

At the Lower Size Limit in Tetrapods: A New Diminutive Frog from Cuba (Leptodactylidae: *Eleutherodactylus*)

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Eleutherodactylus iberia is described from the Cuchillas de Moa in eastern Cuba. At approximately 10 mm snout–vent length, it rivals the Brazilian brachycephalid *Psyllophryne didactyla* in being the smallest species of tetrapod. The new species appears to be most closely related to the Cuban species *E. cubanus*, *E. limbatus*, and *E. orientalis*; and all have the same small clutch size (one). The *limbatus* group is erected to accommodate these four diminutive leaf-litter species. The smallest species of anurans, representing four families (Brachycephalidae, Leptodactylidae, Microhylidae, and Sooglossidae), are compared to examine the effects of miniaturization on morphological and life-history traits. Digital reduction and loss of vomerine teeth are common, and most diminutive species have a high frequency (> 5 kHz) call and lay one or a few eggs on land that undergo direct development.

Se describe *Eleutherodactylus iberia* de la zona de Cuchillas del Toa, en el extremo Este de Cuba. Con aproximadamente 10 mm de longitud hocico–cloaca, esta especie rivaliza al brachicefalido brasileño *Psyllophryne didactyla*, considerado la especie de tetrapodo mas pequeña. La nueva especie parece estar mas estrechamente relacionada a las especies cubanas *E. cubanus*, *E. limbatus* y *E. orientalis*; teniendo todas el mismo tamaño de puesta pequeño (un solo huevo). Se crea el grupo *limbatus*, para acomodar a estas cuatro diminutas especies habitantes de la litera. Son comparadas las especies mas pequeñas de anuros, representantes de cuatro familias (Brachycephalidae, Leptodactylidae, Microhylidae y Sooglossidae), para examinar los efectos de la miniaturizacion sobre los diferentes aspectos de la morfologia y la historia natural. Son comunes las reducciones digitales y la perdida de dientes vomerinos. La mayoría de estas especies diminutas poseen llamadas de alta frecuencia (> 5 kHz) y ponen uno o unos pocos huevos sobre la tierra, los cuales siguen un desarrollo directo.

MANY new species of amphibians and reptiles have been discovered in Cuba, and especially in the eastern provinces, in the past several years. These include snakes (Hedges and Garrido, 1992a, 1992b), anoline lizards (e.g., Estrada and Garrido, 1991; Garrido and Hedges, 1992; Estrada and Hedges, 1995), gekkonid lizards (Thomas et al., 1992; Hedges and Garrido, 1993), frogs (Estrada and Hedges, 1991, 1996; Hedges et al., 1992), and taxa not yet described. The rate of discovery has not declined, and it is apparent that our knowledge of the vertebrate diversity of Cuba is far from complete. Unfortunately, Cuba and other islands in the West Indies have some of the lowest levels of natural forest cover in the world, and their unique flora and fauna is threatened as a result of continued deforestation (Hedges and Woods, 1993).

During an expedition to eastern Cuba in search of the ivory-billed woodpecker (*Campyphilus principalis*) in March and April, 1993, the senior author collected anurans in the region of Monte Iberia in the Cuchillas de Moa. Among

these specimens are four small, dark frogs that clearly represent a new species.

MATERIALS AND METHODS

The following abbreviations are used: SVL = snout–vent length; HL = head length; HW = head width; TYM = tympanum width; EL = eye length; EN = eye–naris distance; IOD = interorbital distance; THL = thigh length; SHL = shank length; and FTW = fingertip (III) width. Museum abbreviations: MNHNCU, Museo Nacional de Historia Natural, Cuba (Havana); CARE (Collection of A. R. Estrada, Havana, Cuba); and USNM, United States National Museum of Natural History, Washington, DC. Measurements were taken with digital calipers (0.01 mm accuracy) and an ocular micrometer. Calls were recorded with a Sony microcassette recorder, and analyses were made with the use of Canary software (Cornell University). Terminology for call parameters follows Duellman and Trueb (1986).



Fig. 1. *Eleutherodactylus iberia*, an adult male from Arroyo Sucio (Anacleto) Arriba, on the western slope of Monte Iberia, Holguín Province, Cuba, 600 m, collected by A. Estrada on 19 April 1993; photographed on a Cuban 10 centavos coin (21 mm diameter) by M. Lammertink.

Eleutherodactylus iberia sp. nov.

Figure 1

Holotype.—MNHNCU 661, an adult male from Arroyo Sucio (Anacleto) Arriba, on the western slope of Monte Iberia, Holguín Province, Cuba, 600 m elevation, collected by A. Estrada on 19 April 1993; original field number CARE 849.

Paratypes.—CARE 847 (male), CARE 850 (male), USNM 335653 (female; original field number CARE 848), paratopotypes with same date and collector as holotype.

Diagnosis.—*Eleutherodactylus iberia* is the smallest species of *Eleutherodactylus* (> 500 species). It can be distinguished from all other members of the genus in the West Indies by its very small size (9.8 mm SVL, males; 10.5 mm SVL, female) and dark coloration. It is a member of the subgenus *Euhyas* (Hedges, 1989) in having a long and pointed left lobe of the liver, and in several morphological characters including smooth to weakly rugose venter and digital tips not enlarged. It is most closely related to *E. limbatus* and *E. orientalis* (new combination; see below), with which it shares a very small body size, small digits and digital tips, dorsal pattern of dorsolateral lines (at least anteriorly), absence of vomerine teeth, and general habitus (Fig. 2). It

differs from those species in having an entirely dark venter (vs completely yellow in *limbatus* or pale yellow in *E. orientalis*), absence of dorsolateral lines posteriorly, smaller body size (vs 10.5 mm SVL in males and 11.6 mm SVL in females of *E. limbatus*; 11.0 mm SVL in males and 11.6 mm SVL in females of *E. orientalis*), and a lower frequency call. In addition, it has a distinctly narrower head than in *E. limbatus* (IOD/SVL = 0.104–0.122 in *E. iberia* vs 0.131–0.157 in *E. limbatus*) and narrower digital tips than in *E. orientalis* (0.20 in *E. iberia* vs 0.32–0.42 in *E. orientalis*).

Description.—Head as wide as body, width equal to length; snout subacuminate in dorsal view, subacuminate in lateral view, overhanging lower jaw; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis rounded, slightly concave in dorsal view; loreal region flat, sloping abruptly; lips not flared; upper eyelid and interorbital space not tuberculate; supratympanic fold weakly defined, concealing upper edge of tympanic annulus; tympanum moderate-sized, round and larger in males, higher than wide and smaller in females, separated from eye by a distance less than its own diameter; post-riotal tubercles elevated, subconical; choanae small, round, partially concealed by palatal shelf of maxillary arch when roof of mouth is viewed from below; vomerine teeth absent; tongue longer than wide, posterior edge without notch,

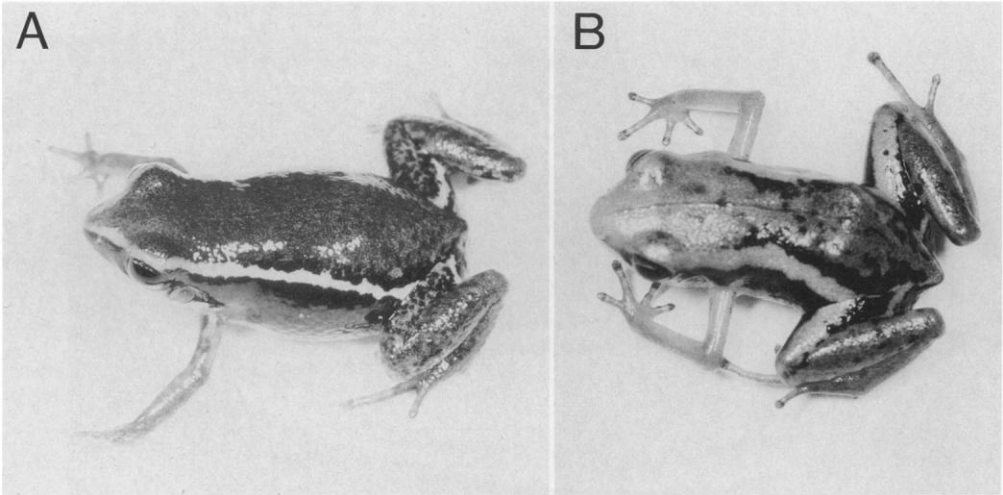


Fig. 2. Two Cuban frogs of the genus *Eleutherodactylus*: (A) *E. limbatus* from Soroa, Pinar del Río Province, and (B) *E. orientalis*, from El Yunque de Baracoa, Guantánamo Province. Photograph by S. B. Hedges.

posterior three-fourths not adherent to floor of mouth; males with vocal slits.

Skin of dorsum very weakly rugose, without dorsolateral folds; skin of flanks similar to dorsum; skin of venter very weakly rugose, without discoidal folds; anal opening not extended in sheath; no glandular areas present; ulnar tubercles absent; palmar tubercle single, about the same size as thenar, thenar tubercle oval, low; no supernumerary tubercles; subarticular tubercles of fingers oval and flat; weak lateral ridge on finger; no fingers with expanded tips; fingertips rounded, circular pad on ventral surface of fingertip; circumferential groove bordering distal two-thirds of finger pad; width of largest pad (III) one-fifth to one-fourth tympanum; first finger shorter than second when adpressed; heel tubercles absent; no tubercles along outer edge of tarsus; metatarsal tubercles elevated, inner (oval) twice size of outer (subconical); no supernumerary plantar tubercles; subarticular tubercles of toes oval and subconical; toes unwebbed; weak lateral ridge on toe; no toes with expanded tips; toetips rounded or pointed; circular or triangular pad on ventral surface of toetip; circumferential groove bordering distal two-thirds of toe pad; heels do not touch when flexed legs are held at right angles to sagittal plane.

In life, dorsal ground color was dark brown with a vivid coppery stripe on the canthal region grading to orange over the eyelids and golden yellow and white behind the eyes; the dorsolateral stripe becomes discontinuous near the vent; loreal region dark brown, flanks dark brown

with discontinuous white line delimiting flank color from ventral color; forelimbs with orange bar on arms; thigh crossed by diagonal white line from the vent to knee; shank dark brown; venter dark purple. In preservative, dorsal and ventral ground color very dark brown; only pattern distinguishable is a faint white stripe from the snout to the first one-third of the dorsolateral region.

Measurements.—See Table 1.

Etymology.—The name *iberia* is in reference to Monte Iberia of the type locality.

Natural history.—The type series was collected during the day and night under leaf litter and among the roots of ferns in a secondary hardwood forest on the western slope of Monte Iberia. The region receives relatively high rainfall (> 1600 mm/year) and is very humid. Frogs were calling during the day and night but were seen active and moving about in the leaf litter only at night. The female was collected within a few centimeters of a single egg, implying a clutch size of one as in *E. limbatus* (Noble, 1931).

Vocalization.—The call of *E. iberia* (Fig. 3A) consists of a series of irregular, high-pitched "chirps," somewhat similar to the calls of *E. limbatus* (Fig. 3B) and *E. orientalis* (Fig. 3C). However, the dominant frequency of *E. iberia* (5.78 ± 0.07 kHz; 1SE, $n = 10$ calls) is lower than that of *E. limbatus* (6.32 ± 0.06 kHz; $n = 10$) and *E. orientalis* (6.56 ± 0.09 kHz; $n = 10$).

TABLE 1. MEASUREMENTS (IN mm) OF *Eleutherodactylus iberia*, *E. limbatus*, AND *E. orientalis*. Shown are means \pm 1 SE and ranges (in parentheses) of adults.

	<i>E. iberia</i>			<i>E. limbatus</i>		<i>E. orientalis</i>	
	Males (3)	Female	Holotype	Males (5)	Females (4)	Males (3)	Females (2)
SVL	9.80 \pm 0.12 (9.6–10.0)	10.5	10.0	10.5 \pm 0.36 (9.8–11.7)	11.6 \pm 0.17 (11.1–11.8)	11.0 \pm 0.26 (10.7–11.5)	11.6 (11.2, 12.0)
HL	3.57 \pm 0.33 (3.5–3.6)	3.7	3.6	2.90 \pm 0.14 (2.7–3.4)	3.35 \pm 0.15 (3.0–3.6)	3.87 \pm 0.07 (3.8–4.0)	3.95 (3.7, 4.2)
HW	3.83 \pm 0.66 (3.7–3.9)	3.6	3.9	3.90 \pm 0.23 (3.3–4.7)	4.03 \pm 0.17 (3.8–4.2)	3.80 \pm 0.10 (3.7–4.0)	3.95 (3.8, 4.1)
TYM	0.90 \pm 0.00 (0.9–0.9)	0.6	0.9	0.96 \pm 0.04 (0.9–1.1)	0.83 \pm 0.09 (0.7–1.1)	0.80 \pm 0.06 (0.7–0.9)	0.75 (0.7, 0.8)
EL	1.43 \pm 0.33 (1.4–1.5)	1.6	1.4	1.44 \pm 0.04 (1.3–1.5)	1.50 \pm 0.41 (1.4–1.6)	1.57 \pm 0.12 (1.4–1.8)	1.75 (1.7, 1.8)
IOD	1.10 \pm 0.58 (1.0–1.2)	1.2	1.1	1.48 \pm 0.04 (1.4–1.6)	1.58 \pm 0.05 (1.5–1.7)	1.43 \pm 0.03 (1.4–1.5)	1.55 (1.5, 1.6)
THL	4.60 \pm 0.58 (4.5–4.7)	4.9	4.7	4.82 \pm 0.20 (4.3–5.5)	5.25 \pm 0.19 (4.9–5.7)	4.97 \pm 0.09 (4.8–5.1)	5.40 (5.2, 5.6)
SHL	4.53 \pm 0.33 (4.5–4.6)	5.0	4.5	4.88 \pm 0.22 (4.3–5.5)	5.53 \pm 0.34 (5.2–6.0)	5.4 \pm 0.15 (5.1–5.6)	5.65 (5.6, 5.7)
FTW	0.20 \pm 0.00 (0.2–0.2)	0.2	0.2	0.30 \pm 0.03 (0.25–0.35)	0.30 \pm 0.03 (0.25–0.35)	0.35 \pm 0.03 (0.32–0.40)	0.38 (0.34, 0.42)

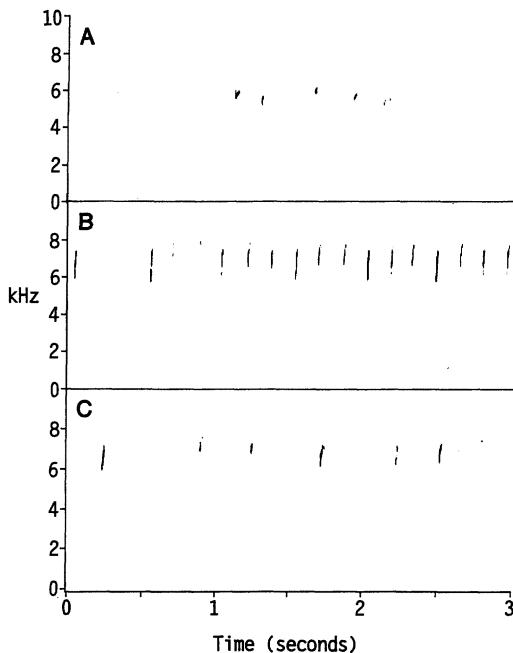


Fig. 3. Audiospectrograms of Cuban *Eleutherodactylus* of the *limbatus* group: (A) *E. iberia*, from the type locality in Holguin province, (B) *E. limbatus* from along the Río Cuzco, near Jagueyones, Guantánamo Province and (C) *E. orientalis*, from El Yunque de Baracoa, Guantánamo Province. A narrow band filter was used with all three. The exact number of individuals calling in each case is unknown, although single males are believed to emit a multiple-note call.

The calls of all three species consist of a single, sharply rising primary note, although the note of *E. iberia* is shorter and rises less sharply than that of *E. limbatus*. Considering the small number of recordings available, the significance of these differences is unclear.

Distribution.—Known only from the type locality. *Eleutherodactylus limbatus* has not yet been collected sympatrically with *E. iberia*. However, typical specimens of *E. limbatus* have been collected within a few kilometers of the type locality of *E. iberia* in the Reserva de Jauganí. The known localities of *E. limbatus* and *E. orientalis* are shown in Schwartz and Henderson (1991).

Remarks.—In the description of *Sminthillus* (= *Eleutherodactylus*) *limbatus orientalis*, Barbour and Shreve (1937) noted only color pattern differences between that taxon and *E. l. limbatus* (coloration in *E. limbatus* also noted by Valdes, 1989). We have found those differences to be consistent in distinguishing specimens of the two taxa (e.g., Fig. 2), especially the middorsal spot preceded by two small dark dots (absent in *E. limbatus*), dorsolateral lines that converge at midbody (straight in *E. limbatus*), pale head and anterior body lacking loreal lines (uniform dark brown head and body with distinct, straight, loreal lines in *E. limbatus*), and broad white bar on anterior face of thigh (narrow or absent in *E. limbatus*). These concordant pattern differ-

ences alone suggest that different species are involved. However, we also note structural differences compatible with recognition of *E. orientalis* at the species level. *Eleutherodactylus orientalis* is a more slender frog than *E. limbatus* and its snout is more rounded (Fig. 2; Barbour and Shreve, 1937:pl. 2). Also, the head is narrower (HL/HW = 0.98–1.02 vs 0.72–0.86 in *E. limbatus*), finger I is shorter than II in *E. orientalis* (approximately equal in *E. limbatus*), and the eye is larger in females of *E. orientalis* (EL/SVL = 0.149–0.150 vs 0.119–0.136 in females of *E. limbatus*).

These three diminutive frogs (*E. iberia*, *E. limbatus*, and *E. orientalis*) share several characteristics that suggest they are each others closest relatives: very small body size, small digits and small digital tips, dorsolateral lines, a similar high-pitched call (Fig. 3), and absence of vomerine teeth. In habitat preference, they also are similar in occupying leaf-litter of the forest floor. In recognition of these similarities, we place them in their own species group, the *limbatus* group, of the subgenus *Euhyas*. Another small (13–14 mm SVL) Cuban species with small digits and digital tips and a clutch size of one, *E. cubanus*, is similar in body shape to *E. limbatus*. After not having been seen since the type series was obtained in the 1930s, a single specimen recently was collected in leaf litter at a new locality on Pico Turquino (Hedges et al., 1995). Those authors tentatively associated *E. cubanus* with *E. limbatus* (and by inference, *E. orientalis* and *E. iberia*), and therefore we include *E. cubanus* in the *limbatus* group as a more distant relative of the three other species. The small size, dorsolateral line pattern (at least in one morph), and terrestrial habits of the widespread Cuban species *E. varleyi* suggest that it, too, may have affinities with the *limbatus* group. However, it is distinctive in possessing dorsolateral rows of tubercles and a long thoracic vocal sac. Until relationships of Cuban *Euhyas* become better known, we consider the *limbatus* group to include only *E. cubanus*, *E. iberia*, *E. limbatus*, and *E. orientalis*.

El Yunque de Baracoa (565 m) is an isolated, flat-top limestone mountain near the coast and surrounded by areas only slightly above sea level. Any significant rise in sea level during the Pliocene or Pleistocene would have created an island and reduced or halted gene flow with other populations of proto-*limbatus*. This probably explains the origin of *E. orientalis* and the gecko *Sphaerodactylus bromeliarum* (Peters and Schwartz, 1977), also endemic to El Yunque de Baracoa. Monte Iberia (709 m) is larger and part of a mountain chain (Cuchillas de Moa), but it also would have been subjected to greater iso-

lation during times of higher sea level, and this may explain the origin of *E. iberia* and another species of frog endemic to that mountain (Es-trada and Hedges, 1996).

DISCUSSION

Among the approximately 25,000 extant species of tetrapods, the smallest bird is the bee hummingbird of Cuba (*Mellisuga helenae*; 64 mm body length; Bond, 1979), and the smallest mammal is a Mediterranean shrew (*Suncus etruscus*; 35 mm body length; Walker, 1975). However, both are large compared to the smallest lizard (a West Indian gecko, *Sphaerodactylus parthenopion*; 17 mm SVL; Thomas, 1965) and salamander (a Mexican plethodontid, *Thorius arboreus*; 17 mm SVL; Hanken and Wake, 1994). The smallest tetrapod is considered to be a brachycephalid frog from southeastern Brazil, *Psyllophryne didactyla*, with a SVL of about 10 mm (Izecksohn, 1971; Duellman and Trueb, 1986). Although the single adult female of *E. iberia* (10.5 mm SVL) is comparable in size to that of *P. didactyla* (10.2 mm SVL; Izecksohn, 1971), males of the latter species appear to average about 1 mm smaller (8–9 mm SVL) than those of *E. iberia* (9–10 mm SVL), although the significance of these differences is unclear considering the small number of individuals. Body size at hatching or metamorphosis has been used as a measure for determining the "smallest frog" (Glaw and Vences, 1992:193), but this measurement is known for relatively few anuran species at this time. Moreover, hatchlings of *E. planirostris*, a species reaching 36 mm SVL, are as small as 4.3 mm (Schwartz and Henderson, 1991), and thus it is likely that hatchlings of other species of *Eleutherodactylus* rival those of *Stumpffia* (3 mm). At present, it would appear that the two smallest known species of tetrapods are the anurans *P. didactyla* and *E. iberia*.

Miniaturization in animals sometimes is accompanied by morphological novelty or greater variability in characters, but more often it is associated with simplification or loss of morphological structures (Hanken and Wake, 1993). This can be seen when comparing some of the smallest species of anurans (Table 2). Because the four neobatrachian families represented (Brachycephalidae, Leptodactylidae, Microhylidae, and Sooglossidae) are not obviously closely related (Hay et al., 1995), any trends observed are unlikely to be the result of phylogeny. A reduction in the normal number of digits in anurans (four on the hand and five on the foot), although rare, is seen in three of the smallest species representing two families (Brachycephalidae and Microhylidae). Likewise, most spe-

TABLE 2. COMPARISON OF SOME DIMINUTIVE SPECIES OF ANURANS.

Species	Adult body size ^a		Digits ^b		Vomerine teeth	Development	Clutch size ^c	Dominant frequency (kHz)	Reference
	Males	Females	Hands	Feet					
<i>Psyllophryne didactyla</i>	8–9	10.2	2	3	absent	direct	1	—	Izecksohn, 1971
<i>Eleutherodactylus iberia</i>	9.8	10.5	4	5	absent	direct	1	5.78	This paper
<i>Sooglossus gardineri</i>	10.2	11.5	4	5	absent	direct	6–13	5.55	Nussbaum et al., 1982; Mitchell and Altig, 1983
<i>E. limbatus</i>	10.5	11.6	4	5	absent	direct	1	6.32	This paper
<i>Stumpffia tridactyla</i>	10–11	—	1	3	absent	larval ^d	—	6.5–9	Glaw and Vences, 1982
<i>E. orientalis</i>	11.0	11.6	4	5	absent	direct	1	6.56	This paper
<i>S. pygmaea</i>	10–12	12	4	5	absent	larval ^d	12–13	5.8–6	Glaw and Vences, 1982; F. Glaw, pers. comm.
<i>Brachycephalus nodoterga</i>	11.8	13.4	2	3	absent	direct	—	—	Heyer et al., 1990
<i>E. thorectes</i>	12.2	14.5	4	5	present	direct	3	6.06	Hedges, 1988, pers. obs.
<i>E. griphus</i>	12.5	17.0	4	5	present	direct	—	—	Crombie, 1986
<i>E. sisypodemus</i>	12.9	16.9	4	5	present	direct	10	—	Crombie, 1977; SBH, pers. obs.

^a Mean SVL (if known) or range; arranged in order of increasing male body size.

^b Functional number, not counting greatly reduced digits.

^c All species have direct development except *Stumpffia pygmaea* (and presumably *S. tridactyla*).

^d Eggs are deposited, and larvae develop, in foam nest in leaf litter.

cies of anurans possess vomerine teeth, but these are absent in the smallest species. The high frequency (5–9 kHz), insectlike, advertisement calls of diminutive anurans is primarily the result of a very small laryngeal apparatus.

Life-history traits also show patterns associated with miniaturization. For example, most anurans lay eggs in water and undergo a larval (tadpole) stage of development; this is considered to be the primitive mode of reproduction (Duellman and Trueb, 1986). In contrast, all of the smallest species lay eggs on land, and all but two undergo direct development within the egg. Even in the microhylid genus *Stumpffia*, larval development (nonfeeding tadpoles) takes place in a terrestrial foam nest, a unique reproductive mode in the family (Glaw and Vences, 1992). As expected, small body size also is associated with the smallest clutch sizes. Several of the diminutive species lay only a single egg, and the larger number for *S. pygmaea* (12–13) is, nonetheless, one of the smallest clutch sizes for a species with larval development (Duellman and Trueb, 1986). At the same time, the clutch size

for *Sooglossus gardineri* (6–13), is relatively large for the small body size of that direct-developing species. Parental care has been noted for *Stumpffia pygmaea* (Glaw and Vences, 1992), *Sooglossus gardineri* (Nussbaum, 1984), and suggested for *E. iberia* (this paper); and it has not been ruled out for the other diminutive species. These data suggest that very small body size, necessarily resulting in small clutches, has increased the relative investment per offspring and therefore created selection for life-history strategies (e.g., terrestrial eggs, direct development, parental care) that increase the survivorship of individual offspring.

COMPARATIVE MATERIAL EXAMINED

Eleutherodactylus limbatus.—Cuba: Santiago de Cuba Prov., Municipio Guamá, La Emajagua, near Pico Turquino (CARE 142); Holguín Prov., Mun. Moa, Farallones de Moa (CARE 294); Holguín Prov., Mun. Moa, Jaguaní (CARE 461-462); Holguín Prov., Mun. Sagua de Tánamo, Cupeyal del Norte (CARE 448); Guantánamo

Prov., Mun. El Salvador, Meseta del Guaso, La Hembrita (CARE 733 and 735). *Eleutherodactylus orientalis*.—Cuba: Guantánamo Prov., El Yunque de Baracoa, SW slope, 360–450 m (USNM 497646–647); El Yunque de Baracoa, summit, 565 m (USNM 497643–645).

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Fusion Complex of Abdominal Vertebrae 1–5 in Boxfishes (Tetraodontiformes; Ostraciidae): Reinterpreting Character Evolution

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Early workers consistently underestimated the number of vertebrae present in Ostraciidae, counting a fusion complex associated with the anterior portion of the vertebral column as the first vertebra. Tyler considered this complex to be reduced by progressive fusion, with these characters forming a linear transformation series from fusion of the first two vertebrae (Araconinae) to fusion of the first four vertebrae (Ostraciinae from the Indo-Pacific), culminating in the fusion of the first five vertebrae (Ostraciinae from the Atlantic). The present analysis, and some of Tyler's own observations, shed doubt on that interpretation, and indicate that the fusion series forms a "character complex" with the fusion of vertebrae 1 + 2 and 3 + 4 being synapomorphic for the Ostraciinae and that the fusion of vertebrae 2 + 3 in *Lactoria* and in *Acanthostracion* + *Lactophrys* are two independent events. Recognition of "complex characters" based on a priori assumptions of progressive evolution can lead to erroneous interpretations of character evolution.

O STRACIINE boxfishes have held the interest of ichthyologists for some time, primarily because their apparently simplified skeleton has been considered a case study in reductive evolution (Tyler, 1963). Cuvier (1805) first noted that *Acanthostracion quadricornis* has an unusually low vertebral count, supposedly 13. Günther (1870) reported that all ostraciine boxfishes had 14 vertebrae. Regan (1903) noted a difference in the counts for *Ostracion* and *Lactophrys*, with the former having 16 and the latter 14 vertebrae. These observations led Jordan

(1905) to conclude that ostraciine boxfishes have the lowest number of vertebrae of all fishes. Fraser-Brunner (1941) examined the same genera as Regan (1903), observed the same number of vertebrae but recognized diagnostic differences between precaudal and caudal elements. LeDanois (1961) later presented contradictory counts for the same fishes, further confusing the issue. Tyler (1963) finally resolved the question of the number of vertebrae, concluding that *A. quadricornis* has 19 whereas all other ostraciine boxfishes have 18 vertebrae. Tyler