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Biogeography of the Sacoglossa (Mollusca, Opisthobranchia)*

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Abstract. The Sacoglossa (Mollusca, Opisthobranchia) comprise almost 400 nominal species level taxa. Of these 284 are considered valid (i.e., no published synonymies) in this study. About half of the nominal species have been described before 1950, and the 10 most productive taxonomists have described about half of the species. Distributions of all valid species are reviewed. The highest diversity is found in the islands of the Central Pacific, though species diversity is almost as high in the Indo-Malayan sub-province. The Caribbean forms another center of species diversity. These three areas are distinguished by the high number of Plakobranchoidea. Similarity among provinces is generally low. Endemicity is high in most provinces, but this may be an artifact of collecting activity. The decrease in number of species with latitude is spectacular, and the number of cold-water endemics is very low, indicating that sacoglossans in cold temperate regions are mostly eurythermic warm water/ tropical species. The highest number of species in cold temperate areas is found in Japan and Southeastern Australia. This coincides with high species diversity of the algal genus *Caulerpa*, which constitutes the diet of all shelled and many non-shelled sacoglossans.

Keywords. Species diversity, endemism.

1. INTRODUCTION

Information on biogeography is important for understanding speciation and phylogeny as well as for making decisions about conservation. Ideally, combining a phylogenetic tree with a distributional map should give information on whether species dispersed from a center of origin or were the result of vicariance events. For most marine invertebrate groups, however, phylogenies are not fully resolved and/or taxonomy is not yet stable, and even information on distributions is incomplete. Species are still being split or synonymized, and new and undescribed species are discovered. In a worst case scenario a distribution map would show the activities of taxonomists rather than actual species distributions. In the present study existing distributional data for the Sacoglossa (Mollusca: Opisthobranchia) is reviewed and analyzed with regard to different biogeographic theories as well as activities of taxonomists over time. Phylogenetic analysis has been performed at the genus level (JENSEN 1996a), and for one genus, *Thuridilla*, at species level (GOSLINER 1995). The relationship of the Sacoglossa to other opisthobranchs has been discussed in several recent publications (JENSEN 1996B; MIKKELSEN 1996, 1998; THOLLESON 1999; WÄGELE et al. 2003).

Sacoglossans are suctorial herbivores; only two or three species are oophagous, feeding on the eggs of other opisthobranchs (JENSEN 1993a, 1997a). This means that they have depth distributions restricted to the photic zone, i.e. generally <100m. Sacoglossans are also dietary specialists, the majority of species feeding on siphonaceous green algae, especially *Caulerpa* spp. (Jensen 1997a). Hence they only occur in the habitats where these algae are found. The total number of valid species is around 300, but new species are still described and other species are synonymized.

2. MATERIALS AND METHODS

Distributional data for all species of Sacoglossa were taken from the literature. The study has included most publications of original descriptions to get the type localities. However, in the case of the oldest descriptions, the publications by SCHMEKEL & PORTMANN (1982) and BOUCHET (1984) have been used. Also, national and regional faunal checklists have been included, as well as records published on the Sea Slug Forum (http://www.-seaslugforum.net/). All nominal species listed in Appendix 1 have been included in the first analysis for bias of taxonomic expertise and scientific activity. In the distributional analyses, however, only species considered valid in this study have been included. As the present study is not a taxonomic analysis, species identifications and synonymizations, with a few controversial exceptions, will not be discussed. Only synonymies that have been published and not subsequently contested are used. Thus species that have only been mentioned once in the literature are, with few exceptions mentioned in the text, considered valid.

Biogeographic regions and provinces were taken from Briggs (1995) (Fig. 1), and sacoglossan distributions among these provinces were recorded. Although it must be assumed that a species occurs continuously between the extreme points of distribution, species were only scored as occurring in a region or province if at least one published record existed. The number of endemic species was determined for each province. As some regions were clearly underrepresented with regards to faunistic studies on opisthobranchs, a few regions have been merged or deleted from the analyses. Similarity between biogeographic regions or provinces was analyzed using three indices: CJ= Jaccard's coefficient= 100(a/(N1+N2-a)) (Valentine 1966), SD= Dice coefficient = 100(2a/(2a+b+c)) (Leal & Bouchet 1991), and I=index of inclusion= 100(a/Nmin) (Golikov 1989). These indices differ in the weight placed on shared species (a) compared to total number of species in the compared regions (N1, N2), and species found exclusively in one or the other of the compared regions (b, c).

3. RESULTS

3.1. Fossil history

After the description of live specimens of bivalved sacoglossan gastropods (Kawaguti & Baba 1959), several papers on fossil species of these sacoglossans appeared. The first reviews of fossil sacoglossans were those of Boettger (1963) and Kay (1968). There have been extensive discussions about the identity of the Recent *Tamanovalva*, *Edenttellina* and *Midorigai* and the Middle Eocene genus *Berthelinia* (e.g. Edmunds 1963; Burn 1998). Keen & Smith (1961) listed several other fossil species and included all in the family Juliidae Dall, 1898, which had previously been located in the Bivalvia. More

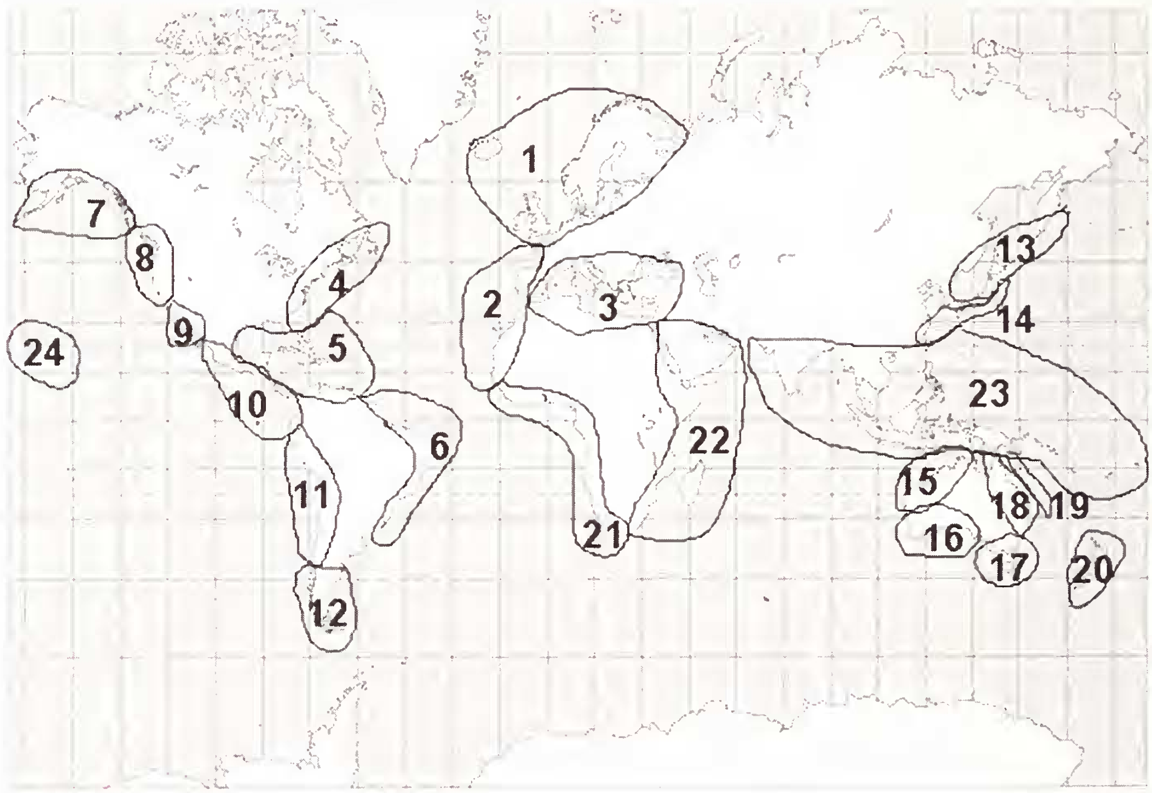

Fig. 1. Map showing biogeographic regions used in the present study. Regions have been modified from Briggs (1995). **1.** Northeast Atlantic. **2.** Lusitanian. **3.** Mediterranean (including the Black Sea). **4.** Northwest Atlantic. **5.** Caribbean. **6.** Southwestern Atlantic tropical and warm temperate. **7.** Aleutian. **8.** Oregonian. **9.** Californian. **10.** Mexican-Panamanian. **11.** Southeastern Pacific warm temperate. **12.** Cold temperate South America. **13.** Northwest Pacific cold temperate. **14.** Northwest Pacific warm temperate. **15.** Northern and northwestern Australia. **16.** Southwestern and southern Australia. **17.** Southeastern Australia. **18.** Northeastern Australia. **19.** Great Barrier Reef. **20.** New Zealand. **21.** Southeast Atlantic. **22.** Western Indian Ocean. **23.** Indo-Polynesian region (including Ryukyu Islands). **24.** Hawaii.

recently several more fossil bivalved sacoglossans have been described (see LE RENARD et al. 1996 for review), and also a single species of *Volvatella* has been described from the Lower Miocene of France (VALDÉS & LOZOUET 2000). Thus there may be two or five Recent genera of bivalved sacoglossans, whereas there are 9 fossil genera extending from the Lower Eocene to Lower Pliocene. Most fossil species have been found in European localities, but a few are from the Caribbean, and one each from Australia and Indonesia. However, no doubt more fossil species will be described in the future.

The temporal and spatial distribution of fossil sacoglossans indicates that they arose as part of the Tethys Sea fauna. As sea level receded and temperatures cooled down, their distribution became more restricted, and today there is only one species of *Berthelinia* in the Caribbean and one in the Panamanian region; the remaining species are Indo-West Pacific. *Julia* has one species in the East Pacific; the remaining species are Indo-West Pacific. For *Volvatella* there is only one species in the Caribbean, one in warm temperate South Africa, and the remaining species are Indo-West Pacific. The disappearance of a major part of the coral reefs at the end of the Cretaceous (BRIGGS 1995) may have created ideal conditions for speciation of siphonaceous green algae when sea level rose again in early Eocene.

3.2. Recent species

Slightly more than half (199 of 387) of the nominal species have been described before 1950. There is a distinct peak around the 1860s and 1870s when PEASE and BERGH were most active describing species from the Indo-West Pacific and Costa and Trinchese worked in the Mediterranean (Fig. 2). After 1950, it is especially the MARCUSes (39 species) and K. BABA (30 species) who dominate the number of new species (Table 1). The 10 most productive authors or groups of authors have described almost 50 % of the species.

Of the 387 nominal species 284 (73%) have been included in the similarity analyses. The number of species recorded from regions and provinces shown in Fig. 1 is listed in Table 2. Some regions are distinctly underrepresented in regards to number of records. This is true for most of the southern cold temperate zone, but also for tropical East Atlantic and southern East Pacific. Most of the biogeographic regions and provinces are supported by the present study as indicated by the percentage of endemic species. The regions and provinces with less than 10% endemism will be discussed below.

The Northeast Atlantic and Mediterranean were the earliest studied areas. The number of species described dur-

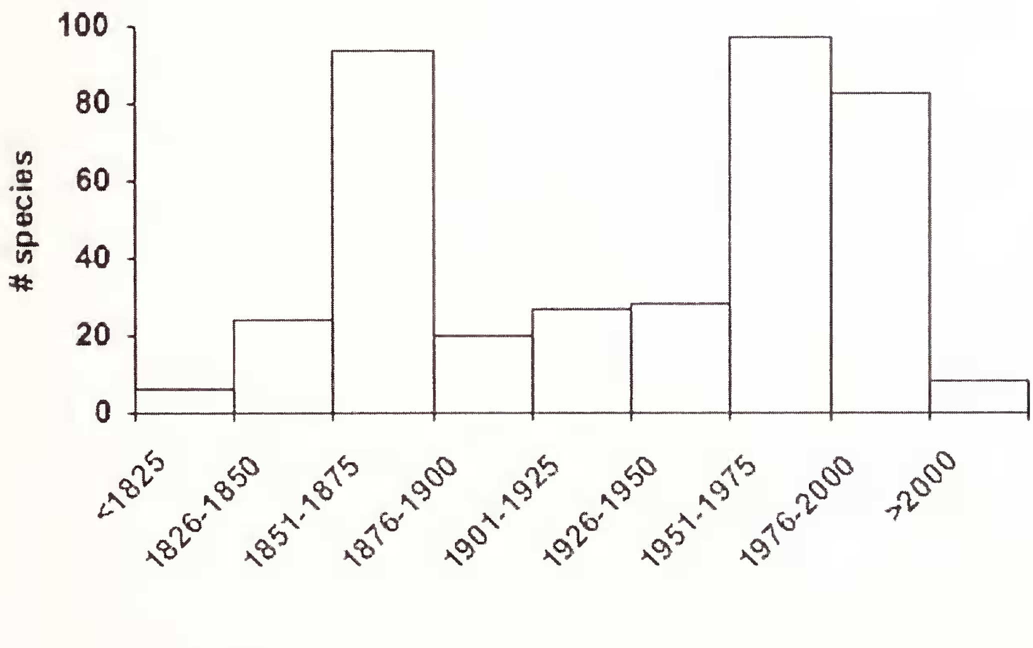

Fig. 2. Frequency of species descriptions through time.

Table 1. Number of species described by different authors (called "group(s)", when with one or several co-authors) through time. All nominal taxa have been included.

Author	# species described
Marcus (& Marcus), 1955–1982	39
Baba (et al.), 1935–1959	30
Jensen (et al.), 1980–1999	23
Bergh, 1871–1905	20
Pease, 1860–1871	17
Ortea (et al.), 1981–2006	15
Trinchese, 1869–1895	14
Ichikawa, 1993	11
Thompson (et al.), 1973–1988	10
A. Costa, 1862-1876	10
Total for 10 authors (groups)	189
Total # nominal species	387
Percentage described by 10 most productive authors (groups)	49
Total # authors (groups)	104
Average # species per author (group)	3.7

ing the 19th century is high, but many species have subsequently been synonymized. New species are still discovered (ORTEA & TEMPLADO 1990; PERRONE 1990; CERVERA et al. 1991), old synonyms resurrected (CERVERA & LOPEZ-GONZÁLEZ 1996; ORTEA & MORO 1998), and the validity of some species, even some of the more recently described ones, is still debated (CERVERA et al. 2006). In addition, species ranges appear to be expanding (THOMPSON 1983; ORTEA et al. 1997; EVERTSEN & BAKKEN 2002). Hence the present analyses represent an *ad hoc* picture of species distributions and diversity.

Three faunal provinces are recognized in the Northeast Atlantic: the warm temperate Mediterranean Sea, including the Black and Azov Seas (no sacoglossans occur in the Caspian and Aral Seas), the warm temperate Lusitanian province and the cold temperate Northeast Atlantic Boreal region (BRIGGS 1995). Three species appear to be endemic to the Northeast Atlantic cold-water region. However, two of these may be identical to Lusitanian and/or Mediterranean species. The possible synonymy of *Ercolania nigra* and *E. viridis* is currently under study by the present author, and it is also likely that *Calliopaea oopha-*

Table 2. Species distribution and endemicity of sacoglossan opisthobranch in biogeographic regions as defined by BRIGGS (1995). Only species considered valid in the present study have been included. n.d. not determined.

Region	# Species	# endemics (%)
1. Northeast Atlantic boreal	11	3* (27)
2. Lusitanian	40	5 (12.5)
3. Mediterranean + Black Sea	37	8 (22)
4. Northwest Atlantic boreal	6	1 (17)
5. Caribbean incl. Florida	49	21 (43)
6. Southwestern Atlantic tropical + warm temperate	19	3 (16)
7. Aleutian	6	0
8. Oregonian	8	0
9. Californian	9	0
10. Mexican-Panamanian	23	9 (39)
11. Southeast Pacific warm temperate	6	0
12. Cold temperate South America	4	2 (50)
13. Northwest Pacific cold temperate	29	5 (17)
14. Northwest Pacific warm temperate	41	9 (21)
15. North and Northwestern Australia	23	4 (17)
16. South and Southwestern Australia	22	6 (27)
17. Southeastern Australia	15	6 (40)
18. Northeastern Australia	18	1 (5.5)
19. Great Barrier Reef	22	0
20. New Zealand	5	1 (20)
21. Southeastern Atlantic	9	4 (44)
22. Western Indian Ocean + Red Sea	32	8 (25)
23. Indo-Polynesian, incl. Ryukyu Islands	107	n.d.
24. Hawaii	25	6 (24)

*Two of these species may be synonymous with Lusitanian and Mediterranean species.

Table 3. Similarity between provinces of the Atlantic Ocean. The Southeast Atlantic is excluded due to lack of information. In this and all following tables only species considered valid in the present study have been included. CJ Jaccard's Coefficient; SD Dice Coefficient; I Index of inclusion; N number of species included; n.d. not determined.

a.

CJ \ SD	**NE Atl cold N=11**	**NW Atl cold N=6**	**Lusitan. N=40**	**Medit N=38**	**Carib N=49**	**Brazil N=19**
NE Atl cold	-	23.5	27.5	28.6	3.33	n.d
NW Atl cold	13.3	-	8.70	9.09	14.5	n.d.
Lusitanian	15.9	4.55	-	66.7	31.5	13.6
Mediterranean	16.7	4.76	50.0	-	23.0	n.d.
Caribbean	1.69	7.84	18.7	13.0	-	47.1
Brazil	n.d.	n.d.	7.27	n.d.	30.8	-

b.

I	**NE Atl cold**	**NW Atl cold**	**Lusitanian**	**Medit**	**Carib**
NE Atl cold	-	-	-	-	-
NW Atl cold	33.3	-	-	-	-
Lusitanian	63.6	33.3	-	-	-
Mediterranean	63.6	33.3	68.4	-	-
Caribbean	9.09	66.7	35.0	26.3	-
Brazil	n.d.	n.d.	21.1	n.d.	84.2

ga Lemche, 1974 is a subtidal variety of *C. bellula* d'Orbigny, 1837. *Limapontia depressa* may be the only endemic from this cold-water region, and even that species may occasionally be found further south on the French Atlantic coast (M. Poddubetskaia, Bordeaux, pers. comm. 2006). The other two species of *Limapontia* only extend into the Lusitanian and/or Mediterranean province (Pruvot-Fol 1954; Schmekel & Portmann 1982); *L. capitata* occurs in all three provinces and *L. senestra* occurs in two provinces. *L. capitata* is also the only sacoglossan recorded from Iceland and the Faroe Islands (Platts 1985). Hence the genus *Limapontia* is probably a cold-water, eurythermal genus, which is endemic to the Northeast Atlantic-Mediterranean region. Various records exist of unidentified species of *Limapontia* from other regions (e.g. Engel et al. 1940; Burn 1973; Schrödl 1996). However, these need confirmation as many species of *Ercolania* lack cerata in juveniles.

One species, *Hermaea variopicta*, has its northern limit along the south coast of the UK (Lemche & Thompson 1974). Two species, *Elysia viridis* and *Calliopaea bellula*, have their northern limit around Trondheimfjord (Brattegard & Holthe 2001). Four species, *Alderia modesta, Placida dendritica, Limapontia capitata* and *L. senestra*, occur in the northernmost part of Norway (Vader 1981; Brattegard & Holthe 2001; Evertsen & Bakken 2002; pers. obs.), and all three species of *Limapontia* plus *Alderia modesta* have been recorded from the White Sea (Roginskaya 2000; Martynov et al. 2006). Prior to 1997 *P. dendritica* had not been recorded from Norway north of the Bergen area (Evertsen & Bakken 2002).

Five species appear to be endemic to the Lusitanian province. These have all been described after 1980, so it is possible that they will be found in neighboring regions in the future. The Canary Islands has the highest species diversity of this region (27 of 40 species have been recorded here). A number of Caribbean species have been recorded from these islands in recent years (Ortea et al. 1998). Since the sacoglossan fauna of these islands has been well documented over many years (Ortea 1981; Fernandez-Ovies & Ortea 1986; Cervera et al. 1988; Ortea et al. 1990; Templado et al. 1990), and only one or a few specimens have been collected at one single time far from their native distribution area, these species have most likely been transported by human activities (Chapman & Carlton 1991). Few species have been recorded from Madeira, Salvage, Cape Verde and Azores Islands (Ortea 1981; Ortea & Templado 1990; Ortea et al. 1988, 1990, 1998; Malaquias & Calado 1997; Jensen 1995, in prep.). There is an old record of the shelled *Ascobulla fragilis* from the Atlantic coast of Spain, which is cited in more recent publications (Pilsbry 1895; Pruvot-Fol 1954; Cervera et al. 2006). As this species feeds exclusively on *Caulerpa*, which does not extend this far north (Doumenge 1995), this needs to be re-examined.

Eight species are endemic to the Mediterranean. Some of these may be synonyms of other species with wider distributions (Schmekel & Portmann 1982; Thompson 1988). Eight amphi-Atlantic (one of which may be cosmopolitan), eight Northeast Atlantic-Lusitanian, and five endemic species do not extend into the eastern basin of the Mediterranean. Only four species found in the eastern basin of the Mediterrnanean do not occur in the western basin; two of these have been described recently (Thompson 1988). The total number of sacoglossans in the eastern basin is only 17 whereas 34 species are known from the western basin (Swennen 1961; Barash & Danin 1971; Schmekel & Portmann 1982; Thompson 1983; Bouchet 1984; Thompson et al. 1985; Thompson 1988; Thompson & Jaklin 1988; Cattaneo-Vietti & Thompson 1989; Cervera et al. 2006). The southern coast of the Mediterranean has been insufficiently studied. It is uncertain whether two or three species extend into the Black and Azov Seas. *Limapontia capitata* and *Calliopaea bellula* (as *Stiliger bellulus*) have been recorded previously (Murina & Artemjeva 1997), but recent pictures on the Sea Slug Forum (Kurakin 2002) have shown that *Ercolania viridis* is present, and it remains to be seen whether the species previously identified as *C. bellula* has been misidentified, or whether both species occur.

The Lusitanian and Mediterranean provinces have very high similarity indices (Table 3). The combined number of species amounts to 52, which is very close to the species diversity found in the Caribbean. However, the number of Plakobranchidae is lower in the eastern Atlantic provinces (Table 9).

Briggs (1995) recognizes one circumpolar Arctic region comprising Spitzbergen, Greenland and the northern coasts of North America and Russia. No sacoglossans have been recorded from Spitzbergen (Gulliksen et al. 1999) or the north coast of North America (Bleakney 1996; Goddard & Foster 2002). The four species occurring in the White Sea also occur in the Russian part of the Barents Sea (Roginskaya 2000; Martynov et al. 2006). In addition, Martynov et al. (2006) mentions an old record of a single juvenile specimen of *Placida dendritica* from Kola Bay. This indicates that this area is influenced by the North Atlantic Current and should be included in the boreal region. The single specimen of *Alderia modesta* recorded from western Greenland (Platts 1985) could be attributed to larvae transported from Canada, which may occasionally be able to find suitable habitats for metamorphosis in Greenland. The latitude of Disko Fjord is about the same as northern Norway, where the species occurs regularly. It should be mentioned that in Danish waters this species seems to have disappeared from localities where prior to 1997 it was abundant (pers. obs.). Whether this is due to habitat deterioration or increased temperature is unknown.

The fauna of the Northwest Atlantic is also very well studied (e.g. Marcus & Marcus 1970; Marcus 1972a,b; Marcus & Hughes 1974; Clark 1975; Jensen & Clark 1983; Bleakney 1996), though new species are still being described from the tropical waters (Ortea & Espinosa 1996, 2000, 2001, 2002; Caballer et al. 2006; Pierce et al. 2006). Only 6 species occur in the cold temperate province; one of these, *Placida dendritica*, may be cosmopolitan (Bleakney 1989) and one, *Alderia modesta*, is circum-boreal. Apparently only one species, *Elysia catulus*, is endemic to the Northwest Atlantic cold water region (Clark 1975). This species feeds on the seagrass *Zostera marina*, which does not occur in Florida. It is possible that *E. catulus* is a dark pigmented variety of the other seagrass feeding species, *Elysia serca* (Jensen 1982), in which case there will be no endemic species for the Northwest Atlantic. *Ercolania fuscata* may occur from Nova Scotia, Canada to Sao Paolo, Brazil, but this distribution is based on synonymization with *E. vanellus* and *E. talis* (Jensen & Clark 1983). Two species, *Elysia chlorotica* and *Hermaea cruciata*, have their southern limit in Florida (Jensen & Clark 1983), i.e., just south of the cold-water region. The former species also occurs in the northern part of the Gulf of Mexico (Boone 1982), and the latter has its northern limit in Massachusetts (Marcus 1972a). The species presently known as *Limapontia zonata*, and known only from its original collection (Gould & Binney 1870), is probably a flatworm; no sacoglossan has transverse pigment bands.

A separate Carolinian province could not be distinguished for sacoglossan opisthobranchs, and no difference is evident between the continental and insular parts of the Caribbean (Clark & DeFreese 1987), including Bermuda (Clark 1984), although these provinces were considered distinct by Briggs (1995). However, the majority of studies involving sacoglossans are from the Caribbean islands. The limit between cold-water and tropical faunas appears to be along the coast of Florida (Jensen & Clark 1983); 36 of the 49 Caribbean species have been recorded from Florida (Thompson 1977; Marcus 1977, 1980; Clark 1982; Clark & DeFreese 1987; Pierce et al. 2006; Valdés et al. 2006). The degree of endemism in the Caribbean is exceptionally high (Table 2). Especially the number of Plakobranchidae is high (Table 9), indicating that speciation in this family has taken place within the province. Five of the 21 endemic species have been described after 1990, so they may be found outside this province in the future or be synonymized with other species. As for the Mediteranean and Lusitanian provinces, synonymies are extensively debated and the status of several species remains uncertain (Jensen & Clark 1983; Marcus 1980; Valdés et al. 2006).

Table 4. Similarity of provinces of East Pacific. Due to the high similarity between Aleutian, Oregonian and Californian provinces, these have been merged (Al+Or+Cal). Other abbreviations as in Table 3.

a.

CJ \ SD	Aleutian N=6	Oregonian N=8	Californian N=9	Al+Or+Cal N=10	Mex-Panam N=23	SE Pacific N=9
Aleutian	-	85.7	66.7	-	27.6	n.d.
Oregonian	75.0	-	82.4	-	38.7	n.d.
Californian	50.0	70.0	-	-	50.0	n.d.
Al+Or+Cal	-	-	-	-	48.5	10.5
Mex-Panam	16.0	24.0	33.3	32.0	-	43.8
SE Pacific	n.d.	n.d.	n.d.	5.56	28.0	-

b.

I	Aleutian	Oregonian	Californian	Al+Or+Cal	Mex-Panam
Aleutian	-	-	-	-	-
Oregonian	100.0	-	-	-	-
Californian	83.3	87.5	-	-	-
Mex-Panam	66.7	75.0	88.9	80.0	-
SE Pacific	n.d.	n.d.	n.d.	11.1	77.8

The genus *Bosellia* appears to be an Atlantic warm-water genus with one amphi-Atlantic, one Canary Islands endemic (Fernandez-Ovies & Ortea 1986), and two Caribbean species (Marcus 1973). There are some scattered reports of *Bosellia* from the Indo-Pacific region (Marcus 1978; Imamoto 2004; Pittman 2004; Riek 2006). However, too few specimens have been recorded to either identify them as one of the described species or decide that they are undescribed species.

Briggs (1995) recognized a tropical Brazilian province extending to just south of Rio de Janeiro. For sacoglossans, most Brazilian species extend south to the area around Sao Paolo (Marcus (Er.) 1955, 1957; Marcus & Marcus 1967; Marcus (Ev.) 1977). This can probably be explained by the extensive collecting activity of the Marcuses around Sao Paolo; 47% of the Brazilian species have been described by them. Furthermore, more than 90% of the Brazilian species also occur in the Caribbean (Table 3b), and the number of endemic species is low (Table 2). This is most likely also due to the activities of the Marcuses in both these regions.

Trowbridge (2002) reviewed the Northeast Pacific sacoglossan fauna. She recognized four provinces, but unfortunately the borders are not exactly the same as suggested by Briggs (1995). This is especially evident for the Californian province, in which Trowbridge records one species of the bivalved genus *Berthelinia* plus a couple of unidentified/ undescribed species. The present study found no endemic species in the Aleutian, Oregonian and California provinces and hence these were merged. Also, no difference was obvious between the Mexican and Panamanian provinces, which have also been merged before comparisons with other provinces (Table 4). In the Mexican-Panamanian province four species have been recorded after the publication of Trowbridge's paper (Behrens & Hermosillo 2005; Krug et al. 2007) and one species, *Ascobulla californica* (originally described as *Cylindrobulla californica* by Hamatani (1971)), was not considered a sacoglossan by Trowbridge (2002). The occurrence of *Alderia modesta* in the Mexican-Panamanian region is probably the recently described species, *Alderia willowi* (Krug et al. 2007), which occurs southwards from central California. The monotypic genus *Olea* is endemic to the Northeastern Pacific region, extending from the Aleutian to the Californian province (Trowbridge 2002). *Hermaea vancouverensis* is a cold-water species, extending across the Bering Strait to the Kurile province (Chernyshev 2005). One species, *Elysia hedgpethi*, occurs from British Columbia, Canada to Chile (Schrödl 1996; Trowbridge 2002), though the occurrence in Chile needs verification.

The species extending into the warm temperate region of the Southeast Pacific almost all are shared with the tropical Mexican-Panamanian region (Schrödl 1996; Trowbridge 2002; Behrens & Hermosillo 2005). *Julia thecaphora* is considered the oldest name for *J. equatorialis*, which was also described from the tropical East Pacific. Only four species have been recorded from cold-temperate South America, one from the Atlantic coast and three from the Pacific (Marcus 1959; Schrödl 1996; Munian & Ortea 1997). Due to the low number of species and sparse collecting activity, the species from the Southeast Pacific coast have been considered as one province for analyses.

Table 5. Similarity of Japanese biogeographic provinces and of Northwest and Northeast Pacific provinces. The Japanese provinces have also been compared to the neighboring Central Pacific sub-province. Abbreviations: see Table 3.

a.

CJ \ SD	Japan cold temp., N=26	Japan warm temp., N=41	Ryukyu N=33	Central Pacif. N=51	NW Pacif. cold temp., N=29	NE Pacif. cold temp. N=10
Japanese cold temp.	-	59.7	27.1	26.0	-	n.d.
Japanese warm temp.	42.6	-	37.8	37.0	n.d.	n.d.
Ryukyu	15.7	23.3	-	38.1	n.d.	n.d.
Central Pacific	14.9	22.7	23.5	-	n.d.	n.d.
NW Pacific cold temp.	-	n.d.	n.d.	n.d.	-	20.5
NE Pacific cold temp.	n.d.	n.d.	n.d.	n.d.	11.4	-

b.

I	Japan cold temp.	Japan warm temp.	Ryukyu	NW Pacif. cold temp.
Japancse cold temp.	-	-	-	-
Japanese warm temp.	76.9	-	-	-
Ryukyu	30.8	42.4	-	-
Central Pacific	38.5	41.5	48.5	-
NE Pacific cold temp	-	n.d.	n.d.	40.0

Four biogeographic regions or provinces can be distinguished along the coasts of Japan. Biogeographically the southernmost archipelago of Ryukyu belongs in the vast tropical Indo-Polynesian province (Briggs 1995), but being under Japanese jurisdiction, the sacoglossan fauna has been studied mostly by Japanese scientists (e.g. Baba 1936; Hamatani 1980; Ichikawa 1993). Hence Ryukyu has been included in both analyses of the Japanese fauna (Table 5) and of the Indo-West Pacific one (Table 7). The warm-water temperate region comprises southern and eastern Japan, including the well studied Seto Inland Sea and Sagami Bay. The corresponding continental coast of China has been insufficiently studied, and only 14 species have been recorded from southern Korea (Koh 2002a,b, 2003, 2005a,b,c; Rudman, Sydney, pers. comm. 2007). The cold-water temperate oriental province includes the central and western coasts of Honshu, whereas the northernmost island of Hokkaido belongs to the Kurile province (Briggs 1995). The cold-temperate fauna of Japan contains more species (N=26) than any other cold-water fauna. A few shelled species extend into this province, which is also seen in southern Australia, but not in other cold-water provinces. Only three additional sacoglossan species have been recorded from the Kurile province (Baba 1935; Chernyshev & Chaban 2005; Trowbridge 2006) and these were only included in the comparison of Northeast and Northwest Pacific cold-water faunas (Table 5). The highest number of species has been recorded from the warm temperate region (e.g. Baba 1949, 1952a,b, 1955, 1957, 1959, 1966; 1968; Hamatani 1968, 1969, 1972, 1976a,b, 1994; Kawaguti & Baba 1959; Hirano et al. 2006); in fact Baba described 59% of the species from this province and 69% of the species from the cold-water region of Japan. A few of the species described by Baba have been synonymized with more widespread Indo-West Pacific species (Baba 1974; Jensen 1985). On the other hand, many of Baba's species have been identified outside Japan (Jensen 1985; Carlson & Hoff 1978, 2003; Burn 1998, 2006).

The Northeast Australian and Great Barrier Reef faunas (Burn 1966b; Thompson 1973; Marshall & Willan 1999; Wägele & Johnson 2001) are so closely related to each other that no endemics have been recorded from the Great Barrier Reef and only one endemic species, *Placida fralila*, has been recorded from Northeast Australia (Table 2). Hence these two provinces were merged for similarity analyses, and the combined province has two endemic species (*Elysia bennettae, P. fralila*). For the Great Barrier Reef 30% of the species were listed as unidentified and/or undescribed (Marshall & Willan 1999). This part of Australia has been included in the Indo-Polynesian province by Briggs (1995). This is supported by the low endemicity, and also, the similarity with the fauna of the South Pacific islands is higher than with any of the other Australian provinces (Tables 6 and 7). The North and Northwestern Australian fauna has rather high similarity to the Western Indian Ocean fauna (Table 7). This is in spite of the fact that almost 40% of the species have been described by the present author within the last 20 years (Jensen 1993b, 1997b,c; Jensen & Wells 1990). The fauna of the South and Southwestern Australia has

Table 6. Similarity of provinces of the Australian continent. Due to the high similarity between the Northeast Australian province and the Great Barrier Reef, these two provinces have been merged (NE Aus+GBR). Abbreviations as in Tab. 3.

a.

CJ \ SD	**NE Austr N=18**	**GBR N=22**	**NE Aus+ GBR N=28**	**N+NW Austr N=23**	**SW+S Austr N=22**	**SE Austr N=15**
NE Australia	-	60.0	-	34.1	30.0	30.3
GBR	42.9	-	-	26.7	18.2	16.2
NE Aus+GBR	-	-	-	31.4	28.0	27.9
N+NW Austr	20.6	15.4	19.0	-	48.8	26.3
SW+S Austr	17.6	10.0	16.3	32.4	-	43.2
SE Austr	17.9	8.82	16.2	15.2	27.6	-

b.

I	**NE Austr**	**GBR**	**NE Aus+GBR**	**N+NW Austr**	**SW+S Austr**
NE Australia	-	-	-	-	-
GBR	66.7	-	-	-	-
NE Aus+GBR	-	-	-	-	-
N+NW Austr	38.9	27.3	34.8	-	-
SW+S Austr	33.3	18.2	31.8	50.0	-
SE Austr	33.3	20.0	40.0	33.3	53.3

the highest affinity to the fauna of North and Northwestern Australia, and the other way around, whereas the fauna of Southeastern Australia (Burn 1958, 1960, 1965, 1974, 1998, 2006) has a higher affinity to the fauna of South and Southwestern Australia than to that of Northeastern Australia and the Great Barrier Reef (Table 6). This may change when the 50% unidentified/undescribed species listed for Southeastern Australia (Burn 2006) are properly named.

Very few sacoglossans have been recorded from New Zealand (Powell 1937; Willan & Morton 1984; Trowbridge 1995a; Spencer & Willan 1995). The fauna consists of widespread species and one endemic (Table 2). Hence this fauna has not been further analyzed in the present study.

The sacoglossan fauna of the Red Sea (Eliot 1908; O'-Donoghue 1929; Heller & Thompson 1983) has about the same affinity to the fauna of the Indian subcontinent as to the Western Indian Ocean, and the index of inclusiveness (I) for the Red Sea and India *sensu lato (s.l.*, see below) is twice that for the Red Sea and the Western Indian Ocean (Table 7b). Also, two out of the ten recorded species are endemic to the Red Sea. Hence the Red Sea should be considered a separate province. In other groups of invertebrates Lessepsian migrants are common. For sacoglossans this appears to be a small and recent problem (Yokes 2001, 2002; Rudman 2002). Except for these few species, the Red Sea does not share any species with the Mediterranean.

The sacoglossans found in southwestern Africa are more closely related to those found in southeastern Africa than to any other region or province (Gosliner 1987a); in fact no species are shared with the Brazilian fauna and only one species, *Placida dendritica*, is shared with the Lusitanian province. Hence this province has been considered in connection with the Western Indian Ocean province. Endemicity is high, but this could be due to the poor knowledge of tropical western Africa. Only one species has been described from this region (Marcus & Marcus 1966), so this was not included in the present study. The East Atlantic species *Elysia viridis* apparently occurs from central Norway (Brattegard & Holthe 2001) to South Africa (Gosliner 1987a), though no records exist between the Senegal (Pruvot-Fol 1953) and South Africa, and Gosliner (1998) has subsequently changed the identification to *Elysia* sp. The species was originally identified in South Africa as the Indian species *E. punctata* by Macnae (1954). Gosliner (1987a) found a distinct faunal separation for opisthobranchs at Port Elizabeth, whereas Briggs (1995) considers the coast between the Cape of Good Hope and north of Durban one province. In the present study Port Elizabeth has been used to separate the faunas of southwestern Africa and the Western Indian Ocean.

The Western Indian Ocean is considered a separate province by Briggs (1995). The sacoglossan fauna of this province has a high similarity with the South Pacific and North and Northwestern Australia (Table 7). The affinity with the fauna of India *s.l.* (India, Sri Lanka and Maldives) is considerably lower, and also the affinity with the Indo-

Table 7. Similarity of provinces of the Australian continent. Due to the high similarity between the Northeast Australian province and the Great Barrier Reef, these two provinces have been merged (NE Aus+GBR). Abbreviations as in Tab. 3.

a.

CJ \ SD	SW Afr. N=8	WIO N=27	Red Sea N=10	India *s. l.* N=20	Indo-Malay N=48	N+NW Austr N=23	Centr. Pac. isl. N=51	NE Aus + GBR N=28	S Pacific N=33	Hawaii N=25	Ryukyu N=33
SW Afr.	-	28.6	11.1	7.14	n.d.	12.9	n.d.	n.d.	9.76	n.d.	n.d.
WIO	16.7	-	27.0	17.0	24.0	32.0	35.9	25.5	36.7	n.d.	n.d.
Red Sea	5.88	15.6	-	26.7	n.d.	18.2	n.d.	n.d.	18.6	n.d.	n.d.
India *s. l.*	3.70	9.30	15.4	- 20.6	14.0	19.7	12.5	22.6	17.8	7.55	
Indo-Malay	n.d.	13.6	n.d.	11.5	-	22.5	50.5	28.9	37.0	19.2	24.7
N+NW Austr	6.90	19.0	10.0	7.50	12.7	-	29.7	31.4	32.1	n.d.	n.d.
Centr. Pac. isl.	n.d.	21.9	n.d.	10.9	33.8	17.5	-	43.0	50.0	42.1	38.1
NE Aus+GBR	n.d.	14.6	n.d.	6.67	16.9	19.0	27.4	-	42.6	n.d.	n.d.
S Pacific	5.13	22.4	10.3	12.8	22.7	19.1	33.3	27.1	-	41.2	24.2
Hawaii	n.d.	n.d.	n.d.	9.76	10.6	n.d.	26.7	n.d.	26.1	-	13.8
Ryukyu	n.d.	n.d.	n.d.	3.92	14.1	n.d.	23.5	n.d.	13.8	7.41	-

b.

I	SW Afr.	WIO	Red Sea	India *s. l.*	Indo-Malay	N+NW Austr.	Centr. Pac. isl.	NE Aus + GBR	S Pacific	Hawai
SW Afr.	-	-	-	- -	-	-	-	-	-	-
WIO	62.5	-	-	- -	-	-	-	-	-	-
Red Sea	12.5	50.0	-	- -	-	-	-	-	-	-
India *s. l.*	12.5	20.0	40.0	- -	-	-	-	-	-	-
Indo-Malay	n.d.	33.3	n.d.	35.0	-	-	-	-	-	-
N+NW Austr	25.0	34.9	30.0	15.0	34.8	-	-	-	-	-
Centr. Pac. isl.	n.d.	51.9	n.d.	35.0	52.1	47.8	-	-	-	-
NE Aus+GBR	n.d.	25.9	n.d.	15.0	39.3	34.8	60.7	-	-	-
S Pacific	25.0	40.7	40.0	30.0	45.5	39.1	63.6	46.4	-	-
Hawaii	n.d.	n.d.	n.d.	20.0	28.0	n.d.	64.0	n.d.	48.0	-
Ryukyu	n.d.	n.d.	n.d.	10.0	30.3	n.d.	48.5	n.d.	24.2	16.0

Malayan sub-province is lower. Endemicity is high (5 of 27 species), though two of these species have sometimes been synonymized with widespread Indo-West Pacific species (GOSLINER 1987b). The majority of species recorded from the Western Indian Ocean have been collected from the southern part of the region, i.e. South Africa (THOMPSON 1979; GOSLINER 1987a,b, 1995), Tanzania (ELIOT 1903, 1904; GOSLINER 1995), Madagascar (GOSLINER 1995) and Mauritius (BERGH 1888; GOSLINER 1995).

A total of 107 species of sacoglossans have been recorded from the vast Indo-Polynesian province. Most of these species are only distributed in part of the province and hence it was subdivided into five sub-provinces: The Indian subcontinent, including Sri Lanka and the Maldive Islands was considered one sub-province (10 endemic species); the Andaman Sea, the South China Sea, Indonesia and the Philippines form an Indo-Malayan sub-province (9 endemic species); the Mariana and Marshall Islands together with Micronesia were considered a Central Pacific sub-province (4 endemic species); Papua New Guinea, Solomon Islands, Fiji, Vanuatu, New Caledonia, Samoa and the Polynesian islands form a South Pacific province (6 endemic species); and as mentioned above the Ryukyu Islands form a separate sub-province (10 endemic species). Many of the endemic species have been described within the last 20 years, so they may actually have wider distributions.

Of the 107 species recorded from the Indo-Polynesian province only 12 have distributions from the Western Indian Ocean and/or the Red Sea to the Central and/or South Pacific islands, two species, *Elysia ornata* and *Ercolania coerulea*, are circum-tropical and one, *Placida dendritica*, may be cosmopolitan. Two of the 12 widespread Indo-West Pacific species are shelled (*Oxynoe viridis* and *Berthelinia schlumbergeri*), seven are plakobranchoids (5 species of *Thuridilla, Elysiella pusilla* and *Plakobranchus ocellatus*) and three are limapontioids *(Cyerce elegans, C. nigricans* and *Polybranchia orientalis*). The widest latitudinal distributions along the West Pacific rim are found in the four species that occur from the cold-temperate part of Japan to the cold-temperate part of Australia. Two of these species are the circum-tropical *Elysia ornata* and the questionably cosmopolitan *Placida dendritica*; the other two are *Elysia obtusa* and *Stiliger smaragdinus*. *P. dendritica* has been synonymized with a number of species described from different places in the Indo-West Pacific (BLEAKNEY 1989), but the synonymy has been doubted (e.g. TROWBRIDGE 1995b). Two species, *Oxynoe viridis* and *Elysiella pusilla*, extend from warm-temperate Japan to southern Australia. Two further species, *Thuridilla splendens* and *Polybranchia orientalis*, extend from warm-temperate Japan to Northeast Australia and the Great Barrier Reef. Four species, *Plakobranchus ocellatus, Thuridilla vatae, T. hoffae* and *Cyerce nigricans*, extend from the Ryukyu Islands to tropical Australia. Most of these species also have wide longitudinal distributions. *Plakobranchus ocellatus* occurs in a number of colour varieties, and it is possible that a complex of sibling species is involved (see discussion on the Sea Slug Forum: http://www.seaslugforum.net/find.cfm?id=13970) (last access 12th of August 2007).

The Indian sub-province has a high proportion of endemic species (50%). This is probably an artifact due to the activities of a few taxonomists who have worked only within this sub-province (KELAART 1858; NEVILL & NEVILL 1869; RAO 1937; RAO & RAO 1963; SARMA 1975). Most of G. & H. NEVILL's species have been synonymized, though not consistently with the same species. Although doubtful, they have been considered valid in the present study. The species described by KELAART have been re-examined several times (ELIOT 1906; O'DONOGHUE 1932) and they are still recognized as valid, mostly widespread Indo-West Pacific species. In spite of the high endemicity, India *s.l.* shows higher similarity to the Indo-Malayan, Central and South Pacific sub-provinces than to the Western Indian Ocean province (Table 7). The highest similarity is found between India *s.l.* and the Red Sea, but this is caused by the low number of species found in the Red Sea, and the high proportion of widespread Indo-West Pacific species.

The Indo-Malayan and Central Pacific sub-provinces have twice the number of species occurring in tropical Australia and the Western Indian Ocean and 50% more species than the South Pacific and Ryukyu Islands. This could be seen as evidence for being a center of origin for evolution of new species. Looking at species composition in the central Pacific islands (data from MARCUS 1965; JOHNSON & BOUCHER 1983; CARLSON & HOFF 2003), it seems more likely that they are "traps", where species dispersing from the Japanese warm-temperate and from tropical and possibly even warm-temperate Australia can find suitable habitats. The Central Pacific sub-province is the only one with less than 10% endemics, but many unidentified and/or undescribed species are known from this sub-province (CARLSON & HOFF 2003; own obs.). Most biogeographic studies indicate that the triangle consisting of Indonesia, Malaysia and the Philippines and sometimes including Papua New Guinea has the highest number of species (EKMAN 1953; BRIGGS 1995, 2005). Information on sacoglossan distributions in the Indo-Malayan sub-province has been collected from numerous sources (e.g. BERGH 1871, 1872, 1905; ELIOT 1917; LIN 1986, 1990; GOSLINER 1995; GOSLINER et al. 1996; DEBELIUS 1996; JENSEN 1998a,b, 2003; SWENNEN et al. 2001). The number of sacoglossan species is slightly lower in this sub-province than in the islands of the Central West Pacific, i.e. Marianas, Marshall Islands and Micronesia. This may be a collecting artifact caused by the activities of Carlson and Hoff in Guam and neighboring islands; they recorded 91 species of which 48 (53%) were identified to species level (CARLSON & HOFF 2003). However, the present similarity analyses also indicate that these islands constitute the center of species diversity. Species described from northern Australia, the South China Sea and southern Japan also occur in the Mariana Islands. The genus *Gascoignella* is endemic to the Indo-Malayan province (JENSEN 1985; SWENNEN 2001), and the genus *Sohgenia* is endemic to the Central Pacific islands (HAMATANI 1991). However, with one exception, these species have been described within the last 20 years, so they may have wider distributions.

BRIGGS (1995) considered the Hawaiian islands a separate region. The Hawaiian islands have a high endemicity (OSTERGAARD 1955; KAY 1967; present study), but the present study has shown that they also have a rather high similarity to the other islands of the Central and South Pacific (Table 7).

The islands of the South Pacific have been rather sporadically studied (PEASE 1861, 1866, 1868, 1871; ELIOT 1899; RISBEC 1928, 1953; BURN 1966a; MILLER 1969; BRODIE & BRODIE 1990; GOSLINER 1995). Hence the total number of species as well as the number of endemics may be considerably higher. GOSLINER & DRAHEIM (1996) estimated that more than 40% of the opisthobranch species from Papua New Guinea are undescribed. For the Fiji Islands 30% of the species have not been identified to species level (BRODIE & BRODIE 1990). For the sacoglossans most of the old species are poorly described and need re-examination.

4. DISCUSSION

Sacoglossans are small, often cryptically colored species and they are therefore difficult to collect. This means that only a few biogeographic provinces have been thoroughly studied. In recent years international workshops and biodiversity programs have greatly increased the number of sacoglossans known from more remote localities, especially in tropical waters (Jensen 1985, 1990, 1993b, 1997b,c, 1999, 2003; Jensen & Wells 1990; Ichikawa 1993; Gosliner 1995; Swennen 1997, 2001; Ortea & Templado 1988; Ortea & Espinosa 1996, 2000, 2001, 2002; Caballer et al. 2006; Munian & Ortea 1997). The present study has reviewed the existing information about sacoglossan distributions and analyzed the data for endemicity and similarity among provinces. Although the data are biased with regards to collecting efforts of a few highly active scientists, several patterns have emerged from these analyses. The collection bias is most obvious in the areas where few other observations have been made, e.g. the Brazilian region where basically all collections have been made by the Marcuses. However, the species richness and endemicity does not differ from that of other tropical regions with no collection bias. The same seems to be true for the Japanese fauna, where Baba has described most of the species. The sacoglossan fauna of the Indian sub-province has been studied by several taxonomists, but in this case endemicity seems remarkably high. One reason for this is that descriptions have been published in local journals and therefore overlooked by other taxonomists.

Overall the distributions of sacoglossans correspond to the biogeographic regions and provinces identified by Briggs (1995). The exceptions have been pointed out above. Some of the provinces identified contain less than 10 species, which means that just one endemic species will yield more than 10% endemicity. Obviously this cannot be used to make conclusions about their distinctiveness.

Table 8. Number of species and endemicity of the tropical provinces and sub-provinces of the Indo-West Pacific region.

Province/ subprovince	# species	# endemics (%)
Western Indian Ocean	27	5 (19)
Red Sea	10	2 (20)
India *s.l.*	20	10 (50)
Indo-Malayan	48	9 (19)
Central Pacific	51	4 (8)
Ryukyu	33	10 (30)
Hawaii	25	6 (24)
S Pacific	33	6 (18)
Northeast Australia + Great Barrier Reef	28	2 (7)
North and Northwestern Australia	23	4 (17)

The records listed in existing literature do not usually have longitude and latitude, and many locality names are ambiguous or oblivious. Consequently it has not been possible to construct a "degree-by-degree" plot of species distributions for analysis. Nevertheless, the latitudinal decrease in species diversity from warm to cold temperate provinces is spectacular. Sacoglossans are dietary specialists and the majority of species feed on siphonaceous green algae, which are much more abundant and diverse in tropical and warm temperate waters. The cold temperate sacoglossan faunas of the North Atlantic as well as the Northeast Pacific Ocean are mostly eurythermic species with wide latitudinal distributions, extending well into neighboring warm water regions; indices of inclusion are over 60% (Tables 3b, 4b). This is also seen in Japan (Table 5b) and southern Africa between the tropical western Indian Ocean and the warm temperate southwestern Africa (Table 7b), but not nearly as pronounced in Australia (Table 6b). This apparently supports Rapoport's rule that species ranges in high latitudes are larger than in low latitudes. However, there are great differences between the provinces. The Northeast Pacific coldwater fauna is 43% of the tropical fauna, the Northeast Atlantic boreal fauna is 21% of the combined Lusitanian and Mediterranean fauna, and the Northwest Atlantic boreal fauna is only 12% of the Caribbean fauna.

The number of amphi-Atlantic species is relatively high, especially for the warm-water/tropical faunas (Ortea et al. 1997; present study): 16 species (about 30%) occur in the Caribbean and the Lusitanian and/or Mediterranean provinces. However, amphi-Atlantic distributions for most of these species have only been recognized in recent years (Templado et al. 1990; Ortea et al. 1988, 1998), and it cannot be excluded that human introductions are involved. Contrary to this, only one cold-temperate species, *Hermaea vancouverensis*, has an amphi-Pacific distribution. *Alderia modesta* has a circum-boreal/arctic distribution. *Elysiella pusilla* has recently been recorded from the Mexican-Panamanian province (Behrens & Hermosillo 2005). However, it cannot be excluded that this is a human introduction. The same is true for *Ercolania boodleae*, a Japanese species, which has been recorded from California (Behrens 1991); this may also be a misidentification (Trowbridge 2002). The so-called circum-tropical species, *Elysia ornata* and *Ercolania coerulea*, are conspicuously absent from tropical eastern Pacific; they extend from the Caribbean to the South and/or Central Pacific islands. *Lobiger souverbii*, which has been synonymized with several Indo-West Pacific species (Kay 1964; Baba 1974; Gosliner 1987a; Gosliner et al. 1996), and which occurs in the Caribbean as well

Table 9. Distribution of species of the Oxynoacea, Plakobranchoidea and Limapontioidea in provinces supported by present study.

Region	Oxynoacea	Plakobranchoidea	Limapontioidea
NE Atlantic	0	1	10
Lusitanian	4	10	26
Mediterranean	3	11	24
NW Atlantic	0	2	4
Caribbean	6	25	23
NE Pacif. warm + cold	0	1	9
Mexican-Panamanian	5	6	12
SE Pacific	4	2	3
Hawaii	7	13	5
Japan cold temp.	3	11	12
Japan warm temp.	9	18	14
Ryukyu Islands	9	15	11
Australia, tropical	9	20	14
Australia, warm + cold	8	10	11
W Indian Ocean	9	18	8
India, Sri Lanka, Maldi.	8	8	4
Indo-Malaya	5	29	14
Central Pacific	10	25	16
SW Pacific	12	17	4

as Mexican-Panamanian province (Behrens 1991; Trowbridge 2002), may be the only truly circum-tropical species. Very few species are shared between the Caribbean and Mexican-Panamanian provinces, but there is probably a sister-taxon relationship between the East Pacific *Elysia diomedea* (formerly *Tridachiella diomedea*) and the Caribbean *E. crispata* (formerly *Tridachia crispata*) and *E. clarki*. Thus the Central American land bridge is as effective a geographical separation as the natural land barrier between the Red Sea and the Mediterranean. Also the few species occurring on both sides of the Isthmus of Panama may have arrived on the Pacific side as hitch-hikers on ships travelling through the Panama Canal.

The subdivision of the Indo-Polynesian province used in the present study may seem rather arbitrary. In many studies Papua New Guinea is considered a part of the Indo-Malayan sub-province, whereas it has been included in the South Pacific sub-province here. Only 14 species have been identified from Papua New Guinea, which is obviously an underrepresentation; Gosliner (1992) gives 61 species for this area, but most are undescribed or have not been identified to species. Only sacoglossans that have been identified to species level can be used for calculating similarities between different sub-provinces. The 14 species are almost all widespread species found in the Indo-Malayan as well as the Central Pacific sub-provinces. The one species that does not occur in these sub-provinces, *Elysia expansa*, has its main distribution in tropical Australia. Geologically Papua New Guinea has been associated with the Australian continent (Briggs 1995).

The number of species decreases with longitude to the west of the Central Pacific islands, from 51 through 48 in the Indo-Malayan sub-province to 20 in the Indian sub-province and 27 in the Western Indian Ocean province. The majority of species in the latter province have widespread distributions, whereas less than half the species in the Indian sub-province belong in this category. A less pronounced longitudinal decrease is seen from 33 species in the South Pacific islands through 28 in northeastern Australia to 23 in northwestern Australia.

The number of species of the Central and South Pacific islands, including Ryukyu, is at least 50% higher than the number of species in tropical East Pacific. This is in spite of the fact that the combined area of these islands is relatively small. On the other hand the endemicity of these islands is relatively low except in the Ryukyu Islands (Table 8). This means that insular isolation has not resulted in extensive speciation (or that subsequent dispersal has obscured such speciation). The high endemicity of Ryukyu is almost entirely attributable to one fairly recent publication: Ichikawa (1993).

Looking at distribution within subordinal taxa of the Sacoglossa, it is obvious that the shelled suborder Oxynoacea, which all feed exclusively on algae of the genus *Caulerpa*, is restricted by the distribution of this alga. In the North Atlantic shelled sacoglossans occur in Bermuda, but there is a questionable record of *Ascobulla fragilis* from the northern part of Spain (see above). In the East Pacific shelled species are found in the Panamanian region, but also in the southernmost part of the Gulf of California. In the West Pacific shelled species occur in the warm temperate region. The only places where shelled species occur in cold temperate waters are Victoria, southeastern Australia and the west coast of central Japan. These places also have species diversity of *Caulerpa* rivaling many tropical and warm temperate provinces (Doumenge 1995; Prud'homme van Reine et al. 1996). The two nonshelled superfamilies, Plakobranchoidea and Limapontioidea, occur in all provinces where sacoglossans are found.

At the family level, the bivalved Juliidae are absent from the eastern Atlantic. Since they are common as fossils from this region, this must be due to extinction. Juliidae and Volvatellidae are rare in the Atlantic and eastern Pacific. On the other hand, Limapontioidea are highly diverse in the northeastern Atlantic and Mediterranean (Table 9). The least studied areas have the fewest Limapontioidae. This is probably due to the very small size (<10 mm) of most of these species. In tropical regions the number of Plakobranchioidea is always higher than the number of species in the other superfamilies. Plakobranchoidea are most diverse in the Caribbean region and in the Indo-Malayan and Central Pacific islands sub-provinces; tropical Australia also has a high proportion of this superfamily (Table 9).

Only rarely are more than two or three species of one genus found in one area. However, for the genera *Elysia* and *Thuridilla* many places have more than 5 species, and in a few cases more than 10 species may co-occur, though on different food algae. Whether this is due to sym- or parapatric speciation or dispersal following allopatric speciation, as suggested by Gosliner (1995), cannot be deducted from existing information. Phylogenetic analysis, preferably including molecular data should be applied to these genera[1].

Some genera are restricted to one or a few neighboring biogeographic provinces. *Limapontia* only occurs in the Northeast Atlantic and Mediterranean region. This may also be the case for the genus *Calliopaea*, though the Japanese *Stiliger pusillus* has been tentatively assigned to this genus (Baba & Hamatani 1970). The monotypic *Platyhedyle* only occurs in the Mediterranean (Wawra 1979), whereas the genus *Gascoignella*, which has been assigned to the same family, Platyhedylidae (Jensen 1996a), seems restricted to the South China Sea (Jensen 1985; Swennen 2001). The monotypic genus *Olea* is restricted to the Northeast Pacific (Trowbridge 2002). The genus *Bosellia* may have its natural distribution restricted to tropical and warm temperate Atlantic and Mediterranean (Marcus 1973; Fernandez-Ovies & Ortea 1986), and the monotypic genus *Sohgenia* has only been found in the Central Pacific islands (Hamatani 1991). Common to all of the above genera is that they have morphological characters that appear to be reduced compared to other genera in the same superfamilies; they either lack or have very reduced rhinophores, cerata or parapodia (or a combination of these). The genera *Roburnella, Plakobranchus* and *Pattyclaya* are Indo-west Pacific endemics, the former furthermore restricted to southern Australia, and *Julia* and *Elysiella* also occur in the eastern Pacific. Within the more speciose genera, many have few (1-3) representatives in the Atlantic Ocean, zero in the East Pacific, and the remaining species are Indo-West Pacific. This is seen in *Volvatella, Thuridilla* and *Costasiella*, indicating that the Atlantic fauna is a Tethyan relict fauna with little subsequent speciation, except in the genus *Elysia* in the Caribbean. However, the high number of limapontioid species seems to contradict this. It is possible that the lack of plakobranchoids first spurred a burst of speciation of limapontioids in the East Atlantic/Mediterranean, whereas the speciation in Caribbean *Elysia* may be a more recent phenomenon.

The present study is a preliminary analysis of biogeographic affinities of sacoglossan opisthobranchs. Nevertheless several patterns have been identified, which should be further investigated using phylogenetic analyses. Also, some obvious gaps in the existing knowledge as well as conflicting and/or questionable records have been identified. There is an urgent need to describe the undescribed species known from the Indo-West Pacific region and to collect sacoglossans from poorly studied regions. Finally, several new hypotheses emerge from the present analyses, which should be tested in the future: the genus *Elysia* has speciated within the Caribbean; warm temperate Australia and Japan are centers of speciation; the appearance of several Caribbean species in the Canary Islands is due to human activities.

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Appendix

List of nominal species of recent Sacoglossa, authorship and type localities. Species are arranged alphabetically within families and superfamilies. Valid species (and species for which synonymy has been contested) are listed with their current generic name. Species considered invalid in the present study are marked with an *.

Species	Author	Type locality
Oxynoacea		
Volvatellidae		
Ascobulla californica	(Hamatani, 1971)	Gulf of California
Ascobulla fischeri	(Adams & Angas, 1864)	"South Australia"
Ascobulla fragilis	(Jeffreys, 1856)	Mediterranean
Ascobulla japonica	(Hamatani, 1969)	Kii, Middle Japan
Ascobulla? pusilla	(Nevill & Nevill, 1869)	Sri Lanka
Ascobulla souverbiei	(Montrouzier in Souverbie & Montrouzier, 1874)	New Caledonia
*Ascobulla? systremma**	(Melvill, 1918)	Gulf of Oman
Ascobulla ulla	(Marcus & Marcus, 1970)	E of Santos, Brazil
*Ascobulla? turtoni**	(Bartsch, 1915)	South Africa
Volvatella angeliniana	Ichikawa, 1993	Sesoko Isl., Ryukyu
Volvatella australis	Jensen, 1997	Darwin Harbour, N Australia
Volvatella ayakii	Hamatani, 1972	Kii, Middle Japan
Volvatella bermudae	Clark, 1982	Bermuda
Volvatella candida	Pease, 1868	French Polynesia
Volvatella cincta	Nevill & Nevill, 1869	Sri Lanka
Volvatella elioti	(Evans, 1950)	Zanzibar
Volvatella evansi	(Kay, 1961)	Oahu, Hawaii
Volvatella ficula	Burn, 1966	Fiji
Volvatella fragilis	Pease, 1860	Sandwich Islands
*Volvatella kawamurai**	Habe, 1946	Japan
Volvatella laguncula	Sowerby, 1894	Port Elizabeth, S Africa
Volvatella omega	(Melvill, 1918)	Gulf of Oman
Volvatella pyriformis	Pease, 1868	Huaheine, French Polynesia
Volvatella ventricosa	Jensen & Wells, 1990	Albany, SW Australia
Volvatella vigourouxi	(Montrouzier, 1861)	New Caledonia
Volvatella viridis	Hamatani, 1976	Amami Islands, Japan
Juliidae		
Berthelinia (Midorigai) australis	(Burn, 1960)	Torquay, Victoria, Australia
Berthelinia (Tamanovalva) babai	(Burn, 1965)	Torquay, Victoria, Australia
Berthelinia caribbea	Edmunds, 1963	Port Royal, Jamaica
Berthelinia chloris	(Dall, 1918)	Baja California, W Mexico
*Berthelinia corallensis**	Hedley, 1920	Queensland, Australia
Berthelinia darwini	Jensen, 1997	Darwin Harbour, N Australia
Berthelinia (Tamanovalva) fijiensis	(Burn, 1966)	Fiji
Berthelinia ganapati	Sarma, 1975	SE India
Berthelinia (Tamanovalva) limax	(Kawaguti & Baba, 1959)	Seto, Japan
Berthelinia pseudochloris	Kay, 1964	Kauai, Hawaii
Berthelinia rottnesti	Jensen, 1993	Rottnest Island, SW Australia
Berthelinia schlumbergeri	Dautzenberg, 1895	Madagascar
Berthelinia (Edenttellina) typica	(Gatliff & Gabriel, 1911)	Port Phillip, Victoria, Australia
Berthelinia waltairensis	Sarma, 1975	SE India
*Julia borbonica**	(Deshayes, 1863)	Reunion
Julia burni	Sarma, 1975	Andaman Islands, India
*Julia cornuta**	(De Folin, 1867)	Mauritius
*Julia equatorialis**	Pilsbry & Olsson, 1944	N of Mancara, Peru
Julia exquisita	Gould, 1862	Hawaiian Islands
Julia japonica	Kuroda & Habe, 1951	Wakayama, Honshu, Japan
Julia mishimaensis	Kawaguti & Yamasu, 1982	Yamaguchi Pref. Japan
Julia thecaphora	(Carpenter, 1857)	Mazatlán, Mexico(?)
Julia zebra	Kawaguti 1981	Yamaguchi Pref. Japan
Oxynoidae		
*Icarus gravesii**	Forbes, 1844	Aegean Sea
*Lobiger corneus**	Mörch, 1863	? (Cuming collection)

*Lobiger cumingi**	(A. Adams, 1850)	Puerto St. Elena, W Colombia
Lobiger nevilli	Pilsbry, 1896	n.n. for L. viridis G. &. H. Nevill, 1869
*Lobiger pellucidus**	A. Adams, 1854	unknown (Cuming collection)
*Lobiger philippi**	Krohn, 1847	Sicily, Italy
*Lobiger pilsbryi**	Schwengel, 1941	Sanibel Isl., Florida
*Lobiger picta**	Pease, 1868	Huaheine, French Polynesia
Lobiger sagamiensis	Baba, 1952	Sagami Bay, Japan
Lobiger serradifalci	(Calcara, 1840)	Sicily, Italy
Lobiger souverbii	Fischer, 1856	Guadeloupe
Lobiger viridis	Pease, 1863	Huahine
*Lobiger viridis**	Nevill & Nevill, 1869	Sri Lanka
*Lophocercus krohnii**	A. Adams, 1854	Hawaiian Islands (Sandwich Islands)
*Lophocercus sieboldii**	Krohn, 1847	Messina, Italy
Lophopleurella capensis	(Thiele, 1912)	S Africa
*Oxynoe aguayoi**	Jaume, 1945	Cuba
Oxynoe antillarum	Mörch, 1863	St. Thomas, USVI
Oxynoe azuropunctata	Jensen, 1980	Florida
Oxynoe benchijigua	Ortea, Moro & Espinosa, 1999	Canary Islands
*Oxynoe brachycephalus**	Mörch, 1863	Based on figure
Oxynoe delicatula	Nevill & Nevill, 1869	Sri Lanka
*Oxynoe hargravesi**	Adams, 1872	New Hebrides
Oxynoe kabirensis	Hamatani, 1980	Ishigaki Isl., Ryukyu Islands
*Oxynoe natalensis**	Smith, 1903	Port Elizabeth, S Africa
Oxynoe olivacea	Rafinesque, 1814	Sicily, Italy
Oxynoe panamensis	Pilsbry & Olsson, 1943	Bocas Isl., Panama
Oxynoe viridis	(Pease, 1861)	Sandwich Islands
Roburnella wilsoni	(Tate, 1889)	Port Phillip Bay, Victoria, Australia
Plakobranchacea		
Plakobranchidae		
*Actaeon elegans**	de Quatrefages, 1844	St. Vaast, France
*Aplysiopterus neapolitanus**	delle Chiaje, 1830	Napoli, Italy
*Elisia marmorata**	Cantraine, 1835	Livorno, italy
Elysia abei	Baba, 1955	Sagami Bay, Japan
*Elysia albomarginata**	Trinchese, 1869	Italy
Elysia amakusana	Baba, 1955	Sagami Bay, Japan
Elysia atroviridis	Baba, 1955	Sagami Bay, Japan
Elysia australis	(Quoy & Gaimard, 1832)	Port Jackson, Sydney, NSW
Elysia babai	Pruvot-Fol, 1946	Ryukyu Islands
Elysia bangtawaensis	Swennen, 1997	Pattani, Gulf of Thailand
*Elysia bedeckta**	MacFarland, 1966	Monterey Bay, California
Elysia bella[3]	(Pease, 1860)	Hawaii
Elysia bennettae	Thompson, 1973	Heron Island, GBR
Elysia canguzua	Marcus, 1955	NE of Santos, Brazil
Elysia catulus	(Gould, 1870)	Massachusetts, USA
*Elysia cauze**	Marcus, 1957	NE of Santos, Brazil
Elysia chilkensis	Eliot, 1916	Chilka Lake, India
Elysia chitwa	Marcus, 1955	NE of Santos, Brazil
Elysia chlorotica	Gould, 1870	Massachusetts, USA
Elysia clarki	Pierce et al., 2006	Florida
*Elysia clena**	Marcus & Marcus, 1970	?Curacao/?Barbados
Elysia coodgeensis	(Angas, 1864)	Port Jackson, Sydney, NSW
*Elysia cornigera**	Nuttall, 1989	Spanish Harbor Key, FL
Elysia crispata	Mörch, 1863	St. Croix, USVI
*Elysia cyanea**	Mamo in Caruana, 1867	Malta
Elysia degeneri	Ostergaard, 1955	Oahu, Hawaii
Elysia diomedea	(Bergh, 1894)	Lower California
*Elysia dubia**	Eliot, 1904	Zanzibar
*Elysia duis**	Marcus & Marcus, 1967	Biscayne Bay, Florida
*Elysia elsiae**	Ostergaard, 1955	Waikiki, Hawaii
Elysia eugeniae	Ortea & Espinosa, 2002	Manzanillo, Costa Rica (Carib)
Elysia evelinae	Marcus, 1957	NE of Santos, Brazil
Elysia kushimotoensis	Baba, 1957	Kushimoto, Kii, Japan
Elysia expansa	(O'Donoghue, 1924)	Abrolhos Islands, NW Australia
*Elysia faustula**	Bergh, 1872	Masoloc, Philippines

Elysia fezi	Vilella, 1968	Barcelona, Spain
Elysia filicauda	Jensen & Wells, 1990	Albany, SW Australia
Elysia flava	Verrill, 1901	Bermuda
Elysia flavipunctata	Ichikawa, 1993	Ishigaki Isl., Ryukyu
Elysia flavomacula	Jensen, 1990	Hong Kong
Elysia furvacauda	Burn, 1958	Torquay, Victoria, Australia
*Elysia fusca**	Philippi, 1844	Palermo, Italy
Elysia gordanae	Thompson & Jaklin, 1988	Rovinj, Yugoslavia
Elysia grandifolia	Kelaart, 1857	Sri Lanka
Elysia grandis[3]	Bergh, 1872	Palau? (Pelew)
Elysia haingsisiana[3]	Bergh, 1905	Haingsisi
*Elysia halimedae**	Macnae, 1954	Port Alfred, S Africa
Elysia hamatanii	Baba, 1957	Seto, Japan
Elysia hedgpethi	Marcus, 1961	Tomales Bay, California
Elysia hendersoni	Eliot, 1899	Samoa
Elysia hetta	Perrone, 1990	Gulf of Taranto, Italy
Elysia hirasei	Baba, 1955	Sagami Bay, Japan
Elysia japonica	Eliot, 1913	Japan
*Elysia latipes**	Marcus, Er. & Marcus, Ev. 1960	Maldives
Elysia leucolegnote	Jensen, 1990	Hong Kong
Elysia lobata	Gould, 1852	Hawaii
*Elysia macnaei**	Ev. Marcus, 1980	Japan?/Australia?
Elysia maoria	Powell, 1937	Auckland, NZ
Elysia margaritae	Fez, 1962	Valencia, Spain
*Elysia marginata**	(Pease, 1871)	Huahcine, French Polynesia
Elysia minima	Ichikawa, 1993	Kuro Isl., Ryukyu
*Elysia minuta**	(Sars, 1835)	Bergensund, Norway
Elysia nealae	Ostergaard, 1955	Waikiki, Hawaii
Elysia nigrocapitata	Baba, 1957	?Osaka/?Seto/?Tsurugu/?Toyama Bay Japan
Elysia nigropunctata	(Pease, 1871)	Tahiti
Elysia nisbeti	Thompson, 1977	Jamaica
Elysia obtusa	Baba, 1938	Seto, Japan
*Elysia ocellata**	Pease, 1860	Hawaii
Elysia oerstedii	Morch, 1859	Puntarenas, Central America
Elysia ornata	(Swainson, 1840)	West Indies
*Elysia ornata**	(Pease, 1860)	Hawaii
*Elysia pagenstecheri**	Marcus, Ev., 1982	Sète, Mediterranean
Elysia papillosa	Verrill, 1901	Bermuda
Elysia patagonica	Munian & Ortea, 1997	San Jorge Gulf, Argentina (45d58'S; 67d34'W)
Elysia patina	Marcus, 1980	Florida Keys
Elysia pilosa	Risbec, 1928	New Caledonia
Elysia pratensis	Ortea & Espinosa, 1996	Eastern part of Yucatan, Mexico
*Elysia pruvotae**	Risbec, 1953	New Caledonia
Elysia punctata	Kelaart, 1857	Sri Lanka
Elysia purchoni	Thompson, 1977	Jamaica
Elysia rufescens	(Pease, 1871)	Tahiti
Elysia serca	Marcus, 1955	NE of Santos, Brazil
Elysia setoensis	Hamatani, 1968	Seto, Japan
Elysia siamensis	Swennen, 1997	Pattani, Gulf of Thailand
Elysia slimora	Marcus & Marcus, 1966	near Sao Tome, W Africa
*Elysia splendida**	Grube, 1861	Cherso, N Adriatic
Elysia subornata	Verrill, 1901	Bermuda
Elysia sugashimae	Baba, 1955	Sagami Bay, Japan
Elysia thompsoni	Jensen, 1993	Rottnest Island, SW Australia
Elysia timida	Risso, 1818	Nice, France Mediterr.
Elysia tokarensis	Baba, 1957	Tokara Islands, Kyushu, Japan
Elysia tomentosa	Jensen, 1997	Abrolhos Islands, NW Australia
Elysia translucens	Pruvot-Fol, 1957	Banyuls, France Mediterr.
Elysia trilobata	Heller & Thompson, 1983	Red Sea
Elysia trisinuata	Baba, 1949	Sagami Bay, Japan
Elysia tuca	Marcus & Marcus, 1967	Biscayne Bay, Florida
*Elysia (Elysiella) verrilli**	Thiele, 1931	n.n. for Elysia (Elysiella catula Verrill
Elysia verrucosa	Jensen, 1985	Hong Kong

Elysia viridis	(Montagu, 1804)	Devonshire, UK
*Elysia viridissima**	Trinchese, 1869	Italy
Elysia vreelandae	Marcus & Marcus, 1970	W Mexico
Elysia yaeyamana	Baba, 1936	Ishigakishima, Ryukyu
Elysia zuleicae	Ortea & Espinosa, 2002	Cuba
Elysiella pusilla	Bergh, 1872	Aibukit, ?Palau (Palaos)
Elysiella stylifera	Jensen, 1997	Darwin Harbour, N Australia
Elysiobranchus mercieri	Pruvot-Fol, 1930	New Caledonia
Elysiobranchus ryukyuensis	Ichikawa, 1993	Sesoko Isl., Ryukyu
Pattyclaya arena	Carlson & Hoff, 1978	Guam
Pattyclaya brycei	Jensen & Wells, 1990	Albany, SW Australia
*Placobranchus argus**	Bergh, 1872	Honolulu, Hawaii
*Placobranchus caminguinus**	Bergh, 1872	Luzon, Philippines
*Placobranchus chlorophagus**	Bergh, 1878	Huaheine
*Placobranchus gracilis**	Pease, 1871	Tahiti
*Placobranchus guttatus**	Stimpson, 1858	Ryukyu Islands
*Plakobranchus ianthobapsus**	Gould, 1852	Honolulu, Hawaii
*Placobranchus laetus**	Bergh, 1872	Masoloc, Philippines
Plakobranchus ocellatus	van Hasselt, 1824	Sunda Strait
*Placobranchus priapinus**	Bergh, 1872	Bohol, Philippines
*Placobranchus punctulatus**	Bergh, 1872	Masoloc, Philippines
*Placobranchus variegatus**	Pease, 1871	Huaheine, French Polynesia
Thuridilla albopustulosa	Gosliner, 1995	Madang, PNG
Thuridilla bayeri	(Marcus, 1965)	Marshall Islands
Thuridilla carlsoni	Gosliner, 1995	Madang, PNG
Thuridilla coerulea	(Kelaart, 1857)	Sri Lanka
Thuridilla decorata	(Heller & Thompson, 1983)	Red Sea
Thuridilla flavomaculata	Gosliner, 1995	Luzon, Philippines
Thuridilla gracilis	(Risbec, 1928)	New Caledonia
Thuridilla hoffae	Gosliner, 1995	Madang, PNG
Thuridilla hopei	(Verany, 1853)	Nice, France Mediterr.
Thuridilla indopacifica	Gosliner, 1995	Aldabra Atoll
Thuridilla kathae	Gosliner, 1995	Madagascar
Thuridilla lineolata	(Bergh, 1905)	Saleyer
Thuridilla livida	(Baba, 1955)	Sagami Bay, Japan
Thuridilla mazda	Ortea & Espinosa, 2000	Manzanillo, Costa Rica (Carib)
Thuridilla moebii	(Bergh, 1888)	Mauritius
Thuridilla multimarginata	Gosliner, 1995	Midway Atoll
Thuridilla neona	Gosliner, 1995	Lanai, Hawaii
Thuridilla picta	(Verrill, 1901)	Bermuda
Thuridilla ratna	(Marcus, 1965)	Palau
Thuridilla splendens	(Baba, 1949)	Sagami Bay, Japan
Thuridilla thysanopoda[3]	(Bergh, 1905)	Tual, Kei Islands, Indonesia
Thuridilla undula	Gosliner, 1995	Madang, PNG
Thuridilla vatae	(Risbec, 1928)	New Caledonia
Thuridilla virgata	(Bergh, 1888)	Mauritius
*Tridachia schrammi**	Mörch, 1863	Guadeloupe
Boselliidae		
Bosellia cohellia[2]	Marcus, 1978	?Red Sea/?Mediterranean
Bosellia corinneae	Marcus, 1973	Key Biscayne, Florida
Bosellia leve	Fernandez-Ovies & Ortea, 1986	Lanzarote, Canary Islands
Bosellia marcusi	Marcus, 1972	Grassy Key & Miami, FL
Bosellia mimetica	Trinchese, 1890	Capri, Italy
Platyhedylidae		
Gascoignella aprica	Jensen, 1985	Hong Kong
Gascoignella jabae	Swennen, 2001	Pattani, Gulf of Thailand
Gascoignella nukuli	Swennen, 2001	Pattani, Gulf of Thailand
Platyhedyle denudata	Salvini-Plawen, 1973	Livorno, italy
Limapontioidea		
Polybranchidae (=Caliphyllidae)		
Caliphylla mediterranea	(A. Costa, 1867)	Napoli, Italy
*Caliphylla tricolor**	Trinchese, 1879	Mediterranean
Cyerce antillensis	Engel, 1927	Tobago(?), Westindien

Cyerce cristallina	(Trinchese, 1881)	Napoli, Italy
Cyerce? edmundsi	Thompson, 1977	Jamaica
Cyerce elegans	Bergh, 1871	Palau? (Palaos)
Cyerce graeca	Thompson, 1988	Greek Ionian Sea
Cyerce habanensis	Ortea & Templado, 1988	Cuba
*Cyerce jheringi**	Pelseneer, 1892	Napoli, Italy
Cyerce kikutarobabai	Hamatani, 1976	Amami Islands, Japan
Cyerce nigra	Bergh, 1871	Palau? (Palaos)
Cyerce nigricans	(Pease, 1866)	Pacific Islands
Cyerce orteai	Valdès & Camacho, 2000)	Puntarenas, Costa Rica
Cyerce pavonina	Bergh, 1888	Mauritius
Cyerce verdensis	Ortea & Templado 1990	Cape Verde
Mourgona germaineae	Marcus & Marcus, 1970	Puerto Rico (aquarium)
Mourgona murca	Marcus & Marcus, 1970	Curacao
Mourgona osumi	Hamatani, 1994	Amami-Oshima Island, SW Japan
Polybranchia borgnini	(Trinchese, 1895)	Mediterranean
Polybranchia orientalis	(Kelaart, 1858)	Sri Lanka
Polybranchia pallens	(Burn, 1957)	Queenscliff, Victoria, Australia
Polybranchia papillosa	(Pease, 1866)	Pacific Islands
Polybranchia pellucida	Pease, 1860	Hawaii
Polybranchia prasinus	(Bergh, 1871)	Luzon, Philippines
*Polybranchia rubicundus**	(Bergh, 1871)	Tor, Red Sea
Polybranchia viridis	(Deshayes, 1857)	Guadeloupe
Polybranchia westralis	Jensen, 1993	Rottnest Island, SW Australia
Sohgenia palauensis	Hamatani, 1991	Palau
Hermaeidae		
Aplysiopsis brattstroemi	(Marcus, 1959)	Chile (23d39'S; 70d25'W)
Aplysiopsis elegans	(Deshayes, 1835)	Banyuls, France Mediterr.
Aplysiopsis enteromorphae	(Cockerell & Eliot, 1905)	San Pedro, California(?)
Aplysiopsis formosa	Pruvot-Fol, 1953	Temara, Marocco
*Aplysiopsis maculosa**	(Trinchese, 1874)	Genova, Italy
Aplysiopsis minor	(Baba, 1959)	Toyama Bay, Japan
Aplysiopsis nigra	(Baba, 1949)	Sagami Bay, Japan
Aplysiopsis orientalis	(Baba, 1949)	Sagami Bay, Japan
Aplysiopsis sinusmensalis	(Macnae, 1954)	Table Bay, S Africa
*Aplysiopsis smithi**	(Marcus, 1961)	Tomales Bay, California
Aplysiopsis toyamana	(Baba, 1959)	Toyama Bay, Japan
*Aplysiopsis zebra**	Clark, 1982	Florida
Hermaea bifida	(Montagu, 1816)	Devonshire, UK
Hermaea boucheti	Cervera, Garcia-Gomez & Ortea, 1991	Pontevedra, SW Spain
*Hermaea carminis**	Fez, 1962	Valencia, Spain
Hermaea coirala	Marcus, 1955	NE of Santos, Brazil
Hermaea cruciata	Gould, 1870	Massachusetts, USA
Hermaea evelinemarcusae	Jensen, 1993	Rottnest Island, SW Australia
Hermaea hillae	Marcus & Marcus, 1967	Sonora, W Mexico
*Hermaea lutescens**	A. Costa, 1866	Napoli, Italy
*Hermaea minor**	Bergh, 1888	Mauritius
Hermaea noto	(Baba, 1959)	?Noto Peninsula/?Toyama Bay Japan
Hermaea oliviae	(MacFarland, 1966)	Monterey Bay, California
Hermaea paucicirra	Pruvot-Fol, 1953	Marocco
*Hermaea polychroma**	(Hesse, 1873)	Brest
Hermaea vancouverensis	O'Donoghue, 1924	Vancouver Isl., Canada
Hermaea variopicta	(A. Costa, 1869)	Napoli, Italy
*Hermaea venosa**	Lovén, 1845	Bohuslän, Sweden
Hermaea wrangeliae	(Ichikawa, 1993)	Kuro Isl., Ryukyu
Hermaea zosterae	(Baba, 1959)	Amakusa, Japan
*Physopneumon carneum**	A. Costa, 1862	Mediterranean
Limapontiidae		
Alderella comosa	(Costa, 1867)	Napoli, Italy
*Alderia harvardiensis**	Gould, 1870	Massachusetts, USA
Alderia modesta	(Lovén, 1844)	Bohuslän, Sweden
*Alderia scaldiana**	Nyst, 1855	Scheldt estuary, Netherlands
Alderia uda	Marcus, Ev. & Marcus, Er., 1956)	SW of Santos, Brazil
Alderia willowi	Krug, Ellingson, Burton & Valdés, 2007	San Pedro, California

Alderiopsis garfio	Caballer, Ortea & Espinosa, 2006	Cuba
Alderiopsis nigra	(Baba, 1937)	Amakusa, Japan
Calliopaea bellula	d'Orbigny, 1837	France
Calliopaea oophaga	Lemche, 1974	Samso, Kattegat, DK
*Calliopaea souleyeti**	Verany, 1853	Nice, France Mediterr.
*Cenia cocksii**	Alder & Hancock, 1848	Falmouth, UK
*Cenia corrugata**	Alder & Hancock, 1848	Falmouth, UK
*Chalidis coeruleus**	de Quatrefages, 1844	Ile de Bréhat, France
*Chalidis nigricans**	Alder & Hancock, 1847	Falmouth, UK
Costasiella formicaria	(Baba, 1959)	Amakusa, Japan
Costasiella illa	(Marcus, 1965)	Caroline Islands, Micronesica
Costasiella iridophora	Ichikawa, 1993	Kuro Isl., Ryukyu
Costasiella kuroshimae	Ichikawa, 1993	Kuro Isl., Ryukyu
*Costasiella lilianae**	(Marcus, Ev. & Marcus, Er., 1969	NE of Santos, Brazil
Costasiella mandurahae	Jensen, 1997	Darwin Harbour, N Australia
Costasiella nonatoi	Marcus & Marcus, 1960	NE of Santos, Brazil
Costasiella ocellifera	(Simroth, 1895)	Bermuda
Costasiella pallida	Jensen, 1985	Hong Kong
Costasiella paweli	Ichikawa, 1993	Miyako Isl., Ryukyu
Costasiella rubrolineata	Ichikawa, 1993	Ishigaki Isl., Ryukyu
Costasiella usagi	Ichikawa, 1993	Ishigaki Isl., Ryukyu
Costasiella vegae	Ichikawa, 1993	Ishigaki Isl., Ryukyu
Costasiella virescens	Pruvot-Fol, 1951	Banyuls, France Mediterr.
*Custiphorus vesiculosus**	Deshayes, 1853	?
*Embletonia mariae**	Meyer & Möbius, 1865	Kieler Bucht
Ercolania boodleae	(Baba, 1938)	Seto, Japan
Ercolania coerulea	Trinchese, 1892	Napoli, Italy
*Ercolania costai**	Pruvot-Fol, 1951	?Banyuls/?Monaco, Mediterranean
*Ercolania cricetae**	(Marcus & Marcus, 1970)	Curacao
Ercolania evelinae	(Marcus, 1959)	Chile (53d22'S; 70d57'W)
*Ercolania emarginata**	Jensen, 1985	Hong Kong
Ercolania endophytophaga	Jensen, 1999	Rottnest Island, SW Australia
Ercolania erbsus	(Marcus & Marcus, 1970)	Madagascar
Ercolania felina	(Hutton, 1882)	New Zealand
*Ercolania funerea**	(Costa, 1867)	Napoli, Italy
Ercolania fuscata	(Gould, 1870)	Massachusetts, USA
Ercolania gopalai	(Rao, 1937)	Madras, E India
Ercolania irregularis	(Eliot, 1904)	Zanzibar
Ercolania lozanoi	Ortea, 1981	Tenerife, Canary Islands
Ercolania margaritae	Burn, 1974	Point Lonsdale, Victoria, Australia
Ercolania nigra	(Lemche, 1936)	Nyborg Fjord, DK
*Ercolania nigrovittata**	(A. Costa, 1866)	Napoli, Italy
*Ercolania nigrovittata**	(Rao & Rao, 1963)	Gulf of Mannar, SE India
*Ercolania pancerii**	Trinchese, 1872	Genova, Italy
Ercolania pica	(Annandale & Prashad, 1922)	Chilka Lake, India
Ercolania raorum	(Marcus & Marcus, 1970)	Gulf of Mannar, SE India
Ercolania selva	Ortea & Espinosa, 2001	Manzanillo, Costa Rica (Carib)
Ercolania siottii	Trinchese, 1872	Genova, Italy
Ercolania subviridis	(Baba, 1959)	Toyama Bay, Japan
*Ercolania talis**	(Marcus & Marcus, 1956)	SW of Santos, Brazil
Ercolania tentaculata	(Eliot, 1917)	Singgora, SE Thailand
Ercolania translucens	Jensen, 1993	Rottnest Island, SW Australia
*Ercolania trinchesii**	Pruvot-Fol, 1951	?Banyuls/?Monaco, Mediterranean
*Ercolania uziellii**	Trinchese, 1872	Genova, Italy
*Ercolania vanellus**	Marcus, 1957	E of Santos, Brazil
Ercolania varians	(Eliot, 1904)	Zanzibar
Ercolania viridis	(A. Costa, 1866)	Napoli, Italy
Ercolania zanzibarica	Eliot, 1903	E Zanzibar
Limapontia capitata	(Müller, 1773)	Baltic Sea
*Limapontia cornuta**	Giard, 1873	?
Limapontia depressa	Alder & Hancock, 1862	Sunderland, UK
*Limapontia nigra**	Johnston, 1836	Berwick Bay, UK
Limapontia senestra	(de Quatrefages, 1844)	Ile de Bréhat, France
Limapontia zonata[1]	(Girard, 1852)	Massachusetts, USA
Olea hansineensis	Agersborg, 1923	Friday Harbor, Washington

*Placida aoteana**	(Powell, 1937)	Auckland, NZ
*Placida babai**	Mareus, Ev., 1982	Seto, Japan
Placida brevicornis	(A. Costa, 1867)	Napoli, Italy
*Placida capensis**	Maenae, 1954	Cape Provinee, S Afriea
Placida cremoniana	(Trinehese, 1892)	Napoli, Italy
Placida daguilarensis	Jensen, 1990	Hong Kong
Placida dakariensis	(Pruvot-Fol, 1953)	Dakar, Senegal
Placida dendritica	(Alder & Haneock, 1843)	Torbay, UK
Placida fralila	Burn, 1966	Queensland, Australia
Placida kingstoni	Thompson, 1977	Jamaiea
*Placida ornata**	(MaeFarland, 1966)	Monterey Bay, California
Placida saronica	(Thompson, 1988)	Greek Aegean Sea
Placida tardyi	(Trinehese, 1873)	Genova, Italy
Placida verticillata	Ortea, 1981	Tenerife, Canary Islands
Placida viridis	(Trinehese, 1873)	Genova, Italy
Stiliger akkeshiensis	Baba, 1935	Akkeshi Bay, Hokkaido, Japan
Stiliger aureomarginatus	Jensen, 1993	Rottnest Island, SW Australia
Stiliger berghi	Baba, 1937	Tomioka, Amakusa, Japan
Stiliger fuscovittatus	Lanee, 1962	San Diego, California
Stiliger llerai	Ortea, 1981	Tenerife, Canary Islands
Stiliger pusillus	Baba, 1959	Osaka Bay, Japan
Stiliger smaragdinus	Baba, 1949	Sagami Bay, Japan
Stiliger ornatus	Ehrenberg, 1828	Red Sea
Stiliger vossi	Mareus & Mareus, 1960	Upper Florida Keys
Stiliger? viridis[2]	(Kelaart, 1858)	Sri Lanka

[1]This species is probably a flatworm rather than a sacoglossan.

[2]The taxonomic status of this species is so uncertain that it has been omitted from the analyses.

[3]This species has been omitted from the analyses due to lack of information.

[4]Since the type locality is uncertain, this species has been omitted from the analyses.