

EVOLUTIONARY ALLOMETRY AND VARIATION IN BODY FORM IN THE SOUTH AMERICAN CATFISH GENUS *CORYDORAS* (CALLICHTHYIDAE)

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Abstract.—The systematic relationships within the speciose genus *Corydoras* have been very difficult to elucidate due to similar body forms among species, lack of discrete morphological features, and uncertain homologies of pigmentation patterns. Most taxa have been described on the basis of pigmentation and of proportional differences in body measurements, which often are variable within and among conspecific populations. Multivariate comparisons of body form among species indicate that both meristic and mensural attributes are highly correlated with body size, thus displaying strong evolutionary allometry. Most ratios of measurements, including those often considered diagnostic among taxa, are as strongly dependent on body size as are untransformed measurements; however, some bivariate ratios reflect multivariate patterns of shape variation and, thus, may be useful in descriptive taxonomic studies. Size-independent variation in form seems to be continuous among species, with no apparent morphological gaps with which to distinguish "natural" species groups. Thus, changes in morphology in these fishes are highly conservative and result from subtle, perhaps heterochronic changes in relative growth rates among body structures. [Allometry; catfishes; morphometrics; principal components analysis; ratios; shape; size; species groups.]

The callichthyid genus *Corydoras* comprises more than 100 nominal species of small South American freshwater catfishes, ranging in distribution from Trinidad to the La Plata drainage and from the foothills of the Andes to the Atlantic coast. The taxonomy of this group has been notoriously difficult to elucidate. Most species have been described on the basis of pigmentation patterns that are often variable both within and among populations, and are difficult to quantify and compare objectively (Nijssen, 1970). The homologies of pigmentation have not been investigated genetically or ontogenetically, and there have been no comprehensive studies of geographic variation in even a single species. There seems to be little qualitative variation in meristic features among species, and there are no other morphological attributes that vary in a sufficiently discrete manner to allow them to be used for phylogenetic reconstruction.

Diagnostic descriptions of morphology have been based primarily on proportional differences in body measurements, expressed as ratios. However, such proportions often have wide numerical ranges,

especially across widely separated localities, and also vary systematically within populations due to growth allometry (Nijssen, 1970). Methodological problems resulting from such natural variation are compounded by inadequate sampling. Available samples of many described species of *Corydoras* are limited to a few specimens from one or a very few localities. As a result there have been no rigorous analyses of morphological variation in *Corydoras* (Weitzman and Nijssen, 1970). Without information on patterns of variation within and among species, it is difficult to formulate and apply consistent and logical criteria with which to diagnose taxa and assess interspecific relationships.

An important objective of a preliminary survey of morphometric variation must be to determine the degree of association of relative body proportions, and other aspects of body form, with body size. Allometry is a nearly universal biological phenomenon, both in ontogenetic development and in the static interspecific scaling of body dimensions among closely related organisms (Gould, 1971, 1975; Sweet,

1980; Cheverud, 1982). Size can be particularly confounding in organisms, such as fishes, having indeterminate growth. Within speciose groups of closely related species (e.g., "adaptive radiations"), variation in body size may account for a large proportion of morphological and ecological variability (Strauss, 1984). Traits or ratios that are strongly correlated with body size are not by themselves useful as taxonomic characters. Discrimination between species must be inherently robust against sampling bias, of which size bias is one unavoidable aspect (Bookstein et al., 1985).

Nijssen and Isbrücker (1980) recently produced a comprehensive taxonomic review of *Corydoras* in which they summarized descriptions of currently recognized species, synonymized a number of others, and partitioned known taxa into hypothetical species groups. In addition, they provided data from a uniformly applied set of body measurements and meristics of type specimens for all recognized taxa. Although these data are in many ways limited and biased, both in the attributes measured and in the choice and quality of preservation of the specimens, they represent a valuable resource for a preliminary survey of variation in body form within the entire genus. The tables of counts and measurements from Nijssen and Isbrücker (1980), and auxiliary references have been utilized for the present study.

This study has four primary objectives: (1) To describe the dependency on body size of each of the meristic and mensural characters used in order to assess their suitability as taxonomic characters. Notable departures from otherwise consistent allometric trends may be of particular value in discriminating among species and in identifying and understanding specific functional adaptations (Strauss, 1984). (2) To describe the amount and directions of size-independent variation in body form among species. A quantitative description of such variation will allow the diagnosis of species according to their positions within the overall patterns. (3) To determine which of the ratios commonly used

in taxonomic descriptions and comparisons of *Corydoras* are consistent with multivariate descriptions of size-free variation in body form, and to identify ratios of potential use in descriptive and comparative taxonomic studies. (4) To determine whether there exist "natural" groupings based on qualitative size-free differences in shape and, in particular, to examine the extent to which the species groups defined by Nijssen and Isbrücker can be discriminated and characterized by body form.

Because the review by Nijssen and Isbrücker (1980) represents the only taxonomic work based upon direct observation of all available material, I use their evaluation of names and relationships as a framework within which to examine the morphology of *Corydoras*. This quantitative descriptive summary is intended to serve as a baseline reassessment for the continuing study of this remarkable group of fishes.

METHODS

Material and morphometric characters.—Data on 12 mensural and 4 meristic characters were provided by Nijssen and Isbrücker (1980, 1982, 1983) for 123 nominal taxa (species and subspecies) of *Corydoras* (Appendix). *Corydoras adolfoi* and *C. robiniae* (Burgess, 1982, 1983) could not be included in this study due to the lack of comparable data in the descriptions of these taxa.

Each taxon is represented by one holotype, lectotype, neotype, or syntype (see Appendix). Specimens were collected over many decades and, because the methods of collection have undoubtedly been diverse and the designation of a type specimen from a sample is inherently subjective, it cannot be assumed that the observed body sizes are necessarily representative of the populations from which they were drawn. However, the specimens are probably not atypical in body form because of the sturdiness of their bony encasement. Due to the limitations of these data, I could not examine differences among species in relation to within-population growth and

variation or to sexual dimorphism. (Such studies on several widespread species are in progress.)

Because all morphometric data were collected by the same researchers, artifactual variation due to differences in technique has been largely avoided. Most characters are illustrated in Nijssen (1970). They are listed here along with their conventional abbreviations: (1) SL, standard length, from snout to caudal end of vertebral column (hypural plate); (2) BD, body depth, from the anterior edge of the azygous predorsal scute to the posteroventral edge of the coracoid; (3) DCP, least depth of the caudal peduncle; (4) BW, body width just anterior to the pectoral spine insertions; (5) CA, width of the coracoid area between the ventral edges of the first (anterior) ventrolateral scutes; (6) HL, head length, from snout (ethmoid) tip to the dorsal edge of the gill opening; (7) SN, snout length, from snout (ethmoid) tip to the nearest edge of the bony orbit; (8) LBO, horizontal length (diameter) of the bony orbit; (9) WI, least width of the interorbital region; (10) FNT, length of cranial (frontal) fontanel, measured along the midsagittal skull; (11) LDS, length of dorsal spine in vertical (extended) position; (12) LPS, length of depressed pectoral spine; (13) DBS, number of dorsolateral body scutes; (14) VBS, number of ventrolateral body scutes; (15) PAS, number of preadipose middorsal scutes, excluding the adipose spine; (16) PFR, number of pectoral fin rays.

Statistical analyses.—Body measurements covary strongly with body size, while in most fishes counts of scutes and fin rays do not change during growth beyond some threshold body size; therefore, mensural and meristic data were treated separately. Principal components of mensural data were computed from the covariance matrix of logarithmically transformed data. The logarithmic transformation preserves allometries, standardizes variances, and produces a scale-invariant covariance matrix (Jolicoeur, 1963a). Because the first principal component (PC1) of these data is a strong size factor, the position (score) of an individual on PC1 is a measure of its

overall body size, while the loadings (coefficients) of characters on the component are proportional to the allometric coefficients of the characters with respect to size (Bookstein et al., 1985). In using PC1 as a size factor, general body size is implicitly defined to be the linear combination of characters that best accounts for joint increase or decrease in all characters simultaneously, in the sense of leaving the smallest mean square residual. Loadings on mensural-character PC1 were rescaled to a mean of 1.0 and interpreted as static allometric coefficients on general size (i.e., average size-related shape differences among taxa; Leamy and Bradley, 1982; Lande, 1985); values greater than unity describe positive allometry, while those less than unity indicate negative allometry.

Fontanel length (FNT) and number of pectoral-fin rays (PFR) were omitted from some analyses because data were lacking for several taxa. Principal components of meristic data were computed from the covariance matrix of logarithmically transformed counts.

Size-independent character variabilities were estimated as the standard deviations of residuals (square root of the mean square error) from linear regressions of log-transformed characters on the size factor, PC1. These values are proportional to coefficients of variation of size-corrected measurements (Lewontin, 1966).

For species-group comparisons, sheared principal components (Humphries et al., 1981) were used to provide size-free discrimination based only on mensural data. Components were sheared by partialing out the pooled within-group size factor (PC1) while maintaining the group centroids. Sheared components are much more stable under substitution of variables than discriminant functions when the variables are of equivalent scale (Bookstein et al., 1985). For combined mensural and meristic data, discriminant functions were used. Because the putative species-groups differ significantly in size, and mensural and meristic data differ in their covariance relationships with size, discriminant functions were calculated using residuals from

regressions of each character separately on the pooled within-group PC1.

All principal-component and canonical loadings are portrayed as vector correlations (directional cosines; Wright, 1954), which are estimated for each character by correlations with projection scores across individuals. Unlike loadings, such correlations are directly comparable across analyses and can be estimated for characters not used in the computation of the components or functions. Correlations between multivariate vectors were computed as inner products (Morrison, 1976).

Standard errors for multivariate allometric coefficients and vector correlations were estimated using a jackknifing technique (Miller, 1974). Principal components analyses were repeated 12 times, each time excluding 10 specimens randomly selected without replacement. For each coefficient, the standard error of the resulting 12 pseudovalues was taken to be an estimate of its standard error (Sokal and Rohlf, 1981). Relatively small standard errors indicate homogeneity within the sample, with little individual variation in character covariance trends. Large standard errors indicate sensitivity to one or more outliers affecting correlations of characters with components.

To investigate the behavior of ratios of characters with respect to principal components, all possible pairs of mensural characters were used to generate 132 ratios (the ratio and its reciprocal for each character pair) for each taxon, and their correlations were examined across taxa with the standard length, the first three mensural principal components, and the first three meristic components. Ratios of raw data were used to be consistent with standard taxonomic practice. Ratios were considered to be satisfactory descriptive variables when they were uncorrelated with mensural PC1 ($|r| \leq 0.10$) but cor-

related with PC2 or PC3 ($|r| \geq 0.30$). For comparison, ratios were logarithmically transformed and then correlated with log (standard length) and the six principal components.

All computations were performed using the Michigan Interactive Data Analysis System (MIDAS).

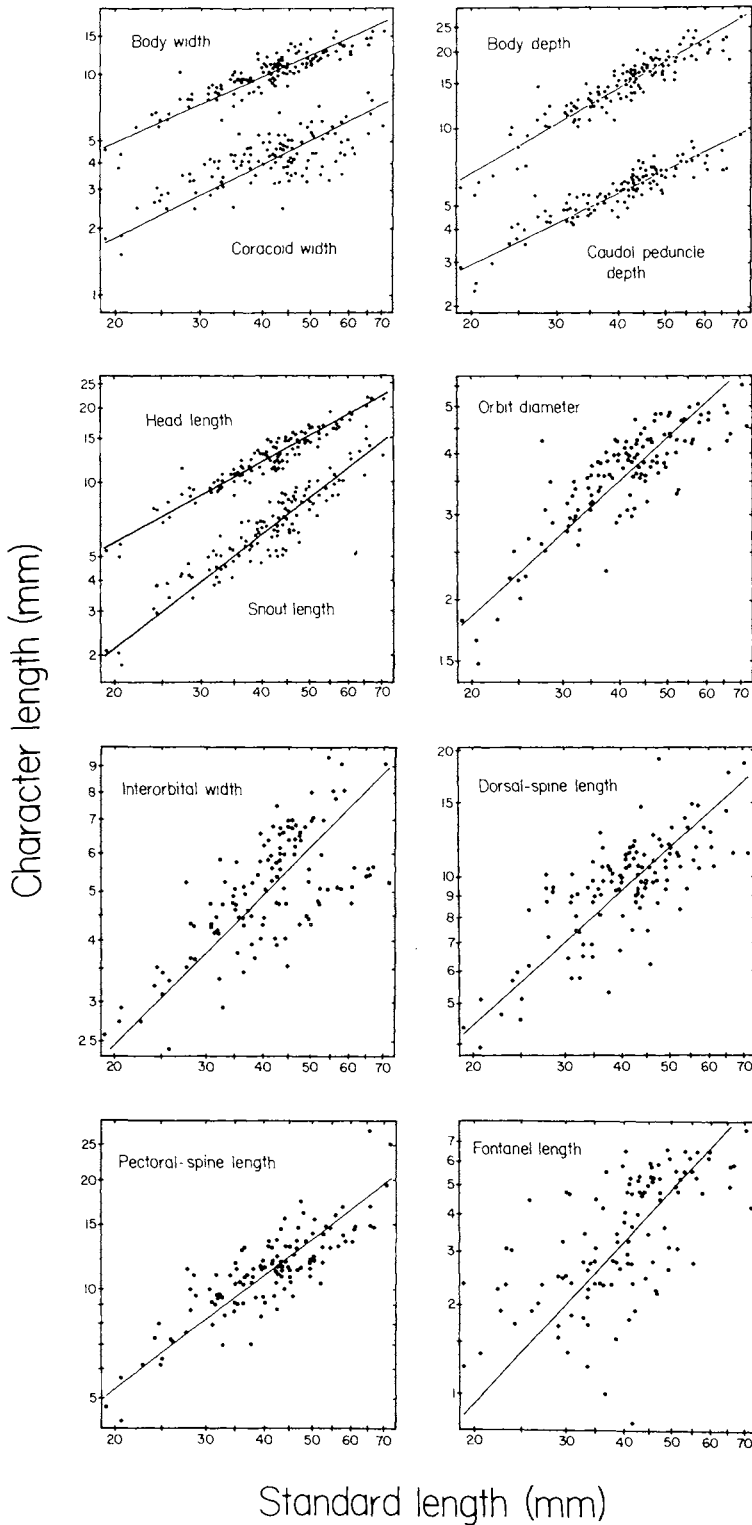
RESULTS

Size and shape variation among taxa.—Most morphometric variation among taxa of *Corydoras* is size-related. Specimens representing taxa vary over a four-fold range in size, from 17.4 mm to 72.3 mm standard length, and the first principal component of the mensural data (described below) accounts for 84% of total variation in the data. All characters, both mensural (Fig. 1) and meristic (Fig. 2), are significantly correlated with standard length, with correlations of log-transformed data ranging from 0.20 for preadipose scutes to 0.96 for head length (Table 1). Cephalic characters, such as snout length and orbit diameter, tend to be more highly correlated with head length than with body length, as expected if these structures are more highly integrated with the body region of which they are a part than with the body as a whole. There are no apparent discontinuities in the variation of any character.

Each of the mensural characters is significantly allometric with respect to general body size (PC1) across species except for three isometric traits: standard length, body width, and length of the pectoral spine. Because standard length is isometric, it serves as a useful proxy for general size in these catfishes. However, general body size (which includes aspects of width and depth) increases faster than standard length in other fishes (Chernoff and Miller, 1982; Strauss and Bookstein, 1982; Humphries, 1984) and, thus, its utility in a particular group must be demonstrated,

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FIG. 1. Relationships between body measurements and standard body length among species. Each point represents a taxon; axes are logarithmic. Correlations and allometric coefficients are given in Table 1.



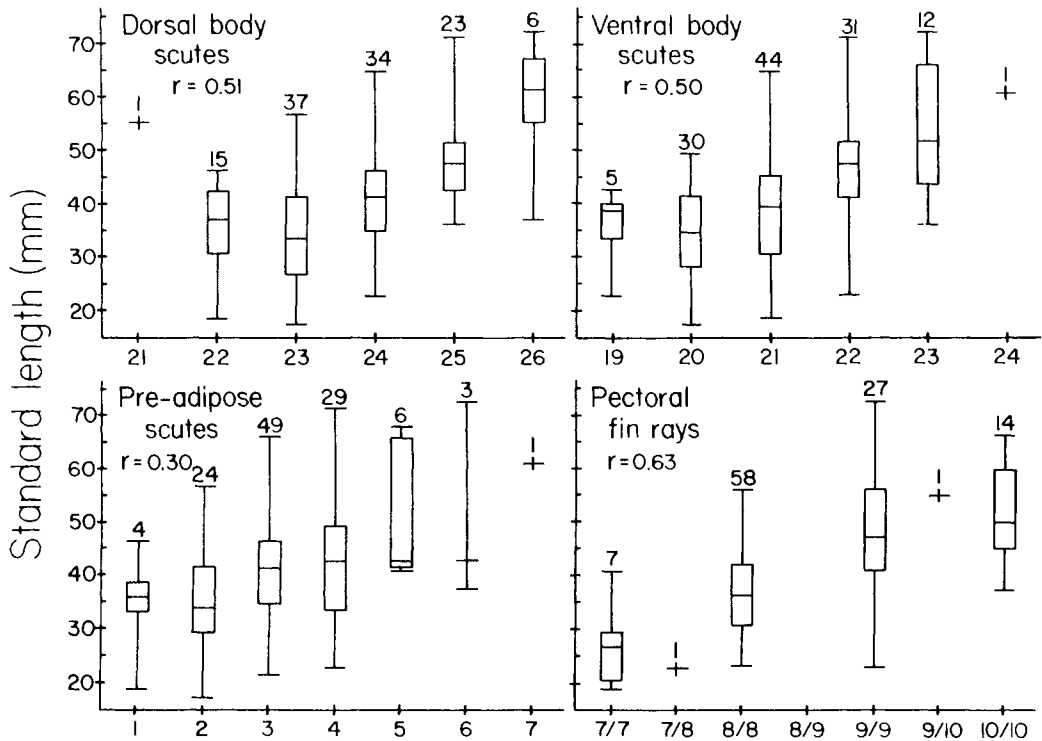


FIG. 2. Relationships between meristic counts and standard body length among species. Each "box plot" indicates range of size variation (outer bars), quartiles (extent of rectangle), and median size (line within rectangle). Size axes are linear. Correlations are given in Table 1.

not assumed. Body depth and three cephalic characters (head length, snout length, and fontanel length) are positively allometric—that is, relatively larger in large individuals than in small individuals. The remainder of the characters are negatively allometric. These significant static allometries, together with the high correlations with body size, indicate that a significant amount of variation in shape among species can be accounted for solely by differences in body size.

Because of their high correlations with body size, relative character variabilities can be compared only after variation in size (PC1) has been partitioned out (Table 1). Fontanel length and number of pre-adipose scutes display the largest amounts of size-free variation among species; inter-orbital width, coracoid width, snout length, and length of dorsal spine display

intermediate levels of variability. As shown below, these characters are among those that load most heavily on the principal components that describe multivariate variation in shape (mensural PC2 and PC3), suggesting the absence of confounding secondary shape factors (Bookstein et al., 1985).

Size-related differences in shape may be visualized by predicting the character-state values for an "average" individual at any body length, based on the regressions of Figure 1. Table 2 shows the predicted values of 11 mensural characters as a function of three arbitrary body lengths covering the observed size range. Ratios of such characters with standard length are often used as "size-free" measures of shape for interspecific comparisons (e.g., Nijssen, 1970). However, these ratios increase with body length for some characters and de-

TABLE 1. Static allometric coefficients (\pm estimated standard errors), correlations with body and head lengths, and measures of size-independent variation of mensural characters. Relative variability is the standard deviation of residuals after regression on mensural PC1.

Character	Static allometric coefficient	Correlation with		Relative variability
		Standard length	Head length	
Standard length	0.99 \pm 0.02	—	0.96	0.083
Body depth	1.12 \pm 0.03	0.92	0.94	0.062
Caudal-peduncle depth	0.92 \pm 0.02	0.92	0.93	0.067
Body width	0.97 \pm 0.04	0.91	0.90	0.086
Coracoid width	0.86 \pm 0.04	0.70	0.70	0.177
Head length	1.07 \pm 0.02	0.96	—	0.062
Snout length	1.44 \pm 0.05	0.93	0.98	0.149
Orbit diameter	0.89 \pm 0.03	0.84	0.90	0.083
Interorbital width	0.81 \pm 0.05	0.69	0.72	0.175
Fontanel length	1.74 \pm 0.14	0.63	0.70	0.384
Dorsal-spine length	0.92 \pm 0.03	0.75	0.80	0.144
Pectoral-spine length	0.97 \pm 0.02	0.86	0.87	0.103
Dorsal body scutes	—	0.47	0.47	0.043
Ventral body scutes	—	0.45	0.45	0.046
Pre-adipose scutes	—	0.20	0.22	0.379
Pectoral-fin rays	—	0.63	0.65	0.079

crease for others, indicating a systematic change in body form with increasing size (Table 2). As expected, the amounts of change in the ratios are highly correlated ($r = 0.89$) with static allometric coefficients. Thus, the greater the allometry (positive or negative) of a given character, the less useful will be a ratio of that character with body length (which is isometric) in discriminating taxa or deducing phylogenetic relationships.

Scatter plots of taxa on the principal components of mensural data (Fig. 3A) reconfirm that: (i) most observed variation is

size-related and can be accounted for solely by variation in body size; and (ii) except for a few outliers, variation in body form is continuous among taxa, with no obvious morphological gaps. Vector correlations of mensural and meristic characters with the components portray the manner in which the first few components account for size and shape variation (Fig. 3B). The first component is a size factor, significantly and positively correlated with all characters and accounting for 84% of total mensural variation. Correlations with PC1 range from 0.63 (fontanel length) to 0.98

TABLE 2. Expected (predicted) values (in millimeters) of mensural characters and their ratios with standard length at each of three arbitrary standard lengths.

Character	Expected value (and ratio) at standard length			Change in ratio ^a
	20 mm	45 mm	70 mm	
Body depth	6.7 (0.336)	16.5 (0.368)	27.1 (0.387)	0.051
Caudal-peduncle depth	2.9 (0.147)	6.3 (0.140)	9.5 (0.136)	-0.011
Body width	5.0 (0.249)	11.1 (0.247)	17.2 (0.245)	-0.004
Coracoid width	2.4 (0.122)	4.5 (0.099)	5.8 (0.083)	-0.039
Head length	5.7 (0.287)	13.9 (0.308)	22.5 (0.322)	0.035
Snout length	2.1 (0.107)	7.4 (0.165)	14.7 (0.210)	0.103
Orbit diameter	1.9 (0.097)	3.9 (0.087)	5.5 (0.079)	-0.108
Interorbital width	3.0 (0.151)	5.6 (0.125)	7.5 (0.107)	-0.044
Fontanel length	0.9 (0.047)	4.0 (0.089)	8.9 (0.127)	0.080
Dorsal-spine length	4.9 (0.239)	10.5 (0.232)	15.6 (0.223)	-0.016
Pectoral-spine length	5.7 (0.283)	12.3 (0.273)	18.6 (0.265)	-0.018

^a Difference between ratios at 70 mm and 20 mm.

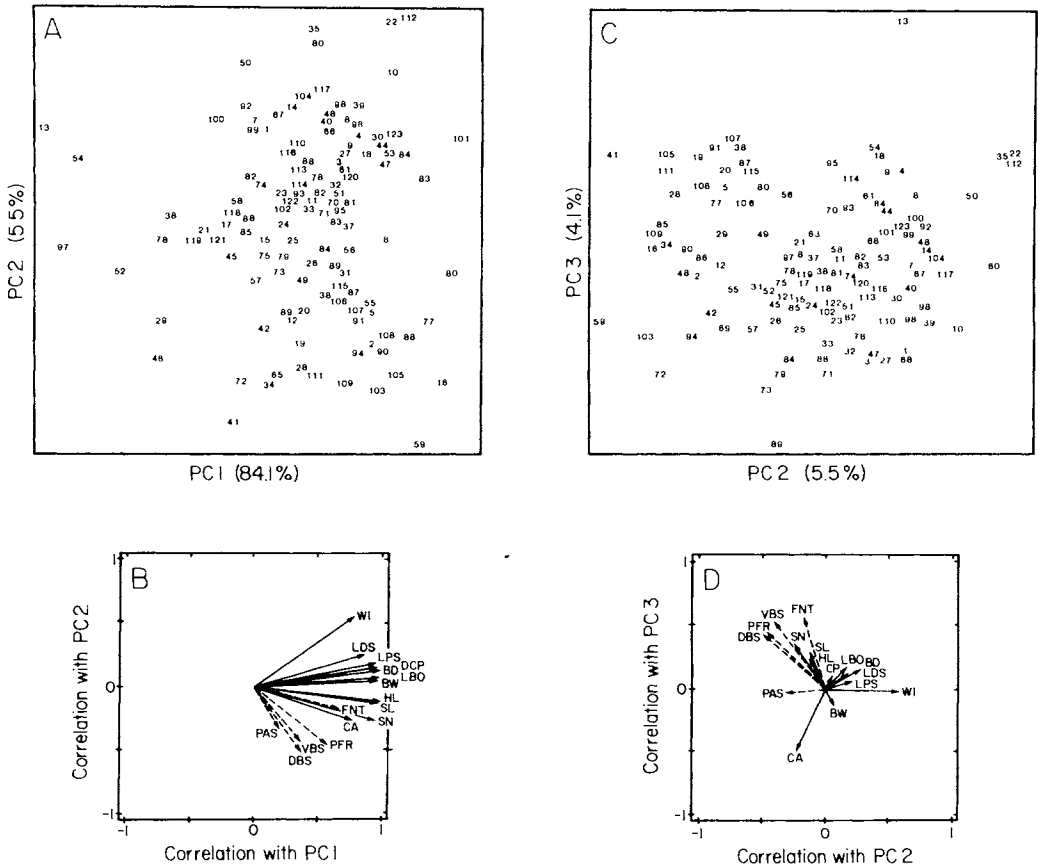


FIG. 3. Principal components analysis of mensural characters. (A, C) Scatters of taxa (see Appendix) on the first three components of mensural characters (excluding fontanel length). (B, D) Corresponding correlations of mensural characters (solid vectors) and others not included in the PC analysis (dotted vectors) with corresponding principal components.

(body depth); the correlation with standard length is 0.96. The greatest amount of size-free shape variation is due to those characters significantly correlated with PC2 or PC3, primarily interorbital width, coracoid width, and snout length. Although not used in the computation of the components, fontanel length and three meristic traits (dorsal and ventral body scutes, number of pectoral-fin rays) are also significantly correlated with the PC2-PC3 plane. However, the importance of meristic characters may be overestimated by this analysis due to their relatively small ranges and discrete values and the lack of any information in this analysis about known

high levels of intraspecific variation (which, for example, explains more than 93% of total meristic variation within and among Paraguayan populations of *Corydoras aeneus*, *C. ellisae*, and *C. polystictus*; Strauss, unpubl. data). Despite the existence of several outlying taxa on the scatter of PC2 and PC3, vector correlations are highly stable; jackknifed standard errors of correlations are all less than 0.02. The first three components together account for 94% of total mensural variation among taxa. The fourth through twelfth components each account for less than 2%.

Ratio descriptions of shape.—In the presence of strong patterns of static allometry,

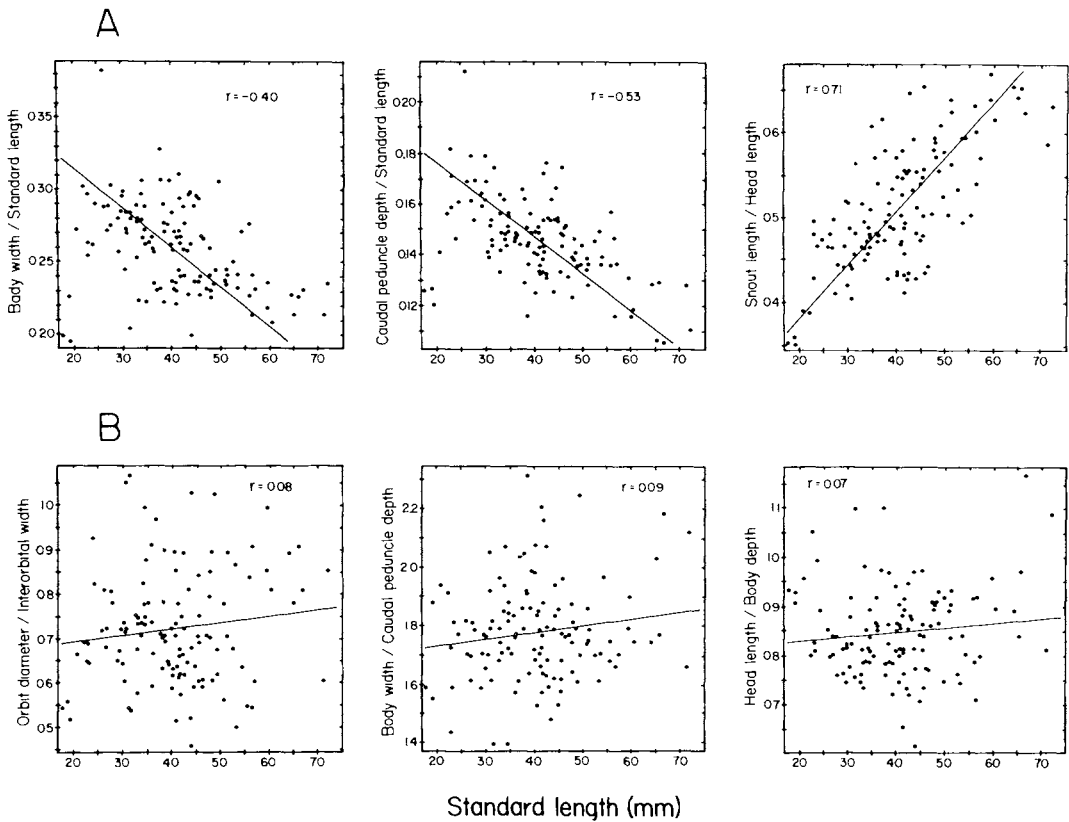


FIG. 4. (A) Examples of commonly used ratios highly correlated with standard body length among species. (B) Examples of less commonly used ratios uncorrelated with standard body length among species, but correlated with shape variation (mensural PC2 and PC3). Each point represents a taxon; axes are linear (r = correlation coefficient).

bivariate ratios of mensural characters may be highly correlated with body size (Table 2, Fig. 4A). Nevertheless, because some ratios are clearly statistically independent of body size (Fig. 4B), an empirical investigation of ratio behavior in relation to multivariate descriptors of size and shape is necessary: (i) to determine which of the ratios commonly used in interspecific descriptions and comparisons of *Corydoras* are truly indicative of size-free differences in form; (ii) to identify ratios of potential use in descriptive taxonomic studies, in the context of the present multivariate analysis; and (iii) to judge whether such a protocol might be useful in studies of morphometric variation in other groups of organisms. Mosimann and James (1979)

have investigated relationships of ratios (in their case, log-ratios) to multivariate factors of non-ratio data.

I considered a ratio to be satisfactory as a descriptive variable when it was uncorrelated with general size but correlated with shape variation. Of the 132 possible ratios generated from raw data, only 26 met these criteria. When both a ratio and its reciprocal were size-free and shape-correlated, the one having the higher root-mean-square correlation with PC2 and PC3 was selected, giving a total of 14 potentially useful ratios (Table 3). In two cases (CA/LBO and CA/LDS) the reciprocals had correlations with general size (-0.14 and -0.16 , respectively) beyond the arbitrary cut-off point. The correlations of log-ratios

TABLE 3. Ratios uncorrelated with mensural PC1 ($|r| \leq 0.1$) but correlated with mensural PC2 or PC3 ($|r| \geq 0.3$), and their correlations with standard lengths and principal component projections. Ratios are listed by decreasing root-mean-square correlation with mensural PC2 and PC3.

Ratio ^a	Standard length	Correlation with					
		Mensural			Meristic		
		PC1	PC2	PC3	PC1	PC2	PC3
CA/LBO ^b	-0.05	-0.06	-0.44	-0.79	-0.13	0.18	0.13
CA/WI	0.07	0.00	-0.76	-0.45	0.23	0.25	-0.05
HL/BD	-0.02	-0.07	-0.72	0.36	0.52	-0.07	0.15
LBO/WI	0.12	0.08	-0.65	0.29	0.51	0.17	-0.21
FNT/BD	0.06	0.02	-0.38	0.60	0.53	-0.20	-0.14
LPS/SL	-0.09	-0.07	0.54	-0.21	-0.44	0.22	0.10
FNT/HL	0.10	0.06	-0.16	0.55	0.42	-0.20	-0.19
FNT/LPS	-0.05	-0.08	0.25	-0.46	-0.43	0.21	0.13
FNT/SL	0.08	0.09	-0.13	0.56	0.40	-0.18	-0.20
BW/LDS	0.04	0.02	-0.27	-0.41	-0.03	0.08	0.01
LPS/BW	0.05	0.07	0.27	0.34	0.05	-0.02	0.07
BW/DCP	0.11	0.09	-0.01	-0.57	-0.26	0.15	0.02
LDS/DCP	-0.03	0.00	0.37	0.11	-0.16	0.02	0.06
CA/LDS ^b	-0.01	-0.05	-0.30	-0.16	0.10	0.01	-0.01

^a Abbreviations given in Methods.

^b Reciprocal ratio does not meet selection criteria. See text

(Jolicoeur, 1963b; Mosimann and James, 1979; Jolicoeur et al., 1984) with the principal components were almost identical with those of the corresponding untransformed ratios. When the same criteria of selection were applied, the same set of 14 ratios resulted, indicating that over the small ranges involved (Table 3), the ratios and log-ratios are highly correlated.

In general, the set of size-free ratios consists of pairs of characters having approximately equal allometries on general size, although the statistical behavior of ratios is also highly dependent on the underlying frequency distributions of the numerator and denominator variables (Atchley et al., 1976). The set of 14 ratios includes only two (LPS/SL and FNT/HL) commonly used in species descriptions and comparisons of *Corydoras* (e.g., Burgess, 1982, 1983; Nijssen and Isbrücker, 1982, 1983). Several of the remaining ratios are of characters anatomically or functionally related, such as CA/WI (two width measurements), HL/BD (a length-to-depth ratio), LBO/WI (two characters describing the morphology of the eyes), and BW/DCP (a width-to-depth ratio). Others, such as CA/LBO, FNT/LPS, BW/LDS, and LDS/DCP, are ratios of character pairs having

no obvious functional relationship to one another and, thus, would tend not to be chosen for descriptive use.

Of the 14 ratios, CA/LBO and HL/BD were selected as the most reasonable descriptive variables for the following reasons: (i) they are uncorrelated with both standard length and general size but have among the highest joint correlations with mensural PC2 and PC3; (ii) the two ratios involve four different characters; (iii) CA/LBO is rather highly correlated with PC3 and moderately correlated with PC2, while the opposite is true for HL/BD; and (iv) the two ratios are not significantly correlated with one another across taxa ($r = 0.11$). Most other pairs of ratios are significantly correlated and, thus, are redundant in their descriptions of shape variation. A scatter of the 123 taxa on the two ratios (Fig. 5A), and corresponding vector correlations with mensural and meristic characters (Fig. 5B), may be of value (for comparative purposes only) in taxonomic studies of *Corydoras*. Note that the plane formed by the two ratio-vectors is almost parallel with the PC2-PC3 plane (Fig. 5B), and that the vectors describing correlations of mensural and meristic characters with the ratios are more regularly distrib-

uted than are the corresponding vectors with the PC2-PC3 plane (Fig. 3B). However, intraspecific variability of bivariate ratios is likely to be much greater than of multivariate factors (e.g., Fig. 3A) because of the inherent sensitivity of ratios to measurement error and individual variation.

Discrimination among species groups.—Nijssen (1970) and Nijssen and Isbrücker (1980) divided the species of *Corydoras* into five phenetic groups. Although no discontinuities were evident in the preceding multivariate analyses of body form, the utility of their groupings can be evaluated by attempting to discriminate among them with respect to their within-group covariance patterns. Two different methods of discriminant analysis, having somewhat different assumptions and properties, were used.

The sheared second (H2) and third (H3) principal components portray size-free discrimination based only on mensural data (Fig. 6A, B). Four of the five groups overlap considerably on the sheared components. The fifth (and most distinctive) is the "acutus" group, identified by Nijssen (1970:58-60) as consisting of the long-snouted species. It is distinct from all but the "barbatus" group, with which it overlaps by 27%. Loadings on the sheared components (Fig. 6B) indicate that the "acutus" species differ primarily in their relatively longer body, head, and fontanel and, to a lesser extent, longer snout and narrower interorbital width. Although the analysis was based on mensural data only, the "acutus" species also tend to have greater meristic counts than other taxa (Fig. 6B).

To test for discrimination based on concurrent mensural and meristic differences, conventional discriminant functions were calculated using size-free residuals of all available data. In the resulting analysis (Fig. 6C, D) the "acutus" species are distinct from the remaining four groups, which overlap among themselves. Vector correlations on the first two canonical variates (Fig. 6D) are consistent with those from the sheared-component analysis, in that the "acutus" species are distinguished primarily by their greater meristic counts

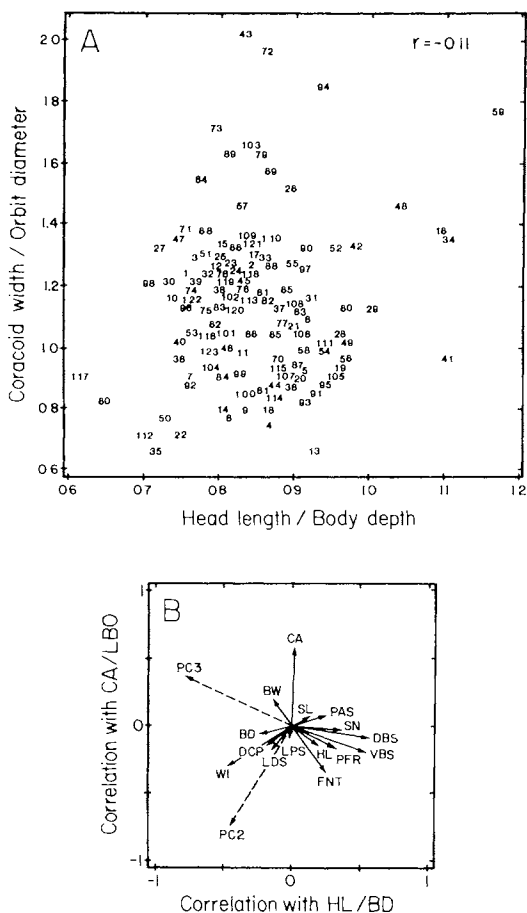


FIG. 5. (A) Scatter of taxa (see Appendix) on two size-independent ratios. Each point represents a taxon; axes are linear. (B) Correlations of mensural and meristic characters (solid vectors) and mensural PC2 and PC3 (dotted vectors) with corresponding ratio axes. Correlations of mensural PC1 with both ratios are insignificant.

and fontanel length and narrower interorbital width and, to a lesser extent, longer body, head, and snout. In fact, the canonical axes of size-corrected data are highly correlated with the sheared principal components, rotated by about 40° (Fig. 6B, D) to account for meristic differences.

DISCUSSION

Allometry, functional scaling, and taxonomic descriptions.—Analyses of the effects of

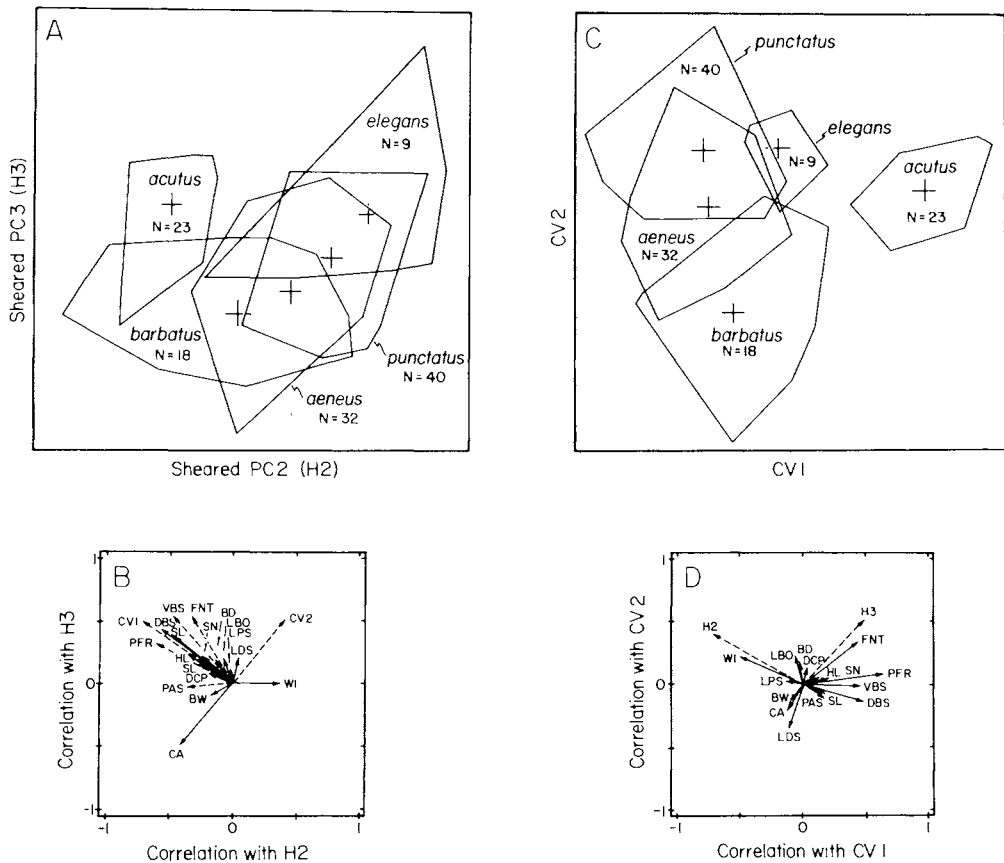


FIG. 6. Discriminant analysis of the five hypothetical species groups. (A) Scatter of the five groups on the second (H2) and third (H3) sheared principal components of mensural data. The convex polygons minimally enclose sets of points for each group; crosses indicate centroids. (B) Correlations of mensural and meristic characters and the first two canonical variates (CV1, CV2) with the corresponding sheared components. (C) Scatter of the five groups on the first two canonical variates from a five-group multiple discriminant analysis of size-independent residuals of meristic and mensural data. (D) Correlations of mensural and meristic characters and the two sheared components (H2, H3) with the corresponding canonical axes.

body size and allometry among species have largely been neglected in morphological investigations of speciose groups of fishes, including the callichthyids. To the extent that morphological variation is continuous across space, time or size, it is unproductive to treat differences as discrete (or necessarily adaptive; Gould, 1984) until one has accounted for the effects of the underlying continuity. Almost all anatomical, physiological, and behavioral traits are size-related in some way (Clutton-Brock and Harvey, 1979). When a change in body size takes place, for neu-

tral or selective reasons, a large number of developmental and morphological relationships will change concomitantly. It is important to ask ecological and evolutionary questions about body size itself (Roff, 1981; Calder, 1983), but if one wishes to examine relationships between features that are inevitably affected by size, it is necessary first to account for its effects and to treat it as a single trait. The presence of allometric scaling may be used as an objective criterion by which to determine whether evolutionary changes in morphology are required correlates of trends

in size variation, or instead possible adaptations to the organisms' modes of life. The null hypothesis of static allometric scaling is not identity of shape, but rather size-correlated difference in shape (Sweet, 1980).

Both mensural and meristic characters in *Corydoras* are highly correlated with body size among species, thus displaying strong static allometry. Because body sizes of these specimens are not necessarily representative of the taxa they represent, and because the ontogenetic development of a large-bodied individual must encompass the entire size range of any smaller taxon, distinctions among species must be robust against such allometric trends.

Expressing morphometric measurements as ratios does not usually remove the scaling effects of body size in the presence of differential allometries. For example, the ratio of snout length to head length is a feature often used in taxonomic keys to the genus (e.g., Gosline, 1940; Nijssen, 1970), but is highly correlated with body length (Fig. 4). If species were to be arbitrarily assigned to one of two categories on the basis of relative snout length above or below a cutoff point of, say, SN/HL = 0.55, the species would be partitioned by standard length at a corresponding length of 45 mm with less than 10% overlap between groups. Thus, relative snout length, measured as a proportion of head length, serves as a proxy for body size and might not have any evolutionary or taxonomic significance in its own right.

It is evident that most of the ratios commonly used in species-level taxonomic descriptions of *Corydoras* do not diagnose taxa. The statistical and biological problems associated with using ratios as "dimensionless" shape descriptors have been described in detail (Pearson, 1897; Atchley et al., 1976; Albrecht, 1978; Atchley, 1978; Atchley and Anderson, 1978; Bookstein et al., 1985). Hence, ratios are best avoided in morphometric studies unless their use has been validated beforehand for a specific problem, which in practice may be more troublesome than proceeding direct-

ly to more informative multivariate procedures using mensural data. The ratios of Table 3 and Figure 5 may be useful for comparative purposes in future taxonomic studies of *Corydoras*, but additional information about magnitudes of ontogenetic and intraspecific variation is needed. Regression coefficients (slopes, intercepts, and corresponding confidence intervals) of logarithmically transformed body measurements would be much more informative than ratios for diagnostic descriptions of species.

Species groups and evolution.—These exploratory analyses have shown that size-free variation in body form seems to be continuous among species, with no apparent morphological gaps with which to distinguish "natural" groupings of species. In particular, four of the five groups proposed by Nijssen and Isbrücker (1980) on the basis of "colour pattern, morphometric, and meristic characters" (Nijssen, 1970) overlap widely in body form and meristics and cannot be discriminated from one another. If these groups are truly informative with respect to qualitative color patterns, then there is little congruence between patterns of pigmentation and size-independent trends of morphological variation. Although Nijssen's "*acutus*" group is distinguishable from the remainder on the basis of a suite of meristic and mensural characters, the species do not have contiguous geographical ranges with respect to the distribution of the genus (Nijssen, 1970:59), and there is little additional evidence that they form a monophyletic group. Scheel et al. (1972) provide some karyotypic and electrophoretic data suggesting that these groups are probably not monophyletic. Thus the distinctiveness of the "*acutus*" groups is most likely the result of convergent evolution.

There is little evidence for other groupings that have been proposed in the past. For example, there seems to be no justification on morphometric grounds for isolating the dwarf taxa (*C. hastatus*, *C. australe*, and *C. pygmaeus*) into a separate genus, as was suggested by Myers (1953). *Corydoras australe* (taxon 13 in Fig. 3) dif-

fers considerably from all other taxa in size-independent form, particularly in its very narrow ventral coracoid separation, but *C. hastatus* (54) and *C. pygmaeus* (97) lie well within the normal patterns of variation for the genus; that is, adults of the two latter species resemble "typical" juveniles of larger species.

Whenever species groups are to be recognized, particularly in the absence of discrete anatomical traits, they should be assessed on the basis of body form rather than body size. This means that: (i) care must be taken not to treat, as biologically meaningful shape differences, attributes that are simply passive allometric consequences of difference in size; and (ii) in order to discover significant differences in "adult" (asymptotic) body size among species, one needs unbiased samples that are truly representative of natural populations.

But even when size-independent variation has been adequately quantified and characterized, by itself it reveals nothing about directions of evolution. In conjunction with an independent hypothesis of phylogenetic relationships, however, such patterns may lead to testable process-oriented hypotheses (Lande, 1982). Because there are so many species of *Corydoras* so closely related, lacking discrete traits and known homologies, it is unlikely that morphology alone will provide much insight into evolutionary relationships. Pigmentation patterns may be of some phylogenetic value once ontogenetic sequences have been described in representative species and putative homologous elements have been identified. The most promising avenue for future phylogenetic work, however, is in the application of cytogenetic techniques. Karyotypic variability in *Corydoras* is among the highest for any genus of fish thus far examined (Gold et al., 1980). Several species have been determined to be chromosomal tetraploids (Hinegardner and Rosen, 1972; Scheel et al., 1972) with reduced duplicate-gene expression (Dunham et al., 1980) and apparently considerable intraspecific variability (B. May, pers. comm.; B. Turner,

pers. comm.). Such a system of directed character-state change, from duplicate gene expression (primitive) to functionally diploid expression (derived), has been fruitfully applied to systematic problems involving other tetraploid fishes (Ferris and Whitt, 1978; Buth, 1979, 1980).

To comprehend the significance of scale-invariant variation among species within a phylogenetic context, it will be necessary to study patterns of ontogenetic allometry and their variability among geographically isolated populations, particularly among different drainage systems. The findings presented here indicate that changes in morphology in *Corydoras* are the result of subtle, perhaps heterochronic changes in relative growth rates among body structures. Under conditions of rapid evolutionary change, and particularly when selection favors differentiation in size apart from morphology, ontogenetic scaling may limit the extent of shape diversity among adults. An adequate assessment of ontogenetic and evolutionary allometry will substantially improve our understanding of *Corydoras* catfishes in particular, and of processes of morphological divergence in general.

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- APPENDIX
- Alphabetical List of Specimens of
Corydoras Included in the Present Study*
- Data from Nijssen and Isbrücker (1980). Synonymies follow Nijssen and Isbrücker (1980) and Nijssen (pers. comm.). The standard length (in millimeters) of each specimen is given, along with species-group abbreviation: ac, acutus; ae, aeneus; ba, barbatus; el, elegans; pu, punctatus.
- (1) *C. acrensis*, 30.0, pu; (2) *C. acutus*, 53.5, ac; (3) *C. aeneus*, 46.6, ae; (4) *C. agassizi*, 47.4, pu; (5) *C. amapaensis*, 56.9, ac; (6) *C. ambiacus*, 43.7, pu; (7) *C. amphibelus*, 27.4, pu; (8) *C. approuaguensis*, 49.4, ae; (9) *C. arcuatus*, 44.6, ae; (10) *C. armatus*, 45.8, pu; (11) *C. atropersonatus*, 38.8, pu; (12) *C. aurofrenatus*, 40.9, ac; (13) *C. australe* (= *hastatus*?), 17.4, el; (14) *C. axelrodi*, 35.9, ae; (15) *C. baderi*, 29.9, ae; (16) *C. barbatus*, 72.3, ba; (17) *C. bicolor*, 25.9, pu; (18) *C. bifasciatus*, 45.6, pu; (19) *C. blochi blochi*, 37.0, ac; (20) *C. blochi vittatus*, 40.9, ac; (21) *C. boehlkei*, 24.1, pu; (22) *C. bolivianus*, 53.1, pu; (23) *C. bondi bondi*, 33.4, ae; (24) *C. bondi coppenamensis*, 35.0, ae; (25) *C. boesemani*, 35.3, ae; (26) *C. carlae*, 41.8, ba; (27) *C. caudimaculatus*, 39.3, pu; (28) *C. cervinus*, 43.9, ac; (29) *C. cochui*, 24.0, ba; (30) *C. concolor*, 42.3, pu; (31) *C. condiscipulus*, 41.5, ae; (32) *C. dubius* (= *trilineatus*), 37.8, pu; (33) *C. ehrhardti*, 42.5, ba; (34) *C. eigenmanni* (= *barbatus*), 37.6, ba; (35) *C. elegans*, 42.8, el; (36) *C. ellisae*, 47.7, ac; (37) *C. ephippifer*, 41.6, pu; (38) *C. episcopi* (= *trilineatus*), 22.3, pu; (39) *C. eques*, 46.6, ae; (40) *C. evelynae*, 40.6, pu; (41) *C. filamentosus*, 31.5, ac; (42) *C. flaveolus*, 33.6, ba; (43) *C. fowleri*, 65.6, ac; (44) *C. funnelli* (= *leopardus*), 49.0, pu; (45) *C. garbei*, 29.3, ba; (46) *C. geryi*, 41.1, pu; (47) *C. gossei*, 49.2, ae; (48) *C. gracilis*, 23.2, el; (49) *C. griseus*, 38.3, ae; (50) *C. guapore*, 33.3, el; (51) *C. guianensis*, 39.0, ae; (52) *C. habrosus*, 20.7, ae; (53) *C. haraldschultzi*, 52.5, pu; (54) *C. hastatus*, 19.0, el; (55) *C. heteromorphus*, 48.1, ae; (56) *C. imitator*, 45.3, ae; (57) *C. julii*, 29.6, pu; (58) *C. juquiaae* (= *nattereri*), 30.5, ba; (59) *C. kronei* (= *barbatus*), 67.2, ba; (60) *C. latus*, 41.5, el; (61) *C. leopardus*, 40.2, pu; (62) *C. leucomelas*, 26.7, pu; (63) *C. macropterus*, 51.5, ba; (64) *C. macrosteus* (= *aeneus*), 44.4, ae; (65) *C. maculifer*, 35.0, ac; (66) *C. marmoratus*, 40.1, ba; (67) *C. melanistius brevirostris*, 33.4, pu; (68) *C. melanistius melanistius*, 35.0, pu; (69) *C. melanotaenia*, 40.9, ae; (70) *C. melini*, 43.4, ae; (71) *C. metae*, 38.0, ae; (72) *C. micracanthus*, 35.9, ba; (73) *C. microcephalus* (= *paleatus*), 38.6, ba; (74) *C. microps* (= *aeneus*), 31.5, ae; (75) *C. multi-maculatus*, 33.1, pu; (76) *C. nanus*, 23.0, el; (77) *C. narcissus*, 64.7, ac; (78) *C. nattereri*, 41.6, ba; (79) *C. nattereri triseriatus* (= *nattereri*), 33.8, ba; (80) *C. octocirrus*, 65.7, ac; (81) *C. oelemariensis* (= *baderi*), 41.1, ae; (82) *C. oia-poquensis*, 38.7, ae; (83) *C. ornatus*, 54.2, pu; (84) *C. orphnopterus*, 57.7, pu; (85) *C. osteocarus*, 30.5, ae; (86) *C. ourastigma*, 60.1, ac; (87) *C. oxyrhynchus*, 47.8, ac; (88) *C. paleatus*, 31.0, ba; (89) *C. panda*, 41.9, ae; (90) *C. pastazensis orcesi*, 55.5, ac; (91) *C. pastazensis pastazensis*, 48.9, ac; (92) *C. polystictus*, 29.4, pu; (93) *C. potaroensis*, 35.9, ae; (94) *C. prionotus*, 51.1, ba; (95) *C. pulcher*, 40.3, pu; (96) *C. punctatus*, 41.8, pu; (97) *C. pygmaeus*, 19.0, el; (98) *C. rabauti*, 45.2, ae; (99) *C. reticulatus*, 30.7, pu; (100) *C. reynoldsi*, 27.3, ae; (101) *C. robustus*, 71.2, pu; (102) *C. sanchesi*, 34.6, ae; (103) *C. saramaccensis*, 51.3, ac; (104) *C. schwartzi*, 34.5, pu; (105) *C. semiaquilus*, 60.1, ac; (106) *C. septentrionalis*, 47.7, ac; (107) *C. simulatus*, 51.0, ac; (108) *C. solox*, 60.6, ac; (109) *C. spilurus*, 46.0, ac; (110) *C. steindachneri*, 40.4, ba; (111) *C. stenocephalus* (= *acutus*), 43.4, ac; (112) *C. sterbai*, 56.4, pu; (113) *C. surinamensis*, 36.6, pu; (114) *C. sychri*, 36.2, pu; (115) *C. treitlii*, 42.8, ac; (116) *C. trilineatus*, 33.7, pu; (117) *C. undulatus*, 43.9, el; (118) *C. venezuelanus* (= *aeneus*), 31.2, ae; (119) *C. virescens* (= *polystictus*), 22.6, pu; (120) *C. weitzmani*, 45.7, ae; (121) *C. wotroi* (= *melanistius*), 26.8, pu; (122) *C. xinguensis*, 32.8, pu; (123) *C. zygatus*, 55.5, ae.