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SUMMARY

Character analysis is performed based on anatomical information on 95 species of Sacoglossa (Mollusca, Opisthobranchia). Functional and developmental information is included, where available. Phylogenetic analysis to generic level is performed. The shelled Oxynoacea is a monophyletic group containing three families, Volvatellidae, Juliidae and Oxynoidae. The family Cylindrobullidae is excluded from the Sacoglossa, but forms a sister taxon. The non-shelled Placobranchacea is also a monophyletic group composed of two monophyletic superfamilies, Placobranchoidea (= Elysioidea) and Limapontioidea (= Stiligeroidea; = Polybranchoidea). Relationships among most genera included in the Placobranchoidea remain unresolved. The family Boselliidae is retained until further examination of the included species has shown whether it should be included in the Placobranchidae. The Platyhedylidae, comprising the genera *Platyhedyle* and *Gascoignella*, is included in the Placobranchoidea. Of the families included in the Limapontioidea, the 'Polybranchiidae' appears to be paraphyletic, though monophyly could be 'forced' by applying extra weight to four characters. The Hermaeidae forms a monophyletic group as does the Limapontiidae. The latter family may contain two or three subfamilies, but this must await further anatomical studies. The families Alderiidae and Costasiellidae are superfluous, the genera clustering within the Limapontiidae.

1. INTRODUCTION

The opisthobranch order Sacoglossa constitutes an ecologically uniform group; almost all species are specialist herbivores feeding suctorially on the cytoplasm of marine plants. About 200 species have been described, most of which are in the size range of 1–3 cm long. The facts that all shelled sacoglossans feed on one algal genus, *Caulerpa*, and that more than 50% of the species are restricted to diets of siphonalean green algae (Greene 1970; Clark & Busacca 1978; Jensen 1980*a*, 1993*a*), have evoked hypotheses on coevolution of the Sacoglossa and their food plants (Kay 1968; Clark & DeFreese 1987).

The Sacoglossa appears to be a well defined monophyletic group. However, classification within the group is highly unstable (Boettger 1954, 1963; Gascoigne 1976, 1985; Boss 1982; Marcus 1982). The name Sacoglossa was introduced by von Ihering (1876) to encompass the shelled family Oxynoidae (= Lophocercidae) as well as the non-shelled families Elysiidae, Placobranchidae, Polybranchiidae (= Phyllobranchidae; = Caliphyllidae), Hermaeidae, and Limapontiidae because these all have a uniseriate radula and a specialized sac on the ventral surface of the pharynx in which the used radular teeth are accumulated. The same conclusion had been reached by Bergh, who coined the name Ascoglossa (Bergh 1877). Most malacologists, however, did not accept the inclusion of the shelled Oxynoidae in the group (Fischer 1883; Vayssière 1885; Pelseneer 1894, 1906; Thiele 1895; Iredale & O'Donoghue 1923). After some convincing anatomical studies (Pruvot-Fol 1926; Russell 1929), Thiele (1931) reunited the Oxynoidae with the non-shelled families. Later the shelled families Volvatellidae (= Arthessidae) and Juliidae were also transferred to the Sacoglossa (Baba 1961, 1966; Boettger 1963; Kay 1968). The position of the genus *Cylindrobulla* has been widely discussed until the genus *Ascobulla* was separated from *Cylindrobulla* (Marcus & Marcus 1956, 1970; Marcus 1972).

Current classifications have been based on external characters, central nervous system, and to some extent reproductive anatomy (Boettger 1954, 1963; Gascoigne 1976, 1985; Clark & Busacca 1978; Marcus 1982; Schmekel & Portmann 1982). These classifications have not distinguished between ancestral and derived characters. This probably explains some of the discrepancies among them. The objective of this study is to analyse the phylogenetic relationships of the Sacoglossa. In particular it is important to test whether the shelled Sacoglossa is a monophyletic or, as usually assumed, paraphyletic group. Reconstruction of sacoglossan phylogeny will allow testing of hypotheses of coevolution of the Sacoglossa and their siphonalean food plants (Jensen 1996); also hypotheses on biogeographical relations can be tested. Recent studies have analysed a number of characters, particularly of the alimentary system; in these studies several parallelisms related to similarity of diets have been identified

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Table 1. *Species used in character analysis in this study, and the source of origin*

(Species are arranged in accordance with current classification.)

taxon	locality	reference
family Volvatellidae Pilsbry 1895		
Ascobulla ulla (Marcus & Marcus 1970)	Florida	personal observation; Marcus 1972
Ascobulla fischeri (Adams & Angas 1864)	Western Australia	Jensen & Wells 1990
Volvatella cf. *vigourouxi* (Montrouzier 1861)	Japan	Baba 1966
Volvatella laguncula Sowerby 1894	South Africa	Thompson 1979
Volvatella bermudae Clark 1982	Bermuda	Clark 1982*a*
Volvatella ventricosa Jensen & Wells 1990	Western Australia	Jensen & Wells 1990
Family Juliidae E. A. Smith 1885		
Julia japonica Kuroda & Habe 1951	Japan	Kawaguti & Yamasu 1962
Berthelinia limax Kawaguti & Baba 1959	Japan	Baba 1961
Berthelinia caribbea Edmunds 1963	Jamaica Florida	Edmunds 1963; personal observation
Berthelinia babai Burn 1965	Victoria, Australia	personal observation
Berthelinia rottnesti Jensen 1993	Western Australia	Jensen 1993*b*
Family Oxynoidae H. Adams & A. Adams 1854		
Oxynoe antillarum Mörch 1863	Florida, St. Thomas	personal observation
Oxynoe azuropunctata Jensen 1980	Florida	Jensen 1980*b*
Oxynoe viridis (Pease 1861)	Western Australia	Jensen & Wells 1990
Lobiger serradifalci (Calcara 1840)	Mediterranean	Gonor 1961*a*
Lobiger souverbiei Fischer 1856	Florida	personal observation
Lobiger sagamiensis Baba 1952	Hong Kong	Jensen 1993*d*
Lobiger viridis Pease 1863	Fiji	Burn 1966
Roburnella wilsoni (Tate 1889)	Victoria, Australia Western Australia	Burn 1966 Jensen 1993*b*
Family Boselliidae Marcus 1982		
Bosellia mimetica Trinchese 1891	Florida, St. Thomas	personal observation
Family Placobranchidae Rang 1829 (= Elysiidae Forbes & Hanley 1851)		
Placobranchus ocellatus van Hasselt 1824	Thailand, Guam	Jensen 1992*a*
Thuridilla hopei (Verany 1853)	Mediterranean	Jensen 1992*a*
Thuridilla ratna (Marcus 1965)	Thailand, Western Australia	Jensen 1992*a*
Thuridilla decorata (Heller & Thompson 1983)	Red Sea	Heller & Thompson 1983; Jensen 1992*a*
Thuridilla vatae (Risbec 1928)	Guam, Western Australia	Jensen 1992*a*
Thuridilla bayeri (Marcus 1965)	Guam	Jensen 1992*a*
Elysiella pusilla Bergh 1872	Thailand, Guam Western Australia	Jensen 1992*a* Jensen & Wells 1990
Elysiella n.sp.	Darwin Harbour, N.T., Australia	personal observation
Elysia timida Risso 1818	Mediterranean	Jensen 1992*a*

Table 1. (*cont.*)

taxon	locality	reference
Elysia filicauda Jensen & Wells 1990	Western Australia	Jensen & Wells 1990
Elysia australis (Quoy & Gaimard 1832)	Western Australia	Jensen & Wells 1990; Jensen 1992*a*
Elysia chilkensis Eliot 1916	Hong Kong	Jensen 1985, 1993*d*
Elysia leucolegnote Jensen 1990	Hong Kong	Jensen 1990, 1992*a*, 1993*d*
Elysia trisinuata Baba 1949	Hong Kong	Jensen 1985, 1992*a*, 1993*d*
Elysia ornata (Swainson 1840)	Florida, Canary Islands, Thailand, Guam, Western Australia	Jensen 1992*a*
Elysia viridis (Montagu 1804)	U.K., Denmark	personal observation
Elysia maoria Powell 1937	Western Australia New South Wales	Jensen 1993*b* Reid 1964
Elysia expansa (O'Donoghue 1924)	Western Australia	Jensen 1993*b*
Pattyclaya arena (Carlson & Hoff 1977)	Guam	Marcus 1982; Jensen 1992*a*
Pattyclaya brycei Jensen & Wells 1990	Western Australia	Jensen & Wells 1990
Family Polybranchiidae O'Donoghue 1929		
Cyerce antillensis Engel 1927	Florida, St. Thomas	personal observation
Cyerce cristallina (Trinchese 1881)	Mediterranean Jamaica	Thompson 1988 Schmekel & Portmann 1982 Thompson 1977
Cyerce verdeensis Ortea & Templado 1990	Cape Verde Islands	Ortea & Templado 1990
Polybranchia orientalis (Kelaart 1858)	Japan	Baba & Hamatani 1971
Polybranchia viridis (Deshayes 1857)	Jamaica	Thompson 1977
Polybranchia prasina (Bergh 1871)	Philippines	Bergh 1871
Polybranchia westralis Jensen 1993	Western Australia	Jensen 1993*b*
Mourgona germaineae Marcus & Marcus 1970	Florida	personal observation
Mourgona murca Marcus & Marcus 1970	Curaçao	Marcus & Marcus 1970
Mourgona osumi Hamatani 1994	Japan	Hamatani 1994
Caliphylla mediterranea Costa 1867	Mediterranean, Florida	Gascoigne 1979*a* personal observation
Sohgenia palauensis Hamatani 1991	Palau	Hamatani 1991
Family Hermaeidae H. Adams & A. Adams 1854		
Aplysiopsis formosa (Pruvot-Fol 1953)	Florida Canary Islands Azores	Clark 1982*b*, personal observation Ortea *et al.* 1990, personal observation Jensen 1995*b*
Aplysiopsis smithi (Marcus 1961)	California	Gonor 1961*b*; personal observation
Aplysiopsis elegans Deshayes 1839–53	Mediterranean	Schmekel & Portmann 1982
Aplysiopsis orientalis (Baba 1949)	Japan	Baba 1949
Aplysiopsis nigra (Baba 1949)	Japan	Baba 1949
Hermaeopsis variopicta Costa 1869	Mediterranean	Gascoigne 1979*b*; Schmekel & Portmann 1982
Hermaea bifida (Montagu 1815)	U.K., Mediterranean	Gascoigne 1976 Schmekel & Portmann 1982

Table 1. (*cont.*)

taxon	locality	reference
Hermaea cruciata Gould 1870	Florida	Jensen 1993*c*
Hermaea hillae Marcus & Marcus 1967	Mexico	Marcus & Marcus 1967
Hermaea coirala Marcus 1955	Brazil	Marcus 1955
Hermaea evelinemarcusae Jensen 1993	Western Australia	Jensen 1993*b*
Family Costasiellidae Clark 1984		
Costasiella virescens Pruvot-Fol 1951	Mediterranean	Marcus 1982
Costasiella ocellifera (Simroth 1895)	Florida, St. Thomas	personal observation
Costasiella nonatoi Marcus & Marcus 1960	Bermuda Brazil	Clark 1984 Marcus 1982
Costasiella formicaria (Baba 1959)	Japan	Baba 1959
Costasiella illa (Marcus 1965)	Micronesia	Marcus 1965
Costasiella pallida Jensen 1985	Hong Kong	Jensen 1990
Family Limapontiidae Gray 1847 (= Stiligeridae Iredale & O'Donoghue 1923)		
Stiliger cf. *ornatus* Ehrenbergh 1831	Japan	Baba & Hamatani 1970*a*
Stiliger llerai Ortea 1981	Canary Islands	Ortea 1981
Stiliger smaragdinus Baba 1949	Western Australia	Jensen 1993*b*
Stiliger aureomarginatus Jensen 1993	Western Australia	Jensen 1993*b*
Placida dendritica (Alder & Hancock 1843)	Mediterranean Australia Japan Oregon, British Columbia	Schmekel & Portmann 1982 Bleakney 1989; Jensen 1993*b* Bleakney 1989 Bleakney 1990
Placida viridis (Trinchese 1873)	Mediterranean	Gascoigne & Sordi 1980
Placida kingstoni Thompson 1977	Florida	personal observation
Placida daguilarensis Jensen 1990	Hong Kong	Jensen 1990
Olea hansineensis Agersborg 1923	Washington	Gascoigne 1975
Calliopaea bellula d'Orbigny 1837	U.K. Mediterranean	Gascoigne & Todd 1977 Schmekel & Portmann 1982
Calliopaea oophaga Lemche 1974	Denmark	personal observation
Limapontia capitata (Müller 1773)	Denmark	personal observation
Limapontia depressa Alder & Hancock 1862	Denmark	personal observation
Limapontia senestra (Quatrefages 1844)	U.K.	Gascoigne 1956
Ercolania funerea (Costa 1867)	Mediterranean	Schmekel & Portmann 1982
Ercolania gopalai (Rao 1937)	India Hong Kong	Rao 1937 Jensen 1985
Ercolania boodleae (Baba 1938)	Japan	Baba & Hamatani 1970*b*
Ercolania coerulea Trinchese 1892	Mediterranean Hong Kong Florida Western Australia	Schmekel & Portmann 1982 Jensen 1985 personal observation Jensen 1993*b*
Ercolania fuscata (Gould 1870)	Eastern U.S.A.	Gascoigne 1978

Table 1. (*cont.*)

taxon	locality	reference
Ercolania nigra (Lemche 1935)	Denmark	Jensen 1993*c*
Ercolania emarginata Jensen 1985	Hong Kong	Jensen 1985, 1993*d*
Ercolania tentaculata (Eliot 1917)	Hong Kong	Jensen 1985
Ercolania margaritae Burn 1974	Victoria, Australia	Gascoigne 1976
Family Alderiidae Pruvot-Fol 1954		
Alderia modesta (Lovén 1844)	U.K. Denmark	Gascoigne 1976; personal observation
Family Platyhedyliidae Salvini-Plawen 1973		
Platyhedyle denudata Salvini-Plawen 1973	Mediterranean	Wawra 1979, 1988*a*, 1991
Family Gascoignellidae Jensen 1985		
Gascoignella aprica Jensen 1985	Hong Kong	Jensen 1985

(Jensen & Wells 1990; Jensen 1991, 1992*a*, 1993*a*,*b*,*c*,*d*). In this study several other characters are analysed and phylogenetic analysis performed.

Classification should be based on monophyletic groups. In this study a classificatory framework, based on shared derived characters, is proposed. However, many genera are poorly described, and the classification presented here will no doubt need adjustments as more genera and species are described.

2. MATERIALS AND METHODS

Information on 95 species (of which the author has examined 66) currently referred to 31 genera and 12 families of Sacoglossa (see table 1) has been included in this study. This is about half of the described species, and all of the genera for which anatomy has been described. Most of the information has been taken from recent systematic and morphological studies. Some new, unpublished, material has also been included.

Character analysis has been performed by outgroup comparison. As outgroup for determining character polarity various 'tectibranchs', in particular the herbivorous genera *Haminaea* (Bullacea) and *Akera* (Anaspidea), have been used (Rudman 1971, 1978; Morton 1972; Brace 1977; Gosliner 1981, 1991; Jensen 1995*a*). Also, information on the enigmatic genus *Cylindrobulla* has been included (Marcus & Marcus 1970; Jensen 1989, 1995*a*). In some instances sacoglossan characters have been compared to the Heterostropha (Ponder 1991) or even the lower Caenogastropoda (Houbrick 1988; Ponder 1988).

Cladistic analysis has been performed using the programme Hennig86, version 1.5. A 'hypothetical cephalaspid ancestor' was used as outgroup and *Cylindrobulla* was also included in the analysis.

3. CLASSIFICATION

Some recent classifications are shown in table 2. Most classifications have three suborders of shelled Sacoglossa, each containing only one family. Thompson (1976) includes the Volvatellidae and Cylindrobullidae in the suborder Oxynoacea, and Gascoigne (1985) places all shelled sacoglossans in one suborder, Conchoidea. The most controversial classification is that of Boettger (1963). Here the genera with reduced shells are included with the shell-less sacoglossans, and moreover, *Oxynoe* is included with the parapodia-bearing families, and *Lobiger* with the cerata-bearing families. This is based primarily on the organization of the nervous system; *Oxynoe* and *Lobiger*, like the non-shelled sacoglossans, have a short visceral loop, *Oxynoe* with three ganglia, and *Lobiger serradifalci* with only two ganglia. This classification considers the Juliacea paraphyletic, and the shell has been lost twice within the Oxynoacea. Figure 1 is a diagrammatic representation of this classification, which was subsequently adopted by Clark & Busacca (1978), and, with slight modification, by Clark *et al.* (1990). Later studies have shown that the family Lobigeridae is superfluous because a third visceral ganglion is found in other species of *Lobiger* and in *Roburnella* (Burn 1966; Jensen 1985, 1993*b*), and most classifications have only one family with reduced shells, Oxynoidae (see table 2) (Thompson 1988; Jensen & Wells 1990).

Excluding the diphyletic origin of the shell-less Sacoglossa, two hypotheses for the phylogeny of the Sacoglossa remain: (i) the shelled families form a monophyletic clade, as do the non-shelled families (see figure 2); and (ii) the shelled families form a paraphyletic grade leading to the monophyletic, shell-less clade (see figure 3).

Schmekel & Portmann (1982) have constructed a tree, in which the shelled Sacoglossa constitutes a monophyletic group. However, the characters used to unite the three shelled suborders are all plesiomorphies. They also considered the non-shelled Sacoglossa as one monophyletic clade. Unfortunately, loss of plesiomorphies has been used to unite these families in one suborder, Elysiacea. The majority of the characters uniting the shelled sacoglossans are connected to the

Table 2. *Recent classifications of the Sacoglossa*

Boettger 1963	Thompson 1976	Marcus 1982	Schmekel & Portmann 1982	Gascoigne 1985
suborder Juliacea	suborder Juliacea	suborder Volvatellacea	suborder Volvatellacea	suborder Conchoidea
superfamily	family Juliidae	family Volvatellidae	family Volvatellidae	family Volvatellidae
Arthessoidea				
(= Volvatelloidea)				
superfamily Julioidea	suborder Oxynoacea	suborder Juliacea	suborder Juliacea	family Tamanovalvidae
	family Volvatellidae	family Juliidae	family Juliidae	(=Juliidae)
suborder Oxynoacea	family Oxynoidae			family Oxynoidae
superfamily Oxynoidea	family Cylindrobullidae	suborder Oxynoacea	suborder Oxynoacea	suborder Aconchoidea
family Oxynoidae		family Oxynoidae	family Oxynoidae	family Elysiidae
family Elysiidae	suborder Elysiacea			family Polybranchiidae
family Placobranchidae	family Elysiidae	suborder Elysiacea	suborder Elysiacea	family Stiligeridae
superfamily	family Placobranchidae	family Elysiidae	family Elysiidae	
Stiligeroidea	family Polybranchiidae	family Plakobranchidae	family Boselliidae	
family Lobigeridae	family Stiligeridae	family Boselliidae	family Caliphyllidae	
family Polybranchiidae	family Oleidae		family Hermaeidae	
family Oleidae	family Limapontiidae		family Limapontiidae	
family Stiligeridae	suborder			
family Limapontiidae		Polybranchiacea		
	family Caliphyllidae			
		family Polybranchiidae		
		family Hermaeidae		
		family Stiligeridae		
		family Alderiidae		
		suborder Platyhedylacea		
		family Platyhedylidae		

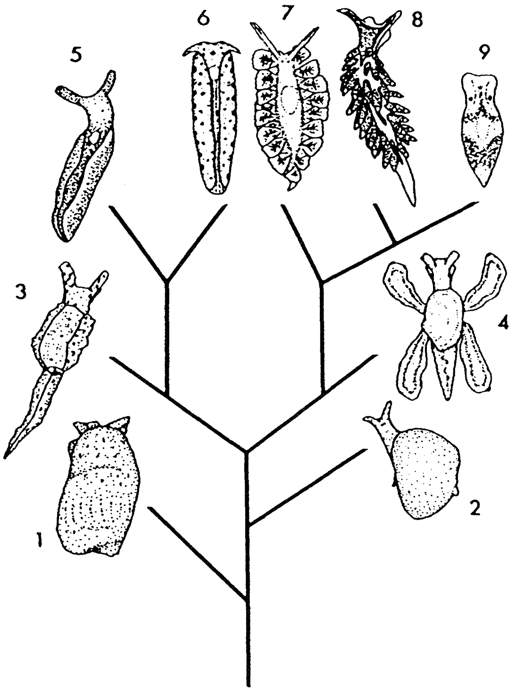

Figure 1. Cladogram based on phylogenetic scheme of Boettger (1963) and Clark & Busacca (1978). 1 Volvatellidae; 2 Juliidae; 3 Oxynoidae; 4 Lobigeridae; 5 Elysiidae; 6 Placobranchidae; 7 Polybranchiidae; 8 Stiligeridae; 9 Limapontiidae.

shell and mantle complex. Most of these also occur in *Cylindrobulla*. Hence they must be considered plesiomorphic within the Sacoglossa (but synapomorphies linking the Cylindrobullidae as a sister group to the Sacoglossa) (Jensen 1995*a*). Only apomorphic characters not related to shell and mantle complex can be used to determine whether the shelled Sacoglossa constitutes a monophyletic or paraphyletic group.

There are a number of other classificatory problems, which have been addressed in various publications (see, for example, Marcus 1982; Clark 1984; Sanders-Esser 1984; Gascoigne 1985; Thompson 1988).

1. Are the monogeneric families Boselliidae, Costasiellidae, and Alderiidae warranted, or could they be accommodated in other families?
2. What is the position of the Platyhedylacea?
3. Are the Polybranchiidae monophyletic?
4. Are the Hermaeidae and Stiligeridae separate families? These questions will all be addressed in this study.

Marcus (1982) listed 22 characters which she considered important for classification of the Sacoglossa. Some of these apply only to certain families, others are useful only at the generic or specific levels. Marcus did not indicate which character states were considered primitive or advanced. Nevertheless, they have been included in this character analysis, indicated by a number prefixed M.

4. NOMENCLATURAL CHANGES

Recent studies have shown that the genus *Placobranchus* should be included in the Elysiidae (Jensen 1992*a*), and that *Limapontia* and *Olea* should be included in the Stiligeridae (Gascoigne 1976, 1985). However, this necessitates some nomenclatural changes.

1. Placobranchidae Rang 1829, precedes Elysiidae

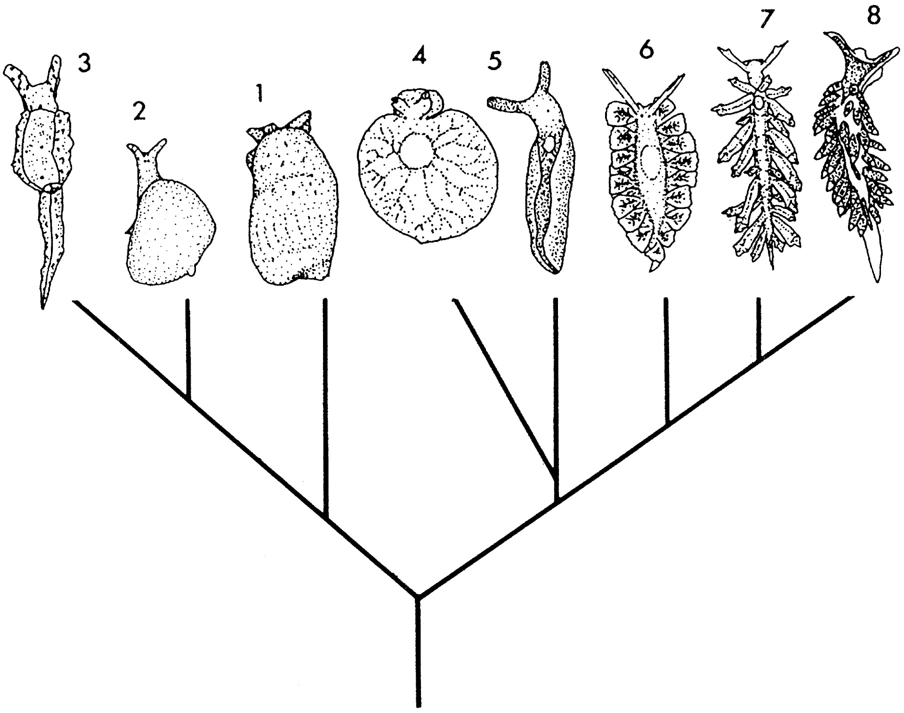

Figure 2. Cladogram depicting the hypothesis that the shelled Sacoglossa are monophyletic, as are the non-shelled Sacoglossa. 1 Volvatellidae; 2 Juliidae; 3 Oxynoidae; 4 Boselliidae; 5 Placobranchidae (= Elysiidae); 6 Polybranchiidae; 7 Hermaeidae; 8 Limapontiidae (= Stiligeridae).

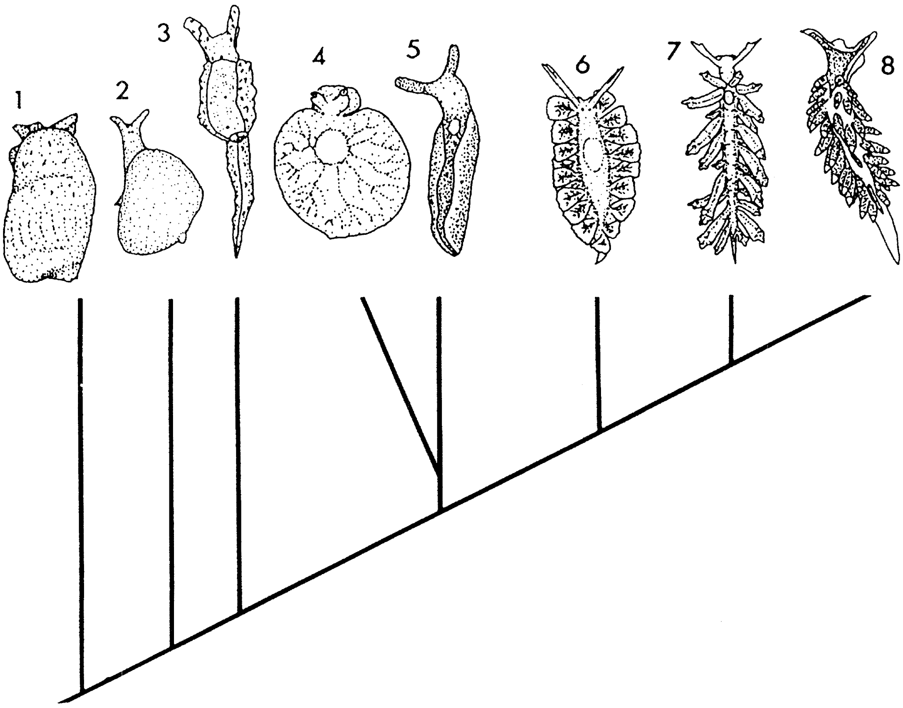

Figure 3. Cladogram depicting the hypothesis that the shelled Sacoglossa are paraphyletic, and the non-shelled Sacoglossa are monophyletic. Numbering as in figure 2.

Forbes & Hanley 1851; hence the family should be renamed Placobranchidae.

2. The oldest family-group name of the genera currently included in the Stiligeridae is – unfortunately – Limapontiidae Gray 1847, which precedes Oleidae Thiele 1931, as well as Stiligeridae Iredale & O'Donoghue 1923. This is unfortunate, because *Limapontia* is the only genus in the cerata-bearing group which does not have cerata!

Concerning names of suborders the law of priority does not apply. Also, names at this level need not be based on generic names. Although the names

Conchoidea and Aconchoidea, as suggested by Gascoigne (1985), are appealingly descriptive, they unfortunately have the suffix -oidea, which should be applied to superfamilies. Hence it is proposed that the suborder of shelled Sacoglossa is named Oxynoacea, as suggested by Odhner (1939), and the non-shelled suborder Placobranchacea, which is an emendation of Elysiacea, also suggested by Odhner (1939).

5. CHARACTER ANALYSIS

(*a*) *External characters*

(i) *Shell (M1)*

The sacoglossan shell is generally thin, lightly calcified, and often has fine fracture lines in live animals. It is covered by a transparent, often yellowish, elastic but strong periostracum, which usually overhangs the shell. In *Ascobulla* and *Volvatella* the shell is relatively large; the animal can be completely contained within the shell. There is a sutural slit and a sutural keel, which is sharp-edged in *Ascobulla*, softly rounded in *Volvatella* (Jensen & Wells 1990). The sutural keel is formed by the reflected inner lip, i.e. it is secreted by the infrapallial lobe. The aperture is narrow posteriorly. In *Oxynoe*, *Lobiger* and *Roburnella* the shell is reduced, covering only the visceral mass. The head can be withdrawn into the shell, but not the long, muscular tail nor the lateral parapodia (Jensen 1993*b*). The aperture is wide. *Berthelinia* and *Julia* differ from all other gastropods by having a bivalved shell. *Berthelinia* has rather thin, fragile shells with a subcentral 'umbo'. *Julia* has thicker, more robust shells with posterior, curved 'umbones' (Kay 1968).

By outgroup comparison the large shell of *Ascobulla* and *Volvatella* is considered plesiomorphic, and the reduced and bivalved shells are apomorphic states. The reduced shell could have arisen by gradual enlargement of the soft parts, whereas the bivalved shell is an innovation. A sutural slit and a sharp-edged sutural keel occur in *Akera* and *Cylindrobulla* (Jensen 1995*a*). In the character matrix (see table 3) it has been listed as apomorphic in *Cylindrobulla* and *Ascobulla*. The shell spout of *Volvatella* appears to be an autapomorphy of the genus.

The Sacoglossa have a paucispiral, sinistral (ultradextral?) protoconch (less than two whorls). In *Ascobulla* the protoconch is located at the bottom of a slightly concave apical area. In *Volvatella* the protoconch is completely hidden in the sunken spire. In both heterostrophy at the transition from protoconch to teleoconch is distinct (see figure 4). In *Oxynoe*, *Lobiger* and *Roburnella* the protoconch is hidden in the sunken spire. In *Oxynoe* and *Roburnella* the shell apex is located posteriorly. In *Lobiger* the apex is towards the left side. In *Julia* and *Berthelinia* the protoconch is distinctly visible, though it may secondarily have broken off in *Julia*.

(ii) *Shell adductor muscles*

In *Ascobulla* and *Volvatella* there is a diagonal shell adductor muscle. Such a muscle occurs also in *Cylindrobulla*. *Akera* has two shell adductor muscles, of which the posterior one, close to the sutural slit, is the largest. The adductor muscle of *Cylindrobulla* is homologous with that of the sacoglossans, based on functional, positional and derivation criteria, and thus is a synapomorphy for these taxa. The adductors of *Akera* are located differently from those of the sacoglossans and, though also derived from the columella muscle, probably are not completely homologous. In

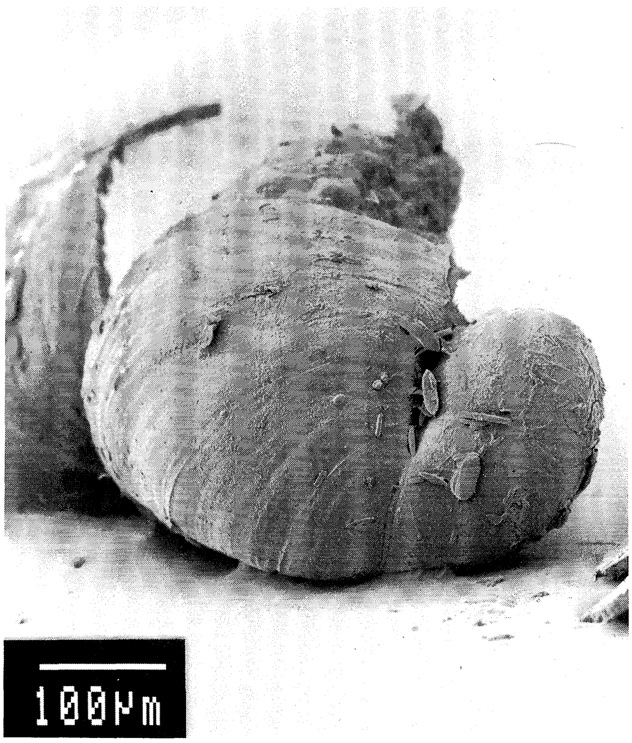

Figure 4. Scanning electron micrograph of protoconch and early teleoconch of *Volvatella ventricosa*.

Berthelinia and *Julia* the shell adductor muscle is transverse and apparently has lost all connection with the columella muscle. This is apomorphic within the Sacoglossa. Species with a reduced shell have apparently lost the shell adductor muscle.

(iii) *Cephalic shield*

Ascobulla has a cephalic shield similar to that of the cephalaspid *Cylichna*. A deep groove separates the left and right side lobes of the shield. The anterior as well as posterior corners are rounded, the posterior ones forming short processes (Hamatani 1969; Jensen & Wells 1990). A similar cephalic shield occurs in *Cylindrobulla* (Marcus & Marcus 1970; Jensen 1989). *Volvatella* does not have a cephalic shield (Baba 1966; Jensen & Wells 1990), and neither do any other sacoglossans. A cephalic shield is an adaptation for burrowing and is weakly developed in several epifaunal Cephalaspidea, for example, *Colpodaspis* and some philinids (Brown 1979; Gosliner 1988). *Ascobulla* and some species of *Volvatella* burrow shallowly, but also venture up among algal assimilators to feed (Thompson 1979; DeFreese 1987; personal observation). *Cylindrobulla* is always found in the sediment (Clark 1994; personal observation). As a cephalic shield occurs in most cephalaspids, its presence has been coded as plesiomorphic (see table 3).

(iv) *Rhinophores (M3, M9)*

Ascobulla is devoid of cephalic processes. *Volvatella* has four cephalic lobes, the length of which differs between species; the anterior ones are longitudinally grooved. Based on this groove and the position of the eyes and penial opening, the anterior lobes are considered homologous to the rhinophores of the remaining Sacoglossa. Innervation has not been studied in the Volvatellidae. The remaining shelled Sacoglossa have long, distinctly rolled rhinophores. This is also seen in numerous non-shelled species. A number of genera, presently referred to the family Polybranchiidae, have bifid rhinophores. In the genera presently referred to the Hermaeidae the rhinophores have a distal non-rolled 'flap', possibly the remains of a bifid tip. Several species of Limapontiidae, have simple or slightly flattened rhinophores, and a few species completely lack rhinophores. In some sacoglossans branches of the digestive gland enter the rhinophores, though this does not seem to have phylogenetic importance, as it varies within one genus.

The homology of the sacoglossan rhinophores has been widely debated (Pruvot-Fol 1932; Hoffmann 1939; Salvini-Plawen 1990; Huber 1993). Cephalic tentacles with chemosensory function are associated with epifaunal habits, whereas the chemosensory epithelium (= Hancock's organ) of burrowing opisthobranchs (Cephalaspidea) is hidden in a groove below the cephalic shield. In the various opisthobranch orders different sections of the Hancock's organ have been included with part of the cephalic shield into chemosensory tentacles. Those innervated by the rhinophoral nerve have been called rhinophores, those innervated by the labio-tentacular nerve are the oral tentacles. In the non-shelled Sacoglossa, which are the only ones in which innervation has been studied, the rhinophores are innervated by the rhinophoral nerve as well as a branch of the labio-tentacular nerve (Russell 1929; Huber 1993). This has been used to claim that the sacoglossan rhinophores are not homologous to those of other opisthobranchs, and should be given a different name (Salvini-Plawen 1990). As the Aplysiomorpha, Acochlidiacea and the Notaspidea-Nudibranchia clade most likely evolved separately from different cephalaspid ancestors (without rhinophores), complete homology of the rhinophores of these groups cannot be inferred, although they are only innervated by the rhinophoral nerve. Hence there is no need for a new name for the sacoglossan rhinophores. In most sacoglossans the rhinophores are in front of the eyes, and there are no oral tentacles. In the genera of the Polybranchiidae and in most species of *Costasiella* the eyes are between the rhinophores, and most polybranchiids also have oral tentacles. Most of the above mentioned opisthobranch groups have oral tentacles, which are innervated by the labio-tentacular nerve. Unfortunately innervation has not been studied in any of the polybranchiid species.

The folded anterior cephalic processes of *Volvatella* are most likely homologous with the rhinophores of the remaining Sacoglossa. Bifid rhinophores appear to be a synapomorphy for the genera of the family Polybranchiidae. They probably arose from rolled rhinophores. Simple rhinophores probably arose by reduction from rolled rhinophores. Lack of rhinophores in shell-less sacoglossans is almost certainly secondary (for example, *Alderia*, *Limapontia*).

(v) *Oral tentacles*

Oral tentacles are absent in most sacoglossans. However, most genera of the Polybranchiidae have oral tentacles, which are usually rolled. The genus *Caliphylla* has very short oral tentacles, often recorded as absent (Gascoigne 1979*a*). Oral tentacles are also present in the limapontiid *Ercolania tentaculata* (Eliot 1917; Jensen 1985). In *Berthelinia* and *Lobiger* the anterior fold of the rhinophores continues down onto the anterior surface of the head (Gonor 1961*a*; personal observation). A similar arrangement occurs in *Volvatella* (personal observation). This indicates that oral tentacles could have arisen independently (from such lobes) several times within the Sacoglossa. It may also explain why a branch of the labio-tentacular nerve is found in the rhinophores.

(vi) *Eyes (M11)*

The eyes of *Ascobulla* and *Volvatella* are located laterally, underneath the cephalic lobes (Jensen & Wells 1990). In *Oxynoe*, *Lobiger* and *Roburnella* the eyes are also lateral, behind the rhinophores (Gonor 1961*a*; Jensen & Wells 1990; Jensen 1993*b*). In *Berthelinia* and *Julia* the eyes are mid-dorsal on a small protuberance behind the rhinophores (Baba 1961; Kawaguti & Yamasu 1962). Median eyes on a small protuberance are also seen in *Placobranchus* (Jensen 1992*a*), and median eyes, though not elevated, occur in most polybranchiids and in all species of *Costasiella* (Marcus 1982; Clark 1984). Lateral eyes are plesiomorphic, and median eyes evolved in parallel at least three times within the Sacoglossa.

(vii) *Foot (M4, M5)*

The foot of *Ascobulla* and *Volvatella* is short i.e. it does not extend beyond the shell (Jensen & Wells 1990). The tail is rounded. In *Berthelinia* and *Julia* the foot is also rather short, but has a pointed tail (Baba 1961; Kawaguti & Yamasu 1962). *Oxynoe*, *Lobiger* and *Roburnella* have long, broad, muscular tails behind the visceral mass (Jensen 1985, 1993*b*; Jensen & Wells 1990). The foot of the Oxynoidae and Juliidae is capable of longitudinal folding (Jensen 1993*b*). In *Volvatella*, *Bosellia* and *Elysiella* the foot sole is adapted for strong adhesion to the substrate (Marcus 1973; Jensen & Wells 1990). In *Cyerce* the foot sole is divided by a transverse groove (Bergh 1871). In many placobranchoids there is also a groove extending part or all the way across the foot sole (Jensen 1992*a*). This groove functions as a spawn groove (see below). Whether the transverse groove of *Cyerce* is homologous to that of the placobranchids is not clear. In *Gascoignella* and *Platyhedyle* the foot is very short, not extending under the visceral mass (Salvini-Plawen 1973; Jensen 1985). This strongly resembles the arrangement of the Acochlidiacea, to which *Platyhedyle* was originally allocated (Salvini-Plawen 1973).

In most sacoglossans the anterior margin of the foot forms distinct pedal lobes used for grasping or probing. Distinct pedal tentacles occur in very few sacoglossans, e.g. *Costasiella virescens* and *Ercolania tentaculata* (Marcus 1982; Jensen 1985), and probably evolved separately in these species.

(viii) *Gill*

The gill of the shelled Sacoglossa is composed of many parallel, simple, ciliated lamellae. These are folds of the epithelium of the mantle roof covering the surface of the kidney. This differs considerably from the plicate gill found in most other shelled opisthobranchs. A lamellate gill on the surface of the kidney occurs also in *Cylindrobulla*, and is another synapomorphy of the Cylindrobullidae and the Sacoglossa (Jensen 1995*a*). Behind the gill are dorsal and ventral ciliated ridges, which continue into the upper whorls. The ciliated ridges have apparently been lost in *Lobiger* (Gonor 1961*a*). A plicate gill occurs in *Acteon* and the Diaphanidae as well as most Bullomorpha and Aplysiomorpha (Brace 1977; Jensen 1995*a*). In *Ringicula buccinea* (Brocchi) the gill is a simple longitudinal lamella on the surface of the kidney (Fretter 1960), but other species of *Ringicula* have 'normal' plicate gills extending from the edge of the kidney (Gosliner 1981). Whether the sacoglossan gill has evolved independently or only after secondary loss of a plicate gill is impossible to determine (Jensen 1995*a*).

(ix) *Osphradium*

An osphradium is often mentioned as a small 'button-like' structure lying in front of the gill, near the adductor muscle (Marcus & Marcus 1956; Baba 1961, 1966). However, its ultrastructure has not been investigated.

(x) *Mantle glands*

In *Ascobulla* and *Volvatella* there is one or two narrow bands of white mucus-secreting glands posterior to the gill. These glands continue into the visceral whorls along the ciliated band (Jensen 1995*a*). A similar band of glands is found behind the gill in the bivalved sacoglossans (Baba 1961; Jensen 1993*b*). In *Oxynoe*, *Lobiger* and *Roburnella* there is a triangular patch of similar white glands distal to the gill (Jensen & Wells 1990; Jensen 1993*b*). Glandular cells accompanying the ciliated band into a pallial caecum are found in several cephalaspideans, for example, *Acteon* (Fretter & Graham 1954), thus their presence is a plesiomorphic character. The reduction to a triangular patch is apomorphic.

(xi) *Infrapallial lobe*

In *Ascobulla* and *Volvatella* there is a long, thin infrapallial lobe, in some species bearing a row of small, regularly spaced, transparent glands. These glands – like corresponding glands along the posterior mantle margin – exude a milky white substance when the animal is disturbed. Similar glands occur in the infrapallial lobe of *Cylindrobulla*. The infrapallial lobe may also contain branches of the digestive gland (Jensen 1995*a*). The 'left mantle lobe' of the Juliidae is probably a modified infrapallial lobe.

(xii) *Ciliated spawn groove*

In *Ascobulla* and *Volvatella*, and also in *Berthelinia* and *Julia*, a ciliated groove extends from the female genital papilla to the mouth area, passing just below the penial opening. In the Juliidae its distal part is covered by an epidermal flap (Baba 1961, 1966; Jensen 1993*b*). Schmekel & Portmann (1982) mention a groove running only to the penial opening of Mediterranean oxynoids. This has not been observed in any other species; *Roburnella* has a groove like that of the Volvatellidae (Jensen 1993*b*), and a groove is absent in *Oxynoe viridis* and *O. azuropunctata* (personal observation). The spawn groove may be homologous to the external sperm groove in cephalaspids, but has a different function in the Sacoglossa. A ciliated sperm groove occurs also in several Heterostropha, which have an external penis, and this character could be considered a plesiomorphy of the entire Heterobranchia (Ponder 1991). Many cerithioid gastropods have a spawn groove to the pedal 'ovipositor' (Houbrick 1988). A ciliated groove from the female aperture has also been described in several basal Pulmonata, e.g. *Onchidium* (Jensen 1992*b*). If the ciliated groove of the shelled Sacoglossa is derived from a sperm groove, the fact that it extends to the mouth area would indicate derivation from cephalaspids with an anterior penis. However, the functional explanation is that the outermost layer of the egg mass is produced by gland cells in the mouth area. Thus homology cannot be unequivocally established.

In the Placobranchoidea there is a ciliated groove running ventrally from the anus/ female aperture and more or less across the anterior end of the foot sole. This groove is also used to guide the egg ribbon into a spiral shape during spawning (Reid 1964; personal observation), and may be derived from the spawn groove of the shelled species.

(xiii) *Parapodia*

Parapodia are absent in *Ascobulla*, *Volvatella* and the bivalved sacoglossans. In *Oxynoe* a pair of fleshy parapodia covers the shell almost completely (Jensen 1980*b*; Jensen & Wells 1990). In *Lobiger* four spatulate parapodia may in part cover the shell, or they may be extended laterally, displaying a brightly coloured marginal band (Gonor 1961*a*; Jensen 1985). These parapodial lobes are in no way related to the cerata of the limapontioid families, though this has sometimes been implied (Boettger 1954; Thompson 1988). In *Roburnella* low parapodia extend along the margins of the shell, and also four elongated, usually rolled, parapodial lobes extend dorsally or laterally (Burn 1966; Jensen 1993*b*). The parapodia of the Oxynoidae seem to be derived solely from pedal tissues. In the shell-less Sacoglossa lateral, wing-like parapodia are characteristic of the family Placobranchidae. However, in these species the parapodia are apparently composed of a pallial and visceral portion as well as a pedal portion, and parts of the digestive and reproductive systems extend into the parapodia (Jensen 1992*a*). *Elysiella* is characterized by having parapodia which do not extend to the tip of the tail (Jensen & Wells 1990). Parapodia occur in many cephalaspids and probably evolved several times in parallel within the Opisthobranchia, and even within the Sacoglossa, i.e. the parapodia of the Oxynoidae have evolved independently of the placobranchid parapodia.

(xiv) *Dorsal lamellae*

In some placobranchids the dorsal surface is densely folded longitudinally (*Placobranchus*) or transversely (*Pattyclaya*). These folds should not be confused with the dorsal vessels (see below); they contain tubules of the digestive gland (Marcus 1982; Jensen 1992*a*). These lamellae are autapomorphies evolved independently in the two genera.

(xv) *Cerata (M2, M9, M10)*

The cerata of the sacoglossans evolved independently of those of the Nudibranchia. In the Polybranchiidae the cerata are more or less flattened, leaflike, and have a marginal row of large, subepidermal gland cells (see figure 5). In *Cyerce* and *Sohgenia* the digestive gland does not enter the cerata, though in *C. verdeensis* there is a branch of the digestive gland at the base of the cerata (Ortea & Templado 1990). The remaining genera of the Polybranchiidae have a branching tubule of the digestive gland in the cerata. The Hermaeidae, Alderiidae, Costasiellidae and Limapontiidae have more or less fusiform cerata, each containing a more or less branching tubule of the digestive gland. In the latter two families the albumen gland may also send a branch into the cerata (Gascoigne 1976; Marcus 1982). Cerata have been secondarily lost in *Limapontia*.

(xvi) *Pericardium (M7)*

In the shelled Sacoglossa the pericardium is located dorsally in the mantle cavity, in front of the gill (and kidney). This is considered plesiomorphic. In the shell-less Sacoglossa the pericardium forms a more or less conspicuous hump on the dorsal surface of the body. In some species (placobranchoids as well as limapontioids) there is an elongate extension of the pericardium containing the kidney; this is then called the renopericardial prominence (Marcus 1980, 1982; Clark 1982*b*; Jensen & Wells 1990). An elongate renopericardium probably derived from an oval pericardium.

(xvii) *Heart (M19)*

In some species of *Volvatella* the heart appears to be more or less transverse within the mantle cavity, at least when viewed in live animals (Jensen & Wells 1990). In all other sacoglossans the heart is completely detorted. A heart has apparently been secondarily lost in a few sacoglossans (*Alderia modesta* and *Placida viridis*) (Evans 1953; Gascoigne & Sordi 1980). However, this is most likely an adaptation to intertidal and/or estuarine living, and has no phylogenetic significance.

(xviii) *Dorsal vessels (M8)*

In most Placobranchoidea a number of tubular, more or less branching vessels enter the renopericardium dorsally. Dorsal vessels are absent in *Platyhedyle*, *Gascoignella* and *Placobranchus*; the latter may be a secondary loss (Jensen 1992*a*). Dorsal vessels also occur in a few limapontioids, for example, *Aplysiopsis*, *Cyerce*, *Costasiella*. The function of these vessels is unknown, but it has been suggested that they form a 'negative gill' in species having functional kleptoplasts i.e. transport oxygen away from the tissues (Clark *et al.* 1981). Their association with pericardium and kidney indicate excretory or osmoregulatory function in addition to circulatory function. In the cladistic analysis it appeared that dorsal vessels are synapomorphic only in the higher Placobranchidae, and have evolved in parallel in *Bosellia* and several limapontioid genera (see table 4).

(xix) *Position of anus (M6)*

In the shelled Sacoglossa the anus is located on a papilla facing posteriorly on the surface of the digestive gland, at the floor of the mantle cavity (Baba 1961, 1966; Jensen 1991). In the shell-less Sacoglossa the anus is often closely in front of the pericardium, but it may also be lateral, above or below the cerata, sometimes on a conspicuous papilla. In the Placobranchoidea the anus is usually at the top of the ciliated groove on the right, anterior side of the body, sometimes on a low papilla. In *Alderia* the long anal papilla is at the posterior end of the body. As a transformation series, and even polarity, is difficult to determine for this character (Jensen 1991), only two states were coded into the data matrix (see tables 3 and 4), though the apomorphic state in the Juliidae (on the right side of a laterally compressed visceral mass), Placobranchoidea (in or at an anterior groove) and Polybranchiidae (on papilla below cerata) are not

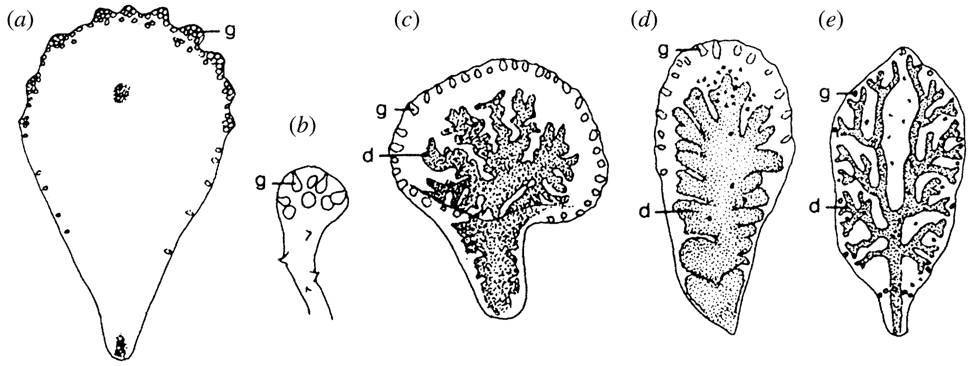

Figure 5. Outline of cerata and digestive gland tubules in genera of the Polybranchiidae. (*a*) *Cyerce antillensis* (redrawn from Marcus & Marcus 1970). (*b*) *Sohgenia palauensis* (redrawn from Hamatani 1991). (*c*) *Polybranchia westralis* (redrawn from Jensen 1993*b*). (*d*) *Mourgona germaineae* (redrawn from Jensen 1984). (*e*) *Caliphylla mediterranea* (redrawn from Gascoigne 1979*a*). Abbreviations: d digestive gland tubule; g marginal, defensive glands.

identical. In this connection it should be mentioned that in the Placobranchoidea (except *Placobranchus*) the anal and oviducal openings are close together, whereas in the Limapontioidea they are separated by some distance.

(xx) *Melanin-black vesicle (M18)*

A black vesicle found close to the kidney opening has been described in a few sacoglossans, notably limapontiids (Gascoigne & Sigurdsson 1977; Jensen 1993*b*). This has been interpreted as the remains of the larval kidney, and thus a plesiomorphic character linking the Sacoglossa with some Heterostropha, in which a corresponding black organ is found (Ponder 1991). In the Sacoglossa as well as the Heterostropha this structure occurs mainly in small species, and could be considered paedomorphic. However, ultrastructural studies are necessary to determine the homology of this structure in the various groups. It has no phylogenetic importance within the Sacoglossa.

(*b*) *Alimentary system*

(i) *Buccal apparatus (M12–14)*

Characters of the buccal apparatus and their polarity have been discussed previously (Jensen 1992*a*, 1993*c*). It is in this character complex that the most important synapomorphies of the Sacoglossa are found. The sacoglossan 'innovations' are no doubt related to increasing feeding efficiency (Jensen 1993*a*,*c*,*d*), and have been instrumental for speciation within the group. It is also in this character complex that the most noteworthy parallelisms are found i.e. blade-shaped teeth, elongation of ascus-muscle, shape of ascus, 'detachment' of posterior ascus-muscle, and loss or enlargement of pharyngeal pouches (Jensen 1993*a*,*c*).

One of the sacoglossan innovations is the retention of all radular teeth throughout the life of the animal. Even the teeth formed in the metamorphosis-competent larvae are retained, though they may be difficult to find in species having a dense heap of teeth in the ascus (Gascoigne 1977; Jensen 1980*b*). The very first teeth in which no cusps have been formed are called preradular teeth (Pruvot-Fol 1926; Edmunds 1963; Hamatani 1969). Often a number of 'transitional' teeth with incomplete cusps are found between the preradular teeth and the fully formed teeth of the adult shape (Gascoigne 1979*a*,*b*). The preradular teeth are formed before any suctorial feeding, and their shape is therefore independent of the structure of the food of the benthic juvenile. The transitional teeth are probably formed while the newly settled larvae make the first attempts at penetrating algal cell walls, and cusp-shape gradually changes into that of the adult animal. The phylogenetic value of the preradular teeth has not been discussed previously. In the non-shelled Sacoglossa several small cuspless teeth are found (see figure 6*d*–*f*). These preradular teeth can be interpreted as tooth bases, because they are smaller than or equal in length to the base of the first transitional or juvenile teeth. This is considered plesiomorphic within the Sacoglossa. In the shelled Sacoglossa only one preradular tooth is formed (see figure 6*a*–*c*). This tooth is a long rod with no morphological resemblance to either bases or cusps of the adult teeth. Also, it is much longer (three to fourfold) than the bases of the first juvenile or transitional teeth. As tooth size generally increases with age in the Sacoglossa, this long, rod-shaped preradular tooth cannot be interpreted as a cuspless tooth, and it must be considered a synapomorphy of the Oxynoacea. Preradular teeth are not found in *Cylindrobulla* (personal observation).

Another sacoglossan innovation is the formation of an epithelium-lined ascus-sac in which the used teeth are accumulated. This structure is probably formed as a consequence of retaining all the radular teeth. In the Sacoglossa the odontophore is attached to the pharynx wall ventrally and also, in part, laterally (Jensen 1993*c*). In *Cylindrobulla* the odontophore is attached to the posterior, and in part lateral, pharynx wall, and the long descending limb of the radula is attached to the ventral surface of the odontophore. No epithelium-lined ascus-sac is formed for the accumulation of used teeth. The heap of discarded teeth found in some specimens of *Cylindrobulla* appears to lie loose between the muscle-strands of the odontophore, and most likely these teeth are periodically shed (Jensen 1995*a*). In *Volvatella* the descending limb of the radula is short and almost vertical. The ascus-sac forms a small boss on the antero-ventral surface of the pharynx, and the posterior

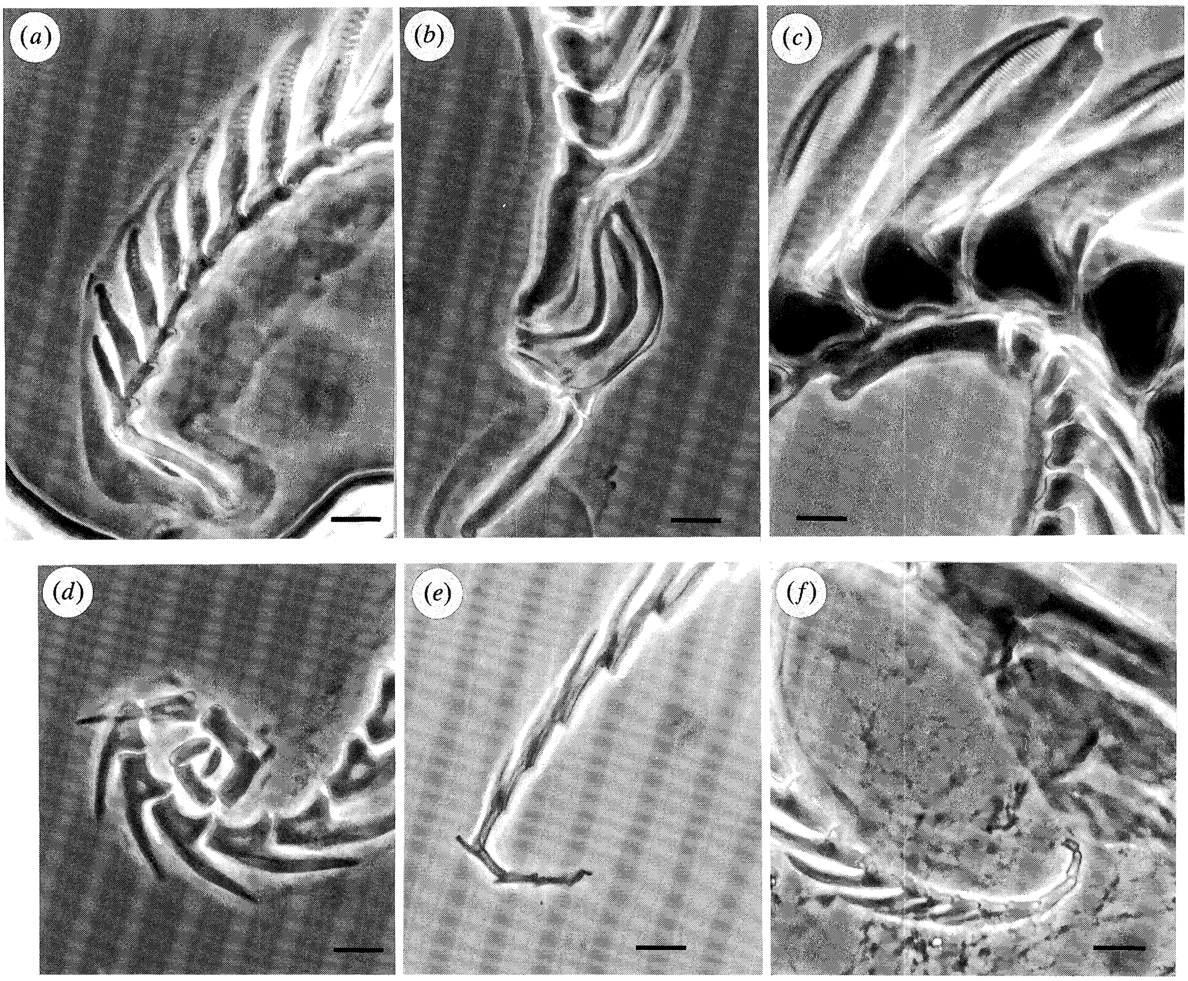

Figure 6. Light micrographs of preradular teeth of sacoglossans. (*a*) *Volvatella bermudae*; 1 rod-shaped preradular tooth and no transitional teeth. (*b*) *Oxynoe antillarum*; 1 rod-shaped preradular tooth and 2–3 transitional teeth. (*c*) *Berthelinia babai*; 1 rod-shaped preradular tooth and no transitional teeth. (*d*) *Elysia subornata*; 3 preradular teeth and 2–3 transitional teeth. (*e*) *Mourgona germaineae*; 3 preradular teeth and 2 transitional teeth. (*f*) *Placida kingstoni*; 3 preradular teeth and 3–4 transitional teeth. Scale lines: 10 μm.

end of the radula (the ascus) forms an almost straight row (personal observation). In *Ascobulla* the descending limb of the radula is longer and has a more horizontal orientation (Jensen 1993*c*). As the ascus-sac is a 'new' structure, not found in *Cylindrobulla* or more distantly related outgroups, a short ascus-sac containing the used teeth in a straight row must be considered plesiomorphic within the Sacoglossa. The most likely transformation series is from a straight row to a spiral, and then, as even more teeth are accumulated, to a heap. However, it is also possible that the two apomorphic character states developed independently from the plesiomorphic state. In the cladistic analysis, unfortunately, this character comes out as apomorphic (heap) in the first node. This is probably because the heap of teeth found in *Cylindrobulla* has been coded as a heap (see table 4), though it is not enclosed in an ascus-sac.

Three types of radular teeth have been described previously (Jensen 1993*a*). The most likely transformation series is from triangular to blade-shaped, which has occurred three times in parallel, and from blade-shaped to sabot-shaped, which has apparently occurred twice within the cerata-bearing genera (Jensen 1993*a*,*c*). The teeth of a few species cannot be fitted into any of these categories; they are short and conical, with more or less pointed tips. These teeth have been called chisel-shaped (Baba & Hamatani 1970*a*; Jensen 1985). These teeth could have developed from triangular as well as blade-shaped teeth. In this study they have been coded as having evolved from blade-shaped teeth (see table 3).

(ii) *Oral tube*

In most sacoglossans the oral tube is a simple, more or less folded structure with glands opening into the lumen. In the Oxynoidae, however, there are some modifications. In *Oxynoe* there are two enormous, muscular bulges in front of the pharynx. These bulges are everted during feeding (Jensen 1980*b*). In *Lobiger* there are a pair of muscular pads attached to the anterior end of the pharynx (Burn 1966; Jensen 1993*d*). Although feeding has not been observed in detail, it must be assumed that they have similar function. The oral tube appears to be eversible in most shelled Sacoglossa. As observations on feeding in the 'primitive' non-shelled sacoglossans are rare, it is not known whether an eversible oral tube occurs in any of these genera. However, none of the more advanced Placobranchacea have an eversible oral tube. Hence this character appears to be an Oxynoacean synapomorphy.

(iii) *Salivary glands*

The salivary glands of most sacoglossans are composed of long, glandular tubules, a salivary duct, and sometimes a reservoir immediately before entering the pharynx (next to the oesophagus). In the Oxynoidae the shape of the salivary glands seems to be of diagnostic value at the generic level: in *Oxynoe* the glands are tassel-shaped with widened ducts (Burn 1966; Jensen 1980*b*); in *Lobiger* they are shaped like small clusters of grapes (Burn 1966; Jensen 1985); and in *Roburnella* they are flattened lobes (Burn 1966; Jensen 1993*b*).

(iv) *Oesophageal pouch (M14)*

An oesophageal pouch occurs in many, if not most sacoglossans. It differs in size as well as muscular and glandular components, but only in the Oxynoidae does it seem to have diagnostic value. In *Roburnella* it is of the 'usual' (plesiomorphic), spherical shape (Burn 1966; Jensen 1993*b*); in *Oxynoe* it is flattened, elongate, and with numerous glandular(?) branchlets (Burn 1966; Jensen 1980*b*); in *Lobiger* it is elongate with broad (glandular?) lobes along one side (Burn 1966). Several polybranchiids also have elongate, but apparently non-glandular oesophageal pouches.

(v) *Digestive gland in mantle/ dorsal lamellae/ cerata (M9)*

Some species of *Volvatella*, and also *Berthelinia*, have tubules of the digestive gland in the mantle fold (Clark 1982*a*; Jensen & Wells 1990; Jensen 1991). This is seen as a precursor for the acquisition of functional kleptoplasty (Clark *et al.* 1990). *Placobranchus* and *Pattyclaya* have tubules of the digestive gland extending into their longitudinal or transversal dorsal lamellae. Most limapontioid sacoglossans have branches of the digestive gland extending into the cerata. This all indicates a general trend of extending the surface area of the digestive gland, but also the pattern of branching indicates the extent of functional kleptoplasty, many narrow tubules harbouring long-term functional chloroplasts, and fewer, wide-lumened tubules indicating short-term or even non-functional chloroplasts. The finely branched network of digestive gland tubules probably evolved in parallel in both non-shelled clades. The capability to sustain functional kleptoplasts, however, was probably present in the placobranchacean ancestor. *Limapontia*, *Platyhedyle* and *Gascoignella*, which do not have any cerata, only have short lobules on the long, wide, main ducts of the digestive gland.

(*c*) **Nervous system (*M15*)**

The pleural ganglia are fused with the cerebral ganglia in all sacoglossans. Also, the ganglionic ring is postpharyngeal (Russell 1929). This appears to be the case also in *Cylindrobulla* (Jensen 1989). In *Ascobulla*, *Volvatella*, *Julia* and *Berthelinia* the visceral chain is long and contains at least three ganglia (subintestinal, abdominal, and supraintestinal) (Baba 1961, 1966; Jensen & Wells 1990). There may be an additional parietal ganglion in some species of *Volvatella* (Burn 1966) and *Ascobulla* (Marcus & Marcus 1956). In all other sacoglossans the visceral chain is short, and contains two or three ganglia (Boettger 1963). The subintestinal ganglion may have fused with the abdominal ganglion several times in parallel, but in most cases where only two ganglia have been reported, the subintestinal ganglion actually sits on top of the abdominal one. Thus a third visceral ganglion has been described from some species of *Lobiger* (Burn 1966), several polybranchiids and hermaeids (Gascoigne 1978, 1979*a*,*b*). Only in the Limapontiidae is the subintestinal ganglion completely fused with the abdominal ganglion (Gascoigne 1978).

(*d*) ***Reproductive system***

(i) *Penis (M17)*

A cuticular penial stylet is found in many sacoglossans. As a stylet occurs in *Ascobulla* as well as *Volvatella* (though not in all species), its presence must be considered plesiomorphic within the Sacoglossa. The penis of *Cylindrobulla* is unarmed. Hence a penial stylet may be a sacoglossan synapomorphy, though penial armature has evolved (and been lost) many times within the Opisthobranchia (Hyman 1967; Thompson 1976). In this study presence of a penial stylet has been coded as apomorphic (see table 3). A penial stylet is also prominent in many non-shelled sacoglossans, e.g. *Placobranchus*, *Bosellia*, *Cyerce*. Most limapontiids have a short, curved penial stylet (Gascoigne 1974, 1976; Jensen 1986*b*, 1993*b*; Bleakney 1988, 1989). *Caliphylla mediterranea* has a long, whip-like extension, called a 'flagellum', at the tip of the penis, armed with a minute stylet (Gascoigne 1979*a*). Minute stylets have also been described for some species of *Polybranchia*, whereas *Cyerce* and *Mourgona* have long, almost straight penial stylets (Bergh 1871; Marcus & Marcus 1970; Gascoigne 1974; Jensen 1993*b*). Penial armature is very rare in *Elysia* spp. (Marcus 1980; Jensen 1986*a*, 1992*a*).

The Sacoglossa have an eversible penis located laterally on the right side. The penial opening is usually below the right eye, or rhinophore. There is a closed vas deferens. In the Volvatellidae, and also in *Cylindrobulla*, the vas deferens is in part embedded in the body wall. The penis itself is rather big, muscular and capable of great extension in the shelled sacoglossans, and also in most non-shelled species. In these species only the tip of the penis is actually inserted during copulation. In the Limapontiidae the penis is usually short and conical. This is considered apomorphic.

(ii) *Prostate gland (M20)*

In the shelled sacoglossans the prostate is simply a glandular part of the vas deferens; in the Placobranchidae the prostate is highly branched throughout

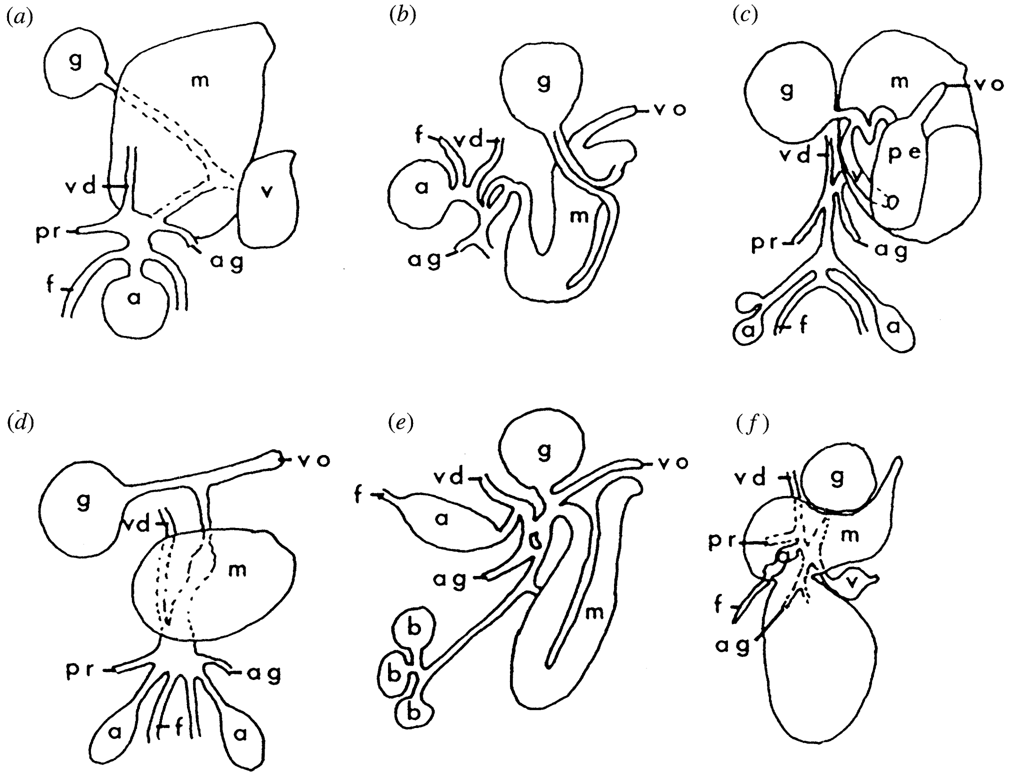

Figure 7. Schematic drawings of anterior reproductive systems (penis excluded) of some sacoglossans with a vaginal opening. (*a*) *Thuridilla hopei* (redrawn from Jensen 1992*a*). (*b*) *Elysia viridis* (redrawn from Schmekel & Portmann 1982). (*c*) *Elysia leucolegnote* (redrawn from Jensen 1990). (*d*) *Elysia australis* (redrawn from Jensen & Wells 1990). (*e*) *Cyerce cristallina* (redrawn from Schmekel & Portmann 1982). (*f*) *Stiliger aureomarginatus* (redrawn from Jensen 1993*b*). Abbreviations: a ampulla; ag duct to albumen gland; b secondary copulatory bursae; f duct to hermaphrodite follicles; g genital receptacle; m mucus gland; pe pericardium; pr duct to prostate gland; v vagina; vd vas deferens; vo vaginal opening.

the body, and in the limapontioids it consists of a few lobes in front of or ventral to the mucus gland (Sanders-Esser 1984; Jensen 1992*a*, 1993*b*). In *Bosellia* the prostate is only slightly branched (Marcus 1973), and in *Platyhedyle* the prostate is an unbranched tubule (Wawra 1991). There is some conflicting information on the prostate in the Polybranchiidae. Schmekel & Portmann (1982) report a highly branched prostate in *Cyerce* and *Caliphylla*, whereas Gascoigne (1979*a*) mentions a compact gland composed of numerous acini in *Caliphylla*. The non-separated prostate of the shelled species is the plesiomorphic state, but whether the highly branched and lobular prostates developed independently from this, or one developed from the other is not clear.

(iii) *Female genital papilla*

In the Oxynoacea there is a large, muscular, female genital papilla, which usually contains the opening of the duct from the genital receptacle as well as the oviducal opening. Also, copulation in these species is definitely through this papilla (personal observation), whereas copulation through the oviducal opening has not been observed in any non-shelled sacoglossan, though it has often been inferred (e.g. Gascoigne 1976, 1979*a*). In these species the female genital opening is not on a distinct papilla. The large papilla in the shelled species may be a 'remnant' of a closed pallial gonoduct as seen in many prosobranchs. If this is the case, then it is a plesiomorphy. However, if it is not a prosobranch inheritance, then it is another synapomorphy for the shelled Sacoglossa. Ponder (1991) lists a simple, slit-like genital opening as plesiomorphic within the Heterobranchia. A large genital papilla is seen also in the diaphanid *Newnesia antarctica* Smith, 1902 (Jensen 1995*a*). However, in this species it also contains an excurrent sperm groove. Hence complete homology with the female papilla of the Oxynoacea cannot be inferred.

(iv) *Vaginal opening (M16)*

Many non-shelled sacoglossans have a separate vaginal opening. If this opening continues with a separate duct conducting the allosperm to the fertilization region (or seminal receptacle), the system is called triaulic (Ghiselin 1966; Gascoigne 1976). However, the arrangement of the vaginal opening, duct, and vagina differs widely among the sacoglossans, and these structures are probably not homologous in the various families, or possibly genera. *Thuridilla* spp. have a dorsal vagina (see figure 7*a*), usually with a separate opening (Jensen 1992*a*). In, for example, *Elysia viridis* the latero-dorsal vaginal opening connects to the mucus gland (see figure 7*b*) (Sanders-Esser 1984), whereas in *E. leucolegnote* it connects through the pericardium to the duct of the genital receptacle (see figure 7*c*) (Jensen 1990), and in *E. australis* the vaginal duct connects directly to the genital receptacle (see figure 7*d*) (Jensen & Wells 1990). In *Cyerce* the vaginal duct connects to the duct of the genital receptacle (see figure 7*e*) (Sanders-Esser 1984). In the limapontiids with a separate vaginal opening, this connects to the seminal receptacle (see figure 7*f*), where present, or to the fertilization region (Gascoigne 1976). Obviously this character cannot be used phylogenetically until homologies have been identified.

(v) *Mucus gland (M20)*

In most sacoglossans the mucus gland is a more or less inflated lump anteriorly in the body. The encapsulated eggs pass through the mucus gland. In *Caliphylla*, *Hermaeopsis* and *Hermaea* it consists of two limbs, a transversal and a longitudinal one (Gascoigne 1979*a*,*b*). In *Aplysiopsis* it is very long, and its lumen functionally separated in two (Gonor 1961*b*; Jensen 1995*b*). In the Limapontiidae it is U-shaped (Gascoigne 1976, 1978). In *Platyhedyle* and *Gascoignella* it is an elongate tube (Jensen 1985; Wawra 1991).

(vi) *Albumen gland (M20)*

The eggs do not traverse the albumen gland in the Sacoglossa. In the shelled Sacoglossa the albumen gland is apparently closely associated with the mucus gland (Baba 1961, 1966; Sanders-Esser 1984). This is also the case in most cephalaspids (Gosliner 1981). In the placobranchoid genera the albumen gland consists of a system of highly branched tubules (Sanders-Esser 1984; Jensen 1992*a*). In the limapontioids the albumen gland may also be tubules following the digestive gland tubules, sometimes even into the cerata. In a few limapontioids, e.g. *Hermaea*, the albumen gland is composed of small clusters of acini connected by narrow ductules, but again these ductules follow the branches of the digestive gland, though not into the cerata (Gascoigne 1976; Sanders-Esser 1984).

(vii) *Hermaphrodite ampulla (M20)*

In most sacoglossans the hermaphrodite ampulla is a widened, more or less coiled, part of the hermaphrodite duct. In the Placobranchidae the ampulla is separate from the hermaphrodite duct, and there may be one, two or more small, spherical ampullae (Jensen 1992*a*). *Placobranchus*, *Pattyclaya* and several species of *Elysia* use many anterior follicles for ampullae, whereas *Thuridilla* and *Elysiella* both have a large median ampulla. A single ampulla apparently also occurs in several species presently referred to *Elysia*, e.g. *E. viridis* and *E. patina*. The problems with this character have been discussed previously (Jensen 1992*a*). The separation of the ampulla is a synapomorphy of the family Placobranchidae.

(viii) *Genital receptacle (M20)*

The structure called genital receptacle in the Sacoglossa (Gascoigne 1976, 1978, 1979*a*,*b*; Jensen 1992*a*, 1993*b*) corresponds to the structure called bursa copulatrix, spermatheca, or gametolytic sac in other opisthobranchs (Ghiselin 1966; Rudman 1978; Gosliner 1981). In no sacoglossan has it been observed that sperm from copulation is actually directed into this vesicle; it usually contains an amorphous or granular bolus of various surplus reproductive products (albumen, yolk, prostatic secretion, excess sperm etc.). In most shelled Sacoglossa the genital receptacle opens by a separate duct to the inside of the female genital papilla, but is not connected to the fertilization region (Baba 1961, 1966). Hence it is difficult to determine whether a triaulic system is plesiomorphic. In most non-shelled sacoglossans the connection of the genital receptacle with the reproductive system has moved from the female opening to a more interior position, but its function is still that of collecting 'surplus' reproductive materials (Gascoigne 1976). In some limapontioids the genital receptacle has a distal as well as a proximal connection (Schmekel & Portmann 1982).

(ix) *Seminal receptacle (M20)*

The generalized hermaphroditic, euthyneuran reproductive system has two vesicles for storing allosperm: a distal bursa copulatrix, receiving the sperm at copulation, and a proximal seminal receptacle, storing the sperm oriented with the heads towards (and embedded in) the wall (Ghiselin 1966). A special structure containing oriented sperm has not been described for any shelled Sacoglossa (Sanders-Esser 1984; personal observation). However, many species have a sperm-filled vesicle near the female genital papilla (Baba 1961; Sanders-Esser 1984; personal observation), which may or may not connect to the duct of the genital receptacle. This is usually called a seminal receptacle, though it most likely functions as a bursa copulatrix. Most genera of cerata-bearing sacoglossans have a true seminal receptacle containing oriented sperm (Sanders-Esser 1984). In the limapontiids this is also the functional bursa copulatrix (Gascoigne 1976). A seminal receptacle does not occur in the Placobranchidae. Instead one or more secondary copulatory bursae may be developed (Jensen 1992*a*). Similar arrangements may occur in *Bosellia* and *Cyerce*, though different types of connections have been described for these genera (Marcus 1973; Sanders-Esser 1984).

It is difficult to identify a plesiomorphic character state for this character. In most cases it has not been stated whether the structure called seminal receptacle actually contained oriented sperm; it has just been called a seminal receptacle, if it had a proximal connection, and/or if a genital receptacle was also present. This is also how the character has been treated in the present study. Ponder (1991) stipulates that early heterobranchs had lost the seminal receptacle. It would seem that a true seminal receptacle with oriented sperm, as in caenogastropods, was the plesiomorphic state, unless this has evolved in parallel in some rather advanced sacoglossans and in other opisthobranchs. Some cerithiids have two seminal receptacles, only one of which contains oriented sperm (Houbrick 1988).

The development of secondary copulatory bursae could have occurred in parallel in several sacoglossan groups.

(x) *Shape of egg mass*

Gascoigne & Wallis (1982) recognized three types of egg masses in the Sacoglossa: (i) a regular spiral; (ii) an irregular 'sausage' or string; and (iii) a flat, lenticular egg mass. Type (i) occurs in most placobranchoids and many limapontioids, type (ii) in oxynoids and many limapontioids, and type (iii) in *Berthelinia* and some small limapontiids (personal observation). The egg masses of *Ascobulla* and *Volvatella* are slightly different; a string is embedded zig-zag-wise within a thick mucus coat, some of which may be secreted by the mouth area and/or the ciliated spawn groove (Jensen & Wells 1990; personal observation). This has been considered plesiomorphic in the present study (see table 3). The spiral egg mass occurs in the majority of sacoglossans and is here considered apomorphic. The irregular 'sausage-shaped' egg mass occurs mostly in species feeding on filamentous algae, and may represent a modification of the regular spiral, which just follows an irregular substrate. It occurs in species without a spawn groove (Limapontioidea and Oxynoidae). The lenticular egg mass is probably not a separate group, but just indicative of small size of the parent animal. The arrangement of eggs within this mass will reveal whether it originates from a bivalved sacoglossan or from a small limapontiid. In the latter case the eggs will be arranged in a helix within the mass (personal observation).

(xi) *Extra-capsular yolk*

In some sacoglossans, notably placobranchids, the eggs are more or less surrounded by a granular mass, often brightly coloured (Clark *et al.* 1979; Boucher 1983; Thompson & Salghetti-Drioli 1984; Jensen 1990). Extra-capsular yolk has also been described in the Chromodorididae (Nudibranchia) (Boucher 1983), but no doubt this is a homoplasy. The question is whether it is a synapomorphy of the Placobranchoidea, the non-shelled sacoglossans, or whether it has developed in parallel within several genera. *Bosellia* has discrete clumps of extra-capsular yolk (Fernandez-Ovies & Ortea 1986). This is also seen in *Elysia maoria*, *E. gordanae* Thompson & Jaklin 1988, *E. ornata* and *E. atroviridis* Baba 1955 (Reid 1964; Jensen 1985; Thompson & Jaklin 1988; K. Jensen, unpublished data). *E. subornata* Verrill 1901, *E. expansa* and *Thuridilla* spp. have a more or less continuous string of extra-capsular yolk (Clark *et al.* 1979; Boucher 1983; Thompson & Salghetti-Drioli 1984; personal observation). In some species the colour of the extra-capsular yolk is the same as the embryonic yolk; in others it is different (Heller & Thompson 1983; Thompson & Jaklin 1988). It is not known where the extra-capsular yolk is produced, hence it is not at the present time possible to determine the phylogenetic importance of the different types of extra-capsular yolk. In the character matrix only absence or presence has been recorded (see table 4).

(*e*) *Other characters*

(i) *Development type (M21)*

Three types of development are usually distinguished in the Opisthobranchia: (i) planktotrophic (free-swimming, feeding veliger, long planktonic stage); (ii) lecithotrophic (free-swimming, non-feeding veliger, short planktonic phase); and (iii) direct development (no planktonic stage) (Thompson 1976). In most opisthobranchs there is an important modification of the third type, because actually a veliger larva is formed within the capsule; only metamorphosis takes place immediately before hatching (Bouchet 1989). All three types of development occur within all three groups of Sacoglossa. The genera of the Limapontiidae, however, have planktotrophic development, except *Limapontia senestra* which has direct development, but without the formation of an intracapsular veliger (Gascoigne 1956; Clark & Jensen 1981). This can probably be explained by the secondary loss in the Limapontiidae of the capability to produce lecithotrophic veligers. Apart from this, development type cannot be used for phylogenetic analysis.

(ii) *Chromosome number (M22)*

Karyological studies have been performed on very few sacoglossans (Mancino & Sordi 1965; Burch & Natarajan 1967). From this it appears that the normal chromosome number is $n = 17$. Only *Bosellia mimetica* differs from this ($n = 7$). This was the main reason for creating the family Boselliidae (Marcus 1982). However, none of the other species of *Bosellia* have been examined. Thus it is not known whether this is a specific or a generic (and thus familial) character.

(iii) *Sperm ultrastructure*

Unfortunately this has not been studied on a systematical basis in the Sacoglossa. Only one published transmission electron micrograph exists of the sperm of a sacoglossan, namely *Elysia australis* (Healy 1993).

6. PHYLOGENY

The characters used in cladistic analysis and their polarity have been listed in table 3. The corresponding character matrix is presented in table 4. Because it was *a priori* suspected that the genus *Elysia* would be paraphyletic (see Jensen 1992*a*), all included species of this genus were at first included in the computer analysis. However, this yielded more than 2000 equally parsimonious trees (overflow of computer RAM). Instead four species of *Elysia* with different morphology were selected for inclusion. Further resolution of the Placobranchidae was subsequently attempted by a separate analysis (see below). Cladistic analysis using Hennig86-algorithms m* and bb* for the data of table 4, gave 196 equally parsimonious trees, a tree-length of 168 steps, and consistency and retention indices of 0.38 and 0.75, respectively. The strict consensus tree (Hennig86-command nelsen) showed a low degree of resolution; the shelled families were unresolved and possibly paraphyletic, and in the monophyletic, non-

Table 3. *Character analysis for the Sacoglossa*

character	plesiomorphic	apomorphic
1. shell	present 0	absent 1
2. shell	univalved 0	bivalved 1
3. shell size	covering whole body 0	reduced 1
4. sharp-edged sutural keel	absent 0	present 1
5. shell adductor muscle	absent 0	present 1
6. plicate gill	present 0	absent 1
7. lamellate gill	absent 0	present 1
8. cephalic shield	present 0	absent 1
9. rhinophores	absent 0	present 1
10. shape of rhinophores	rolled/ folded 0	flattened/simple 1
11. tips of rhinophores	simple 0	bifid 1; with short flap 2
12. oral tentacles	absent 0	present 1
13. eyes	lateral 0	admedian 1
14. transverse groove anteriorly on right side	absent 0	present 1
15. parapodia	absent 0	present 1
16. origin of parapodia	pedal 0	pallial/visceral 1
17. cerata	absent 0	present 1
18. cerata	no digestive gland 0	with digestive gland 1
19. shape of cerata	fusiform 0	flat 1
20. pericardium	in mantle cavity 0	oval 1 elongate 2 absent 3
21. dorsal vessels	absent 0	present 1
22. number of vessels	$\leqslant 4$ pairs 0	> 4 pairs 1
23. anus	dorsal 0	lateral 1
24. pharyngeal pouch	absent 0	present 1
25. shape of pharyngeal pouch	short collar 0	large 1 paired 2
26. epithelium-lined ascus-sac	absent 0	present 1
27. length of ascus-muscle	short 0	long 1
28. attachment of ascus-muscle	attached 0	posteriorly free 1
29. position of ascus	internal 0	external 1
30. shape of ascus	straight 0	spiral 1 heap 2
31. oral tube	non-eversible 0	eversible 1
32. radular teeth	triangular 0	blade-shaped 1 chisel-shaped 2 sabot-shaped 3
33. denticulation	bilateral 0	unilateral 1 medial 2 absent 3
34. tips of teeth	simple 0	bifid 1
35. lateral flanges	absent 0	present 1
36. preradular teeth	absent 0	present 1
37. first preradular	very short 0	long rod 1
38. digestive gland	solid 0	long main tubules 1 short main tubules 2
39. visceral loop	long 0	short 1
40. number of visceral ganglia	$>$ three 0	three 1 two 2
41. penis	long 0	short 1
42. penial stylet	absent 0	present 1
43. vas deferens	embedded in body wall 0	free 1
44. female genital papilla	absent 0	present 1
45. female opening	far from anus 0	close to anus 1
46. prostate	part of vas deferens 0	separate 1
47. prostate	short lobes 0	highly branched 1
48. ampulla	part of duct 0	separate 1
49. seminal receptacle	present 0	absent 1
50. albumen gland	solid 0	following digestive gland 1
51. spawn	‘clump’ 0	spiral 1 ‘sausage’ 2
52. extra-capsular yolk	absent 0	present 1

Table 4. *Character matrix for cladistic analysis of the Sacoglossa*

(Characters and polarity are listed in table 3. ? denotes missing data and – that the character is not applicable for the taxon in question.)

character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
taxon																																																				
ancestor	0	0	0	0	0	0	0	0	0	–	–	0	0	0	0	–	0	–	–	0	0	–	0	0	–	0	–	–	–	–	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0
Cylindrobulla	0	0	0	1	1	1	1	0	0	–	–	0	0	0	0	–	0	–	–	0	0	–	0	0	–	0	–	–	0	2	?	0	0	0	0	0	–	0	?	?	1	0	0	0	0	0	–	0	?	?	?	?
Ascobulla	0	0	0	1	1	1	1	0	0	–	–	0	0	0	0	–	0	–	–	0	0	–	0	1	0	1	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	–	0	0	0	0	0
Volvatella	0	0	0	0	1	1	1	1	0	–	–	0	0	0	0	–	0	–	–	0	0	–	0	1	1	1	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	–	0	0	0	0	0
Oxynoe	0	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	–	–	0	0	–	0	1	0	1	1	0	0	0	1	1	0	0	1	1	1	0	1	1	0	0	1	1	0	0	–	0	0	0	2	0
Lobiger	0	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	–	–	0	0	–	0	1	1	1	1	0	1	2	1	1	0	1	0	?	?	0	1	1	?	0	1	1	0	0	–	0	?	0	2	0
Roburnella	0	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	–	–	0	0	–	0	1	0	1	1	0	0	2	1	1	0	1	1	?	?	0	1	1	1	0	1	1	0	0	–	0	?	0	?	?
Julia	0	1	0	0	1	1	1	1	1	0	0	0	1	0	0	–	0	–	–	0	0	–	1	1	2	1	1	1	1	1	?	1	0	?	?	?	?	0	0	1	?	0	1	1	0	0	–	0	?	0	0	0
Berthelinia	0	1	0	0	1	1	1	1	1	0	0	0	1	0	0	–	0	–	–	0	0	–	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	0	1	1	1	0	0	–	0	0	0	0	0
Bosellia	1	–	–	–	–	1	0	1	1	0	0	0	0	1	0	–	0	–	–	1	1	0	1	1	1	1	0	0	0	1	0	0	0	0	0	1	0	2	1	1	1	1	1	0	1	1	0	0	1	1	1	1
Placobranchus	1	–	–	–	–	1	0	1	1	0	0	0	1	1	1	1	0	–	–	1	0	–	0	1	0	1	0	0	0	2	?	0	0	0	0	1	0	2	1	1	0	1	1	0	0	1	1	1	1	1	2	0
Thuridilla	1	–	–	–	–	1	0	1	1	0	0	0	0	1	1	1	0	–	–	1	1	0	1	1	0	1	0	0	0	1	?	0	0	0	0	1	0	2	1	1	0	0	1	0	1	1	1	1	1	1	1	1
Elysiella	1	–	–	–	–	1	0	1	1	0	0	0	0	1	1	1	0	–	–	2	1	1	1	0	–	1	1	0	1	2	0	0	1	0	0	1	0	2	1	1	0	1	1	0	1	1	1	1	1	1	1	1
Pattyclaya	1	–	–	–	–	1	0	1	1	0	0	0	0	1	1	1	0	–	–	2	1	1	1	0	–	1	1	0	1	0	0	1	2	0	0	1	0	2	1	1	0	0	1	0	1	1	1	1	1	1	?	?
Elysia timida	1	–	–	–	–	1	0	1	1	0	0	0	0	1	1	1	0	–	–	1	1	0	1	0	–	1	1	0	1	2	0	1	2	0	1	1	0	2	1	1	0	0	1	0	1	1	1	1	1	1	1	1
E. australis	1	–	–	–	–	1	0	1	1	0	0	0	0	1	1	1	0	–	–	1	1	0	1	0	–	1	1	0	1	2	0	1	2	0	0	1	0	2	1	1	0	0	1	0	1	1	1	1	1	1	1	0
E. ornata	1	–	–	–	–	1	0	1	1	0	0	0	0	1	1	1	0	–	–	1	1	0	1	0	–	1	0	0	1	2	0	1	3	0	0	1	0	2	1	1	0	0	1	0	1	1	1	1	1	1	1	1
E. expansa	1	–	–	–	–	1	0	1	1	0	0	0	0	1	1	1	0	–	–	2	1	1	1	0	–	1	1	0	1	0	0	1	2	0	0	1	0	2	1	1	0	0	1	0	1	1	1	1	1	1	1	1
Platyhedyle	1	–	–	–	–	1	0	1	0	–	–	0	0	?	0	–	0	–	–	1	0	–	1	0	–	1	?	?	0	2	?	?	?	0	?	?	?	?	1	1	?	1	1	0	1	1	0	0	?	1	?	?
Gascoignella	1	–	–	–	–	1	0	1	0	–	–	0	0	1	0	–	0	–	–	1	0	–	1	0	–	1	1	0	0	2	0	2	3	0	0	?	?	1	1	1	1	1	1	0	1	1	0	0	?	?	2	0
Cyerce	1	–	–	–	–	1	0	1	1	0	1	1	1	0	0	–	1	0	1	1	1	0	0	1	1	1	0	0	0	2	?	0	0	0	0	1	0	0	1	1	?	1	1	0	0	1	0	0	1	?	1	0
Sohgenia	1	–	–	–	–	1	0	1	1	0	1	0	0	0	0	–	1	0	1	1	0	–	0	1	?	?	?	?	?	2	?	0	0	0	0	?	?	?	?	?	?	0	?	0	0	?	?	?	?	?	?	?
Polybranchia	1	–	–	–	–	1	0	1	1	0	1	1	1	0	0	–	1	1	1	1	0	–	1	1	1	1	1	1	1	1	?	0	0	0	0	1	0	1	1	?	0	1	1	0	0	1	0	0	?	1	?	?
Mourgona	1	–	–	–	–	1	0	1	1	0	1	1	1	0	0	–	1	1	1	1	1	–	1	1	0	1	1	1	1	2	0	0	0	0	0	1	0	1	1	?	0	1	1	0	0	1	0	0	?	1	2	0
Caliphylla	1	–	–	–	–	1	0	1	1	0	1	1	0	0	0	–	1	1	1	1	0	–	1	1	1	1	1	1	1	1	0	1	3	0	0	1	0	1	1	1	0	1	1	0	0	1	0	0	0	1	2	0
Hermaeopsis	1	–	–	–	–	1	0	1	1	0	2	0	0	0	0	–	1	1	0	1	0	–	0	0	–	1	1	1	1	1	?	1	3	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	1	?	?
Hermaea	1	–	–	–	–	1	0	1	1	0	2	0	0	0	0	–	1	1	0	1	0	–	0	0	–	1	1	1	1	1	0	1	0	0	1	1	0	1	1	2	0	0	1	0	0	1	0	0	0	1	2	0
Aplysiopsis	1	–	–	–	–	1	0	1	1	0	2	0	0	0	0	–	1	1	0	2	1	1	0	0	–	1	1	1	1	1	0	3	0	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	1	1	2	0
Costasiella	1	–	–	–	–	1	0	1	1	1	0	0	1	0	0	–	1	1	0	1	1	0	0	1	0	1	0	1	1	2	0	1	3	0	0	1	0	1	1	1	0	1	1	0	0	1	0	0	0	1	1	0
Placida	1	–	–	–	–	1	0	1	1	0	0	0	0	0	0	–	1	1	0	1	0	–	0	0	–	1	1	1	1	1	0	1	2	0	0	1	0	1	1	2	1	1	1	0	0	1	0	0	0	1	2	0
Stiliger	1	–	–	–	–	1	0	1	1	0	0	0	0	0	0	–	1	1	0	1	0	–	0	0	–	1	0	1	1	2	0	1	3	0	0	1	0	1	1	2	1	0	1	0	0	1	0	1	0	1	2	0
Calliopaea	1	–	–	–	–	1	0	1	1	1	0	0	0	0	0	–	1	1	0	1	0	–	0	0	–	1	0	1	1	0	0	2	3	0	0	1	0	1	1	2	1	1	1	0	0	1	0	0	0	1	1	0
Olea	1	–	–	–	–	1	0	1	1	1	0	0	0	0	0	–	1	1	0	1	0	–	0	0	–	1	0	0	0	0	0	?	3	0	0	1	0	1	1	2	1	1	1	0	0	1	0	0	0	1	?	0
Alderia	1	–	–	–	–	1	0	1	0	–	–	0	0	0	0	–	1	1	0	3	0	–	0	0	–	1	0	1	1	2	0	3	3	0	0	1	0	1	1	2	1	1	1	0	0	1	0	0	0	1	2	0
Ercolania	1	–	–	–	–	1	0	1	1	1	0	0	0	0	0	–	1	1	0	2	0	–	0	0	–	1	0	1	1	2	0	3	3	0	0	1	0	1	1	2	1	1	1	0	0	1	0	0	0	1	2	0
Limapontia	1	–	–	–	–	1	0	1	1	1	0	0	0	0	0	–	0	–	–	1	0	–	0	0	–	1	0	1	1	2	0	3	3	0	0	1	0	1	1	2	1	1	1	0	0	1	0	0	0	1	2	0

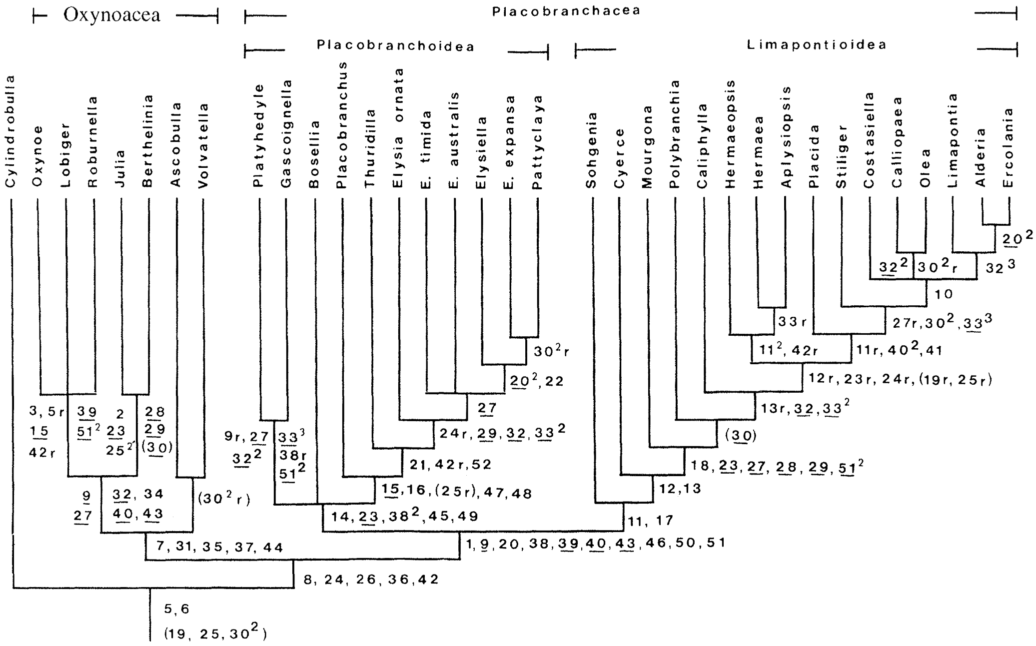

Figure 8. Phylogenetic relationship of the genera of the Sacoglossa. Strict consensus tree from eight equally parsimonious trees of length 176 steps; consistency and retention indices were 0.39 and 0.77 respectively. Characters and their polarity are shown in table 3, and the corresponding character matrix is given in table 4. Characters 14, 44 and 48 were given a weight of 3. Internodal length only signifies the space needed to accommodate the synapomorphies. Numbers correspond to character numbers of table 3; underlined numbers are homoplasies, superscripts denote apomorphic state of multistate characters, and r is reversal.

shelled Sacoglossa the cerata-bearing genera were also highly unresolved; *Platyhedyle* and *Gascoignella* were included in this unresolved group. By applying a weight of only 2 to either character 44 (female genital papilla) or 31 (eversible oral tube) the number of trees decreased to 56 and the shelled Oxynoacea resolved as a monophyletic group; tree-length increased to 169 steps and tree-statistics remained unchanged. By consecutively applying weights to characters uniting the currently accepted families and superfamilies (14, 44, 45, 47, 48), a preferred tree was obtained, which required the minimum amount of manipulation with maximum resolution (see figure 8). This tree is a strict consensus tree from eight equally parsimonious trees of length 176 steps; a weight of 3 was applied to only three characters (14, 44 and 48); consistency and retention indices were 0.39 and 0.77 respectively. This tree supports the hypothesis that the Oxynoacea are monophyletic as in figure 2. Also, the division of the non-shelled Sacoglossa into two monophyletic groups is supported. This division was actually apparent even in the unweighted consensus tree, and the diphyletic origin of the non-shelled Sacoglossa can thus be rejected.

The preferred tree configuration (see figure 8) has four unresolved trichotomies, namely the genera of the Oxynoidae, the base of the Placobranchoidea, within the genus *Elysia* (as expected), and near the top of the Limapontiidae. These will be discussed below. The preferred tree configuration appears very 'robust'; it was obtained from many different combinations of applying extra weight, unordering and deleting problematic characters. The low consistency index indicates a high degree of homoplasy. This and other possible tree configurations will be discussed below.

Three characters, 19, 25 and 30, give problems in the analysis; in spite of their coding in the matrix, they come out as apomorphic in the outgroup. As none of the prerequisites for these characters (i.e. cerata, pharyngeal pouch, ascus) are present in the outgroup, this appears unacceptable, and they have been labelled in parenthesis in figure 8. Neither deleting nor applying extra weight to character 19 changes the preferred tree configuration. Deleting character 25 decreases the number of equally parsimonious trees to four, resolving the Oxynoidae. Deleting character 30, however, increases the number of trees to 147, and many branches are unresolved; unordering character 30 produces 22 equally parsimonious trees, and the Placobranchacea are highly unresolved.

(*a*) *Monophyly of the order*

The monophyly of the Sacoglossa has not been questioned for many years (but see Pruvot-Fol 1929 and Risbec 1930 for discussions on the subject). The only problem seems to be whether the monogeneric family Cylindrobullidae should be included (Marcus 1982; Mikkelsen 1993). *Cylindrobulla* no doubt stands in a sister group relationship with the Sacoglossa (Jensen 1995*a*). It shares a number of synapomorphies, especially in shell and mantle-complex characters (4, 5, 7 of table 3), but it lacks the most important synapomorphies, those of the alimentary system (24–38 of table 3). The teeth of its descending limb do not descend into a pocket on the ventral surface of the pharynx, and the used teeth are not stored in a thinwalled ascus.

Cladistic analysis showed that the Sacoglossa forms a monophyletic group, not including *Cylindrobulla* (see figure 8). If extra weight (5) was applied to the characters assumed to be synapomorphies of *Cylindrobulla* and *Ascobulla* (other character weights as noted above for preferred tree configuration), the former was included in the Volvatellidae (tree statistics: length 204 steps, consistency index 43, retention index 79, four equally parsimonious trees). However, the Volvatellidae then became the most highly derived taxon within the monophyletic Oxynoacea. The same configuration for the Oxynoacea was obtained, if the extra weight of characters 14, 44 and 48 was removed. This is a highly unlikely configuration. Clearly it is most parsimonious to exclude *Cylindrobulla* from the Sacoglossa, though it may mean that a monogeneric order will have to be erected for the Cylindrobullidae; the name Cylindrobullacea is here suggested.

(*b*) *Monophyly of the Oxynoacea*

Until recently, anatomy had only been described for a few species, and still the functional organization of the reproductive system is largely unknown. As mentioned, characters pertaining to shell and mantle-complex cannot be used to elucidate sacoglossan phylogeny. Cladistic analysis using default weight (1) for all characters yielded a totally unresolved, and possibly paraphyletic, Oxynoacea. As mentioned above, monophyly could be obtained by applying a weight of 2 to just one character. Paraphyly was almost impossible to obtain with any degree of resolution in either shelled or non-shelled sacoglossans. Hence the monophyly of the Oxynoacea is well supported. The most important synapomorphies are: the eversible oral tube (31), the long, rod-shaped preradular tooth (37), and the large female genital papilla (44) (see figure 8). The fact that all shelled sacoglossans feed exclusively on *Caulerpa* may also be a 'good' synapomorphy, because the 'primitive' non-shelled sacoglossans apparently feed on Udoteaceae (see below).

(i) *Status of the Volvatellidae*

The Volvatellidae are very 'primitive' even within the opisthobranch clade (see below). Apparently there are no synapomorphies for the family. *Volvatella* and *Ascobulla* have all of the sacoglossan and oxynoacean synapomorphies plus some generic autapomorphies. The shell (periostracum) and mantle fold may be orange or green, but the head-foot is usually unpigmented. Some species of *Volvatella* have branches of the digestive gland in the mantle fold (Clark 1982*a*; Jensen & Wells 1990). It is possible that more detailed studies of the reproductive system of these genera might yield some familial synapomorphies. If no other shelled sacoglossans were known, it would be easy to include *Cylindrobulla* in the family Volvatellidae. It should be noted that *Volvatella* is characterized by several autapomorphies, whereas no 'good' autapomorphies have been described for *Ascobulla*. A cephalic shield was apparently lost in the sacoglossan ancestor (see figure 8). This indicates that the sacoglossan ancestor was not burrowing and more closely resembled *Volvatella* than *Ascobulla*. The occurrence of a cephalic shield in the latter genus must then be interpreted as a reversal in connection with burrowing habits (DeFreese 1987). The separate oesophageal glands of *A. fischeri* (Jensen & Wells 1990) may be a generic autapomorphy, but other species need examination.

(ii) *Status of Oxynoidae and Juliidae*

The other two families of the Oxynoacea are distinctly separated by a series of synapomorphies (see figure 8). Blade-shaped teeth apparently developed in parallel to those of the Placobranchidae, and also those of the Hermaeidae and Limapontiidae. The bifid tips of the radular teeth in some Oxynoidae as well as some Juliidae indicate that the blade-shaped teeth in these two families are homologous. This would not be the case, if the Oxynoacea was a paraphyletic grade, unless these two families were indeed a clade within the grade. The rolled rhinophores apparently also developed in parallel to those of the non-shelled sacoglossans. However, in this case the common ancestor probably had anterior, folded cephalic processes similar to those of *Volvatella* and the diaphanid *Colpodaspis*. The bodies of both the Juliidae and Oxynoidae are bright green, like their food plant (nutritional homochromy). This is another parallelism to many non-shelled sacoglossans. In the latter, however, green colouration is usually caused by the tubules of the digestive gland being visible through a transparent epidermis, whereas colouration in the shelled species is mostly due to epidermal pigment. The Oxynoidae have a short visceral loop of the nervous system; this has evolved in parallel to the short visceral loop of the shell-less sacoglossans. The genera of the Oxynoidae form an unresolved trichotomy in the preferred tree configuration (see figure 8). Attempts at further resolution yielded different results. In some trees *Lobiger* separated from the other two genera, in others *Oxynoe* separated. In the Oxynoidae the oral tube, the pharyngeal pouches, salivary glands and the oesophageal pouch show different development between genera. *Lobiger* has the highest number of generic autapomorphies, but most of the characters shared by *Oxynoe* and *Roburnella* are plesiomorphies. Hence it is considered most prudent to leave the family unresolved until more species have been studied anatomically. The Juliidae have small, paired pharyngeal pouches and, at least in *Berthelinia*, posteriorly separated ascus-muscles.

(*b*) *Monophyly of the shell-less Sacoglossa*

Whereas the Oxynoacea, after character analysis, could be arranged as outlined in figure 2, the Placobranchacea are more difficult to arrange. Not only have a few monogeneric families been left out of figures 2 and 3, but also strict monophyly has been assumed for the included families. The present analysis has shown that this is apparently not the case. Problems are found especially in the cerata-bearing families, which will be discussed below. However, the monophyly of the suborder is very well supported (see figure 8). Even in the highly unresolved, unweighted consensus tree, the Placobranchacea were monophyletic, and also the subdivision into two superfamilies was distinct. Only the genera included at the base of each superfamily changed with different weights being applied to different characters.

Here I will point to some important parallelisms, which have occurred in the placobranchoid as well as the limapontioid line. Blade-shaped radular teeth have evolved in both groups independently. The more primitive members of each group have triangular, laterally denticulate teeth. Blade-shaped teeth in the Oxynoacea usually have fine lateral denticles and often bifid tips. The latter character is not found in the shell-less Sacoglossa, and only a few species of *Hermaea* have very short lateral denticles (Jensen 1993*c*). In the placobranchids the blade-shaped teeth usually have median denticles; the cutting edge of the blade characteristically curves towards one side at the base (see f.x. figure 8 of Jensen 1992*a*). The blade-shaped teeth in the limapontioid line are usually smooth, though a few species have median or lateral denticles. Unfortunately no good frontal view of these teeth has been figured, so it is unknown whether the blade curves near the base. Also, pharyngeal pouches have been lost within both groups. In the species without pharyngeal pouches, the functional separation between the ascending and descending limbs of the radula has been accomplished by slightly different means (Jensen 1993*c*). In the placobranchoids the descending limb of the radula and its surrounding ascus-muscle are attached throughout their lengths; only the thinwalled ascus is free. In most species the ascus-muscle is as long as the pharynx. In the limapontioid line the ascus-muscle is usually unattached posteriorly, and the descending limb of the radula thus steeply inclined to the longitudinal axis of the pharynx.

In the cladistic analysis dorsal vessels appear to be a synapomorphy of the Placobranchidae, and to have evolved in parallel in several limapontioid genera, as well as *Bosellia*. In the case of such a complex structure, parallel loss seems more acceptable than parallel development. Hence it is more likely that these vessels were present in the non-shelled ancestor.

The result of the present cladistic analysis shows that the non-shelled species feeding on *Caulerpa* are not the morphologically primitive species, e.g. *Elysia expansa* and *Pattyclaya* spp. The 'primitive' members of the group almost all feed on *Halimeda* or *Chlorodesmis* (Jensen 1993*a*). Functional kleptoplasty probably evolved in the common placobranchacean ancestor, as it occurs to varying degrees in both major lines (Clark *et al.* 1990).

(i) *Status of the Placobranchoidea* (= *Elysioidea*)

The Placobranchoidea consists of the genera *Platyhedyle*, *Gascoignella*, *Bosellia*, *Placobranchus*, *Thuridilla*, *Elysiella*, *Pattyclaya* and *Elysia*; the monotypic *Tridachia* and *Tridachiella*, which have not been included in the present study, also belong in this clade. Only the first three genera do not have parapodia, but whether this is a primary absence or a secondary loss is unknown. In the preferred tree configuration it is assumed to be a primary absence. All the parapodia-bearing genera have been united in the family Placobranchidae (= Elysiidae) (Jensen 1992*a*).

The base of the placobranchoid clade is an unresolved trichotomy. The genus *Bosellia* shares some apomorphic characters with the parapodia-bearing genera, but also lacks some of the most important ones (separate ampulla and highly branched prostate). As most species of *Bosellia* are poorly described anatomically, the characters included in the character matrix are those of *B. mimetica*. In the unweighted consensus tree *Bosellia* clustered within the Placobranchidae, and *Placobranchus* was the least derived genus. In some of the eight trees used to form the preferred consensus tree *Bosellia* clustered with the Platyhedylidae, in others with the Placobranchidae. The genus *Bosellia* has alternately been included in the Polybranchiidae (Pruvot-Fol 1954; Sanders-Esser 1984) or the Placobranchidae (Marcus 1980; Thompson & Jaklin 1988). This study has clearly confirmed the affinity with the Placobranchidae. The characters linking *Bosellia* with the Polybranchiidae, e.g. the penial stylet and the pharyngeal pouch, are plesiomorphic characters, and the pharyngeal pouch is not found in all species of *Bosellia*. One species has a posterior vaginal opening (Marcus 1973); the others apparently have hypodermic impregnation. Extracapsular yolk is deposited in small discrete clumps along the spiral egg mass (Fernandez-Ovies & Ortea 1986). *Bosellia* has a superficial resemblance with the genus *Elysiella*, which also feeds on *Halimeda*, and has a broad foot and short parapodia. Marcus (1982) erected the monogeneric family Boselliidae primarily because the chromosome number of *Bosellia mimetica* differs from that of the other sacoglossans. However, the chromosome number of the other species of *Bosellia* has not been determined. Additional studies of species of *Bosellia* are obviously needed to elucidate the relationship of this genus with either the Platyhedylidae or the Placobranchidae. Until this has been undertaken, it seems most prudent to retain the family Boselliidae.

The family Placobranchidae comprises the parapodia-bearing genera. Most of these genera are very similar in body shape, and their validity has been discussed for many years (e.g. Thompson & Jaklin 1988; Jensen 1992*a*). It has been suggested that the genus *Elysia* needs to be subdivided (Jensen 1992*a*). *Placobranchus* has previously been separated from the Elysiidae, but recent studies have shown that the major differences between this genus and the elysiid genera are plesiomorphic, and that it shares the most important elysiid synapomorphies i.e. lateral parapodia into which the digestive gland and reproductive system extend; the ampulla is not an integrated part of the hermaphrodite duct; the prostate ramify extensively (Jensen 1992*a*). On the other hand it has a number of autapomorphies (broad, flat head; truncate tail; longitudinal dorsal lamellae), and also the anus is dorsal (reversal?), and dorsal vessels are absent (secondary loss?, see Jensen 1992*a*). However, *Placobranchus* never clustered outside the placobranchid clade, not even in the unweighted consensus tree. This strongly supports its inclusion with the other parapodia-bearing genera.

In the preferred tree configuration the genera *Pattyclaya* and *Elysiella* are included among the *Elysia* spp. This could either be interpreted as lack of support for their generic separation, or as support for the further subdivision of the genus *Elysia*. The latter is also supported by the fact that no apomorphic character has been identified which is shared by all species presently referred to the genus *Elysia*. Further attemps at resolving the top of the placobranchid clade, and including all species of *Elysia* included in this study, did not yield any conclusive results. Even if all the characters pertaining only to the shelled genera, and also the characters of the cerata were deleted, and a number of characters only pertaining to 'elysiids' (size of parapodia, dorsal lamellae, thickness of dorsal septate muscle, position of ascending limb, shape of ascus-muscle, colour of extra-capsular yolk) were added, the clade was still highly unresolved. A few things seem fairly certain, however. *Elysia ornata* stands as the sister taxon of the remaining species included in the present study, indicating the relative primitiveness of this species. Several species with similar external morphology are known, for example *E. grandifolia* Kelaart 1858, *E. rufescens* (Pease 1870), and the monotypic *Tridachia* and *Tridachiella*. However, the anatomy of these species needs to be examined. *Elysia timida* and *E. filicauda* came out as sister species, which is not surprising, as they also share a common diet, *Acetabularia* (Jensen 1992*a*). *Elysia expansa* is a sister taxon of *Pattyclaya*. These species also have similar diets, namely *Caulerpa*, and examination of the Caribbean *Elysia* species complex feeding on *Caulerpa* (Jensen & Clark 1983) would probably elucidate whether these species should be included in *Pattyclaya* or form a separate genus. In most trees *E. australis* and *E. chilkensis* were also sister species; again these species have similar diets and occupy similar habitats (Jensen 1992*a*). The position of *Elysiella* close to the top of the clade is problematic. The genus has retained many plesiomorphic characters, e.g. triangular teeth and one species has a penial stylet (own obs.). It is more likely that the long renal ridge has evolved in parallel in this genus and in the *Caulerpa*-feeding species; a long renal ridge occurs also in *Ercolania*. *Elysiella* should probably separate just after *Thuridilla*. The relationships of the remaining species can only be resolved as more species are studied in sufficient detail.

(ii) *Status of the Platyhedylacea*

Marcus (1982) included the Platyhedylacea as a separate suborder in the Sacoglossa, and Jensen (1985) added the monotypic family Gascoignellidae to this group. The status of the Platyhedylacea is unclear. *Platyhedyle* as well as *Gascoignella* are most likely highly reduced. Both are strongly flattened and devoid of parapodia, cerata and rhinophores. *Platyhedyle* lives interstitially in the Mediterranean (Salvini-Plawen 1973), and *Gascoignella* is intertidal on mangrove mud-flats in Hong Kong (Jensen 1985). However, it is difficult to ascertain whether they are derived from the placobranchoid or the limapontioid clade. The characters shared with either group are almost all plesiomorphies. The present study has shown that the position of the anus and female genital opening close together in an anterior ciliated groove is a placobranchoid synapomorphy. This also occurs in *Platyhedyle* (Wawra 1979) and *Gascoignella* (Jensen 1985), which, with extra weight applied to this character, places them at the base of the placobranchoid clade, though their reproductive systems are highly deviating (Jensen 1985; Wawra 1991). Also, the radular teeth deviate from anything known in the placobranchoid genera. Reexamination of the nervous system of *Platyhedyle* (Wawra 1988*a*) has shown that *Gascoignella* may be contained within the family Platyhedylidae. In the unweighted consensus tree the Platyhedylidae clustered within the Limapontioidea. However, this is almost certainly due to homoplasic reductions; loss of rhinophores as in *Alderia* and some species of *Limapontia*; absence of cerata (and parapodia) as in *Limapontia*; and chisel-shaped radula teeth as in *Calliopaea*. As anal position is an apomorphy shared with the Placobranchoidea, the Platyhedylidae should be in this clade. The only problem with separating the Platyhedylidae at the beginning of this clade is the apparent non-caulerpalean diets; feeding has not been observed in these species, but no Caulerpales are present in the habitat of *Gascoignella*. If, however, the Platyhedylidae are derived from the Boselliidae, at the time when diet radiation took place in the Placobranchidae, this difficulty would be overcome. This, however, is highly speculative.

(iii) *Status of the Limapontioidea*

This no doubt constitutes the most problematic group of the order (Jensen 1993*b*). Most of the genera presently referred to the Polybranchiidae have been poorly defined because of: (i) the scarcity of described species (and material used in species description); (ii) the low density of animals (usually only one or two specimens are collected at one time); and (iii) virtually nothing is known about their biology. On the other hand, the profusion of family-group names applied to various genus-groups is caused by the prolific speciation occurring in connection with: (i) radiation to non-caulerpalean diets; (ii) dispersal into temperate regions; and (iii) reduction in size. Morphological differences between genera, and even among species in one genus, are much larger than in the Placobranchidae. Among the species with cylindrical cerata, many occur in high densities, and the anatomy as well as biology of certain species have been extensively studied (e.g. Gascoigne 1978, 1979*b*; Gascoigne & Sordi 1980; Bleakney 1989, 1990; Trowbridge 1992, 1993*a*,*b*). However, several species appear not to 'fit' into the genus in which they are currently placed. Many characters occur in more than one apomorphic state within one genus, and several genera are poorly known. Hence it is very likely that new genera will have to be described, when more species are studied in detail.

In spite of all this, the clade came out monophyletic even in the unweighted consensus tree. The genera presently included in the family Polybranchiidae form a fully resolved, but paraphyletic, group; the Hermaeidae form a monophyletic group, and the remaining genera form a highly unresolved cluster, including the Platyhedylidae. In the preferred tree configuration the resolution of the Limapontiidae (= Stiligeridae) is somewhat improved, the Platyhedylidae being moved to the placobranchoid clade. *Costasiella* forms part of an unresolved trichotomy within the Limapontiidae.

(iv) *Status of the Polybranchiidae*

In the unweighted as well as the preferred tree configuration the genera usually included in the family Polybranchiidae resolved as a paraphyletic grade. The genera share some seemingly apomorphic characters i.e. flat cerata with marginal defensive glands and bifid rhinophores; most of the genera also have oral tentacles and a lateral anal papilla (below the cerata) (see table 4). However, the genera *Cyerce* and *Sohgenia* are very plesiomorphic, and if only three characters (14, 44 and 45) were given an extra weight of 5, those two genera formed a basal, unresolved grade in addition to the two well-defined placobranchacean clades. A similar position of these two genera could be obtained by deleting character 30 from the preferred tree configuration. However, this also resulted in collapse of several branches within each of the previously well resolved clades. The Polybranchiidae could be 'forced' to resolve as a monophyletic clade by adding a weight of 5 to characters 11, 12 and 19 of the preferred tree configuration. This, however, caused not only the Oxynoacea, but also the family Oxynoidae to become paraphyletic, with *Lobiger* and *Roburnella* forming an unresolved trichotomy with the Placobranchacea. A better resolution, including monophyly of Oxynoacea and Oxynoidae, was obtained by the following settings: weight 3 added to characters 14 and 48 and weight 5 to characters 3, 11, 12, 19 and 44. This yielded 96 equally parsimonious trees of length 204 steps with consistency and retention indices of 0.45 and 0.79 respectively. A part of the resulting strict consensus tree is shown in figure 9. As seen, even this did not result in complete resolution of the Polybranchiidae, and also, the base of the Placobranchacea forms an unresolved trichotomy. Obviously the genera of this family need further examination.

The genera of the Polybranchiidae are usually considered more primitive than those of the other cerata-bearing familes. This is based on the 'holohepatic' arrangement of the digestive gland in *Cyerce* (i.e. no digestive gland tubules in cerata); also, triangular teeth and udoteacean diets dominate (Jensen 1993*a*,*c*), and they occur only in tropical-subtropical regions. As the genera are so poorly known, a brief outline of each genus will be given below.

Cyerce differs in many respects from the other Polybranchiidae, and it probably stands at the base of the limapontioid clade. *Cyerce* is the only limapontioid genus with a transverse groove in the foot sole. Diets, where known, are udoteacean (*Halimeda*, *Chlorodesmis*) (Jensen 1993*a*). Reproductive anatomy has only been studied in *C. cristallina* (Sanders-Esser 1984). This species has secondary copulatory bursae as in the Placobranchoidea, though homology of the bursae has not been established.

The recently described monotypic genus *Sohgenia* superficially resembles a mutilated *Cyerce* (compare figure 1 in Hamatani (1991) with figure 9 in Thompson (1988)). Extremely flattened body-shape, lack of oral tentacles and penial stylet, as well as the small number of very small cerata, may all be explained as mutilation. However, the lack of a transverse groove in the foot sole can hardly be explained in this way. Its reproductive anatomy is unknown.

The genus *Polybranchia* is rather poorly defined, though the anatomy of several species has been examined. The anus is lateral, below the cerata. Diet is unknown, but several species have been collected in association with *Caulerpa* (Jensen 1993*b*; Clark 1994). Bergh's (1871) lengthy description of the reproductive system of *P. prasina* is completely impossible to interpret.

Two of the three known species of the genus *Mourgona* differ very much from one another in buccal anatomy (Marcus & Marcus 1970). Reexamination of *M. germaineae* has shown that in this species there is a small, but distinct pharyngeal pouch (Jensen 1991). The only external difference between *Mourgona* and *Polybranchia* is the shape of the base of the cerata (see figure 5). In *M. germaineae* the reduction of the pharyngeal pouch is accompanied by a conspicuous change in tooth morphology (though still basically triangular) and a non-caulerpalean diet, *Cymopolia barbata* (Jensen 1981). *M. osumi* feeds on *Acetabularia* (Hamatani 1994), another dasycladalean alga. Except for the presence of a straight penial stylet, the reproductive anatomy is unknown.

Caliphylla has a number of autapomorphies. It has retained the large pharyngeal pouches, but the lumina are large and apparently used in connection with buccal regurgitation, another important 'innovation' within the shell-less Sacoglossa (Jensen 1993*d*, 1994). It is the only polybranchiid genus with blade-shaped teeth. The rhinophores contain a branch of the digestive gland. Several characters of the reproductive system are shared with the 'hermaeid' genera, so much that Gascoigne (1985) proposed including *Caliphylla* in the subfamily Hermaeinae under the family Polybranchiidae.

Considering the fact that most genera are so poorly described anatomically, and also that monophyly could be 'forced' without seriously disrupting the other monophyletic groups, it is here proposed that the family Polybranchiidae is retained.

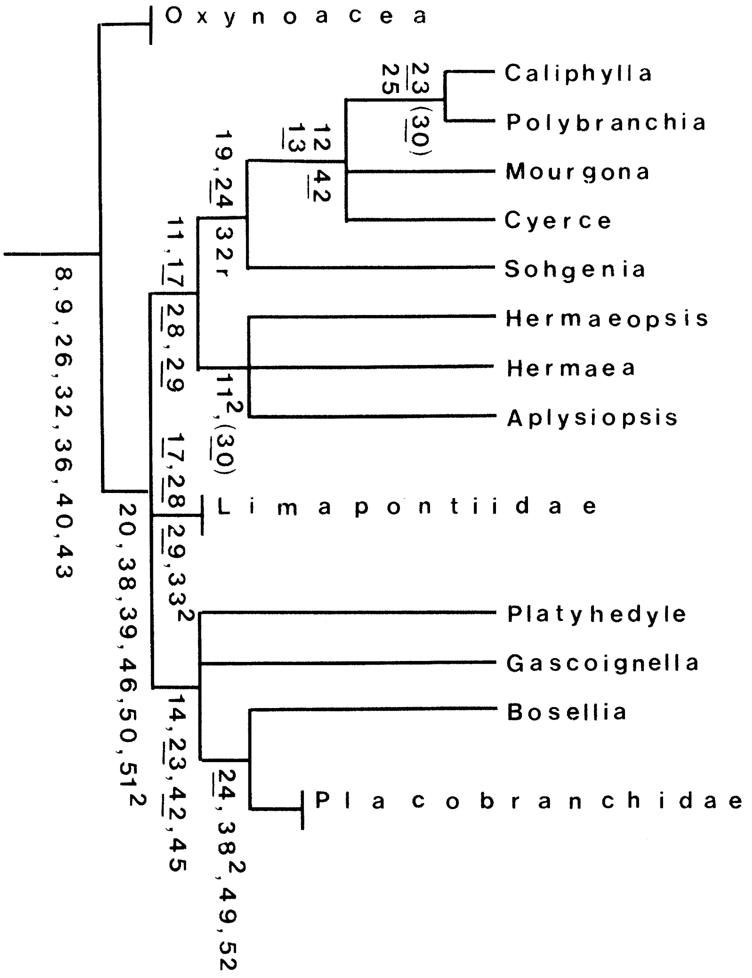

Figure 9. Alternative phylogenetic relationships of the Limapontioidea. Part of a strict consensus tree from 96 equally parsimonious trees of length 204 steps; consistency and retention indices were 0.45 and 0.79 respectively; character weights were set at 3 for characters 14 and 48 and at 5 for characters 3, 11, 12, 19 and 44. Lettering as in figure 8.

(v) *Status of the Costasiellidae, Hermaeidae, Alderiidae and Limapontiidae* (= *Stiligeridae*)

These families have been separated mainly based on reproductive characters (Gascoigne 1976, 1985; Clark 1984). The genera presently referred to the Hermaeidae are *Hermaea*, *Hermaeopsis* and *Aplysiopsis*; the Limapontiidae (= Stiligeridae) comprises the genera *Stiliger*, *Placida*, *Calliopaea*, *Olea*, *Ercolania* and *Limapontia* (Gascoigne 1976, 1985). Most species included in this group are small (less than 1 cm); a few are big (about 4 cm), e.g. '*Stiliger*' *smaragdinus* (which almost certainly is not a *Stiliger*) and *Hermaeopsis variopicta*. Most species in the group have smooth, blade-shaped teeth and non-caulerpalean diets. However, sabot-shaped teeth evolved in this group, and also many species have simple rhinophores. In the preferred tree configuration the common ancestor of the Hermaeidae and Limapontiidae is characterized mainly by reversals. This could indicate a massive event of paedomorphosis. However, it could also indicate that a configuration similar to that of figure 9 is more appropriate for this group.

In *Hermaeopsis* and *Aplysiopsis* (and also in *Caliphylla*) the genital receptacle is connected distally to the oviduct and proximally to the postampullar oviduct (not in *Caliphylla*). In *Hermaea* only this proximal connection exists (Schmekel & Portmann 1982). Gascoigne (1979*b*) did not notice a distal connection of the genital receptacle of *Hermaeopsis*, and he synonymized this genus with *Hermaea*. However, the species which are certainly congeneric with the type species, *H. bifida*, have an albumen gland which differs from that of the other two hermaeid genera; it is composed of numerous discrete acini connected by non-glandular ducts (Marcus & Marcus 1967; Jensen 1993*b*). The teeth in the ascus of the hermaeids form a spiral. However, this occurs in the majority of *Placida* spp., and also in many Polybranchiidae and Placobranchoidea. The digestive gland does not send branches into the rhinophores of the hermaeid genera; there is an anterior transverse branch of the digestive gland on either side sending branches into a short, transverse row of cerata. It is possible that several species for which anatomy is unknown, e.g. *H. paucicirra* Pruvot-Fol 1953, *H. vancouverensis* O'Donoghue 1924, will have to be removed from *Hermaea sensu strictu*, either to *Hermaeopsis* or to a new genus. In the present study the Hermaeidae separated out as a monophyletic group, even in the unweighted analysis. The affinity with *Caliphylla* is seen in the preferred tree configuration (see figure 8) as well as the tree in which monophyly of the Polybranchiidae was 'forced' (see figure 9); in this tree the Hermaeidae and Polybranchiidae share a common ancestor, and the Limapontiidae form a separate clade.

In the preferred tree configuration the limapontiid clade contains an unresolved trichotomy of *Costasiella*, the two oophagous genera (*Olea* and *Calliopaea*), and the genera having sabot-shaped teeth (*Ercolania*, *Limapontia* and *Alderia*). It is interesting that previously four of these genera (*Limapontia*, *Alderia*, *Olea* and *Costasiella*) have been allocated to separate, monogeneric families (Thiele 1931; Gascoigne 1976; Clark 1984). The base of the limapontiid clade is comprised of the externally similar genera *Placida* and *Stiliger*. Most of the species included in these two genera are also ecologically similar, feeding on *Codium* or *Bryopsis* (Jensen 1993*a*,*b*). *Placida cremoniana* (Trinchese, 1892) may represent an intermediate form between the 'hermaeid' and 'stiligerid' reproductive systems (Sanders-Esser 1984); it has a seminal receptacle deep in the body cavity as the hermaeids, but also a functional bursa copulatrix close to the body wall (in addition to the genital receptacle). In most limapontiids the seminal receptacle is located close to the body wall, and it is the functional bursa copulatrix (Gascoigne 1976). In a few species, e.g. *Ercolania margaritae* (Gascoigne 1976), *E. coerulea* (Schmekel & Portmann 1982), and *Calliopaea bellula* (Gascoigne & Todd 1977), there is a vaginal opening, which may connect to the seminal receptacle or to a small vagina. The latter apparently does not store oriented (or unoriented) sperm, and these species do not have a distinct seminal receptacle; sperm may be stored in the vaginal duct leading to the fertilization area. Thus, although the 'stiligerid' reproductive system is very well defined, there are numerous exceptions or modifications.

The monogeneric family Costasiellidae was erected because this genus did not fit into either the Hermaeidae or the Limapontiidae (= Stiligeridae) (Clark 1984). The reproductive system apparently may have two, three or even four openings. The latter has erroneously been called tetraaulic (Clark 1984); the fourth aperture is an outlet from the genital receptacle (Gascoigne 1979*b*). The rhinophores are usually simple, but in some species a small 'flap' occurs at the base of the rhinophores, which indicates reduction from originally folded rhinophores. Folded rhinophores occur in *C. nonatoi*, in which also the eyes are behind the rhinophores (Clark 1984). *Costasiella* shares at least one apomorphy with the Limapontiidae, namely the albumen gland sending branches into the cerata. Some species have long pedal tentacles, and some do not have especially large eyes. However, this genus also has retained many plesiomorphies; several species have a pharyngeal pouch, the ascus-muscle is attached throughout its length, and they have a long, conical penis, which may have a minute stylet (Marcus 1982; Jensen 1990). *Costasiella* also is the only genus within the group, in which some species have lecithotrophic or encapsulated development (Clark & Jensen 1981). Most species feed on *Avrainvillea*. However, *C. pallida* and an undescribed Australian species feed on *Vaucheria* (Jensen 1990; R. Burn, personal communication). These species may form a separate genus.

Oophagy occurs in two genera, *Calliopaea* and *Olea*. Although Gascoigne & Sigurdsson (1977) claimed that *Stiliger vesiculosus* (Deshayes 1864), another oophagous species (Haefelfinger 1962), had sabot-shaped teeth, this almost certainly is due to misidentification of their specimens – most likely *Ercolania funerea* – which often co-occurs with *Calliopaea bellula*. *Calliopaea* occurs in the northeastern Atlantic and the Mediterranean (Schmekel & Portmann 1982). *Olea* occurs in the northeastern Pacific (Gascoigne 1975). Both have 'stiligerid' reproductive systems. The penial stylet of *Calliopaea* is extremely long, that of *Olea* slightly longer than in *Limapontia*. However, in *Olea* as well as *Calliopaea* the penial stylet lies across the tip of the penis when retracted, whereas it is partly retracted into the tip of the penis in most other limapontiids. *Olea* has a very reduced radula, consisting only of two preradular teeth plus three to seven incomplete 'adult' teeth, and often recorded as absent (Gascoigne 1975). The teeth of *Calliopaea* have been called chisel-shaped, and teeth of similar shape occur in some species presently referred to *Hermaea*, e.g. *H. paucicirra*, or to *Stiliger*, e.g. *S. zosterae* Baba 1959 (Baba 1959; Salvat 1968). Diet is not known for any of these species, and they will probably have to be transferred to one or more separate genera. In the present study the two oophagous genera came out as sister taxa within the Limapontiidae.

Sabot-shaped teeth occur almost exclusively in genera which have specialized on diets of Cladophorales and/or Siphonocladales. *Aplysiopsis* clearly clustered with the Hermaeidae, whereas *Alderia*, *Limapontia* and *Ercolania* form the tip of the limapontiid clade (see figure 8). The sabot-shaped teeth of *Aplysiopsis* differ in many ways, especially in the base, from those of the other genera, and they probably evolved in parallel (Jensen 1993*c*), though they must have had a not too distant common ancestor. The diet of *Alderia* is *Vaucheria*, a xanthophyte. This may be a secondary diet change; the tips of the sabot-shaped teeth of *Alderia* are pointed (Bleakney 1988). In this connection it should be noted that the placobranchids which feed on Cladophorales do not have sabot-shaped, but blade-shaped teeth, though with rounded tips.

The genus *Alderia* groups within the genera of the Limapontiidae. It is possible that all the genera having sabot-shaped teeth should form their own subfamily. As several characters occur in more than one apomorphic state within the genus *Ercolania*, this genus may have to be split. However, *Alderia* has been placed in a separate family because of some anatomical peculiarities, e.g. gonad not forming discrete follicles, large hemolymph sinuses, absence of heart (Evans 1953; Gascoigne 1976). *Limapontia*, which for many years had its own family, also has several autapomorphies, and these genera are probably very old. This is supported by molecular data (Theisen & Jensen 1991).

In conclusion, only two families with fusiform cerata can be recognized, i.e. Hermaeidae and Limapontiidae

(= Stiligeridae). The genera *Costasiella* and *Alderia* should be included in the Limapontiidae. A subdivision into subfamilies is not possible with our present knowledge.

(*c*) *The Sacoglossa as heterobranchs and as opisthobranchs*

Several synapomorphies link the Sacoglossa to the Heterobranchia: (i) heterostrophic shell; (ii) ciliated tracts accompanying; and (iii) a secondary gill. Also the hermaphroditic reproductive system is shared with most heterobranchs. Euthyneury is shared with opisthobranchs as well as pulmonates. Sacoglossans share only some of the opisthobranch synapomorphies: (i) a separate left parietal ganglion in a few species; and (ii) a pallial caecum, which differs in many respects from that of other opisthobranchs. They differ from most shelled opisthobranchs in the absence of: (i) plicate gill; (ii) Hancock's organ; (iii) gizzard; and (iv) jaws.

Aside from *Cylindrobulla*, it is not possible to link the Sacoglossa with any other extant opisthobranch clade. Any apparent synapomorphy can be explained as parallel evolution, or not quite homologous structures i.e. sutural slit and keel, shell adductor muscles, and attached pallial caecum, which occur also in *Akera* (Jensen 1995*a*). Because *Akera* differs fundamentally in the organization of central nervous system (it has separate pleural ganglia close to the pedal ganglia) and reproductive system (monaulic) (Gosliner 1991), the above characters are attributed to parallel evolution.

The order Acochlidiacea has sometimes been mentioned as a possible sister group of the Sacoglossa (Gosliner & Ghiselin 1984). This group has so many autapomorphies correlated with small size and interstitial habitat (Salvini-Plawen 1973) that comparison with other opisthobranchs is difficult. Although the genus *Ganitus* has a uniseriate radula, the teeth of which bear some resemblance to those of some sacoglossans (Salvini-Plawen 1990), most acochlidiaceans have a triseriate radula, which may be asymmetrical i.e. two lateral teeth on one side and one on the other side (Wawra 1988*b*). Hence the acochlidiaceans must have split off before the Cylindrobullidae. In addition *Ganitus* has cuticular jaws (Marcus 1953). The Acochlidiacea also have separate pleural ganglia and the nerve-ring is prepharyngeal (Challis 1970).

The Diaphanidae, which has often been named as a possible ancestor of the Sacoglossa (Marcus & Marcus 1956; Thompson 1976; Salvini-Plawen 1990), probably is not a monophyletic group (Jensen 1995*a*). The genera included in the Diaphanidae have separate pleural ganglia, prepharyngeal nerve-ring, monaulic reproductive systems, and the penial opening is anterior, close to the mouth. The genus *Newnesia* has a large, muscular pharynx and a uniseriate radula (Gascoigne & Sartory 1974; Jensen 1995*a*). However, the organization of the odontophore differs widely from that of the sacoglossans, and also the shape of the radular teeth is very different (Jensen 1995*a*).

7. CONCLUSIONS AND CLASSIFICATION

A classificatory framework based on shared apomorphies is proposed (see table 5). This will probably need modifications, especially at generic and subfamily-levels, as more species are described in detail. The following conclusions are made.

1. The Sacoglossa forms a monophyletic clade.
2. The monogeneric Cylindrobullidae is not included in the Sacoglossa, but forms a sister group, Cylindrobullacea.
3. The shelled sacoglossans form a monophyletic suborder Oxynoacea H. & A. Adams 1854.
4. The non-shelled sacoglossans likewise form a monophyletic suborder Placobranchacea Rang 1829.
5. The parapodia-bearing Placobranchidae Rang 1829, together with the Boselliidae and the Platyhedylidae form the monophyletic superfamily Placobranchoidea Rang 1829.
6. The monogeneric family Boselliidae Marcus 1982 is retained until further studies have shown whether it may be included in the Placobranchidae.
7. The relationship of the genera within the Placobranchidae must await revision of the genus *Elysia*.
8. The Platyhedylidae Salvini-Plawen 1973 contains two genera: *Platyhedyle* Salvini-Plawen 1973 and *Gascoignella* Jensen 1985. The family Gascoignellidae Jensen 1985 is now considered a junior synonym of the Platyhedylidae.
9. The cerata-bearing genera form a monophyletic superfamily Limapontioidea Gray 1847.
10. The family Polybranchiidae, O'Donoghue 1929 is apparently paraphyletic. As monophyly can be 'forced' fairly easily in cladistic analysis, it is suggested that the Polybranchiidae be retained until the anatomy of the cerata-bearing genera has been studied in more detail.
11. The cerata-bearing genera with cylindrical cerata may form a monophyletic group mostly characterized by reversals; or, the Hermaeidae may share a common ancestor with the Polybranchiidae. This should be further investigated.
12. The family Hermaeidae H. & A. Adams 1854 forms a monophyletic clade.
13. The family presently known as Stiligeridae also forms a monophyletic group. The name of this family, if based on the oldest available family-name, should, unfortunately, be Limapontiidae Gray 1847. This is unfortunate because *Limapontia* is the only genus without cerata!
14. The family Costasiellidae is not warranted. *Costasiella* may have to be split into more than one genus, thus justifying subfamilial status within the Limapontiidae. This must await anatomical studies of the included species.
15. The family Alderiidae is superfluous; *Alderia* can be included in the Limapontiidae.
16. The relationship between the Sacoglossa, its sister group (Cylindrobullidae), and the remaining opisthobranchs remains elusive; similarities between the Sacoglossa and the Diaphanidae are plesiomorphies

Table 5. *Classification of the Sacoglossa, based on phylogeny*

- order Sacoglossa von Ihering 1876
  - suborder Oxynoacea H. Adams & A. Adams 1854
    - family Volvatellidae Pilsbry 1895
      - genus *Volvatella* Pease 1860
      - genus *Ascobulla* Marcus 1972
    - family Juliidae E.A. Smith 1885
      - genus *Julia* Gould 1862
      - genus *Berthelinia* Crosse 1875
    - family Oxynoidae H. & A. Adams 1854
      - genus *Roburnella* Marcus 1982
      - genus *Oxynoe* Rafinesque 1819
      - genus *Lobiger* Krohn 1847
- suborder Placobranchacea Rang 1829
  - superfamily Placobranchoidea Rang 1829
    - family Placobranchidae Rang 1829 (= Elysiidae Forbes & Hanley 1851)
      - genus *Placobranchus* van Hasselt 1824
      - genus *Thuridilla* Bergh 1872
      - genus *Elysiella* Bergh 1872
      - genus *Pattyclaya* Marcus 1982
      - genus *Elysia s.l.* Risso 1818
    - family Boselliidae Marcus 1982
      - genus *Bosellia* Trinchese 1891
    - family Platyhedylidae Salvini-Plawen 1973
      - genus *Platyhedyle* Salvini-Plawen 1973
      - genus *Gascoignella* Jensen 1985
  - superfamily Limapontioidea Gray 1847
    - family Polybranchiidae O'Donoghue 1929 (= Caliphyllidae Thiele 1931)
      - genus *Sohgenia* Hamatani 1991
      - genus *Cyerce* Bergh 1871
      - genus *Mourgona* Marcus & Marcus 1970
      - genus *Polybranchia* Pease 1860
      - genus *Caliphylla* A. Costa 1867
    - family Hermaeidae H. Adams & A. Adams 1854
      - genus *Hermaea* Lovén 1844
      - genus *Hermaeopsis* A. Costa 1869
      - genus *Aplysiopsis* Deshayes 1839–53
    - family Limapontiidae Gray 1847 (= Stiligeridae Iredale & O'Donoghue 1923)
      - genus *Placida* Trinchese 1876
      - genus *Stiliger* Ehrenberg 1831
      - genus *Costasiella* Pruvot-Fol 1951
      - genus *Calliopaea* d'Orbigny 1837
      - genus *Olea* Agersborg 1923
      - genus *Limapontia* Johnston 1836
      - genus *Alderia* Allman 1846
      - genus *Ercolania s.l.* Trinchese 1872

or parallelisms, between the Sacoglossa and the Anaspidea (*Akera*) are most likely homoplasies, and between the Sacoglossa and the Acochlidiacea convergences due to small size.

Unfortunately the 'problematic' taxa in the Sacoglossa (and probably other groups) are extremely rare animals. Hence further resolution of the phylogenetic relationships may be difficult to obtain. Future studies must concentrate on such characters as ultrastructure of osphradium, spermatozoa, and mantle structures, which have proved very interesting in other heterobranchs (Healy & Willan 1984, 1991; Haszprunar 1985; Foale & Willan 1987; Healy 1993). Also molecular data would be very helpful to solve various remaining problems.

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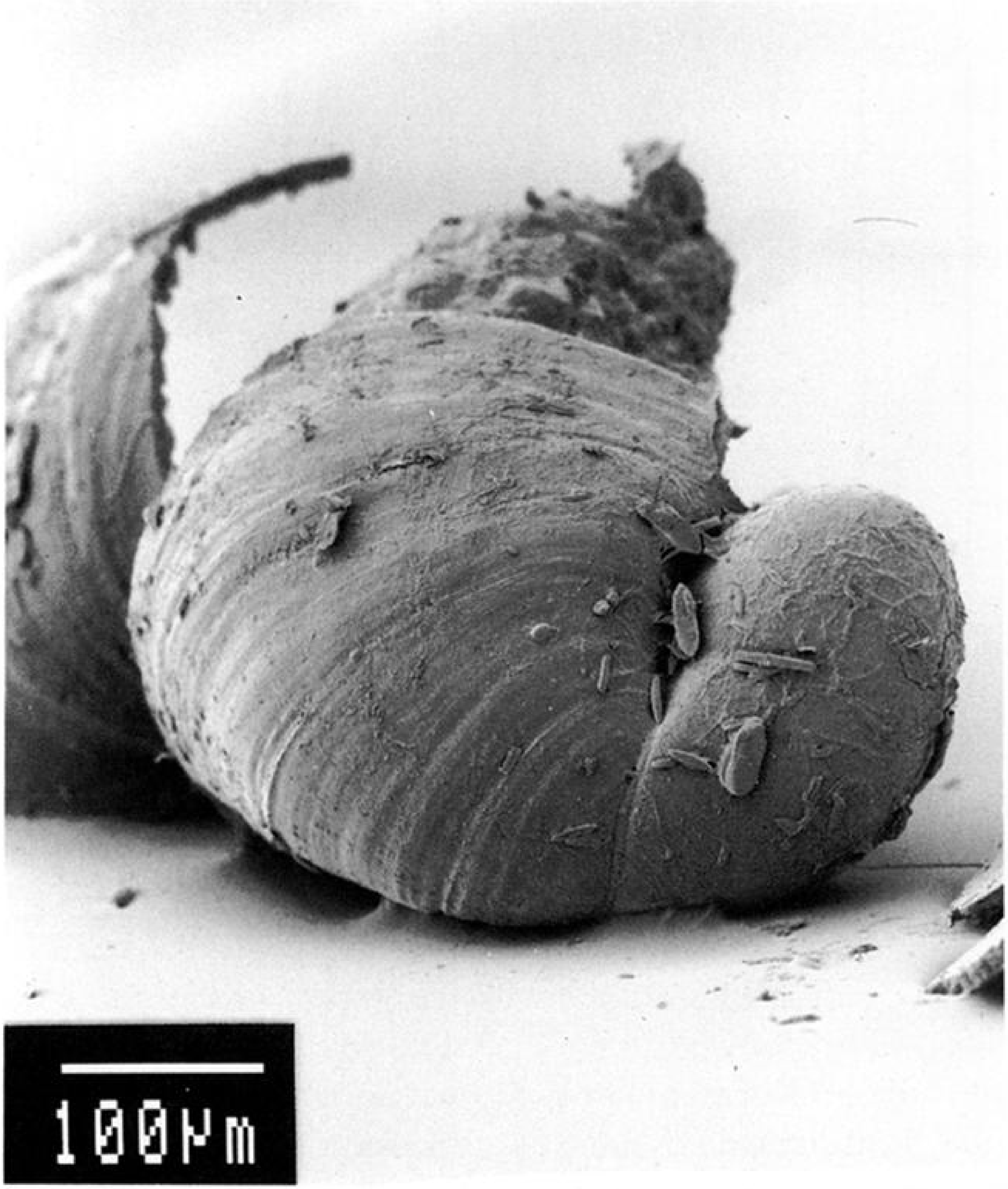
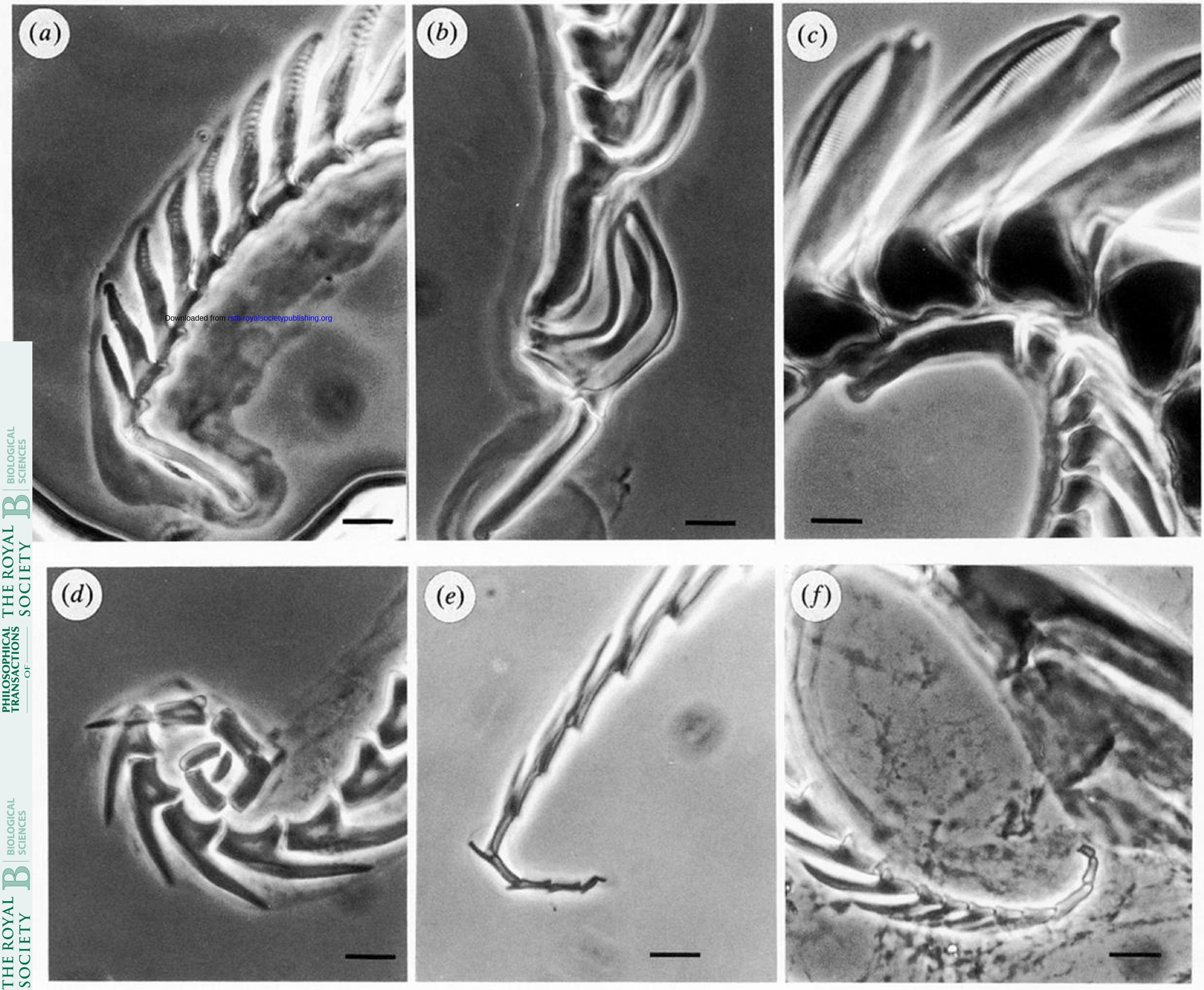


gure 4. Scanning electron micrograph of protoconch and early teleoconch of *Volvatella ventricosa*.



igure 6. Light micrographs of preradular teeth of sacoglossans. (*a*) *Volvatella bermudae*; 1 rod-shaped preradular tooth nd no transitional teeth. (*b*) *Oxynoe antillarum*; 1 rod-shaped preradular tooth and 2–3 transitional teeth. (*c*) *Berthelinia abai*; 1 rod-shaped preradular tooth and no transitional teeth. (*d*) *Elysia subornata*; 3 preradular teeth and 2–3 ransitional teeth. (*e*) *Mourgona germaineae*; 3 preradular teeth and 2 transitional teeth. (*f*) *Placida kingstoni*; 3 reradular teeth and 3–4 transitional teeth. Scale lines: 10 μm.