Discriminant analysis of Indo-West Pacific *Flabellum*

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Stepwise discriminant analysis was performed on 145 specimens of Indo-West Pacific *Flabellum* pertaining to 8 putative species. Posterior classification supported the premise of 8 species at the 99.3% level. Only two characters are needed to distinguish all species at the 0.01 level: lesser calicular diameter and crest height. Among the first 3 canonical variables, which explain most (95.7%) of the variation, 6 characters proved to be most highly weighted: edge angle, crest height, lateral edge length, lesser calicular diameter, greater calicular diameter, and height. Subsequent inclusion of type specimens into the classification revealed that the 5 syntypes of *F. patens* are all different species; the 5 syntypes of *F. pavoninum* represent 2 species, one of which is *F. distinctum*; *F. magnificum*, *F. lamellulosum*, and *F. vaughani* are all distinct species; the east African species is poorly known and difficult to distinguish; and 2 unnamed species remain. Discriminant analysis is highly recommended as a statistical procedure to distinguish species that have few qualitative differences, and to subsequently identify specimens, or assign types, following a preliminary analysis that does not include the type specimens.

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To deal with the statistics of a number of individual forms, proper statistical methods must be employed, or systematic zoology will be thrown into confusion... We have at present no data [method] for determining the range of variation in the species of Flabellum *by statistical methods, and until such data [methods] are available I prefer to place reliance...* equally upon both qualitative and quantitative characters. (Bourne,1905, p.200, commenting on morphometric analysis of Gardiner [1902]).

Despite the difficulties of discriminating morphologically similar species of corals based on a limited set of often highly variable skeletal characters (Lang,1984), few coral systematists have resorted to discriminant analysis. Foster (1984) reviewed the few multivariate statistical techniques that have been applied to scleractinian coral data sets, but, to date, only 2 authors in 5 papers have used discriminant analysis to distinguish coral species: Foster (1980), 4 fossil species of *Siderastrea*; Foster (1984), 5 fossil and Recent species of *Montastrea*; Owens (1984), 14 species of fossil and Recent micrabaciids and fungiids; Foster (1986), 8 species of fossil and Recent poritids; and Foster (1987), 3 species of fossil and Recent *Stephanocoenia*.

Flabellum contains more species than any other azooxanthellate genus: c. 190 described fossil and Recent species (Felix,1929; Zibrowius,1974; Cairns, in press). Within the Scleractinia, species of *Flabellum* are among the most simple and, consequently, the most difficult to distinguish, being solitary; lacking in pali, columella, dissepiments, and costae; and having a simple epithecal wall. Because there are few qualitative characters that can be used to distinguish species, quantitative characters describing corallum size and shape and septal shape and number are employed. Given numerous species and paucity and high variability of characters, great confusion has resulted in intrageneric taxonomy: some authors advocating widespread synonymy of species (Gray,1848; Gardiner,1902; Faustino,1927) and others maintaining separate species (Milne Edwards & Haime,1848; Cairns, in press). The taxonomic confusion has been exacerbated by: 1, repeated widespread synonymy without examination of the type species involved, 2, loss of various type specimens, and 3, mixed syntype lots for critical species.

This paper uses a small subset of *Flabellum* (i.e., the nontruncate smooth-edged species [group 1 of Zibrowius,1974; *Flabellum (Flabellum)* of Cairns, in press]) from the Indo-West Pacific (but excluding Australia) to: 1, test the hypothesis that 8 species are represented in the study material, 2, determine which characters or character combinations best discriminate these species, and 3, classify previously described Indo-West Pacific type-specimens in order to assign names to the putative 8 species. In order to evaluate the morphological data (to be published in detail in Cairns, in press) in light of the previously stated goals, a series of discriminant analyses were performed.

Methods and materials

Statistical methods

Discriminant analysis determines the minimum number of dimensions (axes) that will minimize variance within a group and maximize variance between groups chosen *a priori* (Wiley,1981; Foster,1984). The apparent subjectivity of choosing groups *a priori* is partially mitigated by the posterior classification procedure that calculates the probability of group assignment for each specimen analyzed. It is a technique often used when few qualitative characters are available and quantitative ones have overlapping ranges.

Eight *a priori* groups (putative species) were distinguished among the 145 specimens using traditional morphological criteria, such as those used by Vaughan (1907) and listed in Table 2. Next, discriminant analysis was run on these groupings using the SPSSX (1986) package on an IBM 4381 mainframe computer. A stepwise discriminant analysis was performed using either the criterion of minimizing the residual variance (RV) or maximizing the Mahalanobis Distance (D2) between the closest related groups. The first 4 analyses used the RV and D2 options to analyze: 1, characters 1-11, and 2, all characters plus indices, i.e., characters 1-14. These preliminary results were analyzed with regard to the minimum number of characters needed to distinguish all species and the character loadings (relative weightings of each character in the general equation of the canonical discriminant function) of the first 3 canonical discriminant functions. Based on this analysis 2 discriminant analyses employing the RV and D2 options were done using only the 6 significant characters (Table 3) to determine the correct model. The results were interpreted biologically: character loading of the principal canonical variate axes, classification of specimens, plotting of specimens on canonical variate axes 1 vs 2. Specimens misclassified or classified with a probability of only 50-70% were reexamined. This was considered to be the final working analysis for the specimens examined. In order to provide a check of these results, the same discriminant analysis was run using a different statistical program (SYSTAT, Wilkenson,1986) on an IBM PC. These results were compared to those using SPSSX. Finally, using the results of these analyses, 12 additional type-specimens and one hypotype were classified and the results analyzed.

Material

Non-juvenile, well-preserved specimens were used because the required measurements had to be made on complete specimens inasmuch as available computer packages to perform the discriminant analysis do not allow for specimens with missing data. Consequently, of the 1450 specimens studied, only 145 were analyzed (Table 1). This percentage is low primarily because one large lot of 1100 *F. patens* contained only 25 measurable specimens. The 145 specimens also included 3 syntypes of *F. distinctum* because so few other specimens of that species were available, and the type series of *F. vaughani* was included, these being the only specimens available. Twelve type-specimens and one hypotype (Table 1) were also classified *a posteriori* based on the discriminant analysis. Unfortunately, types of *F. coalitum* Marenzeller,1888, *F. dens* Alcock,1902, and *F. suluense* Alcock,1902, were not available for classification, but they are qualitatively and quantitatively readily distinguishable from the 8 analyzed species.

Thirteen measurements (Table 2, Fig.1) were taken on each specimen, which represents all gross quantifiable characters shared by all species in the genus. Four of the measurements were used to calculate 2 primary indices (SSI and RSS). In addition, 3 secondary ratio indices were calculated from components of the 11 characters, making a total of 14 characters that were used in the preliminary analyses. Measurements were taken with a MAX-CAL electronic digital caliper with a resolution to 0.01mm, but rounded to the closest 0.1mm.

The following abbreviations of museums of specimen deposition are used in Table 1: BM = British Museum (Natural History), London; MNHNP = Muséum National d'Histoire Naturelle, Paris; RGM = National Museum of Geology and Mineralogy, Leiden; USNM = United States National Museum, Washington D.C.; and ZMA = Zoologisch Museum, Amsterdam.

Results and interpretation

Results of the first set of 4 analyses were similar to each other, regardless of whether

Table 1. Specimens analysed (UGR = Ungrouped in original discriminant analyses)

Group	*Cumulative Specimen Number*	*Locality*	*Museum Number and Status*
1	1–11	Alb-5391	USNM 40724
1	12–36	Alb-5392	USNM 40733
1	37	Alb-5393	USNM 81946
1	38	Alb-5212	USNM 40725
2	39	Alb-5523	USNM 81951
2	40	Alb-5590	USNM 81952
2	41	Alb-5412	USNM 40746
2	42	Alb-5118	USNM 40740
2	43	Alb-5116	USNM 81948
2	44	Alb-5280	USNM 81949
2	45–46	Alb-5281	USNM 81950
3	47–48	Alb-4132	USNM 20705-6 *F. pavoninum* typ. of Vaughan (1907)
3	49–50	Alb-?	USNM 20707, 20710 ”
3	51–52	Alb-4080	USNM 20708 ”
3	53–55	Alb-4081	USNM 20702 ”
3	56	Alb-3865	USNM 20711 *F. pavoninum* var. *latum* of Vaughan (1907)
4	57–58	Alb-5289	USNM 40745
4	59	Alb-5173	USNM 40720
5	60	Alb-4115	USNM 20721 Holotype of *F. vaughani*
5	61–65, 69–95, 97	Alb-4080	USNM 20713, 20715 Paratypes of *F. vaughani*
5	66–68	Alb-3937	USNM 20901 ”
5	96	Alb-4081	USNM 20716 ”
6	98–99	Cape Natal	BM 1950.1.11.30 Gardiner (1902)
6	100	N. Kenya Banks	USNM 82133
6	101–107	Durban, S. Afr.	USNM 82134
7	108–109	“Japan”	BM 1840.4.6.81–12 syntypes of *F. distinctum*
7	110	“Japan”	MNHNP 1022 ?syntype of *F. distinctum*
7	111–112	Alb-5312	USNM 40752
8	113–114	Alb-5393	USNM 40754
8	115, 125–127	Alb-5392	USNM 40753, 45485
8	116–117, 128–145	Alb-5273	USNM 45483-4
8	118–119	Alb-5505	USNM 81983
8	120–121	Alb-5212	USNM 40744
8	122–124	Alb-5116	USNM 40738
UGR	146–150	Challenger-192	BM 1880.11.25.79, syntypes of *F. patens*
UGR	151–155	“Sandwich Ids”	MNHNP 372, syntypes of *F. pavoninum*
UGR	156	Valdivia-199	Holotype of *F. magnificum* (measurements from literature)
UGR	157	Siboga-251	ZMA Coel 1215, Holotype of *F. lamellulosum*
UGR	158	Java, Miocene	RGM 3788, hypotype *F. pavoninum* var. *distinctum* of Gerth (1921)

Table 2. List, abbreviations, and descriptions of characters (variables) used in analyses. Six characters used in final analysis indicated with *. Linear measurements in mm; all angular measurements in degrees. Ranges, means, and standard deviations of every character for every species in Cairns (in press).

Character	*Abbreviation*	*Description*
1. Face angle	FAN	Angle made by intersection of two corallum faces.
*2. Edge angle	EAN	Angle made by intersection of two lateral edges (exclusive of pedicel).
*3. Greater calicular diameter	GCD	Linear measure of greater calicular diameter measured between two upper lateral edges.
*4. Lesser calicular diameter	LCD	Linear measure of lesser calicular diameter measured between summits of upper thecal faces.
*5. Corallum height	HT	Linear measure from base of pedicel to point midway between summits of upper thecal faces.
6. Pedicel diameter	PD	Linear measure of greater diameter of pedicel.
*7. Lateral edge length	LEL	Linear measure taken from junction of lateral edge of calice to point of greatest angular inflection associated with pedicel; average.
*8. Crest height	CRE	Linear measure of maximum height attained by crest on lateral edges.
9. Total Number of septa	NS	Count.
10. Septal Sinuosity Index	SSI	Ratio of amplitude of sinuosity of lower inner edge of a major septum to thickness of septum (Fig. 1D).
11. Relative Septal Size Index	RSS	Ratio of width (measured from theca to fossa at widest point) of second largest-cycle septa to that of largest-cycle septa (e.g., S4:S1-3) (x/y of Fig. 1C).
12. Calice shape index	GCD/LCD	Ratio of two characters defined above.
13. GCD/HT	GCD/HT	Ratio of two characters defined above.
14. LEL/HT	LEL/HT	Ratio of two characters defined above.

11 or 14 characters were used or if the RV or the D2 method were used. Percentage classification ranged from 99.3-100; only 2 characters (LCD and CRE) were needed to distinguish all groups at the 0.01 level; and, in the first 3 canonical variables, 7 characters consistently proved to be most highly weighted: EAN, CRE, LEL, LCD, GCD, HT, and GCD/HT (Fig.1, Table 2).

The second set of 2 discriminant analyses to determine the correct model, RV and D2, was based on 6 characters: GCD/HT being removed because both of its component characters were already included in the variables and no reduction in separation or classification occurred when it was omitted. This analysis produced identical results (Table 3, Fig.2). Three canonical variables explained 95.72% of the variation; canonical variables 4-6 explained only 3.66%, 0.39%, and 0.23% of the variation, respectively, and were therefore not analyzed further. The first canonical variable, explaining 59% of the variation had high weightings for EAN, CRE, and LEL: the first 2 characters relating to corallum shape, and the third a function of size. Canonical variable 2 was highly weighted for LCD, a function of corallum size. Canonical variable 3 is highly weighted for the variables of GCD and HT, also a function of size.

All specimens from this analysis were plotted on a bivariate graph (Fig.2) with canonical variables 1 and 2 as the axes, the 8 original groups being encircled. Although overlap of species occurred (Species 2 and 8,

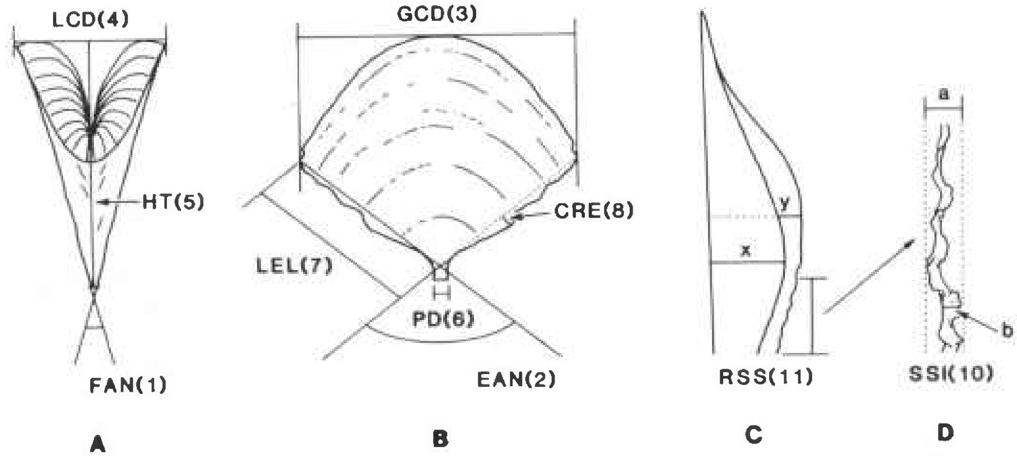

Fig.1. Illustration of characters measured for each specimen. Character abbreviations and numbers as in Table 2. A,B, edge and face of a corallum. C,D, side and edge view of septa. RSS = ratio of width of second largest cycle septa (x) to that of width of largest cycle septa (y), or x/y. SSI = ratio of amplitude of septal sinuosity (a) to thickness of septum (b), or a/b.

and 3 with 6 and 7), it must be remembered that this was only one graph of 2 canonical variables, which together represent 82% of variation. Graphs of canonical variables 1 vs 3 and 2 vs 3 (not illustrated) further distinguished the overlapping groups, except for Species 6 and 7.

The posterior classification based on this discriminant analysis indicated that 99.3%, or 144/145, of the specimens were correctly classified, the only exception being specimen 119 (Fig.2). This specimen was originally assigned to Species 8 but ultimately was classified in Species 4 with a 70% probability and only secondarily with Species 8 with a 30% probability. Re-examination of this specimen from Alb-5505 showed it to have an unusually low EAN and an unusually high CRE, the 2 characters acting together to produce a misclassification into Species 4, even though the plot in Fig.2 places it closer to group 8. Other characters not used in the analysis, including the qualitative character of corallum color, lead me to believe that specimen 119 was originally correctly placed in Species 8. Six other specimens (98, 102, 105, 110, 124, and 145) had relatively low probabilities of correct classification (50-70%) but did classify correctly. When these specimens were re-examined it was usually found that each specimen varied to an extreme in one or two characters, pushing toward a classification with another species. Five of the 7 mis- or poorly classified

Table 3. Standardized/unstandardized canonical discriminant function coefficients for discriminant analyses based on 6 characters.

Original Variable	*Canonical Variable* 1	2	3
EAN	**0.858/ 0.066	-0.375/-0.029	0.398/ 0.031
CRE	*0.687/ 0.925	-0.331/-0.446	-0.484/-0.651
LEL	*0.600/ 0.196	-0.368/-0.120	0.321/ 0.105
LCD	-0.070/-0.021	**1.146/ 0.353	-0.280/-0.086
GCD	-0.078/-0.014	-0.121/-0.022	**0.870/ 0.158
HT	0.109/ 0.024	0.145/ 0.033	*-0.589/-0.134
Constant	-14.289	-2.736	-4.511
Eigenvalue	12.858	5.005	3.109
% Variance	58.68	22.84	14.19
Cum. % Variance	58.68	81.53	95.72

** most heavily weighted in the function
* heavily weighted in the function

specimens related in some way to Species 6.

Discriminant analysis of the same data using SYSTAT was performed to plot specimens on additional axes. Classification analyses performed after the discriminant analysis yielded slightly different results due to differing algorithms. Again, 6 of the 9 specimens mis- or poorly classified concerned Species 6. Several of these specimens indicated that Species 7 was the next closest group, and the stepwise analysis indicated that Species 6 and 7 were indeed most difficult to separate. Re-examination of specimens of Species 6 and 7 and comparisons of their means for all 14 characters (using t tests) showed few statistical differences. Four characters were different at the 0.05 level (HT, LCD, GCD, and CRE), 3 being merely size related: specimens in Species 7 were consistently larger than those in Species 6. However, characters of fossa width, columella, and subtle aspects of corallum shape — characters not used in the analysis and difficult to quantify — lead me to believe that they are different species, a belief substantiated by the ability of the discriminant analysis to distinguish all 8 species, including Species 6. Only 10 specimens were used to characterize Species 6, all from off the east coast of Africa. It is suggested that when more specimens are available of the east African *Flabellum*, a better distinction of species will emerge and Species 6 will be more clearly differentiated from the others.

Classification of the type specimens shows that 5 syntypes of *F. patens* Moseley, 1881, should be classified as 5 different species (1, 3, 4, 5, and 7). This confirms my suspicion that the syntypes represented a mixed lot. The specimen classified as Species 5 (# 148) is poorly preserved, and that classified as Species 7 (# 150) is based on measurements from the literature, and therefore both are suspect. I concur, however, with the classification of the other 3 specimens as Species 1, 3, and 4.

The 5 syntypes of *F. pavoninum* Lesson,1831, classified as 2 species (1 as Species 7; 4 as Species 6). Because the largest specimen, the one most likely to correspond to the original description and figure (and therefore the logical choice of lectotype), is the one classified as Species 7, this species is considered to represent *F. pavoninum*. Because Species 7 includes the types of *F. distinctum* Milne Edwards & Haime,1848, it is considered to be a junior synonym of *F. pavoninum*. The other 4 specimens ('paralectotypes' of *F. pavoninum*) that classified as Species 6 probably represent a different species but not necessarily the *Flabellum* from off the east coast of Africa described as Species 6 (Fig.2). As noted above, there is confusion in characterizing Species 6, and until more specimens are studied from the Indian Ocean these specimens cannot be assigned to a species.

The holotype of *F. magnificum* Marenzeller,1904 (measurements taken from the literature; type lost or misplaced), falls within Species 2 (Fig.2), which coincides with my qualitative observations.

The holotype of *F. lamellulosum* Alcock,1902, classified with 89% probability as Species 3 and 11% probability as Species 8. Examination of the specimen shows that its affinities to Species 3 are purely size related (it is a relatively small specimen), whereas its similarities to Species 8 were based on shape indices (EAN, PD, and CRE), which are not size dependent and are therefore perhaps more diagnostic characters. An assignment to Species 8 would seem logical for this specimen.

Gerth's (1921) Miocene *F. pavoninum* var. *distinctum* classified with 81% probability as Species 1 and 19% probability as Species 6.

Discussion

Gardiner (1902) was among the first to perform a univariate morphometric analysis of Scleractinia — the truncate *Flabellum*. Although he measured many specimens from off eastern Africa, he did not examine the types involved, synonymizing 10 nominal species as *F. rubrum* (Quoy & Guimard,1833). The preface to this paper is Bourne's (1905) comment on Gardiner's statistical methods. Essentially I agree with Bourne that Gardiner indiscriminantly synonymized too many species (see also Squires, 1964 for synonymy of *F. rubrum)*; however, by proper application of discriminant analysis we can now separate and characterize morphologically similar species of *Flabellum* based on variables (characters) and canonical variables (multivariate characters). The foregoing analysis showed that only 6 characters were necessary to discriminate the 8 groups considered and graphically illustrate the groupings and distribution of the specimens.

Another function of discriminant analysis is to classify previously ungrouped specimens, in this case type-specimens. The

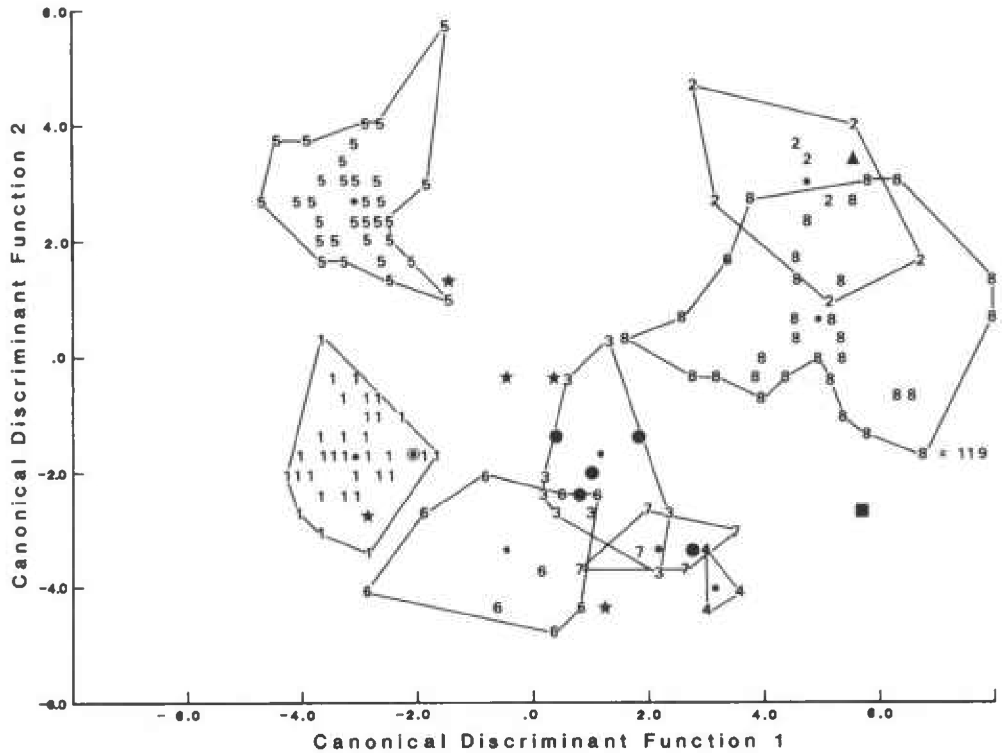

Fig.2. Plot of the first 2 canonical discriminant functions (Table 3) showing intraspecific variation of specimens in each of the numbered taxa and degree of interspecific separation between taxa. Numbered polygons represent the specimens of the taxa listed in Table 1 and as identified in the Discussion section. * denote group centroids. Stars indicate the subsequent classification of the 5 syntypes of *F. patens* (specimens 146-150); solid circles, the 5 syntypes of *F. pavoninum* (specimens 151-155); square, the outlying holotype of *F. lamellulosum* (specimen 157); triangle, the holotype of *F. magnificum* (specimen 156); and solid circle within a circle, Gerth's (1921) *F. pavoninum distinctum* (specimen 158). Controversial specimen 119 indicated.

final results of this paper were therefore to associate names with the 8 *a priori* groups of specimens. To reiterate: Species 1 = unnamed species, to be described by Cairns (in press) ; Species 2 = *F. magnificum* Marenzeller,1904; Species 3 = unnamed species, thus far only known from Hawaii; Species 4 = *F. patens* Moseley,1881, if specimen 146 is chosen as the lectotype (Cairns, in press); Species 5 = *F. vaughani* Cairns,1984; Species 6 = poorly distinguished species from western Indian Ocean, probably not *F. pavoninum*; Species 7 = *F. pavoninum* Lesson,1831 (= *F. distinctum* Milne Edwards & Haime,1848); Species 8 = *F. lamellulosum* Alcock,1902. Using the unstandardized canonical discriminant function coefficients (Table 3) and the raw measurements of a specimen, one can plot and assign any new specimen to one of the 8 species.

Much more information could be extracted from the discriminant analysis and descriptive statistics based on this data set, such as comparison of means, analysis of second highest probability of classifications, and plotting and analysis of other canonical variable axes. An extended analysis based on this data set is presented in a taxonomic revision of the flabellids currently in progress (Cairns, in press).

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