Catalogue of American Amphibians and Reptiles.

Smith, H.M. and D. Chiszar. 2001. *Pliocercus elapoides*.

Pliocercus elapoides Cope
Variegated False Coral Snake

Pliocercus elapoides Cope 1860:253. Type locality, "Jalapa" (= Xalapa), Veracruz, México (amended by Smith and Taylor 1950). Four syntypes, Acad. Nat. Sci. Philadelphia 3810–3, an adult, a subadult, and two juveniles (sex not recorded), collected by R.M. DeOca, date of collection unknown (not examined by authors).
Urotheca elapoides: Boulenger 1894:182.
Urotheca elapoides elapoides: Amaral 1929:177 (part).
Urotheca elapoides: Savage and Crother 1989:352 (part).

• **CONTENT.** Five subspecies (*P. e. elapoides*, *P. e. aequalis*, *P. e. diastema*, *P. e. occidentalis*, *P. e. wilmarai*) are recognized.

FIGURE 1. *Pliocercus elapoides elapoides* (UTA 25830) from Oaxaca, México (photograph courtesy of W.W. Lamar and J.A. Campbell). The strongly triad pattern mimics that of *Micrurus elegans* (Fig. 2).

FIGURE 2. *Micrurus elegans elegans* from Cintalapa, El Mercadito, Chiapas, México (from Roze 1996). Note the contrast in design of the pattern evolved in mimicry of *Micrurus elegans* in *Pliocercus e. elapoides* (triad, Fig. 8) and *P. e. aequalis* (modified monad, with black saddles in the red zones, Fig. 5).

FIGURE 3. *Micrurus diastema diastema* from México (from Roze 1996). This model, sympatric in part with *P. e. elapoides*, is responsible for the monad variant (Fig. 8), whereas *Micrurus elegans* is responsible for the triad variant (Figs. 1 & 8).

FIGURE 4. *Pliocercus elapoides aequalis* PC1 from Huehuetenango, Guatemala (photograph by J.A. Campbell). This pattern class is dominated by mimicry of *Micrurus e. elegans* (Fig. 2).

FIGURE 5. *Pliocercus elapoides aequalis* PC2 (KU 187343) from Izabal, Guatemala (photograph courtesy of J.A. Campbell). This pattern class is dominated by mimicry of several subspecies of *Micrurus diastema* (Fig. 6).

FIGURE 6. *Micrurus diastema sapperi* from 4 km E Chial, Cayo, Belize (photograph by Paul Freed, courtesy of Carnegie Museum of Natural History). This Coral Snake serves as a model for *Pliocercus elapoides aequalis* PC2 (Fig. 5).

FIGURE 7. *Pliocercus elapoides diastema* (UTA 21714) from Quetzaltenango, Guatemala (photograph by D.G. Barker, courtesy of J.A. Campbell). This is the most common variant of the subspecies, mimicking *Micrurus browni importunus* (Fig. 9) and others with similar patterns.

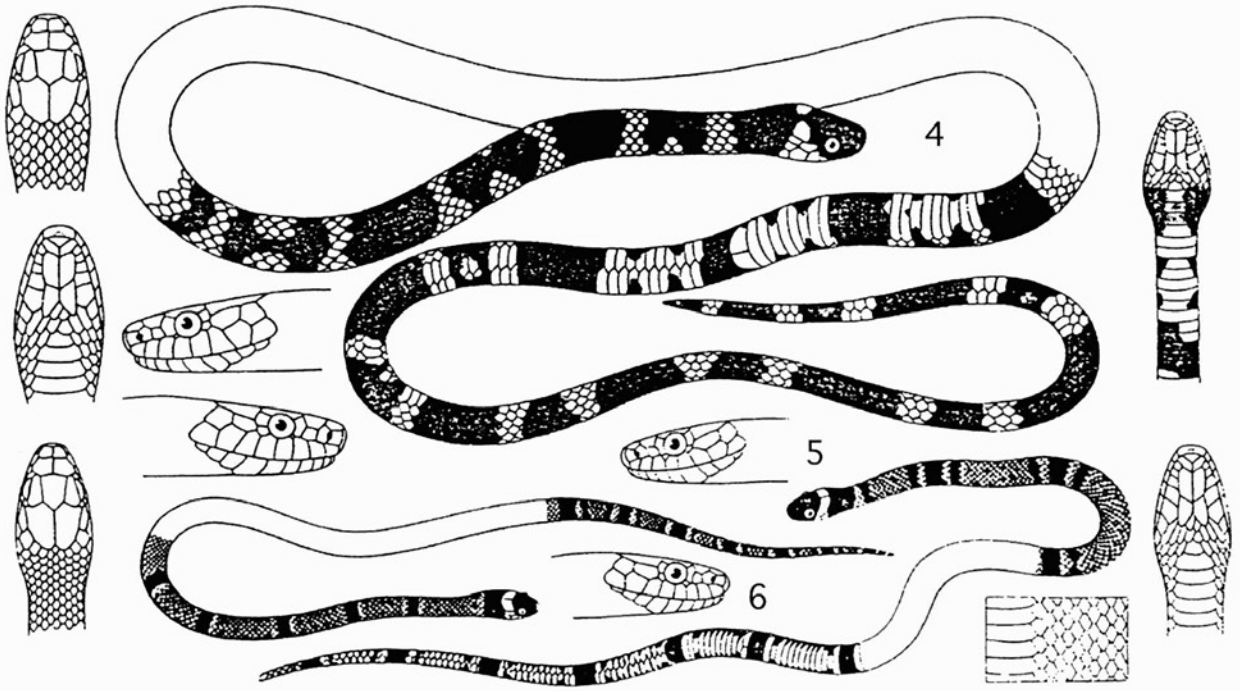
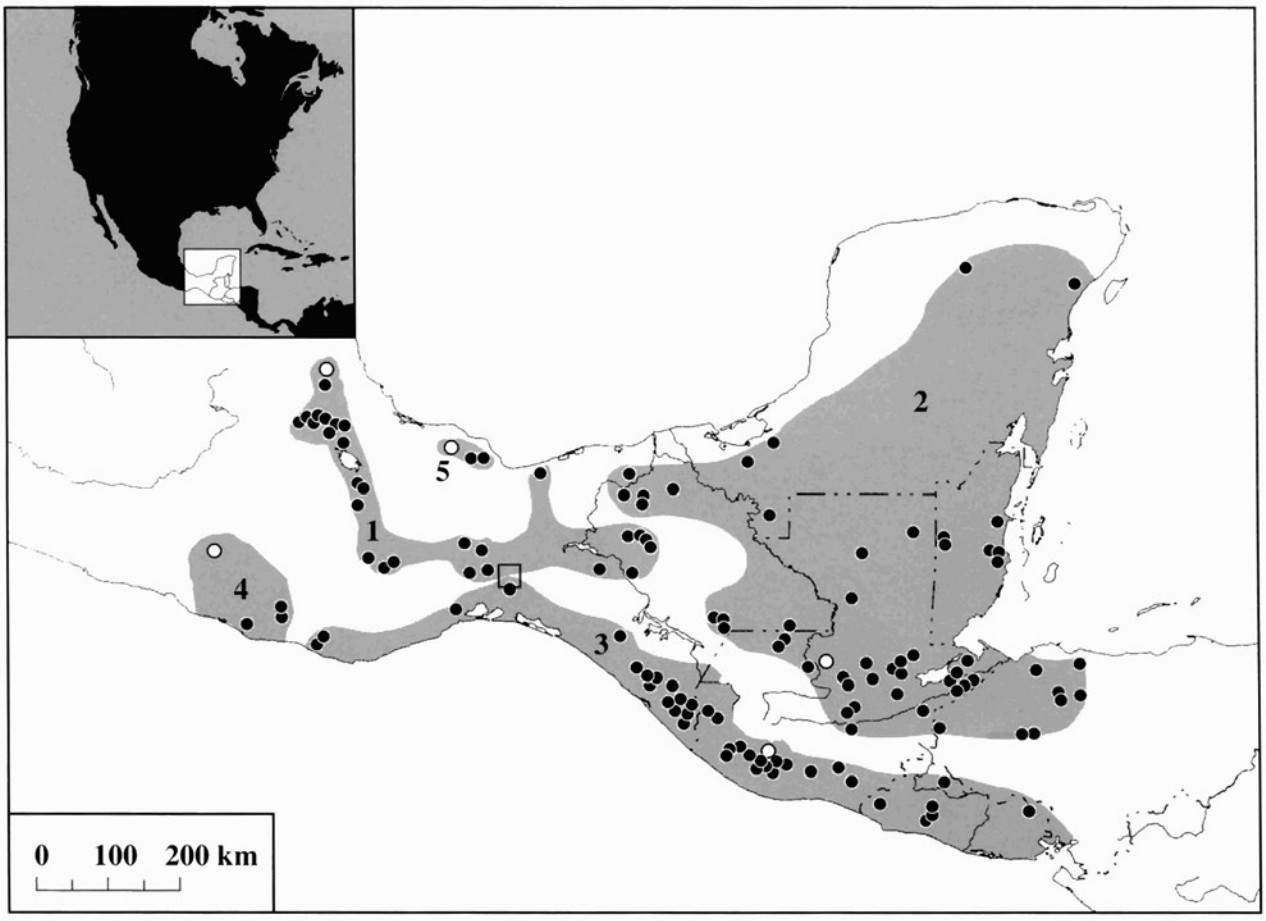


FIGURE 8. Syntypes of *Liophis tricinctus* Jan (= *Pliocercus elapoides elapoides*), from Jan and Sordelli (1866: livr. 18, pl. 4, figs. 4–6), showing three pattern variants and single secondary temporals; no. 4 exemplifies the extreme triad pattern, with the secondary black rings fused across the red rings, much as described by Smith and Langebartel (1949) for a specimen from near La Gloria, Oaxaca; no. 5 exemplifies a normal triad pattern; both nos. 4 and 5 are apparent mimics of *Micrurus elegans*; no. 6 exemplifies reduction of the triads to monads, apparently mimicking *Micrurus diastema*.



MAP. Distribution of *Pliocercus elapoides*; circles indicate type localities, dots other known records.

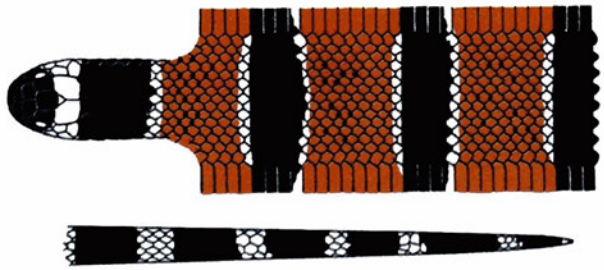


FIGURE 9. *Micrurus browni importunus* from Dueñas, Guatemala (from Roze 1996). This Coral Snake serves as a model for *Pliocercus elapoides diastema* (Fig. 7).

FIGURE 10. *Pliocercus elapoides diastema* (UTA 21716) from Quetzaltenango, Guatemala (photograph by D.G. Barker, courtesy J.A. Campbell). This uncommon variant of the subspecies has yellow rings limited to the ventral surface. The other extreme has exceptionally long yellow rings, as in the holotype of the synonym *P. andrewsi pacificus*. Note that the locality is the same as in Fig. 7. *Micrurus nigrocinctus zunilensis* (Fig. 11) apparently is the model for this pattern variant.

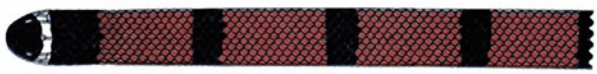


FIGURE 11. *Micrurus nigrocinctus zunilensis* from San Gerónimo, Oaxaca, México (from Roze 1996). This pattern serves as the apparent model for the sort of variant illustrated in Fig. 10.

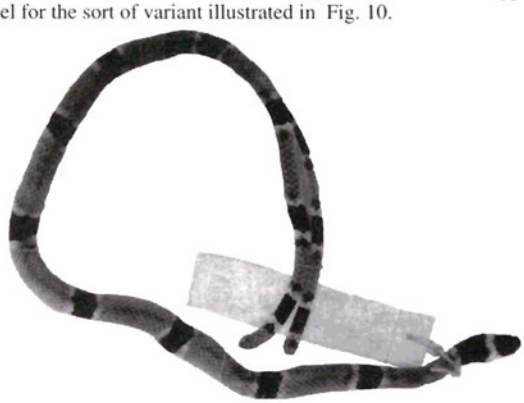


FIGURE 12. *Pliocercus elapoides occidentalis* (UIMNH 61401) from La Concepción, near Putla, Oaxaca, México (from Smith and Landy 1965). This is the only known specimen (of 11) with caudal triads.

FIGURE 13. *Pliocercus elapoides wilmarai* from 9 km ESE Tebanca, Veracruz, México (photograph by R. Powell). This form mimics *Micrurus limbatus limbatus* (Figs. 15–16).

FIGURE 14. *Pliocercus elapoides wilmarai* (UTA 3058) from 9 km ESE Tebanca, Veracruz, México (from Smith and Chiszar 1996). This specimen came from the same litter as that illustrated in Fig. 17. It is bicolored, completely lacking yellow rings, but still belongs to the tricolor complex, apparently a mimic of *Micrurus l. limbatus* (Fig. 15).

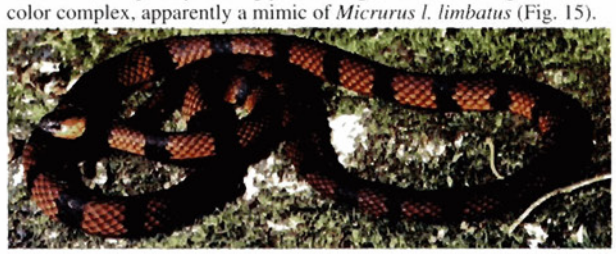


FIGURE 15. *Micrurus limbatus limbatus* from the Estación de Biología Tropical "Los Tuxtlas," Veracruz, México. This subspecies is the apparent model for *Pliocercus elapoides wilmarai* (Figs. 13–14)(photograph by R. Powell, from Greene et al 1998).

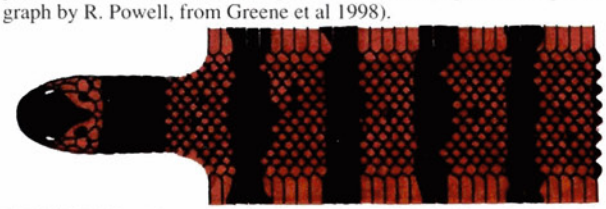


FIGURE 16. *Micrurus l. limbatus* from Volcán Santa Marta, Los Tuxtlas, Veracruz, México (from Roze 1996). This Coral Snake pattern serves as the model for the ringed variant of *Pliocercus elapoides wilmarai* (Figs. 13–14).

FIGURE 17. *Pliocercus elapoides wilmarai* from 9 km ESE Tebanca, Veracruz, México (photograph courtesy of W.F. Pyburn and J.A. Campbell). This nearly patternless variant, represented by the holotype, mimics *Micrurus limbatus spilosomus* (Fig. 18).

FIGURE 18. *Micrurus limbatus spilosomus* from Volcán Santa Marta, Los Tuxtlas, Veracruz, México (photograph courtesy of R.C. Vogt and J.A. Campbell). This subspecies is the apparent model for the nearly patternless variant of *Pliocercus elapoides wilmarai* (Fig. 17).

However, no subspecies are recognized by some recent reviewers (e.g., Wilson and Meyer 1985, Savage and Crother 1989), who also gave this species more extensive parameters, including *P. andrewsi* and *P. bicolor* as here interpreted (see also Smith and Chiszar 2001a).

• **DEFINITION.** *Pliocercus elapoides* is a small, generally tricolored colubrid snake of the tricolor *P. elapoides* complex, with a maximum known SVL of 416 mm (female, A.K. Smith 1969)(TL calculated at about 670 mm, assuming the tail to be the mean of 38% of TL). The tail in males is 38–44% of TL ($\bar{x}$ = 42), in females, 35–41% ($\bar{x}$ = 39)(A.K. Smith 1969).

Head scalation is as follows: supralabials usually 8 (91%, *N* = 607 of 665), occasionally (8%) 9 (*N* = 52), rarely (1%) 7 (*N* = 6); infralabials usually 9 (53%, 340 of 642) or 10 (45%, 286), seldom (2%, 10) or 11 (1%, 6); preoculars usually 2 (84%, 560 of 668), occasionally 1 (9%, 61, in one of which the loreal contacts the eye) or 3 (7%, 47); postoculars usually 2 (99%, 667 of 676), rarely 3 (1%, 9); anterior temporal always single (*N* = 340); secondary temporal single on both sides in 80% (*N* = 271), single on one side and double on the other in 9% (*N* = 30), double on both sides in 11% (*N* = 39); tertiary temporals usually 2 on both sides (94%, 319 of 340), single on one side in 1% (*N* = 3), on both sides in 1% (*N* = 3), triple on one side in 4% (*N* = 12), on both sides in 1% (*N* = 3). Ventral scales in males number 119–132 ($\bar{x}$ = 125.2, *N* = 148), in females 124–139 ($\bar{x}$ = 132.1, *N* = 184). Subcaudal scales in males number 90–121 ($\bar{x}$ = 107.4, *N* = 86), in females 85–112 ($\bar{x}$ = 98.7, *N* = 83). Of the 148 males examined, 58% had complete tails, whereas only 45% of 184 females did.

In life, most populations have yellow rings between red and black rings. Yellow rings vary in length from 0.5–4 scales in length, usually 1 more or less. Primary black rings on body number 2–25, and may be complete or not. Red zones lack black, or may have some or all dorsal scales lightly to heavily black-tipped. Secondary black saddles may be present or absent; when present, they are peripheral in the red zones, forming triads with the primary black rings (in some specimens they extend toward each other across the red zones, and rarely completely replace the red middorsally, although not ventrally, because all secondary black saddles are incomplete ventrally). The nuchal black ring often is somewhat longer than others. A yellow parietal ring is present.

• **DIAGNOSIS.** *Pliocercus elapoides* is a member of the *P. elapoides* complex (with black rings separated from each other by complete red rings, typically bordered by yellow rings separating the black rings from the red rings), thus eliminating all members of the *P. euryzonus* complex (*P. euryzonus*, *P. dimidiatus*). This species is distinguished from other members of the tricolor complex by having the posterior infralabial separate from the posterior labiogenial (thus eliminating *P. bicolor*), and black rings not as few as 7, unless they are much less than half as long as their pale interspaces (thus eliminating *P. andrewsi*). The isolated Los Tuxtlas population (*P. e. wilmarai*) lacks yellow rings, as do some individuals in central western Guatemala and adjacent Chiapas (*P. e. aequalis*), but they are readily distinguished from members of the *P. euryzonus* complex by having the primary black rings much shorter than the pale interspaces.

• **DESCRIPTIONS AND ILLUSTRATIONS.** The most detailed descriptions and illustrations (in black and white) are in Smith and Chiszar (1996). Several color illustrations appear in Campbell and Lamar (1989), where figure 512 is of *P. e. diastema* (as labelled), and figures 513–6 are all of *P. e. aequalis*, as here interpreted (figure 510 depicts *P. bicolor hobartsmithi*, and figure 511 illustrates *P. e. wilmarai*). Color figures of *P. e. elapoides* (figure 1E) and *P. e. aequalis* (figure 1F) appeared in Mertz (1996) and in Greene and McDiarmid (1981); the latter does not show the yellow rings characteristically present (Campbell and Lamar 1989, figures 514–6, even in figure 513, vestiges of yellow rings are present dorsally). Smith and Landy (1965) included black and white illustrations of *P. e. elapoides*, *P. e. diastema*, and *P. e. occidentalis* (reproduced in Smith and Chiszar 1996). *Pliocercus e. aequalis* was illustrated and described in Fischer (1881), Bocourt (1886), and Günther (1893). Weber (1945) showed in color a *P. e. elapoides* in the claws of a White Snake Hawk. Smith and Langebartel (1949) illustrated a *P. e. elapoides* from the Isthmus of Tehuantepec. Jan and Sordelli (1866) illustrated the three syntypes of *Liophis tricinctus* (= *P. e. elapoides*). *Pliocercus e. diastema* was illustrated in Bocourt (1886). *Pliocercus e. aequalis* was depicted in color in Wilson and Meyer (1982, 1985). A black and white figure of *P. e. diastema* is in Alvarez del Toro (1973, 1982), in Smith and Chrapliwy (1957), in Mertens (1952b), and in Hecht and Marien (1956). Greene (1969) portrayed *P. e. wilmarai* in black and white.

• **DISTRIBUTION.** *Pliocercus elapoides* is the southernmost species of the tricolor group of the genus, occurring in rainforest and cloud forest habitats on Atlantic slopes from central Veracruz, México, to western Honduras, and on Pacific slopes from western Oaxaca and perhaps adjacent Guerrero, México, to El Salvador and perhaps Honduras. This geographic range marginally overlaps that of *P. dimidiatus* in western Honduras, and is extensively sympatric with *P. andrewsi* in the northern part of the Yucatán Peninsula. The population in the Los Tuxtlas uplift of southern Veracruz (*P. e. wilmarai*) is completely isolated from all others.

• **FOSSIL RECORD.** None.

• **PERTINENT LITERATURE.** Most of the literature on this species is distributional or variational, and is summarized in the subspecies accounts. Much of the rest concerns mimicry, summarized in Smith and Chiszar (2001a). Morphological variation in the species as a whole was described by Smith and Chiszar (1996). Savage and Crother (1989) also reviewed some aspects of variation, but included *P. andrewsi* and *P. bicolor* with *P. elapoides*. Variation in material from Honduras was described by Wilson and Meyer (1982, 1985). An excellent review of variation in the whole species, although including *P. bicolor*, was included in an unpublished dissertation by A.K. Smith (1969).

The natural history of mostly this species, although covering the whole genus, is reviewed in Smith and Chiszar (1996). Wilson and McCranie (1998) and Pelcastre-Villafuerte and Flores-Villela (1992) summarized habitat preferences. Seib (1980) reported a severe reaction to the venom of *P. e. diastema*, noted by numerous authers (e.g., Minton 1990). Wilson (1968) described and illustrated the fracture plane in the caudal vertebrae of *P. e. aequalis* (reproduced in Bellairs and Bryant, 1985), although Arnold (1984, 1988) and Savage and Crother (1989) argued for intervertebral breakage. Thatcher (1966) reported trematodes. Predation on *P. e. elapoides* by a White Snake Hawk was noted by Weber (1945).

Vernacular names were suggested in Smith and Chiszar (1996), and Greene (1997) applied the name Halloween Snake.

Other literature includes Flores-Villela (1993, keys), Flores et al. (1995, keys), Liner (1994, checklist and common names), Ramírez-Velázquez and Sigler-Morena (1993, Chiapas), Savage (1966, herpetofaunal origins), Wilson and Meyer (1982, 1985, Honduras), and Zhao et al. (1993, name).

Literature explicitly relating to *Pliocercus elapoides elapoides* includes Alvarez del Toro (1960, 1973, 1982, Chiapas), Booth (1959, Chiapas), Campbell et al. (1995, Veracruz), Casas Andreu et al. (1996, Oaxaca, part), Flores et al. (1991, Oaxaca), Fugler and Dixon (1958, Veracruz), González-Romero et al. (1991, Veracruz), Greene (1969, mention), Liner (1960, comparisons), Pelcastre-Villafuerte and Flores-Villela (1992, Veracruz, habitat), Pérez-Higareda and Navarro (1980, Veracruz, barrier), Pérez-Higareda and Smith (1991, Veracruz), Peters and Orejas-Miranda (1970, key), Peters et al. (1986, key), Ramírez-Bautista et al. (1993, Veracruz), Salvin (1861, comparisons), Smith (1941, 1942, 1943, 1987, Veracruz, taxonomy), Smith et al. (1989, comparisons), Smith and Langebartel (1949, Oaxaca), Smith and Smith (1976, 1993, literature), Smith and Taylor (1945, checklist), Smith and Taylor (1950, type localities), Stuart (1950, Guatemala), Tanner (1957, Chiapas), Troschel (1862, literature), Wake and Johnson (1989, Chiapas), and Zhao (1993, list).

Literature explicitly relating to *Pliocercus elapoides aequalis* includes Alvarez del Toro (1973, 1982, Chiapas), Boulenger (1882, Zoological Record), Cadle (1984, molecular systematics, Quintana Roo), Campbell and Vannini (1988, Guatemala, habitat, abundance), Cochran (1961, list of type specimens), Duellman (1963, El Petén, Guatemala), Hahn (1971, Honduras), Henderson and Hoevers (1975, Belize), Jackson (1973, Honduras), Kramer (1978, list of type specimens). Lee (1980, 1996, 2000, Yucatán Peninsula), Markel (1990, color photo), Martín del Campo (1945, Chichén Itzá, Yucatán), Marx (1958, 1976, list of type specimens), McCoy (1966, 1970, Guatemala), Mendelson (1990, Guatemala), Müller (1973, dispersal center), Neill (1965, Belize), Neill and Allen (1961, Belize), Peters and Orejas-Miranda (1970, 1986, keys), Smith (1943, 1987, nomenclature), Smith and Smith (1976, 1993, literature), Smith and Taylor (1945, 1950, checklist, type localities), Stuart (1950, Alta Vera Paz, Guatemala), Taylor (1944, list of type specimens), Wilson (1968, tail fracture plane), Wilson and McCranie (1998, Honduras), and Wilson and Meyer (1985, Honduras).

Literature explicitly relating to *Pliocercus elapoides diastema* includes Alvarez del Toro (1960, 1973, 1980, Chiapas), Campbell and Lamar (1989, photograph), Casas-Andreu et al. (1996, Oaxaca), Greene (1969, 1973, eggs, Senckenberg Museum), Hecht and Marien (1956, pattern, mimicry, photograph), Landy et al. (1966, food, habitat, mimicry), Lynch and Smith (1965, Oaxaca), Maldonado (1953, mention), Martínez-Castellano and Muñoz-Alonzo (1998, mention), Mertens (1952b, El Salvador), Peters and Orejas-Miranda (1970, 1986, keys), Seib (1980, envenomation), Smith (1942, 1959, 1987, key, Guatemala), Smith and Landy (1965, Chiapas, Oaxaca), Smith et al. (1964, list of type specimens), Smith and Smith (1976, 1993, literature), Smith and Taylor (1945, 1950, checklist, type localties), Stuart (1948, 1950, 1963, Guatemala), and Wilson and Meyer (1982, 1985, Honduras).

Literature explicitly relating to *Pliocercus elapoides occidentalis* includes Peters and Orejas-Miranda (1970, 1986, keys), Savage and Crother (1989, rejected), Smith and Smith (1976, 1993, literature), Smith and Taylor (1966, checklist), and Wilson and Meyer (1982, 1985, rejected).

Literature explicitly relating to *Pliocercus elapoides wilmarai* includes Campbell and Lamar (1989, color photograph), Greene et al. (1998, mimicry), Pelcastre-Villafuerte and Flores-Villela (1992, habitat), Pérez-Higadera (*sic*) et al. (1987, Los Tuxtlas herpetology), Pérez-Higareda and Smith (1990, 1991, Los Tuxtlas), Ramírez-Bautista (1978, Los Tuxtlas), Ramírez-Bautista and Nieto-Montes de Oca (1997, Los Tuxtlas), Vogt (1997, serpentine communities, Los Tuxtlas), and Vogt et al. (1997, herpetofaunal list, Los Tuxtlas).

• **REMARKS.** The validity of *P. elapoides* has never been questioned, but its scope and taxonomic content have been a source of considerable disagreement. One extreme is a single species (including *P. bicolor* and *P. andrewsi)*, with no subspecies, as understood by Savage and Crother (1989), as well as many others. The other extreme is exemplified by Smith and Smith (1976), who accepted 9 taxa that we now know are referable to *P. elapoides*. We herein recognize little more than half (5) that number, as initially proposed by Smith and Chiszar (1996), with modifications they adopted later (2000, 2001b).

Although our argument for acceptance of *P. andrewsi* as a separate species may be questioned, we regard the validity of the subspecies we here recognize in *P. elapoides* as the chief bone of contention relative to the tricolor complex of *Pliocercus*. Our recognition of five subspecies rests on the observation that those five units exhibit unique parameters of variation of at least reasonable magnitude (better than 80% separability), and presumably reflect distinctive genetic compositions. Each has evolved unique tendencies apparently influenced for the most part by the associated models for mimicry.

We have been impressed by the relatively minor variation in two of the subspecies (*P. e. diastema*, *P. e. occidentalis*), as compared with the considerable variation in *P. e. elapoides*, and the very extensive variation in *P. e. aequalis* and *P. e. wilmarai*, all apparently correlated with multiple sympatric Coral Snake patterns (whether monads or triads, for example; see discussion in Smith and Chiszar 2001a).

In recognizing five subspecies of *P. elapoides*, we have been influenced by the geographic consistency of certain character-states in each taxon; geographically erratic variants, particularly as in *P. e. aequalis* and *P. e. wilmarai*, we regard as infrataxonomic chromotypes. Our analyses sought geographic character consistencies, whether or not associated with mimicry of Coral Snakes. Thus the perceived geographic ranges of the five subspecies of *P. elapoides* are allopatric. Some taxa (*P. e. wilmarai*) are strongly dichopatric, others parapatric or presumably so. Good intergrades are known from one intermediate locality between the ranges of *P. e. elapoides* and *P. e. diastema (*Smith and Landy 1965*)*; they are to be expected between the latter and *P. e. occidentalis*, but isolation of the latter prevents intergradation with any subspecies except *P. e. diastema*. Intergrades may occur between *P. e. elapoides* and *P. e. aequalis*, but probably not between the latter and *P. e. diastema*, because of the presence of an isolating physiographic/ecological barrier. *Pliocercus e. wilmarai* is isolated from all other congeneric taxa, hence can have no intergrades.

After decades of experience with the Guatemala herpetofauna, Stuart (1963) recognized three populations of *P. elapoides*, although his nomenclature was partly different than that used here. His populations were designated as *P. e. diastema*, exactly the same as interpreted here; *P. e. aequalis*, essentially the same as our *P. e. aequalis* PC1 (pattern class 1); and *P. e. salvini*, essentially the same as our *P. e. aequalis* PC2. More recent material has changed his analysis only by making the latter two inseparable taxonomically, although they remain two different chromotypes.

• **ETYMOLOGY.** Cope's (1860) name *elapoides* is an adjective formed from *elaps* (Latin for "snake"), the generic name of the Coral Snake when Cope worked, and the suffix *-oides*, "like," a Latin term derived from the Greek *-eides*. Thus the first species described in the genus was at once recognized as a mimic of Coral Snakes.

The name *aequalis* is a Latin adjective meaning "equal," and refers to the "equidistant black bands" (Salvin 1861) of the holotype. Salvin (1861) and other early workers did not distinguish between primary and secondary rings, and they also failed to note the presence of yellow rings, interpreting all of the light

areas as red. Bocourt's name *diastema* is a Greek noun meaning "space between" or "interval," and was applied in reference to the widely spaced black rings in the type series. The name is not an adjective and therefore does not change its ending to agree with the gender of the generic name to which it is referred. The Latin word *occidentalis* ("of the west") was applied to its taxon in reference to its geographic position as the westernmost population of the genus on Pacific slopes. The name *wilmarai* is a genitive patronym honoring William P. Mara for his editorial and herpetocultural skills, the latter of which are dedicated to exercise on the present genus, where they are so important to its taxonomy.

• **KEY TO SUBSPECIES.** The two pattern classes of *Pliocercus elapoides aequalis* can be seen to differ substantially, as is evident in the following key. However, because they are inconsistent in geographic occurrence, occurring both together and by themselves over considerable areas, they are not populationally distinctive and hence do not qualify as subspecies. A parallel exists in the distinctive chromotypes of *Lampropeltis getula californiae*.

1. a. No black rings or saddles on body or tail except nuchal and anal; or, if present, no yellow rings, pale zones all red, even ventrally ..... *P. e. wilmarai*
   b. Black rings or saddles present throughout body and tail; yellow rings present at least ventrally between red and black rings or saddles 2

2. a. Minimum middorsal or paravertebral scale lengths in nuchal black ring, posterior to parietals, 6 or more (*P. e. diastema*, 94%; *P. e. occidentalis*, 100%; *P. e. elapoides*, 38%) 3
   b. Minimum middorsal or paravertebral scale lengths in nuchal black ring, posterior to parietals, 5 or fewer (*P. e. aequalis* PC1, 95%; *P. e. aequalis* PC2, 91%; *P. e. elapoides*, 62%) 5

3. a. No distinct triads on tail (82%) ..... *P. e. occidentalis*
   b. Distinct triads on tail (*P. e. diastema*, 92%; *P. e. elapoides*, 97%) 4

4. a. Infralabials 9–9 or fewer (87%); outer rings of triads at least 1.5 dorsal scales in length on at least part of body (74%) ..... *P. e. elapoides*
   b. Infralabials 9–10 or more (80%); outer rings of triads shorter than 1.5 dorsal scales in length throughout body (95%) ..... *P. e. diastema*

5. a. Parietal pale ring narrow, not involving any scale anterior or posterior to parietals (95%) ..... *P. e. elapoides*
   b. Parietal pale ring longer, involving 95% or more of the length of parietals, or parts of scales anterior (frontal, supraoculars, postoculars) or posterior (occipitals) to the parietals (*P. e. aequalis* PC1, 75%; *P. e. aequalis* PC2, 84%) 6

6. a. Primary black rings on body 15 or more (91%); minimum number of subcaudals between primary black rings on complete tail 6 or fewer (91%); maximum number of subcaudals between primary black rings on complete tail 8 or fewer (88%); black rings on tail 10 or more (88%); ratio, middorsal length of the primary black ring on body adjacent to the shortest interval between, over the latter, 34% or more (79%); ratio, middorsal length of the primary black ring on body adjacent to the longest interval, divided by the latter, 38% or more (86%) ..... *P. e. aequalis* PC1
   b. Primary black rings on body 14 or fewer (79%; minimum number of subcaudals between primary black rings on complete tail 9 or more (69%); black rings on tail 9 or fewer (94%); ratio, middorsal length of the primary black ring adjacent to the shortest interval between, divided by the latter, 33% or less (94%); ratio, middorsal length on the primary black ring on body adjacent to the longest interval, divided by the latter, 31% or less (81%) ..... *P. e. aequalis* PC2

1. *Pliocercus elapoides elapoides* Cope
Deppe's False Coral Snake

Pliocercus elapoides Cope 1860:253. See species synonymy.
Elapochrus deppei Peters 1860:293. Type locality, "Mexico," restricted to "Xalapa, Veracruz," by Smith and Taylor (1950). Holotype, Zoologischen Museum Berlin (ZMB) 2411 (Bauer et al. 1995), an adult female, collected by F. Deppe, date of collection unknown, but between 1824 and 1830 (Taylor 1969)(not examined by authors).
Pliocercus deppei: Günther 1862:53.
Liophis (Cosmiosophis) tricinctus Jan 1863a:289. Type locality, "Messico," restricted to "Xalapa, Veracruz," by Smith and Taylor (1950). Syntypes, one adult and two juveniles (sex not recorded), cited in the original description and also by Jan (1863b) to be in the Naturhistorisches Museum in Vienna, the Copenhagen University Museum, and the Museo Civico di Storia Naturale in Milan. Collectors and dates not recorded (not examined by authors).
Urotheca elapoides elapoides: Amaral 1929:177 (part).
Pliocercus elapoides elapoides: Smith 1941:119.
Elapochrous deppei: Smith and Taylor 1945:110. *Lapsus calami*.
Pliocercus elapoides: Greene and McDiarmid 1981:1211 (part).
Urotheca elapoides: Savage and Crother 1989:356 (part).

• **DIAGNOSIS.** This subspecies of *P. elapoides* is distinguished from all others by the combination of a relatively short parietal pale ring not involving scales anterior or posterior to parietals (95%); distinct triads on body (92%) and tail (97%), yellow rings distinct; a relatively short nuchal ring, covering 5 or fewer middorsal or paravertebral scale lengths (66%); and infralabials usually 9–9 or fewer (87%).

• **REMARKS.** This subspecies is extensively mimetic of two very differently patterned Coral Snakes, *Micrurus elegans* (with triads, resulting in evolution of supernumerary black saddles appearing as triads; on the contrary in *P. e. aequalis*, mimicking the same species, they appear usually as modified monads) and *M. diastema* (with monads, resulting in reduction, even loss, of the supernumerary black saddles). Variation in 76 specimens was described by Smith and Chiszar (1996).

2. *Pliocercus elapoides aequalis* (Salvin)
Salvin's False Coral Snake

Pleiocercus aequalis Salvin 1861:227. Type locality, "San Gerónimo and the neighboring mountains ... of Vera Paz," in Baja Vera Paz, Guatemala. Holotype, British Museum of Natural History (BMNH) 1946.1.1.4, an adult female, collected by R. Owen, 1860 (not examined by authors).
Pliocercus aequalis: Cope 1862:72.
Elapochrus aequalis, varietas: Müller 1878a:662.
Pliocercus salvinii Müller 1878a:709 (substitute name for *Elapochrus aequalis*, varietas Müller (1878). Type locality, "Vera Paz, Guatemala." Holotype, Naturhistorischen Museum Berlin (ZMB) 1495, an adult (sex not recorded), col-

lected by G. Bernoulli, date of collection unknown (not examined by authors).
Liophis tricinctus: Müller 1878b:750 (*nec* Jan).
Pliocercus sargii Fischer 1881:225. Type locality, "Cobán," Alta Vera Paz, Guatemala. Holotype, Naturhistorischen Museum Stuttgart 2012, an adult female, collected by F. Sarg, date of collection unknown (not examined by authors).
Liophis elapoides aequalis: Bocourt 1886:637.
Elapochrus aequalis: Günther 1893:106.
Urotheca elapoides aequalis: Werner 1896:348.
Urotheca aequalis: Gadow 1911:17.
Urotheca elapoides elapoides: Taylor 1939 (1940):469 (part).
Pliocercus elapoides laticollaris Smith 1941:122. Type locality, "Tenosique, Tabasco, Mexico." Holotype, National Museum of Natural History (USNM) 110767, an adult female, collected by H.M. Smith, 30 June 1939 (examined by authors).
Pliocercus elapoides schmidti Smith 1942:161. Type locality, "Chichen Itzá, Yucatán, Mexico." Holotype, Museum of Comparative Zoology (MCZ) 26843, an adult female, collected by E.N. Thompson, date of collection unknown (examined by authors).
Pliocercus elapoides semicinctus Schmidt 1941:502. Type locality, "Double Falls, west of Stann Creek, Belize." Holotype, Field Museum of Natural History (FMNH) 72471, an adult female, collected by I.T. Sanderson, 13 December 1939 (examined by authors).
Pliocercus elapoides salvinii: Stuart 1948:67.
Pliocercus elapoides: Stuart 1948:71 (part).
Pliocercus euryzonus aequalis: Stuart 1948:72.
Pliocercus bicolor: Stuart 1948:72 (*nec* Smith).
Pliocercus elapoides elapoides: Smith 1960:223 (*nec* Cope).
Pliocercus laticollaris: Liner 1960:217.
Pliocercus elapoides diastemus: Henderson and Hoevers 1975: 44 (*nec* Bocourt).
Pliocercus aequalis aequalis: Smith 1987:xxxv.
Urotheca elapoides: Savage and Crother 1989:356 (part).
Pliocercus elapoides aequalis: Smith and Chiszar 1996:53.
Urotheca (Pliocercus) elapoides: Stafford 1999:48.
Pliocercus psychoides Smith and Chiszar 1996:34. Type locality, unknown, given as "Brasil or Venezuela," but obviously in error, probably central western Guatemala (Smith and Chiszar 2001b). Holotype, American Museum of Natural History (AMNH) 4433, an adult female, collector and date of collection unknown (examined by authors).

• **DIAGNOSIS.** This subspecies of *P. elapoides* is distinguished from all others by the combination of a short nuchal black ring, usually (91%) extending no more than 6 dorsal scale lengths posterior to the parietals, and a long, pale parietal ring, usually (75% in PC1, 84% in PC2) involving 95% or more of the parietals or parts of scales anterior (frontal, supraoculars, postoculars) or posterior (occipitals) to the parietals.

• **REMARKS.** This subspecies is extensively mimetic of *Micrurus diastema* and *M. hippocrepis* (both tricolor monads; Savage and Slowinski 1990) and *M. elegans* (basically a tricolor triad, but incompletely a tricolor pentad), hence populations are highly variable where both species occur together, but are less so elsewhere.

Two pattern classes occur in this subspecies. Pattern class 1 (PC1) is mostly limited to the range of the tricolor triad species *Micrurus elegans*, where the tricolor modad *M. diastema* also serves as a model, and is characterized by a complex and erratic pattern of numerous black rings or saddles, primary and secondary, more or less matching one or both of the model patterns (see Smith and Chiszar 1996). Black saddles are frequently present in the middle of the red zones, which in some specimens are completely obliterated dorsally. The yellow rings are frequently very short and may be absent dorsally, although always present ventrally. Pattern Class 2 (PC2) occurs mostly outside of the range of *M. elegans*, but also erratically within that range. It mimics the tricolor monad *M. diastema* and is characterized by a simple pattern of widely spaced primary black rings and minimal pigmentation in the intervening zones (see Smith and Chiszar 1996).

Pliocercus e. aequalis has at times been regarded as bicolored, lacking yellow rings, and has been so illustrated in several works (e.g., Günther 1893). This taxon, however, is not a member of the *P. euryzonus* complex. Of 88 specimens of *P. e. aequalis* we examined, 19 (22%) showed no clear dorsal evidence of yellow rings, although in some of those exceptions the yellow may have been too faded or discolored to be evident. However, the yellow rings were evident, at least ventrally, in all. None of the 32 specimens examined of PC2 had yellow rings reduced dorsally; that variation appeared only in some of PC1, mostly in those from Chiapas and in Guatemala from Alta Vera Paz and Baja Vera Paz.

If these two pattern classes were clearly allopatric, they would qualify as subspecies (per Stuart 1963), but we now know that they are populationally inseparable. The situation is much like that in *Lampropeltis getula californiae*.

Variation in 88 specimens was reported by Smith and Chiszar (1966).

3. *Pliocercus elapoides diastema* (Bocourt)
Bocourt's False Coral Snake

Liophis elapoides [*elapoides*]: Bocourt 1886:635 (part; four of five specimens and the figures are of *P. e. diastema*).
Liophis elapoides diastema Bocourt 1886:636. Type locality, "Plateau of Guatemala." Syntypes, adult males, Muséum National d'Histoire Naturelle, Paris (MNHN) 132–133, collector and date of collection unknown (not examined by authors).
Urotheca elapoides elapoides: Slevin 1939:402 (*nec* Cope).
Pliocercus elapoides diastemus: Smith 1941:120. Unjustified emendation of the subspecific name (Mertens 1952b).
Pliocercus elapoides elapoides: Stuart 1948:71 (*nec* Cope).
Pliocercus elapoides diastema: Mertens 1952a:70.
Pliocercus elapoides salvadorensis Mertens 1952a:91. Type locality, "Finca San José, 1150 m, nr Santa Tecla, Depto. La Libertad, El Salvador." Holotype, Natur-Museum Senckenberg (SMF) 42301, an adult female, collected by C. Holtmann, 22 July 1950 (not examined by authors).
Pliocercus andrewsi pacificus Smith and Chrapliwy 1957:233. Type locality, "Finca Custepeque, 40 mi ESE Tonalá, Chiapas, Mexico." Holotype, University of Illinois Museum of Natural History (UIMNH) 40832, an adult male, collected by T. MacDougall, 18 November 1956 (examined by authors).
Pliocercus elapoides elapoides × *diastemus*: Lynch and Smith 1965:168.
Pliocercus elapoides: Greene 1973:151 (part).
Urotheca elapoides: Savage and Crother 1989:356 (part).

• **DIAGNOSIS.** This subspecies of *P. elapoides* differs from others of the species as follows: from *P. e. aequalis* PC1 in having 13 or fewer primary black rings on body (98% in 159 specimens versus 5% in 58); from *P. e. aequalis* PC2 in having a relatively long nuchal ring, at least 6 dorsals long near midline (94% in 160 versus 9% in 32); from *P. e. occidentalis* in having well developed triads on tail (91% in 159 versus 9% in 11); from *P. e. elapoides* in having 9–10 or more infralabials (81% in 155 versus 13% in 69), and triads on body weaker or absent, the outer (incomplete) rings less than 1.5 dorsals long (95% in

160 versus 26% in 74); and from *P. e. wilmarai* in regularly possessing complete yellow rings (versus absence).

• **REMARKS.** This subspecies is extensively mimetic of the tricolor monad Coral Snakes *Micrurus bogerti*, *M. browni*, *M. latifasciatus*, *M. nigrocinctus*, and *M. stuarti*. The minimal variability of *P. e. diastema* is most likely correlated with the basic pattern similarity of all species of sympatric Coral Snake species. The usual pattern in *P. e. diastema* does embrace a variation in number of primary black rings from 6–14, and the yellow rings vary from a maximum of 3–4 dorsal scale lengths to a minimum of complete absence dorsally. These variations to a certain extent reflect different *Micrurus* species with different monad patterns. Variation in 160 specimens was reported by Smith and Chiszar (1996).

4. *Pliocercus elapoides occidentalis* Smith and Landy MacDougall's False Coral Snake

Pliocercus elapoides occidentalis Smith and Landy 1965:1. Type locality, "La Concepción, nr Putla, Oaxaca, Mexico." Holotype, University of Illinois Museum of Natural History (UIMNH) 61410, an immature male, collected by T. MacDougall, 24 May 1965 (examined by authors).
Pliocercus elapoides: Greene and McDiarmid 1981:1211 (part).
Urotheca elapoides: Savage and Crother 1898:356 (part).

• **DIAGNOSIS.** This subspecies of *P. elapoides* differs from *P. e. aequalis* PC1 in having 12 or fewer primary black rings on body (100% versus 2%) and 7 or fewer on tail (100% versus 0%); from *P. e. aequalis* PC2 in having a longer nuchal ring, near midline covering a minimum of at least 6 dorsal scale lengths (100% versus 9%); from *P. e. elapoides* in usually lacking distinct triads on the tail (91% versus 0%), and triads on body weak or absent, outer saddles less than one dorsal scale in length where present (100% versus 8%); from *P. e. wilmarai* in regularly possessing yellow rings (versus absence); and from *P. e. diastema* in usually lacking distinct triads on the tail (91% versus 9%), having a lesser maximum number of subcaudals in the primary black rings (4 or fewer, 89% versus 14%), lesser minimum number of subcaudals in the primary black rings (3 or fewer, 89% versus 35%), and a longer light parietal ring (covering 95% of the parietals, or extending onto scales anterior or posterior to the parietals, 84% versus 33%).

• **REMARKS.** The only species of *Micrurus* likely to occur within the range of *P. e. occidentalis* is *M. b. bogerti* (Roze 1996), although no records exist at present for any Coral Snake in that area. If none occur, their absence may have been influential in the differentiation of *P. e. occidentalis* from the widely distributed *P. e. diastema*, the only other taxon of the genus occuring on Pacific slopes, and sympatric with several species of Coral Snakes. Variation in 11 specimens was reported by Smith and Chiszar (1996).

5. *Pliocercus elapoides wilmarai* Smith, Pérez-Higareda, and Chiszar
Mara's False Coral Snake

Pliocercus elapoides: Greene 1969:27 (part).
Pliocercus elapoides schmidti: Ramírez-Bautista 1977:137 (*nec* Smith).
Pliocercus elapoides salvinii: Pérez-Higareda and Smith 1986: 125 (part).
Pliocercus bicolor: Pérez-Higareda and Smith 1986:127 (*nec* Smith).
Urotheca elapoides: Savage and Crother 1989:356 (part).
Pliocercus wilmarai Smith, Pérez-Higareda, and Chiszar 1996: 76. Type locality, "5.6 road mi ESE Tebanca (= Tabanca), Los Tuxtlas region, southern Veracruz, [México]." Holotype University of Texas at Arlington (UTA) 3159, an adult female, collected by J. Darling, R. Harris, and W.F. Pyburn, 20 June 1966 (examined by authors).
Pliocercus elapoides wilmarai: Smith and Chiszar 2000:18.

• **DIAGNOSIS.** This subspecies of *P. elapoides* differs from all conspecifics by lacking black rings or saddles except for the nuchal and anal marks, or, if they are present, yellow rings are missing both dorsally and ventrally. This subspecies, from the Los Tuxtlas uplift in southern Veracruz, is geographically isolated from all other populations of the genus.

• **REMARKS.** This subspecies is extensively mimetic in its ringless morph of the equally ringless, spotted, sympatric *Micrurus limbatus spilosomus*; and in its ringed morph with the sympatric tricolor triad *M. elegans* and tricolor monads *M. diastema* (oligocricoid) and *M. l. limbatus* (polycricoid). The characteristic loss of yellow rings in *P. e. wilmarai* may have resulted from mimicry of *M. elegans*, in which yellow is not or scarcely evident.

This taxon was regarded in its original description and in Smith and Chiszar (1996) as a full species thought to occur sympatrically in the Los Tuxtlas region with an equally isolated population of *P. e. aequalis* PC1 that Pérez-Higareda and Smith earlier (1986) regarded as *P. bicolor*, because of the absence of yellow rings, before the defining scale character of that species was known. Both taxa mimic the same Coral Snake models and, not surprisingly, resemble one another. They differ, however, in apparently lacking yellow rings both dorsally and ventrally (see color figures in Greene and McDiarmid 1981, and Pérez-Higareda and Smith 1991), whereas apparently all *P. e. aequalis* PC1 possess yellow rings at least ventrally if not dorsally. All chromotypes occur sympatrically within the Los Tuxtlas area (Pérez-Higareda and Smith 1991), hence they are most likely consubspecific. The apparent overlap of variation in the Los Tuxtlas population and *P. e. aequalis* PC1 in reduction of the yellow rings suggests that the two populations are best regarded as distinct subspecies, not species, until considerably more material is at hand.

Most subspecies of *P. elapoides* that we recognize are distinguished on the basis of characters that seem not to be affected by mimicry, but *P. e. wilmarai* is an exception, being distinguished solely on the basis of mimicral features. However, *P. e. wilmarai* is distinct from other taxa of *Pliocercus*, just as *M. limbatus* (and its two distinctive subspecies) is from other Coral Snake species, and both taxa are equally limited geographically. Consequently, recognizing both Los Tuxtlas populations as taxonomically distinct is not unreasonable.

Variation is summarized by Smith et al. (1996) and supplemented by Smith and Chiszar (1996).

• **ACKNOWLEDGMENTS.** We are indebted to Kraig Adler for counsel and bibliographic aid, to Ernest A. Liner for help with the literature, to Frank Van Breukelen for technical assistance, to Deborah Aguiar for preparation of the map, to Comstock Publishing Company for permission to reproduce figures 37, 73, 511, and 515 from Campbell and Lamar (1989), and to Krieger Publishing Company for permission to reproduce patterns 8, 13, 22, and 30 from Roze (1996).

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HOBART M. SMITH, Department of EPO Biology, University of Colorado, Boulder, CO 80309-0334, USA (hsmith@spot.colorado.edu), and **DAVID CHISZAR**, Departmemt of Psychology, University of Colorado, Boulder, CO 80309-0345, USA (chiszar@clipr.colorado.edu).

Primary editor for this account, Robert Powell.

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