ERRATA

Torres-Carvajal, O. 2004. The abdominal skeleton of tropidurid lizards (Squamata: Tropiduridae). Herpetologica 60:75–83.

Page 78. Replace the following names in Table 1: 1. Stenocercus arenarius formosus 2. Stenocercus trieristatus prionotus

THE ABDOMINAL SKELETON OF TROPIDURID LIZARDS (SQUAMATA: TROPIDURIDAE)

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ABSTRACT: Morphological variation in the abdominal skeleton of Tropiduridae was examined from radiographs and cleared-and-stained specimens of 61 species. Based on the numbers of xiphisternal and postxiphisternal inscriptional ribs, as well as the presence of inscriptional ribs articulating ventromedially, seven patterns of rib attachment are described. The distribution of these patterns among the species studied reveals intra- and interspecific variation, which indicates that the abdominal skeleton of lizards is a good source of fixed and polymorphic characters for phylogenetic analyses.

Key words: Abdominal skeleton; Iguania; Morphological variation; Tropiduridae

WITH approximately 100 species, Tropiduridae is one of the most speciose families of neotropical reptiles. Several high-level taxonomic arrangements for iguanian lizards have been proposed during the last 15 yr (Frost and Etheridge, 1989; Frost et al., 2001a; Macey et al., 1997). Herein, I follow Frost et al. (2001a) and recognize the taxon name Tropiduridae. This family includes two primary clades—Tropidurinae and the Stenocercus group (Frost et al., 2001a). Several studies using both morphological and molecular characters have investigated phylogenetic relationships among species of Tropidurinae (Frost, 1992; Frost et al., 2001b; Harvey and Gutberlet, 2000). In contrast, phylogenetic relationships among members of the Stenocercus group have not been resolved, and monophyly of this group remains questionable.

The abdominal skeleton of lizards is composed of inscriptional ribs, which are endochondral elements that originate within the myocommata of the abdominal musculature (Etheridge, 1965). Several names have been used in reference to these cartilaginous elements (e.g., abdominal ribs, parasternum, parasternalia, gastralia, inscriptional ribs; Etheridge, 1965), which articulate with corresponding dorsal bony ribs to form the xiphisternal and anterior postxiphisternal ribs (Fig.

Inscriptional ribs are present in most lizards and extant rhynchocephalians (Etheridge, 1965; Etheridge and de Queiroz, 1988; Hoffstetter and Gasc, 1969). However, patterns of morphological variation of these endochondral elements are poorly known for many subclades. Etheridge (1959) reported some variation in the abdominal skeletons of lizards, especially polychrotids. He also described intraspecific and interspecific variation of xiphisternal ribs in *Sceloporus* (= *Sator*) grandaevus (Etheridge, 1962) and other sceloporine phrynosomatids (Etheridge, 1964).

^{1).} The xiphisternal inscriptional ribs (XIRs) lie posterior to the sternal ribs (i.e., ribs that articulate with lateral margins of sternum) and their distal ends fuse with the xiphisternum, which is composed of paired longitudinal cartilaginous rods that articulate with the posterior margin of the sternum (Etheridge and de Queiroz, 1988). The numbers of sternal and xiphisternal ribs are variable in lizards, but the most frequent condition is three sternal ribs and two xiphisternal ribs (3:2; Hoffstetter and Gase, 1969). All postxiphisternal inscriptional ribs (PIRs) are presacral cartilaginous ribs that are embedded in the abdominal musculature posterior to the xiphisternum, and they may, or may not, articulate with the corresponding dorsal bony ribs. Furthermore, members of one or more pairs of PIRs may articulate medially with each other, forming continuous chevrons.

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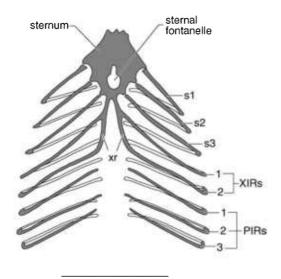


FIG. 1.—Ventral view of sternum, sternal ribs, and inscriptional ribs of a juvenile *Stenocercus guentheri* (KU 147347, SVL = 30 mm). Abbreviations: PIRs, postxiphisternal inscriptional ribs; s, sternal ribs; XIRs, xiphisternal inscriptional ribs; xr, xiphisternal longitudinal rods. Cartilage is indicated in grey. Scale bar = 5 mm.

Similarly, de Queiroz (1987) examined intergeneric variation in the abdominal skeleton of iguanine lizards. After examination of several genera of Iguania, Etheridge (1965) defined four patterns of attachment of inscriptional ribs, but later Etheridge and de Queiroz (1988) grouped previously described patterns into two character states.

In several genera of tropidurid lizards, Etheridge (1965) reported (without referring to species) two patterns of attachment of inscriptional ribs corresponding to the first and second patterns recognized by Etheridge and de Queiroz (1988). In one pattern, pairs of PIRs are not continuous midventrally and each PIR attaches to its corresponding dorsal rib; this condition occurs in *Tropidurus*, *Urano*scodon, Plica, Stenocercus (including Proctotretus and Ophryoessoides), and Uracentron. The second pattern, also observed in Ophryoessoides, differs from the first one only in that members of one or two pairs of PIRs articulate with one another midventrally (forming chevrons). In an attempt to determine whether characters of the abdominal skeleton in lizards are phylogenetically informative within Tropiduridae, I analyzed interspecific variation in numbers and morphology of XIRs and PIRs in that taxon, as well as intraspecific variation in *Stenocercus* guentheri.

MATERIALS AND METHODS

Data for 61 species of Tropiduridae (>50% of the currently recognized species) were obtained from 226 specimens (Appendix I), of which 90 were cleared-and-double-stained following the methodology of Taylor and van Dyke (1985) and Wassersug (1976), and 62 were x-rayed. Institutional abbreviations are listed in Leviton et al. (1985), except for Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ). The radiographs were taken with a FTI Corporation Unit at 5 mA and 50 kV for 40-50 s using Kodak's Industrex SR-1 film. Inscriptional ribs could be seen only in radiographs of specimens >39 mm in snout-vent length (SVL). Data from the remaining 74 specimens were taken from x-ray radiographs provided by Richard Etheridge. Intraspecific variation in the abdominal skeleton was assessed in 45 specimens of S. guentheri, 30-88 mm SVL. Even though size does not always provide an accurate estimate of age in reptiles (Andrews, 1982), it was the only available criterion to determine whether or not ontogenetic variation in the abdominal skeleton exists in this species. Descriptions and illustrations were prepared with the aid of a stereomicroscope equipped with a camera lucida. Measurements were made either with a ruler and recorded to the nearest 1 mm or they were taken from museum collection data. I follow the terminology of Etheridge (1965) for elements of the abdominal skeleton.

RESULTS

Seven patterns of attachment of inscriptional ribs are recognized (Fig. 2). The main criteria for establishing the patterns were: (1) numbers of xiphisternal and postxiphisternal pairs of inscriptional ribs and (2) the presence or absence of chevrons (i.e., PIRs articulating medially). Relative lengths of PIRs and attachment to dorsal bony ribs were criteria used to define subpatterns when applicable. Postxiphisternal inscriptional ribs are considered to be long if they extend midventrally to about the same level of the xiphisternal rods and short if they are less than half this length.

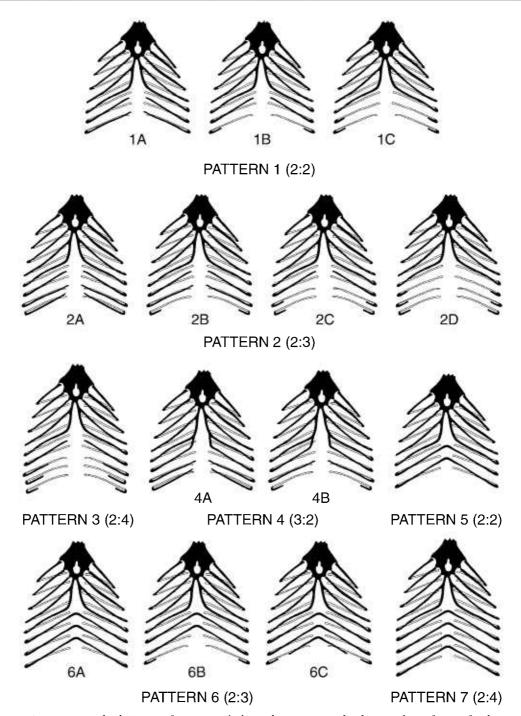


Fig. 2.—Patterns and subpatterns of inscriptional rib attachment in Tropiduridae. Numbers of pairs of xiphisternal incriptional ribs and postxiphisternal inscriptional ribs (PIRs) that distinguish each pattern are shown in parentheses. Patterns 5–7 are characterized by presence of PIRs articulating ventromedially (chevrons). Sternum, sternal ribs, xiphisternum, and inscriptional ribs are shown in black.

 $TABLE \ 1. \\ -Frequencies \ of \ patterns \ and \ subpatterns \ of \ inscriptional \ rib \ attachment \ in \ 61 \ species \ of \ Tropiduridae.$

									Pattern							
Taxon	n	1A	1B	1C	2A	2B	2C	2D	3	4A	4B	5	6A	6B	6C	7
Microlophus																
atacamensis	1	_	_	_	_	_	1.00	_	_	_	_	_	_	_	_	_
M. occipitalis	4	_	_	_	_	0.50	0.50		—	_	_	_	_	_	_	_
M. peruvianus	3	_	_	_	_	_	0.33	0.66	_	_	_	_	_	_	_	_
M. stolzmanni	3	_	_	_	_	0.33	0.33	_	0.33	_	_	_	_	_	_	_
M. theresiae	2	_	_	_	_	_	0.50	0.50		_	_	_	_	_	_	_
Plica plica	1 1	_	_	_	_	_	_	_	1.00	_	1.00	_	_	_	_	_
P. umbra Stenocercus	1	_	_		_		_	_	_		1.00	_		_	_	_
aculeatus	3												0.33	0.33	0.33	
S. angel	1				1.00											
S. apurimacus	3	_	_	_	0.66	_	_	0.33	_	_	_	_		_	_	_
S. arenarius	1	1.00	_	_	_	_	_	_	_	_	_	_	_	_	_	_
S. azureus	3	_	_	0.33	_	_	0.33	0.33	_	_	_	_	_	_	_	_
S. boettgeri	8	_	0.125	_	_	_	0.75	_	_	_	0.125	_	_	_	_	_
S. bolivarensis	2	_	_	_	_	_	_	_	_	0.50	0.50	_	_	_	_	_
S. caducus	2	_	_	_	_	_	_	_	_	_	_	_	1.00	_	_	_
S. chlorostictus	1	1.00	_	_	_	_	_	_	_	_	_	_	_	_	_	_
S. chota	4	_	_	_	1.00	_	_	_	_	_	_	_	_	_	_	_
S. chrysopygus	5	_		_	_	0.40	0.40	_	0.20	_	_	_	_	_	_	_
S. crassicaudatus	10	0.40	0.60	_	_	_	_	_	_	_	_	_	_	_	_	_
S. cupreus	2	_	1.00	_	_	_	_	_	_	_	_	_	_	_	_	_
S. doellojuradoi	3		1.00	_	_	_	_	_	_	_	_	_	_	_	_	_
S. empetrus	3	0.66	0.33	_	_	_	_	_	_	_	_	_	1.00	_	_	_
S. erythrogaster S. festae	$\frac{1}{2}$	_	_			1.00			_	_	_	_	1.00		_	_
S. fimbriatus	1					1.00							1.00			
S. formosus	1	1.00											1.00			
S. guentheri	45	0.07	0.02	_	0.16	0.64	_	_	_	0.07	0.04	_	_	_	_	_
S. ĥaenschi	1	_	_	_	_	1.00	_	_	_	_	_	_	_	_	_	_
S. huancabambae	2	_	_	_	_	_	_	_	_	_	_	0.50	0.50	_	_	_
S. humeralis	4	0.25	0.25	_	_	0.25	0.25	_	_	_	_	_	_	_	_	_
S. imitator	2	0.50	_	_	_	0.50	_	_	_	_	_	_	_	_	_	_
S. iridescens	3	_	_	_	_	_	_	_	_	_	_	_	1.00	_	_	_
S. ivitus	1	_	_	_	_	_	_	_	1.00	_	_	_	_	_	_	_
S. lache	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1.00
S. marmoratus	8		1.00	_	_		_	_	_	_	_	_	_	_	_	_
S. melanopygus	3	0.33	_	_	_	0.66	_	_	_	_	_	_	_	_	_	_
S. moestus	$\frac{1}{4}$	_	0.25	_	0.25	$\frac{1.00}{0.50}$	_	_	_	_	_			_		_
S. nigromaculatus S. ochoai	3	0.33	0.23		0.23	0.33		_	_	_	_	_			_	
S. orientalis	3		0.33		0,33	0.33	0.66	_								
S. ornatissimus	5	0.20			0.20	0.20	0.40									
S. ornatus	5		_	_	0.40	0.60		_	_	_	_	_	_	_	_	_
S. pectinatus	9	_	0.11	0.11	_	_	0.33	0.33	0.11	_	_	_	_	_	_	_
S. percultus	1	1.00	_	_	_	_	_	_	_	_	_	_	_	_	_	_
S. praeornatus	1	1.00	_	_	_	_	_	_	_	_	_	_	_	_	_	_
S. rhodomelas	4	_	_	_	0.75	0.25	_	_	_	_	_	_	_	_	_	_
S. roseiventris	7	1.00	_	_	_	_	_	_	_	_	_	_	_	_	_	_
S. scapularis	1	_	_	_	_	1.00	_	_	_	_	_	_	_	_	_	_
S. simonsii	7	0.58	0.28	_		0.14	_	_	_	_	_	_	_	_	_	_
S. trachycephalus	9	0.33	_	_	0.66	_	_	_	_	_	_	_	_	_	_	_
S. tricristatus	1	_	_	_	_	_	_		_		_	_	_	_	_	1.00
S. variabilis	2	_	_	_	_	1.00	_	_	_	_	_	_	_	_	_	_
S. varius	9	0.22	_	_	0.11	0.55	0.11	_	_	_	_		_	_		_
Tropidurus bogerti	1	_	_	_	_	_	1.00		_	_	_	_	_	_	_	_
T. etheridgei	2	_	_	_	_	_	0.50	0.50	_	_	_	_	_	_	_	_
T. hispidus T. melanopleurus	$\frac{1}{2}$	_	_	_	_	_	_	1.00 1.00	_	_	_	_	_	_	_	_
1. meianopieurus								1.00								

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TABLE	-	-Continue	a

		Pattern														
Taxon	n	1A	1B	1C	2A	2B	2C	2D	3	4A	4B	5	6A	6B	6C	7
T. spinulosus	4	_	0.25	_	_	_		_	_	_	0.75	_	_	_	_	
T. thoracicus	1	_	_	_	_	_	1.00	_	_	_	_	_	_	_	_	_
Uracentron azureum	1	_	_	_	_	_	_	1.00	_	_	_	_	_	_	_	_
U. flaviceps	1	_	_	_	_	_	1.00	_	_	_	_	_	_	_	_	_

Pattern 1.—Two xiphisternal and two postxiphisternal pairs of inscriptional ribs (Fig. 2). Both pairs of PIRs may be long (1A) or short (1C), or only the posterior pair may be short (1B).

Pattern 2.—Two xiphisternal and three postxiphisternal pairs of inscriptional ribs (Fig. 2). Variation within this pattern includes: all PIRs long (2A), either the last (2B) or two last (2C) pairs short, or all pairs short (2D).

Pattern 3.—Two xiphisternal and four post-xiphisternal pairs of inscriptional ribs (Fig. 2). Each pair of PIRs is shorter than the preceding pair.

Pattern 4.—Three xiphisternal and two postxiphisternal pairs of inscriptional ribs (Fig. 2). Both pairs of PIRs may be long (4A) or the posterior pair may be short (4B).

Pattern 5.—Two xiphisternal and two postxiphisternal pairs of inscriptional ribs. The postxiphisternal pairs articulate midventrally (Fig. 2).

Pattern 6.—Two xiphisternal and three postxiphisternal pairs of inscriptional ribs (Fig. 2). Some or all postxiphisternal pairs articulate midventrally, and, in most cases, they are fused to form continuous chevrons. All pairs of PIRs may be continuous medially (6A), or the posterior pair does not articulate midventrally (6B). In addition, one or more pairs can be fused midventrally without articulating laterally with the corresponding dorsal bony ribs (6C), giving the appearance of a "floating chevron" (Etheridge, 1965).

Pattern 7.—Two xiphisternal and four post-xiphisternal pairs of inscriptional ribs. All postxiphisternal pairs articulate midventrally (Fig. 2).

Interspecific Variation

Patterns 1 and 2 are the most common patterns among the species of Tropiduridae examined in this study (Table 1; Fig. 3). Pattern 1 was found in 26 species (n = 66

specimens)—17 species 1A (n = 35), 13 species 1B (n = 29), and 2 species 1C (n =2). Pattern 2 was found in 37 species (n =127)—11 species 2A (n = 29), 19 species 2B (n = 58), 18 species 2C (n = 29), and 8 species 2D (n = 11). Pattern 3 occurs in 5 of the species examined (n = 5). Only 4 species had Pattern 4 (n = 11)—2 species 4A (n = 4) and 4 species 4B (n = 7). Pattern 5 was observed in 1 species (n = 1), whereas pattern 6 was found in 6 species (n = 11)—6 species 6A (n = 9), 1 species 6B (n = 1), and 1 species 6C (n = 1). Only 2 species had Pattern 7 (n = 2). Four pairs of sternal ribs were found in one specimen each of P. plica, T. melanopleurus, T. spinulosus, and S. ornatus; all other specimens (98%), including most S. ornatus, had three pairs of sternal ribs. The xiphisternal longitudinal rods extend posterior to their articulation with the last pair of XIRs in 12 species (n = 15; Fig. 4). These extensions are short in all taxa except S. trachycephalus, Uracentron azureum, and U. flaviceps, in which they are long and curve laterally and anteriorly.

Intraspecific Variation

Multiple patterns or subpatterns occur in 29 species (Table 1). Given that the amount of intraspecific variation might be underestimated because of small sample sizes, I examined a large sample (n = 45) of S. guentheri. This species exhibits three patterns (1, 2, and 4) and six subpatterns (1A, 1B, 2A, 2B, 4A, and 4B), with Pattern 2 and Subpattern 2B being the most common types of rib attachment (80% and 64%, respectively; Fig. 5). Only 9% and 11% of the specimens examined have Patterns 1 and 4, respectively (Table 1). The type of pattern does not appear to be related to size or sex. Free posterior extensions of the xiphisternum (described above) were found only in one specimen (KU 147415). Both the sternum and inscriptional ribs were heavily mineralized in large specimens.

Asymmetry

A few specimens are asymmetrical in the number of xiphisternal and postxiphisternal inscriptional ribs. Nonetheless, loss of one XIR on one side was always accompanied by gain of one PIR on the other side (i.e., the total number of inscriptional ribs was the same on each side). Two adult females, one *S. festae* (KU 134595, SVL = 64 mm) and one *Microlophus atacamensis* (KU 161986, SVL = 87 mm), had 2:3 and 3:2 XIRs/PIRs counts on the right and left sides, respectively. An adult male *S. orientalis* (KU 134460, SVL = 60.5 mm) had 3:2 and 2:3 XIRs/PIRs counts on the right and left sides, respectively.

DISCUSSION

Most species of Tropiduridae examined had three pairs of sternal and two pairs of xiphisternal inscriptional ribs. Except for Anguimorpha, this 3:2 count is usual among lizards. Etheridge (1959) reported this pattern for tropidurid lizards, except for P. plica (4:2) and U. azureum (3:1). A 4:2 count for P. plica (KU 167499) also is reported herein; however, the specimen of *U. azureum* examined had a 3:2 count, which indicates intraspecific variation in the number of xiphisternal ribs. Additionally, P. umbra (KU 146659) had a 3:3 pattern that demonstrates interspecific variation of numbers of sternal and xiphisternal inscriptional ribs in Plica. Four sternal ribs also were found in one specimen each of *T. melanopleurus* and T. spinulosus. Etheridge (1959) found that, regardless of the number of sternal ribs, there are two pairs of XIRs in nearly all iguanians. Tropidurid lizards certainly follow that pattern—three pairs of XIRs were found only in S. boettgeri, S. bolivarensis, and 11% of the specimens of S. guentheri. Phrynosomatids resemble tropidurids in having patterns that include two or three pairs of XIRs, though some phrynosomatid species have only one pair of XIRs (Etheridge, 1964). Another characteristic of the xiphisternum that varies among iguanian lizards is the presence and shape of posterior xiphisternal processes that extend posterior to the articulation between the xiphisternal rods and the last pair of XIRs (Fig. 4). Intra- and interspecific variation in the occurrence of these processes has been reported in Phrynosomatidae (Etheridge, 1962, 1964) and, in less detail, in Tropiduridae and Leiocephalidae (Etheridge, 1966; Pregill, 1992). Furthermore, one of the synapomorphies of *Leiocephalus* is the presence of posterior xiphisternal processes that curve anteriorly and extend to a point either ventral, or anterior, to the last (second) pair of XIRs (Pregill, 1992). I found similar processes in *S. trachycephalus*, *U. azureum*, and *U. flaviceps*; however, unlike *Leiocephalus*, the posterior xiphisternal processes end posterior to the last pair of XIRs in these specimens.

The number and morphology of PIRs in iguanian lizards has been studied in less detail. Although the numbers and lengths of PIRs have been reported to vary among iguanians (Etheridge, 1959, 1965), intraspecific variation has only been described in S. grandaevus (Etheridge, 1962). Four counts of xiphisternalpostxiphisternal ribs were found in S. grandaevus—1:2, 2:2 (the most common), 2:3, and 3:2 (Etheridge, 1962); nonetheless, the frequency of these patterns and differences in the length of PIRs were not discussed. Variation in the abdominal skeleton of tropidurids includes at least four XIRs/PIRs counts (i.e., 2:2, 2:3, 2:4, and 3:2), with the most common (67% of species and 61% of specimens examined in this study) being 2:3 (Pattern 2). If the relative length of each pair of PIRs is considered, variation within each pattern is evident. Thus, Pattern 4, Patterns 1 and 6, and Pattern 2 can be divided into two, three, and four subpatterns, respectively (Fig. 2).

The presence of PIRs articulating medially (i.e., Patterns 5–7) is rare in Tropiduridae and is restricted to the Stenocercus clade. Species with PIRs articulating medially do not exhibit patterns with PIRs not articulating medially (i.e., Patterns 1–4) and vice versa (Table 1). Only eight species currently assigned to Stenocercus have Patterns 5-7, and they include all species that were formerly assigned to Ophryoessoides (as defined by Fritts, 1974) except for S. scapularis, which exhibits Pattern 2. Two other species (S. fimbriatus and S. huancabambae) with PIRs articulating medially have been included in the "Ophryoessoides group" (Cadle, 2001) along with the species previously assigned to Ophryoessoides by Fritts (1974). Although monophyly of the

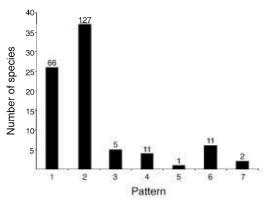


FIG. 3.—Frequency distribution of patterns of rib attachment among species of Tropiduridae examined in this study. Number of individuals is indicated above each box

"Ophryoessoides group" has not been tested, PIRs articulating medially might represent a synapomorphy of this group. However, this character state seems to have originated at least twice in Tropiduridae because it also was found in S. lache, a species that does not belong to the "Ophryoessoides group." In addition, similar patterns have been reported in other iguanian lizards. For example, Etheridge (1959) reported that anoles have 3-11 midventrally fused pairs of PIRs (chevrons); in a few species of anoles, these ribs do not articulate with the corresponding dorsal bony ribs. Similarly, all members of Iguanidae except Sauromalus and Dipsosaurus have continuous chevrons (de Queiroz, 1987; Etheridge, 1965). Also, PIRs

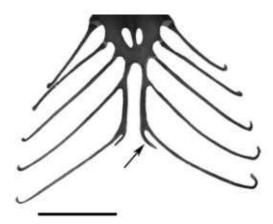


Fig. 4.—Ventral view of abdominal skeleton of Stenocercus cupreus (KU 133974, SVL = 66 mm). Arrow indicates posterior extension of left xiphisternal longitudinal rod. Scale bar = 5 mm.

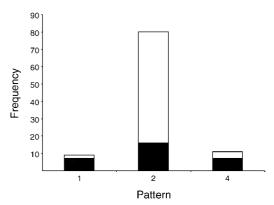


Fig. 5.—Frequency distribution of patterns of rib attachment in *Stenocercus guentheri*. Subpatterns A and B are indicated in black and white, respectively.

articulating medially have been reported in species of Chamaeleonidae, Dibamidae, Cordylidae, Gekkonidae, Gymnophthalmidae, Lacertidae, and Scincidae (Camp, 1923; Etheridge and de Queiroz, 1988; Hoffstetter and Gasc, 1969). Because this character state (i.e., PIRs articulating medially) does not occur in extant rhynchocephalians—the only non-squamate lepidosauromorphs in which inscriptional ribs are known—it is thought to be derived (Estes et al., 1988). Currently, the simplest explanation for the distribution of this character state is independent origins in all the families in which it occurs (Estes et al., 1988).

There is intraspecific variation in the abdominal skeleton of lizards. Etheridge (1962) reported sexual variation in S. grandaevus consisting of males having the highest (3) and females the lowest (1) numbers of XIRs: intermediate numbers (2) were found in both sexes. No indication of sexual variation in S. guentheri was found in this study. Only 11% of the specimens have three pairs of XIRs; the other 89% have two. Both of these two patterns were observed in members of both sexes. Stenocercus guentheri resembles S. grandaevus in that there seems to be no ontogenetic variation in the abdominal skeleton. However, ontogenetic and sexual variation need to be investigated with statistical analyses if appropriate sample sizes become available.

The abdominal skeleton of lizards represents a source of fixed and polymorphic characters of potential use in phylogenetic analyses. Although intraspecific variation in the presence of PIRs articulating ventrome-

dially has been reported in some iguanids (de Queiroz, 1987), this character seems to be fixed in other iguanian taxa, including Tropiduridae. Numbers of PIRs and XIRs, as well as relative length of PIRs, are potentially informative characters for use in phylogenetic studies that have been explored in less detail. Given that these characters are polymorphic, they should be treated accordingly if included in phylogenetic analyses (Smith and Gutberlet, 2001; Wiens, 2000). I have described patterns of morphological variation of the abdominal skeleton in tropidurid lizards; however, large samples of additional taxa will need to be examined in order to determine the morphological diversity and evolution of the abdominal skeleton in Iguania.

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APPENDIX I

Specimens Examined

Taxa are arranged alphabetically. Snout-vent length is indicated in parentheses.

Abbreviations: C&S, cleared-and-double stained; X-R, x-rayed; M, male; F, female.

Microlophus atacamensis.—KU 161986 (87 mm, C&S, F), 161983 (121 mm, C&S, M). M. occipitalis—KU 142735 (27 mm, C&S), 142730 (31 mm, C&S), 142721 (62 mm, C&S, F), 142714 (75 mm, C&S, M). M. peruvianus—KU 134695 (60.5 mm, C&S, M), 134673 (70 mm, C&S, F), 134674 (115 mm, C&S, M). M. stolzmanni—KU 134731 (30 mm, C&S, M), 134704 (63 mm, C&S, F), 134747 (95 mm, C&S, M). M. theresiae—KU 162018 (80 mm, C&S, F), 162012 (107 mm, C&S, M).

Plica plica.—KU 167499 (100 mm, C&S, F). *P. umbra*—KU 146659 (85 mm, C&S, M).

Stenocercus aculeatus.—KU 212628 (79 mm, X-R, M), 212629 (87 mm, X-R, F), 121093 (98 mm, C&S, M). S. angel—QCAZ 1354 (82.6 mm, C&S, M). S. apurimacus-KU 134306 (29 mm, C&S), 134278 (64 mm, C&S, F), 134284 (80.5 mm, C&S, M). S. arenarius—SDSU 1688 (90 mm, X-R, M). S. azureus—AMNH 17013 (66.7 mm, X-R, F), 37357 (54 mm, X-R), 37558 (59 mm, X-R, F). S. boettgeri—AMNH 13626 (66.5 mm, X-R), 13502 (70 mm, X-R), 13504 (74.1 mm, X-R), 13505 (64.6 mm, X-R), 13508 (60.3 mm, X-R); KU 134014 (82 mm, C&S, M); MCZ 8085 (74.8 mm, X-R), 45881 (76.5 mm, X-R). S. bolivarensis— KU 122812 (76 mm, X-R, M), 181994 (81 mm, X-R, M). S. caducus-SDSU 1690 (67 mm, X-R, F), 1689 (79 mm, X-R, M). S. chlorostictus—SDSU 1535 (74 mm, X-R, M). S. chota--- QCAZ 2654 (81 mm, C&S, M), 2655 (51 mm, C&S, F), 2670 (C&S, F), 2671 (C&S, F). S. chrysopygus-AMNH 63475 (63.6 mm, X-R); KU 133906 (59.5 mm, C&S, F), 133895 (65.5 mm, C&S, M); UMMZ 58920 (X-R), 89487 (X-R). S. crassicaudatus—AMNH 23132 (71 mm, X-R), 23143 (79.7 mm, X-R), 23144 (70.7 mm, X-R), 23146 (70.7 mm, X-R); KU 133959 (83.5 mm, C&S, M), 163602 (74 mm, C&S, F); MCZ 12401 (84.4 mm, X-R), 12402 (77.5 mm, X-R), 29303 (77.3 mm, X-R), 45882 (64.2 mm, X-R). S. cupreus-KU 133976 (54.5 mm, C&S, F), 133974 (66 mm, C&S, M). S. doellojuradoi—SDSU 1678 (60 mm, X-R), 3645 (65 mm, X-R, F), 3646 (69 mm, X-R, M). S. empetrus-KU 134421 (35 mm, C&S), 134403 (77 mm, C&S, F), 134401 (87.5 mm, C&S, M). S. erythrogaster—ICN 7970 (87.8 mm, X-R, M). S. festae—KU 134595 (64 mm, C&S, F), 134603 (81 mm, C&S, M). S. fimbriatus-LSUMZ 17519 (X-R). S. formosus-KU 134110 (70.5 mm, C&S, F). S. guentheri—KU 147347 (30 mm; C&S), 147525 (32 mm; C&S), 147520 (35 mm, C&S), 147346 (39 mm, C&S), 147553 (39 mm, X-R), 147516 (44 mm, X-R), 147519 (44 mm, C&S, F), 147542 (45 mm, X-R), 147467 (49 mm, X-R), 147534 (49 mm, C&S, M), 147467 (49 mm, X-R), 147404 (53 mm, X-R), 147445 (55 mm, C&S, F), 147437 (55 mm, F), 147372 (56mm, X-R), 147389 (58 mm, X-R), 147416 (58 mm, X-R), 147433 (60 mm, X-R), 147454 (60 mm, X-R), 147477 (60 mm, C&S, F), 147376 (61 mm, X-R, F), 147374 (62 mm, X-R, F), 147409 (65 mm, C&S, M), 147381 (66 mm, X-R, F), 147326 (66 mm, C&S, F), 147369 (67 mm, C&S, F), 147382 (68 mm, C&S, F), 147396 (68 mm, X-R, F), 147410 (68 mm, X-R, F), 147508 (70 mm, X-R, F), 147487 (70 mm, C&S, M), 147503 (71 mm, X-R, M), 147418 (71 mm, X-R), 147401 (72 mm, X-R, M), 147415 (72 mm, X-R, F), 147475 (74 mm, X-R), 147482 (74 mm, C&S, M), 142713 (78 mm, X-R), 147319 (78.5 mm, C&S, M), 147421 (79 mm, C&S, M), 147513 (80 mm, X-R, M), 147457 (81 mm, X-R, M), 147388 (81 mm, C&S, M), 147488 (81 mm, X-R, M), 147318 (87 mm, X-R, M), 147412 (88 mm, C&S, M). S. haenschi—ZMB 16595 (76 mm, X-R). S. huancabambae—KU 209513 (49 mm, X-R), 212630 (68 mm, X-R, M). S. humeralis—AMNH 27135 (84.7 mm, X-R); KU 134006 (41 mm, C&S), 134001 (92 mm, C&S, F), 134004 (96.5 mm, C&S, M). S. imitator—KU 181912 (79 mm, X-R, M); SDSU 1534 (72 mm, X-R, F). S. iridescens—QCAZ 2205 (95.7 mm, X-R, M), 2212 (94.6 mm, X-R, M), 5310 (82.5 mm, X-R, F). S. ivitus—KU 134653 (65 mm, X-R, F). S. lache—ICN 5756 (87.2 mm, X-R). S. marmoratus-UMMZ 68120 (n = 4, X-R), 68121 (X-R), 68122 (X-R),68124 (n = 2, X-R). S. melanopygus—KU 134036 (29 mm, C&S), 134075 (58 mm, C&S, F), 134058 (75 mm, C&S, M). S. moestus—SDSU 1686 (65 mm, X-R, M). S. nigromaculatus—AMNH 28554 (68.5 mm, X-R), 28954 (78.4 mm, X-R); KU 134089 (55 mm, C&S, F), 134092 (70 mm, C&S, M). S. ochoai-KU 133876 (35 mm, C&S, M), 133878 (64 mm, C&S, F), 133884 (72.5 mm, C&S, M). S. orientalis—KU 134464 (29.5 mm, C&S), 134460 (60.5 mm, C&S, M), 134452 (61.5 mm, C&S, F). S. ornatissimus—AMNH 27136 (65.8 mm, X-R), 27137 (70.1 mm, X-R), 28783 (69.4 mm, X-R); KU 134360 (63 mm, C&S, F), 134351 (75 mm, C&S, M). S. ornatus—KU 121128 (86.5 mm, C&S, M), 134128 (62 mm, C&S, F), 134129 (67 mm, C&S, M), 134139 (66 mm, C&S, F), 134155 (30 mm, C&S). S. pectinatus—SDSU 1679 (54 mm, X-R, F), 3644 (62 mm, X-R, M), 3643 (66 mm, X-R, F); UMMZ 98880 (n = 3, X-R), 98881 (n = 2, X-R); USNM 94093 (63.3 mm,X-R), S. percultus—SDSU 1596 (85 mm, X-R, M), S. praeornatus—KU 134229 (91 mm, C&S, M). S. rhodomelas—KU 152186 (74 mm, C&S, F), 152184 (98 mm, C&S, M); UMMZ 3518 (81.6 mm, X-R), 3521 (68.6 mm, X-R). S. roseiventris-KU 172196 (91.5 mm, C&S, F); UMMZ 68116 (n = 2, X-R), 68117 (n = 2, X-R), 68118 (X-R);USNM 94094 (74 mm, X-R). S. scapularis—SDSU 1691 (70 mm, X-R, F). S. simonsii—KU 134164 (68 mm, X-R, F), 134168 (79 mm, X-R, M); UMMZ 60093 (n = 2, X-R), 60095 (n = 3, X-R). S. trachycephalus—SDNHM 10781 (72.4 mm, X-R, F), 10782 (75.1 mm, X-R, F), 10783 (59 mm, X-R, F); SDSU 1068 (74.5 mm, X-R, F), 1069 (66.1 mm, X-R, F), 1692 (72 mm, X-R, M), 1695 (72 mm, X-R, M), 1693 (79 mm, X-R, M), 1694 (90 mm, X-R, M). S. tricristatus-KU 179058 (88 mm, X-R, F). S. variabilis-KU 134213 (63 mm, C&S, M), 134198 (80 mm, C&S, M). S. varius-AMNH 22190 (70.6 mm, X-R), 22202 (64.7 mm, X-R), 22204 (67.2 mm, X-R), 22206 (66 mm, X-R), 22208 (65.4 mm, X-R), 22210 (71.8 mm, X-R), 22817 (68.8 mm, X-R), KU 121135 (65 mm, C&S, M), 142704 (73 mm, C&S, F).

Tropidurus bogerti.—AMNH 61012 (77.5 mm, X-R). *T. etheridgei*—KU 186113 (79 mm, C&S, F), 186102 (90.5 mm, C&S, M). *T. hispidus*—KU 182742 (31 mm, C&S). *T. melanopleurus*—KU 136370 (63.5 mm, C&S, F), 136371 (94 mm, C&S, M). *T. spinulosus*—KU 97856 (77 mm, C&S, M), MCZ 28633 (83.1 mm, X-R), 28691 (86 mm, X-R), 42525 (67.4 mm, X-R). *T. thoracicus*—KU 163721 (82 mm, X-R, M).

Uracentron azureum.—KU 204989 (72 mm, X-R, M). $U.\ flaviceps$ —KU 175319 (72 mm, X-R, F).