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Reevaluation of the Status of Taxa of Central American Caecilians (Amphibia: Gymnophiona), with Comments on Their Origin and Evolution

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New specimens and a new analysis provide the basis for systematic revision of Central American caecilians. We recognize seven species in the genus *Dermophis* (*oaxacae, mexicanus, gracilior, costaricense, glandulosus, parviceps*, and *occidentalis*). Two species of *Gymnopis* (*syntrema* and *multiplicata*), three of *Oscaecilia* (*osae, elongata*, and *ochrocephala*), and four of *Caecilia* (*nigricans, volcani, isthmica*, and *leucocephala*) occur in Central America. New information about the geology of the region permits reevaluation of the biogeographic history of the group. Data for specimens, distribution maps, and a key are provided.

MORE than 25 years ago, we (Savage and Wake, 1972) reviewed the systematic status and distribution pattern of Mesoamerican caecilians. This effort provided a conservative analysis of then-available material that led to recognition of only eight species: three *Dermophis*, one *Gymnopis*, four *Caecilia* and one *Oscaecilia* in the region. Taylor (1973) correctly predicted that our paper would not be the final word on the matter, because since that time additional specimens from critical localities, especially in lower Central America, have encouraged us to undertake a reassessment of the systematics and biogeography of Mesoamerican gymnophionan taxa.

The current situation is presented by the Savage and Wake (1972) revision, which dealt primarily with geographic variation and the validity of species of the genera *Dermophis* and *Gymnopis*, which had been allocated to three genera and 13 species (one with a subspecies) by Taylor (1968) in his monograph of the world's caecilians. We followed Taylor (1968, 1969) in recognizing *Oscaecilia ochrocephala*, *Caecilia elongata*, *C. nigricans*, *C. tentaculata* and *C. volcani* as valid taxa. The latter are all Panamanian forms, three of which (*O. ochrocephala*, *C. nigricans*, and *C. tentaculata*) were thought to range for varying distances into South America.

Our treatment of *Dermophis* involved the synonymization of many taxa recognized as valid by Taylor (1968). The nominal species *Dermophis balboai* Taylor, 1968, *D. glandulosus* Taylor, 1955, and *D. occidentalis* Taylor, 1955, were regarded as conspecific with *Dermophis parviceps* (Dunn, 1924). *Dermophis costaricense* Taylor, 1955, *D. eburatus* Taylor, 1968, *D. septentrionalis* Taylor, 1968, and *D. mexicanus clarki* (Barbour, 1926) were allocated to the synonymy of *Dermophis mexicanus* (Dumeríl and Bibron, 1841).

Within the genus *Gymnopis*, we regarded *Gymnopis oligozona* (Cope, 1877) as conspecific with *Gymnopis multiplicata* Peters, 1874, and showed that *Gymnopis proxima* (Cope, 1875) intergraded with *G. multiplicata*, with which it was synonymized. In addition, we demonstrated that all caecilians assigned by Taylor to the putative genus *Cryptosophis* Boulenger, 1883, based on *Siphonops simus* Cope, 1877, are representatives of *G. multiplicata*.

In the interim since our work, Taylor (1973) restated the case for recognizing *Dermophis gracilior* as a valid form and reduced *Dermophis eburatus* to subspecific status within *D. mexicanus*. Wake and Campbell (1983) described a new genus and species, *Minasaecilia sartoria* from Guatemala. Nussbaum (1988) indicated that *M. sartoria* was conspecific with *Siphonops syntremus* Cope, 1866, the generic type of Taylor's (1968) putative genus *Copeotyphlinus* and *Gymnopis oligozona* (Cope, 1877) and concluded that the taxon should be recognized as *Gymnopis syntremus*. MHW disagrees with Nussbaum's concept of the genus *Gymnopis* as it relates to *G. syntremus*; she will treat that issue elsewhere. Wake (1985) and Nussbaum and Wilkinson (1989) preferred to assign *Caecilia elongata* to the genus *Oscaecilia*, an option later followed by Lahanas and Savage (1992).

As presently understood, the known Middle American caecilian fauna differs from that recognized in our 1972 paper by the desynonymization of *Dermophis gracilior* and *D. eburatus* (but only as a subspecies), the resurrection of *Gymnopis syntremus* from obscurity, the shift of *C. elongata* to *Oscaecilia*, and the addition of *Caecilia volcani* and *Oscaecilia osae*.

Our review of newly collected or discovered specimens from Guatemala, Nicaragua, Costa Rica, and Panama (Appendix 1) provides more

complete information on characteristics and distributional patterns and indicates that the current systematic arrangement needs revision. As in our earlier work, we are hampered by small sample sizes for several taxa (< 10) that include considerable ontogenetic variation, so that a morphometric treatment is not yet feasible. However, we provide new data and a reanalysis of Middle American caecilians in the light of a more historically informed species concept (Frost and Hillis, 1990) and a revised biogeographic explanation (Savage, 1982). Appendix 2 summarizes our systematic analysis.

Materials and Methods

We reexamined most of the caecilian specimens from Costa Rica and many from other parts of Central America; some information is taken from our previous work and other literature. We measured total lengths of specimens, counted primary and secondary annuli (our counts omit the ''collar'' annuli), and took detailed data on color patterns, condition of the vent, and distances of the eye, tentacle, and nostril from each other. We calculated an index of attenuation (IA = total length/width at midbody) to evaluate body size/shape relationships. We note that pregnant females of the viviparous *Dermophis* and *Gymnopis* usually fall at the upper limit of this index for each species. Data are presented in Tables 1–3. Specimen numbers for the several hundred *Dermophis mexicanus* from southern Mexico and northern Guatemala housed in the Museum of Vertebrate Zoology (MVZ) at the University of California, Berkeley, are not listed in Appendix 1 in the interest of space; the information is available upon request from MVZ, or via their Web site.

Results

Caecilians of the Dermophis mexicanus complex.—In our 1972 paper, we regarded most previously described species as belonging to a single wide-ranging taxon, *Dermophis mexicanus*, except for its relative *Dermophis oaxacae* and the smaller, slender lower Central American form, *Dermophis parviceps*. That this now appears to have been an oversimplification of the situation, especially for lower Central America, will become evident in the following sections of this report.

In the present context, *D. mexicanus*-like caecilians occur in the tropical lowlands on both coasts in Mexico, in northwestern Honduras, eastern Guatemala, and south from Guatemala along the Pacific versant into central Nicaragua (Figs. 1–2; Table 1). Members of this series of populations are large, robust to moderately stout animals reaching a total length of 600 mm and are characterized by having the dorsum gray to olive-brown, the venter yellowish and the annular grooves bordered by blackish lines that extend to ring the body and are especially evident ventrally, in sharp contrast to the otherwise pale venter. The dark transverse lines thus formed are usually complete across the venter but may be interrupted medially on the anterior part of the body. Only two species, *D. mexicanus* and *D. oaxacae*, are currently assigned to this complex (Wake, 1985).

Dermophis oaxacae is clearly distinct from all other samples in the *D. mexicanus* complex (Figs. 1B, 2; Table 1) by having the highest numbers of both primary (119–139) and secondary (101–133) annuli in the genus (total folds 224–258). This species ranges from Jalisco south to western Chiapas along the Pacific versant of Mexico and occurs in upland Michoacán (Wake, 1998a).

Additional material from Central America accumulated since 1972, especially the large series from northwestern Guatemala reported on by Wake (1980), clarifies the status of the remaining populations referred to *D. mexicanus*. The Guatemala series has moderately high annular counts (94–112, $\bar{x} = 105.1$ primaries, 35–85, $\bar{x} = 66.1$ secondaries, and a range of 136–188 total annuli) and encompasses the known range of variation for smaller samples of this group from eastern Mexico and the Pacific slopes of Central America (Table 1).

Recently collected material from the Atlantic slopes of Guatemala and Honduras clarifies the status of the nominal form *Gymnophis* (sic) *clarkii* Barbour, 1926, recognized as a subspecies of *Dermophis mexicanus* by Dunn (1942) and Taylor (1968). Its sole distinguishing feature was the low number of secondary folds, variously reported as 41 (in four specimens) by Dunn (1942) and 40 (for the holotype) by Taylor (1968). In 1972, we regarded these specimens as being at the lower limit of variation for *D. mexicanus* and placed *clarkii* in synonymy. One of the examples of *D. m. clarkii* reported on by Dunn (1942) was from San Pedro Sula (AMNH 49953). Four additional specimens (NSW 5252, TCWC 19159-60, AMNH 33386) from that locality or nearby have 75, 48, 35, and 37 secondaries, respectively. The secondary range for northern Honduras is 35–75 ($\bar{x} = 50.1$). Although lower values than for any other *D. mexicanus* population, these counts overlap those for the largest sample (Pacific Guatemala, Table 2), confirming our earlier conclusion that *D. m.*

TABLE 1. COUNTS AND MEASUREMENTS FOR NORTHERN *Dermophis*.

Populations	*N*	Primary annuli	Secondary annuli	Total annuli	Maximum total length (mm)	IA
oaxacae	18	119–139	101–133	224–258	454	22–34
$\bar{x}$		127.7	120.5	240.7		
mexicanus						
Atl. Mexico	12	104–110	51–72	155–179	393	15–26
$\bar{x}$		105.3	59.3	165.4		
Pac. Mexico	13	102–109	61–80	164–186	450	15–25
$\bar{x}$		105.4	71.0	176.4		
At. Guatemala	10	93–105	50–72	150–172	515	
$\bar{x}$		102.6	50.9	172.9		
Pa. Guatemala	200	94–112	45–85	159–188	600	13–22
$\bar{x}$		106.4	67.2	173.6		
El Salvador	39	102–112	61–88	168–196	412	15–24
$\bar{x}$		103.8	73.3	179.6		
Pac. Honduras	5	100–107	50–71	152–175	406	19–26
$\bar{x}$		103.8	62.4	166.2		
Atl. Honduras	9	99–107	35–75	135–178	543	16–25
$\bar{x}$		103.6	50.1	154.4		
Nicaragua	14	97–107	53–70	152–177	333	16–22
$\bar{x}$		102.9	59.2	162.3		
Total	292	94–112	35–88	152–196		13–26
$\bar{x}$		105.7	66.9	168.6		

clarkii is based on one extreme of variation in the species (Fig. 1B).

The status of Lower Central American Dermophis with numerous secondary folds.—In 1972, there were 38 lower Central American *Dermophis* and two from Colombia available for our study. Only two taxa, *D. mexicanus* and *D. parviceps*, were recognized at that time. An additional 31 examples from Costa Rica have allowed us to substantially revise our treatment of the genus in the region. It is now apparent that none of the caecilians from this area can be referred to *D. mexicanus* (contra Savage and Wake, 1972), nor are all examples previously identified by us as *D. parviceps* properly assigned to that species.

As noted above, *Dermophis mexicanus* is a large (to 600 mm in total length) form characterized by darkly pigmented ventral portions of the annular grooves and relatively high numbers of primary and secondary folds. The populations of Costa Rican and Panamanian caecilians that have numerous secondary folds are moderate-sized gymnophionans (to 405 mm total length) without darkly demarcated annuli on the venter. Although clearly related, two populations, one from the Atlantic and the other from the Pacific slope, differ substantially in the number of primary and secondary folds (Table 2). The Atlantic Costa Rican material is distinguished by its high annular counts and its geographic isolation. Concomitantly, the southwest Costa Rican-

TABLE 2. COUNTS AND MEASUREMENTS FOR COSTA RICAN *Dermophis*.

Species	*N*	Primary annuli	Secondary annuli	Total annuli	Total length (mm)	IA
parviceps	8	85–102	11–26	97–126	112–217	22–28
$\bar{x}$		94.5	17.6	112.1		
occidentalis	8	95–112	29–37	126–149	192–235	30–32
$\bar{x}$		105.8	32.2	138		
glandulosus	22	91–106	37–60	132–159	162–405	21–25
$\bar{x}$		95.7	48.1	144.1		
gracilior	5	91–102	65–78	159–176	255–345	25–31
$\bar{x}$		96.2	70.4	168.5		
costaricense	28	107–117	74–96	186–208	168–387	23–34
$\bar{x}$		112.8	88.2	199.8		

TABLE 3. SALIENT CHARACTERS OF MESOAMERICAN CAECILIANS EXCLUSIVE OF *Dermophis*.

Taxon	Primary annuli	Secondary annuli	Total annuli	Maximum total length	IA (See text)
Caecilia					
isthmica	131–147	12–21	143–168	578	22–31
leucocephala	118–131	32–54	150–185	455	31–41
nigricans	157–189	32–62	196–252	1,030	42–62
volcani	112–124	14–37	126–156	320	30–37
Oscaecilia					
ochrocephala	169–198	7–31	182–218	617	40–60
elongata	226–231	0	226–231	620	83–88
osae	232	0	232	382	91
Gymnopis					
multiplicata	112–133	84–107	201–250	480	23–34
syntrema	128–132	63–93	193–206	305	37–51

northwest Panamanian population with its low primary annular counts and isolated upland distribution is equally distinct from *Dermophis mexicanus*. Because of their disjunct distributions and annular counts that indicate differentiation along separate pathways, we believe that the distinctiveness of these units should be recognized.

Taylor (1955) described the Atlantic slope form as *D. costaricense* (Figs. 1A, 3), which is characterized by a high number of primaries (107–117) and secondaries (74–96). He (1968, 1973) also applied the name *D. gracilior* (Günther, 1902) to the Pacific slope population now diagnosable by having fewer primaries (91–102) and secondaries (65–78) than its Atlantic slope ally. It is possible that future collections may reveal individuals that are intermediate in the annular fold features, indicating that the two nominal taxa represent extremes in variation within a single species. However, the two taxa appear to be completely allopatric and, although overlapping slightly in both primary and secondary fold counts, are always distinguishable by differences in total annular counts (186–208 in *D. costaricense* vs 159–176 in *D. gracilior*).

In 1955, Taylor described *Dermophis glandulosus*, also from Costa Rica, based upon a single juvenile (159 mm in total length). Two additional, somewhat larger specimens (one 250 mm total length) were referred to this species by Taylor (1968). Savage and Wake (1972), perhaps misled by the small size and relatively low secondary counts (37–46), referred *D. glandulosus* to the synonymy of *D. parviceps*. Recently acquired material shows that this form is not

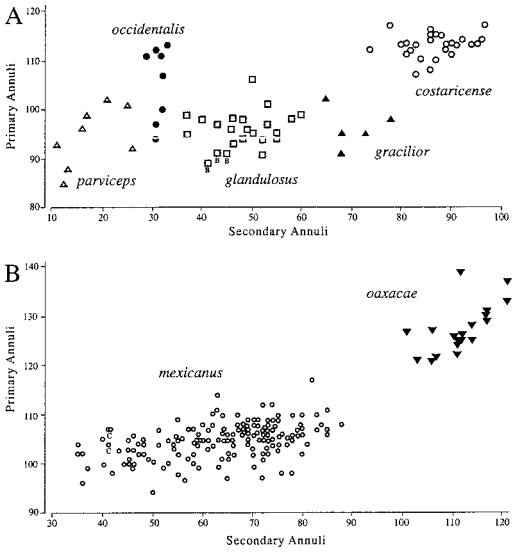

Fig. 1. (A) Primary and secondary annular counts for specimens of *Dermophis parviceps*, *Dermophis occidentalis*, *Dermophis glandulosus*, *Dermophis gracilior*, and *Dermophis costaricense*. The letter "B" denotes the three specimens previously identified as *Dermophis balboai*. (B) Primary and secondary annular counts for *Dermophis mexicanus* and *Dermophis oaxacae*. The letter "C" indicates the three specimens once designated *Dermophis mexicanus clarkii*.

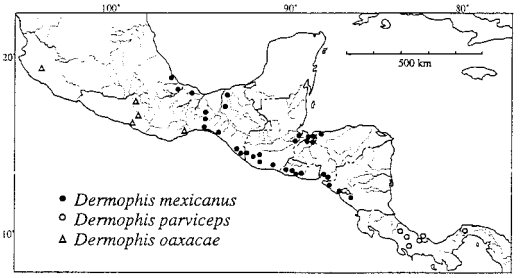

Fig. 2. Distribution of *Dermophis mexicanus*, *Dermophis parviceps*, and *Dermophis oaxacae* from Mexico to Panama.

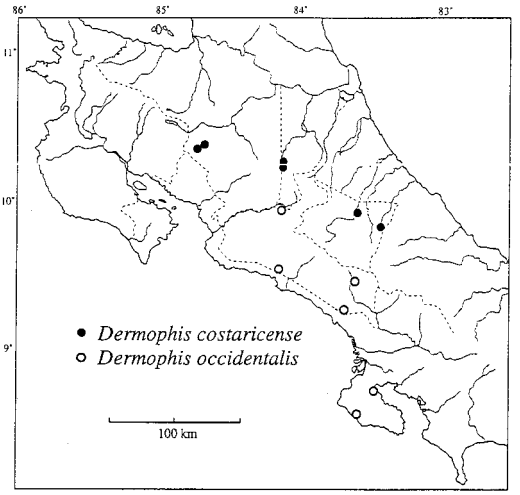

Fig. 3. Distribution of *Dermophis costaricense* and *Dermophis occidentalis* in Costa Rica.

Fig. 4. Distribution of *Dermophis glandulosus*, *Caecilia isthmica*, and *Caecilia leucocephala* from Costa Rica to Colombia.

allied to the smaller *D. parviceps* but rather is a moderate-sized species (up to 405 mm in total length) that resembles *D. gracilior* in the number of primary annuli but has fewer secondaries (37–60 in *D. glandulosus* vs 65–70 in *D. gracilior*; Fig. 1A). In addition, the two are sympatric in the area of San Vito de Jaba–Las Cruces Biological Station, Puntarenas Province, Costa Rica. The nominal species *Dermophis balboai* Taylor, 1968, of eastern Panama and adjacent Colombia resembles *D. glandulosus* in all salient features (Fig. 1A), and we continue to regard the two as conspecific.

Differentiation of Lower Central American Dermophis with few secondary folds.—*Dermophis parviceps* (Dunn, 1924) is a relatively small caecilian lacking dark pigment in the annular grooves. It is unusual among *Dermophis* in having a pinkish-colored head in life which contrasts with the purplish-gray body. After preservation the head and body colors retain the contrast although the pink color of the head fades to pale brown.

In our 1972 paper, we synonymized *Dermophis glandulosus* and *D. occidentalis*, both named by Taylor (1955), with *D. parviceps*. As pointed out in a previous section, we now regard *D. glandulosus* as based upon a much larger species that lacks the contrasting head coloration and has a substantial number of primary and secondary annuli (Figs. 1A, 4; Table 2).

The available material (16 specimens) of small caecilians from Costa Rica and Panama strongly suggests that two forms besides *D. glandulosus* are represented by what we called *D. parviceps* in 1972. All Atlantic versant specimens closely agree in features with the type of *D. parviceps* in having a pale head, very few secondaries (11–26) and relatively few primary annuli (85–101). Pacific slope examples agree with the type of *D. occidentalis* in having more secondaries (29–37) and primaries (95–112; Fig. 1B). One puzzling caecilian (LACM 128533) from near the Las Cruces Biological Station, Puntarenas Province, on the Pacific slope in Costa Rica, is a small (107 mm in total length) caecilian in poor condition having, as best as can be determined, 21 secondaries and 102 primary annuli, which would place it within the variation for the Atlantic slope series in secondaries. That specimen aside, we conclude that *D. parviceps* and *D. occidentalis* represent distinct allopatric species (Figs. 2–3). We tentatively refer LACM 128533 to the former, with question, as additional material from the Pacific slopes of Costa Rica and Panama is required to confirm the occurrence of *D. parviceps* in that area.

Notes on other taxa.—*Dermophis* and *Gymnopis* are essentially Middle American in distribution, with one species, *D. glandulosus*, ranging into northern Colombia. Two primarily South American genera of caecilians, *Caecilia* and *Oscaecilia*, reach their northern limits in lower Central America (Figs. 4–6). Three species of *Caecilia* also found in Colombia range into eastern Panama and one other form is endemic to western Panama. We are unaware of any new locality records for *C. nigricans*, *C. leucocephala*, or *C. isthmica* (= *C. tentaculata* in partim sensu Dunn, 1942, and Taylor, 1968) from Panama. Addition-

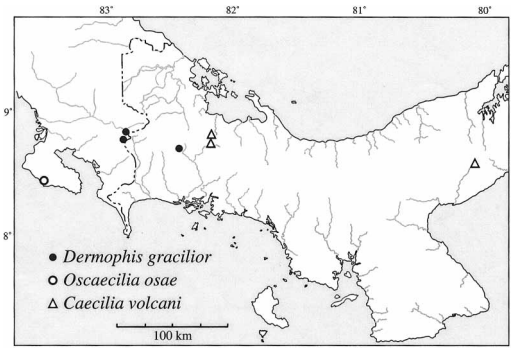

Fig. 5. Distribution of *Dermophis gracilior, Oscaecilia osae,* and *Caecilia volcani* in Costa Rica and Panama.

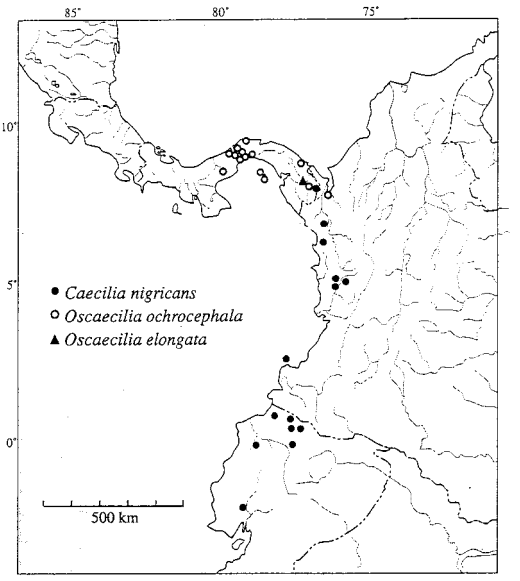

Fig. 6. Distribution of *Caecilia nigricans, Oscaecilia ochrocephala,* and *Oscaecilia elongata* from Panama through Ecuador.

al collections of the western Panamanian species *C. volcani,* previously known only from the type-locality at El Valle de Antón, Coclé Province, are from as far as 220 km west-northwest in the Fortuna Dam area of Chiriquí Province (Fig. 5).

The genus *Oscaecilia* is represented in Central America by two Panamanian species and one endemic to Costa Rica (Figs. 5–6). *Oscaecilia ochrocephala* is known from northwestern Colombia to central Panama. *Oscaecilia elongata,* the other form, is a Panamanian endemic, placed in *Caecilia* by us in 1972. We, however, now follow Taylor (1968), Wake (1985), Nussbaum and Wilkinson (1989), and Lahanas and Savage (1992) in allocating it to *Oscaecilia,* until the limits of the two genera are resolved (see Nussbaum and Wilkinson, 1989; Wake, in press). The discovery of a distinctive new species, *Oscaecilia osae,* from the Peninsula de Osa, Costa Rica (Lahanas and Savage, 1992) extends the known range of the genus 420 km to the west-southwest from central Panama.

Both Dunn (1942) and Taylor (1968) used the name *Caecilia tentaculata* Linné, 1758, for the species we are calling *Caecilia isthmica.* It is clear from their accounts that several taxa are subsumed under that name (*tentaculata*). In addition, no one is sure of the exact application of this name since the type is not extant and two Linnean descriptions (1749 and 1754) using the name appear to be based on two different species (Dunn, 1942:503). One of us (MHW) noticed a specimen labeled *Caecilia tentaculata* in a cabinet in Linné's home in Uppsala, Sweden, and has asked curators in Sweden to ascertain the provenance of the specimen. Although it seems probable that the type-specimen (formerly in the Leiden Museum) came from Suriname, of species known from that country only the form called *C. tentaculata* by Nussbaum and Hoogmoed (1979) appears to be conspecific with the type, a conclusion reached by Dunn (1942). This taxon does not seem to be the same as the one ranging from eastern Panama to northern Colombia. Consequently, we use the name *C. isthmica* for the type (USNM 25188) of that name and a Colombian specimen (MCZ 17376), both placed as *C. tentaculata* by Dunn (1942; Fig. 4).

We recognized a single species of *Gymnopis, G. multiplicata,* in lower Central America in 1972, based on data that indicated gradual intergradation of the Atlantic (nominal *G. proxima*) and Pacific (*G. multiplicata*) populations in the Tilarán region of northwestern Costa Rica. We also considered the completely allopatric population of this genus restricted to eastern Guatemala as referable to *G. multiplicata.* Both Dunn (1942) and Taylor (1968) regarded this population as a distinct species, *Gymnopis oligozona* (Cope, 1877). We (Savage and Wake, 1972: 687) left open the possibility that *G. oligozona* would prove to be a valid form, as dramatically proven by Wake and Campbell (1983) and Nussbaum (1988). Currently this form is placed in *Gymnopis* as *G. syntrema* (Cope, 1866). MHW will treat this problem elsewhere. Recent collections (UTA-A 32979, 47810) establish the occurrence of *G. multiplicata* in northern Guatemala on the slopes of the Sierra de las Minas and in the lower Motagua Valley. At the former locality, it is probably sympatric with *G. syntrema* (Fig. 7).

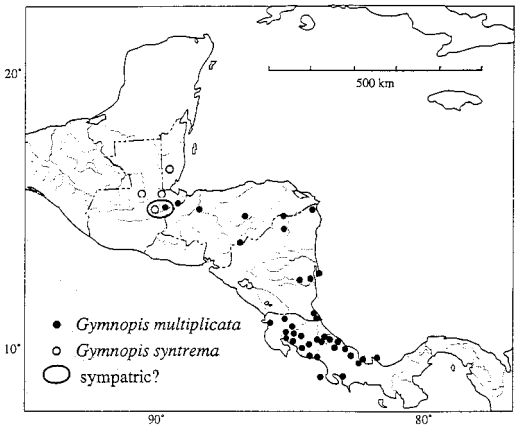

Fig. 7. Distribution of *Gymnopis multiplicata* and *Gymnopis syntrema* from Guatemala and Honduras through Panama. The localities circled may include sympatry of the species.

Discussion

Relationships.—The four currently recognized genera of Central American caecilians are all placed in the family Caeciliidae. This taxon has a broad tropical distribution in India (2 genera), the Seychelle Islands (3 genera), Africa (6 genera), and the Neotropics (10 genera), six of which are restricted to South America (Nussbaum and Wilkinson, 1989; Nussbaum and Hinkel, 1994). Of the Central American genera, *Dermophis* ranges into northern Colombia, whereas *Caecilia* (33 species) and *Oscaecilia* (8 species) are primarily South American in distribution. Within this family, *Dermophis* and *Gymnopis* appear to be sister taxa (Nussbaum and Wilkinson, 1989; Wake, 1992, 1998b), and *Caecilia* and *Oscaecilia* have a similar relationship. Indeed, some realignment of species between these last two genera is to be anticipated because some *Caecilia* appear to be more closely allied to some *Oscaecilia* than to other *Caecilia* species.

In the present state of knowledge, it is not possible to determine the relationships of either the *Dermophis–Gymnopis* clade or the *Caecilia–Oscaecilia* clade to other genera within the family, although there is some resemblance between the former and *Microcaecilia* and *Parvicaecilia*. *Caecilia* and *Oscaecilia*, however, differ from all other members of the family in having the tentacle located under the nostril and from all other American caeciliids in having narial plugs on the tongue. These facts support the notion of a long and independent history of the two clades.

Evaluation of species relationships within *Caecilia* and *Oscaecilia* lies outside the confines of the present study because the majority of forms in these genera are South American. Because *Gymnopis* contains only a pair of species, our comments on species relationships will refer only to *Dermophis*.

On the basis of external morphology we have recognized three groups of species within *Dermophis*: (1) large caecilians with numerous secondary annuli (*D. mexicanus* and *D. oaxacae*); (2) moderate-sized forms with numerous secondary folds (*D. costaricense, D. glandulosus, D. gracilior*); and (3) small to moderate-sized forms with few secondary folds (*D. occidentalis, D. parviceps*).

There seems little question that *D. mexicanus* and *D. oaxacae* are sister taxa differing in color pattern, number of vertebrae and number of secondary folds. They appear to be most closely related to lower Central American forms with high secondary counts. Within the latter group, *D. costaricense* and *D. gracilior* may be regarded as sister taxa and form a sister group to *D. glandulosus*.

Dermophis parviceps remains the most distinctive *Dermophis* in coloration and low secondary fold counts. The relationships of *D. occidentalis* are ambiguous, and possibly this form is more closely related to *D. glandulosus* or *D. gracilior* than to *D. parviceps*.

Biogeographic considerations.—Caecilians are a very ancient group with the oldest fossils being from early Jurassic times in North America, about 200 million years ago (Jenkins and Walsh, 1993) and more recent ones from the late Cretaceous of Bolivia (Rage, 1986) and of the Sudan (Werner, 1994; Evans et al., 1996), the Paleocene of Brazil (Estes and Wake, 1972) and of Bolivia (Rage, 1986), the Miocene of Colombia (Hecht and LaDuke, 1997) and the Quaternary of southern Mexico (Wake et al., 1999). Only the latter is referred to an extant species; most specimens are not referable or even assigned to a new taxon, being based on one or a few vertebrae. These records and the current circumtropical distribution of the order Gymnophiona implies an early Pangean distribution with *Dermophis* and *Gymnopis* the only remaining definitive Laurasian representatives. All other caecilians are derived from Gondwanian ancestors and are restricted to fragments of that ancient land mass except for the Ichthyophiidae, now found in India, Southeast Asia, and the Indo-Malayan region. The wider distribution of this family probably involved dispersal from the Indian plate. Along the same lines, we suspect that the present-day absence of caecilians from Madagascar and Australia represents extinction events.

In his review of the history of the Central American herpetofauna, Savage (1966, 1982)

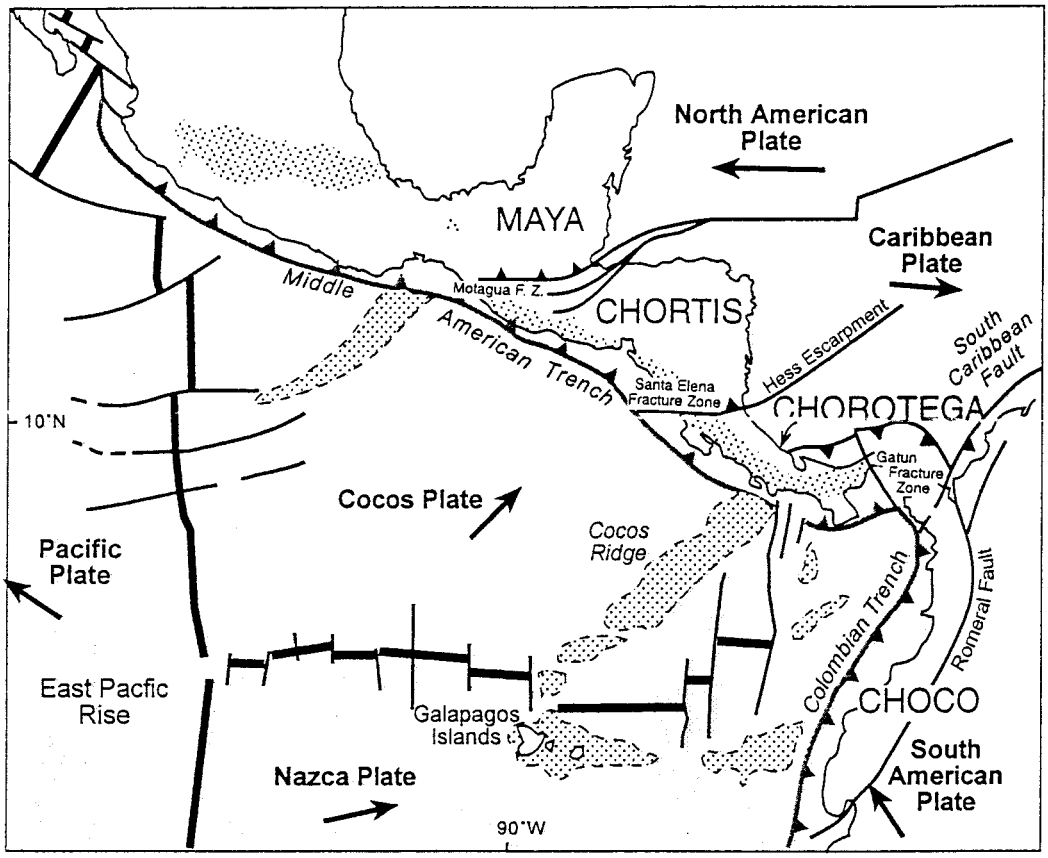

Fig. 8. Tectonic features of Mesoamerica. Crustal blocks: Chocó, Chorotega, Chortis, Maya. Note the locations of faults, fracture zones, and trenches; see text for the relationship to historical biogeography of caecilians. Based primarily on Mann (1995).

proposed that a major vicariance event separated the ancestors of future Middle American endemic genera from their relatives in South America. This event, the breakup of a formerly continuous isthmian link between North and South America in Paleocene times, isolated the ancestor of the *Dermophis–Gymnopis* clade in tropical North America. In addition, it isolated the ancestors of all South American caecilians on the now insular South American continent. Throughout the next 30 million years, the two continents remained separated by the broad and deep Panamanian seaway extending from about what is now the Tehuantepec region of Mexico to a South America far removed to the southeast of its present position.

At this time the Maya block was in its present position as the principal component of what would become eastern Mexico and northern nuclear Central America. The Chortis block, the future southern nuclear Central America lay well to the west. Far to the southwest were a series of volcanic islands that would later coalesce into the Chorotega and Choco blocks. In due course, the former would become today's Costa Rica and western Panama and the later eastern Panama and western Colombia.

By the middle Eocene, the Chortis block had to become sutured to the southern margin of the Maya block. During the late Oligocene and Miocene, the Chorotega and Chocó blocks narrowed the gap between nuclear Central America and South America. Finally, in the middle Pliocene about 3.3 million years ago, the two continents were reconnected by the present Panamanian Isthmus as the result of further uplift of the Chorotega and Chocó blocks by the subducting Cocos Plate (Escalante, 1990; Coates and Obando, 1996). With this very condensed review of Central American geologic history in mind, we could not help being struck by the remarkable fidelity of Central American caecilian core areas of distribution with major tectonic terranes (Fig. 8) as follows: North Ameri-

can Plate, especially the Maya block: *Dermophis* group 1; Chortis block: *Gymnopis*; Chorotega block: *Dermophis* groups 2 and 3; Chocó block: *Caecilia* and *Oscaecilia*.

We postulate that by the early Cenozoic, the ancestors of *Dermophis* and *Gymnopis* were already associated with the Chortis and Maya blocks, respectively. In the case of *Gymnopis*, some expansion of its range northward occurred across the Motagua and Polochic Faults after the suturing of the Chortis block to the Maya block in the Eocene. Subsequent fragmentation of this distribution, probably through the uplift of several east-west trending ranges (most notably the Merendón, Las Minas, Mico, and Chuacús of Atlantic-slope eastern Honduras and adjacent Guatemala), led to the differentiation of *Gymnopis syntrema* to the north and *G. multiplicata* to the south of the suture zone. Range expansion by both forms has brought them into virtual contact today along the lower north slope of the Sierra de Merendón in Guatemala. In addition, *G. multiplicata* has moved southward from the Oligocene onward across the Chortis block onto the emerging isthmian land bridge, where it has penetrated onto the northern portion of the Chorotega block.

The present distribution of *Dermophis* can best be explained by a combination of vicariance and dispersal events. The initial fragmentation of the ancestral range was probably initiated by the uplift of the central backbone of southern Mexico and nuclear Central America beginning in the Oligocene. This event was probably responsible for the differentiation of *Dermophis mexicanus* to the east and *D. oaxacae* to the west of the Tehuantepec Isthmus. In 1972, we proposed a dispersal across the isthmus by *D. mexicanus* onto the Pacific slope and subsequent expansion of its range southward on the Chortis block. Similarly, the range of *D. oaxacae* gradually extended northward up the western Mexican lowlands.

The southern species of *Dermophis* are restricted in distribution to areas south of the Chortis block, principally on the Chorotega block, although two species (*D. glandulosus* and *D. parviceps*) range onto the Chocó block. This dates the origins of *Dermophis* groups 2 and 3 to Miocene time.

Some continuity between the Chortis and Chorotega blocks existed sometime in the Miocene, but by late Miocene, the Nicaragua Depression formed a marine link north of the Chorotega unit. Apparently it was at this time that the isolated ancestors of southern *Dermophis* differentiated from the *D. mexicanus* lineage. Final emergence of the isthmian link allowed dispersal of *Dermophis* onto the Chocó block in Pliocene to Recent time. Differentiation of the southern species appears to have been the result of local orogenic effects (e.g., uplift of the cordilleras of Costa Rica and western Panama).

The representatives of the South American genera *Caecilia* and *Oscaecilia* in the region are the result of relatively recent events following closure of the final segments of the Panamanian seaway in the Pliocene. In Central America, four species are restricted to the Chocó block (*Oscaecilia elongata, Caecilia isthmica, C. leucocephala*, and *C. nigricans*). Two others occur only on the southern portion of the Chorotega block (*Oscaecilia osae* and *O. ochrocephala*) and *C. volcani* and *C. isthmica* appear to be allopatric sister taxa, one each on each of the two isthmian blocks. In summary, the correlation of caecilian distributions with major tectonic terranes provides a more detailed scenario of the historical biogeography of Central American caecilians.

Key to the Caecilians of Mexico and Central America

1a. Tentacle and tentacular foramen lying well posterior to nostril 2
1b. Tentacle and tentacular foramen lying immediately below nostril 10
2a. Tentacle just anterior to eye, tentacular foramen at or near center of maxillary bone; orbit roofed over by squamosal bone; a single splenial tooth on each ramus of lower jaw so that there are two tooth series (dentary and splenial) 3
2b. Tentacle about halfway between eye and nostril, tentacular foramen in anterior margin of maxillary bone; orbit not roofed by bone; no splenial teeth so only one row of teeth on lower jaw 4
3a. Dorsum gray, annular grooves contrasting pink or white; secondary folds 63–93; primary folds 128–132; total folds 193–206 (Northeastern Guatemala, adjacent Belize, and probably northwestern Honduras) ..... *Gymnopis syntrema*
3b. Dorsum and annular rings not contrasting in color; secondary folds 84–107; primary folds 112–133; total folds 201–250 (Atlantic slope Honduras to western Panama and Pacific slope Costa Rica and western Panama) ..... *Gymnopis multiplicata*
4a. Annular grooves marked with dark pigment ventrally, sharply contrasting with lighter venter 5
4b. Annular grooves not contrasting in color with lighter venter 6
5a. Primary folds 119–137; secondary folds 101–133; total folds 224–258 (Jalisco and Michoacán to Chiapas, Mexico) ..... *Dermophis oaxacae*

5b. Secondary folds 35–88; primary folds 94-112; total folds 152–196 (Eastern Mexico, western Mexico to Nicaragua and Atlantic slopes of Guatemala and Honduras ..... *Dermophis mexicanus*
6a. Secondary folds 65–96 7
6b. Secondary folds 11–60 8
7a. Primary folds 91–102; secondary folds 65–78; total folds 159–176 (Southwestern Panama and adjacent Costa Rica) ..... *Dermophis gracilior*
7b. Primary folds 107–112; secondary folds 74–96; total folds 186–208 (Atlantic slope Costa Rica) ..... *Dermophis costaricense*
8a. Small species to 235 mm in total length; 11–37 secondary folds 9
8b. A large species to 405 mm in total length; 37–60 secondary folds; 91–106 primary folds; 132–159 total folds (Southwest Pacific slope of Costa Rica) ..... *Dermophis glandulosus*
9a. Head pink to whitish in life, contrasting with gray dorsum; 11–26 secondary folds; 85–102 primary folds; 97–126 total folds (Atlantic versant from Costa Rica to central Panama) ..... *Dermophis parviceps*
9b. Head not pinkish to whitish in life, not markedly different in color to dorsum; 29-37 secondary folds; 95–112 primary folds; 126–149 total folds (Southwestern Costa Rica) ..... *Dermophis occidentalis*
10a. No secondary folds; 226–232 primary folds 11
10b. Secondary folds present; 112–198 primary folds 12
11a. Dermal scales present in posterior annular grooves (Osa Peninsula, Costa Rica) ..... *Oscaecilia osae*
11b. No dermal scales present in annular grooves (Eastern Panama) ..... *Oscaecilia elongata*
12a. Grooves of primary folds not contrasting to ground color 13
12b. Grooves of primary folds edged with black; 17–31 secondary folds; 169–198 primary folds; total folds 182–218 (Central and eastern Panama) ..... *Oscaecilia ochrocephala*
13a. Secondary folds 12–54; primary folds 112–147; total folds 126–185 14
13b. Secondary folds 42–62; primary folds 150–188; total folds 196–252 (Eastern Panama to northwestern Ecuador ..... *Caecilia nigricans*
14a. Large species, adults to 570 mm in total length; 12–54 secondary folds; 118–147 primary folds; 143–185 total folds 15
14b. A small species, adults 239–320 mm in total length; 14–37 secondary folds; 112–124 primary folds; 126–156 total folds (Western Panama) ..... *Caecilia volcani*
15a. Secondary folds 12–21; primary folds 131–147; total folds 143–168 (Eastern Panama and northern Colombia) ..... *Caecilia isthmica*
15b. Secondary folds 32–54; primary folds 118–131; total folds 150–185 (Eastern Panama and northwestern Colombia) ..... *Caecilia leucocephala*

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APPENDIX 1

Examined specimens reallocated to different species from Savage and Wake (1972) and records for additional material examined that was not available in 1972. Approximate altitudinal ranges of the species as a whole are also indicated. Museum abbreviations follow Leviton et al. (1985), except for CHP (Círculo Herpetológico de Panamá), CRE (Costa Rican Expedition—Jay Savage collection; not yet accessioned), LDW (Larry David Wilson collection; not yet accessioned), and MVUP (Museo de Vertebrados de la Universidad de Panamá).

Dermophis costaricense (1000–1360 m): COSTA RICA: Alajuela: Cinchona, KU 36337–42, 36343 (holotype), 36344–47, 66800, 66809; above Dos Aces, CRE (Costa Rica Expedition: J. M. Savage collection) 7532; Isla Bonita, KU 10854; Peñas Blancas Valley, 100 m, CRE 7533. Cartago: Moravia de Chirripó, KU 36447–48, 66801–08, 66810; 9.6 km E Turrialba, KU 140025.

Dermophis glandulosus (404–2000 m): COSTA RICA: Puntarenas: Limón: Valle de Silencio, MVZ 193582; Las Alturas, UCR 10920; Las Cruces, UCR 2826, 10919, and two unaccessioned

specimens; ± 5 km N Sabanilla, CRE 4706–08; San Vito de Java, CRE 8640–42; El Volcán, S. Minton 532 (private collection). San José: Cerro de la Muerte, UCR 1253; El Jorón, UCR 4219; nr. San Isidro de El General, KU 56070, 29979 (holotype). PANAMA: Chiriquí: Finca Santa Clara, KU 108935. Darién: Tacaracuna (holotype: *Dermophis balboai*), KUMNH 76184. COLOMBIA: Antioquia: Villa Artega, FMNH 78139–40.

Caecilia leucocephala (50–1000 m): PANAMA: Cana, KU 94378; COLOMBIA: Cauca: Río Raposo (transliterated to Río Riposa by collector), W. A. Thornton 583 (private collection) (holotype); ''Central Brazil,'' CAS 66187.

Dermophis gracilior (980–1200 m): COSTA RICA: Puntarenas: Las Cruces, CRE 8639; San Vito de Java, UCR 8494. PANAMA: Chiriquí: ''Chiriqui,'' BMNH 1946.9.5.33 (holotype); Boquete, CAS 79463-64.

Dermophis occidentalis (50–970 m): COSTA RICA: Puntarenas: 3 km W Rincon de Osa, 0.5 km N Old Osa Station, CRE 9245, 9606; Sirena, UCR 13479. San José: 1.5 km NE Alfombra, KU 32696–97, 32698 (holotype); Cerro de la Muerte, UCR 1444; Ciudad Colón, CRE 7032; Pozo Azul, BMNH 1907.6.28.27.

Dermophis parviceps (365–1220 m): COSTA RICA: Cartago: Moravia de Chirripó, KU 36276, 66827–28, UTA 1460. Limón: Parque Nacional Hitoy-Cerre, UCR 11196. Puntarenas: Las Cruces, LACM 128533. PANAMA: Bocas del Toro: La Loma, MCZ 9407 (holotype); Isla Popa, USNM 346903. Panama: Cerro Azul AMNH, 59533–35.

Dermophis mexicanus (2–1100 m): MEXICO: Chiapas: Finca San Jeronimo, N Cachaohatan, MVZ 159320–26, 167178, 177469–72, 179465–93, 191545–47; Tapachula, MVZ 1774678, 132911; Tabasco: Teapa, MVZ 81337–9. GUATEMALA: Guatemala: Zona 16, Santa Rosita, KU 186287. Izabal: 1 km SW El Arenal bridge, UTA 4397; Bandequa, UTA 25396–97; Puerto Barrios: Finca El Jalhaf, UTA 47811–12; Finca El Naranjo, UTA 47813; Morales: Quebradas Las Firmecza, UTA 51487; Tecomate, UTA 18160–62; Tenedores, KU 189564. San Marcos: San Rafael Pie de Cuesta, MVZ (466 specimens, individually recorded). EL SALVADOR: Cuscatlán: 2.5 km E Tanancingo, KU 184387; El Salvador: La Libertad: 10 km N Libertad, KU 85520; El Salvador: San Salvador: San Salvador, KU 184386; El Salvador: Santa Ana: at or nr. Volcán Isalco, CAS 69627–32, 69634, 69636–50, 69652, 69654–55, 69658. HONDURAS: Choluteca: 1 km N Cedeño, KU 394181, LSU 33568, 33587. Cortés: San Pedro Sula, NSW 5252; 3.2 km W San Pedro Sula, TCWC 19159–60; 1 km SSE Tegucigalpita, L. D. Wilson 10990 (private collection). NICARAGUA: Chinandega: San Antonio, KU 85519; Managua : Casa Colorado (Las Nubes), KU 173526–31.

Gymnopis multiplicata (3–1400 m): COSTA RICA: Alajuela: 9 km S Canalete, ANSP 32389; Grutas de Venado, UCR 3629; La Marina, UCR 3606; Peje Vieja, UCR 5408; San José de Upala, UCR 9700; Rincón de Zaragosa, UCR 12037; Guancaste: Cañas, UCR 2902. Heredia: Río Frío, UF 31694; 13.2 km N La Virgen, CRE 4760; La Selva, CRE 4748, 6726. Puntarenas: Golfito, UCR 11195; La Maritima nr. Quepos, UCR 8028; Santa Elena, CRE 4664. San Jose: San Isidro de El General, CRE 4664. GUATEMALA: Izabal: Morales, Sierra de Coral, Adlea San Miguelito, UTA 47810; Las Amates, Adlea San Antonio, UTA 32979. HONDURAS: Atlantida: nr. La Ceiba, SMF 78877. El Paraiso: Arenales, LACM 10979. Olanacho: 4.5 km SE Catacamas, LSU 21324; confluence Quebrada Siksatara and Río Wampú, USNM 530569. Yoro: Progreso District, MCZ 11048. NICARAGUA: Río San Juan: near Isla de Diamante, OMNH 33549–33569. PANAMA: Bocas del Toro: Isla Cristóbal, USNM 348644; Isla Escudo, USNM 347374.

Dermophis oaxacae (1–2100 m): MEXICO: Jalisco: 50 km N Autlán; Michoácan: Zitácuaro, IPN 2273.

Caecilia volcani (550–1180 m): PANAMA: Bocas del Toro: 6.5 km N continental divide on Gualaca-Chiriquí Grande road, USNM 339787. Chiriquí: 12.6 km N Los Planes on Gualaca-Chiriquí Grande road, GRG 2815 (field number in USNM); Quebrada Bonito, Fortuna, MVUP (Museo de Vertebrados de la Universidad de Panamá) 884; Bijau, Fortuna, MVUP 885. Coclé: El Aserradero, El Copé, CHP Círculo Herpetológico de Panamá) 1435; El Valle de Antón, CHP 3375.

Caecilia nigricans (128–914 m): COLOMBIA: Chocó: N slope Alto del Buey, LACM 72741–42.

Caecilia isthmica: PANAMA: San Blas: Atlantic side of Darién, USNM 25188; Colombia: Boyacá: Garagoa, MCZ 17384.

Oscaecilia osae (3 m): COSTA RICA: Puntarenas: Sirena, LACM 138542.

Oscaecilia ochrocephala (0–610 m): PANAMA: Panama: El Llano, LACM 2719–20.

Gymnopis syntrema (440–1000 m): GUATEMALA: Alta Verapaz: Finca Volcán, UMMZ 90928; Izabal: Aldea Vista Hermosa, KU 189565–66 (paratype and holotype, *Minascaecilia sartoria*); HONDURAS: ''Honduras, nr Belize'' (probably Belize), USNM 25187 (holotype, also holotype of *Siphonops oligozona*). Note that Stafford (1994) mentioned a specimen of this species from BELIZE: Cayo: upper Río Raspaculo.

APPENDIX 2. SYSTEMATIC SUMMARY

Caecilia nigricans Boulenger, 1902, Ann. Mag. Nat. Hist. ser. 7, 9:51. Synonyms: *Caecilia intermedia* Boulenger, 1913, Proc. Zool. Soc. London 1913:1026; *Caecilia palmeri* Boulenger, 1913, Proc. Zool. Soc. London 1913:1021.

Caecilia isthmica Cope, 1877, Proc. Amer. Phil. Soc. 17:91, but called *C.tentaculata* by Dunn (1942) and Taylor (1968, 1973).

Caecilia volcani Taylor, 1969, Univ. Kans. Sci. Bull. 98(12):315.

Dermophis costaricense Taylor, 1955, Univ. Kans. Sci. Bull. 37(13):505.

Dermophis glandulosus Taylor, 1955, Univ. Kans. Sci Bull. 37(13):506. Synonym: *Dermophis balboai* Taylor, 1968, Caecilians of the World: 461.

Dermophis gracilior (Günther, 1902), Biol. Central.-Americana:306.

Dermophis mexicanus (Duméril and Bibron, 1841, Erpétol. Général. 8:284. Synonyms: *Gymnophis* (sic) *clarkii* Barbour, 1926, Occ. Paps. Boston Soc. Nat. Hist. 5:191; *Dermophis eburatus* Taylor, 1968, Caecilians of the World: 473; *Dermophis septentrionalis* Taylor, 1968, Caecilians of the World: 513.

Dermophis occidentalis Taylor, 1955, Univ. Kans. Sci. Bull. 37(13):503.

Dermophis oaxacae (Mertens, 1930), Abh. Ber. Mus. Natur.-Heimatk. Magdeburg, 6(3):153.

Dermophis parviceps (Dunn, 1924), Occ. Paps. Boston Soc. Nat. Hist. 5:93.

Gymnopis multiplicata Peters, 1874, Mber. Akad. Wissen. Berlin, 1874:616. Synonyms: *Siphonops proximus*, Cope, 1877, Proc. Amer. Phil. Soc. 1877:90; *Siphonops simus* Cope, 1877, Proc. Amer. Phil. Soc. 1877:91.

Gymnopis syntrema (Cope, 1866), Proc. Acad. Nat. Sci. Philadelphia, 18:129. Synonym: *Siphonops oligozona* Cope, 1877, Proc. Amer. Phil. Soc., 1877:91; *Minascaecilia sartoria* Wake and Campbell, 1983, Copeia 1983(4):858.

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