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ELEVENTH INTERNATIONAL MALACOLOGICAL CONGRESS
(SIENA 30TH AUGUST-5TH SEPTEMBER 1992)

Workshop on Systematic and Ecology in the Opistobranchs

Direttore Responsabile: Fernando Ghisotti

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ELEVENTH INTERNATIONAL MALACOLOGICAL CONGRESS
SIENA 30th AUGUST - 5th SEPTEMBER 1992

WORKSHOP ON SYSTEMATICS AND ECOLOGY IN THE OPISTOBRANCHS

edited by RICCARDO GIANNUZZI-SAVELLI

SOCIETÀ ITALIANA DI MALACOLOGIA - 1993

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SIENA 30th AUGUST - 5th SEPTEMBER 1992

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edited by RICCARDO GIANNUZZI-SAVELLI

FOREWORDS

I am glad to introduce to this volume of the proceedings of the Workshop on Systematics and Ecology in the Opisthobranchs, organized by Riccardo Cattaneo-Vietti duringthe Eleventh International Malacological Congress organized by me in Siena (30th August - 5th September 1992) on behalf of Unitas Malacologica.

This volume and those of the other workshop and symposia of the Congress reflect the strategy of Unitas Malacologica of printing selected papers on subjects which could be of interest to the entire zoological community and particularly large number of malacologists.

As promoter of this new strategy, I hope it will be successful inbroadcasting scientific activity of Unitas Malacologica and its members. I warmly thank all colleagues, who like Riccardo Cattaneo-Vietti not only organized the symposia and workshops but edited the volumes. I must also thank the Società Italiana di Malacologia for agreeing to publish this volume as an issue of its journal, The Bollettino Malacologico, and the Ministero dei Beni Ambientali e Culturali who provided financial support.

FOLCO GIUSTI, Ex-president Unitas Malacologica

PREFAZIONE

Sono lieto di presentare questo volume dei lavori del Workshop sulla Sistematica ed Ecologia degli Opistobranchi, organizzato da Riccardo Cattaneo-Vietti nel corso dell'11° Congresso Internazionale di Malacologia da me organizzato a Siena (30 agosto-5 settembre 1992) per conto dell'Unitas Malacologica. Questo volume e quelli degli altri workshops e simposi rispecchiano la strategia dell'Unitas Malacologica di pubblicare una selezione di lavori che possono interessare tutti gli zoologi e in particolare un gran numero di malacologi.

Quale promotore di questa nuova strategia, spero che la pubblicazione abbia successo nel diffondere l'attività scientifica della Unitas Malacologica e dei suoi membri. Ringrazio caldamente tutti i colleghi che, come Riccardo Cattaneo-Vietti, non solo hanno organizzato i simposi e i workshops, ma hanno anche curato le pubblicazioni. Devo anche ringraziare la Società Italiana di Malacologia per aver accettato di pubblicare questo volume quale fascicolo della rivista Bollettino Malacologico, e il Ministero dei Beni Ambientali e Culturali che ha fornito il supporto finanziario.

FOLCO GIUSTI, Ex-presidente della Unitas Malacologica

Riccardo Cattaneo - Vietti*

WORKSHOP ON SYSTEMATICS AND ECOLOGY IN THE OPISTHOBRANCHS

(Eleventh Internation Malacologica Congress)

During the Eleventh International Malacological Congress, organized by Folco Giusti, President of the Unitas Malacologica, in Siena (30th August - 5th September, 1993), a Workshop on Systematics and Ecology in the Opistobranchs was held.

It was a good oppurtinity for hearing the latest results of many colleagues and for exchanging ideas and discussing problems on this peculiar group of the Mollusca.

Opisthobranchs are indeed, a very good research group, but they are not studied as they could be and we could all try to enlarge our research field.

Today the studies on the Opistobranchs mainly concern taxonomy and with great success: even in such an extensively studied as the Mediterranean Sea, new species and records are still frequent, but a lot has to be done to clarify sunonymies, and studying better specific variabilities in colour patterns, radular apparatus and reproductive systems. Too many species have been described without considering all this and a review of genera and families, preparing better defined diagnosis, could be very useful.

Many researchers have spent a loto of time preparing faunistic catalogues of determinated regions: this led to a deeper understanding of the zoogeography of the group. However more general studies and comparative analysis, particularly among different regions and taking into consideration the numerous physical, chemical and biological factors which play a role in species distribution, are lacking and the available is insufficient.

Few studies have been devoted to the ecology of Opisthobranchs at any stages of their life cycle. Studies on larval behaviour and ecological strategies, such as the relationships between larval metamorphosis and the presence of the prey would be of great interest. The variability in colour patterns of many species is another field in which hypotheses on mimicry, camouflage, prey-predator relationship could be tested.Opisthobranchs have often been used as lab material for research in neurophysiology and behavior, due to their large nerve cells. In biochemistry Opisthobranchs have generally been regarded as mere "chemical factories" producinginteresting substances, and only in a few cases has biochemical study been the basis for research of wider interest to support evolutionary studies and phylogenetic deductions. The excellent results obtained by specialists of other mollusc groups reported in the Symposium in Molecular Techniques and Molluscan Phylogenu of the same Congress, speak strongly in favour of a new research field for Opisthobranchiologists, that of genetic methods

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*Istituto di Zoologia dell'Università degli Studi - via Balbi 5, I-16126 Genova, Italy.

applied to taxonomy and phylogenesis. A good field of research could be the rare species: to analyze why a species is rare, what advantage it has had or if it is only a hybrid seems important, not only in taxonomy. In this, such as in other fields, genetic methods which have not been applied so much, could help to resolve many doubts. Such research would require cooperation between taxonomists and geneticists too.

There were some of the topics touched upon in the Workshop on Systematics and Ecology in Opisthobranchs, but unfortunately not all the partecipants had their papers ready for publication in time. This is why the present volume is small and does not fully represent the scientific content of the workshop. I am not afraid to say that I would have preferred a better collaboration, but I still believe that this type of informal meeting has primarily an important role allowing an exchange of views, ideas and results. So, I very much hope that this kind of meeting will become a regular appointment in the organization of the Congresses of Unitas Malacologica.In closing, I would like to thank my friend and colleague Folco Giusti, the organizer of the Congress and our host in Siena, and Fernando Ghisotti, Honorary President of the Italian Malacological Society and Editor of the Bollettino Malacologico, who both contributed work and economic support to the workshop and the present volume.

Partecipanti at Workshop
"SISTEMATICA ED ECOLOGIA DEGLI OPISTOBRANCHI"

R. CattaneoVietti (Genova)
T. Gascoigne (London)
K.R. Jensen (Copenhagen)
D. Koutsoubas (Thessaloniki)
E.M. Martinez (Oviedo)
P.M. Mikkelsen (Fort Pierce)
G. Rodriguez (Oviedo)
W.B. Rudman (Sydney)
A. Spinella (Napoli)
G. Villani (Napoli)
H. Wägele (Bielefeld)
N. Yonow (Swansea)

Riccardo Cattaneo-Vietti*

WORKSHOP SULLA SISTEMATICA ED ECOLOGIA DEGLI OPISTOBRANCHI

(Undicesimo Congresso Internazionale di Malacologia)

Durante l'undicesimo Congresso Internazionale di Malacologia, organizzato a Siena da Folco Giusti, Presidente dell'Unitas Malacologica, (30 agosto - 5 settembre 1992), è stato tenuto un workshop sulla Sistematica ed Ecologia degli Opistobranchi.

È stata una buona occasione per apprendere i più recenti risultati ai quali sono pervenuti molti colleghi e per avere uno scambio di opinioni sui problemi connessi a questo particolare gruppo di molluschi. In effetti gli Opistobranchi costituiscono un ottimo gruppo di ricerca, ma il loro studio non è ancora approfondito come dovrebbe essere: nostro compito è di ampliare il campo delle nostre ricerche.

Attualmente gli studi sugli Opistobranchi riguardano essenzialmente la tassonomia, con notevoli contributi: persino in un'area profondamente studiata quale è il mare Mediterraneo, sono frequenti le segnalazioni di nuove specie, ma vi è ancora molto lavoro da svolgere per quanto concerne eventuali sinonimie e variabilità specifica di colorazione, struttura dell'apparato radulare e riproduttivo. Troppe specie sono state descritte senza tener conto di ciò e sarebbe veramente auspicabile la pubblicazione di un catalogo faunistico che, descrivendo i vari taxa, presentasse diagnosi più complete che tengano conto di queste variabili.

Sono stati pubblicati cataloghi relativi ad altre aree del globo, i quali hanno contribuito alla conoscenza della zoogeografia del gruppo. Tuttavia studi più generali e di analisi comparativa, in particolare sui fattori - fisici, chimici, biologici - che influiscono sulla distribuzione delle specie, mancano ancora e quanto è disponibile è insufficiente.

Esistono pochi studi dedicati all'ecologia degli Opistobranchi in tutti gli stadi del loro ciclo vitale. Sarebbero di grande interesse studi sul comportamento larvale e sulle strategie ecologiche, quali le relazioni fra la metamorfosi larvale e la presenza di prede. La variabilità della colorazione di molte specie è un altro campo di notevole interesse, nel quale potrebbero essere verificate le ipotesi di mimetismo, camouflage e le relazioni fra predatore e preda.

Gli Opistobranchi sono stati spesso utilizzati come materiale di laboratorio per ricerche comportamentali e di neurofisiologia , date le notevoli dimensioni delle loro cellule nervose. Nel campo della biochimica, gli Opistobranchi sono stati generalmente usati come mere "fabbriche" di nuove e interessanti sostanze e solo in pochi casi gli studi biochimici sono serviti come base per ricerche di più ampio interesse che fornissero elementi in favore dell'evoluzione e deduzione filogenetica.

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* Istituto di Zoologia dell'Università degli Studi - via Balbi 5, I-16126 Genova, Italy.

Gli eccellenti risultati ottenuti da specialisti in altri gruppi di molluschi e riferiti nelle relazioni del simposio su Tecniche Molecolari e Filogenia dei Molluschi dello stesso Congresso, sottolineano l'importanza di un nuovo campo di ricerca per gli studiosi di Opistobranchi, e cioè quello dei metodi genetici applicati alla tassonomia e alla filogenesi. Queste ricerche richiederebbe la cooperazione fra tassonomisti e genetisti.

Altro interessante campo di ricerca potrebbe essere quello delle specie rare: studiare perché una specie è rara e quale ne sia la ragione se lo è veramente, oppure se invece si tratti di un ibrido: sia in questo, sia in altri campi dîndagine non sono stati molto applicati i metodi genetici che potrebbero risolvere molti interrogativi. Anche in questi casi sarebbe auspicabile una cooperazione fra tassonomisti e genetisti.

Alcuni di questi argomenti sono stati trattati nel corso del workshop sulla Sistematica ed Ecologia degli Opistobranchi, ma sfortunatamente non tutti i partecipanti hanno preparato in tempo i loro lavori per la pubblicazione. Questa è la ragione per la quale il presente fascicolo è di dimensioni piuttosto ridotte e non rispecchia appieno il contenuto scientifico del workshop. Avrei effettivamente desiderato una maggiore collaborazione, ma tuttavia sono fermamente convinto che questo tipo di incontri informali assolva l'importante, primaria funzione di consentire scambio di pareri, idee e risultati. Spero quindi veramente che esso sia il primo di una serie da tenersi regolarmente in occasione dei Congressi della Unitas Malacologica.

Desidero infine ringraziare il mio amico e collega Folco Giusti, perfetto organizzatore del Congresso, e nostro ospite a Siena, e Fernando Ghisotti, Presidente onorario della Società Italiana di Malacologia ed editore del Bollettino Malacologico: entrambi hanno prestato la loro opera e il supporto economico per il workshop e il presente volume.

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Paula M. Mikkelsen (*)

MONOPHYLY VERSUS THE CEPHALASPIDEA (GASTROPODA, OPISTHOBRANCHIA) WITH AN ANALYSIS OF TRADITIONAL CEPHALASPID CHARACTERS (**)

KEY WORDS: Cephalaspidea, Opisthobranchia, systematics, cladistics, phylogeny, homoplasy, parallelism, characters.

Abstract

The opisthobranch order Cephalaspidea is well-recognized as an unnatural, paraphyletic group characterized by «evolutionary trends» toward reduction and loss of many features. A survey of 35 key classifications and published phylograms involving cephalaspids revealed a general lack of morphological definition for the order and the tenacious use of traditional characters. Of 49 frequently-used characters, 44 (90%) are problematic for use in modern phylogenetic (cladistic) analyses due to reductive nature, non-homology, incompleteness, or other grounds. Claims of «rampant parallelism» involving a majority of these characters are based on *a priori* decisions and are therefore presently unjustified. The few consistent family groups in published phylograms are most strongly supported by characters correlated with diet, and may therefore also be open to question. Successful resolution of the phylogeny of these and other «lower heterobranchs» will require critical reevaluation of cephalaspid morphology to determine an improved set of taxonomically informative, homologous characters. New areas of investigation are proposed.

Riassunto

L'ordine dei Cephalaspidea è generalmente considerato un raggruppamento innaturale, parafiletico, caratterizzato da «indirizzi evolutivi» che tendono ad una riduzione e perdita di molti caratteri. L'analisi di 35 chiavi di classificazione e degli alberi filogenetici recentemente pubblicati che coinvolgono i cefalaspidei indica una carenza nella definizione morfologica dell'ordine ed il costante uso di caratteri tradizionali.

Dei 49 caratteri più frequentemente usati, 44 (il 90%) sono difficili da utilizzare nella moderna analisi cladistica a causa della loro natura riduttiva, non omogeneità, incompletezza o altro.

Le ipotesi di un «parallelismo ascendente» fatte per la maggior parte sulla base di questi caratteri appaiono sostenute da decisioni aprioristiche e sono dunque, al momento, ingiustificate. Inoltre i pochi raggruppamenti tassonomici di un certo valore sono per la maggior parte sostenuti da caratteri collegati con la dieta e dunque discutibili.

Un'analisi corretta della filogenesi di questo, come di altri gruppi, appartenenti ai «bassi eterobranchi» richiederà una critica rivalutazione della loro morfologia, per definire insiemi di caratteri omologhi d'interesse tassonomico.

A tal proposito, vengono qui presentate nuove aree d'indagine.

(*) Harbor Branch Oceanographic Institution, Inc., 5600 U.S. 1 North, Fort Pierce, Florida, 34546, and Florida Institute of Technology, Melbourne, Florida, USA.

(**) Paper presented at the Eleventh International Malacological Congress (Siena, Italy, 1992) organized by the Unitas Malacologica.

Introduction

Within the opisthobranchs, the Order Cephalaspidea [=Bullomorpha, Tectibranchiata (in part), «bubble-shells»] is morphologically mosaic as a group, and is traditionally considered «basal», or «transitional» between typical prosobranchs and «higher» opisthobranchs (e.g., Boettger, 1955; Schmekel, 1985). Systematics within the order (as well as for the order itself) is currently based upon anagenetic organizational grades, phenetic similarities and «evolutionary trends» rather than upon distinct synapomorphies. Any such assemblage does not meet modern phylogenetic standards and may not be monophyletic. Several authors (e.g., Rudman, 1972; Gosliner, 1992) have already suggested that this is true of Cephalaspidea.

Cephalaspidea was originally introduced by P. Fischer (1883b: 550) as a subdivision (with Anaspidea and Notaspidea) of Tectibranchiata Cuvier, 1812. The new group of nine families (Fig. 1) was distinguished by the presence of «un large disque céphalique». It is now generally agreed (e.g., Brace, 1977a,b) that this and other features of «typical» cephalaspid anatomy are the products of extensive ecophenotypic modification related to burrowing through soft sediment, a habit successfully exploited by most extant members of the present order. These kinds of features could conceivably have evolved in parallel in unrelated taxa under similar circumstances, and as such, may not reflect phylogenetic relationships. Similar statements have also been made for characters associated with diet (Mikkelsen, 1989, 1990), reduction in body size (Ghiselin, 1963, 1966; Haszprunar, 1985), and loss of the shell (Gosliner & Ghiselin, 1984). The apparent high incidence of homoplasy in opisthobranchs led Gosliner & Ghiselin (1984: 263-264; also Gosliner, 1981, 1991) to contend that «rampant parallelism» made it «difficult, if not impossible» to resolve opisthobranch relationships using modern cladistic methods. Although terminology has occasionally implied the use of phylogenetic techniques (Gosliner, 1978, 1991; Haszprunar, 1988), few rigorous analyses of opisthobranchs by modern methods have appeared. Willan's (1987) treatment of Notospidea is a notable exception.

Patterson (1989: 484) contended that «success in systematics requires three things: good data (characters), sound methods of analysis, and criteria for evaluating the results». Phenetic analytical approaches have been unsuccessful in resolving the continual problems in cephalaspid systematics. Further review presented here implicates a second, more basic deficiency, i.e., the tenacious use of traditional characters, most of which are problematic in cephalaspids. This study suggests that successful resolution of this phylogeny may lie more in rigorous character selection than in the use of alternate methodologies.

Material and Methods

Thirty-five key works in cephalaspid systematics were selected and analyzed for agreement in classification or proposed phylogeny presented, the character used (if given), any consistent family groups, and any synap-

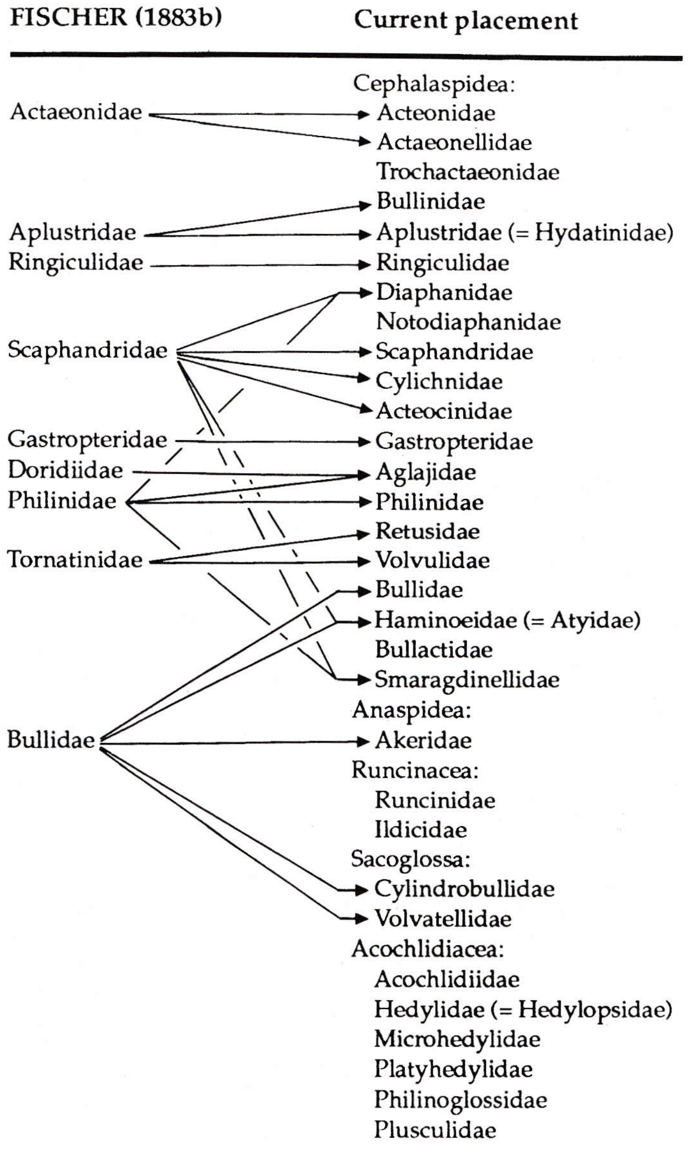


Figure 1. The 31 «traditional» cephalaspid families and their current taxonomic placement (based mainly on Boss, 1982), as derived from Fischer's (1883b) original Cephalaspidea.

omorphies defining family groups. Among them were 17 comprehensive and/or well-recognized classifications [Fischer, 1883b; Pilsbry, 1894-1896; Thiele, 1931; Odhner, 1939; Zilch, 1960; Taylor & Sohl, 1962; Odhner in Franc, 1968; Nordsieck, 1972; Abbott, 1974; Thompson, 1976; Marcus, 1977; Boss, 1982; Long, 1983; Vaught, 1989; Sabelli, *et al.*, 1990-1992; combined Austrian scheme (Haszprunar, 1985; Salvini-Plawen, 1988, 1991a,b); combined Russian scheme (Minichev & Starobogatov, 1979a,b; Golikov & Starabogatov, 1989)], and all known proposed phylograms (18) indicating cephalaspid relationships [Fischer, 1883b: 551; Cossmann, 1895: table; Pilsbry, 1896: vii; Guiart, 1901: 201-202; Boettger, 1955: fig. 1; Morton, 1963: fig. 2; Ghiselin, 1966: fig. 7; Salvini-Plawen, 1970: fig. 1; Beeman, 1977: fig. 15; Gosliner, 1978: pl. 22, fig. 36 (unpublished thesis); Rudman, 1978: figs. 2-6; Kandel, 1979: fig. 2-3; Edlinger, 1980: fig. 9; Haszprunar, 1985: fig. 5; Schmekel, 1985: fig. 17: Poulicek *et al.*, 1991: fig. 1; Salvini-Plawen, 1991a: fig. 15; Salvini-Plawen, 1991b: fig. 5).

The phylograms presented in Figs. 3-5 are redrawings of previously published trees, and do not represent original, cladistically-derived results.

Results and Discussion

Additions and subtractions - a history of Cephalaspidea

Cephalaspidean taxonomic history has been one of repeted inclusions and exclusions, expansions and restrictions. Within the genera and subgenera of Fischer's (1883b) original taxon are found the bases of most (20) of the 31 families which have been assigned to Cephalaspidea since Fischer's time (Fig. 1). Subsequent anatomical studies by Guiart (1901), Bergh (1900-1908) and others induced a proliferation of family-level groups, accompanied by a dizzying rate of taxonomic rearrangement [Fig. 2; Pilsbry, 1894-1896 (10 families); Thiele, 1931 (14); Boettger, 1955 (15, excluding Pyramidellidae and Euthecosomata); Zilch, 1960 (15); Taylor & Sohl, 1962 (15); Odhner in Franc, 1968 (13); Thompson, 1976 (16); Marcus, 1977 (18); Boss, 1982 (13); Long, 1983 (23); Vaught, 1989 (16); Sabelli *et al.*, 1990-1992 (13)]. Most of the activity has focussed on a limited number of families moving back and forth between Cephalaspidea and other opisthobranch groups: (1) Akeridae to Anaspidea (Guiart, 1901; Thompson & Seaward, 1989), (2) Volvatellidae/Cylindrobullidae to Sacoglossa (=Ascoglossa; Evans, 1950; Marcus, 1982), (3) 4-6 families of meiofaunal «sand-nudibranchs» to their own orders, Acochlidiacea and Philinoglossacea, or (in part) to Sacoglossa (Odhner, 1939; Wawra, 1979; Marcus, 1982; Salvini-Plawen, 1973), and (4) Runcinidae/Ildicidae to their own order Runcinacea (Odhner, 1939; Burn, 1963; Odhner in Franc, 1968; Ghiselin, 1963; Thompson & Brodie, 1988).

This continual shifting is partially due to new analyses and new data, but it also stems from our lack of a solid morphology-based definition for the order. High variability is the rule: shell external, internal or absent, thick or thin, involute or with spire exposed; operculum present or absent; mantle cavity anterior or posterior, enclosed or open; parapodia present or absent; gizzard present or absent; jaws usually absent; radula usually present; penis usually retractile; etc. The cephalic shield and Hancock's organ once regarded as synapomorphies for Cephalaspidea (e.g., SCHMEKEL, 1985) are no longer warranted in view of the above-mentioned removals of controversial taxa.

In perhaps the most dramatic rearrangement to date (Table 1), two Austrian workers (HASZPRUNAR, 1985; SALVINI-PLAWEN, 1988, 1991a,b) have suggested removing six families — Acteonidae, Bullinidae, Aplustridae, Ringiculidae, Diaphanidae, and Notodiaphanidae — from the Cephalaspidea mainly on the basis of shared symplesiomorphies (streptoneury, pallial gonoduct, lack of gizzard). Two new groups have been proposed: (1) Architectibranchia, a «conservative» pharaphyletic superorder (HASZPRUNAR, 1985; SALVINI-PLAWEN, 1991b), and (2) Dystectibranchia (including several «non-cephalaspid» groups), «an interrelated stock with mosaic evolution» (SALVINI-PLAWEN, 1991a: 24). The remaining cephalaspid families are treated as the order Bullomorpha, in the derived superorder Paratectibranchia (HASZPRUNAR, 1985; SALVINI-PLAWEN, 1991b). [SALVINI-PLAWEN (1991a) altered this, treating Paratectibranchia as another paraphyletic basal group.] Major divisions of Cephalaspidea reminiscent of this were earlier implied, although never formally proposed, by GUIART (1901; for Acteonidae), GHISELIN (1966; for Acteonidae, Aplustridae), BEEMAN (1978; for Acteonidae), GOSLINER (1978; for Acteonidae, Bulinidae, Aplustridae, Ringiculidae), EDLINGER (1980: fig. 9; for Acteonidae, Aplustridae, Diaphanidae), GOSLINER & GHISELIN (1984: fig. 1; for Acteonidae), and SCHMEKEL (1985: figs. 2,7,9,17; for Acteonidae, Ringiculidae).

HASZPRUNAR (1985) and SALVINI-PLAWEN (1988, 1991a,b) did not define the familial contents nor characteristics of their paratectibranch group Bullomorpha. By process of elimination, 8 families are inferred: Scaphandridae, Philinidae, Gastropteridae, Aglajidae, Retusidae, Bullidae, and Haminoeidae/Smaragdinellidae. Runcinidae/Ildicidae and Philinoglossidae/Plusculidae were also included here (and Retusidae and Philinidae confirmed) by HUBER (1987). From discussion of the larger Paratectibranchia (HASZPRUNAR, 1985), it can be deduced that hervibory and an anterior armed gizzard are regarded as plesiomorphic for Bullomorpha. Beyond this, synapomorphies defining the group have not been recognized and therefore the question of monophyly, as implied by the trees presented by HASZPRUNAR (1985: fig. 5) and SALVINI-PLAWEN (1991a: fig. 15; 1991b: fig. 5), remains open.

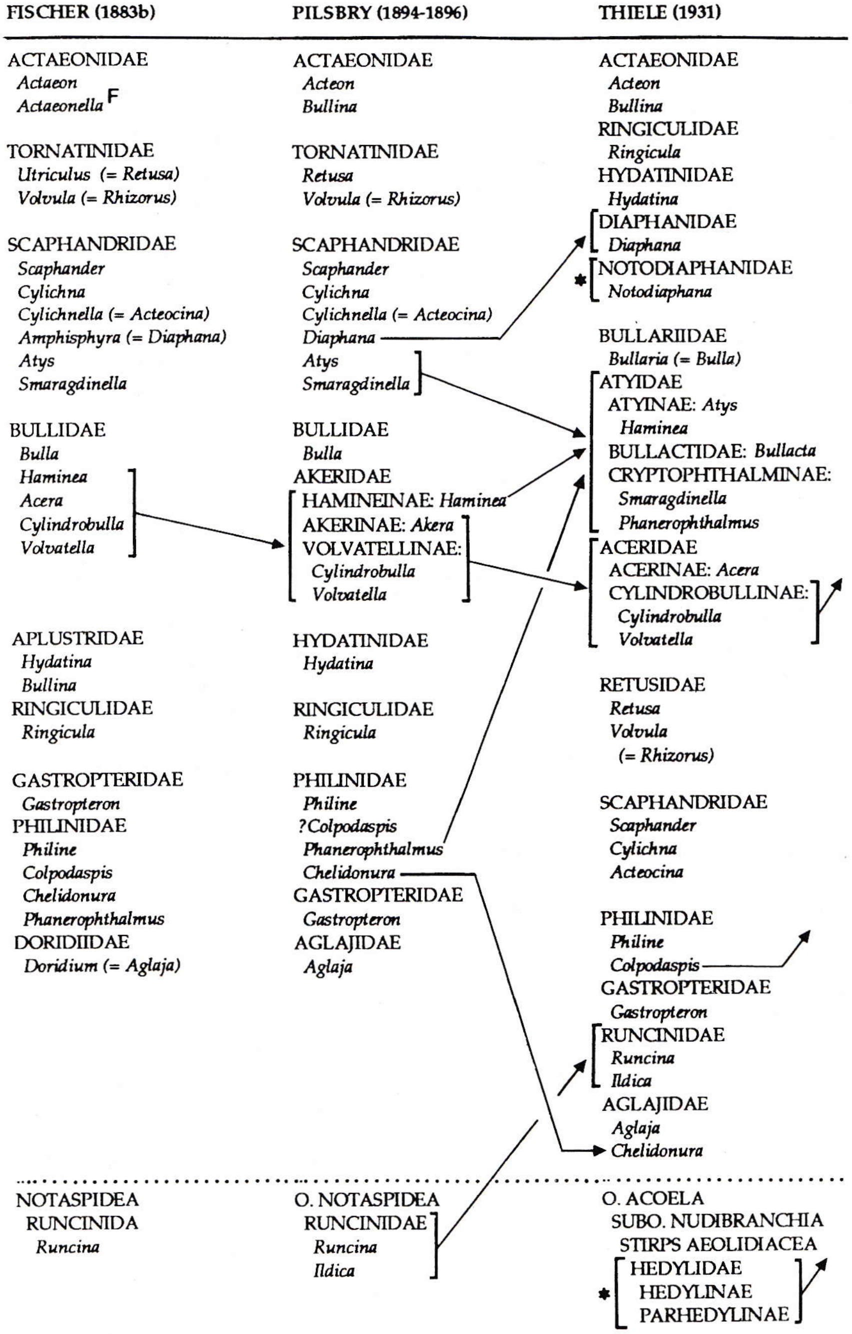
Russian workers (MINICHEV & Starobogatov, 1979a,b; GOLIKOV & STAROBOGATOV, 1989) have independently taken steps similar to those of the Austrians, based almost entirely on reproductive morphology: (a) Ringiculidae in subclass Sinistrobranchia (=Allogastropoda), (b) Acteonidae and Aplustridae in subclass Opisthobranchia: Phyllidiiformii, and (c) the remaining cephalaspids (together with various traditional anaspids, sacoglossans, and notably Diaphanidae/Notodiaphanidae) in Opisthobranchia: Bulliformii. Since the groups proposed by the Russian school were largely undefined, it is impossible to discuss this radical classification further.

Eighteen phylograms defining relationships of and/or among cephalaspideans have appeared in the literature (see list under Materials & Methods). The three earliest versions (FISCHER, 1883b; COSSMAN, 1895;

PILSBRY, 1896) were based on shells, «hard parts» (radula, jaws, gizzard plates), and gross external anatomy, one accounted for stratigraphic appearance of fossil taxa (COSSMANN, 1895), one was restricted to a single superfamily (RUDMAN, 1978), three others were primarily single-organ-system analyses (BOETTGER, 1955; GHISELIN, 1966; EDLINGER, 1980), three were slight modifications of previous trees [SALVINI-PLAWEN, 1970 (of BOETTGER, 1955); BEEMAN, 1977 (of GHISELIN, 1966); POULICEK *et al.*, 1991 (of GHISELIN, 1966)], and one concerned only the relationship of Cephalaspidea to other opisthobranch orders (SCHMEKEL, 1985). None of the 18 trees was generated through cladistic methods.

The three most comprehensive treatments to date [GHISELIN, 1966; SALVINI-PLAWEN's 1970 modification of BOETTGER, 1955; GOSLINER, 1978; redrawn here in cladistic fashion for purposes of discussion and comparison (Figs. 3-5)], are unsatisfactory for a number of reasons. BOETTGER's (1955) tree has been criticized (GOSLINER, 1978,1991; GOSLINER & GHISELIN, 1984) for being based on the shell and nervous system, both believed to contain many characters showing parallel evolution (associated with loss of the shell or reduction in body size). SALVINI-PLAWEN's (1970 updated version of BOETTGER (notably also removing modern families from nodal ancestral positions) still left six major clades (grades) radiating from a single node (Fig. 3). GHISELIN's (1966) originally confusing tree was based largely on a single system (reproductive anatomy), distinguished many opisthobranch groups by undefined «similarities», and united most of the cephalaspideans through traditional «hard-parts» (gizzard plates; Fig. 4). Finally, GOSLINER's (1978) interpretation, although based on a more complete dataset and employing qualitative weighting of characters, left an unresolved octochotomy (in figure; pentachotomy according to text) adding little new information on cephalaspid interrelationships (Fig. 5). Most importantly in modern phylogenetic terms, the Cephalaspidea itself is not monophyletic in any of these three phylograms.

Paraphyly of the Cephalaspidea is not a new discovery. Relative to other opisthobranchs, PILSBRY (1985: 134) early recognized the Tectibranchiata (= Cephalaspidea + Anaspidea + Notaspidea) as «a synthetic type, from which in the remote past, the Nudibranchiata and Pulmonata have no doubt been derived». With the breakup of Tectibranchiata by the 1960's [or the reduced but similar Pleurocoela of THIELE, 1931; not Tectibranchia *sensu* HASZPRUNAR (1935: 33) nor SALVINI-PLAWEN (1991a: 23)], the Cephalaspidea assumed the role of the «ancestral stock» of the opisthobranchs (GOSLINER, 1978; GOSLINER & GHISELIN, 1984). The phylograms of BOETTGER (1955: fig. 1) and SCHMEKEL (1985: fig. 17) are prime examples of this view, with the clearly-paraphyletic Cephalaspidea defined mainly by symplesiomorphies. Although the Austrian-advocated division considers most of the cephalaspids as members of the presumably-monophyletic Bullomorpha, their Architectibranchia and Dystectibranchia still occupy the paraphyletic position once held by the entire Tectibranchiata.



FISCHER (1883b)

ACTAEONIDAE
Actaeon
Actaeonella F

TORNATINIDAE
Utriculus (= Retusa)
Volvula (= Rhizorus)

SCAPHANDRIDAE
Scaphander
Cylichna
Cylichnella (= Acteocina)
Amphisphyra (= Diaphana)
Atys
Smaragdinella

BULLIDAE
Bulla
Haminea
Acera
Cylindrobulla
Volvatella

APLUSTRIDAE
Hydatina
Bullina
RINGICULIDAE
Ringicula

GASTROPTERIDAE
Gastropteron
PHILINIDAE
Philine
Colpodaspis
Chelidonura
Phanerophthalmus
DORIDIIDAE
Doridium (= Aglaja)

NOTASPIDEA
RUNCINIDA
Runcina

PILSBRY (1894-1896)

ACTAEONIDAE
Acteon
Bullina

TORNATINIDAE
Retusa
Volvula (= Rhizorus)

SCAPHANDRIDAE
Scaphander
Cylichna
Cylichnella (= Acteocina)
Diaphana
Atys
Smaragdinella

BULLIDAE
Bulla
AKERIDAE
HAMINEINAE: *Haminea*
AKERINAE: *Akera*
VOLVATELLINAE:
Cylindrobulla
Volvatella

HYDATINIDAE
Hydatina

RINGICULIDAE
Ringicula

PHILINIDAE
Philine
?Colpodaspis
Phanerophthalmus
Chelidonura
GASTROPTERIDAE
Gastropteron
AGLAJIDAE
Aglaja

O. NOTASPIDEA
RUNCINIDAE
Runcina
Ildica

THIELE (1931)

ACTAEONIDAE
Acteon
Bullina
RINGICULIDAE
Ringicula
HYDATINIDAE
Hydatina
DIAPHANIDAE
Diaphana
* NOTODIAPHANIDAE
Notodiaphana

BULLARIIDAE
Bullaria (= Bulla)
ATYIDAE
ATYINAE: *Atys*
Haminea
BULLACTIDAE: *Bullacta*
CRYPTOPHTHALMINAE:
Smaragdinella
Phanerophthalmus
ACERIDAE
ACERINAE: *Acera*
CYLINDROBULLINAE:
Cylindrobulla
Volvatella

RETUSIDAE
Retusa
Volvula
(= Rhizorus)

SCAPHANDRIDAE
Scaphander
Cylichna
Acteocina

PHILINIDAE
Philine
Colpodaspis
GASTROPTERIDAE
Gastropteron
RUNCINIDAE
Runcina
Ildica
AGLAJIDAE
Aglaja
Chelidonura

O. ACOELA
SUBO. NUDIBRANCHIA
STIRPS AEOLIDIACEA
* HEDYLIDAE
HEDYLINAE
PARHEDYLINAE

Figure 2. Cephalaspid classification by key authors, with superfamilies (if any), families, and representative genus-level taxa. Arrows indicate movement of genera, creation of new families, and movement of taxa in and out of Cephalaspidea. Non-cephalaspid groups below dotted line. F = exclusively-fossil taxa. * = first appearance of new additions.

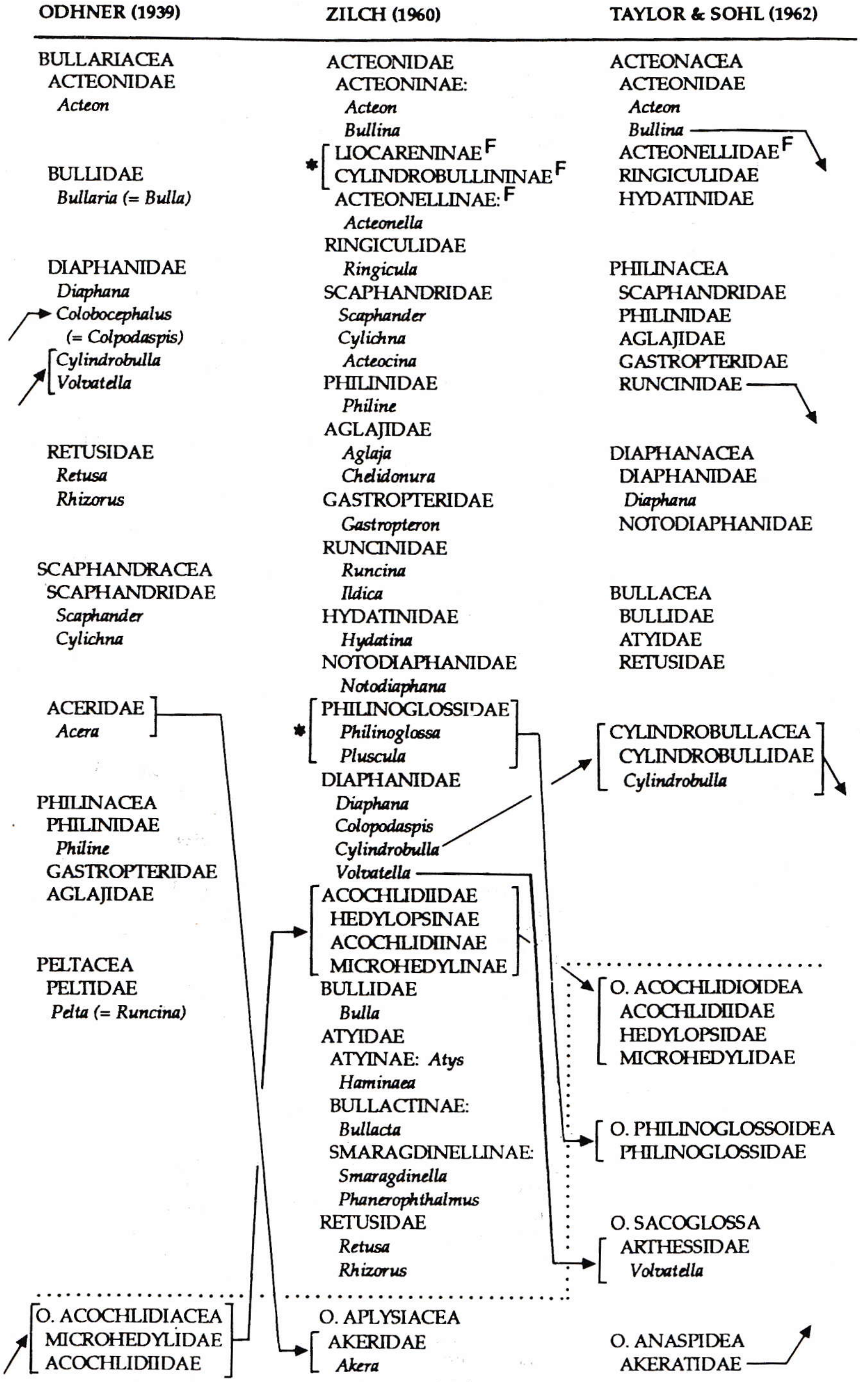
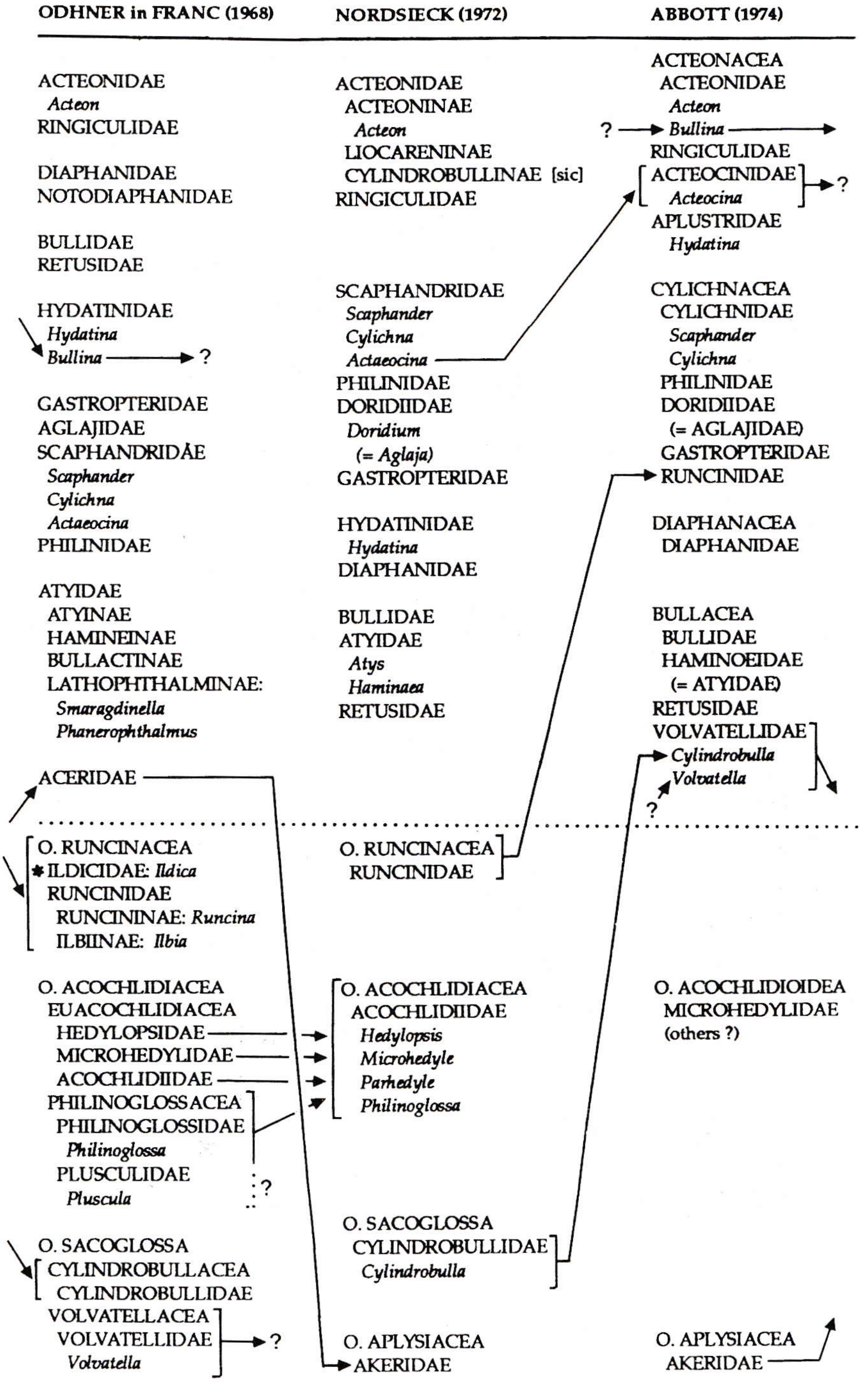


Figure 2 (continued)



ODHNER in FRANC (1968)

ACTEONIDAE
Acteon
RINGICULIDAE

DIAPHANIDAE
NOTODIAPHANIDAE

BULLIDAE
RETUSIDAE

HYDATINIDAE
Hydatina
Bullina → ?

GASTROPTERIDAE
AGLAJIDAE
SCAPHANDRIDAE
Scaphander
Cylichna
Actaeocina
PHILINIDAE

ATYIDAE
ATYINAE
HAMINEINAE
BULLACTINAE
LATHOPHTHALMINAE:
Smaragdinella
Phanerophthalmus

ACERIDAE

O. RUNCINACEA
✱ ILDICIDAE: *Ildica*
RUNCINIDAE
RUNCININAE: *Runcina*
ILBIINAE: *Ilbia*

O. ACOCHLIDIACEA
EUACOCHLIDIACEA
HEDYLOPSIDAE
MICROHEDYLIDAE
ACOCHLIDIIDAE
PHILINOGLOSSACEA
PHILINOGLOSSIDAE
Philinoglossa
PLUSCULIDAE
Pluscula
?

O. SACOGLOSSA
CYLINDROBULLACEA
CYLINDROBULLIDAE
VOLVATELLACEA
VOLVATELLIDAE → ?
Volvatella

NORDSIECK (1972)

ACTEONIDAE
ACTEONINAE
Acteon
LIOCARENINAE
CYLINDROBULLINAE [sic]
RINGICULIDAE

SCAPHANDRIDAE
Scaphander
Cylichna
Actaeocina
PHILINIDAE
DORIDIIDAE
Doridium
(= *Aglaja*)
GASTROPTERIDAE

HYDATINIDAE
Hydatina
DIAPHANIDAE

BULLIDAE
ATYIDAE
Atys
Haminaea
RETUSIDAE

O. RUNCINACEA
RUNCINIDAE

O. ACOCHLIDIACEA
ACOCHLIDIIDAE
Hedylopsis
Microhedyle
Parhedyle
Philinoglossa

O. SACOGLOSSA
CYLINDROBULLIDAE
Cylindrobulla

O. APLYSIACEA
AKERIDAE

ABBOTT (1974)

ACTEONACEA
ACTEONIDAE
Acteon
? → *Bullina* →
RINGICULIDAE
ACTEOCINIDAE → ?
Acteocina
APLUSTRIDAE
Hydatina

CYLICHNACEA
CYLICHNIDAE
Scaphander
Cylichna
PHILINIDAE
DORIDIIDAE
(= AGLAJIDAE)
GASTROPTERIDAE
RUNCINIDAE

DIAPHANACEA
DIAPHANIDAE

BULLACEA
BULLIDAE
HAMINOEIDAE
(= ATYIDAE)
RETUSIDAE
VOLVATELLIDAE
Cylindrobulla
Volvatella
?

O. ACOCHLIDIOIDEA
MICROHEDYLIDAE
(others ?)

O. APLYSIACEA
AKERIDAE

Figure 2 (continued)

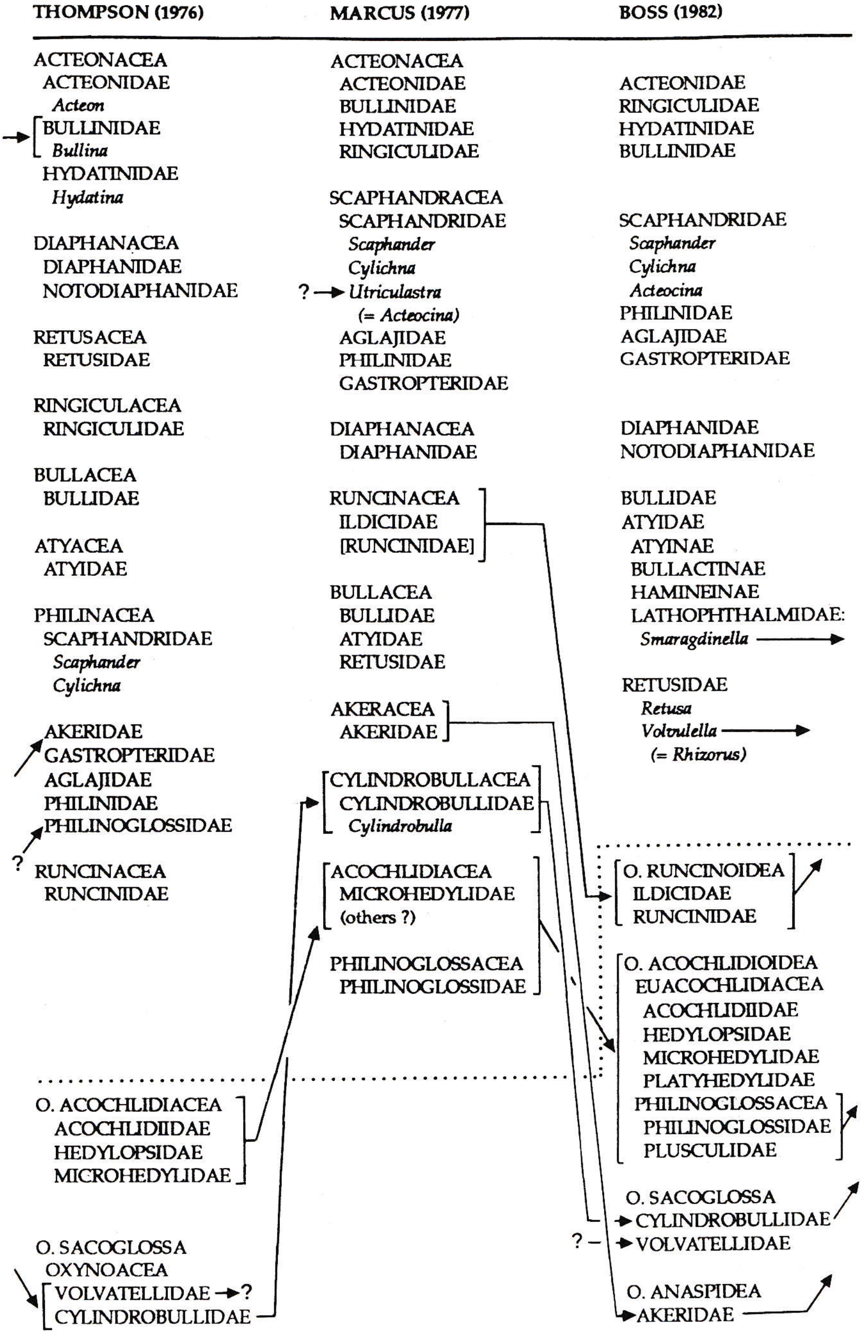
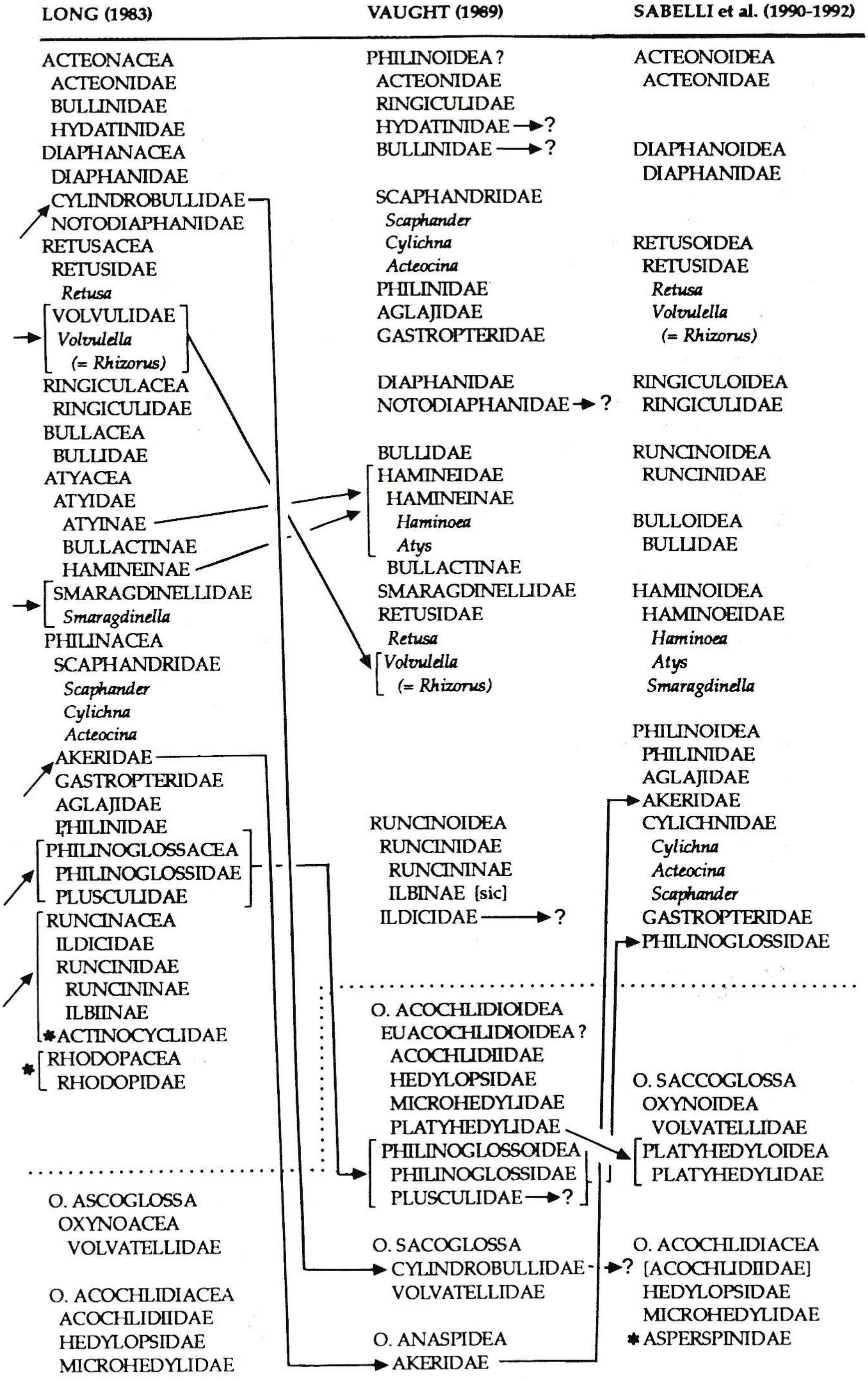


Figure 2 (continued)



LONG (1983)

ACTEONACEA
ACTEONIDAE
BULLINIDAE
HYDATINIDAE
DIAPHANACEA
DIAPHANIDAE
CYLINDROBULLIDAE
NOTODIAPHANIDAE
RETUSACEA
RETUSIDAE
Retusa
VOLVULIDAE
Volvulella
(= Rhizorus)
RINGICULACEA
RINGICULIDAE
BULLACEA
BULLIDAE
ATYACEA
ATYIDAE
ATYINAE
BULLACTINAE
HAMINEINAE
SMARAGDINELLIDAE
Smaragdinella
PHILINACEA
SCAPHANDRIDAE
Scaphander
Cylichna
Acteocina
AKERIDAE
GASTROPTERIDAE
AGLAJIDAE
PHILINIDAE
PHILINOGLOSSACEA
PHILINOGLOSSIDAE
PLUSCULIDAE
RUNCINACEA
ILDICIDAE
RUNCINIDAE
RUNCININAE
ILBIINAE
✱ACTINOCYCLIDAE
✱ RHODOPACEA
RHODOPIDAE

O. ASCOGLOSSA
OXYNOACEA
VOLVATELLIDAE

O. ACOCHLIDIACEA
ACOCHLIDIIDAE
HEDYLOPSIDAE
MICROHEDYLIDAE

VAUGHT (1989)

PHILINOIDEA ?
ACTEONIDAE
RINGICULIDAE
HYDATINIDAE → ?
BULLINIDAE → ?

SCAPHANDRIDAE
Scaphander
Cylichna
Acteocina
PHILINIDAE
AGLAJIDAE
GASTROPTERIDAE

DIAPHANIDAE
NOTODIAPHANIDAE → ?

BULLIDAE
HAMINEIDAE
HAMINEINAE
Haminoea
Atys
BULLACTINAE
SMARAGDINELLIDAE
RETUSIDAE
Retusa
Volvulella
(= Rhizorus)

RUNCINOIDEA
RUNCINIDAE
RUNCININAE
ILBINAE [sic]
ILDICIDAE → ?

O. ACOCHLIDIOIDEA
EUACOCHLIDIOIDEA ?
ACOCHLIDIIDAE
HEDYLOPSIDAE
MICROHEDYLIDAE
PLATYHEDYLIDAE
PHILINOGLOSSOIDEA
PHILINOGLOSSIDAE
PLUSCULIDAE → ?

O. SACOGLOSSA
CYLINDROBULLIDAE → ?
VOLVATELLIDAE

O. ANASPIDEA
AKERIDAE

SABELLI et al. (1990-1992)

ACTEONOIDEA
ACTEONIDAE

DIAPHANOIDEA
DIAPHANIDAE

RETUSOIDEA
RETUSIDAE
Retusa
Volvulella
(= Rhizorus)

RINGICULOIDEA
RINGICULIDAE

RUNCINOIDEA
RUNCINIDAE

BULLOIDEA
BULLIDAE

HAMINOIDEA
HAMINOEIDAE
Haminoea
Atys
Smaragdinella

PHILINOIDEA
PHILINIDAE
AGLAJIDAE
AKERIDAE
CYLICHNIDAE
Cylichna
Acteocina
Scaphander
GASTROPTERIDAE
PHILINOGLOSSIDAE

O. SACCOGLOSSA
OXYNOIDEA
VOLVATELLIDAE
PLATYHEDYLOIDEA
PLATYHEDYLIDAE

O. ACOCHLIDIACEA
[ACOCHLIDIIDAE]
HEDYLOPSIDAE
MICROHEDYLIDAE
✱ASPERSPINIDAE

Figure 2 (continued)

Table 1. New classifications of «cephalaspids» by the Austrian school (HASZPRUNAR, 1985; SALVINI-PLAWEN, 1988, 1991a,b) and the Russian school (MINICHEV & STAROBOGATOV, 1979a,b; GOLIKOV & STAROBOGATOV, 1988). Included families inferred (where indicated) through name of superfamilial taxon and currently-accepted groups. * = «non-cephalaspid», included families not listed here.

AUSTRIAN SCHOOL

- SCL. HETEROBRANCHIA
  - COHORS TRIGANGLIONATA
    - SUPERO. ALLOGASTROPODA*
  - COHORS PENTAGANGLIONATA
    - SUPERO. ARCHITECTIBRANCHIA
      - O. ACTEONOIDEA
        - ACTEONIDAE
        - BULLINIDAE
        - HYDATINIDAE
      - O. RINGICULOIDEA
        - RINGICULIDAE
    - SUPERO. DYSTECTIBRANCHIA
      - O. DIAPHANOIDEA
        - DIAPHANIDAE
        - NOTODIAPHANIDAE
      - O. SACOGLOSSA
        - CYLINDROBULLIDAE
        - VOLVATELLIDAE
        - (others)
      - O. ACOCHLIDIOMORPHA
        - ACOCHLIDIIDAE
        - HEDYLIDAE
        - MICROHEDYLIDAE
        - PLATYHEDYLIDAE
      - O. RHODOPEMORPHA*
    - SUPERO. PARATECTIBRANCHIA
      - O. THECOSOMATA*
      - O. BULLOMORPHA (families inferred)
        - SCAPHANDRIDAE
        - PHILINIDAE
        - GASTROPTERIDAE
        - AGLAJIDAE
        - RETUSIDAE
        - BULLIDAE
        - HAMINOEIDAE
        - SMARAGDINELLIDAE
        - RUNCINIDAE
        - ILDICIDAE
        - PHILINOGLOSSIDAE
        - PLUSCULIDAE
      - O. ANASPIDEA
        - AKERIDAE
        - (others)
      - O. GYMNOSOMATA*
  - COHORS ELEUTHEROBRANCHIA*
  - COHORS CYMNOMORPHA*
  - COHORS PULMONATA*

RUSSIAN SCHOOL (families inferred]

- SCL. SINISTROBRANCHIA
  - SUPERO. ARCHITECTONICIFORMII*
  - SUPERO. MELANELLIFORMII*
  - SUPERO. PYRAMIDELLIFORMII
    - O. RINGICULIFORMES
      - SUBO. RINGICULOIDEI
        - RINGICULIDAE
    - O. PYRAMIDELLIFORMES*
- SCL. OPISTHOBRANCHIA
  - SUPERO. PHYLIDIIFORMII
    - O. ACTEONIFORMES
      - ACTEONIDAE
      - HYDATINIDAE
    - O. PLEUROBRANCHIFORMES*
    - O. PHYLLIDIIFORMES*
    - O. TRITONIIFORMES*
  - SUPERO. POLYBRANCHIFORMII*
  - SUPERO. BULLIFORMII
    - O. BULLIFORMES
      - SUBO. DIAPHANOIDEI
        - DIAPHANIDAE
        - NOTODIAPHANIDAE
      - SUBO. BULLOIDEI
        - BULLIDAE
      - SUBO. SCAPHANDROIDEI
        - SCAPHANDRIDAE
        - PHILINIDAE
        - GASTROPTERIDAE
        - AGLAJIDAE
      - SUBO. PHILINOGLOSSOIDEI
        - PHILINOGLOSSIDAE
      - SUBO. HAMINEOIDEI
        - HAMINOEIDAE
    - O. RUNCINIFORMES
      - RUNCINIDAE
      - ILDICIDAE
    - O. APLYSIIFORMES
      - AKERIDAE
      - (others)
    - O. PNEUMODERMATIFORMES*
    - O. TAMANOVALVIFORMES
      - SUBO. CYLINDROBULLOIDEI
        - CYLINDROBULLIDAE
      - SUBO. VOLVATELLOIDEI
        - VOLVATELLIDAE
      - (others)
- SCL. DEXTROBRANCHIA
  - SUPERO. UMBRACULIIFORMII*
  - SUPERO. ACOCHLIDIIFORMII
    - O. ACOCHLIDIIFORMES
      - SUBO. PLATYHEDILOIDEI
        - PLATYHEDYLIDAE
      - SUBO. HEDYLOPSOIDEI
        - HEDYLOPSIDAE
        - MICROHEDYLIDAE
      - SUBO. ACOCHLIDIOIDEI
        - ACOCHLIDIIDAE
      - (others)
  - SUPERO. PERACLIFORMII*
  - SUPERO. ONCHIDIIFORMII*
- SCL. PULMONATA*

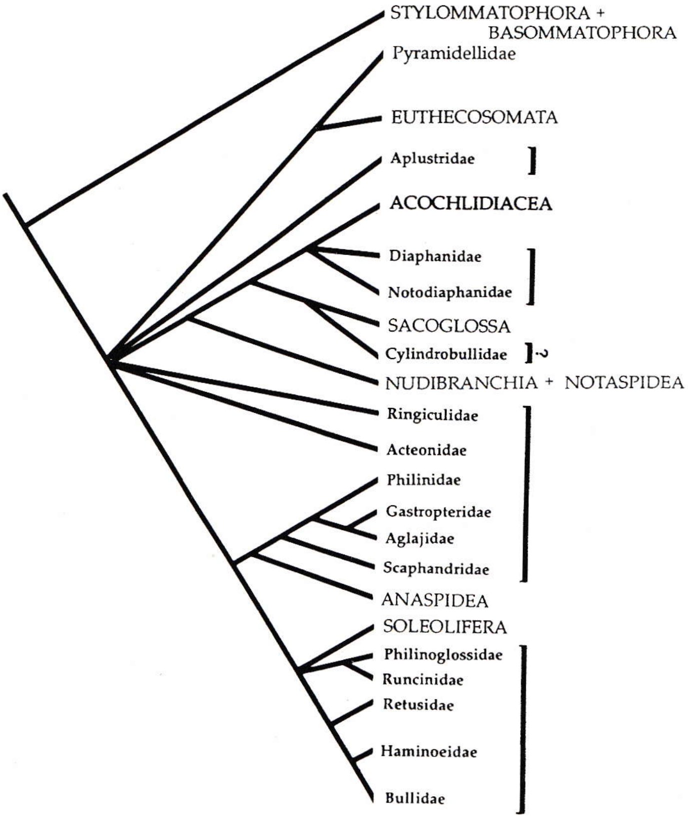


Figure 3. SALVINI-PLAWEN's (1970: fig. 1) phylogeny of euthyneuran gastropods [modified from Boettger (1955: fig. 1)], redrawn as a modern cladogram. Solid horizontal bar denotes present Cephalaspidea.

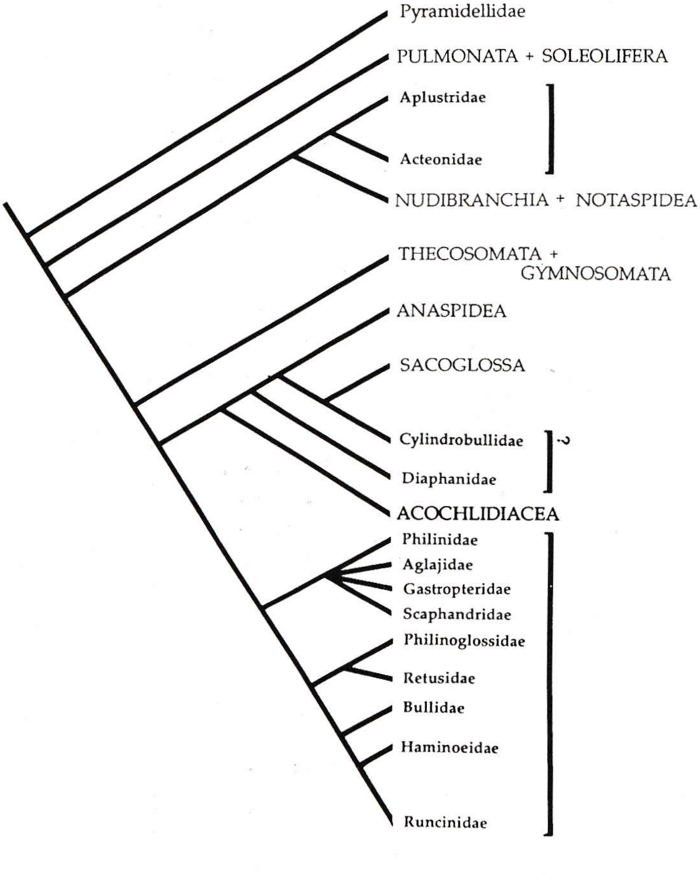


Figure 4. GHISELIN's (1966: fig. 7) «phylogenetic tree» of the Opisthobranchia, (based on a «functional analysis» of characters of the reproductive and alimentary systems), redrawn as a modern cladogram. Solid horizontal bar denotes present Cephalaspidea. Ringiculidae was not included on the original tree due to uncertain affinities.

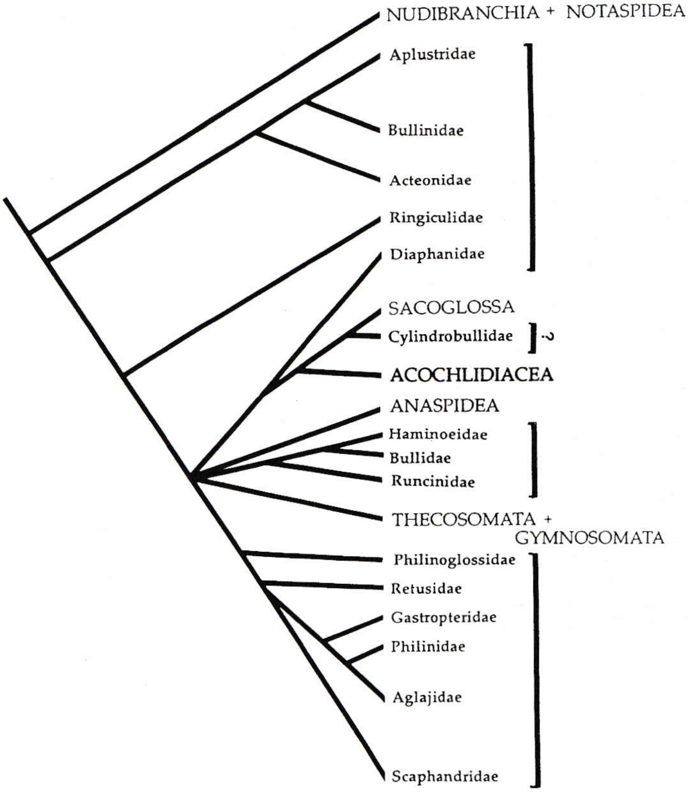


Figure 5. GOSLINER's (1978: pl. 22, fig. 36) phylogeny of the Opisthobranchia, redrawn as a modern cladogram. Solid horizontal bar denotes present Cephalaspidea.

	HP	R	C	F	I	HM
SHELL present/absent	B	x				
SHELL external/internal	B					
SHELL thick/thin	B	x				
SHELL not reduced/reduced	B	x				
SHELL exposed spire/involute/plate-like	B	x				
OPERCULUM present/absent	B	x				
CHROMOSOME number 12/17					x	
RETRACTION complete/incomplete	B		x			
CEPHALIC PROCESSES (form)	B			x		
MANTLE CAVITY position	B					
PALLIAL CAECUM short/long/absent	B					
PARAPODIA absent/weak/strong	B	x				
FOOT long/short	x	x				
POSTERIOR PALLIAL LOBE absent/present						
GILL present/reduced/absent	S	x				
GILL nonplicate/plicate						
HANCOCK'S ORGAN weakly/strongly developed						
HANCOCK'S ORGAN (form)				x		
LIP ORGANS (form)				x		
OSPHRADIUM not reduced/reduced	x?	x				
OSPHRADIUM (form)				x		
RADULA present/absent	D	x				
RADULA (form)	D			x		
RADULA teeth many/few	D	x				
RACHIDIAN present/absent	D	x				
JAWS present/absent	D	x				
JAWS armed/unarmed	D	x				
GIZZARD weakly/strongly developed	D					
GIZZARD PLATES absent/present	D					
GIZZARD PLATES 3/4/many	D					
GIZZARD PLATES (form)	D			x		
SALIVARY GLANDS 1/2 pair	D?					
ESOPHAGEAL DIVERTICULUM absent/present	D					
DIET carnivorous/herbivorous	D		x			
REPRODUCTIVE SYSTEM monaulic/diaulic	x		x			
COPULATORY ORGAN nonretractile/retractile	B					
PROSTATE pallial/penial	x					
SPERM DUCT open/closed	x?					x
EJACULATORY DUCT open/closed	x					
SPERMATIC BULB absent/present	x					
RECEPTACULUM SEMINIS present/absent	x	x				
PALLIAL GONODUCT simple/divided						
GONODUCT pallial/coelomic						
NERVOUS SYSTEM streptoneurous/euthyneurous	S	x				
EYES present/absent	B	x				
NERVE RING pre-pharyngeal/post-pharyngeal	x					
NERVE RING ganglia 6/4	S	x				
VISCERAL LOOP long/short	S	x				
VISCERAL LOOP ganglia 5/4/3	S	x				

Table 2. Traditional cephalaspid characters used by 35 key classifications and proposed phylogenies, with the problems associated with their use in cladistic analysis. **x** = problem noted; **C** = condition; **F** = form; **HM** = homology; **HP** = presumed homoplasy (with suspected agent: **B** = burrowing; **D** = diet; **S** = small size); **I** = incomplete; **R** = reduction.

Traditional cephalaspid characters

Evaluation of the above-mentioned previous descriptions and phylograms yielded 49 frequently-utilized characters (Table 2).

Most the characters have been associated by various authors with the theoretically-homoplastic agents of burrowing (plus shell loss), diet, or small size (Table 2). Their derived states have been claimed to have «evolved» more than once during cephalaspid evolution (BOETTGER, 1955; GHISELIN, 1966; GOSLINER, 1978; GOSLINER & GHISELIN, 1984), giving rise to statements of «rampant parallelism» in the group (GOSLINER & GHISELIN, 1984). Much of this «evolution» is perceived as loss; twenty characters (42%) involve presumed reduction or loss of a feature. It must be argued here that, technically, one cannot invoke homoplasy to explain character distributions before the fact. Homoplasy is a phenomenon recognized through the analytical process, not an intrinsic quality of a character state. Because a rigorous phylogenetic analysis is not yet available for opisthobranchs, all cases of inferred homoplasy are products of *a priori* decisions at this point. One can certainly allow that the potential for homoplasy may be particularly high in certain cases, such as the absence of features, and take appropriate precaution. Absence or weak development of a character could also conceivably represent two different states: primary condition/absence or secondary loss/reduction.

Six characters reflect the general form or shape of a structure. This type of phenetic similarity requires better definition of the homologous characters and character states involved. Three broad functional or physiological «conditions» (carnivorous/herbivorous, monaulic/diaulic, retraction complete/incomplete) are similarly unusable. Each of these suggests probable suites of characters and questions of homology.

«Sperm duct open/closed» has a more obvious homology problem. Based on a reproductively monaulic «mesogastropod» ancestor, GHISELIN (1966: 333) stated that «the open seminal groove has been converted into a closed tube... called the vas deferens». This is a functional interpretation, reflecting analogy rather than homology. Based on positional evidence, the open external sperm groove, from the common genital opening to the copulatory organ opening, is probably not homologous with the closed pallial sperm duct (= «vas deferens»), extending from the common pallial gonoduct, through the prostate gland to the base of the copulatory organ. Both states apparently occur simultaneously in the sacoglossan *Ascobulla ulla* (MARCUS) (MARCUS, 1972). Therefore the connection/separation of the pallial sperm duct (with its associated prostate gland) from the common pallial gonoduct is distinct from the loss/gain of the external seminal groove.

Data on chromosome number are still too incomplete to be successfully used in this dataset, although considerable progress has been made since GHISELIN (1966) first considered its use (PATTERSON, 1969; NATARAJAN, 1970; VITTURI et al., 1985; CURINI-GALLETTI, 1985, 1988). Members of the cephalaspid genera *Bulla, Haminoea, Scaphander, Philine, Smaragdinella, Runcina,* and *Aglaja* have a haploid number of 17 or 18. This range is also generally found in Sacoglossa, Anaspidea, and basommatophoran and soleoliferan Pulmonata. However, Nudibranchia, the most throughly examined group so far (VITTURI *et al.*, 1985) shows a very consistent 13. Members of Notaspidea also possess 12 or 13. The only «architectibranch» examined so far [*Hydatina velum* (Gmelin)] has 15 (NATARAJAN, 1970). [NATARAJAN's (1970) statement that other acteonoideans have 17 chromosomes is apparently based on a species of *Cylichnatys*, now placed in Haminoeidae (BURN, 1978)]. *Philinoglossa praelongata* SALVINI-PLAWEN has 13 (CURINI-GALLETTI, 1985). Within the Heterostropha, Valvatidae reveal 10 and Pyramidellidae 17 (PATTERSON, 1969). In a recent review, VITTURI *et al.* (1985), suggested that chromosome number may be a highly stable character at family or higher taxonomic level in molluscs. But polarity is still in question: low number has been considered plesiomorphic (PATTERSON, 1969) or derived (CURINI-GALLETTI, 1985). This is definitely a character worth investigating further.

In summary, of the 49 traditionally most-used characters, 44 (90%) are here perceived as problematic. It is obvious then, that the dataset presented in Table 2 is insufficient for use in cladistic analysis, and it is therefore no surprise that authors emphasizing these characters have claimed that «it cannot be done».

Monophyletic subgroups?

Given the lack of recognized synapomorphies for Cephalaspidea, and the acknowledgment that only monophyletic taxa be formally recognized in classification, the entire order Cephalaspidea is now difficult to justify. However, in the phylograms generated using the above-discussed characters, are there any family groups which are consistent and/or defined by synapomorphies?

The polychotomies present in SALVINI-PLAWEN's (1970) and GOSLINER's (1978) trees severely limit the identification of possible monophyletic units. However, one consistent grouping is obvious: the superfamily Philinoidea (Philinidae + Scaphandridae + Gastropteridae + Aglajidae), which is also the most consistently recognized group in cephalaspid classifications. But synapomorphies for this group are difficult to discern from the three publications. SALVINI-PLAWEN (1970) and BOETTGER (1955), on which the former was based, identify nothing specific. GOSLINER (1978), who placed major importance on dietary morphology, found flattened gizzard plates to be unique when Retusidae was added to the group. When Philinoglossidae was also considered, a radula with enlarged cusp-like lateral teeth became synapomorphic for Philinoidea. Other superfamilial characteristics (carnivory, pre-pharyngeal nerve ring, monauly, simple mucus gland) were symplesiomorphic according to GOSLINER. GHISELIN (1966) described only phenetic similarities in reproductive system structure and grades in reduction of the shell and radula, and suggested mosaic evolution patterns among the four families; but he also mentioned features at the cellular level (e.g., secretory cells of unknown function in coelomic gonoduct) which seem worthy of additional study. RUDMAN's (1978) discussion of phylogeny within the Philinoidea defined phenetic similarities and grades similar to those of GHISELIN.

The only other cephalaspid superfamily consistently used in classifications is also recognizable in all three trees: Bulloidea (Bullidae + Haminoeidae). SALVINI-PLAWEN (1970) added Retusidae and defined the group by possession of a shortened foot. GHISELIN (1966) added Runcinidae and used herbivory (with its associated esophageal diverticulum, which was however «lost» in Haminoeidae) as a synapomorphy. GOSLINER (1978) defined the same clade as GHISELIN, but added ridged gizzard plates and an elaborated mucus gland to the list of presumed synapomorphies.

In spite of these three attempts to redefine cephalaspids based on new data, most apparent synapomorphies for the few consistent groups are associated with diet, e.g., the «traditional» radulae and gizzard plates. Separate carnivorous and herbivorous lineages of cephalaspids were also advocated by GUIART (1901), PRUVOT-FOL (1954), GHISELIN (1966), RUDMAN (1971), KANDEL (1979), and SALVINI-PLAWEN (1988), HASZPRUNAR (1985) used herbivory and the resultant plate-bearing anterior gizzard as synapomorphies of his superorder Tectibranchia (=Cephalaspidea, plus others). And JENSEN (1991: 149) has acknowledged a number of alimentary characters as phylogenetically informative within the closely-related Sacoglossa (=Ascoglossa) in spite of «many specializations to specific diets». These observations support the belief of T.E. THOMPSON (1976) that dietary needs formed the driving force behind the succesful radiation of opisthobranchs. However, several authors have cautioned against the use of alimentary characters at higher taxonomic levels. HASZPRUNAR (1985) implicated convergence through herbivory for the presence of a muscular stomach in two groups of non-tectibranch heterobranchs. BRACE (1977b: 51) noted «considerable anatomical similarity» in the alimentary systems of herbivorous cephalaspids and pulmonates. The «plasticity» of gastropod radulae in response to prey structure or habitat was summarized for prosobranchs by KOOL (1987). SALVINI-PLAWEN & HASZPRUNAR (1987) expressed the general opinion that characters of the gastropod digestive system are correlated more with diet than phylogeny (although useful characters were found in configuration of the esophagus). As previously mentioned, congruence of radular/gizzard plate morphology with diet has been noted in a preliminary survey of cephalaspids (MIKKELSEN, 1989, 1990). While diet-related morphology may reflect phylogenetic relationship in a well-defined specialist group as the Sacoglossa, the probability of homoplasy is undoubtedly higher for the much larger and ill-defined Cephalaspidea.

Possible New Taxonomic Characters

From the literature, several suggestions may be immediately put forth as potentially useful characters worthy of serious investigation: (1) karyotype (discussed above); (2) cellular morphologies within the reproductive tract (GHISELIN, 1966), e.g.: (a) ciliated strips in the ampullae of Acteonidae and nudibranchs which serve to bypass eggs around stored autosperm, and (b) secretory cells of unknown function noted in the coelomic gonoduct of philinoideans; (3) sperm ulstrastructure and spermiogenesis, studied in only a few cephalaspids (THOMPSON, 1973; HEALY, 1982b), but proven informative in other heterobranch groups (HEALY, 1982a, 1988a,b; HEALY & WILLAN, 1991); (4) structure of spermatophores, reported in *Haminoea* and *Runcina* (Ghiselin, 1966); (5) fine structure of osphradia (Haszprunar, 1986, 1988, and pers.comm.) and Hancock's organ; (6) stomach structure; (7) muscular arrangements of the gizzard or buccal mass (Gosliner & Ghiselin, 1984); and (8) details of the nerve ring complex (Huber, 1987). Some of these data are already accessible or under study, but so far, no synthesis is available.

The complete resolution of problematic cases such as this may ultimately require the use of physiological, biochemical, and/or molecular data. At this taxonomic level, the most appropriate molecular method is currently gene sequencing, with the DNA molecule generally the preferred source (Hillis, 1987; Hillis & Moritz, 1990: table 1). Unfortunately at the present time, these sophisticated techniques are fraught with technical difficulties in mucus-laden mollusks and have not been routinely applied to phylogenetic studies. Attesting to this, the first molecular (RNA-based) phylogenies involving gastropods have only recently been published (Emberton, *et al.*, 1990; Tillier, *et al.*, 1992; summarized by Bieler, 1992). Even when molecular and other novel characters can be practically employed, these do not supersede morphological characters. Biochemical and molecular data are not immune from the effects of homoplasy (Ghiselin, 1988; Murphy, 1988; Swofford & Olsen, 1990), and a sound morphology-based phylogeny must be available upon which to intelligently interpret results derived from other sources. Morphology is also critical to the molluscan systematist for the inclusion of imperfectly-known, rare and fossil taxa in the dataset. An integrated approach utilizing as many types of data as possible should ultimately provide the best resolution.

Conclusions

The chronic confusion in cephalaspid systematics is a direct reflection of the persistent use of traditional characters, which are implicated in a variety of problems and have been thus far unable to demonstrate relationships. Successful resolution of the phylogeny of these and other «lower heterobranchs» will require (1) critical reevaluation of morphology to determine an improved set of taxonomically informative, homologous characters (irregardless of previous claims of homoplasy), and (2) looking beyond morphology to explore the use of innovative, non-traditional characters. Only thorough a through cladistic analysis can suspected parallelisms be confirmed and morphyletic clades identified.

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T. Gascoigne (*)

STYLETS, STYLES, AND OTHER CUTICULAR EXTENSIONS OF THE MALE DUCT IN THE ORDER SACOGLOSSA (GASTROPODA)

KEY WORDS: Sacoglossa, Opisthobranchia, copulation studies, hypodermic injection

Abstract

Sacoglossans form an interesting group of specialized sea slugs. They are vegetarians and feed by slitting open algal cells and sucking out the contents. The radula is the hall mark of the order. They are hermaphrodites. Fertilization is internal and usually reciprocal. There are two genital openings: a male opening and a female opening. When not in action, the penis is enclosed in a penial sheath that is adjacent and posterior to the male opening and along the inside from the penial sheath and is thrust outside the body. The female opening functions only as an outlet for the egg-string on during egg-laying. Apparently there is no vaginal opening in many sacoglossans. The transfer of sperm is effected by a cuticular extension of the male duct. Aided by considerable pressure of the body, a stylet, style or other extension pierces through the body wall of the other conjugant and so sperm is transferred. The process is called *hypodermic injection*. Next follows a section describing the details on the cuticular extensions which the author has dissected. Precise *hypodermic injection* is described. There follows the uses in classification in which the reproductive system is recommended as an important family character. One section especially emphases copulation studies and discusses in merit of other methods.

Riassunto

I Sacoglossi sono un ordine di opistobranchi ermafroditi, con fecondazione interna e generalmente reciproca. Essi presentano due aperture genitali: una maschile ed una femminile. Il pene, quando non è estroflesso, è contenuto in una guaina posta posteriormente all'apertura maschile. Attraverso l'apertura femminile avviene solo la deposizione del nastro ovigero e, apparentemente in molte specie manca una vera e propria apertura vaginale. Il passaggio degli spermi, infatti, avviene attraverso un'iniezione ipodermica del pene grazie anche alla presenza di stili, stiletti ed altri accessori, che vengono descritti in dettaglio. Viene inoltre discussa l'importanza del sistema riproduttore nella sistematica dei sacoglossi e le diverse tecniche necessarie per lo studio di questo ordine.

Introduction

This Introduction is intended to help the reader who may have little or no knowledge of sacoglossan sea slug. This was recommended at the 11° International Malacological Congress at Siena, Italy, in 1992.

The Sacoglossa is a small compact order of about 200 species. Most species are small and their lengths are measured in mm. Styles, styles and other extensions are measured in μm. They are vegetarians and feed on filamentous algae that grow, littorally, in rock pools. Three species have taken to feeding on the eggs of other opisthobranchs. Two species (*Limapontia depressa* and *Alderia modesta*) live on the damp mud of estuarine salt marshes. The order is essentially a tropical or subtropical group, but its range is extensive, from Norway to Australia. 10 species are found along the coast of Great Britain.

(*) 16A, York Grove, Peckham, London SE15 2NY, U.K.

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Some brief remarks now follow for the species n° 1 to 10, depicted in Fig. 1.

1. Elysia viridis (Montagu, 1804)

This large species, 45 mm long, is characterized by a pair of parapodia with which it can balance and move about and even swim a little. Feeds on the seaweed *Codium*.

2. Limapontia capitata (O.F. Müller, 1773)

A very small sacoglossan of length 2 mm. Without rhinophores or cerata. Looks like a bit of dirt when placed in the hand. It will glisten with mucus and slowly crawl with its foot. Two black eyes in pale lemon patches will be seen. Feeds on filamentous seaweed of the genus *Cladophora*.

3. Limapontia cocksi (Alder & Hancock, 1848)

Similar in size and appearance to *L. capitata*, except that it has a pair of rhinophores which form a key character. It feeds on *Cladophora*. It lives in the same habitat as *L. capitata* but it is less common. It is more active than *L. capitata* that seldom strays from its tuft of *Cladophora*. Contrary other sacoglossans which have a veliger, *L. cooksi* shows a direct development.

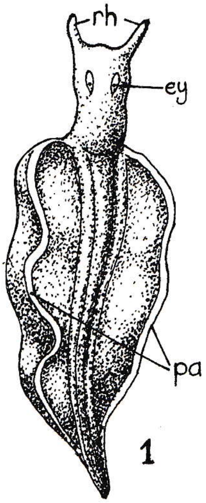
4. Limapontia depressa Alder & Hancock, 1862

Limapontia depressa and *L. capitata* are alike in that they have no external appendages and are small, 2 mm long. *L. capitata* has a slightly raised crest-like head, whereas, the head of *L. depressa* is depressed. This last species lives on the damp mud of estuarine salt marshes whereas *L. capitata* lives in rocky shore pools. Dark forms of *L. depressa* have been mistaken for *L. capitata*, but their stylets are quite different (Figs. 2: 2-5). That of *L. depressa* is squat and has a wide aperture with a rim with 3 or 4 spinules underneath the aperture. The stylet of *L. capitata* is a simple open tube, slightly curved towards the tips. *L. depressa* feeds on *Vaucheria*.

5. Alderia modesta (Lovén, 1844)

Total length: 10 mm. A pair of short stubby ear-like parapodia. With a raised dorsal prominence, cerata are arranged round its posterior border. Key character, a terminal anal spout. Habitat: semi-terrestrial, lives on the dump mud of estuarine salt marshes as for *L. depressa*. Less common than *L. depressa*. It feeds on *Vaucheria*.

Fig. 1. Sacoglossan external features
1. *Elysia viridis*; 2. *Limapontia capitata*; 3. *Limapontia cocksi*; 4. *Limapontia depressa*; 5. *Alderia modesta*; 6. *Tamanovalva limax*; 7. *Hermaea bifida*; 8. *Calliopea bellula*; 9. *Calliopea oophaga*; 10. *Hermaeopsis variopicta*. Abbreviations: **rh**, rhinophores; **pa**, parapodia or sideflaps; **ey**, eye; **as**, anal spout; **sh**, bivalved shell (juvenile length: 1 mm): **gp**, gastropodous foot; **ca**, cerata (plural); **c**, ceras (singular).
(Based on a Figure by GREGORY BROWN in *Biology of Opisthobranchs*, vol 2 by T.E. Thompson and G. Brown).



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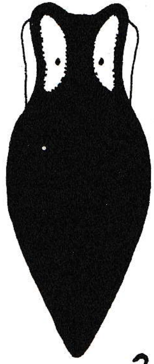

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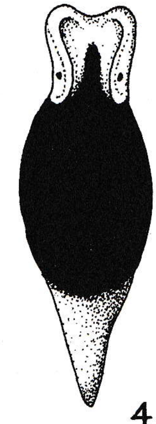

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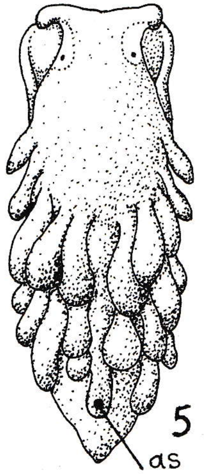

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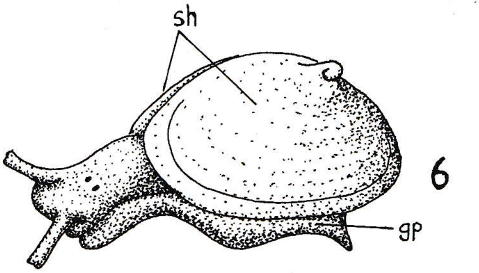

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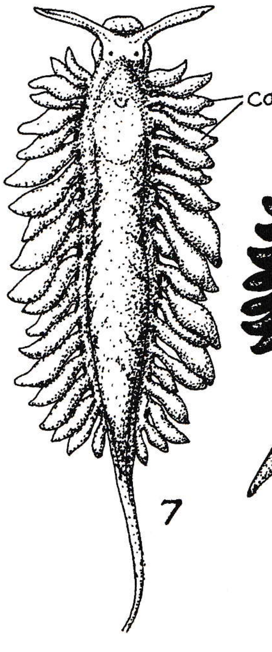

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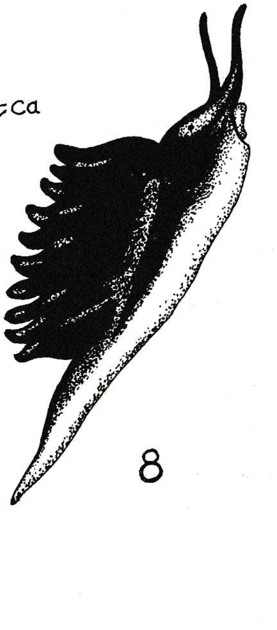

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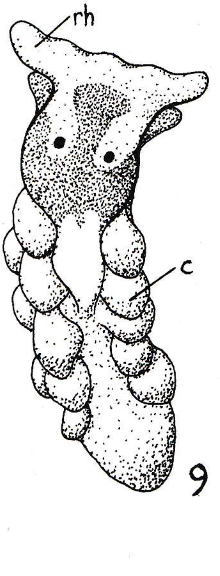

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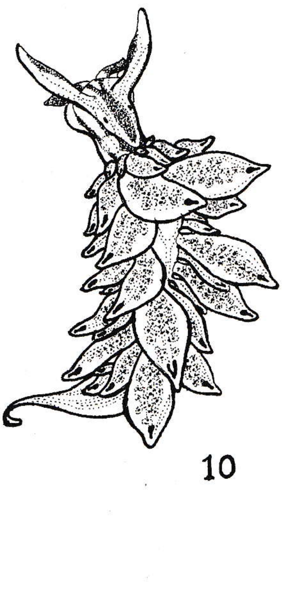

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6. Tamanovalva limax (Kawaguti & Baba, 1951)

Discovered in the Bay of Tamano, Japan, this species was formerly placed in the order Bivalvia. Kawaguti & Baba convincingly showed it was a «bivalved gastropod». Key character, a bivalved shell, width 1 mm, into which it can completely withdraw. It has a bivalved shell and it was placed in the Bivalvia. But it has a gastropodous foot, a sacoglossan radula and is a vegetarian feeding on *Caulerpa*. Also its central nervous system is typically sacoglossan.

7. Hermaea bifida (Montagu, 1815)

This species emits a pungent and obnoxious smell when disturbed.

8. Calliopaea bellula (D'Orbigny, 1837)

This species shows a double row of cerata along each side of the body. Remarkable for its speedy, incessant movement.

9. Calliopaea oophaga (Lemche, 1974)

Total length: 3 mm. It has a single row of six cerata along each side of the body. Moves with the remarkable speed as for *C. bellula*. Juvenile specimens eat the eggs of other opisthobranchs.

10. Hermaeopsis variopicta (A. Costa, 1869)

Beautifully coloured species with orange, purple and creamy white bands.

Fig. 2. Details of the cuticular extensions in Sacoglossans
Stylets

Type A. Length: 20-60 μm. A simple, open tube slightly curved towards its open end. Inflexible. 1: *Limapontia cocksii*. 2: *Limapontia capitata*. The penis is dissected. It shows the anchoring collar and a small ampulla. 3: *Placida dendritica*.

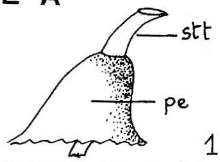
Type B. Length: 10-40 μm. A squat stylet with a wide aperture. Inflexible. 4: *Ercolania margaritae*. 5: *Limapontia depressa*. The wide aperture has an irregular thickened rim. Beneath the aperture are 3-4 recurved spinules. 6: *Alderiopsis nigra*.

Stiles. 7: *Alderia modesta*. Long tube, about 100 μm, slightly curved towards its open end. With about 8 terminal longitudinal rows of tiny pointed spicules (BLEAKNEY, 1988). 8; *Cyerce nigricans*. A long, straight inflexible tube. Note the neat penultimate opening.

Other extensions. 9: *Calliopaea oophaga* Total length: 400 μm. The first half of the cuticular extension is wider than the second part. The inset shows that it has an open end. 10: *Edenttellina typica*. long broad flexible tube with a spur at its base. 11; *Midorigai australis*. long broad flexible tube with a flange at its open end. 12: *Elysia viridis*. long and thread-like extension; flexible. Abbrevations: **ac**, anchoring collar; **ap**, aperture; **ds**, distal section of style; **fl**, flange; **l**, lip; **md**, male duct; **am**, penial ampulla; **pe**, penis; **sp**, spinules; **spi**, spicules; **spr**, basal spur; **st**, style; **stt**, stylet.

STYLETS

TYPE A



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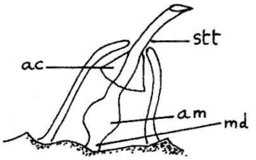

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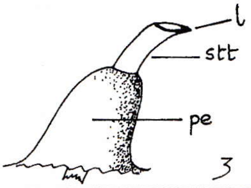

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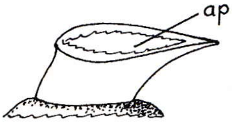
TYPE B



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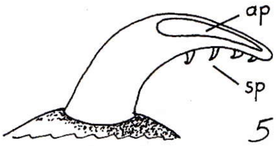

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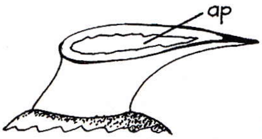

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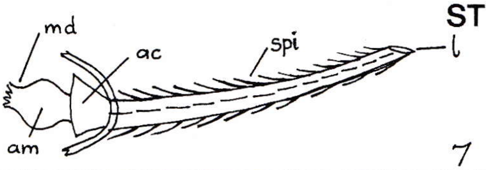

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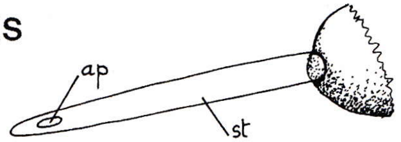

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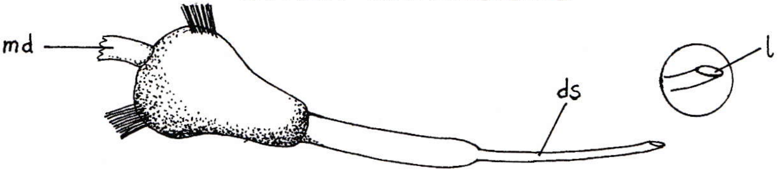
OTHER EXTENSIONS



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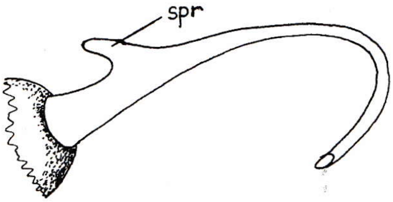

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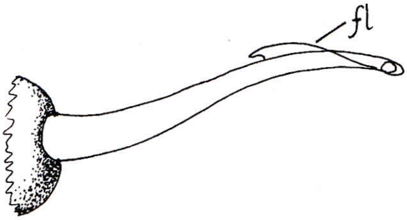

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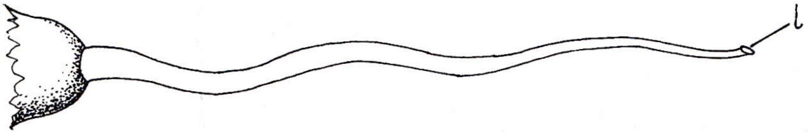

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Cuticular extensions of the male duct in Sacoglossans

Sacoglossans are hermaphrodites. Fertilization is internal and usually reciprocal. In the species that I examined there were only two genital openings on the right side: a male opening just posterior to the right eye and a female opening at some distance posterior to the male opening. When not in action, the penis is enclosed in the penial sheath that extends posteriorly from the male opening, along the inside of body wall. During copulation, the penis is thrust out of its sheath and after copulation the penis retracts inside its sheath. The penis is a conical outpushing of the body wall and contains muscular tissue and a penial nerve. The male duct runs through the penis and extends beyond the tip of the penis as a stylet, style or other cuticular extensions. The male duct has an anchoring collar and sometimes a small ampulla inside the apex of the penis. The female opening functions only as an outlet for the egg string when it passes outside the body during egg-laying. In the species I examined, I did not find a vaginal opening. During copulation, the transfer of sperm is effected by *hypodermic injection*, by means of a cuticular extension of the male duct.

Adult sacoglossans with stylets that I have examined (Fig. 2: 1-6) practice *precise hypodermic injection*. During copulation two specimens come close together in a «head-to-tail» copulatory position, each conjugant with its penis poised over the target area of its partner. The partner's bursa copulatrix is attached to the inside of the body walls. With considerable pressure from both conjugants, each stylet is thrust directly into its partner's bursa copulatrix and so a double tranfer of sperm is achieved. It should be noted that the bursa copulatrix is a vesicle for the reception and storage of foreign sperm. The bursal duct leads to the fertilization chamber. When the exchange of sperm is completed, the conjugants tug themselves apart and each penis with its extension is returned inside its body and is enclosed in its penial sheath. This sheath has been mistaken for the penis by previous researchers.

Alderia modesta exchanges sperm by *imprecise hypodermic injection*. HAND & STEINBERG (1965) published a copulation study of this species. Each conjugant makes repeated jabs over the dorsal surface of its partner and sperms were seen actively swimming in the haemocoelic fluid. REID (1964) described how in *Elysia maoria* the exchange of sperms takes place simply by repeated pressure of the body over the dorsal surface and no cuticular extension was observed. It so this may be an exception that proves the rule.

Uses in Classification

In the 19th century, figures of stylets appeared in the papers of Alder & Hancock, Bergh, Trinchese and other specialists. As far as I can tell, ENGEL *et al.* (1940) were among the first to describe the function of stylets in a paper on *Limapontia depressa* and *Alderia modesta*. GASCOIGNE (1956; 1976) added further details and described six more stylets. MARCUS (1982) published a pamphlet on the systematics of the genera of the order Ascoglossa. It is a comprehensive pamphlet, including 71 figures and 156 references. A novel feature is a key to the genera. It will be a valuable reference work for ascoglossan specialists for many years to come. In the classification, E. Marcus uses only stylets as generic characters; styles and other extensions are omitted. The stylets are not described. Among the 71 figures there is not one of a stylet. E. Marcus refers to the reproductive systems as diaulic, triaulic or pseudodiaulic. I recall that in my 1976 paper, I used diaulic and pseudodiaulic. In this context, diaulic means with two genital openings. Pseudodiaulic was an invention of mine. It refers to the time when a cuticular extension makes a temporary opening by hypodermic injection. I have not used such a technical term since 1976. I suggest two improvements to E. Marcus's classification of the Stiligeridae.

1. Remove the taxon subfamily before the genus *Limapontia*. The pattern of the reproductive system in this genus is stiligerid.
2. Place the genus *Alderia* in a separate family, the Alderidae, as GASCOIGNE (1976) proposed. The Alderidae has only one genus, *Alderia*.

E. Marcus gave a description of *Alderia modesta* and concluded with the comment «with this incomplete description it must be considered as *incertae sedis*». HAND & STEINBERG (1965) studied the copulation of *A. modesta*. They observed that each conjugant made several jabs with a distinctive style, and sperm were seen swimming in the haemocoelic fluid of the partner. GASCOIGNE (1976) in his paper on the reproductive systems and classification of the Stiligeridae, showed that there was a wide gap between the reproductive systems of the Stiligeridae and the Alderidae. These two papers are sufficient to remove the doubts expressed by E. Marcus. More could be added. If a sacoglossan possesses a stylet, it is and indication it belongs to the family Stiligeridae. A few cuticular extensions, such as the styles of *Alderia modesta* and *Cyerce nigricans*, are so distinctive that they may be considered as key characters of their species. Cuticular extensions play a part in maintaining a species in reproductive isolation. The reproductive system, especially the female one, can prove to be a wide gap between the families. For example, between the families Stiligeridae and Alderidae. Unfortunately there are far too few satisfactory descriptions, with figures, of the sacoglossan reproductive system. Most of the figures show a partially dissection lying in a tangled heap that does not reveal the pattern of the system.

Research Methods

There are two main methods: copulation studies and fine dissection.

Copulation studies: an ideal programme

1. Collect about six specimens of the same species. Do not over collect. Avoid collecting too much filamentous seaweed and leave it in the laboratory to stink. You may remove much of the seaslugs habitat.
2. Keep them alive for about 2-3 weeks. Usually the sacoglossans feed before copulating.
3. Note copulatory position: is it head-to-tail or entwined or nondescript? Take no note of juvenile specimens that often jab at random while the adult is in action.
4. Observe the injections: precise or imprecise?
5. Take a pair of copulants and slightly disturb them. This will reveal the exact point of injection.

6. Once a pair starts, the other adults will follow their example. This suggests that, during mating, an attractive chemical substance is secreted.

7. After copulation there is a period of apparent rest. The penis is withdrawn inside the body, into the penial sheath, until egg laying begins. The eggs are laid as an egg-string (flat spiral) or an egg-mass (compressed spiral). Within the envelope of an egg-string, the eggs are arranged on a single helix.

8. Estimate the number of eggs in the egg-string or egg-mass. There may be differences between families.

9. It may be that a species is not a good laboratory animal. If so, I suggest *Elysia viridis or Hermaea bifida.*

Fine dissection

The fine dissection is essential for displaying the pattern of the reproductive system. Do no represent the reproductive system by a confused figure of a partial dissected mass that does not show the pattern of the system. Serial sections can be essential for examining the follicles or acini of the hermaphrodite gland and cellular details. Not recommended for cuticular extensions or ducts which may be cut and displaced or lost in the elaborate process of making sections.

Whole mounts are suitable for cuticular extension of the male duct. Free the penis from the body and mount in Berlese's fluid is recommended. Also the smear technique is useful: from a freshly killed sacoglossan remove the vesicle, or part required and stain appropriately.

Finally electronic microscope methods (TEM and SEM) could be used if they make a cuticular extension clearer than before.

Acknowledgements

I wish to express my grateful thanks to Robin Harvey (Oban) who read my rough notes and arranged them as a paper and typed it; Charles Wethered, artist, he drew the text figures from my imperfect sketches; and John Mc Caig, my guide and secretary when I went to the 11th International Malacological Congress. Finally, I thank John Greatrex for reading the publisher's proof.

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Kathe R. Jensen (*)

EVOLUTION OF BUCCAL APPARATUS AND DIET RADIATION IN THE SACOGLOSSA (OPISTHOBRANCHIA) (**)

Key Words: Sacoglossa; Pharynx; Radular teeth; Opisthobranchia; Evolution

Abstract

The Sacoglossa are suctorial feeders, and the majority of species are stenophagous herbivores, feeding on the cell sap of marine plants. In the Sacoglossa evolution appears to be closely associated with diet radiation. All shelled Sacoglossa feed on the morphologically variable algal genus *Caulerpa*.

Changes in diet has occurred in parallel in the major groups of shell-less Sacoglossa. Pharynx musculature and radular teeth of several species of Sacoglossa are described. Based on this and previous studies, character analysis is performed, and the most important morphological and functional «innovations» are identified. These are: muscular suspension of ascending limb of radula, transverse muscles forming a functional separation of ascending and descending limbs of radula, blade-shaped teeth with median denticles, sabot-shaped teeth, and shift in importance from ascending to descending limb of radula. Radula suspending muscles are found in all sacoglossans, transverse muscles in the shell-less Sacoglossa. Blade-shaped teeth have evolved 2 or 3 times within the major lines of evolution, sabot-shaped teeth only in the stiligeroid line. The functional shift apparently occurred rather late, after the loss of the shell and pharyngeal pouches.

Riassunto

I sacoglossi sono opistobranchi erbivori che si alimentano succhiando il contenuto cellulare di diverse piante marine. La maggior parte di essi è stenofaga. L'evoluzione del gruppo sembra essere strettamente collegata alle loro scelte alimentari. Tutti i sacoglossi conchigliati si alimentano di varie alghe appartenenti al genere *Caulerpa*, mentre tra le specie non conchigliate, parallelamente alla loro evoluzione, è avvenuta una forte specializzazione della dieta.

Viene qui descritta la muscolatura faringea ed i denti radulari di diverse specie di sacoglossi. Grazie a questo ed altri studi, è stato possibile condurre un'analisi dei caratteri, identificando le più importanti «innovazioni» morfologiche e funzionali. Queste sono: la sospensione muscolare del ramo ascendente della radula, i muscoli trasversali che formano una separazione funzionale fra il ramo ascendente e discendente della radula, i denti a forma di lama con denticoli mediani, i denti a forma di zoccolo olandese o cucchiaio (sabot), e la perdita d'importanza del ramo ascendente nei confronti di quello discendente. Muscoli sospensori della radula si rinvengono in tutti i sacoglossi, mentre i muscoli transversali sono presenti solo nei sacoglossi non conchigliati. I denti a forma di lama hanno subito almeno 2-3 cambiamenti evolutivi nell'ambito delle maggiori linee filogenetiche dei sacoglossi, mentre quelli a cucchiaio appaiono solo all'interno del gruppo degli Stiligeroidi.

Il cambiamento funzionale della radula è apparentemente avvenuto piuttosto tardi, dopo la perdita della conchiglia e delle tasche faringee.

(*) Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen, Denmark

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Introduction

The Sacoglossa are suctorial feeders, and the majority of species are stenophagous herbivores, feeding on the cell sap of marine plants. The buccal apparatus in the Sacoglossa consists of the oral tube, the muscular pharynx, and the radula (Fig. 1). The oral tube of most sacoglossans is short and non-muscular. The sacoglossan pharynx and radular teeth show several autapomorphies to distinguish them from other opisthobranchs (JENSEN, 1991, in press).

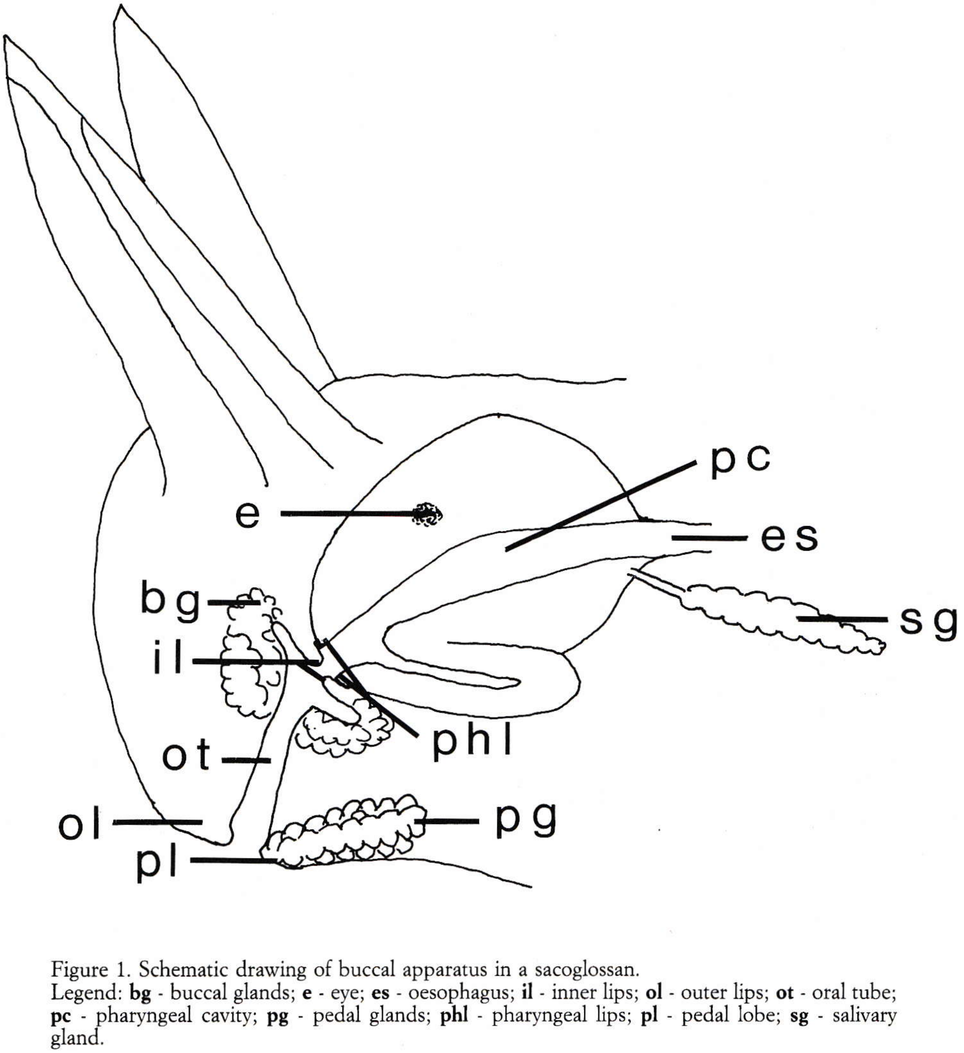

Figure 1. Schematic drawing of buccal apparatus in a sacoglossan.
Legend: **bg** - buccal glands; **e** - eye; **es** - oesophagus; **il** - inner lips; **ol** - outer lips; **ot** - oral tube; **pc** - pharyngeal cavity; **pg** - pedal glands; **phl** - pharyngeal lips; **pl** - pedal lobe; **sg** - salivary gland.

The suctorial pharynx of sacoglossans is composed of 4 muscular units: (1) the dorsal septate muscle, (2) the odontophore, (3) the ventral, longitudinal ascus-muscle, and (4) the pharyngeal pouch. The odontophore contains 2 or 3 functionally distinct groups of musculature: (1) the odontophore muscles (mainly dorso-ventral), (2) the radula suspending muscles (fan-shaped), and (3) the ventral, transverse muscles forming a functional separation between the ascending and descending limbs of the radula (JENSEN, in press).

The sacoglossan radula is uniseriate and composed of (1) an ascending limb completely enclosed within the odontophore musculature, (2) a descending limb of about equal length, surrounded by the ascus-muscle, and (3) an ascus in which old, used teeth are accumulated throughout life, either rolled up into a spiral, or in a densely packed heap (JENSEN, 1991).

Parallel evolution is very common in the opisthobranchs (GOSLINER & GHISELIN, 1984). In the Sacoglossa evolution appears to be closely associated with diet radiation (JENSEN, 1993a in press). All shelled Sacoglossa feed on the morphologically variable algal genus *Caulerpa*. Changes in diet has occurred in parallel in the major groups of shell-less Sacoglossa. This has resulted in several parallelisms of the feeding apparatus (JENSEN, 1993a).

The Sacoglossa contains 3 distinct superfamilies: the shelled Conchoidea, the cerata-bearing Stiligeroidea, and the parapodia-bearing Elysioidea. Previous studies, mainly on the Elysiidae, have shown that all the major muscle groups of the sacoglossan pharynx have evolved differently in the different species (JENSEN & WELLS, 1990; JENSEN, 1992, in press). Also, correlations between shape of radular teeth and diets have been examined (JENSEN, 1993a). In the present study information on pharynx musculature and radular teeth of several species from the major evolutionary lines will be presented. Based on this information as well as that of the previous studies, character analysis is performed. For outgroup comparison the very well studied *Monodonta lineata* and *Philine aperta* have been used (FRETTER & GRAHAM, 1962; HURST, 1965). Functional aspects have been included in the analysis. Also, the parallelisms related to diet changes will be discussed.

Materials and methods

Collecting data for specimens used in the present study are listed in Table 1. Specimens were relaxed in 7% $MgCl_2.6H_2O$ mixed with seawater (1:1). They were fixed in neutral 4% formaldehyde and then transferred to 70% or 80% ethanol. For fine dissection animals were lightly stained with acetocarmine. Radular mounts for SEM were prepared as described in JENSEN (1992). Serial sections of *Caliphylla mediterranea* were generously given to the author by Dr. Tom Gascoigne.

Table 1. List of material used in present study. WA - Western Australia; USVI - U.S. Virgin Islands.

Species	Location	Date	Collector
Ascobulla fischeri	Triggs Isl. WA	30 Mar. 69	S. Slack-Smith WAM186-88
	Albany, WA	Jan. 88	K.R. Jensen
Lobiger sagamiensis	Hong Kong	April 83	K.R. Jensen
Elysia flavomacula	Hong Kong	April 86	K.R. Jensen
Elysia cf. *maoria*	Rottnest Isl. WA	Jan. 91	K.R. Jensen
Caliphylla mediterranea	Livorno, Italy	June 78	T. Gascoigne
Cyerce antillensis	St. Thomas, USVI	April 82	K.R. Jensen
Hermaea cruciata	Florida	Jan. 80	K.R. Jensen
Aplysiopsis formosa	Azores	July 91	K.R. Jensen
Aplysiopsis smithi	California	July 86	K.R. Jensen
Costasiella pallida	Hong Kong	April 86	K.R. Jensen
Ercolania nigra	Denmark	Aug. 89	K.R. Jensen
Ercolania translucens	Rottnest Isl. WA	Feb 81	J.S. Bleakney

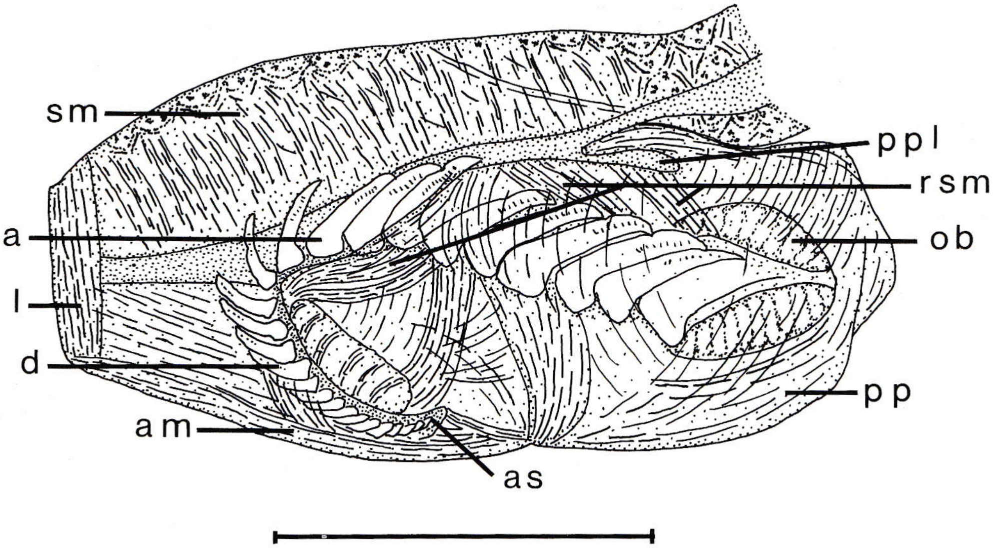

Figure 2. Sagittally sectioned pharynx of *Ascobulla fischeri* (WAM 186-88). Scale line = 0.5 mm. Legend: **a** - ascending limb; ***am*** - ascus-muscle; **as** - ascus; **d** - descending limb; **l** - pharyngeal lips; **ob** - odontoblasts; **pp** - pharyngeal pouch; **ppl** - lumen of pharyngeal pouch; **rsm** - radula suspending muscles; **sm** - dorsal septate muscle.

Results

PHARYNX

The pharynx of the shelled *Ascobulla fischeri* has a flat dorsal septate muscle, a thin ascus-muscle, and a short, collar-like pharyngeal pouch (Fig. 2). The odontophore is positioned rather far back in the pharynx. The ascending limb of the radula is much longer than the descending limb, and the posterior tip of the radular sac extends all the way to the bottom of the pharyngeal pouch. Three to 4 teeth of the ascending limb are visible on the dorsal surface of the odontophore. Only a few radula suspending muscles are located on the dorsal surface of the ascending limb. The most prominent radula suspending muscles are ventral of the ascending limb. The odontophore muscles form dense layers on either side of the radula and appear to be continuous with the muscles of the pharyngeal pouch. About 4 teeth of the descending limb are visible on the anterior free tip of the odontophore. The descending limb ends in a straight row which is located within the odontophore. Dorsal to the descending limb is a distinct muscular «cushion» apparently composed of dorsoventral muscles. Thus there are no transverse muscles separating the ascending and descending limbs of the radula. The posterior tip of the desçending limb is connected to the ascending limb by a strong strand of radula suspending muscle. The lumen of the pharyngeal pouch is only a small pocket at the dorsal part of the pharyngeal pouch, just below the esophagus.

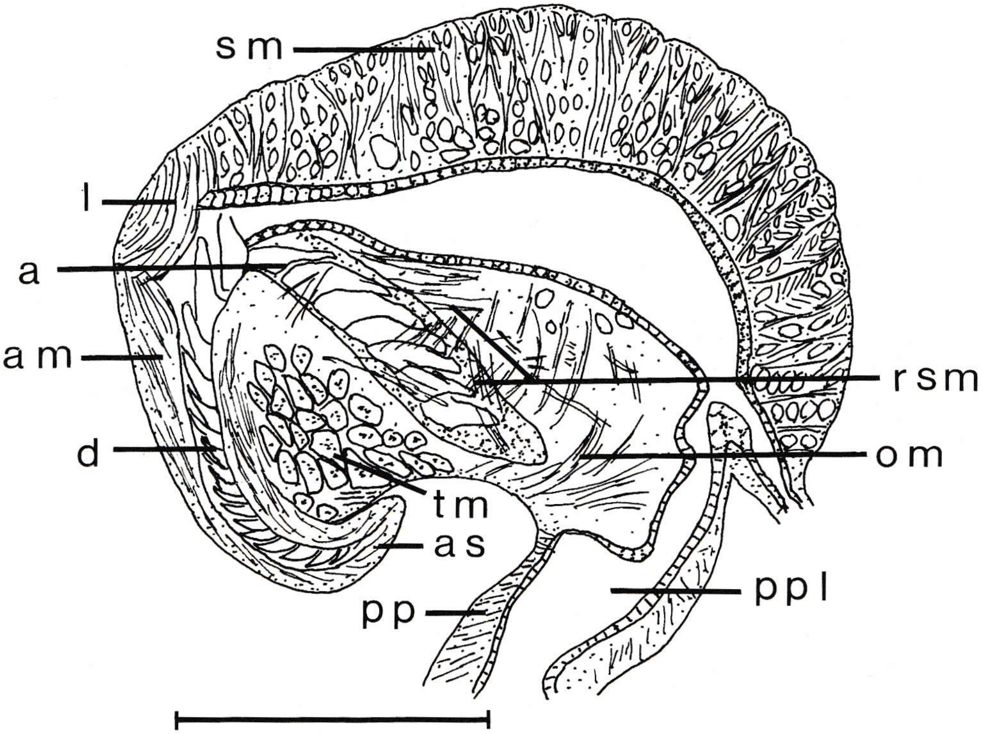

Figure 3. Sagittal section through pharynx of *Caliphylla mediterranea*. Scale line = 0.5 mm. Legend: **a** - ascending limb; **am** - ascus-muscle; **as** - ascus; **d** - descending limb; **l** - pharyngeal lips; **om** - odontophore muscles; **pp** - pharyngeal pouch; **ppl** - lumen of pharyngeal pouch; **rsm** - radula suspending muscles; **sm** - dorsal septate muscle; **tm** - transverse muscles.

Sections of the pharynx of the polybranchiid *Caliphylla mediterranea* (Fig. 3) show that it has a thick dorsal septate muscle and a large pharyngeal pouch. The epithelium of the pharyngeal cavity is pigmented, as is that of the wide, paired lumina of the pharyngeal pouch. There is a distinct dorsal food groove. The ascending limb is rather far towards the ventral surface of the odontophore. There are 3-4 teeth on the free tip of the odontophore. The ascus-muscle is rather short and steeply inclined relative to the longitudinal axis of the pharynx. Its posterior tip is not attached to the ventral pharynx wall. Teeth in the ascus are rolled in a spiral. Most of the radula suspending muscles are dorsal to the ascending limb. A prominent muscle attaches to the anteriormost tooth in the ascending limb and runs along the anteriormost teeth in the descending limb. It continues along the ventral surface of the pharynx to a point behind the tip of the ascus-muscle. Dorsal to this muscle is a thick layer of transverse muscles forming a tall, narrow «stalk» separating the ascending and descending limbs of the radula. The pharyngeal pouch consists of mainly dorso-ventral muscles. The paired lumina of the pharyngeal pouch are narrow in the anterior part of the pharyngeal pouch («stalk») and wide in the posterior part. The pouch is somewhat twisted.

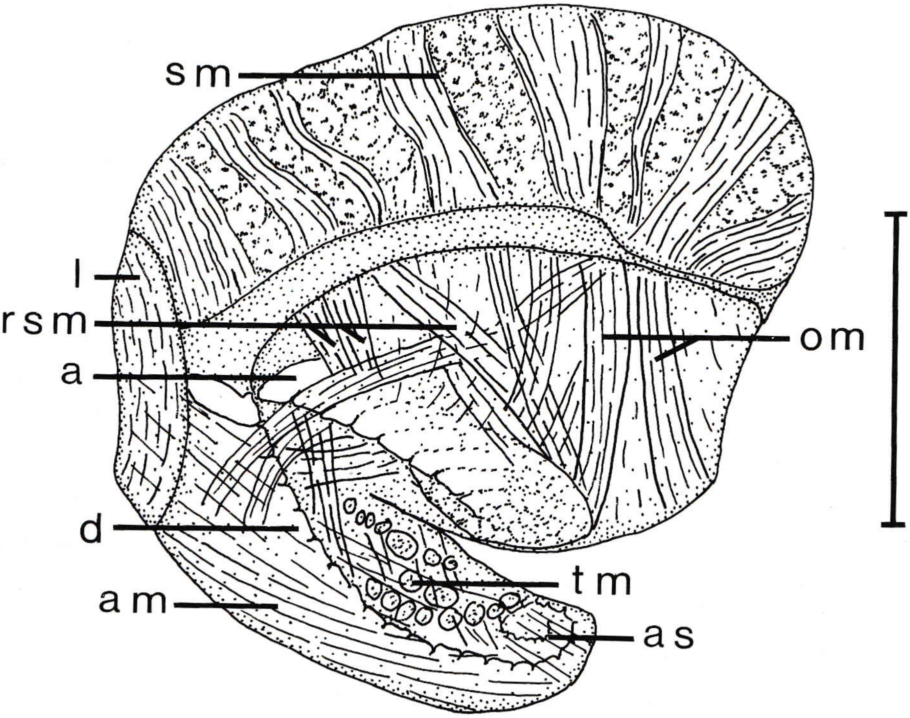

Figure 4. Sagittally sectioned pharynx of *Aplysiopsis formosa*. Scale line = 0.5 mm. Legend: **a** - ascending limb; **am** - ascus-muscle; **as** - ascus; **d** - descending limb; **l** - pharyngeal lips; **om** - odontophore muscles; **rsm** - radula suspending muscles; **sm** - dorsal septate muscle; **tm** - transverse muscles.

The pharynx of *Aplysiopsis formosa* has a thick, distinctly septate dorsal wall (Fig. 4). The odontophore is large, and the ascending limb of the radula is located rather far towards the ventral surface. It does not reach the posterior end of the pharynx. Apparently there are few radula suspending muscles dorsal to the ascending limb. This probably indicates that back and forth movements of the ascending limb are not important. The odontophore muscles behind the ascending limb of the radula are prominente. There is a thick layer of transverse muscles separating the ascending and descending limbs. The longitudinal muscles of the ascus-muscle are very well developed, and it is unattached posteriorly. The teeth in the ascus are rolled up in a spiral. There is no pharyngeal pouch.

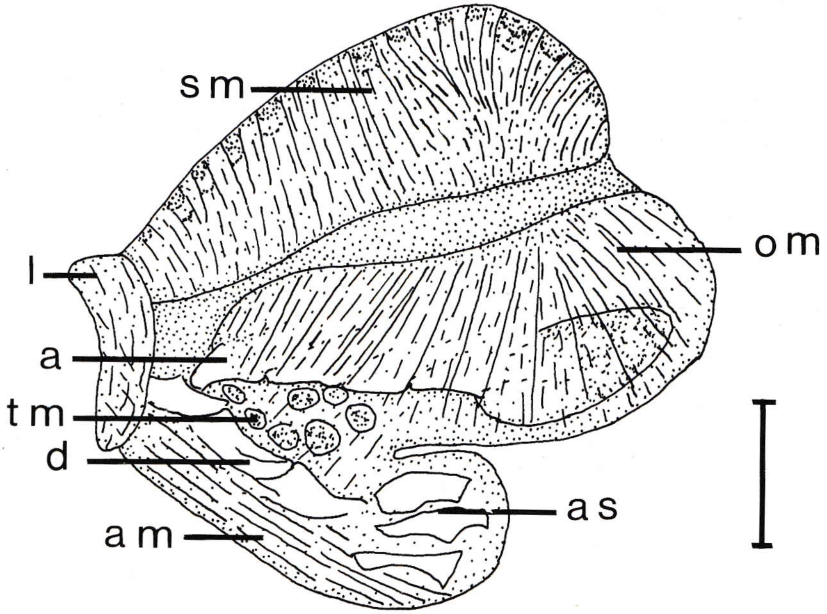

Figure 5. Sagittally sectioned pharynx of *Ercolania translucens* from Rottnest Island, Western Australia. Scale line = 0.1 mm. Legend: **a** - ascending limb; **am** - ascus-muscle; **as** - ascus; **d** - descending limb; **l** - pharyngeal lips; ***om*** - odontophore muscles; **sm** - dorsal septate muscle; ***tm*** - transverse muscles.

Fig. 5 shows the pharynx of *Ercolania translucens* from Rottnest Island, Western Australia. It has a thick dorsal septate muscle. The odontophore is rather flat, and the ascending limb of the radula is located in the ventral part. Radula suspending muscles are indistinct. There is a distinct layer of transverse muscles separating the ascending and descending limbs of the radula. The ascus-muscle is very thick, and its posterior end is unattached. The teeth in the ascus form a densely packed heap. A pharyngeal pouch is absent.

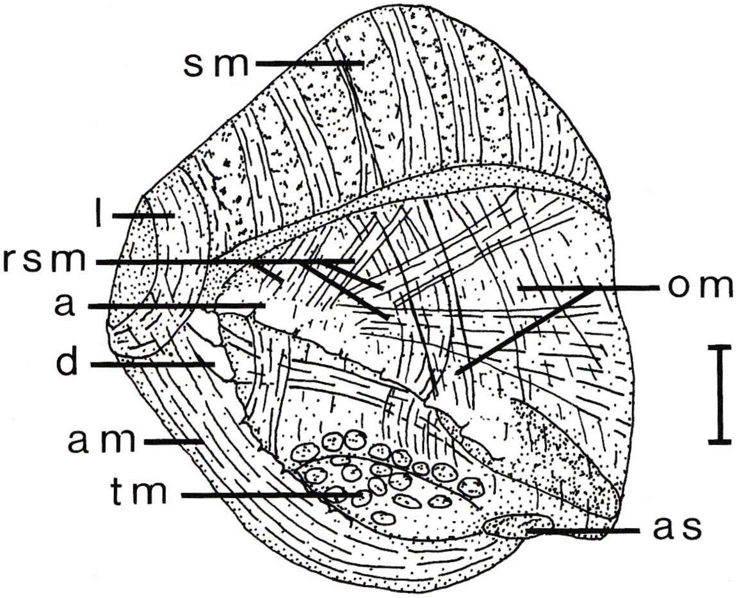

Figure 6. Sagittally sectioned pharynx of *Elysia* cf. *maoria* from Rottnest Island, Western Australia. Scale line = 0.1 mm. Legend: **a** - ascending limb; **am** - ascus-muscle; **as** - ascus; **d** - descending limb; **l** - pharyngeal lips; **om** - odontophore muscles; **rsm** - radula suspending muscles; **sm** - dorsal septate muscle; ***tm*** - transverse muscles.

The pharynx of *Elysia* cf. *maoria* from Rottnest Island (Western Australia) has a tall, thick, domed dorsal septate muscle (Fig. 6). The dorsal and lateral corners of the pharyngeal cavity are pigmented. The odontophore is triangular in outline, and the ascending limb of the radula ascends diagonally from the postero-ventral edge of the pharynx to the antero-dorsal tip of the odontophore. The radula suspending muscles are prominent, especially dorsal to the ascending limb. The odontophore muscles are especially prominent dorsal to the ascending limb. There is a thick layer of transverse muscles separating the ascending and descending limbs of the radula. The ascus-muscle is long, almost as long as the pharnyx, thick and attached to the ventral surface of the pharynx over its entire length, and the thinwalled, densely packed ascus is external. There is no pharyngeal pouch.

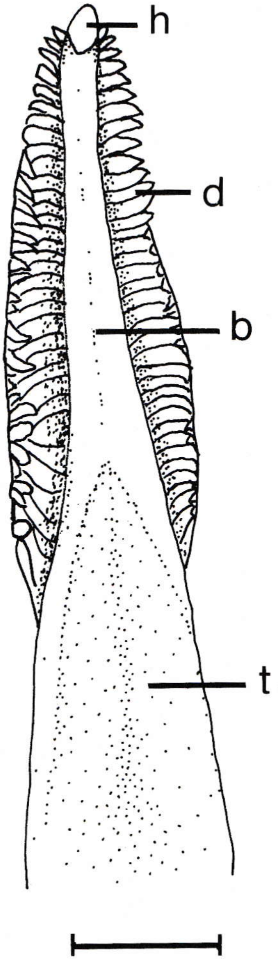

Figure 7. Distal part of tooth of *Ascobulla fischeri* from Albany, Western Australia. Scale line = 10 μm. Legend: **b** - blade; **d** - denticles; **h** - hooked tip; **t** - triangular part of cusp.

RADULAR TEETH

The radular teeth of the Sacoglossa are large, articulating, and interlocking. Only 1-3 teeth are exposed on the anterior, free surface of the odontophore (JENSEN, 1993a). They have a squarish base attached to the radular membrane. There are 3 basic shapes of the cusps of the radular teeth: teeth with triangular cusps with denticles along the lateral margins; blade-shaped teeth with lateral or median denticles, or completely smooth; and sabotshaped teeth with lateral denticles or smooth (JENSEN, 1991, 1993a).

The teeth of *Ascobulla fischeri* (see SEM-photo in Jensen & Wells (1990)) have triangular cusps with long, thin lateral denticles. The denticles extend from the tip and slightly over half the length of the cusp. They originate from ridges along the dorsal edges of the cusp. The lower half of the cusp (Fig. 7) is broadly triangular. The distal part of the cusp is more blade-shaped, with a short, rounded blade. The tip of the cusp is hooked, and the hook fits into a depression on the back of the tooth in front. The base is short and stout, and there is a prominent articulation knob anteriorly (Jensen & Wells, 1990). The cusp is inclined about 35° to the longitudinal axis of the base.

In *Lobiger sagamiensis* the teeth are blade-shaped with lateral denticles (Fig. 8). The denticles are very short and only extend over part of the length of the cusp. The blade is narrow, and the tip of the teeth is bifid. The bifid tips, like the hooked ones, are used to interlock a long row of teeth. The bases are rather short, less than half the length of the cusp. The posterior articulation knobs are more prominent than the anterior one. The blade is 28° inclined to the base.

The teeth of *Cyerce antillensis* have a long, broad base and a rather narrow cusp with coarse denticles along the lateral margins of the distal part (see SEM-photo in Jensen, 1993a). The lower part of the base has a broadly rounded median keel which fits into a cavity on the back of the preceding tooth. Distal to this cavity the back side of the cusp has a rather sharp edge. The articulation knobs anteriorly and posteriorly on the base are prominent. The cusp is only 18° inclined to the base. The teeth of *Caliphylla* are blade-shaped with a smooth edge (Gascoigne, 1979).

The teeth of *Costasiella pallida* (Fig. 9) are blade-shaped with smooth edges. The base is short with the most prominent articulation knobs posteriorly. The blade is long and thin, and the tip is slightly curved. The blade of *C. pallida* is inclined 23° to the base.

Hermaea cruciata has blade-shaped teeth with short lateral denticles (Fig. 10). The denticles are on low flanges which originate at the anterior edges of the base and run obliquely along the blade, almost to the tip. The blade is inclined 30° to the base. The base has prominent articulation knobs anteriorly and posteriorly, and it extends further back than the cusp. *Aplysiopsis smithi* has very peculiar looking radular teeth (Fig. 11). These teeth have been called sabot-shaped because of their resemblance to a Dutch wooden shoe (Gascoigne, 1977). These teeth have a very shallow base and broad cusps with a rounded tip and a prominent dorsal keel over which the tooth behind fits. In *Aplysiopsis* the teeth have denticulate margins. The base is short and the cusp is inclined 55° to the base.

The stiligerid genus *Ercolania* has sabot-shaped teeth. These teeth have a very shallow base, a conspicuous dorsal keel, and a deep cusp with flexible lateral edges. Articulation knobs are small or absent. In *E. nigra* the cusps have a short cutting edge dorsally on the tip of the cusp, and the tip is slightly hooked (Fig. 12).

Like most species of *Elysia*, *E. flavomacula* has bladeshaped teeth with median denticles (Fig. 13). The base is rather short with prominent articulation knobs anteriorly and posteriorly. There are no lateral flanges on the blade. The denticles are fine and have rounded edges. In *Elysia* cf. *maoria* the blade is relatively longer, and the denticles have pointed tips.

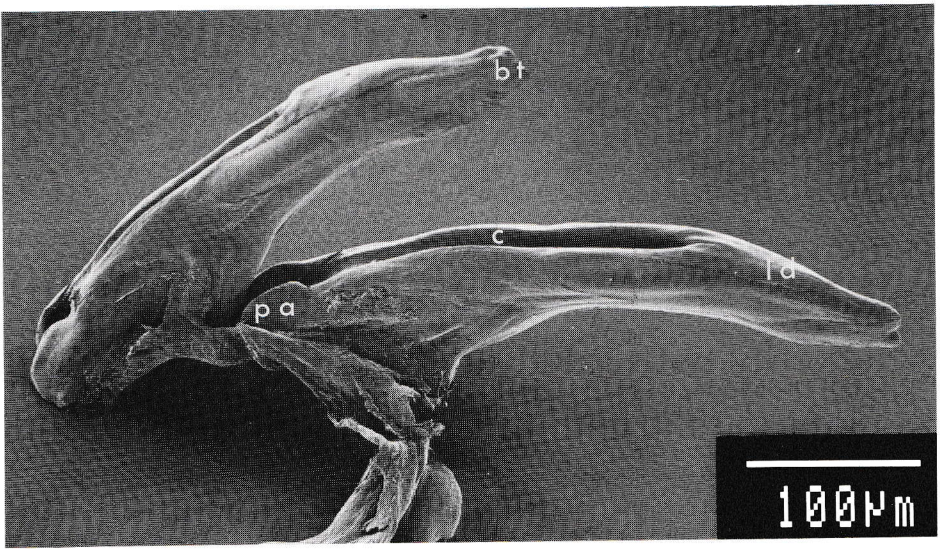

Figure 8. SEM-photo of radular teeth of *Lobiger sagamiensis* from Hong Kong. Legend: **bt** - bifid tip; **c** - dorsal cavity; **ld** - latral denticles; **pa** - posterior articulation knob.

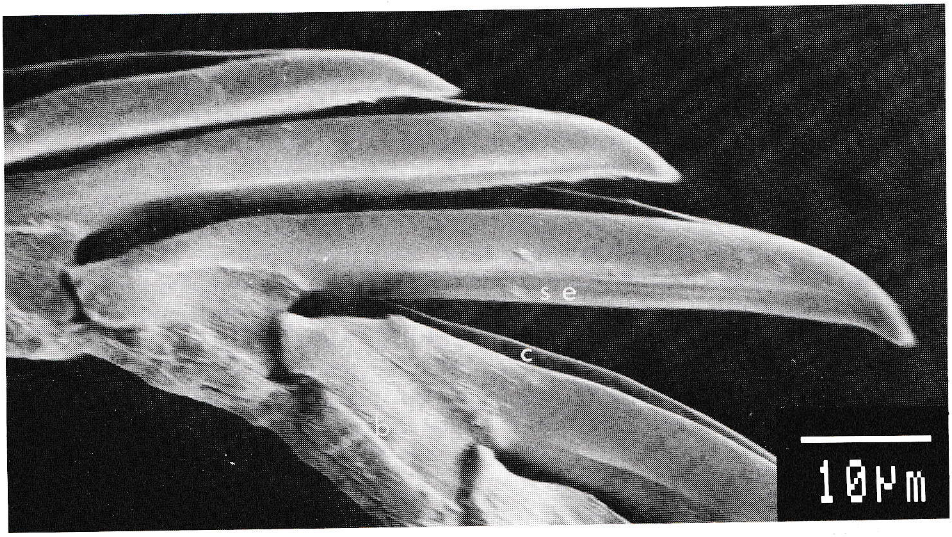

Figure 9. SEM-photo of radular teeth of *Costasiella pallida*. Legend: **b** - base; **c** - dorsal cavity; **se** - smooth edge.

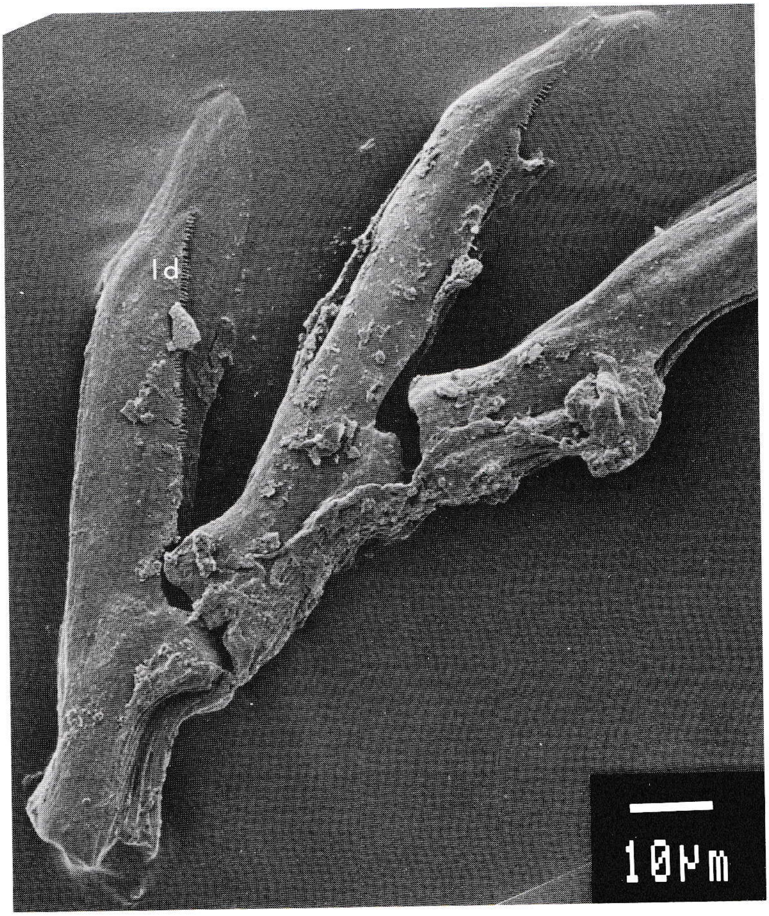

Figure 10. SEM-photo of radular teeth of *Hermaea cruciata*. Legend: **ld** - lateral denticles.

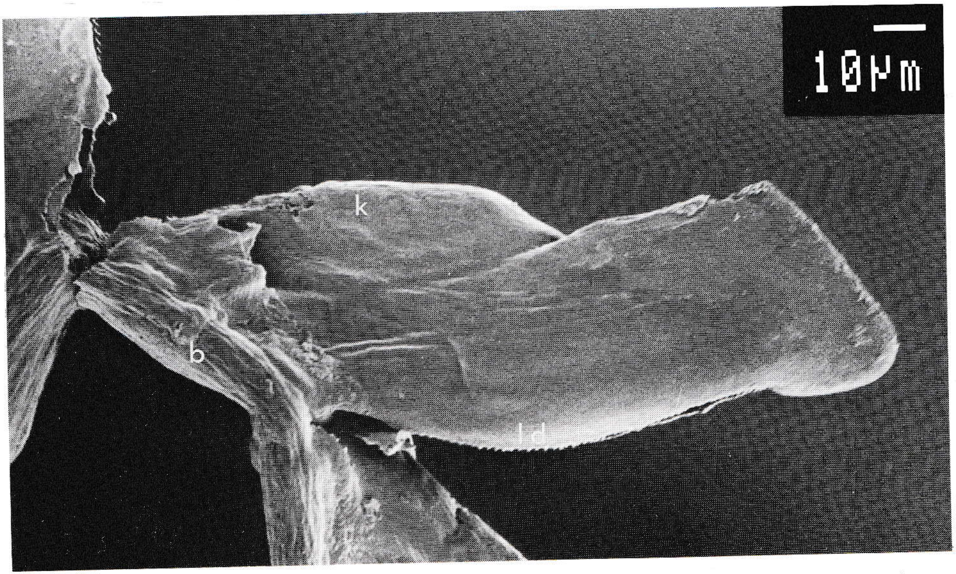

Figure 11. SEM-photo of radular tooth of *Aplysiopsis smithi*. Legend: **b** - base; **k** - dorsal keel; **ld** - lateral denticles.

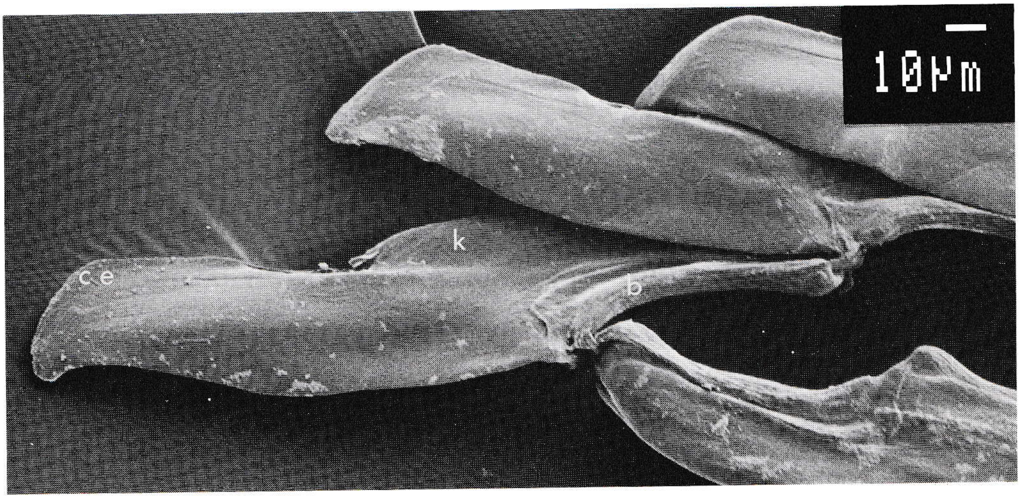

Figure 12. SEM-photo of radular teeth of *Ercolania nigra*. Legend: **b** - base; **ce** - cutting edge; **k** - dorsal keel.

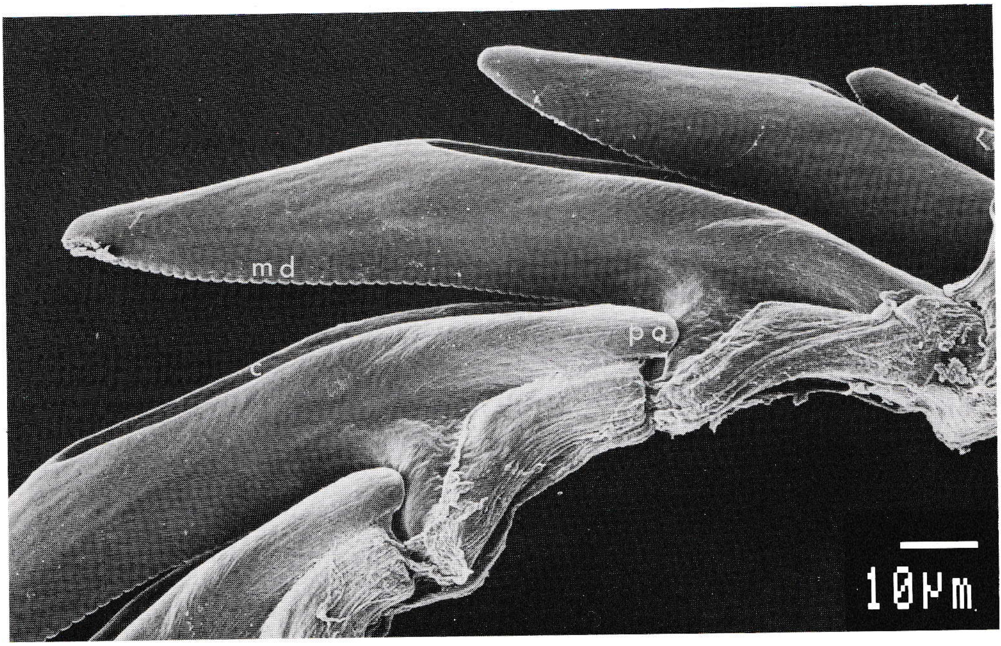

Figure 13. SEM-photo of radular teeth of *Elysia flavomacula*. Legend: **c** - dorsal cavity; **md** - median denticles; **pa** posterior articulation knob.

Discussion

The Sacoglossa have long been recognized as a well defined, monophyletic group. However, phylogenetic relationships within the group are not resolved (see f.ex. MARCUS (1982) and GASCOIGNE (1985)). Recently attempts have been made to describe characters which are useful for phylogenetic analysis (JENSEN & WELLS, 1990; JENSEN, 1991, 1992, 1993a,b in press).

Evolution within the Sacoglossa appears to be closely related to changes in diet (CLARK & BUSACCA, 1978; CLARK & DEFREESE, 1987; JENSEN, 1993a, in press). The shelled Sacoglossa all feed on algae of one single genus, *Caulerpa*. «Diet radiation» probably occurred at several stages of evolution. At all these stages species may have evolved which «reverted» to a more «ancestral» diet. Hence it is necessary to identify some morphological «innovations» in order to distinguish parallelisms from homologies.

The first step in diet radiation was from *Caulerpa* to other genera of the order Caulerpales (Fig. 14). These have similar cell wall structure, but often more complex thallus structure (JENSEN, 1993a). The second step involved a simplification in thallus structure, but a change in cell wall struc-

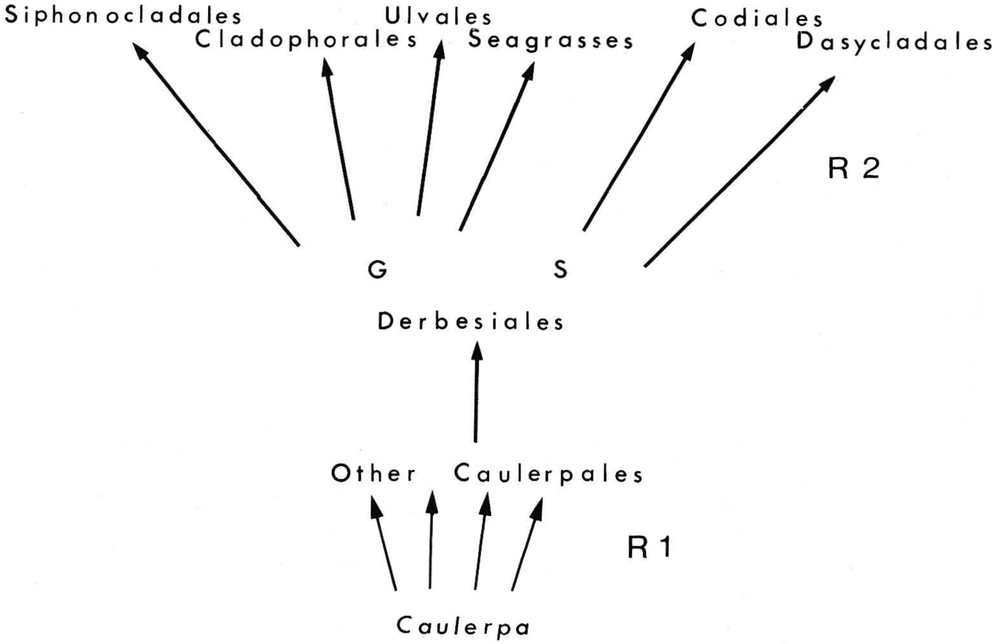

Figure 14. Diagram of diet radiation in the Sacoglossa. Abbreviations: **G** - gametophyte; **S** - sporophyte; **R1** and **R2** - first and second radiation.

ture, namely the filamentous Derbesiales. These have heteromorphic lifecycles in which the gametophyte has xylan (as in the Caulerpales) and cellulose as the structural cell wall polysaccharides, and the sporophyte has mannan. Very few algal genera belong to this order, and this stage in sacoglossan evolution cannot be called a «radiation». However, after some species had adapted well to this food, the third step, which involved tremendous radiation (Fig. 14), could take place. At this stage some species chose to specialize on mannan cell walls and radiated to Codiales and Dasycladales; others specialized on cellulose cell walls and radiated to Siphonocladales, Cladophorales, Ulvales, or seagrasses. This may also be the stage from which diatom-feeding species and species feeding on red algae evolved.

The change from *Caulerpa* to other diets seems to have been associated with the loss of the shell. However, several species of *Elysia* and *Pattyclaya* feed on *Caulerpa*, and at least some species of *Polybranchia* are associated with this algal genus. Also, *Stiliger smaragdinus* feeds on *Caulerpa* (JENSEN, 1993b). Only thorough character analysis can resolve whether these species are morphologically «ancestral» or whether they have reverted to the «ancestral» diet.

CHARACTER ANALYSIS

1. *Dorsal septate muscle*: This is a composite muscle consisting of alternating layers of (semi) circular and radial muscles. The semicircular and radial muscle-bands work antagonistically, alternately constricting and widening the dorsal part of the pharyngeal cavity. In conjunction with the odontophore muscles, this functions as an efficient suction pump. The dorsal pharynx wall of most other gastropods is thin (FRETTER & GRAHAM, 1962), and the flat, indistinctly septate muscle of *Ascobulla* is considered plesiomorphic within the Sacoglossa. A flat dorsal septate muscle also occurs in *Volvatella, Lobiger* and *Thuridilla* (Fig. 15A) (JENSEN & WELLS, 1990; JENSEN, 1992, in press). In most non-shelled Sacoglossa the dorsal septate muscle is thick and domed (Fig. 15B), and in a few species, e.g. *Elysia australis* (Fig. 15C), the radial muscles converge in the central part of the pharyngeal cavity (JENSEN, 1992). This resembles the dorsal pharyngeal pump of some suctorial onchidorids (FORREST, 1953; CRAMPTON, 1977). These are apomorphic states.

2. *Shape of odontophore*: The odontophore takes up the major part of the pharyngeal cavity. Only the anteriormost tip is free. Anteriorly the odontophore is only attached ventrally. Further back the attachment broadens, and the odontophore is attached laterally as well as ventrally, leaving only a narrow, crescent-shaped pharyngeal cavity. In most gastropods the odontophore is located far back in a spacious pharyngeal cavity, and it is only attached to the pharynx wall ventrally (FRETTER & GRAHAM, 1962). In *Ascobulla* the odontophore is located rather far back, and this is considered plesiomorphic. Also, in most shelled Sacoglossa the tip of the odontophore is broadly rounded, and several teeth are exposed anteriorly. In most non-shelled sacoglossans the odontophore reaches all the way to the pharyngeal lips, and the tip is pointed. This is the apomorphic condition. In

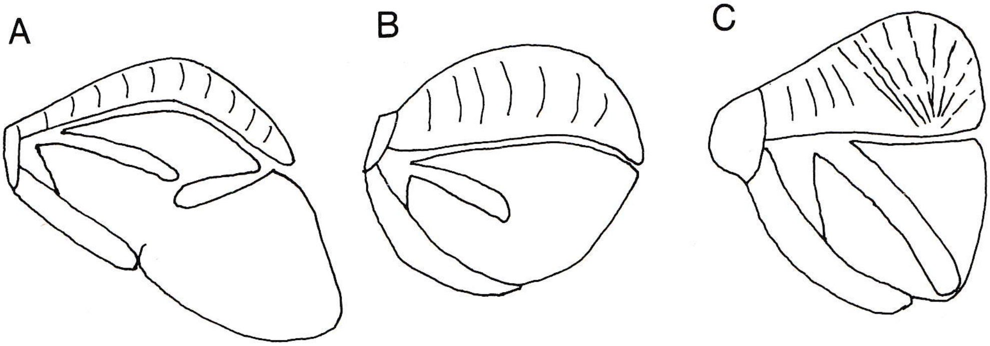

Figure 15. Schematic drawings of different types of pharynx. **A** - flat dorsal septate muscle, pharyngeal pouch, thin ascus-muscle, internal ascus, central ascendind limb. **B** - thick dorsal septate muscle, no pharyngeal pouch, external ascus, central ascending limb. **C** - thick, domed dorsal septate muscle, diagonal ascending limb, no pharyngeal pouch, thick, long ascus-muscle, external ascus.

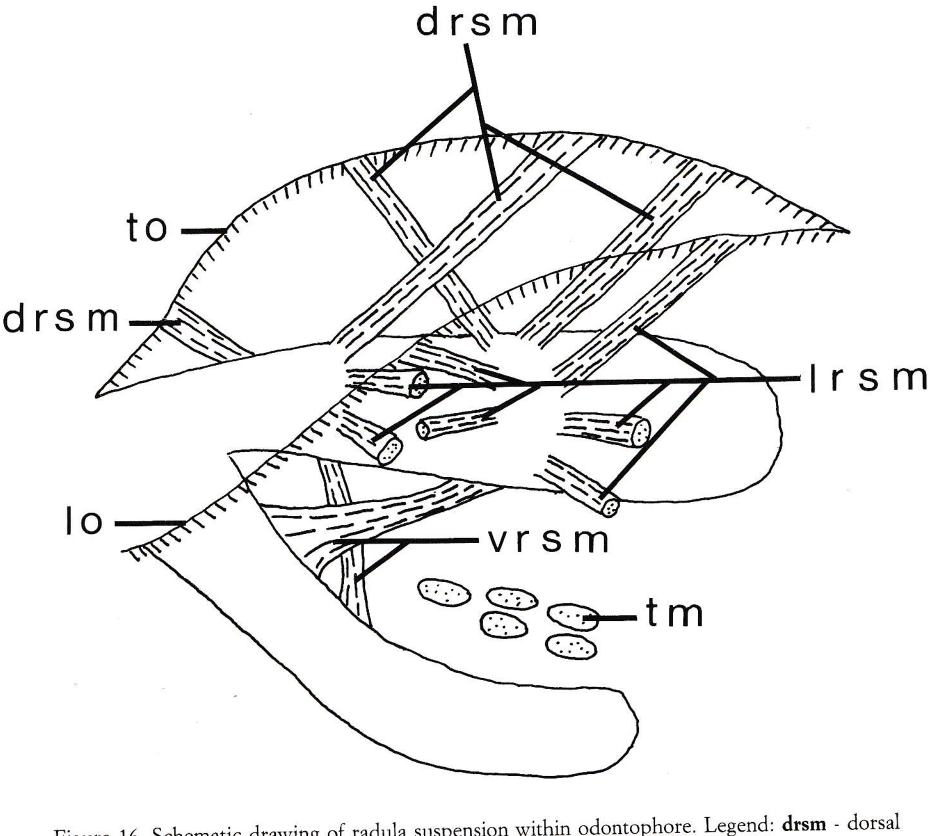

Figure 16. Schematic drawing of radula suspension within odontophore. Legend: **drsm** - dorsal radula suspending muscles; **lo** - lateral attachment of odontophore; **lrsm** - lateral radula suspending muscles; **tm** - transverse muscles; **to** - dorsal surface of odontophore; **vrsm** - ventral radula suspending muscles.

many sacoglossans the dorsal surface of the odontophore is rather flat. In others there is a distinctly pointed, tongue-like anterior part and a thick domed posterior part.

3. *Odontophore muscles*: The odontophore muscles are attached to the dorsal surface of the odontophore and extend to the ventral and lateral pharynx walls. In other gastropods the odontophore muscles are mostly associated with protraction and retraction of the odontophore (HURST, 1965). In the Sacoglossa the odontophore muscles function as a piston moving the dorsal surface of the odontophore up and down during the sucking phase of feeding (JENSEN, in press). Little variation is seen in the arrangement of the odontophore muscles, and function is probably the same throughout the order.

4. *Position of ascending limb*: The ascending limb of the radula is the equivalent of the radular sac in other gastropods. In the sacoglossans it is completely enclosed within the odontophore. In many shelled sacoglossans, e.g. *Ascobulla* and *Lobiger*, the ascending limb is located close to the dorsal surface of the odontophore (JENSEN, in press, present study). As the radular sac is external to the odontophore in most other gastropods (FRETTER & GRAHAM, 1962), this superficial position is considered plesiomorphic within the Sacoglossa. In many species of *Elysia* the ascending limb runs diagonally from the postero-ventral edge of the pharynx to the anterior tip of the odontophore (Figs 6, 15C), in others the ascending limb is located centrally within the odontophore (Fig. 15B). This is also seen in *Thuridilla* (Fig. 15A) (JENSEN, 1992) and many stiligeroids (JENSEN, 1993b). In *Aplysiopsis* the ascending limb is rather short, but steeply inclined within the odontophore. In *Ercolania* the ascending limb is located ventrally in the odontophore (JENSEN, in press, present study).

5. *Radula suspending muscles*: The ascending limb of the radula is attached by a complex system of radula suspending muscles, extending anteriorly and posteriorly in a fan-like manner to the dorsal, lateral, and ventral pharynx wall (Fig. 16). The radula suspending muscles run between the odontophore muscles, forming a dense network within the odontophore. This muscular attachment of the radular sac is a sacoglossan «innovation», and may have been instrumental to the development of suctorial feeding. Alternate contractions of posteriorly oriented and anteriorly oriented muscles move the ascending limb of the radula back and forth, and more differential contractions may allow very precise positioning of the leading tooth (=anteriormost tooth in descending limb). Few radula suspending muscles occur dorsal to the ascending limb in *Ascobulla*, and this is considered the plesiomorphic state. *Ercolania* and *Aplysiopsis* also have few dorsal radula suspending muscles. *Elysia, Thuridilla, Placobranchus* and *Caliphylla* have many dorsal radula suspending muscles (JENSEN, 1992, present study). These differences probably reflect differences in the function of the teeth.

The anteriormost teeth in the descending limb of the radula are the functional teeth. In many sacoglossans they are connected to the posterior end of the ascending limb by a strong radula suspending muscle. This muscle probably functions as a radula retractor muscle, but is clearly a part of the fanshaped arrangement of anteriorly oriented radula suspending muscles, and thus it is inappropriate to give a special name to this muscle. In some sacoglossans there is also a muscle connecting the anteriormost tooth of the ascending limb with some of the anterior teeth in the descending limb. This may correspond to a radula protractor or erector muscle (JENSEN, in press). In *Ascobulla* and *Lobiger* radula suspending muscles apparently attach to the descending limb throughout its lenght, and there are no transverse muscles forming a functional separation between the ascending and descending limbs of the radula (JENSEN, in press, present study).

6. *Transverse muscles*: In most sacoglossans there is a layer of transverse muscles forming a functional separation between the ascending and descending limbs of the radula. This allows independent movements of the two parts of the radula. The development of this thick layer is most likely one of the most important sacoglossan «innovations», and may have been responsabile for the ability to include algae other than *Caulerpa* in the diet. This layer is absent in the shelled sacoglossans studied so far, i.e. *Ascobulla* and *Lobiger* (JENSEN, in press, present study), and its absence is considered plesiomorphic. In many non-shelled sacoglossans, e.g. *Caliphylla*, the transverse muscles form a thick layer, which in transverse sections looks like a «stalk» attaching the ascus-muscle to the ventral surface of the pharynx (JENSEN, 1991).

7. *Ascus-muscle*: The ventral, longitudinal muscle-layer consists of densely set, parallel muscle-strands. Anteriorly the muscles extend from the lateral and ventral part of the pharyngeal lips. Anteriorly they form a rather thin layer around the ventral half of the pharynx. Behind the attachment of the odontophore the ascus-muscle concentrates on the ventral surface of the pharynx, surrounding the descending limb of the radula. In some species only the ventral and lateral surfaces of the descending limb are covered. This is seen mostly in the species having a pharyngeal pouch, and which have a weakly developed (or absent) transverse muscle layer. This is considered the plesiomorphic state. In the species having a thick layer of transverse muscles, the ascus-muscle surrounds the descending limb completely. This is an apomorphic condition. In the Elysiidae the ascus-muscle is long, in many species as long as the pharynx (JENSEN & WELLS, 1990; JENSEN, 1992). In most Stiligeroidea the ascus-muscle is short and the posterior end is not attached to the pharynx (JENSEN, 1993b, in press, present study). These two apomorphic states probably evolved independently. Physical separation of the ascus-muscle from the ventral surface of the pharynx also occurs in *Berthelinia* (JENSEN, 1993b). At the present time it seems most likely that this has occurred independently in the Stiligeroidea and *Berthelinia*.

8. *Shape of ascus*: In some sacoglossans the descending limb of the radula ends in a straight row with only the preradular tooth/ teeth bent over. This is seen in e.g. *Ascobulla, Volvatella, Pattyclaya* and some species of *Elysia* (JENSEN, 1992, present study). In other species the ascus teeth are rolled up in a spiral. This is seen in e.g. *Berthelinia, Caliphylla, Aplysiopsis* and *Thuridilla* (JENSEN, 1992, 1993b, present study). In other species the ascus teeth are densely packed in an irregular heap. This occurs in e.g. *Lobiger, Ercolania, Placobranchus* and most species of *Elysia* (JENSEN, 1992, in press, present study). As an ascus is not found in any other gastropods, the straight row is considered plesiomorphic, and the other 2 conditions are apomorphic. Both apomorphic conditions occur in shelled sacoglossans, hence it is not possible at the present time to determine whether one apomorphic state evolved from another, or whether both evolved from the plesiomorphic condition. Also, both apomorphic states occur in both major superfamilies of non-shelled sacoglossans. Thus they may have evolved several times independently.

9. *Position of ascus*: The ascus may be enclosed within the odontophore musculature as in *Ascobulla, Volvatella, Thuridilla* and *Placobranchus*, or it may be external as in *Lobiger, Caliphylla, Ercolania* and *Elysia* (JENSEN, 1992, in press, present study). This appears to depend on the extension of transverse muscles. The species with little or no transverse muscles usually have the internal ascus, and it is possible that in these species the ascus teeth form the functional separation between ascending and descending limbs. The internal ascus, then, is the plesiomorphic state.

10. *Pharyngeal pouch*: The pharyngeal pouch is almost solid muscle. In the species which have been examined till now, the lumen is paired, and the two narrow slits are separated by a thin epithelial membrane. The lumina may extend through the whole length of the pharyngeal pouch, or be restricted to the base of the pouch. In *Caliphylla* the lumina of the pharyngeal pouch are large (JENSEN, 1991, present study), and may have a different function than in the other species. The muscles of the pharyngeal pouch almost all have the same orientation, which is perpendicular to the longitudinal axis of the pouch. The pharyngeal pouch is usually attached lateral to the posterior end of the ascending limb. Hence the main function of the pouch musculature is probably to assist the ascending limb in piercing the algal cell wall. The musculature of the pouch probably functions in combination with the odontophore and radula suspending muscles, forming a muscular hydrostat (JENSEN, in press). Pharyngeal pouches occur in all shelled sacoglossans as well as the non-shelled family Polybranchiidae (=Caliphyllidae) (JENSEN, 1991), and also in a number of other non-shelled species, e.g. *Bosellia, Placobranchus, Thuridilla* and *Costasiella* (JENSEN, 1990, 1991, 1992). Postero-ventral pharyngeal pouches do not occur in other opisthobranchs, hence are a sacoglossan «innovation». A small, collar-like pouch as that of *Ascobulla, Oxynoe, Placobranchus* or *Costasiella*

must be considered plesiomorphic. Hence the pharyngeal pouch must have been lost several times within the Sacoglossa. It has apparently also evolved into large, «stalked» pouches more than once, e.g. *Lobiger* and *Polybranchia/Caliphylla*. Small, paired pharyngeal pouches occur only in the bivalved Juliidae.

11. *Shape of radular teeth*: Three basic shapes have been described previously (Jensen, 1991, 1993a). The teeth of *Bosellia* are short and broad and have coarse lateral denticles (Marcus, 1973). This is rather similar to the central tooth of many Cephalaspidea, and thus must be considered plesiomorphic. Triangular teeth with lateral denticles also occur in the shelled Volvatellidae, in most Polybranchiidae, and in the elysioid genera *Placobranchus, Thuridilla* and *Elysiella* (Jensen, 1992, 1993a). However, numerous modifications have been observed. The triangular teeth of *Ascobulla* have a distal blade-shaped prominence, and in *Cyerce* there is a basal prominence (present study). Blade-shaped teeth occur in the largest number of species and apparently are not associated with any particular type of food (Jensen, 1993a). They have most likely evolved independently at least 2 or maybe 3 times; in the Conchoidea (with lateral denticles), in the Elysioidea (with median denticles), and in the Stiligeroidea (smooth). In the blade-shaped teeth of the Oxynoidae and Juliidae the edge of the blade arises directly above the center of the anterior margin of the base (see SEM-photos in Jensen & Wells (1990) and Jensen 1993a). In the Elysiidae the edge of the blade bends to one side, usually the left, of the base (see SEM-photos in Jensen & Wells (1990) and Jensen (1992)). The blade-shaped teeth in the Stiligeridae are very similar to those of the Elysiidae, except that the inclination of the cusp to the base is usually much less than 20° in the Elysiidae and more than 20° in the Stiligeridae. The sabot-shaped teeth of *Aplysiopsis* differ in some important respects, i.e. inclination of cusp to base, relative length of base, and shape of tip, from those of the stiligerid genera *Ercolania, Limapontia* and *Alderia*. Sabot-shaped teeth occur almost exclusively in species feeding on algae having cellulose cell walls with micro-fibrillae in a crossed-fibrillar structure (Jensen, 1993a). Thus they may have evolved in parallel in the Stiligeridae and the hermaeid genus *Aplysiopsis*. In *Alderia modesta* the base is somewhat broader than the cusp. At the base of the cusp is a small median crest (see SEM-photo in Bleakney (1988)). The dorsal keel in rather shallow and does not extend all the way to the posterior end of the base. A few stiligerids, e.g. *Calliopaea* spp., and also the genus *Gascoignella* have teeth which do not fit into the above categories. The cusps form simple, smooth cones, like a chisel, and they have been called chisel-shaped (Baba & Hamatani, 1970). These teeth may form a stage which is intermediate between triangular and blade-shaped, or between blade-shaped and sabot-shaped.

12. *Tooth denticulation*: The triangular teeth of *Ascobulla* and *Volvatella* have long lateral denticles on the distal part of the cusp. This is also seen in the polybranchiid *Cyerce antillensis* (JENSEN & WELLS, 1990; JENSEN, 1993a). In *Bosellia, Placobranchus, Thuridilla* and *Polybranchia* the coarse denticles extend over the whole length of the triangular cusp (MARCUS, 1973; JENSEN, 1992, 1993b). The teeth of *Elysiella pusilla* are peculiar in having denticles only along one edge of the narrow triangular teeth (see SEM-photos in JENSEN & WELLS (1990)). Also, the cavity of the cusp is very deep. Only the diatom-feeding *Elysia evelinae* and the seagrass-feeding *Elysia catulus* have smooth, triangular teeth. In the other seagrass-feeding species, *Elysia serca*, denticulation varies among populations (JENSEN, 1981, 1982, 1983, 1993a). Lateral denticles on the blade-shaped teeth of *Oxynoe, Berthelinia* and *Lobiger* originate from flanges near the dorsal side. Some species of *Elysia*, e.g. *E. timida* and *E. filicauda*, also have lateral flanges with small denticles (see SEM-photos in JENSEN & WELLS (1990) and JENSEN (1992)). However, these occur only on the distal part of the blade, and probably are not homologous to those of the shelled species. The lateral denticles in *Hermaea* are also on flanges, but these run obliquely on the blades from the anterior, basal part to the central, distal part (Fig. 10). In most species of *Elysia* the blade-shaped teeth have denticles along the median cutting edge (Fig. 13). A few elysiids, e.g. *Pattyclaya brycei* and *Elysia ornata*, have smooth, blade-shaped teeth (JENSEN & WELLS, 1990; JENSEN, 1992). Many stiligerids have blade-shaped teeth, and in these species the teeth are usually smooth, e.g. *Placida viridis, P. kingstoni, P. daguilarensis* (JENSEN, 1993a). Only a few species, e.g. *Stiliger smaragdinus* and *Placida dendritica* have median denticles (BLEAKNEY, 1989; JENSEN, 1993b). Smooth blade-shaped teeth also occur in the genera *Caliphylla* and *Costasiella* (Fig. 9). The sabot-shaped teeth of *Aplysiopsis* have denticulate edges, whereas those of the Stiligeridae have smooth edges. However, many species of *Ercolania* have one more or less prominent indentation on the lateral edges (JENSEN, 1985, 1993b).

13. *Tip of radular teeth*: In the Volvatellidae the tips of the teeth are hooked. This is used for interlocking the teeth in a row. Interlocking apparently is not important in *Cyerce, Bosellia* and *Placobranchus*; the tips are not hooked, and the dorsal cavities are shallow. In *Thuridilla* the tip of the tooth is slightly hooked, and the distal end of the dorsal cavity partly covers the tip of the tooth in front (JENSEN, 1992). In the species with blade-shaped teeth the dorsal cavity is deep and this locks the tip of the preceding tooth in place. In *Lobiger, Roburnella* and some species of *Berthelinia* the tip is bifid, and this further strengthens the interlocking of the teeth. In the species having sabot-shaped teeth, and also in some species of *Elysia*, e.g. *E. japonica* and *E. verrucosa*, having blade-shaped teeth, the tip is broadly rounded (JENSEN, 1985, present study). This appears to be correlated with diets of Cladophorales, i.e. cellulose cell walls with crossed-fibrillar texture (JENSEN, 1993a).

14. *Articulation*: Posteriorly on the base are usually 2 articulation knobs which fit around the anterior base of the tooth behind. This prevents lateral dislocation of the row of teeth, which may be important when the radula suspending muscles work. Anteriorly is a more or less prominent articulation knob which probably is most important when the tooth pivots on the tip of the odontophore. Articulation knobs are very weakly developed in sabot-shaped teeth. The interlocking system in these species also prevents lateral displacement, and pivoting is probably not important in the function of these teeth. Weak articulation knobs are considered apomorphic.

Conclusions

The present study has shown that the buccal apparatus of the Sacoglossa contains several morphological «innovations» which are connected with diet radiation. Also, several structures have evolved in parallel in major lines of evolution in response to parallel changes in diet. The most important morphological «innovations» are the muscular suspension of the ascending limb of the radula within the odontophore, the development of transverse muscles between the ascending and descending limbs of the radula, blade-shaped teeth with median denticles, and sabot-shaped teeth.

Functionally the shift in importance from ascending to descending limb of the radula is a very important evolutionary event. In the species having pharyngeal pouches the ascus-muscle is usually weakly developed and there is little or no transverse muscles separating the ascending and descending limbs of the radula. In some species the ascending limb is also longer than the descending limb. Functionally the pharynx with pharyngeal pouches and weak separation between ascending and descending limbs of the radula is plesiomorphic within the Sacoglossa. Here the ascending limb is obviously most important in piercing the algal cell wall (JENSEN, in press). Many of these species have triangular teeth with lateral denticles. The «rasping» function of these teeth and the dietary limitations imposed by this method have been described previously (JENSEN, 1993a).

Loss of pharyngeal pouches has occurred in both major shell-less groups of Sacoglossa. This is associated with the development of transverse muscles to form a functional separation between ascending and descending limbs of the radula. Also, the ascus-muscle is very well-developed in these species, surrounding the descending limb of the radula completely.

In the Elysiidae loss of pharyngeal pouches was accompanied by a posterior elongation of the ascus-muscle (and descending limb of radula) to almost the entire length of the pharynx. In many species the ascending limb shifted to a diagonal position, leaving a thick muscle-layer above the radula posteriorly. Also, tooth shape changed from triangular with lateral denticles to blade-shaped with median denticles. Feeding method in these species is probably «cutting», i.e. the algal cell wall is pierced by the tip of the leading tooth and then slit open from the inside (JENSEN, 1993a).

In the Stiligeroidea loss of pharyngeal pouches was preceded by the posterior separation of the ascus-muscle and descending limb of the radula from the ventral surface of the pharynx. In many species the ascending limb has moved to a ventral or anterior position (Jensen, 1993b, present study). In some species the radular teeth are blade-shaped, usually with smooth edges, and feeding method is probably «cutting», as in the elysiids. The most advanced stiligeroids are the species with sabot-shaped teeth. These teeth function in a «piercing» manner (Jensen, 1993a).

As pharyngeal pouches are found in several non-shelled species, in the Elysioidea as well as the Stiligeroidea, the shift in importance from ascending to descending limb must have occurred some time after the loss of the shell. Unfortunately it is not possible to link this shift with any particular change in diet. Except for *Polybranchia* the non-shelled species feeding on *Caulerpa* do not have pharyngeal pouches: they have blade-shaped teeth and distinct transverse muscles separating ascending and descending limbs of the radula. Hence they probably evolved from species which had a non-*Caulerpa* diet, and reverted to the ancestral diet.

Because the sacoglossan pharynx contains so many autapomorphies correlated with suctorial feeding, character analysis must include information on diets as well as functional aspects of feeding to identify parallelism and determine polarity of many characters. Although only a fraction of the known species have been examined in detail, it is hoped that the most important evolutionary changes have been identified in the present study.

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R. Cattaneo-Vietti, S. Angelini & G. Bavestrello (*)

SKIN AND GUT SPICULES IN *DISCODORIS ATROMACULATA* (BERGH, 1880) (MOLLUSCA: NUDIBRANCHIA) (**)

Key Words: Nudibranchs, Doridaceans, calcareous spicules

Summary

The presence of skin spicules inside the notum, the foot or in any other organs of numerous doridaceans is well known, and generally considered a defensive mechanism to diminish the nudibranch attractiveness as food.

About 80 specimens of *Discodoris atromaculata* (Bergh, 1880) (Nudibranchia: Doridina) were collected monthly for a year along the Portofino Promontory (Ligurian Sea), in order to clarify some aspects on the calcareous spicules morphology and the hypothetical use of the siliceous ones coming from diet on the sponge *Petrosia ficiformis.* The specimens' average foot length is 25.4 mm and their average wet weight is 3.2 g. In either morphometric bulk of data (total length, foot length, total width and wet weight) no significative differences can be outlined during the year. It probably occurs because this species shows a wide reproductive season (from April to October) and its life history suggests a biennal cycle.

The *D. atromaculata* notum shows blunt tubercles of various sizes supported by densely packed calcareous spicules covered by the epithelium, others lie in the inter-tubercles spaces. Other spicules are present in foot, gills and rhinophores, more irregularly arranged. A lot of these spicules is slender and spiny, those present in gills and rhinophores are sometimes curved or show a central bulge. Small sphaeroid spicules (diameter 20-80 μm) are always present. The slender spicules show a considerable intra- and interindividual variability that is not related to individual size or season. The average size of the notal slender spicules is 332 μm x 16 μm, while the pedal ones is 260 μm x 16 μm, and this difference is statistically significative ($p < 0.01$: t test and Kolmogorov-Smirnov). Consequently, the spicule length in *D. atromaculata* seems to be influenced by the anatomical localization and its development can be considered in terms of changes in gene regulation caused by the kind of tissue in which it occurs.

The percent value of calcium carbonate is always higher in the notum than the foot ($p < 0.01$), and this quantity does not change during the year, in either of these organs. On the contrary, a slightly negative relationship with the individual size can be underlined mainly in the notum, and this unidirectional percent decrease suggests a natural slowing down of the biomineralization related to the age.

The strong monophagy of *D. atromaculata* on *P. ficiformis* is confirmed by the gut contents analysis, but it does not appear absolute. In fact, one specimen, 25 mm long, with the gut full of spicules of the sponge *Reniera fulva* was collected on this sponge which showed evident signs of predation.

D. atromaculata does not suspend feeding activities during the year: monthly, specimens with the gut full of siliceous spicules were recorded, but the nudibranch never uses these alloctone spicules to firm its notum.

(*) Istituto di Zoologia dell'Università degli Studi, Via Balbi 5 I-16126 Genova, Italy.

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Riassunto

La presenza di spicole calcaree nel notum, nel piede ed in altri organi di numerosi doridacei (Gastropoda: Nudibranchia) è ben nota e generalmente queste strutture vengono considerate elementi difensivi, atti a diminuire l'interesse alimentare della specie nei confronti di un eventuale predatore. Grazie allo studio condotto su oltre 80 individui di *Discodoris atromaculata* (Bergh, 1880) (Nudibranchia: Doridina), raccolti mensilmente per un anno lungo il Promontorio di Portofino (Mar Ligure), è stato possibile chiarire alcuni aspetti della morfologia di queste spicole ed escludere l'utilizzazione di spicole silicee, provenienti dalla dieta, da parte del nudibranco.

La lunghezza media del piede degli esemplari esaminati è di 25.4 mm, con un peso umido medio di 3.2 g. Analizzando il complesso dei dati morfometrici presi in considerazione (lunghezza totale, lunghezza del piede, larghezza, peso umido) non è stato possibile riscontrare differenze significative nelle diverse stagioni dell'anno. Ciò è dovuto al fatto che la specie presenta un ampio periodo riproduttivo (da aprile ad ottobre) con un ciclo probabilmente biennale.

I tubercoli del notum in *D. atromaculata* sono costituiti da strutture subconiche costituite da spicole calcaree coperte dall'epitelio. Gli interspazi tra i tubercoli sono riempiti da altre spicole. La maggior parte delle spicole calcaree sono fusiformi e spinose, mentre quelle presenti nelle branchie e nei rinofori possono talvolta essere più irregolari, con un rigonfiamento centrale. Piccole spicole sferoidali, del diametro di 20-80 μm sono sempre presenti. Le spicole fusiformi presentano un'alta variabilità inter- ed intraindividuale che non sembra essere correlata nè con la stagionalità nè con la taglia. La dimensione media delle spicole presenti nel notum è 332 ± 63 μm x 16 ± 3 μm,, mentre quelle del piede sono statisticamente più piccole (260 ± 43 μm x 16 ± 3 μm). La taglia delle spicole in *D. atromaculata* sembra dunque essere influenzata, più che da fattori ambientali esterni, dal tipo di ambiente cellulare o tissutale in cui vengono a formarsi.

Il valore percentuale di carbonato di calcio presente nel mantello è sempre statisticamente maggiore di quello misurato nel piede, e questa quantità non sembra variare nel corso dell'anno. Al contrario si nota un leggero decremento nel valore percentuale di carbonato di calcio con l'aumento della taglia dell'individuo, suggerendo una leggera, ma significativa riduzione dell'attività di biomineralizzazione legata all'età.

La monofagia di *D. atromaculata* per *Petrosia ficiformis*, pur confermata, non appare assoluta. L'analisi del contenuto stomacale di un individuo di 25 mm di lunghezza ha rivelato la presenza di notevoli quantità di spicole di *Reniera fulva*.

Introduction

The presence of calcareous spicules inside different body regions of numerous doridaceans is well known (KRESS, 1981; GARCIA et al., 1986). They appear in the notum of one mm long juvenile *Cadlina laevis* during the first 3 days after hatching (THOMPSON, 1967), and cannot be considered homologous of the shell, as they appear not only in the notum, but also in the foot, rhinophores and gills. Almost nothing appears to be known about spicules formation and turn-over in nudibranchs, but some information is available on the type of mineralization in few opisthobranchs (LOWENSTAM & WEINER, 1989).

During a field study carried out on some traits of the life history of *Discodoris atromaculata* (Bergh, 1880) (Nudibranchia: Doridina) in the Ligurian Sea, about 80 specimens were sampled along to Portofino Promontory, in order to clarify some aspects on the calcareous spicules morphology of this species, its diet, and the possible utilisation of the siliceous sponge spicules to firm the body.

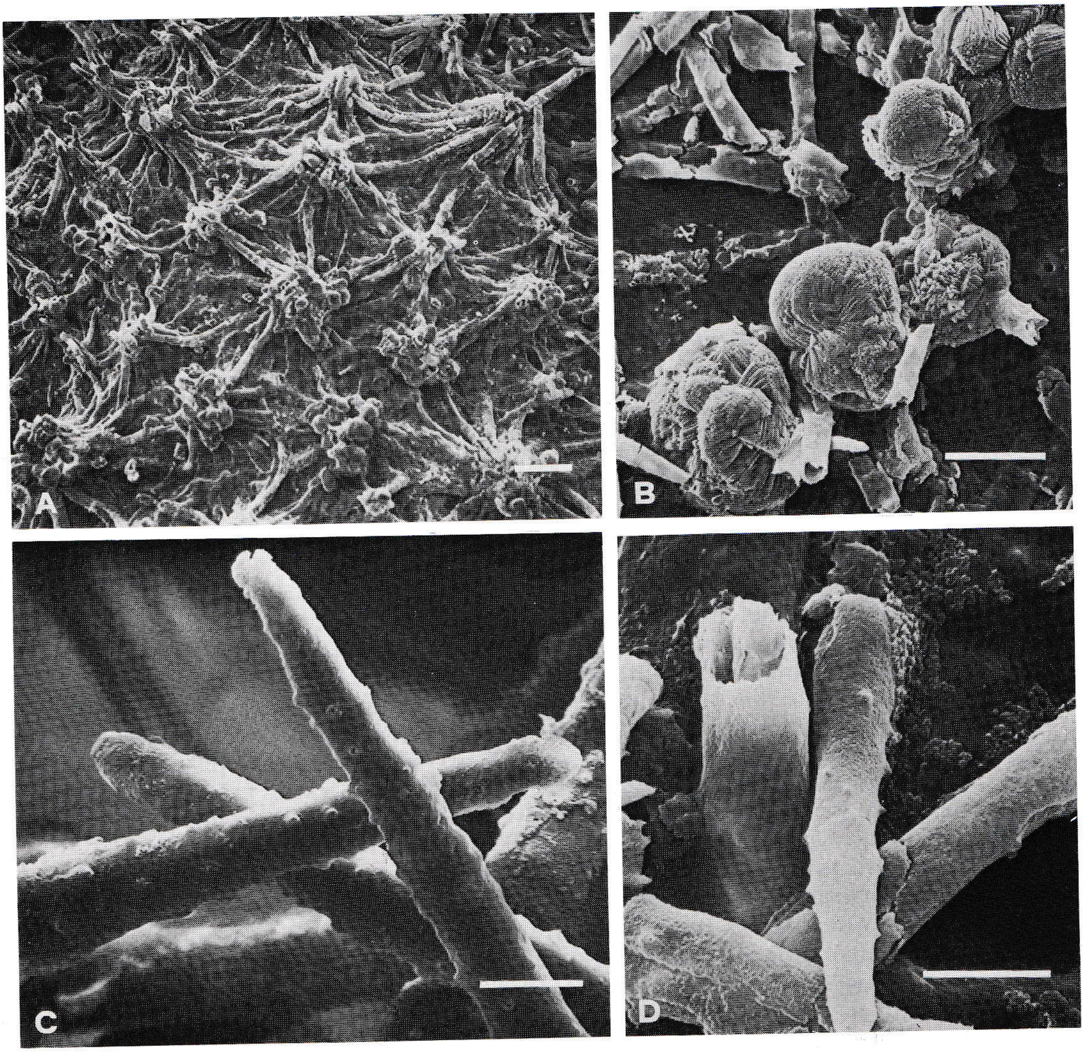

Fig. 1. *Discodoris atromaculata*: calcareous spicules. a) notal subconical tubercles supported by densely packed calcareous spicules. b) small calcium carbonate sphaerules present in the notum. c) slender spicules showing the spiny surface. d) Spicule showing the empty center. Bar length: a=100 μm; b=40 μm; c-d=20 μm.

Tab 1. *Discodoris atromaculata*: Descriptive statistics. Length in mm; weight in g.

	Whole Year			Warm Season			Cold Season		
	n	avg	st.dev.	n	avg	st.dev.	n	avg	st.dev
tot. length	82	39.29	19.36	52	42.59	20.55	30	33.57	15.83
tot. width	82	23.36	12.17	52	26.58	12.85	30	17.79	8.53
wet weight	82	3.18	3.70	52	3.38	3.80	30	2.84	3.56
foot length	82	25.40	11.60	52	26.67	11.64	30	23.20	11.39

Material and methods

82 specimens of *Discodoris atromaculata* were collected from March 1990 during monthly SCUBA dives along the Portofino Promontory (Ligurian Sea), for a year. All the specimens were found in the precoralligenous and coralligenous biocoenoses, at a depth of 15 to 30 m. The siliceous and calcareous spicules present in the digestive system, and in the notum, foot, rhinophores and gills were prepared on slides, respectively after dissolution of tissues by boiling nitric acid and H_2O_2. For each slide, the length and width of 20 spicules were noted for a bulk of data of over 2000 spicules. The percent value of the calcium carbonate present in the notum and foot was determinated in 1 cm^2 dry skin tissue, by weight difference after dissolution of the spicules in 2% hydrofluoric acid.

Results

Population data

Practically the entire studied population, both juveniles and adults, was collected on the common sponge *Petrosia ficiformis* Poiret, 1789, the usual prey of this nudibranch (Schmekel & Portmann, 1982). The descriptive statistics of this population (total length, foot length, total width and wet weight) are summarized in Tab. 1. Data have been divided up into cold (from October to March) and warm season (from April to September) to clarify possible seasonal differences. The foot length varies from 9 mm to 48 mm (with an average value of 25.4 mm), while the wet weight from 0.01 g to 19.7 g (with an average value of 3.18 g). The various multiple range tests available in the SAS ANOVA package gave no statistical differences between the two seasonal groups. It could happen because in this species, which shows its reproductive season from April to October, the larval metamorphosis occurs during a wide period of the year and its life history suggests a biennial cycle.

Morphology of the calcareous spicules

The *Discodoris atromaculata* notum shows blunt tubercles of various sizes supported by densely packed calcareous spicules covered by the epithelium (Fig. 1a). No spicules protrude from it and they are arranged as indian teepees, while others lie in the inter-tubercles spaces. Other spicules are present in the foot, rhinophores and gills, more irregularly arranged.

Tab. 2. Monthly data regarding the length and width of the notal and pedal spicules (in μm).

	n° obs.	Notum length	Notum width	Foot length	Foot width
January	59	416±43	19±2	320±15	16±1
February	60	207±15	15±3	253±57	16±4
March	100	359±44	17±1	253±19	17±1
April	138	296±33	15±2	267±23	17±3
May	99	377±24	21±3	241±44	17±3
June	100	265±64	14±3	219±33	15±2
August	178	374±29	19±3	267±21	16±1
September	100	348±41	14±1	241±27	15±1
November	119	322±28	15±2	258±58	16±5
December	20	358±38	22±3	296±3	296±27

Tab. 3 Average length, width and their ratio in notal and pedal spicules.

	notum	foot
Length (μm)	332.6±63.1	260.1±42.8
Width (μm)	16.6±3.3	16.2±3.2
ratio W/L	0.05±0.01	0.06±0.01

Many calcium carbonate spherules (diameter 20-80 μm) are always present (Fig. 1b), but the main notal and pedal spicules are generally slender, lightly curved and often spiny (Fig. 1c). Those present in gills and rhinophores are sometimes more irregular and can show a central bulge. The spicules seems to be very fragile because have generally an empty center (Fig. 1d), but others show concentric layers inside. Also their walls have a layered structure. Some morphometric data concerning this kind of spicules are summarized in Tab. 2. The average length of the notal ones is 332.6 μm (± 63.1), its width is 16.6 μm (±3.3). Those in the foot are 260.1 μm (±42.8) long and 16.2 μm (±3.2) wide. The difference between the lengths is statistically significative ($P < 0.01$: t test and Kolmogorov-Smirnov test) as well as the width/length ratio, which is consequently higher in the foot (Tab. 3).

The standard deviation high values inside both data suggest a strong inter- and intraindividual variability: strong irregular variations in the spicule length can be, in fact, observed during the year, but no morphological or morphometric changes can be related to the individual size or season.

The percent value of calcium carbonate present in the notum is always higher than in the foot, but this quantity does not change, in either of the structures, notably during the year (Tab. 4). On the contrary, a slightly negative relationship with the individual size can be underlined mainly in the notum (Fig. 2).

Siliceous spicules

The analysis of the gut contents showed the presence of the siliceous spicules of the sponge *Petrosia ficiformis* in almost all the specimens examined. Only one specimen, 25 mm long, collected on the sponge *Reniera fulva* which showed evident scars of predation, had its gut full of spicules of that sponge. The percentage of empty stomachs is constant during the whole year (about 60%) and, consequently, this species does not suspend feeding activities during the year. No siliceous spicules were never found in the notum and foot.

Discussion

The skin spicules, generally considered a defensive mechanism to diminuish the nudibranch attractiveness as food to predators (THOMPSON, 1960; ROS, 1976), have an important role in determining the firmness, structure and architecture of the notum in *Discodoris atromaculata*. In this case no alloctone siliceous spicules occur. Contrary to HAEFELFINGER's (1961) observations, only a type of slender calcareous spicules is present in the Portofino population, even though sizes are statistically different between the notal and pedal spicules. A similar phenomenon occurs in the spicules of demospongiae (BAVESTRELLO et al., 1992) with a variation of the size of the same kind of spicules in different anatomical territories. This plasticity may be ascribed to the phenomenon of phenothypic modulation (SMITH-GILL, 1983) where the environment may modify in *continuo* the genetic expression. The decrease of calcium carbonate in the notum with the size suggests a natural slowing down of the biomineralization with age.

All this suggests that the process of biomineralization in *Discodoris atromaculata* is not directly influenced by seasonal changes (e.g. temperature), but it is better linked to the age of the specimen and the different anatomical localization.

The trophic relationship between the sponge *Petrosia ficiformis* and *D. atromaculata* is generally considered as one of the best examples of monophagy in nudibranchs (CHANGEUX & DELAMARE, 1955; HAEFELFINGER, 1961; VICENTE, 1967; SCHMEKEL & PORTMANN, 1982) and this close relationship was also demonstrated by biochemical results (CIMINO et al., 1980; CASTIELLO et al., 1980) and behavioural experiences (CASTIELLO et al., 1979). This fact can be confirmed, but it does not appear absolute. In fact, the feeding on *Reniera fulva* can create some doubts, because this last species is rarer than *Petrosia ficiformis* along the Portofino Promontory.

Discussion arised on the possibility of using sponge spicules to firm the nudibranch notum (VICENTE, 1967), but in *Discodoris atromaculata* they are confined always to the digestive system and consequently, this hypothesis would seem very unlikely.

Tab. 4 Monthly percentage values of calcium carbonate/cm² of dry notum and foot.

	n° obs.	%$CaCO_3$ notum	 foot
January	3	58±2	43±11
February	2	68±2	56±5
March	9	65±8	49±10
April	10	65±9	54±13
May	11	69±7	50±10
June	4	61±8	46±6
August	8	61±9	51±8
September	5	68±6	47±4
November	8	68±8	41±12
December	3	68±7	58±8

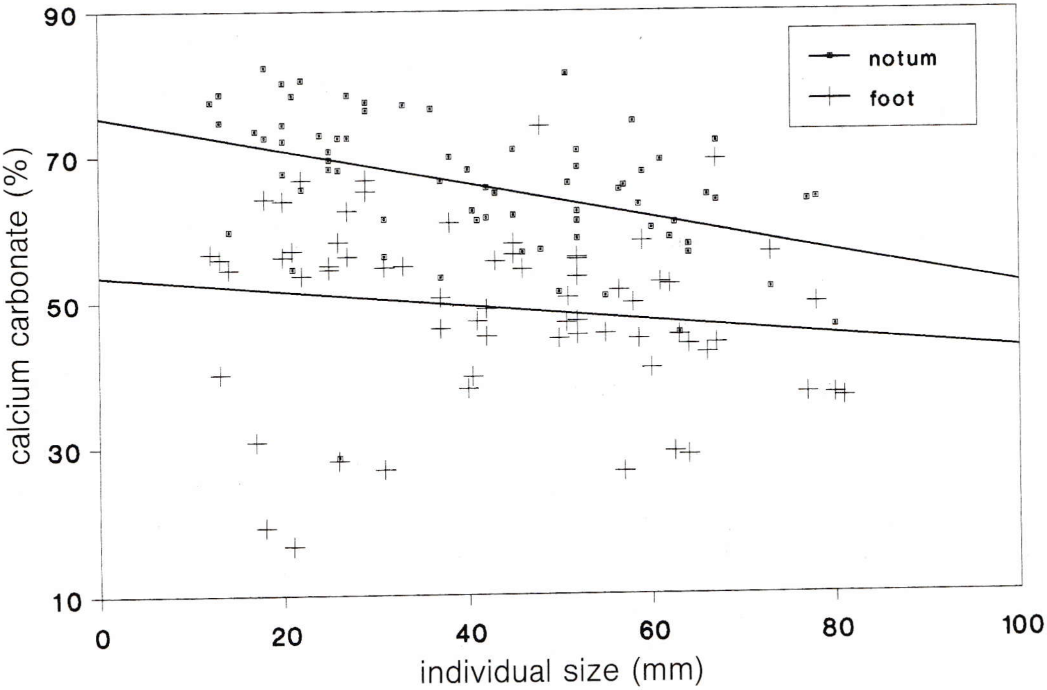

Fig. 2. *Discodoris atromaculata*: Individual size vs per cent calcium carbonate (d.w.) in the notum and foot of 63 specimens.

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Heike Wägele (*)

NEW RESULTS ON THE SYSTEMATICS OF NUDIBRANCHIA (OPISTHOBRANCHIA, GASTROPODA) FROM THE SOUTHERN POLAR SEAS (**)

KEY WORDS: Antarctica, Nudibranchs, Opisthobranchs

Summary

The difficulties when working on Antarctic Nudibranchia are demonstrated with the help of the genus *Austrodoris* Odhner, 1926, and new results are presented. A list of the recently revised nudibranchs genera of the South Polar Sea, with synonyms, and a list with those species collected and described only once or twice from that area, is given.

Riassunto

Lo studio della sistematica dei Molluschi Nudibranchi antartici pone, ancor oggi, notevoli problemi sia per la difficoltà di ottenere esemplari, sia per la copiosa letteratura esistente che, tuttavia, non essendo sempre stata curata da specialisti, è spesso di difficile interpretazione. Ne è un esempio il genere *Austrodoris* Odhner, 1926 che viene qui discusso.

Viene inoltre presentata una lista ragionata delle specie di Nudibranchi oggi considerate valide per l'Oceano Polare Antartico con i relativi sinonimi.

Introduction

The first nudibranchs from Antarctic and Subantarctic waters were already described by BERGH (1884). Since then new species have been described continuously (BERGH, 1898; VAYSSIÈRE, 1906; 1917; ELIOT, 1905; 1907; THIELE, 1912; ODHNER, 1926; 1934; 1944; MINICHEV, 1969; 1972; EV. MARCUS, 1985; CATTANEO-VIETTI, 1991). But it is amazing that, with only few exceptions, they have been described new species. Mainly in the last 20 to 30 years specimens newly collected from the Southern Polar Seas have been assigned to existing species. But very often it is quite difficult to understand the reasons for the assignment to a particular species (VICENTE, 1974; VICENTE & ARNAUD, 1974).

In 1985, when the author started studying Antarctic nudibranchs, 64 nominal species belonging to 24 genera had been described from the southern continent. This is a very small number compared to the large area studied. Many of the early descriptions of Antarctic nudibranch species gave more or less, or exclusively, external features (e.g. *Bathydoris clavigera* Thiele, 1912). Thorough descriptions of the anatomical features are rather exceptional.

(*) Lehrstuhl für Verhaltensforschung, Universität Bielefeld, Postfach 33501, 4800 Bielefeld 1, Germany.

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Some authors justified this practice by saying that they did not want to dissect, and therefore destroy, the most valuable type material (THIELE, 1912).

Therefore it is no wonder that all who have studied Antarctic nudibranchs consider the assignment of newly collected specimens as extremely difficult, or even as impossible.

The author was confronted with these difficulties, when she tried to assign the material she had collected to existing species. Over 600 specimens had been collected, and after each years new cruise by the German-Antarctic Research Vessel «Polarstern», augmented the number considerably.

Between 1987 and the present the author revised several of the most common taxa of Antarctic nudibranchs (WÄGELE, 1987; 1989b; 1989c; 1990a; 1990b; 1991) (tab. 1).

The purpose of this present paper is to demonstrate the difficulties confronting anyone had, or still has, to cope with, when he is working on Antarctic nudibranchs. This is shown with the help of the genus *Austrodoris* Odhner, 1926. In this connection new results are also presented. A list of Antarctic and Subantarctic Nudibranchia, partly with new synonyms, is given (tab. 1).

Results and discussion

To demonstrate the difficulties in identifying newly collected specimens, the methods of clarifying possible synonymies are described. As an example, the species *Austrodoris* Odhner, 1926 is chosen, since this genus is the oldest known from the Antarctic waters and 14 nominal species have been included in the past.

All the nominal species have had a rather limited distribution: e.g. *Austrodoris rubescens* (Bergh, 1898) was known only from the Atlantic sector of the Subantarctic waters. Many species were described from only locality (some only based on one specimen), and never rediscovered subsequently (e.g. *A. mishu* Marcus, 1985; *A. michaelseni* Odhner, 1926; *A. grandis* Minichev, 1972). The distribution of *Austrodoris kerguelenensis*, described by BERGH (1884) under the generic name *Archidoris*, seemed to be restricted to Subantarctic waters (Kerguelen Islands, Herd Islands, Macquarie Islands and Patagonia).

The distinction of the species mainly based on external features (ODHNER, 1926; 1934; EV. MARCUS, 1985; VICENTE, 1974; VICENTE & ARNAUD, 1974): the shape of the body (oval, roundish or elongate); the shape of the tubercles (digitiform, conical or clubshaped); the number of gills (8, 10, or 12); the relation between the length of the body compared to the length of the peribranchial room (the room between the gill's sheath and the caudal margin of the notum: 1/6, 1/8, etc.).

Observations of living animals in special temperature controlled containers showed that many of the external characters, which were thought to be species specific, in fact varied within one and the same individual. Fig. 1 shows the same specimen some days after collection and several weeks later.

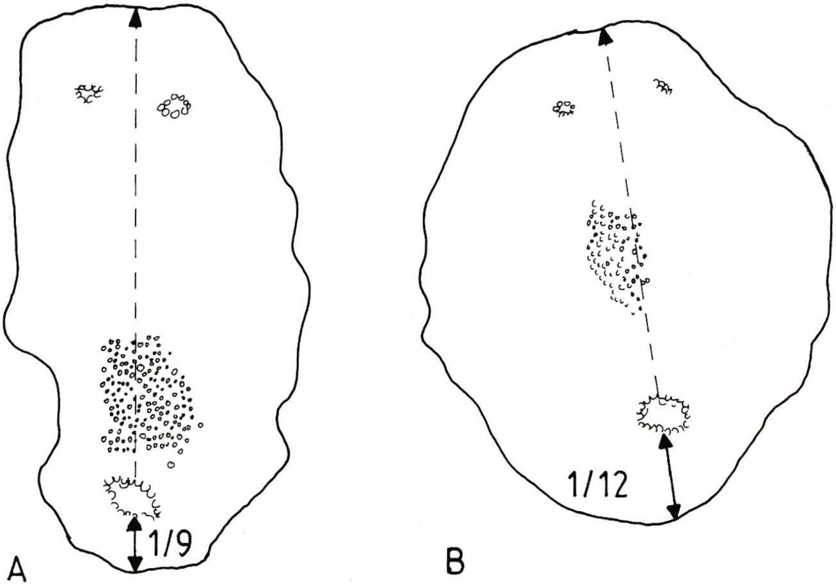

Fig. 1. *Austrodoris kerguelenensis* (Bergh, 1884). Redrawn from a photograph taken on the day of collection (A), and 5 months later (B).

The external features of about 100 specimens of *Austrodoris* were investigated and nearly 50 specimens were partly or completely dissected. Some specimens were also examined by histological means (Wägele, 1989a; 1990a). All organ systems (digestive tract, nervous system, genital tract, excretory system and glands) were taken into account. Specimens from one haul (therefore probably from the same population) of similar size and external features, and of quite different external features were compared with specimens from completely different localities (South Georgia, Antarctic Peninsula, Weddell Sea).

Specimens, which were fixed directly after the haul were compared with others that had been kept in aquaria for several weeks or months.

Re-examination of available type specimens and other material stored in different museums also revealed some new results on the variability of features, a variability that was often overlooked in the past.

A comparison of this museum material with personally collected material led the author (WÄGELE, 1990a) to the conclusion that at least 9 of the 14 nominal species are synonymous with *Austrodoris kerguelenensis* (Bergh, 1884). Some specimens, which were subsequently assigned to different species (*A. rubescens*: det. Odhner 1926; *A. granulatissima*: det. Odhner 1934; *Archidoris kerguelenensis*: det. Burn 1973), could also be assigned to *Austrodoris kerguelenensis*.

The holotype of *Archidoris granulatissima* Vayssière, 1917 was considered a *nomen dubium* by Wägele (1990a) since the type material could not be relocated at that time (pers. comm. P. Bouchet, 1986). A new request to the Muséum National d'Histoire naturelle (Paris) in 1992 was more successful. The types of *Archidoris granulatissima* Vayssière, 1917 and *Archidoris tuberculata* var. Vayssière, 1906 (=*A. tuberculata* var. *antarctica* Vayssière 1917) were sent to me. The re-examination of both species allowed the assignment to *Austrodoris kerguelenensis* (Wägele, unpublished data).

According to the original (and only) description of Minichev (1972), the synonymy of *Austrodoris longa, A. stellata* and *A. grandis* with *A. kerguelenensis* is quite certain. Further distinguishing features (besides those discusses above, which are merely intraspecific variation, s. Wägele, 1990a) mentioned by Minichev (1972), are the number of rhinophoral lamellae in *A. grandis* (25-32), the star-shaped arrangement of the tubercles in *A. stellata* and the features described for the digestive tract of *A. longa*. All these features lay within the variability observed in personal material.

The assignment of *Archidoris kerguelenensis* Bergh, 1884, *Archidoris australis* Bergh, 1884 and *Archidoris rubescens* Bergh, 1898 to the genus *Austrodoris* Odhner, 1926 is still problematical. The genus *Austrodoris* is defined by the extraordinary shape of its vas deferens. This is an extremely long, coiled duct, which lies in a very long, muscular sheath (Odhner, 1926; Wägele, 1989a; 1990a). A glans penis is absent. Odhner designed *Archidoris rubescens* Bergh, 1898 as the type species of the genus *Austrodoris*. He had re-examined the holotype of *A. rubescens*, but he mentioned that the genital organs were missing in the type material.

Odhner had material from the type locality of *Archidoris rubescens* (Punta Arenas) and from the Burdwood Bank, Shag Rock Bank, Falkland Islands and South Georgia. Since that time no other archidorid species were collected in that area.

Bergh's descriptions and (when present) the figures of the genital system are not precise enough.

At Bergh's time (and probably still now) special interest was taken in the shape of the distal vas deferens, the form of the penis and other penial structures, and presence or absence of a prostate gland. But the shape of the vas deferens, which usually has no special features, might have been easily overlooked, before Odhner recognized its peculiarity. In the genus *Archidoris* a glans penis within a penial bulb is present (Bergh, 1878; Odhner, 1934; Schmekel, 1968). For *Archidoris rubescens*, Bergh writes (1898: 503): «Der Samenleiter ohne prostatische Abtheilung, kaum 2 cm lang, vorn in den wenig weiteren ungefähr 2 mm langen Penissack (Vorhaut) übergehend; die kleine Glans Penis am Boden des Penissackes unbewaffnet».

This is typical, when observing the vas deferens without opening the sheath in its complete length. Very often, there is a small enlargement of the sheath just before entering the notal tissue (Wägele, 1990a). This gives the false impression of a small, but separate penial bulb.

The same holds true for *Archidoris kerguelenensis*, which was described 14 years earlier by Bergh (1884) from the Kerguelen Islands. The type locality just at the opposite side of the Atlantic sector of the Antarctic continent probably might be the reason that ODHNER did not choose this species as the type species of his new genus, although he already assigned this species to *Austrodoris* at that time. *Archidoris kerguelenensis* is the only Antarctic dorid for which BERGH figured the distal vas deferens (1884: Pl. I, fig. 12). There is a small enlargement, indicated as a penial bulb, and it looks as if that part represents a small glans penis within a sheath. BERGH (1884: 89) describes the vas deferens of *Archidoris kerguelenensis* as follows: «... which forms several long loops, measuring when extended nearly 3,3 cm by 5 mm, in diameter, and winding on the front and on the inner side of the genital mass. Below the spermatic duct (fig. 12, a) becomes somewhat dilated, and forms the penis (*praeputium*) (fig. 12, b), nearly 2 mm long, the upper half of which is filled with the conical unarmed glans». This again is exactly the picture, when only the distal part of the somewhat dilated «penial» sheath is opened.

BURN (1973) assigned newly collected material from the Heard Islands (close to the Kerguelen Islands) to *Archidoris kerguelenensis*, but a reexamination of his material clearly allowed an assignment to the genus *Austrodoris* (WÄGELE, 1990a). So only recently the vas deferens of *Austrodoris* has been misinterpreted as being of the archidorid type. No archidorid species from the Kerguelen zone are known to me.

Although the type material of BERGH's species seems to be lost (s. WÄGELE, 1990a; K. JENSEN, pers. comm., 1992), the interpretation of the figures and the descriptions, and the fact of the absence of other archidorids in the Antarctic and Subantartict waters, allow to conclude that BERGH's species belong to the genus *Austrodoris* Odhner, 1926.

ODHNER (1926) also mentioned the similarity of *Doris antarctica* Hedley, 1916 to the austrodorid species. According to the figure 102 (plate 9) the protruded vas deferens is very long and also has no separate penis. A protruded vas deferens of a similar length was also observed several times in own material. The assignment of HEDLEY's two specimens to the genus *Austrodoris* therefore seem to be correct. But since nothing is known about the anatomy (except for the radula), it is impossibile to clarify the status of the species.

HEDLEY (1916) also assigned four specimens to *Doris nivalis* (Thiele, 1912), without giving any reasons for doing so. WÄGELE (1990a) considered the name *Archidoris nivalis* Thiele, 1912 as *nomen dubium*, since the description does not allow a re-identification, and the holotype, except for the radula, is lost. Whether Hedley's specimens also belong to *Austrodoris kerguelenensis*, has to be affirmed by examination of his material.

WÄGELE (1990a) already synonymized nine austrodorid species with *Austrodoris kerguelensensis*. The number of synonymous nominal taxa is now extended to 14 (Tab. 1).

Besides revising the genus *Austrodoris*, several other quite common genera of Antarctic nudibranchs were studied by the author (WÄGELE, 1987; 1989b; 1989c; 1990b; 1991). In some of them a rather high degree of intraspecific variation in several features could be observed. A good example is the monotypic genus *Tritoniella* Eliot, 1907 which shows great variation in external morphology as well as in the structure of the rachidian teeth in the radula (Wägele, 1989b). In other genera (e.g. *Bathydoris* Bergh, 1884, *Notaeolidia* Eliot, 1905) the organ systems are relatively consistent in their shape (Wägele, 1989c; 1990b).

Odhner (1934: 233) united the genera *Bathydoris* Bergh, 1884 and *Doridoxa* Bergh, 1900 under the name Gnathodoridacea: «.... these two types have one character in common which separates them from all other Doridacea, viz. the possession of very homogeneous mandibles in the pharynx». Wägele (1989e) showed, that there exists no synapomorphy for the two genera. She removed *Doridoxa* from the Gnathodoridacea and considered the latter as the sister taxon of the Doridacea. The name «Gnathodoridacea» is inadmissable because it is not based on an existing genus (R.C. Willan, pers. comm., 1993). According to the rules of the International Code of Zoological Nomenclature, (Art. 36: Principle of Coordination) the name Bathydoridoidea Bergh, 1891 has to be established, since Bergh described the family Bathydorididae for the first time in 1891.

Although many nations have contributed to our knowledge of the Antarctic benthos, there are still many species that remain known from Antarctic or Subantarctic waters by only one or a few specimens and which have been seldomly re-collected (e.g. *Doto antarctica* Eliot, 1907; *Armodoris antarctica* Minichev, 1972; *Prodoridunculus gaussianus* Thiele, 1912, tab. 1). Nevertheless it can be assumed that ecologists, taxonomists, or other interested people wishing to identify Antarctic nudibranchs will find it much easier now to assign their material to the known nudibranchs species from the south polar seas.

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Table 1: List of species from the southern polar seas, with synonyms.

NUDIBRANCHIA
ANTHOBRANCHIA
DORIDOIDEA

- *Aegires albus* Thiele, 1912; Hedley 1916; Odhner 1926; 1934: Wägele 1987
  - = *Aegires protectus* Odhner, 1934
- *Armodoris antarctica* Minichev, 1972
- *Austrodoris kerguelenensis* (Bergh, 1884); Odhner 1926; 1934; Wägele 1990a
  - = *Austrodoris kerguelensis* Cattaneo-Vietti 1991
  - = *Archidoris kerguelenensis* Bergh, 1884; Bergh 1898
  - = *Archidoris kerguelensis* Bergh 1894
  - = *Archidoris australis* Bergh, 1884
  - = *Austrodoris australis* (Bergh): Odhner 1934
  - = *Archidoris rubescens* Bergh, 1898
  - = *Austrodoris rubescens* (Bergh): Odhner 1926
  - = *Archidoris tuberculata* var. Vayssère, 1906; new synonym
  - = *Archidoris tuberculata* var. *antarctica* Vayssière, 1917; new synonym
  - = *Archidoris granulatissima* Vayssière, 1917; new synonym
  - = *Austrodoris granulatissima* (Vayssière): Odhner 1934; ? Vicente & Arnaud 1977; ? Ev. Marcus 1985
  - = *Austrodoris crenulata* Odhner, 1926
  - = *Austrodoris michaelseni* Odhner, 1926
  - = *Austrodoris macmurdensis* Odhner, 1934; ? Bouchet 1977
  - = *Austrodoris nivium* Odhner, 1934; Minichev 1972; Vicente 1974
  - = *Austrodoris tomentosa* Odhner, 1934; Vicente 1977
  - = *Austrodoris grandis* Minichev, 1972; new synonym
  - = *Austrodoris stellata* Minichev, 1972; new synonym
  - = *Austrodoris longa* Minichev, 1972; new synonym
  - = *Archidoris kerguelenensis* Bergh: Burn 1973; ? Merilees & Burn 1969
  - = *Austrodoris mishu* Ev. Marcus, 1985
  - = *Austrodoris vicentei* Ev. Marcus, 1985
- ? *Austrodoris antarctica* (Hedley, 1916)
- *Cadlina affinis* Odhner, 1934
- *Cadlina falklandica* Odhner, 1926
- *Doris falklandica* (Eliot, 1907)
- *Prodoridunculus gaussianus* Thiele, 1912

BATHYDORIDOIDEA

- *Bathydoris clavigera* Thiele, 1912; Wägele 1989c; 1989d
  - = *B. obliquata* Odhner, 1934; Minichev 1972
  - = *B. argentina* Kaiser, 1980
- *Bathydoris hodgsoni* Eliot, 1907; Hedley 1916; Wägele 1989c
  - = *B. inflata* Eliot, 1907
  - = *B. brownii* Evans, 1914
- *Bathydoris vitjazi* Minichev, 1969
- *Bathydoris patagonica* Kaiser, 1980

SUBORDER CLADOBRANCHIA

SUPERFAMILY DENDRONOTOIDEA

Doto sp. Thiele, 1912

Doto antarctica Eliot, 1907

Marionia cucullata Vicente & Arnaud, 1974; non *M. cucullata* (Gould, 1852): Ev. Marcus 1983

Tritonia australis Bergh, 1898; Ev. & Er. Marcus 1969; Ev. Marcus 1983
= *T. poirieri* Odhner, 1926 (non Rochebrune & Mabille, 1891;

Tritonia appendiculata Eliot, 1905

Tritonia challengeriana Eliot, 1907; Odhner 1926; Minichev, 1972
= *T. antarctica* Pfeffer in Pfeffer & Martens, 1886

Tritonia vorax (Odhner, 1926: as *Duvaucelia*)

Tritoniella belli Eliot, 1907; Odhner 1934; Minichev 1972; Vicente & Arnaud 1974; Wägele 1989b; Cattaneo-Vietti 1991
= *T. sinuata* Eliot, 1907; Hedley 1916; Odhner 1926; 1934; Vicente & Arnaud 1974

ARMINOIDEA

Charcotia granulosa Vayssière, 1906

Pseudotritonia quadrangularis Thiele, 1912; Cattaneo-Vietti 1991; Wägele, 1991

Pseudotritonia gracilidens Odhner, 1944; Cattaneo-Vietti 1991; Wägele 1991

Pseudotritonia antarctica (Odhner, 1934): Cattaneo-Vietti 1991;
= *Telarma antarctica* Odhner, 1934; Wägele 1991;

AEOLIDOIDEA

Coryphella falklandica Eliot, 1907; Odhner 1926; 1944

Cuthona antarctica (Pfeffer, 1884; as *Aeolis*); Martens & Pfeffer 1886; Odhner 1926

Cuthona claviformes Vicente & Arnaud, 1974

Cuthona crinita Minichev, 1972

Cuthona georgiana (Pfeffer, 1884; as *Aeolis*); Martens & Pfeffer 1886; Odhner 1926; 1944; Cattaneo-Vietti 1991

Cuthona georgiana longipapillata: Minichev, 1972

Cuthona paucicirra Minichev, 1972

Cuthona schraderi (Pfeffer, 1884: as *Aeolis*); Martens & Pfeffer 1886

Cuthona schraderi bouvetensis Odhner, 1944

Cuthona arnaudi (Vicente, 1974: as *Eubranchus*); Cattaneo-Vietti 1991

Cuthona macquariensis (Burn, 1973: as *Trinchesia*)

Cuthona modesta (Eliot, 1907: as *Cuthonella*)

Cuthona elioti Odhner, 1944: nom. nov. for *Cuthonella antarctica* Eliot, 1907

Cuthona paradoxa (Eliot, 1907: as *Cuthonella*); Odhner 1944

Eubranchus sp. Vicente & Arnaud, 1974

Eubranchus adarensis Odhner, 1934; Vicente & Arnaud 1974

Eubranchus falklandicus (Eliot, 1907: as *Galvina*)

Galvinella antarctica Eliot, 1907

Galvinella glacialis Thiele, 1912

Guyvalvoria francaisi Vayssière, 1906
Notaeolidia depressa Eliot, 1905; Hedley 1916; Wägele 1990b
= *N. rufopicta* Thiele, 1912
= *N. robsoni* Odhner, 1934; Vicente & Arnaud 1974
= *N. subgigas* Odhner, 1944
= *N. alutacea* Minichev, 1972
= *N. flava* Minichev, 1972
Notaeolidia gigas Eliot, 1905; Wägele 1990b
= *N. purpurea* Eliot, 1905
= *N. subgigas:* Wägele, 1988, non *N. subgigas* Odhner, 1944
Notaeolidia schmekelae Wägele, 1990
Tergipes antarcticus Pelseneer, 1903
Tergipes valentini (Eliot, 1907: as *Cratena*); Cattaneo-Vietti 1991

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Drosos Koutsoubas & Athanasios Koukouras (*)

AN ACCOUNT OF OUR KNOWLEDGE ON THE OPISTHOBRANCH MOLLUSC FAUNA OF THE AEGEAN SEA (**)

KEY WORDS: Mollusca, Gastropoda, Opisthobranchia, Zoogeography, Aegean Sea.

Riassunto

Viene esposto per la prima volta un elenco ragionato della fauna a molluschi opistobranchi del Mare Egeo. 23 specie sono nuove per la malacofauna di questo mare. Fra quest'ultime, 7 non erano conosciute nel Mediterraneo Orientale. Infine è anche discussa la composizione ed il significato biogeografico della malacofauna degli opistobranchi del Mare Egeo.

Abstract

A check list of the opisthobranch molluscs of the Aegean Sea is presented for the first time. 23 species are new records for the mollusc fauna of the Aegean Sea. Among the latter 7 species were not previously known in the Eastern Mediterranean. The systematic composition and zoogeographical status of the opisthobranch mollusc fauna of the Aegean Sea is also discussed.

Introduction

Our knowledge on the Aegean opisthobranch mollusc fauna is rather limited compared with that of other Mediterranean areas. Information about the opisthobranch mollusc fauna in the Aegean Sea is included in a restricted number of papers (DESHAYES, 1835; FORBES, 1844 critically revised by NORDSIECK, 1977; JEFFREYS, 1883; CARUS, 1893; STURANY, 1896; PRUVOT-FOL & FISCHER-PIETTE, 1934; PRUVOT-FOL, 1954; OBERLING, 1960-1962; SALVINI-PLAWEN & STERRER, 1968; GHISOTTI, 1968/78; RAMPAL, 1970; NORDSIEK, 1972; WAWRA, 1974; THOMPSON, 1983, 1985, 1988; THOMPSON & TURNER, 1983; THOMPSON & BROWN, 1984; WÄGELE, 1985; BARASH & DANIN, 1986; THOMPSON & JAKLIN, 1988; TENEKIDIS, 1989; THOMPSON *et al.*, 1990; KOUTSOUBAS *et al.*, 1992, 1993). Some other papers of mainly ecological interest (PÉRÈS & PICARD, 1958; LABOREL, 1960; JACQUOTTE, 1962; LEDOYER, 1966, 1969; KIORTSIS, 1969; GELDIAY & KOCATAS, 1972; FIELDING & EDMUNDS, 1973; BIANCHI & MORRI, 1983; KOUKOURAS *et al.* 1985; THOMPSON *et al.*, 1985) give also scattered information on the opisthobranch mollucs of the Aegean Sea.

(*) Department of Zoology, University of Thessaloniki, 54006 Thessaloniki, Greece.
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According to the information given by the above mentioned authors a total of 114 opisthobranch species is known from the Aegean Sea.

In 1986, a research program on the qualitative composition of the benthic fauna of the North Aegean Sea started. Samplings carried out in that period, in various habitats and depths revealed an important number of opisthobranch species.

The main goal of this study is: (i) to present for the first time an updated check-list of Aegean opisthobranch species, (ii) to give additional information on the opisthobranch mollusc fauna of the Aegean Sea and (iii) to discuss the systematic composition and zoogeographical status of this fauna.

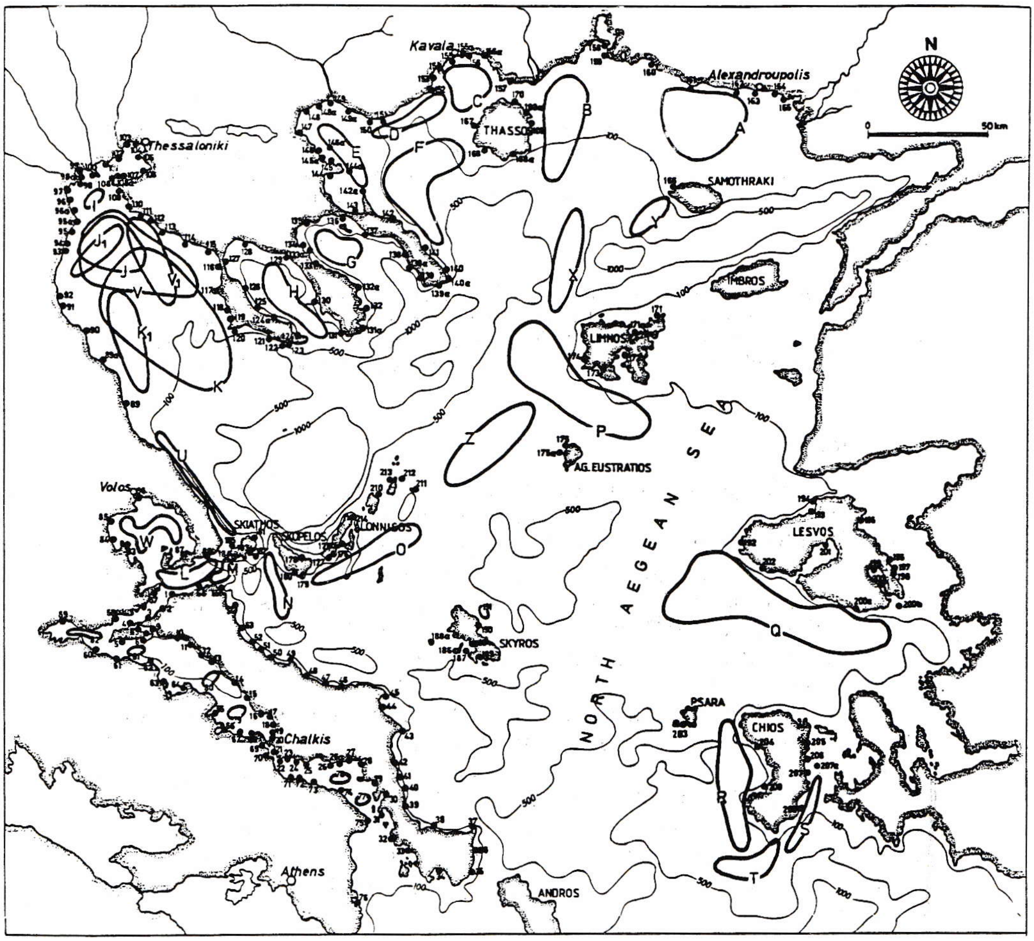

Fig. 1. Map of the North Aegean Sea indicating the sampling stations. (●: sampling stations where the samples were collected by SCUBA diving or grab; ———: sampling stations where the samples were collected by dredge or fishing nets).

Table I. Opisthobranch mollusc species known from the Aegean Sea (A=authors' collection; the authors given in brackets were the first to report the presence of the species in the Aegean Sea; * first record for the North Aegean Sea; ** first record for the Aegean Sea; *** first record for the Eastern Mediterranean).

Order **CEPHALASPIDEA**

	Family **Acteonidae**	
	Acteon tornatilis (Linnaeus, 1758)	[DESHAYES, 1835; A]
***	*Acteon monterosatoi* Dauntzenberg, 1889	[A]
	Crenilabium exile (Forbes in Jeffreys, 1870)	[CARUS, 1893; A]
*	*Liocarenus globulinus* (Forbes, 1844)	[FORBES, 1844; A]
	Japonacteon pusillus (Forbes, 1844)	[FORBES, 1844; A]
	Family **Diaphanidae**	
	Diaphana cretica (Forbes, 1844)	[FORBES, 1844]
	Family **Retusidae**	
	Retusa leptoneilema (Brusina, 1866)	[CARUS, 1893]
	Retusa mammilata (Philippi, 1836)	[FORBES, 1844]
*	*Retusa obtusa* (Montagnu, 1803)	[OBERLING, 1960-62; A]
*	*Retusa semisulcata* (Philippi, 1836)	[FORBES, 1844; A]
	Retusa truncatula (Bruguiere, 1792)	[FORBES, 1844; A]
	Retusa piriformis (Monterosato, 1878)	[NORDSIECK, 1972]
*	*Cylichnina umbilicata* (Montagu, 1803)	[OBERLING, 1960-62; A]
*	*Volvulella acuminata* (Bruguiere, 1792)	[KOUTSOUBAS *et al.*, 1992; A]
	Family **Ringiculidae**	
	Ringicula auriculata (Menard de la Groye, 1811)	[FORBES, 1844; A]
*	*Ringicula conformis* (Monterosato, 1877)	[TENEKIDIS, 1989; A]
**	*Ringicula leptocheila* Brugnone, 1873	[A]
	Family **Bullidae**	
	Bulla striata Bruguiere, 1792	[FORBES, 1844; A]
	Family **Haminaeidae**	
	Haminaea hydatis (Linnaeus, 1758)	[FORBES, 1844; A]
	Haminaea navicula (Da Costa, 1778)	[FORBES, 1844; A]
	Atys brocchi (Michelotti, 1847)	[TENEKIDIS, 1989]
	Atys jeffreysi (Weinkauff, 1868)	[JACQUOTTE, 1962]
*	*Weinkauffia turgidula* (Forbes, 1844)	[FORBES, 1844; A]
	Family **Philinidae**	
	Philine aperta (Linnaeus, 1767)	[DESHAYES, 1835; A]
	Philine catena (Montagu, 1803)	[FORBES, 1844; A]
	Philine punctata (Adams J., 1800)	[FORBES, 1844]
	Johania retifera (Forbes, 1844)	[FORBES, 1844]
	Family **Aglajidae**	
	Philinopsis depicta (Renier, 1804)	[LEDOYER, 1966]
	Family **Akeridae**	
*	*Akera bullata* Mueller O.F., 1776	[FORBES, 1844; A]
	Family **Cylichnidae**	
	Cylichna alba (Brown, 1827)	[TENEKIDIS, 1989]
	Cylichina crossei B.D.D., 1886	[TENEKIDIS, 1989]
*	*Cylichna cylindracea* (Pennant, 1777]	[FORBES, 1844; A]
	Cylichna parvula Jeffreys, 1883	[JEFFREYS, 1883]
	Roxania utriculus (Brocchi, 1814)	[FORBES, 1844; A]
***	*Raxania monterosatoi* Dautzenberg & Fischer, 1986	[A]
	Scaphander lignarius (Linnaeus, 1758)	[FORBES, 1844; A]

Family **Gastropteridae**		
*	*Gastropteron meckeli* Kosse, 1813	[FORBES, 1844; A]
Family **Philinoglossidae**		
	Philinoglossa helgolandica Hertling, 1932	[WAWRA, 1974]
Order **THECOSOMATA**		
Family **Cavolinidae**		
	Cavolinia gibbosa (D'Orbigny, 1835 ex Rang ms)	[FORBES, 1844; A]
	Cavolinia inflexa (Lesueur, 1813)	[FORBES, 1844; A]
	Cavolinia tridentata (Niebuhr, 1775 ex Forskal ms)	[FORBES, 1844; A]
	Diacria trispinosa (Lesueur, 1821)	[RAMPAL, 1970]
	Clio cuspidata (Bosc, 1802)	[FORBES, 1844; A]
	Clio pyramidata Linnaeus, 1767	[FORBES, 1844; A]
	Creseis acicula Rang. 1828	[FORBES, 1844; A]
	Creseis virgula Rang, 1828	[KIORTSIS 1969; A]
	Hyalocylis striata (Rang, 1828)	[FORBES, 1844; A]
	Styliola subula (Quoy & Gaimard, 1827)	[FORBES, 1844]
Family **Limacinidae**		
	Limacina retroversa (Fleming, 1823)	[GHISOTTI, 1968/78]
	Limacina bulimoides (D'Orbigny, 1836)	[CARUS, 1893]
*	*Limacina trochiformis* (D'Orbigny, 1836)	[JEFFREYS, 1883; A]
	Limacina inflata (D'Orbigny, 1836)	[JEFFREYS, 1883; A]
	Limacina helicoides Jeffreys, 1877	[KIORTSIS, 1969]
Family **Cymbuliidae**		
	Cymbulia peronii Lamarck, 1819	[KIORTSIS, 1969; A]
Family **Peraclidae**		
	Peracle reticulata (D'Orbigny, 1836)	[FORBES, 1844]
	Peracle bispinosa Pelseneer, 1888	[KIORTSIS, 1969]
	Peracle triacantha (Fischer P., 1882)	[KIORTSIS, 1969]
Order **SACOGLOSSA**		
Family **Oxynoidae**		
	Oxynoe olivacea Rafinesque, 1814	[FORBES, 1844]
	Lobiger serradifalci (Calcara, 1840)	[TENEKIDIS, 1989]
Family **Volvatellidae**		
*	*Ascobulla fragilis* (Jeffreys, 1856)	[TENEKIDIS, 1989; A]
Family **Elysiidae**		
	Elysia flava Verrill, 1901	[THOMPSON, 1983]
	Elysia timida (Risso, 1818)	[FORBES, 1844]
	Elysia translucens Pruvot-Fol, 1957	[THOMPSON & JAKLIN, 1988]
	Elysia viridis (Montagu, 1804)	[LEDOYER, 1969]
	Thuridilla hopei (Vérany, 1853)	[THOMPSON & JAKLIN, 1988]
Family **Boselidae**		
	Bosellia mimetica Trinchese, 1891	[THOMPSON & JAKLIN, 1988]
Family **Polybranchiidae**		
	Polybranchia bogninii (Trinchese, 1896)	[THOMPSON, 1988]
	Aplysiopsis elegans Deshayes, 1864	[KOUTSOUBAS *et al.*, 1993; A]
	Cyerce graeca Thompson T.E., 1988	[THOMPSON, 1988]
Family **Stiligeridae**		
	Placida saronica (Thompson T.E., 1988)	[THOMPSON, 1988]

Order **NOTASPIDEA**

Family **Umbraculidae**

*	*Umbraculum umbraculum* (Roeding, 1798)	[FORBES, 1844; A]

Family **Tylodinidae**

	Tylodina perversa (Gmelin, 1791)	[PRUVOT-FOL & FISCHER-PIETTE, 1934; A]

Family **Pleurobranchidae**

**	*Pleurobranchus membranaceus* (Montagu, 1815)	[A]
	Berthella aurantiaca (Risso, 1818)	[FORBES, 1844]
	Berthella plumula (Montagu, 1803)	[TENEKIDIS, 1989]
	Berthella stellata (Risso, 1826)	[THOMPSON, 1985; A]
**	*Pleurobranchaea meckelii* Meckel in Leue, 1813	[A]

Order **ACOCHLIDIACEA**

Family **Hedylopsidae**

	Hedylopsis spiculifera (Kowalewsky, 1901)	[PRUVOT-FOL., 1954]

Family **Microhedylidae**

	Microhedyle glandulifera (Kowalewsky, 1901)	[WAWRA, 1974]
	Pontohedyle milatschevitchi (Kowalewsky, 1901)	[WAWRA, 1974]

Order **ANASPIDEA**

Family **Aplysiidae**

**	*Aplysia depilans* Gmelin, 1791	[A]
**	*Aplysia parvula* Guilding in Moerch, 1863	[A]
	Aplysia punctata (Cuvier, 1803)	[PERES & PICARD, 1958; A]
	Aplysia fasciata Poiret, 1789	[FIELDING & EDMUNDS, 1973; A]
	Bursatella leachii Blainville, 1817	[BARASH & DANIN, 1986; A]

Family **Dolabriferidae**

	Notarchus punctatus Philippi, 1836	[FORBES, 1844]
	Petalifera petalifera (Rang, 1828)	[THOMPSON *et al.*, 1985]
	Phyllaplysia lafonti (Fischer P., 1870)	[FORBES, 1844]

Order **NUDIBRANCHIA**

Family **Aegiretidae**

	Aegires punctilucens (D'Orbigny, 1837)	[LEDOYER, 1966]

Family **Gonoiodorididae**

	Okenia elegans (Leuckart, 1828)	[KOUTSOUBAS *et al.*, 1993; A]

Family **Dorididae**

	Doris marmorata Risso, 1818	[KOUTSOUBAS *et al.*, 1993; A]
**	*Doris ocelligera* (Bergh, 1881)	[A]

Family **Archidorididae**

	Archidoris pseudoargus (Rapp, 1827)	[KOUTSOUBAS *et al.*, 1993; A]

Family **Chromodorididae**

**	*Chromodoris krohni* (Vérany, 1846)	[A]
	Chromodoris luteorosea (Rapp. 1827)	[KOUTSOUBAS *et al.*, 1993; A]
**	*Chromodoris purpurea* (Risso in Guérin, 1831)	[A]
***	*Hypselodoris messinensis* (Von Ihering, 1880)	[A]
***	*Hypselodoris tricolor* (Cantraine, 1835)	[A]
*	*Hypselodoris villafranca* (Risso, 1818)	[FORBES, 1844; A]
*	*Hypselodoris webbi* (D'Orbigny, 1839)	[THOMPSON & TURNER, 1983) A]

Family **Discodorididae**		
	Discodoris atromaculata (Bergh, 1880)	[LABORET, 1960; A]
**	*Paradoris indecora* (Bergh, 1881)	[A]
***	*Thordisa filix* Pruvot-Fol., 1951	[A]
Family **Kentrodorididae**		
	Jorunna tomentosa (Cuvier, 1804)	[KOUTSOUBAS *et al.*, 1993; A]
Family **Platydorididae**		
*	*Platydoris argo* (Linnaeus, 1767)	[FORBES, 1844; A]
**	*Baptodoris cinnabarina* Bergh, 1884	[A]
**	*Taringa armata* Swennen, 1961	[A]
Family **Rostangidae**		
*	*Rostanga rubra* (Risso, 1818)	[FORBES, 1844; A]
Family **Polyceridae**		
	Polycera quadrilineata (Mueller, O.F., 1776)	[LEDOYER, 1966]
***	*Limacia clavigera* (Mueller O.F., 1776)	[A]
Family **Dendrodorididae**		
**	*Dendrodoris grandiflora* (Rapp. 1827)	[A]
	Dendrodoris limbata (Cuvier, 1804)	[KOUKOURAS *et al.*, 1985; A]
Family **Phyllidiidae**		
	Phyllidia flava Aradas, 1847	[WÄGELE, 1985; A]
Family Dotidae		
	Doto coronata (Gmelin, 1791)	[FORBES, 1844]
	Doto fragilis (Forbes, 1838)	[FORBES, 1844]
	Doto floridicola Simroth, 1888	[THOMPSON *et al.*, 1990]
	Doto pontica Swennen, 1961	[THOMPSON *et al.*, 1990]
	Doto lemchei Ortea & Urgorri, 1989	[THOMPSON *et al.*, 1990]
	Doto rosea Trinchese, 1881	[THOMPSON *et al.*, 1990]
Family **Hancockiidae**		
	Hancockia uncinata (Hesse, 1872)	[LEDOYER, 1966]
Family **Scyllaeidae**		
	Scyllaea pelagica Linnaeus, 1758	[FORBES, 1844]
Family **Tethyidae**		
	Tethys fimbria Linnaeus, 1767	[FORBES, 1844; A]
Family **Tritoniidae**		
**	*Tritonia manicata* Deshayes, 1853	[A]
	Tritonia plebeia Johnston, 1828	[FORBES, 1844]
**	*Marionia blainvillea* (Risso, 1818)	[A]
**	*Marionia tethydea* (Delle Chiaje, 1822)	[A]
Family **Arminidae**		
	Armina maculata Rafinesque, 1814	[THOMPSON *et al.*, 1990; A]
	Armina neapolitana (Delle Chiaje, 1824)	[KOUTSOUBAS *et al.*, 1993; A]
Damily **Aeolidiidae**		
	Aeolidiella alderi (Cocks, 1852)	[THOMPSON & BROWN, 1984; A]
Family **Facelinidae**		
**	*Facelina rubrovittata* (Costa A., 1886)	[A]
	Cratena peregrina (Gmelin, 1791)	[KOUTSOUBAS *et al.*, 1993; A]

	Family **Flabellinidae**	
*	*Flabellina affinis* (Gmelin, 1791)	[BIANCHI & MORRI, 1983; A]
***	*Coryphella pedata* (Montagu, 1815)	[A]
	Family **Pseudovermidae**	
	Pseudovermis boedeni Salvini-Plawen & Sterrer, 1968	[WAWRA, 1974]
	Pseudovermis kowalewskyi Salvini-Plawen & Sterrer, 1968	[SALVINI-PLAWEN & STERRER, 1968]
	Pseudovermis papillifer Kowalewsky, 1901	[SALVINI-PLAWEN & STERRER, 1968]
	Family **Tergipedidae**	
	Cuthona caerulea (Montagu, 1804)	[LEDOYER, 1966]

Table II. Systematic composition of the opisthobranch mollusc fauna from the Aegean Sea.

Order	Family	Genus	Species
Cephalaspidea	12	22	38 (27.74%)
Thecosomata	4	9	19 (13.87%)
Gymnosomata	0	0	0 (0.00%)
Saccoglossa	6	10	13 (9.49%)
Notaspidea	3	5	7 (5.11%)
Acochlidiacea	2	3	3 (2.19%)
Anaspidea	2	5	8 (5.84%)
Nudibranchia	23	32	49 (35.76%)
Total	52	86	137

Table III. Number of Aegean opisthobranch molluscs in different zoogeographic categories (137 species).

Atlanto-Mediterranean	47 (34.30%)
Boreal	30 (21.90%)
Mediterranean endemics	29 (21.17%)
Cosmopolitan	18 (13.14%)
Subtropical	7 (5.11%)
Circumtropical	6 (4.38%)
Total	137

Materials and Methods

Specimens were collected by SCUBA diving and dredge, grab or fishing nets from 87 sampling stations in various areas of the North Aegean Sea (fig. 1) at depths from 0 to 1000 m. Specimens were preserved in 5% formalin and are deposited in the Museum of the Department of Zoology, University of Thessaloniki. The classification used is that proposed by SABELLI *et al*. (1990).

Results and Discussion

The examination of the collected material (930 live individuals and shells) from the North Aegean Sea revealed the presence of 82 opisthobranch species. 7 of these species are new records for the fauna of the eastern basin of the Mediterranean (eastern of 20°), 16 are new for the fauna of the Aegean Sea and 18 are reported for the first time from the North Aegean Sea.

Besides the 82 opisthobranch species found during this study in the Aegean Sea, 55 more species reported by other authors should be considered. Thus, the total number of the opisthobranch molluscs known from the Aegean Sea becomes 137 species. The opisthobranch mollusc species of the Aegean Sea, known up to now are given in Table I with the relevant literature sources. In this Table, 10 species reported by FORBES (1844) from various localities of the Aegean Sea are not included, either because their systematic identity is doubtful (*Pleurobranchus calyptroides* Forbes, 1844; *Pleurobranchus limacoides* Forbes, 1844; *Pleurobranchus scutatus* Forbes, 1844; *Pleurobranchus sordidus* Forbes, 1844; *Goniodoris regalis* Forbes, 1844; *Goniodoris tenerrima* Forbes, 1844; *Goniodoris vivida* Forbes, 1844; *Doris aurata* Forbes, 1844) or because their presence in the Mediterranean Sea has not been confirmed (*Acanthodoris pilosa* (Abildgaard in Mueller, 1789); *Coryphella verrucosa* (Sars M., 1829).

The systematic composition of the Aegean opisthobranch mollusc fauna is presented in Table II. Nudibranchia are represented by the greatest number of species followed by Cephalaspidea.

It has already been mentioned by CATTANEO-VIETTI & THOMPSON (1989) that there are insufficient data on the zoogeography of the opisthobranchs in the different areas of the Mediterranean Sea. Zoogeographic analyses on the opistobranch mollusc fauna of the Aegean Sea (Table III) revealed that the largest opisthobranch category is the Atlanto-Mediterranean (55 species, 39.86%) followed by Boreal (31 species, 22.46%) and Mediterranean endemics (27 species, 19.56%). It is worth mentioning the absence of Indo-Pacific opisthobranch species from the Aegean, despite the vicinity of this sea to the Levantine basin from where an important number of Indo-Pacific opisthobranch species has been reported (BARASCH & DANIN, 1972, 1986; POR, 1978).

The review of the relevant literature and the results of the present study show that the total number of opisthobranch species in the Aegean Sea is greater than that known from other areas of the Eastern Mediterranean, but it is still lower than that known from certain areas of the Western Mediterranean. However, we believe that the great numerical difference between the opisthobranch species known from the Aegean Sea and those from areas of the Western Mediterranean, will be significantly reduced, when the research in the Aegean becomes more intensive.

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G. Villani (*) & E. Martinez (**)

SOME OBSERVATIONS ON THE OPISTHOBRANCH FAUNA FROM THE FUSARO LAKE, A BRACKISH-WATER LAGOON NEAR NAPLES. (***)

KEY WORD: Opisthobranchs, Lagoon, Mediterranean Sea

Summary

The opisthobranch fauna of Fusaro, a coastal lagoon near Naples (Tyrrhenian Sea), is studied and a comparison with previous data is made. Results show that although the lagoon is heavily polluted, diversity of opisthobranch species is quite high.

Riassunto

È stata studiata la fauna ad Opistobranchi del Lago Fusaro, una laguna costiera vicino Napoli, ed è stata effettuata una comparazione con i dati precedenti. I risultati mostrano che, nonostante l'elevato inquinamento della laguna, la diversità specifica è piuttosto elevata.

Introduction

The Fusaro, a coastal lagoon near Naples, had been previously sampled by SCHMEKEL (1968) in her work about the Opisthobranchia from the Gulf of Naples (see CATTANEO-VIETTI & CHEMELLO, 1991). Several samplings were made in order to widen the knowledge about the opisthocenose of the lagoon, and also to make a comparison with previous works.

The Fusaro lagoon is situated on the Western side of the Gulf of Naples, in the area called «Campi Flegrei» (Fig. 1), and separated from the Tyrrhenian Sea by a barrier formed by a coastal dune. Geologically, the lagoon originates from a secondary vulcanic process.

The lagoon is near 100 ha at the surface, with a water volume of about 3 millions m^3 and a medium depth of 2.5 m (LECCESE & SPEZIALE, 1967). It opens into the Tyrrhenian Sea through three little channels, which penetrate the coastal dune (Fig. 2). The Southernmost one, called Foce Romana, is 750 m long; in the centre, Foce di mezza Chiaia, is the shortest, only 400 m long. Foce Nuova, to the North, is 600 m long. The medium depth of these channels is about 1.5 m, but in some areas of the Foce Romana and specially of the Foce Nuova the bottom is closer to the surface, thus becoming an obstacle for water circulation.

(*) Istituto per la Chimica di Molecole di Interesse Biologico, C.N.R., - Via Toiano, 6. Arco Felice, Napoli, Italy.

(**) Laboratorio de Zoología, Depto, de Biología de Organismos y Sistemas, Universidad de Oviedo. C/ Jesus Arias de Velasco s/n, 33005 Oviedo Spain.

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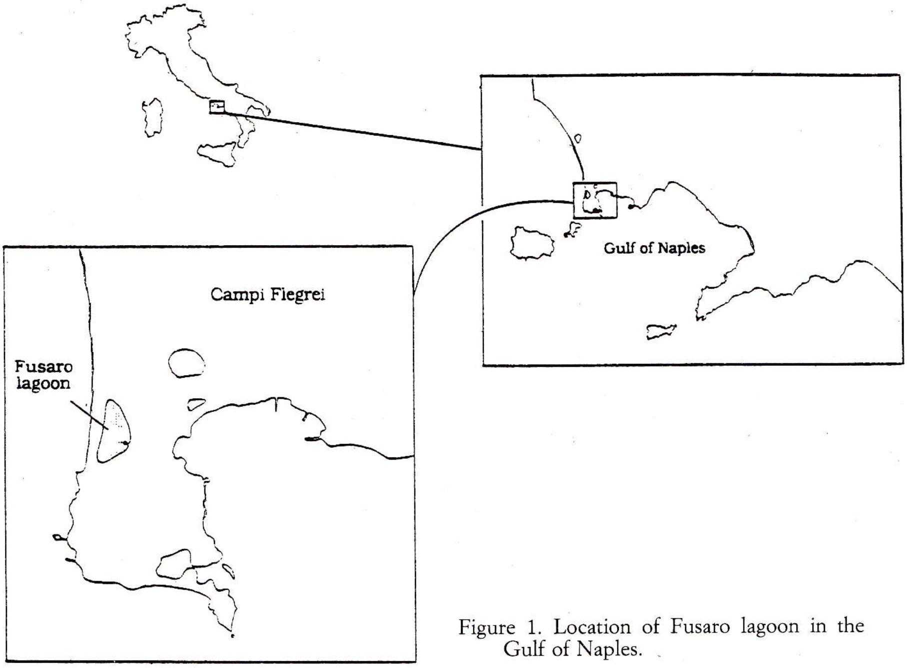

Figure 1. Location of Fusaro lagoon in the Gulf of Naples.

Water re-cycling in the lagoon is only through the tidal action and is extremely reduced owing to the almost total absence of a freshwater contribution. In a 24 h period only about 8.4% of the volume is recycled. All these factors are responsable for the hypersalinity trend in the Fusaro lake.

Muddy bottoms are dominant both in the lagoon and the channels. The lagoon lacks natural shores, but submersed walls surround the lagoon and the channels, constituting the only hard substratum found in the Fusaro, together with an artificial breakwater around Casina Vanvitelliana.

Benthic communities have been previously characterized by RUSSO & FERRO (1980), who found three types of faunistic associations: in hard bottoms the upper 5 cm are dominated by barnacles and mitilids, whereas the infralitoral community consists of serpulids which form a net with their calcareous tubes, which retain sand particles, constituing a microhabitat for some tunicates such as *Ciona intestinalis* and *Microcosmus sulcatus*, actiniarians such as *Bunodactis verrucosa* and *Paranemonia cinerea*, the bryozoa *Bugula neritina* and the bivalves *Ostrea edulis* and *Petricola litophaga*. Soft bottoms are dominated by a bivalve community, mainly *Tapes decussatus, Paphia aurea* and *Cerastoderma edule* (RUSSO & FERRO, 1980); several areas are covered by *Ulva lactuca* and *Chaetomorpha aerea*, although these algae are not fixed to the bottom.

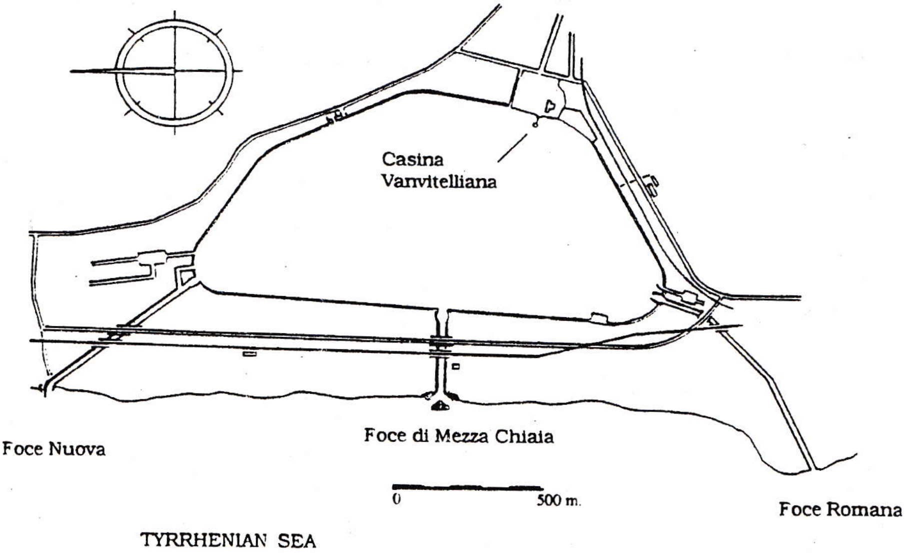

Figure 2. Map of the Fusaro lagoon, showing the location of the three «foce» and the Casina Vanvitelliana.

The malacofauna from the Fusaro has been previously studied by Bellini (1901), Mazzarelli (1921), Ferro & Russo (1981, 1982), but almost only Prosobranchs and Bivalves were reported in these works. The most important contributions concerning opisthobranch fauna are that of Schmekel (1968), who found in the lagoon 13 Sacoglossa and Nudibranchia species, and the revision by Cattaneo-Vietti & Chemello (1991), with 17 species reported.

Material and Methods

Between 1990-91, in the course of several samplings into the Fusaro lagoon in order to collect marine invertebrates for chemical studies, some observations and samplings were made about the Opisthobranch fauna, using scuba-diving techniques. Samples were taken principally on hard substrata, in the three channels and also in the breakwater surrounding the Casina Vanvitelliana, a small Borbonic pavilion built in the inner shores of the lagoon. Animals were caught by direct observations and also by means of algae washing.

Results

A total of 25 species were found (see Table 1), only five of them scarce.

The species most abundant and more frequently recorded are the herbivores. Among them, Cephalaspidea belonging to the *Haminaea* genus make up numerically important populations. Three species can be found: *H. orbignyana*, *H. orteai* and a third, *H. fusari*, recently described by ALVAREZ *et al.* (1993). These *Haminaea* species are found in high densities, specially in spring-summer time, when the reproductive activity is highest. Our observations disagree with those of FERRO & RUSSO (1981), who only recorded one species, *Haminaea hydatis*, with a great phenotypic variation. These authors only studied the shell, whereas our experiences have shown that shell characteristics are not reliable diagnostic features as far as identifying Cephalaspidea species is concerned.

Species	**Channels**	**Breakwater**
Philine aperta	+	-
*Philinopsis depicta**	+	-
Bulla striata	+	-
Haminaea orbignyana	+	+
Haminaea orteai	+	-
Haminaea fusari	+	+
Akera bullata	+	+
Aplysia fasciata	+	-
Aplysia depilans	+	-
Aplysia punctata	+	-
Bursatella leachii	+	-
*Notarchus punctatus**	+	-
*Pleurobranchaea meckelii**	+	-
Elysia viridis	-	+
Ercolania funerea	+	+
Placida dendritica	-	+
Caliphylla mediterranea	-	+
Spurilla neapolitana	+	+
Facelina coronata	+	-
Facelina dubia	+	-
Favorinus branchialis	+	-
Janolus cristatus	+	-
Polycera quadrilineata	+	+
*Polycera dubia**	+	-
*Taringa sp.**	+	-

Table 1. Distribution of Opisthobranch species in the two habitats sampled at the Fusaro lagoon. Those ones considered to be rare are marked with an asterisk.

An interesting and scarcely reported data is the great differences in the spawn among the *Haminaea* species. Thereby, in *H. orbignyana* it is a light yellow ribbon with eggs arranged in regular rows, the heigth of these rows does not vary along the ribbon. *H. orteai* shows eggs arranged also in rows, but variable in heigth. On the other hand, the species *H. fusari* has a bright yellow spawn; eggs are not arranged in rows but irregularly.

Another herbivorous species is *Akera bullata*, found in lower densities than *Haminaea* spp., and that spawns from May to June. The carnivorous *Philine aperta*, also inhabiting soft bottoms, is common and feeds on little bivalves.

Among the Anaspidea, three *Aplysia* species can be found in great quantities: *A. fasciata*, *A. depilans* and *A. punctata* together with *Bursatella leachii*; the latter, now spreading into the Mediterranean Sea from the Indian Ocean, inhabits sheltered areas, such as harbours and lagoons, and thus finds an optimal habitat in the Fusaro. On the contrary, *Notarchus punctatus* is an occasional species, there.

'acoglossa is one of the most abundant group in the lagoon. Life cycles in this order are correlated to those of the algae they feed on. From January to May the cladophoral *Chaetomorpha capillaris* grows, with *Ercolania funerea* and its spawns associated with it. The caulerpal *Bryopsis plumosa* can be found from March to May, coinciding with the presence of *Placida dendritica*, which feeds on this alga together with *Caliphylla mediterranea* and *Elysia viridis*. The almost total absence of Porifera in the Fusaro lagoon is the reason why the number of Nudibranchia species is so reduced. In fact, among eudoridaceans only one *Taringa* species has been found by chance in one of the channels. The widespread species *Polycera quadrilineata* makes up important populations; animals and its spawns are found both on the bryozoa *Bugula neritina* and the sea squirt *Ciona intestinalis*. This species shows a great chromatic variation, thus specimens white in colour with scarce yellow stripes are found together with almost completely orange and black pigmented individuals. *Polycera dubia* was occasionally found in one of the channels, close to the sea.

Facelina coronata is one of the most abundant species in the lagoon, which reaches up to 7 cm in length and is present throughout the year, but with a maximum density from January to May. On the contrary, *Facelina dubia*, and easily-recognized species because of its smooth rinophores, is very scarce in the Fusaro.

The coloration of *Spurilla neapolitana* is darker than usual because of the fact that the Actiniaria on which it feeds in the lagoon are *Bunodactis verrucosa* and *Paraneomonia cinerea*, darker in colour that *Anemonia sulcata*, usually reported as its food. The latter is very rare in the Fusaro and is only present in the channels close to the sea.

From February and through the spring *Janolus cristatus* can be found in the lagoon, usually associated with *Bugula neritina*. This species grows up to 10 cm long in the Fusaro, and the two colour patterns (orange and blue) can be found, the former much more abundant.

Discussion and Conclusions

A phenomenon we can observe in the Fusaro is the existence of a biotic zonation, as it often happens in very «closed» environments, such as coastal lagoons. This means that the number of Opisthobranch species increases as we reach the sea, that is, bigger in the channels area, close to the sea, than in the inner part of the basin, near Casina Vanvitelliana (see Table 1).

Table 2 shows a comparison between the number of Opisthobranch species previously found in the Fusaro and those reported in the present paper. Eleven species already collected were absent in our samples (see Table 3). As far as *Haminaea hydatis* is concerned, the identity of the species is very probably wrong, because only the shell was used as a diagnostic feature; besides it should be pointed out that no *H. hydatis* was found in our samplings despite the fact that another three *Haminaea* species, including a new one, were collected. Very probably, species such as *Limacia clavigera* and *Okenia elegans* are found accidentally, as they are not typical of lagunar environments, and the same would apply to *Taringa* sp. recorded in the present paper. The absence of species such as *Calliopaea bellula* and *Aeolidiella alderi* is more difficult to explain; both of them had been previously recorded here, and are considered as very common in brackish areas.

	Previous works	Present paper
CEPHALASPIDEA	2	7
ANASPIDEA	0	5
NOTASPIDEA	0	1
SACOGLOSSA	6	4
ARMINACEA	1	1
AEOLIDACEA	5	4
DORIDACEA	6	3
TOTAL SPECIES	20	25

Table 2. Comparison between the number of Opisthobranch species from the Fusaro reported in previous works and in the present work.

PRESENT PAPER	ANOTHER SPECIES PREVIOUSLY RECORDED
Cephalaspidea	
Philine aperta	*Haminaea hydatis* [b]
Philinopsis depicta	
Bulla striata [c]	
Haminaea orbignyana	
Haminaea orteai	
Haminaea fusari	
Akera bullata	
Anaspidea	
Aplysia fasciata	
Aplysia depilans	
Aplysia punctata	
Bursatella leachii	
Notarchus punctatus	
Notaspidea	
Pleurobranchaea meckelii	
Sacoglossa	
Elysia viridis [a]	*Placida viridis* [a]
Ercolania funerea [a]	*Limapontia capitata* [a]
Placida denditrica [a]	*Calliopaea bellula* [a]
Caliphylla mediterranea	
Nudibranchia	
Spurilla neapolitana [a]	*Aeolidiella alderi* [d]
Facelina coronata	*Eubranchus exiguus* [a]
Facelina dubia	*Coryphella pedata* [f]
Favorinus branchialis [a]	
Janolus cristatus [a]	
Polycera quadrilineata [a]	*Polycera hedgpethi* [e]
Polycera dubia [a]	*Polycerella emertoni* [a]
Taringa sp.	*Limacia clavigera* [t]
	Okenia elegans [t]

Table 3. Comparison between the species recorded in this work and in previous ones. Abbreviations: a=Schmekel, 1968; b=Ferro & Russo, 1981; c=Ferro & Russo, 1982; d=Schmekel & Portmann, 1982; e=Cervera *et al.*, 1988 f=Cattaneo-Vietti & Chemello, 1991.

We have not found in our samples the species *Polycera hedgpethi*, an Indo-Pacific species first recorded in the Mediterranean Sea by CERVERA et al. (1988), on the basis of specimens from the Fusaro lagoon. This species is often found as a member of the communities inhabiting ship hulls. This could be the way this species reached the Mediterranean Sea.

Although the number of species recorded in the Fusaro may seem small (25), it is larger than that recorded from other coastal Mediterranean lagoons with similar features (see Table 4). Only the Stagnone di Marsala (Sicily) has a rich Opisthobranch population due to its special features (it extensively communicates with the sea and shows a wide range of habitats), but its specific composition is very different to that of the Fusaro: in Marsala eudoridaceans are a well represented group (CATTANEO-VIETTI & CHEMELLO, 1991). In other Mediterranean lagoons with a well known Opisthobranch fauna (Mar Menor, Sète, Orbetello...) several species have been found. It must also be born in mind that the variable knowledge on the fauna in different geographical areas could account for many of differences in the number of species recorded in Mediterranean lagoons.

To sum up, Opisthobranch fauna from the Fusaro can be considered rich in the number of species, specially if we consider the particularly adverse characteristics of the lagoon, with its quick changes of salinity, temperature and disolved oxygen, all those features considered as limitant to the life. At this point we must consider the great pollution of this coastal lagoon, enhanced by the very slow water interchange with the sea and the high summer temperatures, and the eutrophic processes what occurs during summer time, which reduce dramaticaly the disolved oxygen in the lagoon.

MEDITERRANEAN LAGOONS	N° OF SPECIES
Mar Menor (Spain)	15
Calblanque (Spain)	7
Estany des Peix (Formentera, Spain)	15
Sète (Thau, France)	18
Berre (France)	10
Orbetello (Italy)	13
Marsala (Sicily, Italy)	23
Mar Piccolo (Taranto, Italy)	8
Fusaro (Naples, Italy)	25

Table 4. Number of Opisthobranch species present in several Mediterranean lagoons (data after MARIN, 1988; DANTART *et al.*, 1990; CATTANEO-VIETTI & CHEMELLO, 1992; this work).

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