Rev. Biol. Trop., 41 (3): 817-842, 1993

A review of the status and biogeography of the lizard genera *Celestus* and *Diploglossus* (Squamata: Anguidae), with description of two new species from Costa Rica

Jay M. Savage and Karen R. Lips
Department of Biology, University of Miami, P.O. Box 249118, Miami, Florida 33124, USA.

(Rec. 17-IX-1992. Acep. 5-II-1993)

Abstract: Two new species of diploglossine lizards, *Celestus hylaius* and *Celestus orobius*, are described from the Atlantic lowlands and Cordillera de Talamanca of Costa Rica, respectively. The species differ from previously known *Celestus* primarily in coloration but also in details of scutellation (number of middorsal scale rows, lamellae under the 4th toe and/or number of preanal scales). The status of the genera *Celestus* and *Diploglossus* is reviewed. The allocation of species to either of these taxa based on the architecture of the osteoderms is rejected since the presumed differences represent ontogenetic stages. The traditional classification whereby species having claw sheaths are placed in *Diploglossus* and those without in *Celestus* is resurrected. Under this arrangement *Celestus* is composed of 7 Mexican and Central Am rican and 16 Antillean forms while *Diploglossus* includes 6 southern Central and South American and 4 Antillean species. The Hispaniolan endemic genera *Sauresia* (2 species) and *Wetmorena* (1 species) are regarded as derived allies of *Diploglossus*. *Celestus* and *Diploglossus* are sympatric only in lower Central America but *Celestus* occurs in sympatry with *Sauresia* and *Wetmorena* on the island of Hispaniola. The biogeography of diploglossines is reviewed with special emphasis on the Caribbean region. Two conflicting biogeographic models (one dispersal and one vicariance) that purport to explain current distribution patterns (*Celestus* in Mexico, Central America, Jamaica, Cayman Islands and Hispaniola; *Diploglossus* in Lower Central America, South America, Cuba, Puerto Rico, Montserrat and Malpelo Islands, and its allies *Sauresia* and *Wetmorena* on Hispaniola) are examined. Area cladograms and predicted phylogenetic relationships of circum-Caribbean forms based on each model are presented. Rejection, acceptance or modification of either model must await more detailed phylogenetic analyses. The vicariance model, however, is shown to be the most parsimonious explanation of diploglossine biogeography based upon available data.

Key words: Lizards, Anguidae, *Celestus*, *Diploglossus*, new species, biogeography.

In 1959, the first of many field parties from the University of Southern California set out to collect herpetological material in Costa Rica and obtained a single diploglossine lizard from the Cordillera de Talamanca. The specimen was tentatively identified as *Celestus cyanochloris* Cope, a species then known only from the Cordillera Central of Costa Rica, although differing from that form in details of scutellation and colouration. Since that time more material of *C. cyanochloris* has accumulated, and the difference between it and the Talamancan specimen remains. This leads us to regard the latter as representative of a previously unrecognized species. Unfortunately, although considerable effort has been expended in searching for other examples of the new form, none have been forthcoming and its description is based on the unique type.

In addition, some two decades ago another apparently undescribed *Celestus* was discovered by Michael J. Corn (MJC). Corn collected five specimens of the putative new form from the extensive Río Frio banana plantation in Heredia Province. Subsequently, University of Southern California field teams obtained several lizards conspecific with Corn's specimens from the La Selva Biological Station of the Organization for Tropical Studies, also in Heredia Province, as part of an intensive study of the leaf-litter herpetofauna (Lieberman 1986).

Although for some years Corn intended to describe the Atlantic lowland lizards as a new species and had collected considerable data on mainland *Celestus* for that purpose, he ultimately abandoned the project. This was due, at least in part, to his uncertainty regarding variation in *Celestus cyanochloris*, then known from three specimens (counting the holotype), a species that he had not seen in life, and in part, to the relationship of his Atlantic lowland form to *Celestus bivittatus* Boulenger known from a single juvenile from Nicaragua. More importantly, however, he failed to include in his study several scale counts that prove to be decisive in distinguishing among Mexican and Central American members of the genus, and indeed establish the Atlantic Costa Rican population as a distinct species.

The present paper serves to describe these two new species so that they may be included in the senior author's comprehensive handbook on the herpetofauna of Costa Rica. As part of the process of demonstrating the validity of the three Costa Rican taxa we have examined most of the specimens of *Celestus* available from Mexico and Central America. We also redescribe *Celestus cyanochloris* based on newly acquired specimens. Consequently we provide summary characterizations of all mainland forms in the genus and document their distributions. In addition we review the characteristics and status of the genera *Celestus* and *Diploglossus* and develop an original biogeographic hypothesis to explain current patterns of distribution.

MATERIAL AND METHODS

Data used in this paper are from specimens located in several collections. Where reference is made to a particular example, the abbreviation denoting the source follows Leviton *et al.* (1985).

Scale counts were made with a variety of binocular microscopes under different magnifications using a sharp teasing needle. Counts were made following the procedures defined and/or illustrated by Peters (1964), with snout-vent length designated as standard length. Measurements were made to the nearest 0.01 mm with dial calipers.

Colour notes in life for *Celestus cyanochloris* and *C. hylaius* were taken from colour slides projected onto a screen, and diagrammatic figures of colour patterns were sketched from preserved specimens.

Status of the genera *Celestus* and *Diploglossus* on the American mainland: The evolutionary lineage (subfamily Diploglossinae) to which our new species belong contains a single fossil, *Eodiploglossus borealis*, from the Eocene of Wyoming (Gauthier 1982) and 38 extant forms referred to four or five genera. Diploglossines differ from other anguids in the following combination of features: skinklike in habitus; limbs present but variously reduced; body covered by cycloid scales that are underlain by osteoderms having a distinctive, peaked, gliding surface (the basal non-sculptured surface); a thin, pointed, "quill pen-shaped" anterior end of surangular; frontal bones paired; frontal and maxillary bones in contact; and lacking palatine and pterygoid teeth and any evidence of a lateral fold. Three of the genera, *Ophiodes* of central and southern South America east of the Andes, and *Sauresia* and *Wetmorena* of Hispaniola are universally considered valid. Differences of opinion exist, however, concerning the status and species composition of the nominal genera *Celestus* and *Diploglossus;* some authors regard them as forming a single genus while others maintain them as distinct.

Diploglossus Weigmann, 1834 (type by subsequent designation of Fitzinger, 1843: *Tiliqua fasciatus* Gray, 1831) is based on a South American form having the frontal plate in contact anteriorly with three shields (a pair of prefrontals separated medially by a large frontonasal) and the claws on the fingers and toes covered by a scaly (ungual) sheath, so that only the tip is exposed. *Celestus* Gray, 1839 (monotype: *Celestus striatus*, Gray, 1839) was proposed for West Indian members of this complex having the frontal contact anteriorly with a single large shield (the fused prefrontals and frontonasal). In addition, as pointed out by Boulenger (1885), these lizards have the claws exposed for most of their length (i.e. lack a scaly, ungual sheath). Boulenger placed all of the then known species of *Celestus* and *Diploglossus* in a single genus for which he used the latter name. In his key however, he separated the included species into two major groups, based on whether or not they had a large ungual sheath into which the claw could be partially or entirely retracted. Subsequent work has added substantially to the number of species recognized by Boulenger, and representatives of his *"Diploglossus"* are now known to occur from Mexico to Brazil and Bolivia, on all islands in the Greater Antilles, and on several other Neotropical islands as well. During the next 74 years a number of authors (Stejneger 1904; Barbour 1910; Burt and Burt 1932) recognized *Celestus* as distinct, based on the degree of exposure of the claws, but Dunn (1939) preferred Boulenger's arrangement, since the condition of the frontonasal/prefrontal arrangement did not correlate exactly with the claw differences. After examining twenty nominal species from throughout the range of the complex, Underwood (1959) supported Dunn's position. Underwood further suggested that the ungual sheath had been lost in the evolutionary history of this group on several occasions and seriously questioned whether the claw was retractable into the sheath. Most students of mainland anguids continued to recognize *Celestus* (*e.g.* Stuart 1963; Peters and Donoso-Barros 1970; Meyer and Wilson 1973) although Myers (1973) was inclined to follow Underwood's interpretation.

Strahm and Schwartz (1977) established that the claws in these lizards are in no way retractile and presented a new interpretation of the *Celestus-Diploglossus* problem based upon purported differences in the architecture of the canal system of the body osteoderms. As pointed out by these authors, the sculptured free (distal, posterior) portion of each osteoderm contains a relatively simple system of canals that shows striking variation within diploglossines. They called this system the "arbor" and indicated that it is poorly developed in these lizards as compared to other anguids. A second canal system (the "radix") is usually present in the unsculptured basal (anterior proximal) portion of each osteoderm (that portion overlapped by the free margin of the preceeding scale and osteoderm). According to Strahm and Schwartz (1977), members of this complex may be divided into two groups, one in which the radix is absent or consists of a single unit, and one in which the canal system is extensive and complex. Species having the complex radix were placed in the genus *Diploglossus* by these authors and those in which the radix was simple or lacking were referred to *Celestus*.

The resulting classification scheme led to a radical realignment of the group, so that species with exposed claws were placed in each genus. Similarly, each of the putative genera contained forms with both one and three shields bordering the frontal anteriorly under this arrangement. A number of taxa usually regarded as closely related by all previous authors (*e.g.* *cyanochloris* and *rozellae*) were placed in different genera. Because of these variations in the application of the two generic names we do not use binomials in the following several paragraphs.

This interpretation also produced a complex and confused biogeographic picture, with *"Celestus"* having a distribution in Mexico and northern Central America, Jamaica, the Cayman Islands and Hispaniola, and *"Diploglossus"* disjunctly occurring in Central and northwestern South America, eastern Brazil and Bolivia and on the islands of Cuba, Hispaniola, Puerto Rico, Montserrat and Malpelo (off the Pacific coast of Colombia). Fortunately, Strahm and Schwartz provided evidence that the degree of radix development exhibits considerable individual variation. They note that osteoderms from examples of *costatus* of Hispaniola "usually" lack a radix, but six out of 12 (50%) have a small to moderate one. In the holotype of *atitlanensis* a double and reduced radix was found on ventral and lateral osteoderms but a fully developed one on the dorsal osteoderms.

Wilson *et al.* (1986) subsequently showed that there is ontogenetic variation in Strahm and Schwartz's sample as well. Individual variation in radix development is to be expected in other species since these authors examined osteoderms from only a single lizard of each form in all cases except *costatus.* The former demonstrated that the nominal species (according to Strahm and Schwartz) *"Diploglossus" bivittatus* Boulenger, 1895 and *"Celestus" atitlanensis* Smith and Taylor, 1950, are conspecific. The holotype of the former is a juvenile whose osteoderms lack a radix and the holotype of the latter is an adult with two kinds of osteoderm canal systems (Strahm and Schwartz [1977] examined and illustrated osteoderms taken from the two holotypes). Consequently, Wilson *et al.* (1986) concluded that the putative differences in osteoderm canal systems are subject to ontogenetic variation and have no value in estimating relationships. In light of these variations we concur that the degree of radix development is an unreliable diagnostic feature. It should be further noted that no mention is made of this presumed character in subsequent descriptions of new taxa of *Celestus* and *Diploglossus* from Hispaniola by Schwartz and his associates (1979, 1985) and Thomas and Hedges (1989), which are referred to one or the other genus solely on the basis of phenetic resemblence to previously described species.

Our conclusion, while undermining the Strahm and Schwartz classification, does not resolve whether *Celestus* is distinct from *Diploglossus.* In the process of describing the new species, we became convinced that two basic lineages of diploglossines are represented on the American mainland. These two lineages conform exactly to the traditionally diagnosable genera of mainland *Celestus* and *Diploglossus*. Mainland *Celestus* have exposed claws, a reduced ungual scale, and a single subungual scale (Fig. 1A). Mainland *Diploglossus* have the claws covered for most of their length by a compressed claw sheath comprised of an elongate and laterally expanded ungual scale and a pair of subungual scales. In addition, there is an enlarged lateroungual scale lying near the claw base on each side (Fig. 1B). Thus, there are two scales around the base of the claw in mainland *Celestus* and five in *Diploglossus*.

Among West Indian diploglossines the same distinctive features are evident (Table 1). Claw sheaths are absent in a cluster of eight related species from Hispaniola and in all Jamaican forms. All other species from the Antilles, including representatives of the nominal genera *Sauresia* and *Wetmorena,* have sheathed claws. The arrangement of ungual, subungual and lateroungual scales is exactly the same as in mainland lizards with claw sheaths (*Diploglossus*) and without (*Celestus*). The claw sheath features appear to be consistent and invariant for each species, with those species presumed to be related (from analysis of other characteristics) sharing the same sheath condition.

However, Underwood (1959) and Strahm and Schwartz (1977) reported that several forms had the claws "half-sheathed", suggesting that intermediates occur. Myers (1973) also indicated that there may be species differen-

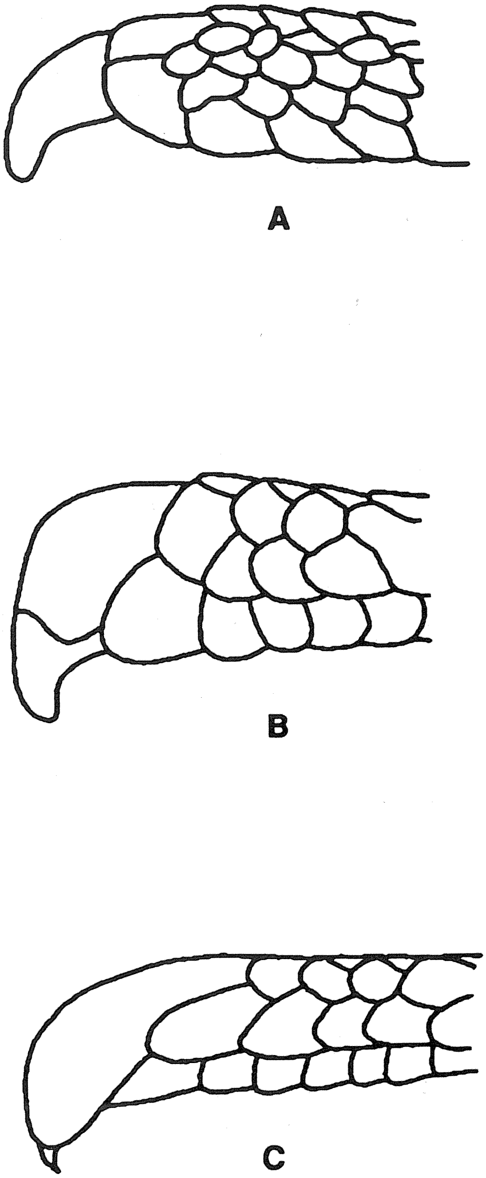

Fig. 1. **Condition of toes in diploglossine lizards. A. Claws exposed *(Celestus);* B. Claw sheathed, more than tip exposed *(Diploglossus millepunctatus);* C. Claw sheathed, only tip exposed (all other *Diploglossus, Sauresia* and *Wetmorena*).**

TABLE 1

Character states and geographic distribution of recent diploglossine lizards

Claws Exposed			Claws Sheathed		No Claws
1 Frontonasal		2 Prefrontals & 1 Frontonasal	1 Frontonasal	2 Prefrontals & 1 Frontonasal	1 Frontonasal
	Celestus		*Diploglossus*		*Ophiodes*
CA	*bivittatus* ±	CA *montanus* –	CA *bilobatus* +, u	CA/NSA *monotropis* +, s	SSA *intermedius* –
M/CA	*enneagrammus* +		CA *montisilvestris* –, s	SA *fasciatus* ± u	SSA *striatus* –
CA	*cyanochloris* +		SA *lessonae* +, s	MO *montisserrati** +, s	SSA *vertebralis* –
CA	*hylaius* +		C *delasagra* +, s	MA *millepunctatus* +, s	SSA *yacupoi* –
CA	*orobius* +		PR *pleei* +,s		
CA	*rozellae* +				
WI	*striatus* -				
H	*anelpistus* -				
H	*carraui* –				
H	*costatus* –		*Sauresia*		
H	*darlingtoni* –	H *darlingtoni* –	H *agasepsoides* -, s		
H	*macrotus* –		H *sepsoides* –, s		
H	*marcanoi* –				
H	*stenurus* –				
H	*warreni* –				
J	*barbouri* –				
JCI	*crusculus* –				
J	*curtissi* –				
J	*duquesneyi* –		*Wetmorena*		
J	*fowleri* –		*H haetiana* –, s		
J	*hewardi* –				
J	*microblepharis* –				
J	*occiduus* –				

C = Cuba, CA = Central America, CI = Cayman Islands, H = Hispaniola, J = Jamaica, M = Mexico, MA = I. Malpelo, MO = I. Montserrat, NSA = Northern South America, SA = South America, SSA = Southern South America, WI = West Indies
I.C. = ungual overlap, s = subungual overlap; naso-rostral contact: + = present, – = absent
* = prefrontal and frontonasal fused posteriorly

ces in the degree of exposure of the claw tip in those forms having sheaths. Species purported to have the claws half-sheathed are the mainland forms *bivittatus* and *enneagrammus*, the Antillean *microblepharis*, and *millepunctatus* of Malpelo Island, Colombia. A review of the situation indicates that Underwood (1959) called two very different conditions half-sheathed. One of these was illustrated for *microblepharis* (his Fig. 3A) in which the ungual scale is somewhat longer than in the typical *Celestus* condition (his Fig. 3C). The second condition is found in *millepunctatus* (Fig. 1B) where more than the tip of the claw is exposed and the elongate and enlarged ungual scale does not completely cover the more ventral areas of the distal portion of the claw. Two scales surround the base of an exposed claw in *microblepharis*, while five scales surround the mostly concealed claw in *millepunctatus*.

Presumably, Strahm and Schwartz (1977) thought that *bivittatus* (and its synonym *atitlanensis*) and *enneagrammus* had claws similar to *microblepharis* since they recorded them as half-sheathed. Significantly, Wilson *et al.* (1986) make no comment regarding the presence of half-sheathed claws in *bivittatus* in their redescription. In our examination of available specimens of these forms we can find no examples that differ in sheath development from other mainland taxa of the *Celestus* group. We can only conclude that the notion that *bivittatus*, *enneagrammus* and *microblepharis* have the claw half-sheathed is based upon misinterpretation or mis-observation, as we would classify all these species as having exposed, unsheathed claws.

The condition of the claw sheath in *millepunctatus* however, remains unique and legitimately may be called a partial or incomplete sheath. Nevertheless, it has an identical number of sheath scales as those mainland *Diploglossus* with complete sheaths, and is much closer in structure to those specimens having the sheathed condition than to any form with completely exposed claws. We interpret this arrangement as indicating its relationship to the lower Central American and South American stock that includes the type species of *Diploglossus*.

In conclusion, we believe that the differences in claw sheathing provide a valid basis for the recognition of two genera, *Celestus* and *Diploglossus*, on the mainland of the Americas. The several insular species may also be placed unequivocally into one or the other genera, and as will be pointed out below, their geographic distribution is consistent with such allocations. These conclusions change the generic assignments for three Hispaniolan taxa *(anelpistus*, *carraui* and *warreni*) listed in Schwartz and Henderson (1988) from *Diploglossus* to *Celestus*.

It should be noted that *C. striatus*, the type species of the genus *Celestus*, is something of an enigma. The only known specimen was supposedly collected in the West Indies (Gray 1839; Boulenger 1885). Boulenger, contrary to Strahm and Schwartz (1977) considered *C. striatus* to be related to (not a synonym of) *Celestus occiduus* (Shaw, 1802) from Jamaica. Schwartz (1970) and Strahm and Schwartz (1977) believed that the type must have come from the mainland. We are dubious of this conclusion because *C. striatus* had three scales bordering the frontal anteriorly and 41 scale rows around the body. *Celestus montanus* of Honduras is the only mainland *Celestus* having the described cephalic scutellation, and no known mainland species has more than 36 scale rows around the body.

A summary of generic allocations of all known diploglossine species, those characteristics involved in determining generic limits in both this and previous reviews, and species distributions are provided (Table 1). In addition to the conditions of the claw sheath and prefrontal/frontonasal features we have indicated whether the nasal shield is in contact with the rostral (+) or separated from it by a dorsal extension of the first supralabial (-), since Underwood (1959) and Strahm and Schwartz (1977) thought the alternate conditions were intraspecifically invariate. For those species with a claw sheath we have also recorded whether the ungual scale overlaps the subungual (*u*) or *vice versa* (*s*), since this character appears to show no intraspecific variation. We have not examined the Antillean *Celestus* for this feature, but in mainland forms the state is uniformly *u*. Strahm and Schwartz (1977) observed that *microblepharis* exhibits the *s* state.

The following key will distinguish among the five recognized genera of living diploglossines.

A KEY TO THE GENERA OF THE LIZARD SUBFAMILY DIPLOGLOSSINAE (FAMILY ANGUIDAE)

1a. Four limbs and claws present 2

1b. No forelimbs, hindlimbs reduced to flaps, no claws; auricular opening small, hidden under scales just behind the angle of the jaw .... *Ophiodes*

2a. Claws hidden within a scaly sheath (Figs. 1B, 1C) 3

2b. Claws exposed for most of their length; 5 fingers and toes; an auricular opening (Fig. 1A) .... *Celestus*

3a. Four fingers and toes 4

3b. Five fingers and toes; an auricular opening .... *Diploglossus*

4a. An auricular opening .... *Sauresia*

4b. No auricular opening .... *Wetmorena*

DESCRIPTIONS OF COSTA RICAN SPECIES OF *CELESTUS*

Celestus orobius n. sp.

Fig. 2A, 4-5

Holotype. - LACM 138540, from the area near Hortensia, Palma and Fortuna on the Carretera Interamericana, southern slope of the Cordillera de Talamanca, Canton Pérez-Zeledón, Provincia de San José, Costa Rica (1500-2000 m). Collected by R. J. Lavenberg and P. H. Starrett, August 15, 1959.

Diagnosis. - This small (standard length 82.85 mm) species appears to be most closely allied to *Celestus cyanochloris* of the Cordilleras Central and Tilarán of Costa Rica. The two forms differ most obviously in colouration, with *C. cyanochloris* having scattered black spots on the dorsum and flanks that do not align to demarcate distinct, light vertical lines as in *C. orobius*. In addition, *C. orobius* has only 8 preanal scales versus 10 to 12 in *C. cyanochloris* (Table 2) and is a more elongate form with the axilla to groin distance 61% of the standard length versus stouter body and axilla to groin distance 53 to 58% of standard length in *C. cyanochloris* (Table 3). In addition to colour pattern differences (Figs. 2-3), *C. orobius* is distinguished from other mainland *Celestus* as follows (features for the compared species in parentheses): from *C. montanus* of Honduras in having a single enlarged plate bordering the frontal shield anteriorly (three scales bordering the frontal anteriorly); from *C. enneagrammus* and *C. bivittatus* of Mexico and Nuclear Central America in having 21 to 22 lamellae under the 4th toe and 66 transverse rows of dorsal scales (18 or fewer lamellae, 78 or more dorsals); from *C. hylaius* by having 66 transverse dorsal and 75 transverse ventral scale rows (76 to 81 dorsal; 84 to 92 ventrals); from *C. rozellae* in having 66 transverse dorsal, and 75 transverse ventral scale rows (73 to 77 dorsals, 78 to 86 ventrals).

Description. - Rostral less than twice as wide as high, distinctly visible above, in contact with nasal; anterior internasals (= supranasals) narrower than posterior; frontonasals and prefrontals fused into a single large scute, wider than long, posterior border straight; frontal narrow, much longer than wide; frontoparietals small, widely separated by frontal; interparietal nearly as large as parietals, separating them widely, touching smaller postparietal; parietal separated from supraoculars by an intercalated scale (*sensu* Myers, 1973); nasal single, nostril pierced in posterior part of scale; a suture from upper edge of nasal to nostril or missing; a pair of small postnasals, occasionally fused into one large postnasal; anterior and posterior loreals fused; canthal (=superior loreal of Taylor, 1956) of similar size, touching a second internasal, a prefrontal, first supraocular, posterior

TABLE 2

Scale counts for the three species of Costa Rican Celestus

	Scales around midbody	Middorsal scales	Scales between postmental and vent	Lamellae of 4th toe	Supra-labials	Supralabials to center of eye	Preanals	Infra-labials
C. cyanochloris								
AMNH 16290	33	65	73	21-20	10 - 10	7 - 7	10	8 - 8
KU 34291	34	70	73	25-23	11 - 11	8 - 7	10	8 - 9
KU 34292	33	73	76	25	10 - 10	7 - 7	10	10 - 9
CRE 4590	34	67	75	20 - 21	11 - 11	7 - 7	10	10 - 9
CRE 10084	32	66	76	23	10 - 10	6 - 8	-	9 - 8
UCR 7375	32	65	73	24 - 23	10 - 11	7 - 7	10	9 - 8
UCR 7376	33	70	77	23 - 22	-	-	10	9 - 9
C. hylaius								
FU 31080	30	80	84	24 - 24	10 - 9	7 - 7	10	8 - 8
FU 31081	32	80	87	26 - 26	10 - 9	7 - 7	12	8 - 8
FU 30538	31	80	90	26	10 - 10	7 - 7	12	8 - 7
FU 75794	30	81	88	27	9 - 9	7 - 7	11	8 - 9
LACM 59202	31	-	-	25	9 - 9	7 - 7	12	9 - 8
KU 125599	33	81	87	27	9 - 9	7 - 8	12	7 - 9
CRE 8380	32	80	89	23 - 24	10 - 11	7 - 8	12	8 - 8
CRE 8381	32	80	86	25 - 26	9 - 9	7 - 7	11	9 - 9
CRE 6711	32	79	88	25 - 27	10 - 9	8 - 7	12	9 - 9
CRE 6707	32	76	89	24 - 24	9 - 9	7 - 7	-	8 - 8
UCR 4544	33	80	92	22 - 22	10 - 11	7 - 8	12	9 - 9
C. orobius								
CRE 277	33	66	75	21 - 22	9 - 9	6 - 7	8	7 - 8

TABLE 3

Standard measurements of Celestus cyanochloris, C. hylaius, *and* C. orobius, *and as percent of standard length (% SL).*

	standard length	total length	% SL	groin axilla	% SL	forelim	% SL	body width	% SL	hindlimb	% SL	head length	% SL	head width	% SL	head height	% SL	palpebral aperature	% SL	ear aperature	%SL
C. cyanchloris																					
AMNH 16290	66.7	142.8	--	37.4	56	17.3	26	13.2	19	21.2	32	15.7	24	10.2	15	8.2	12	4.15	6.2	2.3	3.5
CRE 10084	80.2	--	--	52.4	65	18.5	23	--	--	21.8	27	15.6	19	10.7	13	--	--	3.4	4	1.6	2
CRE 4590	75.85	168.7	222	40.55	54	14.85	20	10.8	14	21.45	28	14.65	19	9.5	13	6.45	9	2.5	3.3	1.3	1.7
KU 34291 juvenile	53.5	135.5	253	30.5	57	7.2	14	6.5	12	9.2	17	11.2	21	6.45	12	4.9	9	2.25	4.2	0.8	1.5
KU 34292	79	156.5	198	46	58	12.8	16	10.1	13	14.1	18	15	19	9.9	13	7.6	10	2.8	3.5	1.2	1.5
UCR 7375	98.6	237.9	241	56.85	58	14.2	14	14.3	15	32.85	33	19.7	20	14.05	14	10.05	10	3.55	3.6	1.75	1.8
UCR 7376	98.55	211.9	215	57.05	58	23.8	24	13.4	14	29.05	30	19.25	20	13.65	14	10.85	11	na	--	1.55	1.6
$\bar{X}$	81.1	182.1	226	46.19	57	14.57	18	11	13	21.33	25	15.96	20	10.71	13	7.97	10	2.78	3.7	1.32	1.6
C. hylaius																					
CRE 6707 juvenile	38.5	90.1	234	21.45	56	8.15	21	--	--	10.6	28	8.7	23	5.6	15	3.95	10	2.45	6.4	1	2.6
CRE 6711	74.45	tail bkn.	--	44.3	60	13.85	19	10.4	14	19	26	13.7	18	9.25	12	7.65	10	--	--	--	--
CRE 8380	106.85	143.7	135	63.8	60	16.3	15	15.8	15	27	25	18.05	17	12	11	10.55	10	3.5	3.3	1.45	1.4
CRE 8381	91.25	158.75	174	55.15	60	16.15	18	14.5	16	22.5	25	15.85	17	10.5	12	8.05	9	3.1	3.4	1.4	1.5
KU 125599	94	168	179	58	62	11.1	12	11.6	12	14.6	16	15.7	17	9.9	11	8.4	9	2.7	2.9	1.4	1.5
LACM 59202	70.5	166.5	236	43.5	62	missing	--	--	--	missing	--	12.3	17	5.8	8	--	--	--	--	--	--
UCR 4544	85.55	119.5	140	54.45	64	17	20	11.2	13	25.4	30	15.65	18	10.4	12	9.05	11	2.9	3.4	1.2	1.4
UF 30538	105.65	154.3	146	63.6	60	17.55	17	14.3	14	23.55	22	18	17	10.5	10	8.75	8	2.95	2.8	1.5	1.4
UF 31080	96.15	153.15	159	59.3	62	16.75	17	14.7	15	23.3	24	16	17	11	11	8.05	8	2.7	2.8	1.3	1.4
UF 31081	103.15	185.6	180	60.4	59	18.4	18	16.3	16	26.65	26	17.65	17	12.45	12	9.45	9	3.25	3.2	1.4	1.4
UF 75794	100.25	198.45	198	63.3	63	15.9	16	12.9	13	24.75	25	16.75	17	9.9	10	8.6	9	2.85	2.8	1.35	1.3
$\bar{X}$	87.85	139.82	178	53.39	61	15.12	17	13.5	14	21.74	25	15.3	18	9.75	11	8.25	9	2.93	3.4	1.33	1.5
C. orobius																					
CRE 277	82.85	tail bkn.	--	50.25	61	19.25	23	13.7	17	25.05	30	16.1	19	10.1	12	7.25	9	3.4	4.1	1.85	2.2

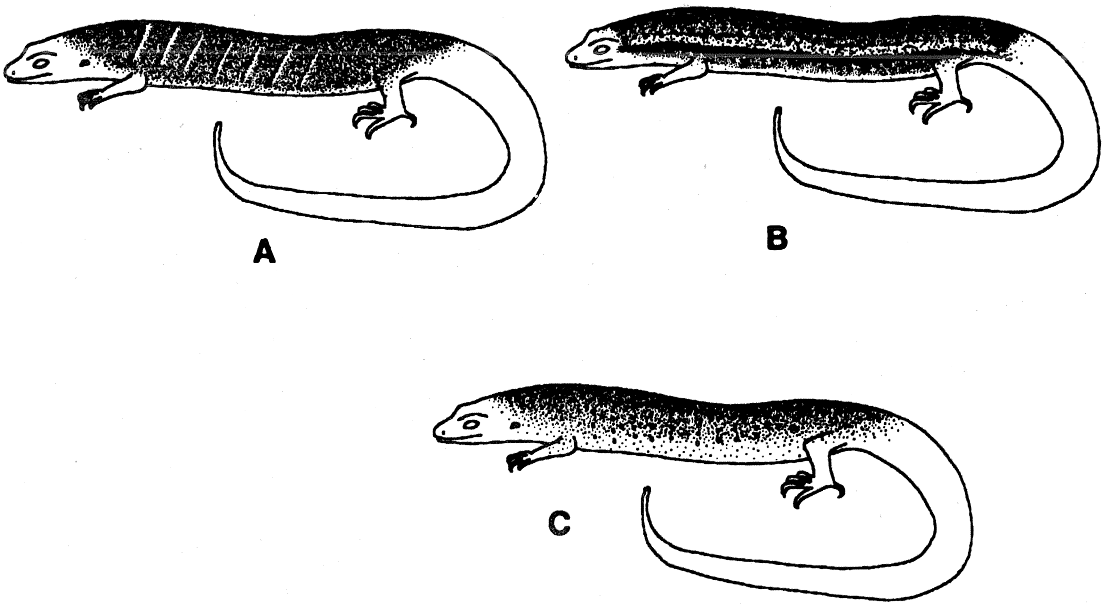

Fig. 2. Diagrammatic representations of dorsal colour patterns in Costa Rican species of *Celestus*. A. *C. orobius*; B. *C. hylaius*; C. *C. cyanochloris*.

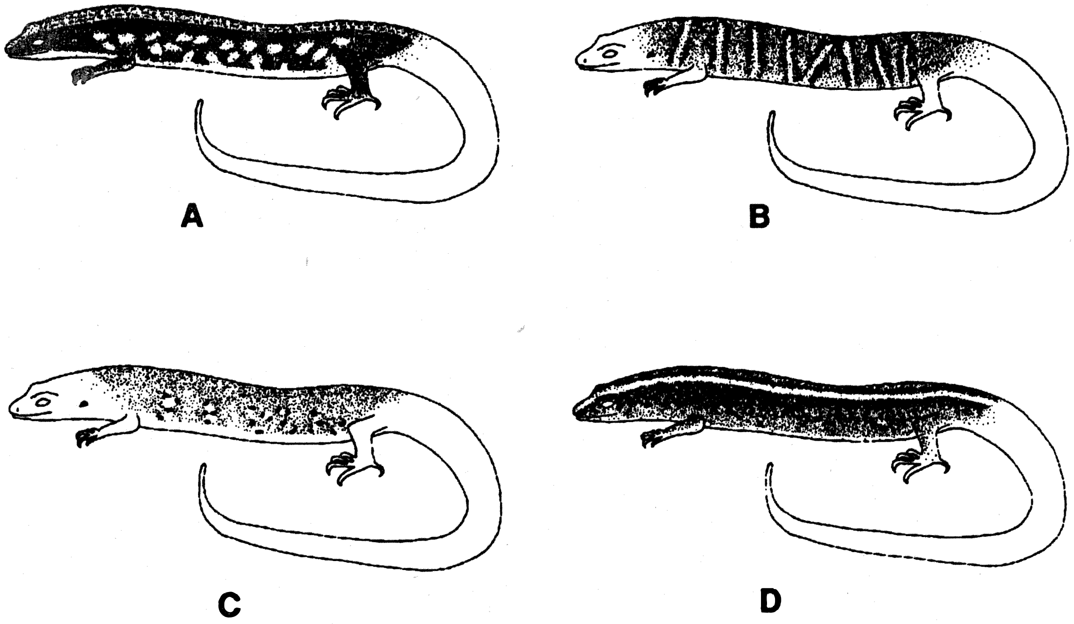

Fig. 3. Diagrammatic representations of typical dorsal colour patterns in Mesoamerican species of *Celestus*. A. *C. enneagrammus* (lateral light spots variably present); B. *C. rozellae* (barring reduced in some large adults); C. *C. montanus* (lateral light spots variably present); D. *C. bivittatus*.

canthal (=first supraciliary of Taylor, 1956), and fused loreal; small to medium-sized preocular; five median supraoculars, 2 and 3 bordering frontal; four lateral supraoculars, anteriormost interpreted as canthal as noted by Myers (1973); subocular nearly 3 times as long as high; a row of four postoculars; nine supralabials, six or seven to a point below middle of eye; seven or eight infralabials; mental narrower than rostral; an azygous postmental; five pairs of chinshields, first pair in contact with one another and second and third labials; second and succeeding pairs separated from each other by one to five scales; 66 dorsal scales from occipital to base of tail, 75 ventral scales between postmental and anterior edge of vent, 30-33 scale rows around midbody; eight scales on anterior edge of vent; pentadactylous; laterally compressed digits with slightly rounded subdigital lamellae; third and fourth fingers of similar length, with 15-17 lamellae; toes relatively long and slender, fourth longest with 21-22 lamellae, each digit terminating in a claw lacking a sheath; upper caudal scales with a median keel.

Colouration in preservative. - Dorsal ground colour olive brown; head uniform olive brown; some scales dark brown, evenly scattered across neck, trunk and tail; dorsal surfaces of limbs uniform brown; definite black-edged, vertical light lines on flanks; venter uniform dark grey.

Measurements in millimeters. - Values in parentheses indicate measurements expressed as percentages of standard length (Table 1). One adult specimen. Standard length 82.85 with broken tail; axilla to groin 50.25 (61%); forelimb (from axilla) 19.25 (23%); hindlimb (from groin) 25 (30%); head length to rear ear opening 16 (19%); greatest width of head (angle of jaw) 10 (12%); head height 7.25 (9%); diameter of ear opening 1.85 (2.2%).

Etymology.- The name *orobius* is from the Greek meaning mountain dweller with reference to the montane origin of the only known specimen.

Distribution. - Known from a single locality in the lower montane rainforest zone of the Cordillera de Talamanca of Costa Rica (1500-2000 m) (Figs. 4-5).

CELESTUS HYLAIUS n. sp.

Figs. 2B, 6

Holotype. - LACM 138541, from the La Selva Biological Station, Canton de Sarapiquí, Provincia de Heredia, Costa Rica, (40 m). Collected by James J. Talbot, December 3, 1973.

Paratypes. - UCR 4544, KU 125599, UF 75794, UF 30538, UF 31080-81, CRE 8380-81, CRE 6707, CRE 6711, LACM 59202. Locality data can be found in the Materials section.

Diagnosis. - A moderate-sized *Celestus* (maximum standard length 106.85 mm) with a dorsal pattern of light and dark spots that tend to align vertically on the flank to form obscure bars and paired longitudinal, lateral stripes on a greenish ground colour. It differs most obviously from the Mexican and Central American species, *Celestus enneagrammus* and *C. bivittatus*, in colouration (Figs. 2-3) and in having 22 to 27 lamellae under the fourth toe, versus 14 to 18 in the other two species (Table 2). The new form is distinguished from the two other Costa Rican species, *C. cyanochloris* and *C. orobius*, by having more transverse dorsal scale rows (76 to 81 versus 65 to 73) and in colouration. The new form is most similar to *C. rozellae* of southern Mexico and northern Central America in scalation (Table 4), but *rozellae* lacks both the light-tipped black scales scattered over the body, and any hint of dorsolateral stripes; and has very distinct, dark-margined, vertical light bars on the neck and often on the flanks. The new species cannot be confused with *C. montanus* of Honduras since that form has three plates (2 prefrontals and a frontonasal) bordering the prefrontal shield anteriorly, while all other mainland *Celestus*, including *C. hylaius*, have a single large shield in that position.

Description. - Rostral less than twice as wide as high, distinctly visible above, in contact with nasal; anterior internasals (= supranasals)

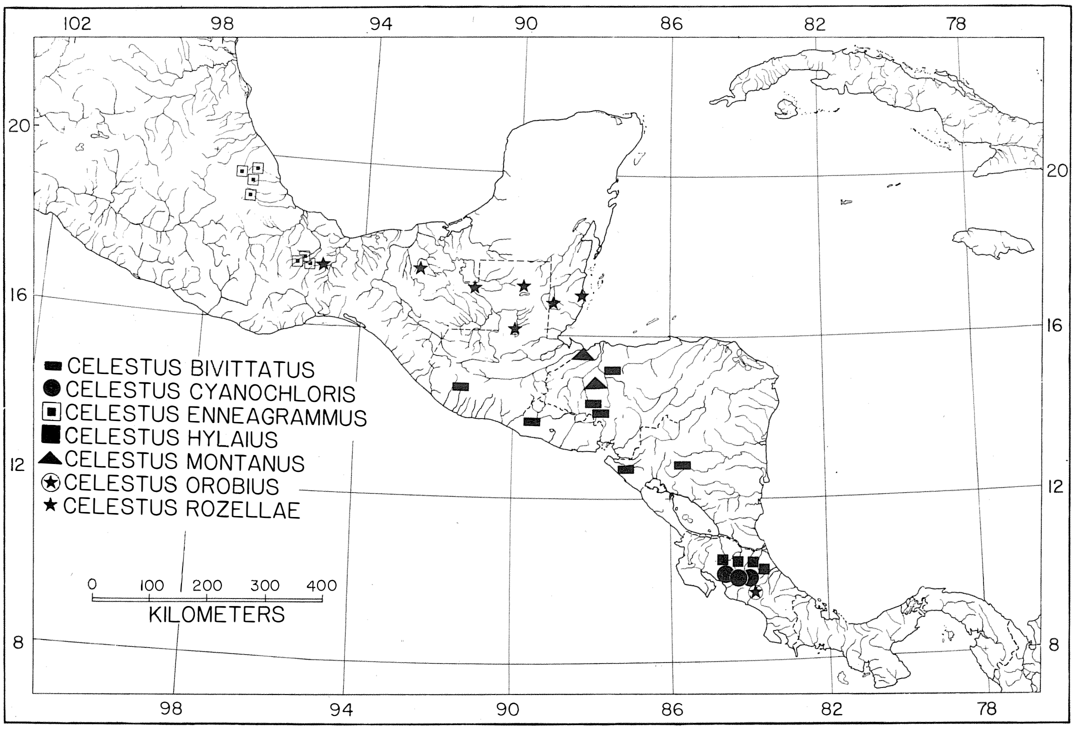

Fig. 4. Distribution of mainland species of *Celestus.*

narrower than posterior, fused in KU 125599; frontonasals and prefrontals fused into a single large scute, wider than long, posterior border somewhat concave to straight, (CRE 8380 and CRE 6707 have two small lateral scales split off from this plate in canthal area); frontal narrow, much longer than wide; frontoparietals small, widely separated by frontal; interparietal nearly as large as parietals, separating them widely, touching much smaller interoccipital; parietal separated from supraoculars by an intercalated scale (*sensu* Myers, 1973); nasal single, nostril pierced in posterior part of scale; a suture from upper edge of nasal to nostril or missing; a pair of small postnasals, occasionally fused into one large postnasal; anterior loreal of equal size to posterior; canthal (superior loreal of Taylor, 1956) of similar size, touching a second internasal, a prefrontal (or a small lateral scale split off from prefrontal in CRE 8380 and CRE 6707), first supraocular, posterior canthal (first supraciliary of Taylor, 1956), and two loreals (anterior and posterior or occasionally posterior and intermediate loreals when four scales occur between postnasals and orbit as in UF 31080-81); small to medium-sized preocular; five (rarely 6) median supraoculars, usually 1, 2 and 3 bordering frontal (rarely 2 and 3); four or five lateral supraoculars, anteriormost interpreted as canthal as noted by Myers (1973); subocular nearly 3 times as long as high; a row of four (rarely three or five) postoculars; nine or 10 (rarely 11) supralabials, seven (rarely six or eight) to a point below middle of eye; eight or nine (occasionally seven) infralabials; mental usually of equal width as rostral; an azygous postmental; five pairs of chinshields, first pair in contact with one another and second and third labials (rarely in contact with 2; 1, 2 and 3; or 1 and 2); second and succeeding pairs separated from each other by one to five scales. Dorsal scales from occipital to base of tail, 76-81; 84-92 ventral scales between postmental and anterior edge of vent; 31-33 scale rows around body; usually 12 (rarely 10 to 11) scales on anterior edge of vent; pentadactylous; laterally compressed digits with slightly rounded subdigital lamellae;

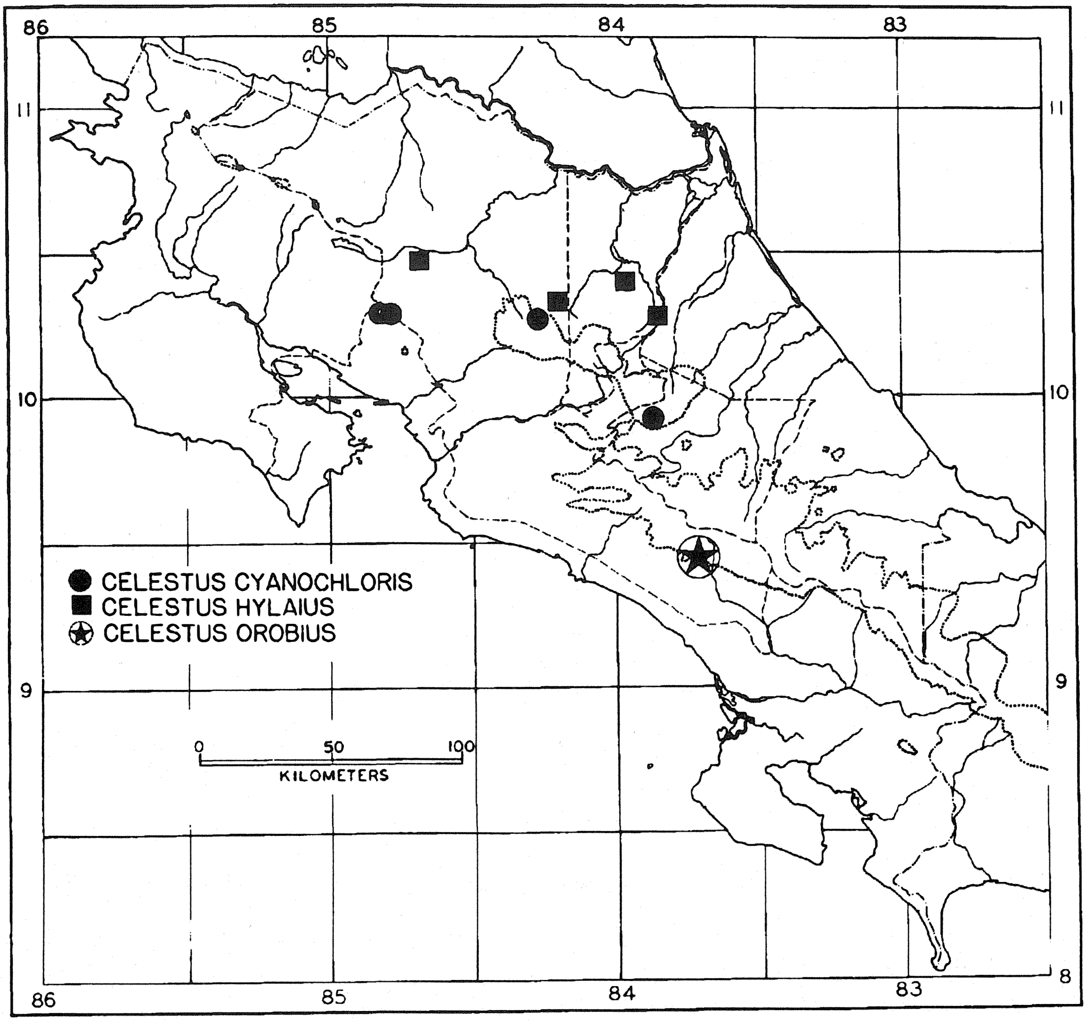

Fig. 5. Distribution of species of *Celestus* in Costa Rica; dotted line indicates 1500 m contour.

third and fourth fingers of similar length, most often with 17-19 (rarely with 15, 16 or 20) lamellae; toes relatively long and slender, fourth longest with 24-27 (rarely with 22 or 23) lamellae, each digit terminating in a claw lacking a sheath; all caudal scales without median keels.

Colouration in life. - Dorsal ground colour coppery brown with numerous small black scales scattered over neck, trunk, and tail, forming black ventrolateral stripes where black colour concentrated from ear to above forelimbs and along trunk to groin; pair of dorsolateral coppery brown stripes indicated where black scales missing. Dorsum of head coppery brown; tip of snout olive green to light coppery brown; upper labials and suboculars bright yellow-green to yellow-blue; posterior edges of supralabials and infralabials bordered by black; thin black line from base of postnasal to corner of eye, along upper edge of suboculars to postoculars, becoming wider and running along area superior to ear then laterally along body. Venter immaculate yellow green; colour reaching supralabials, auricular opening and sides of body at level of axilla. Iris rusty brown.

TABLE 4

Range of values for selected features of mainland Celestus. *Means in parentheses.*

Species	No. Dorsal Scale Rows	No. Ventral Scale Rows	No. Scale Rows Around Body	No. of Lamellae on 4th toe
cyanochloris	65-73 (68)	73-77 (74.7)	32-34 (32.9)	20-25 (22.4)
enneagrammus	78-85 (82.2)	81-91 (86.4)	31-36 (33.2)	15-18 (16.5)
montanus	67-72 (69.5)	78-84 (81)	33 (33)	22-26 (24)
bivittatus	75-79 (77.7)	76-81 (79.0)	29-31 (30.3)	14-18 (16.8)
rozellae	73-77 (75.2)	78-86 (82.2)	31-33 (31.3)	22-26 (23.5)
hylaius	76-81 (79.7)	84-92 (88)	31-33 (31.6)	22-27 (24.7)
orobius	66	75	33	21-22 (21.5)

Colouration in preservative. - Dorsal ground colour olive brown, often with faint wash of light blue dorsolaterally; a pair of dorsolateral light and ventrolateral dark stripes; head uniform olive brown; some scales dark brown, tipped with light blue; evenly scattered across neck, trunk and tail to give speckled appearance; dorsal surfaces of limbs uniform brown with faint hint of blue-tipped scales; venter uniform grey, becoming darker grey-blue dorsally along flank, upper lip and area superior to ear and limbs.

Measurements in millimeters. - Values in parentheses are ranges of measurements expressed as percentages of standard length based on ten adults. Standard length 70.5-106.85, $\bar{x}$=92.78; total length 119.5-198.5, $\bar{x}$=160.8 (135-236%), seven specimens with broken and/or regenerated tails; axilla to groin 43.5-63.8, $\bar{x}$=56.6 (59-64%); forelimb (from axilla to tip of longest toe) 11.1-17.55, $\bar{x}$=15.9 (12-20%); hindlimb (from groin to tip of longest toe) 14.6-27, $\bar{x}$=22.8 (16-30%); head length to rear ear opening 12.3-18, $\bar{x}$=16.0 (17-18%); greatest width of head (at angle of jaw) 5.8-12.5, $\bar{x}$=10.2 (8-12%); head height 8.05-10.55, $\bar{x}$=8.72 (8-11%); diameter of ear opening 1.2-1.45, $\bar{x}$=1.38 (1.3-1.5%). Measurements for the one juvenile specimen (CRE 6707) can be found in Table 3.

Etymology. - *Hylaius* is from the Greek for forest dweller in allusion to the rainforest habitat of the species.

Remarks: One of the paratypes (KU 125599) of this new form was referred to *Celestus cyanochloris* by Strahm and Schwartz (1977) and their figure of a dorsal osteoderm under that name is from this specimen.

Distribution. - Atlantic lowland rainforest of Costa Rica (40-360 m) (Figs. 4-5).

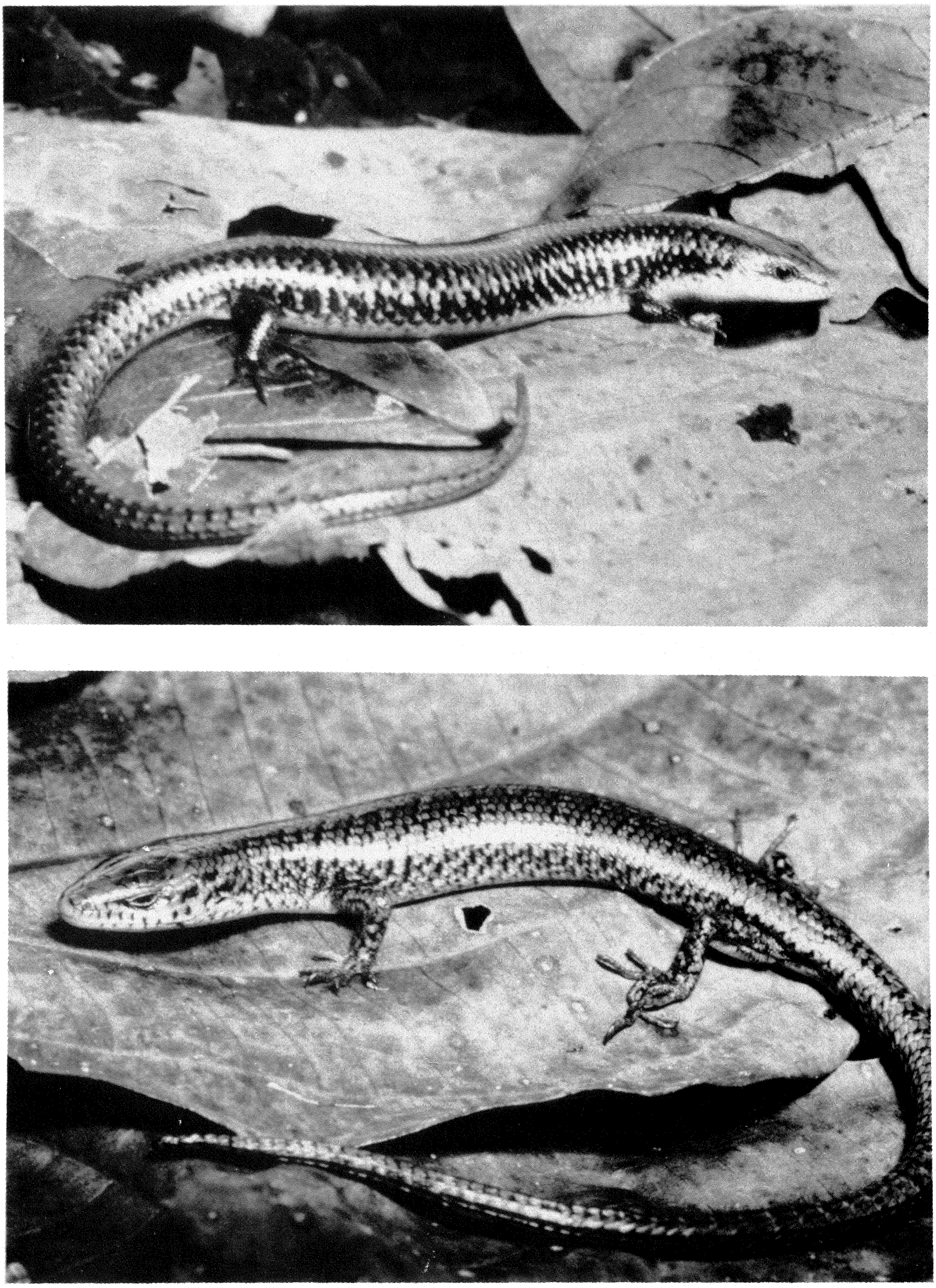

Fig. 6. Upper, *Celestus hylaius;* lower, *Celestus cyanochloris*.

CELESTUS CYANOCHLORIS COPE

Figs. 2C,

Holotype. - AMNH 16270; from Volcán Irazú, Cartago Province, Costa Rica.

Diagnosis. - A relatively small lizard (to 98.6 mm in standard length) most similar to *C. orobius* of the Cordillera de Talamanca of Costa Rica, but differs in having scattered dark spotting, and 10 to 12 preanal scales versus definite, black-margined, vertical light bars on the flanks and eight preanal scales in *C. orobius*. *Celestus cyanochloris* may be separated from all other mainland *Celestus* as follows (characters for the compared forms in parentheses): from *C. montanus* of Honduras in having a single large plate bordering the frontal shield anteriorly (three plates); from *C. bivittatus* of Nuclear Central America and *C. enneagrammus* of Mexico in having 20 to 25 lamellae under the 4th toe (18 or less) and dorsal scales in 65 to 73 transverse rows (75 or more); from *C. rozellae* of northern Central America and *C. hylaius* from Costa Rica in the number of transverse ventral scale rows, 73 to 77 (78 or more). Differences in colouration (Figs. 2-3) provide additional means to distinguish this species from its congeners.

Description. - Rostral less than twice as wide as high, distinctly visible above, in contact with nasal; anterior internasals (= supranasals) narrower than posterior; frontonasals and prefrontals fused into single large scute, wider than long, posterior border somewhat concave; frontal narrow, much longer than wide; frontoparietals small, widely separated by frontal; interparietal nearly as large as parietals, separating them widely, touching much smaller interoccipital; parietal separated from supraoculars by an intercalated scale; nasal single, nostril pierced in posterior part of scale; a suture from upper edge of nasal to nostril; a pair of small postnasals; anterior loreal slightly smaller or of equal size to posterior; canthal (=superior loreal of Taylor, 1956) of similar size, touching a second internasal, prefrontal, first supraocular, posterior canthal (=first supraciliary of Taylor, 1956), and two loreals; small to medium-sized preocular; five median supraoculars, second and third bordering frontal, first excluded from contact; four (rarely three) lateral supraoculars, anteriormost interpreted as canthal as noted by Myers (1973); subocular nearly three times as long as high; a row of four (occasionally three) postoculars; 10 or 11 supralabials, usually seven (sometimes six or eight) to a point below middle of eye; nine (rarely ten sometimes eight) infralabials; mental a little wider, but of less area than rostral; an azygous postmental; five pairs of chinshields, first pair in contact with one another and second and third labials; second and succeeding pairs separated from each other by one to five scales; 65-73 dorsal scales from occipital to base of tail, 73-77 ventral scales between postmental and anterior edge of vent, 32 to 34 scale rows around body; 10 scales on anterior edge of vent; pentadactylous; laterally compressed digits with slightly rounded subdigital lamellae; third and fourth fingers of similar length, both with 16-18 lamellae; toes relatively long and slender, fourth longest with 20-25 lamellae, each digit ending in a claw without sheath; upper caudal scales with a median keel.

Colouration in life. - Dorsal ground colour tan anteriorly becoming darker posteriorly with rusty brown tail; head light brown with few scattered black spots; tip of snout pale yellow-tan; black scales scattered irregularly over body, often forming short irregular stripes across dorsum; not concentrated as lateral stripes running length of body; some black scales tipped with lighter tan; limbs appear mottled with brown, black and light tan, one specimen with leading edge of forelimb yellowish-green; supralabials, infralabials and ventrolateral areas of neck below level of ear ivory to white, one specimen with considerable black flecking in white colouration from ear posterior to axilla; posterior edges of supra- and infralabials bordered with black; thin black line from corner of eye along dorsal edge of suboculars; venter greenish-yellow.

Colouration in preservative. - Olive brown dorsally; sides of head, neck and trunk fading to light brown and becoming blue-grey ventrolaterally; two specimens (KU 34291, CRE 4590) with typical colouration but with numerous black punctations evenly scattered across brown areas of trunk and tail, and two faint dorsolateral stripes weakly indicated where black spots absent, one specimen (CRE 4590) has bluish-green dorsal ground colour, becoming yellow-green posteriorly; venter uniform grey (blue-grey in CRE 4590).

Measurements in millimeters. - Values in parentheses are ranges of measurements expressed as percentage of standard length from six adult specimens (AMNH 16290, CRE 4590, CRE 10084, KU 34292, UCR 7375-6). Standard length (snout-vent) 66.7-98.6, $\overline{x}$=83.2; total length 142.8-238, $\overline{x}$=183.6 (198-241%); axilla to groin 37.4-57, $\overline{x}$=48.4 (54-65%); forelimb (from axilla) 12.8-23.8, $\overline{x}$=16.9 (14-26%); hind limb (from groin) 14-33; $\overline{x}$=23.4 (17-33%); head length to rear ear opening 15-19.7, $\overline{x}$=16.7 (19-24%); greatest width of head (behind corners of mouth) 9.5-14, $\overline{x}$=11.33 (13-15%); head height 6.5-10.9, $\overline{x}$=8.6 (9-12%); diameter of ear opening 1.2-2.3, $\overline{x}$=1.62 (1.5-13.5%). Measurements for the one juvenile (KU 34291) can be found in Table 3.

Etymology. - The name is from the Greek *cyan* (dark blue) and *chloris* (green) with reference to the holotype's colour in preservative.

Remarks. - This species was first described by Cope (1894) along with 11 other new Costa Rican forms based on material in the Museo Nacional de Costa Rica loaned to him by George K. Cherrie, who at that time was a taxidermist and collector for the Museo. The unique types of two of these species (*Hyla cherrei* and *Hyla chrysops*) cannot be located in any collection and must be regarded as lost, but all of the others reached the American Museum of Natural History by some circuitous route and remain safely housed there.

Taylor (1956) was the first worker to refer additional specimens to *C. cyanochloris*. His material (KU 34291-92) is from the slopes of Volcán Irazú in the same mountain range as the holotype (the Cordillera Central). Taylor thought that the holotype of *C. cyanochloris* had been lost but assumed that his material was conspecific with it. Cope's original description did not provide data that would unequivocally distinguish the holotype from other Costa Rican forms but our reexamination of the holotype confirms Taylor's usage.

Cope (1894) described the colouration of *C. cyanochloris* in preservation as follows: "colour above light golden-green, with several indistinct longitudinal rows of paler spots as large as a scale, mingled with as many brown spots as large as a scale. Lower surfaces blue, paler on chin and tail". Preserved specimens from the Cordilleras de Tilarán and Central agree well with this description although usually having more olive than green dorsally. One example (CRE 4590), as described in the section on colouration above, matches closely the colour of the holotype, whose colour has probably dulled somewhat over the last 97 years in preservative. All available examples from these mountain ranges have a definite bluish cast. In preservative *C. hylaius* is olive-brown above and characteristically marked with scattered dark scales tipped with blue. *Celestus orobius* has distinct vertical lateral light bars.

It should be noted that in life *C. cyanochloris* has a tan to brown dorsum marked with scattered black scales and the venter is greenish-yellow. In contrast *C. hylaius* has a bronze to copper dorsal ground colour with a definite greenish cast, numerous bicoloured (black and greenish) scales, and a greenish-yellow venter. In preservative the overall hue of *C. cyanochloris* is bluish-green while *C. hylaius* is brown above and blue-gray below.

The type locality and colouration effectively rule out the possibility that Cope's montane example was a representative of the lowland *C. hylaius*. It also seems highly unlikely that the Volcán Irazú specimen is conspecific with the Cordillera de Talamanca species (*C. orobius*) because of the differences in colouration. Consequently, we follow Taylor in using the name *C. cyanochloris* for the Cordillera Central lizards and conspecifics from the Cordillera Tilarán.

Distribution. - Premontane zone of the Cordilleras de Tilarán and Central of Costa Rica (1200-1550 m) (Figs. 4-5).

It should be noted that the specimen, now lost, reported as *Celestus steindachnerii* by Cope (1893) from Boruca, Puntarenas Province, Costa Rica (550 m) remains an enigma as pointed out by Taylor (1956). Cope described it as having two prefrontals, 36 rows of scales around the midbody, and the body scales smooth anteriorly but stricted and lacking a median keel posteriorly and on the tail. The first listed feature (Table 4) eliminates all mainland Central American species, except *Celestus montanus* (Honduras) from consideration. The second eliminates *C. montanus* and all known Costa Rican forms as possible conspecifics as well. In addition *C. cyanochloris* and *C. orobius* have well-developed median keels on the caudal scales. If the presence of two prefrontals is regarded as a possible anomoly the scale count and the structure of the posterior dorsal and caudal scales are similar to those of *Celestus enneagrammus* (Mexico). Even if the locality data for Cope's example are erroneous identity with *C. enneagrammus* seems a remote possibility. Consequently, we conclude in agreement with Taylor that an undescribed species of *Celestus* may await rediscover from southwestern Costa Rica.

MAINLAND SPECIMENS OF CELESTUS EXAMINED

C. bivittatus: El Salvador: Ahuachapán, Finca El Imposible (*KU 18048); Guatemala: Atitlán; probably San Lucas Atitlán (*MNHP 5206); Nicaragua: Matagalpa: Jérico (*BMNH 1946.8.29.37); Chinandega: Volcán Chongo, Cordillera de los Marrabios (KU 194658); Honduras: Intibucá: La Esperanza (KU 194665-68, †KU 194669-78); Lempira: Gualcince (KU 194679); Yoro: Montaña de Macuzul, above El Portillo (FMNH 236386).

C. cyanochloris: Costa Rica: Cartago: Volcán Irazú (AMNH 16290, holotype); Heredia: Isla Bonita, Volcán Poás (KU 34291-92); Puntarenas: Monteverde (CRE 4590, CRE 10084, UCR 7375-76).

C. enneagrammus: Mexico: "Tehuantepec" (USNM 30189); Vera Cruz: Orizaba (*USNM 6342, *USNM 6603), 5 km SE Perote (*KU 26733); Jalapa (*MCZ 2848); Oaxaca: Sierra Mixe, 0.8 km W (by road) Totontepec (UTACV 12215-19, UTACV 14596); 3.6 mi W (by road) Totontepec (UTACV 7727-29, UTACV 8388, UTACV 9520), 4.9 km W (by road) Totontepec (UTACV 10278).

C. hylaius: Costa Rica: Alajuela: Río Cuarto (UCR 4544); 1.6 km W La Fortuna (KU 125599); Heredia: La Selva (CRE 8380, holotype; CRE 8381; CRE 6707; CRE 6711); Río Frío (UF 75794, UF 30538, *LACM 59202); 3 km SE Puerto Viejo (UF 31080-81).

C. montanus: Honduras: Cortés: "few km S Santa Elena" (LSUMZ 36659, UTACV 9443).

C. orobius: Costa Rica: San José: Interamerican Hwy. between Hortensia and Fortuna (CRE 277, holotype).

C. rozellae: Mexico: Chiapas: Palenque (*USNM 113526); Vera Cruz: Jesús Carranza (KU 27514-15); Guatemala: El Petén: Tikal (UF 13726); 20 km NNW Chinajá (KU 55861-62).

* MJC notes
† Wilson *et al.* (1986) data

A KEY TO THE MAINLAND SPECIES OF THE GENUS *CELESTUS*

1a. Frontal shield bordered anteriorly by a single large plate (fused prefrontals and frontoparietal) 2

1b. Frontal shield bordered anteriorly by three plates (two prefrontals and a frontonasal); small dark spots on dorsum and flanks, sometimes with large, dark-outlined, lime-green light spots on flanks .... *Celestus montanus* (Honduras; 915-1373 m)

2a. 14-18 lamellae under 4th toe 3

2b. 20-27 lamellae under 4th toe 4

3a. A pair of distinct dorsolateral light stripes .... *Celestus bivittatus* (Guatemala to Nicaragua; 800-1882 m)

3b. Dorsum light brown, sharply contrasting with darker flanks that may either be uniform or marked with large light spots... *Celestus enneagrammus* (Mexico; 1200-1900 m)

4a. 78 or more transverse rows of ventral scales; 73 to 81 transverse rows of dorsal scales; caudal scales lack a distinct median keel..5

4b. 77 or fewer transverse rows of ventral scales; 65 to 73 transverse rows of dorsal scales; caudal scales with a distinct median keel 6

5a. Dorsal and lateral pattern includes scattered, light-tipped black scales that sometimes form short longitudinal or vertical lines; side of neck without vertical dark and light bars; a pair of longitudinal greenish dorsolateral and black ventrolateral stripes present... *Celestus hylaius* (Costa Rica; 40-360 m)

5b. Dorsum uniform or with some black flecking; distinct alternating light and dark bars on side of neck and usually on flanks; no indication of longitudinal stripes... *Celestus rozellae* (southern Mexico, Guatemala, Belize; 2-480 m)

6a. 10-12 preanal scales; body pattern of scattered black scales .... *Celestus cyanochloris* (Costa Rica; 1200-1500 m)

6b. 8 preanal scales; body of scattered black scales dorsally and definite black-margined light bars on flanks... *Celestus orobius* (Costa Rica; 1500-2000 m)

DISTRIBUTION AND RELATIONSHIPS

The species of Central American *Celestus* are completely allopatric to one another in distribution. Two species (*C. hylaius* and *C. rozellae*) are found only in humid lowland forests of the Atlantic slope below 500 m in altitude. These lizards do not particularly resemble one another and their ranges are separated by a distance of some 500 km. The remaining five forms are from the uplands above the 1200 m contour and are distributed on isolated upland masses in a linear fashion from north to south as follows: Atlantic drainage slopes eastern and southeastern Mexico *(enneagrammus)*, moderate elevations of the Nuclear Central American highlands from Guatemala to central Nicaragua (*bivittatus*), montane Atlantic slope Honduras (*montanus*), Cordillera de Tiláran and Central of Costa Rica (*cyanochloris*) and Cordillera de Talamanca of Costa Rica *(orobius)*. This sequence does not appear to reflect an easily determined set of phylogenetic relationships. *Celestus bivittatus* and *enneagrammus* show similarities in scale features but are strikingly different in colouration, whereas *C. cyanochloris* and *C. orobius* appear to be allied. *Celestus montanus* does not appear to be closely related to any other form although it resembles the upland Costa Rican forms in some scale features.

A cladistic analysis of the seven Central American species here placed in *Celestus* was undertaken using PAUP (Swofford, 1985) based upon eight characteristics (scale rows around body, number of dorsal scale rows, number of ventral scales, number of preanals, naso-rostral contact, number of fourth toe lamellae, condition of frontonasal, and color pattern). Monophyly was based upon the unsheathed condition of the claws which Underwood (1959), Strahm and Schwartz (1977) and we regard as derived from the sheathed condition in *Diploglossus*. *Diploglossus bilobatus* and *D . monotropis* were used as outgroups. These were especially appropriate choices because the former has a single shield in the prefrontal area (a large frontonasal) and the latter three (2 prefrontals and a frontonasal). In both cases the analysis produced an unresolved polychotomy of all seven species, strongly indicating that some other kinds of data (e.g. molecular) are needed to establish a robust hypothesis of relationships for mainland *Celestus*.

BIOGEOGRAPHIC CONSIDERATIONS

Strahm and Schwartz (1977) proposed a biogeographic model for the major features in the history of diploglossine evolution based on the concept that the ancestor of the living genera was of South American stock having sheathed claws, and an auricular opening. Although other features were attributed to the presumed ancestor (radices, 3 shields bordering the frontal anteriorly and a naso-rostral contact) all of these conditions exhibit intraspecific varia ion in one or more contemporary species and have questionabl utility in establishing relationships. It should be noted however, that a majority of species have a single large frontonasal shield and most forms have the nasal separated from the rostral (see Table 1).

The Strahm and Schwartz biogeographic model is briefly summarized below. The reader should bear in mind however, that according to our analysis their concepts of *"Celestus"* and *"Diploglossus"* are unnatural (non-monophyletic) taxa, since Strahm and Schwartz placed individuals of the same species into different genera and that both nominal genera contain species with and without claw sheaths. Their emphasis on the apparently unreliable and variable osteodermal canal systems as an indicator of relationships is principally responsible for this situation, as they defined *"Diploglossus"* as having radices and *"Celestus"* as lacking them. Similarly, *Sauresia* and *Wetmorena* were related to *"Celestus"* on this basis alone. The salient features of their model are:

1. A widespread tropical American ancestor of South American origin differentiated into the modern genera

2. *Ophiodes* evolved *in situ* in South America

3. *"Celestus"* arose from the ancestor in Central America, probably in association with Miocene or earlier "openings and closings" of the Panamanian Portal

4. *"Diploglossus"* retained the ancestral character states and remained in South America, although now ranging north to Guatemala

5. *"Diploglossus"* invaded the Antilles by overwater transport or island hopping via the Lesser Antilles to the Greater Antilles exclusive of Jamaica and the Cayman Islands

6. *"Celestus"* subsequently dispersed to Jamaica and the Cayman Islands via overwater transport and thence to Hispaniola

7. *Sauresia* and *Wetmorena* evolved from *Celestus in situ* on Hispaniola, and secondarily regained claw sheaths.

This scenario is a classic disperal explanation of a distributional pattern involving a center of origin (South America), a migration (to Central America) and two episodes of overwater dispersion to the West Indies (Fig. 7). It appears to support the long-held view (Simpson 1942, 1 46; Darlington 1957; Williams 1989) that the biota of the Greater Antilles arose by waif dispersal from the mainland and subsequent island hopping along the Lesser Antilles arc. However, before either the Strahm and Schwartz scheme or its congruence (or lack thereof) with the general dispersal hypothesis can be evaluated, it is necessary to elucidate diploglossine distribution as required by our reevaluation of the species content of *Celestus* and *Diploglossus*.

As delimited here, *Diploglossus* occurs in South America, Lower Central America, and on the islands of Malpelo, Montserrat, Puerto Rico and Cuba. Strahm and Schwartz's inclusion of Upper Central America in the range of the genus is based upon reference of *Celestus atitlanensis* (a junior synonym of *Celestus bivittatus*) to *Diploglossus*. Similarly, Hispaniola was included in the distribution of *Diploglossus* based upon the placement of *Celestus warreni* in the genus (the allied Hispaniolan species, *C. anelpistus* and *C. carraui*, were described subsequent to the 1977 paper).

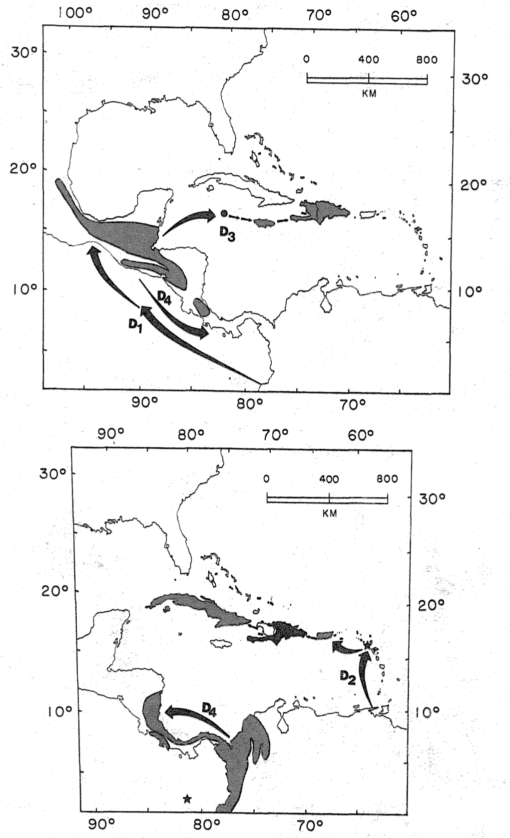

Fig. 7. Dispersal hypothesis of diploglossine biogeography for Mesoamerica and the West Indies. Upper, origin (D_1) and subsequent dispersals of *Celestus;* lower, dispersals of *Diploglossus* (hatched and stars) and origin of its derivatives *Sauresia* and *Wetmorena* on Hispaniola (black).

Celestus as defined in the present paper occurs on Jamaica, the Cayman Islands, and Hispaniola, and from Costa Rica to Mexico on the mainland. *Celestus* and *Diploglossus* are sympatric only on the Atlantic versant of Costa Rica and Nicaragua. No revision in species content or distribution is required for the other diploglossine genera, and the ranges of all five genera are mapped (Fig. 8). However, we regard the endemic genera *Sauresia* and *Wetmorena* as close relatives of *Diploglossus* that have differentiated on Hispaniola and occur sympatrically with *Celestus* on that island. This conclusion raises the possibilities that the species now referred to *Sauresia* and *Wetmorena* actually should be included in *Diploglossus* in spite of their highly specialized habitus (i.e. *Diploglossus* is paraphyletic). A decision on this matter cannot be made here and must await further study of the relationships of the West Indian forms.

The modifications in generic characterizations and composition outlined above do not substantially modify the overall model proposed by Strahm and Schwartz. A revised dispersal model based on our systematic reallocations involves a migration from South to Central America and two overwater dispersals to the West Indies, one along the Lesser Antillean chain and the other from Central America to Jamaica and then to Hispaniola. This conforms to the essential features of the Strahm and Schwartz hypothesis, and is presented in the form of a cladogram of area relationships (Fig. 9). This hypothesis requires a minimum of one vicariant and seven dispersal events, three of which are major. It could be corroborated if the phylogeny of diploglossines were determined to be congruent with the area cladogram, since such a typology is predicted by their model. Unfortunately such a test of the dispersal model must await a rigorous cladistic analysis of diploglossine phylogeny (see below) which is beyond the scope of this paper. We do note with more than a casual interest, that the distribution of diploglossines conforms closely to that expected from Guyer and Savage's (1987) vicariance model of Caribbean biogeography (Fig. 10) based upon an interpretation of recent geologic and biogeographic studies (Rosen 1976; Pindell and Dewey 1982; Savage 1983; Pindell 1985; Sykes *et al.*, 1982; Mann and Burke 1984) and the phylogeny of anole lizards. The salient features of this model as it relates to diploglossine history are:

1. North and South America were connected in the Late Cretaceous-Paleocene by a more or less continuous land connection (the proto-Greater Antilles)

2. The subsequent fragmentation of this block into the precursors of the Greater Antilles and their displacement northeastward by movement of the Caribbean Plate led to the isolation of the two American continents and differentiation of their faunas

3. Differentiation also occurred on the various proto-Greater Antillean fragments

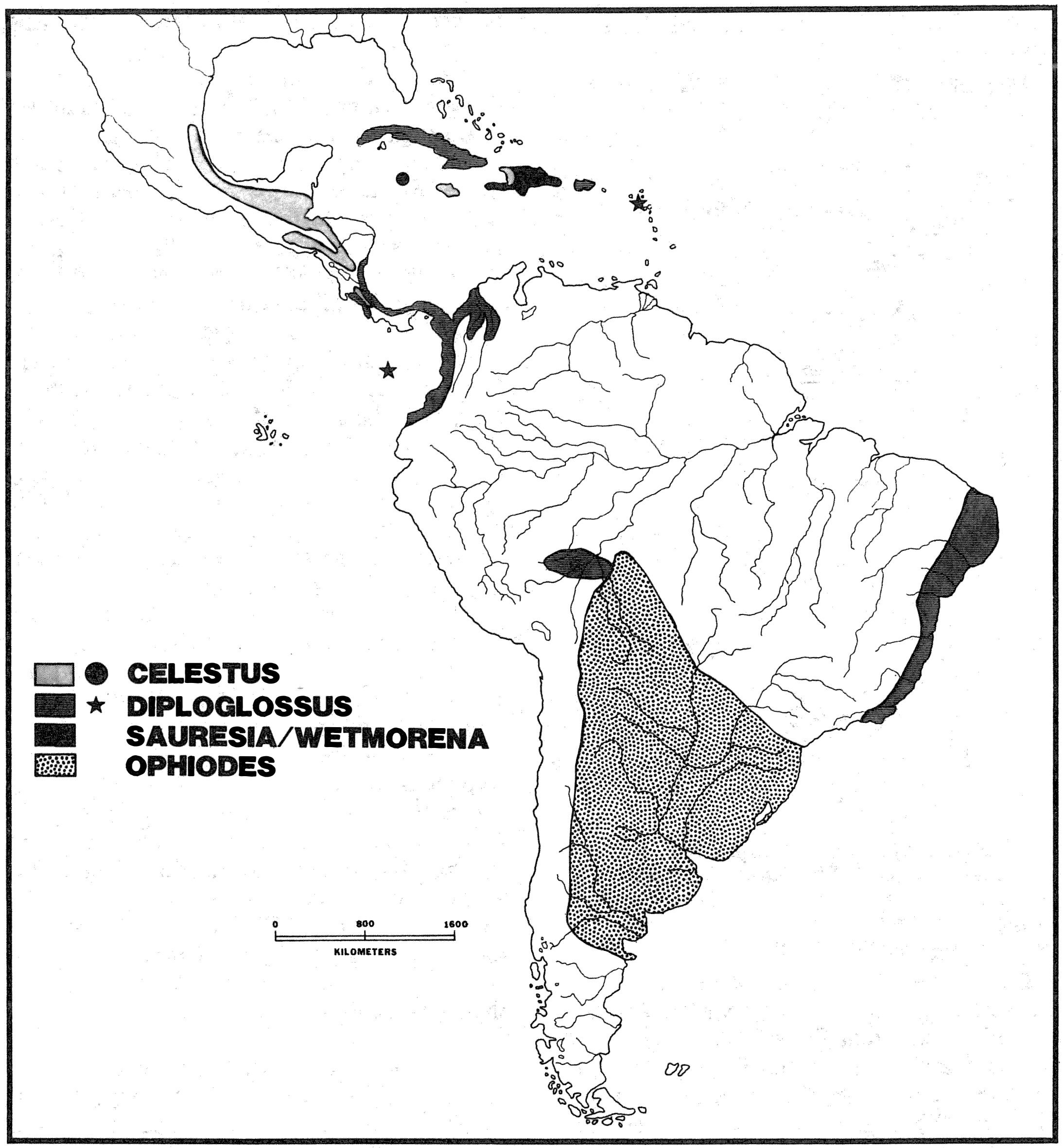

Fig. 8. Distributions of extant genera of diploglossines. *Celestus* is sympatric with *Sauresia* and *Wetmorena* over much of Hispaniola.

4. The fragments that now form the southwestern portion of Hispaniola and Jamaica remained associated with Central America for the longest time

5. Hispaniola is a composite island formed by accretion of several parts, with the southwestern portion added most recently

6. Reconnection of North and South America by the uplift of the Panamanian Isthmus resulted in sympatry between formerly disjunct, allied taxa via dispersal.

The present distribution of diploglossines and their apparent relationships show a close correlation with this series of events as follows:

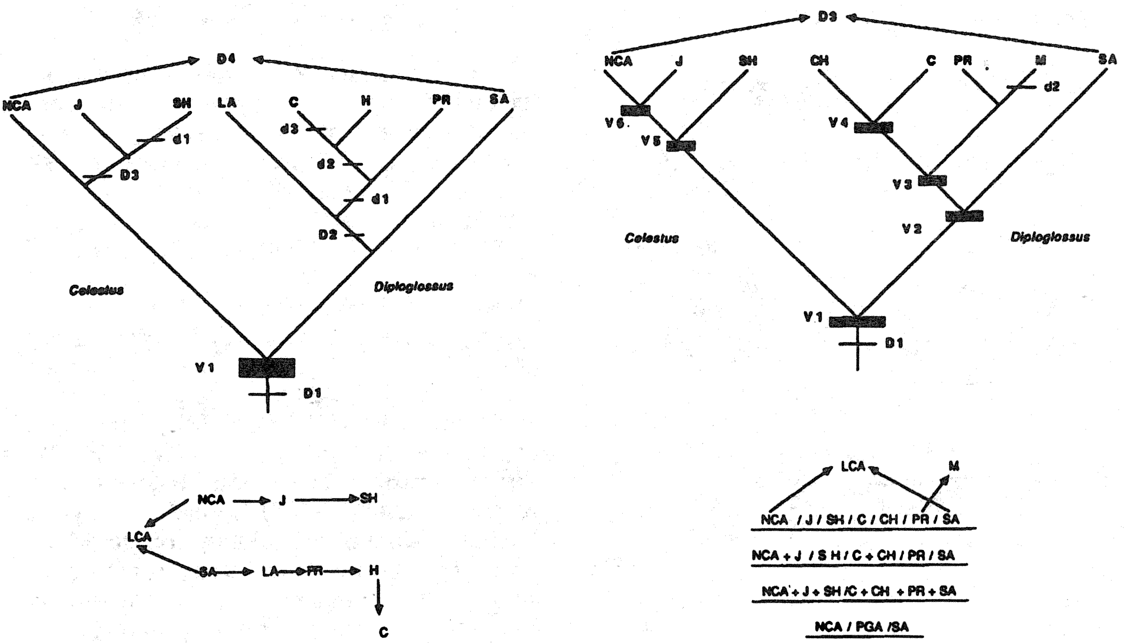

Fig. 9. Cladogram of relationships of *Celestus* and *Diploglossus* predicted by biogeographic hypotheses. Left, dispersal model; right, vicariance model. D = major dispersal event, d = minor dispersal event, V = vicariance event; arrows indicate dispersals, bars vicariance events; C = Cuba, CH = central Hispaniola, H = Hispaniola, J = Jamaica, LA = Lesser Antilles, M = Montserrat, NCA = Nuclear Central America, PR = Puerto Rico, SA = South America, SH = southern Hispaniola. See text for discussion.

1. A widespread ancestor resembling *Diploglossus* in having a claw sheath ranged over tropical America
2. Fragmentation of the proto-Greater Antilles split this stock in two, a southern component in South America and on the fragments that became Puerto Rico, central Hispaniola and Cuba plus a northern unit comprised of Central America, future southwestern Hispaniola and Jamaica
3. *Celestus* differentiated in the northern area; speciation within *Diploglossus* resulted in the origin of the Antillean taxa *Sauresia* and *Wetmorena* on the isolated fragments that were to form Puerto Rico, central Hispaniola and Cuba
4. The fragments that were to become southwestern Hispaniola and Jamaica separately split off from Central America, carrying *Celestus* with them
5. Accretion to the southwestern portion of Hispaniola produced the present sympatry of *Celestus* with *Sauresia* and *Wetmorena*
6. *Diploglossus* and *Celestus* now overlap in Lower Central America following the uplift of the Panamanian Isthmus and their dispersal (north or north and south) into the region.

This model requires only three dispersal events to produce the current pattern (Fig. 10). It is also corroborated by the distribution of other groups of Antillean species, including anoline lizards (Guyer and Savage 1987), butterflies (Miller and Miller 1989) and *Eleutherodactylus* (Hedges 1989), suggesting that the pattern is a general one and that the model may have general explanatory power.

Selection of one of the competing hypotheses of diploglossine biogeography over the other (or rejection in favor of some other hypothesis) is dependent upon a cladistic analysis of diploglossine phylogeny based on osteological and/or molecular characteristics. Rejection or acceptance of the dispersal or vicariance hypothesis is dependent upon how closely the phylogram conforms to the cladogram of area relationships required by the competing hypotheses (Fig. 9).

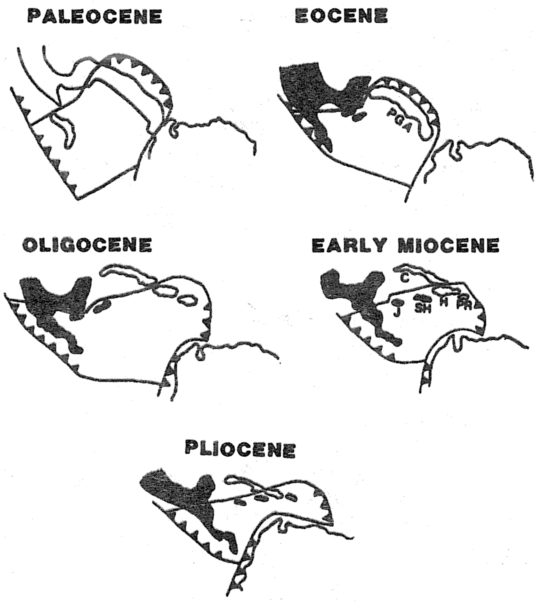

Fig. 10. Guyer and Savage's 1987 vicariance model of Caribbean biogeography as an explanation of diploglossine distribution in the region. Light stipple, distribution of *Diploglossus*-like ancestor (Paleocene) and *Diploglossus;* dark stipple, distribution of *Celestus*. C = Cuba, H = central Hispaniola, J = Jamaica, PGA = Proto-Greater Antilles, PR = Puerto Rico, SH = southern Hispaniola. Scale of Central American Isthmus in Paleocene and Proto-Greater Antilles exaggerated for purposes of illustration. Present distribution of *Celestus* and *Diploglossus* and its allies detailed in Figs. 7-8. See text for further explanation.

In the interim, we invoke the principle of biogeographic parsimony as our basis for favoring one of these hypotheses over the other. This principle states that when two competing biogeographic hypotheses are compared, the one conforming most closely to geographic and geologic data and requiring the fewest *ad hoc* dispersal events should be favored (i.e. it is most parsimonious). In this case there are no major differences in the geologic basis or geographic relationships involved in the two hypotheses, although the dispersal model implies a greater recency of events (*e.g.* after fragmentation of and movement by the Greater and Lesser Antilles into more or less their present positions) than does the vicariance one. However, the vicariance hypothesis provides the more parsimonious explanation of diploglossine biogeography since it requires only three dispersal events compared to eight for the Strahm and Schwartz dispersal hypothesis (Fig. 9).

ACKNOWLEDGEMENTS

We are indebted to the following curators for their cooperation in providing specimens and data for inclusion in this study (abbreviations for catalogued specimens in parentheses): D. L. Auth, University of Florida (UF); J. A. Campbell, University of Texas at Arlington (UTACV); W. E. Duellman, University of Kansas (KU); R. W. McDiarmid, National Museum of Natural History (USNM); C. W. Myers, American Museum of Natural History (AMNH); D. C. Robinson, Universidad de Costa Rica (UCR); D. Rossman, Louisiana State University (LSUMZ); H.K. Voris, Field Museum of Natural History (FMNH); J.W. Wright, Museum of Natural History of Los Angeles County (LACM). Special thanks go to Michael J. Corn of Lake Forest College, whose notes and counts and measurements of additional specimens were most useful in evaluating the status of our specimens. We appreciate the aid of Maureen A. Donnelly, American Museum of Natural History, who provided supplementary data needed for outgroup comparisons, of Michael Fogden who kindly donated color slides of *C. cyanochloris* and *C. hylaius,* and of Joseph B. Slowinski for constructing the parsimony cladogram. We thank M. A. Donnelly and C. Guyer for comments on the manuscript.

RESUMEN

Se describe dos especies nuevas de lagartijas diploglosinas, *Celestus hylaius* y *Celestus orobius*, de las bajuras del Atlántico y de la Cordillera de Talamanca, Costa Rica, respectivamente. Ambas difieren de las descritas previamente para el género *Celestus* fundamentalmente en la coloración, así como en detalles de las escamas (número de filas medio-dorsales, lamelas bajo el cuarto dedo y/o número de escamas preanales). Se revisa el estado taxonómico de ambos géneros. Se rechaza la ubicación de especies en alguno de esos taxones que se basa en la arquitectura de los osteodermos debido a que las supuestas diferencias demostraron ser en realidad variación ontogénica. En cambio, se da nueva validez a la clasificación tradicional que ubicaba en *Diploglossus* las especies con vaina

en las uñas y las carentes de vaina en *Celestus*. Así, *Celestus* tiene siete especies en México y América Central, y 16 en las Antillas. *Diplogolssus* tiene seis en Centro y Sur América y cuatro en las Antillas. Los géneros endémicos de Isla Española, *Sauresia* (dos especies) y *Wetmorena* (una) son parientes derivados de *Diploglossus*. *Celestus* y *Diploglossus* solo son simpátricos en América Central, pero *Celestus* coincide con *Sauresia* y *Wetmorena* en la Española. Se revisa la biogeografía de los diploglosinos haciendo especial referencia al Caribe. Hay dos modelos opuestos, dispersión y vicariancia, que intentan explicar la actual distribución: *Celestus* en México, América Central, Jamaica, Islas Caimán y Española; *Diploglosus* en el sur de América Central, Sur América, Cuba, Puerto Rico, Monserrat y Malpelo, y sus parientes *Sauresia* y *Wetmorena* en la Española. Se muestran cladogramas geográficos y las relaciones filogenéticas predichas para las formas circumcaribeñas con base en ambos modelos. No hay aún suficiente información para decidirse por alguno, aunque el vicariante es más parsimonioso.

REFERENCES

Barbour, T. 1910. Notes on the herpetology of Jamaica. Bull. Mus. Comp. Zool. 52:273-301.

Boulenger, G. A. 1885. Catalogue of the lizards in the British Museum (Natural Histo y). vol. 2, 2nd ed. Taylor and Francis, London.

Boulenger, G. A. "1894". [1895]. Second report on additions to the lizard collection in the Natural-History Museum. Proc. Zool. Soc.of London 1894:722-736.

Burt, C. E. & M. D. Burt. 1932. South American lizards in the collection of the American Museum of Natural History. Bull. Am. Mus. Nat. Hist.61:1-597.

Cope, E.D. 1894. Third addition to a knowledge of the Batrachia and Reptilia of Costa Rica. Proc. Academy of Natural Sciences of Philadelphia 1894:194-206.

Darlington, P. J. 1957. Zoogeography. John Wiley and Sons, Inc. New York, New York.

Dunn, E. R. 1939. Zoological results of the Geor e Vanderbilt South Pacific Expedition of 1937. Part III. The lizards of Malpelo island, Colombia. Notulae Naturae, Academy of Natural Sciences of Philadelphia. 4:1-3.

Fitzinger, L.J.F.J. 1843. Systema reptilium. Wien.

Gauthier, J. A. 1982. Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. Contributions to Geology, University of Wyoming 21:7-54.

Gray, J.E. 1831. Description of a new genus of ophisaurean animal, discovered by the late James Hunter, Esq., in New Holland. Zoological Miscellany 1:14.

Gray, J. E. 1839. A catalogue of the slender-tongued saurians, with descriptions of many new genera and species. Annals and Magazine of Natural History 1:288-293.

Guyer, C. & J. M. Savage. "1986". [1987]. Cladistic relationships among anoles (Sauria: Iguanidae). Systematic Zoology 35:509-531.

Hedges, S.B. 1989. Evolution and biogeography of West Indian frogs of the genus *Eleutherodactylus*: slow-evolving loci and the major groups. *In:* Biogeography of the West Indies. C.A. Woods (ed.). Sandhill Press, Gainesville, Florida.

Leviton, A. E., R. H. Gibb, JR., E. Heal & C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802-832.

Lieberman, S. S. 1986. Ecology of the leaf litter herptofauna of a Neotropical rainforest: La Selva, Costa Rica. Acta Zoologica Mexicana 15:1-72.

Mann, P. & K. Burke. 1984. Neotectonics of the Caribbean. Review of Geophysical and Space Physics 22:309-362.

Meyer, J. R. & L. D. Wilson. 1973. A distributional checklist of the turtles, crocodilians and lizards of Honduras. Contributions to Science, Natural History Museum of Los Angeles County 244: 1-39.

Miller, L.D. & J.Y. Miller. 1989. The biogeography of West Indian butterflies (Lepidoptera: Papilionidea, Hesperioidea): a vicariance model. *In:* Biogeography of the West Indies. C.A. Woods (ed.). Sandhill Press, Gainesville, Florida.

Myers, C. W. 1973. Anguid lizards of the genus *Diploglossus* in Panama, with the description of a new species. American Museum Novitates 2523:1-20.

Peters, J.A. 1964. Dictionary of herpetology. Hafner Publ. Co. New York, New York.

Peters, J. A. & R. Donoso-Barros. 1970. Catalogue of the Neotropical Squamata: Part II. Lizards and Amphisbaenians. Bulletin of the United States National Museum 297:1-193.

Pindell, J. L. 1985. Alleghenian reconstruction and subsequent evolution of the Gulf of Mexico, Bahamas, and Proto-Caribbean. Tectonics 4:1-39.

Pindell, J. L. & J. F. Dewey. 1982. Permo-Triassic reconstruction of western Pangea and the evolution of the Gulf of Mexico/Caribbean region. Tectonics 1:179-211

Rosen, D. E. 1976. A vicariance model of Caribbean biogeography. Systematic Zoology 24:431-464.

Savage, J. M. 1983. The enigma of the Central American herpetofauna: dispersal or vicariance? Annals of the Missouri Botanical Garden 69:464-547.

Schwartz, A. 1970. A new species of large *Diploglossus* (Sauria: Anguidae) from Hispaniola. Proceedings of the Biological Society of Washington 82:777-788.

Schwartz, A. & R. W. Henderson. 1988. West Indian Amphibians and Reptiles: a check-list. Contributions to Biology and Geology, Milwaukee Public Museum 74:1-264.

Schwartz, A., E.D. Graham, JR., & J.J. Duval. 1979. A new species of *Diploglossus* (Sauria: Anguidae) from Hispaniola. Proceedings of the Biological Society of Washington 92: 1-9.

Schwartz, A., S.J. Indravstegui, & R.W. Henderson. 1985. Hispaniolan giant *Diploglossus* (Sauria: Anguidae): description of a new species and notes on the ecology of *D. warreni*. Amphibia-Reptilia 6: 195-201.

Shaw, 1802. General Zoology or Systematic Natural History. Thomas Davison, London.

Simpson, G. G. 1942. A Miocene tortoise from Patagonia. American Museum Novitates 1209:1-6.

Simpson, G. G. 1946. Tertiary land bridges. Transactions of the New York Academy of Science ser. 2, 8:255-258.

Smith, H. M. & E. H. Taylor. 1950. An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. Bulletin of the United States National Museum 199:1-253.

Stejneger, L. 1904. The herpetology of Porto Rico. Annual Report of the United States National Museum 547-724.

Strahm, M. H. & A. Schwartz. 1977. Osteoderms in the anguid lizard subfamily Diploglossinae and their taxonomic importance. Biotropica 9: 58-72.

Stuart, L. C. 1963. A checklist of the herpetofauna of Guatemala. Miscellaneous Publications of the Museum of Zoology, University of Michigan 122:5-150.

Swofford, D.L. 1985. PAUP: Phylogenetic Analysis Using Parsimony, version 2.4. Illinois Natural History Survey, Champaign, Illinois.

Sykes, L. E., W. R. McCann, & A. L. Kafka. 1982. Motion of Caribbean plate during last 7 million years and implications for earlier Cenozoic movements. Journal of Geophysical Research 87: 10656-10676.

Taylor, E. H. 1956. A review of the lizards of Costa Rica. University of Kansas Science Bulletin 38:3-322.

Thomas, R., & S.B. Hedges. 1989. A new *Celestus* (Sauria: Anguidae) from the Chaine de la Selle of Haiti. Copeia 1989: 886-891.

Underwood, G. 1959. A new Jamaican galliwasp (Sauria: Anguidae). Breviora Museum of Comparative Zoology 102:1-13.

Weigmann, A.F.A. 1834. Herpetologica Mexicana. Lüderitz, Berlin

Williams, E. E. 1989. Old problems and new opportunities in West Indian biogeography. *In*: Biogeography of the West Indies. C.A. Woods (ed.). Sandhill Press, Gainesville, Florida.

Wilson, L. D., L. Porras, & J. R. McCranie. 1986. Distributional and taxonomic comments on some members of the Honduran herpetofauna. Contributions to Biology and Geology, Milwaukee Public Museum 66:1-18.