

## Catalogue of American Amphibians and Reptiles.

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

***Pliocercus* Cope**  
False Coral Snakes

*Pliocercus* Cope 1860:253. Type species, *P. elapoides* Cope, by monotypy.

*Elapochrus* Peters 1860:293. Type species, *E. deppei* Peters (= *P. e. elapoides*), by monotypy.

*Pleiocercus*: Salvin 1861:227 (invalid emendation, occupied nomenclaturally).

*Liophis*: Jan 1863:287 (part).

*Liophis* (*Cosmiosophis*) Jan 1863:289 (part). Type species, *L. tricinctus* Jan (= *P. e. elapoides*), by subsequent designation (Smith and Taylor 1945). The other species originally included were *L. splendens* Jan (= *Pliocercus euryzonus* Cope 1862) and *L. lateristriga* Berthold 1859 (now *Urotheca lateristriga*).

*Urotheca*: Boulenger 1894:180 (part).

*Plioceras*: Schmidt 1936:175 (incorrect subsequent spelling, without nomenclatural status).

*Elapochrous*: Smith and Taylor 1945:110 (incorrect subsequent spelling, without nomenclatural status).

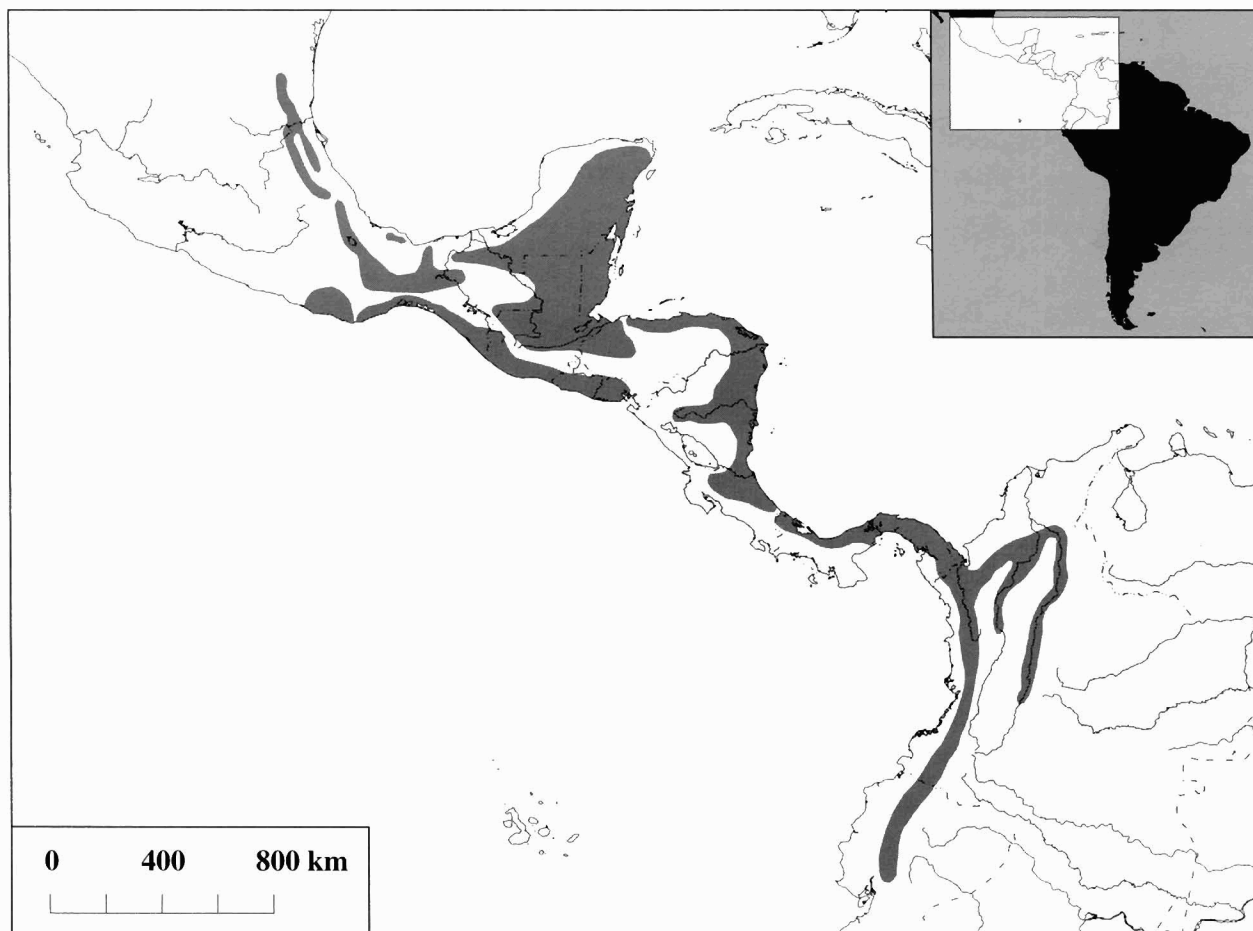
• **CONTENT.** Five species are recognized herein, two of which are monotypic (*P. andrewsi*, *P. dimidiatus*), and three are poly-

typic (*P. bicolor*, *P. elapoides*, *P. euryzonus*) (see **Nomenclatural History and Comments**).

• **DEFINITION.** The most readily observable characteristics of the genus *Pliocercus* are: (1) a distinctive pattern of 2–27 primary black rings or saddles on the body, separated from each other by pale zones that may be interrupted by secondary black saddles and that vary from less than a single scale length to nearly the full length of the body, and from white to yellow and/or red; (2) 17 scale rows throughout the length of the body; (3) all scales without keels; (4) no apical pits; (5) a thick, exceptionally long tail, 34–46% of TL, which terminates in a spine; (6) a fragile tail, readily parted intervertebrally; (7) moderately large eyes, 1.5–2 times larger than the eyes of *Micrurus*, with a vertical diameter equal to or greater than the distance from the lip (much less in *Micrurus*); and (8) a normal complement of head scales.

The hemipenis is unusual in having a conspicuous, small, bare pocket on the asulcate side of the capitulum; spines, increasing in size toward the base, extend two thirds the length of the hemipenis on the asulcate side; the sulcate side has basal spinules, replaced distally by small to medium-sized spines (Savage and Crother 1989). These features are, however, shared with *Urotheca*, as is the unusually long, fragile tail.

The maxilla bears 17–21 subequal, strongly recurved teeth, the rear two slightly enlarged, with a slender, rear flange and usually preceded by a short diastema. The mandibular teeth are subequal. Duvernoy's glands are present, and the venom may

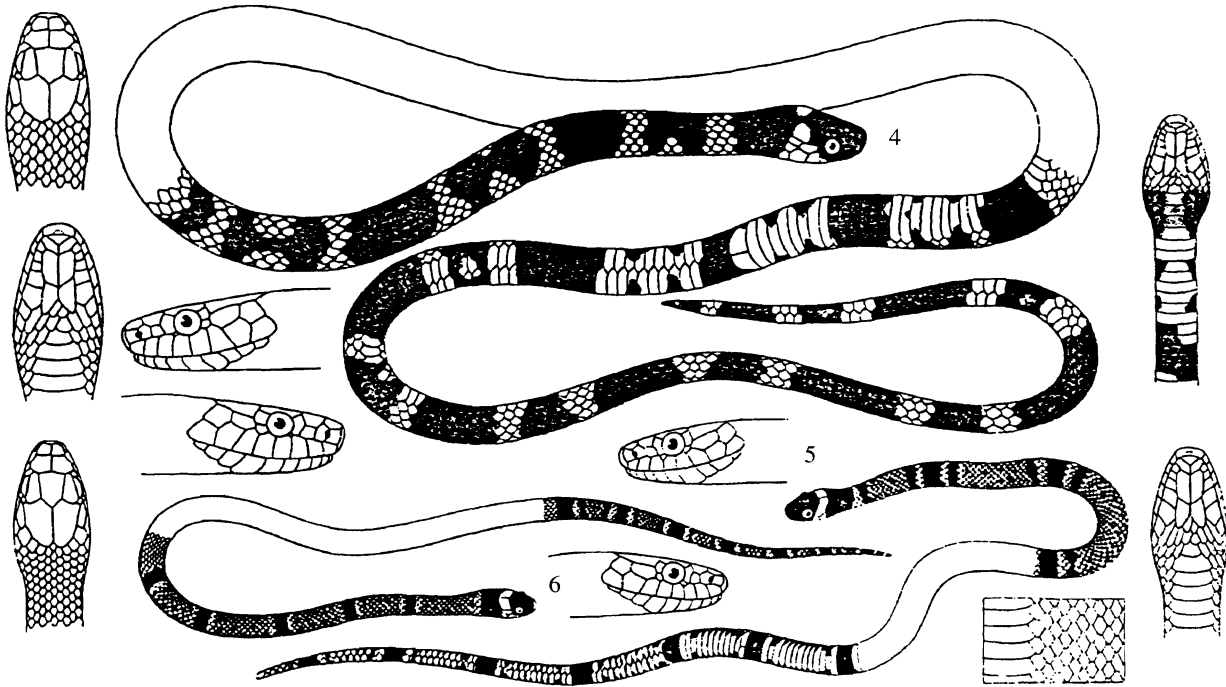


MAP. Distribution of the genus *Pliocercus*.

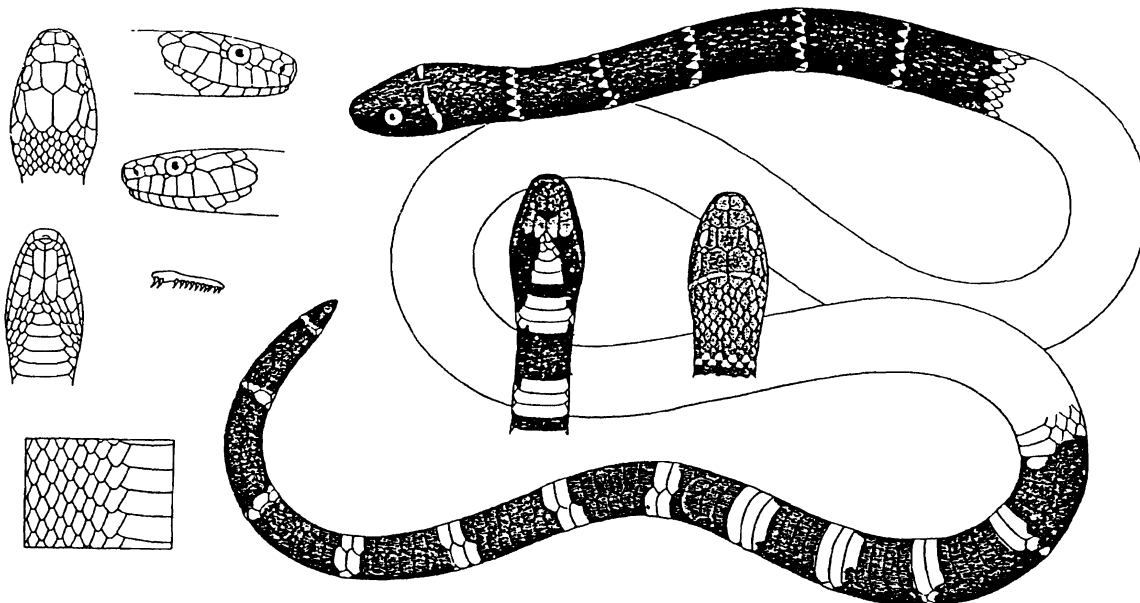
be potent (Seib 1980). No hypapophyses are present on the posterior trunk vertebrae (Savage and Crother 1989).

All members of the genus are small to medium-sized, reaching a maximum of 795 mm TL (*P. dimidiatus*, Savage and Crother 1989). The head is not or scarcely distinguishable from the neck, and the body is cylindrical, not at all flattened. The pupil of the eye is round, the iris black. The supralabials usually number 8, occasionally 9 (0–22% in different taxa), rarely 7 (1% or less); infralabials 8–11, usually 9, 10, or 11, depending on species—they are about equally 9 and 10 in *P. andrewsi*, usually 9 in *P. e. aequalis* (60%), *P. e. elapoides* (90%), and *P. e. occidentalis* (73%), usually 10 in *P. e. diastema* (72%), *P.*

*dimidiatus* (93%), and *P. eurizonus* (92%), and usually 11 in *P. bicolor* (96%); preoculars 1–3, usually 2, except in *P. dimidiatus*, usually with 3; postoculars usually 2, occasionally 3, 1 occurring only in *P. bicolor* (10%); secondary temporals mostly single, two occurring in 0–6% in all taxa except *P. eurizonus* (79%), *P. dimidiatus* (13%), *P. e. diastema* (32%), and *P. e. occidentalis* (41%); one loreal; nasal divided, nostril virtually splitting it more or less equally into two parts, the posterior part indented so that the nostril is directed somewhat posterolaterally; and 2 pairs of elongate chinshields. Ventral scales number 119–137 in males, 124–145 in females, with little clinal variation (Savage and Crother 1989). Caudal scales are divided, 90–122 in males,



**FIGURE 1.** Examples of the tricolor *Pliocercus elapoides* complex: syntypes of *Liophis tricinctus* Jan (from Jan and Sordelli 1866: livr. 18, figs. 4–6), representing *P. e. elapoides*. A common pattern of the subspecies is shown in fig. 5; an extreme reduction in the secondary black rings in fig. 6; and an extreme hypertrophy of the secondary black rings in fig. 4.



**FIGURE 2.** An example of the bicolor *Pliocercus eurizonus* complex: holotype of *Liophis splendens* Jan (from Jan and Sordelli 1866: livr. 18, fig. 1), representing *P. e. eurizonus*. Note the double secondary temporal, incomplete parietal pale ring, and short pale and black rings on the body.

83–120 in females, with higher numbers tending to occur toward the south. The cloacal (anal) scute is divided. The tongue is black.

• **DIAGNOSIS.** *Pliocercus* is most like *Urotheca*. Savage and Crother (1989) found so many unusual apomorphies shared by these two genera that they concluded that they should be regarded as a single genus, *Urotheca*. Their scholarly analysis leaves no doubt of the close relationship and common ancestry of the two divisions, as observed on lesser grounds by earlier workers (e.g., Boulenger 1894, Amaral 1929, Dunn 1928, and Taylor 1939 [1940]). Nevertheless, close common ancestry does not necessarily preclude specialization of one branch to such an extent that it may be regarded as a separate genus.

Smith and Chiszar (1996a) continued to so view *Pliocercus*, which differs from *Urotheca* most importantly by: (1) evolution in all species of a ringed and/or red pattern mimicking various species of *Micrurus* (versus the cryptic, unicolor, or striped patterns of *Urotheca*)—such mimicry is completely unique in related groups, including the speciose genus *Rhadinaea*; (2) a surprisingly potent venom present in *Pliocercus* (versus possibly weak or none in *Urotheca*; observations are lacking), thus possibly constituting reinforcement (Müllerian) as well as simple (Batesian) mimicry; (3) reinforcement suggested also by the slight lateral compression and rear flange on each fang in *Pliocercus* (Smith and Chiszar 1996a)—the fangs of *Urotheca sensu strictu* we have examined (*U. decipiens*, KU 35637; *U. fulviceps*, KU 80266; *U. guentheri*, KU 31939; *U. pachyura*, KU 112458) are cylindrical in cross section and lack a flange; and (4) a terminal tracheal entry into the right lung (versus subterminal in *Urotheca*) is present in *Pliocercus* (fide Van Wallach, in Smith et al. 1995).

Despite these categorical differences, *Urotheca sensu lato* continues to be accepted by various workers (e.g., Brodie 1993; Cadle and Greene 1993; Crother 1992, 2000; Ernst and Zug 1996; Lee 1996, 2000; Liner 1994; McCranie and Villa 1993; Mendelson 1992; Savage and Slowinski 1990, 1992; Slevin 1939; Slowinski and Savage 1995; Stafford 1999, 2000; Stafford and Meyer 2000; Wilson and McCranie 1998; Zhao et al. 1993). Myers and Cadle (1994) and Smith et al. (1995) were among the first to resurrect *Pliocercus* after Savage and Crother (1989) synonymized it with *Urotheca*, and the preponderance of opinion at present appears to favor acceptance of *Pliocercus* (e.g., Campbell 1998; Flores-Villela and Smith 1997; Greene 1997; Liner 1997; Markel 1990; Pérez-Higareda and Smith 1991; Smith and Chiszar 1996a, b; Wallach 1995; Wilson et al. 1996; and many others dealing with single species).

• **DESCRIPTIONS.** Hoffmann (1890), Dunn (1944a), Pérez-Santos and Moreno (1988, 1991), and Smith et al. (1995) gave a brief diagnosis for *Pliocercus*, limited as at present. Boulenger (1894) and Savage and Crother (1989), the latter in much detail, described *Urotheca sensu lato*, including several species now referred to *Pliocercus*.

• **ILLUSTRATIONS.** The hemipenis of *P. euryzonus* was illustrated by a drawing in Savage and Crother (1989). A drawing of a caudal vertebra, showing its hypothesized intravertebral fracture plane, appeared in Wilson (1968), although Arnold (1984, 1988) and Savage and Crother (1989) argued that the tail parts intervertebrally and hence is not regenerated, thus incurring selection pressure for a long tail. Other illustrations depict external features, especially pattern. Exquisite detail appears in the drawings in Jan and Sordelli (1866, livr. 18, pls. 4, 5) for *P. e. elapoides* (3 specimens) and *P. e. euryzonus*, the first (and best) for the genus. The most complete representation of photographs (black and white mostly) is in Smith and Chiszar

(1996a), with all taxa represented. Numerous color photographs of various taxa are in Campbell and Lamar (1989), and a few illustrations are in Greene (1997), Lee (1996, 2000), Markel (1990), Mertz (1996), Pérez-Higareda and Smith (1991), Smith and Chiszar (1996b), Stafford (2000), and Stafford and Meyer (2000) (see also species accounts, Smith and Chiszar 2001a, b, c, d, e).

• **DISTRIBUTION.** The genus *Pliocercus* ranges from central Tamaulipas, México, in foothills along the Atlantic drainage, to Colombia, where it occurs in the Chocó forest not only of Atlantic drainage but also Pacific, as far south as Ecuador. A Pacific slope series of populations, presumably originating at the Isthmus of Tehuantepec from Atlantic slope ancestors, occurs from western Oaxaca (and possibly adjacent Guerrero), México southeastward to El Salvador (and possibly adjacent Honduras). The genus was erroneously stated to occur widely in the Amazonian region (Dixon 1979).

• **FOSSIL RECORD.** None.

• **PERTINENT LITERATURE.** The most nearly complete review of the literature on *Pliocercus*, including its natural history, is in Smith and Chiszar (1996a). The enormous literature on mimicry was reviewed in detail, both pros and cons, in Cloudsley-Thompson (1994), Dunn (1954), Greene and McDiarmid (1981), Hecht and Marien (1956), Mertens (1956, 1957), Pough (1988), Smith and Chiszar (1996a, b), and Wickler (1968). Roze (1983) regarded mimicry as occurring in “nearly 100% of the species and subspecies” of *Pliocercus*. Reinforcement (Müllerian) mimicry may well exist, as suggested by the potent venom and flanged fangs, in addition to simple (Batesian) mimicry. Mertensian (model turned mimic) mimicry was thought unlikely (Pough 1988), but it appears very likely to occur in *P. andrewsi*, whose unique pattern mimics no sympatric *Micrurus*. On the contrary, rare individuals of the latter simulate the *P. andrewsi* pattern to a certain extent, as shown by Lee (1996)—however, Roze (1996) does not note such a variant in his account for the sympatric *Micrurus diastema alienus*. S. Smith (1975, 1977, 1980) concluded that avoidance by predators of the patterns of Coral Snakes and their mimics is not entirely learned, but that a genetic basis has evolved. Brodie (1993) and Brodie and Brodie (1999) agreed.

A considerable potency of *Pliocercus* venom was suggested by the experience reported by Seib (1980), widely cited (e.g., Mitton 1990, 1996), although an allergic response cannot be ruled out.

Greene (1997) adopted the name Halloween Snakes for the genus (as did Hayes et al. 1998), recognizing just two species, the Red Halloween Snake and Black Halloween Snake. The name Harlequin Snakes also has been applied to members of *Pliocercus* (e.g., Stafford 2000).

Few references to anatomy exist. The long, thick tail is adapted to frequent intervertebral breakage (Mendelson 1991), hence cannot be regenerated (Savage and Crother 1989, Slowinski and Savage 1995). Incomplete tails occur least frequently in *P. b. hobartsmithi* (40% of ten) and most frequently in *P. andrewsi* (71% of 14), according to Smith and Chiszar (1996a). The high frequency in the latter species may be influenced by the absence of a similar model.

The maxillary teeth were described by Savage and Crother (1989) and Smith and Chiszar (1996a). Taub (1967) dealt with Duvernoy's glands. The hemipenis was well described by Savage and Crother (1989), and commented on by Wallach (1995). Miller (1968) described the cochlear duct in comparison with the condition in other snakes. Langebartel (1968) reported the presence of a hyoid muscle of erratic occurrence in Serpentes.

Saiff (1975) noted the absence of any preglottal structures in species of *P. euryzonus* complex and their presence in the *P. elapoides* complex. Tracheal entry into the right lung was noted as different in *Pliocercus* and *Urotheca* (*s.s.*) by Van Wallach (in Smith et al. 1995). Baird (1970) reported on the structure of the ear.

Behavioral observations include the general consensus that all *Pliocercus* are diurnal (e.g., Pough 1988), with a rare exception (Greene 1969), in which the snake was probably searching for an oviposition site rather than foraging. Upon capture the tail is generally thrashed vigorously (pers. obs.), perhaps functioning to focus attacks on it rather than on the trunk. The behavior in defensive use of the fangs (Seib 1980) is of special interest.

The literature reveals that *Pliocercus* prefers a moist (750–7000 mm/yr), sciophilic (densely shaded) habitat with temperatures of 12.5–30°C, at altitudes of 0–2750 m. Sources include Campbell and Vannini (1989), Duellman (1966), Johnson (1989), Landy et al. (1966), Martin (1958), Mendelson (1990), Mertens (1952), Pérez-Santos and Moreno (1988, 1991), Stafford (1999), and Wilson and McCranie (1998).

Records of food preference (Landy et al. 1966, Martin 1958, Mertens 1952, Scott 1983, Stuart 1948) indicate that anurans and salamanders are preferred; no accounts record reptiles being eaten, although small lizards and snakes would seem to be likely prey.

Avian predators have been reported by Pough (1964) and Weber (1945), a Laughing Falcon (*Herpetotheres cachinnans*) in Costa Rica by the former, and a “White Snake Hawk” in Tabasco by the latter. Stuart (1948) recorded a specimen in the stomach of a notorious diurnal snake-eater, *Drymarchon corais melanurus*.

Evidence indicates that *Pliocercus* lays its eggs in late June or July, hatching in August (Greene 1969, Köhler 1997, Landy et al. 1966, Martin 1958, Mertens 1952, Stafford 1999).

Thatcher (1966) recorded a trematode, *Ochetosoma ellipticum*, from a *P. e. elapoides* from Tabasco.

Other references to *Pliocercus* occur in Alvarez and Gonzalez (1987), Cadle (1984a, b, molecular confirmation of xenodontine relationship), Cadle and Greene (1993, phylogeny), Casas Andreu and McCoy (1979, key), Cope (1875 [1876], 1894), Deeming (1989, egg residues in the related genus *Urotheca*, as *U. gigas*, perhaps *Cyclagras gigas*), DeLisle (1981, 1982, venomous), Dixon (1980, not in *Liophis*), Dowling (1975, 1995, Dipsadidae, Dipsadinae), Dunn (1928, generic key; 1944a, b), Dunn and Dunn (1940, Cope’s contributions), Flores-Villela (1993), Flores-Villela et al. (1995, keys), Golvan (1962, 1965, list of vertebrate genera), Greene (1976, mimicry), Greene and Seib (1983, envenomation, mimicry), Günther (1893, considered a junior synonym of *Elapochrus* in a generic summary), Jenner (1982, family-group allocation), Lamar (1997, review), Lieb (1993, review), Mattison (1986, 1995, uroautotomy), McKinstry (1983, salivary toxicity), Mertz (1996, mimicry), Minton (1981, toxicophidian evolution, distribution; 1990, colubrid envenomation bibliography), Muñoz (1987, autotomy), Myers (1970, 1974, relationship to *Rhadinaea*), Obst et al. (1988), Parker and Grandison (1977, urotomy), Patrick and Vasse (1994, mimicry), Peters (1960, Ecuador), Peters and Orejas-Miranda (1970, keys, synonymy), Peters et al. (1986, keys, synonymy), Peters (1869, concedes priority over his *Elapochrus*), Pough (1988, envenomation, mimicry), Pough et al. (1998, 2001, Xenodontinae, mimicry), Roze (1983, mimicry), Savage (1966, 1982, zoogeography; 1980, Costa Rica), Smith and Chiszar (1996b, mimicry), Smith and Smith (1976, 1993, literature survey), Smith and Taylor (1950, type localities), Sokolov (1988, name list), Spellerberg (1982), Stuart (1950, 1963, Guatemala), Wallace (1876), Williams and Wallach (1989, generic syn-

onyms), Wilson and McCranie (1998, Middle American herpetogeography), Zaher (1999, in Dipsadinae), and Zug (1993).

• **KEY TO SPECIES.** Numbers of relevant species accounts are given in parentheses.

1. a. Posterior infralabial and posterior labiogenial fused .....  
..... *P. bicolor* (737)
- b. Posterior infralabial and posterior labiogenial separate .. 2
2. a. Parietal pale ring incomplete, absent or very narrow, 15% or less of the length of the parietals (100%); two secondary temporals on one or both sides (90%) .....  
..... *P. euryzonus* (740)
- b. Parietal pale ring complete, 20% or more of the length of parietals (100%); one secondary temporal on both sides (80–92% in different taxa) ..... 3
3. a. Primary black rings on body number 5–7 and are 0.5–1.25 times as long as pale interspaces (secondary black saddles, if present, are counted as part of the pale rings in which they occur) ..... *P. andrewsi* (736)
- b. If primary black rings on body as few as 7 or less, interspaces are more than twice as long as those rings ..... 4
4. a. Primary black rings on body separated by pale rings usually 1–2 scales long, never more than 3.5 .....  
..... *P. dimidiatus* (738)
- b. Primary black rings on body separated by pale rings some or all of which are more than 3.5 scales long .....  
..... *P. elapoides* (739)

• **NOMENCLATURE HISTORY.** By 1886 (Savage and Crother 1989), ten nominal species-group taxa had been named in the genus, although Boulenger (1894) recognized but two as valid. As stated by Savage and Crother (1989), not until 1941 did any more appear in print, but then a flurry of them culminated with 12 more names by 1965, reflecting a diversity of individual patterns that defied ready understanding. Two more nominal species were described by Smith et al. (1996) and Smith and Chiszar (1996b), making a total of 24 species-group names proposed over the span of 136 years. In 1970, Peters and Orejas-Miranda accepted nine taxa, in five species, from Central and South America, and listed five others in México.

By that time, however, recognition that not all of the nominal taxa represented taxonomic populations became evident; some had to be based on individual variants. Greene (1969) was among the earliest to question seriously the stability of supposed defining patterns (on the excellent basis of the only offspring recorded of known female parentage). A.K. Smith (1969) soon followed, examining variation in *P. elapoides*, and concluding that *P. andrewsi pacificus*, *P. e. schmidtii*, *P. e. salvini*, and *P. e. occidentalis* were invalid, although he retained *P. andrewsi*.

In 1981, Greene and McDiarmid concluded that no more than two monotypic species, *P. elapoides* and *P. euryzonus*, could be recognized in the genus. Essentially the same conclusion was maintained by most subsequent workers (e.g., Wilson and Dugas 1972; Savage and Vial 1974; Wilson and Meyer 1982, 1985; and, most influentially, Savage and Crother 1989). Campbell and Lamar (1989) continued to recognize some subspecies, as did Smith (1987) and Smith et al. (1989), but a subsequent generic evaluation (Smith and Chiszar 1996a) recognized seven species, two of which contained two subspecies, and one four subspecies. Since then, Smith and Chiszar (2001f) synonymized one of their species, *P. psychoides*, with *P. elapoides aequalis*, and Smith and Chiszar (2000) reduced another (*P. wilmariai* of

the Los Tuxtlas region, Veracruz) to subspecific rank, *P. e. wilmarai*, lumping the latter with the grossly sympatric specimens they had earlier referred to *P. e. aequalis*.

• **REMARKS.** Savage and Slowinski (1990) proposed a terminology for the basic pattern types occurring in Coral Snakes and their mimics, and introduced for tricolor snakes the new terms monad, dyad, tetrad, and pentad, all referring to the number of black bands between the red rings. That system was expanded by Savage and Slowinski (1992, 1996). Two pattern variants are recognized for the *P. eurizonus* complex (bicolor group), pale interspaces between black rings with red dorsally or lacking red. The *P. elapoides* complex (tricolor group) exhibits seven different patterns, according to this classification (examples ours): (1) unicolor except for a nuchal (and anal) black saddle (*P. e. wilmarai*); (2) black rings alternating with pale interspaces (e.g., *P. e. aequalis* PC [pattern class] 1); (3) bicolor with black spots (e.g., *P. e. wilmarai*); (4) bicolor with black blotches (e.g., *P. e. wilmarai*); (5) tricolor monads, with single black rings flanked by yellow rings (e.g., *P. andrewsi*); (6) tricolor triads, with three black rings in a unit, separated by yellow/white, alternating with red rings (e.g., *P. e. aequalis* PC 1); and (7) tricolor monads, but with black or pale rings incomplete dorsally (e.g., *P. e. aequalis* PC 2).

Pattern type 2 above, as exemplified by some specimens of *P. e. aequalis* PC 1 (Smith and Chiszar 1996a), is not truly bicolored, and of course does not belong to that group. Occasional specimens have the black speckling characteristically present in the center of the red rings so dense that a black saddle is formed, completely obliterating the red rings dorsally and laterally, but not ventrally. Superficially, such snakes appear to belong to the bicolor group, having a simple dorsal pattern of black rings separated by pale rings. Those examples, however, have more numerous bands than most members of the true bicolor group. They are, in other words, generally polycricoid (numerous bands) as opposed to the generally oligocricoid (few bands) bicolor group (terms from Smith and Chiszar 1996a). This pattern was called a double monad by Smith and Chiszar (1996a), but that term is not consistent with Savage and Slowinski's (1992, 1996) concept of a monad. The pattern is better regarded as a modified monad, as it is derived from a simple monad. If the pattern is termed bicolor at all, it should be clearly designated as being secondarily bicolor. *Pliocercus e. wilmarai* also is secondarily bicolor, but in a different fashion, by the absence of yellow or white rings.

*Pliocercus* never has paired black rings separated by a pale ring, as indicated by Minton et al. (1966), a condition occurring, for example, in *Lampropeltis*, and termed a double monad by Brodie (1993).

• **ETYMOLOGY.** The name *Pliocercus* was derived from the Greek words *pleio* and *kerkos*, meaning "more" and "tail," respectively, referring to the characteristically long tail in the genus.

• **COMMENTS.** Our concept of 11 valid species-group taxa lies between the historical extremes of 2 and 24 taxa, but it is not viewed as a compromise per se. Instead, we regard it as an hypothesis that more closely approximates taxonomic reality than either of the extremes.

For many decades, False Coral Snakes were so rarely taken that, in view of their spectacular variation in pattern, almost every individual was interpreted as representing a different species. The hiatus in nominal creation from 1887 to 1940 was a product of exploratory inactivity, and the rapid increase in the number of new names thereafter reflected renewed field activity as well as increased attention. Accumulating series also led

to the realization that the numerous names available did not properly reflect the growing populational concept of species. Boulenger (1894) was ahead of his time in the context of recognizing but two species, and Savage and Crother (1989) epitomized the conviction that far more names were available than valid taxa to receive them.

Wilson and McCranie (1997) vigorously defended Savage and Crother's (1989) conclusions, and equally vigorously attacked the alternative taxonomy of the genus proposed by Smith and Chiszar (1996a). Both schools of thought agree that two major divisions exist in the genus (the basically bicolor *P. eurizonus* complex, extending from Honduras to Ecuador, and the basically tricolor *P. elapoides* complex, extending from México into Honduras and El Salvador), although one interpretation considers them to be species complexes, whereas the alternative view considers them single species. Both schools agree that no taxonomic significance exists in ventral or subcaudal counts or in the number alone of black rings (well summarized in Savage and Crother 1989). Indeed, the absence of differences in these characters, commonly (although not invariably) taxonomically vital, was regarded by Savage and Crother (1989) as strong evidence of no taxonomic differentiation in either the bicolor or tricolor complexes—on the other hand, color and pattern were accepted as valid criteria for distinguishing the two complexes (or species). We agree that color and pattern are valid criteria separating the two complexes, but we view them as equally valid for distinguishing taxa within those two complexes.

Wilson et al. (1996) went so far as to express uncertainty that color and pattern are sufficient to diagnose even the two complexes, suggesting that ultimately but one species would be recognized. That thought, however, apparently stemmed largely from regarding two specimens from La Muralla and Los Planes, Honduras, as bicolored, hence by implication members of the bicolor complex. So interpreted, the concept of allospecificity would indeed be in jeopardy. However, those specimens represent *Pliocercus elapoides aequalis*, a widely distributed tricolor subspecies already known from but a few kilometers from the cited localities. The specimens appear to be more or less intermediate between pattern classes 1 and 2 of that subspecies. An apparently more typical specimen of pattern class 2 was reported simultaneously with the cited specimens from nearby La Fortuna. We have not seen these specimens, but R.I. Crombie (National Museum of Natural History, where the specimens are now cataloged) kindly supplied supplementary information. Both localities extend the known range of *P. e. aequalis* slightly to the east, at the farthest known limit of the species in Honduras. They reinforce the probability of sympatry of the tricolor and bicolor complexes, the latter of which is known from as far west as Tela, Honduras.

At least five fundamentally different factors are involved in the disparity of the 2-taxon and 11-taxon analyses: (1) The number of specimens examined varied substantially in the two principal studies (516 in the 11-taxon analysis, 131 in the 2-taxon analysis), although the discrepancy is insignificant for the bicolor complex (69 versus 70 specimens), because Savage and Crother (1989) focused more strongly there than elsewhere. (2) The studies interpreted differently what constitutes the bicolor complex; Savage and Crother (1989) regarded some Veracruz specimens as bicolor, although not regarding them as members of the bicolor complex. Indeed, they are bicolored, but secondarily so, derived from tricolor types. The two specimens reported by Wilson et al. (1996) as bicolored and dubiously a member of the bicolor complex, also are secondarily bicolored, being variants of a tricolor taxon. The secondary bicolor conditions, variants of the tricolor complex, must be distinguished from the primary bicolor condition. (3) Details of pattern, in

addition to those evidently correlated with mimicry, and some details of scalation, were analyzed by Smith and Chiszar (1996a), but not by Savage and Crother (1989); consequently, geographic correlations of the variation in such details were not considered by the latter. (4) In the 2-taxon point of view, mimicry is regarded as too erratic to be reliable taxonomically, except in the distinction of the bicolor and tricolor complexes. When two radically differently patterned models exist, the results of mimicry per se are irrelevant taxonomically (e.g., as in pattern class 1 of *P. e. aequalis*); however, that fact should not obscure the possibility that other pattern characters, not involved with mimicry and consistent geographically, are valid taxonomic criteria (again, e.g., *P. e. aequalis*).

Mimicry also has been construed as too labile for taxonomic significance. For example, Wilson et al. (1996) stated that mimicry may well be the principal survival strategy of *Pliocercus*, and we agree. They suggest "that variation in color and pattern in *Pliocercus* has much more to do with what species of *Micrurus* occur in a given area to serve as models for mimicry than does the explanation-bare picture of subspecific variation.... Recognizing ...subspecies of these coral snake mimics is, we hope, a thing of the past" (Wilson et al. 1996). However, most species-group taxa are "explanation-bare"—not subspecies alone. Furthermore, although major features of color and pattern are involved in mimicry, lesser features may vary relatively little, as for example the length of the pale and dark parietal/nuchal bands. Such constancies indicate genetic continuity, despite evidence in other contexts of genetic inconstancy. That mimicry by *Pliocercus* of *Micrurus* has been going on perhaps thousands of years is suggested by the tracheal-lung connection, the reinforcement adaptations of a potent venom and flanged fangs, and, if S. Smith (1975, 1977, 1980) and Brodie and Brodie (1999) are correct, the evolution (not simply learning) of predator avoidance.

Species-group differentiation is reasonably viewed as directly or indirectly adaptive in most cases. The obviously adaptive nature of mimicry is not thereby to be regarded as taxonomically insignificant. The famous case of industrial melanism, long thought to exemplify a marked shift within a few decades in adjustment to human activities, is now known to be in error. For the most part, nature changes slowly. Mimicry patterns could have existed for thousands of years; hence, where consistent differences exist, they merit taxonomic evaluation. Populational differentiation generally is accepted as adaptive (although seldom confirmed), and mimicry is obviously adaptive.

In addition to the differences noted previously between the two schools of thought, a fundamental philosophical difference exists. Savage and Crother (1989), Wilson and McCranie (1997), and many other taxonomists today categorically reject subspecies. In part, that view results from an inability or a reluctance to cope with them, for example in large museums where segregation and adjustment to changes in subspecies in vast holdings are impractical or even logistically impossible. Subspecies also are often inconsequential in faunistic studies of limited territories where but one in any given species occurs. However, other reasons exist why "the subspecies has been largely abandoned" in herpetology as "an outmoded concept" (Wilson and McCranie 1997). Wilson and Brown (1953) initiated the slide of the subspecies concept toward disfavor, and this approach was reinforced by, among others, Savage and Heyer (1967) and Wilson and Meyer (1985). However, Wilson (1994) recanted: "I realize now that Brown and I overstated our case in 1953. Some populations can be defined clearly with sets of genetic traits that do change in a concordant, not discordant manner;" he also noted that subspecies are a part of the "taxon cycle."

Two recent advances in biology have contributed to the disfavor in which subspecies are held, cladistic and molecular re-

search. Not being discrete, subspecies are incompatible with cladistic theory or resultant phylogenetic analyses. Molecular techniques are seldom successful in distinguishing subspecies—and when they are, the taxa often are elevated to species rank. In these contexts, the subspecies concept may not be tenable, but in contexts of recognizably distinct populational diversity, concomitant conservation concerns, and evolutionary origin, they remain of strong scientific importance. Exclusion in some contexts does not require exclusion in others. Subspecies should remain a part of taxonomy, recognizable in appropriate situations.

The subspecies concept has been abused at times by its proponents, but the same can be said of every other taxonomic category. The subspecies in *Pliocercus* recognized herein are all distinguished by a geographically consistent suite of character-states, at least one of which exceeds 70% reliability, but distinctly less than total infallibility. In contrast, the species herein recognized are all distinguished by a suite of geographically consistent character-states, at least one of which is invariably distinctive, or nearly so. These concepts are consistent with those expressed by Mayr (2000), who viewed non-Mendelian species and subspecies as approximations to the much more familiar parameters of species and subspecies of sexually reproducing organisms. Mendelian species-group taxa provide the most practical foundation for achievement of common grounds, albeit arbitrary, for non-Mendelian entities. No single, universal species concept can address all situations, inasmuch as the factors involved in evolution and maintenance of populational characteristics are widely different in different organisms. Precise, all-inclusive definitions are unrealistic. Thus the many definitions, variously designated as evolutionary, phylogenetic, recognition, morphological, biological, typological, cohesion, Hennigian, and nominal concepts, among others, emphasize differences of concept rather than the common grounds that should be sought. The most important consideration in all discussions of species and subspecies names is their fundamental role as names for recognizably distinct populational assemblages. All other functions are subordinate.

Although we are confident of the validity of the hypotheses presented herein, on the basis of the data available, new data may require changes. Molecular studies and breeding experiments will be of great importance in a definitive resolution of some of the many uncertainties of *Pliocercus* taxonomy.

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