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TAXONOMIC STUDIES ON *GYRAULUS* (GASTROPODA: PLANORBIDAE)[1]

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ABSTRACT

From 94 mostly Eurasiatic samples, alcohol material of *Gyraulus* snails was compared conchologically and 492 specimens were dissected for anatomical characteristics. Infraspecific shell variation is shown to depend on, among other things, water movement. *G. albus* (Müller) becomes larger in lenitic biotopes than animals with equal whorl numbers in lotic biotopes. In animals killed by immersion in ethanol particularly the length of the penis sheath is shorter than in snails relaxed with pentobarbital.

Characters highly valued for species discrimination are among others: the distribution of pigment cells on the mantle to the right of the kidney; the presence or absence of distinct transverse septa in the tubular portion of the kidney, rendering its margins "undulate" or "straight," respectively; the number of prostate diverticula and their shape and arrangement in the gland; the width of the vas deferens; the length ratio penis sheath : preputium; the shape of the penis tip and stylet, and the position of the penis pore. In certain groups peculiarities occur in various other organs (radula, seminal vesicle, bursa copulatrix, bursa duct, etc.).

Europe harbours five indigenous species of the genus plus six endemic species in Macedonian ancient lakes. North Asia is inhabited by *Gyraulus acronicus* (Férussac) only, while south Asia harbours a "Rassenkreis," i.e. *G. chinensis* (Dunker) (commonly used junior synonyms: *G. convexiusculus* (Hutton), *G. spirillus* (Gould)) with at least eight peripheral isolates. Two new species are described, i.e. *G. eugyne* from Inner Mongolia and *G. malayensis* from Malaya, also occurring in Java and Bali. Abandonment of planispiral growth and formation of several angles or keels on the shell periphery in *Gyraulus* of the ancient lakes is certainly due to convergent evolution. There is strong evidence from anatomy that a species endemic to Lake Biwa in Japan has a history different from that in a group endemic to the Macedonian Lakes Ohrid and Prespa. Two keys are presented: one for identification of the species living in Europe, the second a provisional one for the west, south, and east Asiatic species.

Analysis of relationships according to Hennig's "consequent phylogenetic systematics" revealed the existence of seven subgenera, i.e. *Torquis* Dall (Nearctic and west Palaearctic), *Lamorbis* Starobogatov (west Palaearctic), *Armiger* Hartmann (Holarctic), *Caillaudia* Bourguignat (Ethiopic), *Choanomphalodes* Lindholm (Lake Biwa, Japan), *Carinogyraulus* Polinski (Lakes Ohrid and Prespa, Macedonia), and a provisional "subgenus *Gyraulus* s. str. Charpentier" (cosmopolitan except South America and the Ethiopic region). *Gyraulus* s. str., being a remnant group merely characterized by symplesiomorphies and autapomorphies, cannot be established as a monophyletic taxon. According to Hennig its paraphyletic character is not excluded. Hennig's arguments appear to leave such remnant groups as a general problem of his systematics. In the case of "*Gyraulus* s. str." only chorological implications can help to support monophyletic status in Hennig's sense. Incompatibility is shown between Hennig's "deviation rule" and biological reality in the case of the "Rassenkreis" of *G. chinensis*, which is considered to be the "persisting stem species" of the marginal species that have evolved as peripheral isolates.

The centre of origin and the primary centre of differentiation is probably the west Palaearctic to which all the genera closely related to *Gyraulus* are confined. A secondary centre of differentiation is the Nearctic, a third one the Indo-Malayan region. A redescription of the genus *Gyraulus* Charpentier, 1837, is given using present knowledge on variation of anatomical and conchological characters.

INTRODUCTION

As in other molluscan groups, diversity of shell characters has led to excessive naming of "species" in the planorbid genus *Gyraulus* Charpentier, 1837. For the South African region, Brown & van Eeden (1969) have published an outstanding revision of *Gyraulus*

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[1] Habilitationsschrift, Fachbereich Biologie der Eberhard-Karls-Universität zu Tübingen, 1977.

species; the species endemic to Lake Ohrid (SE Europe) have been revised by Hubendick & Radoman (1959); three species of central Europe have been compared anatomically by Meier-Brook (1964). A synoptic view of Eurasiatic forms was, however, still lacking, although repeatedly called for, particularly by those interested in medical malacology (Burch & Natarajan, 1965; Pace, 1973).

The health impact of *Gyraulus* is their rôle as intermediate hosts of the intestinal flukes *Echinostoma ilocanum* Odhner, 1911 and *E. lindoense* (Sandground & Bonne, 1940), which are pathogenic to *inter alia* man.

The number of names created for Eurasiatic species or subspecies of the genus, or later assigned to it, is not far from 200, and only recently three new species have been described from Thailand (Brandt, 1974).

The goal of the present investigation was to find out to what extent conchological variation is paralleled by anatomical variation. Consequently the studies had to be confined to instances where living or preserved animals were available. A revision of North American forms must be postponed since the huge American collections would require years of study. Moreover, American species have so far not been incriminated as hosts of human helminths. In South America there is only one species of this genus (Paraense, personal communication) and the Australian region will be covered by studies now being undertaken by Dr. D. S. Brown. It would be premature to expect a complete revision and list of synonyms, but I hope that the present study will serve as a basis for a revision where results of further studies can find their appropriate places. Great gaps in knowledge remain from central Asia, viz. Siberia and the Peoples Republic of China, where I could collect some material but was prevented from taking it out of the country.

Material to be studied and compared was selected according to the following criteria: planorbid snails with a hollow stylet on their penis and having a shell with three to four and a half (at most five) rapidly increasing whorls. These features have been accepted as characteristic of the genus *Gyraulus* by all authors who have used this name (Baker, 1945; Hubendick, 1955, etc.).

MATERIALS AND METHODS

Snails were collected alive by various persons at the localities indicated in the text under "Material." The animals were usually sent alive and prepared for study at the laboratory of the Institute of Tropical Medicine of Tübingen University; in some cases animals were relaxed, fixed and preserved by the collectors, as indicated in the text. Where freshly collected material was not available, i.e. from the U.S.S.R. and the Peoples Republic of China, I had to rely on old museum collections.

Unless stated otherwise, living snails were prepared as follows: They were relaxed in a freshly prepared suspension of 5 mg or more pentobarbital in 10 ml of tap water at room temperature, as described by Meier-Brook (1976a). After 6 to 12 hr they were killed and fixed in 4% formalin at appr. 60°C and transferred to 70% ethanol until dissection. This was done under a Wild Zoom Stereomicroscope M7 using pointed forceps, microscissors after Vannas, ophthalmologic scissors, and insect needles of the sizes 0 to 000. Camera lucida drawings were done with a Wild drawing tube. Whole mounts of organs and organ sytems were made on microscope slides in Eukitt. For histological studies organs were removed from the body, dehydrated in a series of graded ethanol, soaked with methyl benzoate (2 × 15 min), benzolum (30 min), benzolum/histoplast-S (56–57°C, Serva) (30 min) and embedded in histoplast-S after 8 hr. Serial sections 7 μm thick were made with a Leitz-microtome and stained in haemalum and azophloxine. When organs were too small for exact orientation during embedding, they were stained in an alcoholic solution of safranin prior to dehydration.

Chromosome Counts.—For determination of chromosome numbers, ovotestes and embryos were used in some cases when living snails were available. Ovotestes were excised in tap water where they remained for 15 to 30 min to make cells swell and thus make better chromosome spreads. Embryos were freed from their egg capsules and treated in the same way.

For fixation, tissues were transferred to a mixture of acetic acid and 96% ethanol, 1:3 parts by volume (according to Patterson, 1971). After 5 min they were stained in a concentrated acetic orcein solution for up to 8 hr and differentiated in 45% acetic acid. Preparations were examined in 45% acetic acid after squashing tissues in a screw clamp. Counts were made under a Zeiss interference microscope at 1200×.

SEM-Studies.—Snails were relaxed in a suspension of pentobarbital for 1 hr, fixed at room temperature in a 2% glutaraldehyde solution, in which the body cavity was opened immediately after immersion. For studies of the penis tip, the penis sheath was cut and the penis drawn out. The organs were fixed for 2–4 days, rinsed in distilled water for 4 × 5 min, dehydrated in 30, 50, 70, 90 and 100% acetone for 10 min each and dried in an ISI critical point drying (CPD) apparatus over carbon dioxide. Critical point drying was performed in the Cytological Laboratory of the Institute of Tropical Medicine, Tübingen, by Dr. H. M. Seitz. SEM studies were performed with a Cambridge Stereoscan Microscope MK2A after coating with C + Pd/Au.

CHARACTERS USED IN *GYRAULUS* TAXONOMY

The biological species concept (Scudder, 1974) is advocated in taxonomical revisions at the infrageneric level. It is subject to a minimum of controversies aside from dealing with fossils and problems stemming from uniparental reproduction. As every taxonomist knows, however, very few species would be accepted at all if biologists relied on only this species concept. In planorbid gastropods, the fact that all members can self-fertilize poses severe problems from crossing experiments. Only in a few cases does a genetic marker, e.g. recessive albinism, enable one to distinguish between the results of self- and cross-fertilization (Richards, 1973b). In most groups, such as *Gyraulus,* albinotic individuals have not yet been found.

The biological species, however, is not defined only as "the largest and most inclusive reproductive community of sexual and cross-fertilizing individuals that share in a common gene pool" (Dobzhansky, 1950); "the essence of the biological species concept is discontinuity due to reproductive isolation" (Mayr, 1974a: 379). Evidence of reproductive isolation between sympatric populations serves to indicate that different species are involved even if other types of data are unavailable.

Examples of reproductive isolation between species of *Gyraulus* hitherto characterized as morphological species are regularly encountered in Europe. In seven of the nine localities where I collected *G. laevis* (Alder), it lived together with *G. albus* (Müller), and not only in the same water body, but in the same square meter. In all of the eight central European lakes where I found *G. acronicus* (Férussac) this species coexisted with *G. albus. G. riparius* (Westerlund), too, was found associated with *G. albus,* and the only European species regularly living alone is the decidedly stenoekous *G. rossmaessleri* (Auerswald) confined to temporary pools. Wherever sympatric species of the genus were examined I never saw intermediate anatomical traits indicating hybridization. Doubts arose when only shell characters were considered. But even if hybrids occurred and these were fertile, this would not necessarily affect our statement on reproductive isolation. "What matters is not whether hybrids can be obtained but whether the Mendelian populations do or do not exchange genes, and if they do whether at a rate which destroys the adaptive equilibrium of the population concerned" (Dobzhansky, 1950: 415 *et seq.*).

Sympatry of pairs of European species of course should not be taken as evidence for sympatric speciation. On the contrary, in the pairs *Gyraulus albus-laevis* and *G. albus-riparius* relationships appear remote enough to regard them as members of different subgenera. Although we are far from recognizing the mechanism of reproductive isolation between them, differences in form and size of the male copulatory organs, as shown later, make copulation unimaginable. This is also the case in the pair *G. albus-acronicus* where differences in size (Tables 1 and 2) though not in general morphology are pronounced. There is no reason to assume that events leading to separate species and subsequently to separate subgenera did not occur in geographical isolation. Allopatric speciation with a later reunion of geographic ranges may be the rule in cases where closely related species coexist, although the possibility of sympatric speciation, for example by disruptive selection (Mayr, 1963: 156; Sperlich, 1973: 52–53, 155), can no longer be denied (Scudder, 1974).

A different situation will be shown for a pair of jointly occurring species that have virtually no anatomical differences: *Gyraulus chinensis* (Dunker)-*tokyoensis* (Mori). Here evidence of reproductive isolation favours the decision for separate species.

In the majority of samples from allopatric populations comparison and evaluation of morphological characters, supported by biological and ecological observations, remain the only practical methods for species discrimination. This approach is considered justifiable as long as the following, expressed by Mayr (1974a: 381), is kept in mind: "Repro-

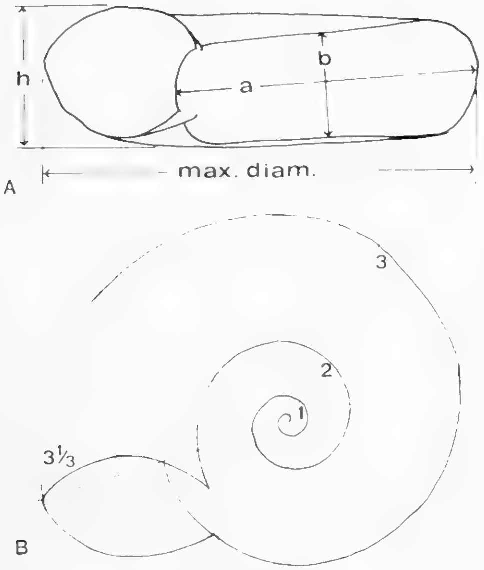


FIG. 1. Dimensions measured (A) and method of counting whorls (B) in *Gyraulus*. Example: *G. laevis*. Kuehren and Ansbach.

ductive isolation is effected by physiological properties which have a genetic basis. Morphological characters are the product of the same gene complex," and as long as priority is given to reproductive isolation: "This inference method is by no means a return to a morphological species concept since reproductive isolation always remains the primary criterion and degree of morphological difference only a secondary indicator, which will be set aside whenever it comes in conflict with the biological evidence."

Morphological characters are subject to variation for various reasons: allometric and seasonally different growth, preparation-dependent changes, and, of course, genotypically- and ecophenotypically-determined ones. Although the latter two reasons cannot be separated in a morphological analysis, I later include several paragraphs titled "Non-Genetic Variation," where undoubted cases of externally induced aberrations are dealt with. However, the inclusion of such paragraphs does not imply that the preceding paragraphs are confined to genetic variation!

Shell Dimensions

Absolute dimensions usually given in taxonomical studies of planorbids are the height and the maximum diameter, height and width of the aperture and the number of whorls. As a measure of flatness the ratio maximum diameter : height is generally indicated. One problem arising in *Gyraulus* and some other genera is caused by the tendency in some groups to deflect the last whorl near the aperture. A slight increase of the deflection angle would result in a highly increased height

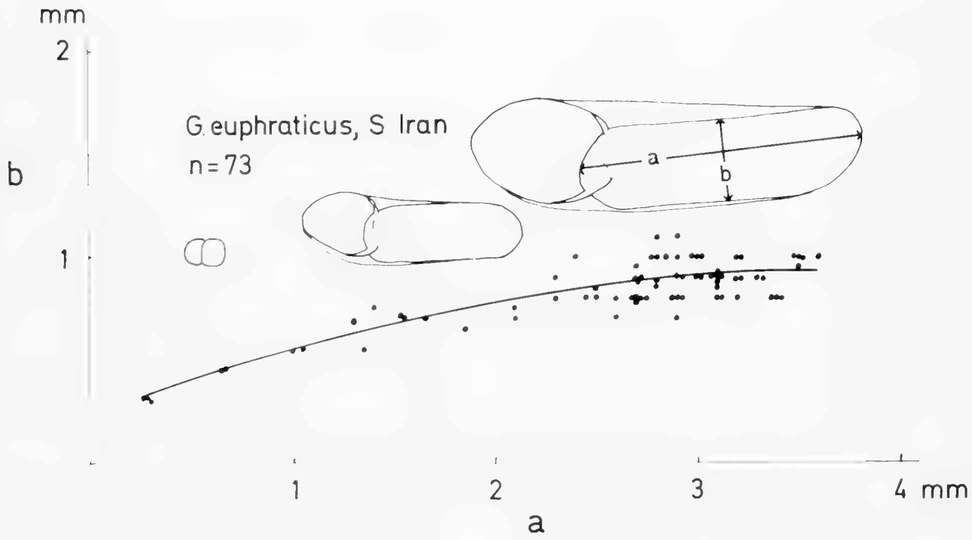


FIG. 2. Dimension b plotted against a in a *Gyraulus*.

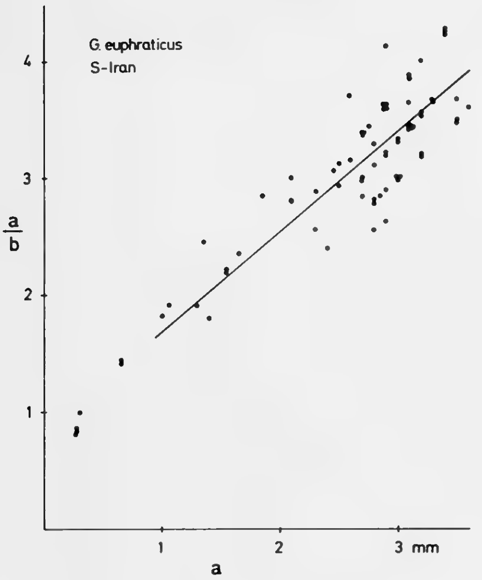


FIG. 3. Graph with a/b plotted against a and regression line. Same sample as Fig. 2. n = 67 (+6 juv. neglected); $y = 0.84 + 0.85x$ ($y = \frac{a}{b}$, $x = a$); $r = 0.921$.

figure and thus in a falsification of the "flatness index." This is avoided by indicating the maximum diameter minus aperture and the height of the last whorl in its middle as seen in apertural view (Fig. 1A, a and b). These dimensions were first used by Brown & van Eeden (1969: figs. 16, 17), who, moreover, plotted the ratio a/b against a, arguing that the degree of flattening of the whorl during (allometric) growth is thus best demonstrated. These authors have not commented on the question of linearity of such a function.

Growth is allometric since individuals are proportionally high in youth and become proportionally lower during growth (Fig. 2). Plotting absolute dimensions, viz. b against a, yields a distribution of points probably following a hyperbolic function (personal communication by Dr. W. U. an der Heiden, Inst. Biomathematics, Tübingen). Although well-fitting curves in such a graph would give a clear idea of the course of growth, it is impractical to construct them or to find appropriate equations that help in comparing populations. Calculating the ratios a/b and plotting these against a indeed appears to be better suited for these purposes, because at $a > 1$ mm, points apparently follow a linear function. Hence regression lines can be drawn and the corresponding equations, $y = f + g \cdot x$, can be tabulated and compared. *The higher the inclination, indicated by g, the lower the relative increase of dimension b,* or the angle between upper and under sides in the growing shell. *The higher f,* indicating the position of the line, *the flatter the shell as a whole* (Fig. 109). Linearity of the regression line in a coordinate system with a/b as the y-axis and a as the x-axis was examined by the F-test (Sachs, 1969: 421 *et seq.*). In the two examples (Figs. 3, 4), the critical F-values at the 5%-level (Fig. 3) or at the 10%-level (Fig. 4) were not attained or exceeded; therefore the test did not disprove the linearity of the regression function. Regression lines are compared in cases where critical F-values on the 5%-level are not reached.

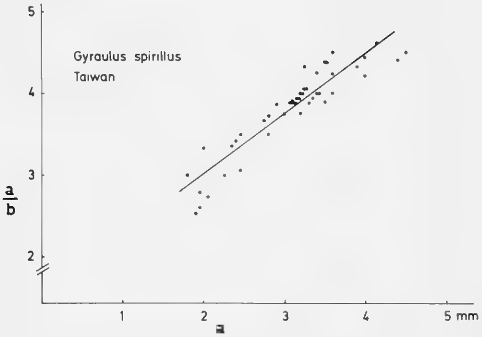


FIG. 4. Same as Fig. 3 but with another species. n = 45; $y = 1.55 + 0.73x$ ($y = \frac{a}{b}$, $x = a$); $r = 0.924$.

There has been some controversial use of the terms upper and under side, due to different orientations—some authors handle planorbid shells as sinistral, most as dextral. It has long been known that all Planorbidae are morphologically sinistral (compare Physidae and Bulininae): genital openings and the anus are on the left. Consequently all *Gyraulus* snails are here considered sinistral.

The number of whorls is determined as usual (Fig. 1B) (Mandahl-Barth, 1954, fig. 2; Pan American Health Organization, 1968: fig. 7). Dimensions, proportions and whorl numbers are important for characterizing species, particularly since they are the main conchological features that, in earlier years, formed the only basis for taxonomy.

As in other groups of fresh-water mol-

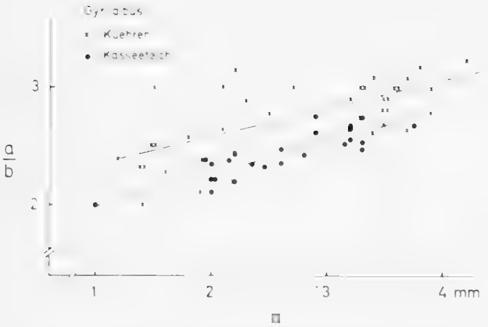


FIG. 5. Variation of a/b plotted against a in two similar biotopes (fish ponds in Holstein, N Germany).

luscs, variation of shell characters within a population is much less than between neighbouring populations, populations being defined as communities of individuals actually interbreeding. Hubendick (1951) convincingly demonstrated this for lymnaeid snails by his "mean photographs."

Intraspecific variation demonstrable with this technique is much less in Planorbidae than in high-spired snail groups, but proportions in two populations of presumably similar biotopes may prove to be so different that their ranges overlap only marginally (Fig. 5). Interpopulational variation of proportions in one species in lakes and in ponds or backwaters is furthermore demonstrated in Fig. 7. Restricted variation is seen particularly in small water bodies where often one or a few individuals have founded a population, which, consequently, has a restricted gene pool (as in cases where the founder-principle becomes effective). Genetic isolation resulting in "a homogeneous genetic constitution" is favoured by self-fertilization of which basommatophoran snails generally are capable (Hubendick, 1951: 31, 32), but probably also by a certain island character of small water bodies (Lassen, 1975; Keddy, 1976; Aho, 1978). The hostile land masses separating ponds and pools may reduce gene flow between limnic populations as compared with gene flow in the vast and continuous populations of many terrestrial animal species. Phenotypic similarity between individuals of such small populations may, furthermore, be caused by the influence of environmental factors that act upon all of them largely to an equal degree, either through selection (e.g. founder effect, as understood by MacArthur & Wilson, 1967: 154, 188) or immediate influence (within the range of reaction norm) upon the growth of individuals.

Non-Genetic Variation of Dimensions and Proportions

Non-genetic variation is due to environmental factors. For any given population it is difficult to assess the influence of selection, as distinct from ecologically induced non-inherited influences, on shell phenotype. For some factors, however, direct action on growth is known. For fresh-water molluscs factors most interacting with shell development are water movement and water chemistry, particularly the calcium content. Calcium deficiency, if not inhibiting occurrence of certain species (Meier-Brook, 1963), may cause shells to become thin and fragile (Hubendick, 1947: 503; Meier-Brook, 1978). Shell thickness in the widely distributed species of *Gyraulus* is, however, regarded not to be significant, neither for taxonomic conclusions nor merely for identification.

Water movement in standing waters generally varies with wind exposure. This means that snails of larger lakes (lotic biotopes) are usually more exposed to water movement than are those in ponds and pools (lenitic biotopes). Reduced shell size in lakes, as shown for *Gyraulus albus* (Figs. 6 and 7), is a plausible consequence, because the planispiral shell offers a large surface to waves. Three ways of size reduction in lotic biotopes are imaginable: (1) Growth generally equals that in lenitic biotopes but individuals die earlier. In this case numbers of whorls must be reduced as well; (2) Snail growth is reduced, because selection has favoured individuals whose diameter grows more slowly; (3) Snail growth is hampered by direct physiological (=non-genetic) action of the environment on each individual. In cases (2) and (3) it could be that whorl numbers are not reduced as compared with snails from still water; then whorls must be narrower and less rapidly increasing.

Fig. 6 depicts ratios of whorl number : diameter in *Gyraulus albus* from some lakes and ponds shows that in these samples situation (1) has not been realized. Whorl numbers are not smaller than in ponds. At least when high whorl numbers (around 4) are reached, pond dwellers have attained more or less greater diameters than lake dwellers. A decision on how far situations (2) or (3) are

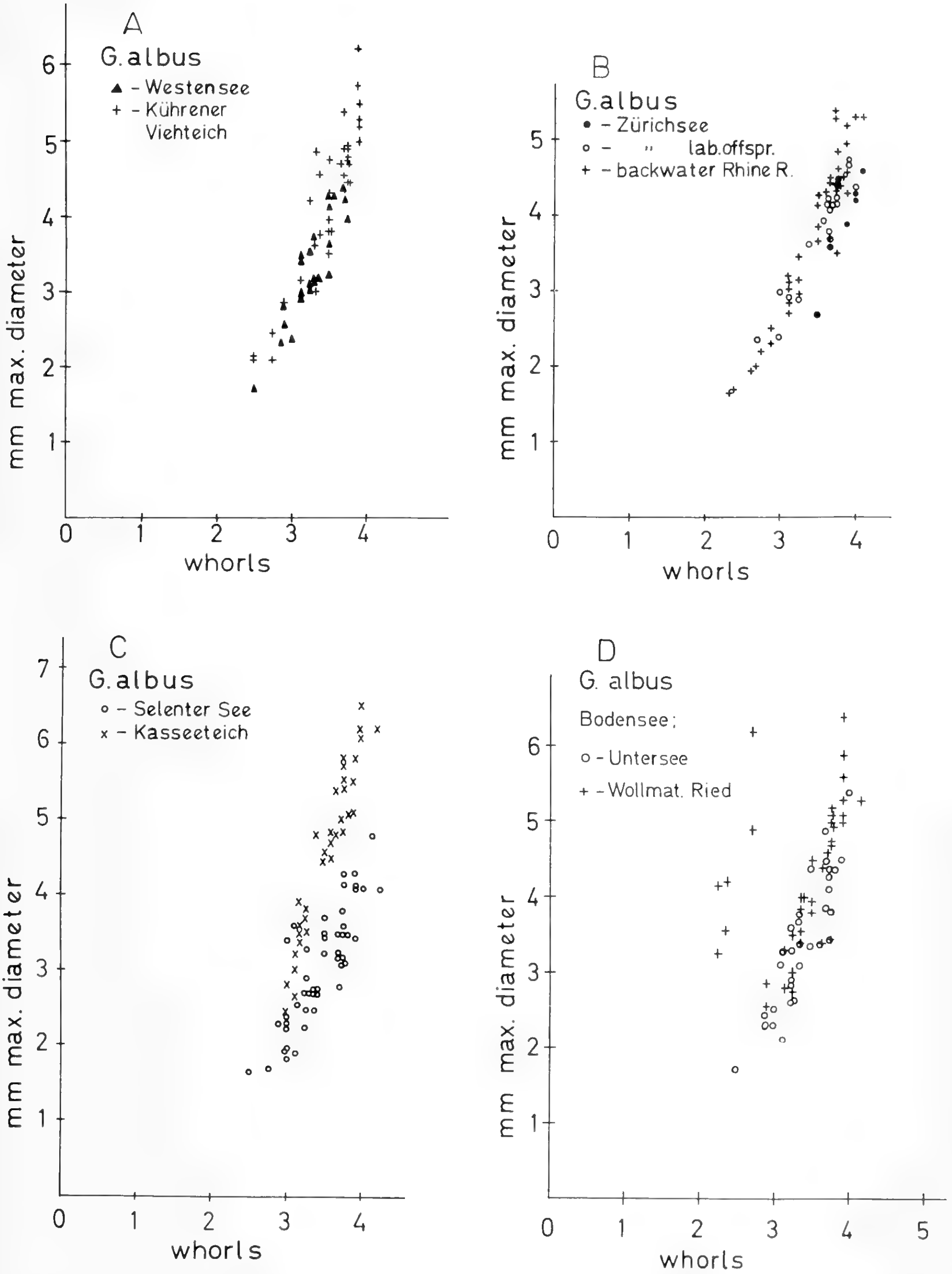


FIG. 6A–D. Comparison of the ratio maximum diameter : whorl number in lotic (o) and lenitic (x, +) biotopes. According to the Hotelling-Test (Anderson, 1958) differences between the centroids are highly significant ($p < 0.001$).

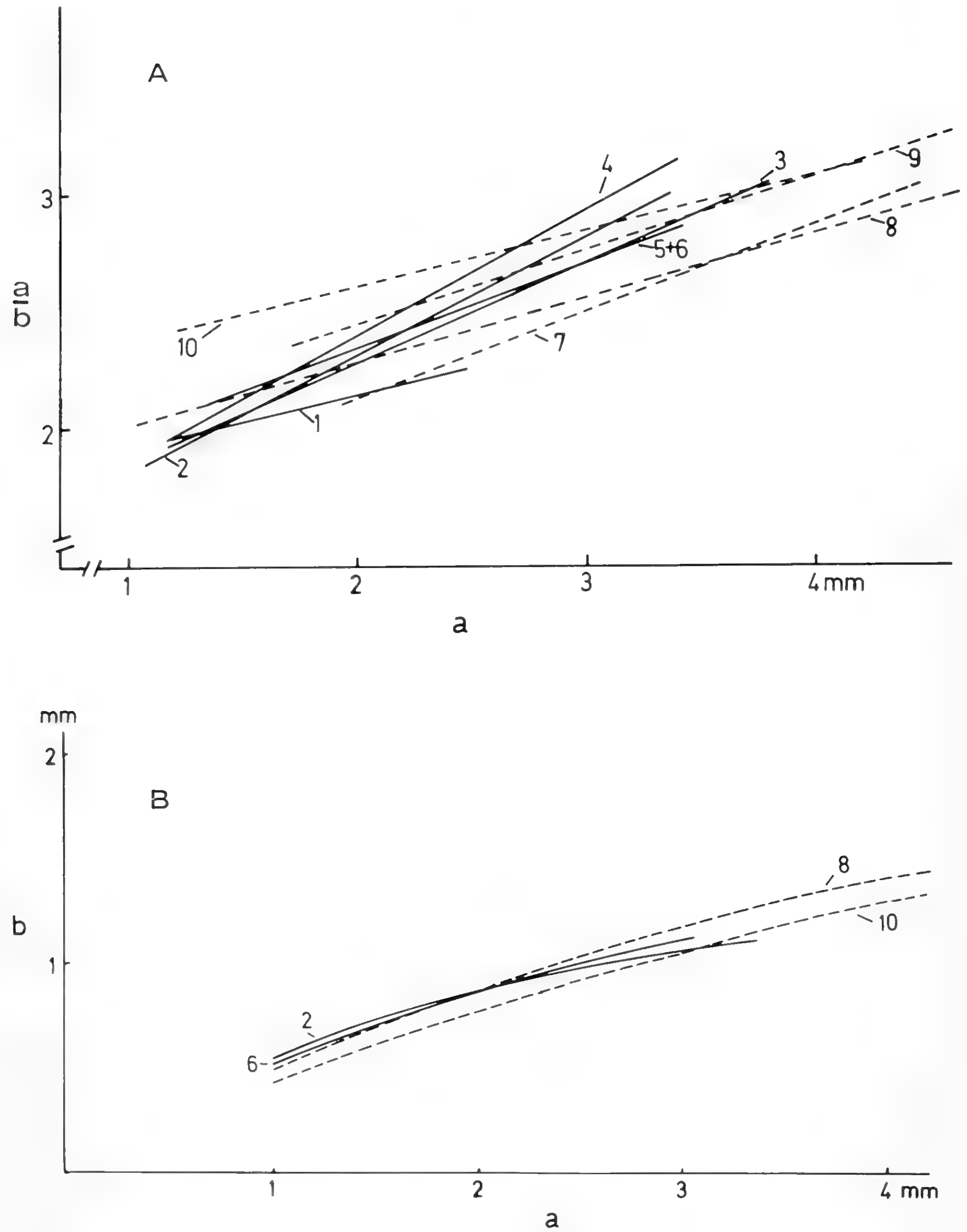


FIG. 7. *Gyraulus albus*. Comparison of shell proportions between lotic (——) and lenitic (-----) biotopes; A: a/b plotted against a; B: b plotted against a. 1—Haslacher See; 2—Selenter See; 3—Titisee; 4—Zürichsee; 5—Lac St. Point; 6—Westensee; 7—Ettenheim; 8—Kasseeteich; 9—Wollmatingen; 10—Kuehren.

involved in size reduction is not possible without laboratory breeding experiments. Differences between snails collected in Zürichsee and their offspring reared in aquaria (Fig. 6B) suggest that reduction of shell size is to some extent reversible and, thus, not inherited. How far genetic fixation of a reduced shell size in lakes has taken place in other populations cannot yet be stated. Neither can the rôle of other ecological conditions, e.g. food, be overlooked at present. Large lakes, such as the Bodensee, offer an opportunity for comparing samples from different habitats of the same water body. In Fig. 6D a sample from a wind-exposed shore in Untersee is compared with one from a bay very rich in vegetation (Phragmition and Potamion) and mud. The two biotopes, approximately 5 km from one another are in the same water body. They are lotic and lenitic with broad overlap. However, the difference visible in the other examples is also distinct here, especially in snails with three and four whorls. Probably a steady gene exchange between the two localities takes place, at least in one direction: from Wollmatinger Ried to Niederzell/Untersee a strong current occurs, i.e. toward the outflow of the Rhine River. The strange aberration of six specimens that have attained large diameters despite a low whorl number must thus far remain unexplained. The sample size was not sufficient to support the real existence of a gap between two portions or perhaps generations in the population.

Fig. 6A–C shows, furthermore, that variation of the ratio is greater in lakes than in ponds and other small water bodies. This can have two causes: (1) a larger gene pool in lakes as compared with that in small water bodies (see above: founder principle!), and (2) the fact that every lake has, besides lotic microhabitats, also lenitic ones where vegetation or stones protect animals from direct surf or wave action. Therefore lakes have a greater variety of ecological conditions than ponds, etc., and, consequently, a greater range of ecophenotypes.

One of the other parameters underlying variation is the flatness index (Fig. 7). A comparison of lakes (solid lines) with ponds and similar lenitic biotopes (broken lines) does not bring to light significant differences in the position of regression lines. But there is some evidence that regression coefficients are higher in lakes. What does this mean in terms of shell morphology? In each two examples of lake and pond populations the corresponding curves in a system with a and b as the coordinates (Fig. 7B) show that young snails are slightly higher in lakes than in ponds. The necessity for young and weak snails to increase musculature for increased resistance to moving water may be the cause: bigger muscles in the cephalopedal mass require a larger volume of the last whorl (the so-called body-whorl) since in danger the latter must be able to take up the whole head-foot complex. For some time b grows well with growing a, but later growth of b is necessarily lowered (otherwise growth would result in snails with two completely conical umbilici). Reduced growth of b gradually takes place when a certain number of whorls is reached. Lake dwellers then usually have a smaller diameter than pond dwellers, as shown above (Fig. 6).

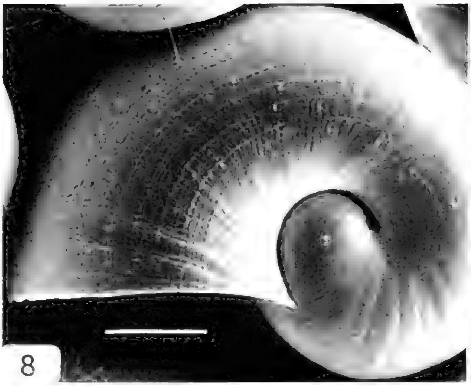
Extreme growth was attained in the laboratory by reducing population density and offering optimal nutrition (food according to Standen, 1949). These giant forms are rarely encountered in nature. Field-collected giant individuals were in some cases trematode-infected. Parasitic castration may be the cause of giantism. Deformations such as open coiling eventually occur. They may be caused by external or internal (genetic) factors and are left out of further consideration here.

Shell Surface

The presence or absence of a peripheral *angle* and a periostracal *fringe* as well as the colour and the presence or absence of spiral striae have been used for species discrimination. Spiral striae, together with growth lines, form a reticulate surface which is appropriately termed "Gitterskulptur" in the German literature. A *keel,* typical in *Planorbis carinatus* Müller but also present in the genus *Anisus,* has rarely been developed in *Gyraulus* outside the old lakes (Lakes Prespa, Ohrid, and Biwa).

Some species never produce an angle (example: *Gyraulus albus, G. laevis*), others always have an angle (example: *G. riparius*) and usually also a fringe at the same site (*G. tokyoensis*). Species are also found with shells varying from entirely rounded to angulate at the periphery. Thus the absence or presence of an angle may be significant in one group and insignificant in another. The same applies to reticulate sculpture, which is always present e.g. in *G. albus,* always absent e.g. in *G. laevis,* as a rule present in *G. acronicus,* and rarely present in *G. chinensis.*

It must be stressed that embryonic shells (=nuclear whorls of authors) have to be exempted from consideration. On these shells spiral striation occurs in all species examined (Figs. 8 and 47b) including those that are smooth in later stages. Moreover, this micro-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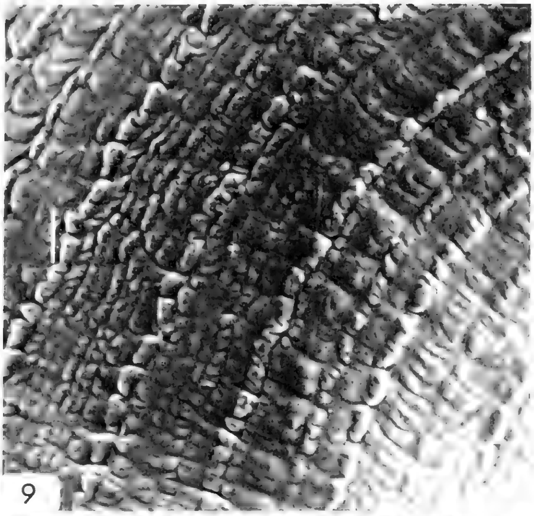
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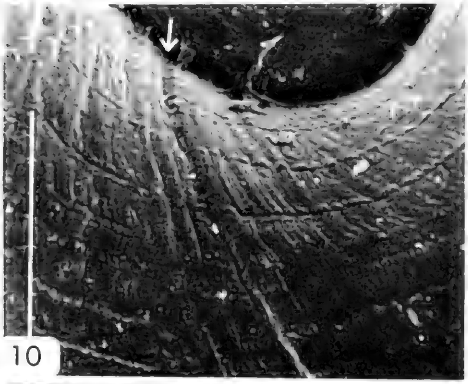
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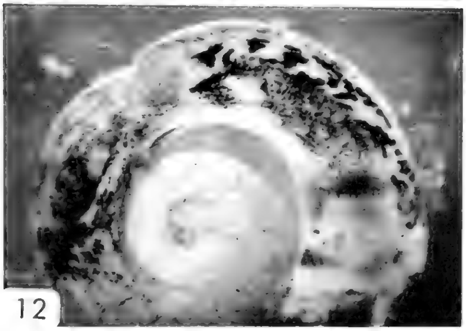
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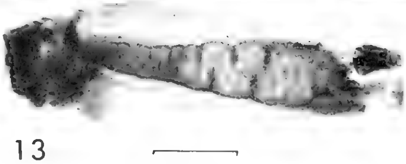
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FIGS. 8–13. 8. Shell of freshly hatched individual showing spiral striae. *G. spirillus*, Taiwan. SEM. Scale = 0.1 mm. 9. Part of shell shown in Fig. 8. SEM. Scale = 0.01 mm. 10. Continuation of spiral striae from embryonic to juvenile shell (arrow pointing to transition line between these) in *G. albus*, Zürichsee. SEM. Scale = 0.1 mm. 11. Pigmentation of cephalopedal mass and mantle (diffuse). *G. albus*, Sjaelland. 12. Mantle pigmentation with distinct pattern. *G. chinensis*, Hong Kong. 13. Undulate margins of kidney in *G. parvus*, Speyer.

sculpture was present in all European species examined of *Anisus* s. str., *Planorbis* s. str., as well as in *Armiger* and members of different planorbid tribes (*Hippeutis*, *Segmentina*, *Planorbarius*). The distribution of microsculpture in other planorbid groups and in other basommatophoran families has been reviewed by Walter (1962).

Striation on embryonic shells may consist of spirally arranged nodules (Figs. 8, 9) visible in the periostracum, continuous periostracal folds, as shown for *Bulinus tropicus*

(Krauss) by Hamilton-Attwell & van Eeden (1971: fig. 5), round pits ("punctation" in other *Bulinus* spp., Walter, 1962: fig. 1) or regularly spaced transverse (=same direction as growth lines) pits (e.g. in *Biomphalaria glabrata* (Say)).

Though I agree with Walter's (1962: 128) statement "that punctae are lacking in most planorbids," it is likely that the various forms of spiral striation, viz. nodules, folds, round or transverse pits, are not so fundamentally different that a different origin must be assumed. Observations show that folds or initially continuous series of nodules gradually become undulate, loosen to round pits and into transverse pits, which finally become weaker and weaker before totally disappearing during juvenile growth. This can best be observed in *Hippeutis complanatus* (L.) (Meier-Brook, unpublished). Spiral striation of embryonic shells is so universal in various basommatophoran groups that it can be regarded as an ancestral structure. Consequently, smooth or glossy adult shells consistently present in planorbid groups may be regarded as derived from spirally striated ancestors. This view is supported by two facts: (1) striation does not cease abruptly after hatching in adult-smooth groups, but is continued onto the first parts of the juvenile shell; (2) in these as well as in adult-striated groups postembryonic striae form an immediate continuation of embryonic striae (e.g. in *Gyraulus albus,* Fig. 10).

Gyraulus costulatus from Liberia was reported as having "a total lack of punctation" (Walter, 1962: 128). Examination of the same species, also from Liberia, revealed that continuous striae are present on the nuclear whorl, which later (but still before hatching) break up into small nodules similar to those in *G. spirillus* and other species.

Reticulate sculpture on the shell surface is sometimes, though not necessarily, accompanied by hair-like protrusions formed by the periostracum. They regularly occur in *Gyraulus albus* (Fig. 36) and occasionally in *G. acronicus* (Fig. 62B).

Wherever peculiar periostracal structures occur in *Gyraulus,* corresponding, but weaker, shell sculpture is found below these. A peripheral fringe of periostracum never decorates an equally rounded periphery; striated periostracum does not cover a completely smooth shell surface, as could be shown in shells devoid of their periostracum. Below a distinct fringe there is at least a distinct peripheral angle, if not even a keel (Fig. 87).

Thickness of shells was not measured. Unusual thickness probably plays a rôle only in ancient lakes where additional angles and keels can be used to characterize species.

Shell color varies from light corneous to reddish brown to light brown, but the color range is too narrow to provide reliable characters for species determination. The degree of transparency is apparently also of equally low value.

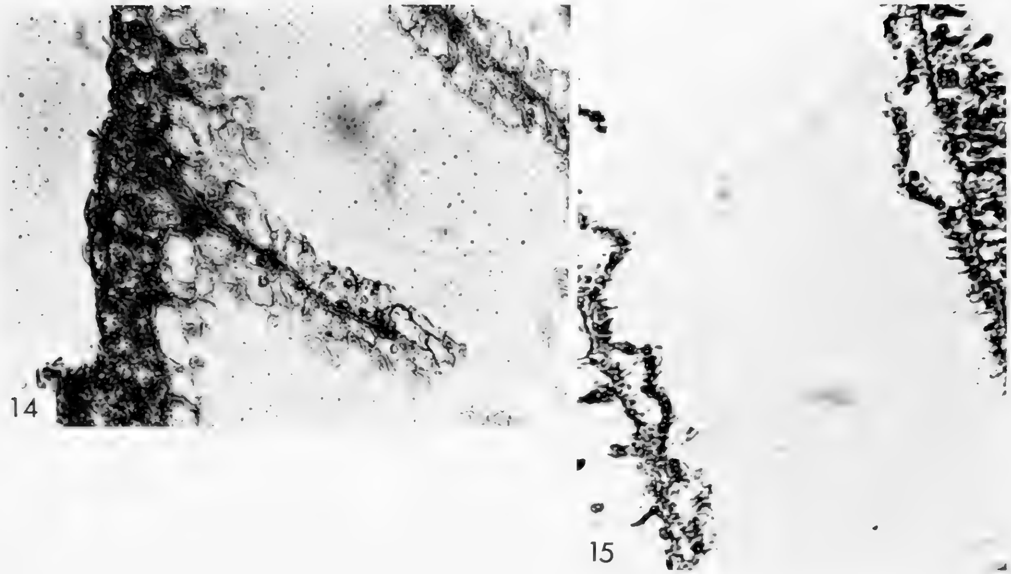
There were no apparent correlations between shell surface characters and environmental conditions except where the reticulate sculpture was slightly worn in surf zones of sandy lake shores.

Body Pigmentation

Pigmentation of the cephalopedal mass shows slight variation, from colorless with scattered spots (Fig. 89) to homogeneously light grey. However, pigmentation of the mantle roof in most cases can be categorized (1) as diffuse and with poor contrast (example *Gyraulus albus,* Fig. 11) or (2) with distinct patterns, and thus with rich contrast (example *G. chinensis,* Fig. 12). These patterns are most distinct on the right side between the kidney and the darker region where the prostate gland, uterus and oesophagus run along the inner side of the whorl. Although pigment patterns are highly variable, there were usually no doubts about which category was involved. In *G. acronicus* the pigment pattern is not as rich in contrast as in *G. chinensis*; in some populations of *G. acronicus* a clear decision was impossible and identification had to be based on other characters (shell, male copulatory organ). But as a rule the nature of mantle pigmentation can readily be categorized and serves as a helpful character.

Pallial Organs

The only pallial organ that proved to have a shape characteristic for certain taxa is the kidney. It has conspicuously "undulate" margins (Fig. 13) in some species, whereas in most species the margins are straight. In unrelaxed individuals the margins of the shrunken kidney seemed to be more or less undulate in all species (perhaps the reason that the significance of this peculiarity has gone unreported, e.g. Hubendick (1955: 456)



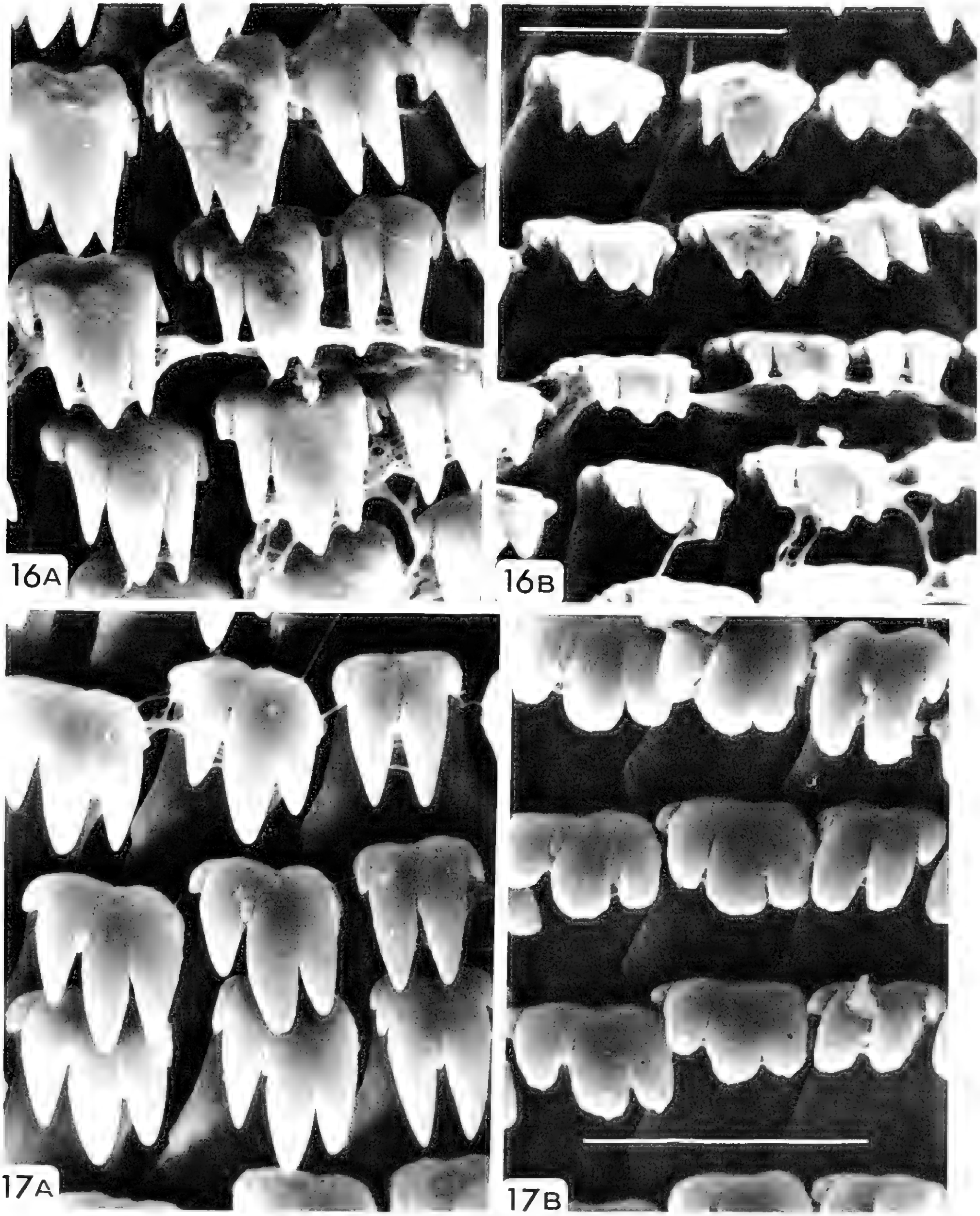
FIGS. 14–15. 14. Septate kidney in tangential section. *G. laevis*, Kuehren. Hematoxylin and eosin. (M 123). 15. Non-septate kidney in tangential section. *G. euphraticus*, S Iran. Hematoxylin and eosin. (M 140).

stressed "that details of the form and size of the kidney are . . . not reliable as taxonomic characters"). In individuals fixed after relaxation as well as in living ones, however, the difference is obvious. Histological investigation revealed that in *Gyraulus laevis* and *G. parvus* (Say) real septa protrude into the renal lumen alternating from both sides. Probably these septa have developed from folds of the renal walls, but fusion (Fig. 14) has taken place that is evidently irreversible. No such septa can be detected in most other species (Fig. 15), even when contraction yields a form like "undulate" margins.

Alimentary Tract

The jaw and radula have long been the main non-conchological characters used in gastropod taxonomy. In rare cases, however, these parts have contributed to differential diagnosis at the infrageneric level. This is the situation in *Gyraulus*. Except for a small group of species endemic to ancient lakes in Macedonia, radular teeth are uniform throughout the genus. Should species differences really occur these must be so insignificant that they are masked by individual variation. Although great hopes used to be placed on the radula for species discrimination, many authors (e.g. Annandale & Rao, 1925; Roszkowski, 1929; Wagner, 1931) came to the same conclusion: the value of the radula for species discrimination has been exaggerated. Most regrettably variation of radular characters is not quantifiable in our genus, so that the above statements could only be supported by a great number of additional figures. SEM micrographs of radulae documenting its low value have been deposited at the Senckenberg-Museum, Frankfurt.

On this occasion it is necessary to caution against misinterpretations of scanning electron micrographs. Owing to the great depth of focus it is very difficult to tell the degree of inclination of part of a radula. To demonstrate the effect of varying directions of observation two micrographs of the same region of one individual radula is shown (Fig. 16). Hence, statements about "long" and "short" cusps on radulae, judged from SEM photos, should be regarded with caution. Furthermore differences occur between younger and older portions of a radula where teeth are worn and, thus, may lack the sharp edges of their cusps (Fig. 17). To save space I refrain from giving descriptions of radular teeth for all species except for the type-species of the genus and the aberrant species from ancient lakes. The number of teeth per



FIGS. 16–17. 16. Identical part of radula in perpendicular view (A) and with 37° inclination (B). *G. parvus*, W Iceland. SEM. Scale = 0.01 mm. 17. Unworn (A) and worn (B) central and lateral teeth in different regions of the same radula. *G. albus*, Sjaelland. SEM. Scale = 0.01 mm.

transverse row appears to be highly size-dependent and is almost worthless for taxonomic purposes (Bertram & Meier-Brook, in preparation).

The oesophagus, crop, stomach, caecum, and digestive gland are devoid of taxonomically significant characters within our genus. Striking variation occurs in the size and form

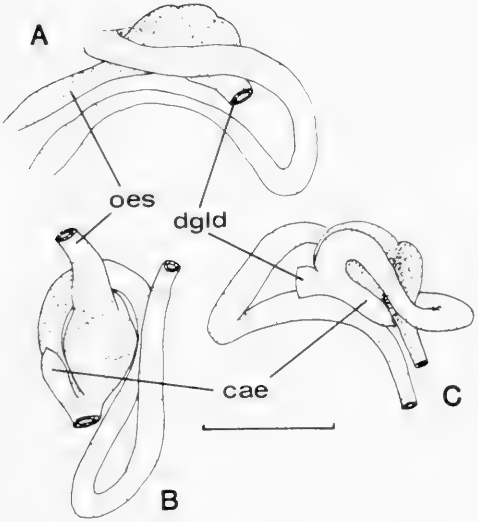


FIG. 18. Intestinal loop, viewed from the left (A), ventral view (B) and viewed from the right (C). *G. albus*, Sjaelland (M 286).

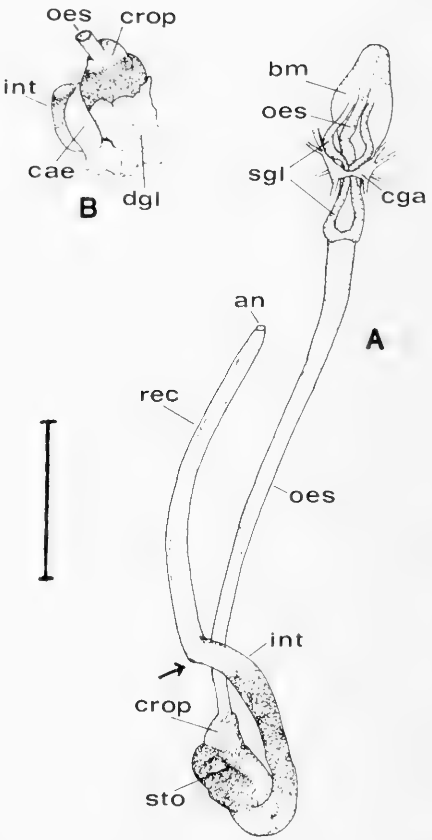


FIG. 19. (A) Omission of intestinal loop, *G. laevis*, Kuehren. The arrow indicates the site at which a loop usually is intercalated. (B) Same; stomach region in ventral view. Key to lettering p. 27.

of the intestinal loop. Normally (Fig. 18) the intestine, after leaving the pyloric region of the stomach, runs anteriad on the right side of the animal, bends to the left, passes over the oesophagus, bends once more, runs backward on the left side, forms an elongate loop embedded in the large digestive gland, and finally runs anteriorly after passing the stomach on its left side again, to terminate as the rectum. In portions of the lots examined of *Gyraulus laevis* and in all specimens dissected of *G. parvus* the loop was absent, and the intestine showed only a slight indication of flexure where the loop is usually intercalated (Fig. 19A, arrow). Transitional stages occur. Presence or absence of a loop is not strongly correlated with more invariable species characters and, thus, is not considered to be a reliable character. In most species presence and absence seems to be randomly distributed, even within the same population. In a few species percent omission is increased (e.g. *G. parvus*); in others the loop is well developed in all individuals examined (e.g. *G. acronicus, G. rossmaessleri*). Therefore, in certain cases presence or absence of an intestinal loop may serve as a supporting character, and in future studies further attention should be devoted to it. Richards (1973a), studying *Biomphalaria glabrata* with both absence and presence of a loop in the same stock, found that omission is inherited. This may be the case in *Gyraulus* also, but inheritance, of course, does not necessarily mean taxonomic significance.

Reproductive Organs

The number of lobes in the ovotestis (hermaphroditic gland), a character used in the taxonomy of at least one group of planorbid snails, viz. *Biomphalaria* (e.g. by Paraense, 1966; Pan American Health Organization, 1968), is difficult to determine, because the lobes are insufficiently differentiated in the most apical portion of the ovotestis. The value of lobe numbers is especially low if variation between species is low and there is overlap; this is the case in *Gyraulus* (mostly between 28 and 32).

The length of the spermoviduct (hermaphroditic duct) (sod in Fig. 43) and of its parts has not proven to be of value as a character, particularly since the seminal vesicle can be lengthened by stretching to more than twice its dimension in the resting state. The shape of the seminal vesicle coils may be characteristic, being either rounded and bulbous or more delicate and studded with spiny humps (Fig. 20). Though in many cases a decision is difficult, extreme formations can be found to be constant.

The seminal vesicle (vs in Figs. 43, 57) can be exceptionally voluminous and appear larger than the prostate gland and uterus together (e.g. *Gyraulus riparius*). The portion of the spermoviduct between the seminal vesicle and the carrefour (=distal spermoviduct), which is usually very thin, in certain cases can be wider than the vas deferens and may then have diagnostic value (e.g. *G. laevis*).

In the carrefour (car in Fig. 43) and the parts of the female tract down to the vagina (vag in Fig. 43), no characters useful for taxonomic purposes have been found. The vagina in many cases is much inflated, partly below the zone of fusion with the duct of the bursa copulatrix. This inflation may be absent, but it has, as yet, been impossible to recognize any regularity. Intra- and interpopulational variation of the bursa copulatrix and its duct are usually greater than interspecific variation. Therefore it has lower value than in other planorbid genera (e.g. *Planorbis*, Meier-Brook, 1976c), but an extremely slender bursa (e.g. *Gyraulus laevis, G. parvus*) or an unusually inflated one (e.g. *G. eugyne* n. sp.) is a good species character.

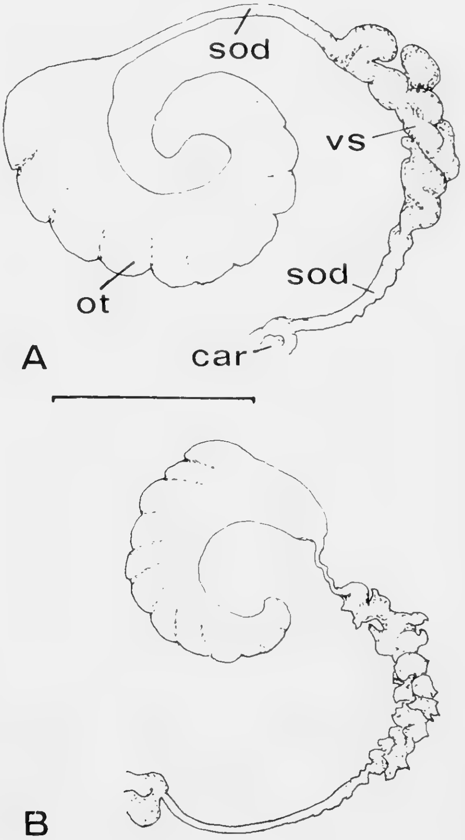


FIG. 20. Coiling of seminal vesicle: bulbous (A; *G. parvus*, Speyer) (M 275); spinous (B; *G. hiemantium*, Hanechi-son) (M 260).

In the male reproductive tract the length of the free sperm duct (free spd in Fig. 48), relative to other parameters, is of restricted value, but the prostate gland has been judged as bearing one of the most reliable characters for species discrimination in the genus since counting the numbers of diverticula was introduced into taxonomic work (Baker, 1945; Meier-Brook, 1964; Brown & van Eeden, 1969; Pace, 1973). Numbers of diverticula extend over a wide range in the genus, from <10 to >30, and they can be determined without trouble (Tables 1 and 2). They are rendered invaluable, because they appear to be age—or size—independent (Fig. 21). In immature individuals diverticula may be difficult to recognize, but they are formed in definitive number early in ontogeny. Variation generally is low enough to permit the indication of mean diverticula numbers even in smaller samples (Fig. 22). Diverticula are usually unbranched, except the most distal one, two or three, which may incidentally be bifid. The remaining diverticula were almost exclusively found unbranched in most species (e.g. *Gyraulus acronicus, G. euphraticus* (Mousson)). Here and there, along the whole prostate, bifid diverticula were regularly noticed in *G. parvus* (Fig. 50). Another constant feature in the prostate gland is the mode of grouping. Diverticula are usually spaced closely and regularly (Fig. 23), whereas in certain groups they emerge from the prostate duct with gaps and in changing directions (e.g. *G. laevis, G. parvus*, Figs. 48, 50).

The length of the vas deferens is occasionally useful as a standard parameter for comparison with the proper male copulatory or-

TABLE 1. Reproductive organs of *Gyraulus albus*. Data from Meier-Brook (1964) are included.

				Male copulatory organ						
	No. prost. divert.			Total length (mm)			Ratio psh:prp		Bursa copulatrix	
Locality	n	range	x̄ ± s.d.	n	range	x̄ ± s.d.	range	x̄ ± s.d.	clb. el.	clb. sph.
Sjaelland	18	7–16	11.9 ± 3.6	14	0.8–1.3	1.0 ± 0.1	1.2–1.8	1.6 ± 0.2	+	
Bodensee	—	(indiscernible)		2	0.9 + 1.4		1.3 + 1.4		+	
Zürichsee	3	17 + 19 + 20		3	1.4 + 1.4 + 1.0					+
Greifensee	3	16 + 18 +18		3	1.4 + 1.2 + 1.7		2.0 + 2.0 + 2.0			+
Fischau	1	8		4	0.9–1.2	1.0	1.4–1.7	1.5	+	
Ursee	—	(indiscernible)		6	1.1–1.5	1.3 ± 0.1	1.4–2.2	1.9 ± 0.3	+	
Kuehren	2	13 + 15		1	0.9		2.0		+	+
Wollmatingen	—	(indiscernible)		2	1.8 + 1.5		1.3 + 1.2		+	
Ettenheim	4	15–22	17.5	4	1.3–1.8	1.6	1.4–2.0	1.7	+	
Windgfällw.	—	(indiscernible)		4	1.3–1.5	1.4	1.6–1.8	1.8	+	
Total	31	7–22	13.8 ± 4.3	43	0.8–1.8	1.2 ± 0.3	1.2–2.2	1.6 ± 0.3		
excl. Sjaell.	13	8–22	16.5 ± 3.5	29	0.9–1.8	1.3 ± 0.3	1.2–2.2	1.7 ± 0.3		

TABLE 2. Characters of *Gyraulus* in Europe and N Asia; spt. ki. = septate kidney.

				Male copulatory organ					
	No. prost. divert.			Total length (mm)			Ratio psh:prp		
Species	n	range	x̄ ± s.d.	n	range	x̄ ± s.d.	range	x̄ ± s.d.	spt. ki.
albus (Table 2)	31	7–22	13.8 ± 4.3	43	0.8–1.8	1.2 ± 0.3	1.2–2.2	1.6 ± 0.3	–
laevis, Kuehr.	9	9–15	12.4 ± 2.7	11	1.0–1.7	1.3 ± 0.2	1.2–2.5	1.9 ± 0.4	+
laevis, Haarl.	7	6–13	9.1 ± 2.7	11	0.6–1.9	0.9 ± 0.4	1.0–2.1	1.6 ± 0.3	+
parvus, centr. Eur.	15	9–17	12.1 ± 2.5	15	0.9–2.0	1.4 ± 0.3	1.2–2.3	1.6 ± 0.3	+
parvus, Iceld.	9	6–14	10.7 ± 2.7	11	1.0–1.6	1.35 ± 0.2	1.5–2.5	2.0 ± 0.3	+
rossm., Alsace	12	8–14	11.3 ± 2.1	14	1.1–2.0	1.4 ± 0.3	0.4–0.6	0.5 ± 0.1	+
rossm., Pl. W.[1]	7	15–21	18.2 ± 2.2	7	1.8–2.3	2.0 ± 0.2	0.3–0.4	0.35 ± 0.0	+
riparius	4	7–10	8.3	4	0.7–0.9	0.8	0.6–0.9	0.75	+
crista, Kuehr.	see text p. 42			11	0.6–1.0	0.8 ± 0.2	1.1–2.4	1.5 ± 0.4	+
acron., centr. Eur.	15	21–39	26.9 ± 5.3	16	2.1–4.7	3.5 ± 1.0	1.2–1.7	1.5 ± 0.2	–
acron., N Eur. + As.[1]	13	20–30	25.3 ± 3.1	25	1.9–3.2	2.5 ± 0.4	1.1–2.4	1.5 ± 0.3	–

[1] Unrelaxed.

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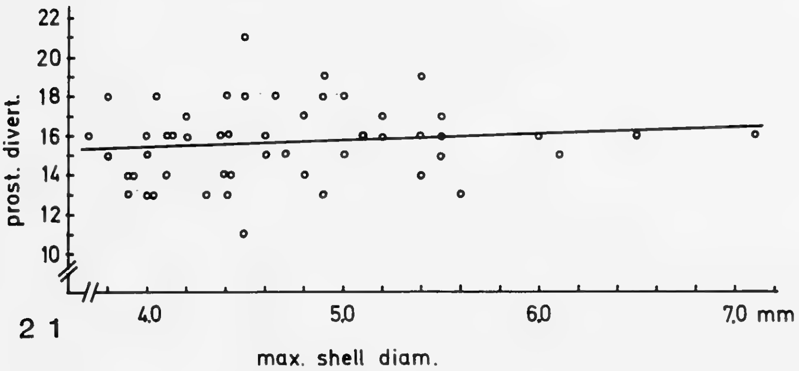

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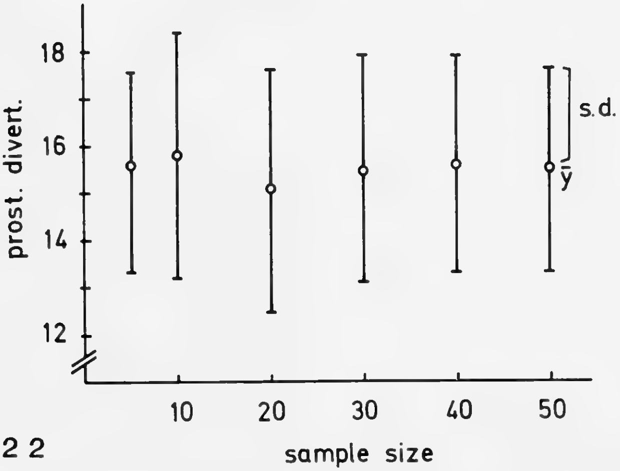
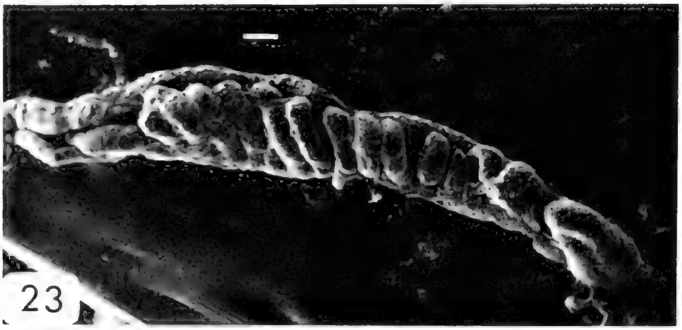


FIGS. 21–22. 21. Numbers of prostate diverticula in snails of various sizes. *G. spirillus*, Taiwan. $y = 14.1 + 0.33x$; $n = 51$; $r = 0.1245$ (significance limit for $p = 0.1$ is 0.2329). 22. Progress of mean numbers of prostate diverticula and standard deviations with increasing sample size. *G. spirillus*, Taiwan.

gan because it is a nonmuscular organ and, thus, not subject to contraction during fixation (Meier-Brook, 1976b). In *Gyraulus* the length could not be determined exactly in the majority of cases. Delamination is easy in *Planorbis* (Meier-Brook, 1976c; fig. 1), namely between the upper end of the penis sheath and the point of fusion of the sperm duct and the prostate duct. In *Gyraulus* this point is much less discernible.

The width of the vas deferens is uniformly low through the vast majority of *Gyraulus* species, but in some species from Lake Ohrid and the Malayan Archipelago it is constantly greater, and in one species (*G. parvus*) in the proximal half it is ⅓ to ½ of that in the distal half (both measured in the middle, Fig. 51). In these few cases characters of the vas deferens can serve for the discrimination of taxa.

The form and total length of the male copulatory organ as well as the ratio of length of penis sheath : length of preputium are of great taxonomic value and have been highly valued in planorbid taxonomy since they were used for discriminating among *G. acronicus*, *G. rossmaessleri* and *G. albus* (Meier-Brook, 1964; Hudec, 1967; Brown & van Eeden, 1969). This is in contradiction to Hubendick's (1955: 457 *et seq.*) opinion that it is "worthless to make measurements of its (male copulatory organ) different parts and then to base comparisons on details of proportion." The total length can be related to other dimensions and expressed by indicating the position of its upper end in relaxed individuals in situ (Fig. 44; Meier-Brook, 1964: figs. 21, 22). The ratio total length of the ♂ copulatory organ : greatest width of penis sheath, as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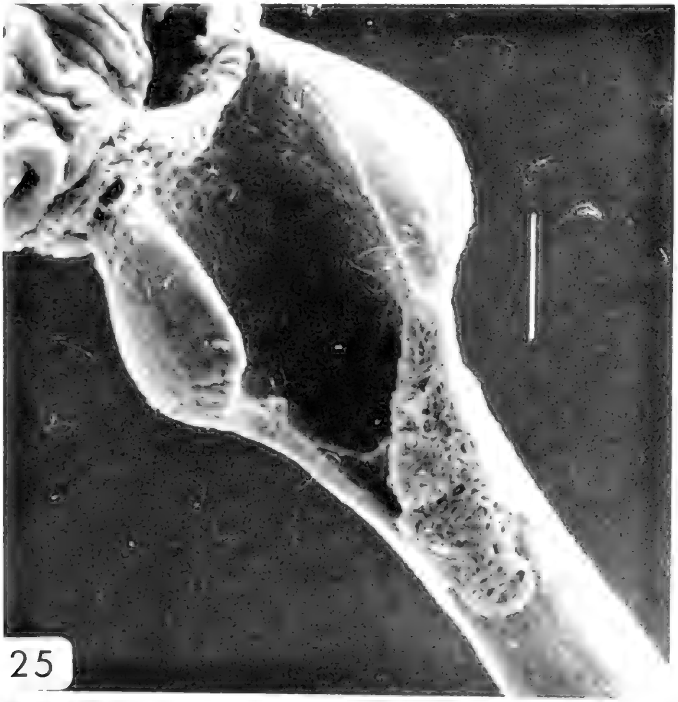
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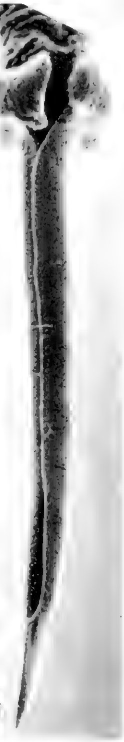
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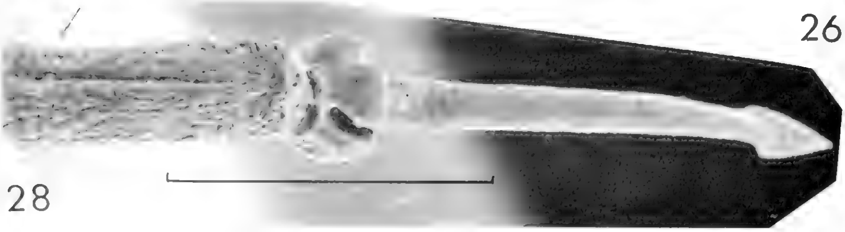
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tentatively used in a previous paper (Meier-Brook, 1964), is considered to be unnecessary, since drawings demonstrate differences better than numerical data in this case.

The penis provides two significant characters: the position of the penis pore, i.e. the aperture of the sperm canal and the shape of the penis tip. The penis tip is usually equipped with a bulbous thickening, resembling the mammalian glans penis (Fig. 45, etc.); in a few groups the thickening may be less distinct, in others there is a conical narrowing instead of a thickening (e.g. in *Gyraulus rossmaessleri,* Fig. 55; Meier-Brook, 1964: figs. 24, 27). The penis pore almost always is situated near or in the bulbous thickening and generally has a well defined site: (1) subterminal or in the distal half of the thickening (*G. albus*), (2) near the proximal end of the thickening or in its upper half (*G. acronicus,* almost all groups from S and SE Asia). Rarely it is situated above the middle of the whole penis, as described for *G. lychnidicus* by Hubendick & Radoman (1959: 236) and observed in the present study only in *G. malayensis* n. sp. from Bali, Java and Malaysia. In every case there is a more or less wide open groove running down from the penis pore to the proximal opening of the stylet (Fig. 24). During copulation the sperm traverses the groove to the stylet. The stylet leads it out of the everted copulatory organ through the hole in the papilla (Fig. 29). The stylet is so uniform in the whole genus as well as in closely related genera that it is not attributed interspecific significance, except in a few cases where it is reduced in size and form: the "hob-nail stylet" of *G. rossmaessleri, G. riparius,* and *G. crista* (L.).

Hubendick & Radoman (1959: 231–234) report on differences between two species, *G. crenophilus* Hubendick & Radoman and *G. fontinalis* Hubendick & Radoman, in the proximal end of the stylet. The basal part is said to have chitinized internal bars in the one and no such bars in the other species. When these species are reexamined, attention should be directed towards these alleged differences. According to my experiences such differences could occur depending on where one happens to section. In the middle of the wider basis (Fig. 25) a cross section may look like a horseshoe, as stated for *G. fontinalis* (Hubendick & Radoman, 1959: 234); a few μm towards the penis tissue the picture should be quite different. A continuous series of sections might have been impossible at that time because of the resistant stylet material.

The basal opening may vary a little from comparatively wide to narrower (Fig. 26). This figure, by the way, clearly demonstrates that the stylet is a hollow tube formed out of a thin blade by rolling up in a clockwise sense. The sperm leaves the stylet through a slit left open near the stylet tip (Fig. 27), which in this view appears extremely acute although it is of lancet-shape when viewed after being turned 90° (Fig. 28). In everted organs of individuals of various species only this tiny stylet tip penetrated the hole in the papilla (Brown & van Eeden, 1969, fig. 6). This hole (Fig. 29) is so small that most of the stylet (including its base) probably cannot pass through it, not to mention the penis tip itself. However, a penis extending into the preputium has been reported by Wright (1963: 463) as a characteristic of *Gyraulus costulatus* from Angola. Unfortunately he did not mention how frequently this condition was seen. I have found no more than one such case, which I could not explain, in adult *Gyraulus.*

In immature animals the stylet is positioned in the distal portion of the ♂ copulatory organ; this is the rule. In early stages of development there is no clear distinction between the future penis sheath and the preputium. The developing penis with the stylet, which is formed in its definitive size (Hubendick, 1958: 429; Meier-Brook, 1964: 238), extends distally to near the male genital pore.

←

FIGS. 23–28. 23. Prostate gland with closely spaced diverticula. *G. spirillus,* Taiwan. Most distal diverticulum two-branched, others unbranched. CPD; SEM. Scale = 0.1 mm. 24. Penis pore (arrow) and groove leading to stylet aperture. *G. euphraticus,* S Iran. CPD; SEM. Scale = 0.01 mm. 25. Stylet base is "horseshoe-shaped" in cross section. *G. chinensis,* Chongpyong. SEM. Scale = 0.01 mm. 26. Stylet showing apertures and edge of rolled up blade. *G. euphraticus,* S Iran. CPD; SEM. Scale = 0.1 mm. 27. Distal aperture of stylet. *G. euphraticus,* S Iran, different individual. CPD; SEM. Scale = 0.01 mm. 28. Penis tip showing penis pore (arrow) and stylet with basal aperture and lancet tip. *G. euphraticus,* S Iran, same spec. as in Fig. 26. CPD; SEM. Scale = 0.1 mm.

FIG. 29. Papilla showing hole through which the stylet tip is pushed for copulation. Copulatory organ broken between papilla and diaphragm. *G. spirillus*, Taiwan. CPD; SEM. Scale = 0.01 mm.

Later, when the copulatory organ begins to differentiate the stylet is still seen in the preputium surrounded by the tissue producing it (Meier-Brook, 1964, fig. 35).

During longitudinal growth of the whole organ the penis tip and the stylet then gradually withdraw, before differentiation of papilla and diaphragm takes place. In trematode-infected individuals, which were externally adult, but occasionally retarded in sexual development (microphally), I have observed portions of the penis extended into the preputium. Possibly an event like parasite-induced retardation would also explain Wright's (1963) statement. This is regarded the more probable since Brown & van Eeden (1969), investigating a large series of specimens of *G. costulatus* (Krauss) from South Africa, did not find the stylet position noticed by Wright.

In immature snails the stylet may be unrecognizable until a rather late developmental stage. This was first observed in *G. parvus* from Speyer (Germany). The first specimens received appeared to be fully grown. Notwithstanding, a stylet could not be detected, and the snails were tentatively placed in the genus *Promenetus.* In a few specimens the distal area of the penis sheath was found chitinized internally, a condition never reported in the literature. After keeping the remaining snails in aquaria for some weeks, all developed a normal stylet, while the chitinized region of the penis sheath was no longer observed. The shells had not noticeably grown in the meantime but body pigmentation had turned dark. The phenomenon, subsequently also found in *G. parvus* from Iceland and *G. laevis* from Germany, has not been investigated further. Observations suggest that the development of the stylet in these two species does not follow the pattern described for other species by Hubendick (1958) and confirmed in the majority of *Gyraulus* species in the present and a previous study (Meier-Brook, 1964). Possible differences in the site and mode of stylet formation that should be studied in detail may prove to support other differences on the subgeneric level. They are not so different that stylets in the differing groups could be regarded to be non-homologous. Otherwise, *G. parvus* and *G. laevis* could not be placed in the genus *Gyraulus.*

Any consistent lack of a distinct stylet in a species would indicate that it does not belong in the genus *Gyraulus.* Several African planorbid species were previously placed in *Gyraulus* and its close relative, *Anisus,* on conchological grounds, but in spite of the lack of a stylet. They have later turned out to be members of two separate genera, described as new by Brown & Mandahl-Barth (1973).

In two of three new *Gyraulus* species described by Brandt (1974: 241–243) the penis is said to lack a stylet. Anatomical features of these species are not figured; therefore it is impossible to determine their generic position.

Other species previously regarded as *Gyraulus,* but devoid of a penial stylet, could be placed in *Planorbis,* e.g. *Gyraulus macedonicus* Sturany (Hubendick & Radoman, 1959: 243), *G. presbensis* Sturany and *G. intermixtus* Mousson (Meier-Brook, 1976c).

The preputium usually contains two muscular pilasters, formed as an invagination of the preputial inner epithelium (cf. Meier-Brook, 1964: figs. 28–31). The interspace is filled with parenchyma, sufficiently extensible to permit eversion of the preputium for copulation. Presence and site of pilasters are normally indicated in external view by a particularly dense longitudinal pigmentation of the preputium. This pigmentation is evidently a result of folding of an outer epithelium which is rich in pigment anyway. In species with small ♂ copulatory organs pilasters may be absent. Doubtful cases occur and are exclud-

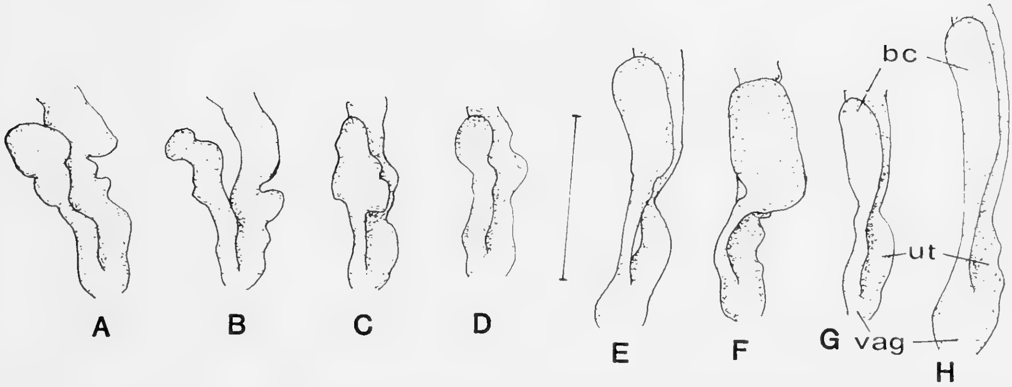


FIG. 30. Shapes of vagina and bursa copulatrix in contracted (A–D) and extended (E–H) individuals of *G. spirillus*, Taiwan.

ed from decisions. Clear absence may be consistent and is then used for characterizing species (compare also definitions!).

Non-Genetic Variation in Reproductive Organs

Effects of Fixation.—Since form and dimensions of soft parts underlie different amounts of contraction depending on fixing conditions it was necessary to evaluate the rôle of preparation methods commonly used.

Anatomical characters generally used in taxonomical studies of planorbid snails were compared in (1) individuals killed by immersion in 70% ethanol and in (2) those killed in warm (60–70°C) 4% formalin after relaxation with pentobarbital (according to Meier-Brook, 1976a, 1976b) for 12 hr. Both cohorts were selected at random from the same stock of laboratory reared snails. Comparison was made as to the shape of the bursa copulatrix and vagina and to the proportions of parts of the ♂ copulatory organ.

The bursa copulatrix in the example used (*Gyraulus spirillus* from Taiwan) has a more irregular shape in contracted (unrelaxed) individuals than in extended (relaxed) ones (Fig. 30) and is smaller. These alterations are evidently caused by external pressure exerted by surrounding tissues of the shrinking animals. Active contraction is unlikely because this organ lacks muscular tissue.

While the preputium (prp in Table 3) loses an insignificant portion of its length, it is mainly the penis sheath (psh in Table 3) that is reduced in length by 25% on average. Consequently the ratio psh:prp is also altered significantly. These results differ from those found in a *Planorbis* species (Meier-Brook, 1976b), where the penis sheath is smaller and much less muscularized. Why the preputium in *Gyraulus* contracted to a lesser degree than expected after the experiences with *Planorbis* is not clear. Histologically these parts do not differ fundamentally in the two genera. There is good reason not to transfer exact data of length reduction from *Gyraulus spirillus* to other species of the genus.

Alterations not given in the table are seen in the length and shape of the penis (Fig. 31). The penis in most cases coils within the penis sheath, which, in its turn, shortens and widens by contraction of the spirally arranged longitudinal musculature (Fig. 32).

Circulatory and Nervous Systems

The circulatory and nervous systems of all groups have been examined for taxonomically valuable characters. I examined the heart, sections of the aorta, and the central nervous system. There were no unique character states enabling species discrimination. Dense pigmentation of the heart is constant in *Gyraulus laevis*, rendering the heart the darkest part of the animal beside the stomach and parts of the intestine. The heart has little pigmentation or is unpigmented in all other species studied.

Chromosomes

The karyotype has proved useful in some planorbid groups, particularly in the problem-

TABLE 3. Dimensions (mm) and ratios of parts of the male copulatory organ in *G. spirillus* from Taiwan, fixed in relaxed (fully extended) and unrelaxed (contracted) states.

Fixing state	Whorl number		Length of psh	t-test	Length of prp	t-test	Ratio psh:prp	t-test
	n	x̄ ± s.d.	x̄ ± s.d.	p	x̄ ± s.d.	p	x̄ ± s.d.	p
fully extended	21	4.11 ± 0.32	1.21 ± 0.20 (range 0.8–1.5)	<0.001	0.68 ± 0.16 (range 0.4–1.0)	<0.05	1.85 ± 0.43 (range 1.33–3.00)	<0.01
contracted	20	4.11 ± 0.28	0.91 ± 0.20 (range 0.6–1.2)		0.66 ± 0.15 (range 0.3–0.9)		1.42 ± 0.36 (range 0.75–2.33)	

atic taxonomy of *Bulinus* species, where the usual planorbid chromosome number of 2n = 36 has undergone various multiplications (Burch, 1964, 1967). Burch (1960) was the first to show tetraploidy (2n = 72) in a *Gyraulus* species (*G. parvus,* in the original publication misidentified as *G. circumstriatus* (Tryon) (Natarajan et al., 1965: 251)). In the present study *G. parvus* from Mainz was found to have n = 36 and 2n = 72. A cytological examination of *G. laevis,* considered closely related to *G. parvus* on morphological grounds, was not possible though most desirable; animals did not survive transport to the laboratory. *G. euphraticus* from southern Iran and *G. spirillus* (Gould) from Taiwan had n = 18 and 2n = 36. Burch *et al.* (1964: 221) reviewed chromosome numbers of five *Gyraulus* species, stating that in *G. tokyoensis* two of five specimens studied had 19 instead of 18 bivalents in meiotic cells; one of them even had 19 bivalents plus a univalent. Apart from chromosome numbers, the karyotype does not appear to differ between species using my techniques.

Biochemical Approaches

Biochemical data are well suited to support or disprove hypotheses about relationships between taxa including species (Davis & Lindsay, 1967; Grossu, 1977). Electrophoretic studies, for example, require living material, because samples should, whenever possible, be examined simultaneously. Since living snails were available only from a restricted number of species application of chemotaxonomic methods had to be postponed until sufficient material is successfully cultivated in the laboratory.

Parasitological Evidence

Parasitological data have been used to support or weaken conclusions about relationships to an increasing extent in several groups of animals (Fahrenholz's Rule, Eichler, 1941). Echinostomatid rediae were regularly observed during these studies, but a species identification would have required establishing life cycles in the laboratory. The expected value of the findings, however, would not have justified the expense.

Number of Eggs per Egg Mass

The number of eggs per egg mass was determined for species reared in the laboratory. Results so far seem to indicate that egg

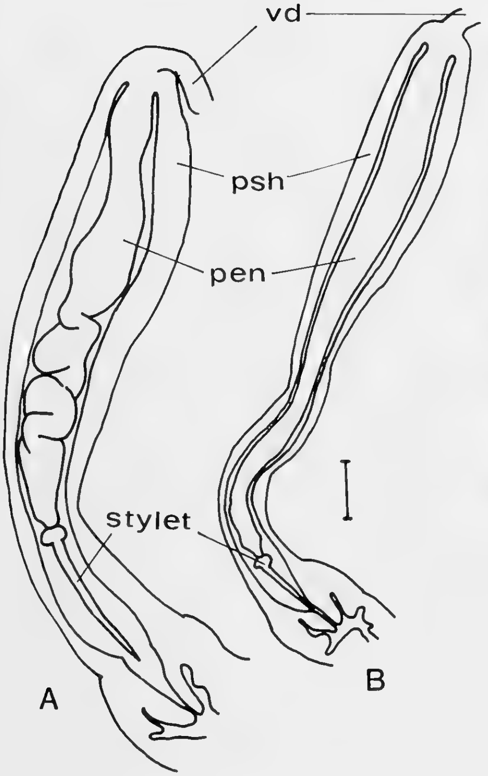


FIG. 31. Penis sheath and penis in an individual fixed without (A) and with (B) relaxation. *G. spirillus*, Taiwan. Scale = 0.1 mm.

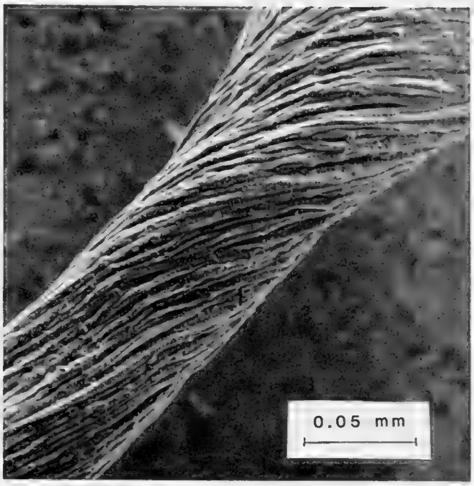


FIG. 32. Spirally arranged longitudinal muscles of penis sheath in an unrelaxed, contracted individual, fixed in ethanol. *G. chinensis*, Chongpyong. CPD; SEM.

numbers per mass in general are correlated with snail size and are, thus, of restricted value. Nevertheless, in certain cases, when species of approximately equal sizes are compared, such as *Gyraulus albus, G. laevis,* and *G. parvus,* highly significant differences in egg numbers per mass (Table 4) are found. These support conclusions drawn anatomically. Aquarium conditions were kept constant and as similar as possible for all species: 25°C, 12 hr/12 hr light-dark regime; 2 liters of hard water (24° German hardness, ≅8.56 mval/l); fortnightly water change; twisted fresh lettuce ad libitum daily; medium population density (appr. 20 to 40 mature snails in 2 liters of water).

Differences reported here between *G. albus* and *G. parvus* correspond well with those

TABLE 4. Numbers of eggs per egg mass in *Gyraulus* species.

Species, origin, counting date	n masses counted	range	eggs/mass x̄ ± s.d.
albus, Zürichsee 23-IV-1974	105	1–10	6.1 ± 1.5
laevis, Haarlem 21-IX-1977	32	1–7	4.6 ± 1.2
parvus, Mainz 22-III-1974	231	1–4	2.3 ± 0.7
dto. 17-XII-1974	103	1–4	2.3 ± 0.7
dto. 30-IX-1975	140	1–5	2.4 ± 0.9
costulatus, Liberia 8-I-1975	253	2–6	4.1 ± 0.7
ehrenbergi, Cairo 7-XI-1974	119	2–8	5.0 ± 1.2
euphraticus, S Iran 19-III-1975	167	1–11	5.1 ± 2.0
chinensis, Kwekers 2-XI-1977	152	2–12	5.8 ± 1.9
spirillus, Taiwan 12-VI-1976 (density: 105 ind./2 l)	139	2–14	5.8 ± 2.2
dto., 7-X-1976 (7 ind./2 l)	88	3–14	7.4 ± 2.1

t-test: *albus/parvus, albus/laevis, parvus/laevis,* and *spirillus* high/low density $p < 0.001$.

described in the literature. Bondesen (1950: 54) even observed up to 16 eggs per mass in *G. albus*, and Krull (1931: 5), for *G. parvus* from Michigan, wrote that "masses of two or three are the most common but those of one or four are also found."

Population density greatly affects egg production as shown by data obtained at high and low densities of *Gyraulus spirillus* (Table 4). The differences between 5.8 and 7.4 are very highly significant ($p < 0.001$). Mean values of 6.1, 6.4, and 6.5 were found at intermediate densities.

Ecological Differences

Very little is known about ecological differences between *Gyraulus* species. In the case of stenotopic snails, I attach taxonomic significance to differences in physiological requirements that now probably prevent gene flow. Examples of such species are *Gyraulus rossmaessleri* with its preponderance in astatic water bodies, and *G. laevis* which appears to be favoured by a high nitrate content and often reaches high abundance in slightly brackish water. The importance of such differences in chemical and physical requirements as well as behavioural differences "in maintaining (possibly not in initiating) isolation between populations" has been pointed out for most groups of organisms (Prosser, 1974: 359). Of course, in the Planorbidae the situation is certainly not as simple as in *Paramaecium aurelia*, where Sonneborn & Dippell (1943) distinguished no fewer than 16 physiological varieties, each of which "has a potentially common gene pool which is effectively cut off from the gene pool of every other variety" and two of which are distinguished by the temperatures optimal for their growth and reproduction (Sonneborn, 1974: 173).

Although we cannot yet define the specific ecological preferences of most species, the situation in the pair of sibling species, *Gyraulus parvus* and *G. laevis* is an example of differing ecologies. My objections to the view of conspecificity of these species as represented by Jaeckel (1962: 69) initially were based on differences in ecological range, which is much wider in *G. parvus* than in *G. laevis*. As mentioned above, the latter species is both rather stenotopic and rare, while the former species is nearly ubiquitous (Clarke, 1973: 403). *G. parvus* regularly lives in pools of botanical and zoological gardens in Europe, since 1973 constantly in a ground-water lake near Speyer (W. Germany), and in May 1977 it was collected in a forest pool near Stuttgart (S. Germany) and hence outside man-controlled water bodies in central Europe. It readily propagates in aquaria. *G. laevis*, on the other hand, is difficult to rear and is obviously diminishing in its original distribution area. These observations support the view that environmental requirements differ between the two species.

Characterization of Anatomically Examined Species

A detailed description of taxonomically relevant organs including generic characters is given for the type-species of the genus, *Gyraulus albus*. Descriptions of other species are confined to characters of diagnostic importance. Quantifiable data are listed in tables or demonstrated in graphs as much as possible.

Before conclusions are drawn as to species delimitations, species are dealt with under provisional names. These are mostly in conformance with common use in the respective geographical areas. Type-localities are added in parentheses.

For clarity, treatment of species is subdivided according to its origin in the generally accepted zoogeographical regions ("realm") (de Lattin, 1967, fig. 87): the Palaearctic, the Oriental and, as isolated relics of Tertiary origin and foci of advanced speciation, the ancient lakes. As the borderline between Palaearctic and Orient, as found for most groups of animals, does not fit the distribution patterns in *Gyraulus* completely, chapters are headed "Europe and North Asia" and "South and East Asia."

Synonyms, even those generally accepted as correctly identified by authorities, are omitted unless I could examine preserved specimens or shells in original series, and when their identification was beyond all doubt.

Under "material" collection localities are written in short form. More detailed information on the locations is listed alphabetically in the Appendix. Spelling of names follows The Times Atlas of the World (1967) if entered there. Material preserved without relaxation and hence in a contracted state is marked "unrelaxed." All individuals without this note were relaxed and fixed, as described above. Symbols specifying material are included in parentheses.

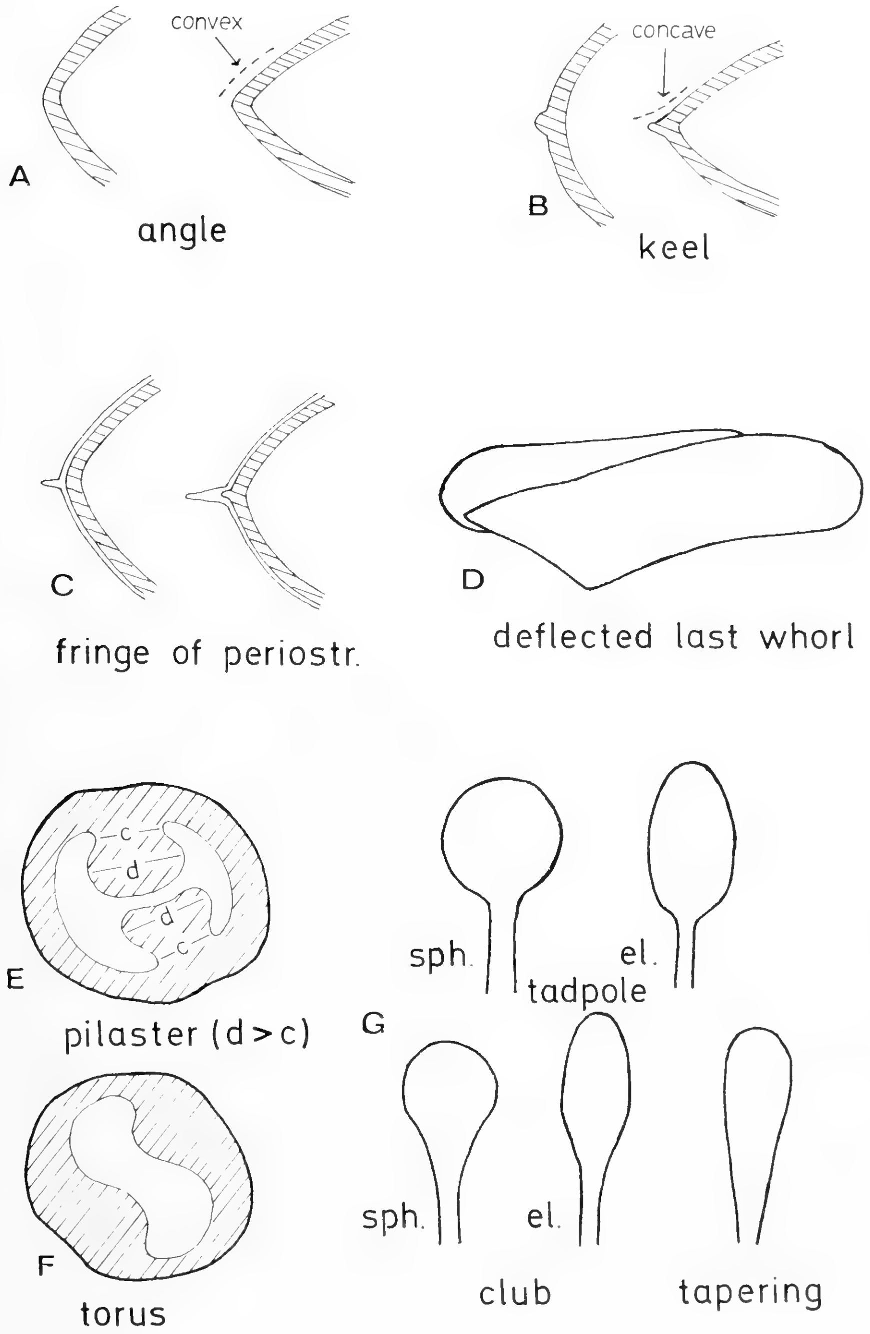


FIG. 33. Definitions. A–C: outlines of shell periphery in cross section; D: deflected last whorl (example: *G. acronicus*, Bodensee); E–F: preputial wall in cross section; G: shapes of bursa copulatrix (from top left): tadpole spherical, tadpole elongate, club spherical, club elongate, tapering.

In the figures, scales measure 1 mm unless stated otherwise. In the drawings, shaded areas indicate sectioned tissues.

MUSEUM ABBREVIATIONS

ANSP—Academy of Natural Sciences of Philadelphia
BMNH—British Museum (Natural History), London
IRSNB—Institut Royal des Sciences Naturelles de Belgique, Bruxelles
M or MG—no. in the author's collection of microsc. preparations
NHMG—Naturhistoriska Museet Göteborg
NHRMS—Naturhistoriska Riksmuseet Stockholm
MHNG—Musée d'Histoire Naturelle Genève
NMC—National Museum of Canada, Ottawa
NMV—National Museum of Victoria, Melbourne
RMNH—Rijksmuseum van Natuurlijke Historie, Leiden
SMF—Senckenberg-Museum Frankfurt/M.
ZMA—Zool. Museum Amsterdam
ZMZ—Zoologisches Museum Zürich
ZSI—Zoological Survey of India, Calcutta

DEFINITIONS AND SYNONYMOUS TERMS

The following alphabetical list of terms used here for morphological analysis, including synonymous terms, is provided to enable recognition of and the position of organs or parts of organs, and to delimit them from other organs connected or attached to them. Definitions do not include functional aspects. Terms in common and uncontroversial use in planorbid taxonomy are exempted.

angle—any interruption of a regular rounding (Fig. 33A).

club elongate (bursa copulatrix)—an elongate bursa with gradual transition to bursa duct, but not evenly tapering (Fig. 33G).

club spherical (bursa copulatrix)—a balloonlike bursa with gradual transition to bursa duct (Fig. 33G).

copulatory organ—penis + penis sheath + preputium.

deflected whorl—a whorl leaving the planispiral phase of growth toward the upper side (=under side in the sense of many previous authors, therefore: deflected = bent down) (Fig. 33D).

diaphragm—the muscular ring proximally terminating the preputium, resembling a sphincter; =velum sensu Hubendick, 1955; =Ringwulst sensu Buchner, 1891; =diaphragm or muscular ring sensu Baker, 1945.

distal—situated towards outside.

embryonic whorl—the whorl formed within the egg shell; =nuclear whorl (Fig. 10, up to arrow).

free sperm duct—the portion of the sperm duct not covered by the prostate gland.

fringe (of periostracum)—a periostracal collar on the periphery of a shell, attached to an angle or keel (Fig. 33C).

height—the maximum dimension measured perpendicular to the plane in which the whorls grow (Fig. 1).

keel—a calcareous collar on the periphery of a shell, resulting in a concave outline in cross section (Fig. 33B).

maximum diameter—measured from peristome ("outer lip") of the aperture through the innermost (nuclear) whorl (Fig. 1).

papilla—the conical to hemispherical tissue distally terminating the penis sheath, carrying a hole which is penetrated by the stylet for copulation (Fig. 29); =sarcobelum sensu Hubendick, 1955; Stilettscheide sensu Buchner, 1891; =papilla sensu Baker, 1945.

penis sheath—the proximal portion of the ♂ copulatory organ harbouring the penis, delimited proximally by the end of the vas deferens, distally by the widened lumen between papilla and diaphragm. This is the hinge-point for eversion of the preputium; =penis sac in Pan American Health Organization, 1968; =vergic sac sensu Baker, 1945; =phallotheca II auctorum (P2 Hudec, in Macha, 1963); =distale (!) Phallotheca sensu Hudec, 1967.

pilaster—a longitudinal ridge running along the inner wall of the preputium and reaching a width greater than at the site of connection with preputial wall (Fig. 33E); =muscular pillar sensu Hubendick, 1955; =Muskelpfeiler sensu Meier-Brook, 1964. (The term pilaster is preferred to pillar, because there is always a connection with the wall along its full length, whereas "pillar" implies partial detachment from the wall.)

preputium—the distal portion of the ♂ copulatory organ, delimited proximally by a weak zone between papilla and diaphragm, distally by the body integument; =phallotheca I auctorum; =proximale (!) Phallotheca or Praeputium sensu Hudec, 1967.

proximal—situated towards the inner whorls.

tadpole elongate (bursa copulatrix)—an elongate bursa with bursa duct distinctly set off (Fig. 33G).

tadpole spherical (bursa copulatrix)—a balloon-like bursa with bursa duct distinctly set off (Fig. 33G).

tapering (towards the vagina: bursa copulatrix)—a bursa evenly tapering, without a clear distinction of bursa and bursa duct (Fig. 33G).

under side—under side in a shell held with its aperture on its left side (as in apertural views of figures in the present paper); =morphological under side or conchological upper side or functional right side sensu Hubendick & Radoman, 1959; =right side sensu Pan American Health Organization, 1968.

upper side—upper side in a shell held with its aperture on its left side; =morphological upper side or conchological under side or functional left side sensu Hubendick & Radoman, 1959; =left side sensu Pan American Health Organization, 1968.

KEY TO LETTERING

agl	albumen gland
an	anus
aur	auricle
bc	bursa copulatrix
bm	buccal mass
cae	caecum
car	carrefour
cga	cerebral ganglion
dgl	digestive gland
dgld	common duct of digestive gland portions
dia	diaphragm
free spd	free sperm duct
h	heart
int	intestine
intl	intestinal loop
ki	kidney
mbo	mantle border
mcol	columellar muscle
mrp	penis retractor muscle
ngl	nidamental gland
od	oviduct
oes	oesophagus
ot	ovotestis
pa	papilla
pc	pericardium
pen	penis
pgm	male genital pore
pnst	pneumostome
pp	penis pore
prp	preputium
psb	pseudobranch
psh	penis sheath
pst	prostate gland
pstd	prostate duct
rec	rectum
ret	renal tube (tubular portion of kidney)
sgl	salivary gland
ski	saccular portion of kidney
sod	spermoviduct
spd	sperm duct
st	stylet
sto	stomach
uo	external opening of ureter
ut	uterus
vag	vagina
vd	vas deferens
ventr	ventricle
vep	pulmonary vein
ver	renal vein
vs	seminal vesicle

SPECIES OF EUROPE AND NORTH ASIA

Gyraulus albus (Müller, 1774)

Planorbis albus Müller, 1774: 164, No. 350 (Fig. 34) (Fridrichsdal, Sjaelland, Denmark).

Planorbis hispidus Draparnaud, 1805.

Planorbis crosseanus Bourguignat, 1862: 42.

Gyraulus albus, Ehrmann, 1933: 170, pl. 8, fig. 104 (but not including "*G. a. acronicus* (=*Planorbis deformis* Hartmann)" listed hereunder!).

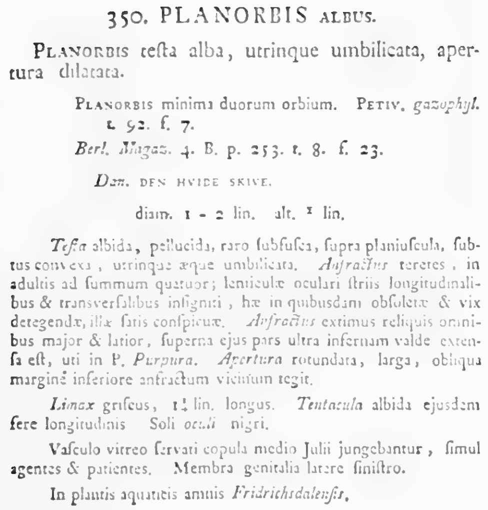
Gyraulus albus, Hubendick, 1949: 43, figs. 83–85.

Gyraulus albus, Jaeckel, 1962: 68 (but not including *G. deformis* (Hartm.) and *G. tenellus* (Hartmann)!).

P. hispidus Draparnaud was designated by Dall (1870) as the type-species of *Gyraulus.*

Material—Jorløse, Sjaelland (Denmark), 18 specs.; Switzerland: Zürichsee, 3 specs.; Greifensee, 3 specs.; Fischau (Austria), 4 specs. (unrelaxed); Germany: Kuehren, 2 specs.; Bodensee, 2 specs.; Dobersdorfer See, 2 specs.; Ettenheim, 4 specs.; Wollmatingen, 2 specs.; Ursee, 9 specs.; Windgfällweiher, 6 specs.

Shell (Fig. 35)—The shell is planispiral, of medium size (4–7 mm maximum diameter), relatively high (1.2–1.8 mm) and has 3½ (at most 4 or 4¼) whorls, which rapidly increase



350. PLANORBIS ALBUS.

PLANORBIS teſta alba, utrinque umbilicata, apertura dilatata.

PLANORBIS minima duorum orbium. PETIV. *gazophyl.* t. 92. f. 7.

Berl. Magaz. 4. B. p. 253. t. 8. f. 23.

Dan. DEN HVIDE SKIVE.

diam. 1 - 2 lin. alt. ½ lin.

Teſta albida, pellucida, raro ſubfuſca, ſupra planiuſcula, ſubtus convexa, utrinque æque umbilicata. *Anfractus* teretes, in adultis ad ſummum quatuor; lenticulæ oculari ſtriis longitudinalibus & transverſalibus inſigniti, hæ in quibusdam obſoletæ & vix detegendæ, illæ ſatis conſpicuæ. *Anfractus* extimus reliquis omnibus major & latior, ſuperna ejus pars ultra infernam valde extenſa eſt, uti in P. *Purpura*. *Apertura* rotundata, larga, obliqua margine inferiore anfractum vicinum tegit.

Limax griſeus, 1¼ lin. longus. *Tentacula* albida ejusdem fere longitudinis. Soli *oculi* nigri.

Vaſculo vitreo ſervati copula medio Julii jungebantur, ſimul agentes & patientes. Membra genitalia latere ſiniſtro.

In plantis aquaticis amnis *Fridrichsdalenſis*.

FIG. 34. Facsimile of O. F. Müller's description of *Planorbis albus* (1774: 164).

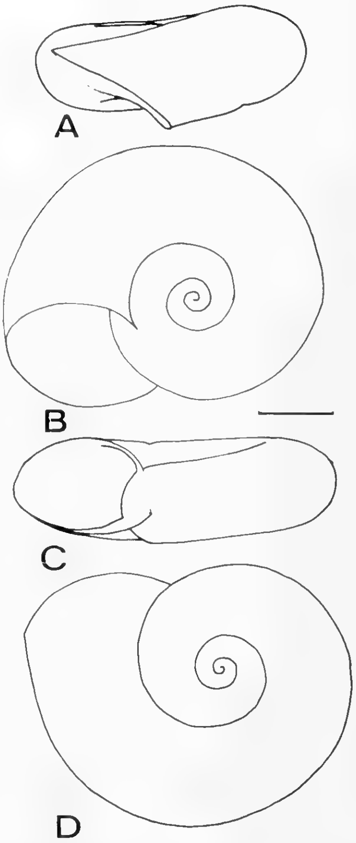


FIG. 35. *G. albus*, Sjaelland. Shell shape: A—lateral view, B—upper side, C—apertural view, D—under side (SMF 246 302).

in width. The last whorl expands towards the aperture and ends in a broadening bend. The whorls are a little wider than high, giving the aperture an ovoid shape. Each whorl scarcely embraces the preceding one; the whorls are equally rounded on each side as well as peripherally and rarely have a trace of an angle. The shell is slightly concave on the under side and deeply concave on the upper side. The last whorl is not or very little deflected.

Growth lines are arcuate, crossed by spiral striae, both forming a reticulate surface sculpture (Fig. 36A, B). This sculpture is usually well developed; when weakly developed it is visible at least on the upper side of the shell. The surface is never glossy; the periostracum sometimes has short hair-like protrusions; these are part of the periostracal ridges formed on growth lines, the ridges being stretched out to triangular laminae on the nodules formed at the crossing points. "Hairs" thus follow the spiral striae (Fig. 36C). The color is light-corneous.

Animal (Fig. 37)—The animal is light to medium grey. The pigment is distributed not quite evenly on the cephalopedal mass that comprises body portions extended out of the shell during crawling. The tentacles are lighter, except for a central line that is darker; pigmentation is cloudy on the remaining parts. The anterior mantle roof (Figs. 11 and 37) is diffusely pigmented, showing a cloudy pattern. The mantle roof is dark grey on the right side, in a zone parallel to the columellar muscle. Pigmentation is weaker and diffuse to almost absent in between this densely pigmented zone and the peripheral region. At the periphery there is a narrow longitudinal unpigmented stripe indicating the position of the pulmonary vein (Fig. 37A, vep); next to it the kidney roof is densely pigmented. The renal vein (Fig. 37A, ver), again devoid of pigment, delimits the kidney on its left side. The remaining portion of the left mantle side is weakly pigmented, only a few scattered pigment cells being present.

Pallial Organs (Fig. 38)—The pallial cavity extends back from the thickened mantle border (mbo) to about ⅔ of the last whorl. The dorsal part of the mantle roof is occupied by the kidney. The kidney consists of the very short saccular portion (ski) situated to the left of the pericardium (in dorsal view) and the long renal tube (ret). Anteriorly, the kidney tapers off and ends in a reflected ureter, discharging (uo) behind the pneumostome (pnst). In extended individuals the kidney has straight margins; there are no septa in the lumen of the renal tube. None of the three pallial ridges regularly found in other planorbid groups is developed.

The mantle border is partially connected with the roof of the cephalopedal mass by connective tissue (Fig. 39). The pallial cavity opens on the left side through the pneumostome (pnst) formed by the mantle lobe, which in the living snail is held against the mantle border (mbo), together with the pseudobranch (psb). The pseudobranch is triangular to rectangular and carries a longitudinal fold. The rectum ends (an) near the base of the pseudobranch on the right of this fold.

Alimentary Tract—The jaw is composed of numerous chitinized bars, approximately 12 in the median part, and 15 to 20 in each of the lateral portions (Fig. 40).

The radula of a sexually mature animal consists of approximately 150 transverse rows of teeth. The almost straight rows are formed by 27 to 35 single teeth (Fig. 41); the central tooth is bicuspid (Fig. 17). A small additional denticle regularly occurs between the cusps; similar denticles are found on both sides of the tooth, but nearer to the base. The base broadens posteriorly. The lateral teeth are tricuspid. The mesocone is the longest one; the endocone is a little shorter and the ectocone the shortest. Again there are additional denticles between each cusp and on both sides of a tooth. The base of the lateral teeth has parallel edges directed obliquely towards the lateral posterior region of the radula. About the 10th or 11th lateral tooth shows the first signs of a conversion to marginal teeth. These are pluricuspid, but the three cusps of the lateral teeth, particularly the mesocone, are still pronounced, though narrower. The denticles increase in number and size (Fig. 42). Cusps and denticles together total a dozen or even more. Variation of radula characters is slight.

The oesophagus emerges from the dorsal part of the buccal mass and penetrates the ring of the central nervous system as a narrow tube. A short distance behind the central nervous system it widens abruptly and runs backwards along the right side of the body,

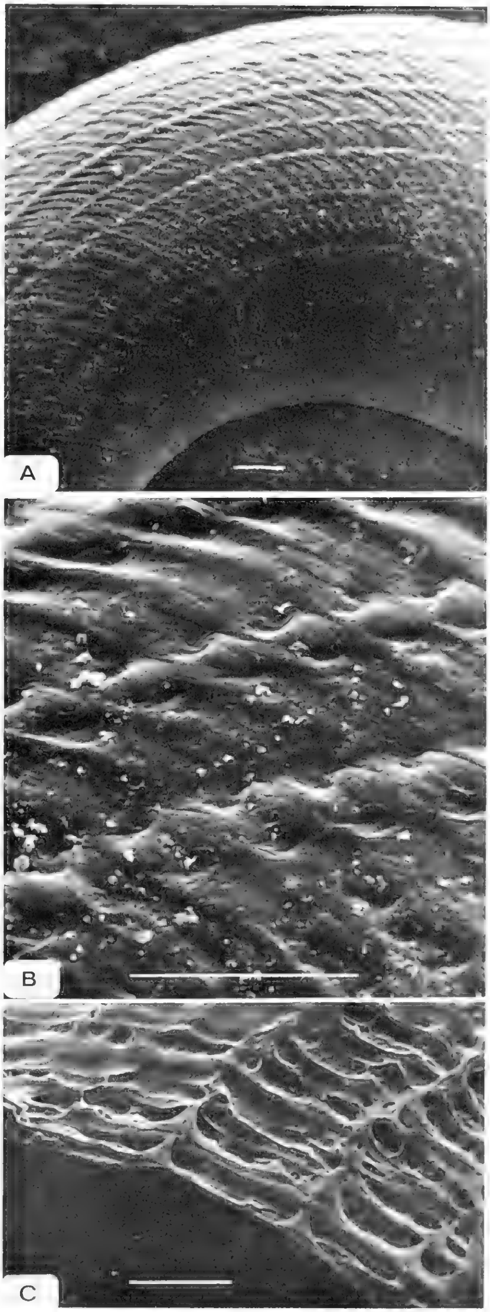


FIG. 36. Shell surface of *G. albus*, Sjaelland, with characteristic reticulate sculpture (A, B) or "hairs" (C). Scales = 0.1 mm.

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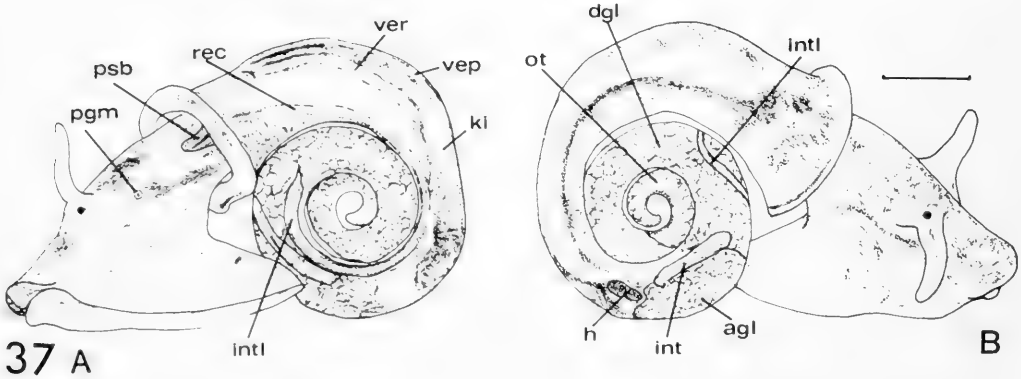

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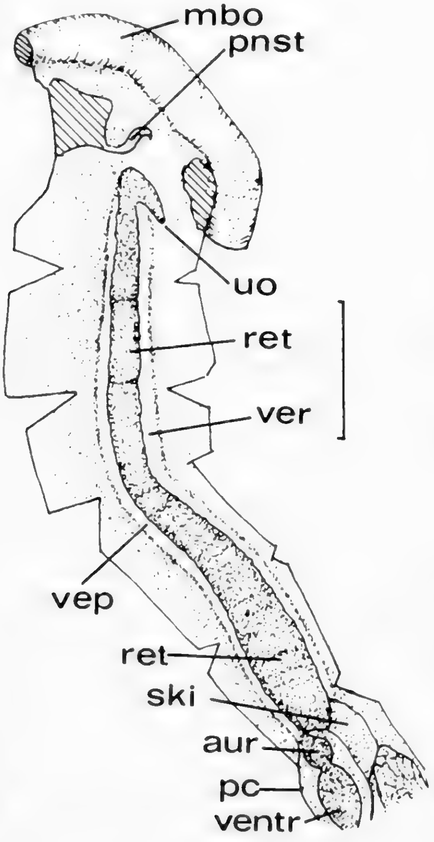

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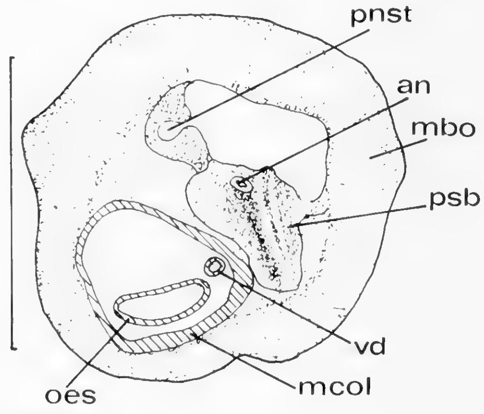

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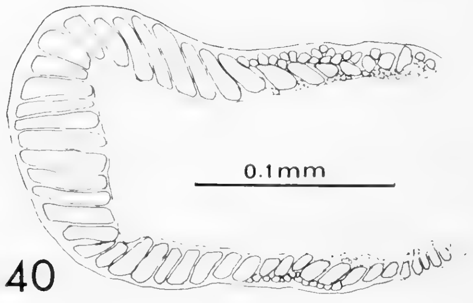
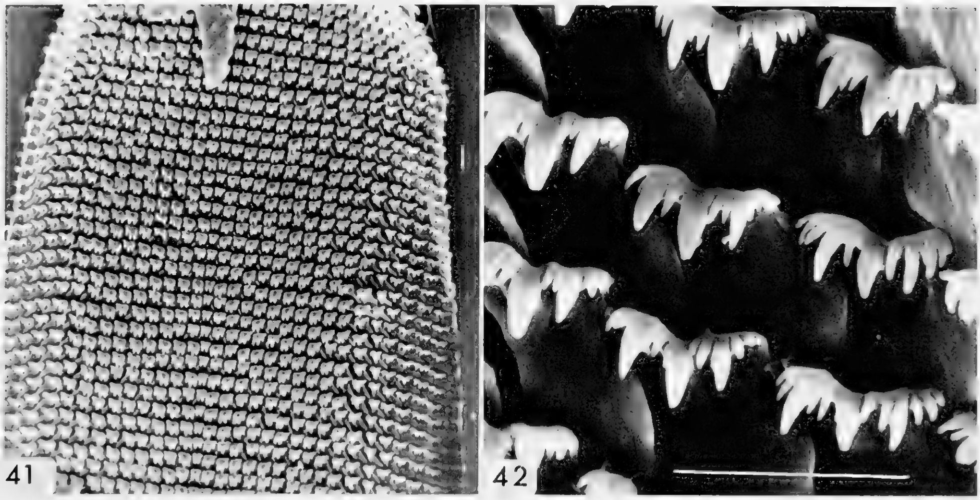


FIGS. 37–40. *G. albus*. Sjaelland. 37. Animal with shell removed, viewed from the left and right, to show pigmentation and position of organs visible externally. 38. Ceiling of mantle cavity showing kidney region. Ventral view (SMF 246 301). 39. Mantle border in frontal view. Cephalopedal mass and portion behind mantle border cut off. Relaxed individual with widely dilated pallial opening. 40. Jaw (M 289).

usually attached to the exterior side of the prostate gland. Behind the end of the pallial cavity it turns to the middle and widens, forming a crop. This leads to the strong muscular part of the stomach (the gizzard) that is always filled with sand grains.

The intestine leaves the stomach on its right posterior side and bends anteriorly (Fig. 18).



FIGS. 41–42. *G. albus,* Sjaelland. 41. Transverse rows of radular teeth. SEM. Scale = 0.01 mm. 42. Marginal teeth nos. 13–15. SEM. Scale = 0.01 mm.

At the bending point the short duct of the digestive gland merges into the intestine. A caecum, in the anteriad direction, follows immediately. The intestine then follows the course described above as an intestinal loop (Fig. 18). The rectum makes its way to the pseudobranch on the extreme left side of the floor of the pallial cavity.

The salivary glands insert on the dorsal part of the buccal mass, close to the oesophagus. They penetrate the nerve ring together with the oesophagus, buccal retractor muscles and cephalic arteries. The two unequal parts of the digestive gland (Fig. 37B, dgl) almost fill the whole space from the central part of the stomach to the middle of the ovotestis. Only the intestinal loop and the spermoviduct with the seminal vesicle are embedded in it.

The intestinal loop may be more or less well developed, i.e. longer or shorter. Complete lack of the loop has not been observed in *Gyraulus albus.*

Reproductive System (Fig. 43)—The ovotestis (ot) consists of a double row of 20 to 30 lobes. The anterior part of the ovotestis is situated on the left side of the posterior end of the digestive gland. The spermoviduct (sod) is embedded ventrally in the middle of the latter. It leaves the ovotestis as an initially wide and delicate tube, then narrowing and, after a short distance, coiling up to form the seminal vesicle (vs), where sperm is stored after production. A narrow distal part, considerably longer than the proximal one, follows and enters the rather voluminous carrefour (car). This is a complex hollow organ, entered also by the tiny duct of the albumen gland (agl). The albumen gland is a compact organ, convex dorsally, concave ventrally, composed of numerous small acini.

Distal to the carrefour the female and the male tracts of the reproductive system separate. The oviduct leaves the carrefour on the left side as a wide and irregularly shaped tube.

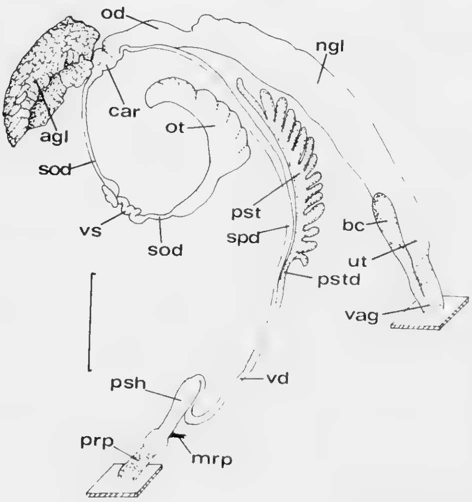


FIG. 43. Reproductive system of *G. albus,* Sjaelland. Max. shell diameter 5 mm, 4¼ whorls (M 286). Key to lettering p. 27.

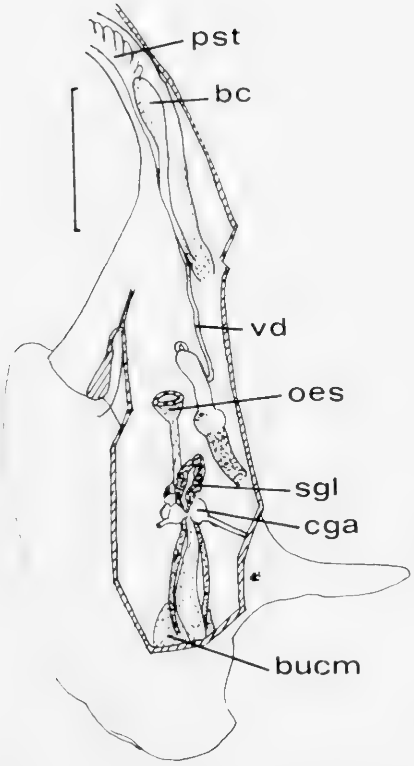


FIG. 44. Position of distal genitalia in a fully extended *G. albus*, Sjaelland. Roof of cephalopedal mass and posterior portion of oesophagus removed (SMF 246 301). Key to lettering p. 27.

Its transition to the part joined by the nidamental gland is mostly invisible from the outside. Under favourable circumstances the nidamental gland can be distinguished from the oviduct by its opaque yellowish appearance. The uterus can be told from the nidamental gland by a more transparent and colorless appearance. The uterus finally narrows abruptly towards the vagina, which is uninflated or, at most, weakly inflated near the ♀ genital pore. Here the bursa copulatrix branches off with a duct of moderate width. The bursa is club-shaped in *Gyraulus albus*, usually elongate, rarely more spherical. It is always narrower than the uterus.

The male tract emerges from the carrefour on the right ventral side. The sperm duct is always considerably narrower than any part of the female tract. It lies close to the oviduct and is joined by the duct of the prostrate gland. Their fusion takes place gradually so that it cannot be clearly located in many cases. The prostate duct is longer than half the sperm duct. A number of diverticula merges into the duct. These are densely arranged in a single row and are not separable histologically from the prostate duct. Diverticula are unbranched in the vast majority of examined individuals; the bifid condition rarely occurs. A more scattered, irregular and less dense arrangement of diverticula was observed in several individuals of one population (Sjaelland, Denmark). Numbers of prostate diverticula usually vary from 13 to 20. In one population, numbers as low as 7 were counted (Table 1).

The vas deferens, extending between the point of fusion of the prostate duct with the sperm duct and the ♂ copulatory organ, is relatively wide.

The ♂ copulatory organ is comparatively short. In relaxed and well extended animals of *Gyraulus albus* its proximal end at most reaches up to the bursa copulatrix, but often not even to the vagina (Fig. 44). The penis sheath (psh) is 1.5 to 2.0 times the length of the preputium (Table 2). It is club-shaped in outline, being narrowest near its middle. A knob-like thickening of the copulatory organ in the region of the papilla and diaphragm indicates the border between the two portions in external view. A single retractor muscle inserts at the penis sheath near its distal end.

The preputium has relatively thin walls that are folded inwards, but too little to form pilasters (see definitions). The preputial lumen is oval in cross section or slightly S-shaped. The male copulatory organ opens outwards a short distance behind the left tentacle (Fig. 37A, pgm).

The penis is enclosed in the penis sheath. It consists of a long tube, uniform except at its tip. Distally the penis is thickened on one side (see Meier-Brook, 1964, figs. 25, 28). The orifice of the sperm canal (pp) is in the distal half of the thickening, and is often subterminal. Variation in the form of the penis tip and position of the penis pore, is moderate (Fig. 45). The groove between the penis pore and the opening of the stylet is wide and shallow, not narrow as shown for *Gyraulus euphraticus* (Fig. 28). The stylet varies a little in size and shape, but is generally similar to that figured from other species (Figs. 25–28).

As to the histology of the ♂ copulatory organ, I refer to the excellent account by Buchner (1891: 78–84, pl. V: 1) for *Anisus vortex*.

Remarks—*Gyraulus albus* is so well sep-

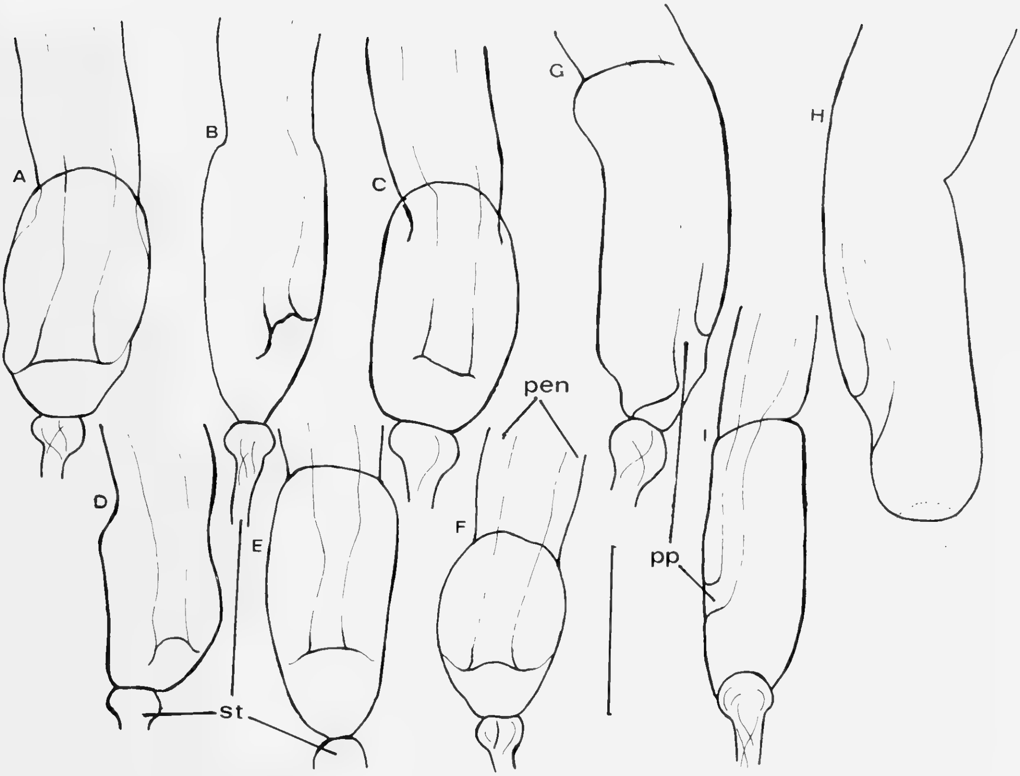


FIG. 45. Variation in shape of penis tip and position of penis pore in *G. albus*. A–F: Sjaelland (M 286); G–H: Ettenheim (M 288); I: Kuehren (M 90). Scale = 0.1 mm.

arated from any other species of the genus that problems arise neither in delimitation nor in recognition. Shell characters alone are sufficient to distinguish this species from others. *G. albus* is distributed all over Europe; it is most frequent in temperate climates. It extends far to the east. Khazannikov (1973: fig. 1) figured ♂ copulatory organs clearly proving correct identification of this species from the River Terek Basin (northeast of the Caucasus), but so far this is the most eastern record of anatomically-identified specimens. All records from Central or East Asia seem to have been published by authors who only knew *G. albus* from descriptions and insufficient illustrations, or had little experience with this species. Thus, the species named *Anisus* (*Gyraulus*) *albus* by Mori (1938: 294, pl. 16: 13) was doubtlessly misidentified, as judged from the description and figures. Kuroda's listing of *G. albus* (1963: 23) and of *G. spirillus* as one of its synonyms was evidently based on Mori's paper. Consequently it is highly probable that this species does not live in Japan.

Yen (1939: 69) claimed that *Gyraulus albus* was frequently found in N and S China. I examined the material in the Senckenberg-Museum, Frankfurt. The shells in the three lots named *G. albus* from Sagsagyr/Ordos, Peak/Hongkong and Pok-Fulam/Hongkong (Yen, 1939, pl. 6, fig. 6) are devoid of any spiral striation and cannot be distinguished from the material anatomically examined and identified as *G. chinensis* in this study.

It must be conceded, however, that at that time—and until recently (Jaeckel, 1962: 68)—*Planorbis deformis* Hartmann was considered a variety of *Gyraulus albus,* and that in E Asia there are indeed snails resembling *P. deformis* at first glance. *P. deformis* has, in the meantime, proven to be a synonym of *G. acronicus* (Meier-Brook, 1964). Whether *G. albus* is conspecific with North American forms such as *G. deflectus* (Say, 1824) and *G. hirsutus* (Gould, 1839) cannot yet be an-

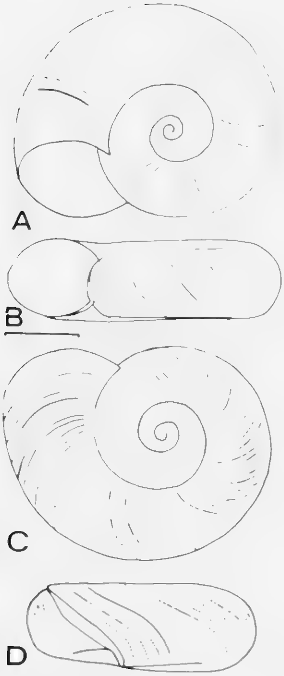


FIG. 46. *G. laevis*, Kuehren. Shell. A—upper side, B—apertural view, C—under side, D—lateral view (SMF 246 308).

swered satisfactorily. Species identity of these has been claimed by Dall (1905) and Baker (1928), but other authors have questioned this on conchological grounds (Miller, 1966; Clarke, 1973). Judging by Baker's (1945: pls. 15, 16) anatomical figures, the two American species have a ♂ copulatory organ at least twice the length of that of *G. albus*.

Gyraulus laevis (Alder, 1838)

Planorbis laevis Alder, 1838: 337 (Whitley Quarries near Newcastle).
Planorbis thermalis Westerlund, 1885: 83 (Bad Villach).
Gyraulus laevis, Ehrmann, 1933: 170, pl. 8, fig. 105.
Gyraulus laevis, Jaeckel, 1962: 69.

Material—Kuehren (Germany, 16 specs., including 5 trematode-infected ones with underdeveloped reproductive organs; Haarlem (Netherlands), 12 specs.; Bad Villach (Austria), 10 specs. (*Gyraulus thermalis*).

Shell (Fig. 46)—The shell is a little smaller than in *Gyraulus albus* (4 mm maximum diameter), relatively high (1.3 mm); it has 3½ whorls, which increase regularly in width, the last one not expanding towards the aperture. The whorls are scarcely wider than high and separated by deep sutures; the aperture is roundish. The periphery is rounded, never keeled or angled. The shell is deeply concave on the upper side; on the under side, the whorls interior to the penultimate one are also concave; the whorls are more rounded on the under side than on the upper side. Growth lines are less arcuate than in *G. albus* and irregular. The surface is smooth (Fig. 47) and

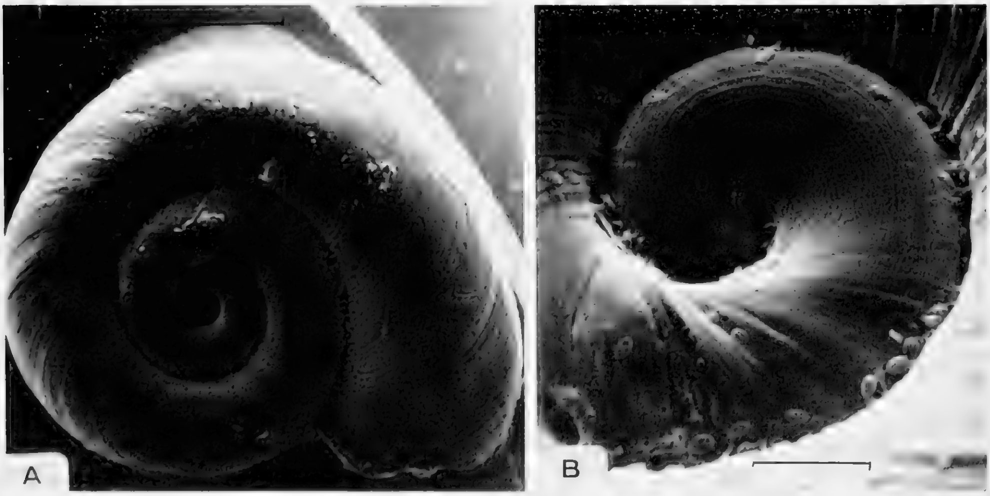


FIG. 47. *G. laevis*, Kuehren. Shell surface, SEM. A—whole shell. B—spiral striation on embryonic whorl. Scale = 0.1 mm.

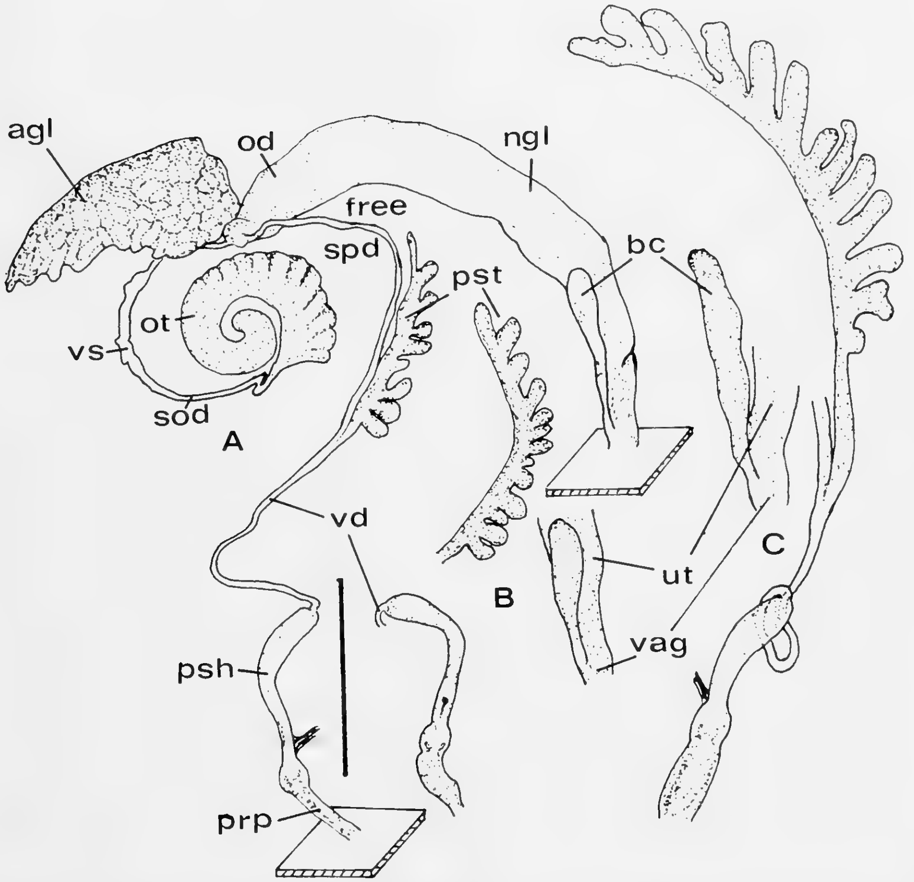


FIG. 48. *G. laevis*, Kuehren. Reproductive system. Maximum shell diameter: A—3.4 mm (SMF 246 309), B—3.6 mm (M 290), C—5.4 mm (M 66). Key to lettering p. 27.

slightly glossy; spiral striae are absent except on the nuclear whorl, as in all species. The color is brownish.

In the population at Bad Villach named *Gyraulus thermalis* shells are smaller, 2 to 3 mm in diameter, 0.9 to 1.0 mm in height, with 3 to 3¼ whorls.

Animal—The animal is moderately grey and scarcely pigmented; the mantle roof is virtually unpigmented except on the kidney and lateral borders of the accompanying veins where scattered pigment cells are found. The mantle border is unpigmented. The extreme right portion of the mantle covering the reproductive tract is more densely pigmented. Conspicuously dark pigmentation is present only in the heart, stomach and intestine between stomach and flexion (Fig. 19, arrow).

There are several distinct septa in the kidney giving it an undulate shape (Fig. 14). The jaw and radula are not fundamentally different from those described for *Gyraulus albus*. An intestinal loop was lacking (Fig. 19) in ten individuals and well developed in six from the population at Kuehren.

In the reproductive system (Fig. 48), the distal portion of the spermoviduct is wider (0.030–0.033 mm) than the two halves of the vas deferens in their respective middle parts (proximal half ~ 0.012 mm; distal half ~ 0.018 mm) and also wider than the sperm duct. The bursa copulatrix is inconspicuous, elongate club-shaped or tapering. The prostate gland is so delicate that it is almost impossible to detach it from the female tract without damage. It shows two unusual features: the scattered arrangement of diverticula and their changing shape. The number of diverticula seems to be slightly less than in *Gyraulus albus* (Table 2). The vas deferens is similarly narrow in both halves (see above). The ♂ copulatory organ is not longer than that in *G. albus* (Table 2). Microphally was observed in trematode-infected individuals (x̄ = 0.60 ± 0.2 mm). The length ratio penis sheath : preputium is also similar to that in *G. albus*. The preputium cannot be distinguished from that of *G. albus*.

The penis shows considerable variation in shape. In larger individuals (e.g. Fig. 48C) it is nearly congruent with those figured for *Gyraulus albus* in Fig. 45E and similar forms. In smaller individuals 3.3–4.0 mm in diameter, the distal thickening is regularly undeveloped; the tip is rather conical in shape, and the penis pore is lateral rather than subterminal. This shape and penis pore position is possibly a sign of immaturity although an orange color in all individuals indicates that copulation has taken place. The question deserves further attention. Smaller individuals with an incompletely differentiated stylet and a colorless bursa copulatrix have been exempted from evaluation.

Remarks—*Gyraulus laevis* has been defined as a distinct species conchologically for a long time. Doubts can arise, where *G. laevis* and *G. albus* occur together and the latter has weak spiral striation. However, the septate kidney and the irregular prostate diverticula provide good characters for safe distinction. *G. laevis* is closely related, though not identical, with the North American *G. parvus,* which is included here for comparison and because it lives on Iceland and has been introduced to Europe. The only anatomical description of *G. laevis* thus far published is by Soos (1935: 26, fig. 3). From his figure it can be seen that his Hungarian material resembles that presented here in the irregular prostate diverticula, their number (11), the short ♂ copulatory organ, and the club-shaped bursa copulatrix. Soos, however, expressed the opinion that *G. laevis* differs anatomically from *G. albus* only to a negligible degree.

Gyraulus thermalis has been given the rank of a subspecies of *G. laevis* or a species endemic to the thermal spring of Villach (Klemm, 1960: 12; Jaeckel, 1962: 69; Jaeckel, 1967: 103). However, the small size of *G. thermalis* appears to be the only character by which it constantly differs from *G. laevis.* In this connection it may be noted that there are more instances in the genus where thermal springs harbor snails significantly smaller than those that occur in cooler waters. One is *G. acronicus* from Paratunka (Kamchatka): the snails were collected "near hot springs"; the biggest of 97 individuals was 4.7 mm in diameter, whereas samples from other Siberian localities contained snails exceeding 6 or 6.5 mm in diameter. The other example is *G. parvus* from a warm spring in Iceland (about 30°C, as estimated by the collector). Snails from two shipments were transferred to aquaria at 25°C in attempts to raise larger individuals for anatomical studies. They all died before growing larger than 2.5–3.0 mm diameter. As the sample also never contained empty shells larger than these, I assume that they do not exceed this size in their natural habitat. The mechanism causing dwarfism in warm springs is not yet understood. At any rate it is unlikely that a process of speciation has been initiated here. Only in such a case would it be justified to raise a dwarf form, such as *thermalis,* to subspecies rank. Experimental analysis should clear up how far in phenotypical dwarfism genetically fixed characters are involved. It seems preferable to deal with *thermalis* as merely an ecological form.

Snails diagnosed as *Gyraulus laevis* have been recorded from Europe and Asia as far east as Kamchatka. According to Alzona (1971) the species is said to live all over Italy, and other records were published on its distribution in other Mediterranean countries, sometimes under names such as *G. agraulus* and *G. numidicus.* In one case an anatomical figure was published of "*Gyraulus agraulus.*" This figure clearly proves that the material does not belong in *Gyraulus* (Giusti, 1968).

In attempts to obtain more material of *Gy-*

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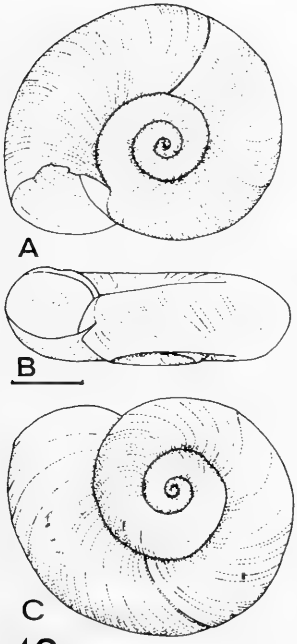
FIGS. 49–52. *G. parvus.* 49. Ann Arbor (U.S.A.). Shell (SMF 246 310). A—upper side; B—apertural view; C—under side. 50. Variation in prostate glands. A, B: Ann Arbor (M 30), C: W Iceland (M 198), D: SE Iceland (MG 208). 51. ♂ copulatory organ (Speyer) and characteristic vas deferens being wide in the distal half (0.050 mm in its middle) and narrow in the proximal half (0.018 mm) (M 227). Scale = 0.1 mm. 52. Variation in shape of penis tips and position of penis pore. A, B: Ann Arbor (M 81, 83); C, D: W Iceland (M 199); E, F: SE Iceland (M 274); G, H: Speyer (M 275). Scale = 0.1 mm.


A
B
C

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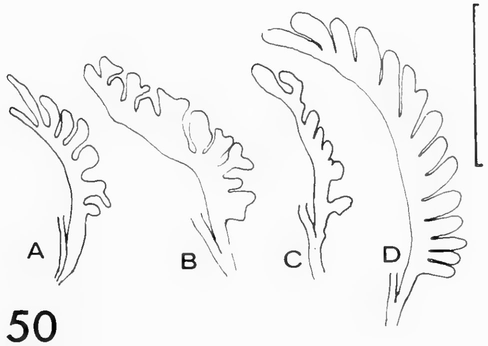
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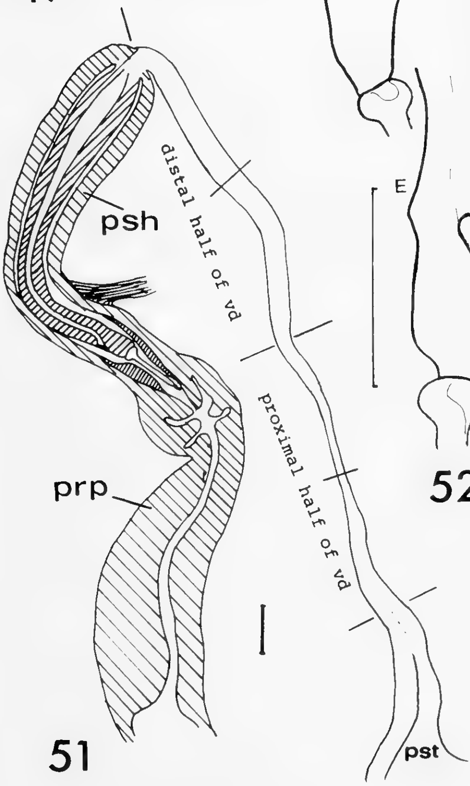
psh
distal half of vd
prp
proximal half of vd
pst

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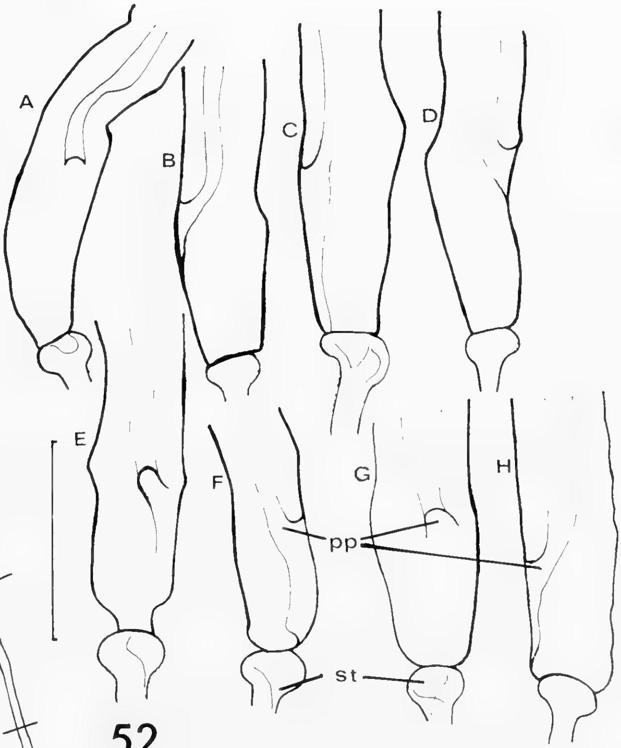
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TABLE 5. Reproductive organs of *Gyraulus parvus.*

	Male copulatory organ								Bursa copul.		
	No. prost. divert.			Total length (mm)			Ratio psh:prp				
Locality	n	range	x ± s.d.	n	range	x̄ ± s.d.	range	x̄ ± s.d.	clb. el.	clb. sph.	tap.
Ann Arbor	5	7–10	8.5 ± 1.1	6	1.1–1.6	1.4 ± 0.2	1.1–2.5	1.6 ± 0.6	+	+	+
Abitibi-R[1]				3	0.8 + 0.8 + 1.2		1.5 + 1.7 + 2.3			+	+
Lesser Slave L.[1]	2	10 + 12		2	1.4 + 1.8		1.6 + 1.0			+	+
W Iceland	4	6–9	8.0	4	1.0–1.3	1.1	1.9–2.3	2.1	+		+
SE Iceland	5	12–14	12.8	7	1.2–1.6	1.5 ± 0.1	1.5–2.5	2.0 ± 0.3	+		+
Mainz	9	9–17	12.1 ± 2.9	8	0.9–1.7	1.2 ± 0.2	1.3–2.3	1.8 ± 0.3	+		+
Speyer	6	10–16	12.2 ± 2.0	7	1.3–2.0	1.6 ± 0.2	1.2–2.0	1.5 ± 0.3	+		+
Total	31	7–17	11.0 ± 2.7	32[2]	0.8–2.0	1.4 ± 0.2	1.1–2.5	1.8 ± 0.4			

[1] Unrelaxed.

[2] Excl. unrelaxed individuals from Canada.

raulus laevis, I have dissected snails identified as *G. laevis.* Moreover, I checked drawings of material studied and kindly provided by Dr. Giusti from various Mediterranean islands. Specimens from Crete, Corfu, Rhodos, Elba, Montecristo, Corsica, Sardinia, Mallorca and, moreover, from Madeira had anatomical features of the genus *Planorbis*; it is therefore doubted that *G. laevis* lives in the Mediterranean region. The occurrence of this species in Asia must also be doubted unless anatomical evidence proves the contrary.

Gyraulus parvus (Say, 1817)

Planorbis parvus Say, 1817: pl. 1, fig. 5 (Delaware River, near Philadelphia).

Material—Ann Arbor (U.S.A.), 13 specs.; Abitibi River (Canada), 3 specs. (unrelaxed); Lesser Slave Lake (Canada), 2 specs. (unrelaxed); W Iceland, 5 specs.; SE Iceland, 3 specs.; Germany (introduced): Speyer, 11 specs.; Mainz, 11 specs.

Shell—The shell is small, deeply umbilicate on the upper side; on the under side the penultimate whorl is strikingly elevated (Fig. 49). Both the inner whorls and the last whorl are sunken or deflected respectively. This character state is more strongly developed in *Gyraulus parvus* than in *G. laevis.* The whorls are rounded or nearly angled on the under side; the sutures are deep. The surface is smooth and glossy; no spiral striation is present. The color is light-corneous to brownish.

Animal—The animal is very weakly pigmented, like *Gyraulus laevis.* The kidney has distinctly undulate margins. The intestinal loop was lacking in all individuals seen. The seminal vesicle is inconspicuous to slightly bulbous; the distal portion of the spermoviduct is as narrow as in *G. albus.* The vagina is not or scarcely inflated. The bursa copulatrix is as narrow (and relatively long) as in *G. laevis,* mostly tapering or elongate club-shaped, rarely spherical club-shaped. The number of prostate diverticula is insignificantly less than in *G. laevis* (Table 5). The shape of the diverticula is still more irregular than in *G. laevis* (Fig. 50A–C), often branched, but in two populations (SE Iceland, Speyer), regularly and closely spaced diverticula occasionally occurred (Fig. 50D). The most consistent character state in *G. parvus* is the strikingly changing width of the vas deferens (Fig. 51). In its course it narrows in between as usual in most species, but in its distal half it widens so much that its diameter becomes twice that of the proximal half (width ratio distal : proximal half: $\bar{x} = 2.1 \pm 0.5$, range 1.3–3; $n = 22$).

The ♂ copulatory organ is similar to that of *Gyraulus laevis*; its total length as well as proportions are of the same order of magnitude. The preputium does not have pilasters, but its lumen is S-shaped. The penis, in most cases, has a slight terminal thickening (Fig. 52A–E), less distinct than that shown for *G. albus* (Fig. 45), but incidentally such a thickening may be indiscernible (Fig. 52F, H). The penis pore lies within the terminal thickening or corresponding region, but its position varies to some degree.

Remarks—The question of species identity of *Gyraulus laevis* and *G. parvus* has repeatedly been raised because of their conchological similarities. Anatomical investigations show that common shell characters are evidently not a result of convergent evolution, as they share a number of derived characters to the extent that they can be considered sibling species, one living in Europe, the other in North America. The common characters, most of which I regard as derived, are: (1) whorls almost circular in cross section; (2) lack of spiral striation; (3) deeply umbilicated upper side; (4) lack of mantle pigmentation left and right of kidney; (5) black pigmentation of heart, stomach and intestine; (6) lack of marked thickening of penis tip; (7) delicate, irregularly shaped and loosely arranged prostate diverticula; (8) narrow and long bursa copulatrix, and (9) undulate kidney margins.

Of these, characters 7 and 9 are unique in the *Planorbis*-tribe; they have not been observed in related genera, *Anisus, Bathyomphalus,* and *Planorbis.* Placement in their own subgenus is justified. A subgenus name created by Dall (1905: 86) with *Planorbis parvus* Say as the type-species is available: *Torquis.* A diagnosis will be given in a later chapter. According to Dall there are some more species in North America to be placed here. I have not examined other North American species. In Europe, *Gyraulus laevis* is the only representative of *Torquis. G. parvus* is distributed all over North America; "its northern limit corresponds fairly well with the tree line" (Clarke, 1973: 403). As shown here, its range includes Iceland as well. The occurrence in Europe is without doubt due to a quite recent introduction, probably together with aquarium plants. Characters separating *G. parvus* from *G. laevis* are: (1) the elevated penultimate whorl, and (2) the marked widening of the distal half of the vas deferens as compared with that of the proximal half. These two traits of *G. parvus* are unique in the tribus and thus they must be regarded as derived. In addition, (3) the distal portion of the spermoviduct is not wider than the widest portion of the sperm duct, and (4) the euryoekous character of *G. parvus* clearly distinguishes it from *G. laevis.*

My observation that all individuals examined lack an intestinal loop agrees with Baker's (1945: 74) statement "no intestinal loop in *Torquis.*" This may hold true for American species of the subgenus, but not for *Gyraulus laevis.*

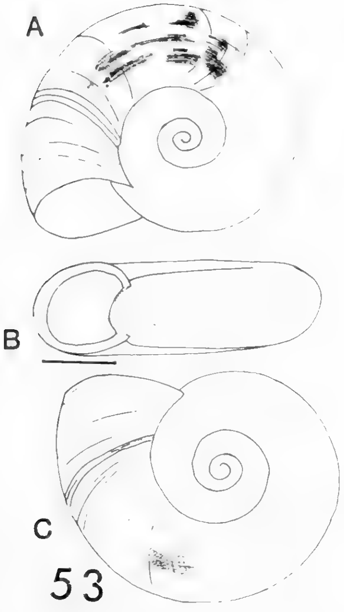
Gyraulus rossmaessleri (Auerswald, 1851)

Planorbis rossmaessleri Auerswald, 1851: 179 (Leipzig).

Material—Beside the material dealt with previously (Meier-Brook, 1964), further specimens were studied from Drusenheim (France), 3 specs. (unrelaxed); Sessenheim/Soufflenheim (France), 1 spec.; and Pleistinger Wörth (Germany), 7 specs. (unrelaxed).

Shell—The shell (Fig. 53) is small- to medium-sized, usually not exceeding 4 mm in diameter and 1.3 mm in height. It is similar to *Gyraulus laevis* in shape, but less deeply umbilicate; the sutures are less deep, the whorls are rounded, never angled or keeled. The aperture has a characteristic thickened lip (that does not necessarily terminate growth!). Growth marks indicating growth interruptions are regularly present (desiccation of habitat!). The surface is not smooth, but rather dull, with a very fine reticulate sculpture (spiral striae very close to each other). The color is red-brown.

Animal—The animal is similar to *Gyraulus albus* insofar as diffuse pigmentation is concerned. The heart is not dark, but so sparsely pigmented that it contrasts with its grey surroundings by its light appearance. The kidney has undulate margins. The intestinal loop is present in all individuals. The seminal vesicle is voluminous, with spiny coiling. The distal spermoviduct is long and very slender (Fig. 54). The bursa copulatrix is elongate club-shaped or tapering, in one population (Pleistinger Wörth) being almost of the elongate tadpole type. The bursa duct is wide, not narrower than the vagina. The sperm duct is



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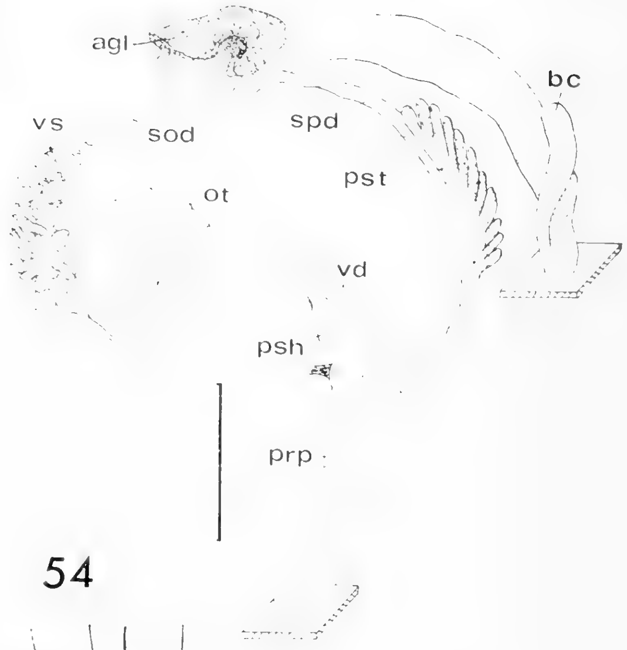

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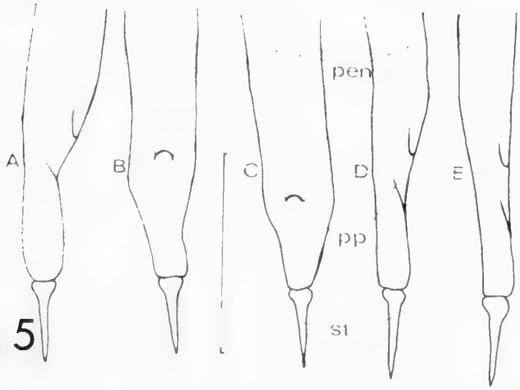

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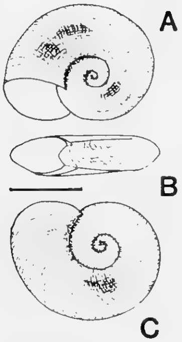
FIGS. 53–55. *G. rossmaessleri.* 53. Shell, Drusenheim. 54. Reproductive system. Soufflenheim. Maximum shell diameter 4.3 mm, 3¾ whorls (M 291). 55. Variation in shape of penis tip and position of penis pore. A: Soufflenheim (M 292); B–D: Pleistinger Wörth (M 293); E: Drusenheim (SMF 246 312). Scale = 0.1 mm.

wide. The prostate gland has a low to moderate number of diverticula (Table 2), which are closely spaced and regular in form. The length of the ♂ copulatory organ is about the same as in *G. albus* or longer (Pleistinger Wörth). The penis sheath which is extremely short and narrow is scarcely set off from the vas deferens. The preputium is considerably wider and longer, the ratio psh:prp being far below one. The penis is correspondingly tiny and slender. The penis tip is tapering where in *G. albus* and other species the thickening occurs. The penis pore lies where tapering begins. The stylet is hob-nail shaped (Fig. 55).

Remarks—Beside my previous studies on *Gyraulus rossmaessleri* there is only one further paper figuring the reproductive system of this species, as found in a Czechoslovakian population by Hudec (in Macha, 1963: 87). In the shape of the bursa copulatrix, its wide duct, and in the ♂ copulatory organ there is agreement with the present finding. As the status of *G. rossmaessleri* as a separate species had not been acknowledged for a



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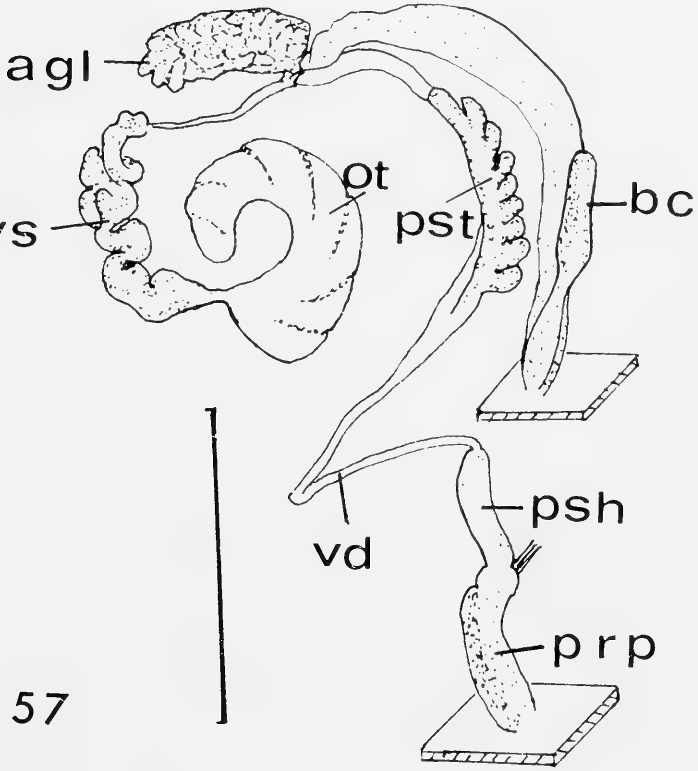

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FIGS. 56–57. *G. riparius*, Kolksee. 56. Shell. 57. Reproductive system. Maximum shell diameter 2.2 mm, 2¾ whorls (SMF 246 313).

long time (compare Meier-Brook, 1964: 233, 238 and following), distribution data in the literature will have to be revised. This is a strictly European species.

Gyraulus riparius (Westerlund, 1865)

Planorbis riparius Westerlund, 1865: 106 (Ronneby).

Material—Kolksee (Germany), 4 specs.

Shell—The shell (Fig. 56) is very small and delicate; most do not exceed 2.3 mm in diameter and 0.6 mm in height; it is discus-like, resembling a young *Hippeutis complanatus* in general shape. The three whorls increase rapidly; they are flattened. The periphery is angled; the aperture is spindle-shaped in its exterior portion. The growth lines are arcuate. The surface is silky in texture and has very fine, but relatively remote spiral striae.

Animal—The animal is weakly pigmented; the cephalopedal mass is light grey, and the mantle including the kidney is almost unpigmented. The kidney margins are undulate. An intestinal loop was present in the specimens examined. The ovotestis is large as compared with the remaining parts of the reproductive system (Fig. 57). The proximal portion of the spermoviduct is extremely short. The seminal vesicle has bulbous coils and is very voluminous, approaching or exceeding the albumen gland in size. The bursa copulatrix is elongate club-shaped to cylindrical, its duct being proximally narrow, but inflated towards its orifice, giving it the same width as the vagina itself. The prostate has 7 to 10 diverticula, which are closely spaced and of regular shape. The ♂ copulatory organ is comparatively long (0.7, 0.8, 0.8, 0.9 mm). The preputium is wide; its lumen is S-shaped. The penis (Fig. 58) is very similar to that described for *Gyraulus rossmaessleri*, with almost no variation in the four individuals.

Remarks—This rare species was placed in *Hippeutis* for a long time. Odhner (1929) was the first to find a stylet and therefore included

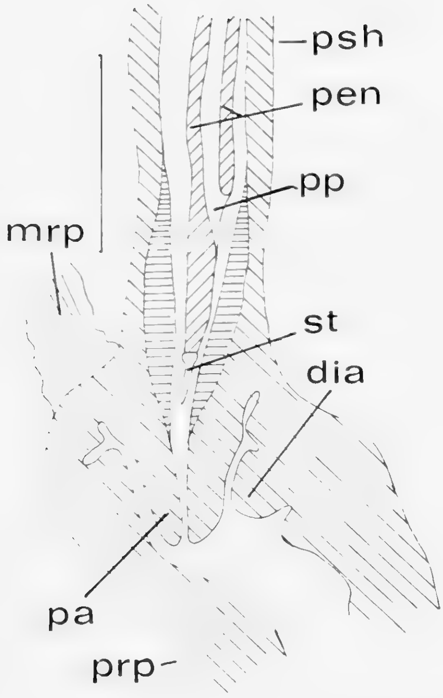


FIG. 58. *G. riparius*, Kolksee, region of transition between penis sheath/preputium and penis tip. Same specimen as in Fig. 57. Horizontal shading: columnar epithelium in distal area of penis sheath. Scale = 0.1 mm. Key to lettering p. 27.

the species in *Gyraulus*. His figure (Odhner, 1929, reproduced in 1956: fig. 2d) shows the general shape of the ♂ copulatory organ found in the German specimens, but (certainly due to the restricted optical facilities then available) his drawing is too poor to permit further comparison in detail.

Because of the ♂ copulatory organ, which undoubtedly was derived from the type seen in *Gyraulus* by size reduction of the penis and penis sheath, and retention of preputium size, it appears justified to place *Gyraulus riparius* in its own subgenus.

Starobogatov (1967: 296) named a new subgenus of *Choanomphalus* (!) with *Planorbis riparius* as the type-species: *Lamorbis*. He also wanted to place *Gyraulus rossmaessleri* in *Lamorbis* but gave no reasons. This will be discussed later.

Gyraulus crista (Linnaeus, 1758)

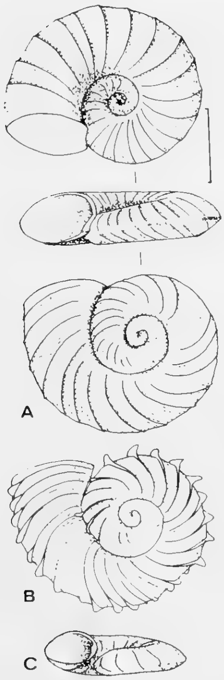
Nautilus crista Linnaeus, 1758: 709, no. 234.
Turbo nautileus Linnaeus, 1767: 1241, no. 654.
Planorbis imbricatus Müller, 1774: 165, no. 351.
Planorbis paladilhi Moitessier, 1867: 424, pl. 22, figs. 7–14.
Armiger crista, Ehrmann, 1933: 172, fig. 105.
Gyraulus (*Armiger*) *crista,* Soos, 1935: 28, fig. 4.
Armiger crista, Baker, 1945: 75, pl. 18, figs. 6–11.

Material—Kuehren (Germany), 15 specs.; Tübingen (Germany), 5 specs.; Wollmatingen (Germany), 4 specs.

Shell (Fig. 59)—The shell is very small, 2.2 to 2.8 (rarely >3 mm) in diameter and 0.75 to 0.9 mm in height. It has 2½ to 2⅞ rapidly increasing whorls. The under side of the whorls are ± flattened; the upper side is well rounded. The periphery is angled, the angle being nearer to the under side. The last whorl does not embrace the penultimate whorl as in all other planispiral species of the genus, but is loosely attached to its upper side, the peristome thus being continuous. The shell is almost flat or very slightly convex on its under side and deeply concave on its upper side. The whorls are traversed by ridges, these sometimes carrying periostracal fringes projecting peripherally (Fig. 59B). Reticulate sculpture is absent.

Animal—The animal is weakly pigmented, the cephalopedal mass being light grey and the mantle showing a light and diffuse pigmentation. The kidney margins are distinctly undulate. An intestinal loop was present in all specimens studied. The ovotestis and seminal vesicle vary in size. The female tract is short and wide (Fig. 60). The bursa copulatrix is long and slender and is club-shaped. The prostate diverticula are reduced in length, so that the gland merely consists of the prostate duct (Fig. 60B); only in one of the individuals studied were there vestiges of 7 diverticula (Fig. 60A) that indicated that, before reduction, these must have been regularly and densely arranged. The penis sheath is long and slender, being always longer than the preputium (compare Table 2). The diaphragm is very muscular, giving the knoblike thickening between the penis sheath and the preputium a particularly pronounced look. The penis has a conical tip and a hob-nail stylet (Fig. 60C, D). The penis pore lies near the tip.

Remarks—The reproductive system of this well-defined species was previously figured



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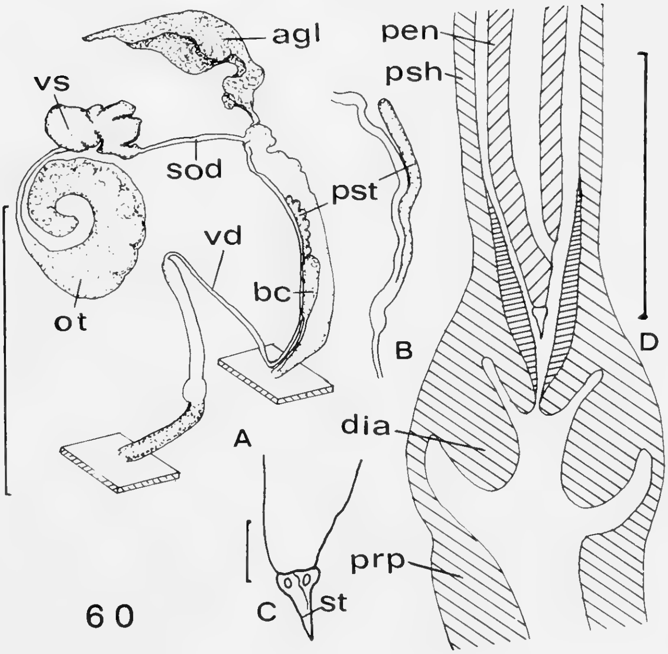

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FIGS. 59–60. *G. crista.* 59. Shell. A—ditch near Wallnau/Fehmarn (SMF 248 548); B—form found in lenitic biotopes, Wollmatingen (SMF 248 547); C—lake form, Dobersdorfer See (SMF 248 549). 60. A—reproductive system, Kuehren (SMF 248 543); B—prostate gland of another specimen from Kuehren (SMF 248 543); C—penis tip with stylet, Tübingen (M 302); D—middle part of ♂ copulatory organ, Kuehren, shading as in Fig. 58 (M 313). Scales: 1 mm in A and B, 0.01 mm in C, 0.1 mm in D.

by Soos (1935: fig. 4) and Baker (1945, pl. 18). There is general agreement with the present findings. Differences concerning the armament of the penis tip and the form of the prostate gland exist between Baker's (1945) figures and my findings. Soos showed 9 and Baker 13 prostate diverticula of normal length. There is possibly greater variation in this character than seen in the material I studied, but considering the smallness of the animal, I consider the possibility that the presence of well-defined and long prostate diverticula in all closely related taxa fired these authors' imagination. This is more plausible considering that in contracted animals transverse folds are commonly found in the female tract to which the prostate gland adheres. Greater concentrations of pigment cells at these sites could indeed simulate the picture of prostate diverticula.

Gyraulus crista has usually been regarded as a member of a separate genus, *Armiger.* This idea was based on the really aberrant form of the shell and supported by the statements of previous students who did not recognize a penial stylet. Baker (1945: 76) spoke of a "pointed fleshy papilla" instead of a stylet, and Odhner (1956) observed what he called a "small cuticular cap" or a "bulbous tip." The alleged lack of a stylet led both authors to exclude the species from *Gyraulus.* The only publication mentioning the presence of a stylet in *G. crista* was the one by Hubendick (1955: 466), but Odhner (1956) believed that Hubendick had mistaken a *G. riparius* for *G. crista,* arguing that *Armiger crista* did not occur in Hubendick's collecting place. Whatever may be the truth, the smallness of the two species in question may have hampered thorough studies. In light section the true nature of the stylet must indeed remain obscure. Only an extraction of the penis from

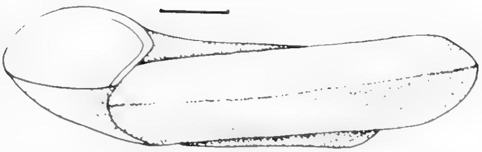


FIG. 61. *G. acronicus,* Bodensee near Überlingen (loc. typ.), shell.

its sheath, which was successful for the first time during the present studies, revealed that the armament of the penis tip in *G. crista* does not differ fundamentally from that in *G. riparius* and *G. rossmaessleri.* In one stylet of *G. crista* (Fig. 60C) there is even a tinge of the brown colour typical for the stylet of *Gyraulus.* Other features, found with the aid of oil immersion and phase contrast microscopy, are the well-defined border between the penis tissue and the base of the stylet, two double refractive areas in the base and a trace of a longitudinal line indicating that the stylet is formed by a rolled blade as in those other taxa of the *Planorbis* tribe which are equipped with a stylet. Therefore, there is no doubt that the stylet of *G. crista* has the same origin as the stylet in any other *Gyraulus* species.

The possession of such a stylet alone would not necessarily place the species in the genus *Gyraulus,* as I shall explain later. But, besides the shell character state "rapidly increasing whorls" there is at least one other feature that leaves no alternative but placing *Nautilus crista* in *Gyraulus,* i.e. the distinctly undulate kidney margin. As will become clearer in the cladistic analysis, the undulate kidney margin is a character very probably having evolved only once in the *Planorbis* tribe. It does not occur in any others of its genera. *G. crista* must have evolved from a parent species carrying this character state. This stem species must have been identical or a descendant of the one from which the species *G. parvus, G. laevis, G. rossmaessleri,* and *G. riparius* evolved. According to Hennig's quite correct and convincing arguments against Mayr's (1974b) criticism (Hennig, 1974), a taxon can only be regarded as monophyletic if *all* descendants of one parent species are included in this taxon. Accordingly *G. crista* must not be grouped in a separate genus.

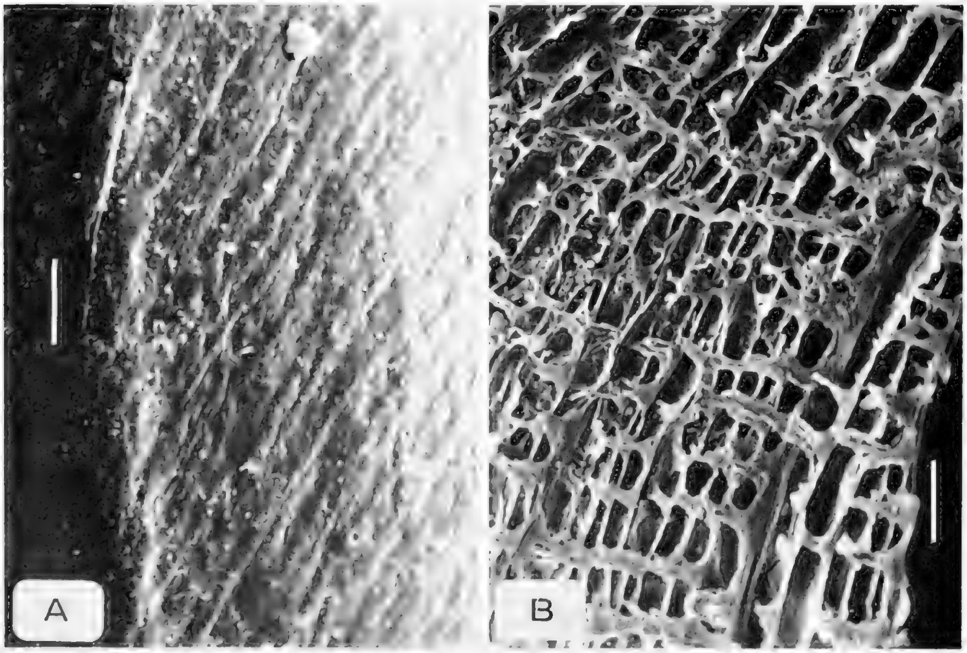


FIG. 62. *G. acronicus,* shell surface. A—Bodensee, faint spiral striae and weak keel; B—Vikarsjön, "hairs" protruding from periostracal ridges on growth lines. Scale = 0.1 mm.

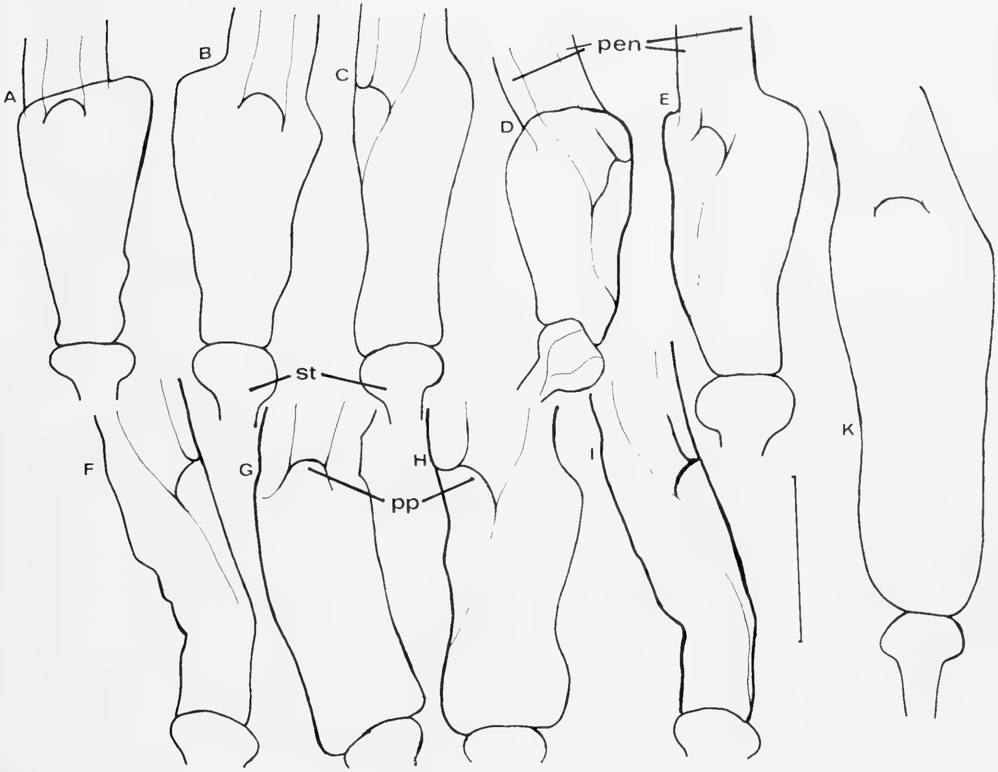


FIG. 63. *G. acronicus*, variation in shape of penis tip and position of penis pore. A—Tärna; B—Ragunda; C—Tulom; D—Krasnojarsk; E—Valtjärn; F—Ragunda; (A–F unrelaxed; microscopic preparations under respective reg. no. in museum collections, see Appendix); G—Siggen (M 46); H—Dobersdorfer See (M 41); I—Vikarsjön (unrel.); K—Bodensee (M 48). Scale = 0.1 mm.

Gyraulus acronicus (Férussac, 1807)

Planorbis acronicus Férussac, 1807: 105 (Bodensee near Überlingen).
Gyraulus deformis Hartmann, 1844: 95, pl. 27, figs. 1–5.
Planorbis gredleri Gredler, 1859: pl. 5, figs. 1a–d.
Planorbis borealis (Lovén Ms) Westerlund, 1875: 77–79.
Gyraulus albus acronicus, Ehrmann, 1933: 170, pl. 7, figs. 107, 107a.
Gyraulus gredleri, Ehrmann, 1933: 171, pl. 8, figs. 106, 106a.
Gyraulus albus deformis, Jaeckel, 1962: 68.
Gyraulus acronicus, Jaeckel, 1962: 69.

Material—In addition to the material previously studied (Meier-Brook, 1964: 235), unrelaxed snails were available from the following localities, partially under the name *Planorbis borealis* Lovén: Sweden: Vikarsjön, 2 specs.; Ragunda, 3 specs.; Valtjärn, 2 specs.; Vojmån, 3 specs.; Tärna, 3 specs.; USSR: Karabella, 2 specs. (named *Gyraulus rossmaessleri,* det. Westerlund); Tulom, 3 specs. (named *borealis,* det. Odhner); Dudinska, 1 + 2 specs. (2 lots; named *borealis,* det. Odhner); Krasnojarsk, 3 specs. (named *borealis,* det. Odhner); Paratunka, 2 specs. (unnamed).

Shell—The shell (Fig. 61) is large, usually reaching 7 mm in diameter or more and 2 mm in height; it has 4–4¾ whorls, is not deeply umbilicate, with sutures not deep and whorls flattened. The periphery is angled or rounded, sometimes with a small periostracal fringe. The aperture is ellipsoid, usually oblique. The last whorl is regularly deflected, thus giving the shell the appearance of being deformed. The surface is dull, and is reticulately sculp-

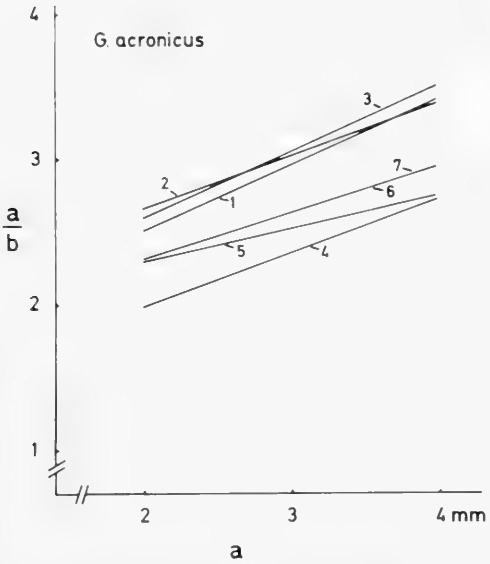


FIG. 64. *G. acronicus*, a/b plotted against a in three central European and four N European or N Asiatic populations. 1—Bodensee (n = 117); 2—Siggen (n = 38); 3—Dobersdorfer See (n = 40); 4—Vojmån (n = 25); 5—Tulom (n = 13); 6—Rasno-volok (n = 14); 7—Krasnojarsk (n = 18). Correlations significant: no. 5: $p < 0.05$, all other samples: $p < 0.001$.

tured. The sculpture sometimes is almost indiscernible, sometimes stronger, but never coarse as in *Gyraulus albus*. Spiral striae are less remote than in *G. albus*. Fine periostracal "hairs" can be present (Fig. 62). The color is light-corneous, like *G. albus*.

Animal—The animal is moderately grey on the cephalopedal mass. The mantle roof has a distinct pattern, which is sometimes weakly developed. The kidney margins are straight. An intestinal loop was developed in all individuals checked. The seminal vesicle varies in shape. The bursa copulatrix is elongate club-shaped. The prostate gland has a high number of diverticula (compare Table 2), which are closely spaced, have a regular shape and are unbranched. The ♂ copulatory organ is very long (Table 2) and usually bent twice (Meier-Brook, 1964: figs. 6–10) The penis tip can be faintly thickened. The penis pore lies near the proximal end of the thickening or in its proximal half (Fig. 63).

Remarks—*Gyraulus acronicus* was long considered a peculiar lake form of *G. albus* until its identity with *G. gredleri* was proved by Odhner and Forcart (compare Meier-Brook, 1964). *G. borealis* (Lovén, Ms) (Westerlund, 1875) was for a long time recognized as a larger boreal-subarctic form of *G. gredleri*, and now of *G. acronicus*. It cannot be overlooked that *G. borealis* is persistently different in shell characters from the temperate European forms of *G. acronicus*. In central Europe the whorls of *G. acronicus* are flattened, the last whorl is more deflected, the periphery is distinctly angled or weakly keeled. In N Europe and boreal-subarctic Asia, the whorls are more rounded, the last whorl is less deflected, the periphery slightly angled though often decorated by a delicate periostracal fringe.

A latitudinal cline is demonstrated in Fig. 64, where flatness and relative height increase are expressed by regression lines for 3 central European (1–3) and 4 boreal-subarctic samples.

Gyraulus acronicus is the largest European species of the genus. It is characterized by the long, slender and bent ♂ copulatory organ and by its mantle pigmentation, showing a distinct pattern although this is less strong than in *G. chinensis* (Fig. 12). It is the only European indigenous species with such a pattern. Hubendick's (1955: 479) misidentification of *G. albus* as *G. acronicus* was pointed out previously (Meier-Brook, 1964: 236). The only study of the anatomy of this species from outside central Europe is the one published by Khazannikov (1973, fig. 4) from River Erek Basin, Caucasus. In the shape of the figured ♂ copulatory organs there is close agreement with my previous figures of *G. acronicus* (Meier-Brook, 1964, figs. 6–10). Khazannikov's printed drawings, however, are too poor to allow comparison of internal details.

Final Notes on European Species

The main results of anatomical studies on the European *Gyraulus* species, except the endemic species from Macedonia, which will be dealt with in a separate chapter on ancient lakes species, are summarized in Table 2. Provisional grouping into subgenera will be substantiated after discussion of relationships between all taxa studied (see below). A key is included as an aid to identification of species indigenous to or introduced to Europe outside the Macedonian lake basin. It is based on diagnostic characters. These are not necessarily indicators of relationship. The dendrograms (Figs. 107, 111, 112) showing phylogenetic relationships are suitable for identification as well.

Key to the *Gyraulus* Species Living in Europe Excluding Macedonia

1A. Periphery angled 2
1B. Periphery rounded 5
2A. Shell diameter not exceeding 3 mm; mantle pigmentation diffuse or lacking; kidney with undulate margins 3
2B. Shell diameter exceeding 4 mm, mantle pigmentation with distinct pattern, kidney margins straight 4
3A. Angle approximately in the middle between upper and under side; shell therefore discus-shaped; surface with silky lustre; penis sheath shorter than preputium, not widened proximally; prostate gland with 7 to 10 regular diverticula which are densely arranged .... *G.* (*L.*) *riparius*
3B. Angle near under side, therefore shell ± flat on under side, whorls well rounded on upper side; last whorl not embracing the penultimate, but loosely attached to its upper side; whorls traversed by ridges (costae) at greater intervals; sometimes ridges peripherally projecting to spiny lamellae; penis sheath longer than preputium; prostate diverticula lacking or vestigial .... *G.* (*A.*) *crista*
4A. Shell rough and not glossy, usually with distinct reticulate sculpture, spiral striae relatively distant; prostate gland with 20 to 40 diverticula; pigmentation of mantle poor in contrast .... *G.* (*G.*) *acronicus*
4B. Shell smooth and glossy, at most faintly reticulate sculpture, then spiral striae very fine and dense; prostate gland with 8 to 20 (exceptionally up to 24; in Europe so far only between 12 and 18) diverticula; pigmentation pattern on mantle distinct and rich in contrast; introduced from Asia to rice fields in N Italy and Camargue; also found in West Frisia (Netherlands) .... *G.* (*G.*) *chinensis*
5A. Shell surface smooth, glossy, aperture rounded, kidney margins undulate, ♂ copulatory organ 1 to 2 mm long, penis sheath distinctly longer than preputium, widening proximally, prostate diverticula mostly irregular and not closely spaced 6
5B. Shell surface with fine or coarse spiral striation or, if appearing glossy, aperture with white lip; kidney margins straight or undulate; ♂ copulatory organ of varying length; penis sheath distinctly shorter and narrower than preputium, not widening proximally, prostate diverticula regular and closely spaced 7
6A. Penultimate whorl distinctly elevated, distal portion of spermoviduct slender, not wider than widest portion of sperm duct; distal half of vas deferens much wider (2:1 on an average) than proximal half (introduced from N America) .... *G. parvus*
6B. Penultimate whorl not or not distinctly elevated, distal portion of spermoviduct wider than widest portion of sperm duct and vas deferens, distal half of vas deferens not conspicuously widened (1:1) .... *G. laevis*
7A. Aperture circular, with white callous lip, shell surface with very fine spiral striation, almost glossy, color red-brown, penis sheath distinctly shorter and narrower than preputium, not widening proximally, penis narrowing distally .... *G. rossmaessleri*
7B. Aperture ovoid, without callous lip, shell surface with fine or rough spiral striation, color whitish to light-corneous, penis sheath distinctly longer than preputium, widening proximally, penis thickening distally 8
8A. Shell with fine spiral striation, prostate gland with 20 to 40 diverticula, ♂ copulatory organ longer than 2 mm, usually bent twice (S-form), penis pore near proximal end of thickened penis tip or in its proximal half .... non-angled form of *G. acronicus*
8B. Shell with coarse spiral striation, prostate gland with less than 22 diverticula, ♂ copulatory organ shorter than 2 mm, bent at most once, penis pore subterminal in thickened penis tip or in its distal half .... *G. albus*

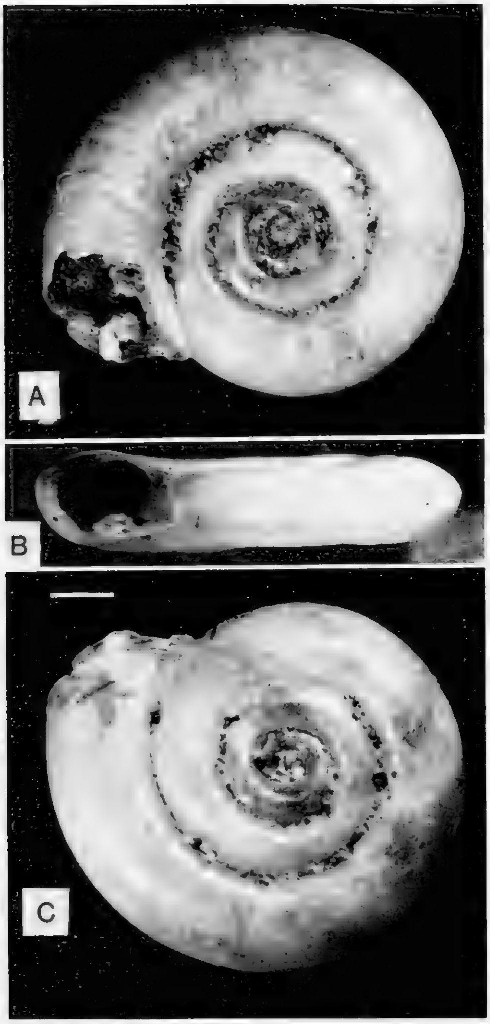


FIG. 65. *G. euphraticus*, Samava, lectotype ZMZ 521 181.

SPECIES OF SOUTH AND EAST ASIA

Before conclusions are drawn as to species delimitations material is treated under preliminary names that are widely used in the literature.

Gyraulus euphraticus (Mousson, 1874)

Planorbis (*Gyraulus*) *devians* Porro var. *euphratica* Mousson, 1874: 40 (Samava/Euphrates).

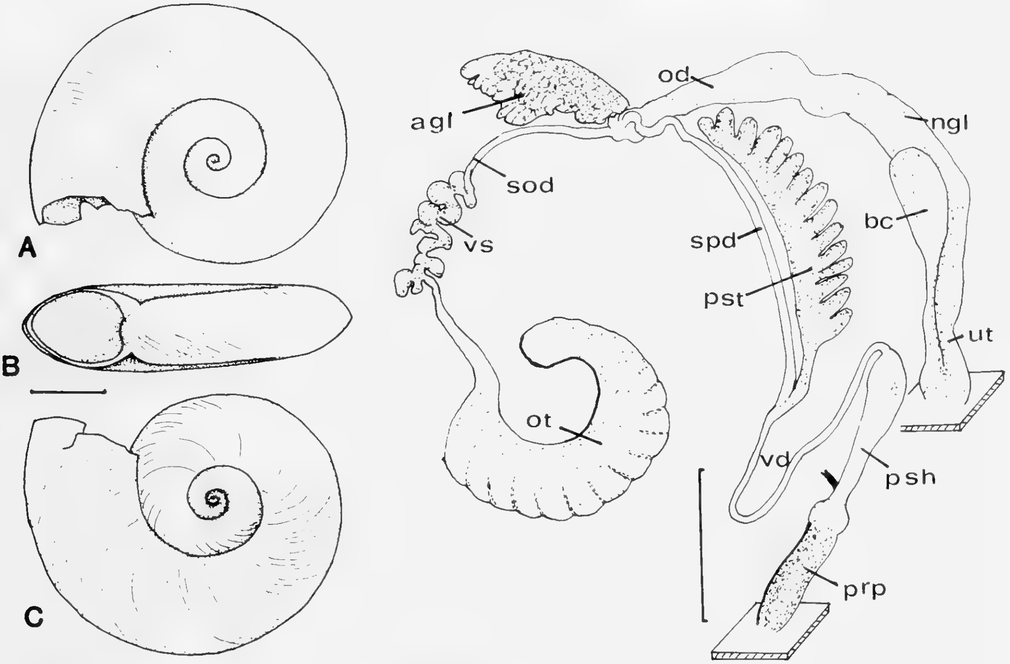
The original series on which Mousson's description is undoubtedly based (Mousson's handwriting kindly confirmed by Dr. Zilch) consists of two lots with identical labels. One contains hundreds of shells, obviously unsorted (ZMZ 521 180) and mixed with mud particles, in the other one (ZMZ 521 181) Mousson has sorted out 33 specimens (probably the "beautiful" ones, as usual at that time). A lectotype has been selected from the latter one (Fig. 65). A second specimen from lot no. 521 180 is also figured here (Fig. 66) to demonstrate the extreme conchological variation in the original series. There are all transitional shell forms between the figured ones, and the full range of variation is even wider. No gap is visible within the range.

Material—S Iran, 30 specs.

Dr. Massoud, who kindly put at my disposal living snails and preserved specimens from the collecting site in S Iran was unable to give more precise information on the locality. The stock had been kept in his laboratory for parasitological research since previous epidemiological surveys in Khuzistan. At least this is not far distant from the type-locality of *Gyraulus euphraticus*. The shell form in this stock resembles Mousson's original series and can therefore be identified with his species (Fig. 85, lines 7 + 8). The following description is based on both series, as far as shell characters are concerned.

Shell—The shell is of medium size, the maximum diameter scarcely reaching 7 mm; it is rather flat (<1.5 mm high). As the last whorl is only exceptionally deflected, it is possible to give a reliable figure of the ratio maximum diameter : height: in 100 randomly selected shells between 2.5 and 5.2 mm diameter and mean values of 3.76 and 1.10 mm (ZMZ 521 180) it is 3.42. Three and a half to 4½ whorls are rapidly (Fig. 66) or slowly (Fig. 65) increasing, in the latter case nearly approaching *Anisus* in appearance. The whorls are slightly or considerably wider than high. The periphery is angled. The shell is not deeply umbilicate. The surface is smooth, glossy; no reticulate sculpture is present. The color is light-corneous.

Animal—The animal is light grey, the mantle pigmentation showing a distinct pattern, similar to that figured in *Gyraulus chinensis* (Fig. 12). The kidney margins are straight. An intestinal loop is absent or reduced in size. The seminal vesicle is bulbous (Fig. 67) or slightly spinous. The bursa copulatrix has a spherical club shape and is sometimes taper-



66 67

FIGS. 66–67. *G. euphraticus*. 66. Samava, paralectotype (ex ZMZ 521 180). 67. S Iran. Reproductive system. Maximum shell diameter 3.7 mm, 3½ whorls (M 121).

ing though inflated at its upper end. The vagina is inflated in most specimens. The prostate gland bears 9 to 18 diverticula (cf. Table 6). The ♂ copulatory organ is similar to that of *G. acronicus* in general, but shorter, bent no more than once with the penis sheath relatively longer (cf. Tables 2 and 6). The penis tip and the position of the penis pore are indistinguishable from those in *G. acronicus*. Preputial pilasters are present.

Remarks—Mousson's description is so insufficient ("Fere regularis, pallide corneo-hyalina"), like most attempts at verbal characterizations of shells, and moreover, the description suggests similarity to *Gyraulus devians* Porro (which is probably a synonym of *G. acronicus*) that misidentifications are understandable. The first and as yet only anatomical account of a snail called *G. euphraticus* was published in 1919 by Annandale & Prashad. These authors, complaining about frequent confusions, "because conchologists have rarely seen specimens from the original localities" (Annandale & Prashad, 1919: 52) probably succumbed to the same error. The shell figured from Quetta, Baluchistan, (30°15′N; 67°00′E), and said to "agree closely with shells of Mousson's *G. devians* var. *euphratica* recently collected by Captain C. L. Boulenger in Mesopotamia," measures 8.9 mm in max. diameter and 2.55 mm in height(!). It does not fall in the range of variation shown in Mousson's original series. Moreover, the distance between Quetta and Samava is 2160 km, and there are large deserts between the localities, so that great doubts arise as to their identification. The figures of the reproductive system prove that the animals dissected were indeed *Gyraulus* but further details are lacking due to the insufficient optical facilities of that time. The fact, by the way, that Annandale & Prashad's fig. 5D—of a penis sheath of *G. euphraticus* (according to the caption)—is not that of a *Gyraulus*, is evidently due to an accidental exchange of letters D and F. The shell figured by Annandale & Prashad (1919: fig. 7A) is so similar in size, shape and proportions to shells in the British Museum of Natural History (no registration number) under the name of *Plan-*

TABLE 6. Reproductive organs of *Gyraulus* in S and E Asia.

	No. prost. diverticula			Male copulatory organ				
				Total length (mm)			Ratio psh:prp	
Provis. species name, locality	n	range	x̄ ± s.d.	n	range	x̄ ± s.d.	range	x̄ ± s.d.
euphraticus, S Iran	16	9–18	13.1 ± 2.5	18	1.6–2.6	2.1 ± 0.2	1.3–2.9	1.9 ± 0.5
hebraicus, Kumluca + Limyra[1]	6	11–15	13.3 ± 1.4	10	1.2–1.9	1.6 ± 0.2	0.8–2.3	1.4 ± 0.4
piscinarum, Diyarbakir[1]	4	12–16	14.0	4	1.8–2.7	2.4	1.2–2.0	1.5
mareoticus, Cairo	18	14–19	16.6 ± 1.4	13	1.9–2.8	2.5 ± 0.3	1.4–2.3	1.9 ± 0.3
Alexandria[1]	4	15–19	17.3	4	1.2–2.0	1.8	1.2–2.2	1.6
convexiusculus, Maur. + Afgh.[1]	7	12–15	13.8 ± 1.1	8	1.2–2.1	1.7 ± 0.4	1.3–1.6	1.4 ± 0.2
India[1]	4	20–24	22.3	6	1.5–2.7	1.9	1.0–1.3	1.2
Thailand[1]	5	10–15	12.7 ± 2.5	7	1.1–1.6	1.35 ± 0.3	1.3–1.8	1.6 ± 0.1
chinensis, Hong Kong[1]	8	11–15	12.9 ± 1.7	13	1.1–2.3	1.45 ± 0.3	1.1–2.1	1.5 ± 0.4
spirillus, Onna-son[1]	5	12–16	14.0 ± 1.6	5	1.4–2.0	1.7 ± 0.3	1.1–1.7	1.4 ± 0.3
Motobu-cho[1]	5	16–20	17.8 ± 1.6	5	1.7–2.6	2.0 ± 0.4	1.2–3.2	2.0 ± 0.7
Taiwan	54	11–21	15.7 ± 2.1	33[2]	1.4–3.0	2.0 ± 0.3	1.1–2.6	1.6 ± 0.4
Chongpyong	15	8–18	14.0 ± 2.4	15	1.6–2.7	2.1 ± 0.3	1.1–2.0	1.6 ± 0.3
Kaejong	4	13–16	14.0	5	1.4–2.3	2.0 ± 0.4	1.4–2.4	1.9 ± 0.4
Kunsan	8	9–19	14.0 ± 3.0	8	1.9–3.7	2.5 ± 0.6	1.3–2.3	1.6 ± 0.3
tokyoensis, Tomigusuku-son[1]	10	11–18	15.0 ± 2.3	13	1.6–2.7	2.1 ± 0.4	1.1–2.6	1.9 ± 0.5
Sashiki-son[1]	7	12–19	15.6 ± 2.3	7	1.4–2.2	1.9 ± 0.3	0.9–1.8	1.5 ± 0.3

[1] Unrelaxed.

[2] Unrelated individuals excluded.

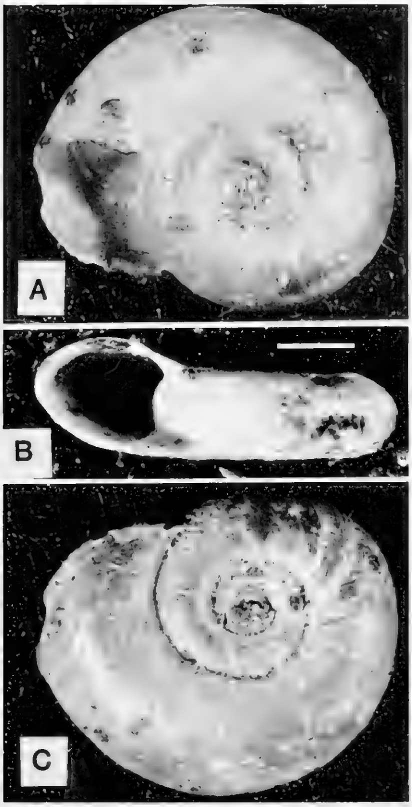


FIG. 68. *G. hebraicus,* Bahr el Houlé, Syria; lectotype (MHN Genève).

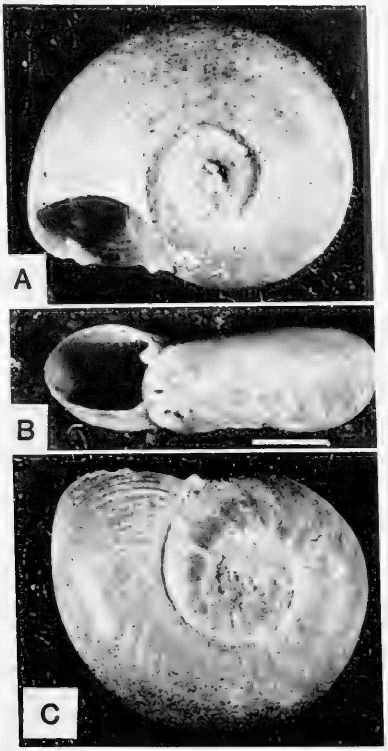


FIG. 69. *G. piscinarum,* Baalbeck, Lebanon; lectotype (MHN Genève).

orbis nanus that species identity is probable. The lot is labelled: "*Planorbis nanus* Sowerby, Loc. Ganges, India. H. Cuming colln. 3 specs, Acc. no. 1829—Apparently not the specimens figured in Reeve, Conch. Icon. XX, *Planorbis,* Pl. 9, Sp. 75." The largest of the 3 shells measures 8 mm in diam. and 2.5 mm in height. The anatomy of *P. nanus,* however, could not be examined for comparison.

The question of a relationship between *G. euphraticus* and *G. chinensis* will be discussed later.

Gyraulus hebraicus (Bourguignat, 1852)

Planorbis hebraicus Bourguignat, 1852: 23, Nr. 3 (Bahr-el-Houlé, Syria).

A lectotype is designated here from Bourguignat's original lot in Musée d'Histoire Naturelle Genève (no registration number) labelled "*Planorbis hebraicus* Bourg., type, Bahr-el-Houlé (Syrie)" (Bourguignat's handwriting kindly identified by Dr. Zilch). The lot contains 2 shells of 5.9 mm diameter and 1.55 mm height, and 4.85 mm diameter and 1.50 mm height; the smaller one has been selected (Fig. 68).

Material—Since alcohol material from Syria or Lebanon was not obtainable, material tentatively identified as G. *hebraicus* from the geographically least distant localities in Turkey was examined: Kumluca, 2 specs., Limyra, 8 specs. (all unrelaxed).

Shell—The shell (Fig. 68) is small to medium-sized, rather flat, usually 3 to 5 mm in diameter and 1.2 to 1.6 mm in height with 3¼ to 4 whorls which increase rather rapidly, flattened and wider than high. The shell is equally concave on both sides. The periphery is slightly angled. The surface is smooth, glossy; reticulate sculpture is absent. The color is light-corneous.

Animal—The animal is light grey, the mantle pigmentation showing a distinct pattern that is marbled but not as contrasting as in Fig. 12. The kidney character state was not determined in the contracted animals. An intestinal loop was present in all individuals. The bursa copulatrix has a club shape. The prostate gland bears 11 to 15 closely spaced and regular diverticula. The ♂ copulatory organ, as judged from the contracted material, is not much shorter than in *Gyraulus euphraticus* (Table 6), the ratio penis sheath : preputium similar to that in *G. euphraticus*. The position of the penis pore was not discerned due to poor fixation.

Remarks—There are few records of *Gyraulus hebraicus* in the literature. Beside the type lot there is one other lot in MHNG identified by Bourguignat from "fossés près du camp Deer (almost illegible) pins, près de Beyrouth. Mahmoud," containing 7 shells. The shells are similar to those of *G. euphraticus,* though slightly higher. If the material anatomically examined were from the type-locality I should not hesitate in considering *euphraticus* a junior synonym of *G. hebraicus*. But before a widely used name such as *G. euphraticus* is withdrawn, one should wait for an opportunity to study topotypes of *G. hebraicus*.

Gyraulus piscinarum (Bourguignat, 1852)

Planorbis piscinarum Bourguignat, 1852: 22, no. 2 (Baalbeck, Lebanon).

A lectotype is designated here (Fig. 69) from the lot labelled "type" by Bourguignat (MHNG, no registration number), from Baalbeck. The lot includes 63 paralectotypes.

Material—Diyarbakir (Turkey) 5 specs. (unrelaxed).

Shell—The shell is of medium size, 5 to 6 mm in diameter, and relatively high due to a largely deflected last whorl, with a height often up to 2.5 mm. Three to four whorls rapidly increase. The whorls are not flattened (Fig. 85, regression line 2). The periphery is rounded or at most slightly angled (Fig. 70). The under side is convex and hardly umbilicate. The upper side is deeply umbilicate. The last whorl is slightly to strongly deflected. The aperture is oblique. The surface is moderately smooth and silky. In the sample anatomically examined there is very faint reticulate sculpture. The color is dark-corneous to light brown. *Gyraulus piscinarum* is pronouncedly thick-shelled.

Animal—The animal is dark grey, with diffuse and dark mantle pigmentation. The kidney margins are straight. An intestinal loop was present in the individuals seen. The ovotestis is large (Fig. 71). The seminal vesicle is of the usual size and spinous. The bursa copulatrix is of the spherical tadpole type, with a long and narrow duct. The prostate gland bears 12–16 closely spaced, fleshy diverticula. The vas deferens is equally narrow over its full length. The ♂ copulatory organ is relatively long (Table 6), with a varying ratio penis sheath : preputium. The penis tip has normal thickening, the penis pore being situated in its middle part or the proximal half (Fig. 72).

Remarks—*Gyraulus piscinarum* is a well-defined species, even on purely conchological grounds. Its convex under side makes it one of the most easily recognizable species in the genus. It is the only Asiatic species seen in this study having diffuse mantle pigmentation. Its bursa copulatrix of the tadpole type seems to be a species-specific character state. Nevertheless, *G. piscinarum* has often been confused in the literature and in collections. Bourguignat himself erroneously used this name for material of two lots. One contained one specimen from "fossés près de Beyrouth, Mahmoud" (probably from the same locality as *G. hebraicus,* see above), which is *G. hebraicus*. The other lot from "le Danube à Ibraila" contained one shell of *G. rossmaessleri*. Records of *G. piscinarum* in the literature are quite common, but in my opinion Bourguignat's types were insufficiently known to many authors, and *G. piscinarum* probably has a wider distribution in the literature than in nature.

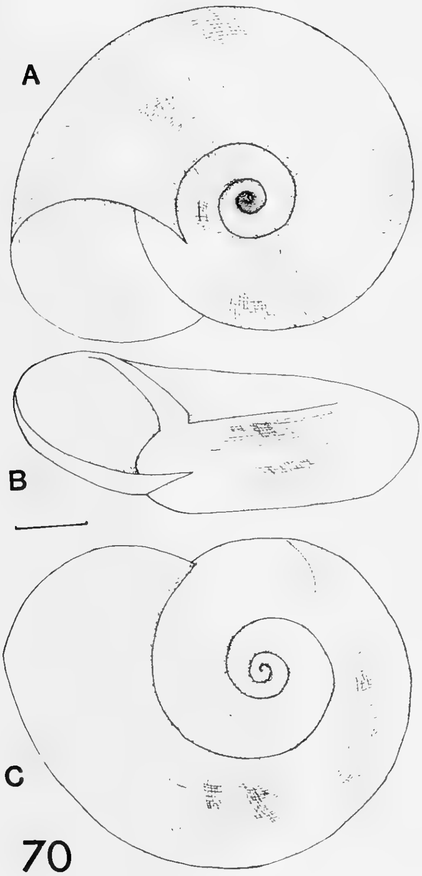
Gyraulus ehrenbergi (Beck, 1837)

Planorbis ehrenbergi Beck, 1837: 119.
Planorbis mareoticus Innes, 1884: 339.

Material—Cairo (Egypt) 13 specs.; Alexandria (Egypt) 4 specs. (unrelaxed).

Shell (Fig. 73)—The shell is small, usually not exceeding 4 mm in diameter, but relatively high: 1.3 mm (Fig. 85, line 1); 3½ whorls increase rapidly. The periphery is slightly angled, with a small, but distinct fringe of periostracum. The last whorl is scarcely deflected. The surface is smooth and silky. Growth lines are very fine. No reticulate sculpture is present. The color is pale-whitish.

Animal—The animal is almost hyaline, almost lacking pigment. The cephalopedal mass is almost white. The mantle pigmenta-



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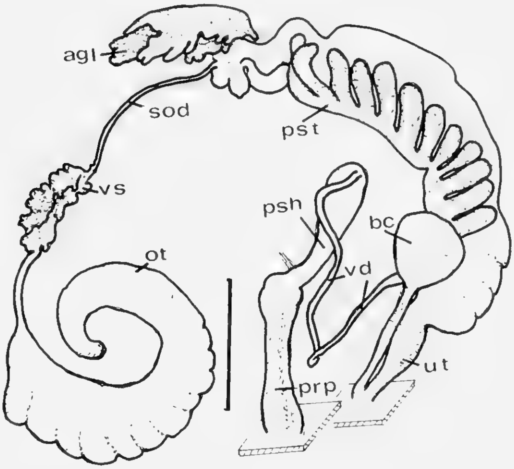

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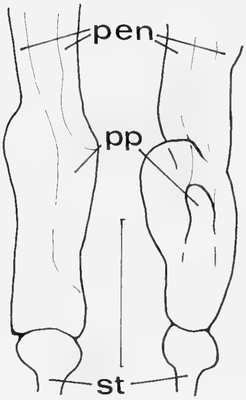

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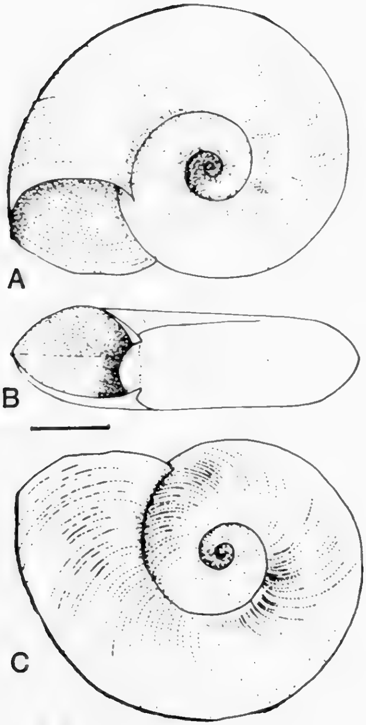
FIGS. 70–72. *G. piscinarum*, Diyarbakir. 70. Shell (SMF 246 318). 71. Reproductive system; maximum shell diameter 5.0 mm, 3⅔ whorls (SMF 246 317). 72. Penis tips (M 294). Scale = 0.1 mm.

tion has a distinct, though weakly developed, pattern. The kidney, heart, stomach and preputium which in most other *Gyraulus* species are darkly pigmented, bearing only scattered black spots. The kidney margins are straight. An intestinal loop is present. The bursa copulatrix is of the elongate club type, with a duct about half as wide as the bursa itself (Fig. 74). The prostate gland bears 14 to 19 diverticula (Table 6), which are closely spaced. The vas deferens is equally narrow over its full length. The ♂ copulatory organ is relatively long. The ratio penis sheath : preputium is high (Table 6). The penis tip is normally thickened, the penis pore lying in its proximal half.

Remarks—The snails studied of the Egyptian populations belong to a well-defined species, without close affinity to the W Asiatic species dealt with on the preceding pages. Apart from their relative height they do not have many character states in common with *Gyraulus piscinarum*, as might be implied by Jaeckel's (1962: 104) considering *G. piscinarum* as a subspecies of *G. ehrenbergi*. *G. ehrenbergi* differs from G. *piscinarum* not only in shell characters, but also in pigmentation, width of the bursa duct and numbers of prostate diverticula.

A close relationship of *Gyraulus ehrenbergi* with other African species, anatomically known as *G. costulatus* (Krauss) and *G. connollyi* Brown & van Eeden, is improbable. For comparison, *G. costulatus* is briefly characterized below.



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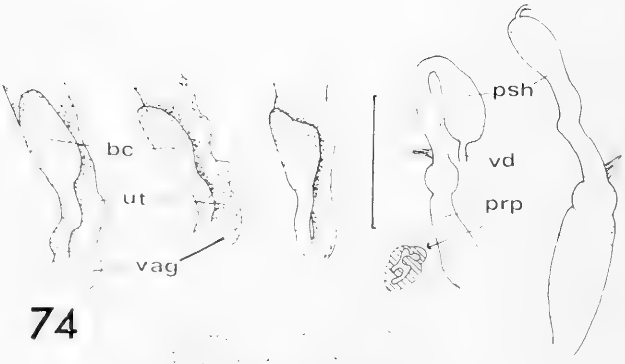

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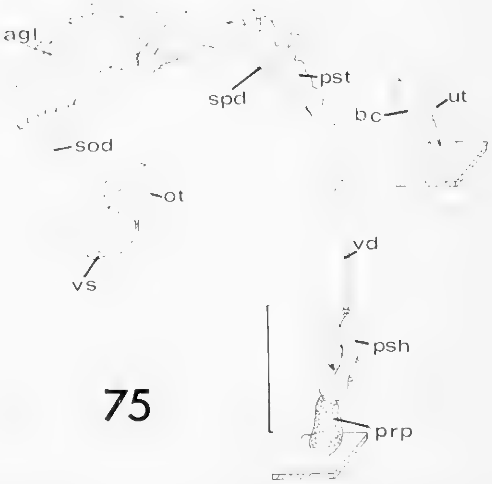

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FIGS. 73–75. *G. ehrenbergi*, Cairo, shell (SMF 246 319). 74. *G. ehrenbergi*, Cairo, shape of 3 bursae copulatrices and 2 ♂ copulatory organs. 75. *C. costulatus*, Liberia: reproductive system; maximum shell diameter 4.9 mm, height 1.3 mm, 3⅔ whorls.

Gyraulus costulatus (Krauss, 1848)

Planorbis costulatus Krauss, 1848: 83, pl. 5, fig. 3 (Umgeni Valley, Natal).

Material—Liberia, five specs.

Shell—The shell is small- to medium-sized, scarcely reaching 5 mm in diameter and of moderate height (1.3 mm). Three and two thirds whorls increase rapidly. The periphery is angled, with a small fringe of periostracum. The surface is glossy, with regular costae in the direction of the growth lines.

Animal—The animal is uniformly light grey. The mantle has many well-defined small pigmented areas. The kidney has some tiny septa which, however, do not render its margins undulate. An intestinal loop is present. The entire reproductive system (Fig. 75) is delicate and slender: the ovotestis is very small. The spermoviduct is long and slender. The seminal vesicle is inconspicuous. The albumen gland is composed of few long acini. The bursa copulatrix is tiny and is of an elongate club shape or tapering. The sperm duct is extremely narrow. The prostate gland bears 5 to 8 diverticula, which are irregular in shape and arrangement, the most distal one not touching the bursa copulatrix as in all Palaearctic species, but distant from it. The ♂ copulatory organ is of the normal form, but very short, scarcely exceeding 1 mm in length. The penis sheath is approximately the same length as the preputium or is slightly longer. The proximal end of the penis sheath does not reach the vagina in fully extended animals.

Remarks—The anatomy of this widely distributed tropical and southern African species has been well known since various authors have dealt with it (Fraga de Azevedo *et al.*, 1961; Wright, 1963; Brown, 1965). A particularly comprehensive study has at the same time shown that there is a South African species resembling *Gyraulus costulatus* in many details, but clearly separated (Brown & van Eeden, 1969).

A comparison of the two African species, *Gyraulus costulatus* and *G. connollyi* with Palaearctic species shows several striking deviations from character states usually seen in the genus, namely the extremely small ovotestis, the tiny seminal vesicle, the very narrow sperm duct, the number of prostate diverticula that is by far lower (in Ethiopia no more than three, according to Brown, 1965), and the long distance between the most distal diverticulum and the bursa copulatrix. These character states, evidently commonly derived in *G. costulatus* and *G. connollyi*, strongly suggest the existence in Africa of a separate subgenus. Bourguignat (1883: 99) has established a genus *Caillaudia* with the type-species *G. angulata* Bourguignat. *G. angulata* is commonly accepted as a junior synonym of *P. costulatus*. Thus *Caillaudia* is available as a subgenus name for at least the two African species mentioned above.

Gyraulus convexiusculus (Hutton, 1849)

Planorbis convexiusculus Hutton, 1849: 657 (Candahar, Afghanistan).

Hutton's notes on habitats begin with "Occurs plentifully at Candahar in tanks." Localities further listed by him are Quettah, Kojuck Pass, river Helmud at Girishk (all in Afghanistan) and, furthermore, the Gangetic provinces, at Tope Chancey, Pinjore below Simla. I consider Candahar the type-locality.

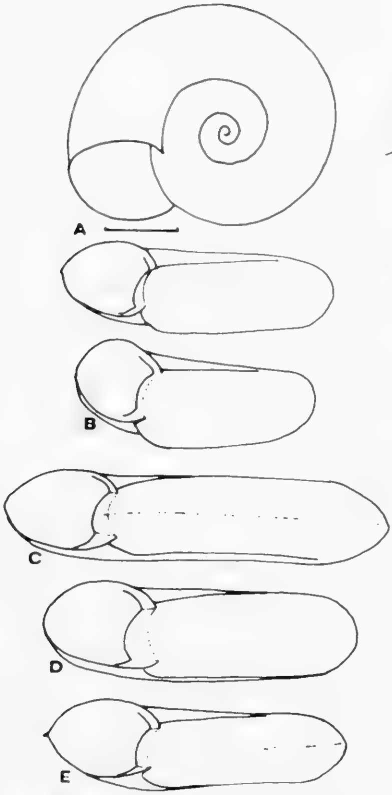
Material—Sayedabad, 3 specs. (unrelaxed); Gawargin (both Afghanistan), 2 specs. (unrelaxed), Mauritius, 3 specs. (named *G. mauritianus* (Morelet) by G. Mandahl-Barth) (unrelaxed); Bangalore, 6 specs. (unrelaxed); Bharatpur (both India), 4 specs. (unrelaxed); Thailand, 2 localities: 4 + 4 individuals (unrelaxed); further alcohol material was seen from Ceylon, but authorities of the Nat. Hist. Mus. Vienna did not permit dissection.

Shell (Fig. 76)—The shell is small- to medium-sized, 4 to 5 mm in diameter and relatively high (1.2 to 1.8 mm). Three and a half to 3¾ whorls increase rapidly. The umbilicus on the upper side is deep, on the under side shallow. The sutures are not very deep. The last whorl is slightly deflected. The periphery is rounded or angled, sometimes with a fringe of periostracum. The surface is smooth and glossy, without reticulate sculpture. The color is light to dark corneous.

Animal—The animal is light to very dark grey. The mantle has a distinct pigmentation pattern, in intensity varying from very dark (Sayedabad, Mauritius) to light (Gawargin, Bangalore, Thailand). The kidney has straight margins. An intestinal loop is absent or present. The bursa copulatrix is small, spherical or elongate, its duct in most individuals being wide and not distinctly set off; the duct is as wide as the bursa itself (Fig. 77). The prostate gland bears 10 to 15 ($\bar{x} = 13.1 \pm 1.7$) (in Bangalore 20–24) closely spaced and regularly shaped diverticula, which are occasionally bifid. The vas deferens is as narrow as in most species. The ♂ copulatory organ is of the usual shape and 1–2 mm long. The penis sheath is as long or slightly longer than the preputium. Preputial pilasters are present. The penis tip has a thickening, with the penis pore in varying positions, in two individuals from Thailand virtually terminal (Fig. 78D), in the other ones subterminal, in the distal half of the thickening or near its middle.

Remarks—I have not seen the full range of characters in the few (unrelaxed) individuals I had available and better knowledge of variation will require study of additional material. Original material of Hutton's collection was to be found neither in ZSI, Calcutta, nor in BMNH, London. Annandale & Prashad (1919: 53) figured *G. convexiusculus* from Quetta, one of the localities indicated in Hutton's description. Their shell (Annandale & Prashad, 1919, fig. 7B) measures about 10 mm in maximum diameter, whereas Hutton (probably measuring one of the largest individuals, as usual at that time) speaks of 6.25 mm ("¼ of an inch"). The differences are striking, and the question may be raised again, whether Annandale & Prashad examined *Planorbis nanus* Sowerby, as has been suggested with their "*G. euphraticus.*" Starmühlner (1974: 168–171) figured organs of a snail from Ceylon, which is evidently conspecific with those anatomically examined in the present study. The shape and proportions of the ♂ copulatory organ as well as the narrow width of the vas deferens agree with those observed by me.

A more flattened and strongly angled form, usually considered *Gyraulus convexiusculus* "var. *compressus* Hutton," has not been ex-



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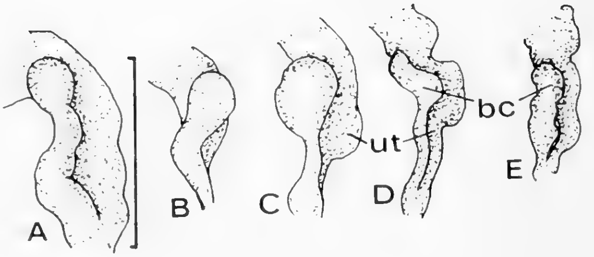

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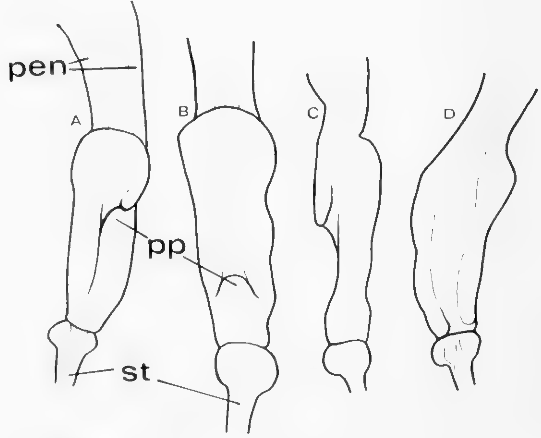

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FIGS. 76–78. *G. convexiusculus*. 76. Variation in shell shape. A—Thailand (SMF 193 798); B—Thailand (SMF 197 350/15); C—Bangalore; D—Sayedabad; E—Gawargin. 77. Variation in shape of bursa copulatrix. A—Sayedabad (M 297); B, C—Gawargin (M 298); D—Bangalore; E—Thailand (SMF 193 798). 78. Variation in penis tip and position of penis pore. A—Gawargin (M 298); B—Sayedabad (M 297); C—Bangalore (M 299); D—Thailand (SMF 193 798).

amined anatomically. Their affinity can, thus, not yet be judged.

Character states of the reproductive system studied from Bangalore (India) are in good accordance with Baker's (1945, pl. 19, fig. 2) drawing of a specimen from Calcutta. Congruence even includes the number of prostate diverticula (23), which, as seen in the present study, is higher in Bangalore (20–24) than in Afghanistan (12–15) and Thailand (10–14). The data are, however, too restricted to generalize.

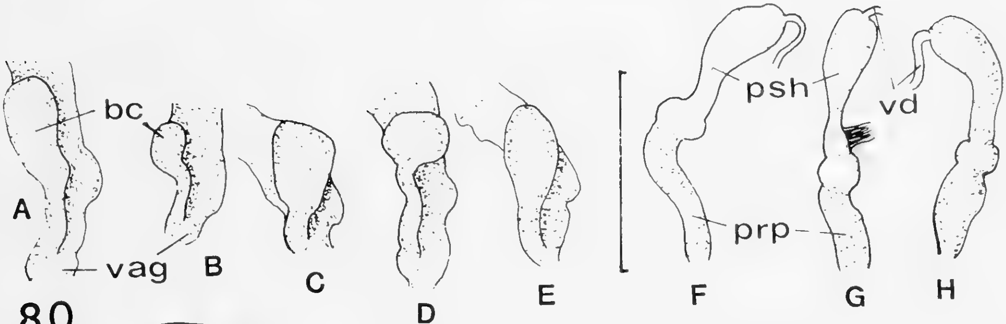
Gyraulus chinensis (Dunker, 1848)

Planorbis chinensis Dunker, 1848: 41 (Hong Kong).

Material—Hong Kong, 13 specs. (unrelaxed).

Shell (Fig. 79)—The shell is small- to medium-sized, 3.5–4 mm in maximum diameter and 1.2–1.3 mm in height. Three and three quarter whorls increase rapidly in width. The last whorl is not or slightly deflected. The periphery is rounded to moderately angled. A small periostracal fringe is present on some of the 28 specimens available from this population. The surface is not glossy, with growth lines irregular and pronounced. Fine spiral striae are present in most individuals. The colour is light to brownish-corneous.

Animal—The animal is light grey, the cephalopedal mass with small scattered black patches. There is a distinct pattern in the



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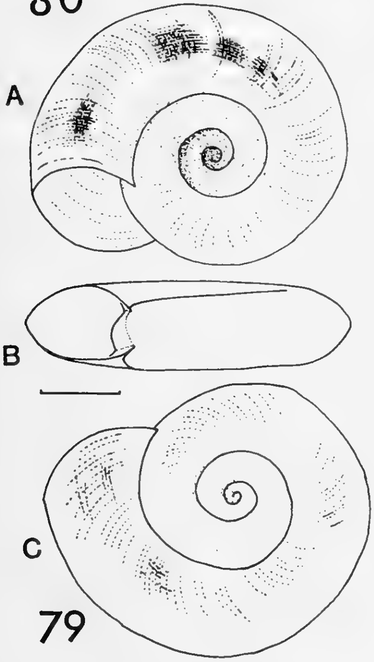

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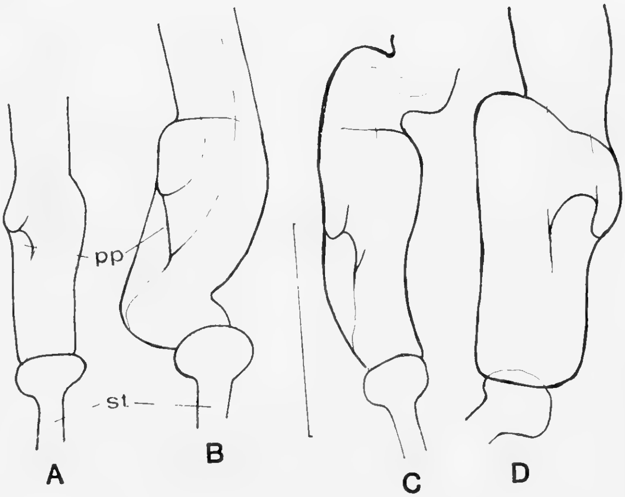

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FIGS. 79–81. *G. chinensis,* Hong Kong. 79. Shell (SMF 246 321). 80. Variation in shape of bursa copulatrix and ♂ copulatory organ (SMF 246 322 and M 300). 81. Variation in shape of penis tip and position of penis pore (M 300). Scale = 0.1 mm.

mantle pigmentation (Fig. 12). The kidney margins are straight. An intestinal loop is present. The seminal vesicle is bulbous to slightly spinous. The bursa copulatrix (Fig. 80) is elongate or spherical club-shaped and sometimes large. The bursa duct is as wide as the vagina. The prostate gland bears 11 to 15 closely spaced diverticula. The vas deferens is equally narrow over its full length. The ♂ copulatory organ has the usual shape (Fig. 80) and is between 1 and 2 mm long. Preputial pilasters are present. The penis sheath is slightly longer than the preputium. The penis has a distal thickening, in which the penis pore is situated laterally at various sites (Fig. 81).

Remarks—Dunker's original material could be located neither in the Zoological Museum of Humboldt-University, Berlin (personal communication, Dr. R. Kilias) nor in BMNH, London. According to Dunker's description. snails in the type-series reached 4.75 mm in diameter and 1.15 mm in height, which is only slightly larger than in the present sample. The animals examined correspond to the original description except for the weak spiral striation that is not mentioned by Dunker, probably due to his poor optics.

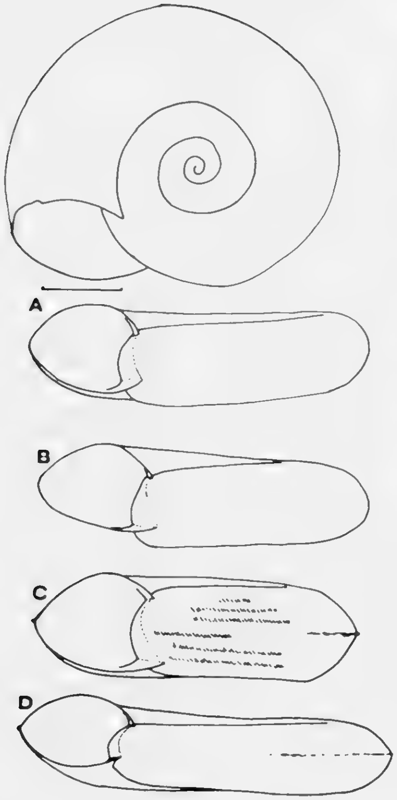


FIG. 82. *G. spirillus*, variation in shell shape. A—Onna-son (ANSP A453); B—Chongpyong (SMF 246 323); C—Kunsan (SMF 246 324); D—Taiwan (SMF 246 325).

FIG. 83. *G. spirillus*, Taiwan; shell surface on upper side and periphery. SEM. Scale = 0.01 mm.

Gyraulus spirillus (Gould, 1859)

Planorbis spirillus Gould, 1859: 40 (Ousima; =Amami-O-Shima, Ryukyu Islands, appr. 28°08′N, 129°19′E).

Material—Motobu-cho (Okinawa; as the locality nearest to Ryukyu-Islands), 5 specs. (unrelaxed); Taiwan, 60 specs. (20 of which unrelaxed); Korea: Chongpyong, 15 specs.; Kaejong, 5 specs.; Kunsan, 8 specs.

Shell (Fig. 82)—The shell is small to medium in size, rarely exceeding 5 mm in diameter and variable in height: rather flat, 1.2 to 1.4 mm in height (Fig. 85, lines 8 and 10), or less flat, 1.3 to 1.5 mm in height (lines 3 and 4). Three and a half to 4½ whorls, slowly (Taiwan) or more rapidly (other localities) increasing in size. The last whorl is more or less deflected. The periphery is angled, usually with a distinct fringe of periostracum. The surface is smooth (Fig. 83) (Taiwan. Only one of several hundred shells from a laboratory stock had clear spiral striation!) or with reticulate sculpture. Spiral striae are faint to pronounced; in the latter case the surface has periostracal lamellae on growth lines, protruding in spiral rows (Fig. 82C) like the "hairs" of *Gyraulus albus* (Fig. 36C). The colour is light to brownish-corneous.

Animal—The animal is light grey, the cephalopedal mass being uniformly light grey or with many small black dots. The mantle pigmentation has a distinct pattern. The seminal vesicle is bulbous or spinous. The bursa copulatrix is extremely variable (Fig. 84), from slender and tapering to spherical club-shaped. The bursa duct likewise varies from narrow to wide. The vagina is usually inflated. The prostate gland bears 11 to 21 (Taiwan) or 8 to 19 (Korea) closely spaced diverticula (Table 6). The diverticula are two-branched. The vas deferens is narrow. The ♂ copulatory organ is of the usual shape, around 2 mm in length. The length of the penis sheath is 1.5 to 2 times that of the preputium. Pilasters are present in the latter. The penis tip is thickened, the position of the penis pore situated at various sites laterally in thickening.

Remarks—The lectotype of Gould's *Planorbis spirillus*, designated and figured by Johnson (1964, pl. 44, fig. 7), is very similar to the flat population from Taiwan or Kaejong; it carries some spiral striae ("lirae" in Gould's description).

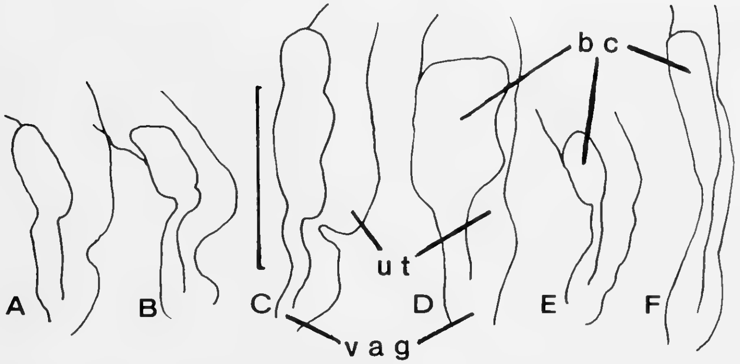


FIG. 84. *G. spirillus,* variation in shape of bursa copulatrix. A—Motobu-cho; B—Onna-son; C, D—Kunsan; E—Kaejong; F—Chongpyong. For Taiwanese specimens see Fig. 30.

Pace (1973: 79) figured the reproductive system of a species under this name from Taiwan, noting that the Taiwanese specimens have fewer than 20 prostate diverticula (cf. Table 6); his fig. 16 is completely in line with my observations. Pace, at the same time, poses the question again that has frequently been asked: are *Gyraulus spirillus, G. chinensis, G. convexiusculus,* and *G. euphraticus* forms of the same species? This question must be considered anew in the light of anatomical characters. As Table 6 shows, there are no essential differences between these four species in (1) mean numbers of prostate diverticula, (2) length of the copulatory organ, (3) ratio penis sheath : preputium. Moreover the shapes of the bursa copulatrix and a usually wide bursa duct as well as the penis tip do not show differences so consistent that species discrimination could be based on them. Nevertheless essential differences in shell characters exist, as Rensch (1934: 210–211) already pointed out. He expressed the height of the last whorl in its middle as a percentage of the maximum diameter, stating (translated): "In 24 typical *euphraticus* this percentage was 16.9–23.0%, mean 20.3%, in 57 typical *convexiusculus,* on the other hand, it was 21.9–35.5%, mean 27.4%." My own measurements of *G. euphraticus* from southern Iran yielded results similar to Rensch's (Figs. 85, 88). It is interesting to note that the other extremely flat shells of the group in question occur at the other end of the Asiatic continent: in Taiwan and Korea (Fig. 85, lines 9 and 10). Both the Iranian and the Taiwanese snails have smooth shells without spiral striation, and it would be difficult to tell one from another, if the Taiwanese shells did not regularly carry a tiny, but distinct, fringe of periostracum, which is always absent in *G. euphraticus.* In the whole southern Asiatic region between Iran and the Far East flat and smooth forms with anatomical features of this group seem to be unknown.

In view of the slight differences in the group

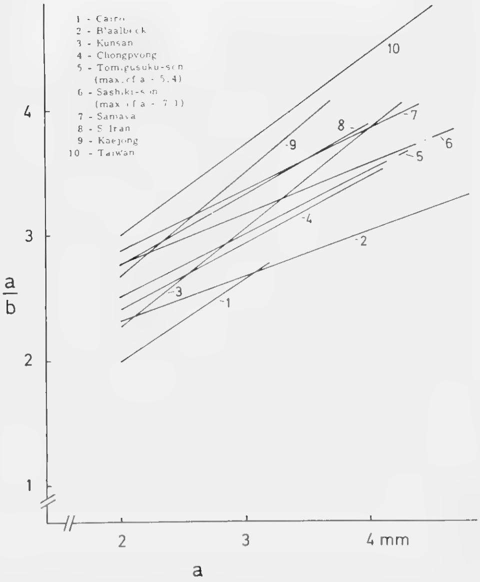


FIG. 85. a/b plotted against a in samples from S and E Asia. The right upper end of the regression lines indicates the maximum value of a in the sample.

FIG. 86. *G. tokyoensis,* Sashiki-son, shell shape, apertural view.

it would seem reasonable to treat *Gyraulus euphraticus, G. convexiusculus, G. chinensis,* and *G. spirillus* as geographical races or subspecies of one species. One exception, however, must probably be made. According to observations made by Dr. Mandahl-Barth and co-workers, Charlottenlund, *G. euphraticus* is sympatric with *G. convexiusculus* in Iran, where they are said to occur in the same water bodies (J. E. Jelnes, personal communication, VIII-1977). This, of course, would be a strong argument for reproductive isolation between these groups and, thus, for separate species status of *G. euphraticus.* Hence, the group dealt with under the names of *G. convexiusculus, G. chinensis* and *G. spirillus* and perhaps some others form a separate network of races in south and east Asia. I want to apply the term Rassenkreis for this chain, as coined by Rensch (1929: 13, translated): "A Rassenkreis is a complex of geographical races having immediately developed from each other, geographically vicariating and showing unrestricted fertility between neighbouring races." We do not yet know whether *G. convexiusculus, G. chinensis* and *G. spirillus* are reproductively isolated. If they are reproductively isolated they would have to be considered sibling species. It would, in this case, not be justified to call the group of these three a superspecies, as defined by Mayr who replaced Rensch's "Artenkreis" by this term: "A superspecies consists of a monophyletic group of entirely or essentially allopatric species that are morphologically too different to be included in a single species" (Mayr, 1963: 499). As shown above, morphological differences between the three groups are negligible.

A similar observation was made by Hubendick (1951) who studied a great number of races of the lymnaeid snail *Radix auricularia* (L.), which have a distribution like *Gyraulus chinensis,* etc. The races, previously regarded as species, are defined on shell characters, but show virtually no consistent differences in anatomy. He found geographic overlap of races with transitional forms occurring here and there. In western Burma and Assam, for example, the Indian race *R. a. rufescens* appears to grade into the Chinese race *R. a. swinhoei* (Hubendick, 1951: 154). In his discussion, Hubendick saw most reason for steering a middle course between the two alternatives: "geographical races constituting one species" or "separate though closely related species, all of which . . . form one superspecies." Finally he apparently decided to speak of a superspecies, whereas I am tending to consider the *Gyraulus* widely distributed over south and east Asia members of one Rassenkreis. The reason is that the *Gyraulus* taxa called races are hardly discernible from each other, even on the basis of shell characters. The oldest available name for this taxon is *G. chinensis* (Dunker).

FIG. 87. *G. tokyoensis,* Tomigusuku-son, shell periphery with keel and weak reticulate sculpture; periostracum removed. SEM. Scale = 0.01 mm.

In the material collected by G. M. Davis on Okinawa there are snails that I should identify as *Gyraulus hiemantium.* They are almost congruent with Mori's figure of this species (Mori, 1938, pl. 15, fig. 9). Anatomically they do not show any substantial deviations.

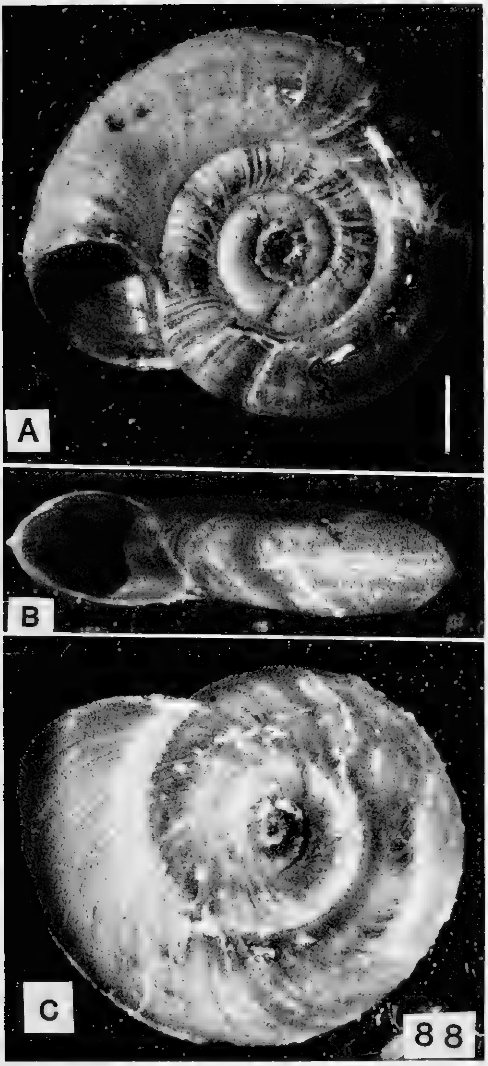


FIG. 88A–C. *G. malayensis* n. sp., shell. Holotype (SMF 246 333).

Should topotypes of *Planorbis hiemantium* Westerlund, 1883 from Hiroshima show the same characters, *G. hiemantium* may also be included in the *chinensis*-Rassenkreis as a very flat form of the race *G. ch. spirillus.*

Gyraulus tokyoensis (Mori, 1938)

Anisus (*Gyraulus*) *tokyoensis* Mori, 1938: 290 (Tokyo).

Material—Tomigusuku-son (Okinawa), 13 specs. (unrelaxed); Sashiki-son (Okinawa), 7 specs. (unrelaxed).

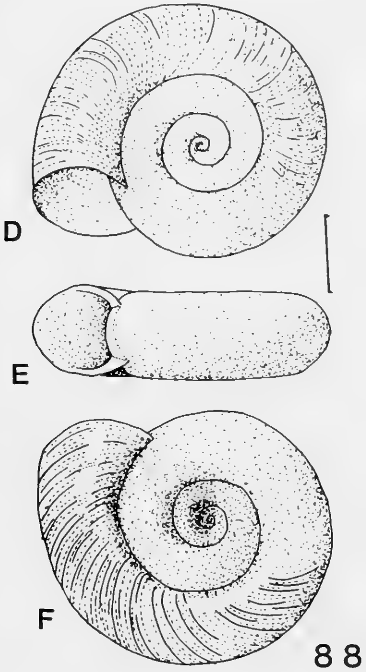


FIG. 88D–F. *G. malayensis* n. sp., shell. Paratype, Bukateja, Java (RMNH 9056/alcohol).

Shell (Fig. 86)—The shell is large, regularly exceeding 7 mm in diameter, relatively flat (2 mm in height), with 4¼ to 4½ rapidly increasing whorls. The last whorl is not or only slightly deflected. The periphery is distinctly angled and keeled (Fig. 87), carrying a wide fringe of periostracum (removed in Fig. 87 to show the keel). The surface shows weak reticulate sculpture. Anatomical characters (Table 6) are like those of *G. chinensis.*

Remarks—The lack of anatomical differences between *Gyraulus tokyoensis* and the *G. chinensis*-group suggests very close relationship. There are two reasons for maintaining *G. tokyoensis* as a separate species: (1) Size and a strongly keeled periphery distinguish *G. tokyoensis* from the *G. spirillus* race. Extreme forms within the *chinensis*-Rassenkreis differ from each other not to the same extent. (2) The two species live in the same region, e.g. on Okinawa. Here Davis & Yamaguchi (1969: 147) collected *Gyraulus* at 29 localities. Of these, 23 had *G. ch. spirillus* and 7 had *G. tokyoensis,* while at one site the two forms were found together. This could also mean that they are ecophenotypes of one species, but according to these authors

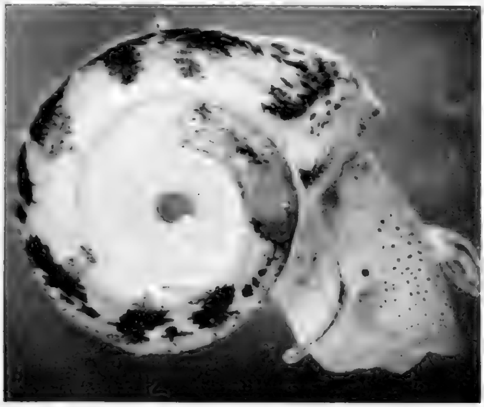


FIG. 89. *G. malayensis* n. sp., paratype, Kuala Lumpur, body pigmentation (shell removed).

"there was no gradation of *G. spirillus* into *G. tokyoensis*." Consequently *G. tokyoensis* apparently complies with the biospecies criterion of reproductive isolation from its closest relative.

Gyraulus malayensis Meier-Brook, n. sp.

Diagnosis—A species of the genus *Gyraulus* which differs from all known species by its extremely wide vas deferens, the penis sheath being not much wider than the vas deferens, and the penis pore being situated near the middle or in the proximal half of the penis.

Shell (Fig. 88A–F)—The shell is medium-sized to large, 3.5 to 6.5 mm in diameter, of varying height, the smaller snails being relatively high, 1 to 1.25 mm (Bukateja, Tasik Madu), the larger relatively flat, 1.2 to 1.55 mm (Kuala Lumpur). Three and three quarters to 5 whorls increase moderately fast. The periphery is rounded or slightly angled, angled forms having a wide fringe of periostracum (Kuala Lumpur). The last whorl is hardly deflected. The aperture is round to ovoid. The upper side is almost flat with shallow sutures. The under side is deeply concave with deep sutures. The surface is smooth to glossy, occasionally (Kuala Lumpur) carrying faint spiral striae. Growth lines are ± irregular. The colour is pale corneous.

Animal—The animal is light grey, the cephalopedal mass has distinct black spots (Fig. 89). The mantle pigmentation shows a distinct pattern, either with large black areas (Fig. 89) or smaller patches like those in *Gyraulus chinensis* (Fig. 12). The pseudobranch is large. The kidney margins are straight. An intestinal loop is present. Ovotestis, seminal vesicle, and albumen gland are of the usual size and form (Fig. 90). The female tract is long and narrow. The bursa copulatrix is elongate club-shaped. The bursa duct is long and relatively wide (about the width of the vagina). The vagina is slightly inflated. The free sperm duct is conspicuously long. The prostate gland bears 17 to 25 (Kuala Lumpur) or 21 to almost 30 (Tasik Madu, not exactly determined in contracted specimens) or 29 and 33 (Bukateja) diverticula, which are densely and regularly arranged. The vas deferens is equally wide throughout its length (Fig. 90, 91A–B); its width is 0.12 to 0.20 (Kuala Lumpur), 0.10 to 0.14 (Tasik Madu) or 0.08 to 0.11 mm (Bukateja). The penis sheath is not considerably wider than the vas deferens, its widest portion being 0.14 to 0.24 (Kuala Lumpur), 0.16 to 0.20 (Tasik Madu) or 0.14 to 0.16 mm (Bukateja) wide. The preputium is of the usual form. Preputial pilasters are present. The penis sheath is longer than the preputium: the ratio penis sheath : preputium in Kuala Lumpur is $\bar{x} = 1.5 \pm 0.4$ ($n = 8$); Tasik Madu (unrelaxed!) $\bar{x} = 1.8$, ($n = 3$); Bukateja (unrelaxed!) $\bar{x} = 1.5$ ($n = 4$). The penis gradually tapers from about the middle of its length. The penis pore lies near the middle of the penis length or in its proximal half (Fig. 91C). The stylet has the normal form.

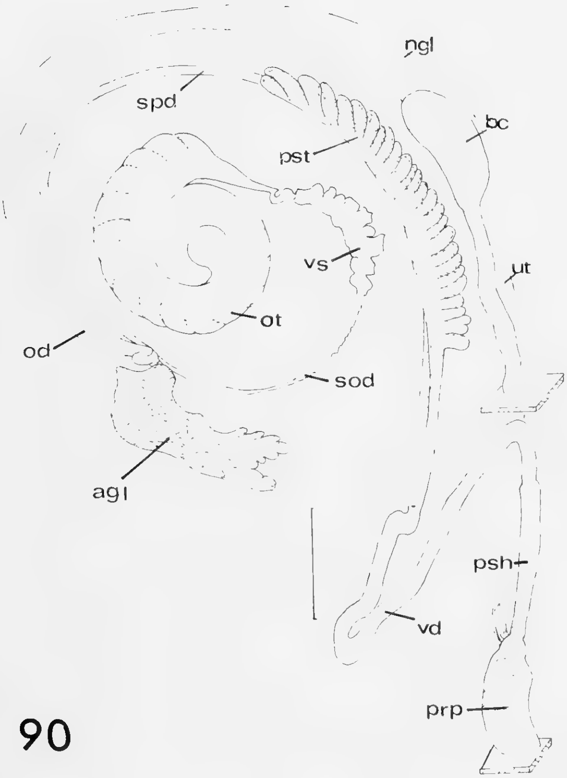
Type-locality—Kuala Lumpur (Malaysia), 5 km from the city, large abandoned tin-mining pool. On grass and *Eichhornia*. J. K. Lie legit, VI-1973.

Holotype (Fig. 88A)—6.1 mm in diameter, 1.5 mm high; a:b = 4.6:1.25 mm, 4⅞ whorls. Deposited in SMF 246 333/1.

Paratypes—SMF 246 334/4 and 246 326 (microscopical preparation); RMNH, Leiden (alcohol), no. 9055/4 from Kuala Lumpur. SMF 246 335/3 from Tasik Madu, N Bali: Lovina Beach, legit K. Y. T. Tjhen, VI-1976, RMNH Leiden (alcohol) no. 9056/2 from Bukateja, south-central Java, Tjhen legit, VI-1976 (Fig. 88B)

Additional paratypes are in the author's collection. Material examined anatomically: Kuala Lumpur (Malaysia) 11 specs., Tasik Madu (Bali) 4 specs. (unrelaxed); Bukateja (Java) 4 specs. (unrelaxed).

Conchologically, this new species appears to fall in the range of variation of what has usually been called *Gyraulus convexiusculus*. The expert for Indonesian mollusks, Dr. van der Feen van Benthem-Jutting of Domburg



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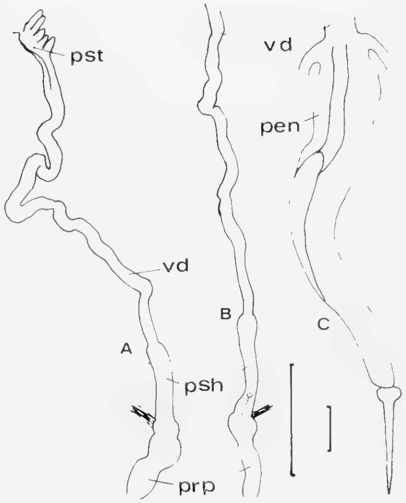

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FIGS. 90–91. *G. malayensis* n. sp. 90. Paratype, Kuala Lumpur, reproductive system (SMF 246 326). 91. Paratypes. A, B—♂ copulatory organs with vas deferens from Tasik Madu, Bali and Bukateja, Java. C—penis of a specimen from Tasik.

(Netherlands), was kind enough to check the shells of the Javanese and Balinesian samples and to give me her opinion (*in litt.* 22-XI-1976), before I began to study their anatomy. She used to attribute the name *G. convexiusculus* to snails of this form. In her monograph of Javanese mollusks (van Benthem-Jutting, 1956: 463) she mentions only two *Gyraulus* species: *G. convexiusculus* and *G. terraesacrae* Rensch. *G. terraesacrae* is a tiny species not exceeding 2.2 mm in diameter and is probably a separate species. Whether the Indonesian material in the various collections named *G. convexiusculus* really belongs to this species or rather to *G. malayensis* n. sp. cannot be judged without extensive anatomical studies. It is hoped that future studies will also reveal reliable conchological differences between *G. chinensis* and *G. malayensis* n. sp.

Most characters of the animal of the new species shared by *Gyraulus chinensis* are symplesiomorphous within the subgenus *Gyraulus* and thus of little value, but the distinct pattern of mantle pigmentation and perhaps also the relatively wide bursa duct are synapomorphous within the subgenus. These synapomorphies indicate close relationship between *G. chinensis* and *G. malayensis*. Moreover, there is a high probability that in Indo-China there has never been any other taxon from which *G. malayensis* could have split off than the parent species *G. chinensis*. And the presence of *G. malayensis* in Malaysia and in Indonesia strongly suggests that isolation took place somewhere in or near the Malayan peninsula.

Reproductive isolation between *Gyraulus chinensis* and *G. malayensis* is not only understandable because of the fundamental difference in the copulatory organs but also because their geographical ranges overlap in at least one region: a sample from Malacca, approximately 120 km SSE of Kuala Lumpur,

FIG. 92. *G. eugyne* n. sp., holotype (NHRM Stockholm 2198).

recently received from Mr. Sigurdsson, contained the species common in S Asia: *G. chinensis*. From this finding it is probable that the two species are sympatric in Malaysia. One of the most exciting questions now is whether they are sympatric also in Sumatra, Java, Bali, and Borneo, which according to Rensch (1936: 267) and other zoogeographers (de Lattin, 1967, fig. 58; Illies, 1971: 53–54) were separated from Java, Sumatra and the continent at the end of the Pleistocene.

Gyraulus eugyne Meier-Brook, n. sp.

Diagnosis—A species of the genus *Gyraulus* which differs from all known species by its extraordinarily inflated bursa copulatrix.

Shell (Figs. 92, 93)—The shell is medium-sized to relatively large and has 3¾ to 4¼ whorls with the periphery rounded. The last whorl is deflected. The aperture is slightly oblique and round to ovoid. The shell is deeply umbilicate on the upper side and slightly concave on the under side. Fine growth lines are present. The surface is almost smooth, with at most a few faint spiral striae. The sutures are deep and the whorls are rounded laterally.

Animal—The cephalopedal mass is almost dark grey. The mantle pigmentation consists of a weak pattern, similar to that in *Gyraulus acronicus*. In the reproductive system of three paratypes the prostate gland had 17, 15 and 14 diverticula; the ♂ copulatory organ (1.8, 3.4 and 2.2 mm long) is of the ordinary type, the length ratio penis sheath : preputium (1.4, 1.6, 1.9) being in the range of *G. acronicus*. The penis pore has not been located exactly but seems to be at the base of the bulbous thickening. The bursa copulatrix in all three individuals showed enormous inflation, comparable to the "spherical tadpole type" in some *Planorbis*-species (cf. Meier-Brook, 1976c), which has to this extent never been observed in any other *Gyraulus* species. This amount of inflation cannot solely be caused by recent copulation. It greatly exceeds the amount observed in freshly mated individuals of other species. Moreover, the characteristic orange color of the bursa contents, as is usually seen in freshly mated individuals, was absent here.

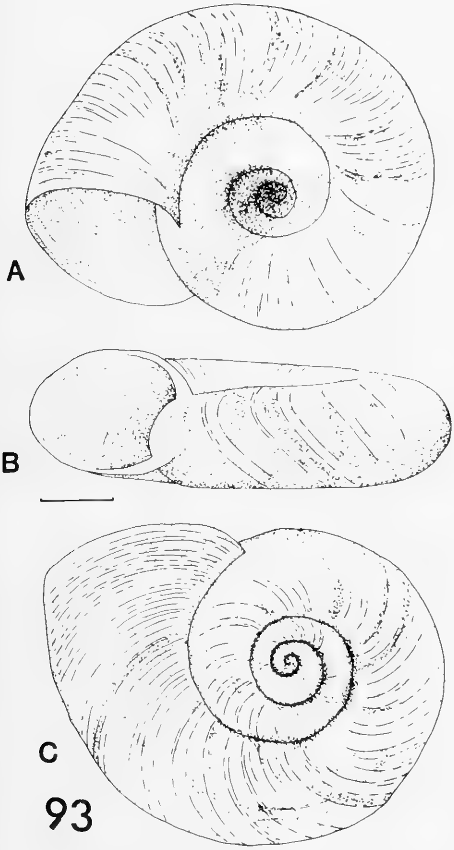
Type-locality—Inner Mongolia ("Läger XI" Honnen-tjaggan-tschollogol; Sven Hedin-Expedition, 1927).

Holotype—NHRM Stockholm no. 2198 (Fig. 92); 5.9 mm maximum diameter, 4⅛ whorls; 2.3 mm height; a:b = 4.25:1.55 mm.

Paratype no. 1—6.2 mm diameter; 2.1 mm height; a:b = 4.5:1.35; Paratype no. 2—5.7 mm diameter; 2.2 mm height; a:b = 4.15:1.5; Paratype no. 3—5.7 mm diameter; 2.2 mm height; a:b = 3.9:1.5 (Fig. 93); Paratype no. 4—5.6 mm diameter, 2.0 mm height; a:b = 4.1:1.5; Paratype no. 5—6.6 mm diameter; 2.1 mm height, a:b = 4.3:1.45.

Relationship—Conchologically, there is superficial resemblance between *Gyraulus eugyne* and *G. piscinarum*, both having a mean ratio a:b of 4.2:1.5 in adult specimens. Anatomically the size and shape of the bursa copulatrix (Figs. 71 and 94) also show some affinity. The mean number of prostate diverticula lies within the range of that in *G. piscinarum* and *G. chinensis* with subgroups, while shell characters are quite different from those in the latter species.

So far as we know, *Gyraulus piscinarum* has a restricted distribution in the Near East. Its occurrence, as an eastern race, in Mongolia, approximately 7000 km distant from the Near East, appears improbable. The shells could be compared with the east Siberian forms of *G. acronicus*, but the number of prostate diverticula does not fall in its range. However, close relationship with *G. acronicus* cannot be excluded. Of the many *Gyraulus* species described from China there is none that is conchologically similar except, perhaps, *G. zilchianus* Yen. As long as the



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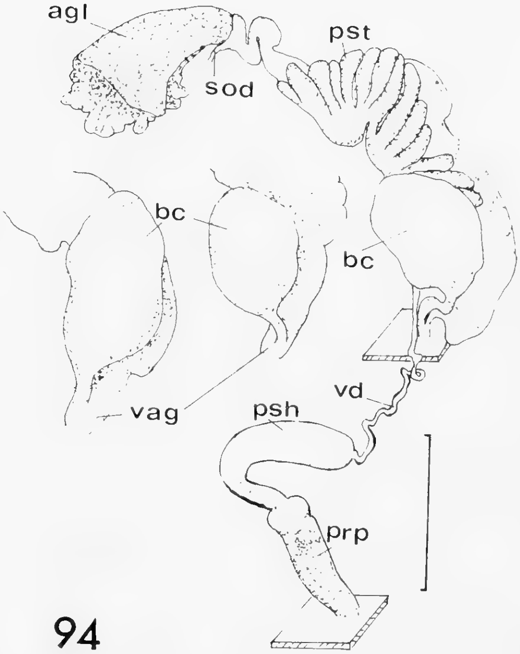

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FIGS. 93–94 *G. eugyne* n. sp. 93. Paratype no. 3; (NHRMS 2198). 94. Reproductive system, including shapes of two further bursae copulatrices. Paratypes (NHRMS 2198).

chance of studying Chinese material anatomically is virtually zero (my attempt to collect in Soochow, the type-locality of *G. zilchianus,* was obstructed) I dare not identify the only anatomically known species from China with a conchologically defined species from a locality more than 1300 km distant. Thus, I prefer to run the risk of creating another synonym in order to avoid misidentification of this species.

Concluding Remarks on South Asiatic Species

Our knowledge of anatomical characters in *Gyraulus* species must still be called sporadic with regard to the dimensions and geomorphological heterogeneity of the southern part of Asia. We may state that there is one Rassenkreis extending from Middle to Far East: *G. chinensis.* There is also no doubt that the Near East harbours at least two species clearly separated from *G. chinensis,* viz. *G. piscinarum* and *G. ehrenbergi.* There is probably also a third one, *G. euphraticus.* In the Far East there is one taxon considered here as a separate species though with close affinity to *G. chinensis*: *G. tokyoensis.* Possibly Japan is inhabited by more than these two species, apart from the endemic species of Lake Biwa. It is, of course, premature to claim that in the entire south Asiatic region any *Gyraulus* must be a member of the Rassenkreis of *G. chinensis.* Conchological variation, e.g. in the Chinese *Gyraulus* fauna (Yen, 1939, pl. 6, figs. 1–8), suggests that there are a few more separate species, as the discovery of *G. eugyne* n. sp. from Inner Mongolia implies. No further conclusions, however, are reasonable without anatomical studies of more material from this region.

Although I am far from having full knowledge of the species inhabiting the Orient, I provide a provisional key. Users should be aware of its incompleteness and of possible weaknesses, e.g. a sure distinction between *Gyraulus chinensis* and *G. euphraticus*. As pointed out above there are forms of *G. chinensis*, such as the Taiwanese population dealt with here under the name *G. spirillus*, that are almost indistinguishable from *G. euphraticus*. Unfortunately there are not even anatomical characters constant enough to support a decision, so that only geographical distribution offers help.

A Provisional Key to the *Gyraulus* Species Inhabiting Continental Southwest, South and East Asia

1A. Mantle pigmentation diffuse, without a distinct pattern and poor in contrast, underside of shell flat or slightly concave or convex, upper side deeply concave, aperture ± oblique; 3 to 4 whorls rapidly increasing, diameter 5 to 6 mm, periphery rounded; surface dull . . . . *G. piscinarum*

1B. Mantle pigmentation with a distinct pattern rich in contrast, though sometimes weakly developed (± pale), surface ± shiny 2

2A. Vas deferens wide, not much narrower than penis sheath, not well set off against it; penis tapering towards its tip; penis pore in middle or proximal half of penis . . . . *G. malayensis*

2B. Vas deferens slender, considerably narrower than penis sheath, always well set off against it; penis with ± distinct distal thickening with the penis pore in or close to it 3

3A. Shell scarcely >4 mm in diameter, relatively high: 1.3 mm; 3½ whorls very rapidly increasing, periphery slightly angled, with a small fringe of periostracum; animal poor in pigment, but pattern, though poor in contrast, discernible on mantle . . . *G. ehrenbergi*

3B. Shell larger, >4 mm in diameter, mantle pigmentation rich in contrast 4

4A. Bursa copulatrix much inflated (balloon-like), wider than uterus, bursa duct narrow; shell 5 to 6 mm in diameter, scarcely concave on under side, deeply concave on upper side; about 4 whorls rapidly increasing, periphery rounded . . . . *G. eugyne*

4B. Bursa copulatrix ± elongate, not wider than uterus, bursa duct ± wide; shell periphery often angled 5

5A. Shell large, >6 to 7 mm in diameter, 4¼ to 4½ whorls rapidly increasing, periphery keeled, with a conspicuous fringe of periostracum . . . . *G. tokyoensis*

5B. Shell small, usually < 5 to 6 mm in diameter, periphery rounded or angled 6

6A. Shell flat, height at most 23% of diameter; surface glossy, spiral striation absent . . . . *G. euphraticus* (? = *G. hebraicus*?)

6B. Shell usually biconcave, height usually >25% of diameter, periphery rounded or angled, fringe of periostracum often present, surface usually glossy; fine spiral striation sometimes present . . . . *G. chinensis*

SPECIES OF ANCIENT LAKES

Molluscs are one of those groups of organisms that first drew biologists' attention to highly distinctive endemic taxa in lakes of Tertiary origin. Examples of lakes with well known endemic molluscan faunas are Lake Tanganyika, Lake Titicaca, Lake Biwa, Lake Baikal, and Lake Ohrid. Regarding the *Planorbis*-tribe (sensu Hubendick, 1955), endemic taxa have been described from the three last mentioned lakes, all situated in the Palaearctic region. The genus *Choanomphalus* was established as the first representative of ancient lake planorbids (Gerstfeldt, 1859). A striking character of this genus is its pseudo-dextrality caused by hyperstrophy. Subsequently, the first planorbid snail endemic to Lake Ohrid was described as *Planorbis* (*Gyrorbis*) *macedonicus* by Sturany

(1894) who pointed out its great similarity to *Choanomphalus*. Finally, a new species was discovered in Lake Biwa and relegated to *Choanomphalus* (Preston, 1916). The possibility that a peculiar planorbid genus was common to three ancient lakes so far distant from one another opened up exciting aspects as to the origin and evolution of such a group. Studies on the Baikalian snails revealed that *Choanomphalus* is anatomically distinct from *Gyraulus*, because of the acquisition of a distal accessory gland complex at the male copulatory organ, which gives the genus a unique status in the family (Hubendick, 1954, 1955). There are other features, however, such as the penial stylet, that leave no doubt that it is the group around *Gyraulus* that must have given rise to the seven Baikalian *Choanomphalus* species. Surprisingly, Lake Baikal has no endemic species of the genus *Gyraulus* itself. The *Gyraulus* species inhabiting the lake has been identified by previous authors as *G. gredleri* (=*G. acronicus*) (Kozhov, 1963: 159). Unfortunately, no material from Lake Baikal was available for my anatomical studies.

Species of *Gyraulus* from Lake Ohrid have been examined thoroughly as regards morphology (Hubendick & Radoman, 1959). There are four species of *Gyraulus* in the Ohrid basin similar to each other and strikingly distinct from European species outside the Ohrid basin. A fifth species resembles the usual *Gyraulus* species, but has been described as *G. albidus* (Radoman, 1953). The first of the four unusual Ohrid species relegated to a new subgenus, *Carinogyraulus*, was *G. trapezoides* (Polinski, 1929). A new species described from neighbouring Lake Prespa (*G. stankovici*) was considered to be *Carinogyraulus* (Hadžišče, 1953). No doubt the remaining three species of the Ohrid basin, *G. lychnidicus* Hesse, *G. crenophilus*, and *G. fontinalis* (but not including *G. albidus*) can be united in this subgenus. Probably a fifth species, *G. paradoxus* Sturany, 1894, belongs here. Hubendick & Radoman's (1959) information was so ample that further investigations on Ohrid species did not appear urgent, and my studies are thus restricted to the dissection of one individual of *G. lychnidicus* (see below).

The species described as *Choanomphalus japonicus* and *Gyraulus biwaensis* by Preston (1916) have not been previously examined anatomically. Information on these forms is given below.

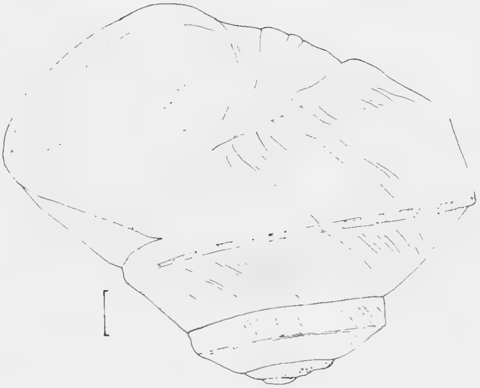


FIG. 95. *G. lychnidicus*, Lake Ohrid, shell (in coll. W. Rähle). Scale = 1 mm.

Gyraulus lychnidicus Hesse, 1928

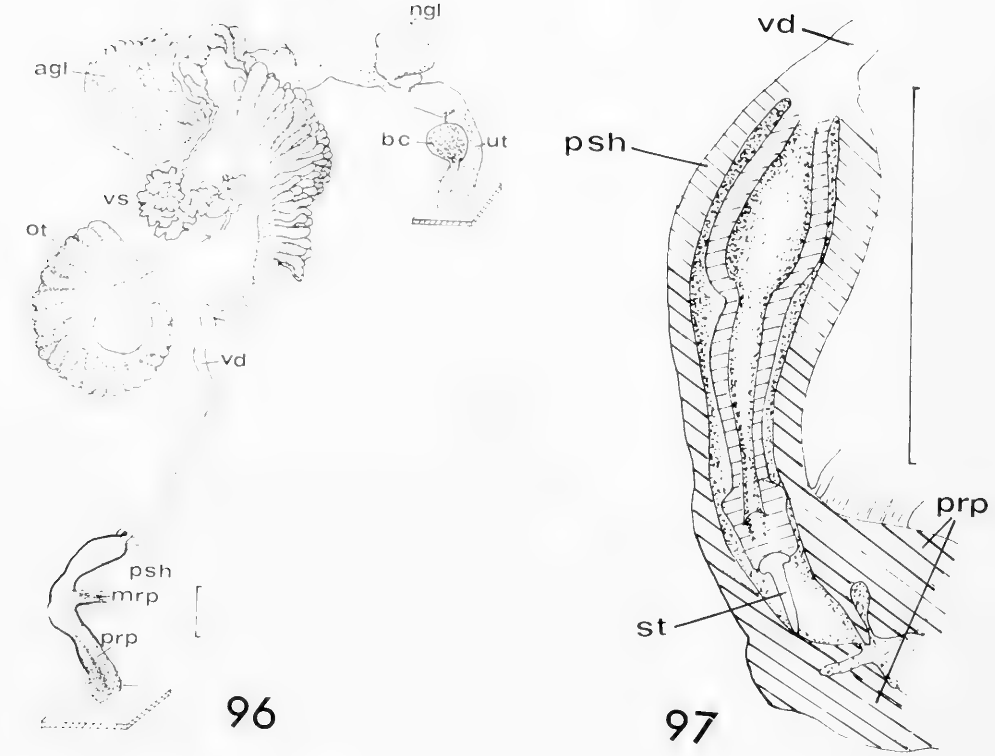
Gyraulus lychnidicus Hesse, 1928: 6, pl. 1, fig. 4a–c (Lake Ohrid).

Material—One spec. (unrelaxed) collected by W. Rähle on the shore of L. Ohrid between Trpejica and Sveti Zaum (shell in coll. Rähle).

Shell (Fig. 95)—The shell is pseudo-dextral, very large compared with other *Gyraulus* species, 10 mm in width and 8 mm in height; the whorls are angled and keeled, first at their greatest diameter, secondly and more weakly on their highest elevation forming the crest of the funnel-like depression (umbilicus). *G. lychnidicus* is a thick-shelled species.

Animal—The animal is light to dark grey on the head-foot complex; the mantle is nearly uniformly black, both on the kidney and on both sides of it. Strong pigmentation is also present on the alimentary tract except the digestive gland where it is merely pale. Of the reproductive organs also the preputium, the vagina, and the bursa copulatrix are covered by dense pigmentation in the individual dissected, while the vas deferens and the spermoviduct including the seminal vesicle are completely devoid of pigment. All other parts of this system show scattered pigmentation.

The reproductive system (Fig. 96) is characterized by a conspicuous seminal vesicle with bulbous coiling, a prostate gland in which more than 60 diverticula are arranged in several rows, and a relatively wide vas deferens, reaching more than 0.2 mm in width. The pe-



FIGS. 96–97. *G. lychnidicus,* Lake Ohrid. 96. Reproductive system (M 270). 97. Proximal portion of ♂ copulatory organ.

nis sheath and preputium in this contracted individual are of equal length, viz. 1.8 mm, and of usual width, 0.5–0.6 mm. The penis (Fig. 97) has a bulbous thickening, in the middle of which the penis pore is situated.

The radula (Fig. 98), as already stated by Hubendick & Radoman (1959), has unicuspid teeth (except in some marginals), as in *Gyraulus crenophilus* Hubendick & Radoman, *G. fontinalis* Hubendick & Radoman, and *G. trapezoides* Polinski.

Remarks—While Hubendick & Radoman's (1959) fig. 21 might suggest that in the prostate gland the diverticula are arranged like the rays in a fan, I found that in the individual dissected the diverticula emerged from the whole length of the prostate duct although in cross sections one would see an arrangement as in a fan. Finding the penis pore closer to the penis tip is in contrast with Hubendick & Radoman's (1959) statement that it "normally seems to be located well above the middle of the penis in large sized specimens."

Gyraulus stankovici Hadžišče, 1953

Gyraulus stankovici Hadžišče, 1953: 175, figs. 3–4 (Lake Prespa).

Material—One spec. (unrelaxed) dredged by W. Rähle in Lake Prespa, Macedonia, at Oteševo (7 June 1973); 12 specs. (poorly preserved) collected by W. Maassen at the same locality (May 1976).

Shell (Fig. 99)—The shell is pseudo-dextral, rather small, 3.8 mm maximum diameter, 1.3 mm high; the 3¼ whorls are provided with three strong keels: the first delimits the funnel (umbilicus) on the upper side; the second forms the periphery of a whorl; the third delimits the almost completely flat under side. At the site of the keels the shell is acutely angled so that it appears concave between keel 1 and 2 and between 2 and 3. *Gyraulus* *stankovici* is not as thick-shelled as indicated for *G. lychnidicus.* The shell surface is coarse. Irregular growth marks and a faint spiral striation form a reticulate sculpture.

Animal—The animal is light grey on the head-foot complex, dark grey at the lateral margins of the kidney, almost black in the region of the reproductive organs on the right side, but nearly pigmentless in the remaining mantle parts. Rather dense pigmentation is present on most parts of the alimentary system.

The reproductive system as found in the one well preserved individual is shown in Fig. 100. It is too early to give a general description, but it can be said from examination of this specimen that the prostate diverticula are arranged in a single row and are few in number (here 14). The radula of several individuals examined shows characteristics intermediate between the usual *Gyraulus* type and the Ohrid species. A few central teeth are bicuspid, most are unicuspid and tend to elongate. The lateral teeth are mostly tricuspid, but the mesocone is usually enlarged, while the endocone has almost disappeared and the ectocone is greatly reduced (Fig. 101).

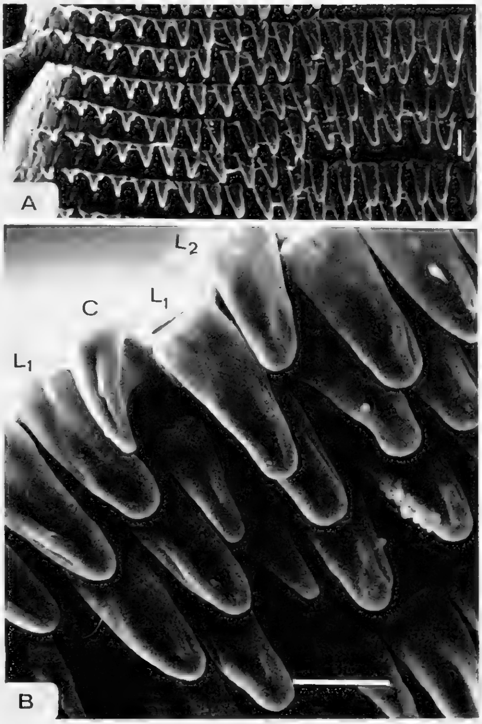


FIG. 98. *G. lychnidicus,* Lake Ohrid, Parts of radula, with (A) lateral and marginal teeth and (B) central (C) and first lateral teeth (L). SEM. Scale = 0.01 mm.

Gyraulus biwaensis (Preston, 1916)

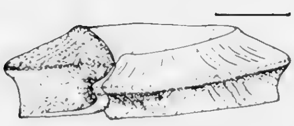
Choanomphalus japonicus Preston, 1916: 160, pl. 9, figs. 2–2c (*non Planorbis compressus japonicus* v. Martens, 1867 [a *Gyraulus*]).
Choanomphalus japonicus perstriatulus Preston, 1916: 161, pl. 9, figs. 1–1c.
Planorbis (*Gyraulus*) *biwaensis* Preston, 1916: 161, pl. 9, figs. 3–3c.
Anisus (*Gyraulus*) *biwaensis,* Mori, 1938: 292, pl. 16, fig. 11a–f.
Gyraulus biwaensis, Kuroda, 1963: 22.

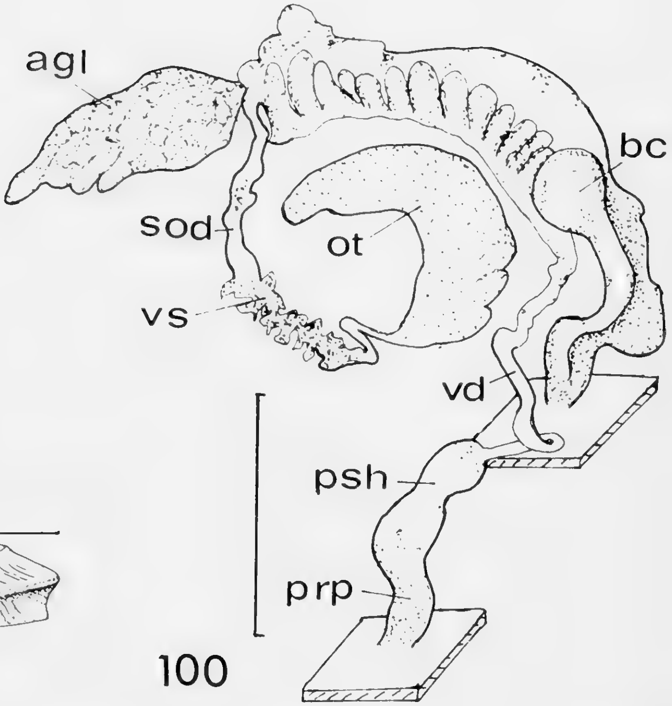
Material—Lake Biwa (Japan) at Eizan (10 extended specs. collected by H. D. Boeters on 19 February 1975); Lake Biwa at Oura (2 retracted specs. collected by T. Miura on 12 June 1975).

Shell (Fig. 102)—The shell is pseudo-dextral, but the spire is not considerably elevated above the last whorl. This thick-shelled (0.04 mm in periphery of the last whorl) species is relatively small: width 3–3.5, height 1.5–2 mm; apertural height 1.2–1.5 mm. There are usually three keels. The middle keel lies on the periphery and the upper and lower ones are about equidistant from it. The upper keel delimits the funnel leading to the deep umbilicus. The lower keel surrounds the more or less flat underside that is only interrupted by relatively deep sutures. There are usually three to five spiral striae between every two keels.

Animal—The animal is relatively uniformly pigmented. The head-foot complex is light grey, the mantle roof is similarly pigmented, as described for *Gyraulus lychnidicus* but not as dark. There is no pronounced pigment pattern.

The whorls are relatively short, wide and high; most organs are likewise short and wide (Fig. 103). This is the case with the albumen gland, the free sperm duct, the prostate gland (7–12 diverticula, $\bar{x} = 10.1 \pm 1.7$), the oviduct and uterus. The striking exception is made by the male copulatory organ that is—in its extended state—so long that its upper end nearly reaches the carrefour. The penis sheath is slightly longer (psh = 0.9–1.2 mm, $\bar{x} = 1.0 \pm 0.1$) than the preputium (prp = 0.75–1.05 mm, $\bar{x} = 1.0 \pm 0.1$) (psh:prp =





FIGS. 99–100. *G. stankovici*, Lake Prespa. 99. Shell, apertural view. 100. Reproductive system (M 281).

1.1–1.3). The bulbous thickening of the penis tip is inconspicuous. The penis pore is situated in its upper half (Fig. 104). Preputial pilasters are well developed.

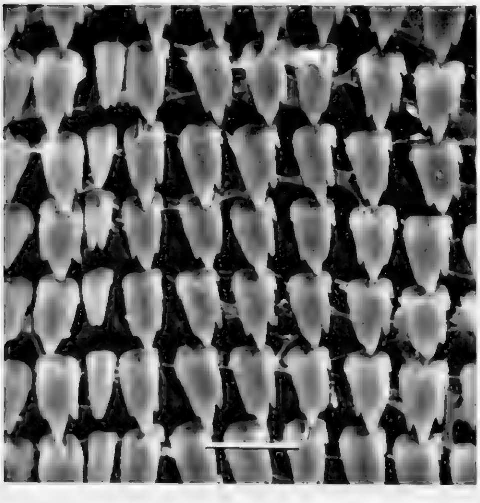
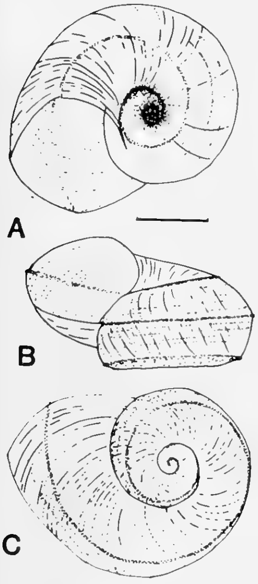


FIG. 101. *G. stankovici*, Lake Prespa, central and lateral teeth of radula. SEM. Scale = 0.01 mm.

The radula formula is 13/14-1-13/14. The teeth are basically of the usual type in the genus (Fig. 105).

Remarks—The proportionally long ♂ copulatory organ gives *Gyraulus biwaensis* a unique position within the genus. This and the lack of a distinct pigment pattern make it unlikely that it has a common origin with the *G. chinensis* group. Thus these taxa do not appear very closely related. Its placement in the genus *Choanomphalus* has already been refuted by Mori (1938: 294) in a radula study, and by Kozhov (1963: 132–133) on conchological grounds. Anatomical study confirms this. The organization is even closer to the non-endemic group of *Gyraulus* than to the Macedonian endemic subgenus *Carinogyraulus* as the following considerations will demonstrate.

The marked multiserial arrangement of prostate diverticula, their great number, the unusual width of the vas deferens, and the unicuspid central and lateral teeth of the radula appear to be the character states common to the non-planispiral *Gyraulus* species of Lake Ohrid. Neither of these characteristics is found in *G. biwaensis* where, on the



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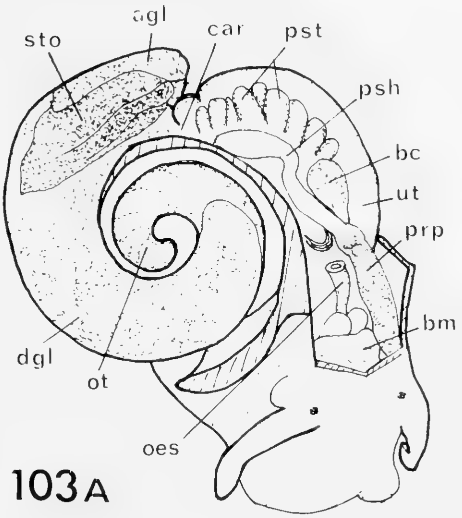

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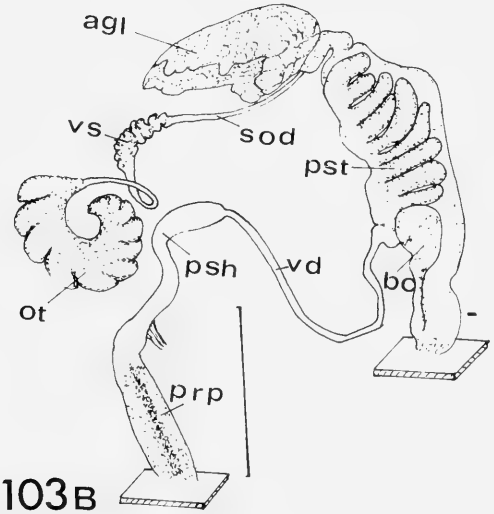

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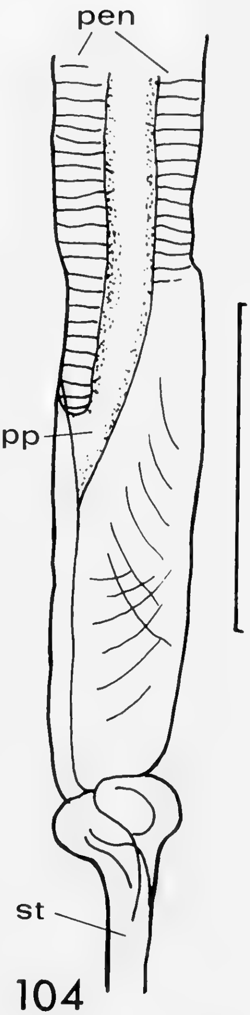

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FIGS. 102–104. *G. biwaensis,* Lake Biwa at Eizan. 102. Shell. 103A: Reproductive organs in situ demonstrating the relative length of the ♂ copulatory organ (mantle roof and esophagus removed); B: Reproductive system. 104. Penis tip. Scale = 0.1 mm.

contrary, the prostate diverticula are arranged uniserially and are relatively few in number. The vas deferens in *G. biwaensis* is as narrow as in *G. albus* and in any species outside Macedonia and the Malay Archipelago except *G. parvus,* where, as described above, the inferior half is largely thickened.

Nomenclature—The three names for this species, *Choanomphalus japonicus, Choanomphalus japonicus perstriatulus,* and *Planorbis biwaensis* were introduced in the same publication. The first revising author, Mori (1938), stated that these are synonyms. He chose to use the name *G. biwaensis.* Kuroda (1963: 22) followed him, though pointing out that *G. perstriatulus* chosen by Preston as a subspecies name would have line priority. According to article 24 (a)(i) of the International Code of Zoological Nomenclature, Mori's choice of *G. biwaensis* must stand.

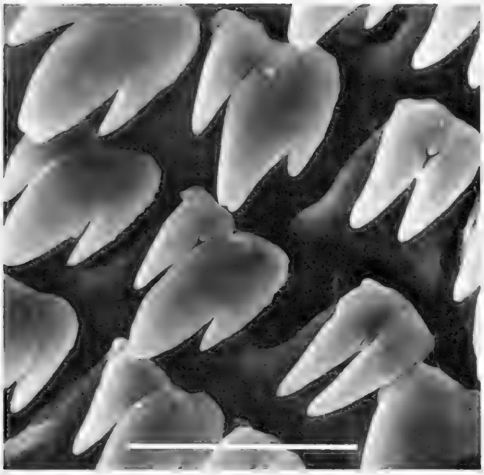

FIG. 105. *G. biwaensis*, Lake Biwa, central and first lateral radula teeth. SEM. Scale = 0.01 mm.

Concluding Notes on the Ancient Lakes Species

The similarity of *Gyraulus* species from Lake Ohrid, Lake Prespa and Lake Biwa, that led conchologists to assume that they had a common origin, apparently is restricted to shell characters. Conchological features in common are the abandonment of planispiral growth and a tendency to form angles and keels. These character states appear to be unique in any planorbid genus and can be considered derived. As long as they were the only characters known for these species it would have been plausible to assume them to be *common* derived characters and to consider the four Ohridan species plus *G. stankovici* plus *G. biwaensis* to be synapomorphous in Hennig's sense. Anatomical differences show that the assertions based on conchology cannot be accepted.

The ancient lakes were, as today, large and it is probable that wave action selected for planorbids with shells hydrodynamically suited to such an environment, i.e. with more globose than planispiral shells, and with a trend towards thickening and reinforcing angles and keels. It is thus not surprising that shells with such attributes arose in geographically separated lakes by convergent evolution.

The conditions necessary for developing these shell forms was sufficient time in a stable habitat, i.e. where populations did not need to frequently adapt to changing environmental conditions, as is the case in virtually all inland waters that are—geologically speaking—ephemeral.

Similar phenomena can be observed in other groups of ancient lakes molluscs, where a general trend in forming angles, keels, sculptures and other reinforcing shell structures is obvious. Convergent evolution in these groups has partly led to shells of such a striking resemblance with marine groups that, for a long time, the Tanganykan endemic prosobranch snails were considered immediately derived from marine ancestors (Hubendick, 1952). To a lesser extent convergent evolution in various lakes has also been demonstrated in basommatophoran snails. A good example is the freshwater limpets *Acroloxus macedonicus* Hadžišče from Lake Ohrid, and *A. kobelti* (Dybowski) and *A. boettgerianus* (Lindholm) from Lake Baikal, which have radial ribs making them appear like small Siphonariidae.

After thorough anatomical examination, Hubendick (1960, 1969) concluded that the Ohridan and Baikalian *Acroloxus* species have evolved independently and that "evolution has obviously run parallelly in the two groups" (Hubendick, 1969: 66). It is interesting to state that also in the Acroloxidae a trend is visible towards reduction of radular cusp numbers. But according to Hubendick (1969: 66), "this process has resulted in mostly bicuspid laterals in the Baikal species and unicuspid laterals in the Ohrid species." As shown above, four of the five *Gyraulus* species in Lake Ohrid have unicuspid centrals and laterals. Since bicuspid centrals and tricuspid laterals are the rule not only throughout the genus but in the whole family Planorbidae as well, there can be no doubt about the direction evolution proceeded: somewhere in the Macedonian region a reduction of cusp numbers must once have taken place, and that *before* speciation within the Ohrid basin began (Fig. 106).

Concerning the fifth Ohridan species, *Gyraulus albidus*, it would seem that it has a different origin and closer relationship with *Gyraulus albus*. While Radoman (1953: 58) originally suggested that his species be conchologically and anatomically compared with *G. albus*, *G. laevis* and *G. gredleri*, in 1959 (Hubendick & Radoman, 1959: 239–243) he did not comment further on this aspect, and most recently (*in litt.* 2 February 1977) he expressed the opinion that *G. albidus* cannot be separated from the group of Ohridan *Carinogyraulus* species. I have specified the conchological and anatomical features separating *G. albidus* from the other Ohridan species above, and the decision on whether *G. albidus* is to be included in this group may depend on the width or narrowness of the scope of a subgenus. Until *G. albidus* can be examined anew the question must remain open (Fig. 106). For now the subgenus *Carinogyraulus* will include no more than the Ohridan species (except *G. albidus*) plus *G. stankovici* from Lake Prespa. The latter is included here mainly because of the obvious reduction seen in radula cusp numbers. This reduction and the short distance of Lake Prespa from Lake Ohrid make it improbable that *G. stankovici* and the four peculiar Ohrid species evolved independently. Because of the probable close ancestry of these species I assume that the conchological similarities likewise attest to a close relationship, i.e. were not derived by convergent evolution. The character state that distinguishes *G. stankovici* from the Ohridan forms is the uniserial arrangement of prostate diverticula and their low number. This evidence indicates that *G. stankovici* diverged after cusp reduction had been initiated, but before increase of number of prostate diverticula and speciation in the Ohrid basin began. The Biwa species, *G. biwaensis,* on the other hand, must have evolved from a different ancestral group within the genus. It is necessary to place it in a separate subgenus, namely *Choanomphalodes,* a name erected by Lindholm (1927) as a subgenus of *Choanomphalus.*

It is strange that an endemic subgenus of *Gyraulus* has not evolved in Lake Baikal. *Gyraulus* must have been present throughout Asia during the Tertiary (according to Zilch (1960: 110) since the Paleocene). This "gap" would not exist, however, if the following assumption proves true: evolution of an endemic subgenus of *Gyraulus* may have taken place in the past but has continued until a still more aberrant group has been formed, namely *Choanomphalus* with its seven species endemic to Lake Baikal and one species endemic to Lake Khubsugul (=Kosogol). Indeed there are character states common to *Choanomphalus* and *Gyraulus* that can be regarded to be synapomorphous[2] within the *Planorbis*-tribe. These are the generally similar structure of the ♂ copulatory organ, including the hollow penial stylet formed by a rolled blade. Moreover, a lack of pallial folds in *Choanomphalus* (Hubendick, 1954: 504) relegates this species to the *Planorbis*-tribe. The genera of this tribe are united by the synapomorphy "loss of pallial folds." Characters giving *Choanomphalus* a unique state in the family are an additional gland complex opening immediately beside the ♂ genital pore, a greatly concentrated central nervous system, and the lack of a reflected ureter. None of these characters run counter to assuming its origin in the *Anisus-Gyraulus* group. Also Hubendick (1954: 508; 1955: 531–532) concluded that "the morphology of *Choanomphalus* seems to indicate that the genus is most closely related to *Anisus* and *Gyraulus* but has undergone a further evolution." This view is shared by Kozhov (1963: 133) and Starobogatov (1958).

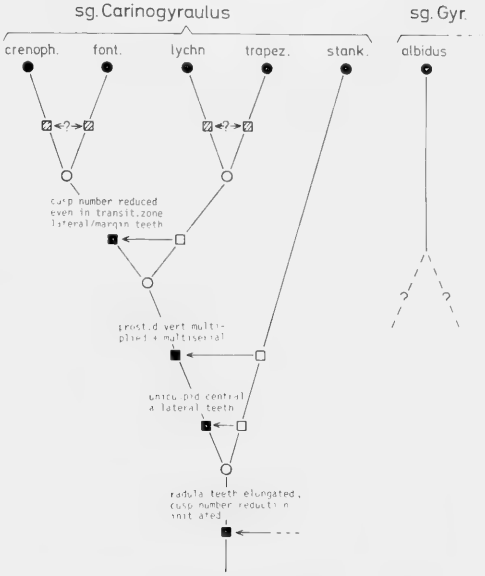

FIG. 106. Probable phylogenetic relationship in Macedonian *Gyraulus* species. Arrows are from plesiomorphous (open squares) to apomorphous characters (black squares). Shaded squares—direction of change uncertain. Open circles—hypothetical stem species. Black circles—contemporary species.

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[2] We will call the characters or character conditions from which transformation started in a monophyletic group *plesiomorphous*, and the derived conditions *apomorphous*. . . . We will call the presence of plesiomorphous characters symplesiomorphy, the presence of apomorphous characters *synapomorphy*, always with the assumption that the compared characters belong to one and the same transformation series" (Hennig, 1966: 89).

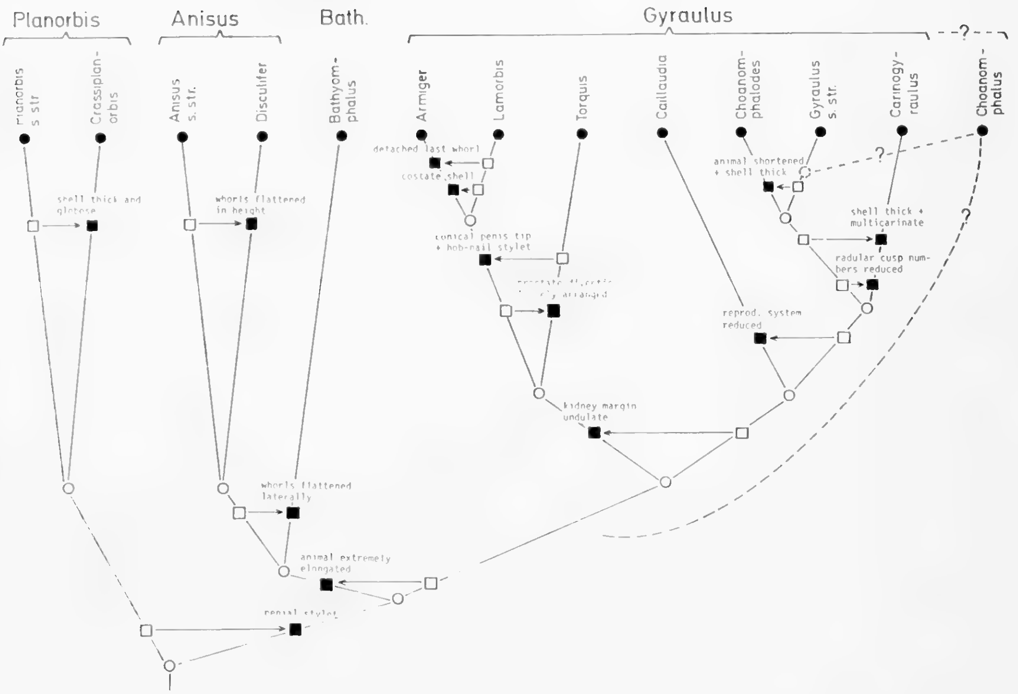

FIG. 107. The probable kinship relations in the *Planorbis*-tribe. For symbols see Fig. 106.

The question whether the *Choanomphalus* clade diverged before or after the parent species common to all recent *Gyraulus* species came into being, cannot yet be answered. If it diverged *after*, then it must show synapomorphies that are shared with a subgroup of *Gyraulus*. In this case *Choanomphalus* would have to be included in *Gyraulus* as a subgenus according to Hennig's (1966: 73) definition of monophyly: "A monophyletic group is a group of species descended from a single ("stem") species, and which includes all species descended from this stem species." Which group of *Gyraulus* species could have given rise to formation of a new clade in the Baikal basin? *Torquis* and *Lamorbis* occur in the Palaearctic but do not reach as far as Central Asia (Fig. 116). These two subgenera are sufficiently recognizable from shell characters that their past distribution in the Baikal region can be excluded as well. The only subgenera having reached Central Asia are *Armiger* and *Gyraulus* s. str. *Armiger* has too aberrant traits to be considered derived from a stem species shared with *Choanomphalus*. Thus only *Gyraulus* s. str. is left. This subgenus, however, is characterized exclusively by synapomorphies, thus forming a "remnant group" whose monophyletic status sensu Hennig cannot be proven. Should, one day, synapomorphous character states be found in *Gyraulus* species occurring, in past and present, in the Baikal region and should these synapomorphies be located in *Choanomphalus*, too, there would be no argument against including *Choanomphalus* in *Gyraulus* as a subgenus (Fig. 107, straight broken line). The genus *Gyraulus* would otherwise not keep its monophyletic status in Hennig's sense, as was also argued in the case of *Armiger*. If *Choanomphalus* branched off *before* the parent species of all recent *Gyraulus* species existed it must furthermore be regarded as a separate genus (Fig. 107, curved broken line), as all authors have done (Lindholm, 1927; Baker, 1945; Hubendick, 1954, 1955; Zilch, 1960).

Let us briefly consider the possibility that *Choanomphalus* branched off from a trunk that led to other genera of the tribe. *Planorbis, Anisus,* and *Bathyomphalus* presently extend to the Baikal region. The past existence of a species ancestral to—and only to—*Planorbis* and *Choanomphalus* giving them the status of sister genera would mean: a structure as complex as the penial stylet in all genera of the tribe except *Planorbis,* would have developed twice independently. This is so unlikely that I can exclude it. *Anisus* and *Bathyomphalus* possess a derived character state not shared by *Choanomphalus*: an extreme elongation of the total body. In a branch leading to *Choanomphalus* this elongation would have had to revert to the shortened state. Such a reversion is not impossible, as *Gyraulus biwaensis* demonstrates. But it is improbable that all organs re-shorten to the same extent. The unusually long ♂ copulatory organ in *G. biwaensis* is an example of this partial re-shortening. In *Choanomphalus* there is no indication of a partial re-shortening (Hubendick, 1954). Consequently I should think it equally improbable to assume a common ancestor for *Choanomphalus* and *Anisus* or *Bathyomphalus* that is shared only by them (as a condition for finding sister groups).

The question of why there is no endemic subgroup of the genus in Lake Titicaca and Lake Tanganyika is, in the former case, easily answered: The Andes region has evidently been devoid of members of the genus *Gyraulus* at all times. From Lake Tanganyika a few records of "*Anisus*" or "*Gyraulus*" species are found in the literature. At least one such species was assigned to a different genus by Brown & Mandahl-Barth (1973), namely *Afrogyrorbis natalensis* (Krauss).[3] Lake Tanganyika was probably outside the geographical range of real *Anisus* or *Gyraulus* during most of its history. It is of interest, though, that a strongly carinate form, described as *Gyraulus bicarinatus* Mandahl-Barth (1954: 91) and somewhat ressembling ancient lake forms from other parts of the world, has been discovered in Lake Albert. However, *G. bicarinatus* belongs to *Afrogyrorbis,* too (Brown & Mandahl-Barth, 1973).

Finally the question of an affinity between ancient lake *Gyraulus* and fossil groups deserves attention. Shells from the Upper Miocene of Steinheim/Albuch, Württemberg, Germany, cover a wide range of forms from flat and almost planispiral to turreted and extremely pseudo-dextral. These fossil taxa have been placed in a single species, *Gyraulus trochiformis* (Stahl, 1824) (synonym: *Poecilospira multiformis* (Zieten, 1830)). Comparing shell characters of the Steinheim species with those in the *Planorbis* tribe, particularly with thick-shelled and angled forms of ancient lakes, I do not object to grouping them in this tribe. However, the similarity of *P. multiformis* to *Gyraulus* is not greater than similarity to Paleocene *Carinulorbis* Yen, 1949. Even if we consider that *P. multiformis* may really have had anatomical characters in common with *Anisus* and *Gyraulus,* conchological differences between the Steinheim-group and any ancient lake *Gyraulus* would be greater than between distantly related standard *Gyraulus* species.

The probability substantiated above of an independent evolution of multicarinate and non-planispiral *Gyraulus* species in different parts of the world is one more reason not to overemphasize the possibility of a common evolution of Ohridan species and the Steinheim series, as was done by Polinski (1932) and accepted by Stankovič (1960: 244).

CLADISTIC ANALYSIS

Character Weighting

My study of morphological characteristics has revealed a number of qualitative or quantitative character states enabling me to distinguish species from each other. The use of such character states for characterizing and, thus, for identifying species, as discussed above, does, however, not necessarily mean that they are suited as tools in the analysis of genealogical relationship. One such character, to mention an example, is size. Within a certain range, enlargement or reduction of size appears to have happened independently in various groups where one observes giants or dwarfs. In a discussion on weighting of the "hob-nail-stylet" I shall show that isolated occurrences of dwarf-forms in the genus are encountered in Europe, Australia, Java, and Samoa. Of course, this does not preclude that splitting up of a tiny parent species may result in two sibling species maintaining their small size. Whether evolution took this course must be decided on two bases: (1) the occurrence of other derived characters common to these and only to these, and (2) a contact or overlapping of their geographical ranges at least in the past.

There are a number of processes besides convergent evolution that invalidate the re-

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[3] *Afrogyrorbis* Starobogatov, 1967, described with the same type-species, *Planorbis natalensis* Krauss, has priority over *Ceratophallus* Brown & Mandahl-Barth, 1973.

sulting characters or lower the value of such characters for phylogenetic conclusions, although not for the discrimination of species. These are, among others, mosaic evolution, and gradual and sporadic reappearance of traits once lost during phylogeny.

Recognition of mosaic evolution (Mayr, 1975: 208) requires a great variety of characters undergoing transformation during evolution *after* the existence of the stem species of a taxon. In *Gyraulus* few characters of this kind have been observed, so that it cannot be judged whether or not mosaic evolution happened.

The problem arising through the second event mentioned above as limiting the value of a character may be elucidated by examining reticulate sculpture. Spiral striae, which in adult snails form this structure together with transverse striae (growth lines), are encountered in embryonic shells of all Planorbidae studied so far, as stated above. Since they occur in many other basommatophoran taxa, too, one may suspect that this sculpture once was common in adult shells of a taxon at the stem of the Basommatophora or one of their higher subordinate taxa. If this were the case (fossil records in support of this have not systematically been examined) then its complete absence in most planorbid shells including those of the closest relatives of *Gyraulus* must be secondary and its presence in several *Gyraulus* species either is due to reappearance of the ancestral structure or to a new acquisition. The observation that spiral striae on adult shells are an immediate continuation of embryonic striae supports the assumption of a reappearance. This would also facilitate an explanation of the obviously independent occurrence of spiral striae here and there (sg. *Lamorbis, Choanomphalodes, Gyraulus* s. str., *Carinogyraulus*), even in usually smooth-shelled groups, such as *G. chinensis spirillus.*

A new acquisition, however, can not be entirely excluded. The new striae could have started from the embryonic striae because the shell-forming mantle edge was functionally prepared for the formation of striae just at these sites. If my concept, established on several reliable characters (Fig. 107), is correct, new formations of striae, however, would have had to arise several times independently, since *Caillaudia, Torquis,* and *Armiger* always lack spiral striae.

The above speculation shows how difficult a decision is on what presence or absence of reticulate sculpture tells us about phylogenetic relationships. As long as there is no palaeontological evidence for spiral striation being ancestral, the problem must remain open. The value of the structure for cladistic analysis is, thus, zero. The suitability of a distinct reticulate sculpture for characterization and recognition of species, such as *Gyraulus albus* and *G. acronicus,* is not affected by this difficulty.

Characters particularly useful in the evaluation of relationship are all those that, besides a high stability, show (1) clear alternatives (example: undulate/straight kidney margins), (2) can be categorized as ancestral or derived with as little doubt as possible (example: pluricuspid/unicuspid radula teeth) and (3) tie in well with the geographical distribution of their bearers (example: the hob-nail-stylet in *Armiger* and *Lamorbis*).

Analytical Procedure

I have attempted to group species in supraspecific taxa according to a system expressing relationships and resulting in monophyletic groups. By relationship one means "overall similarity" as discussed by most authors (e.g. Hennig, 1966: 74). This can even be expressed in terms of mathematics and, consequently, meets the demand of modern biology for quantification, e.g. as in numerical taxonomy (Sokal & Sneath, 1963). Proceeding in this way one may establish a reasonable classification, but this does not necessarily yield groups united by relationship in a genealogical sense. Moreover, groups established in this way are "monophyletic" only in a sense that is not unequivocally defined. It was Hennig's (1950 and later) great contribution to recognize a logical and consequent way of phylogenetic research permitting clear-cut and reproducible decisions. Of his many thoughts at least one has been generally accepted: the superiority of synapomorphous over symplesiomorphous characters in judging relationship, i.e. for the reconstruction of the actual course of the evolutionary process. Hennig's arguments in favour of this procedure are well known and need not be repeated here; they have not seriously been contradicted. Hennig's conception of monophyly (Hennig, 1950: 307 *et seq.*; 1966: 207; 1969: 17; 1974: 283), however, has not found general agreement. Inasmuch as the first thought in his definition is concerned, there is little controversy: "Only groups of species that can ultimately be traced back to a common stem species can be called monophyletic'' (Hennig, 1966: 207). Similar definitions have been in use a long time, with one minor, though important, difference. The generally accepted use of the term monophyly was sketched by Simpson (1961: 124): ''Monophyly is the derivation of a taxon through one or more lineages . . . from one immediately ancestral taxon of the same or lower rank.'' Hennig defended his conception against this definition by pointing out that ''the device of bisexual reproduction makes the species the real unit. New species can arise only through the breakdown of individually existing species'' (Hennig, 1966: 207).

There has been much argument about the second part of Hennig's definition: ''. . . it must be added that not only must a monophyletic group contain species derived from a common stem species, but it must also include *all* species derived from this stem species'' (Hennig, 1966: 207). Acceptance of this postulate means that one has to break with familiar views about ''natural groupings'' as they appear to every unprejudiced observer. Reptilia, for example, cease to be a monophyletic taxon, whereas extremely dissimilar organisms, such as crocodiles and birds, are united in one taxon as Mayr (1975: 72–75) pointed out. Hence, the overwhelming majority of taxonomists disagreed with Hennig, i.e. all those who concentrated on the degree of divergence and not the stem group. Their sticking to a definition of monophyly excluding the demand for all species derived from the stem species being included was criticized by Hennig (1974: 283) with the simple, but irrefutible comment (translated): ''Each pair of whatever species has a common ancestor. Following this criterion one may establish arbitrary grouping. It is only the postulate that animal species must have an ancestor common only to them in order to be members of a monophyletic group that makes definition clear and workable.''

Actually, Hennig's conception has the advantage of being logical and allowing objective and reproducible conclusions and statements on phylogenetic relationships. It avoids decisions about the degree of overall similarity or dissimilarity which, in my opinion, must always be subjective because there will never be general agreement about which yardstick has to be used. Even mathematical methods will not be able to help in this respect, as drastic differences result depending on which method of computation is employed using identical data (according to Mayr, 1975: 187).

The decision between (1) the logically consequent concept held by the ''cladists'' as Mayr calls them and based on a biological theory and (2) the ''evolutionists''' conception of monophyly, taking into account the ''dual nature of evolutionary change,'' but up to now based on no clear theory, is perhaps a matter of confession. For the analysis of relationship between taxa dealt with here I accept Hennig's principle and his definition of monophyly, although I acknowledge that there are some weaknesses in his works as, for example, the ''deviation rule.'' Concerning the deviation rule Hennig himself (in Schlee, 1971: 28) more recently explained how his thoughts should be understood. He did not refuse Schlee's (1971: 27) remark, that this rule contributes to mastering a merely semantic problem.

Plesiomorphy and Apomorphy

''Recognition that species or species groups with common apomorphous characters form a monophyletic group rests on the assumption that these characters were taken over from a stem species that only they share in common, and which already possessed these characters prior to the first cleavage'' (Hennig, 1966: 90). What criteria can be used to distinguish between plesiomorphous and apomorphous characters? (1) Apomorphous characters by definition appear later in geological time, i.e. in younger fossils, than plesiomorphous characters. (2) Plesiomorphous characters also occur in closely and distantly related taxa. Apomorphous characters are unique or rare and restricted to relatively small groups. (3) In groups with low vagility a character is probably apomorphous if it predominates in a restricted geographic area whereas taxa with the corresponding symplesiomorphous character have a wider distribution.

In the literature, a number of other criteria are offered, for example, in a paper dealing with relationships in advanced snakes (Marx & Rabb, 1972). In their work, the authors enumerate a total of 10 criteria for derivativeness. Several of them more or less repeat each other so that their number can be reduced. At least one of them, in my opinion, is open to circular reasoning, viz. ''Correlation of derived states. A character state is derived if its occurrence is positively correlat-

TABLE 7. Characters in genera of the *Planorbis*-tribe. From left to right in columns: supposed direction of evolutionary change in characters within the tribe. +—regularly occurring; (+)—rarely occurring.

	1 Kidney margins		2 Mantle pigmentat.		3 Prost. div. number		4 Prost. div. arrangement		5 Vas deferens		6 Shape of penis sheath		
	straight	undulate	diffuse	patchy	high	low	closely spaced	loose	narrow	wide	cylindr.	club-shape	cylindr. again
Planorbis	+		+		+[1]		+		+		+		
Anisus	+		+		+[2]		+		+			+	
Bathyomphalus	+		+		+[3]		+		+			+	
Gyraulus	+	(+)	+	(+)	(+)	+	+	(+)	+	(+)		+	(+)
Choanomphalus	?		?		?		?		+[4]			?	

	7 Penis tip thickening			8 Penis pore situated		9 Hollow penial stylet			10 Bursa copulatrix		11 Reticul. sculpt. (adult shell)	
	absent	present	reduced again	near tip	distant fr. tip	absent	present	"hob-nail"	elong.	inflated	absent	present
Planorbis	+			+		+			+	(+)	+	
Anisus		+		+			+		+		+	
Bathyomphalus		+		+			+		+		+	
Gyraulus		+	(+)	+	(+)		+	(+)	+	(+)	+	+
Choanomphalus		?		+[4]			+[4]		?		+	(+)

[1] 19–57, Meier-Brook, 1976c.
[2] 13–80, Hudec, 1967.
[3] 26–43, Meier-Brook, unpubl.
[4] Hubendick, 1954.

ed with derived states of other characters. Such correlation of derived states of different characters probably results from common genetic history of taxa" (Marx & Rabb, 1972: 5). One should at least add ". . . correlated with *undoubted* derived states of other characters."

Of the three criteria mentioned above, the one based on fossil records does not help much in our case. The only characters preserved in the fossil state are those of the shell, and as shown in these studies, almost all reliable characters in this group are hidden in the animal.

Concerning the second criterion, i.e. the distribution of characters in *Gyraulus* and in other genera of the same tribe, I refer to Table 7. A character common to all of them is the lack of pallial folds. This synapomorphy does not appear in the table.

Most of the unique character states confined to small groups within the *Planorbis*-tribe occur solely in *Gyraulus* but these are not even in the majority of species. The following character states are regarded as apomorphous: undulate kidney margins, a patchy mantle pigmentation, a loose and irregular arrangement of prostate diverticula, an extremely wide vas deferens, the penis pore lying remote from the penis tip, an inflated bursa copulatrix. As to the number of prostate diverticula (Table 7, column 3), this is a quantitative character that may be subject to repeated reduction. Reduction or disappearance of an organ is therefore considered by many authors to greatly lower its value for phylogenetic analyses. But diverticula numbers in the *Planorbis*-tribe are not so unstable that extreme reduction would lack any significance for relationship. For example, the two African *Gyraulus* species, *G. costulatus* and *G. connollyi,* which are very similar in other characters, have extremely reduced diverticula numbers. It is very improbable that reduction took place independently after branching of their common stem species. Most probably their stem species already had reproductive organs greatly reduced in size and complexity and, among others, expressed in very low diverticula numbers.

The problem arising with an interpretation of shell surface structure (Table 7, column 11) has been discussed above. The completely smooth surface in postlarval shells of all genera of the tribe except in some subgroups of *Gyraulus* and *Choanomphalus* is striking. All other Recent planorbid genera have a smooth shell as well. Only few exceptions occur (e.g. *Bulinus reticulatus* Mandahl-Barth, 1954).

Since spiral striation incidentally appears or reappears in various species there is no clear decision in what direction transformation took place. Consequently the question has been left open (Fig. 112, shaded squares between *G. albus* and *G. piscinarum*).

In another case (Table 7, column 6) a rare character is seemingly shared by *Planorbis* and subgroups of *Gyraulus.* There is strong evidence that the *cylindrical penis sheath* in *G. riparius, G. rossmaessleri,* and moreover less regularly in *G. crista* and *G. malayensis* had their origin in the club-shaped penis sheath typical of *Gyraulus, Anisus,* and *Bathyomphalus*: in *G. crista* and *G. malayensis,* transitions between shapes are frequently found. On the other hand, the cylindrical shape of the penis sheath in *Planorbis* (Meier-Brook, 1976c, figs. 1, 6a), corresponds to the shape found throughout all other tribes of the family (Hubendick, 1955).

The form of the *penis tip* shows the same phenomenon (Table 7, column 7). A distal thickening of the penis in groups of the *Planorbis*-tribe as described above is unique in the family. Its lack in *Planorbis* is consistent with the state common to all other planorbid tribes. Within the genus *Gyraulus* intermediary stages are observed (Figs. 52, 63) between presence (Figs. 45, 72, 78, 81) and absence of the thickening (Figs. 55, 58, 60, 91). This suggests that its absence in certain *Gyraulus* species is secondary.

A *penial stylet* (Table 7, column 9) is absent in *Planorbis.* It is absent in the vast majority of Planorbidae though not in all of them. Its presence in various planorbid groups suggests that the question be examined whether stylets more probably have a common origin or have developed independently. A tendency to sclerotize the penis tip is observed in one or the other group, according to Hubendick (1955) in *Polypylyis* (*Segmentina*-tribe), *Planorbula* and *Promenetus* (*Helisoma*-tribe) as well as in *Physastra* (*Physastra*-tribe). Comparison of structure shows that all these stylets are solid and evenly transient from the penis tissue, both in form and in consistency. A picture of the penis tip of a *Physastra* species demonstrates this (Fig. 108). Stylets have also been reported from quite different groups, as in sacoglossan Opisthobranchia, where, according to Gascoigne (1974), there is a variety of stylets serving for transfer of sperm, either by conducting it to the bursa

FIG. 108. Stylet in *Physastra* sp., L. Barracuta.

copulatrix or simply by hypodermic injection. None of these stylets has the exact characteristics of structure found in the four genera of the *Planorbis*-tribe listed in the table, i.e. the sharp delimitation against the penis tissue where it is, to a certain extent, movable like a door on a hinge. The broad base and the stylet itself consist of a rolled blade, leaving a tube inside and one proximal and one distal opening (Figs. 25 to 27). It is highly improbable that a stylet of such a complex construction has been formed more than once. Of all synapomorphies encountered in the tribe, the stylet is the one with the highest probability of being derived.

Probably two other genera with a sclerotized penis tip belong in the *Planorbis*-tribe: *Afrogyrus* Brown & Mandahl-Barth, 1973, and *Afrogyrorbis* Starobogatov, 1967. Pallial ridges are not mentioned; their lack would clearly place them here. The sclerotized tip of the penis in these two genera (Brown & Mandahl-Barth, 1973: fig. 4) is again so different that I conclude that it must have formed independently. An origin from a stem species that had the *Gyraulus* stylet is unthinkable. Let us assume that *Afrogyrus* and *Afrogyrorbis* belong in the *Planorbis*-tribe. Then they must have branched off somewhere between the stem species of the tribe (Fig. 107, basal circle) and the stem species of all *Planorbis* species.

The *hob-nail stylet* undoubtedly arose from the usual stylet by size reduction, associated with a narrowed penis sheath and penis, and a loss of the distal thickening of the latter. These reductions in size could be understood as a consequence of extreme size reduction of the whole animal as seen in the tiny species, *Gyraulus riparius* and *G. crista.* Accordingly, one might conclude that the origin of hob-nail stylets in these species took place independently, by convergent evolution, were there not a *Gyraulus* species with normal dimensions, i.e. *G. rossmaessleri,* which also has a hob-nail stylet. The fact that a species has these features although it could have maintained the normal penis, makes it likely that the following happened. Size reduction culminating in the evolution of *G. crista* and *G. riparius* took place independently (Fig. 111). So the hob-nail stylet came into being before such size reduction. Or, at least, hob-nail stylet formation was not an immediate consequence of an overall reduction in animal size.

Initially I hesitated to place *Gyraulus rossmaessleri* in the same subgenus as *G. riparius.* The reason was that conchologically *G. rossmaessleri* is so similar to *G. laevis* that paleontologists would find it difficult to tell them apart. On the other hand, there was the aberrant ♂ copulatory organ also shared by *G. riparius.* The undulate kidney also seemed to support the conchological decision. Later, when the undulate kidney was found to be present in *G. riparius* and *G. crista,* too, it became clear what had probably happened. The formation of prominent kidney septa took place when the parent species common to the subgenera *Torquis, Lamorbis,* and *Armiger* came into being. This parent species had the normal size of a *Gyraulus* and the normal rounded whorls. These shell characters are, therefore, symplesiomorphous to *G. rossmaessleri* and the subgenus *Torquis,* and are, thus, not suited to prove a close relationship between these. Moreover, abandonment of the closely and regularly arranged prostate diverticula, a process leading to the synapomorphy of the *Torquis* species, did not take place in *G. rossmaessleri.* Size reduction of the whole animal, including the shell plus flattening towards a peripheral angulation on the other hand, is a process occurring repeatedly in species in different parts of the world, so that its independent occurrence in *G. crista* and *G. riparius* is not too unlikely. The different types of angulation (=formation of an edge) in the two species (Figs. 56 and 59) support independent formation of edges.

It would be of great interest to see how other species of the genus that have drastically reduced their size have managed the problems of housing the penis in the ♂ copulatory organ. There are tiny snails—evidently members of the genus *Gyraulus*—in different parts of the world, e.g. *Planorbis singularis* Mousson on Samoa (1.6 mm in diameter), *Gyraulus terraesacrae* Rensch in central Java (2.2 mm in diameter) and a species in Australia (2.5 mm in diameter). The only character common to these is their small size, so that independent reduction of size is highly probable. Do they possess a narrowed penis sheath and a conical penis tip with a hob-nail stylet?

Regarding the Australian species, here called *G.* sp. 1, I could examine specimens from two samples recently provided by Dr. B. J. Smith, of Melbourne. My prediction that size reduction does not necessarily cause formation of a conical penis tip and a hob-nail stylet, proved true. The distal part of the penis has a distinct though slight thickening with the penis pore near its middle and a "miniature edition" of a stylet in the normal form. The space problem in the actually narrow penis sheath has evidently been solved by stretching in length: the distal thickening is proportionally longer than usual in the genus.

The *bursa copulatrix* is of an elongate form in most Planorbidae. Inflated bursae are much rarer than in the Lymnaeidae, for example. There is a reasonable explanation for differences in abundance of the inflated bursa. The body whorl in lymnaeid snails leaves sufficient space for increased volume of organs, whereas in planorbid snails it is simply too narrow. When whorls are not so much flattened one can indeed find a more rounded bursa, e.g. in *G. piscinarum* (Fig. 71) and the more or less globose snails of ancient lakes (Fig. 96, 100, 103). On the other hand, as seen in *G. ehrenbergi* (Fig. 74) increase of whorl height does not automatically lead to inflation of the bursa. And an extreme inflation, as in *G. eugyne* (Fig. 94), certainly goes far beyond what is plausible as a simple consequence of whorl height increase. When an external or functional causative agent for an extreme morphological change is not obvious, the value of an otherwise apparently insignificant character is raised.

Two of the character states considered apomorphous on the strength of rarity within the *Planorbis*-tribe require some comment. These are the undulate kidney margins and the patchy mantle pigmentation. These characters force us to reconsider the problem of irreversibility. The question has already been discussed in connection with reticulate sculpture.

As shown above the *undulate kidney margins* are caused by distinct septa protruding into the lumen of the tubular kidney. According to Baker (1945: 12) in the Planorbidae the "central tube . . . is regularly marked by internal septa which project into the lumen for a greater or less distance." This would mean that the presence of septa is the rule in this family, and thus their absence rendering margins straight is the derived state. Baker's remark could imply that the formation of septa in subgroups of *Gyraulus* is merely a reversal of a loss, which, from time to time, occurred during evolution. Baker's figures of kidneys from a great variety of planorbid genera (Baker, 1945, pls. 44–47) do not show any sign of transverse septa except in a *Gyraulus* (*G. circumstriatus* (Tryon) (which is a *Torquis* species, where it has been placed by other authors on a conchological basis)) and two species of *Helisoma.* In the latter case I am not even sure whether it is not an artifact caused by fixation. I myself have never observed distinct septa in any living planorbid snail except in the case detected during the present studies. Should real septa be discovered in other planorbid groups these will probably prove to be non-homologous to those described here. The undulate kidney margins in some *Gyraulus* species are justifiably called apomorphous.

A probable reversal in evolutionary change is seen in the patchy pattern of mantle pigmentation. It is the rule in Planorbidae as well as in other basommatophoran families and also in various prosobranch groups. The patchy pigment is probably ancestral. Since a pigment pattern is not a complex structure only a small step is necessary from a distinct pattern to diffuse pigmentation and back again. Nevertheless this step has not occurred as frequently as one might suspect. Otherwise, the two alternate states should be distributed at random. In Lymnaeidae we see two patterns. These are (1) a distinct pattern or (2) a more uniform pigmentation with small cutouts. These alternatives are usually clearly distributed and consistent within genera (genera have been generally retained by authors in spite of Hubendick's (1951) opinion), e.g. *Radix* and *Stagnicola*, respectively. The diffuse pigmentation of *Planorbis, Anisus, Bathyomphalus* and several *Gyraulus* species is at least so constant that it may be considered ancestral within the *Planorbis*-tribe. Accordingly the reappeared pattern is derived. This conclusion is supported by the geographic distribution of species with the patchy pigment pattern as it relates to the present systematic analysis of species. The patchy pigment pattern is missing in *Armiger, Lamorbis, Torquis, Choanomphalodes,* and *Carinogyraulus*. In the African subgenus *Caillaudia* the patchy pigment consists of a great number of unusually small spots, so that its independent derivation from diffuse pigmentation is not improbable. In the remaining species, tentatively united in a subgenus *Gyraulus* s. str. a patchy pigment pattern occurs only in N Europe, Asia and Indonesia. Of the two Australian species I have seen none[4] having mantle pigmentation at all, so that a decision is impossible. Whether the patchy pigment pattern occurs in the North American species is an important question that has not yet been examined. So far we may assume that reappearance of the patchy mantle pigmentation in *Gyraulus* has probably happened only once, in western Eurasia. From this point the first species with the patchy pattern spread and split up into a northern (*G. acronicus*) and a southern branch (the stem species of all species living in southwest, south, southeast and east Asia including Indonesia: *G. ehrenbergi, G. euphraticus* etc.) (Fig. 112). These two branches may have dispersed mainly in an easterly direction. While *G. acronicus* evidently did not evolve into isolated species, the southern stem species, on its way to the east, branched off several times. The latter process may have been favoured by the irregular shape of the continent south of the great mountain chain (Caucasus, Elburz, Hindukush, Himalaya). The many large peninsulas facilitated formation of peripheral isolates, of which Mayr (1963: 513) says: "... most peripheral isolates do *not* evolve into new species, but *when* a new species evolves, it is almost invariably from a peripheral isolate." This is likely to be the case in S Asiatic *Gyraulus*. Secondary contact of peripheral isolates with the parental populations proved that reproductive isolation had not been completely achieved and thus we see the races of *G. chinensis*. In a few cases isolation was complete enough, and sibling species of *G. chinensis* (*G. euphraticus, G. tokyoensis*), or morphologically more dissimilar species evolved (*G. malayensis* and the diverse species of Sumatra and New Guinea) (Rensch, 1934; van Benthem-Jutting, 1963).

In summary, the more important apomorphous characters in the *Planorbis*-tribe may be categorized as follows: (1) Characters of high frequency in the tribe (but absence or rarity in other tribes of Planorbidae and related families), e.g. the hollow penial stylet; the thickened penis tip; the club shaped penis sheath. (2) Characters of low frequency in the tribe as well as in the family and order, or of low frequency in the tribe and scattered occurrence in the higher taxa indicating reversal of evolutionary change, e.g. the undulate kidney margins, loosely and irregularly arranged prostate diverticula, the penis pore being remote from the penis tip, the extremely widened vas deferens, the patchy mantle pigmentation. (3) Quantitative characters that lie beyond the usual range of variation, e.g. an extremely low or high number of prostate diverticula, an extremely inflated bursa copulatrix, a constant and distinct reticulate sculpture in the adult shell.

Characters listed under (1) serve to define relationships between the subgroups of the *Planorbis*-tribe. Characters listed under (2) mainly contribute to defining subgroups of the genus *Gyraulus*, whereas the characters of category (3) predominantly (though not exclusively) are autapomorphies[5] of species.

The nearly complete restriction of the category (3) characters to autapomorphies in this study is fortuitous. Each apomorphous feature, when appearing for the first time, is autapomorphous in one species (Hennig, 1966: 90). When it is stable enough, as required, this feature becomes the synapomorphy of

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[4] After completion of the manuscript I found the patchy pattern in *G. essingtonensis* (Smith) from the Kimberley region, West Australia (J. Walker legit 1979).

[5] An autapomorphy is a derived character state confined to one individual taxon. A synapomorphy is a derived character connecting two or more taxa.

all succeeding species. The extremely lowered number of prostate diverticula in the two (or more?) species of the genus *Caillaudia* is one example. Even genera can be established from quantitative characters alone, as will be substantiated in the next chapter. In any case the point is: what is the probability of having the character *because* the common stem species had it? The probability should be high.

Cladograms

In his ''scheme of argumentation of phylogenetic systematics'' Hennig (1966, fig. 22; 1969, fig. 2) establishes a phylogeny by working backwards from the synapomorphous character states seen in recent taxa to the character states in stem taxa. The procedure consists of three steps. (1) Collect information on all characters that occur in more than one state in a group. (2) Decide what state is plesiomorphous and what is apomorphous. (3) Arrange species (or higher taxa) so that every two or more species lie together if they share apomorphous character states (Hennig, 1966, fig. 22). A result of proceeding this way is a picture of the sequence of changes of character states (''transformation of characters'' in Hennig, 1966). In the cladograms (Figs. 106, 107, 111) squares indicate pairs of character states in the positions resulting from Hennigian arguments. White squares indicate the plesiomorphous state, black squares the apomorphous character state. All Recent species branching off one trunk carry the total number of character states (squares) indicated on the lines leading to them in the cladograms. In some cases where the direction of character transformation is not clear, squares are shaded. If two characters are uncorrelated, transformations of states are depicted by two pairs of squares, e.g. Fig. 106, transformation of pluricuspid to unicuspid radula teeth and of uniserial to multiserial prostate diverticula. When two apomorphous character states are probably linked, there is only one pair of squares, e.g. Fig. 107, transformation of thickened to conical penis tip and of the standard stylet to hob-nail stylet during evolution of the stem species of *Armiger* and *Lamorbis*.

It is evident that transformations of character states could only have happened in a sequence as shown in Figs. 106, 107, 111. One exception is made, i.e. when multiple new character states appear in the same stem species it is impossible to tell in what sequence. But finding the sequence of transformation events between two branching points is irrelevant for relationship research.

The sequence of transformations determined in a branch does not necessarily indicate absolute points of time that can be compared with those in a neighbouring branch. This can only be found in palaeontological studies. Hence the ordinate in Figs. 106, 107, 111, and 112 does not provide absolute measures; it indicates only the relative sequence within each single branch.

Hennig's method of phylogenetic reasoning does not involve measures of divergence or overall similarity. The positioning of taxa in a cladogram has no meaning as regards closeness of relationship. Each two branches originating from the same stem species can be exchanged, and the direction of arrows in the cladogram is accordingly random. In order not to express degrees of similarity, Recent taxa are shown at equal distances.

Subgroups in the *Planorbis* Tribe and in the Genus *Gyraulus*

To determine if *Gyraulus* is monophyletic (sensu Hennig) one must study its closest relatives. The *Planorbis*-tribe is unquestionably a monophyletic taxon. The synapomorphies of its species are the lack of the three pallial ridges present in the other Planorbidae, short marginal radula teeth, and the presence of a separate prostate duct.

The hollow penial stylet is a distinct synapomorphy characterizing the majority of tribe members (Fig. 107). Other synapomorphies, not shown in the cladogram, due to lack of space, are the club-shaped penis sheath and the thickened penis tip. There is a limited number of species living in Europe and west Asia that share a character state belonging in the third category of apomorphies listed above i.e. extreme elongation of the body. This is not unique in the family. There are species similar in external appearance in South America, but remotely related to the *Planorbis*-tribe, namely *Drepanotrema* species. Besides some *Drepanotrema* species and those of *Anisus* and *Bathyomphalus* there are, as far as I know, no other planorbid groups with an extremely elongated body.

Although convergent changes to an elongated body in species from South America and Eurasia is proved, there is no evidence of a selective value for this character state

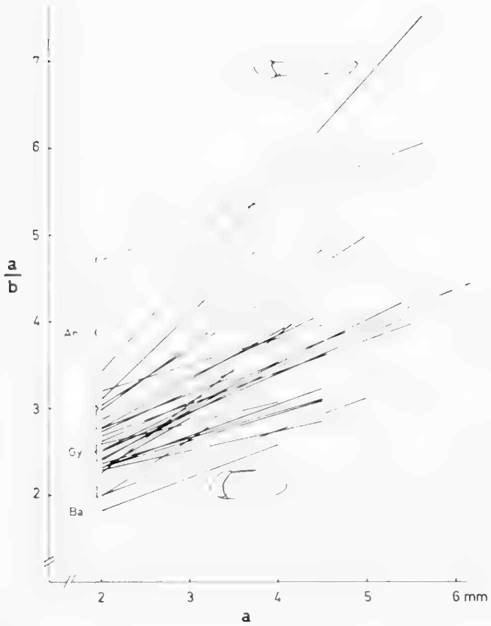

FIG. 109. "Flatness indices" in *Gyraulus* (Gy) and related genera, *Anisus* (An = 2 × *vortex*, 1 × *spirorbis*, 2 × *leucostomus*) and *Bathyomphalus contortus* (Ba).

that could explain the convergence. If elongation and slenderness had a selective value, convolution of such an animal would, in my opinion, invalidate any advantage. On the basis of similarity of relative body length I conclude that this transformation happened only once in the *Planorbis*-tribe. In the next clade one daughter species retained its roundish body cross section while the other became flattened laterally, yielding an unusually thick snail with a relatively low diameter, namely *Bathyomphalus* (Fig. 109, Ba). The daughter species with the plesiomorphous body form then divided once more resulting in the stem species of the two (three?) Recent species of the subgenus *Anisus* s. str. and that of the species *Anisus vortex* and *A. vorticulus* (sg. *Disculifer* C. Boettger). In the latter subgenus whorls are flattened as well but perpendicular to the direction seen in *Bathyomphalus*. Referring to the "flatness-index," all of the four (five?) *Anisus* species lie beyond the range of variation in *Gyraulus* (Fig. 109, An).

The width of the last whorl as a percentage of the total diameter is a good parameter to illustrate differences. Fig. 110 shows a broad gap between *Bathyomphalus* plus *Anisus* and *Gyraulus*. Class frequencies are distributed not only bimodally but also without contact or overlapping. The genus *Planorbis* is not inserted in the figure to avoid confusion. *Planorbis* lies well within the range of *Gyraulus* species with 27% (*Planorbis planorbis*), 28% (*P. intermixtus*) and 33% (*P. carinatus*).

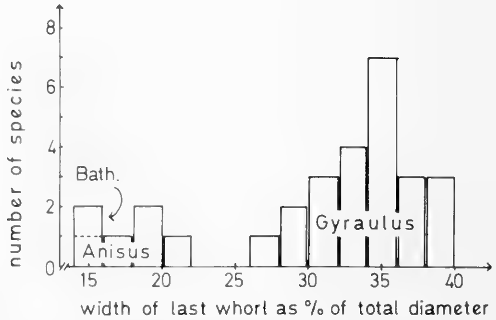

FIG. 110. Relations between whorl width and snail diameter in the stylet-bearing genera of the *Planorbis*-tribe.

I see no objection to conceiving the whole group of stylet-bearers as one genus, *Anisus*, as has been done by some authors. The group is clearly a monophyletic taxon. On the other hand, the gap (Fig. 110) separating *Gyraulus* and *Anisus/Bathyomphalus* justifies acceptance, at least of *Gyraulus*, as a separate genus (Mayr, 1969: 233). If *Gyraulus* has monophyletic status I prefer to leave it at the rank of a genus as most authors have done. A practical reason is the following. Indication of "*Gyraulus* sp." in publications provides much more information than "*Anisus* sp." or even "*Planorbis* sp."

Finding an apomorphy that is shared by all *Gyraulus* species but not by *Anisus* and *Bathyomphalus* would help to clearly state the monophyletic character of *Gyraulus*. Such an apomorphy would prove that *Anisus* and *Bathyomphalus* must have branched off the common trunk before the stem species of *Gyraulus* existed. One character state that should be synapomorphous to all *Gyraulus* species has not entered the cladogram (Fig. 107), because I am not sure enough about its reliability, but it should at least be considered. Two of the three *Planorbis* species have an angle or keel that is quite close to the upper side of the shell. This side is more or less plane, the whorls being flattened. The *Anisus* species have this flattened upper side as well;

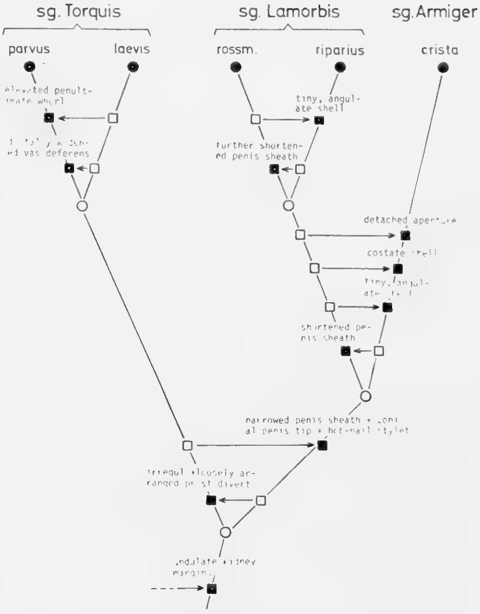

FIG. 111. The probable kinship relations in the *Gyraulus* species bearing undulate kidney margins.

moreover they have an angle or keel at exactly the same place as *Planorbis* (except *A. vorticulus* that is so extremely flattened that the angle appears to be in the middle). Thus the asymmetric shell seems to be plesiomorphous. Whenever a *Gyraulus* forms an angle or keel, this is situated symmetrically in the middle of the shell. Even in multicarinate species of old lakes, where additional angles or keels may appear near the under and upper side, their position is always different from that in *Planorbis* and *Anisus,* because the upper side is not plane, but marginally convex and centrally deeply concave (Figs. 99, 102). If one were able to accept this central angulation or carination or at least a tendency to form it as an apomorphy, there would be no question that *Gyraulus* is a monophyletic group in Hennig's sense, even when *Anisus* and *Bathyomphalus* are regarded as separate genera.

Summarizing the above discussions, according to the concept of so-called evolutionists (a higher taxon is an aggregate of related species separated from others by a discontinuity; Mayr, 1969: 88) there would be no doubt that *Gyraulus, Anisus* and *Bathyomphalus* are well separated genera. The strict monophyly concept of Hennig postulates synapomorphies uniting taxa to monophyletic higher taxa: "The possession of plesiomorphous characters (symplesiomorphy) does not justify the conclusion that the bearers of these characters form a monophyletic group" (Hennig, 1966: 90). The proof could perhaps be the central angulation or carination or a tendency towards this formation, if this can be accepted as a synapomorphy of *Gyraulus* species. If this character is not accepted as a synapomorphy (because there are *Gyraulus* groups constantly lacking an angled shell periphery), this would of course not be evidence against the monophyletic status of *Gyraulus.* A lack of synapomorphies merely means that proof of monophyly cannot be furnished.

Proceeding on the assumption that *Gyraulus* is in fact a monophyletic group, the further progress of evolution in most lines appears to be conclusive on the basis of synapomorphies discussed above (Fig. 107). Several of the probable evolutionary events have been presented in the remarks following descriptions of individual species. One problematic group, however, is left, i.e. the group of *Gyraulus* species placed in the provisional subgenus *Gyraulus* s. str. Again, the monophyly of this group cannot be proved. Its pathway is marked by nothing but plesiomorphous character states. Following this pathway it is evident that in one lineage there is the group acquiring an undulate kidney (*Armiger, Lamorbis, Torquis*; Figs. 107, 111). After another branching a drastic reduction in volume and complexity of almost all reproductive organs occurred, i.e. in *Caillaudia.* The peculiar ancient lake species with distinct synapomorphies (*Carinogyraulus*) or an autapomorphy (*Choanomphalodes*) originated in two other such lineages. Consequently, the group called *Gyraulus* s. str. is a remnant group. The subgenus formation, shown in Fig. 107, namely *Carinogyraulus* and then *Choanomphalodes* and *Gyraulus,* could thus also have taken place in a different sequence. The sequence shown in Fig. 107 is, however, most likely from a geographical standpoint.

The ancestral stem species of Recent *Gyraulus* spread over wide parts of Laurasia after the stylet-bearing species diverged into two sister lineages, one producing elongated animals, the other keeping its normal body proportions (or perhaps producing the apomorphy of a central angle or keel). In the west part of Laurasia an organism evolved undulating kidney margins, i.e. the stem species of Recent *Armiger, Lamorbis,* and *Torquis.* In the marginal southern zone of Laurasia a species branched off forming the stem species of *Caillaudia* with small and simple reproductive organs. In or near the present Ohrid basin a lineage appeared with thick-shelled and multicarinate snails reducing their radula cusps, i.e. the stem species of Recent *Carinogyraulus.* In Japan, finally, the stem species of *Choanomphalodes* branched off. What remained was *Gyraulus* s. str. retaining the plesiomorphous character states corresponding to the apomorphies mentioned above.

When Hennig's principle is applied the problem arises again and again that some species remain that carry only autapomorphies and are connected only by symplesiomorphies. "That a common stem form is shared by a group of species (a condition for a "monophyletic group" . . .) can be proved only by means of synapomorphous characters, not with symplesiomorphous characters" (Hennig, 1966: 90). *Gyraulus* s. str. therefore is considered here only a provisional subgenus. There is one reason why *Gyraulus* s. str. has probably to be considered even a "paraphyletic" group. The paraphyletic groups "have no ancestor in common only to them, and thus also no point of origin in time common only to them in the true historical course of phylogeny" (Hennig, 1966: 146–147). *Gyraulus* s. str. could be monophyletic (sensu Hennig) in two cases, namely (1) if *Carinogyraulus* and *Choanomphalodes* had a synapomorphy and, together, formed the sister group of the remaining *Gyraulus* species, or (2) if both *Carinogyraulus* and *Choanomphalodes* had split off from one and the same ancestor species. Concerning case (1), the derived character states in *Carinogyraulus* and *Choanomphalodes* turned out to have formed by convergence very probably. They are not sister groups. Concerning case (2), regarding the long distance from Europe to Japan it is probable that the species migrating eastward split into several lineages. The stem species of *Choanomphalodes* would then be not the same as the stem species of *Carinogyraulus.* These are the problems as regards the monophyletic status of a subgenus *Gyraulus* s. str. in a cladistic analysis according to Hennig. In contrast, the "evolutionists" and the numerical taxonomists accept paraphyletic groups (sensu Hennig) as monophyletic groups in their sense. Basing their taxa on morphological similarity and separating their taxa on morphological divergence they would not face troubles in conferring monophyletic status to a subgenus *Gyraulus* s. str. as characterized in my study.

Within my provisional subgenus *Gyraulus* s. str. a monophyletic subgroup can be distinguished, namely the group of species with the synapomorphy "patchy mantle pigmentation" (Fig. 112, the seven species from the right). The two species carrying the plesiomorphous character state "diffuse mantle pigmentation," however, form the remnant group in this case, i.e. *G. albus* and the Near East species *G. piscinarum.* (A species with diffuse mantle pigmentation was, by the way, collected by Dr. H. Schütt in Turkey recently. It will have to be described as a new species showing that the remnant group consists of more than *G. albus* and *G. piscinarum.*) Should this group prove to be monophyletic it would have to bear the subgenus name *Gyraulus* s. str., whereas the group with the synapomorphy "patchy mantle pigmentation" would have to be in a new subgenus. For the time being, I prefer to wait for opportunities to examine more material from southwest, south and east Asia, hoping especially that samples from the Near East and North America will yield further insights. Only then will it be time to draw further conclusions about the remnant group. Finally the question must be asked: why not leave *Armiger* in genus rank? Mayr's (1974b) call that divergent evolution be considered in the reconstruction of dendrograms would favor a genus *Armiger.* Hennig replying to Mayr emphasized what he had explained in detail in previous works (among others Hennig, 1950: 308, and 1969: 17–20): "In reality there is a categorial difference between the monophyletic groups . . . , possessing a stem species common *only to them,* and the non-monophyletic (paraphyletic and polyphyletic) groupings whose components also possess a stem species common to them but *not only to them*" (Hennig, 1974: 284, translated). Consequently raising *Armiger* to generic rank, although it has synapomorphous characters in common with the *Gyraulus* subgenera *Torquis* and *Lamorbis,* would mean that the genus *Gyraulus* would cease to be a monophyletic taxon in Hennig's sense. It would mean that *Gyraulus* in this case becomes a paraphyletic taxon. The distinction between paraphyletic and polyphyletic groupings, on the

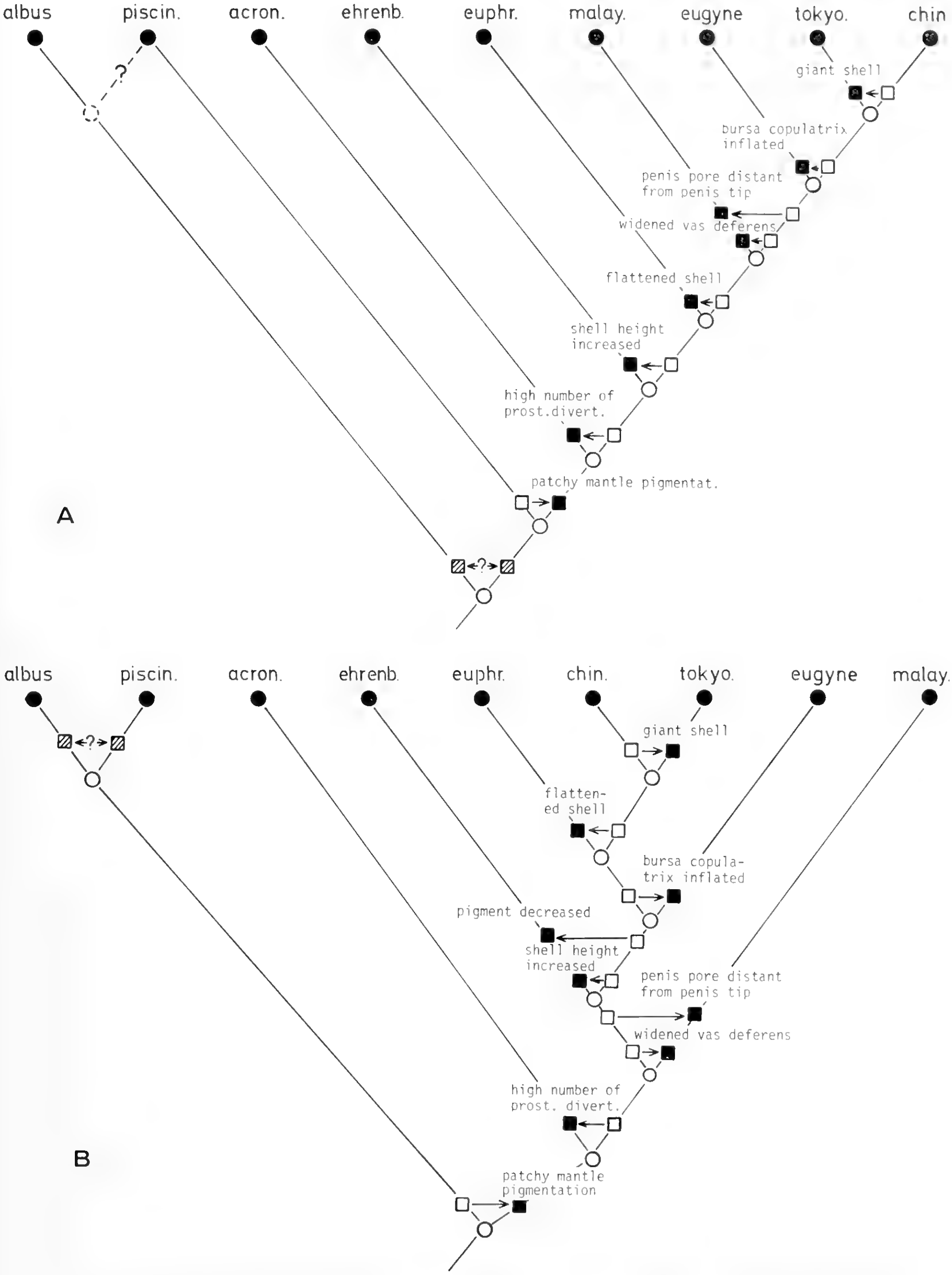

FIG. 112. Two of the several possible kinship relations in the provisional subgenus *Gyraulus* s. str.

other hand, is only a methodological one and does not mean fundamental differences in genealogical relations, as has been demonstrated by Hennig (1969: 19; 1974: 284). As to the former genus name *Armiger,* there is no objection against its use as a subgenus. As illustrated in the dendrogram (Fig. 107) there is good reason to accept *Armiger* as the sister subgenus of *Lamorbis.*

Hennig (1966: 154) advanced the demand "that objects to which the same label is given must be comparable in some way" against the arbitrary treatment of ranking generally performed in the literature. Seeing the enormous difficulties in applying this principle to groups as different as annelids and mammals one will welcome his confinement to the demand that at least "sister groups must have the same rank" (Hennig, 1966: 159). This is reasonable and feasible. In practice, however, when interpreting Fig. 107, problems arise. The cladogram shows *Lamorbis* and *Armiger* as subgenera; they are sister groups. Together they form a group whose sister group is named *Torquis.* Thus *Torquis* does not rank at the same level as *Armiger.* It is desirable not to suppress the independence of the monophyletic group *Torquis* being expressed. Consequently *Torquis* could be raised to generic rank. Its sister group would be a genus "*Armiger* s.l." The two genera "*Armiger* s.l." and *Torquis* would perhaps present a group intermediate between a genus and a tribe. The sister group of this genus group would be the one comprising the groups named *Caillaudia* etc. through *Carinogyraulus.* In this group there would be a genus *Caillaudia,* whose sister genus would comprise the groups named *Choanomphalodes,* "*Gyraulus* s. str.," and *Carinogyraulus.* The next lower taxon not necessarily carrying a category name would be the group consisting of *Choanomphalodes* and "*Gyraulus* s. str." whose sister group is *Carinogyraulus.* If one sees a need for retaining the subgenera *Choanomphalodes* and "*Gyraulus* s. str.," *Carinogyraulus* could no longer stay at subgeneric rank because it does not hold the same level as e.g. *Choanomphalodes.* It would, strictly speaking, have a lower rank than generic and a higher one than subgeneric. This would, however, not contradict speaking of an unnamed category with a single subgenus, which has to carry the name *Carinogyraulus.* As ranking in one group is not dependent on how often branching occurred in its sister group, one must do what has unexpressedly been done by systematists since long ago: (1) acknowledge a series of hierarchical intermediate categories (as many as branchings maximally occur), which may be named or unnamed; (2) in branches that have not split up as frequently as their sister branches insert an assumed additional "stem species" at the same level where in the sister group a branching point occurs. When doing so the difficulty seen above is easily solved: *Armiger* and *Lamorbis* are subgenera, together forming a taxon higher by one level, say "taxon of order Y." *Torquis* is a subgenus and that the only one of the sister "taxon of order Y." The three subgenera form a "taxon of order X," which, together with its sister "taxon of order X," forms the genus *Gyraulus.* Proceeding in this way, one avoids contradictions arising from strict consequences of applying Hennig's quite justified rule for equal ranking of sister groups. This is the procedure usual in handling monotypic taxa.

Absolute Age of Subgenera

The question as to how old the subgenera are arises because Hennig (1950: 255–261) had postulated that the absolute age of origin of a taxon should determine its rank. In the meantime manifold criticism apparently led him to abandon this concept or at least to mitigate it: ". . . phylogenetic systematics must be content with a much coarser time scale for its correlations" (Hennig, 1966: 183).

Determination of fossil snails should, of course, only be relied on when shells are characteristic enough to preclude errors. As confusion of many snail groups (*Planorbis, Afrogyrus, Promenetus,* and others) in Recent material demonstrates, a safe identification of *Gyraulus* in fossil samples seems to be impossible. This may explain fossil records of "*Gyraulus* s. str." from as early as the "Jurassic, ? Upper Cretaceous, Paleocene" (Zilch, 1960: 110). At least the two Mesozoic references are presumably erroneous. Subgenera that can more reliably be determined have been indicated from the Pleistocene (*Caillaudia*), Pliocene (*Carinogyraulus*), and Miocene (*Armiger*). Zilch (1960: 111) moreover records *Torquis* from the Miocene, but *Torquis* is often misidentified (confused with small *Planorbis*), even in Recent samples, as shown above.

Given current information on sea-floor-spreading (Scrutton, 1976; Thenius, 1977:

99), the disintegration of Laurasia into Palaearctic and Nearctic became complete in the Eocene. Accordingly, the ancestors of the European and American *Torquis* have lived in the Eocene at the latest. A migration, e.g. during the Pleistocene, via the Bering-bridge is highly improbable because there is no evidence that *Torquis* ever lived in Central and NE Asia.

As in the preceding case snails from other tribes are sometimes misidentified as *Planorbis,* because *Planorbis* has the plesiomorphous shell form that is shared by many other Planorbidae. According to Zilch (1960: 108) the oldest record for *Planorbis* is from the Upper Oligocene. Other close relatives of *Gyraulus* were recorded from Miocene (*Bathyomphalus*), Upper Miocene (subgenus *Anisus* s. str.) and Upper Pliocene (subgenus *Disculifer*). In view of the scattered nature of palaeontological data there is, at least for the time being, no chance of tracing the successive origin of taxa in geological time.

Speciation in *Gyraulus*

The probable course of speciation in the Ohrid basin group and in the group having the "undulate kidney margin" was previously discussed. The genus *Lamorbis* appears to consist of only two species, *Gyraulus rossmaessleri* and *G. riparius.* North America has many *Gyraulus* species not examined by me, but Baker (1945, pl. 15–19) figured the reproductive organs of most of them, and there is no evidence that any one of them has the features of the ♂ copulatory organ peculiar to *Lamorbis.*

The situation is apparently different in the subgenus *Torquis.* There is at least one more species in North America. Of the two sibling species, *Gyraulus parvus* and *G. laevis,* the North American one (*G. parvus*) has a wide distribution and a wide ecological range while the vicariant species in Europe (*G. laevis*) has a limited distribution and a narrow ecological range. A hypothetical explanation for such a difference could be the following. The common stem species of *G. parvus* and *G. laevis* was widely distributed in the now North American portion of Laurasia, where it was adapted to a wide range of habitats. A small peripheral section of the population split off and became reproductively isolated (either before or after complete separation of North America and Europe). This isolate spread over parts of Europe and invaded a limited number of habitat types, and that either (1) because of its restricted gene pool as compared with the large remaining population of their stem species or (2) because it found the majority of suitable ecological niches occupied already, perhaps by other *Gyraulus* species. Both factors may have contributed.

The phenomenon of pairs of vicariant subspecies or species strikingly different in distribution and environmental requirements is not rare. Hennig (1966: 59) quotes the situation in insects where cases are commonly encountered "in which, in addition to a common widely distributed euryoekous species, there is a second species that is very little different, less widely distributed and stenoekous." This is exactly the situation in the pair *Gyraulus parvus* and *G. laevis.*

Unlike the species of the subgenera *Torquis, Lamorbis* and *Armiger,* most species of *Gyraulus* s. str. lack distinct apomorphies. In this group at least two species have maintained the diffuse mantle pigmentation, *G. albus* (Europe, W Asia) and *G. piscinarum* (SW Asia). *G. albus* has distinct reticulate sculpture, *G. piscinarum* does not. It is not yet possible to decide which of these characters is more derived. All species of the Asiatic continent have patchy mantle pigmentation. I regard this to be their synapomorphy. Unfortunately all other apomorphies hitherto observed in the group are autapomorphies of species. The problematic situation for the phylogeneticist who deals with a group having only symplesiomorphies and species-autapomorphies can be well demonstrated with this group (Fig. 112). The sequence of evolutionary changes cannot be determined from morphology, and theoretically none of the n! (where n is the number of species with nothing but symplesiomorphies and autapomorphies) possibilities (5040 different sequences in our case, where n = 7) would have a higher probability than the other ones. My assumption is that a species most probably living in Europe or W Asia once developed patchy mantle pigmentation. This assumption increases the probability that the first splitting led to a northern branch, which did not split any more (at least not into reproductive isolates), i.e. *G. acronicus,* and a southern branch. We may thus assume that *G. acronicus* had its origin near the base of the tree of patchily pigmented species, as depicted in Fig. 112. The remaining six species could have arisen, theoretically, via 720 alternatives of sequences, two of which are represented as Fig. 112A and B.

If my assumption is correct that the stem species of the southern branch spread to S Asia from W to E, two main alternative modes of further speciation are conceivable. (1) During dispersal in an easterly direction the southern branch split up several times leaving behind a series of species with limited distribution: *Gyraulus ehrenbergi, G. euphraticus, G. malayensis,* etc. (as shown in Fig. 112A, or something similar). This sequence would be consistent with the observation that "speciation apparently always goes parallel with a progression in space" (Hennig, 1966: 134). (2) Initially the southern branch spread into a vast area, as seen presently, and in the course of time peripheral isolates arose as has been shown for many animal groups, e.g. the tree snake *Dendrophis pictus,* the sandfly *Phlebotomus papatasii* (Hennig, 1966: figs. 16–17), and several groups of birds (Mayr, 1963: 496). It is unimportant whether the peripheral isolates are "only" subspecies or "already" reproductively isolated communities. If the stem species of all Asiatic *Gyraulus* at first spread from W to E Asia, we cannot even say whether an eastern isolate arose before a western, and the sequence may be completely random (Fig. 112B). At any rate it is obvious that the widespread species (the Rassenkreis or polytypic species *G. chinensis*) has maintained the most plesiomorphous characters and, thus, has diverged from its stem species to a lesser degree than the other S Asiatic species.

Reflexion about the first alternative, i.e. splitting of several species during easterly dispersal, brings us again to a discussion of the deviation rule. Hennig established it by stating: A species ceases to exist as a species when it breaks up into two species by partial ending of tokogenetic relations between its individuals" (Hennig, 1950: 102, translated). This rule has meantimes been heavily attacked by other taxonomists (among others Mayr, 1974b). In 1966, Hennig largely withdrew from this formulation, but he was still speaking of the "deviation rule, which is derived from the similarity distribution within species groups and which says when a species splits, one of the daughter species tends to deviate more strongly than the other from the common stem species (or from the common original condition)" (Hennig, 1966: 207). This is self-evident, and nobody has ever believed that two daughter species would deviate to an exactly equal degree from their stem species! But Hennig sticks to a change of *both* daughter species in any case. There is one fact that makes it impossible to disprove Hennig's deviation rule. Our most objective species concept, the biospecies concept, can only be applied to contemporary organisms, not to organisms from different geological periods, as Hennig's disciple, Schlee, points out: "Concerning the species definition of the remaining population there is an uncertainty whether it is really identical—in a very strict sense—with the original population of the stem species. Species identity or unidentity, however, cannot be proved, because a biological species definition as a potential reproductive community is valid only for a point of time (temporal cross-section) and populations of successive times are, naturally, not open to crossing experiments" (Schlee, 1971: 28–29, translated).

The question whether a stem species can continue to exist, although new species have split off, is answered by Hennig as follows: "Stem species, from which two or more recent species have arisen (by whatever type of speciation), do not occur in the hierarchic system of recent species. They can be provided only by paleontology" (Hennig, 1966: 64). I do not concur because I consider *Gyraulus chinensis* as the continuously existing stem species of *G. ehrenbergi, G. euphraticus, G. malayensis,* etc. (Fig. 112). According to Hennig's deviation rule the stem species A of the S Asiatic *Gyraulus* species would have split at first into, let us say, *G. ehrenbergi* and a different new stem species A1. In a second cleavage the two species *G. euphraticus* and A2 would have appeared. Thus, in the five or more splitting processes the former stem species A would have changed five or more times. If unrestricted fertility between *Gyraulus* from Afghanistan and Korea should prove true, the existence of a biospecies *G. chinensis* would be clear. This would disprove the justification of Hennig's deviation rule, unless one assumes that the product of the latest splitting, A5 (or A6 or so) is the Recent species *G. chinensis. G. chinensis* then would have had to spread back from E Asia to W Asia covering the vast area now inhabited, which appears extremely improbable.

Would Hennig have voided the "rule" in our case? Probably not. Rather, he would warn us not to mix biological and genealogical systems (Hennig in Schlee, 1971: 28). In my opinion, this is the point where dialectics begin.

Schlee apparently has a more realistic view of the situation at the species level such as in the *Gyraulus* group, saying "In monophyletic groups containing a taxon that is characterized by nothing but plesiomorphies, this taxon can be the stem species" (Schlee, 1971: 34, translated). This obviously applies to our *G. chinensis* and the group of its probable descendants. And this perhaps applies even to the relation between *Gyraulus albus* or *G. piscinarum* and the whole genus. (That *G. albus* has been designated type-species of the genus and is probably the species with the greatest similarity to the stem species of the genus, is, of course, a mere coincidence!)

Briefly returning to our alternatives of evolutionary processes in the S Asiatic region, one should see that there is fundamentally the same incompatibility of biological reality and the consequence of Hennig's deviation rule. A series of peripheral isolates would have to be graphically represented in the same way, for example like that in Fig. 112B. It would likewise raise the question: why should the stem species of the marginal new species have ceased to exist?

DISTRIBUTION AND CHOROLOGICAL ASPECTS

A combination of morphological and distributional features has long been used in phylogenetic arguments. The geographical implications in taxonomic research climax in the books of Rensch, particularly in his opus founding the "Rassenkreislehre" (1929). Our knowledge has recently been summarized in Hennig's (1966: 133) sentence: "Every species originally occupies a certain area, and the breaking up of a species into several reproductive communities usually, if not always, is closely related to the dispersal of the species in space." I will first discuss the distribution of Eurasiatic species of *Gyraulus,* as far as it is known, and of the species of the closely related genera.

The distribution maps (Fig. 113A–C) clearly indicate that the genera related to *Gyraulus* are restricted to the Palaearctic. The species of the genera *Planorbis* and *Anisus* primarily inhabit Europe; they only marginally extend into the central areas of Asia. The only species reaching as far as the Pacific coast is *Bathyomphalus contortus* (Linnaeus). They all have in common a southern limit in the Mediterranean region, Turkey or the Black Sea, the Caucasus or Transcaucasia, the regions of the Caspian and Aral Seas and a line roughly crossing Kazakhstan and Mongolia. Fossil records remote from the Recent distribution areas have become known in *Planorbis planorbis* (Linnaeus), viz. from the Sudan and Ethiopia (Brown, 1965: 67). *Planorbis* species not mapped here are *P. presbensis* Sturany and *P. macedonicus* Sturany, both endemic to two Macedonian ancient lakes, and the group of *P. atticus* Bourguignat and *P. intermixtus* Mousson which live in the circummediterranean countries, eastward to Iran. They are probably not separate from each other (Meier-Brook, 1976c) but well isolated from *P. planorbis,* with which they share great parts of their geographical ranges.

As more or less all Planorbidae were once included in the genus "*Planorbis*" there was also a time when a great heterogeneous group of Planorbidae was named "*Anisus.*" It might, therefore, appear as if I had not included the entire group of *Anisus* in the maps. Bollinger (1914) described an endemic species, *Planorbis sarasinorum,* from Lake Lindoe, Celebes, for example, which later usually was called "*Anisus*" *sarasinorum.* Its shell does not show any similarity with real *Anisus* species. The few whorls increase very rapidly, even more than usual for *Gyraulus.* Its aperture is trumpet-like. A sharp angle with a keel is situated in the middle of the periphery (material studied in ZMA). Moreover, Hubendick (1955) found a big gland in the preputium, which has not been found in any member of the *Planorbis*-tribe. Unfortunately I cannot discern from his semi-schematic figures the nature of the stylet. As has been shown above, formation of stylets has occurred independently in several groups of the family. It is highly improbable that "*Planorbis*" or "*Anisus*" *sarasinorum* is closely related to any *Anisus* species. Another question which cannot be answered is whether "*Anisus*" *sarasinorum* could have originated in the genus *Gyraulus.*

Another species recently referred to the genus *Anisus* is "*A.*" *pauxillus* van Benthem-Jutting, 1963. This tiny snail from New Guinea, which its author classified in *Anisus* "only tentatively, because no soft parts are available," indeed has less rapidly increasing whorls than does Indonesian *Gyraulus* but still

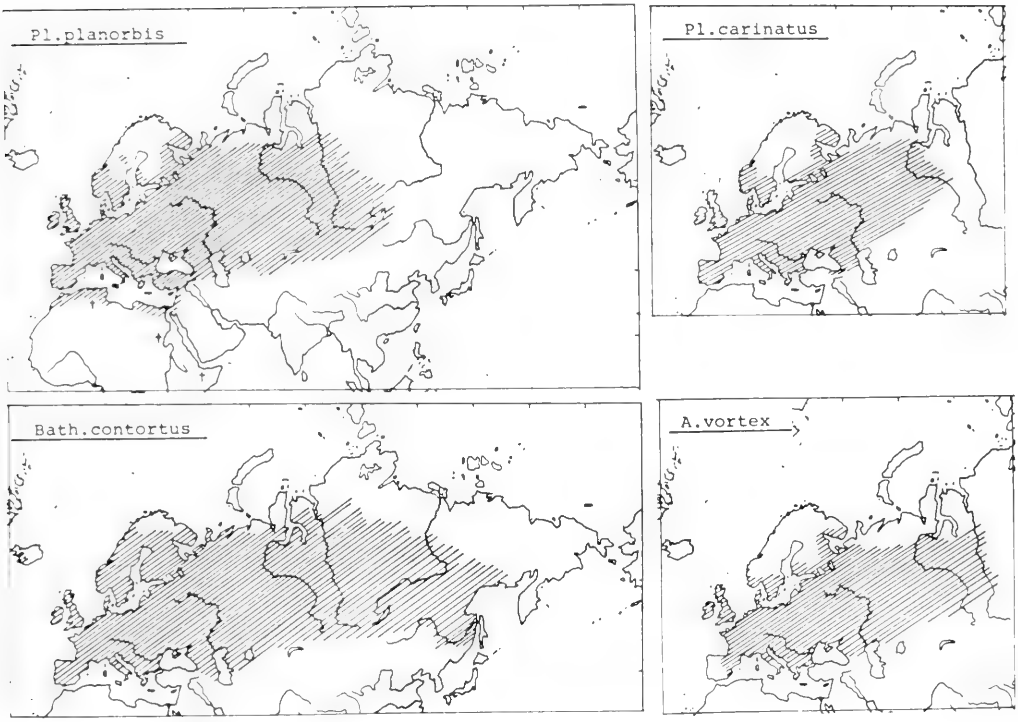

FIG. 113A. World distribution of *Planorbis*, *Anisus* and *Bathyomphalus*.

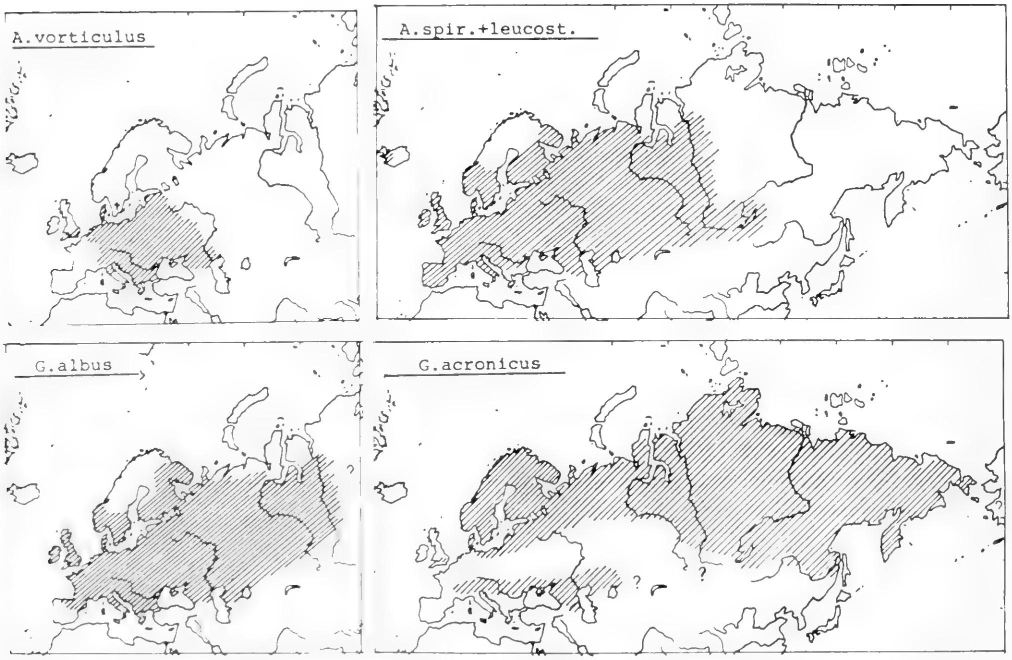

FIG. 113B. World distribution of *Anisus* and Palaearctic *Gyraulus*.

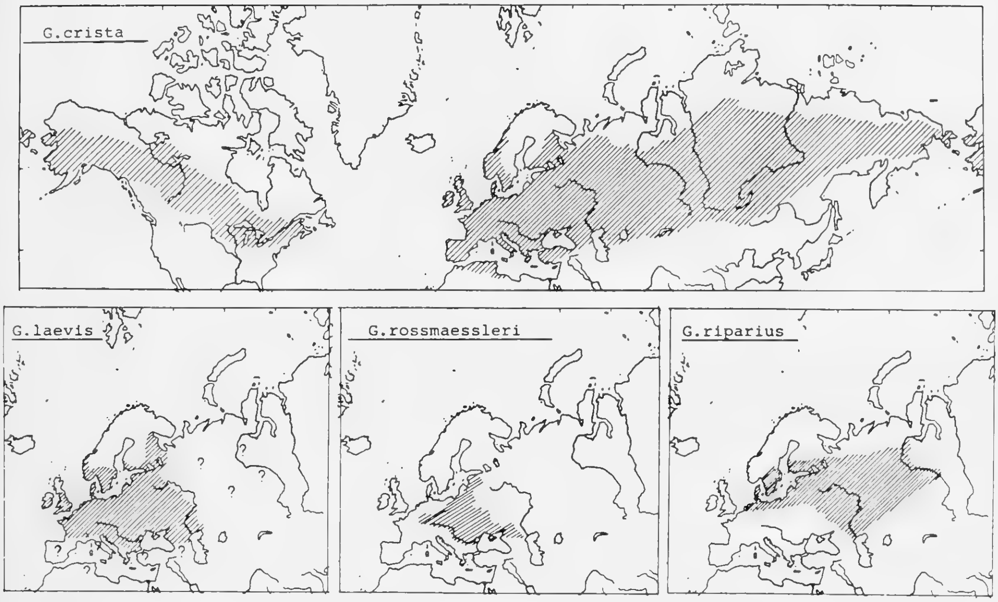

FIG. 113C. World distribution of Palaearctic *Gyraulus*.

decidedly more than in any of the European *Anisus* species. I expect that anatomical examination will reveal its close relationship with *Gyraulus* species. The nature of mantle pigmentation could supply the clue: if it shows a distinct pattern (besides other features of *Gyraulus*) it belongs in *Gyraulus*, because hitherto all *Gyraulus* snails seen from S and E Asia and the islands S of Asia have patchy mantle pigmentation. All four species of *Anisus*, on the other hand, lack this pattern. Some other snails listed as "*Anisus* species" by Baker (1945: 60) may either turn out to have only superficial resemblance with or to be merely synonyms of the European *Anisus* species. Presumably, the only other good species is *Anisus strauchianus* (Clessin). Being confined to S Russia, it fits within the distribution area of the genus. Fossil records, also of extinct species, do not lie beyond the Recent geographical limits of the genus.

We can thus state that all but one genus belonging to the *Planorbis*-tribe are restricted to the Palaearctic. The only genus that has spread to nearly every continent is *Gyraulus*. Should further studies reveal that the African genera *Afrogyrus* and *Afrogyrorbis* are also members of this tribe these would be further exceptions. North America, the Oriental, the Malay Archipelago, Australia, New Zealand and the Pacific Islands harbour *Gyraulus* only.

Of the *Gyraulus* species living in Europe only one has a Holarctic distribution: *G. crista*. The species with the second widest distribution is *G. acronicus*. It extends farthest to the N and displays a typical boreo-alpine disjunction, as is known for many organisms. Representatives of limnic animals with a similar distribution (accord. to Thienemann, 1950) are the water bug *Arctocorisa carinata* Sahlb., the chironomid midges *Paratrichocladius alpicola* Zett., *Pseudodiamesa nivosa* (Goethgh.), the copepod *Heterocope borealis* (S. Fischer), and several turbellarians. The boreal portion of the range of *G. acronicus* extends farther southward than that of the examples mentioned. It comprises the circum-Baltic countries as far as the Baltic terminal moraines reach. This area is shared by the cladoceran *Holopedium gibberum* Zadd., and two plant species typically associated with it: *Lobelia dortmanna* L. and *Isoetes lacustris* L. (Thienemann, 1950: 161). The only difference is that these three organisms exclusively inhabit lakes poor in lime, whereas *G. acronicus* requires a higher calcium concentration. Thienemann joins Ekman in applying the term glacial "pseudo-relics" to these species, previously often labelled "glacial relics." Since "glacial relics" should be restricted to species whose present distribution coincides with that during glaciation, Ekman introduced his term, defining it as follows (according to, and slightly modified, by Thienemann, 1950: 194, translated): "Pseudo-relics are faunal elements that are not relics in a certain area but have immigrated to it in the past when natural conditions, presently no longer existing, allowed access to the area." As to fresh-water molluscs this is true not only for *G. acronicus,* but also for some pill clams: *Pisidium lilljeborgii* Clessin, *P. conventus* Clessin, and probably also *P. hibernicum* Westerlund.

The two species of the subgenus *Lamorbis, Gyraulus rossmaessleri* and *G. riparius,* are not only stenoekous (or rather stenotopic, since the determining ecological factors are unknown) but also have a very limited distribution. *G. laevis* may be called central European. *G. crista* is apparently the only species of the *Planorbis*-tribe with a Holarctic distribution (Fig. 113C). There is, however, a strange difference in distributional character in the continents. *G. crista* is almost ubiquitous in the Palaearctic. In central Europe it is encountered in almost every water body (if not extremely soft); in constancy and abundance it is outdone at most by the lymnaeid snails *Radix peregra* and *R. ovata,* and perhaps also by *Anisus vortex*. In the Nearctic it is extremely scattered and rare. Clarke (1973: 406–409) surveying the fresh-water mollusc fauna of the Canadian Interior Basin found it in only two localities (of a total of 577 stations). He states that the species is "rare and local in distribution" in his investigation area "and probably in North America as a whole." He quotes La Rocque who lists 18 eastern North American localities from which this species has been recorded, but 15 of these are from Pleistocene sediments and only 3 represent living specimens. From this he concludes that "the relative abundance of *Armiger crista* in North America appears to have declined substantially since the Pleistocene." In eastern North America *G. crista* is particularly sporadic. It does not extend into the milder and warm climates, whereas the same species in the Old World inhabits circum-Mediterranean regions as far S as NW Africa. Its northern distribution, low abundance and low constancy in North America, together with its continuous distribution over N Asia, the Chukotskiy Peninsula, Alaska, and Canada strongly suggest that *G. crista* has reached the Nearctic continent via NE Asia. *G. crista* is certainly one of the fresh-water molluscs with the highest vagility. Its extremely small size, its costae and spines and its quasi-omnipresence in water vegetation render it particularly suited for passive dispersal, e.g. by birds, to whose feathers it probably adheres easily. Since no older fossil records than from the Pleistocene seem to be known in North America (according to Clarke, 1973: 406) it may well be possible that the species was introduced to the North American continent after the connection (Bering-bridge) in the last glacial period in the Pleistocene had been formed that permitted considerable exchange of animals and plants (Thenius, 1977: 22). If this hypothesis is true, two (alternative or, more probably, joint) factors may determine the limited distribution and ecological range of *G. crista* in North America. (1) Only those individuals of the Palaearctic populations that were sufficiently adapted to a cold climate crossed the periglacial environment (tundra, steppe) of the Bering-bridge. Hence this would mean a restricted gene pool of the American population, but not by chance (as responsible for the founder principle) but by selection. (2) Similarly, as hypothetically assumed for the European member of *Torquis* (*G. laevis*), the newcomer, *G. crista,* found most ecological niches occupied and could not settle as well as it might have done earlier.

The actual distribution of the SW, S and E Asiatic species is far too little known to present maps for them. I merely wish to demonstrate the relative uniformity of one taxonomically significant organ in the majority of samples (Fig. 114). I have omitted only those cases where several samples from neighbouring localities were checked, e.g. from Korea and Okinawa. All animals in these samples had the patchy mantle pigmentation indicating their evidently common origin. The majority of them have been included in *Gyraulus chinensis* in this study. Some marginal populations are considered separate species although the form of the penis sheath, penis tip, vas deferens and the position of the penis pore are virtually indistinguishable. These species, regarded as having originated as peripheral isolates (Fig. 115), are *G. euphraticus* (Fig. 116A; 115, 2), a species probably endemic to the Seychelles (nomenclature not as yet clear) (Fig. 114, D; Fig. 115, 3), *G. tokyoensis* (Fig. 115, 5; not drawn in Fig. 114, due to lack of space), *G. brongersmai* (Fig. 114, N; Fig. 115, 8); *G. tondanensis* (Fig. 116, Q; the penis was not recognizable, due to poor preservation, but the vas deferens and the penis sheath suggest conformity with the species mentioned so far; Fig. 115, 7). *G. eugyne* (Fig. 115, 4) is probably also a peripheral isolate of the *G. chinensis*-Rassenkreis; but one should take into account that *G. acronicus* in this region probably almost reaches the range of *chinensis* (cf. Agócsi & Pintér, 1971); it could, thus, also be that *G. eugyne* is a peripheral isolate of *G. acronicus;* this should be examined in future studies.

The species examined from Mauritius under the name *G. mauritianus* shown to be identical with *G. chinensis* is obviously a recent introduction to the island through human activities. According to Starmühlner (personal communication) the fauna and flora of Mauritius is rich in anthropochorous elements from India. Brown (personal communication) claimed that Mauritius has in fact an endemic *Gyraulus* species, which has to carry the name *G. mauritianus* (Morelet) and which is said to be identical with the species of the Seychelles. I have not followed this question further; but in any case the *Gyraulus* inhabiting Mauritius and the Seychelles are distinctly different from any African *Gyraulus,* while anatomically it is very similar to the S Asiatic group. This suggests a close relationship that agrees with other biogeographic observations. Mani (1974: 645) lists a number of insect species endemic to the Seychelles but belonging in genera indigenous to India. Faunistic affinities to the Madagascan region are much smaller. According to Scrutton (1976) the Seychelles (unlike Mauritius) are most probably a fragment of the continental lithosphere that was left when India broke off and started to drift northward, about 60 to 70 millions of years ago. Up to that time, however, India was part of Gondwanaland and there would be no faunal relationship to taxa living in Laurasia. The present *Gyraulus* species of India certainly immigrated to the subcontinent only after India's fusion with the Asiatic continent. As long as Pangaea was intact, on the other hand, up to the Jurassic, *Gyraulus* certainly did not yet exist. The question concerning where the Seychelles received the stem species of their endemic *Gyraulus* species thus far remains unanswered.

The *Gyraulus* fauna of the Malay Archipelago deserves special attention. Since the pioneer work by Wallace this region has aroused biogeographers' interest. A sharp borderline, the Wallace line between faunal regions, runs between Bali and Lombok, between Borneo and the Celebes. West of it there are nearly exclusively Oriental elements with a very low proportion of Australian-Papuan elements; from Bali to Lombok there is an increase in Australian-Papuan elements and a decrease in Oriental elements. A less sharp line, Lydekker's line, between Australia/New Guinea and the Lesser Sunda Islands characterizes the eastern limit of Oriental elements, e.g. of the flying lizard *Draco lineatus* (Hennig, 1966: 136). Both lines coincide with the seacoast lines during periods of glaciation in the Pleistocene associated with a eustatic dropping of sea level. In between there are gradients in either direction. This region, named "indoaustralisches Zwischengebiet" by Rensch (1936: 251), is generally assigned the status of a different faunal region, the Wallacea (de Lattin, 1967: 273; Illies, 1971: 53). A line designating about equal portions of the respective faunal elements, Weber's line, is without interest here. It must be stated, however, that Wallacea has a number of genera and species of its own, including non-marine mollusks (Bollinger, 1914; Rensch, 1936).

While in Wallacea elements of Indo-Malayan and of Australian origin used to meet and overlap in many groups of organisms, Australia cannot be regarded as a source of *Planorbis*-tribe members. Consequently, spreading of *Gyraulus* in the Malayan Archipelago should have taken place mainly in easterly and southerly directions. The Australian *Gyraulus* fauna could have originated from only two continents: Asia and Africa. From South America, S of Venezuela, there are known neither Recent nor fossil *Gyraulus* species. One mode of extension of S Asian *Gyraulus* obviously was via Malacca to the Greater Sunda Islands. At present only four samples have been examined, one of which being *G. chinensis* from Malacca (Fig. 114, H), the remaining three belong to species with the aberrant characters in the ♂ copulatory organ, *G. malayensis* (Fig. 114, R, S, T). It is important to learn whether *G. chinensis* itself or a close relative with the corresponding plesiomorphous characters entered the Greater Sunda Islands and Bali at all. If not, the other *Gyraulus* species endemic to Sumatra (*G. proclivis* von Martens, *G. sumatranus* von Martens, *G. feuerborni* Rensch) and to Java (*G. terraesacrae* Rensch) probably share the striking features of *G. malayensis.* Spread of *G. malayensis* is likely to have ended at Wallace's line (distance be-


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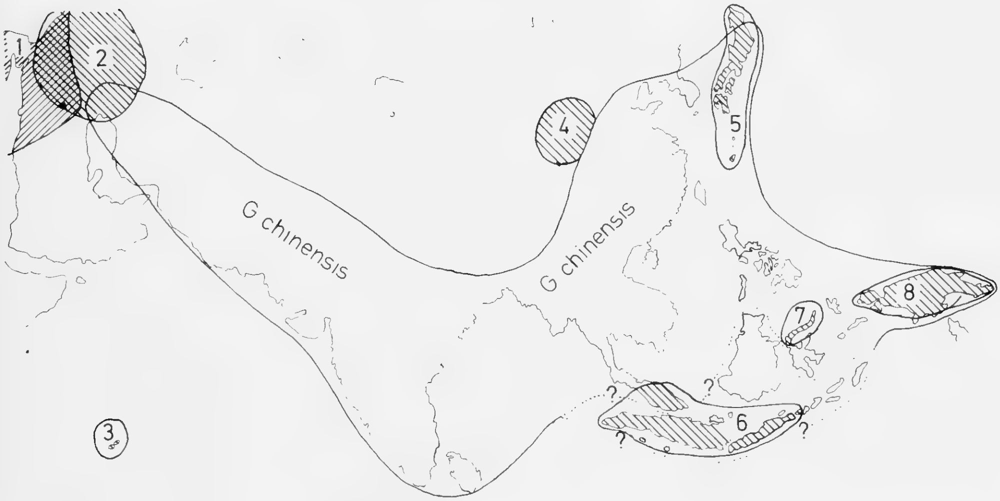

FIG. 115. A tentative map of the approximate distribution of the southern branch of *Gyraulus* species with a patchy mantle pigmentation. White encircled area: *G. chinensis*. Shaded areas: peripheral isolates. 1 = *G. ehrenbergi;* 2 = *G. euphraticus;* 3 = a species endemic to the Seychelles; 4 = *G. eugyne* n. sp.; 5 = *G. tokyoensis*; 6 = *G. malayensis* n. sp. plus endemic spp. of Sumatra and Java; 7 = *G. tondanensis*; 8 = *G. brongersmai* plus endemic spp. of New Guinea.

tween Bali and Lombok scarcely 30 km, but depth of sea 300 m). Australia has evidently not received its *Gyraulus* fauna this way. The copulatory organ in the two Australian species studied is of the normal, i.e. plesiomorphous, form. The second route by which *Gyraulus* could have arrived at the Australian continent is the one via New Guinea. Firstly, *G. chinensis* itself has been encountered here (Fig. 114, P) (van Benthem-Jutting, 1963: 494), and secondly I note the similarity in essential anatomical features between (1) *G. chinensis,* (2) a species endemic to New Guinea, and (3) one of the Australian species examined. The New Guinean species in question is *G. brongersmai* van Benthem-Jutting (Fig. 115, N); the Australian species I wish to provisionally call *G.* sp. 2 (loc.: Bombala, New South Wales). These two share a rather unusual shell form, recalling at first glance a *Segmentina* or *Hippeutis* in outline and even in surface character. I expect that study of more material will reveal that *G. brongersmai* and the Australian *G.* sp. 2 are sister species. Material of the other species described as endemic to New Guinea was not available for dissection.

How *Gyraulus chinensis* reached New Guinea from the Asian continent is a question not easily answered. *G. chinensis* is present in the Philippines (Fig. 114, O). *G. tondanensis* from North Celebes (Fig. 114, Q) has the general shape of the ♂ copulatory organ of *G. chinensis* as well. Moreover, Bollinger reported *Planorbis compressus* Hutton from the Celebes, which is probably a synonym of *G. chinensis.* Pleistocene land bridges between New Guinea and the Philip-

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FIG. 114. Shapes of penis sheath and vas deferens and penis plus positions of penis pore in *Gyraulus* samples from S and E Asia. A—*G. euphraticus;* B, C, E through M, O, P—*G. chinensis;* D—*G.* sp., probably endemic to the Seychelles; N—*G. brongersmai* van Benthem-Jutting, 1963 (paratype); Q—*G. tondanensis* (Quoy & Gaimard, 1834); R, S, T—*G. malayensis* n. sp. Equal magnification in all figures. Localities: A—S Iran; B—Sayedabad; C—Mauritius; D—Seychelles; E—Bharatpur; F—Bangalore; G—Thailand; H—Malacca; I—Hong Kong; K—Kaejong; L—Motobu-cho; M—Taiwan; N—L. Tage, West Irian; O—Mindanao; P—Merauke, West Irian; Q—Tondano, Sulawesi; R—Kuala Lumpur; S—Bukateja, Java; T—Tasik Madu, Bali.

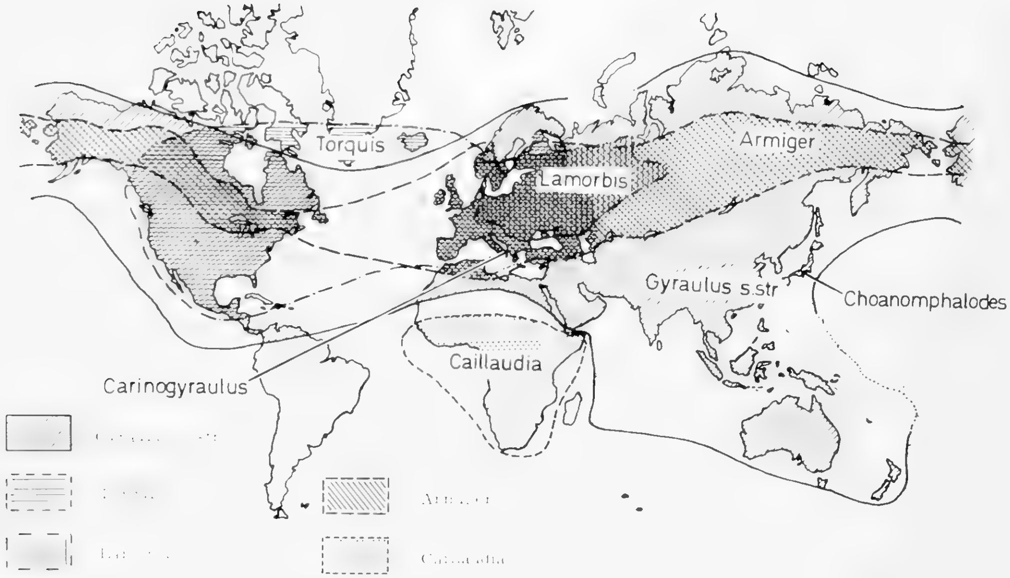

FIG. 116. World distribution of *Gyraulus* subgenera.

pines cannot have existed considering the great depth of the sea between the islands. Moreover, the period since the Pleistocene seems to be rather short in view of the extensive speciation that has evidently taken place in New Guinea. Hence it follows that passive dispersal, probably by birds, remains the only explanation for the existence of *Gyraulus* in New Guinea.

Particularly close biogeographic relations between New Guinea and Australia on the one hand, and a very low affinity between the Australian fauna and that of the Greater Sunda Islands on the other have been well established in various groups of plants and animals (Keast, 1959; McMichael & Iredale, 1959: 241). My preliminary data presented so far as a by-product seem to be in line with these statements.

The second possible origin of Australian *Gyraulus* to be discussed is that from Africa. A prerequisite of this assumption would be (1) that transfer from Africa at least to the transantarctic continent happened before the Upper Jurassic/Lower Cretaceous, and (2) that snails were able to reach Gondwanaland from Laurasia despite their separation by the Tethys Sea. The probability of both is extremely low.

Surprisingly, however, I found a great reduction of portions of the reproductive system (e.g. two prostate diverticula!) recalling the apomorphous characters of the African species (subgenus *Caillaudia*) in one of the Australian species examined. It is the species, provisionally named *G.* sp. 1, from Benambra, E Victoria, mentioned above. Although shell characters are quite dissimilar, future students should pay particularly thorough attention to further similarities between this species and the African ones before the conclusion is drawn that similarities are merely a result of convergent evolution.

Finally, where were the centre of origin and the centre of differentiation? The following hypothesis is given. As the genera branching off near the base of the tribe (Fig. 107) are exclusively Palaearctic in distribution far beyond the present limits (except *Planorbis planorbis* in Africa), there can be no doubt that the stem species of all recent *Gyraulus* species lived in the Palaearctic region (Fig. 116). The stem species of the subgenera *Armiger, Lamorbis,* and *Torquis* split off, split once more, and the stem species of *Torquis* spread westward, joined by the plesiomorphous remnant group (with "straight kidney margins"), far beyond the limits of the present Palaearctic. In the Nearctic part of the then Laurasian continent speciation began, both in "*Gyraulus* s. str." and in *Torquis.* The European *Torquis* species, *G. laevis,* spread in the counter-direction settling in the Palaearctic. *Lamorbis* remained limited to Europe; *Armiger* primarily inhabited the Palaearctic only and, if the above reflexions are correct, reached the Nearctic only during the Pleistocene.

A southern portion of the remnant plesiomorphous species, having reached Africa, was isolated by the formation of the Sahara desert. The remaining species having spread over the whole Palaearctic continent gave rise to a peculiar group in the Balkan region, and, independently, to that of another taxon in Japan. When, by the end of the Pleistocene, glaciations began, the stem species of *Carinogyraulus* and *Choanomphalodes* withdrew in the refugia of the Recent Lakes Ohrid/Prespa and Lake Biwa respectively.

The group that remained then split off a species developing the patchy mantle pigmentation. After another cleavage the two branches spread eastward separately, N and S of the great mountain chains. The southern branch cleft several times resulting in a greater number of peripherally isolated species.

A relatively basic (=early) diversification leading to the Recent subgenera took place in the European/West Asiatic region (3 subgenera, plus a subgenus in 2 Macedonian ancient lakes plus a subgenus probably immigrated from the Nearctic plus a marginal one in the south: *Caillaudia* (see Fig. 116)). Another, though minor, centre of differentiation can be located in the North American region (two subgenera plus one, probably more recent, immigrant). The large area of S and E Asia plus the Malayan Archipelago and Australia harbour species of only one subgenus, although extensive speciation (=differentiation) occurred.

We may, therefore, state that the centre of origin of the genus *Gyraulus* was probably the West Palaearctic. A primary centre of differentiation was in the same area, a secondary one in the Nearctic, and another one in the Indo-Malayan region.

Two of the main tasks of future research in taxonomy of the group will, consequently, be an elaboration of phylogenetic relations between the Palaearctic and the Nearctic taxa, and a study of speciation and dispersal in the Malayan Archipelago. Moreover, it is hoped that further knowledge of certain characters (especially the mantle pigmentation) in North American species will help to solve the question of a further division of the species group provisionally united in a "subgenus *Gyraulus* s. str."

DIAGNOSES OF SUBGENERA

1. Sg. *Gyraulus* s. str.

Type-species: *Planorbis hispidus.* Draparnaud 1805, designated by Dall (1870) (=*Planorbis albus* Müller, 1774).

The nominate subgenus, comprising the vast majority of *Gyraulus* species, differs from the other subgenera by the lack of characters typical for these other subgenera. The shell is always planispiral although the last whorl may descend towards the aperture. The aperture is more or less oval. The periphery is equally rounded, angled or keeled and may carry a periostracal fringe. The shell surface may be smooth, but in most species shows spiral striation, resulting in reticulate sculpture, usually visible at least on the upper side. The kidney has straight margins. The prostate diverticula, between 8 and 40 in number, are regularly and closely spread in a single row. The monophyletic status of this subgenus is uncertain because the character states common to all of its members are plesiomorphous ones. Of the Eurasiatic species examined the following are assigned to the nominate subgenus: *G. albus, G. acronicus, G. chinensis* with diverse races, *G. euphraticus, G. ehrenbergi, G. piscinarum, G. tokyoensis, G. eugyne* n. sp., *G. malayensis* n. sp.

2. Sg. *Torquis* Dall, 1905

Genus *Planorbis* subgenus *Gyraulus* section *Torquis* Dall, 1905: 83, 86.

Type-species: *Planorbis parvus* Say, by original designation.

Torquis differs from all other subgenera by the following characters: A planispiral shell with a nearly round aperture and the periphery neither angled, keeled nor fringed. The shell surface is always smooth, due to lack of spiral striation. The kidney is distinctly septate, thus appearing to have undulate margins. The prostate diverticula are arranged irregularly and usually scattered in a single row.

Eurasiatic species assigned here are: *G. laevis, G. parvus.*

3. Sg. *Lamorbis* Starobogatov, 1967

Genus *Choanomphalus* subgenus *Lamorbis* Starobogatov, 1967: 296.

Type-species: *Planorbis riparius* Westerlund, by original designation.

Lamorbis differs from all other subgenera by a cylindrical penis sheath which is, moreover, distinctly shorter than the preputium, by a tapering penis tip with a hob-nail shaped stylet, a position of the penis pore relatively remote from the distal end of the penis, and a distinctly septate kidney as in *Torquis*. Species assigned here: *G. riparius, G. rossmaessleri.*

4. Sg. *Armiger* Hartmann, 1844

Genus *Armiger* Hartmann, 1844: 172, 219.

Type-species: *Nautilus crista* Linnaeus, by original designation.

Armiger differs from all other subgenera by its last whorl not embracing the penultimate whorl, but rather being ± loosely attached to the upper side of the latter, the peristome thus being continuous. *Armiger* has undulate kidney margins, a tapering penis tip with a hob-nail shaped tiny stylet. There is probably only one species: *G. crista.*

5. Sg. *Carinogyraulus* Polinski, 1929

Genus *Gyraulus* subgenus *Carinogyraulus* Polinski, 1929: 161.

Type-species: *Gyraulus trapezoides* Polinski, by original designation.

Carinogyraulus differs from the other subgenera by a non-planispiral pseudodextral shell, a spire raised or flat, the left side carrying a funnel-like deep umbilicus delimited by an angle or keel. The whorls of the thick-shelled species of the subgenus are sometimes reinforced by up to three keels. Central and lateral teeth of the radula are unicuspid, or cusp numbers at least partially reduced. Prostate diverticula are as in sg. *Gyraulus* s. str. or closely spaced in more than one row, totalling more than 40. The vas deferens is wider than in most species of the other subgenera.

Species assigned here are *G. stankovici* from Lake Prespa and *G. crenophilus, G. fontinalis, G. lychnidicus, G. trapezoides* from Lake Ohrid.

6. Sg. *Choanomphalodes* Lindholm, 1927

Genus *Choanomphalus* subgenus *Choanomphalodes* Lindholm, 1927: 182.

Type-species: *Choanomphalus japonicus* Preston (=*G. biwaensis*), by original designation.

Choanomphalodes differs from the other subgenera by a non-planispiral, pseudodextral shell, whose spire is flat to weakly raised. The periphery is tricarinate to rounded. The radula, vas deferens, and prostate are as in the sg. *Gyraulus* s. str., but the male copulatory organ differs from that in all other groups by its enormous length.

If *G. amplificatus* (Mori) should prove to be identical with *G. biwaensis*, the subgenus is monotypic.

7. Sg. *Caillaudia* Bourguignat, 1883

Genus *Caillaudia* Bourguignat, 1883: 99.

Type-species: *Caillaudia angulata* Bourg. (=*Planorbis costulatus* Krauss) by original designation.

The subgenus *Caillaudia* differs from all other subgenera by reproductive organs largely reduced in size and complexity: a tiny ovotestis, inconspicuous seminal vesicle, prostate diverticula reduced in length and number (3 to 12), irregular in shape and arrangement, the most distal one lying distinctly remote from the bursa copulatrix. Species assigned here: *G. costulatus, G. connollyi,* both in Africa south of the Sahara (Australian species?).

REDESCRIPTION OF *GYRAULUS*

The genus name was introduced in a publication by Charpentier (1837). He lists a subgenus "*Gyraulus* Ag. (Msc.)" of the genus *Planorbis* on p. 21 of his Catalogue des Mollusques terrestres et fluviatiles de la Suisse. A description or diagnosis is not added. The first species listed thereunder is *Planorbis hispidus* Drap.; as a synonym "*Pl. albus* Stud." is mentioned. *Pl. hispidus* Draparnaud, 1805, as the type-species was formally chosen by Dall in 1870.

The planorbid genus *Gyraulus* is conchologically and anatomically briefly defined by the following characters.

Shell—The shell is planispiral or, exceptionally (only in some ancient lakes), pseudodextral with elevated spire. The shell is small, 2 to 10 mm in maximum diameter. In planispiral species the mean height is ⅕ to ⅓ of the maximum diameter. The shell has 3 to 5 rapidly increasing whorls. The shell is deeply concave on the upper side, less concave or nearly flat on the under side. The aperture is roundish, ovoid or spindle-shaped at its outer margin. The surface is smooth to dull, with or without spiral striation. The color is light to dark corneous.

Animal—The animal is of a light to moderate grey. The mantle pigmentation is diffuse to conspicuously patchy ("distinct pattern"). The kidney is long and narrow, with straight or undulate margins. The ureter is reflected. The pseudobranch is triangular to rectangular, with one longitudinal dorsal fold. The anus lies immediately to the right of this fold. The jaw is composed of a number of chitinized platelets. The radula formula is 12-1-12 to 27-1-27; the central teeth are bicuspid, with 3 additional denticles (2 lateral, 1 intermediate); the lateral teeth are tricuspid with usually 4 (2 lateral, 2 interstitial) additional denticles; the marginal teeth have up to 12 cusps formed by the 3 cusps of the lateral teeth and additional denticles which are increased in size and number. Cusp numbers are reduced (to one in central and lateral teeth) in forms endemic to Lake Ohrid basin, Macedonia. The alimentary tract has a more or less developed intestinal loop which is sometimes omitted. The ovotestis is composed of up to 40 lobes, which are arranged in 2 (rarely 3) rows. The proximal end of the spermoviduct is shorter than that distal to the seminal vesicle. The seminal vesicle has bulbous or spinous coils. The albumen gland is elongate triangular, convex dorsally, concave ventrally (the concavity harbouring the stomach). The female tract has no externally visible distinctions into oviduct, nidamental gland and uterus. The vagina is narrower, but often inflated close to the ♀ genital pore. The bursa copulatrix is narrow and cylindrical to inflated, the bursa duct being usually long and of varying width. The sperm duct is narrower than the oviduct. The prostate gland is separated from the sperm duct, with 3 to 40 diverticula emerging from the prostate duct. The diverticula are densely or loosely arranged in one row (exceptions with up to 70 or more diverticula, arranged in several rows, occur in species of the Lake Ohrid basin). The vas deferens usually narrows not far from the zone where the prostate duct branches off the sperm duct, then slightly widening, but still narrow towards the ♂ copulatory organ. In at least one species the vas deferens widens to approximately twice the diameter of the proximal half. In some species the vas deferens does not narrow, but is equally wide down to the ♂ copulatory organ; the ♂ copulatory organ is in shape well divided into a penis sheath and a preputium by a knob-like thickening. The penis sheath usually has a club-shaped proximal end, which is well set off against the vas deferens (exceptions in forms of the Malay Archipelago, where it is scarcely wider than the unusually wide vas deferens). The penis sheath is more cylindrical and lacks a distinct club-like proximal thickening, but is nevertheless well distinguished from the vas deferens, in two European species (*G. riparius, G. rossmaessleri*). The distal end of the penis sheath is nearly closed by a muscular papilla of hemispherical shape. The preputium begins with a muscular ring called the diaphragm. The lumen of the preputium distal to the diaphragm is wide; towards the middle its lumen is usually narrowed by longitudinal, introverted folds which usually form pilasters; folds can be so weak that the preputial lumen appears nearly round. The penis sheath is usually of once to twice the length of the preputium (only in the two European species mentioned above distinctly shorter than the preputium). The penis is as long as the penis sheath, usually with a more or less conspicuous distal thickening (instead of the thickening there may be a conical tapering). The penis tip is equipped with a chitinized hollow stylet, which is clearly delimited against the penis tissue. The penis pore usually lies in varying portions of the thickened penis tip, exceptionally near the middle of the penis (forms of the Malay Archipelago, probably—according to Hubendick & Radoman, 1959—also in a species from Lake Ohrid).

SUMMARY

1. An approach is made towards basing the classification of the planorbid snail genus *Gyraulus* on as many characters as possible. The study is focussed on taxa inhabiting Europe and Asia with observations pertaining to other continents.

2. Shell proportions, as expressed by a "flatness-index" (introduced by Brown & van Eeden) and the ratio maximum shell diameter : whorl number are demonstrated in diagrams to show interspecific and infraspecific (both genotypical and ecophenotypical) variation. In one species, *G. albus,* shells of equal whorl numbers in lenitic biotopes are larger in diameter than in lotic biotopes (Fig. 6).

3. Influence of the usual fixing techniques on anatomical data is elaborated in one example. The length of the penis sheath is greatly affected by immersion of living *Gyraulus* snails in 70% ethanol, as compared with values for snails fixed after relaxation with

pentobarbital. The preputium does not appear to be significantly shortened.

4. Characters highly valued for species discrimination are among others: the distribution of pigment cells on the mantle to the right of the kidney; the presence or absence of distinct transverse septa in the tubular portion of the kidney rendering its margins "undulate" or "straight," respectively; the number of prostate diverticula, their shape and arrangement in the gland; the width of the vas deferens; the length ratio penis sheath : preputium; the shape of the penis tip and stylet, and the position of the penis pore. In certain groups peculiarities may occur in various other organs (radula, seminal vesicle, bursa copulatrix, bursa duct, etc.).

5. Europe outside Macedonia harbours five indigenous species. For their identification a key is presented which also permits recognition of two species recently introduced to Europe.

6. In Asia the number of species is much greater. N Asia is inhabited by *G. acronicus* (Fér.) only. A huge area of S Asia, from Iran to Japan and New Guinea, harbours forms so little different both conchologically and anatomically that they are probably not reproductively isolated and must, thus, be regarded as races of one polytypic species or "Rassenkreis": *G. chinensis* (Dunker) (synonyms: *G. convexiusculus* (Hutton), *G. spirillus* (Gould) and others). Species anatomically indistinguishable, but conchologically more or less distinctly different, are *G. tokyoensis* Mori and *G. euphraticus* (Mousson). They are considered separate species because they are said to be sympatric with *G. chinensis,* thus indicating reproductive isolation. There are some more species whose anatomical similarity suggests close relationship with *G. chinensis*; they are conchologically divergent species mostly endemic to island groups (Seychelles, Celebes, New Guinea). One species, on the other hand, conchologically so far indistinguishable, has quite aberrant anatomical features giving it a unique status. It is known from Malaya, Java and Bali and is described as a new species: *G. malayensis.* Another species named here is *G. eugyne* n. sp. from Inner Mongolia.

7. Abandonment of planispiral growth and formation of several angles or keels on the shell periphery in *Gyraulus* of ancient lakes is certainly due to convergent evolution. There is strong evidence that a species endemic to Lake Biwa in Japan has a history different from that in a group endemic to the Macedonian Lakes Ohrid and Prespa.

8. For an analysis of phylogenetic relationships, Hennig's (1950 and later) recommendations are followed in a "search for the sister group" and a hierarchic system expressing the "recency of common ancestry" of taxa. Tools used in the analysis are common derived characters ("synapomorphies"). Moreover, Hennig's concept of monophyly is followed in this study.

9. Criteria for judging the apomorphous character states are discussed. Highly valued as being derived are characters of uniqueness or low abundance in the genus or in the family or higher taxa. Qualitative characters meeting these requirements are relatively rare in the genus, so that quantitative ones must be used in addition. In some cases, these are even used as synapomorphies of subgenera or genera, provided they display extreme values and appear to be sufficiently stable, e.g. the extreme elongation of the body in the genera *Anisus* and *Bathyomphalus.*

10. The systematic position of *Gyraulus* in the *Planorbis*-tribe is examined (Fig. 107). The species group bearing a hollow penial stylet (*Anisus, Bathyomphalus, Gyraulus*) is clearly a monophyletic group within the *Planorbis*-tribe. Since *Gyraulus* is likely to be a monophyletic group, too, maintenance of the three genera mentioned above is recommended because of clear gaps in their range of variation. *Anisus* and *Bathyomphalus* together form the sister group of *Gyraulus.*

11. Phylogenetic analysis in the genus *Gyraulus* reveals the existence of seven subgenera: *Torquis* Dall (Nearctic and W Palaearctic), *Lamorbis* Starobogatov (W Palaearctic), *Armiger* Hartmann (Holarctic), *Caillaudia* Bourguignat (Ethiopic), *Choanomphalodes* Lindholm (Lake Biwa, Japan), *Carinogyraulus* Polinski (Lakes Ohrid and Prespa, Macedonia), and a provisional "subgenus *Gyraulus* s. str." (cosmopolitan except South America and the Ethiopic region) (Figs. 107, 116). *Gyraulus* s. str. being a remnant group merely characterized by plesiomorphous character states is likely to be a paraphyletic group in Hennig's sense. Diagnoses of subgenera are given.

12. The impossibility of deriving sequences of evolutionary steps in groups sharing only in plesiomorphous characters is demonstrated in the remnant group, the provisional

"subgenus *Gyraulus* s. str." Sequences may, with a certain probability, be supposed from dispersal pathways only.

13. Incompatibility is shown between Hennig's "deviation rule" and biological reality in the case of peripheral isolates. The example advanced is the polytypic species ("Rassenkreis") *Gyraulus chinensis,* with marginal species such as *G. euphraticus, G. tokyoensis, G. malayensis* and others. *G. chinensis* is considered to be their "persisting stem species" although, according to this "rule," it ought to have changed its species status once at each time a peripheral isolate split off. A "persistent stem species of Recent species" is inconsistent with the deviation rule.

14. A limited geographical distribution and a narrow ecological range of the only *Torquis* species indigenous to Europe suggests that the subgenus primarily inhabited the western part of the former Laurasian continent and that *Gyraulus laevis,* the sister species of the Nearctic *G. parvus,* was split off from their common stem species as a small marginal portion of a large reproductive community. This is similar to phenomena encountered in insect groups where in pairs of vicariant species or subspecies one is often much less widely distributed and displays a much narrower ecological range than the other.

15. The centre of origin of the genus *Gyraulus* is probably the W Palaearctic, to which all its closely related genera are confined. With three subgenera of wider distribution plus one subgenus endemic to two ancient lakes in Macedonia plus one marginal subgenus in the Ethiopic plus one subgenus probably originating in the Nearctic, the W Palaearctic is at the same time regarded as the primary centre of differentiation. In the Nearctic there is a secondary one: two subgenera plus one subgenus probably acquired not before the Pleistocene. A third centre of differentiation, though only on the species level in a single subgenus, is the Indo-Malayan region (Fig. 116). Expansion probably took place radially from the W Palaearctic to the Nearctic, Africa, N Asia, and S Asia. Australia received its poor *Gyraulus* fauna evidently from Southeast Asia via New Guinea. An African offshoot in the Australian *Gyraulus* fauna, though unlikely, cannot yet be completely excluded.

16. A redescription of the genus *Gyraulus* Charpentier, 1837, is given using present knowledge on the variation of anatomical and conchological characters.

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LITERATURE CITED

AGÓCSI, P. & PINTÉR, L., 1971, Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei. *Annales Historico-Naturales Musei Nationalis Hungarici, Pars Zoologica,* 63: 153–158.

AHO, J., 1978, Freshwater snail populations and the equilibrium theory of island biogeography. I. A case study in southern Finland. *Annales Zoologici Fennici,* 15: 146–154.

ALDER, J., 1838, Supplement to a catalogue of the land and freshwater testaceous Mollusca, found in the vicinity of Newcastle. *Transactions of the Natural History Society of Northumberland,* 1838: 337–342.

ALZONA, C., 1971, Malacofauna Italica. Catalogo e bibliografia dei Molluschi viventi, terrestri e d'acqua dolce. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano,* 111: 1–433.

ANDERSON, T. W., 1958, *An Introduction to Multivariate Analysis.* New York, Wiley, 374 p.

ANNANDALE, N. & PRASHAD, B., 1919, The Mollusca of the inland waters of Baluchistan and of Seistan, with a note on the liver fluke of sheep in Seistan. *Records of the Indian Museum,* 18: 17–63.

ANNANDALE, N. & RAO, H. S., 1925, Materials for a revision of the Recent Indian Limnaeidae (Mollusca Pulmonata). *Records of the Indian Museum,* 27: 137–152.

AUERSWALD, B., 1851, in SCHMIDT, A., Malakologische Mitteilungen. *Zeitschrift für Malakozoologie,* 8: 179–192.

BAKER, F. C., 1928, *The fresh-water Mollusca of Wisconsin. Pt. 1. Gastropoda.* Wisconsin Academy of Science, Arts & Letters, xx + 507 p.

BAKER, F. C., 1945, *The molluscan family Planorbidae.* University of Illinois Press, Urbana, xxxvi + 530 p.

BECK, H. H., 1837, *Index Molluscorum praesentis aevi Musei Principis Augustissimi Christiani Frederici.* Fasc. I–II. *Mollusca Gastropoda Pulmonata,* 124 p.

BENTHEM-JUTTING, W. S. S. VAN, 1956, Systematic studies on the non-marine Mollusca of the Indo-Australian Archipelago. V. Critical-revision of the Javanese fresh-water gastropods. *Treubia,* 23: 259–477.

BENTHEM-JUTTING, W. S. S. VAN, 1963, Non-marine Mollusca of West New Guinea. Part I. Mollusca from fresh and brackish water. *Nova Guinea, Zoology,* 20: 409–521, pl. 24–25.

BOLLINGER, G., 1914, Süsswasser-Mollusken von Celebes. *Revue Suisse de Zoologie,* 22: 557–579, pl. 18.

BONDESEN, P., 1950, A comparative morphological-biological analysis of the egg capsules of freshwater pulmonate gastropods. *Natura Jutlandica,* 3: 1–208.

BOURGUIGNAT, J. R., 1852, *Testacea novissima quae Cl. de Saulcy in itinere per orientem annis 1850 et 1851 collegit.* Lutetiae, 31 p.

BOURGUIGNAT, J. R., 1862, *Malacologie du Lac des Quatre-Cantons et de ses environs.* Paris, 72 p.

BOURGUIGNAT, J. R., 1883, Histoire malacologique de l'Abyssinie. *Annales des Sciences Naturelles, Zoologie,* 15: 47–162.

BRANDT, R. A. M., 1974, The non-marine aquatic Mollusca of Thailand. *Archiv für Molluskenkunde,* 105: iv + 423 p.

BROWN, D. S., 1965, Freshwater Gastropod Mollusca from Ethiopia. *Bulletin of the British Museum (Natural History),* 12: 37–94.

BROWN, D. S. & EEDEN, J. A. VAN, 1969, The molluscan genus *Gyraulus* (Gastropoda: Planorbidae) in southern Africa. *Zoological Journal of the Linnean Society,* 48: 305–331.

BROWN, D. S. & MANDAHL-BARTH, G., 1973, Two new genera of Planorbidae from Africa and Madagascar. *Proceedings of the Malacological Society of London,* 40: 287–302.

BUCHNER, O., 1891, Beiträge zur Kenntnis des Baues der einheimischen Planorbiden. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg,* 47: 35–118.

BURCH, J. B., 1960, Chromosomes of *Gyraulus circumstriatus,* a freshwater snail. *Nature* (London), 186: 497–498.

BURCH, J. B., 1964, Cytological studies of Planorbidae (Gastropoda: Basommatophora). I. The African subgenus *Bulinus* s.s. *Malacologia,* 1: 387–400.

BURCH, J. B., 1967, Chromosomes of intermediate hosts of human bilharziasis. *Malacologia,* 5: 127–135.

BURCH, J. B. & NATARAJAN, R., 1965, Cytological studies of Taiwan freshwater pulmonate snails. *Bulletin of the Institute of Zoology, Academia Sinica,* 4: 11–17.

BURCH, J. B., WILLIAMS, J. E., HISHINUMA, Y. & NATARAJAN, R., 1964, Chromosomes of some Japanese Freshwater Snails (Basommatophora: Branchiopulmonata). *Professional Report 406th Medical Laboratory United States Army Medical Command, Japan,* p. 214–232.

CHARPENTIER, J. DE, 1837, Catalogue des Mollusques terrestres et fluviatiles de la Suisse.

Denkschrift der Schweizer Gesellschaft für Naturwissenschaften, Neuchâtel, 1: 1–28.

CLARKE, A. H., 1973, The freshwater molluscs of the Canadian interior Basin. *Malacologia,* 13: 1–509.

DALL, W. H., 1870, On the genus *Pompholyx* and its allies, with a revision of the Limnaeidae of authors. *Annals of the Lyceum of Natural History of New York,* 9: 333–361.

DALL, W. H., 1905, Land and fresh-water mollusks of Alaska and adjoining regions. In: *HARRIMAN Alaska Expedition Series,* 13: 1–171, 2 pl.

DAVIS, G. M. & LINDSAY, G. K., 1967, Disc electrophoretic analysis of molluscan individuals and populations. *Malacologia,* 5: 311–334.

DAVIS, G. M. & YAMAGUCHI, S., 1969, The freshwater Gastropoda of Okinawa. *Venus,* 28: 137–152.

DOBZHANSKY, T., 1950, Mendelian populations and their evolution. *American Naturalist,* 84: 401–418.

DRAPARNAUD, J. P. R., 1805, *Histoire naturelle des Mollusques terrestres et fluviatiles de la France.* Paris, 116 p.

DUNKER, G., 1848, Diagnoses specierum novarum generis *Planorbis* collectionis Cumingianae. *Proceedings of the Zoological Society of London,* 16: 40–43.

EHRMANN, P., 1933, Weichtiere, Mollusca. In: BROHMER, P., EHRMANN, P. & ULMER, G., *Die Tierwelt Mitteleuropas,* 1: 1–264.

EICHLER, W., 1941, Korrelationen in der Stammesentwicklung von Wirten und Parasiten. *Zeitschrift für Parasitenkunde,* 12: 94.

FÉRUSSAC, J. B. L., 1807, *Essai d'une méthode conchyliologique appliquée aux mollusques terrestres et fluviatiles.* Paris, xvi + 142 p.

FRAGA DE AZEVEDO, J., MEDEIROS, L. D. DE, FARO, M. M. DA COSTA, XAVIER, M. DE LOURDES, GANDARA, A. F. & MORAIS, T., 1961, *Os Moluscos de Água Doce do Ultramar Português. III. Molluscos do Moçambique.* Lisboa (Junta de Investigacões do Ultramar): 1–394.

GASCOIGNE, T., 1974, A note on some sacoglossan penial styles (Gastropoda: Opisthobranchia). *Zoological Journal of the Linnean Society,* 55: 53–59.

GERSTFELDT, G., 1859, Über Land- und Süßwassermollusken Sibiriens und des Amur-Gebietes. *Mémoires des Savans étrangers* (St. Pétersbourg), 9: 507–548.

GIUSTI, F., 1968, Notulae malacologicae.—IV. L'Isola di Montecristo e lo Scoglio d'Africa. *Atti della Società Toscana di Scienze Naturali,* B75: 239–254.

GOULD, A. A., 1859, Shells of the North Pacific Exploring Expedition. *Proceedings of the Boston Society of Natural History,* 7: 40–45.

GREDLER, V. M., 1859, Tirol's Land- und Süsswasser-Conchylien. II. Die Süsswasser-Conchylien. *Verhandlungen der Zoologisch-Botanischen Gesellschaft Wien,* 9: 213–308.

GROSSU, A. V., 1977, Le polymorphisme des gastéropodes et la possibilité d'identifier et de limiter l'espèce avec des méthodes biochimiques. *Malacologia,* 16: 15–19.

HADŽIŠČE, S., 1953, Prilog poznavanju Gastropoda Prespanskog i Ohridskog Jezera. *Bioloski glasnik,* II/B7: 174–177.

HAMILTON-ATTWELL, V. L. & EEDEN, J. A. VAN, 1971, A preliminary study on the microsculpture of the shell of some freshwater Basommatophora (Mollusca). *Proceedings South African Electron Microscopy Society,* Pretoria, 1971: 41–42.

HARTMANN, J. D. W., 1844, *Erd- und Süsswassergastropoden der Schweiz.* St. Gallen, 227 p.

HENNIG, W., 1950, *Grundzüge einer Theorie der phylogenetischen Systematik.* Berlin, Deutscher Zentralverlag, 370 p.

HENNIG, W., 1966, *Phylogenetic systematics.* University of Illinois Press, Urbana, Chicago, London, 263 p.

HENNIG, W., 1969, *Die Stammesgeschichte der Insekten.* Kramer, Frankfurt, 436 p.

HENNIG, W., 1974, Kristische Bemerkungen zur Frage: "Cladistic analysis or cladistic classification?" *Zeitschrift für zoologische Systematik und Evolutionsforschung,* 12: 279–294.

HESSE, P., 1928, Mazedonische Gastropoden, gesammelt von Herrn Prof. Dr. F. Doflein. *Zoologische Jahrbücher; Abt. für Allgemeine Zoologie,* 45: 1–30.

HUBENDICK, B., 1947, Die Verbreitungsverhältnisse der limnischen Gastropoden in Südschweden. *Zoologiska Bidrag från Uppsala,* 24: 419–559.

HUBENDICK, B., 1949, *Våra snäckor.* Bonnier, Stockholm, 100 p.

HUBENDICK, B., 1951, Recent Lymnaeidae. Their variation, morphology, taxonomy, nomenclature, and distribution. *Kungliga Svenska Vetenskapsakademiens Handlingar,* (4)3: 1–223, 5 pl.

HUBENDICK, B., 1952, On the evolution of the so-called thalassoid molluscs of Lake Tanganyika. *Arkiv för Zoologi,* (2)3: 319–323.

HUBENDICK, B., 1954, On the anatomy of *Choanomphalus* (Moll. Pulm.). *Arkiv för Zoologi,* (2)6: 503–509.

HUBENDICK, B., 1955, Phylogeny in the Planorbidae. *Transactions of the Zoological Society of London,* 28: 453–542.

HUBENDICK, B., 1958, The development of the penial stylet in *Gyraulus* (Moll. Pulm.). *Arkiv för Zoologi,* (2)11: 427–429.

HUBENDICK, B., 1960, The Ancylidae of Lake Ochrid and their bearing on intralacustrine speciation. *Proceedings of the Zoological Society of London,* 133: 497–529.

HUBENDICK, B., 1969, The Baikal limpets and their phylogenetic status. *Archiv für Molluskenkunde,* 99: 55–68.

HUBENDICK, B. & RADOMAN, P., 1959, Studies on the *Gyraulus* species of Lake Ochrid. Morphology. *Arkiv för Zoologi,* (2)12: 223–243.

HUDEC, V., 1967, Bemerkungen zur Anatomie von

Arten aus der Gattung *Anisus* Studer, 1820, aus slowakischen Populationen (Mollusca, Pulmonata). *Biològia (Bratislava)*, 22: 345–364.

HUTTON, T., 1849, Notices of some land and fresh water shells occurring in Afghanistan. *Journal of the Asiatic Society (Bengal)*, 18: 649–661.

ILLIES, J., 1971, *Einführung in die Tiergeographie*. Fischer, Uni-Taschenbücher, Stuttgart, 91 p.

INNES, W., 1884, Récensement des Planorbes et des Valvées de l'Egypte. *Bulletin de la Société Malacologique de France*, 1: 329–352.

JAECKEL, S. G. A., 1962, Ergänzungen und Berichtigungen zum rezenten und quartären Vorkommen der mittel-europäischen Mollusken. In BROHMER-EHRMANN-ULMER, *Die Tierwelt Mitteleuropas*. Quelle & Meyer, Leipzig, p. 27–294.

JAECKEL, S. G. A., 1967, Gastropoda. In ILLIES, J., *Limnofauna Europaea*. Fischer, Stuttgart, p. 89–104.

JOHNSON, R. I., 1964, The Recent Mollusca of August Addison Gould. *United States National Museum Bulletin*, 239: 1–182.

KEAST, A., 1959, The Australian environment. In KEAST, A., CROCKER, R. L. & CHRISTIAN, C. S., *Biogeography and ecology in Australia*. Junk, Den Haag, p. 15–35.

KEDDY, P. A., 1976, Lakes as islands: The distributional ecology of two aquatic plants, *Lemna minor* L. and *L. trisulca* L. *Ecology*, 57: 353–359.

KHAZANNIKOV, E. A., 1973, Mollusks of the genus *Gyraulus* (Gastropoda, Planorbidae) from the River Terek Basin. *Sbornik zoologićeskih' rabot (Ordzhonikidze)*, 1973: 129–137.

KLEMM, W., 1960, Mollusca. In STROUHAL, H., *Catalogus faunae Austriae*. Springer, Wien, VIIa, 1–VIIa 59.

KOZHOV, M., 1963, *Lake Baikal and its life*. Junk, The Hague, vii + 344 p.

KRAUSS, C. F., 1848, *Die Südafrikanischen Mollusken*. Ebner & Seubert, Stuttgart, 140 p.

KRULL, W. H., 1931, Importance of laboratory-raised snails in Helminthology with life history notes on *Gyraulus parvus*. *Occasional Papers of the Museum of Zoology, University of Michigan*, No. 226: 1–10.

KURODA, T., 1963, *A catalogue of the non-marine mollusks of Japan*. Malac. Soc. Japan, Tokyo, 71 p.

LASSEN, H. H., 1975, The diversity of freshwater snails in view of the equilibrium theory of island biogeography. *Oecologia*, 19: 1–8.

LATTIN, G. DE., 1967, *Grundriss der Zoogeographie*. Fischer, Stuttgart, 602 p.

LINDHOLM, W., 1927, Kritische Studien zur Molluskenfauna des Baikalsees. *Travaux de la Commission d'Etudes du Lac Baical*, 2: 139–189.

LINNAEUS, C., 1758, *Systema naturae. Regnum animale*, ed. 10, Lipsiae, 824 p.

LINNAEUS, C., 1767, *Systema naturae per regna tria naturae*, ed. 12. Holmiae, 532 p.

MacARTHUR, R. H. & WILSON, E. O., 1967, *The theory of island biogeography*. Univ. Press, Princeton, xi + 203 p.

MACHA, S., 1963, Neue Kenntnisse von der Weichtierfauna des Hultschiner Hügellandes. *Acta Musei Silesiae*, ser. A, 1963: 85–93.

MANDAHL-BARTH, G., 1954, The freshwater mollusks of Uganda and adjacent territories. *Annales du Musée Royal du Congo Belge Tervuren, Sciences Zoologiques*, 32: 1–206.

MANI, M. S., 1974, Biogeography of the peninsula. In: MANI, M. S., ed., *Ecology and biogeography in India*. Junk, The Hague, p. 614–647.

MARTENS, E. VON, 1867, Über die ostasiatischen Limnaeaceen. *Malakozoologische Blätter*, 14: 211–227.

MARX, H. & RABB, C. B., 1972, Phyletic analysis of fifty characters of advanced snakes. *Fieldiana Zoology*, 63: 1–319.

MAYR, E., 1963, *Animal species and evolution*. Harvard Univ. Press, Cambridge, Mass., xiv + 797 p.

MAYR, E., 1969, *Principles of systematic zoology*. McGraw-Hill, New York etc., xi + 428 p.

MAYR, E., 1974a, Difficulties and importance of the biological species concept. In MAYR, E., ed., *The species problem*. Arno Press, New York 371–388.

MAYR, E., 1974b, Cladistic analysis or cladistic classification? *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 12: 95–128.

MAYR, E., 1975, *Grundlagen der zoologischen Systematik*. Parey, Hamburg, Berlin, 370 p.

McMICHAEL, D. F. & IREDALE, T., 1959, The land and freshwater Mollusca of Australia. In KEAST, A., CROCKER, R. L. & CHRISTIAN, C. S., *Biogeography and ecology in Australia*. Junk, Den Haag, p. 224–245.

MEIER-BROOK, C., 1963, Über die Mollusken der Hochschwarzwald-und Hochvogesengewässer. *Archiv für Hydrobiologie Suppl.*, 28: 1–46.

MEIER-BROOK, C., 1964, *Gyraulus acronicus* und *G. rossmaessleri*, ein anatomischer Vergleich (Planorbidae). *Archiv für Molluskenkunde*, 93: 233–242.

MEIER-BROOK, C., 1976a, An improved relaxing technique for mollusks using pentobarbital. *Malacological Review*, 9: 115–117.

MEIER-BROOK, C., 1976b, The influence of varied relaxing and fixing conditions on anatomical characters in a *Planorbis* species. *Basteria*, 40: 101–106.

MEIER-BROOK, C., 1976c, The generic position of *Planorbis* (*Gyraulus*) *intermixtus* Mousson, 1874, and *Planorbis presbensis* Sturany, 1894 (Gastropoda, Basommatophora). *Basteria*, 40: 107–118.

MEIER-BROOK, C., 1978, Calcium uptake by *Marisa cornuarietis* (Gastropoda; Ampullariidae), a predator of schistosome bearing snails. *Archiv für Hydrobiologie*, 82: 449–464.

MILLER, B. B., 1966, Five Illinoian molluscan faunas from the southern Great Plains. *Malacologia*, 4: 173–260.

MOITESSIER, P.-A., 1867, Histoire malacologique du département de l'Hérault. *Revue et Magazin de Zoologie,* sér. 2, 19: 421–445.

MORI, S., 1938, Classification of the Japanese Planorbidae. *Memoirs of the College of Science, Kyoto Imperial University,* ser. B, 14: 279–300.

MOUSSON, M. A., 1874, Coquilles terrestres et fluviatiles recueillies par M. le Dr. Alex. Schlaefli dans l'Orient. *Journal de Conchyliologie,* 22: 5–60.

MÜLLER, O. F., 1774, Vermium terrestrium et fluviatilium seu animalium infusorium helminthicorum et testaceorum non marinorum succincta historia. Heineck & Faber, off. Mölleriana, Hauniae et Lipsiae 2: xxxvi + 214 p.

NATARAJAN, R., BURCH, J. B. & GISMANN, A., 1965, Cytological studies of Planorbidae (Gastropoda: Basommatophora). II. Some African Planorbinae, Planorbininae and Bulininae. *Malacologia,* 2: 239–251.

ODHNER, N. H., 1929, Die Molluskenfauna des Tåkern. *Sjön Tåkerns. Fauna och Flora,* 8: 1–129.

ODHNER, N. H., 1956, Distinctions between *Anisus* (*Armiger*) *crista* (L.) and *Anisus* (*Gyraulus*) *riparius* (West.). *Proceedings of the Malacological Society of London,* 32: 127–131.

PACE, G. L., 1973, The freshwater snails of Taiwan (Formosa). *Malacological Review Suppl.,* 1: 1–118.

PAN AMERICAN HEALTH ORGANIZATION, 1968, A guide for the identification of the snail intermediate hosts of schistosomiasis in the Americas. *Pan American Health Organization, Scientific Publication,* 168: ix + 122 p.

PARAENSE, W. L., 1966, "*Biomphalaria amazonica*" and "*B. cousini,*" two new species of neotropical planorbid molluscs. *Revista Brasileira de Biologia,* 26: 115–126.

PATTERSON, C. M., 1971, A karyotype technique using freshwater snail embryos. *Malacological Review,* 4: 27.

POLINSKI, W., 1929, Die reliktäre Gastropodenfauna des Ochrida-Sees. *Glas Srpske Kraljevske Akademije,* 173: 131–178.

POLINSKI, W., 1932, Die reliktare Gastropodenfauna des Ochrida-Sees. *Zoologische Jahrbücher, Abteilung für Systematik Ökologie und Geographie der Tiere,* 62: 611–666.

PRESTON, H. B., 1916, Descriptions of new freshwater shells from Japan. *The Annals and Magazine of Natural History,* (8)17: 159–163.

PROSSER, C. L., 1974, The species problem from the viewpoint of a physiologist. In MAYR, E., ed., *The species problem.* Arno Press, New York p. 339–369.

RADOMAN, P., 1953, Contribution à la connaissance des gastéropodes du Lac d'Ohrid (Macédoine). *Archiv of Biological Sciences (Beograd),* 5: 55–59.

RENSCH, B., 1929, *Das Prinzip geographischer Rassenkreise und das Problem der Artbildung. Bornträger,* Berlin, 206 p.

RENSCH, B., 1934, Süsswasser-Mollusken der Deutschen Limnologischen Sunda-Expedition. *Archiv für Hydrobiologie Suppl.* 13 (Tropische Binnengewässer Bd. 5): 203–257.

RENSCH, B., 1936, *Die Geschichte des Sundabogens. Eine tiergeographische Untersuchung.* Bornträger, Berlin, 318 p.

RICHARDS, C. S., 1973a, Inherited variability in the course of the intestine in *Biomphalaria glabrata. Malacological Review,* 6: 133–138.

RICHARDS, C. S., 1973b, Genetics of *Biomphalaria glabrata* (Gastropoda: Planorbidae). *Malacological Review,* 6: 199–202.

ROSZKOWSKI, W., 1929, On the systematic position and the geographical distribution of the genus *Myxas. Annales Zoologici Musei Polonici Historiae Naturalis,* 8: 64–97.

SACHS, L., 1969, *Statistische Auswertungsmethoden.* Springer, Berlin, 2. Aufl., xxxii + 677 p.

SAY, T., 1817, *Nicholson's Encyclopedia,* 1st American edition.

SCHLEE, D., 1971, *Die Rekonstruktion der Phylogenese mit Hennig's Prinzip.* Kramer, Frankfurt, 62 p.

SCRUTTON, R. A., 1976, Fragmente der kontinentalen Lithosphäre. *Endeavour* (dtsch. Ausg.), 35: 99–103.

SCUDDER, G. G. E., 1974, Species concepts and speciation. *Canadian Journal of Zoology,* 52: 1121–1134.

SIMPSON, G. G., 1961, *Principles of animal taxonomy.* Columbia Univ. Press, New York, xii + 247 p.

SOKAL, R. R. & SNEATH, P. H. A., 1963, *Principles of numerical taxonomy.* Freeman, San Francisco, 359 p.

SONNEBORN, T. M., 1974, Breeding systems, reproductive methods, and species problems in Protozoa. In MAYR, E., ed., *The species problem.* Arno Press, New York, p. 155–324.

SONNEBORN, T. M. & DIPPELL, R. V., 1943, Sexual isolation, mating types, and sexual responses to diverse conditions in variety 4, *Paramecium aurelia. Biological Bulletin,* 85: 36–43.

SOOS, A., 1935, Morphologie and Histologie des Geschlechtsapparates der ungarischen *Planorbis*-Arten. *Allattani Közlemények (Budapest),* 32: 21–46.

SPERLICH, D., 1973, Populationsgenetik. Grundlagen und experimentelle Ergebnisse. Fischer, Stuttgart, ix + 197 p.

STANDEN, O. D., 1949, Experimental schistosomiasis. The culture of the snail vectors *Planorbis boissyi* and *Bulinus truncatus. Annals of Tropical Medicine and Parasitology,* 43: 13–22.

STANKOVIČ, S., 1960, The Balkan Lake Ochrid and its living world. Junk, Den Haag, 357 p.

STARMÜHLNER, F., 1974, The freshwater gastropods of Ceylon. *Bulletin of the Fisheries Research Station, Sri Lanka,* 25: 97–181.

STAROBOGATOV, Y. I., 1958, The system and phylogeny of Planorbidae (Gastropoda Pulmonata). *Bulletin of the Moscow Naturalists Society, Biological Department,* 63: 37–53.

STAROBOGATOV, Y. I., 1967, On the systematization of freshwater pulmonate molluscs. *Akademiia Nauk USSR Trudy Zoologičeskogo Instituta,* 42: 280–304.

STURANY, R., 1894, Zur Molluskenfauna der europäischen Türkei. *Annalen des k.k. naturhistorischen Hofmuseums Wien,* 9: 369–390.

THENIUS, E., 1977, *Meere and Länder im Wechsel der Zeiten.* Springer, Berlin, etc., x + 200 p.

THIENEMANN, A., 1950, *Verbreitungsgeschichte der Süsswassertierwelt Europas. Versuch einer historischen Tiergeographie der europäischen Binnengewässer.* Schweizerbart, Stuttgart, xvi + 809 p.

TIMES ATLAS OF THE WORLD, 1967, Comprehensive edition. London, 123 pl., 272 p.

WAGNER, A. J., 1931, Anatomische, biologische und systematische Beiträge zur Kenntnis der ungarischen Limnaeen. *Annales Historico-Naturales Musei Nationalis Hungarici,* 27: 71–157.

WALTER, H. J., 1962, Punctuation of the embryonic shell of Bulininae (Planorbidae) and its possible taxonomic-phylogenetic implications. *Malacologia,* 1: 115–137.

WESTERLUND, C. A., 1865, *Sveriges Land- och Sötvatten-Mollusker.* Gleerups, Lund, 146 p.

WESTERLUND, C. A., 1873, *Fauna molluscorum terrestrium et fluviatilium Sueciae, Norvegiae et Daniae. Sveriges, Norges och Danmarks Land- och Sötvatten-Mollusker. II. Sötvattenmollusker.* Stockholm, 651 p.

WESTERLUND, C. A., 1875, Malakologische Studien, Kritiken und Notizen. *Malakozoologische Blätter,* 22: 51–98.

WESTERLUND, C. A., 1883, Von der Vega-Expedition in Asien gesammelte Binnenmollusken. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft,* 15: 48–59.

WESTERLUND, C. A., 1885, *Fauna der in der palaearctischen Region lebenden Binnenconchylien. 5. Succinidae, Auriculidae, Limnaeidae, Cyclostomidae & Hydrocenidae.* Hakan Ohlsson, Lund, 135 p., Reg. 1–12.

WRIGHT, C. A., 1963, The freshwater gastropod Mollusca of Angola. *Bulletin of the British Museum (Natural History) Zoology,* 10: 447–528.

YEN, T.-C., 1939, Die chinensischen Land- und Süsswasser-Gastropoden des Natur-Museums Senckenberg. *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft,* 444: 1–233.

YEN, T. C., 1949, A new name for *Carinorbis* Yen. *Journal of Paleontology,* 23: 573.

ZILCH, A., 1960, Gastropoda Euthyneura. In SCHINDEWOLF, *Handbuch der Paläozoologie* 6, pt. 2: xii + 834 p.

APPENDIX. Alphabetical List of Collecting Sites (short forms listed in the text)

Locality (reg. no. of mus. coll.)	Other data about local.; collector, sampling date	Nearest place entered in Times Atlas	Lat. ° ′	Long. ° ′
Abitibi R. (NMC 25150)	Canada: Ontario: A. River at Hwy. 579, appr. 27 km N of Cochrane; A. H. Clarke VII-1961	Clute	49.13N	81.00W
Alexandria	Egypt: Ezbet Belal 25 km S of Alex.; Demian III-1966	Alexandria	31.13N	29.55E
Ann Arbor	USA: Michigan. Woods-pool at Zeeb Rd., Te V-1974	Ann Arbor	42.18N	83.43W
Ansbach	Germany: Bavaria: Scheerweiher, 3 km W of Ansbach; H. Stocker I-1966	Ansbach	49.18N	10.36E
Baalbeck	Lebanon (collector and date not indicated)	Ba'albek	34.00N	36.12E
Bad Villach	see Villach			
Bahr-el-Houlé	Syria: running and standing waters near Bahr-el-Houlé (Lake Samachonitides); Bourguignat (no date)	?		
Bangalore	India: Bangalore; Muraleedharan, XII-1973 Mandahl-Barth dedit	Bangalore	12.58N	77.35E
Barracuta (L.)	Australia: East Victoria; Neboiss I-1975	?		

APPENDIX. Continued

Locality (reg. no. of mus. coll.)	Other data about local.; collector, sampling date	Nearest place entered in Times Atlas	Lat. ° ′	Long. ° ′
Benambra	Australia: Corryong Rd., 8 km N of B.; in water beside road; Dartmouth Survey X-1973	Corryong	36.11S	147.58E
Bharatpur	India: Bird sanctuary near Bh.; D. Haas I-1974	Bharatpur	27.14N	77.28E
Biwa (L.)	Japan: Lake Biwa; at Shiotsu and Oura: T. Miura VI-1975; at Eizan: H. D. Boeters II-1975	Kinomoto Otsu	35.33N 35.00N	136.12E 135.50E
Bodensee	Germany: Lake of Constance at Sipplingen/Überlingen; Meier-Br. IX-1961	Überlingen	47.46N	9.10E
Bombala (NMV 2305)	Australia: New S Wales: Saucy Ck.; 10 km S of B., on Cann Valley Hwy.; A.B.R.S. Snail Survey IV-1975	Bombala	36.55S	149.16E
Bukateja	S-central Java; Tjhen VI-1976	Purbolinggo	7.22S	109.15E
Cairo	Egypt: Drain in Giza near pyramids; Demian X-1974	Giza Pyram.	29.59N	31.07E
Chongpyong	Rep. of Korea: Kyong-gi-do: fish pond; Meier-Brook VI/XII-1970	Kapyong	37.53N	127.30E
Diyarbakir	Turkey: Vilayet Diyarbakir; Paydak VI-1972; H. Schütt dedit	Diyarbakir	37.55N	40.14E
Dobersdorfer See	N Germany: Holstein: Probsteierhagen; Meier-Brook IX-1960	Schönberg	54.24N	10.23E
Drusenheim	France: Bas Rhin; Meier-Brook III-1961	Drusenheim	48.46N	7.58E
Dudinska	U.S.S.R.: Siberia: Dudinka/Yenisey, Swed. Sib. Exped. VII-1876	Dudinka	69.27N	86.13E
Ettenheim	SW Germany: Baden; fishpond; Meier-Brook VI-1961	Ettenheim	48.16N	7.52E
Fehmarn	see Wallnau			
Fischau	Austria: Therme Bad Fischau; Meier-Br. IX-1968; Jungbluth X-1974	Bad Fischau	47.50N	16.11E
Gawargin	Afghanistan: Prov. of Helmand (31.26N 64.20E), alt. "750 m" (according to Times Atlas, coordinates are between 200 and 500 m in alt.!); Kawata IX-1968; Mandahl-Barth dedit	Zaras	31.18N	64.13E
Greifensee	Switzerland: E of Zürich; Meier-Brook VII-1961	Greifensee	47.18N	8.42E
Haarlem	Netherlands: "Lake" in Kennemerduinen; R. Bank VIII-1977	Haarlem	52.23N	4.38E
Hanechi-son (ANSP A288)	Japan: Okinawa: channel and ditch along rt. 124 betw. Maeshine and Gabusoka; Davis III-1968	Nakaoshi	26.43N	127.57E

APPENDIX. Continued

Locality (reg. no. of mus. coll.)	Other data about local.; collector, sampling date	Nearest place entered in Times Atlas	Lat. ° ′	Long. ° ′
Haslacher See	Germany: Bavaria: near Burggen; Meier-Brook VIII-1959	Schongau Lech	47.49N	10.54E
Hong Kong	Hong Kong: Island peak in mountain stream; A. J. Brandt IV-1974	Victoria	22.16N	114.13E
Iceland, SE	A. Skaftaffellssysla; pond on Stapasandur, nr. Thveit; Einarsson VIII-1976; dedit Sigurdsson	Bjarnarnes	64.19N	15.13W
Iceland, S	Arnessysla: Opnur, Stora-saurbae, Ölfus; Sigurdsson VII-1976	Kaldadarnes	63.56N	21.10W
Iceland, W	Snaefellsnessysla: Stadarsveit, Kúka & Hofgardatjörn, Yovi-Gardar; Sigurdsson VII-1976	Stadastadur	64.49N	23.00W
Inner Mongolia	See Läger XI			
Iran, S	locality? III-1975 Massoud dedit	?		
Kaejong	Rep. of Korea: Cholla-puk-do; ditch W of rd. Iri-Kunsan; Meier-Brook IX-1970	Kunsan	35.57N	126.42E
Karabella	U.S.S.R.: Kola Peninsula; on Ribatski; Sandebergs Exped. VII-1877	?		
Kasseeteich	Germany: Holstein: near Probsteierhagen; Meier-Brook III-1960	Kiel	54.20N	10.08E
Kolksee	N Germany: Holstein: forest lake near rd. Preetz-Plön; Meier-Br. VII-74	Preetz	54.14N	10.17E
Krasnojarsk (NHRMS 404)	U.S.S.R.: Siberia; Swed. Sib. Exped. 1876	Karsnojarsk	56.05N	92.46E
Kuala Lumpur	Malaysia: 5 km from K.L., large unused tin-mining pool. On grass and *Eichhornia.* J. K. Lie VI-1973	Kuala Lumpur	3.08N	101.42E
Kuehren	N Germany: Holstein: Kührener Viehteich; Meier-Brook VIII-1974	Preetz	54.14N	10.17E
Kumluca	Turkey: well NE Kumluca; Kinzelbach VIII-1975	Kumluca	36.23N	30.17E
Kunsan	Rep. of Korea: Cholla-puk-do: reservoir betw. K. and Air base; Meier-Brook VIII-1970	Kunsan	35.57N	126.42E
Kwekerslaan	Netherlands: greenhouses in Kw., Haarlem; R. Bank VII-1977	Haarlem	52.23N	4.38E
Lake . . .	see proper name			
Läger XI (NHRMS 2198)	P. R. China: Inner Mongolia: Honnentjaggan-tschollogol, a northern tributary of Hoang-ho; Sven Hedin Exped.; Hummel VIII-1927	(?) Ch'ing-tai	41.46N	113.29E
Lesser Slave Lake (NMC 29922)	Canada: Alberta: Slave Lake; Athearn; VII-1965 A. H. Clarke id. et dedit	(?) Slave Lake	55.17N	114.43W

APPENDIX. Continued

Locality (reg. no. of mus. coll.)	Other data about local.; collector, sampling date	Nearest place entered in Times Atlas	Lat. ° ′	Long. ° ′
Liberia	Centra Liberia; Höfler et Knüttgen V-1974	?		
Limyra	Turkey: mouth of a creek 5 km E of Limyra near Finike; Kinzelbach VIII-1975	Finike	36.18N	30.08E
Mainz	W Germany: pond in Bot. Garden Mainz Univ.; Kinzelbach 1973–1974	Mainz	50.00N	8.16E
Malacca	Malaysia: 20 km inland from M., stream running through paddy-field; J. B. Sigurdsson II-1977	Malacca	2.14N	102.14E
Mauna-gawa	Japan: Okinawa; branch of Mauna-gawa, E of Teguchi-village; Davis III-1968	Toguchi	26.40N	127.53E
Mauritius	Beau Bassin, canal; C. N. Courtois VI-1973	Rose Hill	20.14S	57.27E
Merauke (RMNH 5322)	West Irian (New Guinea): pool N of M. in swampy area (cf. v. Benth.-J., 1963: 494); Holthuis III-1955	Merauke	8.30S	140.22E
Mindanao (NHRMS 4166)	Philippines: Davao Penal Colony, 40 km N of Davao City, creek; B. Hubendick VII-1952	Davao	7.05N	125.38E
Motobu-cho (ANSP A266)	Japan: Okinawa: E of Teguchi-village Davis III-1968	Tohuchi	26.40N	127.53E
Niederzell/Untersee	Germany: Lake of Constance: Island of Reichenau (also called Unterzell)	Radolfzell	47.44N	8.59E
Ohrid (L.)	Yugoslavia: Macedonia: Lake Ohrid near Sveti Zaum; Rähle VI-1973	Ohrid	41.06N	20.49E
Onna-son (ANSP A 453)	Japan: Okinawa: paddy field W of Atsuta, along Rt. 1; Davis IV-1968	Atsuta	26.30N	127.50E
Paratunka (NHRMS 3727)	U.S.S.R.: Kamchatka: hot springs near P.; Hultén II-1921	Paratunka	52.58N	158.14E
Pleistinger Wörth	S Germany: Bavaria: island in Donau; Hässlein VIII-1965	Vilshofen	48.38N	13.12E
Prespa (L.)	Yugoslavia: Macedonia: Lake Prespa, Rähle VI-1973; Maassen V-1976	Resen	41.05N	21.01E
Ragunda (NHMG 11249)	Sweden: Jmt.: SW Stormoberget, Ammeråns N strand; Waldén et Wanntorp VII-1961	Ragunda	63.06N	16.25E
Rasno-volok (NHRMS 347)	U.S.S.R.: Kola-peninsula; turbid marsh; Sandebergs Exped. VII-1877	?		
Rhine River Backwater	Germany: Baden: Plittersdorf; Meier-Brook III-1961	Rastatt	48.51N	8.13E

APPENDIX. Continued

Locality (reg. no. of mus. coll.)	Other data about local.; collector, sampling date	Nearest place entered in Times Atlas	Lat. ° ′	Long. ° ′
St. Point (Lac)	France: Dép. Jura: Lac de St. Point F. Geissert 1959	St. Point	46.49N	6.17E
Samava	Iraq: As Samawah/Euphrates; Schlaefli 1873	As Samawah	31.18N	45.18E
Sashiki-son (ANSP A374)	Japan: Okinawa; ditch in Fusozaki along Kaneku-ko Bay; Davis III-1968	Baten	26.12N	127.46E
Sayedabad	"Afghanistan" (30.49N 67.51E); (according to Times Atlas, 1967, these coordinates are in West Pakistan, Quetta Prov.), alt. 2500 m; Kawata VIII-1968; Mandahl-Barth dedit	?Hindubagh	30.51N	67.50E
Selenter See	Germany: Holstein; Meier-Br. III-1960	Lütjenburg	54.17N	10.36E
Seychelles (IRSNB I.G. 25.536)	Ile de Mahé, Riv. Sèche (Route de Misère), Sta. 40; G. Marlier X-1976	Mahé I.	4.41S	55.30E
Siggen	S Germany: Allgäu: Krs. Wangen; Neuweiher near Siggen; Meier-Brook IV-1974	Isny	47.42N	10.02E
Sjaelland	Denmark: lake 1 km N of Jorløse, E of rd. Kalundborg-Slagelse; Burgemeister VII-1976	Jerslev	55.37N	11.15E
Soufflenheim	France: Bas Rhin; inundated meadow NE rd. S Sessenheim; Meier-Brook V-1963	Soufflenheim	48.50N	7.57E
Speyer	SW Germany: Autobahnsee NE Speyer; Fischenich III-1974; Kinzelbach ded.	Speyer	49.18N	8.26E
Stuttgart	Germany: Württemberg: forest pool near Stuttgart-Büsnau; Meier-Brook V-1977	Stuttgart	48.47N	9.12E
Tärna	Sweden: Ly Lpm., SE Granås; 500 m SE of Granås; H. Waldén, Svensson, and Wanntorp VIII-1962	?		
Tage (L.) (RMNH alc. 4985)	West Irian (New Guinea): Lake Tage, near missionary post Tage, Wissel Lake region (cf. v. Benth.-J., 1963: 497); L. D. Brongersma XII-1954	between Uwapa and Mbambawa	3.46S 3.42S	135.31E 137.31E
Taiwan	Rice fields near Hualien-Airport; Lo VI-1975	Hualien	23.58N	121.53E
Tasik Madu	N Bali: Lovina-beach; Tjhen VI-1976	Singaradja	8.06S	115.07E
Thailand (SMF 193798)	Bangkok: Zoolog. Garden; R. Brandt VI-1965	Bangkok	13.44N	100.30E

APPENDIX. Continued

Locality (reg. no. of mus. coll.)	Other data about local.; collector, sampling date	Nearest place entered in Times Atlas	Lat. ° ′	Long. ° ′
Thailand (SMF 197350)	Klong Killard, 4.7 km from Grabi to Khao Thong; R. Brandt X-1969	Krabi	8.04N	98.52E
Titisee	Germany: Baden: Schwarzwald; Meier-Brook X-1961	Titisee	47.55N	8.10E
Tomigusukuson (ANSP A416)	Japan: Okinawa; ditch near Iraha, 1.6 km S Naha air base; Davis III-1968	Oroku/Naha	26.10N	127.40E
Tondano (ZMA)	Sulawesi (Celebes): River near Tondano; Siboga Expedition	Tondano	1.19N	125.56E
Tübingen	S Germany: Quarry pool near Wendelsheim, 6 km W of T.; Meier-Brook VI-1973	Tübingen	48.32N	9.04E
Tulom River (NHRMS 350)	U.S.S.R: Kola peninsula: Tulom R. 10 to 20 verst from Kola; Sandebergs Exped. VII-1877	Kola	68.53N	33.01E
Untersee	see Niederzell			
Ursee	SW Germany: bog in Schwarzwald between Feldberg and Lenzkirch; Meier-Brook IV/VIII-1963	Lenzkirch	47.52N	8.13E
Valtjärn (NHMG 66-11.853)	Sweden: Jmt, 1300 m N of Mattmar K:a, creek just W of Valtjärn; Waldén IX-1966	Mattmar	63.19N	13.45E
Vikarsjön (NHMG 64-11490)	Sweden: Hrj, Vikarsjön S. str. v. Kvarnåns utfl.; Waldén, Svensson and Wanntorp VIII-1962	?		
Villach	Austria: Kärnten: Therme Bad Villach; Mildner VIII-1974	Villach	46.37N	13.51E
Vojmån (NHMG 67-11.982)	Sweden: Ås Lpm, northern part of Gotajaure; Waldén and Hultin VIII-1968	?		
Wallnau/Fehmarn	Germany: Holstein: Island of Fehmarn; Meier-Brook III-1960	Orth	54.27N	11.04E
Westensee	Germany: Schleswig; J. Rentner V-1961	Flemhude	54.20N	9.58E
Windgfällweiher	SW Germany: tarn in Schwarzwald between Feldberg a. Lenzkirch; Meier-Brook VI/IX-1964	Lenzkirch	47.52N	8.13E
Wollmatingen	S Germany: Wollmatinger Ried, part of Bodensee near Reichenau; Meier-Brook VI-1961	Konstanz	47.40N	9.10E
Zürichsee	Switzerland; J. Walter IV-1974	Zürich	47.23N	8.33E

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A REVIEW OF THE NUDIBRANCHS OF THE CALIFORNIA COAST

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ABSTRACT

All of the named species of nudibranchs reported from the California coast are described, including five unnamed species and one previously reported but unnamed species, a total of 101 species comprising 50 genera and 32 families. The species descriptions use the same terminology and present information in the same order to facilitate comparison. An extensive synonymy is given for each species, along with a detailed bibliography. A dichotomous key to aid in identification and drawings of the radula of each species are presented. Location of type-specimens, geographic ranges on the west coast of North America, type-locality, habitat, and food data are also presented. Recent publications and study have resulted in a number of generic reallocations and in changed names due to the law of priority.

INTRODUCTION

This study describes all of the valid species of nudibranchs presently known along the California coast. Five species are included which have not previously been reported from California. It is quite possible that these five species are described from other geographic areas; presently they are identified only to genus until further investigation determines if they are assignable to an already described species. Listing them thus would seem best, as has been done by other workers (e.g. Marcus & Marcus, 1967a: 32), rather than to name them as new species at this time.

At present no publication describes all of the California nudibranch species. Two publications, MacFarland (1966), and Marcus (1961) each treated many, but not nearly all of the species for California. Unfortunately, neither publication presents a key to aid in identification of species.

MacFarland (1966) studied specimens collected over many decades and from numerous localities along the coast. The majority of species were seen alive and color paintings were made. The volume by MacFarland (1966) is based on his extensive notes which were organized by his wife and workers at the California Academy of Sciences after his death in 1951. In the 15 years between his death and the publication of his work, six of his new species were collected and named by other workers. Roller (1970a) found six other species to be junior synonyms of older species. Since MacFarland's work was unfinished at the time of his death, the coverage of species is highly variable; some were described in great detail, while others were only briefly described.

The basis for the study by Marcus (1961) was a collection of preserved specimens collected over a relatively short span of time, mostly from Dillon Beach, Marin Co., and San Diego, California, and sent to Marcus in Brazil. Observation of living specimens is most desirable when preparing descriptions of new species of nudibranchs. Unfortunately, Marcus received only preserved material and never saw any of the species alive. The study is thus of limited usefulness and is deficient in species coverage since only 37 of the total 101 California species are described.

METHODS AND MATERIALS

My personal collection forms the major basis for the present study. The collection contains several thousand specimens collected over a period of ten years. The majority of specimens in the collection is from the central California coast (Pescadero Point, San Ma-

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teo Co., to Pismo Beach, San Luis Obispo Co.), but localities all along the California coast are represented. In addition, the collections of the Department of Invertebrate Zoology, California Academy of Sciences (CAS-IZ) and the collections of the Moss Landing Marine Laboratories were frequently used. Most of the live specimens examined were from the central California coast (viz. Monterey and San Luis Obispo counties); however, some specimens from northern and southern California were also examined alive. Only material which was preserved is listed under material examined.

For two species (viz. *Aeolidiella takanosimensis* and *Cadlina limbaughi*) neither live nor preserved specimens were available for study. In these cases published descriptions were relied upon for information, and color photographs were available for study.

Live specimens were relaxed in 2-phenoxyethanol and preserved in ethanol and butylated hydroxytoluene.

The radula from at least one specimen of each available species was examined. The buccal mass was removed and macerated successively in 10% potassium hydroxide and Clorox (5.25% sodium hypochlorite), cleaned with forceps and teasing needles, rinsed in distilled water and mounted in Turtox CMC-9AF on a microscope slide. Radulae were usually mounted whole to facilitate determination of the radular formula. For certain species it was necessary to separate out individual teeth to facilitate observation of tooth shape. The radula of each species was drawn with the aid of a drawing tube on a Wild M-20 microscope. The radulae are arranged in the figures roughly in taxonomic groups so that similarities and differences may readily be seen. Drawings consist either of an entire half row of the radula, or in cases where teeth are numerous and very similar (e.g. Eudoridacea) of only a few representative teeth.

The body of this work is organized so that a brief generic diagnosis is given first, followed by descriptions of the species, based on observations of both live and preserved specimens and on the literature. In some cases it was not possible to discern certain characters such as the location of the anus (certain aeolids). The descriptions present as complete information about external morphology and coloration as is practicable. Information concerning internal morphology and anatomy is presented only where it may be useful in identification of species. Odhner (1934: 229), in discussing the nudibranchs of the 'Terra Nova' Expedition, said:

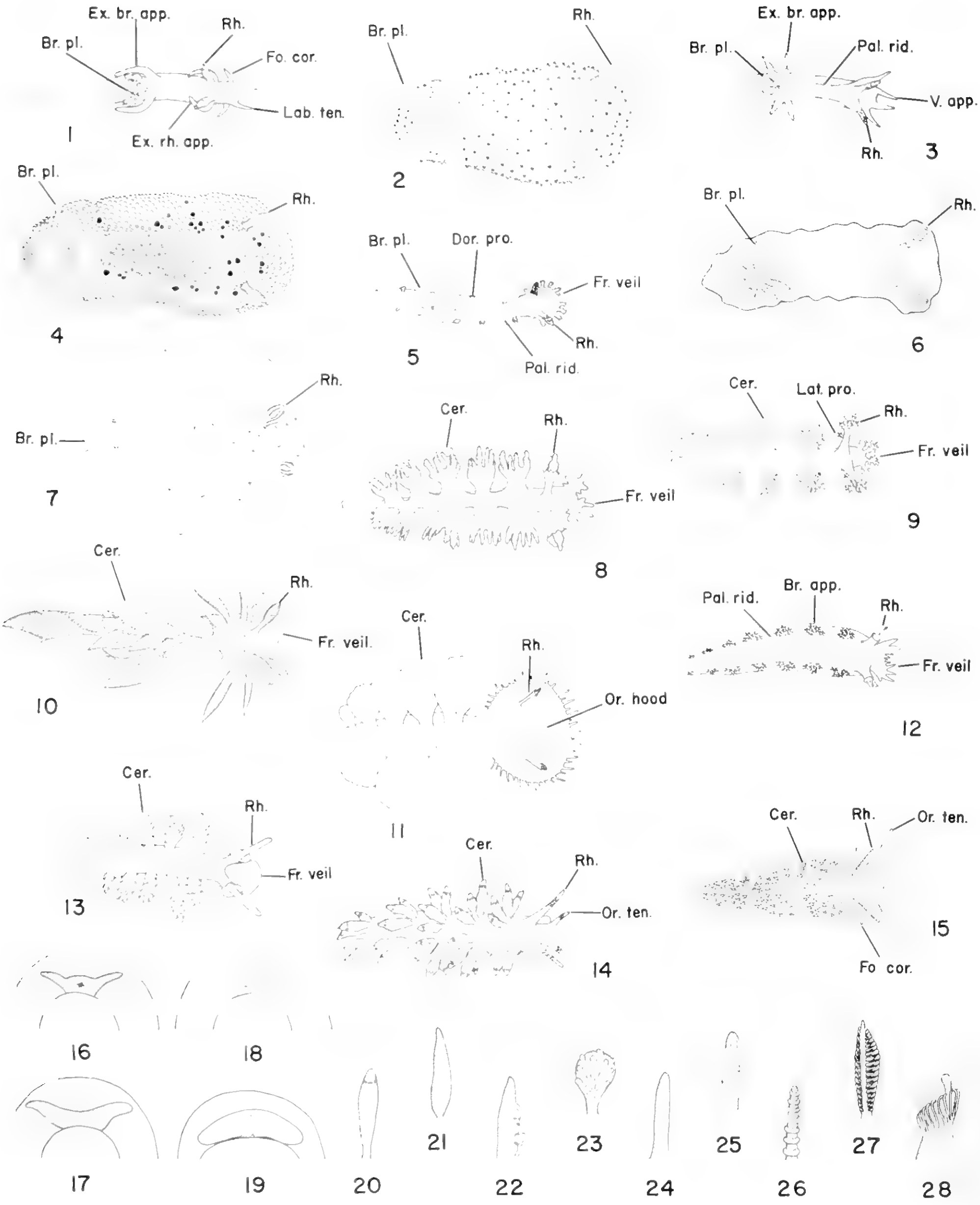
> ". . . I think it necessary to give good figures of the whole animal, and not of details only in the ancient manner of Bergh. His method of description is followed by later authors with the result that one is often very little informed as to the essential external appearance of a species described, and this is the more to be regretted as external shape and features provide not only an immediate means of recognition, but often also important systematic characters."

The descriptions are arranged in alphabetical order so that they may be quickly found. Because the higher taxa are still in a state of flux, it was felt that this arrangement would be more useful than a taxonomic arrangement which may become obsolete in a few years. The species descriptions present information in the same sequence for each species and use the same term for a given structure throughout. Many of the terms used are illustrated in Figs. 1 to 28.

The range limits are listed as exactly as possible in the hope that future collections will show whether the present known ranges are increasing or are still imperfectly known. It must be kept in mind that published ranges for animals frequently better reflect the ranges of collectors than those of the animals.

The total lengths (indicated by T.L.) given are a rough average for California specimens, based on personal observations and the literature. However, individuals may vary widely from the average, and individuals from other areas may regularly be larger or smaller than these averages. A case in point is *Discodoris sandiegensis* which regularly reaches lengths over 100 mm in Elkhorn Slough, California, while 20 miles north and south of this area specimens average 25 mm in length.

The habitat and food notes are based upon the literature and personal observation. While the food habits of some species have been studied in some detail (e.g. *Aeolidia papillosa*), the food of some other species is totally unknown. As a result, the food data given herein are highly variable, but I feel that even stating that a species feeds upon an unidentified ascidian is better than no data. The same sort of variability applies to the habitat information. Some species are very limited (e.g. *Cumanotus beaumonti* is found almost exclusively on *Tubularia crocea* in bays) while



FIGS. 1–28. External morphology. 1, *Trapania*. 2, *Acanthodoris*. 3, *Polycera*. 4, *Anisodoris*. 5, *Triopha*. 6, *Chromodoris*. 7, *Corambe*. 8, *Hancockia*. 9, *Dendronotus*. 10, *Dirona*. 11, *Melibe*. 12, *Tritonia*. 13, *Doto*. 14, *Eubranchus*. 15, *Phidiana*. 16, digitiform labial tentacles. 17, auriculate labial tentacles. 18, labial tentacles absent. 19, crescent-shaped oral veil. 20, clavate ceras. 21, spindle-shaped ceras. 22, ceras with sail-like expansion (*Fiona pinnata*). 23, ceras showing plume-like gill (*Doto*). 24, smooth rhinophore. 25, verrucose rhinophore. 26, annulate rhinophore. 27, perfoliate rhinophore. 28, rhinophore of *Rostanga pulchra*. Abbreviations: Br. app.: branchial appendage; Br. pl.: branchial plumes; Cer.: cerata; Dor. pro.: dorsal process; Ex. br. app.: extra branchial appendage; Ex. rh. app.: extra-rhinophoral appendage; Fo. cor.: foot corner; Fr. veil: frontal veil; Lab. ten.: labial tentacle; Lat. pro.: lateral process; Or. hood: oral hood; Or. ten.: oral tentacle; Pal. rid.: pallial ridge; Rh.: rhinophore; V. app.: velar appendage.

others are found in many areas (e.g. *Phidiana crassicornis*).

Each synonymy lists all the literature dealing with the species, especially publications of taxonomic interest. The synonymies are derived from those previously published, with the addition of new publications and new synonyms. While it is virtually impossible to cite every paper which mentions a given species, the synonymies are as complete as time and facilities would allow, and are the most complete yet published for any of the species discussed. Popular books (viz. Johnson & Snook, 1927; Ricketts & Calvin, 1968; Miner, 1950) which mention various species, have not been cited in the synonymies, except in cases where they give important taxonomic information. They are, however, cited in the bibliography. Publications dealing with the biology of molluscs or opisthobranchs in general (viz. Hoffman, 1932–1940; Fischer *et al.,* 1968; Thiele, 1931; Hyman, 1967; Purchon, 1968; Wilbur & Yonge, 1964, 1966; Morton, 1967) are likewise not listed in the synonymies as they would cause an inordinate increase in the length of the synonymies, but are listed in the bibliography. It is presumed that anyone seeking information about a given species will consult these general references as well as those listed in a synonymy.

The location of type-specimens is listed for those species for which it could be determined.

The key presented should enable the nonspecialist, with a minimum of difficulty, to identify any named species of nudibranch found along the California coast. The key is based on the one in Light's Manual (McDonald, 1975a), but with minor corrections and the addition of eight more species. Using the key requires living specimens, as it is based almost entirely on external morphology and coloration. Preserved specimens are unsuitable as they quickly lose their color and become shrivelled and contorted. Preservation also renders observation of important characters difficult, or even impossible (e.g. number of branchial plumes or number of rhinophore lamellae). Some species are highly variable in color and may not always perfectly fit a key couplet. Further, there are always new and undescribed species being found, as well as occasional specimens with damaged cerata or rhinophores, or other abnormalities.

Four species of nudibranchs which have been described from California are not described herein. *Janolus coeruleopictus* Cockerell & Eliot, 1905, corresponds very closely to *Antiopella barbarensis* (Cooper, 1863b), the only important difference being that in *A. barbarensis* the masticatory margin of the mandibles is denticulate, while in *J. coeruleopictus* it is non-denticulate. This seems sufficient reason to distinguish the two species. Steinberg (1963a: 66) has suggested that *J. coeruleopictus* be considered a *nomen dubium,* based on the meager description.

Tritonia palmeri Cooper, 1863a comes close to *Tritonia diomedea* Bergh, 1894, but since the description of *T. palmeri* is so incomplete, and since *T. palmeri* was found in the intertidal and *T. diomedea* is not reported from the intertidal in southern California, it would be very difficult to consider the two conspecific. Cockerell (1903: 117) and Thompson (1971: 334) consider *T. palmeri* a *nomen dubium.*

Doris alabastrina Cooper (1863a: 204) is described as alabaster white with 12 simple branchial plumes. The only named species from California which approaches *D. alabastrina* is *Cadlina modesta* MacFarland, 1966. However, the description of *D. alabastrina* is so poor that it is best to consider it a *nomen dubium* as suggested by Steinberg (1961: 59).

Chromodoris glauca Bergh, 1879e is discussed with *Hypselodoris californiensis* (*q.v.*).

RESULTS AND DISCUSSION

In attempting to review any group of animals, systematic, nomenclatorial, and other difficulties arise. With the nudibranchs one is confronted at the outset with many problems: several different systems of classification, vast numbers of synonyms, improperly described species, many poorly described species, preoccupied names, a relatively large and widely scattered literature ("There is also the great hydra of literature to be wrestled with . . ." Winckworth, 1932: 217), and a vast and often confusing terminology in which several different terms may refer to the same entity. Furthermore, nudibranchs have few hard parts which can be used as taxonomic characters. This review is intended to help clarify some of these problems.

There are two points which require discussion. First, the use of the radula as a taxonomic character, and second, the difficulties presented by the current classification.

The radula is one of the very few seemingly conservative characters in nudibranchs. As one of the very few hard structures which will remain almost unchanged by preservation, it has been much used in classifying nudibranchs. Radulae have a number of parameters which may be used: the number of transverse rows of teeth, the number of teeth per row, the number of denticles on the teeth, and the shape of the teeth. At present it would appear that the number of denticles and the shape of the radular teeth are useful taxonomic characters at the species level in the Aeolidoidea and Arminoidea and are slightly less useful in the Dendronotoidea and Anadoridacea. In the Eudoridacea the teeth are usually all hamate and little different among species and therefore of little use in separating species. Bertsch (1976b) discusses and documents variation in nudibranch radulae. In comparing the radulae of a number of specimens of *Triopha maculata,* I found that both the number of teeth per transverse row and the number of rows increased with size of the animal. Ferreira (1977) found that the radular teeth increase in size with increased animal size but did not find a significant correlation between number of rows of teeth and animal size. Ontogenetic variation such as found in the radulae of *T. maculata* would account for the discrepancies between previously published radular formulae and those reported here. Another cause of discrepancy is that the rachidian teeth may be vestigial and not obvious unless the radula is properly stained when mounted. More detailed studies are necessary to determine how much the radula varies within a species and within an individual over time. Only then can the real value of radulae as taxonomic characters be determined.

While the classification used herein is not perfect, I feel that it probably best represents the present understanding of the relationships of the nudibranchs. O'Donoghue (1926: 22) in listing the species occurring along the Pacific coast of North America stated:

> "Classifications are by their nature tentative, for they express to a large extent the opinions of their authors regarding relationships and are subject to revision in the light of additional knowledge."

Baba (1937a: 195), in describing the Opisthobranchia of Japan, summarized quite well the state of systematics in the Opisthobranchia when he said:

> "The classification and nomenclature of the Opisthobranchia are serious problems still not satisfactorily solved. Subsequent investigations therefore will render it necessary to alter some of the accounts of the species, genera, or even families contained in this paper, but care has been taken to make them as accurate as possible. The systematic arrangement here adopted is mainly that of Dr. J. Thiele (1931), with some necessary emendations in accordance with the current workers' opinions and on the basis of my study."

More than 40 years later, this statement is still largely true and applies equally well to the present paper except that the systematic arrangement is mainly that of Fischer *et al.* (1968) rather than of Thiele (1931).

Certain of the taxa in the present classification seem ambiguous or inappropriate, for example, the tribes of the Aeolidoidea (viz. Pleuroprocta: anus lateral, outside and beneath the liver branches; Acleioprocta: anus between the right liver and the left liver branches, in the interhepatic space; and Cleioprocta: anus more or less within or behind the second group of cerata). While Odhner (1939: 50) felt that these tribes are clearly distinguished, it now appears that such is not the case. Edmunds (1964: 7) described the new genus *Selva* which has the anus in the cleioproct position but has an armed penis, cuspidate radular teeth, smooth rhinophores, rounded foot, and 2 short rows of cerata to the anterior liver, which are all characteristic of the acleioproct family Cuthonidae. Miller (1971: 312), in discussing the aeolids of the Flabellinidae and Eubranchidae from New Zealand, stated that although Odhner's tribes show evolutionary stages, they cut across the aeolid families rather than separating them. He further stated that at least 2 of the 3 anal positions occur in several families and that there is considerable variation of each of the anal positions. Thus it would seem that the position of the anus may not be a good taxonomic character for division of the Aeolidoidea into tribes. This is especially true since it is a character which is very difficult to observe and is hence not recorded for some species. Schmekel (1970: 134) in an extensive study of the genital organs of nudibranchs concluded that the Acleioprocta form a distinct group, while the Cleioprocta and Pleuroprocta form another distinct group. For this latter group Schmekel formed the infraorder Heteroprocta. While Schmekel's system seems more realistic at present than Odhner's system, the resulting two groups are still not as clearly separated as one might wish. It would thus appear that until the characters used for division of higher taxa are reevaluated and perhaps changed, certain higher taxa are apt to remain in a state of flux. While the existing classifications are not perfect, it is not my intention to propose a better system, but only to place the California species into the existing system as best as possible. Ideally, in order to improve and somewhat stabilize the classification it is necessary to study all species of nudibranchs worldwide, decide which characters best distinguish the various taxa, and then to arrange them in a taxonomic hierarchy.

CLASSIFICATION OF THE NUDIBRANCHS KNOWN TO OCCUR IN CALIFORNIA

> ". . . there is nothing to be done in the wide boundless field of natural history without a system."—Gilbert White

This classification is taken largely from Fischer *et al.* (1968), with addition of some new taxa and corrections due to nomenclatorial changes.

- ORDER—NUDIBRANCHIA
  - SUBORDER—Doridoidea Odhner, 1934 (=Holohepatica Bergh, 1881)
    - Superfamily—Anadoridacea Odhner, 1939 (=Phanerobranchia Fischer, 1883)
      - Tribe—Suctoria Bergh, 1892
        - Family—Corambidae Bergh, 1892
          - *Corambe* Bergh, 1869
          - *Doridella* Verrill, 1870
        - Family—Goniodorididae H. & A. Adams, 1854
          - Subfamily—Okeniinae Iredale & O'Donoghue, 1923
            - *Okenia* Menke, 1830, ex Leuckart in Bronn, Ms.
          - Subfamily—Anculinae Pruvot-Fol, 1954
            - *Ancula* Lovén, 1846
            - *Trapania* Pruvot-Fol, 1931
          - Subfamily—Hopkinsiinae Odhner, 1968
            - *Hopkinsia* MacFarland, 1905
        - Family—Onchidorididae Alder & Hancock, 1845
          - *Acanthodoris* Gray, 1850
          - *Onchidoris* Blainville, 1816
      - Tribe—Nonsuctoria Bergh, 1892
        - Family—Triophidae Odhner, 1941
          - Subfamily—Triophinae Odhner, 1968
            - *Crimora* Alder & Hancock, 1862
            - *Triopha* Bergh, 1880
        - Family—Aegiretidae Fischer, 1883
          - *Aegires* Lovén, 1844
        - Family—Polyceratidae Alder & Hancock, 1845
          - *Laila* MacFarland, 1905
          - *Polycera* Cuvier, 1817
    - Superfamily—Eudoridacea Odhner, 1934 (=Cryptobranchia Fischer, 1883)
      - Family—Cadlinidae Bergh, 1891
        - Subfamily—Cadlininae
          - *Cadlina* Bergh, 1878
      - Family—Chromodorididae Bergh, 1891
        - *Chromodoris* Alder & Hancock, 1855
        - *Hypselodoris* Stimpson, 1855
      - Family—Actinocyclidae Pruvot-Fol, 1934
        - *Hallaxa* Eliot, 1909
      - Family—Conualeviidae Collier & Farmer, 1964
        - *Conualevia* Collier & Farmer, 1964
      - Family—Aldisidae Odhner, 1939
        - *Aldisa* Bergh, 1878
      - Family—Rostangidae Pruvot-Fol, 1951
        - *Rostanga* Bergh, 1879
      - Family—Dorididae Rafinesque, 1815
        - *Doris* Linnaeus, 1758
      - Family—Archidorididae Bergh, 1892
        - *Archidoris* Bergh, 1878
        - *Atagema* Gray, 1850
      - Family—Discodorididae Bergh, 1891
        - Subfamily—Discodoridinae Bergh, 1891
          - *Anisodoris* Bergh, 1898
          - *Discodoris* Bergh, 1877
          - *Thordisa* Bergh, 1877
      - Family—Asteronotidae Thiele, 1931
        - *Sclerodoris* Eliot, 1904
      - Family—Platydorididae Bergh, 1891
        - Subfamily—Platydoridinae Bergh, 1891
          - *Platydoris* Bergh, 1877

Superfamily—Porodoridacea Odhner, 1968
(=Porostomata, Bergh, 1892)
Family—Dendrodorididae O'Donoghue, 1924
Dendrodoris Ehrenberg, 1831
SUBORDER—Dendronotoidea Odhner, 1936
Family—Tritoniidae Lamarck, 1809
Tochuina Odhner, 1963
Tritonia Cuvier, 1798
Family—Hancockiidae MacFarland, 1923
Hancockia Gosse, 1877
Family—Dendronotidae Sars, 1878
Dendronotus Alder & Hancock, 1845
Family—Tethyidae Fischer, 1883
Melibe Rang, 1829
Family—Dotidae Gray, 1853
Doto Oken, 1815
SUBORDER—Arminoidea Odhner, 1934
Superfamily—Euarminacea Odhner, 1968
Family—Arminidae Pruvot-Fol, 1927
Armina Rafinesque, 1814
Superfamily—Metarminacea Odhner, 1968
Tribe—Pachygnatha
Family—Dironidae MacFarland, 1912
Dirona Eliot in Cockerell & Eliot, 1905 ex MacFarland, Ms.
Family—Zephyrinidae
Antiopella Hoyle, 1902
SUBORDER—Aeolidoidea Odhner, 1934
Superfamily—Eueolidacea Odhner, 1968
Tribe—Pleuroprocta Odhner, 1939
Family—Coryphellidae Bergh, 1892
Coryphella Gray, 1850
Tribe—Acleioprocta Odhner, 1939
Family—Eubranchidae Odhner, 1934
Subfamily—Cumanotinae Odhner, 1968
Cumanotus Odhner, 1907
Subfamily—Eubranchinae Odhner, 1934
Eubranchus Forbes, 1838
Family—Cuthonidae Odhner, 1934
Subfamily—Precuthoninae Odhner, 1968
Precuthona Odhner, 1929
Subfamily—Cuthoninae Odhner, 1934
Cuthona Alder & Hancock, 1855
Tenellia Costa, 1866
Family—Fionidae Alder & Hancock, 1855
Fiona Alder & Hancock, 1855
Tribe—Cleioprocta Odhner, 1939
Family—Phidianidae Odhner, 1968
Subfamily—Phidianinae Miller, 1974
Phidiana Gray, 1850
Subfamily—Babakininae Roller, 1973
Babakina Roller, 1973
Family—Aeolidiidae Orbigny, 1834
Aeolidia Cuvier, 1797
Aeolidiella Bergh, 1867
Cerberilla Bergh, 1873
Family—Spurillidae Odhner, 1939
Spurilla Bergh, 1864

KEY TO THE SPECIES OF NUDIBRANCHS KNOWN TO OCCUR IN CALIFORNIA

"If one does not know the names, one's knowledge of things is useless."—Isidorus

1. Gills (branchial plumes) located posteriorly on dorsum (Figs. 1–6) or in 3 groups directed posteriorly 2
1′. Gills (branchial plumes) not located posteriorly on dorsum; respiratory surface otherwise 52
2.(1) With extra-branchial appendages (Figs. 1, 3) 3
2′. Without extra-branchial appendages 9
3.(2) With extra-rhinophoral appendages (Fig. 1); branchial plumes 3 4
3′. Without extra-rhinophoral appendages; branchial plumes usually more than 3 . . . 6
4.(3) Each rhinophore shaft with 1 extra-rhinophoral appendage (Fig. 1); ground color whitish; longitudinal brownish lines running most of the length of body; distal tips of rhinophores, oral tentacles, tips of branchial plumes, extra-branchial and extra-rhinophoral appendages orange-yellow . . . . *Trapania velox*

4.′ Each rhinophore shaft with 2 extra-rhinophoral appendages 5
5.(4′) With 1 extra-branchial appendage on each side; ground color translucent tan to whitish; head, tail, and sides of body with irregular patches of dark reddish-brown . . . . *Ancula lentiginosa*
5′. With 4 or more extra-branchial appendages on each side; ground color translucent yellowish-white; 3 longitudinal yellow lines running most of the length of body; rhinophores and extra-branchial appendages with subapical orange-yellow band . . . . *Ancula pacifica*
6.(3′) Body covered with numerous tubercles; yellow spots on body and on tips of low tubercles; body color dark brownish; branchial plumes 3–5 . . . . *Polycera zosterae*
6′. Body not covered with numerous tubercles 7
7.(6′) Overall body color translucent grayish-white; velar appendages (Fig. 3) and extra-branchial appendages with black on proximal third and a yellow ring immediately distal of black pigment; branchial plumes 5–6, blackish with yellow lines . . . . *Polycera tricolor*
7′. Overall body color blackish 8
8.(7′) With oblong orange spots occurring between longitudinal black lines running the length of the body; branchial plumes 7–11 . . . . *Polycera atra*
8′. With closely set small black dots on body; rhinophores, corners of foot, velar and extra-branchial appendages with yellowish-orange; caudal crest and upper edge of foot with streaks of yellow-orange; branchial plumes 7–9 . . . . *Polycera hedgpethi*
9.(2′) Rhinophores smooth (Fig. 24); ground color opaque white 10
9′. Rhinophores not smooth; ground color variable 11
10.(9) Dorsum with large cylindrical tubercles; usually with many irregularly scattered dark brown to black spots; branchial plumes 3; rhinophore sheaths with 5–6 high, rounded tubercles . . . . *Aegires albopunctatus*
10′. Dorsum nearly smooth, tubercles minute; lacking any brown or black; branchial plumes about 8; rhinophores long and tapered (Fig. 24); lateral edge of dorsum with opaque white glands . . . . *Conualevia alba*
11.(9′) With dorsal processes (Fig. 5) other than tubercles or papillae on dorsum or sides of body 12
11′. Dorsum without dorsal processes, but with tubercles (Fig. 4) or papillae (Fig. 5) or entirely smooth (Fig. 6) 19
12.(11) Dorsal processes simple 13
12′. Dorsal processes bifurcated, branched or tuberculate distally 16
13.(12) Body color entirely rose pink; with many long dorsal processes covering entire dorsum; branchial plumes 7–14 and usually darker pink than dorsal processes . . . . *Hopkinsia rosacea*
13′. Body color not pink 14
14.(13′) Dorsal processes club-shaped and tipped with orange-red; branchial plumes 5; ground color white to pale yellow; white or orange low tubercles medially on dorsum; rhinophores tipped with orange-red . . . . *Laila cockerelli*
14′. Dorsal processes not club-shaped, not tipped with orange-red 15
15.(14′) Dorsum with a single median process; branchial plumes 8–11; body flattened dorso-ventrally; ground color whitish with minute brownish spots; 5 marginal processes on each side . . . . *Okenia plana*
15′. Dorsum with 5–7 median processes; branchial plumes 5–7; body limaciform; ground color translucent white with small yellow flecks and greenish-gray patches; with numerous rather long papillae . . . . *Okenia angelensis*
16.(12′) Dorsum with tubercles or processes medially, in addition to dorso-lateral and frontal marginal processes; ground color whitish 17
16′. Dorsum smooth medially; with dorso-lateral and frontal marginal processes; ground color yellow or orange 18
17.(16) Dorsal processes and frontal marginal processes with a subapical orange ring and often tipped with black; branchial plumes 3 . . . . *Crimora coneja*

17′. Dorsal processes and frontal marginal processes orange tipped; branchial plumes 5 . . . . *Triopha catalinae*

18.(16′) Branchial plumes whitish with reddish tips; ground color pale yellow to yellowish-brown, dorsal processes tipped with reddish-orange; powder blue spots on dorsum . . . . *Triopha occidentalis*

18′. Branchial plumes yellowish with orangish tips; ground color orange to orange-brown, usually quite dark; dorsal processes usually tipped with dark orange; dorsum with numerous small blue dots in larger specimens . . . . *Triopha maculata*

19.(11′) Branchial plumes in 2 semicircles (∩∩) or in 3 groups directed posteriorly 20

19′. Branchial plumes in a single circlet 21

20.(19) Branchial plumes 16–32, in form of 2 semicircles united anteriorly (∩∩); ground color brownish-white, usually with 2–3 irregular longitudinal brownish stripes on dorsum; many large, conspicuous tubercles on dorsum . . . . *Onchidoris bilamellata*

20′. Branchial plumes 3, directed posteriorly from beneath 3 thick, bluntly triangular lobes; ground color raw umber with many small dark brown to black spots on dorsum; dorsum with many small, hispid papillae; dorsum with a prominent, irregular ridge extending along midline . . . . *Atagema alba*

21.(19′) Labial tentacles (Fig. 16) absent or minute and rudimentary (Fig. 18) 22

21′. Labial tentacles present, in form of tentacles or veil 25

22.(21) Ground color white to grayish-white 23

22′. Ground color yellow to orange or chestnut brown 24

23.(22) Ground color white; dorsum with numerous brown to black, irregular blotches and flecks; mantle margin undulating; body rather long and narrow . . . . *Dendrodoris* sp. b

23′. Ground color grayish-white; dorsum with numerous minute, brownish flecks which are more concentrated medially; about 4–5 opaque white blotches dorso-laterally on dorsum . . . . *Dendrodoris nigromaculata*

24.(22′) Branchial plumes white to pale yellowish; tubercles on dorsum with a small, apical, white dot; ground color yellow to chestnut brown . . . . *Dendrodoris albopunctata*

24′. Branchial plumes orangish; white dots on dorsum and on tubercles; ground color yellow-orange . . . . *Dendrodoris* sp. a

25.(21′) Body color red, or if orange, then dorsum velvety (with minute papillae) and branchial plumes 8 or more and same color as body 26

25′. Body color not red; if orange, then dorsum with distinct tubercles or papillae . . . 28

26.(25) Clavus of rhinophores with a blunt cylindrical process above the lamellae (Fig. 28), nearly one fourth the length of the entire rhinophore; frequently with minute brownish-black dots on dorsum . . . . *Rostanga pulchra*

26′. Rhinophores perfoliate (Fig. 27), lacking blunt cylindrical process above lamellae 27

27.(26′) With 1–2 black spots on midline of dorsum, one just posterior of rhinophores and the other just anterior of branchial plumes (rarely one or both may be absent) . . . . *Aldisa sanguinea*

27′. Lacking black spots; dorsum deep dark red, rather velvety smooth; body greatly flattened dorso-ventrally . . . . *Platydoris macfarlandi*

28.(25′) Ground color blue or deep violet; dorsum smooth, lacking any obvious tubercles or papillae 29

28′. Ground color not blue or deep violet; dorsum with tubercles or papillae or smooth 31

29.(28) Ground color deep violet; dorsum with 3 longitudinal, bright yellow lines; edge of dorsum with a submarginal white band . . . . *Chromodoris macfarlandi*

29′. Ground color blue 30

30.(29′) Dorsum with 2 longitudinal series of about 7 yellow to golden spots; anterior edge of dorsum and sides of foot also with yellow spots . . . . *Hypselodoris californiensis*

30′. Dorsum with 2 longitudinal bright yellow stripes, ending anteriorly at the rhinophores, and a single bright yellow stripe anterior of rhinophores; a median light blue line extending from between rhinophores to branchial plumes; margin of dorsum with a narrow white band .... *Chromodoris porterae*

31.(28′) Labial tentacles large and auriculate (Fig. 17) extending nearly to edge of dorsum; dorsum thickly set with long papillae 32

31′. Labial tentacles small and digitiform (Fig. 16) to triangular, extending less than half way to edge of dorsum, or in form of small crescent-shaped veil; dorsum with or without papillae 37

32.(31) Ground color orange; dorsum with numerous flecks of yellow; branchial plumes 9, whitish .... *Acanthodoris lutea*

32′. Ground color not orange 33

33.(32′) Ground color brownish, flecked with irregular blotches of black; branchial plumes 7, tipped with lemon yellow .... *Acanthodoris brunnea*

33′. Ground color white to grayish-white 34

34.(33′) Dorsal papillae tipped with black 35

34′. Dorsal papillae tipped with yellow 36

35.(34) Edge of dorsum with an outer yellow and an inner black band; branchial plumes 5; rhinophores and branchial plumes tipped with reddish-brown to black .... *Acanthodoris rhodoceras*

35′. Edge of dorsum without an outer yellow and an inner black band; branchial plumes 5–9 .... *Acanthodoris pilosa*

36.(34′) Rhinophores and branchial plumes tipped with brown or maroon; branchial plumes 7–9 .... *Acanthodoris nanaimoensis*

36′. Rhinophores and branchial plumes tipped with yellow; branchial plumes 5; edge of dorsum with yellow band .... *Acanthodoris hudsoni*

37.(31′) Dorsum with black or brown pigment, not including rhinophores or branchial plumes 38

37′. Dorsum lacking black or brown pigment 46

38.(37) Dorsum with a lateral series of small brown to black dots with yellow centers; ground color salmon to yellowish-pink; branchial plumes 12 ...... *Cadlina sparsa*

38′. Dorsum lacking black dots with yellow centers 39

39.(38′) Rhinophores tipped with maroon to brownish-black; dorsum with small tubercles, largest of which are tipped with brown; ground color yellowish .... *Hallaxa chani*

39′. Rhinophores not tipped with maroon to brownish-black 40

40(39′) Branchial plumes 8–10, tripinnate, sprinkled with minute brownish flecks, whitish distally; blackish pigment in form of many very small dots, with a single major concentration just anterior of branchial plumes; ground color yellowish to yellowish-brown; tubercles small .... *Discodoris heathi*

40′. Branchial plumes less than 8; blackish pigment not in a single major concentration forming a blotch on dorsum 41

41.(40′) Dorsum with small tubercles which give dorsum a velvety appearance 42

41′. Dorsum with large, conspicuous tubercles 43

42.(41) With numerous, minute flecks of opaque white on margin of dorsum, forming a diffuse band; dorsum with irregularly oval, light brown spots and numerous minute light brown flecks; branchial plumes 6 .... *Doris* (s.l.) sp.

42′. Lacking diffuse white band around margin of dorsum; dorsum with brown to almost black rings, or occasionally blotches, of various sizes; branchial plumes 6–7 .... *Discodoris sandiegensis*

43.(41′) Dorsum with numerous large, irregular tubercles which bear smaller tubercles; ground color light yellowish-tan; dorsum with irregularly round, dark tan to brown blotches between the large tubercles; ventral surface of foot and mantle margin with flecks of brown; branchial plumes 7 .... *Sclerodoris tanya*

43′. Dorsum with numerous large rather regular tubercles which do not bear smaller tubercles 44

44.(43′) Dorsum with 2 brown to blackish blotches formed of smaller spots on midline; ground color whitish to yellow or orange; dorsum with many papillae; branchial plumes 6 .... *Thordisa bimaculata*

44′. Dorsum lacking 2 brown to blackish spots on midline 45

45.(44′) Blackish pigment in blotches on both dorsum and tubercles; branchial plumes 7, yellowish; ground color light yellow to orange-yellow . . . *Archidoris montereyensis*

45′. Blackish blotches on dorsum only, not on tubercles; branchial plumes 6, whitish; ground color light yellow to yellow-orange . . . . *Anisodoris nobilis*

46.(37′) Clavus of rhinophores brown to black 47

46′. Clavus of rhinophores white to yellow 48

47.(46) Branchial plumes brown to black; ground color whitish; dorsal and ventral surfaces of foot and sides of body with minute black spots . . . . *Cadlina limbaughi*

47′. Branchial plumes white to yellow; ground color whitish to yellow; lateral edges of dorsum with 6–10 yellow dots on each side, anterior-most dot usually posterior of rhinophores . . . . *Cadlina flavomaculata*

48.(46′) Dorsum with yellow band around edge and with yellow tipped tubercles; ground color whitish to pale yellow; branchial plumes 6, tipped with yellow . . . . *Cadlina marginata*

48′. Dorsum lacking yellow band around edge 49

49.(48′) Dorsum with many long, slender papillae giving animal a fuzzy appearance; branchial plumes 9–12, unipinnate; ground color white to yellowish-white; dorsum with many opaque white flecks . . . . *Onchidoris hystricina*

49′. Dorsum lacking long, slender papillae 50

50.(49′) Dorsum with many bulbous tubercles which appear nearly spherical; ground color yellowish-white to yellow-orange; rhinophores orange-yellow, with yellow tips; tubercles tipped with orange . . . . *Onchidoris* sp.

50′. Tubercles, if present, not bulbous, not appearing spherical 51

51.(50′) Ground color pure white with white tubercles of various sizes on dorsum; branchial plumes 7, white, rather fluffy in appearance . . . . *Archidoris odhneri*

51′. Ground color pale yellow; branchial plumes 10–12, yellowish-white; dorsum with several small, yellow dots along lateral edges, anterior-most dots extending anterior of rhinophores . . . . *Cadlina modesta*

52.(1′) With cerata (Figs. 8–11, 13–15), or with branched branchial plumes arranged laterally on dorsum (Fig. 12) 53

52′. Without cerata 98

53.(52) Cerata or branchial plumes branched (Figs. 8, 9, 12) 54

53′. Cerata not branched (Figs. 10, 11, 13–15) 62

54.(53) Cerata palmately branched, each with 4–26 digitiform projections (Fig. 8); cerata in 4–7 pairs; head with a broad palmate velar lobe on either side, each with 6–10 or more unequal digitiform processes; ground color reddish-brown in mature individuals, younger individuals translucent greenish-brown . . . . *Hancockia californica*

54′. Cerata not palmately branched 55

55.(54′) Processes on frontal veil simple (Fig. 12) or lacking 56

55′. Processes on frontal veil branched (Fig. 9) 58

56.(55) Dorsum distinctly tuberculate, each tubercle tipped with white; ground color deep orange-yellow to yellow-brown; body margins with an irregular series of low white branchial plumes; foot edged with narrow white band . . . . *Tochuina tetraquetra*

56′. Dorsum not distinctly tuberculate 57

57.(56′) Ground color white to yellowish-white; frontal veil (Fig. 12) with 7–12 digitiform processes; body margins with 11–15 branchial plumes on each side; fine reticulate opaque white lines on dorsum; foot edged with a narrow band of opaque white . . . . *Tritonia festiva*

57′. Ground color rose pink; frontal veil with 10–30 white processes; body margins with about 20–30 branchial plumes; margins of foot, margins of dorsum, and edge of rhinophore sheath bear a narrow white line . . . . *Tritonia diomedea*

58.(55′) Rhinophore shaft with a lateral process (Fig. 9) 59

58′. Rhinophore shaft lacking a lateral process; frontal veil with 4–6 stout, branched processes; margin of rhinophore sheath with 5–7 short, blunt processes which are shorter than clavus; dorsum with 4 distinct longitudinal light brown lines running from posterior of rhinophore shaft to tip of tail; ground color extremely variable, may be yellow, brown, orange, greenish, or white; 3–6 pairs of cerata . . . . *Dendronotus subramosus*

59.(58) Posterior face of rhinophore shaft with vertical row of 3–6 small, slightly branched processes; lateral process arising near base of rhinophore shaft; usually 4 pairs of branched velar processes; dorsal edge of foot usually with an opaque white line; ground color may be white, gray, brownish, orange-red, or maroon; 4–7 pairs of cerata which may be tipped with orange, yellow, or purple . . . . *Dendronotus iris*

59′. Posterior face of rhinophore shaft lacking vertical row of small, slightly branched processes; margin of rhinophore sheath usually with 5 long processes 60

60.(59′) With a narrow, median, opaque white line extending posteriorly from between the last cerata to tip of tail 61

60′. Without a white line dorso-medially on tail; ground color variable, translucent grayish-white, greenish, or even brownish; cerata in 3–9 pairs; frontal veil usually with 3 pairs of branched processes . . . . *Dendronotus frondosus*

61.(60) Frontal veil with 2 pairs of branched processes; general ground color translucent grayish-white; 4–8 pairs of cerata . . . . *Dendronotus albus*

61′. Frontal veil with 3 pairs of branched processes; ground color translucent grayish-white or lilac; 4–5 pairs of cerata . . . . *Dendronotus diversicolor*

62.(53′) With large oral hood (Fig. 11), having 2 rows of cirri on margin; about 5–6 pairs of petal-like cerata; ground color yellowish-brown to greenish-brown . . . . *Melibe leonina*

62′. Lacking large oral hood with cirri 63

63.(62′) Rhinophores perfoliate (Fig. 27) or annulate (Fig. 26), not smooth or verrucose . . . 64

63′. Rhinophores smooth (Fig. 24) or verrucose (Fig. 25), not perfoliate or annulate . . . 75

64.(63) Cerata extending well in front of rhinophores and same color as rhinophores . . . 65

64′. Cerata not extending well in front of rhinophores 67

65.(64) Cerata spindle-shaped (Fig. 21); lacking frontal veil; oral tentacles present; cerata with a subapical band of yellow-orange, tips blue or white; an orange-red crest between rhinophores; ground color translucent grayish-white . . . . *Antiopella barbarensis*

65′. Cerata lanceolate (Fig. 10); with a distinct frontal veil; oral tentacles absent 66

66.(65′) Cerata usually with irregular bumps; ground color light brown to greenish-gray with fine yellowish-white, olive green, and pink dots; a pale red spot on outer side of each ceras . . . . *Dirona picta*

66′. Cerata smooth, lateral margin of each with an opaque white line; anterior edge of frontal veil and median crest of tail with opaque white line; ground color translucent grayish-white . . . . *Dirona albolineata*

67.(64′) Rhinophores arising from a single median stalk, Y-shaped; cerata pinkish-red on proximal half, followed distally by a wide band of opaque white, then a narrow band of yellow-orange below translucent tip; ground color whitish to pinkish . . . . *Babakina festiva*

67′. Rhinophores not on a single, common shaft 68

68.(67′) With an opalescent blue line along edge of foot; double opalescent blue median lines running the length of body and enclosing a bright orange-yellow elongate spot between and posterior of rhinophores and another in cardiac region; cerata with a subapical band of orange-yellow, cores extremely variable in color . . . . *Phidiana crassicornis*

68′. Lacking opalescent blue lines 69

69.(68′) Rhinophores annulate 70

69′. Rhinophores perfoliate 72

70.(69) Oral tentacles brilliant vermilion to scarlet-red or yellow to deep cadmium orange distally 71

70′. Oral tentacles encrusted with opaque white dots distally; rhinophores pale yellowish-green distally; cerata with subterminal band of rich brown, cores deep olive-green to brownish-green . . . . *Coryphella pricei*

71.(70) With an opaque white line dorso-medially and similar lines dorso-laterally; tips of cerata whitish, cores usually reddish to orange, occasionally brownish . . . . *Coryphella trilineata*

71′. Lacking opaque white lines on dorsum; ground color light pinkish; with an irregular band of scarlet-orange to vermilion on either side of head and a band of similar color below tip of each ceras . . . . *Phidiana stearnsi*

72.(69′) Ground color deep purple; rhinophores perfoliate, lamellae deep maroon; cerata violet proximally, grading to flaming scarlet or orange distally . . . . *Coryphella iodinea*

72′. Ground color not deep purple 73

73.(72′) With a narrow orange-red line between and on the proximal half of the oral tentacles; cerata with pink tinge throughout, cores dark brown to black . . . . *Phidiana hiltoni*

73′. Lacking narrow red line between oral tentacles 74

74.(73′) Cerata orange-red with white tips; ground color grayish-white; dorsum along midline free of cerata; head usually with a pale orange spot . . . . *Spurilla oliviae*

74′. Cerata cores greenish-brown, cerata with pink tinge, tipped with white; ground color dull orange; midline of dorsum with irregular patches of opaque white; oral tentacles very stout . . . . *Spurilla chromosoma*

75.(63′) Oral tentacles present and digitiform 77

75′. Oral tentacles rudimentary or absent or in the form of a frontal veil 76

76.(75′) Rhinophore sheath calyciform (Fig. 13); cerata large and bulbous with a plume-like gill on inner surface (Fig. 13) 78

76′. Rhinophore sheath absent; cerata lacking plume-like gill 80

77.(75) Each ceras with thin sail-like expansion on posterior edge (Fig. 22); ground color translucent gray to brownish . . . . *Fiona pinnata*

77′. Cerata lacking posterior sail-like expansion 81

78.(76) With brown to black on body 79

78′. Lacking brown to black on body or cerata; cerata cores orange to pinkish, cerata rather bulbous; ground color pale yellowish-white; tubercles on cerata elongate . . . . *Doto amyra*

79.(78) Cerata with black rings at base of tubercles; upper border of rhinophore sheaths smooth; ground color whitish with brown on head, dorsum, and sides . . . . *Doto columbiana*

79′. Cerata lacking black rings at base of tubercles; upper border of rhinophore sheaths somewhat scalloped; ground color white to yellowish; cerata long with yellowish to brown cores . . . . *Doto kya*

80.(76′) Cerata usually in groups of 1–2, longest cerata shorter than body length; ground color white to yellowish-white; a few black specks on dorsum . . . *Tenellia adspersa*

80′. Cerata very long, longest about equal to body length, some groups with more than 2 cerata; ground color grayish-green to light brownish; cerata cores brownish-yellow to bluish-green, with network of similar colored lines on dorsum between groups . . . . *Cumanotus beaumonti*

81.(77′) Dorsum with a distinct (sometimes discontinuous) opaque white line medially . . . 82

81′. Dorsum without a distinct opaque white line medially 83

82.(81) Usually with a greenish-blue patch anterior and to the left of cardiac region; cerata with few, very minute, opaque white dots; cerata cores reddish-brown; ground color translucent grayish-white with pink tinge . . . . *Coryphella cooperi*

82′. Lacking a greenish-blue patch in cardiac region; cerata with numerous opaque white dots; cerata cores pinkish-brown distally and greenish-brown proximally; ground color translucent grayish-white without pink tinge . . . . *Coryphella* sp.

83.(81′) Rhinophores with various amounts of orange to red 84

83′. Rhinophores lacking orange to red 87

84.(83) Dorsum with distinct opaque white blotches medially; foot corners distinct; vermilion on oral tentacles, rhinophores, head, and dorsum; cerata tipped with white and with a narrow white band below tip, cores brownish . . . . *Aeolidiella takanosimensis*

84′. Dorsum lacking distinct opaque white blotches medially; foot corners indistinct . . . 85

85.(84′) Oral tentacles with white on at least distal half; tail with median opaque white line 86

85′. Oral tentacles orange-red with white tips; tail lacking median opaque white line; cerata recumbent with broad, opaque white band extending from base to tip of each ceras, covering distal third, cores brownish .... *Cuthona columbiana*

86.(85) Rhinophores white distally; light orange covering front of head, extending one quarter of the way up rhinophores and on bases of oral tentacles; cerata with small, opaque white spots, cores brownish to dark green .... *Cuthona flavovulta*

86′. Rhinophores orange-red for nearly entire length; large orange-red spot between oral tentacles and anterior of rhinophores; cerata with orange-red tips and blackish cores .... *Cuthona lagunae*

87.(83′) Cerata irregularly inflated, warty in appearance (Fig. 14) 88

87′. Cerata not irregularly inflated, not warty 90

88.(87) Anterior foot corners tentaculiform; rhinophores frequently with 2–3 brown rings; oral tentacles frequently with a subterminal, brown ring; numerous distinct brown dots on dorsum, extending up onto cerata; each ceras with a subapical yellow ring .... *Eubranchus misakiensis*

88′. Anterior foot corners not produced into tentaculiform processes 89

89.(88′) With a fairly broad, wavy band of deep olive green dorso-medially on the dorsum; cerata cores deep olivaceous green; rhinophores frosted with small, opaque white dots distally and with a subterminal band of brownish to olivaceous green; body color pale, translucent yellowish-green, with numerous light brown spots .... *Eubranchus olivaceus*

89′. Lacking a band of deep olive green dorso-medially on dorsum; rhinophores and oral tentacles with subapical band of brownish to light gray or greenish; sides of body with small yellow dots .... *Eubranchus rustyus*

90.(87′) With 2 median light orange oval spots, one spot anterior and one posterior of base of rhinophores; opaque white dots on distal third of rhinophores and oral tentacles; an irregular, longitudinal series of white blotches medially on dorsum; cerata with 3 dark brownish-black bands, cores ochre ...... *Phidiana morroensis*

90′. Lacking median light orange spots anterior and posterior of rhinophores 91

91.(90′) With band of purple midway on oral tentacles and rhinophores; cerata cores yellowish proximally, olive green to brown medially, and yellow distally .... *Cuthona abronia*

91′. Lacking purple band midway on rhinophores and oral tentacles 92

92.(91′) Cerata frosted with opaque white on outer two thirds; dorsum encrusted with opaque white; cerata cores pale green to raw umber; distal third of rhinophores encrusted with white .... *Cuthona albocrusta*

92′. Cerata not frosted with opaque white on distal two thirds 93

93.(92′) With yellow band near tips and bases of cerata, or with yellow on frontal margin between tentacles 94

93′. Lacking yellow bands on cerata or between oral tentacles 95

94.(93) With yellow on frontal margin between oral tentacles; cerata with orange flecks, cores green with some brown; rhinophores and oral tentacles with white dots on distal half .... *Cuthona virens*

94′. Lacking yellow on frontal margin; cerata with yellow band near tip and another near base, cores yellow-brown to dark brown, surface of cerata with white dots .... *Cuthona fulgens*

95.(93′) With band of opaque white subapically on each ceras; cerata cores greenish-brown to brown; dorsum and cerata with opaque white dots .... *Cuthona* sp.

95′. Lacking band of opaque white subapically on each ceras 96

96.(95′) Cerata slightly flattened, not round in cross section 97

96′. Cerata not flattened, but round in cross section, cores dark chocolate brown to reddish-brown, to pink 100

97.(96) With a triangular to crescentic patch of encrusting white to cream in the area between the rhinophores and oral tentacles and in cardiac region; body color dirty white, dull gray, mauve, rose, or pink .... *Aeolidia papillosa*

FIGS. 29–65. Radulae. 29, *Acanthodoris brunnea;* (a) sixth (outermost) marginal; (b) fifth marginal; (c) fourth marginal; (d) third marginal; (e) second marginal; (f) first marginal; (g) lateral. 30, *Acanthodoris hudsoni:* (a) fifth (outermost) marginal; (b) fourth marginal; (c) third marginal; (d) second marginal; (e) first marginal; (f) lateral. 31, *Acanthodoris lutea:* (a) fourth (outermost) marginal; (b) third marginal; (c) second marginal; (d) first marginal; (e) lateral. 32, *Acanthodoris nanaimoensis:* (a) fourth (outermost) marginal; (b) third marginal; (c) second marginal; (d) first marginal; (e) lateral. 33, *Acanthodoris pilosa:* (a) fourth (outermost) marginal; (b) third marginal; (c) second marginal; (d) first marginal; (e) lateral. 34, *Acanthodoris rhodoceras:* (a) fifth (outermost) marginal; (b) fourth marginal; (c) third marginal; (d) second marginal; (e)

97′. Lacking a patch of white to cream between rhinophores and oral tentacles or in cardiac region; ground color translucent grayish-white, encrusted with brown to reddish-brown .... *Cerberilla mosslandica*

98.(52′) Dorsum with undulating longitudinal ridges of white on a pinkish-brown background; gills located laterally below dorsum edge on either side; edge of dorsum with an antero-median notch through which the rhinophores project; clavus of rhinophores with many longitudinal grooves .... *Armina californica*

98′. Dorsum without undulating longitudinal ridges; gills located postero-ventrally (Fig. 7); ground color pale gray, with small yellowish-brown blotches and reticulate lines 99

99.(98′) Dorsum with posterior notch through which gills may be seen; rhinophore shaft with plate-like expansion .... *Corambe pacifica*

99′. Dorsum without posterior notch; rhinophores smooth and tapered .... *Doridella steinbergae*

100.(96′) Distal half of rhinophores and dorsal surface of oral tentacles encrusted with opaque white; ground color translucent white .... *Cuthona cocoachroma*

100′. Lacking opaque white on rhinophores and oral tentacles; ground color translucent cream to brownish-pink .... *Precuthona divae*

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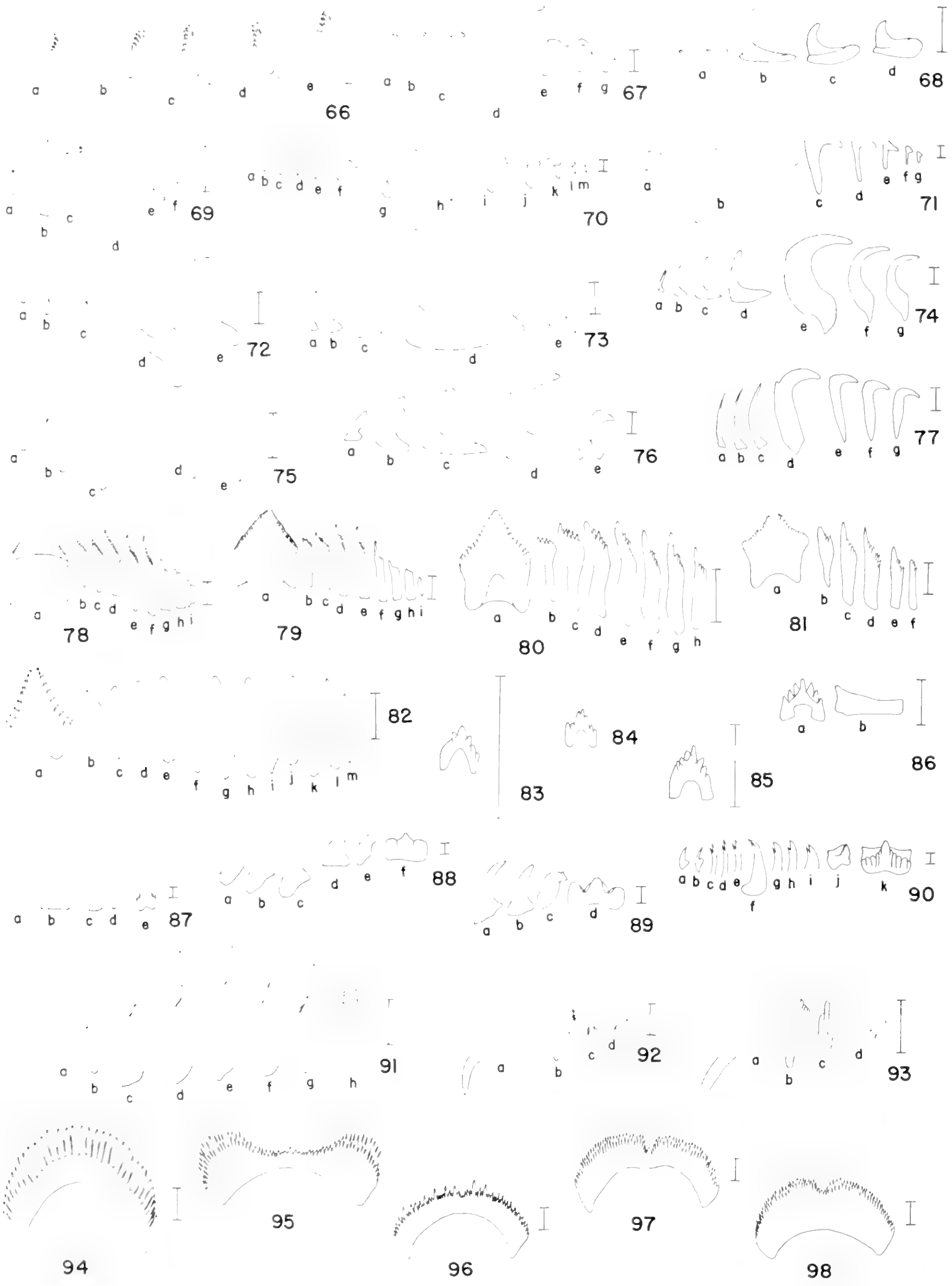
first marginal; (f) lateral. 35, *Onchidoris bilamellata:* (a) marginal; (b) lateral; (c) rachidian. 36, *Onchidoris hystricina:* (a) marginal; (b) lateral; (c) rachidian. 37, *Onchidoris* sp.: (a) fifth (outermost) marginal; (b) fourth marginal; (c) third marginal; (d) second marginal; (e) first marginal; (f) lateral. 38, *Doridella steinbergae:* (a) fifth (outermost) marginal; (b) fourth marginal; (c) third marginal; (d) second marginal; (e) first marginal; (f) lateral. 39, *Corambe pacifica:* (a) sixth (outermost) marginal; (b) fifth marginal; (c) fourth marginal; (d) third marginal; (e) second marginal; (f) first marginal; (g) lateral. 40, *Okenia angelensis:* (a) marginal; (b) lateral. 41, *Okenia plana:* (a) marginal; (b) lateral. 42, *Trapania velox:* lateral. 43, *Ancula pacifica:* (a) marginal; (b) lateral. 44, *Ancula lentiginosa:* (a) marginal; (b) lateral. 45, *Laila cockerelli:* (a) first lateral; (b) second lateral; (c) first marginal; (d) third marginal. 46, *Triopha catalinae:* (a) fourteenth marginal; (b) thirteenth marginal; (c) twelfth marginal; (d) eleventh marginal; (e) tenth marginal; (f) ninth marginal; (g) first marginal; (h) fourteenth (outermost) lateral; (i) thirteenth lateral; (j) first lateral; (k) second rachidian; (l) first rachidian. 47, *Triopha occidentalis:* (a) twelfth (outermost) marginal; (b) eleventh marginal; (c) tenth marginal; (d) ninth marginal; (e) eighth marginal; (f) seventh marginal; (g) sixth marginal; (h) fifth marginal; (i) fourth (outermost) lateral; (j) first lateral; (k) second rachidian; (l) first rachidian. 48, *Triopha maculata:* (a) eighth (outermost) marginal; (b) seventh marginal; (c) sixth marginal; (d) second marginal; (e) first marginal; (f) fifth (outermost) lateral; (g) second lateral; (h) first lateral; (i) second rachidian; (j) first rachidian. 49, *Crimora coneja:* (a) fourteenth marginal; (b) eleventh marginal; (c) second marginal; (d) first marginal; (e) second lateral. 50, *Hopkinsia rosacea:* (a) lateral; (b) marginal. 51, *Aegires albopunctatus:* (a) twentieth lateral; (b) first lateral. 52, *Polycera atra:* (a) first lateral; (b) second lateral; (c) first marginal; (d) second marginal. 53, *Polycera hedgpethi:* (a) first lateral; (b) second lateral; (c) first marginal; (d) second marginal; (e) third marginal; (f) fourth (outermost) marginal. 54, *Polycera tricolor:* (a) first lateral; (b) second lateral; (c) first marginal; (d) second marginal; (e) third marginal; (f) fourth (outermost) marginal. 55, *Polycera zosterae:* (a) first lateral; (b) second lateral; (c) first marginal; (d) second marginal; (e) third marginal; (f) fourth marginal; (g) fifth (outermost) marginal. 56, *Aldisa sanguinea:* (a) fourth lateral; (b) distal portion of lateral. 57, *Rostanga pulchra:* (a) sixth-seventh lateral; (b) fortieth lateral; (c) fourteenth lateral; (d) third lateral; (e) second lateral; (f) first lateral. 58, *Cadlina flavomaculata:* (a) rachidian; (b) first lateral; (c) twenty-first lateral; (d) twenty-fifth (outermost) lateral. 59, *Cadlina limbaughi:* (a) rachidian; (b) first lateral; (c) thirtieth lateral; (d) forty-fourth (outermost) lateral; after Lance (1962a). 60, *Cadlina modesta:* (a) rachidian; (b) first lateral; (c) second lateral; (d) eighteenth lateral; (e) twenty-seventh lateral; (f) twenty-eighth (outermost) lateral. 61, *Cadlina sparsa:* (a) rachidian; (b) first lateral; (c) second lateral; (d) twelfth lateral; (e) nineteenth lateral. 62, *Cadlina marginata:* (a) rachidian; (b) first lateral; (c) thirty-seventh lateral; (d) fifty-eighth lateral; (e) fifty-ninth lateral; (f) sixtieth (outermost) lateral. 63, *Hallaxa chani:* (a) lateral; (b) first marginal; (c) sixth marginal; (d) fourteenth marginal; (e) fifteenth (outermost) marginal. 64, *Hypselodoris californiensis:* (a) first lateral; (b) twenty-ninth lateral; (c) one-hundred and tenth lateral; (d) one-hundred and eighteenth (outermost) lateral. 65, *Chromodoris macfarlandi:* (a) rachidian; (b) first lateral, dorsal view; (c) second lateral, dorsal view; (d) first lateral, lateral view; (e) second lateral, lateral view; (f) fifty-third (outermost) lateral. Scale lines 50 μm long.



FIGS. 66–98. Radulae. 66, *Chromodoris porterae:* (a) first lateral; (b) seventh lateral; (c) twenty-third lateral; (d) twenty-sixth lateral; (e) twenty-ninth lateral. 67, *Atagema alba:* (a) first lateral; (b) second lateral; (c) third lateral; (d) ninth lateral; (e) nineteenth lateral; (f) twentieth lateral; (g) twenty-first (outermost) lateral. 68, *Conualevia alba:* (a) first lateral; (b) thirty-sixth lateral; (c) sixty-sixth lateral; (d) sixty-seventh (outermost) lateral. 69, *Thordisa bimaculata:* (a) sixth (outermost) marginal; (b) second marginal; (c) first marginal; (d) twenty-seventh lateral; (e) fifth lateral; (f) first lateral. 70, *Archidoris montereyensis:* (a) first lateral; (b) second lateral; (c) third lateral; (d) fourth lateral; (e) fifth lateral; (f) sixth lateral; (g) twenty-sixth

SYSTEMATIC ACCOUNT

"Nomina se pereunt, perit et cognitio rerum."—Linnaeus

Acanthodoris Gray, 1850

Body rather soft and doridiform, broadly rounded anteriorly, somewhat tapered posteriorly; dorsum densely covered with numerous large, conical papillae. Margin of dorsum covers foot everywhere except posteriorly where postero-dorsal tip of foot is visible when animal is actively crawling. Labial tentacles large and auriculate, extending nearly to edge of dorsum. Rhinophores rather long and perfoliate, retractile into low sheaths bordered by low papillae. Branchial plumes usually 5–9, usually bi- or tripinnate, arranged in a circle around postero-dorsal anus, they are non-retractile below dorsum but are contractile.

Armature of labial disc consists of minute hooks below with projecting thickenings of the cuticle. Radular formula n.1.0.1.n, lateral large and hooked distally, with or without denticles. Marginals small and frequently pointed distally.

Penis unarmed, vagina usually very long. Buccal crop with pharyngeal teeth.

Type-species: *Acanthodoris pilosa* (Abildgaard in Müller, 1789).

Acanthodoris brunnea MacFarland, 1905

Acanthodoris brunnea MacFarland, 1905: 52. MacFarland, 1906: 146–147, pl. 20, figs. 81–88a; pl. 21, fig. 104; pl. 29, figs. 20–21. Berry, 1907: 35. O'Donoghue, 1921: 171–172, pl. 4, figs. 41–42. O'Donoghue, 1924: 24. MacFarland, 1925: 53–55. MacFarland, 1926: pl. 2, fig. 7. O'Donoghue, 1926: 218. O'Donoghue, 1927a: 6. Smith & Gordon, 1948: 180. LaRocque, 1953: 256. MacFarland, 1966: 118–120, pl. 20, figs. 5–6. Hurst, 1967: 255 ff, text fig.

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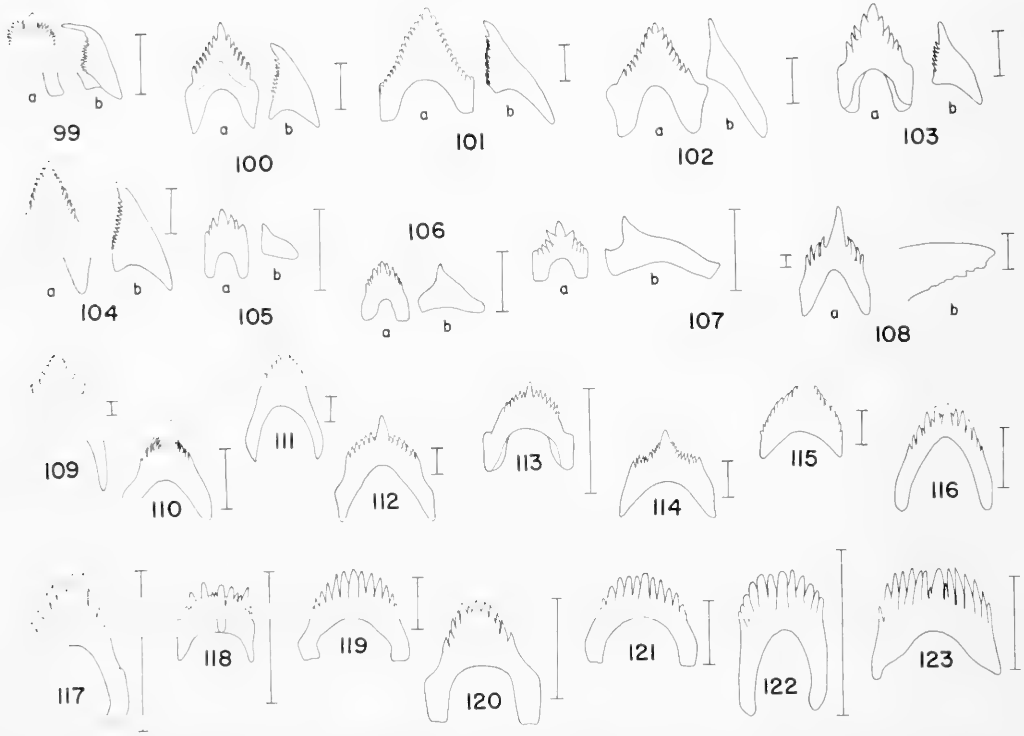
lateral; (h) thirty-first lateral; (i) thirty-second lateral; (j) thirty-third lateral; (k) thirty-fourth lateral; (l) thirty-fifth lateral; (m) thirty-sixth (outermost) lateral. 71, *Archidoris odhneri:* (a) first lateral; (b) twenty-sixth lateral; (c) fortieth lateral; (d) forty-first lateral; (e) forty-second lateral; (f) forty-third lateral; (g) forty-fourth (outermost) lateral. 72, *Sclerodoris tanya:* (a) thirty-fourth (outermost) lateral; (b) thirty-third lateral; (c) thirty-second lateral; (d) ninth lateral; (e) first lateral. 73, *Doris* (s.l.) sp.: (a) twenty-fifth (outermost) lateral; (b) twenty-fourth lateral; (c) twenty-third lateral; (d) fourteenth lateral; (e) first lateral. 74, *Discodoris sandiegensis:* (a) thirty-first (outermost) lateral; (b) thirtieth lateral; (c) twenty-ninth lateral; (d) twenty-eighth lateral; (e) eleventh lateral; (f) second lateral; (g) first lateral. 75, *Platydoris macfarlandi:* (a) seventieth (outermost) lateral; (b) sixty-ninth lateral; (c) sixty-eighth lateral; (d) seventh lateral; (e) first lateral. 76, *Anisodoris nobilis:* (a) forty-third (outermost) lateral; (b) forty-second lateral; (c) forty-first lateral; (d) fifteenth lateral; (e) first lateral. 77, *Discodoris heathi:* (a) nineteenth (outermost) lateral; (b) eighteenth lateral; (c) seventeenth lateral; (d) eleventh lateral; (e) third lateral; (f) second lateral; (g) first lateral. 78, *Dendronotus albus:* (a) rachidian; (b) first lateral; (c) second lateral; (d) third lateral; (e) fourth lateral; (f) fifth lateral; (g) sixth lateral; (h) seventh lateral; (i) eighth (outermost) lateral. 79, *Dendronotus diversicolor:* (a) rachidian; (b) first lateral; (c) second lateral; (d) third lateral; (e) fourth lateral; (f) fifth lateral; (g) sixth lateral; (h) seventh lateral; (i) eighth (outermost) lateral. 80, *Dendronotus frondosus:* (a) rachidian; (b) first lateral; (c) second lateral; (d) third lateral; (e) fourth lateral; (f) fifth lateral; (g) sixth lateral; (h) seventh (outermost) lateral. 81, *Dendronotus subramosus:* (a) rachidian; (b) first lateral; (c) second lateral; (d) third lateral; (e) fourth lateral; (f) fifth (outermost) lateral. 82, *Dendronotus iris:* (a) rachidian; (b) first lateral; (c) second lateral; (d) third lateral; (e) fourth lateral; (f) fifth lateral; (g) sixth lateral; (h) seventh lateral; (i) tenth lateral; (j) fifteenth lateral; (k) sixteenth lateral; (l) seventeenth lateral; (m) eighteenth (outermost) lateral. 83, *Doto amyra,* rachidian. 84, *Doto columbiana,* rachidian; after O'Donoghue (1921). 85, *Doto kya,* rachidian. 86, *Hancockia californica:* (a) rachidian; (b) lateral. 87, *Tochuina tetraquetra:* (a) one-hundred sixty-second (outermost) marginal; (b) one-hundred twenty-fourth marginal; (c) seventeenth marginal; (d) lateral; (e) rachidian. 88, *Tritonia diomedea:* (a) eighty-fourth (outermost) marginal; (b) eighty-third marginal; (c) seventy-third marginal; (d) first marginal; (e) lateral; (f) rachidian. 89, *Tritonia festiva:* (a) twenty-fourth (outermost) marginal; (b) sixth marginal; (c) lateral; (d) rachidian. 90, *Armina californica:* (a) sixty-third (outermost) marginal; (b) sixty-second marginal; (c) fifty-fourth marginal, distal portion; (d) fifth-second marginal, distal portion; (e) fiftieth marginal, distal portion; (f) thirty-eighth marginal; (g) tenth marginal, distal portion; (h) ninth marginal, distal portion; (i) eighth marginal, distal portion; (j) lateral; (k) rachidian. 91, *Antiopella barbarensis:* (a) fourteenth (outermost) lateral; (b) thirteenth lateral; (c) twelfth lateral; (d) fourth lateral; (e) third lateral; (f) second lateral; (g) first lateral; (h) rachidian. 92, *Dirona albolineata:* (a) marginal; (b) lateral; (c) rachidian; (d) rachidian, lateral view. 93, *Dirona picta:* (a) marginal; (b) lateral; (c) rachidian; (d) rachidian, lateral view. 94, *Aeolidia papillosa,* rachidian. 95, *Aeolidiella takanosimensis,* rachidian; after Ferreira & Bertsch (1973). 96, *Cerberilla mosslandica,* rachidian. 97, *Spurilla chromosoma,* rachidian. 98, *Spurilla oliviae,* rachidian. Scale lines 50 μm long.



FIGS. 99–123. Radulae. 99, *Cumanotus beaumonti:* (a) rachidian; (b) lateral. 100, *Coryphella cooperi:* (a) rachidian; (b) lateral. 101, *Coryphella iodinea:* (a) rachidian; (b) lateral. 102, *Coryphella pricei:* (a) rachidian; (b) lateral. 103, *Coryphella trilineata:* (a) rachidian; (b) lateral. 104, *Coryphella* sp.: (a) rachidian; (b) lateral. 105, *Eubranchus misakiensis:* (a) rachidian; (b) lateral. 106, *Eubranchus olivaceus:* (a) rachidian; (b) lateral. 107, *Eubranchus rustyus:* (a) rachidian; (b) lateral. 108, *Phidiana crassicornis:* (a) rachidian; (b) rachidian, median cusp, lateral view of distal portion. 109, *Phidiana hiltoni,* rachidian. 110, *Phidiana morroensis,* rachidian. 111, *Phidiana stearnsi,* rachidian. 112, *Fiona pinnata,* rachidian. 113, *Tenellia adspersa,* rachidian. 114, *Babakina festiva,* rachidian. 115, *Precuthona divae,* rachidian. 116, *Cuthona abronia,* rachidian. 117, *Cuthona albocrusta,* rachidian. 118, *Cuthona columbiana,* rachidian. 119, *Cuthona flavovulta,* rachidian. 120, *Cuthona fulgens,* rachidian. 121, *Cuthona lagunae,* rachidian. 122, *Cuthona virens,* rachidian. 123, *Cuthona* sp., rachidian. Scale lines 50 μm long.

1, pl. 26, fig. 1; fig. 24-5. Haderlie, 1968: 333, 339. Sphon & Lance, 1968: 75. Roller & Long, 1969: 429. Haderlie, 1969: tab. 2. Bernard, 1970: 85. Robilliard, 1971a: 164, 165. Abbott, 1974: 361, text fig. 4306. McDonald & Nybakken, 1978: 111. Haderlie & Donat, 1978: 52, 60.

Type-specimens: U. S. Nat. Mus., no. 181293.

Foot oval, bluntly rounded and bilabiate anteriorly, rounded posteriorly. Rhinophores with 20–28 lamellae, deep blue-black to brownish, tipped with pale yellow. Branchial plumes 7, bipinnate, light brown, with 2 longitudinal dark brown lines on inner surface, tipped with yellow. General ground color brown, to almost black in occasional specimens; dorsum sprinkled with irregular blotches of black and numerous minute flecks of lemon yellow. T.L.: 12 mm.

Radular formula of specimen examined 13(5–6.1.0.1.5–6), MacFarland (1966: 119) reports 24–28(6–7.1.0.1.6–7). Laterals (Fig. 33e) bear 8–12 denticles in specimen examined, MacFarland (1966: 119) reports 14–19 denticles on laterals.

Type-locality: Monterey Bay, California.

Range and habitat: Nanaimo, British Columbia, Canada (Robilliard, 1971a), to Santa Monica Bay, Los Angeles Co., California (personal observation). Intertidal to 110 m, rare in rocky intertidal in California. Occasionally found in rocky subtidal or dredged from muddy bottom in deeper water. Kozloff

(1973: 93) states that it feeds upon bryozoans.

Remarks: The specimens reported by Haderlie (1968, 1969) and by Haderlie & Donat (1978), based on the rarity of *A. brunnea* and on the habitat to which their specimens were found, may prove to be *Onchidoris bilamellata.*

Acanthodoris hudsoni MacFarland, 1905

Acanthodoris hudsoni MacFarland, 1905: 51. MacFarland, 1906: 144–146, pl. 20, figs. 73–80. O'Donoghue, 1921: 170–171. O'Donoghue, 1922b: 164. MacFarland, 1925: 51–53. MacFarland, 1926: pl. 2, fig. 1. O'Donoghue, 1926: 218. O'Donoghue, 1927a: 6. Smith & Gordon, 1948: 180. LaRocque, 1953: 256. Steinberg, 1963b: 70. Hurst, 1967: 255 ff, text fig. 2, pl. 26, fig. 2. Lee & Brophy, 1969: 220. Robilliard, 1969a: 290. Bernard, 1970: 85. McDonald, 1970: 375. Roller, 1970b: 482. Robilliard, 1971a: 164. Bertsch *et al.,* 1972: 302. Sphon, 1972a: 154. Gosliner & Williams, 1973b: 352–354. Abbott, 1974: 362. Lambert, 1976: 294, 296. Thompson, 1976a: 79, text figs. 38a–b. Nybakken, 1978: 135.
Cadlina luteomarginata MacFarland. Kozloff, 1973: pl. X.

Type-specimens: U. S. Nat. Mus., no. 181289.

Foot oval, bluntly rounded and bilabiate anteriorly, rounded posteriorly. Rhinophores bear 22–24 lamellae, clavus lemon yellow. Branchial plumes 5, bipinnate, grayish white, tipped with lemon yellow. General ground color translucent yellowish white. Dorsal papillae tipped with lemon yellow; mantle margin with band of same color. T.L.: 15 mm.

Radular formula of specimens examined 18(5–6.1.0.1.5–6), MacFarland (1925: 51) reports 27(5–6.1.0.1.5–6). Laterals (Fig. 30f) large and hooked, bearing 5–8 denticles on cusp.

Type-locality: Point Pinos, Monterey Co., California.

Range and habitat: Porcher Island, British Columbia, Canada (Lambert, 1976), to Gaviota, Santa Barbara Co., California (Lee & Brophy, 1969). Intertidal to 215 m, rare in rocky intertidal in California.

Acanthodoris lutea MacFarland, 1925

Acanthodoris lutea MacFarland, 1925: 60–65. MacFarland, 1926: pl. 2, figs. 2, 6, 8; pl. 3, figs. 3, 6. O'Donoghue, 1927a: 7. Lance, 1961: 67. Steinberg, 1963b: 70. MacFarland, 1966: 120–121, pl. 32, fig. 15. Marcus & Marcus, 1967a: 202. Farmer, 1967: 342. Sphon & Lance, 1968: 76. Turner *et al.,* 1969: 132, append. 1, 2. Roller & Long, 1969: 425. Roller, 1970b: 482. Gosliner & Williams, 1970: 176. Bertsch *et al.,* 1972: 303. Abbott, 1974: 362. Michel, 1976: 46, fig. 4. Nybakken, 1978: 144.

Type-specimens: not listed, may be at CASIZ.

Foot oval, bluntly rounded and bilabiate anteriorly, rounded posteriorly. Rhinophores bear about 26 lamellae, orange-red to red. Branchial plumes 9, bipinnate, grayish white. General ground color orange to red-orange, papillae of same color. Dorsum sprinkled with numerous minute lemon yellow flecks. T.L.: 22 mm.

Radular formula of specimens examined 33–36(4–5.1.0.1.4–5), MacFarland (1966: 120) reports 34–39(5–6.1.0.1.5–6). Laterals (Fig. 31e) bear 5–7 denticles on cusp, MacFarland (1966: 120) reports 2–4 denticles on laterals.

Type-locality: Cayucos, San Luis Obispo Co., California.

Range and habitat: Dillon Beach, Marin Co., California (Steinberg, 1963b), to 12.9 km S of Cabo Colonet, Baja California, Mexico (Farmer, 1967). Intertidal to 500 m.

Remarks: This species frequently gives off a quite pungent odor of sandalwood or cedar.

Acanthodoris nanaimoensis
O'Donoghue, 1921

Acanthodoris nanaimoensis O'Donoghue, 1921: 172–174, pl. 10, figs. 43–44. O'Donoghue, 1922a: 126. O'Donoghue, 1922b: 164. O'Donoghue & O'Donoghue, 1922: 139. O'Donoghue, 1926: 218. MacFarland, 1926: 100. O'Donoghue, 1927a: 7. La Rocque, 1953: 256. Steinberg, 1963a: 64. Steinberg, 1963b: 70. MacFarland, 1966: 123. Hurst, 1967: 255 ff, text fig. 3, pl. 26, fig. 3; fig. 24-8. Lance, 1968: 11. Lee & Brophy, 1969: 220. Roller & Long, 1969: 425. Roller, 1970a: 371. Bernard, 1970: 85. Gosliner & Williams, 1970: 176. Holleman, 1972a: 60. Bertsch *et al.,* 1972: 303. Sphon, 1972a: 154–155. Abbott, 1974: 362. Lambert, 1976: 294, 296. Thompson, 1976a: 79, text fig. 38c. Thompson, 1976b: 42. McDonald & Nybakken, 1978: 111.
Acanthodoris columbina MacFarland, 1926: 94–100, pl. 2, figs. 5, 9–10; pl. 3, figs. 1–

2, 5. O'Donoghue, 1927a: 3, 4, 7. Steinberg, 1963a: 64. MacFarland, 1966: 121–123, pl. 32, fig. 16. Roller, 1970a: 371.

Type-specimens: Mus. Dominion Biol. Stat., Nanaimo, B. C., Canada.

Foot oval, bluntly rounded and unilabiate anteriorly and rounded posteriorly. Rhinophores bear 22–26 lamellae, shaft brownish, clavus deep wine red to maroon, entire rhinophore sprinkled with lemon yellow flecks. Branchial plumes 7–9, bipinnate, light gray-brown, tipped with wine red to maroon. General ground color translucent grayish-white to dirty brownish-mauve in larger specimens; dorsal papillae grayish-white to brownish, tipped with lemon yellow. Mantle margin with band of lemon yellow all around. T.L.: 30 mm.

Radular formula of specimens examined 36–37(4.1.0.1.4), O'Donoghue (1921b: 173) reports 35(6–7.1.0.1.6–7), while MacFarland (1966: 122) reports 40–43(5.1.0.1.5) for *A. columbina*. Laterals (Fig. 32e) bear 2 denticles on cusp in specimens examined, MacFarland (1966:122) reports 6–8 denticles on laterals, while O'Donoghue (1921: 173) reports no denticles.

Type-locality: Jesse Island, Vancouver Island, British Columbia, Canada.

Range and habitat: Wales Island, British Columbia, Canada (Lambert, 1976), to Purisima Point, Santa Barbara Co., California (Lee & Brophy, 1969). Intertidal to 10 m, quite rare south of Pigeon Point, San Mateo Co., California, more common northward. Feeds upon an unidentified encrusting ascidian.

Acanthodoris pilosa
(Abildgaard in Müller, 1789)

Doris pilosa Abildgaard in Müller, 1789: 3, pl. 85, figs. 5–8. Gmelin in Linnaeus, 1791: 3106. Cuvier, 1804: 451, 470. Blainville 1819: 449. Lamarck, 1819: 312. Rapp, 1827: 517. Bosc, 1830: 111. Cuvier, 1834, 115. Bouchard-Chantereaux, 1835: 139–140. Lamarck, 1836: 464. Johnston, 1838a: 54. Johnston, 1838b: pl. 2, figs. 9–10. Thompson, 1840: 86. Hassall, 1842: 133. Thompson, 1844: 250. Alder & Hancock, 1851c: fam. 1, pl. 1, figs. 1, 3–5, 12; pl. 2, figs. 2–6; pl. 15. Hancock & Embleton, 1852: 208 ff, pl. 11, figs. 4, 6; pl. 13, figs. 6–12; pl. 14, fig. 4; pl. 16, figs. 1, 3–7; pl. 17, fig. 8. Gosse, 1853: 62. Byerly, 1854: 44. Alder & Hancock, 1855: 4, 27, 31, 32, 43. Gosse, 1856: 105. Thompson, 1856: 274. Collingwood, 1859: 463–464. E. Wright, 1859: 88. Collingwood, 1860: 202. Collingwood, 1861: 114. Hancock & Norman, 1864: 49, 51, 53. Meyer & Möbius, 1865: 63–67, pl. 5. McIntosh, 1865: 390. Robertson, 1868: 205. Jeffreys 1869: 93. Dall, 1870: 249. Gould, 1870: 232. Sauvage, 1873: 29. McIntosh, 1874: 432. McIntosh, 1875: 89. Friele & Hansen, 1876: 71, pl. II, fig. II. Tiberi, 1880: 207. Leslie & Herdman, 1881: 312. Hertzenstein, 1885: 709. Locard, 1886: 27. Higgins, 1886: 25. Haddon, 1886: 530. Herdman & Clubb, 1892: 148. Hecht, 1893: XIV, XVI. Cooke, 1899: 64. Colgan, 1908: 110. Colgan, 1909: 174. Pelseneer, 1911: 55, pl. 15, fig. 24; pl. 16, figs. 1–4. Chumley, 1918: 55, 169. White, 1938: 15. Volodchenko, 1955: 250, pl. 48, fig. 6.

Doris stellata Gmelin in Linnaeus, 1791: 3107. Cuvier, 1804: 449 ff, 470. Blainville, 1819: 449. Lamarck, 1819: 311. Rapp, 1827: 517. Bosc, 1830: 113. Cuvier, 1834: 114. Bouchard-Chantereaux, 1835: 139. Philippi, 1836: 105. Lebert, 1846: 444. Alder, 1850: 110.

Doris nigricans Fleming, 1820: 618. Fleming, 1828: 283. Johnston, 1838a: 55. Hassall, 1842: 133. Alder, 1850: 110. Herdman, 1886: 269.

Doris flemingii Forbes, 1838: 3, pl. 1, figs. 2–3.

Doris sublaevis Thompson, 1840: 87, pl. 2, fig. 1.

Doris similis Alder & Hancock, 1842: 32–33. Alder, 1850: 111.

Doris subquadrata Alder & Hancock, 1845c: 313–314. Alder & Hancock, 1851c: fam. 1, pl. 16. Forbes & Hanley, 1851: 571. Alder & Hancock, 1855: 31, 43. Collingwood, 1860: 200, 202. Collingwood, 1861: 113. Collingwood & Byerley, 1862: 189. McIntosh, 1865: 390. Jeffreys, 1869: 93.

Doris fusca Müller. Lovén, 1846: 136.

Doris tomentosa Cuvier. Lovén, 1846: 136.

Doris laevis. Gray, 1850: pl. 214, fig. 6.

Doris rocinela Leach in Gray, 1852: 19–20.

Acanthodoris pilosa (Abildgaard in Müller). Adams & Adams, 1854: 56, pl. 63, fig. 4. Chenu, 1859: 404, fig. 3045. Mörch, 1868: 203. Sars, 1878: 308–309, 364, 383, 390, 402, pl. XIV, fig. 4. Bergh, 1879a: 359. Bergh, 1880a: 240–246, pl. 10, figs. 12–15; pl. 11, figs. 1–2; pl. 12; pl. 13, figs. 2–5. Bergh, 1880b: 91–97, pl. 10, figs. 12–15; pl. 11, figs. 1–2; pl. 12; pl. 13, figs. 2–5. Bergh, 1881a: pl. L, figs. 1–5. Verrill, 1882b: 549. Herdman, 1886: 269, 277. Fischer, 1887: 519, text fig. 282. Herdman

& Clubb, 1889: 226. Garstang, 1889: 178. Carus, 1889–1893: 224. Garstang, 1890: 446–447. Norman, 1890: 72. Bergh, 1890b: 989–990. Bergh, 1892: 1151 (159). Herdman & Clubb, 1892: 133, 146, pl. 6, figs. 4–5. Garstang, 1894: 226. Tregelles, 1896: 220. Herdman *et al.,* 1896: 446. Gamble, 1896: 132, 133. Cooke, 1899: 66. Beaumont, 1900: 849. Nichols, 1900: 596. Knight, 1901: 207. Conchol. Soc., 1901: 26. Johansen, 1902: 387. Farran, 1904: 3. Mar. Biol. Assoc., 1904: 284. Cockerell & Eliot, 1905: 32. Norman & Scott, 1906: 217. Nordgaard, 1907: 33. Odhner, 1907: 72. Eliot, 1907: 327 ff. Elmhirst, 1908: 228. Walton, 1908: 238. Balch, 1909: 36. Farran, 1909: 17. Eliot, 1910: 4, 8, 13, 28, 155. Colgan, 1911: 25. Walton, 1913: 110. Sumner *et al.,* 1913: 705. Farran, 1915: 10, 67. Johnson, 1915: 173. Evans & Evans, 1917: 110. Bardarson, 1919: 73. Bardarson, 1920: 108. Odhner, 1922: 24. Elmhirst, 1922: 42. Iredale & O'Donoghue, 1923: 222–223. O'Donoghue, 1924: 30–31. Larsen, 1925: 28–30, text figs. 20–21, pl. figs. 4a–c. Odhner, 1926b: 25. O'Donoghue, 1926: 219. Jutting, 1927: LXXXVIII. Løyning, 1927: 246, 247, 250–252, 262. O'Donoghue, 1927a: 6. Derjugin, 1928: 320. Lemche, 1928: 15–16. O'Donoghue, 1929: 776. Fisher, 1931: 198. Mar. Biol. Assoc., 1931: 274. Monod & Dollfus, 1932: 163, 191. Winckworth, 1932: 234. Leigh-Sharpe, 1933: 114. Renouf, 1934: 400. Fisher, 1935: 249. Baba, 1935b: 115, 117–119, pl. 7, figs. 5–7. Baba, 1937a: 199. Baba, 1937b: 294. Moore, 1937: 190. Millott, 1937: 406 ff. White, 1938: 15, 17. Lemche, 1938: 21–22 ff. Odhner, 1939: 39. Volodchenko, 1941: 60, 61. McMillan, 1944: 161. Jutting, 1947: 64. Purchon, 1947: 292 ff. Cornet & Marche-Marchad, 1951: 32. Jaeckel, 1952: 28 ff. Stock, 1952: 58. Forrest, 1953: 232, text fig. 5b. Williams, 1954: 106. Graham, 1955: 152, Clark & Milne, 1955: 180. Mar. Biol. Assoc., 1957: 310. Baba, 1957: 8, 13, text fig. 5. Thompson, 1959: 240. Marcus, 1959: 61. Swennen, 1959: 57, 58. Buznikov, 1960: 374. Thompson, 1960b: 126–127, text fig. 1. Buznikov & Manukhin, 1961: 226, text fig. 2. Thompson, 1961: 236. Marcus, 1961: 26. Miller, 1961: 107, 114. Swennen, 1961: 200. Roginskaya, 1962a: 88, 92, figs. 1.4–1.5. Roginskaya, 1962b: 203, 212, 213, fig. 1.4. Miller, 1962: 552–553, text fig. 6. Zenkevitch, 1963: 112. Bruce *et al.,* 1963: 202–203. Steinberg, 1963b: 70. Thompson, 1964: 280 ff. Marcus & Marcus, 1967a: 202. Miller, 1967: 9. Thompson, 1967: 9. Morse, 1967: 770. Morse, 1968: 305–319, text figs. 1–9. Edmunds, 1968b: 131. Barrett, 1969: 69. Loveland *et al.,* 1969: 418. Franz, 1970: 172 ff. Hughes, 1970b: 81, 82. Kress, 1971: 326, 336–338, text figs. 8–10. Meyer, 1971: 137–139. Holman, 1972: 179–183. Platts, 1973: 383, 385. Rasmussen, 1973: 267–268, 447. Harris, 1973: 217, 221, 246–247. Abbott, 1974: 361, pl. 16, fig. 4305. Roginskaya, 1974b: 998. Rozsa, 1974: 8. Clark, 1975: 36–37. Franz, 1975a: 81. Thompson & Brown, 1976: 90, fig. 46. Thompson, 1976a: 36. Thompson, 1976b: 70, 92, 80, fig. 7. Crampton, 1977: 49. Garlo, 1977: 24, 25, 27. Bleakney & Saunders, 1978: 82. McDonald & Nybakken, 1978: 111. Clark & Goetzfried, 1978: 290. Ortea, 1979: 47.

Acanthodoris subquadrata (Alder & Hancock). Adams & Adams, 1854: 56. Abraham, 1877: 228. Bergh, 1879a: 360. Bergh, 1880a: 240. Bergh, 1880b: 91. Bergh, 1892: 1151 (159). Cooke, 1899: 66. Conchol. Soc., 1901: 26. Eliot, 1910: 155. Iredale & O'Donoghue, 1923: 222. MacFarland, 1925: 49. Winckworth, 1932: 234. White, 1938: 17. Thompson, 1964: 290.

?"*Lamellidoris Elfortiana* Blv.?" Mörch, 1868: 204.

Doris quadrangulata Alder & Hancock. Jeffreys, 1869: 93–94.

Doris bifida Verrill, 1870: 406–407. Verrill, 1872: 210. Verrill, 1873: 307, 333, 664–665, pl. 25, fig. 176.

Doris pilosa var. *stellata* Gmelin in Linnaeus. Sauvage, 1873: 30.

Acanthodoris citrina Verrill, 1879: 313–314. Verrill, 1882b: 549. Bergh, 1892: 1151 (159).

Acanthodoris ornata Verrill, 1879: 314. Verrill, 1882b: 549. Bergh, 1892: 1151 (159).

Acanthodoris stellata (Gmelin in Linnaeus). Verrill, 1879: 313. Verrill, 1882b: 549.

Acanthodoris pilosa var. *albescens* Bergh, 1880a: 246–247, pl. 10, figs. 14–15; pl. 11, fig. 2; pl. 12, figs. 13–16. Bergh, 1880b: 97, pl. 10, figs. 14–15; pl. 11, fig. 2; pl. 12, figs. 13–16. Bergh, 1892: 1151 (159). O'Donoghue, 1921: 168. O'Donoghue, 1922b: 164. O'Donoghue, 1926: 219. O'Donoghue, 1927a: 6.

Acanthodoris pilosa var. *purpurea* Bergh, 1880a: 247–252, pl. 12, figs. 1–9. Bergh, 1880b: 98–103, pl. 12, figs. 1–9. Bergh, 1892: 1151 (159). O'Donoghue, 1924: 31.

O'Donoghue, 1926: 219. O'Donoghue, 1927a: 6.

Acanthodoris quadrangulata (Alder & Hancock). Herdman, 1886: 269. Herdman, 1896: 49. Herdman *et al.*, 1896: 446. Conchol. Soc., 1901: 26.

Doris (*Acanthodoris*) *pilosa.* Herdman, 1890a: pl. 6, fig. 2.

Acanthodoris pilosa var. *nov. zealandiae* Bergh, 1905a: 94–97, pl. 6, figs. 23–26, pl. 7, fig. 1.

Acanthodoris pilosa var. *pallida* Bergh, 1905a: 97–98, pl. 6, figs. 27–29; pl. 7, fig. 2. Eliot, 1907: 329.

Acanthodoris pilosa ornata Verrill. Johnson, 1915: 173. Johnson, 1934: 157. LaRocque, 1953: 257.

Acanthodoris pilosa pilosa. Johnson, 1934: 157. LaRocque, 1953: 256.

Acanthodoris pilosa var. *fusca* Lovén. Odhner, 1939: 39.

Acanthodoris pilosa albescens Bergh. LaRocque, 1953: 256.

Acanthodoris pilosa purpurea Bergh. LaRocque, 1953: 257. Marcus & Marcus, 1967a: 202.

Type-specimens: not listed.

Foot oval, bluntly rounded and bilabiate anteriorly and rounded posteriorly. Rhinophores bear 18–25 lamellae, translucent grayish-white with numerous small brown flecks which are most concentrated on clavus, with a few small yellow flecks, tips whitish. Branchial plumes 5–9, tripinnate, grayish-white, densely covered with small, brownish flecks, and a lesser number of yellow and white flecks. General ground color translucent grayish-white; dorsum densely covered with numerous brown flecks and a lesser number of yellow flecks. Dorsal papillae tipped with black. Color quite variable in specimens from Europe and Atlantic coast of North America. T.L.: 25 mm.

Radular formula of specimens examined 28(3–4.1.0.1.3–4), Baba (1935b: 118) reports 24(4.1.0.1.4). Laterals (Fig. 33e) bear 4–7 denticles on cusp, Baba (1935b: 118) reports 4 denticles on laterals.

Type-locality: "Mari Norvegico."

Range and habitat: Kiska Island, Alaska (Bergh, 1880a) to Morro Bay, San Luis Obispo Co., California (personal observation); circumboreal; Atlantic coast of North America (Franz, 1975a); Japan (Baba, 1935b); Europe (Pruvot-Fol, 1954); Okhotsk Sea (Volodchenko, 1955). Intertidal to 270 m, relatively uncommon in California. Usually found in rocky areas and on floating docks in bays. Feeds upon the bryozoans *Alcyonidium gelatinosum, Alcyonidium hirsutum, Alcyonidium polyoum, Alcyonidium* spp., *Callopora dumerili, Cryptosula pallasiana, Electra pilosa, Flustrellidra hispida, Membranipora, Porella concinna, Schizoporella unicornis, Smittina reticulata* (Barrett, 1969; Bleakney & Saunders, 1978; Bruce *et al.*, 1963; Jaeckel, 1952; Meyer, 1971; Miller, 1961; Morse, 1968; Swennen, 1961; Thompson, 1964; Thompson & Brown, 1976).

Remarks: This is a highly variable species on the Atlantic coast of North America and in Europe. Further investigation may well show several California species of *Acanthodoris* to be junior synonyms of *A. pilosa* (viz. *A. hudsoni, A. nanaimoensis,* and *A. rhodoceras*).

Dr. T. E. Thompson (personal communication) states that Gregory H. Brown has examined the types of *Doris subquadrata,* and found that they present no significant differences from *A. pilosa.*

Acanthodoris rhodoceras Cockerell in Cockerell & Eliot, 1905

Acanthodoris rhodoceras Cockerell in Cockerell & Eliot, 1905: 38. MacFarland, 1925: 55–60. MacFarland, 1926: pl. 2, figs. 3–4; pl. 3, fig. 4. Marcus, 1961: 26–27, 58, pl. 5, figs. 84–88. Lance, 1961: 67. Paine, 1963a: 4. Farmer & Collier, 1963: 62. Steinberg, 1963b: 70. Paine, 1964: 385. Paine, 1965: 607. Marcus & Marcus, 1967a: 202. Sphon & Lance, 1968: 76. Roller & Long, 1969: 425. Roller, 1970b: 482. Gosliner & Williams, 1970: 176. Abbott, 1974: 362. Haderlie & Donat, 1978: 60.

Acanthodoris rhodocera Cockerell & Eliot. O'Donoghue, 1926: 219 (*lapsus*).

Acanthodoris sp. MacGinitie & MacGinitie, 1949: 363.

Type-specimens: not listed.

Foot oval, bluntly rounded and bilabiate anteriorly and rounded posteriorly. Rhinophores bear about 13–17 lamellae, translucent grayish-white, clavus yellowish to brown, tipped with white, occasionally with a subterminal black band. Branchial plumes 5, bi- and tripinnate, translucent grayish-white, tipped with yellow to brown. Posterior-most branchial plume on either side bears an accessory branch nearly as large as an independent plume. General ground color translucent grayish-white; dorsum may be finely sprinkled with tiny flecks of yellow and dark brown to black. Dorsal papillae tipped with dark brown to black. Mantle margin with yellow band and with a black band just inside yellow band. One or both of these marginal bands may be discontinuous or indistinct in some specimens. T.L.: 15 mm.

Radular formula of specimens examined 28–31(5.1.0.1.5), MacFarland (1925: 57) reports 32–36(5–6.1.0.1.5–6). Laterals (Fig. 34f) bear 3–6 denticles on cusp.

Type-locality: San Pedro, Los Angeles Co., California.

Range and habitat: Dillon Beach, Marin Co., California (Marcus, 1961), to Punta Mesquite, Baja California, Mexico (Farmer & Collier, 1963). Intertidal to 25 m. Usually found on floating docks in bays and in rocky intertidal areas, frequently in association with an unidentified ascidian upon which it may feed.

Aegires Lovén, 1844

Body rather limaciform and somewhat rigid, dorsum with numerous tubercles. Margin of dorsum indistinct and tuberculate; frontal margin narrow and tuberculate. Labial tentacles small and lobiform. Rhinophores smooth and retractile into oblique, tuberculate sheaths. Branchial plumes few, retractile, tripinnate, arranged around the anus, each protected by a peculiar individual lobe.

Armature of labial disc consists of a band of minute rods close to buccal aperture below; large mandible present above. Radular formula 0.n.0.n.0, laterals numerous and uniformly hooked.

Penis armed with hooks.

Type-species: *Aegires punctilucens* (Orbigny, 1837).

Aegires albopunctatus MacFarland, 1905

Aegires albopunctatus MacFarland, 1905: 45. Cockerell & Eliot, 1905: 32, 44–45. MacFarland, 1906: 133, pl. 19, figs. 41–44. Guernsey, 1912: 75, fig. 39F. O'Donoghue, 1926: 213. O'Donoghue, 1927a: 7–9, pl. 1, figs. 7–9. O'Donoghue, 1927b: 95–96. Costello, 1938: tabs. 1–5. Marcus, 1961: 20–21, pl. 4, figs. 65–66. Lance, 1961: 66. Paine, 1963a: 4. Farmer & Collier, 1963: 62. Steinberg, 1963b: 70. Paine, 1964: 385. MacFarland, 1966: 101–103, pl. 18, figs. 5–8; pl. 31, figs. 1–5. Lance, 1966: 73–76. Farmer, 1967: 341. Sphon & Lance, 1968: 76. Haderlie, 1968: 339. Lance, 1969: 34, 37. Long, 1969c: 232. Roller & Long, 1969: 425. Haderlie, 1969: tabs. 1, 2. Turner *et al.*, 1969: 132. Gosliner & Williams, 1970: 176. Bernard, 1970: 85. North, 1971: 57. Keen, 1971: 829, pl. 21, fig. 1. Bertsch *et al.*, 1972: 304. Harris, 1973: 281, 289. Abbott, 1974: 358. Haderlie *et al.*, 1974: tab. 4. Michel, 1976: 4b, fig. 1. Lambert, 1976: 294, 296. Nybakken, 1978: 135, 144. Haderlie & Donat, 1978: 52, 60. Bertsch, 1980: 223–224, figs. 1–6.

Cregires albopunctatus MacFarland. Berry, 1907: 35 (*lapsus*).

Aegires albopunctata. O'Donoghue, 1927b: 77 (*lapsus*).

Aegirus (*Aegires*) *albopunctatus* MacFarland. Smith & Gordon, 1948: 180.

Type-specimens: U. S. Nat. Mus., no. 181282.

Dorsum densely covered everywhere with large, cylindrical tubercles which may be slightly expanded apically, and are arranged in irregular longitudinal rows; they may be somewhat reduced in occasional specimens, especially in small individuals from the rocky intertidal. Foot narrow and elongate, distinctly set off from sides of body. Labial tentacles small and lobe-like. Rhinophores completely smooth, cylindrical, and truncated apically; white to lemon yellow with small, opaque white flecks. Borders of rhinophore sheaths bear 5–6 rounded tubercles which are higher on lateral surface than on medial surface. Branchial plumes 3, non-retractile, white to cream. A large irregularly tuberculate lobe occurs lateral of branchial plumes, and a similar lobe occurs anterior of median branchial plume. General ground color white to pale yellowish-white or cream, dorsum and sides of body generally sprinkled with small, irregularly scattered dark brown to black flecks, though these may be lacking in some individuals. Dorsum also bears small, opaque white flecks scattered between the tubercles. T.L.: 13 mm.

Radular formula of specimens examined 17–18(22–24.0.22–24), MacFarland (1966: 103) reports 16–22(17.0.17). Laterals (Fig. 51) hamate.

Type-locality: Monterey Bay, California.

Range and habitat: Porcher Island, British Columbia, Canada (Lambert, 1976), to Islas Coronados, Baja California, Mexico (Lance, 1961). Intertidal to 30 m. Most common on docks and pilings in bays, occasional in rocky intertidal and subtidal. Bertsch (1980: 223) reports that it feeds upon the sponge *Leucilla nuttingi.* It is also frequently found upon the sponge *Leucosolenia eleanor* which it probably also eats.

Remarks: Smith & Gordon (1948: 180) list one of the localities at which *A. albopunctatus* has been found as: "extreme low water, on stones, at Santa Cruz (Cooper)." This reference appears to be taken from Cooper (1870: 56) who cited *Doris albopunctata* (an old name for *Doriopsilla albopunctata*) from: "Santa Cruz, rare on stone, extreme l.w.."

Aeolidia Cuvier, 1797

Body aeolidiform, broadest anteriorly and tapered posteriorly. Wide foot rounded and bilabiate anteriorly, lateral margins extend beyond body margins; anterior foot corners slightly elongate. Cerata flattened and lanceolate, pointed apically and broadest near base; they occur in numerous transverse rows, with little space between rows. Cnidosacs present. Rhinophores smooth and non-retractile.

Masticatory border of mandibles non-denticulate. Radula uniseriate, with pectinate teeth.

Penis unarmed. Anus cleioproct.

See ICZN (1966: opinion 779), *Aeolidia* placed on Official List.

Type-species: *Aeolidia papillosa* (Linnaeus, 1761).

Aeolidia papillosa (Linnaeus, 1761)

Doris spinis mollibus hirsuta Baster, 1760: 81, pl. 10, fig. 1.

Limax papillosus Linnaeus, 1761: 508, no. 2093. Linnaeus, 1767: 1082. Mohr, 1786: 115. Cuvier, 1817: 16. Bruguière & Lamarck, 1830: 114. Lemche, 1938: 1. Lemche, 1964b: 116, 117.

Doris bodoensis Gunnerus, 1770: 170, unnumbered pl., figs. 11–16. Cuvier, 1817: 16. Bruguière & Lamarck, 1830: 114. (*Non*) Möller, 1842: 5.

Doris papillosa Müller, 1776: 229, no. 2775. Fabricius, 1780: 345. Stewart, 1801–1802: 336. Montagu, 1815: 16, pl. 4, fig. 3. Cuvier, 1817: 16, 25. Bruguière & Lamarck, 1830: 114, 115. Lemche, 1964b: 116. (*Non*) Kelaart, 1858: 101. (*Non*) Pease, 1860: 30.

Tritonia papillosa (Linnaeus). Pennant, 1777: 81. Bosc, 1802: 91. Jameson, 1809: 556. Fleming, 1820: 619. Bosc, 1830: 105.

Doris vermigera Turton, 1807: 132.

Eolis cuvieri Lamarck, 1819: 302. Start, 1828: 69. Bouchard-Chantereaux, 1835: 33. Lamarck, 1936: 450. Thompson, 1844a: 250.

Eolida papillosa Fleming, 1823a: 295. Fleming, 1828: 285.

Eolidia bodoensis (Gunnerus). Cuvier, 1834: 122.

Eolidia papillosa (Linnaeus). Cuvier, 1834: 122. Johnston, 1835: 376–378, text fig. 35. Sars, 1835: 68. Johnston, 1838b: 118–120. Thompson, 1840: 89. Kroyer, 1847: 116. Gray, 1857: 225. Herdman & Clubb, 1892: 146. Herdman *et al.*, 1896: 446. Daro, 1969: 136.

Eolis Cuverii Lamarck. Bouchard-Chantereaux, 1835: 129–132 (*lapsus*).

Eolidia cuvierii. Blainville, 1825: 486. Bruguière & Lamarck, 1830: 115. Johnston, 1838b: 120–121, pl. 3, figs. 9–11.

Eolida zetlandica Forbes & Goodsir, 1839: 647.

Eolis rosea Alder & Hancock, 1842: 34. Alder, 1850: 114.

Eolis obtusalis Alder & Hancock, 1842: 34. Alder, 1850: 114. Collingwood, 1859: 466.

Aeolis murrayana MacGillivray, 1843: 193.

Aeolis lesliana MacGillivray, 1843: 194.

Aeolis papillosa (Linnaeus). MacGillivray 1843: 192. Lovén, 1846: 139. Sars, 1850: 193. Adams & Adams, 1854: 73, pl. 65, fig. 8. Norman, 1860: 7243. Meyer & Möbius, 1865: 29–32, pl. 2. Hogg, 1868: pl. 10. Mörch, 1868: 205. Gould, 1870: 238–240. Verrill, 1873: 486, 495, 499, 666. Verrill, 1874b: 132. Sars, 1878: 318–319 ff, pl. XV, fig. 8. Collin, 1884: 50. Locard, 1886: 43–44. Fischer, 1887: 532, 540, text figs. 290, 298. Garstang, 1890: 432–433. Norman, 1890: 81. Hecht, 1893: XIII. Garstang 1894: 226. Tregelles, 1896: 222. Mansel-Pleydell, 1898: 27. Nichols, 1900: 587. Allen & Todd, 1900: 165 ff. Whiteaves, 1901: 204–205. Grosvenor, 1903: 468 ff. Todd, 1903: 544, 556. Farran, 1904: 6. Odhner, 1907: 77. Eliot, 1907: 327. Colgan, 1908: 108. Colgan, 1911: 23. Retzius, 1914: 13–15, pl. 4, figs. 1–15. Colgan, 1914: 177–178. Chumley, 1918: 74, 169. Bardarson, 1919: 72. Bardarson, 1920: 110. Løyning, 1922: 2. Odhner, 1926a: 25. Derjugin, 1928: 321. Lonnberg, 1931: 19–20. Ellis, 1933: 189. Linke, 1937: 232–236, text figs. 1–6. Volodchenko, 1941: 60. Kepner, 1943: 305. Homans & Needler, 1944: 37, 38. Schafer, 1950: 9–14, text figs. 1–5. Fischer, 1950: 234 ff. Schonenberg, 1969: 288. (*Non*) Hagg, 1905: 104.

Eolis papillosa (Linnaeus). Thompson, 1844: 250. Hancock & Embleton, 1845: 2 ff, pl. 1, figs. 1, 5–11; pl. 2, figs. 1–2, 4–5, 7, 9, 12, 14; pl. 3, figs. 5–7; pl. 4, figs. 4–9; pl. 5, figs. 7–14, 16. Alder & Hancock, 1847: fam. 3, pl. 8. Alder, 1850: 105, 114. Forbes & Hanley, 1851–1852: 590. Alder & Hancock, 1852: fam. 3, pl. 9. Hancock & Embleton, 1852: 236, 237. Gosse, 1853: 12, 16. Dalyell, 1853: 314–317, pl. 45, figs. 23–27. Gosse, 1854: 105, 125. Byerley, 1854: 45. Alder & Hancock, 1855: 3, 23, 26, 31, 32, 48. Thompson, 1856: 277. Collingwood, 1859: 466. E. Wright, 1859: 87. T. Wright, 1859: 39. Collingwood, 1860: 199, 202. Collingwood, 1861: 114. Kinahan, 1861: 31. Wright, 1863: 53. McIntosh, 1865: 392. Hogg, 1868: 103. Robertson, 1868: 206. Jeffreys, 1869: 37–38, pl. 2, fig. 3. Gould, 1870: pl. 18, figs. 258, 261. Sauvage, 1873: 25, 34–35. McIntosh, 1874: 428. McIntosh, 1875: 85. Friele & Hansen, 1876: 74. Leslie & Herdman, 1881: 310. Verrill, 1882a: 340. Herdman, 1886: 273, 277. Higgins, 1886: 26. Herdman & Clubb, 1889: 232, pl. 12, figs. 4–6. Garstang, 1889: 190–191. Hecht, 1896: 543 ff. Gamble, 1896: 132. Boutan, 1898: XXXVII–XLII. Cooke, 1899: 60. Liverpool Mar. Biol. Comm., 1899: 55. Knight, 1901: 206. Conchol. Soc., 1901: 24. Grosvenor, 1903: 462. Cuenot, 1907: 87, 94. Fleure & Walton, 1907: 219. Elmhirst, 1908: 227. Pelseneer, 1911: 55–57, pl. 16, figs. 5–14. Colgan, 1913: 165–166. Farran, 1913: 6. Farran, 1915: 10, 67. Engel, 1925: 33. Pelseneer, 1928: 179. White, 1938: 16. Arvy, 1950: 159. Humes & Stock, 1973: 167, 168.

Eolidia cuvieri (Lamarck). Leach, 1852: 23, pl. 7, fig. 3. Gray, 1857: 225.

Eolis farinacea Stimpson ex Gould Ms, 1853: 25. Gould, 1870: pl. 18, figs. 257, 259, 260, 262, 263.

Eolis plumata Dalyell, 1853: 300, pl. 44, figs. 1–2.

Aeolis Cuvieri (Lamarck). Adams & Adams, 1854: 73. Chenu, 1859: 411, fig. 3070. Locard, 1886: 44.

Eolis cuvierii (Lamarck). Thompson, 1856: 277.

Aeolis farinacea. Stimpson, 1862: 4.

Eolis papillata. Baudelot, 1863: 212–213 ff, pl. 5, figs. 5–6.

Aeolidia serotina Bergh, 1873a: 618–620, pl. 9, figs. 14–17; pl. 10, figs. 4–12. Bergh, 1879b: 74. Bergh, 1879c: 130. Bergh, 1892: 1019 (27). Bergh, 1898: 541–544, pl. 31, figs. 26–31. Eliot, 1907: 327, 351–352. Odhner, 1921: 225. Odhner, 1926a: 25, 29. Powell, 1951: 54.

Aeolidia papillosa (Linnaeus). Bergh, 1860: 309–331, pl. 8. Bergh, 1868: 174, 184, 200–203, pl. 1, figs. 1–20. Dall, 1870: 249. Bergh, 1874: 396. Bergh, 1877c: 822. Bergh, 1879b: 74–77, pl. 1, figs. 1–6. Bergh, 1879c: 130–131, pl. 1, figs. 1–6. Trinchese, 1881: 33. Dall, 1884: 341. Bergh, 1890a: 28. Bergh, 1892: 1019 (27). Hecht, 1893: XVI. Lundbeck, 1893: 175. Bergh, 1894: 127. Bergh, 1898: 540–541. Cooke, 1899: 65. Beaumont, 1900: 833. Vayssière, 1901: 301. Johansen, 1902: 387. Mar. Biol. Assoc., 1904: 278. Cockerell & Eliot, 1905: 32. Eliot, 1907: 327, 352. Walton, 1908: 228–229. Balch, 1909: 37. Farran, 1909: 3–4. Eliot, 1910: 5, 7, 11, 36, 50–59, 175, text fig. 7. Sumner *et al.*, 1913: 705. Walton, 1913: 110. Johnson, 1915: 162. Evans & Evans, 1917: 109. O'Donoghue, 1921: 199–201, pl. 3 (9), fig. 31. Odhner, 1921: 225. O'Donoghue & O'Donoghue, 1922: 135–136, pl. 3, fig. 1. O'Donoghue, 1922b: 165. O'Donoghue, 1922d: 141. Løyning, 1922: 70–73, 94, text figs. 51–54, pl. 4, figs. 14–15. Elmhirst, 1922: 40. Iredale & O'Donoghue, 1923: 201. Odhner, 1926a: 29. Odhner, 1926b: 28. O'Donoghue, 1926: 232. Jutting, 1927: LXXXVIII. Løyning, 1927: 262. Carter, 1927: 5 ff. Cuenot, 1927: 261–262. Carter, 1928: 97 ff. O'Donoghue, 1929: 742. Russell, 1929: 210 ff, text figs. 2–3, pls. 6, 8–10. Lemche, 1929: 18–19. Carter, 1929: 561. Mar. Biol. Assoc., 1931: 268. Rousseau, 1931: 954–956. Winckworth, 1932: 238. Nobre, 1932: 28, pl. 9, fig. 2. Monod & Dollfus, 1932: 138 ff. Renouf, 1934: 400. Rousseau, 1934: 677. Chambers, 1934: 602 ff. Johnson, 1934: 154. MacGinitie, 1935: 740. Baba, 1935b: 116, 121–123, pl. 8, figs. 3–5. Leigh-Sharpe, 1935: 48. Nobre, 1936: 20. Baba, 1937a: 199. Baba, 1937b: 335. Millott, 1937: 406 ff. Moore, 1937: 11, 194. Hewatt, 1937: 200. White, 1938: 16, 17. Lemche, 1938: 28 ff. Graham, 1938: 267 ff, text fig. 11. Odhner, 1939: 84–85, text figs. 49–50. Cockerell, 1940: 503. Russell, 1942: 80–81. McMillan, 1942a: 324. McMillan, 1942b: 327. McMillan, 1944: 162. Jutting, 1947: 65. Pruvot-Fol, 1951a: 54. Cornet & Marche-Marchad, 1951: 37–38. Stehouwer, 1952: 161–170. Jaeckel, 1952: 24 ff. Stock, 1952: 58, 59. Braams & Geelen, 1953: 242 ff. LaRocque, 1953: 248. Williams, 1954: 107. Pruvot-Fol, 1954: 426–427, text fig. 167. Graham, 1955: 153. Franzén, 1955: 428. Mar. Biol.

Assoc., 1957: 318. Baba, 1957: 9. Aboul-Ela, 1959: 442. Swennen, 1959: 58. Thompson, 1960b: 125. Haaften & Verwey, 1960: 493 ff. Pruvot-Fol, 1960: 160, 194. Swennen, 1961: 223–225. Miller, 1961: 98 ff. Thompson, 1961: 237. Marcus, 1961: 54 ff, pl. 10, figs. 193–195. Robson, 1961: 685–690. Lance, 1961: 68. Buznikov & Manukhin, 1961: 226. Kohn, 1961: 299. McLean, 1962: 111. Roginskaya, 1962a: 88, 104, 106, figs. 5.6–5.7. Roginskaya, 1962b: 209–211, 213, 214. Sakharov, 1962: 311. Miller, 1962: 562–563. Roginskaya, 1963: 1179. Bruce *et al.*, 1963: 209. Paine, 1963a: 4. Paine, 1963b: 71. Steinberg, 1963b: 72. de Vries, 1963: 137 ff. Thompson, 1964: 279 ff. Gonor, 1965: 231. Baba & Hamatani, 1965: 107. Ghiselin, 1965: 345 ff. Sakharov, 1966: 957. Edmunds, 1966: 28 ff. Ross, 1967: 313. Hurst, 1967: 255 ff, text figs. 10a–d, pl. 29, fig. 13, pl. 33, fig. 29; fig. 24-10. Wolter 1967: 277 ff, text figs. 6, 19, 34–36. Franz, 1968: 11. Mauzey *et al.*, 1968: 617. Beeman, 1968b: 268. Bebbington & Thompson, 1968: 10. Sphon & Lance, 1968: 76. Streble, 1968: 357 ff. Thompson & Hinton, 1968: pl. 2, figs. A–C. Burn, 1968: 91. Rosin, 1969: 74, 76. Tardy, 1969: 34. Barrett, 1969: 68–69. Daro, 1969: 147. Roller & Long, 1969: 425. Loveland *et al.*, 1969: 419. Franz, 1970: 172 ff. Hughes, 1970b: 81, 82, text figs. 5, 7, 8, 23. Schmekel, 1970: 158. Rosin, 1970: 47. Tardy, 1970: 352. Bernard, 1970: 85. Gosliner & Williams, 1970: 176. Daro, 1970: 168–169. Waters, 1971a: 32. Waters, 1971b: 33. Harris, 1971a: 79–80, 81. Harris, 1971b: 699. Harris, 1971c: 22. Meyer, 1971: 148–149. Keen, 1971: 839, fig. 2385. Kress, 1971: 326, 342–345, text fig. 14. Salvini-Plawen, 1972: 394, 396. Korobtsov & Sakharov, 1972: 198. Bertsch *et al.*, 1972: 304. Holleman, 1972a: 60. Humes & Stock, 1973: 167, 168. Thompson & Bebbington, 1973: 148, 149. Navoni, 1973: 1334, 1352. Waters, 1973: 174–192. Morse, 1973: 1334. Harris, 1973: 217 ff. Mariscal, 1974: 163. Roginskaya, 1974b: 998, text fig. 1. Bertsch, 1974: 3–6, figs. 1–4. Nybakken, 1974: 371. Hinegardner, 1974: 452. Edmunds *et al.*, 1974: 939–947. Abbott, 1974: 380, pl. 16, fig. 4470. Rozsa, 1974: 7, 8. Rozsa, 1975: 3. Belcik, 1975: 276. 277. Franz. 1975a: 81, 82. Zack. 1975a: 271. Clark, 1975: 37. Kalker & Schmekel, 1976: 42 ff. Roginskaya, 1976: 26. Edmunds *et al.*, 1976: 65 ff. Harris, 1976: 301. Lambert, 1976: 296. Michel, 1976: 48, fig. 10. Thompson, 1976a: 36, 39, 50, text figs. 21b–h. Thompson, 1976b: 64, 71, 77, 80, 87, fig. 1. Thompson & Brown, 1976: 160, fig. 85. Barletta & Melone, 1976: 204, 205, 230–231, 233. Barletta & Melone, 1977: 320–324, text figs. 1–2. Hoc & Fricke, 1977: 362, text fig. 9b. Dunn, 1977: 70. Garlo, 1977: 24, 26, 27. Moreteau, 1977: 369 ff. Tardy, 1977: 255–258. Nybakken, 1978: 133, 135. Bonar, 1978: 187. McDonald & Nybakken, 1978: 115. Haderlie & Donat, 1978: 52, 60. Day & Harris, 1978: 105 ff. Howe & Harris, 1978: 551 ff. Brewer, 1978: 8. Williams, 1978: 58. Harris & Howe, 1979: 138 ff. Russo, 1979: 46, 47. Boyle & Cohen, 1980: 2130. Cockburn & Reid, 1980: 275 ff. Gosliner, 1980: 72. Porter & Rivera, 1980: 217 ff, figs. 1, 2, 6–8, 11–12. Williams, 1980: 99 ff, text fig. 1b.

Aeolidia papillosa var. *pacifica* Bergh, 1879b: 75–77, pl. 1, figs. 1–6. Bergh, 1879c: 131–133, pl. 1, figs. 1–6.

Aeolidia herculea Bergh, 1894: 128–129, pl. 1, figs. 8–12. Bergh, 1898: 540. Cockerell & Eliot, 1905: 32. O'Donoghue, 1922d: 141. Marcus, 1961: 54.

Aeolidiella papillosa. Balch 1909: 36.

Eolis papillosa var. *albina* Dautzenberg & Durouchoux, 1913: 8.

Aeolidida papillosa. O'Donoghue, 1921: 199. Jaeckel, 1952: 45 (*lapsus*).

Aeolidia hercules Bergh. Smith & Gordon, 1948: 181 (*lapsus*).

Aeolidia papillosa var. *serotina* Bergh. Marcus, 1959: 3 ff, 81–84 ff, figs. 191–196. Marcus, 1961: 56.

Aeolidia pappilosa (Linné). Almaca, 1960: 209–211 (*lapsus*).

Aeolidia papillosa herculea Bergh. MacFarland, 1966: 370–373, pl. 72, figs. 1–8.

Aaeolidia papillosa. Daro, 1969: 139 (*lapsus*).

Aerolidia papillosa. Platts, 1973: 384 (*lapsus*).

Aeolodia papillosa. Kalker & Schmekel, 1976: 41 (*lapsus*).

Type-specimens: not listed.

Body tapered to a short, broad, pointed tail which extends posteriorly just beyond the cerata. Oral tentacles slightly shorter than rhinophores, same color as body. Rhinophores usually a slightly darker shade of body color. Cerata occur in numerous (19–24 or more) transverse rows, usually about one third of the cerata rows occur anterior of the rhinophores. Cardiac region lacks cerata, remainder of dorsum so densely covered with cerata as to make individual rows almost indistinguishable. Cerata recumbent when animal is actively crawling. Color of body and cerata highly variable, most commonly dirty white, but individuals which are dull gray, mauve, rose, or pink have been collected. Area between oral tentacles and rhinophores with triangular to crescentic patch of encrusting white to cream, this patch may be prolonged onto dorsal surface of oral tentacles. Area of similar pigment occurs posterior of rhinophores and extends to cardiac region. Core of cerata usually brownish to mauve or umber, but quite variable. T.L.: 40 mm.

Anus located dorso-laterally on right, between the ninth and tenth rows of cerata. Renal pore ventral of first post-anal row of cerata. Genital aperture on right side, between fifth to tenth rows of cerata. Penis conical and unarmed.

Radular formula of specimen examined 23(0.0.1.0.0), with 36–38 denticles on each tooth (Fig. 94). MacFarland (1966: 371) reports 18(0.1.0), with 38–43 denticles on each tooth, while Marcus (1961: 54) reports 21(0.1.0), with up to 58 denticles on each tooth. Masticatory border of mandible smooth.

Type-locality: "Mari Norvegico."

Range and habitat: Widely distributed in the northern hemisphere (Lance, 1961), Atlantic (Franz, 1975a) and Pacific (Lance, 1961) coasts of North America; Japan (Baba, 1935b), Europe (Pruvot-Fol, 1954). Intertidal to 870 m. Most commonly found on docks and pilings in bays; occasionally found in rocky intertidal. Feeds on various species of sea anemones: '*Actinia*,' *Actinia equina, Actinothoe sphyrodeta, Aiptasia couchi*, '*Anthea*,' *Anemonia sulcata, Anthopleura artemisia, Anthopleura balli, Anthopleura elegantissima, Anthopleura xanthogrammica, Cereus pedunculatus, Corynactis californica, Corynactis viridis, Diadumene cincta, Diadumene luciae, Epiactis prolifera, Metridium dianthus*, '*Metridium marginatus*,' *Metridium marginatum, Metridium senile, Sagartia elegans, Sagartia troglodytes, Sagartiogeton undata, Stomphia coccinea, Tealia coriacea, Tealia crassicornis, Tealia felina, Tealiopsis stella* (Bertsch *et al.*, 1972; Bruce *et al.*, 1963; Clark, 1975; Day & Harris, 1978; Dunn, 1977; Eliot, 1910; Harris, 1971b; Harris, 1973; Howe & Harris, 1978; Harris & Howe, 1979; Kalker & Schmekel, 1976; McMillan, 1942b; Miller, 1961; Robson, 1961; Russell, 1942; Swennen, 1961; Thompson, 1964; Thompson & Brown, 1976; Waters, 1973). In addition, Miller (1961) and Salvini-Plawen (1972) list the hydroid *Tubularia indivisa* as a food item. Jaeckel (1952) also lists worms, tunicates, and young *Mytilus* as prey. Alder & Hancock (1855) found several small specimens of the common mussel in the stomach. McIntosh (in Grosvenor, 1903) found that the cod (*Gadus callarius*) would eat *Aeolidia papillosa*. Homans & Needler (1944: 37) found the stomachs of a fairly large sample of young haddock (*Melanogrammus aeglifinus*) filled exclusively with *A. papillosa*.

Aeolidiella Bergh, 1867

Body aeolidiform, tapered posteriorly. Foot somewhat rounded anteriorly, anterior foot corners somewhat produced into triangular lobes. Cerata numerous, cylindrical, slightly clavate, and decumbent, arranged in slightly oblique rows which are very close together; the cerata bear cnidosacs. Rhinophores nonretractile, smooth or with a few shallow, oblique lamellae.

Masticatory border of mandibles smooth or striate, nondenticulate. Radula uniseriate, rachidian teeth rather bilobed, with a somewhat prominent median denticle, with lateral denticles largest on medial portion of either lobe.

Penis unarmed. Anus cleioproct.

Type-species: *Aeolidiella soemmerringii* (Leuckart, 1828).

Aeolidiella takanosimensis Baba, 1930

Eolis sp. Ijima, 1925: 615, fig. 740B.

Aeolidiella takanosimensis Baba, 1930: 122, 124, text figs. 4a–b, pl. 4, figs. 5a–c. Komori, 1932: 395–397, text figs. 3–4. Baba, 1949: 20, 111–112, 183–184, text figs. 154–155, pl. XLIX, fig. 167. Baba & Hamatani, 1952: 10. Abe, 1964: 72–73, pl. 36, fig. 129. Marcus & Marcus, 1967a: 117. Schmekel, 1968a: 122, 123, 145. Usuki, 1969: 8. Schmekel, 1970: 135, 155, 156, fig. 16b. Schmekel, 1971: 122, text fig. 2b. Sphon, 1971a: 368–369. Salvini-Plawen, 1972: 394. Mulliner, 1972a: 38. Mulliner, 1972b: 4, figs. Abbott, 1974: 380. Keen & Coan, 1975: 45. Ferreira & Bertsch, 1975: 329, fig. 19. McDonald & Nybakken, 1978: 115. Bertsch, 1979a: 59. Baba, 1979a: 12–18, figs. 1–6. Baba, 1979b: 7.

Eolidina (*Eolidina*) *takanosimensis* (Baba). Baba, 1937b: 336. Baba, 1938: 3.

Aeolidiella takanosimiensis Baba. Gosliner, 1980: 63–64, 72, text figs. 16A–B (*lapsus*). (*Non*) *Aeolidiella* (?*takanosimensis* K. Baba). Risbec, 1956: 31–32, pl. 21, figs. 110–115. Marcus, 1961: 56 (=*Spurilla risbeci* Marcus, 1961).

Type-specimens: missing (Baba, personal communication).

Foot elongate, rather rounded and bilabiate anteriorly, tapered posteriorly to moderate, pointed tail. Oral tentacles long, cylindrical, and slightly tapered to blunt tips, vermilion distally with an opaque white tip. Rhinophores smooth, cylindrical, and tapered to bluntly pointed tips; colored as oral tentacles. Cerata arranged in about 28 or more oblique rows dorso-laterally on either side of dorsum leaving dorsum free antero-medially, posterior groups of cerata less separated medially. General ground color translucent grayish-white with a vermilion tinge. A broad band of vermilion occurs dorso-laterally on either side, between base of oral tentacles and base of rhinophores. Dorsum vermilion in cardiac region; with about 3 or more rather symmetrical, white blotches dorso-medially. Each ceras bears a subapical band of opaque white below light vermilion tip; core light brown. T.L.: 25 mm.

Anus dorso-lateral on right, between ninth and tenth rows of cerata. Genital aperture on right side, ventral of third row of cerata.

Baba (1930: 122) reports the radular formula 16(0.1.0), Baba (1979: 14) reports 12–20(0.1.0), and Gosliner (1980: 63) reports 15–17(0.1.0), while Ferreira & Bertsch (1975: 329) report 32(0.1.0). Baba (1930: 122) reports 24–34 denticles on either side of median denticle of the rachidian tooth, Baba (1979a: 14) reports 15–20 denticles, and Gosliner (1980: 63) reports 16–19 denticles, while Ferreira & Bertsch (1975: 329) report approximately 67 denticles per tooth. Masticatory border of mandibles smooth.

Type-locality: Takanosima, Tateyama Bay, Japan.

Range and habitat: Palos Verdes Peninsula, Los Angeles Co., California (Sphon, 1971a), to San Diego, San Diego Co., California (Sphon, 1971a); Bahía San Marte, Baja California, Mexico (Ferreira & Bertsch, 1975); Japan (Baba, 1930); Gulf of Naples, Italy (Schmekel, 1971); Hawaii (Gosliner, 1980); Fanning Atoll, Line Islands (Gosliner, 1980). Usually found on floating docks in bays. Schmekel (1968a: 145) and Salvini-Plawen (1972: 394) report that it feeds upon the sea anemone *Sagartia* sp.

Aldisa Bergh, 1878

Body doridiform, dorsum covered with numerous small papillae. Labial tentacles small and auriform or tuberculiform. Rhinophores perfoliate and retractile into sheaths. Branchial plumes retractile, uni- to tripinnate, arranged in a circle around anus.

Labial disc unarmed. Radular formula 0.n.0.n.0, laterals quite elongate and bear numerous fine denticles distally, appearing whisk-like.

Penis armed with small hooks.

Type-species: *Aldisa zetlandica* (Alder & Hancock, 1854).

Aldisa sanguinea (Cooper, 1863)

Doris (*Asteronotus*) *sanguinea* Cooper, 1863a: 204. Carpenter, 1864: 608. Steinberg, 1961: 59.

Doris sanguinea Cooper. Cooper, 1867: 14. Abraham, 1877: 203. Orcutt, 1885: 545. Kelsey, 1907: 39.

Asteronotus (?) *sanguinea* (Cooper). Bergh, 1890b: 917.

Asteronotus sanguineus (Cooper). Bergh, 1891: 137. Pruvot-Fol, 1954: 269.

Asteronotus (?) *sanguineus* (Cooper). Bergh, 1892: 1103 (111).

Aldisa sanguinea (Cooper). MacFarland, 1905: 42. MacFarland, 1906: 123–125, pl. 18, figs. 25–26; pl. 21, figs. 112, 114; pl. 24, fig. 7. Kelsey, 1907: 33. O'Donoghue, 1926: 206, 209. O'Donoghue, 1927a: 10. O'Donoghue, 1927b: 84–85, pl. 1, figs. 16–19. Boone, 1929: 38. Costello, 1938: tabs. 1–3, 5. Smith & Gordon, 1948: 181. Pruvot-Fol, 1954: 269. Steinberg, 1961: 59. Marcus, 1961: 16, 57, pl. 3, figs. 50–53. Lance, 1961: 66. Cook, 1962: 196. Steinberg, 1963b: 70. MacFarland, 1966: 169–171, pl. 25, fig. 8; pl. 29, fig. 11; pl. 35, figs. 17–22. Sphon & Lance, 1968: 76. Long, 1969c: 232. Fournier, 1969: 74. Roller, 1969a: 280–281, text fig. 1. Roller & Long, 1969: 425. Robilliard & Baba, 1972: 409–413, fig. 1A. Abbott, 1974: 354, text fig. 4236. Ferreira & Bertsch, 1975: 327–328, figs. 11–14. Belcik, 1975: 276. Keen & Coan, 1975: 43. Bloom, 1976: 293, 295. Nybakken, 1978: 135. McDonald & Nybakken, 1978: 110, 112. (*Non*) Farmer & Collier, 1963: 62. (=*Thordisa bimaculata* Lance, 1966.)

Type-specimens: not listed; Geological survey coll. (Cooper, 1863a).

Foot oval, bluntly rounded and bilabiate anteriorly, slightly more acutely rounded posteriorly. Labial tentacles short and auriform, with a distinct external groove. Rhinophores reddish, with 12–15 lamellae. Branchial plumes 8–10, unipinnate, light red to crimson. General ground color light red to dark crimson, occasionally yellow-orange to yellow-green; dorsum sprinkled with very minute dark brown to black dots; with 1–2 larger black spots on median line of dorsum, one just posterior of rhinophores and the other just anterior of branchial plumes, one or both spots may be absent, especially in small individuals. Laterally on either side of dorsum, about two thirds of the distance from anterior end occur (especially in large individuals) patches of yellow to yellow-green; a similar patch frequently occurs just posterior of branchial plumes. T.L.: 17 mm.

Radular formula of specimen examined 55(89–107.0.89–107), MacFarland (1966: 170) reports 70(75–100.0.75–100). Laterals (Fig. 56) long and rod-like, with numerous fine denticles distally.

Type-locality: San Diego Bay, California.

Range and habitat: Bodega Bay, Sonoma Co., California (Marcus, 1961), to San Diego, San Diego Co., California (Cooper, 1863a); Punta Prieta, W. Isla Espíritu Santo, Mexico (Ferreira & Bertsch, 1975). Intertidal to 10 m. Usually found in the rocky intertidal under rocks. Feeds upon the sponge *Hymendesmia brepha* (McDonald & Nybakken, 1978: 110), also found on *Ophlitaspongia pennata* (Fournier, 1969).

Comments: This species should be closely compared to *Aldisa banyulensis* Pruvot-Fol, 1951. *Aldisa sanguinea cooperi* differs from *A. sanguinea sanguinea* by being lemon yellow to cadmium orange, and usually less densely dotted with black points than *A. s. sanguinea.* The black spots on the midline of the dorsum are usually less prominent and more numerous in *A. s. cooperi* than in *A. s. sanguinea.*

A subspecies has recently been named and the synonymy for that subspecies is given so that it may be separated from *Aldisa sanguinea sanguinea.*

Aldisa sanguinea cooperi Robilliard & Baba, 1972

Doris sanguinea Cooper. (*Asteronotus.*) Cooper, 1863b: 58.

Doris sanguinea Cooper. Carpenter, 1864: 609.

Aldisa sanguinea (Cooper). Baba, 1940: 103–104, figs. 1–2. Baba, 1949: 62–63, 150, text fig. 75, pl. 24, fig. 86. Baba, Hamatani & Hisai, 1956: 211, fig. 6. Baba, 1957: 9.

Aldisa sanguinea cooperi Robilliard & Baba, 1972: 409–413, figs. 1B, 2–4. Lambert, 1976: 294, 296.

Ancula Lovén, 1846

Body limaciform and smooth, highest just anterior of branchial plumes. Foot abruptly rounded anteriorly, rather narrow and elongate, tapered to narrow tail. Labial tentacles short and lobe-shaped. Rhinophores non-retractile, perfoliate; base of each rhinophore bears 2 digitiform extra-rhinophoral appendages. Branchial plumes 3, non-retractile, bi- and tripinnate, arranged in semi-circle around anus. On either side, lateral of branchial plumes are one to several slightly clavate, extrabranchial appendages.

Armature of labial disc consists of rows of separate, imbricated hooks. Radular formula 1.1.0.1.1, lateral large and broad with a denticulate inner margin, marginals much smaller and subtriangular.

Penis armed with very small hooks. Buccal crop sessile.

Type-species: *Ancula gibbosa* (Risso, 1818).

Ancula lentiginosa Farmer in Farmer & Sloan, 1964

Ancula lentiginosa Farmer in Farmer & Sloan, 1964: 148–150, pl. 18, figs. 1–2; text figs. 1–2. Lance, 1966: 78. Sphon & Lance, 1968: 76. Roller & Long, 1969: 425. Keen, 1971: 829. Marcus, 1972b: 299. Abbott, 1974: 364. Nybakken, 1978: 135. Jaeckle, 1981: 240.

Type-specimens: Calif. Acad. Sci., IZ no. 13.

Labial tentacles short, slender, and blunt. Rhinophores with 4–7 lamellae, translucent tan to off-white, with various amounts of reddish-brown dots. The 2 extra-rhinophoral appendages about half as long as rhinophores and tan to off-white with various amounts of reddish-brown dots. Branchial plumes 3, tripinnate, tan to off-white with various amounts of reddish-brown dots. On either side is a single extra-branchial appendage which is colored as the extra-rhinophoral appendages. General ground color tan to off-white, with various amounts of reddish-brown dots on dorsum, head, tail, and sides of body; these dots are usually clustered in groups forming a pattern. T.L.: 5 mm.

Radular formula of specimen examined 23(1.1.0.1.1); Farmer & Sloan (1964: 148) report 36(1.1.0.1.1). The laterals of the specimen examined (Fig. 44b) bear 12–14 denticles, Farmer & Sloan (1964) report 13 denticles. The marginals (Fig. 44a) are roughly triangular and bear a stout hook apically.

Type-locality: Salt water system (pipes) of Scripps Institution of Oceanography, La Jolla, San Diego Co., California.

Range and habitat: Frontier Arts Nature Reserve, Marin Co., California (Jaeckle, 1981), to La Jolla, San Diego Co., California (Farmer & Sloan, 1964); also reported from Bahía de los Ángeles, Baja California, Mexico (Lance, 1966). Intertidal and subtidal, usually in bays on floating docks and pilings. Quite uncommon, but when found usually occurs in numbers.

Ancula pacifica MacFarland, 1905

Ancula pacifica MacFarland, 1905: 53. MacFarland, 1906: 148–149, pl. 20, figs. 89–92; pl. 21, figs. 93–96; pl. 30, fig. 23. Guernsey, 1912: 75, fig. 39G. Hilton, 1919: 34. Odhner, 1926a: 46. O'Donoghue, 1926: 221. Smith & Gordon, 1948: 180. Pruvot-Fol, 1951a: 28. Marcus, 1961: 28–29, 58, pl. 6, figs. 97–102. Lance, 1961: 67. Steinberg, 1963b: 71. Farmer & Sloan, 1964: 148 ff. MacFarland, 1966: 123–124, pl. 21, fig. 1; pl. 29, figs. 2–3. Sphon & Lance, 1968: 82. Long, 1969c: 232. Roller & Long, 1969: 425. Gosliner & Williams, 1970: 176. Behrens, 1971a: 297–298. Robilliard, 1971a: 162–163, 164. Abbott, 1974: 364, fig. 4336. Nybakken, 1978: 135. McDonald & Nybakken, 1978: 110, 111.

Type-specimens: U. S. Nat. Mus., no. 181280.

Labial tentacles short, slender, blunt and slightly flattened. Rhinophores perfoliate with about 8–10 lamellae, lamellae yellowish, tip of clavus orange. The 2 extra-rhinophoral appendages nearly as long as rhinophores; white with subapical ring of yellow to orange. Branchial plumes 3, bi- and tripinnate, yellowish-white with orange tips. On either side are 4–5 or more extra-branchial appendages which are yellowish-white on proximal two-thirds and yellow on distal third, with orange tips. General ground color yellowish-white. A narrow, orange line extends postero-medially from between the rhinophores to branchial plumes and continues from posterior of branchial plumes to tip of tail. A similar orange line on each side extends posteriorly along the dorso-lateral margin, from the rhinophores to the extra-branchial appendages; this same line continues between extra-branchial appendages and for a short distance posterior of them. T.L.: about 10 mm.

Radular formula of specimen examined 32(1.1.0.1.1), MacFarland (1966: 124) and Marcus (1961: 29) both report 35(1.1.0.1.1). The laterals (Fig. 43b) of the specimen examined bear 11–14 denticles; MacFarland (1966: 124) reports 11–17 denticles on laterals.

Type-locality: Monterey Bay, California.

Range and habitat: San Juan Island, Puget Sound, Washington (Robilliard, 1971a), to Point Loma, San Diego Co., California (Lance, 1961). Intertidal and subtidal, more commonly found on floating docks and pilings in bays than on the rocky open coast in California. Feeds upon the entoproct *Barentsia ramosa* (McDonald & Nybakken, 1978: 110).

Remarks: The description of *Ancula pacifica* in MacFarland (1966: 123–124) agrees almost perfectly with that of *Ancula cristata* in Alder & Hancock (1847: fam. 1, pl. 25). The external coloration is identical except for the yellow-orange line on the dorso-lateral margin of *A. pacifica,* which is not mentioned by Alder & Hancock (1847) for *A. cristata.* This line is sometimes so discontinuous in *A. pacifica* that it is almost absent (Robilliard, 1971a: 162–163), and Herdman & Clubb (1892: 134) state that the variation in coloration of *A. cristata* "is very great, and the larger specimens are almost invariably white, light grey or almost colourless, while the smaller ones are more or less conspicuously ornamented with bright yellow." The number of branchial plumes (3) is the same in both species, as is the number of rhinophore lamellae (8–10). *A. pacifica* has 4–5 extra-branchial appendages and *A. cristata* usually has 5 but may have 4–7 (Alder & Hancock, 1855; Meyer & Möbius, 1865). The radular formula of *A. pacifica* is 35(1.1.0.1.1) (MacFarland, 1966) while that for *A. cristata* is 25–27(2.0.2) (Alder & Hancock, 1855). MacFarland (1966) reports 11–17 denticles on the laterals of *A. pacifica* while Alder & Hancock (1855: pl. 46 suppl.) show 12 denticles on the laterals of *A. cristata,* and Meyer & Möbius (1865: pl. 4) show 13–15 denticles.

There seem to be no significant differences between these two species. Meyer (1971: 140) considers both *A. cristata* and *A. sulphurea* Stimpson, 1853 as junior synonyms of *A. gibbosa* (Risso, 1818). However, specimens from Britain, the Mediterranean, and New England must be compared to those from California before the synonymy is certain.

Anisodoris Bergh, 1898

Body doridiform, rather evenly rounded anteriorly and posteriorly; dorsum covered with numerous large, low, rounded tubercles. Labial tentacles digitiform. Rhinophores perfoliate and retractile into low sheaths which are bordered by low tubercles. Branchial plumes tri- or quadripinnate, retractile, arranged in a circle around anus.

Labial disc smooth. Radular formula 0.n.0.n.0, laterals numerous and hamate.

Penis unarmed. Prostate gland large, set off from the efferent duct.

Type-species: *Anisodoris punctuolata* (Orbigny, 1837).

Remarks: Thompson (1975) synonymized *Anisodoris* with *Discodoris*. I here retain *Anisodoris* for reasons discussed under *Discodoris* (*q.v.*).

Anisodoris nobilis (MacFarland, 1905)

Montereina nobilis MacFarland, 1905: 38–39. Abbott, 1974: 351, pl. 17, no. 4215.

Anisodoris nobilis (MacFarland). MacFarland, 1906: 116–118, pl. 18, figs. 6–11; pl. 22, figs. 1–2. Eliot, 1907: 338. Berry, 1907: 34. Bovard & Osterud, 1918: 133–134. O'Donoghue, 1921: 156–158, pl. 1 (7), figs. 9–10. O'Donoghue, 1922a: 126. O'Donoghue & O'Donoghue, 1922: 137. O'Donoghue, 1922b: 163. O'Donoghue, 1924: 1, 22–23, 28–29. O'Donoghue, 1926: 207. O'Donoghue, 1927b: 81, pl. 1, figs. 4–5. Fraser, 1932: 67. Hewatt, 1937: 178 ff. Hewatt, 1938: 287. Costello, 1938: 325, 329–332, tabs. 2, 5, pl. 1, fig. 16. Smith & Gordon, 1948: 181. Rigg & Miller, 1949: 343. Fischer, 1950: 199. LaRocque, 1953: 259. Bousfield, 1958: 109. Marcus, 1959: 45, 47. Eyerdam, 1960: 45. Marcus, 1961: 17–18, pl. 3, figs. 56–58. Lance, 1961: 66. McLean, 1962: 111. Paine, 1963a: 4. Farmer & Collier, 1963: 62. Steinberg, 1963b: 70. Pequegnat, 1964: 279. Willows, 1965: 707 ff. MacFarland, 1966: 188–190, pl. 28, figs. 1, 3; pl. 29, figs. 16–17; pl. 37, figs. 22–27. Marcus & Marcus, 1967a: 71. Gorman *et al.*, 1967: 329. Sphon & Lance, 1968: 76. Turner *et al.*, 1969: 133. Roller & Long, 1969: 425. Gorman & Mirolli, 1969: 615 ff. Marmor & Gorman, 1969: 293. Robilliard, 1969a: 290. Mirolli, 1970: 141a. Gosliner & Williams, 1970: 177. Marmor & Salmoiraghi, 1970: 834. Marmor & Gorman, 1970: 65. Bernard, 1970: 84. McBeth, 1970: 28. Gorman & Marmor, 1970a: 897, 898. Gorman & Marmor, 1970b: 919. Gorman & Marmor, 1971: 323. Gorman & Mirolli, 1971: 137a. Marmor, 1971: 575. North, 1971: 57. Bertsch *et al.*, 1972: 304. Holleman, 1972a: 60. Baker, 1972: 45. McBeth, 1972a: 55 ff. Gorman & Marmor, 1972: 319. Partridge, 1973: 349. Gosliner & Williams, 1973b: 352. Mirolli & Gorman, 1973: 423. Gorman & Marmor, 1974a: 36. Gorman & Marmor, 1974b: 50. Marmor, 1975: 169 ff. Belcik, 1975: 276. Schuler, 1975: 33. Bloom, 1975: 311–314. Bloom, 1976: 289 ff. Guy & Connor, 1976: 146. Partridge & Stevens, 1976: 315, 316. Thompson & Smith, 1976: 153. Williamson & Crill, 1976a: 217, 219. Bloom & Bloom, 1977: 296–299. Eckert *et al.*, 1977: 1748. Eyerdam, 1977: 110. Hargens, 1977: 363. Nybakken, 1978: 134 ff. Haderlie & Donat, 1978: 60. Eckert & Tillotson, 1978: 178a. McDonald & Nybakken, 1978: 110, 112. Partridge & Connor, 1978: C155. Fuhrman *et al.*, 1979: 290 ff. Partridge *et al.*, 1979: 70 ff. Connor, 1979: 41 ff. Harris & Howe, 1979: 145. Aldrich *et al.*, 1979a: 508 ff. Aldrich *et al.*, 1979b: 532 ff. Bertsch, 1980: 224. Fuhrman *et al.*, 1980: 193.

Anisodoris (*Montereina*) *nobilis*. Eliot, 1907: 338.

Archidoris nobilis. Michel, 1976: 46, fig. 3.

Type-specimens: U. S. Nat. Mus., no. 181284.

Foot oval, bluntly rounded and bilabiate anteriorly, slightly more acutely rounded posteriorly; foot slightly lighter in color than dorsum. Rhinophores bear 18–24 lamellae, yellow on shaft and yellow-orange on clavus. Branchial plumes 6, tri- and quadripinnate, grayish-white, tipped with opaque white. General ground color varies from light yellow to deep orange-yellow, dorsum sprinkled with numerous irregular, dark brown to black blotches which do not extend up onto any of the tubercles. T.L.: 35 mm, but specimens up to 200 mm have been collected.

Radular formula of specimens examined

20–22(40–44.0.40–44), MacFarland (1966: 189) reports 26(55–60.0.55–60), while Marcus (1961: 18) reports 23–27(55–62.0.55–62). Laterals (Fig. 76) hamate.

Type-locality: Monterey Bay, California.

Range and habitat: Washington Bay, Kuiu Island, Alaska (Eyerdam, 1977), to Ensenada, Baja California, Mexico (Farmer & Collier, 1963). Intertidal to 250 m. Common in rocky intertidal and subtidal zones; occasional small specimens may be found on docks and pilings in bays. Feeds upon the sponges: *Halichondria panicea, Haliclona permollis, Lissodendoryx firma, Mycale adhaerens, Mycale macginnitiei, Myxilla agennes, Paresperella psila, Prianos* sp., and *Zygerphe hyaloderma* (Bloom, 1976: McBeth, 1971; McDonald & Nybakken, 1978).

Remarks: Additional references which mention *Anisodoris* and presumably refer to *A. nobilis* are: Both *et al.,* 1976; Connor & Stevens, 1971a, 1971b, 1971c; Gutknecht, 1970; Williamson & Crill, 1976b.

Antiopella Hoyle, 1902

Body rather flattened, broadest anteriorly. Cerata spindle-shaped, rather inflated. Rhinophores non-retractile, perfoliate, with an inter-rhinophoral crest (or caruncle).

Masticatory border of mandibles denticulate. Radular formula 0.n.1.n.0, laterals slightly hooked distally and may bear denticles.

Penis generally thick and conical, unarmed. Anus located postero-medially on dorsum.

Type-species: *Antiopella cristata* (Delle Chiaje, 1841).

Antiopella barbarensis (Cooper, 1863)

Aeolis barbarensis Cooper, 1863b: 59–60. Carpenter, 1864: 609. Cooper, 1867: 14. Yates, 1890: 41. O'Donoghue, 1922d: 140. Steinberg, 1963a: 65.

Janolus (*Aeolis*) *barbarensis* (Cooper). O'Donoghue, 1922d: 140–141. O'Donoghue, 1924: 19.

Janolus barbarensis (Cooper). O'Donoghue, 1922d: 140. O'Donoghue, 1926: 228. Marcus, 1958: 40. Lance, 1961: 68. Steinberg, 1963a: 65–66. Abbott, 1974: 373.

Janolus fuscus O'Donoghue, 1924: 16–19, pl. 2, figs. 18–20. O'Donoghue, 1926: 228. Steinberg, 1963a: 65.

Antiopella aureocincta MacFarland, Mss. Johnson & Snook, 1927: 500–501. Steinberg, 1963a: 66.

Antiopella aureocincta Johnson & Snook. Costello, 1938: 321, tabs. 1, 5. Marcus, 1958: 40.

Antiopella (*Janolus*) *fuscus* O'Donoghue. Pruvot-Fol, 1954: 375.

Antiopella fusca (O'Donoghue). Marcus, 1958: 40. Steinberg, 1963a: 65. Lambert, 1976: 294–295, 296. Robilliard & Barr, 1978: 153.

Antiopella barbarensis (Cooper). Steinberg, 1963a: 65–66. Paine, 1963a: 4. Farmer, 1967: 342. Sphon & Lance, 1968: 76. Lance, 1969: 36. Roller & Long, 1969: 425. Turner *et al.,* 1969: 134. Burn & Miller, 1969: 30. Roller, 1970a: 372. Gosliner & Williams, 1970: 177. Keen, 1971: 835, pl. 21, fig. 4. Bertsch *et al.,* 1972: 304. Sphon, 1972a: 155. Nybakken, 1974: 371. Birkeland, 1974: 218. Ferreira & Bertsch, 1975: 328, figs. 15–16. Lambert, 1976: 294. Nybakken, 1978: 135. McDonald & Nybakken, 1978: 110, 114. Russo, 1979: 44, 48.

Antiopella aureocincta MacFarland, 1966: 303–308, pl. 57, figs. 1–5: pl. 63, figs. 13–30; pl. 64, figs. 11–17. Sphon & Lance, 1968: 76. Roller, 1970a: 372. Bernard, 1970: 86. Lambert, 1976: 294.

Hermissenda crassicornis. Buchsbaum & Milne, 1967: pl. 62.

Type-specimens: not listed; state coll. species 978 (Cooper, 1863b).

Body somewhat aeolidiform, rounded and broadest anteriorly, tapered posteriorly to pointed tail. Foot bilabiate and widest anteriorly, and tapered posteriorly to tail. Labial tentacles cylindrical, short, and blunt. Margin of dorsum covers foot everywhere, resulting in a distinct groove between margin of dorsum and foot. Rhinophores bear about 10–14 lamellae, clavus usually bears a subterminal ring of orange-gold, with tip either white or blue. Cerata spindle-shaped, arranged in longitudinal rows along margin of dorsum, leaving medial area of dorsum free of cerata; they extend anterior of rhinophores. General ground color translucent grayish-white to pinkish-gray. In specimens from northern California and Washington, cerata are tipped with opaque white, below which is a subterminal band of orange. In specimens from California south of Santa Barbara, cerata tipped with bright, metallic blue, below which is a subterminal band of metallic gold. In central California, in the area of Monterey Bay, both variations in color of cerata are found, as well as occasional specimens whose cerata are intermediate in color, with very light blue tips. Cerata cores are raw umber. Caruncle is yellow-orange. T.L.: 20 mm.

Anus located medially, well back on dorsum. Genital aperture located midway on right side. Penis cylindrical and tapered distally, unarmed.

Radular formula of specimen examined 16(14–21.1.14–21), MacFarland (1966: 305) reports 20–22(18–22.1.18–22). Rachidian tooth (Fig. 91h) bears a single, median denticle, with 6–8 small denticles on either side. Laterals (Fig. 91a–g) are slightly hooked distally, inner laterals with 12–17 minute denticles. Masticatory border of the large, thick mandibles bears 8–14 denticles.

Type-locality: Santa Barbara, Santa Barbara Co., California.

Range and habitat: Klu Bay, Revillagigedo Island, Alaska (Robilliard & Barr, 1978), to Bahía San Quintín, Baja California, Mexico (Keen, 1971); between Isla San Diego and Isla San José, Gulf of California, Mexico (Ferreira & Bertsch, 1975); Bahía de los Angeles, Baja California, Mexico (Keen, 1971). Intertidal to 30 m. Found in rocky intertidal as well as on floating docks and pilings in bays. Feeds upon the hydroid *Corymorpha palma* and the bryozoan *Bugula californica* (MacGinitie & MacGinitie, 1949: McDonald & Nybakken, 1978).

Remarks: O'Donoghue (1924: 16–19) named *Janolus fusca* from Galiano Island, British Columbia, Canada. In comparing O'Donoghue's description of this species with MacFarland's (1966: 303–308) description of *Antiopella aureocincta* (a junior synonym of *A. barbarensis*) I note a number of similarities. The number of denticles of the masticatory border of the mandible is 10–12 for *J. fusca* (O'Donoghue, 1924: 18) and 8–14 for *A. aureocincta* (MacFarland, 1966: 305). O'Donoghue (1924: 17) reports the radular formula 21(4–22.1.4–22) for the latter species. O'Donoghue (1924: 18) reports 10–14 minute serrations on the inner side of the first 3–4 laterals and 2–3 denticles on the outer side of same, while MacFarland (1966: 305) reports 12–17 small pointed denticles on the inner hook of the first 3 inner laterals and occasionally a few similar denticles on the outer face of the first lateral. O'Donoghue (1924: 16) states that a line of intense, opaque white spots runs from the last cerata to the tip of the tail of *J. fusca*; while MacFarland (1966: 306) reports the dorsum of tail with a narrow, median, longitudinal band of white in *A. aureocincta*. O'Donoghue (1924: 16) states that "near the end on the cerata where the core stops is a very striking, opaque, bright orange band. The pointed tip is transparent for a short distance and then is covered with opaque, intensely white spots." MacFarland (1966: 306) states "tips of the papillae pure white encircled below by a band of yellow orange." O'Donoghue's (1924: pl. 2, figs. 18–20) drawings of the mandibles and radula correspond very well to those by MacFarland (1966: pl. 63, figs. 13–25). In comparing the mandibles and radula of a specimen from Friday Harbor, Washington with those of a specimen from Hazard Canyon, San Luis Obispo Co., California, I can see no significant differences between the two. Therefore, *Janolus fusca* is a junior subjective synonym of *Antiopella aureocincta,* and since Sphon & Lance (1968: 76) consider the latter a junior synonym of *Antiopella barbarensis,* the correct name for the species which has been known by the above three names is *Antiopella barbarensis* by the law of priority.

O'Donoghue (1922d: 141) felt that *Janolus coeruleopictus* Cockerell & Eliot, 1905, should be considered a synonym of *A. barbarensis,* and stated that Eliot agreed with him. The description of *J. coeruleopictus* is quite brief but is fairly close to *A. barbarensis,* the only major difference being that the former has tessellated, nondenticulate mandibles (Cockerell & Eliot, 1905) while the latter has denticulate mandibles. Unless this difference in the mandibles can be explained, I feel that Steinberg (1963a: 66) was correct in stating that because of the poor description of *J. coeruleopictus* it should be declared a *nomen dubium.*

Archidoris Bergh, 1878

Body somewhat soft, doridiform, rather evenly rounded anteriorly and posteriorly; dorsum covered with numerous low, rounded tubercles of various sizes. Labial tentacles short and thick, with an external longitudinal groove. Rhinophores perfoliate and retractile into low sheaths with tuberculate margins. Branchial plumes retractile, tri- to quadripinnate, arranged in a circle around anus.

Labial disc unarmed. Radular formula 0.n.0.n.0, laterals hamate.

Penis unarmed, pleurembolic; glans penis distinct. Vas deferens glomerate.

Type-species: *Archidoris tuberculata* (Cuvier, 1804) (*non* Müller, 1778).

Archidoris montereyensis (Cooper, 1863)

Doris montereyensis Cooper, 1863a: 204. Cooper, 1863a: 58. Carpenter, 1864: 608, 609. Cooper, 1867: 14. Cooper, 1870: 56. Dall, 1871: 137.

Doris tuberculata Cuvier. Abraham, 1877: 203–204. O'Donoghue, 1926: 206. O'Donoghue, 1927b: 80.

Archidoris montereyensis (Cooper). Bergh, 1878b: 624, pl. 68, fig. 24. Bergh, 1879b: 107–108. Bergh, 1879c: 163–164. Bergh, 1880a: pl. 8 (16), figs. 10–11. Bergh, 1880b: pl. 8(16). Bergh, 1880c: 34. Bergh, 1891: 128. Bergh, 1892: 1092 (100). Bergh, 1898: 501. MacFarland, 1905: 37. Cockerell & Eliot, 1905: 34. MacFarland, 1906: 114–116, pl. 18, figs. 1–5; pl. 23, fig. 4. Berry, 1907: 34. Cockerell, 1908: 106. O'Donoghue, 1921: 154–156, pl. 1 (7), figs. 7–8. O'Donoghue, 1922a: 126. O'Donoghue & O'Donoghue, 1922: 137, pl. 3, fig. 5. O'Donoghue, 1924: 22, 28. O'Donoghue, 1926: 206–207. Odhner, 1926a: 64, 67. O'Donoghue, 1927b: 80. Fraser, 1932: 67. Costello, 1938: 324 ff, tabs. 1–5; pl. 1, fig. 5; pl. 2, figs. 28, 41. Smith & Gordon, 1948: 181. LaRocque, 1953: 259. McGowan & Pratt, 1954: 261–276. Goodwin & Fox, 1955: 1086. Marcus, 1957: 471. Marcus, 1961: 16–17, pl. 3, figs. 54–55. Lance, 1961: 66. Cook, 1962: 194–196. Paine, 1963a: 4. Steinberg, 1963b: 70. deVries, 1963: 124. Willows, 1965: 707 ff. MacFarland, 1966: 181–182, pl. 27, fig. 8; pl. 37, figs. 1–10. Thompson, 1967: 9. Hurst, 1967: 255 ff, text figs. 4a–b; pl. 27, fig. 5; pl. 34, fig. 33; fig. 24-18. Sphon & Lance, 1968: 76. Burn, 1968: 91, 92. Lee & Brophy, 1969: 220. Roller & Long, 1969: 426. Nicaise, 1969: 2601, pl. 1, fig. 1. Robilliard, 1969a: 290. Gosliner & Williams, 1970: 177. Bernard, 1970: 85. Crane, 1971: 57. Harris, 1971a: 84. North, 1971: 57. Holleman, 1972a: 60. Bertsch *et al.*, 1972: 305. Sphon, 1972a: 155. McBeth, 1972a: 56. Harris, 1973: 219 ff. Burn, 1973: 40, fig. 7c. Partridge, 1973: 349. Chia & Skeel, 1973: 153. Crane, 1973: 17. Haderlie *et al.*, 1974: tab. 4. Abbott, 1974: 351, pl. 17, no. 4211. Robilliard, 1974b: 989. Hinegardner, 1974: 452. Belcik, 1975: 276. Bloom, 1975: 311–314. Lambert, 1976: 296. Bloom, 1976: 289 ff. Elvin, 1976: 194. Partridge & Stevens, 1976: 315, 316. Thompson & Smith, 1976: 153. Williamson & Crill, 1976a: 217, 219. Bloom & Bloom, 1977: 296–299. Connor, 1977a: 43a. Connor, 1977b: 487 ff. Connor & Ahmed, 1978: 186a. Nybakken, 1978: 134 ff. Haderlie & Donat, 1978: 60. McDonald & Nybakken, 1978: 112, 116. Idler *et al.*, 1978: 163 ff. Partridge & Connor, 1978: C155. Clark & Goetzfried, 1978: 290. Dehnel & Kong, 1979: 1843. Aldrich *et al.*, 1979a: 508 ff. Aldrich *et al.*, 1979b: 532 ff. Fuhrman *et al.*, 1979: 291 ff. Partridge *et al.*, 1979: 70 ff. Connor, 1979: 41 ff. Ahmed & Connor, 1979a: 61 ff. Ahmed & Connor, 1979b: 265a. Connor & Ahmed, 1979: 265a. Ahmed & Connor, 1980a: 2038. Ahmed & Connor, 1980b: 403 ff.

Doris (*Archidoris*) *montereyensis* (Cooper). Bergh, 1880a: 232. Bergh, 1880b: 83. Orcutt, 1885: 545.

Archidoris nyctea Bergh, 1900: 222–224, pl. 21, figs. 70–72. MacFarland, 1966: 182. Burn, 1968: 91.

Archodoris montereyensis (Cooper). O'Donoghue, 1922b: 163 (*lapsus*).

Anisodoris nobilis (MacFarland). Guberlet, 1962: 255.

Type-specimens: not listed; Geological survey coll. (Cooper, 1863a).

Foot elliptical, bluntly rounded and bilabiate anteriorly, bluntly rounded posteriorly. Labial tentacles relatively small and auriculate. Rhinophores bear 20–30 lamellae, yellow to orange. Branchial plumes 7, tri- to quadripinnate, yellow to orange. General ground color variable, light yellow to dark orange, dorsum bears many irregular blotches of brown to black which extend up onto the tubercles. T.L.: 25 mm, but specimens up to 150 mm have been collected.

Radular formula of specimen examined 20(34–37.0.34–37), MacFarland (1966: 181) reports 33(42–49.0.42–49), while Marcus (1961: 17) reports 33(42–65.0.42–65), and Bloom (1976: 292) gives the range 27–36(42–70.0.42–70). Laterals (Fig. 70) hamate.

Type-locality: Monterey Bay, California.

Range and habitat: Jackson Point, Port Valdez, Alaska (Robilliard, 1974b), to La Jolla, San Diego Co., California (Cockerell & Eliot, 1905). Intertidal to 256 m. Fairly common in rocky intertidal, also found on docks and pilings in bays; also occurs well up into Elkhorn Slough, Monterey Co., California, where it feeds upon a yellow sponge which grows on muddy bottom. This sponge has been tentatively identified as *Halichondria bowerbanki* (McDonald & Nybakken, 1978). Cook (1962: 196) reports that it feeds upon *Halichondria panicea.*

Remarks: This species should be closely compared to *Archidoris tuberculata* (Cuvier, 1804), which occurs in England and very closely resembles *A. montereyensis.*

Additional references which mention *Archidoris* and are presumably referring to *A. montereyensis* are Both *et al.* (1976) and Stevens (1969).

Archidoris odhneri (MacFarland, 1966)

Austrodoris odhneri MacFarland, 1966: 173–179, pl. 26, fig. 1; pl. 29, fig. 14; pl. 36, figs. 1–19. Hurst, 1967: 255 ff, text fig. 5, pl. 26, fig. 4; pl. 33, figs. 31–32; fig. 24-24. Sphon & Lance, 1968: 77. Burn, 1968: 90–92. Roller, 1970a: 371. Robilliard, 1971a: 164. Partridge, 1973: 349–350, fig. 1c–d.

Archidoris odhneri (MacFarland). Burn, 1968: 90–92. Roller & Long, 1969: 425. Roller, 1970a: 371. Robilliard, 1971a: 164, 165. Bertsch *et al.,* 1972: 305. Burn, 1973: 40, fig. 7f. Robilliard, 1974b: 989–990. Abbott, 1974: 351. Belcik, 1975: 276. Lambert, 1976: 296. Bloom, 1976: 289 ff. McDonald & Nybakken, 1978: 112. Robilliard & Barr, 1978: 153. Fuhrman *et al.,* 1979: 291 ff. Bertsch, 1980: 224. Andersen & Sum, 1980: 797–800.

Archidoris (=*Austrodoris*) *odhneri* (MacFarland). Robilliard, 1971a: 164.

Type-specimens: type material at Calif. Acad. Sci.

Dorsal tubercles larger medially and smaller near edge of dorsum. Foot elliptical, bluntly rounded and bilabiate anteriorly, and bluntly rounded posteriorly. Labial tentacles slightly triangular to digitiform. Rhinophores bear 20–24 lamellae and are white to very light dusty yellow. Branchial plumes 7, tri- to quadripinnate, very finely divided, appearing quite feathery and delicate, white to very light yellow. General ground color pure white, occasional individuals may be very light dusty yellow. Dorsum dusted with numerous minute, opaque flecks of the ground color. T.L.: 100 mm, but specimens over 200 mm have been collected.

Radular formula of specimen examined 20(44.0.44), MacFarland (1966: 176) reports 34(55.0.55). Laterals (Fig. 71) hamate.

Type-locality: Monterey Bay, California.

Range and habitat: Port Dick, Kenai Peninsula, Alaska (Robilliard & Barr, 1978), to Point Loma, San Diego Co., California (Robilliard, 1974b). Intertidal to 25 m. Most commonly found subtidally in kelp (*Macrocystis pyrifera*) bed areas, quite rare intertidally in California. Feeds upon the sponges: *Craniella* sp., *Halichondria panicea, Mycale adhaerens, Myxilla incrustans, Stylissa stipitata, Syringella amphispicula, Tedania* sp. and a hexactinellid (possibly *Rhabdocalyptus* sp.) (Bloom, 1976; Robilliard, 1971a).

Armina Rafinesque, 1814

Body ovate, rounded anteriorly and tapered posteriorly to a pointed tail. Dorsum bears numerous longitudinal ridges which occur along the entire length of dorsum; sculpture of dorsum is different in a few species, consisting of a few widely separated ridges, or of numerous tubercles. Foot broadly rounded anteriorly and tapered posteriorly to pointed tail. Anterior margin of dorsum generally has a rounded median notch through which the rhinophores project. Rhinophores closely appressed, nearly united at base, retractile beneath mantle margin, and bear vertical perfoliations. Branchiae consist of longitudinally directed lamellae, arranged antero-laterally just below edge of dorsum; there may be smaller lamellae between the larger lamellae.

Masticatory border of mandibles denticulate. Radular formula usually n.1.1.1.n; rachidian tooth bears a strong denticle, with smaller denticles on either side; lateral denticulate or not; marginals more elongate and denticulate or not.

Penis unarmed. Anus on right side, below mantle margin, usually posterior of branchiae.

Type-species: *Armina tigrina* Rafinesque, 1814.

Armina californica (Cooper, 1863)

Pleurophyllidia californica Cooper, 1863a: 203–204. Bergh, 1866: 33, pl. 1. Cooper, 1867: 14. Bergh, 1869: 229. Bergh, 1876a: 2. Bergh, 1890a: 3–8, pl. 1, figs. 1–6; pl. 2, figs. 1–2. Bergh, 1892: 1063 (71). Bergh, 1894: 154–157, pl. 3, figs. 14–15; pl. 4, figs. 7–12. MacFarland, 1897: 227, 229–

244, pl. 18, figs. 1–10; pl. 19, figs. 11–20; pl. 20, figs. 21–23. Bergh, 1904: 19–20, pl. 4, figs. 23–26. Kelsey, 1907: 47. O'Donoghue, 1921: 178–180, pl. 5 (11), figs. 49–50. O'Donoghue, 1922a: 124. O'Donoghue, 1926: 222. Fraser, 1932: 67. Norris & Rao, 1935: 787. MacFarland, 1966: 205. Hinegardner, 1974: 452.

Pleurophyllidea californica Cooper. Carpenter, 1864: 608, 647 (*lapsus*).

Pleurophyllidia vancouverensis Bergh, 1876a: 3, 5–9, pl. 1, figs. 8–17. MacFarland, 1966: 205.

Armina columbiana O'Donoghue, 1924: 11–14, pl. 2, figs. 13–17. O'Donoghue, 1926: 222. LaRocque, 1953:260. Marcus, 1961: 43–44, 58, pl. 8, figs. 151–154. Lance, 1962c: 54. Steinberg, 1963a: 64–65. MacFarland, 1966: 206.

Armina vancouverensis (Bergh). O'Donoghue, 1926: 222. LaRocque, 1953: 260. Marcus, 1961: 44. Lance, 1962c: 54. Steinberg, 1963a: 64–65. MacFarland, 1966: 206. Marcus & Marcus, 1967b: 215.

Armina californica (Cooper). O'Donoghue, 1926: 222. O'Donoghue, 1927a: 11. LaRocque, 1953: 260. Marcus, 1961: 41–43, 44, 56, pl. 8, figs. 147–150. Lance, 1961: 67. Lance, 1962c: 54. Steinberg, 1963a: 64–65. Steinberg, 1963b: 71. Lance, 1966: 69. MacFarland, 1966: 198–206, pl. 38, figs. 1–6; pl. 43, figs. 37–44; pl. 44, figs. 6–7. Marcus & Marcus, 1967b: 215. Hurst, 1967: 255 ff, text figs. 11a–c, pl. 29, fig. 14; pl. 34, figs. 34–35; fig. 24-20. Farmer, 1967: 342. Sphon & Lance, 1968: 77. Mauzey *et al.*, 1968: 606. Bertsch, 1968: 440–441. Lance, 1969: 34. Roller & Long, 1969: 429. Turner *et al.*, 1969: 133. Bernard, 1970: 85. Keen, 1971: 834. Holleman, 1972a: 60. Thompson & Bebbington, 1973: 148, pl. 10, figs. a–d. Thompson, 1973: 167, 172, 179, 186, text fig. 9. Gosliner & Williams, 1973b: 354. Bertsch, 1973: 110. Abbott, 1974: 372, fig. 4400. Birkeland, 1974: 211 ff. Kastendiek, 1975: 784. Thompson, 1976a: 39, pl. 2, fig. d. Thompson, 1976b: 16, 47. Kastendiek, 1976: 519 ff, text fig. 7. Poorman & Poorman, 1978: 373. McDonald & Nybakken, 1978: 114. Dorsett, 1978: 307–324.

Armina (*Pleurophyllidia*) *californica* (Bergh). Smith & Gordon, 1948: 181.

Armina digueti Pruvot-Fol, 1955: 464–465, text figs. 8–10. Marcus, 1961: 44. Steinberg, 1963a: 65. Marcus & Marcus, 1967b: 216.

Armina (=*Pleurophyllidia*) *californica* (Cooper). Willows, 1965: 707 ff.

Type-specimens: not listed, Geological Survey coll. (Cooper, 1963a).

Dorsum bears about 18–25 longitudinal ridges. Head consists of a transverse head shield which is broadly rounded anteriorly, with undulating margins. Rhinophores bear 30–40 lamellae and are grayish-pink with white on tip and on margins of lamellae. Branchiae 15–30 on either side. General ground color light pinkish-brown, longitudinal dorsal ridges light pinkish-brown to cream, and area between ridges gray to grayish-brown. Margin of dorsum edged with white to cream. Dorsal surface of head shield gray to grayish-brown. T.L.: 30 mm.

Radular formula of specimen examined 25(39–44.1.1.1.39–44), MacFarland (1966: 202) reports 30(45.1.45) to 52(81.1.81), and Marcus (1961: 42) reports 41(60.1.1.1.60). Rachidians (Fig. 90k) bear 3–4 (rarely up to 8) denticles on either side of median denticle.

Type-locality: San Diego Bay, California.

Range and habitat: Hecate Strait, British Columbia, Canada (O'Donoghue, 1921), to Panama (Bergh, 1894). Found on sandy-mud bottom in 1 to 230 m, usually in association with the sea pansy *Renilla kollikeri* (*vide* Bertsch 1968: 440) or the pennatulacean *Ptilosarcus gurneyi*, both of which it feeds upon (Bertsch, 1968; Birkeland, 1974; Kastendiek, 1976; MacFarland, 1966; Turner *et al.*, 1969; McDonald and Nybakken, 1978).

Additional references: Anderson & Chase (1975) mention *Armina*, presumably referable to *A. californica*.

Atagema Gray, 1850

Body rather firm, doridiform, rather evenly rounded anteriorly and posteriorly. Dorsum spiculose, bears a medial ridge. Labial tentacles somewhat digitiform or triangular. Rhinophores perfoliate and retractile into sheaths. Branchial plumes few, tri- or quadripinnate, located just anterior of anus.

Radular formula 0.n.0.n.0, laterals hook-shaped.

Penis unarmed.

Type-species: *Atagema carinata* (Quoy & Gaimard, 1832).

Atagema alba (O'Donoghue, 1927)

Glossodoridiformia alba O'Donoghue, 1927b: 87–89, pl. 1, figs. 29–32. Lance, 1961: 66.

Atagema quadrimaculata Collier, 1963: 73–75, text figs. 1–5. Smith, 1964: 172. Sphon & Lance, 1968: 82. Roller & Long, 1969: 429. Roller, 1970a: 371. Abbott, 1974: 351.
Petelodoris spongicola MacFarland, 1966: 183–187, pl. 27, figs. 1–5; pl. 30, fig. 16; pl. 37, figs. 11–21. Lee & Brophy, 1969: 220. Roller, 1970a: 371.

Type-specimens: not listed.

Dorsum densely covered with numerous minute, hispid papillae. An irregular ridge extends posteriorly on dorsum from between rhinophores to just anterior of branchial plumes; a few smaller irregular ridges extend laterally from a median prominence on the ridge. Edge of dorsum somewhat crenulate or undulating. Foot elliptical, somewhat elongated; bluntly rounded and bilabiate anteriorly, and bluntly rounded posteriorly. Labial tentacles triangular, thin, and tapered to blunt tips. Rhinophores bear 15–18 lamellae, clavus very pale green. Rhinophore sheaths with bluntly rounded margins and covered with small, hispid papillae. Branchial plumes 3–5, bi- to tripinnate, projecting posteriorly from beneath 3 thick, bluntly triangular lobes on anterior and antero-lateral margins of branchial sheath; branchial plumes pale raw umber. General ground color raw umber, with small, dark brown to black spots between the papillae on dorsum, and with very small flecks of pink along mid-dorsal ridge. T.L.: 22 mm.

Radular formula of specimen examined 15(17–20.0.17–20), MacFarland (1966: 185) reports 15(20–23.0.20–23), while Collier (1963: 74) reports 18(18–19.0.18–19), and O'Donoghue (1927b: 88) reports 17–18(25–26.0.25–26). Laterals (Fig. 67) strongly hooked.

Type-locality: Laguna Beach, Orange Co., California.

Range and habitat: Point Pinos, Monterey Co., California (MacFarland, 1966), to San Diego, San Diego Co., California (Collier, 1963). Intertidal to 210 m. Quite rare throughout most of its range. It quite probably feeds upon encrusting sponges upon which it has been found. Most commonly found in extreme low intertidal zone, in areas of heavy surf.

Remarks: O'Donoghue (1927b: 87–89) described *Glossodoridiformia alba* from Laguna Beach, California, but the species has not been recognized since. However, upon closely comparing O'Donoghue's original description with that of *Atagema quadrimaculata* Collier (1963: 73–75) and that of its junior synonym *Petelodoris spongicola* MacFarland (1966: 183–187), it seems quite certain that they are synonymous. The general ground color (white to raw umber) is essentially the same in all three species. The dorsum bears small papillae in all three cases. The number of rhinophore lamellae is comparable, about 15 in *G. alba,* 16–18 in *P. spongicola,* and 16 in *A. quadrimaculata.* The foot is anteriorly bilabiate and deeply notched in all three cases. The number of branchial plumes is comparable, five in *G. alba,* three with two basal branches in *P. spongicola,* and five in *A. quadrimaculata.* The branchial sheath of *G. alba* was described by O'Donoghue (1927b: 88) as: ". . . a large pocket with a raised rim, which is papillated right up to the margin like the rhinophore sheath, but this part of the animal had been damaged in life and part of the rim and sides of the sheath torn off and partially healed, giving the animal a superficial likeness to a phanerobranchiate form." Certainly the branchial lobes and posteriorly projecting branchial plumes of *A. quadrimaculata* and *P. spongicola* could give the appearance described by O'Donoghue. The radular formulae are comparable in all three cases: 17–18(25–26.0.25–26) in *G. alba,* 15(20–23.0.20–23) in *P. spongicola,* and 18(18–19.0.18–19) in *A. quadrimaculata.* The shape and relative sizes of the teeth are also comparable in all three cases.

From the above facts it seems obvious that *G. alba* is conspecific with *A. quadrimaculata,* the correct name being *Atagema alba* (O'Donoghue, 1927) by the law of priority. *Glossodoridiformia* O'Donoghue, 1927, is therefore a junior synonym of *Atagema* Gray, 1850.

Babakina Roller, 1973

Body aeolidiform, broadest anteriorly and tapered posteriorly to pointed tail. Foot corners very produced. Cerata fusiform, arranged in numerous oblique rows on either side of dorsum. Rhinophores non-retractile, joined together basally for half their length.

Masticatory border of mandibles denticulate. Radula uniseriate, rachidians bear prominent median cusp, with smaller denticles on either side.

Penis unarmed. Anus pleuroproct.

Type-species: *Babakina festiva* (Roller, 1972).

Babakina festiva (Roller, 1972)

Babaina festiva Roller, 1972: 416–418, text figs. 1–9. Miller, 1974: 40.

Babakina festiva (Roller). Roller, 1973: 117–118.

Type-specimens: Calif. Acad. Sci., no. 486.

Foot rather narrow, linear, somewhat emarginate anteriorly and tapered posteriorly to tail. Foot corners produced into rather long, tentaculiform processes with a shallow groove. Oral tentacles long and cylindrical, slightly tapered to blunt points; dark pinkish-red on proximal half and very light yellow on distal half. Rhinophores perfoliate with 30–35 lamellae. Rhinophore shaft light pink, clavus yellow to brownish with a pink vertical line on proximal half of anterior face and with a number of small, encrusting, yellow dots distally, which extend in a postero-medial line on distal half. With a small, yellow to brownish knob projecting above clavus. Cerata cylindrical, slightly clavate, somewhat decumbent, and arranged in about 22 oblique rows from just anterior of rhinophores, nearly to tip of tail. Antero-medial area of dorsum free of cerata. General ground color translucent grayish-white with a pinkish tinge, which is more pronounced in some specimens. Head region may be quite pinkish-red in some specimens, and very pale in others. A medial line of yellow-white passes from base of rhinophores to between oral tentacles. Cardiac region bears numerous spots of opaque white. Dorsal tip of tail yellowish. Cerata pinkish-red on proximal half, with a subapical band of cadmium yellow, and just below this, a wide band of rather diffuse, opaque white dots; the tips are translucent grayish-white; cores dark pinkish-red. T.L.: 15 mm.

Anus on right, just posterior of cardiac region. Genital aperture on right side, ventral of fourth row of cerata. Penis unarmed.

Radular formula of specimen examined 14(0.0.1.0.0), Roller (1972: 418) reports 16(0.0.1.0.0). Rachidian tooth (Fig. 114) bears 6–11 small denticles on either side of large, median cusp. Masticatory border of mandibles bears several rows of long denticles.

Type-locality: White's Point, Palos Verdes Peninsula, Los Angeles Co., California.

Range and habitat: Malibu Reef, Los Angeles Co., California (Roller, 1972), to La Jolla, San Diego Co., California (Roller, 1972); Matenchén, Nayarit, Mexico (personal observation); Japan (Roller, 1972). Intertidal to 5 m in rocky areas. Quite rare in California.

Cadlina Bergh, 1878

Body doridiform, somewhat elongate, bluntly rounded anteriorly and less bluntly rounded posteriorly. Dorsum frequently minutely granular, occasionally tuberculate. Labial tentacles more or less triangular. Rhinophores perfoliate and retractile into sheaths. Branchial plumes uni- to tripinnate, retractile, arranged in a circle around anus.

Labial disc armed with minute hooks. Radular formula 0.n.1.n.0, rachidians each bear a few denticles, laterals usually denticulate.

Penis usually armed with hooks.

Type-species: *Cadlina laevis* (Linnaeus, 1767).

See ICZN (1967, Opinion 812), *Cadlina* validated.

Cadlina flavomaculata MacFarland, 1905

Cadlina flavomaculata MacFarland, 1905: 43. Cockerell & Eliot, 1905: 35. MacFarland, 1906: 126–128, pl. 19, figs. 32–37; pl. 21, fig. 110; pl. 25, fig. 9. Kelsey, 1907: 35. Cockerell, 1908: 106. O'Donoghue & O'Donoghue, 1922: pl. 3, fig. 4. O'Donoghue, 1922b: 154–155, 165, pl. 6, figs. 16–18. O'Donoghue, 1924: 23, 29. O'Donoghue, 1926: 210. O'Donoghue, 1927a: 10. O'Donoghue, 1927b: 85–86, pl. 1, figs. 20–24. Fraser, 1932: 67. Baba, 1935a: 343. Baba, 1937c: 75. Costello, 1938: 324–326, tabs. 1–3, 5. Smith & Gordon, 1948: 180. LaRocque, 1953: 259. Marcus, 1955: 122. Marcus, 1961: 14, pl. 3, figs. 41–42. Lance, 1961: 65. Lance, 1962a: 157. Paine, 1963a: 4, 7. Steinberg, 1963b: 69. Farmer, 1964: 24. MacFarland, 1966: 140, 143, 144–147 ff, pl. 23, fig. 1; pl. 29, fig. 12; pl. 33, figs. 12–21. Marcus & Marcus, 1967a: 169. Sphon & Lance, 1968: 77. Lee & Brophy, 1969: 220. Roller & Long, 1969: 426. Gosliner & Williams, 1970: 177. Bernard, 1970: 85. Schmekel, 1970: 194. North, 1971: 57. Keen, 1971: 823. Bertsch *et al.*, 1972: 305. Abbott, 1974: 356, fig. 4262. Belcik, 1975: 276. Thompson, 1976b: 92. Nybakken, 1978: 135. Haderlie & Donat, 1978: 60. McDonald & Nybakken, 1978: 110, 112. Fuhrman *et al.*, 1979: 291. Bertsch, 1980: 224. Chamberlain & Behrens, 1980: 284.

Cardlina flavomaculata MacFarland. Ingram, 1935: 48 (*lapsus*).

Type-specimens: U. S. Nat. Mus., no. 181279.

Dorsum covered with numerous very small, low tubercles. Foot narrow and linear, broadly rounded anteriorly and bluntly pointed posteriorly. Labial tentacles short and bluntly auriculate, with a groove on external margin. Rhinophores bear 8–12 lamellae, which are brown to almost black, causing entire clavus to appear brown. Branchial plumes 10–12, uni- to bipinnate, light cream to yellow. General ground color light cream to light yellow. A series of 6–10 or more small, lemon yellow dots occurs longitudinally on either side of dorsum, from just posterior of rhinophores to just posterior of branchial plumes. T.L.: 15 mm.

Radular formula of specimen examined 51(28.1.28), MacFarland (1966: 145) reports 77(23.1.23), while Marcus (1961: 14) reports 68–77(22–27.1.22–27). Rachidian teeth (Fig. 58a) may bear 2–3 denticles on inner margin and 4–7 denticles on outer margin. Outer laterals (Fig. 58b–d) may bear 11–15 denticles on margin.

Type-locality: Monterey Bay, California.

Range and habitat: Vancouver Island, British Columbia, Canada (O'Donoghue, 1922b), to Punta San Eugenio, Baja California, Mexico (Lance, 1961); northern end of Gulf of California, Mexico. Intertidal to 220 m. Not uncommon in rocky intertidal zone in central California. Feeds upon the sponge *Aplysilla glacialis* (McDonald & Nybakken, 1978: 110).

Cadlina limbaughi Lance, 1962

Cadlina sp. Lance, 1961: 66.

Cadlina limbaughi Lance, 1962a: 155–157, text figs. 1–3. Shields, 1966: 189. Marcus & Marcus, 1967a: 169. Sphon & Lance, 1968: 77. North, 1971: 57. Abbott, 1974: 357. Michel, 1976: 48, fig. 11.

Type-specimens: Calif. Acad. Sci., Paleo. type coll. no. 12′396.

Dorsum nearly smooth, bearing very small tubercles. Foot rather linear, broadly rounded and slightly bilabiate anteriorly, and tapered posteriorly to bluntly rounded tail. Labial tentacles thick, triangular and auriform, with a groove on external margin. Rhinophores bear 11–18 lamellae, clavus dark reddish-brown. Branchial plumes 6–8, bi- and tripinnate, whitish at base and dark reddish-brown on distal two thirds, except for the most posterior plume which is white. General ground color whitish, with numerous opaque white dots on dorsum. Sides of body and dorsal and ventral surfaces of foot bear a few minute black dots. T.L.: 15 mm.

Lance (1962a: 156) gives the radular formula 102(0.44.1.44.0). Rachidian teeth (Fig. 59a) bear 4–6 denticles. Innermost laterals (Fig. 59b) bear 3 denticles on inner margin and 6 denticles on outer margin. Outer laterals (Fig. 59c) somewhat hooked with about 14 denticles below cusp; the outermost laterals (Fig. 59d) lack a cusp and bear about 9 denticles.

Type-locality: La Jolla, San Diego Co., California.

Range and habitat: Coal Oil Point, Santa Barbara Co., California (Sphon & Lance, 1966), to Islas Coronados, Baja California, Mexico (Lance, 1961). Subtidal, 9–43 m, in rocky areas. This species is relatively uncommon.

Cadlina marginata MacFarland, 1905

Cadlina marginata MacFarland, 1905: 43. Cockerell & Eliot, 1905: 35. MacFarland, 1906: 125–126, pl. 18, figs. 27–31; pl. 25, figs. 10–12. Kelsey, 1907: 35. Berry, 1907: 35. Cockerell, 1908: 106. O'Donoghue, 1921: 161–162, pl. 1 (7), figs. 13–14. O'Donoghue & O'Donoghue 1922: 138. O'Donoghue, 1922b: 164. O'Donoghue, 1924: 24, 29. O'Donoghue, 1927a: 10. O'Donoghue, 1927b: 86–87, pl. 1, figs. 25–28. Fraser, 1932: 67. Baba, 1935a: 343. Hewatt, 1937: 200. Baba, 1937c: 75. Costello, 1938: 324 ff, tabs. 1–3, 5, pl. 1, figs. 4, 6, 10, 22; pl. 2, fig. 32. Smith & Gordon, 1948: 180. Rigg & Miller, 1949: 343. LaRocque, 1953: 259. Marcus, 1955: 122. Marcus, 1961: 15. Lance, 1961: 66. Lance, 1962a: 157. McLean, 1962: 110. Steinberg, 1963b: 69. Paine, 1963a: 4. Willows, 1965: 707 ff. MacFarland, 1966: 140. Marcus & Marcus, 1967a: 170. Robilliard, 1969a: 290. North, 1971: 57. Abbott, 1974: 357, fig. 4263. (*Non*) *Doris marginata* Montagu, 1804: 79, pl. 7, fig. 7 (=*Cadlina laevis* Linnaeus, 1767).

Cadlina luteomarginata MacFarland, 1966: 140–144, pl. 23, figs. 2–4; pl. 29, figs. 13–13a; pl. 33, figs. 1–11. Sphon & Lance, 1968: 77. Roller & Long, 1969: 426. Bertsch, 1969: 231. Gosliner & Williams, 1970: 177. Bernard, 1970: 85. Schmekel, 1970: 194. Bertsch *et al.,* 1972: 305. Robilliard, 1974b: 990. Belcik, 1975: 276. Bloom, 1976: 289 ff. Thompson, 1976b: 92. Nybakken, 1978: 135, 144. Haderlie & Donat, 1978: 60. McDonald & Nybakken, 1978: 112. Dehnel & Kong, 1979: 1835 ff.

Type-specimens: U. S. Nat. Mus., no. 181287.

Dorsum covered with numerous low, rounded tubercles. Foot nearly linear, broadly rounded and bilabiate anteriorly, and bluntly pointed posteriorly. Labial tentacles short, flattened, and triangular, with a groove on external margin. Rhinophores bear 15–18 lamellae which are cream to light yellow. Branchial plumes six, bipinnate, cream to light yellow. General ground color cream to very pale yellow. Dorsal tubercles tipped with lemon yellow, and a band of similar color occurs on both the dorsal and ventral surfaces of mantle margin and also on edge of foot. T.L.: 25 mm.

Radular formula of specimen examined 89(57–63.1.57–63), MacFarland (1966: 142) reports 90–114(47–58.1.47–58). Rachidian teeth (Fig. 62a) bear 4–7 denticles. Inner laterals (Fig. 62b) hooked and bear 4–14 denticles.

Type-locality: Monterey Bay, California.

Range and habitat: Auke Bay, Alaska (Robilliard, 1974b), to Punta San Eugenio, Baja California, Mexico (Lance, 1961). Intertidal to 45 m in rocky areas. Feeds upon the sponges: *Halichondria panicea, Higginsia* sp., and *Myxilla incrustans* (Bloom, 1976: 294).

Remarks: MacFarland (1966: 140) emended the specific epithet to *luteomarginata*, based on *Doris marginata* Montagu, 1804, being a junior synonym of *Cadlina laevis* (Linnaeus, 1767). He felt that this made the epithet *marginata* unavailable in the genus *Cadlina*. However his emendation is unjustified because the specific epithet *marginata* is not currently used in the genus *Cadlina*. The present species therefore should be referred to as *Cadlina marginata* MacFarland, 1905, not as *Cadlina luteomarginata* MacFarland, 1905.

Cadlina modesta MacFarland, 1966

Cadlina modesta MacFarland, 1966: 140, 143, 147–152, pl. 30, figs. 14–15; pl. 33, figs. 22–31. Sphon & Lance, 1968: 77. Bertsch, 1969: 231–232. Roller & Long, 1969: 426. Gosliner & Williams, 1970: 170. Schmekel, 1970: 194. Robilliard, 1971a: 163, 164. Bertsch *et al.*, 1972: 305. Abbott, 1974: 357. Thompson, 1976b: 43, 92. Nybakken, 1978: 135, 144. Haderlie & Donat, 1978: 60. McDonald & Nybakken, 1978: 110, 112.

Type-specimens: type material at Calif. Acad. Sci.

Dorsum covered with numerous relatively inconspicuous, low tubercles of various sizes. Foot narrow and nearly linear, broadly rounded and bilabiate anteriorly, and less rounded posteriorly. Labial tentacles triangular and lobe-like, with a groove on external margin. Rhinophores bear 10–12 lamellae which are cream to light yellow. Branchial plumes 10–12, unipinnate, cream to light yellow. General ground color cream to light yellow, occasionally tinted with orange and pink. A series of 16–20 or more small, lemon yellow dots occurs longitudinally on either side of dorsum extending anterior of rhinophores and posterior of branchial plumes. T.L.: 15–20 mm.

Radular formula of specimen examined 43(28.1.28), MacFarland (1966: 148) reports 70–94(21–24.1.21–24). Rachidian teeth (Fig. 60a) bear 5–7 denticles, the median of which is largest. First laterals (Fig. 60b) have 5–7 denticles, innermost of which is usually largest. The most external laterals (Fig. 60f) bear 11–15 denticles.

Type-locality: Point Pinos, Monterey Co., California.

Range and habitat: Nanaimo, Vancouver Island, British Columbia, Canada (Robilliard, 1971a), to La Jolla, San Diego Co., California (MacFarland, 1966). Intertidal to 10 m, in rocky areas. Feeds upon the sponge *Aplysilla glacialis* (McDonald & Nybakken, 1978: 110).

Cadlina sparsa (Odhner, 1921)

Juanella sparsa Odhner, 1921: 225–226, text fig. 3, pl. 8, figs. 13–14. Odhner, 1926a: 56–57.

Cadlina sparsa (Odhner). Odhner, 1926a: 56–57. Marcus, 1955: 122. Marcus, 1958: 21. Marcus, 1959: 3, 7, 27–29, 87, 93, text figs. 39–44. Lance, 1961: 66. Marcus, 1961: 15, pl. 3, figs. 43–45. Lance, 1962a: 157. Marcus & Marcus, 1967a: 169. Sphon & Lance, 1968: 77. Roller & Long, 1969: 426. Keen, 1971: 823. Abbott, 1974: 357. Nybakken, 1978: 135.

Type-specimens: not listed.

Dorsum covered with numerous small, low, rounded tubercles. Foot narrow and nearly linear, broadly rounded and bilabiate anteriorly, and bluntly pointed posteriorly. Labial tentacles tapered, somewhat triangular-conical, with a groove on external margin. Rhinophores bear about 8–12 lamellae, which are light yellow to yellowish-tan. Branchial plumes 12, unipinnate, light yellow to light yellowish-tan. General ground color cream to very light yellow. An irregular series of 7–13 or more small, brown to black dots with yellow centers occurs longitudinally on either side of the dorsum, from just posterior of rhinophores to just posterior of branchial plumes. T.L.: 15–20 mm.

Radular formula of specimen examined 37(24.1.24), Marcus (1961: 15) reports 56–69(28.1.1.1.28), and Odhner (1921: 225) reports 54(20.1.1.1.20). Rachidian teeth (Fig. 61a) bear 3–4 relatively small denticles. First laterals (Fig. 61b) have 6 denticles, innermost of which is usually largest. The most external laterals (Fig. 61e) bear up to 19 denticles.

Type-locality: Juan Fernandez Island, Chile.

Range and habitat: Monterey, Monterey Co., California (personal observation), to San Pedro, Los Angeles Co., California (Marcus, 1961); Juan Fernández and Chiloé Islands, Chile (Marcus, 1961). Intertidal to 40 m, in rocky areas. Relatively rare in California.

Cerberilla Bergh, 1873

Body aeolidiform, rather compressed dorso-ventrally. Foot wide, anterior foot corners tentaculiform. Cerata usually somewhat flattened and decumbent. Oral tentacles usually quite long, cylindrical and tapered distally. Rhinophores non-retractile and smooth.

Masticatory border of mandibles smooth. Radula uniseriate, rachidian teeth very distinctive, each bears numerous unequal larger denticles, between which (or on which) are smaller denticles.

Penis unarmed. Anus pleuroproct.

Type-species: *Cerberilla longicirrha* Bergh, 1873.

Cerberilla mosslandica McDonald & Nybakken, 1975

Cerberilla mosslandica McDonald & Nybakken, 1975: 378–382, text figs. 1–2. McDonald, 1975b: 55. McDonald & Nybakken, 1978: 115.

Type-specimens: Calif. Acad. Sci., no. CASIZ 596.

Foot broad, rounded anteriorly and slightly tapered posteriorly to short, abruptly pointed tail; foot corners produced into tentaculiform processes. Oral tentacles quite long, cylindrical, and tapered to pointed tips; translucent grayish-white and encrusted with brownish to reddish-brown proximally, and encrusted with numerous opaque white dots on distal half. Rhinophores non-retractile, smooth, and tapered to blunt tips; encrusted with brownish to reddish-brown proximally and with opaque white on tips. Cerata are slightly flattened and decumbent, arranged in 8–10 crescent-shaped, transverse rows on dorsum. Anterior 3–4 rows have a median space which leaves cardiac region free of cerata. General ground color translucent grayish-white. Dorsum, dorsal surface of foot margin, and head are encrusted with brownish to reddish-brown. Cerata encrusted with brownish to reddish-brown and tips encrusted with white. T.L.: 7 mm.

Anus on right, approximately ventral of fourth row of cerata. Genital aperture on right side, just ventral of second row of cerata. Penis unarmed.

Radular formula of specimen examined 10(0.0.1.0.0). Rachidian tooth (Fig. 96) bears 11–16 large denticles, between which occur 17–27 small denticles. Masticatory border of mandibles smooth.

Type-locality: Monterey Bay, California.

Range and habitat: Monterey Bay, California (McDonald & Nybakken, 1975). Found on a mud-sand bottom in 16–63 m. May feed upon a burrowing sea anemone (McDonald & Nybakken, 1975b: 380).

Chromodoris Alder & Hancock, 1855

Body doridiform, evenly rounded anteriorly and posteriorly, sometimes rather elongate; usually with an ample projecting mantle margin. Dorsum soft and smooth, without tubercles or papillae. Labial tentacles small and rather conical. Rhinophores perfoliate, retractile into sheaths with smooth borders. Branchial plumes retractile, usually unipinnate, arranged in a circle around anus. Most species are brightly colored.

Labial armature consists of minute rods which are usually bifid at tip. Radula broad, without a strongly developed rachidian tooth (vestiges may be detectable). Laterals more or less hamate, first laterals are each denticulate on both inner and outer margins, remaining laterals denticulate on outer margins only. Outermost laterals denticulate at apex only. Teeth do not have bifid cusps.

Penis unarmed.

Type-species: *Chromodoris magnifica* (Quoy & Gaimard, 1832).

The genera *Chromodoris* and *Hypselodoris* are sometimes difficult to separate, as characters can overlap. I use here the distinctions put forward by Odhner (1957) and further elaborated by Thompson (1972b). Bertsch (1977) erected the genus *Mexichromis* and included in it *Chromodoris porterae*. While *Chromodoris* is a large genus, in need of study and possible division into several subgenera or new genera, it would seem unwise to erect new genera based on study of species from a limited geographic area (i.e. the Pacific coast of North America). The Chromodoridinae are largely tropical and the 15 species found on the Pacific coast of North America are but a fraction of the number of species found worldwide. Bertsch (1977: 113) distinguished *Mexichromis* with acuspid, pectinate radular teeth from *Chromodoris* with unicuspid, serrate radular teeth. However, a cursory perusal of the literature shows that there is gradation from one type of radular tooth to the other. *Chromodoris tryoni* Garrett, 1873 (Bergh, 1877a: pl. 54, fig. 2) is very distinctly unicuspid, while *Chromodoris paupera* Bergh, 1877 (Bergh, 1976b: pl. 53, fig. 21) and *Chromodoris carnea* Bergh, 1889 (Bergh, 1889: pl. 83, fig. 26) are slightly less unicuspid. *Chromodoris vicina* Eliot, 1904 (Edmunds, 1971: text fig. 16E) is even less unicuspid and *Chromodoris petechialis* (Gould, 1852) (Kay & Young, 1969: text fig. 440) is acuspid. A range of variation such as this would seem to make it difficult or impossible to separate these species into two distinct genera based on this character.

Chromodoris macfarlandi Cockerell, 1901

Chromodoris mcfarlandi Cockerell, 1901c: 79–80. Cockerell, 1902: 19–21. Costello, 1947: 232. Costello, 1950: 430–431. MacFarland, 1966: 158. Bertsch, 1976a: 157–158. Bertsch, 1977: 114, text fig. 3D. Bertsch, 1978a: 313–317, 315, figs. 7, 13–15, 37–40. McDonald & Nybakken, 1978: 112.

Chromodoris macfarlandi (Cockerell). Cockerell & Eliot, 1905: 36. Kelsey, 1907: 37. Cockerell, 1908: 106. Hewatt, 1946: 198. Costello, 1947: 232. Costello, 1950: 430–431. Marcus & Marcus, 1967a: 178. Lance, 1969: 37. Roller & Long, 1969: 425, 429. Roller, 1970a: 371. Roller, 1970b: 482. Long, 1970: 19. Hertz, 1970: 6. McBeth, 1970: 28. Schmekel, 1970: 194. North, 1971: 57. Keen, 1971: 822. Bertsch *et al.*, 1973: 287. Schuler, 1975: 33. Michel, 1976: 47, fig. 8. Hargens, 1977: 363, 365. Bertsch, 1978a: 314. Bertsch, 1979b: 44, fig. 3D.

Chromodoris (sp.?). Berry, 1907: 35.

Glossodoris macfarlandi (Cockerell). Cockerell, 1908: 106. O'Donoghue, 1926: 212. O'Donoghue, 1927a: 10. O'Donoghue, 1927b: 89–90, 116, pl. 2, figs. 33, 37. Pruvot-Fol, 1951b: 120. Pruvot-Fol, 1951c: 152. Lance, 1961: 66. McLean, 1962: 111. Paine, 1963a: 4 ff. Farmer & Collier, 1963: 62. Steinberg, 1963b: 69. Farmer, 1964: 24. MacFarland, 1966: 153–157, pl. 22, figs. 1–5; pl. 34, figs. 1–11. Sphon & Lance, 1968: 79. Roller, 1970a: 371. Abbott, 1974: 354, fig. 4239. Bloom, 1976: 292, 294.

Glossodoris mcfarlandi (Cockerell). Costello, 1947: 232.

Type-specimens: not listed.

Lateral edges of dorsum thin and undulating, projecting well beyond foot. Foot rather elongate, rather truncate and bilabiate anteriorly, tapered posteriorly to blunt pointed tail. Labial tentacles short and lobe-like, with an obscure groove on external margin. Rhinophores bear 16–20 lamellae, and are pale violet on shaft and deep red-violet on clavus. Branchial plumes 10–14, unipinnate, violet proximally and deep violet-garnet distally. General ground color deep, vivid violet (somewhat paler in occasional specimens). A narrow median stripe of yellow-gold extends posteriorly from just anterior of rhinophores to just anterior of branchial plumes; a similar stripe occurs antero-laterally on either side of dorsum, from just posterior of rhinophores to just posterior of branchial plumes, where both stripes unite. A similar yellow-gold band occurs along margin of dorsum, and a white band occurs just inside the yellow-gold band around dorsum. Ventral edge of dorsum bears a white band. T.L.: 25–35 mm.

Radular formula of specimen examined 57(50–55.1.50–55), MacFarland (1966: 155) reports 62(47–50.1.47–50), and Bertsch (1978a: 316) reports 36–76(16–50.1.16–50). Rachidian teeth (Fig. 65a) smaller than laterals, each bears a single, median denticle, and is roughly triangular in shape. First laterals (Fig. 65b, d) bear 3–6 denticles; the number of denticles increases on outer laterals to about 15 or more.

Type-locality: San Pedro, Los Angeles Co., California.

Range and habitat: Monterey, Monterey Co., California (MacFarland, 1966), to Bahía Magdalena, Baja California, Mexico (Bertsch, 1978a). Intertidal to 27–34 m, in rocky areas. Quite rare in northern part of range, more common in southern California. Bloom (1976: 294) reports that it is found in association with and may feed upon the sponges *Gellius* sp. and *Haliclona* sp.

Remarks: See ICZN (1954, Opinion 221) for emendation to *Chromodoris macfarlandi.*

Chromodoris porterae Cockerell, 1901

Chromodoris porterae Cockerell, 1901c: 79. Cockerell, 1902: 19–21. MacFarland, 1905: 44–45. Cockerell & Eliot, 1905: 36. MacFarland, 1906: 129–130, pl. 26, figs. 13–14. Kelsey, 1907: 37. Baily, 1907: 92. Guernsey, 1912: 74–75, fig. 39B. Crozier, 1922: 304. O'Donoghue, 1926: 212. O'Donoghue, 1927b: 91–92. Costello, 1947: 232. ICZN, 1954: 118. MacFarland, 1966: 163–165, pl. 24, figs. 4–5; pl. 34, figs. 24–31. Roller, 1970a: 371. Bertsch & Ferreira, 1974: 344. Schuler, 1975: 33. Bertsch, 1976a: 158. Michel, 1976: 48, fig. 13. Bertsch, 1977: 113. Bertsch, 1978b: 80. McDonald & Nybakken, 1978: 112.

Glossodoris porterae (Cockerell). O'Donoghue, 1926: 212. O'Donoghue, 1927a: 11. O'Donoghue, 1927b: 91–92. Pruvot-Fol, 1951c: 134. Lance, 1961: 66. Steinberg, 1963b: 70. Sphon & Lance, 1968: 79. North, 1971: 57. Abbott, 1974: 355, pl. 17, no. 4252.

Glossodoris (*Chromodoris*) *porterae* (Cockerell). Smith & Gordon, 1948: 180.

Hypselodoris porterae (Cockerell). Lance, 1969: 37. Roller & Long, 1969: 425, 429. Roller, 1970a: 371. Harris, 1973: 240. Bertsch *et al.,* 1973: 287.

Mexichromis porterae (Cockerell). Bertsch, 1977: 113, 114, text fig. 3J. Bertsch, 1978b: 80, 82–84, figs. 55–56. Bertsch, 1979b: 44, fig. 3J.

Type-specimens: not listed.

Foot broadly rounded and deeply notched anteriorly, tapered posteriorly to long, pointed tail. Rhinophores bear 12–14 lamellae, and are ultramarine blue on shaft and darker on clavus. Branchial plumes 9–12, unipinnate, ultramarine blue. General ground color ultramarine blue. A median stripe of pale blue extends from between the rhinophores to just anterior of branchial plumes and continues for a short distance just posterior of branchial plumes; a similar stripe occurs dorso-medially on posterior portion of foot which extends beyond dorsum. A stripe of yellow-orange extends longitudinally on either side of dorsum from just posterior of rhinophores to posterior of branchial plumes, where the stripes meet; a line of similar color forms an arc just anterior of rhinophores. Dorsum edged with a narrow, white line. A number of small, hemispherical, submarginal glandular prominences occur posteriorly. T.L.: 15 mm.

Radular formula of specimen examined 50(38.0.38), Bertsch (1978b: 83) reports 38–68(23–36.0.23–36). Laterals (Fig. 66) bear 5–8 denticles on one edge, the terminal one or two frequently longer than the remaining denticles which are all about equal in size.

Type-locality: La Jolla, San Diego Co., California.

Range and habitat: Monterey Bay, California (MacFarland, 1966), to Isla Cedros, Baja California, Mexico (Lance, 1961). Intertidal to 18 m, in rocky areas. Occasionally found on the sponge *Dysidea amblia* upon which it may feed (McDonald & Nybakken, 1978).

Conualevia Collier & Farmer, 1964

Body soft and doridiform, equally rounded anteriorly and posteriorly. Dorsum smooth or minutely papillate. Labial tentacles short and stout. Rhinophores smooth, retractile below dorsum but no sheath margin is obvious. Branchial plumes uni- to tripinnate, arranged in a circle around anus.

Labial cuticle thin or absent. Radular formula (0.n.0.n.0); laterals hamate.

Penis unarmed.

Type-species: *Conualevia marcusi* Collier & Farmer, 1964.

Conualevia alba Collier & Farmer, 1964

Conualevia alba Collier & Farmer, 1964: 383–385, pl. 3, text figs. 2a–d. Lance, 1966: 75. Marcus & Marcus, 1967a: 186. Sphon & Lance, 1968: 77. Keen, 1971: 821, pl. 19, fig. 8. Ferreira, 1972: 53–54. Abbott, 1974: 358.

Type-specimens: Calif. Acad. Sci., no. 29.

Dorsum varies from smooth to minutely papillate. Foot rounded and bilabiate anteriorly and rather rounded posteriorly. Rhinophores appear white, but are faintly ringed with minute black dots. Branchial plumes 8, tripinnate, white. General ground color white. An irregular row of opaque white glands occurs around lateral edges of dorsum on either side. T.L.: 12 mm.

Radular formula of specimen examined 47(68.0.68), Collier & Farmer (1964: 385) report 34(56.0.56). Laterals (Fig. 68) simple hooks.

Type-locality: Newport Bay, Orange Co., California.

Range and habitat: Cypress Point, Pacific Grove, Monterey Co., California (Ferreira, 1972), to Bahia Tortugas, Baja California, Mexico (Lance, 1966); Galapagos Islands, Ecuador (Sphon, 1972b). Intertidal to 17 m, in rocky areas, usually under rocks.

Corambe Bergh, 1869

Body elliptical in outline, quite flattened and disc-like. Margin of dorsum wide and thin, extending well beyond foot; a median notch occurs in posterior margin. Dorsum smooth. Foot emarginate anteriorly and rounded posteriorly. Labial tentacles short, rather blunt lobes. Rhinophores bear an inner pair of wing-like expansions and are retractile into sheaths. Branchial plumes unipinnate, arranged on either side of the postero-median anus, between dorsum and foot.

Labial cuticle bears two lateral thickenings. Radular formula n.1.0.1.n; laterals large and bear denticles below cusp. Marginals small and lack denticles below cusp.

Penis unarmed.

Type-species: *Corambe sargassicola* Bergh, 1871.

Corambe pacifica MacFarland & O'Donoghue, 1929

Corambe pacifica MacFarland & O'Donoghue, 1929: 1–27, pls. 1–3. Smith & Gordon, 1948: 180. Marcus, 1955: 164 ff. Marcus, 1959: 62. Steinberg, 1960: 49. Lance, 1961: 67. Lance, 1962b: 36, 37. Paine, 1963a: 4. Steinberg, 1963b: 71. MacFarland, 1966: 130–132 ff, pl. 22, figs. 6–8; pl. 29, fig. 20, pl. 32, figs. 13–14. Marcus & Marcus, 1967b: 206 ff. Sphon & Lance, 1968: 77. Roller & Long, 1969: 426. Gosliner & Williams, 1970: 177. Bernard, 1970: 84. Anderson, 1972: 19. Abbott, 1974: 365, text fig. 4342. Seed, 1976: 2. McDonald & Nybakken, 1978: 111.

Carambe pacifica MacFarland & O'Donoghue. Haderlie & Donat, 1978: 60 (*lapsus*).

Type-specimens: Calif. Acad. Sci., no. 634.

Foot equally rounded anteriorly and posteriorly, with an antero-lateral notch. Labial tentacles short and blunt. Rhinophores bear a plate-like expansion on anterior and lateral sides, extending from distal portion anteriorly, downward to posterior face of shaft; within area enclosed by this expansion is another pair of smaller plate-like expansions, one on either side of shaft; a third, unpaired ridge occurs postero-medially on shaft within area enclosed by smaller plate-like expansions. Rhinophores translucent grayish, stalk may have a few spots of yellow, garnet, or black. Branchial plumes 6–14, translucent grayish, and may be seen through postero-median notch in dorsum. General ground color translucent grayish. Dorsum bears numerous irregular lines of pale yellow which become small spots on central area of dorsum. Between yellow lines are indian red spots edged with black. Scattered small black to dark green flecks also occur, especially centrally on dorsum. A thin, white line occurs around margin of foot. In all, the color pattern of the dorsum very closely resembles the colonies of the bryozoan *Membranipora* spp. upon which the animal feeds. T.L.: 5 mm.

Radular formula of specimen examined 26(6.1.0.1.6), MacFarland (1966: 132) reports 38–40(4–5.1.0.1.4–5). Laterals (Fig. 39g) are large and bear 3–7 denticles below large distal cusp. Marginals (Fig. 39a–f) decrease in size outward, each having a single, simple hook.

Type-locality: Pacific Grove, Monterey Co., California.

Range and habitat: Nanaimo, Vancouver Island, British Columbia, Canada (MacFarland & O'Donoghue, 1929), to Punta San Eugenio, Baja California, Mexico (Lance, 1961). Intertidal to 5 m, almost always found on the kelp *Macrocystis pyrifera* which is encrusted with the bryozoan *Membranipora* spp. Feeds upon *Membranipora villosa* (MacFarland, 1966; MacFarland & O'Donoghue, 1929); also found on *Membranipora serrilamella* (Lance, 1961).

Coryphella Gray, 1850

Body aeolidiform and gradually tapered posteriorly to tail. Foot corners somewhat produced. Cerata cylindro-conical, pointed apically, arranged transversely in simple or irregularly divided rows along edge of dorsum, and bear cnidosacs. Edge of dorsum usually well defined. Oral tentacles usually relatively long. Rhinophores non-retractile, may be smooth, verrucose, annulate, perfoliate, or papillate.

Masticatory border of mandibles denticulate. Radula triseriate, with denticles on rachidian and usually on laterals.

Penis unarmed. Anus pleuroproct.

Type-species: *Coryphella rufibranchialis* (Johnston, 1832).

Coryphella cooperi Cockerell, 1901

Coryphella cooperi Cockerell, 1901a: 85–86. O'Donoghue, 1926: 229. Marcus, 1961: 48. Steinberg, 1961: 62. Lance, 1961: 68. Marcus & Marcus, 1967a, 221 ff. Farmer, 1967: 342. Abbott, 1974: 374. Cooper, 1978: 8. Cooper, 1980: 284.

Type-specimens: not listed.

Foot widest and bilabiate anteriorly and tapered posteriorly to pointed tail. Foot corners prolonged into tentaculiform processes. Oral tentacles about as long as rhinophores, cylindrical and tapered distally to blunt points; translucent grayish-white, very pale orange distally, with a few minute, opaque white dots. Rhinophores verrucose, cylindrical, and slightly tapered to tips; colored as oral tentacles. Cerata arranged in about 5–7 groups on dorso-lateral body margin, leaving dorsum free medially; one group occurs anterior of cardiac region, the others are posterior. General ground color translucent grayish-white with a pink tinge, head in area of rhinophores pale pinkish-orange. A greenish-blue patch occurs between first and second cerata rows, just anterior and to left of cardiac region. A distinct, sometimes discontinuous, dorsomedial white line occurs on dorsum. Cerata greenish at base with white tips and a few minute, opaque white flecks on surface, cores reddish-brown. T.L.: 20 mm.

Anus on right, ventral of first post-cardiac group of cerata. Genital aperture on right side, ventral of first group of cerata.

Radular formula of specimen examined 11(0.1.1.1.0). Rachidian teeth (Fig. 100a) bear 7–10 denticles on either side of median cusp. Laterals (Fig. 100b) roughly triangular with 7–10 denticles below cusp.

Type-locality: San Pedro, Los Angeles Co., California.

Range and habitat: Elkhorn Slough, Monterey Co., California (personal observation), to Bahía San Quintín, Baja California, Mexico (Farmer, 1967). Intertidal in bays and estuaries on floating docks and mudflats. Usually on the hydroid *Tubularia crocea*. Cooper (1978) states that it eats the polyps and gonophores of *Tubularia crocea*. Very rare in California.

Coryphella iodinea (Cooper, 1863)

Aeolis (*Phidiana*?) *iodinea* Cooper, 1863a: 205. O'Donoghue, 1922d: 139.

Phidiana iodinea (Cooper). Cooper, 1863b: 60. Carpenter, 1864: 609. Cooper, 1867: 14. Cooper, 1870: 57. Bergh, 1873a: 615. Yates, 1890: 41. O'Donoghue, 1922d: 139.

Aeolis (?*Phidiana*) *iodinea* Cooper. Carpenter, 1864: 608.

Flabellina iodinea (Cooper). Bergh, 1873a: 615. Bergh, 1879b: 79–81, pl. 1, figs. 15–17; pl. 2, fig. 16. Bergh, 1879c: 135–137, pl. 1, figs. 15–17; pl. 2, fig. 16. Hilton, 1919: 34. O'Donoghue, 1922d: 139. O'Donoghue, 1927a: 11. O'Donoghue, 1927b: 103. Coe, 1932: 63. Ingram, 1935: 48, 49. Coe & Allen, 1937: 126. Smith & Gordon, 1948: 181. LaRocque, 1953: 249. Goodwin & Fox, 1955: 1086. Lance, 1961: 68. Pequegnat, 1963: 427. Farmer & Collier, 1963: 63. Paine, 1963a: 4. Steinberg, 1963b: 72. Paine, 1964: 385. Farmer, 1967: 342. Marcus & Marcus, 1967a: 226. Harris, 1971a: 84. North, 1971: 57. Nybakken, 1978: 133.

Coryphella iodina (Cooper). Cockerell, 1901b: 121 (*lapsus*).

Aeolis iodinea Cooper. Kelsey, 1907: 33.

Flabellina (*Aeolis*) *iodinea* Cooper. O'Donoghue, 1922d: 138.

Coryphella iodinea (Cooper). O'Donoghue, 1922d: 139. Marcus & Marcus, 1967a: 218–220, 238, text figs. 68–69. Farmer, 1970: 78. Schmekel, 1970: 141. Abbott, 1974: 374. Bertsch & Ferreira, 1974: 347. Keen & Coan, 1975: 45. Thompson, 1976a: 28. Thompson, 1976b: 58. Cowen & Laur, 1978: 292–294. Poorman & Poorman, 1978: 373.

Flabellinopsis iodinea (Cooper). MacFarland, 1966: 308–313, pl. 58, figs. 1–2; pl. 65, figs. 1–8; pl. 66, figs. 1–6. Sphon & Lance, 1968: 79. Roller & Long, 1969: 427. Lance, 1969: 33. Turner *et al.*, 1969: 136. DuShane & Brennan, 1969: 361. Gosliner & Williams, 1970: 178. Grigg & Kiwala, 1970: 151. Bernard, 1970: 86. McBeth, 1970: 28. McBeth, 1971: 158, 159. Keen, 1971: 836–837, pl. 22, fig. 1. Baker, 1972: 44 ff. McBeth, 1972a: 55 ff. Harris, 1973: 246,

281. Hinegardner, 1974: 452. Kitting, 1974: 32. Michel, 1976: 47, fig. 9. McDonald & Nybakken, 1978: 114. Russo, 1979: 44 ff.
Flabellinopsis iodinia (Cooper). Lance, 1968: 7. McBeth, 1972a: 56 (*lapsus*).
Flabellina (*Flabellinopsis*) *iodinea* (Cooper). McBeth, 1972a: 65.
Flabellina (=*Flabellinopsis*) *iodinea* (Cooper). Harris, 1973: 239.
Flabillinopsis iodinea (Cooper). Kastendiek, 1976: 531 (*lapsus*).
Coryphella sabulicola Cowen & Laur, 1978: 292–294.

Type-specimens: not listed; Geological Survey coll. (Cooper, 1863a).

Dorsum separated from foot by well defined, longitudinal groove; body high and much compressed laterally. Foot linear, quite narrow, slightly rounded anteriorly and tapered posteriorly to rather long, bluntly pointed tail. Oral tentacles elongate, slender, and tapered, up to one third of body length, colored as body, pale distally. Rhinophores perfoliate with 40–80 lamellae, shaft colored as body, clavus maroon to orange-red, with opaque white, antero-median ridge. Cerata pedunculate, borne upon 5–8 or more pairs of low, crescent-like longitudinal elevations of the dorsum edge. General ground color translucent purple. Cerata purple on proximal one quarter to one third, shading gradually to brilliant orange distally; cores burnt sienna. T.L.: 30 mm.

Anus on right, postero-ventral of second group of cerata. Genital aperture on right side, just postero-ventral of first group of cerata.

Radular formula of specimen examined 16(0.1.1.1.0), MacFarland (1966: 310) reports 17(0.1.1.1.0), and Marcus & Marcus (1967a: 219) report 22(0.1.1.1.0). Rachidian teeth (Fig. 101a) bear 12–16 denticles on either side of median cusp. Laterals (Fig. 101b) have 11–22 denticles below cusp. Masticatory border of mandibles bears numerous, tubercle-like denticles.

Type-locality: San Diego Bay, California.

Range and habitat: Vancouver Island, British Columbia, Canada (Bernard, 1970), to Cabo San Quintín, Baja California, Mexico (Farmer, 1967). Intertidal to 39 m, found in rocky areas and on pier pilings along relatively open coast. McBeth (1971: 158) reports that it feeds upon the hydroid *Eudendrium ramosum* and MacGinitie & MacGinitie (1949: 76) state that it feeds to some extent on the ascidian *Diplosoma pizoni*. *C. iodinea* is capable of swimming.

Remarks: Marcus & Marcus (1967a: 220) state that the peduncles upon which the cerata are borne, are not visible on the single preserved specimen available to them, nor could they see the peduncles on two color photographs. On this basis they assigned this species to the genus *Coryphella*. In the more than 20 specimens which I examined the peduncles were quite obvious; however, I feel that the character pedunculate cerata is not sufficient to distinguish a separate genus. Since pedunculate cerata are the only character which separates *Flabellinopsis* MacFarland, 1966, from *Coryphella* Gray, 1850, the former is a junior synonym of the latter. *C. iodinea* was also once placed in *Flabellina* Voigt, 1834. However, the type-species of *Flabellina*, *F. affinis* (Gmelin, 1791), has a penial stylet (Bergh, 1875a: 647–651), is acleioproct, and has a somewhat different radula than does *Coryphella* which lacks a penial stylet and is pleuroproct. Therefore, while *Coryphella* and *Flabellina* are somewhat similar in general shape and may have pedunculate cerata, they are not closely related.

Cowen & Laur (1978: 292–294) described *Coryphella sabulicola* which they distinguished from *C. iodinea* almost solely on the basis of starch-gel electrophoresis data. They used the heads of starved animals of both species, and found that 11 of the *C. iodinea* had a cathode attracted protein which was absent from all 12 *C. sabulicola*. They do not mention what happened in the case of the other specimen of *C. iodinea*. A morphometric comparison was made of 8 specimens of both species in which total numbers of cerata on the left side, total length, oral tentacle length, number of cerata groups, and lengths of longest and shortest cerata were recorded. Only the total number of cerata relative to length showed any significant difference between the two species. Number of cerata is not normally (if ever) used to differentiate species, as it is highly variable. The number of denticles on the rachidian and on the lateral teeth, as well as number of rhinophore lamellae are not significantly different in the two species. The somewhat lighter body color of *C. sabulicola* and the other slight differences, including habitat, certainly do not seem sufficient to separate two species. In addition, information concerning the reproductive system, presence or absence of a penial stylet, location of anus, or nature of masticatory border of the mandibles, all of which are characters normally used to differentiate species of aeolids, are not given. They also place *C. sabulicola* in the acleioproct family Flabellinidae rather than in the pleuroproct family Coryphellidae which contains all the other species of *Coryphella.*

Certainly, the intraspecific variation in electrophoretic data is not yet very well understood. It therefore seems quite unadvisable to use such data as virtually the only basis for separating two species. Certainly the slight morphological differences between the two species are well within the limits of variation found in many aeolids, and could easily be the result of different habitats or food. Therefore, *C. sabulicola* is a junior synonym of *C. iodinea.*

Coryphella pricei MacFarland, 1966

Coryphella pricei MacFarland, 1966: 313–318 ff, pl. 58, fig. 6; pl. 65, figs. 9–13; pl. 66, figs. 8–9. Marcus & Marcus, 1967a: 223. Gosliner & Williams, 1970: 177. Schmekel, 1970: 141. Miller, 1971: 315. Abbott, 1974: 374. Lambert, 1976: 295, 296.

Type-specimens: type material at Calif. Acad. Sci.

Foot widest anteriorly and tapered posteriorly to pointed tail; margins of foot rather wide and distinct from sides of body. Foot corners rather stout, tapered, and pointed distally, ventral surface of each grooved. Oral tentacles slender and tapered to blunt tips, longer than rhinophores, translucent grayish with encrusting, opaque white dots. Rhinophores annulate with 8–11 complete annuli which alternate with more or less incomplete annuli which occur on posterior face of clavus; rhinophores taper to blunt tip and are translucent grayish with pale yellow-green on distal half. Cerata slightly flattened laterally and directed obliquely posteriorly, arranged in 9–12 or more transverse rows dorso-laterally on dorsum. Rows posterior of cardiac region well separated from each other in crescent-shaped rows, each of which is on a common, elevated base. The 5–8 rows which are anterior of cardiac region are less distinctly separated. General ground color translucent grayish-white. An irregularly broken band of opaque white occurs dorsally on edge of foot. Occasional specimens have a pale orange spot dorsally on head. Cerata tipped with opaque white and bear a subterminal band of rich brown which grades into yellow below; cores deep olive-green to brownish-green. T.L.: 22 mm.

Anus located dorso-laterally on right, just above lowermost cerata bases of first post-cardiac row of cerata. Genital aperture on right side, ventral of pre-cardiac group of cerata. Penis short and bluntly conical.

Radular formula of specimens examined 21–25(0.1.1.1.0), MacFarland (1966: 315) reports 19(0.1.1.1.0). Rachidian teeth (Fig. 102a) bear 6–9 denticles on either side of median cusp. Laterals (Fig. 102b) without denticles and in form of broadly triangular plates. Masticatory border of mandibles bears a row of approximately 26 blunt denticles.

Type-locality: Monterey Bay, California.

Range and habitat: Pearse Island, British Columbia, Canada (Lambert, 1976), to Point Fermin, San Pedro, Los Angeles Co., California (Sphon, 1972b). Intertidal to 19 m. A relatively rare species in California, taken occasionally in rocky intertidal areas. One specimen was found crawling on hydroids upon which it probably feeds.

Coryphella trilineata O'Donoghue, 1921

Coryphella trilineata O'Donoghue, 1921: 197–198, pl. 3 (9), figs. 29–30. O'Donoghue, 1924: 25. O'Donoghue, 1926: 229. LaRocque, 1953: 250. Marcus, 1961: 48. Steinberg, 1963a: 66. Steinberg, 1963b: 72. Lance, 1966: 69. Marcus & Marcus, 1967a: 222, 226. Hurst, 1967: 263. Sphon & Lance, 1968: 77. Haderlie, 1969: tab. 1. Roller & Long, 1969: 426. Long, 1969c: 232. Gosliner & Williams, 1970: 177. Bernard, 1970: 86. Keen, 1971: 836. Bridges & Blake, 1972: 293–297. Bertsch *et al.*, 1972: 305. Sphon, 1972a: 155. Bertsch & Ferreira, 1974: 347. Nybakken, 1974: 371. Abbott, 1974: 374. Lambert, 1976: 297. McDonald & Nybakken, 1978: 114. Cooper, 1978: 8. Cooper, 1980: 284.

Coryphella piunca Marcus, 1961: 47–49, 57, pl. 9, figs. 161–167. Lance, 1961: 68. Farmer & Collier, 1963: 63. Steinberg, 1963a: 66. Lance, 1966: 69. Marcus & Marcus, 1967a: 222, 226. Schmekel, 1970: 141. Miller, 1971: 315.

Coryphella fisheri MacFarland, 1966: 318–322, pl. 58, figs. 3–5; pl. 65, figs. 14–18; pl. 66, figs. 10–20. Marcus & Marcus, 1967a: 226. Roller, 1970a: 372. Edmunds, 1970: 47. Miller, 1971: 315. Schuler, 1975: 33.

Coryphella fischeri MacFarland. Marcus, 1970: 213 (*lapsus*).

Type-specimens: Museum of Dominion Biol. Stat., Nanaimo, British Columbia, Canada.

Foot narrow, widest anteriorly; margins of foot narrow, distinct from sides of body. Foot corners short and rather triangular. Oral tentacles of moderate length and tapered to blunt tips, translucent grayish, yellow to deep cadmium orange on distal half of most specimens. Rhinophores annulate with 7–10 complete annuli which alternate with more or less incomplete annuli which occur on posterior face of clavus; rhinophores tapered to blunt tips and translucent grayish with yellow to deep cadmium orange on distal half. Cerata arranged in 6–8 transverse rows dorso-laterally on either side of dorsum, leaving mid-dorsal area free; first row occurs anterior of cardiac region, while remaining rows occur posterior of cardiac region. General ground color translucent grayish-white. A narrow, opaque white line extends longitudinally from tip of each oral tentacle, along its mid-dorsal surface to its base, where the two unite and pass posteriorly, mid-dorsally to tip of tail; similar lines extend longitudinally on either side of body, just ventral of cerata, from first row of cerata to just posterior of last row of cerata, where they unite with the median white line. Cerata cores usually red-orange, deepening in intensity distally to cadmium yellow tip. T.L.: 22 mm.

Anus located laterally on right, just ventral of first post-cardiac row of cerata. Genital aperture on right side, just ventral of most anterior row of cerata. Penis bluntly conical.

Radular formula of specimen examined 20(0.1.1.1.0), MacFarland (1966: 320) reports 18(0.1.1.1.0), and Marcus (1961: 47) reports 16–25(0.1.1.1.0). Rachidian teeth (Fig. 103a) bear 5–8 denticles on either side of median cusp. Laterals (Fig. 103b) broadly triangular with 5–12 denticles below cusp. Masticatory border of mandibles bears numerous blunt, conical denticles.

Type-locality: Nanoose Bay, Vancouver Island, British Columbia, Canada.

Range and habitat: Porcher Island, British Columbia, Canada (Lambert, 1976), to Los Coronados Islands, Baja California, Mexico (Lance, 1961). Intertidal to 50 m. Frequently found in rocky intertidal, often on the hydroid *Eudendrium* sp. Also sporadically abundant on floating docks in bays, usually on the hydroid *Tubularia crocea,* the polyps and gonophores of which it eats according to Cooper (1978).

Coryphella sp.

Foot narrow, rather truncated anteriorly and tapered posteriorly to rather long tail. Foot corners prolonged into tentaculiform processes. Oral tentacles rather long, cylindrical, and tapered to pointed tips, translucent grayish-white, encrusted with opaque white flecks distally. Rhinophores verrucose, translucent grayish-white with a slight brownish-orange hue and encrusted with minute white flecks distally. Cerata arranged in 6–8 transverse rows on dorsum, borne upon low, longitudinal ridges. Anterior rows of cerata separated medially, leaving cardiac area free. General ground color translucent grayish-white. An opaque white line extends from base of either oral tentacle to between rhinophores, where they unite and continue dorso-medially to tip of tail as an irregular, often discontinuous line which is rather broad in cardiac region. Dorsum also bears a number of irregular, opaque white dots. Cerata bear numerous opaque white dots, tips translucent grayish-white, cores pinkish-brown distally and greenish-brown proximally. T.L.: 25 mm.

Anus on right side, ventral and just posterior of cardiac region. Genital aperture on right side, midway between first group of cerata and cardiac region.

Radular formula of specimens examined 15–17(0.1.1.1.0). Rachidian teeth (Fig. 104a) bear 7–9 denticles on either side of median cusp. Laterals (Fig. 104b) have 11–13 denticles below cusp.

Range and habitat: This species has been found only during October and November of 1972, in Elkhorn Slough, Monterey Co., California, on the hydroid *Tubularia crocea* on floating docks (personal observation).

Remarks: These specimens may be found to be a slight variation of *Coryphella cooperi.* However, they lack the greenish-blue patch between the first and second cerata rows which is typical of *C. cooperi*; they also have 11–13 denticles on the laterals while *C. cooperi* has 7–10.

Crimora Alder & Hancock, 1862

Body limaciform and elongate. Dorsum bears dorsal processes. Frontal veil bears numerous, usually bifid or compound processes. Labial tentacles short and blunt. Rhinophores perfoliate and retractile into sheaths. Branchial plumes 3, non-retractile, bi- or tripinnate, arranged in an arch around anus.

Mandibles absent, but labial cuticle present. Radula bears a number of types of teeth. Rachidian tooth spurious or absent. Inner laterals triangular, laterals hooked distally, inner marginals roughly rectangular and bear a cusp, outer marginals very elongate and bear small denticles.

Penis armed with small hooks.

Type-species: *Crimora papillata* Alder & Hancock, 1862.

Crimora coneja Marcus, 1961

Crimora coneja Marcus, 1961: 25–26, 57, pl. 5, figs. 77–83. Lance, 1961: 67. Paine, 1963a: 4. Lance, 1969: 36. Abbott, 1974: 361.

Type-specimens: Dept. Zool., Fac. Philos., Sci., Let., Univ. São Paulo, Brazil (Marcus, personal communication).

Dorsum and dorsal surface of tail bear numerous rather long processes of various sizes which may be simple, bifid, or slightly branched distally. Frontal margin slightly expanded into a veil-like process which bears along its margin about 10 processes which are slightly branched distally, and about 10 shorter processes which are very slightly or not at all branched distally; both sets of processes are orange distally. Foot rather narrow, bilabiate anteriorly and tapered posteriorly to long, pointed tail. Rhinophores bear about 9–12 lamellae, clavus inclined slightly posteriorly and orange, shaft translucent grayish-white. Branchial plumes tripinnate, translucent grayish-white. General ground color translucent grayish-white. Some dorsal processes tipped with dark brown to black, and may bear a subterminal band of orange, others tipped with orange. T.L.: 10 mm.

Radular formula of specimen examined 45(15.7–8.1.(1).1.7–8.15), Marcus (1961: 25) reports 53(9.6.2.(1).2.6.9). Spurious rachidian plate does not constitute a true tooth and is quite difficult to see. First laterals, which are small, rounded triangles, were not visible on the single radula available for study. Second laterals (Fig. 49e) relatively large, hooked with a large, blunt denticle near base. Inner marginals (Fig. 49c, d) roughly rectangular with a blunt cusp. Outer marginals (Fig. 49a, b) very elongate, rod-like, slightly curved, and minutely denticulate.

Type-locality: Point Loma, San Diego Co., California.

Range and habitat: Point Loma, San Diego Co., California (Marcus, 1961). Also, a specimen identified from a photograph, collected near Humboldt Bay, Humboldt Co., California (personal observation). Intertidal in rocky areas, very rare.

Cumanotus Odhner, 1907

Body rather aeolidiform, rather high and short. Foot rather wide, and somewhat truncate anteriorly and tapered posteriorly to rather long tail. Anterior foot corners slightly produced. Cerata quite long, cylindro-conical, rather wide at base and tapered distally; first rows occur anterior of rhinophores. A short, truncated frontal veil bears the nearly rudimentary, short oral tentacles at its anterodistal corners. Rhinophores non-retractile, arising close together on a slight prominence, long, cylindrical, smooth, and tapered to pointed tips.

Masticatory border of mandibles denticulate. Radula triseriate, rachidian teeth each bear a rather long median denticle with smaller denticles on either side, laterals denticulate on inner margin.

Penis unarmed. Bursa copulatrix bears on the upper and lower margins a circular pad armed with about 12 small cones which terminate in small hooks. Anus pleuroproct.

Type-species: *Cumanotus beaumonti* (Eliot, 1906).

See ICZN (1966, Opinion 783), *Cumanotus* placed on Official List.

Cumanotus beaumonti (Eliot, 1906)

Coryphella beaumonti Eliot, 1906c: 361–363, pl. 11, figs. 15–16. Lemche, 1964c: 125, 126.

Cumanotus laticeps Odhner, 1907: 26–29. Odhner, 1910: 82–84. Eliot, 1910: 6. White, 1938: 17. Lemche, 1964c: 125.

Cumanotus beaumonti (Eliot). Eliot, 1908: 313–314. Eliot, 1910: 125–127, 169, pl. 8, figs. 1–5. Odhner, 1910: 82–84. Iredale & O'Donoghue, 1923: 209. Cuenot, 1927: 264. Mar. Biol. Assoc., 1931: 270. Winckworth, 1932: 237. White, 1938: 17. Lemche, 1938: 38. Pruvot-Fol, 1954: 424–425. Mar. Biol. Assoc., 1957: 315. Thompson, 1964: 294. Hurst, 1967: 255 ff, text fig. 14, pl. 30, fig. 17; pl. 35, fig. 39; fig. 24-6. Bebbington & Thompson, 1968: 10. Roller, 1970b: 482. Gosliner & Williams, 1970: 177. Robilliard, 1971a: 164. Thompson & Brown, 1976: 172, fig. 92. Thompson, 1976a: 28, text fig. 38f. Thompson, 1976b: 55, 60, 62, 80, fig. 4. McDonald &

Nybakken, 1978: 114, 116. Cooper, 1978: 8. Cooper, 1980: 284. Tardy & Gantes, 1980: 204 ff.

Cumanotus species. Sphon & Lance, 1968: 78.

Type-specimens: not listed.

Foot rather wide and somewhat truncate anteriorly, tapered posteriorly to rather long, pointed tail. Foot corners produced into extremely short processes. Rhinophores translucent grayish-white, with slight orange tint. Cerata quite long, cylindrical, and tapered to fine points; arranged in about 7–8 poorly defined rows dorso-laterally on dorsum. General ground color translucent grayish-white. A few reticulate bands of yellowish-brown to bluish-green occur on dorsum. Cerata translucent grayish-white, with a subapical band of opaque white; cores yellowish-brown to bluish-green. T.L.: 8 mm.

Anus dorso-lateral on right, anterior of seventh cerata row.

Radular formula of specimen examined 12(0.1.1.1.0). Rachidian teeth (Fig. 99a) bear 8–12 denticles on either side of median cusp. Laterals (Fig. 99b) somewhat triangular with a hooked cusp distally, and about 18 denticles. Masticatory border of mandibles bears 2–3 rows of denticles.

Type-locality: Barn Pool, Plymouth, England.

Range and habitat: San Juan Islands, Puget Sound, Washington (Hurst, 1967), to San Diego, San Diego Co., California (Roller, 1970b); England (Eliot, 1906c). This species was probably introduced along with *Tubularia crocea.* Intertidal to 5 m, usually on bay boat landings. Almost always found upon the hydroid *Tubularia crocea* upon which it feeds, and whose polyps it rather resembles (McDonald & Nybakken, 1978; Cooper, 1978).

Remarks: The specimens of *Cumanotus* which are found in California do not perfectly match the description of *Cumanotus beaumonti,* but until specimens from England can be compared with specimens from the Pacific coast of North America, it seems best to refer the specimens from North America to *C. beaumonti,* rather than name a new species.

Cuthona Alder & Hancock, 1855

Body aeolidiform, somewhat compressed, and tapered posteriorly. Foot narrow, linear, rounded anteriorly and tapered posteriorly; foot corners rounded, usually slightly expanded. Cerata cylindrical, tapered to pointed tips, and arranged in transverse rows dorso-laterally on dorsum. Oral tentacles cylindrical and tapered to blunt tips. Rhinophores non-retractile, usually smooth, and slightly tapered to blunt tips.

Masticatory border of mandibles bears denticles or numerous minute bristles. Radula uniseriate, rachidian teeth each bear a strong median cusp which may or may not be raised above the lateral denticles; smaller denticles may be present between the lateral denticles.

Penis may be armed with a stylet or unarmed. Anus acleioproct.

Miller (1977) combined *Catriona* Winckworth, 1941, and *Trinchesia* Ihering, 1879, and a number of smaller genera under the name *Cuthona,* stating that the characters used to separate the two genera (mandible dentition, cusp of rachidian tooth, penial stylet, etc.) overlap in the various species such that there is no good set of characters to separate *Trinchesia* from *Catriona.*

Type-species: *Cuthona nana* (Alder & Hancock, 1842).

See ICZN (1966a, Opinion 773), *Cuthona* placed on Official List.

Cuthona abronia (MacFarland, 1966)

Cratena abronia MacFarland, 1966: 347–351, pl. 59, figs. 3–4; pl. 68, figs. 18–22; pl. 70, figs. 1–5. Long, 1969b: 281. Roller, 1970a: 372.

Trinchesia abronia (MacFarland). Roller, 1969b: 421, text fig. 1. Roller & Long, 1969: 428. Roller, 1970a: 372. Gosliner & Williams, 1970: 179. Robilliard, 1971a: 164, 165. Bertsch *et al.,* 1972: 308. Sphon, 1972a: 156. Nybakken, 1974: 371. Abbott, 1974: 376, text fig. 4449.

Trinchesia (=*Cratena*) *abronia* (MacFarland). Robilliard, 1971a: 164.

Cuthona abronia (MacFarland). Williams & Gosliner, 1979: 208, 215.

Type-specimens: type material at Calif. Acad. Sci.

Sides of body distinct from margins of foot. Oral tentacles bear a band of purple midway along their length, with a pale yellow ring proximal of this and also encrusting distal one third of tentacles, frequently with diffuse purple proximally. Rhinophores smooth, colored as oral tentacles. Cerata erect, cylindrical, and tapered to blunt tips, arranged in about 9 transverse rows dorso-laterally on body margin. General ground color translucent grayish-white, dorsum encrusted with a few opaque white to pale yellow dots, a blotch of the same color occurs just posterior of rhinophores and a line of similar color occurs dorsomedially on tail. Cerata bear about 3, sometimes incomplete, narrow bands of encrusting white to pale yellow which form boundaries between colored segments of cores. Cores pale yellow in distal third, medial third olive green to brown, and proximal third maroon to carmine. T.L.: 8 mm.

Anus on right, just posterior of cardiac region. Genital aperture on right side, just ventral of second row of cerata. Penis armed with chitinous stylet.

Radular formula of specimen examined 25(0.0.1.0.0), MacFarland (1966: 348) reports 33(0.0.1.0.0). Rachidian teeth (Fig. 116) bear 4–9 large denticles on either side of median cusp, with lesser denticles between the larger denticles. Masticatory border of mandibles bears a single series of 18–28 denticles.

Type-locality: Point Pinos, Monterey Co., California.

Range and habitat: Mukkaw Bay, Washington (Robilliard, 1971a), to Pismo Beach, San Luis Obispo Co., California (Long, 1969b). Usually found in rocky intertidal zone on hydroids.

Cuthona albocrusta (MacFarland, 1966)

Cratena albocrusta MacFarland, 1966: 340–344, pl. 61, figs. 1–4; pl. 67, figs. 13–22; pl. 69, figs. 4–5a. Hurst, 1967: 255 ff, text figs. 26a–b, 29; fig. 25-1. Haderlie, 1968: 333 ff. Sphon & Lance, 1968: 78. Roller, 1970a: 372. Robilliard, 1971a: 164.

Trinchesia albocrusta (MacFarland). Roller, 1969b: 421, text fig. 1. Roller & Long, 1969: 428. Haderlie, 1969: tab. 1. Roller, 1970a: 372. Gosliner & Williams, 1970: 179. Robilliard, 1971a: 165. Bertsch *et al.*, 1972: 308. Sphon, 1972a: 156. Nybakken, 1974: 371. Abbott, 1974: 376, text fig. 4443. Haderlie & Donat, 1978: 52, 60. Cooper 1978: 8.

Trinchesia (=*Cratena*) *albocrusta* (MacFarland). Robilliard, 1971a: 164.

Catrena albocrusta. Thiriot-Quiévreux, 1977: 186 (*lapsus*).

Cuthona albocrusta MacFarland. Williams & Gosliner, 1979: 208, 215. Cooper, 1980: 284.

Type-specimens: type material at Calif. Acad. Sci.

Sides of body distinctly separated from foot by a longitudinal groove. Oral tentacles translucent grayish-white with a few scattered flecks of opaque white. Rhinophores smooth, bearing various amounts of encrusting white distally. Cerata cylindrical, somewhat inflated, pointed at tips, and decumbent; arranged in 6–7 transverse rows dorso-laterally on body margin. General ground color translucent grayish-white. Dorsum encrusted with opaque white extending from head to posterior row of cerata, and from there postero-medially, as a broken line, to tail. Irregular spots of opaque white are scattered on sides of body. Cerata encrusted with opaque white on distal two thirds, leaving tips free, cores vary from pale or deep green to pale or deep raw umber. T.L.: 5 mm.

Anus on right, just anterior of innermost ceras of first post-cardiac group. Genital aperture on right side, between rhinophores and first row of cerata. Penis armed with chitinous stylet.

Radular formula of specimen examined 49(0.0.1.0.0), MacFarland (1966: 342) reports 56–70(0.0.1.0.0). Rachidian teeth (Fig. 117) bear 4–5 denticles on either side of median cusp. Masticatory border of mandibles bears a single row of about 18 triangular denticles.

Type-locality: Point Pinos, Monterey Co., California.

Range and habitat: Friday Harbor, Washington (Hurst, 1967), to Point Fermin, Palos Verdes Peninsula, Los Angeles Co., California (Sphon, 1972b). Intertidal to 30 m, usually in rocky intertidal areas, especially on hydroids at base of the algae *Laminaria* spp.; also occasional on floating docks in bays. Cooper (1980) reports that it eats *Tubularia crocea*.

Cuthona cocoachroma
Williams & Gosliner, 1979

Cuthona cocoachroma Williams & Gosliner, 1979: 203–215, text figs. 1A, 3, 4, 5, 6A.

Type-specimens: Calif. Acad. Sci., no. CASIZ 00715, 00716.

Oral tentacles encrusted with opaque white dorsally. Rhinophores smooth, with opaque white on the distal half. Cerata digitiform, elongate, and somewhat acute apically, arranged in 9–11 rows on each side of the body with 1–7 cerata per row. General ground color translucent white. Cerata tipped with opaque white, cores vary from deep reddish-brown to dark chocolate brown. T.L. 12 mm.

Anus on right, antero-dorsal of fourth or fifth row of cerata, posterior of inter-hepatic space. Genital aperture on right side between and ventral of the first and second rows of cerata. Penis unarmed.

Radular formula 20–39(0.0.1.0.0), rachidian teeth bear 4–5 lateral denticles on either side of median cusp (Williams & Gosliner, 1979). Masticatory border of mandibles bears a single row of approximately 16 triangular or rounded denticles.

Type-locality: Coleman Beach, Sonoma Coast State Park, Sonoma Co., California.

Range and habitat: Known only from Duxbury Reef, Marin Co., California, and Coleman Beach, Sonoma Co., California. Found in lower rocky intertidal zone.

Cuthona columbiana (O'Donoghue, 1922)

Amphorina (?) sp. Eliot, 1913: 4, 43. Baba, 1937b: 328.

Amphorina columbiana O'Donoghue, 1922b: 160–161, 165, pl. VI, figs. 23–24. Edmunds, 1968a: 207. Williams & Gosliner, 1979: 212.

Galvina columbiana O'Donoghue, 1922b: 161.

Cuthona (*Cuthona*) sp. Eliot. Baba, 1937b: 328.

Cratena columbiana (O'Donoghue). LaRocque, 1953: 249. Bernard, 1970: 85.

Catriona columbiana (O'Donoghue). Marcus, 1958: 50. Marcus, 1961: 52. Edmunds, 1968a: 207. Williams & Gosliner, 1979: 208, 212, 213, 214.

Cuthona alpha Baba & Hamatani, 1963b: 339–343, pl. 11, figs. 1–12. Lance, 1966: 79. Sphon & Lance, 1968: 78. Edmunds, 1968a: 207. Roller, 1969b: 422. Miller, 1977: 197, 198, 207–211, text figs. 3–4, pl. 1, fig. B. Williams & Gosliner, 1979: 212.

Cratena spadix MacFarland, 1966: 351–354, pl. 60, fig. 4; pl. 68, figs. 12–17; pl. 69, figs. 6–7a. Sphon & Lance, 1968: 78. Edmunds, 1968a: 207. Roller, 1969b: 422–423. Roller, 1970a: 372. Williams & Gosliner, 1979: 212.

Catriona alpha (Baba & Hamatani). Edmunds, 1968a: 207. Roller, 1969b: 422–423. Roller & Long, 1969: 426. Roller, 1970a: 372. Gosliner & Williams, 1970: 177. Robilliard, 1971a: 163–165. Sphon, 1972a: 155. Nybakken, 1974: 371. Abbott, 1974: 376, fig. 4439. Lambert, 1976: 295, 296. McDonald & Nybakken, 1978: 114. Cooper, 1978: 8. Williams & Gosliner, 1979: 212.

Cuthona columbiana (O'Donoghue). Cooper, 1980: 284.

Type-specimens: not listed.

Dorsum separated from foot by a shallow, longitudinal groove. Oral tentacles about same length as rhinophores, tapered to blunt points and white distally and proximally with a wide, red-orange band on medial three quarters. Rhinophores smooth, distal two thirds red-orange, with white tips, proximal third white. Cerata arranged in 9–14 transverse rows, recumbent and overlapping. Four rows of cerata occur anterior of cardiac region and remainder occur posterior of cardiac region. General ground color translucent grayish-white. Opaque white flecks occur on head and extend in a line along dorsal surface of oral tentacles. A broad band of encrusting white occurs from base to tip of each ceras, becoming wider distally until it covers distal third of each ceras; core brown (burnt sienna to deep burnt umber). Occasional specimens collected from floating docks in bays and estuaries may be somewhat paler, especially with respect to red-orange of rhinophores and oral tentacles and opaque white of cerata. T.L.: 8 mm.

Anus dorso-lateral, on right, just posterior of cardiac elevation. Genital aperture on right side, ventral of first and second rows of cerata. Penis conical and somewhat curved, armed with a very small, non-protruding chitinous stylet.

Radular formula of specimen examined 66(0.0.1.0.0), MacFarland (1966: 352) reports 127 (0.0.1.0.0), and Baba & Hamatani (1963b: 340) report about 80(0.0.1.0.0), while O'Donoghue (1922b: 161) reports 65–69(0.0.1.0.0). Median denticle of rachidian teeth (Fig. 118) raised well above level of lateral denticles which number about 2–6 on either side, there may be very small denticles between the larger lateral denticles. Masticatory border of mandibles bears numerous, minute, rod-like structures, the surface of which bears minute spines.

Type-locality: Gabriola Pass, Gabriola Island, British Columbia, Canada.

Range and habitat: Pearse Island, British Columbia, Canada (Lambert, 1976), to Mission Bay, San Diego, San Diego Co., California (Lance, 1966); Japan (Baba & Hamatani, 1963b); New Zealand (Miller, 1977). Intertidal to 30 m, most frequently found on floating docks in bays, frequently on the hydroid *Tubularia crocea,* upon which it feeds (Cooper, 1980). Feeds upon *Tubularia marina* and *Tubularia* sp. (Robilliard, 1971a), also found on *Tubularia larynx, Obelia* sp., and *Syncoryne eximia* (Miller, 1977; Robilliard, 1971a). This species is rather rare in California.

Remarks: The radula of *Cuthona alpha* Baba & Hamatani (1963b: pl. 11, fig. 3) is virtually identical to that of *Amphorina columbiana* O'Donoghue (1922b: pl. 6, fig. 24). Although O'Donoghue's description of the coloration of *A. columbiana* is very incomplete, it approaches the description of *C. alpha.* O'Donoghue (1922b: 161) states that the penis of *A. columbiana* is armed with a small, somewhat flattened spine. The penis of *C. alpha* was originally described as unarmed; however, upon re-examination of paratype material by Dr. Baba (Roller, 1969b: 422) a short non-protruding stylet was found. Since there are no significant differences between the two, *A. columbiana* is conspecific with *C. alpha,* the latter being a junior subjective synonym of the former, the proper name is therefore *Cuthona columbiana* (O'Donoghue, 1922) by the law of priority. Williams & Gosliner (1979: 212–213) also agree that *A. columbiana* and *C. alpha* are conspecific.

Cuthona flavovulta (MacFarland, 1966)

Cratena flavovulta MacFarland, 1966: 336–337, pl. 60, fig. 2; pl. 67, figs. 7, 12; pl. 69, figs. 2–2a. Roller, 1970a: 372.
Trinchesia flavovulta (MacFarland). Roller, 1969b: 421, text fig. 1. Roller & Long, 1969: 428. Roller, 1970a: 372. Gosliner & Williams, 1970: 179. Nybakken, 1974: 371. Abbott, 1974: 376, fig. 4446.
Cuthona flavovulta (MacFarland). Williams & Gosliner, 1979: 208, 215.

Type-specimens: type material at Calif. Acad. Sci.

Sides of body distinctly separated from foot by longitudinal groove. Oral tentacles light orange to red on proximal third, and distal two thirds encrusted with white. Rhinophores smooth, light orange to red on proximal fourth, and distal three fourths encrusted with white. Cerata cylindrical, slightly inflated, tapered to blunt tips, and rather erect; arranged in 9 or more transverse rows dorsolaterally on body margin. General ground color translucent grayish-white to cream. A light orange blotch covers front of head, extending onto rhinophores and oral tentacles. An opaque white line occurs dorso-medially on tail. Cerata encrusted with opaque white flecks distally, and a line of orange occurs longitudinally on lateral edge of each ceras; cores usually brownish, rarely green. T.L.: 8 mm.

Anus located on right, just anterior of innermost ceras of first post-cardiac group. Genital aperture on right side, ventral of second row of cerata. Penis armed with chitinous stylet.

Radular formula of specimen examined 66(0.0.1.0.0), MacFarland (1966: 336) reports 70(0.0.1.0.0). Rachidian teeth (Fig. 119) bear 5–7 denticles on either side of median cusp. Masticatory border of mandibles bears a single row of rounded denticles.

Type-locality: Monterey Bay, California.

Range and habitat: Palomarin, Marin Co., California (Gosliner & Williams, 1970), to Shell Beach, San Luis Obispo Co., California (Roller & Long, 1969). Intertidal in rocky areas, usually on hydroids at base of the algae *Laminaria* spp.

Cuthona fulgens (MacFarland, 1966)

Cratena fulgens MacFarland, 1966: 337–340, pl. 60, fig. 3; pl. 67, figs. 8–11; pl. 69, figs. 3–3a. Roller, 1970a: 372.
Trinchesia fulgens (MacFarland). Roller, 1969b: 421, text fig. 1. Long, 1969a: 10. Roller, 1970a: 372. Roller, 1970b: 483. Gosliner & Williams, 1970: 179. Nybakken, 1974: 371. Abbott, 1974: 376, fig. 4447.
Cuthona fulgens (MacFarland). Williams & Gosliner, 1979: 208, 215.

Type-specimens: type material at Calif. Acad. Sci.

Sides of body distinct from margins of foot. Oral tentacles translucent grayish-white and encrusted with opaque white on distal portion. Rhinophores smooth, colored as oral tentacles. Cerata cylindrical, tapered to blunt tips, and slightly decumbent; arranged in 6–8 transverse rows dorso-laterally on either side of dorsum. General ground color translucent grayish-white to pale cream. An irregular line of opaque white may occur dorsomedially on tail. Cerata bear encrusting white dots on surface; cores yellow-brown, raw umber, or dark brown medially with a yellow band both proximal and distal of medial brown area, tips white. T.L.: 6 mm.

Anus on right, just anterior of innermost ceras of first post-cardiac group. Genital aperture on right side, ventral of first and second groups of cerata. Penis armed with chitinous stylet.

Radular formula of specimens examined 16–25(0.0.1.0.0), MacFarland (1966: 338) reports 59(0.0.1.0.0). Rachidian teeth (Fig. 120) bear 5–6 denticles on either side of median cusp. Masticatory border of mandibles bears single row of about 21 small, angular denticles.

Type-locality: Point Pinos, Monterey Co., California.

Range and habitat: Duxbury Reef, Marin Co., California (Long, 1969a), to Shell Beach, San Luis Obispo Co., California (Long, 1969a). Found in rocky intertidal, usually on hydroids at base of the algae *Laminaria* spp.

Cuthona lagunae (O'Donoghue, 1926)

Hervia sp. ? Guernsey, 1912: 78, fig. 39l. Steinberg, 1961: 62. Steinberg, 1963a: 66.

Hervia lagunae O'Donoghue, 1926: 232. Steinberg, 1961: 62. Steinberg, 1963a: 66.

Catriona ronga Marcus, 1961: 52, pl. 10, figs. 185–187. Steinberg, 1963a: 66.

Catriona lagunae (O'Donoghue). Steinberg, 1963a: 66. Steinberg, 1963b: 72. Farmer, 1967: 342. Sphon & Lance, 1968: 77.

Cratena rutila MacFarland, 1966: 332–336, pl. 60, fig. 1; pl. 67, figs. 1–6a; pl. 69; figs. 1–1a; pl. 71, fig. 21. Sphon & Lance, 1968: 77. Roller, 1969b: 421, text fig. 1. Roller, 1970a: 372.

Trinchesia lagunae (O'Donoghue). Roller, 1969b: 421. Roller & Long, 1969: 428. Roller, 1970a: 372. Gosliner & Williams, 1970: 179. Bertsch *et al.*, 1972: 308. Nybakken, 1974: 371. Abbott, 1974: 376, fig. 4445.

Cuthona lagunae (O'Donoghue). Williams & Gosliner, 1979: 208, 215.

Type-specimens: not listed.

Sides of body distinctly separated from foot by a longitudinal groove. Oral tentacles translucent grayish-white with encrusting opaque white on distal two thirds. Rhinophores smooth, orange-red with extreme tips slightly lighter. Cerata cylindrical, slightly clavate, and somewhat decumbent; arranged in 8–9 transverse rows dorso-laterally on dorsum. General ground color translucent grayish-white to cream. Top of head bears a large, rhomboidal, orange-red blotch. An irregular, opaque white line occurs dorso-medially on tail. Cerata bear a few opaque white dots, tips orange-red; cores vary from ochre to almost black. T.L.: 8 mm.

Anus on right, just anterior of innermost ceras of first post-cardiac group. Genital aperture on right side, just ventral of third row of cerata. Penis armed with chininous stylet.

Radular formula of specimen examined 71(0.0.1.0.0), MacFarland (1966: 333) reports 81(0.0.1.0.0). Rachidian teeth (Fig. 121) bear 5–6 denticles on either side of median cusp. Masticatory border of mandibles bears a single series of rather coarse denticles.

Type-locality: Laguna Beach, Orange Co., California.

Range and habitat: Palomarin, Marin Co., California (Gosliner & Williams, 1970), to Rosarito Beach, Baja California, Mexico (Farmer, 1967). Intertidal to 8 m, in rocky areas, frequently in association with hydroids at base of the algae *Laminaria* spp.

Cuthona virens (MacFarland, 1966)

Cratena virens MacFarland, 1966: 344–347, pl. 61, fig. 5; pl. 68, figs. 8–11; pl. 70, figs. 6–8. Roller, 1970a: 372.

Trinchesia virens (MacFarland). Roller, 1969b: 421. Long, 1969a: 9, fig. 1. Roller, 1970a: 372. Roller, 1970b: 483. Abbott, 1974: 376, fig. 4448. Gosliner & Williams, 1973b: 353, 354.

Cuthona virens (MacFarland). Williams & Gosliner, 1979: 208, 215.

Type-specimens: type material at Calif. Acad. Sci.

Sides of body distinctly separated from foot by a shallow, longitudinal groove. Oral tentacles translucent grayish-white with minute white dots on distal half. Rhinophores smooth, translucent grayish-white, with pale yellow on proximal half and distal half paler and encrusted with minute, white dots. Cerata cylindrical, somewhat spindle-shaped, tapered to pointed tips and somewhat decumbent; arranged in about 7 transverse rows dorso-laterally on dorsum. General ground color translucent grayish-white, with a tinge of yellow around and posterior of bases of rhinophores. Anterior margin between oral tentacles bordered with light yellow. Cerata bear occasional flecks of orange or yellow; cores grass green with orange-yellow tips. T.L.: 5 mm.

Anus on right, just anterior of innermost ceras of first post-cardiac group. Genital aperture on right side, just ventral of second row of cerata. Penis armed with chitinous stylet.

Radular formula of specimen examined

33(0.0.1.0.0), MacFarland (1966: 346) reports 46(0.0.1.0.0). In examining MacFarland's microscope slide of the radula of the holotype, I found only 33 teeth; however, some may have been lost in mounting since MacFarland states that the radula had 46 teeth. Rachidian teeth (Fig. 122) bear 4–6 denticles on either side of median cusp. Masticatory border of mandibles bears a few triangular denticles.

Type-locality: Point Pinos, Monterey Co., California.

Range and habitat: Duxbury Reef, Marin Co., California (Gosliner & Williams, 1970), to Shell Beach, San Luis Obispo Co., California (Long, 1969a). Found in rocky intertidal areas.

Remarks: This is the rarest member of the genus in California. Only two or three specimens have been recorded thus far.

Cuthona sp.

Oral tentacles translucent grayish-white with small, opaque white flecks. Rhinophores smooth, translucent grayish-white with numerous small, opaque white flecks which are more concentrated distally. Cerata cylindrical, slightly inflated, and tapered to blunt tips; arranged in 6–10 transverse rows dorso-laterally on dorsum. General ground color translucent grayish-white to cream. Dorsum bears numerous minute, opaque white flecks. Cerata bear numerous opaque white flecks and a band of similar color well below tips, which may be frosted with opaque white; cores olivaceous-green to brownish. T.L.: 7 mm.

Anus on right, just posterior of cardiac region. Genital aperture on right side, just ventral of second group of cerata.

Radular formula of specimen examined 28(0.0.1.0.0). Rachidian teeth (Fig. 123) bear 5–10 denticles on either side of median cusp.

Range and habitat: San Francisco Bay, California (personal observation). Found on floating docks, in association with the sea anemone *Haliplanella luciae* upon which it may feed.

Remarks: Additional study is needed to determine if this species is a named species which has been introduced into San Francisco Bay, or whether it is a species new to science.

Dendrodoris Ehrenberg, 1831

Body doridiform, rather evenly rounded anteriorly and posteriorly; dorsum may be smooth or tuberculate, and is usually rather translucent. Labial tentacles very rudimentary, mouth pore-like. Rhinophores perfoliate and retractile into sheaths. Branchial plumes tri- to quadripinnate, retractile, arranged in a circle around anus.

Radula absent.

Penis armed with spines.

Eliot (1906b: 663) states that in *Dendrodoris* the buccal ganglia beneath the esophagus are located at a constriction of the esophagus, some distance posterior of the main body of the central nervous system, and are united to the nerve-collar by rather long connectives, while in *Doriopsilla* Bergh, 1880, the buccal ganglia beneath the esophagus lie immediately posterior of the main body of the central nervous system. This seems to be the only recognizable difference between *Dendrodoris* and *Doriopsilla.* The location of the buccal ganglia seems a rather poor and insufficient character for use in separating two genera. Steinberg (1961: 58) states that "Until it can be shown that the condition of the central nervous system may be successfully used in separating genera in this very difficult family, I do not consider it wise to maintain *Doriopsilla* as generically distinct from *Dendrodoris.*" Further, Thompson (1975: 500) synonymizes *Doriopsilla* with *Dendrodoris,* stating: "The distinction is based upon several features of the morphology which appear to me to be inadequate."

Type-species: *Dendrodoris lugubris* Ehrenberg, 1831.

Dendrodoris albopunctata (Cooper, 1863)

Doris albopunctata Cooper, 1863b: 58. Carpenter, 1864: 609. Cooper, 1867: 14. Cooper, 1870: 56. Abraham, 1877: 209. Orcutt, 1885: 545. Yates, 1890: 41. O'Donoghue, 1922d: 143. Steinberg, 1961: 58.

Doriopsis reticulata Cockerell in Cockerell & Eliot, 1905: 41–42, pl. 7, fig. 5. Eliot, 1906a: 366. O'Donoghue, 1922d: 143.

Doriopsis fulva MacFarland, 1905: 45. MacFarland, 1906: 130–131, pl. 19, figs. 38–40; pl. 22, fig. 3. Berry, 1907: 35. Guernsey, 1912: 77, fig. 38B. O'Donoghue, 1922d: 142–144. O'Donoghue, 1926: 212. O'Donoghue, 1927b: 92–93. Shelford *et al.,* 1935: 283. Norris & Rao, 1935: 787. Costello, 1938: 330, pl. 1, fig. 3. Steinberg, 1961: 62. Fuhrman *et al.,* 1979: 290.

Doriopsilla reticulata (Cockerell & Eliot). Eliot, 1906b: 665.

Doridopsis fulva MacFarland. Eliot, 1907: 330, 349. Steinberg, 1961: 58.

Doris sp. Guernsey, 1912: 78, fig. 38C. O'Donoghue, 1927b: 78. Steinberg, 1961: 62.

Doriopsis albopunctata (Cooper). O'Donoghue, 1922d: 143.

Dendrodoris fulva (MacFarland). O'Donoghue, 1922d: 142. O'Donoghue, 1926: 212. O'Donoghue, 1927b: 92–93. Costello, 1938: 324, 327, 329, tabs. 1–3, 5. Worley & Worley, 1943: 367, pl. 3, fig. 13. Steinberg, 1961: 57. Marcus, 1961: 30, 58, pl. 6, figs. 107–108. McLean, 1962: 111. MacFarland, 1966: 194–196, pl. 28, fig. 2; pl. 29, figs. 18–19. Roller, 1970a: 371. Hertz, 1970 6. Michel, 1970: 7. McBeth, 1970: 28. McBeth, 1971: 158, 159. McBeth, 1972a: 55 ff. Harris, 1973: 264. Poorman & Poorman, 1978: 373. Fuhrman *et al.*, 1979: 290.

Doriopsilla albopunctata (Cooper). O'Donoghue, 1922d: 142–144. O'Donoghue, 1926: 205. O'Donoghue, 1927b: 93–95. Ingram, 1936: 48. Steinberg, 1961: 57. Marcus & Marcus, 1967a: 98–99, 189, 204–205, 238. Roller, 1970a:372. McBeth, 1970: 28. Gosliner & Williams, 1970: 178. Keen, 1971: 830. Bertsch *et al.*, 1972: 306. McBeth, 1972a: 55 ff. Abbott, 1974: 366, fig. 4351. Haderlie *et al.*, 1974: tab. 4. Bloom, 1976: 295. Nybakken, 1978: 134 ff. McDonald & Nybakken, 1978: 113. Haderlie & Donat, 1978: 60. Poorman & Poorman, 1978: 373. Fuhrman *et al.*, 1979: 290 ff. Russo, 1979: 44, 48. Bertsch, 1980: 224. McCosker, 1980: 30.

Doriopsilla fulva (MacFarland). Andrews, 1945: 26, 34. Pequegnat, 1963: 427. Marcus & Marcus, 1967a: 204. Hargens, 1977: 363.

Dendrodoris (*Doriopsis*) *fulva* (MacFarland). Smith & Gordon, 1948: 181.

Dendrodoris albopunctata (Cooper). Lance, 1961: 67. Farmer & Collier, 1963: 62. Steinberg, 1963b: 71. Paine, 1963a: 4. Paine, 1964: 385. Ghiselin, 1965: 345. Lance, 1966: 69. MacFarland, 1966: 196–197, pl. 28, fig. 4. Sphon & Lance, 1968: 78. Turner *et al.*, 1969: 133. Roller, 1970a: 371. North, 1971: 57. Fuhrman *et al.*, 1979: 290.

Dendrodoris albopunctatus (Cooper). Farmer, 1964: 24. Paine, 1965: 607 (*lapsus*).

Dendrodoris (*Doriopsilla*) *albopunctata* (Cooper). Ghiselin, 1964: 45–46.

Dendrodoris (*Doriopsila*) *albopunctata* (Cooper). Ghiselin, 1965: 335 (*lapsus*).

Doriopsilla ? *albopunctata* (Cooper). Roller & Long, 1969: 427.

Type-specimens: not listed; state coll. species 1000 (Cooper, 1863b).

Body rather elongate. Foot elongate and elliptical, anterior margin bilabiate. Rhinophores bear 11–20 lamellae, and are pale yellow to yellow-orange on shaft, clavus rather brownish-yellow. Rhinophore sheaths have low, smooth, thin margins. Branchial plumes 5, tripinnate, whitish to very pale yellow. General ground color varies from pale yellow to yellow-orange or chestnut brown, low tubercles on dorsum each bear a small, apical, white dot. Some specimens are brownish medially on dorsum. T.L.: 25 mm.

Type-locality: Santa Barbara, Santa Barbara Co., California.

Range and habitat: Van Damme, Mendocino Co., California (Gosliner & Williams, 1970), to Punta San Eugenio, Baja California, Mexico (Lance, 1961). Intertidal to 46 m. One of the most common dorids found in the rocky intertidal zone in central California. McBeth (1971: 158) reports that it feeds upon the sponges: *Acarnus erithacus, Cliona celata, Ficulina suberea,* and *Suberites* sp.

Remarks: Roller (1970a: 371) and Steinberg (1961: 58) synonymized *Dendrodoris fulva* with *Dendrodoris albopunctata*. This may well be warranted as it is very difficult to determine from Cooper's brief description what *D. albopunctata* really is. There are, however, other species of yellow porostomes which occur along the California coast which are very much like *D. albopunctata* as described by Cooper, but yet are not like *D. fulva* as described by MacFarland, and are different from the animals which are currently accepted as *D. albopunctata* (vide *Dendrodoris* sp. a). In addition, there are occasionally found specimens of a eudoridacean which externally resembles *D. albopunctata*. It may be distinguished from *D. albopunctata* by the 8–10 bipinnate, rather vertical branchial plumes, the digitiform labial tentacles, and the rather narrow foot; it is firmer than *D. albopunctata,* and is usually less than 20 mm in length.

Dendrodoris nigromaculata (Cockerell in Cockerell & Eliot, 1905)

Doridopsis vidua (?), Bergh. Cockerell & Eliot, 1905: 40–41. O'Donoghue, 1922d: 143.

Doris nigromaculata Cockerell in Cockerell & Eliot, 1905: 40–41.
Doridopsis nigromaculata Cockerell & Eliot (*vidua* Bergh, var. (?)). Cockerell, 1908: 106. O'Donoghue, 1922d: 143.
Doriopsis nigromaculata Cockerell & Eliot. O'Donoghue, 1922d: 143.
Dendrodoris vidua (Bergh). O'Donoghue, 1926: 212.
Doriopsis vidua Bergh. Kelsey, 1907: 39. O'Donoghue, 1926: 212–213.
Doridopsis nigromaculata Cockerell. O'Donoghue, 1926: 213.
Dendrodoris nigromaculata (Cockerell). Steinberg, 1961: 59.
Doriopsilla nigromaculata (Cockerell & Eliot). Abbott, 1974: 366. Bertsch, 1977: 112.

Type-specimens: not listed.

Dorsum smooth. Foot bluntly rounded anteriorly and tapered posteriorly to blunt tail. Rhinophores bear about 5–6 inclined lamellae and are grayish-white. Branchial plumes 5–6, bi- and tripinnate, whitish. General ground color translucent grayish-white, dorsum bears numerous minute, brownish flecks which are more concentrated medially. About 4–5 opaque white blotches occur in a line dorso-laterally on either side of dorsum, between rhinophores and branchial plumes. T.L.: 10 mm.

Type-locality: La Jolla, San Diego Co., California.

Range and habitat: La Jolla, San Diego Co., California (Cockerell & Eliot, 1905). This species occurs in rocky intertidal, and is quite rare.

Remarks: *Doriopsilla rowena* Marcus & Marcus, 1967a is quite probably a synonym of *D. nigromaculata*. However, since no specimens of *D. rowena* or *D. nigromaculata* from the known geographic range of the former were available for study, I hesitate to synonymize the two.

Dendrodoris sp. a

Body quite broad and ovate, foot elliptical. Rhinophores bear 13–18 inclined lamellae and are orange to brownish-orange. Branchial plumes 5, tripinnate, orangish. General ground color varies from orange to brownish-orange, dorsum somewhat darker medially. Dorsum bears numerous small, opaque white dots which occur over all the dorsum and are not confined to the apex of each tubercle as in *Dendrodoris albopunctata*. T.L.: 40 mm.

Range and habitat: Elkhorn Slough, Monterey Co., California (personal observation), to southern California. Vast majority of specimens are subtidal, usually in rocky areas, but also found in sloughs.

Remarks: The nidosome of this species is very different from that of *Dendrodoris albopunctata*. That of *D. albopunctata* is typical of dorids; it is a yellow spiral which is attached to the substrate by the narrow edge of the ribbon. The nidosome of *Dendrodoris* sp. a is also a spiral, but is usually more yellow-orange than that of *D. albopunctata,* and it is attached to the substrate by the broad surface of the ribbon.

Dendrodoris sp. b

Dendrodoris sp. Lee & Brophy, 1969: 220.

Body quite elongate with nearly parallel sides, and equally rounded anteriorly and posteriorly; dorsum nearly smooth. Foot quite elongate and rounded anteriorly and posteriorly. Rhinophores bear 8–10 lamellae and are white to cream. Rhinophore sheaths have low, smooth margins. Branchial plumes 5, tripinnate, white to cream. General ground color white to very pale cream. Dorsum bears a number of irregular, chocolate-brown blotches of various sizes, usually with the larger blotches concentrated in three groups, one just anterior of branchial plumes, one mid-dorsally, and one just posterior of rhinophores; occasionally another concentration may occur anterior of rhinophores near anterior margin of dorsum. Sides of body, between mantle margin and foot, bear an irregular, longitudinal row of about 4–8 small, chocolate-brown dots. T.L.: 20 mm.

Range and habitat: Pescadero Point, Carmel Bay, Monterey Co., California (personal observation), to Point Loma, San Diego Co., California (personal observation). Intertidal to 46 m, usually in rocky areas.

Dendronotus Alder & Hancock, 1845

Body limaciform. Cerata arborescent, arranged in a longitudinal row along either edge of dorsum, usually in 3–8 opposite pairs; cnidosacs absent. Oral tentacles as such absent. Anterior margin of body bears a veil which usually has 2–5 pairs of velar processes which are normally branched. Rhinophores perfoliate, clavus contained within a campanulate sheath which bears a number of more or less branched processes.

Labial disc armed with small rodlets or filaments. Masticatory border of mandibles normally denticulate. Rachidian teeth usually denticulate but may be smooth; laterals narrow and usually denticulate.

Penis unarmed. Anus located between first and second cerata on right side.

Type-species: *Dendronotus frondosus* (Ascanius, 1774).

Dendronotus albus MacFarland, 1966

Dendronotus albus MacFarland, 1966: 256, 272, 274, 275–279, pl. 40, fig. 1; pl. 46, figs. 1–4; pl. 47, figs. 8–11; pl. 48, figs. 7–8; pl. 49, fig. 5; pl. 50, fig. 4; pl. 51, figs. 6–7. Sphon & Lance, 1968; 78. Long, 1969c: 232. Roller & Long, 1969: 426. Robilliard, 1970: 466–470, pl. 64, fig. 34, text figs. 2, 4–6, 22–24. Schmekel, 1970: 180. Bertsch *et al.*, 1972: 305. Robilliard, 1972: 421 ff. Nybakken, 1974: 371. Haderlie *et al.*, 1974: tab. 4. Abbott, 1974: 368. Lambert, 1976: 296, 297. Thompson, 1976b: 92. Nybakken, 1978: 135. McDonald & Nybakken, 1978: 113. Robilliard & Barr, 1978: 153.

Type-specimens: type material at Calif. Acad. Sci.

Body rather high, and tapered to pointed tail. Foot narrow, rounded anteriorly and tapered posteriorly to pointed tail. Frontal veil bears 4 long, branched, tapered processes on a low, horseshoe-shaped ridge, 2 processes on either side of median line; medial pair longer; below this series may occur a variable number of small, less branched appendages. Rhinophores bear 12–14 lamellae. A short, simple process is directed obliquely upward midway on cylindrical rhinophore shaft. Margin of rhinophore sheath bears 5 slender, tapered, branched processes, the longest of these processes is posterior. Clavus and distal half of the processes of rhinophore sheath usually orange-red to brownish, rarely opaque white; rhinophore shaft translucent grayish-white. The 4–8 opposite pairs of cerata have rather long branches, anterior pairs more branched than posterior pairs. First pair of cerata occurs immediately anterior of cardiac region, second pair occurs immediately posterior of cardiac region. Hepatic diverticulae in 3–5 pairs of cerata. General ground color tanslucent grayish-white. A narrow, median, opaque white line extends posteriorly from between fourth cerata to tip of tail. Velar processes and cerata branches opaque white, usually tipped with orange-red to brownish. T.L.: 25 mm.

Anus on right, about midway between first and second cerata. Genital aperture on right side, ventral and anterior of first ceras.

Radular formula of specimen examined 37(7–8.1.7–8), MacFarland (1966: 278) reports 36–38(7–9.1.7–9), and Robilliard (1970: 468) reports 32–38(6–8.1.6–8). Rachidian teeth (Fig. 78a) bear 16–20 small, blunt denticulations on either side. First laterals (Fig. 78b) have 5–11 denticles on external margin. Outermost 2–3 laterals (Fig. 78h, i) bear only a single cusp and no denticles. Masticatory border of mandibles bears 70–80 transverse, plate-like ridges.

Type-locality: Point Pinos, Monterey Co., California.

Range and habitat: Port Dick, Kenai Peninsula, Alaska (Robilliard & Barr, 1978), to Islas Coronados, Baja California, Mexico (Robilliard, 1970). Intertidal to 30 m, usually found in rocky intertidal and subtidal. Feeds upon the hydroid *Thuiaria argentea* Robilliard, 1970: 470), and also found on *Abietinaria amphora* and *Plumularia* sp. (Robilliard & Barr, 1978; McDonald & Nybakken, 1978). This species is capable of swimming.

Remarks: *Dendronotus albus* is frequently quite difficult to distinguish from *Dendronotus diversicolor* and may possibly be conspecific with it, but present data are insufficient to determine this.

Dendronotus diversicolor Robilliard, 1970

Dendronotus diversicolor Robilliard, 1970: 470–475, pl. 64, figs. 35–36, text figs. 4–6, 25–28. Gosliner & Williams, 1970: 177. Robilliard, 1972: 421 ff. Robilliard, 1974a: 335–336. Abbott, 1974: 368. Lambert, 1976: 296, 298. Thompson, 1976b: 92. Michel, 1976: 47, fig. 7. McDonald & Nybakken, 1978: 113.

Type-specimens: Calif. Acad. Sci., no. 416.

Body quite compressed laterally. Foot narrow, rounded anteriorly and tapered posteriorly to sharply pointed tail. Frontal veil bears 6 slender, slightly branched processes, medial pair is longest. Rhinophores bear 16–21 lamellae. A small, simple lateral process occurs between one third and one half way up rhinophore shaft, it is usually about one quarter the length of rhinophore shaft, but may be shorter or even absent. Margin of rhinophore sheath bears 5 tall, slender, simply branched processes, longest of which is posterior. Distal one third of posterior rhinophore sheath processes and posterior surface of rhinophore sheath may be orange or opaque white; rhinophore shaft translucent grayish-white to lilac. The 4–5 opposite pairs of cerata are tall, slender, and sparsely branched. First pair of cerata occurs immediately anterior of cardiac region, second pair occurs immediately posterior of cardiac region. First 3 pairs about equal in height, fourth pair about one half to two thirds as high, and fifth pair, if present, consists of short papillae. Hepatic diverticulae in anterior 2 pairs of cerata. General ground color translucent grayish-white or lilac. A narrow, median, opaque white line extends posteriorly from between last pair of cerata to tip of tail. Velar processes and cerata branches tipped with orange or opaque white. T.L.: 40 mm.

Anus on right, midway between first and second cerata. Genital aperture on right side, ventral and anterior of first ceras.

Radular formula of specimen examined 38(6–7.1.6–7), Robilliard (1970: 472) reports 33–38(6–9.1.6–9). Rachidian teeth (Fig. 79a) bear 13–25 small, blunt denticulations on either side. First four laterals (Fig. 79b) have 4–11 denticles on external margin. Fifth lateral (Fig. 79f) rarely bears any denticles below the single distal cusp. Outermost 1–3 laterals (Fig. 79g–i) have only a single cusp and no denticles. Masticatory border of mandibles bears 40–61 transverse ridges.

Type-locality: San Juan Island, Puget Sound, Washington.

Range and habitat: Porcher Island, British Columbia, Canada (Lambert, 1976), to Point Loma, San Diego Co., California (Robilliard, 1974a). Intertidal to 19 m, in rocky areas. Found on various hydroids: *Abietinaria* spp., *Hydrallmania distans,* and *Sertularella tricuspidata* (Robilliard, 1970: 474). This species is capable of swimming.

Remarks: The white phase of this species is very difficult to differentiate from *Dendronotus albus.*

Dendronotus frondosus (Ascanius, 1774)

Amphitrite frondosa Ascanius, 1774: 155, pl. 5, fig. 2.

Doris arborescens Müller, 1776: 229. Fabricius, 1780: 346. Mohr, 1786: 116. Cuvier, 1804: 449. Thienemann, 1824: 156. Bosc, 1830: 112. Odhner, 1936: 1109.

Doris cervina Gmelin in Linnaeus, 1791: 3105, no. 12.

Doris frondosa. Cuvier, 1804: 449. Bosc, 1830: 112.

Tritonia arborescens Cuvier, 1805: 435, pl. 61, figs. 8–10. Cuvier, 1817: 28, figs. 8–10. Lamarck, 1819: 304. Fleming, 1823b: 254. Grant, 1826: 165, 185–186. Fleming, 1828: 284. Stark, 1828: 68. Cuvier, 1834: 119. Lamarck, 1836: 454. Johnston, 1838a: 46. Johnston, 1838b: 115. Gould, 1841: 5. Thompson, 1844: 276. Alder & Hancock, 1846b: 65. Kroyer, 1847: 116. Alder & Hancock, 1855: 4.

Tritonia cervina. Bosc, 1830: 106.

Tritonia reynoldsii Couthouy, 1838: 74, pl. 2, figs. 1–4.

Tritonia lactea Thompson, 1840: 88, pl. 2, fig. 3. Thompson, 1856: 275, 276, 485.

Tritonia pulchella Alder & Hancock, 1842: 33. Alder, 1850: 114.

Tritonia felina Alder & Hancock, 1842: 33. Alder, 1850: 114.

Tritonia ascanii Möller, 1842: 78.

Tritonia reynoldsi Couthouy. DeKay, 1843: 8, pl. 5, fig. 94.

Dendronotus arborescens (Müller). Alder & Hancock, 1845a: 644. Alder & Hancock, 1845b: fam. 3, pl. 3. Reid, 1846: 377 ff. Alder & Hancock, 1846a: fam. 3, pl. 2. Lovén, 1846: 138–139. Alder, 1850: 105, 113. Stimpson, 1853: 26. Adams & Adams, 1854: 65, pl. 64, fig. 7. Byerley, 1854: 45. Alder & Hancock, 1855: 21, 31, 32, 47. Gosse, 1856: 103. Thompson, 1856: 485. Carpenter, 1857: 313. Gray, 1857: 219. Chenu, 1859: 407, fig. 3059. Collingwood, 1859: 464–465. Hyndman, 1859: 286. E. Wright, 1859: 88. Collingwood, 1860: 202. Norman, 1860: 7243. Collingwood, 1861: 114. Collingwood & Byerley, 1962: 189. McIntosh, 1865: 391. Meyer & Möbius, 1865: 43–47, pl. 5, pl. 3. Robertson, 1868: 206. Mörch, 1868: 204. Hogg, 1868: pl. 10, fig. 38. Jeffreys, 1869: 62–63, pl. 2, fig. 2. Gould, 1870: 234–236, pl. 22, figs. 311–313. Dall, 1870: 250. Sauvage, 1873: 25, 33–34. Verrill, 1873: 495, 499, 665. Verrill, 1874a: 43. McIntosh, 1874: 430. McIntosh, 1875: 86. Friele & Hansen, 1876: 73. Smith & Harger, 1876: 8, 13. Mörch, 1877: 436. Garner, 1878: 93. Jones, 1878: 326. Sars, 1878: 314–315 ff, pl. XV, fig. 3. Bergh, 1879b: pl. 2, figs. 13–15; pl. 3, fig. 1; pl. 4, figs. 1–4. Bergh, 1879c: pl. 2, figs. 13–15; pl. 3, fig. 1; pl. 4, figs. 1–4. Verrill, 1880: 385, 386. Leslie & Herdman, 1881, 310. Verrill, 1882a: 339. Bush, 1883: 245. Hertzenstein, 1885: 710. Krause, 1885: 295. Becher, 1886: 14. Locard, 1886: 40–41. Higgins, 1886: 26. Haddon, 1886: 530. Herdman, 1886: 271, 277. Holm, 1887: 156

ff. Fischer, 1887: 535, text fig. 292. Bergh, 1887: 25–35, pl. 2, figs. 12–28. Herdman & Clubb, 1889: 228–231, pl. 12, figs. 1–3, 7. Garstang, 1889: 185. Herdman, 1890a: 46, 54, pl. 7, figs. 16–21. Herdman, 1890b: 202. Bergh, 1890a: 56. Garstang, 1890: 425. Bergh, 1892: 1051 (59). Herdman & Clubb, 1892: 136 ff, pl. 6, fig. 14. Lundbeck, 1893: 175. Herdman, 1894: 14. Bergh, 1894: 137–139. Clubb, 1895: 220–234, pls. 14–15. Herdman *et al.*, 1896: 446. Sumner, 1896: 49. Vanhoffen, 1897: 188, 193. Posselt, 1898: 248. Cooke, 1899: 61–62. Liverpool Mar. Biol. Comm., 1899: 55. Beaumont, 1900: 847. Whiteaves, 1901: 206. Vayssière, 1901: 296. Johansen, 1902: 387. Todd, 1903: 544, 556. Cockerell & Eliot, 1905: 32. Walton, 1908: 237–238. Colgan, 1903: 106, 112. Farran, 1909: 14. Eliot, 1910: 13. Pelseneer, 1911: 63–64, pl. 18, figs. 2–13. Sumner *et al.*, 1913: 704. Chumley, 1918: 103, 149, 169. Bardarson, 1919: 72. O'Donoghue, 1921: 184, pl. 4 (10), fig. 45; pl. 5 (11), figs. 51–53. O'Donoghue, 1922a: 124. Scott, 1922: 49. White, 1938: 14. Volodchenko, 1955: 248, pl. 48, fig. 1. MacFarland, 1966: 254 ff. Storch & Welsch, 1969: 528 ff. Daro, 1969: 141, 147. Zaitseva, 1978: 498 ff.

Amphitridea facrici. Kroyer, 1847: 114.

Dendronotus reynoldsii (Couthouy). Alder & Hancock, 1855: 28. Mörch, 1857: 78. Stimpson, 1862: 4. Mörch, 1875: 125. Mörch, 1877: 436.

Tritonia (*Dendronotus*) *arborescens.* Carpenter, 1857: 218.

Dendronotus pulchella (Alder & Hancock). Gray, 1857: 219.

Dendronotus felina (Alder & Hancock). Gray, 1857: 219.

Campaspe pusilla Bergh, 1863: 471–478, pl. 12, figs. 28–35. Mörch, 1857: 125. Mörch, 1877: 437. Bergh, 1892: 1050 (58). Vanoffen, 1897: 193. Posselt, 1898: 251. Odhner, 1907: 64. Løyning, 1927: 249. Odhner, 1936: 1108.

Dendronotus luteolus Lafont, 1871–1872: 267, pl. 17, fig. 1. Fischer, 1872: 14. Locard, 1886: 41. Bergh, 1892: 1051 (59). Odhner, 1936: 1108.

Dendronotus purpureus Bergh, 1879b: 89–94, pl. 1, figs. 18–20; pl. 3, figs. 7–12. Bergh, 1879c: 145–150, pl. 1, figs. 18–20; pl. 3, figs. 7–12. Bergh, 1892: 1051 (59). Bergh, 1903: 15–18, pl. 2, figs. 10–12. Odhner, 1936: 1108. LaRocque, 1953: 253. MacFarland, 1966: 257.

Dendronotus arborescens var. *aurantiaca* Friele, 1879: 284.

Dendronotus elegans Verrill, 1880: 385–386. Verrill, 1882b: 551.

Dendronotus pulchellus (Alder & Hancock). Locard, 1886: 41.

Dendronotus lacteus (Thompson). Becher, 1886: 14. Bergh, 1892: 1051 (59). Eliot, 1910: 112, 151. Odhner, 1936: 1108. White, 1938: 18.

Campaspe major Bergh, 1887: 21–24, pl. 1, figs. 23–26; pl. 2, figs. 1–11. Bergh, 1892: 1051 (58). Odhner, 1936: 1108. Løyning, 1927: 249.

Dendronotus frondosus (Ascanius). Norman, 1890: 78. Tregelles, 1896. 221. Cooke, 1899: 66. Herdman *et al.*, 1900: 46. Nichols, 1900: 592. Conchol. Soc., 1901: 25. Knight, 1901: 207. Farran, 1904: 5. Mar. Biol. Assoc., 1904: 282. Odhner, 1907: 66. Balch, 1909: 36. Eliot, 1910: 161. Crawshay, 1912: 372. Vayssière, 1913: 7–10, pl. figs. 7–18. Johnson, 1915: 169. Evans & Evans, 1917: 109. Bardarson, 1920: 109. Elmhirst, 1922: 41. Iredale & O'Donoghue, 1923: 216. Larsen, 1925: 38–42, text figs. 30–33, pl. figs. 9a–d. Odhner, 1926b: 17–19, text fig. 13. O'Donoghue, 1926: 223, Cuenot, 1927: 266. Jutting, 1927: LXXXVIII. Løyning, 1927: 246–249, 262. Derjugin, 1928: 319–320. Lemche, 1929: 8–9. Lonnberg, 1931: 20. Mar. Biol. Assoc., 1931: 272. Winckworth, 1932: 235–236. Chambers, 1934: 636. Odhner, 1936: 1063 ff, text figs. 3–4, 39. Moore, 1937: 191–192. White, 1938: 14, 18. Lemche, 1938: 13–14 ff. Graham, 1938: 300. Odhner, 1939: 45–46. Lemche, 1941a: 23–24. Lemche, 1941b: 15–18. Jutting, 1947: 64. Fischer, 1950: 199. Jaeckel, 1952: 24 ff. La Rocque, 1953: 252. Williams, 1954: 106. MacGinitie, 1955: 66, 97, 101, 102, 175. Franzén, 1955: 428, text fig. 96. Graham, 1955: 153. Baba, 1957: 9. Mar. Biol. Assoc., 1957: 313. Swennen, 1959: 58. MacGinitie, 1959: 144–145, pl. 3, fig. 1. Thompson, 1960a: 24–26, text figs. 1–2. Thompson, 1960b: 126–127. Buznikov, 1960: 373. Buznikov & Manukhim, 1960: 1414–1416. Miller, 1961: 100, 105. Thompson, 1961: 236. Swennen, 1961: 207–209. Marcus, 1961: 34–36 ff, pl. 7, figs. 121–124. Lance, 1961: 67. Buznikov & Manukhim, 1961: 226, 232. Miller, 1962: 562. Sakharov, 1962: 310, 311. Roginskaya, 1962a: 88, 93–95, 106, figs. 2.1–2.3. Roginskaya, 1962b: 205–206, 211–212 ff, fig. 1.5. Paine, 1963a: 4. Steinberg, 1963b: 71. Arronet, 1963: 11. Zenkevitch, 1963: 112. Bruce *et al.,* 1963: 205. Thompson, 1964: 281 ff. Buznikov, 1964: 1243. Abe, 1964: 57, 87, pl. 29, fig. 100. Ghiselin, 1965: 351 ff. MacFarland, 1966: 254 ff. Brattegard, 1966: 20. Sakharov, 1966: 957. Hurst, 1967: 255 ff, text fig. 15, pl. 30, fig. 18; fig. 25-5. Marcus & Marcus, 1967a: 212. Thompson, 1967: 12. Carefoot, 1967: 628 ff. Buchsbaum & Milne, 1967: pl. 63. Sphon & Lance, 1968: 91. Bebbington & Thompson, 1968: 9. Marcus & Marcus, 1969: 27. Turner *et al.,* 1969: 135, append. 1, 2. Loveland *et al.,* 1969: 418. Haderlie, 1969: tab. 1. Long, 1969c: 232. Roller & Long, 1969: 426. Morse, 1969: 38. Roller, 1970a: 372. Robilliard, 1970: 441–446, text figs. 7–9, pl. 63, fig. 29. Gosliner & Williams, 1970: 177. Franz, 1970: 172 ff. Hughes, 1970b: 81, 82. Bernard, 1970: 85. Buznikov *et al.,* 1970: 550, 557. North, 1971: 57. Meyer, 1971: 142. L. Williams, 1971: 166–171, text figs. 1–5. Keen, 1971: 832. Bertsch *et al.,* 1972: 305. Holleman, 1972a: 60. Sphon, 1972a: 155. Gascoigne, 1972: 259. Robilliard, 1972: 421 ff. Salvini-Plawen, 1972: 393. Voogt, 1973: 479 ff. Rasmussen, 1973: 27, 268, 460. Platts, 1973: 384. Harris, 1973: 217, 292–293. Thompson & Bebbington, 1973: 148, 149, pl. 9, figs. c–d. Robilliard, 1974a: 335. Rozsa, 1974: 8. Nybakken, 1974: 371. Abbott, 1974: 367, pl. 16, fig. 4357. Roginskaya, 1974b: 998, text fig. 1. Harris *et al.,* 1975: 264. Robilliard, 1975a: 59. Robilliard, 1975b: 44–47. Sneli & Steinnes, 1975: 13. Clark, 1975: 40–41. Franz, 1975a: 81. Rozsa, 1975: 3. Belcik, 1975: 276. Michel, 1976: 49, fig. 14. Lambert, 1976: 296. Thompson & Brown, 1976: 66, fig. 29. Thompson, 1976a: 39. Thompson, 1976b: 8, 34, 72, 92. Thiriot-Quiévreux, 1977: 178. Edmunds, 1977: 306, 307. Garlo, 1977: 23 ff. McDonald & Nybakken, 1978: 113. Chamberlain & Behrens, 1980: 283. (*Non*) Odhner, 1936: 1105–1109 (=*Dendronotus dalli* Bergh, 1879, *Dendronotus rufus* O'Donoghue, 1921).

Dendronotus frondosus elegans Verrill. Johnson, 1915: 170. Johnson, 1934: 156.

Dendronotus frondosa. Dahlgren, 1925: 436 (*lapsus*).

Dendronotus frondosus frondosus. Johnson, 1934: 156.

Dendronotus purpurascens Bergh. Odhner, 1936: 1109 (*lapsus*).

Dendronotus frondosus var. *purpureus* Bergh. MacFarland, 1966: 255.

Dendronotus venustus MacFarland, 1966: 271–275, pl. 40, fig. 2; pl. 46, figs. 9–12; pl. 47, figs. 1–2; pl. 49, fig. 6; pl. 50, fig. 3; pl. 52, figs. 3–6. Roller, 1970a: 372. Schmekel, 1970: 180.

(*Non*) *Dendronotus frondosus* var. *dalli.* Zenkevitch, 1963: 134 (=*Dendronotus dalli* Bergh, 1879).

Type-specimens: not listed.

Foot narrow, rounded anteriorly and tapered posteriorly to short, pointed tail. Frontal veil bears 4–8 branched, tapered processes; of these, two on either side of median line are larger and relatively constant; between these may occur smaller, less branched processes. Rhinophores bear 6–14 lamellae. A short process with short branches distally occurs near base of rhinophore shaft on external surface. Rhinophore sheath bears 4–5 branched processes, postero-medial process longest and most branched. Rhinophores translucent grayish-green, with irregular patches of yellow-green to brown-green, clavus slightly darker shade of grayish-green. The 3–9 opposite pairs of cerata bear rather short branches, anterior pairs slightly more branched than posterior pairs. First pair of cerata occurs immediately anterior of cardiac region, second pair occurs immediately posterior of cardiac region. General ground color translucent grayish-white, tending toward greenish or brownish in most specimens. Irregular patches of yellow-green to brown-green occur on body, with smaller spots of olive to pale green and pale yellow to bright orange. Low conical papillae on body are tipped with yellow. On occasional specimens, a series of opaque white blotches occurs medially on dorsum between successive pairs of cerata. Distal ends of cerata branches flecked with numerous small, yellow dots, cores light green to brown. T.L.: 25 mm, may attain 100 mm.

Anus on right, dorso-laterally, between first and second cerata. Genital aperture on right side, ventral and anterior of first ceras.

Radular formula of specimen examined 32(8–9.1.8–9), MacFarland (1966: 272) reports 28–34(6–7.1.6–7), and Robilliard (1970: 443) reports 33–48(7–11.1.7–11). Rachidian teeth (Fig. 80a) bear 10–13 small denticles on either side. Laterals (Fig. 80b–h) have 3–6 denticles on external margin, innermost denticles usually longest. Masticatory border of mandibles bears 27–40 transverse, ridgelike denticles.

Type locality: Norway?

Range and habitat: Nearly cosmopolitan in northern hemisphere (Lance, 1961); east (Franz, 1975a) and west (Robilliard, 1970) coasts of North America, British Isles (Mar. Biol. Assoc., 1957), Europe (Cuenot, 1927), China (Thompson & Brown, 1976), Japan (Baba, 1957). Intertidal to 400 m. Occasionally found in rocky intertidal; more commonly found on floating docks and pilings in bays. Feeds upon the hydroids: *Bougainvillia glorietta, Coryne* sp., *Dynamena pumila, Hydractinia echinata, Hydrallmania falcata, Obelia commissuralis, Obelia* spp., *Sertularia argentea, Sertularia cupressina, Sertularia dichotoma, Sertularia pumila, Syncoryne eximia, Tubularia crocea, Tubularia indivisa,* and *Tubularia larynx* (Carefoot, 1967; Clark, 1975; Collingwood, 1859; Grant, 1826; Harris, 1973; Harris *et al.,* 1975; Herdman, 1886; Kozloff, 1973; Meyer, 1971; Miller, 1961; Robilliard, 1970; Swennen, 1961; Thompson, 1964; Thompson & Brown, 1976). Also found on the hydroids: *Abietinaria abietina, Aglaophenia* sp., *Laomedea geniculata,* and *Obelia flabellata* (Garlo, 1977; Herdman, 1890a; Marcus, 1961; Rasmussen, 1944, 1973). Morse (1969: 38) reports that it has been observed eating the ascidian *Botryllus schlosseri.* This species is capable of swimming. Volodchenko (1955: 248) states that it is preyed upon by fish.

Dendronotus iris Cooper, 1863

Dendronotus iris Cooper, 1863b: 59. Carpenter, 1864: 609. Cooper, 1867: 14. Yates, 1890: 41. Bergh, 1892: 1052(59). O'Donoghue, 1926: 224. Odhner, 1936: 1105, 1107, 1109, pl. 1, fig. 9, text figs. 40–41. Lance, 1961: 67. Marcus, 1961: 36. Steinberg, 1963b: 71. MacFarland, 1966: 254–265 ff, pl. 47, figs. 12–18; pl. 48, figs. 1–6; pl. 49, fig. 4; pl. 50, fig. 1; pl. 51, figs. 1–5. Powell, 1966: 115. Marcus & Marcus, 1967a: 210, 212, 213. Hurst, 1967: 255 ff, pl. 30, fig. 19; pl. 38, figs. 49–50; fig. 25-2. Sphon & Lance, 1968: 78. Lee & Brophy, 1969: 220. Roller & Long, 1969: 429. Wobber, 1970: 383–387, pl. 55, figs. 1–2; pl. 56, figs. 3–4; pl. 57, fig. 5. Roller, 1970b: 482. Robilliard, 1970: 446–450, pl. 63, fig. 30, text figs. 4–6, 10–12. Bernard, 1970: 85. Schmekel, 1970: 180, 181. Crane, 1971: 57. Robilliard, 1972: 421 ff. Gosliner & Williams, 1973b: 352, 353. Harris, 1973: 221 ff. Thompson, 1973: 167 ff, text fig. 8. Abbott, 1974: 367. Lambert, 1976: 296. Thompson, 1976a: 28, pl. 3, figs. c, d. Thompson, 1976b: 13, 58. McDonald & Nybakken, 1978: 113.

Dendronotus giganteus O'Donoghue, 1921: 187–190, pl. 4 (10), fig. 47; pl. 5 (11) figs. 57–59. O'Donoghue, 1922b: 165. Agersborg, 1922a: 257. Agersborg, 1922b: 439. O'Donoghue, 1924: 24. Agersborg, 1925: 167. O'Donoghue, 1926: 223. Fraser, 1932: 67. Odhner, 1936: 1105 ff. Hewatt, 1937: 178 ff. Smith & Gordon, 1948: 181. LaRocque, 1953: 253. Marcus, 1961: 36. Kohn, 1961: 293 ff. MacFarland, 1966: 255, 258. Farmer, 1970: 79. Harris, 1973: 260.

Dendronotus iris (=*giganteus*). Thompson, 1976b: 92.

Type-specimens: not listed; state coll. species 959 (Cooper, 1863b).

Foot relatively wide, rounded anteriorly and tapered posteriorly to short, bluntly rounded tail. Frontal veil bears 4–8 processes, which are relatively sparsely branched. Rhinophores bear 15–31 lamellae. A stout, branched process occurs near base of rhinophore shaft. Two to six (usually 4) small, branched papillae are arranged vertically on posterior face of rhinophore shaft. Rhinophore sheath bears 2–5 long, branched processes, the longest of which is posterior. Clavus translucent grayish white to orange or maroon, usually tipped with opaque white. The 4–7 opposite pairs of cerata bear numerous long branches, anterior pairs larger and somewhat more branched than posterior pairs. First pair occurs immediately anterior of cardiac region. Second pair occurs immediately posterior of cardiac region. There are two color phases commonly found in California. In the first, general ground color translucent grayish-white and cerata tipped with opaque white with subterminal band of brownish-orange, below which a band of lighter orange. In the second, general ground color deep maroon or reddish-purple, cerata tipped with orange. In both phases, an opaque white line extends around dorsal margin of foot, and velar processes tipped with metallic orange, maroon, yellow or purple, or white. T.L.: 60 mm, but specimens up to 200 mm have been collected.

Anus on right, midway between first and second cerata. Genital aperture on right side, ventral and just anterior of first ceras.

Radular formula of specimen examined 35(12–20.1.12–20), MacFarland (1966: 262) reports 34–36(11–20.1.11–20), and Robilliard (1970: 448) reports 41–61(11–21.1.11–21). Rachidian teeth (Fig. 82a) bear 9–18 pointed denticles on either side. First laterals (Fig. 82b) have 1–8 denticles, while remaining laterals (Fig. 83c–m) lack denticles, and bear only the single, terminal cusp. Masticatory border of mandibles bears 85–100 large denticles.

Type-locality: Santa Barbara, Santa Barbara Co., California.

Range and habitat: Unalaska, Alaska (Robilliard, 1970), to Islas Coronados, Baja California, Mexico (Lance, 1961). Intertidal to 215 m. Most commonly found subtidally (ca. 10 m) in association with the tube-dwelling sea anemone *Pachycerianthus fimbriatus* upon which it feeds (Powell, 1966; Wobber, 1970). This species is capable of swimming.

Dendronotus subramosus MacFarland, 1966

Dendronotus subramosus MacFarland, 1966: 255, 265–270 ff, pl. 40, fig. 3; pl. 46, figs. 5–8; pl. 47, figs. 3–7; pl. 49, figs. 1–3; pl. 50, fig. 2; pl. 52, figs. 1–2. Sphon & Lance, 1968: 78. Roller & Long, 1969: 426. Haderlie, 1969: tab. 1. Gosliner & Williams, 1970: 177. Robilliard, 1970: 462–466, pl. 64, fig. 33, text figs. 3, 4, 6, 19–21. Schmekel, 1970: 180. Robilliard, 1972: 421 ff. Nybakken, 1974: 371. Abbott, 1974: 367–368. Thompson 1976b: 92. McDonald & Nybakken, 1978: 113.

Type-specimens: type material at Calif. Acad. Sci.

Foot narrow, rounded anteriorly and bluntly pointed posteriorly. Frontal veil bears 4–6 short, slightly branched processes, medial pair longest. Rhinophores bear 9–14 lamellae. No processes on rhinophore shaft, as opposed to other species of this genus in California. Margin of rhinophore sheath bears 5 short, blunt processes, longest of which is posterior and may bear small tubercle-like branches, but remaining processes are unbranched. Clavus and shaft translucent grayish-white to brownish-white. The 3–6 opposite pairs of cerata are stout, anterior pairs more branched than posterior pairs. First pair occurs immediately anterior of cardiac region, second pair occurs immediately posterior of cardiac region. General ground color translucent grayish-white to brownish-white to white or even dark brown. Body sprinkled with numerous lemon yellow or orange dots, especially on cerata and velar processes; with a smaller number of brown, red-brown, gold, green, and white dots. Four distinct, light to dark brown stripes occur longitudinally on dorsum. Outermost stripe on either side runs from lateral base of rhinophore shaft to lateral base of each ceras, and continues on to tail; innermost stripe on either side runs from medial base of rhinophore shaft to medial base of each ceras, and continues on to tail where the 4 stripes unite. These stripes may be lacking in occasional specimens. T.L.: 25 mm.

Anus on right between first and second cerata. Genital aperture on right side, ventral and anterior of first ceras.

Radular formula of specimen examined 31(5–6.1.5–6), MacFarland (1966: 266) reports 56–72(5–7.1.5–7), and Robilliard (1970: 464) reports 54–62(2–5.1.2–5). Rachidian teeth (Fig. 81a) bear 7–12 long, blunt, heavy denticles on either side. First laterals (Fig. 81b) have 1–3 irregular denticles, remaining laterals (Fig. 81c–f) bear 0–8 irregular denticles. Masticatory border of mandibles bears about 120 transverse, smooth, crescentic ridges.

Type-locality: Monterey Bay, California.

Range and habitat: San Juan Islands, Puget Sound, Washington (Robilliard, 1970), to Islas Coronados, Baja California, Mexico (Robilliard, 1970). Intertidal to 107 m. Most commonly found in rocky intertidal, occasionally on floating docks and pilings in bays. Feeds upon the hydroid *Aglaophenia struthionides* (Robilliard, 1970: 466).

Dirona Eliot in Cockerell & Eliot, 1905, ex MacFarland, MS.

Body limaciform, rather broad, bluntly rounded anteriorly and tapered posteriorly to short, pointed tail. Cerata lanceolate, pointed apically; arranged in closely set, irregular dorso-lateral rows on dorsum, leaving mid-dorsal area free. Cerata extend anterior of rhinophores, but do not meet antero-medially, and they extend posteriorly where they meet medially. Cnidosacs absent. Labial tentacles as such absent, in their place a broad, undulating frontal veil. Rhinophores non-retractile, perfoliate.

Masticatory border of massive mandibles smooth. Radular formula 1.1.1.1.1, rachidian teeth bear a single, non-denticulate, median denticle. Laterals somewhat hooked and bear a few denticles. Marginals large and hooked, with no denticles. Labial cuticle covered with thick-set, hair-like processes.

Penis unarmed. Anus on a papilla far back on right side, just ventral of cerata.

Type-species: *Dirona picta* Eliot in Cockerell & Eliot, 1905, ex MacFarland, Ms.

Dirona albolineata Eliot in Cockerell & Eliot, 1905, ex MacFarland, Ms.

Dirona albolineata MacFarland in Cockerell & Eliot, 1905: 46. MacFarland, 1912: 518–533, pl. 30, fig. 2; pl. 31, figs. 11–19; pl. 32, fig. 21. O'Donoghue, 1921: 181–183, pl. 2 (8), figs. 23–24. O'Donoghue, 1922a: 124. O'Donoghue & O'Donoghue, 1922: 132–134, pl. 3, fig. 2. O'Donoghue, 1922b: 164. O'Donoghue, 1924: 24, 31. O'Donoghue, 1926: 224. O'Donoghue, 1927b: 102–103, pl. 3, figs. 64–67. Smith & Gordon, 1948: 181. LaRocque, 1953: 260. Marcus, 1961: 46–47, pl. 9, figs. 159–160. Lance, 1961: 68. Steinberg, 1963b: 71. Paine, 1963a: 4. Willows, 1965: 707 ff. Hurst, 1966: 9 ff. MacFarland, 1966: 298–302, pl. 30, fig. 13; pl. 56, figs. 1–4; pl. 63, figs. 9–12; pl. 64, figs. 4–10. Lance, 1966: 79. Hurst, 1967: 255 ff, text figs. 16, 31, pl. 30, fig. 20; pl. 36, fig. 41; fig. 24-2. Marcus & Marcus, 1967a: 217. Sphon & Lance, 1968: 82. Mauzey *et al.*, 1968: 609. Roller & Long, 1969: 426. Robilliard, 1969a: 290. Robilliard, 1969b: 23. Turner *et al.*, 1969: 135, append. 1, 2. Gosliner & Williams, 1970: 178. Bernard, 1970: 86. Schmekel, 1970: 188. Robilliard, 1971c: 429 ff. Sphon, 1972a: 155. Blair & Seapy, 1972: 119. Goddard, 1973: 9. Abbott, 1974: 373. Belcik, 1975: 276. Schuler, 1975: 33. Lambert, 1976: 296, 298. Thompson, 1976a: 39, pl. 3, fig. 6, text fig. b. Thompson, 1976b: 17, 47, 71. Nybakken, 1978: 135. McDonald & Nybakken, 1978: 114. McCosker, 1980: 31. (*Non*) Baba, 1935b: 116, 120–121, pl. 7, figs. 11–16; pl. 8, figs. 1–2. (*Non*) Baba, 1937b: 321. (*Non*) Volodchenko, 1941: 60. (*Non*) Volodchenko, 1955: 251–252, pl. 48, fig. 10. (=*Dirona akkeshiensis*, Baba, 1957).

Dirona sp. MacGinitie & MacGinitie, 1949: 364.

Type-specimens: Mus. Invert. Zool., Stanford Univ.

Rhinophores bear 16–20 lamellae, conical clavus occupies about half the rhinophore; rhinophore shaft clear white, lamellae delicate ochre; inner face of rhinophore shaft bears an opaque white line, starting just below clavus, passing down shaft, between rhinophores and up opposite shaft. Cerata smooth, and somewhat flattened antero-posteriorly. Medial cerata are longest, reaching about one half body length. General ground color translucent whitish. Cerata also translucent whitish, with an opaque white line on lateral margin of each. Frontal veil bears a band of opaque white along anterior margin, and crest of tail bears a similar line medially. Large individuals may have a few small, opaque white flecks on body and cerata. T.L.: 25 mm, but specimens up to 180 mm have been collected.

Anus on right, near posterior end, in outermost row of cerata. Genital aperture on right side, below cerata, about one third of the distance from anterior end. Penis unarmed, but bears a spiral row of soft, conical prominences.

Radular formula of specimens examined 23–25(1.1.1.1.1), MacFarland (1966: 299) reports 29–32(1.1.1.1.1), and Marcus (1961: 47) reports 22(2.1.2). Rachidian teeth (Fig. 92c, d) small, and each bears a single, long, thin, median denticle. Laterals (Fig. 92b) somewhat hooked, with 2–5 denticles. Marginals (Fig. 92a) large and greatly hooked with no denticles. Mandibles quite large, masticatory border smooth.

Type-locality: Monterey Bay, California.

Range and habitat: Porcher Island, British Columbia, Canada (Lambert, 1976), to La Jolla, San Diego Co., California (Lance, 1966). Intertidal to 37 m, usually in rocky areas. Rather uncommon in central California. Robilliard (1971c: 419) reports that it is an unselective predator, scraping up bryozoans, hydroids, small crustaceans, sponges, barnacles, and tunicates, and that it feeds upon the snails *Margarites pupillus, Margarites helicinus,* and *Lacuna carinata.*

Dirona picta Eliot in Cockerell & Eliot, 1905, ex MacFarland, Ms.

Dirona picta MacFarland in Cockerell & Eliot, 1905: 46–48, pl. 7, figs. 6–11. MacFarland, 1912: 517, 518, 520–533, pl. 30, fig. 1; pl. 31, figs. 1–10; pl. 32, figs. 20, 22–24. Hilton, 1919: 34. O'Donoghue, 1926: 224–225. O'Donoghue, 1927b: 101, 102, pl. 3, figs. 60–63. Baba, 1937b: 320. Hewatt, 1937: 188, 200. Smith & Gordon, 1948: 181. Marcus, 1961: 44–46, 47, pl. 9, figs. 155–158. Lance, 1961, 68. Farmer &

Collier, 1963: 62. Steinberg, 1963b: 71. Paine, 1963a: 4. Paine, 1964: 385. Paine, 1965: 604, 607. Hurst, 1966: 9 ff. Lance, 1966: 69. MacFarland, 1966: 295–299, pl. 56, figs. 5–7; pl. 63, figs. 1–8; pl. 65, figs. 1–3. Farmer, 1967: 342. Marcus & Marcus, 1967a: 216–218, 238, fig. 67. Sphon & Lance, 1968: 78. Haderlie, 1968: 339. Roller & Long, 1969: 426. Gosliner & Williams, 1970: 178. Schmekel, 1970: 188. Salvini-Plawen, 1972: 393. Holleman, 1972a: 60. Goddard, 1973: 9. Abbott, 1974: 373, fig. 4406. Belcik, 1975: 277. Thompson, 1976a: 35. Nybakken, 1978: 135. McDonald & Nybakken, 1978: 114.

Dirona picta Eliot in Cockerell & Eliot, 1905, ex MacFarland, Ms. Keen, 1971: 835, pl. 22, fig. 4.

Type-specimens: Mus. Invert. Zool., Stanford Univ.

Rhinophores bear 8–10 lamellae, clavus occupies one third to one half of total rhinophore; rhinophore shaft light yellowish-brown to burnt umber, lamellae a lighter shade of same color. Cerata inflated and rather tuberculate. Medial cerata are longest, reaching about one half of body length. General ground color light yellowish-brown to burnt umber, occasional specimens may be greenish. Small pink and cream dots or dark brown, dull green, and yellow dots may occur on body. Cerata same color as body, with a pale red spot on outer side of each ceras, about one third of the distance from base. T.L.: 25 mm.

Anus on right, near posterior end, in outermost row of cerata. Genital aperture on right side below cerata, about one third of the distance from anterior end. Penis unarmed, but bears a spiral row of soft, conical prominences.

Radular formula of specimen examined 24(1.1.1.1.1), MacFarland (1966: 298) reports 32–35(1.1.1.1.1), and Marcus (1961: 45) reports 24(2.1.2). Rachidian teeth (Fig. 93c, d) small, each bears a single, thin, median denticle which is shorter than that in *Dirona albolineata* (Fig. 92c, d). Laterals (Fig. 93b) somewhat hooked, with 3–7 denticles. Marginals (Fig. 93a) largest and greatly hooked, with no denticles. Mandibles quite large, masticatory border slightly roughened.

Type-locality: Dead Man's Island, San Pedro, Los Angeles Co., California.

Range and habitat: Dillon Beach, Marin Co., California (Marcus, 1961), to Puerto Rompiente, Baja California, Mexico (Farmer & Collier, 1963); Puerto Peñasco, Sonora, Mexico (Farmer, 1967); Puertecitos, Baja California, Mexico (Farmer & Collier, 1963): also reported from Japan (Baba, 1937b). Intertidal to 10 m, usually in rocky intertidal areas, occasional on floating docks in bays. May feed upon bryozoans such as *Thaumatoporella* sp. Marcus (1961: 45) found several cheilostomatous bryozoans, e.g. *Celleporella hyalina,* in the digestive tract. Bertsch *et al.* (1972: 306) found the avicularia of a "*Bugula*-type bryozoan" in the stomach of one specimen. Salvini-Plawen (1972: 393) reports that it feeds upon the hydroid *Aglaophenia* sp.

Remarks: Volodchenko (1955: 252) reports the radular formula (4.1.4). Since MacFarland (1912: 516) states that the radular formula in the genus *Dirona* is (2.1.2), this casts doubt on the identification of Volodchenko's specimens with *D. picta.* Further, Volodchenko's specimens have a distinct circle of processes at the base of each rhinophore, which is absent in specimens of *D. picta* from California. In addition, Volodchenko's figure (1955: pl. 48, fig. 11) appears to be copied from MacFarland (1912: pl. 30, fig. 1), with the addition of the processes at the bases of the rhinophores. Therefore, it is difficult to know how closely Volodchenko's specimens resemble *D. picta.* This makes the reports of *D. picta* by Volodchenko (1941: 60; 1955: 252) rather dubious.

Discodoris Bergh, 1877

Body doridiform, rather evenly rounded anteriorly and posteriorly; dorsum densely covered with numerous very small tubercles. Labial tentacles cylindro-conical. Foot broadly rounded and bilabiate anteriorly and somewhat more acutely rounded posteriorly. Rhinophores retractile, perfoliate. Branchial plumes retractile, tripinnate, arranged in a circle around anus; branchial aperture slightly crenulate, stellate, or bilabiate.

Radular formula 0.n.0.n.0, inner laterals hamate, those nearer margin less hooked.

Penis unarmed; prostate large.

Type-species: *Discodoris boholiensis* Bergh, 1877.

Remarks: Thompson (1975: 481, 487) synonymized *Diaulula* Bergh, 1880, and *Anisodoris* Bergh, 1898, with the older genus *Discodoris* Bergh, 1877, stating that *Discodoris* has hemispherical papillae and that all three genera "contain species of similar size, shape, texture, mode of life, radula and reproductive organs and must be merged, because these similarities far outweigh the differences between them (chiefly the presence of rod-like differentiations in the labial cuticle of some forms, absent in others)." However, Bergh (1877b: 518) described the dorsum of *Discodoris* as finely granulate. (. . . "die Rückenseite ist fein granulirt;") rather than bearing hemispherical papillae as stated by Thompson (1975: 487). This would seem sufficient to exclude *Anisodoris nobilis,* which has hemispherical papillae, from inclusion in the genus *Discodoris.* The type-species of *Anisodoris* [*Anisodoris punctuolata* (Orbigny, 1847)] also has hemispherical or short cone-shaped papillae on the dorsum (". . . der Rücken uberall bis an den Rand mit Kleinen, halbkugelformigen oder kurz kegelformigen Papeln bedeckt . . ." (Bergh, 1898: 509). Until specimens of the types of the genera *Discodoris* and *Anisodoris* can be compared, it seems best to maintain them as distinct genera.

In the case of *Diaulula* Bergh, 1880, it is much more difficult to differentiate from *Discodoris.* Both genera have basically the same texture of the dorsum, *Dicodoris* is described as finely granulate (Bergh, 1877b: 518) and *Diaulula* as villous (Bergh, 1880a: 189). The radular teeth of *Diaulula sandiegensis* (Cooper, 1863) have virtually the same form as *Discodoris boholiensis* (Bergh, 1877b: pl. 61, figs. 8–12), the type of the genus. Bergh (1880a: 189) states: "In their general form the *Diaululae* somewhat resemble the *Discodorides* . . ." and that "The radula nearly agrees with that of the *Discodorides* . . . ." Furthermore, *Diaulula* presently contains only about 4 species. On these bases, I agree with Thompson (1975) that *Diaulula* is a junior synonym of *Discodoris.*

The Eudoridacea contains a number of poorly defined and often small genera which further study may show should best be combined into a few broader, well defined genera.

Discodoris heathi MacFarland, 1905

Discodoris heathi MacFarland, 1905: 39–40. MacFarland, 1906: 118–119, pl. 18, figs. 12–17; pl. 23, fig. 6. O'Donoghue, 1922b: 151–152, 165, pl. 5, figs. 8–11. O'Donoghue, 1924: 23. O'Donoghue, 1926: 207. O'Donoghue, 1927b: 82, pl. 1, figs. 6–9. Hewatt, 1937: 200. Costello, 1938: 324, tabs. 2, 3, 5, pl. 1, figs. 9, 23; pl. 2, fig. 29. Smith & Gordon, 1948: 181. LaRocque, 1953: 259. Marcus, 1955: 150. Marcus, 1961: 17, 19–20, pl. 3, figs. 62–64. Lance, 1961: 66. Farmer & Collier, 1963: 62. Steinberg, 1963b: 70. MacFarland, 1966: 192–193, pl. 27, fig. 7; pl. 35, figs. 26–33. Marcus & Marcus, 1967a: 80, 82, 87, 188, 189. Farmer, 1967: 341. Sphon & Lance, 1968: 79. Turner *et al.,* 1969: 135. Thompson, 1969: 763. Roller & Long, 1969: 427. Long, 1969c: 232. Gosliner & Williams, 1970: 178. Bernard, 1970: 85. Bertsch *et al.,* 1972: 306. Gosliner & Williams, 1973b: 352. Abbott, 1974: 352, pl. 17, no. 4220. Thompson, 1975: 487. Belcik, 1975: 276. Lambert, 1976: 297–298. Bloom, 1976: 289 ff. Bertsch, 1977: 109. Nybakken, 1978: 134 ff. McDonald & Nybakken, 1978: 110, 112.

Archidoris montereyensis. Ricketts & Calvin, 1968: text fig. 86.

Type-specimens: U. S. Nat. Mus., no. 181282.

Rhinophores bear 10–16 lamellae and are light yellow to dusky yellow on shaft and clavus. Rhinophore sheaths low with a slightly sinuous margin. Branchial plumes 8–10, tripinnate, light yellow to dusky yellow, sprinkled with minute brownish flecks, rather whitish on tips. General ground color varies from light yellow to a more dusky yellow-tan or raw umber, dorsum usually darker medially. Dorsum sprinkled with numerous minute red-brown and brown to black dots, usually with a major concentration just anterior of branchial plumes. T.L.: 30 mm.

Radular formula of specimen examined 20(16–20.0.16–20), MacFarland (1966: 192) reports 20(36–42.0.36–42), and Marcus (1961: 19) reports 20–22(9–10.31.0.31.9–10), while Bloom (1976: 293) gives the range 20–22(36–42.0.36–42). Laterals (Fig. 77) strongly hooked, but become long, thin and only slightly curved near margin of radula.

Type-locality: Monterey Bay, California.

Range and habitat: Porcher Island, British Columbia, Canada (Lambert, 1976) to Bahía San Quintín, Baja California, Mexico (Farmer, 1967). Intertidal to 8 m, usually found in rocky areas, rarely found on floating docks and pilings in bays. Feeds upon the sponges: *Adocia gellindra, Halichondria panicea,* and *Myxilla incrustans* (Bloom, 1976; McDonald & Nybakken, 1978).

Remarks: Marcus (1961: 20) states that

Discodoris fulva O'Donoghue, 1924, is probably a young specimen of *D. heathi.*

Discodoris sandiegensis (Cooper, 1863)

Doris (*Actinocyclus*?) *sandiegensis* Cooper, 1863a: 204. Cooper, 1863b: 58.
Doris (?*Actinocyclus*) *sandiegensis* Cooper. Carpenter, 1864: 608.
Doris sandiegensis Cooper. Carpenter, 1864: 609. Cooper, 1867: 14. Kelsey, 1907: 39. Odhner, 1926a: 88.
Doridopsis sandiegensis (Cooper). Abraham, 1877: 240. O'Donoghue, 1922d: 143.
Diaulula sandiegiensis (Cooper). Bergh, 1878a: 567 (*lapsus*).
Diaulula sandiegensis (Cooper). Bergh, 1879a: 344. Bergh, 1879b: pl. 5, figs. 3–5. Bergh, 1879c: pl. 5, figs. 3–5. Bergh, 1880a: 189–193. Bergh, 1880b: 40–44. Bergh, 1891: 132. Bergh, 1892: 1097 (105). Bergh, 1894: 172. MacFarland, 1897: 227, 245–257, pl. 20, figs. 24–31; pl. 21, figs. 33–44; pl. 22, figs. 45–46. MacFarland, 1905: 41. MacFarland, 1906: 122–123, pl. 18, figs. 22–24; pl. 23, fig. 5. Eliot, 1907: 356. Baily, 1907: 92. Berry, 1907: 35. O'Donoghue, 1921: 159–161, pl. 1 (7), figs. 11–12. O'Donoghue, 1922a: 126. O'Donoghue & O'Donoghue, 1922: 137–138. O'Donoghue, 1922b: 163–164. O'Donoghue, 1922d: 143. O'Donoghue, 1924: 23, 29. O'Donoghue, 1926: 209. Odhner, 1926a: 88, 89. O'Donoghue, 1927a: 10. O'Donoghue, 1927b: 83–84, pl. 1, figs. 14–15. Fraser, 1932: 67. Ingram, 1935: 48, 49. Hewatt, 1937: 200. Costello, 1938: 321, 323–327 ff, tabs. 1–4; pl. 1, figs. 1, 2, 8, 12, 14, 18; pl. 2, figs. 24–25, 36–37. Hewatt, 1946: 193, 198. Smith & Gordon, 1948: 181. LaRocque, 1953: 258. Baba, 1957: 9, 13, text fig. 6. Marcus, 1959: 53. Marcus, 1961: 18–19, 57, pl. 3, figs. 59–61. Steinberg, 1961: 58. Lance, 1961: 66. Cook, 1962: 196. Paine, 1963a: 4. Steinberg, 1963b: 70. Farmer, 1963: 24. Willows, 1965: 707 ff. Lance, 1966: 69. MacFarland, 1966: 190–192, pl. 27, fig. 6; pl. 29, fig. 15; pl. 30, fig. 17; pl. 35, figs. 23–25. Hurst, 1967: 255 ff, text fig. 4a, pl. 27, fig. 6; pl. 35, fig. 40; fig. 24-17. Marcus & Marcus 1967a: 189, 238. Beeman, 1968b: 268–269. Sphon & Lance, 1968: 78. Roller & Long, 1969: 426. Turner *et al.*, 1969: 135. Bertsch, 1969: 231. Robilliard, 1969a: 290. Gosliner & Williams, 1970: 177. Bernard, 1970: 85. Michel, 1970: 7. North, 1971: 57. Keen, 1971: 825. Holleman, 1972a: 60. Bertsch *et al.*, 1972: 305–306. Sphon, 1972a: 155. Goddard, 1973: 9. Haderlie *et al.*, 1974: tab. 4. Abbott, 1974: 353, pl. 17, no. 4234. Ferreira & Bertsch, 1975: 327. Schuler, 1975: 33. Belcik, 1975: 276. Bloom, 1976: 289 ff. Elvin, 1976: 194–198. Lambert, 1976: 296. Michel, 1976: 48, fig. 12. Thompson, 1976b: 33. Behrens & Tuel, 1977: 33, 35. O'Clair, 1977: 443. Nybakken, 1978: 134 ff. McDonald & Nybakken, 1978: 113, 116. Fuhrman *et al.*, 1979: 291 ff.
Diaulula sandiegensis (Cooper) var. Bergh, 1879b: pl. 5, figs. 6–9. Bergh, 1879c: pl. 5, figs. 6–9. Bergh, 1880a: 193–195. Bergh, 1880b: 44–46. Bergh, 1894: 173–175, pl. 6, figs. 2–5.
Doris (*Diaulula*) *sandiegensis* (Cooper). Orcutt, 1885: 548.
Diaululua sandiegensis (Cooper). Kelsey 1907: 39 (*lapsus*).
Peltodoris mauritiana Bergh. Baba, 1935a: 346. Baba, 1935b: 119.
Dialulu sandiegensis (Cooper). MacGinitie & MacGinitie, 1949: 362, 379 (*lapsus*).
Dialula sandiegensis (Cooper). McLean, 1962: 111. Harris, 1973: 282, 287. Russo, 1979: 48. (*lapsus*).
Dilella sandiegagenesis. Hargens, 1977: 363 (*lapsus*).
Discodoris sandiegensis (Cooper). Bertsch, 1980: 224.
(*Non*) *Diaulula sandiegensis* var. *pallida* Bergh, 1894: 172–175, (=*Diaulula vestita* (Abraham, 1877)).

Type-specimens: not listed; Geological Survey coll. (Cooper, 1863a).

Labial tentacles small and digitiform. Rhinophores bear 12–30 lamellae, and are ochre to raw umber. Branchial plumes 6–7, grayish-white to dusky with whitish tips. General ground color varies from almost white to chocolate brown, but is most commonly pale cream to raw umber; dorsum marked with brown to almost black rings or occasionally irregular blotches of various sizes, number, and position. Most commonly these rings are arranged in 2 longitudinal rows, one on either side of median line, 3–4 in each row, but this is highly variable, especially in specimens from the northern part of the range. One specimen which was collected lacked rings or blotches. Specimens from slough or bay areas are typically darker than specimens from open coast areas. T.L.: 25 mm, but specimens up to 150 mm have been collected from Elkhorn Slough, Monterey Co., California.

Radular formula of specimen examined 13(29–31.0.29–31), MacFarland (1966: 191) reports 19–22(26–30.0.26–30), and Marcus (1961: 19) reports 19–23(25–34.0.25–34). Laterals (Fig. 74) hamate.

Type-locality: San Diego Bay, California.

Range and habitat: Unalaska, Alaska (Bergh, 1894), to Cabo San Lucas, Baja California, Mexico (Lance, 1961); Japan (Baba, 1957). Intertidal to 37 m, commonly found in rocky intertidal, occasional in sloughs and sometimes found on pilings and docks in bays. Bloom (1976: 195) reports that it is found in association with and probably feeds upon the sponges: *Halichondria panicea, Haliclona permollis, Myxilla incrustans,* and *Petrosia dura.* McDonald and Nybakken (1978: 116) report it from *Halichondria bowerbanki.* Cook (1962: 196) states that in the laboratory it was observed feeding upon *Haliclona* sp.; Elvin (1976) reports that it feeds upon *Haliclona permollis.*

Doridella Verrill, 1870

Body elliptical in outline, quite depressed and flattened, dorsum entirely smooth and extends well beyond foot. No postero-median notch in margin of dorsum such as occurs in *Corambe.* Labial tentacles short and tapered. Rhinophores retractile, smooth or with a few vertical lamellae. Branchial plumes unipinnate or ridge-like, arise posteriorly from ventral surface of dorsum on either side of median anus.

Radular formula n.1.0.1.n, laterals large, with denticles below cusp; marginals smaller and may bear small denticles.

Penis unarmed.

Type-species: *Doridella obscura* Verrill, 1870.

Doridella steinbergae (Lance, 1962)

Corambella sp. Steinberg, 1960: 49. Lance, 1961: 67.

Corambella steinbergae Lance, 1962b: 35–38, pl. 1, text figs. 6–10. Steinberg, 1963b: 71. Sphon & Lance, 1968: 77. McBeth, 1968: 145–146. Gosliner, 1968: 147. Thompson, 1976a: 36, pl. 4, fig. c.

Corambella bolini MacFarland, 1966: 133, 134–139, pl. 22, figs. 9–11; pl. 29, fig. 21; pl. 32, figs. 1–12. Sphon & Lance, 1968: 77. Roller, 1970a: 371.

Doridella steinbergae (Lance). Franz, 1967: 75. Marcus & Marcus, 1967b: 208, 209. Roller & Long, 1969: 427. Roller, 1970a: 371. Gosliner & Williams, 1970: 178. Bernard, 1970: 84. Anderson, 1972: 19. Abbott, 1974: 365. Thompson, 1976b: 48. Seed, 1976: 1 ff. McDonald & Nybakken, 1978: 111. Bickell & Chia, 1979a: 291 ff. Bickell & Chia, 1979b: 957.

Type-specimens: Calif. Acad. Sci., Paleo. type coll. no. 12′404.

Anterior margin of foot bluntly rounded or only slightly emarginate. Labial tentacles short, slender, and tapered distally. Rhinophores smooth and tapered to blunt tips, translucent grayish-white, retractile into rather high sheaths with thin, entire margins. Branchial plumes 2–4, translucent grayish-white; larger, innermost plumes consist of a rather triangular stalk which bears 3–4 small lamellae, outermost plumes bear fewer or no lamellae. General ground color translucent grayish-white. Dorsum with approximately 7–10 broken, irregular, longitudinal, opaque white lines which are borne upon ridges medially; marginally dorsum bears similar lines which are shorter, more broken and more irregular. Between these lines are scattered small, irregular blotches of reddish-brown. In all, the color pattern quite resembles the colonies of *Membranipora* upon which the animal is most often found. T.L.: 5 mm.

Radular formula of specimen examined 31(4–5.1.0.1.4–5), MacFarland (1966: 135) reports 40–60(5.1.0.1.5). Laterals (Fig. 38f) largest, bearing 3–8 denticles. Marginals (Fig. 38b–e) smaller with minute denticles, outermost marginals (Fig. 38a) smallest and nondenticulate.

Type-locality: San Diego, San Diego Co., California.

Range and habitat: British Columbia, Canada (50° N latitude) (Bernard, 1970), to Islas Coronados, Baja California, Mexico (Lance, 1961). Intertidal and subtidal, almost always found on the brown alga *Macrocystis pyrifera,* where it feeds upon an encrusting bryozoan of the genus *Membranipora* (McBeth, 1968: 145); Lance (1962b: 38) states that it feeds upon *Membranipora serrilamella.*

Doris Linnaeus, 1758

Body doridiform, rather evenly rounded anteriorly and posteriorly; dorsum tuberculate. Labial tentacles short and digitiform. Rhinophores perfoliate, retractile into sheaths with tuberculate margins. Branchial plumes retractile, arranged in circle around anus.

Radular formula 0.n.0.n.0, laterals hamate.

Penis acrembolic, no glans penis; vas deferens widened to a prostatic canal.

Type-species: *Doris verrucosa* Linnaeus, 1758.

Doris (s.l.) sp. MacFarland, 1966

Doris (s.l.) species MacFarland, 1966: 179–181, pl. 25, figs. 1–6. Sphon & Lance, 1968: 79.

Material upon which MacFarland based his description is at Calif. Acad. Sci.

Dorsum densely covered with numerous small papillae, giving dorsum a velvety or villous appearance. Dorsal papillae each encircled by a row of vertical spicules. Foot elongate, elliptical and bilabiate anteriorly, upper lip notched medially. Labial tentacles slender and pointed distally. Rhinophores bear 8–18 lamellae, and are white to cream. Branchial plumes 6, tripinnate, white or cream, tipped with light brownish. General ground color off white to cream tan, dorsum bears a number of large, irregularly oval, light brown spots and numerous flecks of same color; numerous minute, opaque white flecks occur on margin of dorsum, forming a diffuse band. T.L.: 25 mm.

Radular formula of specimen examined 16(22–23.0.22–23). Laterals (Fig. 73) are hamate.

Type-locality: Newport Bay, Orange Co., California.

Range and habitat: Pescadero Point, Monterey Co., California (personal observation), to Newport Bay, Orange Co., California (MacFarland, 1966). Intertidal to 6 m in rocky areas, occasionally found upon the sponge *Dysidea amblia* upon which it may feed. A relatively rare species in California.

Remarks: This rather enigmatical species in many respects (viz. radular teeth, dorsal papillae, and coloration) resembles *Discodoris sandiegensis,* and may well be conspecific with it. The coloration and radula are also much like that of the widely distributed species *Jorunna tomentosa* (Cuvier, 1804), with which it may possibly be synonymous. More extensive study is necessary to determine the position of *Doris* (s.l.) sp.

Doto Oken, 1815

Body limaciform and highly arched. Foot narrow, linear, rounded anteriorly and tapered posteriorly to short, blunt tail; anterior foot corners rounded and not produced. Cerata bulbous, tuberculate, rather club-shaped, arranged in dorso-lateral series on either side of dorsum; the larger, anterior pairs bear a plume-like "gill" on their inner surface. Cerata lack cnidosacs and are deciduous. Oral tentacles as such are absent; in their place is a rounded frontal veil. Rhinophores smooth and bluntly tapered, retractile into calyciform rhinophore sheaths.

Masticatory border of thin mandibles smooth. Radula uniseriate, with numerous teeth which are somewhat asymmetrical and bear a few denticles.

Penis unarmed. Anus on right side, in line of cerata.

Type-species: *Doto coronata* (Gmelin, 1791).

See ICZN (1964, Opinion 697) for validation of generic name and designation of type-species.

Doto amyra Marcus, 1961

Doto amyra Marcus, 1961: 38, pl. 7, figs. 130–134. Steinberg, 1963a: 65. Steinberg, 1963b: 71. Marcus & Marcus, 1967a: 214, 238. Sphon & Lance, 1968: 79. Schmekel, 1968b: 6. Long, 1969c: 232. Gosliner & Williams, 1970: 178. Schmekel, 1970: 184. Keen, 1971: 832. Thompson, 1972a: 75. Nybakken, 1974: 371. Abbott, 1974: 371. McDonald & Nybakken, 1978: 113.

Doto ganda Marcus, 1961: 39, 57, pl. 7, figs. 135–138. Farmer & Collier, 1963: 63. Schmekel, 1970: 184. Abbott, 1974: 371.

Doto wara Marcus, 1961: 40–41, 57, pl. 8, figs. 143–146. Schmekel, 1970: 184. Thompson, 1972a: 75. Abbott, 1974: 371.

Doto amyra ? Marcus. Roller & Long, 1969: 427.

Doto gauda Marcus. Thompson, 1972a: 75 (*lapsus*).

Type-specimens: Dept. Zool., Univ. São Paulo, Brazil.

Frontal veil smooth, rounded, and slightly laterally expanded, with an entire margin. Rhinophore sheaths have rather smooth margins. Rhinophores and sheaths both pigmented distally with numerous small, opaque white dots. The 5–7 opposite pairs of cerata bear numerous rather long, well spaced tubercles which occur in 3–7 rings around each ceras. General ground color translucent cream-white. Cerata cores vary from cream to pink, yellow, or light orange. T.L.: 8 mm.

Anus on a high papilla on right, in line of cerata, near second ceras. Genital aperture on right side, just ventral of first ceras.

Radular formula of specimen examined 87(0.0.1.0.0), Marcus (1961: 38) reports about 70 teeth on radula. Rachidian teeth (Fig. 83) asymmetrical, usually with 1–3 denticles on either side of median denticle.

Type-locality: Monterey Bay, California.

Range and habitat: Dillon Beach, Marin Co., California (Marcus, 1961), to Ensenada, Baja California, Mexico (Farmer & Collier, 1963). A single specimen has been reported from Puerto Penasco, Sonora, Mexico (Marcus, 1967a: 214). Intertidal and subtidal, frequently found on the hydroids: *Aglaophenia struthionides* and *Sertularia furcata* upon which it may feed; Marcus (1961: 39) found one specimen on *Obelia*.

Doto columbiana O'Donoghue, 1921

Doto columbiana O'Donoghue, 1921: 204–205, pl. 3 (9), fig. 33. O'Donoghue, 1926: 235. Odhner, 1936: 1119. Marcus, 1961: 36–38 ff, pl. 7 figs. 125–129. Steinberg, 1963b: 71. MacFarland, 1966: 288–289, 295. Gosliner & Williams, 1970: 178. Bernard, 1970: 85. Schmekel, 1970: 184. Marcus, 1972b: 303. Abbott, 1974: 371. Belcik, 1975: 276. Lambert, 1976: 297, 298.

Idulia columbiana (O'Donoghue). O'Donoghue, 1926: 235. LaRocque, 1953: 251.

Type-specimens: Mus. Dominion Biol. Stat., Nanaimo, British Columbia, Canada.

Frontal veil rounded and slightly laterally expanded, with a few small tubercles dorsally and an entire margin. Rhinophore sheaths have smooth margins. Rhinophores and sheaths translucent grayish-white. The 5–7 opposite pairs of cerata bear numerous short, flat tubercles which occur in 4–5 rings around each ceras. General ground color translucent grayish-white to pale grayish-yellow. Irregular, scattered lines of black occur on dorsum and sides of body. Tubercles on cerata each bear a black ring at their base. T.L.: 10 mm.

Anus on right, just anterior of second ceras. Genital aperture on right side, just ventral of first ceras.

Marcus (1961: 37) gives the radular formula 83(0.0.1.0.0), and MacFarland (1966: 288–289) reports 86–96(0.0.1.0.0). Rachidian teeth (Fig. 84) asymmetrical, usually with 3–5 denticles on either side of median denticle.

Type-locality: Nanoose Bay, Vancouver Island, British Columbia, Canada.

Range and habitat: Pearse Island, British Columbia, Canada (Lambert, 1976), to Duxbury Reef, Marin Co., California (Gosliner & Williams, 1970). Intertidal to 60 m, usually found on hydroids.

Doto kya Marcus, 1961

Dota kya Marcus, 1961: 39–40, pl. 8, figs. 139–142. Steinberg, 1963b: 71. Haderlie, 1968: 333, 339. Schmekel, 1968b: 6. Haderlie, 1969: tabs. 1–2. Roller & Long, 1969: 427. Roller, 1970a: 372. Schmekel, 1970: 184. Thompson, 1972a: 75. Bertsch *et al.*, 1972: 306. Nybakken, 1974: 371. Abbott, 1974: 371.

Doto varians MacFarland, 1966: 288, 289–295, pl. 42, figs. 1–8: pl. 44, figs. 8–17; pl. 48, figs. 9–13 (*partim*). Roller, 1970a: 372–373. Bernard, 1970: 85. Schmekel, 1970: 184. Abbott, 1974: 371.

Type-specimens: Dept. Zool., Univ. São Paulo, Brazil.

Frontal veil smooth and slightly laterally expanded, margin entire. Rhinophore sheaths have scalloped margins which are slightly expanded anteriorly. Rhinophores and sheaths both bear numerous, small, opaque white dots distally. The usually 8, opposite pairs of cerata bear numerous ovoid tubercles which occur in 4–5 rings around each ceras. General ground color translucent yellowish white. Dorsum, sides of body, and cerata bear numerous brownish-black spots and blotches. Cerata cores usually brownish. T.L.: 8 mm.

Anus on right, just anterior of second ceras. Genital aperture on right side, ventral of first ceras.

Radular formula of specimen examined 61(0.0.1.0.0), Marcus (1961: 40) reports 95(0.0.1.0.0). Rachidian teeth (Fig. 85) asymmetrical, usually with 2–3 denticles on either side of median denticle.

Type-locality: Point Pinos, Monterey Bay, California.

Range and habitat: Duxbury Reef, Marin Co., California (Gosliner & Williams, 1970), to Shell Beach, San Luis Obispo Co., California (Roller & Long, 1969). Intertidal and subtidal, usually found upon the hydroid *Aglaophenia struthionides* upon which it may feed.

Remarks: The species of the genus *Doto* found along the California coast are presently quite confused. Marcus (1961: 38–41) named four new species of *Doto* (*D. amyra, D. ganda, D. kya,* and *D. wara*) from California. While further study is necessary, I recognize only *D. amyra* and *D. kya* and consider *D. ganda* and *D. wara* synonyms of *D. amyra.* MacFarland (1966: 289–295) named *Doto varians* which appears to be, in part at least, a junior synonym of *D. kya,* and also possibly of *D. amyra.* A detailed study of the California species of *Doto* is needed to clearly define and differentiate the species of the genus found in California. Preliminary evidence from development and larval morphology seems to indicate that there are more valid species of *Doto* in California than are accepted in this paper. However, no clearly defined morphological differences have yet been observed which will clearly distinguish more than the three species herein recognized.

Eubranchus Forbes, 1838

Body aeolidiform, rather high and narrow. Foot narrow, linear, and elongate, tapered posteriorly to tail; anterior foot corners usually rounded and not produced, but at least one species (*E. misakiensis*) has produced foot corners. Cerata long, cylindrical, somewhat clavate, and rather irregularly inflated. Oral tentacles cylindrical and tapered slightly to blunt tips. Rhinophores non-retractile, long, smooth, and tapered slightly to blunt tips.

Masticatory border of mandibles denticulate. Radula triseriate, rachidian teeth bear a few denticles on either side of median cusp; laterals rather thin, with a single, non-denticulate cusp.

Penis armed with a chitinous stylet in most species. Anus acleioproct.

Type-species: *Eubranchus tricolor* Forbes, 1838.

See ICZN (1966b, Opinion 774), *Eubranchus* placed on Official List.

Eubranchus misakiensis Baba, 1960

Eubranchus misakiensis Baba, 1960b: 300–301, pl. 34, figs. 2a–g. Hamatani, 1961: 353, 358–361, text figs. 5–8. Baba, 1964: 287. Burn, 1964: 14. Thompson, 1967: 9. Edmunds & Kress, 1969: 907. Behrens, 1971b: 214–215. Baba, 1971: 63–64, 66, pl. 6, figs. 1–6. Behrens & Tuel, 1977: 33, 35. Clark & Goetzfried, 1978: 290.

Type-specimens: Biol. Lab., Imperial Palace, Japan.

Foot corners produced into rather long, tentaculiform processes. Oral tentacles colored as rhinophores but usually bear only 0–1 chocolate brown bands. Rhinophores translucent yellowish-white, with a number of small, chocolate brown dots which may be concentrated into 2–3 bands. Cerata arranged in about 6 oblique rows dorso-laterally on either side of dorsum. General ground color translucent yellowish-white. Dorsum, sides of body, and cerata bear numerous small, round, chocolate brown dots. Cerata bear yellow to brown subapical ring, cores bluish-green. T.L.: 5 mm.

Anus just anterior of third group of cerata, slightly to right of midline. Genital aperture on right side, just ventral and posterior of first group of cerata. Penis unarmed.

Radular formula of specimen examined 46(0.1.1.1.0), Baba (1960b: 301) reports 40(0.1.1.1.0). Rachidian teeth (Fig. 105a) bear 3–4 denticles on either side of median cusp. Laterals (Fig. 105b) rather thin plates with a single, triangular cusp. Masticatory border of mandibles bears a single row of about 15 denticles.

Type-locality: Misaki, Sagami Bay, Japan.

Range and habitat: Introduced into San Francisco Bay, California (Behrens, 1971b); originally described from Japan. Most often on floating docks and pilings in bays, rather rare in California.

Eubranchus olivaceus (O'Donoghue, 1922)

Galvina olivacea O'Donoghue, 1922b: 158–160, 165, pl. 6, figs. 21–22.

Eubranchus olivaceus (O'Donoghue). O'Donoghue & O'Donoghue, 1922: 135, pl. 4, fig. 7. O'Donoghue, 1924: 25–26. O'Donoghue, 1926: 230. LaRocque, 1953: 251. Steinberg, 1963b: 72. Hurst, 1967: 255 ff, text fig. 20; pl. 32, fig. 26; pl. 38, fig. 51; fig. 25-3. Edmunds & Kress, 1969: 907. Bernard, 1970: 86. Nybakken, 1974: 371. Abbott, 1974: 375. Lambert, 1976: 298. Rivest & Harris, 1976: 146–147. Thompson, 1976a: 79, text fig. 38g. McDonald & Nybakken, 1978: 114.

Type-specimens: not listed.

Foot corners rounded, not produced. Oral tentacles colored as, and shorter than rhinophores. Rhinophores translucent yellow-white with a subterminal band of brownish to olivaceous-green, and encrusted with white dots which are more concentrated distally, Cerata arranged in about 4–7 indistinct groups on dorsum. First group contains about 4–6 cerata, posterior of first group, cerata are nearly alternately arranged. General ground color pale translucent yellow-green to yellow-white. An irregular network of reddish-brown lines occurs on dorsum, along with a faint, irregular, dorso-medial band of olive green. A few opaque white dots occur on head and dorsal surface of tail. Cerata slightly frosted with white and bear an indistinct, subterminal band of reddish-brown to olivaceous-green, cores deep olivaceous green. T.L.: 8 mm.

Radular formula of specimen examined 35(0.1.1.1.0), O'Donoghue (1922b: 159) reports 32–33(0.1.1.1.0). Rachidian teeth (Fig. 106a) bear 5–6 denticles on either side of median cusp. Laterals (Fig. 106b) rather thin plates with a single triangular cusp. Masticatory border of mandibles finely denticulate.

Anus just anterior of third group of cerata, slightly to right of midline. Genital aperture on right side, postero-ventral of first group of cerata.

Type-locality: Jesse Island, Vancouver Island, British Columbia, Canada.

Range and habitat: Vancouver Island, British Columbia, Canada (O'Donoghue, 1922b), to Asilomar Beach, Pacific Grove, Monterey Co., California (Nybakken, 1974: personal observation). Intertidal to 10 m. Rare in rocky intertidal zone in California. O'Donoghue (1922b: 159) states that it is usually found on the hydroid *Obelia longissima* growing at the base of *Zostera marina*. Although Sphon (1972b: 64) gives the geographic range of *E. olivaceus* as Bamfield, British Columbia, Canada, to Bahía de los Ángeles, Baja California, Mexico, this is the range of *Eubranchus rustyus* (Robilliard, 1971a; Lance, 1961). Since *E. rustyus* is not included in Sphon's (1972b) list of nudibranchs of the west coast of North America and it is reported elsewhere in the literature to occur south of Asilomar Beach, Monterey Co., California, it seems certain that *E. rustyus* and *E. olivaceus* were inadvertently combined into a single entry using the name of the latter and the range of the former in Sphon's list.

Remarks: Meyer (1971: 147–148) reported *E. olivaceus* from Maine. However, Rivest & Harris (1976: 146–147) suggest that she collected *Eubranchus exiguus* (Alder & Hancock, 1848) rather than *E. olivaceus*.

Eubranchus rustyus (Marcus, 1961)

Capellinia rustya Marcus, 1961: 49–50, 57, pl. 9, figs. 168–172. Lance, 1961: 68. Steinberg, 1963b: 72. Paine, 1963a: 4. Lance, 1966: 69. Sphon & Lance, 1968: 82. Roller & Long, 1969: 426. Roller, 1970a: 372. Abbott, 1974: 375.

Eubranchus occidentalis MacFarland, 1966: 323–326, pl. 62, fig. 7; pl. 65, figs. 19–25; pl. 66, fig. 7. Roller, 1970a: 372.

Eubranchus rustyus (Marcus). Edmunds & Kress, 1969: 907. Gosliner & Williams, 1970: 178. Robilliard, 1971a: 163, 165. Keen, 1971: 837. Bertsch *et al.*, 1972: 306. Nybakken, 1974: 371. Keen & Coan, 1975: 45. Lambert, 1976: 298. McDonald & Nybakken, 1978: 114.

Eubranchus (=*Capellinia*) *rustyus* (Marcus). Robilliard, 1971a: 163–164.

Type-specimens: Dept. Zool., Univ. São Paulo, Brazil.

Foot corners rounded, not produced. Oral tentacles just over one half the length of the rhinophores; colored as rhinophores with a similar subapical band. Rhinophores a light shade of body color with translucent whitish tips and a subapical band of brownish to light gray or greenish, and a few small, irregular spots of the same color. Cerata may bear tubercles, and are arranged in 4–6 groups on either side of dorsum, with 2–6 cerata in each group. General ground color varies from grayish-white to light cream or yellowish to a light brownish-yellow, numerous irregular specks of brownish to light gray or greenish over body and on cerata. Cerata each bear a diffuse, subapical band of brownish to light gray or greenish, and whitish tip; cores vary from yellowish-green to brown. T.L.: 8 mm.

Anus just posterior of second group of cerata, slightly to right of midline. Genital aperture on right side, just ventral of first group of cerata. Penis armed with a chitinous stylet.

Radular formula of specimen examined 59(0.1.1.1.0), Marcus (1961: 49) reports 50–60(0.1.1.1.0), and MacFarland (1966: 324) reports 58–62(0.1.1.1.0). Rachidian teeth (Fig. 107a) bear 3–5 denticles on either side of median cusp. Laterals (Fig. 107b) are rather thin plates with a single, triangular cusp. Masticatory border of mandibles bears a single row of about 10 transverse, ridge-like denticles which may bear 12–20 small denticulations.

Type-locality: Monterey Bay, California.

Range and habitat: Vancouver Island, British Columbia, Canada (Robilliard, 1971a), to Punta Abreojos, Baja California, Mexico (Keen, 1971); Bahía de los Angeles, Gulf of California, Mexico (Lance, 1961). Intertidal and subtidal, most common on floating docks in bays, where it is usually found on the hydroids *Obelia* spp. Occasionally found in rocky intertidal. It has been found on the hydroids: *Obelia* sp., *Plumularia lagenifera,* and on *Hydractinia* sp. at the base of the alga *Cystoseira osmundacea* (MacFarland, 1966; Marcus, 1961; Robilliard, 1971a).

Fiona Alder & Hancock, 1855

Body aeolidiform, elongate, and broadest medially. Foot rounded anteriorly and tapered posteriorly to rather long tail, margins thin and extend laterally well beyond body. Anterior foot corners rounded, not produced. Cerata cylindrical and tapered, the majority bear a thin, sail-like expansion on proximal three quarters of posterior surface; cnidosacs present. Oral tentacles cylindrical and tapered to blunt tips. Rhinophores non-retractile and smooth.

Masticatory border of mandibles denticulate. Radula uniseriate, with denticles on either side of median cusp.

Penis unarmed. Anus acleioproct.

Type-species: *Fiona pinnata* (Eschscholtz, 1831).

Fiona pinnata (Eschscholtz, 1831)

Limax marinus Forskål, 1775: 99. Cuvier, 1817: 25. O'Donoghue, 1922d: 145. Lemche, 1964a: 37. (*Non*) Gunnerus, 1770: 170.

Doris fasiculata Gmelin in Linnaeus, 1791: 3104. (*Non*) Müller, 1776: 229, no. 2772.

Eolis fasciculata. Lamarck, 1819: 302.

Eolis leuconotus Hasselt in Férussac, 1824a: 82.

Eolidia alba Hasselt in Férussac, 1824b: 239. O'Donoghue, 1922d: 145.

Eolidia fasciculata. Bruguière & Lamarck, 1830: 115.

Eolidia pinnata Eschscholtz, 1831: 14, pl. 19, fig. 1. Carpenter, 1857: 173. O'Donoghue, 1922d: 145.

Eolidia longicauda Quoy & Gaimard, 1832: 288–290, pl. 21, figs. 19–20. Finlay, 1927: 441.

Oithona nobilis Alder & Hancock in Forbes & Hanley, 1851a: 589. Alder & Hancock, 1851b: 291. Hancock, 1852: 74. Chenu, 1859: 413, fig. 3078. O'Donoghue, 1922d: 145. Pruvot-Fol, 1927: 45.

Fiona nobilis (Alder & Hancock). Adams & Adams, 1854: 77, pl. 67, fig. 1. Alder & Hancock, 1855: 31, 32, 53, fam. 3, pl. 38a, app. 23. Gosse, 1856: 100. Gray, 1857: 227. Bergh, 1859: 8–9. Jeffreys, 1869: 35, pl. 2, fig. 2. Verrill, 1881: 300. Verrill, 1882a: 339. Verrill, 1882b: 551–552. Locard, 1886: 52. Tempere, 1900: 116. Vayssière, 1901: 305. Grosvenor, 1903: 470. Pruvot-Fol, 1927: 45. White, 1938: 16.

Aeolis pinnata (Eschscholtz). Carpenter, 1857: 313.

Fiona atlantica Bergh, 1858: 273–337, pls. 2–3. Bergh, 1859: 9–16, pl. 1, figs. 1–29; pl. 2, figs. 30–53. Bergh, 1871: 1287–1288, pl. 13, fig. 8. O'Donoghue, 1922d: 145. Pruvot-Fol, 1927: 45.

Fiona longicauda (Quoy & Gaimard). Bergh, 1859: 16–18. Bergh, 1892: 1035 (43). Bergh, 1894: 130. Simroth, 1895: 184.

Hymenaeolis elegantissima Costa, 1867: 29–30, pl. 1, figs. 1–3. O'Donoghue, 1922d: 145. Iredale & O'Donoghue, 1923: 231.

Fiona pinnata (Eschscholtz). Bergh, 1859: 3. Bergh, 1873a: 606–610, pl. 8, figs. 2–11; pl. 9, fig. 13. Bergh, 1873b: 87, pl. 12, fig. 45. Bergh, 1892: 1035 (43). Bergh, 1894: 130. Iredale & O'Donoghue, 1923: 212–213. O'Donoghue, 1926: 234. Finlay, 1927: 441. Pruvot-Fol, 1927: 45. O'Donoghue, 1929: 754. Winckworth, 1932: 237. Johnson, 1934: 155–156. Baba, 1937a: 197, 200. Baba, 1937b: 333. Graham, 1938: 300. White, 1938: 16, 18. Smith & Gordon, 1948: 181. Baba, 1949: 101, 176, pl. 43, fig. 149. Tokioka, 1952: 13–14, text figs. 1–8. Baba & Hamatani, 1952: 9. LaRocque, 1953: 251. Graham, 1955: 153. Haefelfinger, 1960: 341. Marcus, 1961: 50, 56, pl. 10, figs. 173–179. Lance, 1961: 68. Steinberg, 1963b: 72. Bayer, 1963: 460–465, figs. 5–7. Thompson, 1964: 277 ff. Bennett, 1966: 46, pl. 11, fig. 2; pl. 12, figs. 1–2. Edmunds, 1966: 31 ff. Bieri, 1966: 166, 168. MacFarland, 1966: 355–358, pl. 68, figs. 23–28; pl. 70, figs. 11–11a, 12, 12-1′. 12-2′. Burn, 1966: 24. Burn, 1967a: 116–117, figs. 1–2. Marcus & Marcus, 1967a: 109, 124. Marcus & Marcus, 1967b: 216. Rees, 1967: 218. Sphon & Lance, 1968: 79. Schmekel, 1968a: 121, 147. Schmekel, 1968b: 5. Roller & Long, 1969: 429. Gosliner & Williams, 1970: 178. Edmunds, 1970: 54, 55. Bernard, 1970: 86. Schmekel, 1970: 136, 169–170, text figs.

32–33. Keen, 1971: 837. Harris, 1971a: 84. Schmekel, 1971: 123. Zeiller & Compton, 1971: 377. Holleman, 1972b: 142–146, text fig. 5. McBeth, 1972a: 55. Salvini-Plawen, 1972: 388, 392. Abbott, 1974: 377. Bingham & Albertson, 1974: 220, 223. Edmunds, 1975: 269. Ros, 1975: 340, 358. Thompson & Brown, 1976: 192, fig. 104. Thompson, 1976a: 35. Thompson, 1976b: 51, 67. Marcus, 1977: 14. McDonald & Nybakken, 1978: 115. Ros, 1978a: 153 ff. Ros, 1978b: 25 ff. Bertsch, 1979a: 58.

Eolis armoricana Hesse, 1872: 347.

Fiona marina var. *pacifica* Bergh, 1879b: 86–88, pl. 1, figs. 7–8. Bergh, 1879c: 142–144, pl. 1, figs. 7–8. Bergh, 1894: 130–132, pl. 1, figs. 13–15. O'Donoghue, 1922d: 145. Marcus, 1959: 89. MacFarland, 1966: 355.

Fiona elegantissima (Costa). Tiberi, 1880: 236.

Cratena plicata Hutton, 1882: 166, pl. 6, fig. 1.

Fiona marina (Forskål). Bergh, 1877c: 823–824. Bergh, 1884a: 9–10, pl. 11, fig. 1. Fischer, 1887: 541. Herdman & Clubb, 1889: 225, 235. Carus, 1889–1893: 215. Bergh, 1892: 1035 (43). Herdman & Clubb, 1892: 146. Bergh, 1894: 130. Simroth, 1895: 165, 184. Herdman, 1896: 49. Herdman *et al.*, 1896: 446. Tregelles, 1896: 223. Bergh, 1898: 560–561. Cooke, 1899: 65. Bergh, 1900: 239. Conchol. Soc., 1901: 25. Casteel, 1904a: 325–405, pls. 21–35. Casteel, 1904b: 505. Eliot, 1910: 5, 166. Eliot, 1913: 44–45. Sumner *et al.*, 1913: 706. Johnson, 1915: 168. Scott, 1922: 49. O'Donoghue, 1922d: 145–147. Finlay, 1927: 441. Pruvot-Fol, 1927: 45. Issel, 1928: 3–7. Russell, 1929: 219 ff, pl. 7. Kropp, 1931: 120. White, 1938: 18. Marcus, 1959: 93. Thompson, 1961: 237. Burn, 1962: 106. MacFarland, 1966: 355. Franz, 1975b: 250.

Fiona alba (Hasselt). Bergh, 1892: 1035 (43). Simroth, 1895: 184.

Fiona ? *alba* (Hasselt). Bergh, 1894: 130.

Fiona primata (Eschscholtz). Simroth, 1895: 184 (*lapsus*).

Cratena ? spec. ? Simroth, 1895: 170–171, pl. 20, figs. 11–22.

Cratena longicauda Heinke, 1897: 249, text fig. 4.

Aeolis longicauda Quoy & Gaimard. O'Donoghue, 1922d: 145.

Dolicheolis longicauda (Quoy & Gaimard). Finlay, 1927: 441.

Aeolis. Savilov, 1956: pl. fig. 5, text fig. 8.

Fiona. Bieri, 1970: 305.

Fione pinnata. Thiriot-Quiévreux, 1977: 178 (*lapsus*).

Type-specimens: not listed.

Oral tentacles about same length as rhinophores and colored as body. Rhinophores rather long with blunt tips, translucent grayish-white to cream. Cerata borne upon thin, marginal expansion of dorsum, with 4–6 or more cerata in each transverse row. General ground color translucent grayish-white; body varies somewhat from pale cream to rather pale raw umber, with a slight pinkish cast between and anterior of rhinophores. Cerata colored as body, cores vary from brown to raw umber; or bluish-purple in specimens which have been feeding upon *Velella velella*. T.L.: 20 mm.

Anus medial, slightly anterior of middle of body. Genital aperture on right side, well forward and ventral of area between oral tentacles and rhinophores.

Radular formula of specimen examined 35(0.0.1.0.0), MacFarland (1966: 356) reports 40(0.0.1.0.0), and Marcus (1961: 50) reports 36–40(0.0.1.0.0). Rachidian teeth (Fig. 112) bear 5–7 small denticles on either side of large, median cusp. Masticatory border of mandibles bears one row of round to crescent-shaped denticles.

Type-locality: Sitka, Alaska.

Range and habitat: Nearly cosmopolitan (Lance, 1961), pelagic on floating objects, especially on logs with the barnacles *Lepas* spp. Feeds upon the barnacles: *Lepas anatifera*, *Lepas anserifera*, and *Lepas* sp., and upon the chondrophorans: *Porpita* sp. and *Velella velella* (Bergh, 1880b; Bieri, 1966; Burn, 1966; Eliot, 1910; Kropp, 1931; Marcus, 1961; McDonald & Nybakken, 1978; Rees, 1967; Savilov, 1956; Schmekel, 1968a; Thompson & Brown, 1976). Kropp (1931: 121) also mentions that it feeds upon small jellyfishes and crustaceans when it occurs in the intertidal.

Hallaxa Eliot, 1909

Body doridiform, rather evenly rounded anteriorly and posteriorly; dorsum may be smooth or tuberculate. Labial tentacles short and somewhat variable in form. Rhinophores perfoliate, retractile into sheaths. Branchial plumes unipinnate, retractile, arranged in a circle around anus.

Labial disc bears spines. Radular formula n.1.1.1.n, rachidian teeth large and bear a large cusp and a few smaller denticles below. Marginals bear denticles below cusp.

Penis unarmed.

Type-species: *Hallaxa decorata* (Bergh, 1878).

Eliot (1909) proposed *Hallaxa* to replace *Halla* Bergh (1878a), the latter being preoccupied.

Hallaxa chani Gosliner & Williams, 1975

Hallaxa sp. McDonald, 1975a: 529, 540.
Hallaxa chani Gosliner & Williams, 1975: 396–405, text figs. 1–10. Nybakken, 1978: 135. McDonald & Nybakken, 1978: 110, 112. Bertsch, 1980: 222. Jaeckle, 1981: 240.

Type-specimens: Calif. Acad. Sci., no. 674.

Dorsum covered with numerous tubercles which are larger and more numerous near margin. Foot relatively narrow and elongate, anterior corners slightly extended laterally, bluntly rounded posteriorly. Rhinophores bear 8–12 lamellae, and are pale yellow with brownish-maroon distally. Branchial plumes 12–14, translucent yellowish-white with small reddish-maroon spots near base of each plume. General ground color light lemon yellow, varying from dull grayish-yellow in small specimens to richer yellow in larger specimens. Dorsum bears numerous reddish-brown flecks of various sizes, and is somewhat darker medially; an irregular series of larger, dark brown spots occurs medially, anterior of branchial plumes. Some specimens bear a thin, marginal band of golden-brown on dorsum. T.L.: 15 mm.

Radular formula of specimen examined 45(6–18.1.1.1.6–18), Gosliner & Williams (1975: 401) report 35–36(7–14.1.1.1.7–14). Rachidian teeth small and vestigial. Laterals (Fig. 63a) each bear one large cusp and 3–5 small, blunt denticles. Marginals (Fig. 63b–e) have 5–9 small denticles below cusp.

Type-locality: Duxbury Reef, Marin Co., California.

Range and habitat: Abalone Beach, Humboldt Co., California (Jaeckle, 1981), to Shell Beach, San Luis Obispo Co., California (Gosliner & Williams, 1975). Most individuals have been found in rocky intertidal zone, but it is also occasionally found on floating docks and pilings in bays. Feeds upon the ascidian *Didemnum carnulentum* (McDonald & Nybakken, 1978).

Hancockia Gosse, 1877

Body rather limaciform, somewhat elongate, and compressed. Cerata digitate lobes, arranged dorso-laterally on either side of dorsum. Oral tentacles as such are absent; frontal veil prolonged into digitate lobes. Clavi of rhinophores perfoliate and retractile into sheaths on rhinophore shafts.

Labial disc armed with small rodlets. Masticatory border of mandibles denticulate. Radula triseriate. Rachidian teeth bear a few denticles on either side of median cusp. Laterals somewhat rectangular plates with a single cusp.

Anus located between first and second cerata on right side. Penis unarmed.

Type-species: *Hancockia eudactylota* Gosse, 1877.

Hancockia californica MacFarland, 1923

Hancockia californica MacFarland, 1923: 65–104, pls. 1–6. O'Donoghue, 1926: 225. Odhner, 1936: 1068 ff, text fig. 9. Smith & Gordon, 1948: 181. Forrest, 1953: 234. Marcus, 1957: 451, 454. Marcus, 1961: 33–34, 57, 58, pl. 7, figs. 119–120. Lance, 1961: 67. Steinberg, 1963b:71. deVries, 1963: 129. Ghiselin, 1965: 350. MacFarland, 1966: 245, 246–254, pl. 38, figs. 7–9; pl. 43, figs. 45–50; pl. 49, fig. 7; pl. 50, fig. 5; pl. 52, figs. 7–7a; pl. 53, figs. 1–6. Sphon & Lance, 1968: 82. Roller & Long, 1969: 427. Thompson, 1972a: 70, 72. Nybakken, 1974: 371. Abbott, 1974: 369, fig. 4376.

Type-specimens: not listed.

Dorsum separated from foot by a well defined, longitudinal groove. Foot narrow, linear, bluntly rounded anteriorly with a narrow, median notch, and slightly tapered posteriorly to bluntly rounded tail which bears a slight, median notch. Anterior margin of body bears, on either side, a broad, palmate, velar lobe which bears 6–10 or more unequal, digitiform processes. Clavi of rhinophores bear 6–8, vertical lamellae, and a short blunt apex. Six to nine irregularly spaced, rounded ridges occur along the thin margin of calyciform rhinophore sheath. Rhinophores colored as body. Cerata palmate distally, with 4–16 digitiform processes arranged in a horseshoe shape; the larger digitiform processes may bear numerous, nodular tuberosities. Cerata occur in 4–7 pairs, first pair opposite, those on right side successively more posterior, such that posterior pairs are alternate. General ground color reddish-brown, varying from light to dark in different specimens, occasional specimens (especially young individuals) may be greenish to greenish-brown. Red, red-brown, and yellow blotches, which are formed of minute dots, occur on body. Rhinophores may bear scattered white spots. The convex, dorsal sides of cerata bear oval patches of white. T.L.: 15 mm.

Anus on right, between first and second cerata. Genital aperture on right side, antero-ventral of first ceras.

Radular formula of specimen examined 47(0.1.1.1.0), MacFarland (1966: 247) reports 50–62(0.1.1.1.0). Rachidian teeth (Fig. 86a) bear 3–5 large denticles on either side of median cusp. Laterals (Fig. 86b) rather flat, rectangular plates, each with a single cusp. Masticatory border of mandibles bears 20–30 blunt denticulations.

Type-locality: Monterey Bay, California.

Range and habitat: Dillon Beach, Marin Co., California (Lance, 1961), to Punta Abreojos, Baja California, Mexico (Lance, 1961). Intertidal to 6 m, usually found in rocky areas along open coast, frequently in the alga *Gigartina* sp. Also found offshore on drifting masses of the kelp *Macrocystis pyrifera*.

Hopkinsia MacFarland, 1905

Body basically doridiform, elongate-elliptical in outline, abruptly rounded anteriorly and posteriorly, and quite depressed and flattened dorso-ventrally. Dorsum densely covered with numerous very long, gently tapered processes. Labial tentacles very broad, forming a veil-like expansion. Rhinophores non-retractile, perfoliate. Branchial plumes unipinnate, arranged in a semi-circle around anus.

Labial disc bears very short, thickened rods. Radular formula 1.1.0.1.1. Laterals long and hooked distally. Marginals flattened and denticulate.

Penis armed with minute hooks.

Type-species: *Hopkinsia rosacea* MacFarland, 1905.

Hopkinsia rosacea MacFarland, 1905

Hopkinsia rosacea MacFarland, 1905: 54. Cockerell, 1905: 131. MacFarland, 1906: 149–151, pl. 21, figs. 97–103; pl. 31, figs. 24–25. Baily, 1907: 92. Berry, 1907: 35. Kelsey, 1907: 41. O'Donoghue, 1926: 222. O'Donoghue, 1927b: 100–101, pl. 2, figs. 57–59. Hewatt, 1937: 178 ff. Hewatt, 1938: 287. Costello, 1938: 320, 325, 327–330, tabs. 1, 3, 5, pl. 1, fig. 20. Smith & Gordon, 1948: 180. Strain, 1949: 206–209. Goodwin & Fox, 1955: 1086. Marcus, 1961: 29–30, pl. 6, figs. 103–106. Lance, 1961: 67. Steinberg, 1963b: 71. Paine, 1963a: 4. Paine, 1964: 385. MacFarland, 1966: 125–126, pl. 21, figs. 2–3; pl. 31, figs. 32–36. Sphon & Lance, 1968: 79. Roller & Long, 1969: 427. Lance, 1969: 37. Gosliner & Williams, 1970: 178. McBeth, 1970: 28. McBeth, 1971: 158–159. Harris, 1971a: 84. McBeth, 1972a: 55. Bertsch *et al.*, 1972: 307. Harris, 1973: 239, 240. Abbott, 1974: 364, pl. 17, fig. 4339. Schuler, 1975: 33. Nybakken, 1978: 135. McDonald & Nybakken, 1978: 111. Fuhrman *et al.*, 1979: 292. Russo, 1979: 44.

Hopkinsea rosacea MacFarland. O'Donoghue, 1927a: 11 (*lapsus*).

Type-specimens: U. S. Nat. Mus., no. 181275.

Foot broad, truncated anteriorly with a deep triangular notch, and abruptly rounded posteriorly. Rhinophores bear 18–24 lamellae, and are rose-pink on shaft, and somewhat darker pink on clavus. Branchial plumes 7–14, dark rose-pink. General ground color everywhere rose-pink, dorsal processes same color, or occasionally a lighter shade of same color. T.L.: 20 mm.

Radular formula of specimen examined 22(1.1.0.1.1), MacFarland (1966: 125) and Marcus (1961: 30) both report 16(1.1.0.1.1). Laterals (Fig. 50a) flattened, very elongate triangles, with a small, blunt hook apically. Marginals (Fig. 50b) small and somewhat triangular, usually with a single small cusp.

Type-locality: Monterey Bay, California.

Range and habitat: Coos Bay, Coos Co., Oregon (Steinberg, 1963b), to Ensenada, Baja California, Mexico (Farmer & Collier, 1963). Intertidal to 6 m, usually in rocky areas. McBeth (1971: 58) reports that it feeds upon the rose pink bryozoan *Eurystomella bilabiata*.

Hypselodoris Stimpson, 1855

Body basically doridiform, quite elongate, somewhat compressed laterally; sides of body quite high and lateral mantle margins quite narrow, making body somewhat quadrilateral in cross section. Dorsum soft and smooth, without tubercles or papillae. Labial tentacles short and cylindro-conical. Rhinophores perfoliate, retractile into sheaths. Branchial plumes retractile, usually unipinnate, arranged in a circle around anus. Most species are brightly colored.

Labial armature minute rods which are usually bifid at tip. Radula broad, without rachidian tooth. Laterals have bifid cusps, sometimes with denticles below cusp, especially on teeth nearest margin of radula.

Penis unarmed.

This genus is very closely related to *Chromodoris* Alder & Hancock, 1855 (*q.v.*).

Type-species: *Hypselodoris obscura* (Stimpson, 1855).

Hypselodoris californiensis (Bergh, 1879)

Chromodoris californiensis Bergh, 1879b: 72, 109, 112–114. Bergh, 1979c: 128, 165, 168–170. Bergh, 1880a: 274, pl. 6 (14), figs. 5–15. Bergh, 1880b: 125, pl. 6 (14), figs. 5–15. Bergh, 1881b: 220. Bergh, 1884b: 649. Orcutt, 1885: 545. Bergh, 1890b: 940. Bergh, 1890c: 168, pl. 3, fig. 14. Bergh, 1891: 141. Bergh, 1892: 1110 (118). Bergh, 1898: 533. Bergh, 1905a: 71. Bergh, 1905b: 156. Cockerell & Eliot, 1905: 36, 37–38. MacFarland, 1906: 129–130. Kelsey, 1907: 37. Cockerell, 1908: 106. Ingram, 1935: 48. Costello, 1947: 232. Pruvot-Fol, 1951b: 79. MacFarland, 1966: 154, 157–162 ff, pl. 24, figs. 1–3; pl. 34, figs. 12–23. Marcus & Marcus, 1967a: 176–178, text figs. 30–33. Russell, 1968: 140–141. Roller, 1970a: 371. Schmekel, 1970: 194. North, 1971: 57. Schuler, 1975: 33. Bloom, 1976: 293, 294. Bertsch & Burn, 1979: 253 ff. (*Non*) Bergh, 1894: 181–182, pl. 7, figs. 23–28 (=*Hypselodoris ghiselini* Bertsch, 1978).

Chromodoris calensis Bergh, 1879a: 341. Bergh, 1879e: 103. Bergh, 1879f: 3. Bergh, 1880a: 274, pl. 6 (14), figs. 5–15. Bergh, 1880b: 125, pl. 6 (14), figs. 5–15. Costello, 1947: 232. MacFarland, 1966: 157. Russell, 1968: 140–141.

Chromodoris universitatis Cockerell, 1901c: 79. Cockerell, 1902: 19–20. Cockerell & Eliot, 1905: 36, 37–38. MacFarland, 1906: 129–130. Kelsey, 1907: 37. Hilton, 1919: 34. Crozier, 1922: 304. Costello, 1947: 232. Pruvot-Fol, 1951b: 90. MacFarland, 1966: 158, 163.

Chromodoris sp. Guernsey, 1912: 75, figs. 39C–D. O'Donoghue, 1927b: 78.

Glossodoris californiensis (Bergh). O'Donoghue, 1926: 211. O'Donoghue, 1927a: 10. O'Donoghue, 1927b: 90–91, pl. 2, figs. 38–42. Cockerell, 1940: 504. Costello, 1947: 232. Pruvot-Fol, 1951b: 89–90. Pruvot-Fol, 1951c: 152. White, 1952: 114. Lance, 1961: 66. Steinberg, 1961: 62. Farmer & Collier, 1963: 62. Paine, 1963a: 4, 8. Steinberg, 1963b: 69. Lance, 1966: 69, 70, 72. Farmer, 1967: 341. Sphon & Lance, 1968: 79. North, 1971: 57. Abbott, 1974: 355, fig. 4250.

Glossodoris (*Chromodoris*) *californiensis* (Bergh). Smith & Gordon, 1948: 180.

Glossodoris calensis (Bergh). Pruvot-Fol, 1951b: 89.

Glossodoris universitatis (Cockerell). Pruvot-Fol, 1951b: 90. Pruvot-Fol, 1951c: 152.

Hypselodoris californiensis (Bergh). Marcus & Marcus, 1967a: 59, 176–178 (*partim*), 238, text fig. 30, (*non*) text fig. 31, (*non*) pp. 176–178 (*partim*) (=*Hypselodoris agassizii* (Bergh, 1894)). Roller & Long, 1969: 429. McBeth, 1970: 28. Roller, 1970a: 371. Long, 1970: 19. Farmer, 1971: 19. McBeth, 1971: 158. Sphon, 1971b: 214. Keen, 1971: 823, pl. 20, fig. 1, (*non*) fig. 2335 (=*H. agassizii*). Sphon & Mulliner, 1972: 150. Harris, 1973: 240. Bertsch *et al.*, 1973: 287. Bertsch, 1973: 109. Marcus & Hughes, 1974: 520. Ferreira & Bertsch, 1975: 326, 327. Bertsch, 1976a: 158. Bertsch, 1977: 114, text fig. 3M. McDonald & Nybakken, 1978: 112. Bertsch, 1978c: 241–244, figs. 27, 29–31, 61–64. Fuhrman *et al.*, 1979: 292. Bertsch & Burn, 1979: 255. Russo, 1979: 43. Bertsch, 1979b: 46, fig. 3M.

Chromodoris universitates (=*Hypselodoris californiensis*). Harris, 1973: 240 (*lapsus*).

Type-specimens: not listed.

Anterior portion of dorsum widened and somewhat expanded, forming a broad undulating velum. Foot narrow and elongate, rounded and bilabiate anteriorly, and tail rather prolonged and rounded. Posterior margin of dorsum bears 5–9 prominent, hemispherical, glandular elevations ventrally, each whitish with a central pore-like opening. Rhinophores bear about 17–20 lamellae, clavus bears a vertical ridge both anteriorly and posteriorly; the low sheath has a smooth margin. Rhinophores very dark blue. Branchial plumes 9–12, usually unipinnate, very dark blue. General ground color rich dark ultramarine blue, margins of dorsum and foot are bright cobalt blue. Dorsum bears numerous round to oblong spots of bright yellow-orange, frequently in lateral series on either side of dorsum and more irregularly placed posterior of branchial plumes. Sides of body bear about 10 round to oval spots of bright yellow-orange. T.L.: 40 mm.

Radular formula of specimen examined 75(118.0.118), MacFarland (1966: 159) reports 74(114.0.114), and Bertsch (1978c: 243) reports 42–92(63–150.0.63–150), while Bloom (1976: 293) reports the range 82–92(98–132.0.98–132). Laterals (Fig. 64) somewhat hooked and shallowly to deeply bifurcated distally, thus forming 2 cusps; each tooth bears 5–10 rather tuberculiform denticles below the lower cusp.

Type-locality: Santa Catalina Island, California.

Range and habitat: Monterey, Monterey Co., California (MacFarland, 1966), to Bahía Magdalena, Baja California, Mexico (Bertsch, 1978c) 24°11′N, 109°55′W (La Paz), Baja California, Mexico (Bergh, 1894); throughout Gulf of California, Mexico. Rare north of Point Conception, Santa Barbara Co., California. Intertidal to 31 m, usually in rocky areas of open coast, occasional on floating docks and pilings in bays. Frequently found on the sponge *Dysidea amblia* upon which it may feed (McDonald & Nybakken, 1978). McBeth (1971: 158) reports that it feeds upon the sponges: *Stelletta estrella* and *Haliclona* sp.

Remarks: *H. californiensis* has been confused in the literature with 2 other species, *Hypselodoris agassizii* (Bergh, 1894) and *Hypselodoris ghiselini* Bertsch, 1978 (see Bertsch, 1978c for discussion).

Bertsch (1978c: 241) and Bertsch & Burn (1979) consider *Chromodoris glauca* Bergh, 1879 a synonym of *Hypselodoris californiensis*. However, *C. glauca* was originally described by Bergh (1879e: 107) as having a double white line on the edge of the dorsum ("Der ziemlich schmale Mantlerand mit ziemlich schmaler weisser Doppellinie."), and Bergh (1879c: 168) said that in *H. californiensis* a "fine line seemed to border the margin of the mantle-edge . . .," while for *Hypselodoris agassizii* Bergh (1894: 182) mentions 2 narrow white lines on the edge of the dorsum (. . . "an dem Ruckenrande selbst zwei schmale, ringsum continuirliche weissliche linien."). *C. glauca* and *H. agassizii* are both described as having numerous small yellow flecks on the dorsum and side of the body, while *H. californiensis* has fewer and larger yellow spots. Bergh (1879e: 106) was apparently not sure of the locality where *C. glauca* was collected, as it was listed as: "Hab. M. pacif. or. (California," and as "Californien." Since California and Baja California were frequently not clearly distinguished by early collectors, *C. glauca* may well have been collected in Baja California, where *H. californiensis* and *H. agassizii* are both known to occur. Bertsch (1978b: 80) mentions a similar situation when he rejects Bergh's listing of Puget Sound, Washington as the type-locality of *Chromodoris dalli* and proposes a location south of Puertecitos, Baja California, Mexico as the type-locality. Since the radula and internal anatomy of *C. glauca* are unknown, only the external coloration is available for comparing it to *H. agassizii* and *H. californiensis*. From the above descriptions, it seems certain that *C. glauca* much more closely resembles *H. agassizii* than *H. californiensis*.

Laila MacFarland, 1905

Body doridiform, quite depressed dorsoventrally, rounded anteriorly and posteriorly. A flattened subpallial ridge occurs on either side of anterior end of body, just posterior and dorsal of labial tentacles. Margin of dorsum bears numerous elongate, rather clavate processes. Labial tentacles short and digitiform, grooved distally. Rhinophores retractile into sheaths, perfoliate. Branchial plumes non-retractile, tripinnate, arranged in circle around anus.

Labial armature absent. Radular formula n.2.1.2.n. Rachidian teeth spurious plates. First laterals hooked, second laterals quite large. Marginals smaller and flattened.

Penis armed with small hooks in irregular longitudinal rows.

Type-species: *Laila cockerelli* MacFarland, 1905.

Laila cockerelli MacFarland, 1905

Laila cockerelli MacFarland, 1905: 47. Cockerell, 1905: 132. Cockerell & Eliot, 1905: 43–44. MacFarland, 1906: 134–145, pl. 19, figs. 45–50; pl. 27, fig. 15. Berry, 1907: 35. Kelsey, 1907: 41. Guernsey, 1912: 77, fig. 39A. Guernsey, 1913a: 88–92, text figs. 1–2. Guernsey, 1913b: 137–157, figs. 1–5. O'Donoghue, 1921: 163–165, pl. 2 (8), figs. 15–17. O'Donoghue, 1922b: 164. O'Donoghue & O'Donoghue, 1922: 138–139, pl. 4, fig. 8. O'Donoghue, 1924: 30. O'Donoghue, 1926: 213. O'Donoghue, 1927a: 11. O'Donoghue, 1927b: 99–100, pl. 2, figs. 54–56. Clayton, 1932: 6. Fraser, 1932: 67. Hewatt, 1937: 178 ff. Costello, 1938: 320 ff, tabs. 1, 5. Smith & Gordon, 1948: 180.

LaRocque, 1953: 257. Marcus, 1961: 21–22, pl. 4, figs. 67–70. Lance, 1961: 66. Paine, 1963a: 4. Steinberg, 1963b: 70. MacFarland, 1966: 104–106, pl. 20, fig. 4; pl. 29, fig. 1; pl. 31, figs. 6–12. Lance, 1966: 69. Sphon & Lance, 1968: 79. Roller & Long, 1969: 427. Lance, 1969: 37. Robilliard, 1969a: 290. Gosliner & Williams, 1970: 178. Hertz, 1970: 6. Long, 1970: 19. Keen, 1971: 827, pl. 21, fig. 3. Bertsch *et al.*, 1972: 307. Baker, 1972: 49. Sphon, 1972a: 155. Bertsch & Ferreira, 1974: 346. Abbott, 1974: 359, pl. 17, fig. 4282. Haderlie *et al.*, 1974: tab. 4. Belcik, 1975: 276. Thompson, 1976a: 51, pl. 7, fig. d. Thompson, 1976b: 77. Michel, 1976: 47, fig. 6. Nybakken 1978: 135. Poorman & Poorman, 1978: 373. McDonald & Nybakken, 1978: 110, 112. Bertsch, 1980: 224.

Lialla. Clayton, 1932: 12 (*lapsus*).

Leilla cockerelli. Marcus, 1966: 58 (*lapsus*).

Type-specimens: U. S. Nat. Mus., no. 181290.

Dorsal processes usually arranged in rather oblique rows of about 3–4, inner medial processes generally longer than outer, lateral processes. Anterior processes may occasionally bear small tubercles distally. Processes translucent white to yellowish-white, tipped with red-orange. Foot linear; truncate, bilabiate, and slightly emarginate anteriorly, abruptly pointed posteriorly. Rhinophores bear 9–14 lamellae, shaft whitish and clavus red-orange. Rhinophore sheaths have smooth edges. Branchial plumes 5, whitish, tipped with red-orange flecks. General ground color translucent grayish-white to yellowish-white. In specimens from the northern part of range, dorsum bears numerous small, randomly distributed, white tubercles medially; while in specimens from the southern part of range dorsum bears a median row of larger tubercles which are tipped with red-orange. Southern specimens are darker red-orange than are northern specimens. In Monterey Bay, California, specimens which bear tubercles intermediate in size and number between the northern and southern forms are occasionally found, some of the tubercles are white and some red-orange. Tail may also be tipped with red-orange distally. T.L.: 15 mm.

Penis armed with 10–12 slightly irregular, longitudinal rows of minute, thorn-like hooks.

Radular formula of specimen examined 67(10.2.1.2.10), MacFarland (1966: 105) reports 76–82(10–13.2.1.2.10–13), and Marcus (1961: 21) reports 74–88(10–14.2.1.2.10–14). Rachidian teeth very rudimentary, small, flat rectangular, nearly colorless plates. First laterals (Fig. 45a) long and thin with a distal hook. Second laterals (Fig. 45b) large, quite massive, with two distal cusps; below larger cusp is a rounded prominence; lower part of shaft bears a blunt projection. Marginals (Fig. 45c, d) quadrate in outline with a rather large, broad cusp.

Type-locality: Monterey Bay, California.

Range and habitat: Mudge Island, Strait of Georgia, British Columbia, Canada (O'Donoghue, 1921), to Cabo San Lucas, Baja California, Mexico (Lance, 1961); Bahía de los Ángeles, Baja California, Mexico (Keen, 1971). Intertidal to 34 m, occasional in rocky, open coast areas, usually under rocks. Feeds upon the bryozoan *Hincksina velata* (McDonald & Nybakken, 1978: 110).

Remarks: Since the northern and southern forms, and individuals which are intermediate between the two, occur in Monterey Bay, California, it seems fairly certain that they are a single species and not two species as has occasionally been suggested, nor geographic subspecies as suggested by Keen (1971: 827).

Melibe Rang, 1829

Body limaciform, somewhat laterally compressed, and tapered posteriorly. Foot corners and oral tentacles as such absent. Head separated from body by narrow neck and expanded into an enormous oral hood. Margin of hood bears cirri. Cerata spatulate, without basal gills, and arranged in a longitudinal row on either side of dorsum.

Radula absent, mandibles absent or rudimentary.

Type-species: *Melibe rosea* Rang, 1829.

Melibe leonina (Gould, 1852)

Chioraera leonina Gould, 1852: 310–311, pl. 26, fig. 404. Adams & Adams, 1854: 71. Carpenter, 1857: 210, 213, 313. Adams & Adams, 1858: 633, pl. 138, fig. 1. Chenu, 1859: 414, fig. 3083. Cooper, 1863b: 60. Carpenter, 1864: 609. Cooper, 1867: 14. O'Donoghue, 1921: 192. O'Donoghue, 1922a: 125. O'Donoghue & O'Donoghue, 1922: 134–135, pl. 4, fig. 8. O'Donoghue, 1922b: 165. O'Donoghue, 1922d: 148. O'Donoghue, 1929: 716. Johnson, 1964: 54, 100. MacFarland, 1966: 280–287, pl.

71, figs. 1–7; pl. 54, figs. 1–10. Schmekel, 1970: 178. North, 1971: 57.

Chioraera leontina Gould. Fewkes, 1889: 141. Yates, 1890: 41. O'Donoghue, 1922d: 148. (*lapsus*).

Melibe pellucida Bergh, 1904: 11–13, pl. 4, figs. 33–34. O'Donoghue, 1922d: 148. Odhner, 1936: 1117. Burn, 1960: 70. MacFarland, 1966: 280.

Melibe leonina (Gould). Bergh, 1875b: 364. Bergh, 1880d: 161. Fischer, 1887: 534, text fig. 291. Bergh, 1890b: 882. Bergh, 1892: 1043 (51). Bergh, 1907: 95. Agersborg, 1919: 269. Agersborg, 1921a: 222–253, text figs. 1–12. Agersborg, 1921b: 50–57. O'Donoghue, 1922d: 150. Agersborg, 1922b: 439. Agersborg, 1923a: 507–592, pls. 27–37. Agersborg, 1923b: 86–96, pls. 2–5. Agersborg, 1923c: 135. Agersborg, 1923d: 346. Agersborg, 1924: 216–229, pls. 6–7. O'Donoghue, 1924: 24–25. Agersborg, 1925: 167. Guberlet, 1928: 163–170. Fosbert, 1929: 135, text figs. a–c. Fraser, 1932: 67. Chambers, 1934: 602, 604. Wismer & Swanson, 1935: 341. Odhner, 1936: 1068, 1113, 1117, text fig. 8. Smith & Gordon, 1948: 181. LaRocque, 1953: 252. Forrest, 1953: 234. Graham, 1955: 153. Comfort, 1957: 226. Burn, 1960: 70. Eyerdam, 1960: 45. Lance, 1961: 67. deVries, 1963: 107 ff. Steinberg, 1963b: 71. Paine, 1963a: 4. Lance, 1966: 69, 78–79. Hurst, 1967: 255 ff, text figs. 7a–b, pl. 27, fig. 8; fig. 24–16. Hurst, 1968: 151–166, text figs. 1–8. Sphon & Lance, 1968: 80. Waidhofer, 1969: 295, 296. Roller & Long, 1969: 427. Long, 1969c: 232. Gosliner & Williams, 1970: 179. Farmer, 1970: 78. Bernard, 1970: 85. Ghelardi, 1971: 411, 415. Ajeska, 1971: 13. Keen, 1971: 833, pl. 21, fig. 6. Baker, 1972: 49. Thompson, 1972a: 75. Harris, 1973: 258 ff. Abbott, 1974: 370, fig. 4378. Birkeland, 1974: 218. Ajeska & Nybakken, 1976: 19–26, figs. 4, 6–10. Lambert, 1976: 297. Thompson, 1976a: 28, text figs. 12b, 14a. Thompson, 1976b: 58. Poorman & Poorman, 1978: 373. McDonald & Nybakken, 1978: 113. Bonar, 1978: 191.

Chioraera dalli Heath, 1917: 137–148, pls. 11–13. O'Donoghue, 1922d: 148. MacFarland, 1966: 280 ff.

Melibe lenina. Bovard & Osterud, 1918: 134 (*lapsus*).

Melibe (*Chioraera*) *leonina* (Gould). O'Donoghue, 1922d: 145–150.

Chicoraera leonina. O'Donoghue, 1924: 24 (*lapsus*).

Melibe dalli (Heath). Odhner 1936: 1117.

Type-specimens: not listed.

Foot narrow, linear; rounded anteriorly and tapered slightly posteriorly to blunt tail; foot separated from body by lateral groove. Oral hood elliptical and arched dorsally. Margin of hood bears two rows of outwardly directed cirri, outermost longer, innermost half the length of outermost series and alternates with it. Within the previous series is an inwardly directed series of shorter, more numerous cirri, arranged at equal intervals. Rhinophores perfoliate with 5–6 lamellae; they are located anteriorly on oral hood, shaft long and cylindrical and bears a thin, triangular, sail-like expansion on inner face; clavus retractile into a campanulate sheath at tip of shaft. Cerata laterally flattened, broadly ovate to round in outline, and arise from a short, stout stalk; the slightly truncate tips bear 2–6 small, acute points. There are usually 5–6 cerata on either side of dorsum. First pair is opposite, and remaining pairs are more or less alternate. They are readily dehiscent; the delicate network of liver branches in the cerata may easily be seen. General ground color, including cerata, oral hood, and rhinophores is translucent yellowish-brown, occasionally with a slight blue-green tinge. Body irregularly dotted with numerous small, bluish-white dots. Liver branches usually light green to brown. T.L.: 100 mm, but specimens up to 300 mm have been collected.

Anus on right, between and slightly ventral of first and second cerata. Genital aperture on right, antero-ventral of first ceras. Penis unarmed.

Type-locality: Port Discovery, Puget Sound, Washington.

Range and habitat: Dall Island, Alaska (Heath, 1917), to Punta Abreojos, Baja California, Mexico (Lance, 1966), and throughout the Gulf of California, Mexico. Intertidal to 37 m, usually found on the alga *Macrocystis pyrifera,* or on the eelgrass *Zostera marina,* occasionally found on floating docks in bays. The large oral hood is used to capture small crustaceans, especially copepods which dwell on the blades of *Macrocystis.* Feeds upon copepods and amphipods (gammarids and caprellids) (Ajeska & Nybakken, 1976; Hurst, 1968; MacGinitie & MacGinitie, 1949).

Remarks: This species is capable of swimming, and it releases a rather pungent fruity odor.

Okenia Menke, 1830, ex Leuckart in Bronn, Ms.

Body usually limaciform and elongated. Lateral edge of dorsum bears a few elongate dorsal processes. Labial tentacles as such are absent. Rhinophores non-retractile, perfoliate (lamellae sometimes few and incomplete), and rather large. Branchial plumes uni- to bipinnate, non-retractile, arranged around anus.

Labial disc armed with small hooks. Radular formula 1.1.0.1.1., laterals hook shaped, with or without denticles. Marginals smaller, with a small cusp.

Penis armed.

Type-species: *Okenia elegans* Leuckart, 1828.

See ICZN (1974, Opinion 1014), *Okenia* placed on Official List.

Okenia angelensis Lance, 1966

Okenia angelensis Lance, 1966: 76–78, text figs. 9–12. Burn, 1967b: 55. Sphon & Lance, 1968: 80. Roller & Long, 1969: 427. Keen, 1971: 829, pl. 21, fig. 2. Abbott, 1974: 363. Schmekel, 1979: 357.

Cargoa angelensis (Lance). Vogel & Schultz, 1970: 389.

Type-specimens: Calif. Acad. Sci., no. 101.

Body somewhat compressed laterally, with rather high, vertical sides. Dorsum bears a few cylindrical, elongate, blunt tipped processes, 6–9 of which occur dorso-laterally along pallial ridge on either side; a pair of processes occurs medially on dorsum between rhinophores and branchial plumes. Foot elongate, rather narrow, and truncate anteriorly; sides nearly parallel, and tail rather blunt. Antero-lateral corners of head prolonged into a pair of rather triangular lobes. Rhinophores long and slightly tapered to blunt tips, they bear 1–3 incomplete lamellae on posterior face, and are translucent grayish-white with minute yellowish to white dots distally and minute brownish dots proximally. Branchial plumes 5–7, uni- to bipinnate, arranged in an irregular semi-circle, they are translucent grayish-white with a few flecks of yellow and brown. General ground color translucent grayish-white, with a few flecks of yellow to white on dorsum and sides of body, and with irregular patches of reddish-brown dots on dorsum. Occasional specimens may bear scatterings of bluish-green on dorsum. T.L.: 5 mm.

Radular formula of specimen examined 18(1.1.0.1.1), Lance (1966: 77) reports 21(1.1.0.1.1). Laterals (Fig. 40b) hamate and bear 14–30 denticles on margin of hook. Marginals (Fig. 40a) oval to subquadrate with a single, distal hook.

Type-locality: Bahía de los Ángeles, Baja California, Mexico.

Range and habitat: San Francisco Bay, California (Lance, 1966), to Mission Bay, San Diego Co., California (Lance, 1966); Bahía de los Ángeles, Baja California, Mexico (Lance, 1966). Intertidal and subtidal, most commonly found on floating docks and pilings in bays. Not uncommon, but easily overlooked, as it is small and blends well with the substrate.

Okenia plana Baba, 1960

Okenia sp. Steinberg, 1960: 49.

Okenia plana Baba, 1960a: 80–81, pl. 7, figs. 2a–d. Steinberg, 1963a: 65. Steinberg, 1963b: 71. Burn, 1967b: 55. Gosliner & Williams, 1970: 179. Abbott, 1974: 363. Schmekel, 1979: 357.

Cargoa plana (Baba). Vogel & Schultz, 1970: 389.

Type-specimens: Dr. K. Baba's Laboratory, Japan (Baba, personal communication).

Body rather doridiform, quite depressed dorso-ventrally, rather equally rounded anteriorly and posteriorly. Dorsum bears a single median, elongate, cylindrical, blunt tipped, dorsal process just anterior of branchial plumes; it is translucent grayish-white with a number of irregular, chocolate-brown flecks on proximal two thirds to three quarters, some of which are concentrated into an irregular subapical band below the distal one quarter to one third which is opaque white. A row of 5 similarly shaped and colored dorsal processes occurs dorso-laterally on either side, the first just anterior of rhinophores, the next 3 in a line between rhinophores and branchial plumes, and the last just posterior of branchial plumes. Foot elliptical in outline; head expanded into a semi-circular oral veil. Rhinophores bear about 9–13 lamellae and are translucent grayish-white, somewhat yellowish distally, and bear a few irregular chocolate brown flecks proximally on shaft. Branchial plumes 8–11, unipinnate, arranged in a semi-circle, translucent yellowish-white with a number of irregular chocolate brown flecks. General ground color translucent grayish-white. Dorsum bears numerous irregular, chocolate brown flecks. T.L.: 8 mm.

Radular formula of specimen examined 18(1.1.0.1.1), Baba (1960a: 81) reports 30(1.1.0.1.1). Laterals (Fig. 41a) hooked and non-denticulate. Marginals (Fig. 41b) smaller, somewhat quadrate with a rather large denticle below which are 4–5 denticles. Labial disc bears an incomplete ring of jagged hooks.

Type-locality: Toba, Japan.

Range and habitat: San Francisco Bay, California (Steinberg, 1963b); originally described from Japan, from where it was probably introduced into California. Intertidal and subtidal, usually on floating docks and pilings in bays.

Onchidoris Blainville, 1816

Body doridiform, dorsum tuberculate or papillate. Labial tentacles as such are absent; they are fused into an oral veil. Rhinophores perfoliate and retractile into sheaths with smooth margins. Branchial plumes retractile and unipinnate.

Labial disc unarmed. Radular formula varies among the numerous species, 1.1.0.1.1, 1.1.1.1.1, or 2.1.1.1.2, etc.

Penis unarmed.

Type-species: *Onchidoris bilamellata* (Linnaeus, 1767).

Onchidoris bilamellata (Linnaeus, 1767)

Doris bilamellatus Linnaeus, 1767: 1083. Tonning, 1768, *vide* 1769: 484.

Doris fusca Müller, 1776: 229, no. 2768. Müller, 1788: pl. 47, figs. 1–9. Cuvier, 1804: 449. Lamarck, 1819: 312. Blainville, 1819: 452. Rapp, 1827: 520. Bosc, 1830: 110. Cuvier, 1834: 114. Gray, 1842: pl. 67, fig. 15. Adams & Adams, 1854: 51. Løyning, 1927: 250. Lemche, 1938: 1. (*Non*) Lovén, 1846: 136 (? =*Acanthodoris pilosa*).

Doris verrucosa Pennant, 1777: 43, pl. 21, fig. 23. Turton, 1807: 133. Pennant, 1812: 82, pl. 23, fig. 2. Fleming, 1828: 282. Thiele, 1931: 434, fig. 533. (*Non*) Linnaeus, 1768: 653.

Doris elfortiana Blainville, 1816: 95. Leach, 1852: 20, pl. 7, fig. 1.

Onchidorus leachii Blainville, 1816: 97.

Doris leachii Blainville, 1819: 450. Rapp, 1827: 520.

Onchidoris leachii Blainville. Blainville, 1825: 489. Blainville, 1827: pl. XLVI, fig. 8. Cuvier, 1834: 117.

Doris obvelata Bouchard-Chantereaux, 1835: 42. (*Non*) Müller, 1776.

Doris bilamellata Linnaeus. Cuvier, 1804: 448, 449. Johnston, 1838a: 54. Johnston, 1838b: pl. 2, fig. 8. Thompson, 1840: 86. Hassall, 1842: 133. MacGillivray, 1843: 198. Thompson, 1844: 250. Reid, 1846: 377 ff, pl. 10, figs. 1–13, 15–21, 25. Alder, 1850: 105, 110. Forbes & Hanley, 1851: 567. Alder & Hancock, 1851c: fam. 1, pl. 1, fig. 13. Hancock & Embleton, 1852: 208 ff, pl. 11, fig. 2; pl. 12, fig. 5; pl. 14, fig. 8; pl. 17, figs. 6–7. Gosse, 1853: 12, 13–14, 62, 83, 232. Gosse, 1854: 107. Adams & Adams, 1854: 51. Byerley, 1854: 44. Alder & Hancock, 1855: 20, 31, 32, 43. Gosse, 1856: 105. Thompson, 1856: 272. Collingwood, 1859: 463, 470. E. Wright, 1859: 88. Collingwood, 1860: 202. Norman, 1860: 7242. Collingwood, 1861: 114. Collingwood & Byerley, 1862: 189. McIntosh, 1865: 390. Robertson, 1868: 205. Jeffreys, 1869: 90. Gould, 1870: 228–229, pl. 21, figs. 305–309. Dall, 1870: 249. Verkruzen, 1872: 375. Sauvage, 1873: 25, 29. McIntosh, 1874: 432. McIntosh, 1875: 89. Friele & Hansen, 1876: 71. Jeffreys, 1877: 337. Leslie & Herdman, 1881: 312. Locard, 1886: 28. Hertzenstein, 1885: 709. Higgins, 1886: 25. Herdman, 1890b: 201. Bergh, 1891: 103. Herdman & Clubb, 1892: 153, 159, 162. Lundbeck, 1893: 175. Cooke, 1899: 64. Colgan, 1908: 106, 111. Eliot, 1910: 16. Pelseneer, 1911: 53–55, pl. 15, figs. 5–23. Chumley, 1918: 87, 169. Pelseneer, 1923: 28–32, text figs. 1–4. Løyning, 1927: 250. White, 1938: 14. Lemche, 1938: 1.

Doris affinis Thompson, 1840: 85–86. Thompson, 1856: 272. (*Non*) Gmelin in Linnaeus, 1791: 3106.

Doris liturata Beck in Möller, 1842: 78. Mörch, 1857: 6. Stimpson, 1862: 4. Bergh, 1878b: 607.

Doris vulgaris Leach, 1847: 268. Leach, 1852: 19.

Doris coronata Agassiz, 1850: 191. Gould, 1870: pl. 20, figs. 285, 286; pl. 21, figs. 297, 299.

Oncidoris (*doris*) *bilamellata* (Linnaeus). Hogg, 1868: pl. 10, fig. 43 (*lapsus*).

Lamellidoris n. sp. vel var. praecedentis ? Mörch, 1868: 204.

Lamellidoris bilamellata (Linnaeus). Mörch, 1868: 203. Abraham, 1877: 198. Bergh, 1878b: 605, 606–609, pl. 64, fig. 13; pl. 64, figs. 1–5. Sars, 1878: 306–307 ff, pl. XIII, fig. 5. Bergh, 1879a: 364. Bergh, 1880a: 210. Bergh, 1880b: 61. Herdman 1886: 268, 277. Fischer, 1887: 524, text fig. 286. Garstang, 1889: 179. Garstang, 1890: 447. Bergh, 1890b: 985. Norman, 1890: 73. Bergh, 1892: 1152 (160). Herdman & Clubb, 1892: 132 ff. Bergh, 1894: 192. Garstang, 1894: 226. Bergh, 1894: 173. Herdman *et al.*, 1896: 446. Tregelles, 1896: 220. Cooke, 1899: 66. Beaumont, 1900: 850. Nichols, 1900: 597. Allen & Todd, 1900: 181, 212. Vayssière, 1901: 297. Conchol. Soc., 1901: 26. Knight, 1901: 207. Johansen, 1902: 387. Mar. Biol. Assoc., 1904: 284. Farran, 1904: 3. Cockerell & Eliot, 1905: 32. Bergh, 1905a: 101. Eliot, 1906c: 346. Woodland, 1907: 45, pl. 5, fig. 6. Odhner, 1907: 74. Walton, 1908: 239. Elmhirst, 1908: 228. Farran, 1909: 17–18. Eliot, 1910: 13, 28, 156, 346. Colgan, 1911: 25. Walton, 1913: 110. Farran, 1915: 10, 67. Johnson, 1915: 175. Renouf, 1916: 12–15. Evans & Evans, 1917: 109. Bardarson, 1919: 73. Bardarson, 1920: 108. O'Donoghue, 1921: 174–176, pl. 2 (8), fig. 21. O'Donoghue, 1922a: 126–129, pl. 2. O'Donoghue & O'Donoghue, 1922: 139, pl. 4, fig. 6. Odhner, 1922: 24–25. O'Donoghue, 1924: 24. O'Donoghue, 1926: 221. O'Donoghue, 1927a: 3, 10. Jutting, 1927: LXXXVIII. Derjugin, 1928: 320. Fraser, 1932: 67. White, 1938: 19. Volodchenko, 1941: 60. Stock, 1952: 58. Pruvot-Fol, 1954: 296–297, figs. 116a–f. Swennen, 1959: 56, 58. Swennen, 1961: 197–199. Zenkevitch, 1963: 112. Hadfield, 1963: 91. Daro, 1969: 136 ff. Daro, 1970: 168. Voogt, 1973: 479 ff.

Lamellidoris liturata (Beck in Möller). Mörch, 1875: 125. Mörch, 1877: 436.

Lamellidoris bilamellata var. *liturata* Beck. Bergh, 1878b: 609–613, pl. 64, figs. 14–19; pl. 65, figs. 6–13.

Lamellidoris bilamellata var. *pacifica* Bergh, 1880a: 211–216, pl. 5, fig. 10; pl. 11, figs. 3–9. Bergh, 1880b: 62–67, pl. 5, fig. 10; pl. 11, figs. 3–9. Bergh, 1894: 192–193. Bergh, 1905a: 101.

Lamellidoris billamellata var. *pacifica*. Dall, 1884: 341 (*lapsus*).

Doris (*Lamellidoris*) *bilamellata* Linnaeus. Vanoffen, 1897: 187, 193.

Onchidorus fusca (Müller). Iredale & O'Donoghue, 1923: 220. Mar. Biol. Assoc., 1931: 273. Johnson, 1934: 156. Renouf, 1934: 400. LaRocque, 1953: 254.

Onchidoris fusca (Müller). O'Donoghue, 1924: 24. Winckworth, 1932: 234. Steven, 1938: 60, 62. White, 1938: 14, 19. McMillan, 1944: 162. Barnes & Powell, 1951: 381. Forrest, 1953: 233, text fig. 5d. Barnes & Powell, 1954: 361–363, pl. 2. Williams, 1954: 106. Marcus, 1955: 129. Graham, 1955: 152. Mar. Biol. Assoc., 1957: 310. Thompson, 1959: 240. Thompson, 1960b: 126–127. Miller, 1961: 111, 112. Thompson, 1961: 234, 236, text fig. 1A. Tarasov, 1961: 8, 25, 54. Miller, 1962: 553–554, fig. 7. Roginskaya, 1962a: 88, 92, 105, fig. 1.3. Hadfield, 1963: 88–93. Bruce *et al.*, 1963: 203. Thompson, 1964: 279 ff. Miller, 1967: 9. Thompson, 1967: 9, 11, text fig. 7E. Edmunds, 1968b: 122 ff. Barrett, 1969: 69. Hughes, 1970a: 609 ff. Hughes, 1970b: 81, 82, text figs. 15, 16. Potts, 1970: 269–292, pls. 1–2, text figs. 1–8. Meyer, 1971: 139–140. Holleman, 1972b: 142. Harris, 1973: 217 ff. Roginskaya, 1976: 23–26. Perron & Turner, 1977: 182, 183. Eyerdam, 1977: 110. Chia & Koss, 1978: 118. Nybakken, 1978: 129, 143. Dehnel & Kong, 1979: 1843.

Onchidorus bilamellatus (Linnaeus). Odhner, 1926b: 26.

Onchidorus bilamellata (Linnaeus). Løyning, 1927: 262. Lemche, 1929: 17.

Onchidorus fuscus (Müller). O'Donoghue, 1927a: 3, 9–10.

Onchidoris bilamellata (Linnaeus). Lemche, 1938: 19–20 ff. Odhner, 1939: 40–41. Lemche, 1941b: 20–22. Marcus, 1958: 27–28, text figs. 44–45. Marcus, 1961: 27–28, 57, pl. 5, figs. 92–96. Steinberg, 1963b: 70. Hurst, 1967: 255 ff, pl. 28, fig. 9; pl. 37, fig. 45; fig. 24-15. Burn, 1968: 91. Robilliard, 1969a: 290. Roller, 1970a: 482. McDonald, 1970: 375. Connell, 1970: 54 ff. Gosliner & Williams, 1970: 179. Bernard, 1970: 85. Franz, 1970: 172 ff. Dayton, 1971: 383. Thompson & Bebbington, 1973: 148, pl. 8, fig. b. Birkeland, 1974: 218. Rozsa, 1974: 7, 8. Clark, 1975: 45. Franz, 1975a: 81, 83. Belcik, 1975: 276. Lambert, 1976: 297. Thompson & Brown, 1976: 96, fig. 49. Thompson, 1976a: 33, 36, 93, text fig. 41e. Thompson, 1976b: 66 ff. Garlo, 1977: 23 ff. Crampton, 1977: 48 ff, text figs. 1–17. Bleakney & Saunders, 1978: 82–85. McDonald & Nybakken, 1978: 111. Mumaw, 1978: 74. Clark & Goetzfried, 1978: 290. Todd, 1979a: 59. Todd, 1979b: 213 ff. Todd, 1979c: 65 ff.

Lamellidoris fusca (Müller). Baba, 1957: 9. Abbott, 1974: 362.

Lamellidoris (*Lamellidoris*) *fusca* (Müller). Baba, 1957: 9, 11, text fig. 2B.

Onchidoris (*Lamellidoris*) *fusca* (Müller). Hadfield, 1963: 86.

Type-specimens: not listed.

Body equally rounded anteriorly and posteriorly, dorsum covered with numerous large, round tubercles, which decrease in size near margin. Foot rather broad, rounded to almost truncate anteriorly, and somewhat tapered posteriorly to rather bluntly rounded tail. Crescent-shaped oral veil extends laterally nearly to edge of dorsum. Rhinophores bear 14–20 lamellae and are encrusted with brown except at translucent grayish-white tips. Rhinophore sheaths low, with smooth margins. Branchial plumes 16–32 or more, unipinnate, arranged in 2 semi-circles just anterior of anus; they are encrusted with dark brown. General ground color translucent brownish-white, dorsum encrusted with irregular blotches of light rusty brown to dark chocolate brown, occasionally in the form of 2–3 irregular longitudinal stripes. T.L.: 15 mm.

Radular formula of specimen examined 21(1.1.1.1.1), Marcus (1961: 27) reports 24–30(1.1.1.1.1). Rachidian teeth (Fig. 35c) narrow, roughly rectangular plates which lack a cusp or denticles. Laterals (Fig. 35b) large, each with a long, tapered cusp. Marginals (Fig. 35a) each bear a small cusp.

Type-locality: Oceano Norvegici.

Range and habitat: Kiska Island, Aleutian Islands, Alaska (Bergh, 1894), to Morro Bay, San Luis Obispo Co., California (McDonald, 1970); Japan (Baba, 1957), Greenland (Pruvot-Fol, 1954), Europe (Pruvot-Fol, 1954), Atlantic coast of North America (Franz, 1975a). Intertidal to 250 m, sporadically abundant on pilings and floating docks in bays, usually in association with the barnacles *Balanus* spp. Feeds upon the barnacles: *Balanus balanoides, Balanus crenatus, Balanus porcatus, Elminius modestus,* and *Verruca stroemia* (Barnes & Powell, 1954; Barrett, 1969; Bleakney & Saunders, 1978; Bruce *et al.*, 1963; Clark, 1975; McDonald & Nybakken, 1978; Meyer, 1971; Miller, 1961; Potts, 1970; Swennen, 1961; Thompson & Brown, 1976; Todd, 1979b). Juveniles have also been reported to feed upon the bryozoans: *Cryptosula* and *Umbonula* (Thompson & Brown, 1976). Allan Fukuyama presented for identification two specimens of this species from the stomach of a female oldsquaw duck (*Clangula hyemalis*) collected at Homer, Alaska; and 14 specimens from a Steller's eider (*Polysticta stelleri*) collected at Nelson Lagoon, Alaska.

Remarks: Edmunds (1968b: 123) reports that this species secretes acid of pH 1.

Lemche (1938: 20) discusses reasons for maintaining the name *O. bilamellata* in preference to *O. fusca.*

Onchidoris hystricina (Bergh, 1878)

Lamellidoris hystricina Bergh, 1878b: 605, 614, pl. 68, figs. 17–23. Bergh, 1879a: 365. Bergh, 1880a: 219–221. Bergh, 1880b: 70–72. Bergh, 1890b: 985. Bergh, 1892: 1153 (161). Abbott, 1974: 362.

Onchidorus hystericina (Bergh). O'Donoghue, 1926: 221 (*lapsus*).

Onchidoris hystricina (Bergh). Marcus, 1961: 28, 57, pl. 5, figs. 89–91. Paine, 1963a: 4. Steinberg, 1963b: 71. Farmer, 1967: 342. Sphon & Lance, 1968: 80. Roller & Long, 1969: 427. Gosliner & Williams, 1970: 179. Keen, 1971: 838. Eyerdam, 1977: 110. Nybakken, 1978: 135.

Onchidoris hystericina (Bergh). 1970: 85 (*lapsus*).

Type-specimens: not listed.

Body has rather parallel sides, and is bluntly rounded anteriorly, and more acutely rounded posteriorly; dorsum thickly set with numerous long, slender, white to yellowish-white papillae which give animal a fuzzy appearance. Foot truncate and bilabiate anteriorly and tapered posteriorly to rounded tail. Oral veil rather crescent-shaped. Rhinophores bear 7–20 lamellae, and are yellowish-white. Branchial plumes 9–12, unipinnate, yellowish-white, arranged in a circle around anus. General ground color yellowish-white to cream, dorsum and dorsal surface of tail may bear small flecks of opaque white. T.L.: 8 mm.

Radular formula of specimens examined 27–32(1.1.1.1.1), Marcus (1961: 28) reports 32–34(1.1.1.1.1). Rachidian teeth (Fig. 36c) narrow, roughly rectangular plates which lack cusp or denticles. Laterals (Fig. 36b) large, each bearing a cusp which bears 12–15 denticles, Marcus (1961: 28) reports 6–11 denticles on cusp. Marginals (Fig. 36a) somewhat quadrate and each bears a short cusp.

Type-locality: Kiska Island, Aleutian Islands, Alaska.

Range and habitat: Kiska Island, Aleutian Islands, Alaska (Bergh, 1880a) to 12.9 km south of Cabo Colonet, Baja California, Mexico (Farmer, 1967). Intertidal to 30 m, sporadically abundant in rocky intertidal; occasional on floating docks and pilings in bays. May feed upon the bryozoan *Tubulipora* sp.

Remarks: The specimens which I have examined are in some ways intermediate between *Onchidoris hystricina* (Bergh) and *Onchidoris varians* (Bergh, 1878). Bergh (1880a: 217, 221) mentions 6–8 denticles on the laterals of the former and about 20 for the latter species, while the specimens I examined had 12–15 denticles on the laterals. Bergh (1880a: 216) describes *O. varians* as very similar to *O. hystricina,* the only real differences being the number of denticles on the laterals, and *O. hystricina* bears numerous spicules in the dorsum, while *O. varians* has very few spicules. Since the specimens which I examined had numerous spicules in the dorsum, I feel that they more closely resemble *O. hystricina* than *O. varians.* Further study of these two species may well show them to be conspecific.

Onchidoris sp.

Onchidoris spec. Roller & Long, 1969: 427.
Onchidoris muricata (Müller). Roller, 1970b: 482. McDonald, 1975a: 531, 540. McDonald & Nybakken, 1978: 111 (*partim*), 116. Nybakken, 1978: 135.

Body equally rounded anteriorly and posteriorly, dorsum covered with numerous tubercles which are somewhat constricted basally and bulbous apically, appearing rather spherical. Foot rather broad, rounded, almost truncated anteriorly, broadly rounded posteriorly. Oral veil crescent-shaped extending laterally nearly to edge of dorsum. Rhinophores perfoliate with 9–15 lamellae, lemon yellow; rhinophore sheaths with smooth margins. Branchial plumes 10–13, unipinnate, light to dark yellow, arranged in incomplete circle around anus. General ground color lemon yellow, tubercles slightly darker than dorsum. T.L.: 5 mm.

Radular formula of specimens examined 34–39(5–6.1.0.1.5–6). Each lateral (Fig. 37f) bears a long, curved hook with 11–21 small denticles. Marginals (Fig. 37a–e) each have a single cusp.

Range and habitat: Friday Harbor, Washington (Roller, 1970b), to Lion Rock, San Luis Obispo Co., California (Roller, 1970b). Intertidal to 10 m. Usually found upon the encrusting bryozoan *Reginella mucronata* which it matches closely in color and upon which it probably feeds (McDonald & Nybakken, 1978).

Remarks: Externally this species closely resembles *Adalaria proxima* (Alder & Hancock, 1854) or *Onchidoris muricata* (Müller, 1776), but the denticulate laterals exclude it from *A. proxima* and the lack of a rachidian excludes it from both of the above. Further study is needed to determine whether or not it is a new species.

Phidiana Gray, 1850

Body aeolidiform, gradually tapered posteriorly to the pointed tail. Anterior foot corners usually produced into elongate, tentaculiform processes, but may be rounded. Cerata cylindrical and slightly clavate; arranged in regular rows. Rhinophores non-retractile, may be smooth, papillate, verrucose, annulate, or perfoliate.

Masticatory border of mandibles denticulate. Radula uniseriate, with denticles on either side of median cusp.

Penis may be armed with a stylet or spines or may be unarmed. Anus cleioproct.

Miller (1974) united a number of similar genera (e.g. *Hermissenda* Bergh, 1878, *Facelina* Alder & Hancock, 1855, *Emarcusia* Roller, 1972, *et al.*) under the name *Phidiana,* stating that the characters which had been used to separate these genera overlap and do not seem sufficient to distinguish separate genera. I agree with Miller's definition of *Phidiana.*

Type-species: *Phidiana patagonica* (d'Orbigny, 1837).

Phidiana crassicornis (Eschscholtz, 1831)

Cavolina crassicornis Eschscholtz, 1831: 15, fig. 1. Carpenter, 1857: 173. Trinchese, 1881: 31. O'Donoghue, 1922c: 76. O'Donoghue, 1922d: 133–135.
Facelina crassicornis (Eschscholtz). Gray, 1857: 224. Adams & Adams, 1858: 633.
Flabellina crassicornis (Eschscholtz). Carpenter, 1857: 313.
Aeolis (*Flabellina*?) *opalescens* Cooper, 1863a: 205. O'Donoghue, 1922c: 75, 76.
Flabellina opalescens (Cooper). Cooper,

1863b: 60. Carpenter, 1864: 609. Cooper, 1867: 14. Bergh, 1975a: 649. O'Donoghue, 1922c: 75, 76. O'Donoghue, 1922d: 134.

Aeolis (?*Flabellina*) *opalescens* Cooper. Carpenter, 1864: 608.

Eolis opalescens (Cooper). Dall, 1871: 137.

Hermissenda opalescens (Cooper). Bergh, 1879b: 81–85, pl. 1, figs. 9–12; pl. 2, figs. 1–6. Bergh, 1879c: 138–141, pl. 1, figs. 9–12; pl. 2, figs. 1–6. Bergh, 1879d: 573. Bergh, 1890a: 37. Bergh, 1892: 1030 (38). Cockerell, 1901a: 86. Cockerell, 1901b: 122. Cockerell & Eliot, 1905: 50–51. Guernsey, 1912: 78, fig. 39J. O'Donoghue, 1921: 201–204, pl. 3 (9), fig. 32. O'Donoghue, 1922a: 125–126. O'Donoghue & O'Donoghue, 1922: 136–137, pl. 3, fig. 3. O'Donoghue, 1922b: 165. O'Donoghue, 1922c: 75–76. O'Donoghue, 1922d: 134. Agersborg, 1922b: 425. Agersborg, 1923c: 134. O'Donoghue, 1924: 26, 31. Agersborg, 1925: 167. Costello, 1938: 321 ff, tabs. 1, 3, 5; pl. 1, fig. 19; pl. 2, figs. 33–34, 42–43.

Aeolidia (*Hermissenda*) *opalescens* (Cooper). Bergh, 1880a: 232. Bergh, 1880b: 83.

Facelina (*Cavolina*) *crassicornis* Eschscholtz. Trinchese, 1881: 31.

Aeolis opalescens Cooper. Fischer, 1887: 559. Kelsey, 1907: 33.

Hermissenda crassicornis (Eschscholtz). O'Donoghue, 1922a: 125–126. O'Donoghue, 1922c: 76. O'Donoghue, 1922d: 133–135. Agersborg, 1923e: 349. O'Donoghue, 1924: 26, 31. Agersborg, 1925: 167–180, text figs. 1–22. O'Donoghue, 1926: 233. O'Donoghue, 1927b: 107–108, pl. 3, figs. 74–76. Fraser, 1932: 67. Ingram, 1935: 48, 49. MacGinitie, 1935: 740. Hewatt, 1937: 178 ff. Volodchenko, 1941: 60. Worley & Worley, 1943: 367, pl. 3, figs. 7, 9–12. Hewatt, 1946: 191, 198. Smith & Gordon, 1948: 181. Pruvot-Fol, 1951a: 59, fig. 36. LaRocque, 1953: 248. Marcus, 1961: 52–54, pl. 10, figs. 188–192. Lance, 1961: 68. Kohn, 1961: 292 ff. Lance, 1962c: 52. McLean, 1962: 111. Farmer & Collier, 1963: 63. Steinberg, 1963b: 72. Paine, 1963a: 1, 4, pl. 1. Barth, 1964: 312. Paine, 1964: 385. Farmer, 1964: 24. Burgin, 1965: 205, 215, text figs. 1–9. Ghiselin, 1965: 336 ff. Paine, 1965: 604 ff. MacFarland, 1966: 358–365, 368, pl. 55, fig. 1; pl. 70, figs. 13–14; pl. 71, figs. 1–14. Lance, 1966: 69, 79–80. Dennis, 1967a: 1441 ff. Dennis, 1967b: 259. Hurst, 1967: 255, text fig. 4a, pl. 31, fig. 22; fig. 24-3. Eakin *et al.*, 1967: 349 ff. Marcus & Marcus, 1967a: 226–227, 238. Buchsbaum & Milne, 1967: pl. 64 (*non* pl. 62 =*Antiopella barbarensis*). Mauzey *et al.*, 1968: 607. Beeman, 1968a: 96. Beeman, 1968b: 268. Sphon & Lance, 1968: 79. Haderlie, 1968: 333 ff. DuShane & Sphon, 1968: 244. Turner *et al.*, 1969: 136, text fig. 52, append. 1, 2. Haderlie, 1969: tabs. 1, 2. Roller & Long, 1969: 427. Stensaas *et al.*, 1969: 510 ff. Robilliard, 1969a: 290. Williams & Gosliner, 1970: 33. Gosliner & Williams, 1970: 178. Grigg & Kiwala, 1970: 149, 151. Bernard, 1970: 85. Hughes, 1970b: 80. Michel, 1970: 7. Schmekel, 1970: 154. Fager, 1971: 243, 246. Robilliard, 1971c: 429. Crane, 1971: 57. Farmer, 1971: 19. Harris, 1971a: 80, 84–85, 88. North, 1971: 57. Bertsch *et al.*, 1972: 306–307. Mulliner, 1972b: 2, fig. Holleman, 1972a: 60. Alkon & Fuortes, 1972: 631. Baker, 1972: 45, 47. Blair & Seapy, 1972: 121 ff. Harris, 1973: 226 ff. Thompson, 1973: 167 ff, text fig. 9. Thompson & Bebbington, 1973: 148, 149, pl. 12, fig. c. Goddard, 1973: 9. Alkon, 1973a: 444 ff. Alkon, 1973b: 185, 197. Alkon & Bak, 1973: 620–634. Detwiler & Alkon, 1973: 618 ff. Willows, 1973b: 205. Gosliner & Williams, 1973b: 352. Nybakken, 1974: 371. Abbott, 1974: 379, fig. 4463. Miller, 1974: 43. Haderlie *et al.*, 1974: tab. 4. Alkon, 1974a: 1083. Alkon, 1974b: 70, text figs. 1–2. Birkeland, 1974: 211 ff. Chase, 1974a: 707. Mariscal, 1974: 163. Murray & Lewis, 1974: 156. Zack, 1975a: 271–275. Zack, 1975b: 238 ff, text fig. 1. Belcik, 1975: 276. Alkon, 1975a: 46. Alkon, 1975c: 507. Detwiler & Fuortes, 1975: 107, 108. Harris, 1975: 539. Masukawa, 1975: 359. Schuler, 1975: 33. Alkon, 1976b: 341. Alkon, 1976c: 410 ff. Detwiler, 1976: 691. Michel, 1976: 49, fig. 15. Anderson, 1976: 407 ff. Akaike & Alkon, 1977: 171. Defelice & Alkon, 1977b: 613. Alkon & Grossman, 1977: 171. Crow & Alkon, 1978b: 191. Cooper, 1978: 8. Schmidt *et al.*, 1978: 136a. McDonald & Nybakken, 1978: 115. Bonar, 1978: 187. Harrigan & Alkon, 1978a: 430 ff. Harrigan & Alkon, 1978b: 299. Heldman & Alkon, 1978: 117 ff. Williams, 1978: 58. Crow & Alkon, 1978a: 1239. Alkon & Grossman, 1978b: 1329 ff. Alkon, 1979b: 810–816. Crow & Harrigan, 1979: 179 ff. Harrigan *et al.*, 1979: 1001. Grossman *et al.*, 1979: 24 ff. Oakes, 1979: 28–29. Harris & Howe, 1979: 145. Heldman *et al.*, 1979: 153 ff. Baba, 1979a: 17. Baba, 1979b: 7. Russo, 1979: 44, 46, 48. Crow *et al.*, 1979: 181–195. Susswein & Bennett, 1979: 523 ff. Akaike & Alkon, 1980: 501 ff. Williams, 1980: 99 ff, text figs. 1a, 2–7. Crow & Alkon, 1980b: 412 ff. Stommell *et al.*, 1980: 2104. Neary, 1980: 2166. Crow & Alkon, 1980a: 596. Lederhendler *et al.*, 1980: 218 ff. Cockburn & Reid, 1980: 275 ff. Hodge & Adelman, 1980: 220 ff.

Hermisisenda crassicornis (Eschscholtz). O'Donoghue, 1927a: 11 (*lapsus*).

Cuthona (*Hervia*) *emurai* Baba, 1937b: 329–331, text fig. 16A–D. Baba, 1937a: 199. Marcus, 1958: 62. Baba & Hamatani, 1965: 109. Baba, 1979a: 17. Baba, 1979b: 7.

Hermissenda (*Cavolina*) *crassicornis* Eschscholtz. Pruvot-Fol, 1951a: 58.

Hervia emurai (Baba). Baba, 1957: 9.

Dondice emurai (Baba). Abe, 1964: 70, 89, pl. 35, fig. 125.

Shinanoeolis emurai (Baba). Baba & Hamatani, 1965: 109.

Hermissenda crassicornis (Eschscholtz in Rathke). Keen, 1971: 840, pl. 2, fig. 6.

Hermissenda crassicornis (Eschscholtz). Oakes, 1979: 27. Jerussi & Alkon, 1980: 596 (*lapsus*).

Phidiana crassicornus (Eschscholtz). Cooper, 1980: 284.

Type-specimens: not listed.

Foot rather broad, thickened, bilabiate, and broadest anteriorly, tapered posteriorly to tail. Margins of foot are thin and extend laterally beyond body. Oral tentacles translucent grayish-white. Rhinophores weakly perfoliate, with 8–24 lamellae, shaft translucent grayish-white, clavus opalescent white to very pale blue. Cerata arranged in 5–11 groups dorsolaterally on either side of dorsum; first 2 groups separated medially by cardiac region, more posterior groups less well separated medially. General ground color translucent grayish-white. A median band of brilliant cadmium orange occurs between oral tentacles and passes between rhinophores, where it is narrowest, to anterior of cardiac region. An opalescent blue line occurs dorsally on either oral tentacle, becoming broader and bifurcating proximally. Inner portion of blue line extends between rhinophores, on either side of orange line, and continues dorso-medially to tip of tail. Outer portion of these blue lines extends dorso-laterally to tip of tail, and is interrupted by each group of cerata. Just ventral of this last blue line is an orange line on either side of head, extending from bases of oral tentacles to first group of cerata. A narrow, opalescent blue line extends posteriorly along dorsal margin of foot, from foot corners to tip of tail. Cerata tipped with white and each bears a subterminal band of cadmium orange which becomes lighter below. Occasionally specimens may bear a bluish-white band longitudinally on anterior surface of each ceras. Cerata cores usually light burnt umber to deep brown; occasionally specimens may be found which have greenish-gray cores. I have found these specimens on mudflats in pools with phoronids and presume they feed upon the phoronid lophophores. T.L.: 25 mm.

Anus on right, dorso-laterally, between second and third groups of cerata. Genital aperture on right side, ventral of first group of cerata. Penis unarmed.

Radular formula of specimen examined 25(0.0.1.0.0), MacFarland (1966: 361) reports 22–25(0.0.1.0.0), and Marcus (1961: 53) reports 28(0.0.1.0.0). Rachidian teeth (Fig. 108a) bear 3–6 rather long denticles on either side of large median cusp which bears 6–15 minute, irregular serrulations on distal ventral surface (Fig. 108b). Masticatory border of mandibles has about 50 denticles.

Type-locality: Sitka, Alaska.

Range and habitat: Sitka, Alaska (Bergh, 1879b), to Punta Eugenia, Baja California, Mexico (Lance, 1961); Isla Ángel de la Guarda, Gulf of California, Mexico (Farmer & Collier, 1963); Japan (Baba, 1937b); common in northern Gulf of California, Mexico (Keen, 1971). Intertidal to 37 m. Common in rocky intertidal and on floating docks and pilings in bays, occasional on mudflats in bays. Feeds upon various hydroids such as *Obelia* spp. (Harris, 1973). Harris (1971a) reports that it also eats small crustaceans and other nudibranchs. Birkeland (1974) reports that it feeds upon the pennatulacean *Ptilosarcus gurneyi*, the ascidian *Aplidium californicum*, and stranded specimens of the scyphozoans *Phacellophora camtschatica* and *Cyanea capillata*. Harrigan & Alkon (1978) raised specimens in the laboratory on *Ciona intestinalis*, mantle muscles of *Loligo pealii*, and *Mytilus edulis*. Cooper (1978) found that it eats the polyps and gonophores of the hydroid *Tubularia crocea*. Oakes (1979) fed it the hydroids *Aglaophenia struthionides* and *Sertularia furcata* in the laboratory. Also occasionally cannibalistic in captivity. This is probably the most common aeolid in California.

Remarks: The stomach of a buffalo sculpin (*Enophrys bison*) which was captured near the P. G. & E. outfall at Moss Landing, Monterey Co., California, contained numerous specimens of *P. crassicornis*, along with two specimens of the sea anemone *Anthopleura elegantissima*.

Additional references which mention *Hermissenda* and are certainly referable to *P. crassicornis* are: Alkon, 1975b; 1976a; 1979a; Alkon & Grossman, 1978a; Alkon *et al.*, 1978; Budelmann, 1976; DeFelice & Alkon, 1977a; Fuortes & O'Bryan, 1972; Kennedy, 1967; Mellon, 1974; Zack, 1974a; 1974b.

Dr. K. Baba (1979 and personal communication) agrees that the form which has a bluish-white band longitudinally on anterior surface of each ceras is identical with *Shinanoeolis emurai* (Baba, 1937), the latter therefore being a junior subjective synonym of *P. crassicornis*.

Phidiana hiltoni (O'Donoghue, 1927)

Facelina hiltoni O'Donoghue, 1927b: 104–105, pl. 3, figs. 70–71. Marcus, 1958: 59. Steinberg, 1961: 62.

Phidiana sp. Lance, 1961: 68.

Phidiana pugnax Lance, 1962a: 157–159, pl. 38, text figs. 4–8. Paine, 1963a: 4. Farmer & Collier, 1963: 63. Steinberg, 1963b: 72. Sphon, 1966: 245. Sphon & Lance, 1968: 80. Roller & Long, 1969: 427. Roller, 1970a: 372. Keen, 1971: 840. North, 1971: 58. Robilliard, 1971c: 429. Baker, 1972: 46, 48. Nybakken, 1974: 371. Abbott, 1974: 379, text fig. 4465. Bertsch & Ferreira, 1974: 351. Fitch & Lavenberg, 1975: 115. Thompson, 1976a: 33. Thompson, 1976b: 51, 66. McDonald & Nybakken, 1978: 115, 116. Russo, 1979: 46, 48. McCosker, 1980: 31.

Phidiana nigra MacFarland, 1966: 366–370, pl. 62, figs. 1–3; pl. 70, figs. 15–16a; pl. 71, figs. 15–20. Sphon & Lance, 1968: 80. Roller, 1970a: 372. Schmekel, 1970: 154. Nybakken, 1978: 135. Childs, 1980: 53.

Type-specimens: not listed.

Foot relatively broad, and thickened, bilabiate, and broadest anteriorly, and tapered posteriorly to tail; foot extends laterally well beyond body and is separated from it by a longitudinal groove. Oral tentacles bluish-white with a red-orange line on dorso-basal portion, which extends over mouth to opposite tentacle. Large specimens may also bear a short line of same color mid-ventrally on oral tentacles. Rhinophores perfoliate, with 14–22 lamellae and are pale orange-yellow with rich orange-yellow on proximal lamellae. Cerata cylindrical and slightly clavate, arranged in about 30 rows dorso-laterally. About first 10 rows are anterior of cardiac region and are separated by it medially. Remaining rows are posterior of cardiac region and not well separated medially. General ground color translucent grayish-white, with a slight opalescent blue cast on dorsal surface of foot. Large specimens may have an area of suffused orange-yellow anteriorly on head. Cerata rose pink distally, fading in intensity proximally, and tipped with white or gold; cores dark brown to almost black, rarely very dark green. T.L.: 40 mm.

Anus on right just anterior of second group of cerata. Genital aperture on right side, ventral of posterior edge of first group of cerata. Penis armed with minute, black chitinous hook.

Radular formula of specimen examined 17(0.0.1.0.0), MacFarland (1966: 367) reports 21(0.0.1.0.0). Rachidian teeth (Fig. 109) bear 3–4 small denticles on either side, just below cusp, and 4–6 larger denticles on either side below the smaller denticles. Masticatory border of mandibles bears 25–30 irregular, blunt denticles.

Type-locality: Laguna Beach, Orange Co., California.

Range and habitat: Monterey Bay, California (MacFarland, 1966), to Puerto Rompiente, Baja California, Mexico (Farmer & Collier, 1963); Gulf of Mexico (Childs, 1980). Intertidal to 220 m, sporadically abundant in rocky intertidal areas. McDonald & Nybakken (1978: 116) report that it feeds upon the hydroid *Hydractinia* sp. Lance (1962a: 159) states that it attacks other aeolids. Fitch & Lavenberg (1975: 115) state that they have found only nudibranchs, including *Phidiana pugnax*, in stomachs of the fish *Chirolophis nugator*.

Remarks: O'Donoghue (1927b: 104–105) described *Facelina hiltoni* from Laguna Beach, California. Except for references to the original description, this species has not been mentioned in the literature since the original description. O'Donoghue's description fails to mention some important characters (e.g. location of anus, penial stylet, etc.) but the information given seems sufficient to distinguish the species. In comparing the description of *F. hiltoni* with those of *P. pugnax* and its junior synonym *P. nigra,* I can find no significant differences. The shape of the radular teeth is certainly very similar (O'Donoghue, 1922b: fig. 71; Lance, 1962a: fig. 6; MacFarland, 1966: pl. 71, figs. 17–20). The radular formulae are similar, *P. pugnax* has 19 teeth and 6 or 7 denticles on either side of the median denticle (Lance, 1962b: 158), *P. nigra* has 21 teeth and 7–10 denticles on either side of the median denticle (MacFarland, 1966: 367), and *P. hiltoni* has 19 teeth and 7–8 denticles on either side of the median denticle (O'Donoghue, 1927b: 105). The masticatory border of the mandibles is denticulate in all three cases and the rhinophores are perfoliate. *P. pugnax* has 6 major groups of cerata with black cores (Lance, 1962b: 157–158); *P. nigra* has 5 groups of cerata with brown to black cores (MacFarland, 1966: 366–368); and *P. hiltoni* has 6 oblique rows of cerata with chocolate brown cores (O'Donoghue, 1927b: 104). The type-locality for *P. pugnax* is Point Loma, San Diego Co., California which is less 100 km from that of *P. hiltoni.* Although MacFarland's description of *P. nigra* was not published until 1966, he mentions having collected 10 specimens in 1932, showing that *P. pugnax* was known on the California coast at about the same time that *P. hiltoni* was described. The type-locality of *P. hiltoni* is also within the geographic range reported for *P. pugnax.* The above evidence is sufficient to establish the synonymy of *P. pugnax* with the previously enigmatic *P. hiltoni.* The fact that no other aeolid which even vaguely resembles *P. hiltoni* has been reported from the Pacific coast of North America lends additional support to the synonomy of the two species. Therefore, *P. pugnax* is a junior subjective synonym of *P. hiltoni,* the latter being the correct name by the law of priority.

Phidiana morroensis (Roller, 1972)

Emarcusia morroensis Roller, 1972: 420–423, text figs. 19–28.

Type-specimens: Calif. Acad. Sci., no. 490.

Foot linear, slightly wider than body, rather truncate and bilabiate anteriorly and tapered posteriorly to tail. Oral tentacles long, cylindrical, and slightly tapered to rather bluntly pointed tips, translucent grayish-white with numerous opaque white dots on distal third. Rhinophores smooth, pale orange on proximal two thirds and translucent grayish-white with numerous opaque white dots on distal third. Cerata arranged in 7–9 transverse rows which occur on slightly elevated ridges on either side of dorsum. Four or five rows occur anterior of cardiac region, and 3–4 rows are posterior of cardiac region. General ground color translucent grayish-white. Two oval, light orange spots occur dorso-medially on head, one just anterior and one just posterior of rhinophores; in occasional specimens these two spots may be connected by a narrow, light orange line which passes between rhinophores. A narrow, light orange line passes antero-laterally on either side of head, from anterior-most cerata onto proximal two thirds of oral tentacles. An irregular series of white dots occurs medially from head to posterior of cardiac region; an irregular, white line extends medially from posterior of cardiac region to posterior-most cerata row. Cerata translucent whitish, cores light ochre with scattered, dark brownish-black spots which are often concentrated in 3 bands, distal band darkest. A distinct reddish-brown band often occurs at bases of cerata; surface of cores bears numerous, opaque white dots. T.L.: 10 mm.

Anus on right in first post-cardiac row of cerata. Genital aperture on right side, ventral of second and third cerata rows. Penis armed with short, straight stylet.

Radular formula of specimen examined 24(0.0.1.0.0), Roller (1972: 422) reports 15–22(0.0.1.0.0). Rachidian teeth (Fig. 110) bear 6–10 very long denticles on either side of large, median cusp. Masticatory border of mandibles bears 2 rows of denticles, inner row with about 23 short denticles, and outer row with about 13 very small denticles.

Type-locality: Morro Bay, San Luis Obispo Co., California.

Range and habitat: Elkhorn Slough, Monterey Co., California (Roller, 1972), to San Diego, San Diego Co., California (Roller, 1972). Intertidal to 19 m, usually found in bays on floating docks and pilings, in association with hydroids upon which it probably feeds.

Phidiana stearnsi (Cockerell, 1901)

Facelina stearnsi Cockerell, 1901a: 86. Eliot, 1907: 331. O'Donoghue, 1926: 230. O'Donoghue, 1927b: 105–107, pl. 3, figs. 72–73. Marcus, 1958: 58. Steinberg, 1961: 62.

Type-specimens: not listed.

Foot rather narrow, bilabiate and rounded anteriorly and tapered posteriorly to sharp, pointed tail. Anterior foot corners bear a groove on ventral margin. Oral tentacles cream on distal third, scarlet-orange on medial third, and maroon-pink on proximal third. Rhinophores annulate with 10–13 annuli; tips cream-yellow, distal half scarlet-orange, shading to maroon-pink basally. Cerata cylindro-conical, quite long, and tapered distally to acute tips; arranged in 5–8 rows on slightly elevated ridges dorso-laterally on either side of dorsum. General ground color transcluent pinkish-white. An irregular, longitudinal band of brilliant vermilion to scarlet-orange occurs on either side of head, from base of oral tentacles to base of rhinophores, and a similar band occurs dorso-medially on tail. Irregular blotches of scarlet-orange to vermilion occur on either side of dorsum, between groups of cerata. Minute cream to white flecks occur between and posterior of bases of rhinophores. Foot corners colored as oral tentacles. Cerata translucent pinkish-maroon, each with a subapical band of scarlet-orange to vermilion below whitish tip which bears maroon flecks. Opaque white occurs below the subapical band and becomes more diffuse proximally; cores dark maroon-brown to pale olivaceous gray. T.L.: 15 mm.

Anus on right, just ventral and anterior of second group of cerata. Genital aperture on right side, just ventral of first group of cerata.

Radular formula of specimen examined 26(0.0.1.0.0), O'Donoghue (1927b: 106) reports 21–23(0.0.1.0.0). Rachidian teeth (Fig. 111) bear 4–6 denticles on either side of median cusp. Masticatory border of mandibles denticulate.

Type-locality: San Pedro, Los Angeles Co., California.

Range and habitat: Santa Barbara, Santa Barbara Co., California (preserved specimen, Calif. Acad. Sci.), to La Jolla, San Diego Co., California (personal observation). Intertidal in rocky areas and occasionally on mudflats. Quite uncommon.

Platydoris Bergh, 1877

Body doridiform, rather compressed dorso-laterally, equally rounded anteriorly and posteriorly. Dorsum smooth or minutely granular. Anterior margin of foot bilabiate. Labial tentacles digitiform. Rhinophores perfoliate and retractile. Branchial plumes 6 or 8, arranged in a circle around anus, retractile into a sheath with valvular lobes.

Labial disc unarmed. Radular formula 0.n.0.n.0, laterals numerous and hamate.

Penis armed with short spines.

Type-species: *Platydoris argo* (Linnaeus, 1758).

Platydoris macfarlandi Hanna, 1951

Platydoris macfarlandi Hanna, 1951: 1–3, pl. 2, figs. 1–5. Lance, 1961: 66. Steinberg, 1963b: 70. Roller & Long, 1969: 429. Abbott, 1974: 357.

Type-specimens: Calif. Acad. Sci., no. 9510.

Dorsum almost smooth, closely set with very minute papillae, causing dorsum to appear velvety. Foot truncate anteriorly and tapered posteriorly to a point. Labial tentacles well developed. General ground color deep, dark red. T.L.: 30 mm.

Radular formula of specimen examined 46(69–76.0.69–76). Laterals (Fig. 75) hamate.

Type-locality: Pismo Beach, San Luis Obispo Co., California.

Range and habitat: Off Pismo Beach, San Luis Obispo Co., California (Hanna, 1951); subtidal to 157 m.

Remarks: This species is known only from the original 3 specimens described by Hanna (1951). No further specimens have been reported and little is known about the species.

Polycera Cuvier, 1817

Body limaciform, highest in branchial region; with a dorso-lateral pallial ridge on either side. Anterior margin of head somewhat expanded, forming a frontal veil which bears digitiform processes. Labial tentacles short and lobiform. Rhinophores non-retractile and perfoliate. Branchial plumes non-retractile, arranged in a circle or semi-circle around anus. Extra-branchial appendages present.

Mandibles bear a wing-like process. Radular formula n.2.0.2.n. Laterals hamate, second lateral much larger than first. Marginals smaller and flattened.

Penis armed with small hooks.

Type-species: *Polycera quadrilineata* (Müller, 1776).

Polycera atra MacFarland, 1905

Polycera atra MacFarland, 1905: 50–51. MacFarland, 1906: 142–143, pl. 20, figs. 65–72; pl. 21, figs. 105, 111; pl. 29, fig. 22. Berry, 1907: 35. Hilton, 1919: 34. O'Donoghue, 1926: 217. Ingram, 1935: 48. Hewatt, 1937: 200. Costello, 1938: tab. 1. Odhner, 1941: 13, 17. Smith & Gordon, 1948: 180. Marcus, 1955: 159. Lance, 1961: 66. Steinberg, 1963b: 70. Paine, 1963a: 4. Collier & Farmer, 1964: 389. Paine, 1964: 385. Paine, 1965: 604, 607. MacFarland, 1966: 115–118, pl. 18, figs. 1–4; pl. 31, figs. 27–31. Marcus & Marcus, 1967a: 196–198. Sphon & Lance, 1968: 80. Haderlie, 1968: 333 ff. Haderlie, 1969: tabs. 1–2. Roller & Long, 1969: 428. Turner *et al.*, 1969: 137. Long, 1969c: 232. Gosliner & Williams, 1970: 179. Schmekel, 1970: 202. Robilliard, 1971b: 242. Keen, 1971: 827. Abbott, 1974: 359, pl. 17, fig. 4283. Lewbel & Lance, 1975: 346. Thompson, 1976a: 35. Nybakken, 1978: 135. Haderlie & Donat, 1978: 52, 60. McDonald & Nybakken, 1978: 112. (*Non*) Bernard, 1970: 85 (=*Polycera zosterae* O'Donoghue, 1924).

Type-specimens: U. S. Nat. Mus., no. 181278.

Pallial ridges extend from posterior of rhinophores to posterior of branchial plumes, where they unite and continue postero-medially as caudal crest, bearing a few small tubercles. Each pallial ridge bears five or more tubercles which are usually yellowish. Frontal veil bears 4–8 tapered, pointed processes, the medial being longest, and those located laterally shorter; these processes are dusky grayish-white with an orange-yellow band medially. Foot relatively narrow. Rhinophores bear 8–12 lamellae, and are translucent grayish-white, with a slightly dusky gray hue, each bears a subterminal band of orange-yellow on clavus, and a large triangular spot of like color on inner surface of shaft near base. Branchial plumes 7–11, unipinnate, dusky grayish, each with an orange spot distally on outer face, a larger spot proximally and a pale orange spot at base of inner face. There are usually 2–4 extra-branchial appendages borne upon the pallial ridge on either side of branchial plumes, the appendages are yellow-orange with grayish-white tips. General ground color pale grayish, with longitudinal black lines of various widths on dorsum and sides. Oblong spots of yellowish-orange occur everywhere between black lines, which may branch somewhat. T.L.: 12 mm.

Radular formula of specimen examined 9(2–4.2.0.2.2–4), MacFarland (1966: 117) reports 9–11(2–4.2.0.2.2–4). Laterals (Fig. 52a, b) hamate, first laterals (Fig. 52a) smaller and each bears a triangular expansion about midway on shaft, below cusp. Second laterals (Fig. 52b) larger and each has a rather triangular expansion proximally on shaft. Marginals (Fig. 52c, d) roughly triangular, they decrease in size outwardly, and each bears a longitudinal crest. Mandibles bear a thickened, oval cutting surface.

Type-locality: Monterey Bay, California.

Range and habitat: Limantour Estero, Marin Co., California (Gosliner & Williams, 1970), to Islas Coronados, Baja California, Mexico (Lance, 1961). Intertidal to 18 m, occasionally in rocky coastal areas, but more common on floating docks and pilings in bays where it feeds upon the bryozoan *Bugula pacifica* (MacFarland, 1966; McDonald & Nybakken, 1978); also reported to feed upon the encrusting bryozoan *Membranipora membranacea* and the gorgonian *Lophogorgia chilensis* (Lewbel & Lance, 1975; MacGinitie & MacGinitie, 1949).

Polycera hedgpethi Marcus, 1964

Polycera hedgpethi Marcus, 1964: 128–131, text figs. 1–4. Collier & Farmer, 1964: 389. Lance, 1966: 76. Marcus & Marcus, 1967a: 200. Sphon & Lance, 1968: 80. Roller & Long, 1969: 428. Robilliard, 1971b: 242. Farmer, 1971:19. Keen, 1971: 827, fig. 2352. Gosliner & Williams, 1973b: 354. Abbott, 1974: 359. Poorman & Poorman, 1978: 373. McDonald & Nybakken, 1978: 112.

Type-specimens: U. S. Nat. Mus., no. 575603.

Pallial ridges extend from posterior of frontal veil to posterior of branchial plumes where they unite and continue posteriorly as caudal crest. Frontal veil bears 4–6 cylindrical, tapered, pointed processes which are translucent grayish-white proximally and distally, with a narrow, subterminal band of gray-black dots and a wider proximal band of yellow; there are frequently gray-black dots scattered throughout the length of the processes. Foot relatively narrow, anterior corners slightly produced. Rhinophores bear 8–12 lamellae, clavus tipped with white and bears a subterminal band of yellow and numerous closely set gray-black dots proximally, which continue down onto shaft. Branchial plumes 7–9, tripinnate, translucent grayish-white, densely covered with numerous gray-black dots, and with a little yellow distally. There are 2–3 cylindrical, bluntly pointed, extra-branchial appendages on either side of branchial plumes; they converge somewhat posteriorly, and are translucent grayish-white, covered with various amounts of gray-black dots, especially proximally, and in a more or less distinct subterminal band, and with a band of yellow proximal of gray-black subterminal band. General ground color translucent grayish-white; dorsum, sides of body, head, and dorsal surface of tail densely covered with grayish-black dots, giving the animal an overall gray-black appearance. Pallial ridge and caudal crest are nearly devoid of grayish-black dots and may bear a few yellow dots. Tip of tail usually yellow. T.L.: 15 mm.

Radular formula of specimen examined 14(3–4.2.0.2.3–4), Marcus (1964: 131) reports 17(3–4.2.0.2.3–4). First laterals (Fig. 53a) hooked distally and each bears a low tubercle near the base. Second laterals (Fig. 53b) slightly larger and each is hooked at tip and bears a larger tubercle near base. Marginals (Fig. 53c–f) roughly rectangular. Masticatory border of mandibles smooth and thickened.

Type-locality: Tomales Bay, Marin Co., California.

Range and habitat: Tomales Bay, Marin Co., California (Marcus, 1964), to Mission Bay, San Diego Co., California (Lance, 1966); Bahía de los Ángeles, Gulf of California, Mexico (Lance, 1966). Intertidal to at least 5 m, usually on floating docks and pilings in bays, where it feeds upon the bryozoan *Bugula pacifica* (McDonald & Nybakken, 1978; Robilliard, 1971b).

Remarks: *Polycera gnupa* Marcus & Marcus (1967a: 198) is probably a synonym of *P. hedgpethi.*

Polycera tricolor Robilliard, 1971

Polycera sp. Lance, 1969: 3.
Polycera tricolor Robilliard, 1971b: 235–243, text figs. 1–10. Thompson, 1976b: 41.

Type-specimens: Calif. Acad. Sci., no. 447.

Pallial ridges extend from posterior of frontal veil to extra-branchial appendages, posterior of which they unite and continue postero-medially as caudal crest. Dorsum and sides of body bear a few scattered, low tubercles which are translucent grayish-white to pale yellow. Frontal veil bears 8–11 cylindrical, tapered, pointed processes, the medial processes longest and lateral processes shorter; they are white tipped, with a yellow band on distal one half to two thirds, and black on base and continuing onto frontal veil. Foot relatively narrow, anterior corners somewhat produced. Rhinophores bear 10–20 lamellae, clavus tipped with white with a subterminal band of yellow and proximal of this, a medial band of black. Branchial plumes 5–6, bi- and tripinnate, yellow on distal quarter to half and pale to deep black on proximal half to three quarters. There are 4–6 cylindrical, tapered, extra-branchial appendages borne on either side of branchial plumes; they converge posteriorly and are white tipped with a subterminal band of yellow on distal half to two thirds and translucent grayish-white proximally. General ground color translucent grayish-white; a yellow line extends around margin of foot, and may be discontinuous in some specimens; a dorso-medial line of the same color occurs on caudal crest. A narrow, discontinuous line of yellow occurs along pallial ridge; and a dorso-medial row of yellow tubercles occurs on dorsum, and a few scattered yellow tubercles occur elsewhere on dorsum and sides of body. T.L.: 15 mm.

Radular formula of specimen examined 13(3–4.2.0.2.3–4), Robilliard (1971b: 240) reports 9–16(3.2.0.2.3). First laterals (Fig. 54a) are hooked and each bears a denticle near base. Second laterals (Fig. 54b) are hooked but lack any distinct denticles. Marginals (Fig. 54c–f) roughly rectangular. Masticatory border of mandibles smooth and thickened.

Type-locality: Bamfield, Barkley Sound, British Columbia, Canada.

Range and habitat: Ucluelet, Vancouver Island, British Columbia, Canada (Robilliard, 1971b), to La Jolla, San Diego Co., California (Robilliard, 1971b). Subtidal to 60 m, usually in rocky areas. Relatively rare in central California. Robilliard (1971b: 240) states that it preys upon bryozoans.

Polycera zosterae O'Donoghue, 1924

Polycera zosterae O'Donoghue, 1924: 7–10, pl. 1, figs. 5–9. O'Donoghue, 1926: 217. Baba, 1937b: 291. Odhner, 1941: 17. LaRocque, 1953: 258. Marcus, 1957: 434. Steinberg, 1963b: 70. Collier & Farmer, 1964: 389. Bernard, 1970: 85. Robilliard, 1971b: 242. Gosliner & Williams, 1973a: 252–253. Abbott, 1974: 359. McDonald & Nybakken, 1978: 112.
Polycera atra MacFarland. Bernard, 1970: 85.

Type-specimens: not listed.

Pallial ridges extend from oral veil to branchial plumes, and both bear a series of low tubercles which are translucent grayish-white, encrusted with yellow and dark brown dots, the yellow being more concentrated distally. Similar tubercles occur elsewhere on dorsum and sides of body and are largest and most abundant just anterior of branchial plumes. Frontal veil bears 5–6 anterior tubercles on either side; these tubercles are grayish-white, encrusted with yellow dots. Foot relatively narrow. Rhinophores bear about 6 lamellae, and are translucent brownish with encrusting yellow and dark brown to black dots. Branchial plumes 3–5, bi- and tripinnate, dusky brownish-white, tipped with yellow dots and a scattering of dark brown to black dots. There are about 3–6 extra-branchial appendages on either side, postero-lateral of branchial plumes, they are whitish with yellow dots; the 3 posterior-most appear to arise from a common base. A dorso-medial row of tubercles passes from posterior of branchial plumes to tail. General ground color translucent grayish-white, with numerous small, brown to black dots and a lesser number of yellow dots over entire body, except ventral surface of foot. T.L.: 10 mm.

Radular formula of specimen examined 13(5.2.0.2.5), O'Donoghue (1924: 8) reports 15(5–6.2.0.2.5–6). Laterals are hamate, first laterals (Fig. 55a) smaller and each bears a denticle about midway on shaft, and a smaller denticle just below cusp. Second laterals (Fig. 55b) larger and each bears a small denticle near base. Marginals (Fig. 55c–g) roughly quadrangular and decrease in size outward. Mandibles bear a thickened cutting surface.

Type-locality: Newcastle Island, Vancouver Island, British Columbia, Canada.

Range and habitat: Shushartie Bay, Vancouver Island, British Columbia, Canada (Robilliard, 1971b), to Bodega Bay, Sonoma Co., California (Gosliner & Williams, 1973a). Intertidal and subtidal, in bays on floating docks and pilings, and on eelgrass (*Zostera marina*). This species occurs upon the bryozoan *Bowerbankia gracilis* var. *aggregata*, upon which it may feed. Robilliard (1971b: 242) reports that it feeds upon the bryozoan *Membranipora* sp.

Precuthona Odhner, 1929

Body aeolidiform. Anterior foot corners rounded, not produced. Cerata cylindrical, linear, and tapered to blunt tips, arranged in closely set transverse to slightly oblique dorso-lateral rows. Oral tentacles cylindrical and tapered to blunt tips. Rhinophores non-retractile, smooth, cylindrical, rather long, and tapered distally.

Masticatory border of mandibles denticulate. Radula uniseriate, with a few denticles on either side of median cusp.

Penis unarmed. Anus acleioproct.

Type-species: *Precuthona peachii* (Alder & Hancock, 1848).

Precuthona divae Marcus, 1961

Precuthona divae Marcus, 1961: 50–52, pl. 10, figs. 180–184. Steinberg, 1963b: 72. Sphon & Lance, 1968: 80. Roller & Long, 1969: 428. Roller, 1970a: 372. Gosliner & Williams, 1970: 179. Robilliard, 1971a: 164, 165. Bertsch *et al.*, 1972: 307. Nybakken, 1974: 371. Abbott, 1974: 377, text fig. 4454. Harris *et al.*, 1975: 264, 267. Christensen, 1977: 131. McDonald & Nybakken, 1978: 114. Williams & Gosliner, 1979: 214.

Cuthona rosea MacFarland, 1966: 326–332, pl. 59, figs. 1–2; pl. 68, figs, 1–7; pl. 70, figs. 9–10. Sphon & Lance, 1968: 80. Roller, 1970a: 372. Abbott, 1974: 377.

Cuthona divae (Marcus). Williams & Gosliner, 1979: 208, 210, 214, 215.

Type-specimens: Dept. Zool., Univ. São Paulo, Brazil.

Body slightly compressed dorso-ventrally, sides of body distinct from margin of foot. Foot elongate, widest and rounded anteriorly, tapered posteriorly to short, pointed tail. Oral tentacles long, cylindrical, and tapered to blunt tips, translucent cream to pinkish-brown. A true frontal veil is absent, but head broad and flattened ventrally and slightly extended laterally. Rhinophores colored as oral tentacles. Cerata rows widely separated antero-medially but converge postero-medially. First 2–3 rows anterior of rhinophores and consist of 3–4 cerata on either side. General ground color translucent cream to brownish-pink, cerata same color, tips encrusted with opaque white, cores reddish-brown to pink or burnt umber. T.L.: 15 mm.

Anus on right, just anterior of medial end of eighth row of cerata. Genital aperture on right side between fourth and fifth rows of cerata.

Radular formula of specimen examined 23(0.0.1.0.0), MacFarland (1966: 327) reports 28–32(0.0.1.0.0), and Marcus (1961: 51) reports 21 (0.0.1.0.0). Rachidian teeth (Fig.

115) each bear a large median cusp with 8–10 (rarely as few as 3) smaller denticles on either side. Masticatory border of mandibles bears a single row of 10–15 blunt denticles.

Type-locality: Dillon Beach, Marin Co., California.

Range and habitat: San Juan Island, Puget Sound, Washington (Robilliard, 1971a), to Dume Rock, Paradise Cover, Malibu, Los Angeles Co., California (personal observation). Intertidal to 18 m, occasional in rocky intertidal areas. Feeds upon the hydroid *Hydractinia* sp. (Christensen, 1977; Harris *et al.*, 1975; MacFarland, 1966) which it somewhat resembles.

Remarks: This species very closely resembles *Precuthona peachii* (Alder & Hancock, 1848) with which it may be conspecific.

Rostanga Bergh, 1879

Body doridiform, rather equally rounded anteriorly and posteriorly; dorsum densely covered with numerous minute papillae. Labial tentacles digitiform. Rhinophores perfoliate, retractile into sheaths. Branchial plumes retractile, usually unipinnate, arranged in a circle around anus.

Labial disc armed with small hooks. Radular formula 0.n.0.n.0. Inner laterals strongly hooked, grading to outer laterals which are thin and elongate.

Penis unarmed.

Type-species: *Rostanga coccinea* Forbes in Alder & Hancock, 1848.

Rostanga pulchra MacFarland, 1905

Rostanga pulchra MacFarland, 1905: 40–41. MacFarland, 1906: 119–122, pl. 18, figs. 18–21; pl. 24, fig. 8. Eliot, 1907: 330, 339–341. Berry, 1907: 34. Guernsey, 1912: 77, fig. 38A. Eliot, 1913: 20. O'Donoghue, 1922b: 152–154, 165, pl. 5, figs. 12–15. O'Donoghue, 1924: 23, 29. O'Donoghue, 1926: 208. O'Donoghue, 1927b: 82–83, pl. 1, figs. 10–12. deLaubenfels, 1927: 266. Boone, 1929: 38. Baba, 1933: 277. Baba, 1935a: 344, 345. Ingram, 1935: 48, 49. Baba, 1937e: 3. Costello, 1938: 327 ff, tabs. 1–5, pl. 1, figs. 13–15. Hewatt, 1946: 191, 193, 198. Smith & Gordon, 1948: 180. Rigg & Miller, 1949: 344. LaRocque, 1953: 258. Marcus, 1958: 25. Marcus, 1959: 3, 7, 35–37 ff, figs. 65–68. Marcus, 1961: 15–16, 57, pl. 3, figs. 46–49. Lance, 1961: 66. Cooke, 1962: 194–196. Farmer & Collier, 1963: 62. Steinberg, 1963b: 70. Paine, 1963a: 4. MacFarland, 1966: 165–169, 170, pl. 25, fig. 7; pl. 29, figs. 7–10; pl. 35, figs. 1–16. Lance, 1966: 69, 72. Hurst, 1967: 255 ff, text fig. 9, pl. 28, fig. 11; pl. 37, fig. 47; fig. 24-21. Sphon & Lance, 1968: 81. DuShane & Sphon, 1968: 244. Miller, 1968: 134. Roller & Long, 1969: 428. Long, 1969c: 232. Marcus & Marcus, 1969: 20–21. Fournier, 1969: 74. Burn, 1969: 82. Robilliard, 1969a: 290. Gosliner & Williams, 1970: 179. Marcus & Marcus, 1970: 202–203. Long, 1970: 19. Bernard, 1970: 85. Keen, 1971: 821. Harris, 1971a: 82, 85. Bertsch *et al.,* 1972: 307–308. Baker, 1972: 49. Sphon, 1972a: 156. Harris, 1973: 239–240, 269. Navoni, 1973: 1334. Anderson, 1973: 121, 122. Abbott, 1974: 353, pl. 17, fig. 4238. Haderlie, 1974: tab. 4. Thompson, 1975: 489, 490. Lambert, 1976: 297, 299. Bloom, 1976: 293, 295. Behrens & Tuel, 1977: 33, 35. Chia & Koss, 1978: 109–119, figs. 1–4. Hadfield, 1978: 167. Chia, 1978: 283. Nybakken, 1978: 134 ff. McDonald & Nybakken, 1978: 112. Bickell & Chia, 1979a: 306, 310.

Rostangia pulchra. Hewatt, 1937: 178 ff (*lapsus*).

Type-specimens: U. S. Nat. Mus., no. 181292.

Dorsum thickly set with numerous small, hispid papillae. Foot abruptly rounded and deeply bilabiate anteriorly, and slightly tapered posteriorly to short, bluntly pointed tail. Labial tentacles digitiform, long, and slender. Rhinophores bear 16–24 nearly vertical lamellae, shaft prolonged above clavus and bluntly tipped. Rhinophore sheaths bear papillate margins. Rhinophores orange to scarlet, lamellae darker shade of same color. Branchial plumes 8–12, unipinnate, orange to scarlet. General ground color orange to bright red or scarlet, although occasional specimens are light salmon pink. Dorsum sprinkled with minute dots of brown to black, the amount of which is quite variable. T.L.: 10 mm.

Radular formula of specimen examined 70(0.75.0.75.0), MacFarland (1966: 167) reports 68–80(81.0.81), and Marcus (1961: 16) reports 80(75–90.0.75–90), while Bloom (1976: 293) reports 65–80(39–90.0.39–90). First laterals (Fig. 57f) strongly hooked and bear 4–11 small denticles on hook. Succeeding about 10 laterals (Fig. 57c–e) strongly hooked. From about twelfth lateral outward, the hook lengthens and becomes more slender and less curved. Outermost laterals (Fig. 57a) quite elongate, with 1–7 very long denticles, appearing almost whisk-like.

Type-locality: Monterey Bay, California.

Range and habitat: Dundas Island, British Columbia, Canada (Lamber, 1976), to Point Loma, San Diego Co., California (Marcus, 1961); Bahía de los Ángeles, Gulf of California, Mexico (Lance, 1966); Chiloé Island, Chile (Marcus, 1961); Camarones Bay, Argentina (Marcus & Marcus, 1969). Intertidal to 102 m, frequent in rocky intertidal areas. Feeds upon the encrusting red sponges: *Acarnus erithacus, Esperiopsis originalis, Ophlitaspongia pennata, Plocamia karykina,* and *Plocamia lithophoenix* (Chia & Koss, 1978; Cook, 1962; deLaubenfels, 1927; MacFarland, 1966).

Remarks: Baba (1933: 277; 1935a: 344) synonymized *R. pulchra* with *Rostanga muscula* (Abraham, 1877), the latter being a synonym of *Rostanga arbutus* (Angas, 1864). However, Marcus (1958: 25; 1959: 36–37), Marcus & Marcus (1969: 21), and Burn (1969: 82) give ample evidence, based on the radula, for maintaining *R. pulchra* as a distinct species.

Sclerodoris Eliot, 1904

Body doridiform, rather equally rounded anteriorly and posteriorly; dorsum rough, with tubercles, pits, depressions and reticulate ridges developed to varying degrees. Spiculate sessile caryophyllidia and/or tubercles with retractile papillae may be present. Rhinophores perfoliate, retractile into crenulate sheaths. Branchial plumes retractile, tripinnate and bushy.

Radular formula 0.n.0.n.0. Laterals hamate, usually nondenticulate, outermost 3–4 teeth small and may be pectinate or serrated distally.

Type-species: *Sclerodoris tuberculata* Eliot, 1904.

I use here *Sclerodoris* sensu Rudman (1978). Bertsch (1981) gives ample evidence for the placement of the following species in this genus.

Sclerodoris tanya (Marcus, 1971)

Doris tanya Marcus, 1971: 357–362, text figs. 4–8. Sphon, 1973: 5. Marcus, 1973: 5.
Halgerda sp. Hertz, 1978: 90, fig. 1.
Sclerodoris tanya (Marcus). Bertsch, 1981: 217–220, figs. 2–7.

Type-specimens: Dept. Zool., Univ. São Paulo, Brazil (Marcus, personal communication).

Dorsum thickly set with numerous large, irregular tubercles which bear smaller tubercles. Foot rounded anteriorly and posteriorly, unilabiate anteriorly. Labial tentacles rather flattened and rounded distally. Rhinophores bear about 40 lamellae, clavus yellowish-tan, occasionally with a few darker tan markings. Branchial plumes 7, multi-pinnate, colored as dorsum, with a few tan to brownish flecks. General ground color light yellowish-tan, a number of darker tan to brown, irregularly round spots occur on dorsum between tubercles, smaller spots of similar color occur on tubercles. Ventral surfaces of foot and of mantle margin bear numerous irregular flecks of brown. T.L.: 30 mm.

Radular formula of specimen examined 29(32–37.0.32–37), Marcus (1971: 358) reports 23(0.33.0.33.0) and Bertsch (1981: 219) reports 21–26(25–43.0.25–43). Laterals (Fig. 72) hamate.

Type-locality: Newport Bay, Orange Co., California.

Range and habitat: Newport Bay, Orange Co., California (Marcus, 1971), to San Diego Flood Control Channel, Mission Bay, San Diego Co., California (personal observation); also Gulf of California, Mexico (Bertsch, 1981). Intertidal to 5 m in bays.

Spurilla Bergh, 1864

Body aeolidiform, broadest anteriorly and tapered posteriorly. Foot truncate anteriorly, anterior foot corners somewhat produced into triangular lobes. Cerata numerous, arranged in numerous transverse or oblique rows, and frequently decumbent; cnidosacs present. Rhinophores non-retractile, perfoliate, lamellae very oblique.

Masticatory border of mandibles smooth. Radula uniseriate, rachidian teeth rather bilobed and pectiniform, with the lateral denticles largest on the medial portion of either lobe.

Penis unarmed. Anus cleioproct.

The only character which seems to separate *Spurilla* from *Aeolidiella* Bergh, 1867, is the rhinophores, which are smooth in *Aeolidiella* and perfoliate in *Spurilla*. It should be determined whether any other characters exist which sufficiently distinguish the two genera. If none can be found, the shape of the rhinophores alone is probably not sufficient to separate genera. If this should be the case, they should be united under the oldest name, *Spurilla* Bergh, 1864.

Type-species: *Spurilla neapolitana* (Delle Chiaje, 1841).

Spurilla chromosoma Cockerell in Cockerell & Eliot, 1905

Spurilla chromosoma Cockerell in Cockerell & Eliot, 1905: 32, 51–52. Marcus, 1961: 54–56, 57, pl. 10, figs. 196–199. Steinberg, 1961: 62. Lance, 1961: 68. Farmer & Collier, 1963: 63. Paine, 1963a: 4. Lance, 1966: 80. Marcus & Marcus, 1967a: 227 (*partim*). Sphon & Lance, 1968: 81. DuShane & Sphon, 1968: 244. Burn, 1969: 97, 98. DuShane & Brennan, 1969: 361. Bertsch, 1970: 16. Williams & Gosliner, 1970: 33. Bertsch & Smith, 1970: 19. Farmer, 1971: 19. Keen, 1971: 839, pl. 22, fig. 2. Harris, 1973: 265. Bertsch, 1973: 110. Abbott, 1974: 381. Michel, 1976: 46, fig. 2. Poorman & Poorman, 1978: 373. McDonald & Nybakken, 1978: 115.

Spurilla sp. Guernsey, 1912: 78, fig. 39K. O'Donoghue, 1927b: 78. Steinberg, 1961: 62.

Eolidina chromosoma (Cockerell & Eliot). O'Donoghue, 1926: 234.

Eolidina orientalis O'Donoghue, 1927b: 109–110, pl. 3, fig. 78. Steinberg, 1961: 62.

Eolidina (*Spurilla*) *chromosoma* Cockerell & Eliot. O'Donoghue, 1927b: 109.

Type-specimens: not listed.

Foot broad, broadly rounded and bilabiate anteriorly, and tapered posteriorly to rather long, pointed tail; margins are thin and undulating and extend laterally beyond body. Foot corners produced into rather long, tentaculiform processes. Oral tentacles cylindrical, tapered, quite long, and white. Rhinophores bear about 10–12 lamellae, clavus red with white tip. Cerata arranged in about 13 crescentic, transverse rows. General ground color translucent grayish-white. Head orange dorsally. A row of opaque white blotches occurs dorso-medially between cerata rows. Anterior cerata have an orangish hue, tips are white and cores are greenish-gray. T.L.: 20 mm.

Anus on right, just posterior of sixth row of cerata. Genital aperture on right side, just ventral of third and fourth rows of cerata.

Radular formula of specimen examined 24(0.0.1.0.0), Marcus (1961: 55) reports 21(0.0.1.0.0). Rachidian teeth (Fig. 97) pectiniform with 24–32 denticles on either side of median denticle.

Type-locality: San Pedro, Los Angeles Co., California.

Range and habitat: Purisima Point, Santa Barbara Co., California (Sphon & Lance, 1968), to Tenacatita, Jalisco, Mexico (Keen, 1971). Intertidal to 18 m, usually found in rocky intertidal areas. Harris (1973: 265) reports that it feeds upon the sea anemone *Metridium senile.*

Spurilla oliviae (MacFarland, 1966)

Aeolidiella oliviae MacFarland, 1966: 373–377, pl. 62, figs. 4–6; pl. 72, figs. 9–14. Sphon & Lance, 1968: 81. Roller, 1970a: 372. Harris, 1973: 221, 260, 265. Schuler, 1975: 33.

Spurilla oliviae (MacFarland). Sphon & Lance, 1968: 81. Roller & Long, 1969: 428. Roller, 1970a: 372. Gosliner & Williams, 1970: 179. G. Williams, 1971: 215–216, text fig. 1. Nybakken, 1974: 371. Abbott, 1974: 381, fig. 4477. McDonald & Nybakken, 1978: 115.

Spurilla chromosoma Cockerell & Eliot. Marcus, 1961: 54–55 (*partim*). Nybakken, 1974: 371.

Type-specimens: type material at Calif. Acad. Sci.

Foot rather broad, somewhat thickened and bilabiate anteriorly and tapered posteriorly to moderately long tail; margins are thin and extend laterally beyond body. Foot corners produced into rather long, tentaculiform processes which bear a shallow groove. Oral tentacles cylindrical, about twice as long as rhinophores, and tapered to blunt tips; translucent grayish-white with encrusting white on distal half. Rhinophores bear 10–14 oblique lamellae which are orange-vermilion, shaft rather short and translucent grayish-white. Cerata decumbent and arranged in about 17 oblique rows, leaving dorsum free anteromedially, posterior groups less separated medially. General ground color translucent grayish-white, becoming rather cream on dorsum. A blotch of pale vermilion occurs on head and another occurs in cardiac region. Encrusting white occurs anteriorly on foot margin. Cerata chrome orange with white tips, cores raw umber. T.L.: 20 mm.

Anus right of cardiac region, between fifth and sixth rows of cerata. Genital aperture on right side, ventral of sixth and seventh rows of cerata.

Radular formula of specimen examined

27(0.0.1.0.0), MacFarland (1966: 374) reports 24(0.0.1.0.0). Rachidian teeth (Fig. 98) pectiniform with 20–35 denticles on either side of median denticle.

Type-locality: Point Pinos, Monterey Co., California.

Range and habitat: Duxbury Reef, Marin Co., California (Gosliner & Williams, 1970), to Point Fermin, Palos Verdes Peninsula, Los Angeles Co., California (Sphon, 1972b). Usually found under rocks in rocky intertidal zone. Harris (1973: 265) reports that it feeds upon the sea anemone *Metridium senile.*

Remarks: The range of variation in the color of this species is such that it may prove to be conspecific with *Spurilla chromosoma.*

Tenellia A. Costa, 1866

Body aeolidiform and rather narrow. Anterior foot corners not produced. Cerata cylindrical, slightly tapered distally, arranged in groups of 1–4, laterally along either edge of dorsum; cnidosacs present. Oral tentacles as such absent, in their place a frontal veil. Rhinophores non-retractile and smooth.

Masticatory border of mandibles finely denticulate. Radula uniseriate, rachidian teeth bear a few denticles on either side of median cusp.

Penis armed with a chitinous stylet. Anus acleioproct.

Type-species: *Tenellia adspersa* (Nordmann, 1845).

Tenellia adspersa (Nordmann, 1845)

Tergipes adspersus Nordmann, 1844: 270. Nordmann, 1845: 498, pl. 1, figs. 4–5. Nordmann, 1846: 110. Adams & Adams, 1854: 76. Gray, 1857: 229. Ostroumoff, 1893: 246. Sowinsky, 1904: 15, 144–145, 150, 310. Milachewitch, 1916: 132. Chukhchin, 1960: 111, text fig. 25. Gomoiu, 1961: 1251, fig. 4B. Gomoiu, 1966: 145, 146. Turpaeva, 1972: 168–185. Lemche, 1973: 90. Roginskaya, 1974a: 139.

Terpiges lacinulatus Blainville. Schultze, 1849: 268, text figs. 1–11. Roginskaya, 1974a: 138. Bonar, 1978: 178.

Eolis ventilabrum Dalyell, 1853: 318, pl. 45, fig. 28.

Embletonia pallida Alder & Hancock, 1854: 105. Byerley, 1854: 45. Alder & Hancock, 1855: 31, 32, 53, append. p. xii. Gosse, 1856: 100. Adams & Adams, 1858: 635. Collingwood, 1859: 469. Collingwood, 1860: 196, 202. Collingwood, 1861: 114. Sanford, 1861: fig. 1. Collingwood & Byerley, 1862: 189. Meyer & Möbius, 1865: 17–18, pl. Hensche, 1866: 105–106. Jeffreys, 1869: 36. Sars, 1878: pl. XVI, fig. 11. Bergh, 1885: 34–37, pl. 2, figs. 14–19; pl. 3, figs. 11–13; pl. 4, fig. 12; pl. 5, fig. 7. Herdman, 1886: 276, 277. Higgins, 1886: 26. Bergh, 1890a: 33. Bergh, 1893: 1026 (34). Herdman & Clubb, 1892: 146. Herdman, 1896: 49. Herdman *et al.,* 1896: 446. Cooke, 1899: 65. Conchol. Soc., 1901: 25. Odhner, 1907: 30, 81. Eliot, 1910: 1, 128–129, 171, pl. 6, figs. 1–2. Colgan, 1913: 165, 167. Sumner *et al.,* 1913: 706. Colgan, 1914: 181–182. Løyning, 1922: 65–69, 94, text figs. 44–50, pl. 3, figs. 13a–b. Iredale & O'Donoghue, 1923: 207. Naville, 1925: 812. Naville, 1926: 252–255, text figs. 1–2. Hoffmann, 1926: 18. Poisson, 1927: 68–69. Cuenot, 1927: 263. Jutting, 1927: LXXXVIII, XCVI. Løyning, 1927: 262. Winckworth, 1932: 237. Nicol, 1935: 215. Engel, 1936: 107. Lemche, 1938: 39. White, 1938: 15. Rasmussen, 1944: 207, figs. 15–20. Jutting, 1947: 64. Marcus & Marcus, 1955: 230, 238–242, pl. 38, figs. 23–31. Marcus & Marcus, 1958: 94, 95. Swennen, 1959: 59. Jaeckel, 1961: 140, fig. 2. Swennen, 1961: 217. Thompson, 1961: 236. Coomans, 1962: 222. Coomans & de Coninck, 1962: 1. Hadfield, 1963: 93. Thompson, 1964: 284 ff. Ghiselin, 1965: 351. Thompson, 1967: 12, 14, 18. Lawinski, 1968: 410, figs. 1–6. Bebbington & Thompson, 1968: 10. Tardy, 1970: 303. Salvini-Plawen, 1972: 394. Suckow, 1972: 193–194, figs. 1, 3, 4. Rasmussen, 1973: 22, 25, 29, 269–270, 447, 449. Lemche, 1973: 90. Harris, 1973: 217 ff. Roginskaya, 1974a: 138. Thompson, 1976a: 85, 86. Thompson, 1976b: 79. Bonar, 1978: 178. Harris *et al.,* 1980: 70.

Embletonia hyalina "(Alder & Hancock)." Sanford, 1861: 152, 153.

Tenellia mediterranea Costa, 1866: 76, pl. 3, fig. 7. Carus, 1889–1893: 211. Iredale & O'Donoghue, 1923: 231. Tardy, 1970: 359. Roginskaya, 1974a: 138.

Galvina adspersa (Nordmann). Bergh, 1868: 220.

Embletonia grayi Kent, 1869: 109, pl. 8. Gray, 1869: 247. Conchol. Soc., 1901: 25. Iredale & O'Donoghue, 1923: 207.

Embletonia ? pallidus (Alder & Hancock). Mörch, 1871: 184.

Eubranchus pallidus (Alder & Hancock). Jaeckel, 1952: 28.

Embletonia mediterranea (Costa). Bergh, 1892: 1026 (34). Poisson, 1927: 68. O'Donoghue, 1929: 747. Vannucci & Hosoe, 1953: 103–120, pls. 1–6. Hadfield, 1963: 92. Thompson, 1967: 9. Tardy, 1970: 303. Bonar, 1978: 178.

Tenellia ventilabrum (Dalyell). Pruvot-Fol, 1954: 413, text figs. 160a–d, g–l. Steinberg, 1963a: 65. Schmekel, 1968a: 121, 149. Schonenberg, 1969: 252. Tardy, 1970: 303 ff. Schmekel, 1970: 136, 169, text fig. 30b. Schmekel, 1971: 126. Abbott, 1974: 372. Barletta & Melone 1976: 226, 233. Bonar, 1978: 185, 190.

Tenellia pallida (Alder & Hancock). Marcus, 1957: 467. Marcus & Marcus, 1958: 95. Marcus & Marcus, 1960: 180–182, fig. 80. Steinberg, 1963a: 65. Steinberg, 1963b: 72. Baba & Hamatani, 1963a: 337–338, text fig. 1. Franz, 1968: 10. Marcus, 1970: 216. Marcus, 1972a: 314, fig. 8E. Roginskaya, 1974a: 139. Franz, 1975b: 253. Thompson & Brown, 1976: 180, fig. 97. Marcus, 1977: 15. Clark & Goetzfried, 1978: 289. Bonar, 1978: 178. McDonald & Nybakken, 1978: 114. Eyster, 1979: 133 ff. Eyster, 1980: 582 ff. Williams, 1980: 113.

Embletonia sp. Steinberg, 1960: 49.

Tergipes. Gomoiu, 1961: 1251, text fig. 4B.

Tenellia sp. Steinberg, 1963a: 65.

Stiliger bellulus (d'Orbigny). Chukhchin, 1963a: 149. Chukhchin, 1963b: 197. Chukhchin, 1963c: 218. Chukhchin, 1967: 102.

Tenellia adspersa (Nordmann). Turpaeva, 1969: 415. Roginskaya, 1970: 167–172, text figs. 1–4. Maksimov *et al.*, 1971: 902–907. Roginskaya, 1974a: 139. Turpaeva & Simkina, 1975: 1149, 1152. Turpaeva & Lebedeva, 1976: 1437, 1444. Cooper, 1978: 8. Williams & Gosliner, 1979: 215. Brown, 1980: 251–252, text fig. 7B. Cooper, 1980: 284.

Type-specimens: not listed.

Foot narrow, rather linear, quite truncate anteriorly and tapered posteriorly to short, bluntly pointed tail. Circular frontal veil extends slightly laterally beyond body. Rhinophores rather short, translucent grayish-white. Cerata cylindrical, only slightly tapered to blunt tips, arranged dorso-laterally on either side of dorsum in 5–6 groups of 1–2 cerata each. General ground color translucent yellowish-white, usually with a few small, black flecks on dorsum. Cerata translucent yellowish-white, occasionally tipped with orange and occasionally with a pale, powder blue hue distally; cores light yellowish to yellowish-brown. T.L.: 5 mm.

Anus on right, between second and third groups of cerata. Genital aperture on right side, ventral of first and second groups of cerata. Penis armed with chitinous stylet.

Radular formula of specimen examined 27(0.0.1.0.0), Eliot (1910: 129) reports 40(0.1.0). Rachidian teeth (Fig. 113) bear 5–8 denticles on either side of median cusp. Masticatory border of mandibles finely denticulate.

Type-locality: Black Sea, U.S.S.R.

Range and habitat: San Francisco Bay, California (Steinberg, 1963a), to Monterey Harbor, Monterey Co., California (Steinberg, 1963b); Europe (Marcus & Marcus, 1960); Japan (Baba & Hamatani, 1963a); Black Sea (Nordmann, 1845); Cananeia, Brazil (Marcus & Marcus, 1960). Intertidal to 8 m, usually in bays or estuaries on floating docks and pilings. Feeds upon the hydroids: *Bougainvillia glorietta, Bougainvillia muscoides, Cordylophora caspia, Cordylophora lacustris, Corydendrium dispar, Gonothyraea loveni, Laomedia gelatinosa, Laomedia longissima, Laomedia loveni, Obelia* sp., *Obelia dichotoma, Perigonimus megas, Podocoryne* sp., *Protohydra leuckarti,* and *Psammohydra* sp. (Cooper, 1980; Marcus & Marcus, 1955; Naville, 1926; Rasmussen, 1973; Salvini-Plawen, 1972; Sanford, 1861; Schmekel, 1968; Swennen, 1961; Thompson, 1964; Thompson & Brown, 1976; Turpaeva, 1972). This species is quite rare in central California.

Remarks: See ICZN (1977, Opinion 1084), *Tergipes adspersus* placed on Official List.

Thordisa Bergh, 1877

Body doridiform, rather evenly rounded anteriorly and posteriorly; dorsum usually papillate or granular. Anterior margin of foot bilabiate. Labial tentacles short and digitiform. Rhinophores perfoliate and retractile. Branchial plumes retractile and arranged in circle around anus.

Labial disc smooth. Radula bears numerous laterals and a few marginals. Laterals hamate, marginals bear numerous bristles distally.

Penis may be armed or not.

Type-species: *Thordisa maculigera* Bergh, 1877.

Thordisa bimaculata Lance, 1966

? *Thordisa.* Paine, 1963a: 4.
Aldisa sanguinea (Cooper). Farmer & Collier, 1963: 62.
Thordisa bimaculata Lance, 1966: 72–75, figs. 1–8. Sphon & Lance, 1968: 81. Roller & Long, 1969: 429. Abbott, 1974: 357.

Type-specimens: Calif. Acad. Sci., no. 100.

Dorsum thickly set with numerous, spiculate papillae of various sizes, which are larger medially and smaller marginally; larger papillae may be constricted at base. Foot rounded and bilabiate anteriorly, and slightly tapered posteriorly to bluntly pointed tail. Labial tentacles relatively short and digitiform. Rhinophores bear 14–16 lamellae which are bright orange to dull yellow with a brownish tinge, shaft colored as clavus but lacks brownish tinge. Rhinophore sheaths have papillate margins. Branchial plumes 6, bi- and tripinnate, somewhat lighter in color than dorsum and bear a few brown flecks on rachis and are encrusted with white. General ground color varies from bright orange to dull yellowish. Two concentrations of brown dots occur medially on dorsum, one just posterior of rhinophores and the other just anterior of branchial plumes. T.L.: 25 mm.

Penis armed with 7–10 longitudinally oriented, large spines.

Radular formula of specimen examined 32(6.25.0.25.6), Lance (1966: 74–75) reports 32(8.34.0.34.8) and 31(6.29.0.29.6). Innermost laterals (Fig. 69f) small and hamate, the laterals increase in size towards outermost laterals (Fig. 69d). Marginals (Fig. 69a–c) slightly hooked and bear numerous bristles distally. Labial disc has a tessellated surface.

Type-locality: Windnsea Reef, La Jolla, San Diego Co., California.

Range and habitat: Carmel, Monterey Co., California (Lance, 1966), to Isla de Natividad, Baja California, Mexico (Lance, 1966). Intertidal to 30 m, usually in rocky areas. This species is rare, especially in the northern part of its range.

Tochuina Odhner, 1963

Body limaciform, rather subquadrate, somewhat depressed dorso-ventrally and tapered posteriorly. The numerous branchial appendages are plumose and arranged dorso-laterally along either margin of dorsum. Dorsum tuberculate. Foot broad. Anterior margin of head somewhat expanded, forming a frontal veil which is tuberculate. Rhinophores retractile, and bear plumose processes distally.

Masticatory border of mandibles smooth. Radular formula n.1.1.1.n. Rachidian teeth bear a blunt cusp. Laterals short, blunt hooks; marginals rather hamate.

Penis unarmed. Anus on right side, beneath margin of dorsum.

Type-species: *Tochuina tetraquetra* (Pallas, 1788).

Tochuina tetraquetra (Pallas, 1788)

Limax tetraquetra Pallas, 1788: 237, 239, pl. 5, fig. 22. Odhner, 1963: 50.
Doris tetraquetra (Pallas). Gmelin in Linnaeus, 1791: 3106.
Tritonia tetraquetra (Pallas). Bosc, 1830: 108. Bergh, 1879b: 98–105, pl. 3, figs. 13–16; pl. 4, figs. 5–12; pl. 5, figs. 1–2. Bergh, 1879c: 154–161, pl. 3, figs. 13–16; pl. 4, figs. 5–12; pl. 5. figs. 1–2. Bergh, 1881b: 237. Bergh, 1884b: 701, 726–727. Bergh, 1892: 1068 (76). Cockerell & Eliot, 1905: 33. O'Donoghue, 1922b: 146–149, 165, pl. 5, figs. 1–5. Odhner, 1926a: 32. Odhner, 1936: 1080. Baba, 1937a: 197. Marcus, 1961: 32. Willows, 1965: 707 ff. Willows, 1968: 226. Willows & Dorsett, 1975: 118. Willows, 1976: 329 ff.
Tritonia sp. Eliot, 1901: 163–165, text figs. 1–2.
Tritonia gigantea Bergh, 1904: 26–28, pl. 4, figs. 29–32. Cockerell & Eliot, 1905: 33. Odhner, 1926a: 32. Marcus, 1961: 32. Odhner, 1963: 50. MacFarland, 1966: 241.
Sphaerostoma tetraquetra (Pallas). O'Donoghue, 1924: 3. O'Donoghue, 1926: 204. LaRocque, 1953: 261.
Tritoniopsis tetraquetra (Pallas). Odhner, 1926a: 32, 33. Odhner, 1936: 1080. Marcus, 1961: 32. Odhner, 1963: 50. Steinberg, 1963b: 71.
Tritoniopsis gigantea (Bergh). Odhner, 1936: 1080.
Tritoniopsilla tetraquetra (Pallas). Baba, 1937b: 312.
Duvaucelia tetraquetra (Pallas). Baba, 1937a: 197, 199. Smith & Gordon, 1948: 180. MacFarland, 1966: 207, 208–218 ff, pl. 30, figs. 3–8; pl. 39, figs. 8–10; pl. 43, figs. 1–9; pl. 44, fig. 1; pl. 45, figs. 1–5. Roller, 1970a: 372. Bernard, 1970: 85.
Tritoniopsis aurantia Mattox, 1955: 8–13, pls.

4–5. Marcus, 1961: 32. Lance, 1961: 67. Sphon & Lance, 1968: 81.

Tochuina tetraquetra (Pallas). Odhner, 1963: 50. Sphon & Lance, 1968: 81. Baba, 1969b: 134. Roller & Long, 1969: 429. Roller, 1970a: 372. Thompson, 1971: 334–335, text fig. 1. Wicksten & DeMartini, 1973: 195. Abbott, 1974: 369. Birkeland, 1974: 212. Belcik, 1975: 276. Lambert, 1976: 297. Thompson & Brown, 1976: 2. Thompson, 1976a: 3. Thompson, 1976b: 6, 7, 91. McDonald & Nybakken, 1978: 113.

Trochuina tetraquetra (Pallas). Baba, 1968a: 257–258, text figs. 1–5 (*lapsus*).

Tritonia (*Tochuina*) *tetraquetra* (Pallas). Robilliard, 1969a: 290.

Type-specimens: not listed.

Dorsum bears numerous white tipped tubercles. Foot nearly as broad as dorsum and rather linear, bilabiate and rather truncate anteriorly, and slightly tapered posteriorly to short bluntly rounded tail; margins project laterally beyond sides of body. Upper surface of foot well set off from sides of body, orange-yellow to yellowish-brown, slightly lighter than dorsum and bears white tipped tubercles; sole of foot light salmon pink to yellow, dorsal margin edged with a band of white. Antero-dorsal surface expanded into broad frontal veil which extends laterally as thin, rounded lobes; dorsal surface bears a few white tipped tubercles, and is a slightly lighter shade of color of dorsum, ventral surface a slightly darker shade of foot color. Labial tentacles are almost obscure, located at outer angle of frontal veil, they are short and externally grooved. Rhinophores bear 6–10 short, vertical, bi- to tripinnate plumose processes which encircle shaft below tip, posterior-most process adnate to shaft, others free. The tapered rhinophore shaft terminates distally in a blunt, cylindrical tip. Rhinophores retractile into high sheaths with thick walls and thin, nearly smooth margins; outer surface of sheath tuberculate, antero-lateral margins cleft. A single, irregular series of white, bi- and tripinnate plumose branchial appendages occurs along undulating body margins on either side, from the area of rhinophores, posteriorly to tip of foot. General ground color orange-yellow to brownish-yellow or almost gray-yellow. T.L.: 120 mm, but specimens over 300 mm have been collected.

Anus on right side, close beneath dorsolateral margin, posterior of genital aperture.

Radular formula of specimen examined 64(162–212.1.1.1.162–212), MacFarland (1966: 213) reports 50–94(225–312.1.225–312). Rachidian teeth (Fig. 87e) slightly elongated, with a blunt cusp posteriorly and deeply notched anteriorly. Laterals (Fig. 87d) somewhat elongated. Marginals (Fig. 87a–c) somewhat hooked.

Type-locality: Kuril Islands, U.S.S.R.

Range and habitat: Unalaska, Alaska (Bergh, 1879b), to Santa Catalina Island, California (Mattox, 1955); northern Japan (Baba, 1969b), to Kuril Islands. Subtidal to 363 m, usually in areas of rocky or mud and cobble bottom. Feeds upon the alcyonacean *Gersemia rubiformis* (Wicksten & DeMartini, 1973: 195), and the pennatulacean *Ptilosarcus guerneyi* (Birkeland, 1974: 212; Thompson, 1971: 335).

Remarks: Bergh (1879c: 154) quotes Pallas as saying he obtained the animal from the Kuril Islands, "where the inhabitants eat it, raw or cooked, and where it is known by the name of Tochni."

Trapania Pruvot-Fol, 1931

Body limaciform, elongate, smooth, and arched dorsally. Anterior foot corners tentaculiform. Labial tentacles rather long and digitiform. Rhinophores non-retractile and perfoliate; at base of each is a digitiform extra-rhinophoral appendage. Branchial plumes non-retractile, arranged around anus. On either side, lateral of branchial plumes, occurs a digitiform extra-branchial appendage.

Labial disc armed with denticles. Radular formula 0.1.0.1.0, laterals rather broad with a denticulate margin.

Penis armed with spines.

Type-species: *Trapania fusca* (Lafont, 1874).

Trapania velox (Cockerell, 1901)

Thecacera velox Cockerell, 1901a: 87. Kelsey, 1907: 50. Cockerell, 1908: 106. O'Donoghue, 1922d: 139–140. O'Donoghue, 1926: 217. O'Donoghue, 1927a: 11. MacFarland, 1931: 32.

Drepania velox (Cockerell). MacFarland, 1929: 487–496, pl. 35, figs. 1–15. Baba, 1935a: 337–338.

Drepanida velox (Cockerell). MacFarland, 1931: 32.

Trapania velox (Cockerell). Marcus, 1957: 443. Lance, 1961: 67. Steinberg, 1963b:

71. Paine, 1963a: 4. Lance, 1966: 78. MacFarland, 1966: 127–129, pl. 20, figs. 1–3; pl. 32, figs. 17–24. Sphon & Lance, 1968: 81. Roller & Long, 1969: 428. Kress, 1970: 115. Marcus, 1972b: 297. Abbott, 1974: 364, text fig. 4340.

Type-specimens: not listed.

Foot elongate, linear, and set off from body by a narrow, thin ridge; anterior margin broadly emarginate, bearing a series of small, anteriorly directed, whitish papillae. Foot corners produced into long, tapered, blunt tentaculiform processes which are whitish and are slightly grooved ventrally. Labial tentacles cylindrical, long, and tapered to blunt tips; with a broad, medial band of cadmium yellow to orange, leaving tip and base white. Rhinophores bear 10–12 lamellae; clavus cadmium yellow to orange on distal half and whitish on proximal half and on shaft. On external base of rhinophore shaft is a horizontal, cylindrical, bluntly pointed extra-rhinophoral appendage with a subterminal ring of cadmium yellow to orange and a wide, oblique band of dark brown just proximal of subterminal ring. Branchial plumes 3, uni- and bipinnate, whitish with cadmium yellow to orange distally, and with a dark brown, rather oval spot on outer basal surface of rachis of each plume. A horizontal digitiform extra-branchial appendage occurs immediately antero-laterally of branchial plumes on either side; distal third of each is cadmium yellow to orange, leaving extreme tip white, a dark brown line extends along dorsal surface of proximal half of each appendage. General ground color translucent grayish-white. A narrow, median dark brown line extends posteriorly from frontal margin, between rhinophores to anterior of branchial plumes, where it joins the two lines from the extra-branchial appendages. A similar line extends from posterior of branchial plumes to tip of tail which bears a subterminal band of yellow, the extreme tip white. Another similar dorso-lateral line extends longitudinally on either side from just posterior of rhinophores nearly to tip of tail, being interrupted just ventral of branchial plumes. All of these brown lines vary in width and continuity. T.L.: 15 mm.

Penis armed with curved spines.

Radular formula of specimen examined 22(0.1.0.1.0), MacFarland (1966: 128) reports 24(0.1.0.1.0). Laterals (Fig. 42) somewhat convex, bearing 8–24 irregular denticles along one edge, usually with one denticle considerably longer than the others.

Type-locality: La Jolla, San Diego Co., California.

Range and habitat: Hazard Canyon, San Luis Obispo Co., California (Roller & Long, 1969), to San Diego, San Diego Co., California (Lance, 1961). Intertidal to 6 m, usually found in rocky intertidal and subtidally on a white sponge on pier pilings. Quite rare in California.

Remarks: Cockerell (1901a: 87) mentions that this species swims with an undulating motion on the surface of the water.

Triopha Bergh, 1880

Body limaciform and elongate. An indistinct dorso-lateral pallial ridge on either side of dorsum bears a number of irregular (tuberculate or short-branched) processes. Frontal margin somewhat expanded into a veil-like process, the margin of which bears processes similar to those on pallial ridge. Labial tentacles short, blunt, and auriform, usually with a longitudinal groove on distal half. Rhinophores perfoliate, retractile into rather prominent sheaths. Branchial plumes non-retractile, usually tripinnate, arranged around anus, usually five in number.

Mandibular plates triangular, with short, closely-set rodlets. Radular formula n.n.2–4.n.n. Rachidian plates spurious. Laterals hooked; marginals quadrilateral.

Penis armed with minute hooks.

Type-species: *Triopha catalinae* (Cooper, 1863).

Triopha catalinae (Cooper, 1863)

Triopa catalinae Cooper, 1863b: 59. Carpenter, 1864: 609. Cooper, 1870: 56. Abraham, 1877: 230. Ferreira, 1977: 388.

Triopa carpenteri Stearns, 1873a: 78, fig. 2. Stearns, 1873b: 209, fig. 2. Abraham, 1877: 230. Ferreira, 1977: 388.

Triopha carpenteri (Stearns). Bergh, 1880a: 262. Bergh, 1880b: 112. Tryon, 1883: 376. Bergh, 1892: 1140 (146). Bergh, 1894: 184. MacFarland, 1905: 48–49. Cockerell & Eliot, 1905: 43. MacFarland, 1906: 135–137, pl. 19, figs. 51–55; pl. 21, figs. 108, 113; pl. 27, figs. 16–17. Berry, 1907: 35. Cockerell, 1908: 107. Cockerell, 1915: 228–229. O'Donoghue, 1921: 167. O'Donoghue, 1922b: 164. O'Donoghue, 1922d: 136–138. O'Donoghue, 1926: 214, 238.

O'Donoghue, 1927b: 96–97, pl. 2, figs. 45–47. Hewatt, 1937: 200. Costello, 1938: 321 ff, tabs. 1–3, 5, pl. 1, figs. 11, 21; pl. 2, figs. 26, 31, 38–40. Hewatt, 1946: 195, 198. Smith & Gordon, 1948: 180. Baba, 1957: 8, 11, text figs. 1, 2A. Marcus, 1961: 22–23, 57, pl. 4, fig. 71. Thompson, 1961: 235. Steinberg, 1961: 60. Lance, 1961: 66. McLean, 1962: 110. Paine, 1963a: 4. Steinberg, 1963b: 70. Willows, 1965: 707 ff. MacFarland, 1966: 106–109, 115, pl. 19, figs. 3–4; pl. 29, figs. 4–6; pl. 31, figs. 13–18. Ghiselin, 1966: 333, 345. Hurst, 1967: 255 ff, pl. 28, fig. 12; fig. 24-9. Buchsbaum & Milne, 1967: pl. 67. Sphon & Lance, 1968: 81. Roller & Long, 1969: 428. Haderlie, 1969: tab. 2. Turner *et al.*, 1969: 137–138. Long, 1969c: 232. Robilliard, 1969a: 290. Gosliner & Williams, 1970: 179. McBeth, 1970: 28. Bernard, 1970: 85. Thompson, 1971: 334. McBeth, 1971: 158, 159. Bertsch *et al.*, 1972: 308. Sphon, 1972a: 156. McBeth, 1972a: 55 ff. McBeth, 1972b: 69. Thompson & Bebbington, 1973: 148, pl. 14, figs. a–b. Harris, 1973: 240, 281, 287. Abbott, 1974: 360, pl. 17, 4295. Robilliard, 1974b: 990. Birkeland, 1974: 218. Belcik, 1975: 276. Lambert, 1976: 297. Thompson, 1976a: pl. 2, fig. a. Thompson, 1976b: 37, 70. Nybakken & Eastman, 1977: 279–289. Ferreira, 1977: 387–391. O'Clair, 1977: 443. Nybakken, 1978: 134 ff. Haderlie & Donat, 1978: 60. McDonald & Nybakken, 1978: 111. Fuhrman *et al.*, 1979: 292. Dickinson, 1979: 277 ff, text figs. 1A–B. Russo, 1979: 48.

Triopha modesta Bergh, 1880a: 261–266, pl. 14, figs. 17–20; pl. 15, figs. 1–11. Bergh, 1880b: 113–117, pl. 14, figs. 17–20; pl. 15, figs. 1–11. Bergh, 1892: 1140 (146). Bergh, 1894: 184–187, pl. 7, fig. 29; pl. 8, figs. 2–12; pl. 9, figs. 1–12. MacFarland, 1905: 49. Cockerell & Eliot, 1905: 43. MacFarland, 1906: 137, 141. O'Donoghue, 1922d: 137–138. O'Donoghue, 1926: 215. Thiele, 1931: 424. LaRocque, 1953: 258. Marcus, 1961: 22–23. MacFarland, 1966: 106, 109, 115. Ferreira, 1977: 388, 390.

Triopa modesta. Fischer, 1887: 527.

Triopha catalinae (Cooper). Cockerell, 1915: 229. O'Donoghue, 1922d: 138. O'Donoghue, 1926: 214. Smith & Gordon, 1948: 180. Marcus, 1961: 23, 56. Steinberg, 1961: 60. Lance, 1961: 66. Abbott, 1974: 360. Ferreira, 1977: 388, 389–396, figs. 1–11, 16. Bertsch, 1977: 109.

Triopha scrippsiana Cockerell, 1915: 228–229. O'Donoghue, 1922d: 137–138. O'Donoghue, 1926: 215. Marcus, 1961: 23. Steinberg, 1961: 60. Lance, 1961: 66. Abbott, 1974: 360. Ferreira, 1977: 388, 390.

Triopha elioti O'Donoghue, 1921: 165–167. Marcus, 1961: 23. Steinberg, 1961: 60. Steinberg, 1963b: 70. MacFarland, 1966: 115. Ferreira, 1977: 388, 390.

Type-specimens: not listed, State Coll. species 1002 (Cooper, 1863b).

Pallial ridge bears 4–9 slightly prolonged, large orange tubercles which bear very small branches or tubercles. Dorsum, dorsal surface of tail, and sides of body bear a number of irregular, orange tubercles and blotches of various sizes. Margin of frontal veil bears 7–16 or more irregularly lobed, orange processes. Foot rounded anteriorly and elongate with nearly parallel margins extending to abruptly pointed tail. Rhinophores bear 20–30 lamellae, clavus inclined slightly posteriorly, orange, shaft translucent grayish-white. Rhinophore sheaths bear thin, smooth margins. Branchial plumes 5, tripinnate, translucent grayish-white with orange tips. General ground color translucent grayish-white, very large specimens may occasionally be quite grayish. T.L.: 40 mm.

Radular formula of specimen examined 45(12–14.14.4.14.12–14), MacFarland (1966: 107) reports 33(9–14.9–18.4.9–18.9–14), and Marcus (1961: 23) reports 29–33(9–20.9–18.4.9–18.9–20). Rachidian plates (Fig. 46k–l) very rudimentary and thin, innermost quadrangular, outer triangular. Laterals (Fig. 46h–j) strongly hooked, marginals (Fig. 46a–g) quadrilateral.

Type-locality: Santa Catalina Island, California.

Range and habitat: Auke Bay, Alaska (Robilliard, 1974b), to San Diego, San Diego Co., California (Lance, 1961); Japan (Baba, 1957). Intertidal to 80 m. Common in rocky intertidal and subtidal areas, occasional on floating docks and pilings in bays. Feeds upon the bryozoans: *Bugula mollis, Caulibugula ciliata, Cauloramphus spiniferum, Cellaria mandibulata, Crisia occidentalis, Crisia serrulata, Dendrobeania laxa, Filicrisia franciscana, Scrupocellaria californica, Scrupocellaria diegensis,* and *Tricellaria* sp. (McBeth, 1971; Nybakken & Eastman, 1977).

Triopha maculata MacFarland, 1905

Triopha maculata MacFarland, 1905: 49. Cockerell & Eliot, 1905: 43. MacFarland, 1906: 137–139, pl. 19, figs. 55a–59; pl. 21, figs. 106–107; pl. 28, fig. 18. Berry, 1907: 35. Baily, 1907: 92. Cockerell, 1915: 229. O'Donoghue, 1922b: 165. O'Donoghue, 1922d: 137–138. O'Donoghue, 1926: 214–215. O'Donoghue, 1927b: 98–99, pl. 2, figs. 51–53. Hewatt, 1937: 200. Costello, 1938: 321 ff, tabs. 1–3, 5. Smith & Gordon, 1948: 180. Marcus, 1961: 23–24, pl. 4, figs. 72–76. Steinberg, 1961: 61. Lance, 1961: 66. Farmer & Collier, 1963: 62. Paine, 1963a: 4. Steinberg, 1963b: 70. Paine, 1964: 385. Paine, 1965: 607. MacFarland, 1966: 109–112, 115, pl. 19, figs. 5–6; pl. 31, figs. 19–21. Farmer, 1967: 341. Sphon & Lance, 1968: 81. Roller & Long, 1969: 428. Gosliner & Williams, 1970: 180. North, 1971: 58. Bertsch *et al.,* 1972: 308, tabs. 1–5. Harris, 1973: 281. Abbott, 1974: 360, pl. 17, fig. 4296. Ferreira, 1977: 396–400, figs. 12–15, 17–18 (*partim*). Bertsch, 1977: 109. Bloom & Bloom, 1977: 296. Nybakken, 1978: 134 ff. Haderlie & Donat, 1978: 60. McDonald & Nybakken, 1978: 112. Fuhrman *et al.,* 1979: 292. Russo, 1979: 48.

Triopha aurantiaca Cockerell, 1908: 107. Cockerell, 1915: 229. O'Donoghue, 1922d: 137–138. O'Donoghue, 1926: 214. Fraser, 1932: 67. LaRocque, 1953: 258. Marcus, 1961: 115. Steinberg, 1961: 60–61. Lance, 1961: 66. MacFarland, 1966: 115. Bernard, 1970: 85. Abbott, 1974: 360. Ferreira, 1977: 387, 388, 396.

Triopha sp. Cockerell & Eliot, 1905: 42–43. Sphon & Lance, 1968: 81. Roller & Long, 1969: 428. Bertsch *et al.,* 1972: 308, tabs. 2, 4, 5. Ferreira, 1977: 387, 396.

Type-specimens: U. S. Nat. Mus., no. 181276.

Pallial ridge bears 4–6 orange to vermilion, slightly prolonged processes which are slightly branched or bear tubercles distally. Margin of frontal veil bears 10–12 stout processes which bear a few tubercles distally and are orange. Foot bluntly rounded anteriorly, elongate with nearly parallel margins extending to abruptly pointed tail. Rhinophores bear about 16–18 lamellae, clavus inclined slightly posteriorly, orange; shaft slightly lighter orange. Rhinophore sheaths bear thin, smooth margins. Branchial plumes 5–7, tripinnate, orange, tipped with darker orange to vermilion. General ground color varies from clear, light orange in young specimens to darker orange or yellow brown in larger specimens. In larger specimens, dorsum bears numerous round to oval, pale blue spots and more numerous small, dark brown dots. T.L.: 15 mm.

Radular formula of specimen examined 14(8–10.1–5.4.1–5.8–10), MacFarland (1966: 110) reports 14(7–8.4–5.4.4–5.7–8), and Marcus (1961: 24) reports 13–17(7–10.3–5.4.3–5.7–10). Rachidian plates (Fig. 48i–j) very rudimentary and thin. Laterals (Fig. 48f–h) strongly hooked. Marginals (Fig. 48a–e) quadrangular.

Type-locality: Monterey Bay, California.

Range and habitat: Bodega Bay, Sonoma Co., California (Marcus, 1961), to Ensenada, Baja California, Mexico (Farmer & Collier, 1963). Intertidal to 28 m, quite common in rocky intertidal areas in central California. Nybakken & Eastman (1977: 288) report that it feeds upon the bryozoans: *Bugula mollis, Caulibugula ciliata, Cauloramphus spiniferum, Crisia occidentalis, Dendrobeania laxa, Filicrisia franciscana, Membranipora membranacea, Scrupocellaria californica,* and *Tricellaria* sp.

Triopha occidentalis (Fewkes, 1889)

Cabrilla occidentalis Fewkes, 1889: 140–141, fig. O'Donoghue, 1926: 215. Steinberg, 1961: 60. Ferreira, 1977: 389.

Triopha grandis MacFarland, 1905: 50. Cockerell & Eliot, 1905: 43. MacFarland, 1906: 139–141, pl. 19, figs. 60–64; pl. 28, fig. 19. Cockerell, 1915: 229. O'Donoghue, 1922b: 165. O'Donoghue, 1922d: 137–138. O'Donoghue, 1926: 214. O'Donoghue, 1927b: 97–98, pl. 2, figs. 48–50. Costello, 1938: 321, 325, tabs. 1–3, 5, pl. 1, fig. 7. Smith & Gordon, 1948: 180. Lance, 1961: 66. Marcus, 1961: 23. Steinberg, 1963b: 70. MacFarland, 1966: 112–115, pl. 19, figs. 1–2; pl. 31, figs. 22–26. Farmer, 1967: 341. Sphon & Lance, 1968: 81. Haderlie, 1968: 333, 338. Haderlie, 1969: tabs. 1, 2. Roller & Long, 1969: 428. Gosliner & Williams, 1970: 180. Mulliner, 1972a: 38. Mulliner, 1972b: 3, figs. Abbott, 1974: 360, pl. 17, fig. 4297. Ferreira, 1977: 387, 388, 396, 397.

Triopha maculata MacFarland. Ferreira, 1977: 396–400, figs. 12–15, 17–18 (*partim*).

Type-specimens: not listed.

Pallial ridge bears 4–6 irregular, prolonged processes which bear small branches or tubercles, and are yellow-orange to vermilion. Margin of frontal veil bears 7–12 tuberculate or branched, yellow-orange to vermilion or pale burnt sienna processes. Foot rounded anteriorly, elongate with nearly parallel margins extending to abruptly pointed tail. Rhinophores bear 15–20 lamellae, clavus inclined slightly posteriorly and is yellow-orange to vermilion, shaft slightly paler. Rhinophore sheaths bear thin, smooth, slightly flared margins. Branchial plumes 5–6, tri- and quadripinnate, pale yellow-orange to almost white with yellow-orange to vermilion tips. General ground color varies from pale yellow-ochre to dark yellow-brown, with yellow orange being most frequent. Dorsum bears numerous light powder blue spots which may be almost white, or extremely faint in some specimens: T.L.: 40 mm.

Radular formula of specimen examined 11(2–8.2–4.2.2–4.2–8), MacFarland (1966: 113) reports 18(8.7.2.7.8). Rachidian plates (Fig. 47k–l) extremely rudimentary, thin, and squarish. Laterals (Fig. 47i–j) strongly hooked. Marginals (Fig. 47a–h) rather quadrilateral.

Type-locality: Prisoner's Harbor, Santa Cruz Island, California.

Range and habitat: Limantour Estero, Drakes Bay, Marin Co., California (Gosliner & Williams, 1970), to San Quintín, Baja California, Mexico (Farmer, 1967). Intertidal to 30 m, occasional on floating docks in bays, in association with the alga *Macrocystis pyrifera*; also in offshore kelp (*M. pyrifera* and *Nereocystis luetkeana*) beds.

Remarks: Ferreira (1977: 396) considered *Triopha grandis* a junior synonym of *Triopha maculata.* In reviewing his reasons for doing so, I feel that the evidence which he presents is insufficient to synonymize the two species. Especially since I have seen juveniles and adults of both species and feel that they are reasonably easily separable. The correlation between the number of hooks vs. number of plates per half-row of radula (Ferreira, 1977: 399) does not seem sufficient reason to consider the two species synonymous. Further study is certainly necessary to resolve the question.

Fewkes (1889: 139–141) described the new genus and species *Cabrilla occidentalis* on the basis of a single specimen from Santa Cruz Island, California. Although a number of authors (O'Donoghue, 1926; Steinberg, 1961; Ferreira, 1977) have felt that the description is very poor and therefore difficult to compare to known species, it seems that the description corresponds very closely to that of *Triopha grandis* MacFarland, 1905. The body color of *C. occidentalis* is greenish-brown covered with light green spots (Fewkes, 1889: 140) while that of *T. grandis* varies from pale yellow-ochre to dark yellow-brown with light blue spots (MacFarland, 1966: 113). *C. occidentalis* has 4 large processes on either edge of the dorsum anterior of the branchial plumes and 2 smaller ones posterior of the branchial plumes, while *T. grandis* has 4–6 processes on either side of the dorsum (MacFarland, 1966: 112). The figure of *C. occidentalis* (Fewkes, 1889: 140) shows 7 or 8 velar processes, and *T. grandis* has 8–12 processes. Fewkes (1889: 140) states that *C. occidentalis* has "lens-like bodies" on the apex of the dorso-lateral processes, MacFarland (1966: 112) mentions that *T. grandis* has a dim white mass at the apex of each appendage "probably the 'lens' of Fewkes." The number of branchial plumes in *C. occidentalis* is not mentioned by Fewkes; he says simply: "The branchiae are stellate, bipinnate, consisting of primary arms and lateral branches, of white color, transparent." *T. grandis* has 5–6 pale yellow-orange to white, tri- to quadripinnate branchial plumes. The bipinnate branchial plumes and their lateral branches (of *C. occidentalis*) may be considered as tri- or quadripinnate plumes. The type-locality of *C. occidentalis* is within the range known for *T. grandis,* and *C. occidentalis* was found on the anchor of a buoy, while *T. grandis* is most often found on buoys, floating docks, or in kelp holdfasts. These facts seem to indicate that *C. occidentalis* is conspecific with *T. grandis,* in which case the latter is a junior subjective synonym of the former, the proper name being *Triopha occidentalis* (Fewkes, 1889) by the law of priority. Further, specimens have been collected which match the description of *C. occidentalis* much more closely than that of *T. grandis* (i.e. they are brownish with light green spots and the rhinophores are brownish distally, as described for *C. occidentalis*). It therefore seems certain that *C. occidentalis* is a valid species, and although some may consider it distinct from *T. grandis,* I consider them conspecific.

Tritonia Cuvier, 1798

Body limaciform, rather subquadrilateral, and somewhat depressed dorso-ventrally. Branchial appendages plumose and arranged in a longitudinal series, dorso-laterally on either side of dorsum. Dorsum smooth or bears small tubercles. Foot broad. Antero-dorsal surface expanded into broad frontal veil which extends laterally and may be rounded or bilobed and usually bears digitiform processes. Rhinophores retractile into high sheaths, and bear a few plumose processes distally.

Masticatory border of mandibles denticulate. Radular formula n.1.1.1.n. Rachidian teeth bear a median cusp and are broader than in *Tochuina.* Laterals short, blunt hooks; marginals hamate.

Penis unarmed. Anus on right side, beneath margin of dorsum.

Type-species: *Tritonia hombergi* Cuvier, 1803 (see ICZN, 1963, Opinion 668).

Tritonia diomedea Bergh, 1894

Tritonia diomedea Bergh, 1894: 146–150, pl. 2, figs. 10–11; pl. 3, figs. 6–10; pl. 4, figs. 1–5. Cockerell & Eliot, 1905: 33. Marcus, 1959: 68. Marcus, 1961: 57. Steinberg, 1963b: 71. Sakharov, 1966: 957. Dorsett, 1967: 140. Michelson, 1970: 108. Thompson, 1971: 335–336, text fig. 2. Sanchis & Castro, 1972: 181. Dorsett *et al.,* 1973: 287. Thompson, 1976a: 23, pl. 5, fig. d. Thompson, 1976b: 55, 59. Kempf & Willows, 1977: 261 ff. Getting, 1977: 325 ff. Bonar, 1978: 178. McDonald & Nybakken, 1978: 113. Harrigan & Alkon, 1978b: 299. Taghert & Willows, 1978: 253 ff. Audesirk & Audesirk, 1979: 79 ff, text figs. 2A–F. Dickinson, 1979: 278, text fig. 1D. Bulloch & Dorsett, 1979: 20. Strathmann & Leise, 1979: 524 ff. Lennard *et al.,* 1980: 165 ff. Getting *et al.,* 1980: 151 ff.

Tritonia exsulans Bergh, 1894: 150–152, pl. 3, figs. 11–12; pl. 4, fig. 6. Cockerell & Eliot, 1905: 33. O'Donoghue, 1921: 152–154, pl. 1 (7), figs. 4–6. Baba, 1937b: 310–312, text fig. E. Baba, 1957: 9. Marcus, 1959: 68. Marcus, 1961: 32–33, 56, 57, pl. 6, figs. 115–118. Lance, 1961: 67. Steinberg, 1963b: 71. Willows, 1965: 707 ff. Hurst, 1967: 255 ff, text figs. 18a–d, pl. 31, fig. 24; pl. 37, fig. 48; fig. 24-14. Marcus & Marcus, 1967a: 123. Sphon & Lance, 1968: 81. Willows, 1968: 242. Roller & Long, 1969: 428. Roller, 1970a: 372. Thompson, 1971: 336–337. Keen, 1971: 834. Bertsch *et al.,* 1972: 308. Holleman, 1972a: 60. Goddard, 1973: 10. Gosliner & Williams, 1973b: 354. Abbott, 1974: 368. Willows & Dorsett, 1975: 118.

Tritonia diomedia Bergh. O'Donoghue, 1921: 151–152, pl. 1 (7), figs. 1–3. Volodchenko, 1955: 249, pl. 48, fig. 3. Veprintsev *et al.,* 1964: 352, 354. Borovyagin *et al.,* 1965: 104 ff. Sakharov *et al.,* 1965: 660 ff. Sakharov, 1965: 365. Borovyagin & Sakharov, 1965a: 642 ff. Borovyagin & Sakharov, 1965b: 458, 463. Gerasimov & Magura, 1965: 360, 363. Antonov *et al.,* 1965: 1200. Manokhina, 1966: 93 ff. Turpayev *et al.,* 1967: 619, 621. Dorsett, 1967: 140. Sakharov & Turpaev, 1968: 305. Borovyagin & Sakharov, 1968: 3 ff. Kostyuk, 1968: 146. Bezruchko *et al.,* 1969: 1107 ff. Bezruchko *et al.,* 1970: 1073 ff. Bezruchko *et al.,* 1971: 460 ff. Minichev, 1971: 282, 284. Willows, 1971: 69. Abraham & Willows, 1971: 271, 272. Junge, 1972: 975. Krasts & Veprintsev, 1972: 289–290. Adzhimolaev *et al.,* 1972: 79 ff. McCaman *et al.,* 1973: 129. Willows *et al.,* 1973a: 207. Willows *et al.,* 1973b: 255 ff. Willows *et al.,* 1973c: 461. Faugier & Willows, 1973: 244. Adzhimolaev *et al.,* 1973a: 60. Adzhimolaev *et al.,* 1973b: 129. Getting & Willows, 1973: 424. Hoyle & Willows, 1973: 239, 240. Willows, 1973b: 200. Weinreich *et al.,* 1973: 970 ff. Adzhimolaev *et al.,* 1973c: 131 ff. Getting, 1974: 846. Chase, 1974a: 707. Chase, 1974b: 721. Getting & Willows, 1974: 858. Grieshaber *et al.,* 1974: 168. Willows & Dorsett, 1975: 117 ff. Zack, 1975b: 239. Chase, 1975: 37. Getting, 1975: 128. Dorsett, 1975: 292, 309. Partridge, 1975: 161 ff. Willows, 1976: 329 ff. Getting 1976: 271 ff. Hoyle, 1976: 33, fig. 2. Kuz'min *et al.,* 1976: 231. Thompson, 1977: 465 ff. Tomosky-Sykes *et al.,* 1977: 99. Willows, 1978: 155 ff. Audesirk, 1978a: 259 ff. Audesirk, 1978b: 541 ff. Audesirk, 1979: 71 ff. Audesirk, McCaman & Willows, 1979: 87 ff. Gakhova *et al.,* 1979: 313 ff. McCaman, Ono & McCaman, 1979: 1111 ff (*lapsus*).

Sphaerostoma diomedia (Bergh). O'Donoghue, 1924: 3. LaRocque, 1953: 261 (*lapsus*).

Sphaerostoma exsulans (Bergh). O'Donoghue, 1924: 3. O'Donoghue, 1926: 204. LaRocque, 1953: 261.

Sphaerostoma diomedea (Bergh). O'Donoghue, 1926: 204.

Duvaucelia diomedea (Bergh). Odhner, 1926a: 35. MacFarland, 1966: 241 ff. Bernard, 1970: 85.

Duvaucelia exsulans (Bergh) . Odhner, 1926a: 35. Baba, 1937a: 199. Smith & Gordon, 1948: 180. MacFarland, 1966: 212, 223, 226–235 ff, pl. 30, figs. 9–10; pl. 39, fig. 7; pl. 43, figs. 20–26; pl. 44, figs. 3–4. Roller, 1970a: 372. Bernard, 1970: 85.

Duvaucelia (*Duvaucelia*) *exsulans* (Bergh). Baba, 1937b: 310–312, text fig. 9. Baba, 1937d: 391. Baba, 1957: 9.

Duvaucelia (*Duvaucelia*) *diomedea* (Bergh). Baba, 1937d: 391.

Duvaucelia (*Duvaucelia*) *septemtrionalis* Baba, 1937d: 391–392, text figs. 1A–E.

Duvaucelia gilberti MacFarland, 1966: 223, 224, 235–243, pl. 30, figs. 1–2; pl. 43, figs. 27–36; pl. 44, fig. 5; pl. 45, fig. 6. Roller, 1970a: 372.

Tritonia gilberti (MacFarland). Willows, 1967a: 570, 571. Willows, 1967b: 796. Willows & Hoyle, 1967: 327. Willows, 1968: 219, 242. Mauzey *et al.*, 1968: 609. Willows & Hoyle, 1968: 443. Willows & Hoyle, 1969: 1549. Dorsett *et al.*, 1969: 711. Robilliard, 1969a: 290. Roller, 1970a: 372. Konishi, 1971: 60. Rose, 1971: 185. Harris, 1973: 228 ff. Birkeland, 1974: 212.

Tritonia primorjensis Minichev, 1971: 282–284, text figs. 1–5.

Tritonia (*Duvaucelia*) *diomedea* (Bergh). Abbott, 1974: 368.

Tritonia (*Duvaucelia*) *gilberti* MacFarland. Abbott, 1974: 369.

Tritonia esculans. Willows, 1976: 349 (*lapsus*).

Tritonia diamedia. Audesirk, 1978b: 541 ff (*lapsus*).

Type-specimens: not listed.

Dorsum covered with numerous, very small tubercles. Foot somewhat broader than dorsum and rather linear, rounded and bilabiate anteriorly and slightly tapered posteriorly to short, rather blunt tail. Foot margins but slightly set off from body. Margin of slightly bilobed frontal veil bears about 10–30 light pink to almost white, digitiform processes; lateral processes somewhat longer than medial processes, lateral-most process on either side bears a ventral longitudinal groove. Rhinophores bear about 20 short, vertical, bipinnate, plumose, very pale yellow to brownish processes which encircle shaft below tip, posterior processes adnate to shaft, others free distally. The slightly tapered rhinophore shaft terminates in a white, blunt tip. Rhinophore sheaths bear thin, nearly smooth, white margins. A single, irregular series of very pale yellow to brownish, bi- to tripinnate plumose branchial appendages occurs dorso-laterally on either side of dorsum, from just posterior of rhinophores to tip of foot. General ground color pinkish, dorsum a deep rose-pink, sides of body and frontal veil lighter. A narrow white line borders edge of foot; a similar line occurs on anterior edge of frontal veil. An indistinct, broken line of white may occur on dorso-lateral body margins, between branchial appendages. A white line occurs vertically on inner surface of rhinophore sheath and continues down onto frontal veil. T.L.: 150 mm.

Anus on right, close beneath dorso-lateral margin, posterior of genital aperture.

Radula formula of specimen examined 69(87–95.1.1.1.87–95), MacFarland (1966: 229) reports 44–55(64–82.1.1.1.64–82), Baba (1937b: 312) reports 65(75–95.1.1.1.75–95), and O'Donoghue (1921: 153) reports 45–52(60–64.1.1.1.60–64). Rachidian teeth (Fig. 88f) tricuspidate with median cusp longer than lateral cusps. Marginals (Fig. 88a–d) hooked.

Type-locality: Shumagin Bay, Aleutian Islands, Alaska.

Range and habitat: Shumagin Bay, Aleutian Islands, Alaska (Bergh, 1894), to Bay of Panama, Panama (Sphon, 1972b); Japan (Baba, 1957); Okhotsk Sea (Volodchenko, 1955); Florida (Marcus, 1961). Intertidal to 656 m. Not uncommonly taken in bottom trawls on mud-sand bottom in central California. Feeds upon the pennatulaceans: *Ptilosarcus gurneyi* and *Virgullaria* sp. (Audesirk & Audesirk, 1979; Birkeland, 1974; Thompson, 1971; Willows, 1978).

Remarks: Thompson (1971: 333) reviewed the family Tritoniidae from the North American Pacific coast and found that the only possible character for separating *Tritonia diomedea* and *Tritonia exsulans* is the shape of the penis. The difference in shape, which Thompson observed, could easily be attributed to differences in preservation technique. Since all other observable characters fail to differentiate the two species, and since they occur in the same area, they are here considered conspecific and the name *Tritonia diomedea* is used since it has priority by being described on the pages immediately preceding the description of *Tritonia exsulans. Tritonia palmeri* Cooper, 1863, while possibly synonymous with *T. diomedea,* has been declared a nomen dubium by Thompson (1971: 334) because the original description is so poor. Minichev (1971) described *Tritonia primorjensis* from the northern part of the Sea of Japan, stating that it may be differentiated from *T. diomedea* most of all by its narrower radula and by the lobed edge of the rhinophore cavities and the spiny jaws. The radular formula for *T. primorjensis* is 50–75(89–100.1.1.1.89–100) (Minichev, 1971: 282) and the total body length is 8–18 cm (Minichev, 1971: 282), while Thompson (1971: 336) gives the radula formula 65(89.1.89) for a 16 cm specimen of *T. diomedea.* Minichev (1971: 283) states that the lobed edge of the rhinophore cavities distinguishes *T. primorjensis* from *T. diomedea.* However, MacFarland (1966: 235) states that *T. gilberti* (a junior syonym of *T. diomedea*) has irregularly crenulate rhinophore sheaths. The masticatory border of the mandibles of *T. primorjensis* bears plates which grade into spines (Minichev, 1971: 282) while the mandibles of *T. exsulans* bear large conical denticles grading to plate-like markings (MacFarland, 1966: 229). It is apparent that Minichev (1971) compared his specimens only with the description of *T. diomedea* in Bergh (1894) and not with any of the more recent descriptions of specimens of *T. diomedea.* From the above discussion it is obvious that *T. primorjensis* is a junior subjective synonym of *T. diomedea.* In addition, Soviet workers have continued to use the name *T. diomedea* and have not used *T. primorjensis* at all. Baba (1937d) described *Duvaucelia* (*Duvaucelia*) *septemtrionalis* from the Sea of Okhotsk. He distinguished it from *T. diomedea* by its larger radular formula, 80(100–115.1.1.1.100–115), and larger number of branchial plumes (29–30). However, Bergh (1894: 148) gives the radular formula 73(140–150.1.1.1.140–150) in the original description of *T. diomedea.* Thompson (1971: 335) mentions 7–8 major gills and 20–24 smaller plumes on either side of the dorsum. It is therefore obvious that *T. septemtrionalis* does not differ significantly from *T. diomedea* and is therefore a junior subjective synonym of *T. diomedea.*

Additional references which mention *Tritonia* sp., and are referable to *T. diomedea* are: Dorsett, 1976; Field & MacMillan, 1973; Gulrajani & Roberge, 1978; Harth *et al.*, 1975; Kennedy *et al.*, 1969; Lloyd, 1979; Manokhina & Kuz'mina, 1972; Martin & Manning, 1974; McCaman, McCaman, & Stetzler, 1979; Mellon, 1974; Pentreath, 1977; Pentreath & Barry, 1977; Plant, 1979; Salanki & Willows, 1978; Veprintsev *et al.*, 1966; Veprintsev & D'yakanova, 1967; Willows, 1973a.

Tritonia festiva (Stearns, 1873)

Lateribranchiaea festiva Stearns, 1873a: 77–78, text fig. 1. O'Donoghue, 1926: 218. Costello, 1938: 321, 324, tabs. 1, 5.

Lateribranchiaia festiva Stearns. Stearns, 1873b: 209, text fig. 1 (*lapsus*).

Tritonia reticulata Bergh, 1881b: 239–250, pl. 8, figs. 7–20; pl. 9, figs. 1–12; pl. 10, figs. 1–10. Bergh, 1884b: 727. Baba, 1937b: 310. MacFarland, 1966: 241.

Sphaerostoma undulata O'Donoghue, 1924: 3–6, pl. 1, figs. 1–4. O'Donoghue, 1926: 205. LaRocque, 1953: 261. Steinberg, 1961: 62. Marcus, 1961: 57. MacFarland, 1966: 241.

Duvaucelia reticulata (Bergh). Odhner, 1927a: 34.

Duvaucelia undulata (O'Donoghue). Odhner, 1936: 1078. Baba, 1940: 107.

Duvaucelia (*Duvaucelia*) *undulata* var. *muroranica* Baba, 1940: 106–107, text figs. 6A–C.

Tritonia undulata (O'Donoghue). Marcus, 1959: 69.

Lateribranchia festiva Stearns. Steinberg, 1961: 61 (*lapsus*).

Sphaerostoma festiva (Stearns). Steinberg, 1961: 61.

Tritonia festiva (Stearns). Marcus, 1961: 31–32, 57, pl. 6, figs. 109–114. Steinberg, 1961: 61–62. Lance, 1961: 67. Paine, 1963a: 4. Steinberg, 1963b: 71. Willows, 1965: 707 ff. Willows, 1968: 226. Baba, 1968b: 258–259, figs. 1–2. Sphon & Lance, 1968: 81. Baba, 1969a: 132–134, fig. 1. Bertsch, 1969: 231. Roller & Long, 1969: 428. Long, 1969c: 232. Robilliard, 1969a: 290. Roller, 1970a: 372. Gosliner & Williams, 1970: 180. Thompson, 1971: 337–338, text fig. 3. North, 1971: 58. Bertsch *et al.*, 1972: 308. Sphon, 1972a: 156. Gomez, 1973: 163–165, text fig. 1. Harris, 1973: 305. Thompson, 1973: 167 ff, text fig. 8, pl. 2, fig. F. Nybakken, 1974: 371. Abbott, 1974: 368, text fig. 4366. Birkeland, 1974: 211 ff. Lewbel & Lance, 1975: 346. Belcik, 1975: 276. Willows & Dorsett, 1975: 118. Lambert, 1976: 297, 299. Michel, 1976: 47, fig. 5. Thompson, 1976a: 17, text fig. 11b. Thompson, 1976b: 71. Nybakken, 1978: 135. McDonald & Nybakken, 1978: 110, 113. Robilliard & Barr, 1978: 153. Bertsch, 1980: 224.

Duvaucelia festiva (Stearns). MacFarland, 1966: 212, 218–226 ff, pl. 39, figs. 1–6; pl. 43, figs. 10–19; pl. 44, fig. 2; pl. 45, figs. 7–8. Grigg & Kiwala, 1970: 151. Bernard, 1970: 85.

Type-specimens: not listed.

Dorsum smooth, lacking tubercles. Foot somewhat broader than dorsum, rather linear; rounded and slightly bilabiate anteriorly and tapered posteriorly to rather blunt tail.

Margin of slightly bilobed frontal veil bears about 7–12 long, tapered, white processes; lateral processes somewhat longer than medial processes; lateral-most process on either side bears a ventral longitudinal groove. Rhinophores bear about 8–10 vertical, uni- to bipinnate, plumose, yellowish processes which encircle shaft below tip, posterior-most process adnate to shaft, others free, at least distally. Tapered rhinophore shaft terminates distally in blunt, white tip. Rhinophore sheaths bear thin, undulating, white margins. A single, rather irregular, undulating series of about 11–15, yellowish, bi- to tripinnate, plumose branchial appendages occurs dorso-laterally on either side of dorsum, from just posterior of rhinophores, posteriorly almost to tail. General ground color varies from pure white to cream, light cadmium yellow, or occasionally, burnt sienna. A series of white, reticulate lines and loops occurs on dorsum. An opaque white line occurs along edge of foot; similar lines occur on anterior margin of frontal veil and transversely on head between rhinophores up onto rhinophore sheaths. T.L.: 20 mm.

Anus on right, close beneath dorso-lateral margin, posterior of genital aperture, and ventral of fifth or sixth branchial appendage.

Radular formula of specimen examined 32(16–34.1.1.1.16–34), MacFarland (1966: 221) reports 57(49.1.49), and Marcus (1961: 31) reports 37(33.1.1.1.33). Rachidian teeth (Fig. 89d) tricuspidate with median cusp longer than lateral cusps. Laterals (Fig. 89c) broadly triangular with a slight hook distally. Marginals (Fig. 89a, b) compressed hooks. Masticatory border of mandibles bears 3–9 rows of denticles.

Type-locality: Point Pinos, Monterey Co., California.

Range and habitat: Port Dick, Kenai Peninsula, Alaska (Robilliard & Barr, 1978), to Islas Coronados, Baja California, Mexico (Lance, 1961); Japan (Baba, 1969a). Not uncommon in low rocky intertidal to 10 m under rocks and ledges, often in areas of heavy surf. Feeds upon the pennatulacean *Ptilosarcus gurneyi*, the gorgonian *Lophogorgia chilensis*, and the alcyonarian *Clavularia* sp. (Birkeland, 1974; Gomez, 1973; McDonald & Nybakken, 1978).

Remarks: Thompson (1971: 337) reports that this species is capable of swimming, and Birkeland (1974: 224) states that it escapes from its asteroid predators *Crossaster papposus* and *Solaster dawsoni* by swimming off the substratum.

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REFERENCES CITED

ABBOTT, R. T., 1974, *American seashells, the marine Mollusca of the Atlantic and Pacific coasts of North America.* Ed. 2, Van Nostrand Reinhold, New York, 633 p., 24 pl.

ABE, T., 1964, *Opisthobranchia of Toyama Bay and adjacent waters.* Hokuryu-kan, Tokyo, ix + 99 p., 36 pl.

ABILDGAARD, P. C., 1789, *In* MÜLLER, O. F., *Zoologica Danica.* Ed. 3, 3: 1–71, pl. 81–120.

ABOUL-ELA, I. A., 1959, On the food of nudibranchs. *Biological Bulletin,* 117: 439–442.

ABRAHAM, F. D. & WILLOWS, A. O. D., 1971, Plasticity of a fixed action pattern in the sea slug *Tritonia diomedia. Communications in Behavioral Biology,* (A) 6: 271–280.

ABRAHAM, P. S., 1877, Revision of the anthobranchiate nudibranchiate Mollusca, with descriptions or notices of forty-one hitherto undescribed species. *Proceedings of the Zoological Society of London,* 1877: 196–269, pl. 27–30.

ADAMS, H. & ADAMS, A., 1854, *The genera of recent Mollusca; arranged according to their organization.* London, 2: 1–92, pl. 61–72.

ADAMS, H. & ADAMS, A., 1858, *The genera of recent Mollusca; arranged according to their organization.* London, 2: 541–660, pl. 129–138.

ADZHIMOLAEV, T. A., BEZRUCHKO, S. M. & VOZHENINA, N. I., 1972, Effect of electrical stimulation on the incorporation of tritiated uridine and tritiated lysine into the cells of the isolated nervous system of *Tritonia. Biophysics,* 17: 78–87.

ADZHIMOLAEV, T. A., MURAV'EV, R. A., PIRUZYAN, L. A. & ROGOVIN, V. V., 1973a, Electron microscopic cytochemistry of peroxidase activity in giant neurons of the mollusk *Tritonia diomedia. Journal of Evolutionary Biochemistry and Physiology,* 9: 60–62.

ADZHIMOLAEV, T. A., MURAV'EV, R. A. & ROGOVIN, V. V., 1973b, Electron cytochemistry of acid phosphatase in giant nerve cells of the mollusk *Tritonia diomedia. Journal of Evolutionary Biochemistry and Physiology,* 8: 129–134.

ADZHIMOLAEV, T. A., MURAV'EV, R. A. & ROGOVIN, V. V., 1973c, Electron cytochemistry of acid phosphatase in giant neurons of the mollusk *Tritonia diomedia. Neuroscience and Behavioral Physiology,* 6: 131–138.

AGASSIZ, L., 1850, Notes in minutes of November 7, 1849 meeting of Boston Society of Natural History, drawings of *Doris diademata, D. coronata, D. tenella, D. pallida,* all new Agassiz species exhibited and *Meliboea arbuscula* reported from Gay Head, Mass. *Proceedings of the Boston Society of Natural History,* 3: 191.

AGERSBORG, H. P. V. W. K., 1919, Notes on *Melibe leonina* (Gould). *Publications of the Puget Sound Marine Biological Station,* 2: 269–277, pl. 49, 50.

AGERSBORG, H. P. V. W. K., 1921a, Contributions to the knowledge of the nudibranchiate mollusk, *Melibe leonina* (Gould). *American Naturalist,* 55: 222–253.

AGERSBORG, H. P. V. W. K., 1921b, On the status of *Chioraera* (Gould). *Nautilus,* 35: 50–57.

AGERSBORG, H. P. V. W. K., 1922a, Notes on the locomotion of the nudibranchiate mollusk *Dendronotus giganteus* O'Donoghue. *Biological Bulletin,* 42: 257–266.

AGERSBORG, H. P. V. W. K., 1922b, Some observations on qualitative chemical and physical stimulations in nudibranchiate mollusks, with special reference to the role of the "rhinophores." *Journal of Experimental Zoology,* 36: 423–444.

AGERSBORG, H. P. V. W. K., 1923a, The morphology of the nudibranchiate mollusk *Melibe* (syn. *Chioraera*) *leonina* (Gould). *Quarterly Journal of Microscopical Science,* new series, 67: 507–592, pl. 27–37.

AGERSBORG, H. P. V. W. K., 1923b, A critique on Professor Harold Heath's *Chioraera dalli,* with special reference to the use of the foot in the nudibranchiate mollusk, *Melibe leonina* Gould. *Nautilus,* 36: 86–96, pl. 2–5.

AGERSBORG, H. P. V. W. K., 1923c, Notes on a new cladohepatic nudibranch from Friday Harbor, Washington. *Nautilus,* 36: 133–138, pl. 6.

AGERSBORG, H. P. V. W. K., 1923d, The sex of the nudibranchiate Mollusca. I. With special reference to germ cell secretions in *Melibe leonina* (Gould). *Anatomical Record,* 26: 346.

AGERSBORG, H. P. V. W. K., 1923e, The sensory receptors and their structure in the nudibranch mollusk *Hermissenda crassicornis* (Eschscholtz) s. *Hermissenda opalescens* Cooper. *Anatomical Record,* 26: 349.

AGERSBORG, H. P. V. W. K., 1924, The sex of the nudibranchiate Mollusca, (I). With special reference to germ cell secretions in *Melibe leonina* (Gould). *Archives de Biologie,* 34: 215–233, pl. 6–7.

AGERSBORG, H. P. V. W. K., 1925, The sensory receptors and the structure of the oral tentacles of the nudibranch mollusk *Hermissenda crassicornis* (Eschscholtz, 1831) syn. *Hermissenda opalescens* Cooper, 1862, 1863. *Acta Zoologica Internationell Tidskrift för Zoologi utgiven av Nils Holmgrem,* 6: 167–182.

AHMED, Z. & CONNOR, J. A., 1979a, Measurement of calcium influx under voltage clamp in molluscan neurones using the metallochromic dye arsenazo III. *Journal of Physiology,* 286: 61–82.

AHMED, Z. & CONNOR, J. A., 1979b, Buffering of internal hydrogen ions in neurons. *Biophysical Journal* 25(2 part 2): 265a.

AHMED, Z. & CONNOR, J. A., 1980a, Measurement of internal calcium ion and rapid calcium ion buffer capacity of molluscan neurons. *Federation of American Societies of Experimental Biology, Federation Proceedings,* 39: 2038.

AHMED, Z. & CONNOR, J. A., 1980b, Intracellular pH changes indicated by calcium influx during electrical activity in molluscan neurons. *Journal of General Physiology,* 75: 403–426.

AJESKA, R. A., 1971, Notes on the biology of *Melibe leonina* (Gould). *The Echo, Western Society of Malacologists,* 4: 13.

AJESKA, R. A. & NYBAKKEN, J. W., 1976, Contributions to the biology of *Melibe leonina* (Gould, 1852) (Mollusca: Opisthobranchia). *Veliger,* 19: 19–26.

AKAIKE, T. & ALKON, D. L., 1977, Interaction of chemosensory, visual and statocyst pathways in *Hermissenda crassicornis. Neuroscience Abstract,* 3: 171.

AKAIKE, T. & ALKON, D. L., 1980, Sensory convergence on central visual neuron in *Hermissenda. Journal of Neurophysiology,* 44: 501–513.

ALDER, J., 1850 [''1848''], Catalogue of the Mollusca of Northumberland and Durham. *Transactions of the Tyneside Naturalist's Field Club,* 1: 97–209, 358–365.

ALDER, J. & HANCOCK, A., 1842, Descriptions of several new species of nudibranchous Mollusca found on the coast of Northumberland. *Annals and Magazine of Natural History,* 9:31–36.

ALDER, J. & HANCOCK, A., 1845a, On a new genus of Mollusca Nudibranchiata. *Anthenaeum,* no. 922: 644.

ALDER, J. & HANCOCK, A., 1845b, *Monograph of the British nudibranchiate Mollusca,* pt. 1, fam. 1, pl. 4, 5, 26; fam. 3, pl. 3, 21, 24, 26, 34–46. Ray Society, London.

ALDER, J. & HANCOCK, A., 1845c, Notice of new genus and several new species of nudibranchiate Mollusca. *Annals and Magazine of Natural History,* 16: 311–316.

ALDER, J. & HANCOCK, A., 1846a, *Monograph of the British nudibranchiate Mollusca,* pt. 2, fam. 1, pl. 10, 13, 18, 23; fam. 3, pl. 1, 2, 4, 6, 12, 15, 23, 30, 42. Ray Society, London.

ALDER, J. & HANCOCK, A., 1846b, On a new genus of Mollusca Nudibranchiata. *Report 15th Meeting of the British Association for the Advancement of Science,* Cambridge, 1845, Notices and Abstr. Comm. Sec., p. 65.

ALDER, J. & HANCOCK, A., 1847, *Monograph of the British nudibranchiate Mollusca,* pt. 3, fam. 1, pl. 6, 8, 19, 25; fam. 2, pl. 3; fam. 3, pl. 1a, 7, 8, 19, 28, 31, 33. Ray Society, London.

ALDER, J. & HANCOCK, A., 1851a, In FORBES, E. & HANLEY, S. C. T., *A history of British Mollusca, and their shells,* 3: 562–612, pl. Y.Y., Z.Z., 1851; pl. A.A.A., B.B.B., 1852.

ALDER, J. & HANCOCK, A., 1851b, Descriptions of two new species of nudibranchiate Mollusca, one of them forming the type of a new genus. With the anatomy of the genus by A. Hancock. *Annals and Magazine of Natural History,* ser. 2, 8: 290–302, pl. 9–10.

ALDER, J. & HANCOCK, A., 1851c, *Monograph of the British nudibranchiate Mollusca,* pt. 5, fam. 1, pl. 1, 2, 12, 15, 16, 22; fam. 2, pl. 4; fam. 3, pl. 5, 16, 17, 27, 37, 39, 43. Ray Society, London.

ALDER, J. & HANCOCK, A., 1852, *Monograph of the British nudibranchiate Mollusca,* pt. 6, fam. 1, pl. 3, 9, 11, 17; fam. 3, pl. 9, 10, 18, 22, 29, 32, 41, 44. Ray Society, London.

ALDER, J. & HANCOCK, A., 1854, Notice of some new species of British Nudibranchiata. *Annals and Magazine of Natural History,* ser. 2, 14: 102–105.

ALDER, J. & HANCOCK, A., 1855, *Monograph of the British nudibranchiate Mollusca,* pt. 7: 1–54, fam. 1, pl. 21a, 27; fam. 2, pl. 1, 2; fam. 3, pl. 38a, 45–48, appendix, pp. I-XXVIII. Ray Society, London.

ALDRICH, P. W., Jr., GETTING, P. A. & THOMPSON, S. H., 1979a, Inactivation of delayed outward current in molluscan neuron somata. *Journal of Physiology,* 291: 507–530.

ALDRICH, P. W., JR., GETTING, P. A. & THOMPSON, S. H., 1979b, Mechanisms of frequency-dependent broadening molluscan neurone soma spikes. *Journal of Physiology,* 291: 531–544.

ALKON, D. L., 1973a, Neural organization of a molluscan visual system. *Journal of General Physiology,* 61: 444–461.

ALKON, D. L., 1973b, Intersensory interactions in *Hermissenda. Journal of General Physiology,* 62: 185–202.

ALKON, D. L., 1974a, Sensory interaction in the nudibranch mollusk *Hermissenda crassicornis. Federation Proceedings, Federation of American Societies for Experimental Biology,* 33: 1083–1090.

ALKON, D. L., 1974b, Associative training in *Hermissenda. Journal of General Physiology,* 64: 70–84.

ALKON, D. L., 1975a, Neural correlates of associative training in *Hermissenda. Journal of General Physiology,* 65: 46–56.

ALKON, D. L., 1975b, A dual synaptic effect on hair cells in *Hermissenda. Journal of General Physiology,* 65: 385–397.

ALKON, D. L., 1975c, Responses of hair cells to statocyst rotation. *Journal of General Physiology,* 66: 507–530.

ALKON, D. L., 1976a, Signal transformation with pairing of sensory stimuli. *Journal of General Physiology,* 67: 197–211.

ALKON, D. L., 1976b, Neural modification by paired sensory stimuli. *Journal of General Physiology,* 68: 341–358.

ALKON, D. L., 1976c, The economy of photoreceptor function in a primitive nervous system. *In* ZETTLER, F. & WEILER, R., eds., *Proceedings of life sciences neural principles in vision, Symposium. Munich, West Germany, Sept. 15–20,* 1975. Springer-Verlag, Berlin, p. 410–426.

ALKON, D. L., 1979a, Voltage dependence of calcium and potassium photoreceptor currents during and after light steps. *Biophysical Journal,* 25(2 part 2): 268a.

ALKON, D. L., 1979b, Voltage-dependent calcium and potassium ion conductances: a contingency mechanism for an associative learning model. *Science,* 205: 810–816.

ALKON, D. L., AKAIKE, T. & HARRIGAN, J., 1978, Interaction of chemosensory, visual, and statocyst pathways in *Hermissenda crassicornis. Journal of General Physiology,* 72: 177–194.

ALKON, D. L. & BAK, A., 1973, Hair cell generator potentials. *Journal of General Physiology,* 61: 619–637.

ALKON, D. L. & FUORTES, G. F., 1972, Responses of photoreceptors in *Hermissenda. Journal of General Physiology,* 60: 631–649.

ALKON, D. L. & GROSSMAN, Y., 1977, Prolonged inhibition and excitation in the *Hermissenda* eye. *Neuroscience Abstracts,* 3: 171.

ALKON, D. L. & GROSSMAN, Y., 1978a, Evidence for nonsynaptic neuronal interaction. *Journal of Neurophysiology,* 41: 640–653.

ALKON, D. L. & GROSSMAN, Y., 1978b, Long-lasting depolarization and hyperpolarization in eye of *Hermissenda. Journal of Neurophysiology,* 41: 1328–1342.

ALLEN, E. J. & TODD, R. A., 1900, The fauna of the Salcombe Estuary. *Journal of the Marine Biological Association of the United Kingdom,* new series, 6: 151–217.

ALMACA, C., 1960, Sobre a distribuicao de *Aeolidia pappilosa* (Linné) (Moll. Gast. Opist.). *Boletim da Sociedad Portuguesa de Ciencias Naturais,* 2 ser., 8: 209–211.

ANDERSEN, R. J. & SUM, F. W., 1980, Farnesic acid glycerides from the nudibranch *Archidoris odhneri. Tetrahedron Letters,* 21: 797–800.

ANDERSON, E. S., 1973, A method for marking nudibranchs. *Veliger,* 16: 121–122.

ANDERSON, G., 1972, Some aspects of the biology of the nudibranchs *Doridella steinbergae* and *Corambe pacifica. The Echo, Western Society of Malacologists,* 5: 19.

ANDERSON, P. A. V. & CHASE, J. F., 1975, Electrical activity associated with luminescence and other colonial behavior in the pennatulid *Renilla kollikeri. Biological Bulletin,* 149: 80–95.

ANDERSON, W. W., 1976, Endogenous bursting in *Tritonia* neurons at low temperature. *Brain Research,* 103: 407–411.

ANDREWS, H. L., 1945, The kelp beds of the Monterey region. *Ecology,* 26: 24–37.

ANTONOV, V. F., KURELLA, G. A. & YAGLOVA, L. G., 1965, Distribution of Na^{22} between cytoplasm and nucleus in giant neurones of *Tritonia diomedia* Bergh. *Biophysics,* 10: 1200–1202.

ARRONET, N. J., 1963, Reaction to heating of the ciliated cells of some gastropod molluscs larvae. *International Symposium on Cytoecology, Leningrad, Abstr.* p. 11–12.

ARVY, L., 1950, Activité nucléolaire et vitellogenèse chez *Eolis papillosa* L. *Bulletin de la Société Zoologique de France,* 75: 159–160.

ASCANIUS, P., 1774, Beskrivelse over en Norske sneppe og et sodyr. *Det Kongelige Norske Videnskabernes Selskabs Skrifter,* Trondhjem, 5: 153–158, pl. 5.

AUDESIRK, G., 1978a, Properties of central motor neurons exciting locomotory cilia in *Tritonia diomedea. Journal of Comparative Physiology, A Sensory, Neural and Behavioral Physiology,* 128: 259–267.

AUDESIRK, G., 1978b, Central neuronal control of cilia in *Tritonia diamedia. Nature,* 272: 541–543.

AUDESIRK, G., McCAMAN, R. E. & WILLOWS, A. O. D., 1979, The role of serotonin in the control of pedal ciliary activity by identified neurons in *Tritonia diomedea. Comparative Biochemistry and Physiology, C Comparative Pharmacology,* 62: 87–91.

AUDESIRK, T., 1979, Oral mechanoreceptors in *Tritonia diomedea* I. Electrophysiological properties and location of receptive fields. *Journal of Comparative Physiology, A Sensory, Neural and Behavioral Physiology,* 130: 71–78.

AUDESIRK, T. & AUDESIRK, G. J., 1979, Oral mechanoreceptors in *Tritonia diomedea* II. Role in feeding. *Journal of Comparative Physiology, A Sensory, Neural and Behavioral Physiology,* 130: 79–86.

BABA, K., 1930, Studies on Japanese nudibranches (3). A. Phyllidiidae. B. Aeolididae. *Venus,* 2: 117–125, pl. 4.

BABA, K., 1933, Supplementary note on the Nudibranchia collected in the vicinity of the Amakusa Marine Biologial Laboratory. *Annotationes Zoologicae Japonenses,* 14: 273–283.

BABA, K., 1935a, Report on the biologial survey of Mutsu Bay (27). Nudibranchia of Mutsu Bay. *Science Reports Tohoku Imperial University,* ser. 4, *Biology,* 10: 331–360, pl. 5–7.

BABA, K., 1935b, The fauna of Akkeshi Bay pt. 1, Opisthobranchia. *Journal of the Faculty of Science, Hokkaido University,* ser. 6, *Zoology,* 4: 115–125, pl. 7–8.

BABA, K., 1937a, Opisthobranchia of Japan (I). *Journal Department of Agriculture, Kyushu Imperial University,* 5: 195–236, pl. 4.

BABA, K., 1937b, Opisthobranchia of Japan (II). *Journal Department of Agriculture, Kyushu Imperial University,* 5: 289–344, pl. 1–2.

BABA, K., 1937c, Two new species of the nudibranchiate genus *Cadlina* from Sagami Bay, Japan. *Venus,* 7: 75–80.

BABA, K., 1937d, *Duvaucelia septemtrionalis* nov. sp., a nudibranchiate mollusc from the Sea of Okhotsk. *Zoological Magazine,* Japan, 49: 391–392.

BABA, K., 1937e, Note on the color variation of a dorid, *Rostangia arbutus* (Angas, 1864). *Venus,* 7: 1–4.

BABA, K., 1938, Opisthobranchia of Kii, middle Japan. *Journal Department of Agriculture, Kyushu Imperial University,* 6: 1–19.

BABA, K., 1940, Some additions to the nudibranch fauna of the northern part of Japan. *Bulletin of the Biogeographical Society of Japan,* 10: 103–111.

BABA, K., 1949, *Opisthobranchia of Sagami Bay Collected by His Majesty the Emperor of Japan.* Iwanami Shoten, Tokyo. 194 p., 50 pl.

BABA, K., 1957, A revised list of the species of Opisthobranchia from the northern part of Japan, with some additional descriptions. *Journal of the Faculty of Science, Hokkaido University,* ser. 6, *Zoology,* 13: 8–14.

BABA, K., 1960a, The genera *Okenia, Goniodoridella* and *Thecacera* from Japan (Nudibranchia—Polyceridae). *Publications of the Seto Marine Biological Laboratory,* 8: 79–83, pl. 6.

BABA, K., 1960b, Two new species of the genus *Eubranchus* from Japan. *Publications of the Seto Marine Biological Laboratory* 8(2): 299–302, pl. 34.

BABA, K., 1964, Description of *Eubranchus inabai* n. sp., from Mukaishima, Japan (Nudibranchia—Eolidoidea). *Publications of the Seto Marine Biological Laboratory,* 12: 285–287.

BABA, K., 1968a, A collection of *Trochuina tetraquetra* (Pallas, 1788) from Shirikishinai, Hokkaido, Japan (Gastropoda: Nudibranchia). *Collecting & Breeding,* 30: 257–258 (in Japanese).

BABA, K., 1968b, On the identification of *Tritonia festiva* (Stearns, 1873) in Japan (Gastropoda: Nudibranchia). *Collecting & Breeding,* 30: 258–259 (in Japanese).

BABA, K., 1969a, Notes on the collection of *Tritonia festiva* (Stearns, 1873) from the seas of Japan (Gastropoda: Nudibranchia). *Veliger,* 12: 132–134.

BABA, K., 1969b, Range extension of *Tochuina tetraquetra* (Pallas, 1788) to Hokkaido, North Japan (Gastropoda: Nudibranchia). *Veliger,* 12: 134.

BABA, K., 1971, Review of the anatomical aspects of *Eubranchus misakiensis* Baba, 1969 from Mukaishima, Japan (Nudibranchia: Eolidoidea: Eubranchidae). *Venus,* 30: 63–66, pl. 6.

BABA, K., 1979a, Short account of the anatomy of a nudibranchiate mollusk, *Aeolidiella takanosimensis* Baba, 1930 from Japan (Eolidoidea: Aeolidiidae). *Veliger,* 22: 12–18.

BABA, K., 1979b, Brief comment on the identification of a nudibranchiate mollusk, *Aeolidiella takanosimensis* Baba, 1930, from Amakusa, Japan (Eolidoidea: Aeolidiidae). *Publications of Amakusa Marine Biological Laboratory,* 5: 1–7.

BABA, K. & HAMATANI, I., 1952, List of the species of the Opisthobranchia from Kii, middle Japan. *Nanki-Seibutsu Supplement. Nanki Biological Society, Wakayama,* no. 1: 1–11.

BABA, K. & HAMATANI, I., 1963a, A short account of the species, *Tenellia pallida* (A. & H.) taken from Mukaishima, Japan (Nudibranchia—Eolidoidea). *Publications of the Seto Marine Biological Laboratory* 11: 337–338.

BABA, K. & HAMATANI, I., 1963b, A cuthonid, *Cuthona alpha* n. sp. with a radula of *Catriona* type (Nudibranchia—Eolidoidea). *Publications of the Seto Marine Biological Laboratory,* 11: 339–344, pl. 11.

BABA, K. & HAMATANI, I., 1965, The anatomy of *Sakuraeolis enosimensis* (Baba, 1930), n. g. (=*Hervia ceylonica* (?) Eliot, 1913) (Nudibranchia—Eolidoidea). *Publications of the Seto Marine Biological Laboratory,* 13: 103–113, pl. 8–10.

BABA, K., HAMATANI, I. & HISAI, K., 1956, Observations on the spawning habits of some Japanese Opisthobranchia. 2. *Publications of the Seto Marine Biological Laboratory,* 5: 209–220, pl. 24–26.

BAILY, J. L., JR., 1907, Shells of La Jolla, California. *Nautilus,* 21: 92–93.

BAKER, N. W., 1972, The sea slugs unlikely showoffs of the sea. *Oceans Magazine,* 5(4): 44–49.

BALCH, F. N., 1909, A spring collecting trip. Notes on New England nudibranchs II. *Nautilus,* 23: 33–38.

BARDARSON, G. G., 1919, Sae-lindry vid island

(Mollusca marina Islandiae). *Skýrsla um hid Íslenzka nátturufraedisfélag,* 1917–18: 45–75.

BARDARSON, G. G., 1920, Om den marine molluskfauna ved vestkysten af Island. *Det Kongelige Danske Videnskabernes Selskabs, Biologiske Meddelelser,* 2(3): 1–139, map.

BARLETTA, G. & MELONE, G., 1976, Nudibranchi del Promontorio di Portofino (Genova) (Gastropoda Nudibranchia). *Natura,* 67: 203–236.

BARLETTA, G. & MELONE, G., 1977, Sulla accertata presenza di *Aeolidia papillosa* (L.) in Mediterraneo. *Atti della Società Italiana di Scienze Naturale e del Museo Civico di Storia Naturale in Milano,* 118: 320–324.

BARNES, H. & POWELL, H. T., 1951, The growth-rate of juvenile *Asterias rubens* L. *Journal of the Marine Biological Association of the United Kingdom,* 30: 381–385.

BARNES, H. & POWELL, H. T., 1954, *Onchidoris fusca* (Muller), a predator of barnacles. *Journal of Animal Ecology,* 23: 361–363, pl. 2.

BARRETT, B. E., 1969, Canada's northeast coast. *Oceans Magazine,* 2(2): 65–73.

BARTH, J., 1964, Intracellular recording from photoreceptor neurons in the eyes of a nudibranch mollusc (*Hermissenda crassicornis*). *Comparative Biochemistry and Physiology,* 11: 311–315.

BASTER, J., 1760, *Opuscula subseciva, observationes miscellaneas de animalculis et plantis quibusdam marinis, eorumque ovariis et seminibus continentia,* 1(2): 53–97, pl. 1–10.

BAUDELOT, E., 1863, Recherches sur l'appareil générateur des mollusques gastéropodes. *Annales des Sciences Naturelles,* Paris, ser. 4, 19: 135–222, 268–294, pl. 2–5.

BAYER, F. M., 1963, Observations on pelagic mollusks associated with the siphonophores *Velella* and *Physalia. Bulletin of Marine Science of the Gulf and Caribbean,* 13: 454–466.

BEAUMONT, W. I., 1900, XII.—Report on the opisthobranchiate Mollusca. *In* SCHARFF, R. F., The fauna and flora of Valencia Harbour on the west coast of Ireland. *Proceedings of the Royal Irish Academy,* ser. 3, 5: 832–854.

BEBBINGTON, A. & THOMPSON, T. E., 1968, Note sur les opisthobranches du Bassin d'Arcachon. *Actes de la Société Linnéenne de Bordeaux,* ser. A, 105(5): 1–35.

BECHER, E., 1886, Mollusken von Jan Mayen, gesammelt von Dr. F. Fischer, Arzt der osterreichischen Expedition auf Jan Mayen. *Die internationale Polarforschung* 1882–83, Vienna, 3: 1–16, pl. 6.

BECK, H. H., 1842, *In* Möller, H. P. C., *Index molluscorum Groenlandiae naturhistorisk Tidsskrift.* Kjobenhavn, 4: 78.

BEEMAN, R. D., 1968a, The order Anaspidea. *Veliger,* 3 (suppl): 87–102.

BEEMAN, R. D., 1968b, The use of succinylcholine and other drugs for anesthetizing or narcotizing gastropod molluscs. *Pubblicacioni della Stazione Zoologica di Napoli,* 36: 267–270.

BEHRENS, D. W., 1971a, The occurrence of *Ancula pacifica* MacFarland in San Francisco Bay. *Veliger,* 13: 297–298.

BEHRENS, D. W., 1971b, *Eubranchus misakiensis* Baba, 1960 (Nudibranchia: Eolidacea) in San Francisco Bay. *Veliger,* 14: 214–215.

BEHRENS, D. W. & TUEL, M., 1977, Notes on the opisthobranch fauna of south San Francisco Bay. *Veliger,* 20: 33–36.

BELCIK, F. P., 1975, Additional opisthobranch mollusks from Oregon. *Veliger,* 17: 276–277.

BENNETT, I., 1966, Some pelagic molluscs and associated animals in south-eastern Australian waters. *Journal of the Malacological Society of Australia,* no. 9: 40–51, pl. 8–13.

BERGH, L. S. R., 1858, Anatomisk Untersogelse af *Fiona atlantica,* Bgh. *Videnskabelige Meddeleser fra Danske Naturhistorisk Forening,* Kjobenhavn, p. 273–337, pl. 2–3.

BERGH, L. S. R., 1859, *Contributions to a monograph of the genus* Fiona, *Hanc.* Copenhagen, 1–20 p., pl. 1–2.

BERGH, L. S. R., 1860, Om Forekomsten af Neldefiim hos Mollusker. *Videnskabelige Meddeleser fra Danske Naturhistorisk Forening.* Kjobenhavn, p. 309–331, pl. 8.

BERGH, L. S. R., 1863, *Campaspe pusilla,* en ny Slaegstform af Dendronotidernes Gruppe, samt Bemaerkniger om Dotidernes Familie. *Naturhistorisk Tidsskrift Stiftet af Henrik Kroyer,* ser. 3, 1: 471–483, pl. 12.

BERGH, L. S. R., 1866, Bidrag til en Monographi af Pleurophyllidierne, en Familie af de Gastraeopode Mollusker. *Naturhistorisk Tidsskrift Stiftet af Henrik Kroyer,* ser. 3, 4: 1–81, pl. 1–4.

BERGH, L. S. R., 1868 ["1864"], Anatomiske Bidrag til kundskab om aeolidierne. *Det Kongelige Danske Videnskabernes Selskabs Skrifter.* (5) *Naturvidenskabelig og Mathematisk Afdeling,* Kjobenhaven, 7: 139–316, 9 pl.

BERGH, L. S. R., 1869, Anatomische Untersuchungen der *Pleurophyllidia formosa. Verhandlungen der königlich-kaiserlich Zoologisch-botanischen Gesellschaft in Wien (Abhandlungen),* 19: 225–244, pl. 1–3.

BERGH, L. S. R., 1871, Beiträge zur Kenntniss der Mollusken des Sargassomeeres. *Verhandlungen der königlich-kaiserlich Zoologisch-botanischen Gesellschaft in Wien (Abhandlungen),* 21: 1273–1308, pl. 11–13.

BERGH, L. S. R., 1873a, Beiträge zur Kenntniss der Aeolidiaden. I. *Verhandlungen der königlich-kaiserlich zoologisch-botanischen Gesellschaft in Wien (Abhandlungen),* 23: 597–628, pl. 7–10.

BERGH, L. S. R., 1873b, Neue Nacktschnecken der Südsee, malacologische Untersuchungen. *Journal des Museum Godeffroy,* 1(2): 65–96(137–168), pl. 9–12.

BERGH, L. S. R., 1874, Beiträge zur Kenntniss der Aeolidiaden. II. *Verhandlungen der königlich-kaiserlich Zoologisch-botanischen Gesellschaft in Wien (Abhandlungen),* 24: 395–416, pl. 8–11.

BERGH, L. S. R., 1875a, Beiträge zur Kenntniss der Aeolidiaden III. *Verhandlungen der königlich-*

kaiserlich Zoologisch-botanischen Gesellschaft in Wien (Abhandlungen), 25: 633–658, pl. 13–15.

BERGH, L. S. R., 1875b, Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate.* Band 2, Theil 1, Heft 9: 345–376, pl. 45–48.

BERGH, L. S. R., 1876a, Neue Beiträge zur Kenntniss der Pleurophyllidien. *Malakozoologische Blätter,* 23: 1–14, pl. 1.

BERGH, L. S. R., 1876b, Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate.* Band 2, Theil 2, Heft 10: 377–427, pl. 49–53.

BERGH, L. S. R., 1877a, Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate.* Band 2, Theil 2, Heft 11: 429–494, pl. 54–57.

BERGH, L. S. R., 1877b, Malacologische Untersuchungen. In *Reisen im Archipel der Phillippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate.* Band 2, Theil 2, Heft 12: 495–546, pl. 58–61.

BERGH, L. S. R., 1877c, Beiträge zur Kenntniss der Aeolidiaden. V. *Verhandlungen der königlich-kaiserlich Zoologisch-botanischen Gesellschaft in Wien (Abhandlungen),* 27: 807–840, pl. 11–13.

BERGH, L. S. R., 1878a, Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate.* Band 2, Theil 2, Heft 13: 547–601, pl. 52–65.

BERGH, L. S. R., 1878b, Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate.* Band 2, Theil 2, Heft 14: 603–645, I–L, pl. 66–68.

BERGH, L. S. R., 1879a, Gattungen Nordische Doriden. *Archiv für Naturgeschichte,* 45: 340–369, pl. 19.

BERGH, L. S. R., 1879b, On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska, pt. 1. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 31: 71–132, pl. 1–8.

BERGH, L. S. R., 1879c, On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska. *Scientific Results of the Exploration of Alaska* 1, Art. 5, pt. 1: 127–188, pl. 1–8.

BERGH, L. S. R., 1879d ["1878"], Beiträge zur Kenntniss der Aeolidiaden. VI. *Verhandlungen der königlich-kaiserlich Zoologisch-botanischen Gesellschaft in Wien (Abhandlungen),* 28: 553–584, pl. 6–8.

BERGH, L. S. R., 1879e, Neue Chromodoriden. *Malakozoologische Blätter,* Neue Folge, 1: 87–116, pl. 4.

BERGH, L. S. R., 1879f, Neue Nacktschnecken der Südsee, Malacologische Untersuchungen. IV. *Journal des Museum Godeffroy,* 5(14): 1–50, pl. 1–5.

BERGH, L. S. R., 1880a, On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska. *Scientific Results of the Exploration of Alaska* 1, Art. 6, pt. 2: pl. 9–16.

BERGH, L. S. R., 1880b, On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska, pt. 2. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 32: 40–127, pl. 9–16.

BERGH, L. S. R., 1880c, Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate,* Band 2, Theil 4, Heft 1: 1–78, pl. A–F.

BERGH, L. S. R., 1880d, Beiträge zur Kenntniss der japanischen Nudibranchien. I. *Verhandlungen der königlich-kaiserlich Zoologisch-botanischen Gesellschaft in Wien (Abhandlungen),* 30: 155–200, pl. 1–5.

BERGH, L. S. R., 1881a, Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate,* Band 2, Theil 4, 2 Suppl., Heft 2: 79–128, pl. G, H, J–L.

BERGH, L. S. R., 1881b, Beiträge zur Kenntniss der japanischen Nudibranchien. II. *Verhandlungen der königlich-kaiserlich Zoologisch-botanischen Gesellschaft in Wien (Abhandlungen),* 31: 219–254, pl. 6–10.

BERGH, L. S. R., 1884a, Report of the Nudibranchiata. *Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–1876. Zoology,* vol. 10, no. 1, *Challenger Zoological Reports,* pt. 26: 1–154, pl. 1–14.

BERGH, L. S. R., 1884b, Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate.* Band 2, Theil 3, Heft 15: 647–754, pl. 69–76.

BERGH, L. S. R., 1885, Beiträge zur Kenntniss der Aeolidiaden. VIII. *Verhandlungen der königlich-kaiserlich Zoologisch-botanischen Gesellschaft in Wien (Abhandlungen),* 35: 1–60, pl. 1–7.

BERGH, L. S. R., 1887, 8. Die Nudibranchien gesammelt warhrend der Fahrten des "Willem-Barents" in das nordliche Eismeer. *Bijdragen tot de Dierkunde afleverung,* Amsterdam. *Onderzoekingstochter van de "Willem-Barents" Exped. Gedeelte,* 13(4): 1–37, pl. 1–3.

BERGH, L. S. R., 1889, Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate.* Band 2, Theil 3, Heft 16, 2 Halfte: 815–872, pl. 82–84.

BERGH, L. S. R., 1890a, Die cladohepatischen Nudibranchien. *Zoologische Jahrbücher, Abtheilung für Systematik Geographie und Biologie der Thiere,* 5: 1–75.

BERGH, L. S. R., 1890b, Die nudibranchien des

"Sunda-Meeres." Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate.* Band 2, Theil 3, Heft 17: 873–991, pl. 85–89.

BERGH, L. S. R., 1890c, Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–1878), and in the Caribbean Sea (1879–1880), by the U.S. Coast Survey Steamer "Blake," Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. XXXII. Report on the nudibranchs. *Bulletin of the Museum of Comparative Zoology at Harvard College,* 19: 155–181, pl. 1–3.

BERGH, L. S. R., 1891, Die cryptobranchiaten Dorididen. *Zoologische Jahrbücher, Abtheilung für Systematik Geographie und Biologie der Thiere,* 6: 103–144.

BERGH, L. S. R., 1892. Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate.* Band 2, Theil 3, Heft 18: 995–1165 (3–173).

BERGH, L. S. R., 1894, Die Opisthobranchien. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U. S. Fish Commission steamer "Albatross," during 1891, Lieut. Commander Z. L. Tanner, U.S.N. commanding. *Bulletin of the Museum of Comparative Zoology at Harvard College,* 25: 125–235, pl. 1–12.

BERGH, L. S. R., 1898, Die Opisthobranchier der Sammlung Plate. *Zoologische Jahrbücher Supplement,* 4: 481–582, pl. 28–33.

BERGH, L. S. R., 1900, Ergebnisse einer Reise nach dem Pacific (Schauinsland 1896–1897). Die Opisthobranchier. *Zoologische Jahrbücher,* 13: 207–246, pl. 19–21.

BERGH, L. S. R., 1904, Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate.* Band 9, Theil 6, Lief. 1: 1–56, pl. 1–4.

BERGH, L. S. R., 1905a, Malacologische Untersuchungen. In *Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper.* Zweiter Theil. *Wissenschaftliche Resultate.* Band 9, Theil 6, Lief. 2: 57–115, pl. 5–8.

BERGH, L. S. R., 1905b, Die Opisthobranchiata der Siboga Expedition. *Siboga Expeditie* 50: 1–248, pl. 1–20.

BERGH, L. S. R., 1907, The Opisthobranchiata of South Africa. *Transactions of the South African Philosophical Society,* 17: 1–144, pl. 1–14. In *Marine investigations of South Africa* 5(1).

BERNARD, F. R., 1970, A distributional checklist of the marine molluscs of British Columbia: based on faunistic surveys since 1950. *Syesis,* 3: 75–94.

BERRY, S. S., 1907, Molluscan fauna of Monterey Bay, California. *Nautilus,* 21: 34–35.

BERTSCH, H., 1968, Effect of feeding by *Armina californica* on the bioluminescence of *Renilla koellikeri. Veliger,* 10: 440–441.

BERTSCH, H., 1969, *Cadlina modesta*: a range extension, with notes on habitat and a color variation. *Veliger,* 12: 231–232.

BERTSCH, H., 1970, Natural history and occurrence of opisthobranchs of Las Cruces, Baja California, Mexico, and vicinity. *Echo, Western Society of Malacologists,* 3: 16.

BERTSCH, H., 1973, Distribution and natural history of opisthobranch gastropods from Las Cruces, Baja California del Sur, Mexico. *Veliger,* 16: 105–111.

BERTSCH, H., 1974, Descriptive study of *Aeolidia papillosa* with scanning electron micrographs of the radula. *Tabulata, Santa Barbara Malacological Society,* 7: 3–6.

BERTSCH, H., 1976a, A new species of *Chromodoris* (Opisthobranchia: Nudibranchia) from tropical west America. *Veliger,* 19: 156–158.

BERTSCH, H., 1976b, intraspecific and ontogenetic radular variation in opisthobranch systematics (Mollusca: Gastropoda). *Systematic Zoology,* 25: 117–122.

BERTSCH, H., 1977, The Chromodoridinae nudibranchs from the Pacific coast of America.—Part I. Investigative methods and supra-specific taxonomy. *Veliger,* 20: 107–118.

BERTSCH, H., 1978a, The Chromodoridinae nudibranchs from the Pacific coast of America.—Part II. The genus *Chromodoris. Veliger,* 20: 307–327, pl. figs. 33–50.

BERTSCH, H., 1978b, The Chromodoridinae nudibranchs from the Pacific coast of America.—Part III. The genera *Chromolaichma* and *Mexichromis. Veliger,* 21: 70–86.

BERTSCH, H., 1978c, The Chromodoridinae nudibranchs from the Pacific coast of America.—Part IV. The genus *Hypselodoris. Veliger,* 21: 236–250, pl. figs. 63–68.

BERTSCH, H., 1979a, Tropical fauna affinities of opisthobranchs from the Panamic province (eastern Pacific). *Nautilus,* 93: 57–61.

BERTSCH, H., 1979b, The eastern Pacific chromodorids (Opisthobranchia: Chromodoridinae). *Festivus, San Diego Shell Club,* 11: 44–46.

BERTSCH, H., 1980, The nudibranch *Aegires albopunctatus* (Polyceratacea: Aegiretidae) preys on *Leucilla nuttingi* (Porifera: Calcarea). *Veliger,* 22: 222–224.

BERTSCH, H., 1981, Rectification of the generic placement of *Sclerodoris tanya* (Marcus, 1971), comb. nov., a nudibranch from southern California, with a range extension to the Gulf of California, Mexico. *Veliger,* 23: 217–220.

BERTSCH, H. & BURN, R., 1979, *Chromodoris californiensis* Bergh, 1879 (May): proposed conservation over *Chromodoris glauca* Bergh, 1879 (March) (Mollusca: Gastropoda). Z.N.(S.) 2253.

Bulletin of Zoological Nomenclature, 35: 253–256.

BERTSCH, H. & FERREIRA, A. J., 1974, Four new species of nudibranchs from tropical west America. *Veliger,* 16: 343–353.

BERTSCH, H., FERREIRA, A. J., FARMER, W. M. & HAYES, T. L., 1973, The genera *Chromodoris* and *Felimida* (Nudibranchia: Chromodorididae) in tropical west America: distributional data, description of a new species, and scanning electron microscope studies of radulae. *Veliger,* 15: 287–294.

BERTSCH, H., GOSLINER, T., WHARTON, R. & WILLIAMS, G., 1972, Natural history and occurrence of opisthobranch gastropods from the open coast of San Mateo county, California. *Veliger,* 14: 302–314.

BERTSCH, H. & SMITH, A. A., 1970, A habitat note on *Navanax inermis* (Opisthobranchia: Cephalaspidea). *Tabulata, Santa Barbara Malacological Society,* 3: 19.

BEZRUCHKO, S. M., ADZHIMOLAEV, T. A., VOZHENINA, N. I. & GAZARYAN, K. G., 1971, Effect of temperature on membrane potential and the incorporation of tritiated uridine and tritiated lysine in the cells of the ganglia of *Tritonia diomedia. Biophysics,* 16: 459–466.

BEZRUCHKO, S. M., VOZHENINA, N. I., ADZHIMOLAEV, T. A. & GAZARYAN, K. G., 1970, Localization and kinetics of RNA and protein synthesis in isolated nervous system of *Tritonia diomedia. Biophysics,* 15: 1073–1081.

BEZRUCHKO, S. M., VOZHENINA, N. I., GAZARYAN, K. G., KUL'MINSKAYA, A. S. & KUKHTIN, V. A., 1969, Autoradiographic study of DNA synthesis in giant neurones of *Tritonia diomedia. Biophysics,* 14: 1107–1111.

BICKELL, L. R. & CHIA, F.-S., 1979a, Organogenesis and histogenesis in the planktotrophic veliger of *Doridella steinbergae* (Opisthobranchia, Nudibranchia). *Marine Biology,* 52: 291–313.

BICKELL, L. R. & CHIA, F.-S., 1979b, Gut metamorphosis in the planktotrophic larva of the nudibranch, *Doridella steinbergae* (Opisthobranchia). *American Zoologist,* 19: 957.

BIERI, R., 1966, Feeding preferences and rates of the snail, *Ianthina prolongata,* and barnacle, *Lepas anserifera,* the nudibranchs, *Glaucus atlanticus* and *Fiona pinnata,* and the food web in the marine neuston. *Publications of the Seto Marine Biological Laboratory,* 14: 161–170, pl. 3–4.

BIERI, R., 1970, The food of *Porpita* and niche separation in three neuston coelenterates. *Publications of the Seto Marine Biological Laboratory,* 17: 305–307.

BINGHAM, F. O. & ALBERTSON, H. D., 1974, Observations on beach strandings of the *Physalia* (Portuguese-man-of-war) community. *Veliger,* 17: 220–224.

BIRKELAND, C. E., 1974, Interactions between a sea pen and seven of its predators. *Ecological Monographs,* 44: 211–232.

BLAINVILLE, H. M. D. DE, 1816, Quatrième mémoire sur les mollusques, de l'ordre des cyclobranches. *Bulletin des Sciences par la Société Philomathique,* 13: 93–97.

BLAINVILLE, H. M. D. DE, 1819, In *Dictionnaire des sciences naturelles* . . . . Paris, 13: 1–578.

BLAINVILLE, H. M. D. DE, 1825, *Manuel de Malacologie et de Conchyliologie.* Leurault, Paris. viii + 664 p.

BLAINVILLE, H. M. D. DE, 1827, *Manuel de Malacologie et de Conchyliologie. Planches* 1–87, Leurault, Paris.

BLAIR, G. M. & SEAPY, R. R., 1972, Selective predation and prey location in the sea slug *Navanax inermis. Veliger,* 15: 119–124.

BLEAKNEY, J. S. & SAUNDERS, C. L., 1978, Life history observations on the nudibranch mollusc *Onchidoris bilamellata* in the intertidal zone of Nova Scotia. *Canadian Field Naturalist,* 92: 82–85.

BLOOM, S. A., 1975, The motile escape response of a sessile prey: a sponge-scallop mutualism. *Journal of Experimental Marine Biology and Ecology,* 17: 311–321.

BLOOM, S., 1976, Morphological correlation between dorid nudibranch predators and sponge prey. *Veliger,* 18: 289–301.

BLOOM, S. & BLOOM, C. F., 1977, Radular variation in two species of sponge-rasping dorid nudibranchs. *Journal of Molluscan Studies,* 43: 296–300.

BONAR, D. B., 1978, Morphogenesis at metamorphosis in opisthobranch molluscs. In CHIA, F.-S. & RICE, M. E., eds., *Settlement and metamorphosis of marine invertebrate larvae,* Proceedings of the symposium on settlement and metamorphosis of marine invertebrate larvae . . . . Elsevier, New York, p. 177–196.

BOONE, E. S., 1929, Five new polyclads from the California coast. *Annals and Magazine of Natural History,* ser. 10, 3: 33–46, pl. 2–3.

BOROVYAGIN, V. L. & SAKHAROV, D. A., 1965a, Electron microscopy of glial cells in the molluscs, *Tritonia diomedia* Bergh. *Tsitologiia,* 7: 641–645 (in Russian).

BOROVYAGIN, V. L. & SAKHAROV, D. A., 1965b, Submicroscopical morphology of trophospongium in the ganglion of the nudibranchiate mollusc. *Zhurnal Obshchei Biologii,* 26: 458–463 (in Russian).

BOROVYAGIN, V. L. & SAKHAROV, D. A., 1968, *Ultrastructure of giant nerve cells of* Tritonia *(an atlas).* Nauka, Moscow, 32 p., pl. 4–75 (in Russian).

BOROVYAGIN, V. L., SAKHAROV, D. A. & VEPRINTSEV, B. N., 1965, On the intracellular inclusion in nerve cell of the nudibranch mollusc, *Tritonia diomedia* Bergh. *Biophysics,* 10: 104–108.

BOSC, L. A. G., 1802, *Histoire naturelle des vers, contenant leur description et leurs moeurs; avec figures dessinées d'après nature,* 1.

BOSC, L. A. G., 1830, *Histoire naturelle des vers,* *contenant leur description et leurs moeurs.* Ed. 2, Vol. 1.

BOTH, R., FINGER, W. & CHAPLAIN, R. A., 1976, Model predictions underlying the beating and bursting pacemaker characteristics of molluscan neurons. *Biologial Cybernetics,* 23: 1–11.

BOUCHARD-CHANTEREAUX, N. R., 1835, Catalogue des mollusques marins observés, jusqu'à ce jour, à l'état vivant, sur les côtes du Boulonnais. *Mémoires de la Société d'Agriculture de Boulogne-sur-Mer Sciences et Arts,* III. *Histoire Naturelle Zoologie,* p. 101–168.

BOUSFIELD, E. L., 1958, Ecological investigations on shore invertebrates of the Pacific coast of Canada, 1955. *National Museum of Canada, Annual Report,* 1955–1956, *Bulletin,* 147: 104–115, 2 pl.

BOUTAN, L., 1898, Moeurs de l'*Eolis papillosa* Linné. *Archives de Zoologie Expérimentale et Générale,* Paris, ser. 3, 6: XXXVII–XLII.

BOVARD, J. F. & OSTERUD, H. L., 1918, Partial list of the animals yielding embryological material at the Puget Sound Biological Station. *Publications of the Puget Sound Marine Biological Station,* 2: 127–137.

BOYLE, M. B. & COHEN, L. B., 1980, Birefringence signals that monitor membrane potential in cell bodies of molluscan (*Aeolidia papillosa*) neurons. *Federation of American Societies for Experimental Biology, Federation Proceedings,* 39: 2130.

BRAAMS, W. G. & GEELEN, H. F. M., 1953, The preference of some nudibranchs for certain coelenterates. *Archives Néerlandaises de Zoologie,* 10: 241–264.

BRATTEGARD, T., 1966, The natural history of the Hardangerfjord. 7. Horizontal distribution of the fauna of rocky shores. *Sarsia,* 22: 1–54.

BREWER, B., 1978, The association between an endoparasitic rhabdocoel (family Fecampidae) and the nudibranch *Aeolidia papillosa. Western Society of Malacologists, Annual Report* 11: 8.

BRIDGES, C. & BLAKE, J. A., 1972, Embryology and larval development of *Coryphella trilineata* O'Donoghue, 1921 (Gastropoda: Nudibranchia). *Veliger,* 14: 293–297.

BROWN, G. J., 1980, British species of the aeolidacean family Tergipedidae (Gastropoda: Opisthobranchia) with a discussion of the genera. *Zoological Journal of the Linnean Society,* 69: 225–255.

BRUCE, J. R., COLMAN, J. S. & JONES, N. S., 1963, Marine fauna of the Isle of Man and its surrounding seas. *Liverpool Marine Biological Committee, Memoir,* 36: ix + 307 p., charts A–F.

BRUGUIÈRE, J. G. & LAMARCK, J. B. P. A. DE M., 1830, *Encyclopédie méthodique. Histoire naturelle des vers,* 2: vii + 594 p.

BUCHSBAUM, R. & MILNE, L. J., 1967, *The lower animals, living invertebrates of the world.* Doubleday, N. Y., 303 p., 144 pl.

BUDELMANN, B.-U., 1976, *Equilibrium receptor systems in molluscs.* In MILL, P. J., ed., *Structure and function of proprioceptors in the invertebrates.* Chapman & Hall, London, p. 529–566.

BULLOCK, A. G. M. & DORSETT, D. A., 1979, The functional morphology and motor innervation of the buccal mass of *Tritonia hombergi. Journal of Experimental Biology,* 79: 7–22.

BURGIN, U. F., 1965, The color pattern of *Hermissenda crassicornis* (Eschscholtz, 1831) (Gastropoda: Opisthobranchia: Nudibranchia). *Veliger,* 7: 205–215.

BURN, R. F., 1960, New names for two Victorian opisthobranch molluscs. *Journal of the Malacological Society of Australia,* no. 4: 70.

BURN, R. F., 1962, Descriptions of Victorian nudibranchiate Mollusca, with a comprehensive review of the Eolidacea. *Memoirs of the National Museum, Melbourne* 25: 95–128.

BURN, R. F., 1964, Descriptions of Australian Eolidacea (Mollusca: Opisthobranchia). 2. The genera *Nossis, Eubranchus, Trinchesia* and *Toorna. Journal of the Malacological Society of Australia,* no. 8: 10–22.

BURN, R. F., 1966, Descriptions of Australian Eolidacea (Mollusca: Opisthobranchia). 4. The genera *Pleurolidia, Fiona, Learchis,* and *Cerberilla* from Lord Howe Island. *Journal of the Malacological Society of Australia,* no. 10: 21–34, text figs. 1–16.

BURN, R. F., 1967a, First record of a pelagic eolid from Victoria. *Victorian Naturalist,* 84: 116–117.

BURN, R. F., 1967b, Descriptions of two new species of *Okenia* (Nudibranchia, Doridacea) from south-eastern Australia. *Proceedings of the Royal Zoological Society of New South Wales,* 1965–1966, p. 52–57, pl. 10–11.

BURN, R. F., 1968, *Archidoris odhneri* (MacFarland, 1966) comb. nov., with some comments on the species of the genus on the Pacific coast of North America. *Veliger,* 11: 90–92.

BURN, R. F., 1969, A memorial report on the Tom Crawford collection of Victorian Opisthobranchia. *Journal of the Malacological Society of Australia,* 12: 64–106, pl. 4.

BURN, R. F., 1973, Opisthobranch molluscs from the Australian sub-Antarctic territories of Macquarie and Heard Islands. *Royal Society of Victoria, Melbourne, Proceedings,* 86: 39–46.

BURN, R. F. & MILLER, M. C., 1969, A new genus, *Caldukia,* and an extended description of the type species, *Proctonotus* ? *affinis* Burn, 1958 (Mollusca Gastropoda: Arminacea, Antiopellidae). *Journal of the Malacological Society of Australia,* 12: 23–31, pl. 2.

BUSH, K. J., 1883, Catalogue of Mollusca and Echinodermata dredged on the coast of Labrador by the expedition under the direction of Mr. W. A. Stearns, in 1882. *United States National Museum, Proceedings,* 6: 236–247, pl. 9.

BUZNIKOV, G. A., 1960, Cholinesterase in the embryogenesis of nudibranchiate molluscs. *Doklady Akademiia Nauk S.S.S.R., Biological Sciences, Moscow,* 132: 373–375.

BUZNIKOV, G. A., 1964, Use of tryptamine derivatives in the study of the role of 5-oxytryptamine (serotonin) during embryonic development of invertebrates. *Doklady Akademiia Nauk S.S.S.R., Biological Sciences, Moscow,* 152: 1243–1246.

BUZNIKOV, G. A., KOST, A. N., KUCHEROVA, N. F., MNDZHOYAN, A. L., SUVOROV, N. N & BERDYSHEVA, L. V., 1970. The role of neurohumours in early embryogenesis. III. Pharmacological analysis of the role of neurohumours in cleavage divisions. *Journal of Embryology and Experimental Morphology,* 23: 549–569.

BUZNIKOV, G. A. & MANUKHIM, B. N., 1960, The "inhibitory substance" of mollusc embryos and its role in the regulation of embryonal motility. *Doklady Akademiia Nauk S.S.S.R., Biological Sciences, Moscow,* 144: 1414–1417 (in Russian).

BUZNIKOV, G. A. & MANUKHIM, B. N., 1961, Serotonin-like substances in the embryogenesis of some gastropods. *Zhurnal Obshchei Biologii,* 22: 226–232.

BYERLEY, I., 1854, The fauna of Liverpool. *Proceedings of the Literary and Philosophical Society of Liverpool,* no. 8, append., p. 1–125, 1 pl.

CAREFOOT, T. H., 1967, Growth and nutrition of three species of opisthobranch molluscs. *Comparative Biochemistry and Physiology,* 21: 627–652.

CARPENTER, P. P., 1857, Report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. *Report 26th Meeting of the British Association for the Advancement of Science,* p. 159–368.

CARPENTER, P. P., 1864, Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. *Report 33rd Meeting of the British Association for the Advancement of Science,* p. 517–686.

CARTER, G. S., 1927, On the nervous control of the velar cilia of the nudibranch veliger. *British Journal of Experimental Biology,* 4: 1–26, pl. 1–3.

CARTER, G. S., 1928, On the structure of the cells bearing the velar cilia of the nudibranch veliger. *British Journal of Experimental Biology,* 6: 97–109.

CARTER, G. S., 1929, The structure of the ciliated cells of the velum in the veliger of *Aeolidia papillosa. Report 96th Meeting of the British Association for the Advancement of Science,* p. 561.

CARUS, J. V., 1889–1893, *Prodromus faunae Mediterraneae* . . . . 2: i–ix, 1–854. Schweizerbart'sche Verlagshandlung (E. Koch), Stuttgart.

CASTEEL, D. B., 1904a, The cell lineage and early larval development of *Fiona marina,* a nudibranchiate mollusk. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 56: 325–405, pl. 21–35.

CASTEEL, D. B., 1904b, The development of the germ layers in a nudibranch mollusc. *American Naturalist,* 38: 505–506.

CHAMBERLAIN, R. & BEHRENS, D. W., 1980, Deep water collections of opisthobranchs in central California. *Veliger,* 22: 282–285.

CHAMBERS, L. A., 1934, Studies on the organs of reproduction in the nudibranchiate mollusks, with special reference to *Embletonia fuscata* Gould. *Bulletin of the American Museum of Natural History,* 66: 599–641, pl. 28–31.

CHASE, R., 1974a, The electrophysiology of photoreceptors in the nudibranch mollusc, *Tritonia diomedia. Journal of Experimental Biology,* 60: 707–719, pl. 1.

CHASE, R., 1974b, The initiation and conduction of action potentials in the optic nerve of *Tritonia. Journal of Experimental Biology,* 60: 721–734.

CHASE, R., 1975, The suppression of excitatory synaptic responses by ethyl alcohol in the nudibranch mollusc, *Tritonia diomedia. Comparative Biochemistry and Physiology, C Comparative Pharmacology,* 50: 37–40.

CHENU, J. C., 1859, *Manuel de conchyliologie et de paléontologie conchyliologique,* 1: i–vii, 1–508. Masson, Paris.

CHIA, F.-S., 1978, Perspectives: settlement and metamorphosis of marine invertebrate larvae. In CHIA, F.-S. & RICE, M. E., eds., *Settlement and metamorphosis of marine invertebrate larvae,* Proceedings of the symposium on settlement and metamorphosis of marine invertebrate larvae . . . . Elsevier, New York, p. 283–285.

CHIA, F.-S. & KOSS, R., 1978, Development and metamorphosis of planktotrophic larvae of *Rostanga pulchra* (Mollusca: Nudibranchia). *Marine Biology,* 46: 109–119.

CHIA, F.-S. & SKEEL, M., 1973, The effect of food consumption on growth, fecundity, and mortality in a sacoglossan opisthobranch, *Olea hansineensis. Veliger,* 16: 153–158.

CHILDS, T. W., 1980, The silver lining. *Oceans Magazine,* 13(2): 50–54.

CHRISTENSEN, H., 1977, Feeding and reproduction in *Precuthona peachi* (Mollusca Nudibranchia). *Ophelia,* 16: 131–142.

CHUKHCHIN, V. D., 1960, Pelagic larvae of gastropod molluscs of the Black Sea. *Akademiia Nauk SSSR. Sevastopolskoi Biologicheskoi Stantsii, Trudy,* 13: 92–113 (in Russian).

CHUKHCHIN, V. D., 1963a, In: STAROSTIN, I. V. & TURPAEVA, E. P., Settlement of larvae of fouling organisms at the water work of metallurgical plant (Sea of Azov). *Trudy Instituta Okeanologii, Akademiia Nauk SSSR,* 70: 142–150.

CHUKHCHIN, V. D., 1963b, In: TURPAEVA, E. P., Tolerance of the Azov Sea nudibranch mollusc *Stiliger bellulus* (D'Orbigny) to water at different salinity. *Trudy Instituta Okeanologii, Akademiia Nauk SSSR,* 70: 197–215.

CHUKHCHIN, V. D., 1963c, In: SIMKINA, R. G., On the ecology of *Perigonimum megas* Kinne (Hydroidea, Athecata)——a new species in the fauna of the U.S.S.R. *Trudy Instituta Okeanologii, Akademiia Nauk SSSR,* 70: 216–224.

CHUKHCHIN, V. D., 1967, In: SIMKINA, R. G., Settlement, growth and nutrition of *Perigonimus megas* Kinne (Hydroidea, Athecata). *Trudy Instituta Okeanologii, Akademiia Nauk SSSR,* 85: 98–111.

CHUMLEY, J., 1918, *The fauna of the Clyde Sea area being an attempt to record the zoological results obtained by the late Sir John Murray and his assistants on board the S. Y. "Medusa" during the years 1884 to 1892.* Glasgow University Press, vi + 200 p.

CLARK, K. B., 1975, Nudibranch life cycles in the northwest Atlantic and their relationship to the ecology of fouling communities. *Helgoländer wissenschaftliche Meeresuntersuchungen,* 27: 28–69.

CLARK, K. B. & GOETZFRIED, A., 1978, Zoogeographic influences on development patterns of North Atlantic Ascoglossa and Nudibranchia, with a discussion of factors affecting egg size and number. *Journal of Molluscan Studies,* 44: 283–294.

CLARK, R. B. & MILNE, A., 1955, The sublittoral fauna of two sandy bays on the Isle of Cumbrae, Firth of Clyde. *Journal of the Marine Biological Association of the United Kingdom,* 34: 161–180.

CLAYTON, D. E., 1932, A comparative study of the non-nervous elements in the nervous system of invertebrates. *Journal of Entomology and Zoology, Pomona College, Claremont, California,* 24: 3–22, pl. 1–4.

CLUBB, J. A., 1895, Notes on some points in the structure of the cerata of *Dendronotus arborescens. Liverpool Biological Association, Proceedings and Transactions,* 9: 220–234, pl. 14–15.

COCKBURN, T. C. & REID, R. G. B., 1980, Digestive tract enzymes in two aeolid nudibranchs (Opisthobranchia: Gastropoda). *Comparative Biochemistry and Physiology, B Comparative Biochemistry,* 65: 275–281.

COCKERELL, T. D. A., 1901a, Three new nudibranchs from California. *Journal of Malacology,* 8: 85–87.

COCKERELL, T. D. A., 1901b, Notes on two Californian nudibranchs. *Journal of Malacology,* 8: 121–122.

COCKERELL, T. D. A., 1901c, Pigments of nudibranchiate Mollusca. *Nature,* 65: 79–80.

COCKERELL, T. D. A., 1902, Three new species of *Chromodoris. Nautilus,* 16: 19–21.

COCKERELL, T. D. A., 1903, Note on *Tritonia palmeri* Cooper, 1882. [sic]. *Nautilus,* 16: 117.

COCKERELL, T. D. A., 1905, Californian nudibranchs. *Nautilus,* 18: 131–132.

COCKERELL, T. D. A., 1908, Mollusca of La Jolla, California. *Nautilus,* 21: 106–107.

COCKERELL, T. D. A., 1915, The nudibranchiate genus *Triopha* in California. *Journal of Entomology and Zoology, Pomona College, Claremont, California,* 7: 228–229.

COCKERELL, T. D. A., 1940, The marine invertebrate fauna of the California islands. *Sixth Pacific Science Congress, Proceedings,* 3: 501–504.

COCKERELL, T. D. A. & ELIOT, C. N. E., 1905, Notes on a collection of Californian nudibranchs. *Journal of Malacology,* 12: 31–53, pl. 7–8.

COE, W. R., 1932, Season of attachment and rate of growth of sedentary marine organisms at the pier of the Scripps Institution of Oceanography, La Jolla, California. *Bulletin, Scripps Institution of Oceanography. Technical series,* 3: 37–74, pl. 1–6.

COE, W. R. & ALLEN, W. E., 1937, Growth of sedentary marine organisms on experimental blocks and plates for nine successive years at the pier of the Scripps Institution of Oceanography. *Bulletin, Scripps Institution of Oceanography. Technical Series* 4: 1-0–135, pl. 1–2.

COLGAN, N., 1908, Dublin Marine Biological Committee. General account of dredging operations, 1907. With special notes on the Mollusca. *Irish Naturalist,* 17: 105–114.

COLGAN, N., 1909, Dublin Marine Biological Committee report for 1908 with special notes on the Mollusca. *Irish Naturalists' Journal,* 18: 166–177.

COLGAN, N., 1911, A biological survey of Clare Island in the county of Mayo, Ireland and of the adjoining district. Section 2. Marine Mollusca, part 22. *Proceedings of the Royal Irish Academy,* 31: 1–36.

COLGAN, N., 1913, Some additions to the nudibranch fauna of Co. Dublin. *Irish Naturalist,* 22: 165–168.

COLGAN, N., 1914, The opisthobranch fauna of the shores and shallow waters of County Dublin. *Irish Naturalist,* 23: 161–204.

COLLIER, C. L., 1963, A new member of the genus *Atagema* (Gastropoda: Nudibranchia). *Veliger,* 6: 73–75.

COLLIER, C. & FARMER, W. M., 1964, Additions to the nudibranch fauna of the east Pacific and the Gulf of California. *Transactions of the San Diego Society for Natural History,* 13: 377–396, pl. 1–6.

COLLIN, J., 1884, *Om Limfjordens tidligere og nuvaerende marine fauna, med Saerligt Hensyn til Bloddyrfaunaen.* Kjobenhavn. 168 p., 1 pl.

COLLINGWOOD, C., 1859, The estuary of the Mersey considered as a locality for nudibranchiate Mollusca. *Annals and Magazine of Natural History, ser. 3,* 3: 461–470.

COLLINGWOOD, C., 1860, On the nudibranchiate Mollusca inhabiting the estuary of the Dee. *Annals and Magazine of Natural History,* ser. 3, 6(33):196–202.

COLLINGWOOD, C., 1861, On the nudibranchiate Mollusca of the Mersey and Dee. Report. *30th Meeting of the British Association for the Advancement of Science,* p. 113–114.

COLLINGWOOD, C. & BYERLEY, I., 1862, Preliminary report of the Dredging Committee for the Mersey and Dee. *Report 31st Meeting of the British Association for the Advancement of Science,* p. 188–189.

COMFORT, A., 1957, The duration of life in mollusks. *Proceedings of the Malacological Society of London*, 32: 219–241.

CONCHOLOGICAL SOCIETY OF GREAT BRITAIN & IRELAND, 1901, List of British marine Mollusca & Brachiopoda. *Journal of Conchology*, 10: 9–27.

CONNELL, J. H., 1970, A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecological Monographs*, 40: 49–78.

CONNOR, J. A., 1977a, Calcium and calcium activated ion influx in isolated somata of molluscan neurons. *Biophysical Journal*, 17: 43a.

CONNOR, J. A., 1977b, Time course separation of two inward currents in molluscan neurons. *Brain Research*, 119: 487–492.

CONNOR, J. A., 1979, Calcium current in molluscan neurones: measurement under conditions which maximize its visibility. *Journal of Physiology*, 286: 41–60.

CONNOR, J. A. & AHMED, Z., 1978, Colorimetric determination of calcium and pH changes under voltage clamp in molluscan neurons. *Biophysical Journal*, 21: 186a.

CONNOR, J. A. & AHMED, Z., 1979, Intracellular calcium regulation by molluscan (*Archidoris montereyensis*) neurons. *Biophysical Journal*, 25(2 part 2): 265a.

CONNOR, J. A. & STEVENS, C. F., 1971a, Inward and delayed outward membrane currents in isolated neural somata under voltage clamp. *Journal of Physiology*, 213: 1–19.

CONNOR, J. A. & STEVENS, C. F., 1971b, Voltage clamp studies of a transient outward membrane current in gastropod neural somata. *Journal of Physiology*, 213: 21–30.

CONNOR, J. A. & STEVENS, C. F., 1971c, Prediction of repetitive firing behavior from voltage clamp data on an isolated neurone soma. *Journal of Physiology*, 213: 31–53.

COOK, E. F., 1962, A study of food choices of two opisthobranchs, *Rostanga pulchra* McFarland [sic] and *Archidoris montereyensis* (Cooper). *Veliger*, 4: 194–197.

COOKE, A. H., 1899, Notes on the nomenclature of the British Nudibranchiata, with a detailed classification of the group. *Journal of Malacology*, 7: 59–66.

COOMANS, A., 1962, *Embletonia pallida*, nudibranche nouveau pour la faune Belge. *Société Royale Zoologique de Belgique*, 92: 222–223.

COOMANS, A. & CONINCK, L. DE, 1962, *Embletonia pallida*, nudibranche nouveau pour la faune Belge. *Institut Royal des Sciences Naturelles de Belgique, Bulletin* 38: 1–4, pl. 1.

COOPER, J. G., 1863a [''1862''], Some new genera and species of California Mollusca. *Proceedings of the California Academy of Sciences*, 2: 202–207.

COOPER, J. G., 1863b, On new or rare Mollusca inhabiting the coast of California. 2. *Proceedings of the California Academy of Sciences*, 3: 56–60.

COOPER, J. G., 1867, *Geographical catalogue of the Mollusca found west of the Rocky Mountains, between latitudes 33° and 49° north*. San Francisco, Towne & Bacon, Printers, 40 p.

COOPER, J. G., 1870, Notes on Mollusca of Monterey Bay, California. *American Journal of Conchology*, 6: 42–70.

COOPER, J. W., 1978, Feeding ecology and life histories of aeolid nudibranchs from Elkhorn Slough, California. *Western Society of Malacologists, Annual Report* 11: 8.

COOPER, J. W., 1980, The influence of predation upon *Tubularia crocea*. In: TARDENT, P. & TARDENT, R., eds., *Developmental and cellular biology of coelenterates*. Elsevier/North-Holland Biomedical Press, p. 281–286.

CORNET, R. & MARCHE-MARCHAD, I., 1951, Inventaire de la faune marine de Roscoff Mollusques. *Travaux de la Station Biologique de Roscoff*, 5: 1–80.

COSTA, A., 1866 [''1863''], Saggio sui molluschi eolididei del Golfo di Napoli. *Annuario del Museo Zoologico della Università di Napoli*, 3: 59–80, pl. 1–3.

COSTA, A., 1867 [''1864''], Sui molluschi eolididei del Golfo di Napoli. *Annuario del Museo Zoologico della Università de Napoli*, 4: 26–37, pl. 1–2.

COSTELLO, D. P., 1938, Notes on the breeding habits of nudibranchs of Monterey Bay and vicinity. *Journal of Morphology*, 63: 319–344, pl. 1–2.

COSTELLO, D. P., 1947, On the interpretation of article 19 of the Règles Internationales in relation to the name *Chromodoris mcfarlandi* Cockerell, 1902 (class Gastropoda, order Opisthobranchia). *Bulletin of Zoological Nomenclature* 1: 232–233.

COSTELLO, D. P., 1950, The trivial name ''*mcfarlandi*'' as published in the binomial combination ''*Chromodoris mcfarlandi*'' (class Gastropoda, order Opisthobranchia): emendation to ''macfarlandi'' under article 19. *Bulletin of Zoological Nomenclature* 4: 430–431.

COUTHOUY, J. P., 1838, Descriptions of new species of Mollusca and shells, and remarks on several Polypi found in Massachusetts Bay. *Boston Journal of Natural History*, 2: 53–111, pl. 1–2.

COWEN, R. K. & LAUR, D. R., 1978, A new species of *Coryphella* (Nudibranchia: Flabellinidae) from Santa Barbara, California. *Veliger*, 20: 292–294.

CRAMPTON, D. M., 1977, Functional anatomy of the buccal apparatus of *Onchidoris bilamellata* (Mollusca: Opisthobranchia). *Zoological Society of London, Transactions*, 34: 46–86.

CRANE, S., 1971, The feeding and reproductive behavior of the sacoglossan gastropod *Olea hansineensis* (Agersborg, 1923). *Veliger*, 14: 57–59.

CRANE, S., 1973, Vital stains: a marking technique for nudibranchs. *Echo, Western Society of Malacologists*, 6: 17.

CRAWSHAY, L. R., 1912, On the fauna of the outer western area of the English Channel. *Journal of the Marine Biological Association of the United Kingdom,* 9: 292–393, pl. 6.

CROW, T. J. & ALKON, D. L., 1978a, Retention of an associative behavioral change in *Hermissenda. Science,* 201: 1239–1241.

CROW, T. J. & ALKON, D. L., 1978b, Neural correlates of an associative behavioral change in *Hermissenda crassicornis. Society for Neuroscience Abstracts,* 4: 191.

CROW, T. J. & ALKON, D. L., 1980a, Neural correlates of a long-term associative behavioral modification in *Hermissenda crassicornis. Federation Proceedings, Federation of American Societies for Experimental Biology,* 39(3 part I): 596.

CROW, T. J. & ALKON, D. L., 1980b, Associative behavioral modification in *Hermissenda*: cellular correlates. *Science,* 209: 412–414.

CROW, T. J. & HARRIGAN, J. F., 1979, Reduced behavioral variability in laboratory-reared *Hermissenda crassicornis* (Eschscholtz, 1831) (Opisthobranchia: Nudibranchia). *Brain Research,* 173: 179–184.

CROW, T. J., HELDMAN, E., HACOPIAN, V., ENOS, R. & ALKON, D. L., 1979, Ultrastructure of photoreceptors in the eye of *Hermissenda* labeled with intracellular injections of horseradish peroxidase. *Journal of Neurocytology,* 8: 181–195.

CROZIER, W. J., 1922, Correspondence of skin pigments in related species of nudibranchs. *Journal of General Physiology,* 4: 303–304.

CUENOT, L., 1907, L'origine des nematocystes des eolidiens. *Archives de Zoologie Expérimentale et Générale, Paris,* ser. 4, 6: 73–102, pl. 3.

CUENOT, L., 1927, Contributions à la faune du Bassin d'Arcachon. IX. Revue général de la faune et bibliographie. *Bulletin de la Station Biologique d'Arcachon, Université,* 24: 229–305.

CUVIER, G. L. C. F. D., 1804, Mémoire sur le genre *Doris. Annales de Muséum National d'Histoire Naturelle, Paris* 4: 447–473, pl. 73–74.

CUVIER, G. L. C. F. D., 1805, Mémoire sur la *Scyllée,* l'*Eolide* et le *Glaucus* avec des additions au mémoire sur la *Tritonie. Annales de Muséum National d'Histoire Naturelle, Paris* 6: 416–436, pl. 61.

CUVIER, G. L. C. F. D., 1817, Mémoire sur la *Scyllée,* l'*Eolide* et le *Glaucus,* avec des additions au mémoire sur la *Tritonie.* In: *Mémoires pour servir à l'histoire et à l'anatomie des Mollusques,* Paris, p. 1–16, 25–29, 1 pl.

CUVIER, G. L. C. F. D., 1834, Das Thierreich, geordnet nach seiner Organisation, vol. 3, die Mollusken. Leipzig, xviii + 621 p.

DAHLGREN, U., 1925, The biologial survey of the Mount Desert Island (Maine) region. *Science,* 61: 435–436.

DALL, W. H., 1870, Revision of the classification of the Mollusca of Massachusetts. *Proceedings of the Boston Society of Natural History,* 13: 240–257.

DALL, W. H., 1871, Descriptions of sixty new forms of mollusks from the west coast of North America and the North Pacific Ocean, with notes on others already described. *American Journal of Conchology,* 7: 93–160, pl. 13–16.

DALL, W. H., 1884, Contribution to the history of the Commander Islands. No. 3. Report on the Mollusca of the Commander Islands, Bering Sea, collected by Leonhard Stejneger in 1882 and 1883. *Proceedings of the United States National Museum,* 7: 340–349.

DALYELL, J. G., 1853, *The powers of The Creator displayed in the creation ....* London, van Voorst, 2: i–xii, 1–359, pl. 1–46.

DARO, M. H., 1969, Etude écologique d'un briselames de la côte Belge. I. Description et zonation des organismes. *Société Royale Zoologique de Belgique, Annales,* 99: 111–152.

DARO, M. H., 1970, Etude écologique d'un briselames de la côte Belge: II. Biologie et développement saisonnier des espèces. *Société Royale Zoologique de Belgique, Annales,* 100: 159–190.

DAUTZENBERG, P. & DUROUCHOUX, P., 1913, Les mollusques de la Baie de Saint-Malo. *La Feuille des Jeunes Naturalistes,* ser. 5, 43: suppl. p. 1–8.

DAY, R. M. & HARRIS, L. G., 1978, Selection and turnover of coelenterate nematocysts in some aeolid nudibranchs. *Veliger,* 21: 104–109.

DAYTON, P. K., 1971, Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs,* 41: 351–389.

DEFELICE, L. J. & ALKON, D. L., 1977a, Noise spectra from hair cells of the *Hermissenda* statocyst. *Biophysical Journal,* 17: 19a.

DEFELICE, L. J. & ALKON, D. L., 1977b, Voltage noise from hair cells during mechanical stimulation. *Nature,* 269: 613–615.

DEHNEL, P. A. & KONG, D. C., 1979, The effect of temperature on developmental rates in the nudibranch *Cadlina luteomarginata. Canadian Journal of Zoology,* 57: 1835–1844.

DEKAY, J. E., 1843, Zoology of New York. Vol. 1, Zoology, Part V Mollusca. Albany, 271 p., 40 pl.

DELAUBENFELS, M. W., 1927, The red sponges of Monterey Peninsula, California. *Annals and Magazine of Natural History,* ser. 9, 19: 258–266.

DENNIS, M. J., 1967a, Electrophysiology of the visual system in a nudibranch mollusc. *Journal of Neurophysiology,* 30: 1439–1465.

DENNIS, M. J., 1967b, Interactions between the five receptor cells of a simple eye. In WIERSMA, C. A. G., ed., *Conference on invertebrate nervous systems: their significance for mammalian neurophysiology.* University of Chicago Press, p. 259–262.

DERJUGIN, K. M., 1928, Fauna of the White Sea and its conditions of life. *Explorations des Mers d'U.R.S.S.*, no. 7–8: i–xii, 1–511 (in Russian).

DETWILER, P. B., 1976, Multiple light-evoked conductance changes in the photoreceptors of *Hermissenda crassicornis. Journal of Physiology,* 256: 691–708.

DETWILER, P. B. & ALKON, D. L., 1973, Hair cell interactions in the statocyst of *Hermissenda. Journal of General Physiology,* 62: 618–642.

DETWILER, P. B. & FUORTES, M. G. F., 1975, Responses of hair cells in the statocyst of *Hermissenda. Journal of Physiology,* 251: 107–129, pl. 1–3.

DEVRIES, J. B., 1963, Contribution to the morphology and histology of the nudibranch *Melibe rosea* Rang. *Universiteit Stellenbosch, Annale,* ser. A, 38: 105–153.

DICKINSON, P. S., 1979, Homologous neurons control movements of diverse gill types in nudibranch molluscs. *Journal of Comparative Physiology, A Sensory, Neural and Behavioral Physiology,* 131: 277–283.

DORSETT, D. A., 1967, Giant neurons and the axon pathways in the brain of *Tritonia. Journal of Experimental Biology,* 46: 137–151.

DORSETT, D. A., 1975, Some aspects of neural organization in molluscs. In: USHERWOOD, P. N. R. & NEWTH, D. R., *'Simple' nervous systems.* Edward Arnold, London, xvi + 490 p.

DORSETT, D. A., 1976, The structure and function of proprioceptors in soft-bodied invertebrates. In: MILL, P. J., ed., *Structure and function of proprioceptors in the invertebrates.* Chapman & Hall, London, p. 443–483.

DORSETT, D. A., 1978, Neurons controlling foot and mantle movements in *Armina californica. Marine Behaviour and Physiology,* 5: 307–324.

DORSETT, D. A., WILLOWS, A. O. D. & HOYLE, G., 1969, Centrally generated nerve impulse sequences determining swimming behaviour in *Tritonia. Nature,* 224: 711–712.

DORSETT, D. A., WILLOWS, A. O. D. & HOYLE, G., 1973, The neuronal basis of behavior in *Tritonia.* IV. The central origin of a fixed action pattern demonstrated in the isolated brain. *Journal of Neurobiology,* 4: 287–300.

DUNN, D. F., 1977, Locomotion by *Epiactis prolifera* (Coelenterata: Actinaria). *Marine Biology,* 39: 67–70.

DUSHANE, H. & BRENNAN, E., 1969, A preliminary survey of mollusks for Consag Rock and adjacent areas, Gulf of California, Mexico. *Veliger,* 11: 351–363, 1 map.

DUSHANE, H. & SPHON, G. G., 1968, A checklist of intertidal mollusks for Bahia Willard and the southwestern portion of Bahía San Luis Gonzaga, State of Baja California, Mexico. *Veliger,* 10: 233–236, pl. 35, 1 map.

EAKIN, R. M., WESTFALL, J. A. & DENNIS, M. J., 1967, The fine structure of the eye of nudibranch mollusc *Hermissenda crassicornis. Journal of Cell Science,* 2: 349–358.

ECKERT, R. & TILLOTSON, D., 1978, Outward current component associated with intracellular calcium accumulation in aequorin injected voltage clamped dorid neurons. *Biophysical Journal,* 21: 178a.

ECKERT, R., TILLOTSON, D. & RIDGWAY, E. B., 1977, Voltage dependent facilitation of Ca^{2+} entry in voltage-clamped, aequorin-injected molluscan neurons. *Proceedings of the National Academy of Sciences of the United States of America,* 74: 1748–1752.

EDMUNDS, M., 1964, Eolid Mollusca from Jamaica, with descriptions of two new genera and three new species. *Bulletin of Marine Science of the Gulf and Caribbean,* 14: 1–32.

EDMUNDS, M., 1966, Protective mechanisms in the Eolidacea (Mollusca Nudibranchia). *Journal of the Linnean Society, London (Zoology),* 47: 27–71, pl. 1–4.

EDMUNDS, M., 1968a, Eolid Mollusca from Ghana, with further details of west Atlantic species. *Bulletin of Marine Science,* 18: 203–219.

EDMUNDS, M., 1968b, Acid secretion in some species of Doridacea (Mollusca, Nudibranchia). *Proceedings of the Malacological Society of London,* 38: 121–133.

EDMUNDS, M., 1970, Opisthobranchiate Mollusca from Tanzania II. Eolidacea (Cuthonidae, Piseinotecidae and Facelinidae). *Proceedings of the Malacological Society of London,* 39: 15–57.

EDMUNDS, M., 1971, Opisthobranchiate Mollusca from Tanzania (suborder: Doridacea). *Zoological Journal of the Linnean Society, London,* 50: 339–396, pl. 1.

EDMUNDS, M., 1975, An eolid nudibranch feeding on Bryozoa. *Veliger,* 17: 269–270.

EDMUNDS, M., 1977, Larval development, oceanic currents, and origins of the opisthobranch fauna of Ghana. *Journal of Molluscan Studies,* 43: 301–308.

EDMUNDS, M. & KRESS, A., 1969, On the European species of *Eubranchus* (Mollusca Opisthobranchia). *Journal of the Marine Biological Association of the United Kingdom,* 49: 879–912, pl. 1–2.

EDMUNDS, M., POTTS, G. W., SWINFEN, R. C. & WATERS, V. L., 1974, The feeding preferences of *Aeolidia papillosa* (L.) (Mollusca, Nudibranchia). *Journal of the Marine Biological Association of the United Kingdom,* 54: 939–947.

EDMUNDS, M., POTTS, G. W., SWINFEN, R. C. & WATERS, V. L., 1976, Defensive behaviour of sea anemones in response to predation by the opisthobranch mollusc *Aeolidia papillosa* (L.). *Journal of the Marine Biological Association of the United Kingdom,* 56: 65–83.

ELIOT, C. N. E., 1901, Notes on a remarkable nudibranch from north-west America. *Proceedings of the Malacological Society of London,* 4: 163–165, text figs. 1–2.

ELIOT, C. N. E., 1906a, The genus *Doriopsilla* Bergh. *Journal of Conchology,* 11: 366–367.

ELIOT, C. N. E., 1906b, On the nudibranchs of southern India and Ceylon, with special reference to the drawings by Kelaart and the collections belonging to Alder and Hancock preserved in the Hancock Museum at Newcastle-on-Tyne. *Proceedings of the Zoological Society of London,* 1906: 636–691, pl. 42–47.

ELIOT, C. N. E., 1906c, Notes on some British nudibranchs. *Journal of the Marine Biological Association of the United Kingdom,* new ser., 7: 333–382, pl. 11–12.

ELIOT, C. N. E., 1907, Nudibranchs from New Zealand and the Falkland Islands. *Proceedings of the Malacological Society of London,* 7: 327–361, pl. 28.

ELIOT, C. N. E., 1908, On the genus *Cumanotus. Journal of the Marine Biological Association of the United Kingdom,* new ser., 8: 313–314.

ELIOT, C. N. E., 1909, Notes on a collection of nudibranchs from Ceylon. *Spolia Zeylanica, Colombo,* 6: 79–95.

ELIOT, C. N. E., 1910, *A monograph of the British nudibranchiate Mollusca: with figures of the species. Part* VIII (*supplementary*). *Figures by the late Joshua Alder and the late Albany Hancock, and others.* Ray Society, London, 198 p., 8 pl.

ELIOT, C. N. E., 1913, Japanese nudibranchs. *Journal of the College of Science, Imperial University of Tokyo,* 35: 1–47, pl. 1–2.

ELLIS, E. A., 1933, Sea-slugs. *Transactions of the Suffolk Naturalist's Society,* 2: 188–189.

ELMHIRST, R., 1908, Notes on nudibranchiate molluscs. *Annals of Scottish Natural History,* no. 68: 227–230.

ELMHIRST, R., 1922, Notes on the breeding and growth of marine animals in the Clyde Sea area. *Scottish Marine Biological Association, Glasgow, Annual Report,* p. 19–43.

ELVIN, D. W., 1976, Feeding of a dorid nudibranch, *Diaulula sandiegensis,* on the sponge *Haliclona permollis. Veliger,* 19: 194–198.

ENGEL, H., 1925, Westindische opisthobranchiate Mollusken. Bijdragen tot de kennis der fauna van Curacao. Resultaten eener reis van Dr. C. J. van der Horst in 1920. *Bijdragen tot de Dierkunde, Koninklijk Zoologisch Genootschap,* 24: 33–80.

ENGEL, H., 1936, The Netherlands nudibranchiate Mollusca. *Zoologische Mededelingen uitgegeven* (Vanwegen, door's, door het) (Rijks Museum, Rijksmuseum) *van Natuurlijke Historie te Leiden,* 19: 103–116.

ESCHSCHOLTZ, J. F., 1831, *Zoologischer Atlas* .... Berlin, Reiner, pt. 4: 1–19, pl. 16–20.

EVANS, W. & EVANS, W. E., 1917, Some nudibranchs, including *Hermaea dendritica,* and *Lamellidoris aspera* from the Forth area. *Scottish Naturalist,* no. 65: 105–110.

EYERDAM, W. J., 1960, Mollusks and brachiopods from Afognak and Sitkalidak Islands, Kodiak group, Alaska. *Nautilus,* 74: 41–46.

EYERDAM, W. J., 1977, A collection of mollusks from Washington Bay, Alaska. *Of Sea and Shore,* 8: 109–110.

EYSTER, L. S., 1979, Production and developmental variability in the opisthobranch *Tenellia pallida. Marine Biology,* 51: 133–140.

EYSTER, L. S., 1980, Distribution and reproduction of shell-less opisthobranchs from South Carolina. *Bulletin of Marine Science,* 30: 580–599.

FABRICIUS, O., 1780, *Fauna Groenlandica.* Hafniae et Lipsiae, xiv + 452 p., 1 pl.

FAGER, E. W., 1971, Pattern in the development of a marine community. *Limnology and Oceanography,* 16: 241–253.

FARMER, W. M., 1964, One hundred common marine animals of San Diego. *Occasional Papers of the San Diego Society of Natural History,* 14: 1–47.

FARMER, W. M., 1967, Notes on the Opisthobranchia of Baja California, Mexico, with range extensions—II. *Veliger,* 9: 340–342.

FARMER, W. M., 1970, Swimming gastropods (Opisthobranchia and Prosobranchia). *Veliger,* 13: 73–89.

FARMER, W. M., 1971, Eveline Marcus; and Puerto de Lobos, Sonora, Mexico (an 8-minute film). *Echo, Western Society of Malacologists,* 4: 19.

FARMER, W. M. & COLLIER, C. L., 1963, Notes on the Opisthobranchia of Baja California, Mexico, with range extensions. *Veliger,* 6: 62–63.

FARMER, W. M. & SLOAN, A. J., 1964, A new opisthobranch mollusk from La Jolla, California. *Veliger,* 6: 148–150, pl. 18.

FARRAN, G. P., 1904, The marine fauna of the west coast of Ireland. Part I. The nudibranchiate molluscs of Ballynakill and Bofin Harbours, Co. Galway. *Report on the Sea and Inland Fisheries of Ireland for 1901,* pt. 2, append. 8: 1–10, pl. 18–19.

FARRAN, G. P., 1909, Nudibranchiate Mollusca of the trawling grounds of east and south coasts of Ireland. *Department of Agriculture and Technical Instruction for Ireland Fisheries Branch. Dublin. Scientific Investigation,* no. 6: 1–18 ("*Fisheries Ireland Sci. Invest.*" 1907, VI (1909)).

FARRAN, G. P., 1913, Clare Island Survey. 45. Marine Entomostraca, *Proceedings of the Royal Irish Academy,* 31(2): 1–20, pl. 1–3.

FARRAN, G. P., 1915, Results of a biological survey of Blacksod Bay, Co. Mayo. *Department of Agriculture and Technical Instruction for Ireland Fisheries Branch. Dublin. Scientific Investigations, 1914,* no. 3: 1–72, 1 pl.

FAUGIER, S. & WILLOWS, A. O. D., 1973, Behavioral and nerve cell membrane effects of an epileptic agent (metrazol) in a mollusk. *Brain Research,* 52: 243–260.

FERREIRA, A. J., 1972, Range extensions of *Conualevia alba* Collier and Farmer, 1964. *Veliger,* 15: 53–54.

FERREIRA, A. J., 1977, A review of the genus *Triopha* (Mollusca: Nudibranchia). *Veliger,* 19: 387–402.

FERREIRA, A. J. & BERTSCH, H., 1975, Anatomical and distributional observations of some opisthobranchs from the Panamic faunal province. *Veliger,* 17: 323–330.

FEWKES, J. W., 1889, New Invertebrata from the coast of California. *Essex Institute, Salem, Bulletin* 21: 99–146, pl. 1–7.

FIELD, L. H & MacMILLAN, D. L., 1973, An electrophysiological and behavioural study of sensory responses in *Tritonia* (Gastropoda, Nudibranchia). *Marine Behaviour and Physiology,* 2: 171–185.

FINLAY, H. J., 1927, A further commentary on New Zealand molluscan systematics. *Transactions of the New Zealand Institute,* 57: 320–485, pl. 18–23.

FISCHER, E., FRANC, A., MARTOJA, M., TERMIER, G. & TERMIER, H., 1968, *Traité de zoologie. Anatomie, systématique, biologie.* Tome 5, *Mollusques gastéropodes et scaphopodes* (fascicule 3). Paris, Masson, 1083 p., 1 pl.

FISCHER, P., 1872, Catalogue des nudibranches et cephalopodes des côtes océaniques de la France (2ᵉ supplement). *Journal de Conchyliologie,* ser. 3, 20: 5–26.

FISCHER, P., 1887, *Manuel de Conchyliologie et de Paléontologie conchyliologique ou histoire naturelle des Mollusques vivants et fossiles suivi d'un appendice sur les Brachiopodes.* Paris, Savy, 1369 p., 23 pl.

FISCHER, P. H., 1950, *Vie et Moeurs des Mollusques.* Payot, Paris, 312 p.

FISHER, N., 1931, Nudibranch records from N. E. Ireland. *Irish Naturalists' Journal,* 3: 198.

FISHER, N., 1935, Notes on the spawning of *Acanthodoris pilosa* (Abildgaard). *Proceedings of the Malacological Society of London,* 21: 249.

FITCH, J. E. & LAVENBERGH, R. J., 1975, *Tidepool and nearshore fishes of California,* University of California Press, 156 p., 8 pl.

FLEMING, J., 1820, In: BREWSTER, D., *The Edinburgh encyclopaedia . . . .* 14(2).

FLEMING, J., 1823a, Gleanings of natural history gathered on the coast of Scotland during a voyage in 1821. *Edinburgh Philosophical Journal,* 8: 294–303.

FLEMING, J., 1823b, Gleanings of natural history gathered on the coast of Scotland during a voyage in 1821. *Edinburgh Philosophical Journal,* 9: 248–254.

FLEMING, J., 1828, *A history of British animals . . . .* Edinburgh, xxiii + 565 p.

FLEURE, H. J. & WALTON, C. L., 1907, Notes on the habits of some sea anemones. *Zoologischer Anzeiger,* 31: 212–220.

FORBES, E., 1838, *Malacologia monensis . . . .* 63 p., 3 pl.

FORBES, E. & GOODSIR, J., 1839, Notice of zoological researches in Orkney and Shetland during the month of June, 1839. *The Athenaeum,* no. 618, p. 647.

FORBES, E. & HANLEY, S. C. T., 1851–1852, *A history of British Mollusca, and their shells.* 3: 1–616, pl. Y.Y., Z.Z., 1851; pl. A.A.A., B.B.B., 1852.

FORREST, J. E., 1953, On the feeding habits and the morphology and mode of functioning of the alimentary canal in some littoral dorid nudibranchiate Mollusca. *Proceedings of the Linnean Society of London,* 164: 225–235.

FORSKÅL, P., 1775, Vermes. 1. Mollusca. In: *Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium quae in itinere orientali observavit Petrus Forskål. Hauniae,* p. 99–140.

FOSBERG, F. R., 1929, Preliminary notes on the fauna of the giant kelp. *Journal of Entomology and Zoology, Pomona College, Claremont, California,* 21: 133–135.

FOURNIER, A., 1969, Anatomie, histologie, et histochimie du tube digestif de *Peltodoris atromaculata* Bergh. *Vie et Milieu,* 20: 73–93.

FRANZ, D. R., 1967, On the taxonomy and biology of the dorid nudibranch *Doridella obscura. Nautilus,* 80: 73–79.

FRANZ, D. R., 1968, Occurrence and distribution of New Jersey Opisthobranchia. *Nautilus,* 82: 7–12.

FRANZ, D. R., 1970, Zoogeography of northwest Atlantic opisthobranch molluscs. *Marine Biology,* 7: 171–180.

FRANZ, D. R., 1975a, An ecological interpretation of nudibranch distribution in the northwest Atlantic. *Veliger,* 18: 79–83.

FRANZ, D. R., 1975b, Opisthobranch culture. In: SMITH, J. L. & CHANLEY, M. H., eds., *Culture of marine invertebrate animals.* Plenum Press, N.Y., p. 245–256.

FRANZÉN, Å., 1955, Comparative morphological investigations into the spermiogenesis among Mollusca. *Zoologiska bidrag från Uppsala,* 30: 399–456, pl. 1–2.

FRASER, C. M., 1932, A comparison of the marine fauna of the Nanaimo region with that of the San Juan archipelago. *Transactions of the Royal Society of Canada,* ser. 3, 26(sec. 5): 49–70.

FRIELE, H., 1979, Catalog der auf der norwegischen Nordmeerexpedition bei Spitzbergen gefundenen Mollusken. *Deutsche Malakozoologische Gesellschaft Jahrbücher,* 6: 264–286.

FRIELE, H. & HANSEN, G. A., 1876 [''1875''], Bidrag til kundskaben om de Norske nudibranchier. *Videnskabs-Selskabet Fordhandlinger, Christiania,* p. 69–80, pl. 2.

FUHRMAN, F. A., FUHRMAN, G. J. & DeRIEMER, K., 1979, Toxicity and pharmacology of extracts from dorid nudibranchs. *Biological Bulletin,* 156: 289–299.

FUHRMAN, F. A., FUHRMAN, G. L., KIM, Y. H., PAVELKA, L. A. & MOSHER, H. S., 1980, Doridosine: a new hypotensive N-methylpurine riboside from the nudibranch *Anisodoris nobilis. Science,* 207: 193–195.

FUORTES, M. G. F. & O'BRYAN, P. M., 1972, *Generator potentials in invertebrate photoreceptors.* In: FUORTES, M. G. F., ed., *Handbook of sensory physiology,* vol. 8/2. *Physiology of pho-*

toreceptor organs, p. 279–319. Springer-Verlag, Berlin.

GAKHOVA, E. N., JERELOVA, O. M., KISLOV, A. N., KRASTS, I. V., CHEMERIS, N. K. & VEPRINTSEV, B. N., 1979, Isolated neurons in nudibranchia mollusc: kinetices of Ca and Na currents upon action potential generation. *Comparative Biochemistry and Physiology, A Sensory, Neural, and Behavioral Physiology,* 64: 313–316.

GAMBLE, F. W., 1896, Notes on a zoological expedition to Valencia Island, Co. Kerry. Shore-collecting and dredging. *Irish Naturalist,* 5: 129–136.

GARLO, E. V., 1977, Opisthobranchs found off Little Egg Inlet, New Jersey, with notes on three species new to the state. *Nautilus,* 91: 23–28.

GARNER, R., 1978, Professor Edward Forbes and his country. *Midland Naturalist,* 1: 67–70, 90–94.

GARSTANG, W., 1889, Report on the nudibranchiate Mollusca of Plymouth Sound. *Journal of the Marine Biological Association of the United Kingdom,* new ser., 1: 173–198.

GARSTANG, W., 1890, A complete list of the opisthobranchiate Mollusca found at Plymouth; with further observations on their morphology, colours, and natural history. *Journal of the Marine Biological Association of the United Kingdom,* new ser., 1: 399–457, pl. 27–28.

GARSTANG, W., 1894, Faunistic notes at Plymouth during 1893–4. With observations on the breeding seasons of marine animals, and on the periodic changes of the floating fauna. *Journal of the Marine Biological Association of the United Kingdom,* new ser., 3: 210–235.

GASCOIGNE, T., 1972, Some additions to the aquatic fauna list of the inner Farne. *Transactions of the Natural History Society of Northumberland, Durham, and Newcastle-upon-Tyne,* 17: 259.

GERASIMOV, V. D. & MAGURA, I. S., 1965, Electrical activity of giant neurons of nudibranchiate mollusc *Tritonia diomedia. Zhurnal Evoliutsionnoi Biokhimiii Fiziologii,* 1: 360–363 (in Russian).

GETTING, P. A., 1974, Modification of neuron properties by electronic synapses. I. Input resistance, time constant, and integration. *Journal of Neurophysiology,* 37: 846–857.

GETTING, P. A., 1975, *Tritonia* swimming; triggering of a fixed action pattern. *Brain Research,* 96: 128–133.

GETTING, P. A., 1976, Afferent neurons mediating escape swimming of the marine mollusc, *Tritonia. Journal of Comparative Physiology, A. Sensory, Neural and Behavioral Physiology,* 110: 271–286.

GETTING, P. A., 1977, Neuronal organization of escape swimming in *Tritonia. Journal of Comparative Physiology, A. Sensory, Neural and Behavioral Physiology,* 121: 325–342.

GETTING, P. A., LENNARD, P. R. & HUME, R. I., 1980, Central pattern generator mediating swimming in *Tritonia.* I. Identification and synaptic interactions. *Journal of Neurophysiology,* 44: 151–164.

GETTING, P. A. & WILLOWS, A. O. D., 1973, Burst formation in electrically coupled neurons. *Brain Research,* 63: 424–429.

GETTING, P. A. & WILLOWS, A. O. D., 1974, Modification of neuron properties by electrotonic synapses. II. Burst formation by electrotonic synapses. *Journal of Neurophysiology,* 37: 858–868.

GHELARDI, R. J., 1971, "Species" structure of the animal community that lives in *Macrocystis pyrifera* holdfasts. In: NORTH, W. J., ed., The biology of giant kelp beds (*Macrocystis*) in California. *Beihefte zur Nova Hedwigia,* Heft 32: 381–420.

GHISELIN, M. T., 1964, Feeding of *Dendrodoris* (*Doriopsilla*) *albopunctata,* an opisthobranch gastropod. *American Malacological Union, Inc., Annual Report,* 1964: p. 45–46.

GHISELIN, M. T., 1966, Reproductive function and the phylogeny of opisthobranch gastropods. *Malacologia,* 3: 327–378.

GMELIN, J. F., 1791, *Caroli a Linne Systema naturae per regna tria naturae.* Editio decima tertia. Leipzig, Germany, 1(6): cl. 6, Vermes, p. 3021–3910.

GODDARD, J., 1973, Opisthobranchs of San Francisco Bay. *Tabulata. Santa Barbara Malacological Society,* 6: 8–10.

GOMEZ, E. D., 1973, Observations on feeding and prey specificity of *Tritonia festiva* (Stearns) with comments on other tritoniids (Mollusca: Opisthobranchia). *Veliger,* 16: 163–165.

GOMOIU, M.-T., 1961, Contributii la Cuoasterea Citorva Nudibranchiate (Gastropoda—Opisthobranchia) Din Partea Vestica a Marii Negre. *Communicarile Academiei Republicii Populare Romine. Bucharest,* Nr. 10, Tomul 11: 1247–1255.

GOMOIU, M.-T., 1966, *Speciile de opisthobranchiate din Marea Neagra. Hidrobiologia. Bucuresti,* 7: 141–147.

GONOR, J. J., 1965, Predator-prey reactions between two marine prosobranch gastropods. *Veliger,* 7: 228–232.

GOODWIN, T. W. & FOX, D. L., 1955, Some unusual carotinoids from two nudibranch slugs and a lamprid fish. *Nature,* 175: 1086–1087.

GORMAN, A. L. F. & MARMOR, M. F., 1970a, Contributions of the sodium pump and ion gradients to the membrane potential of a molluscan neurone. *Journal of Physiology,* 210: 897–917.

GORMAN, A. L. F. & MARMOR, M. F., 1970b, Temperature dependence of the sodium-potassium permeability ratio of a molluscan neuron. *Journal of Physiology,* 210: 919–931.

GORMAN, A. L. F. & MARMOR, M. F., 1971, A biphasic potential produced by L-glutamic acid in a giant molluscan neuron. *Federation Proceedings, Federation of American Societies for Experimental Biology,* 30: 323.

GORMAN, A. L. F. & MARMOR, M. F., 1972, Relative contribution of the electrogenic Na⁺ ion pump to a neuronal membrane potential under steady state and Na⁺ ion loaded conditions. *Federation Proceedings, Federation of American Societies for Experimental Biology,* 31: 319.

GORMAN, A. L. F. & MARMOR, M. F., 1974a, Steady-state contribution of the sodium pump to the resting potential of a molluscan neuron. *Journal of Physiology,* 242: 35–48.

GORMAN, A. L. F. & MARMOR, M. F., 1974b, Long-term effect of ouabain and sodium pump inhibition on a neuronal membrane. *Journal of Physiology,* 242: 49–60.

GORMAN, A. L. F. & MIROLLI, M., 1969, The input-output organization of a pair of giant neurones in the mollusc, *Anisodoris nobilis* (MacFarland). *Journal of Experimental Biology,* 51: 615–634, pl. 1.

GORMAN, A. L. F. & MIROLLI, M., 1971, New estimates of the specific membrane resistance and capacitance of molluscan neurons. *Biophysical Society, Annual Meeting, Abstracts,* 15: 137a.

GORMAN, A. L. F., MIROLLI, M. & SALMOIRAGHI, G. C., 1967, Unusual characteristics of an inhibitory potential recorded intracellularly from a molluscan nerve cell. *Federation Proceedings, Federation of American Societies for Experimental Biology,* 26: 329.

GOSLINER, T. M., 1968, A new record of *Corambella steinbergae* Lance, 1962. *Veliger,* 11: 147.

GOSLINER, T. M., 1980, The systematics of the Aeolidacea (Nudibranchia: Mollusca) of the Hawaiian Islands, with descriptions of two new species. *Pacific Science,* 33: 37–77.

GOSLINER, T. M. & WILLIAMS, G. C., 1970, The opisthobranch mollusks of Marin County, California. *Veliger,* 13: 175–180.

GOSLINER, T. M. & WILLIAMS, G. C., 1973a, The occurrence of *Polycera zosterae* O'Donoghue, 1924 in the Bodega Bay region, California, with notes on its natural history (Gastropoda: Nudibranchia). *Veliger,* 15: 252–253.

GOSLINER, T. M. & WILLIAMS, G. C., 1973b, Additions to the opisthobranch fauna of Marin County, California, with notes on their natural history. *Veliger,* 15: 352–354.

GOSLINER, T. M. & WILLIAMS, G. C., 1975, A genus of dorid nudibranch previously unrecorded from the Pacific coast of the Americas, with the description of a new species. *Veliger,* 17: 396–405.

GOSSE, P. H., 1853, *A naturalist's rambles on the Devonshire coast.* London, xvi + 451 p., 28 pl.

GOSSE, P. H., 1854, *Natural history. Mollusca.* Society for Promoting Christian Knowledge, viii + 328 p.

GOSSE, P. H., 1856, *A manual of marine zoology for the British Isles.* London, 2: 1–239.

GOULD, A. A., 1841, *Report on the Invertebrata of Massachusetts.* Cambridge, Mass., xii + 373 p.

GOULD, A. A., 1852, *United States Exploring Expedition. During the years 1838, 1839, 1840, 1841, 1842. Under the command of Charles Wilkes, U. S. N. Vol. XII. Mollusca & shells,* xv + 510 p. Atlas of plates, 1856.

GOULD, A. A., 1870, *Report on the Invertebrata of Massachusetts* . . . . Ed. 2, comprising the Mollusca. Ed. by BINNEY, W. G., v + 524 p., pl. 16–27.

GRAHAM, A., 1938, The structure and function of the alimentary canal of aeolid molluscs, with a discussion on their nematocysts. *Transactions of the Royal Society of Edinburgh,* 59: 267–307.

GRAHAM, A., 1955, Molluscan diets. *Proceedings of the Malacological Society of London,* 31: 144–159.

GRANT, R. E., 1826, On the sounds produced under water by the *Tritonia arborescens. Edinburgh Philosophical Journal,* 14: 165, 185–186.

GRAY, J. E., 1857, *Guide to the systematic distribution of Mollusca in the British Museum.* London, pt. I: i–xii, 1–230.

GRAY, J. E., 1869, Nudibranchs in fresh water. *The Annals and Magazine of Natural History,* ser. 4, 3: 247–248.

GRAY, M. E., 1842, Figures of molluscous animals, selected from various authors. London, 1, pl. 1–78.

GRAY, M. E., 1850, Figures of molluscous animals, selected from various authors. London, 3, pl. 200–312.

GRIESHABER, J., BARBER, R. & VAUGHN, J., 1974, Morphological techniques for the study of neurons in *Tritonia diomedia. Journal of Ultrastructure Research,* 48: 168.

GRIGG, R. W. & KIWALA, R. S., 1970, Some ecological effects of discharged wastes on marine life. *California Fish and Game,* 56: 145–155.

GROSSMAN, Y., ALKON, D. L. & HELDMAN, E., 1979, A common origin of voltage and generator potentials in statocyst hair cells. *Journal of General Physiology,* 73: 23–48, text figs. 1–13.

GROSVENOR, G. H., 1903, On the nematocysts of aeolids. *Proceedings of the Royal Society of London,* 72: 462–486.

GUBERLET, J. E., 1928, Observations of the spawning habits of *Melibe leonina* (Gould). *Publications of the Puget Sound Marine Biological Station,* 6: 262–270.

GUBERLET, M. L., 1962, *Animals of the seashore.* Binfords & Mort, Portland, Oregon, xxi + 450 p.

GUERNSEY, M., 1912, Some of the Mollusca of Laguna Beach. *First Annual Report of the Laguna Marine Laboratory at Laguna Beach, Orange County, California.* Pomona College, p. 68–82.

GUERNSEY, M., 1913a, The circulatory system of *Laila cockerelli. Journal of Entomology and Zoology, Pomona College, Claremont, California,* 5: 88–92.

GUERNSEY, M., 1913b, The anatomy of *Laila cockerelli. Journal of Entomology and Zoology, Pomona College, Claremont, California,* 5: 137–157.

GULRAJANI, R. M. & ROBERGE, F. A., 1978, Possible mechanisms underlying bursting pacemaker discharges in invertebrate neurons. *Federation Proceedings, Federation of American Societies for Experimental Biology,* 37: 2146–2152.

GUNNERUS, J. E., 1770, Nogle smaa rare, mestendelen nye norske Sodyr., beskrevne. *K. Danske Selskab Skrift.* D. 10: 166–176.

GUTKNECHT, J., 1970, The origin of bioelectrical potentials in plant and animal cells. *American Zoologist,* 10: 347–354.

GUY, H. R. & CONNOR, J. A., 1976, A study of the effects of ρ-chloro-mercuribeneze sulfonic acid on acetylcholine-induced responses of molluscan neurons. *Journal of Pharmacology and Experimental Therapeutics,* 198: 146–154.

HAAFTEN, J. L. V. & VERWEY, J., 1960, The role of water currents in the orientation of marine animals. *Archives Néerlandaises de Zoologie,* 13: 493–499.

HADDON, A. C., 1886, Preliminary report on the fauna of Dublin Bay. *Proceedings of the Royal Irish Academy,* ser. 2, 4: 523–531.

HADERLIE, E. C., 1968, Marine fouling and boring organisms in Monterey Harbor. *Veliger,* 10: 327–341, pl. 49.

HADERLIE, E. C., 1969, Marine boring and fouling organisms in Monterey Harbor. II. Second year of investigation. *Veliger,* 12: 182–192.

HADERLIE, E. C. & DONAT III, W., 1978, Wharf piling fauna and flora in Monterey Harbor, California. *Veliger,* 21: 45–69.

HADERLIE, E. C., MELLOR, J. C., MINTER III, C. S. & BOOTH, G. C., 1974, The sublittoral benthic fauna and flora of Del Monte Beach, Monterey, California. *Veliger,* 17: 185–204.

HADFIELD, M. G., 1963, The biology of nudibranch larvae. *Oikos, Acta Oecologia Scandinavica,* 14: 85–95.

HADFIELD, M. G., 1978, Metamorphosis in marine molluscan larvae: an analysis of stimulus and response, In CHIA F.-S. & RICE, M. E., eds., *Settlement and metamorphosis of marine invertebrate larvae,* Proceedings of the symposium on settlement and metamorphosis of marine invertebrate larvae . . . . Elsevier, New York, p. 165–175.

HAEFELFINGER, H.-R., 1960, Catalogue des opisthobranches de la Rade de Villefranche-sur-Mer et des environs (Alpes Maritimes). *Revue Suisse de Zoologie,* 67: 323–351.

HAGG, R., 1905, Mollusca und Brachiopoda gesammelt von der schwedischen zoologischen Polarexpedition nach Spitzbergen, dem nordostlichen Gronland und Jan Mayen im Jahre 1900. *Arkiv for Zoologi,* 2: 1–136, pl. 1.

HAMATANI, I., 1961, Notes on veligers of Japanese opisthobranchs (4). *Publications of the Seto Marine Biological Laboratory,* 9: 353–361.

HANCOCK, A., 1852, Descriptions of two new species of nudibranchiate Mollusca, one of them forming the type of a new genus. *Report, 21st Meeting of the British Association for the Advancement of Science,* 1851: 74.

HANCOCK, A. & EMBLETON, D., 1845, On the anatomy of *Eolis,* a genus of mollusks of the order Nudibranchiata. *Annals and Magazine of Natural History,* 15: 1–10, 77–78, pl. 1–5.

HANCOCK, A. & EMBLETON, D., 1852, On the anatomy of *Doris. Philosophical Transactions of the Royal Society, London,* 142: 207–252, pl. 11–18.

HANCOCK, A. & NORMAN, A. M., 1864, On *Splanchnotrophus,* an undescribed genus of Crustacea, parasitic in nudibranchiate Mollusca. *Transactions of the Linnean Society of London,* 24: 49–60, pl. 15–16.

HANNA, G. D., 1951, A new west American nudibranch mollusk. *Nautilus,* 65: 1–3, pl. 2.

HARGENS, A. R., 1977, Pressure volume relationships on dehydrating animal tissues. *Comparative Biochemistry and Physiology,* 56(3A): 363–367.

HARRIGAN, J. F. & ALKON, D. L., 1978a, Larval rearing, metamorphosis, growth and reproduction of the eolid nudibranch *Hermissenda crassicornis* (Eschscholtz, 1831) (Gastropoda: Opisthobranchia). *Biological Bulletin,* 154: 430–439.

HARRIGAN, J. F. & ALKON, D. L., 1978b, Laboratory cultivation of *Haminoea solitaria* (Say, 1822) and *Elysia chlorotica* (Gould, 1870). *Veliger,* 21: 299–305.

HARRIGAN, J. F., CROW, T. J. & ALKON, D. L., 1979, Statocyst development in *Hermissenda crassicornis. American Zoologist,* 19: 1001.

HARRIS, L. G., 1971a, Nudibranch associations as symbioses. In CHENG., T. C., ed., *Aspects of the biology of symbiosis.* University Park Press, Baltimore, p. 77–90.

HARRIS, L. G., 1971b, Ecological observations on a New England nudibranch-anemone association. *American Zoologist,* 11: 699.

HARRIS, L. G., 1971c, Ecological observations on a New England nudibranch-anemone association. *Echo, Western Society of Malacologists,* 4: 22.

HARRIS, L. G., 1973, Nudibranch associations. In CHENG, T. C., *Current topics in comparative pathobiology.* Academic Press, p. 213–315.

HARRIS, L. G., 1975, Studies on the life history of two coral-eating nudibranchs of the genus *Phestilla. Biological Bulletin,* 149: 539–550.

HARRIS, L. G., 1976, Comparative ecological studies of the nudibranch *Aeolidia papillosa* and its anemone prey *Metridium senile* along the Atlantic and the Pacific coasts of the USA. *Journal of Molluscan Studies,* 42: 301.

HARRIS, L. G. & HOWE, N. R., 1979, An analysis of the defensive mechanisms observed in the anemone *Anthopleura elegantissima* in response to its nudibranch predator *Aeolidia papillosa. Biological Bulletin,* 157: 138–152.

HARRIS, L. G., POWERS, M. & RYAN, J., 1980, Life history of the estuarine nudibranch *Tenellia fuscata* (Gould, 1870). *Veliger,* 23: 70–74.

HARRIS, L. G., WRIGHT, L. W. & RIVEST, B. R., 1975, Observations on the occurrence and biology of the aeolid nudibranch *Cuthona nana* in New England waters. *Veliger,* 17: 264–268.

HARTH, E., LEWIS, N. S. & CSERMELY, T. J., 1975, The escape of *Tritonia*: dynamics of a neuromuscular control mechanism. *Journal of Theoretical Biology,* 55: 201–228.

HASSALL, A. H., 1842, A list of the Invertebrata found in Dublin Bay and its vicinity. *Annals and Magazine of Natural History,* 9: 132–134.

HASSELT, J. C. VAN, 1824a, In FERUSSAC, A. E. J. P. J. F. D'A. DE, Extrait d'une lettre de J. C. van Hasselt sur les mollusques de l'île de Java, adressée au Prof. van Swinderen à Groninque. *Bulletin des Sciences Naturelles et de Géologie,* 3: 81–87.

HASSELT, J. C. VAN, 1824b, In FERUSSAC, A. E. J. P. J. F. D'A. DE, Extrait d'une lettre du Dr. J. C. van Hasselt au Prof. van Swinderen sur mollusques de Java. *Bulletin des Sciences Naturelles et de Géologie,* 3: 237–248.

HEATH, H., 1917, The anatomy of an eolid *Chioraera dalli. Proceedings of the Academy of Natural Sciences of Philadelphia,* 69: 137–148, pl. 11–13.

HECHT, E., 1893, Note sur un nouveau copépode parasite de nudibranches. *Archives de Zoologie Expérimentale et Générale,* Paris, ser. 3, 1: XIII–XVI.

HECHT, E., 1896 ["1895"], Contribution à l'étude des nudibranches. *Mémoires de la Société Zoologique de France,* 8: 539–711, pl. 1–5.

HEINCKE, F., 1897, Nachtrage zur Fisch- und Molluskenfauna Helgolands 1 (Nr. 7 der Beiträge zur Meeresfauna von Helgoland). *Wissenschaftliche Meeresuntersuchungen.* Neue Folge, 2: 233–252.

HELDMAN, E. & ALKON, D. L., 1978, Neurotransmitter synthesis in the nervous system of the mollusc *Hermissenda. Comparative Biochemistry and Physiology, C Comparative Pharmacology,* 59: 117–126.

HELDMAN, E., GROSSMAN, Y., JERUSSI, T. P. & ALKON, D. L., 1979, Cholinergic features of photoreceptor synapses in *Hermissenda. Journal of Neurophysiology,* 42(1 part 1): 153–165.

HENSCHE, A., 1866, Dritter Nachtrag zur Mollusken-Fauna Preussens. *Schriften der Physikalisch-ökonomischen Gesellschaft zu Konigsberg,* 7: 99–106.

HERDMAN, W. A., 1886, Report on the Nudibranchiata of the L. M. B. C. district. *The first report upon the fauna of Liverpool Bay and the neighbouring seas,* p. 267–277.

HERDMAN, W. A., 1890a, On the structure and functions of the cerata or dorsal papillae in some nudibranchiate Mollusca. *Quarterly Journal of Microscopical Science,* 31: 41–63, pl. 6–10.

HERDMAN, W. A., 1890b, Some experiments on feeding fishes with nudibranchs. *Nature,* 42: 201–203.

HERDMAN, W. A., 1894, Dredging expeditions. *7th Annual Report of the Liverpool Marine Biological Committee, Biological Station Port Erin,* p. 13–20.

HERDMAN, W. A., 1896, *Handbook to Liverpool and the neighbourhood; prepared by various authors for the Publications sub-committee, and* ed. by W. A. HERDMAN. British Assoc., Liverpool, 191 p.

HERDMAN, W. A. & CLUBB, J. A., 1889, Second report of the Nudibranchiata of the L. M. B. C. district. *Proceedings and Transactions of the Liverpool Biological Club,* 3: 225–239, pl. 12.

HERDMAN, W. A. & CLUBB, J. A., 1892, Third report upon the Nudibranchiata of the L. M. B. C. district. *Liverpool Marine Biological Committee, Report,* 3: 131–169, pl. 6–9.

HERDMAN, W. A., THOMPSON, I. C. & CHADWICK, H. C., 1900, Fauna distribution lists for the south end of the Isle of Man. *14th Report, Marine Biological Station, Port Erin,* p. 23–26, 36–58, 7 pl.

HERDMAN, W. A. *et al.,* 1896, The marine zoology, botany, and geology of the Irish Seas—Fourth and final report of the committee . . . . *Report 66th Meeting of the British Association for the Advancement of Science,* p. 417–450.

HERTZ, C. M., 1970, A weekend in Santo Tomas. *Festivus, San Diego Shell Club,* 1(10): 5–6.

HERTZ, J., 1978, Unusual find. *Festivus, San Diego Shell Club,* 10(11): 99, 1 fig.

HERTZENSTEIN, S. M., 1885, Material of fauna of the Murmanske coast and the White Sea. I. Mollusca. Leningrad. *Société des Naturalistes (St. Petersburg), Transactions,* 16: 635–814 (in Russian).

HESSE, M., 1892, Diagnose de nudibranches nouveaux des côtes de Bretagne. *Journal de Conchyliologie,* ser. 3, 20: 345–348.

HEWATT, W. G., 1937, Ecological studies on selected marine intertidal communities of Monterey Bay, California. *American Midland Naturalist,* 18: 161–206, pl. 1–2.

HEWATT, W. G., 1938, Notes on the breeding seasons of the rocky beach fauna of Monterey Bay, California. *Proceedings of the California Academy of Sciences,* ser. 4, 23: 283–288.

HEWATT, W. G., 1946, Marine ecological studies on Santa Cruz Island, California. *Ecological Monographs,* 16: 185–210.

HIGGINS, H. H., 1886, List of the Nudibranchiata of the Mersey and the Dee. In *Pioneers in local biology. The first report upon the fauna of Liverpool Bay L.M.B.C.,* no. 1: 25–26.

HILTON, W. A., 1919, Opisthobranch mollusks from Laguna Beach. *Journal of Entomology and Zoology, Pomona College, Claremont, California,* 11: 34.

HINEGARDNER, R., 1974, Cellular DNA content of the Mollusca. *Comparative Biochemistry and Physiology,* 47A: 447–460.

HOC, S. & FRICKE, J., 1977, Schneckenzungen. *Mikrokosmos,* 66: 360–363.

HODGE, A. J. & ADELMAN JR., W. J., 1980, The neuroplasmic network in *Loligo* and *Hermissenda* neurons. *Journal of Ultrastructure Research,* 70: 220–241.

HOFFMANN, H., 1926, Opisthobranchia. In GRIMPE, G. & WAGLER, E., *Die Tierwelt der Nord- und Ostsee.* Sect. 3, Pt. 9: 1–152.

HOFFMANN, H., 1932, In BRONN, H. G., *Klassen und Ordnungen des Tierreichs.* 3. Band: *Mollusca,* II. Abteilung: *Gastropoda,* 3. Buch: *Opisthobranchia,* Teil 1. I Lieferung, p. 1–152.

HOFFMANN, H., 1933, *op. cit.,* 2 Lieferung, p. 153–312, pl. 1.

HOFFMANN, H., 1934, *op. cit.,* 3 Lieferung, p. 313–488.

HOFFMANN, H., 1935, *op. cit.* 4 Lieferung, p. 489–640.

HOFFMANN, H., 1936, *op. cit.* 5 Lieferung, p. 641–864.

HOFFMANN, H., 1938, *op. cit.* 6 Lieferung, p. 865–1104.

HOFFMANN, H., 1939, *op. cit.* 7 Lieferung, p. 1105–1247.

HOFFMANN, H., 1940, *op. cit.* Teil 2, 1 Lieferung, p. 1–90.

HOGG, J., 1868, The lingual membrane of Mollusca, and its value to classification. *Transactions of the Royal Microscopical Society,* new ser., 16: 92–104, pl. 8–11.

HOLLEMAN, J. J., 1972a, Opisthobranch mollusks dredged in San Francisco Bay during the period 1966 to 1972. *Veliger,* 15: 59–60.

HOLLEMAN, J. J., 1972b, Observations on growth, feeding, reproduction, and development in the opisthobranch *Fiona pinnata* (Eschscholtz). *Veliger,* 15: 142–146.

HOLM, H. T., 1887, Beretning om de paa Fylla's Togti i 1884 foretagne zoologiske Undersogelser i Gronland. *Meddelelser om Gronland,* pt. 8, no. 5: 151–172.

HOLMAN, J. A., 1972, The ultrastructure and activity of sperm in *Acanthodoris pilosa,* a nudibranchiate mollusk. *Marine Biology,* 12: 179–183.

HOMANS, R. E. S. & NEEDLER, A. W. H., 1944, Food of the haddock (*Melanogrammus aeglifinus* Linnaeus). *Nova Scotian Institute of Science, Proceedings,* 21(2): 15–49.

HOWE, N. R. & HARRIS, L. G., 1978, Transfer of the sea anemone pheromone, anthopleurine, by the nudibranch *Aeolidia papillosa. Journal of Chemical Ecology,* 4: 551–561.

HOYLE, G., 1976, Approaches to understanding the neurophysiological bases of behavior. In FENTRESS J. C., ed., *Simpler networks and behavior.* Sinauer Assoc., Inc., p. 21–38.

HOYLE, G. & WILLOWS, A. O. D., 1973, Neuronal basis of behavior in *Tritonia.* II. Relationship of muscular contraction to nerve impulse pattern. *Journal of Neurobiology,* 4: 239–254.

HUGHES, H. P. I., 1970a, The spectral sensitivity and absolute threshold of *Onchidoris fusca* (Müller). *Journal of Experimental Biology,* 52: 609–618.

HUGHES, H. P. I., 1970b, A light and electron microscope study of some opisthobranch eyes. *Zeitschrift für Zellenforschung und mikroskopische Anatomie,* 106: 79–98, 21 pl.

HUMES, A. G. & STOCK, J. H., 1973, A revision of the family Lichomolgidae Kossman, 1877, cyclopoid copepods mainly associated with marine invertebrates. *Smithsonian Contributions to Zoology,* 127: i–v, 1–384.

HURST, A., 1966, A description of a new species of *Dirona* from the north-east Pacific. *Veliger,* 9: 9–15, pl. 2.

HURST, A., 1967, The egg masses and veligers of thirty northeast Pacific opisthobranchs. *Veliger,* 9: 255–288, pl. 26–38.

HURST, A., 1968, The feeding mechanism and behaviour of the opisthobranch *Melibe leonina. Symposia of the Zoological Society of London,* no. 22: 151–166.

HUTTON, F. W., 1882, Notes on some branchiate Mollusca. *Transactions and Proceedings of the New Zealand Institute,* 14: 162–167, pl. 6–7.

HYMAN, L. H., 1967, *The invertebrates,* volume VI, *Mollusca* I. *Aplacophora, Polyplacophora, Monoplacophora, Gastropoda. The coelomate Bilateria.* McGraw-Hill, vii + 792 p.

HYNDMAN, G. C., 1859, Report of the Belfast Dredging Committee. *Report 28th Meeting of the British Association for the Advancement of Science for 1858,* p. 282–291.

I.C.Z.N., 1954, Opinion 221. Emendation to *macfarlandi* of the specific name published as *mcfarlandi* Cockerell, 1902 in the combination *Chromodoris mcfarlandi* (class Gastropoda). *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature,* 4: 117–123.

I.C.Z.N., 1963, Opinion 668. *Tritonia* Cuvier, (1797) (Gastropoda): designation of a type-species under the plenary powers. *Bulletin of Zoological Nomenclature,* 29: 272–273.

I.C.Z.N., 1964, Opinion 697. *Doto* Oken, 1815 (Gastropoda): validated under the plenary powers. *Bulletin of Zoological Nomenclature,* 21: 97–100.

I.C.Z.N., 1966a, Opinion 773. *Tergipes* Cuvier, 1805 (Gastropoda): validated under the plenary powers. *Bulletin of Zoological Nomenclature,* 23: 84–86.

I.C.Z.N., 1966b, Opinion 774. *Eubranchus* Forbes 1838 (Gastropoda): added to the Official List with suppression of several nomina dubia. *Bulletin of Zoological Nomenclature,* 23: 87–90.

I.C.Z.N., 1966c, Opinion 779. *Aeolidia* Cuvier, 1797 (Gastropoda): placed on the Official List of Generic Names. *Bulletin of Zoological Nomenclature,* 23: 100–101.

I.C.Z.N., 1966d, Opinion 783. Four nudibranch gastropod genera: placed on the Official List of Generic Names. *Bulletin of Zoological Nomenclature,* 23: 108–109.

I.C.Z.N., 1967, Opinion 812. *Cadlina* Bergh 1878

(Gastropoda): validated under the plenary powers. *Bulletin of Zoological Nomenclature*, 24: 91–92.

I.C.Z.N., 1974, Opinion 1014. *Okenia* Menke, 1830 (Mollusca, Opisthobranchia): placed on the Official List of Generic Names. *Bulletin of Zoological Nomenclature*, 31: 13–15.

I.C.Z.N., 1977, Opinion 1084. *adsperus, Tergipes*, Nordmann, 1845 (Mollusca, Opisthobranchia) placed on Official List of Specific Names in Zoology. *Bulletin of Zoological Nomenclature*, 34: 33–34.

IDLER, D. R., KHALIL, M. W., BROOKS, C. J. W., EDMONDS, C. G. & GILBERT, J. D., 1978, Studies of sterols from marine molluscs by gas chromatography and mass spectrometry. *Comparative Biochemistry and Physiology, B Comparative Biochemistry*, 59: 163–168.

IJIMA, I., 1925, *Manual of zoology*. Dai-Nippon-Tosho, ed. 4, 950 + 30 p.

INGRAM, W. M., 1935, Notes on egg masses associated with eight nudibranchs from Laguna Beach, California. *Journal of Entomology and Zoology, Pomona College, Claremont, California*, 27: 48–49.

IREDALE, T. & O'DONOGHUE, C. H., 1923, List of British nudibranchiate Mollusca. *Proceedings of the Malacological Society of London*, 15: 195–233.

ISSEL, R., 1928, Sulla relazioni etologiche fra sifonofori (*Velella spirans* Eschr.) e gasteropodi nudibranchi (*Fiona marina* (Forsk.)) nel Mare Ligure. *Bollettino dei Musei di Zoologica e Anatomia Comparata della R. Università de Genova*, ser. 2, 8(23): 1–7.

JAECKEL, S. Jr., 1952, Zur Oekologie der Mollusken-fauna in der westlichen Ostsee. *Schriften des Naturwissenschaftlichen Vereins fur Schleswig-Holstein*, 26: 18–50.

JAECKEL, S. Jr., 1961, Nudibranchia. In *Excursionsfauna von Deutschland. Wirbellose* 1. *Mollusca-Weichtiere*, p. 137–142.

JAECKLE, W. B., 1981, New distributional records for two California nudibranchs. *Veliger*, 23: 240.

JAMESON, R., 1809, Catalogue of animals, of the class Vermes, found in the Firth of Forth, and other parts of Scotland. *Memoirs Wernerian Natural History Society*, 1: 556–565.

JEFFREYS, J. G., 1869, *British conchology* . . . . 5: 1–259, pl. 1–5, 1–102. van Voorst, London.

JEFFREYS, J. G., 1877, New and peculiar Mollusca of the Eulimidae and other families of Gastropoda, as well as Pteropoda, procured in the Valorous Expedition. *Annals and Magazine of Natural History*, ser. 4, 19: 317–339.

JERUSSI, T. P. & ALKON, D. L., 1980, Light responses of motor units in a marine mollusk. *Federation Proceedings, Federation of American Societies for Experimental Biology* 39(3 part I): 596.

JOHANSEN, A. C., 1902, On the Mollusca between tide-marks at the coasts of Iceland. *Videnskabelige Meddeleser fra Danske Naturhistorisk Forening. Kjobenhavn*, 54: 385–392.

JOHNSON, C. W., 1915, Fauna of New England. 13. List of the Mollusca. *Occasional Papers of the Boston Society of Natural History*, 7: 1–231.

JOHNSON, C. W., 1934, List of marine Mollusca of the Atlantic coast from Labrador to Texas. *Proceedings of the Boston Society of Natural History*, 40: 1–204.

JOHNSON, M. E. & SNOOK, H. J., 1927, *Seashore animals of the Pacific coast*. MacMillan, N.Y., xiv + 659 p., pl. 1–11.

JOHNSON, R. I., 1964, The recent Mollusca of Augustus Addison Gould. *United States National Museum, Bulletin* 239: 1–182, pl. 1–45.

JOHNSTON, G., 1835, Illustrations in British Zoology. London. *Magazine of Natural History and Journal of Zoology, Botany, Mineralogy, Geology, and Meteorology*, 8: 376–380.

JOHNSTON, G., 1838a, Miscellanea zoologica. IV.—The Scottish Mollusca Nudibranchia. *Annals of Natural History, or Magazine of Zoology, Botany, & Geology*, 1: 44–56, pl. 2–3.

JOHNSTON, G., 1838b, Miscellanea zoologica. *Annals of Natural History, or Magazine of Zoology, Botany, & Geology*, 1: 114–125, pl. 2–3.

JONES, J. M., 1878, Mollusca of Nova Scotia, (corrected to date, 1877). *Nova Scotian Institute of Natural Science. Proceedings*, 4: 321–330 (421–330, sic).

JUNGE, D., 1972, Increased k-conductance as proximate cause of post-stimulus hyperpolarization in *Tritonia* neurones. *Comparative Biochemistry and Physiology*, 42(4A): 975–981.

JUTTING, T. van B., 1927, Lijst van gemeenten als vindplaatsen van Nederlandsche mollusken. *Tijdschrift der Nederlandsche Dierkunde vereeniging*, ser. 2, 20: LXXXIII–XCVI.

JUTTING, W. S. S. van B., 1947, Lijst van gemeenten als vindplaatsen van Nederlandsche mollusken. *Basteria*, 11: 54–86.

KALKER, H. & SCHMEKEL, R. L., 1976, Bau und Funktion des Cnidosacks der Aeolidoidea (Gastropoda Nudibranchia). *Zoomorphologie*, 86: 41–60.

KASTENDIEK, J., 1975, Predator-prey relationships of 3 subtidal sandbottom invertebrates. *American Zoologist*, 15: 784.

KASTENDIEK, J., 1976, Behavior of the sea pansy *Renilla kollikeri* Pfeffer (Coelenterata: Pennatulacea) and its influence on the distribution and biological interactions of the species. *Biological Bulletin*, 151: 518–537.

KAY, E. A. & YOUNG, D. K., 1969, The Doridacea (Opisthobranchia; Mollusca) of the Hawaiian Islands. *Pacific Science*, 23: 172–231.

KEEN, A. M., 1971, *Sea shells of tropical west America: marine mollusks from Baja California to Peru*. Ed. 2. Stanford University Press, Stanford, California, xiv + 1066 p.

KEEN, A. M. & COAN, E. V., 1974, *Marine molluscan genera of western North America, an illustrated key*. Ed. 2, p. 1–208, Stanford University Press, Stanford, California.

KEEN, A. M. & COAN, E. V., 1975, "Sea shells of tropical west America" additions and corrections to 1975. *Western Society of Malacologists, Occasional Papers,* 1: 1–66.

KELAART, E. F., 1858, Description of new and little known species of Ceylon nudibranchiate molluscs and zoophytes. *Journal of the Royal Asiatic Society, Ceylon Branch, Colombo,* 3: 84–139, 2 pl.

KELSEY, F. W., 1907, Mollusks and brachiopods collected in San Diego, California. *Transactions of the San Diego Society for Natural History,* 1: 31–55.

KEMPF, S. C. & WILLOWS, A. O. D., 1977, Laboratory culture of the nudibranch *Tritonia diomedea* Bergh (Tritoniidae: Opisthobranchia) and some aspects of its behavioral development. *Journal of Experimental Marine Biology and Ecology,* 30: 261–276.

KENNEDY, D., 1967, Small systems of nerve cells. *Scientific American,* 216: 44–52.

KENNEDY, D., SELVERSTON, A. I. & REMLER, M. P., 1969, Analysis of restricted neural networks. *Science,* 164: 1488–1496.

KENT, W. S., 1869, On a new British nudibranch (*Embletonia grayi*). *Proceedings of the Zoological Society of London,* p. 109–111, pl. 8.

KEPNER, W. A., 1943, The manipulation of the nematocysts of *Pennaria tiarella* by *Aeolis pilata. Journal of Morphology,* 73: 297–310, pl. 1.

KINAHAN, J. R., 1861, Report of the committee appointed to dredge Dublin Bay. *Report 30th Meeting of the British Association for the Advancement of Science for* 1860, p. 27–31.

KITTING, C. L., 1974, A subtidal predator-prey system: *Flabellinopsis iodinea* (Nudibranchia) and its hydroid prey. *Western Society of Malacologists, Annual Report,* 7: 32–33.

KNIGHT, G. A. F., 1901, Marine Mollusca and Brachiopoda. In ELLIOT, G. F. S., LAURIE, M. & MURDOCH, J. B., eds., *Fauna, flora and geology of the Clyde area.* Published by the local committee for the meeting of the British Association 1901, p. 189–208.

KOHN, A. J., 1961, Chemoreception in gastropod molluscs. *American Zoologist,* 1: 291–308.

KOMORI, S., 1932, Origin of the eolidian nematocysts from the standpoint of regeneration. *Annotationes Zoologicae Japonenses,* 13: 391–397.

KONISHI, M., 1971, Ethology and neurobiology. *American Scientist,* 59: 56–63.

KOROBSTSOV, G. N. & SAKHAROV, D. A., 1972, The role of ionic environment in the nervous and hormonal control of ciliary beating in molluscan larvae. *Journal of Evolutionary Biochemistry and Physiology,* 7: 198–200.

KOSTYUK, P. G., 1968, Ionic background or activity in giant neurons of molluscs. In SALANKI, J., ed., *Neurobiology of invertebrates.* Plenum Press, p. 145–167.

KOZLOFF, E. N., 1973, *Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago.* pp. i–ix, 1–282, pls. I–XXVIII. *University Washington Press,* ix + 282 p., 28 pl.

KRASTS, I. V. & VEPRINTSEV, B. N., 1972, The giant neurons of *Tritonia*: its electrical properties and the ionic dependence of the action potential. *Comparative Biochemistry and Physiology,* 41(2A): 289–296.

KRAUSE, A., 1885, Ein Beitrag zur Kenntniss der Mollusken-Fauna des Beringsmeeres. *Archiv für Naturgeschichte,* 51: 256–302, pl. 16–18.

KRESS, A., 1970, A new record of *Trapania pallida* (Opisthobranchia, Gastropoda) with a description of its reproductive system and a comparison with *T. fusca. Proceedings of the Malacological Society of London,* 39: 111–116.

KRESS, A., 1971, Über die Entwicklung der Eikapselvolumina bei verschiedenen Opisthobranchier-Arten (Mollusca, Gastropoda). *Helgoländer wissenschaftliche Meeresuntersuchungen,* 22: 326–349.

KROPP, B., 1931, The pigment of *Velella spirans* and *Fiona marina. Biological Bulletin,* 60: 120–123.

KROYER, H. N., 1847, Zoologisches. 1. Aus Koniglichen Musaen. *Amtlicher Bericht Deutscher Naturforscher und Aerzte in Kiel,* 24: 109–124.

KUZ'MIN, S. M., TIMKIN, V. N., BEZRUCHKO, S. M. & ADZHIMOLAEV, T. A., 1976, Dynamic aspects of RNA metabolism in ganglia of mollusks during electrical effects. *Journal of Evolutionary Biochemistry and Physiology,* 11: 231–238.

LAFONT, A., 1871–1872, Note pour servir à la faune de la Gironde contenant la liste des animaux marins dont la présence a été constatée à Arcachon pendant les années 1869–70. *Actes de la Société Linneenne de Bordeaux,* ser. 3, 28: 237–280, pl. 13–17.

LAMARCK, J. B. P. A. DE M., 1819, Histoire naturelle des animaux sans vertèbres . . . . 6(1): i–vi, 1–343. Paris.

LAMARCK, J. B. P. A. DE M., 1836, Histoire naturelle des animaux sans vertèbres. 2. edition . . . . par G. P. DESHAYES et H. MILNE EDWARDS, 7: 1–735.

LAMBERT, P., 1976, Records and range extensions of some northeastern Pacific opisthobranchs (Mollusca: Gastropoda). *Canadian Journal of Zoology,* 54: 293–300.

LANCE, J. R., 1961, A distributional list of southern California opisthobranchs. *Veliger,* 4: 64–69.

LANCE, J. R., 1962a, Two new opisthobranch mollusks from southern California. *Veliger,* 4: 155–159, pl. 38.

LANCE, J. R., 1962b, A new *Stiliger* and a new *Corambella* (Mollusca: Opisthobranchia) from the northwestern (sic) Pacific. *Veliger,* 5: 33–38, pl. 6.

LANCE, J. R., 1962c, A new species of *Armina* (Gastropoda: Nudibranchia) from the Gulf of California. *Veliger,* 5: 51–54.

LANCE, J. R., 1966, New distributional records of some northeastern Pacific Opisthobranchiata with descriptions of two new species. *Veliger,* 9: 69–81.

LANCE, J. R., 1968, New Panamic nudibranchs (Gastropoda Opisthobranchia) from the Gulf of California. *Transactions of the San Diego Society for Natural History,* 15(2): 1–13, pls. 1–2.

LANCE, J. R., 1969, Portraits of California's colorful sea slugs. *Oceans Magazine,* 1(5): 33–37, 11 figs.

La ROCQUE, A., 1953, Catalogue of the Recent Mollusca of Canada. *National Museum of Canada, Bulletin,* No. 129, (Biol. Ser. No. 44), p. i–ix, 1–406.

LARSEN, M., 1925, Nudibranchfaunaen i Drobaksundet. 2. Holo-Cladohepatica (excl. fam. Aeolididae). *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo 1. Matematisk-Naturvidenskapelig klasse* No. 2, p. 1–60, 1 pl.

LAWINSKI, L., 1968, Spostrzenia nad *Embletonia pallida* (A. et H.), morskim slimakiew nagoskrzelnym (Nudibranchia) wystepujacym w Martwej Wisle. *Przeglad Zoologiczny,* 12(4): 410–413.

LEACH, W. E., 1847, The classification of the British Mollusca. *Annals and Magazine of Natural History,* 20: 267–273.

LEACH, W. E., 1852, In: GRAY, J. E., *A synopsis of the Mollusca of Great Britain.* London, p. i–xvi, 1–376, pl. 1–13.

LEBERT, H., 1846, Beobachtungen über die Mundorgana einiger Gastropoden. *Archiv für Anatomie und Physiologie,* p. 435–477, pl. 12–14.

LEDERHENDLER, I. I., BARNES, E. S., & ALKON, D. L., 1980, Complex responses to light of the nudibranch *Hermissenda crassicornis* (Gastropoda: Opisthobranchia). *Behavioral and Neural Biology,* 28: 218–230.

LEE, R. S. & BROPHY, P., 1969, Additional bathymetric and locality data for some opisthobranchs and an octopus from Santa Barbara County, California. *Veliger,* 12: 220–221.

LEIGH-SHARPE, W. H., 1933, A second list of parasitic Copepoda of Plymouth with a description of three new species. *Parasitology,* 25: 113–118.

LEIGH-SHARPE, W. H., 1935, A list of British invertebrates with their characteristic parasitic and commensal Copepoda. *Journal of the Marine Biological Association of the United Kingdom,* 20: 47–48.

LEMCHE, H., 1929, Gastropoda Opisthobranchiata. In JENSEN, A. S., LUNDBECK, W., MORTENSEN, T. & SPARCK, R., eds., *The zoology of the Faroes,* no. 53: 1–35.

LEMCHE, H., 1938, Gastropoda Opisthobranchia. In FRIORIKSSON, A. & TUXEN, S. L., eds., *The zoology of Iceland,* 4(61): 1–54.

LEMCHE, H., 1941a, Gastropoda Opisthobranchiata. The zoology of east Greenland. *Meddelelser om Grønland,* 121(7): 1–50.

LEMCHE, H., 1941b, The Godthaab Expedition 1928. Gastropoda Opisthobranchiata (excl. Pteropoda). *Meddelelser om Grønland,* 80(7): 1–65.

LEMCHE, H., 1964a, Proposed use of the plenary powers to grant precedence to the family-group name Cuthonidae over Tergipedidae and to stabilize some specific names in the genus known as *Eubranchus* Forbes, 1838 (class Gastropoda). Z.N. (S.) 1044. *Bulletin of Zoological Nomenclature,* 21: 35–39.

LEMCHE, H., 1964b, *Aeolidia* Cuvier, 1797 (Gastropoda), proposed addition to the Official List. Z.N. (S.) 1097. *Bulletin of Zoological Nomenclature,* 21: 116–117.

LEMCHE, H., 1973, *Embletonia pallida* Alder and Hancock, 1854. The specific name to be protected against the nomen oblitum *Tergipes adspersus* Nordmann, 1845. (Mollusca, Opisthobranchia) Z.N. (S.) 2010. *Bulletin of Zoological Nomenclature,* 30: 90.

LENNARD, P. R., GETTING, P. A. & HUME, R. I., 1980, Central pattern generator mediating swimming in *Tritonia.* II. Initiation, maintenance, and termination. *Journal of Neurophysiology,* 44: 165–173.

LESLIE, G. & HERDMAN, W. A., 1881, The invertebrate fauna of the Firth of Forth. 3. Comprising the Porifera, Coelenterata (pars), Vermes, Pycnogonida and Mollusca. *Proceedings of the Royal Physical Society of Edinburgh,* 6: 269–315.

LEWBEL, G. S. & LANCE, J. R., 1975, Detached epidermal sheaths of *Lophogorgia chilensis* as a food for *Polycera atra. Veliger,* 17: 346.

LINKE, O., 1937, Die Fortpflanzung der Gemeinen Fadenschnecke (*Aeolis papillosa* L.) der Nordsee. *Natur und Volk,* 67: 232–236.

LINNAEUS, C., 1758, *Systema Naturae,* ed. 10, vol. 1, 824 p.

LINNAEUS, C., 1761, *Fauna Svecica sistens animalia Sveciae regni,* ed. 2, p. 1–578, pl. 1–2.

LINNAEUS, C., 1767, *Systema Naturae per regna tria naturae.* Edito duodecima, reformata. Stockholm, vol. 1, *Regnum animale.* Pt. 2, p. 533–1327.

LIVERPOOL MARINE BIOL. COMM., 1899, Price list of specimens, etc., supplied by the Marine Biological Station at Port Erin (Isle of Man). *12th Annual Report of the Liverpool Marine Biological Committee, Biological Station Port Erin,* p. 49–56.

LLOYD, P. E., 1979, Central peptide-containing neurons modulate gut activity in the gastropod, *Tritonia. Journal of General Physiology,* 74: 9a–10a.

LOCARD, A., 1886, *Catalogue général des mollusques vivants de France—mollusques marin. Prodrome de Malacologie Française,* p. i–x, 1–778, Lyon, Georg.

LONG, S. J., 1969a, Records of *Trinchesia virens, Trinchesia fulgens,* and *Placida dendritica* from San Luis Obispo county, California. *Tabulata, Santa Barbara Malacological Society,* 2(4): 9–12.

LONG, S. J., 1969b, Two new records of *Cratena abronia. Veliger,* 11(3): 281.

LONG, S. J., 1969c, A note on the opisthobranchs of Santa Cruz Island, California. *Veliger,* 12: 232.

LONG, S. J., 1970, A note on the opisthobranch mollusks of Santa Catalina Island, California. *Tabulata, Santa Barbara Malacological Society,* 3(2): 19.

LONNBERG, E., 1931, Untersuchungen über das Vorkommen carotinoider Stoffe bei marinen Evertebraten. *Arkiv för Zoologi,* 22A(14): 1–49.

LOVELAND, R. E., HENDLER, G. & NEWKIRK, G., 1969, New records of nudibranchs from New Jersey. *Veliger,* 11: 418–420.

LOVÉN, S. L., 1846, Index molluscorum litora Scandinaviae occidentalia habitantium. *Ofversigt of Kongl. Vetenskaps Akademiens Forhandlinger. Stockholm,* 3: 135–160.

LØYNING, P., 1922, Nudibranchfaunaen i Drøbaksundet. I. Fam. Aeolididae. *Videnskapsselskapets Skrifter.* I. *Matematisk Naturvidenskapelig klasse,* no. 6, p. 1–103, pl. 1–4.

LØYNING, P., 1927, Nudibranchs from Bergen, collected in the neighborhood of the Biological Station at Herdla. *Nyt Magazin for Naturvidenskaberne. Christiana,* 65: 243–264.

LUNDBECK, W., 1893, Beretning om Fiskeriundersogelser—paa de islandske Fjorde i Sommeren 1893. *Fiskeri-Beretning for 1892–93 Kbh.,* p. 152–178.

MACFARLAND, F. M., 1897, Cellulare Studien an Mollusken-eiern. I. Zur Befruchtung der von *Pleurophyllidia californica* (Cooper) Bergh. II. Die Centrosomen bei der Richtungs Korperbildung im Ei von *Diaulula sandiegensis* (Cooper) Bergh. *Zoologische Jahrbucher, Abtheilung für Morphologie,* 10: 227–264, pl. 18–22.

MACFARLAND, F. M., 1905, A preliminary account of the Dorididae of Monterey Bay, California. *Proceedings of the Biological Society of Washington,* 18: 35–54.

MACFARLAND, F. M., 1906, Opisthobranchiate Mollusca from Monterey Bay, California, and vicinity. *Bulletin of the United States Bureau of Fisheries,* 25: 109–151, pl. 18–31.

MACFARLAND, F. M., 1912, The nudibranch family Dironidae. *Zoologische Jahrbucher Supplement,* 15: 515–536, pl. 30–32.

MACFARLAND, F. M., 1923, The morphology of the nudibranch genus *Hancockia. Journal of Morphology,* 38: 65–104, pl. 1–6.

MACFARLAND, F. M., 1925, The Acanthodorididae of the California coast. *Nautilus,* 39: 49–65.

MACFARLAND, F. M., 1926, The Acanthodorididae of the California coast. *Nautilus,* 39: 94–103, pl. 2–3.

MACFARLAND, F. M., 1929, *Drepania* a genus of nudibranchiate mollusks new to California. *Proceedings of the California Academy of Sciences,* 18: 485–496, pl. 35.

MACFARLAND, F. M., 1931, *Drepanida,* new name for *Drepania* Lafont, preoccupied. *Nautilus,* 45: 31–32.

MACFARLAND, F. M., 1966, Studies of opisthobranchiate mollusks of the Pacific coast of North America. *California Academy of Sciences, Memoirs,* 6: 1–546, pl. 1–72.

MACFARLAND, F. M. & O'DONOGHUE, C. H., 1929, A new species of *Corambe* from the Pacific coast of North America. *Proceedings of the California Academy of Sciences,* ser. 4, 18: 1–27, pl. 1–3.

MACGILLIVRAY, W., 1843, *A history of the molluscous animals of the counties of Aberdeen, Kincardine and Banff . . . .* London, xxiv + 372 p.

MACGINITIE, G. E., 1935, Ecological aspects of a California marine estuary. *American Midland Naturalist,* 16: 629–765.

MACGINITIE, G. E., 1955, Distribution and ecology of the marine invertebrates of Point Barrow, Alaska. *Smithsonian Miscellaneous Collections,* 128: i–iv, 1–201, pl. 1–8.

MACGINITIE, G. E. & MACGINITIE, N. L., 1949, *Natural history of marine animals.* McGraw-Hill, N.Y., xii + 473 p.

MACGINITIE, N. L., 1959, Marine Mollusca of Point Barrow, Alaska. *Proceedings of the United States National Museum,* 109: 59–208, pl. 1–27.

MAKSIMOV, V. N., TURPAEVA, E. P. & SIMKINA, R. G., 1971, Intensity of the effect of several factors acting simultaneously on the population of the barnacle *Balanus improvisus* Darwin. *Oceanology of the Academy of Sciences of the U.S.S.R.,* 11: 902–907.

MANOKHINA, M. S., 1966, Cytochemical study of giant neurons in *Tritonia diomedia* Bergh. I. Nucleic acids, proteins, polysaccharides and lipides. *Arkhiv Anatomii, Gistologii i Embriologii, Moscow,* 50: 93–101 (in Russian).

MANOKHINA, M. S. & KUZ'MINA, L. V., 1972, Distribution of biogenic monoamines in the central nervous system of the nudibranch *Tritonia* sp. *Journal of Evolutionary Biochemistry and Physiology,* 7: 296–301.

MANSEL-PLEYDELL, J. C., 1898, *The Mollusca of Dorsetshire.* Dorchester, xxxii + 110 p.

MARCUS, E., 1955, Opisthobranchia from Brazil. *Boletim de Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo* 207, 20: 89–261, pl. 1–30.

MARCUS, E., 1957, On Opisthobranchia from Brazil (2). *Journal of the Linnean Society, London (Zoology),* 43: 390–486.

MARCUS, E., 1958, On western Atlantic opisthobranchiate gastropods. *American Museum of Natural History, Novitates* No. 1906: 1–82.

MARCUS, E., 1959, Reports of the Lund University Chile Expedition 1948–49. 36. Lamellariaçea und Opisthobranchia. *Lunds Universitets Årsskrift* N.F., Avd. 2, 55(9): 1–134.

MARCUS, E., 1961, Opisthobranch mollusks from California. *Veliger,* 3(Suppl. I): 1–85, pl. 1–10.

MARCUS, E., 1964, A new species of *Polycera* (Nudibranchia) from California. *Nautilus,* 77: 128–131.

MARCUS, E. & MARCUS, E. DU B. R., 1967a, American opisthobranch mollusks. Part 1, tropical American opisthobranchs. Part 2, opisthobranchs from the Gulf of California. *Studies in Tropical Oceanography, Institute of Marine Science, Miami,* 6: 1–256.

MARCUS, E. DU B. R., 1970, On some opisthobranchs from Cananeia, Brazil. *Boletim de Zoo-*

logia e Biologia Marinha, N.S., 27: 207–228, pl. 1–4.

MARCUS, E. DU B. R., 1971, On some euthyneuran gastropods from the Indian and Pacific Oceans. *Proceedings of the Malacological Society of London,* 39: 355–369.

MARCUS, E. DU B. R., 1972a, Notes on some opisthobranch gastropods from the Chesapeake Bay. *Chesapeake Science,* 13: 300–317.

MARCUS, E. DU B. R., 1972b, On some opisthobranchs from Florida. *Bulletin of Marine Science of the Gulf and Caribbean,* 22: 284–308.

MARCUS, E. DU B. R., 1973, On the scientific names of new species. *Tabulata, Santa Barbara Malacological Society,* 6(1): 5.

MARCUS, E. DU B. R., 1977, An annotated checklist of the Western Atlantic warm water opisthobranchs. *Journal of Molluscan Studies, Supplement* 4: 1–23.

MARCUS, E. DU B. R. & HUGHES, H. P. I., 1974, Opisthobranch mollusks from Barbados. *Bulletin of Marine Science,* 24: 498–532.

MARCUS, E. DU B. R. & MARCUS, E., 1955, Über Sand-Opisthobranchia. *Kieler Meeresforschungen,* 11: 230–243, pl. 36–38.

MARCUS, E. DU B. R. & MARCUS, E., 1958, Opisthobranchia aus dem Schill von Helgoland. *Kieler Meeresforschungen,* 14: 91–96, pl. 18.

MARCUS, E. DU B. R. & MARCUS, E., 1960, Opisthobranchs from American Atlantic warm waters. *Bulletin of Marine Science of the Gulf and Caribbean,* 10: 129–203.

MARCUS, E. DU B. R. & MARCUS, E., 1967b, Some opisthobranchs from Sapelo Island, Georgia, U.S.A. *Malacologia,* 6: 199–222.

MARCUS, E. DU B. R. & MARCUS, E., 1969, Opisthobranchian and lamellarian gastropods collected by the "Vema." *American Museum of Natural History, Novitates* No. 2368: 1–33.

MARCUS, E. DU B. R. & MARCUS, E., 1970, Some gastropods from Madagascar and West Mexico. *Malacologia,* 10: 181–223.

MARINE BIOLOGICAL ASSOCIATION, 1904, Plymouth marine invertebrate fauna. *Journal of the Marine Biological Association of the United Kingdom,* new ser., 7: 155–298.

MARINE BIOLOGICAL ASSOCIATION, 1931, *Plymouth marine fauna ....* Marine Biological Association of the United Kingdom, ed. 2, 371 p.

MARINE BIOLOGICAL ASSOCIATION, 1957, *Plymouth marine fauna ....* Marine Biological Association of the United Kingdom, ed. 3, xliii + 457 p.

MARISCAL, R. N., 1974, Nematocysts. In MUSCATINE, L. & LENHOFF, H. M., eds., *Coelenterate biology: reviews and new perspectives.* Academic Press, New York, p. 129–178.

MARMOR, M. F., 1971, The effects of temperature and ions on the current-voltage relation and electrical characteristics of a molluscan neurone. *Journal of Physiology,* 218: 573–598.

MARMOR, M., 1975, The membrane of giant molluscan neurons electrophysiologic properties and the origin of the resting potential. *Progress in Neurobiology,* 5: 167–195.

MARMOR, M. & GORMAN, A. L. F., 1969, Ionic and metabolic components of a neuronal membrane potential. *Physiologist,* 12: 293.

MARMOR, M. & GORMAN, A. L. F., 1970, Membrane potential as the sum of ionic and metabolic components. *Science,* 167: 65–67.

MARMOR, M. & SALMOIRAGHI, G. C., 1970, Electrogenic sodium transport and current voltage relations in a molluscan neuron. *Federation Proceedings, Federation of American Societies for Experimental Biology,* 29: 834.

MARTIN, H. F., III & MANNING, J. W., 1974, Burst firing of flexor neurons in *Tritania* (sic) escape swimming. *Federation Proceedings, Federation of American Societies for Experimental Biology,* 33(3 part 1): 361.

MASUKAWA, L. M., 1975, Potassium ion conductance increase during inhibitory synaptic potentials in photo receptor cells of *Hermissenda crassicornis. Federation Proceedings, Federation of American Societies for Experimental Biology,* 34: 359.

MATTOX, N. T., 1955, Studies on the Opisthobranchiata. 1. A new species of the genus *Tritoniopsis* from southern California. *Bulletin of the Southern California Academy of Sciences,* 54: 8–13, pl. 4–5.

MAUZEY, K. F., BIRKELAND, C. & DAYTON, P. K., 1968, Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. *Ecology,* 49: 603–619.

McBETH, J. W., 1968, Feeding behavior of *Corambella steinbergae. Veliger,* 11: 145–146.

McBETH, J. W., 1970, Pigmentation of nudibranchs. *Echo,* 3: 28.

McBETH, J. W., 1971, Studies on the food of nudibranchs. *Veliger,* 14: 158–161.

McBETH, J. W., 1972a, Carotenoids from nudibranchs. *Comparative Biochemistry and Physiology,* 41(1B): 55–68.

McBETH, J. W., 1972b, Carotenoids from nudibranchs—II. The partial characterization of hopkinsiaxanthin. *Comparative Biochemistry and Physiology,* 41(1B): 69–77.

McCAMAN, M. W., McCAMAN, R. E. & STETZLER, J., 1979, A rapid radioenzymatic assay for dopamine and N-acetyldopamine. *Analytical Biochemistry,* 96: 175–180.

McCAMAN, M. W., ONO, J. K. & McCAMAN, R. E., 1979, Dopamine measurements in molluscan ganglia and neurons using a new, sensitive assay. *Journal of Neurochemistry,* 32: 1111–1113.

McCAMAN, M. W., WEINREICH, D. & McCAMAN, R. E., 1973, The determination of picomole levels of 5-hydroxytryptamine and dopamine in *Aplysia, Tritonia* and leech nervous tissues. *Brain Research,* 53: 129–137.

McCOSKER, J. E., 1980, Academically speaking: gaudy slugs of the sea. *Pacific Discovery,* 33(2): 29–31.

McDONALD, G. R., 1970, Range extensions for *Acanthodoris hudsoni* MacFarland, 1905, and *Onchidoris bilamellata* (Linnaeus, 1767). *Veliger*, 12: 375.

McDONALD, G. R., 1975a, Key D: Sacoglossa and Nudibranchia. In: SMITH, R. I. & CARLTON, J. T., eds., *Light's manual, intertidal invertebrates of the central California coast*. University of California Press, p. 522–542, pl. 121–123.

McDONALD, G. R. & NYBAKKEN, J. W., 1975b, *Cerberilla mosslandica*. A new eolid nudibranch from Monterey Bay, California (Mollusca: Opisthobranchia). *Veliger*, 17: 378–382.

McDONALD, G. R., 1975b, *Cerberilla mosslandica* McDonald and Nybakken, 1975, a new species of nudibranch from Monterey Bay, California, with comments on other enigmatic or undescribed species from California. *Bulletin of the American Malacological Union*, 1975: 55.

McDONALD, G. R. & NYBAKKEN, J. W., 1978, Additional notes on the food of some California nudibranchs with a summary of known food habits of California species. *Veliger*, 21: 110–118.

McGOWAN, J. A. & PRATT, I., 1954, The reproductive system and early embryology of the nudibranch *Archidoris montereyensis* (Cooper). *Bulletin of the Museum of Comparative Zoology at Harvard College*, 111: 261–276, pl. 1–2.

McINTOSH, W. C., 1865, On the nudibranchiate Mollusca of St. Andrews; *Edwardsia*; and the polyps of *Alcyonium digitatum*. *Proceedings of the Royal Physical Society of Edinburgh*, 5: 387–393.

McINTOSH, W. C., 1874, On the marine invertebrate fauna and fishes of St. Andrews. *Annals and Magazine of Natural History*, ser. 4, 13: 420–432.

McINTOSH, W. C., 1875, *The marine invertebrates and fishes of St. Andrews*. Adam & Charles Black, Edinburgh, vi + 186 p., 9 pl.

McLEAN, J. H., 1962, Sublittoral ecology of kelp beds of the open coast area near Carmel, California. *Biological Bulletin*, 122: 95–114.

McMILLAN, N. F., 1942a, Spawn of *Aeolidia papillosa* (L.). *Journal of Conchology*, 21: 324.

McMILLAN, N. F., 1942b, Food of nudibranchs. *Journal of Conchology*, 21: 327.

McMILLAN, N. F., 1944, The marine Mollusca of Greenisland Co. Antrim. *Irish Naturalists' Journal*, 8: 158–164.

MELLON, D., JR., 1974, Integrative and organizational aspects of synaptic function in molluscs. *Progress in Neurobiology*, 3: 163–189.

MEYER, H. A. & MÖBIUS, K., 1865, *Fauna der Kieler Bucht. Die Hinterkiemer oder Opisthobranchier*. Leipzig, Engelmann 1: i–xxx, 1–88, pl. 1–26.

MEYER, K. B., 1971, Distribution and zoogeography of fourteen species of nudibranchs of northern New England and Nova Scotia. *Veliger*, 14: 137–152.

MICHEL, N., 1970, A good day's dive. *Festivus, San Diego Shell Club*, 1(8): 7–8.

MICHEL, N., 1976, A fantastic dive. *Festivus, San Diego Shell Club*, 7(8): 46–49.

MICHELSON, M. J., 1970, On the possible changes in the mutual disposition of cholinoreceptors in the course of evolution. In: EIGENMANN, R., ed., *Proceedings of the 4th International Congress on Pharmacology*, Schwabe, Basel, vol. 5, symposia, p. 103–115.

MILACHEWITCH, K. O., 1916, *Les mollusques des mers Russes*. Tome 1: i–xii, 1–312, pl. 1–11.

MILLER, M. C., 1961, Distribution and food of the nudibranchiate Mollusca of the south of the Isle of Man. *Journal of Animal Ecology*, 30: 95–116.

MILLER, M. C., 1962, Annual cycles of some Manx nudibranchs, with a discussion of the problem of migration. *Journal of Animal Ecology*, 31(3): 535–569.

MILLER, M. C., 1967, Grazing carnivores—some sea slugs feeding on sedentary invertebrates. *Poirieria, Conchology Section Auckland Institute and Museum*, 3: 1–11.

MILLER, M. C., 1971, Aeolid nudibranchs (Gastropoda: Opisthobranchia) of the families Flabellinidae and Eubranchidae from New Zealand waters. *Zoological Journal of the Linnean Society, London*, 50: 311–337, 1 pl.

MILLER, M. C., 1974, Aeolid nudibranchs (Gastropoda: Opisthobranchia) off the family Glaucidae from New Zealand waters. *Zoological Journal of the Linnean Society, London*, 54: 31–61; 1 pl.

MILLER, M. C., 1977, Aeolid nudibranchs (Gastropoda: Opisthobranchia) of the family Tergipedidae from New Zealand waters. *Zoological Journal of the Linnean Society, London*, 60: 197–222, 1 pl.

MILLER, R. L., 1968, Some observations on the ecology and behavior of *Lucapinella callomarginata*. *Veliger*, 11: 130–134, pl. 16.

MILLOTT, N., 1937, On the structure and function of the wandering cells in the wall of the alimentary canal of nudibranchiate Mollusca. *Journal of Experimental Biology*, 14: 405–412.

MINER, R. W., 1950, *Field book of seashore life*. Putnam's Sons, New York, xv + 888 p., 251 pl., 24 col. pl.

MINICHEV, YU, S., 1971, *Tritonia primorjensis* sp. n. (Gastropoda, Opisthobranchia), a suitable subject for neurophysiological and biophysical investigations studies. *Zoologicheskii Zhurnal*, 50: 282–284.

MIROLLI, M., 1970, Geometrical factors determining the electrotonic properties of a folded nerve fiber. *Journal of Cell Biology*, 47(2 part 2): 141a.

MIROLLI, M. & GORMAN, A. L. F., 1973, The extracellular space of a simple molluscan nervous system and its permeability to potassium. *Journal of Experimental Biology*, 58: 423–435, pl. 1–3.

MOHR, N., 1786, *Forsog til en Islandsk Naturhistoire, med adskillige oekonomiske samt andre Anmaerkninger*. Kjobenhavn, xvi + 413, 7 pl.

MÖLLER, H. P. C., 1842, *Index molluscorum Groenlandiae,* Hafniae, 138 p.

MONOD, T. & DOLLFUS, R.-PH., 1932, Les copépodes parasites de mollusques. *Annales de Parasitologie Humaine et Comparée,* 10: 129–204.

MONTAGU, G., 1804, Description of several marine animals found on the south coast of Devonshire. *Transactions of the Linnean Society of London,* 7: 61–85, pl. 6–7.

MONTAGU, G., 1815, Descriptions of several new or rare animals, principally marine, discovered on the south coast of Devonshire. *Transactions of the Linnean Society of London,* 11: 1–26, pl. 1–5.

MOORE, H. B., 1937, Marine fauna of the Isle of Man. *Proceedings and Transactions of the Liverpool Biological Society,* 50: 1–293.

MÖRCH, O. A. L., 1857, In RINK, H. J., *Gronland geographisk og statistisk beskrevet. Prodromus fauna moluscorum Gronlandiae. Fortegnelse over Gronland Bloddyr.* Bd. 2, pt. 4: 75–100.

MÖRCH, O. A. L., 1868, Faunula molluscorum Islandiae. Oversigt over Islands Bloddyr. *Videnskabelige Meddeleser fra Danske Naturhistorisk Forening,* p. 185–227.

MÖRCH, O. A. L., 1871, Synopsis molluscorum marinorum Daniae. Fortegnelse over de i danske Have forenkommende Bloddyr. *Videnskabelige Meddeleser fra Danske Naturhistorisk Forening, Kjobenhavn,* ser. 3, 3: 157–225.

MÖRCH, O. A. L., 1875, In RINK, H. J., *Prodromus faunae molluscorum Groenlandiae,* p. 125.

MÖRCH, O. A. L., 1877, Synopsis of the Greenland fauna. IV. Mollusca. In RINK, H. J., *Danish Greenland its people and its products,* p. 435–442.

MORETEAU, J.-C., 1977, Etude sur l'alimentation d'*Aeolidia papillosa* L. *Cahiers de Biologie Marine,* 18: 369–383.

MORSE, M. P., 1967, Functional morphology of the digestive system of the nudibranch mollusc *Acanthodoris pilosa. American Zoologist,* 7: 770.

MORSE, M. P., 1968, Functional morphology of the digestive system of the nudibranch mollusc *Acanthodoris pilosa. Biological Bulletin,* 134: 305–319.

MORSE, M. P., 1969, On the feeding of the nudibranch, *Coryphella verrucosa rufibranchialis,* with a discussion of its taxonomy. *Nautilus,* 83: 37–40.

MORSE, M. P., 1973, Fine structure of the vascular inclusions of the stomach cells in the opisthobranch mollusk *Aeolidia papillosa. American Zoologist,* 13: 1334.

MORTON, J. E., 1967, *Molluscs.* Hutchinson University Library, London, ed. 4 rev., 244 p.

MÜLLER, O. F. 1776, *Zoologiae Danicae* . . . . xxxii + 282 p.

MÜLLER, O. F., 1788, *Zoologica Danica* . . . . ed. 3, 2: 1–56, pl. 41–80.

MULLINER, D. K., 1972a, Breeding habits and life cycles of three species of nudibranchs from the eastern Pacific. *Echo, Western Society of Malacologists,* 5: 38.

MULLINER, D. K., 1972b, Breeding habits and life cycles of three species of nudibranchs from the eastern Pacific. *Festivus, San Diego Shell Club,* 3(9): 1–5.

MUMAW, L. M., 1978, Effects of oil on nudibranch development. *College of Fisheries, University of Washington, Annual Report* 1977, *Res. Fish., Contr.* No. 480: 74–75.

MURRAY, M. J. & LEWIS, E. R., 1974, Sensory control of prey capture in *Navanax inermis. Veliger,* 17: 156–158.

NAVILLE, A., 1925, Sur la présence d'une *Embletonia* (mollusque, nudibranche) dans le canal de Caen à la mer; origine exogène de ses nematocystes. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris,* 181: 812–813.

NAVILLE, A., 1926, Notes sur les éolidiens. Un éloidien d'eau saumatre. Origine des nematocystes. Zooxanthelles et homochromie. *Revue Suisse de Zoologie, Annales de la Société Zoologique Suisse et du Muséum d'Histoire Naturelle de Genève,* 33: 251–289.

NAVONI, L., 1973, Der chemische Sinn der Nudibranchier (Gastropoda Opisthobranchia). *Revue Suisse de Zoologie, Annales de la Société Zoologique Suisse et du Muséum d'Histoire Naturelle de Genève,* 79: 1333–1379, pl. 1–2.

NEARY, J. T., 1980, Protein phosphorylation in the nervous system of the nudibranch mollusk *Hermissenda crassicornis. Federation Proceedings, Federation of American Societies for Experimental Biology,* 39: 2950.

NICAISE, G., 1969, Detection histochimique de cholinesterases dans les cellules gliales et interstitielles des Doridiens. *Comptes Rendus Société de Biologie de Lyon,* 163: 2600–2604, pl. 1–2.

NICHOLS, A. R., 1900, A list of the marine Mollusca of Ireland. *Proceedings of the Royal Irish Academy,* ser. 3, 5: 477–662.

NICOL, E. A. T., 1935, The ecology of a salt-marsh. *Journal of the Marine Biological Association of the United Kingdom,* new ser., 20: 203–261.

NOBRE, A., 1932, *Moluscos Marinhos de Portugal.* Instituto de Zoologia da Universidade do Porto, 466 p., 80 pl.

NOBRE, A., 1936, *Moluscos Marinhos de Portugal.* Companhia Editora do Minho, Barcelos, 2: vii + 378 p., pl. 81–86.

NORDGAARD, O., 1907, Mofjordens Naturforhold. *Det Kongelige Norske Videnskabernes Selskabs Skrifter,* Trondhiem, 1906: no. 9: 1–42, pl. 1.

NORDMANN, A. VON, 1844, Versuch einer Monographie des *Tergipes edwardsi,* ein Beitrag zur Natur und Entwicklungsgeschichte der Nacktkiemer. *Bulletin de la classe Physico-Mathématique de l'Académie Impériale des Sciences de Saint Pétersbourg,* 3: 270–271.

NORDMANN, A. VON, 1845, Versuch einer Natur-und Entwicklungsgeschichte des *Tergipes Edwardsii.* Akademiia Nauk SSSR. Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg, ser. 6, seconde partie, 4: 497–602, pl. 1–5.

NORDMANN, A. VON, 1846, Essai d'une monographie du *Tergipes edwardsii.* Annales des Sciences Naturelles. *Zoologie et Biologie Animale,* ser. 3, 5: 109–160, pl. 1.

NORMAN, A. M., 1860, The Mollusca of the Firth of Clyde. *The Zoologist, A Popular Miscellany of Natural History,* 18: 7238–7248.

NORMAN, A. M., 1890, Revision of British Mollusca. *Annals and Magazine of Natural History,* ser. 6, 6: 60–91.

NORMAN, A. M. & SCOTT, T., 1906, *The Crustacea of Devon and Cornwall.* London, xv + 232 p., 24 pl.

NORRIS, E. R. & RAMA RAO, D. A. R., 1935, Phosphatases of marine invertebrates. *Journal of Biological Chemistry,* 108: 783–790.

NORTH, W. J., 1971, Introduction and background. In NORTH, W. J., ed., The biology of giant kelp beds (*Macrocystis*) in California. *Beihefte zur Nova Hedwigia,* (32): i–xiii, 1–600.

NYBAKKEN, J. W., 1974, A phenology of the smaller dendronotacean, arminacean and aeolidacean nudibranchs at Asilomar State Beach over a twenty-seven month period. *Veliger,* 16: 370–373.

NYBAKKEN, J. W., 1978, Abundance, diversity and temporal variability in a California intertidal nudibranch assemblage. *Marine Biology,* 45: 129–146.

NYBAKKEN, J. W. & EASTMAN, J., 1977, Food preference, food availability and resource partitioning in *Triopha maculata* and *Triopha carpenteri* (Opisthobranchia: Nudibranchia). *Veliger,* 19: 279–289.

OAKES, J. V., 1979, Distribution of ^{14}C-labeled food material through the bodies of various gastropods. *Wasmann Journal of Biology,* 37: 27–29.

O'CLAIR, C. E., 1977, Marine invertebrates in rocky intertidal communities. In MERRITT, M. L. & FULLER, R. G., eds., *The environment of Amchitka Island, Alaska. Tech. Information Cent., ERDA.* TID-26712, p. 395–449.

ODHNER, N. H., 1907, Northern and Arctic invertebrates in the collection of the Swedish State Museum (Riks Museum). 3. Opisthobranchia and Pteropoda, Stockholm. *Kungl. Svenska Vetenskaps Adademiens Handlingar,* Neue Folge, 41(4): 1–113, pl. 1–3.

ODHNER, N. H., 1910, Some notes on the genus *Cumanotus. Journal of the Marine Biological Association of the United Kingdon,* new ser., 9: 82–84.

ODHNER, N. H., 1921, Mollusca from Juan Fernandez and Easter Island. In SKOTTSBERG, C. J. F., *Natural History of Juan Fernandez and Easter Island,* 3: 219–254, pl. 8–9.

ODHNER, N. H., 1922, Norwegian opisthobranchiate Mollusca in the collections of the Zoological Museum of Kristiania. *Nyt Magazin for Naturvidenskaberne, Christiana,* 60: 1–47.

ODHNER, N. H., 1926a, Die Opisthobranchien. In *Further zoological results of the Swedish Antarctic Expedition 1901–1903 under the direction of Dr. Otto Nordenskjold,* 2: 1–100, pl. 1–3.

ODHNER, N. H., 1926b, Nudibranchs and lamellariids from the Trondhjem Fjord. *Det Kongelige Norske Videnskabernes Selskabs Skrifter, Trondhjem* 1926, N. R. 2. *Meddelelse fra Trondhjems Biologiske Statsjon* N. R. 24, p. 1–36, pl. 1.

ODHNER, N. H., 1934, The Nudibranchiata. *British Antarctic ("Terra Nova") Expedition, 1910. British Museum (Natural History) Natural History Report. Zoology,* 7: 229–310, pl. 1–3.

ODHNER, N. H., 1936, Nudibranchia Dendronotacea—A revision of the system. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique,* ser. 2, fasc. 3: 1057–1128, pl. 1.

ODHNER, N. H., 1939, Opisthobranchiate Mollusca from the western and northern coasts of Norway. *Det Kongelige Norske Videnskabernes Selskabs Skrifter, Trondheim,* no. 1: 1–93.

ODHNER, N. H., 1941, New polycerid nudibranchiate Mollusca and remarks on this family. *Meddelanden fran Götesborgs Musei Zoologiska Avdeling,* 91: 1–20. (*Gotesborgs Kgl. Vetensk. Vitterh. Samh. Handl.* (b) 1 (11)).

ODHNER, N. H., 1957, *Chromodoris* contra *Glossodoris* a systematic-nomenclatorial controversy. *Proceedings of the Malacological Society of London,* 32: 250–253.

ODHNER, N. H., 1963, On the taxonomy of the family Tritoniidae (Mollusca: Opisthobranchia). *Veliger,* 6: 48–52.

O'DONOGHUE, C. H., 1921, Nudibranchiate Mollusca from the Vancouver Island region. *Transactions of the Royal Canadian Institute,* 13: 147–209, pl. 7–11 (1–5).

O'DONOGHUE, C. H., 1922a, Notes on the nudibranchiate Mollusca from the Vancouver Island region. I. Colour variations. *Transactions of the Royal Canadian Institute,* 14: 123–130, pl. 2.

O'DONOGHUE, C. H., 1922b, Notes on the nudibranchiate Mollusca from the Vancouver Island region. III. Records of species and distribution. *Transactions of the Royal Canadian Institute,* 14: 145–167, pl. 5–6.

O'DONOGHUE, C. H., 1922c, Notes on the taxonomy of nudibranchiate Mollusca from the Pacific coast of North America. I. On the identification of *Cavolina* (i.e. *Hermissenda*) *crassicornis* of Eschscholtz. *Nautilus,* 35: 74–77.

O'DONOGHUE, C. H., 1922d, Notes on the taxonomy of nudibranchiate Mollusca from the Pacific coast of North America. *Proceedings of the Malacological Society of London,* 15: 133–159.

O'DONOGHUE, C. H., 1924, Notes on the nudibranchiate Mollusca from the Vancouver Island region. IV. Additional species and records. *Transactions of the Royal Canadian Institute,* 15: 1–33, pl. 1–2.

O'DONOGHUE, C. H., 1926, A list of the nudibranchiate Mollusca recorded from the Pacific coast of North America, with notes on their distribution. *Transactions of the Royal Canadian Institute*, 15: 199–247.

O'DONOGHUE, C. H., 1927a, Notes on the nudibranchiate Mollusca from the Vancouver Island region. V. Two new species and one new record. *Transactions of the Royal Canadian Institute*, 16: 1–12, pl. 1.

O'DONOGHUE, C. H., 1927b, Notes on a collection of nudibranchs from Laguna Beach, California. *Journal of Entomology and Zoology, Pomona College, Claremont, California*, 19: 77–119, pl. 1–3.

O'DONOGHUE, C. H., 1929, Report on the Opisthobranchiata. In: Zoological results of the Cambridge Expedition to the Suez Canal, 1924. *Transactions of the Zoological Society of London*, 22: 713–841.

O'DONOGHUE, C. H. & O'DONOGHUE, E., 1922, Notes on the nudibranchiate Mollusca of the Vancouver Island region. II. The spawn of certain species. *Transactions of Royal Canadian Institute*, 14: 131–143, pl. 3–4.

ORCUTT, C. R., 1885, Notes on the mollusks of the vicinity of San Diego, California, and Todos Santos Bay, Lower California. *Proceedings of the United States National Museum*, 8: 534–552, pl. 24.

ORTEA, J. A., 1979, *Onchidoris sparsa* (Alder & Hancock, 1846) in Asturias, northern Spain. *Veliger*, 22: 45–48.

OSTROUMOFF, A. A., 1893, Catalogue des Mollusques de la Mer Noire et d'Azow, observés jusqu'à ce jour à l'état vivant. *Zoologischer Anzeiger*, 16: 245–247.

PAINE, R. T., 1963a, Food recognition and predation on opisthobranchs by *Navanax inermis* (Gastropoda: Opisthobranchia). *Veliger*, 6: 1–9, pl. 1.

PAINE, R. T., 1963b, Trophic relationships of 8 sympatric predatory gastropods. *Ecology*, 44: 63–73.

PAINE, R. T., 1964, Ash and calorie determinations of sponge and opisthobranch tissues. *Ecology*, 45: 384–387.

PAINE, R. T., 1965, Natural history, limiting factors and energetics of the opisthobranch *Navanax inermis*. *Ecology*, 46: 603–619.

PALLAS, P. S., 1788 ["1794"], Marina varia nova et rariora. *Nova Acta Academiae Scientiarum Imperialis Petropolitanae*, St. Petersburg, 2: 229–250, pl. 5–7.

PARTRIDGE, L. D., JR., 1973, A note on the anatomy of the circumesophageal ganglion complex of several Doridacea nudibranchs. *Veliger*, 15: 349–351.

PARTRIDGE, L. D., JR., 1975, Pentylenetetrazol induced bursting activity in the absence of a negative conductance characteristic. *Brain Research*, 94: 161–166.

PARTRIDGE, L. D., JR. & CONNOR, J. A., 1978, A mechanism for minimizing temperature effects on repetitive firing frequency. *American Journal of Physiology*, 234: C155–C161.

PARTRIDGE, L. D., JR. & STEVENS, C. F., 1976, A mechanism for spike frequency adaptation. *Journal of Physiology*, 256: 315–332.

PARTRIDGE, L. D., JR., THOMPSON, S. H., SMITH, S. J. & CONNOR, J. A., 1979, Current-voltage relationships of repetitively firing neurons. *Brain Research*, 164: 69–80.

PEASE, W. H., 1860, Descriptions of new species of Mollusca from the Sandwich Islands. *Proceedings of the Zoological Society of London*, pt. 28: 18–37.

PELSENEER, P., 1911, Recherches sur l'embryologie des gastropodes. *Mémoires de l'Académie Royal de Belgique. Classe de Sciences*, ser. 2, 3: 1–167, pl. 1–22.

PELSENEER, P., 1923 ["1922"], Sur une habitude de *Doris bilamellata*. *Société Royale Zoologique de Belgique, Annales*, 53: 28–32.

PELSENEER, P., 1928, Les parasites des mollusques et les mollusques parasites. *Bulletin de la Société Zoologique de France*, 53: 158–189.

PENNANT, T., 1777, *The British zoology*, 4: i–viii, 1–154, pl. 1–93.

PENNANT, T., 1812, *British zoology. Crustacea, Mollusca, Testacea*. 4: i–xvi, 1–380, pl. 1–94.

PENTREATH, V. W., 1977, 5-Hydroxytryptamine in identified neurons. *Biochemical Society, Transactions*, 5: 854–858.

PENTREATH, V. W. & BERRY, M. S., 1977, Electrotonic synapsis in the visceral ganglion of *Planorbis*. *Experientia*, 33: 354–356.

PEQUEGNAT, W. E., 1963, Population dynamics in a sublittoral epifauna. *Pacific Science*, 17: 424–430.

PEQUEGNAT, W. E., 1964, The epifauna of a California siltsone reef. *Ecology*, 45: 272–283.

PERRON, F. E. & TURNER, R. D., 1977, Development, metamorphosis, and natural history of the nudibranch *Doridella obscura* Verrill (Corambidae: Opisthobranchia). *Journal of Experimental Marine Biology and Ecology*, 27: 171–185.

PHILIPPI, R. A., 1836, *Enumeratio Molluscorum Siciliae* . . . . Berolini, xiv + 267 p., 12 pl.

PLANT, R. E., 1979, Temporal pattern generation in coupled oscillators—model for the *Tritonia* trigger group. *Mathematical Biosciences*, 43: 239–263.

PLATTS, E., 1973, Notes on some Irish intertidal nudibranchs collected off the coast of Co. Down. *Irish Naturalists' Journal*, 17: 382–386.

POISSON, R., 1927, Sur la présence d'*Embletonia pallida* Ald. et Hanc. (Mollusque Nudibranche) dans le Canal de Caen à la mer. *Bulletin Mensuel de la Société Linnéenne de Normandie, Caen*, ser. 7, 9: 68–70.

POORMAN, F. L. & POORMAN, L. H., 1978, Additional molluscan records from Bahia de los Angeles, Baja California Norte. *Veliger*, 20: 369–374.

PORTER, K. J. & RIVERA, E. R., 1980, The golgi apparatus in epidermal mucoid and ellipsoid-vacuolate cells of *Aeolidia papillosa* and *Coryphella rufibranchialis* (Nudibranchia). *Protoplasma,* 102: 217–233.

POSSELT, H. J., 1898, Conspectus Faunae Groenlandicae. Brachiopoda et Mollusca .... *Meddelelser om Grønland,* 23: i–xix, 1–298, 2 pl., 1 map.

POTTS, G. W., 1970, The ecology of *Onchidoris fusca* (Nudibranchia). *Journal of the Marine Biological Association of the United Kingdom,* 50: 269–292, pl. 1–2.

POWELL, A. W. B., 1951, Antarctic and subantarctic Mollusca: Pelecypoda and Gastropoda collected by the ships of the Discovery Committee during the years 1926–1937. *Discovery Reports,* 26: 47–196, pl. V–X.

POWELL, D. C., 1966, Notes on the care and nutrition of the giant red nudibranch *Dendronotus iris* at Steinhart Aquarium. In JARVIS, C., ed., *International Zoo Yearbook,* 6: 115.

PRUVOT-FOL, A., 1927, Sur quelques mollusques nudibranches de la côte atlantique du Maroc, récoltés principalement par MM. J. Liouville et R. Ph. Dollfus. *Bulletin de la Société des Sciences Naturelles et Physiques du Maroc,* 7: 39–49, pl. 5.

PRUVOT-FOL, A., 1951a, Etudes des nudibranches de la Méditerranée. 2. *Archives de Zoologie Expérimentale et Générale,* 88: 1–80, pl. 1–4.

PRUVOT-FOL, A., 1951b, Revision du genre *Glossodoris* Ehrenberg. *Journal de Conchyliologie,* 91: 76–132.

PRUVOT-FOL, A., 1951c, Revision du genre *Glossodoris* Ehrenberg. *Journal de Conchyliologie,* 91: 133–164.

PRUVOT-FOL, A., 1954, Mollusques opisthobranches. *Faune de France,* 58: 1–460, pl. 1.

PRUVOT-FOL, A., 1955, Les Arminidae (Pleurophyliidiadae ou Diphylliadidae des anciens auteurs). *Muséum National d'Histoire Naturelle Paris, Bulletin,* (2)27: 462–468.

PRUVOT-FOL, A., 1960, Les organes génitaux des opisthobranches. *Archives de Zoologie Expérimentale et Générale,* 99: 135–224, pl. 1–4.

PURCHON, R. D., 1947, Studies on the biology of the Bristol Channel. XVII. The littoral and sublittoral fauna of the northern shores, near Cardiff. *Proceedings of the Bristol Naturalist's Society,* 27: 285–310.

PURCHON, R. D., 1968, *The biology of the Mollusca.* Pergamon Press, xxv + 560 p.

QUOY, J. R. C. & GAIMARD, J. P., 1832–1833, *Voyage de découvertes de l'Astrolabe ....* Zool., Mollusca, 2: 1–686, 1832, 1833; Atlas, pl. 1–26, 1833.

RAPP, W. L. VON, 1827, Ueber das Molluskengeschlecht *Doris* und Beschreibung einiger neuen Arten derselben, von Prof. Rapp. *Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher,* 13: 515–522, pl. 26–27.

RASMUSSEN, E., 1944, Faunistic and biological notes on marine invertebrates I. The eggs and larvae of *Brachystomia rissoides* (Hanl.), *Eulimella nitidissima* (Mont.), *Retusa truncatula* (Brug.) and *Embletonia pallida* (Alder and Hancock), (Gastropoda marina). *Videnskabelige Meddeleser fra Danske Naturhistorisk Forening, Kjobenhavn,* 107: 207–333.

RASMUSSEN, E., 1973, Systematics and ecology of the Isefjord marine fauna (Denmark) with a survey of the eelgrass (*Zostera*) vegetation and its communities. *Ophelia,* 11: 1–495.

REES, W. J., 1967, A brief survey of the symbiotic associations of Cnidaria with Mollusca. *Proceedings of the Malacological Society of London,* 37: 213–231.

REID, J., 1846, On the development of the ova of the nudibranchiate Mollusca. *Annals and Magazine of Natural History,* 17: 377–389, pl. 10.

RENOUF, L. P. W., 1916, Note on the occurrence of two generations of the nudibranchiate Mollusca *Lamellidoris bilamellata* (Linn.) and of *Archidoris tuberculata* (Cuvier) in the course of the year. *Proceedings of the Royal Physical Society of Edinburgh,* 20: 12–15.

RENOUF, L. P. W., 1934, Tectibranchs and nudibranchs on the south coast of Cork. *Annals and Magazine of Natural History,* ser. 10, 14: 399–400.

RETZIUS, G., 1914, Über die Struktur des Protoplasmas in den Eiren der Mollusken und anderer Evertebraten. *Biologische Untersuchungen,* Jena, 18: 13–18, pl. 4–5.

RICKETTS, E. F. & CALVIN, J., 1968, *Between Pacific tides.* Stanford University Press, Stanford, California, ed. 4, xiv + 614 p., 8 col. pl.

RIGG, G. B. & MILLER, R. C., 1949, Intertidal plant and animal zonation in the vicinity of Neah Bay, Washington. *Proceedings of the California Academy of Sciences,* ser. 4, 26: 323–351.

RISBEC, J., 1956, Nudibranches du Viet-Nam. *Archives du Muséum National d'Histoire Naturelle, Paris,* 7(4): 1–34, pl. 1–22.

RIVEST, B. R. & HARRIS, L. G., 1976, *Eubranchus tricolor* Forbes in the western Atlantic. *Nautilus,* 90: 145–147.

ROBERTSON, D., 1868, On the nudibranchiate Mollusca of the shores of the Cumbraes. *Natural History Society of Glasgow, Proceedings,* 1: 204–207.

ROBILLIARD, G. A., 1969a, A method of color preservation in opisthobranch mollusks. *Veliger,* 11: 289–291.

ROBILLIARD, G. A., 1969b, Predation by the nudibranch, *Dirona albolineata,* on three species of prosobranchs. *Echo, Western Society of Malacologists,* 2: 23.

ROBILLIARD, G. A., 1970, The systematics and some aspects of the ecology of the genus *Dendronotus. Veliger,* 12: 433–479, pl. 63–64.

ROBILLIARD, G. A., 1971a, Range extensions of some northeast Pacific nudibranchs (Mollusca: Gastropoda: Opisthobranchia) to Washington and British Columbia, with notes on their biology. *Veliger,* 14: 162–165.

ROBILLIARD, G. A., 1971b, A new species of *Polycera* (Opisthobranchia: Mollusca) from the northeastern Pacific, with notes on other species. *Syesis,* 4: 235–243.

ROBILLIARD, G. A., 1971c, Predation by the nudibranch *Dirona albolineata* on three species of prosobranchs. *Pacific Science,* 25: 429–435.

ROBILLIARD, G. A., 1972, A new species of *Dendronotus* from the northeastern Pacific with notes on *Dendronotus nanus* and *Dendronotus robustus* (Mollusca: Opisthobranchia). *Canadian Journal of Zoology,* 50: 421–432.

ROBILLIARD, G. A., 1974a, Range extension for *Dendronotus diversicolor* (Mollusca: Opisthobranchia). *Veliger,* 16: 335–336.

ROBILLIARD, G. A., 1974b, Range extensions of some northeastern Pacific nudibranch molluscs. *Canadian Journal of Zoology,* 52: 989–992.

ROBILLIARD, G. A., 1975a, The nudibranch *Dendronotus frondosus*: is it one species or four? *Bulletin of the American Malacological Union,* 1975: 59.

ROBILLIARD, G. A., 1975b, The nudibranch *Dendronotus frondosus*: one species or four? *Festivus, San Diego Shell Club,* 6: 44–47.

ROBILLIARD, G. A. & BABA, K., 1972, *Aldisa sanguinea cooperi* subspec. nov. from the coast of the state of Washington, with notes on its feeding and spawning habits (Nudibranchia: Dorididae: Aldisinae). *Publications of the Seto Marine Biological Laboratory,* 19: 409–414.

ROBILLIARD, G. A. & BARR, L., 1978, Range extensions of some nudibranch molluscs in Alaskan waters. *Canadian Journal of Zoology,* 56: 152–153.

ROBSON, E. A., 1961, The swimming response and its pacemaker system in the anemone *Stomphia coccinea. Journal of Experimental Biology,* 38: 685–694.

ROGINSKAYA, I. S., 1962a, The nudibranchiate mollusks of the White Sea in the region of the Biological Station of MSU. In ZENKEWITCH, L. A., ed., *Biology of the White Sea. Reports of the White Sea Biological Station of the State University of Moscow,* 1: 88–108 (in Russian).

ROGINSKAYA, I. S., 1962b, The egg-masses of nudibranchs of the White Sea. In ZENKEWITCH, L. A., ed., *Biology of the White Sea. Reports of the White Sea Biological Station of the State University of Moscow* 1: 201–214 (in Russian).

ROGINSKAYA, I. S., 1963, Reproductive biology and life cycle of *Cuthona pustulata* (Gastropoda, Nudibranchia). *Akademiia Nauk SSSR. Doklady: Biological Sciences,* 146: 1178–1181.

ROGINSKAYA, I. S., 1970, *Tenellia adspersa,* a nudibranch new to the Azov Sea, with notes on its taxonomy and ecology. *Malacological Review,* 3: 167–174.

ROGINSKAYA, I. S., 1974a, Comment on the proposal to conserve the specific name *pallida* Alder & Hancock, 1854 as published in the binomen *Embletonia pallida* Z. N. (S.) 2010. *Bulletin of Zoological Nomenclature,* 30: 138–140.

ROGINSKAYA, I. S., 1974b, Chromosome numbers of 13 species of Nudibranchia from the White and the Barents Seas. *Zoologicheskii Zhurnal,* 53: 998–1001 (in Russian).

ROGINSKAYA, I. S., 1976, Opisthobranchia on the Sosnovetz Island (White Sea). *Zoologicheskii Zhurnal,* 55: 23–28 (in Russian).

ROLLER, R. A., 1969a, A color variation of *Aldisa sanguinea. Veliger,* 11: 280–281.

ROLLER, R. A., 1969b, Nomenclatural changes for the new species assigned to *Cratena* by MacFarland, 1966. *Veliger,* 11: 421–423.

ROLLER, R. A., 1970a, A list of recommended nomenclatural changes for MacFarland's "Studies of opisthobranchiate mollusks of the Pacific coast of North America." *Veliger,* 12: 371–374.

ROLLER, R. A., 1970b, A supplement to the annotated list of opisthobranchs from San Luis Obispo county, California. *Veliger,* 12: 482–483.

ROLLER, R. A., 1972, Three new species of eolid nudibranchs from the west coast of North America. *Veliger,* 14: 416–423.

ROLLER, R. A., 1973, *Babakina,* new name for *Babaina* Roller, 1972, preoccupied. *Veliger,* 16: 117–118.

ROLLER, R. A. & LONG, S. J., 1969, An annotated list of opisthobranchs from San Luis Obispo county, California. *Veliger,* 11: 424–430.

ROS, J., 1975, Opisthobranquios (Gastropoda: Euthyneura) del litoral iberico. *Investigacion Pesquera,* Barcelona, 39: 269–372, pl. 1–4.

ROS, J., 1978a, La alimentacion y el sustrato en los opistobranquios ibericos. *Oecologia aquatica,* 3: 153–166.

ROS, J., 1978b, Distribució en l'espai i en el temps dels opistobranquis *Ibèrics, amb especial referència als del litoral Català. Butlleti de la Instutucio catalana d'Historia Natural,* 42 (Sec. Zool. 2): 23–32.

ROSE, R. M., 1971, Patterned activity of the buccal ganglion of the nudibranch mollusc *Archidoris pseudoargus. Journal of Experimental Biology,* 55: 185–204.

ROSIN, R., 1969, Escape response of the sea-anemone *Anthopleura nigrescens* (Verrill) to its predatory eolid nudibranch *Herviella* Baba, spec. nov. *Veliger,* 12: 74–77.

ROSIN, R., 1970, On Aeolidoidea, Coelenterata and nematocysts. *Argamon,* 1: 43–50.

ROSS, D. M., 1967, Behavioural and ecological relationships between sea anemones and other invertebrates. *Oceanography and Marine Biology, an Annual Review,* 5: 291–316.

ROUSSEAU, C., 1931, Sur la presence de zooxanthelles chez les Eolidiens. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris,* 193: 954–956.

ROUSSEAU, C., 1934, Sur la structure de l'épithélium hépatique des Eolidiens. *Comptes Rendus*

Hebdomadaires des Séances de l'Académie des Sciences, Paris, 198: 677–679.

ROZSA, R., 1974, Preliminary checklist of the nudibranchs and Sacoglossa of Long Island. *New York Shell Club Notes,* no. 200: 7–8.

ROZSA, R., 1975, Long Island nudibranch and sacoglossan supplement. *New York Shell Club Notes,* no. 214: 2–4.

RUDMAN, W. B., 1978, The dorid opisthobranch genera *Halgerda* Bergh and *Sclerodoris* Eliot from the Indo-west Pacific. *Zoological Journal of the Linnean Society,* 62(1): 59–88, pl. 1.

RUSSELL, H. D., 1942, Observations on the feeding of *Aeolidia papillosa* L., with note on the hatching of the veligers of *Cuthona amoena* A. & H. *Nautilus,* 55: 80–82.

RUSSELL, H. D., 1968, *Chromodoris californiensis* and *C. calensis. Nautilus,* 81: 140–141.

RUSSELL, L., 1929, The comparative morphology of the elysioid and aeolidioid types of the molluscan nervous system, and its bearing on the relationships of the ascoglossan nudibranchs. *Proceedings of the Zoological Society of London,* pt. 2: 197–233, pl. 1–10.

RUSSO, R., 1979, A salute to sea slugs. *Oceans Magazine,* 12(4): 42–49.

SAKHAROV, D. A., 1962, Giant nerve cells in nudibranchiate mollusks *Aeolidia papillosa* and *Dendronotus frondosus. Zhurnal Obshchei Biologii,* 23: 308–311 (in Russian).

SAKHAROV, D. A., 1965, Functional organization of giant neuron of molluscs. *Uspekhi Sovremennoi Biologii* 60, 3: 364–383 (in Russian).

SAKHAROV, D. A., 1966, Recent studies of the properties of nudibranch nerve cells. *Comparative Biochemistry and Physiology,* 18: 957–959.

SAKHAROV, D. A., BOROVYAGIN, V. L. & ZS.-NAGY, I., 1965, Light fluorescence and electron microscope studies on "neurosecretion" in *Tritonia diomedia* Bergh (Mollusca, Nudibranchiata). *Zeitschrift für Zellforschung und mikroskopische Anatomie,* 68: 660–673.

SAKHAROV, D. A. & TURPAEV, T. M., 1968, Evolution of cholinergic transmission. In SALANKI, J., *Neurobiology of invertebrates.* Plenum Press, N. Y., p. 305–314.

SALANKI, J. & WILLOWS, A. O. D., 1978, Sensory modification of neuronal activity in the central nervous system of *Tritonia. Acta physiologica Academiae Scientiarum hungaricae,* Budapest, 51: 180.

SALVINI-PLAWEN, L., 1972, Cnidaria as food-sources for marine invertebrates. *Cahiers de Biologie Marine,* 13: 385–400, pl. 1.

SANCHIS, C. A. & CASTRO, R. J., 1972, Morphometric characterization of center molluscan neurons. *Experientia,* 28: 181–182.

SANFORD, W. A., 1861 ["1860"], Notice of *Embletonia pallida,* of a new hydrozoon, and a new infusorium. *Somersetshire Archaeological and Natural History Society, Taunta. Proceedings,* 10: 152–154.

SARS, G. O., 1878, *Bidrag til kundskaben om Norges Arktiske fauna. I. Mollusca Regionis Arcticae Norvegiae . . . .* Universitetsprogram, Christiania, xiii + 466 p., 34 + xviii pl.

SARS, M., 1835, *Beskrivelser og Iagttagelser over nogle maerkelige eller nye i Havet ved den Bergenske kyst levende Dyr af Polypernes, Acaliphernes, Radiaternes, Annelidernes og Molluskernes Classer . . . .* Bergen, xii + 81 p., 15 pl.

SARS, M., 1850, Beretning om i Sommeren 1849 forentagen Zoologisk Feise i Lofoten og Finmarken. *Nyt Magazin for Naturvidenskaberne,* Christiana, 6: 121–211.

SAUVAGE, H. E., 1873, Catalogue des nudibranches des Côtes du Boulonnais, dressé, d'après les notes de Bouchard-Chantereaux. *Journal de Conchyliologie,* ser. 3, 21: 25–36.

SAVILOV, A. I., 1956, The swimming biocenoses in the Pacific Ocean based on the material from the Expedition of the Institute of Oceanology, Academy of Sciences in the Pacific Ocean on the "Vityaz." *Priroda,* Sofiya, 45: 62–68, 1 pl. (in Russian).

SCHAFER, W., 1950, Nahrungsaufnahme und ernahrungsphysiologische Umstimmung bei *Aeolis papillosa. Archiv für Molluskenkunde,* 79: 9–14.

SCHMEKEL, R. L., 1968a, Ascoglossa, Notaspidea und Nudibranchia im Litoral des Golfes von Neapel. *Revue Suisse de Zoologie,* 75: 103–155.

SCHMEKEL, R. L., 1968b, *Doto doerga* Marcus, 1963 (Gastr. Nudibranchia) aus dem Karibischen Meer im Golf von Neapel. *Pubblicazioni della Stazione Zoologica di Napoli,* 36: 1–7.

SCHMEKEL, R. L., 1970, Anatomie der Genitalorgane von Nudibranchiern (Gastropoda Euthyneura). *Pubblicazioni della Stazione Zoologica di Napoli,* 38: 120–217.

SCHMEKEL, R. L., 1971, Histologie und Feinstrucktur der Genitalorgane von Nudibranchiern (Gastropoda, Euthyneura). *Zeitschrift für Morphologie und Ökologie der Tiere,* 69: 115–183.

SCHMEKEL, R. L., 1979, First record of *Okenia impexa* Marcus, 1957, from the western Atlantic in the Mediterranean. *Veliger,* 21: 355–360.

SCHMIDT, J. A., GROSSMAN, Y. & ALKON, D. L., 1978, Effects of external Ca on the photoresponse of a nudibranch mollusk. *Biophysical Journal,* 21: 136a.

SCHONENBERGER, N., 1969, Beitrage zur Entwicklung und Morphologie von *Trinchesia granosa* Schmekel (Gastropoda, Opisthobranchia). *Pubblicazioni della Stazione Zoologica di Napoli,* 37: 236–292.

SCHULER, M., 1975, A dawn trip to the tidepools. *Festivus, San Diego Shell Club,* 6: 33.

SCHULTZE, M. S., 1849, Ueber die Entwicklung des *Tergipes lacinulatus. Archiv für Naturgeschichte,* 15: 268–279, pl. 5.

SCOTT, A., 1922, Various nudibranchs. *Proceedings and Transactions of the Liverpool Biological Society,* 36: 49–50.

SEED, R., 1976, Observations on the ecology of *Membranipora* (Bryozoa) and a major predator *Doridella steinbergae* along the fronds of *Lami-*

naria saccharina at Friday Harbor, Washington. *Journal of Experimental Marine Biology and Ecology,* 24: 1–18.

SHELFORD, V. E., WEESE, A. O., RICE, L. A., RASMUSSEN, D. I. & MacLEAN, A., 1935, Some marine biotic communities of the Pacific coast of North America. Part I. General survey of the communities. *Ecological Monographs,* 5: 251–332.

SHIELDS, N., 1966, A new record of *Cadlina limbaughi* (Nudibranchia: Doridacea). *Veliger,* 8: 189.

SIMROTH, H., 1895, Opisthobranchia Gymnobranchia. In: Die Gastropoden der Plankton-Expedition. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung,* Band 2, F. d.: 1–206, pl. 1–22.

SMITH, A. G., 1964, A correction. *Veliger,* 6: 172.

SMITH, A. G. & GORDON Jr., M., 1948, The marine mollusks and brachiopods of Monterey Bay, California, and vicinity. *Proceedings of the California Academy of Sciences,* ser. 4. 26: 147–245, pl. 3–4.

SMITH, S. I. & HARGER, O., 1876, Report on the dredgings in the region of St. George's Banks in 1872. *Transactions of the Connecticut Academy of Arts and Sciences,* 3: 1–57, pl. 1–7.

SNELI, J.-A. & STEINNES, A., 1975, Marine Mollusca of Jan Mayen Island. *Astarte (Zoological Department, Tromsoe Museum),* 8: 7–16.

SOWINSKY, W. K., 1904, Introduction to the study of the Ponto-Caspian-Aralian marine basin considered as a separate zoogeographic province. Zapiski Kievskogo Obshchestva Estestvoispytateleĭ 18: i–xiii, 1–487, pl. 1–4; suppl.: 1–216 (in Russian).

SPHON, G. G., 1966, Material contained in the molluscan type collection of the Santa Barbara Museum of Natural History. *Veliger,* 9: 244–246.

SPHON, G. G., 1971a, New opisthobranch records for the eastern Pacific. *Veliger,* 13: 368–369.

SPHON, G. G., 1971b, The reinstatement of *Hypselodoris agassizi* (Bergh, 1894) (Mollusca: Opisthobranchia). *Veliger,* 14: 214.

SPHON, G. G., 1972a, Some opisthobranchs (Mollusca: Gastropoda) from Oregon. *Veliger,* 15: 153–157.

SPHON, G. G., 1972b, An annotated checklist of the nudibranchs and their allies from the west coast of North America. *Opisthobranch Newsletter,* 4: 53–79.

SPHON, G. G., 1973, Siamese tails #2. *Tabulata,* 6: 5.

SPHON, G. G. & LANCE, J. R., 1968, An annotated list of nudibranchs and their allies from Santa Barbara County, California. *Proceedings of the California Academy of Sciences,* ser. 4, 36: 73–84.

SPHON, G. G. & MULLINER, D. K., 1972, A preliminary list of known opisthobranchs from the Galapagos Islands collected by the Ameripagos Expedition. *Veliger,* 15: 147–152.

STARK, J., 1828, *Elements of natural history . . . .* Edinburgh, 2 vols.

STEARNS, R. E. C., 1873a, Descriptions of a new genus and two new species of nudibranchiate mollusks from the coast of California. *Proceedings of the California Academy of Sciences,* 5: 77–78.

STEARNS, R. E. C., 1873b, Remarks on the nudibranchiate, or naked-gilled, mollusks. *California Horticulturist and Floral Magazine,* 3: 208–209.

STEHOUWER, H., 1952, The preference of the slug *Aeolidia papillosa* (L.) for the sea anemone *Metridium senile* (L.). *Archives Néerlandaises de Zoologie,* 10: 161–170.

STEINBERG, J. E., 1960, Rare and little known opisthobranch mollusks from the west coast of North America. *Veliger,* 3: 49.

STEINBERG, J. E., 1961, Notes on the opisthobranchs of the west coast of North America. I. Nomenclatural changes in the order Nudibranchia (southern California). *Veliger,* 4: 57–63.

STEINBERG, J. E., 1963a, Notes on the opisthobranchs of the west coast of North America. III. Further nomenclatorial changes in the order Nudibranchia. *Veliger,* 6: 63–67.

STEINBERG, J. E., 1963b, Notes on the opisthobranchs of the west coast of North America. IV. A distributional list of opisthobranchs from Point Conception to Vancouver Island. *Veliger,* 6: 68–75.

STENSAAS, L. J., STENSAAS, S. S. & TRUJILLO-CENOZ, O., 1969, Some morphological aspects of the visual system of *Hermissenda crassicornis* (Mollusca: Nudibranchia). *Journal of Ultrastructure Research,* 27: 510–532.

STEVEN, D., 1938, The shore fauna of Amerdloq Fjord, West Greenland. *Journal of Animal Ecology,* 7: 53–70, pl. 5–6.

STEVENS, C. F., 1969, Voltage clamp analysis of a repetitively firing neuron. In: JASPER, H. H., WARD, A. A. & POPE, A., eds., *Basic mechanisms of the epilepsies.* Little, Brown, p. 76–82.

STEWART, C., 1801–1802, *Elements of natural history . . . .* Vol. 2, Containing the fifth and sixth classes, viz. V. Insects. and VI. Vermes. London, Cadell & Davies, vi + 491 p., pl. 7–12.

STIMPSON, W., 1853, Synopses of the marine Invertebrata of Grand Manan: or the region about the mouth of the bay of Fundy, New Brunswick. *Smithsonian Contributions to Knowledge,* 6(art. V): 1–67, pl. 1–3.

STIMPSON, W., 1862, Check list of the shells of North America. East coast: Arctic seas to Georgia. *Smithsonian Miscellaneous Collections,* 2: 1–6.

STOCK, J. H., 1952, On a semiparasitic copepod from a Dutch nudibranch. *Basteria,* 16: 58–59.

STOMMEL, E. W., STEPHENS, R. E. & ALKON, D. L., 1980, Motile statocyst cilia transmit rather than transduce mechanical stimuli. *Federation of American Societies for Experimental Biology, Federation Proceedings,* 39: 2104.

STORCH, V. & WELSCH, U., 1969, Uber Bau und Funktion der Nudibranchier-Rhinophoren. *Zeit-*

schrift fur Zellforschung und mikroskopisch Anatomie, 97: 528–536.

STRAIN, H. H., 1949, Hopkinsiaxanthin, a xanthophyll of the sea slug *Hopkinsia rosacea. Biological Bulletin,* 97: 206–209.

STRATHMANN, R. & LEISE, E., 1979, On feeding mechanisms and clearance rates of molluscan veligers. *Biological Bulletin,* 157: 524–535.

STREBLE, H., 1968, Bau und Bedeutung der Nesselsacke von *Aeolidia papillosa* L., der Breitwarzigen Fadenschnecke (Gastropoda, Opisthobranchia). *Zoologischer Anzeiger,* 180: 356–372, 12 pl.

SUCKOW, R., 1972, Weit verbreitet-wenig bekannt: *Embletonia pallida,* eine Fadenschnecke der Nord- und Ostsee. *Mikrokosmos,* 61: 193–194.

SUMNER, F. B., OSBURN, R. C. & COLE, L. J., 1913, A biological survey of the waters of Woods Hole and vicinity. Section III. A catalogue of the marine fauna of Woods Hole and vicinity. *Bulletin of the United States Bureau of Fisheries,* 31: 549–794.

SUMNER, J. C., 1896, In HERDMAN, W. A., Other faunistic work. *9th Annual Report of the Liverpool Marine Biological Committee, Biological Station Port Erin,* p. 46–50.

SUSSWEIN, A. J. & BENNETT, M. V. L., 1979, Plasticity of feeding behavior in the opisthobranch mollusk *Navanax inermis. Journal of Neurobiology,* 10: 521–534.

SWENNEN, C., 1959, The Netherlands coastal waters as an environment for Nudibranchia. *Basteria,* 23(suppl.): 56–62.

SWENNEN, C., 1961, Data on distribution, reproduction and ecology of the nudibranchiate Mollusca occurring in the Netherlands. *Netherlands Journal of Sea Research,* 1: 191–240.

TAGHERT, P. H. & WILLOWS, A. O. D., 1978, Control of a fixed action pattern by single, central neurons in the marine mollusk, *Tritonia diomedea. Journal of Comparative Physiology, A. Sensory, Neural and Behavioral Physiology,* 123: 253–260.

TARASOV, N. I., 1961, Fouling in the Soviet waters of the Japan sea. *Trudy Instituta okeanologii. Akademiia Nauk SSSR,* 49: 3–59 (in Russian).

TARDY, J. P., 1969, Etude systématique et biologique sur trois espèces d'Aeolidielles des côtes européennes (Gastéropodes Nudibranches). *Bulletin de l'Institut Océanographique,* Monaco, 68(1389): 1–40, pl. 1–15.

TARDY, J. P., 1970, Contribution à l'étude des metamorphoses chez les nudibranches. *Annales des Sciences Naturelles (Zoologie),* 12: 299–370.

TARDY, J. P., 1977, Contribution à la connaissance de la biologie des nudibranches: développement et metamorphose; vie prédatrice: II. Les premiers stades benthiques d'*Aeolidia papillosa* (Linné) (Mollusque Nudibranche). *Haliotis, Société Française de Malacologie,* 6: 255–259.

TARDY, J. P. & GANTÈS, H., 1980, Un mollusque nudibranche peu connu: *Cumanotus cuenoti* A. Pruvot-Fol, (1948); redescription, biologie. *Bulletin de la Société Zoologique de France,* 105: 199–207, pl. 1–2.

TEMPERE, J. A., 1900, Ruban linguale et radule des Gastéropodes et Céphalopodes. Le Micrographe Préparateur. *Journal de Micrographie,* 8: 112–118, pl. 13–14.

THIELE, J., 1931, *Handbuch der systematischen Weichtierkunde.* Asher, Amsterdam, reprint 1963. Band 1: i–vi, 1–788.

THIENEMANN, F. A. L., 1824–1827. Reisen im Norden Europas vorzuglich in Island . . . . Leipzig, Reclam. 2 Abth., 27 pl.

THIRIOT-QUIÉVREUX, C., 1977, Veligère planctotrophe de doridien *Aegires punctilucens* (D'Orbigny) (Mollusca: Nudibranchia: Notodorididae): description et metamorphose. *Journal of Experimental Marine Biology and Ecology,* 26: 177–190.

THOMPSON, S. H., 1977, Three pharmacologically distinct potassium channels in molluscan neurones. *Journal of Physiology,* 265: 465–488.

THOMPSON, S. H. & SMITH, S. J., 1976, Depolarizing afterpotentials and burst production in molluscan pacemaker neurons. *Journal of Neurophysiology,* 39: 153–161.

THOMPSON, T. E., 1959, Feeding of nudibranch larvae. *Journal of the Marine Biological Association of the United Kingdom,* 38: 239–248.

THOMPSON, T. E., 1960a, On a disputed feature of the anatomy of the nudibranch *Dendronotus frondosus* Ascanius. *Proceedings of the Malacological Society of London,* 34: 24–26.

THOMPSON, T. E., 1960b, Defensive adaptations in opisthobranchs. *Journal of the Marine Biological Association of the United Kingdom,* 39: 123–134.

THOMPSON, T. E., 1961, The importance of the larval shell in the classification of the Sacoglossa and the Acoela (Gastropoda: Opisthobranchia). *Proceedings of the Malacological Society of London,* 34: 233–238.

THOMPSON, T. E., 1964, Grazing and the life cycles of British nudibranchs. In: Grazing in terrestrial and marine environments. *British Ecological Society Symposium,* no. 4: 275–297.

THOMPSON, T. E., 1967, Direct development in a nudibranch, *Cadlina laevis,* with a discussion of developmental processes in Opisthobranchia. *Journal of the Marine Biological Association of the United Kingdom,* 47: 1–22.

THOMPSON, T. E., 1969, Acid secretion in Pacific ocean gastropods. *Australian Journal of Zoology,* 17: 755–764.

THOMPSON, T. E., 1971, Tritoniidae from the North American Pacific coast. *Veliger,* 13: 333–338.

THOMPSON, T. E., 1972a, Eastern Australian Dendronotoidea (Gastropoda: Opisthobranchia). *Zoological Journal of the Linnean Society,* London, 51: 63–77.

THOMPSON, T. E., 1972b, Chromodorid nudibranchs from eastern Australia (Gastropoda, Opisthobranchia). *Journal of Zoology*, 166: 391–409, pls. 1–4.

THOMPSON, T. E., 1973, Euthyneuran and other molluscan spermatozoa. *Malacologia*, 14: 167–206, 443–444, pl. 1–16.

THOMPSON, T. E., 1975, Dorid nudibranchs from eastern Australia (Gastropoda, Opisthobranchia). *Journal of Zoology*, 176: 477–517, pl. 1.

THOMPSON, T. E., 1976a, Biology of opisthobranch molluscs. Ray Society, London, no. 151, 1: 1–207, pl. 1–21.

THOMPSON, T. E., 1976b. Nudibranchs. T. F. H. Publication, New Jersey, 96 p., 30 pls.

THOMPSON, T. E. & BEBBINGTON, A., 1973, Scanning electron microscope studies of gastropod radulae. *Malacologia*, 14: 147–165, 14 pl.

THOMPSON, T. E. & BROWN, H., 1976, British opisthobranch molluscs. Mollusca: Gastropoda. *Synopsis of the British fauna* (*new ser.*) no. 8, *Linnean Society of London*, 203 p., pl. 1.

THOMPSON, T. E. & HINTON, H. E., 1968, Stereoscan electron microscope observations on opisthobranch radulae and shell sculpture. *Bijdragen tot de Dierkunde*, 38: 91–92, pl. 1–4.

THOMPSON, W., 1840, Contributions towards a knowledge of the Mollusca Nudibranchia and Mollusca Tunicata of Ireland, with descriptions of some apparently new species of Invertebrata. *Annals and Magazine of Natural History*, 5: 84–102, pl. 2.

THOMPSON, W., 1844, Report on the fauna of Ireland: division Invertebrata. *Report 13th Meeting of the British Association for the Advancement of Science*, p. 245–291.

THOMPSON, W., 1856, *The natural history of Ireland. Mammalia, reptiles, and fishes. Also Invertebrata.* London, Bohn, Covent Garden, 4: i–xxxii, 1–516.

TIBERI, N., 1880, I molluschi nudibranchi del Mediterraneo. *Bullettino della Società Malacologica Italiana*, 6: 182–242.

TODD, C. D., 1979a, Reproductive energetics of two species of dorid nudibranchs with planktotrophic and lecithotrophic larval strategies. *Marine Biology*, 53: 57–68.

TODD, C. D., 1979b, The population ecology of *Onchidoris bilamellata* (L.) (Gastropoda: Nudibranchia). *Journal of Experimental Marine Biology and Ecology*, 41: 213–255.

TODD, C. D., 1979c, Annual cycles of two species of *Onchidoris* (Opisthobranchia, Nudibranchia). In NAYLOR, E. & HARTNOLL, R. G., eds., *Cyclic phenomena in marine plants and animals. Proceedings of the 13th European Marine Biology Symposium.* Pergamon Press, p. 65–72.

TODD, R. A., 1903, Notes on the invertebrate fauna and fish-food of the bays between the Start and Exmouth. *Journal of the Marine Biological Association of the United Kingdom*, new ser., 6: 541–561.

TOKIOKA, T., 1952, Record of *Fiona pinnata* (Eschscholtz). *Nanki-Seibutsu*, Suppl. no. 1: 13–14.

TOMOSKY-SYKES, T. K., JARDINE, I., MUELLER, J. F. & BUEDING, E., 1977, Sources of error in neurotransmitter analysis. *Analytical Biochemistry*, 83: 99–108.

TONNING, H., 1768, Rariora Norvegiae. Reprinted in: *Linnaei Amoenitates Academica* VII Holmiae 1769, p. 466–486.

TREGELLES, G. F., 1896, The marine Mollusca of Cornwall. *Journal of Conchology*, 8: 191–225.

TRINCHESE, S., 1881, Per la fauna marittime italiana . . . Aeolididae e famiglie affini. *Atti della Reale Accademia dei Lincei*, ser. 3, Della classe di Scienze Fisiche, Matematiche e Naturali. Rome (Memorie), 11: 3–142, pl. 1–80.

TRYON, G. W., Jr., 1883, *Structural and systematic conchology* . . . . Philadelphia, vol. II, 430 p., 91 pl.

TURNER, C. H., EBERT, E. E. & GIVEN, R. R., 1969, Man-made reef ecology. *California Department of Fish and Game. Fish Bulletin*, 146: 1–221.

TURPAEVA, E. P., 1969, Symphysiological relations in the oligomixt biocenosis of the sea fouling. *Doklady Akademiia Nauk S.S.S.R., Biological Sciences, Moscow*, 189: 415–417.

TURPAEVA, E. P., 1972, A system of symphysiological relationships in the biocoenosis of marine fouling. Bonitation of the world ocean. Issue 2. Distribution of plankton, nekton and benthos in the oceans and open seas. *Proceedings of the All-Union Research Institute of Marine Fisheries and Oceanography* (VNIRO), Moscow, Pischevaya Promyshlennost, 77: 168–185 (in Russian).

TURPAEVA, E. P. & LEBEDEVA, L. P., 1976, Numerical modeling of the dynamics of a population of nudibranchs *Tenellia adspersa. Zoologicheskii Zhurnal* 55: 1437–1444 (in Russian).

TURPAEVA, E. P. & SIMKINA, R. G., 1975, Size weight characteristics, energy equivalent of mass and intensity of metabolism in mass species of encrusting organisms of the Sea of Azov. *Zoologicheskii Zhurnal*, 54: 1149–1153.

TURPAYEV, T. M., NISIRAIOVA, S. N. & SAKHAROV, D. A., 1967, Evolution of the cholinergic regulation of the cardiac activity in molluscs. *Zhurnal Obshchei Biologii*, 28: 618–626 (in Russian).

TURTON, W., 1807, *British fauna, containing a compendium of the zoology of the British Islands.* London, 1: i–vii, 1–230.

USUKI, I., 1969, Opisthobranch fauna in the Sado districts of the Japan Sea. *Niigata Daigaku. Sado Museum Memoirs*, 18: 3–14, 3 pl.

VANHOFFEN, E., 1897, Die Fauna und Flora Gronlands. In DRYGALSKI, *Gronland-Expedition der Gesellschaft für Erdkunde zu Berlin 1891–1893*, 2: i–x, 1–571, pl. 1–8.

VANNUCCI, M. & HOSOE, K., 1953, Sobre *Embletonia mediterranea* (Costa), nudibranquio de regiao Lagunar de Cananeia. *Boletim do Instituto Oceanografico, Universidade de São Paulo, Brazil*, 4: 103–120, pl. 1–6.

VAYSSIÈRE, A. J. B. M., 1901, Etude comparée des opisthobranches des côtes françaises de l'Océan Atlantique et de la Manche avec ceux de nos côtes Mediterranéenes. *Bulletin Scientifique de la France et de la Belgique,* 34: 281–315.

VAYSSIÈRE, A. J. B. M., 1913, Etude sur quelques opisthobranches nus rapportés de côtes de la Nouvelle-Zemble par la Mission Ch. Benard en 1908. *Annales de l'Institut océanographique,* 5(8): 1–15, 1 pl.

VEPRINTSEV, B. N. & D'YAKONOVA, T. L., 1967, Cytological changes in the neurones of the nudibranchial mollusc *Tritonium* during generation of action potentials. *Biophysics,* 12: 119–130.

VEPRINTSEV, B. N., GERASIMOV, V. D., KRASTS, I. V. & MAGURA, I. S., 1966, Effect of the ionic composition of the medium on the action potentials of the giant neurons of the nudibranchiate mollusc *Tritonium. Biophysics,* 11: 1145–1153.

VEPRINTSEV, B. N., KRASTS, I. V. & SAKHAROV, D. A., 1964, Nerve cells of the nudibranchiate mollusc *Tritonia diomedia* Bergh. *Biophysics,* 9: 351–361.

VERKRUZEN, T. A., 1872. Dredging-excursion to Iceland in June and July 1872. *Annals and Magazine of Natural History,* ser. 4, 10: 371–376.

VERRILL, A. E., 1870, Contributions to zoology from the Museum of Yale College. No. 8—Descriptions of some New England Nudibranchiata. *American Journal of Science and Arts,* ser. 2, 50: 405–408.

VERRILL, A. E., 1872, Brief contributions to zoology, from the Museum of Yale College. No. XIX.—Recent additions to the molluscan fauna of New England and the adjacent waters, with notes on other species. *American Journal of Science and Arts,* ser. 3, 3: 209–214, pl. 6–7.

VERRILL, A. E., 1873, Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. In BAIRD, S. F., *U.S. Commission Fish and Fisheries.* Part I. *Report on the condition of the sea fisheries of the south coast of New England in 1871 and 1873,* p. 295–778, 38 pls.

VERRILL, A. E., 1874a, Brief contributions to zoology from the Museum of Yale College. No. XXVI. Results of recent dredging expeditions on the coast of New England. No. 4. *American Journal of Science and Arts,* ser. 3, 7: 38–46.

VERRILL, A. E., 1874b, Brief contributions to zoology from the Museum of Yale College. No. XXVII.—Results of dredging expeditions on the coast of New England. No. 5. *American Journal of Science and Arts,* ser. 3, 7: 131–138.

VERRILL, A. E., 1879, Notice of recent additions to the marine fauna of the east coast of North America. No. 4. *American Journal of Science and Arts,* ser. 3, 17: 309–315.

VERRILL, A. E., 1880, Notice of recent additions to the marine Invertebrata of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others. Part II—Mollusca, with notes on Annelida, Echinodermata, etc., collected by the United States Fish Commission. *Proceedings of the United States National Museum,* 3: 356–405.

VERRILL, A. E., 1881, Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England, No. 2. *American Journal of Science and Arts,* ser. 3, 22: 292–303.

VERRILL, A. E., 1882a, Notice of recent additions to the marine Invertebrata of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others. Part IV.—Additions to the deep-water Mollusca, taken off Martha's Vineyard, in 1880 and 1881. *Proceedings of the United States National Museum,* 5: 315–343.

VERRILL, A. E., 1882b, Catalogue of marine Mollusca added to the fauna of the New England region, during the past ten years. *Transactions of the Connecticut Academy of Arts and Sciences,* 5: 447–587, pl. 42–44, 57, 58.

VOGEL, R. & SCHULTZ, L. P., 1970, *Cargoa cupella,* new genus and new species of nudibranch from Chesapeake Bay and the generic status of *Okenia* Menke, *Idalia* Leuckart and *Idalla* Ørsted. *Veliger,* 12: 388–393.

VOLODCHENKO, N. I., 1941, New species of nudibranch molluscs from the far eastern seas of the U.S.S.R. *Investigations of the far eastern seas of the U.S.S.R.* 1: 53–72, pl. 1–4 (in Russian).

VOLODCHENKO, N. I., 1955, Subclass Opisthobranchia. In PAVLOVSKII, E. N., ed., *Atlas of the invertebrates of the far eastern seas of the USSR.* Akademiia Nauk SSSR. Zoologicheskii Institut, p. 1–324, pl. 1–66. (Transl. 1966, Israel Prog. Sci. Transl.).

VOOGT, P. A., 1973, Investigations of the capacity of synthesizing 3β-sterols in Mollusca: XI. Biosynthesis and composition of 3β-sterols in some Acoela (Opisthobranchia). *International Journal of Biochemistry,* 4: 479–488.

WAIDHOFER, C., 1969, Anatomische Untersuchungen des Zentralnervensystems von *Fimbria fimbria* und *Melibe leonina. Malacologia,* 9: 295–296.

WALTON, C. L., 1908, Nudibranchiata collected in the North Sea by the S.S. 'Huxley' during July and August 1907. *Journal of the Marine Biological Association of the United Kingdom,* new ser., 8: 227–240.

WALTON, C. L., 1913, The shore fauna of Cardigan Bay. *Journal of the Marine Biological Association of the United Kingdom,* new ser., 10: 102–113.

WATERS, V. L., 1971a, Food preferences of *Aeolidia papillosa. Echo, Western Society of Malacologists,* 4: 32.

WATERS, V. L., 1971b, The effect of the defenses of the prey on the food preference of *Aeolidia papillosa. Echo, Western Society of Malacologists,* 4: 33.

WATERS, V. L., 1973, Food preference of the nudibranch *Aeolidia papillosa*, and the effect of the defenses of the prey on predation. *Veliger,* 15: 174–192.

WEINREICH, D., McCAMAN, M. W., McCAMAN, R. E. & VAUGHN, J. E., 1973, Chemical enzymatic and ultrastructural characterization of 5-hydroxytryptamine-containing neurons from the ganglia of *Aplysia californica* and *Tritonia diomedia. Journal of Neurochemistry,* 20: 969–976.

WHITE, K. M., 1938, The nomenclature of British nudibranchiate Mollusca by Alder and Hancock and by Eliot correlated with that of British marine Mollusca by Winckworth. *Journal of Conchology,* 21: 14–19.

WHITE, K. M., 1952, On a collection of mollusks from the Dry Tortugas, Florida. *Proceedings of the Malacological Society of London,* 29: 106–120, pl. 6.

WHITEAVES, J. F., 1901, *Catalogue of the marine Invertebrata of eastern Canada.* Ottawa, Geological Survey of Canada, no. 772: 1–271.

WICKSTEN, M. K. & DeMARTINI, J. D., 1973, Observations of the feeding habits of *Tochuina tetraquetra* (Pallas) (Gastropoda: Tritoniidae). *Veliger,* 15: 195.

WILBUR, K. M. & YONGE, C. M., eds., 1964, *Physiology of Mollusca.* Academic Press, N.Y., 1: i–xii, 1–473.

WILBUR, K. M. & YONGE, C. M., 1966, *Physiology of Mollusca.* Academic Press, N.Y. 2: i–xii, 1–645.

WILLIAMS, G., 1954, Fauna of Strangford Lough and neighboring coasts. *Proceedings of the Royal Irish Academy,* sec. B, 56: 29–133, pl. 2–4.

WILLIAMS, G. C., 1971, New record of a color variation in *Spurilla oliviae. Veliger,* 14: 215–216.

WILLIAMS, G. C. & GOSLINER, T. M., 1970, Notes on the ecology and distribution of opisthobranchiate mollusks of the San Carlos Bay region, Gulf of California. *Echo, Western Society of Malacologists,* 3: 33.

WILLIAMS, G. C. & GOSLINER, T. M., 1979, Two new species of nudibranchiate molluscs from the west coast of North America, with a revision of the family Cuthonidae. *Zoological Journal of the Linnean Society,* 67: 203–223.

WILLIAMS, L. G., 1971, Veliger development in *Dendronotus frondosus* (Ascanius, 1774) (Gastropoda: Nudibranchia). *Veliger,* 14: 166–171.

WILLIAMS, L. G., 1978, Development and feeding in the larvae of two species of aeolid nudibranchs, *Hermissenda crassicornis* and *Aeolidia papillosa. Bulletin of the American Malacological Union,* 1978: 58.

WILLIAMS, L. G., 1980, Development and feeding of larvae of the nudibranch gastropods *Hermissenda crassicornis* and *Aeolidia papillosa. Malacologia,* 20: 99–116.

WILLIAMSON, T. L. & CRILL, W. E., 1976a, The effects of pentylenetetrazol on molluscan neurons: I. Intramuscular recording and stimulation. *Brain Research,* 116: 217–229.

WILLIAMSON, T. L. & CRILL, W. E., 1976b, The effects of pentylenetetrazol on molluscan neurons: II. Voltage clamp studies. *Brain Research,* 116: 231–249.

WILLOWS, A. O. D., 1965, Giant nerve cells in the ganglia of nudibranch molluscs. *Comparative Biochemistry and Physiology,* 14: 707–710.

WILLOWS, A. O. D., 1967a, Behavioral acts elicited by stimulation of single, identifiable brain cells. *Science,* 157: 570–574.

WILLOWS, A. O. D., 1967b, The function of single nerve cells in the control of behavior. *American Zoologist,* 7: 796.

WILLOWS, A. O. D., 1968, Behavioral acts elicited by stimulation of single identifiable nerve cells. In CARLSON, F. D. ed., *Physiological and biochemical aspects of nervous integration.* Prentice-Hall, New Jersey, p. 217–243.

WILLOWS, A. O. D., 1971, Giant brain cells in mollusks. *Scientific American,* 224: 68–75.

WILLOWS, A. O. D., 1973a, Interactions between brain cells controlling swimming in a mollusc. In SALANKI, J., ed., *Neurobiology of invertebrates mechanisms of rhythm regulation.* Akad. Kiado, Budapest, p. 233–247.

WILLOWS, A. O. D., 1973b, Learning in gastropod mollusks. In CORNING, W. C., DYAL, J. A. & WILLOWS, A. O. D., eds., *Invertebrate learning,* vol. 2, *arthropods and gastropod mollusks.* Plenum Press, N. Y., p. 187–274.

WILLOWS, A. O. D., 1976, Trigger neurons in the mollusk *Tritonia.* In HERMAN, R. M., GRILLNER, S., STEIN, P. G. S., & STUART, D. G., eds., *Neural control of locomotion. Advances in Behavioral Biology.* Plenum Press, N. Y., p. 327–349.

WILLOWS, A. O. D., 1978, Physiology of feeding in *Tritonia.* I. Behaviour and mechanics. *Marine Behaviour and Physiology,* 5: 115–135.

WILLOWS, A. O. D. & DORSETT, D. A., 1975, Evolution of swimming behavior in *Tritonia* and its neurophysiological correlates. *Journal of Comparative Physiology, A. Sensory, Neural and Behavioral Physiology,* 100(2A): 117–134.

WILLOWS, A. O. D., DORSETT, D. A. & HOYLE, G., 1973a, The neuronal basis of behavior in *Tritonia.* I. Functional organization of the central nervous system. *Journal of Neurobiology,* 4: 207–237.

WILLOWS, A. O. D., DORSETT, D. A. & HOYLE, G., 1973b, The neuronal basis of behavior in *Tritonia.* III. Neuronal mechanism of a fixed action pattern. *Journal of Neurobiology,* 4: 255–285.

WILLOWS, A. O. D., GETTING, P. A. & THOMPSON, S., 1973c, Bursting mechanisms in molluskan locomotion. In STEIN, R. B., PEARSON, K. G., SMITH, R. S. & REDFORD, J. B., eds., Control of posture and locomotion. *Advances in Behavioral Biology,* 7: 457–475.

WILLOWS, A. O. D. & HOYLE, G., 1967, Neural geography of the giant cells in the central ganglia of a nudibranch mollusc. *Federation Proceedings, Federation of American Societies for Experimental Biology,* 26: 327.

WILLOWS, A. O. D. & HOYLE, G., 1968, Correlation of behavior with the activity of single identifiable neurons in the brain of *Tritonia*. In: SALANKI, J. *Neurobiology of invertebrates*. Plenum Press, N. Y., p. 443–461.

WILLOWS, A. O. D. & HOYLE, G., 1969, Neuronal network triggering a fixed action pattern. *Science*, 166: 1549–1551.

WINCKWORTH, R., 1932, The British marine Mollusca. *Journal of Conchology*, 19: 211–252.

WISMER, N. M. & SWANSON, J. H., 1935, Some marine biotic communities of the Pacific coast of North America. Part II. A study of the animal communities of a restricted area of soft bottom in the San Juan Channel. *Ecological Monographs*, 5: 333–354.

WOBBER, D. R., 1970, A report on the feeding of *Dendronotus iris* on the anthozoan *Cerianthus* sp. from Monterey Bay, California. *Veliger*, 12: 383–387, pl. 55–57.

WOLTER, H., 1967, Beiträge zur Biologie, Histologie und Sinnesphysiologie (insbesondere der Chemorezeption) einiger Nudibranchier (Mollusca, Opisthobranchia) der Nordsee. *Zeitschrift für Morphologie und Ökologie der Tiere*, 60: 275–337.

WOODLAND, W., 1907, Studies in spicule formation. VI.—The scleroblastic development of the spicules in some Mollusca and in one genus of colonial ascidians. *Quarterly Journal of Microscopical Science*, 51: 45–53, pl. 5.

WORLEY, L. G. & WORLEY, E. K., 1943, Studies of the supravitally stained golgi apparatus. I. Its cycle in the tectibranch mollusc, *Navanax inermis* (Cooper). *Journal of Morphology*, 73: 365–399, pl. 1–5.

WRIGHT, E. P., 1859, Notes on the Irish Nudibranchiata. *The Natural History Review and Quarterly* 6(2) Proc. of Soc., p. 86–88.

WRIGHT, T. S., 1859, On the cnidae or thread-cells of the Eolidae. *Proceedings of the Royal Physical Society of Edinburgh*, 2: 38–40.

WRIGHT, T. S., 1863, On the urticating filaments of the Eolidae. *Quarterly Journal of Microscopical Science*, new ser., 3: 52–55.

YATES, L. G., 1890, The Mollusca of Santa Barbara County, California. *Bulletin, Santa Barbara Society of Natural History*, 1: 37–45.

ZACK, S., 1974a, The effects of food deprivation on agonistic behavior in an opisthobranch mollusc, *Hermissenda crassicornis*. *Behavioral Biology*, 12: 223–232.

ZACK, S., 1974b, Sequences of agonistic behavior patterns and food deprivation in *Hermissenda*. *Behavioral Biology*, 12: 525–532.

ZACK, S., 1975a, A preliminary study of the effects of nematocyst removal on agonistic behavior in *Hermissenda*. *Veliger*, 17: 271–275.

ZACK, S., 1975b, A description and analysis of agonistic behavior patterns in an opisthobranch mollusc, *Hermissenda crassicornis*. *Behaviour; an international journal of comparative ethology*, 53: 238–267.

ZAITSEVA, O. V., 1978, Characteristics of the neuronal composition of the central nervous system in nudibranch molluscs from the White Sea. *Zhurnal Evoliutsionnoi Biokhimii i Fiziologii*, 14: 497–504.

ZEILLER, W. & COMPTON, G., 1971, The purple wind. *Sea Frontiers*, 17: 373–377.

ZENKEVITCH, L., 1963, *Biology of the seas of the U.S.S.R.* Translated by Sophia Botcharskaya. Allen & Unwin, London, 955 p.

APPENDIX: MATERIAL EXAMINED

This list includes most of the material examined during this study; some material examined alive and returned to the field is not included. Data concerning each species are listed in the following order: accession number, locality of collection, date of collection, collector, and number of specimens. Accession numbers beginning with an M and followed by four groups of digits separated by hyphens (e.g. M71-8-31-2) indicate specimens in my personal collection. Accession numbers beginning with an M and followed by four digits (e.g. M0135) indicate specimens in the Moss Landing Marine Laboratories. Specimens preceded by CASIZ are in the California Academy of Sciences, Department of Invertebrate Zoology. Specimens preceded by LACM are in the Los Angeles County Museum of Natural History. The asterisks indicate the lots from which radulae were taken.

Acanthodoris brunnea

M71-8-31-2, Santa Monica Bay, Los Angeles Co., Calif., 31 Aug. 1971, S. Anderson, 1. M71-8-31-7, Santa Monica Bay, Los Angeles Co., Calif., 31 Aug. 1971, S. Anderson, 1. M71-8-31-8, Santa Monica Bay, Los Angeles Co., Calif., 31 Aug. 1971, S. Anderson, 1. M71-10-7-1, Santa Monica Bay, Los Angeles Co., Calif., 7 Oct. 1971, S. Anderson, 1. *M71-10-7-4, Santa Monica Bay, Los Angeles Co., Calif., 7 Oct. 1971, S. Anderson, 1. M72-3-22-3, Monterey Breakwater, Monterey Co., Calif., 22 Mar. 1972, G. McDonald, 1. M72-12-9-1, Monterey Bay, Calif., 9 Dec. 1972, G. McDonald, 2. M74-3-25-1, Monterey Bay, Calif., 25 Mar. 1974, G. McDonald, 1.

Acanthodoris hudsoni

M70-10-16-1, Asilomar, Monterey Co., Calif., 16 Oct. 1970, G. McDonald, 1. M69-6-3-1, S of Spooner's Cove, San Luis Obispo Co., Calif., 3 June 1969, G. McDonald, 1. M72-1-15-1, Asilomar, Monterey Co., Calif., 15 Jan. 1972, G. McDonald, 1. M75-10-4-3, Monastery Beach, Monterey Co., Calif., 4 Oct. 1975, Andrea McDonald, 1. M76-1-17-1, Monastery Beach, Carmel, Monterey Co., Calif., 17 Jan. 1976, G. McDonald, 1. M78-8-24-3, Monastery Beach, Carmel, Monterey Co., Calif., 24 Aug. 1978, G. McDonald, 2. M0135, Asilomar, Monterey Co., Calif., 16 Oct. 1970, G. McDonald, 1.

Acanthodoris lutea

*M69-9-14-2, Morro Bay, San Luis Obispo Co., Calif., 14 Sept. 1969, G. McDonald, 5. M70-12-12-1, Santa Cruz Harbor, Santa Cruz Co., Calif., 12 Dec. 1970, S. Anderson, 1. M71-1-25-7, Sunset Palisades, San Luis Obispo Co., Calif., 25 Jan. 1971, G. McDonald, 2. M71-1-26-2, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 2. M71-9-21-1, Pt. Fermin, Los Angeles Co., Calif., 21 Sept. 1971, S. Anderson, 1. M71-12-28-2, Sunset Palisades, San Luis Obispo Co., Calif., 28 Dec. 1971, G. McDonald, 2. M71-12-31-3, Shell Beach, San Luis Obispo Co., Calif., 31 Dec. 1971, G. McDonald, 1. M75-11-3-5, Pigeon Pt., San Mateo Co., Calif., 3 Nov. 1975, G. McDonald, 3. M75-12-1-2, Pigeon Pt., San Mateo Co., Calif., 1 Dec. 1975, Andrea McDonald, 2. M77-12-9-1, Terrace Pt., Santa Cruz Co., Calif., 9 Dec. 1977, G. McDonald, 1. M0018, Pt. Fermin, Los Angeles Co., Calif., 21 Sept. 1971, S. Anderson, 1. M0134, Santa Cruz Harbor, Santa Cruz Co., Calif., 12 Dec. 1970, S. Anderson, 1.

Acanthodoris nanaimoensis

M71-3-6-1, Pigeon Pt., San Mateo Co., Calif., 6 Mar. 1971, invert. class, 1. M71-6-24-1, Bodega Bay, Sonoma Co., Calif., 24 June 1971, J. Nybakken, 2. M71-7-25-5, Morro Bay, San Luis Obispo Co., Calif., 25 July 1971, G. McDonald, 1. *M72-9-0-1, San Francisco Bay, Calif., Sept. 1972, G. Huey, 1. M75-11-3-1, Pigeon Pt., San Mateo Co., Calif., 3 Nov. 1975, G. McDonald, 5. M75-12-1-1, Pigeon Pt., San Mateo Co., Calif., 1 Dec. 1975, G. & A. McDonald, 9. M76-12-20-1, Scott Cr., Santa Cruz Co., Calif., 20 Dec. 1976, A. K. McDonald, 1. M77-11-11-3, Scott Cr., Santa Cruz Co., Calif., 11 Nov. 1977, G. McDonald, 1.

Acanthodoris pilosa

M70-11-27-1, Morro Bay, San Luis Obispo Co., Calif., 27 Nov. 1970, G. McDonald, 1. M70-11-8-4, Morro Bay, San Luis Obispo Co., Calif., 8 Nov. 1970, G. McDonald, 1. *M71-10-23-1, Elkhorn Slough, Monterey Co., Calif., 23 Oct. 1971, G. McDonald, 1. M75-6-27-1, Moss Landing, Monterey Co., Calif., 27 June 1975, R. Christiansen. M0143, Monterey Bay, Calif., 7 May 1971, class, 1. M76-12-19-1, Pescadero Pt., San Mateo Co., Calif., 19 Dec. 1976, G. McDonald, 4. M77-11-11-4, Scott Cr., Santa Cruz Co., Calif., 11 Nov. 1977, G. McDonald, 1.

Acanthodoris rhodoceras

M71-10-17-9, Morro Bay, San Luis Obispo Co., Calif., 17 Oct. 1971, G. McDonald, 1. M71-11-2-1, S of Spooner's Cove, San Luis Obispo Co., Calif., 2 Nov. 1971, G. McDonald, 1. M71-11-22-4, Morro Bay, San Luis Obispo Co., Calif., 22 Nov. 1971, R. Roller, 1. *M71-12-28-1, Sunset Palisades, San Luis Obispo Co., Calif., 28 Dec. 1971, G. McDonald, 6. M71-12-31-2, Shell Beach, San Luis Obispo Co., Calif., 31 Dec. 1971, G. McDonald, 3. M72-4-8-1, Elkhorn Slough, Monterey Co., Calif., 8 Apr. 1972, G. McDonald, 1. M75-6-25-3, La Jolla, San Diego Co., Calif., 25 June 1975, G. McDonald, 1. M0127, Dillon Beach, Marin Co., Calif., 9 July 1971, J. Nybakken, 1.

Aegires albopunctatus

M69-9-14-1, Morro Bay, San Luis Obispo Co., Calif., 14 Sept. 1969, G. McDonald, 2. M70-6-5-4, Pirate's Cove, San Luis Obispo Co., Calif., 5 June 1970, G. McDonald, 1. M70-10-14-4, Asilomar, Monterey Co., Calif., 14 Oct. 1970, G. McDonald, 1. M71-2-15-1, Monterey Harbor, Monterey Co., Calif., 15 Feb. 1971, G. McDonald, 3. M71-2-24-8, Morro Bay, San Luis Obispo Co., Calif., 24 Feb. 1971, G. McDonald, 1. M71-7-25-3, Morro Bay, San Luis Obispo Co., Calif., 25 July 1971, G. McDonald, 1. M71-11-4-5, Carmel Pt., Monterey Co., Calif., 4 Nov. 1971, G. McDonald, 1. M72-1-5-2, Malibu, Los Angeles, Co., Calif., 5 Jan. 1972, S. Anderson, 4. M72-1-16-3, Monterey Breakwater, Monterey Co., Calif., 16 Jan. 1972, R. Hilaski, 1. M72-3-22-1, Monterey Breakwater, Monterey Co., Calif., 22 Mar. 1972, G. McDonald, 4. M72-5-17-9, Carmel Pt., Monterey Co., Calif., 17 May 1972, G. McDonald, 1. *M72-7-9-2, Shell Beach, San Luis Obispo Co., Calif., 9 July 1972, G. McDonald, 20. M73-6-5-16, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 1. M75-10-26-3, Morro Bay, San Luis Obispo Co., Calif., 26 Oct. 1975, G. McDonald, 1. M77-12-10-11, Asilomar, Monterey Co., Calif., 10 Dec. 1977, G. McDonald, 1.

Aeolidia papillosa

M70-10-22-2, Moss Landing, Monterey Co., Calif., 22 Oct. 1970, S. Anderson, 1. M70-11-14-1, Elkhorn Slough, Monterey Co., Calif., 14 Nov. 1970, G. McDonald, 1. M71-1-26-12, Morro Bay, San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 3. M71-1-32-1, Monterey Harbor, Monterey Co., Calif., Jan. 1971, S. Anderson, 1. M71-2-15-3, Monterey Harbor, Monterey Co., Calif., 15 Feb. 1971, S. Anderson, 1. M71-7-7-3, Morro Bay, San Luis Obispo Co., Calif., 7 July 1971, G. McDonald, 1. M71-8-8-2, Asilomar, Monterey Co., Calif., 8 Aug. 1971, G. McDonald, 1. M71-10-17-11, Morro Bay, San Luis Obispo Co., Calif., 17 Oct. 1971, G. McDonald, 2. *M71-10-22-3, Monterey Harbor, Monterey Co., Calif., 22 Oct. 1971, G. McDonald, 5. M71-11-1-4, Hazard Can., San Luis Obispo Co., Calif., 1 Nov. 1971, G. McDonald, 1. M71-11-17-8, Elkhorn Slough, Monterey Co., Calif., 17 Nov. 1971, G. McDonald, 1. M71-11-22-5, Morro Bay, San Luis Obispo Co., Calif., 22 Nov. 1971, G. McDonald, 1. M74-3-13-1, Monterey Bay, Calif., 13 Mar. 1974, G. McDonald, 1. M75-10-26-5, Morro Bay, San Luis Obispo Co., Calif., 26 Oct. 1975, G. McDonald, 2. M75-11-4-2, Fanshell Beach, Monterey Co., Calif., 4 Nov. 1975, G. McDonald, 2.

Aldisa sanguinea

M71-6-13-2, Monterey Breakwater, Monterey Co., Calif., 13 June 1971, S. Anderson, 1. M71-6-13-3, Monterey Breakwater, Monterey Co., Calif., 13 June 1971, S. Anderson, 1. M71-6-13-5, Monterey Breakwater, Monterey Co., Calif., 13 June 1971, S. Anderson, 1. M71-8-15-1, Port San Luis, San Luis Obispo Co., Calif., 15 Aug. 1971, G. McDonald, 1. M71-12-2-8, Carmel Pt., Monterey Co., Calif., 2 Dec. 1971, G. McDonald, 1. M71-12-28-5, Dume Rock, Los Angeles Co., Calif., 28 Dec. 1971, S. Anderson, 2. M72-3-19-2, Asilomar, Monterey Co., Calif., 19 Mar. 1972, G. McDonald, 1. M72-4-17-1, Asilomar, Monterey Co., Calif., 17 Apr. 1972, G. McDonald, 1. *M72-4-26-3, Monterey Breakwater, Monterey Co., Calif., 26 Apr. 1972, G. McDonald, 2. M72-5-14-1, Rocky Pt., Monterey Co., Calif., 14 May 1972, G. McDonald, 1. M72-5-17-8, Carmel Pt., Monterey Co., Calif., 17 May 1972, G. McDonald, 2. M72-7-18-1, Spooner's Cove, San Luis Obispo Co., Calif., 18 July 1972, G. McDonald, 1. M72-12-18-1, Asilomar, Monterey Co., Calif., 18 Dec. 1972, G. McDonald, 1. M72-12-20-1, Asilomar, Monterey Co., Calif., 20 Dec. 1972, G. McDonald, 2. M73-1-0-1, Los Angeles Harbor, Los Angeles Co., Calif., Jan. 1973, R. Fay, 1. M73-4-9-1, Carmel Pt., Monterey Co., Calif., 9 Apr. 1973, G. McDonald, 3. M67-11-17-1, Hazard Can., San Luis Obispo Co., Calif., 17 Nov. 1967, R. Roller, 1. M71-1-8-8, White's Pt., Los Angeles Co., Calif., 8 Jan. 1971, R. Roller, 2. M73-4-9-8, Carmel Pt., Monterey Co., Calif., 9 Apr. 1973, G. McDonald, 2. M73-5-5-10, Asilomar, Monterey Co., Calif., 5 May 1973, G. McDonald, 1. M75-11-2-4, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 1.

Ancula lentiginosa

*M71-10-22-6, Monterey Harbor, Monterey Co., Calif., 22 Oct. 1971, G. McDonald, 5. M71-11-4-2, Asilomar, Monterey Co., Calif., 4 Nov. 1971, G. McDonald, 1. M71-11-17-1, Elkhorn Slough, Monterey Co., Calif., 17 Nov. 1971, G. McDonald, 2. M71-11-22-6, Morro Bay, San Luis Obispo Co., Calif., 22 Nov. 1971, G. McDonald, 2. M71-12-4-2, Elkhorn Slough, Monterey Co., Calif., 4 Dec. 1971, G. McDonald, 3.

Ancula pacifica

M70-6-5-1, Pirate's Cove, San Luis Obispo Co., Calif., 5 June 1970, G. McDonald, 1. M70-6-28-3, Pirate's Cove, San Luis Obispo Co., Calif. 28 June 1970, G. McDonald, 1. M70-7-18-2, Shell Beach, San Luis Obispo Co., Calif. 18 July 1970, G. McDonald, 2. M70-7-18-3, Shell Beach, San Luis Obispo Co., Calif., 18 July 1970, G. McDonald, 3. M70-10-14-2, Asilomar, Monterey Co., Calif., 14 Oct. 1970, G. McDonald, 3. M71-1-26-23, Morro Bay, San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 1. M71-2-8-2, Asilomar, Monterey Co., Calif., 8 Feb. 1971, G. McDonald, 1. M71-11-1-2, Hazard Can., San Luis Obispo Co., Calif., 1 Nov. 1971, G. McDonald, 2. M73-5-5-2, Asilomar, Monterey Co., Calif., 5 May 1973, G. McDonald, 1. M73-5-6-2, Pt. Pinos, Monterey Co., Calif., 6 May 1973, G. McDonald, 2. M73-6-5-13, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 1. *M75-11-2-3, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 5. M78-6-22-9, Carmel Pt., Monterey Co., Calif., 22 June 1978, G. McDonald, 1.

Anisodoris nobilis

M70-12-12-7, Santa Cruz Harbor, Santa Cruz Co., Calif. 12 Dec. 1970, S. Anderson, 1. M70-12-12-8, Pigeon Pt., San Mateo Co., Calif., 12 Dec. 1970, G. McDonald, 1. M70-

12-12-10 Santa Cruz Harbor, Santa Cruz Co., Calif., 12 Dec. 1970, S. Anderson, 1. M71-1-25-8, Pirate's Cove, San Luis Obispo Co., Calif., 25 Jan. 1971, G. McDonald, 2. *M71-1-26-1, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 5. M71-1-26-19, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 1. M71-5-26-3, Asilomar, Monterey Co., Calif., 26 May 1971, G. McDonald, 1. M71-11-2-7, Spooner's Cove, San Luis Obispo Co., Calif., 2 Nov. 1971, G. McDonald, 1. M72-1-16-2, Monterey Breakwater, Monterey Co., Calif., 16 Jan. 1972, R. Hilaski, 1. M73-6-5-2, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 1. M75-10-5-1, Carmel Pt., Monterey Co., Calif., 5 Oct. 1975, G. McDonald, 4. M0012, Anacapa Is., Calif., Oct. 1968, P. Brophy, 1. M0015, Asilomar, Monterey Co., Calif., 3 Nov. 1971, J. Nybakken, 1. M0167, Pt. Pinos, Monterey Co., Calif., 25 Apr. 1967, V. Mansfield, 1. M0169, Moss Beach, Monterey Co., Calif., 16 Oct. 1966, J. Nybakken, 1.

Antiopella barbarensis
M71-1-26-10, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 1. M71-2-1-5, Port San Luis, San Luis Obispo Co., Calif., 1 Feb. 1971, G. McDonald, 1. M71-8-8-4, Asilomar, Monterey Co., Calif., 8 Aug. 1971, G. McDonald, 1. M71-12-30-4, Hazard Can., San Luis Obispo Co., Calif., 30 Dec. 1971, G. McDonald, 3. M69-10-18-1, San Juan Is., Wash., 18 Oct. 1969, G. Robilliard, 6.

Archidoris montereyensis
M71-1-25-6, Pirate's Cove, San Luis Obispo Co., Calif., 25 Jan. 1971, G. McDonald, 1. M71-1-26-20, Morro Bay, San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 2. M71-11-1-1, Hazard Can., San Luis Obispo Co., Calif., 1 Nov. 1971, G. McDonald, 1. M71-11-16-2, Elkhorn Slough, Monterey Co., Calif., 16 Nov. 1971, G. McDonald, 1. M71-11-17-5, Elkhorn Slough, Monterey Co., Calif., 17 Nov. 1971, G. McDonald, 1. M71-12-4-1, Elkhorn Slough, Monterey Co., Calif., 4 Dec. 1971, G. McDonald, 1. M72-1-16-8, Elkhorn Slough, Monterey Co., Calif., 16 Jan. 1972, G. McDonald, 3. M72-11-1-6, Moss Landing, Monterey Co., Calif., 1 Nov. 1972, G. McDonald, 4. M75-8-6-1, Elkhorn Slough, Monterey Co., Calif., 6 Aug. 1975, B. Antrim, 1. M75-8-8-1, Pacific Grove, Monterey Co., Calif., 8 Aug. 1975, M. E. Anderson, 1. M0139, Elkhorn Slough, Monterey Co., Calif., Nov. 1970, G. McDonald, 1. M0176, Carmel Pt., Monterey Co., Calif., 15 Oct. 1970, J. Nybakken, 1.

Archidoris odhneri
M71-1-27-2, Sunset Palisades, San Luis Obispo Co., Calif., 27 Jan. 1971, G. McDonald, 1. *M71-7-3-2, Sunset Palisades, San Luis Obispo Co., Calif., 3 July 1971, G. McDonald, 2. M71-7-3-3, Sunset Palisades, San Luis Obispo Co., Calif., 3 July 1971, P. Clark, 1. M72-7-16-1, Pirate's Cove, San Luis Obispo Co., Calif., 16 July 1972, G. McDonald, 5. M75-9-28-3, Monastery Beach, Monterey Co., Calif., 28 Sept. 1975, A. McDonald, 2. M0237, Monastery Beach, Monterey Co., Calif., 25 Nov. 1970, E. Stark, 1. M0523, Hopkin's Reef, Monterey Co., Calif., 8 Dec. 1974, D. Hunt, 2.

Armina californica
M71-4-10-4, Monterey Bay, Calif., 10 Apr. 1971, G. McDonald, 1. M71-5-4-1, Monterey Bay, Calif., 4 May 1971, G. McDonald, 1. M71-10-0-1, Zuma Beach, Los Angeles Co., Calif., Oct. 1971, S. Anderson, 1. M71-11-18-1, Monterey Bay, Calif., 18 Nov. 1971, D. Varoujean, 1. M71-11-15-1, Santa Monica Bay, Los Angeles Co., Calif., 26 Nov. 1971, S. Anderson, 3. M72-1-7-4, Santa Monica Bay, Los Angeles Co., Calif., 7 Jan. 1972, S. Anderson, 2. M69-8-27-2, Friday Harbor, Wash., 27 Aug. 1969, R. Roller, 1. M73-4-16-1, Monterey Bay, Calif., 16 Apr. 1973, G. McDonald, 1. M0022, Año Nuevo Pt., San Mateo Co., Calif., 3 Aug. 1971, D. Ventresca, 1. M0321, Monterey Bay, Calif., 8 Mar. 1972, G. Kukowski, 1. M0322, Monterey Bay, Calif., 8 Mar. 1972, G. Kukowski, 1.

Atagema alba
M69-7-31-1, Sunset Cliffs, San Diego Co., Calif., 31 July 1969, R. Roller, 1. *M73-10-0-1, Escondido Can., San Diego Co., Calif., Oct. 1973, M. Patton, 1. CASIZ, radula of holotype of *Petelodoris spongicola.*

Babakina festiva
M71-10-0-9, Los Angeles Co., Calif., Oct. 1971, S. Anderson, 1. *M71-11-0-4, Malibu, Los Angeles Co., Calif., Nov. 1971, S. Anderson, 1. M75-1-25-2, Matanchen, Nayarit, Mexico, 25 Jan. 1975, C. Boone, 4.

Cadlina flavomaculata
M69-10-26-8, Pirate's Cove, San Luis Obispo Co., Calif., 26 Oct. 1969, G. McDonald, 2. M71-1-25-4, Sunset Palisades,

San Luis Obispo Co., Calif., 25 Jan. 1971, G. McDonald, 1. M71-12-28-4, Dume Rock, Los Angeles Co., Calif., 28 Dec. 1971, S. Anderson, 2. M71-12-31-4, Shell Beach, San Luis Obispo Co., Calif., 31 Dec. 1971, G. McDonald, 2. M73-6-5-7, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 2. M75-10-5-6, Carmel Pt., Monterey Co., Calif., 5 Oct. 1975, G. McDonald, 2. M75-11-2-10, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 1. M0318, Asilomar, Monterey Co., Calif., 15 May 1972, J. Nybakken, 1.

Cadlina marginata
M70-2-5-3, Field Ranch, San Luis Obispo Co., Calif., 5 Feb. 1970, G. McDonald, 2. M70-10-17-2, Pacific Grove, Monterey Co., Calif., 17 Oct. 1970, G. McDonald, 1. M70-12-12-6, Pigeon Pt., San Mateo Co., Calif., 12 Dec. 1970, G. McDonald, 2. M71-1-26-3, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 1. M71-12-29-1, Pirate's Cove, San Luis Obispo Co., Calif., 29 Dec. 1971, G. McDonald, 2. M72-5-14-2, Rocky Pt., Monterey Co., Calif., 14 May 1972, J. Nybakken, 1. *M73-4-9-7, Carmel Pt., Monterey Co., Calif., 9 Apr. 1973, G. McDonald, 1. M75-9-28-1, Monastery Beach, Monterey Co., Calif., 28 Sept. 1975, A. McDonald, 1. M75-10-4-1, Monastery Beach, Monterey Co., Calif., 4 Oct. 1975, A. McDonald, 5. M75-11-2-1, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 3. M0131, Monastery Beach, Monterey Co., Calif., 18 Nov. 1970, E. Stark, 1. M0164, Carmel Pt., Monterey Co., Calif., 15 Oct. 1970, J. Nybakken, 1. M0189, Pt. Pinos, Monterey Co., Calif., 27 Apr. 1967, V. Mansfield, 2. M0311, Rocky Pt., Monterey Co., Calif., 14 May 1972, J. Nybakken, 2.

Cadlina modesta
M69-10-26-6, Pirate's Cove, San Luis Obispo Co., Calif., 26 Oct. 1969, G. McDonald, 1. M70-10-17-3, Pacific Grove, Monterey Co., Calif., 17 Oct. 1970, G. McDonald, 2. M71-1-26-4, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 6. M71-11-2-3, Spooner's Cove, San Luis Obispo Co., Calif., 2 Nov. 1971, G. McDonald, 1. M71-12-29-2, Pirate's Cove, San Luis Obispo Co., Calif., 29 Dec. 1971, G. McDonald, 3. M73-6-5-6, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 1. M75-10-5-5, Carmel Pt., Monterey Co., Calif., 5 Oct. 1975, G. McDonald, 2. M75-11-2-8, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 4. M0174, Asilomar, Monterey Co., Calif., 10 Nov. 1970, G. McDonald, 1. M0219, Carmel Pt., Monterey Co., Calif., 15 Oct. 1970, J. Nybakken, 1.

Cadlina sparsa
M71-12-27-1, Malibu, Los Angeles Co., Calif., 27 Dec. 1971, S. Anderson, 1. M72-3-22-2, Monterey Breakwater, Monterey Co., Calif., 22 Mar. 1972, G. McDonald, 1. M72-10-22-1, Asilomar, Monterey Co., Calif., 22 Oct. 1972, J. Nybakken, 2. *M73-6-5-5, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 1. M75-6-25-2, La Jolla, San Diego Co., Calif., 25 June 1975, G. McDonald, 1. M77-11-11-1, Scott Cr., Santa Cruz Co., Calif., 11 Nov. 1977, G. McDonald, 1.

Cerberilla mosslandica
M71-11-10-1, Monterey Bay, Calif., 21 Aug. 1971, 1; 10 Nov. 1971, 1; 3 Feb. 1972, 1. M72-8-23-6, Monterey Bay, Calif., 23 Aug. 1972, G. McDonald, 2. M72-8-23-9, Monterey Bay, Calif., 23 Aug. 1972, G. McDonald, 2. M0323, Monterey Bay, Calif., 10 May 1972, G. McDonald, 7. M0481, Monterey Bay, Calif., 1971–1972, Sea Grant, approx. 100. M0482, Monterey Bay, Calif., 3 Feb. 1972, Sea Grant, 1, paratype. M0483, Monterey Bay, Calif., 20 Aug. 1971, Sea Grant, 1, paratype. CASIZ no. 596, Monterey Bay, Calif., 10 May 1972, Sea Grant, 1. holotype. CASIZ no. 597, Monterey Bay, Calif., Sea Grant, 3, paratypes. LACM 1725, 1726, Monterey Bay, Calif., Sea Grant, 3, paratypes.

Chromodoris macfarlandi
*M70-7-9-1, Sunset Palisades, San Luis Obispo Co., Calif., 9 July 1970, G. McDonald, 1. M70-7-9-2, Sunset Palisades, San Luis Obispo Co., Calif., 9 July 1970, G. McDonald, 1. M70-7-26-1, Sunset Palisades, San Luis Obispo Co., Calif., 26 July 1970, G. McDonald, 1. M71-12-2-13, La Jolla, San Diego Co., Calif., 2 Dec. 1971, S. Anderson, 1. M75-6-25-7, La Jolla, San Diego Co., Calif., 25 June 1975, G. McDonald, 1. M78-8-17-5, Monterey Breakwater, Monterey Co., Calif., 17 Aug. 1978, A. K. McDonald, 1.

Chromodoris porterae
M71-8-2-1, Malibu, Los Angeles Co., Calif., 2 Aug. 1971, S. Anderson, 1. M71-8-2-5, Malibu, Los Angeles Co., Calif., 2 Aug. 1971, S. Anderson, 1. M71-8-2-6, Malibu, Los Angeles Co., Calif., 2 Aug. 1971, S. Anderson,

1. M71-9-14-3, Malibu, Los Angeles Co., Calif., 14 Sept. 1971, S. Anderson, 1. *M71-10-0-5, Malibu, Los Angeles Co., Calif., Oct. 1971, S. Anderson, 4. M71-11-23-2, Malibu, Los Angeles Co., Calif., 23 Nov. 1971, S. Anderson, 1. M72-3-2-1, Malibu, Los Angeles Co., Calif., 2 Mar. 1972, S. Anderson, 1. M71-11-23-5, Malibu, Los Angeles Co., Calif., 23 Nov. 1971, S. Anderson, 1.

Conualevia alba
*M71-9-21-2, Pt. Fermin, Los Angeles Co., Calif., 21 Sept. 1971, S. Anderson, 2. M71-1-8-7, White's Pt., Los Angeles Co., Calif., 8 Jan. 1971, 2. M71-10-20-4, Los Angeles Co., Calif., 20 Oct. 1971, S. Anderson, 2. M71-10-22-8, Los Angeles Co., Calif., 22 Oct. 1971, S. Anderson, 1. M75-1-23-8, Cruz de Huanacaxtle, Nayarit, Mexico, 23 Jan. 1975, G. McDonald, 15. M77-11-12-2, Carmel Pt., Monterey Co., Calif., 12 Nov. 1977, R. Slutz, 1. M0363, Carmel Pt., Monterey Co., Calif., 9 Apr. 1973, G. McDonald, 1.

Corambe pacifica
M70-10-7-3, Monterey Bay, Calif., 7 Oct. 1970, G. McDonald, 12. M70-11-27-2, Morro Bay, San Luis Obispo Co., Calif., 27 Nov. 1970, G. McDonald, 2. M71-1-26-21, Morro Bay, San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 1. M71-10-17-10, Morro Bay, San Luis Obispo Co., Calif., 17 Oct. 1971, G. McDonald, 12. *M71-11-22-3, Morro Bay, San Luis Obispo Co., Calif., 22 Nov. 1971, G. McDonald, 4. M69-11-15-1, Morro Bay, San Luis Obispo Co., Calif., 15 Nov. 1969, R. Roller, 2. M73-6-21-1, Pirate's Cove, San Luis Obispo Co., Calif., 21 June 1973, G. McDonald, 1. M75-10-14-4, Monterey Bay, Calif., 14 Oct. 1975, G. McDonald, 1. M75-10-26-10, Morro Bay, San Luis Obispo Co., Calif., 26 Oct. 1975, 7. M78-8-17-6, Monterey Breakwater, Monterey Co., Calif., 17 Aug. 1978, G. McDonald, 12.

Coryphella cooperi
*M70-11-16-3, Elkhorn Slough, Monterey Co., Calif., 16 Nov. 1970, G. McDonald, 1. M70-11-16-8, Elkhorn Slough, Monterey Co., Calif., 16 Nov. 1970, G. McDonald, 1. M70-12-7-1, Elkhorn Slough, Monterey Co., Calif., 7 Dec. 1970, G. McDonald, 1. M76-11-12-1, Elkhorn Slough, Monterey Co., Calif., 12 Nov. 1976, J. Cooper, 3. M76-11-20-1, Elkhorn Slough, Monterey Co., Calif., 20 Nov. 1976, G. McDonald, 1.

Coryphella iodinea
M70-6-13-1, Port San Luis, San Luis Obispo Co., Calif., 13 June 1970, G. McDonald, 1. M71-2-1-2, Port San Luis, San Luis Obispo Co., Calif., 1 Feb. 1971, G. McDonald, 1. M71-2-1-3, Port San Luis, San Luis Obispo Co., Calif., 1 Feb. 1971, G. McDonald, 1. M71-2-2-1, Port San Luis, San Luis Obispo Co., Calif., 2 Feb. 1971, G. McDonald, 1. M71-2-2-2, Port San Luis, San Luis Obispo Co., Calif., 2 Feb. 1971, G. McDonald, 1. M71-2-2-4, Port San Luis, San Luis Obispo Co., Calif., 2 Feb. 1971, G. McDonald, 1. M71-7-3-1, Sunset Palisades, San Luis Obispo Co., Calif., 3 July 1971, G. McDonald, 1. M71-8-18-3, Santa Monica Bay, Los Angeles Co., Calif., 18 Aug. 1971, R. S. Anderson, 2. M71-8-31-5, Santa Monica Bay, Los Angeles Co., Calif., 31 Aug. 1971, R. S. Anderson, 2. M71-11-26-3, Santa Monica Bay, Los Angeles Co., Calif., 26 Nov. 1971, R. S. Anderson, 1. *M72-7-9-1, Shell Beach, San Luis Obispo Co., Calif., 9 July 1972, G. McDonald, 5. M75-6-26-3, La Jolla, San Diego Co., Calif., 26 June 1975, M. U. Purdue, 1. M75-11-23-1, Pacific Grove, Monterey Co., Calif., 23 Nov. 1975, A. K. McDonald, 1. M0186, Del Monte Beach, Monterey Co., Calif., 1 Apr. 1967, V. Mansfield, 1. M0362, Carmel Pt., Monterey Co., Calif., 9 Apr. 1973, G. McDonald, 1.

Coryphella pricei
*M71-11-0-1, Zuma Beach, Los Angeles Co., Calif., Nov. 1971, S. Anderson, 1.

Coryphella trilineata
M70-2-26-2, Morro Bay, San Luis Obispo Co., Calif., 26 Feb. 1970, G. McDonald, 1. M70-11-8-1, Morro Bay, San Luis Obispo Co., Calif., 8 Nov. 1970, G. McDonald, 2. M70-11-13-3, Elkhorn Slough, Monterey Co., Calif., 13 Nov. 1970, G. McDonald, 1. M70-11-16-2, Elkhorn Slough, Monterey Co., Calif., 16 Nov. 1970, G. McDonald, 1. M70-11-16-6, Elkhorn Slough, Monterey Co., Calif., 16 Nov. 1970, G. McDonald, 5. M71-10-17-6, Morro Bay, San Luis Obispo Co., Calif., 17 Oct. 1971, G. McDonald, 1. M71-11-17-7, Elkhorn Slough, Monterey Co., Calif., 17 Nov. 1971, G. McDonald, 2. M71-12-2-5, Carmel Pt., Monterey Co., Calif., 2 Dec. 1971, G. McDonald, 1. M72-10-18-9, Elkhorn Slough, Monterey Co., Calif., 18 Oct. 1972, G. McDonald, 4. M72-11-1-2, Elkhorn Slough, Monterey Co., Calif., 1 Nov. 1972, G. McDonald, 3. M75-10-21-3, Elkhorn Slough,

Monterey Co., Calif., 21 Oct. 1975, G. McDonald, 6. M0197, Elkhorn Slough, Monterey Co., Calif., 13 Nov. 1970, G. McDonald, 1. M0198, Elkhorn Slough, Monterey Co., Calif., 13 Nov. 1970, G. McDonald, 1. M0207, Carmel Pt., Monterey Co., Calif., 15 Oct. 1970, J. Nybakken, 1.

Coryphella sp.
*M72-10-18-2, Elkhorn Slough, Monterey Co., Calif., 18 Oct. 1972, G. McDonald, 15. M72-10-18-7, Elkhorn Slough, Monterey Co., Calif., 18 Oct. 1972, G. McDonald, 2. M72-10-19-1, Elkhorn Slough, Monterey Co., Calif., 19 Oct. 1972, G. McDonald, 5. M72-10-19-2, Elkhorn Slough, Monterey Co., Calif., 19 Oct. 1972, G. McDonald, 10.

Crimora coneja
M75-6-25-1, La Jolla, San Diego Co., Calif., 25 June 1975, G. McDonald, 2. *Prepared radula of specimen, Pt. Loma, San Diego Co., Calif., 25 Apr. 1973, R. Roller, 1.

Cumanotus beaumonti
M70-10-28-1, Elkhorn Slough, Monterey Co., Calif., 28 Oct. 1970, G. McDonald, 1. M70-11-13-1, Elkhorn Slough, Monterey Co., Calif., 13 Nov. 1970, G. McDonald, 1. M70-11-13-2, Elkhorn Slough, Monterey Co., Calif., 13 Nov. 1970, G. McDonald, 6. M70-11-16-1, Elkhorn Slough, Monterey Co., Calif., 16 Nov. 1970, G. McDonald, 3. *M70-11-16-7, Elkhorn Slough, Monterey Co., Calif., 16 Nov. 1970, G. McDonald, 5. M72-10-18-1, Elkhorn Slough, Monterey Co., Calif., 18 Oct. 1972, G. McDonald, 30. M72-10-18-5, Elkhorn Slough, Monterey Co., Calif., 18 Oct. 1972, G. McDonald, 7. M72-10-18-6, Elkhorn Slough, Monterey Co., Calif., 18 Oct. 1972, G. McDonald, 6. M72-11-1-3, Elkhorn Slough, Monterey Co., Calif., 1 Nov. 1972, G. McDonald, 8. M75-10-21-1, Elkhorn Slough, Monterey Co., Calif., 21 Oct. 1975, G. McDonald, 9. M75-10-21-5, Elkhorn Slough, Monterey Co., Calif., 21 Oct. 1975, G. McDonald, 18. M0201, Elkhorn Slough, Monterey Co., Calif., 13 Nov. 1970, G. McDonald, 6. M0203, Elkhorn Slough, Monterey Co., Calif., 28 Oct. 1970, G. McDonald, 1.

Cuthona abronia
*M67-9-6-1, Duxbury Reef, Marin Co., Calif., 6 Aug. 1967, T. Gosliner, 10. M72-8-9-2, Asilomar, Monterey Co., Calif., 9 Aug. 1972, G. McDonald, 1. M73-3-0-4, Los Angeles Co., Calif., Mar. 1973, R. Fay, 1. M73-5-6-6, Pt. Pinos, Monterey Co., Calif., 6 May 1973, G. McDonald, 4. M73-6-2-2, Pescadero Pt., Monterey Co., Calif., 2 June 1973, G. McDonald, 1. M78-7-21-5, Pt. Pinos, Monterey Co., Calif., 21 July 1978, G. McDonald, 8.

Cuthona albocrusta
M71-5-25-3, Asilomar, Monterey Co., Calif., 25 May 1971, G. McDonald, 1. *M71-10-22-4, Monterey Harbor, Monterey Co., Calif., 22 Oct. 1971, G. McDonald, 2. M72-10-18-4, Elkhorn Slough, Monterey Co., Calif., 18 Oct. 1972, G. McDonald, 2. M73-6-5-19, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald 1. M75-10-26-12, Morro Bay, San Luis Obispo Co., Calif., 26 Oct. 1975, G. McDonald, 2. M76-11-20-2, Elkhorn Slough, Monterey Co., Calif., 20 Nov. 1976, G. McDonald, 4. M78-7-21-7, Pt. Pinos, Monterey Co., Calif., 21 July 1978, G. McDonald, 1.

Cuthona columbiana
M70-11-16-4, Elkhorn Slough, Monterey Co., Calif., 16 Nov. 1970, G. McDonald, 1. M71-1-13-1, Elkhorn Slough, Monterey Co., Calif., 13 Jan. 1971, G. McDonald, 9. *M71-1-13-2, Elkhorn Slough, Monterey Co., Calif., 13 Jan. 1971, G. McDonald, 15. M71-5-25-5, Asilomar, Monterey Co., Calif., 25 May 1971, G. McDonald, 1. M71-6-26-3, Asilomar, Monterey Co., Calif., 26 June 1971, G. McDonald, 1. M71-12-2-7, Carmel Pt., Monterey Co., Calif., 2 Dec. 1971, G. McDonald, 1. M72-5-15-9, Asilomar, Monterey Co., Calif., 15 May 1972, G. McDonald, 1. M72-10-22-4, Asilomar, Monterey Co., Calif., 22 Oct. 1972, G. McDonald, 1. M72-11-1-1, Elkhorn Slough, Monterey Co., Calif., 1 Nov. 1972, G. McDonald, 1. M73-5-5-6, Asilomar, Monterey Co., Calif., 5 May 1973, J. Nybakken, 1. M73-6-5-17, Asilomar, Monterey Co., Calif., 5 June 1973, M. Silberstein, 1. M76-11-20-3, Elkhorn Slough, Monterey Co., Calif., 20 Nov. 1976, G. McDonald, 3. M78-7-21-6, Pt. Pinos, Monterey Co., Calif., 21 July 1978, G. McDonald, 1.

Cuthona flavovulta
M70-10-14-10, Asilomar, Monterey Co., Calif., 14 Oct. 1970, G. McDonald, 1. *M71-1-26-22, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 2. M71-5-25-2, Asilomar, Monterey Co., Calif., 25 May 1971, G. McDonald, 1. M71-8-8-6, Asilomar, Monterey Co., Calif., 8 Aug. 1971, G. Mc-

Donald, 1. M71-10-5-3, Asilomar, Monterey Co., Calif., 5 Oct. 1971, G. McDonald, 1. M71-10-22-5, Monterey Harbor, Monterey Co., Calif., 22 Oct. 1971, G. McDonald, 1. M73-6-5-18, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 2. M0313, Asilomar, Monterey Co., Calif., 15 May 1972, G. McDonald, 1.

Cuthona fulgens

*M71-5-25-4, Asilomar, Monterey Co., Calif., 25 May 1971, G. McDonald, 1. M73-5-5-7, Asilomar, Monterey Co., Calif., 5 May 1973, G. McDonald, 3. M73-6-5-20, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 6. M78-7-21-8, Pt. Pinos, Monterey Co., Calif., 21 July 1978, G. McDonald, 1. M0366, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 1.

Cuthona lagunae

M70-7-18-4, Shell Beach, San Luis Obispo Co., Calif., 18 July 1970, G. McDonald, 1. M71-1-26-14, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 5. M71-5-25-1, Asilomar, Monterey Co., Calif., 25 May 1971, G. McDonald, 4. M71-5-26-1, Asilomar, Monterey Co., Calif., 26 May 1971, G. McDonald, 6. M71-6-26-4, Asilomar, Monterey Co., Calif., 26 June 1971, G. McDonald, 1. M71-7-25-7, Morro Bay, San Luis Obispo Co., Calif., 25 July 1971, G. McDonald, 1. M71-8-8-7, Asilomar, Monterey Co., Calif., 8 Aug. 1971, G. McDonald, 1. M72-3-19-1, Asilomar, Monterey Co., Calif., 19 Mar. 1972, G. McDonald, 1. *M72-5-15-8, Asilomar, Monterey Co., Calif., 15 May 1972, G. McDonald, 4. M68-8-8-1, Hazard Can., San Luis Obispo Co., Calif., 8 Aug. 1968, R. A. Roller, 2. M73-5-5-8, Asilomar, Monterey Co., Calif., 5 May 1973, G. McDonald, 4. M73-5-6-5, Pt. Pinos, Monterey Co., Calif., 6 May 1973, G. McDonald, 1. M73-6-5-4, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 5. M0192, Asilomar, Monterey Co., Calif., 14 Oct. 1970, R. Ajeska, 1. M0312, Asilomar, Monterey Co., Calif., 15 May 1972, G. McDonald, 2.

Cuthona virens

*CASIZ, radula of holotype, 1.

Cuthona sp.

*M72-9-20-1, Palo Alto, Santa Clara Co., Calif., 20 Sept. 1972, M. Silberstein, 5. M72-9-20-2, Palo Alto, Santa Clara Co., Calif., 20 Sept. 1972, M. Silberstein, 2.

Dendrodoris albopunctata

M70-10-17-4, Pacific Grove, Monterey Co., Calif., 17 Oct. 1970, G. McDonald, 1. M70-12-12-4, Pigeon Pt., San Mateo Co., Calif., 12 Dec. 1970, G. McDonald, 1. M71-6-29-1, Pirate's Cove, San Luis Obispo Co., Calif., 29 June 1971, G. McDonald, 1. M71-8-2-2, Malibu, Los Angeles Co., Calif., 2 Aug. 1971, R. S. Anderson, 1. M71-9-24-1, Malibu, Los Angeles Co., Calif., 24 Sept. 1971, R. S. Anderson, 1. M72-1-16-1, Monterey Breakwater, Monterey Co., Calif., 16 Jan. 1972, R. Hilaski, 2. M72-12-16-2, Shell Beach, San Luis Obispo Co., Calif., 16 Dec. 1972, G. McDonald, 1. M73-4-9-2, Carmel Pt., Monterey Co., Calif., 9 Apr. 1973, G. McDonald, 2. M73-6-5-3, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 6. M75-6-24-1, La Jolla, San Diego Co., Calif., 24 June 1975, G. McDonald, 3. M75-6-26-5, La Jolla, San Diego Co., Calif., 26 June 1975, G. McDonald, 1. M75-8-8-4, Pacific Grove, Monterey Co., Calif., 8 Aug. 1975, M. E. Anderson, 1. M75-10-17-2, Pescadero Pt., Monterey Co., Calif., 17 Oct. 1975, M. Silberstein, 1. M75-11-2-17, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 3. M0132, Pacific Grove, Monterey Co., Calif., 17 Oct. 1970, G. McDonald, 1. M0141, Carmel Pt., Monterey Co., Calif., 15 Oct. 1970, J. W. Nybakken, 1. M0166, Pt. Pinos, Monterey Co., Calif., 26 Apr. 1967, V. Mansfield, 1. M0168, Pigeon Pt., San Mateo Co., Calif., 30 Oct. 1966, J. W. Nybakken, 1.

Dendrodoris nigromaculata

M75-6-26-4, La Jolla, San Diego Co., Calif., 26 June 1975, G. McDonald, 2.

Dendrodoris sp. a.

M72-7-16-2, Pirate's Cove, San Luis Obispo Co., Calif., 16 July 1972, G. McDonald, 1. M73-11-12-1, Pirate's Cove, San Luis Obispo Co., Calif., 12 Nov. 1973, G. McDonald, 1. M72-9-23-1, Elkhorn Slough, Monterey Co., Calif., 23 Sept. 1972, G. McDonald, 1. M75-0-0-1, 17 Mile Dr., Monterey Co., Calif., 1975, J. Harvey, 1.

Dendrodoris sp. b.

M71-7-7-6, Santa Monica Bay, Los Angeles Co., Calif., 7 July 1971, S. Anderson, 1. M71-10-20-2, Los Angeles Co., Calif., 20 Oct. 1971, S. Anderson, 1. M71-10-9-1, Malibu, Los Angeles Co., Calif., 9 Oct. 1971, S. Anderson, 2. M75-10-17-1, Pescadero Pt., Monterey Co., Calif., 17 Oct. 1975, M. Silberstein, 1.

Dendronotus albus

M70-4-3-1, Pirate's Cove, San Luis Obispo Co., Calif., 3 Apr. 1970, G. McDonald, 1. M70-6-5-2, Pirate's Cove, San Luis Obispo Co., Calif., 5 June 1970, G. McDonald, 1. M70-6-5-3, Pirate's Cove, San Luis Obispo Co., Calif., 5 June 1970, G. McDonald, 1. *M70-7-18-1, Shell Beach, San Luis Obispo Co., Calif., 18 July 1970, G. McDonald, 2. M71-5-26-4, Asilomar, Monterey Co., Calif., 26 May 1971, G. McDonald, 5. M72-5-15-4, Asilomar, Monterey Co., Calif., 15 May 1972, G. McDonald, 1. M72-7-11-1, Pirate's Cove, San Luis Obispo Co., Calif., 11 July 1972, G. McDonald, 3. M73-5-6-3, Pt. Pinos, Monterey Co., Calif., 6 May 1973, G. McDonald, 2. M73-6-5-8, Asilomar, Monterey Co., Calif., 5 June 1973, 2. M78-7-21-3, Pt. Pinos, Monterey Co., Calif., 21 July 1978, G. McDonald, 2. M0214, Asilomar, Monterey Co., Calif., 25 May 1971, G. McDonald, 2.

Dendronotus diversicolor

*M0506, Asilomar, Monterey Co., Calif., 14 Nov. 1974, J. Nybakken, 1. M76-8-2-3, Otter Bay, British Columbia, Canada, 2 Aug. 1976, P. Lambert, 1.

Dendronotus frondosus

M70-2-26-1, Morro Bay, San Luis Obispo Co., Calif., 26 Feb. 1970, G. McDonald, 2. M70-2-26-4, Morro Bay, San Luis Obispo Co., Calif., 26 Feb. 1970, G. McDonald, 1. M70-3-29-1, Morro Bay, San Luis Obispo Co., Calif., 29 Mar. 1970, G. McDonald, 1. M70-9-21-1, Monterey Bay, Calif., 21 Sept. 1970, S. Anderson, 3. *M70-10-7-1, Monterey Bay, Calif., 7 Oct. 1970, G. McDonald, 4. M71-11-17-9, Elkorn Slough, Monterey Co., Calif., 17 Nov. 1971, G. McDonald, 1. M75-10-14-1, Monterey Bay, Calif., 14 Oct. 1975, G. McDonald, 3. M75-10-23-1, Monterey Bay, Calif., 23 Oct. 1975, P. Slattery, 20. M78-7-21-20, Elkhorn Slough, Monterey Co., Calif., 21 July 1978, G. McDonald, 1. M0213, Monterey Bay, Calif., 7 Oct. 1970, G. McDonald, 4. M0215, Monterey Bay, Calif., 21 Sept. 1970, S. Anderson, 15. M0499, Monterey Bay, Calif., 8 Oct. 1974, G. McDonald, 1.

Dendronotus iris

M71-2-15-4, Monterey Harbor, Monterey Co., Calif., 15 Feb. 1971, G. McDonald, 1. M71-5-23-1, Monterey Breakwater, Monterey Co., Calif., 23 May 1971, G. McDonald, 1. M71-5-23-2, Monterey Breakwater, Monterey Co., Calif., 23 May 1971, P. Clark, 1. M71-5-23-3, Monterey Breakwater, Monterey Co., Calif., 23 May 1971, G. McDonald, 2. M71-5-23-4, Monterey Breakwater, Monterey Co., Calif., 23 May 1971, P. Clark, 1. M70-8-18-1, Morro Bay, San Luis Obispo Co., Calif., 18 Aug. 1970, R. Roller, 1. M72-1-7-1, off Topanga Can., Los Angeles Co., Calif., 7 Jan. 1972, S. Anderson, 2. M72-3-22-5, Monterey Breakwater, Monterey Co., Calif., 22 Mar. 1972, G. McDonald, 2. M72-3-22-6, Monterey Breakwater, Monterey Co., Calif., 22 Mar. 1972, G. McDonald, 2. M73-3-0-2, Los Angeles Co., Calif., Mar. 1973, R. Fay, 2. M78-8-4-1, Monterey Breakwater, Monterey Co., Calif., 4 Aug. 1978, G. McDonald, 4. M69-8-0-3, Friday Harbor, Wash., Aug. 1969, R. Roller, 1. M0221, Monterey Breakwater, Monterey Co., Calif., 23 May 1971, G. McDonald, 1.

Dendronotus subramosus

M71-7-25-6, Morro Bay, San Luis Obispo Co., Calif., 25 July 1971, G. McDonald, 1. M71-8-8-3, Asilomar, Monterey Co., Calif., 8 Aug. 1971, G. McDonald, 3. M71-11-1-5, Hazard Can., San Luis Obispo Co., Calif., 1 Nov. 1971, G. McDonald, 1. M71-11-4-3, Asilomar, Monterey Co., Calif., 4 Nov. 1971, D. Shonman, 2. M72-5-15-3, Asilomar, Monterey Co., Calif., 15 May 1972, G. McDonald, 1. M72-5-17-7, Carmel Pt., Monterey Co., Calif., 17 May 1972, G. McDonald, 1. M75-8-8-2, Pt. Pinos, Monterey Co., Calif., 8 Aug. 1975, M. E. Anderson, 1. M75-11-2-7, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 1. M0210 Asilomar, Monterey Co., Calif., 25 May 1971, G. McDonald, 2. M0314, Asilomar, Monterey Co., Calif., 15 May 1972, G. McDonald, 1.

Dirona albolineata

M70-12-12-2, Pigeon Pt., San Mateo Co., Calif., 12 Dec. 1970, G. McDonald, 1. M71-5-25-7, Asilomar, Monterey Co., Calif., 25 May 1971, G. McDonald, 1. *M71-6-26-1, Asilomar, Monterey Co., Calif., 26 June 1971, G. McDonald, 1. M71-10-5-2, Asilomar, Monterey Co., Calif., 5 Oct. 1971, G. McDonald, 1. M68-7-11-1, Shell Beach, San Luis Obispo Co., Calif., 11 July 1968, R. A. Roller, 3. M72-5-15-2, Asilomar, Monterey Co., Calif., 15 May 1972, G. McDonald, 2. M75-11-3-4, Pigeon Pt., San Mateo Co., Calif., 3 Nov. 1975, G. McDonald, 1.

Dirona picta

M70-2-26-6, Morro Bay, San Luis Obispo Co., Calif., 26 Feb. 1970, G. McDonald, 1. M70-12-11-1, Asilomar, Monterey Co., Calif., 11 Dec. 1970, G. McDonald, 1. M71-1-26-5, Morro Bay, San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 2. M71-1-26-17, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 1. M71-2-8-1, Asilomar, Monterey Co., Calif., 8 Feb. 1971, G. McDonald, 3. M71-2-24-4, Morro Bay, San Luis Obispo Co., Calif., 24 Feb. 1971, G. McDonald, 2. M71-2-24-5, Morro Bay, San Luis Obispo Co., Calif., 24 Feb. 1971, G. McDonald, 1. *M71-5-26-5, Asilomar, Monterey Co., Calif., 26 May 1971, G. McDonald, 3. M71-7-25-4, Morro Bay, San Luis Obispo Co., Calif., 25 July 1971, G. McDonald, 1. M71-10-7-3, Marina del Rey, Los Angeles Co., Calif., 7 Oct. 1971, R. S. Anderson, 3. M71-12-1-2, Asilomar, Monterey Co., Calif., 1 Dec. 1971, D. Shonman, 1. M71-12-30-3, Hazard Can., San Luis Obispo Co., Calif., 30 Dec. 1971, G. McDonald, 1. M72-5-17-3, Carmel Pt., Monterey Co., Calif., 17 May 1972, G. McDonald, 1. M75-11-2-15, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 2. M78-7-21-11, Pt. Pinos, Monterey Co., Calif., 21 July 1978, A. K. McDonald, 2. M0220, Asilomar, Monterey Co., Calif., 11 Nov. 1970, R. S. Anderson, 1.

Discodoris heathi

M70-6-28-2, Pirate's Cove, San Luis Obispo Co., Calif., 28 June 1970, G. McDonald, 1. M70-10-16-3, Asilomar, Monterey Co., Calif., 16 Oct. 1970, G. McDonald, 1. M70-12-12-11, Pigeon Pt., San Mateo Co., Calif., 12 Dec. 1970, J. Hansen, 1. M71-1-26-7, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 1. M71-2-1-6, Port San Luis, San Luis Obispo Co., Calif., 1 Feb. 1971, G. McDonald, 1. M71-11-2-2, Spooner's Cove, San Luis Obispo Co., Calif., 2 Nov. 1971, G. McDonald, 1. M71-11-2-9, Spooner's Cove, San Luis Obispo Co., Calif., 2 Nov. 1971, G. McDonald, 1. *M71-12-29-4, Pirate's Cove, San Luis Obispo Co., Calif., 29 Dec. 1971, G. McDonald, 1. M75-11-2-9, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 5. M77-12-10-15, Asilomar, Monterey Co., Calif., 10 Dec. 1977, G. McDonald, 5. M0165, Pt. Pinos, Monterey Co., Calif., 26 Apr. 1967, V. Mansfield, 1. M0486, Carmel Pt., Monterey Co., Calif., 22 June 1974, M. E. Anderson, 1.

Discodoris sandiegensis

M69-9-3-10, San Diego, San Diego Co., Calif., 3 Sept. 1969, G. McDonald, 1. M69-10-26-4, Pirate's Cove, San Luis Obispo Co., Calif., 26 Oct. 1969, G. McDonald, 2. M70-6-28-5, Pirate's Cove, San Luis Obispo Co., Calif., 28 June 1970, G. McDonald, 1. M70-10-14-1, Asilomar, Monterey Co. Calif., 14 Oct. 1970, G. McDonald, 1. M70-10-17-1, Pacific Grove, Monterey Co., Calif., 17 Oct. 1970, G. McDonald, 2. M70-12-12-5, Pigeon Pt., San Mateo Co., Calif., 12 Dec. 1970, G. McDonald, 1. M71-1-25-3, Pirate's Cove, San Luis Obispo Co., Calif., 25 Jan. 1971, G. McDonald, 1. M71-11-2-4, Spooner's Cove, San Luis Obispo Co., Calif., 2 Nov. 1971, G. McDonald, 1. M71-11-2-8, Spooner's Cove, San Luis Obispo Co., Calif., 2 Nov. 1971, G. McDonald, 1. *M71-12-31-1, Shell Beach, San Luis Obispo Co., Calif., 31 Dec. 1971, G. McDonald, 5. M72-1-16-4, Monterey Breakwater, Monterey Co., Calif., 16 Jan. 1972, R. Hilaski, 1. M72-1-16-9, Elkhorn Slough, Monterey Co., Calif., 16 Jan. 1972, G. McDonald, 4. M73-6-5-1, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 2. M75-7-18-1, Elkhorn Slough, Monterey Co., Calif., 18 July 1975, G. McDonald, 1. M75-10-21-4, Elkhorn Slough, Monterey Co., Calif., 21 Oct. 1975, D. Ituarte, 1. M75-11-2-2, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 3. M75-11-4-1, Pescadero Pt., Monterey Co., Calif., 4 Nov. 1975, G. McDonald, 2. M0160, Del Monte Beach, Monterey Co., Calif., 1 Apr. 1967, V. Mansfield, 1. M0487, Monterey Breakwater, Monterey Co., Calif., 8 July 1974, M. E. Anderson, 1.

Doridella steinbergae

*M71-7-7-4, Morro Bay, San Luis Obispo Co., Calif., 7 July 1971, G. McDonald, 6. M73-6-21-2, Pirate's Cove, San Luis Obispo Co., Calif., 21 June 1973, G. McDonald, 40. M75-10-14-3, Monterey Bay, Calif., 14 Oct. 1975, G. McDonald, 20.

Doris (s.l.) sp.

M71-9-14-1, Malibu, Los Angeles Co., Calif., 14 Sept. 1971, R. S. Anderson, 1. M71-9-14-2, Malibu, Los Angeles Co., Calif., 14 Sept. 1971, R. S. Anderson, 1. *M71-12-2-12, La Jolla, San Diego Co., Calif., 2 Dec. 1971, R. S. Anderson, 4. M75-6-26-1, La Jolla, San Diego Co., Calif. 26 June 1975, G. McDonald, 1. M75-6-26-6, Pescadero Pt., Monterey Co., Calif., 26 June 1975, M. Silberstein, 1.

Doto amyra

*M72-5-15-5, Asilomar, Monterey Co., Calif., 15 May 1972, G. McDonald, 3. M73-5-5-9, Asilomar, Monterey Co., Calif., 5 May 1973,

G. McDonald, 4. M73-6-5-12, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 4. M78-6-22-4, Carmel Pt., Monterey Co., Calif., 22 June 1978, G. McDonald, 5. M0315, Asilomar, Monterey Co., Calif., 15 May 1972, G. McDonald, 2.

Doto kya

*M71-10-17-2, Morro Bay, San Luis Obispo Co., Calif., 17 Oct. 1971, G. McDonald, 1. M73-5-6-7, Pt. Pinos, Monterey Co., Calif., 6 May 1973, G. McDonald, 1. M73-6-5-15, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 6. M75-10-26-2, Morro Bay, San Luis Obispo Co., Calif., 26 Oct. 1975, G. McDonald, 12.

Eubranchus misakiensis

*Mukaishima, Inland Sea of Seto, Japan, 22 Mar. 1962, K. Baba, 2.

Eubranchus olivaceus

*M73-5-5-4, Asilomar, Monterey Co., Calif., 5 May 1973, G. McDonald, 1.

Eubranchus rustyus

M70-11-16-5, Elkhorn Slough, Monterey Co., Calif., 16 Nov. 1970, G. McDonald, 1. M71-1-26-8, Morro Bay, San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 3. M71-6-26-5, Asilomar, Monterey Co., Calif., 26 June 1971, G. McDonald, 1. M71-10-17-3, Morro Bay, San Luis Obispo Co., Calif., 17 Oct. 1971, G. McDonald, 1. *M73-5-5-1, Asilomar, Monterey Co., Calif., 5 May 1973, G. McDonald, 7. M73-5-5-2, Asilomar, Monterey Co., Calif., 5 May 1973, G. McDonald, 2. M73-5-6-1, Pt. Pinos, Monterey Co., Calif., 6 May 1973, G. McDonald, 8. M75-10-19-1, Monterey Breakwater, Monterey Co., Calif., 19 Oct. 1975, A. K. McDonald, 2. M75-10-26-8, Morro Bay, San Luis Obispo Co., Calif., 26 Oct. 1975, G. McDonald, 4. M78-6-22-10, Carmel Pt., Monterey Co., Calif., 22 June 1978, G. McDonald, 1. M0316, Asilomar, Monterey Co., Calif., 15 May 1972, J. W. Nybakken, 1.

Fiona pinnata

M70-9-21-2, Monterey Bay, Calif., 21 Sept. 1970, R. S. Anderson, 2. M70-10-5-5, Monterey Bay, Calif., 5 Oct. 1970, G. McDonald, 4. M70-10-5-6, Monterey Bay, Calif., 5 Oct. 1970, G. McDonald, 11. M70-11-1-1, Monterey Bay, Calif., 1 Nov. 1970, R. S. Anderson, 6. *M70-11-1-3, Monterey Bay, Calif., 1 Nov. 1970, R. S. Anderson, 9. M70-11-1-4, Monterey Bay, Calif., 1 Nov. 1970, R. S. Anderson, 3. M72-8-9-1, Monterey Bay, Calif., 9 Aug. 1972, G. McDonald, 14. M0031, Monterey Bay, Calif., Sept. 1971, 2. M0193, Monterey Bay, Calif., 1 Nov. 1970, R. S. Anderson, 7. M0194, Monterey Bay, Calif., 8 Nov. 1970, R. S. Anderson, 7. M0195, Monterey Bay, Calif., 12 Sept. 1970, R. S. Anderson, 9. M0199, Monterey Bay, Calif., 5 Oct. 1970, G. McDonald, 9.

Hallaxa chani

M71-12-30-2, Hazard Can., San Luis Obispo Co., Calif., 30 Dec. 1971, G. McDonald, 2. M71-12-31-6, Shell Beach, San Luis Obispo Co., Calif., 31 Dec. 1971, G. McDonald, 2. M72-1-15-2, Asilomar, Monterey Co., Calif., 15 Jan. 1972, G. McDonald, 1. *M72-10-22-2, Asilomar, Monterey Co., Calif., 22 Oct. 1972, G. McDonald, 1. M75-10-26-4, Morro Bay, San Luis Obispo Co., Calif., 26 Oct. 1975, G. McDonald, 3. M77-11-11-2, Scott Cr., Santa Cruz Co., Calif., 11 Nov. 1977, G. McDonald, 1.

Hancockia californica

M70-9-21-3, Monterey Bay, Calif., 21 Sept. 1970, R. S. Anderson, 3. M70-10-14-3, Asilomar, Monterey Co., Calif., 14 Oct. 1970, G. McDonald, 1. M71-5-25-6, Asilomar, Monterey Co., Calif., 25 May 1971, G. McDonald, 1. M71-6-26-2, Asilomar, Monterey Co., Calif., 26 June 1971, G. McDonald, 1. M71-7-25-2, Morro Bay, San Luis Obispo Co., Calif., 25 July 1971, G. McDonald, 12. *M71-8-8-1, Asilomar, Monterey Co., Calif., 8 Aug. 1971, G. McDonald, 25. M71-7-25-10, Morro Bay, San Luis Obispo Co., Calif., 25 July 1971, G. McDonald, 3. M72-8-9-3, Asilomar, Monterey Co., Calif., 9 Aug. 1972, G. McDonald, 2. M73-6-5-10, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 3. M75-8-8-3, Pacific Grove, Monterey Co., Calif., 8 Aug. 1975, M. E. Anderson, 1. M76-11-21-1, Asilomar, Monterey Co., Calif., 21 Nov. 1976, G. McDonald, 1. M78-7-21-1, Pt. Pinos, Monterey Co., Calif., 21 July 1978, G. McDonald, 6. M0206, Monterey Bay, Calif., 12 Sept. 1970, R. S. Anderson, 5.

Hopkinsia rosacea

M70-6-28-1, Pirate's Cove, San Luis Obispo Co., Calif., 28 June 1970, G. McDonald, 1. M70-6-28-4, Pirate's Cove, San Luis Obispo Co., Calif., 28 June 1970, G. McDonald, 1. M71-1-25-1, Sunset Palisades, San Luis Obispo Co., Calif., 25 Jan. 1971, G. McDonald, 1. M71-1-26-8, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 1. M71-11-2-10, Spooner's Cove, San Luis Obispo Co., Calif., 2 Nov. 1971, G. McDonald, 1. M71-11-2-11, Spooner's Cove, San Luis Obispo Co., Calif., 2 Nov. 1971, G. McDonald, 1. M72-5-17-2, Carmel Pt., Monterey Co., Calif., 17 May 1972, G. McDonald, 2. M73-4-9-5, Carmel Pt., Monterey Co., Calif., 9 Apr. 1973, G. McDonald, 3. M73-6-1-1, Pacific Grove, Monterey Co., Calif., 1 June 1973, G. McDonald, 4. M75-10-5-2, Carmel Pt., Monterey Co., Calif., 5 Oct. 1975, G. McDonald, 10. M0136, Asilomar, Monterey Co., Calif., 11 Nov. 1970, G. McDonald, 1. M0188, Pacific Grove, Monterey Co., Calif., 16 Oct. 1966, J. W. Nybakken, 1. M0202, Pt. Pinos, Monterey Co., Calif., 27 Apr. 1967, V. Mansfield, 1.

Hypselodoris californiensis

M71-8-16-1, Malibu, Los Angeles Co., Calif., 16 Aug. 1971, R. S. Anderson, 1. M71-8-2-3, Malibu, Los Angeles Co., Calif., 2 Aug. 1971, R. S. Anderson, 1. M71-8-2-4, Malibu, Los Angeles Co., Calif., 2 Aug. 1971. R. S. Anderson, 1. *M71-10-0-2, Malibu, Los Angeles Co., Calif., Oct. 1971, R. S. Anderson, 1. M71-10-0-3, Malibu, Los Angeles Co., Calif., Oct. 1971, R. S. Anderson, 1. M71-10-0-4, Malibu, Los Angeles Co., Calif., Oct. 1971, R. S. Anderson, 1. M71-11-23-1, Malibu, Los Angeles Co., Calif., 23 Nov. 1971, R. S. Anderson, 1. M71-11-23-4, Malibu, Los Angeles Co., Calif., 23 Nov. 1971, R. S. Anderson, 1.

Laila cockerelli

M70-2-5-2, Pecho, San Luis Obispo Co., Calif., 5 Feb. 1970, G. McDonald, 2. *M71-5-25-8, Asilomar, Monterey Co., Calif., 25 May 1971, G. McDonald, 1. M71-6-10-1, Monterey Breakwater, Monterey Co., Calif., 10 June 1971, D. B. Lewis, 1. M71-10-5-1, Asilomar, Monterey Co., Calif., 5 Oct. 1971, G. McDonald, 2. M71-11-3-1, Carmel Pt., Monterey Co., Calif., 3 Nov. 1971, G. McDonald, 5. M71-11-4-4, Carmel Pt., Monterey Co., Calif., 4 Nov. 1971, G. McDonald, 1. M71-12-2-11, Carmel Pt., Monterey Co., Calif., 2 Dec. 1971, G. McDonald, 2. M69-7-30-1, Pt. Loma, San Diego Co., Calif., 30 July 1969, R. A. Roller, 1. M72-1-16-7, Monterey Breakwater, Monterey Co., Calif., 16 Jan. 1972, R. Hilaski, 1. M72-2-14-1, Asilomar, Monterey Co., Calif., 14 Feb. 1972, G. McDonald, 1. M72-5-15-6, Asilomar, Monterey Co., Calif., 15 May 1972, G. McDonald, 1. M72-5-17-6, Carmel Pt., Monterey Co., Calif., 17 May 1972, G. McDonald, 2. M73-4-9-4, Carmel Pt., Monterey Co., Calif., 9 Apr. 1973, G. McDonald, 1. M73-5-6-4, Pt. Pinos, Monterey Co., Calif., 6 May 1973, G. McDonald, 1. M73-6-1-3, Pacific Grove, Monterey Co., Calif., 1 June 1973, G. McDonald, 2. M75-6-25-4, La Jolla, San Diego Co., Calif., 25 June 1975, G. McDonald, 1. M75-10-5-3, Carmel Pt., Monterey Co., Calif., 5 Oct. 1975, G. McDonald, 1. M75-11-2-14, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 8. M0212, Carmel Pt., Monterey Co., Calif., 15 Oct. 1970, E. Stark, 1.

Melibe leonina

M69-10-3-1, Morro Bay, San Luis Obispo Co., Calif., 3 Oct. 1969, G. McDonald, 3. M70-10-7-2, Monterey Bay, Calif., 7 Oct. 1970, G. McDonald, 1. M70-12-2-2, Monterey Bay, Calif., 2 Dec. 1970, G. McDonald, 2. M75-10-14-5, Monterey Bay, Calif., 14 Oct. 1975, J. Harvey, 1. M0218, Monterey Bay, Calif., 7 Oct. 1970, G. McDonald, 1. M0496, Elkhorn Slough, Monterey Co., Calif., Sept. 1974, C. Keusink, 1.

Okenia angelensis

M70-11-8-2, Morro Bay, San Luis Obispo Co., Calif., 8 Nov. 1970, G. McDonald, 1. M70-11-27-3, Morro Bay, San Luis Obispo Co., Calif., 27 Nov. 1970, G. McDonald, 2. M71-1-26-13, Morro Bay, San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 3. M71-2-24-2, Morro Bay, San Luis Obispo Co., Calif., 24 Feb. 1971, G. McDonald, 2. M71-2-24-7, Morro Bay, San Luis Obispo Co., Calif., 24 Feb. 1971, G. McDonald, 3. *M71-10-17-7, Morro Bay, San Luis Obispo Co., Calif., 17 Oct. 1971, G. McDonald, 13. M71-10-22-7, Monterey Harbor, Monterey Co., Calif., 22 Oct. 1971, G. McDonald, 7. M72-10-29-1, Morro Bay, San Luis Obispo Co., Calif., 29 Oct. 1972, G. McDonald, 4. M69-11-23-1, Morro Bay, San Luis Obispo Co., Calif., 23 Nov. 1969, R. A. Roller, 1. M69-10-12-4, Morro Bay, San Luis Obispo Co., Calif., 12 Oct. 1969, R. A. Roller, 4. M75-10-26-7, Morro Bay, San Luis Obispo Co., Calif., 26 Oct. 1975, G. McDonald, 10. M0025, Monterey Harbor, Monterey Co., Calif., 21 Oct. 1971, G. McDonald, 14. M0171, Morro Bay, San Luis Obispo Co., Calif., 8 Nov. 1970, G. McDonald, 1.

Okenia plana

*M72-11-0-1, Pt. Richmond, San Francisco Bay, Calif., Nov. 1972, E. Lyke, 2.

Onchidoris bilamellata

*M70-10-22-1, Moss Landing, Monterey Co., Calif., 22 Oct. 1970, R. S. Anderson, 10. M70-10-22-3, Moss Landing, Monterey Co., Calif., 22 Oct. 1970, R. S. Anderson, 11. M70-10-22-5, Moss Landing, Monterey Co., Calif., 22 Oct. 1970, R. S. Anderson, 12. M71-2-15-2, Monterey Harbor, Monterey Co., Calif., 15 Feb. 1971, G. McDonald, 1. M71-11-17-3, Elkhorn Slough, Monterey Co., Calif., 17 Nov. 1971, G. McDonald, 2. M72-2-10-1, Elkhorn Slough, Monterey Co., Calif., 10 Feb. 1972, G. McDonald, 7. M65-4-3-1, England, 3 Apr. 1965, T. E. Thompson, 1. M75-7-18-2, Elkhorn Slough, Monterey Co., Calif., 18 July 1975, G. McDonald, 1. M0129, Moss Landing, Monterey Co., Calif., 22 Oct. 1970, R. S. Anderson, 14. M0172, Moss Landing, Monterey Co., Calif., 22 Oct. 1970, R. S. Anderson, 6. M0173, Moss Landing, Monterey Co., Calif., 22 Oct. 1970, R. S. Anderson, 20.

Onchidoris hystricina

M70-7-18-5, Shell Beach, San Luis Obispo Co., Calif., 18 July 1970, G. McDonald, 3. M70-7-18-6, Shell Beach, San Luis Obispo Co., Calif., 18 July 1970, G. McDonald, 3. *M71-6-28-2, Morro Bay, San Luis Obispo Co., Calif., 28 June 1971, R. A. Roller, 3. M71-7-7-2, Morro Bay, San Luis Obispo Co., Calif., 7 July 1971, G. McDonald, 1. M71-10-17-5, Morro Bay, San Luis Obispo Co., Calif., 17 Oct. 1971, G. McDonald, 2. M75-10-26-9, Morro Bay, San Luis Obispo Co., Calif., 26 Oct. 1975, G. McDonald, 1. M78-8-4-3, Monterey Breakwater, Monterey Co., Calif., 4 Aug. 1978, G. McDonald, 2. M0126, Asilomar, Monterey Co., Calif., 14 Oct. 1970, J. W. Nybakken, 1.

Onchidoris sp.

*M71-1-26-15, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 3. M69-8-24-2, Friday Harbor, Wash., 24 Aug. 1969, R. A. Roller, 1. M71-12-30-1, Hazard Can., San Luis Obispo Co., Calif., 30 Dec. 1971, G. McDonald, 2. M75-0-0-1, Monastery Beach, Monterey Co., Calif., 1975, A. K. McDonald, 3. M0505, Monastery Beach, Monterey Co., Calif., 18 Jan. 1975, A. K. McDonald, 5.

Phidiana crassicornis

M69-10-26-9, Pirate's Cove, San Luis Obispo Co., Calif., 26 Oct. 1969, G. McDonald, 3. M69-10-26-11, Pirate's Cove, San Luis Obispo Co., Calif., 26 Oct. 1969, G. McDonald, 1. M70-3-29-2, Morro Bay, San Luis Obispo Co., Calif., 29 Mar. 1970, G. McDonald, 1. M70-10-17-5, Elkhorn Slough, Monterey Co., Calif., 17 Oct. 1970, G. McDonald, 1. M70-10-28-3, Elkhorn Slough, Monterey Co., Calif., 28 Oct. 1970, G. McDonald, 1. M71-10-22-1, Monterey Harbor, Monterey Co., Calif., 22 Oct. 1971, G. McDonald, 2. M71-11-17-6, Elkhorn Slough, Monterey Co., Calif., 17 Nov. 1971, G. McDonald, 1. M71-11-29-1, Morro Bay, San Luis Obispo Co., Calif., 29 Nov. 1971, G. McDonald, 1. M72-10-18-3, Elkhorn Slough, Monterey Co., Calif., 18 Oct. 1972, G. McDonald, 5. M72-10-18-8, Elkhorn Slough, Monterey Co., Calif., 18 Oct. 1972, G. McDonald, 3. M75-10-5-7, Carmel Pt., Monterey Co., Calif., 5 Oct. 1975, G. McDonald, 1. M75-10-26-6, Morro Bay, San Luis Obispo Co., Calif., 26 Oct. 1975, G. McDonald, 1. M75-11-2-16, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 1. M76-7-0-1, E. Redonda Island, B. C., Canada, July 1976, M. E. Anderson, 6. M0191, Pt. Pinos, Monterey Co., Calif., 26 Apr. 1967, V. Mansfield, 1. M0204, Elkhorn Slough, Monterey Co., Calif., 17 Oct. 1970, G. McDonald, 2.

Phidiana hiltoni

M69-10-26-7, Pirate's Cove, San Luis Obispo Co., Calif., 26 Oct. 1969, G. McDonald, 1. *M71-1-25-2, Sunset Palisades, San Luis Obispo Co., Calif., 25 Jan. 1971, G. McDonald, 6. M71-1-26-6, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 6. M71-12-2-10, Carmel Pt., Monterey Co., Calif., 2 Dec. 1971, G. McDonald, 1. M71-12-28-3, Sunset Palisades, San Luis Obispo Co., Calif., 28 Dec. 1971, G. McDonald, 3. M72-5-17-4, Carmel Pt., Monterey Co., Calif., 17 May 1972, G. McDonald, 1. M75-10-4-2, Monastery Beach, Monterey Co., Calif., 4 Oct. 1975, A. K. McDonald, 1. M75-11-2-11, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 2. M78-7-21-12, Pt. Pinos, Monterey Co., Calif., 21 July 1978, G. McDonald, 1. M0187, Carmel Pt., Monterey Co., Calif., 26 May 1967, R. Schinoke, 1. M0310, Carmel Pt., Monterey Co., Calif., 17 May 1972, G. McDonald, 1.

Phidiana morroensis

M71-10-17-4, Morro Bay, San Luis Obispo Co., Calif., 17 Oct. 1971, G. McDonald, 1. M71-11-17-2, Elkhorn Slough, Monterey Co., Calif., 17 Nov. 1971, G. McDonald, 5. M71-12-4-3, Elkhorn Slough, Monterey Co., Calif., 4 Dec. 1971, G. McDonald, 5. *M72-9-21-1, Monterey Bay, Calif., 21 Sept. 1972, J. Oliver, 3. M72-11-1-5, Elkhorn Slough, Monterey Co., Calif., 1 Nov. 1972, G. McDonald, 3.

Phidiana stearnsi

M75-6-0-1, La Jolla, San Diego Co., Calif., June 1975, J. R. Lance, 1. *CASIZ, Santa Barbara, Santa Barbara Co., Calif., Aug. 1966, J. E. Steinberg, 1.

Platydoris macfarlandi

*CASIZ 9511, Pismo Beach, San Luis Obispo Co., Calif., 23 Oct. 1950, W. E. Ripley *et al.*, 1, paratype. CASIZ 9512, Pismo Beach, San Luis Obispo Co., Calif., 23 Oct. 1950, W. E. Ripley *et al.*, 1, paratype.

Polycera atra

M70-2-26-7, Morro Bay, San Luis Obispo Co., Calif., 26 Feb. 1970, G. McDonald, 1. M70-3-31-1, Morro Bay, San Luis Obispo Co., Calif., 31 Mar. 1970, G. McDonald, 1. M70-10-22-4, Monterey Harbor, Monterey Co., Calif., 22 Oct. 1970, G. McDonald, 1. M70-10-28-2, Elkhorn Slough, Monterey Co., Calif., 28 Oct. 1970, G. McDonald, 1. M71-1-26-16, Morro Bay, San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 1. M71-7-25-9, Morro Bay, San Luis Obispo Co., Calif., 25 July 1971, G. McDonald, 1. M71-10-17-8, Morro Bay, San Luis Obispo Co., Calif., 17 Oct. 1971, G. McDonald, 2. M71-11-22-1, Morro Bay, San Luis Obispo Co., Calif., 22 Nov. 1971, G. McDonald, 2. *M72-3-12-1, Morro Bay, San Luis Obispo Co., Calif., 12 Mar., 1972, G. McDonald, 2. M72-11-1-4, Elkhorn Slough, Monterey Co., Calif., 1 Nov. 1972, G. McDonald, 1. M75-10-21-2, Elkhorn Slough, Monterey Co., Calif., 21 Oct. 1975, D. Ituarte, 2. M75-10-26-1, Morro Bay, San Luis Obispo Co., Calif., 26 Oct. 1975, G. McDonald, 2. M75-11-11-1, Elkhorn Slough, Monterey Co., Calif., 11 Nov. 1975, B. S. Antrim, 4. M0209, Elkhorn Slough, Monterey Co., Calif., 28 Oct. 1970, G. McDonald, 1.

Polycera hedgpethi

M70-11-8-3, Morro Bay, San Luis Obispo Co., Calif., 8 Nov. 1970, G. McDonald, 1. M71-6-28-1, Morro Bay, San Luis Obispo Co., Calif., 28 June 1971, R. A. Roller, 2. *M71-7-7-5, Morro Bay, San Luis Obispo Co., Calif., 7 July 1971, G. McDonald, 2. M71-9-20-1, Redondo Beach, Los Angeles Co., Calif., 20 Sept. 1971, R. S. Anderson, 1. M71-11-22-2, Morro Bay, San Luis Obispo Co., Calif., 22 Nov. 1971, G. McDonald, 1. M71-1-26-26, Morro Bay, San Luis Obispo Co., Calif., 26 Jan. 1971, R. A. Roller, 1.

Polycera tricolor

*M71-8-31-3, Santa Monica Bay, Los Angeles Co., Calif., 31 Aug. 1971, R. S. Anderson, 1. M71-8-31-4, Santa Monica Bay, Los Angeles Co., Calif., 31 Aug. 1971, R. S. Anderson, 1. M71-11-26-1, Santa Monica Bay, Los Angeles Co., Calif., 26 Nov. 1971, R. S. Anderson, 1. M71-11-26-2, Santa Monica Bay, Los Angeles Co., Calif., 26 Nov. 1971, R. S. Anderson, 1.

Polycera zosterae

*Prepared slide of radula, Friday Harbor, Wash., 23 Apr. 1973, R. A. Roller, 1.

Precuthona divae

M71-8-8-5, Asilomar, Monterey Co., Calif., 8 Aug. 1971, G. McDonald, 1. M71-11-2-6, Spooner's Cove, San Luis Obispo Co., Calif., 2 Nov. 1971, G. McDonald, 3. M71-11-4-1, Asilomar, Monterey Co., Calif., 4 Nov. 1971, D. Shonman, 1. M72-1-5-1, Dume Rock, Los Angeles Co., Calif., 5 Jan. 1972, R. S. Anderson, 1. M72-5-17-5, Carmel Pt., Monterey Co., Calif., 17 May 1972, G. McDonald, 2. M76-8-5-1, Lasqueti Island, B. C., Canada, 5 Aug. 1976, M. E. Anderson, 5. M0196, Asilomar, Monterey Co., Calif., 11 Dec. 1970, J. W. Nybakken, 1.

Rostanga pulchra

M70-4-3-5, Pirate's Cove, San Luis Obispo Co., Calif., 3 Apr. 1970, G. McDonald, 1. M70-11-11-1, Asilomar, Monterey Co., Calif., 11 Nov. 1970, G. McDonald, 1. M71-1-25-5, Pirate's Cove, San Luis Obispo Co., Calif., 25 Jan. 1971, G. McDonald, 1. M71-1-26-9, Hazard Can., San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 3. M71-1-27-1, Shell Beach, San Luis Obispo Co., Calif., 27 Jan. 1971, G. McDonald, 1. M71-6-13-1, Monterey Breakwater, Monterey Co., Calif., 13 June 1971, G. McDonald, 1. M71-11-1-3, Hazard Can., San Luis Obispo Co., Calif., 1 Nov. 1971, G. McDonald, 1. M71-12-2-9, Carmel Pt., Monterey Co., Calif., 2 Dec. 1971, G. McDonald, 2. M71-12-28-6, Dume Rock, Los Angeles Co., Calif., 28 Dec. 1971, R. S. Anderson, 2. M71-12-29-3, Pirate's Cove, San Luis Obispo Co., Calif., 29 Dec. 1971, G. McDonald, 2. M71-12-31-5, Shell Beach, San Luis Obispo Co., Calif., 31 Dec. 1971, G. McDonald, 2. M73-1-16-1, Asilomar, Monterey Co., Calif., 16 Jan. 1973, G. McDonald, 1. M73-6-5-9, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 3. M75-11-3-3, Pigeon Pt., San Mateo Co., Calif., 3 Nov. 1975, G. McDonald, 1. M76-2-21-1, Monastery Beach, Monterey Co., Calif., 21 Feb. 1976, A. K. McDonald, 3. M0163, Pt. Pinos, Monterey Co., Calif., 27 Apr. 1967, V. Mansfield, 1. M0308, Rocky Pt., Monterey Co., Calif., 14 May 1972, J. W. Nybakken, 1. M0309, Rocky Pt., Monterey Co., Calif., 14 May 1972, G. McDonald, 2.

Sclerodoris tanya
M74-3-27-1, Mission Bay, San Diego Co., Calif., 27 Mar. 1974, J. Patton, 1. *M73-9-0-1, Mission Bay, San Diego Co., Calif., Sept. 1973, M. Patton, 1.

Spurilla chromosoma
*M73-4-18-2, Puertecitos, Baja Calif., Mex., 18 Apr. 1973, M. Silberstein, 1. M75-1-26-3, Punta Mita, Nayarit, Mex., 26 Jan. 1975, G. McDonald, 1.

Spurilla olivae
M70-3-3-1, San Simeon, San Luis Obispo Co., Calif., 3 Mar. 1970, P. Clark, 1. M71-1-26-11, Morro Bay, San Luis Obispo Co., Calif., 26 Jan. 1971, G. McDonald, 1. M71-5-26-2, Asilomar, Monterey Co., Calif., 26 May 1971, R. S. Anderson, 1. M71-6-10-2, Monterey Breakwater, Monterey Co., Calif., 10 June 1971, G. McDonald, 1. *M71-9-14-4, Malibu, Los Angeles Co., Calif., 14 Sept. 1971, R. S. Anderson, 2. M71-10-22-2, Monterey Harbor, Monterey Co., Calif., 22 Oct. 1971, G. McDonald, 1. M71-11-22-10, Malibu, Los Angeles Co., Calif., 22 Nov. 1971, R. S. Anderson, 1. M73-4-7-1, Asilomar, Monterey Co., Calif., 7 Apr. 1973, G. McDonald, 1. M73-4-9-3, Carmel Pt., Monterey Co., Calif., 9 Apr. 1973, G. McDonald, 1. M0024, Monterey Harbor, Monterey Co., Calif., 21 Oct. 1970, G. McDonald, 1. M0217, Monterey Breakwater, Monterey Co., Calif., 18 May 1971, S. Pace, 1.

Tenellia adspersa
*M0580, Elkhorn Slough, Monterey Co., Calif., 3 June 1977, J. W. Cooper, 5.

Thordisa bimaculata
M74-4-3-1, Escondido Can., San Diego Co., Calif., 3 Apr. 1974, M. Patton, 1. *M75-6-26-2, La Jolla, San Diego Co., Calif., 26 June 1975, G. McDonald, 1.

Tochuina tetraquetra
M76-7-30-1, Roffey Island, B. C., Can., 30 July 1976, P. Lambert, 1. M0472, Monterey Bay, Calif., 10 Mar. 1974, G. McDonald, 1. M0500, Monterey Bay, Calif., 8 Oct. 1974, G. McDonald, 1.

Trapania velox
M71-2-1-1, Port San Luis, San Luis Obispo Co., Calif., 1 Feb. 1971, G. McDonald, 5. *M71-2-1-4, Port San Luis, San Luis Obispo Co., Calif., 1 Feb. 1971, G. McDonald, 5. M71-2-2-3, Port San Luis, San Luis Obispo Co., Calif., 2 Feb. 1971, G. McDonald, 7.

Triopha catalinae
M69-10-12-1, Port San Luis, San Luis Obispo Co., Calif., 12 Oct. 1969, G. McDonald, 1. M69-10-12-2, Port San Luis, San Luis Obispo Co., Calif., 12 Oct. 1969, G. McDonald, 1. M70-1-6-7, Sunset Palisades, San Luis Obispo Co., Calif., 6 Jan. 1970, G. McDonald, 1. M70-10-14-7, Asilomar, Monterey Co., Calif., 14 Oct. 1970, G. McDonald, 1. M71-5-25-9, Asilomar, Monterey Co., Calif., 25 May 1971, G. McDonald, 1. M71-7-7-1, Morro Bay, San Luis Obispo Co., Calif., 7 July 1971, G. McDonald, 1. M71-12-2-6, Carmel Pt., Monterey Co., Calif., 2 Dec. 1971, G. McDonald, 1. *M72-1-16-6, Monterey Breakwater, Monterey Co., Calif., 16 Jan. 1972, R. Hilaski, 1. M72-4-26-4, Monterey Breakwater, Monterey Co., Calif., 26 Apr. 1972, P. Clark, 1. M72-5-17-1, Carmel Pt., San Luis Obispo Co., Calif., 17 May 1972, G. McDonald, 1. M73-6-5-14, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 1. M75-11-2-12, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 2. M0161, Pigeon Pt., San Mateo Co., Calif., 30 Oct. 1966, J. W. Nybakken, 1. M0162, Carmel Pt., Monterey Co., Calif. 26 May 1967, R. Schinoke, 1. M0211, Asilomar, Monterey Co., Calif., 14 Oct. 1970, G. McDonald, 1.

Triopha occidentalis
M70-2-26-3, Morro Bay, San Luis Obispo Co., Calif., 26 Feb. 1970, G. McDonald, 1. M70-2-26-8, Morro Bay, San Luis Obispo Co., Calif., 26 Feb. 1970, G. McDonald, 1. M70-10-14-6, Asilomar, Monterey Co., Calif., 14 Oct. 1970, G. McDonald, 1. *M71-7-25-8, Morro Bay, San Luis Obispo Co., Calif., 25 July 1971, G. McDonald, 1. M72-1-9-1, Monterey Breakwater, Monterey Co., Calif., 9 Jan. 1972, R. Hilaski, 1. M73-11-11-1, Morro Bay, San Luis Obispo Co., Calif., 11 Nov. 1973, G. McDonald, 4. M73-11-11-4, Morro Bay, San Luis Obispo Co., Calif., 11 Nov. 1973, G. McDonald, 2. M75-6-25-5, La Jolla, San Diego Co., Calif., 25 June 1975, G. McDonald, 1. M0170, Monterey Bay, Calif., 20 Dec. 1970, G. McDonald, 1.

Triopha maculata
M69-10-26-2, Pirate's Cove, San Luis Obispo, Calif., 26 Oct. 1969, G. McDonald, 4. *M69-10-26-5, Pirate's Cove, San Luis

Obispo, Calif., 26 Oct. 1969, G. McDonald, 8. M70-7-18-8, Shell Beach, San Luis Obispo Co., Calif., 18 July 1970, G. McDonald, 3. M70-10-14-5, Asilomar, Monterey Co., Calif., 14 Oct. 1970, G. McDonald, 1. M70-10-16-2, Asilomar, Monterey Co., Calif., 16 Oct. 1970, G. McDonald, 1. M71-2-24-6, Morro Bay, San Luis Obispo Co., Calif., 25 Feb. 1971, G. McDonald, 1. M72-1-16-5, Monterey Breakwater, Monterey Co., Calif., 16 Jan. 1972, R. Hilaski, 1. M73-6-5-11, Asilomar, Monterey Co., Calif., 5 June 1973, G. McDonald, 1. M75-11-2-13, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 2. M75-11-4-3, Fanshell Beach, Monterey Co., Calif., 4 Nov. 1975, G. McDonald, 3. M75-10-5-4, Carmel Pt., Monterey Co., Calif., 5 Oct. 1975, G. McDonald, 1. M0175, Carmel Pt., Monterey Co., Calif., 15 Oct. 1970, J. W. Nybakken, 1.

Tritonia diomedea

M71-4-10-1, Monterey Bay, Calif., 10 Apr. 1971, G. McDonald, 1. M71-4-10-2, Monterey Bay, Calif., 10 Apr. 1971, G. McDonald, 1. M71-4-10-3, Monterey Bay, Calif., 10 Apr. 1971, G. McDonald, 1. M71-8-32-1, Santa Monica Bay, Los Angeles Co., Calif., Aug. 1971, P. Brophy, 1. M71-10-7-2, Marina del Rey, Los Angeles Co., Calif., 7 Oct. 1971, R. S. Anderson, 1. M72-1-7-2, Santa Monica Bay, Los Angeles Co., Calif., 7 Jan. 1972, R. S. Anderson, 1. M74-3-0-3, Monterey Bay, Calif., Mar. 1974, D. Rold, 1. M76-1-16-1, Monterey Bay, Calif., 16 Jan. 1976, B. Alford, 1. M0223, Monterey Bay, Calif., 5 Nov. 1970, L. Talent, 1. M0471, Monterey Bay, Calif., 13 Mar. 1974, G. McDonald, 1. M0494, Monterey Bay, Calif., 14 Aug. 1974, G. McDonald, 1.

Tritonia festiva

M69-10-26-3, Pirate's Cove, San Luis Obispo Co., Calif., 26 Oct. 1969, G. McDonald, 8. M69-10-26-12, Pirate's Cove, San Luis Obispo Co., Calif., 26 Oct. 1969, G. McDonald, 1. M70-12-12-3, Pigeon Pt., San Mateo Co., Calif., 12 Dec. 1970, G. McDonald, 1. M71-11-4-6, Carmel Pt., Monterey Co., Calif., 4 Nov. 1971, G. McDonald, 1. M73-6-2-1, Pescadero Pt., Monterey Co., Calif., 2 June 1973, G. McDonald, 1. M75-11-2-5, Carmel Pt., Monterey Co., Calif., 2 Nov. 1975, G. McDonald, 1. M75-11-3-2, Pigeon Pt., San Mateo Co., Calif., 3 Nov. 1975, G. McDonald, 7. M75-12-2-1, Pigeon Pt., San Mateo Co., Calif., 2 Dec. 1975, A. K. McDonald, 4. M0190, Pt. Pinos, Monterey Co., Calif., 26 Apr. 1967, V. Mansfield, 1. M0200, Pigeon Pt., San Mateo Co., Calif., 12 Dec. 1970, G. McDonald, 1. M0208, Asilomar, Monterey Co., Calif., 27 Apr. 1971, J. W. Nybakken, 1. M0216, Pirate's Cove, San Luis Obispo Co., Calif., 26 Oct. 1969, G. McDonald, 1. M0364, Carmel Pt., Monterey Co., Calif., 4 May 1973, G. McDonald, 1.

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FACTORS REGULATING THE DISTRIBUTION OF FRESH-WATER SNAILS (GASTROPODA) IN NORWAY[1]

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ABSTRACT

Environmental factors and snail faunas were investigated in about 1,000 lakes. Abundance of species was estimated according to a time-catch method.

Single factor analyses showed that 18 species tolerated total hardness values down to 1°dH, and 13 species down to 0.5°dH. The number of species tended to decrease with a decrease in pH. The drop in species number was particularly noticeable at about pH 6.0 and no species occurred in lakes with a pH below 5.2. Total hardness, pH, macro-vegetation in the water, and substratum showed a high correlation with the snail fauna and were considered primary factors of direct importance to the snails.

Bivariate analyses showed that both total hardness and pH affected the snail fauna *per se.* Lakes without gastropods tended to be more acid than those where snails were found, regardless of the level of total hardness. Furthermore, it appears that the snails' tolerance to low pH increases with increasing total hardness.

Stepwise multiple regression analyses demonstrated that total hardness and water vegetation were the two most significant independent variables that accounted for the number of species found and total time-catch abundance. Total hardness, water vegetation and pH were listed as steps 1, 2, 3, respectively, in the analyses for low total hardness lakes (≤ 1°dH).

The data suggest that acidification of lakes will adversely affect snail species. This implies that snails can be used as "early warning" organisms of acidification. Since snails are important fish-food items, their disappearance will cause a reduction in fish production.

Key words: acidification; distribution; ecology; environment; fresh-water snails; hydrogen-ion concentration; Norway; pH.

INTRODUCTION

Field investigations on fresh-water snails have recently been focused upon because they are sensitive to low pH and consequently are affected by acid precipitation. Fieldwork for the present study was begun in 1953, long before problems connected with acid rain became evident. Inspiration for this investigation came from studies of the habitats of fresh-water Mollusca in Britain by Boycott (1936) and those on the distribution patterns of fresh-water snails in South Sweden by Hubendick (1947). The main purpose of this study was to elucidate the importance of various environmental factors for the geographical and microgeographical distribution of fresh-water snails in Norway.

Some of the results from this investigation have already been published (J. Økland, 1969, 1979a, b; J. Økland & K. A. Økland, 1979). Most of the material collected is still being studied and these results will be published later. The present contribution considers mainly the snail fauna as a unit. It also includes much of the background material used in two short synopses dealing with the fresh-water fauna and acidification problems (J. Økland, 1980b; J. Økland & K. A. Økland, 1980). The possible effects of acidification are discussed.

MATERIALS AND METHODS

About 1,500 lakes, rivers, ponds, etc. were investigated from 1953 to 1973. The distribution of these localities is shown in Fig. 1. Only lakes, of which there were about 1,000, will be considered here. Two thirds of the lo-

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[1] Only slightly updated since presentation at the Seventh International Malacological Congress, 31 August–7 September, 1980.

FIG. 1. Map of Norway indicating the distribution of approximately 1,500 fresh-water localities where environmental parameters were recorded and bottom fauna investigated. Area S comprises southeastern Norway.

calities (including approx. 600 lakes) are located in the southeastern part of Norway. Within this fairly restricted area environmental conditions are extremely diverse.

Each locality was usually studied once, during the summer (1 June–30 September). In each lake only one habitat was investigated and defined as a stretch of shore about 200 m long. This habitat was described by ten environmental parameters and surveyed down to a depth of 1.5 m. The major collecting device among vegetation and on soft bottom was a sieve mounted on a rod about 1.8 m in length. Stones, branches and other items were also picked up by hand and inspected for snails.

The abundance of the snails was estimated according to a time-catch method, i.e. number of individuals collected per half-hour. The level of chemical environmental factors refers to the summer values from surface water.

RESULTS

Single Factor Analyses

Of the 27 species of fresh-water snails in Norway, 18 species tolerated total hardness ("calcium" content) down to 1°dH, which equals 10 mg "CaO"/l, and 13 species tolerated values down to 0.5°dH (Fig. 2). Tolerance is defined as the presence of a species in a lake with a recorded value for a particular environmental parameter, or presence in lakes with both the lower and higher values for that parameter. From Fig. 2 it appears that the snail fauna has no problems existing in a lake so long as the total hardness is above approximately 1°dH.

Fig. 3 indicates the number of species of snails which tolerate a given pH. Twenty species were found at pH 7.0. There was a decline in the number of species in lakes with a pH below 7.0 and a pronounced decrease in the number at about pH 6.0 and below.

Fig. 4 shows the correlation between environmental parameters and number of species of snails present. For those parameters exhibiting discontinuous variation abbreviations have sometimes been used to describe the category (see the caption). Details on the discrimination between categories will be given later in connection with a further treatment of these data. The data in Fig. 4 are self-explanatory. Therefore, only a few com-

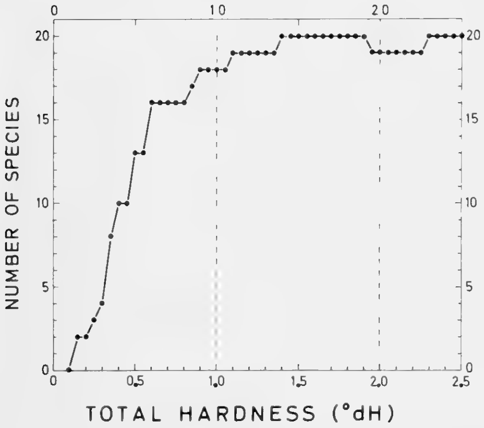

FIG. 2. Species tolerance to total hardness, range 0–2.5°dH (1°dH = 10 mg "CaO"/l) of snails. Material: 959 lakes investigated.

ments will be made. With regard to geology, lakes which belong to category A have from two to twelve species with an average of about six species, while those that belong to category D have a maximum of four species. Under the parameters with continuous variation it was found that at different elevations above sea level lowland lakes could have few or many species, while high-altitude lakes always had few.

The correlation between environmental parameters and total time-catch abundance of snails is shown in Fig. 5. The bar graphs represent the number of individuals collected during a half-hour period. Among those lakes which are influenced by unaltered Cambro-Silurian rocks (IIA), there was a fairly large number of the lakes investigated in which more than 150 individuals were collected. However, in those lakes influenced by strongly altered Cambro-Silurian rocks (C), or by Precambrian rock (D), the number of lakes with such a high population density was negligible.

Pearson correlation matrices were made for ten environmental parameters and number of species of snails (Table 1) and total time-catch abundance of snails (Table 2). In order to include parameters with discontinuous variation (such as geology) into the calculations, categories of such parameters were given numbers from one and upwards, ranking the categories from favourable to unfavourable for the snails using the frequency deviation method described by J. Økland (1969, 1979a). Correlation coefficients for such parameters versus snail parameters were therefore all negative.

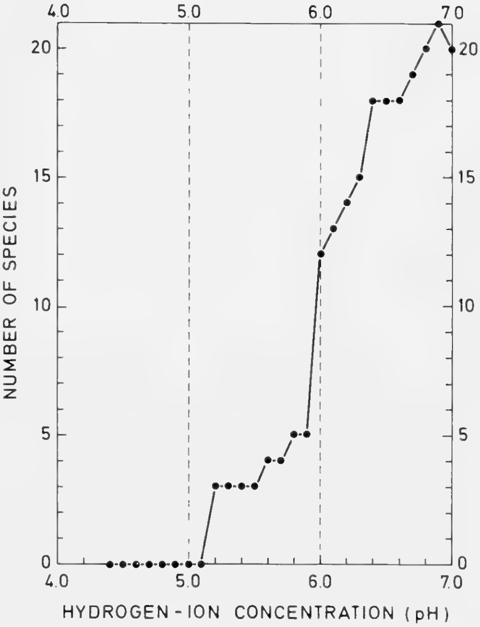

FIG. 3. Species tolerance to pH range 4.0 to 7.0 of snails from the same lakes as in Fig. 2.

The bottom row of each of the two parts in Tables 1–2 shows how the snail parameters are correlated with the various environmental parameters. The correlation coefficients describing correlation between environmental factors with continuous variation (pH, total hardness (=log°dH), elevation, and temperature give some idea of the types of lakes which were studied.

Table 3 compares Pearson and Kendall correlation coefficients. Since the material is large (594 lakes) significant values are often obtained. Therefore major attention should be focused on the magnitude of the coefficients and not on significance/non-significance. Total hardness, macro-vegetation in the water, pH, and substratum have high correlation coefficients and are primary factors. High correlations are also found between the snail fauna and two secondary factors, i.e. geology and terrestrial vegetation.

Bivariate Analyses

Cursory examination of Fig. 6 which represents low-calcium lakes in southeastern

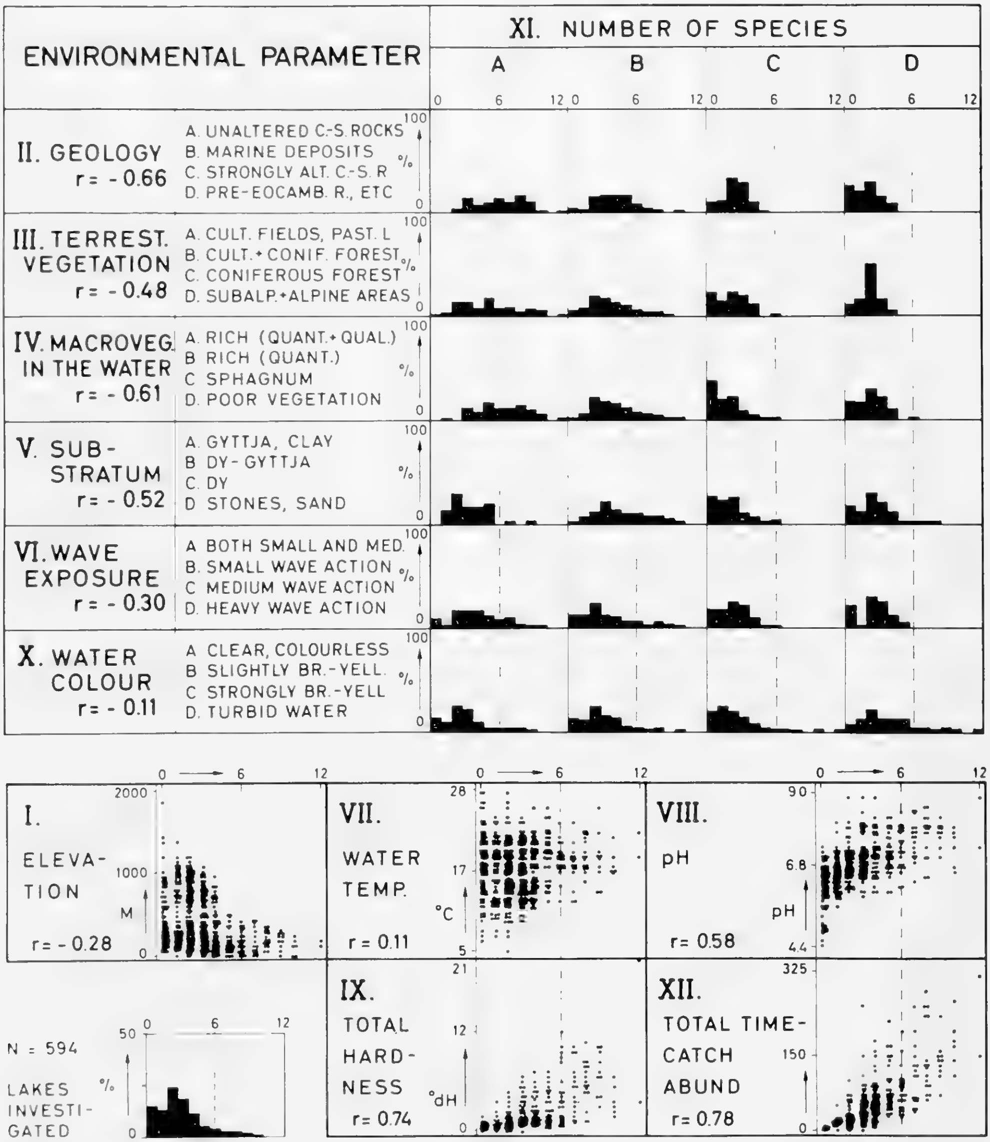

FIG. 4. Correlations of ten environmental parameters and number of species of snails found in 594 lakes in southeastern Norway. The upper part of the figure represents six parameters with non-continuous variation (geology, etc.) and the lower part four parameters with continuous variation (elevation, etc.). The frequency distribution of investigated lakes according to number of species present is presented in the lower left and the total time-catch abundance correlated with number of species is found in the bottom right corner. The Pearson correlation coefficient (r) is indicated for each of the 11 sets of correlations. Abbreviations for categories representing parameters with non-continuous variation: For: *geology:* A. Unaltered Cambro-Silurian rocks, C. Strongly altered Cambro-Silurian rocks, D. Precambrian rocks, and Permian plutonic and effusive rocks of the Oslo region. For *terrestrial vegetation:* A. Cultivated fields, pasture lands, B. Both cultivated fields and coniferous forests. For *water colour:* B. Slightly brownish-yellowish water, C. Strongly brownish-yellowish water.

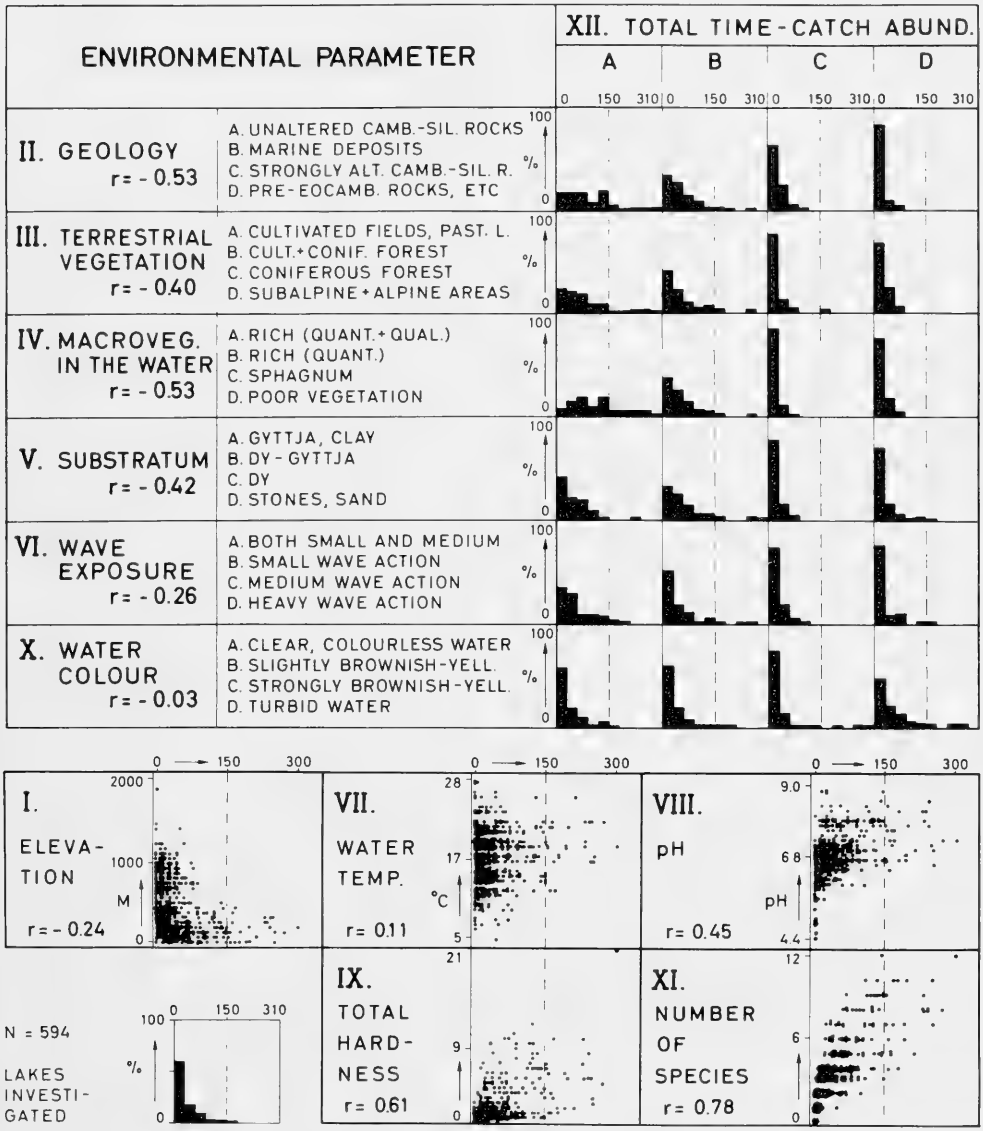

FIG. 5. Correlations of ten lake parameters with total time-catch abundance of snails (number of individuals collected per half-hour). The parameters and calculations are the same as those described in Fig. 4.

Norway shows that most of the lakes in which snails were found were in the pH range 6.0 to 7.0 and had a total hardness above 0.25° dH. Lakes without gastropods tended to be more acidic than those in which snails were present, regardless of the level of total hardness.

Furthermore, lakes in the pH range 6.0–7.0 without gastropods tended to have a lower total hardness than those in which snails were present.

Study of data from all parts of Norway revealed that nine of the eleven most commonly found species increased their tolerance to

TABLE 1. Pearson correlation matrices for ten lake parameters and number of species of snails in lakes from southeastern Norway.

ALL LAKES. N = 594.

		pH 1	Log dH 2	Elevation 3	Geology 4	Terrestrial vegetation 5	Macro-vegetation 6	Substratum 7	Wave exposure 8	Tempera-ture 9	Colour 10
pH	1	1.00									
Log dH	2	.70	1.00								
Elevation	3	−.02	−.27	1.00							
Geology	4	−.56	−.72	.27	1.00						
Terrestrial vegetation	5	−.23	−.42	.66	.48	1.00					
Macro-vegetation	6	−.40	−.50	.26	.56	.52	1.00				
Substratum	7	−.34	−.44	.25	.51	.43	.60	1.00			
Wave exposure	8	−.19	−.31	.15	.26	.28	.30	.17	1.00		
Temperature	9	.04	.15	−.56	−.21	−.44	−.16	−.08	−.28	1.00	
Colour	10	−.15	−.04	.09	.14	.18	.20	.21	.03	−.07	1.00
No. species	11	.58	.74	−.28	−.66	−.48	−.61	−.52	−.30	.11	−.11

LOW TOTAL HARDNESS LAKES (< 1°dH). N = 403.

		pH 1	Log dH 2	Elevation 3	Geology 4	Terrestrial vegetation 5	Macro-vegetation 6	Substratum 7	Wave exposure 8	Tempera-ture 9	Colour 10
pH	1	1.00									
Log dH	2	.40	1.00								
Elevation	3	.11	−.32	1.00							
Geology	4	−.22	−.33	.17	1.00						
Terrestrial vegetation	5	−.07	−.37	.71	.39	1.00					
Macro-vegetation	6	−.27	−.24	.13	.42	.36	1.00				
Substratum	7	−.20	−.22	.16	.37	.32	.56	1.00			
Wave exposure	8	−.02	−.17	.11	.10	.19	.12	.02	1.00		
Temperature	9	−.13	.10	−.57	−.13	−.43	−.03	.02	−.28	1.00	
Colour	10	−.19	−.06	.04	.20	.18	.26	.22	.04	−.03	1.00
No. species	11	.45	.53	−.20	−.41	−.36	−.45	−.39	−.13	−.05	−.18

TABLE 2. Pearson correlation matrices for ten lake parameters and total time-catch abundance of snails in lakes from southeastern Norway.

ALL LAKES. N = 549.

		pH 1	Log dH 2	Elevation 3	Geology 4	Terrestrial vegetation 5	Macro-vegetation 6	Substratum 7	Wave exposure 8	Temper-ature 9	Colour 10
pH	1	1.00									
Log dH	2	.70	1.00								
Elevation	3	−.02	−.27	1.00							
Geology	4	−.56	−.72	.27	1.00						
Terrestrial vegetation	5	−.23	−.42	.66	.48	1.00					
Macro-vegetation	6	−.40	−.50	.26	.56	.52	1.00				
Substratum	7	−.34	−.44	.25	.51	.43	.60	1.00			
Wave exposure	8	−.19	−.31	.15	.26	.28	.30	.17	1.00		
Temperature	9	.04	.15	−.56	−.21	−.44	−.16	−.08	−.28	1.00	
Colour	10	−.15	−.04	.09	.14	.18	.20	.21	.03	−.07	1.00
Time-catch	11	.45	.61	−.24	−.53	−.40	−.53	−.42	−.26	.11	−.03

LOW TOTAL HARDNESS LAKES (≤1°dH). N = 403.

		pH 1	Log dH 2	Elevation 3	Geology 4	Terrestrial vegetation 5	Macro-vegetation 6	Substratum 7	Wave exposure 8	Temper-ature 9	Colour 10
pH	1	1.00									
Log dH	2	.40	1.00								
Elevation	3	.11	−.32	1.00							
Geology	4	−.22	−.33	.17	1.00						
Terrestrial vegetation	5	−.07	−.37	.71	.39	1.00					
Macro-vegetation	6	−.27	−.24	.13	.42	.36	1.00				
Substratum	7	−.20	−.22	.16	.37	.32	.56	1.00			
Wave exposure	8	−.02	−.17	.11	.10	.19	.12	.02	1.00		
Temperature	9	−.13	.10	−.57	−.13	−.43	−.03	.02	−.28	1.00	
Colour	10	−.19	−.06	.04	.20	.18	.26	.22	.04	−.03	1.00
Time-catch	11	.38	.40	−.16	−.32	−.27	−.34	−.27	−.08	−.04	−.10

TABLE 3. Pearson and Kendall correlation coefficients from one-factor analyses of environmental parameters correlated with snail parameters (number of species and time-catch abundance). Data from 594 lakes in southeastern Norway. Kendall values are put in parentheses. Pearson correlations are significant $\neq 0$ at 0.001 level if $|r| \geq 0.126$ (symbol ●), at 0.05 level if $|r| \geq 0.067$ (assuming normal distributions). Kendall correlations significant $\neq 0$ at 0.001 level if $|t| \geq 0.11$ (symbol ●), at 0.05 level if $|t| \geq 0.05$. All tests are one-tailed.

	Number of species		Total time-catch abundance	
Environmental parameter	Pearson r	Kendall t	Pearson r	Kendall t
High Correlations				
A. *PRIMARY FACTORS (IN THE WATER)*				
Total hardness	0.74●	(0.56●)	0.61●	(0.49●)
Macro-vegetation	−0.61●	(−0.49●)	−0.53●	(−0.45●)
pH	0.58●	(0.47●)	0.45●	(0.41●)
Substratum	−0.52●	(−0.40●)	−0.42●	(−0.34●)
B. *SECONDARY FACTORS (OUTSIDE THE WATER)*				
Geology	−0.66●	(−0.51●)	−0.53●	(−0.43●)
Terrestrial vegetation	−0.48●	(−0.39●)	−0.40●	(−0.33●)
Low Correlations				
Wave exposure	−0.30●	(−0.22●)	−0.26●	(−0.23●)
Elevation	−0.28●	(−0.21●)	−0.24●	(−0.16●)
No or negligible Correlations				
Water temperature	0.11	(0.05)	0.11	(0.02)
Water colour	−0.11	(−0.11)	−0.03	(−0.06)

low pH as the total hardness level increased. This pattern, as well as tendencies described in connection with Fig. 6, is shown in Fig. 7.

Multiple Regression Analyses

Multiple regression analyses may be used to show the relative importance of environmental factors to explain variability in the data. Using stepwise multiple regression analyses, where the number of species and total time-catch abundance, respectively, were dependent variables and the ten environmental parameters independent variables, ranking lists of the various environmental factors were obtained. Table 4 gives results for number of species and Table 5 for time-catch abundance. An increase in r reflects improvement of the model by the addition of more parameters. Total hardness and macro-vegetation in the water had the greatest explicatory value both for "all lakes" and "low total hardness lakes" in both tables. pH appears in Step 3 in the low calcium groups, but is insignificant for "all lakes."

DISCUSSION

Calcium concentration and pH level are important factors for determining presence and well-being of snails (Boycott, 1936; Hubendick, 1947; Aho, 1966, 1978; J. Økland, 1969, 1979a, b; J. Økland & K. A. Økland, 1979). The decline in species number with decreasing values for total hardness (Fig. 2) and pH (Fig. 3) is, therefore, in agreement with previous information.

The concept "species tolerance" was used in relation to values of total hardness and pH of lakes. If a given species was collected from a lake with a particular parameter value, it was considered to tolerate this value or conditions associated with this value. When the species was not found in lakes where the parameter was below a given value, and a sufficiently large number of lakes below this value were investigated with negative results, we assumed that this condition was not tolerated by the species. In those cases where the species was recorded in only one or a few lakes having the lowest value of a particular

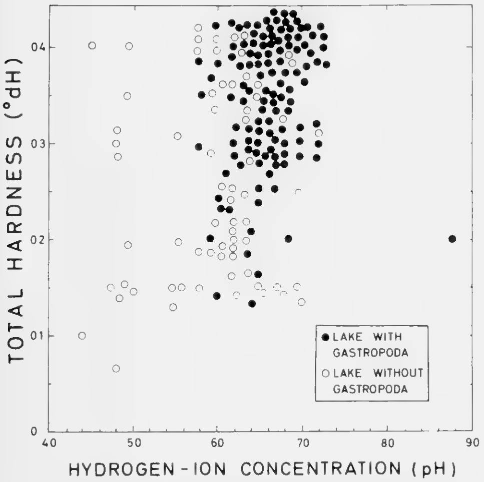

FIG. 6. Presence/absence of snails in low calcium lakes of southeastern Norway with a given pH and total hardness.

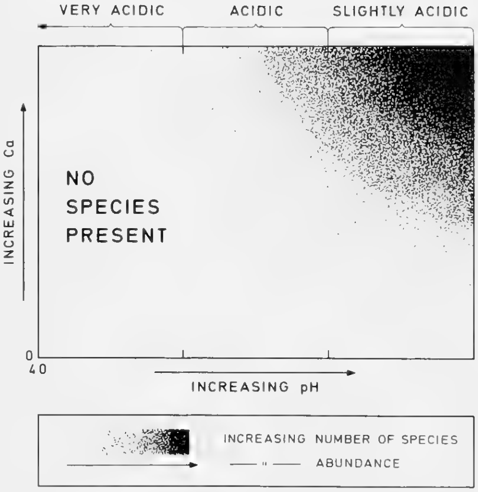

FIG. 7. Schematic diagram of lakes with measured values for pH and calcium concentration containing widespread species of snails (N = 9), small mussels (N = 10), and the crustacean *Gammarus lacustris*. Approximately 1,000 lakes investigated.

parameter, these lakes were considered to be *marginal habitats* for the species. The curves in Figs. 2–3 represent such marginal habitats.

The bivariate analyses in Fig. 7 allow us to make some general statements about the dependence of the snail fauna on pH and calcium concentration. Since this figure is based on a large amount of data for abundance of widespread species from all parts of Norway, it includes data from Fig. 6 which only represents presence/absence data from a restricted part of the calcium spectrum and limited to southeastern Norway.

We note that at a given value of calcium the number of species and abundance increase with increasing pH.

At a given pH value the number of species, and abundance, increase with increasing calcium content.

It may, therefore, be concluded that both pH and calcium concentration are important factors, *per se,* in spite of the fact that they are correlated (Table 1).

Marginal habitats for the snails are represented by dots bordering the white area. It is evident that these dots form a curved line which extends further to the left—towards more acid water—when calcium concentration is medium or high, and further downwards—towards lower calcium concentration—when pH is medium or high. This implies that in those habitats where pH is minimal for a given species, total hardness is above minimum—and in those habitats where total hardness is minimal, pH is above minimum. The species accordingly does not tolerate more than one minimal factor at the same time. If one factor approaches the tolerance limit of the species, other factors have to be favourable.

The single factor analyses in Table 3 places those factors showing a high correlation with the snail fauna into the following groups: *Primary factors,* those directly influencing the snails (total hardness, macro-vegetation in the water, pH, and substratum), and *Secondary factors,* those which affect the species indirectly through other factors for example: geology influences total hardness. Following a model for direct/indirect action of environmental factors on the snail fauna (J. Økland, 1979a) the effect of a given factor was considered a direct one when its action did not necessarily involve a step through any of the other factors.

It also appears from Table 3 that wave exposure and elevation above sea level had low correlations with the snail fauna, while no or negligible correlations were found for water temperature and water colour.

Correlations may reflect causality either directly between the given environmental fac-

TABLE 4. Stepwise multiple regression analyses of number of species of snails (dependent variable) and ten lake parameters (independent variables) from 594 lakes in southeastern Norway ("all lakes"), and from low total hardness lakes (N = 403). The parameters are: (1) elevation above sea level, (2) water temperature, (3) geology, (4) terrestrial vegetation, (5) macro-vegetation in the water, (6) substratum, (7) wave exposure, (8) water colour, (9) total hardness (log°dH), and (10) hydrogen-ion concentration (pH). Sequence and selection of environmental parameters are listed according to decreasing prediction value.

		r	Percent of variability accounted for
ALL LAKES	Step 1. Log°dH*	0.74	54.7
	Step 2. Macro-vegetation	0.79	62.0
	Step 3. Geology	0.79	63.0
	Step 4. Substratum	0.80	63.7
	Step 5. pH	0.80	64.1
	Step 6. Terr. vegetation	0.80	64.6
	Step 7. Water temp.	0.81	65.0
	Step 8. Wave exposure	0.81	65.2
	Step 9. Elevation	0.81	65.4
LOW TOTAL HARDNESS LAKES (≤1°dH)	Step 1. Log°dH*	0.53	27.9
	Step 2. Macro-vegetation	0.63	39.1
	Step 3. pH	0.66	43.0
	Step 4. Geology	0.67	44.7
	Step 5. Substratum	0.68	45.7
	Step 6. Water temp.	0.68	46.2
	Step 7. Elevation	0.69	47.7
	Step 8. Wave exposure	0.69	48.1

* Total hardness ("calcium").

tor and the snails or indirectly through other factors which are influenced by the environmental factor in question. Causality can only be proven, however, by experimentation or corroborated by knowledge of the ecology and physiology of the species.

It is of special importance to verify causality for the primary factors, which had high correlations with the snail fauna. Low values of total hardness may be critical, since snails need calcium for their shells. Limnic organisms (fish) are affected by low pH through changes in the ion balance, creating lower concentrations of Na and Cl in the blood plasma with secondary effects at the cellular level (Leivestad *et al.*, 1976; Leivestad &

TABLE 5. Stepwise multiple regression analysis of total time-catch abundance of snails (dependent variable) and ten lake parameters (independent variables) of 594 lakes in southeastern Norway ("all lakes"), and low total hardness lakes (N = 403). Same parameters etc. as indicated in Table 4.

		r	Percent of variability accounted for
ALL LAKES	Step 1. Log°dH*	0.61	37.3
	Step 2. Macro-vegetation	0.66	44.1
	Step 3. Terr. vegetation	0.67	44.5
	Step 4. Water colour	0.67	44.8
	Step 5. Substratum	0.67	45.1
LOW TOTAL HARDNESS LAKES (≤1°dH)	Step 1. Log°dH*	0.40	15.7
	Step 2. Macro-vegetation	0.47	21.9
	Step 3. pH	0.51	25.9
	Step 4. Geology	0.52	27.2
	Step 5. Elevation	0.53	27.8
	Step 6. Water temp.	0.54	29.3

* Total hardness ("calcium").

Muniz, 1976). Much work on the physiology of the snails seems to be needed in order to understand how low calcium concentration and low pH affect the snail fauna. Dussart & Kay (1980) point out that the precise way in which fresh-water gastropods respond to their chemical environment at a cellular level has yet to be discovered.

The importance of the macro-vegetation is probably connected to different ecological mechanisms. A rich growth of macro-vegetation creates sheltered conditions and reduces wave action. It also provides organic matter to feed on, including attached algae, and suitable substratum to crawl upon. Different types of macro-vegetation reflect different trophic states which in indirect ways (through chemical factors, etc.) may affect the snail fauna.

Substratum also had a high correlation with the snail fauna. Gyttja and dy-gyttja represent more productive lakes. Algae growing on these types of sediment may serve as food for several species, a few also using the organic material in the substratum *per se.* A loose dy sediment is obviously a disadvantage for all species which to some extent are in need of a substratum to crawl upon.

From the stepwise regression analyses (Tables 4 and 5), it appears that regarding "all lakes" most of the variability in the data can be explained by two environmental factors, total hardness and macro-vegetation in the water. If only low-calcium lakes are considered (bottom part of the tables), these same two factors top the list, but pH should not be disregarded. These three factors together account for much of the variation in the data. The increase in importance of pH in the groups of low total hardness lakes is reasonable, since the effect of pH is connected with acid water which almost always has a hardness value below 1°dH.

The sequence of the first three environmental factors in the low total hardness lakes in Tables 4–5 (total hardness, macro-vegetation, pH) suggests that a change in pH will affect the snail populations. In a situation of acidification, a slight increase in total hardness has been observed in some lakes. If macrovegetation should change, it would be towards adverse conditions for the snails. A slight increase in total hardness is, however, not sufficient to maintain snail populations unaffected during acidification since the number of species tolerating given values for pH decreases drastically with decreasing pH (Fig. 3). Since we have seen that pH affects the snail fauna *per se* and not through total hardness with which it is correlated we conclude that decreasing pH may cause snails to disappear.

Thousands of lakes both in Europe and in North America have been acidified during the last decades mainly by the impact of acid precipitation (Drabløs & Tollan, 1980). In Norway more than one thousand lakes have lost their fish populations (Sevaldrud *et al.,* 1980). Only low-calcium lakes become acidified, particularly those with total hardness below 0.5°dH, but sometimes lakes with values up to 1°dH (Henriksen, 1979; J. Økland, 1980a; J. Økland & K. A. Økland, 1980). Since 13 of the Norwegian species of fresh-water snails tolerate hardness values down to 0.5°dH, at least one-half of the Norwegian species may be influenced, if acidification continues.

Snails form an important part of the diet of fresh-water fish. They are more sensitive to low pH than fish, which means that they will disappear before the fish become extinct. It has been suggested that the disappearance of snails will reduce fish production (J. Økland & K. A. Økland, 1980). Snails may also be used as biological indicators or "early warning" organisms for monitoring acidification (J. Økland, 1980b).

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REFERENCES CITED

AHO, J., 1966, Ecological basis of the distribution of the littoral freshwater molluscs in the vicinity of Tampere, South Finland. *Annales Zoologici Fennici,* 3: 287–322.

AHO, J., 1978, Freshwater snail populations and the equilibrium theory of island biogeography. II. Relative importance of chemical and spatial variables. *Annales Zoologici Fennici,* 15: 155–164.

BOYCOTT, A. E., 1936, The habitats of fresh-water Mollusca in Britain. *Journal of Animal Ecology,* 5: 116–186.

DRABLØS, D. & TOLLAN, A., eds., 1980, *Ecological impact of acid precipitation.* Proceedings of an international conference, Sandefjord, Norway, March 11–14, 1980. SNSF project, Norway, 383 p.

DUSSART, G. & KAY, R., 1980, Relationships between water chemistry and respiration rate in several populations of *Lymnaea peregra* Müller (Gastropoda: Mollusca). *Hydrobiologia,* 69: 57–65.

HENRIKSEN, A., 1979, A simple approach for identifying and measuring acidification of freshwater. *Nature,* 278: 542–545.

HUBENDICK, B., 1947, Die Verbreitungsverhältnisse der limnischen Gastropoden in Südschweden. *Zoologiska Bidrag från Uppsala,* 24: 419–559.

LEIVESTAD, H., HENDREY, G., MUNIZ, I. P. & SNEKVIK, E., 1976, Effects of acid precipitation on freshwater organisms. In: BRÆKKE, F. H., ed., *Impact of acid precipitation on forest and freshwater ecosystems in Norway.* SNSF project FR6/76, Oslo-Ås, Norway, p. 87–111.

LEIVESTAD, H. & MUNIZ, I. P., 1976, Fish kill at low pH in a Norwegian river. *Nature,* 259: 391–392.

ØKLAND, J., 1969, Distribution and ecology of the fresh-water snails (Gastropoda) of Norway. *Malacologia,* 9: 143–151.

ØKLAND, J., 1979a, Distribution of environmental factors and fresh-water snails (Gastropoda) in Norway: use of European Invertebrate Survey principles. *Malacologia,* 18: 211–222.

ØKLAND, J., 1979b, Kalkinnhold, surhetsgrad (pH) og snegler i norske innsjøer. Abstract in English: Total hardness, hydrogen-ion concentration (pH) and Gastropoda in Norwegian lakes, with remarks on acidification of watercourses. *Fauna (Oslo),* 32: 96–111.

ØKLAND, J., 1980a, Acidification in 50 Norwegian lakes. *Nordic Hydrology,* 11: 25–32.

ØKLAND, J., 1980b, Environment and snails (Gastropoda): studies of 1,000 lakes in Norway. In DRABLØS, D. & TOLLAN, A., eds., *Ecological impact of acid precipitation.* Proceedings of an international conference, Sandefjord, Norway, March 11–14, 1980. SNSF project, Oslo-Ås, Norway, p. 322–323.

ØKLAND, J. & ØKLAND, K. A., 1979, Use of freshwater littoral fauna for environmental monitoring: aspects related to studies of 1,000 lakes in Norway. In: *The Use of Ecological Variables in Environmental Monitoring. The National Swedish Environment Protection Board, Report PM* 1151, p. 168–183.

ØKLAND, J. & ØKLAND, K. A., 1980, pH level and food organisms for fish: studies of 1,000 lakes in Norway. In DRABLØS, D. & TOLLAN, A., eds., *Ecological impact of acid precipitation.* Proceedings of an international conference, Sandefjord, Norway March 11–14, 1980. SNSF project, Oslo-Ås, Norway, p. 326–327.

SEVALDRUD, I. H., MUNIZ, I. P. & KALVENES, S., 1980, Loss of fish populations in southern Norway. Dynamics and magnitude of the problem. In DRABLØS, D. & TOLLAN, A., eds., *Ecological impact of acid precipitation.* Proceedings of an international conference, Sandefjord, Norway, March 11–14, 1980. SNSF project, Oslo-Ås, Norway, p. 350–351.

POSTSCRIPT

TOTAL HARDNESS, CALCIUM AND MAGNESIUM

Values for total hardness represent calcium plus magnesium. For 514 lakes, calcium and magnesium were also measured separately. Based on this material, average concentration of calcium and magnesium in Norwegian lakes can be calculated for given values of total hardness. Some examples are given below.

Given values for total hardness		Calculated empirically	
°dH (1°dH = 10 mg "CaO"/l)	"CaO" mg/l	Ca mg/l	mg/l
0.2	2	1.2	0.2
0.4	4	2.2	0.4
0.6	6	3.2	0.7
0.8	8	4.2	0.9
1.0	10	5.2	1.2
5.0	50	30.8	3.0
10.0	100	62.4	5.6
20.0	200	125.6	10.6

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THE PREDATORY BEHAVIOUR OF *MARISA CORNUARIETIS* ON EGGS AND NEONATES OF *BIOMPHALARIA GLABRATA*, THE SNAIL HOST OF *SCHISTOSOMA MANSONI*[1]

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ABSTRACT

The predatory behaviour of *Marisa cornuarietis* (L.) was evaluated as an agent for the control of *Biomphalaria glabrata* (Say). The results show that predation by *Marisa* is influenced both by endogenous and exogenous factors. Although some *Marisa* preyed deliberately on *Biomphalaria* eggs and juveniles, a minority did not do so during the experiment. There is evidence that *Marisa* predation tends to increase with experience, age and onset of sexual maturity. Mature females ingest significantly more eggs than mature males. Predation is also enhanced by the presence of plant food in flow systems but depressed by heterotypic conditioning. The possible cause of these effects is discussed. The above considerations, and the fact that the rate of predation by *Marisa* does not increase with egg density, shows that *Marisa* is not a good predator. The conclusion that *Marisa* can only be effective as a predator if it is present at high densities, of about 1 per 150–300 cm^2, is supported by field observations.

INTRODUCTION

The feeding behaviour of freshwater snails that serve as hosts of human schistosomes, and those proposed as agents for their control, has received little detailed attention (Ferguson, 1977; Brown, 1980). Whilst it is generally assumed that freshwater pulmonate and prosobranch snails feed mainly on living or dead plant material as well as small animals associated with epilithic and epiphytic algae (World Health Organization, 1965), recent detailed studies (Ndifon, 1979; Ndifon & Ukoli, 1980) have shown that animal material, including protozoa, gastrotrichs, copepods, ostracods, rotifers, nematodes and even chironomid larvae, may become dominant in the diets of the pulmonate *Bulinus globosus* (Morelet), at certain times at least. There is also evidence that snail species, such as *Marisa cornuarietis* (L.), *Helisoma duryi* (Wetherby), *Physa acuta* (Drap.) and *Pomacea* spp., are predators, as eggs and juveniles of pulmonate snails feature in their diets (Oliver-Gonzalez *et al.,* 1956; Frandsen & Madsen, 1979; Paulinyi & Paulini, 1972; Ferguson, 1977). Before their potential as control agents can be properly evaluated, it is important that their predatory behaviour be better understood.

The present paper concerns the predatory behaviour of *Marisa cornuarietis* and attempts to answer the following questions. Firstly, does *Marisa* deliberately feed on the eggs and juveniles of the snail hosts? According to Oliver-Gonzalez *et al.* (1956) and Chernin *et al.* (1956) the ingestion of egg masses is incidental while *Marisa* is feeding on plant material on which they have been deposited. Demian & Lutfy (1965, 1966) take the opposite view and claim that predation by *Marisa* is intentional, although no quantitative evidence is provided. Secondly, is *Marisa* an obligate omnivore, or does it cease to feed on eggs when plant food is present in abundance? Thirdly, to what extent is predation by *Marisa* dependent on media conditioning, previous experience, age and sex? Fourthly, does *Marisa* show any of the attributes of an efficient predator?

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MATERIALS AND METHODS

The methods used for culturing the albino, Venezuelan strain of *Biomphalaria glabrata* (Say), and the Puerto Rican strain of *Marisa cornuarietis,* have been described by Thomas (1973) and Cedeño-León (1975). Both species were maintained in 40 aquaria containing aerated, filtered tap-water maintained at a temperature of 26 ± 1°C and a photoperiod of 12 hr light and 12 hr dark. They were fed lettuce daily. As *Marisa* tends to pollute its environment, the tap-water was replaced by means of a 'drip-feed' (8 ml min^{-1}) and an overflow.

The experiments described below were designed to answer the questions raised above.

1. The influence of experience, and location of egg masses, on predation by *Marisa*

In the first treatment six juvenile *Marisa* 12 ± 2 mm in shell diameter, which had previously coexisted with *Biomphalaria* for three months, were placed, together with an equal number of adult *Biomphalaria* (14 ± 1 mm), in plastic buckets containing 1.2 l of Standard Snail Water (SSW2) (Thomas *et al.*, 1975). The second treatment resembled the first in all respects, except that the *Marisa* had not previously encountered eggs, juveniles or adults of *Biomphalaria.* The snails in the first and second treatments were designated experienced and non-experienced predators respectively. As a control, six adult *Biomphalaria* in the same size range as those used in the treatments were placed in 600 ml of SSW2 in a plastic bucket. Each treatment and control were replicated six times.

The SSW2 was changed every three days. An excess of lettuce was provided as food. Uneaten remains were removed each day before adding new portions. The number of egg masses laid on different kinds of substrates, the total number of egg masses and the number of juvenile *Biomphalaria* present were counted at three day intervals for a period of 15 days.

2. The influence of egg deposition substrate and media conditioning on predation by *Marisa*

If egg masses are only consumed accidentally during feeding, then obviously they should be safe from attack if laid on non-food substrates. To test this, 14 plastic buckets, each containing 10 adult *Biomphalaria* fed on an excess of lettuce, were left for 4 days in an environmental unit at a temperature of 26 ± 1°C. During this period they deposited between 12 and 20 egg masses in each of the containers. The snails were then removed, and the number of egg masses in each container recorded. The water was carefully decanted and replaced by 600 ml of fresh SSW2. Six non-experienced juvenile *Marisa* (14–17 mm shell diameter) were introduced into each of ten buckets and lettuce was added in excess. Four buckets without snails were used as controls. The media were changed every third day.

The number of *Biomphalaria* egg masses and juveniles present in each container was counted every day for seven days.

3. Influence of experience and *Biomphalaria* egg density on egg predation by juvenile *Marisa*

In these experiments the functional response (Solomon, 1949; Holling, 1959a, b) was investigated by measuring the extent of predation on varying numbers of *Biomphalaria* eggs by individually isolated, experienced and non-experienced juvenile *Marisa* (shell diameter 17–23 mm).

To familiarise *Marisa* with *Biomphalaria* eggs, two groups of 20 juvenile *Marisa* were maintained separately at 26 ± 1°C in the aerated flow-through aquaria previously described. Approximately 500 *Biomphalaria* egg masses, deposited on floating transparent plastic sheets, were introduced into each aquarium. Initially, the snails were deprived of food and remained on the sediment, making no attempt to prey on the egg masses. From the fourth day onwards they were provided with lettuce below the level deemed to be in excess. As a result, all the lettuce was eaten by the end of the day. After this change in feeding regime, the rate of consumption of egg masses increased from zero to a stable level of 1.81 ± 0.19 egg masses per *Marisa* per day. The snails were maintained under these conditions for eight weeks.

After this treatment, the experienced *Marisa* were placed individually, with a 1 cm diameter lettuce disc, in buckets containing approximately 50, 100, 150, 200 and 250 *Biomphalaria* eggs in 200 ml SSW2. Each treatment was replicated four times. A parallel experiment was set up with non-experienced snails. The experimental snails were maintained under the standard conditions already described. The number of eggs remaining uneaten was counted after 24 hr.

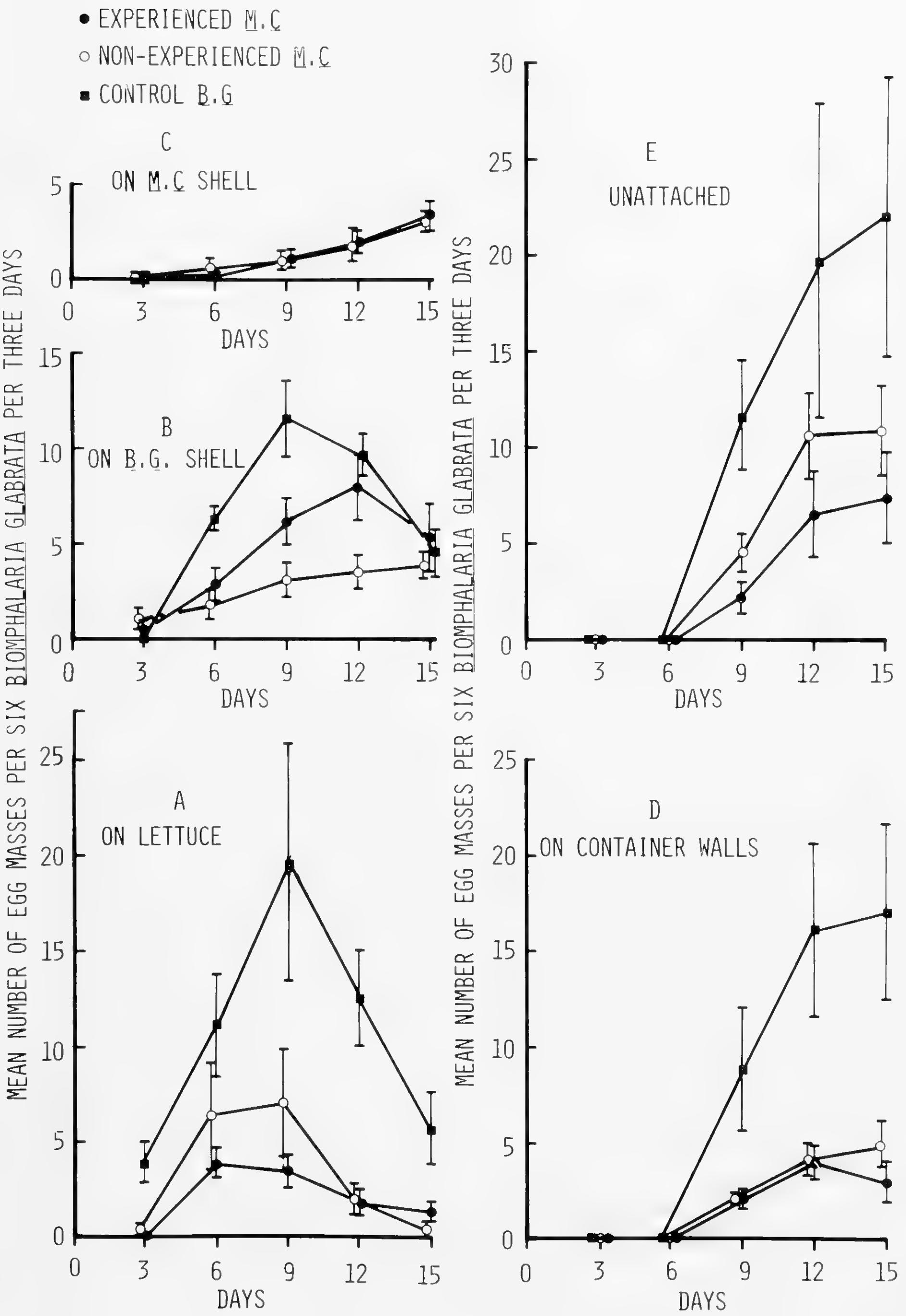

FIG. 1. The cumulative mean number ($\bar{X}$ ± S.E.) of egg masses laid by six *Biomphalaria* on various substrates in three treatments (control: *Biomphalaria* on their own, *B. glabrata* with experienced *Marisa*, and *B. glabrata* with non-experienced *Marisa*). Key: *B. glabrata* = B.g; *M. cornuarietis* = M.c.).

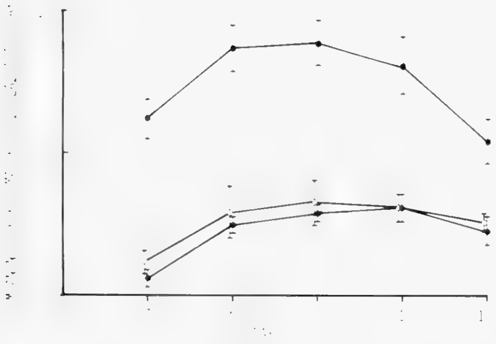

FIG. 2. The mean number ($\bar{X}$ ± S.E.) of *Biomphalaria* egg masses counted each day in the three treatments described in Fig. 1. (Key as in Fig. 1.)

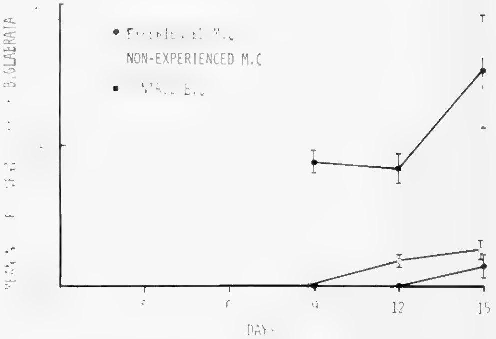

FIG. 3. The mean number ($\bar{X}$ ± S.E.) of neonate *B. glabrata* present in the three treatments described in Fig. 1 after day 9 of the experiment. (Key as in Fig. 1.)

4. Influence of previous experience, and variation in *Biomphalaria* egg density, on egg predation by adult *Marisa*

A procedure similar to the one described for juvenile *Marisa* was used for adults (34–40 mm shell diameter), except that the treatments consisted of 100, 200, 300, 400 and 500 *Biomphalaria* eggs and the snails were provided with two 1 cm diameter lettuce discs each.

RESULTS

1. The influence of experience and location of egg masses on predation by *Marisa*

It was found that *Biomphalaria* deposited egg masses on all possible substrates, namely lettuce leaves, shells of their conspecifics, *Marisa* shells and the walls of the containers. From day nine onwards many egg masses were found loose on the bottom of the containers, but as *Biomphalaria* cannot oviposit without attaching the egg masses to a substrate, it can be assumed that they had become detached after oviposition. As the egg masses do not attach very firmly to lettuce leaves, it is probable that most, if not all, of the detached egg masses originated from the lettuce. When the excess lettuce leaves were removed each day, the portions of the leaf containing the egg masses were left in the container.

The cumulative mean number of detached egg masses and those found on the various substrates are given separately for the two treatments and the control in Fig. 1. The data which were subjected to a three-way analysis of variance revealed the following trends.

There were statistically significant tendencies for the mean number of eggs deposited by *Biomphalaria* on all four substrates to increase progressively until the ninth day. Thereafter the number of egg masses counted on the *Marisa* shells and container walls continued to increase, whereas the mean numbers on lettuce and *Biomphalaria* shells declined. This decline was due, in part, to the *Biomphalaria* eggs becoming detached, as Fig. 1 shows that the mean number of unattached eggs counted on the floor of the container increased throughout the period of observation, in both the control and the two treatments. Lettuce is clearly the preferred oviposition site and the substrates may be ranked in order of preference, as follows: lettuce > container wall > *Biomphalaria* shells > *Marisa* shells. The number of egg masses found was always significantly lower on the treatments containing *Marisa* than in the controls ($P < 0.001$), but there were no significant differences between the mean number of egg masses in treatments containing experienced and non-experienced *Marisa.*

Fig. 2 shows the mean number of *Biomphalaria* eggs found in the two treatments and the control. These values are based on the total number of eggs counted in each replicate at each observation time, irrespective of the substrate on which they were laid. It can be seen that there was a significant tendency ($P < 0.01$) for the number of eggs to decline in the control after the twelfth day. There were significantly more *Biomphalaria* egg masses in the controls than in the treatments containing *Marisa* ($P < 0.001$). However, there

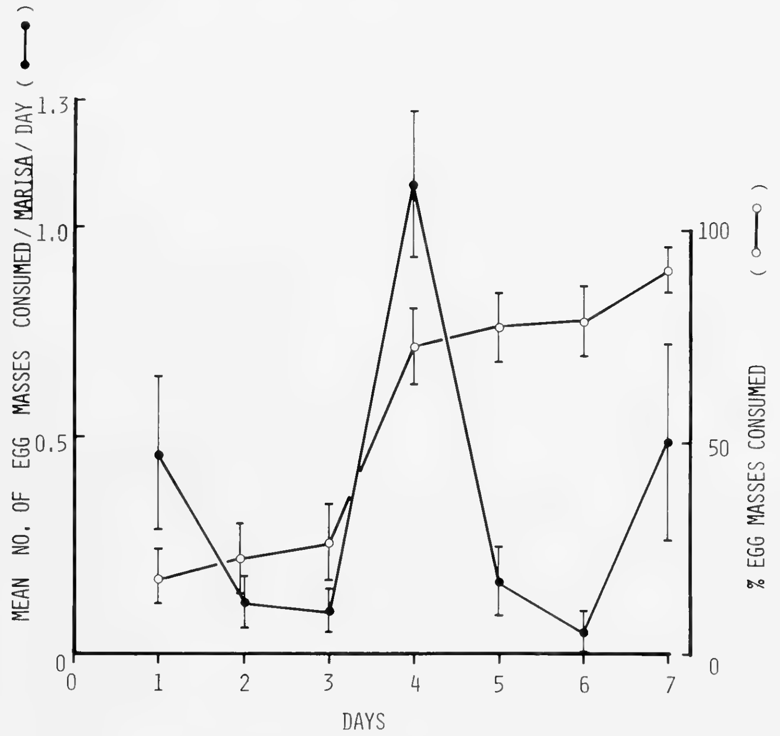

FIG. 4. The mean daily number ($\bar{X} \pm$ S.E.) and mean cumulative percentage ($\bar{X} \pm$ S.E.) of *B. glabrata* egg masses consumed by individual *Marisa* over a period of seven days.

were no significant differences at any time between the values in the treatments containing experienced and non-experienced *Marisa*.

Fig. 3 shows the mean number of neonate *Biomphalaria* found in the control and the two treatments, from the time they appeared in the control until the end of the experiment. Significantly more neonates were found in the controls than in either of the two treatments on both days 12 and 15 ($P < 0.01$). There were fewer neonates in the treatment containing experienced *Marisa* than in that containing their non-experienced conspecifics on days 12 and 15; but the differences were only statistically significant on day 12 ($P < 0.05$).

2. The influence of egg deposition, substrate and media conditioning on predation by *Marisa*

The mean rate of consumption of egg masses per day by *Marisa* were higher on days 1, 4 and 7 (the days after the media were changed) than on other days. The values on day 4 were significantly higher ($P < 0.05$) than on other days. Fig. 4 also shows that there was a progressive increase in the percentage of eggs eaten, and by the end of the experiment 90.5% ± 5.3 had been consumed. As might be expected, there were significantly more juveniles in the control than in the treatment containing *Marisa* ($P < 0.001$) from the fourth day onwards (Fig. 5).

3. Influence of experience, and *Biomphalaria* egg density, on egg predation by juvenile *Marisa*

Fig. 6 shows that the number of eggs eaten per day does not change significantly with increase in egg density. Although experienced *Marisa* ate more *Biomphalaria* eggs than their non-experienced conspecifics (with one exception), the differences were only statistically significant ($P < 0.05$) in the 50 egg treatment. The high standard errors indicate the high level of individual variation in predatory activity. In fact, several of the *Marisa* did not prey on egg masses.

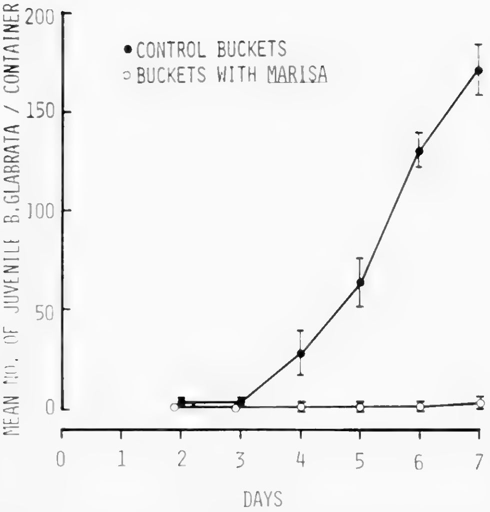

FIG. 5. The mean number (X̄ ± S.E.) of juvenile *B. glabrata* per container, counted each day over a seven day period.

4. Influence of previous experience and variation in *Biomphalaria* egg density on egg predation by adult *Marisa*

Fig. 7 shows that the number of eggs eaten per day by adult *Marisa* did not vary significantly with egg density. Neither could any significant differences be detected between the number of egg masses consumed by experienced and non-experienced *Marisa,* although, as with juveniles, there was a tendency (with one exception) for experienced snails to eat more egg masses than their non-experienced conspecifics. The standard errors indicate that, as with juveniles, there was a great deal of individual variability in predatory activity.

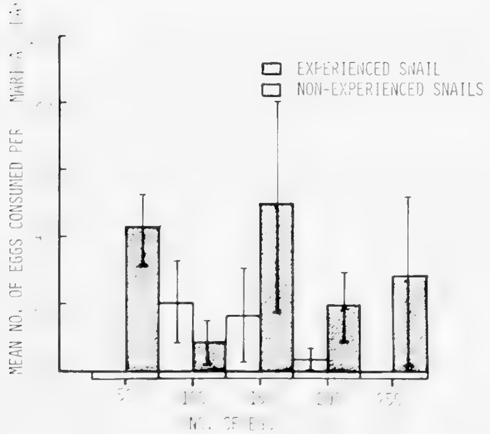

FIG. 6. The mean number (X̄ ± S.E.) of egg masses consumed per juvenile *Marisa* per day in the various egg density treatments.

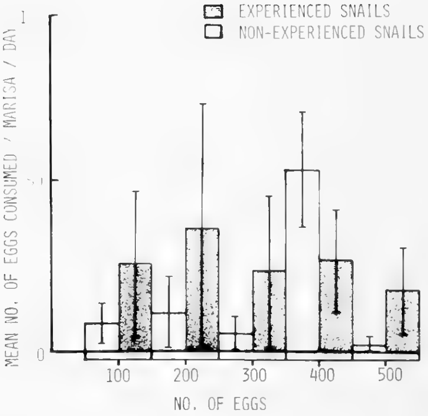

FIG. 7. The mean number (X̄ ± S.E.) of egg masses consumed per adult *Marisa* per day in the various egg density treatments.

Table 1 shows that mature female *Marisa* ate more *Biomphalaria* eggs than mature males. A two-way analysis of variance indicates that the differences between the sexes were highly significant ($P < 0.001$). However, there were no significant differences attributable to experience of egg eating, or to interactions between the sex differences and experience.

DISCUSSION

The results of the first 15 day experiment show that significantly fewer *Biomphalaria* eggs were invariably found in the treatment containing *Marisa* than in controls. These differences may have been caused directly by *Marisa* preying on the eggs, or indirectly by *Marisa* causing a decline in egg production by *Biomphalaria* as a result of competition. Although Cedeño-León (1975) showed that conditioning of the media and competition for resources by *Marisa* does impair the growth and reproduction of *Biomphalaria,* the results of experiments 2–4 in the present investigation show unequivocally that *Marisa* preys significantly on both eggs and juveniles of *Biomphalaria.* These results confirm those of Oliver-Gonzalez *et al.* (1956), Chernin *et al.* (1956), Demian & Lutfy (1965, 1966), Huben-

TABLE 1. Response of female and male *Marisa cornuarietis* to an increasing density of *Biomphalaria glabrata* eggs, measured as number of eggs consumed for *M. cornuarietis* per day ($\bar{X} \pm$ S.E.).

	Female	Male
Experienced snails	40.91 ± 15.35	7.88 ± 6.56
Non-experienced snails	35.40 ± 11.41	4.14 ± 2.82

dick (1966), Msangi & Kihaule (1972) and strengthen the suspicion of Jobin (1970) that the decline in *Biomphalaria* populations in nature, following the introduction of *Marisa*, was largely due to predation.

Biomphalaria has a catholic taste for oviposition sites (Ferguson, 1977). In this investigation these snails deposited their egg masses on the following substrates in order of preference: the plant food (lettuce) > walls of the container > *Biomphalaria* shells > *Marisa* shells. Although predation pressure is likely to be greater on the egg masses deposited on the lettuce, the results show that *Marisa* will also prey on egg masses deposited on non-food substrates. This observation supports the contention of Demian & Lutfy (1965, 1966) that predation by *Marisa* is intentional, not accidental, as claimed by Chernin *et al.* (1956) and Oliver-Gonzalez *et al.* (1956).

However, the present results demonstrate that the predatory behaviour of *Marisa* is an extremely plastic phenomenon that may be influenced by environmental factors, as well as by genotype, age and the physiological state of the snail. The experiments involving plant food shed some light on the predatory activity of *Marisa.* The first experiment shows that the presence of plant food does not deter *Marisa* from preying on egg masses or juveniles of *Biomphalaria.* On the contrary, the experiments in flow aquaria demonstrate that *Marisa* will only prey on egg masses when plant food is present. The increased predatory activity in the presence of plant food may be caused by kairomones, diffusing from the lettuce, acting as arousal factors. Alternatively, increased activity following the ingestion of lettuce could be the cause. Further experiments are needed to test these hypotheses. The behaviour of *Marisa* differs in this respect from that of *Pomacea,* which continues to feed on *Biomphalaria* eggs and juveniles even in the absence of plant food (Paulinyi & Paulini, 1972).

In contrast to the effects of lettuce, conditioning of the SSW2 by snails feeding on lettuce is followed by a decline in the predatory activity of *Marisa.* The reason is unknown, but it is possibly caused by the accumulation of certain chemical species such as H^+ or ammonia (as NH_4^+ or free NH_3) or to a decrease in the concentration of Ca^{2+}. There is experimental evidence that such changes do occur in media conditioned by *Biomphalaria* and *Marisa* (Thomas, Goldsworthy & Benjamin, 1974; Cedeño-León, 1975). These chemical changes may act by lowering the metabolic activity of the *Marisa,* or by creating background "noise" thus making the detection of egg masses difficult. Demian & Lutfy (1966) have postulated that both egg masses and juveniles release attractants, but there is no experimental evidence for their existence.

There is also a great deal of variability in the responses shown by *Marisa* to *Biomphalaria* eggs. This is reflected in the high standard errors of the mean values. There is some evidence that predatory behaviour might be an individual characteristic, as a minority of the snails never preyed on egg masses. Further experiments are needed to ascertain whether this is a consistent, genetically determined trait. There is also the possibility that the variability in response is due to individual snails having learnt to eat egg masses, while others have not. Complex manifestations of learning have recently been demonstrated and partially analysed in gastropod molluscs (Davis & Gillette, 1978; Chang & Gelperin, 1978). The higher level of predation by experienced *Marisa* provides some support for this hypothesis. However, the differences between experienced and non-experienced *Marisa* were only statistically significant in one case. The lack of statistically significant differences in other cases may have been due to the high variances.

Predatory activity tends to increase with age, and is significantly higher in sexually mature females than males. It is plausible to attribute this change to the need for higher quality food when the snails enter the reproductive phase. The differences between the sexes might be explained by the higher costs of reproduction in the females. There is therefore a greater need for females to select food rich in the galactogen and protein required for egg formation. There is some evidence that other snails may supplement their plant diet with protein rich food, particularly when they mature. Thus Bovbjerg (1968) found that although lymnaeid snails feed primarily on plant food, they will also feed on carrion when available. Animal food also figures prominently in the diets of snail species such as *Physa acuta, Helisoma duryi* and *Pomacea* sp. (Ferguson, 1977), which have been proposed as agents for biological control of the snail hosts. It has been shown under experimental conditions, both in the field (Eisenberg, 1966, 1970), and in the laboratory (Frank, 1963; and El Emam & Madsen, in prep.), that improved food quality is followed by an increase in the growth and natality of pulmonate snails. Generally, higher protein food appears essential for maximizing egg production. Further detailed work on the feeding habits and dietary requirements of aquatic snails is clearly needed.

In view of the probabilitistic nature of predation by *Marisa,* it is necessary to question whether it has the attributes needed as a predator for successful biological control. A good predator should respond to an increase in prey density in three major ways. Firstly, individual predators should ingest proportionately more prey as density increases, as described in the type III functional response of Holling (1959a, b). Secondly, they should be capable of a numerical response by aggregating in the vicinity of the high prey densities. Thirdly, their reproductive response should be sufficiently strong to enable them to control the prey species in a density dependent manner.

Unfortunately, *Marisa* does not appear to satisfy these requirements. Thus the predatory activity of the individual does not increase over the range of egg densities used. It is possible that a functional response could arise if smaller numbers of egg masses were used. Secondly, it is unlikely that *Marisa* could show a numerical response because *Biomphalaria* deposits its eggs over a wide range of substrates. Thirdly, the active space within which the egg masses can be discerned is likely to be very small. Finally, it seems improbable from the information given by Ferguson (1977) that *Marisa* can show a sufficiently strong reproductive response to increasing numbers of *Biomphalaria.* Detailed demographic studies are needed to verify this last assumption.

It can be concluded that to optimize on the predatory activity of *Marisa* for biological control it is necessary to introduce them at high densities. There have, in fact, been cases where *Marisa* has been used successfully. For example, Jobin (1970) and Demian & Kamel (1978) introduced them at densities of one per 163 cm^2, and one per 225 cm^2 respectively. These densities are very similar to those used in the present experiments, namely one per 283 cm^2. However, it should be remembered that *Marisa* can also induce other detrimental effects on *Biomphalaria,* by acting as a competitor for resources, and by producing allelopathic factors. Possible methods of maximising these attributes will be considered in subsequent papers.

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LITERATURE CITED

BOVBJERG, R. V., 1968, Responses to food in lymnaeid snails. *Physiological Zoology,* 41:412–423.

BROWN, D. S., 1980, *Freshwater snails in Africa and their medical importance.* Taylor and Francis, London, 487 p.

CEDEÑO-LEÓN, A., 1975, *Interactions between* Biomphalaria glabrata *(Say) and* Marisa cornuarietis *(L.) under laboratory conditions.* Ph.D. thesis, University of Sussex, England.

CHANG, J. T. & GELPERIN, A., 1978, Learned modification of a molluscan feeding resonse produced in the isolated nervous system. *Society for Neuroscience Abstracts,* 4: 189.

CHERNIN, E., MICHELSON, E. H. & AUGUSTINE, D. L., 1956, Studies on the biological control of schistosome-bearing snails, I. The control of *Australorbis glabratus* populations by the snail *Marisa cornuarietis,* under laboratory conditions. *American Journal of Tropical Medicine and Hygiene,* 5: 297–307.

DAVIS, W. J. & GILLETTE, R., 1978, Neural correlate of behavioural plasticity in command neurones of *Pleurobranchaea*. *Science,* 199: 801–804.

DEMIAN, E. S. & KAMEL, E. G., 1978, Displacement of *Bulinus truncatus* by *Marisa cornuarietis* under semi-environmental conditions in Egypt. *Proceedings of the International Conference on Schistosomiasis,* p. 731–739.

DEMIAN, E. S. & LUTFY, R. G., 1965, Predatory activity of *Marisa cornuarietis* against *Biomphalaria alexandrina* under laboratory conditions. *Annals of Tropical Medicine and Parasitology,* 59: 337–339.

DEMIAN, E. S. & LUTFY, R. G., 1966, Factors affecting the predation of *Marisa cornuarietis* on *Bulinus (B.) truncatus, Biomphalaria alexandrina* and *Lymnaea caillaudi. Oikos,* 17: 212–230.

EISENBERG, R. M., 1966, The regulation of density in a natural population of the pond snail, *Lymnaea elodes. Ecology,* 47: 889–906.

EISENBERG, R. M., 1970, The role of food in the regulation of the pond snail *Lymnaea elodes. Ecology,* 51: 680–684.

EL EMAM, M. A. & MADSEN, H., 1983, The effect of temperature, darkness, starvation and various food types on the growth and reproduction of *Helisoma duryi*: (Wetherby), *Biomphalaria alexandrina* (Ehrenberg) and *Bulinus truncatus* (Audouin) (Pulmonata: Planorbidae). *Hydrobiologia,* 88: 265–275.

FERGUSON, F. F., 1977, *The role of biological agents in the control of schistosome-bearing snails.* U.S. Department of Health, Education and Welfare, Atlanta, Georgia.

FRANDSEN, F. & MADSEN, H., 1979, A review of *Helisoma duryi* in biological control. *Acta Tropica,* 36: 67–84.

FRANK, G. H., 1963, Some factors affecting the fecundity of *Biomphalaria pfeifferi* (Krauss) in glass aquaria. *Bulletin World Health Organization,* 29: 531–537.

HOLLING, C. S., 1959a, The components of predation as revealed by a study of small mammal predation of the european pine sawfly. *Canadian Entomology,* 91: 293–320.

HOLLING, C. S., 1959b, Some characteristics of simple types of predation and parasitism. *Canadian Entomology,* 91: 385–398.

HUBENDICK, B., 1966, Some aspects of vector snail control. *Malacologia,* 5: 31–32.

JOBIN, W. R., 1970, Population dynamics of aquatic snails in three farm ponds of Puerto Rico. *American Journal of Tropical Medicine and Hygiene,* 19: 1038–1048.

MSANGI, A. S. & KIHAULE, P. M., 1972, Prospects of biological control of schistosomiasis in East Africa. In: ANDERSON, C. & KILAMA, W. L. (eds.), *Parasitoses on man and animals in Africa.* Nairobi, East African Literature Bureau, p. 439–447.

NDIFON, G. T., 1979, *Studies on the feeding biology, anatomical variations and ecology of vectors of schistosomiasis and other freshwater snails in South Western Nigeria.* Ph.D. thesis, University of Ibadan, Nigeria.

NDIFON, G. T. & UKOLI, F. M. A., 1980, Studies on the dietary habits of naturally occurring populations of *Bulinus (P.) globosus* (Pulmonata, Planorbidae): the snail host of *Schistosoma haematobium. The 3rd European multicolloquium of Parasitology,* Cambridge, England, p. 90.

OLIVER-GONZALEZ, J., BANMAN, P. M. & BENENSON, A. S., 1956, Effect of the snail *Marisa cornuarietis* on *Australorbis glabratus* in natural bodies of water in Puerto Rico. *American Journal of Tropical Medicine and Hygiene,* 5: 290–296.

PAULINYI, H. M. & PAULINI, E., 1972, Laboratory observations on the biological control of *Biomphalaria glabrata* by a species of *Pomacea* (Ampullariidae). *Bulletin of World Health Organization,* 46: 243–247.

SOLOMON, M. E., 1949, The natural control of animal populations. *Journal of Animal Ecology,* 18: 1–35.

THOMAS, J. D., 1973, Schistosomiasis and the control of molluscan hosts of human schistosomes with particular reference to possible self-regulatory mechanisms. *Advances in Parasitology,* 11: 307–394. Academic Press, London and New York.

THOMAS, J. D., GOLDSWORTHY, G. J. & BENJAMIN, M., 1974, Chemical conditioning of the environment by the freshwater pulmonate snail *Biomphalaria,* and its effect on growth and natality rates. *Journal of Zoology,* London, 172: 443–467.

THOMAS, J. D., LOUGH, A. S. & LODGE, R. W., 1975, The chemical ecology of *Biomphalaria glabrata* (Say), the snail host of schistosomiasis: The search for factors in their media conditioned by snails which inhibit their growth and reproduction. *Journal of Applied Ecology,* 12: 421–436.

WORLD HEALTH ORGANIZATION, 1965, Snail control in the prevention of bilharziasis. *WHO Monograph Series No.* 50, Geneva.

MALACOLOGIA, 1983, 24(1–2): 298–311

CONCHIOLIN LAYERS AMONG THE UNIONIDAE AND MARGARITIFERIDAE (BIVALVIA): MICROSTRUCTURAL CHARACTERISTICS AND TAXONOMIC IMPLICATIONS

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ABSTRACT

The purposes of this paper are to determine the function of the conchiolin layers deposited within the shell of the freshwater bivalve families Unionidae and Margaritiferidae, whether they contain species-specific characteristics, and whether the microstructure of these layers supports inclusion of the margaritiferids within the family Unionidae, as proposed by Davis & Fuller (1981). Scanning electron microscope observations were conducted on 23 unionids and three margaritiferids. In addition, fossil unionids from the Eocene and Late Jurassic of Wyoming were examined to determine whether the microstructure of such layers is preserved and can be used as a taxonomic character among fossils.

The results indicate that unionids possess two types of conchiolin layers within the shell: thin, homogeneous and thick, more complex layers. The latter attain their highest degree of complexity within the Unionidae: Ambleminae, especially *Elliptio.* Unionid complex layers can be divided into three distinct regions. Margaritiferids, on the other hand, possess only one type of layer, also divisible into three distinct regions, which closely resembles the periostracum in ultrastructure.

Species examined possess highly individualistic conchiolin layer characteristics, with the exception of some members of the recently radiating *Elliptio,* among which overlaps in both reticulate region characteristics and inter-population variability occur. Placement of the margaritiferids within the family Unionidae is considered incompatible with the differences observed among the taxa.

The conchiolin layers prevent rapid shell dissolution in acidic or poorly buffered waters. Bivalves collected from habitats in which dissolution is severe often show significantly greater numbers of conchiolin layers per millimeter of shell thickness than do conspecific populations from habitats where dissolution is less severe. This indicates that these bivalves exercise control over the frequency of layer deposition, but the mechanism that actuates formation of layers other than damage-response layers remains obscure.

Unionid fossils from the Eocene of Wyoming have remarkably well preserved conchiolin layers. Overall characteristics of these layers are highly consistent with those that occur among Recent taxa examined. When preserved, this feature should allow discrimination of relationships among fossil taxa, and estimation of some environmental parameters, such as water acidity.

Key words: conchiolin layers; microstructure; Unionidae; Margaritiferidae; taxonomy.

INTRODUCTION

The occurrence of conchiolin layers within the shells of freshwater bivalves of the families Unionidae and Margaritiferidae has been documented for some time (e.g. Gray, 1833; Tolstikova, 1974), and recent studies suggest that possession of such conchiolin layers increases resistance of these bivalves to shell dissolution after the periostracum has worn away (Tevesz & Carter, 1980; Kat, 1982). Examination of specimens of *Elliptio complanata* indicated that two types of conchiolin layers are present within the shell of this species: thin, undifferentiated and thick, differentiated layers which can be subdivided into three regions. I proposed (Kat, 1982) that the microstructure of the thick conchiolin layers, especially characteristics of the central reticulate region, might be useful as a taxonomic character at the species level. The purpose of this paper is to test that hypothesis with a number of Atlantic Slope unionids representing two subfamilies, the Anodontinae and the Ambleminae (sensu Davis & Fuller, 1981).

In addition, Tolstikova (1974) indicated a substantial difference between the Unionidae and the Margaritiferidae with respect to both shell and conchiolin layer microstructure. Davis & Fuller (1981) recently included North American margaritiferids within the family Unionidae, which seems to contradict Tolstikova's evidence. Conchiolin layer microstructure of three margaritiferids is compared to that of a number of unionids to determine whether the differences observed by Tolstikova (1974) are compatible with subfamilial status of the margaritiferids.

Taxonomic problems among the Unionacea are especially pronounced among fossil forms. Loss of all soft-part characteristics, as well as evidence of ecophenotypic plasticity has led to much taxonomic uncertainity among these fossil taxa (Haas, 1969). If microstructure of conchiolin layers is preserved, discrimination among fossil species should be simplified. Three fossils, one from the Late Jurassic and two from the Eocene of Wyoming, were examined to study the taxonomic value of conchiolin layer microstructure in fossils.

METHODS

The classification and collection locations of the specimens used in this study are listed in the Appendix. All shells were embedded in clear plastic, radially sectioned with a circular rock saw, polished with carborundum grit, and etched for 5 seconds with 5% HCl in preparation for scanning electron microscopy (SEM). During SEM, the specimens were tilted to reveal clearly the microstructure of the reticulate portions of the conchiolin layers; the relative thickness of the uppermost homogeneous region of the conchiolin layers thus is slightly distorted.

Variability within a species and within a population of a species was studied by examining seven populations of *Elliptio complanata* and four individuals within each of four populations of this species (Ellenwood, French Lake, Norwich, Bull Run). *E. complanata* was chosen for this survey of variability because it is one of the most variable unionid species in terms of shell shape, soft-part characteristics such as stomach anatomy and siphonal papillation, and molecular genetics of the Atlantic Slope unionid assemblage (Davis et al., 1981; Kat & Davis, in press). Variability of conchiolin layer characteristics occurring in this species thus might similarly represent an upper limit to that occurring in other species.

RESULTS

The results of this study indicate the existence of two separate groups within the bivalves examined; as indicated by Tolstikova (1974), the conchiolin layers among the Margaritiferidae have a different structural organization from those in the Unionidae.

A) Margaritiferidae (*Margaritifera margaritifera,* Fig. 1C; *M. falcata,* Fig. 1E; *Cumberlandia monodonta,* Fig. 1F)

The shell of the margaritiferids contains only one type of layer, a thick (35 to 80 μm) conchiolin band (Fig. 1A) which is composed of three distinct regions (Fig. 1C). An outermost homogeneous region of approximately 10 to 16 μm in thickness surmounts a vacuolated region approximately 10 to 20 μm thick. The third region is composed of rather widely spaced organic lamellae, between which fit blocks of subprismatic shell material. This innermost region is the thickest of the three and varies from about 15 to 40 μm. The general appearance of the conchiolin layers of the margaritiferids is very similar to that of the periostracum among these bivalves (Tolstikova, 1974; see also Tevesz & Carter, 1980).

Among the Margaritiferidae examined, *Margaritifera margaritifera* (Fig. 1C) has the thickest layers, which show the best definition of the three regions. *Cumberlandia monodonta* (Fig. 1F) also has good definition of each region, but the layers are only about half as thick as those deposited in the shell of *M. margaritifera*. Finally, *M. falcata* (Fig. 1E) has layers equally thick to those of *C. monodonta,* but the vacuolated region generally is poorly developed in most individuals, and the lamellae seem more randomly placed.

B) Unionidae

Anodontinae (*Anodonta gibbosa,* Fig. 2A; *A. c. cataracta,* Fig. 2B; *A. c. fragilis,* Fig. 2C; *A. implicata,* Fig. 2D; *Strophitus undulatus,* Fig. 2E; *Alasmidonta undulata,* Fig. 2F)

Ambleminae: Lampsilini (*Lampsilis radiata,* Fig. 2G, H; *L. splendida,* Fig. 2I; *L.* sp., Fig. 2J; *L. teres,* Fig. 3A; *L. dolabraefor-*

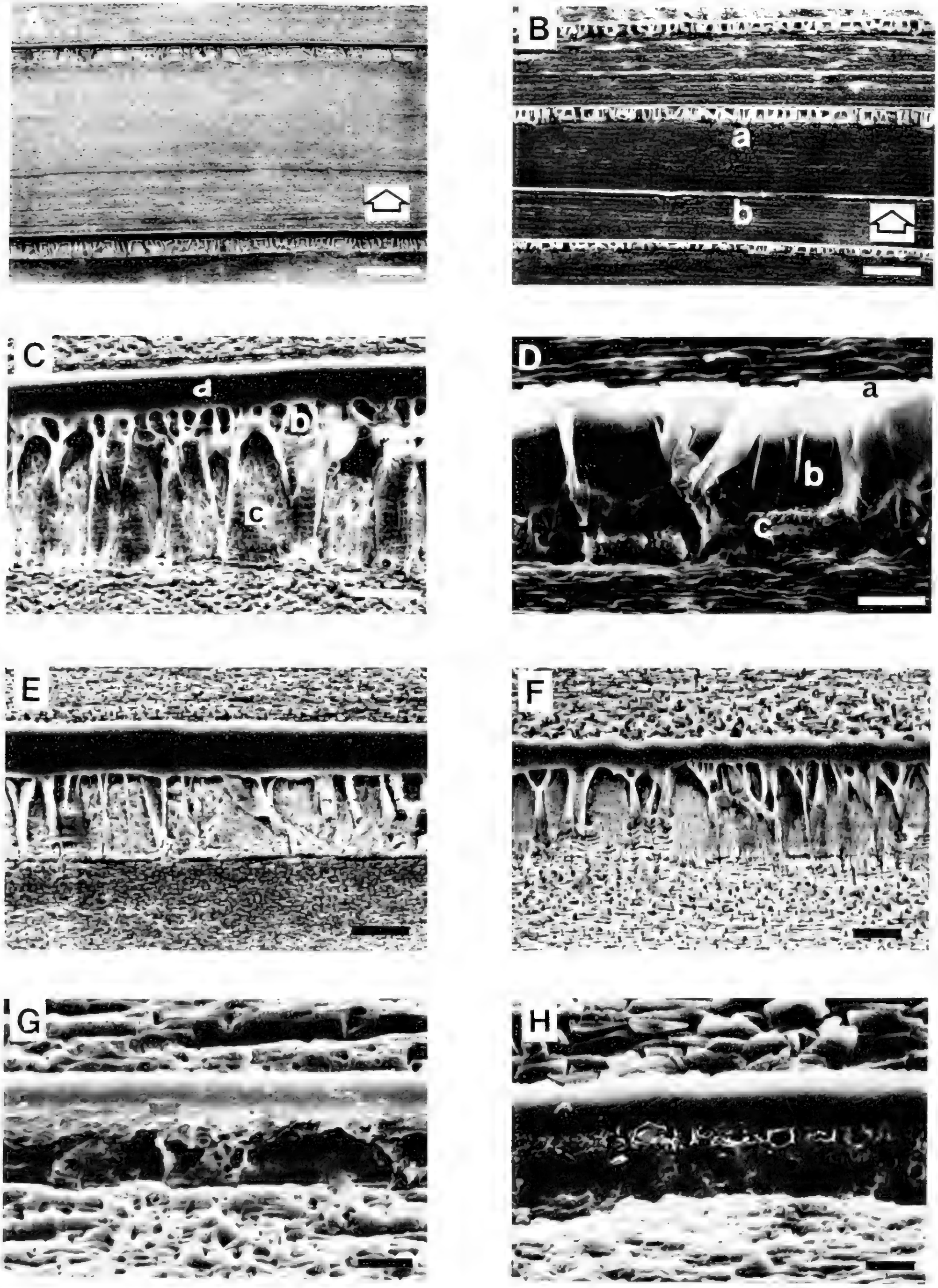

FIG. 1. A. Shell of *Margaritifera falcata* illustrating the exclusive presence of thick conchiolin layers in the shell. The arrow indicates the direction to the outside of the shell; scale bar = 100 μm. B. Shell of *Elliptio complanata* illustrating the presence of thick (a) and thin (b) conchiolin layers characteristic of the unionids. The arrow indicates the direction to the outside of the shell; scale bar = 50 μm. C. Thick conchiolin layer of *Margaritifera margaritifera* illustrating the three regions present in each layer: upper homogeneous (a),

mis, Fig. 3B; *Ligumia nasuta,* Fig. 3C; *Villosa delumbis,* Fig. 3D)

Ambleminae: Pleurobemini (*Elliptio hopetonensis,* Fig. 3E; *E. shephardiana,* Fig. 3F; *E. spinosa,* Fig. 3G; *E. lanceolata,* Fig. 3H; *E. fisheriana,* Fig. 3I; *E. folliculata,* Fig. 3J; *E. dariensis,* Fig. 4A; *E. arctata,* Fig. 4B; *E. complanata,* Fig. 4C–I)

The conchiolin layers of the Anodontinae are among the simplest observed in this study. The shell contains two types of layers; simple, thin (2.5–5 μm), homogeneous layers and slightly more complex layers composed of at most three partially defined regions: an outermost homogeneous region (about 3 μm thick), a reticulate region composed of rather poorly defined chambers, and an innermost, thin, homogeneous sheet. The reticulate region in particular is not very well developed; for example, in *Anodonta gibbosa* (Fig. 2A) thin lamellae form only partial chambers, and in *Strophitus undulatus* (Fig. 2E) the chambers are small and highly irregular in shape. The reticulate region varies in thickness from about 7 μm in *A. gibbosa* to about 5 μm in *S. undulatus.*

The Ambleminae form a cohesive group characterized by possession of two types of layers: thin, homogeneous (2–5 μm) and thick, complex (5–18 μm). Thick and thin layers commonly alternate, but thin shells, such as those of *Lampsilis splendida, Elliptio fisheriana,* and *Ligumia nasuta,* frequently have only one thick layer among several thin ones. Formation of these two layers seems rather similar; thick layers could result from elaboration of thin layers. The dimensions of the homogeneous upper portions of the thick layers are certainly similar to those of the thin layers, and thin layers sometimes have an incomplete reticulate region.

In the Ambleminae thick conchiolin layers consist of three regions: an outermost, homogeneous portion, which varies in thickness from about 2 to about 8 μm; a central, reticulate portion (ranging in thickness from about 3 to about 14 μm) composed of chambers of various shapes formed by sheet-like lamellae; and a lowermost, thin homogeneous region. The reticulate region contains calcareous material within the chambers formed by the lamellae ("irregularly shaped polyhedra" according to Tolstikova, 1974), which largely dissolved when the specimens were etched with HCl, but remains visible, for example, in Fig. 4H. The reticulate region of the conchiolin layers seems best developed in the genus *Elliptio.* The various features of a thick conchiolin layer characteristic of the Unionidae are illustrated in Fig. 5.

The fossil specimen of Late Jurassic age had a highly altered shell in which neither conchiolin layer microstructure nor shell microstructure was preserved. In contrast, both Eocene specimens (Fig. 1G, H) were exceptionally well preserved in that they seemed to retain the original conchiolin and contained both thin, undifferentiated and thick, differentiated layers. These conchiolin layers are similar to those of Recent Ambleminae, especially the Lampsilini, but are quite plesiomorphic in that the lamellae and chambers are poorly developed, and the entire reticulate region presents a disorganized appearance.

Based on the observed variability of conchiolin layer microstructure, it is possible to define a set of characters that determine plesiomorphic and apomorphic conditions among the Unionidae (Table 1). Highly plesiomorphic characters appear mainly among the Anodontinae; the Lampsilini and some Pleurobemini have some plesiomorphic characters; and most other Pleurobemini have apomorphic characters. This division agrees in a general fashion with the previously proposed times of origin of these taxa: The Anodontinae appeared during the Upper Cretaceous, the Lampsilini appeared during the Oligocene, and the Pleurobemini appeared during the Pleistocene (Haas, 1969; Davis *et al.,* 1981).

Tolstikova (1974) noted no differences among the microstructures of *Unio tumidus*

⟵

central vacuolated (b), and lowermost lamellar (c). Scale bar = 20 μm. D. Thick conchiolin layer of *Elliptio waccamawensis* illustrating the presence of three regions: uppermost homogeneous (a), central lamellar (b), and lowermost thin homogeneous (c). Scale bar = 10 μm. E. Thick conchiolin layer of *Margaritifera falcata.* Scale bar = 15 μm. F. Thick conchiolin layer of *Cumberlandia monodonta.* Scale bar = 15 μm. G. Thick conchiolin layer of a *Pseudelliptio* from the Eocene of Wyoming. Scale bar = 7 μm. H. Thick conchiolin layer of a *Pseudelliptio* from the Eocene of Wyoming. Scale bar = 5 μm.

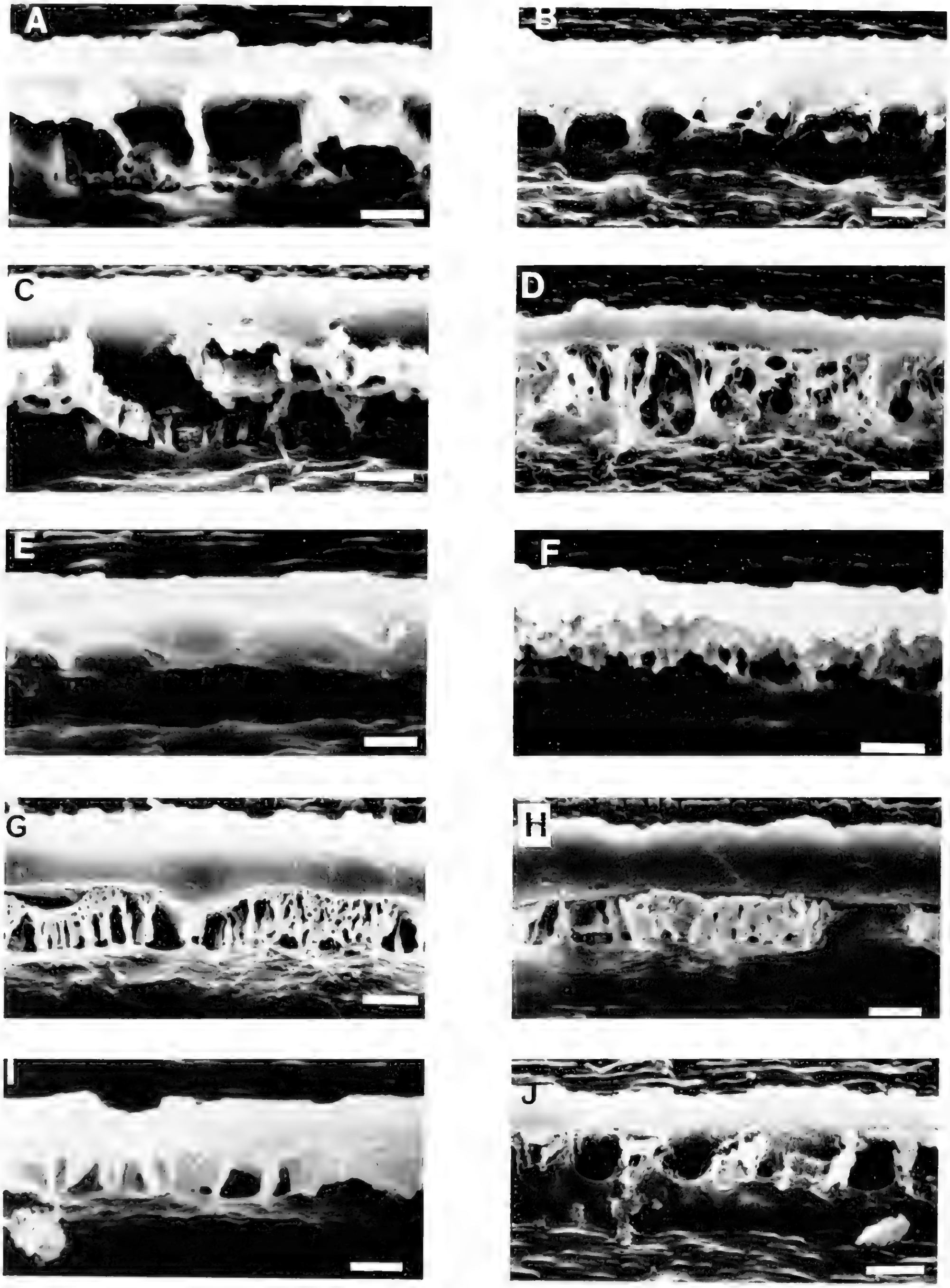

FIG. 2. A. Thick conchiolin layer of *Anodonta gibbosa*. Scale bar = 4 μm. B. Thick conchiolin layer of *Anodonta cataracta cataracta*. Scale bar = 4 μm. C. Thick conchiolin layer of *Anodonta cataracta fragilis*. Scale bar = 6 μm. D. Thick conchiolin layer of *Anodonta implicata*. Scale bar = 5 μm. E. Thick conchiolin layer of *Strophitus undulatus*. Scale bar = 3 μm. F. Thick conchiolin layer of *Alasmidonta undulata*. Scale bar = 5 μm. G. Thick conchiolin layer of *Lampsilis radiata* (Locality 1). Scale bar = 4 μm. H. Thick conchiolin layer of *Lampsilis radiata* (Locality 2). Scale bar = 3 μm. I. Thick conchiolin layer of *Lampsilis splendida*. Scale bar = 3 μm. J. Thick conchiolin layer of *Lampsilis* sp. Scale bar = 4 μm.

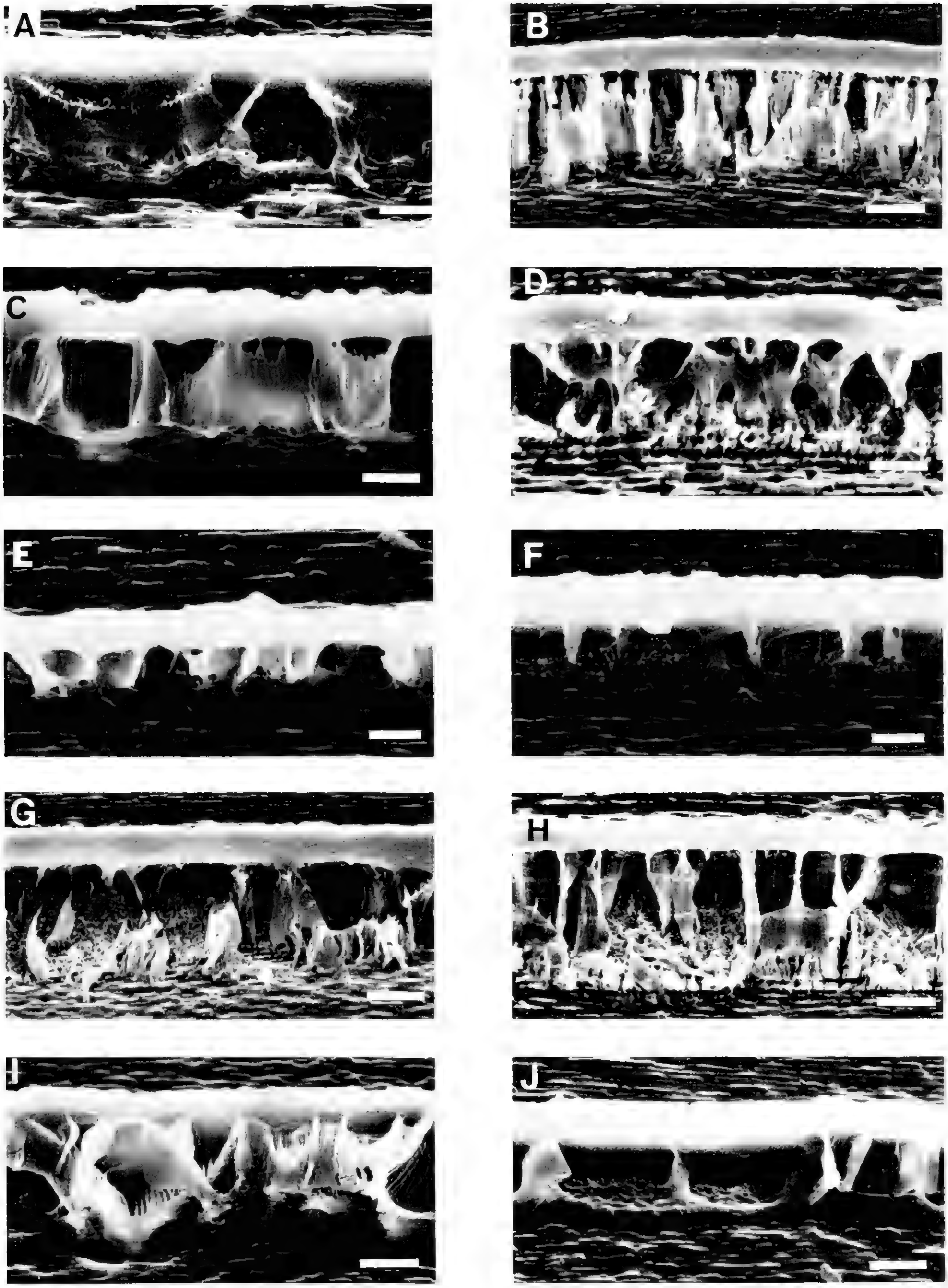

FIG. 3. A. Thick conchiolin layer of *Lampsilis teres*. Scale bar = 3 μm. B. Thick conchiolin layer of *Lampsilis dolabraeformis*. Scale bar = 7 μm. C. Thick conchiolin layer of *Ligumia nasuta*. Scale bar = 5 μm. D. Thick conchiolin layer of *Villosa delumbis*. Scale bar = 5 μm. E. Thick conchiolin layer of *Elliptio hopetonensis*. Scale bar = 3 μm. F. Thick conchiolin layer of *Elliptio shephardiana*. Scale bar = 3 μm. G. Thick conchiolin layer of *Elliptio spinosa*. Scale bar = 7 μm. H. Thick conchiolin layer of *Elliptio lanceolata*. Scale bar = 7 μm. I. Thick conchiolin layer of *Elliptio fisheriana*. Scale bar = 5 μm. J. Thick conchiolin layer of *Elliptio folliculata*. Scale bar = 5 μm.

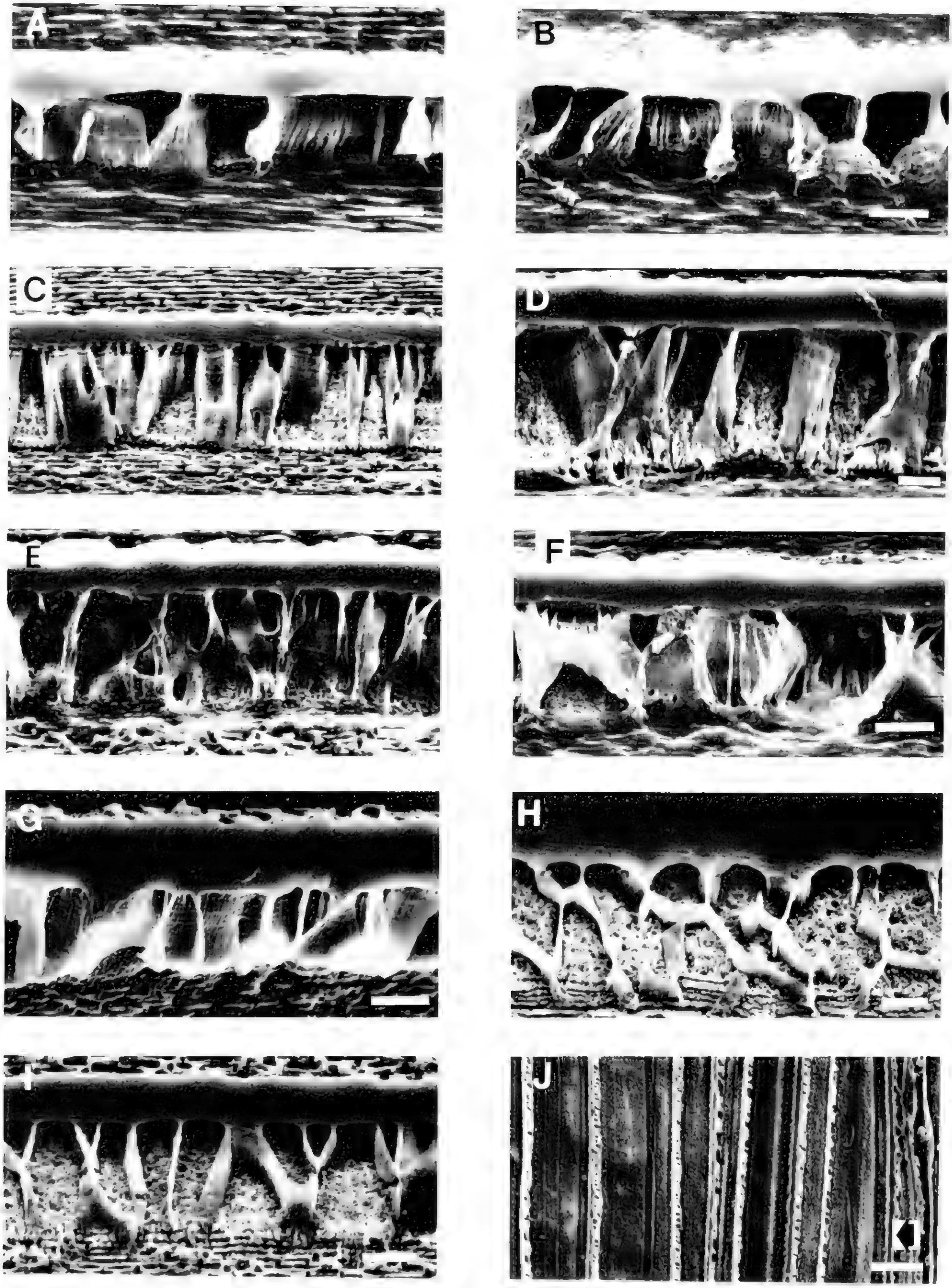

FIG. 4. A. Thick conchiolin layer of *Elliptio dariensis*. Scale bar = 5 μm. B. Thick conchiolin layer of *Elliptio arctata*. Scale bar = 5 μm. C. Thick conchiolin layer of *Elliptio complanata* (Locality 1). Scale bar = 7 μm. D. Thick conchiolin layer of *Elliptio complanata* (Locality 2). Scale bar = 5 μm. E. Thick conchiolin layer of *Elliptio complanata* (Locality 3). Scale bar = 6 μm. F. Thick conchiolin layer of *Elliptio complanata* (Locality 4). Scale bar = 7 μm. G. Thick conchiolin layer of *Elliptio complanata* (Locality 5). Scale bar = 7 μm. H. Thick conchiolin layer of *Elliptio complanata* (Locality 6). Scale bar = 6 μm. I. Thick conchiolin layer of *Elliptio complanata* (Locality 7). Scale bar = 7 μm. J. Presence of many conchiolin layers in shells from

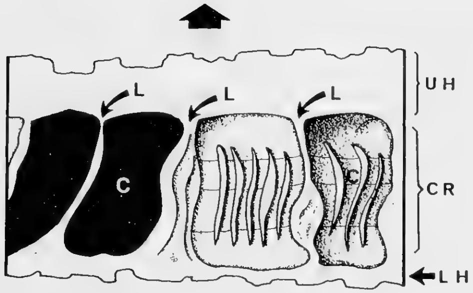

FIG. 5. Semi-diagrammatic representation of a unionid thick conchiolin layer. Illustrated are the upper (or outermost) homogeneous region (UH), the central reticulate region (CR), and the lower (or innermost) homogeneous region (LH). The reticulate region is composed of chambers (C), which are separated by lamellae (L). The back walls of the chambers are illustrated on the right; each chamber was filled with calcareous material which dissolved during HCl etching. The arrow at the top indicates the direction to the outside of the shell.

TABLE 1. Plesiomorphic and amorphic characteristics of the reticulate portion of unionid conchiolin layers.

A. Plesiomorphic characters.
   1. Absence of lamellae, or presence of coarse lamellae which vary in width or length.
   2. Absence of chambers, presence of poorly defined chambers formed by partial lamellae, or presence of variously sized chambers.
   3. Reticulate portion only slightly thicker than the upper homogeneous portion of the conchiolin layer.

B. Apomorphic characters.
   1. Presence of well-developed lamellae of rather uniform length and appearance.
   2. Presence of well-defined chambers of generally equal dimensions.
   3. Reticulate portion considerably thicker than the upper homogeneous portion of the conchiolin layer.

from different provinces in the U.S.S.R., but such differences are evident when populations of the phenotypically plastic and genetically variable *Elliptio complanata* are compared. In eastern Canada, for example, populations from the Sydney and Nine Mile Rivers and from French Lake have variously spaced, approximately vertical lamellae (with respect to the homogeneous layer) within the reticulate portion of the conchiolin layer (Fig. 4C, D, E), while the populations from Placide and Ellenwood Lakes possess curved lamellae (Fig. 4F, G). In contrast, Bull Run (Virginia) and Norwich Creek (Maryland) populations are characterized by lamellae that are interwoven in a variably complex network (Fig. 4H, I). Individuals in a population, however, resemble each other closely.

Resemblance in conchiolin layer microstructure can occur among different species of *Elliptio.* For example, *E. arctata* is similar to *E. dariensis* (Fig. 4A, B). Despite such similarities, pronounced differences usually occur. For example, the lanceolate forms *E. lanceolata, E. folliculata, E. fisheriana, E. shephardiana,* and *E. arctata* are clearly different (Fig. 3H, J, I, F, and 4B, respectively).

Variability among populations of *Elliptio complanata* and overlap of characteristics among species of this genus contrasts with conservatism among the Lampsilini and Anodontinae. For example, *L.* sp., an undescribed species from Lake Waccamaw, North Carolina, is different in reticulate region characteristics from both *L. radiata* and *L. splendida,* the species found in the drainages around Lake Waccamaw and from which *L.* sp. presumably was derived (Fig. 2G, H, I, J) (Kat, in press a).

Despite the high degree of plesiomorphy among the Anodontinae, it is possible to discriminate among anodontine species. For example, *Anodonta c. cataracta* differs in reticulate region characteristics from *A. c. fragilis,* hypothetically a closely related anodontine from Nova Scotia (Fig. 2B, C) (Clarke & Rick, 1963). *A. implicata* (Fig. 2D) is an exception to the plesiomorphic trend among the anodontines; while the reticulate portion still presents a somewhat disorganized picture, the lamellae are thin and the chambers complete.

DISCUSSION

Functional Significance

The presence of thick conchiolin layers in bivalve shells usually has been associated

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habitats in which dissolution is severe. Specimen is *Elliptio complanata* from Locality 5. The arrow indicates the direction to the outside of the shell; scale bar = 50 μm.

(e.g. by Lewy & Samtleben, 1979) with resistance to both predation by boring gastropods and shell dissolution. In the limited case of the unionids and margaritiferids the function of the shell layers has been proposed to fall in the latter category; after the periostracum has been worn away from the umbonal region (which is the oldest part of the bivalve shell), these successive organic layers might retard shell dissolution sufficiently to permit compensatory shell deposition under most conditions (Kat, 1982). For instance, as a result of possession of such layers, unionids can survive with minimal shell damage in habitats where *Corbicula* experience considerable mortality due to excessive shell dissolution because their shells lack conchiolin layers (Kat, 1982). In addition, when the unionid shell is damaged, similar conchiolin layers are deposited to seal off the affected area (Beedham, 1965; Tevesz & Carter, 1980; personal observations). These damage-response layers can be distinguished from other conchiolin layers by the presence of an underlying prismatic layer (Tevesz & Carter, 1980).

With the exception of damage-response layers, it is uncertain what actuates formation of these conchiolin layers. Layers are deposited mainly in small patches in the region of the umbo, and usually end abruptly (Fig. 1B). There is a suggested relationship between frequency of conchiolin layers within the shell and water acidity, although confirmation of this trend requires measurement of inter-population variability in conchiolin layer abundance with both the averages and standard deviations of environmental parameters such as water pH and hardness. Nevertheless, bivalves from habitats in which shell dissolution is extensive (such as Lake Waccamaw, North Carolina; various mesotrophic and oligotrophic lakes in Nova Scotia; and certain small creeks in Georgia and Florida) often have more bands per millimeter of shell (Fig. 4J) than do conspecifics in habitats where minimal shell dissolution occurs (Fig. 1B); it thus appears that these bivalves exercise some degree of control over frequency of layer deposition. There is no evidence that these layers correspond to growth stops as proposed by Tolstikova (1974).

Russell-Hunter *et al.* (1981) found no relationships between total organic content and water hardness in several populations of freshwater limpets from habitats in which hardness varied by an order of magnitude. Their methods, however, are open to some criticism: the variance of environmental parameters such as water pH and hardness apparently was not taken into account, limpets of various size classes were lumped (large limpets could have had eroded shells), and tissues were not extracted from the shells prior to determination of organic content. It is not known whether any freshwater gastropods deposit conchiolin layers within their shells to counter dissolution. Various other relationships among shell calcium and water hardness were presented by Russell-Hunter *et al.* (1981); it is apparent that freshwater molluscs have a variety of responses in terms of shell components and their relationships to environmental parameters.

Taxonomic Significance

Species-level Discrimination

SEM examinations of conchiolin layer microstructure reveal that features of the reticulate region, in particular, can often be used to discriminate among species within a genus. Exceptions to this trend occur among some species of the genus *Elliptio,* which vary considerably in characteristics among geographic subgroups and some overlap of characteristics among species. Conchiolin layer discriminants among anodontine species could be fewer and/or more equivocal because the Anodontinae examined here usually lack a well-defined reticulate region.

The overlap of characteristics among some species of *Elliptio* and the variability among geographic subgroups of *E. complanata* are not surprising. The genus apparently is undergoing a Recent radiation, and levels of molecular genetic resemblance among some species are not different from those that characterize different populations of a wide-ranging species. For example, species within the *E. complanata* "group" defined by Davis *et al.* (1981) are genetically cohesive with identity values (Nei, 1972) ranging from 0.90 to 0.99. Populations of morphologically defined *E. complanata* from various locations, on the other hand, show genetic identity values ranging from 0.82 to 0.99 (Kat & Davis, in press), and I propose elsewhere (Kat, in press b) that *E. companata* should be regarded as a highly polytypic species presently distributed as a Rassenkreis, or ring species, around the Appalachian mountain chain. This pattern of close interspecific and variable intraspecific resemblances generally has been considered to be indicative of rapid speciation and little time since divergence of species within a genus (Avise *et al.*, 1975; Avise, 1976; Davis *et al.*, 1981; Kat, in press a). Morphological characters such as conchiolin layer microstructure therefore could show overall similarity among species unless those genetic changes that accompanied speciation directly or indirectly (through pleiotropy) affected loci that regulate pattern and process of conchiolin layer deposition or unless such differences accumulated since divergence. The latter process seems to be responsible for accumulated differences among widely-separated (and presumably reproductively isolated) populations of *E. complanata*, but it is not possible to determine which process is responsible for observed differences between species which are well separated genetically. For example, *E. folliculata* and *E. fisheriana* are distantly related (I = 0.64; Davis *et al.*, 1981) and exhibit considerable differences in conchiolin layer microstructure (Fig. 3I, J), but it is not possible to determine by which pathway (directly associated with a punctuated process of speciation or as a result of divergence over time) the differences arose.

Three species within *Elliptio* (*E. shephardiana, E. hopetonensis, E. spinosa*; Fig. 3E, F, G) show considerable plesiomorphy in conchiolin layer microstructure when compared with other members of the genus examined here. All three species are endemic to the ancient Altamaha River drainage (Johnson, 1970) and could represent a group of species that diverged from ancestral *Elliptio* early in time and thus retained some plesiomorphic characters.

Members of the Anodontinae and Ambleminae: Lampsilini do not show such variability. Both groups are characterized by rather plesiomorphic conchiolin layers, but there are some exceptions to this overall trend. *Lampsilis dolabraeformis* (Fig. 3B), for instance, has the most apomorphic conchiolin layers among the lampsilines examined. This species can be characterized as "advanced" with respect to other features as well; for example, the mantle flap and marsupium show highly derived conditions. *Anodonta implicata* (Fig. 2D) is an exception to the plesiomorphic trend among the anodontines; the lamellae in this species are thin and complete, and the chambers are quite regular. I have proposed separation of *A. implicata* from the subgenus *Pyganodon* (which includes all other *Anodonta* examined here) because of electrophoretic and soft-part characteristic differences (Kat, 1983); the differences observed in conchiolin layer microstructure support this separation. I also described a substantial difference between *A. c. cataracta* and *A. c. fragilis*; the latter "subspecies" differs considerably from the former in electrophoretic and soft-part characters (in fact, *A. c. fragilis* shows close affinity to the European *A. cygnea* with respect to stomach morphology); conchiolin layer characteristics again positively correlate with other discriminants (Fig. 2B, C).

TABLE 2. Characteristics of the conchiolin layers which differentiate the Unionidae and Margeritiferidae.

Unionidae

1. Presence of two types of conchiolin layers within the shell: thin, undifferentiated, and thick, differentiated.
2. Thick, differentiated layers can always be divided into three or more or less distinct layers: an uppermost homogeneous portion; a central reticulate portion, and a lowermost thin homogeneous portion.
3. Chambers of various sizes are present within the reticulate portion of the conchiolin bands, which are filled with unconsolidated, chalky shell material.

Margaritiferidae

1. Presence of one type of conchiolin layer within the shell: thick, differentiated.
2. Differentiated layers can be divided into three layers: an uppermost homogeneous portion, a central vacuolated portion, and a lowermost lamellar portion. The appearance of the conchiolin layers is similar to that of the periostracum.
3. Chambers of various sizes are formed within the lamellar portion, which are filled with blocks of subprismatic shell material.

Taxonomic concepts based on conchiolin layer similarities, however, sometimes disagree with relationships suggested by electrophoresis: for example, *Lampsilis* sp. seems more closely related to *L. splendida* than to *L. radiata* with respect to overall conchiolin layer microstructure (Fig. 2H, I, J) while the reverse relationship is suggested by electrophoretic and soft-part similarities (Kat, in press a).

Higher-order Taxonomy

Two very distinct categories can be defined on the basis of characteristics of the conchiolin layers among the species examined (Table 1). The Unionidae show varying degress of elaboration of the conchiolin layers, which appear to be the most complex among the Ambleminae. Also, all unionids possess thin, undifferentiated bands, which could be indicative of plesiomorphy. The margaritiferids show very different, periostracum-like bands, which are unlike any encountered among the unionids examined. Tolstikova (1974) was equally convinced of the differences between unionids and margaritiferids with respect to this character and described some additional significant differences in shell microstructure.

I propose two hypotheses to explain these differences:

(1) Recent margaritiferids show conchiolin layers that are as highly derived from an ancestral state as those of the Pleurobemini are; in other words, the fact that these layers are now very different does not mean that they could not once have been very similar. This hypothesis is rejected for two reasons. First, while the conchiolin layers of the Pleurobemini can be regarded as apomorphic, the simultaneous presence of thin, undifferentiated layers within the shell, as well as the presence of features that link differentiated and undifferentiated bands among the unionids, points to common ancestry. This is supported by close resemblance of conchiolin layer microstructure between Recent species and Eocene taxa. A similar argument cannot be constructed for the margaritiferids; they lack all but differentiated layers, and these layers exhibit few features in common with those of the unionids. Second, conchiolin layers of the margartiferids resemble the periostracum in ultrastructure, while those of the unionids do not.

(2) Recent margaritiferids have conchiolin layers that are derived from a very different ancestral condition; in other words, they arose in a lineage different from that of the Unionidae. This hypothesis is most compatible with the data.

It appears that there have been two distinctly different pathways taken by different unionacean lineages towards the solution of the common problem of shell dissolution. Ancestral unionids likely laid down simple to slightly elaborated conchiolin layers, similar to those encountered among Recent anodontines. Elaboration of such bands is encountered among Recent *Lampsilis* and *Elliptio*. Ancestral margaritiferids likely formed layers similar to the periostracum. Recent margaritiferids continue to have this ancestral condition. This hypothesis should be testable in the fossil record.

The classification of Davis & Fuller (1981), which relegates the margaritiferids to subfamilial status within the Unionidae, is therefore rejected; the margaritiferids have conchiolin layer microstructural differences suggestive of an early divergence from the unionid lineage, and on the basis of this character I propose restoration of familial status. On the other hand, similarities among the Lampsilini and Pleurobemini with respect to conchiolin layer microstructure should constitute additional evidence to support including them in the same subfamily (Ambleminae) as proposed by Davis & Fuller (1981).

Placement of the margaritiferids within the Unionidae was based on molecular genetic and some morphologic data (Davis & Fuller, 1981). First, genetic similarity was found to be higher than expected if the taxa belonged to different families (comparative data were derived from comparisons of different gastropod families), especially because fossil evidence indicated that the divergence could have begun before the Cretaceous (Haas, 1969). With respect to electrophoretically determined genetic distances, remaining similarities among distantly related taxa generally are found among slowly evolving loci (Sarich, 1977). Divergence times based on genetic distances that include such loci must include a large margin of error, because rates of differentiation for such loci are unknown, because it is unknown to what extent natural selection maintains similarities among such loci, and because it is not intuitively obvious why genetic distances between distantly related taxa should continue to increase in a regular fashion. In fact, the strict applicability of the molecular clock has recently been questioned: sea urchin species pairs separated by the Isthmus of Panama reveal radically different genetic distances, even though they have presumably been isolated for exactly the same amount of time (Lessios, 1979, 1981). Some taxa thus might diverge more rapidly than others. Cluster-ordination analysis of immunoelectrophoretic distances also indicates high levels of similarity between the Ambleminae and *Margaritifera* (Davis & Fuller, 1981). In sum, the combined electrophoretic and immunoelectrophoretic data indicate that the taxa proabably are not of polyphyletic origin, but the distinct differences observed between the Margaritiferidae and the Unionidae in conchiolin layer microstructure must place the taxa in different families, which I propose shared a common ancestor before the Cretaceous (Fig. 6).

Second, similarities exhibited by the margaritiferids to the unionid morphological groundplan, including the glochidial larval type, could imply similarity of response to similar selective pressures. Margaritiferids and unionids share identical habitats, and parasitize identical hosts (fishes); it is thus entirely likely that, given a similar ancestral bivalve groundplan, the taxa now resemble each other in a general fashion. It must be noted that margaritiferid glochidia are much smaller than those found among the unionids, and that careful comparative observations have not been made to support contentions of their similarity. An initial examination of soft-part characteristics of margaritiferids and unionids reveals significant differences between the taxa. Siphonal papillae among the margaritiferids are both muscular and arborescent, a condition not encountered among unionids thus far examined (although some Amblemini apparently possess arborescent papillae; see Davis & Fuller, 1981); margaritiferids possess no true septa or water tubes in their lamellae; and examination of characteristics of the margaritiferid stomach reveals that it is simple in structure, resembles those of the anodontines, but differs from the unionids thus far examined in possession of a sorting pouch beneath the minor typhlosole fold (Kat, 1983; personal observations).

Fossils

According to Haas (1969), loss of all soft-part characters, evidence of a high degree of phenotypic plasticity of unionacean shell shape, and gaps in knowledge of Recent forms contribute to render classification of fossil forms an extremely difficult endeavor. In addition, fossil specimens often are fragmentary, or preserved only as casts or molds, which further reduces the amount of information that can be deduced from them. Preservation of microstructural characteristics of the conchiolin layers within shells that have undergone little replacement, or replacement with little deformation of the original microstructure of the shell, would allow identification of species as well as degree of phenotypic plasticity shown by such species, even from fragmentary material. Such information is important in that it allows assessment of fossil species diversity, determination of relationships between fossil and Recent taxa, and because the number of layers deposited in the shell seem related to water acidity, some environmental reconstruction. Unfortunately, preservation of conchiolin layer microstructure requires rather exceptional conditions, which might only seldom be met; permineralization which faithfully replicates the conchiolin layer could be extremely rare. The Eocene fossils studied were exceptionally well preserved, and appear to have retained the original components of the conchiolin layers (Fig. 1G, H). In contrast, a fossil specimen from the Late Jurassic had been extensively altered. Preservation of taxonomically valuable characters might thus be limited to specimens of Tertiary or younger age. Nevertheless, good preservation of conchiolin layer microstructure observed in this preliminary study of fossil forms is extremely encouraging, and should provide a useful way to discriminate among previously problematical fossil taxa.

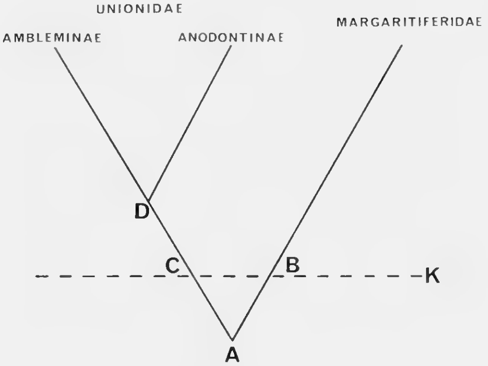

FIG. 6. Relationships among North American Unionacea based on conchiolin layer microstructure. In the diagram, a generalized unionacean ancestor A gives rise to descendant groups B and C, present during the Cretaceous (K). Group B is characterized by deposition of conchiolin layers which resemble the periostracum in ultrastructure, and is ancestral to the Margaritiferidae. Group C is characterized by deposition of simple, non-differentiated layers within the shell, and is ancestral to the Unionidae. This group then diverges (D) into the Ambleminae, which has differentiation of conchiolin layers into separate portions, and the Anodontinae, which largely retain simple layers.

SUMMARY

Thick conchiolin layers within the shells of the Unionidae and the Margaritiferidae seem to serve a common purpose: prevention of rapid shell dissolution in the region of the umbo once the protective periostracum has worn away. Most species examined, with the exception of some recently diverging taxa within the genus *Elliptio,* seem to possess highly individualistic characteristics of especially the reticulate regions of the layers. Placement of the margaritiferids within the Unionidae as proposed by Davis & Fuller (1981) is considered incompatible with the significant differences observed in the microstructure of the conchiolin layers of these taxa; there seem to have been two distinctly different pathways taken by the different lineages toward the solution of the common problem of shell dissolution. The margaritiferids deposit layers that resemble the periostracum, while the unionids lay down simple and variably complex chambered conchiolin layers, which do not resemble the periostracum.

Preservation of conchiolin layer microstructure among Eocene taxa suggests the existence of a powerful tool to discriminate among fossil forms, and should facilitate fossil classification. Such discriminatory ability should additionally allow estimates of fossil assemblage diversity, relationships among fossil and Recent taxa, and reconstruction of some environmental parameters such as water pH.

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REFERENCES CITED

AVISE, J. C., 1976, Genetic differentiation during the speciation process. In AYALA, F. J. (ed.), *Molecular Evolution.* Massachusetts, Sinauer Press, p. 106–122.

AVISE, J. C., SMITH, J. J. & AYALA, F. J., 1975, Adaptive differentiation with little genetic change between two native California minnows. *Evolution,* 29: 411–426.

BEEDHAM, G. E., 1965, Repair of the shell in species of *Anodonta. Proceedings of the Zoological Society of London,* 145: 107–124.

CLARKE, A. H. & RICK, A. M., 1963, Supplementary records of Unionacea from Nova Scotia with a discussion of the identity of *Anodonta fragilis* Lamarck. *National Museum of Canada Bulletin* 199.

DAVIS, G. M. & FULLER, S. L. H., 1981, Genetic relationships among Recent Unionacea (Bivalvia) of North America. *Malacologia,* 20: 217–253.

DAVIS, G. M., HEARD, W. H., FULLER, S. L. H. & HESTERMAN, C., 1981, Molecular genetics and speciation in *Elliptio* and its relationships to other taxa of North American Unionidae (Bivalvia). *Biological Journal of Linnean Society,* 15: 131–150.

GRAY, J. E., 1833, Some observations on the economy of molluscous animals, and on the structure of their shells. *Philosophical Transactions of the Royal Society of London,* 123: 771–819.

HAAS, F., 1969, Superfamily Unionacea. In MOORE, R. C. (ed.), *Treatise on Invertebrate Paleontology,* Part N. Mollusca, 6: Vol. 1 (of 3): N411–N470.

JOHNSON, R. I., 1970, The systematics and zoogeography of the Unionidae (Mollusca: Bivalvia) of the Southern Atlantic Slope region. *Bulletin of the Museum of Comparative Zoology,* 149: 263–447.

KAT, P. W., 1982, Shell dissolution as a significant cause of mortality for *Corbicula fluminea* (Bivalvia: Corbiculidae) inhabiting acidic waters. *Malacological Review,* 15: 129–134.

KAT, P. W., 1983, Genetic and morphological divergence among nominal species of North American *Anodonta* (Bivalvia: Unionidae). *Malacologia,* 23: 361–374.

KAT, P. W., in press a, Genetics, morphological divergence, and speciation in *Lampsilis* (Bivalvia: Unionidae). *Journal of Molluscan Studies.*

KAT, P. W., in press b, Patterns of electrophoretic and morphologic variability among widely distributed species. I. An initial survey of variability in *Elliptio complanata* (Bivalvia: Unionidae). *Netherlands Journal of Zoology,* 33:

KAT, P. W. & DAVIS, G. M., in press, Genetic divergence of peripheral populations of Nova Scotian Unionidae. *Biological Journal of the Linnean Society.*

LESSIOS, H. A., 1979, Use of Panamanian sea urchins to test the molecular clock. *Nature,* 280: 599–601.

LESSIOS, H. A., 1981, Divergence in allopatry: molecular and morphological differentiation between sea urchins separated by the Isthmus of Panama. *Evolution,* 35: 618–634.

LEWY, Z. & SAMTLEBEN, C., 1979, Functional morphology and palaeontological significance of the conchiolin layers in corbulid gastropods. *Lethaia,* 12: 341–351.

NEI, M., 1972, Genetic distance between populations. *American Naturalist,* 106: 283–292.

RUSSELL-HUNTER, W. D., BURKY, A. J. & HUNTER, R. D., 1981, Interpopulation variation in calcareous and proteinaceous shell components in the stream limpet, *Ferrissia rivularis. Malacologia,* 20: 255–266.

SARICH, V. M., 1977, Rates, sample sizes, and the neutrality hypothesis for electrophoresis in evolutionary studies. *Nature,* 265: 24–28.

TEVESZ, M. J. & CARTER, J. C., 1980, Environmental relationships of shell form and structure of Unionacean bivalves. In RHOADS, D. C. & LUTZ, R. A. (EDS.), *Skeletal Growth of Aquatic Organisms.* Plenum Press, New York, p. 295–322.

TOLSTIKOVA, N. V., 1974, Microstructural characteristics of freshwater bivalves (Unionidae). *Paleontological Journal* [translation of *Paleontologicheskii Zhurnal*], 8: 55–60.

APPENDIX. Classification and collection localities of the species studied

Recent Taxa

Unionidae
  Anodontinae
      Anodonta gibbosa Say, 1824
        Ocmulgee River, Ben Hill Co., Georgia
      Anodonta cataracta cataracta Say, 1817
        Pickering Creek, Chester Co., Pennsylvania
      Anodonta cataracta fragilis Lamarck, 1819
        Nowlans Lake, Digby Co., Nova Scotia, Canada
      Anodonta implicata Say, 1829
        Fletcher Lake, Halifax Co., Nova Scotia, Canada
      Strophitus undulatus (Say, 1817)
        Norwich Creek, Talbot Co., Maryland
      Alasmidonta undulata (Say, 1817)
        Norwich Creek, Talbot Co., Maryland
  Ambleminae
    Lampsilini
      Lampsilis radiata (Gmelin, 1791)
        1. Shubenacadie Grand Lake, Halifax Co., Nova Scotia, Canada
        2. Newville Lake, Cumberland Co., Nova Scotia, Canada
      Lampsilis splendida (Lea, 1838)
        Ocmulgee River, Ben Hill Co., Georgia
      Lampsilis dolabraeformis (Lea, 1838)
        Ocmulgee River, Ben Hill Co., Georgia
      Lampsilis teres (Say, 1834)
        Withlacoochee River, Lacoochee, Pasco Co., Florida
      Lampsilis sp.
        Lake Waccamaw, Columbus Co., North Carolina
      Ligumia nasuta (Say, 1817)
        Norwich Creek, Talbot Co., Maryland
      Villosa delumbis (Conrad, 1834)
        Fountain Mill, Pulaski Co., Georgia
    Pleurobemini
      Elliptio complanata (Lightfoot, 1786)
        1. Sydney River, Cape Breton Co., Nova Scotia, Canada
        2. French Lake, Sunbury Co., New Brunswick, Canada
        3. Nine Mile River, Halifax Co., Nova Scotia, Canada
        4. Ellenwood Lake, Yarmouth Co., Nova Scotia, Canada
        5. Placide Lake, Digby Co., Nova Scotia, Canada
        6. Norwich Creek, Talbot Co., Maryland
        7. Bull Run, Prince William Co., Virginia
      Elliptio fisheriana Ortmann, 1919
        Norwich Creek, Talbot Co., Maryland
      Elliptio waccamawensis (Lea, 1863)
        Lake Waccamaw, Columbus Co., North Carolina
      Elliptio hopetonensis (Lea, 1838)
        Ocmulgee River, Ben Hill Co., Georgia
      Elliptio spinosa (Lea, 1836)
        Ocmulgee River, Ben Hill Co., Georgia
      Elliptio shephardiana (Lea, 1834)
        Ocmulgee River, Ben Hill Co., Georgia
      Elliptio lanceolata (Lea, 1820)
        Fountain Mill, Pulaski Co., Georgia
      Elliptio dariensis (Lea, 1842)
        Bowens Mill, Ben Hill Co., Georgia
      Elliptio arctata (Conrad, 1834)
        Mosquito Creek, Gadsden Co., Florida
      Elliptio folliculata (Lea, 1858)
        Lake Waccamaw, Columbus Co., North Carolina
Margaritiferidae
      Margaritifera margaritifera (Linnaeus, 1758)
        Maccan River, Cumberland Co., Nova Scotia, Canada
      Margaritifera falcata (Gould, 1850)
        Deschutes River, Deschutes Co., Oregon
      Cumberlandia monodonta (Say, 1829)
        Clinch River, Hancock Co., Tennessee

Fossil Taxa

Genus?
  Jurassic: Lower Morrison Formation, East Como Bluff, Albany Co., Wyoming. Johns Hopkins University M-COMO-CLM-1
Pseudelliptio sp.
  Eocene: Willwood Formation, Elk Creek, Big Horn Co., Wyoming. Johns Hopkins University W-KC-PSE-1

MALACOLOGIA, 1983, 24(1–2): 312–322

INDEX TO TAXA IN VOLUME 24

An asterisk (*) denotes a new taxon

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MALACOLOGIA, VOL. 24

CONTENTS

AWARDS FOR STUDY AT
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The Academy of Natural Sciences of Philadelphia, through its Jessup and McHenry funds, makes available each year a limited number of awards to support students pursuing natural history studies at the Academy. These awards are primarily intended to assist predoctoral and immediate postdoctoral students. Awards usually include a stipend to help defray living expenses, and support for travel to and from the Academy. Application deadlines are 1 April and 1 October each year. Further information may be obtained by writing to: Chairman, Jessup-McHenry Award Committee, Academy of Natural Sciences of Philadelphia, 19th and the Parkway, Philadelphia, Pennsylvania 19103, U.S.A.

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6. Manuscripts must be typed on one side of good quality white paper, double-spaced throughout (including the references, tables and figure captions), and with ample margins. Tables and figure captions should be typed on separate pages and put at the end of the manuscript. Make the hierarchy of headings within the text simple and consistent. Avoid internal page references (which have to be added in page proof).

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8. Provide a concise and informative Abstract summarizing not only contents but results. A separate summary generally is superfluous.

9. Supply between five and eight key (topic) words to go at the end of the Abstract.

10. Use the metric system throughout. Micron should be abbreviated μm.

11. Illustrations are printed either in one column or the full width of a page of the journal, so plan accordingly. The maximum size of a printed figure is 13.5 × 20.0 cm (preferably not as tall as this so that the caption does not have to be on the opposite page).

12. Drawings and lettering must be dark black on white, blue tracing, or blue-lined paper. Lines, stippling, letters and numbers should be thick enough to allow reduction by ½ or ⅓. Letters and numbers should be at least 3 mm high after reduction. Several drawings or photographs may be grouped together to fit a page. Photographs are to be high contrast. High contrast is especially important for histological photographs.

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VOL. 24, NOS. 1–2 MALACOLOGIA 1983

CONTENTS