

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3033, 68 pp., 44 figures February 24, 1992

Phylogenetic Analysis and Taxonomy of the *Tropidurus* Group of Lizards (Iguania: Tropiduridae)

DARREL R. FROST^{1,2}

ABSTRACT

Phylogenetic relationships among 44 species of the South American *Tropidurus* group of lizards are analyzed using standard cladistic techniques. Seventy-seven transformation series of osteology, squamation, color, and hemipenes are polarized (when possible) using as first and second outgroups the *Stenocercus* group and *Leiocephalus*. Thirty-six equally parsimonious trees (length 169, ci = 0.568) are discovered, of which one is also the strict and Adams consensus tree of the other 35. *Tropidurus* is demonstrated to be paraphyletic with respect both to *Tapinurus* and to a monophyletic group composed of *Plica*, *Strobilurus*, and *Uracentron*. With the exception of *T. koepckeorum*, all species of *Tropidurus* west of the Andes (the former *T. occipitalis* and *T. peruvianus* species

groups) are parts of a single monophyletic group. Excepting *Uranoscodon*, all species of the *Tropidurus* group east of the Andes are part of a single monophyletic group. *Microlophus* is resurrected for former species of *Tropidurus* west of the Andes, excepting *T. koepckeorum*, which is placed in a monotypic genus *Plesiomicrolophus*, in polytomy with *Microlophus* and *Tropidurus*. *Tropidurus* is redefined to include as synonyms *Plica*, *Strobilurus*, *Uracentron*, and *Tapinurus*. Two new tribes are diagnosed, Tropidurini, equivalent to the *Tropidurus* group, and Stenocercini, equivalent to the former *Stenocercus* group ("*Ophryoessoides*," "*Stenocercus*," and *Proctotretus*). Within Stenocercini, *Proctotretus* and *Ophryoessoides* are synonymized with *Stenocercus*.

INTRODUCTION

Tropiduridae is a medium-sized family of Neotropical iguanian lizards composed of

three subfamilies: Liolaeminae (*Liolaemus*, *Ctenoblepharys*, *Phymaturus*), Leiocephali-

¹ Assistant Curator, Department of Herpetology and Ichthyology, American Museum of Natural History.

² This paper developed from part of a dissertation completed at the Museum of Natural History, University of Kansas.

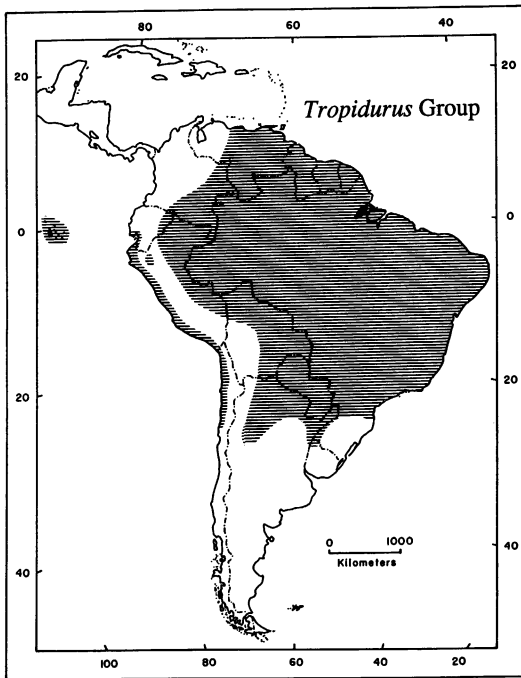


Fig. 1. Distribution of the *Tropidurus* group.

nae (*Leiocephalus*), and Tropidurinae. Tropidurinae is composed of two monophyletic taxa, the *Stenocercus* group (“*Ophryoesoides*,”³ “*Stenocercus*,” *Proctotretus*) and the *Tropidurus* group (fig. 1) (*Tropidurus*, *Tapinurus*, *Uranoscodon*, *Uracentron*, *Strobilurus*, and *Plica*) (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989). Etheridge and de Queiroz (1988), Frost and Etheridge (1989), and Pregill (in press) have substantiated the sister-taxon relationship of these two groups, and the relationship of the Tropidurinae with the Leiocephalinae (fig. 2). The purpose of this study is to formulate a hypothesis based on all available evidence, compare the results with the current hypothesis of intragroup relationships (Etheridge and de Queiroz, 1988), and provide a taxonomy logically consistent (Hull, 1964; Wiley, 1981) with recovered history.

³ Quotation marks surround names of supraspecific taxa that are not demonstrably monophyletic (Wiley, 1979; Kluge, 1989a). For purposes of clarity, all taxa in the *Tropidurus* group will be considered monophyletic unless demonstrated to be otherwise.

ACKNOWLEDGMENTS

For loan of and/or access to specimens I thank: Charles W. Myers and Richard G. Zweifel, American Museum of Natural History (AMNH) (prior to my joining the staff at the AMNH); E. Nicholas Arnold, The Natural History Museum, London (BMNH); Robert C. Drewes, Jacques Gauthier, Alan Leviton, and Jens Vindum, California Academy of Sciences (CAS); Raymond Laurent, Fundación Miguel Lillo (FML); William E. Duellman, Joseph T. Collins, and John E. Simmons, Museum of Natural History, University of Kansas (KU); Robert L. Bezy and John W. Wright, Natural History Museum of Los Angeles County (LACM); Douglas A. Rossman, Museum of Natural Science, Louisiana State University (LSUMZ); Mark Norrell, American Museum of Natural History (MAN private osteology collection); Ernest E. Williams and José Rosado, Museum of Comparative Zoology, Harvard University (MCZ); Teresa C. de Avila Pires, Museu Paraense Emilio Goeldi (MPEG); Stephen D. Busack, David Good, Harry W. Greene, and David Wake, Museum of Vertebrate Zoology, University of California (MVZ); Richard Etheridge, San Diego State University (REE private osteology collection and SDSU); Gregory K. Pregill, San Diego Natural History Museum (SDSNH); James R. Dixon, Texas A&M University (TCWC); Arnold G. Kluge and Greg Schneider, Museum of Zoology, University of Michigan (UMMZ); Norman J. Scott, University of New Mexico (UNM); Ronald I. Crombie, Roy W. McDiarmid, Robert Reynolds, and George R. Zug, National Museum of Natural History (USNM); and Jonathan A. Campbell, University of Texas at Arlington (UTA).

Richard Etheridge, Gregory K. Pregill, and John W. Wright have been of considerable help through their discussions and comments, although this should not be construed necessarily as acceptance of conclusions in this manuscript. Besides these, several others have provided helpful criticism of this manuscript at various stages of its development: Maureen A. Donnelly, William E. Duellman, Arnold G. Kluge, Mathias Lang, Roy W. McDiarmid, Tom Titus, Linda Trueb, and E. O. Wiley. I also thank John Cadle for let-

ting me read his *Stenocercus* manuscript; his comments therein regarding some overstatements in my dissertation have helped me to refine this manuscript. Anne Musser executed figure 18. Permission to use photographs was granted by: David C. Cannatella, Martha L. Crump, James R. Dixon, William E. Duellman, Roy W. McDiarmid, Charles W. Myers, Laurie J. Vitt, and Richard G. Zweifel.

HISTORICAL REVIEW

Prior to the publication of Etheridge's informal tree of relationships within the former "Iguanidae" (Etheridge in Paull et al., 1976), questions of phylogeny in the *Tropidurus* group (*Uranoscodon*, *Tropidurus*, *Plica*, *Tapinurus*, *Strobilurus*, and *Uracentron*) were imbedded in larger discussions of relationships within the former "Iguanidae" (i.e., Crotaphytidae, Corytophanidae, Hoplocercidae, Iguanidae, Phrynosomatidae, Polychridae, Tropiduridae) and former tropidurine iguanids (= Tropiduridae) (Etheridge, 1964, 1966, 1967).

Boulenger (1885) listed the genera of the *Tropidurus* group nonalphabetically, thereby implying some concept of relationship, but it was not until Etheridge and de Queiroz (1988) published their systematic review of "Iguanidae" (sensu lato) that the *Tropidurus* group, within tropidurine iguanids, had been diagnosed sufficiently well to permit detailed discussion. Subsequently, Frost and Etheridge (1989) partitioned the likely paraphyletic "Iguanidae" and recognized these genera (listed above) as parts of one of its constituent groups, Tropiduridae.

A discussion of the taxonomic history of the genera and species of the *Tropidurus* group is hampered by its complexity and historical confusion. Because of this, I will discuss this history in convenient nomenclatural clusters: *Uranoscodon* and *Plica*; *Uracentron* and *Strobilurus*; and *Tapinurus* and *Tropidurus*.

Uranoscodon and *Plica*

Etheridge (1970a) provided an extensive review of the taxonomic history of *Plica*; with minor changes that review is paraphrased here. Linnaeus (1758) named all of the currently named species within this nomenclatural

cluster: *Lacerta plica* (now *Plica plica*), *L. umbra* (now *Plica umbra*), and *L. superciliosa* (now *Uranoscodon superciliosus*).

Laurenti (1768) provided a junior synonym of *L. plica* in his *Iguana chalcidica*. Latreille (1801) placed *L. umbra* and *L. superciliosa* in *Iguana*, and *L. plica* in *Stellio*. In the following year, Daudin (1802) considered all three species to be in the genus *Agama*, along with most smaller scansorial non-chameleon iguanians. Merrem (1820) also included all three species under *Agama*, but supplied a substitute name, *Agama tigrina*, for *Iguana superciliosa* Latreille, 1801 (= *L. superciliosa* Linnaeus, 1758). Opperl (1811) transferred Daudin's (1802) species of *Agama* and *Iguana* into *Lophyrus* Duméril (1806).

Kaup (1825) erected the name *Uranoscodon* (unjustifiably emended to *Uraniscodon* by Boie, 1825), based on *L. superciliosa*, but also including the Linnaean species *L. plica* and *L. umbra*. Boie (1825) suggested that *Agama catenata* Wied-Neuwied (1821) and *Agama picta* Wied-Neuwied (1825) (both species currently in *Enyalius* [Polychridae]) should be included in a genus with *L. superciliosa*. He noted that his name *Ophryessa*, or *Uraniscodon*, could be used. However, he excluded *plica* and *umbra* from this genus.

Spix (1825) named *Lophyrus ochrocollaris* (a junior of *Lacerta umbra*, considered a subspecies of *P. umbra* by Etheridge, 1970a), *Lophyrus panthera* (a junior synonym of *Lacerta plica*), and *Lophyrus xiphosurus* and *Lophyrus aureonitens* (both junior synonyms of *Lacerta superciliosa*) from Brazil. Subsequently, Kaup (1826) synonymized *Lophyrus xiphosurus* Spix and *L. aureonitens* Spix with *L. superciliosa* Linnaeus. He also provided a more detailed characterization of the genus (as *Uraniscodon*) and included, in addition to *superciliosa*, *picta*, and *umbra*, a number of names currently referable to *Enyalius* and *Tropidurus hispidus* (Spix). Boie (1825), dealing with the same species, placed in *Ophryessa* the species *superciliosa*, *ochrocollaris* (= *umbra*), *panthera* (= *plica*), *aureonitens* (= *superciliosa*), *catenata* (= *Enyalius catenatus*), and *margariticeus* (= *Enyalius pictus*).

Fitzinger (1826) recognized a new genus, *Ecphymotes* (type species subsequently designated by Fitzinger, 1843, as *acutirostris*),

for *plica*, *undulatus* (= *Anisolepis undulatus* [Polychridae]), *pictus* (= *Enyalius pictus* [Polychridae]), and *acutirostris* (= *Polychrus acutirostris* [Polychridae]), but he retained Boie's *Ophryessa*, in which he included *superciliosa*, *catenatus* (= *Enyalius catenatus*), *margaritaceus* (= *Enyalius catenatus*), and *umbra*. Kaup (1827) responded by recommending that *Uraniscodon* be partitioned into three subgenera: *Uraniscodon* for *Agama hispida* Spix (= *Tropidurus hispidus*); *Pneustes* for *picta*, *umbra*, and *plica*; and *Ophryessa* for *superciliosa*, *catenata*, and *margaritaceus*. The number of subgenera recommended (3) is probably significant, because Kaup was pre-evolutionary in his views, believing that 3s and 5s had a deep natural significance (Mertens, 1973).

Wagler (1830) erected the genus *Hypsibatus* for *plica*, *umbra*, and *picta*. Subsequently, Wiegmann (1835) replaced *Hypsibatus* with *Hypselophus*, thinking that *Hypsibatus* was preoccupied by *Hypsibates* Nitsch. Under the current Code of Nomenclature (1985) no such preoccupation exists. However, Etheridge (1970a) considered, by reason of Article 23b of the 1961 International Code of Zoological Nomenclature, that *Hypsibatus* was precluded for competing in synonymy by reason of its long lack of use. Contrary to a comment made by Frost and Etheridge (1989), this suppression is continued under the 1985 Code by Article 79(c)iii which states that actions taken under 23b of the 1961 Code are to be upheld unless acted upon by the Commission.

Gray (1827) described *Lophyrus agamoides*, which he later (1831) considered to be a synonym of *Lacerta plica*. *Plica* was erected by Gray (1831) as a subgenus of *Ophryessa* (an unjustified emendation of *Ophryessa* Boie) to include *brasiliensis* (= *Enyalius catenatus* [Polychridae]), *picta* (= *Plica umbra*, in this case, according to Etheridge, 1970a), and *plica*. Gray erected a subgenus, *Xiphura*, of *Ophryessa*, for *superciliosa*, *margaritaceus* (= *Enyalius pictus*), and *rhombifer* (= *Enyalius catenatus*). Gray's confusion between *Agama picta* Wied-Neuwied (= *Enyalius pictus*) and *Plica plica* and *P. umbra* was continued by Schinz (1833).

Duméril and Bibron (1837) employed *Hypsibatus* Wagler for *H. agamoides* and the new *H. punctatus*, both synonyms of *Plica*

plica. In the same work they erected a new genus, *Uperanodon*, to include part of *Plica* Gray and part of *Hypsibatus* Wagler: *ochrocollare* (= *P. umbra*) and *pictum* (= *Enyalius pictus*). *Ophryoessa* (an unjustified emendation of *Ophryessa*) was used by these authors to accommodate the single species *superciliosa*. In the same year, Gravenhorst (1837) followed Wiegmann (1835) and used *Hypselopus* (an unjustified emendation) as the generic name for *plica*.

Fitzinger (1843) treated *Enyalius* (for *catenatus* and *margaritaceus*), *Hypsibatus* (for *umbra*), *Uperanodon* (for *pictus*), *Dryophilus* (for *bilineatus*), and *Ophryoessa* (for *superciliosa*) as subgenera within *Hypsibatus*. He also erected a new genus, *Ptychosaurus*. Because Fitzinger recognized two synonyms of *plica* as distinct species, he erected different subgenera within *Ptychosaurus* for each: *Ptychosaurus* (for *Hypsibatus punctatus* Duméril and Bibron) and *Ptychopleura* (for *L. plica*). A third subgenus of *Ptychosaurus*, *Tritopsis*, was erected for *Tropidogaster blainvillii* Duméril and Bibron (1837) (= *Chalarodon madagascariensis*, fide Etheridge, 1969a). In 1864, Fitzinger regarded his subgenus *Ptychopleura* (of *Ptychosaurus*) as a genus distinct from the nominate subgenus, even though they had the same biological type species.

Gray (1845) referred *umbra* and *picta* to *Uraniscodon*, but referred *umbra* (under the misidentification of *plica*) and *punctata* (= *plica*) to *Plica*. Following Fitzinger (1843), he retained *superciliosa* in *Ophryoessa* (an unjustified emendation of *Ophryessa*).

Boulenger (1885) was the first to group together exclusively *plica* and *umbra*—albeit in *Uraniscodon*. *Ophryoessa* was considered to be a monotypic genus for *superciliosa*. Stejneger (1901) noted the incongruity of the arrangement; *Uraniscodon* Kaup was based on *superciliosa*, even though Kaup included both *umbra* and *plica*. Boie's (1825) *Uraniscodon* included only *superciliosa* of the originally included species; Stejneger (1901) regarded this as tantamount to fixation of a type species. Burt and Burt (1931) followed Stejneger (1901) in the use of the name *Uraniscodon superciliosa*. Etheridge (1970a) formally designated *L. superciliosa* Linnaeus as the type species of *Uraniscodon*, and placed three names in the synonymy of *Plica umbra*: *Tropidurus uncarinatus* Werner (1899), *T. hol-*

otropis Boulenger (1912), and *Plica tuberculatum* Andersson (1918). He also excluded one species, *Plica stejneri* Burt and Burt (1930) (= *Tropidurus spinulosus*), from *Plica*. Etheridge's (1970a) revision of *Plica* was the first to characterize the genus adequately. Most recently, *Plica lumaria* was discovered and named by Donnelly and Myers (1991) and (as *Plica nigra*, a junior synonym) by Mägdefrau (1991). This species, phenotypically similar but also plesiomorphic in some respects of squamation to *Plica plica*, is from Cerro Guaiquinima in southern Venezuela.

Uracentron and *Strobilurus*

Linnaeus (1758) named *Lacerta azurea*, mistakenly thought to be from Africa. Subsequently, Latreille (1802) named *Stellio brevicaudatus*, a junior synonym of *L. azurea*. He placed this species and *L. azurea* in *Stellio*, along with other spiny-tailed lizards. This arrangement was followed by Daudin (1802) and Fitzinger (1826). Merrem (1820) placed *azurea* in *Uromastix* (another genus of spiny-tailed lizard), and supplied a replacement name, *Uromastix caeruleus*.

Kaup (1826) introduced the name *Uracentron* for *azurea* (and *caerulea*). Wagler (1830) emended the name to *Urocentron*, which enjoyed common usage prior to 1968 (e.g., Fitzinger, 1843; Mertens, 1925; Dunn, 1944; Valdivieso and Tamsitt, 1963; Peters, 1967). Other emendations of *Uracentron* were *Uranocentron* (Gray, 1831, 1845), *Uranocentron* (O'Shaughnessy, 1881), and *Urocentron* (Boulenger, 1894; Werner, 1900). Cuvier (1829) supplied *Doryphorus* as a substitute name, and it enjoyed some popularity (Schinz, 1835; Duméril and Bibron, 1837; Guichenot, 1855; Duméril, 1856; Cope, 1870). Gray (1831) placed *Uracentron* (as *Uranocentron*) as a subgenus of *Ophryessa*, along with *Plica*.

Wiegmann (1834b) named a new genus and species of spiny-tailed lizard, *Strobilurus torquatus*, from Brazil. Guichenot (1855) inadvertently renamed this species as *Doryphorus spinosus*, but in the same paper he named a second species, *Doryphorus flaviceps*, that is currently in *Uracentron*. Fitzinger (1843) placed *Strobilurus* as a subgenus of *Steironotus*, which also included a few species currently allocated to *Leiocephalus* and *Stenocercus*. Schlegel (1858) transferred *azurea*,

along with other spiny-tailed species, to *Hoplurus*.

O'Shaughnessy (1881) correctly placed *Doryphorus flaviceps* Guichenot in *Uracentron* (as *Uranocentron*). Boulenger (1885) recognized three species of *Uracentron*: *U. azureum* (Linnaeus, 1758), *U. flaviceps* (Guichenot, 1855), and *U. castor* (Cope, 1870). Also, he recognized that *Doryphorus spinosus* is a junior synonym of *Strobilurus torquatus*.

Burt and Burt (1933), following Fitzinger (1843) and Tschudi (1845), confused *Uracentron* and *Phymaturus*, and mistakenly included *palluma* in *Uracentron*. They also included *Urocentron meyeri* Werner (1900), which subsequently was demonstrated to be a member of *Stenocercus* (Etheridge, 1968).

Etheridge (1968) reviewed both *Strobilurus* and *Uracentron*. He maintained the monotypic status of *Strobilurus* and recognized four species in *Uracentron*: *azureum*, *guentheri*, *wernerii*, and *flaviceps*. Greene (1977) reevaluated the status of the species of *Uracentron* and regarded *guentheri* and *wernerii* as subspecies of *azureum*.

Tropidurus and *Tapinurus*

Unlike those in the other genera within the *Tropidurus* group, most of the species in *Tropidurus* and *Tapinurus* have become known only relatively recently. Wied-Neuwied (1820) described *Stellio torquatus* from Brazil; subsequently, he (1825) erected a new genus, *Tropidurus*, for this species. Lichtenstein (1822) named *torquatus* (fide Rodrigues, 1987) as *Agama operculata*, and Raddi (1822) named it as *Agama brasiliensis*. Spix (1825) named several new species from Brazil: *Agama hispida* (now *Tropidurus hispida*), *A. nigrocollaris* (a synonym of *A. hispida*, fide Peters, 1877), *A. cyclurus* (a synonym of *A. hispida*, fide Peters, 1877), *A. semitaeniatus* (now *Tapinurus semitaeniatus*), and *A. tuberculata* (a synonym of *Tropidurus torquatus*, fide Rodrigues, 1987). Kaup (1826) mistakenly transferred *A. hispida* into *Uraniscodon* with species currently allocated to *Uraniscodon* and *Plica*.

Fitzinger (1826) recognized *Tropidurus* Wied-Neuwied (1820), but he included *schreibersi* (nomen nudum = *Pristinotus schreibersi* Gravenhorst, 1837 = *Leiocephalus schreibersi*), along with *torquatus*.

Wagler (1830) erected *Platynotus* for *Agama semitaeniata* Spix, and recognized an enlarged *Tropidurus* that contained *torquatus* (including *tuberculata* and *hispidus* as synonyms), *nigrocollaris* (with *cyclurus* considered a synonym), and a few other species currently allocated to the generalized scansorial genera *Sceloporus* and *Oplurus*. This arrangement was followed by Gray (1831), who retained *A. hispidus* Spix as a distinct species, but reallocated *semitaeniatus* to *Tropidurus*.

Lesson (1831) named *Stellio peruvianus* and *Lophyrus araucanus* (both = *peruvianus*, fide Ortiz-Zapata, 1980a), the first species currently allocated to *Tropidurus* to be named from west of the Andes. Wiegmann (1834a) named two more species from west of the Andes, *Tropidurus heterolepis* and *T. microlophus* (= *peruvianus*), and for the first time associated species from both sides of the Andes under *Tropidurus*. Wiegmann (1834b) continued to recognize *Platynotus semitaeniatus* and maintained Wagler's (1830) concept of *Tropidurus*, only adding the two new species and some species currently referable to *Liolaemus*.

Duméril and Bibron (1837) erected *Microlophus* for their new species *M. lessonii*; they regarded all other species from west of the Andes (i.e., *peruvianus*, *microlophus*, *heterolepis*), as synonyms. For *Tropidurus torquatus* they suggested *Ecphymotes* (not of Fitzinger, 1826) as a replacement generic name. Surprisingly, I have been unable to find any mention of *A. semitaeniata* Spix in this classic work.

Bell (1843) named the first of the Galapagos *Tropidurus* from material collected by Darwin as *Leiocephalus grayii*. Fitzinger (1843) erected *Steirolepis* as a rough equivalent of *Microlophus* Duméril and Bibron (1837), including *microlophus*, *heterolepis*, and *peruviana*, but also including *semitaeniata*, presumably because *semitaeniatus* shares small scales with these other taxa. He retained *Tropidurus* for *torquatus* (including *hispidus* and *tuberculata* as synonyms) and *microlepidotus* (probably a synonym of *torquatus*; including *nigrocollaris* and *cyclurus*).

Tschudi (1845) followed Fitzinger's (1843) use of *Steirolepis* and added four new species names from Peru: *xanthostigma* (= *peruvianus*), *quadrivittata* (type locality in a region transferred to Chile in 1878), *thoracica*, and

tigris. In the same year, Gray (1845) replaced *Tropidurus* with a new name, *Taraguira*, and added two new species names: *smithii* (= *hispidus*) and *darwinii* (= *torquatus*). He recognized *Microlophus* for *peruvianus* and transferred *grayii* to *Leiocephalus* in the subgenus *Holotrophis*.

Gray (1845) named two junior synonyms, *Taraguira smithii* (= *Tropidurus hispidus*, fide Boulenger, 1885) and *Taraguira darwinii* (= *T. torquatus*, fide Boulenger, 1885). Berthold (1859) named another junior synonym of *Tropidurus hispidus*, *Proctotretus toelsneri*, and in 1861, two more were named: *Trachycylus superciliaris* Günther (1861) and *Tropidurus macrolepis* Reinhardt and Lütken (1861). Reinhardt and Lütken (1861) also named a currently recognized species, *T. hygomi*, from Brazil, as well as *Tropidurus macrolepis* (= *T. hispidus*, fide Rodrigues, 1987). Cope (1862) named *Microlophus spinulosus* (now *Tropidurus spinulosus*), from Paraguay.

With remarkable insight, Peters (1871) returned *grayii* to *Tropidurus* and named two new species, *bivittata* (from the Galapagos) and *occipitalis* (from western Ecuador). He also conceived of *Tropidurus* as composed of four subgenera: *Craniopeltis* (*grayii* and *bivittata*), *Laemopristsis* (*occipitalis*), *Microlophus* (*microlophus* and *heterolepis*), and *Tropidurus* (*torquatus* and *macrolepis*).

Bocourt (1874) named *Aneuoporus occipitalis*, which is identical to *Laemopristsis occipitalis* Peters (1871).

Steindachner (1876) described *Tropidurus* (*Craniopeltis*) *pacificus pacificus* and *T. (C.) p. habelii* from the Galapagos, following Peters' (1871) subgeneric arrangement. In the same year, Cope (1876) placed *occipitalis* into *Craniopeltis*, thereby synonymizing *Laemopristsis* Peters. In the same paper, Cope named *Microlophus inguinalis* (= *peruvianus*) and transferred *heterolepis* to *Microlophus*.

Günther (1877), staying with Bell's (1843) earlier judgment, returned *pacificus* and *grayii* (including *bivittata*) to *Leiocephalus*. In the same year, Peters (1877), regarded *Platynotus* as a subgenus of *Tropidurus*.

O'Shaughnessy (1879), following Günther (1877), named *Leiocephalus* (*Craniopeltis*) *variegatus*, a junior synonym of *Microlophus spinulosus* Cope, 1862. Boettger (1885) followed Peters (1871) and regarded *Microlophus* as a subgenus of *Tropidurus*.

In the *Catalogue of Lizards in the British Museum (Natural History)*, Boulenger (1885) considered all of the generic names based on species within the nomenclatural cluster composed of current *Tropidurus* and *Tapinurus* to be synonyms of *Tropidurus*. In *Tropidurus* he recognized 11 species: (1) *grayii* (including *bivittata*); (2) *pacificus*; (3) *occipitalis*; (4) *bocourtii* (a new species, synonymous with *occipitalis*); (5) *peruvianus* (including *araucanus*, *microlophus*, *heterolepis*, *lessonii*, *xanthostigma*, *thoracica*, *quadrivittata*, and *inguinalis*); (6) *spinulosus* (including *variegatus*); (7) *torquatus* (including *tuberculata*, *microlepidotus*); (8) *hygomi*; (9) *hispidus* (including *smithii*, *nigrocollaris*, *cyclusus*, *toelsneri*, *superciliaris*, *macrolepis*); (10) *semitaeniatus*; and (11) *blainvillii* (= *Chalarodon madagascariensis* according to Etheridge, 1969a). With the exception of the controversial status of *Platynotus* (= *Tapinurus*), competition between generic arrangements is absent after Boulenger's catalog (1885).

Cope (1889) named *Tropidurus lemniscatus* (a junior synonym of *T. bivittatus*) from the Galapagos. Subsequently, Baur (1890) described five new *Tropidurus* species from the Galapagos: *albemarlensis*, *indefatigabilis* (= *albemarlensis*), *delanonis*, *duncanensis*, and *abingdonensis* (= *pacificus*). Boulenger (1891) responded to Cope's (1889) and Baur's (1890) treatments of Galapagos *Tropidurus* by recognizing only three Galapagos species: *bivittatus* (including *abingdonensis* as a synonym), *pacificus* (including *lemniscatus* in synonymy), and *grayii* (including as synonyms Baur's *albemarlensis*, *indefatigabilis*, *delanonis*, and *duncanensis*). Consistent with his view of a multiplicity of species in the Galapagos, Baur (1892) elevated *T. pacificus habelii* to species status, supplied an unneeded replacement name for *T. delanonis* (*T. hoodensis*), and named two new taxa: *T. jacobii* (= *T. a. albemarlensis*) and *T. barringtonensis* (= *T. albemarlensis barringtonensis*).

Heller (1903) added *T. grayii magnus* (= *T. a. albemarlensis*) to the list of described taxa from the Galapagos, and regarded *T. barringtonensis* to be a race of *grayii* and *T. abingdonensis* Baur to be a synonym of *T. pacificus*.

Van Denburgh and Slevin's (1913) revision set the current taxonomy of Galapagos

Tropidurus. They recognized seven species in the Galapagos: *pacificus*, *duncanensis*, *habelii*, *bivittatus*, *delanonis*, *grayii*, and *albemarlensis* (with two subspecies, *albemarlensis* and *barringtonensis*).

On the mainland, Steindachner (1891) named *T. stolzmanni* from Peru. Ten years later, Steindachner (1901) named *T. theresiae* from Peru, and subsequently (1902) amplified the description. Boulenger (1900) named *Tropidurus thomasi* (a junior synonym of *T. thoracicus*) from Peru, and, subsequently in 1902 he named *T. melanopleurus* from Bolivia. Roux (1907) named *T. tschudii* (a synonym of *T. occipitalis*) from Peru. Müller (1924) named *T. continentalis* (a synonym of *T. occipitalis*) from Ecuador and *T. pictus* and *T. praeornatus* from Bolivia (both synonymous with *T. melanopleurus*).

Burt and Burt (1930) placed *hispidus* in the synonymy of *torquatus*, and placed *T. tschudii* Roux, *T. continentalis* Müller, and *T. bocourti* Boulenger into the synonymy of *T. occipitalis*. In 1931 they placed *T. hygomi* in the synonymy of *T. torquatus*.

Amaral (1933) recognized a new genus, *Tapinurus*, for a new species, *scutipunctatus*, from Brazil. Schmidt and Inger (1951) considered this name to be a junior synonym of *Platynotus semitaeniatus*. Recently, Rodrigues (1984b) showed that *Platynotus* was a preoccupied name and that *Tapinurus* Amaral (1933) had priority. In addition, Rodrigues named a new Brazilian species, *Tapinurus pinima*. Subsequently, Manzini and Abe (1990) described another *Tapinurus*, *T. helenae*.

Mertens (1956) produced a study of the Peruvian species of *Tropidurus* west of the Andes, recognizing five species in Peru: *holotropis* (= *Plica umbra*, fide Etheridge, 1970a), *occipitalis*, *theresiae*, *peruvianus*, and *thoracicus*. Mertens considered *tigris* to be a subspecies of *peruvianus*, and *stolzmanni* to be a subspecies of *occipitalis*. He also named *T. occipitalis koepckeorum* (now *T. koepckeorum*) and *T. peruvianus salinicola*. Donoso-Barros (1966), working in Chile, named five new taxa: *T. peruvianus mamiñensis*, *T. p. marianus*, *T. p. atacamensis*, *T. theresioides*, and *T. tarapacensis*. Also, he reduced *heterolepis* and *quadrivittatus* to the status of subspecies of *peruvianus*. Dixon and Wright (1975) reviewed the *Tropidurus* of Peru and

revised the arrangement of Mertens (1956). They recognized that *T. occipitalis koepckeorum* and *T. o. stolzmanni* were distinct species and also named two subspecies of *T. thoracicus*: *talarae* and *icae*.

Ortiz-Zapata (1980b) reviewed the taxonomic status of *Tropidurus* species in Chile. He synonymized *T. peruvianus mamiñensis* with *T. theresioides*, named *T. yanezi*, and revalidated the species status of *T. quadrivittatus* and *T. heterolepis*. Subsequently, Ortiz-Zapata (1980c) elevated *T. peruvianus atacamensis* to species status and regarded *T. p. marianus* as a synonym.

East of the Andes, Roze (1958) named *Tropidurus bogerti* from Venezuela. Donoso-Barros (1968) treated it, without discussion, as a species of *Plica*, but this view was rejected by Etheridge (1970a).

Vanzolini and Gomes (1979) started the dismemberment of *T. torquatus* (sensu Burt and Burt, 1931), by revalidating *T. hygomi*, of eastern Brazil (although *T. hygomi* had earlier been recognized by Etheridge, 1970b, without explanation). Cei (1982) followed by describing *T. etheridgei* from Argentina, and Gudynas and Skuk (1983) named *T. catalanensis* from Uruguay. Rodrigues's (1987) study of the species of *Tropidurus* similar to *T. torquatus* from south of the Rio Amazonas went far to sorting the species masquerading under the name *T. torquatus*. He recognized *hygomi*, *torquatus* (including *catalanensis* as a synonym), *etheridgei*, *hispidus*, and described a number of new species: *T. cocorobensis*, *T. erythrocephalus*, *T. insulanus*, *T. itambere*, *T. montanus*, *T. mucujensis*, and *T. oreadicus*. Later, Rodrigues et al. (1988) recognized another new species, *T. psammonastes*, similar to *T. hygomi* and *T. cocorobensis*.

Laurent (1982) demonstrated that *T. pictus* Müller and *T. praeornatus* Müller are junior synonyms of *T. melanopleurus*, although this synonymy had been made, without discussion, by Etheridge (1970b). Rodrigues (1988) disputed the synonymy of *T. pictus* (including *T. praeornatus*) with *T. melanopleurus*.

Surprisingly, three species from Brazil have come to light that are apparently not closely related to the *Tropidurus torquatus* group. These are *Tropidurus nanuzae* Rodrigues (1981), *T. amathites* Rodrigues (1984a), and

T. divaricatus Rodrigues (1986), which Rodrigues (1986) considered to be closely related. The evolution of this group has been discussed by Rodrigues (1986) and Kasahara et al. (1987).

MATERIALS AND METHODS

The methodology for formulating general phylogenetic hypotheses in this study is parsimony analysis (Kluge and Farris, 1969; Farris and Kluge, 1985, 1986; Farris, 1983; Churchill et al., 1985), with its underlying assumption that the weight of all available evidence must be followed (Kluge, 1989b). For polarizing hypotheses of transformation, outgroup comparison has been shown to be the most general method (e.g., Stevens, 1980; Farris, 1982; Kluge, 1984, 1985; Brooks and Wiley, 1985). In particular, a first outgroup of the group in question, and the outgroup of that combined group are required for adequate transformation polarity (Watrous and Wheeler, 1981; Maddison et al., 1984). Fortunately, previous studies (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Pregill, in press) have shown that for the *Tropidurus* group the "*Stenocercus*" group ("*Stenocercus*," "*Ophryossoides*," and *Proctotretus*) is the first taxonomic outgroup, *Leioccephalus* is the second taxonomic outgroup, and the *Liolaemus* group (*Liolaemus*, *Phymaturus*, and *Ctenoblepharys*) is the third taxonomic outgroup (fig. 2).

The hypothesized character transformations in this analysis fall into four categories: (1) polarized (additive); (2) unpolarized (additive); (3) unordered (nonadditive), ancestor hypothesized; (4) unordered (nonadditive), ancestor not hypothesized. Polarized transformations may be of two characters (of which one is hypothesized as ancestral to the other) or more, but in all cases the additivity of transformation is maintained and the ancestral condition is hypothesized. Unless noted otherwise, analyzed transformations were polarized (additive). Unpolarized transformations are those in which the ancestral condition cannot be deduced, but for reason of being either a two-character transformation or a multicharacter transformation in which the order of transformation is hypothesized

on ontogenetic grounds or by reason of morphological intermediacy, additivity is maintained (i.e., regardless of the ancestral condition it takes two steps to go from character 0 through character 1 to character 2). Unordered transformations may have the ancestral condition hypothesized, but additivity is not assumed (i.e., any change from one homolog to another is counted as one step), for reason of lack of evidence of any particular polarity between a number of characters. Unpolarized and unordered transformations must be included in the character analysis because the objective of any analysis is to explain all of the data at hand. Additionally, both of these "nontraditional" kinds of transformations have substantial roles to play in the development of the most parsimonious unrooted network of terminal taxa. The only difference between these kinds of transformations and standard polarized transformations is that they do not necessarily contribute to the polarity vector that determines rooting of the network to make a tree.

Occasionally, a particular species could not be assessed for a particular character because of damage to a specimen or because of logical incongruencies (e.g., shape of a scale in a lizard lacking that particular scale). In these cases, the character was coded as "unknown" for that taxon. Analytical programs used (discussed below) allow this by hypothesizing the "unknown" to be equivalent to the least rejected assignment in any particular network topology.

The transformation series have been arranged into a data matrix that was subjected to analysis using the PAUP 3.0 (Phylogenetic Analysis Using Parsimony) program of Swofford (1989) and HENNIG86 1.1 (Farris, 1988). Because the data matrix is too large for evaluating all possible trees or using the branch-and-bound method of Hendy and Penny (1982), only heuristic methods were used to analyze the data. Within PAUP a number of alternatives of taxon addition, character optimization, and swapping methods were used. In HENNIG86, extended branch-breaking was used. For trees produced by PAUP, alternative rooting points were checked using MacClade (Maddison and Maddison, 1987). The Dos Equis (XX) utility in HENNIG86 was also used to check alter-

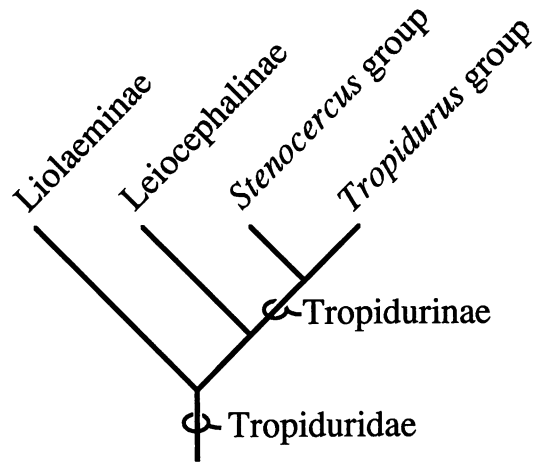


Fig. 2. Cladogram of the Tropiduridae.

native rooting points and character support for stems. Once sources of cladogram instability were identified it was possible to discover cladograms unidentified by either analytical program. Tree optimization was obtained using the consistency index (ci) of Kluge and Farris (1969). Further discussion of analytical techniques can be found under Results. Only stems supported under some character optimization method were considered to be supported; no topologies dependent on "empty" stems are discussed.

Because some members of the *Tropidurus* group are rare (e.g., *Strobilurus torquatus*) or in collections not available to me (e.g., *T. psammonastes*, *T. amathites*), I was unable to see adequate series of, or, in some cases, any specimens of some species. Additionally, many identifications applied to previously prepared skeletons (e.g., *Tropidurus peruvianus* and *T. torquatus*) are dubious, given the recent taxonomic disarray of this group—especially if explicit locality data are not supplied. Thus, with the exception of a few species (e.g., *T. occipitalis*), the amount of material available was limited. Because of this I have tried to be conservative in characterizations.

Skeletons, alcoholics, hemipenes, and cleared and double-stained specimens of almost all taxa (see Appendix 1—Specimens Examined) were examined for interspecific variation that could be hypothesized to be

apomorphies relative to outgroups (see Methods).

Members of the *Tropidurus* group that were not examined are:

1. *Tropidurus tarapacensis*. This is a member of the anagenetically tightly knit *T. peruvianus* group of species (Ortiz-Zapata, 1980a, 1980c). This species is phenotypically so similar to *T. tigris*, *T. yanezi*, and *T. theresioides* that its absence probably has little effect on the analysis.

2. *Tropidurus psammonastes*. This is one of the recently described species (Rodrigues et al., 1988) of the *Tropidurus torquatus* group from Brazil that is, according to the original description, closely similar to *T. hygomi*. Additionally, although I had access to alcoholic material of *T. cocorobensis*, *T. insulanus*, and *T. mucujensis* (Rodrigues, 1987) I was unable to prepare skeletons or hemipenes of these (although X-rays were available).

3. *Tropidurus amathites* Rodrigues (1984b) and *T. divaricatus* Rodrigues (1986). These two recently described Brazilian species presumably are close to *T. nanuzae* Rodrigues, 1981, sharing with it a reduced sternal fontanelle (Rodrigues, 1986) and a presumably derived karyotype (Kasahara et al., 1987). Like the recently described Brazilian species in the *Tropidurus torquatus* group, *T. psammonastes*, these were not available to me.

4. *Tapinurus helenae* Manzini and Abe (1990). This Brazilian species is clearly closely related to the other highly apomorphic species of *Tapinurus*, and appears to differ from *Tapinurus semitaeniatus* only in color pattern and minor aspects of squamation.

TRANSFORMATION SERIES

In this section I will neither give an exhaustive summary of the morphology and anatomy of members of the *Tropidurus* group, nor will I solely summarize variation that can be characterized successfully in transformation series. Rather, I will present a brief summary of the features that can be characterized in ways that allow phylogenetic inferences to be drawn; those that cannot be characterized successfully now, but that may be of interest to successive systematists, are noted where appropriate. Additionally, I will occasionally digress into areas that may be of no great

importance to the systematics of the *Tropidurus* group, but may have some bearing on larger questions of iguanian relationships. In polarized transformations below, "0" denotes the hypothesized plesiomorphic condition and "1" (and higher integers) refers to hypothesized apomorphies. In unpolarized and unordered transformations the integer assignment is arbitrary.

Throughout this discussion I will use the following collective terms (species not examined noted with a †):

(1) *Tropidurus occipitalis* group: *Tropidurus grayii* complex (*T. albemarlensis*, *T. duncanensis*, *T. delanonis*, *T. grayii*, and *T. pacificus*), *T. bivittatus*, *T. habelii*, *T. koepckeorum*, *T. occipitalis*, and *T. stolzmanni*.

(2) *Tropidurus peruvianus* group: *Tropidurus atacamensis*, *T. heterolepis*, *T. peruvianus*, *T. quadrivittatus*, †*T. tarapacensis*, *T. theresiae*, *T. theresioides*, *T. thoracicus*, *T. tigris*, *T. yanezi*.

(3) Western *Tropidurus* group: *Tropidurus occipitalis* group + *T. peruvianus* group.

(4) Eastern *Tropidurus* group (or *Tropidurus* group east of the Andes)⁴: †*Tropidurus amathites*, †*T. divaricatus*, *T. torquatus* group (see below for content), *T. melanopleurus*, *T. nanuzae*, *T. spinulosus*, *Plica*, *Strobilurus*, *Tapinurus*, *Uracentron*, *Uranoscodon*.

(5) *Tropidurus torquatus* group: *T. bogerti*, *T. cocorobensis*, *T. erythrocephalus*, *T. etheridgei*, *T. hispidus*, *T. hygomi*, *T. insulanus*, *T. itambere*, *T. montanus*, *T. mucujensis*, *T. oreadicus*, †*T. psammonastes*, *T. torquatus*.

CRANIAL CHARACTERS

1. Skull size: (0) adult males with head length < 23 percent of snout-vent length; (1) adult males with head length > 23 percent of snout-vent length. Members of the *Tropidurus* group east of the Andes, excluding *Uranoscodon*, have relatively large heads, particularly when compared to the *Tropidurus* group west of the Andes. The "*Stenocercus*" group and species of *Leiocephalus* also have relatively small heads.

⁴ I recognize that the easternmost "western" *Tropidurus*, *T. stolzmanni*, is found east of the continental divide in the Huancabamba Depression Region. However, this generalization of "eastern" and "western" is so convenient that I overlook the geographical anomaly.

2. Skull elevation (fig. 3): (0) skull not elevated at level of orbits (skull height < 39% of skull length)—postorbital bone not rotated to form a flange; (1) skull elevated at level of orbits (skull height > 39% of skull length)—postorbital bone rotated outward to form a flange. *Uranoscodon superciliosus* and *Plica umbra* have noticeably elevated skulls compared with the remainder of the *Tropidurus* group and the outgroups. This elevation is correlated with the enlargement of the orbits and concomitant rotation of the postorbital bones to form postorbital flanges. Although some members of the outgroups (e.g., some "*Ophryoessoides*") show moderate elevation, these species are removed phylogenetically from the base of the "*Stenocercus*" group; therefore, the similar condition is considered homoplastic.

3. Skull compression (fig. 3): (0) not compressed—skull height > 30 percent of skull length; (1) compressed—skull height \leq 25 percent of skull length. *Tapinurus* shows extreme dorsoventral compression of the skull (and body) relative to all other members of the *Tropidurus* group and outgroups.

4. Rostrum length (fig. 3): (0) long; (1) shortened. Within the *Tropidurus* group, only *Plica umbra* and *Uranoscodon superciliosus* show any perceptible shortening of the rostrum (preorbital length of the skull). In both of these species this may be correlated with elevation of the skull in the orbital region. A related characteristic, rostrum shape, has defied adequate characterization. Upon casual inspection, *Uranoscodon* appears to have a blunt rostrum. What causes this illusion is the extreme elevation of the skull at the level of the orbits; *Uranoscodon* has an acute snout. Only individuals of *Plica* exhibit a blunt snout. However, *Plica lumaria* does not exhibit this feature and *P. plica* is sexually dimorphic in this character. Males (e.g., MAN 76, MCZ 43865) have a snout relatively more acute than females. Only female *Plica plica* (e.g., AMNH 61314, KU 167499) could be coded as having blunt snouts. However, the fact that this is sexually dimorphic in *Plica plica*, absent in the almost identical *P. lumaria*, and not sexually dimorphic in *Plica umbra* makes me suspicious that these features are not homologous, and, therefore, I have not used them in my analysis.

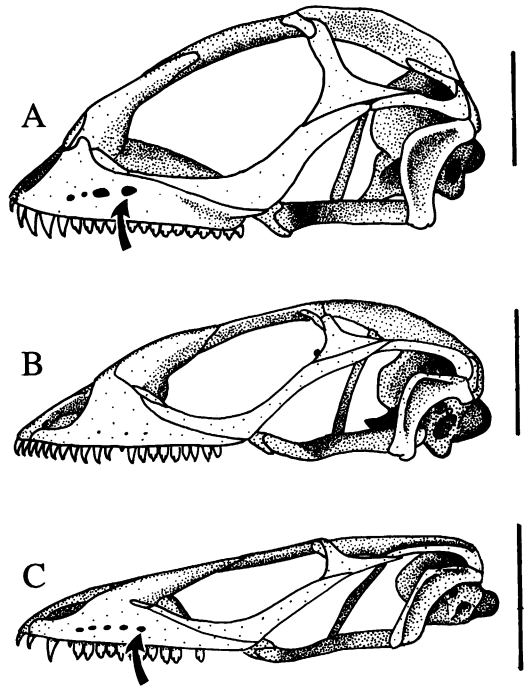


Fig. 3. Lateral views of skulls. A: *Plica umbra*, KU 146659, showing great skull elevation and shortening of rostrum. B: *Tropidurus atacamensis*, KU 161986, showing no pronounced elevation of skull or shortening of rostrum. C: *Tapinurus semitaeniatus*, LSUMZ 39519, showing great skull compression. Scales = 5 mm. Arrows show enlarged maxillary nutritive foramina.

5. Premaxilla (fig. 4): (0) nasal spine narrow—dentigerous part of premaxilla broad; (1) nasal spine broad—dentigerous part of premaxilla narrow. In *Plica*, *Strobilurus*, *Uracentron*, and *Uranoscodon* the dentigerous part of the premaxilla is narrowed with respect to the remaining *Tropidurus* group and outgroups. One would expect this feature to be highly correlated with the number of premaxillary teeth a priori, but this is not so; see Transformation Series 19. Although autapomorphic, *T. spinulosus* has a particularly narrow nasal spine relative to all other members of *Tropidurus* east of the Andes.

6. Nasal bones (fig. 5): (0) not reduced—external choana does not approach level of anterior extent of prefrontal; (1) reduced—excavated to a point approaching the anterior part of the prefrontal in *T. bogerti*; (2) ex-

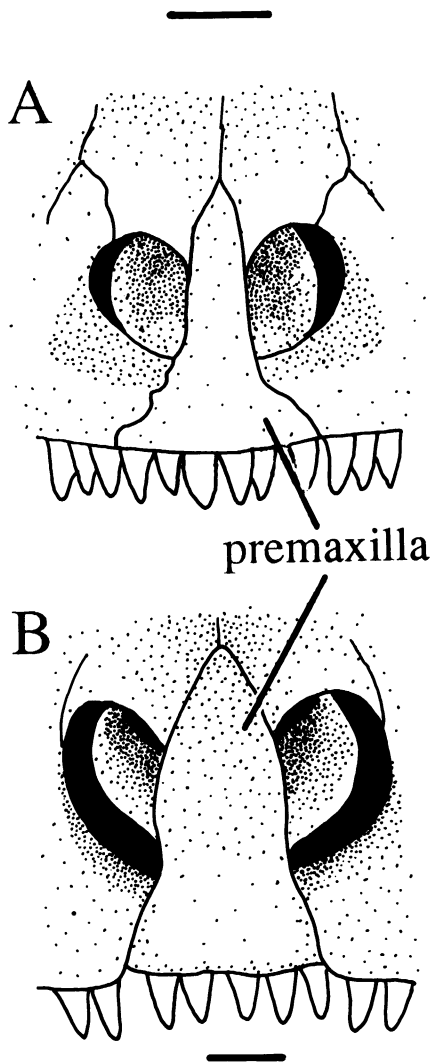


Fig. 4. Anterior views of premaxilla. A: *Tropidurus melanopleurus*, KU 136370. B: *Plica plica*, MAN 76. Scales = 1 mm.

cavated to a point where the prefrontal contacts the margin of the external choana in *Tapinurus*. Although short-snouted members of the *Tropidurus* group (i.e., *Plica*, *Uranoscodon*) appear upon cursory glance to have the nasal bones reduced, more careful examination shows that this is not the case. This is an illusion caused by the extreme hypertrophy in size of the orbits in these species. Only *Tropidurus bogerti* and *Tapinurus* (most extreme) show any retreat of the nasals.

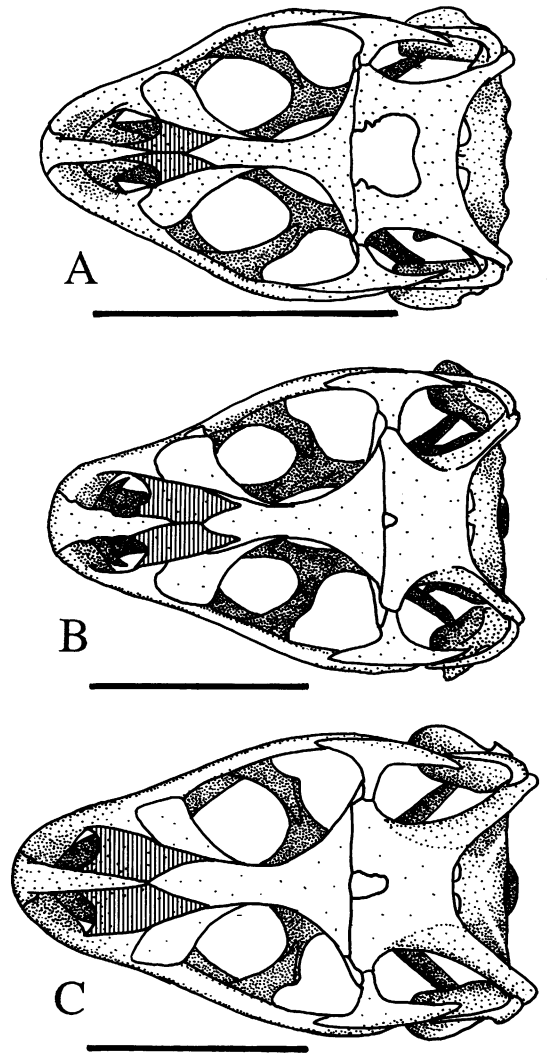


Fig. 5. Dorsal views of skulls. Nasal bones are shaded. A: *Tapinurus semitaeniatus*, LSUMZ 39519, extreme excavation of nasals. B: *Tropidurus bogerti*, RWM 11662, some excavation of nasals. C: *Tropidurus stolzmanni*, KU 134747, no excavation of nasals. Scales = 10 mm.

7. Nutritive foramina of maxillary (fig. 3): (0) small, inconspicuous; (1) enlarged, conspicuous. The characteristic of greatly enlarged nutritive foramina along the lateral surface of the maxilla is unique among iguanians and characteristic of the *Tropidurus* group east of the Andes, excluding *Uranoscodon*.

8. Maxillopalatine foramen (infraorbital

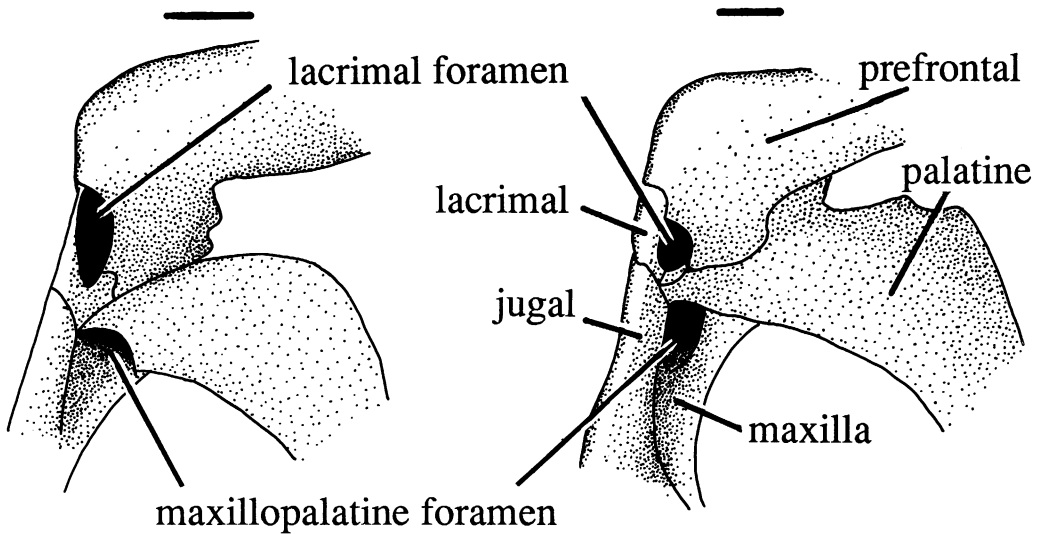


Fig. 6. Posterior view of anterior margin of left orbit showing maxillopalatine foramina. Left: *Tropidurus atacamensis*, KU 161986. Right: *Plica plica*, MAN 76. Scales = 1 mm.

canal of Jollie, 1960) (fig. 6): (0) much smaller than lacrimal foramen; (1) enlarged and dorsoventrally expanded—frequently subequal in size to lacrimal foramen. In the outgroups (as well as in most iguanians) the maxillopalatine foramen is considerably smaller than the lacrimal canal. However, in *Plica*, *Uracentron*, and *Strobilurus* the maxillopalatine foramen is usually considerably enlarged dorsoventrally and as large as, or larger than, the lacrimal foramen. Some individuals of *T. koepckeorum*, *T. hispidus*, and *T. hygomi* show somewhat enlarged maxillopalatine foramina that are expanded laterally but I do not regard this as a homologous condition.

9. Pineal foramen: (0) present; (1) absent. Although some members of the “*Stenocercus*” group lack the pineal foramen (e.g., “*Stenocercus*” *empetrus*), these species are removed from the “base” of “*Stenocercus*,” so this similarity is likely homoplastic with respect to this feature in the *Tropidurus* group. Within the *Tropidurus* group this is an autapomorphy of *Uracentron azureum* (but present rudimentarily in one specimen of *U. azureum* examined, AMNH 60330).

10. Squamosal shape and skull width (fig. 7): (0) squamosal bone relatively straight, reflected in the posterior apex of the temporal fenestra forming an acute angle; (1) squa-

mosal bone curved around the posterior end of the temporal fenestra—the posterior apex of the temporal fenestra forming a smooth curve. This is reflected in shape changes of the temporal fenestra in the three species of *Plica*.

11. Superior fossa of quadrate (fig. 8): (0) relatively small, a process of the squamosal fitting into the fossa like a peg in a hole; (1) relatively enlarged, the squamosal not penetrating the fossa. In the *Tropidurus* group the superior fossa of the quadrate is enlarged. The functional significance is unknown; however, as noted elsewhere, members of the *Tropidurus* group are distinctive within the iguanians for their general delicateness of bone structure. The increase in size of the fossa and the failure of the squamosal to develop enough of a quadrate process to fit into the hole may well be a result of this trend. The “*Stenocercus*” group and *Leiocephalus* show some approach to this condition relative to the remaining iguanians but even in these a process of the squamosal penetrates into the superior fossa of the quadrate.

MANDIBULAR CHARACTERS

12. Alveolar shelf of mandible (fig. 9): (0) forming a well-defined ridge; (1) alveolar ridge

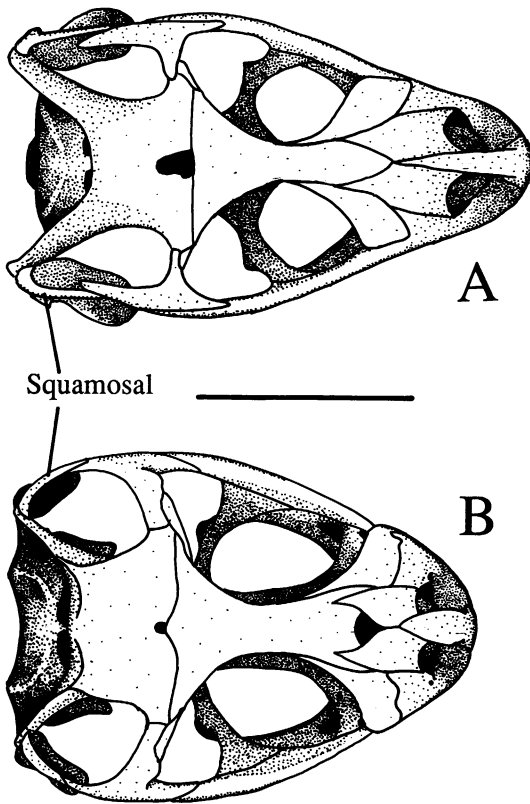


Fig. 7. Dorsal views of skulls. A: *Tropidurus stolzmanni*, KU 134747. B: *Plica umbra*, KU 146659. Scale = 10 mm.

rounded—erosion of thickness of mandible below level of alveolar ridge; (2) alveolar ridge poorly defined—medially approaches ventral margin of mandible. In outgroups, the alveolar shelf of the mandible is well defined. However, in the *Tropidurus* group, the alveolar shelf is slightly eroded. In *Uranoscodon* and *Tropidurus* west of the Andes, the degree of erosion is not as great as that seen in the remaining *Tropidurus* group.

13. Lingual coronoid process of dentary (fig. 9): (0) not overlapping anterior lingual "leg" of coronoid; (1) overlapping anterior lingual "leg" of coronoid. Unique among iguanians examined, members of the *Tropidurus* group, excepting *Uranoscodon*, exhibit a process of the dentary that overlaps part of the anterior labial "leg" of the coronoid. In some members of the "*Stenocercus*" group

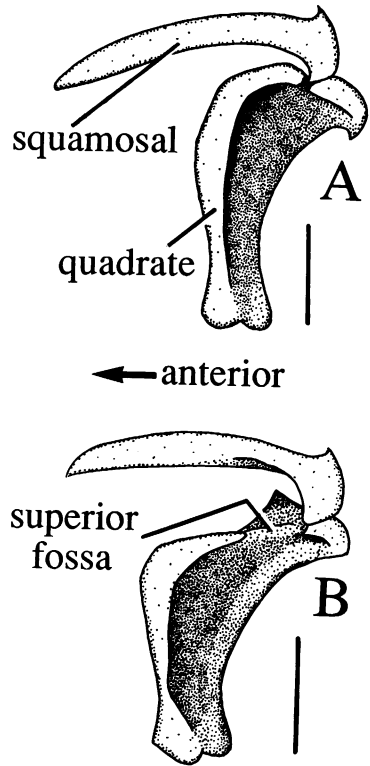


Fig. 8. Squamosal-quadrates articulations. A: *Leiocephalus carinatus*, UMMZ 149104; superior fossa of quadrate small. B: *Tropidurus bogerti*, RWM 11662; superior fossa of quadrate enlarged. Scales = 2 mm.

there is very weak overlap and members of the *Tropidurus* group east of the Andes (except *Uranoscodon*) tend to have stronger development of the process than members of the *Tropidurus* group west of the Andes. However, this is subject to considerable variation, which prevents me from hypothesizing a shift from weak development to strong development as a transformation series.

14. Posterior extent of dentary (fig. 10): (0) dentary extending < 50 percent of the length from apex of coronoid to anterior edge of articular; (1) extending > 50 percent of the length from the apex of the coronoid to the anterior edge of the articular. Excluding *Uranoscodon*, the *Tropidurus* group east of the Andes exhibits a more posterior extension of the dentary than the *Tropidurus* group west

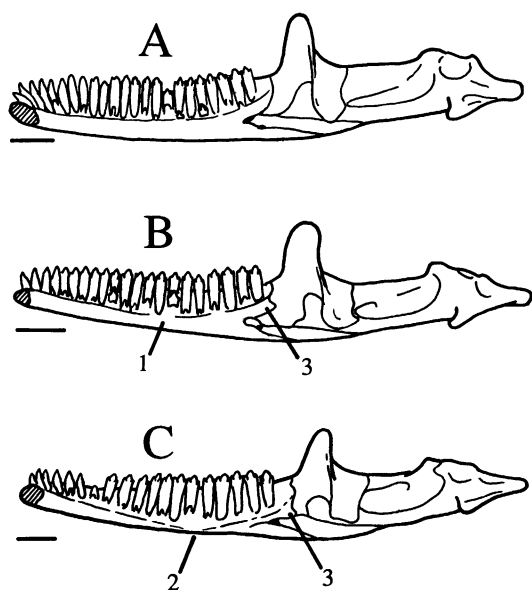


Fig. 9. Lingual views of mandibles. A: "*Stenocercus*" *apurimacus*, KU 134284. B: *Tropidurus stolzmanni*, KU 134747. C: *Plica plica*, MAN 76. Shown: (1) weakly eroded alveolar shelf; (2) strongly eroded alveolar shelf; (3) lingual coronoid process of dentary. Scales = 2 mm.

of the Andes or the outgroups ("*Stenocercus*" group and *Leiocephalus*). Some *Leiocephalus* species approach "1" but they still lack the condition as seen in the *Tropidurus* group.

15. Anterior surangular foramen (fig. 10): (0) not captured by contact of the coronoid and dentary posterior to the foramen; (1) "captured" by contact of the coronoid and surangular posterior to the anterior surangular foramen. Excepting *Uranoscodon* and *Tropidurus bogerti*, the *Tropidurus* group east of the Andes is characterized by enclosure of the anterior surangular foramen between the coronoid and dentary. *Leiocephalus* also has the anterior surangular foramen enclosed by posterior contact of the coronoid and dentary, but the "*Stenocercus*" group and the *Tropidurus* group west of the Andes lack this contact. Outgroup comparison is insufficient to polarize this transformation series; therefore it is treated as unpolarized (i.e., the "ancestor" is coded as "unknown") in this analysis.

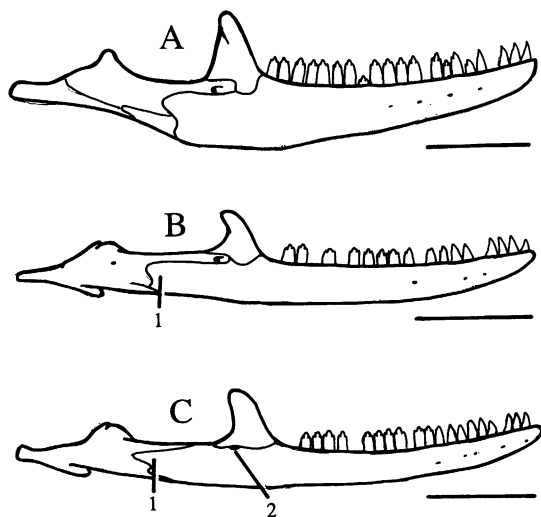


Fig. 10. Labial views of dentaries. A: *Uranoscodon superciliosus*, REE 16600. B: *Tropidurus bogerti*, RWM 11662. C: *Tropidurus melanopleurus*, KU 136367. Scales = 5 mm. Shown: (1) extensive posterior extent of dentary; (2) capture of anterior surangular foramen between coronoid and dentary.

16. Angular condition (fig. 11): (0) large, distinct; (1) reduced (limited to below surangular-prearticular suture) or lost. *Uranoscodon* and *Tropidurus* from west of the Andes have relatively large angulars identical to those in the outgroups. East of the Andes, all members of the *Tropidurus* group (excluding *Uranoscodon*) show some reduction in size of the angular, but inter- and intraspecific variation in shape and presence or absence is confusing; it will be discussed here but not placed in any transformation series. Of those with a reduced angular, some *Tapinurus semitaeniatus* (MCZ 79805) and *T. spinulosus* show the least reduction of the angular; it is only moderately reduced from the plesiomorphic condition. However, in some other *T. spinulosus* (e.g., CAS 49843) the angular apparently is fused with the prearticular and not visible. In *Plica plica* and *P. lumaria* the angular and splenial apparently are fused and this composite bone contacts the surangular, although in MCZ 85313 (*Plica plica*) there is a slight separation of the splenial and angular. In *Plica umbra*, most *Tapinurus semitaenia-*

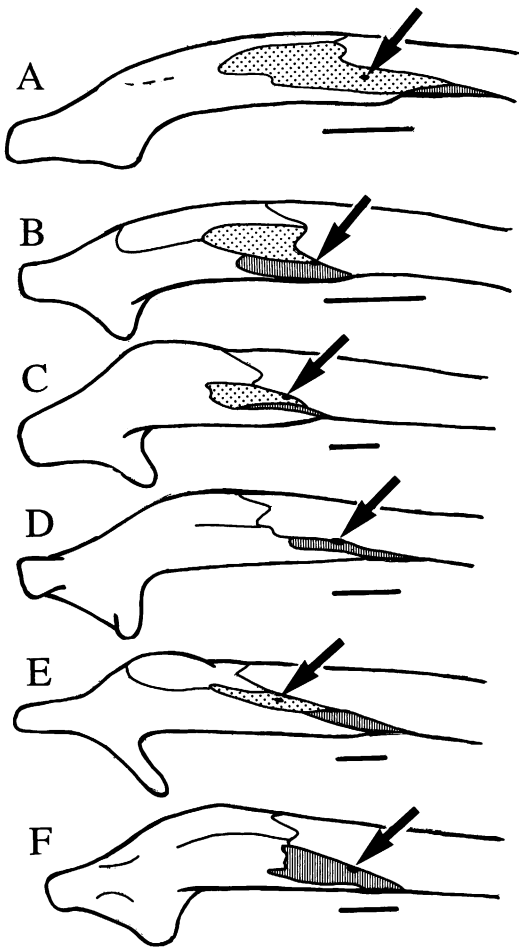


Fig. 11. Ventral views of right mandibles: angulars and posterior mylohyoid foramina. **A:** *Uranoscodon superciliosus*, REE 16600. **B:** *Tropidurus bivittatus*, LACM 10637. **C:** *Tropidurus spinulosus*, USNM 125166. **D:** *Tropidurus melanopleurus*, KU 136367. **E:** *Uracentron flaviceps*, KU 175317. **F:** *Plica plica*, MAN 76. Scales = 2 mm. Nominal angulars are stippled. Nominal splenials are vertically screened. Posterior mylohyoid foramina denoted with arrows.

tus, *Tropidurus bogerti*, and *Uracentron*, the angular is present as a small flake of bone that actually may be a dissociated piece of the splenial. In the remaining *Tropidurus* group the angular is absent or is fused either to the splenial or prearticular. In this group the splenial can be widely separated from the

prearticular (*T. hispidus*, *T. itambere*) or closely approach it (*T. erythrocephalus*, *T. etheridgei*, *T. hygomi*, *T. melanopleurus*, *T. nanuzae*, *T. torquatus*, and *Strobilurus torquatus*) although characterization of this transformation would be difficult because of intraspecific variation.

17. Posterior mylohyoid foramen, osseous contact (fig. 11): (0) posterior mylohyoid foramen penetrating angular or between dentary and angular; (1) between angular and splenial; (2) between dentary and splenial. In outgroups and the *Tropidurus* group west of the Andes (and *Uranoscodon*) the anterior mylohyoid foramen is invariably in contact with the angular. Within this category several conditions obtain that cannot be polarized because of variation in the outgroups. Most of the *T. occipitalis* group and the *T. peruvianus* group show the posterior mylohyoid foramen either penetrating the angular or penetrating between the dentary and angular. However, *T. habellii* and *T. bivittatus* have the posterior mylohyoid foramen penetrating between the angular and splenial, presumably an apomorphy uniting these species. All of the *Tropidurus* group east of the Andes, except for *Uranoscodon*, *T. spinulosus*, and *Uracentron*, exhibit a condition where the posterior mylohyoid foramen is excluded from contact with the angular (or even the topographic "angular region" when the angular is absent).

18. Posterior mylohyoid foramen, position (fig. 11): (0) at the level of anterior end of mandibular fossa; (1) placed more posteriorly, about 33 percent of the length of the mandibular fossa back from the anterior end. The position of the mylohyoid foramen varies considerably in iguanians and may be of wide systematic application. In the outgroups (*Leiocephalus* and "Stenocercus" group) and most members of the *Tropidurus* group, the posterior mylohyoid foramen is on the ventral surface of the dentary at the level of the anterior end of the adductor fossa. In *Uracentron* and *Tapinurus*, however, it is displaced considerably posteriorly. In MCZ 172948 (*T. erythrocephalus*) the posterior mylohyoid foramen is displaced posteriorly, though not to the extent found in *Uracentron* and *Tapinurus*.

DENTITION

19. Premaxillary teeth, number (fig. 4): (0) 6–7; (1) 4–5. In most of the *Tropidurus* group, as well as the outgroups, the premaxilla normally bears 6–7 teeth. In *Uracentron*, *Strobilurus*, *Tapinurus*, *Uranoscodon*, *Plica plica*, and *P. lumaria*, this number is reduced to 5 or 4. The trend is for those species with narrow premaxillae (see Transformation Series 5) to have fewer premaxillary teeth, but this correlation is not perfect. Although *Plica umbra* is coded as “0”, the condition may not be homologous with other “0” conditions, inasmuch as the medial premaxillary teeth in *Plica umbra* are frequently very small, allowing the conjecture that they are in a sense “supernumerary.”

20. Anterior maxillary teeth, enlargement (Boulenger, 1885; Etheridge, 1970a) (fig. 3): (0) not or only feebly enlarged in older adults; (1) enlarged in older adults, forming caniniform teeth. Within the *Tropidurus* group many species show ontogenetic enlargement of the anteriormost few maxillary teeth, concomitant with an upward tilting of the lower margin of the premaxilla, resulting in the appearance of “canines.” There is some evidence of this trend in *Leiocephalus* (G. Pregill, personal commun.) and some species in the “*Stenocercus*” group (e.g., “*S.*” *festae*, *Proctotretus pectinatus*) show ontogenetic elevation of the premaxilla without concomitant lengthening of anterior maxillary teeth. Premaxillary elevation such as this is widespread outside of the Tropidurinae, such as in some *Crotaphytus* (Crotaphytidae), *Ctenosaura* (Iguanidae), and *Phymaturus* (Tropiduridae: Liolaeminae), and it cannot be characterized or polarized in any satisfactory way. However, all species of the *Tropidurus* group east of the Andes (except *Uranoscodon* and some individuals of *Tropidurus melanopleurus* [taxon coded as “1” because present in older individuals]) exhibit “canine” formation well advanced over that seen in the outgroups or the species of *Tropidurus* found west of the Andes. Greatest development may be in *Plica umbra*, although this is approached in *Uracentron flaviceps*. Small sample size precludes the recognition of multiple characters within this transformation series.

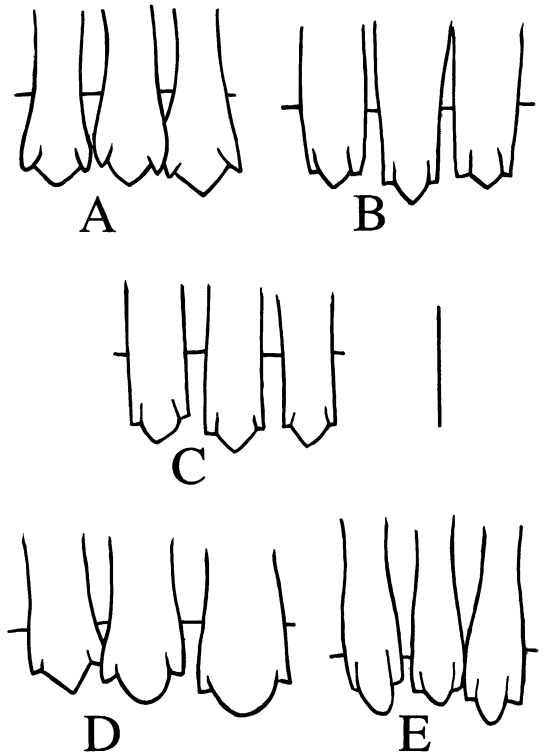


Fig. 12. Posterior maxillary dentition. A: *Leiocephalus carinatus*, UMMZ 149104. B: *Uranoscodon superciliosus*, REE 16600. C: *Tropidurus melanopleurus*, KU 136367. D: *Plica umbra*, KU 146659. E: *Plica plica*, MAN 76. Scale = 1 mm.

21. Posterior maxillary and dentary teeth, crown flaring (Etheridge, 1966, 1968, 1970a; Etheridge and de Queiroz, 1988) (fig. 12): (0) shaft parallel-sided with crowns not or weakly flared; (1) crowns flared. The shape of the crowns of cheek teeth is difficult to describe and is beset with outgroup comparison problems. *Leiocephalus* has flared teeth, but the “*Stenocercus*” group exhibits all conditions from weakly flared and tricuspid (e.g., “*S.*” *guentheri*) to peglike with poorly developed cusps (e.g., *Proctotretus pectinatus*). The variation among conditions within the *Tropidurus* group is necessarily nonpolarized.

Beyond the nonflared-flared dichotomy, characterization of the tooth shape of species in the *Tropidurus* group is difficult to assess

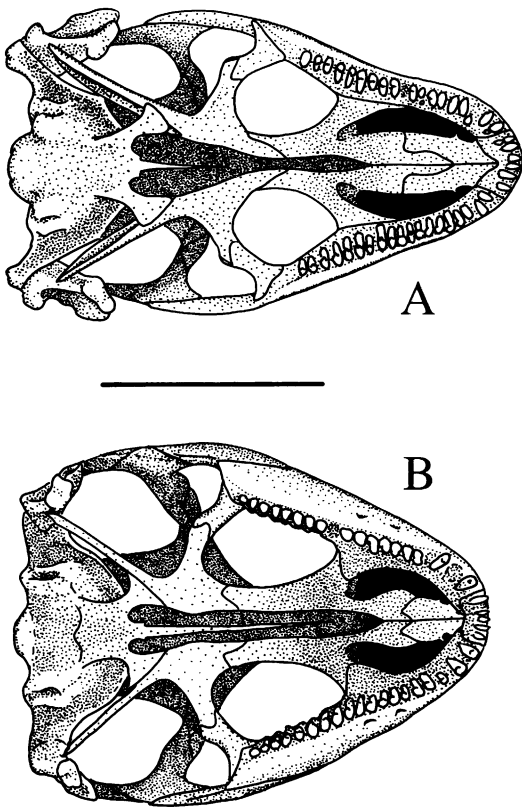


Fig. 13. Ventral views of skulls. A: *Tropidurus stolzmanni*, KU 134747. B: *Plica umbra*, KU 146659. Scales = 10 mm.

and essentially continuous. I will discuss the species as if they fall into four groups; the distinctions among them are fuzzy. Within the *Tropidurus* group, only *Uranoscodon* (fig. 12) and *Tropidurus theresiae* show constriction of the crown of the tooth relative to the shaft. A larger group exhibits posterior maxillary teeth that are, or are nearly, parallel-sided: *T. bogerti*, *T. cocorobensis*, *T. erythrocephalus*, *T. insulanus*, *T. itambere*, *T. melanopleurus* (fig. 12), *T. montanus*, *T. nanuzae*, *T. spinulosus*, *T. torquatus*, and all of the *T. occipitalis* group and *T. peruvianus* group, except *T. theresiae*. Of these, *T. bivittatus* approaches the condition of being slightly flared. Some *Tapinurus semitaeniatum*, some *Plica umbra* (fig. 12), some *Uracentron azureum*, *Tropidurus hygomi*, and *T. spinulosus* could be called slightly flared. Etheridge (1966, 1968, 1970a) used the presence

of tooth flaring as a diagnostic feature uniting *Plica*, *Strobilurus*, and *Uracentron*, and, as a modality (i.e., in *Plica umbra* and *Uracentron azureum*), I agree. *Tapinurus* and *Tropidurus hispidus* also have (predominantly) flared teeth.

22. Posterior maxillary teeth, elevations: (0) posterior maxillary teeth apparently hypsodont, extending above the edge of the maxilla more than the width of a tooth; (1) posterior maxillary teeth brachydont, not extending far above the level of the maxilla. In *Tropidurus nanuzae*, *Uracentron flaviceps*, and *Plica* a crest of bone along the ventral edge of the maxilla deepens the dental gutter, making the teeth appear shorter when viewed laterally.

23. Posterior maxillary teeth, orientation (fig. 13): (0) posterior maxillary teeth set obliquely on the maxilla; when viewed from the ventral side most of the length of the individual teeth can be seen; (1) posterior maxillary teeth set more vertically on maxilla (not to be confused with recurving of the teeth as seen in some other taxa such as some *Leiocephalus*); when viewed from the ventral side, much of the length of the tooth is hidden from view; additionally, the orbital margins of the jugal form "cheeks" that, as evidenced by their outward rotation, are structurally part of the inward rotation of the dental row. In some members of the *Tropidurus* group (i.e., *Uranoscodon*, *Plica*, *Tropidurus nanuzae*, *Strobilurus*, and *Uracentron*) the jugal and maxilla are exceptionally broad in the region of the posteriormost teeth (reflected also in Transformation Series 22). *Uranoscodon*, *Plica plica*, and *P. lumaria* differ slightly from the other taxa coded as apomorphic in this regard by not having the teeth set quite so vertically. None of the remaining species in the *Tropidurus* group, nor outgroups, exhibits this condition.

24. Pterygoid teeth (Etheridge, 1966): (0) present; (1) absent. Although several species of *Leiocephalus* lack pterygoid teeth, other species phylogenetically more "basal" in that genus have them (e.g., *L. carinatus*) (Pregill, in press); therefore I have considered *Leiocephalus* to plesiomorphically have pterygoid teeth. "*Stenocercus*" group members have pterygoid teeth, with the exception in my material of some "*S.*" *nigromaculatus*

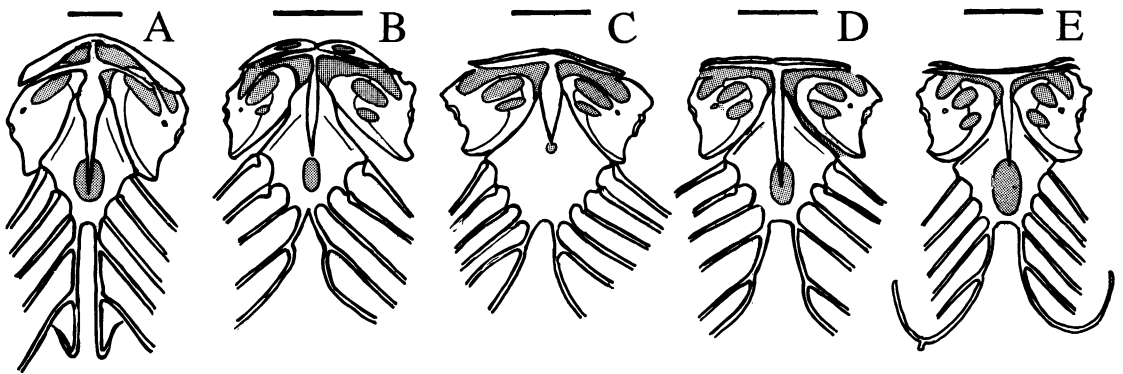


Fig. 14. Pectoral girdles and ribs. A: *Leiocephalus schreibersi*, KU 93358. B: *Tropidurus stolzmanni*, KU 134704. C: *Tropidurus hispidus*, KU 167513. D: *Tropidurus bogerti*, RWM 11663. E: *Tapinurus semitaeniatus*, LSUMZ 39519. Scales = 5 mm.

and several members of the derived “*S.*” *humeralis* group (e.g., “*S.*” *boettgeri*, “*S.*” *crassicaudatus*, and “*S.*” *humeralis*). Presence is therefore considered the plesiomorphic condition within the *Tropidurus* group, in which *Tropidurus bogerti*, *Plica umbra*, *Strobilurus torquatus*, *Tapinurus semitaeniatus*, and *Uracentron azureum* lack pterygoid teeth.

PECTORAL GIRDLE

25. Clavicle (Etheridge and de Queiroz, 1988) (fig. 14): (0) strongly flanged, frequently fenestrate; (1) weakly flared or cylindrical, never fenestrate. In the outgroups, all of the *Tropidurus* group west of the Andes, and, of those east of the Andes, *Tropidurus nanuzae*, *Plica umbra*, *Uranoscodon*, and *Uracentron*, the clavicle has a well-developed posteroventral blade that approaches the lateral processes of the interclavicle. Predominantly in these, the flange is penetrated by a fenestra. In some *Tropidurus occipitalis* (e.g., KU 142714 and 142721) and in *Uracentron flaviceps* these fenestrae are not present. Plesiomorphically within the “*Stenocercus*” group, the clavicle is flanged, although it is uncommonly fenestrate in adults (as in “*S.*” *praeornatus*). *Leiocephalus* also has a weakly flanged clavicle, so, within the *Tropidurus* group this condition must be considered plesiomorphic.

Whether the presence of a clavicular fenestra is an attribute useful for this phylogenetic reconstruction is arguable. Species that do not have a clavicular flange cannot be assessed as to whether they would have a cla-

vicular fenestra if they had a place to put it. Therefore, clavicular fenestration cannot be placed with any assuredness at any particular level of universality.

26. Sternum, fenestration (Rodrigues, 1986) (fig. 14): (0) single fenestration present; (1) fenestra absent. With the exception of *Tropidurus nanuzae* (and *T. divaricatus* and *T. amathites*, according to Rodrigues, 1986 [not seen by me]) all members of the Tropidurinae have medially fenestrate sterna, which otherwise may be a synapomorphy of Tropiduridae and Phrynosomatidae (Frost and Etheridge, 1989). Sternal fontanelles are also absent in some members of the Liolaeminae, including *Liolaemus occipitalis* (Keller and Krause, 1986) as well as several other species (R. Etheridge, personal commun.).

27. Posterior process of the interclavicle anterior to the sternum (fig. 14): (0) “free” part of the posterior process of the interclavicle > 25 percent of the total length of the sternum (i.e., the sternum is small); (1) “free” part of the posterior process of the interclavicle < 25 percent of the total length of the sternum (i.e., the sternum is enlarged). Among iguanians, only the Phrynosomatidae and the *Tropidurus* group show this apomorphic manifestation of enlargement of the sternum. *Tropidurus spinulosus* most closely approaches the plesiomorphic condition within the *Tropidurus* group at 24 percent. Most other species are from 12 to 19 percent with *T. nanuzae* at 0 percent.

Other aspects of the interclavicle require some discussion. Across the Iguania varia-

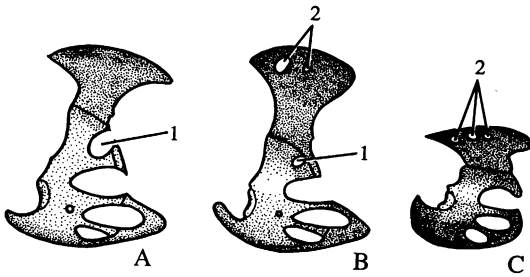


Fig. 15. Lateral view of right scapulocoracoids. A: *Tropidurus albemarlensis*, LACM 196261. B: *Tropidurus spinulosus*, KU 97856. C: *Tapinurus semitaeniatus*, LSUMZ 39519. (1) scapular fenestra; (2) suprascapular fenestrae.

tion in the angle made by the lateral and posterior processes of the interclavicle is continuous and extremely difficult to characterize. However, within this restricted set of groups, characterization proved difficult only within the *T. peruvianus* group; additional specimens examined may show that I have erred in my evaluation of these species. Most of the “*Stenocercus*” group have anchor-shaped interclavicles, the angle varying between 70 and 75°; *Leiocephalus* is somewhat more acute, around 65–70°. The modal interval within the *Tropidurus* group is similar to that in the “*Stenocercus*” group plesiomorphically, but about 80° in the *T. peruvianus* group and, except for *T. nanuzae* (65°), the *Tropidurus* group east of the Andes. *Tapinurus* is exceptional in that the angle formed is greater than 100°. Unfortunately, interspecific variation is extensive enough that it overwhelms any attempt to recognize discrete steps for analysis.

A related character, length of lateral processes of the interclavicle, also proved too variable for use in a transformation series. Most species have the lateral processes not extending to the medial portion of the primary coracoid ray (i.e., *Leiocephalus*, most “*Stenocercus*” group, *T. grayii* complex, *T. bivittatus*, most *T. peruvianus* group, *T. koepckeorum*, some *T. occipitalis*, *T. stolzmanni*, some *T. etheridgei*, some *Plica umbra*, and *Uranoscodon*), or extending only to the medial extent of primary coracoid ray (i.e., *T. habelii*, *T. atacemensis*, some *T. occipitalis*, *T. bogerti*, some *T. etheridgei*, *T. hispidus*, *T. hygomi*, *T. torquatus*, some *Plica*

plica, and *Uracentron*), but a few show extension far beyond the primary coracoid ray (i.e., *Tapinurus semitaeniatus*, *Tropidurus itambere*, some *Plica plica*, *T. melanopleurus*). Further work on this character may prove fruitful.

28. Interclavicle median process (Etheridge, 1964; Etheridge and de Queiroz, 1988) (fig. 14): (0) posterior process of the interclavicle extending as a broad process posteriorly well beyond the posterolateral corners of the sternum; (1) posterior process of the interclavicle not extending posteriorly beyond the posterolateral corners of the sternum. In the *Tropidurus* group, except for *Tropidurus bogerti*, *T. spinulosus*, and *Uracentron azureum*, the posterior process of the interclavicle stops short of the level of the lateral corners of the sternum. In both the “*Stenocercus*” group and *Leiocephalinae*, the posterior process of the interclavicle extends well past this level.

29. Scapular deflection and fenestration of scapulocoracoid (Lecuru, 1968; Etheridge and de Queiroz, 1988) (fig. 15): (0) scapular fenestra present, large, and scapula not bent; (1) scapular fenestra present, reduced, scapula weakly bent; (2) scapular fenestra absent, with no room for fenestra in scapula because extremely bent. In some *Tropidurus* (e.g., *T. bogerti*, *T. melanopleurus*, and *T. spinulosus*) the scapula is deflected noticeably inward, causing the scapulocoracoid to form a more acute bend than normally seen in outgroup species. Concomitantly, this bend reduces the size of the scapular fenestra to the point that it is absent as an individual variation in *T. melanopleurus* and *T. spinulosus*. *Tapinurus* shows an even more apomorphic condition; in this case the scapulocoracoid is bent almost in half, with no room for the scapular fenestra at all. Other lizards that live in cracks in rocks have a strongly inflected shoulder girdle, but in *Phymaturus* (*Liolaeminae*) and *Sauromalus* (*Iguanidae*) the inflection is at the scapula-suprascapula suture (R. Etheridge, personal commun.).

30. Suprascapular fenestrations (fig. 15): (0) absent, or very tiny; (1) large. Within the suprascapula in species of the *Tropidurus* group east of the Andes (excluding *Uracentron*), nonossified, nonchondrified fenestrae appear. Within the “*Stenocercus*” group I

have seen these fenestrae only in "*Stenocercus*" *praeornatus*, which is not phylogenetically near the "base" of the "*Stenocercus*" group (i.e., it is in a derived monophyletic group containing, among others, "*S.*" *humeralis* and "*S.*" *empetrus*). I have not seen these fenestrations within *Leiocephalus*. *Tropidurus koepckeorum* and *T. occipitalis* may have tiny fenestrations along the suprascapular margin as an individual variation. Strictly speaking these "fenestrations" are zones of connective tissue that lack either chondrification or ossification and are not actually holes, but appear as clear windows in double-stained specimens.

31. Rib formula (fig. 14): (0) five ribs in contact with the sternum and xiphisternum: 3 sternal ribs + 2 xiphisternal ribs; (1) six ribs in contact with the sternum and xiphisternum (3 sternal ribs + 3 xiphisternal ribs, or 4 sternal ribs + 2 xiphisternal ribs), with the insertion of the fourth sternal rib being very close to the insertion of the xiphisternal rods or conversely in the case of only three sternal ribs, the first xiphisternal rib inserting very close to the insertion of the xiphisternal rods on the sternum. In most species and the outgroups, there are three sternal ribs and two xiphisternal ribs. *Leiocephalus* is apomorphic in that the second xiphisternal rib bears a posteriorly directed and recurved rod.

In *Tropidurus atacamensis*, *T. bogerti*, *T. hispidus*, *T. itambere*, *T. montanus*, *T. torquatus*, *T. melanopleurus*, *T. spinulosus*, *Plica plica*, *P. lumaria*, *Strobilurus torquatus*, and *Uracentron* there are six total sternal + xiphisternal ribs. The fourth in the series can be attached, as an individual variation, either very near to the xiphisternal bar on the sternum or very near the sternum on the xiphisternal bar. In UMMZ 129418 (*Uracentron azureum*) the last xiphisternal rib is anomalously reduced to a free bar attached only to the xiphisternal bar. *Plica umbra* and *Uracentron azureum* share the condition of the sternum and postxiphisternal inscriptional bars being elongated posteriorly, making the postxiphisternal elements appear "stretched" posteriorly.

32. Recurved xiphisternal-pectoral ribs (fig. 14): (0) absent or present as short spurs associated with the medial part of the pectoralis musculature; (1) present, long, asso-

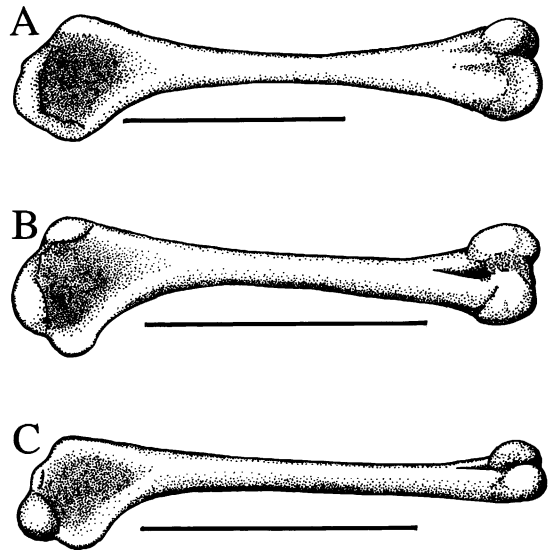


Fig. 16. Left humeri. A: *Uranoscodon superciliosus*, MCZ 58340. B: *Tropidurus peruvianus*, SDSNH 30843. C: *Tropidurus melanopleurus*, KU 136367. All scales = 10 mm.

ciated with entire origin of the pectoralis musculature. *Tapinurus*, unique among iguanians examined, has long cartilaginous rods that follow the origin of the m. pectoralis to form recurved bars that pass from connection with the xiphisternum ventrally across the posteriormost xiphisternal ribs. Short extensions from the postxiphisternal bars, associated with ventral origin of the m. pectoralis, can also be seen in most specimens of most species of the *Tropidurus* group east of the Andes (excluding *Uranoscodon*) and, although not coded as a transformation because of intraspecific variation, is likely a synapomorphy of this more inclusive group. *Leiocephalus* has superficially similar (non-homologous) bars that are not associated with the pectoralis musculature and pass dorsally to the posteriormost xiphisternal ribs.

LIMBS

33. Humerus, head (fig. 16): (0) articular surface scroll-like; (1) somewhat elevated, ovate; (2) ball-shaped and very elevated. Members of the *Tropidurus* group, excluding *Uranoscodon*, effectively have a ball-and-socket shoulder joint, which is, to my knowl-

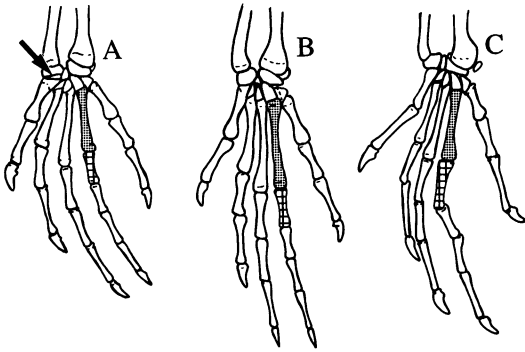


Fig. 17. Dorsal views of left hands. A: *Tropidurus bivittatus*, LACM 106307; arrow points to medial centrale; fourth metacarpal (stippled) shorter than third metacarpal; first phalanx of fourth finger (cross-hatched) distinctly shorter than first phalanx of third finger. B: *Tropidurus hispidus*, KU 167508; medial centrale absent; fourth metacarpal elongated; first phalanx of fourth finger not elongated. C: *Uracentron flaviceps*, KU 175317; medial centrale absent; fourth metacarpal elongate; first phalanx elongate.

edge, unique among lizards. Members of the *Tropidurus* group west of the Andes have the ball-and-socket less well developed than in *Tropidurus* east of the Andes, *Strobilurus*, *Plica*, and *Uracentron*. *Leiocephalus* is here regarded as having the plesiomorphic condition, but it is apomorphic in its own way by having a lateral rotation of the head of the humerus.

34. Medial centrale (fig. 17): (0) present; (1) absent. The loss of the medial centrale is unique among iguanians. All species of the *Tropidurus* group east of the Andes (excluding *Uranoscodon*), exhibit the loss of the medial centrale.

35. Fourth metacarpal and first phalanx of fourth finger (fig. 17): (0) fourth metacarpal distinctly shorter than third metacarpal—first phalanx of fourth finger distinctly shorter than first phalanx of third finger; (1) fourth metacarpal equal to length of third metacarpal—first phalanx of fourth finger distinctly shorter than first phalanx of third finger; (2) fourth metacarpal equal to length of third metacarpal—first phalanx of fourth finger subequal to first phalanx of third finger. All of the *Tropidurus* group east of the Andes (except *Uranoscodon*) exhibit elongation of the fourth

finger relative to the third. This elongation is primarily the result of elongation of the fourth metacarpal to approximate equal length with the third metacarpal. In *Uranoscodon*, *Tropidurus* west of the Andes, and the outgroups, the fourth metacarpal is distinctly shorter than the third.

A subset of the elongate fourth metacarpal group has continued elongation of the fourth finger by lengthening the first phalanx. *Tropidurus bogerti*, *T. spinulosus*, *T. melanopleurus*, *Plica*, *Strobilurus*, *Tapinurus*, and *Uracentron*. *Tropidurus etheridgei*, *T. hygomi*, and *T. torquatus* approach this condition.

36. Claw of first toe: (0) weakly flexed; (1) strongly flexed, recurved. *Plica*, *Strobilurus*, and some *Tropidurus* show some degree of recurving of the claw of the first toe. Only in *Uracentron*, however, can this feature be characterized adequately. As noted by Etheridge (1970a), another feature, digits bent strongly at their articulations (they appear to be “physically challenged”), is a characteristic of *Plica* and some *Tropidurus*. I found this feature widespread within species east of the Andes, but impossible to characterize across all taxa, although there is increased incidence of, and maximal development in, some specimens of *T. spinulosus*, *Plica*, and *Uracentron*.

37. Fringe on fourth toe: (0) absent; (1) present. Unique within the *Tropidurus* group and the outgroups, *Uranoscodon* has the scales of the edges of the fourth developed into fringes, much as in *Basiliscus* (Corytophanidae).

AXIAL SKELETON

38. Pubic symphysis, anterior margin: (0) acute; (1) flattened. In the outgroups and most of the *Tropidurus* group, the anterior margin of the pubis is acute, but in *Uracentron* and *Strobilurus* the anterior margin is relatively flat. Possibly this is associated with caudal musculature in these lizards with heavily armed tails.

39. Anterior caudal vertebrae, neural spines (fig. 18): (0) moderate to high; (1) very depressed. Although the neural spines of the caudal vertebrae are variably developed in the *Tropidurus* group, *T. bogerti* and *Tapinurus* have effectively reduced the neural

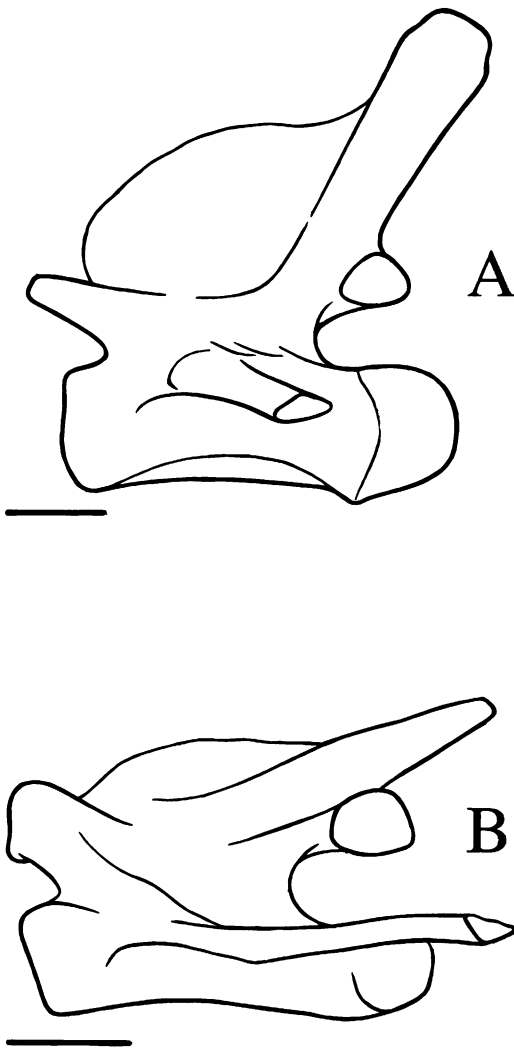


Fig. 18. Lateral views of third caudal vertebrae, showing development of neural spines. **A:** *Tropidurus hispidus*, KU 135268. **B:** *Tropidurus bogerti*, RWM 11662. Scales = 2 mm.

spines of the anterior caudal vertebrae to a minimum.

40. Caudal vertebrae, autotomy fracture planes (Etheridge, 1967): (0) present; (1) absent. Unique in the *Tropidurus* group, *Uracentron* lacks caudal autotomy fracture planes.

NARIAL CHARACTERS

41. Nostrils (fig. 19): (0) exposed postero-laterally and key-hole shaped or some other

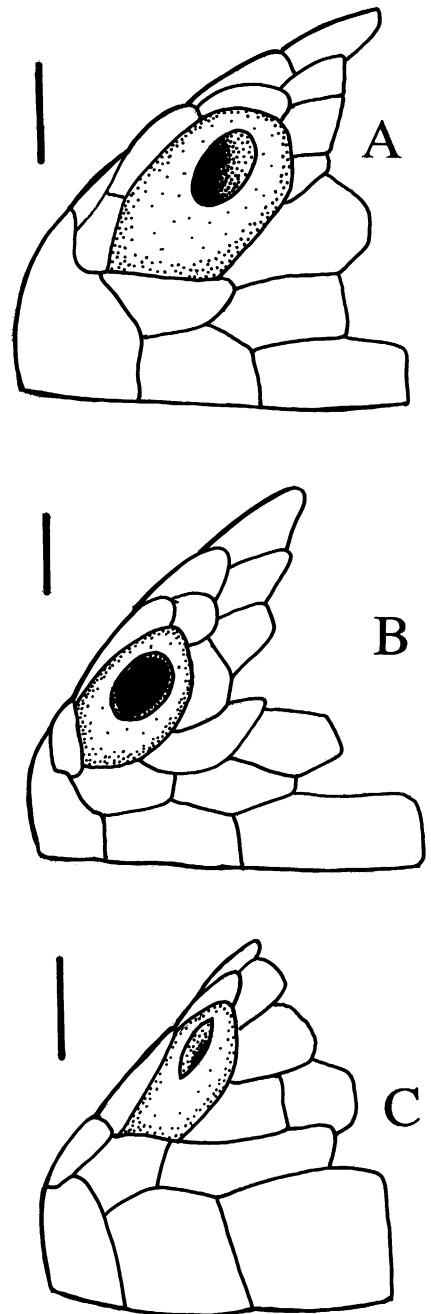


Fig. 19. Lateral view of snouts showing nostril morphology and exposure. **A:** *Tropidurus theresioides*, LACM 134136. **B:** *Tropidurus melanopleurus*, KU 183472. **C:** *Uracentron azureum*, KU 204989. Nasal scale stippled. Scales = 2 mm.

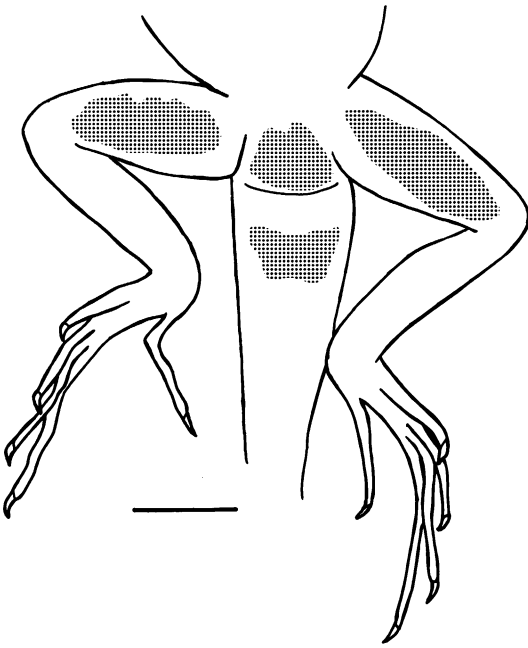


Fig. 20. Pigmented thigh patches. Ventral view of *Tropidurus bogerti*, RWM 11659. Scale = 10 mm.

modification thereof; (1) exposed laterally and widely open; (2) directed anteriorly or anterolaterally and unconstricted. As in the “*Stenocercus*” group and *Leiocephalus* (as well as other iguanians examined), the *Tropidurus* group plesiomorphically has the edges of the nostril produced posterovertically and has a nasal constriction within the nostril that gives the nostril a key-hole or oblong shape. Also, in outgroups and in most of the *Tropidurus* group the nostril is exposed dorsolaterally. However, in *Tropidurus bogerti*, *T. melanopleurus*, and *Tapinurus* the nostril is exposed more laterally and is more widely open, with the normally produced edges of the nostril reduced. In *Plica*, *Strobilurus*, and *Uracentron* the nostrils are directed more anterodorsally. I have left this transformation series unordered because, beyond condition “0” being plesiomorphic, I have no compelling reason to polarize conditions “1” and “2”.

COLORATION

Members of the *Tropidurus* group vary in coloration in ways that mostly defy transla-

tion into transformation series. For example, most have faint to bold black transverse chest bars not found in the outgroups. Evaluation of the presence of this feature is difficult because of various modifications. Presumably this coloration is a synapomorphy of the *Tropidurus* group, excluding *Uranoscodon*. Within the *Tropidurus occipitalis* and *T. peruvianus* groups of species, longitudinal paravertebral light stripes are common, particularly from the eye to over the shoulder. Similar stripes are present in some species of *Leiocephalus* and in the “*Stenocercus*” group, so the status of this feature is arguable. I have found only one feature of coloration that is amenable to placement in a transformation series.

42. Ventral thigh and preanal pigmented region (Rodrigues, 1987) (fig. 20): (0) thighs without a well-defined ventral pigmented spot; (1) thigh and preanal region with a well-defined yellow or greenish spot; (2) thigh and preanal region with a well-defined brown to black spot. Although some members of the “*Stenocercus*” group show fairly extensive “flash” markings on the ventral side of the thighs, these marks are never the well-defined spots seen in the *Tropidurus* group and are actually more similar to markings found in some *Sceloporus* (Phrynosomatidae). None of the *T. peruvianus* group or *T. occipitalis* group shows any kind of thigh spotting, nor does *Uranoscodon*. In some taxa the well-defined thigh spots are yellow or greenish (i.e., *Tropidurus nanuzae*, *T. melanopleurus*, *T. spinulosus*, *Plica* [with less sharp edges in *Plica plica* and *P. lumaria*], and *Strobilurus*). In other taxa (i.e., *Tropidurus bogerti*, *T. cocorobensis*, *T. erythrocephalus*, *T. etheridgei*, *T. hispidus*, *T. insulanus*, *T. hygomi*, and *T. torquatus*, and *Tapinurus*) the thigh markings are dark. Additionally, some species (i.e., *T. etheridgei*, *T. itambere*, and some *T. cocorobensis*) show an additional melanistic fleck on the belly. However, characterization is sufficiently difficult that I have considered the transformation as unordered, although the thigh markings are likely homologous regardless of hue.

HEMIPENES

Hemipenes in lizards have been poorly examined since the early work by Cope (1897)

(but see Böhme, 1988), but they provide some evidence here. Arnold (1984) noted that the *Tropidurus* group is characterized by an accessory dorsal hemipenial muscle, found otherwise only in polychrids. I have not evaluated this character in all species, but because Arnold (1984) saw it in *Uranoscodon superciliosus*, *Uracentron flaviceps*, *Strobilurus torquatus*, *Plica umbra*, *Tropidurus peruvianus*, and *T. torquatus*, I consider this a synapomorphy of the *Tropidurus* group.

43. Hemipenes, condition (Böhme, 1988) (fig. 21): (0) no terminal disks on hemipenial lobes; (1) terminal disks present on hemipenial lobes. In outgroups and members of the *Tropidurus* group east of the Andes the lobes of the hemipenis do not end in a terminal bare disk. With the exception of *Tropidurus koepckeorum*, all *Tropidurus* group west of the Andes have distinctive terminal disks on the lobes of the hemipenis. *T. koepckeorum* has long hemipenial lobes more like eastern *Tropidurus*.

44. Hemipenes, length of lobes (fig. 21): (0) short; (1) long. *Leiocephalus* has single-headed, single-sulcate hemipenes that are incipiently divided. All members of the “*Stenocercus*” group examined have short-lobed, bisulcate, bilobate hemipenes. Although with respect to outgroups, all members of the *Tropidurus* group have elongate hemipenial lobes, those from west of the Andes, excluding *T. koepckeorum*, have the shortest hemipenial lobes. *Tropidurus koepckeorum* and all species of the group east of the Andes have elongate lobes (although *T. koepckeorum* is on the short side of this variation). Because, within the *Tropidurus* group, lobe length and dinking appear to be causally related I have refrained from recognizing any transformation other than a general elongation of the hemipenial lobes that is a likely synapomorphy of the *Tropidurus* group.

45. Hemipenes, ornamentation: (0) calyces start below crotch between lobes; (1) calyces start at a level well above the crotch between the hemipenial lobes. Within the *Tropidurus* group, as in the “*Stenocercus*” group, calyces ornament the lobes of the hemipenes. In the *Tropidurus peruvianus* and *T. occipitalis* groups, and *T. nanuzae*, ornamentation penetrates on the posterior side of the shaft of the hemipenis below the crotch

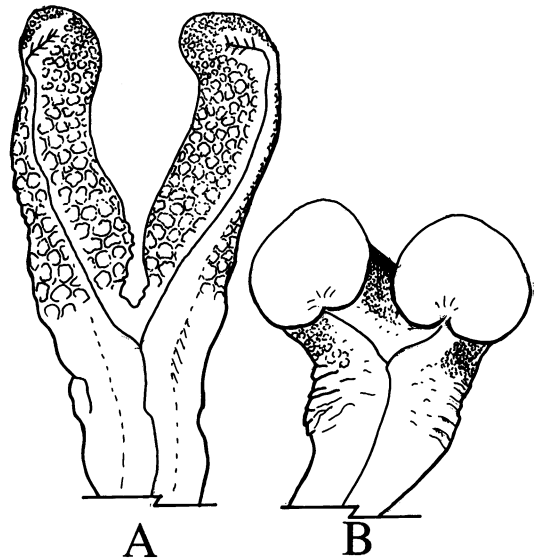


Fig. 21. Hemipenes. A: *Plica umbra*, KU 147947. B: *Tropidurus tigris*, KU 167352. Both $\times 10$.

between the hemipenial lobes. In *Leiocephalus* ornamentation extends far down the shaft of the hemipenis. Therefore, outgroup comparison is insufficient to determine the polarity of this particular transformation. For purposes of this study I regard this transformation as nonpolarized (i.e., the “ancestor” is coded as “unknown”).

POCKETS AND FOLDS

The nomenclature of neck and throat folds in iguanian lizards is sufficiently chaotic that I will define my terms. Generally speaking, the folds on the necks of lizards are relatively conservative in topographic position; this nomenclature is applicable to all lizard groups. See figure 25 for a generalized lizard and the nomenclature of folds. More specifically:

A. The *antehumeral fold* extends anteriorly over the shoulder and may be (usually is) confluent with the gular fold should it be present. An interesting exception is in *Leiocephalus*, the “*Stenocercus*” group, and in many members of the *Tropidurus* group. That is, the antehumeral fold, bordered by small scales, extends obliquely under the gular fold (bordered by large scales) which becomes obsolete or may extend anterodorsally all the way to the oblique neck fold. In other words, this arrangement of the lateral edges of the gular fold extending

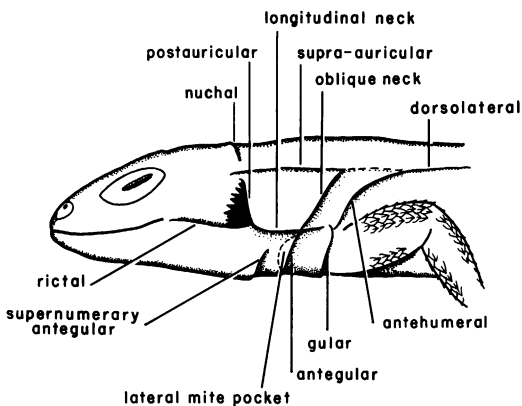


Fig. 22. Standardized nomenclature of folds.

over the antehumeral fold may be a synapomorphy of the Tropidurinae + Leiocephalinae. In *Phymaturus* and *Liolaemus* something near this condition obtains, but the antehumeral fold goes over the gular fold. This may be correlated with the fatty pouches on the sides of the neck in that group.

B. The *gular fold* extends immediately anterior to the insertion of the arm and may be confluent with the antehumeral fold. This fold is associated plesiomorphically with a discontinuity in scale size. I have seen "gular" folds that are not associated with this discontinuity but I suspect nonhomology of appearance in these cases. *Plica umbra* has its gular fold interrupted medially. What confuses the issue is the antegular fold being displaced backwards over the topographic position of the gular fold. *Plica plica*, *P. lumaria*, and *Uracentron* do have a complete gular fold. To my mind, only structural gular folds, that is, folds distinguished by scale discontinuities are easily characterized.

C. The *dorsolateral fold* extends longitudinally anteriorly along the sides and over the insertion of the arm. The dorsolateral fold is usually confluent with the antehumeral fold, but sometimes continues forward (as a supra-auricular fold) to a point over the tympanum. In all species with sufficiently small body scales the dorsolateral fold is evident for much of the length of the body.

D. The *supra-auricular fold* is the continuation of the dorsolateral fold anterior to the antehumeral fold to a position over the tympanum.

E. The *oblique neck fold* is what Fritts (1974) referred to as the neck fold. This is frequently confluent with the antegular fold. The oblique neck fold may be connected to the antehumeral fold by a longitudinal neck fold. The oblique neck fold in *Leiocephalus* is very similar to that found in the *T. occipitalis* group (particularly *T. bivittatus* and

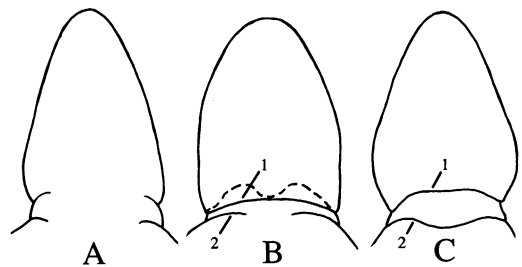


Fig. 23. Ventral view showing antegular and gular folds. A: *Tropidurus torquatus*, USNM 207684 (antegular and gular folds medially incomplete). B: *Tropidurus spinulosus*, USNM Field (NJS) 126026 (antegular complete and closely approximating gular fold, ventral mite pockets outlined by dashed line). C: *Uracentron flaviceps*, KU 175317 (antegular and gular fold complete). (1) Antegular fold; (2) gular fold.

T. habelii) and some "*Stenocercus*" (e.g., "*S.*" *variabilis*). It is under this fold (or its lower extent, the antegular fold) that mite pockets form in phrynosomatids and in eastern *Tropidurus*.

F. The term *antegular fold* represents possibly two nonhomologs. Generally speaking, the antegular fold is a transverse continuation of the oblique neck fold. In some species, like *T. stolzmanni*, supernumerary antegular folds are variably present. When mite pockets form, the fold of the antegular (continued as the oblique neck fold) forms a lobe in front of the scaleless pocket. When two mite pockets obtain underneath the antegular fold they are separated by a smaller fold that divides the "mite zone." However, in taxa such as *Cophosaurus* (Phrynosomatidae) or some members of the western *Tropidurus* group the mite pocket can be very shallow and is detectable only on close inspection. Alternatively, in some species, like many *Sceloporus* (Phrynosomatidae) or *Tropidurus koepckeorum* (as well as many of the *T. peruvianus* group), a lateral antegular fold extends anteriorly under the angle of the jaws where they parallel the longitudinal axis. A fold of sorts sometimes connects these in an "H" shape. In *Plica* and *T. spinulosus* (to a lesser degree), the antegular fold is displaced backwards to approach or overlap the gular fold.

G. A *longitudinal neck fold* frequently is confluent with the postauricular fold.

H. A *postauricular fold* is a continuation of the longitudinal neck fold that crosses the oblique neck fold. The postauricular fold may be confluent with the nuchal fold if the latter is present.

I. The *nuchal fold* is the fold at the back of the cephalic scales so evident in *Leiocephalus*, many

iguonids, and *Uranoscodon*. Sometimes the nuchal fold is confluent with the postauricular fold.

J. A rictal fold is present in *Plica plica*, *P. lumaria*, *Uracentron*, *Strobilurus*, *T. melanopleurus*, *Tapinurus*, *T. spinulosus*, and *T. bogerti* as an "upward" fold connecting the corner of the mouth with the bottom of the ear. Apparently its development is in part correlated with the development of underlying jaw adductor musculature.

The following transformation series (46–53) are based on variation within these folds and pockets.

46. Gular fold (fig. 22, 23): (0) incomplete medially; (1) complete medially. Both *Leiocephalus* and the "*Stenocercus*" group have gular folds that are incomplete medially. *Plica plica*, *P. lumaria*, *Uracentron*, and *Uranoscodon* are the only members of the *Tropidurus* group with a medially complete gular fold.

47. Antegular fold (fig. 22, 23): (0) absent or weak and variable; (1) present, strong, well anterior to gular fold; (2) present, strong, closely approximating or overlapping gular fold. In the outgroups plesiomorphically and in many species of the *Tropidurus* group a medially complete antegular fold is absent. *Plica*, *Tropidurus stolzmanni*, *T. spinulosus*, *T. melanopleurus*, *Uracentron*, and *Uranoscodon* all exhibit a strong antegular fold. More difficult to characterize, all members of the *Tropidurus peruvianus* group (with the exception of *T. tigris*), and *T. bogerti* show weak "complete" antegular folds that are individually variable in their completeness. I have coded only those species with strong antegular folds to have the apomorphic condition. Although *Leiocephalus* lack an antegular fold, in the species of the "*Stenocercus*" group that have an antegular fold (e.g., "*S.*" *humeralis*, "*S.*" *crassicaudatus*) the fold is placed well anterior to the gular fold. Also, I am unaware of any iguanian, other than *Plica plica*, *P. lumaria*, *P. umbra*, and *T. spinulosus*, that has an antegular fold that approximates or overlaps the gular fold. The posterior extension of the antegular fold over the topographic position of the gular fold in *Plica* has caused it to be called a gular fold and has also resulted, in part, in the misidentification of many *Tropidurus spinulosus* as *Plica plica*. The "position" of an antegular fold is evaluated in taxa that lack this fold in a manner

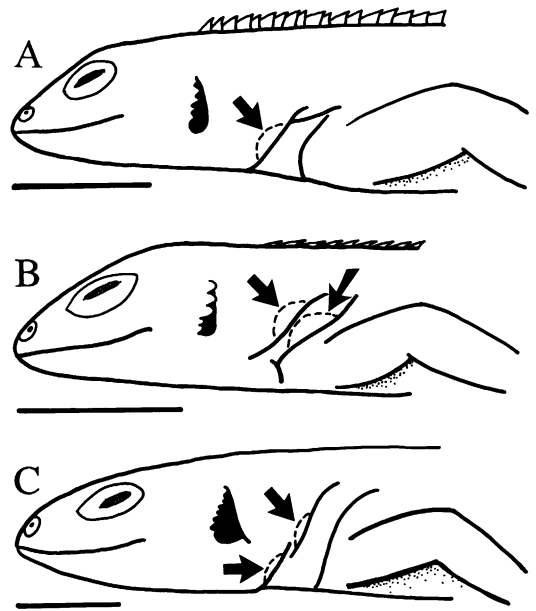


Fig. 24. Lateral mite pockets. A: *Tropidurus koepckeorum*, LACM 49102; showing single mite pocket. B: *Tropidurus nanuzae*, USNM 213514; showing mite pockets under oblique neck fold and antehumeral fold. C: *Tropidurus torquatus*, USNM 207684; showing double mite pockets under oblique neck fold and lateral extent of antegular fold.

analogous to how size of fused "interparietal" scales is compared with taxa that lack enlarged (= fused) "interparietals." The topography of folds on the sides of the neck (fig. 22) indicates expected position of the antegular fold with some accuracy.

48. Antegular-oblique neck fold mite pockets, condition (fig. 24): (0) weak single mite pocket (*T. occipitalis* group, *Strobilurus torquatus*); (1) no mite pocket; complex neck folding (*Tropidurus peruvianus* group, *T. bogerti*, *Uracentron*, *Tapinurus*); (2) a well-developed mite pocket in the upper position (see following transformation); (3) ventrolateral mite pockets (*Tropidurus melanopleurus*, *T. spinulosus*, *Plica* [weak in *P. umbra*]); (4) no obvious mite pocket, although weak depressions are in the ventrolateral side of antegular fold (*Uranoscodon*).

The characterization of mite pockets and the recognition of transformation series with the recognized interspecific variation is

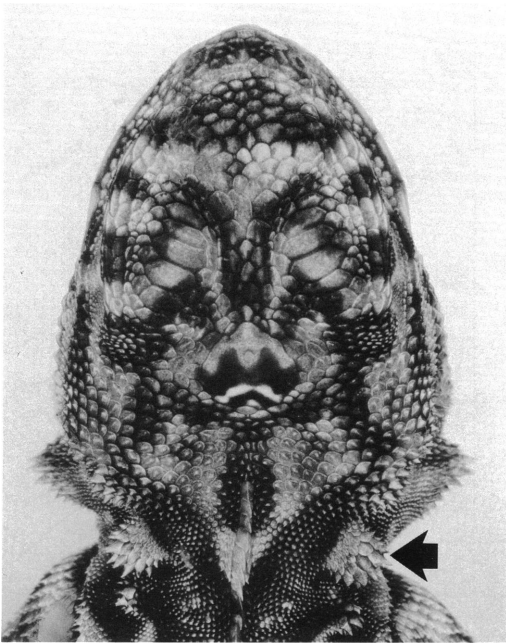


Fig. 25. Neck spines. *Plica plica*, AMNH 107590.

astonishingly difficult, particularly because it is just these structures that are so useful in species identification. Mite pockets are regions of reduced (or absent) squamation in pockets of variable depth, usually located under the antegular-oblique neck fold. Generally, these pockets are inhabited by dense colonies of brightly colored mites. Complicating the issues of homology and polarity of transformation is the uncertainty of topology owing to the modification between taxa of the arrangement of neck folds. Classes of conditions exist that can be discussed, but their phylogenetic relationships remain mysterious.

West of the Andes, the *Tropidurus peruvianus* group lacks mite pockets, although the complex folds on the sides of the neck may have obscured these pockets. All members of the *T. occipitalis* group have invaginations behind the oblique neck fold that are invested with reduced scales and are presumably homologous with pockets behind the lateral neck folds found elsewhere in the *Tropidurus* group. A similar condition obtains in *Strobilurus*. *Uranoscodon* lacks obvious mite pockets, although two shallow depressions in the ante-

gular fold on the ventrolateral side may be homologous with the mite pockets of other taxa. *Uracentron*, *Tropidurus bogerti*, and *Tapinurus* lack mite pockets for much the same reason as the *T. peruvianus* group, elaboration of complex neck folds. *Plica plica* also has complex lateral neck folds, but like *P. umbra*, which does not have complex lateral neck folds, it has modified the position of the gular and antegular folds to such a degree that homology of some structures is questionable. However, *Plica* shares with *Tropidurus spinulosus* and *T. melanopleurus* the development of ventrolateral mite pockets under the antegular fold. None of these taxa has lateral mite pockets as in other taxa; on topographic grounds these ventrolateral pockets are likely homoplastic with the lateral mite pockets of other taxa.

In the *Tropidurus torquatus* group, development of mite pockets shows considerable variation. In these species two regions of pocket development can be seen behind the oblique neck fold, generally separated by a secondary vertical fold. In *T. etheridgei* and *T. cocorobensis* both of these pockets are weakly developed (most weakly in the Argentinian populations); these two pockets are better defined and much deeper in *T. hygomi*. In *T. torquatus* the upper pocket is well developed and the lower is poorly developed. This is similar to the condition in *T. erythrocephalus*, *T. insulanus*, *T. itambere*, *T. montanus*, *T. oreadicus*, and *T. hispidus* in which the lower region of reduced scales is largely absent (presumably concomitant with enlargement of neck scales). The mite pocket is extremely enlarged dorsoventrally in *T. oreadicus* and *T. montanus*.

For purposes of this study I divide this variation into characters of unknown relationship to each other. Although I suspect that the "ancestral" condition for the *Tropidurus* group was "0", I have coded the "hypothetical ancestor" used for rooting as "unknown."

49. Oblique neck fold mite pocket, condition (fig. 24): (0) two mite pockets (*T. etheridgei* [weak in some individuals, particularly in Argentina], *T. cocorobensis*, *T. hygomi*, *T. torquatus* [lower reduced]); (1) a single well-developed mite pocket in the upper position indicated (*T. erythrocephalus*, *T.*

hispidus, *T. itambere*, *T. mucujensis*, *T. nanuzae*); (2) single, very enlarged mite pocket (*T. montanus* and *T. oreadicus*). This additional transformation allows resolution of homology hypotheses not possible under the previous transformation. See discussion under previous transformation.

50. Mite pocket in antehumeral fold (fig. 24): (0) absent; (1) present laterally; (2) present ventrolaterally in antehumeral-antegular fold. *Tropidurus nanuzae* exhibits a very deep antehumeral mite pocket, unique among the iguanians examined. A likely nonhomologous condition obtains in *Plica plica* and *P. lumaria* in which ventrolateral mite pockets appear under the gular fold. Because in these two species the gular and antehumeral folds are continuous, I have coded these conditions as part of an unordered transformation, although I consider it unlikely on topographic grounds that these are homologous.

51. Tufts of spines on sides of neck (fig. 25): (0) absent; (1) present. This transformation series is more difficult to assess than one would think. At least in *Tropidurus spinulosus* the development of the spines is ontogenetic and has a strong geographic component of variation. All species showing some development have spines in the same topographic position relative to lateral neck folds. No development is seen in the outgroups or *Tropidurus* west of the Andes. *Tropidurus torquatus* and *T. montanus* show slightly enlarged scales in the topographic position of the spine tufts, as do *T. melanopleurus*, *Uracentron flaviceps*, and *Uranoscodon*. *Tropidurus bogerti*, *T. mucujensis*, *T. spinulosus*, *Plica plica*, *P. lumaria*, *Strobilurus torquatus*, and *Tapinurus semitaeniatus* develop distinct tufts of spines in older adults. Expression of tufts is apparently strongly influenced by changes in lateral neck scale size. Regardless, species such as members of the *T. peruvianus* group, which have small lateral neck scales, lack "tufting." Therefore, "tufting" is likely apomorphic for the *Tropidurus* group east of the Andes, excluding *Uranoscodon*, or some subset thereof.

52. Rictal fold (fig. 22): (0) absent; (1) present. In *Plica plica*, *P. lumaria*, *Strobilurus*, *Tapinurus*, *Uracentron*, *Tropidurus bogerti*, *T. melanopleurus*, and *T. spinulosus*, a distinctive "upward-pointing" fold extends from

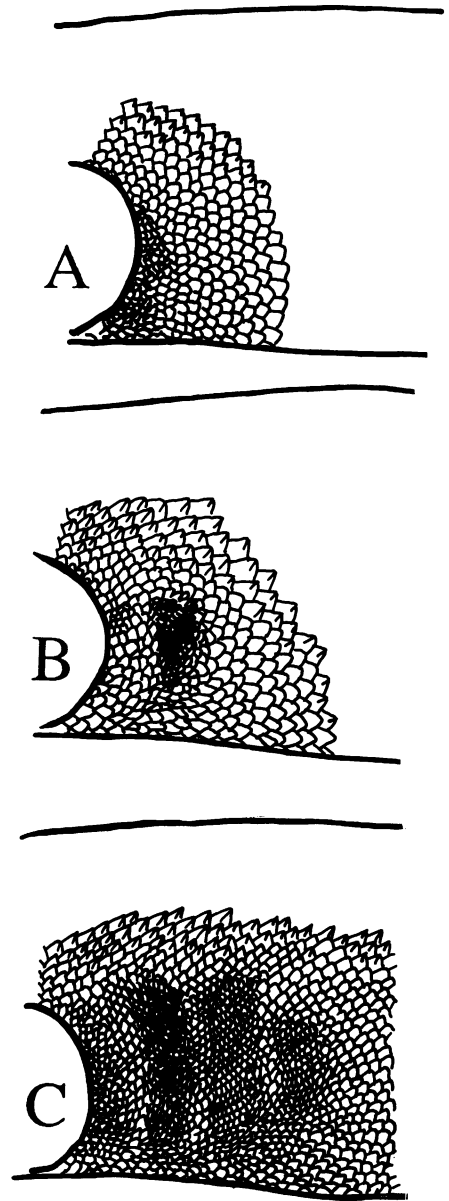


Fig. 26. Axillary squamation. A: *Tropidurus hygomi*. B: *Tropidurus hispidus*, showing single axillary pocket. C: *Tropidurus torquatus*, showing multiple axillary pockets. Redrawn from Rodrigues (1987). Anterior is to the left.

the corner of the mouth to under the ear; it is not found in the remainder of the *Tropidurus* group, or members of the outgroups.

53. Supra-auricular fold (fig. 22): (0) absent or poorly developed; (1) present, well

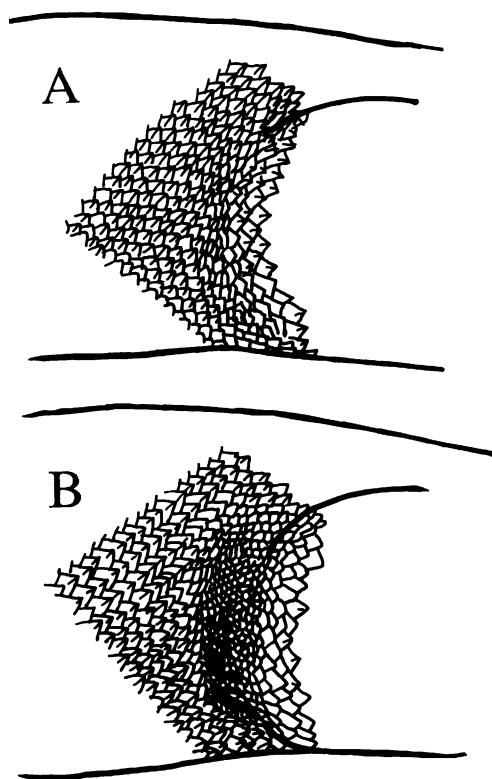


Fig. 27. Groin squamation. A: *Tropidurus hispidus*. B: *Tropidurus torquatus*, showing groin pocket. Redrawn from Rodrigues (1987). Anterior is to the left.

developed. Although present in some members of the outgroups (e.g., “*Stenocercus*” *formosus*), a supra-auricular fold (from the top of the ear to confluence with the dorsolateral fold) is well developed within the *Tropidurus* group only within the *T. peruvianus* group. Weak (but uncoded) development also can be seen in some specimens of *T. bogerti* and *T. melanopleurus*.

54. Axillary pocket, presence (fig. 26): (0) absent; (1) present. See discussion of variation in axillary pockets under the following Transformation Series. Although there is considerable variation in the form of axillary pockets, I have coded them as putative homologs.

55. Axillary pocket, condition (fig. 26) (Rodrigues, 1987): (0) present, single; (1) multiple, usually 3, sometimes only 2. Axillary pockets are absent in *Leiocephalus* and

variably present in the “*Stenocercus*” group although this is not the plesiomorphic condition in that group. The multiple axillary pockets of *Tropidurus torquatus* and *Tapiurus* are visible, but weakly developed in *T. bogerti* and *T. mucujensis*. Of the taxa considered, only *T. erythrocephalus*, *T. hispidus*, and *T. insulanus* have a single (“keyhole”) axillary pocket. Some specimens of *T. montanus*, however, show single mite pockets and some *T. “hispidus”* from the Guyana Region have doubled ones, and some specimens of *T. torquatus* have the folds reduced to a condition almost identical to that in *T. montanus*. Some individuals of *T. itambere* (e.g., MCZ 172883) show axillary depressions that approach the condition found in small *T. montanus*; for this reason *T. itambere* is coded as “unknown.” *T. bogerti* has granular regions topographically in the position of the pockets of other taxa; for this reason I have coded it as apomorphic.

56. Inguinal granular pocket (fig. 27) (Rodrigues, 1987): (0) absent or represented solely by a nongranular fold; (1) present. All species in the outgroups and within the *Tropidurus* group that have relatively small scales have something of an inguinal fold so care must be taken in the evaluation of this feature. The difference between distinctly preinguinal and inguinal mite pockets (Rodrigues, 1987) is difficult to characterize because of intraspecific and geographic variation. I have therefore only coded presence or absence of the pocket. Because *T. bogerti* has a granular fold in the topographic position of the femoral pocket of other species I have coded it as apomorphic.

SQUAMATION

Nomenclature of scales follows Smith (1946).

57. Rostral scale, height (Etheridge, 1970a): (0) rostral scale 1.5 to 2× height of adjacent supralabials; (1) rostral scale height reduced, less than 1.5 height of adjacent supralabials. In the *Leiocephalinae* and “*Stenocercus*” group, the rostral scale is well elevated. In *T. bogerti*, *Plica*, *Uracentron*, and *Uranoscodon* the rostral scale is reduced to nearly the level of the adjacent supralabials. *Tropidurus melanopleurus* and *T. spinulosus*

(somewhat more frequently and with a geographic component) also show reduction in height of the rostral scale, but because these do not exhibit the same degree of reduction I have coded these species as plesiomorphic.

Although Etheridge (1966) noted variation in nasal-rostral contact within the *Tropidurus* group, except in clear cases of anomalies, all members of the *Tropidurus* group have the rostral separated from the nasal scale by at least one row of postrostral scales.

58. Mental scale (fig. 28): (0) enlarged, extending posteriorly well beyond level of adjacent infralabials; (1) reduced, not extending posteriorly well beyond level of adjacent infralabials. In *Leiocephalus* and the “*Stenocercus*” group the mental scale is much larger than the adjacent infralabials. This condition obtains in most of the *Tropidurus* group also. However, in *Plica* and *T. spinulosus* the mental scale is reduced and does not extend far beyond the level of the anteriormost infralabials. Although the mental scale of *Uracentron* appears on casual inspection to be reduced, this perception is due to the great enlargement of the adjacent infralabials and postmentals.

59. Postmental series (Etheridge, 1968, 1970a) (fig. 28): (0) well defined; (1) poorly defined or absent. In *Leiocephalus* and the “*Stenocercus*” group a distinct postmental series of scales is evident. This is also the condition in most of the *Tropidurus* group, except for *Strobilurus*, *Plica*, *Uranoscodon*, *Tropidurus spinulosus*, and *T. melanopleurus* in which the postmental series is difficult to discern from adjacent gulars and subinfralabials. Of this group, *T. melanopleurus* has the most evident postmentals; I have coded this species as “1” because the postmental series is reduced and because of the unusual position of these scales; these mildly enlarged scales may not be homologous with the enlarged postmentals of other species.

60. Infralabial scales, number (fig. 29): (0) 6; (1) 8–9. In outgroups and most of the *Tropidurus* group there are 6 infralabial scales. In the *Tropidurus peruvianus* group, however, there are 8–9.

61. Infralabials, expansion (Etheridge, 1968) (fig. 29): (0) infralabials not ventrally expanded; (1) infralabials greatly expanded ventrally. In *Leiocephalus* and the “*Steno-*

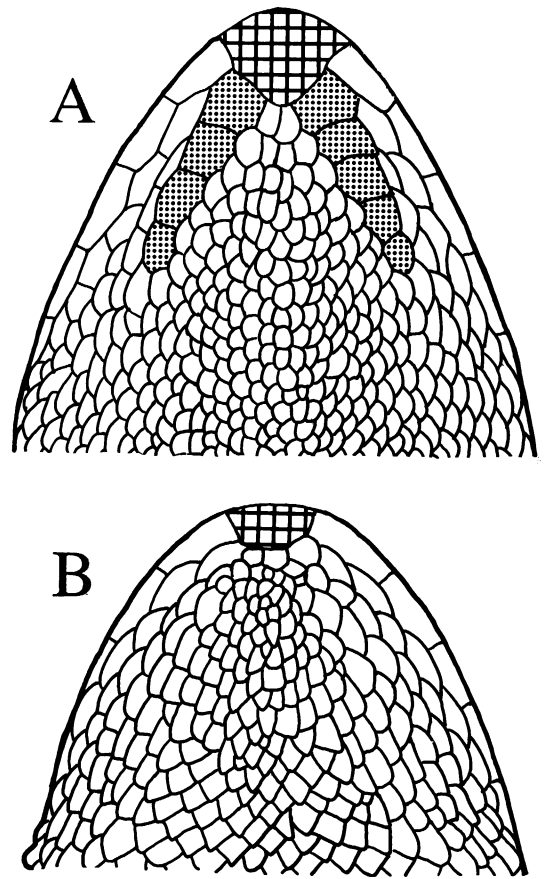


Fig. 28. Ventral views of chins showing mental (cross-hatched) and postmental scales (stippled). A: *Tropidurus torquatus*, UNSM 207684. B: *Plica umbra*, KU 126778.

cercus” group the infralabials are not expanded. This is also the condition in most species in the *Tropidurus* group. Although *Tropidurus bogerti*, *T. melanopleurus*, *Strobilurus torquatus*, and *Tapinurus* exhibit some ventral expansion of the infralabials with respect to the adjacent supralabials, this condition is approached by other *Tropidurus* (e.g., *T. torquatus*, *T. hispidus*), making characterization of a transformation series impossible. *Uracentron* carries this expansion to a much greater degree and has the only condition here coded as apomorphic.

62. Lateral gular scales: (0) imbricate posteriorly; (1) imbricate laterally. In *Leiocephalus* and the “*Stenocercus*” group, the lateral gular scales are imbricate posteriorly. Within

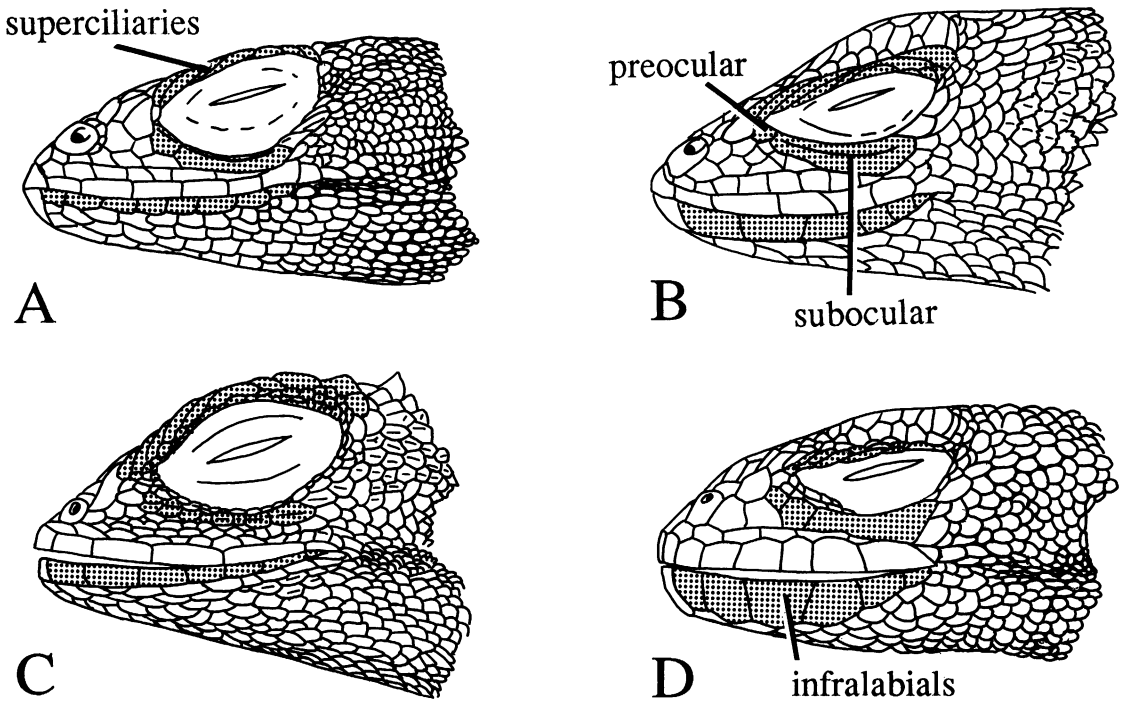


Fig. 29. Scale characters of the side of the head. A: *Tropidurus atacamensis*, KU 161982. B: *Tropidurus hispidus*, KU 127227. C: *Plica umbra*, KU 126778. D: *Uracentron flaviceps*, KU 126781. Infralabials, superciliaries, and preocular-subocular series shaded on each view, although only labeled once.

the *Tropidurus* group this is also true in *Uracentron* and *T. bogerti*. All other species of the *Tropidurus* group have the scales imbricate posterolaterally. In some species of the *T. peruvianus* group the lateral gulars are granular but still show evidence of lateral orientation.

63. Scales of frontonasal region (fig. 25): (0) imbricate posteriorly or no imbrication evident; (1) weakly imbricate anteriorly; (2) all head shields strongly imbricate anteriorly. Unique within the iguanians examined, *Tropidurus spinulosus*, *T. melanopleurus*, *Strobilurus*, *Plica*, *Tapinurus*, and *Uracentron* have the scales of the frontonasal region imbricate in an anterior direction. In some individuals of *Plica umbra* and *Uracentron*, the anterior direction of imbrication is only detectable by lifting the stratum corneum with a probe. *Tropidurus bogerti* is coded as "unknown" because some individuals appear to have some subtle anterior imbrication and others do not. *Plica plica* and *P. lumaria* show

the extreme condition and additionally have the direction of imbrication of the head shields reversed over the entire head.

Possibly this imbrication would increase the handling time of predatory snakes, which are known to take cues from the direction of scale imbrication of prey items (Greene, 1976).

64. Superciliary scales (Etheridge, 1970a) (fig. 29): (0) not or only weakly produced vertically to form a longitudinal crest; (1) produced vertically to form a longitudinal crest. The superciliaries of *Plica* and *Uranoscodon* are produced vertically conspicuously more than in other members of the *Tropidurus* group or outgroups.

65. Circumorbital series (fig. 30): (0) in one row between the supraoculars and the median head shield; (1) in two rows between the supraoculars and the median head shield. In most species of the *Tropidurus* group as well as *Leiocephalus* and relevant members of the "*Stenocercus*" group there is only one row of

circumorbitals separating the supraoculars from the median head shields. However, in *Tropidurus melanopleurus*, *T. spinulosus*, *Plica*, *Strobilurus*, and *Uracentron* there are two distinct rows or circumorbitals, at least posteriorly. Because a circumorbital series is autapomorphically indistinguishable from the supraoculars in *Uranoscodon* this species was coded as “unknown” in the analysis.

66. Circumorbitals (fig. 30): (0) small; (1) enlarged at the expense of the supraoculars. In *Uracentron* the circumorbitals, normally small in the other members of the *Tropidurus* group and outgroups, are enlarged at the expense of the supraocular scales.

67. Interparietal (Smith, 1946; Etheridge and de Queiroz, 1988) (fig. 33): (0) not enlarged, smaller than interorbital distance; (1) enlarged, larger than interorbital distance. With the exception of the Phrynosomatidae, the *Tropidurus* group is unique in the possession of an “enlarged” interparietal. “Enlargement” is not really an appropriate term because the interparietal of the *Tropidurus* group is clearly a sutured aggregation of parietal scales as in other iguanians. In *Uranoscodon* the individuality of the scales is evident because of their separate elevation regardless of their edge-to-edge suturing. In most specimens of western *Tropidurus*, there is generally some evidence of incomplete suturing around the periphery of the interparietal scale (fig. 30). Etheridge (1970a: 242) noted that *Uranoscodon* has a relatively small interparietal, but because it does not obviously have the “enlarged” interparietal composed of fewer subsidiary scales than in other members of the *Tropidurus* group, I have not used this difference in my analysis.

68. Interparietal length (Etheridge, 1968) (fig. 30): (0) subequal to significantly less than width; (1) significantly longer than wide. In order to evaluate the polarity of this feature I circumscribed the “parietal scales” in the outgroups so as to estimate the dimensions of the “enlarged” interparietal (see discussion in previous transformation series). *Uracentron* and *T. itambere* are unique within the *Tropidurus* group in having an interparietal substantially longer than wide.

69. Rows of scales between subocular and supralabials (Etheridge, 1970a [part]) (fig. 29):

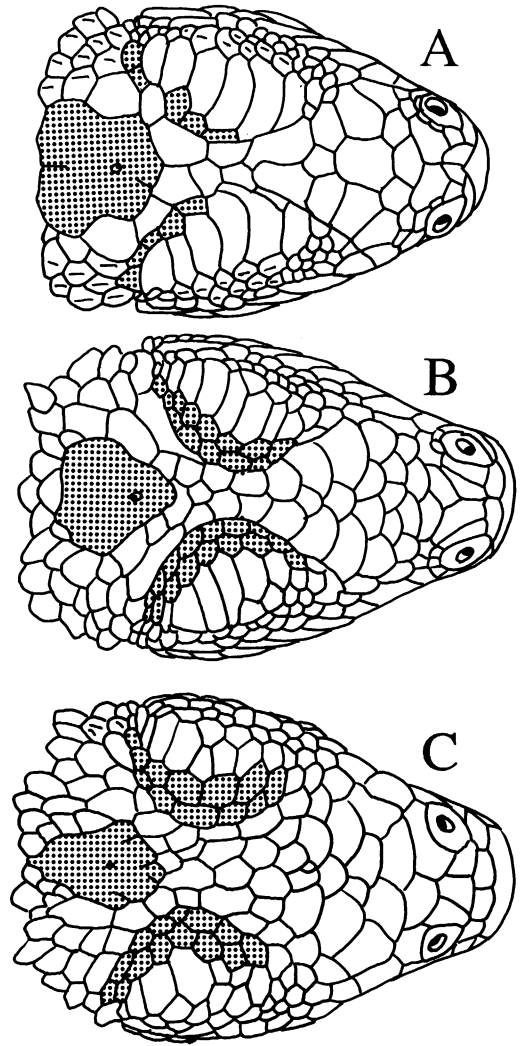


Fig. 30. Dorsal head squamation; circumorbitals and interparietals shaded. A: *Tropidurus koepckeorum*, LACM 49102 (frontonasal scales paved). B: *Tropidurus spinulosus*, LACM 126318 (frontonasal scale imbricated anteriorly). C: *Uracentron flaviceps*, KU 175318 (frontonasal scales imbricated anteriorly).

(0) 0–1; (1) 2 or more. In both *Leiocephalus* and the “*Sternocercus*” group, as well as most of the *Tropidurus* group, there is no more than one row of loreolabials between the subocular and the supralabials. In *Plica* there are at least two rows of loreolabials penetrating between the subocular and supralabials. In

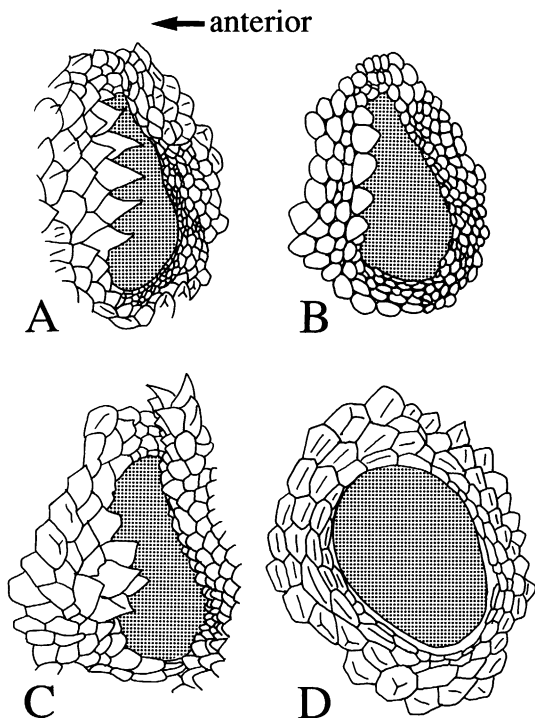


Fig. 31. Auricular fringing and lobing. A: *Tropidurus koepckeorum*, LACM 49102. B: *Tropidurus atacamensis*, KU 161980. C: *Tropidurus spinulosus*, USNM Field 99128. D: *Uranoscodon superciliosus*, KU 127230.

occasional specimens (uncoded) of *Tropidurus spinulosus* more than one row of scales may penetrate between the supralabials and subocular. *Uranoscodon* may appear, on cursory examination, to have multiple rows of scales below the subocular. This illusion is caused by uncertainty as to what constitutes a subocular, because this species has a highly fragmented subocular series. However, occasional specimens show enough enlargement of the subocular series so that it can be seen that only one scale row penetrates between this row and the supralabials.

70. Subocular (Etheridge, 1970a) (fig. 29): (0) entire—0–1 preoculars; (1) divided—at least 2 preoculars in contact with the orbit; (2) subocular-preocular series so fragmented as to be obscure. In the “*Stenocercus*” group and *Leiocephalus*, the orbit is underlain by an elongate subocular and (variably) by a single preocular in the same series. Also, this

condition obtains in most of the *Tropidurus* group. However, in *Plica*, *Strobilurus*, *Uracentron*, and *Uranoscodon* the orbit is underlain by at least three scales caused by fragmentation of the preocular-subocular series. *Uranoscodon* and *Plica umbra* have continued this fragmentation to the point that the preocular-subocular series is obscure.

71. Preauricular fringe (fig. 31): (0) present, ear canal deep, a continuous fringe of scales partially to nearly completely covering ear opening; (1) reduced, ear canal deep; (2) auricular scales reduced, ear canal deep, a lower lobule with several short spines present; (3) auricular fringe absent, the ear canal shallow. In relevant members of the outgroups and most of the *Tropidurus* group, the external ear canal is partially covered by a fringe of scales. In the *T. peruvianus* group the fringe is reduced through “granularization” concomitantly with the granularization of body scales. In some species (i.e., *Tropidurus spinulosus*, *T. bogerti*, *T. melanopleurus*, *Plica plica*, *P. lumaria*, *Strobilurus*, and *Tapinurus*) the fringe is reduced, and a short lobule on the ventral limit of the anterior margin of the ear canal is present. *Tapinurus semitaeniatus* is intermediate between “0” and “2” but was coded as “2”, because it exhibits the fleshy lobe. *Plica umbra*, *Uranoscodon*, and *Uracentron* have a more reduced condition; the entire fringe or lobule is absent. Because the “reduced” condition (2) involves the elaboration of a fleshy lobule also not seen in condition “3”, it does not follow necessarily that absence (3) must be derived from condition “1” rather than “0” or “2”. I have therefore regarded these conditions as an unordered set, although the “ancestral” condition is clearly “0”.

72. Middorsal scale row (Etheridge, 1966 [part]): (0) present; (1) absent. I have not taken degree of development (i.e., scale enlargement or elevation) into consideration in this transformation series because variation in development is continuous and exceedingly difficult to characterize. In *Leiocephalus* (except *L. pratensis*) and plesiomorphically in the “*Stenocercus*” group (as in all iguanians) the middorsal scale row is present and enlarged. In the *T. torquatus* group, *Tapinurus*, and *Uracentron* the middorsal scale row is

not identifiable. In the *T. heterolepis* subgroup (*T. atacamensis*, *T. heterolepis*, *T. quadrivittatus*, and *T. theresiae*) of the *T. peruvianus* group, the middorsal scale row is usually identifiable on the neck (though not enlarged) but is usually unidentifiable along the back.

73. Paravertebral scales (Boulenger, 1885): (0) keeled; (1) not keeled. In the outgroups and most of the *Tropidurus* group, the paravertebral scales are imbricate and keeled. In the *Tropidurus peruvianus* group, *Tapinurus*, *Tropidurus melanopleurus*, and *Uracentron azureum* these scales are extremely weakly keeled or unkeeled.

74. Lateral body scales: (0) imbricate, keeled; (1) granular and juxtaposed. In both outgroups and most of the *Tropidurus* group, the lateral body scales are imbricate and mucronate. In the *Tropidurus peruvianus* group, though, the lateral body scales are granular ("pebbly") and juxtaposed. *Tapinurus* approaches this condition, but is not "pebbly" as in the *Tropidurus peruvianus* group.

75. Caudal scales (fig. 32): (0) tail unarmed, longer than head + body; (1) tail armed with heavy mucrons, roughly terete and subequal to length of head + body; (2) tail armed with heavy mucrons, dorsoventrally flattened and shorter than head + body. In *Leiocephalus* and plesiomorphically within the "*Stenocercus*" group the caudal scales are only weakly mucronate. In *Strobilurus*, and even more so in *Uracentron*, the caudal scales are so strongly mucronate that their tails should be considered armed and dangerous.

76. Ventral scales: (0) smooth; (1) keeled. With the exception of the few derived species of "*Ophryoessoides*," *Proctotretus azureus*, and *Leiocephalus herminieri* the keeled ventral scales of *Uranoscodon superciliosus* and *Plica umbra* are unique among the *Tropidurus* group and the immediate outgroups.

77. Upper thigh scales: (0) not heavily mucronate; (1) heavily mucronate. *Strobilurus*, unique within the *Tropidurus* group and derived with respect to the outgroups, has heavily armed thigh scales. *Tropidurus itambere* also has strongly mucronate scales on the legs, but nothing approaching the condition in *Strobilurus*.

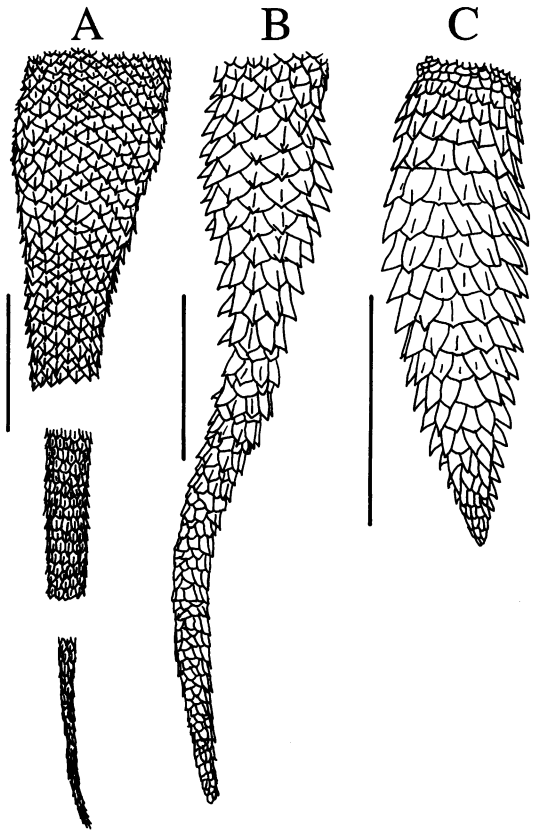


Fig. 32. Caudal scales in dorsal view. A: *Tropidurus etheridgei*, KU 73442 (SVL = 65, tail = 91). B: *Strobilurus torquatus*, MCZ 154241 (SVL = 45, tail = 40). C: *Uracentron azureum*, KU 204988 (SVL = 36, tail = 19). Scales = 10 mm.

RESULTS AND DISCUSSION OF POSSIBLE ERRORS

RESULTS

For the characters under analysis *Tropidurus heterolepis*, *T. quadrivittatus*, and *T. theresiae* were identical to *T. atacamensis*. *Tropidurus thoracicus*, *T. theresioides*, *T. tigris*, and *T. yanezi* were identical to *T. peruvianus*. *Tropidurus habellii* was equivalent to *T. bivittatus*, *Tropidurus etheridgei* equivalent to *T. hygomi*, and *Tapinurus pinima* equivalent to *T. semitaeniatus*. *Plica lumaria* is identical to *Plica plica* for characters under discussion. *Tropidurus cocorobensis* as characterized in the data matrix differs from *T. hygomi* solely by "unknown" assignments.

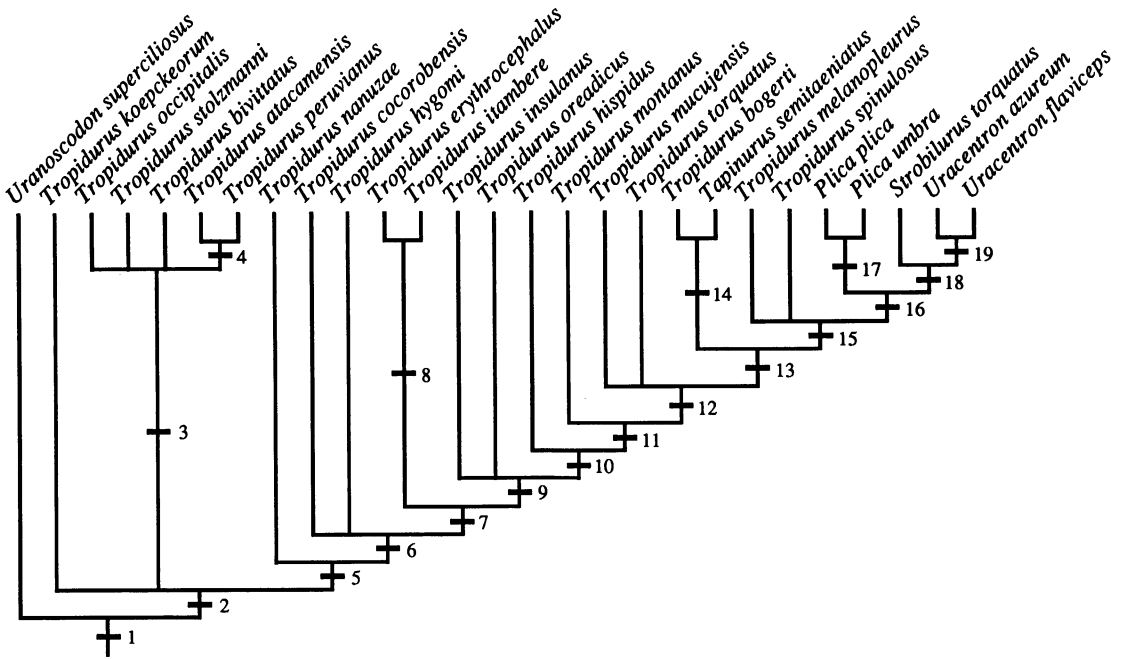


Fig. 33. Strict consensus tree, and one of the 36 equally parsimonious trees generated for the *Tropidurus* group data. Length = 169, ci = 0.568. Numbers on stems are noted in Appendices 3 and 4 and discussed under Results.

The reduced data matrix was subjected to analysis as described under "Methods." One tree was discovered (fig. 33) that was parsimonious under both accelerated and delayed transformation. Thirty-six equally parsimonious trees (length = 169, ci = 0.568; length = 157, ci = 0.535, excluding a priori autapomorphies and group synapomorphies) were discovered that had some justification under either accelerated or delayed character optimization. Another 16 trees could have been counted in this number but they depended on "justification" from arbitrary assignment of an "unknown" character. The number of unrejected trees, i.e., those whose topologies were logically consistent with the data but whose topologies went beyond data support numbered 26,588, this dependent on 6 "regions" in the cladogram of alternative but unsupported arrangements. Of the 36 supported trees only one was supported unambiguously (i.e., not dependent on method of character optimization). This tree (fig. 33) is the same as the strict (Sokal and Rohlf, 1981) and Adams (1972) consensus of the 36 sup-

ported trees discovered. The "regions" of supported alternative topology are depicted in figure 34.

The following discussion refers to figure 33. Stem 1 (the *Tropidurus* group) is well supported by five unreversed transformations: 11.1 (general reduction of bone mass resulting, among other things, in the reduction of the quadrate process of the squamosal as well as the enlargement of the superior fossa of the quadrate), 12.1 (mild reduction in the definition of the alveolar shelf of the mandible [possibly related to transformation 11]), 27.1 (enlargement of the sternum), 44.1 (elongation of the hemipenes), and 67.1 (fusion of parietal scales to form a large, distinct interparietal scale). Additionally, this stem is supported by 28.1 (a shortening of the interclavicle median process), which is reversed in *Tropidurus bogerti*, *T. spinulosus*, and *Uracentron azureum*, and 62.1 (lateral imbrication of the throat scales), which is reversed in *T. bogerti* and Stem 19 (*Uracentron*). This is a well-corroborated group.

Uranoscodon superciliosus is supported as

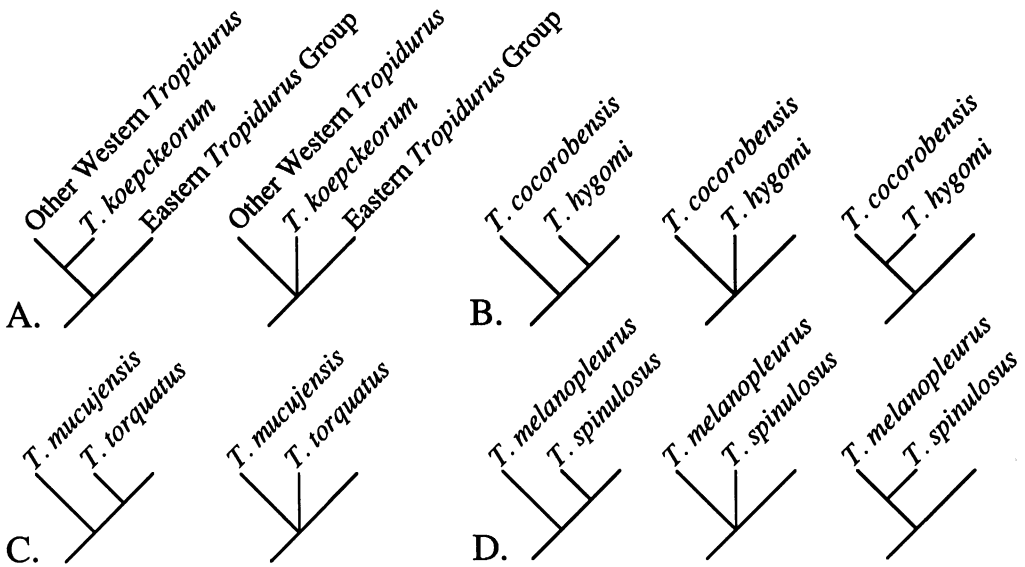


Fig. 34. Supported alternatives for various parts of the cladogram.

the sister taxon of the rest of the *Tropidurus* group (Stem 2). Autapomorphies are numerous (17), although only one (37.1), fringed toes, seems to be unique to this taxon. A surprising number of shared homoplasies with *Plica umbra* (20) as well as other species in its "neighborhood" make it understandable that these taxa have been considered closely related by many authors. Stem 2, the sister taxon of *Uranoscodon* is corroborated by only two synapomorphies, although these are unique and unreversed and easily characterized: 13.1 (development of a lingual coronoid process of the dentary overlapping the anterior lingual leg of the coronoid), and 33.1 (elevation of the head of the humerus). To this meager list can be added one other feature, black transverse bars across chest and upper arms. This feature is difficult to characterize a priori and is obscured in numerous species by increasing black and other obscuring patterns. However, *Uranoscodon* clearly does not have anything like transverse black bars on the chest and all of the remaining species patristically near the "base" of *Tropidurus* do, both east and west of the Andes.

Stem 2 subtends a trichotomy, although under some optimizations *Tropidurus koepckeorum* is placed as the sister taxon of

Stem 3 (other species of western *Tropidurus*). *T. koepckeorum* is not characterized by any apomorphies here analyzed but some of its features are likely apomorphic (see below). Stem 3, subtending the members of the *Tropidurus occipitalis* and *T. peruvianus* groups of Dixon and Wright (1975) is corroborated by a single, but striking feature, hemipenis with terminal disks (43.1). There is currently no evidence for the monophyly of the *T. occipitalis* group, even excluding the former member, *T. koepckeorum*. The *T. peruvianus* group (Stem 4), however, is well corroborated by three unique, unreversed synapomorphies: 53.1 (supra-auricular fold), 60.1 (8–9 infra-labial scales), and 74.1 (granular lateral body scales). Additionally, 48.1 (complex neck folding), also known homoplastically in *T. bogerti*, *Tapinurus*, and *Uracentron*, 71.1 (reduced preauricular fringing [presumably related to reduction of body scales in general], found in a number of other species homoplastically, and 73.1 (reduced scale keeling), also found homoplastically in *Tapinurus*, *Tropidurus melanopleurus*, and *Uracentron azureum*, support this clade. The *Tropidurus heterolepis* subgroup (*T. atacamensis*, *T. heterolepis*, *T. quadrivittatus*, and *T. theresiae*) of the *T. peruvianus* group has its monophyly supported by 72.1 (loss of middorsal enlarged

scale row), also seen in the former *Tropidurus torquatus* group and *Uracentron*. The monophyly of this group is not particularly surprising inasmuch as all species seem to be predominantly intertidal feeders (Dixon and Wright, 1975; Ortiz-Zapata, 1980a).

Stem 5 (*Tropidurus* and generic satellites east of the Andes) is highly corroborated by nine unique unreversed synapomorphies: 1.1 (increased skull size), 7.1 (conspicuously enlarged nutritive foramina of maxilla), 12.2 (alveolar shelf of mandible strongly eroded), 14.1 (long posterior extension of dentary), 16.1 (angular reduced), 20.1 (enlargement of anterior maxillary teeth), 33.2 (ball-like head of humerus), 34.1 (loss of medial centrale), and 35.1 (elongation of fourth metacarpal). To the list can be added: 15.1 (anterior surangular foramen captured by contact of coronoid and surangular), reversed in *T. bogerti*, 17.2 (posterior mylohyoid foramen between splenial and dentary), reversed in *T. spinulosus* and *Uracentron* (Stem 19), 30.1 (suprascapular fenestrations), reversed in *Uracentron* (Stem 19), and 48.2 (lateral mite pocket), reduced and modified a number of places above this level in the cladogram. Additionally, a synapomorphy of this clade is pigmented thigh patches. This is, after Stem 1, the most highly corroborated stem in the analysis.

Tropidurus nanuzae has two unreversed synapomorphies: 26.1 (loss of sternal fontanelle) and 50.1 (mite pocket in antehumeral fold). A third feature, 22.1 (posterior maxillary teeth appear brachydont from the labial side) is also shared with *Uracentron flaviceps*, *Plica*, and *Uranoscodon superciliosus*. I have been unable to see *T. amathites* or *T. divaricatus*, both species considered close to *T. nanuzae* by Rodrigues (1986) on the basis of the loss of the sternal fontanelles. Apparently, *T. amathites* has antehumeral mite pockets and *T. divaricatus* lacks them. Also, the three species in the *T. nanuzae* group of Rodrigues (1986) share a presumptively apomorphic karyotype (Kasahara et al., 1987). As it stands, *T. nanuzae* does not "fit" well anywhere, and sufficient homoplasy shared with the *Plica-Uracentron-Strobilurus* region of the cladogram may suggest that I have misplaced it badly (see comment below).

Stem 6 has no unique unreversed apomorphies but is supported by 25.1 (clavicle not flanged), reversed in *Plica umbra* and *Uracentron* (Stem 19), 45.1 (ornamentation of hemipenes starts above crotch between lobes), also in *Uranoscodon*, and 72.1 (loss of middorsal enlarged scale row), apparently regained at Stem 15, then lost again in *Uracentron* (Stem 19) and also appearing in the *Tropidurus heterolepis* subgroup. This feature has traditionally been the sole justification of the "*Tropidurus torquatus* group," which at this point has little other support.

Stem 7 is united by only two features, 49.1 (single large mite pocket on neck) and 54.1 (axillary pocket present), both with homoplasy; 49 is modified frequently elsewhere and 54 is reversed on Stem 15. Axillary pockets are extremely difficult to characterize for phylogenetic analysis and this stem is very poorly corroborated. The same is true of Stem 8, supporting the monophyly of *T. itambere* and *T. erythrocephalus* which is supported by the homoplastic feature 56.1 (groin granular pocket) which appears elsewhere in the former *T. torquatus* group. I consider this association, along with most other phylogenetic structure within the former *T. torquatus* group to be poorly corroborated. That *T. itambere* resembles *T. etheridgei* in aspects of form and coloration that are difficult to characterize for phylogenetic analyses only strengthens this suspicion.

Stem 9 is supported solely by rib formula (31.1). Although Etheridge (1962, 1964) has documented that this can be astonishingly variable in *Sator* and other phrynosomatids, modalities can be established that seem to be informative. Nevertheless, the sample sizes examined here were small and, although I found no intraspecific variation, it is conceivable that taxa have been mischaracterized.

Stem 10 is justified by the single character 55.1 (double axillary mite pocket). This feature is reversed on Stem 15 concomitant with the reversal in Transformation 54 to 54.0 (axillary pocket absent). This character is peculiar and surprisingly difficult to characterize. That some specimens of *T. "hispidus"* from the Guyana Region have double axillary pockets and that some *T. montanus* are

annectent between the 1- and 2-pocket condition make this a difficult transformation. Stem 11, like Stem 10, is poorly corroborated, with only one homoplastic character justifying it: 56.1 (groin granular pocket), this feature being found also on Stem 8, leading to *T. itambere* and *T. erythrocephalus*. Stem 12 is supported by scale "tufting" on the sides of the neck. This is lost in *Plica umbra*, *Uracentron azureum*, and apparently similar but weakly developed squamation can be seen in *Uranoscodon superciliosus*.

Stem 13 is well corroborated by two unreversed unique apomorphies: 35.2 (fourth metacarpal lengthened) and 63.1 (scales of frontonasal region imbricate anteriorly), although *T. bogerti* was coded "unknown" for this feature because of characterization problems. Additionally, several other homoplastic features support this stem's reality: 29.1 (scapular deflection with concomitant reduction of the scapular fenestra of the scapulo-coracoid), reversed on Stem 16, 52.1 (presence of a rictal fold), reversed in *Plica umbra*, and 71.2 (auricular scales reduced), this being further modified in *Plica umbra* and *Uracentron* (Stem 19). Stem 14, uniting *T. bogerti* with *Tapinurus*, is supported by two non-homoplastic features associated with being flat: 6.1 (nasal bones reduced) and 39.1 (depressed neural spines of tail vertebrae) as well as 24.1 (loss of pterygoid teeth), which is highly homoplastic. *Tapinurus* is a highly apomorphic group of three species of which the following are synapomorphies rather than autapomorphies of *T. semitaeniatus*: 3.1 (skull compressed), 6.2 (nasal bones very reduced), 18.1 (posterior position of posterior mylohyoid foramen), also in *Uracentron* (Stem 19), 19.1 (premaxillary teeth 4–5), also homoplastic in alternative placement elsewhere, 21.1 (flaring maxillary teeth), also in *T. hispidus* and at Stem 16, 29.2 (strongly flexed scapulo-coracoid), 31.0 (reversal to 3 sternal ribs), and 32.1 (long xiphisternal rods associated with the pectoral musculature).

Stem 15 is well corroborated, but only one of its synapomorphies is unique and unreversed: 65.1 (circumorbital scales in two rows). Others include 42.1 (ventral thigh region with yellow patches), also in *T. nanuzae*, 47.1 (complete antegular fold), also in *T. stolz-*

manni, 54.0 (loss of axillary pocket), 56.0 (loss of groin pocket), 59.1 (postmental series reduced), reversed in *Uracentron* (Stem 19), and 72.1 (middorsal scale row present).

Stem 16 has a number of synapomorphies: 5.1 (nasal spine of premaxilla broad), also in *Uranoscodon*, 8.1 (maxillopalatine foramen very large), 21.1 (flaring posterior maxillary teeth), also in *Tapinurus* and *T. hispidus*, and 23.1 (posterior maxillary teeth set vertically), also in *T. nanuzae*, 29.0 (scapular deflection reversed), 41.2 (nostrils directed anterolaterally or anteriorly and unconstricted), and 70.1 (subocular scale divided), also in *Uranoscodon*.

Plica (Stem 17) is supported by only two nonhomoplastic characters, 10.1 (squamosal bone curved around posterior end of temporal fenestra) and 69.1 (two or more rows of scales between the subocular and the supralabials). Other features that support the monophyly of this group are: 22.1 (posterior teeth appear brachydont when viewed from the labial side), also in *T. nanuzae* and *Uracentron flaviceps*, 47.2 (antegular fold overlaps gular fold), also in *T. spinulosus*, 58.1 (mental scale reduced), also in *T. spinulosus*, and 64.1 (superciliary scales produced vertically to form a crest), also in *Uranoscodon*. The members of the *Plica plica* group (*P. plica* and *P. lumaria*) are otherwise extremely different from *Plica umbra* in almost all other ways. *Plica lumaria* and *P. plica* are associated by all features that are treated as autapomorphies of *Plica plica* in this analysis.

Like the three species of *Plica*, *Strobilurus* and *Uracentron* have long been associated with each other, although the resemblances when enumerated are not overwhelming; almost as much associates *Plica umbra* with *Uracentron* as does *Strobilurus* with *Uracentron* (i.e., a one-step difference in total tree length). However, the weight of the evidence does support a special relationship between *Strobilurus* and *Uracentron*. This associative Stem 18 is supported by two synapomorphies: 38.1 (anterior margin of pubis not acute) and 75.1 (armed caudal scales). The tail structure is otherwise quite dissimilar; *Strobilurus* has a terete tail as is found in such species as *Stenocercus roseiventris* and *Uracentron* has a spatulate tail similar in some

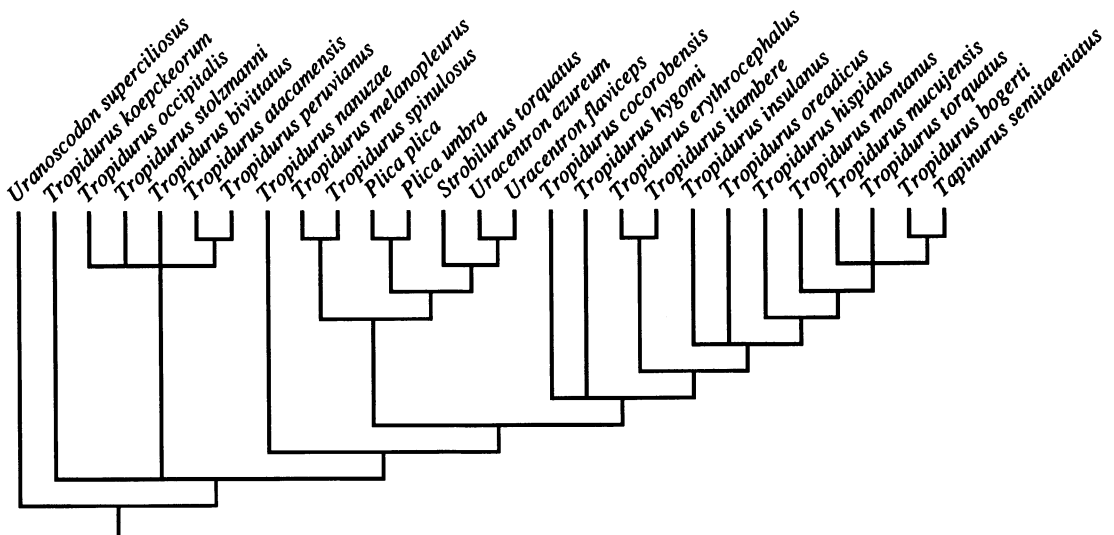


Fig. 35. Alternative tree, length = 171.

ways to that in *Hoplocercus* (Hoplocercidae). *Uracentron* monophyly is not problematical, supported by four unique apomorphies and a plethora of others: 17.0 (posterior mylohyoid foramen between dentary and angular), also in *T. spinulosus*, 18.1 (posterior mylohyoid foramen placed far back on mandible), also in *Tapinurus*, 25.0 (clavicle strongly flared), also in *Plica umbra*, and plesiomorphy below Stem 6, 30.0 (reversal to no suprascapular fenestrae), 36.1 (claw of first toe strongly flexed), 40.1 (no fracture planes in caudal vertebrae), 42.0 (thighs without ventral pigmented patches), 46.1 (gular fold complete medially), also in *Plica* and *Uranoscodon*, 59.0 (reversal to postmental series enlarged), 61.1 (infralabials greatly expanded), 62.0 (lateral gular scales imbricated posteriorly), also in *T. bogerti*, 66.1 (circumorbitals enlarged), 68.1 (interparietal much longer than wide), also in *T. itambere*, 71.3 (auricular fringe absent, ear canal shallow), 72.1 (middorsal scale row absent), also in the former *Tropidurus torquatus* group, and 75.2 (spatulate tail).

COMMENT ON THE *TROPIDURUS TORQUATUS*
GROUP AND ON STABILITY OF
THE CLADOGRAM

That the most parsimonious cladogram (fig. 33) is unstable is obvious. Figure 35 shows

a cladogram of length 171 (two steps longer than the 169-step preferred cladogram). This allows monophyly of the *Tropidurus torquatus* group (including *Tapinurus*); that is, the traditional synapomorphy of the *T. torquatus* group + *Tapinurus*, loss of middorsal scale row, is judged unreversed. The enlarged medial dorsal scale row of *T. melanopleurus*, *T. spinulosus*, *Plica*, and *Strobilurus* would be judged plesiomorphic rather than derived from the *T. torquatus* condition. Also, reversals having to do with axillary and groin granular pockets would disappear and both groups of thigh colors (yellow vs. dark brown or black) would be historically connected rather than have the yellow hue appear independently in *T. nanuzae* and in the *T. melanopleurus*-*Uracentron* group. As evidenced by the increased tree length, however, the cost is a reduction of parsimony, showing itself in additional homoplasy in rib formula (additional change from 3 to 4 sternal ribs in the stem leading to *T. melanopleurus*, *T. spinulosus*, *Plica*, *Strobilurus*, and *Uracentron*, as well as within the *T. torquatus* group); scapulocoracoid flexing would have to occur independently in the *T. melanopleurus*-*T. spinulosus* clade as well as in the *T. bogerti*-*Tapinurus* clade (both of which are notably saxicolous clades). The elongation of the fourth metacarpal would have to occur twice: in the *T. bogerti*-*Tapinurus* clade and inde-

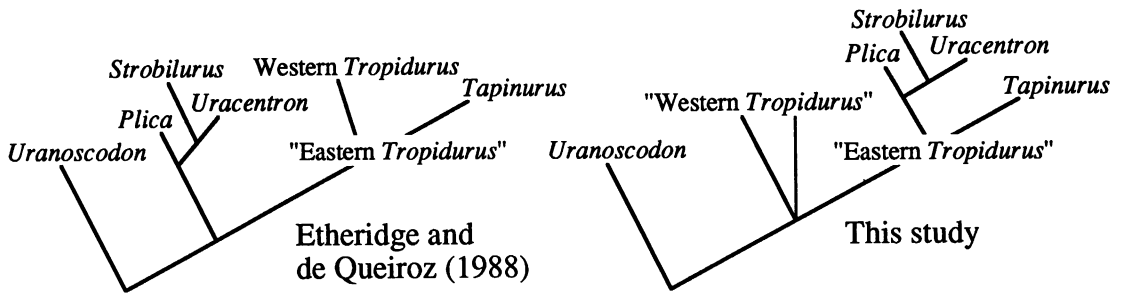


Fig. 36. *Tropidurus* group tree of Etheridge and de Queiroz (1988) and of the present study.

pendently in the *T. melanopleurus*–*Uracentron* clade. Neck spine tufting and the appearance of the rictal fold (associated with underlying muscle development) would also have increased homoplasy. So, even if rib formula (Transformation 31), scapulocoracoid flexion (Transformation 29), elongation of the fourth metacarpal (Transformation 35), rictal fold (Transformation 52), and neck scale tufting (Transformation 51) are excluded from the analysis, this alternative tree is still only marginally more parsimonious (i.e., two steps shorter) than the preferred cladogram, and would still leave *Tropidurus* paraphyletic, even though a modified *T. torquatus* group (including *Tapinurus*) would survive. And, inasmuch as the most parsimonious cladogram correlates well with trends in overall similarity and longer trees do not, there is little that should drive us to prefer a longer tree than we are required to. Regardless of the choice of overall cladograms, the phylogenetic structure among species within the former *Tropidurus torquatus* group is arguable, with considerable homoplasy, and is so unstable as to not promote much confidence in its accuracy.

COMPARISON WITH THE HYPOTHESIS OF ETHERIDGE AND DE QUEIROZ (1988)

The only previous hypothesis of relationship within the *Tropidurus* group is that proposed by Etheridge and de Queiroz (1988). Their tree and a diagrammatic rendition of my most parsimonious tree are shown in figure 36. The two trees concur in the placement of *Uranoscodon* as the sister taxon of the remaining *Tropidurus* group as well as in the

relationship of *Plica* with *Strobilurus* and *Uracentron*. They disagree, however, in the placement of this combined group and the western *Tropidurus* group. Etheridge and de Queiroz (1988) thought the *Plica*–*Uracentron*–*Strobilurus* group to be the sister taxon of *Tropidurus* + *Tapinurus*. This is based on the view that a medially incomplete gular fold is a synapomorphy of *Tropidurus* + *Tapinurus*. However, a medially incomplete gular fold is a synapomorphy of the Tropiduridae and is a plesiomorphy at this level of universality (Frost and Etheridge, 1989). Once this problem is removed the only point of logical inconsistency is in the placement of the western *Tropidurus* group, which Etheridge and de Queiroz (1988) derived from the eastern *Tropidurus* group. None of the features documented in my study that place western *Tropidurus* outside a group composed of eastern *Tropidurus*, *Plica*, *Uracentron*, *Strobilurus*, and *Tapinurus* were available to these authors, so, with the exception of the gular fold character, their evidence can be viewed as less complete rather than in conflict with that presented here.

CONCLUSION

This analysis has forced the data to yield only some of its historical signal. Well-corroborated monophyletic groups are: (1) the *Tropidurus* group; (2) western *Tropidurus*, excluding *T. koepckeorum*; (3) the *T. peruvianus* group; (4) the *T. heterolepis* subgroup of the *T. peruvianus* group; (5) the taxon subtended by Stem 5 in figure 33 (the traditional *T. torquatus* group, *T. melanopleurus*, *T. spinulosus*, *Tapinurus*, *Plica*, *Strobilurus*, and

Uracentron); (5) *T. bogerti* + *Tapinurus*; (6) *T. melanopleurus* + *T. spinulosus* + *Plica* + *Strobilurus* + *Uracentron*; (7) *Plica* + *Strobilurus* + *Uracentron*; (9) *Uracentron*. Evidence for or against a monophyletic *T. torquatus* group (including *Tapinurus*) is equivocal without resorting to adaptation arguments. Other supported but still arguable relationships are *Plica* and *Strobilurus* + *Uracentron*.

TAXONOMY PROPOSED

It is clear that the current generic taxonomy of the *Tropidurus* group is not logically consistent (Hull, 1964; Wiley, 1981) with the hypothesized consensus phylogeny of the group presented (fig. 33), or with any of the most parsimonious trees discovered (or even with trees that are not particularly parsimonious, e.g., fig. 35). In designing a generic taxonomy of the *Tropidurus* group, I have been guided by two constraints: (1) The taxonomy adopted must be logically consistent with the recovered phylogenetic pattern (i.e., the taxonomy must not mislead about recovered phylogenetic history); (2) The taxonomy should be minimally perturbable, that is, questionable stems should, as much as possible, remain unnamed. I have not felt obliged to name all suprageneric or subgeneric taxa. There are two attractive alternatives for the taxonomy to be selected:

(1) Two genera: *Uranoscodon* and a single genus, *Tropidurus*, for the group now composed of *Tropidurus*, *Tapinurus*, *Uracentron*, *Plica*, and *Strobilurus*. The advantages of this arrangement are that only nine species have their generic names changed, although these nine species are highly apomorphic and dissimilar from the traditional *eidos* of *Tropidurus*.

(2) Four genera: *Uranoscodon*, *Microlophus* for species of former *Tropidurus* having disked hemipenes, a new genus for *Tropidurus koepckeorum*, and *Tropidurus* for species east of the Andes (including former *Tapinurus*, *Plica*, *Uracentron*, and *Strobilurus*), other than *Uranoscodon*. One might argue that because *T. koepckeorum* is the likely sister taxon of other species of western *Tropidurus*, it would be more prudent to place it in a collective, *Microlophus** (a metataxon sensu

Gauthier, 1986), defined solely by plesiomorphy with respect to its presumptive sister taxon, *Tropidurus*. The problem with this approach is that it does not invite additional evaluation of the proposition of monophyly of western *Microlophus* + *T. koepckeorum* and is merely an easy bookkeeping convention. The advantage of partitioning *Tropidurus* is that the stem supporting *Tropidurus* east of the Andes (Stem 5) is highly corroborated and without partitioning would be overlooked. At this time I think it prudent to take the second, four-genus alternative:

(1) *Uranoscodon*: a monotypic genus with at least one unique autapomorphy and the sister taxon of the remaining *Tropidurus* group.

(2) *Plesiomicrolophus*: a monotypic genus for *Tropidurus koepckeorum*.

(3) *Microlophus*: a genus for all species of former western *Tropidurus*, excluding *Plesiomicrolophus koepckeorum*, diagnosed by having disked hemipenes.

(4) *Tropidurus*: a genus for all former *Tropidurus* east of the Andes as well as the species formerly in *Tapinurus*, *Plica*, *Uracentron*, and *Strobilurus*.

Additionally, I propose that the *Tropidurus* group be recognized formally as a tribe, Tropidurini, the sister taxon of a new tribe Stenocercini (the former *Stenocercus* group) within the Tropidurinae of the Tropiduridae (Frost and Etheridge, 1989). See Taxonomic Accounts (below) for diagnoses of these taxa.

TAXONOMIC ACCOUNTS AND DIAGNOSES

The taxonomic accounts are designed to be nested within those provided by Frost and Etheridge (1989) for taxa of more general universality. The diagnostic features listed below mention "useful" characteristics, regardless of level of universality; apomorphies are in bold type. The Tropidurinae account is included only as a referent collective for Stenocercini and Tropidurini.

TROPIDURINAE BELL, 1843

Tropiduridae Bell, 1843: 1. Type genus: *Tropidurus* Wied-Neuwied, 1825. See comment under Tropidurinae.

Ptychosauri Fitzinger, 1843: 16. Type genus: *Ptychosaurus* Fitzinger, 1843 (= *Plica* Gray, 1831).

Steirolepides Fitzinger, 1843: 17. Type genus: *Steirolepis* Fitzinger, 1843 (= *Tropidurus* Wied-Neuwied, 1825).

?*Heterotropides* Fitzinger, 1843: 17. Type genus: *Heterotropis* Fitzinger, 1843 (a nomen dubium) (= *Ophryoessoides* Duméril and Duméril, 1851).

DIAGNOSIS: (1) **Hemipenes bilobate with distinctly divided sulci** (also in polychrids); (2) **nasal concha fused to roof of nasal chamber.**

CONTENT: Stenocercini, new tribe, and Tropidurini, new tribe.

DISTRIBUTION: Most of tropical and subtropical South America, excluding high elevations in the Andes and Patagonia.

COMMENT: Further documentation and characterization of the subfamilial taxonomy of the Tropiduridae can be found in Frost and Etheridge (1989).

STENOCERCINI, NEW TRIBE

?*Heterotropides* Fitzinger, 1843: 17. Type genus: *Heterotropis* Fitzinger, 1843 (a nomen dubium) (= *Stenocercus* Duméril and Bibron, 1837?).

DIAGNOSIS: (1) Superior fossa of quadrate not enlarged (not penetrated by a quadrate process of the squamosal); (2) alveolar shelf of mandible robust; (3) posterior process of the interclavicle anterior to contact with the sternum long; (4) **hemipenial sheath musculature extensive** (Arnold, 1984), lacking dorsal accessory muscle; (5) gular scales imbricate posteriorly; (6) interparietal not enlarged or absent.

CONTENT: *Stenocercus* Duméril and Bibron, 1837.⁵

⁵ With the exception of *Proctotretus* Duméril and Bibron, 1837 (which has hyperossified phalanges and metacarpals [*Proctotretus doellojuradoi* not examined as of this writing]), the other genera that compose the Stenocercini, "*Ophryoessoides*" Duméril and Duméril, 1851, and "*Stenocercus*" Duméril and Bibron, 1837, are not natural taxa. "*Stenocercus*" (sensu Fritts, 1974) shares the diagnosis of the Stenocercini and is paraphyletic with respect to "*Ophryoessoides*" and *Proctotretus* (see below). "*Ophryoessoides*" is characterized by features that are either of arguable polarity or homology, or variably distributed in some "*Stenocercus*" and *Proctotretus*. These include keeled ventral scales (also in *Proctotretus azureus* and so weak in "*O.*" *iridescens* as to approach the condition in "*S.*" *trachycephalus*) and more than two elongate postxiphisternal inscriptional ribs (each of which is

DISTRIBUTION: Western South America from northern Colombia and coastal Ecuador to Bolivia, coastal Argentina, and the Upper Amazon Basin of Brazil; coastal southern Brazil and Uruguay (fig. 37).

COMMENT: Should *Heterotropis* Fitzinger, 1843, be demonstrated conclusively to be a junior synonym of *Stenocercus* (and a senior

composed of a bony section and its confluent elongated costal cartilage), of which at least the anterior pair is fused at the midline (Fritts, 1974; but see Etheridge, 1966). However, unlike "*O.*" *aculeatus* and "*O.*" *caducus*, in which the anteriormost inscriptional cartilages are well calcified and join seamlessly at the midline, at least "*O.*" *iridescens* and "*O.*" *scapularis* show anteriormost inscriptional costal cartilages that variably closely approximate each other or are connected medially only by poorly chondrified connective tissue. In several "*Stenocercus*" (e.g., "*S.*" *apurimacus*, "*S.*" *festae*, "*S.*" *ornatus*, "*S.*" *rhodomelas*, and "*S.*" *trachycephalus*), a similar condition obtains of multiple, closely approximating postxiphisternal inscriptional ribs. For this reason Etheridge (1966) had considered species showing this condition to be members of a larger "*Ophryoessoides*" than that subsequently conceived of by Fritts (1974). However, only the more plesiomorphic inscriptional rib pattern as seen in most other "*Stenocercus*" and in *Proctotretus* is found in the type species of "*Ophryoessoides*," "*O.*" *tricristatus* (not examined by Etheridge, 1966, but who mentioned the possibility that this species might not be closely related to other "*Ophryoessoides*"). The reduced antehumeral and oblique neck folds of "*Ophryoessoides*" are also found in *Proctotretus* (more so in *P. azureus* than *P. pectinatus*, which retains small antehumeral folds) and several species of "*Stenocercus*" (including those listed above). *Proctotretus* species also share certain apomorphic scale characteristics (e.g., dorsolateral scale ridges) seen in some "*Ophryoessoides*." A synapomorphy of "*Stenocercus*" has yet to be suggested. Without digressing further into a revision of the Stenocercini, it seems clear that "*Ophryoessoides*" and *Proctotretus* are derived from "*Stenocercus*." Because several workers describing new species in this tribe have expressed some concern over generic definition in the group, and some have seemed inclined to publish revisions based on comments in unpublished sections of my dissertation, it seems best to me at this time to synonymize *Ophryoessoides* and *Proctotretus* with *Stenocercus* (stating *Stenocercus* to have priority over *Proctotretus* under Article 24 [Principle of the First Revisor] of the International Code of Zoological Nomenclature, 1985). Although many species pairs, or even monophyletic groups of more species, could now be recognized generically, without a cladogram of the entire tribe these actions would result only in the concomitant recognition of unsupported and/or paraphyletic "taxa."

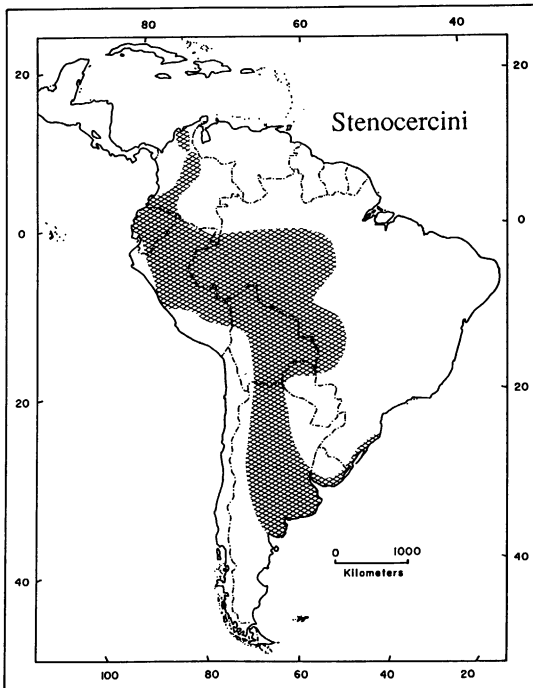


Fig. 37. Distribution of *Stenocercini*.

synonym of *Ophryoessoides* Duméril and Duméril, 1851), the family-group name of *Stenocercini* would become *Heterotropidini*.

TROPIDURINI BELL, 1843

Tropiduridae Bell, 1843: 1. Type genus: *Tropidurus* Wied-Neuwied, 1825.

Ptychosauri Fitzinger, 1843: 16. Type genus: *Ptychosaurus* Fitzinger, 1843 (= *Plica* Gray, 1831).

Steirolepides Fitzinger, 1843: 17. Type genus: *Steirolepis* Fitzinger, 1843 (= *Tropidurus* Wied-Neuwied, 1825).

DIAGNOSIS: (1) Superior fossa of quadrate enlarged (not penetrated by a quadrate process of the squamosal); (2) alveolar shelf of mandible somewhat eroded; (3) posterior process of the interclavicle anterior to contact with the sternum long; (4) elongate hemipenes (also in polychrids); (5) hemipenes with dorsal accessory muscle (also in polychrids); (5) gular scales imbricate posterolaterally to laterally (except in *Tropidurus bogerti*); (6) interparietal enlarged (also in phrynosomatids).

CONTENT: *Microlophus* Duméril and Bibron, 1837; *Plesiomicrolophus*, new genus;

Tropidurus Wied-Neuwied, 1825; *Uranoscodon* Kaup, 1826.

DISTRIBUTION: Tropical and subtropical South America, excluding northern and western Colombia and northeastern Venezuela, south to ca. 32°S (fig. 1).

GENUS *URANOSCODON* KAUP, 1825

Uranoscodon Kaup, 1825: 590. Type species: *Lacerta superciliosa* Linnaeus, 1758, by subsequent designation of Etheridge (1970a: 240).

Ophryessa Boie, 1825: 1090. Type species: *Lacerta superciliosa* Linnaeus, 1758, by subsequent designation of Fitzinger (1843: 16).

Uraniscodon Boie, 1825: 1090. Unjustified emendation of *Uranoscodon* Kaup, 1825.

Lophyrus Gray, 1827: 208 (not of Poli, 1791 [Mollusca], or Oppel, 1811). Substitute name for *Uranoscodon* Kaup, 1825.

Ophryoessa Wagler, 1830: 149. Unjustified emendation of *Ophryessa* Boie, 1825.

Ophryessa Gray, 1831: 39. Unjustified emendation of *Ophryessa* Boie, 1825.

DIAGNOSIS: (1) Skull highly elevated at level of orbits; (2) nutritive foramina of maxilla not strikingly enlarged; (3) lingual process of dentary absent, not extending over lingual dentary process of coronoid; (4) angular not reduced; (5) medial centrale present; (6) "flash" marks on underside of thighs absent; (7) circumorbitals not distinct from other small supraorbital scales; (8) lateral fringe developed on both sides of fourth toes; (9) hemipenes attenuate, without apical disks.

CONTENT: *Uranoscodon superciliosus* (Linnaeus, 1758) (fig. 38).

DISTRIBUTION: Amazonian and Guianan regions of South America (fig. 39).

ETYMOLOGY: Greek: *ouranos* (vault [= roof of the mouth]) + *osco* (mouth) + *-odon* (tooth): in reference to the presence of pterygoid teeth. The gender is masculine.

PLESIOMICROLOPHUS, NEW GENUS

TYPE SPECIES: *Tropidurus koepckeorum* Mertens, 1956.

DIAGNOSIS: (1) Skull not highly elevated at level of orbits; (2) nutritive foramina of maxilla not strikingly enlarged; (3) lingual process of dentary present, extending over lingual dentary process of coronoid; (4) angular not strongly reduced; (5) medial centrale present; (6) "flash" marks on underside of thighs ab-

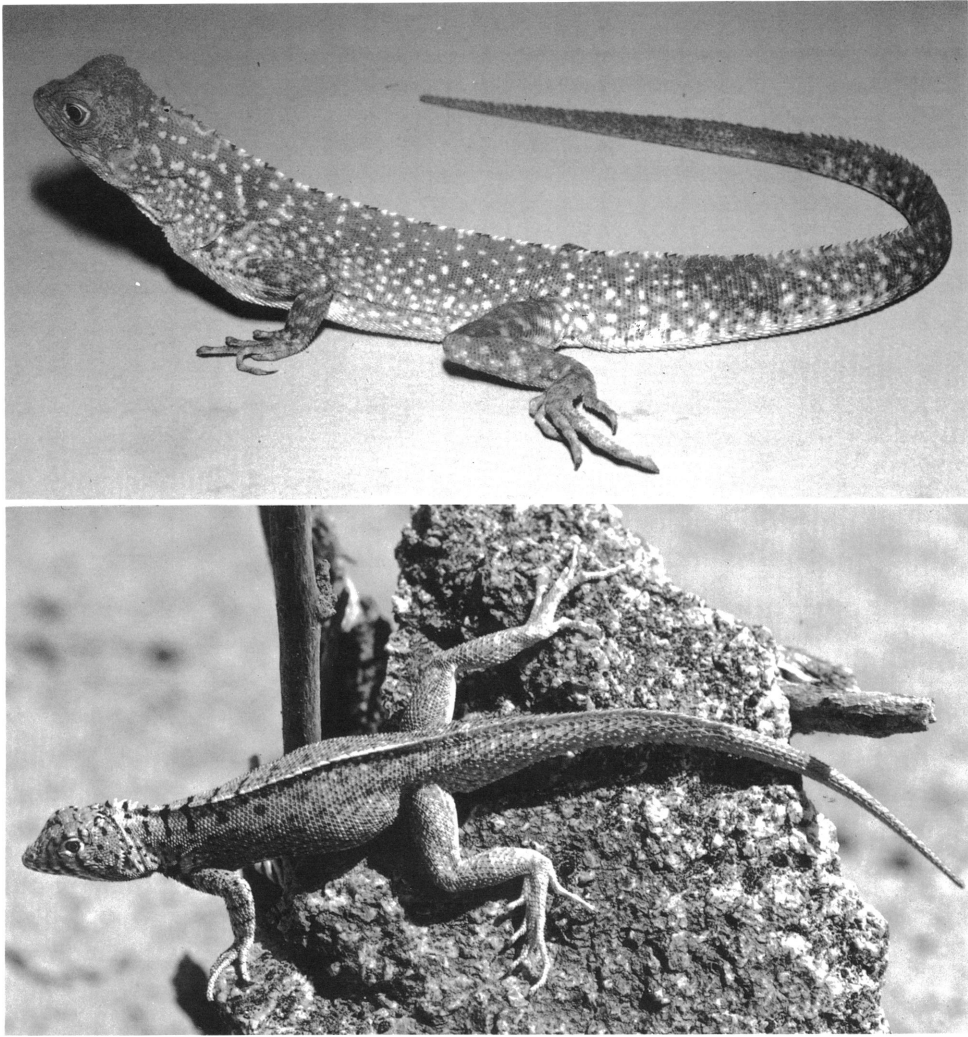


Fig. 38. Some members of the Tropidurini in life. **Top:** *Uranoscodon superciliosus*, KU 130218 (KU photo 3715). Photograph by M. L. Crump. **Bottom:** *Plesiomicrolophus koepckeorum*, J. R. Dixon photograph 105.

sent; (7) circumorbitals distinct from other small supraorbital scales, forming a single series; (8) lateral fringe not developed on both sides of fourth toes; (9) hemipenes attenuate, without apical disks.

CONTENT: *P. koepckeorum* (Mertens, 1956) (fig. 38).

DISTRIBUTION: As for the single species: foothills along the eastern side of the Sechura Desert, south to the Río Shigiay, in Peru (fig. 40).

ETYMOLOGY: Greek: *plesios* (near) + *Mi-*

crolophus (see below), referencing the similarity and possible phylogenetic propinquity of this lineage to the *Microlophus* clade. The gender is masculine.

COMMENT: Although first described as a subspecies of *Microlophus occipitalis*, as *Tropidurus occipitalis koepckeorum*, this species is almost completely plesiomorphic in all features examined and could be considered diagnostically “ancestral” to the clade composed of *Tropidurus* and *Microlophus*. My conjecture is that future work will show

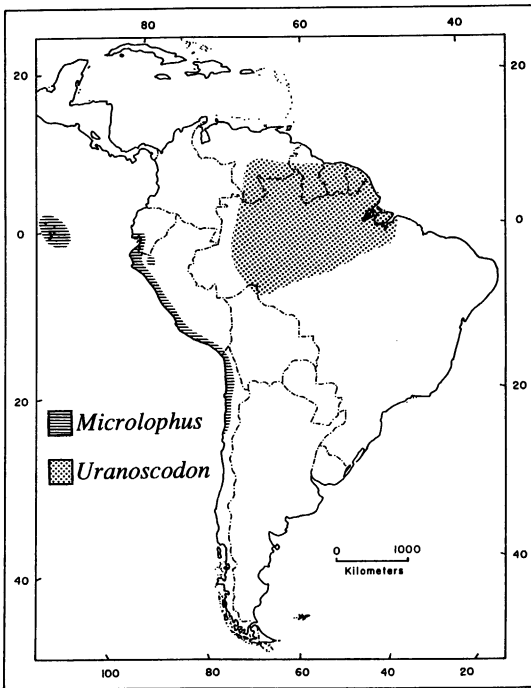


Fig. 39. Distribution of *Microlophus* and *Uranoscodon*.

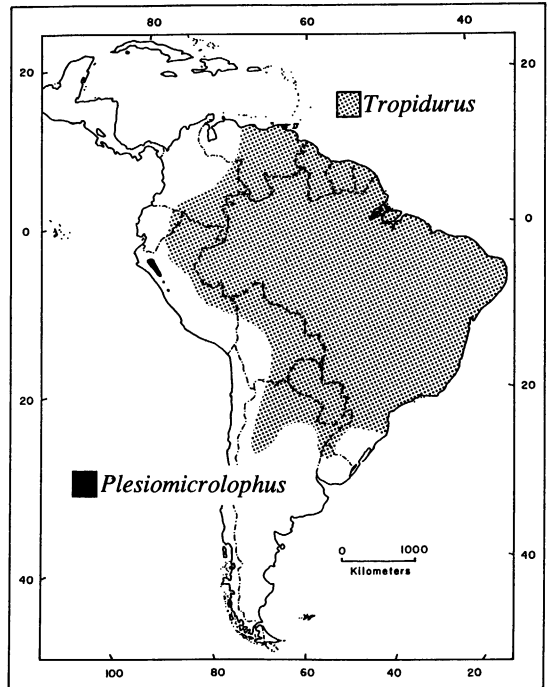


Fig. 40. Distribution of *Plesiomicrolophus* and *Tropidurus*.

it to be the sister taxon of *Microlophus*, in which case it could justifiably be considered a junior synonym of *Microlophus*. Although *Plesiomicrolophus* has no unambiguous apomorphies, what evidence there is (Dixon and Wright, 1975) supports the notion that it is a single lineage. That the "genus" lacks apomorphies is strictly an artifact of the nomenclature convention. With other aspects of color pattern, like narrow transverse dorsal bars, gular spotting in this species is likely apomorphic, although very similar (homologous?) spotting occurs in members of the *Microlophus grayii* complex (see below). Characterization of these patterns is extremely difficult and has not been included in this analysis.

I agree with the principle discussed by Ax (1985), that stem species do not survive lineage splitting, here exemplified by the fact that the population that was ancestral to *Plesiomicrolophus*, *Microlophus*, and *Tropidurus* must be taken to currently be composed of these three genera, not any one of the descendants, although it is possible that one of these may share a diagnosis with the ancestral

"stem" species. That the diagnoses of the organisms constituting *Plesiomicrolophus* are equivalent, or nearly so, to those in the ancestral species is irrelevant, inasmuch as statements about ancestry apply to supraorganismal entities and not to organismal diagnoses.

GENUS *MICROLOPHUS*
DUMÉRIL AND BIBRON, 1837

Microlophus Duméril and Bibron, 1837: 334. Type species: *Microlophus lessonii* Duméril and Bibron, 1837 (= *Stellio peruvianus* Lesson, 1831), by monotypy.

Steirolepis Fitzinger, 1843: 72. Type species: *Tropidurus microlophus* Wiegmann, 1835 (= *Stellio peruvianus* Lesson, 1831), by original designation.

Craniopeltis Peters, 1871: 645. Type species: *Tropidurus bivittatus* Peters, 1871, by monotypy.

Laemopristsis Peters, 1871: 645. Type species: *Tropidurus occipitalis* Peters, 1871, by monotypy.

Aneuoporus Bocourt in Duméril, Bocourt, and Mocquard, 1874: 215. Type species: *Aneuoporus occipitalis* Bocourt, 1874, by monotypy.

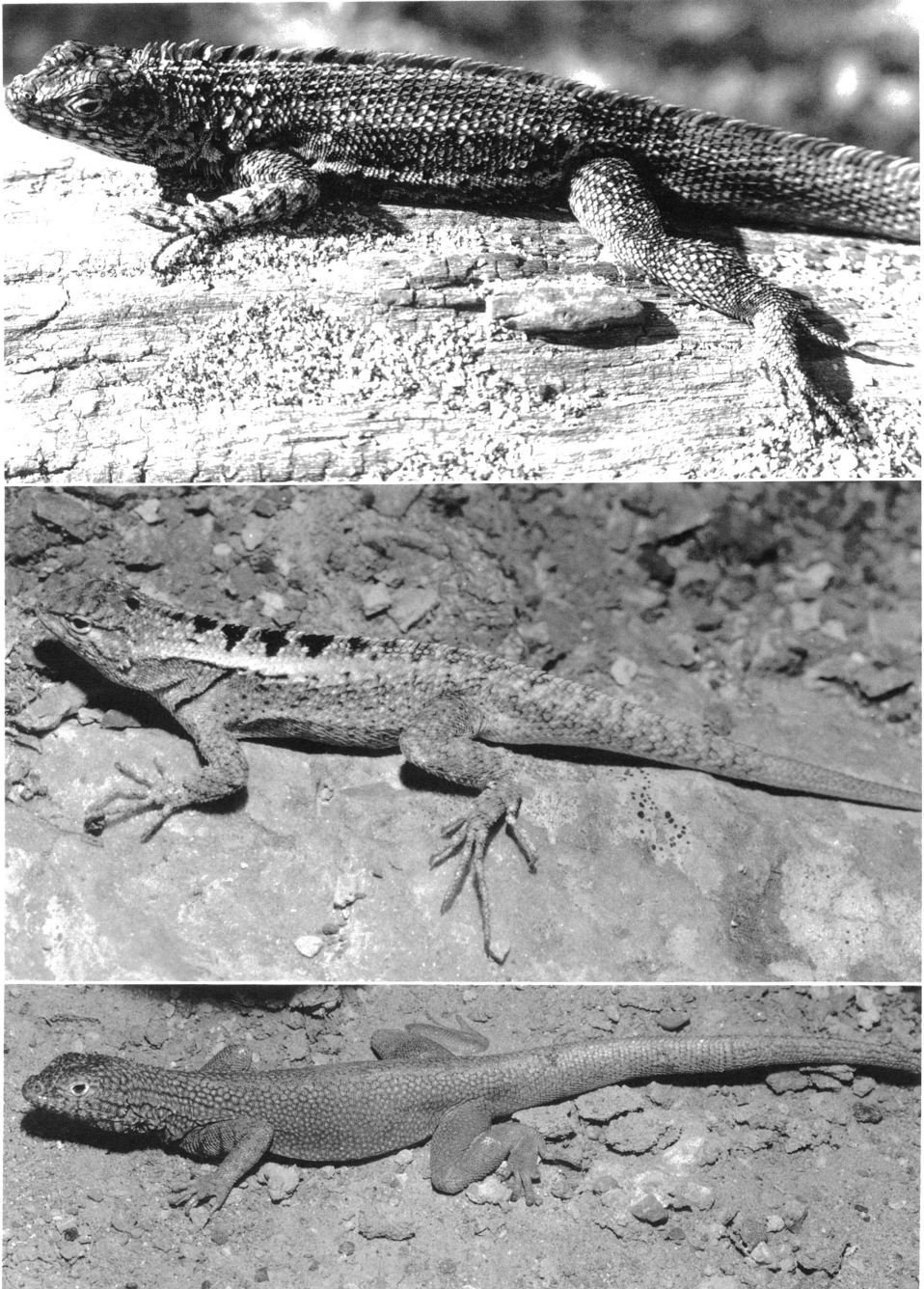


Fig. 41. Some members of the Tropidurini in life. **Top:** *Microlophus albemarlensis*, R. G. Zweifel photograph. **Middle:** *M. occipitalis*, KU 212667 (KU photo 8456), W. E. Duellman photograph. **Bottom:** *M. theresioides*, KU 162002 (KU photo 4940), W. E. Duellman photograph.

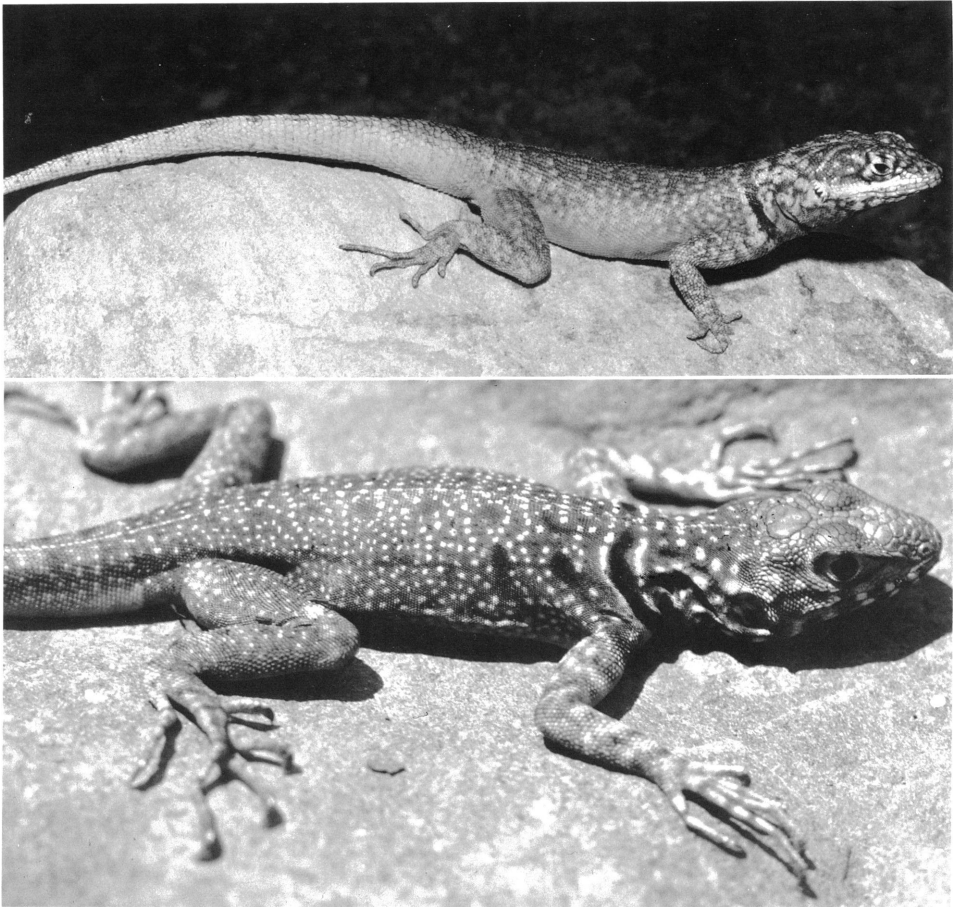


Fig. 42. Some members of the Tropidurini in life. **Top:** *T. etheridgei*, KU 160145 (KU photograph 4739), W. E. Duellman photograph. **Bottom:** *Tropidurus melanopleurus*, KU 182998 (KU photograph 6552 by D. C. Cannatella).

DIAGNOSIS: (1) Skull not highly elevated at level of orbits; (2) nutritive foramina of maxilla not strikingly enlarged; (3) lingual process of dentary present, extending over lingual dentary process of coronoid; (4) angular not strongly reduced; (5) medial centrale present; (6) "flash" marks on underside of thighs absent; (7) circumorbitals distinct from other small supraorbital scales, forming a single series; (8) lateral fringe not developed on both sides of fourth toes; (9) **hemipenes with apical disks.**

CONTENT: *Microlophus albemarlensis* (Baur, 1890) (fig. 41) (see comment below); *M. atacamensis* (Donoso-Barros, 1966); *M. bivittatus* (Peters, 1871); *M. delanonis* (Baur, 1890) (see comment below); *M. duncanensis*

(Baur, 1890) (see comment below); *M. grayii* (Bell, 1843) (see comment below); *M. habelii* (Steindachner, 1876); *M. heterolepis* (Wiegmann, 1834); *M. occipitalis* (Peters, 1871) (fig. 41); *M. pacificus* (Steindachner, 1876) (see comment below); *M. peruvianus* Lesson, 1831; *M. quadrivittatus* (Tschudi, 1845); *M. stolzmanni* (Steindachner, 1891); *M. tarapacensis* (Donoso-Barros, 1966) (not seen but provisionally allocated here); *M. theresiae* (Steindachner, 1901); *M. theresioides* (Donoso-Barros, 1966) (fig. 41); *M. thoracicus* (Tschudi, 1845); *M. tigris* (Tschudi, 1845); *M. yanezi* (Ortiz-Zapata, 1980).

DISTRIBUTION: Galapagos Islands; South America west of the Andes from southern Ecuador to northern Chile; east of the con-

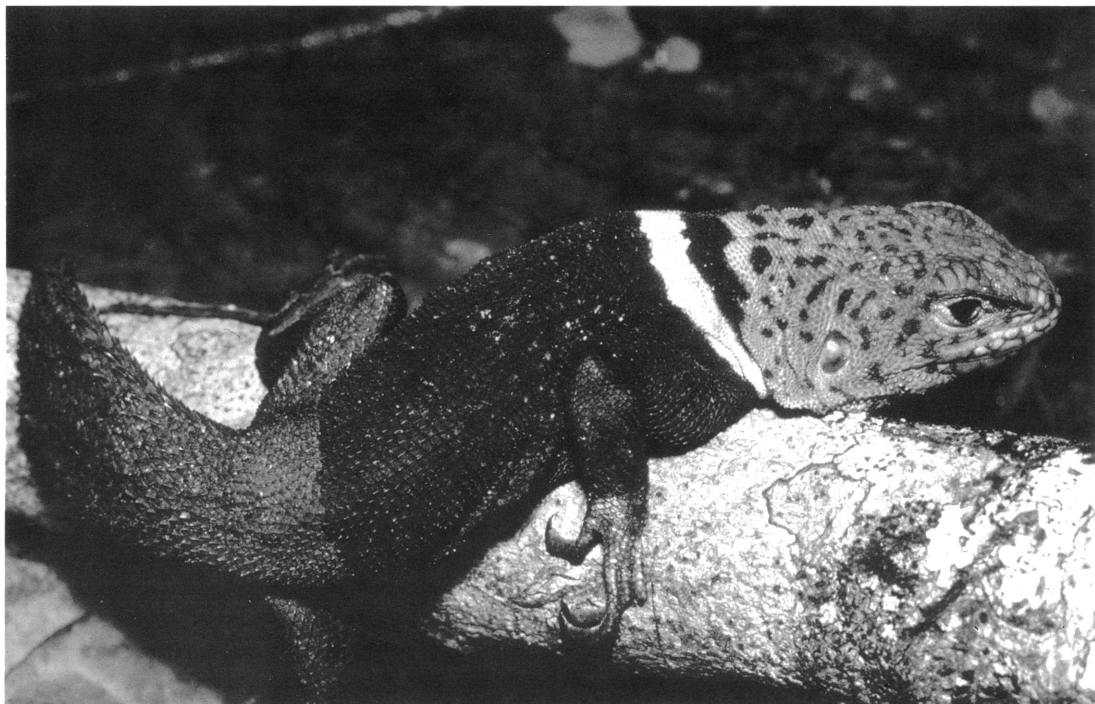


Fig. 43. *Tropidurus flaviceps*, R. W. McDiarmid photograph 18872.

tinental divide only in the Huancabamba Depression Region of northern Peru (fig. 39).

ETYMOLOGY: Greek: *mikros* (small) + *lophos* (crest); in reference to the reduced dorsal crest in the type species, *M. peruvianus*. The gender is masculine.

COMMENT: As in most archipelago species complexes, the current taxonomy of Galapagos *Microlophus* has inherent difficulties. Each island has its own population(s) that differs in some respect from all other island populations (Wright, 1983). That some of the recognized species (e.g., *Microlophus albe-marlensis*) are found on several islands and are lumped together under one binomial because of overall similarity (Van Denburgh and Slevin, 1913) may reflect grouping by plesiomorphy rather than on an understanding of the historical relationships of these island forms. Work by Wright (1983) on allozyme distances, although not dealing explicitly with species distinction, has made it arguable that only three species, composing two monophyletic groups, could be recognized: *Microlophus habelii* and *M. bivittatus* possibly representing the fruits of one invasion of the

islands from the mainland, and *M. grayii* representing the other. However, if the assumption of clocklike molecular evolution is not made for purposes of data analysis, the cladistic structure of the allozymic data is murky. An alternative would be to recognize all diagnosable allopatric populations on the islands as species (*sensu* Frost and Hillis, 1990). The inter- and intrainland variation in squamation and coloration documented by Van Denburgh and Slevin (1913) makes this alternative attractive. However, although I think that a taxonomic treatment of this complex is needed, because this group was not the focus of this study I resist taking the obvious step of recommending a three-species or multiple-species model of Galapagos lava lizard taxonomy without additional study.

GENUS *TROPIDURUS*
WIED-NEUWIED, 1825

Tropidurus Wied-Neuwied, 1825: 131. Type species: *Stellio torquatus* Wied-Neuwied, 1820, by subsequent designation of Fitzinger (1843: 17).
Uracentron Kaup, 1826: 88. Type species: *Uracentron brevicaudatum* Kaup, 1826 (= *Lacerta*

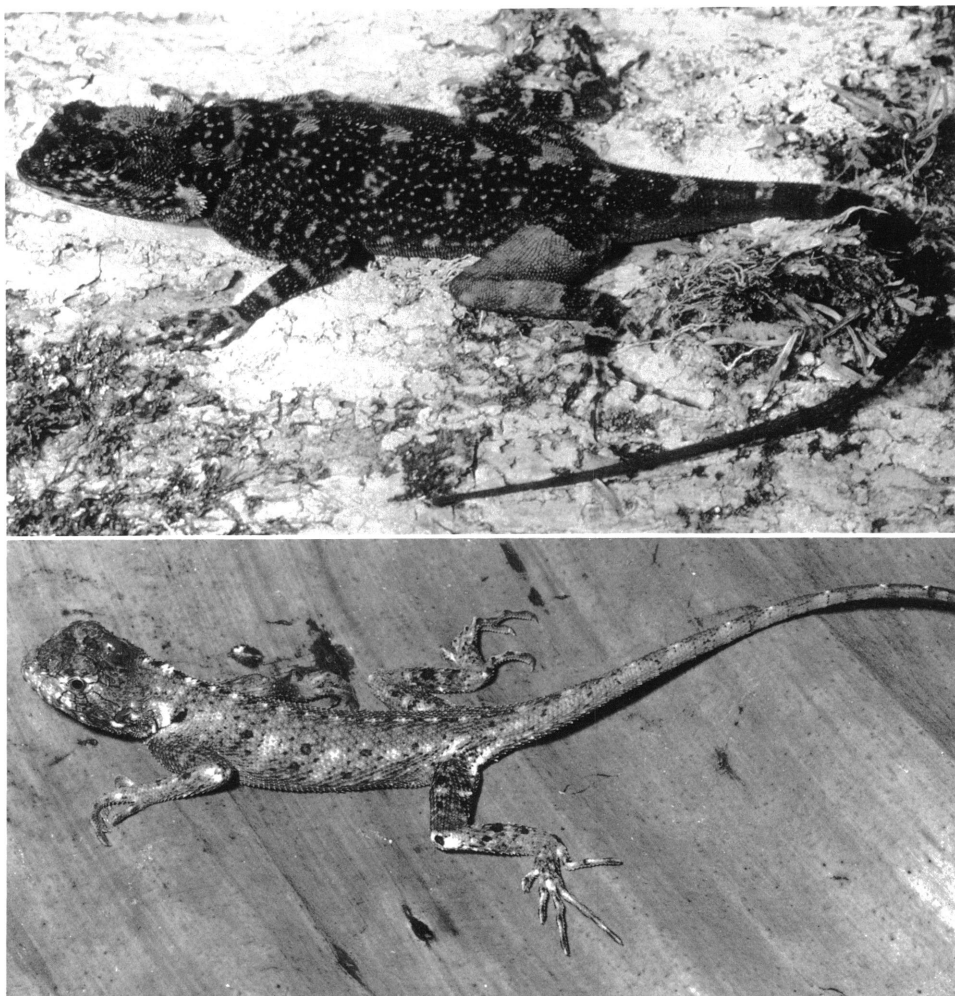


Fig. 44. **Top:** *Tropidurus plica*, L. J. Vitt photograph. **Bottom:** *T. umbra*, R. W. McDiarmid photograph 13411.

azurea Linnaeus, 1758), by subsequent designation of Fitzinger (1843: 17).
Doryphorus Cuvier, 1829: 34. Type species: *Stellio brevicaudatus* Latreille, 1802 (= *Lacerta azurea* Linnaeus, 1758), by monotypy.
Hypsibatus Wagler, 1830: 150. Type species: *Lacerta umbra* Linnaeus, 1758, by subsequent designation of Fitzinger, 1843: 16.
Platynotus Wagler, 1830: 146. Type species: *Agama semitaeniata* Spix, 1825, by monotypy. Pre-occupied by *Platynotus* Fabricius, 1801 (Coleoptera).
Plica Gray, 1831: 40. Type species: *Lacerta plica* Linnaeus, 1758, by subsequent designation of Etheridge (1970a: 241).
Strobilurus Wiegmann, 1834b: 18. Type species:

Strobilurus torquatus Wiegmann, 1834b, by monotypy.
Hypselophus Wiegmann, 1835: 289. Substitute name for *Hypsibatus* Wagler, 1830.
Hypselopus Gravenhorst, 1837: 717. Unjustified emendation of *Hypselophus* Wiegmann, 1835.
Uperanodon Duméril and Bibron, 1837: 247. Type species: *Lophyrus ochrocollaris* Spix, 1825 (= *Lacerta umbra* Linnaeus, 1758), by monotypy.
Ptychosaurus Fitzinger, 1843: 59. Type species: *Hypsibatus punctatus* Duméril and Bibron, 1837 (= *Lacerta plica* Linnaeus, 1758), by original designation.
Ptychopleura Fitzinger, 1843: 59. Type species: *Hypsibatus plica* Wagler, 1830 (= *Lacerta plica* Linnaeus, 1758), by original designation.

Taraguira Gray, 1845: 219. Type species: none designated.

Hyperanodon Agassiz, 1847: 190. Substitute name for *Uperanodon* Duméril and Bibron, 1837.

Tapinurus Amaral, 1933: 65. Type species: *Tapinurus scutipunctatus* Amaral, 1932 (= *Agama semitaeniata* Spix, 1825), by original designation.

DIAGNOSIS: (1) Skull not highly elevated at level of orbits (except in *T. umbra*); (2) nutritive foramina of maxilla strikingly enlarged; (3) lingual process of dentary present, extending over lingual dentary process of coronoid; (4) angular strongly reduced; (5) medial centrale absent; (6) "flash" marks on underside of thighs present, yellow to black (obscured or lost in *T. azureus* and *T. flaviceps*); (7) circumorbitals distinct from other small supraorbital scales, in one or two rows; (8) lateral fringe not developed on both sides of fourth toes; (9) hemipenes attenuate, without apical disks.

CONTENT: *T. amathites* Rodrigues, 1984 (not seen but provisionally allocated here); *T. azureus* (Linnaeus, 1758); *T. bogerti* Roze, 1958; *T. cocorobensis* Rodrigues, 1987; *T. divaricatus* Rodrigues, 1986 (not seen but provisionally allocated here); *T. erythrocephalus* Rodrigues, 1987; *T. etheridgei* Cei, 1982 (fig. 42); *T. flaviceps* (Guichenot, 1855) (fig. 43); *T. helenae* (Manzini and Abe, 1990) (not seen but clearly allocated here); *T. hispidus* (Spix, 1825); *T. hygomi* Reinhardt and Lütken, 1861; *T. insulanus* Rodrigues, 1987; *T. itambere* Rodrigues, 1987; *T. lumarius* (Donnelly and Myers, 1991); *T. melanopleurus* Boulenger, 1902 (fig. 42); *T. montanus* Rodrigues, 1987; *T. mucujensis* Rodrigues, 1987; *T. nanuzae* Rodrigues, 1981; *T. oreadicus* Rodrigues, 1987; *T. pinima* (Rodrigues, 1984); *T. plica* (Linnaeus, 1748) (fig. 44); *T. psammonastes* Rodrigues et al., 1988 (not seen but provisionally allocated here); *T. semitaeniatus* (Spix, 1825); *T. spinulosus* (Cope, 1862); *T. strobilurus*, new name (for *Strobilurus torquatus* Wiegmann, 1834; the combination *Tropidurus torquatus* is preoccupied; see next entry); *T. torquatus* Wied-Neuwied, 1825; *T. umbra* (Linnaeus, 1758) (fig. 44).

DISTRIBUTION: Tropical to temperate South America east of the Andes (fig. 40).

ETYMOLOGY: Greek: *tropido-* (keeled) +

ourus (tail), referring to the keeled squamation on the tails of most species.

REFERENCES

- Adams, E. N.
1972. Consensus techniques and the comparison of taxonomic trees. *Syst. Zool.* 21: 390–397.
- Agassiz, A.
1847. *Nomenclator zoologici universalis*. . . . Soloduri, Jent and Gassman. viii, 393 pp.
- Amaral, A.
1933 "1932." Estudos sobre lacertílios neotrópicos. I. Novos generos e especies de lagartos do Brasil. *Mem. Inst. Butantan* 7(1932): 51–74.
- Andersson, L. G.
1918. New lizards from South America. Collected by Nils Holmgren and A. Roman. *Ark. Zool.* 11(16): 1–9.
- Arnold, E. N.
1984. Variation in the cloacal and hemipenial muscles of lizards and its bearing on their relationships. *Symp. Zool. Soc. London* 53: 47–85.
- Ax, P.
1985. Stem species and the stem lineage concept. *Cladistics* 1: 279–287.
- Baur, G.
1890. Das Variieren der Eidechsen—Gattung *Tropidurus* auf den Galapagos Inseln und Bemerkungen über den Ursprung der Inselgruppe. *Biol. Centralblatt.* 10: 475–483.
1892. Das Variieren der Eidechsen—Gattung *Tropidurus* auf den Galapagos-Inseln. *In* Festschrift zum Siebenzigsten Geburtstag Rudolf Leukarts, pp. 259–277. Leipzig.
- Bell, T.
1843. *Zoology of the voyage of the H.M.S. Beagle, under the command of Captain Fitzroy, R. N., during the years 1832 to 1836.* Edited and superintended by Charles Darwin . . . naturalist to the expedition. Part 5. Reptiles. London: Smith, Elder & Co, vi + 51 pp., atlas.
- Berthold, A. A.
1859. Einige neue Reptilien des Akad. zoolog. Museums in Göttingen. *Nachr. Georg-Augustus Univ. K. Ges. Wiss. Göttingen* 1859(17): 179–181.
- Bocourt, M. F.
1874. *In* A. Duméril, M. F. Bocourt, and F. Mocquard. 1870–1909. *Mission scientifique au Mexique et dans l'Amérique*

Centrale. . . . Recherches zoologiques. Troisième partie. Première section. Etudes sur les Reptiles. Paris: Imprimerie Nationale, xiv + 1012 pp. (17 livraisons).

Boettger, O.

1885. Liste von Reptilien und Batrachien aus Paraguay. Z. Naturwiss. Halle 58: 213–248.

Böhme, W.

1988. Zur Genitalmorphologie der Sauria: Funktionelle und stammesgeschichtliche Aspekte. Bonn. Zool. Monogr. 27: 1–176.

Boie, H.

1825. Zu Kaup's Aufsatz über Lurche. Isis von Oken 17: 1089–1090.

Boulenger, G. A.

1885. Catalogue of the lizards in the British Museum (Natural History), ed. 2. vol. 2. London: Taylor and Francis, xiii + 497 pp.

1891. On the Galapagos lizards of the genus *Tropidurus*. Ann. Mag. Nat. Hist., ser. 6, 7: 501–503.

1894. Second report on additions to the lizard collection in the Natural History Museum. Proc. Zool. Soc. London 1894: 722–736.

1900. Description of new batrachians and reptiles collected by Mr. P. O. Simons in Peru. Ann. Mag. Nat. Hist., ser. 7, 6: 181–186.

1902. Descriptions of new batrachians and reptiles from the Andes of Peru and Bolivia. Ann. Mag. Nat. Hist., ser. 7, 10: 394–402.

1912. Descriptions of new reptiles from the Andes of South America preserved in the British Museum. Ann. Mag. Nat. Hist., ser. 8, 10: 420–424.

Brooks, D. R., and E. O. Wiley

1985. Theories and methods in different approaches to phylogenetic systematics. *Caldistics* 1: 1–12.

Burt, C. E., and M. D. Burt

1930. The South American lizards in the collection of the United States National Museum. Proc. U.S. Natl. Mus. 78(6): 1–52.

1931. South American lizards in the collection of the American Museum of Natural History. Bull. Am. Mus. Nat. Hist. 61: 227–395.

1933. A preliminary check list of the lizards of South America. Trans. Acad. Sci. St. Louis 28: 1–104.

Cei, J. M.

1982. A new species of *Tropidurus* (Sauria,

Iguanidae) from the arid Chacoan and western regions of Argentina. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 97: 1–10.

Churchill, S. P., E. O. Wiley, and L. A. Hauser

1985. Biological realities and the proper methodology: a reply to Duncan. *Taxon* 34: 124–130.

Cope, E. D.

1862. Catalogues of the reptiles obtained during the explorations of the Parana, Paraguay, Vermejo and Uruguay Rivers by Capt. Thos. J. Page, U.S.N., and of those procured by Lieut. N. Michler, U.S. Top. Eng., commander of the expedition conducting the survey of the Atrato River. Proc. Acad. Nat. Sci. Philadelphia 14: 346–359.

1870. Eighth contribution to the herpetology of tropical America. Proc. Am. Philos. Soc. 11: 553–559.

1876. Report on the reptiles brought by Professor James Orton from the middle and upper Amazon, and western Peru. J. Acad. Nat. Sci. Philadelphia, ser. 2, 8: 159–188.

1889. Scientific results of explorations by the U.S. Fish Commission Steamer *Albatross*. No. III.—report on the batrachians and reptiles collected in 1887–'88. Proc. U.S. Natl. Mus. 12: 141–147.

1897 “1896.” On the hemipenes of the Sauria. Proc. Acad. Nat. Sci. Philadelphia 48: 461–467.

1900. The crocodylians, lizards, and snakes of North America. Annu. Rep. U.S. Natl. Mus. 1898: 151–1294.

Cuvier, G.

1829. Le règne animal distribué d'après son organisation, . . . Nouvelle édition, . . . Tome II. Paris: Déterville & Crochard, xv + 406 pp.

Daudin, F. M.

1802. Histoire naturelle, générale et particulière des Reptiles; ouvrage faisant suite à l'Histoire naturelle générale et particulière composée par Leclerc de Buffon; et rédigée par C. S. Sonnini, membre de plusieurs sociétés savantes. vol. 3, 4. F. Dufart.

Dixon, J. R., and J. W. Wright

1975. A review of the lizards of the iguanid genus *Tropidurus* in Peru. Contrib. Sci. Nat. Hist. Mus. Los Angeles Cty. 271: 39 pp.

Donnelly, M. A., and C. W. Myers

1991. Herpetological results of the 1990 expedition to the summit of Cerro Guai-

- quinima, with descriptions of new tepui reptiles. *Am. Mus. Novit.* 3107: 54 pp.
- Donoso-Barros, R.
1966. *Reptiles de Chile*. Santiago: Univ. Chile, 458 + cxlvi.
1968. The lizards of Venezuela (check list and key). *Caribb. J. Sci.* 8: 105–122.
- Duméril, A. H. A.
1856. Descriptions des reptiles nouveaux ou imparfaitement connus de la collection du Musée d'Histoire Naturelle et remarques sur la classification et les caractères de reptiles. Deuxième Mémoire: troisième, quatrième et cinquième familles de l'ordre de sauriens (Geckotiens, Varaniens et Iguaniens). *Arch. Mus. Hist. Nat., Paris* 8: 437–588.
- Duméril, A. M. C.
1806. *Zoologie analytique, ou méthode naturelle de classification des animaux rendue plus facile à l'aide de tableau synoptiques*. Paris: Alais, 344 pp.
- Duméril, A. M. C., and G. Bibron
1837. *Erpétologie générale ou histoire naturelle complète des reptiles*. Vol. 4. Paris: Roret, ii + 571 pp.
- Duméril, A. M. C., and A. H. A. Duméril
1851. *Catalogue méthodique de la collection des reptiles du Muséum d'Histoire Naturelle*. Paris: Gide & Boudry, iv + 224 pp.
- Dunn, E. R.
1944. Los generos de anfibios y reptiles de Colombia, II. Reptiles, orden de los saurios. *Caldasia* 3: 155–223.
- Etheridge, R.
1962. Skeletal variation in the iguanid lizard *Sator grandaevus*. *Copeia* 1962: 613–619.
1964. The skeletal morphology and systematic relationships of sceloporine lizards. *Copeia* 1964: 610–631.
1966. The systematic relationships of West Indian and South American lizards referred to the iguanid genus *Leiocephalus*. *Copeia* 1966: 79–91.
1967. Lizard caudal vertebrae. *Copeia* 1967: 699–721.
1968. A review of the iguanid genera *Uracentron* and *Strobilurus*. *Bull. Br. Mus. (Nat. Hist.)*, Zool. 17: 45–64.
1969a. *Tropidogaster blainvillii* Duméril & Bibron, 1837 (Reptilia, Sauria): proposed suppression under the Plenary Powers. *Bull. Zool. Nomencl.* 25: 224–226.
1969b. A review of the iguanid lizard genus *Enyalius*. *Bull. Br. Mus. (Nat. Hist.)*, Zool. 18: 231–260.
1970a. A review of the South American iguanid genus *Plica*. *Bull. Br. Mus. Nat. Hist. (Zool.)* 19: 237–256.
1970b. *Tropidurus*. In J. A. Peters and R. Donoso-Barros, *Catalogue of the Neotropical Squamata*. Part II. Lizards and amphisbaenians, pp. 264–270. *Bull. U.S. Natl. Mus.* 297 (pt. 2): viii + 293.
- Etheridge, R., and K. de Queiroz
1988. A phylogeny of Iguanidae. In R. Estes and G. K. Pregill (eds.), *Phylogenetic relationships of lizard families: Essays commemorating Charles L. Camp*, pp. 283–268. Stanford, CA: Stanford Univ. Press.
- Fabricius, J. C.
1801. *Systema Eleutheratorum secundum Ordines, Genera, Species: Adjectis synonymis, locis, observationibus, descriptionibus*. 2 vols. Kiliae.
- Farris, J. S.
1982. Outgroups and parsimony. *Syst. Zool.* 31: 328–334.
1983. The logical basis of phylogenetic systematics. In N. I. Platnick and V. A. Funk (eds.), *Advances in cladistics*, Vol. 2. New York: Columbia Univ. Press.
1988. HENNIG86, Version 1.5. Reference. Privately printed.
- Farris, J. S., and A. G. Kluge
1985. Parsimony, synapomorphy, and explanatory power: a reply to Duncan. *Taxon* 34: 130–135.
1986. Synapomorphy, parsimony, and evidence. *Taxon* 35: 298–306.
- Fitzinger, L. I.
1826. *Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften nebst einer Verwandts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des k. k. Zoologischen Museum zu Wien*. Wien: J. G. Hübner, vii + 66 pp.
1843. *Systema Reptilium. Fasciculus primus*. Wien: Baumüller and Seidel, 106 pp.
1864. *Bilder-Atlas zur wissenschaftlich-populären Naturgeschichte der Amphibien in ihren Sämtlichen Hauptformen*. Wien: Kaiserl. Königl. hof- und Staatsdruckerei.
- Fritts, T. H.
1974. A multivariate evolutionary analysis of the Andean iguanid lizards of the genus *Stenocercus*. *Mem. San Diego Soc. Nat. Hist.* 7: 1–89.
- Frost, D. R., and R. Etheridge
1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* 81: 1–65.

- Frost, D. R., and D. M. Hillis
1990. Species in concept and practice: herpetological applications. *Herpetologica* 46: 87–104.
- Gauthier, J. A.
1986. Saurischian monophyly and the origin of birds. In K. Padian (ed.), *The origin of birds and the evolution of flight*, pp. 1–55. *Mem. California Acad. Sci.* 8: i–vii, 1–98.
- Gravenhorst, J. L. C.
1837. Beiträge zur genauern Kenntniss einiger Eidechsegattungen. *Nova Acta Acad. Leop. Carol.*, Halle 18(2): 712–784.
- Gray, J. E.
1827. A description of new species of saurian reptiles; with a revision of the species of chamaeleons. *Philos. Mag. Ann.*, ser. 2, 2: 207–214.
1831. A synopsis of the species of the Class Reptilia, vol. 9, Pt. 2: 110 pp. In E. Griffith and E. Pidgeon (eds.), *The animal kingdom arranged in conformity with its organisation by the Baron Cuvier, with additional descriptions of all the species hitherto named, and of many others*. London: Whittaker, 16 vols.
1845. *Catalogue of the specimens of lizards in the collection of the British Museum*. London: Edward Newman, xxviii + 289 pp.
- Greene, H.
1976. Scale overlap, a directional sign stimulus for prey ingestion by ophiophagous snakes. *Z. Tierpsychol.* 41: 113–120.
1977. Lizards of the genus *Uracentron* (Iguanidae) in east-central Colombia. *Herpetologica* 33: 256–260.
- Gudynas, E., and G. Skuk
1983. A new species of the iguanid lizard genus *Tropidurus* from temperate South America (Lacertilia: Iguanidae). *C. E. D. Orione Contrib. Biol.* 10: 1–10.
- Guichenot, A.
1855. Animaux nouveaux ou races recueillis pendant l'expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro à Lima, et de Lima à Pará; exécutée par ordre du gouvernement français pendant les années 1843 à 1847, sous la direction du Comte Francis de Castelnau, vol. 2. *Reptiles*. Paris, 95 pp.
- Günther, A.
1861. Account of the reptiles sent by dr. Wucherer from Bahia. *Proc. Zool. Soc. London* 1861: 12–18.
1877. Accounts of the zoological collection made during the visit of H. M. S. 'Peterel' to the Galapagos Islands. II. *Reptiles*. *Proc. Zool. Soc. London* 1877: 66–67.
- Heller, E.
1903. Papers from the Hopkins Stanford Galapagos Expedition, 1898–1899. XIV. *Reptiles*. *Proc. Washington Acad. Sci.* 5: 39–98.
- Hendy, M. D., and D. Penny
1982. Branch and bound algorithms to determine minimal evolutionary trees. *Math. Biosci.* 59: 277–290.
- Hull, D. L.
1964. Consistency and monophyly. *Syst. Zool.* 13: 1–11.
- International Commission on Zoological Nomenclature
1961. *International Code of Zoological Nomenclature*, adopted by the XV International Congress of Zoology. International Trust for Zoological Nomenclature, London, 176 pp.
1985. *International Code of Zoological Nomenclature*, Third Edition, adopted by the XX General Assembly of the International Union of Biological Sciences. International Trust for Zoological Nomenclature, London, 338 pp.
- Jollie, M. T.
1960. The head skeleton of the lizard. *Acta Zool.*, Stockholm 41: 1–64.
- Kasahara, S., Y. Yononaga-Yassuda, and M. T. Rodrigues
1987. Karyotype and evolution of the *Tropidurus nanuzae* species group (Sauria, Iguanidae). *Rev. Bras. Genet.* 10: 185–197.
- Kaup, J. J.
1825. Einige Bemerkungen zu Merrems Handbuch. *Isis von Oken* 16: 589–593.
1826. Beiträge zu Amphibiologie und Ichthyologie. *Ibid.* 18–19: 87–89.
1827. *Zoologische Monographien*. *Ibid.* 19: 610–625.
- Keller, C., and L. Krause
1986. The appendicular skeleton of *Liolaemus occipitalis* Boulenger, 1885 (Sauria, Iguanidae). *Rev. Brasil. Biol.*, Rio de Janeiro 46(4): 727–740.
- Kluge, A. G.
1984. The relevance of parsimony to phylogenetic inference. In T. Duncan and T. F. Stuessy (eds.), *Cladistics: perspectives on the reconstruction of evolutionary history*, pp. 24–38. New York: Columbia Univ. Press.
1985. *Ontogeny and phylogenetic systematics*. *Cladistics* 1: 13–28.
1989a. *Metacladistics*. *Cladistics* 5: 291–294.
1989b. A concern for evidence and a phyloge-

- netic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Syst. Zool.* 38: 7–25.
- Kluge, A. G., and J. S. Farris
1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.* 18: 1–32.
- Latreille, P. A.
1801. *In* C. S. Sonnini and P. A. Latreille, Histoire naturelle des Reptiles, avec Figures dissinées d'après Nature. Vol. 1. Paris, xxii + 280 pp.
1802. *In* C. S. Sonnini and P. A. Latreille, *Ibid.*, Vol. 2. Paris, 332 pp.
- Laurent, R.
1982. Variacion y dimorfismo sexual en el complejo *Tropidurus melanopleurus-pictus* (Iguanidae). *Acta VIII Congr. Latinoam. Zool.* 1: 621–626.
- Laurenti, J. N.
1768. Specimen medicum exhibens Synopsis Reptilium emendatum cum experimentis circa venena et antidota reptilium austriacorum. Wien: Trattner, 214 pp.
- Lecuru, S.
1968. Remarques sur les scapulo-coracoide des lacertiliens. *Ann. Sci. Nat., Zool.* 10: 475–510.
- Lesson, R. P.
1831. *In* L. I. Duperrey (ed.). 1826–1838. Voyage autour du Monde, exécuté par Ordre du Roi, sur la Corvette de sa Majesté, La Coquille, pendant les années 1822, 1823, 1824, 1825. Zoologie and Atlas. Paris: Arthur Bertrand.
- Lichtenstein, M. H. K.
1822. Die Werke von Maregrave und Piso über die Naturgeschichte Brasiliens Erläutert aus den wieder aufgefundenen. *Abh. Preuss. Akad. Wiss. Berlin 1820–1821:* 237–254.
- Linnaeus, C.
1758. *Systema Naturae per Regna tria Naturae secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis.* Ed. 10. vol. 1. Stockholm.
- Maddison, W. P., and D. R. Maddison
1987. MacClade. Version 2.1. User's manual. Privately printed.
- Maddison, W. P., M. J. Donoghue, and D. R. Maddison
1984. Outgroup analysis and parsimony. *Syst. Zool.* 33: 83–103.
- Mägdefrau, H.
1991. *Plica nigra*, ein neuer Leguan von Guaiquinima Tepui (Venezuela) (Sauria, Iguanidae). *Spixiana* 14: 229–234.
- Manzini, P. A., and A. S. Abe
1990. A new species of *Tapinurus* from the Caatinga of Piaui, northeastern Brazil (Squamata: Tropiduridae). *Herpetologica* 46: 462–467.
- Merrem, B.
1820. Tentamen Systematis Amphibiorum. Versuch eines Systems der Amphibien. Marburg: J. C. Krieger, 191 pp.
- Mertens, R.
1925. Zwei neue Eidechsen aus Venezuela. *Senckenb. Biol.* 7: 75–78.
1956. Studien über die Herpetofauna Perus I. Zur Kenntniss der Iguaniden—Gattung *Tropidurus* in Peru. *Senckenb. Biol.* 37: 101–136.
1973. Leopold Fitzinger: his life and herpetological work. *In* K. Adler (ed.), Fitzinger's Systema Reptilium. Facsimile Repr. Herpetol., Soc. Study Amph. Rept. Misc. Publ., pp. iii–vi.
- Müller, L.
1924. Über neue oder seltene Mittel- und süd-amerikanische Amphibien und Reptilien. *Mitt. Zool. Mus. Berlin* 11: 75–93.
- Oppel, M.
1811. Die Ordnung, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. München: Lindauer, xii + 87 pp.
- Ortiz-Zapata, J. C.
1980a. Le statut taxonomique de *Lophyrus araucanus* Lesson, 1831 (Sauria, Iguanidae). *Bull. Mus. Natl. Hist. Nat., Paris (Zool. Biol. Ecol. Anim.)* 2(2), 1980: 599–601.
1980b “1977.” Revision taxonomica del género *Tropidurus* en Chile. *Reunion Iberoam. Zool. Vertebr.* 1: 355–377.
1980c. Estudios comparativos de algunas poblaciones de *Tropidurus* de la costa chilena. *An. Mus. Hist. Nat. Vaparaíso* 13: 267–279.
- O'Shaughnessy, A. W. E.
1879. Descriptions of new species of lizards in the collection of the British Museum. *Ann. Mag. Nat. Hist., ser. 5, 4:* 295–303.
1881. An account of the collection of lizards made by Mr. Buckley in Ecuador, and now in the British Museum, with descriptions of the new species. *Proc. Zool. Soc. London* 1881: 227–245.
- Paull, D., E. E. Williams, and W. P. Hall
1976. Lizard karyotypes from the Galapagos Islands: chromosomes in phylogeny and evolution. *Breviora* 441: 31 pp.
- Peters, J. A.
1967. The lizards of Ecuador, a check list and key. *Proc. U.S. Natl. Mus.* 119: 1–49.

- Peters, W.
 1871. Über einige Arten der herpetologischen Sammlund des Berliner zoologischen Museums. Monatsber. Preuss. Akad. Wiss. Berlin 1871: 644–652.
 1877. Herpetologische Notizen. I. Über die von Spix in Brasilien gesammelten Eidechsen des Königlichen Naturalien-Kabinetts zu München. II. Bemerkungen über neue oder weniger bekannten Amphibien. Monatsber. Preuss. Akad. Wiss. Berlin 1877: 407–423.
- Poli, G. S.
 1791. Testacea utriusque Siciliae eorumque historia et anatome. Vol. 1. Parma.
- Pregill, G. K.
 In press. Systematics of the West Indian lizards *Leiocephalus* (Squamata: Iguania: Tropiduridae). Misc. Publ. Mus. Nat. Hist. Univ. Kansas no. 84.
- Raddi, G.
 1822. Continuazione della descrizione dei rettili brasiliani indicati nella memoria inseriata nel secondo fascicolo delle memorie di fisica del precedente volume XVIII. Atti. Soc. Ital. Sci. Modena 19: 53–73.
- Reinhardt, J., and C. Lütken
 1861. Bidrag til Kundskab om Brasiliens Padder og Krybdyr. Første Afdeling Padder og Öglerne. Vidensk. Medd. Dansk Naturhist. Foren. Kjobenhavn 1861: 143–242.
- Rodrigues, M. T.
 1981. Uma nova espécie de *Tropidurus* do Brasil (Sauria, Iguanidae). Pap. Avulsos Zool., São Paulo 34: 145–149.
 1984a. Sobre *Platynotus* Wagler, 1830, pré-ocupado substituído por *Tapinurus* Amaral, 1933, com a descrição de uma nova espécie (Sauria, Iguanidae). Pap. Avulsos Zool., São Paulo 35: 367–373.
 1984b. Uma nova espécie brasileira de *Tropidurus* com crista dorsal (Sauria, Iguanidae). Pap. Avulsos Zool., São Paulo 35: 169–175.
 1986. Um novo *Tropidurus* com crista dorsal do Brasil, com comentários sobre suas relações, distribuição e origem (Sauria, Iguanidae). Pap. Avulsos Zool., São Paulo 36: 171–179.
 1987. Sistemática, ecologia e zoogeografia dos *Tropidurus* do grupo *Torquatus* ao sul do Rio Amazonas (Sauria, Iguanidae). Arq. Zool., São Paulo 31: 105–230.
 1988. Distribution of lizards of the genus *Tropidurus* in Brazil (Sauria, Iguanidae). In W. R. Heyer and P. E. Vanzolini (eds.), Proceedings of a workshop on Neotropical distribution patterns, pp. 305–315. Rio de Janeiro: Acad. Brasil. Cienc.
- Rodrigues, M. T., S. Kasahara, and Y. Yonenaga-Yassuda
 1988. *Tropidurus psammonastes*: uma nova espécie do grupo *torquatus* com notas sobre seu cariótipo e distribuição (Sauria, Iguanidae). Pap. Avulsos Zool., São Paulo 36: 307–313.
- Roux, J.
 1907. Revision de quelques espèces de reptiles et amphibiens du Perou, décrites par Tschudi en 1844–1846. Rev. Suisse Zool. 15: 293–303.
- Roze, J. A.
 1958. Resultados zoológicos de la expedición de la Universidad Central de Venezuela a la región del Ayantépuí, Venezuela, basándose en las colecciones de las expediciones de Phelps-Tate, del American Museum of Natural History, 1937–1938, y de la Universidad Central de Venezuela, 1956. Acta Biol. Venezuelica 2: 243–270.
- Schinz, H. R.
 1833–35. Naturgeschichte und Abbildungen der Reptilien. Leipzig: Wiedmann, 250 + iv pp.
- Schlegel, H.
 1858. Handleiding tot de Beoefening der Dierkunde, vol. 2. Natuurkundige Leercursus ten Gebruike der Koninklijke Militaire Akademie. xx, 628 pp.
- Schmidt, K. P., and R. F. Inger
 1951. Amphibians and reptiles of the Hopkins-Brunner Expedition to Brazil. Fieldiana: Zool. 31: 439–465.
- Smith, H. M.
 1946. Handbook of lizards. Ithaca, NY: Comstock, xxi + 557 pp.
- Sokal, R. R., and F. J. Rohlf
 1981. Taxonomic congruence in the Leptopodomorpha re-examined. Syst. Zool. 30: 309–325.
- Spix, J. B. von
 1825. Animalia nova sive species nova laceratarum quas in itinere per Brasiliam annis MDCCCXVII–MDCCCXX jussu et auspicio Maximiliani Josephi I Bavariae Regis suscepto collegit et descripsit Dr. J. B. de Spix. Lipsiae: T. O. Weigel, 26 pp.
- Steindachner, F.
 1876. Die Schlangen und Eidechsen der Galapagos-Inseln. Festschr. Zool. Bot. Ges. Wien 1876: 303–329.

1891. Ueber neue und seltene Lacertiden aus den herpetologischen Sammlung des k. k. naturhistorisches Hofsmuseums. Ann. k. k. Hofmus. Wien 6: 371–378.
1901. Herpetologische und ichthyologische Ergebnisse einer Reise nach Südamerika mit einer Einleitung von Therese Prinzessin von Bayern. Anz. Akad. Wiss. Wien 38: 194–196.
1902. Herpetologische und ichthyologische Ergebnisse einer Reise nach Südamerika, mit einer Einleitung von Therese Prinzessin von Bayern. Denkschr. Akad. Wiss. Wien 72: 89–148.
- Stejneger, L.
1901. An annotated list of batrachians and reptiles collected in the vicinity of Guaira, Venezuela, with description of two new species of snakes. Proc. U.S. Natl. Mus. 24: 179–192.
- Stevens, P. F.
1980. Evolutionary polarity of character states. Annu. Rev. Ecol. Syst. 11: 333–358.
- Swofford, D. L.
1989. PAUP—Phylogenetic Analysis Using Parsimony. Version 3.01. User's Manual. Privately Published.
- Tschudi, J. J. von
1845. Reptilium conspectum quae in republica Peruana reperiuntur et pleraque observata vel collecta sunt in itinere. Arch. Naturgesch. 11: 150–170.
- Valdivieso, D., and J. R. Tamsitt
1963. Records and observations on Colombian reptiles. Herpetologica 19: 28–29.
- Van Denburgh, J., and J. R. Slevin
1913. Expedition of the California Academy of Sciences to the Galapagos Islands, 1905–1906. IX. The Galapagoan lizards of the genus *Tropidurus* with notes on iguanas of the genera *Conolophus* and *Amblyrhynchus*. Proc. California Acad. Sci., ser. 4, 2: 132–202.
- Vanzolini, P. E., and N. Gomes
1979. On *Tropidurus hygomi*: redescription, ecological notes, distribution and history (Sauria, Iguanidae). Pap. Avulsos Zool., São Paulo 32: 243–259.
- Wagler, J. G.
1830. Natürliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vögel. München, Stuttgart, and Tübingen: J. G. Cotta, vi + 354 pp.
- Watrous, L. E., and Q. D. Wheeler
1981. The outgroup comparison method of character analysis. Syst. Zool. 30: 1–11.
- Werner, F.
1899. Beschreibung neuer Reptilien und Batrachier. Zool. Anz. 22: 479–484.
1900. Reptilien und Batrachier aus Peru und Bolivien. Abh. Ber. K. Zool. Anthropol. Ethnol. Mus. Dresden 9: 1–4.
- Wied-Neuwied, M., Prinz zu
1820–21. Reise nach Brasilien en den Jahren 1815 bis 1817. 2 vols. Frankfurt a. M.: H. L. Brönner.
1825. Beiträge zur Naturgeschichte von Brasilien, vol. 1. Weimar: Gr. H. S. priv. Landes-Industrie-Comptoirs.
- Wiegmann, A. F. A.
1834a. Beiträge zur Zoologie gesammelt auf einer Reise um die Erde, von Dr. F. J. F. Meyen. Siebente Abhandlung. Amphibien. Nova Acta Acad. Caesar. Leop. Carol., Halle 17: 185–268.
1834b. Herpetologica Mexicana seu descriptio amphibiorum Novae Hispaniae. Pars prima. Saurorum species. Berlin: Lüderitz, vi + 54 pp.
1835. Bericht über die Fortschritte der Zoologie in Jahre 1834. Amphibien. Arch. Naturgesch. 1: 273–296.
- Wiley, E. O.
1979. An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. Syst. Zool. 28: 308–337.
1981. Convex groups and consistent classifications. Syst. Bot. 6: 346–358.
- Wright, J. W.
1983. The evolution and biogeography of the lizards of the Galapagos Archipelago: evolutionary genetics of *Phyllodactylus* and *Tropidurus* populations. In R. I. Bowman et al. (eds.), Patterns of evolution in Galapagos organisms, pp. 123–155. AAAS Symposium vol., San Francisco.

APPENDIX 1 SPECIMENS EXAMINED

Abbreviations for names of collections are: AMNH American Museum of Natural History; BMNH The Natural History Museum, London; CAS California Academy of Sciences; KU Museum of Natural History, University of Kansas; LACM Natural History Museum of Los Angeles County; LSUMZ Museum of Natural Science, Louisiana State University; MAN Mark A. Norell private osteology collection; MCZ Museum of Comparative Zoology, Harvard University; MPEG Museu Paraense Emilio Goeldi, Belem, Brazil; MVZ Museum of Vertebrate Zoology, University of California; REE Richard E. Etheridge osteology collection; RWM Roy W. McDiarmid field series (to be accessioned into USNM); SDSNH San Diego Natural History Museum; TCWC Texas Cooperative Wildlife Collection, Texas A&M University; UMMZ Museum of Zoology, University of Michigan; UNM Museum of Southwestern Biology, University of New Mexico; USNM National Museum of Natural History, Smithsonian Institution. Abbreviations for specimens are: A Alizarin stained skeleton, AA Alcian blue-alizarin red stained postcranial skeleton, CAA complete alcian blue-alizarin red skeleton, D dry skeleton, S dry skull, SN skin, H hemipenial preparation or dissection, AL alcoholic specimen, X X-ray photograph. All special preparations (e.g., injected hemipenes, skeletons) are listed but AMNH and KU alcoholic material is not noted. Additionally, although much iguanian material of virtually all genera (except for chamaeleonids) has been examined at one time or another, only material representing my ingroup and immediate outgroups is here listed.

Tropidurini

Microlophus albemarlensis: CAS 11153 (S); LACM 106243–49 (AL), 106250 (AA, S), 106251–60 (AL), 106261 (AA, S), 196261 (D); MCZ 28475 (D), 36928 (D); MVZ 77323 (D), 77467 (D), 77469 (D); SDSNH 7211–12 (D), 7220 (D). *M. atacamensis*: KU 161983 (AA, S, H), 161986 (AA, S). *M. bivittatus*: AMNH 20499 (H); LACM 106302 (AL, H), 106303 (AA, S), 106305–06 (AL), 106307 (AA, S), 106308 (AL); SDSNH 7192 (2) (D). *M. delanonis*: AMNH 92731 (AL, H), MCZ 9204 (D), 36909 (2) (D), 36910 (D); SDSNH 10065 (D), 10073 (D), 10241 (D), 22108 (D). *M. duncanensis*: CAS 12202 (D); SDSNH 10194 (D). *M. grayii*: CAS 11620 (D). *M. habelii*: LACM 106380–87 (AL), 106388 (AL, H), 106389–90 (AL), 106391 (AA, S), 106392–93 (AL), 106394 (AA, S), 106395–96 (AL). *M. heterolepis*: AMNH 65331–42 (AL, X). *M. occipitalis*: KU 142714 (AA, S, SN), 142721 (AA, S), 142735 (CAA), 163630 (H); LACM 48870 (AL), 48874 (AL, H), 48902 (AL), 48904–05 (AL); REE 668 (D), 1847 (D), 1860 (D). *M. pacificus*: CAS 12480 (D); MCZ 28495 (2) (D); SDSNH 10224 (D), 10230 (D). *M. peruvianus*: KU 134673 (AA, 2), 134674 (AA, S, H), 134679 (H), 134695 (AA, S), 163640 (H), 164055–56 (D); LACM 49016 (AL, H), 49018 (AL, H), 49021 (AL), 49051 (AL, H), 49053 (AL, H); SDSNH 30843 (D), 30893 (D), 30911 (D). *M. quadrivittatus*: REE unnumbered (3) (AL, X). *M. stolzmanni*: KU 134701 (H), 134704 (AA, S), 134731 (CAA), 134747 (AA, S); LACM 49105 (AL, H), 49119 (AL, H), 49121 (AL, H), 49129 (AL, H), 49132 (AL, H). *M. theresiae*: LACM 49060–61 (AL), 49064 (AL), 49070 (AL), 49076–77 (AL), 122696 (AL), 122702 (AL), 122706 (AL), 122707–08 (AA, S), 122710 (AL).

M. theresioides: KU 162012 (AA, S), 162018 (AA, S); LACM 134136–41 (AL). *M. thoracicus*: KU 163721 (AA, S), 163724 (AA, S); LACM 48914 (AL), 48917 (AL), 48922 (AL). *M. tigris*: KU 163752 (H), 163753 (AA, S), 163756 (AA, S); SDSNH 47031 (D). *M. yanezi*: MVZ 92938–39 (D, SN), 92945 (D, SN). *Plesiomicrolophus koepckeorum*: LACM 49080–81 (AL), 49082 (CAA), 49083 (AL, H), 49084 (AL), 49085 (AA, S), 49086–87 (AL), 49088 (AA, S), 49089–104 (AL), 109569 (AL), 122584 (AL), 122588 (AL), 122590–91 (AL); TCWC 28687–88 (AL, H), 28697 (AL, H), 28700 (AL, H). *Tropidurus azureus*: AMNH 60330 (S, AA), 61014 (S, AA); MAN 47 (D); UMMZ 129418 (A). *T. bogerti*: RWM 11659–61 (AL), 11662 (D, SN), 11663 (CAA), 11664 (AL, H). *T. cocorobensis*: MCZ 172946–47 (AL, X). *T. erythrocephalus*: MCZ 172948 (S, AA), 172949–50, 172952, 172954 (AL, X). *T. etheridgei*: AMNH 172948 (S, AA), 17949–50 (AL, X); KU 160145 (H), 186102 (AA, S), 186113 (AA, S); LACM 73991 (AL, H); UNM 98982 (D). *T. flaviceps*: AMNH 71101–02 (AL, X); KU 126781 (H), 175317 (AA, S). *T. hispidus*: CAS 49549 (D); KU 167508 (AA, S, H), 167513 (AA, S); MCZ 3133 (D), 3438 (D), 38536 (D), 43869 (D), 49529 (D); SDSNH 34882–83 (D); USNM 159200–05 (AL, X). *T. hygomi*: AMNH 37542 (S, AA), 37538–41 (AL, X); USNM 209643 (AL, X), 209644 (AA, S), 209645–46 (AL, X). *T. insularis*: MCZ 172879–82 (AL, X). *T. itambere*: USNM 148773 (S, AA), 148775–77 (AL, X); MCZ 172883 (AL, X), 172885–87, 172892 (S, AA). *T. lumarius*: AMNH 136177 (S, AA), 136176 (H). *T. melanopleurus*: KU 136367 (D), 136370–71 (AA, S), 136374 (D), 183469 (H); REE 2612 (D), 2616 (D). *T. montanus*: USNM 218204–9 (AL, X), 218210 (S, AA); MCZ 172893–94,

172896, 172901–02. *T. mucujensis*: MCZ 172944–45 (AL, X). *T. nanuzae*: MCZ 160243 (AA, S, SN), 160244–45 (AL); USNM 213514–15 (AL, H). *T. oreadicus*: UMMZ 56805 (S, AA), 188632–33 (S); USNM 188632–33 (D). *T. pinima*: AMNH 131862–63 (AL, X). *T. plica*: AMNH 61314 (D), 85313 (D), 107590 (AL); KU 117088 (H), 167499 (AA, S); MAN 76 (D); MCZ 6100 (D), 9001 (D), 43865 (D); UMMZ 149129 (D). *T. semitaeniatus*: AMNH 131864–66 (AL, X); CAS 49386–88 (AL), 49455 (AL), 49468–69 (AL), 49471–72 (AL), 49473 (D), 49474–76 (AL); LSUMZ 39519 (AA, S); MCZ 79805 (D), 131890–91 (D). *T. spinulosus*: AMNH 101490–91 (S, AA); CAS 49843 (D); KU 97853 (H), 97856 (AA, S); LACM 126315–16 (AL), 126318 (AL), 126321 (AA, S); UNM-ALA 237 (D); UNM 99121 (AL, S), 99128 (AL); USNM 125166 (AL, S), 126016 (AL), 126029 (AL, S), 126703 (D), 126705 (D), 126707 (D), 126941 (D), 128312 (AL, S), 128987 (D). *T. strobilurus*: BMNH 1903.10.16.23 (D); MCZ 154211 (AL, X), 133243 (D); MPEG unnumbered (AL, H, X). *T. torquatus*: AMNH 62148 (S, AA); KU 128205 (H); MVZ 92970 (D, SN); USNM 98593–98 (AL), 207683–85 (AL, X). *T. umbra*: AMNH 61239 (D), 61436 (D); KU 135267 (D), 146659 (AA, S, H), 147946 (H); LACM 49140 (AL, H); MCZ 152184 (D). *Uranoscodon superciliosus*: AMNH 61304 (D); KU 128215 (D), 128216 (H), 128218 (H), 135269 (D); LACM 44474 (AL, H); MCZ 9318 (D), 58340 (D); REE 16600; UMMZ 149312 (D); USNM 202682 (S).

Stenocercini

Stenocercus aculeatus: KU 121093 (AA, S); MCZ 8061 (S); UMMZ 149102 (D). *S. apurimacus*: KU 134244 (H), 134284 (AA, S), 134288 (H), 134306 (CAA). *S. boettgeri*: KU 134011 (H), 134014 (AA, S); MCZ 45843 (D). *S. caducus*: AMNH 37907 (CAA); MCZ 20625–26 (AL); UMMZ 149105–06 (D). *S. chrysopygus*: KU 133895 (AA, S), 133906 (AA, S), 134315 (H); MCZ 45832. *S. crassicaudatus*: AMNH 23132 (D); KU 133959 (AA, S),

163602 (AA, S). *S. cupreus*: KU 133974 (AA, S), 133976 (AA, S); MCZ 43789 (D). *S. empetrus*: KU 134401 (AA, S), 134403 (AA, S), 134421 (CAA), 181909 (H). *S. erythrogaster*: MCZ 36877 (S); UMMZ 149107 (D). *S. festae*: KU 134588 (H), 134595 (AA, S), 134603 (AA, S), 141161 (H). *S. formosus*: KU 134110 (AA, S), 134112 (H); MCZ 11295 (S). *S. guentheri*: KU 147319 (AA, S), 147326 (AA, S), 147347 (CAA), 179426 (H), 202940 (H); MCZ 8418 (D), 8423 (D), 8427 (D). *S. humeralis*: KU 121136 (H), 134001 (AA, S), 134004 (AA, S). *S. iridescens*: AMNH 21993 (AA, S), 112989 (AA, S), 112990 (AA, S); MCZ 8412 (S), 84162 (D), 84165 (D), 84167 (D). *S. marmoratus*: UMMZ 149276 (D). *S. melanopygus*: KU 134058 (AA, S), 134075 (AA, S). *S. nigromaculatus*: KU 134089 (AA, S), 134092 (AA, S), 134105 (H); MCZ 18767 (D). *S. ochoai*: KU 133876 (CAA), 133878 (AA, S), 133884 (AA, S, H), 139267 (H). *S. orientalis*: KU 134452 (AA, S), 134460 (AA, S), 134464 (CAA). *S. ornatissimus*: KU 134351 (AA, S), 134360 (AA, S). *S. ornatus*: KU 121128 (AA, S), 134128 (AA, S), 134130 (H), 134155 (CAA). *S. praeornatus*: KU 134225 (H), 134229 (AA, S). *S. rhodomelas*: KU 142699 (H), 152184 (AA, S), 152186 (AA, S). *S. roseiventris*: KU 134156 (H), 172196 (AA, S). *S. scapularis*: AMNH 56770 (AA, S), 56777 (AA, S). *S. simonsii*: KU 134163 (H). *S. trachycephalus*: AMNH 131223 (S, AA), 131227 (S, AA); MCZ 17144 (D). *S. variabilis*: KU 134178 (H), 134198 (AA, S), 134213 (AA, S). *S. varius*: KU 121135 (H), 134563 (H), 142704 (AA, S).

Leiocephalinae

Leiocephalus carinatus: UMMZ 149103–04 (D); USNM 81709 (D). *L. greenwayi*: UMMZ 149108 (D). *L. inaguae*: UMMZ 149133 (D). *L. loxogrammus*: KU 192293 (D); UMMZ 149134 (D). *L. psammodromus*: UMMZ 149109 (D). *L. punctatus*: UMMZ 149110 (D). *L. raviceps*: UMMZ 149111 (D). *L. schreibersi*: KU 93358 (CAA). *L. vittatus*: CAS 39304 (S).

APPENDIX 2
DATA MATRIX

	1	111111112	222222223	333333334	444444445	555555556	666666667	7777777
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
Ancestor	000000000	0000?00000	?000000000	0000000000	0000?00?0	0000?00000	0000000000	00000000
<i>Uranoscodon</i>	0101100000	1100000010	0110001101	0000001000	00011114?0	1000?01010	0101001002	3000010
<i>Tropidurus</i>								
<i>atacamensis</i>	0000000000	1110000000	0000001100	0010000000	00110001?0	0010?00001	0100001000	1111000
<i>T. peruvianus</i>	0000000000	1110000000	0000001100	0010000000	00110001?0	0010?00001	0100001000	1011000
<i>T. koepckeorum</i>	0000000000	1110000000	0000001100	0010000000	00010000?0	0000?00000	0100001000	0000000
<i>T. occipitalis</i>	0000000000	1110000000	0000001100	0010000000	00110000?0	0000?00000	0100001000	0000000
<i>T. stolzmanni</i>	0000000000	1110000000	0000001100	0010000000	00110010?0	0000?00000	0100001000	0000000
<i>T. bivittatus</i>	0000000000	1110001000	0000001100	0010000000	00110000?0	0000?00000	0100001000	0000000
<i>T. nanuzae</i>	1000001000	1211112001	0100011101	0021100000	0101000211	0000?00000	0100001000	0000000
<i>T. cocorobensis</i>	1000001000	12??????01	0000101101	0021100000	02?1?00200	0000?00000	0100001000	0100000
<i>T. hygomi</i>	1000001000	1211112001	0000101101	0021100000	0201100200	0000?00000	0100001000	0100000
<i>T. erythrocephalus</i>	1000001000	1211112001	0000101101	0021100000	02???00210	0001010000	0100001000	0100000
<i>T. hispidus</i>	1000001000	1211112001	1000101101	1021100000	0201100210	0001100000	0100001000	0100000
<i>T. insulanus</i>	1000001000	12??????01	0000101101	1021100000	0201?00210	0001000000	0100001000	1100000
<i>T. itambere</i>	1000001000	1211112001	0000101101	0021100000	0201100210	000??10000	0100001100	0100000
<i>T. montanus</i>	1000001000	1211112001	0000101101	1021100000	0201100220	0001110000	0100001000	0100000
<i>T. mucujensis</i>	1000001?00	12??????01	0000101101	1021100000	02???00210	1001110000	0100001000	0100000
<i>T. oreadicus</i>	1000001000	1211112001	0000101101	1021100000	0201100220	0001000000	0100001000	0100000
<i>T. torquatus</i>	1000001000	1211112001	0000101101	1021100000	0201100200	1001110000	0100001000	0100000
<i>T. bogerti</i>	1000011000	1211012001	0001101011	1021200010	12011001?0	1101111000	00?0001000	2100000
<i>T. melanopleurus</i>	1000001000	1211112001	0000101111	1021200000	11011013?0	1100?00010	0110101000	2010000
<i>T. spinulosus</i>	1000001000	1211110001	0000101011	1021200000	01011023?0	1100?00110	0110101000	2000000
<i>Tapinurus</i>								
<i>semitaeniatus</i>	1010021000	1211112111	1001101121	0121200010	12011001?0	1101110000	0110001000	2110000
<i>Plica plica</i>	1000101101	1211112011	1110101101	1021200000	21011123?2	1100?01110	0121101011	2000000
<i>P. umbra</i>	1101101101	1211112001	1111001101	1021200000	20011023?0	0000?01110	0111101012	3000010
<i>Strobilurus</i>	1000101100	1211112011	1011101101	1021200100	21011000?0	1100?00010	0110101001	2000101
<i>Uracentron azureum</i>	1000101110	1211110111	1011001000	1021210101	20011111?0	0100?01000	1010111101	3110200
<i>U. flaviceps</i>	1000101100	1211110111	1110001100	1021210101	20011111?0	1100?01000	1010111101	3100200

APPENDIX 3
Changes by Transformation Series for Figure 33

Character changes noted by a double dagger (‡) are of equally parsimonious placement elsewhere. In the case of terminal taxa even though the character assignment is not equivocal, the plesiomorphic member of the transformation pair may have alternative placement in the topology of the tree. Transformation Series denoted with parentheses () are unpolarized (additive) in the analysis; those surrounded by brackets [] are unordered (nonadditive).

Trans. series	ci	Steps	Character change	Along stem
1	1.000	1	0 → 1	5
2	0.500	1	0 → 1	<i>Uranoscodon superciliosus</i>
		1	0 → 1	<i>Plica umbra</i>
3	1.000	1	0 → 1	<i>Tapinurus semitaeniatus</i>
4	0.500	1	0 → 1	<i>Uranoscodon superciliosus</i>
		1	0 → 1	<i>Plica umbra</i>
5	0.500	1	0 → 1	<i>Uranoscodon superciliosus</i>
		1	0 → 1	16
6	1.000	1	0 → 1	14
		1	1 → 2	<i>Tapinurus semitaeniatus</i>
7	1.000	1	0 → 1	5
8	1.000	1	0 → 1	16
9	1.000	1	0 → 1	<i>Uracentron azureum</i>
10	1.000	1	0 → 1	17
11	1.000	1	0 → 1	1
12	1.000	1	0 → 1	1
		1	1 → 2	5
13	1.000	1	0 → 1	2
14	1.000	1	0 → 1	5
15	0.500	1	0 → 1	5
		1	1 → 0	<i>T. bogerti</i>
16	1.000	1	0 → 1	5
[17]	0.500	1	0 → 1	<i>T. bivittatus</i>
		1	0 → 2	5
		1	2 → 0	<i>T. spinulosus</i>
		1	2 → 0	19
18	0.500	1	0 → 1	<i>Tapinurus semitaeniatus</i>
		1	0 → 1	19
19	0.250	1	0 → 1	<i>Uranoscodon superciliosus</i>
		1	0 → 1	<i>Tapinurus semitaeniatus</i>
		1	0 → 1‡	16
		1	1 → 0‡	<i>Plica umbra</i>
20	1.000	1	0 → 1	5
(21)	0.333	1	0 → 1	<i>T. hispidus</i>
		1	0 → 1	<i>Tapinurus semitaeniatus</i>
		1	0 → 1	16
22	0.250	1	0 → 1	<i>Uranoscodon superciliosus</i>
		1	0 → 1	<i>T. nanuzae</i>
		1	0 → 1	17
		1	0 → 1	<i>Uracentron flaviceps</i>
23	0.500	1	0 → 1	<i>Uranoscodon superciliosus</i>
		1	0 → 1	16
24	0.250	1	0 → 1	14
		1	0 → 1‡	16
		1	1 → 0‡	<i>Plica plica</i>
		1	1 → 0‡	<i>Uracentron flaviceps</i>

APPENDIX 3
Changes by Transformation Series for Figure 33—(Continued)

Trans. series	ci	Steps	Character change	Along stem
25	0.333	1	0 → 1	6
		1	1 → 0	<i>Plica umbra</i>
		1	1 → 0	19
26	1.000	1	0 → 1	<i>T. nanuzae</i>
27	1.000	1	0 → 1	1
28	0.250	1	0 → 1	1
		1	1 → 0	<i>T. bogerti</i>
		1	1 → 0	<i>T. spinulosus</i>
		1	1 → 0	<i>Uracentron azureum</i>
29	0.667	1	0 → 1	13
		1	1 → 2	<i>Tapinurus semitaeniatus</i>
		1	1 → 0	16
30	0.333	1	0 → 1	<i>Uranoscodon superciliosus</i>
		1	0 → 1	5
		1	1 → 0	19
31	0.500	1	0 → 1	9
		1	1 → 0	<i>Tapinurus semitaeniatus</i>
32	1.000	1	0 → 1	<i>Tapinurus semitaeniatus</i>
33	1.000	1	0 → 1	2
		1	1 → 2	5
34	1.000	1	0 → 1	5
35	1.000	1	0 → 1	5
		1	1 → 2	13
36	1.000	1	0 → 1	19
37	1.000	1	0 → 1	<i>Uranoscodon superciliosus</i>
38	1.000	1	0 → 1	18
39	1.000	1	0 → 1	14
40	1.000	1	0 → 1	19
[41]	0.667	1	0 → 1‡	13
		1	1 → 0	<i>T. spinulosus</i>
		1	1 → 2	16
[42]	0.400	1	0 → 1‡	5
		1	1 → 2‡	6
		1	2 → 1	15
		1	1 → 0	<i>Plica umbra</i>
		1	1 → 0	19
43	1.000	1	0 → 1	3
44	1.000	1	0 → 1	1
(45)	0.500	1	0 → 1‡	<i>Uranoscodon superciliosus</i>
		1	0 → 1	6
46	0.333	1	0 → 1	<i>Uranoscodon superciliosus</i>
		1	0 → 1	<i>Plica plica</i>
		1	0 → 1	19
47	0.333	1	0 → 1	<i>Uranoscodon superciliosus</i>
		1	0 → 1	<i>T. stolzmanni</i>
		1	0 → 1	15
		1	1 → 2	<i>T. spinulosus</i>
		1	1 → 2	17
		1	1 → 0	<i>Strobilurus torquatus</i>

APPENDIX 3
Changes by Transformation Series for Figure 33—(Continued)

Trans. series	ci	Steps	Character change	Along stem
[48]	0.571	1	0 → 4‡	<i>Uranoscodon superciliosus</i>
		1	0 → 1	4
		1	0 → 2	5
		1	2 → 1‡	13
		1	1 → 3‡	15
		1	3 → 0‡	18
		1	0 → 1‡	19
[49]	0.500	1	0 → 1	7
		1	1 → 2	<i>T. montanus</i>
		1	1 → 0	<i>T. torquatus</i>
[50]	1.000	1	1 → 2	<i>T. oreadicus</i>
		1	0 → 1	<i>T. nanuzae</i>
51	0.250	1	0 → 2	<i>Plica plica</i>
		1	0 → 1	<i>Uranoscodon superciliosus</i>
52	0.500	1	0 → 1	12
		1	1 → 0	<i>Plica umbra</i>
		1	1 → 0	<i>Uracentron azureum</i>
		1	0 → 1	13
53	1.000	1	1 → 0	<i>Plica umbra</i>
54	0.500	1	0 → 1	4
(55)	1.000	1	0 → 1	7
		1	1 → 0	15
56	0.333	1	0 → 1	10
57	0.250	1	0 → 1	8
		1	0 → 1	11
		1	1 → 0	15
58	0.500	1	0 → 1	<i>Uranoscodon superciliosus</i>
		1	0 → 1	<i>T. bogerti</i>
		1	0 → 1‡	16
		1	1 → 0	<i>Strobilurus troquatus</i>
59	0.333	1	0 → 1	<i>T. spinulosus</i>
		1	0 → 1	17
60	1.000	1	0 → 1	<i>Uranoscodon superciliosus</i>
		1	0 → 1	15
		1	1 → 0	19
61	1.000	1	0 → 1	4
62	0.333	1	0 → 1	19
		1	0 → 1	1
		1	1 → 0	<i>T. bogerti</i>
63	1.000	1	1 → 0	19
		1	0 → 1	12
64	0.500	1	1 → 2	<i>Plica plica</i>
		1	0 → 1	<i>Uranoscodon superciliosus</i>
65	1.000	1	0 → 1	17
66	1.000	1	0 → 1	15
67	1.000	1	0 → 1	19
68	0.500	1	0 → 1	1
		1	0 → 1	<i>T. itambere</i>
69	1.000	1	0 → 1	19
			0 → 1	17

APPENDIX 3
Changes by Transformation Series for Figure 33—(Continued)

Trans. series	ci	Steps	Character change	Along stem
70	0.500	2	0 → 2	<i>Uranoscodon superciliosus</i>
		1	0 → 1	16
		1	1 → 2	<i>Plica umbra</i>
[71]	0.500	1	0 → 3	<i>Uranoscodon superciliosus</i>
		1	0 → 1	4
		1	0 → 2	13
		1	2 → 3	<i>Plica umbra</i>
		1	2 → 3	19
		1	0 → 1	<i>T. insulanus</i>
72	0.250	1	0 → 1	<i>T. atacamensis</i>
		1	0 → 1	6
		1	1 → 0	15
		1	0 → 1	19
73	0.250	1	0 → 1	4
		1	0 → 1	<i>Tapinurus semitaeniatus</i>
		1	0 → 1	<i>T. melanopleurus</i>
		1	0 → 1	<i>Uracentron azureum</i>
74	1.000	1	0 → 1	4
75	1.000	1	0 → 1	18
		1	1 → 2	19
76	0.500	1	0 → 1	<i>Uranoscodon superciliosus</i>
		1	0 → 1	<i>Plica umbra</i>
77	1.000	1	0 → 1	<i>Strobilurus torquatus</i>

APPENDIX 4

Apomorphy List by Stem (Taxon) Noted in Figure 33

Transformations noted by a double dagger (‡) are of equally parsimonious placement elsewhere. In the case of terminal taxa even though the character assignment is not unequivocal, the plesiomorphic member of the transformation pair may have alternative placement in the topology of the tree.

Branch	Trans. series	Steps	ci	Change	
1	11	1	1.000	0 → 1	
	12	1	1.000	0 → 1	
	27	1	1.000	0 → 1	
	28	1	0.250	0 → 1	
	44	1	1.000	0 → 1	
	62	1	0.333	0 → 1	
	67	1	1.000	0 → 1	
<i>Uranoscodon superciliosus</i>	2	1	0.500	0 → 1	
	4	1	0.500	0 → 1	
	5	1	0.500	0 → 1	
	19	1	0.250	0 → 1	
	22	1	0.250	0 → 1	
	23	1	0.500	0 → 1	
	30	1	0.333	0 → 1	
	37	1	1.000	0 → 1	
	45	1	0.500	0 → 1‡	
	46	1	0.333	0 → 1	
	47	1	0.333	0 → 1	
	48	1	0.571	0 → 4‡	
	51	1	0.250	0 → 1	
	57	1	0.250	0 → 1	
	59	1	0.333	0 → 1	
	64	1	0.500	0 → 1	
	70	2	0.500	0 → 2	
71	1	0.500	0 → 3		
76	1	0.500	0 → 1		
2	13	1	1.000	0 → 1	
	33	1	1.000	0 → 1	
3	43	1	1.000	0 → 1	
4	48	1	0.571	0 → 1	
	53	1	1.000	0 → 1	
	60	1	1.000	0 → 1	
	71	1	0.500	0 → 1	
	73	1	0.250	0 → 1	
	74	1	1.000	0 → 1	
	<i>T. atacamensis</i>	72	1	0.250	0 → 1
	<i>T. stolzmanni</i>	47	1	0.333	0 → 1
	<i>T. bivittatus</i>	17	1	0.500	0 → 1
	5	1	1	1.000	0 → 1
7		1	1.000	0 → 1	
12		1	1.000	1 → 2	
14		1	1.000	0 → 1	
15		1	0.500	0 → 1	
16		1	1.000	0 → 1	
17		1	0.500	0 → 2	
20		1	1.000	0 → 1	
30		1	0.333	0 → 1	
33		1	1.000	1 → 2	
34		1	1.000	0 → 1	
35		1	1.000	0 → 1	

APPENDIX 4
Apomorphy List by Stem (Taxon) Noted in Figure 33—(Continued)

Branch	Trans. series	Steps	ci	Change
	42	1	0.400	0 → 1‡
	48	1	0.571	0 → 2
<i>T. nanuzae</i>	22	1	0.250	0 → 1
	26	1	1.000	0 → 1
	50	1	1.000	0 → 1
6	25	1	0.333	0 → 1
	42	1	0.400	1 → 2‡
	45	1	0.500	0 → 1
	72	1	0.250	0 → 1
7	49	1	0.500	0 → 1
	54	1	0.500	0 → 1
8	56	1	0.333	0 → 1
<i>T. itambere</i>	68	1	0.500	0 → 1
9	31	1	0.500	0 → 1
10	55	1	1.000	0 → 1
<i>T. hispidus</i>	21	1	0.333	0 → 1
11	56	1	0.333	0 → 1
<i>T. montanus</i>	49	1	0.500	1 → 2
12	51	1	0.250	0 → 1
<i>T. torquatus</i>	49	1	0.500	1 → 0
13	29	1	0.667	0 → 1
	35	1	1.000	1 → 2
	41	1	0.667	0 → 1‡
	48	1	0.571	2 → 1‡
	52	1	0.500	0 → 1
	63	1	1.000	0 → 1
	71	1	0.500	0 → 2
14	6	1	1.000	0 → 1
	24	1	0.250	0 → 1
	39	1	1.000	0 → 1
<i>Tapinurus semitaeniatus</i>	3	1	1.000	0 → 1
	6	1	1.000	1 → 2
	18	1	0.500	0 → 1
	19	1	0.250	0 → 1
	21	1	0.333	0 → 1
	29	1	0.667	1 → 2
	31	1	0.500	1 → 0
	32	1	1.000	0 → 1
	73	1	0.250	0 → 1
<i>T. bogerti</i>	15	1	0.500	1 → 0
	28	1	0.250	1 → 0
	57	1	0.250	0 → 1
	62	1	0.333	1 → 0
15	42	1	0.400	2 → 1
	47	1	0.333	0 → 1
	48	1	0.571	1 → 3‡
	54	1	0.500	1 → 0
	56	1	0.333	1 → 0
	59	1	0.333	0 → 1
	65	1	1.000	0 → 1
	72	1	0.250	1 → 0
<i>T. melanopleurus</i>	73	1	0.250	0 → 1

APPENDIX 4
Apomorphy List by Stem (Taxon) Noted in Figure 33—(Continued)

Branch	Trans. series	Steps	ci	Change	
<i>T. spinulosus</i>	17	1	0.500	2 → 0	
	28	1	0.250	1 → 0	
	41	1	0.667	1 → 0‡	
	47	1	0.333	1 → 2	
	58	1	0.500	0 → 1	
	16	5	1	0.500	0 → 1
		8	1	1.000	0 → 1
		19	1	0.250	0 → 1‡
		21	1	0.333	0 → 1
		23	1	0.500	0 → 1
		24	1	0.250	0 → 1‡
		29	1	0.667	1 → 0
		41	1	0.667	1 → 2
		57	1	0.250	0 → 1‡
		70	1	0.500	0 → 1
17	10	1	1.000	0 → 1	
	22	1	0.250	0 → 1	
	47	1	0.333	1 → 2	
	58	1	0.500	0 → 1	
	64	1	0.500	0 → 1	
	69	1	1.000	0 → 1	
<i>Plica plica</i>	24	1	0.250	1 → 0‡	
	46	1	0.333	0 → 1	
	50	1	1.000	0 → 2	
	63	1	1.000	1 → 2	
<i>P. umbra</i>	2	1	0.500	0 → 1	
	4	1	0.500	0 → 1	
	19	1	0.250	1 → 0‡	
	25	1	0.333	1 → 0	
	42	1	0.400	1 → 0	
	51	1	0.250	1 → 0	
	52	1	0.500	1 → 0	
	70	1	0.500	1 → 2	
	71	1	0.500	2 → 3	
	76	1	0.500	0 → 1	
	18	38	1	1.000	0 → 1
		48	1	0.571	3 → 0‡
75		1	1.000	0 → 1	
<i>S. torquatus</i>	47	1	0.333	1 → 0	
	57	1	0.250	1 → 0‡	
	77	1	1.000	0 → 1	
	19	17	1	0.500	2 → 0
		18	1	0.500	0 → 1
25		1	0.333	1 → 0	
30		1	0.333	1 → 0	
36		1	1.000	0 → 1	
40		1	1.000	0 → 1	
42		1	0.400	1 → 0	
46		1	0.333	0 → 1	
48		1	0.571	0 → 1‡	
59		1	0.333	1 → 0	
61	1	1.000	0 → 1		

APPENDIX 4
Apomorphy List by Stem (Taxon) Noted in Figure 33—(Continued)

Branch	Trans. series	Steps	ci	Change
	62	1	0.333	1 → 0
	66	1	1.000	0 → 1
	68	1	0.500	0 → 1
	71	1	0.500	2 → 3
	72	1	0.250	0 → 1
	75	1	1.000	1 → 2
<i>Uracentron azureum</i>	9	1	1.000	0 → 1
	28	1	0.250	1 → 0
	51	1	0.250	1 → 0
	73	1	0.250	0 → 1
<i>Uracentron flaviceps</i>	22	1	0.250	0 → 1
	24	1	0.250	1 → 0‡
<i>T. insulanus</i>	71	1	0.500	0 → 1
<i>T. oreadicus</i>	49	1	0.500	1 → 2

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates*, *Bulletin*, and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024.