Phylogeny of the Cocculinoidea (Mollusca, Gastropoda)

Ellen E. Strong,[1,a] M.G. Harasewych,[2] and Gerhard Haszprunar[3]

[1]Bell Museum of Natural History, Department of Fisheries, Wildlife and Conservation Biology,
University of Minnesota, St. Paul, MN 55108, USA
[2]Smithsonian Institution, National Museum of Natural History, Washington, DC 20013-7012, USA
[3]Zoologische Staatssammlung München, Münchhausenstrasse 21, D-81247 München, Germany

Abstract. The superfamily Cocculinoidea is a group of marine, deep-water, limpet-like gastropods. Recent speculation surrounding their affinities has concentrated on their placement within the Gastropoda. However, phylogenetic relationships within the Cocculinoidea, especially the monophyly of families and genera within the group, remain poorly understood. Phylogenetic analysis of 31 morphological characters for 15 cocculinoidean taxa and 2 outgroups resulted in a single most parsimonious tree, length=70, CI=0.62, and RI=0.71. Monophyly of the Cocculinoidea, Cocculinidae, and the genera *Cocculina* and *Coccopigya* was supported; *Paracocculina* and *Coccocrater* were found to be paraphyletic. Character optimization demonstrates that many characters often cited as diagnostic of various taxa, are often homoplastic and/or synapomorphies at different hierarchical levels.

*Additional key words:* morphology, cladistics, deep-sea

The Superfamily Cocculinoidea is a group of marine, deep-water limpets that inhabit primarily bathyal to hadal depths. Following a series of studies near the turn of the century (Dall 1882; Dautzenberg & Fischer 1900; Pelseneer 1900; Thiele 1903, 1908, 1909), the anatomy and systematics of these limpets remained essentially ignored for more than 50 years. After this long hiatus, interest in the poorly known group was vitalized by the investigations of Moskalev (1971, 1976), Hickman (1983) and Marshall (1986), with much of our detailed anatomical knowledge resulting from the work of Haszprunar (1987, 1988a, 1998). Currently, the superfamily is subdivided into 2 families: Cocculinidae DALL 1882 (*Fedikovella, Coccocrater, Coccopigya, Cocculina, Macleaniella, Paracocculina,* and *Teuthirostria*) and Bathysciadiidae DAUTZENBERG & FISCHER 1900 (*Bathysciadium, Bathypelta, Xenodonta* and *Bonus*). The Cocculinidae contains the majority of taxa that have been studied morphologically (Dall 1882; Thiele 1903; Haszprunar 1987, 1988a; Strong & Harasewych 1999). Published comprehensive anatomical accounts of other cocculinoidean taxa are limited to that of Thiele (1908) and a study by Pelseneer (1900) that contained many errors (Thiele 1908; Haszprunar 1987, 1998).

The relative scarcity of anatomical studies of this large and diverse superfamily has rendered phylogenetic relationships of its component taxa somewhat difficult to determine. Hypotheses of phylogenetic relationships have relied primarily on feeding biology and accompanying modifications of the radula and alimentary system (Haszprunar 1988a). However, monophyly of the Cocculinidae has remained untested and it has been suggested that familial separation of cocculinids and bathysciadiids may not be justified (Haszprunar 1987). Moreover, current generic divisions within the Cocculinidae have been regarded as provisional given that distinguishing genera requires knowledge of both internal and external anatomy (Haszprunar 1987)—information that is lacking for most cocculinoidean species. Thus, monophyly of the family and the genera within it have remained uncertain.

The goal of the present investigation is to combine the results of previous studies with new anatomical information to generate a phylogeny for the Cocculinoidea based on morphological data. This will allow us to re-evaluate the current nomenclatorial status of the families within the group and begin to address the status of recognized genera for which anatomical information is available. In addition, the character matrix provided herein can serve as a framework for future investigations into the biology and evolutionary history of this morphologically diverse group of deep-sea gastropods.

[a] Author for correspondence. E-mail: stron016@umn.edu
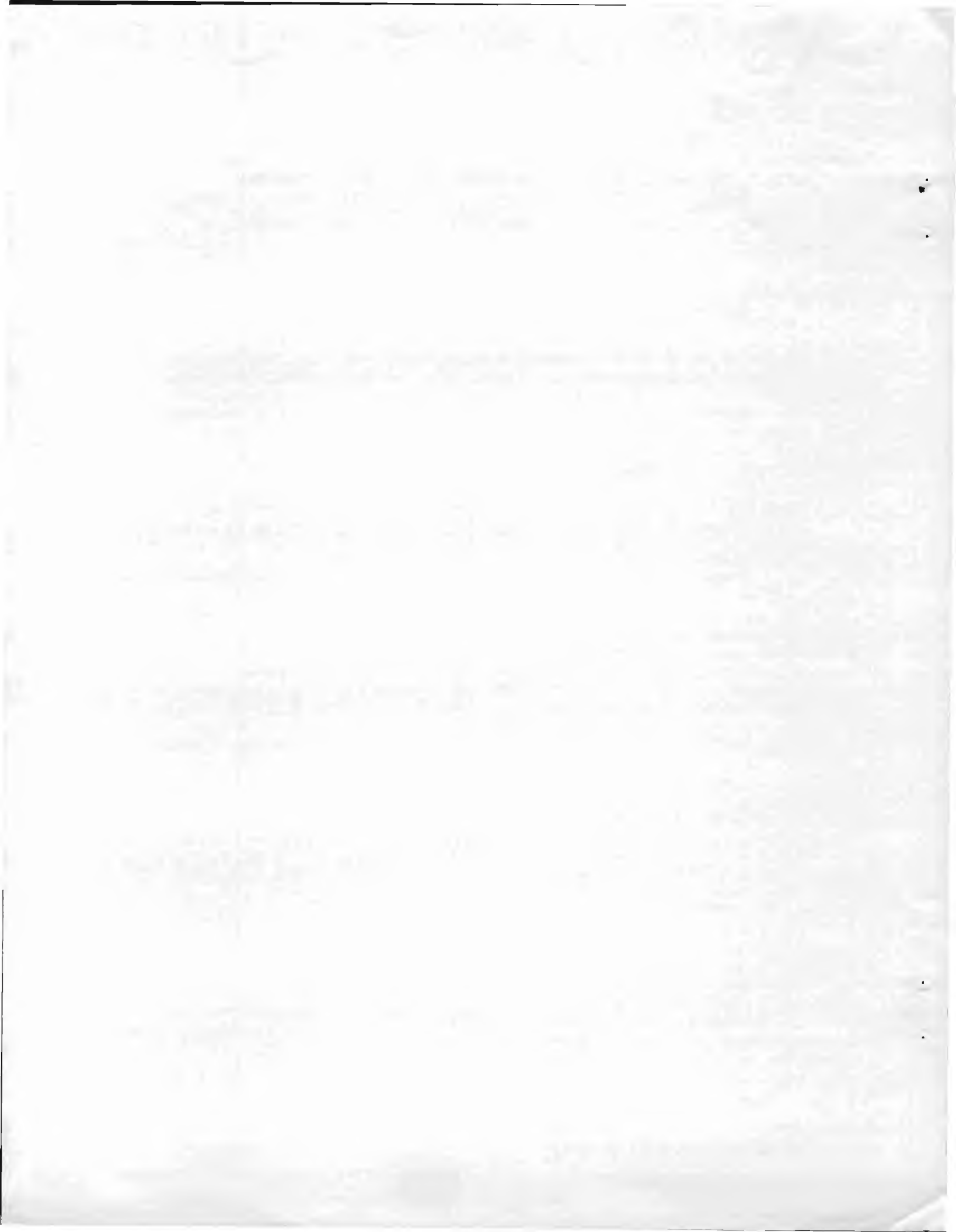
Methods

Outgroups

Despite their divergent morphologies, non-cladistic classifications generally have agreed on an archaeogastropod grade of organization for limpets within the Cocculiniformia HASZPRUNAR 1987, a group that includes the Cocculinoidea and the Lepetelloidea, another superfamily of deep-sea limpets. Pelseneer (1900) suggested an affinity between *Bathysciadium* and the "Docoglossa," but this was founded on his erroneous anatomical account of *B. costulatum*. Thiele (1908) placed the Cocculinoidea within the "Archaeogastropoda" based on the presence of a modified rhipidoglossate radula. Similarly, Haszprunar (1987, 1988a) concluded that the Cocculiniformia represent a primitive offshoot at the archaeogastropod grade of organization, second to the Docoglossa. McLean (1985) hypothesized a more derived position for the Cocculiniformia, intermediate between the archaeogastropod and mesogastropod grades.

Recent cladistic studies have only intensified the debate. One study based on morphological data suggests that the Cocculiniformia may be diphyletic (Ponder & Lindberg 1996, 1997), with the Cocculinoidea forming the sister group to the Neritimorpha, and the Lepetelloidea being a basal offshoot of the Vetigastropoda. Other analyses based on molecular data suggest a basal position for a monophyletic Cocculiniformia near the Patellogastropoda (Harasewych et al. 1997; Harasewych & McArthur 2000).

Thus, at present, there is no consensus on the historical cohesiveness of cocculiniform limpets, or their placement within the Gastropoda. For this analysis, 2 outgroups were chosen to reflect alternative competing hypotheses (Haszprunar 1987, 1988a; Ponder & Lindberg 1996, 1997) of sister group relationship—*Pseudococculina gregaria* as a representative of the Lepetelloidea, and *Theodoxus fluviatilis* representing the Neritimorpha.

Characters

Outgroup taxa were coded from Haszprunar (1988b) for *Pseudococculina gregaria* and Strong (in press) for *Theodoxus fluviatilis*. Anatomical data for the Bathysciadiidae were obtained from Thiele's (1908) account of *B. pacificum*, supplemented with unpublished data (Haszprunar). *Teuthirostria cancellata* and *Fedikovella caymanensis* were coded using unpublished data (Haszprunar). All remaining species were coded primarily from Haszprunar (1987, 1988a, 1998) and Strong & Harasewych (1999) as well as several additional sources (Thiele 1903, 1909; Hickman 1983;

Marshall 1986, 1996; McLean 1987, 1992; Dantart & Luque 1994; McLean & Harasewych 1995; Leal & Harasewych 1999).

Shell. Cocculinoideans share rather uniform shell morphology, consisting of a simple, cap-shaped shell. However, the position of the apex (character 2) may be subcentral to posterior (Figs. 1A,B). Development of the periostracum (character 1) is also somewhat uniform, but a spinose periostracum has been used to diagnose members of the genus *Coccopigya* (Jeffreys 1883; McLean & Harasewych 1995) and a fringed periostracum occurs in the Bathysciadiidae.

Reticulate protoconch sculpture (character 4) has figured prominently in distinguishing cocculinoidean taxa. But both *Teuthirostria cancellata* (Moskalev 1976) and *Macleaniella moskalevi* (Leal & Harasewych 1999) lack reticulate protoconch sculpture, placing the utility of this feature for resolving higher order relationships in question. *T. cancellata* and *Fedikovella caymanensis* are unique among cocculinoideans in possessing reticulate teleoconch sculpture (character 3) rather than the smooth to beaded or pitted radial sculpture common within the group.

External anatomy. Oral cuticular hairs (character 6), while known to occur in the Neritidae (Haszprunar 1987), are thought to comprise a synapomorphy of the Cocculinidae and are lacking in the Bathysciadiidae. Epipodial sense organs (character 5), previously hypothesized to be homologous to epipodial tentacles in vetigastropods and now believed to be homologous to epipodial sensory structures (Haszprunar, unpubl. data), are present in most cocculinids, but are lacking in *Coccopigya*. Subpallial glands (character 7) are variably developed in many cocculinoidean taxa, and are absent in the outgroups.

Pallial cavity. The pallial cavity of cocculinoideans contains a number of structures that are highly modified and unique among gastropods (Fig. 1C–E). Most possess a folded pseudoplicatid gill (character 8) that is not composed of serially arranged leaflets, as are typical ctenidia. However, there are several exceptions. *Macleaniella moskalevi* possesses a small pseudoplicatid gill that forms a simple, ciliated papilla (Fig. 1D). The gill of *Fedikovella caymanensis* comprises a series of respiratory leaflets (Fig. 1E), while *Teuthirostria cancellata* bears a simple ciliary tract within the pallial roof which functions in ventilating the mantle cavity. The hypobranchial gland (characters 9, 10) may be solid or, more typically, may be contained within a small to large pouch that ventrally encloses the rectum—the Manteldrüse condition described by Thiele (1903). Development of this gland has been considered a useful feature for distinguishing species (Haszprunar 1987).
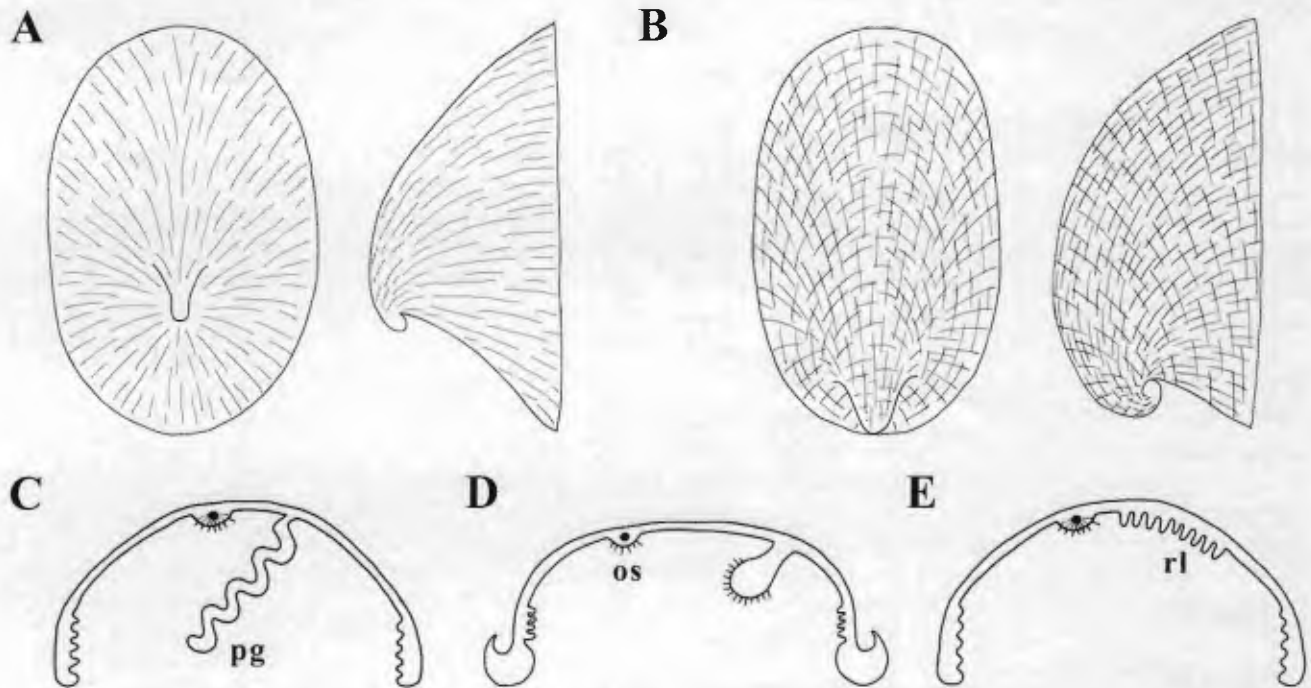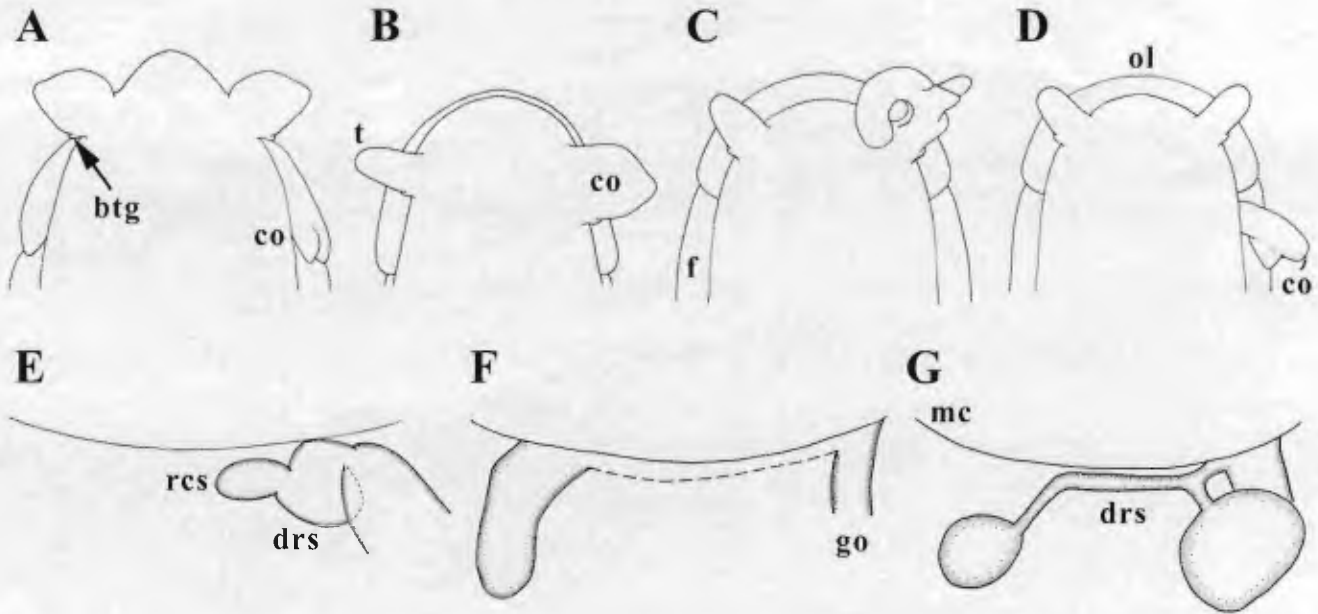
Fig. 1. External morphology of cocculinoideans; shell (A–B) and mantle cavity (C–E) characters. **A.** Shell with subcentral apex (character 2[0]) (*Paracocculina cervae*; modified after Marshall 1986). **B.** Shell with posterior apex (character 2[1]) (*Macleaniella moskalevi*; after Leal & Harasewych 1999). **C.** Large, folded pseudoplicatid gill (character 8[0]) and osphradium with discrete sensory epithelium (character 30[1]). **D.** Small, papillate pseudoplicatid gill (character 8[3]) and osphradium lacking discrete epithelium. **E.** Respiratory leaflets (character 8[2]). Abbreviations: (os) osphradium, (pg) pseudoplicatid gill, (rl) respiratory leaflets.

Reproductive system. The hermaphroditic reproductive system of cocculinoideans is highly variable and has provided numerous characters for generic diagnoses. It is characterized by a regionally differentiated gonad that simultaneously produces both egg and sperm. A seminal groove (character 14), absent in some taxa (*Macleaniella moskalevi*, *Coccocrater agassizii*), leads from the genital aperture to a copulatory organ (character 11) formed by or associated with the right cephalic tentacle, (*Bathypelta pacificum*, *M. moskalevi*, *Teuthirostria cancellata*, *Fedikovella caymanensis*, *Coccocrater radiata*, *C. agassizii*, *Coccopigya viminensis*, *C. hispida*), the foot (*Paracocculina cervae*), or the oral lappet (*P. laevis*, *Cocculina baxteri*, *C. cowani*, *C. ovata*, *C. rathbuni*) (Figs. 2A–D). Seminal receptacles vary in number (character 13) from 1–2, and are found on the left, right, or both sides of the body (Figs. 2E–G). The glandular gonoduct may be massive or have gland cells in a tubular arrangement around a central duct (character 15). A pallial brood pouch (character 12), a rear-facing pocket within the mantle roof, is present in all cocculinoideans except *F. caymanensis*, *T. cancellata*, *B. pacificum*, and *Cocculina craigsmithi*.

Alimentary system. Radular morphology has been

important in differentiating bathysciadiids from cocculinids. The highly modified radula diagnostic of bathysciadiid taxa is characterized by the absence of marginal teeth and a broad, plate-like, acuspate rachidian tooth. These features were autapomorphic and not included in the analysis. The most conspicuous radular character that varies among the included cocculinoideans is the overhanging cusp of the rachidian, which may be present or obsolete (character 16). Radular cartilages (character 18) comprise a single pair, in contrast to other basal gastropods with ≥2 pairs of cartilages. Jaws (character 19) typically consist of a single, small, unpaired plate on the anterior buccal cavity roof, while *Teuthirostria cancellata* possesses a robust jaw. Outgroups often possess distinct, paired jaws.

Although early studies reported salivary glands as absent in Cocculinoidea (Haszprunar 1987, 1988a; Strong & Harasewych 1999), it is now recognized that the salivary glands (character 20) form simple, glandular pouches on the posterior roof of the buccal cavity (Haszprunar 1998). However, *Teuthirostria cancellata* and *Fedikovella caymanensis* possess prominent to tubular salivary glands. In conjunction with the evolution of pouch-like salivary glands, the sublingual

Fig. 2. Reproductive system morphology of cocculinoideans: copulatory organ (A–D) and receptaculum seminis (E–G) characters. **A.** Copulatory organ on right oral lappet (character 11[0]) (*Cocculina rathbuni*; modified after McLean & Harasewych 1995). **B.** Modified right cephalic tentacle as copulatory organ (character 11|1]) (*Macleaniella moskalevi*). **C.** Copulatory organ on right cephalic tentacle (character 11[1]) (*Coccopigya hispida*; adapted from Marshall 1986). **D.** Copulatory organ on foot (character 11[2]) (*Paracocculina cervae*; after Marshall 1986). **E.** Single, right receptaculum seminis (*Macleaniella moskalevi*; after Strong & Harasewych 1999). **F.** Single, left receptaculum seminis (*Coccopigya hispida*; after Haszprunar 1987). **G.** Paired receptaculae (*Cocculina ovata*; after Haszprunar 1987). Abbreviations: (btg) basitentacular gland, (co) copulatory organ, (f) foot, (ol) oral lappet, (t) cephalic tentacle.

cavity has become highly glandular (character 18). The configuration of the fore- and midgut in Cocculinoidea displays some intriguing variability (see discussion below). In most taxa, the posterior esophagus is deflected to the left and opens to the midgut posteriorly (character 21), (*Macleaniella moskalevi, Paracocculina, Coccopigya, Coccocrater, Cocculina*). However, in *F. caymanensis, T. cancellata,* and *Bathypelta pacificum,* the esophagus is straight, opening ventrally to the midgut (Fig. 3A.B).

Circulatory system. The circulatory system in Cocculinoidea is characterized by a rectum that does not penetrate the ventricle (character 22). The aortic vessel (character 23), a contractile vessel connecting the pedal and cephalic hemocoels, is uniquely developed in cocculinoideans: it remains unknown whether this feature occurs in bathysciadiids. A bilobed hemal gland (character 24) is commonly associated with this vessel, but is absent in *Bathypelta pacificum, Fedikovella caymanensis,* and *Teuthirostria cancellata;* the gland may be small or massive (character 25).

Nervous system and sensory structures. Cocculinoideans display unusual diversity in the configuration of ganglia around the circum-esophageal nerve ring (character 26) and visceral loop (character 27): 1)
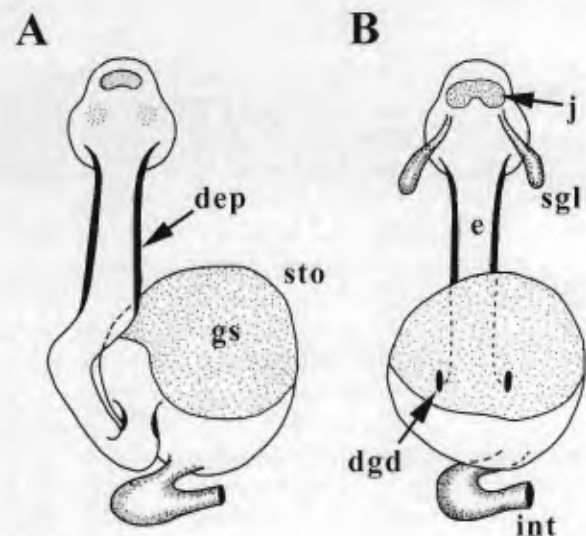
Fig. 3. Alimentary system morphology of cocculinoideans. **A.** Alimentary system with reduced jaw, pouch-like salivary glands and esophageal bending (*Macleaniella moskalevi;* modified after Strong & Harasewych 1999). **B.** Alimentary system with robust jaw, tube-like salivary glands, and straight esophagus (e.g. *Teuthirostria cancellata*). Abbreviations: (dep) ducts of esophageal pouches, (dgd) digestive gland duct, (e) esophagus, (gs) gastric shield, (int) intestine, (j) jaw, (sgl) salivary gland, (sto) stomach.
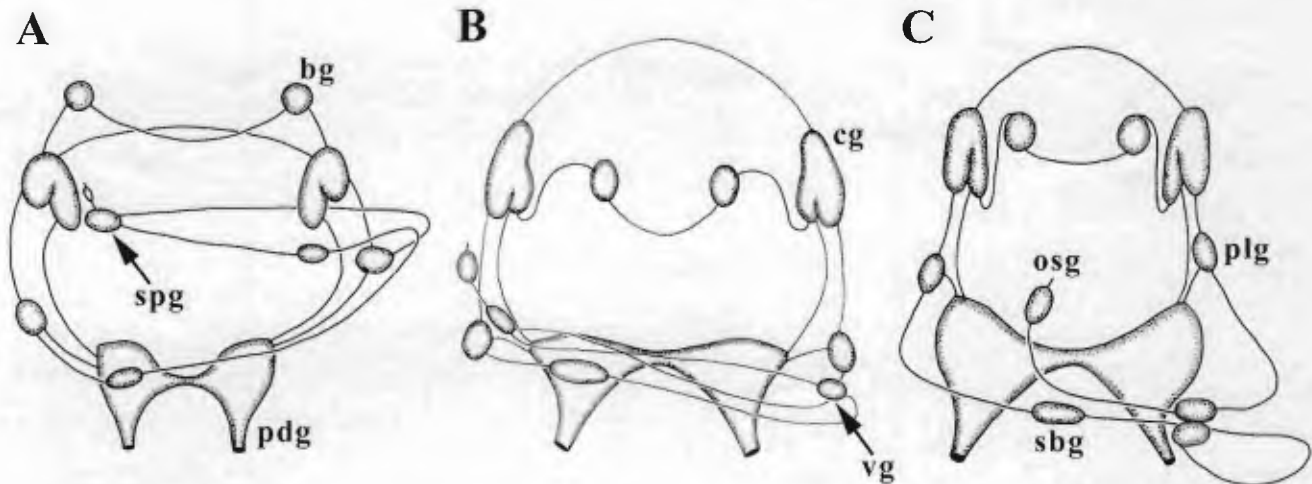
Fig. 4. Nervous system morphology of cocculinoideans. **A.** Central nerve ring (with subesophageal, supraesophageal and osphradial ganglia on left, visceral ganglion on right, and unfused supraesophageal and visceral ganglia) and weakly dystenoid (e.g. *Macleaniella moskalevi*; modified after Strong & Harasewych 1999). **B.** Central nerve ring and hypoathroid on left and right (e.g. *Coccopigya hispida*; after Haszprunar 1987). **C.** Shifted nerve ring (with subesophageal and osphradial ganglia near midline, and supra-esophageal ganglion fused with visceral ganglion on right) weakly dystenoid (e.g. *Cocculina ovata*; after Haszprunar 1987). Abbreviations: (bg) buccal ganglion, (cg) cerebral ganglion, (osg) osphradial ganglion, (pdg) pedal ganglion, (plg) pleural ganglion, (sbg) subesophageal ganglion, (spg) supraesophageal ganglion, (vg) visceral ganglion.

hypoathroid on the left and right, with un-fused supra-esophageal and visceral ganglia (Fig. 4A) (*Bathypelta pacificum, Coccopigya, Paracocculina, Coccocrater*), 2) weakly dystenoid with un-fused visceral and supra-esophageal ganglia (Fig. 4B) (*Macleaniella moskalevi, Teuthirostria cancellata, Fedikovella caymanensis*), and, 3) weakly dystenoid, with fused visceral and supra-esophageal ganglia (Fig. 4C) (*Cocculina*). In addition, the sub-esophageal, supra-esophageal and osphradial ganglia may be located left of the midline (*Coccocrater, Coccopigya, Paracocculina, M. moskalevi, T. cancellata, F. caymanensis, B. pacificum*), or may be displaced to the right (*Cocculina*). However, the shift in position of these ganglia to the right and the fusion of the sub-esophageal and visceral ganglia have an identical distribution among the taxa studied in this analysis, occurring only in *Cocculina*. Thus, these characters are not likely to be independent and are subsumed within a single character (character 27).

Sensory structures include osphradia, statocysts, and modified eyes. Most cocculinoideans possess a distinct osphradium in the pallial roof (character 28); however, *Macleaniella moskalevi* lacks a discrete osphradial epithelium and the osphradium is lacking entirely in *Bathypelta pacificum*. Cocculinoideans are unusual among basal gastropods because they possess statocysts bearing a single statolith (character 29) (Ponder & Lindberg 1997). The only exception is *M. moskalevi*, which is polymorphic for this feature. Eyes may be absent, present or modified into the mucus-secreting basitentacular gland with a narrow to broad duct (characters 30, 31).

Phylogenetic analysis

The data matrix comprises 31 characters for 15 cocculinoidean taxa and 2 outgroups, *Theodoxus fluviatilis* and *Pseudococculina gregaria. Bathypelta pacificum* is the single bathysciadiid for which comprehensive comparative anatomy is known and was included in the analysis to assess monophyly of the family Cocculinidae. The data matrix is listed in Table 1; character descriptions are listed in the appendix. The polymorphic character relating to the condition of the statocysts in *Macleaniella moskalevi* is indicated with "*" in the data matrix and was analyzed as both "0" and "1"; choice of coding had no effect on the result. Unknown information is indicated with "?"; inapplicables are indicated with "-".

Morphological characters were coded using reductive coding (Wilkinson 1995; Strong & Lipscomb 2000) and edited with DADA 1.97 (Nixon 1995). The matrix was analyzed using NONA 1.6 (Goloboff 1993), which suppresses persistent arbitrary resolutions (Nixon & Carpenter 1996). Tree searches were accomplished using the heuristic search option "hold 100; hold/25; mult*20." All characters were analyzed as unordered. Character optimizations were examined in CLADOS (Nixon 1995) under ACCTRAN. Bremer support was calculated with TreeRot (Sorenson 1999)

Table 1. Data matrix for 15 cocculinoidean taxa and 2 outgroups. Inapplicable characters are indicated with "-"; missing characters are indicated with "?". Polymorphic character is indicated with "*".

Taxa	Characters						
	1	.....	2	.....	3	.	
Theodoxus fluviatilis	0--00	0010-	30312	000--	0000-	10100	-
Pseudococculina gregaria	01401	001--	10-12	02020	0000-	10010	-
Bathypelta pacificum	10010	0100-	10210	11000	01?0-	10000	-
Coccocrater agassizii	000?1	100??	11000	01000	1111?	10101	1
Coccocrater radiata	00011	10010	11210	01000	11110	10100	-
Coccopigya hispida	21110	11011	11110	11000	11111	10101	1
Coccopigya viminensis	21110	11010	11110	11000	11110	10101	1
Cocculina baxteri	01011	10010	01111	11000	11110	01101	1
Cocculina cowani	01211	10011	01111	11000	11110	01101	1
Cocculina craigsmithi	00011	10010	00111	01000	1110-	01100	-
Cocculina ovata	00011	10010	01010	01000	11110	01101	1
Cocculina rathbuni	00011	10010	01010	01000	11110	01101	0
Fedikovella caymanensis	01311	1120-	10210	01101	0110-	00100	-
Macleaniella moskalevi	01001	1100-	11200	01000	11110	001*1	0
Paracocculina cervae	01011	11011	21110	11000	11111	10101	1
Paracocculina laevis	00011	11011	01110	11000	11111	10101	1
Teuthirostria cancellata	01301	1030-	10110	01111	0110-	00100	-

using a heuristic search option with 10 random addition sequences and tree-bisection-reconnection. The cladogram was drawn using WINCLADA (Nixon 1999).

Results

A single most parsimonious tree was obtained with a length of 70, CI=0.62, and RI=0.71 (Fig. 5). The analysis supports monophyly of the Cocculinoidea and the Cocculinidae. *Fedikovella caymanensis* and *Teuthirostria cancellata* are sister groups, forming the most basal cocculinid offshoot; *Macleaniella moskalevi* is the sister group to all remaining cocculinids. Among the genera represented by more than a single exemplar, monophyly of *Coccopigya* and *Cocculina* is supported, but *Coccocrater* and *Paracocculina* are paraphyletic.

Bremer support for all nodes is low, with values of ≤3 (see Fig. 5). The node supporting monophyly of the Cocculinoidea is supported by a Bremer value of 3; the node supporting monophyly of the Cocculinidae is supported by a Bremer value of 1.

The Cocculinoidea is highly distinct compared to outgroup taxa and is united by numerous synapomorphies, including: a teleoconch with smooth radial ribs (3[0]), reticulate protoconch sculpture (4[1]), the presence of a subpallial gland (7[1]), a pseudoplicatid gill (8[0]), a single, right receptaculum seminis (13[2]), a gonoduct with massive glands (15[0]), a single pair of radular cartilages (17[1]), a single, small jaw (19[0]), a rectum that does not penetrate the pericardium

(22[1]), and the presence of the aortic vessel (23[1]). Optimization of the aortic vessel is ambiguous at this node due to missing data for *Bathypelta pacificum*.

Monophyly of the Cocculinidae is weakly supported by 2 characters: the presence of oral cuticular hairs (6[1]), and a circum-esophageal nerve ring that is weakly dystenoid (26[0]). The latter only optimizes to this node under ACCTRAN. The presence of epipodial tentacles (5[1]) also optimizes to this node under DELTRAN, but optimization is ambiguous due to variation among the outgroups.

New data for *Teuthirostria cancellata* and *Fedikovella caymanensis* confirm the distinctiveness and cohesiveness of these unusual genera. They are united unambiguously by: a reticulate teleoconch sculpture (3[3]), a non-glandular sublingual cavity (18[1]), and prominent to tube-like salivary glands (20[1]). Condition of the gill (character 8) is dependent upon optimization method, reflecting the autapomorphic character states in both taxa.

The node uniting *Macleaniella moskalevi* and all remaining cocculinids, excluding *Teuthirostria cancellata* and *Fedikovella caymanensis*, is supported by 4 synapomorphies: the presence of a pallial brood pouch (12[1]), a deflected posterior esophagus (21[1]), a hemal gland (24[1]), and a basitentacular gland (30[1]).

Optimization of the condition of the hemal gland and basitentacular gland at this node demonstrates a problematic phenomenon associated with reductive coding, noted by Strong & Lipscomb (2000), namely, the decoupling of presence/absence characters and
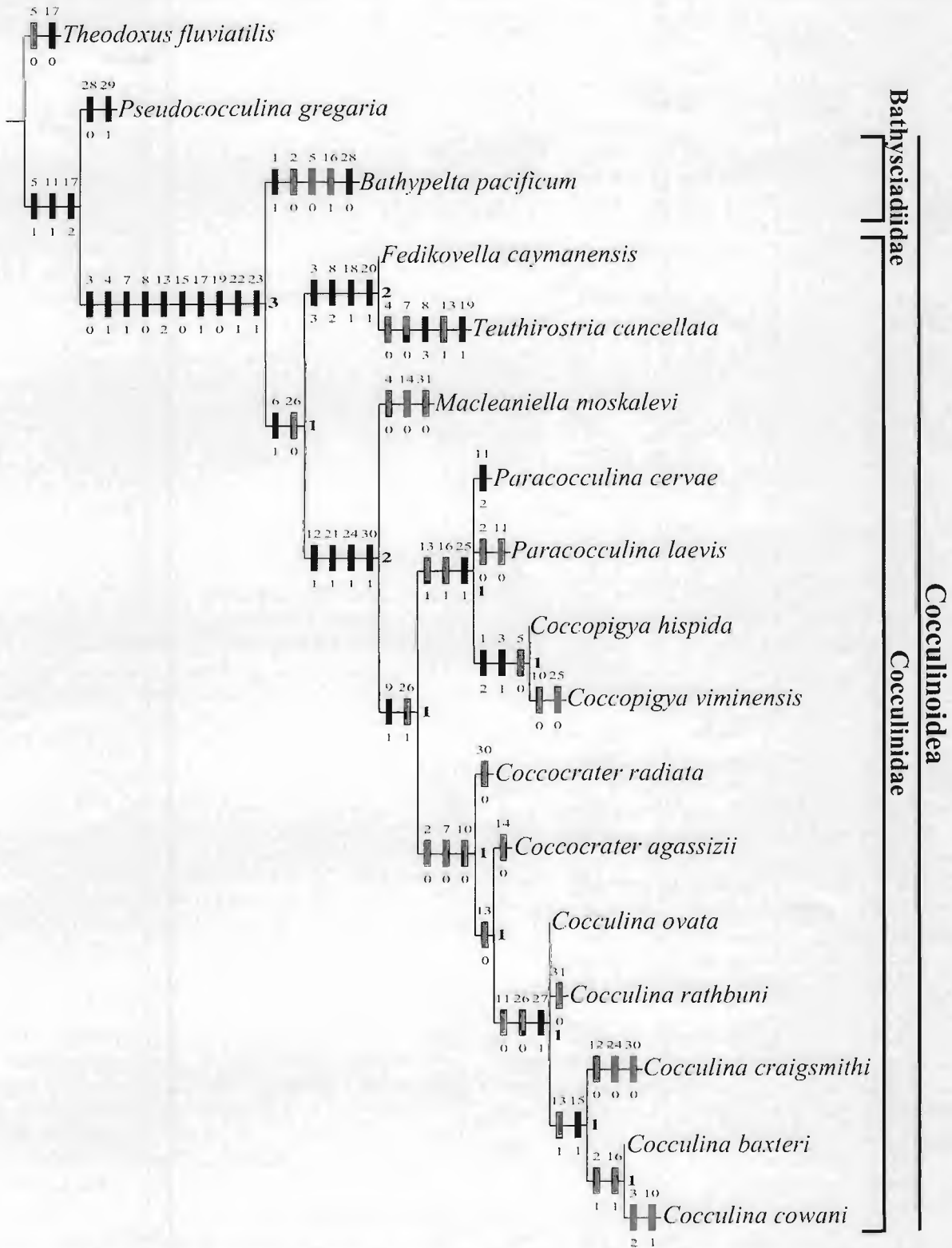
Fig. 5. Single most parsimonious tree. length = 70. CI = 0.62, RI = 0.71. Characters are optimized using ACCTRAN. Black hash-marks indicate forward changes; grey hash-marks indicate forward homoplasies. Values in bold at nodes indicate Bremer support.

their modifiers. For example, the weak development of the hemal gland (character 25|0|) and the broad size of the basitentacular gland duct (character 31|1|) should optimize at this node as well; observations of absence and presence do not exist in isolation. However, because of missing values at the base of the tree reflecting absence of these features, development of the hemal gland and size of the basitentacular gland duct are optimized as symplesiomorphies. As noted by Strong & Lipscomb (2000), this should have no misleading influence on tree construction, but is problematic from the point of view of character interpretation.

Discussion

Character analysis

The utility of features that have figured in the supra-generic classification of Cocculinoidea was assessed in light of these results, namely, protoconch sculpture, radular and salivary gland morphology, and presence/absence of oral cuticular hairs, pseudoplicatid gill, and brood pouch (Haszprunar 1987). Features routinely cited as diagnostic of genera were evaluated as well, including development of the periostracum, teleoconch sculpture, presence/absence of epipodial sense organs and subpallial glands, position of the copulatory organ, arrangement of the reproductive glands, and condition of the nerves (Marshall 1986; Haszprunar 1987; McLean & Harasewych 1995; Leal & Harasewych 1999; Strong & Harasewych 1999).

The presence of oral cuticular hairs is a feature commonly cited as diagnostic of cocculinid taxa. In the present analysis, this feature is uniform and confirmed as a synapomorphy of the family. However, other features are not so straightforward. For example, reticulate protoconch sculpture has been used to characterize cocculinids and bathysciadiids (e.g., Haszprunar 1998). The fact that *Macleaniella moskalevi* (Leal & Harasewych 1999) and *Teuthirostria cancellata* (Moskalev 1976) among others lack this characteristic sculpture casts doubt upon the utility of this feature in the higher order taxonomy and phylogeny of the group. Cladistic analysis indicates that reticulate protoconch sculpture (4|1|) indeed unites the Cocculinoidea. Consequently, although the feature is homoplastic within the group, it does represent a synapomorphy of the superfamily.

Condition of the gill is yet another character with uncertain status in light of new anatomical investigations. Until recently, the presence of a pseudoplicatid gill was thought to comprise a synapomorphy of the Cocculinoidea (Haszprunar 1988). However, *Fedikovella caymanensis* and *Teuthirostria cancellata* are now confirmed to possess unique gill morphologies; *F. cay-*

manensis possesses respiratory leaflets and *T. cancellata* bears only a ciliary tract (Haszprunar, unpubl. data). Despite the unique conditions in these taxa, the analysis reveals that, similar to protoconch sculpture, the pseudoplicatid gill indeed represents a cocculinoidean synapomorphy but is variable and not diagnostic of cocculinioidean taxa.

Reproductive characters are most often used in generic classification of cocculinoideans. However, the unique pallial brood pouch has been used at higher hierarchical levels to distinguish the Cocculinidae from the Bathysciadiidae. In addition to bathysciadiids, new data has confirmed that *Teuthirostria cancellata* and *Fedikovella caymanensis* lack the brood pouch (Haszprunar, unpubl. data), further distinguishing these taxa. This character supports the basal placement of the Bathysciadiidae, *F. caymanensis* and *T. cancellata*, and unites all remaining cocculinids. Thus, a pallial brood pouch does not unite the family but is a synapomorphy of a more exclusive clade than previously thought.

Among alimentary characters, absence of marginal teeth, producing the characteristic "bathysciadiid" radula, is autapomorphic for *Bathypelta pacificum* and, therefore, not included in this analysis. However, such characters are likely to be important in the future for testing monophyly of the Bathysciadiidae. The presence of prominent to tube-like salivary glands is unique to *Teuthirostria cancellata* and *Fedikovella caymanensis*, also highlighting the distinctiveness of these taxa. Optimization of simple, pouch-like salivary glands is ambiguous and interpreted as plesiomorphic within the Cocculinoidea because of the presence of pouch-like glands in *Pseudococculina gregaria* and the absence of glands in *Theodoxus fluviatilis*. For this character, determination of its status as a synapomorphy or symplesiomorphy awaits resolution of the sister group relationship to the Cocculinoidea.

Condition of the nervous system is often given high systematic value, not only within the Cocculinoidea, but within the Gastropoda in general, due to its conservatism. Historically, classifications have relied on such presumably conservative characters, at times to the exclusion of all other information, reflecting the assumption that such characters are reliable in delineating monophyletic groups. This analysis provides an interesting case study that highlights the pitfalls of such approaches. Although the shift of the nervous system to the right, with the concomitant fusion of the supra-esophageal and visceral ganglia, unites *Cocculina*, the evolution of a dystenoid nerve ring primarily denotes grades rather than clades. Under ACCTRAN, the hypoathroid condition is interpreted as plesiomorphic within the group with 2 independent deriva-

tions of the dystenoid condition, once in the grade including *Teuthirostria cancellata, Fedikovella caymanensis, and Macleaniella moskalevi,* and once in the *Cocculina* clade, supporting monophyly of the latter, with a reversal to the hypoathroid condition in the grade including *Paracocculina, Coccopigya,* and *Coccocrater.* In this instance, conditions of the nervous system are homoplastic and do not identify exclusively monophyletic taxa.

In general, features commonly cited as useful for suprageneric classification of cocculinoideans have demonstrated a consistent utility in supporting large clades. Yet, the refinement of character distributions for the pivotal taxa *Fedikovella caymanensis* and *Teuthirostria cancellata,* as well as the basal placement of these taxa with the Bathysciadiidae, have an important influence on character interpretation. Characters previously thought diagnostic of superfamily membership are revealed to be synapomorphies of more exclusive clades than previously thought (e.g., pallial brood pouch). Other features are now confirmed to be homoplastic (e.g., nervous system). However, the analysis illustrates that many such characters, although variable, remain important synapomorphies in higher order systematics of the group (e.g., reticulate protoconch sculpture, condition of the gill).

For genera, this analysis indicates that shell characters are of rather limited utility, yet provide important synapomorphies at lower hierarchical levels. With rare exception, cocculinoideans possess smooth, radial ribs and a simple periostracum. Elaboration of the periostracum has occurred independently in *Bathypelta pacificum* and *Coccopigya,* but the presence of a distinctive, hirsute periostracum supports monophyly of the latter. The periostracal spine bases may be associated with distinct pits along the radial ribs, which are uniquely derived in *Coccopigya.* Reticulate teleoconch sculpture supports monophyly of *Teuthirostria cancellata* and *Fedikovella caymanensis.*

Features of external anatomy and structures within the pallial cavity have been emphasized in generic classifications because they are readily accessible and visible with standard light and scanning electron microscopy. In contrast to their standard use, such features are homoplastic and/or do not consistently provide unambiguous synapomorphies for genera as currently conceived. For example, loss of epipodial sense organs has occurred independently in bathysciadiids and *Coccopigya,* but supports monophyly of the latter. Loss of the subpallial gland has occurred within *Teuthirostria cancellata, Cocculina,* and *Coccocrater,* uniting the latter genera in a large clade. The presence of a hypobranchial gland pocket (Manteldrüse condition) unites a large clade including *Coccocrater, Coc-*

copigya, Paracocculina, and *Cocculina.* Thus, with rare exception these features unite large clades. Even when they indeed represent synapomorphies of genera, they are commonly homoplastic at higher taxonomic levels and cannot be used in isolation to diagnose monophyletic groups.

Similarly, the condition of the copulatory organ is capable of resolving several monophyletic groups but is not always diagnostic of current genera. The use of a modified or unmodified right cephalic tentacle as a copulatory organ is supported as plesiomorphic within the Cocculinioidea and is found in many taxa including *Bathypelta pacificum, Teuthirostria cancellata, Fedikovella caymanensis, Macleaniella moskalevi, Coccocrater,* and *Coccopigya. Paracocculina laevis* is now confirmed to possess a verge on the right oral lappet (Haszprunar, unpubl. data), which has evolved independently in *Cocculina.* A pedally innervated copulatory organ is unique to *P. cervae.* Detailed copulatory organ structure, although often autapomorphic and thus not included here, may become informative in the future with the inclusion of more taxa.

Conditions of the receptaculum seminis appear useful for recognizing monophyletic groups, but also are rarely indicative of generic level taxa. For example, a single, right receptaculum seminis is a synapomorphy of the Cocculinoidea, shared by *Bathypelta pacificum, Fedikovella caymanensis, Macleaniella moskalevi,* and *Coccocrater radiata.* A single, left receptaculum is present in *Teuthirostria cancellata* and has evolved independently in the clade uniting *Paracocculina* and *Coccopigya.* The presence of paired receptaculae has evolved once and supports a grade, not a clade, including *Coccocrater agassizii, Cocculina ovata,* and *C. rathbuni.* Similarly, a massive glandular gonoduct is a synapomorphy of the Cocculinioidea; tubular glands unite a clade including *Cocculina craigsmithi, C. cowani,* and *C. baxteri.* Thus, in contrast to their standard use, these features denote grades or suprageneric clades and cannot be used in isolation to reliably indicate phylogenetic affinity.

Non-torsional asymmetries

Non-torsional rearrangements of organs or organ systems seem to be a common theme in the history of the Mollusca (Lindberg & Ponder 1996). Although poorly studied among gastropods, the best-documented example is the rift limpet *Neomphalus fretterae,* in which asymmetries are apparent in the digestive system, nerves and pericardium (Fretter et al. 1981). Lindberg & Ponder (1996) first discussed the phylogenetic significance of such rearrangements, emphasizing higher taxonomic levels, but also drew attention

to digestive system asymmetries apparent between lepetelloideans and cocculinoideans as described by Haszprunar (1988a). Despite the fact that this and other cited examples involve taxa that have assumed a limpet-like morphology, Lindberg & Ponder (1996) stressed that such rearrangements are unlikely to be restricted to limpets, nor necessary for the adoption of a limpet-like habit. Indeed, Strong (in press) has demonstrated that such asymmetries are capable of providing important phylogenetic information in the Caenogastropoda, cutting across patterns of shell shape.

The intriguing revelation of the present analysis is that configuration of the alimentary system provides important synapomorphic information within the Cocculinoidea. A change in the disposition of the alimentary system apparently has been produced through a non-torsional rotation of the organ system along a longitudinal axis. The manifestations of this process are evident in the morphology of the posterior esophagus (straight vs. deflected) and position of the esophageal aperture (ventral vs. posterior) (Fig. 3). Here, esophageal deflection (character 21), and the inferred rotation of the midgut, bringing the esophageal aperture from a ventral position into a posterior position, forms a synapomorphy uniting all cocculinoideans to the exclusion of *Teuthirostria cancellata, Fedikovella caymanensis,* and *Bathypelta pacificum.* These latter taxa display the plesiomorphic condition—a straight esophagus opening ventrally to the midgut. Thus, the present analysis confirms the utility of such characters at lower taxonomic levels.

Conclusions

Thorough morphological investigation of cocculinoidean taxa is still in its infancy (Haszprunar 1987, 1988a, unpubl. data; Strong & Harasewych 1999). New character combinations are revealed with each study, even among features thought to be conservative at higher taxonomic levels within the Gastropoda, such as the nervous system. Thus, despite its size, the group is extraordinarily morphologically diverse. Moreover, the 15 species for which such information is available represent 8 of 10 nominal genera, and only 23% of the ~60 cocculinoidean species presently known (Haszprunar 1998). The Bathysciadiidae, in particular, remain poorly known.

Given this important caveat, adequacy of the current generic classification must be questioned in light of the results of this cladistic analysis. In particular, the genera *Paracocculina* and *Coccocrater* were found to be paraphyletic. However, given the low Bremer support for these nodes, restructuring the classification is premature and may be overturned with additional anatomical investigations. On the other hand, new morphological data for *Fedikovella caymanensis* and *Teuthirostria cancellata* reveal the anatomical distinctiveness of these taxa; cladistic analysis supports a sister group relationship between them and a basal placement within the Cocculinidae. In addition, monophyly of the Cocculinidae is confirmed. Although the node separating Cocculinidae and Bathysciadiidae is supported by only 2 characters and has a Bremer value of 1, many features were rendered autapomorphic by the inclusion of only a single bathysciadiid representative and were not included in the analysis (e.g., unique features of alimentary system). Thus, this study cannot address the justification for familial separation of these groups.

Character analysis demonstrates that features identified as "diagnostic" of cocculinoidean taxa, are useful in delineating monophyletic groups within the context of a phylogenetic analysis, but are often homoplastic or are synapomorphies at different hierarchical levels than previously thought. Consequently, this analysis emphasizes the fact that it is not reliance on a few essential diagnostic features, *per se,* that provides the key to identifying groups, but the unique combinations of plesiomorphies and apomorphies shared by those taxa as revealed through phylogenetic analysis.

Appendix

Characters used in phylogenetic analysis.

1. Periostracum, (0) Smooth, (1) Fringed, (2) Spinose.
2. Apex position, (0) Subcentral, (1) Posterior.
3. Teleoconch sculpture, (0) Smooth radial ribs, (1) Pitted radial ribs, (2) Beaded radial ribs, (3) Reticulate, (4) Concentric.
4. Protoconch sculpture, (0) Smooth, (1) Reticulate.
5. Epipodial sense organs, (0) Absent, (1) Present.
6. Oral cuticular hairs, (0) Absent, (1) Present.
7. Subpallial gland, (0) Absent, (1) Present.
8. Gill condition, (0) Pseudoplicatid, (1) Respiratory and ventilatory leaflets, (2) Solely respiratory leaflets, (3) Ciliary tract.
9. Hypobranchial gland pocket, (0) Absent, (1) Present.
10. Hypobranchial gland pocket, (0) Small, (1) Large.
11. Copulatory organ, (0) Oral lappet, (1) Right cephalic tentacle, (2) Foot, (3) Cephalic lappet.
12. Pallial brood pouch, (0) Absent, (1) Present.

13. Receptaculum seminis, (0) Paired, (1) Single left, (2) Single right, (3) Pallial oviduct.

14. Seminal groove, (0) Absent, (1) Present.

15. Gonoduct, (0) Massive, (1) Tubular, (2) Not glandular.

16. Rachidian, (0) Cusped, (1) Acuspate.

17. Radular cartilages, (0) 7, (1) 1 pair, (2) 2 pairs.

18. Sublingual Cavity, (0) Glandular, (1) Non-glandular.

19. Jaws, (0) Single small, (1) Single robust, (2) Paired.

20. Salivary Glands, (0) Simple pouches, (1) Prominent to tube-like.

21. Esophageal deflection, (0) Straight, (1) Deflected.

22. Heart-rectum penetration, (0) Penetration, (1) Passing.

23. Aortic vessel, (0) Absent, (1) Present.

24. Hemal gland, (0) Absent, (1) Present.

25. Hemal gland, (0) Weakly developed, (1) Strongly developed.

26. Circumesophageal nerve ring condition, (0) Weakly dystenoid, (1) Hypoathroid.

27. Condition of visceral loop, (0) Central, (1) Shifted right.

28. Osphradium, (0) Absent, (1) Present.

29. Statocyst, (0) Statolith, (1) Statoconia.

30. Basitentacular gland, (0) Absent, (1) Present.

31. Basitentacular gland duct, (0) Narrow, (1) Broad.

References

Dall WH 1882. On certain limpets and chitons from the deep waters off the eastern coast of the United States. Proc. U.S. Natl. Mus. 4: 400–414.

Dantart L & Luque A 1994. Cocculiniformia and Lepetidae (Gastropoda: Archaeogastropoda) from Iberian Waters. J. Moll. Stud. 60: 277–313.

Dautzenberg P & Fischer H 1900. Description d'un mollusque nouveau. Bull. Soc. Zool. Fr. 24: 207–209.

Farris JS 1988. HENNIG86: a PC-DOS program for phylogenetic systematics. Port Jefferson, NY.

Fretter V, Graham A, & McLean JH 1981. The anatomy of the Galapagos Rift Limpet, *Neomphalus fretterae*. Malacologia. 21: 337–361.

Goloboff P 1993. *NONA*. Noname, version 1.6. Program and documentation. Computer program distributed by Carpenter JM, Department of Entomology, American Museum of Natural History, New York.

Harasewych MG & McArthur A 2000. A molecular phylogeny of the Patellogastropoda (Mollusca: Gastropoda). Mar. Biol. 137: 183–194.

Harasewych MG, Adamkewicz SL, Blake JA, Saudek D, Spriggs T & Bult CJ 1997. Phylogeny and relationships of pleurotomariid gastropods (Mollusca: Gastropoda): an assessment based on partial 18S rDNA and cytochrome c oxidase I sequences. Mol. Mar. Bio. Biotech. 6: 1–20.

Haszprunar, G 1987. Anatomy and affinities of cocculinid

limpets (Mollusca, Archaeogastropoda). Zool. Scr. 16: 305–324.

——— 1988a. Comparative anatomy of cocculiniform gastropods and its bearing on archaeogastropod systematics. Mal. Rev. Suppl. 4: 64–84.

——— 1988b. Anatomy and affinities of pseudococculinid limpets (Mollusca, Archaeogastropoda). Zool. Scr. 17: 161–179.

——— 1998. Superorder Cocculiniformia. In: Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5, Part B. Beesley PL, Ross GJB, & Wells A. eds., pp. 653–664.

Hickman CS 1983. Radular patterns systematics diversity and ecology of deep-sea limpets. Veliger. 26: 73–92.

Jeffreys JG 1883. On the Mollusca procured during the Cruise of HMS Triton between the Hebrides and Faroes in 1882. Proc. Zool. Soc. Lond. 1883: 389–399.

Leal JH & Harasewych MG 1999. Deepest Atlantic mollusks: hadal limpets (Gastropoda: Cocculiniformia) from the northern boundary of the Caribbean Plate with descriptions of a new genus and two new species. Invert. Bio. 118: 116–136.

Lindberg DR & Ponder WF 1996. An evolutionary tree for the Mollusca: branches or roots? In: Origin and Evolutionary Radiation of the Mollusca. Taylor J, ed., pp. 67–75. Oxford University, Oxford.

Marshall BA 1986. Recent and Tertiary Cocculinidae and Pseudococculinidae from New Zealand and New South Wales. N. Z. J. Zool. 12: 505–546.

——— 1996. A new subfamily of the Addisoniidae associated with cephalopod beaks from the tropical southwest Pacific, and a new pseudococculinid associated with chondrichthyan egg cases from New Zealand (Mollusca: Lepetelloidea). The Veliger. 39: 250–259.

McLean JH 1985. The archaeogastropod family Addisoniidae Dall 1882: life habit and review of species. The Veliger. 28: 99–108.

McLean JH 1987. Taxonomic descriptions of cocculinid limpets: two new species and three rediscovered species. Zool. Scr. 16(4): 325–333.

McLean JH 1992. Cocculiniform limpets (Cocculindae and Pyropeltidae living on whale bone in the deep sea off California. J. Moll. Stud. 58: 401–414.

McLean JH & Harasewych MG 1995. Review of western Atlantic species of cocculinid and pseudococculinid limpets with descriptions of new species (Gastropoda: Cocculiniformia). Contrib. Sci. (Los Ang.) 453: 1–33.

Moskalev LI 1971. New data on the systematic position of the gastropod molluscs of the order of the Cocculinida Thiele 1908. In: Molluscs: ways, methods, and results of their investigation (autoabstracts of reports of the 4th Conference on the Investigation of Molluscs. Academy of Sciences of the USSR, Leningrad). (In Russian, English translation by Shkurkin GV.)

——— 1976. Concerning the generic diagnosis of the Cocculinidae (Gastropoda Prosobranchia). Trudy P.P. Shirshov Inst. Okeanol. 99: 59–70. (In Russian, English translation by Shkurkin GV.)

Nixon KC 1995. *DADA*, version 1.0. Program and docu-

mentation. Published by the author. Trumansburg, New York.

———— 1999. WINCLADA (BETA) ver. 0. 9. 9 Published by the author, Ithaca, N.Y.

Nixon KC & Carpenter JM 1996. On simultaneous analysis. Cladistics. 12: 221–241.

Pelseneer P 1900. Note sur l'organisation du genre *Bathysciadium*. Bull. Soc. Zool. Fr. 24: 209–211.

Ponder WF & Lindberg DR 1996. Gastropod phylogeny— Challenges for the 90s. In: Origin and Evolutionary Radiation of the Mollusca. Taylor J, ed., pp. 135–154. Oxford University, Oxford.

———— 1997. Towards a phylogeny of gastropod mollusks— an analysis using morphological characters. Zool. J. Linn. Soc. Lond. 119: 83–265.

Sorenson MD 1999. *TreeRot*, version 2. Boston University, Boston.

Strong EE In press. Refining molluscan characters: morphology, character coding and the phylogeny of the Caenogastropoda (Gastropoda). Zool. J. Linn. Soc. Lond.

Strong EE & Lipscomb DL 2000. Character coding and inapplicable data. Cladistics. 15: 363–371.

Strong EE & Harasewych MG 1999. Anatomy of the hadal limpet *Macleaniella moskalevi* (Gastropoda, Cocculinoidea). Invert. Bio. 118: 137–148.

Thiele J 1903. Die Anatomie und systematische Stellung der Gattung *Cocculina*. Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia' 7: 147–179.

———— 1908. Über die Anatomie und systematische Stellung von *Bathysciadium*, *Lepetella* und *Addisonia*. Bull. Mus. Comp. Zool. Harv. Univ. 52: 81–90.

———— 1909. Cocculinoidea und die Gattungen *Phenacolepas* und *Titiscania*. In: Systematisches Conchylien-Cabinet von Martini & Chemnitz. Vol. 2. Kuster HC, Kobelt W, & Haas F, eds., pp. 1–48.

Wilkinson M 1995. A comparison of two methods of character construction. Cladistics. 11: 297–308.