

A New Spiny-tailed Iguana from Honduras, with Comments on Relationships within *Ctenosaura* (Squamata: Iguania)

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Ctenosaura oedirhina is described from specimens formerly referred to *C. bakeri* collected on Isla de Roatán, Honduras. A phylogenetic analysis of relationships within *Ctenosaura* based on 21 morphological characters indicates that although the new species is part of a monophyletic subgroup also containing *C. bakeri*, *C. clarki*, *C. defensor*, *C. palearis*, and *C. quinquecarinata*, it may not be the closest relative of *C. bakeri*. The results of the phylogenetic analysis also indicate that the taxon *Enyaliosaurus* is not phylogenetically separate from *Ctenosaura*; the former is a subgroup of the latter.

THE spiny-tailed iguanas, *Ctenosaura*, are iguanine lizards that inhabit arid to sub-humid lowlands of Mexico and Central America (Bailey, 1928; Etheridge, 1982). Bailey's (1928) revision of *Ctenosaura* is the most recent for this genus, but subsequently four of the species recognized by him—*brachylopha*, *brevirostris*, *erythromelas*, and *parkeri*—have been synonymized with other species (Smith, 1935, 1949; Duellman, 1965). No new species have been described since Bailey's revision.

Ctenosaura bakeri was described by Stejneger (1901) from two specimens collected on "Utila Island" (Isla de Utila), the westernmost of the Islas de la Bahía off the northern coast of Honduras. Bailey (1928) suggested that *C. bakeri* may also occur on nearby "Ruatan Island" (Isla de Roatán), and subsequent authors have either included Isla de Roatán as part of the range of *C. bakeri* (Barbour, 1928; Peters and Donoso-Barros, 1970; Etheridge, 1982) or referred specimens from this island to this taxon (Wilson and Hahn, 1973; Meyer and Wilson, 1973).

The specimens from Isla de Roatán referred to *C. bakeri* differ from those of Isla de Utila, the type locality, in several important morphological characters. Although morphological differences between organisms in allopatric populations could represent geographic variation within a single species, the particular differences between the specimens from these two islands suggest that the two populations may not even be one another's closest relatives. These differences include the absence, in the Roatán specimens, of two of the characters that are supposedly diagnostic for *C. bakeri*. Therefore, I describe a new species for the specimens from Isla de Roatán.

Ctenosaura oedirhina, n. sp.
(Figs. 1-2)

Ctenosaura bakeri Stejneger: Barbour, 1928:56 (in part); Peters and Donoso-Barros, 1970:105 (in part); Wilson and Hahn, 1973:114 (in part); MacLean et al., 1977:4 (in part); Etheridge, 1982:17 (in part).

Enyaliosaurus bakeri: Meyer and Wilson, 1973:24 (in part).

Holotype.—UF 28532, an adult female collected on 19 Aug. 1969 by D. E. Hahn approx. 4.8 km (converted from 3 miles) west of Roatán on the path to Flowers Bay, Isla de Roatán, Departamento de las Islas de la Bahía, Honduras, near sea level (less than 20 m elevation) (Fig. 3).

Paratypes.—UF 28530 (skeleton), 28531, 28533, same data as holotype; LSUMZ 22367-22371 (5 specimens), same locality and date as holotype, collected by L. D. Wilson; UF 28553, near French Harbor, Isla de Roatán, Departamento de las Islas de la Bahía, Honduras, collected 20 Aug. 1969 by D. E. Hahn; LSUMZ 22399, near Roatán, Isla de Roatán, Departamento de las Islas de la Bahía, Honduras, collected 20 Aug. 1969 by L. D. Wilson; BMNH 1938.10.4.82, Isla de Santa Elena, Departamento de las Islas de la Bahía, Honduras, collected 24 Oct. 1937 (?) by J. S. Coleman.

Etymology.—The specific epithet is an adjective from the Greek "oedos," a swelling, plus "rhinos," nose, in reference to the profile of the snout compared with those of other *Ctenosaura*.



Fig. 1. *Ctenosaura oedirhina*, n. sp. Photograph of the holotype, dorsal view.

Diagnosis.—*Ctenosaura oedirhina* is distinguished from all other *Ctenosaura* by its blunt, rounded snout (Fig. 2) resulting from inflation of the nasal capsule. In addition, *C. oedirhina* is distinguished from *C. acanthura*, *C. hemilopha*, *C. pectinata*, and *C. similis* by the enlargement of the scales on the proximal anterodorsal surface of the shank, a character shared with *C. bakeri*, *C. clarki*, *C. defensor*, *C. palearis*, and *C.*

quinquecarinata. *Ctenosaura oedirhina* can be distinguished from *C. clarki*, *C. defensor*, and *C. quinquecarinata* within this latter group by its larger maximum size (Table 1), mode of 24 rather than 25 presacral vertebrae, possession of four rather than two postmental scales, and separation of more than one of the first 10 whorls of enlarged and spinous caudal scales by two rather than one row of smaller scales. These



Fig. 2. *Ctenosaura oedirhina*, n. sp. Photographs of the head of the holotype, left, dorsal view, right, lateral view. Bar = 1 cm.

TABLE 1. MAXIMUM RECORDED SNOUT-VENT LENGTHS OF THE SPECIES OF *Ctenosaura*.

Species	Maximum recorded snout-vent length	Sex	Museum number	Reference
<i>acanthura</i>	243 mm	M	CAS 3858	This study
<i>bakeri</i>	210 mm	F	USNM 25324	Bailey, 1928
<i>clarki</i>	155 mm	M	CAS 143041	This study
<i>defensor</i>	155 mm	M	HM 3420	Bailey, 1928
<i>hemilopha</i>	ca 400 mm	M	—	Smith, 1972
<i>oedirhina</i>	247 mm	M	BMNH 1938.10.4.82	This study
<i>palearis</i>	254 mm	M	CAS 69308	This study
<i>pectinata</i> ^a	311 mm	M	MVZ 128902	This study
<i>quinquecarinata</i>	169 mm	M	—	Gicca, 1983
<i>similis</i>	489 mm	M	—	Fitch and Henderson, 1977

^a A skeleton (MVZ 39403) is estimated to have come from a specimen at least 400 mm snout-vent length.

characters occur also in *C. bakeri*, and all but the last occur also in *C. palearis*. *Ctenosaura oedirhina* is distinguished from *C. bakeri* and *C. palearis* by its relatively slightly compressed dorsal crest scales and the absence of a pendulous dewlap. Other comparisons are presented in the sections on differences between *C. bakeri* and *C. oedirhina* and the phylogenetic relationships of *C. oedirhina*.

Description of holotype.—The holotype is an adult female with a snout-vent length of 203 mm. The tail measures 291 mm, but the tip may be missing.

Head 41.5 mm from tip of snout to anterior margin of auricular opening; 35 mm wide at broadest point. Snout region enlarged; snout blunt in lateral view (Fig. 2). Scales in dorsal snout region enlarged relative to other head scales, smooth and slightly convex. Rostral subrectangular, ca two and one-quarter times as wide as deep, larger than mental. Nostrils large, directed laterally. Nasals separated from rostral by at least two postrostrals. Supraorbital semicircles separated medially by two rows of frontals at narrowest point. Supraoculars decreasing in size laterally. Frontoparietal region concave medially. Interparietal larger than surrounding scales; parietal organ visible externally. Temporal region rugose, temporals larger than nuchals. Canthal series consisting of a larger anterior canthal and a smaller, slightly keeled posterior canthal. Anterior canthal separated from nasal by narrow postnasal. Eight (left) and nine (right) superciliaries. Anterior superciliaries elongate and strongly overlapping. One preocular separating posterior canthal from first subocular. Six enlarged suboculars, first five

keeled, second subocular ca five times longer than tall. Loreals flat; lorilabials in three or four rows below loreals, decreasing to two rows below second subocular. Ten supralabials on left, nine on right. Nine sublabials. Four postmentals, lateral pair small, squarish, medial pair larger and crescentic. One pair of enlarged chinshields posterior to postmentals. Scales in gular region elongate laterally, rounded medially. Medial gulars smaller than ventral body scales. Gular fold distinct; scales within fold small and granular. Dewlap absent.

Neck thicker than head; neck skin loose and folded laterally. Body stout. Dorsal body scales on neck granular, increasing slightly in size and becoming flattened and slightly imbricate posteriorly, those on posterior two-thirds of body faintly keeled. Scales of middorsal row strongly keeled and forming a low crest, which is interrupted for ca 0.5 cm in sacral region. Maximum height of crest scales ca 2 mm, maximum length ca 2.5 mm, reached in shoulder region. Ventral body scales larger than dorsals, slightly imbricate and unkeeled.

Scales of forelimb small, imbricate, and slightly carinate dorsally; smaller, less imbricate, and unkeeled ventrally. Subdigital scales of manus tricarinate. Thigh scales largest anteriorly, smaller dorsally and ventrally; those of dorsal surface faintly keeled. Ten femoral pores on each side. Shank bears patch of enlarged, strongly keeled scales on proximal anterodorsal surface. Pedal subdigital scales mostly tricarinate; some of proximal subdigitals of digits three and four lacking central keel. Subdigital scales of digits two and three with enlarged anterior keels, especially those of proximal phalanx.

Tail not strongly constricted at insertion. Tail bears whorls of enlarged, spinous scales con-

fined to dorsal and lateral surfaces. First three whorls of enlarged, spinous scales separated by two rows of smaller scales (intercalary scales) dorsally, next six separated by one such row, the remainder separated by two rows. Intercalary scales gradually increasing in size and spinosity relative to enlarged, spinous scales posteriorly until distinction vanishes and tail is encircled by consecutive whorls of spinous scales. Whorls themselves become indistinct at distal end of tail.

In alcohol, dorsal head and body chocolate brown with large, cream (medially) to white (laterally) blotches arranged in bands on trunk; small, cream-colored spots covering more than one scale on neck, shoulders, and posterior part of trunk; and small cream-colored flecks confined to one or part of one scale on head. Arms and legs more or less uniform chocolate brown dorsally, paler brown ventrally. Ventral surface of head uniform chocolate brown; ventral surface of body also chocolate brown but with a few small, cream-colored spots laterally. Ground color of dorsal surface of tail dark brown proximally, becoming progressively paler distally; scales with paler coloration, which are cream-colored proximally but pale brown distally, localized to form bands. Bands most distinct in middle of tail. Ventral surface of tail paler than dorsal and banding less distinct.

The holotype has seven premaxillary teeth and tricuspid posterior marginal teeth. A radiograph of the holotype reveals that it has 24 presacral vertebrae, two sacral vertebrae, 50 caudal vertebrae, eight cervical vertebrae, four cervical ribs, four sternal ribs, two xiphisternal ribs, one pair of midventrally continuous postxiphisternal inscriptional ribs that are continuous with their corresponding bony ribs, and one pair of postxiphisternal inscriptional ribs that fail to meet midventrally and fail to connect with their corresponding bony ribs dorsally. All trunk vertebrae bear articulating ribs. The phalangeal formula of manus is 2:3:4:5:3; that of the pes is 2:3:4:5:4. The distal phalanges of right pedal digit five and left pedal digit four are missing. The specimen contains numerous, irregular, radio-opaque masses of dust shot; its left femur is shattered distally; and its ventral surface has three incisions into the body cavity. The colon of this specimen has been described by Iverson (1980).

Variation (means in parentheses).—Snout-vent lengths in *C. oedirhina* range from 58 mm in UF 28553 to 247 mm in BMNH 1938.10.4.82. In-

flation of the nasal capsule is not obvious in specimens less than 100 mm snout-vent length. One or two scales separate nasal and rostral. In one specimen, UF 28553, a single median row of frontals separates the supraorbital semicircles. The frontoparietal region undergoes an ontogenetic change from convex to flat to concave. Rugosity of the temporal region also increases ontogenetically. Two or three canthals, one or two keeled. Eight to 12 (9.7) superciliaries. Four to seven (5.5) suboculars second usually largest, rarely first or third. All or all but last subocular keeled. Rarely (one side of one out of 12 specimens) two preoculars separate first subocular and posterior canthal. Rarely (one out of 12 specimens) minimum of three rows of lorilabials below suboculars. Eight to 10 (9.7) supralabials. Eight to 11 (9.6) sublabials. Three or usually four postmentals; medial pair subequal to or larger than lateral pair. Neck thicker than head only in holotype; most specimens less robust than holotype. Height of scales of mid-dorsal crest varies ontogenetically and possibly sexually: crest scales longer than tall in juveniles, increasing in relative height ontogenetically until they become ca three times as tall as long. Maximum height of crest scales ca 6 mm. In LSUMZ 22399 the middorsal scale row is not interrupted in the sacral region. Nine to 13 (11.2) femoral pores. Ratio of tail length to snout-vent length ranges from 1.61–2.16 (1.86) in specimens with entire tails. Number of intercalary scale rows between whorls of enlarged, spinous scales variable, usually two between first two whorls and always one in at least some of the first 10 whorls.

In alcohol, head and body of specimens 71 mm SVL or less are uniform dark brown dorsally, paler ventrally. Specimens from 110–163 mm SVL have alternating brown and grey bands on the body, sometimes with whitish spots along the posterior edges of the brown (darker) bands. All specimens over 172 mm SVL have alternating cream-colored and dark brown bands, but the size of the cream-colored bands varies considerably. The tail is banded in all specimens, but the distinctness of the banding is variable. The ventral body surface becomes darker with age until it is nearly as dark as the brown of the dorsal surface.

The number of premaxillary teeth ranges from 6–7 (6.8). Radiographs of five specimens with complete tails reveal a range from 54–61 (58) caudal vertebrae.

Distribution.—*Ctenosaura oedirhina* is known only

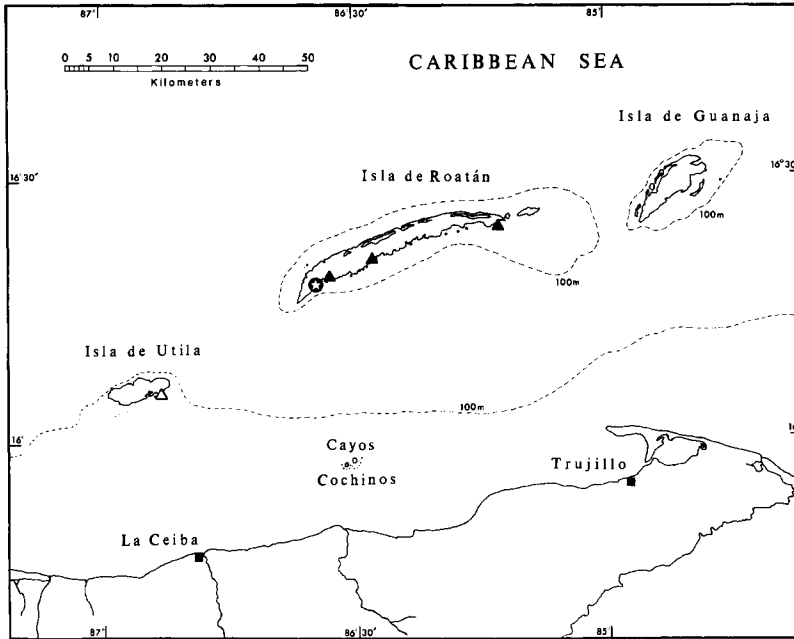


Fig. 3. Distribution of *Ctenosaura oedirhina* and *C. bakeri* in the Islas de la Bahía, Honduras. Locality records for *C. oedirhina* are designated with black triangles and a star (type locality); that for *C. bakeri* is designated with an open triangle.

from Isla de Roatán and its satellite Isla de Santa Elena, Departamento de Islas de la Bahía, Honduras (Fig. 3). In addition to the type locality, ca 5 km west of Roatán, specimens have been collected near Roatán, near French Harbor, and on Isla de Santa Elena (no further data). Although these localities span the length of the island, they are all on its south side.

Natural History.—Little is known about the natural history of *C. oedirhina*. Wilson and Hahn (1973) reported that most of the 11 specimens collected by them were taken on large coral accumulations along the beach. They also collected a juvenile further inland sleeping suspended on a portion of the whorl of thorns on the trunk of a thorn palm.

Half of the 12 specimens of *C. oedirhina* had mites in their nasal passageways that could be seen by looking into the external nares. During skeletal preparation of one of these specimens (UF 28530), 20 mites were removed from the nasal passageways. Mites may be present deeper in the nasal passageways of those specimens in which the mites could not be seen by looking into the external nares. The inflation of the nasal capsule in *C. oedirhina* may in some way be related to the presence of large numbers of

nasal mites. Two specimens had ticks attached in the sacral region, one dorsally and the other ventrally.

Differences between C. bakeri and C. oedirhina.—Although formerly considered to be part of *C. bakeri*, *C. oedirhina* can be distinguished from *C. bakeri* by several characters. The middorsal scale row of *C. bakeri* consists partly of large, strongly compressed, flap-like scales, which are most prominent in the neck and shoulder regions. The scales of the middorsal row in *C. oedirhina* are smaller and are not strongly compressed and flap-like. The middorsal scales of *C. bakeri* develop their characteristic morphology in post-embryonic ontogeny, and those of juveniles are relatively small and are not strongly compressed. Nevertheless, juveniles of the two species can be distinguished by the fact that in *C. bakeri* the individual scales of the middorsal row are separated by gaps, while in *C. oedirhina* they follow one another immediately. Another difference between *C. bakeri* and *C. oedirhina* is that in the former the nasal and rostral are separated by three scales, while in the latter the nasal and rostral are separated by one or two scales.

Other characters differ consistently between

TABLE 2. DIFFERENCES BETWEEN *Ctenosaura bakeri* AND *C. oedirhina* IN NUMBERS OF FEMORAL PORES AND NUMBERS OF LORILABIAL SCALE ROWS SEPARATING LARGEST SUBOCULAR AND SUPRALABIALS.

	Number of femoral pores				t	Number of lorilabial scale rows				
	N	Range	Mean	SD		N	Range	Mean	SD	t
<i>C. bakeri</i>	5*	15–19	16.8	1.64	5.5*	4	2–3	2.1	0.29	6.2*
<i>C. oedirhina</i>	12	19–26	22.5	2.07		12	3	3	0.00	

* $P < 0.005$.

* Additional data from Bailey (1928).

C. bakeri and *C. oedirhina* but are less effective for identifying individual specimens because they develop in post-embryonic ontogeny and, therefore, cannot be used with juveniles. Two such characters are a small dewlap, which develops in *C. bakeri* (Stejneger, 1901; Bailey, 1928: Pl. 22a) but not in *C. oedirhina* (Fig. 2), and an inflated nasal capsule, which develops in *C. oedirhina* (Fig. 2) but not in *C. bakeri* (Bailey, 1928: Pl. 22a).

There are also significant differences between the two species in the number of femoral pores and the number of lorilabial rows below the suboculars (Table 2), but the ranges overlap so that although these characters can be used to distinguish populations, they cannot necessarily be used to identify individual specimens.

Phylogenetic relationships of C. oedirhina.—*Ctenosaura oedirhina* not only differs from *C. bakeri*, with which it was formerly considered to be conspecific, but it also lacks two derived characters that *C. bakeri* shares with *C. palearis*, presence of a dewlap and a flap-like middorsal crest

scales. These characters suggest that *C. oedirhina* and *C. bakeri* are not even one another's closest relatives. Elsewhere (de Queiroz, 1985) I analyzed relationships within *Ctenosaura* excluding *C. oedirhina*. I now present a reanalysis of relationships within this taxon, including the new species, based on the following 21 characters representing a minimum of 25 phylogenetic transformations. The polarities of these characters were inferred using other iguanines as outgroups. Character state codes are as follows: 0 = ancestral, 1 = derived, 2 = derived from 1, etc. Letter codes are used for characters whose polarities were uncertain based on the outgroup evidence.

1) Maximum snout–vent length (Table 1): 0) greater than 190 mm; 1) less than 190 mm.

2) Modal number of presacral vertebrae (Table 3): 0) 24; 1) 25.

3) Modal number of premaxillary teeth (Table 4): 0) seven; 1) five.

4) Contacts of bones in the anterior orbital region (de Queiroz, 1985): A) lacrimal contacts palatine behind lacrimal foramen; B) prefrontal contacts jugal behind lacrimal foramen.

TABLE 3. NUMBERS OF PRESACRAL VERTEBRAE IN DIFFERENT SPECIES OF *Ctenosaura*. Figures given are percentages of the total numbers of specimens. Modes are underlined. Numbers between columns represent specimens with sacral asymmetries.

Species	N	Number of presacral vertebrae			
		24	25	26	27
<i>acanthura</i>	5	<u>100</u>			
<i>bakeri</i>	4	<u>100</u>			
<i>clarki</i>	10		<u>90</u>	10	
<i>defensor</i>	5		<u>40</u>	20	20
<i>hemilopha</i>	22	<u>100</u>			
<i>oedirhina</i>	11	<u>100</u>			
<i>palearis</i>	8	<u>100</u>			
<i>pectinata</i>	13	<u>100</u>			
<i>quinquecarinata</i>	12	8	<u>92</u>		
<i>similis</i>	6	<u>83</u>	17		

TABLE 4. NUMBERS OF PREMAXILLARY TEETH IN DIFFERENT SPECIES OF *Ctenosaura*. Figures given are percentages of the total numbers of specimens. Modes are underlined.

Species	N	Number of premaxillary teeth				
		5	6	7	8	9
<i>acanthura</i>	5			<u>80</u>	20	
<i>bakeri</i>	4		25	<u>75</u>		
<i>clarki</i>	9	11	11	<u>67</u>		11
<i>defensor</i>	5	<u>80</u>	20			
<i>hemilopha</i>	15			<u>100</u>		
<i>oedirhina</i>	11		18	<u>82</u>		
<i>palearis</i>	8			<u>100</u>		
<i>pectinata</i>	24		4	<u>83</u>	8	4
<i>quinquecarinata</i>	11	9	18	<u>73</u>		
<i>similis</i>	18		11	<u>67</u>	17	6

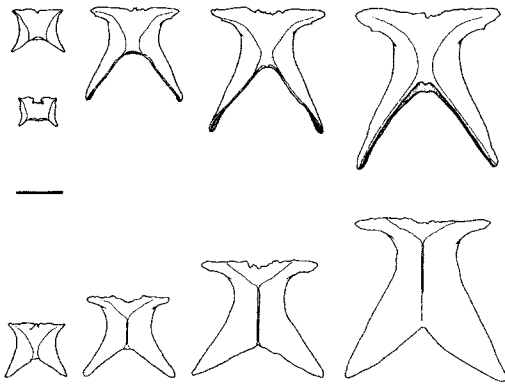


Fig. 4. Dorsal views of the parietal bones from ontogenetic series of *Ctenosaura similis* (top) and *C. pectinata* (bottom). Museum numbers for *C. similis* (smallest to largest): MCZ 22662, 27207, 25993, MVZ 79583, 40119; for *C. pectinata*: MCZ 11350, 2176, 5016, 5015. Bar = 1 cm.

5) Cristae cranii (de Queiroz, 1985): 0) form smooth curve from frontal to prefrontal; 1) frontal portion protrudes anteriorly forming a step from frontal to prefrontal.

6) Parietal roof (Fig. 4) (Smith, 1949; Ray and Williams, unpubl.): 0) remains deeply notched posteriorly throughout ontogeny so that the braincase is broadly exposed in dorsal view; 1) extends posteriorly during postembryonic ontogeny so that the braincase comes to be largely covered in dorsal view.

7-8) Crowns of posterior marginal teeth (de Queiroz, 1985): A0) with a maximum of four cusps; B0) with a maximum of five or more cusps; A1) with a maximum of three cusps.

9) Number of postmental scales: A) usually four; B) usually two.

10) Pendulous dewlap (Bailey, 1928): 0) absent; 1) present but small; 2) present and large.

11) Parietal eye (de Queiroz, 1985): 0) conspicuous externally; 1) external signs inconspicuous or absent.

12) Dorsal crest scales I (Bailey, 1928): 0) not strongly compressed; 1) strongly compressed.

13) Dorsal crest scales II (Ray and Williams, unpubl.): 0) large scales not separated by smaller scales; 1) large scales separated by one or more smaller scales.

14) Dorsal crest scales III (Ray and Williams, unpubl.): 0) conform in color and pattern with adjacent body scales; 1) uniform in color and not conforming in color and pattern with adjacent body scales.

15) Dorsal crest scales IV (Bailey, 1928): 0)

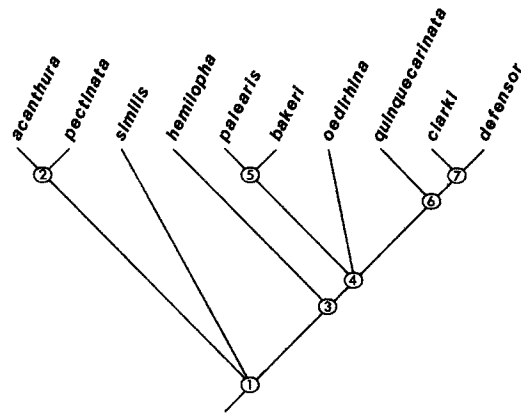


Fig. 5. Cladogram of relationships within *Ctenosaura*. Synapomorphies of the various taxa are given below with number and letter codes corresponding with those in the character list. Homoplastic characters are underlined. Node 1: see de Queiroz (1985); Node 2: 6-1; Node 3: 20-1; Node 4: 17-1; Node 5: 10-1, 12-1; Node 6: 1-1, 2-1, 9-B, 20-2; Node 7: 15-1, 16-1 (polymorphism), 19-1; *acanthura*: no synapomorphies identified; *pectinata*: no synapomorphies identified; *similis*: no synapomorphies identified; *hemilopha*: 16-1; *palearis*: 10-2, 13-1, 14-1, 20-2; *bakeri*: 8-1; *oedirhina*: 8-1, 21-1; *quinquecarinata*: 8-1; *clarki*: 4-B; *defensor*: 3-1, 5-1, 7-A, 11-1, 17-2, 18-1, 20-3.

high-keeled, large, and conspicuous, at least in neck region of large males; 1) low-keeled to flat, inconspicuous throughout length of crest even in large males.

16) Middorsal scale row (Ray and Williams, unpubl.): 0) continuous from neck onto tail or narrowly interrupted in sacral region; 1) broadly discontinuous in lumbosacral region.

17) Scales on anterodorsal surface of leg (Bailey, 1928): 0) neither enlarged nor spinous; 1) enlarged and strongly keeled or spinous on shank but not or only slightly enlarged and spinous on thigh; 2) enlarged and spinous on both shank and thigh.

18) Subdigital scales at the base of pedal digit III (de Queiroz, 1985): 0) with anterior keels subequal to posterior keels or anterior keels enlarged but not united at bases; 1) with enlarged anterior keels united at their bases to form a comb.

19) Tail (Ray and Williams, unpubl.; de Queiroz, 1985): 0) strongly spinose proximally but not distally, always longer than body (snout-length/total length = 0.27-0.45), and with more than 30 caudal vertebrae; 1) tail strongly spinose throughout its length, almost same

TABLE 5. DISTRIBUTION OF CHARACTER STATES OF 21 CHARACTERS AMONG SPECIES OF *Ctenosaura* AND THREE CLOSE AND TWO MORE DISTANT OUTGROUPS. Character state codes correspond with those in the character list. A dash indicates lack of data; N indicates a noncomparable condition in the outgroup.

Taxon	Character																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<i>acanthura</i>	0	0	0	A	0	1	A	0	A	0	0	0	0	0	0	0	0	0	0	0	0
<i>bakeri</i>	0	0	0	—	—	0	A	1	A	1	0	1	0	0	0	0	1	0	0	0	1,0
<i>clarki</i>	1	1	0	B	0	0	A	0	B	0	0	0	0	0	1	0,1	1	0	1	2	0
<i>defensor</i>	1	1	1	A	1	0	B	0	B	0	1	0	0	0	1	0,1	2	1	1	3	0
<i>hemilopha</i>	0	0	0	A	0	0	A	0	A	0	0	0	0	0	0	1	0	0	0	1	0
<i>oedirrhina</i>	0	0	0	A	0	0	A	1	A	0	0	0	0	0	0	0	1	0	0	1,0	1
<i>palearis</i>	0	0	0	A	0	0	A	0	A	2	0	1	1	1	0	0	1	0	0	2	0
<i>pectinata</i>	0	0	0	A	0	1	A	0	A	0	0	0	0	0	0	0	0	0	0	0	0
<i>quinquecarinata</i>	1	1	0	A, B	0	0	A	1	B	0	0	0	0	0	0	0	1	0	0	2	0
<i>similis</i>	0	0	0	A	0	0	A	0	A	0	0	0	0	0	0	0	0	0	0	0	0
Galápagos iguanas	0	0	0	B	0, 1	0	A	0, 1	A, N	0	0	0	0, 1	0	0	0	0	0	0*	N	0
<i>Iguana</i> and <i>Cyclura</i>	0	0	0 ^b	A, B	0	0	B	0	A, B	1, 2	0	0	0	0	0	0	0, 1	0, 1	0*	0, N	0, 1
<i>Sauromalus</i>	0	0	1 ^c	A	0	0	B	0	A, B	0	0	N	N	N	N	1 ^d	0 ^e	0	0*	N	0
<i>Dipsosaurus</i>	1	0	0	A	0	0	A	0	B	0	0	0	0	0	1	0	0	0	0*	N	0
<i>Brachylophus</i>	0	0	0	A	0	0	A	0, 1	—	0, 1	0	0	0	0	0	0	0	0	0*	N	0

* Among the outgroups, spinose tails occur only in *Cyclura*.

^b Greater than seven in *Cyclura*.

^c Some species have modes of four and six.

^d Middorsal row entirely absent.

^e Slightly enlarged and keeled in *S. aspidus*.

length as body (snout-vent length/total length = 0.48–0.56), and with fewer than 30 caudal vertebrae.

20) First 10 whorls of strongly spinous caudal scales: 0) separated from one another by at least two rows of intercalary scales; 1) at least some separated by only one intercalary scale row, others by two or more; 2) except sometimes the first, all separated by one intercalary scale row; 3) intercalary scales reduced or absent.

21) Snout region: 0) not inflated, sloping gradually downward; 1) inflated and sloping abruptly downward.

The distributions of these characters among the species of *Ctenosaura* and three near and two more distant iguanine outgroups (de Queiroz, 1985) are given in Table 5. The phylogenetic relationships within *Ctenosaura* suggested by these characters are presented in Figure 5. This cladogram is the result of an attempt to minimize the number of character transformations required by the data. Because of the relatively high congruence among characters, the minimum step cladogram was determined without the use of a computer program. Characters whose polarities could not be determined by outgroup comparison were placed on the cladogram after it was constructed from the characters whose polarities could be determined.

Ctenosaura oedirhina appears to belong to a monophyletic group within *Ctenosaura* composed of itself, *hemilopha*, *palearis*, *bakeri*, *quinquecarinata*, *clarki*, and *defensor* (node 3, Fig. 5). Members of this monophyletic group are distinguished from other ctenosaurs by a reduction in the number of intercalary scale rows between the whorls of enlarged, spinous caudal scales (character 20-1, 2, or 3). Within this monophyletic group, *C. oedirhina* also belongs to a less inclusive monophyletic group composed of all of the species in the first group except *hemilopha* (node 4, Fig. 5). Members of this less inclusive group are distinguished from other ctenosaurs by their possession of enlarged, spinous scales on the anterodorsal surface of the shank (17-1 or 2). Various authors (Gray, 1845; Smith and Taylor, 1950; Villa R. and Scott, 1967; Peters and Donoso-Barros, 1970; Meyer and Wilson, 1973) have recognized part or all of this monophyletic group as a separate genus, *Enyaliosaurus*. Nevertheless, because the most recent common ancestor of the species of *Ctenosaura* also appears to be an ancestor of *Enyaliosaurus*, a monophyletic (sensu

Hennig, 1966) *Ctenosaura* must contain *Enyaliosaurus* as a subgroup, and the latter cannot then be a separate taxon.

Within this less inclusive monophyletic group (node 4, Fig. 5), the relationships of *C. oedirhina* are uncertain. The new species shares a derived reduction in marginal tooth cusps (8-1) with *C. bakeri* and *C. quinquecarinata*; however, the distributions of other characters and the relationships implied by them suggest that this similarity is homoplastic. *Ctenosaura bakeri* shares the presence of a dewlap (10-1 or 2) and highly compressed crest scales (12-1) with *C. palearis*. These derived characters are absent in *C. oedirhina*. Although *C. oedirhina* and *C. bakeri* occur only about 40 km apart and both species are endemic to the Islas de la Bahía, distributional and bathymetric data are equally consistent with a sister group relationship between *C. bakeri* and *C. palearis* as suggested by the morphological characters. A population of *C. palearis* occurs only about 75 km from Utila Island, where *C. bakeri* occurs, in the valley of the Río Aguán, Honduras (Meyer and Wilson, 1973). Furthermore, Utila lies within the 100 m depth contour of the mainland (Fig. 3). Because sea level in the Caribbean dropped 100–120 m below its present level during the Pleistocene glacial periods (Pregill and Olson, 1981; Buskirk, 1985; and references therein), Utila was probably continuous with the Central American mainland at some time or times during the Pleistocene. In contrast, Roatán lies outside the 500 m depth contour of the mainland and presumably has been separated from the mainland for a longer time.

Ctenosaura quinquecarinata shares a reduced body size (1-1), an increase in the modal number of presacral vertebrae (2-1), a reduction in the number of postmental scales (9-B), and a reduction in the number of intercalary scales between whorls of enlarged caudal scales (20-2 or 3) with *C. clarki* and *C. defensor*. Again, these derived characters are absent in *C. oedirhina*. Except for the last character, which is present in *C. palearis*, they are also absent in *C. bakeri* and *C. palearis*. *Ctenosaura quinquecarinata* and its closest relatives are geographically more distant from *C. oedirhina* than are *C. bakeri* and *C. palearis*. *Ctenosaura clarki* occurs in the valley of the Río Tepalcatepec, Michoacán, Mexico (Duellman and Duellman, 1959); *C. defensor* is found in the Yucatán Peninsula in the Mexican states of Campeche and Yucatán (Duellman, 1965); and *C. quinquecarinata* is made up of dis-

junct populations distributed from the Tehuantepec area of Oaxaca, Mexico to the province of Guanacaste, Costa Rica (Gicca, 1983).

Thus, the weight of the evidence suggests that *C. bakeri* is most closely related to *C. palearis* and that *C. quinquecarinata* is most closely related to *C. clarki* and *C. defensor*. If these relationships are accepted, then the shared reduction in marginal tooth cusps in *C. bakeri*, *C. oedirhina*, and *C. quinquecarinata* has either arisen separately in these three taxa or it was present in the most recent common ancestor of all the taxa united above node 4 (Fig. 5) and, therefore, provides no information about relationships within this group. The second alternative also requires that greater cuspsation was reevolved in two separate lineages, one leading to *C. palearis* and the other leading to *C. clarki* and *C. defensor*.

Because *C. oedirhina* lacks the derived characters shared by *C. bakeri* and *C. palearis* (node 5, Fig. 5) as well as those shared by *C. quinquecarinata*, *C. clarki*, and *C. defensor* (node 6; Fig. 5), the new species cannot be considered to belong to either of these monophyletic groups. Nevertheless, it is possible that *C. oedirhina* is the sister group of one or the other of these two monophyletic groups, although none of the characters used in the present analysis support such relationships.

Another possibility is that *C. oedirhina* is the sister group of all the other taxa stemming from node 4. This possibility is supported by the derived tail morphology (20-2 or 3) shared by all taxa, except the new species and *C. bakeri*, stemming from node 4. If *C. bakeri* is the sister group of *C. palearis*, then some form of homoplasy is involved in this character. Perhaps the former taxon has reevolved secondarily a seemingly primitive tail. Alternatively, *C. bakeri* may retain a relatively primitive tail morphology, in which case the derived conditions seen in *C. palearis* on the one hand and the group composed of *C. quinquecarinata*, *C. clarki*, and *C. defensor* would be interpreted as convergent. Under the second interpretation, however, there is no reason to think that *C. oedirhina* is the sister group of all the other taxa stemming from node 4.

Considering alternative interpretations of character transformations suggests another possibility about relationships within this group (node 4). *Ctenosaura palearis* may be the sister group of the group composed of *C. quinquecarinata*, *C. clarki*, and *C. defensor*, a relationship suggested by the derived tail morphology (20-

2 or 3) shared by these taxa. *Ctenosaura bakeri* and *C. oedirhina* lack this derived condition, and a sister group relationship between them is suggested by a shared, derived tooth crown morphology (8-1), which would be interpreted as convergent in *C. quinquecarinata*. These relationships would require the presence of a dewlap (10-1) and a derived dorsal crest scale morphology (12-1) are convergent in *C. bakeri* and *C. palearis*. In light of this alternative hypothesis of relationships, a more conservative view of relationships within *Ctenosaura* than that presented in Figure 5 would not recognize a sister group relationship between *C. bakeri* and *C. palearis*. Instead, it would leave unresolved the relationships among *C. bakeri*, *C. palearis*, *C. oedirhina*, and the monophyletic group composed of *C. quinquecarinata*, *C. clarki*, and *C. defensor*.

Ctenosaura oedirhina possesses at least one character that is derived relative to all other *Ctenosaura*, an inflated snout region (21-1). Consequently, *C. oedirhina* must be considered a monophyletic species; that is, it cannot be considered ancestral to any other known species of *Ctenosaura*.

MATERIAL EXAMINED

Ctenosaura acanthura: AMNH 46483, CAS 3858, MVZ 129245, SDSNH 47004, 59542-3, USNM 220217-8. *C. bakeri*: LSMZ 22275, 22293, UF 28437, 28471. *C. clarki*: CAS 143041, JMS 1544, MCZ 22454, MVZ 76689-95, 79256, 79293, 160015-6, 162068-72, 164865-6, 164923, RE 57, 184, USNM 21450. *C. defensor*: UF 41534, KU 70261-2, 75528, MCZ 7095. *C. hemilopha*: JMS 287-9, 291, X366, X631-2, X634-5, MVZ 21923, 136691, RE 325, 491, 497-8, 502, 1087, 1341, 1386, 1887, 1964, SDSNH 48480, 48976, 55290, 57114. *C. oedirhina*: BMNH 1938.10.4.82, LSMZ 22367-71, 22399, UF 28530-33, 28553. *C. palearis*: CAS 69297, 69299, 69307-8, 69310, MCZ 22390, 22399, MVZ 162073-5, 162304-5. *C. pectinata*: JMS 238, 242, 250, 269, 692, 696, 704, 1252, MCZ 2176, 5013-21, 11350, MVZ 39403, 44990-1, 128902, RE 56, 419-21, 490, 641, SDSNH 55291. *C. quinquecarinata*: AMNH 77640, CAS 73554-62, MCZ 24903, MVZ 79294, 128903. *C. similis*: AMNH 38949, JMS 178, MCZ 5011, 5457, 5799, 9566, 10312, 21742, 22662, 25993, 26968, 27207, 36830, 139421, MVZ 40119, 79583, 79847-8, RE 469, 2003, 2233, 2238.

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