

## Preliminary study on molecular phylogeny of Sacoglossa and a compilation of their food organisms\*

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**Abstract.** The first molecular analysis of the Sacoglossa based on the 16Sr DNA gene (partial), with 39 species and 59 specimens analysed, is presented. A saturation of substitution is observed, as well as conflict in the data concerning certain taxa. Therefore the phylogenetic relationship presented here has to be considered as preliminary. Many results are congruent with the analysis of JENSEN (1996) based on morphological characters. Plakobranchacea are monophyletic. *Elysiella pusilla* is nested within the genus *Elyisia* and therefore synonymy of *Elysiella* with *Elyisia* confirmed. The position of *Plakobranchus* remains unclear, but a closer affinity to *Elyisia* than to *Thuridilla* seems most likely. Major differences lie in the paraphyly of the Oxynoacea, but only few members of this taxon have been included. A compilation of available data on food algae is presented and the data are discussed under the light of the phylogenetic relationship presented here.

**Keywords.** Opisthobranchia, molecular systematics, SplitsTree, Chlorophyta, evolution, 16S rDNA.

### 1. INTRODUCTION

Sacoglossa is a small group of Opisthobranchia with about 250 to 300 described species (JENSEN 1997a). Animals are small and species larger than 30 mm are rare. The monophyly of this group is well supported (JENSEN 1996) although their phylogenetic position relating to other groups of Opisthobranchia is unresolved (DAYRAT et al. 2001; DAYRAT & TILLIER 2002; GRANDE et al. 2004; VON-NEMANN et al. 2005; WÄGELE & KLUSSMANN-KOLB 2005).

The first and only phylogeny of Sacoglossa based on morphological data was presented by JENSEN (1996) applying Hennigian principles. Her analysis was performed on genus level, except for the genus *Elyisia* with four included species. One of her results was a differentiation into two major clades, the shelled Oxynoacea and the shell-less Plakobranchacea. The latter comprise the monophyletic Plakobranchioidea and the monophyletic Limapontioidea. *Cylindrobulla* appeared as the most basal taxon within her analysis. GOSLINER (1995) performed a morphologically based analysis concentrating on the genus *Thuridilla*. An analysis of the family Plakobranchidae based on a genetic marker (COI) was published lately (BASS & KARL 2006). No further phylogenetic analyses have been performed up to now.

Sacoglossa is feeding nearly exclusively on siphonocladal or siphonocladalean Chlorophyta. They penetrate the cell wall with their uniseriate radula and suck out the cell sap. Noteworthy is the possibility of several sacoglossans to incorporate the chloroplasts from their food intracellularly in their digestive gland and partially perform photosynthesis. This was first recorded by KAWAGUTI & YAMASU (1965) and most recently analysed by EVERTSEN et al. (2007) (for a review see RUMPHO et al. 2000). For several sacoglossans reception of polysaccharides and amino acids from these chloroplasts is documented (TRENCH 1973; WILLIAMS & WALKER 1999 after Grecne & Muscatine 1972). In addition, many members of the Sacoglossa are able to incorporate secondary metabolites from their food and use these as a chemical defense (CIMINO & GHISELIN 1998; CIMINO et al. 1999; GAVAGNIN & FONTANA 2000; MARIN & ROS 2004; CIMINO & GAVAGNIN 2006).

JENSEN (1997a: 313) was the first who discussed a possible correlation between the evolution of morphological characters of the Sacoglossa and the possible evolution of the food plants. She argued that more investigations are needed: "Rigorous application of cladistic methodology in coevolution analysis requires fully resolved phylogenies of the 'hosts' as well as the 'associates'." Intention

of this study was to fill this gap by analysing the phylogeny of Sacoglossa with molecular data and by including many more species. New available data on food organisms in Sacoglossa are presented, which might help to elaborate co-evolutionary processes.

## 2. MATERIALS AND METHODS

### 2.1. Biological material

58 specimens including 38 species of sacoglossans were used for the phylogenetic reconstruction. Locality, date of collection and accession numbers are indicated in Table 1. According to the results of JENSEN (1996) and unpublished data of the senior author, *Cylindrobulla beaultii* (Cylindrobullidae, Opisthobranchia) was chosen as out-group species. *Cylindrobulla* and Sacoglossa share synapomorphies (presence of a shell, adductor muscle, and a lamellate gill (JENSEN 1996)), but also lack synapomorphies of the Sacoglossa (e.g. ascus), and show plesiomorphic characters (e.g. triangular shaped teeth, large shell).

### 2.2. DNA extraction, amplification and sequencing

DNA was extracted from alcohol-preserved specimens by means of NucleoSpin<sup>®</sup> Tissue-Kit by Machery-Nagel or Dneasy<sup>®</sup> Blood and Tissue Kit by Quiagen, guided by the enclosed protocol. A segment of the 16Sr DNA gene was amplified with primer pairs, LR-J-12887 5'-GGA GCT CCG GTT TGA ACT CAG ATC-3' and LR-N-13398 5'-CGG CCG CCT GTT TAT CAA AAA CAT-3'. Amplification reactions (50µl) consisted of 39.15µl ddH<sub>2</sub>O, 5µl 10X PCR Buffer without MgCl<sub>2</sub> (Fermentas), 4µl MgCl<sub>2</sub> (25mM), 0.15µl Taq-Polymerase (5U/µl), 0.4µl of each Primer (10pmol/µl) and 0.5µl DNA. The PCR was carried out in the Gene Amp PCR System 9600 by Perkin Elmer<sup>®</sup> under following conditions: 95°C for 240s, followed by 9 Touch-down-cycles of 45s at 94°C, 45s at 56(-1)°C, 90s at 72°C, followed by 25 amplification-cycles of 45s at 94°C, 45s at 48°C, 90s at 72°C and a final extension at 72°C for 10min followed by cooling down to 4°C. Amplicons were purified by means of NucleoSpin<sup>®</sup> Extract II by Machery-Nagel, guided by the enclosed protocol. The mass of the amplicons was estimated by comparing ethidium bromide staining intensity of 5µl of each purified reaction.

Cycle sequencing reactions (Cycle Sequencing Kit BigDye<sup>®</sup> Terminator v1.1 by Applied Biosystems) were carried out in the Gene Amp PCR System 9600 by Perkin Elmer<sup>®</sup> under following conditions: 96°C for 120s followed by 15 cycles of 10s at 96°C, 5s at 50°C, 150s at

60°C followed by cooling down to 4°C. Reaction products were purified by adding 40µl water containing Dextranblau, 5µl natriumacetate (3M, pH4.6) and 125µl pure ethanol, centrifuging for 15min, taking supernatant, adding 500µl fresh 70% ethanol, centrifuging for 5min, taking supernatant, and were dried at 37°C for 30-40min. The fluorescently labeled products were size sorted and visualized using an ABI Prism<sup>™</sup> 377 DNA Sequencer by Applied Biosystems. The sequences were extracted with Sequencing Analysis 3.0. The sequences of the reverse primer were complemented with Factura 2.0.1 and sequences of both strands were compared and synchronised with Sequence Navigator.

The gene fragments were aligned by applying Muscle3.7 (EDGAR 2004a; EDGAR 2004b) and the resulting alignment was verified by eye. Length of the alignment was 478 base pairs.

### 2.3 Phylogentic reconstruction

A Bayesian analysis was performed with MrBayes 3.1.2 (HUELSENBECK & RONQUIST 2001; HUELSENBECK & BOLLBACK 2001). Maximum Parsimony analysis, Neighbor-joining analysis and Maximum likelihood analysis have been performed with PAUP\* 4.0b10. Modeltest 3.7 (POSADA & BUCKLEY 2004) selected as best-fit model the GTR+G+I-model (AIC). Therefore, neighbour-joining analysis was conducted on a GTR-model and Maximum Likelihood analysis and Bayesian analysis on a GTR+G+I-model. Saturation of substitutions was tested against patristic distances as well as against distances obtained with the GTR-model. A posteriori statistical analysis could not be performed due to long calculation time of bootstrapping methods. For visualizing conflict in the data set, which seemed obvious after the analyses, Splits-Tree4 (HUSON & BRYANT 2006) was applied. A Neighbour-Net analysis was performed applying the K2P-model.

## 3. RESULTS

Saturation in substitutions of the partial 16Sr DNA obtained by using the GTR model is shown in Figure 1. The graph approaches a plateau indicating a saturation of substitutions. When splitting the data set into subgroups (family or genera), saturation was less evident for most groups, but not e.g. the genus *Elysia* or *Thuridilla*. Substitution rates were also less saturated, when using p-distances (not shown here).

### 3.1. Phylogenetic reconstruction

A maximum parsimony analysis produced 81 shortest topologies with a length of 1401 steps. The 50%-Majority-Rule tree is shown in Figure 2. Within the monophyletic Plakobranchea, the family Polybranchiidae and the polybranchiid genus *Cyerce* are also monophyletic. The monophyletic genus *Ercolania* appears as the sistertaxon to the Polybranchiidae. The families Plakobrancheidae and Limapontiidae are not monophyletic, the genera *Elysia* and *Thuridilla* are also paraphyletic. *Plakobrancheus* groups as sistertaxon of several *Elysia* species. The shelled Oxynoacea are basal. They are paraphyletic as well as the family Juliidae and Oxynoidae. The position of *Oxynoe viridis* is unresolved.

In the Neighbor-joining analysis (not presented here), Plakobranchea are monophyletic, as well as the family Polybranchiidae and the genus *Thuridilla*. *Bosellia mimetica* (Boselliidae) groups in the family Plakobrancheidae, rendering this family paraphyletic. Limapontiidae is paraphyletic again, since *Ercolania* and *Stiliger* do not group together. The genus *Elysia* again comprises *Elysiella* and *Plakobrancheus* and is polyphyletic in this analysis. *Plakobrancheus* is sistertaxon to the same *Elysia*-complex as in the maximum parsimony analysis. Similar to the maximum parsimony analysis, *Elysia benettae* is the sistertaxon to *Elysiella pusilla*. Monophyletic *Ercolania* appears as the most basal genus of the Plakobranchea.

Oxynoacea are basal and paraphyletic. The families Juliidae and Oxynoidae again are not monophyletic. Similar as in the MP analysis, *Tamanovalva* is the sistertaxon to the Plakobranchea. The position of *Oxynoe viridis* is unclear.

Two identical trees were found in the Maximum-likelihood analysis; the resulting tree is shown in Figure 3. Plakobranchea is monophyletic, as well as the families Plakobrancheidae and Polybranchiidae. Boselliidae is sistertaxon to the Plakobrancheidae. The genus *Thuridilla* is monophyletic. *Elysiella pusilla* with *Elysia benettae* as sistertaxon groups in the genus *Elysia*, rendering this genus paraphyletic. In this analysis *Plakobrancheus ocellatus* is the sistertaxon to all *Elysia*-species (including *Elysiella*) and monophyletic *Thuridilla* to this *Plakobrancheus/Elysia* clade. Limapontiidae again is paraphyletic. Contrary to the other analyses, *Ercolania* is not monophyletic. The two species represent the most basal Plakobranchea. The Oxynoacea and Oxynoidae are paraphyletic again, but contrary to all other analyses, the Juliidae with the genera *Julia* and *Tamanovalva* represent a monophyletic group. The position of *Oxynoe viridis* is unresolved.

The cladogram based on the analysis with MrBayes is shown in Figure 4. Plakobranchea is monophyletic, but resolution within that taxon is low. *Elysia* (without *E. benettae*), *Elysiella/Elysia benettae* complex and *Plakobrancheus* form a monophyletic clade, but their position is

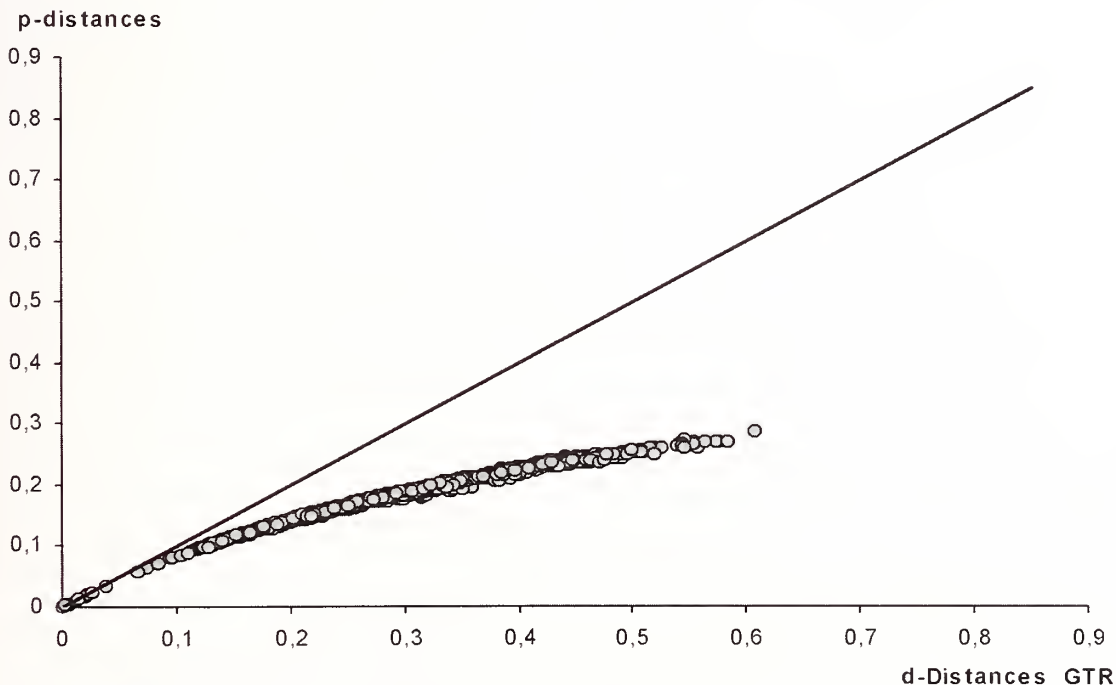


Fig. 1. Saturation of substitution of the 16Sr DNA gene (partial) used in this analysis. The straight line is the bisector. Distances are calculated as patristic distances (y-axis) against d-distances calculated by applying the GTR model (x-axis).

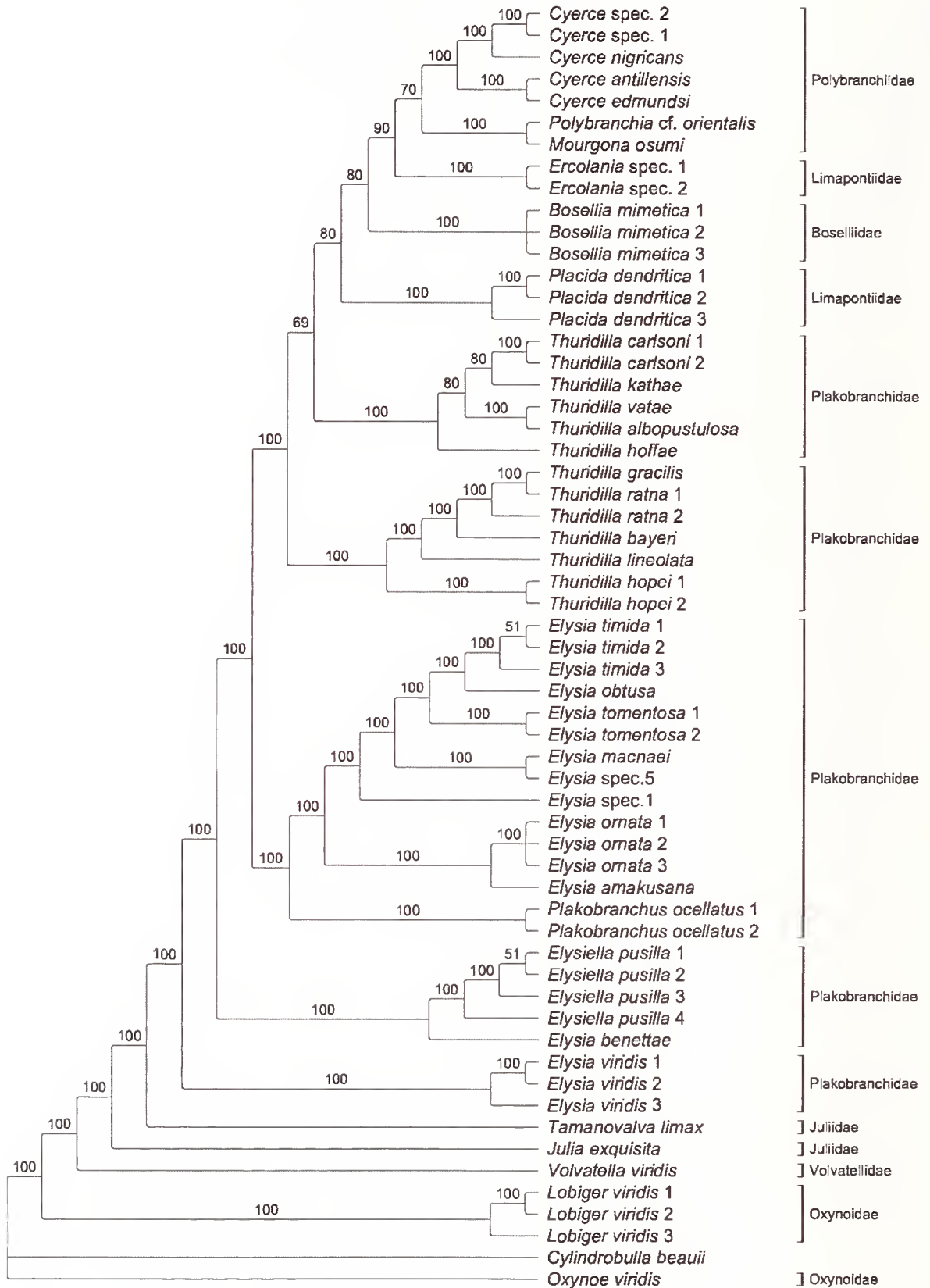


Fig. 2. Sacoglossa; 16Sr DNA gene; Maximum Parsimony analysis, 50% Majority Rule consensus tree.

unresolved. This complex and two *Thuridilla* complexes (representing all Plakobranchidae) and *Bosellia* form the next higher unresolved monophyletic clade.

Polybranchiidae and within that family the genus *Cyerce*, is monophyletic. The family Limapontiidae and the limapontiid genus *Ercolania* are paraphyletic. The Oxynoacea and Oxynoidae are paraphyletic. The Juliidae are not resolved and the position of *Oxynoe viridis* remains again unclear.

The analysis of the dataset with SplitsTree visualises the incongruencies in the dataset and the resulting incongruencies in the different cladograms. Figure 5 shows a network connecting all terminal taxa. Parallel edges of same length within the network visualise a split between two groups. Members of each group share same characters (assumed apomorphic nucleotides for that group). Fit value of the analysis is 95.06, indicating that actually all conflicts are visualised in the figure. No long branch taxa can be identified. Very well supported is the split between Oxynoacea + *Cylindrobulla* and Plakobranchacea, indicated by the long edges. Also well supported are splits between species (e.g. *Placida dendritica*, *Elysia timida* or *Elysia viridis*) and the rest of the sequences. No split between outgroup taxon *Cylindrobulla* and Sacoglossa exists (Fig. 5 and Fig. 6, the latter showing the analysis with a reduced data set for better visualisation). But a split between *Cylindrobulla* + *Tamanovalva limax* + *Oxynoe viridis* against all other sequences can be observed (Fig. 5). Phylogenetic signal (shown as splits) is already low on genus level (e.g. *Ercolania*), or not existing (e.g. *Cyerce*, *Elysia* or *Thuridilla*). A separate analysis of all *Thuridilla* species (Fig. 7) shows the close affinities of *T. ratna* and *T. gracilis*, whereas *T. bayeri* appears separate.

### 3.3. Food spectrum in Sacoglossa

A compilation of available data on food organisms of sacoglossans is presented in Table 2. Food organisms of *Cylindrobulla* are not known. All members of Oxynoacea feed on species of *Caulerpa*. In contrast, species of the Plakobranchacea have a much wider food spectrum:

Members of the family Boselliidae seem to be restricted to the order Caulerpales (Bryopsidophyceae), mainly feeding on *Halimeda*. Within Plakobranchidae, *Elysia* shows the widest range on food organisms, containing Heterokontophyta (*Vaucheria*, *Padina*, *Biddulphia*) and angiosperms (seagrasses). *Elysia timida* and *Elysia filicauda* feed on *Acetabularia* (Dasycladales). KREMER and JANKE (1988) claimed that chloroplasts of the algal genus *Codium* have been found in *Elysia timida* as well. Only for one species of *Thuridilla*, *T. hopei*, data are available:

*Derbesia* and *Cladophora*. The only two references for *Plakobrauchus ocellatus* are based on observations in the laboratory (JENSEN 1980a after Switzer-Dunlap 1975; HIROSE 2005 after Adachi 1991). This species feeds on *Chlorodesmis* and *Udotea*. Interesting is the food organism of *Pattyclaya*, which, according to JENSEN (1992), is *Caulerpa*.

Polybranchiidae feed on species of the orders Bryopsidales and Caulerpales (Bryopsidophyceae) except for *Mourgonia* (*Cymopolia* (JENSEN 1981; CLARK 1994) and *Acetabularia* (HAMATANI 1994), Dasycladales, Dasycladophyceae). Hermacidae also exhibit a broader spectrum of food organisms: The genus *Hermaca* is characterized by feeding on Rhodophyta (GRAHAM 1955 after Pelseneer 1935; TAYLOR 1968; TAYLOR 1971; KREMER & SCHMITZ 1976; KREMER & SCHMITZ 1976 after Cornet & Marché-Marchad 1951; JENSEN & CLARK 1983; JENSEN 1993a, b; WILLIAMS & WALKER 1999 after JENSEN 1983) except *Hermaca vanconverensis* consuming *Isthmia nervosa*, a diatom (WILLIAMS & GOSLINER 1973). *Aplysiopsis* feeds on algae belonging to the orders Cladophorales (JENSEN 1980a after Gonor 1961; JENSEN 1980a after Greene 1970; JENSEN 1993a; TROWBRIDGE 1993; JENSEN 1995; WILLIAMS & WALKER 1999 after Jensen 1983) or Ulvales (JENSEN 1980a after Gonor 1961; JENSEN 1980a after Greene 1970; TROWBRIDGE 1993), *Costasiella* feeds on algae belonging to the orders Bryopsidales (CLARK & BUSACCA 1978; JENSEN 1980a, 1981; CLARK et al. 1981; CLARK 1984; JENSEN 1993a; CLARK 1994; WILLIAMS & WALKER 1999 after Jensen 1980, 1981, 1983) and Caulerpales (JENSEN 1981; WILLIAMS & WALKER 1999 after Jensen 1980, 1981, 1983) (Bryopsidophyceae), Cladophorales (WILLIAMS & WALKER 1999 after Jensen 1980, 1981, 1983) and *Vaucheria* (Heterokontophyta) (JENSEN 1990a, b). Limapontiidae show the most extraordinary food range. Species of the genus *Limapontia* feed on Cladophorales (GRAHAM 1955 after Gascoigne 1952; JENSEN 1975, 1980a after Gascoigne 1956), but also Bryopsidales (JENSEN 1975, 1980a after Gascoigne 1956), Ulvales (GRAHAM 1955 after Gascoigne 1952) and the heterokontophyte *Vaucheria* (GRAHAM 1955 after Gascoigne 1954; GASCOIGNE & SARTORY 1974; JENSEN 1980a after Gascoigne 1956; HARTOG 1959). *Alderia* also feeds on *Vaucheria* (EVANS 1953; GRAHAM 1955 after Gascoigne 1954; CLARK 1975; JENSEN 1980a after Hartog 1959; KRUG & MANZI 1999), but there is one reference for the cladophoralean *Rhizoclonium* (GRAHAM 1955 after Gascoigne 1954). The genus *Placida* mainly feeds on species of Bryopsidales (BRÜEL 1904; GRAHAM 1955 after Gascoigne 1954; BLEAKNEY 1989 after Thompson 1976 and after Millen 1980; JENSEN 1980a; JENSEN 1980a after Monselise & Mienis 1977 and after Schmekel 1982, JENSEN 1981, 1990b; MARZO, DI et al. 1993; TROWBRIDGE 2004 after Willan & Morton 1984, after Burn 1989 and after Trow-

bridge 1998b) and *Codium* (BRÜEL 1904 after Hecht 1895; GRAHAM 1955 after Gascoigne 1954; CLARK 1975; TROWBRIDGE 2004 after Willan & Morton 1984, after Burn 1989 and after Trowbridge 1998b; BEHRENS 2004) (Bryopsidophyceae). BRÜEL (1904) referenced to TRINCHESE 1876 that *Placida dendritica* feeds on *Ulva* doubting this fact at the same time. The observation that *Placida dendritica* ate another sacoglossa (MARCUS DU BOIS-REYMOND 1972) seems to be a particular case. *Placida kingstoni* extended its diet to *Cladophora* (JENSEN 1981). The genus

*Ercolania* prefers Cladophorales (CLARK 1975; JENSEN 1980a; JENSEN 1980a after Trinchese 1872, after Rao 1937, after Schmekel 1968, after Rasmussen 1973 and after Usuki 1977; JENSEN 1981; MARIN & ROS 1992 after Marin & Ros 1988; JENSEN 1993a; MARZO, DI et al. 1993; CLARK 1994; JENSEN 1999; GRZYMBOWSKI et al. 2007), one reference for *Caulerpa* (JENSEN 1980a after Edmunds 1963) is not confirmed again. *Stiliger fuscovittatus* feeds on red algae (JENSEN 1980a after Lance 1962). Unusual feeding strategies in the family show *Calliopea oophaga*, *Olea hiansineensis* and *Stiliger vesiculosus*, they consume eggs of other Opisthobranchia (JENSEN 1986; LEMCHE 1974; CRANE 1971; JENSEN 1999 after Haefelfinger 1962).

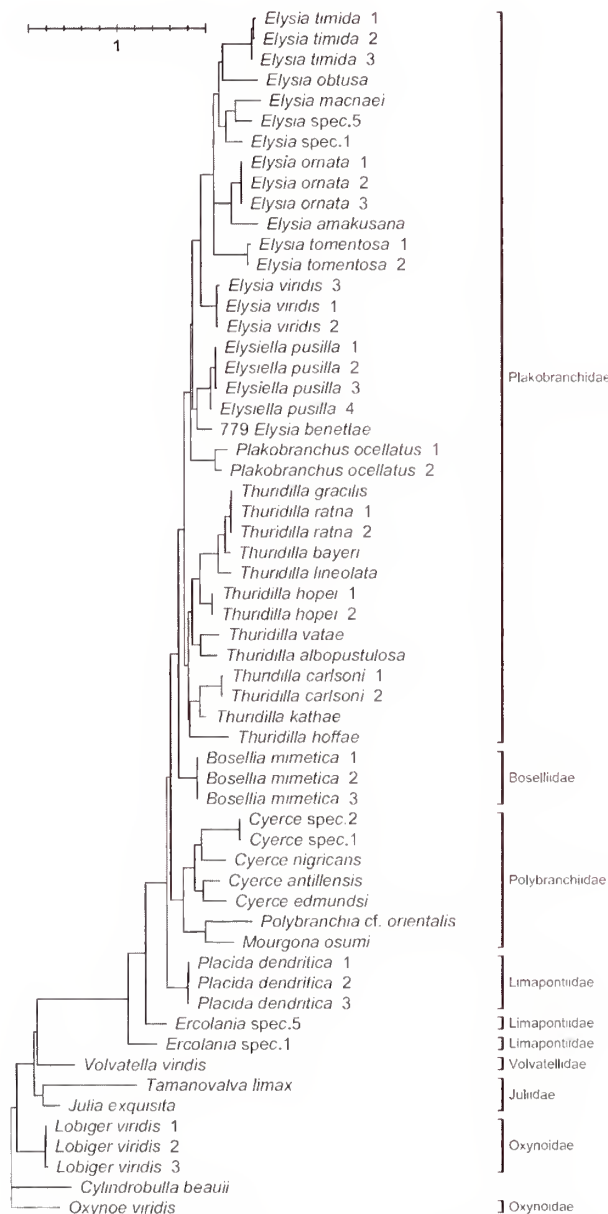


Fig. 3. Sacoglossa, 16S rDNA gene: Maximum Likelihood tree (GTR+G+I-model, AIC).

In Figure 8, the available data of higher food taxa are mapped onto the cladogram of the Maximum Likelihood analysis. Two references are not included: KREMER and JANKE (1988) determined chloroplasts in *Elysia timida* as chloroplasts of *Codium* neither describing the origin of the included REM-slide nor giving a reference. *Elysia timida* was never described feeding on *Codium*, a misdetermination of the chloroplasts is therefore likely. BRÜEL (1904) already doubted Trinchese's information that *Placida dendritica* feeds on *Ulva*. Trinchese's observation was never confirmed over the following years.

## 4. DISCUSSION

### 4.1. Phylogeny of Sacoglossa

The Oxynoacea, comprising the shelled sacoglossans, are paraphyletic in all phylogenetic analyses. Applying SplitsTree, there exists no information for a split *Cylindrobulla* against Sacoglossa. But according to the very long edges, there is much information for a split *Cylindrobulla* + Oxynoacea against Plakobranchacea. JENSEN (1996) mentioned an eversible oral tube, a long, rod-shaped preradular tooth and a large female genital papilla as synapomorphies for the Oxynoacea. These characters are not present in *Cylindrobulla*. Using a cephalaspid as outgroup and including *Cylindrobulla* as part of the ingroup is not applicable for this gene, since it shows already a high substitution rate for the present data set. But the position of *Cylindrobulla* as member of the Oxynoacea has to be reconsidered by using a more conservative gene, as 16S has proven to be. COI is also not apt for this investigation, since it shows high substitution rates on nucleotide level and is not informative on amino acid level (unpublished data of the authors). The unresolved position of *Oxynoë viridis* at the base of the cladograms is peculiar. The genus never groups with *Lobiger*, both usually united under the Oxynoidea. A contamination is unlikely due to high affinity with opisthobranch sequences. SplitsTree visualizes uniting positions with *Cylindrobul-*

*la* and *Tamanovalva limax*, which might present homoplastic characters. The Juliidae are monophyletic only in the Maximum Likelihood analysis, but support is present in the SplitsTree analysis. According to JENSEN (1996) the bivalved shell and small, paired pharyngeal pouches are autapomorphies of this family. It is most unlikely that the bivalved shell has evolved several times independently, as several phylogenetic analyses presented here would suggest.

In all analyses, the Plakobrancheacea sensu JENSEN (1996) are monophyletic and this is visualized very well by the long edges separating this taxon from Oxynoacea + *Cylindrobulla*. But this is not the case for the higher ranking taxa Plakobranchoidea and Limapontioidea. Whereas the former taxon was recognized at least in the maximum likelihood and MrBayes analyses, the Limapontioidea with the genera *Placida* and *Ercolania* (both members of the Limapontiidae) never appeared monophyletic. This is of special interest taking into consideration the ongoing discussion on the validity of *Placida*, *Ercolania* and *Stiliger* as three separate genera (e.g. MARCUS DU BOIS-REYMOND 1982; JENSEN 1985). In JENSEN's (1996) analysis, the Limapontiidae and the genus *Costasiella* (Costasiellidae) form a partly unresolved group. Limapontiidae is characterized by two visceral ganglia instead of three or more (JENSEN 1996).

Contrary to Jensen's analysis, the Polybranchiidae form a monophyletic group with exactly the same branching pattern of the six species (three genera) in all analyses, although no support can be seen in the splits graph. Interesting is the sister taxa relationship of the two Atlantic *Cyerce* species, *C. antillensis* and *C. edmundsi*. MARCUS DU BOIS-REYMOND (1982) and HAMATANI (1994) considered *Cyerce edmundsi* Thompson, 1977 as synonymous with *Mourgona germaineae* Marcus & Marcus, 1970. Assignment of *Cyerce edmundsi*, as described by THOMPSON (1977), to the genus *Cyerce* contradicts diagnostic features of this genus: „The cerata proved to contain abundant lobules of the digestive gland“ (THOMPSON 1977: 137). *Cyerce* is separated from the other Polybranchiidae by having no branches of the digestive gland in the cerata (MARCUS DU BOIS-REYMOND 1982 after Eliot 1910). According to the results of this study, *Cyerce edmundsi* is related to *Cyerce* and not *Mourgona*. A re-arrangement of the genera and species is too early, more taxa of Limapontioidea with the families Polybranchiidae, Hermaeidae, Costasiellidae, and Limapontiidae have to be added in future investigations to clarify validity of these taxa.

Within the usually monophyletic Plakobranchoidea, two families have been considered, the monogeneric Boselliidae and the species rich family Plakobrancheidae. The genus *Bosellia* comprising only five species (JENSEN 1997a) was always a taxon to debate. PRUVOT-FOL (1954) settled *Bosellia* within the family Polybranchiidae. She interpreted the dorsal apertures on the surface as a reminiscence of lost cerata: „Des «orifices» semés sur la partie dorsale font penser que l'animal décrit est incomplet, c'est-à-dire qu'il a perdu ses papilles.“ (PRUVOT-FOL 1954: 180). However, PRUVOT-FOL has not examined a specimen of *Bosellia* by herself but followed the first description of TRINCHESE written in 1891. PORTMANN (1958) re-described the species and denied the existence of pores on the dor-

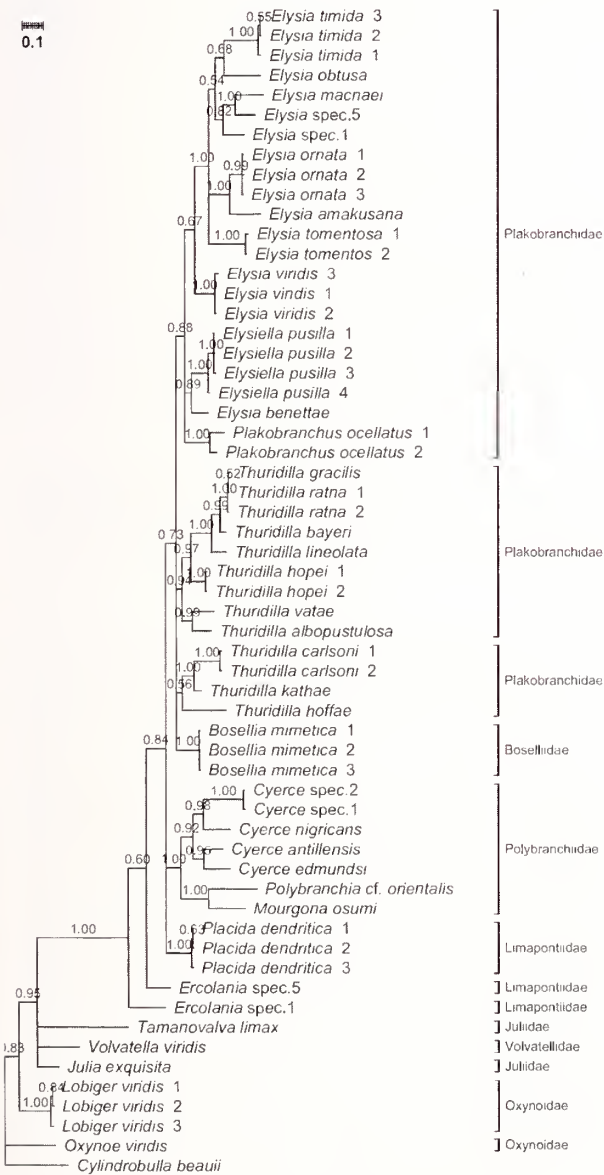
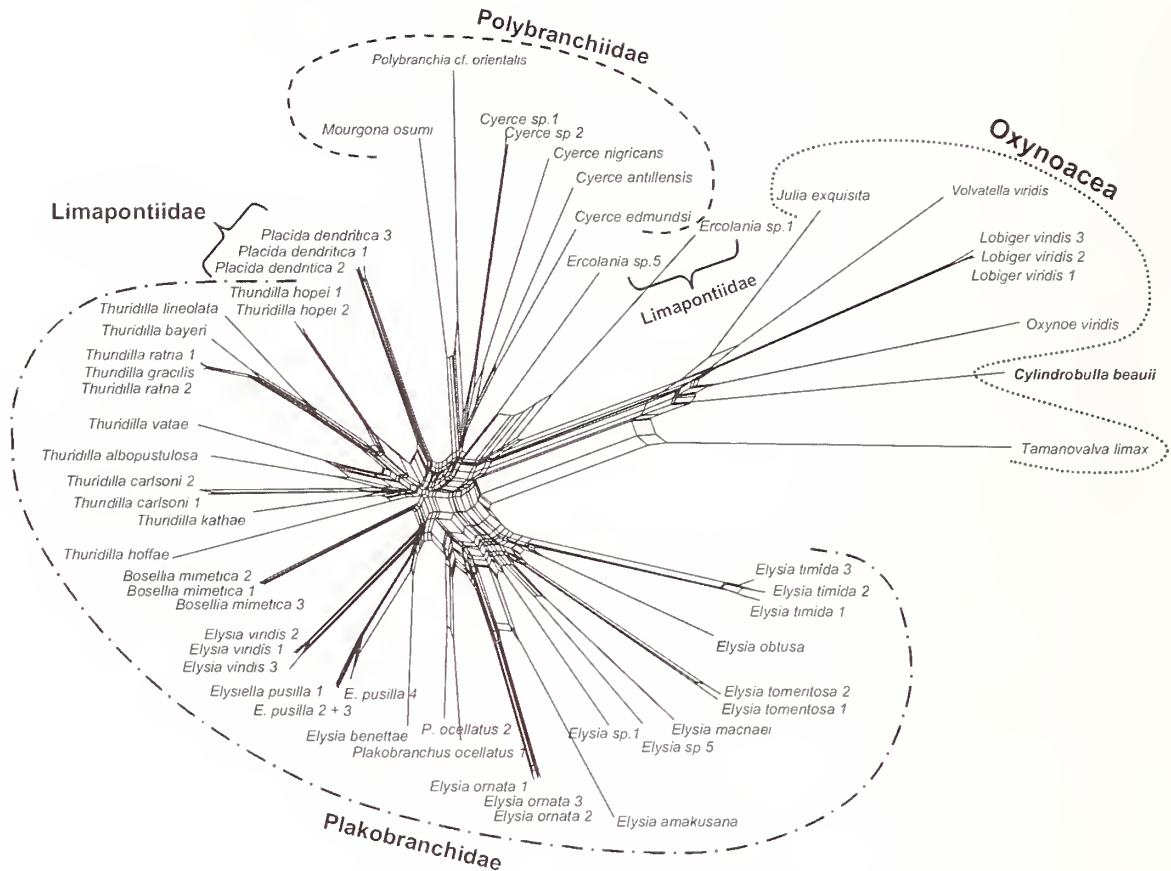


Fig. 4. Sacoglossa; 16Sr DNA gene: Bayesian Analysis, 50%-Majority Rule consensus tree with posterior probabilities (GTR+G+I-model, AIC).



**Fig. 5.** Sacoglossa: Neighbor network analysis applying SplitsTree4 to visualize conflict in the whole sacoglossan data set. Parallel edges with same length indicate a split and visualize the distances between the two groups involved. Note the long edges between the Plakobranchia and the Oxynoacea + *Cylindrobulla*. Fit value: 95.85.

sal surface. MARCUS DU BOIS-REYMOND (1980) and later THOMPSON and JAKLIN (1988) positioned *Bosellia* in the family Plakobranchidae, but MARCUS DU BOIS-REYMOND (1982) transferred it in its own family Boselliidae based on the difference in number of chromosomes in *Bosellia* ( $n=7$ ) and other sacoglossans ( $n=17$ ), as well as the lack of parapodia. JENSEN (1996) criticized that the number of chromosomes is only known for the species *Bosellia mimetica* and not for other species of this genus but decided to retain the family status until the phylogenetic position of the genus is solved. According to our results, *Bosellia* seems to represent an own evolutionary line, independent of the family Plakobranchidae (with the genera *Elysia*, *Thuridilla* and *Plakobranchus*), but its position varies within the Plakobranchacea. The result of the Maximum Likelihood analysis places *Bosellia* as sister-taxon of Plakobranchidae, similar to the results obtained by JENSEN (1996). BASS and KARL (2006) used *Bosellia mimetica* and *Bosellia marcusi* in their phylogenetic analysis of Plakobranchidae. Similar to our results, *B. mimetica* forms the sister taxon to the further included genera

*Elysia*, *Elysiella*, *Plakobranchus* and *Thuridilla*. But the other included member of *Bosellia*, *B. marcusi*, represents the sister-taxon to *Elysia timida*. The authors considered a wrong determination of their animal.

The family Plakobranchidae appears monophyletic only in the Maximum Likelihood analysis. This is in accordance with JENSEN's analysis (1996). She mentioned as most important autapomorphies the parapodia in which the digestive gland and the reproduction system reach. In the SplitsTree analysis support of the split Plakobranchidae versus rest of Sacoglossa is not found at all. Within the Plakobranchidae, the genus *Thuridilla* is monophyletic in the NJ- and ML-analysis and branching pattern is identical. The Bayesian analysis produced two of these monophyletic *Thuridilla* complexes but could not resolve their positions in detail. Also in the Splits analysis, no split *Thuridilla*/rest of Sacoglossa is visible. GOSLINER (1995: 45) mentioned following apomorphic features: „elongate rhinophores, single, thick, darkly pigmented ampulla, non-muscular, unarmed penis, bursa copulatrix with separate



gonopore and orange or red eggs." A darkly pigmented ampulla could not be confirmed in the Mediterranean *Thuridilla hopei* (own unpublished data). It is possible that only Indopacific species have a pigmented ampulla, since Gosliner dealt with these species. *Elysia viridis* also lays „reddish yellow“ eggs when feeding on *Chaetomorpha* (TROWBRIDGE & TODD 2001: 222). One particular clade was found in all analysis: (*T. bayeri* (*T. ratna* 2 (*T. ratna* 1 / *T. gracilis*))). The species are only distinguished by different colouration (GOSLINER 1995). JENSEN (1992: 278) found „slight differences in the size of the pharyngeal pouch.“ BRODIE and BRODIE (1990) considered *T. bayeri* as synonym with *T. ratna*. GÖSLINER (1995: 9) mentioned that "Internally, there is little difference between *Thuridilla bayeri* [and] *Thuridilla ratna*“, "... these data strongly suggest that the described differences between *T. bayeri* and *T. ratna* are simply variations within a single species that is extremely variable in its colouration." Concerning *Thuridilla gracilis*, GOSLINER (1995) complained about the insufficient description of Risbec in 1928, hampering a correct assignment. RUDMAN (2000) stated that "Contrary to Gosliner (1995), I consider *T. bayeri* to be a synonym of *Thuridilla gracilis*." Our study supports the synonymisation of *T. ratna* with *T. gracilis* Risbec, 1928. But synonymisation of *Thuridilla bayeri* with *Thuridilla gracilis* seems preliminary, since we have no information on in-

traspecific variability of the gene. According to our splits analysis, there are affiliations also between *T. bayeri* and *T. lineolata* (Fig. 7). Comparison of GOSLINER's data (1995) with our data is hardly possible due to small overlap of included species. In agreement is the sister taxa relationship of *Thuridilla vatae* and *Thuridilla albopustulosa*.

JENSEN (1997a) estimated the number of *Plakobranchnus*-species from 1 to 14. In this study two specimens of *Plakobranchnus ocellatus* were used. Although all analyses published yet (GOSLINER 1995; JENSEN 1996; BASS & KARL 2006) assign *Plakobranchnus* to other members of the family Plakobranchnidae, its position varies considerably. A unique character of the genus in relation to other members of Plakobranchnidae is the dorsal position of the anus (JENSEN 1992).

In all analyses on Plakobranchnidae (JENSEN 1996; BASS & KARL 2006; this study), *Elysiella pusilla* is always located among *Elysia* species, *E. benettiae* usually forming its sistertaxon. JENSEN and WELLS (1990: 324) emphasized the validity of an own genus *Elysiella*: "this species shows so many differences from other species of *Elysia* that it definitely belongs to a different genus." But all phylogenetic analyses indicate the invalidity of this genus, there-

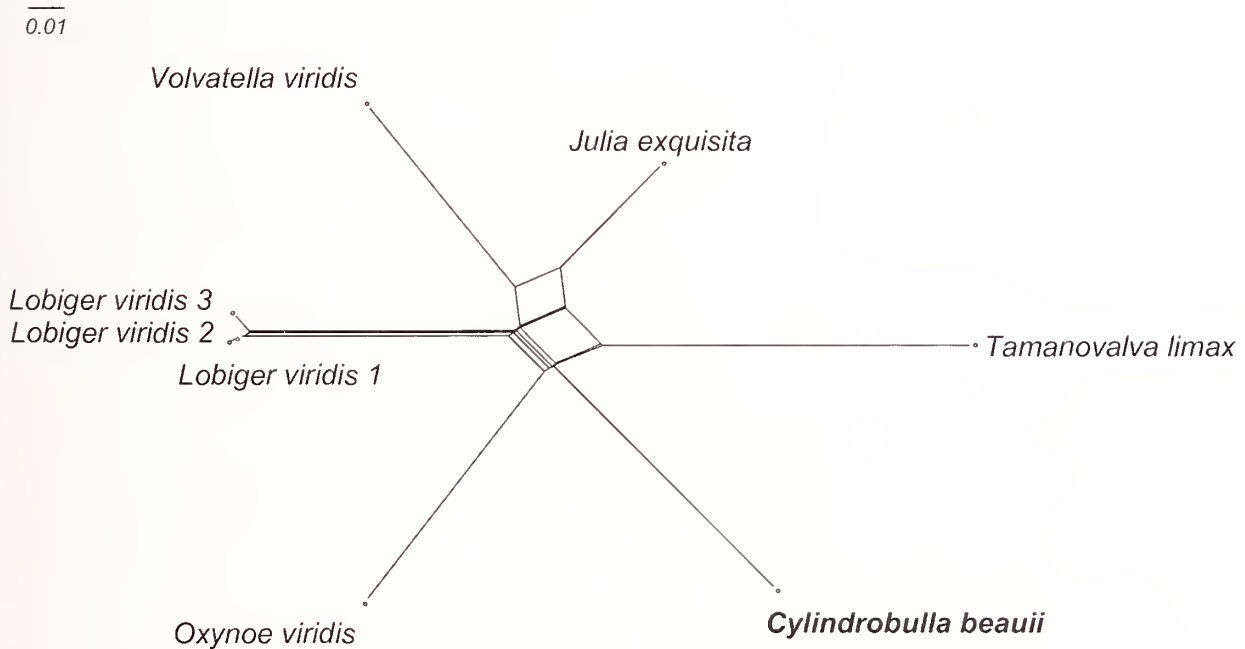
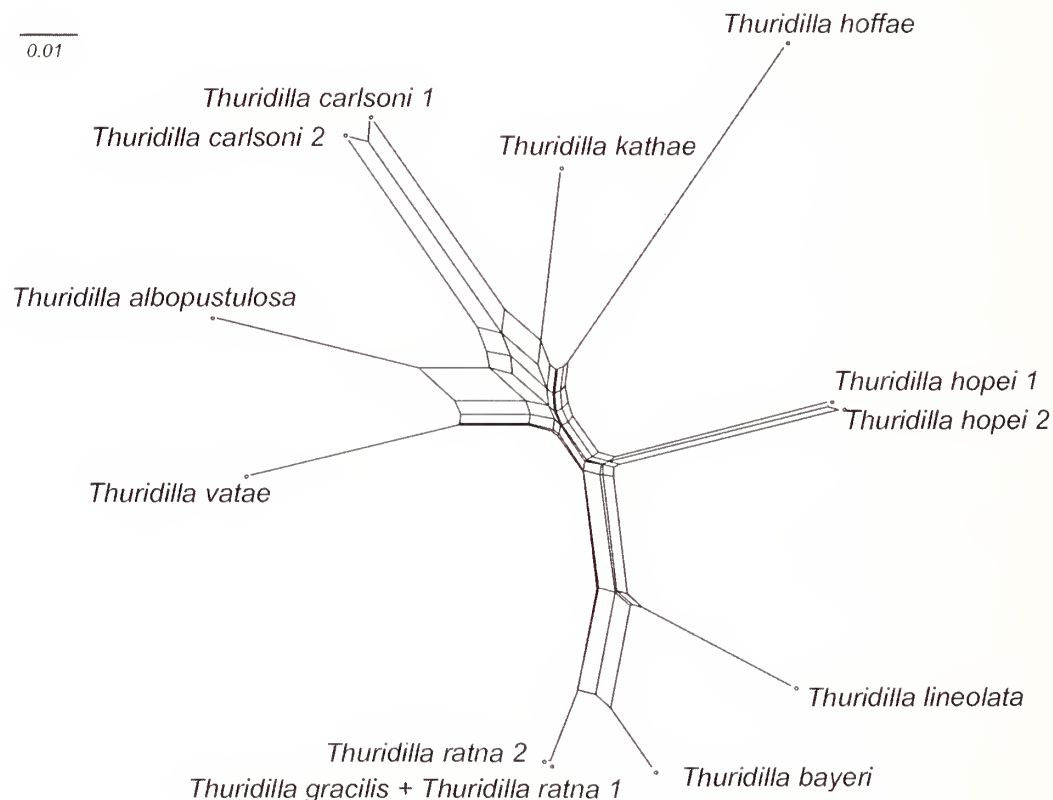


Fig. 6. Neighbor network analysis applying SplitsTree4 to visualize conflict in the reduced data set, comprising only Oxynoacea and the outgroup taxon *Cyliindrobulla beauii*. Note that there is no split separating *Cyliindrobulla beauii* from the Oxynoacea. Similar long edges connecting *Volvatella*, *Julia* and *Tamanovalva* indicate the lack of signal of the taxon Juliidae. Fit value: 98.53.

fore *Elysiella pusilla* is named from hereon as *Elysia pusilla* (Bergh, 1872). Several species, described under the genus name *Elysia* (*Elysia dubia* Eliot, 1904, *Elysia halimeda* Maena, 1954, *Elysia latipes* Marcus & Marcus, 1960 and *Elysia macnaei* Marcus, 1982) are mentioned to be synonymous to *Elysia pusilla* (see JENSEN & WELLS 1990). MARCUS DU BOIS-REYMOND (1980) distinguished material identified as *Elysia halimeda* by Baba (1957) and Burn (1972) from the original *E. halimeda* Maena, 1954 from South Africa by the presence of papillate rhinophores in the latter. She re-named the material misidentified as *E. halimeda* and established the name *E. macnaei* Marcus, 1980. Our study includes a specimen from the Zoologische Staatssammlung München, collected in Sulawesi and identified by courtesy by Michael Schrödl as *E. macnaei*. This specimen does not group with *Elysia pusilla* indicating that *E. macnaei* is not synonymous with *E. pusilla*.

Comparing our results with the only available phylogenetic hypothesis on Sacoglossa elaborated by JENSEN (1996), the results of the Maximum Likelihood analysis come closest to her results. Both analyses support monophyly of the Plakobranchacea, Plakobranchioidea, Plakobranchidae as well as the genera *Elysia* (with *Elysiella* as a synonym) and *Thuridilla*. *Plakobranchus* and *Bosellia* form distinct evolutionary lines. Juliidae are also monophyletic. The two hypotheses contradict in the paraphyly (this study) versus monophyly (JENSEN 1996) of the Oxynoacea, Oxynoidae and Limapontiidae. But it has to be emphasized that these taxa are underrepresented in our study and future analyses have to be performed with more representatives of these groups. Furthermore, other genes have to be used for analysing deeper nodes of Sacoglossa, since the 16Sr DNA gene (this study), as well as the COI gene (unpublished results) show saturation on higher level.



**Fig. 7.** Neighbor network analysis applying SplitsTree4 to visualize similarity of species in a reduced data set, comprising only members of the genus *Thuridilla*. Note the one edge leading to the 2 specimens of *Thuridilla ratna* and the one specimen of *T. gracilis*. No conflict occurs, indicating the synonymy of these 2 species. *Thuridilla bayeri* is separate, nevertheless the long edges characterizing the split *Thuridilla gracilis* / *T. ratna* / *T. bayeri* indicate its closer affinity to *T. gracilis*, than the shorter edge characterizing the split *T. bayeri* / *T. lineolata*. Fit value: 98,12.

4.2. Food spectrum of Sacoglossa

Several authors emphasized that sacoglossans have a very narrow food spectrum (e.g. THOMPSON 1964; CLARK 1975, 1994). However, the contrary was also stated: „..., some species feed on several different food items (...), and food spectra are not so narrow as previously assumed.“ (JENSEN 1980a: 73). „Tropical Ascoglossa are relatively

non-specific feeders, possibly because of the higher diversity of (see Table 2) foods in tropical seas.“ (CLARK & BUSACCA 1978: 281). That food spectrum varies in different taxa is evident in the genus *Elysia* with species feeding exclusively on one food species (e.g. *Elysia translucens* on *Flabellia* (former *Udotea*) *petiolata*, see MARIN & ROS 2004) or on a high variety of food species belonging to completely different phyla (e.g. *Elysia crispata* feed-

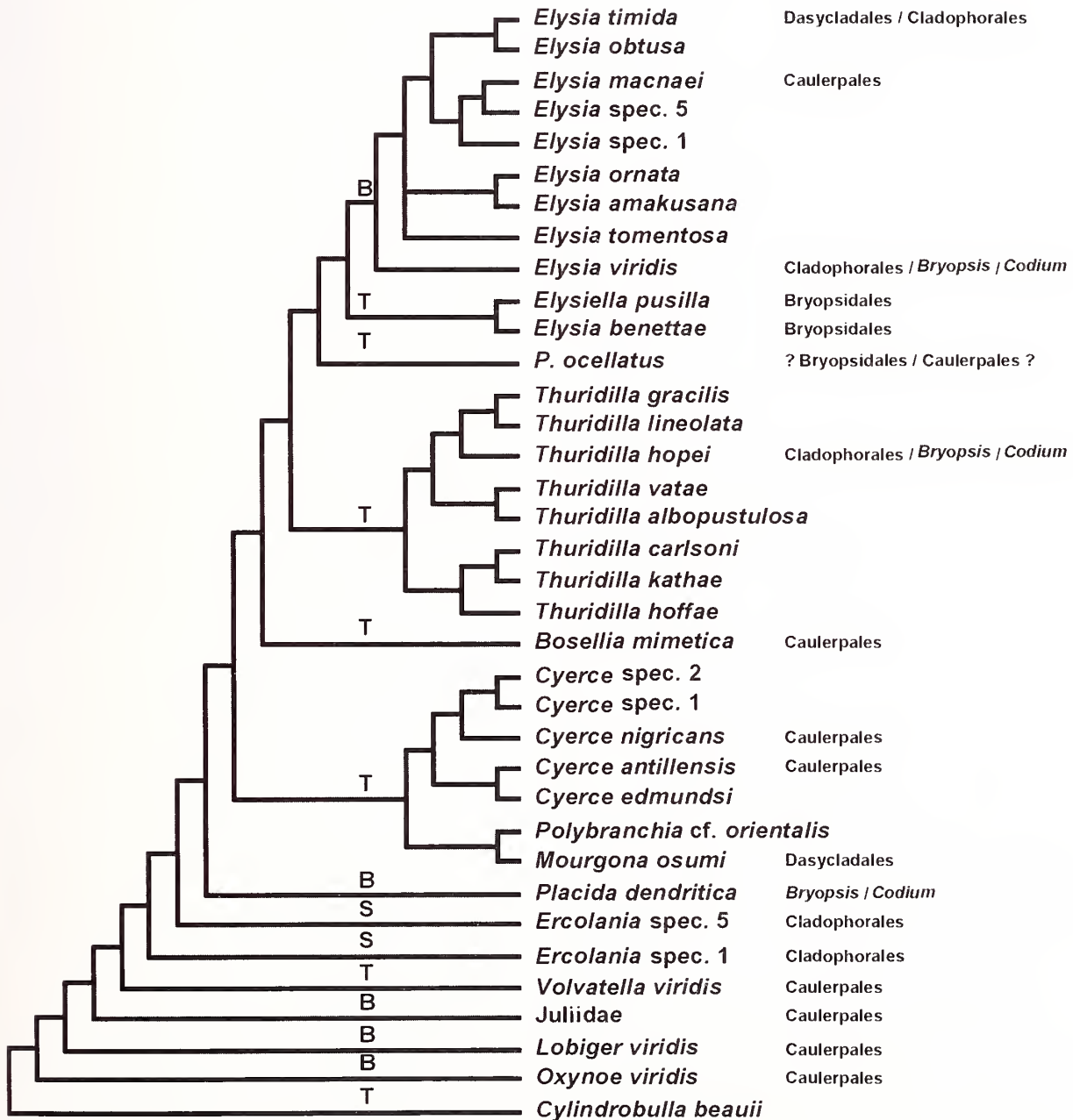


Fig. 8. Phylogeny of Sacoglossa (redrawn after the Maximum Likelihood phylogram, see Fig. 3) with food (higher taxa level) and tooth form mapped on the tree. T Triangular shaped teeth, S sabot shaped teeth, B blade shaped teeth.

ing on the siphonalean heterokontophyte *Vaucheria*, the siphonocladalean *Chaetomorpha* (Cladophorales), the siphonalean *Batophora* (Dasycladales), on different siphonalean Halimedales and members of the taxon Bryopsidales). In few species, an ontogenetic food switch is described, (e.g. juvenile *Elysia timida* feeds on *Cladophora dalmanica*, adults on *Acetabularia acetabulum* (MARÍN & ROS 1993)).

Oxynoacea, representing about 20% of Sacoglossa (JENSEN 1997a), exclusively feed on the genus *Caulerpa*. Members of the Caulerpales with xylan in the cell wall remain the main food source of sacoglossans, even in the highly evolved Plakobanchidae (see Table 2). Some plakobanchids do not feed solely on Caulerpales, but seem to forage additionally on Cladophorales, which have cellulose in their cell wall. *Ercolania* and other limapontiids have switched to the Cladophorales as the main food source, Hermaeidae focus on Rhodophyta, and few sacoglossans are oophagous (consuming eggs of other opisthobranchs). A switch to Dasycladales with mannan in the cell wall is seldom (e.g. *Elysia timida*, *E. filicandula*) and for these species other food sources (Caulerpales) are also recorded. Only species of *Momgona* seem to focus on Dasycladales.

JENSEN (1997a) assumed that the evolution of the sacoglossans was linked to the structure of cell walls in their food organisms. Within evolution of Plakobanchacea, members of this taxon could only change their food spectrum from Caulerpales and Udotaceae (containing xylan) to Codiales and Dasycladales (with mannan) or Cladophorales/Siphonocladales (with cellulose) by exploring Derbesiales (actual taxonomy: Bryopsidales) with cell walls of xylan in the haplonts and cell walls of mannan in the diplonts. According to JENSEN (1993a), 12% of the sacoglossans are able to feed on several algal species with different cell wall structure. She described populations of *Elysia viridis* feeding on *Chaetomorpha* (Cladophorales) with cell walls containing cellulose and populations on *Codium* (Bryopsidales) with cell walls containing mannan (JENSEN 1989a). In experiments, she transferred *Elysia viridis* collected from *Codium* to *Chaetomorpha* and vice versa. Some specimens accepted the other algal species but still preferred the one that was their original food.

In choice experiments, TROWBRIDGE and TODD (2001) confirmed this behaviour of possible food switch. They showed that *E. viridis* collected on the native food *Cladophora rupestris* preferred this alga, but were able to switch to introduced species of *Codium fragile* ssp. *tomentosoides* and *C. fragile* ssp. *atlanticum*. They also demonstrated that the F1 generation also preferred *C. fragile* in laboratory experiments, independent whether the parents

were cultivated on *Cladophora rupestris* or *Codium fragile*. Juveniles grew faster on the introduced species. They concluded, that "slug performance is much better on the introduced host *Codium fragile* than on native *Cladophora*." (TROWBRIDGE & TODD 2001: 234).

#### 4.3. Food spectrum and tooth shape

BLEAKNEY (1990) detected different types of teeth in *Placida dendritica* in correlation with different kinds of food. JENSEN (1993a, 1997a) also found a positive correlation of tooth shape and algal diet. Within Oxynoacea (feeding exclusively on *Caulerpa*) the plesiomorphic triangular shaped tooth occurs as well as the blade-shaped tooth form. The triangular type is only found in those species, which feed on algae with xylan or mannan in the cell wall, but not cellulose. The blade-shaped tooth evolved several times within Sacoglossa, and this tooth type seems to be adapted for feeding on all types of algae. Only the sabot-shaped tooth seems to be restricted to those species mainly feeding on algae with cellulose. In an experiment JENSEN (1993a) could show that phenoplastic variation of teeth underlies environmental factors. *Elysia viridis* collected from *Codium* (Bryopsidales with mannan) was offered *Chaetomorpha* (Cladophorales with cellulose) as only food source for one year. The newly formed teeth in the upper limb of the radula were similar to those teeth of *Elysia viridis* specimens collected from *Chaetomorpha*. Mapping tooth shape and algal food on the cladogram obtained by the ML analysis (Fig. 8) does not reveal correlation of slug evolution and tooth shape, nor toothshape in correlation with consumed algal taxon.

#### 4.4. Food spectrum and phylogeny

Based on her phylogenetic hypothesis, JENSEN (1997a) postulated that the ancestor of the Sacoglossa foraged on a filamentous calcified member of the udotacean *Halimeda* (Caulerpales), since all basal Plakobanchacea are feeding on this type of algae. The monophyletic Oxynoacea switched to the uncalcified genus *Caulerpa*, on which the shelled sacoglossans exclusively feed. In this hypothesis, JENSEN (1997a) assumed that *Cylindrobulla* also feeds on *Halimeda*, which would strengthen her hypothesis. But this was never observed. Actually, her note that "*Cylindrobulla* is apparently associated with the non-photosynthetic, uncalcified rhizoids of *Halimeda*" (JENSEN 1997a: 319) could indicate that *Cylindrobulla* forages on epibenthic algae associated with *Halimeda*. Her description on tooth morphology (JENSEN 1989b), as well as the lack of a suctorial pump (JENSEN 1996, 1997a) also suggests grazing as a feeding mode, and not piercing cell walls and

sucking out the cytoplasmatic contents. According to our analysis and the resulting phylogenetic hypothesis, another evolutionary scenario can be discussed, in which uncalcified *Caulerpa* is the original food source of Sacoglossa. This conforms to the hypotheses of CLARK & BUSACA (1978), JENSEN (1980a) and CLARK & DE FREESE (1987). *Caulerpa* seems to be attractive even for sacoglossans that do not feed on that genus *in situ*. In experiments, JENSEN (1988) demonstrated that many slugs chose a cell homogenate of *Caulerpa* as food. But mapping radula morphology as described by JENSEN (1996) on our cladogram (Fig. 8) produces incongruencies especially concerning the re-evolution of the triangular tooth shape.

Fossil records of Sacoglossa are rare, but shelled Juliidae have been recorded from the Oligocene (JANSSEN 1979). JENSEN (1997a) dated back the origin of Sacoglossa in the Cretaceous because the fossil record of the calcified *Haliueda* dates back so far. She further noted that Sacoglossa then had to exist before the origin of *Haliueda* itself. We do not follow this statement since *Haliueda* could have existed long before the first sacoglossan slug evolved and foraged on this particular food. CLARK & DE FREESE (1987) hypothesized that *Haliueda* was already calcified when the first sacoglossan appeared and that feeding did not influence the grade of calcification significantly. In contrast, JENSEN (1997a) assumed an increasing calcification as a mechanical defense of the alga as an answer to predation by Sacoglossa and the adaptation of the buccal apparatus of Sacoglossa to deal with this mechanical defense. Calcification does not only appear in algae predated by Sacoglossa but is a wide spread phenomenon in Rhodophyta or Phaeophyceae since it gives mechanical stability in areas with strong current or strong swell (e.g. dictyoalean *Padina pavonica*, Corallinacea, etc.). The mediterranean Coralligène is produced mainly by the red alga *Mesophyllum alternans* and *Lithophyllum frondosum* with a high calcification rate and no recorded predation (BALLESTEROS 2006).

#### 4.5. Conclusions

In future analyses, more taxa especially of the Oxynoacea and Limapontioidea have to be included to test the two different hypotheses presented by JENSEN (1996) based on morphology and the one outlined earlier by other authors and the present study based on molecular markers. Since both mitochondrial genes, 16S rDNA (presented here) and COI (not included in this study), show a high substitution rate already on higher taxa level, genes with lower evolutionary rates, e.g. nuclear genes as 18S and 28S, have to be analysed additionally. Further investigation on food organisms is also needed to analyse a possible co-evolution of slugs and algae. This can only be done with a rigorous identification of ingested algae, e.g. by analysing

algal chloroplast genes in the slugs, which would exclude those algae used only as substrat.

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**Addendum:** After receiving the proofs, GRZYMBOWSKI et al. 2007 was published, and a name for *Ercolania spec. I* is available now. The species is called *Ercolania kencolesi* Grzybowski, Stemmer & Wägele, 2007.



**Table 1.** Specimens used in the phylogenetic analysis with accession numbers. ZSM Zoologische Staatssammlung Munich.

Family	Taxon	Origin	Accession number
<b>outgroup</b>			
	Cylindrobullidae Thiele, 1931 P. Fischer, 1856	<i>Cylindrobulla beaulti</i> Miama, 03-2005	EU140897
<b>OXYNOACEA</b>			
Volvatellidae Pilsbry 1895	<i>Volvatella viridis</i> Hamatani, 1976	South Island, Lizard Island/Australia, 12-07-2006	EU140890
Juliidae E.A. Smith 1885	<i>Julia exquisita</i> (Gould, 1862) <i>Tamanovalva limax</i> Kawaguti & Baba, 1959	South Island, Lizard Island/Australia, 11-07-2006 Casuarina Beach, Lizard Island/Australia, 13-07-2006	EU140895 EU140896
Oxynoidae H. Adams & A. Adams 1854	<i>Oxynoe viridis</i> (Pease, 1861) <i>Lobiger viridis</i> 1 Pease, 1863 <i>Lobiger viridis</i> 2 Pease, 1863 <i>Lobiger viridis</i> 3 Pease, 1863	South Island, Lizard Island/Australia, 10-07-2006 Lizard Island/Australia, 10-07-2006 Fiji Island, 26-08-2006 (ZSM 20061650) Coconut Beach, Lizard Island/Australia, 12-08-2006	EU140891 EU140892 EU140893 EU140894
<b>PLAKOBRANCHACEA</b>			
<b>Plakobranchoidea</b>			
Boselliidae Marcus 1982	<i>Bosellia mimetica</i> 1 Trinchese, 1891 <i>Bosellia mimetica</i> 2 Trinchese, 1891 <i>Bosellia mimetica</i> 3 Trinchese, 1891	Baretta del Abre near Mataró/Spain, 23-05-2006 Banyuls-sur-mer/Southern France, 11-05-2006 Tossa/Spain, 29-08-2003	EU140872 EU140873 EU140874
Plakobranchoidea Rang 1829	<i>Elysia amakusana</i> Baba, 1955 <i>Elysia benettae</i> Thompson, 1973 <i>Elysia macnaei</i> Marcus E. duB.-R., 1980 <i>Elysia obtusa</i> Baba, 1938 <i>Elysia ornata</i> 1 (Swainson, 1840) <i>Elysia ornata</i> 2 (Swainson, 1840) <i>Elysia ornata</i> 3 (Swainson, 1840) <i>Elysia timida</i> 1 (Risso, 1818) <i>Elysia timida</i> 2 (Risso, 1818) <i>Elysia timida</i> 3 (Risso, 1818) <i>Elysia tomentosa</i> 1 Jensen, 1997 <i>Elysia tomentosa</i> 2 Jensen, 1997	Lizard Island/Australia, 04-03-2005 Samoa, 06-08-2005 (ZSM 20060293) NW-Sulawesi/Indonesia, 23-07-2003 (ZSM 20033821) Samoa, 20-08-2005 (ZSM 20060257) Lizard Island/Australia, 09-2002 North Point, Lizard Island/Australia, 14-07-2006 Lizard Island/Australia, 18-03-2005 Banyuls-sur-mer/Southern France, 02-05-2006 near Roses/Spain, 22-05-2006 near Tossa/Spain, 25-05-2006 Lizard Island/Australia, 13-09-2004 Lizard Island/Australia, 21-03-2005	EU140851 EU140868 EU140854 EU140860 EU140849 EU140850 EU140848 EU140857 EU140858 EU140859 EU140852 EU140853

Family	Taxon	Origin	Accession number
	<i>Elysia viridis</i> 1 (Montagu, 1804)	Roscoff/Bretagne, Northern France, 2006	EU140861
	<i>Elysia viridis</i> 2 (Montagu, 1804)	Tossa/Spain, 19-05-2006	EU140862
	<i>Elysia viridis</i> 3 (Montagu, 1804)	Banyuls-sur-mer/Southern France, 06-05-2006	EU140863
	<i>Elysia</i> spec.1 (see WÄGELE et al. 2006)	Lizard Island/Australia, 25-07-2005	EU140856
	<i>Elysia</i> spec. 5	South Island, Lizard Island/Australia, 24-07-2006	EU14085
	<i>Elysiella pusilla</i> 1 Bergh, 1872	Maledives, 04-2006	EU140864
	<i>Elysiella pusilla</i> 2 Bergh, 1872	Maledives, 04-2006	EU140866
	<i>Elysiella pusilla</i> 3 Bergh, 1872	Maledives 04-2006	EU140865
	<i>Elysiella pusilla</i> 4 Bergh, 1872	South Island, Lizard Island/Australia, 10-07-2006	EU140867
	<i>Plakobranchnus ocellatus</i> 1 Van Hasselt, 1824	Lizard Island/Australia, 21-03-2005	EU140875
	<i>Plakobranchnus ocellatus</i> 2 Van Hasselt, 1824	Lizard Island/Australia, 21-03-2005	EU140876
	<i>Thuridilla albopustulosa</i> Gosliner, 1995	NW-Sulawesi/Indonesia, 17-07-2003 (ZSM 20033615)	EU140889
	<i>Thuridilla bayeri</i> (Marcus, 1965)	NW-Sulawesi/Indonesia, 17-07-2003 (ZSM 20033612)	EU140886
	<i>Thuridilla carlsoni</i> 1 Gosliner, 1995	Lizard Island/Australia, 13-09-2004	EU140877
	<i>Thuridilla carlsoni</i> 2 Gosliner, 1995	Lizard Island/Australia, 25-06-2006	EU140878
	<i>Thuridilla gracilis</i> (Risbec, 1928)	Lizard Island/Australia, 18-03-2005	EU140883
	<i>Thuridilla hoffae</i> Gosliner, 1995	Samoa, 16-08-2005 (ZSM 20060224)	EU140880
	<i>Thuridilla hopei</i> 1 (Verany, 1853)	Elba, 07-2001	EU140881
	<i>Thuridilla hopei</i> 2 (Verany, 1853)	Baretta del Abre near Mataró/Spain, 24-05-2006	EU140882
	<i>Thuridilla kathae</i> Gosliner, 1995	Lizard Island/Australia, 13-09-2004	EU140879
	<i>Thuridilla lineolata</i> Bergh, 1905	NW-Sulawesi/Indonesia, 07- 2003	EU140887
	<i>Thuridilla ratna</i> 1 (Marcus, 1965)	Lizard Island/Australia, 25-06-2005	EU140884
	<i>Thuridilla ratna</i> 2 (Marcus, 1965)	Lizard Island/Australia, 13-09-2004	EU140885
	<i>Thuridilla vatae</i> (Risbec, 1928)	Samoa, 11-08-2005 (ZSM 20060088)	EU140888
<b>Limapontioidea</b>			
Polybranchiidae O'Donoghue 1929	<i>Cyerce antillensis</i> Engel, 1927	Azores, 09-2001	EU140841
	<i>Cyerce edmundsi</i> (Thompson, 1977)		EU140842
	<i>Cyerce nigricans</i> (Pease, 1866)	Channel, Lizard Island/Australia, 13-07-2006	EU140843

Family	Taxon	Origin	Accession number
	<i>Cyerce</i> spec. 1 (see WÄGELE et al. 2006)	Lizard Island/Australia, 25-07-2005	EU140845
	<i>Cyerce</i> spec. 2 (see WÄGELE et al. 2006)	Lizard Island/Australia, 13-09-2004	EU140844
	<i>Polybranchia</i> cf. <i>orientalis</i> (Kelaart, 1858)	Lizard Island/Australia, 01-09-2004	EU140846
	<i>Mourgona osumi</i> Hamatani, 1994	North Point, Lizard Island/Australia, 14-07-2006	EU140847
Limapontiidae Gray 1847	<i>Placida dendritica</i> 1 (Alder & Hancock, 1843)	Tossa/Spain, 20-05-2006	EU140869
	<i>Placida dendritica</i> 2 (Alder & Hancock, 1843)	Tossa/Spain, 20-05-2006	EU140870
	<i>Placida dendritica</i> 3 (Alder & Hancock, 1843)	Tossa/Spain, 20-05-2006	EU140871
	<i>Ercolania</i> spec.1	Casuarina Beach, Lizard Island/Australia, 02-07-2006	EU140840
	<i>Ercolania</i> spec.5	Casuarina Beach, Lizard Island/Australia, 07-07-2006	EU140839

Table 2. Sacoglossan food organisms compiled from literature.

Species	Food	Reference
<b>OXYNOACEA</b>		
<u>Volvatellidae</u>		
<i>Ascobulla fischeri</i>	<i>Caulerpa</i> spp.	GASCOIGNE & SARTORY 1974 after Burn 1972
<i>Ascobulla fragilis</i>	<i>Caulerpa prolifera</i>	MARIN & ROS 2004
<i>Ascobulla ulla</i>	<i>Caulerpa racemosa</i>	JENSEN 1980a
	<i>Caulerpa racemosa</i> , <b>Laboratory:</b>	JENSEN 1981
	<i>Caulerpa sertularoides</i> ,	
	<i>Caulerpa cupressoides</i> , <i>Caulerpa verticillata</i>	
	<i>Caulerpa racemosa</i>	CLARK 1994
<i>Volvatella australis</i>	<i>Caulerpa</i>	JENSEN 1997b
<i>Volvatella bermudae</i>	<i>Caulerpa racemosa</i>	CLARK 1994
<i>Volvatella pyriformis</i>	<i>Caulerpa</i> spp.	GASCOIGNE & SARTORY 1974 after Burn 1972
<i>Volvatella</i>	<i>Caulerpa</i>	FONTANA et al. 1999
<u>Juliidae</u>		
<i>Edentellina typica</i>	<i>Caulerpa scalpelliformis</i>	GONOR 1961 after Burn 1960b
	<i>Caulerpa brownii</i>	BURN 1965
	<i>Caulerpa scalpelliformis</i>	GASCOIGNE & SARTORY 1974 after Burn 1972
<i>Berthelinia caribbea</i>	<i>Caulerpa verticillata</i>	EDMUNDS 1963
	<i>Caulerpa verticillata</i>	JENSEN 1980a after Grahamc 1969
	<i>Caulerpa verticillata</i>	CLARK 1994
<i>Berthelinia darwini</i>	<i>Caulerpa</i> sp.	JENSEN 1997b
<i>Berthelinia ganapati</i>	<i>Caulerpa racemosa</i>	JENSEN 1980a after Sarma 1975
<i>Berthelinia rotnesti</i>	<i>Caulerpa simpliciuscula</i>	JENSEN 1993b
	<i>Caulerpa racemosa</i>	WILLIAMS & WALKER 1999
<i>Julia japonica</i>	<i>Caulerpa ambigua</i>	JENSEN 1980a after Kawaguti & Yamasu 1966
<i>Midorigai australis</i>	<i>Caulerpa simpliciuscula</i>	GASCOIGNE & SARTORY 1974
	<i>Caulerpa simpliciuscula</i>	JENSEN 1980a after Burn 1960
<i>Tamanovalva babai</i>	<i>Caulerpa scalpelliformis</i> , <i>Caulerpa geminata</i>	GASCOIGNE & SARTORY 1974 after Burn 1972
	<i>Caulerpa scalpelliformis</i> , <i>Caulerpa geminata</i>	JENSEN 1980a after Burn 1960, 1965
<i>Tamanovalva limax</i>	<i>Caulerpa okamurai</i>	JENSEN 1980a after Kawaguti & Baba 1959

Species	Food	Reference
<b>Oxynoidae</b>		
<i>Lobiger serradifalci</i>	<i>Caulerpa prolifera</i>	GONOR 1961
	<i>Caulerpa prolifera</i>	MARIN & ROS 2004
<i>Lobiger souverbii</i>	<i>Caulerpa racemosa</i>	JENSEN 1980a
<i>Oxynoe antillarum</i>	<i>Caulerpa racemosa</i>	JENSEN 1980b
	<i>Caulerpa racemosa</i> , <b>Laboratory:</b>	JENSEN 1980a; JENSEN 1980a after Marcus &
	<i>Caulerpa sertularioides</i>	Hughes 1974; CLARK & BUSACCA 1978
<i>Oxynoe azuropunctata</i>	<i>Caulerpa paspaloides</i> , <i>C. cupressoides</i> ,	JENSEN 1980b
	<i>C. sertularioides</i> , <b>Laboratory:</b> <i>C. racemosa</i>	
	<i>Caulerpa paspaloides</i>	CLARK 1994
<i>Oxynoe olivacea</i>	<i>Caulerpa prolifera</i>	MARIN & ROS 2004
<i>Oxynoe panamensis</i>	<i>Caulerpa sertularioides</i>	JENSEN 1980a after Lewin 1970
	<i>Caulerpa sertularioides</i>	JENSEN 1993e after
		Doty & Aguilar-Santos 1970
<i>Oxynoe viridis</i>	<i>Caulerpa</i> spp.	GASCOIGNE & SARTORY 1974
<i>Roburnella wilsoni</i>	<i>Caulerpa</i>	JENSEN 1993b
<b>PLAKOBRANCHIACEA</b>		
<b>Plakobranchioidea</b>		
<b>Boselliidae</b>		
<i>Bosellia corinnae</i>	<i>Halimeda</i>	JENSEN 1993a
<i>Bosellia marcusii</i>	<i>Halimeda opuntia</i>	JENSEN & CLARK 1983
<i>Bosellia mimetica</i>	<i>Halimeda tuna</i>	PORTMANN 1958
	<i>Udotea</i> , <i>Halimeda</i>	THOMPSON & JAKLIN 1988
<b>Plakobranchidae</b>		
<i>Elysia atroviridis</i>	<i>Codium fragile</i>	KAWAGUTI & YAMASU 1965
<i>Elysia australis</i>	<i>Enteromorpha</i> , <i>Cladophora</i> , <i>Chaetomorpha</i>	JENSEN 1992 after Jensen 1991
	<i>Enteromorpha</i> , <i>Cladophora</i> , <i>Rhizoclonium</i>	JENSEN 1993a
	<i>Acetabularia penicillus</i> , <i>Chaetomorpha</i> ,	WILLIAMS & WALKER 1999 after Hinde 1983
	<i>Rhizoclonium</i> , <i>Enteromorpha</i>	and after Jensen 1990
<i>Elysia benettae</i>	<i>Chlorodesmis</i>	JENSEN 1993a
<i>Elysia canguzua</i>	<i>Codium</i> sp.	JENSEN 1980a after Marcus 1955
	<i>Bryopsis plumosa</i> , <i>Codium</i> sp.	JENSEN & CLARK 1983 after Marcus 1955
	<b>Laboratory:</b> <i>Chaetomorpha</i>	JENSEN & CLARK 1983
<i>Elysia catulus</i>	<i>Zostera marina</i>	CLARK 1975
<i>Elysia chilkinsis</i>	most probably <i>Enteromorpha</i>	JENSEN 1993e
<i>Elysia chlorotica</i>	<i>Cladophora</i> sp.	FRANZ 1968
	<i>Cladophora</i> spp., <i>Vaucheria</i> spp.	CLARK 1975
	<i>Chaetomorpha</i> sp.	JENSEN & CLARK 1983 after West 1977
	<i>Vaucheria litorea</i>	RUMPHO et al. 2000 after Mujer et al. 1996 and
		after Pierce et al. 1996
<i>Elysia crispata</i>	<i>Halimeda</i> sp., <i>Bryopsis plumosa</i> ,	CLARK & BUSACCA 1978
	<i>Penicillus</i> sp., <i>Batophora oerstedii</i>	
	<i>Halimeda</i> sp., <i>Bryopsis plumosa</i> ,	JENSEN 1980a
	<i>Penicillus</i> sp., <i>Batophora oerstedii</i> ,	
	<i>Caulerpa verticillata</i>	
	<b>Laboratory:</b> <i>Caulerpa verticillata</i> ,	THOMPSON & JARMANN 1989
	<i>C. racemosa</i> , <i>Halimeda discoidea</i> ,	
	<i>Chaetomorpha</i> sp.	
	<i>Vaucheria litorea</i>	PIERCE et al. 2003
	<i>Penicillus capitatus</i> , <i>Halimeda incrassata</i> ,	CURTIS et al. 2005 after Curtis et al. 2003
	<i>H. monile</i>	
	<i>Bryopsis plumosa</i> , <i>Derbesia tenuissima</i>	CURTIS et al. 2005
	<i>Bryopsis plumosa</i>	CURTIS et al. 2005
<i>Elysia degeneri</i>	<i>Udotea</i>	HORGEN et al. 2000

Species	Food	Reference
<i>Elysia diomedea</i>	<i>Padina</i> sp.	JENSEN 1980a after Bertsch & Smith 1973
<i>Elysia evelinae</i>	<i>Biddulphia</i> sp., ? <i>Dictyota</i>	JENSEN 1980a; JENSEN 1980a after Marcus 1957
	<i>Biddulphia</i>	JENSEN 1993a
<i>Elysia expansa</i>	<i>Caulerpa</i>	JENSEN 1993b
	<i>Caulerpa racemosa</i> , <i>C. cupressoides</i>	WILLIAMS & WALKER 1999
<i>Elysia filicauda</i>	? <i>Acetabularia peniculus</i>	JENSEN & WELLS 1990
	<i>Acetabularia</i>	JENSEN 1992 after Schmekel 1968 and after Nuttall 1989
	<i>Caulerpa racemosa</i> , <i>C. cupressoides</i> cf. <i>Cladophora</i>	WILLIAMS & WALKER 1999 WÄGELE & JOHNSON 2001 after Marin & Ros 1988
<i>Elysia flava</i>		JENSEN 1990a
<i>Elysia flavomaculata</i>	<b>Laboratory:</b> <i>Chaetomorpha antennina</i> , <i>Cladophoropsis</i> sp.	
<i>Elysia fusca</i>	<i>Codium</i> sp.	JENSEN 1980a after Schmekel 1968
<i>Elysia gordanae</i>	<i>Cladophora</i> sp.	WÄGELE & JOHNSON 2001 after Marin & Ros 1988
<i>Elysia hedgpethi</i>	<i>Codium fragile</i> , <i>Bryopsis corticulans</i>	GREENE 1970
<i>Elysia japonica</i>	<i>Chaetomorpha</i> , <i>Cladophoropsis</i> sp.	JENSEN 1993a
<i>Elysia leucolegnote</i>	<i>Boodleopsis pusilla</i>	JENSEN 1990a, JENSEN 1990b
<i>Elysia macnaei</i>	<i>Halimeda cuneata</i>	MACNAE 1954
	<i>Halimeda macroloba</i>	PAUL & ALSTYNE 1988
<i>Elysia maoria</i>	<i>Codium</i>	JENSEN 1980a after Reid 1964
	<i>Codium convolutum</i> ,	WILLIAMS & WALKER 1999
	<i>Codium fragile</i> ssp. <i>tomentosoides</i>	after Trowbridge 1995
<i>Elysia ornata</i>	<i>Bryopsis plumosa</i>	JENSEN 1981
	<i>Bryopsis</i> sp.	HÖRGEN et al. 2000
	<i>Bryopsis</i> sp.	FONTANA et al. 2001 after Hamann & Scheuer 1993 and after Hamann et al. 1996
<i>Elysia papillosa</i>	<i>Penicillus</i> spp.	JENSEN 1980a
	<i>Halimeda</i> ssp., <i>Penicillus</i> , <i>Udotea flabellum</i>	CLARK 1984
	<i>Penicillus</i> , <i>Udotea</i> , <i>Halimeda</i>	JENSEN 1993a
<i>Elysia patagonica</i>	adult: <i>Codium</i>	SCHRÖDL 1996
	adult: <i>Bryopsis plumosa</i> ; veliger:	MUNIAIN et al. 2001
	<i>Nanochloropsis</i> sp.	
<i>Elysia patina</i>	<i>Penicillus</i> , <i>Halimeda</i>	JENSEN 1993a
	<i>Udotea</i>	CLARK 1994
<i>Elysia punctata</i>	<i>Codium</i> spp.	MACNAE 1954
<i>Elysia rufescens</i>	<i>Bryopsis</i> sp.	HÖRGEN et al. 2000
	<i>Bryopsis</i> sp.	FONTANA et al. 2001 after Hamann & Scheuer 1993 and after Hamann et al. 1996
<i>Elysia serca</i>	<i>Halodule wrightii</i> , <i>Ulva lactuca</i>	JENSEN 1980a; JENSEN 1980a after Horsoe 1956
	<i>Halophila engelmanni</i> , <i>Thalassia testudinum</i> ,	JENSEN 1982
	<i>Halodule wrightii</i>	
	<i>Syringodium filiforme</i>	WILLIAMS & WALKER 1999 after Jensen 1983
<i>Elysia subornata</i>	<i>Caulerpa ashmeadii</i> , <i>C. mexicana</i> ,	CLARK & BUSACCA 1978
	<i>C. paspaloides</i> , <i>C. racemosa</i>	
	<i>Caulerpa ashmeadii</i> , <i>C. racemosa</i> ,	JENSEN 1980a
	<i>C. sertularioides</i> ,	
	<b>Laboratory:</b> <i>C. cupressoides</i> , <i>C. mexicana</i> ,	
	<i>C. paspaloides</i>	
<i>Elysia thompsoni</i>	<i>Caulerpa</i>	JENSEN 1993b

Species	Food	Reference
<i>Elysia timida</i>	<i>Codium</i>	KREMER & JANKE 1988
	<i>Acetabularia acetabulum</i> juvenil: <i>Cladophora dalmatica</i> , adult: <i>Acetabularia acetabulum</i>	MARIN & ROS 1992 MARIN & ROS 1993
<i>Elysia translucens</i>	<i>Flabellia</i> (as <i>Udotea</i> ) <i>petiolata</i>	MARIN & ROS 2004
<i>Elysia trisinuata</i>	<i>Codium</i>	JENSEN 1992
<i>Elysia tuca</i>	<i>Halimeda</i> spp., <i>Caulerpa sertularioides</i> , <i>C. mexicana</i> , <i>C. racemosa</i> , <i>Avrainvillea nigricans</i> , <i>Udotea</i> sp.	CLARK & BUSACCA 1978
	<i>Halimeda discoidea</i>	STIRTS & CLARK 1980
	<i>Halimeda discoidea</i> , <i>H. incrassata</i>	WAUGH & CLARK 1986
	<i>Halimeda incrassata</i>	CLARK & DEFRESE 1987
	<i>Halimeda incrassata</i>	CLARK 1994
	<i>Codium tomentosum</i>	TAYLOR 1968
	<i>Codium</i>	BOUCHET 1984
	<i>Codium fragile</i>	TRENCH et al. 1973
	<i>Codium tomentosum</i>	THOMPSON & JAKLIN 1988
	<i>Codium</i> , <i>Chaetomorpha</i>	JENSEN 1989a
<i>Elysia viridis</i>	<i>Codium</i> spp., <i>Bryopsis plumosa</i> , <i>Chaetomorpha linum</i>	JENSEN 1980a; JENSEN 1980a after Fretter 1941 and after Rasmussen 1973; JENSEN 1994 after Jensen 1990
	<i>Codium tomentosum</i> , <i>Bryopsis</i> spp., <i>Cladophora rupestris</i>	TROWBRIDGE & TODD 2001
	<i>Halimeda</i> spp.	RUDMAN 2003 after Jensen 2003
	<b>Laboratory:</b> <i>Udotea</i> , <i>Chlorodesmis</i>	JENSEN 1980a after Switzer-Dunlap 1975
	<b>Laboratory:</b> <i>Udotea javensis</i> , <i>Bryopsis</i> sp.	HIROSE 2005 after Adachi 1991
	<i>Caulerpa</i> spp.	JENSEN 1992
	<i>Caulerpa</i> spp.	JENSEN 1992
	<i>Derbesia tenuissima</i>	MARIN & ROS 2004
	<i>Derbesia tenuissima</i>	CIMINO & GHISELIN 1998 after Gavagnin et al. 1994b
	<i>Cladophora vagabunda</i>	WÄGELE & JOHNSON 2001 after Marin & Ros 1988, 1989
<b>Limapontioidea</b>		
<b>Polybranchiidae</b>		
<i>Caliphylia mediterranea</i>	<i>Bryopsis plumosa</i>	BRÜEL 1904
	<i>Bryopsis</i>	CLARK & BUSACCA 1978
	<i>Bryopsis</i>	GASCOIGNE 1979
	<i>Bryopsis plumosa</i>	MARZO, DI et al. 1993
	<i>Penicillus</i> spp., <i>Halimeda</i> spp.	JENSEN 1980a
<i>Cyerce antillensis</i>	<i>Penicillus</i> , <i>Udotea</i> , <i>Halimeda</i>	JENSEN 1993
	<i>Penicillus dumetosus</i> , <i>Halimeda</i> ssp.	CLARK 1994
	<i>Chlorodesmis comosa</i>	MILLER 1969
<i>Cyerce nigra</i>	<i>Chlorodesmis fastigiata</i>	HAY et al. 1989
<i>Cyerce nigricans</i>	<i>Chlorodesmis</i>	CIMINO & GHISELIN 1998 after Roussis et al. 1990
<i>Mourgona germaineae</i>	<i>Cymopolia barbata</i>	JENSEN 1981
	<i>Cymopolia barbata</i>	CLARK 1994
<i>Mourgona osumi</i>	<i>Acetabularia ryukyuensis</i>	HAMATANI 1994
<i>Polybranchia viridis</i>	? <i>Caulerpa</i> spp.	JENSEN 1980a after Bertsch & Smith 1973
	<i>Caulerpa racemosa</i>	CLARK 1994
<b>Hermacidae</b>		
<i>Aphysiopsis enteromorphae</i>	<i>Chaetomorpha</i> sp., <i>Cladophora</i> , <i>Urospora</i> , <i>Rhizoclonium</i>	TROWBRIDGE 1993
<i>Aphysiopsis formosa</i>	<i>Cladophora prolifera</i>	JENSEN 1995

Species	Food	Reference
<i>Aplysiopsis smithi</i>	<i>Rhizoclonium</i> sp., <i>Cladophora</i> sp., <i>Chaetomorpha</i> sp., <i>Urospora</i> sp.	JENSEN 1980a after Gonor 1961; JENSEN 1980a after Greene 1970
<i>Aplysiopsis zebra</i>	<i>Cladophora</i>	JENSEN 1993a
<i>Hermæa bifida</i>	<i>Cladophora fuliginosa</i> , <i>Chaetomorpha</i> <i>Griffithsia</i> <i>Griffithsia</i> , <i>Delesseria</i> , <i>Heterosiphonia</i> <i>Griffithsia flosculosa</i> <i>Griffithsia flosculosa</i> <i>Bornetia secundiflora</i>	WILLIAMS & WALKER 1999 after Jensen 1983 GRAHAM 1955 after Pelseneer 1935 TAYLOR 1968 TAYLOR 1971 KREMER & SCHMITZ 1976 KREMER & SCHMITZ 1976 after Cornet & Marche-Marchad 1951 JENSEN & CLARK 1983 JENSEN 1993a
<i>Hermæa cruciata</i>	<i>Griffithsia</i> sp. <i>Griffithsia</i> <i>Griffithsia</i> , <i>Dasya</i> <i>Griffithsia</i> cf. <i>ovalis</i>	WILLIAMS & WALKER 1999 after Jensen 1983 JENSEN 1993b
<i>Hermæa evelinemarcusae</i>	<i>Isthmia nervosa</i>	WILLIAMS & GOSLINER 1973
<i>Hermæa vancouverensis</i>		
<u>Costasiellidae</u>		
<i>Costasiella nonatoi</i>	<i>Avrainvillea</i>	JENSEN 1993a
<i>Costasiella ocellifera</i>	<i>Avrainvillea nigricans</i> <i>Avrainvillea nigricans</i> <i>Avrainvillea</i> , <b>Laboratory:</b> <i>Caulerpa fastigiata</i> <i>Avrainvillea nigricans</i> <i>Avrainvillea</i> <i>Avrainvillea nigricans</i> , <i>Caulerpa fastigiata</i> , <i>Cladophora</i> <i>Avrainvillea</i> <i>Avrainvillea nigricans</i>	CLARK & BUSACCA 1978 JENSEN 1980a JENSEN 1981 CLARK et al. 1981 CLARK 1984 WILLIAMS & WALKER 1999 after Jensen 1980, 1981, 1983 JENSEN 1993a CLARK 1994 JENSEN 1990a, 1990b
<i>Costasiella pallida</i>	<i>Vaucheria vipera</i>	
<u>Limapontiidae</u>		
<i>Alderia modesta</i>	<i>Vaucheria</i> spp. <i>Vaucheria</i> , <i>Rhizoclonium</i> <i>Vaucheria</i> spp. <i>Vaucheria</i> spp. <i>Vaucheria longicaulis</i>	EVANS 1953 GRAHAM 1955 after Gascoigne 1954 CLARK 1975 JENSEN 1980a after Hartog 1959 KRUG & MANZI 1999 JENSEN 1986
<i>Calliopaea oophaga</i>	Eggs of <i>Philine denticulata</i> , <b>Laboratory:</b> eggs of <i>Polycera quadrilineata</i> , <i>Alderia modesta</i> , <i>Ercolania nigra</i> , <i>Limapontia capitata</i> , <i>Retusa truncatula</i> , <i>Turritella communis</i> Eggs of <i>Philine denticulata</i> and <i>Retusa truncatula</i>	LEMICHE 1974 (Appendix of GASCOIGNE & SARTORY 1974)
<i>Ercolania boodleae</i>	<i>Chaetomorpha aerea</i> , <i>C. moniligera</i> , <i>Cladophora</i> spp.	JENSEN 1980a after Usuki 1977
<i>Ercolania coerulea</i>	<i>Valonia</i> sp. <i>Valonia</i> sp., <i>Dictyosphaeria cavernosa</i> , juvenile: <i>Cladophoropsis</i> sp. <i>Dictyosphaeria</i> , <i>Valonia</i> , <i>Cladophoropsis</i>	JENSEN 1980a after Schmekel 1968 JENSEN 1981 JENSEN 1993a JENSEN 1993a
<i>Ercolania emarginata</i>	<i>Chaetomorpha</i> , <i>Cladophoropsis</i>	JENSEN 1999
<i>Ercolania endophytophaga</i>	<i>Struvea plumosa</i> (native), <b>Laboratory:</b> <i>Valonia</i> spec.	
<i>Ercolania fuscata</i>	<i>Cladophora</i> spp., <i>Chaetomorpha limum</i>	CLARK 1975
<i>Ercolania gopalai</i>	<i>Chaetomorpha</i> sp.	JENSEN 1980a after Rao 1937
<i>Ercolania nigra</i>	<i>Chaetomorpha limum</i>	JENSEN 1980a; JENSEN 1980a after Rasmussen 1973
<i>Ercolania translucens</i>	<i>Rhizoclonium</i>	JENSEN 1997b
<i>Ercolania vanellus</i>	? <i>Caulerpa verticillata</i>	JENSEN 1980a after Edmunds 1963

Species	Food	Reference
<i>Ercolania viridis</i>	<i>Chaetomorpha</i> sp. <i>Chaetomorpha</i> spp., <i>Cladophora</i> spp. <i>Chaetomorpha linum</i> <i>Chaetomorpha</i> , <i>Cladophora</i> , <i>Cladophoropsis</i> <i>Chaetomorpha capillaris</i> , <i>Chaetomorpha linum</i>	JENSEN 1980a after Trinchese 1872 JENSEN 1980a MARIN & ROS 1992 after Marin & Ros 1988 JENSEN 1993a, Jensen 1981
<i>Ercolania</i> spec.1	<i>Boergesenia</i> cf. <i>forbesii</i>	MARZO, DI et al. 1993
<i>Ercolania</i> spec.5	<i>Boodleia</i> sp.	GRZYMBOWSKI et al. 2007
<i>Ercolania</i> sp. (CLARK 1994)	<i>Cladophoropsis</i>	Unpublished data HW CLARK 1994
<i>Limapontia capitata</i>	<i>Cladophora arcta</i> , <i>Enteromorpha</i> <i>Cladophora</i> spp., <i>Chaetomorpha linum</i> , <i>Bryopsis plumosa</i> <i>Cladophora</i> spp., <i>Chaetomorpha linum</i> , <b>Laboratory:</b> <i>Bryopsis plumosa</i>	GRAHAM 1955 after Gascoigne 1952 JENSEN 1975 JENSEN 1980a after Gascoigne 1956 and after Jensen 1975
<i>Limapontia senestra</i>	<i>Cladophora rupestris</i>	GRAHAM 1955 after Gascoigne 1952 and after Gascoigne 1954 GASCOIGNE & SARTORY 1974 JENSEN 1980a after Gascoigne 1956
<i>Limapontia depressa</i>	<i>Vaucheria</i> , <i>Rhizoclonium</i> , <i>Conferva</i> <i>Vaucheria</i> spp., <i>Rhizoclonium riparium</i>  <b>Laboratory:</b> <i>Chaetomorpha</i> <i>Vaucheria</i>	GRAHAM 1955 after Gascoigne 1954 JENSEN 1980a after Gascoigne 1956 and after Hartog 1959 JENSEN 1994 GASCOIGNE & SARTORY 1974
<i>Olea hansineensis</i>	Opisthobranchia-eggs Eggs of <i>Haminoea virescens</i> , <i>Aglaja diomedea</i> , <i>Gastropteron pacificum</i> , <b>Laboratory:</b> Eggs of <i>Archidoris montereyensis</i> , <i>Hermisenda crassicornis</i> , <i>Dendronotus iris</i>	JENSEN 1999 after Haefelfinger 1962 CRANE 1971
<i>Placida aoteana</i>	<i>Codium fragile</i> , <i>Codium convolutum</i> , <i>Bryopsis vestita</i>	TROWBRIDGE 2004 after Trowbridge 1998b, after Willan & Morton 1984, after Burn 1989
<i>Placida capensis</i>	specimens of <i>Codiaceae</i>	MACNAE 1954
<i>Placida dagnilarensis</i>	<i>Bryopsis</i> sp., <i>Derbesia</i> sp.	JENSEN 1990b
<i>Placida dendritica</i>	<i>Bryopsis plumosa</i> <i>Ulva</i> <i>Codium tomentosum</i> <i>Codium tomentosum</i> , <i>Bryopsis</i> <i>Hermatea paucicirra</i> <i>Codium tomentosum</i> <i>Codium</i> sp., <i>Bryopsis plumosa</i>  <i>Bryopsis</i>  <i>Bryopsis plumosa</i> <i>Codium adhaerens</i> , <i>Codium tomentosum</i> , <i>Codium vermilare</i> , <i>Bryopsis plumosa</i> , <i>Bryopsis hypnoides</i> , (introduced) <i>Codium fragile</i> <i>Codium</i> spp., <i>Bryopsis plumosa</i> , <i>Bryopsis corticulans</i>	BRÜEL 1904 BRÜEL 1904 after Trinchese 1876b BRÜEL 1904 after Hecht 1895 GRAHAM 1955 after Gascoigne 1954 MARCUS, E. DuB.-R. 1972 after Salvat 1968 CLARK 1975 JENSEN 1980a after Fretter 1941 and after Greene 1970 BLEAKNEY 1989 after Thompson 1976 and after Millen 1980 MARZO, DI et al. 1993 TROWBRIDGE 2004 after Alder & Hancock 1843 and after Thompson 1976 WILLIAMS & WALKER 1999 after Jensen 1980 and Trowbridge 1991a, 1992, 1995
<i>Placida kingstoni</i>	<i>Bryopsis</i> sp. <i>Bryopsis plumosa</i> , <i>Cladophora</i> <i>Bryopsis plumosa</i>	JENSEN 1980a JENSEN 1981
<i>Placida viridis</i>	<i>Bryopsis plumosa</i>	JENSEN 1980a after Schmckel 1968 and after Monselise & Mienis 1977
<i>Placida</i> sp. (BEHRENS 2004)	<i>Codium magnum</i>	BEHRENS 2004
<i>Stiliger fuscovittatus</i>	<i>Polysiphonia pacifica</i>	JENSEN 1980a after Lance 1962
<i>Stiliger vesiculosus</i>	eggs of <i>Favorinus branchialis</i>	JENSEN 1980a after Haefelfinger 1962



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