BEAUFORTIA

SERIES OF MISCELLANEOUS PUBLICATIONS

ZOOLOGICAL MUSEUM - AMSTERDAM

No. 128 Volume 10 Aug. 14, 1964

Notes on the Facelinacea

II. On the systematic position of *Hervia serrata* Baba, 1949 and *Favorinus horridus* Macnae, 1954 (Mollusca Nudibranchia)

CARLOS J. RISSO-DOMINGUEZ

I. INTRODUCTION

The systematic position of *Favorinus horridus* MACNAE, 1954 and *Hervia serrata* BABA, 1949, is a subject on which widely diverse views have been held by different workers, as far as the family and genus are concerned. Additionally, it is invariably admitted that both forms belong to the Facelinacea.

These discrepancies account for the present chaotic condition of the classification and nomenclature of the facelinid eolids, resulting from the rigid adoption by MACNAE (1954) and MARCUS (1957, 1958) of the taxonomic principles established by ODHNER (1939). I have briefly discussed this subject in a previous paper (RISSO-DOMINGUEZ, 1962).

Favorinus horridus was originally described by MACNAE (1954, p. 19) as a favorinid on the basis of a supposed resemblance of the radular teeth, but there has been a great deal of controversy as to the proper genus to which this species belongs. It has been removed from *Favorinus* by MARCUS (1958, p. 59) for obvious reasons and previously united with *Hervia serrata* by BABA (1955, p. 56) on account of the many resemblances.

The generic name *Hervia* cannot be maintained since there is no clear diagnosis of it, nor a real type species. It was probably based upon a specimen of *Facelina drummondi* (ODHNER in MACNAE, 1954, p. 8). Accordingly, the species formerly ascribed to this genus must be distributed among other facelinid genera (MACNAE, 1954, p. 9). Concerning the controversy about

Received November 22, 1963.

the use of the name *Cratena* instead of *Rizzolia,* I regard WINCKWORTH's view (1941) as untenable. This subject will be fully treated in a separate paper in this series.

Rizzolia serrata (BABA, 1949) and *Dondice horridus* (MACNAE, 1954) might be given as the proper names in the light of the most recent literature. Nevertheless, these merely are additional superfluous synonyms, since *Hervia serrata* does not belong to *Rizzolia* TRINCHESE, 1877, nor can *Favorinus horridus* be ascribed to *Dondice* MARCUS, 1958.

Obviously, *Hervia serrata* is not congeneric with *Rizzolia peregrina,* the type species of *Rizzolia,* nor can it be placed in any of the other facelinid genera, since the characteristic serrate structure of the radular teeth is absent in the Facelinacea. I institute, therefore, the new genus **Babaiella** with *Hervia serrata* BABA, 1949 as type species. It is with much pleasure that I designate this genus honouring Dr. Kikutaro Baba, whose name will always be connected with the history of the Indo-Pacific nudibranch fauna.

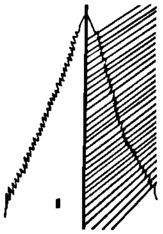
As far as *Dondice* is concerned, I think that this genus is a most unsatisfactory one in many respects, and the principles used by MARCUS (1958) to establish it, were rather arbitrary for the purpose. Strangely enough this genus was constituted upon specimens which are not referable beyond doubt to *Caloria occidentalis* ENGEL, 1925, designated as type species. MARCUS himself (1958, p. 65) recognized that there are some differences between the types from Jamaica and specimens from Cananeia in Southern Brazil, at a considerable distance from the type locality. I do not wish to question the identity of the specimens, nor am I entitled to do so. In such a matter it is difficult to express any opinion without an examination of the actual specimens, especially when these are only contracted preserved specimens. I merely stress the importance of reliable procedures in the taxonomy and nomenclature of the Nudibranchiata. Too many inconveniences have already been added to the nomenclature by the careless procedures of some older authors, especially R. Bergh.

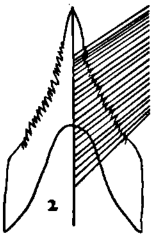
But still more perplexing is the heterogeneous nature of the six additional species assigned to *Dondice.* At a glance, none of them appears to be congeneric with the type species. *Facelina veranyana* Bergh, 1875 is a mere synonym of *Rizzolia peregrina,* type species of *Rizzolia,* as Bergh (1880, p. 156) clearly recognized. A better procedure might have been to admit that the presence of "double rouws" of papillae (if this term could be properly applied) is also known from specimens of *R. peregrina.* Moreover, *Rizzolia modesta* BERGH, 1880 [= *Cuthona japonica* BABA, 1937 = *Hervia japonica* (BABA 1937) BABA, 1949 = *Godiva modesta* (Bergh, 1880), MACNAE, 1954 = *Dondice modesta* (Bergh, 1880), MARCUS, 1958] and *Rizzolia ceylonica* (Farran, 1905) [= *Cuthona ceylonica* (Farran, 1905), BABA, 1937 = *Hervia ceylonica* (Farran, 1905), BABA, 1949 = *Godiva ceylonica* (Farran, 1905), MACNAE, 1954 = *Dondice ceylonica* (Farran, 1905), MARCUS, 1958] are congeneric with *R. peregrina* in the light of actual knowledge.

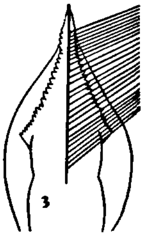
The argument used by MARCUS (1958) for excluding *Facelina veranyana* (= *Rizzolia peregrina*), *Rizzolia modesta* and *Rizzolia ceylonica* from the genus *Rizzolia,* is quite striking. I cannot find any evidence that the mere presence of additional papillae in an arch alternating in a zig-zag line, or even simulating an arrangement in two different parallel lines ("double rows" of MARCUS and MACNAE), can have any diagnostic value for separating subfamilies, genera and species (See RISSO-DOMINGUEZ, 1962). It is noteworthy that MARCUS (1957, p. 478—479) did not use this argument in his description of *Berghia coerulescens* from Brazil, quite overlooking that this species bears a double row of papillae in the anterior arches. It is evident that the illustrated specimen (fig. 238) only bears a "single row" of papillae, while European specimens clearly have a "double row", this peculiarity being emphasized by TRINCHESE (1882, p. 14: "..disposte in due file..") and clearly illustrated by BERGH (1882, pl. I fig. 1) and TRINCHESE (1882, pl. II fig. 1). If this difference was not judged by Marcus to be of sufficient importance for specific separation, it can hardly be justified that this same argument can be used to separate the eolids into different subfamilies or genera. Moreover, the specimen of *Rizzolia modesta* illustrated by BERGH (1880, pl. I fig. 1) bears a "triple row" of papillae in the distal parts of the arches. Thus, if the above discussed principles are maintained, it must be recognized that such specimens should be separated from that of BABA (1949, p. 105 fig. 140) which only bears double rows. It must be questioned whether in the Facelinacea two genera can be separated upon the basis of a single or an alternate arrangement of the papillae only. If some diagnostic value is given to this feature, this can only be proved by the examination and comparison of a large number of specimens. Until this is done it is not only very inconvenient to the taxonomist but contrary to the best principles of scientific research to separate these species, since the actual knowledge does not support such procedure, nor can the presence of rows instead of arches be used in similar attempts. If the taxonomic principles stressed by Macnae and Marcus are accepted and exaggerated diagnostic value is given to the arrangement of the papillae, then a most artificial classification of the eolid nudibranchs would arise (RISSO-DOMINGUEZ, 1962).

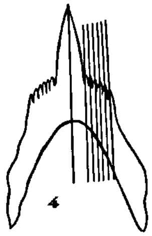
If the diagnosis of *Favorinus* by MACNAE (1954, p. 19) is maintained, then *Favorinus pacificus* BABA, 1937 must be excluded from the genus. Obviously, this is untenable, since this species can hardly be distinguished from *Favorinus albus,* type species of *Favorinus,* as pointed out by BABA (1937, p. 334). It possesses the colouring and morphological features of the European species and only differs in the arrangement of the papillae, viz. arches in *albus* and single rows in *pacificus.* No author will separate into different genera these two species on account of this difference. Consequently, it must be admitted that arches and single rows can occur within the limits of a genus. The strong resemblance between the species of *Acanthopsole* and *Echinopsole fulvus* MACNAE, 1954, leads to analogous results concerning the claimed taxonomic value of the arrangement of the papillae in arches or in crowded transverse rows. Similar examples have been studied in the Aeolidiellidae (RISSO-DOMINGUEZ, 1964 b).

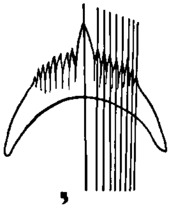
The many striking similarities between *Rizzolia peregrina, Rizzolia ceylonica* and *Rizzolia modesta* suggest very forcibly that they all belong to one genus or subfamily. The separation of these species into different groups cannot be maintained. It is, therefore, quite clear that, unless further research can demonstrate a sharp distinction between eolids bearing arches with single

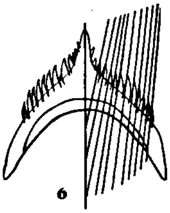

1

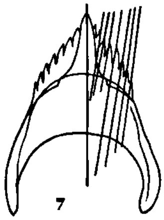

2


3

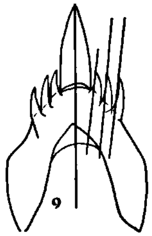

4

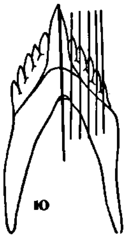

5

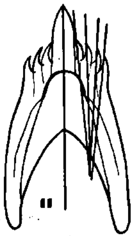

6

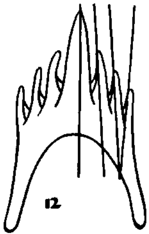

7

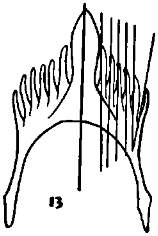

8


9

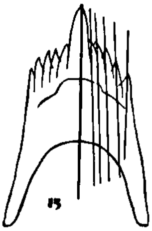

10

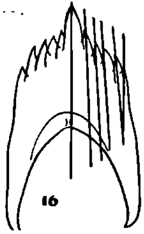

11

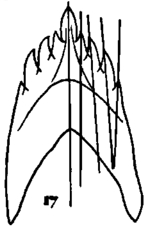

12

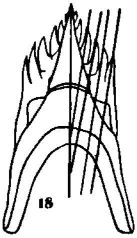

13

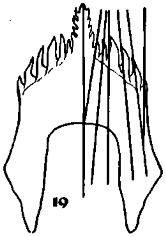

14

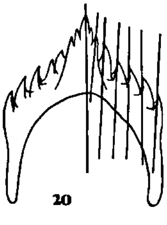

15

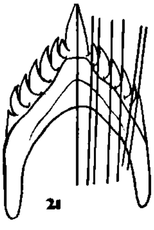

16

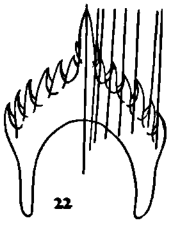

17

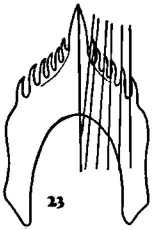

18


19

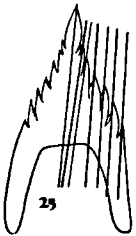

20

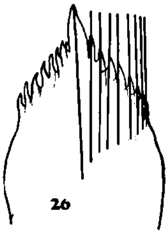

21

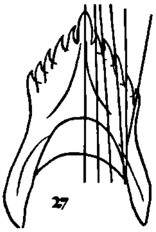

22


23

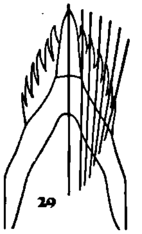

24

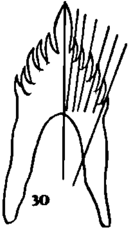

25


26


27


28


29


30

or double rows, *Rizzolia modesta* and *R. ceylonica* cannot be generically separated from *R. peregrina* on the basis of this single peculiarity.

Marcus also mentioned the possibility of including in *Dondice, Hervia emurai* BABA, 1937 and *H. inconspicua* BABA, 1938. Neither of these species can be congeneric with *Caloria occidentalis* or *Caloria maculata,* nor can they be ascribed to *Rizzolia.* Many peculiarities of *H. emurai* are inconsistent with the rizzoliid character and present noticeable affinities with the true facelinids (jaws, teeth, crowding of papillae in the third group, three general and separated groups of papillae, etc.). As to *H. inconspicua,* the description does not allow a clear generic allocation.

Finally, we have to consider the systematic position of *Favorinus horridus* MACNAE, 1954. This eolid, which was erroneously ascribed to *Favorinus* by the original author, and more recently to *Dondice* by MARCUS, 1958, upon the basis of misconceptions of the taxonomic value of distinctive pecularities in the *Facelinacea,* requires careful attention. It appears to me useless to discuss the assignment to *Favorinus* since no author would actually include it in this genus. The mere absence of *Favorinus*-like jaws is sufficient to exclude it from the Favorinidae. Regarding its allocation to *Dondice,* it is necessary to give some consideration to the striking statements by MARCUS (1958, p. 61—62). It can be said that: (1) there is no *Favorinus*-like tooth in *horridus,* but a *Phyllodesmium*-like radula, which is quite different; (2) a *Favorinus*-like radula and *Favorinus*-like jaws are sufficient characters to justify the generic allocation; this is the experience of one century of research on facelinids, and it is only upon the basis of this distinctive character that the favorinids can be safely and easily identified; (3) it must be questioned whether it is allowed to include species bearing smooth and denticulate edges of the jaws (or those with single and multiple series of denticles) in the same genus (RISSO-DOMINGUEZ, 1962).

It was only on account of a supposed resemblance that Odhner, Macnae and Marcus have regarded the teeth of *H. serrata* and *F. horridus* as having a *Favorinus*-like shape.

Figs. 1—30. A comparison of radulae from phyllodesmids and facelinids: 1, *Phyllodesmium xeniae* (after GOHAR & ABOUL-ELA, 1957); 2, *Babaiella serrata* (after BABA, 1949); 3, *Phyllodesmiopsis horridus* (after MACNAE, 1954); 4, *Favorinus albus* (after VAYSSIÈRE, 1888); 5, *Globiferina noumeae* (after RISBEC, 1953); 6, *Pteraeolidia semperi* (after BABA, 1949); 7, *Dondice occidentalis* (after MARCUS, 1958); 8, *Moridilla brockii* (after BERGH, 1888); 9, *Nanuca sebastiani* (after MARCUS, 1957); 10, *Caloria maculata* (after PRUVOT-FOL, 1954); 11, *Rizzolia kaoruae* (after MARCUS, 1957); 12, *Godiva quadricolor* (after MACNAE, 1954); 13, *Amanda armata* (after MACNAE, 1954); 14, *Phestilla sibogae* (after BERGH, 1905); 15, *Facelinella quadrilineata* (after BABA, 1949); 16, *Rizzolia modesta* (after BABA, 1949); 17, *Rizzolia ceylonica* (after BABA, 1949); 18, *Phidiana inca* (after MARCUS, 1959); 19, *Phidiana selencae* (after BERGH, 1879); 20, *Echinopsole fulvus* (after MACNAE, 1954); 21, *Acanthopsole rubrovittata* (after TRINCHESE, 1879); 22, *Acanthopsole olivacea* (after MACNAE, 1954); 23, *Acanthopsole lugubris* (after BERGH, 1882); 24, *Facelina bostoniensis* (after BERGH, 1885); 25, *Facelina annulata* (after MACNAE, 1954); 26, *Facelina coronata* (after BERGH, 1878); 27, *Facelina punctata* (after TRINCHESE, 1882); 28, *Rolandia hispanica* (after PRUVOT-FOL, 1951); 29, *Facelina elegans* (after ALDER & HANCOCK, 1855); 30, *Facelinopsis marioni* (after VAYSSIÈRE, 1888).

Neither *Babaiella serrata* nor *F. horridus* can find a place among the Facelinacea, since the serrata type of teeth is absent in this tribe. On the other hand, these species do not appear to be congeneric because of the differences in the jaws. Because the jaws of *horridus* are not figured by Macnae, it is only with some hesitation that I propose to separate these species generically. Nevertheless, Macnae's statement is conclusive concerning the smooth character of the jaw's masticatory edges. Thus, I constitute a new genus **Phyllodesmiopsis** with *F. horridus* MACNAE, 1954 as type species.

As has been remarked before, neither *H. serrata* nor *F. horridus* can be regarded as favorinids of rizzoliids, nor as belonging to the Facelinacea, and hence the systematic position of *Babaiella* and *Phyllodesmiopsis* among the Aeolidioidea has to be discussed, I now put forward a third suggestion which differs completely from either of the preceding ones.

II. *Phyllodesmium* EHRENBERG, 1831, *Babaiella* GEN. NOV AND *Phyllodesmiopsis* GEN. NOV., MEMBERS OF THE PHYLLODESMIACEA, NEW SUPERFAMILY OR TRIBE

It is evident from a glance at the figures depicting living specimens (BABA, 1937, pl. II fig. 5; BABA, 1949, pl. XLVI fig. 157; MACNAE, 1954, pl. I fig. 4; GOHAR & ABOUL-ELA, 1957, pl. I fig. 1) that one cannot overlook the striking resemblances in external morphology and colouring between *Phyllodesmium, Babaiella* and *Phyllodesmiopsis*: (1) A quite uniform colouring of the body, head, tentacles, rhinophores and papillae of a typical opaque or semiopaque iridiscent bluish, lilac or pinkish colour. The complete absence of the sharp and bright pigmentation commonly found in the Facelinacea appears characteristic of all known phyllodesmids, including uncertain forms, such as *Phidiana tenuis* ELIOT, 1905 and *Aeolidia poindemiei* RISBEC, 1928. This colouring has been stressed by authors who have had occasion to see living animals. (2) The phyllodesmid type of papillae is typical and cannot be mistaken. It is not found in other eolids: they are unusually long, flattened and curved, with a vermiform aspect and characteristic knobs. By these papillae phyllodesmids can be identified, even from undetailed figures. (3) A short head as compared with either the facelinid or aeolidiellid type of head. (4) A relatively depressed body.

Closer examination of the anatomy and of details of the morphology also reveals additional interesting features: (5) A very anterior position of the genital pore, almost under the rhinophores. This character is very rare in the Aeolidioidea. (6) A very typical structure of the radular teeth, which requires a separate consideration. (7) Papillae which are easily cast off at the slightest disturbance. (8) A curious structure of the liver diverticula. It is expected that histological studies will reveal with greater details more important differences and the reasons of that aberrant structure, which undoubtedly may be connected with the alcyonarian diet. Perhaps the structure already described by RISBEC (1928, p. 247, fig. 78) may be general in this group. (9) An ample fulcrum in the jaws as in the aeolidiellids.

Accordingly, it can be said that many of these characteristics are unique and mostly absent in the Facelinacea or other eolid tribes. These structures appear on the whole to be absolutely distinctive of the phyllodesmids, which thus, merely on the basis of conspicuous external features, are sharply separated from all other eolid tribes. The phyllodesmids probably thus form an extremely homogeneous group, the characters of which are for the greater part constant and not found duplicated in any other tribe. Consequently it appears advisable to separate them from the Facelinacea into a new tribe or superfamily, the Phyllodesmiacea. This is constituted on the same principles used to separate the Facelinacea from the Aeolidiacea.

III. THE RADULA OF THE PHYLLODESMIACEA AND ITS TAXONOMIC SIGNIFICANCE

An examination of the figs. 1—30 on the plate shows clearly that in the Phyllodesmiacea the axes of the lateral serrations or pseudodenticles diverge from the axis of the median cusp in a very pronounced angle (more than 40°), whereas in the Facelinacea the axes of the lateral denticles are almost parallel with that of the median cusp, so that the angle, if any, is practically negligible (not more than 20°). This appears to be a general feature in the Facelinacea and so far as I have observed there are no exceptions.

Apparently, there is no intergradation (angles from 20° to 45°) between these two types of teeth. Consequently, it may be quite pertinently argued that this noteworthy peculiarity can be used as a sharp distinguishing character with high diagnostic value, and solely upon the basis of this character the phyllodesmids may be identified with or separated from the Facelinacea. It is necessary to search in other distant tribes to find similar examples of somewhat related types of teeth with a similar divergency of the lateral denticles, perhaps only the Cuthonacea can offer some examples (e.g. *Piseinotecus* MARCUS, 1955).

This remarkable difference between the Facelinacea and the Phyllodesmiacea can be easily understood if we consider the respective functions of the teeth, which in the facelinids clearly have a different function from that in the phyllodesmids. The hook-shaped central cusp or few uniform denticles of the facelinidean teeth merely serve the purpose of hooking the small hydroid polyp already cut off and extirpated from the stem by the powerful and unusually rapid action of the jaws. The radula plays a quite secondary role: merely pulling or discharging the complete polyp into the oesophagus, the real predatory act being restricted to the activity of the jaws.

On the contrary, such remarkably distinct structures as the serrated teeth of the Phyllodesmiacea or the pectinate ones of the Aeolidiacea, with their broadly displayed lacerating edge, are intended for a very different function: they play a direct role in the predatory act, boring into and tearing off the flesh of a large anthozoan polyp, of equal or larger size than the predator. Considering this special structure it is not difficult to realize that the Aeolidiacea exclusively prey on sea anemone-like coelenterates, the Aeolidiellidae on Actiniaria, the Aeolidiopsidae on Zoantharia. Although there is no report extant concerning the specific prey of the Cerberillidae, there can be little doubt about the anthozoan nature of their food.

As might be expected, the phyllodesmids also prey on large polyps. GOHAR

& ABOUL-ELA (1957, p. 133) have given some interesting details on the predaceous habits of *Phyllodesmium* upon *Heteroxenia* and *Xenia*[1]). Consequently, it seems obvious that the curious phyllodesmid serrated teeth are intended for feeding on Alcyonaria, very possibly on a few specific families or genera, a class of food which resembles the prey of the Aeolidiacea in size and considerably differs from the much smaller size of the prey of the Facelinacea. It is evident that a polyp of practically the same size as the slug cannot be completely swallowed at once, as is done with the specific food of the Facelinacea, the small hydranths of Hydrozoa. This explains the apparent resemblance between the teeth of *Phyllodesmium* and those of the aeolidiellids, an argument used by older authors for referring Phyllodesmium to this family.

It is evident from the figures of BERGH (1861), GOHAR & ABOUL-ELA (1957), BABA (1949) and MACNAE (1954) that *Phyllodesmium, Babaiella* and *Phyllodesmiopsis* have a similar type of tooth[2]). As MACNAE (1954, p. 20) has correctly pointed out, there are only serrations and no denticles, and the name *serrata* applied by Baba clearly accounts for this noticeable peculiarity. The rather schematic or undetailed figures do not permit the distinction of structural differences which are to be regarded as of taxonomic value for generic distiction. We do not know whether the higher number of denticles in *Phyllodesmium* really is typical for this genus. In the light of the meagre data available there is an apparent homogeneity in the radular shape. The bluish colouring of teeth reported by GOHAR & ABOUL-ELA (1957, p. 136) may suggest that the colour of the radula could have some diagnostic value (see RISSO-DOMINGUEZ, 1962) since it is a distinguishing character in other nudibranchs. Slow acting polyamines to isolate radulae (RISSO-DOMINGUEZ, 1964 a) will be employed with success for mounting radulae in their natural colours and obtaining the necessary data for comparative studies in this group.

Variation from what may be called the basic facelinidean type of radula,

---

[1]) It is interesting to note that this was known since Ehrenberg, being apparently overlooked in the course of the last 100 years. However, BERGH (1858, p. 33, foot-note) clearly mentioned: "Aeolidierne synes meest at leve af Hydroider (Lovén, Öfvers, 1844, p. 50); Ehrenberg angiver dog *Phyllodesmium hyalinum* levende af Xenier; SARS (Wiegm. Arch., 1840, **1**, p. 209) *Aeolidia bodoënsis* naerende sig af *Actinia viduata,* M., og Quatrefages (Ann. Sc. nat. Zool., **19**, 1843, p. 284) fandt i Maven af en med hans *Eolidina* beslaegtet Form et i begyndende Oplösningstilstand vaerende Skelet af en Fisk; jeg selv har i Maven af en grönlandisk Aeolidie fundet flere större Muslingkrebs (Cyprider) indblandede mellem Hydroider." Consequently, it is evident that GOHAR & ABOUL-ELA quite overlooked this fact already pointed out by Ehrenberg more than a century ago, since these authors do not mention this previous discovery. Incidentally, this revealing note by BERGH, very forcibly suggests that *Eolidina* is a synonym of *Calma,* as already claimed by ODHNER (1939).

[2]) This peculiarity of the phyllodesmids is so conspicuous and characteristic that ENGEL & VAN EEKEN (1962) immediately associated *horridus* with a new phyllodesmid from the Red Sea, which appears distinct from the South African species. The generic allocation of *brevitentaculatus* ENGEL & VAN EEKEN, 1962 can only be established with certainty upon the basis of further studies. There is no information regarding the cutting edges of the jaws.

occurs in two opposite lines. One merely is a further step in the facelinid line of specialization, viz. for manipulation of the small hydroid polyp; no real divergency arises since the prey remains the same. The hook-shaped structure becomes more exaggerated by dispensing with the lateral denticles and throwing all the work on the median cusp, coming to a climax in the *Favorinus*-like tooth (see VAYSSIÈRE, 1888, pl. 4 figs. 30, 31, 32). Thus, the favorinids must be retained in the *Facelinacea.*

On the other hand, the second type results from a real divergency since there is a notable change of food: larger sized polyps or anthozoarian prey. The facelinidean feeding mechanism is useless in this case. There is a considerable increase in the number of lateral denticles and loss of the active role played by the jaws in predation. The predatory act is executed by the radula, and the jaws merely seize the prey. Since there are many types of anthozoarian food, there is not a single or homogeneous divergent line of specialization, but parallelism arises following the same general plan. Theoretically speaking there will be as many smaller divergencies or parallel lines as there are general morphological classes of anthozoarian food. It can be said in general, and neglecting smaller lines or differences, that two main lines of specialization are actually known: *Phyllodesmium*-Alcyonaria and *Aeolidia*-Actiniaria.

Accordingly, the two opposite extremes are *Favorinus* which represents the first type, and *Aeolidia, Baeolidia* and *Phyllodesmiopsis* for the second. It is clear from the observation of such extremes as *Favorinus* and *Baeolidia,* that reduction or disappearing of denticles in radular teeth leads to strong jaws with long and highly denticulated cutting edges, whereas broadening and increasing of denticles in teeth, is associated with decreasing or total disappearance of denticles in the cutting edges (i.e. smooth jaws) (Aeolidiacea and *Phyllodesmiopsis*) or eventually with a type of jaws which bears few denticles, but of much greater size for more effective seizing (*Phyllodesmium).*

Although, as early as 1855, ALDER & HANCOCK (p. 12) pointed at these relationships of the buccal elements in the Nudibranchiata and their prey, their significance in classification unfortunately was overlooked by modern taxonomists, hence the artificial character of many modern systematic arrangements. It is, in this respect, a striking fact that the most specialized member of the Phyllodesmiacea (*Phyllodesmiopsis horridus*) has been described as a *Favorinus*, this genus representing the extreme in the opposite line of specialization. The species shows no resemblance, no convergence, but on the contrary great differences in functions and structures to the genus *Favorinus.* This is an instructive example of the contradictory conclusions resulting from undervaluing the chitinous buccal parts in classification. Thus it seems not justified to include species with smooth jaws and such with denticulated ones in the same genus, or to claim that the radula and jaws "only in a few exceptional cases can be validly used" for classification (see RISSO-DOMINGUEZ, 1962, 1964 b, for a more complete consideration of the Macnae and Marcus classifications and a critique of the principles implied).

I thus reject the views of Macnae and Marcus regarding the arrangement of the Aeolidioidea. Our discussion will make clear the importance of the diet in a natural classification of the Nudibranchiata. If we accept that variations and divergencies in nudibranch morphology result from adaptations to specific types of food, the taxonomic significance of radulae and jaws becomes apparent. These features are intimately connected with often slight differences in prey.

IV. RELATIONSHIPS OF THE PHYLLODESMIDS

Little attention has been paid to these strange eolids in the last century of research on nudibranchs. Surprisingly, ALDER & HANCOCK (1855) did not include the genus *Phyllodesmium* in their Synopsis, although Ehrenberg's other genera were included. Since 1861 not much work has been done on the Phyllodesmiacea. The anatomical account by BERGH (1861) still remains the most important source of knowledge on *Phyllodesmium,* since it was based on the original type material collected by Ehrenberg and examined by Bergh in 1858 during a short visit to the Berlin Museum. BERGH (1892) in his "System" definitely placed this genus among the Aeolidiellids or "Aeolidiidae propriae", but later he only included *Phyllodesmium* with doubt in this group (BERGH, 1905, p. 222). THIELE (1931) merely separated *Phyllodesmium* into a possible subfamily, the Phyllodesminae.

Since Ehrenberg only a few workers have had the opportunity to observe living phyllodesmids (CROSSLAND in ELIOT, 1905; RISBEC, 1928; BABA, 1933; MACNAE, 1954; GOHAR & ABOUL-ELA, 1957 and BURN, 1962). In none of these descriptions detailed anatomical descriptions or even definite data on the external morphology are included. For example, there is no clear figure depicting the shape of the head in details. This is an important gap, since good illustrations of living specimens of members of the Coryphellacea, Cuthonacea, Calmacea, Fionacea, Facelinacea and Aeolidiacea have been known since Alder & Hancock.

It is quite possible that some rare and little known eolids from the Indo-Pacific region may belong to the Phyllodesmiacea and form interesting new genera. Because of the very imperfect descriptions their phyllodesmid nature may easily have been overlooked. A thorough study of the many incompletely described eolids from that region will probably show that several phyllodesmids have already been reported. Two examples are discussed here: (1) *Phidiana tenuis* ELIOT, 1905. Obviously, this form does not belong to *Phidiana,* nor to the Facelinacea, since there is no member in this tribe with thin, transparent and smooth jaws. On the contrary, facelinids have intensively coloured, strong and conspicuously denticulated jaws, because the success of their predaceous habits chiefly depends upon the force exerted by their buccal parts. Moreover, the genus *Phidiana* is restricted to American waters. This eolid does not belong to the Aeolidiacea since it has no pectinate teeth. A good number of characters lead me to suspect its phyllodesmid nature: a) long papillae and the structure of the liver diverticula; b) phyllodesmid-type of colouring; c) a radula clearly agreeing with that of the phyllodesmids; d) smooth jaws; e) easily cast off papillae; f) the rhinophores are only slightly annulated in the distal halves, as in *Phyllodesmium* (cf. GOHAR & ABOUL-ELA, 1957, p. 136). It is noteworthy that the specimens come from the same site and depth, and possibly from the same habitat, as Crossland's specimen of *Phyllodesmium* (cf. Eliot, 1905, p. 287-289). The imperfect description does not permit its reference to *Phyllodesmiopsis* nor the institution of a new genus with *Ph. tenuis* as type species. Its generic position will remain uncertain until more specimens can be studied.

(2) *Aeolidia poindimiei* Risbec, 1928. The typical general aspect and colouring (Risbec, 1928, pl. IX fig. 3), the flattened and very long papillae, the shape of the radular teeth, the structure of the liver diverticula and other details very strongly suggest its phyllodesmid nature. If the characteristic ramifications of the liver described by Risbec (1928, p. 246) and other distinctive characters are also found in *Babaiella serrata,* it would not surprise me when these species prove to be synonyms or at least congeneric. Because we are in almost complete ignorance of the change in the number of serrations by age in the phyllodesmid teeth, there is no sufficient reason for separating it from *Babaiella* at present. The low number of serrations could be common in young specimens. Risbec's specimen only measured 20 mm, whereas the average adult size in phyllodesmids is around 40 mm.

It is unfortunately impossible to treat the relationships between the three genera and other eolid groups with the accuracy one would desire, because the available data are extremely scanty and a good number of phyllodesmid genera have probably still not yet been discovered. I have endeavoured below to give some observations which arose from the study of the actual data; it is to be hoped that thus a beginning has been made towards an understanding of the relationships of the phyllodesmids. There are no data concerning the variability of the most conspicuous features and the criteria to be applied for classification, therefore, remain doubtful until more numerous specimens and species can be studied. The three known genera may be separated principally on the basis of the structure of the cutting edges of the jaws. In *Phyllodesmium* the denticles are enormous and this is a unique peculiarity among eolids. Specimens included in this genus by Ehrenberg, Bergh, Eliot, Baba and Gohar & Aboul-Ela, display no perceptible variations in this feature and it thus appears to be a good diagnostic character for generic identification. *Babaiella,* on the contrary, only bears small facelinid-like denticles, and *Phyllodesmiopsis* constitutes an extreme form by the absence of these structures. Apparently, both *Phyllodesmium* and *Phyllodesmiopsis* followed divergent lines of specialization. The former probably uses the long denticles to retain what they have seized with unrelaxing grip, whereas in *Phyllodesmiopsis* the mechanism is probably similar to that of the aeolidiellids.

Differences of this kind have justified family separation in other tribes and it seems plausible to the writer that at least two families could be distinguished in this taxon, but our knowledge is not yet sufficiently advanced to adopt this course. For practical reasons the three genera may be provisionally included in one single family, the Phyllodesmidae. Theoretically the higher variability displayed by the various groups of the Alcyonaria might suggest that the Phyllodesmiacea will show much more variation than the Aeolidiacea, bearing in mind the differences shown by the aeolidiellids, aeolidiopsids and cerberillids. Being mimetic animals, as demonstrated by GOHAR & ABOUL-ELA (1957, p. 133), they are probably much more numerous than they appear to be, and may continue to furnish new and strange forms to workers in the tropical Pacific. Further studies on these possible new genera will then show if a separation between the Babaiellidae and the Phyllodesmiopsidae has to be established.

In *Phyllodesmium* the egg-capsules only contain a single embryo (GOHAR & ABOUL-ELA, 1957) while in *Phyllodesmiopsis* there are 3 embryos per egg-capsule (MACNAE, 1954, p. 20). Accordingly, there appears to be a striking parallelism with the Aeolidiacea. Here the number of embryos per egg-capsule increases with specialization. This parallelism between *Phyllodesmiopsis* and the more specialized aeolidiellids does not, in my opinion, mean that *Phyllodesmium* should be taken as the less specialized member, nor does it suggest a parallel between *Berghia* and *Phyllodesmium,* since the increase of denticle size in the jaws also has to be considered as an adaptation in the mechanism for seizing the prey (which does not occur in *Phyllodesmiopsis*). These divergencies between the lines of specialization represented by *Phyllodesmium* and *Phyllodesmiopsis* merely point to the fact that the Alcyonaria display a much higher variety of forms than the Actiniaria, also from the point of view of a predator eolid.

Aeolidiellids and phyllodesmids are sharply distinguished from other eolids because they possess in common a number of conspicuous peculiarities which are almost absent or very rare in other tribes. The following are easily noticed: 1) broadening of the lacerating edges and increase of the number of denticles in radular teeth; 2) development of an ample fulcrum in the jaws; 3) loss of denticulated jaw edges; 4) loss of the bright and sharply defined colouring of the Facelinacea; 5) flattening of papillae and higher ramification of liver diverticula. Although there is remarkable parallelism between both groups, the resemblances appear to be almost entirely superficial and adaptive, and not due to a close relationship. For example, flattening of the papillae is a noticeable result of specialization in aeolidiform opisthobranchs when a wider exchange surface with the exterior is required and well developed in Hermaeidae, Calyphyllidae, Myrrhinidae, Phyllodesmidae and Aeolidiellidae. This is easily understood for the aeolidiellids and phyllodesmids since the volume and more toxic character of the anthozoarian food may present physiological problems which are absent or of little importance in the case of the small hydroid prey. Individually, smooth jaws, diffusion of pigmentation, broadening of radular teeth, etc. can hardly be regarded as characters exclusively belonging to one group, they may arise every time when an adaption to anthozoarian food takes place in the Nudibranchiata.

A noteworthy peculiarity of the highly specialized Aeolidiacea (cf. RISSO-DOMINGUEZ, 1964 b) is the tendency towards increase of density of populations as they become more specialized (from *Berghia* to *Aeolidia*), or more adapted to a successful predation on sea anemones. This also appears to be a character of the Phyllodesmiacea. *Phyllodesmium* may be the most abundant eolid in the Red Sea; it was one of the earliest eolid genera discovered in tropical or foreign waters. The report by GOHAR & ABOUL-ELA (1957) strongly supports this view. *Phyllodesmiopsis horridus* is a very common eolid in South African waters (MACNAE, 1954, p. 19). As for *Babaiella serrata*, no conclusions can be drawn due to the particular character of Sagami Bay, which apparently happens to be an occasional locality where tropical nudibranchs may live which normally inhabit more southern waters (BABA, 1949).

The complete tribe Phyllodesmiacea appears to belong exclusively to tropical waters as already reported (RISSO-DOMINGUEZ, 1962, p. 165), being confined to the Indo-Pacific area, as is also the case with the Myrrhinacea. It seems to me that the term "Indo-Pacific nudibranch fauna" must be chiefly applied to the very rich nudibranch fauna which inhabits the Asiatic and African continental coastal waters, or to be more exact to the area inhabited by the aberrant polycerid family Kalingidae. This remark appears necessary because the term Indo Pacific Nudibranch Fauna has often been used in a rather wide sense, including most of the Pacific region with as only exclusion the West American coasts. Although the nudibranch fauna of numerous islands in the central Pacific has a clear Indo-Pacific origin, such regions must be excluded if this term is used in its correct and restricted sense. The paucity of forms from islands which have never been connected with a continent (ELIOT, 1903, p. 573), a fact clearly explained by RISBEC (1928, p. 314), may help to establish definite boundaries between both regions. Concerning the character of the distribution of *Phyllodesmium* after GOHAR & ABOUL-ELA (1957) and other claims for a Red Sea origin, it appears advisable to emphasize that actual evidence does not support such views. On the contrary, *Phyllodesmium hyalinum* may have a rather wide distribution in the Indo-Pacific continental waters, as wide as *Kalinga ornata*, from East Africa to Japan. It is curious that GOHAR & ABOUL-ELA (1957, p. 133) have stressed the association of *Phyllodesmium* with *Heteroxenia* and *Xenia*, and overlooked the fact that these alcyonarian genera are not uniformly spread in the Indo-Pacific (HICKSON, 1903). It seems obvious that the abundance of a predator eolid must closely follow that of the prey, particularly in the case of such intimate associations. Further workers searching for phyllodesmids must take into account the statements by HICKSON (1903, p. 477—478) concerning the favourable areas for the growth of these alcyonarian colonies in the Indo-Pacific region.[3])

V. CONCLUDING REMARKS

It is strongly recommended:

(1) that workers in the tropical and subtropical Pacific, when collecting Alcyonaria, give careful attention to the eolid predators associated with them. Owing to the mimetic character of the phyllodesmids it may be

---

[3]) This explains the preponderance of the Phyllodesmiacea in the Red Sea, but does not support GOHAR & ABOUL-ELA's claims. It seems obvious that there are several other suitable areas for phyllodesmids in the equatorial Indo-Pacific region.

expected that the number of undiscovered genera and even families is still important,

(2) that *Babaiella serrata* and *Phyllodesmiopsis horridus* will be thoroughly studied in the details of their anatomy and histology as well as in their predatory activities,

(3) that marine biologists give special attention to the associations between phyllodesmids and Alcyonaria. The classical relationships between the predaceous eolids and certain definite coelenterate groups (sea anemones, hydroids and medusae) are known since the earlier studies on the Nudibranchiata, being pointed out by GOSSE (1854, p. 124—125; 112—116) more than a hundred years ago. A good amount of knowledge is already available concerning these unusually interesting subjects through the works of many authors. Strangely enough, little or no data have been advanced during one century of research on nudibranchs regarding eolid predators upon other coelenterate groups. Recent discoveries, such as the aberrant genus *Aeolidiopsis* PRUVOT-FOL, 1956, which preys on the zoantharian *Palythoa*, and the association between *Phyllodesmium* and the alcyonarian genera *Xenia* and *Heteroxenia* rediscovered by GOHAR & ABOUL-ELA (1957), clearly point to the conclusion that most groups of coelenterates will have typical and taxonomically well defined eolid predators,

(4) that it is of considerable importance that studies such as made by BURGIN-WYSS (1961) on other eolids should be undertaken on phyllodesmids. The uniformity of pigmentation displayed by known phyllodesmids (*Phyllodesmium, Babaiella* and *Phyllodesmiopsis*) and the parallelism shown with the most specialized aeolidiellids (*Puelchaeolidia, Baeolidia, Spurilla* and *Aeolidia*) clearly point to the fact that the relationships in pigmentation in the association 'phyllodesmidian predator - alcyonarian prey' will have a great resemblance to that recorded by RISSO-DOMINGUEZ (1964 b) for *Puelchaeolidia.*

VI. SUMMARY

The eolids described under the names *Hervia serrata* BABA, 1949 and *Favorinus horridus* MACNAE, 1954, which were recently ascribed to other facelinid genera, such as *Godiva* (cf. MACNAE, 1954) and *Dondice* (cf. MARCUS, 1958), because of misconceptions on the taxonomic value of distinctive peculiarities in the Facelinacea, require a proper generic designation according to the author. Therefore the new genera *Babaiella* and *Phyllodesmiopsis* were constituted with *H. serrata* and *F. horridus* as type species. The distinguishing serrate teeth and other significant features exclude both genera from the Facelinacea and indicate a closer relationship with *Phyllodesmium,* a relatively abundant but very imperfectly known form, which was included among the aeolidiellids by BERGH (1892) upon the basis of an apparent resemblance of the radular teeth, which character, however, is considered to be the result of a remarkable parallelism due to the anthozoarian diet. The radula of the phyllodesmids is clearly different from the radular shapes of both the facelinids and aeolidiellids. From the former group it differs in having serrations (not denticles) which display a high degree of divergence from the axis of the median cusp. Even on external characters the phyllodesmids are already unmistakably characterized and cannot be confused with other eolids. There are thus substantial reasons for believing that the Phyllodesmiacea form a characteristic and close group which must be separated from both the Facelina-

cea and the Aeolidiacea, and their degree of specialization parallels the stage attained by the most specialized aeolidiellids. Our imperfect knowledge of this group does not yet allow further comparative studies; detailed anatomical and histological accounts will be necessary before our point of view can be placed on a more sure scientific basis. The phyllodesmids appear to belong exclusively to the Indo-Pacific region and a good number of new forms can be expected, because they are mimetic animals and little or no extensive collecting has been made on the most promising coasts until recently.

LITERATURE

ALDER, J. & A. HANCOCK
1855 A monograph of the British nudibranchiate Mollusca, **7**, 9 pls. (Ray Society, London).

BABA, K.
1933 Supplementary note on the Nudibranchia collected in the vicinity of the Amakusa Marine Biological Laboratory. — Annot. zool. japon., **14** : 273—283, figs. 1—8.
1937 Opisthobranchia of Japan, II. — J. Dept. Agric. Kyushu Imp. Univ., **5** : 289—344, figs. 1—18, pls. 1—2.
1938 Opisthobranchia of Kii, Middle Japan. — J. Dept. Agric. Kyushu Imp. Univ., **6** : 1—19, figs. 1—14.
1949 Opisthobranchia of Sagami Bay collected by His Majesty the Emperor of Japan: 1—201, pls. 1—50. (Iwanami Shoten, Tokyo).
1955 Opisthobranchia of Sagami Bay, supplement: 1—59, pls. 1—20. (Iwanami Shoten, Tokyo).

BERGH, R.
1858 Anatomisk undersögelse af Fiona atlantica Bgh. — Vidensk. Medd. Dansk naturh. Foren., **1875**: 1—65, pls. I—II.
1861 Anatomisk undersögelse af Phyllodesmium hyalinum, Ehrberg. — Vidensk. Medd. Dansk naturh. Foren., **1860**: 103—116, pl. 2.
1878 Beiträge zur Kenntnis der Aeolidiaden, 5. — Verh. K. K. zool. - bot. Ges. Wien, **27**, 807—840, pls. XI—XIII.
1879 Beiträge zur Kenntnis der Aeolidiaden, 6. — Verh. K. K. zool. - bot. Ges. Wien, **28**, 553—584, pls. VI—VIII.
1880 Beiträge zur Kenntnis der japanischen Nudibranchien, 1. — Verh. K. K. zool. - bot. Ges. Wien, **30**: 155—200, pls. I—V.
1882 Beiträge zur Kenntnis der Aeolidiaden, 7. — Verh. K. K. zool. - bot. Ges. Wien, **32**: 7—74, pls. I—VI.
1885 Beiträge zur Kenntnis der Aeolidiaden, 8. — Verh. K. K. zool. - bot. Ges. Wien, **35**: 1—60, pls. I—VII.
1888 Beiträge zur Kenntnis der Aeolidiaden, 9. — Verh. K. K. zool. - bot. Ges. Wien, **38**: 673—706, pls. XVI—XX.
1892 System der Nudibranchiaten Gasteropoden. Malacologische Untersuchungen, **3** — 18: 995—1168, in: SEMPER, C. (ed.) Reisen im Archipel der Philippinen, 2, Wiss. Res. (Wiesbaden).
1905 Die Opisthobranchiata der Siboga-Expedition. — Siboga-Exp., **50**: 1—248, pls. 1—20.

BURGIN-WYSS, U.
1961 Die Rückenanhänge von Trinchesia coerulea (Montagu). Eine morphologische Studie über Farbmuster bei Nudibranchiern. — Rev. suisse Zool., **68**: 461—582, pl. I figs. 1—49.

BURN, R.
1962 Descriptions of Victorian Nudibranchiate Mollusca, with a comprehensive review of the Eolidacea. Mem. nation. Mus. Vict. **25**: 95—128.

ELIOT, C.
1903 Nudibranchiata, etc. — in J. STANLEY GARDINER ed.: The fauna and geography of the Maldive and Laccadive archipelagoes, **2** (1): 540—573, pl. XXXII. (Cambridge).
1905 On some nudibranchs from East Africa and Zanzibar, 6. — Proc. zool. Soc. London, **1904** (2): 268—298, pls. XVI—XVII.

ENGEL, H. & C. J. VAN EEKEN
1962 Red Sea Opisthobranchia from the coast of Israel and Sinai. — Bull. Sea Fish. Res. Stat. Haifa, **30**: 15—34, figs. 1—7.

GOHAR, H. A. F. & I. A. ABOUL-ELA
1957 On a new nudibranch "Phyllodesmium xeniae" (from the Red Sea, with a description of its development). — Publ. mar. biol. Stat. Al Ghardaqa, **9**: 131—144, 1 pl. figs. 1—9.

GOSSE, P. H.
1854 (Natural History). Mollusca: 1—328. (Soc. Promot. Christian Knowledge, London).

HICKSON, S. J.
1903 The Alcyonaria of the Maldives, 1 — in J. STANLEY GARDINER: The fauna and geography of the Maldive and Laccadive archipielagoes, **2** (1): 473—502, pls. XXVI—XXVII. (Cambridge).

MACNAE, W.
1954 On some eolidacean nudibranchiate molluscs from South Africa. — Ann. Natal Mus., **13** (1): 1—50, pls. I—II figs. 1—32.

MARCUS, E.
1955 Opisthobranchia from Brazil. — Bol. Fac. Fil. Univ. Sao Paulo (Zool.), **20**: 89—200, figs. 1—285.
1957 Opisthobranchia from Brazil (2). — J. Linn. Soc. London (Zool.), **43**: 390—486, figs. 1—246.
1958 On West Atlantic Opisthobranchia. — Amer. Mus. Nov. **1906**: 1—82, figs. 1—111.
1959 Lamellariacea und Opisthobranchia. Reps. Lund Univ. Chile Exp. 1948-49, **36**. — Lunds Univ. Årsskr., (N.F.) (2) **55** (9): 1—134, figs. 1—192.

ODHNER, N. H.
1939 Opisthobranchiate Mollusca from the western and northern coasts of Norway. — Kgl. Norske vidensk. Selsk. Skr., **1939** (1): 1—93.

PRUVOT-FOL, A.
1951 Etude des Nudibranches de la Méditerranée. — Arch. Zool. exp. gén., **88** (1): 1—79, pls. I—IV figs. 1—42.
1954 Mollusques Opisthobranches. — Faune de France, **58**: 1—460, 1 pl., 173 figs. (P. Lechevalier, Paris).
1956 Un Aeolidien nouveau des mers tropicales: Aeolidiopsis ransoni n.g. n.sp. — Bull. Mus. nation. Hist. nat. Paris, (2) **28**, 2: 228—231.

RISBEC, J.
1928 Contribution à l'étude des Nudibranches néo-calédoniens. — Faune Col. Franç., **2** (1): 1—238, figs. 1—98, 3 maps, pls. I—XII and A—D.
1953 Mollusques Nudibranches de la Nouvelle-Calédonie. — Faune Union Franç., **15**: 1—189, figs. 1—126.

RISSO-DOMINGUEZ, C. J.
1962 Notes on the Facelinacea, 1. Introduction. — Ann. Mus. civ. Stor. nat. Genova, **73**: 141—171.
1964a The use of alkylene polyamines to isolate radulae, 2. Practice of the technique. — Stain Techn., in press.
1964b On the new genus Puelchaeolidia, with notes on the taxonomy of the Aeolidioidea. — In press.

THIELE, J.
1931 Handbuch der systematischen Weichtierkunde, **1**: 1—778, I—VI, figs. 1—783. (G. Fischer, Jena).

TRINCHESE, S.
1879 Aeolididae e famiglie affini del porto di Genova, Atlante, 1. — Atti R. Univ. Genova, **2**: 1—94, pls. 1—40.
1882 Aeolididae e famiglie affini del porto di Genova, Testo, 2. — Atti R. Accad. Lincei, (3) **10**: 1—142, pls. 1—80.

VAYSSIÈRE, A.
1888 Recherches zoologiques et anatomiques sur les Mollusques Opithobranches du Golfe de Marseille, 2: Nudibranches et Ascoglosses. — Ann. Mus. Hist. nat. Marseille, (Zool.) **3** (4): 5—160, pls. I—VII.

WINCKWORTH, R.
1941 The name Cratena. Proc. malac. Soc. London, **24** 4: 146—149.

CARLOS J. RISSO-DOMINGUEZ
Azcuénaga 1872
Buenos Aires
Argentina