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Redescription of *Ctenoblepharys adspersa* Tschudi, 1845, and the Taxonomy of Liolaeminae (Reptilia: Squamata: Tropiduridae)

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ABSTRACT

Ctenoblepharys adspersa is a highly derived aricolous lizard that inhabits the sandy coast of central Peru. It differs from other Tropiduridae, and the outgroups Phrynosomatidae and Opluridae, in numerous autapomorphies of the skull and vertebral column, but shares no derived characteristics with either *Phymaturus* or *Liolaemus* other than those that diagnose Liolaeminae. The relationships of *Ctenoblepharys*, *Liolaemus*, and *Phymaturus* are unresolved. All species of Liolaeminae that have been described in, or referred to *Ctenoblepharys*, other than *C. adspersa*, exhibit the synapomorphies that diagnose *Liolaemus*, and should be referred to that genus. All of the species

that have been placed in the genera *Abas*, *Ceio-laemus*, *Helocephalus*, *Pelusauros*, *Phrynosaura*, *Velosaura*, and *Vilcunia* and all of the species that have been placed in the subgenera *Eulaemus*, *Rhytidodeira*, *Mesolaemus*, and *Ortholaemus* also exhibit the diagnostic synapomorphies of *Liolaemus* and, although some of these may represent monophyletic subsets of *Liolaemus*, they should not be used as formal names for taxa until their monophyletic status has been verified by cladistic analysis. *Phymaturus indistinctus*, *P. nevadoi*, *P. patagonicus*, *P. payunae*, *P. somuncurensis*, and *P. zapalensis*, all formerly subspecies of *P. patagonicus*, are elevated to species status.

RESUMEN

Ctenoblepharys adspersa es un lagarto arenícola altamente derivado que habita en la costa arenosa de Centro Perú. Se diferencia de otros Tropiduridae y de los grupos externos Phrynosomatidae y Opluridae en numerosas autapomorfías del cráneo

y de la columna vertebral, pero no comparte ningún carácter derivado con *Phymaturus* o *Liolaemus* excepto los que se diagnostican Liolaeminae. Las relaciones de *Ctenoblepharys*, *Liolaemus*, y *Phymaturus* no están resueltas aún. Todas las es-

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pecies de *Liolaeminae* que han sido descritas en, o referido a *Ctenoblepharys*, excepto *C. adspersa*, exhiben sinapomorfías que diagnostican *Liolaemus*, y deben ser referidas a ese género. Todas las especies que han sido incluídas en los géneros *Abas*, *Ceiolaemus*, *Helocephalus*, *Pelusauros*, *Phrynosaura*, *Velosaura*, y *Vilcunia*, y todas las especies que han sido incluídas en los subgéneros *Eulaemus*, *Rhytidodeira*, *Mesolaemus*, y *Ortholaemus* también exhiben las sinapomorfías

diagnósticas de *Liolaemus* y aunque algunas de estas sinapomorfías representan un subgrupo de *Liolaemus*, no deben ser usados como nombres formales para taxones hasta que su estado monofilético haya sido comprobado por medio del análisis cladístico. *Phymaturus indistinctus*, *P. nevadoi*, *P. patagonicus*, *P. payunae*, *P. somuncurensis*, y *P. zapalensis*, todos antiguamente subespecies de *P. patagonicus*, son elevado al rango de especies.

INTRODUCTION

In 1845, Tschudi described the iguanian lizard *Ctenoblepharys adspersa* from the Pacific coast of central Peru, where it appears to be restricted to coastal sand dunes and beaches (Mertens, 1956; J. Wright, personal commun., 1989). The species is rare in collections and has never been adequately described, but the genus has since had a long and complicated taxonomic history, with 12 species, including 15 specific names, having been described in or transferred to *Ctenoblepharys*: *multimaculatus* Duméril and Bibron, 1837; *nigriceps* Philippi, 1860; *marmoratus* Burmeister, 1861 (non Gravenhorst, 1837); *jamesi* Boulenger, 1891; *stolzmanni* Steindachner, 1891; *anomalus* Koslowsky, 1896; *reichei* Werner, 1907; *wernerii* Müller, 1928 (= *anomalus* fide Cei, 1979a); *schmidtii* Marx, 1960; *erroneus* Núñez and Yáñez, 1984a; *lentus* Gallardo, 1966 (= *anomalus* fide Cei, 1979a); *donosobarrosi* Cei, 1974; *rabinoi* Cei, 1974; *auditovelatus* Núñez and Yáñez, 1983; and *pseudoanomalus* Cei, 1981 (substitute name for *marmoratus* Burmeister, 1861). Additionally, at various times some of these same forms have been referred to *Abas* Núñez and Yáñez, 1984b; *Ceiolaemus* Laurent, 1984a; *Eulaemus* Girard, 1858; *Helocephalus* Philippi, 1860; *Liolaemus* Wiegmann, 1834; *Ortholaemus* Girard, 1858; *Phrynosaura* Werner, 1907; and *Velosaura* Núñez and Yáñez, 1984b.

In recent years, Cei (1979b) considered that *Ctenoblepharys* contained the species *adspersa*, *nigriceps*, *reichei*, and *stolzmanni*, Núñez and Yáñez (1984a) and Veloso and Navarro (1988) included *adspersa*, *stolzmanni*, *erroneus*, and *nigriceps*, and it was considered monotypic, containing only *C. adspersa*, by Laurent (1984a), Etheridge and de

Queiroz (1988), Frost and Etheridge (1989) and Núñez and Jaksic (1992). This disagreement in the allocation of species to the genus *Ctenoblepharys* appears to have been due, at least in part, to the lack of an adequate description of the type species, to its rarity and thus unavailability to all workers, and to the fact that Boulenger (1885) based his characterization of *Ctenoblepharys*, and of the species *C. adspersa*, on a specimen of *Liolaemus*. Furthermore, it is clear that various authors have held different, mutually exclusive views as to what constitutes "generic characters."

Ctenoblepharys adspersa is one of over 135 species of austral South American lizards which, together with *Phymaturus* and *Liolaemus*, were referred to the tropidurid subfamily *Liolaeminae* by Frost and Etheridge (1989). *Phymaturus* includes five species, one with six allopatric subspecies that are treated as species in this work (see below). Frost and Etheridge (1989) considered *Ctenoblepharys* to be monotypic, and all but this species and those of *Phymaturus* were referred to *Liolaemus*, including all of the species that at one time or another had been referred to *Abas*, *Ceiolaemus*, *Ctenoblepharys*, *Eulaemus*, *Helocephalus*, *Mesolaemus*, *Ortholaemus*, *Pelusauros*, *Rhytidodeira*, *Phrynosaura*, *Velosaura*, and *Vilcunia*. In their cladistic analysis, Frost and Etheridge (1989) found two equally parsimonious topologies of relationships: (*Liolaemus* (*Ctenoblepharys* + *Phymaturus*)), and (*Phymaturus* (*Ctenoblepharys* + *Liolaemus*)). Laurent (1984a, 1984b, 1985a), employing morphometric data, and Núñez and Yáñez (1984b), using different combinations of characters, have expressed very different, mutually exclusive ideas about the content of *Ctenoblepharys* and its rela-

tionships to other Liolaeminae. Therefore, the question of the content of *Ctenoblepharys* and its relationships to other Liolaeminae is not a trivial one. If *Ctenoblepharys* or *Ctenoblepharys* + *Phymaturus* is the sister taxon of *Liolaemus*, then the characteristics of *C. adspersa* are important for the process of polarizing character state transformations within the extremely speciose genus *Liolaemus*.

My purpose here is to review the taxonomic history of *Ctenoblepharys*, to describe the external and skeletal morphology of *C. adspersa*, to compare *C. adspersa* with other species that have been referred to *Ctenoblepharys*, to comment on the possible relationships of the genera of Liolaeminae, and to discuss the taxonomic status of various generic and subgeneric names that have been used within the subfamily.

A formal phylogenetic analysis of Liolaeminae is in preparation, but is beyond the scope of the present study. Nevertheless, it is hoped that the characters described here, and their potential utility as synapomorphies (summarized in an indented classification, Appendix 2) will facilitate future work on this large and important component of the austral South American herpetofauna.

HISTORICAL REVIEW

What follows is a chronological account of the taxonomic literature relating to *Ctenoblepharys*.

Ctenoblepharys adspersa was described by Tschudi (1845), from Hacienda Acaray, 2 leagues from Huacho (11°07'S, 77°37'W) on the Pacific coast of Peru. A moderately detailed description of the genus, and a very brief description of the color pattern of the species was provided in Latin. The generic description was repeated and the species description amplified the following year (Tschudi, 1846).

Boulenger (1885) included *Ctenoblepharys adspersa* in his Catalogue of Lizards in the British Museum, changing the spelling to *Ctenoblepharis adspersus*, an emendation followed by most subsequent authors until it was found to be unjustified by Frost and Etheridge (1989). Boulenger's (1885) description was based on a specimen from Arequipa, Peru, at an altitude of 7500 ft (2286 m). Ac-

cording to Boulenger's (1885) description, this specimen differs from *C. adspersa* in a number of ways: the digits have smooth subdigital lamellae, the tail is a little shorter than the head and body, the adpressed hind limb reaches the neck, the digits are short, and the dorsal scales are transversely suboval; in *C. adspersa* the subdigital lamellae are keeled, the tail is longer than the head and body, the adpressed hind limb reaches beyond the external auditory meatus, the digits are exceptionally long, and the dorsal scales are rounded. Additionally, the locality for this specimen is well to the south of the known range of *C. adspersa*, inland, and at a much higher altitude. The identity of this specimen is unknown, but specimens of a possibly new species of *Liolaemus* from Arequipa (3 km SW Uchumayo, 2150 m, KU 163589, 1635902-4, SDSU 1945; 18 km N Matarani, 1000 m, KU 163595) possess all of the features described by Boulenger (1985) for *C. adspersa*.

Boulenger (1891) described a second species of *Ctenoblepharys*, *C. jamesi*, (spelled *jamesii* on the figure) from Tarapacá, Chile, at an altitude of 10,000–12,000 ft (3280–3937 m). Later, Boulenger (1901), following his description of *Liolaemus annectens*, said that "this species is very nearly related to *L. multififormis*, Cope, from which it is to be distinguished by the larger dorsal scales. The two species establish a passage from *Liolaemus* to *Ctenoblepharis*, especially through *C. Jamesii*, Blg." Subsequently *L. annectens* was synonymized with *L. multififormis* Cope, 1876, by Burt and Burt (1933), which was in turn synonymized with *L. signifer*, Duméril and Bibron, 1837, by Laurent (1992), who considered *L. annectens* to be a subspecies of *L. signifer*.

Steindachner (1891) described *Ctenoblepharys stolzmanni* from "Hoch Peru," based on three syntypes in Vienna (NMW 13580[3]), and provided a brief description of a specimen he referred to as the "typische Exemplar" of *Ctenoblepharys adspersa* in the Vienna Museum. This specimen appears to have been one of three upon which Tschudi based his description (Ortiz-Zapata, 1989a).

Werner (1907), in his description of the new genus and species *Phrynosaura reichei*, suggested that the genus closest to *Phrynosaura* was *Ctenoblepharys*.

Burt and Burt (1933) listed *Ctenoblepharys adspersa*, *C. jamesi*, and *C. stolzmanni* as members of the genus.

Donoso-Barros (1958a) did not have a specimen of *Ctenoblepharys adspersa* available, but using the illustration of this species in Tschudi (1846) for comparison, he concluded that although it showed certain similarities with *Phrynosaura reichei*, the characteristics of *C. adspersa* listed by Boulenger (1885) permitted separation of the two genera. Additionally, he (Donoso-Barros, 1958a) stated that the differences between *C. jamesi* and *Phrynosaura reichei* were so great that there was no point in discussing them. Shortly thereafter, Donoso-Barros (1958b) recognized two species of *Ctenoblepharys* in Chile, *C. adspersa* and *C. jamesi*, citing Hellmich's (1934) statement that *C. adspersa* was a problematic member of the herpetofauna of Chile. In the same work (Donoso-Barros, 1958b) he provided measurements and descriptions of an adult male, female, and juvenile, and photographs of an adult female of *C. jamesi*. He pointed out that Codoceo (1950) had listed this species under the name *Liolaemus multiformis multiformis*, and believed the error was due to their possession of convergent structures. Donoso-Barros (1958b) then listed the differences that distinguish *Ctenoblepharys* from *Liolaemus multiformis*.

Marx (1960) described *Ctenoblepharys schmidtii* from 40 miles east of San Pedro de Atacama, Antofagasta Province, Chile. Following Donoso-Barros (1958b), he recognized *C. adspersa*, *C. stolzmanni*, and *C. jamesi* as belonging to the genus, and provided a key to these four species.

Donoso-Barros (1966) provided a brief description of *Ctenoblepharys*; however, although *C. adspersa* was mentioned as the nominal form of the genus, no description of the species was given because only the lizards of Chile were included. In the same work, he transferred *Helocephalus nigriceps* Philippi, 1860, of the Atacama desert of Chile, to *Ctenoblepharys*. This species has had a long and complex taxonomic history tangled with that of *Ctenoblepharys*. Boulenger (1885) recognized *Helocephalus nigriceps* but considered *Leiosaurus multipunctatus* Burmeister, 1861, and *Liolaemus marmoratus* Burmeister, 1861, to be its synonyms. *Leiosaurus mul-*

tipunctatus is currently considered a synonym of *Pristidactylus scapulatus* (Etheridge and Williams, 1985). Burmeister's (1861) *Liolaemus marmoratus* was transferred to *Phrynosaura* by Müller (1928), to *Ctenoblepharys* by Cei (1974), and back to *Liolaemus* by Cei (1980a); then Cei (1981) provided it with the substitute name *L. pseudoanomalus* because of the preoccupation of *L. marmoratus* Burmeister, 1861, by *L. marmoratus* Gravenhorst, 1837 (= *Tropidurus nitidus* Wiegmann, 1834). Laurent (1984a) placed this species in his newly described genus *Ceiolema*, thus reverting the name to *Ceiolema marmoratus*. Lataste (1892) considered *Helocephalus nigriceps* to be a synonym of *Ctenoblepharys adspersa*, Koslowsky (1898) considered it to be a variety of *Liolaemus signifer* Duméril and Bibron, 1837, and Burt and Burt (1933) referred to it as a subspecies of *L. signifer*. Hellmich (1934) recognized *Helocephalus* as a subgenus of *Liolaemus*.

Donoso-Barros (1969) synonymized *Liolaemus lentus* Gallardo, 1966, with *Phrynosaura wernerii* Müller, 1928, and transferred *Liolaemus anomalus* Koslowsky, 1896, to *Ctenoblepharys*, based on its presumed morphological and ecological similarities with *C. nigriceps* and *C. schmidtii*. This action was followed by Peters and Donoso-Barros (1970), who stated that their justification had not yet been published, but was in a manuscript prepared by Donoso-Barros; the latter presumably referred to the work, cited above, that had actually appeared in the previous year. Donoso-Barros (1971, 1972) examined a specimen said to be the type of *Ctenoblepharys adspersa* in the Museum of Natural History of Neuchâtel, and the type specimen of *Phrynosaura reichei* in the Zoological Museum of the University of Concepción, Chile. He concluded that both species were valid, but that they were congeneric, and so placed *Phrynosaura* in the synonymy of *Ctenoblepharys*.

Cei (1974) reviewed the taxonomic history of *Ctenoblepharys* and recognized 11 species in the genus: *C. adspersa*, *C. anomalus*, *C. marmoratus*, *C. nigriceps*, *C. schmidtii*, *C. wernerii*, *C. reichei*, *C. jamesi*, *C. stolzmanni*, and two described as new from central Argentina, *C. donosobarrosi* and *C. rabinoi*. In

the following year, Cei et al. (1975) recognized the similarity of *Liolaemus multima-culatus* and *Ctenoblepharys rabinoi*, and transferred the former to *Ctenoblepharys*. Cei (1979a) returned *C. anomalus* to *Liolaemus*, and placed *Phrynosaura werneri* in its synonymy. Subsequently Cei (1979b) reexamined the basis for placing the remaining species in *Ctenoblepharys*, and concluded that these forms "exhibit a spectrum of common structural characteristics that are apparently adaptive to live in an arid, sandy environment" and also that "several unrelated, geographically noncontiguous groups of species are involved." He limited *Ctenoblepharys* to include only *C. adspersa*, *C. stolzmanni*, *C. reichei*, and *C. nigriceps* and returned the remaining forms to *Liolaemus*.

Núñez and Yáñez (1983) described *Ctenoblepharys audituvelatus* from San Pedro de Atacama on the Atacama Plateau, Segunda Región, northern Chile, referring it to this genus on the basis of the characteristics cited by Cei (1979b). The same authors (Núñez and Yáñez, 1984b) then described two new genera from northern Chile, *Abas* and *Velosaura*, resurrected the genus *Phrynosaura*, and redefined *Ctenoblepharys*. In the genus *Abas* were placed *A. anomalus*, *A. pseudoanomalus*, *A. insolitus* Cei and Péfaur, 1982, and *A. fabiani* Yáñez and Núñez, 1983. In *Velosaura* were placed *V. aymararum* Veloso et al., 1982, and *V. jamesi*. In *Phrynosaura* were placed *P. reichei* and *P. audituvelatus*, in *Ctenoblepharys* were placed *C. adspersa*, *C. nigriceps*, and *C. stolzmanni*, and all others were referred to *Liolaemus*. A fourth species of *Ctenoblepharys*, *C. erroneus*, probably from near San Pedro de Atacama in northern Chile, was then added by Núñez and Yáñez (1984a).

Laurent (1984a), primarily based on morphometric comparisons with other Liolaeminae, considered *Ctenoblepharys* to be monotypic, containing only *C. adspersa*. In *Liolaemus* he placed *L. nigriceps*, *L. jamesi*, and *L. schmidtii*. *Ctenoblepharys* and *Phrynosaura* were said to be "closely related," but he stated that there is a wide gap between *C. adspersa* on the one hand and *P. reichei*, *C. stolzmanni*, and *C. audituvelatus* on the other, and thus the latter two were transferred to *Phrynosaura*. He (Laurent, 1984a) also proposed a new genus, *Ceiolaemus*, for *Lio-*

laemus pseudoanomalus and *L. anomalus*, thus removing these species from *Ctenoblepharys* and revalidating the name *Liolaemus marmoratus* Burmeister, 1861, for *Liolaemus pseudoanomalus* Cei, 1981. He (Laurent, 1984a) also agreed with Cei (1979b) that *Ctenoblepharys rabinoi*, *Liolaemus multima-culatus* (Duméril and Bibron, 1837), and *L. riojanus* Cei, 1979b, are not related to *Ctenoblepharys*, and considered these, together with *L. occipitalis* Boulenger, 1885, *L. lutzae* Mertens, 1938, *L. scapularis* Laurent, 1982, *L. wiegmanni* (Duméril and Bibron, 1837), and *L. cranwelli* Donoso-Barros, 1973, to form "a natural group, for which the generic name *Ortholaemus* Girard is available, should it deserve generic or subgeneric recognition." Laurent (1984a) and Núñez and Yáñez (1984b) apparently were not aware of each others' works.

Ortiz-Zapata and Núñez (1986) followed Núñez and Yáñez (1984b) in transferring *C. audituvelatus* to *Phrynosaura*. Ortiz-Zapata (1989a), after studying the lizards in the collection of the Museum of Natural History of Neuchâtel, stated that the description of *Ctenoblepharys adspersa* (Tschudi, 1845) was based on three specimens. He designated one of these, a male (MHNN 2291-1), as the lectotype, and the other two, both females, as paralectotypes, one of which (MHNN 2291-2) remains in the museum at Neuchâtel, the other (NHMW 18905) having been transferred to the Natural History Museum in Vienna.

In their cladistic analyses of iguanian lizards, Etheridge and de Queiroz (1988), and Frost and Etheridge (1989) followed Laurent (1984a) in recognizing *Ctenoblepharys* as monotypic. Etheridge and de Queiroz (1988) considered *Ctenoblepharys* to be the sister taxon of *Vilcunia* + *Liolaemus*. Frost and Etheridge (1989) included *Vilcunia* in the genus *Liolaemus*, and considered the relationships of *Ctenoblepharys*, *Liolaemus*, and *Phymaturus* to be unresolved.

Laurent (1992) summarized his earlier morphometric studies of the genus *Liolaemus* (Laurent, 1984a, 1984b, 1985a), and recognized two large species groups that he earlier (1983a) had referred to as the Chileno and Argentino groups, as subgenera, *L. (Liolaemus)* for the former, and *L. (Eulaemus)*

for the latter. Within *Eulaemus* he recognized a *fitzingerii* group and a *signifer* group, the latter containing *L. jamesi*, *L. schmidtii* and *L. nigriceps*.

MATERIALS AND METHODS

This study was based on an examination of 15 preserved specimens of *Ctenoblepharys adspersa* and two complete skeletons prepared by hand from preserved specimens. Preserved specimens of 107 species of *Liolaemus* and eight species of *Phymaturus*, and skeletons of 86 species of *Liolaemus* and six species of *Phymaturus* were also examined. These specimens, together with exemplars of the putative outgroups *Leiocephalinae* + *Tropidurinae*, *Phrynosomatidae* and *Opluridae*, are listed in Appendix 1. Some data were obtained from literature accounts of species not examined; these also are listed in Appendix 1.

Squamation terminology follows Smith (1946), and osteological terminology follows Oelrich (1956) for the skull, and Etheridge (1964, 1965, 1966) for the postcranial skeleton. Terminology of lateral neck folds follows Frost (1992).

No formal analysis of the internal relationships of *Liolaeminae* was undertaken. However, for the purpose of discussing possible synapomorphies for groups within *Liolaeminae*, the outgroup method was used for the polarization of character-state transformations (Watrous and Wheeler, 1981; Maddison et al., 1984). All remaining *Tropiduridae* (= *Leiocephalinae* + *Tropidurinae*) constitute the first outgroup for *Liolaeminae* (Frost and Etheridge, 1989). According to Pregill (1992), the best candidate for the least apomorphic extant species of *Leiocephalus* is *L. carinatus*, and this species, plus *L. schreibersi* and *L. cubensis* were used as exemplars for *Leiocephalinae*. No phylogeny for the *Stenocercus* group is available, so *S. crassicaudatus*, *S. praeornatus*, *S. chlorostictus*, *S. chrysopygus*, *S. empetrus*, *S. guentheri*, *S. imitator*, *S. modestus*, *S. percultus*, and *S. roseiventris* were used as exemplars of the group. Following the phylogeny of the *Tropidurus* group presented by Frost (1992), *Uranoscodon superciliosus*, *Microlophus occip-*

italis, *M. peruvianus*, *Tropidurus etheridgei*, and *T. hygomi* were used as exemplars.

Of the 12 unrooted networks discovered by Frost and Etheridge (1989), *Opluridae* was the first and *Phrynosomatidae* the second outgroup of *Tropiduridae* in nine; in one (*Opluridae* + *Polychrotidae*) was the first, and *Phrynosomatidae* the second outgroup of *Tropiduridae*; in one, *Phrynosomatidae* was the first and (*Opluridae* + *Polychrotidae*) the second; and in one, *Opluridae* was the first and *Polychrotidae* the second outgroup. For the purpose of this study, *Phrynosomatidae* and *Opluridae* were considered potential second outgroups for *Liolaeminae*. Relationships within *Polychrotidae* have not been resolved (Frost and Etheridge, 1989), and this family was not considered due to time constraints. In the absence of an explicit phylogeny for *Opluridae*, the exemplars chosen were *Chalarodon madagascariensis*, *Oplurus cuvieri*, *O. cyclurus*, *O. quadrimaculatus*, and *O. saxicola*. The studies of Montanucci (1987), de Queiroz (1992), and Wiens (1993a, 1993b) formed the basis for selection of phrynosomatids examined: *Petrosaurus mearnsi*, *P. thalassinus*, *Uta stansburiana*, *U. palmeri*, *Urosaurus graciosus*, *U. nigricaudus*, *U. lah-teli*, *U. ornatus*, *Phrynosoma asio*, *P. douglassii*, *P. orbiculare*, *P. coronatum*, *Uma notata*, *U. exsul*, and *U. scoparia*.

Illustrations of the skulls and vertebrae were prepared by Callie Mack using a camera lucida.

GENUS CTENOBLEPHARYS TSCHUDI, 1845

Ctenoblepharys Tschudi, 1845: 150. Type species: *Ctenoblepharys adspersa* Tschudi, 1845, by monotypy.

Ctenoblepharis: Boulenger 1885: 165. Unjustified emendation of *Ctenoblepharys* Tschudi, 1845 (but see text).

Ctenoblepharys adspersa Tschudi Figures 1, 2

Ct.[enoblepharys] adspersa Tschudi, 1845: 150 (type locality: not given; lectotype [Ortiz, 1989] MHNN 229-1).

Ct.[enoblepharys] adspersa: Tschudi, 1846: 36 (restricted type locality: Hacienda Acaray (11°07'S–77°37'W), 2 leagues from Huacho, in the coastal region).

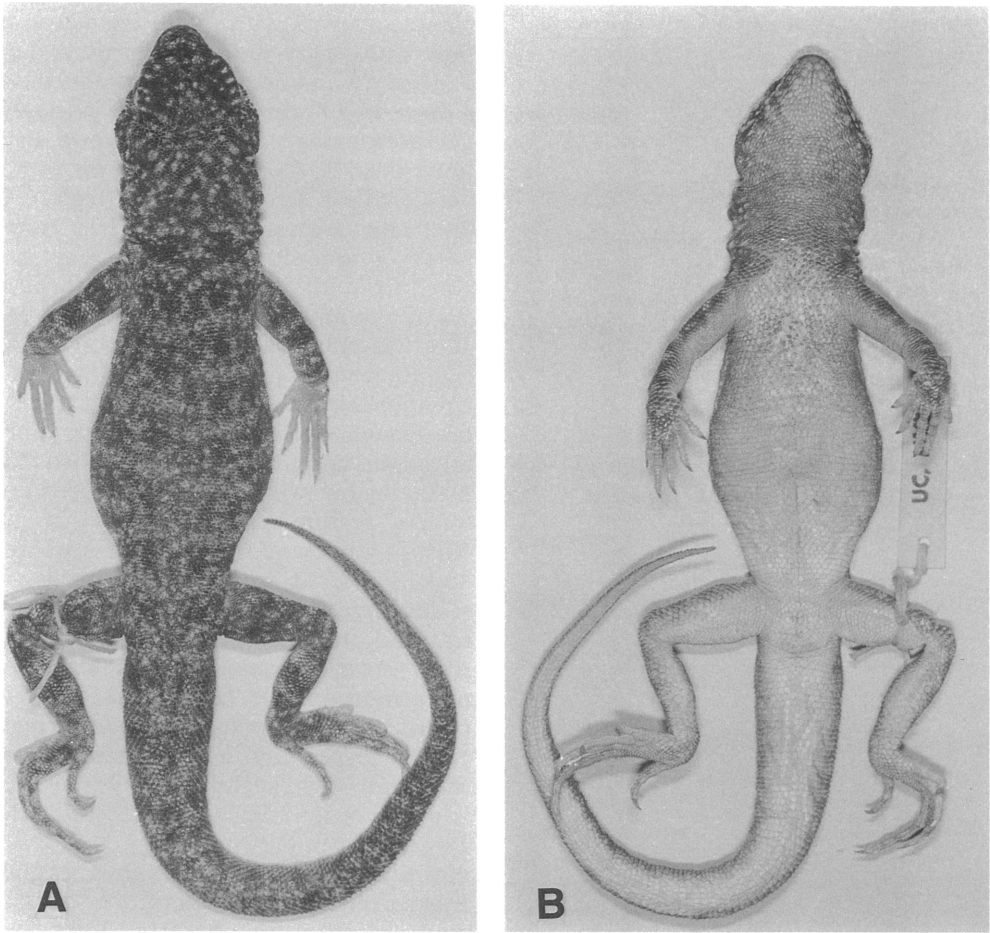


Fig. 1. Adult male *Ctenoblepharys adspersa* (MVZ 85415) from 5.5 km NE San Bartolo, Peru.

Ctenoblepharis adspersus: Boulenger, 1885: 165.
Unjustified emendation of *Ctenoblepharys adspersa* Tschudi, 1845 (but see text).

ETYMOLOGY: The generic name is formed from the Greek words *ktenos*, meaning comb, and *blepharis*, meaning eyelash, presumably in reference to the pronounced, serrate comb formed by the pointed and projecting outer ciliaries. The specific name is from the Latin word *adspersus*, meaning a sprinkling, probably in reference to the dorsal color pattern that is dominated by numerous, scattered whitish dots.

DISTRIBUTION: Sandy beaches and dunes of the Pacific coast of Peru, from Hacienda Acaray (~ 11°05'S, 77°32'W) southward to Paracas (~ 13°50'S, 76°14'W). A specimen

from 6 km N Tacna at 1000 m elevation, was identified by Pearson and Ralph (1978) as *Ctenoblepharys* sp. This locality is about 470 km SW of Paracas, and 46 km inland from the coast, and would represent a considerable range extension if the specimen was one of *C. adspersa*.

DIAGNOSIS: *Ctenoblepharys adspersa* is a lizard of the family Tropiduridae, subfamily Liolaeminae (Frost and Etheridge, 1989) which differs from other members of the subfamily (i.e., *Phymaturus* and *Liolaemus*) in having a wider skull, larger orbits, wider temporal fenestrae, prefrontals wider than long, lacrimal foramen large, a wide maxillary process of the palatines, a short ectopterygoid, the maxillary process of the ectopterygoid

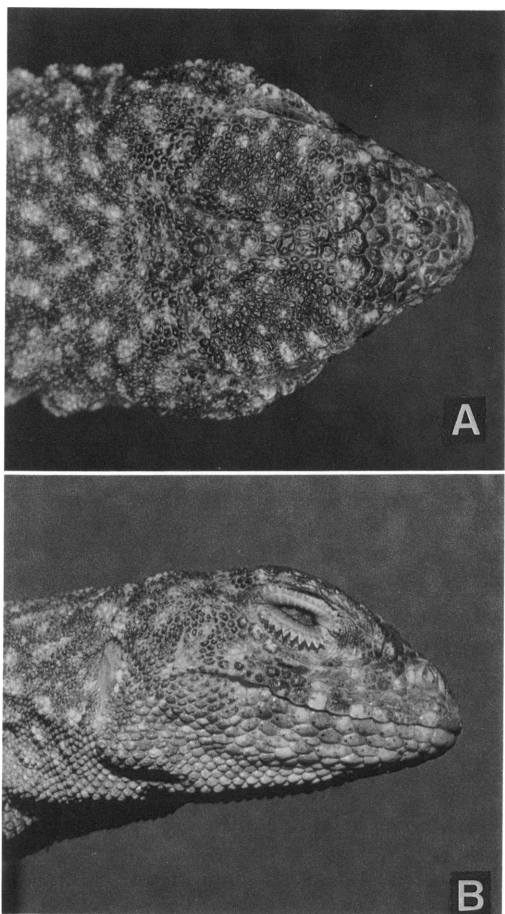


Fig. 2. (A) Dorsal view; (B) lateral view of head of an adult male *Ctenoblepharys adspersa* (MVZ 85415). Scale = 0.5 cm.

truncate, the retroarticular process of the mandible much shorter than the angular process, the parapophyses of the atlas flat and oriented posterolaterally, and the neural arches of the body vertebrae very wide. It further differs from *Liolaemus* in having the lateral borders of the orbitonasal fenestra formed by the prefrontals rather than the frontals, the supratemporal exposed on the lateral surface of the supratemporal process of the parietal, a shorter dentary, a longer angular, and no posterior coracoid fenestra. It further differs from *Phymaturus* in having tricuspid marginal teeth with tapered crowns and small secondary cusps rather than ex-

panded crowns with large secondary cusps, three rather than four sternal ribs, and a slender body with a long, slender tail rather than a depressed body with a short, spinose tail.

DESCRIPTION: Squamation and Proportions (figs. 1, 2): Head large, distinct from neck, widest across temporal region, 0.82–0.92 times wider (as measured across widest part of temporal region) than long (as measured from inferior apex of external auditory meatus to anterior surface of rostral). Snout short (as measured from tip of snout to anterior corner or orbit), 0.29–0.35 times head length, projecting slightly beyond lower jaws; orbit (as measured along its greatest horizontal length) large, 0.43–0.47 times head length. Nasal region swollen, convex in profile; frontonasal region slightly concave in profile. Rostral narrow, 2.60–3.50 times wider than high, bordered by 5–7 postrostrals. Nasal scales large, projecting, separated from rostral and anterior supralabials by two scale rows; nostril oriented anterolaterally, occupying most of scale. Dorsal head scales small, poorly differentiated, somewhat irregularly convex, especially in frontonasal region; in some specimens slightly concave (perhaps due to preservation). Supraorbital semicircles apparent only in prefrontal region; 2 or 3 irregular scale rows, or 1–3 azygous frontals between orbits; supraoculars all very small, subequal, mostly hexagonal, 10–13 in a horizontal line across widest part of supraocular region between superciliaries and frontals; interparietal a little larger than adjacent parietal scales, bordered by 9 or 10 scales, with a distinct “eye”; no pair of enlarged parietals posterior to interparietal. Superciliaries short, not strongly keeled, about 2–3 times longer than wide, anterior 6–7 with oblique sutures, followed by a row of 6–8 small, nonoverlapping scales, preceded by one large anterior and one slightly smaller posterior canthal. Palpebrals small, convex, juxtaposed; inner ciliaries rectangular, about twice as high as wide; outer ciliaries of lower lid 11–14, triangular, sharply pointed distally, altogether forming a strongly projecting serrate comb; outer ciliaries of upper lid 13–18, the anterior and posterior ones triangular, but not as sharply pointed or as strongly projecting as those of lower lid, those in middle of lid more nearly rectangular, scarcely projecting, with

a convex margin. Scales of preocular-subocular-postocular arc 7–10, the third, fourth, or fifth distinctly elongate, about 2–3 times longer than high and with a blunt keel, or none distinctly elongate; suboculars and postoculars swollen, forming an interrupted, strongly projecting shelf. A single row of 9–11 lorilabials, slightly smaller than supralabials, separating suboculars from supralabials. Anterior loreals about equal in size to lorilabials, followed by row of much smaller, often elongate scales between anterior suboculars and lorilabials. Supralabials 7–11, subequal. Temporals small, convex, juxtaposed, with minute interstitial granules, about 14–16 between postocular and anterior margin of ear. External auditory meatus large, obovate, 1.54–1.87 times higher than greatest width, vertical diameter 0.41–0.50 times longitudinal diameter of orbit, bordered by small, convex scales, some slightly enlarged anteriorly, or not differentiated from posterior temporals. Mental small, 0.51–0.76 times as wide as rostral, bordered by two infralabials and two postmentals, not in contact with anterior sublabials. Infralabials 9–10. Gulars small, smooth, convex, oval or rounded, with minute interstitial granules.

Dorsal scales of neck and body small, flat or in some specimens slightly concave (perhaps due to state of preservation), aligned in more-or-less transverse rows, nonoverlapping, with tiny interstitial granules, becoming smaller and strongly convex on the sides, grading gradually into smooth, flat, subimbricate ventral scales. Ventrals rhomboidal with rounded corners, about three times larger than largest dorsals, becoming scarcely imbricate with interstitial granules on posterior abdomen. Scales of precloacal region (fig. 3 A, B) similar to posterior ventrals in both sexes. Precloacal pores 6–8 (\bar{x} = 7.1, sd = 0.8), present in males (N = 8) only. Scales around midbody 95–119 (\bar{x} = 103.9, sd = 6.6); middorsal scales from occiput to point even with anterior margin of thigh 113–135 (\bar{x} = 120.8, sd = 7.0). Lateral nuchal skin folds well-developed and complex: two short folds, one (possibly postauricular) originating at superior, the other at inferior apex of external auditory meatus, converging posteriorly to form, with posterior border of external auditory meatus, a shallow depression, and

continuing posteriorly as longitudinal neck fold, crossed by oblique neck fold and antehumeral fold; no supra-auricular, supernumerary antegular, or antegular folds; gular fold represented laterally by short folds separate medially by 10–12 scales. Lateral nuchal pouches absent.

Limbs moderately slender; hind limbs 0.64–0.78 times snout-vent length. Brachial and antebrachial scales, except preantebrachials, convex, nonoverlapping, with interstitial granules, about equal in size to lateral body scales; several longitudinal rows of smooth, flat, rhomboidal, imbricate preantebrachials, about equal in size to ventral body scales. Suprafemorals, postfemorals, and posterior infrafemorals similar in form to dorsal body scales but smaller; prefemorals similar to ventral body scales, grading into smooth, rounded posterior infrafemorals, with interstitial granules. Supratibials and pretibials small, convex, similar to dorsal body scales; posttibials and infratibials smooth, flat, subimbricate, about equal in size to ventral body scales. Supracarpals and supratarsals smooth, rhomboidal, imbricate; infracarpals and infratarsals imbricate, somewhat projecting, mucronate, some with a tridentate margin. Supradigitals smooth, imbricate, with a slightly concave distal margin on manus, horizontal or slightly convex on pes; distal margin of terminal supradigitals distinctly notched. Lateral digitals triangular, forming a serrate comb, more pronounced on pes. Subdigital lamellae with three or four low, blunt keels, each terminating in a blunt mucron; subdigital lamellae of fourth toe 33–38. Claws long and slender, variable in length perhaps due to wear between shedding cycles; fourth toe claw about as long as 3–5 distal supradigitals.

Tail rather thick and somewhat depressed, 0.53–0.60 percent total length in males, 0.53–0.57 in females; proximal 86–90 percent of tail wider than high, rounded distally. Dorsal and lateral caudal scales like those of dorsal body, becoming subimbricate on middle third of tail, bluntly keeled and weakly mucronate on distal third; ventral caudals, like ventral body scales, becoming more distinctly imbricate, bluntly keeled and mucronate on distal third of tail. Autotomic part of tail with five dorsal and four ventral transverse rows

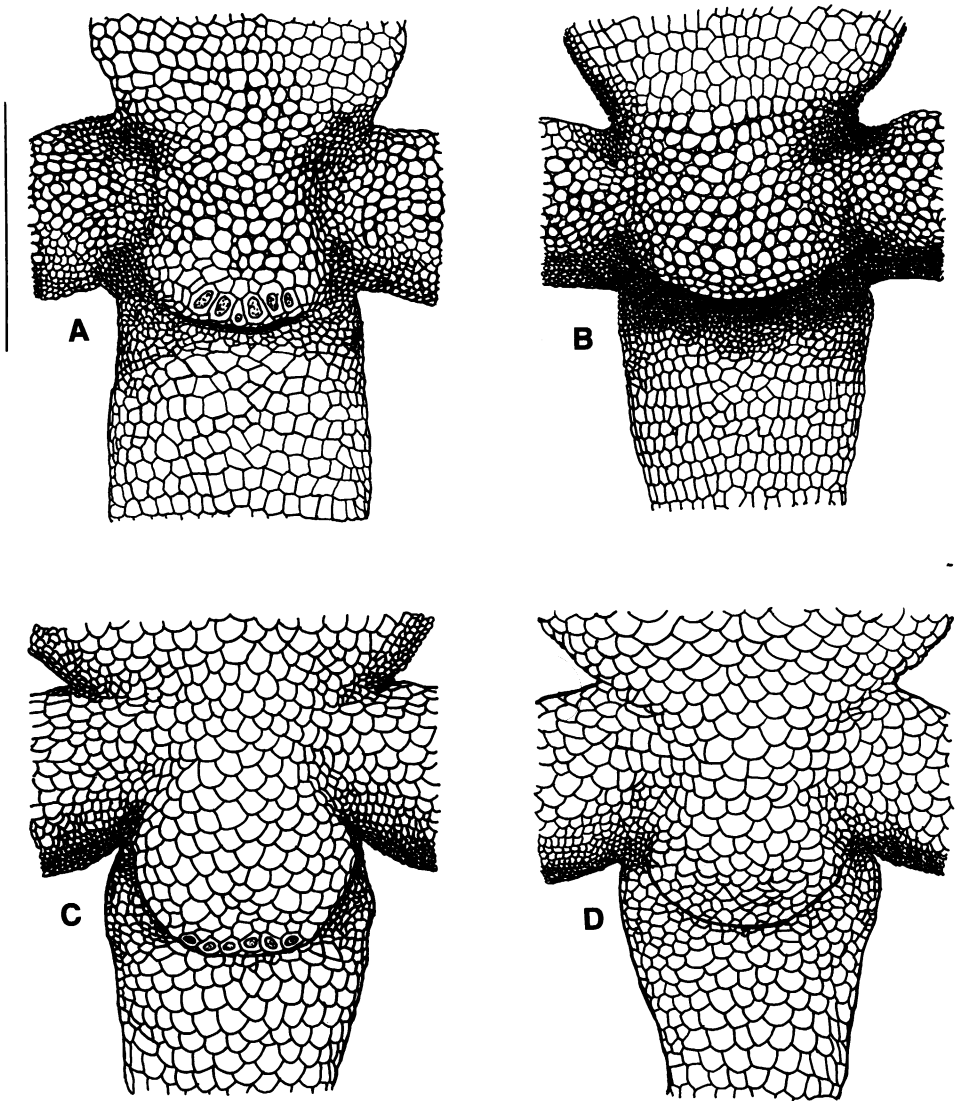


Fig. 3. Ventral view of pygal area of (A) male (MVZ 85415), (B) female (FML 0464) of *Ctenoblepharys adspersa*; and (C) male (SDSU 1532), and (D) female (SDSU 1319) of *Liolaemus multicolor*. Scale = 1.0 cm.

in each segment, the first two dorsal rows in each segment above the first ventral row.

Color Pattern (figs. 1, 2): In preservative, dorsal and lateral surfaces of head medium brown with scattered whitish dots. Palpebrals whitish, those of upper lid with small brown spots; inner ciliaries dark brown proximally, fading to pale tan distally; upper and lower surfaces of outer ciliaries of upper lid, and dorsal surfaces of outer ciliaries of lower lid

pale tan with small brown spots; lower surfaces of lower ciliaries white. Outer ciliaries each with a single light brown scale organ, most of them subterminal in position. Dorsal surfaces of neck, body and tail speckled, with indistinct crossbands of brown or dark gray, alternating with light tan, two on neck and six on body, becoming progressively more obscure distally on tail; banded pattern rendered indistinct by numerous small, whitish

dots. Upper surfaces of limbs similarly banded, also with small, whitish dots. In males, throat and chest light grayish-brown with scattered, small whitish spots, especially prominent on sides; an ill-defined unpigmented zone on anterior chest, between forelimb insertions; remainder of abdomen and ventral surfaces of limbs and tail whitish. Throat of females as in males, other ventral surfaces unpigmented. Color photograph of living individual from Paracas Beach with pattern as above; dark crossbands brownish gray, light background color yellowish tan.

Measurements: Snout-vent length (SVL) of largest male (LACM 49145) 75 mm, tail incomplete; largest female (SMF 75966) 67 mm, tail 80 mm. Measurements of an adult male (MVZ 85415) in millimeters: SVL 72, tail length 110, forelimb 31, hind limb 49, head length (inferior apex of external auditory meatus to rostral) 18.0, maximum head width (across temporal region) 16.2, snout length (anterior corner of orbit to rostral) 5.8, diameter of orbit (between posterior and anterior corner of orbit) 7.5, vertical diameter of external auditory meatus 3.7.

Skeleton: The following descriptions are based on two complete skeletons prepared from preserved specimens. The larger, LACM 49147, is a male 68 mm SVL, with a skull 15.8 mm long. The occipital sutures are partly fused at the condyle, the remaining braincase sutures unfused; scapulocoracoid sutures fused, acetabular sutures partly fused, epiphyses of long bones not fused to diaphyses. Based on these observations, this individual had not attained maximum size. The smaller specimen, REE 2513, is a female, 57 mm SVL, with a skull 13.8 mm long. All sutures remain unfused.

Skull (fig. 4A–C) short and broad, 1.27–1.29 times longer than wide; orbit large, its greatest longitudinal diameter 0.49–0.50 times skull length; snout short, 0.29 times skull length; postorbital part of skull short, 0.20–0.22 times skull length. Nasal process of premaxilla not extremely wide or narrow, posteriorly clamped between nasals; arch formed by premaxillary processes of nasals and nasal process of premaxilla separated from underlying septomaxilla by a wide gap. Nasals wide, not tapering to a point posteriorly between frontal and prefrontals, their

suture with one another extending posteriorly well beyond level of anterior corner of orbits, their sutures with the frontal forming a shallow W. Descending prefrontal processes of frontals short, widely separated from palatines, prefrontals contributing to lateral walls of orbitonasal fenestra. Prefrontal short and wide, much wider than long, flat above, with a slight medial concavity; antorbital process of prefrontal flattened, posterolaterally oriented, strongly projecting. Parietal short and wide, width of anterior margin 1.1–1.4 times length as measured from anterior margin to posterior extremity of supratemporal processes. Parietal foramen formed by a median notch in anterior margin of parietal and an apposing notch in posterior margin of frontal. Postfrontals very small, not or scarcely visible in dorsal view. Supratemporal exposed on lateral face of supratemporal process of parietal, not hidden within groove on ventral face of latter; supratemporal fenestra wide, 1.5–1.6 times longer than wide. Supratemporal process of squamosal without a dorsal hooklike process, separated from contact with parietal by supratemporal.

Lacrimal very small, scarcely visible in lateral view; lacrimal foramen very large, its inferior margin formed by maxilla so that prefrontal fails to contact lacrimal below. Maxillary process of jugal slopes distinctly outward, its lateral aspect tapered anteriorly almost to a point where it contacts the lacrimal.

Interpterygoid vacuity miter-shaped, wide posteriorly, abruptly narrowing at the palatopterygoid suture, continuing forward to separate palatines and posterior portion of vomers from medial contact. Infraorbital fenestra obovate, its anterior margin nearly horizontal due to wide maxillary process of palatine, its posterior margin formed by relatively short, anterolaterally oriented ectopterygoid. Maxillary process of ectopterygoid anteriorly truncate, not tapered to a point. Basisphenoid short and wide, its pterygoid processes short and widely divergent, its speno-occipital processes short, not extending to speno-occipital tubercles.

Meckel's groove unfused, its upper and lower borders in contact between teeth 10–14, open from tooth 9 to mandibular symphysis, occupied by splenial under teeth 15–

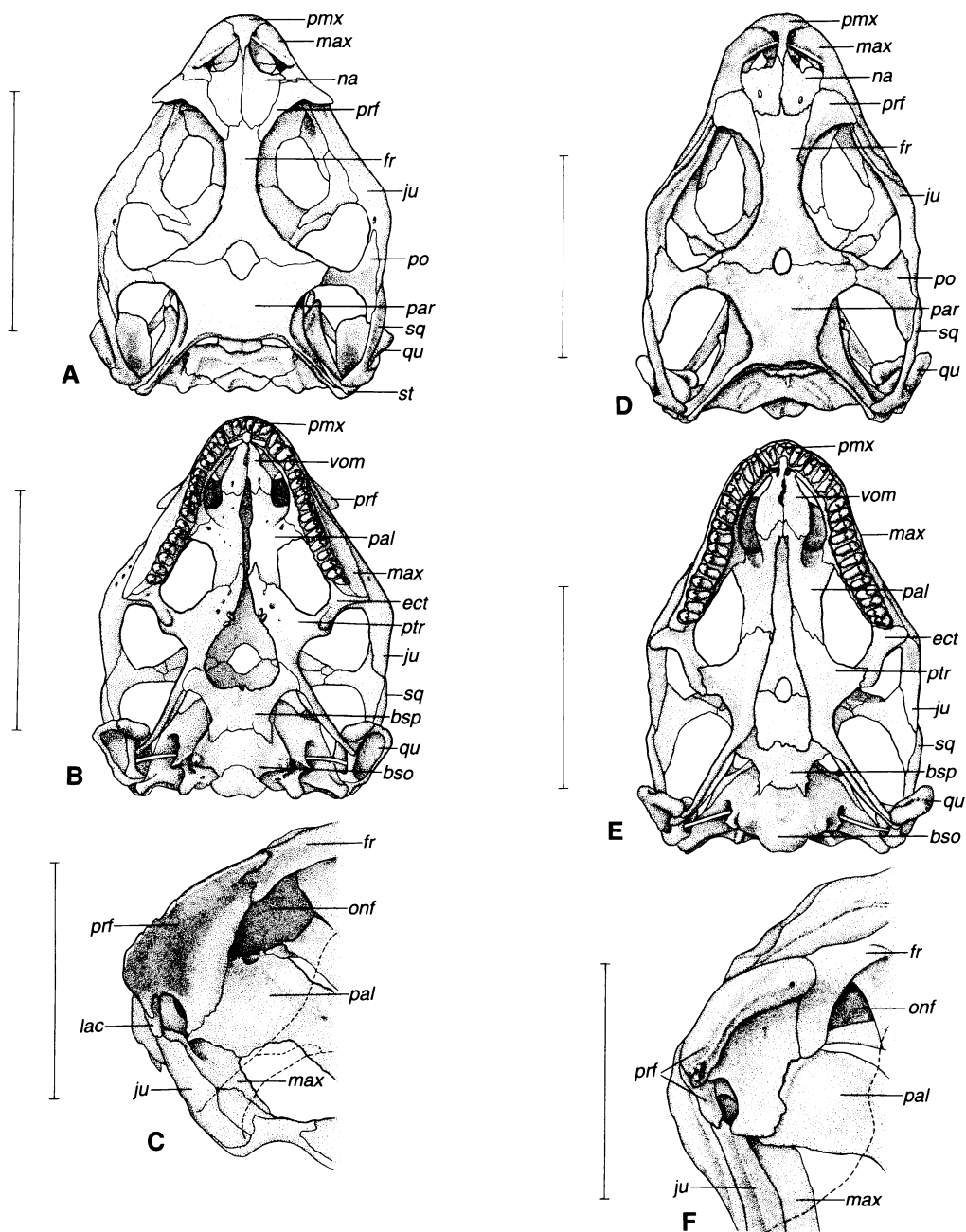


Fig. 4. Skulls of (A-C) *Ctenoblepharys adspersa* (LACM 49147) and (D-F) *Liolaemus nigriceps* (REE 2537); A, D dorsal view; B, E ventral view; C, F view of anterior wall of left orbit. Abbreviations: bso—basioccipital, bsp—basisphenoid, ect—ectopterygoid, fr—frontal, ju—jugal, lac—lacrimal, max—maxilla, na—nasal, onf—orbitonasal fenestra, par—parietal, pmx—premaxilla, po—postorbital, prf—prefrontal, ptr—pterygoid, qu—quadrate, sq—squamosal, st—supratemporal, vom—vomer. Scales for A, B, D and E = 1 cm; for C and F = 0.5 cm.

20. Angular large, labial process wide, lingual process narrow, extending forward to position of last tooth of dentary; posterior mylohyoid foramen not apparent. Splenial large, extending forward between inferior apex of posterior lingual process of coronoid to level of dentary tooth number 15; anterior mylohyoid foramen represented by one or two openings between inferior margin of anterior splenial and dentary; anterior inferior alveolar foramen represented by a notch in dentary, with superior margin of anterior splenial forming inferior border. Posterior limit of dentary on labial face of mandible about even with posterior margin of posterior lingual process of coronoid. Labial process of coronoid constricted proximally, well separated from anterior supra-angular foramen. Retroarticular process short, shorter than angular process.

All marginal teeth slightly tapered, with crowns slightly compressed linguolabially, and slightly curved inward. Both upper and lower jaws with 20 teeth on each side. Premaxilla with six simply pointed teeth; first four maxillary teeth similar to premaxillary teeth, followed by 13 tricuspid teeth with small secondary cusps. Anterior 6–8 dentary teeth simply pointed, followed by 12–14 tricuspid teeth with small secondary cusps. Pterygoids with 1–3 small, pointed teeth; palatine teeth absent.

Parapophyses of atlas somewhat flattened, posteriorly oriented and tapering distally. Presacral vertebrae 23, all with an unusually wide neural arch and slight constriction between zygapophyses (fig. 5A). Ratios based on measurements of 11th vertebra are: (1) maximum length of neural arch, including zygapophyses, divided by narrowest width of arch between zygapophyses 0.98–1.00; (2) maximum length of neural arch divided by maximum width across prezygapophyses 0.78–0.88; (3) ventral length of centrum, excluding condyle, divided by narrowest width of neural arch between zygapophyses 0.69. Caudal vertebrae 43, the first eight nonautotomic, with posterolaterally oriented processes, the anterior ones projecting not quite as far as sacral diapophyses; remaining autotomic caudal numbers 9–23 with slender, laterally oriented processes, numbers 24–32 with anterolaterally oriented processes; all

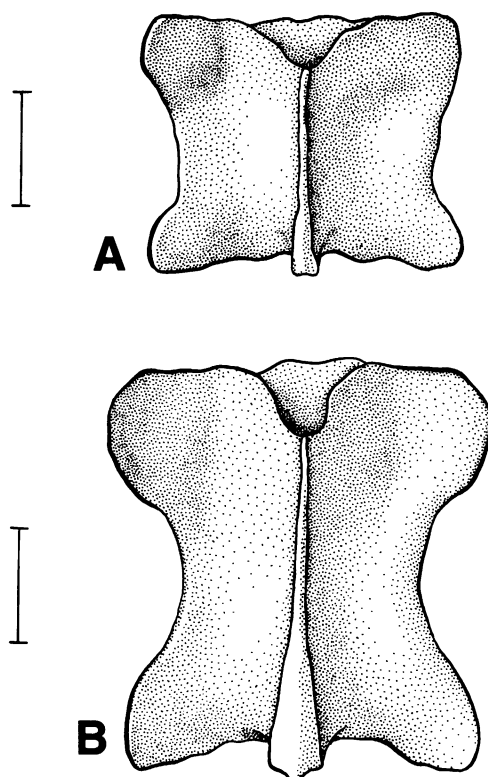


Fig. 5. Dorsal view of the 11th body vertebra of (A), *Ctenoblepharys adspersa* (LACM 49247); and (B), *Liolaemus nigriceps* (REE 2537). Scale = 1.0 mm.

processes gradually reduced in length posteriorly, absent on vertebrae 33 through 43.

Proximal (interclavicle) process of clavicle expanded posteriorly to form a thin plate, fenestrate or not on one or both sides, with posterior margin irregular or forming a smooth curve; proximal process about equal in length to distal (suprascapular) process, the latter narrow and rounded. Interclavicle arrow-shaped, proximal 65 percent of lateral processes contacting posterior margins of clavicles, medial process widest just anterior to sternum, extending posteriorly into sternal fontanelle to about level of articulations of second pair of sternal ribs. Scapulocoracoid and primary coracoid fenestrae large; scapular fenestra absent, with no trace of thinning in the scapula; secondary coracoid fenestra absent, but a thin region present between secondary coracoid ray and coracoid plate. Su-

prascapula curves gradually dorsomedially above scapula-suprascapular suture. Sternum pentagonal, articulating laterally with three pair of sternal ribs and posteriorly with xiphisternal rods; fontanelle a narrow oval, about three times longer than wide. Two pair of xiphisternal ribs, lacking free posterior extensions of xiphisternal rod. Pubic tubercle of pelvis flattened vertically.

Long bones of appendicular skeleton gracile; metacarpal of fourth digit about as long as combined length of metacarpal and proximal phalanx of fifth digit; proximal and distal phalanges of fifth digit about equal in length; femur with a distinct sigmoid curve; tibia without a posterior distal bladeliike process; distal extremity of distal penultimate phalanx of fifth toe extends slightly beyond distal extremity of metatarsal of fourth toe. Plantar tubercles of fifth metatarsal widely separated. Claws slightly over 1.5 times length of penultimate phalanx.

Muscles (fig. 6A): Medial head of *M. flexor tibialis internus* exposed, not covered by hypertrophied *M. puboischiotibialis*. Insertion of *M. tibialis anterior* not hypertrophied. Melanic pigment not present within median portion of epimysium of *M. pterygomandibularis*.

RELATIONSHIPS OF *LIOLAEMUS*, *CTENOBLEPHARYS*, AND *PHYMATURUS*

For the purpose of this discussion, and in the remainder of this work, all of the species of *Liolaeminae* except for *Ctenoblepharys adspersa* and those referred to *Phymaturus*, are included in the genus *Liolaemus* (sensu lato). Evidence for monophyly of this taxon will be given below. Thus, the generalizations as to character states of *Liolaemus* described below also apply to the species that have, at one time or another, been referred to *Ctenoblepharys* (except the type), as well as to those referred to *Abas*, *Ceiolaemus*, *Eulaemus*, *Mesolaemus*, *Ortholaemus*, *Pelusaemus*, *Phrynosaura*, *Rhytidodeira*, *Velosaura*, and *Vilcunia*. This action does not necessarily imply that any one of these taxa is not monophyletic, but rather that all of them are members of a single clade that does not include *Phymaturus* or *Ctenoblepharys adspersa*. I

also point out here that the status of *Ctenoblepharys erroneus* remains uncertain. The unique type, which I have not examined, is said to lack projecting outer ciliaries and the tail is shorter than the snout-vent length, but it has poorly differentiated cephalic scales and a truncate snout (Núñez and Yáñez, 1984b). In view of its lack of a ciliary comb and its short tail, and its locality in the Atacama desert of northern Chile, it seem unlikely that this species will be referred to *Ctenoblepharys*.

Cei (1986) recognized four species of *Phymaturus* under the generic name *Centrura*: *P. flagellifer* (= *P. palluma*), *P. mallimaccii*, *P. punae* and *P. patagonicus*, the latter with six subspecies: *P. p. patagonicus*, *P. p. indistincta*, *P. p. nevadoi*, *P. p. payunae*, *P. p. somuncurensis*, and *P. p. zapalensis*. Pereyra (1985, 1991) recently described a fifth species, *P. antofagastensis*. The subspecies of *P. patagonicus* are diagnosable on the basis of squamation, proportions, color pattern, and the presence or absence of sexual dichromatism; and, they are all allopatric, with no evidence of intergradation (Cei and Castro, 1973; Cei and Roig, 1975; Cei, 1986). They therefore appear to meet the criteria for evolutionary species sensu Frost and Hillis (1990) and Frost et al. (1992), and for this reason are here elevated to specific rank. Nevertheless, the species of *Phymaturus* fall into two groups that are phenetically similar in squamation and skeletal morphology, the *P. palluma* group (*P. antofagastensis*, *P. palluma*, *P. punae*, and *P. mallimaccii*) characterized by a larger adult body size (maximum snout-vent length 95–110 mm), more strongly spinose caudal scales, and more fragmented head scales, including several rows of lorilabials and the absence of an elongate subocular, an open Meckel's groove, and a large splenial that extends at least as far forward as the midpoint of the dentary tooth row. The *P. patagonicus* group (*P. patagonicus*, *P. indistinctus*, *P. nevadoi*, *P. payunae*, *P. somuncurensis*, and *P. zapalensis*) is characterized by the alternatives to the above character states.

Comparisons of the skeleton and integument of *Ctenoblepharys adspersa* with *Phymaturus* and *Liolaemus* indicate that *C. adspersa* possesses a large number of charac-

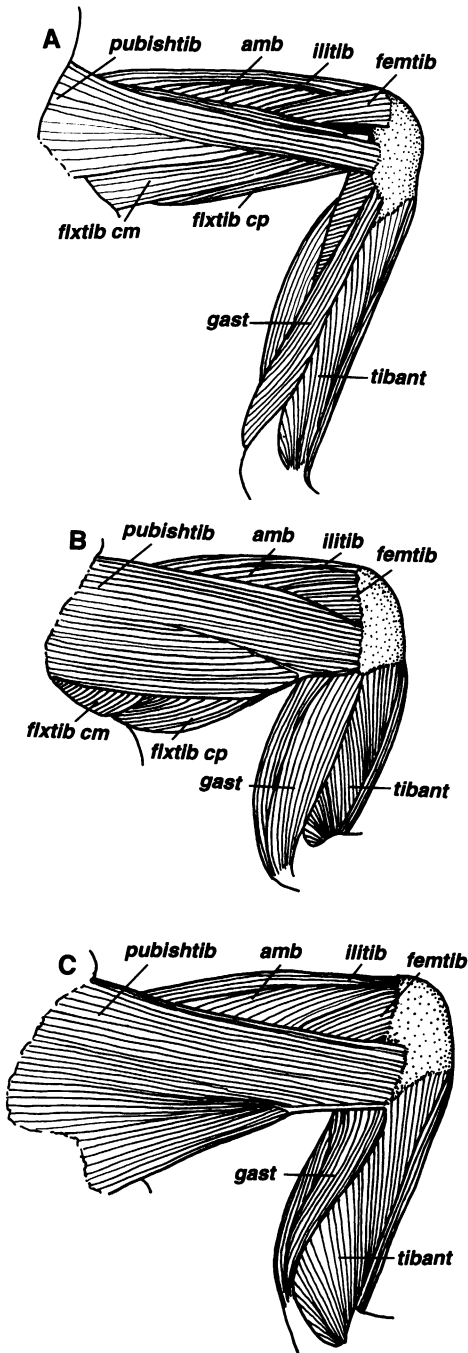


Fig. 6. Dorsal view of the musculature of the right hind limb of (A) male *Ctenoblepharys adspersa* (LACM 49147), (B) female *Liolaemus fuzingerii*, (SDSU 1191) and (C) male *Liolaemus elongatus* (SDSU 1857). Abbreviations: amb—M. ambiens, femtib—M. femorotibialis, flxtib cm—M. flexor tibialis internus capitis medialis, flxtib

teristics, chiefly of the skeleton, not found elsewhere in Liolaeminae. These are (1) skull wide, length/width ratio 0.77–0.79 (0.63–0.72 in *Phymaturus*, 0.63–0.74 in *Liolaemus*); (2) orbit large, skull/orbit ratio 1.99–2.04 (2.18–2.92 in *Phymaturus*, 2.12–2.72 in *Liolaemus*); (3) temporal fenestra wide, length/width ratio 1.49–1.59 (1.78–3.10 in *Phymaturus*, 1.72–3.57 in *Liolaemus*); (4) median suture between nasal bones extends posteriorly far beyond level of anterior corner of orbits (rather than to about level of anterior corner of orbits), (5) prefrontal much wider than long, the antorbital process prominent and strongly projecting (approached in some species of *Liolaemus*, e.g., *L. anomalus*, *L. pseudoanomalus*); (6) lacrimal bone reduced, not forming inferior margin of lacrimal foramen (rather than large and forming inferior margin of lacrimal foramen; lacrimal absent in *L. nigriceps*); (7) lacrimal foramen very large; (8) maxillary process of jugal externally tapering almost to a point (rather than truncate); (9) orbital surface of jugal slopes strongly outward (rather than vertical or slopes slightly outward); (10) palatines and posterior vomers not in medial contact (rather than vomers always in full contact and usually also palatines in contact anteriorly); (11) anterior margin of infraorbital fenestra nearly horizontal due to wide maxillary process of palatine (rather than rounded, with narrow maxillary process of palatine); (12) ectopterygoid short, that part forming posterior margin of infraorbital fenestra shorter than that part of palatine forming medial margin of foramen (rather than long, that part forming posterior margin of infraorbital foramen longer than that part of palatine forming medial margin of foramen); (13) ectopterygoid orientation more nearly lateral than anterolateral; (14) dorsal aspect of maxillary process of ectopterygoid truncate (rather than pointed); (15) retroarticular process of mandible much shorter than angular process (rather than equal to or longer); (16) par-

←

cp—M. flexor tibialis internus capitis posterior, gast—M. gastrocnemius, ilitib—M. ilirotibialis, pubishtib—M. puboischiotibialis, tibant—M. tibialis anterior.

apophyses of atlas flat and oriented posterolaterally (rather than round and laterally oriented); and (17) neural arch of body vertebrae very wide, arch of 11th vertebra length/width ratio 0.98–1.08 (1.26–1.84 in *Phymaturus*, 1.12–1.81 in *Liolaemus*).

There appear to be no characteristics of squamation in *Ctenoblepharys adspersa* that are unique within Liolaeminae, although several are found in only a few species. The small, undifferentiated head scales, including numerous subequal supraoculars and parietals of *C. adspersa*, appear to occur in only *Liolaemus erroneus*. As in *Ctenoblepharys adspersa*, the mental is narrower than the rostral in most individuals of *Phymaturus*, and in those species of *Liolaemus* assigned to *Ortholaemus* by Laurent (1984a), but in the latter the mental has a different shape due to its contact with the anterior sublabials. A subocular fragmented into several short scales also occurs in the *Phymaturus palluma* group and in *Liolaemus stolzmanni* and *L. erroneus*. The pattern of dorsal body scales in *Ctenoblepharys adspersa*, i.e., small, flat, oval or rounded, nonoverlapping scales arranged in more-or-less transverse rows with conspicuous interstitial granules, is not exactly matched in any other Liolaeminae, although similar patterns of subimbricate to nonoverlapping scales with interstitial granules occur in a number of species of *Liolaemus*, e.g., *L. anomalus*, *L. audituvelatus*, *L. pseudoanomalus*, *L. stolzmanni*, *L. schmidtii*, *L. insolitus*, *L. nigriceps*, *L. reichei*, and *L. andinus*.

Osteological character states shared by *Ctenoblepharys adspersa* and *Phymaturus*, but not found in *Liolaemus*, are: (1) lateral borders of orbitonasal fenestra formed by prefrontals (fig. 4A), (2) supratemporal exposed on lateral face of paraoccipital process of parietal, (3) dentary short, not extending posteriorly beyond posterior lingual process of coronoid, (4) anterior process of angular long, extending forward to level with posterior dentary tooth, and (5) posterior coracoid fenestra absent. Alternative states of these characters found in *Liolaemus* are: (1) lateral borders of orbitonasal fenestra formed entirely or almost entirely by frontal downgrowths (fig. 4F), (2) supratemporal mostly or entirely enclosed within a deep groove on

the ventral surfaces of the paroccipital process of parietal (Frost and Etheridge, 1989; fig. 2C), (3) dentary long, extending well beyond posterior lingual process of coronoid (except in a single specimen of *L. sylvanae* [MCZ 156906]), (4) anterior process of angular reduced or absent, not extending forward beyond level of posterior lingual process of coronoid, and (5) posterior coracoid fenestra present (rarely absent as an individual variant).

In *Ctenoblepharys adspersa* and *Phymaturus*, the cloacal region (the triangular region between the hind limb insertions and vent) of males is about the same size as in females, but in *Liolaemus* it is much larger in males, due to the anterior location and hypertrophy of the anterior retractor muscles of the hemipenes (Arnold, 1984) (fig. 3C, D). In most *Liolaemus* males the scales in the central part of this region are approximately the same size as the ventral body scales, whereas they are conspicuously reduced in females. In *C. adspersa* and *Phymaturus* the scales of this region are the same size in both sexes. Although Arnold (1984) stated that the anterior retractor muscle was larger in *Ctenoblepharys* and *Liolaemus* than in *Phymaturus*, he has informed me (Arnold, personal commun., 1989) that his specimens of *Ctenoblepharys adspersa* were, in fact, specimens of *Liolaemus monticola chillensis* (BMNH 1910.9.20.7–9).

Although absent in *Phymaturus* and *Ctenoblepharys adspersa*, in a large number of *Liolaemus*, melanic pigment is present within the median portion of the epimysium of the M. ptergomandibularis, the medial head of the M. flexor tibialis internus is covered by a hypertrophied M. puboischiotibialis, and the insertion of the M. tibialis anterior is hypertrophied in association with the presence of a sharp, blade-like process of the tibia (Ceï, 1993: fig. 36) (fig. 6C). The tibial blade character was first described and illustrated for *Liolaemus occipitalis* by Keller and Krause (1986). These character states have been confirmed in 58 species of *Liolaemus* (Appendix 2), including *L. multimaculatus*, *L. nigriceps*, *L. jamesi*, *L. schmidtii*, *L. donosobarrosi*, *L. rabinoi*, and *L. audituvelatus*, all of which, at one time or another, have been referred to *Ctenoblepharys*. A pigmented epimysium of

the *M. pterygomandibularis* and a hypertrophied *M. puboischiotibialis* also occur in *L. anomalus* and *L. pseudoanomalus*, but a tibial blade and a hypertrophied *M. tibialis anterior* are lacking in these species. All other *Liolaemus* examined (57 species), as well as *Ctenoblepharys*, *Phymaturus*, other Tropiduridae, Phrynosomatidae, and Opluridae, lack melanic pigment in the epimysium of *M. pterygomandibularis*, a tibial blade is lacking, and the *M. puboischiotibialis* and *M. tibialis anterior* are not hypertrophied (Hoyos, 1990; personal obs.).

Of the character states found in *Ctenoblepharys adspersa* that are unique within Liolaeminae, the following likewise do not occur in other Tropiduridae, nor in Opluridae or Phrynosomatidae, and are thus presumed to be autapomorphies for the species: (1) skull wide, length/width ratio 0.77–0.79 (0.57–0.71 in other Tropiduridae, 0.58–0.73 in Phrynosomatidae, 0.62–0.70 in Opluridae), (2) orbit large, skull/orbit ratio 1.99–2.04 (2.08–2.48 in other Tropiduridae, 2.13–2.64 in Phrynosomatidae, 2.13–2.61 in Opluridae); (3) median suture between nasals extends posteriorly far beyond anterior corner of orbits, (4) lacrimal bone very small, not forming part of inferior margin of lacrimal foramen (lacrimal absent in some phrynosomatids), (5) lacrimal foramen large, (6) anterior margin of infraorbital fenestra nearly horizontal due to wide maxillary process of palatine, (7) maxillary process of ectopterygoid truncate, (8) parapophysis of atlas flat and oriented posterolaterally, and (9) neural arch of body vertebrae very wide, length/width ratio of 11th vertebra 0.98–1.08 (1.53–2.04 in other Tropiduridae, 1.46–1.62 in Phrynosomatidae, 1.57–1.71 in Opluridae).

All of the character states listed earlier as shared by *Ctenoblepharys* and *Phymaturus* to the exclusion of *Liolaemus* are judged to be plesiomorphic based on comparisons with other Tropiduridae, Phrynosomatidae, and Opluridae, and the alternative states listed for *Liolaemus* are therefore interpreted as evidence for the monophyly of those Liolaeminae exclusive of *Phymaturus* and *Ctenoblepharys adspersa*, i.e., *Liolaemus sensu lato*.

The question of relationships of *Phymaturus*, *Ctenoblepharys*, and *Liolaemus* re-

mains. In their cladistic analysis, Frost and Etheridge (1989) found two topologies that are independent of network. In Topology 1, *Phymaturus* was the sister taxon of *Ctenoblepharys* + *Liolaemus*, and in Topology 2 *Liolaemus* was the sister taxon of *Phymaturus* + *Ctenoblepharys*. In Topology 1 the linkage of *Ctenoblepharys* with *Liolaemus* was supported by the supratemporal fitting in a groove of the supratemporal process of the parietal. Unfortunately, this character was incorrectly coded for *Ctenoblepharys*. In *Ctenoblepharys*, as in *Phymaturus*, the supratemporal occupies its primitive position on the lateral face of the supratemporal process of the parietal. In Topology 2, the linkage of *Ctenoblepharys* with *Phymaturus* is supported by the presence of a divided subocular, present in *C. adspersa* and in the *P. palluma* group, but not the *P. patagonicus* group. Frost and Etheridge (1989) also pointed out that Arnold (1984) noted the presence of a well-defined fleshy insertion of the *M. retractor lateralis* posterior of the hemipenis as a possible synapomorphy for the *Liolaemus* group (i.e., Liolaeminae), and that it is better developed in *Ctenoblepharys* and *Liolaemus* than in *Phymaturus*. However, as pointed out above, Arnold's specimen representative of *Ctenoblepharys* was actually a specimen of *Liolaemus monticola*. Thus, there are no known derived features shared by *Phymaturus* and *Ctenoblepharys* to the exclusion of *Liolaemus*, nor are there any derived features shared by *Ctenoblepharys* and *Liolaemus* to the exclusion of *Phymaturus*, or by *Phymaturus* and *Liolaemus* to the exclusion of *Ctenoblepharys*. Relationships of the three Liolaeminae genera therefore remain unresolved.

COMMENTS ON THE STATUS OF THE
GENERA *ABAS*, *CEIOLAEMUS*,
PELUSAURUS, *PHRYNOSAURA*,
RHYTIDODEIRA, *VELOSAURA*, AND
VILCUNIA, AND THE SUBGENERA
EULAEMUS, *LIOLAEMUS SENSU*
STRICTO, *MESOLAEMUS*, AND
ORTHOLAEMUS

Monophyly of *Liolaemus* appears to be well supported by the possession of frontal downgrowths that exclude (or nearly exclude) the

prefrontals from the orbitonasal fenestra, the supratemporal mostly or entirely enclosed within a deep groove on the ventral surface of the paroccipital process of the parietal, a long dentary that extends posteriorly well beyond the posterior lingual process of the coronoid, the anterior process of the angular reduced or absent, the presence of a posterior coracoid fenestra, and the anterior location and hypertrophy of the anterior retractor muscles of the hemipenes. However, generic or subgeneric status has been proposed for several groups of species within *Liolaemus*. In this section, their status as monophyletic subsets of *Liolaemus* will be discussed.

ABAS

Núñez and Yáñez (1984b) described *Abas*, and included in it *L. anomalus*, *L. pseudoanomalus*, *L. insolitus* Cei and Péfaur, 1982, and *L. fabiani* Yáñez and Núñez, 1983, the latter designated as the type. The genus was characterized as having (1) eyelids with a short comb, (2) diameter of eye less than length from anterior border of eye to rostral scale, (3) tail equal to or longer than snout-vent length, (4) head scales differentiated, (5) profile isognathus, (6) loreal region slightly depressed, and (7) dorsal scales imbricate and smooth, without companion scales (my translation). My examination of these species indicates that not all of them have a short comb on the eyelid; the outer lower ciliaries of *L. anomalus* and *L. pseudoanomalus* are more projecting and more nearly pointed than in *L. fabiani* and *L. insolitus*. In most species of *Liolaemus* the diameter of the orbit is less than the length of the snout, the head scales are differentiated, the profile is isognathus, and the loreal region is slightly depressed. The tail is shorter than the snout-vent length in *L. insolitus* (also shown by the measurements in Cei and Péfaur [1982: table 2]) and in female *L. pseudoanomalus*, and the dorsal body scales are nonoverlapping, with conspicuous interstitial granules in all four species. The characteristics said to be shared by the species allocated to *Abas* (Núñez and Yáñez, 1984b) either do not apply to all of them, or are shared with most other species of *Liolaemus*. Furthermore, *L. fabiani* and *L. insolitus* possess a tibial blade and hyper-

trophied *M. tibialis* anterior, while *L. anomalus* and *L. pseudoanomalus* do not. Thus, monophyly of *Abas* is unsupported.

CEIOLAEMUS

Laurent (1984a) described *Ceiolaemus*, including in it *C. anomalus* and *C. marmoratus* (= *pseudoanomalus*), and designated the latter as its type species. It was distinguished from *Phymaturus* by its larger and less numerous scales and from other *liolaemine* genera by a number of morphometric characters, plus palatine teeth and smooth dorsal scales. Palatine teeth do not occur in any tropidurid lizards, and it seems likely that this actually was a reference to the presence of pterygoid teeth, which are present in most *Liolaemus*, including both *Liolaemus anomalus* and *L. pseudoanomalus*. Also, smooth dorsal scales occur in a number of other *Liolaemus*. The two species are, however, phenetically extremely similar in squamation, skeletal morphology, and dorsal color pattern, and may well be sister taxa.

PELUSAURUS

Donoso-Barros (1973) described *Pelusauros*, and *P. cranwelli* as its only species, based on a single female from Macho, Nueva Moka (17°19'S, 63°33'W), Santa Cruz Prov., Bolivia. Laurent (1983b) pointed out the similarity of this species to *Liolaemus wiegmanni* (Duméril and Bibron, 1837), and assigned it to the subgenus *Ortholaemus*. I have compared the unique type (MACN 3632) with specimens of *L. wiegmanni* and find the squamation and color pattern of the type to be well within the limits of variation of *L. wiegmanni*, although Laurent (1983b) indicated that there may be proportional differences. The locality for *L. wiegmanni* most proximate to that of *L. cranwelli* is Yuto (23°38'S, 64°28'W), Depto Ledesma, Prov. Jujuy, Argentina (FML 256[2], 258[5]), approximately 680 km to the south. *Pelusauros cranwelli* may be a synonym of *Liolaemus wiegmanni*, or if valid, likely its sister taxon.

PHRYNOSAURA

Werner (1907) described *Phrynosaura*, and its only species, *P. reichei*. Müller (1928) sub-

sequently designated *P. reichei* as its type species. He also included in the genus *P. marmoratus* and his newly described *P. werneri*, a synonym of *Liolaemus anomalus* according to Cei (1979a). Núñez and Yáñez (1984b) restricted the genus to *P. reichei* and *P. audituvelatus*, the latter transferred from *Ctenoblepharys*. They cited as characteristics of the genus (1) eyelid with a conspicuous comb, (2) diameter of eye greater than length between anterior border of eye and rostral, (3) tail shorter than snout-vent length, (4) head scales poorly differentiated, (5) jaws isognathus, (6) loreal region depressed, and (7) dorsal scales imbricate, smooth, and with accompanying scales (my translation). My observations of these two species are in accord with this list of characters, except that the head scales of both species are as well differentiated as in many species of *Liolaemus*, e.g., supraorbital semicircles are distinct, separated from transversely expanded supraocular by a distinct arc of circumorbitals, interparietal prominent, flanked by a pair of larger parietal scales, etc. Compared with most other *Liolaemus*, the snout is distinctly truncate, and the ciliary fringe is very prominent. Laurent (1984a) included *L. reichei*, *L. audituvelatus*, and *L. stolzmanni* in *Phrynosaura*, and distinguished the genus from *Ctenoblepharys*, *Liolaemus* (sensu stricto), and *Ceio-laemus* by its differentiated supraoculars and a number of morphometric differences. *Liolaemus reichi* and *L. audituvelatus* possess a tibial blade and hypertrophied M. tibialis anterior, but the condition in *L. stolzmanni* is unknown. However, the prominent ciliary fringe and truncated snout may prove to be synapomorphies for the three species placed in *Phrynosaura* by Laurent (1984a).

RHYTIDODEIRA

Girard (1858) proposed the genus *Rhytidodeira* for six previously described species of *Liolaemus*: *Proctotretus kingii* Bell, 1842, *P. magellanicus* Duméril and Duméril, 1851, *P. bibronii* Bell, 1842, *P. wiegmanni*, *Tropidurus nigromaculatus* Wiegmann, 1834, and *T. oxycephalus* Wiegmann, 1834 (= *L. nigromaculatus*). Subsequently, Laurent (1985a) resurrected *Rhytidodeira*, designated *L. kingii* as its type species, and suggested

that it may be used as a species-group name for *L. kingii*, *L. archeforus* Donoso-Barros and Cei, 1971, and *L. ruizleali* Donoso-Barros and Cei, 1971 (= *L. kingii* fide Cei and Scolaro, 1987). *Liolaemus kingii* and *L. archeforus* have all of the synapomorphies that diagnose *Liolaemus*, and, according to Laurent (1985a), differ from other *Liolaemus* in being "primitive." No derived characters are known to unite *L. kingii* and *L. archeforus*, the species assigned to *Rhytidodeira* by Laurent (1985a).

VELOSAURA

Núñez and Yáñez (1984b) described *Velosaura*, including in it *L. aymararum* Veloso et al., 1982, and *L. jamesi*, designating the former as its type species. Earlier, Veloso et al., (1982), proposed the generic name *Jararancus* for these two species, but failed to provide a description. Thus, *Jararancus* is a nomen nudum. Núñez and Yáñez (1984b) characterized *Velosaura* as having (1) eyelid with a short comb, (2) diameter of eye larger than the length from anterior border of eye to rostral, (3) tail equal to or longer than snout-vent length, (4) head scales differentiated, (5) profile isognathus, (6) loreal region slightly depressed, and (7) dorsal scales separated, leaving spaces between them, the borders rounded, with slight keels only on some scales. My notes on the holotype of *L. jamesi* (BMNH 90.6.9.2 [RR1946.8.12.39]; see also Boulenger [1891, pl. 1]) are in accord with these observations except that the dorsal body scales are subimbricate with faint, blunt keels. Additionally, both species possess a tibial blade and associated hypertrophied M. tibialis anterior, and although data are not available for *L. aymararum*, *L. jamesi* also has a hypertrophied M. puboischiotibialis and pigmented epimysium of the M. pterygomandibularis. Laurent (1992) referred both species to the *signifer* group of the subgenus *Eulaemus* (see below), but Núñez and Jaksic (1992) and Núñez (1992) continued to recognize *Velosaura* as a valid genus. None of the characters listed for *L. aymararum* and *L. jamesi* are unique to them, although the combination itself may be. Evidence for monophyly of *Velosaura* appears to be weak or lacking. *Liolaemus aymararum* and *L. ja-*

mesi are extremely similar phenetically, and may be synonymous, or, if valid, sister species.

VILCUNIA

Donoso-Barros and Cei (1971) described *Vilcunia*, with a single species, *V. sylvanae*, and indicated that it differed from *Liolaemus* by its tail shorter than snout-vent length, short hind limbs, presence of hemigular fold, absence of precloacal pores in both sexes and posterior border of the thigh not granular. A second species, *V. periglacialis*, was added to the genus by Cei and Scolaro (1982), who indicated that the primary character separating *Vilcunia* from *Liolaemus* was the presence of lateral mucrons on the dorsal scales, giving them a "trifid" appearance, but also pointed out that *Liolaemus lineomaculatus* Boulenger, 1885, lacks precloacal pores as well, and sometimes exhibits dorsal scales slightly notched on the edges (see Cei and Scolaro, 1982: fig. 4; Cei, 1986: fig. 56k-m). On the basis of morphometric studies, Laurent (1985a) recognized *Vilcunia* and transferred *Liolaemus lineomaculatus* to it. *Vilcunia* was recognized by Etheridge and de Queiroz (1988) based on its lack of precloacal pores and tridentate dorsal scales, both presumed to be synapomorphies, and its possession of a shorter dentary, thought to be a plesiomorphic state shared with *Phymaturus* (a longer dentary thought to be a synapomorphy for *Liolaemus*); however, they included in the genus only *V. sylvanae* and *V. periglacialis*. Frost and Etheridge (1989) considered *Vilcunia* to be a synonym of *Liolaemus* because, while not doubting the monophyly of *Vilcunia*, a short dentary, which formed the basis for its exclusion from *Liolaemus*, was found to be variable within the genus, and because all preliminary analyses of liolaemine relationships (Etheridge, unpubl.) had found *Vilcunia* nested well within *Liolaemus*. Of the characters listed for *Vilcunia* by Donoso-Barros and Cei (1971), all but the tridentate dorsal scales and lack of precloacal pores occur in a number of other species of *Liolaemus*. The "hemigular fold" presumably refers to the lateral vestiges of the medially interrupted transverse gular fold, found in almost all Liolaeminae. The post-

femoral scales of Liolaeminae are small, convex, and nonoverlapping in most species, but in those with large, strongly imbricate and lanceolate dorsal body scales, e.g., *Liolaemus chiliensis*, *L. gravenhorstii*, *L. lemniscatus*, and *L. nitidus*, the postfemorals are flat and subimbricate, as in *Vilcunia*. The distinctly tridentate dorsal scales do indeed appear to be unique within Liolaeminae (Cei and Scolaro, 1982), and apparently also within Tropiduridae, and may well represent a synapomorphy for *L. sylvanae*, *L. periglacialis*, and *L. lineomaculatus*. However, precloacal pores are also lacking in both sexes of *Liolaemus coeruleus* (Cei and Ortiz-Zapata, 1983) and *L. cristiani* (Navarro and Núñez, 1992), and in some males of several other species (Laurent, 1984a) that do not otherwise bear a close resemblance to *Vilcunia*.

EULAEMUS AND LIOLAEMUS, SENSU STRICTO

Within *Liolaemus*, Laurent (1983b) recognized two large species groups that included the majority of species in the genus. He referred to them as the Argentino group and the Chileno group. The Chileno group contained 37 species, most of them occurring in Chile, with some extending into Argentina, Bolivia, and southern Peru. The Argentino group contained 28 species, most of them from Argentina, but with some species in Chile, Bolivia, Paraguay, and Peru. He stated that if these groups eventually were to be recognized at the generic or subgeneric level, the name *Eulaemus* Girard, 1858 (type species *Proctotretus fitzingerii* Duméril and Bibron, 1837) was available for the Argentino group, and *Liolaemus* sensu stricto (type species *Calotes chiliensis* Lesson, 1830) should be used for the Chileno group. These groupings were based primarily on his morphometric studies, which he summarized two years later (Laurent, 1985a), and proposed the formal recognition of *Eulaemus* and *Liolaemus* sensu stricto as subgenera.

In 1992, Laurent characterized the two subgenera and listed the species assigned to each. *Liolaemus* (48 species) was characterized as having fewer precloacal pores (\bar{x} = 2.19 and < 5 in 91% of specimens *Liolaemus* versus \bar{x} = 6.40 and > 4 in 92% of specimens

of *Eulaemus*), lateral rather than dorsolateral nostrils, generally flat and long supralabials, the fourth below the eye with an oblique border, rather than short, high supralabials, fifth-seventh below the eye, with posterior border vertical. The supralabials of *Liolaemus* usually number only four, all of them slender and at least twice as long as wide, the fourth usually the most elongate, more than three times longer than wide, with its posterior margin oblique, whereas in *Eulaemus* the supralabials characteristically number five or more, the anterior ones square or not much longer than wide, none of them more than three times longer than wide, and the posterior one with its posterior margin nearly vertical. Laurent (1992) also listed the distance between the upper border of the subocular and lip as distinct: less than the distance between the nasal plates in *Liolaemus*, greater in *Eulaemus*. However, this difference results from the combined effects of two previously mentioned characters, i.e., the nasals being lateral, and therefore closer together, and the supralabials narrower in *Liolaemus* than in *Eulaemus*.

As indicated earlier, a large number of *Liolaemus* (sensu lato) possess melanistic pigment within the median portion of the epimysium of the M. pterygomandibularis, the medial head of the M. flexor tibialis internus is covered by an hypertrophied M. puboischiotalis, and the insertion of the M. tibialis anterior is hypertrophied in association with the presence of a sharp, bladelike process of the tibia. These characters, all unique within Tropiduridae, Phrynosomatidae, and Opluridae, and apparently also unique within Iguania, are present in the 35 species listed for *Eulaemus* by Laurent (1992), save for *L. chacoensis* Shreve, 1948, which lacks them all. They are also present in all species of *Ortholaemus* (see below). The alternative, and presumably plesiomorphic states, of these musculoskeletal characters occur in the 24 species listed for *Liolaemus* sensu stricto, except *L. duellmani* Cei, 1978, which has them. The plesiomorphic state is present in all other Liolaeminae as well.

Other differences between the subgenera appear as trends or tendencies, the polarities of which are uncertain. The proximal (interclavicle) process of the clavicle is slender in

Liolaemus sensu stricto but in *Eulaemus* it usually is anteroposteriorly expanded, often with an irregular posterior margin, and occasionally fenestrate. The latter condition occurs in *Ctenoblepharys* but not *Phymaturus* or other *Liolaemus* sensu lato. Meckel's groove is fused in *Liolaemus* sensu stricto, unfused in *Eulaemus* except in about 60% of *L. darwini* Bell, 1843 (sensu Etheridge, 1993). The polarity of this character is uncertain because of interspecific variation in other *Liolaemus* (sensu lato) and *Phymaturus*. In some species of both groups the body scales are moderately small, rhomboidal, and imbricate, with granular lateral nuchal scales and complex lateral nuchal skin folds; however, within *Liolaemus* sensu stricto, most species exhibit varying degrees of more sharply keeled, strongly imbricate, lanceolate dorsal body scales, and larger, keeled, imbricate lateral nuchal scales accompanied by the reduction or disappearance of lateral nuchal skin folds. In contrast, within *Eulaemus* many species exhibit, to varying degrees, dorsal body scales that are rounded or oval, subimbricate to nonoverlapping, often with conspicuous interstitial granules, and the lateral nuchal scales are granular with prominent skin folds. Other species of *Liolaemus* sensu lato exhibit interspecific variation in these characteristics of the dorsal body and lateral nuchal scales.

In the same work, Laurent (1992) recognized within *Eulaemus* a *fitzingerii* group, characterized by the presence of a patch of enlarged scales on the posterior thigh, and a *signifer* group characterized by its absence. The femoral patch referred to as characteristic of the *fitzingerii* group is a patch of abruptly enlarged, often spiny scales on the posterior proximal surface of the thigh, which is otherwise beset with small, nonoverlapping scales. It is present in both sexes, and in adult males the patch forms a hemispherical bulge due to even greater hypertrophy of the proximal part of the M. puboischiotalis (Etheridge, 1993: pl. 1.3). As Laurent (1992) pointed out, the patch of enlarged scales is unique within Tropiduridae, and it occurs elsewhere within Iguania only in the phrynosomatid genus *Uma* (in which the thigh muscles are normal) and is almost certainly derived within Liolaeminae.

A femoral patch, underlain by a hypertrophied *M. puboischiotibialis*, that characterizes the *fitzingerii* group, as well as the musculoskeletal characteristics of other *Eulaemus*, also occur in the species assigned by Laurent (1983a) to the subgenus *Ortholaemus* (see below). As indicated above, the musculoskeletal characters that distinguish *Eulaemus* from *Liolaemus* sensu stricto, i.e., pigmented epimysium of the *M. pterygomandibularis*, hypertrophy of *M. puboischiotibialis*, and presence of a tibial blade associated with a hypertrophied *M. tibialis* anterior, appear to be unique within Iguania, and provide evidence for the monophyly of a clade composed of *Eulaemus* + *Ortholaemus*. Furthermore, the femoral patch with an underlying hypertrophied thigh muscle also appears to be unique within Iguania, and may be considered a potential synapomorphy of a clade formed by *Ortholaemus* + the *fitzingerii* group of *Eulaemus*. However, the recognition of *Eulaemus* and *Ortholaemus* as subgenera would render *Eulaemus* paraphyletic. Indeed, Laurent (1983a) considered *Ortholaemus* obviously to have been derived from the Argentino group, e.g., *Eulaemus*. Thus, without *Ortholaemus* as a subset of *Eulaemus* there are no known synapomorphies that would unite the species assigned to *Eulaemus* by Laurent (1992).

Monophyly of the subgenus *Liolaemus* is more problematic. Of the characters that distinguish *Liolaemus* from *Eulaemus*, the absence of a hypertrophied *M. puboischiotibialis*, tibial blade and hypertrophied *M. tibialis* anterior, and pigmented *M. pterygomandibularis* epimysium are clearly plesiomorphic. Several characteristics of the group probably are derived within Liolaeminae: the presence of a fused Meckel's groove; supralabials narrow, the fourth the most posterior and greatly elongated; and precloacal pores usually four or fewer (or absent). However, outgroup comparisons indicate that the polarity of these states is equivocal. Precloacal pore numbers are high (5–15) in *Eulaemus*, *Ortholaemus*, *Ctenoblepharys*, and *Phymaturus*. Meckel's groove is open in *Eulaemus* (except in some *Liolaemus darwini*), *Ortholaemus* (except *Liolaemus occipitalis* [Keller and Krause, 1986]), *Ctenoblepharys*, and the *Phymaturus paluma* group, but precloacal pores are lacking in oth-

er iguanians except for a few Agaminae, and in other Tropiduridae Meckel's groove is fused and the labials are narrow.

MESOLAEMUS

In a brief note, Laurent (1985b) proposed the new subgeneric name *Mesolaemus* for *Liolaemus cuyanus* Cei and Scolaro, 1980. The reason stated for this action was that *L. cuyanus* "is similar to *Ortholaemus* in one important character, but also is similar to *Eulaemus* in another, no less important character" (my translation). He further stated that "the data considered does not permit one to decide if *Mesolaemus* is the sister group of *Ortholaemus*, of *Eulaemus*, or of a part of *Eulaemus* . . ." (my translation). The characters referred to, and the data considered, were not specified.

Liolaemus cuyanus was initially described as a subspecies of *L. fitzingerii* (Cei and Scolaro, 1980), and raised to full species status by Laurent (1983b). Presumably, the character referred to by Laurent (1985b) as a similarity between *L. cuyanus* and *Orytholaemus*, is the contact of the mental with six scales, i.e., the sublabials in addition to the anterior infralabials and postmentals. *L. cuyanus* is otherwise a typical member of the *fitzingerii* group of Laurent (1992), and is phenetically very similar to *L. fitzingerii*, *L. canqueli*, *L. melanops*, and *L. xanthoviridis*, but it is unlike any species of *Ortholaemus* in its squamation, large body size (maximum SVL 98 mm [Etheridge, 1992]), and expanded, deeply tricuspid posterior marginal teeth. It is uncertain, as Laurent (1985b) pointed out, whether the sublabial-mental contact is a synapomorphy for *L. cuyanus* + *Ortholaemus*, or is homoplastic. However, recognition of *Mesolaemus* as a monotypic subgenus of *Liolaemus* seems unwarranted.

ORTHOLAEMUS

Cei (1979b) pointed out that *Liolaemus rabinoi*, *L. multimaculatus*, and *L. riojanus* (as *L. multimaculatus riojanus*; see Etheridge, 1993) "appear to represent a very specialized group of psammophilous lizards," and stated that should the group "be accorded special, formal recognition, the subgeneric name *Ortholaemus* (Girard 1858; type species *Ortho-*

laemus beaglyi Girard 1858 = *Liolaemus multimaculatus*) is available." This appears to be the first formal designation of a type species for *Ortholaemus*. Laurent (1983a) added *L. scapularis*, *L. lutzae*, *L. occipitalis*, *L. wiegmanni* and *L. cranwelli* to *Ortholaemus*, and characterized the group as having (1) more than one row of scales between the subocular and supralabials (although in *L. scapularis* the subocular is often separated from the labials by a single scale), (2) mental in contact with six (at times eight) scales instead of four, (3) mental much narrower than rostral, (4) mental wider posteriorly than at the border with the lip, and (5) claws longer and yellowish in the arenicolous species. He also pointed out that in *L. cuyanus* Cei and Scolari, 1980, the rostral is bordered by six scales, but that it is not narrower posteriorly, and there is a single row of scales between the subocular and supralabials. Laurent (1984a) formally proposed the recognition of *Ortholaemus* as a subgenus of *Liolaemus*, and added to it *L. rabinoi* and *L. riojanus*. He also designated *Ortholaemus fitzroyii* Girard 1858 = (*Proctotretus wiegmanni* Duméril and Bibron 1837), as the type species, apparently having overlooked Cei's (1979b) earlier designation of *Liolaemus multimaculatus* as the type species. Later, Laurent (1986) described *Liolaemus salinicola* as a new species in the subgenus *Ortholaemus*.

As indicated above, the species of *Ortholaemus* have all of the apomorphic states that diagnose the *fitzingerii* group of *Eulaemus*, i.e., melanic pigment within the epimysium of the M. pterygomandibularis, the medial head of the M. flexor tibialis internus covered by an hypertrophied M. puboischiotibialis, and the insertion of the M. tibialis anterior hypertrophied in association with the presence of a sharp, bladelike process of the tibia. Additionally, they differ from all other *Liolaemus* in having smaller lorilabial scales, usually in two or more rows between the subocular and supralabials, flat or concave infralabials (personal obs.), and the mental scale narrower anteriorly than posteriorly, and from all other *Liolaemus* except *L. cuyanus* in having six, rather than four scales in contact with the mental, resulting from contact between the mental and sublabials. Thus, *Ortholaemus* may well be a monophyletic group.

In summary, the species that have been

referred to *Abas*, *Ceiolaemus*, *Eulaemus*, *Mesolaemus*, *Ortholaemus*, *Pelusaemus*, *Phrynosaura*, *Rhytidodeira*, *Velosaura*, and *Vilcunia* exhibit all of the synapomorphies that distinguish *Liolaemus* from other Liolaeminae. Furthermore, there is some evidence that *Vilcunia*, *Ceiolaemus*, and *Phrynosaura* may represent monophyletic groups within *Liolaemus*. There also is evidence that *Ortholaemus* is a monophyletic group, which, together with the other species that possess a femoral patch (i.e., *fitzingerii* group), forms a more inclusive clade. This clade, together with *Eulaemus*, forms a still more inclusive clade (see Appendix 2).

DISCUSSION AND SUMMARY

Ctenoblepharys adspersa is a moderate-size (maximum SVL 74 mm) iguanian lizard endemic to the sandy beaches and sand dunes of the Pacific coast of central Peru between about 11°05' and 13°50'S. Little is known of its habits except that it runs swiftly over the sand and that its color pattern is highly cryptic on this substrate. It possesses a number of derived characteristics that are unique within Tropicuridae and its putative outgroups Phrynosomatidae and Opluridae; six of these autapomorphies involve the skull, and two the vertebral column. Additionally, *C. adspersa* differs from most other Liolaeminae in having small, nonoverlapping dorsal body scales arranged in more-or-less transverse rows, and numerous, poorly differentiated head scales, including small, subequal supraoculars and several suboculars, but with greatly elongate, triangular outer ciliaries that form a prominent comb. *Ctenoblepharys adspersa*, along with *Phymaturus*, lacks the synapomorphies that specify a clade consisting of all other Liolaeminae, the species of which are here referred to *Liolaemus*. Furthermore, *C. adspersa* and *Phymaturus* are not known to share any derived characteristics to the exclusion of *Liolaemus*, nor does *Liolaemus* share any derived characteristics with either *Ctenoblepharys* or *Phymaturus* to the exclusion of the other, and thus relationships of *Ctenoblepharys*, *Phymaturus*, and *Liolaemus* are unresolved.

All of the species of Liolaeminae that have been described in or referred to *Ctenoblepharys*, with the possible exception of *L. er-*

roneus, lack the autapomorphies of *C. adspersa*, and furthermore all of them possess the synapomorphies that diagnose *Liolaemus*. This is also true for those species that have been described in, or referred to, other genera of Liolaeminae, or as subgenera and species groups of *Liolaemus*. Evidence for monophyly of some of these groups is lacking, while others may well represent clades within *Liolaemus*. However, until such time as the historical relationships of the species of *Liolaemus* have been determined by cladistic analysis, it would seem to be the wisest course to avoid using these names as formally recognized taxa. To do so could lead to the formation of a paraphyletic group formed by the remaining species that then would compose the genus *Liolaemus*.

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APPENDIX 1 SPECIMENS EXAMINED

Preserved specimens and skeletons of *Ctenoblepharys adpersa* examined are listed below, followed by their localities. Preserved specimens and skeletons of *Phymaturus* and *Liolaemus* examined for comparison with *Ctenoblepharys adpersa*, and specimens of outgroup species examined for comparison with *Liolaeminae*, are also listed below. Museum acronyms follow Leviton et al. (1985). Numbers preceded by REE are all skeletons; skeletons preceded by other acronyms are indicated by "sk."

Species unavailable for examination, for which some data were obtained from the literature, include: *Liolaemus anomalus ditadai* (Cei, 1993), *L. archeforus gallardoi* (Cei, 1986), *L. a. sarmientoi* (Cei, 1986), *L. aymararum* (Veloso et al., 1982), *L. belli araucaniensis* (Müller & Hellmich, 1939a), *L. b. neuquensis* (Müller & Hellmich, 1932a), *L. ceii* (Cei, 1986), *L. cristiani* (Núñez et al., 1991), *L. cyanogaster brattstroemi* (Donoso-Barros, 1961), *L. erroneus* (Núñez and Yáñez, 1984b), *L. hellmichi* (Donoso-Barros, 1975), *L. isabelae* (Navarro and Núñez, 1993), *L. lativittatus* (Werner, 1904), *L. islugensis* (Ortiz-Zapata and Marquet, 1987), *L. maldonadae* (Núñez et al., 1991), *L. melanopleurus* (Philippi, 1860), *L. modestus* (Philippi, 1860), *L. nigroviridis minor* (Müller and Hellmich, 1932b), *L. n. nigroroseus* (Donoso-Barros, 1966), *L. ortizi* (Laurent, 1982), *L. patriciaturrae* (Navarro and Núñez, 1993), *L. pictus ar-*

gentinus (Müller and Hellmich, 1939b), *L. p. major* (Boulenger, 1885), *L. p. talcanensis* (Urbina and Zúñiga, 1977), *L. pseudolemniscatus* (Lam-borot and Ortiz-Zapata, 1990), *L. rosenmanni* (Núñez and Navarro 1992), *L. silvai* (Ortiz-Zapata, 1989b), *L. vallecurensis* (Pereyra, 1992), *L. zapallarensis sieversi* (Donoso-Barros, 1954), *Phymaturus mallimaccii* (Cei, 1980b), *P. indistinctus* (Cei and Castro, 1973), *P. nevadoi* (Cei and Roig, 1975).

Liolaeminae

Ctenoblepharys adpersa: Peru: Ventanilla, near Lima, SMF 75966–69; between Ventanilla and Puente Piedras, SMF 64373–74; Playa Ventanilla near Lima, REE 2513; near Ancón north of Lima, SMF 64369–70; 5.5 km NE San Bartolo, 100 m, MVZ 85415–16; Ciudad de Dios, FML 0368, 0464; Ica: beach south of Paracas, within 100–200 m of ocean, MCZ 145039–40; Museo Paracas, 30.2 km S Pisco, 7.2 km SW Paracas, LACM 49145–6, 49147(sk); Peru (no additional data), NMW 13578, 18905.

Liolaemus abaucan: SDSU 1446–64, REE 2845. *L. alticolor*: SDSU 1697–707, REE 2520, 2641–50. *L. andinus andinus*: FML 1764(10). *L. a. poecilochromus*: SDSU 1597–99, REE 2548, 2670–78. *L. anomalus anomalus*: SDSU 1674–75. *L. archeforus archeforus*: MCZ 162002–03,

- 164001(sk). *L. audituvelatus*: MNHNC 980-81. *L. austromendocinus*: SDSU 1799-80, REE 2340-47, 2358-59. *L. belli belli*: SDSU 1802, REE 1559. *L. b. moradoensis*: SDSU 1803-04. *L. bibronii*: SDSU 1805-13, REE 2305, 2351-55, 2380, 2406-09, 2461. *L. bisignatus*: SDSU 1814, REE 2535. *L. bitaeneatus*: SDSU 1815-17, REE 2597-600. *L. boulengeri*: SDSU 1212-16, MVZ 125722-26, 125728, 125730-48, 125750-57. AMNH 17022, 46431, 95960, REE 2348-50, 2396-97, 2404-05, 2458-60. *L. buergeri*: MVZ 188691, 188716. *L. canqueli*: KU 182038, 187513, FML 795, 1607, 2115, 2786(3), 2874(7 + 1 sk), 2915, IBAUNC 861-9. *L. capillitas*: SDSU 1818-22. *L. chacoensis*: SDSU 1823-25, FMNH 44162-70, REE 2549. *L. chiliensis*: SDSU 1837-42, REE 2515. *L. coeruleus*: SDSU 1826-32, REE 2545. *L. constanzae*: SDSU 1834-45, REE 2516. *L. copiapiensis*: SDSU 1846-47, REE 2560, 2765, 2833. *L. cranwelli*: MACN 15.233. *L. curicensis*: SDSU 1848. *L. curis*: SDSU 1849-51, REE 2564. *L. cuyanus*: SDSU 1010, 1051-55, 1089-95, 1229-31, 1465-508, FML 2097(24), REE 2316-20, 2723-2727. *L. cyanogaster*: SDSU 1833-36, REE 2525. *L. darwini*: SDSU 1249-50, 1443-45, REE 2321-22, 2493-95. *L. disjunctus*: FML 1201(5). *L. donosobarrozi*: SDSU 1188, FML 2687(2), 2770(3), 2871(5 + 1sk). *L. donosoi*: FML 1340. *L. dorbigny*: SDSU 1625-29, FML 1757(17), REE 2541, 2668-69, 2679-84. *L. duellmani*: KU 161126. *L. eleodori*: SDSU 1609-12, REE 2368-79. *L. elongatus elongatus*: SDSU 1857-61, REE 2291-96, 2366-67, 2386-89. *L. e. petrophilus*: SDSU 1862-64, REE 2423-32. *L. exploratorum*: MLP 571. *L. fabiani*: DBGUCH 0350, 0336. *L. famatinae*: SDSU 1624, FML 1720(14), REE 2542. *L. fitzkau*: FML 1612. *L. fitzgeraldi*: SDSU 1865, MVZ 186557-58. *L. fitzingerii*: SDSU 1191-93, MVZ 181615-18, 188785-94, KU 182043-44, FML 2128(13), 2130(4), REE 2457. *L. forsteri*: FML 2211. *L. fuscus*: SDSU 1866-68, REE 2529. *L. gracilis*: SDSU 1869. *L. gravenhorstii*: SDSU 1870-72, 2081-83, REE 2528, 2831, 2892-95. *L. griseus*: FML 1354(4), 1502, 1586(4). *L. hernani*: SDSU 1874-76, REE 2565. *L. huacahuasicus*: SDSU 1623, FML 2303(4), 2246(3), 2297(3), REE 2543. *L. insolitus*: CV-ULA IV-0641-49, 2434-36. *L. irregularis*: SDSU 1194-210, MVZ 126523-47, REE 2656-2667. *L. jamesi*: SDSU 2623, FML 1193, KU 161741, LACM 134120. *L. kingii kingii*: SDSU 1671-72, REE 2479-86. *L. k. baguali*: FML 1247. *L. k. somuncurae*: SDSU 1669-70, REE 2390-95. *L. koslowskyi*: SDSU 1005-09, 1041-50, 1067-69, 1096-97, 1409-23, 1431-42, REE 2705-06. *L. kriegi*: SDSU 1877, REE 2412-2422. *L. kuhlmanni*: SDSU 1878-81, REE 2526. *L. laurenti*: SDSU 1013, 1024-1038, 1070-88, 1114-17, 1121-44, 1159-67, REE 2741-50. *L. lemniscatus*: SDSU 1882-86, 2079-80, REE 2530, 2889-91. *L. leopardinus*: MVZ 187765, 187767. *L. lineomaculatus*: SDSU 1666-68, REE 2463-69. *L. lutzae*: SDSU 1187, 2047-51, MCZ 46241-42, 46963, 79136-40, 92772-74, 119880, AMNH 70922-24, 92870-72, FML 1287(7), REE 2524, 2860, CAS 15802(sk). *L. magellanicus*: SDSU 1673, MVZ 180134-35, 180136(sk), 180118, REE 2517. *L. melanops*: SDSU 1178, KU 182045-48, FML 1609(2), REE 2411. *L. montanus*: SDSU 1621, FML 1723(9), REE 2540. *L. monticola monticola*: SDSU 1888-96, REE 2527. *L. m. chil-lanensis*: SDSU 1898, REE 2596. *L. m. villaricensis*: SDSU 1897, REE 2566. *L. multicolor*: SDSU 1314-19, 1520-32, REE 2547, 2634-40. *L. multimaculatus*: SDSU 1181-1185, 1312, 1756-79, FML 1596(20), 1826(18), REE 2550, 2846. *L. nigriceps*: SDSU 1620, FML 1635(10), AMNH 131845-46, REE 2537. *L. nigromaculatus*: SDSU 1903-05, REE 2551, 2832. *L. nigroviridis nigroviridis*: SDSU 1906-08, REE 2558. *L. n. campanae*: SDSU 1908, REE 2595. *L. nitidus*: SDSU 1899-1902, REE 2519, 2834, 2841. *L. occipitalis*: SDSU 1186, 2052-57, MCZ 96034, 154189-90, KU 176526-31, CAS 87093-94, REE 2521, 2859. *L. olongata*: SDSU 1099-104, 1424-30, 1708-17, REE 2844. *L. orientalis orientalis*: AMNH 80076. *L. o. chlorostictus*: SDSU 1613-1619, REE 2653-55, 2685-96. *L. ornatus*: SDSU 1232-48, 1320-38, AMNH 131849, KU 160034-35, 160210-15, 161182, 183459-68, REE 2522, 2623-33. *L. paulinae*: SDSU 1910-11, REE 2561. *L. periglacialis*: SDSU 1677, MCZ 162007, 162009-10, 162008(sk). *L. pictus pictus*: SDSU 1912-15, REE 1874, 1890, 1894-99, 2704, 2842. *L. p. chil-oeensis*: SDSU 1916-18, REE 2592. *L. platei*: SDSU 1919-23, REE 2523. *L. polystictus*: FML 1683(2). *L. pseudoanomalus*: SDSU 1040, 1310-11, 1676, REE 2728-29. *L. pulcherrimus*: FML 2184(7), 1961. *L. quilmes*: SDSU 1013-16, 1021, 1058-59, 1251-73, 1340-408, 1533, REE 2578-86, 2707-08. *L. rabinoi*: IBAUNC 818.1-2, 1296. *L. ramonensis*: SDSU 1887. *L. reichei*: LACM 9312. *L. riojanus*: SDSU 1105-13, 1146-58, 1169-74, KU 182057, MLP 2730, 2734, 2636, 2752, REE 2532, 2730-37. *L. robertmertensi*: SDSU 1313, 1518-19, 2587-88. *L. robustus*: FML 1682(2). *L. rothi*: SDSU 1175-77, KU 161166, 187517-18, MVZ 180041, 188087-94, 18824-39, REE 2398-403. *L. ruibali*: SDSU 1604-08, REE 2297-2304. *L. salinicola*: SDSU 1011-12, 1189-1190, FML 1909(10), 1912(9), 1807(13), 2020(21), REE 2568, 2738-39. *L. sanjuanensis*: FML 1016. *L. saxatilis*: SDSU 1736-39. *L. scapularis*: SDSU 1017-19, 1022-23, 1057, 1060-62, 1220-28, 1274-303, REE 2569-77, 2709-22. *L. schmidtii*: SDSU 1602-03, FMNH 5759-60, AMNH 131850-61, REE 2518. *L. schroederi*: MVZ

187760–61. *L. signifer signifer*: SDSU 1600, AMNH 90457–60, 90464–68, REE 1825–29, 2562. *L. s. annectens*: FML 1543. *L. stoltzmanni*: NMW 13580(3). *L. sylvanae*: MCZ 162004–06, 156906(sk), KU 190418(sk). *L. tacnae*: SDSU 1924, REE 2533, 2697. *L. tenuis tenuis*: SDSU 1925–35, 2084–89, REE 1817, 2591, 2857. *L. t. punctatissimus*: SDSU 1936, REE 2536. *L. us-pallatensis*: FML 1541(10), MVZ 126869, 188858, 188860–63, 188859(sk). *L. variegatus*: KU 133862–71. *L. velosoi*: IZUC uncataloged. *L. walkeri*: SDSU 1937, REE 1818, 2534. *L. wiegmannii*: SDSU 1168, 1217–19, CAS 174160–200, REE 2567, 2601–04. *L. williamsi*: FML 1701. *L. xanthoviridis*: SDSU 1179, KU 182049, 187514. *L. zapallarensis zapallarensis*: SDSU 1938, 2040–46, REE 2769, 2843. *L. z. ater*: SDSU 1939–42, REE 2850–56.

Phymaturus palluma: SDSU 1946–79, REE 1950, 2306–15, 2323–28, 2361–62. *P. antofagatensis*: SDSU 1991. *P. patagonicus*: SDSU 1980, REE 2471–72. *P. payune*: SDSU 1981–84, REE 2330–39, 2360. *P. punae*: SDSU 1978–79, REE 2356–57, 2383–85. *P. somuncurensis*: SDSU 1780–84, REE 2433–40. *P. zapalensis*: SDSU 1985–90, REE 2451–53.

Leiocephalinae + Tropicurinae

Leiocephalus carinatus: SDSU 1996–97, REE 1469, 1805, 1816. *L. cubensis*: SDSU 1999–2001. *L. schreibersi*: SDSU 1998, REE 1808. *Stenocercus chlorostictus*: SDSU 1535. *S. crassicaudatus*: SDSU 1680–83, REE 2286, 2593. *S. empetris*: SDSU 3059. *S. guentheri*: SDSU 1685. *S. imitator*: SDSU 1534. *S. modestus*: SDSU 1686. *S. percultus*: SDSU 1596. *S. praeornatus*: REE 2544.

S. roseiventris: SDSU 1686, REE 2284. *Microlophus occipitalis*: SDSU 2028–29, 3060–61, REE 649, 658, 1859, 1861–62. *M. peruvianus*: SDSU 2031–32. *Tropidurus etheridgei*: SDSU 2014–17, REE 1954. *T. hygomi*: SDSU 2022, REE 275. *Uranoscodon superciliosus*: SDSU 2110–14, REE 2589, 2883–84.

Opluridae

Chalarodon madagascariensis: SDSU 2123–29, USNM 149311, REE 455, 457, 547. *Oplurus cuvieri*: REE 620, 558, 1835. *O. cyclurus*: USNM 149330. *O. quadrimaculatus*: SDSU 2120–22, REE 658. *O. saxicola*: SDSU 2119.

Phrynosomatidae

Petrosaurus mearnsi mearnsi: SDSU 2253, REE 287–88, 351, 761, 1557–58. *P. m. sleveni*: REE 655. *P. thalassinus*: REE 575, 765–66, 797, 1381. *Uta stansburiana*: SDSU 2522–30, REE 274–75, 1877–78, 1892. *Uta palmeri*: SDSU 2520–21, REE 1990. *Urosaurus graciosus*: SDSU 2543–46, REE 271, 1544, 1547, 1625. *U. nigricaudus*: SDSU 2536–37, REE 492, 494. *U. lahteli*: SDSU 2854–55. *U. bicarinatus*: SDSU 2533. *U. ornatus*: SDSU 2534–35, 2538–42, 2547–53, REE 403, 757, 1553, 1556, 1559. *Phrynosoma asio*: SDSU 2308–09, REE 1489, 1580, 1676. *P. douglassii*: SDSU 2283–84. *P. orbiculare*: SDSU 1109, 1181, 1725, 1931. *P. coronatum*: SDSU 2305–07, REE 28, 188, 609, 1108, 1439, 1501, 1786, 1999. *Uma notata*: SDSU 2554–72, REE 263–64, 316, 396, 1535–38. *U. exsul*: SDSU 2274–77, REE 2880–81. *U. scoparia*: REE 509, 551.

APPENDIX 2

AN INDENTED CLASSIFICATION OF LIOLAEMINAE

Part A. A tentative classification of Liolaeminae, intended to represent historical interesting, is presented here in indented form. The conventions of Wiley (1979) that are applicable (conventions 1–4) are followed. An abbreviated indented classification is presented first to avoid confusion that may result from the large number of species listed in Part B. Supraspecific groups are followed by characters that are likely synapomorphies based on comparisons with the putative outgroups Leiocephalinae + Tropicurinae, Phrynosomatidae and Opluridae. On the same basis, characters not listed are considered plesiomorphic, or their status is equivocal. Species-group names are chosen arbitrarily, in most cases using one of

the oldest names. Formal generic or subgeneric names have been proposed for some of these (e.g., *Vilcunia* Donoso-Barros and Cei = the *sylvanae* group), but their use is discouraged at this time. The term “group” is employed for collations of taxa that are thought to be monophyletic. Species names separated by an arrow (→) refer to the species pairs or polytomies listed alphabetically in Part B.

Phymaturus sedis mutabilis: head and body flattened; body wide; lateral nuchal skin folds obscured by fat-filled pouches; tail with regular whorls of spinose scales; interclavicle short; suprascapula medially inflected; four sternal ribs; marginal teeth,

including at least some premaxillary teeth, expanded, with three (sometimes four) large cusps.

palluma group: superciliaries short; five or more subequal suboculars; three or four rows of lorilabials; mental narrower than rostral, usually in contact with sublabials, sometimes fragmented; caudal spines very well developed, two annuli per segment. *palluma* → *punae*

patagonicus group: splenial short; Meckel's groove fused. *indistinctus* → *zapalensis*

Ctenoblepharys sedis mutabilis: head short and broad; superciliaries short; outer ciliaries strongly projecting, triangular on lower lid; skull wide (about $1.3 \times$ longer than wide); orbit large (about $0.43\text{--}0.47 \times$ skull length); snout short (about $0.29 \times$ skull length); temporal fenestrae wide ($1.5\text{--}1.6 \times$ longer than wide); prefrontals wider than long; lacrimal foramen large; maxillary process of palatine wide; ectopterygoid short; maxillary process of ectopterygoid truncate distally; retroarticular process of mandible much shorter than angular process; parapophyses of atlas flat and oriented posterolaterally; neural arches of body vertebrae very wide. *adspersa*

Liolaemus sedis mutabilis: frontal downgrowths reach, or almost reach, palatines excluding prefrontals from orbitonasal fenestra; supratemporals mostly enclosed in groove along inferior margin of supratemporal processes of parietal; dentary extends posterior to superior apex of coronoid; lingual process of angular short or absent; secondary coracoid fenestra present; pygal region of males much larger than in females, scales of pygal region usually smaller in females than in males; hemipenial retractor muscles located anteriorly and hypertrophied. *archeforus* → *kingii*

nitidus group: supralabials narrow, width equal to or less than that of lorilabials, usually four, the posterior one elongate and usually upturned posteriorly. *magellanicus*

lineomaculatus group: precloacal pores lost; at least some dorsal scales tridentate. *lineomaculatus*

sylvanae group: lateral nuchal scales keeled and imbricate; postfemoral scales subimbricate. *periglacialis* → *sylvanae*

chiliensis group: precloacal pores usually four or fewer, rarely absent; Meckel's groove fused. *alticolor* → *zapallarensis*

signifer group: epimysium of M. pterygomanibularis pigmented; medial head of M. flexor tibialis internus covered by hypertrophied M. puboischiotibialis. *anomalus* → *pseudooanomalus*

montanus group: a sharp, bladelike process on posterior distal tibia, associated with greatly

hypertrophied M. tibialis anterior. *andinus* → *williamsi*

boulengeri group: a patch of abruptly enlarged, spinose scales on the posterior medial surface of thigh, bulged out in adult males due to hypertrophy of underlying M. puboischiotibialis. *abaucan* → *xanthoviridis*

wiegmannii group: lorilabials distinctly smaller than supralabials, usually in two rows between subocular and supralabials; supralabials narrow, but posteriormost not elongate; sublabials contact mental scale, mental widest posteriorly; infralabials flat to concave. *cranwelli* → *wiegmannii*

Part B. It is intended that the following list include all specific and subspecific names in current usage, except *Liolaemus erroneus*, within Liolaeminae. Subspecific names are included for the sake of completeness, without reference to their status as unitary evolving entities. Inclusion and placement of species and subspecies not examined are based on data available from the literature. These species and the bibliographic sources of their data are given in the introduction to Appendix 1.

Phymaturus Gravenhorst, 1838, *sedis mutabilis*

palluma group

antofagastensis Pereyra, 1985

mallimaccii Cei, 1980

palluma (Molina, 1782)

punae Cei, Etheridge & Videla, 1983

patagonicus group

indistinctus Cei & Castro, 1973

nevadoi Cei & Castro, 1975

patagonicus Koslowsky, 1898

payunae Cei & Castro, 1973

somuncurensis Cei & Castro, 1973

zapalensis Cei & Castro, 1973

Ctenoblepharys Tschudi, 1845, *sedis mutabilis*

adspersa Tschudi, 1845

Liolaemus Wiegmann, 1834, *sedis mutabilis* *archeforus*

a. archeforus Donoso-Barros & Cei, 1975

a. gallardoi Cei & Scolaro, 1982

a. sarmientoi Donoso-Barros, 1973

kingii

- k. kingii* (Bell, 1843)
k. baguali Cei & Scolaro, 1983
k. somuncurae Cei & Scolaro, 1981
nitidus group
magellanicus (Hombron & Jacquinot, 1847)
lineomaculatus group
lineomaculatus Boulenger, 1885
sylvanae group
periglacialis (Cei & Scolaro, 1982)
sylvanae (Donoso-Barros & Cei, 1971)
chiliensis group
alticolor Barbour, 1909
atacamensis Müller & Hellmich, 1933
austromendocinus Cei, 1974
bellii
bellii bellii Gray, 1845
b. araucaniensis Müller & Hellmich, 1932
b. moradoensis Hellmich, 1950
b. neuquensis Müller & Hellmich, 1939
bibronii (Bell, 1843)
bisignatus (Philippi, 1860)
bitaeniatatus Laurent, 1984
buergeri Werner, 1907
capillitas Hulse, 1979
ceii Donoso-Barros, 1971
chacoensis Shreeve, 1948
chiliensis (Lesson, 1831)
coeruleus Cei & Ortiz-Zapata, 1983
constanzae Donoso-Barros, 1961
copiapensis Müller & Hellmich, 1933
cristiani Núñez et al., 1991
curicensis Müller & Hellmich, 1938
curis Núñez & Labra, 1985
cyanogaster
c. cyanogaster (Duméril & Bibron, 1837)
c. brattstroemi Donoso-Barros, 1961
donosoi Ortiz-Zapata, 1975
elongatus
e. elongatus Koslowsky, 1896
e. petrophilus Donoso-Barros & Cei, 1971
exploratorum Cei & Williams, 1984
fitzgeraldi Boulenger, 1899
fuscus Boulenger, 1885
gracilis (Bell, 1843)
gravenhorstii (Gray, 1845)
hellmichi Donoso-Barros, 1975
hernani Sallaberry et al, 1982
kriegi Müller & Hellmich, 1939
kuhlmanni Müller & Hellmich, 1932
lativittatus Werner, 1904
lemniscatus Gravenhorst, 1837
leopardinus Müller and Hellmich, 1932
lorenzmuelleri Hellmich, 1950
maldonadae Núñez et al., 1991
modestus (Philippi, 1860)
monticola
m. monticola Müller & Hellmich, 1932
m. chillanensis Müller & Hellmich, 1932
m. villaricensis Müller and Hellmich, 1932
nigromaculatus (Wiegmann, 1834)
nigroviridis
n. nigroviridis Müller & Hellmich, 1932
n. campanae Hellmich, 1950
n. minor Müller & Hellmich, 1932
n. nigroroseus Donoso-Barros, 1966
nitidus (Wiegmann, 1834)
paulinae Donoso-Barros, 1961
pictus
p. pictus (Duméril & Bibron, 1837)
p. argentinus Müller & Hellmich, 1939
p. chiloensis Müller & Hellmich, 1939
p. major Boulenger, 1885
p. talcanensis Urbina & Zuñiga, 1977
platei Werner, 1898
pseudolemniscatus Lamborot & Ortiz-Zapata, 1990
ramonensis Müller & Hellmich, 1932
robertmertensi Hellmich, 1964
sanjuanensis Cei, 1982
saxitilis Avila et al, 1992
schroederi Müller & Hellmich, 1938
silvai Ortiz-Zapata, 1989
tacnae (Shreve, 1941)
tenuis
t. tenuis (Duméril & Bibron, 1837)
t. punctatissimus Müller & Hellmich, 1933
valdesianus Hellmich, 1950
variegatus Laurent, 1984
velosoi Ortiz-Zapata, 1987
walkeri Shreve, 1938
zapallarensis

z. zapallarensis Müller & Hellmich, 1933

z. ater Müller & Hellmich, 1933

z. sieversi Donoso-Barros, 1954

***signifer* group**

anomalus

a. anomalus Koslowsky, 1896

a. ditadai Cei, 1986

pseudoanomalus Cei, 1981

***montanus* group**

andinus

a. andinus Koslowsky, 1895

a. poecilochromus Laurent, 1986

auditovelatus Núñez & Yáñez, 1983

aymararum Veloso et al., 1982

disjunctus Laurent, 1990

dorbignyi Koslowsky, 1898

duellmani Cei, 1978

eleodori Cei et al., 1983

fabiani Yáñez & Núñez, 1983

famatinae Cei, 1980

fitkauui Laurent, 1986

forsteri Laurent, 1982

griseus Laurent, 1984

huacahuasicus Laurent, 1985

insolitus Cei & Péfaur, 1982

isabelae Navarro & Núñez, 1993

islugensis Ortiz-Zapata & Marquet, 1987

jamesi (Boulenger, 1891)

melanopleurus (Philippi, 1860)

montanus Koslowsky, 1898

multicolor Koslowsky, 1898

nigriceps (Philippi, 1860)

orientalis

o. orientalis Müller, 1923

o. chlorostictus Laurent, 1993

ortizi Laurent, 1982

patriciaiturrae Navarro and Núñez, 1993

polystictus Laurent, 1991

pulcherrimus Laurent, 1993

reichei (Werner, 1907)

robustus Laurent, 1991

rosenmanni Núñez & Navarro, 1992

ruibali Donoso-Barros, 1961

schmidti (Marx, 1960)

signifer

s. signifer (Duméril & Bibron, 1837)

s. annectens Boulenger, 1901

stolzmanni (Steindachner, 1891)

vallecurensis Pereyra, 1992

williamsi Laurent, 1992

***boulengeri* group**

abaucan Etheridge, 1993

boulengeri Koslowsky, 1898

canqueli Cei, 1975

cuyanusi Cei & Scolaro, 1989

darwinii (Bell, 1843)

donosobarrosi (Cei, 1974)

fitzingerii (Duméril & Bibron, 1837)

irregularis Laurent, 1986

koslowskyi Etheridge, 1993

laurenti Etheridge, 1992

melanops Burmeister, 1888

olongasta Etheridge, 1993

ornatus Koslowsky, 1898

quilmes Etheridge, 1993

rothi Koslowsky, 1898

uspallatensis Macola & Castro, 1982

xanthoviridis Cei & Scolaro, 1980

***wiegmanni* group**

cranwelli (Donoso-Barros, 1973)

lutzae Mertens, 1938

multimaculatus (Duméril & Bibron, 1837)

occipitalis Boulenger, 1885

rabinoi (Cei, 1974)

riojanus Cei, 1979

salinicola Laurent, 1986

scapularis Laurent, 1982

wiegmanni (Duméril & Bibron, 1837)

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