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Author(s): Sharon B. Emerson
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Frog Postcranial Morphology: Identification of a Functional Complex

SHARON B. EMERSON

Three features that have traditionally been treated as independent characters in frog systematic studies belong to a single functional complex. Ilial length, posterior transverse process length and condition of the dorsal crest on the ilium are significantly correlated with degree of sacral expansion. Those frog species with expanded diapophyses have long ilia and short posterior processes. Species which lack sacral expansion have relatively shorter ilia, longer transverse processes and a dorsal crest on the ilium. The correlated characters are part of a functional complex involved with directional movement at the ilio-sacral joint. Expanded diapophyses, long ilia and short transverse processes are associated with pelvic movement in the horizontal plane at the joint in both antero-posterior and lateral directions. Cylindrical diapophyses, short ilia and longer processes are found in frog species that have, predominantly, vertical rotation of the pelvis at the sacrum.

THE uncovering of new morphological characters and the identification of correlated features of a functional complex are two ways that functional morphologists may provide assistance for workers in systematic biology. The potential value of additional characters is selfevident. The importance of identifying component structures of a functional complex is that without knowledge of function such features might be treated as independent characters. There are, however, few cases to date where functional studies have actually fulfilled these potential roles, and thus examples illustrating the interface between functional morphology and systematics are noteworthy (Liem and Greenwood, 1981). The purpose of this paper is to provide such as example, drawn from a functional analysis of the ilio-sacral articulation of frogs.

The ilio-sacral joint morphology of frogs has been found to display three complex morphological patterns (Whiting, 1961; Emerson, 1979). One type is characterized by an external ligament with no insertion on the sacrum, running from ilium to ilium superficial to the dorsal back musculature (Type I, Emerson, 1979), and a second by an internal ligament originating on the anterior portion of the ilium and inserting directly on the sacral diapophysis (Type II, Emerson, 1979). Furthermore, there are two subgroups of frogs with an internal ligament attachment. One has a narrow, short, internal ligament which attaches on the distal aspect of the sacral diapophysis (Type IIB), and the other a broad, long internal ligament which attaches near the midline of the sacrum (Type IIA).

In addition to ligament shape and attachment site, the three articulations (one with an external ligament, two with internal ligaments) are differentiated by the shape of the articular sesamoids, the origin and insertion sites of the ilio-lumbaris muscle and degree of sacral expansion (Figs. 1–3). A biomechanical analysis of this region reveals that each articulation is correlated with a difference in direction of movement at the ilio-sacral joint, and that these differences are important in locomotor behavior (Emerson, 1979; Emerson and DeJongh, 1980).

This paper presents data that identify three additional aspects of postcranial morphology as belonging to the ilio-sacral functional complex: relative length of the ilia, relative lengths of the posterior transverse processes and condition of the dorsal crest on the ilium. These three features have traditionally been treated as independent characters in anuran systematic studies (Lynch, 1971; Inger, 1972; Heyer, 1975). That these characters are not independent, but rather part of a single ilio-sacral functional complex, may be demonstrated by the fact that the morphological characters are significantly correlated with each other, and the characters interact biomechanically within a single system.

MATERIALS AND METHODS

Forty-one species representing 36 genera from 15 families were selected for study (Table 1). Fourteen species from seven families possess

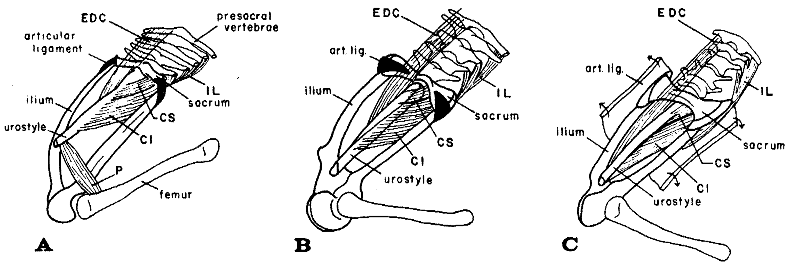

Fig. 1. Diagrammatic representations of the three ilio-sacral articulation patterns. A) Type IIB. B) Type IIA. C) Type I. The ligaments are shown in black. Abbreviations: IL—ilio-lumbaris muscle, CS—coccygeo-sacralis muscle, CI—coccygeo-illacus muscle, P—pyriformis muscle, EDC—extensor digitorum communis muscle (from Emerson and DeJongh, 1980).

a type I articulation pattern; fifteen species from seven families have a type IIA pattern, and 12 species from six families have the IIB type. These particular species were chosen because their articulation type could be confirmed by dissection of preserved (alcohol) specimens, the degree of sacral expansion could be accurately measured (see below), and because the species encompassed a wide diversity of frog morphology and locomotor types. All measurements except degree of sacral expansion were taken from skeletal material. Measurements were obtained to the nearest tenth of a millimeter with dial calipers. The following measurements were taken on each specimen: snout–vent length, length of right ilium, anterior inter-ilial width, length of the last presacral transverse processes (Zug, 1972; Trueb, 1977, provide definitions and illustrations of these standard measurements). Dorsal crest of the ilium was simply recorded as present or absent.

The lateral borders of most frog sacral diapophyses are cartilaginous, and these cartilages are usually lost when specimens are skeletonized. Measurements of sacral expansion taken from only the bony part of the diapophysis of dried skeletons are insufficient to characterize sacral morphology because both the cartilage and the bony part of the sacrum determine the total degree of sacral expansion (Emerson, 1979:Fig. 9). To include the cartilages in the measurement of sacral expansion, camera lucida drawings were made of the right sacral diapophyses of dissected, preserved specimens and the angle of expansion was measured (in degrees) from the drawings with a protractor. (The preserved specimens were selected such that their snout–vent lengths were the same as those of the dried skeletons used for the other measurements.)

Estimates of intraspecific variation for the angle measurement show coefficients of variation between 5 and 10 in three species (Emerson, 1979 and unpubl. data). Measurements of sacral expansion taken from the bony part of the sacrum showed intraspecific coefficients of variation between 10 and 15 in males and females of *Hyla lanciformis* (Trueb, 1977).

The species under study ranged in adult snout–vent length from 20 to 200 millimeters. The original measurements were, therefore, transformed to correct for the potentially confounding affects of allometry and size related variation. This was accomplished as follows. Ilial length, transverse process length and snout–vent length were transformed to logarithms (base 10), and for each of the three articulation type groups, $\log_{10}$ ilial length and $\log_{10}$ transverse process length were regressed against $\log_{10}$ snout–vent length. For both ilial length and transverse process length, the slopes of the three groups were within 95% confidence limits of each other, and the mean of the three slopes was used for the slope of a 'master equation' for each variable. The y-intercept for each master equation was calculated from the mean log y and mean log x of the articulation type I group. For each of the 41 species, in the total sample, $\log_{10}$ snout–vent length was inserted into the two master equations to calculate an expected $\log_{10}$ ilial length and $\log_{10}$ transverse process length. The expected values were subtracted from the actual $\log_{10}$ values to yield log transformed residuals which were then antilogged to give the transforms used in this paper (Table 1). Subsequent use of the word 'trans-

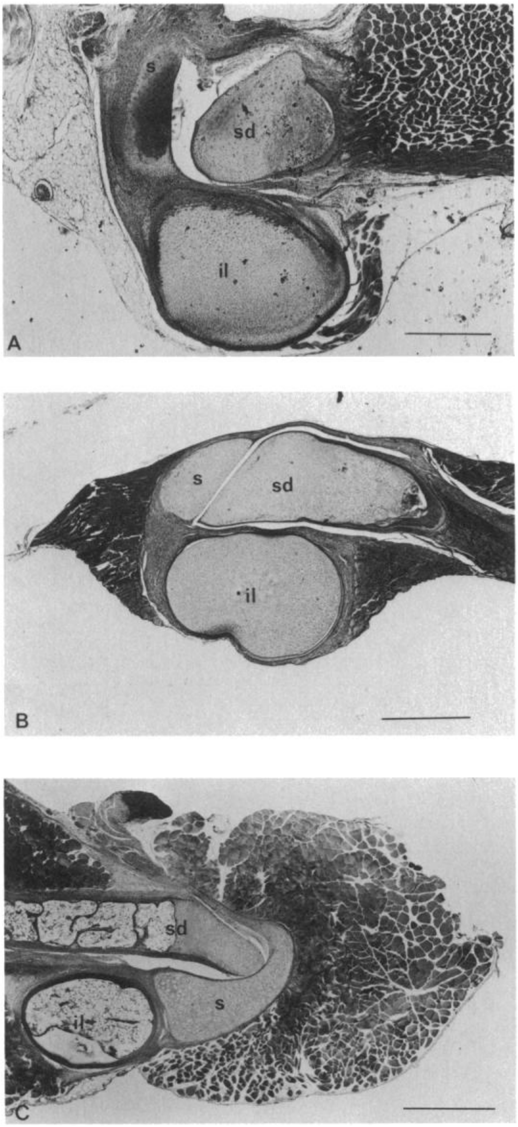

Fig. 2. Cross sections at the sacral diapophyses to illustrate the variation in sesamoid morphology. A) histological cross section of the left sacral diapophysis of a type IIB articulation pattern. B) histological cross section of the left sacral diapophysis of a type IIA articulation pattern. C) histological cross section of the right sacral diapophysis of a type I articulation pattern. Abbreviations: il—ilium, sd—sacral diapophysis, s—sesamoid. Bar = 1 mm.

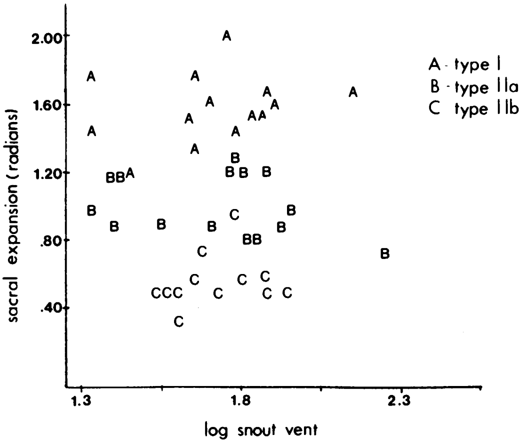

Fig. 3. A graphical representation of the relationship between sacral expansion (measured in radians) and snout–vent length for 41 species of frogs.

form' in this paper refers to data that have been treated by this procedure. These transforms are a measure of relative length (i.e., actual length compared to expected length from the master equation) of the ilium and the transverse processes, but are not ratios as commonly used. This use of residuals is similar to an analysis of covariance in which log snout–vent length is used as the covariate, and it is a common approach used for comparing morphological variables in animals of different size (Bauchot and Stephan, 1966; Jerison, 1973; Emerson, and Radinsky, 1980).

Sample sizes larger than one are uncommon for many species in osteological collections, and data for each species in this study are from a single adult individual.

It is therefore important to examine the consequences of using a sample in which each species is represented by a single specimen. The use of such a sample for inferences about interspecific variation is predicated on the assumption that the component of parametric variance between species means is much greater that the variance within species. In general, the observed variance among species (i.e., among species means) estimates the variance within species, σ^2, plus the product of the true variance among species means, $\sigma_A{}^2$, and the number of individuals sampled per species [or if these are unequal, the corrected average number per species (Sokal and Rolf, 1969:Chapter 8)]. In the present case the sample per species

TABLE 1. TRANSFORMED VARIABLES FROM 41 SPECIES.

Species	Articulation type	Sacral angle (radians)	Ilial length transform*	Transverse process length transform**
Pipidae				
Xenopus laevis	I	1.69	1.0973	0.8269
Pipa pipa	I	1.70	1.0307	0.9230
Ascaphidae				
Ascaphus truei	IIB	0.35	0.6691	0.8562
Discoglossidae				
Bombina orientalis	I	1.29	0.9995	0.8416
Discoglossus pictus	IIA	0.79	1.0020	0.9073
Pelobatidae				
Pelobates fuscus	I	2.01	0.9188	0.7754
Scaphiopus couchii	I	1.40	1.0663	0.8303
Megophrys monticola	I	1.57	1.0119	1.7872
Bufonidae				
Bufo boreas	IIA	0.87	0.9544	1.1204
Bufo blombergi	IIA	0.70	0.8659	1.7312
Bufo calamita	IIA	1.22	0.9283	0.9487
Bufo americanus	IIA	0.80	0.9690	1.2287
Atelopus varius	IIA	0.87	1.0615	2.1373
Melanophryniscus stelzneri	IIA	0.96	0.8628	1.0509
Oreophrynella quelchii	I	1.40	0.8475	1.4771
Mybatrachidae				
Notoden bennetti	IIA	1.22	1.1038	0.8515
Kankanophryne occidentalis	IIA	1.22	0.9412	0.8512
Leptodactylidae				
Physalaemus pustulosus	IIA	1.22	1.1030	1.0983
Leptodactylus melanonotus	IIB	0.45	0.8428	1.5376
Eleutherodactylus rhodopis	IIB	0.45	0.9447	1.6224
Telmatobius marmoratus	IIB	0.49	0.8136	1.2072
Rhinophrynidae				
Rhinophrynus dorsalis	IIA	1.22	1.0804	0.7655
Rhinodermatidae				
Rhinoderma darwinii	I	1.22	0.9592	1.3718
Hylidae				
Pseudacris triseriata	IIA	0.87	0.8999	0.9168
Hyla cinerea	I	1.57	1.0278	0.8898
Phrynohyas venulosa	IIA	0.96	0.9829	0.7565
Agalychnis callidryas	I	1.48	0.9960	1.1057
Pachymedusa dacnicolor	I	1.48	0.9217	1.2789
Dendrobatidae				
Dendrobates tinctorius	IIB	0.52	1.0234	1.8580
Ranidae				
Rana clamitans	IIB	0.44	0.9284	1.2151
Rhacophoridae				
Polypedates leucomystax	IIB	0.52	0.8933	1.1484
Rhacophorus pardalis	IIB	0.52	0.8813	1.2784
Chiromantis rufescens	IIB	0.44	0.9016	0.9898

TABLE 1. CONTINUED.

Species	Articulation type	Sacral angle (radians)	Ilial length transform*	Transverse process length transform**
Hyperolidae				
Hyperolius marmoratus	IIB	0.44	0.9698	0.8929
Leptopelis aubryi	IIB	0.70	0.9229	1.2465
Leptopelis bocagii	IIB	0.96	0.9085	1.2791
Kassina senegalensis	IIA	0.87	0.9013	0.8289
Microhylidae				
Kaloula pulchra	I	1.48	0.9758	0.8400
Hypopachus muelleri	IIA	1.31	1.0039	0.7951
Gastrophryne carolinensis	I	1.75	1.1674	0.8407
Phrynomerus bifasciata	I	1.75	1.0232	0.7520

* Ilial transform equation: $\log y = 1.0476 \log x - 0.4864$.
** Transverse process transform equation: $\log y = 1.0947 \log x - 1.0688$.

is one so the observed variance between specimens estimates $\sigma^2 + \sigma_A^2$. The transform data indicate that the variance between species, σ_A^2, is much greater than the variance within species, σ^2. This can be seen by comparing the variance in a sample of 12 adult *Bufo valliceps* (six males and six females) with the variance among the total sample of 41 specimens (representing 41 species). In the *B. valliceps* sample there was no significant sexual dimorphism in any of the characters. Using the sample to estimate the average variance within species, σ^2, the total variance among species is found to be 4–40 times greater (Table 2). Thus the total sample, even though each species is represented by a single specimen, will give a reasonable approximation of interspecific variance. Furthermore because this sample is drawn from a diverse array of families, it may be reasonably free from taxonomic bias.

Repeatability of measurements was assessed by twice remeasuring four skeletons of *Rana pipiens* over a month's time. A one way analysis of variance on these measurements gave intraclass correlation coefficient values of 0.9942 for ilial length and 0.998 for length of the transverse processes. Intraclass correlation coefficients are a measure of repeatability with values

TABLE 2. TRANSFORM VARIATION AND MEAN VALUES.

	Mean value	Variance	F
I. Intraspecific transform variation (*Bufo valliceps*) (N = 12)			
a. Ilial length	0.9429	0.0013	
b. Transverse process length	1.4226	0.0018	
II. Interspecific transform variation			
a. Type I (N = 14)			
i. Ilial length	1.0031	0.0063	4.84
ii. Transverse process length	0.9810	0.0595	33.43
b. Type IIA (N = 15)			
i. Ilial length	0.9774	0.0066	5.04
ii. Transverse process length	0.9323	0.0222	12.47
c. Type IIV (N = 12)			
i. Ilial length	0.8916	0.0079	6.04
ii. Transverse process length	1.2067	0.0566	31.81
d. Pooled data (N = 41)			
i. Ilial length	0.9611	0.0087	6.69
ii. Transverse process length	1.1137	0.1183	65.14

TABLE 3. CORRELATION COEFFICIENTS.

	Ilial transform	T. process transform
I. Pooled data (41 species)		
a. Transformed variable correlation		
Sacral angle	.548***	−.356**
b. Partial correlation (untransformed data)		
^{r}(sacral angle) (ilium) (snout–vent length) = .559***		
^{r}(sacral angle) (t. process) (snout–vent length) = −.393**		

	Ilial transform	T. process transform	Ilial width transform
II. Intra-articulation type correlation coefficients			
a. Type I			
i. Sacral angle	.247	−.408	.764***
ii. Ilial transform	—	−.444	—
b. Type IIA			
i. Sacral angle	.491*	−.494*	.790***
ii. Ilial index	—	−.020	—
c. Type IIB			
i. Sacral angle	.273	.165	−.009
ii. Ilial index	—	.502*	—

* = $P < .05$.
** = $P < .01$.
*** = $P < .001$.

close to one indicating highly repeatable measurements (Falconer, 1960).

A common problem with osteological material is that parts of the skeleton are often disarticulated. In some cases, it was necessary to 'reconstruct' the skeleton in order to measure snout–vent length. To assess the accuracy of such reconstruction, a study was undertaken with six preserved specimens of *Rana pipiens*. The snout–vent length was measured for each individual and then skeletons were prepared by the use of a dermestid colony. The disarticulated skeletons were then reconstructed twice, snout–vent lengths measured and the values compared with those obtained from the original measurement. A one way analysis of variance gave an intraclass correlation coefficient of 0.9204, indicating that the measurements were highly repeatable.

Degree of sacral expansion was used to represent the ilio-sacral articulation types. Fig. 3 illustrates the relationship between sacral expansion and articulation type for the 41 species. This measurement separates the three articulation types and is the only continuously variable component of the ilio-sacral functional complex. The characters of ligament position, origin and insertion of the ilio-lumbaris muscle and shape of the articular sesamoids do not lend themselves so easily to quantification.

Degree of association of characters was determined both by calculating correlation coefficients between sacral angle and the transformed variables of ilial length and transverse process length and by the use of partial correlations where size was held constant. In the latter case, correlation coefficients were calculated from the raw data. Correlation coefficients were initially calculated on the pooled data from the forty-one species to establish which aspects of postcranial morphology were part of the ilio-sacral functional complex. Secondly, correlation coefficients were calculated between morphological variables from species of each ilio-sacral articulation type. *T*-tests were used to test for differences in transformed variables among the three articulation types.

RESULTS

In the total sample of 41 species there is a significant positive correlation between degree of sacral expansion and relative length of the ilium, and a significant negative correlation between degree of sacral expansion and relative length of the posterior presacral transverse processes (Table 3). A dorsal crest on the ilium occurs only in those species with a type IIB articulation pattern.

Within any articulation type, the situation is more complicated (Table 3). For type I species, there is an inverse relationship between the relative length of the ilia and the relative length of the transverse processes, but no significant correlation between sacral angle and relative ilial length or sacral angle and relative transverse process length. Species with a type IIA articulation pattern show a significant negative correlation between sacral angle and relative length of the transverse processes. There is, however, no significant correlation between relative ilial length and relative transverse process length. For Type IIB species, there is no significant correlation between sacral angle and relative length of the ilia or relative length of the transverse processes.

T-tests show no significant differences (95% level) in relative length of the ilia or relative

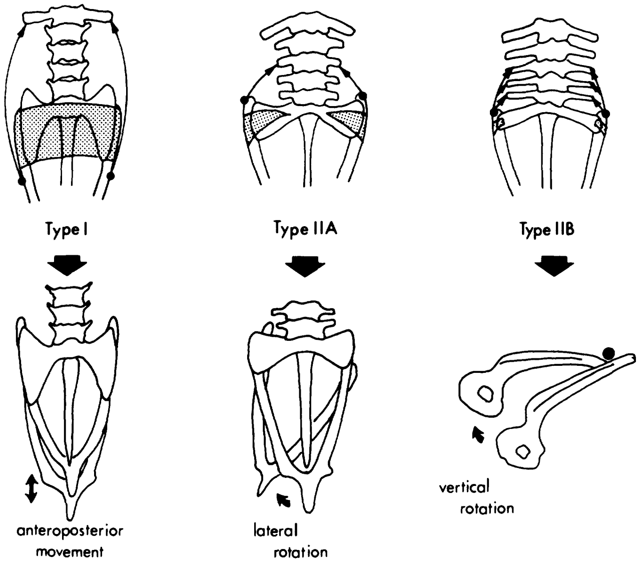

Fig. 4. A diagrammatic representation of the relationship between ilio-sacral articulation type and preferred movement at the joint during locomotion. The dark arrows show the origin and insertion of the ilio-lumbaris muscle. The stippling represents the different ligament patterns.

length of posterior transverse processes between type I and type IIA articulation species. But, relative ilial length and relative transverse process length in type IIB species are significantly different from those of both type I and type IIA. Articulation types I and IIA have relatively longer ilia and shorter presacral transverse processes than articulation type IIB (Table 2), and the differences are significant.

Discussion

Biomechanical analysis.—Correlated morphological characters do not, necessarily, belong to a single functional complex (Inger, 1972). For example, high crowned teeth and elongate distal leg segments are correlated features among ungulate mammals. Yet, they are components of two distinct functional complexes: one involved in feeding and the other in locomotion. For this reason, it is necessary to demonstrate that the correlated morphological characters interact biomechanically if they are to be considered to be part of a single functional complex.

Cineradiographic and electromyographic analyses show that degree of sacral expansion, sesamoid shape and size, articular ligament shape and size and origin and insertion of the ilio-lumbaris muscle determine the type of directional movement at the ilio-sacral joint of a frog (Emerson, 1979; Emerson and DeJongh, 1980). Diagrammatic representations of the morphology of the three articulation types, and the predominant directional movement for each structure during various types of locomotion illustrate the link between ilial length, posterior presacral transverse process length and presence/absence of the dorsal crest of the ilium to the other characters of the ilio-sacral functional complex (Fig. 4).

As shown in Fig. 1, articulation type I species are characterized by a broad cuff-like ligament running from ilium to ilium, anteroposterior elongate, expanded sacral diapophyses, a hook shaped articular sesamoid and an ilio-lumbaris muscle which originates one third the distance down the ilium and inserts on the transverse processes of presacral vertebrae 4–6. This sliding joint produces considerable movement in the horizontal plane, but restricted vertical rotation. The greatest degree of movement is in the antero-posterior direction during swimming (with up to a 20% change in body length), but during walking, some lateral rotation also occurs (Emerson, 1979).

During swimming, the ilia slide antero-posteriorly along the track formed by the expanded, ventrally inclined sacral diapophyses (Emerson, 1979; Emerson and DeJongh, 1980).

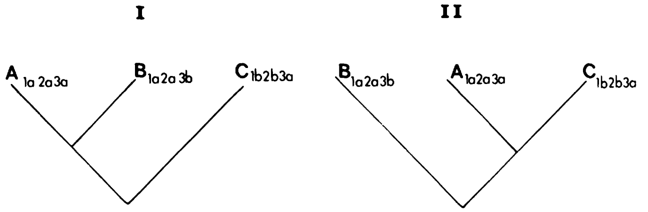

Fig. 5. Two alternative cladograms of relationship for three taxa, A, B and C, based on shared derived character states from three characters.

The results of the present study indicate that species of articulation type I have relatively long ilia, relatively short posterior presacral transverse processes and lack a dorsal crest on the ilium. Long ilia increase the potential distance of movement in the antero-posterior direction. Shortened transverse processes on the posterior presacral vertebrae prevent physical interference with the forward moving ilia.

Articulation type IIA species have a broad ligament inserting on the medial aspect of the sacral diapophysis, a wedge shaped sesamoid, and an ilio-lumbaris muscle which originates on the antero-lateral aspect of the ilium and inserts on the transverse processes of presacral vertebrae 4–7. This arrangement also forms a sliding joint, but, in this case, the predominant direction of movement is lateral rotation in the horizontal plane (Emerson, 1979; Emerson and DeJongh, 1980). Species with articulation type IIA generally use walking, hopping and burrowing locomotions.

During walking, there is an asynchronous contraction of the ilio-lumbaris muscles causing lateral rotation of the pelvic girdle relative to the sacrum and vertebral flexure of the presacral column. The lateral edges of the arc shaped diapophyses act as guides for the rotating ilia. Species with this articulation type have relatively long ilia, relatively short posterior transverse processes and lack a dorsal crest. Longer ilia increase the potential degree of lateral rotation, and, as is the case for articulation type I, the shorter posterior transverse processes preclude interference of the processes with the rotating ilia. Unlike the situation of articulation type I, the length of the transverse processes in articulation type IIA must change regularly with increases in sacral expansion to prevent physical interference (Fig. 4).

Type IIB species are characterized by short ligaments inserting on the distal edges of cylindrical, non-expanded sacral diapophyses, oval shaped articular sesamoids and an ilio-lumbaris muscle which originates on the antero-lateral aspect of the ilium and inserts on the transverse processes of every presacral vertebra. This morphology forms a rotating joint restricting movement in the horizontal plane, but maximizing vertical rotation. Type IIB species are jumpers and do not use walking locomotion.

During jump takeoff the contraction of the coccygeo-iliacus muscle produces a counterclockwise rotation of the presacral vertebral column on the pelvic girdle (Emerson and DeJongh, 1980). This vertical rotation results in an alignment of the anterior part of the frog's body along the long axis of the pelvic girdle, paralleling the direction of propulsive force. The force of contraction of the coccygeo-iliacus muscles shows a significant positive correlation with jump height, and degree of vertical rotation and jump performance are also positively correlated (Whiting, 1961; Emerson and DeJongh, 1980). All species with articulation IIB show the presence of a dorsal crest on the ilium. The presence of this crest is correlated with increased size (measured as cross sectional area) of the coccygeo-iliacus muscle (Emerson and DeJongh, 1980). Type IIB species have relatively shorter ilia and relatively longer transverse processes than species of articulation types I and IIA. There is no movement in the horizontal plane with this morphology. Physical interference between the transverse processes and ilia is not a problem.

Complexity of morphological patterns.—The biomechanical analysis identifies the correlated characters as belonging to a single functional complex. However, the present study shows that the relationships among those morphological characters are complex. Among the frog species studied, relative lengths of the ilia and transverse processes are significantly correlated with sacral angle, but the correlation coefficients are relatively low (Table 3). Second, the intensity of relationship between the variables varies according to each articulation type (Table 3). By including species from a large number of families the probability that the character associations are the result of only phylogenetic proximity has been minimized. This approach does introduce complications, however, as species of different families are likely, for historical reasons, to show different patterns of variation in the morphological characters. The relatively low correlation coefficients and their variability among articulation types may be a reflection of both functional and historical influences.

In general, an increase in sacral expansion is correlated with a decrease in the relative length of the posterior presacral transverse processes. The functional explanation for this relationship is that the lateral rotation and antero-posterior movement in the horizontal plane of the pelvic girdle in species with expanded sacral diapophyses (articulation types I and IIA) could not occur if the processes were not shorter than the distance between the anterior tips of the ilia. Two predictions of correlation within articulation types follow from the biomechanical analysis: 1) there should be a higher correlation between relative ilial width and relative transverse process length in articulation I and IIA species (those types with movement in the horizontal plane) than in type IIB species, and 2) articulation type IIA species should show the highest correlation between relative transverse process length and sacral expansion because only with lateral rotation would the precise length of the transverse processes in relation to degree of sacral expansion be functionally important. With anterior-posterior movement and elongate sacral diapophyses (Type I) it is only necessary for the processes to be shorter than the width of the ilia (Fig. 4), and, obviously, with vertical rotation (as in species of type IIB) interference in the horizontal plane is not a problem at all. Examination of Table 3 shows that both predictions regarding intra-articulation type correlation are supported. Relative ilial width and relative length of the transverse processes are significantly correlated in species of both articulation types I and IIA, but not among species of type IIB. Only in species of articulation type IIA is there a significant (negative) correlation between sacral expansion and the relative length of the processes.

In this example, one has the following situation from a functional perspective: in articulation type IIB length of the transverse processes is not significant in relation to girdle rotation; in articulation type I the processes must be shorter than a certain length, (i.e., distance between the anterior tips of the ilia), and in type IIA precise length of the transverse processes is important. In other words, transverse process length may vary independent of functional constraints among species of type IIB, partially independent among type I species, and not at all independent among type IIA species. And the degree to which the morphological character is subject to functional constraints may influence the expression of variation due to other causes, such as historical relationships.

The morphological characters are not uniquely grouped by articulation type. For example most species of type IIB have narrow sacral diapophyses, but one species, *Leptopelis bocagei,* has relatively expanded sacral diapophyses. While most type IIA species have relatively short transverse processes, *Atelopus varius* (IIA) has relatively long transverse processes. *Dendrobates tinctorius* (IIB) has relatively long ilia compared to other species of type IIB. These exceptions to the general distribution of characters are correlated with differences in locomotion for these species relative to the typical locomotor behaviors found in the other species of each articulation type. *Leptopelis bocagei* is a burrower whereas articulation IIB species are generally jumpers (Table 1). *Dendrobates* is a hopper instead of a jumper, and covers a shorter distance per effort than other type IIB species of similar size (Zug, 1978). *Atelopus* is a long legged, stiff backed walker in contrast to most IIA species which are short legged flexed back hoppers.

Significance for systematics.—Discussions regarding the role of functional morphology in systematics often involve simple examples, such as two alternative cladograms, with the question: "How does knowledge of the functional significance of the characters give useful information for choosing between these two hypotheses?" Such an example is presented in Fig. 5 for three characters, each of which has two character states. For all characters, "a" represents the derived condition. In this example, following the rule of parsimony, alternative one would be selected as most probable because it assumes fewer cases of convergence than alternative two. If, however, characters one and two were found to be part of a single functional complex and significantly correlated with each other, the situation would no longer involve such a clear choice.

An actual example of this situation is provided by data from Lynch's (1973) study on the relationships of frog families. The case involves five families, the Leptodactylidae (exclusive of Telmatobinii), Dendrobatidae, Pseudidae, Hylidae and Centrolenidae, and four characters: atlantal intercondylar distance (this character #5), sacral expansion (#6), length of the posterior transverse processes (#9), and condition of the intercalary cartilage (#16). All four characters were assumed by Lynch to be independent.

The Dendrobatidae, Leptodactylidae and Pseudidae share derived character states for 5, 6 and 9. The Hylidae and Centrolenidae share derived character states for 5 and 9 with these groups, but not character state 6. (Lynch defined his character states for transverse process length differently than I have in this paper. As a result, 9 can occur independently of 6, but 6 cannot occur independently of 9. This complication does not, however, alter the basic point that I am making.) The hypothesis of relationship from this distribution of shared, derived character states would show the Pseudidae, Leptodactylidae, and Dendrobatidae as most closely related. However, the Pseudidae, Hylidae and Centrolenidae also share three derived character states, in this case: 5, 9 and 16, while the Dendrobatidae and Leptodactylidae share derived character states for 5 and 9 but not 16 with the other three groups. From these data, an alternative hypothesis could be constructed, placing the Pseudidae with the Hylidae and Centrolenidae. These alternative hypotheses are based on the same number of shared derived character states among groups, and are, therefore, equally probable under the rule of parsimony. At this point, the correlation between character 6 and 9 becomes pertinent as it reduces the number of shared derived character states in the first hypothesis to those from two independent characters and therefore provides information for choosing a more probable cladogram (that grouping the Pseudidae with the Hylidae and Centrolenidae). If this simple example were extended to a case involving all seven correlated characters of the ilio-sacral functional complex it is easy to image that given alternative hypotheses of relatedness based on seven shared character states versus one, if there were no knowledge of function and through it character association, most workers would choose the first alternative because it has the highest number of shared, derived character states.

SUMMARY

This study shows how functional analysis may provide insights into the identification of characters belonging to a single functional complex. Sacral expansion, presence/absence of a dorsal crest on the ilium, relative ilial length and relative transverse process length have been treated as independent characters in studies of frog systematics. However they do not vary independently among frogs but rather are correlated in three modes related to differences in movement at the ilio-sacral joint.

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Department of Biological Sciences, Box 4348, University of Illinois at Chicago Circle, Chicago, Illinois 60680. Accepted 30 July 1981.

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Rediscovery of *Anisotremus moricandi* (Perciformes: Haemulidae), Including a Redescription of the Species and Comments on its Ecology and Distribution

Arturo Acero P. and Jaime Garzón F.

The third western Atlantic species of *Anisotremus*, last reported in 1925 from Panamá, was rediscovered on the Caribbean coast of Colombia. New information has led us to its redescription as *A. moricandi* (Ranzani). Ecology and distribution of the species are discussed. It differs from its two western Atlantic congeners mainly in the presence of six narrow white stripes on the brown background of its body and a dark blotch on the sides of the caudal peduncle; furthermore it has more pored lateral line scales (56–58). *A. moricandi* seems to have rather restricted ecological preferences, as so far it has only been observed in turbid waters around shallow rocky reefs. The species is now known from Panamá, Colombia and Brasil. *A. moricandi* is the smallest species of its genus, and its distinctive color pattern results from the retention of the juvenile pattern.

THE Haemulidae (=Pomadasyidae auctorum) was recently reviewed for the western central Atlantic by Courtenay and Sahlman (1978) who recorded 22 species in 6 genera. *Anisotremus* was said to include 2 Atlantic species [*A. surinamensis* (Bloch) and *A. virginicus* (Linnaeus)], in agreement with earlier authors (Cervigón, 1966; Böhlke and Chaplin, 1968; Randall, 1968). In the course of studies on the reef fauna in the Colombian Caribbean, we noted a third species of the genus. A review of the older literature had led us to identify this species as *Anisotremus moricandi* (Ranzani), which was last reported by Meek and Hildebrand (1925) as *A. bicolor.*

Herein we redescribe the species, discuss some aspects of its biology, and compare it with its western Atlantic congeners. Counts and measurements are as defined by Courtenay (1961). The specimens examined are deposited in the fish collections of the Instituto de Investigaciones Marinas de Punta de Betín (INVEMAR-P), Santa Marta, Colombia; the University of Miami, School of Marine and