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

RICHARD ETHERIDGE

ABSTRACT

*Ctenoblepharys adspersa* is a highly derived arenicolous 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*, *Ceioilaemus*, *Helocephalus*, *Pelusaurus*, *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. somuncurenensis*, and *P. zapalensis*, all formerly subspecies of *P. patagonicus*, are elevated to species status.

RESUMEN

*Ctenoblepharys adspersa* es un lagarto arenicolo 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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1 Professor Emeritus, Department of Biology, San Diego State University, San Diego, California, 92182-0057.
pecies de Liolaeminae que han sido describidas en, o referido a Ctenoblepharys, excepto *C. adspersa*, exhiben sinapomorfías que diagnósticas de *Liolaemus* y anque 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. payuna*, *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: multimagulatus* Duméril and Bibron, 1837; *nigriceps* Philippi, 1890; *marmoratus* Burmeister, 1851 (non Gravenhorst, 1837); *jamesi* Boulenger, 1891; *stolzmanni* Steindachner, 1891; *anomalus* Koslosky, 1896; *reichei* Werner, 1907; *werneri* Müller, 1928 (= *anomalus* fide Cei, 1979a); *schmidtii* Marx, 1960; *erroneus* Núñez and Yáñez, 1984a; *lentus* Gallardo, 1966 (= *anomalus* fide Cei, 1979a); *donosobarr佐si* Cei, 1974; *rabinoi* Cei, 1974; *audituvelatus* 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, 1948b; Ceilolaemus Laurent, 1984a; Eulaemus Girard, 1858; Holocephalus Philippi, 1860; Liolaemus Wiegmann, 1834; Ortholaemus Girard, 1858; Phrynosaursa Werner, 1907; and Velosaura Núñez and Yáñez, 1984b.

In recent years, Cei (1979b) considered that *Ctenoblepharys* contained the species *adspersa, nigriceps, reicheli, 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 Jaksc (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 allopatic 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, Ceilolaemus, Ctenoblepharys, Eulaemus, Holocephalus, Mesolaemus, Ortholaemus, Pelusaurus, Rhytidodeira, Phrynosaursa, Velosaura, and Vilecina*. 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 adpersus, 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). According 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. multiformis, 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. multiformis 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. jamiş, 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. jamiş 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. jamiş, 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. jamiş. He pointed out that Codoceo (1950) had listed this species under the name Liolaemus multiform is 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 schmidt i from 40 miles east of San Pedro de Atacama, Antofagasta Province, Chile. Following Donoso-Barros (1958b), he recognized C. adspersa, C. stolzmanni, and C. jamiş 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 multipunctatus 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 Ceiolaemus, thus reverting the name to Ceiolaemus marmoratus. Latastes (1892) considered Helocephalus nigriceps to be a synonym of Ctenoblepharys adspersa, Koslosky (1898) considered it to be a variety of Liolaemus signif er Dumérit 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 werneri Müller, 1928, and transferred Liolaemus anomalus Koslosky, 1896, to Ctenoblepharys, based on its presumed morphological and ecological similarities with C. nigriceps and C. schmidt i. 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.

the following year, Cei et al. (1975) recognized the similarity of Liolaemus multimaclulus 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. jami. 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. erroneous, 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 Liolaemus 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 multimaclulus (Duméril and Bibron, 1837), and L. riojanus Cei, 1979b, are not related to Ctenoblepharys, and considered these, together with L. occipitalis Boulenger, 1885, L. lutzai Mertens, 1938, L. scapularis Laurent, 1982, L. wiegmanni (Duméril and Bibron, 1837), and L. cranwellii 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.


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. schrei- bersi and L. cubensis were used as exemplars for Leiocephalinae. No phylogeny for the Stenocercus group is available, so S. crassicaudatus, S. praerornatus, 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 occipitalis, 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: Petrobasis mearnsi, P. thalassinus, Uta stansburiana, U. palmeri, Urosaurus gracilus, U. nigriacus, U. lahteli, U. ornatus, Phrynosoma asio, P. douglasii, P. orbicularis, P. coronatum, Uma notata, U. exsul, and U. scoparia.

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

GENUS CTENOBLEPHARYS

TSCHUDI, 1845

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

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

Ctenoblepharys adspersa Tschudi

Figures 1, 2


ETHERIDGE: REDESCRIPTION OF *CTENOLEPHARUS ADSPERSA*

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

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*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...
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 expanded 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 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; supraoculares 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, elongate scales between orbit, bordered by small, convex scales, some slightly enlarged anteriorly, or not differentiated from posterior temporals. Mental scales, 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. Ventral scales rhomboidal with rounded corners, about three times larger than largest dorsals, becoming scarcely imbricate with interstitial granules on posterior abdomen. Scales of preocular region (fig. 3 A, B) similar to posterior ventrals in both sexes. Preocular pores 6–8 (x = 7.1, sd = 0.8), present in males (N = 8) only. Scales around midbody 95–119 (x = 103.9, sd = 6.6); middorsal scales from occiput to point even with anterior margin of thigh 113–135 (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
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 palate, 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 spheno-occipital processes short, not extending to spheno-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. Retrotartricular 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 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 (supracapular) 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.
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 bladelike 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, Pelusaurus, Phrynosaura, Rhytidodiera, 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 Yañez, 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 spino-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-
ETHERIDGE: REDescription of *CTENOBLEPHARUS ADSPERSA*

Characteristics, 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-

Fig. 6. Dorsal view of the musculature of the right hind limb of (A) male *Ctenoblepharys adspersa* (LACM 49147), (B) female *Liolaemus fitzingerii*, (SDSU 1191) and (C) male *Liolaemus elongatus* (SDSU 1857). Abbreviations: amb—M. ambiens, femtib—M. femerotibialis, flxtib cm—M. flexor tibialis internus capitis medialis, flxtib cp—M. flexor tibialis internus capitis posterior, gast—M. gastrocnemius, illitib—M. iliobibialis, pubishtib—M. puboischiobibialis, 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 fragment 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. aninus.

Osteological character states shared by Ctenoblepharys adspersa and Phymaturus, but not found in Liolaemus, are: (1) lateral borders of orbitalnaal fenestra formed by prefrontals (fig. 4A), (2) supratemporal exposed on lateral face of paroccipital 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 orbitalnaal 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 pigments 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. puboischiotiobals, and the insertion of the M. tibialis anterior is hypertrophied in association with the presence of a sharp, bladelike process of the tibia (Cei, 1993: fig 36) (fig. 6C). The tubial 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 width, 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 palate, (7) maxillary process of ectopterygoid truncate, (8) parapophysis of atlas flat and oriented posteroilaterally, 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 remains. 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 Cej 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 Cej 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 hypertrophied 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 Pelusaurus, 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 wiegmannii (Du-Méril and Bibron, 1837), and assigned it to the subgenus Ortholaemus. I have compared the unique type (MACN 3632) with specimens of L. wiegmannii and find the squamation and color pattern of the type to be well within the limits of variation of L. wiegmannii, although Laurent (1983b) indicated that there may be proportional differences. The locality for L. wiegmannii 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. Pelusaurus cranwelli may be a synonym of Liolaemus wiegmannii, 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. mar- 
moratus* and his newly described *P. wernerii*, 
a synonym of *Liolaemus anomalus* according to 
Cei (1979a). Núñez and Yáñez (1984b) 
restricted the genus to *P. reichei* and *P. au-
dituvelatus*, the latter transferred from *Cte-
noblepharys*. They cited as characteristics of 
the genus (1) eyelid with a conspicuous comb, 
(2) diameter of eye greater than length be-
tween anterior border of eye and rostral, (3) 
tail shorter than snout-vent length, (4) head 
scales poorly differentiated, (5) jaws isogna-
thus, (6) loreal region depressed, and (7) dor-
sal scales imbricate, smooth, and with ac-
companying scales (my translation). My ob-
servations of these two species are in accord 
with this list of characters, except that the 
head scales of both species are as well differ-
entiated as in many species of *Liolaemus*, 
e.g., supraorbital semicircles are distinct, se-
parated from transversely expanded supraocu-
lar by a distinct arc of circumorbitalbs, inter-
parietal prominent, flanked by a pair of larger 
parietal scales, etc. Compared with most oth-
er *Liolaemus*, the snout is distinctly truncate, 
and the ciliary fringe is very prominent. Lau-
rent (1984a) included *L. reichei*, *L. auditu-
velatus*, and *L. stolzmannii* in *Phrynosaura*, 
and distinguished the genus from *Ctenoble-
pharys, Liolaemus* (sensu stricto), and *Cei-
olaemus* by its differentiated supraoculares 
and a number of morphometric differences. *Li-
olaemus reichi* and *L. audituvelatus* possess 
a tibial blade and hypertrophied M. tibialis an-
terior, but the condition in *L. stolzmannii* 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).

**RHYTIDOIDEIRA**

Girard (1858) proposed the genus *Rhyti-
dodeira* for six previously described species 
of *Liolaemus*: *Proctotretus kingii* Bell, 1842, 
*P. magellanicus* Duméril and Duméril, 1851, 
*P. bibronii* Bell, 1842, *P. wiegmannii*, *Tro-
pidurus nigromaculatus* Wiegmann, 1834, and 
*T. oxycephalus* Wiegmann, 1834 (= *L. ni-
gromaculatus*). 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-Bar-
ros and Cei, 1971 (= *L. kingii* fide Cei and 
Scolaro, 1987). *Liolaemus kingii* and *L. ar-
cheforus* have all of the synapomorphies that 
diagnose *Liolaemus*, and, according to Lau-
rent (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 Lau-
rent (1985a).

**VELOSAURA**

Núñez and Yáñez (1984b) described *Ve-
losaura*, including in it *L. ayamararum* Veloso 
et al., 1982, and *L. jamesi*, designating the 
former as its type species. Earlier, Veloso et 
al., (1982), proposed the generic name *Jar-
arancus* 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. tibi-
alis anterior, and although data are not avail-
able for *L. ayamararum, L. jamesi* also has a 
hypertrophied M. puboischiobialis and pig-
mented epimysium of the M. pterygoman-
dibularis. Laurent (1992) referred both spe-
cies to the *signifer* group of the subgenus *Eu-
laemus* (see below), but Núñez and Jaksic 
(1992) and Núñez (1992) continued to rec-
ognize *Velosaura* as a valid genus. None of 
the characters listed for *L. ayamararum* 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 ayamararum* and *L. ja-
mesi are extremely similar phenetically, and may be synonymous, or, if valid, sister species.

VILOCUNIA

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 pleisiomorphic state shared with *Phymaturus* (a longer dentary thought to be a synapomorhpy 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 chilensis*, *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 coerules* (Cei and Ortiz-Zapata, 1983) and *L. cristiani* (Navarro and Nuñez, 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 chilensis* 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 melanin 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. puboischiotibialis, 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. chaconensis 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. darwinii 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 fitzingeri 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 fitzingeri 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. puboischiotibialis (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* + *Eulaemus* + *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 preocular pores usually four or fewer (or absent). However, outgroup comparisons indicate that the polarity of these states is equivocal. Preocular pore numbers are high (5–15) in *Eulaemus, Ortholaemus, Ctenoblepharys*, and *Phymaturus*. Meckel’s groove is open in *Eulaemus* (except in some *Liolaemus darwinii*), *Ortholaemus* (except *Liolaemus occipitalis* [Keller and Krause, 1986]), *Ctenoblepharys*, and the *Phymaturus paluma* group, but preocular pores are lacking in other 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 *Ortholaemus*, 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-"
L. beaglli 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 Ortho-
laemus, 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 Scolaro, 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 Ortho-
laemus 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 design-
ination 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 Ortho-
laemus have all of the apomorphic states that diagnose the fitzingerii group of Eu-
laemus, 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 pres-
ence of a sharp, bladelike process of the tibia. Additionally, they differ from all other Lio-
laemus in having smaller lorilabial scales, usually in two or more rows between the sub-
ocular and supralabials, flat or concave in-
fralabials (personal obs.), and the mental scale narrower anteriorly than posteriorly, and from all other Liolaemus except L. cuyanus in hav-
ing six, rather than four scales in contact with the mental, resulting from contact between the mental and sublabials. Thus, Ortho-
laemus may well be a monophyletic group.

In summary, the species that have been referred to Abas, Ceiolaemus, Eulaemus, Mesolaemus, Ortholaemus, Pelusaurus, Phrynosaura, Rhytidodeira, Velosauro, and Vilcunia exhibit all of the synapomorphies that distinguish Liolaemus from other Liolaeminae. Furthermore, there is some evidence that Vilcunia, Ceiolaemus, and Phry-
osaura may represent monophyletic groups within Liolaemus. There also is evidence that Ortholaemus is a monophyletic group, which, together with the other species that pos-
sess a femoral patch (i.e., Fitzingerii group), forms a more inclusive clade. This clade, to-
gether with Eulaemus, forms a still more in-
clusive clade (see Appendix 2).

DISCUSSION AND SUMMARY

Ctenoblepharys adspersa is a moderate-size (maximum SVL 74 mm) iguanian lizard en-
demic 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 crypt-
ic on this substrate. It possesses a number of derived characteristics that are unique within Tropiduridae and its putative out-
groups Phrynosomatidae and Opluridae; six of these autapomorphies involve the skull, and two the vertebral column. Additionally, C. adspersa differs from most other Liolaem-
inae in having small, nonoverlapping dor-
sal body scales arranged in more-or-less transverse rows, and numerous, poorly differ-
entiated head scales, including small, sub-
equal supraoculares and several suboculars, but with greatly elongate, triangular outer cil-
iiaries that form a prominent comb. Ctenoblepharys adspersa, along with Phymatu-
rus, 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 Phy-
maturus are not known to share any derived characteristics to the exclusion of Liolaemus, nor does Liolaemus share any derived char-
acteristics with either Ctenoblepharys or Phymaturus to the exclusion of the other, and thus relationships of Ctenoblepharys, Phymat-
urus, and Liolaemus are unresolved.

All of the species of Liolaeminae that have been described in or referred to Cteno-
blepharys, 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 adspersa* examined are listed below, followed by their localities. Preserved specimens and skeletons of *Phymaturus* and *Liolaemus* examined for comparison with *Ctenoblepharys adspersa*, 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.”


*Liolaeminae*

*Ctenoblepharys adspersa*: Peru: Ventanilla, near Lima, SMF 75966–69; between Ventanilla and Puerta 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 abauan*: SDSU 1446–64, REE 2845.


*L. anomalus anomalus*: SDSU 1674–75. *L. archeforus archeforus*: MCZ 162002–03,


Leiocephalinae + Tropidurinae


Opluridae


Phrynosomatidae


APPENDIX 2

AN INDENTED CLASSIFICATION OF LIOLAEINAE

Part A. A tentative classification of Liolaeinae, intended to represent historical interestings, 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 + Tropidurinae, 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; supraascapula 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 suboculairs; 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 × longer than wide); orbit large (about 0.43–0.47 × skull length); snout short (about 0.29 × skull length); temporal fenestrae wide (1.5–1.6 × longer than wide); prefrontals wider than long; lacrimal foramen large; maxillary 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. *adspera*

*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; posttemporal scales subimbricate. *periglacialis → sylvanae*

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

**signifer group**: epimyxis of M. pterygomandibularis pigmented; medial head of M. flexor tibialis internus covered by hypertrophied M. puboischiotibialis. *anomalus → pseudoanomalus*

**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. *abauca → 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 erreus*, 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

**nitidus group**: *mallimaccii* Cei, 1980

**palluma** (Molina, 1782) *punae* Cei, Etheridge & Videila, 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

**signifer** *a. gallardoi* Cei & Scolaro, 1982

**montanus** *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. nequensis Müller & Hellmich, 1939
bibronii (Bell, 1843)
bisignatus (Philippi, 1860)
bitaeniatus Laurent, 1984
buergeri Werner, 1907
capillitas Hulse, 1979
ccei Donoso-Barros, 1971
chacoensis Shreeve, 1948
chilensis (Lesson, 1831)
coeruleus Cei & Ortiz-Zapata, 1983
constanzae Donoso-Barros, 1961
copiapensis Müller & Hellmich, 1933
christiani Nuñez et al., 1991
curicensis Müller & Hellmich, 1938
curis Nuñez & Labra, 1985
cyanogaster
c. cyanogaster (Duménil & Bibron, 1837)
c. brattstroemi Donoso-Barros, 1961
donosoi Ortiz-Zapata, 1975
elongatus
e. elongatus Koslowsky, 1896
e. petrophilus Donoso-Barros & Cei, 1971
exploratorium Cei & Williams, 1984
fitzgeraldi Boulenger, 1899
fusculus 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
lorenzmulleri Hellmich, 1950
maldonadae Nuñez 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)
nigrovidiris
n. nigrovidiris 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 (Duménil & 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
sanzuanensis Cei, 1982
saxitilis Avila et al, 1992
schroederi Müller & Hellmich, 1938
silvai Ortiz-Zapata, 1989
tacnae (Shreve, 1941)
tenuis
t. tenuis (Duménil & 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

audituvelatus 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

fitkauí 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

rubali Donoso-Barros, 1961

schmidtii (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

canquelí Cei, 1975

cuyanus 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

**wiegmannii 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

wiegmannii (Duméril & Bibron, 1837)
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