Novafabricia brunnea (Hartman, 1969), New Combination, with an Update on Relationships among Fabriciinae Taxa (Polychaeta: Sabellidae)

KIRK FITZHUGH¹

ABSTRACT. The fabriciin sabellid species, *Fabricia brunnea* Hartman, 1969, from central California, is assigned to the genus *Novafabricia* Fitzhugh, 1990, based on information provided by recently collected specimens. In particular, thoracic notosetal pseudospatulate setae were found to be limited to setigers 3–5, a feature not ascertainable from the type series. Support for this change comes from a cladistic analysis involving *N. brunnea* and other Fabriciinae genera and species. The number of *Novafabricia* species is raised to at least seven. As part of this analysis, the status and relationships of the monotypic genus, *Pseudofabricia* Cantone, 1972 (type species *P. aberrans*), *Novafabricia bilobata* Martin and Giangrande, 1991, and *Augeneriella alata* Hartmann-Schröder, 1991, are evaluated. Based on the original description, *A. alata* is a member of the undescribed taxon "Genus A" (*sensu* Fitzhugh, 1989). Results of the analysis support the recognition of *Pseudofabricia*, including *N. brunnea*, are analyzed and discussed. A key to *Novafabricia* species is provided.

INTRODUCTION

As part of my recent revision (Fitzhugh, 1990a) of the genus *Fabricia* Blainville, 1828, I included a partial redescription of *Fabricia brunnea* Hartman, 1969, based on syntype material from Moss Beach, central California. At that time, I regarded this species as *incertae sedis* as the distribution of thoracic notopodial pseudospatulate setae were neither indicated by Hartman (1969) nor could it subsequently be determined from the syntypes, most notosetae having been broken off. The purpose of the present paper is, in part, to redescribe this species based on recent material.

My revision (Fitzhugh, 1990a) of Fabricia limited the taxon to a single species, Fabricia stellaris (Müller, 1774), including several subspecies of questionable status. Given the evidence at hand, I suggested that such *incertae sedis* species as *F. brunnea* and *F. oregonica* Banse, 1956, would likely be shown to be members of other genera. As such, I noted that Fabricia might very well be monotypic, not allowing definition of the genus in terms of synapomorphy. Taking this situation into account and in conjunction with results from recent cladistic analyses (i.e., Fitzhugh, 1991a, 1992b) of Fabriciinae genera (*sensu* Fitzhugh, 1991a), the generic placement of *F. brunnea* must be judged relative to other fabriciin taxa. This is accomplished here by extending the cladistic analyses of fabriciin genera and species by Fitzhugh (1991a, 1992b) to include *F. brunnea*.

As part of this analysis, validity of the monotypic genus, *Pseudofabricia* Cantone, 1972, can now be assessed as a result of the redescription of *P. aberrans* by Giangrande and Cantone (1990). The original description of this species was based on specimens lacking a branchial crown, and the description of setal forms was too incomplete to have allowed inclusion of the species in earlier cladistic analyses. Attention is also given here to the species *Novafabricia bilobata* Martin and Giangrande, 1991, again for the purpose of confirming the generic placement of this species. Also of relevance to this analysis is a preliminary examination of the generic status of *Augeneriella alata* Hartmann-Schröder, 1991.

Material examined for this study was either obtained from or has been deposited in the Allan Hancock Foundation Polychaete Collection of the Los Angeles County Museum of Natural History (LACM-AHF).

Novafabricia brunnea (Hartman, 1969), new combination

Fabricia brunnea Hartman, 1969:695–696, figs. 1– 5; Fitzhugh, 1990a:9–12, figs. 2–4.

^{1.} Invertebrates Section, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007.



Figure 1. Novafabricia brunnea (LACM-AHF 1651). Entire animal in lateral view (right side; right half of branchial crown removed); figure is split between setigers 6 and 7. Abbreviations: apr, anterior peristomial ring; vc, ventral lobe-like extension of anterior peristomial ring; dl, dorsal lip; ppr, posterior peristomial ring; vl, ventral lip-like process.

MATERIAL EXAMINED. California, San Luis Obispo County; 5 complete and 1 incomplete (branchial crown missing) specimens (LACM-AHF 1651). Syntypes of *Fabricia brunnea* (LACM-AHF 3380), 12 specimens.

DESCRIPTION. All specimens in good condition with 8 thoracic and 3 abdominal setigers. Total length ranges from about 2.0 to 3.0 mm, branchial crown comprises about 0.5 mm of this length. Three pairs of radioles with filamentous distal ends of same width as pinnules. Each radiole with 5–6 pairs of pinnules, all terminating at about same height as radioles. Dorsal lips low, distally rounded; inner margin distinctly fused to most proximal pinnule of dorsal radiole. Ventral lip-like process present



Figure 2. Slightly schematic view of the inner margin of the branchial crown, indicating possible states of dorsal-lip development in fabriciin taxa (cf. character 2, Table 2): A, dorsal lip as a triangular lobe, with dorsal margin well separated from proximalmost pinnule of dorsal radiole; B, dorsal lip with dorsal margin fused with proximalmost pinnule; C, dorsal lip absent. Abbreviations: d, dorsal body margin; dl, dorsal lip; pl, proximalmost pinnule of dorsal radiole; v, ventral body margin.

at base of most proximal pinnule of ventral radiole. Body cylindrical, anterior and posterior ends slightly tapered. Peristomial eyes dark gray, rounded to crescentic, obscured by body-wall pigment; pygidial eyes black, rounded. Anterior margin of anterior peristomial ring a low ridge dorsally and laterally; ventrally a broad, tongue-like lobe, lateral margins only slightly tapered, distally rounded, about 3.5-4 times length of remainder of anterior ring. Anterior peristomial ring (excluding ventral lobe) distinctly narrower than posterior ring. Posterior ring about 2-2.5 times longer than anterior ring. Annulation between rings distinct except along middorsum. Setiger 1 about same width as posterior peristomial ring, wider than long; setigers 2-6 or 7 successively longer, setiger 5 about as wide as long; setiger 8 about same length as setiger 6. Setiger 9 about one-half length of setiger 8; setigers 10-11 successively shorter. Pygidium roughly triangular, rounded, about same length as setiger 11. Superior thoracic notosetae elongate, narrowly hooded; 5-6 per fascicle. Inferior thoracic notosetae with pseudospatulate setae in setigers 3-5; 1 per fascicle; other setigers with elongate, narrowly hooded setae. Abdominal neurosetae modified, elongate, narrowly hooded; 2-4 per fascicle. Thoracic acicular uncini in single or irregular double rows; 6-9 per fascicle; large tooth above main fang; hood present. Abdominal uncini with 5-6 teeth in profile, 4-5 teeth per row; manubrium twice as long as dentate region; manubrium constricted below dentate region, slight proximal expansion to rounded or quadrangular base; 10-13 per fascicle. Entire or proximal half of branchial crown light brown; peristomial rings and setigers 1-2 dark brown, pigmentation diminishing in posterior thoracic setigers; remaining setigers cream colored. Tube material absent; no brooding observed. Methyl green staining produces no distinct patterns.

DISTRIBUTION AND HABITAT. Central California, San Mateo County, Moss Beach, tide pool

Table 1.	Current	generic	distributions	of species	described in	Augeneriella.
A GOLO II		8		or opened		

Species currently recognized as members of <i>Augeneriella</i> (<i>sensu</i> Fitzhugh 1989, 1990e)	Augeneriella species assignable to "Genus A" (sensu Fitzhugh, 1989)
A. hummelinki hummelinki Banse, 1957	A. dubia Hartmann-Schröder, 1965
A. hummelinki indica Banse, 1959	A. cf. dubia (sensu Rouse, 1990)
A. lagunari Gitay, 1970	A. alata Hartmann-Schröder, 1991
A. bansei Hartmann-Schröder, 1986	
A. pectinata Fitzhugh, 1990e	
A. basifurcata Fitzhugh, 1990e	
A. mossambica (Day, 1957)	

among other sabellids (type locality); San Luis Obispo County, Montana de Oro State Park (35°16'16"N, 120°53'15"W), small cove adjacent to recreational area, exposed rock bench at low tide, in crevices among clumps of dense, low-growing green algae.

In addition to the type specimens, Hartman (1969: 693) also includes in *Fabricia brunnea* some of the specimens identified as *F. sabella* (*non* Ehrenberg, 1836) by Berkeley (1930) from Nanaimo, British Columbia, Canada. While I have not pursued this matter, it appears likely that Hartman did not base this conclusion on an actual examination of these specimens but, instead, relied on illustrations in Berkeley's paper, leaving open the question of such a northern distribution.

REMARKS. With the placement of *Fabricia* brunnea in Novafabricia Fitzhugh, 1990, the latter genus now contains at least seven species (e.g., Table 3, Fig. 3). The status of N. gerdi (Hartmann-Schröder, 1974) as a possible junior synonym of *Fabricia bansei* Day, 1961, has yet to be resolved (Fitzhugh, 1990d:12–13). Support for this new combination comes from the cladistic analyses presented below. In short, the features determining the generic placement of Novafabricia brunnea include the presence of pseudospatulate setae in setigers 3–5, also seen in N. gerdi, N. infratorquata (Fitzhugh, 1983), and N. triangularis Fitzhugh, 1990, and the reduced condition of dorsal lips, which is the synapomorphy defining the genus (see below).

The specimens of Novafabricia brunnea described here are virtually identical to the syntypes except that the former have a darker pigmented anterior end. While the ventral lobe of the anterior peristomial ring shows the same pronounced elongation (Fig. 1) seen in *N. chilensis* (Hartmann-Schröder, 1962), the distribution of pseudospatulates is different (setigers 3–6 in *N. chilensis*), as is the dentition pattern in abdominal uncini (cf. Fitzhugh, 1990d). Both species do, however, show the same ventral lip-like outgrowths at the bases of the ventralmost radioles (Fitzhugh, 1990a:fig. 3B, 1990d: fig. 6B; Fig. 1).

Development of the dorsal lips also appears to be slightly greater in *Novafabricia brunnea* (Fig. 1; Fitzhugh, 1990a:fig. 3B) than is seen in *N. chilensis* (Fitzhugh, 1990d:fig. 6B). For example, I originally noted (Fitzhugh, 1990a:12) that in *N. brunnea* the "dorsal lips are not as well developed as those of *Fabricia stellaris*, but are more distinct than what is seen in [other species of *Novafabricia*]." Unfortunately, this generalization is not sufficient to describe any particular dissimilarities or structural relationships between dorsal-lip forms in Fabriciinae taxa.

At this time, three states can be recognized among Fabriciinae taxa for dorsal lips (Fig. 2): (1) welldeveloped, triangular lobes that are distinctly separated from the dorsalmost radioles by a deep, V-shaped notch (Fig. 2A; e.g., Fabricia, Fabriciola Friedrich, 1939, Augeneriella Banse, 1957); (2) poorly to relatively well-developed ridges that are distinctly fused to the most proximal pinnule of the dorsal radioles, leaving only a shallow, U-shaped groove between the lip and pinnule (Fig. 2B; e.g., Novafabricia, some species of Pseudofabriciola Fitzhugh, 1990); or (3) dorsal lips are completely absent (Fig. 2C; e.g., Fabricinuda Fitzhugh, 1990). Distinguishing dorsal lips on the basis of separation from the dorsal radioles provides a more definite means of identifying different states.

A REAPPRAISAL OF CLADISTIC RELATIONSHIPS AMONG FABRICIINAE TAXA

Cladistic relationships among fabriciin taxa have recently been analyzed at several hierarchical levels (Fitzhugh, 1991a, 1991b, 1992a, 1992b) subsequent to results of a cladistic analysis of Sabellidae (sensu lato) genera by Fitzhugh (1989). As a result of a series of revisions of fabriciin genera (i.e., Fitzhugh, 1990a, 1990b, 1990c, 1990d, 1990e), I examined (Fitzhugh, 1991a) relationships among most fabriciin taxa, the results of which support the monophyly of all included genera. A similar analysis was later performed (Fitzhugh, 1992b) with the inclusion of Monroika africana (Monro, 1939) and a new genus and species from Australia, Parafabricia ventricingulata Fitzhugh, 1992. With the addition of several new species as well as redescriptions of some older species, further work on cladistic relationships at the specific level has been carried out for Pseudofabriciola (Fitzhugh, 1991b; Fitzhugh et Table 2. Characters and states used to determine cladistic relationships of Fabriciinae taxa. State "0" is plesiomorphic based on out-group comparisons (see text). Order of multistate characters does not imply any views on transformation series.

- 1. Ventral filamentous appendages: (0) absent; (1) nonvascularized, unbranched; (2) vascularized, unbranched; (3) vascularized, branched.
- 2. Dorsal lips: (0) well-developed, triangular lobes, with dorsal margins well separated from proximalmost pinnules of dorsal radioles; (1) with dorsal margins fused with proximalmost radioles, forming low to moderately narrow ridges; (2) absent.
- 3. Position of branchial crown: (0) extends over entire anterior end; (1) shifted dorsally somewhat; (2) extensively shifted dorsally.
- 4. Branchial lobe shape: (0) wide and short; (1) narrow and elongate and/or with a peduncle-like process.
- 5. Anterior margin of anterior peristomial ring: (0) low ridge dorsally and laterally, ventrally as a narrow lobe; (1) low membranous collar; (2) membranous collar low dorsally and laterally, higher ventrally; (3) very high membranous collar of even width; (4) very high membranous collar that flares anteriorly; (5) low ridge dorsally and laterally, ventrally as a broad lobe; (6) low ridge dorsally and laterally, ventrally, ventrally as a tongue-like lobe; (7) low ridge all around; (8) low ridge all around except for dorsolateral lobes.
- 6. Middorsal collar condition: (0) separate; (1) entire and distinctly grooved; (2) entire and surface smooth.
- 7. Middorsal collar margin: (0) separate; (1) entire; (2) notched.
- 8. Dorsolateral incisions on anterior margin of anterior peristomial ring collar: (0) absent; (1) present.
- 9. Anterior peristomial ring dimensions: (0) wider than long; (1) at least as long as wide.
- 10. Peristomial eyes in lateral view: (0) well developed and round; (1) poorly developed and crescentic; (2) absent.
- Distribution of inferior thoracic pseudospatulate notosetae, in setigers 2-8: (0) absent; (1) 2-5; (2) 3-5; (3) 3-6; (4) 3-7; (5) 3-8; (6) broadly hooded, flagellate in 3-7.
- 12. Thoracic uncini: (0) without large tooth above main fang; (1) large tooth above main fang.
- 13. Thoracic uncini main fang: (0) slender; (1) swollen.
- 14. Abdominal uncini teeth: (0) > 1 row of teeth; (1) 1 row of teeth.
- 15. Abdominal uncini breast: (0) oriopsis-like; (1) manubrium about 2.0 times longer than dentate region;(2) manubrium about 1.5 times longer than dentate region; (3) manubrium same length as dentate region.
- 16. Pygidial eyes: (0) absent; (1) present.
- 17. Radioles: (0) 3 or more pairs; (1) 2 pairs.
- 18. Body-wall spicules: (0) absent; (1) present.
- 19. Branchial hearts: (0) absent; (1) present.
- 20. Displaced pinnules (e.g., Manayunkia, Monroika):(0) absent; (1) present.
- 21. Thoracic uncini shape: (0) typical fabriciin shape; (1) Manayunkia/Genus A-type.
- 22. Pinnule arrangement: (0) distinctly pectinate; reduced

Table 2. Continued.

to two (1) to four (2) pinnules at bases of branchial lobes.

23. Abdominal neuropodial pin-head setae: (0) absent; (1) present.

al., 1993) and *Fabriciola* (Fitzhugh, 1992a). The present cladistic analysis is a compilation of these studies and provides the empirical basis for revising the generic status of *Fabricia brunnea*.

A taxon that has not been considered in past cladistic analyses is the monotypic genus *Pseudofabricia* Cantone. The original description of the type species, *P. aberrans*, was based on specimens lacking a branchial crown, and details of thoracic notosetal types and distributions were vague. With the discovery of complete specimens, Giangrande and Cantone (1990) have thoroughly redescribed the species. Giangrande and Cantone did, however, assume the validity of *Pseudofabricia* relative to other fabriciin genera without any rigorous analysis of the relationship of *P. aberrans* to other fabriciin species. Inclusion of *P. aberrans* in the present analysis will determine the support for recognizing this genus.

Similarly, in their description of Novafabricia bilobata, Martin and Giangrande (1991) placed this species in Novafabricia in accordance with Fitzhugh's (1990d; see also Fitzhugh, 1991a, 1992b) suggestion that monophyly of the genus rests on the reduction of dorsal lips to low, narrow ridges. This dorsal-lip condition is, however, not unique to Novafabricia but is commonly seen in Pseudofabriciola species (e.g., Fitzhugh, 1990d, 1991b; Fitzhugh et al., 1993). Thus, Novafabricia bilobata is included in this analysis to assess its placement in this genus.

Augeneriella alata, from the Great Barrier Reef, was recently described by Hartmann-Schröder (1991) on the basis of a single specimen characterized by the absence of peristomial and pygidial eyes, eight thoracic and four abdominal setigers, a pair of unbranched, vascularized, ventral filamentous appendages, and the anterior peristomial ring collar being ventrally developed into a broad, lip-like extension. These features, along with Hartmann-Schröder's (1991:fig. 91) illustration of thoracic uncini, clearly indicate this is a species belonging to "Genus A" (sensu Fitzhugh, 1989), which is in the process of being formally described (Fitzhugh and Rouse, in prep.). When originally described by Fitzhugh (1989), "Genus A" was known to comprise A. dubia Hartmann-Schröder, 1965, and an undescribed species from the Indian Ocean.

Hartmann-Schröder (1991) noted similarities between A. alata and A. dubia, including the presence of four (as opposed to three) abdominal setigers and the absence of peristomial and pygidial eyes, but allied these species with A. bansei Hartmann-

Table 3.	Character-state matrix for the 43 fabriciin species	based on character states presented in Table 1. Species
included in	in the analysis for the first time are indicated in bold.	. Augeneriella bansei Hartmann-Schröder is not included
since it is	based on a single, incomplete specimen.	

	Characters and states																							
										1	1	1	1	1	1	1	1	1	1	2	2	2	2	
Species	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Manayunkia speciosa	2	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	
M. baicalensis	2	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	
M. aestuarina	2	0	0	0	2	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	0	
M. brasiliensis	2	0	0	0	2	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	2	0	
M. polaris	2	0	0	0	2	0	0	0	0	0	3	0	0	0	1	0	1	0	1	0	1	1	0	
Monroika africana	2	0	0	0	2	0	0	0	0	2	2	1	0	0	3	0	1	0	1	1	0	0	0	
Augeneriella dubia	2	0	0	0	5	0	0	0	0	2	0	0	0	0	1	0	0	1	1	0	1	0	0	
Genus A sp.	2	0	0	0	5	0	0	0	0	2	0	0	0	0	1	0	0	1	1	0	1	0	0	
Fabriciola baltica	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	
F. berkeleyi	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	
F. ghardaqa	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	
F. tonerella	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	?	
F. mediaseta	1	0	0	0	1	0	0	0	0	0	6	0	0	0	1	1	0	0	1	0	0	0	1	
F. brevibranchiata	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	
F. cf. berkeleyi	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	
Pseudofabriciola australiensis	2	0	0	1	4	2	2	1	0	0	0	0	1	0	3	1	0	0	1	0	0	0	0	
P. longa	0	1	0	1	3	2	1	0	0	0	0	0	0	0	3	1	0	0	1	0	0	0	0	
P. incisura	2	0	0	1	4	2	2	1	0	0	0	0	1	0	3	1	0	0	1	0	0	0	0	
P. capensis	0	0	0	1	3	1	1	1	0	0	0	1	0	0	3	1	0	0	1	0	0	0	0	
P. filamentosa	0	?	0	1	3	2	1	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	
P. californica	0	0	0	1	3	1	1	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0	
P. analis	0	1	0	1	4	2	1	1	0	0	0	0	0	0	3	1	0	0	1	0	0	0	0	
P. longipyga	?	?	?	?	4	2	2	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	
Fabricia stellaris	0	0	0	0	5	0	0	0	0	0	4	1	0	0	1	1	0	0	1	0	0	0	0	
Pseudofabricia aberrans	0	0	0	0	5	0	0	0	0	0	0	1	0	0	3	1	0	0	1	0	0	0	0	
Augeneriella hummelincki	3	0	0	0	5	0	0	0	0	0	3	1	0	0	1	1	0	0	1	0	0	0	0	
A. lagunari	3	0	0	0	5	0	0	0	0	1	4	1	0	0	3	1	0	0	1	0	0	0	0	
A. pectinata	3	0	0	0	5	0	0	0	0	0	3	1	0	0	3	1	0	0	1	0	0	0	0	
A. basifurcata	3	0	0	0	5	0	0	0	0	1	4	1	0	0	3	1	0	0	1	0	0	0	0	
A. mossambica	3	0	0	0	5	0	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0	0	
Novafabricia chilensis	0	1	0	0	6	0	0	0	0	0	3	1	0	1	3	1	0	0	1	0	0	0	0	
N. gerdi	0	1	0	0	5	0	0	0	0	0	2	1	0	1	3	1	0	0	1	0	0	0	0	
N. infratorquata	0	1	0	0	5	0	0	0	0	0	2	1	0	0	1	1	0	0	1	0	0	0	0	
N. triangularis	0	1	0	0	5	0	0	0	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	
N. tenuiseta	0	1	0	0	5	0	0	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0	
N. bilobata	0	1	0	0	5	0	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0	0	
N. brunnea	0	1	0	0	6	0	0	0	0	0	2	1	0	0	1	1	0	0	1	0	0	0	0	
Parafabricia ventricingulata	0	0	0	0	5	0	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0	0	
Fabricinuda limnicola	2	2	0	0	7	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0	
F. bikinii	2	2	2	0	8	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0	
F. trilobata	2	2	1	0	8	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0	
F. pseudocollaris	2	2	0	0	8	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0	
F. pseudopalpa	0	0	0	0	8	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0	

Schröder, 1986, as all these species have unbranched ventral filamentous appendages. Unfortunately, Hartmann-Schröder (1991) neither commented on nor cited my (Fitzhugh, 1989; see also Fitzhugh, 1991a, 1992b) finding that *A. dubia* is clearly a member of "Genus A" and cladistically is quite far removed from *Augeneriella*. Furthermore, no mention was made of my (Fitzhugh 1990e) revision of Augeneriella, where I predicted that the presence of unbranched ventral filamentous appendages in the holotype of A. bansei, the only known specimen of the species, is likely an anomalous feature. Hartmann-Schröder (1991) also failed to mention or compare A. alata to Rouse's (1990)



Figure 3. Strict consensus cladogram for fabriciin taxa based on 1,418 minimum-length cladograms. Monotypic genera are indicated in bold.

numerous specimens of A. cf. *dubia*, also from the Great Barrier Reef, though she does cite this paper in relation to *Oriopsis* Caullery and Mesnil, 1896. Thus, for the purposes of the present analysis, A. *alata*, although recognized as a member of "Genus A" (Table 1), is not included in the analysis since distinctions between species of that group are still being determined (Fitzhugh and Rouse, in prep.).

METHODS AND MATERIALS

The analysis includes 43 fabriciin species distributed among 11 genera. Most genera are represented by all described species except in the cases of *Manayunkia* Leidy, 1858, *Fabriciola*, and *Augeneriella* (see Fitzhugh, 1992b, for details). *Fabricia* is only represented by the nominate subspecies, *F. stellaris stellaris* (Müller, 1774; see Fitzhugh, 1990a). *Pseudofabricia aberrans* is included on the basis of preserved specimens and the description by Giangrande and Cantone (1990). Data used for the inclusion of *Novafabricia bilobata* are from the original description (Martin and Giangrande, 1991).

A total of 45 apomorphic states were used, distributed among 23 characters. Characters and states are presented in Table 2. Most characters are the same as those used by Fitzhugh (1992b), though some modifications have been incorporated as a result of studies by Fitzhugh (1991b, 1992a) and Fitzhugh et al. (1993).

States for character 2 have been modified. In previous studies, state 2(1) was described as "dorsal lips low, narrow ridges" and the plesiomorphic state as "well-developed, triangular lobes." As noted above, the dorsal lips of *N. brunnea* are slightly more developed than in other members of this genus. The separation between character states 2(0) and 2(1) is here shifted to indicate the degree of fusion with the first radioles (i.e., showing a conspicuous demarcation as opposed to being distinctly fused to the first radioles; Table 2).

The distribution of states among taxa is pre-

Figure 4. One of 1,418 minimum-length cladograms for fabriciin taxa (species indicated but not named), illustrating one possible pattern of relationship of *Pseudofabricia* to other genera. Character-state changes are only shown for those characters indicating the monophyly of *Augeneriella*, *Novafabricia*, *Fabricinuda*, and *Pseudofabriciola* relative to the monotypic genera *Fabricia*, *Pseudofabricia*, and *Parafabricia*. Slashes = synapomorphies, \times 's = homoplasies. Ambiguous character-state assignments are shown at nodes. See Table 2 for explanations of character states.





Figure 5. A portion of a cladogram of fabriciin taxa (cf. Fig. 4), illustrating one possible pattern of relationship of *Pseudofabricia* to other genera. Character-state changes are only shown for those characters indicating the monophyly of *Augeneriella*, *Novafabricia*, *Fabricinuda*, and *Pseudofabricial* relative to the monotypic genera *Fabricia*, *Pseudofabricia*, and *Parafabricia*. See Fig. 4 for explanations of character-state changes and Table 2 for descriptions of character states.

sented in Table 3. Character-state polarities are based on out-group comparisons as performed by Fitzhugh (1991a, 1991b, 1992a, 1992b), and multistate characters were treated as nonadditive.

Cladograms were constructed using the combination of commands **mhennig***; **bb*** in the computer program Hennig86, developed by Farris (1988). Lengths, consistency, and retention indices (ci and ri, respectively) and character-state transformation series were determined with the **xsteps** command using the **h** and **c** options.

RESULTS

A total of 1,418 minimum-length cladograms was produced, which is only a subset of the total number of cladograms possible using the **mhennig*; bb*** tree-building commands; the limiting factor in this case was the amount of available computer memory. Each cladogram has a length of 68 steps, with a ci of 0.66 and ri of 0.86.

The inclusion of *Pseudofabricia* allows for a greater degree of instability at the generic level, which contributes to the larger number of cladograms (Fig. 3) than previously reported (Fitzhugh, 1991a, 1992b). Specific-level topologies appear to be roughly similar to what have been described by Fitzhugh (1991a, 1991b, 1992a, 1992b) and Fitz-

hugh et al. (1993) except in the case of Novafabricia, which is examined in greater detail in the analysis below. Six of the seven non-monotypic genera clearly remain monophyletic (Fig. 3). The one exception, involving the relationship of the monotypic genus Monroika Hartman, 1951, to Manayunkia, has been analyzed and discussed in detail by Fitzhugh (1992b). The validity of the three remaining monotypic genera—Fabricia, Pseudofabricia, and Parafabricia—is upheld. (Fig. 3).

In all topologies, *Pseudofabricia* is a member of the clade containing *Fabricia*, *Parafabricia*, *Augeneriella*, *Novafabricia*, *Fabricinuda*, and *Pseudofabriciola* (Figs. 3–6); this clade is defined by the presence of a large tooth above the main fang in thoracic uncini [state 12(1); Fig. 4]. The placement of *Pseudofabricia* within this clade is quite variable. For example, the genus can form a basal trichotomy with several genera (Figs. 4–5) or can have a more exclusive relationship to some other genera within this clade (Fig. 6).

With Novafabricia still defined by the reduction of the dorsal lips to low ridges [state 2(1)], the new combination N. brunnea is upheld, as is Martin and Giangrande's (1991) placement of N. bilobata in this genus (Figs. 3–6). The results of additional analyses on the relationships of Novafabricia species are presented below.



Figure 6. A portion of a cladogram of fabriciin taxa (cf. Fig. 4), illustrating one possible pattern of relationship of *Pseudofabricia* to other genera. Character-state changes are only shown for those characters indicating the monophyly of *Augeneriella*, *Novafabricia*, *Fabricinuda*, and *Pseudofabricial* relative to the monotypic genera *Fabricia*, *Pseudofabricia*, and *Parafabricia*. See Fig. 4 for explanations of character-state changes and Table 2 for descriptions of character states.

CLADISTIC RELATIONSHIPS AMONG NOVAFABRICIA SPECIES

A more detailed analysis of relationships among the seven *Novafabricia* species is presented here to examine more accurately the variability of these relationships, especially relative to results of previous analyses (e.g., Fitzhugh, 1991a, 1992b).

METHODS AND MATERIALS

The present analysis involved the seven Novafabricia species in the previous analysis. From the results of that latter analysis, five characters (Table 4) are instrumental in discerning relationships among Novafabricia species. Note, however, that the plesiomorphic state for character 11 (distribution of thoracic pseudospatulate setae) in Table 4 has been altered from what is shown in Table 2. This modification is in accord with the plesiomorphic state as determined in the previous analysis. All multistate characters were, however, treated as nonadditive. The distribution of character states among species is presented in Table 5. Cladograms were constructed using the **ie*** command in Hennig86.

RESULTS

Four minimum-length cladograms (Fig. 7) were produced using the data matrix in Table 5, each Table 4. Characters and states used in the determination of cladistic relationships among *Novafabricia* species. Characters are numbered as in Table 1, though the general character-state polarity for character 11 is based on the cladistic results obtained from the matrix in Table 2. State "0" is plesiomorphic based on these out-group comparisons (see text). Order of multistate characters does not imply any views on transformation series.

- 2. Dorsal lips: (0) triangular lobes with dorsal margins well separated from first radiole; (1) dorsal margins fused with proximalmost radiole of first radiole forming low to moderate narrow ridge.
- Anterior margin of anterior peristomial ring: (0) low ridge dorsally and laterally, ventrally as a broad lobe;
 (1) low ridge dorsally and laterally, ventrally as a tongue-like lobe.
- 11. Distribution of inferior thoracic pseudospatulate notosetae in setigers 2-8: (0) 3-7; (1) 3-5; (2) 3-6; (3) absent.
- 14. Abdominal uncini teeth: (0) > 1 row of teeth; (1) 1 row of teeth.
- 15. Abdominal uncini breast: (0) manubrium same length as dentate region; (1) manubrium about 1.5 times longer than dentate region; (2) manubrium about 2.0 times longer than dentate region.

Table 5. Character-state matrix for all species of *No-vafabricia* based on character states presented in Table 3.

	Characters and states											
Species		2	5	11	14	15						
Outgroup		0	0	0	0	0						
N. bilobata		1	0	0	0	0						
N. brunnea		1	1	1	0	2						
N. chilensis		1	1	2	1	0						
N. gerdi		1	0	1	1	0						
N. infratorquata		1	0	1	0	2						
N. tenuiseta		1	0	3	0	1						
N. triangularis		1	0	1	0	1						

with a length of 9 steps and a ci and ri of 0.88 and 0.80, respectively. Among these cladograms, only the placements of Novafabricia bilobata and a clade containing N. chilensis and N. gerdi are stable. Novafabricia bilobata is the sister group to all other species by way of having thoracic pseudospatulate setae in setigers 3-7 [state 11(0)]. The N. chilensis-N. gerdi clade is defined by the presence of a single row of teeth in abdominal uncini [state 14(1)]. In three topologies (Fig. 7A-C) this clade is the sister group to the clade containing N. infratorquata, N. brunnea, N. tenuiseta Fitzhugh, 1990, and N. triangularis. In the fourth topology (Fig. 7D), the N. chilensis-N. gerdi clade forms a trichotomy with a clade containing N. infratorquata and N. brunnea and another clade with N. tenuiseta and N. triangularis.

DISCUSSION

The increased lack of resolution at the generic level as well as the larger number of cladograms produced in the first analysis as compared to what are reported in earlier studies (e.g., Fitzhugh, 1991a, 1992b) is directly related to the inclusion of *Pseudofabricia aberrans* and *Novafabricia bilobata*. Being primarily characterized by plesiomorphic features, especially the absence of thoracic pseudospatulate setae [state 11(0); Table 2], the placement of *Pseudofabricia* is quite unstable and allows for a larger number of topologies involving this genus and *Augeneriella*, *Novafabricia*, *Fabricinuda*, and *Pseudofabriciola* (cf. Fitzhugh, 1991a, 1992b).

As noted by Martin and Giangrande (1991), Novafabricia bilobata is very distinct from other Novafabricia species by the presence of pseudospatulate setae in setigers 3–7 [state 11(4); Table 2]. In relating Novafabricia species to other fabriciin taxa, the presence of character state 11(4) within Novafabricia has resulted in substantial changes in patterns of relationship among these species as well as resultant hypotheses of transformation series.

For example, in the analyses conducted by Fitzhugh (1991a, 1992b; Fig. 8B, C) for the then known five species, the presence of pseudospatulate setae



Figure 7. Possible minimum-length cladograms for *Novafabricia* species. All character-state changes are shown in A. Character-state changes in B–D are as in A except where indicated. See Fig. 4 for explanations of character-state changes and Table 4 for descriptions of character states.



Figure 8. Past and present patterns of relationships among *Novafabricia* species, indicating the presence, distribution, and polarity of thoracic pseudospatulate setae: **A**, strict consensus cladogram of the four topologies in Fig. 7; **B**, topology from Fitzhugh (1991a:fig. 9); **C**, topology from Fitzhugh (1992b:fig. 5).

is a derived condition within *Novafabricia* as well as being homoplasious relative to other fabriciin genera. The nature of this transformation series resulted from the absence of pseudospatulates in *N. tenuiseta*, which was the sister group to all other *Novafabricia* species. Thus, *N. tenuiseta* displays the more general fabriciin condition of lacking pseudospatulates.

With the inclusion of Novafabricia bilobata, however, the transformation series for pseudospatulates is altered, as is shown in the present analysis of relationships among Novafabricia species (Figs. 7–8), such that the presence of pseudospatulates in setigers 3–7 [state 11(0); Table 4] is now the plesiomorphic condition for the genus. An additional result is the placement of N. tenuiseta at a more exclusive sister-group position by the presence of only elongate, narrowly hooded setae in setigers 2– 8 [state 11(3); Table 4]. Relative to other fabriciin taxa, this setal distribution is hypothesized to be a reversal.

KEY TO SPECIES OF NOVAFABRICIA

- 1a. Inferior thoracic notosetae of setigers 2–8 short, elongate, narrowly hooded

- b. Pseudospatulates in setigers 3-6 or 3-7 ... 3
- b. Pseudospatulates in setigers 3–7 N. bilobata Martin and Giangrande
- b. Ventral extension as a broad, tongue-shaped lobe
- ... N. brunnea (Hartman), new combination 5a. Abdominal uncini viewed *in situ* with promi-
- nent, single proximal row of teeth distally surmounted by 1–2 multidentate rows
- b. Abdominal uncini with at least several rows of

- b. Manubrium of abdominal uncini two times longer than dentate region
 - N. infratorquata (Fitzhugh)

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