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COMPARATIVE STUDIES OF SUPRAOCULAR LEPIDOSIS IN SQUAMATA (REPTILIA) AND ITS RELATIONSHIPS WITH AN EVOLUTIONARY TAXONOMY

ESTUDIOS COMPARATIVOS DE LA LEPIDOSIS SUPRA-OCULAR EN SQUAMATA (REPTILIA) Y SU RELACIÓN CON LA TAXONOMÍA EVOLUCIONARIA

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RESUMEN

Observaciones morfológicas previas sobre un gran número de especies permiten establecer una correspondencia entre la peculiaridad de los patrones sistemáticos de las escamas supraoculares de Squamata y la posición evolutiva de cada taxón considerado en los cladogramas propuestos por Estes et al. (1988). Aparte del significado biológico general de estos hallazgos, incluso para discutidas orientaciones taxonómicas, la lepidosis supraocular llega a refrendar una decisión sistemática con su evidencia. Así, en Iguania, la familia Leiosauridae, propuesta por Frost et al. (2001), aparece sostenida hasta en el detalle de su división en las subfamilias Leiosaurinae y Enyaliinae. Siempre en Iguania Pleurodonta se evidencian ejemplos como los inconfundibles patrones de escamas supraoculares de Opluridae, Leucocephalidae, Polychrotidae, Tropiduridae. A nivel específico la interdependencia en Iguanidae de los géneros Iguana, Cercosaura, Brachylophus, Conolophus, puede llevar a postular pretéritos acontecimientos paleogeográficos. También amerita énfasis la llamativa separación, según este criterio morfológico, entre Iguania y Scleroglossa, la uniforme lepidosis de centenares de Gekkota, o la excepcional fisonomía de Autarchoglossa, en sus ramas tan individualizadas de Scincomorpha (Lacertoidea; Teiioidea; Scincoidea) o Anguimorpha.

***Palabras clave:** diagnosis, escamas supraoculares, patrón específico lepidosis, Pleurodonta, Squamata, taxonomía*

SUMMARY

Former observations on characteristic patterns of supraocular scutellation in different specific or supraspecific taxa of Squamata are extended and analyzed in this general critical review. A relationship between a defined morphological supraocular lepidosis in a particular taxon and its evolutionary position in a classificatory system, such as the cladograms obtained by Estes *et al.* (1988), was tested and confirmed. Supraocular scales of Squamata are not morphological elements at random, but can be assumed as morphological scale characters, useful in systematic comparative examinations and able to strengthen some discussed new systematic assessments, such as the family status of Leiosauridae and its subfamilies in Pleurodont Iguanians, proposed by Frost et al. (2001), as well as in several other cases.

Key words: Squamata, supraocular scutellation, specific lepidosis pattern, diagnosis, Pleurodonta, taxonomy

INTRODUCTION

The selection of significant somatic morphological characters (shape, size, structure) will play an essential role in providing a systematic herpetological arrangement, at least to species level: furthermore it can apply also to more elevated ranks of the herpetological classification. We are pointing out here some interesting aspects of the so-called lepidosis, or cutaneous scale covering of Reptilia, mainly in Lacertilian lizards. More exactly, the differentiated scales bilaterally located in the supraocular region of the head, bounded inside by the orbital semicircles, and by the ciliary eye border outside (Figure 1). Given the noticeable position of these supraocular scales in the head scutellation of Squamata, their presence has generally been reported in many diagnostic descriptions of species. Nevertheless, no true emphasis was ever placed on their peculiar taxonomic significance: either as an important generic characteristic structure of the dorsal head lepidosis, or as distinctive supraocular patterns in separated systematic groups, from different genera to families and higher categories. A preliminary paper was provided on this matter (Cei, 2003), dealing with supraocular scales in species and genera of Iguania, as

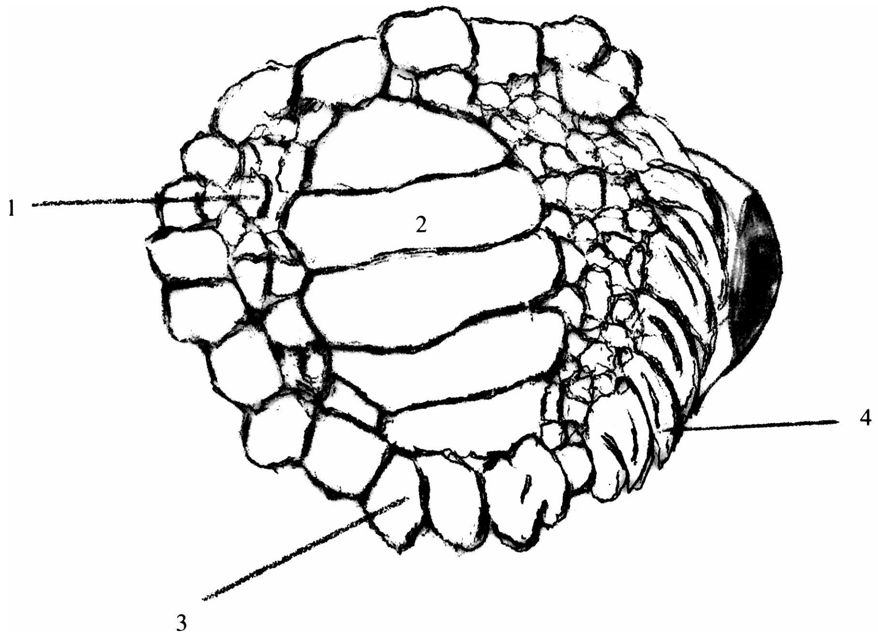

Figure 1. Sketched fundamental morphology of supraocular scutellation in Squamata, Pleurodonta: 1. supraorbital semicircles, 2. supraocular scales, 3. intermediate supraorbital scales and 4. superimposed superciliaries

Figura 1. Esquema fundamental de la morfología de la escutelación supraocular en Squamata, Pleurodonta: 1. semicírculos supraorbitales, 2. escalas supraoculares, 3. escalas supraorbitales intermedias y 4. superciliares superimpuestos

well as in some far-away taxonomic categories, such as Scleroglossa Teiid lizards. Thus, considering the remarkable number of past and recent species descriptions, a detailed review and discussion of such a noticeable but still disregarded anatomical peculiarity could be a very interesting job, postulating a distribution pattern not at random but in agreement with the phylogenetic subdivisions of well-known modern classificatory essays.

Some isolated reports about specific supraocular scutellation in Reptiles, besides a preliminary paper (Cei, 2003), deal with circumorbitals in one row or in two rows between supraoculars and median head shields, as emphasized in Frost‘s (1992) taxonomic revision of *Tropidurus* groups of lizards that points out discrimination among the genera *Uranoscodon*, *Microlophus*, *Plesiomicrolophus* and *Tropidurus*. Likely in Etheridge‘s (1970) comparative research the systematic differences in supraciliaries were suitably applied to discriminate *Plica* and *Uranoscodon* from other members of the *Tropidurus* groups. However, apart from these interesting but limited citations, a whole zoological discussion and critical valuation of lacertilian supraocular scutellation is yet wanting to our knowledge. The present work will attempt to reach better and conclusive information on such a suggestive and little analyzed subject.

MATERIAL AND METHOD

Given the aim of this work, its outcome is a detailed representation of the postulated relationships between the supraocular scutellation patterns and the taxonomic categories of Squamata. Our comparative graphic documentation, exposed in Figures, was mainly obtained from careful observations and drawings of preserved specimens, or in some case from careful adaptations of controlled reproductions by reliable authors. The available materials above all have been the specimens of a personal collection (JMC-DC: José M. Cei Diagnostic Collection), occasionally complemented by past studies of species from the Herpetological Collections of some Museums or Scientific Institutions whose list and acronyms are following. IBA-UNC: Collections of the Instituto de Biología Animal, Universidad Nacional de Cuyo, Mendoza, Argentina; MZUSP: Museo de Zoologia, Universidade de São Paulo, Brasil; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, USA; NMNH: National Museum of Natural History, Smithsonian Institution, Washington, USA; FMNH: Field Museum of Natural History, Chicago, USA; MNHN Paris: Museum Nationale Histoire Naturelle, Paris; UNNE: Universidad Nacional del Nordeste, Corrientes, Argentina.

Given the Figures including the total samples drawn that support our present report and discussion, a separated list of the examined specimens would be prolix and unnecessary. Moreover the general localities of samples were opportunely indicated in the Figures. When it was necessary, morphological details of the lizards were drawn under a dissecting microscope. Peter‘s Dictionary (1964) was a reference for morphological and anatomical nomenclature, as well as the several Etheridge‘s papers, i.e. his *Ctenoblepharis adspersa* redescription (1995). The drawings of the Figures have been all more or less slightly magnified: we believe that individual magnification of symbols in every identified drawing scale is useless to our purposes. Besides the specimens documented in the Figures, hundreds of specimens corresponding to the patterns have been observed and compared, for improving the truthfulness and significance of our samples.

Among the most important literature supporting the harvesting, arranging and discussion of our representative samples, we wish to highlight the useful, good or outstanding papers or reviews by Anderson (1999), Angel (1942), Blarc (1977), Brygoo (1971, 1978), Dixon (1973), Donnelly and Myers (1991), Greer (1970), Grismer *et al.* (1994), Haas and Werner (1969), Halliday and Adler (2002), Hoogmoed (1973), Kluge (1974), Leviton *et al.* (1992), Mertens (1958, 1959), Pregill (1992), Ruibal (1964), Savage (1963), Tayer (1956), Van Demburg (1978), Vanzolini *et al.* (1965, 1980) and Wiens (1993).

RESULTS

Analytical review of comparative reports on supraocular lepidosis in Squamata

As pointed out in the Introduction, the aim of this research was to put in evidence a correlative relationship between a classificatory system and a significant set of data on supraocular scutellation in Squamata reptiles. The phylogenetic indented taxonomy exhibited in the valuable conclusive statements by Estes *et al.* (1988) was considered as a suitable model (Figure 2), together with the reassessment of Iguania by Frost *et al.* (2001). Such taxonomy has been followed here for comparison with our detailed morphological observations, far away from any aprioristic personal opinion. Then, without disregarding other interesting systematic contributions, as the recent paper by Schulte *et al.* (2003), in full agreement with our findings, we recognize the taxon Pleurodonta and its included families as in the mentioned Frost *et al.*'s (2001) arrangement. On the contrary, the opposite general taxon Iguanidae (*sensu* Boulenger, 1895) postulated in the paper by Schulte *et al.*, based on bio-molecular and morphological researchs, is fully discordant with our results.

In the following 27 Figures, specific supraocular scutellation patterns belonging to genera and families of the major taxa listed in the indented taxonomy are reported. Evidently it was impossible to check the thousands of living species of lizards, but significantly representative drawings of enough generic and specific taxa, are provided.

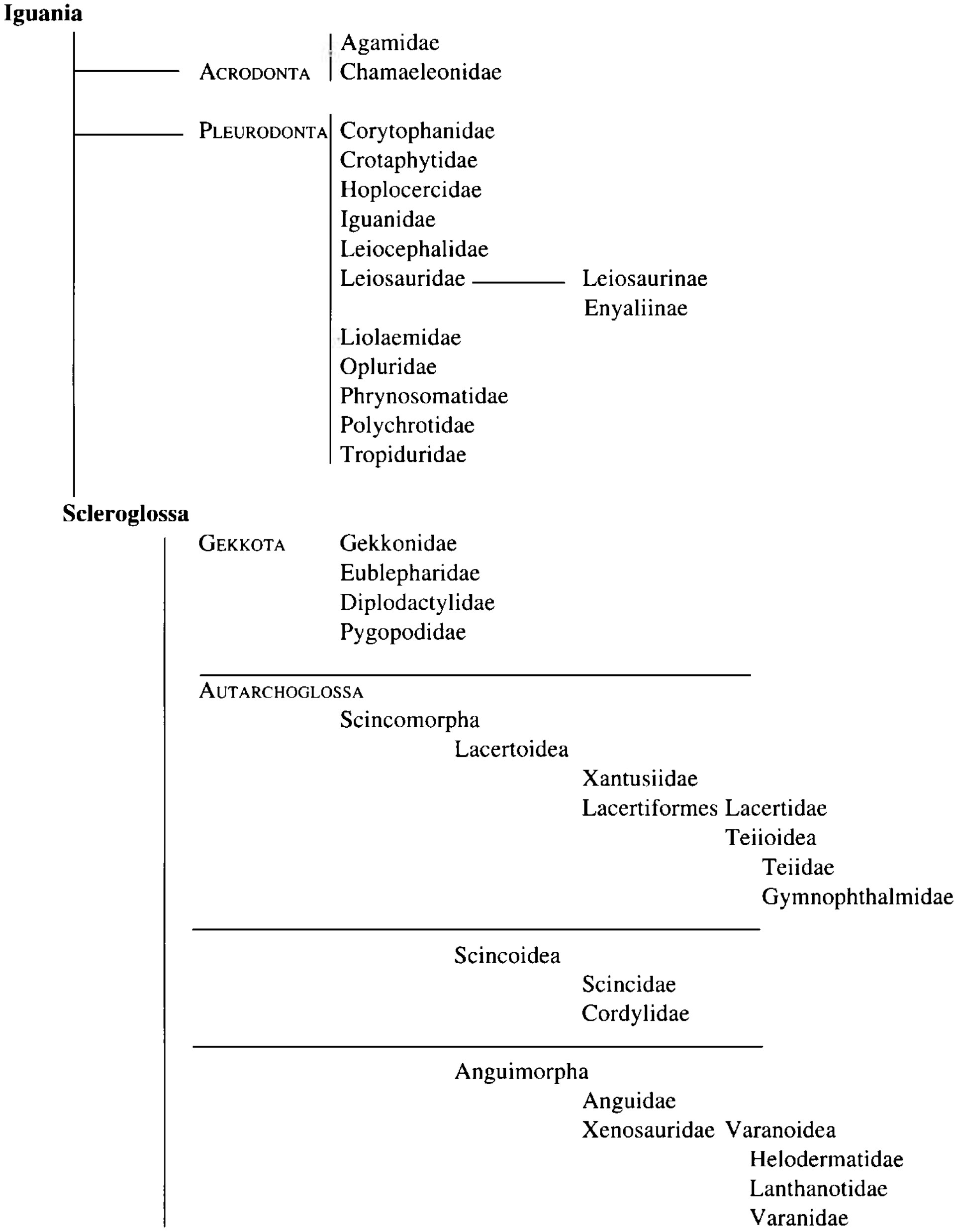

Figure 2. Squamata: phylogenetic indented taxonomy according to Estes *et al.* (1988). The taxon Iguania was adapted in accordance with Frost *et al.* (2001)

Figura 2. Squamata: taxonomía filogenética indentada según Estes et al. (1988). El taxón Iguania fue adoptado de acuerdo con Frost et al. (2001)

Two opposed major systematic categories stand out in the Squamata indented taxonomy: Iguania and Scleroglossa, sustained by anatomical, mostly osteological characters. Acrodonta and Pleurodonta are a subdivision of Iguania, likewise countersigned by osteological differences. We can anticipate that a fairly simple supraocular scutellation belongs to Acrodonta, but a remarkable variety of differentiated supraocular scales is shown by the Pleurodonta families.

Agamidae and Chamaeleonidae are two large and widespread Acrodont families. With more than 50 genera and 400 species, Agamidae are found in the African, Euro-Asiatic and Australian continents, with an extraordinary morpho-ecological diversification. But a relatively uniform covering of rudely roundish or enlarged scales appears in their supraocular region, the circumorbital semicircles being scarcely evident and the supraciliaries moderately prominent or sharp-pointed, with some important exceptions like the smart or spiny supraciliaries of *Lyriocephalus*, *Phrynocephalus* and *Draco*. In Figure 3 several examples of these lizards are given, significant enough for the multiple species of the Acrodonta generic taxa. Representativeness of these patterns has been strengthened by their direct control in many other agamid specimens, or by other careful documentary reports by reliable authors. Agamid patterns of Figure 3 have been compared and confirmed in other 15 African and Indian taxa of the genus *Agama*, in 15 Asiatic taxa of *Draco*, in 4 Indian taxa of *Calotes* whose irregular supraocular scales appear noticeably bulky, in 70 Australian taxa of the genera *Goniocephalus*, *Amphibolurus*, *Tympanocryptis*, *Chelosania*, *Dipariphera*, *Physignathus* and *Lophognathus*.

Chamaeleonidae, a specialized, mostly arboreal family, with more than 130 species but only 6 genera are distributed in Africa, Madagascar, Arabia, India and Sri Lanka. The protruding eyes of Chameleons, covered with scaly lids, are unique: in Figure 4, the supraoculars of *Chamaeleo* and *Brookesia* from Madagascar are emphasized. A fundamental analogy between the *Chamaeleo* pattern and the agamid supraocular scutellation is evident from its general lining of irregular scales, distinct supraciliary border and almost indistinguishable inner circumorbital semicircles. The examples of *Brookesia* taxa in Figure 4 point out the peculiar feature of dermal cranial ossifications in these advanced

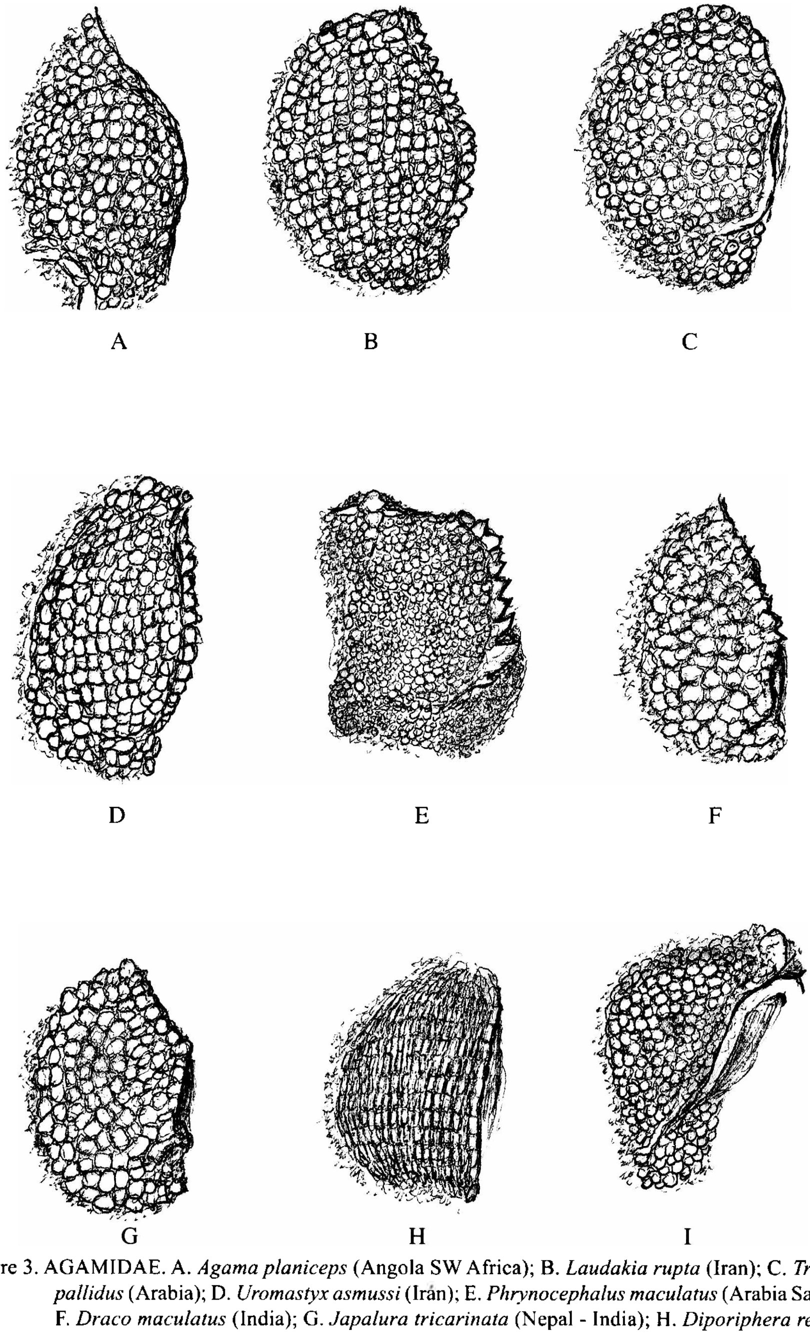

Figure 3. AGAMIDAE. A. *Agama planiceps* (Angola SW Africa); B. *Laudakia rupta* (Iran); C. *Trapelus pallidus* (Arabia); D. *Uromastyx asmussi* (Iran); E. *Phrynocephalus maculatus* (Arabia Saudita); F. *Draco maculatus* (India); G. *Japalura tricarinata* (Nepal - India); H. *Diporiphera reginae*; I. *Amphibolurus vadnappa* (S Australia)

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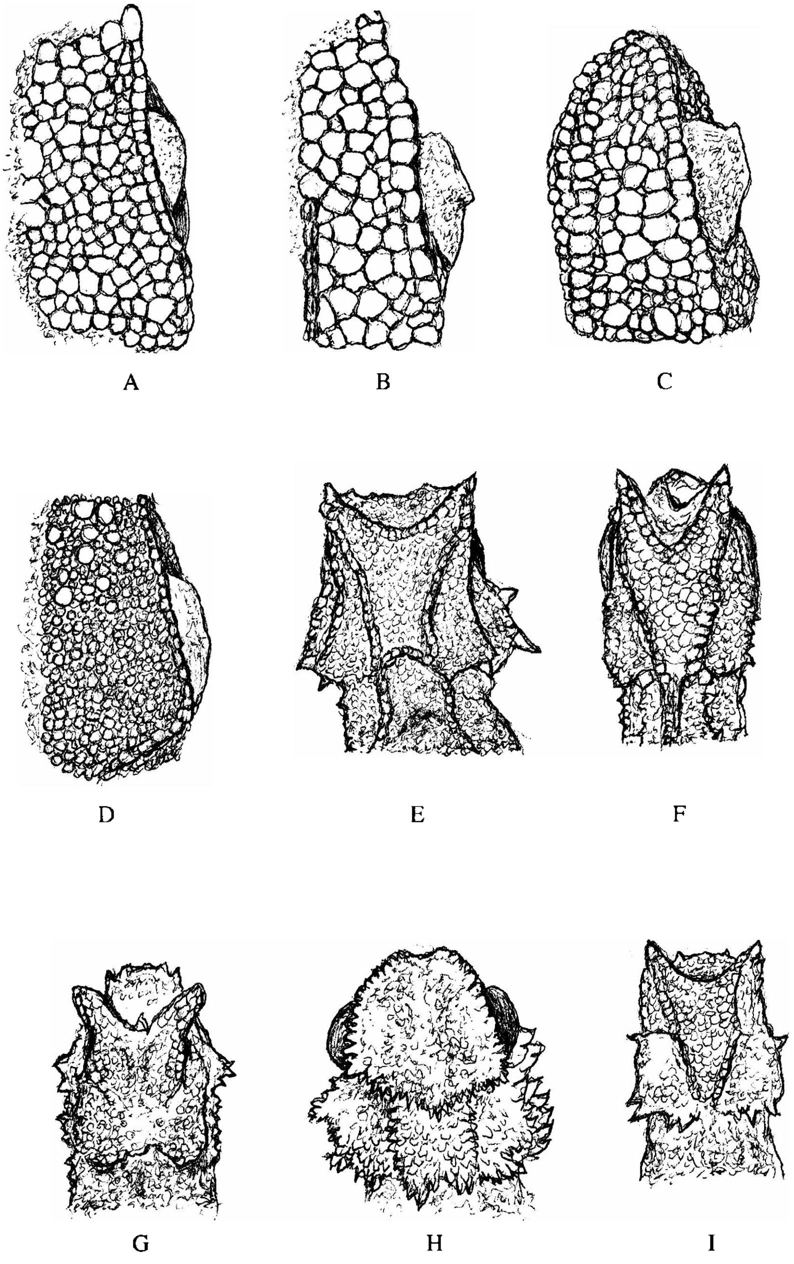

Figure 4. CHAMAELEONIDAE. A. *Chamaeleo bifidus* (E Madagascar); B. *Chamaeleo cephalolepis* (I. Comore-Madagascar); C. *Ch. lateralis* (Madagascar); D. *Chamaeleo cucullatus* (NE Madagascar); E. *Brookesia decaryi* (Madagascar); F. *Brookesia thieli* (Madagascar); G. *Brookesia ebenaui* (Madagascar); H. *B. perarmatz* (Madagascar); I. *Brookesia stumpffi* (Madagascar)

Figura 4. CHAMAELEONIDAE. A. Chamaeleo bifidus (E Madagascar); B. Chamaeleo cephalolepis (I. Comore-Madagascar); C. Ch. lateralis (Madagascar); D. Chamaeleo cucullatus (NE Madagascar); E. Brookesia decaryi (Madagascar); F. Brookesia thieli (Madagascar); G. Brookesia ebenaui (Madagascar); H. B. perarmatz (Madagascar); I. Brookesia stumpffi (Madagascar) chamaeleontids, leading to a striking masking of their supraocular scale coating, here illustrated for several species of uncommon lizards from the isolated Madagascar.

The partition of the Pleurodonta evolutionary stock is remarkable. Also remarkable are our findings about a corresponding association between different supraocular scale patterns and the different families listed in the indented taxonomy exposed in Figure 2. These families have been discussed in a serial issue of herpetological contributions: from the paper by Frost and Etheridge (1989) to the successive works by Frost (1992) and Frost *et al.* (2001). Without any intentional attempt of phylogenetic references, every family shall be analyzed now with regard to its supraocular lepidosis.

In Figure 5, upper row, Leiocephalidae is only limited to the genus *Leiocephalus* from West Indies. Formerly related to Tropiduridae, its family status was established by Frost *et al.* (2001). In its different insular taxa, the well differentiated supraocular lepidosis prevailing in Pleurodonta is maintained, with minor specific differences. A longitudinal central row of large supraocular scale stretches is evident between a narrow row of supraciliaries and moderate, regular circumorbital semicircles inside. In the same Figure 5, midmost and inferior rows, representative of the family Polychrotidae, are shown: *Polychrus* with few neotropical species and *Anolis* with more than 230 species, spread with several characteristic groups from south eastern United States to West Indies, northern Mexico, southwards through Central and South America to about 20°S latitude. A true "Polychrotidae" pattern (*sensu* Frost *et al.*, 2001) is recognizable in the Figure 5, bearing impressive large circumorbital semicircles and few very variable internal, small shields, surrounded by many minute scales, and very diminished supraciliaries outside. The foreseeable specific variation in the multiple *Anolis* is emphasized in Figure 5 by some taxa from Cuba and Colombia.

Two families with few genera and species are registered in the upper and inferior rows of Figure 6. In Opluridae from Madagascar and Comore islands, the monotypic genus *Chalarodon* and some species of *Oplurus* keep a rather simple supraocular pattern reminiscent of Acrodont scutellations. Both very similar examples of *Oplurus* in this Figure exhibit irregular supraocular scales decreasing from their almost

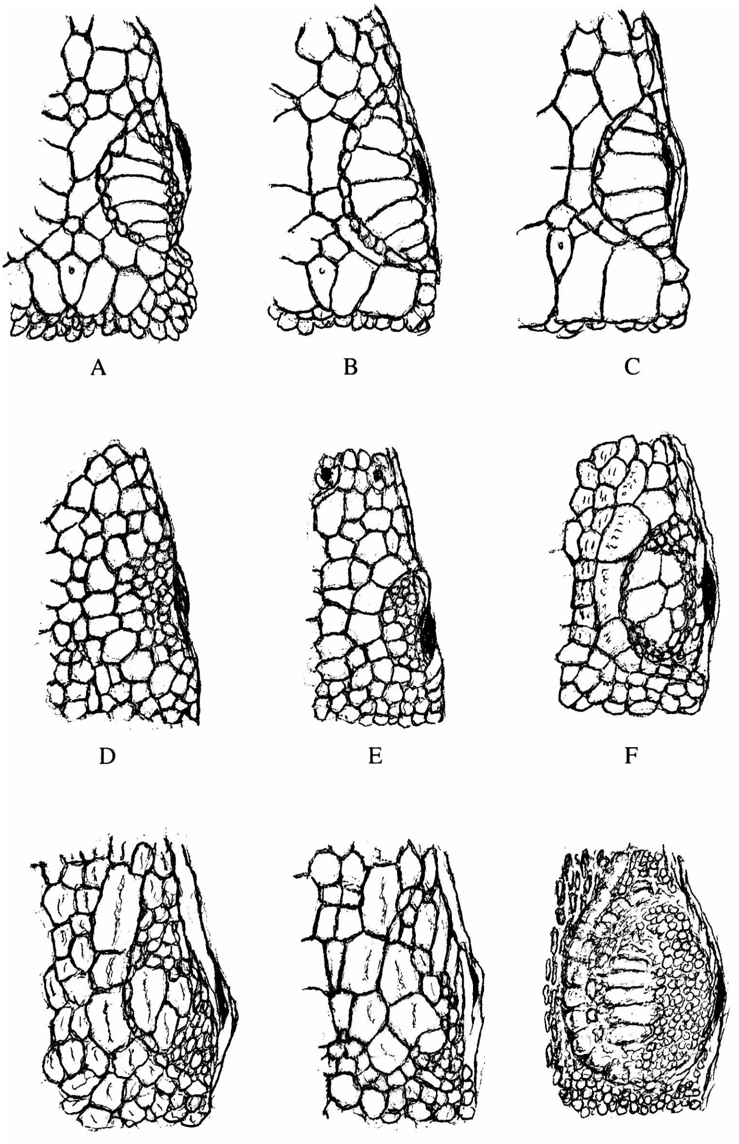

Figure 5. LEIOCEPHALIDAE. A. *Leiocephalus psammodromus* (W Indies - Caicos Isl.); B. *Leiocephalus stictigaster* (Cuba); C. *L. barahonensis* (Republica Dominicana);
POLYCHROTIDAE. D. *Polychrus acutirostris* (Pernambuco, Brasil); E. *Anolis isolepis* (Guantanamo, Cuba); F. *Anolis alutaceus* (Guantanamo, Cuba); G. *A. cyanopleurus* (Guantanamo, Cuba); H. *Anolis spectrum* (Matanzas, Cuba); I. *Anolis biporcatus* (Colombia)

Figura 5. LEIOCEPHALIDAE. A. Leiocephalus psammodromus (W Indies - Caicos Isl.); B. Leiocephalus stictigaster (Cuba); C. L. barahonensis (Republica Dominicana);
POLYCHROTIDAE. D. Polychrus acutirostris (Pernambuco, Brasil); E. Anolis isolepis (Guantanamo, Cuba); F. Anolis alutaceus (Guantanamo, Cuba); G. A. cyanopleurus (Guantanamo, Cuba); H. Anolis spectrum (Matanzas, Cuba); I. Anolis biporcatus (Colombia)

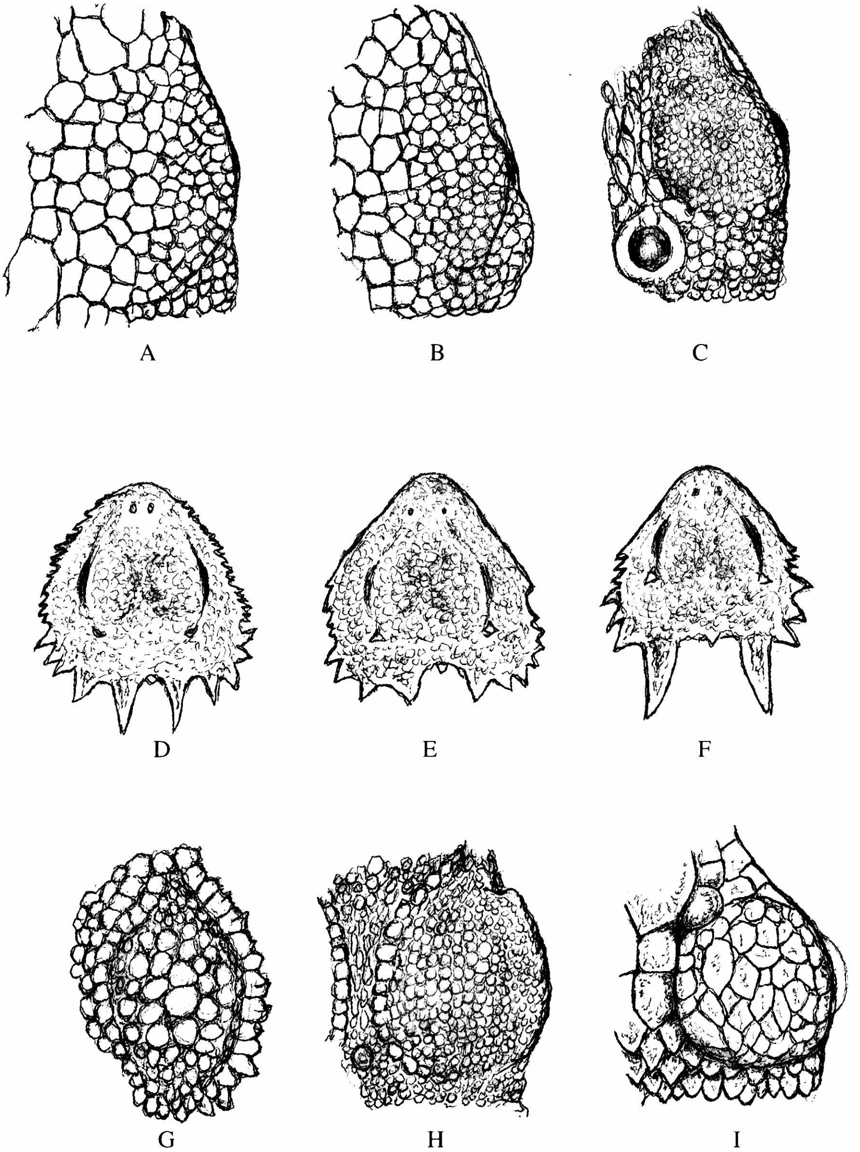

Figure 6. OPLURIDAE. A. *Oplurus cyclurus* (Madagascar); B. *Oplurus fierinensis* (Madagascar); C. *Chalarodon madagascariensis* (Madagascar).
PHRYNOSOMATIDAE. D. *Prhynosoma modestum* (New Mexico, USA); E. *Prhynosoma douglassi* (Montana, USA); F. *Prhynosoma cornutum* (Texas, USA).
CORYTOPHANIDAE. G. *Corytophanes cristatus* (Costa Rica); H. *Basiliscus plumifrons* (Costa Rica); I. *Laemanctus serratus* (Mexico)

Figura 6. OPLURIDAE. A. Oplurus cyclurus (Madagascar); B. Oplurus fierinensis (Madagascar); C. Chalarodon madagascariensis (Madagascar).
PHRYNOSOMATIDAE. D. Prhynosoma modestum (New Mexico, USA); E. Prhynosoma douglassi (Montana, USA); F. Prhynosoma cornutum (Texas, USA).
CORYTOPHANIDAE. G. Corytophanes cristatus (Costa Rica); H. Basiliscus plumifrons (Costa Rica); I. Laemanctus serratus (Mexico)

indistinct circumorbital semicircles to their equally indistinguishable supraciliaries. In *Chalarodon madagascariensis* a quite uniform supraocular layer of small rounded scales is better delimited by narrow circumorbital semicircles and a recognizable border of very small supraciliaries. Corytopharidae from Mexico and Central America likewise include only three genera with few species each. Irregular supraocular scales are broader in *Corytophanes* and *Laemanctus*, small in *Brasiliseus*. Circumorbital semicircles and supraciliaries, sharp-pointed in *Corytophanes*, stand out in this family. Striking in central row of Figure 6 is the undifferentiated supraocular surface of the horny skull roof of some *Phrynosoma*, odd genus of the family Phrynosomatidae, exposed in the following Figures. Several genera, found from south western North America southward to Panama, were assembled in Phrynosomatidae.

In Figure 7 the mentioned "Pleurodont pattern" is recognizable for the about fifty taxa of the spiny *Sceloporus*, distinguished by their expanded circumorbital semicircles and prominent superciliaries, surrounding 5-6 broad supraocular scales. A somewhat diverging morphology can be observed, as in *Sceloporus orcutti* and *S. olivaceus*. Interesting to remark is the finding of these kinds of supraocular scutellation here reported for other genera of such heterogeneous family, like *Uma*, *Uta*, *Holbrookia*, with analogous geographic distribution. Likewise related but peculiar supraocular lepidosis may be pointed out for the arboreal *Urosaurus* (Figure 8), so carefully reviewed by Wiens (1993) for the same arid environment. Their variable six broad longitudinal supraocular scales, the other adherent rows of minor scales as well as the shape and size of circumorbital semicircles and supraciliaries, support an unmistakable generic identity. Similar valuation can be made for the related *Petrosaurus* species inhabiting mainly the same Californian territories. Even in Figure 8, inferior row, the supraocular lepidosis in Crotaphytidae can be observed. Collared lizards and Leopard lizards (*Crotaphytus* and *Gambelia*) also from the subdesert rocky or sandy habitats of southwestern North America are unmistakable for their nearly smooth supraocular covering by very minute circumorbital semicircles and sprinkled by some insignificant scales.

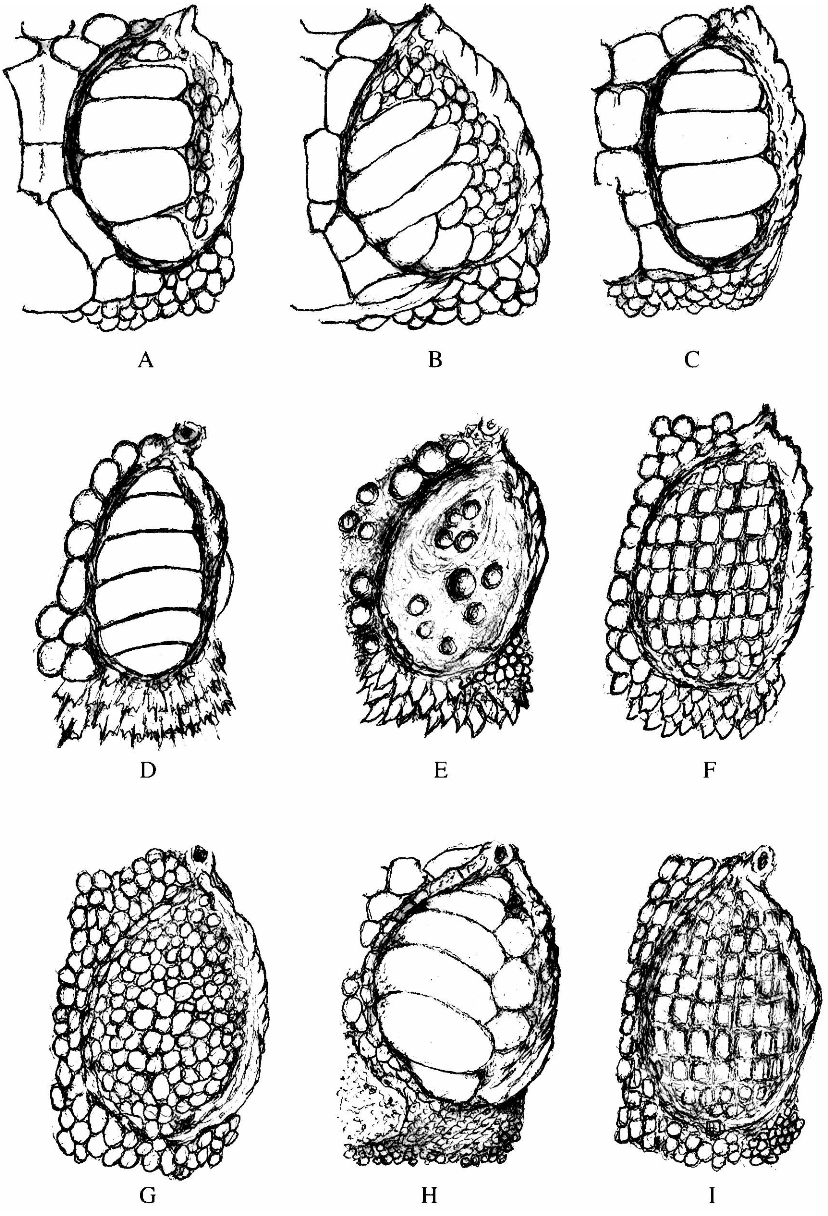

Figure 7. PHRYNOSOMATIDAE. A. *Sceloporus merriami* (Texas, USA); B. *Sceloporus poinsetti* (Texas, USA); C. *Sceloporus clarki* (Arizona, USA); D. *S. magister* (S California, USA); E. *S. orcutti* (S. California, USA); F. *Sceloporus olivaceus* (Texas, USA); G. *Uma notata* (S. California, USA); H. *Uta stamburiana* (S. California, USA); I. *Holbrookia texana* (Texas, USA)

Figura 7. PHRYNOSOMATIDAE. A. Sceloporus merriami (Texas, USA); B. Sceloporus poinsetti (Texas, USA); C. Sceloporus clarki (Arizona, USA); D. S. magister (S California, USA); E. S. orcutti (S. California, USA); F. Sceloporus olivaceus (Texas, USA); G. Uma notata (S. California, USA); H. Uta stamburiana (S. California, USA); I. Holbrookia texana (Texas, USA)

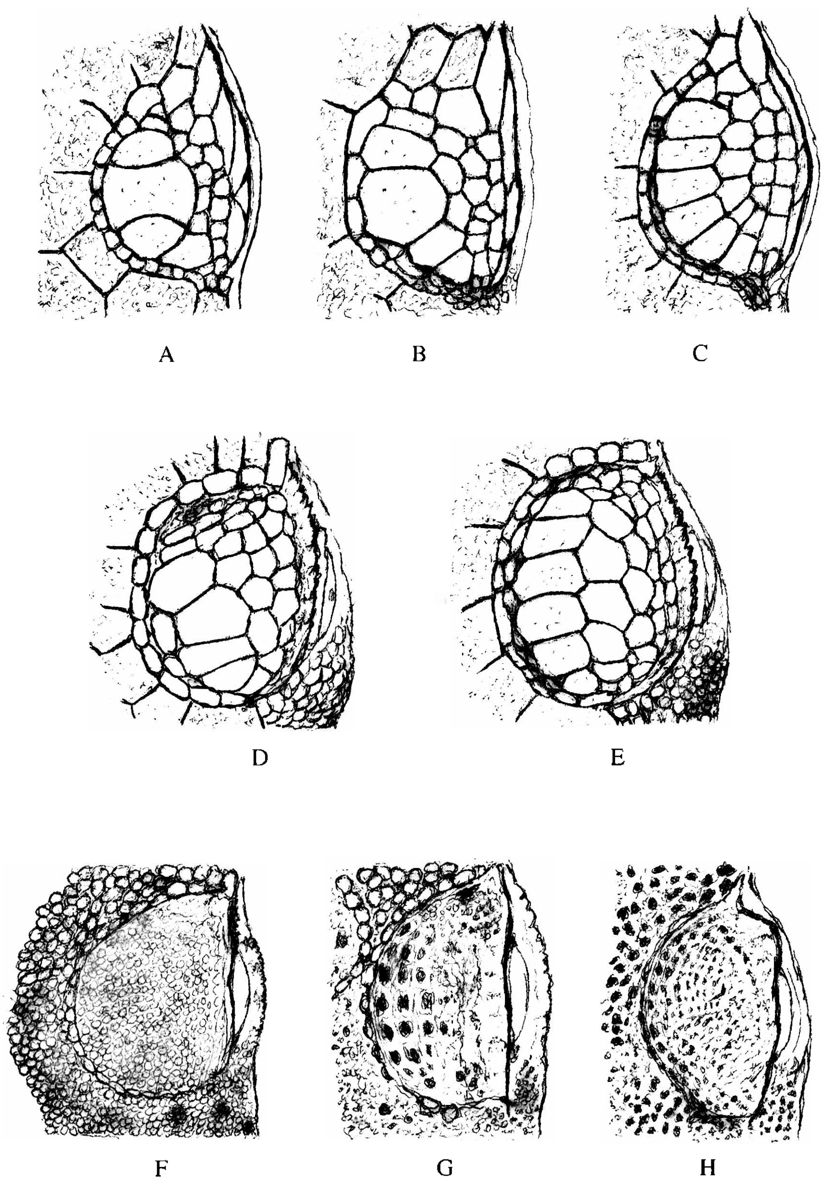

Figure 8. PHRYNOSOMATIDAE. A. *Urosaurus ornatus* (Arizona, USA); B. *Urosaurus nigricaudus* (Baja California, USA); C. *Urosaurus graciosus* (California, USA); D. *Petrosaurus mearnsi* (California, USA); E. *Petrosaurus thalassinus* (California, USA).

CROTAPHYTIDAE. F. *Crotaphytus insularis* (S. California, USA); G. *Crotaphytus collaris* (Texas, USA); H. *Gambelia wislizenii* (Baja California, USA)

Figura 8. PHRYNOSOMATIDAE. A. Urosaurus ornatus (Arizona, USA); B. Urosaurus nigricaudus (Baja California, USA); C. Urosaurus graciosus (California, USA); D. Petrosaurus mearnsi (California, USA); E. Petrosaurus thalassinus (California, USA).

CROTAPHYTIDAE. F. Crotaphytus insularis (S. California, USA); G. Crotaphytus collaris (Texas, USA); H. Gambelia wislizenii (Baja California, USA)

Two families of Pleurodonta with a common general supraocular lepidosis are documented in Figure 9. Belonging to the neotropical Hoplocercidae, with a dozen species, the three queer genera *Hoplocercus*, *Morunasaurus* and *Enyalioides* show always very distinct circumorbital semicircles and supraciliaries, sharp pointed in *Enyahioides*. Supraocular scales are undifferentiated, but with three central quadrangular rows in *Morunasaurus*. Similar lepidosis, though with visible tendency to polymorphism is shown by the interesting taxon Iguanidae (*sensu* Frost *et al.*, 2001), whose genera hold no more than two species each.

Minor differences among the South American *Iguana*, *Cercosaura* and *Dipsosaurus* depend upon the shape and size of supraocular scales, whose more or less regular rows are encircled by evident supraciliaries, and behind by circumorbital semicircles, very enlarged in *Iguana*. They show the differences between the almost undifferentiated probably primitive patterns of the insular Pacific *Brachylophus* and *Conolophus*, and the more differentiated lepidosis in *Iguana iguana* from neotropical forests. Evolutionary factors of primeval distribution in geological times are likely related with the actual conservative conditions of the isolated insular taxa as the Polynesian lizards (*Brachylophus fasciatus*, *B. vitiensis*) or the peculiar *Conolophus* from the Galapagos Archipelago.

The important family Liolaemidae, exemplified in Figures 10-11, was also established in the cited assessment by Frost *et al.* (2001): it comprises the genera *Ctenoplepharis*, *Phymaturus* and *Liolaemus* from southern South America. As stated by Etheridge (1995) in his redescription of *Ctenoblepharis adspersa* from desert landscapes of Peru, the unresolved relationships of such highly derived arenicolous reptiles with *Phymaturus* and *Liolaemus* are emphasized as differential characters by their small, subequal supraoculars. That is congruent with our drawing in Figure 10. Other drawings illustrate several species of the rock-climbing genus *Phymaturus*, all similar enough for the scarcely differentiated supraocular scutellation. Notwithstanding, the species of the *patagonicus* group (those drawn here are: *indistinctus*, *patagonicus*, *somuncurensis*, *payuniae*) have more enlarged supraorbital scales along the circumorbital semicircles. *Liolaemus* assembles about 160 taxa, mainly Andean and Sub-Andean in many cases likely of Pleistocene or post-glacial

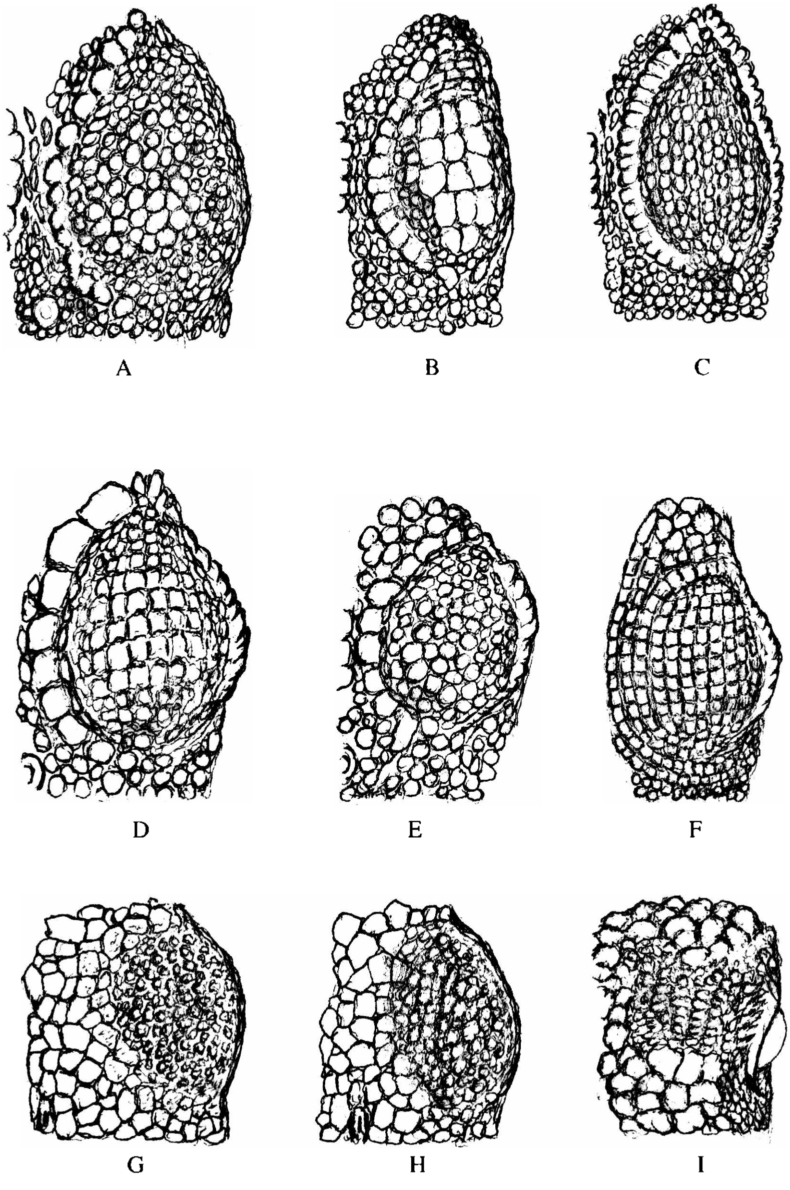

Figure 9. HOPLOCERCIDAE. A. *Hoplocercus spinosus* (Brazil); B. *Morunasaurus annularis* (Rio Santiago, Ecuador): C. *Enyalioides heterolepis* (Ecuador).
IGUANIDAE. D. *Iguana iguana* (Brazil); E. *Cercosaura similis* (Central America); F. *Dipsosaurus dorsalis* (South California, USA); G. *Brachylophus fasciatus* (Orchid Isl., Polynesia); H. *B. vitiensis* (Orchid Isl., Polynesia); I. *Conolophus subvristatus* (Galapagos Isl.)

Figura 9. HOPLOCERCIDAE. A. Hoplocercus spinosus (Brazil); B. Morunasaurus annularis (Rio Santiago, Ecuador): C. Enyalioides heterolepis (Ecuador).
IGUANIDAE. D. Iguana iguana (Brazil); E. Cercosaura similis (Central America); F. Dipsosaurus dorsalis (South California, USA); G. Brachylophus fasciatus (Orchid Isl., Polynesia); H. B. vitiensis (Orchid Isl., Polynesia); I. Conolophus subvristatus (Galapagos Isl.)

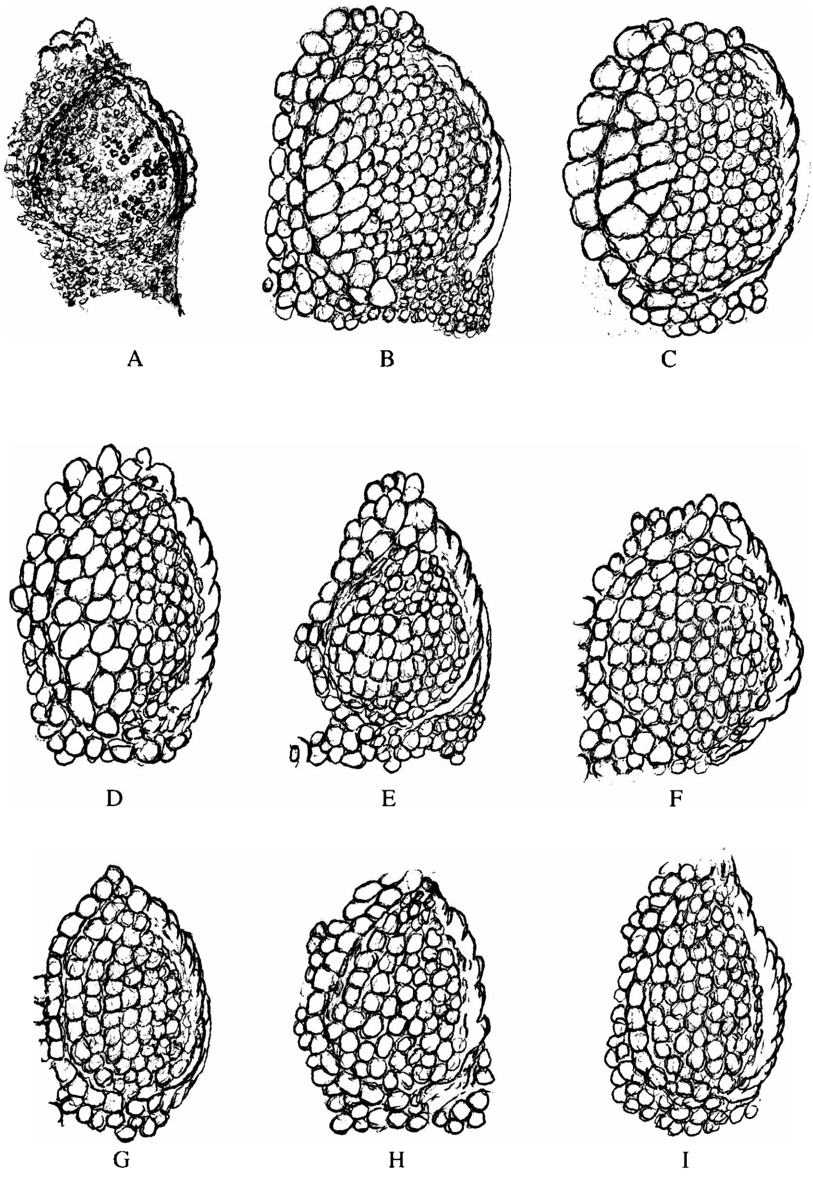

Figure 10. LIOLAEMIDAE. A. *Ctenoblepharis adspersa* (Peru); B. *Phymaturus indistinctus* (Chubut, Argentina); C. *Phymaturus patagonicus* (Chubut, Argentina); D. *Ph. somuncurensis* (Rio Negro, Argentina); E. *Ph. payuniae* (Payunia, Argentina); F. *Ph. punae* (San Juan, Argentina); G. *Ph. mallimaccii* (La Rioja, Argentina); H. *Ph. verdugo* (South Mendoza, Argentina); I. *Ph. antofagastensis* (Catamarca, Argentina)

Figura 10. LIOLAEMIDAE. A. Ctenoblepharis adspersa (Peru); B. Phymaturus indistinctus (Chubut, Argentina); C. Phymaturus patagonicus (Chubut, Argentina); D. Ph. somuncurensis (Rio Negro, Argentina); E. Ph. payuniae (Payunia, Argentina); F. Ph. punae (San Juan, Argentina); G. Ph. mallimaccii (La Rioja, Argentina); H. Ph. verdugo (South Mendoza, Argentina); I. Ph. antofagastensis (Catamarca, Argentina) speciation. Its more characterizing feature is, alongside the very evident circumorbital semicircles, the longitudinal row of 5-6 broad supraocular scales, not as irregular and confused as in the *Phymaturus patagonicus* group (Figure 11). In few eastern Brazilian arenicolous taxa, as *Liolaemus occipitalis*, a diverging pattern of undifferentiated scales, perhaps primitive, may be pointed out.

Before moving to the complex family Tropiduridae of which some taxa as Liolaemidae and Leiocephalidae have already been referred to (Frost and Etheridge, 1989), we must pay attention to the Pleurodont lizards Leiosauridae, as well included in Polychrotidae prior to the remembered reclassification by Frost *et al.* (2001).

Parted into two subfamilies, Leiosaurinae and Enyaliinae, a number of genera and a variety of patterns pertain to this unusual iguanian systematic entity, to which Figures 12 and 13 are dedicated. In Leiosauridae, three peculiar genera are known, *Pristidactylus*, *Diplolaemus* and *Leiosaurus*, of very ancient lineage: *Leiosaurus* is found fossil in Pliocene layers of Argentina, *Pristidactylus* down right in the Miocene sediments of Chubut (Argentina).

Pristidactylus, the purpose of our recent review (Cei *et al.*, 2004), as well as *Diplolaemus* (Cei *et al.*, 2003), are the most undifferentiated members of the subfamily. All the recognized species of *Pristidactylus* were analyzed in detail in our revision, adding three analogous forms to the four Argentine entities reported in Figure 12. *Pristidactylus nigroiugulus* from Chubut exhibits an acrodont-like pattern, somewhat modified in *P. scapulatus* and *P. araucanus*, but equal in *P. achalensis*, *P. casuhatiensis* from Argentina and *P. alvaroi* from Chile. However in *P. fasciatus*, from the arid scrub of central Argentina, a lepidosis very similar to those of the other two genera is found, evoking probably evolutionary genetic relationships. In Figure 12 a unique, just mentioned, iguanian supraocular lepidosis is shown, both in *Diplolaemus* and *Leiosaurus*, with a central rounded bouquet of larger scales in a very homogeneous field of diminished scales. In neotropical Enyaliinae the here commented extant conditions of morphological supraocular uniformity appear altered enough. In Brazilian *Enyalius* the homogeneous pattern of *E. perditus* is replaced by a condition almost repeating that of *Pristidactylus fasciatus* or

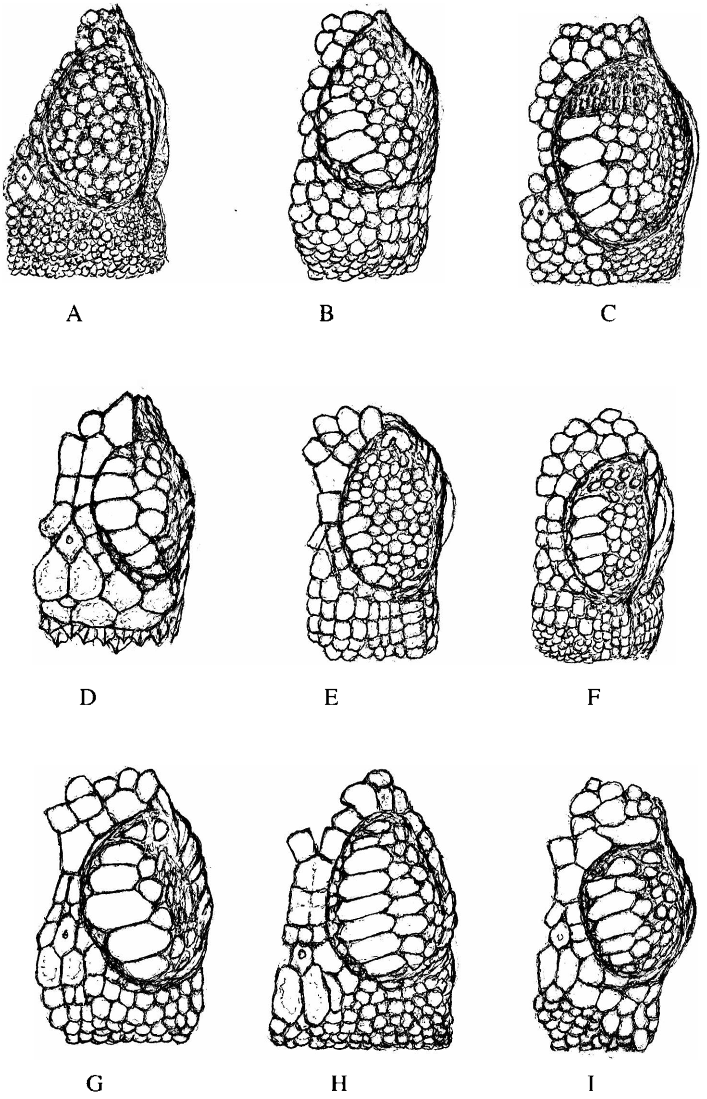

Figure 11. LIOLAEMIDAE. A. *Liolaemus occipitalis* (Rio Grande do Sul, Brazil); B. *Liolaemus wiegmanni* (Tucuman, Argentina); C. *L. nigriceps* (Antofagasta, Chile); D. *L. chiliensis* (Concepcion, Chile); E. *L. ruibali* (San Juan, Argentina); F. *L. kingi* (Santa Cruz, Argentina); G. *L. silvanae* (S. Cruz, Argentina); H. *L. fitzingeri* (Chubut, Argentina); I. *Liolaemus elongatus* (Neuquen, Argentina)

Figura 11. LIOLAEMIDAE. A. Liolaemus occipitalis (Rio Grande do Sul, Brazil); B. Liolaemus wiegmanni (Tucuman, Argentina); C. L. nigriceps (Antofagasta, Chile); D. L. chiliensis (Concepcion, Chile); E. L. ruibali (San Juan, Argentina); F. L. kingi (Santa Cruz, Argentina); G. L. silvanae (S. Cruz, Argentina); H. L. fitzingeri (Chubut, Argentina); I. Liolaemus elongatus (Neuquen, Argentina)

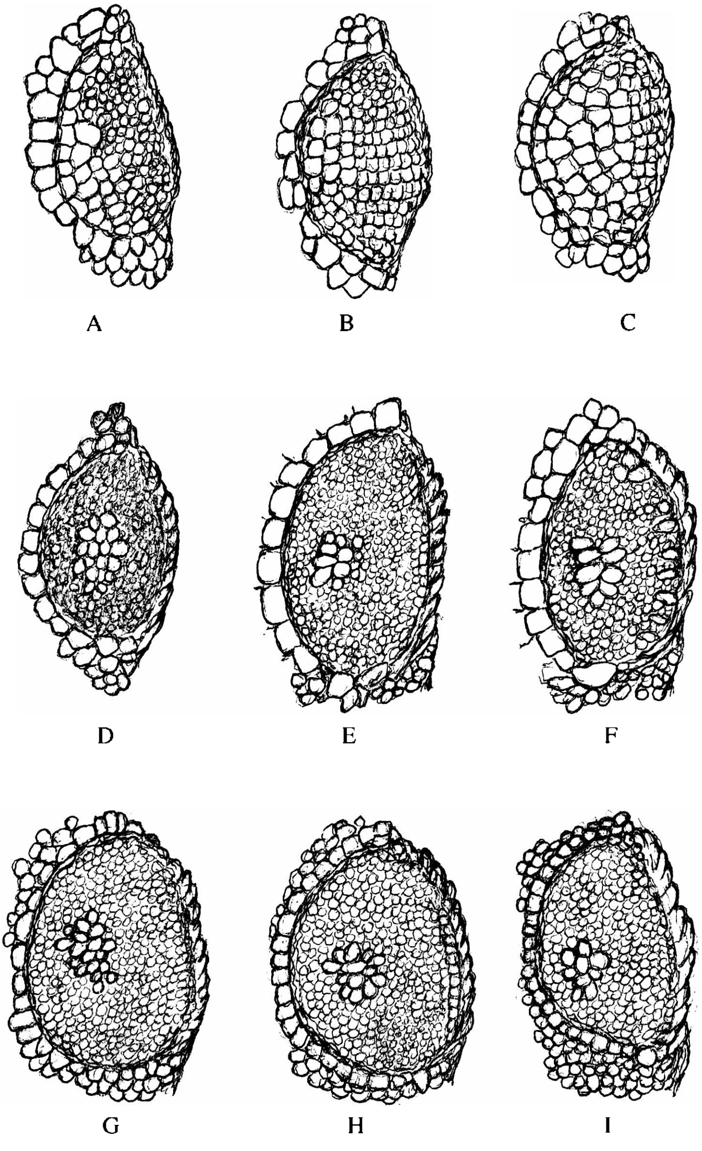

Figure 12. LEIOSAURIDAE. Leiosaurinae. A. *Pristidactylus scapulatus* (Mendoza, Argentina); B. *P. araucanus* (Neuquen, Argentina); C. *P. nigroiugulus* (Chubut, Argentina); D. *P. fasciatus* (Mendoza, Argentina); E. *Diplolaemus bibroni* (Santa Cruz, Argentina); F. *Diplolaemus darwini* (S. Cruz, Argentina); G. *Leiosaurus catamarcencis* (San Juan, Argentina); H. *L. paronae* (Mendoza, Argentina); I. *Leiosaurus belli* (Chubut, Argentina)

Figura 12. LEIOSAURIDAE. Leiosaurinae. A. Pristidactylus scapulatus (Mendoza, Argentina); B. P. araucanus (Neuquen, Argentina); C. P. nigroiugulus (Chubut, Argentina); D. P. fasciatus (Mendoza, Argentina); E. Diplolaemus bibroni (Santa Cruz, Argentina); F. Diplolaemus darwini (S. Cruz, Argentina); G. Leiosaurus catamarcencis (San Juan, Argentina); H. L. paronae (Mendoza, Argentina); I. Leiosaurus belli (Chubut, Argentina)

Diplolaemus (Figure 13), as in *E. brasiliensis*, *E. iheringi* and likewise in *Urostrophus*. More intriguing is the genus *Anisolepis*, whose specific patterns can look alike to that of *Urostrophus vautieri* (i.e. *Anisolepis grillii*), superficially to that of the Corythophanid *Basiliscus plumifrons* (i.e. *Anisolepis undulatus*), and strikingly alike to those of the genera *Urosaurus* and *Petrosaurus* of the family Phrynosomatidae (i.e. *Anisolepis longicauda*).

Remodeled as subfamily by Frost (1992), Tropiduridae was confirmed as a family by Frost *et al.* (2001) without making clear the definitive position (subfamily or tribe) of the diversified Stenocercini tribe. The supraocular lepidosis in *Tropidurus* appears to be the most significant pattern of Iguanian Pleurodonta (Figures 14, 15, 16). Two strongly diverging types are distinguishable. The type of the genus *Uranoscodon* from tropical South America is present too in the Stenocercini tribe, with *Stenocercus guentheri* from Ecuador, *Ophryessoides caducus* from Northern Argentina, *Proctotetrus pectinatus* and *P. doellojuradoi* from central Argentina, the last three lizards considered as *Stenocercus* in the cited Frost's paper (1992). Its fundamental feature is a complete supraocular lining of imbricate keeled scales, together with evident keeled circumorbital semicircles, and variable supraciliaries, showy and sharp-pointed in *Uranoscodon*, superimposed in Stenocercini taxa. The other prevailing *Tropidurus* type shows in the similar genera *Microlophus, Plesiomicrolophus* and *Tropidurus* a general unfolding of longitudinal rows of 4-6 broad supraocular scales, of different size and flanked by minor, rounded, irregular scales. A remarkable variation is even observed in the evident circumorbital semicircles which are more moderate in Stenocercini taxa. Always particularly distinct in our drawings is the interparietal scale and its "eye", more or less developed (*crf.* Frost *et al.*, 2001: p.21). The unifying tendency of Frost`s assessment (1992) led to extend the generic *Tropidurus* name to some taxa known as *Strobilurus* and *Plica*, now *Tropidurus strobilurus*, *T. plica* and *T. umbra.* A third *Plica*, now *Tropidurus lumaria* from Venezuelan Tepui, was well documented by Donnelly and Myers (1991).

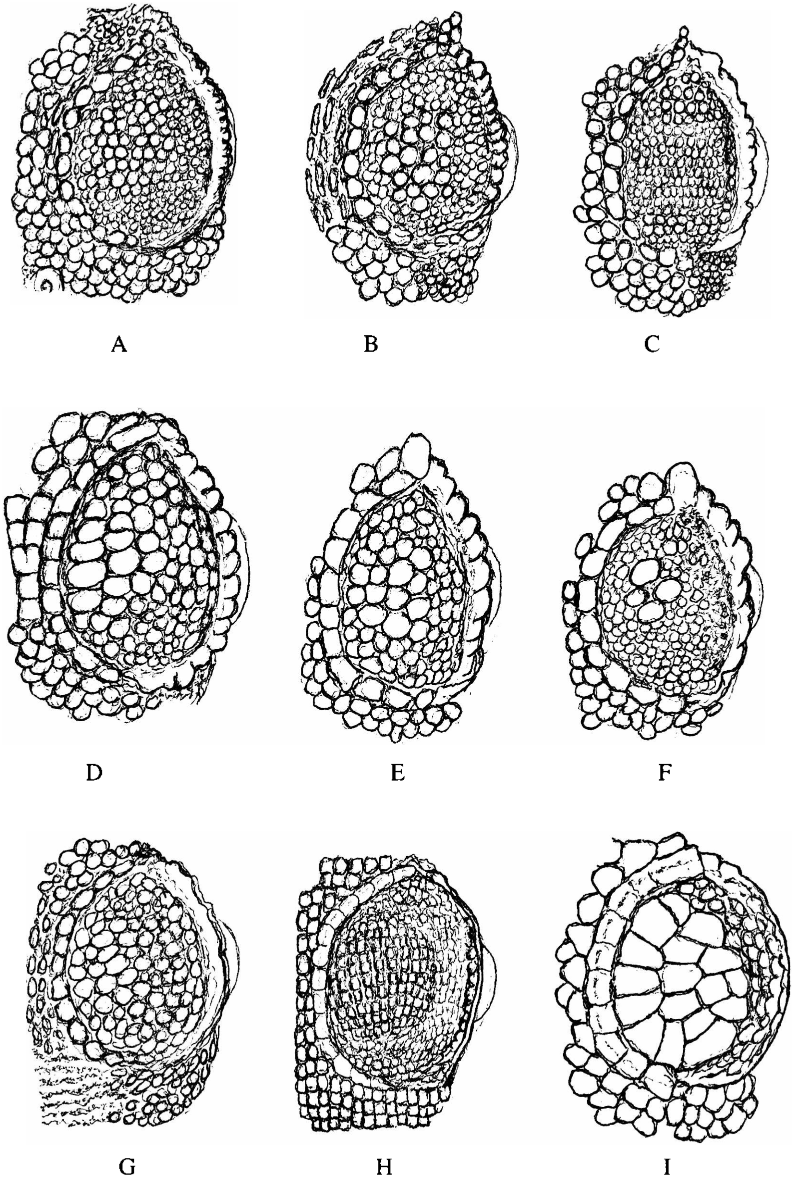

Figure 13. LEIOSAURIDAE. Enyaliinae. A. *Enyalius brasiliensis* (Espirito Santo, Brazil); B. *Enyalius iheringi* (Sao Paulo, Brazil); C. *E. perditus* (Brazil); D. *Urostrophus vautieri* (Sao Paulo, Brazil); E. *Urostrophus iheringi* (S. Paulo, Brazil); F. *U. gallardoi* (Cordoba, Argentina); G. *Anisolepis grillii* (S. Paulo, Brazil); H. *Anisolepis undulatus* (S. Paulo, Brazil); I. *A. longicauda* (Corrientes, Argentina)

Figura 13. LEIOSAURIDAE. Enyaliinae. A. Enyalius brasiliensis (Espirito Santo, Brazil); B. Enyalius iheringi (Sao Paulo, Brazil); C. E. perditus (Brazil); D. Urostrophus vautieri (Sao Paulo, Brazil); E. Urostrophus iheringi (S. Paulo, Brazil); F. U. gallardoi (Cordoba, Argentina); G. Anisolepis grillii (S. Paulo, Brazil); H. Anisolepis undulatus (S. Paulo, Brazil); I. A. longicauda (Corrientes, Argentina)

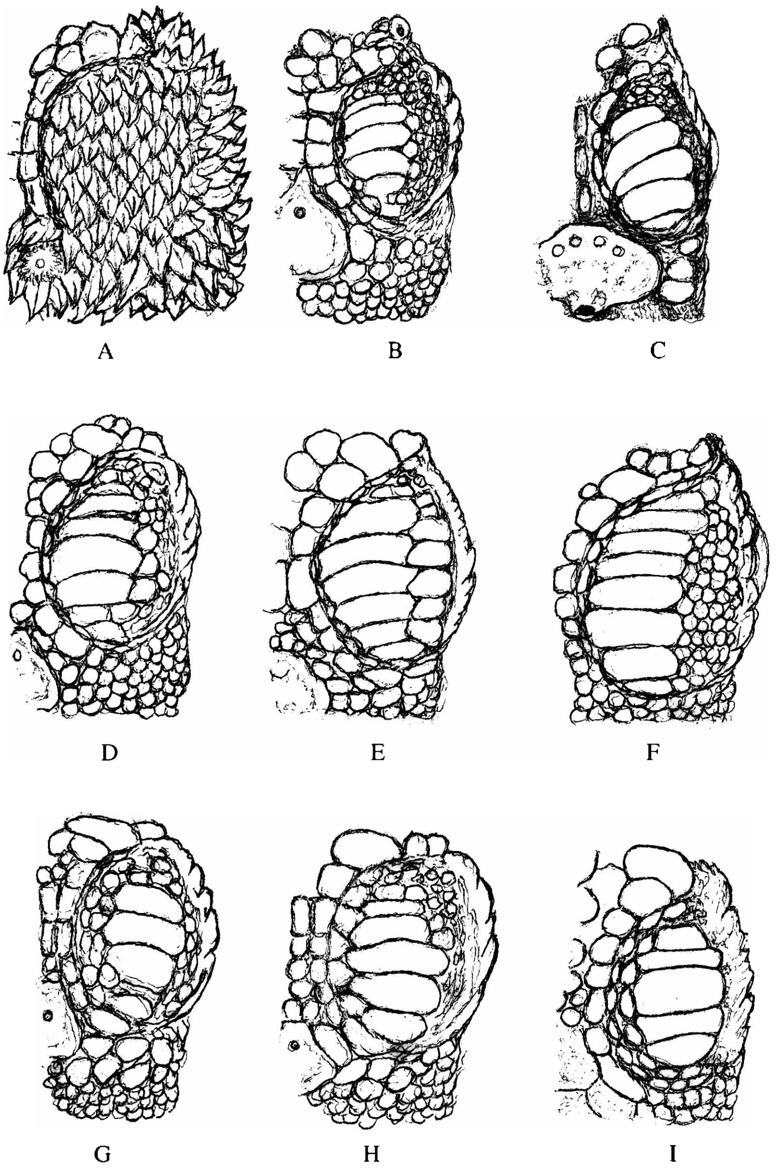

Figure 14. TROPIDURIDAE. Tropidurini. A. *Uranoscodon superciliosus* (Northern S. America); B. *Microlophus peruvianus* (Arica, Chile); C. *Microlophus occipitalis* (Ecuador); D. *Tropidurus hispidus* (Venezuela); E. *Tropidurus torquatus* (S. Paulo, Brazil); F. *T. etheridgei* (La Rioja, Argentina); G. *T. spinulosus* (Formosa, Argentina); H. *T. spinulosus* (Cordoba, Argentina); I. *Tropidurus guarani* (Asuncion, Paraguay)

Figura 14. TROPIDURIDAE. Tropidurini. A. Uranoscodon superciliosus (Northern S. America); B. Microlophus peruvianus (Arica, Chile); C. Microlophus occipitalis (Ecuador); D. Tropidurus hispidus (Venezuela); E. Tropidurus torquatus (S. Paulo, Brazil); F. T. etheridgei (La Rioja, Argentina); G. T. spinulosus (Formosa, Argentina); H. T. spinulosus (Cordoba, Argentina); I. Tropidurus guarani (Asuncion, Paraguay)

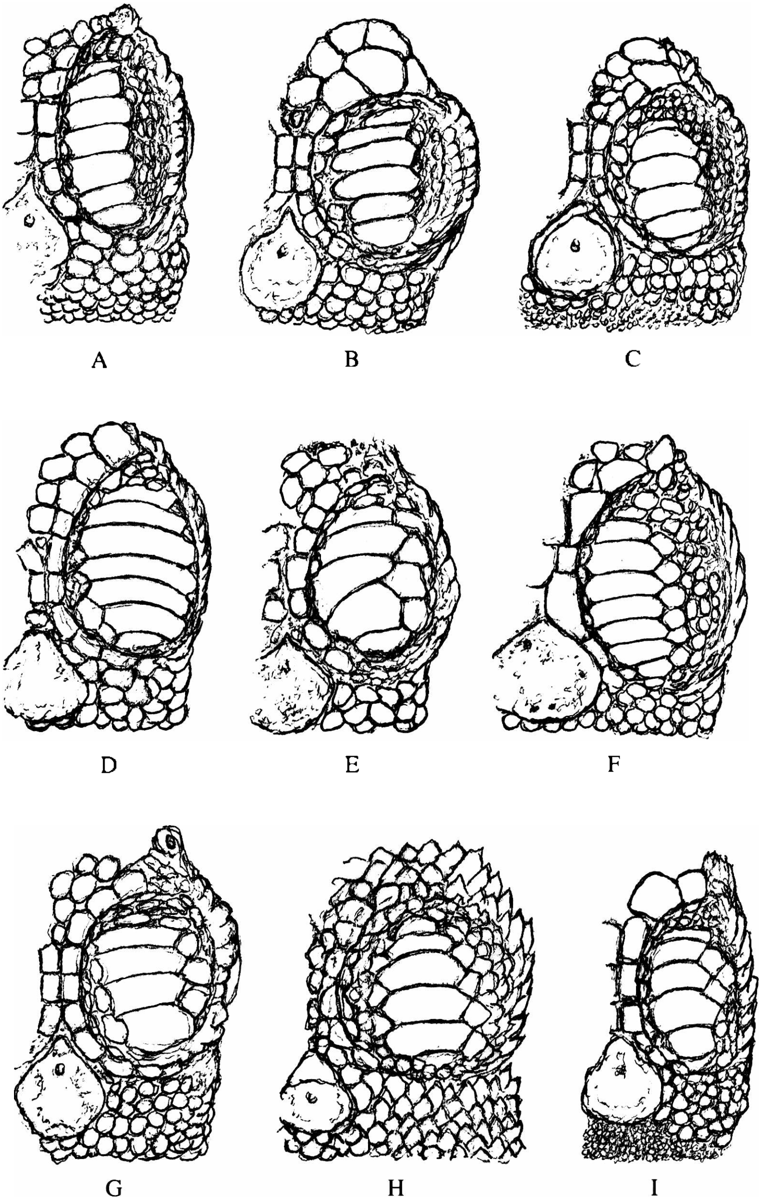

Figure 15. TROPIDURIDAE. Tropidurini. A. *Tropidurus semitaeniatus* (Bahia, Brazil); B. *Tropidurus pictus* (male; Salta, Argentina); C. *T. pictus* (female; Salta, Argentina); D. *Tropidurus hygomi* (Sergipe, Brazil); E. *Tropidurus bogerti* (Bolivar, Venezuela); F. *Tropidurus amathites* (Bahia, Brazil); G. *Tropidurus strobilurus* (NW Brazil); H. *Tropidurus plica* (Para, Brazil); I. *Tropidurus umbra* (French Guyana)

Figura 15. TROPIDURIDAE. Tropidurini. A. Tropidurus semitaeniatus (Bahia, Brazil); B. Tropidurus pictus (male; Salta, Argentina); C. T. pictus (female; Salta, Argentina); D. Tropidurus hygomi (Sergipe, Brazil); E. Tropidurus bogerti (Bolivar, Venezuela); F. Tropidurus amathites (Bahia, Brazil); G. Tropidurus strobilurus (NW Brazil); H. Tropidurus plica (Para, Brazil); I. Tropidurus umbra (French Guyana)

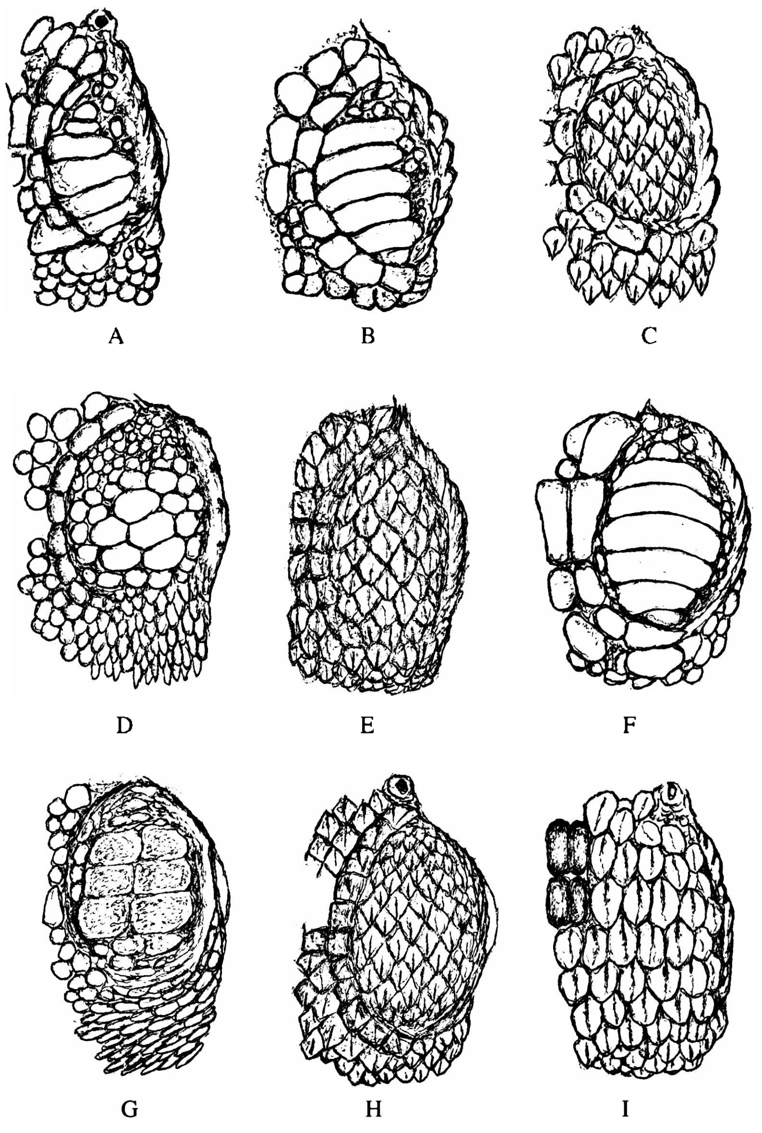

Figure 16. TROPIDURIDAE. Stenocercini. A. *Stenocercus ornatus* (Guayaquil, Ecuador); B. *Stenocercus trachycephalus* (Bogota, Colombia); C. *S. guentheri* (Ecuador); D. *S. varius* (Pichincha, Ecuador); E. *Ophryoessoides caducus* (Jujuy, Argentina); F. *O. iridescens* (Esmeralda, Ecuador); G. *Stenocercus roseiventris* (Salta, Argentina); H. *Stenocercus pectinatus* (Rio Negro, Argentina); I. *S. doellojuradoi* (Santiago del Estero, Argentina)

Figura 16. TROPIDURIDAE. Stenocercini. A. Stenocercus ornatus (Guayaquil, Ecuador); B. Stenocercus trachycephalus (Bogota, Colombia); C. S. guentheri (Ecuador); D. S. varius (Pichincha, Ecuador); E. Ophryoessoides caducus (Jujuy, Argentina); F. O. iridescens (Esmeralda, Ecuador); G. Stenocercus roseiventris (Salta, Argentina); H. Stenocercus pectinatus (Rio Negro, Argentina); I. S. doellojuradoi (Santiago del Estero, Argentina)

Critical reports and annotations on so extensive *Iguania* stem of the followed indented taxonomy are finished. We must comment now on the next major embranchment, Scleroglossa, then parted into two natural lineages: Gekkota and Autarchoglossa. The families attributed to Gekkota are the like, ecologically versatile Gekkonidae, Diplodactylidae, Eublepharidae and the unusual snake-like fossorial Pygopodidae, reviewed by Kenge (1974) in a prolix fashion. Obviously it is impossible to offer here proportional scutellation samples for taxa having some 320 species and 88 genera, such as the almost cosmopolitan Gekkonidae, or for the 120 species and 15 genera of Diplodactylidae from New Zealand and Australia, or the 22 species and 6 genera of Eublepharidae, scattered across the SW of North America, Central America, Africa and Southern Asia. However the examples of Figure 17 are efficacious in expressing the general simplicity of supraocular scutellation of all these Gekkota, given the modest specific or generic variation in their uniform small scales even reduced to short spots, or almost absent. Also the circumorbital semicircles have been restrained to a nearly concealed structure. Very different in size and shape are the supraciliaries, mostly linear and narrow, in some notched (*Rhinogecko misonnei*, *Homonota fasciata*), or sharp-pointed species (*Phyllurus platurus*, *Diplodactylus ciliaris*). Sometimes growths or tubercles appear on the supraocular surface, as in *Phyllurus cornutus*, *Ph. caudiannulatus*, *Nephrurus asper* from Queensland and *Nephrurus wheeleri* from W Australia. Besides Australian examples, these investigations were extended to several other samples from Africa, Middle East India, Iran and America. Our research on Gekkonidae, Diplodactylidae, Eublepharidae has thus been carried out on about a hundred and twenty specimens.

Strongly dissimilar are the more than 30 species and 8 genera belonging to the snake-like Pygopodidae from Australia and New Guinea. These really unusual lizards are represented in Figure 18, pointing out their enlarged cephalic shields and the extreme reduction of their supraocular scales: only one in *Aclys*, *Aprasia* and *Paradelma*, two in *Delma*, *Pygopus* and *Pletholax*, where evident supraciliaries are shown. A most impressive reduction is found in *Lialis* and *Ophidiocephalus*. Lastly, nothing can be added concerning the evolutionary relationships of Pygopodidae with the other Gekkota, anatomical considerations being the decisive factor in this classification.

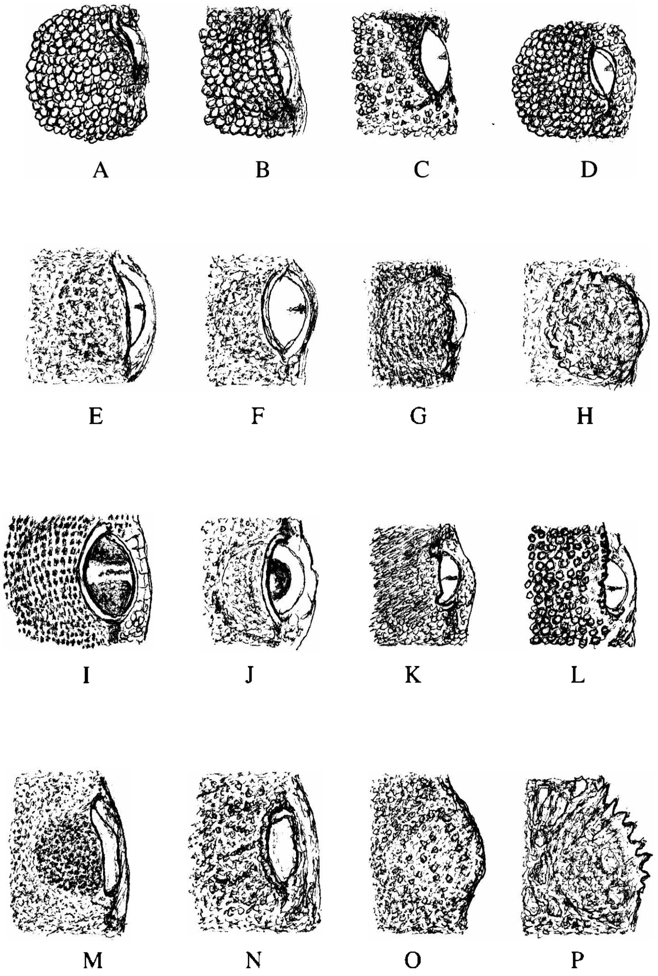

Figure 17. GEKKOTA. GEKKONIDAE. A. *Cyrtopodion heterocercum* (Iran); B. *Rhinogecko misonnei* (Pakistan); C. *Briba brasiliana* (Minas Gerais, Brazil); D. *Phyllopezus pollicaris* (Pernambuco, Brazil); E. *Hemidactylus turcicus* (Mediterranean region); F. *Hemidactylus persicus* (Saudi Arabia); G. *Gonatodes concinnatus* (Napo, Ecuador); H. *Stenodactylus grandiceps* (Jordan, Middle East); I. *Homonota underwoodi* (San Juan, Argentina); J. *Homonota whitii* (Cordoba, Argentina); K. *Homonota darwini* (Payunia, Argentina); L. *Homonota fasciata* (Cordoba, Argentina).
EUBLEPHARIDAE. M. *Coleonyx brevis* (Texas, USA); N. *Eublepharis macularius* (Pakistan); O. *Eublepharis turcmenicus* (Iran).
DIPLODACTYLIDAE. P. *Phyllurus platurus* (South Australia)

Figura 17. GEKKOTA. GEKKONIDAE. A. Cyrtopodion heterocercum (Iran); B. Rhinogecko misonnei (Pakistan); C. Briba brasiliana (Minas Gerais, Brazil); D. Phyllopezus pollicaris (Pernambuco, Brazil); E. Hemidactylus turcicus (Mediterranean region); F. Hemidactylus persicus (Saudi Arabia); G. Gonatodes concinnatus (Napo, Ecuador); H. Stenodactylus grandiceps (Jordan, Middle East); I. Homonota underwoodi (San Juan, Argentina); J. Homonota whitii (Cordoba, Argentina); K. Homonota darwini (Payunia, Argentina); L. Homonota fasciata (Cordoba, Argentina).
EUBLEPHARIDAE. M. Coleonyx brevis (Texas, USA); N. Eublepharis macularius (Pakistan); O. Eublepharis turcmenicus (Iran).
DIPLODACTYLIDAE. P. Phyllurus platurus (South Australia)

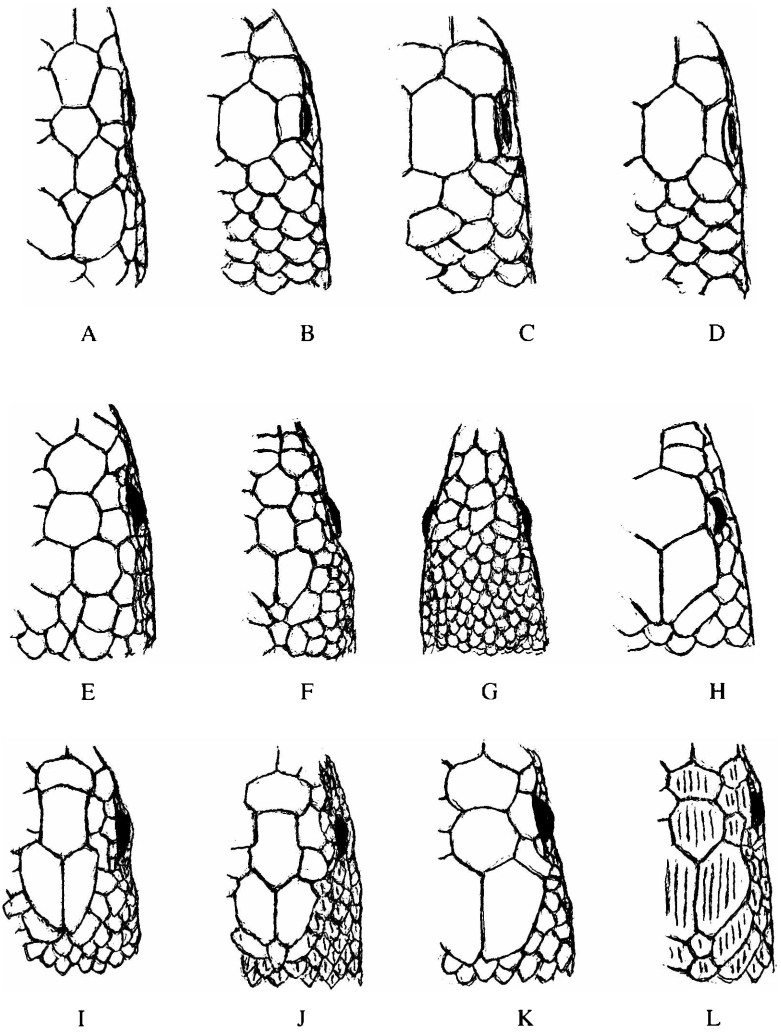

Figure 18. PYGOPODIDAE. A. *Aclys concinna* (W Australia); B. *Aprasia aurita* (SE Australia); C. *Aprasia parapulchella* (SE Australia); D. *Aprasia repens* (SW Australia); E. *Delma australis* (W Australia); F. *Delma elegans* (W Australia); G. *Lialis jicari* (New Guinea); H. *Ophidiocephalus taeniatus* (N Australia); I. *Pygopus nigriceps* (Australia); J. *Pygopus lepidopodus* (SW Australia); K. *Paradelma orientalis* (Queensland, Australia); L. *Pletholax gracilis* (SW Australia)

Figura 18. PYGOPODIDAE. A. Aclys concinna (W Australia); B. Aprasia aurita (SE Australia); C. Aprasia parapulchella (SE Australia); D. Aprasia repens (SW Australia); E. Delma australis (W Australia); F. Delma elegans (W Australia); G. Lialis jicari (New Guinea); H. Ophidiocephalus taeniatus (N Australia); I. Pygopus nigriceps (Australia); J. Pygopus lepidopodus (SW Australia); K. Paradelma orientalis (Queensland, Australia); L. Pletholax gracilis (SW Australia)

Drastic morphological changes, facing examined Iguania supraocular patterns, shall now be commented upon for the successive branches of Autarchoglossa, foreseen in our indented taxonomy, beginning with Scincomorpha and its noticeable lines Lacertoidea and Scincoidea. Without any doubt, observing their cephalic lepidosis, some evolutionary trends are difficult to understand at first sight between the night lizards Xantusidae and the Lacertiformes Lacertidae and Teiioidea of Lacertoidea, as well as the families Scincidae and Cordylidae, of Scincoidea. Studied formerly by Savage (1963), who firstly assigned them to Gekkota, these viviparous, secretive reptiles, with their genera *Lepidophyma*, *Xantusia* and *Cricosaura* (Figure 19), live in crevices or cracks of granite flakes, in forested regions of Mexico, Central America, Southern and Western United States, and there being only one species confined to Cuba, the monotypic *Cricosaura* (*C. typica*). From Figure 19 we can note that in *Xantusia vigilis* circumorbital semicircles are absent, as in *X. henshawi* or *X. arizonae*, besides the other genera, and that the supraocular scales consist of a narrow longitudinal row near the eye border, with no evident supraciliaries; that in *Xantusia riversiana* (ancient *Klauberina* Savage 1957) and *Cricosaura typica* two narrow adjacent rows on the eye border are visible, the external narrower; almost rudimentary in the two adjacent supraocular rows of *Cercosaura*; that in *Lepidophyma flavimaculatum*, the reduction of the supraocular scales is extreme, to "a narrow fleshy ridge above the eye" (Savage, 1963).

Leaving so exceptionally modified scale features, the specimens reported in the inferior drawings of Figure 19 introduce us to the great American stem of Lacertiformes, the Teiioidea, to whose taxon Teiidae belong the reproduced species of the genus *Tupinambis*, still justifying a systematic definition as subfamily. The specific variation in the pattern of *Tupinambis* anticipates here a general distribution of supra-ocular scales dominant in Scincomorpha, with major or minor alteration. Lacking a definition of circumorbital semicircles, 4-5 supraocular scales, somewhat different in size, stretch out on the eye border, edged by one or two narrower linear supraciliary rows. That simple scheme, of the large-sized, powerful *Tupinambis* shall be commented upon, more or less modified, in the following Figures of Teiioidea, Lacertidae and Scincoidea. Fossil remains of *Tupinambis* from South American early Miocene to late Miocene are very suggestive records stating the significant evolutionary lineage of Teiid forms in the continent (Albino *et al.* 2006).

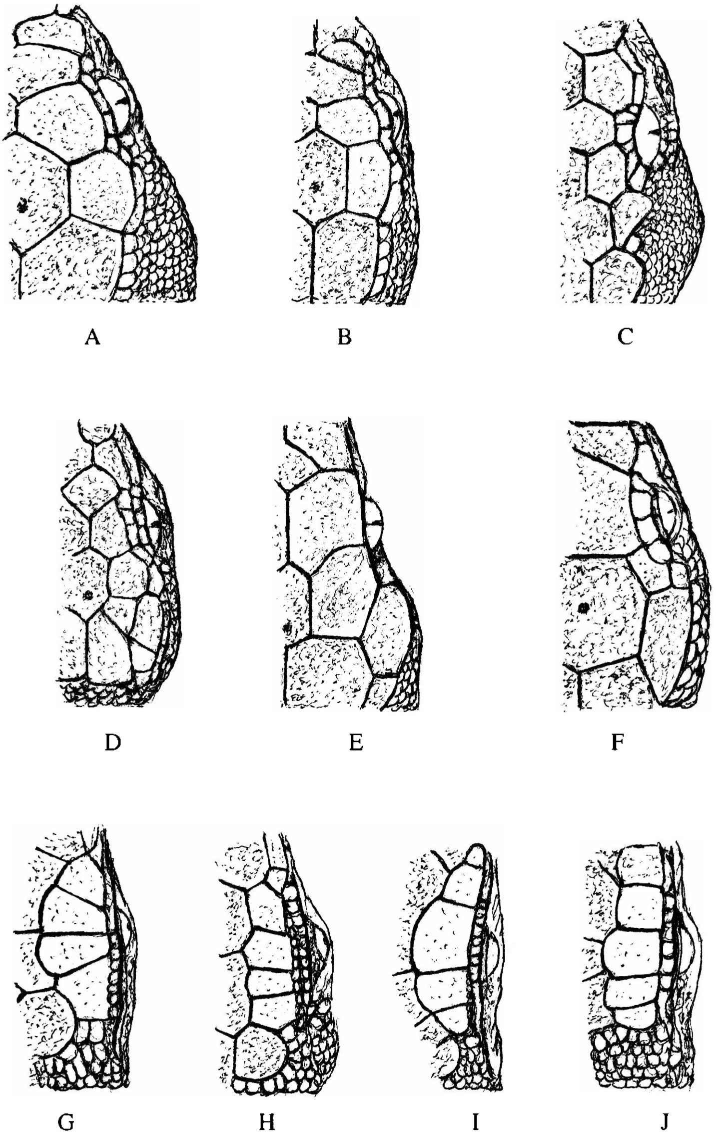

Figure 19. XANTUSIIDAE. TEIIDAE. XANTUSIIDAE. A. *Xantusia vigilis* (SW USA); B. *Xantusia vigilis* (Lower California, USA); C. *X. henshawi* (SW USA); D. *X. riversiana* (SW California, USA); E. *Lepidophyma flavimaculatum* (Costa Rica); F. *Cricosaura typica* (E Cuba). TEIIDAE. G. *Tupinambis nigromaculatus* (Barinas, Venezuela); H. *T. teguixin* (E Brasil); I. *T. merianae* (Bs. Aires, Argentina); J. *Tupinambis rufescens* (Mendoza, Argentina)

Figura 19. XANTUSIIDAE. TEIIDAE. XANTUSIIDAE. A. Xantusia vigilis (SW USA); B. Xantusia vigilis (Lower California, USA); C. X. henshawi (SW USA); D. X. riversiana (SW California, USA); E. Lepidophyma flavimaculatum (Costa Rica); F. Cricosaura typica (E Cuba). TEIIDAE. G. Tupinambis nigromaculatus (Barinas, Venezuela); H. T. teguixin (E Brasil); I. T. merianae (Bs. Aires, Argentina); J. Tupinambis rufescens (Mendoza, Argentina)

In Figure 20, upper row, the greatest Teiid species are documented. Five supraocular scales with much reduced circumorbital semicircles and relatively wide supraciliaries are shown by *Ameiva* and *Callopistes*: 6-5 supraocular scales and a narrower supraciliary row characterize *Dracaena*. Taxa of *Dicrodon* and *Kentropyx*, on the intermediate row, exhibit 3-2 larger broad scales with a very small terminal scale, reduced or absent circumorbital semicircles, but evident overlapping supraciliaries. On the inferior row of the figure, the repeated Teiid lepidosis accounts for the 3 supraocular scales of *Teius*, with circumorbital semicircles and overlapping supraciliaries. For the numerous and so variable whiptails (*Cnemidophorus*) we reported 4-3 supraocular scales and developed supraciliaries: only for *Cnemidophorus ocellifer* the circumorbital semicircle was drawn here.

Corresponding to the old subdivision into Microteiids and Macroteiids, the family Gymnophthalmidae was established for the many small-sized forms distributed with more than 150 species and 35 genera in Central and South America. Figures 21-22 deal with those lizards having 4, 3, 2 supraocular scales, mainly lacking circumorbital semicircles but putting in evidence a more or less wide supraciliary border. Through the careful Dixon's research (1973) it was possible to remark the evolutionary process leading to loss of the supraocular scales in the gymnophthalmid genus *Bachia*: a process whose progressive steps have been already accomplished, i.e., in *Gymnophthalmus underwoodi* from Surinam or *Heterodactylus imbricatus* from SE Brazil. In Figure 22 we can point out the reduced but still recognizable two supraocular scales of *Bachia heteropa* (Venezuela), *B. flavescens* (Guyana), *B. pallidiceps* (Panama, Colombia), and also their elimination from *Bachia talpa* (Colombia) to *B. intermedius* (Peru), with narrow supraciliaries remaining in the end. Differences in body, scales, ecological relationships and evolutionary trends within the genus, related to fossorial adaptation, were preliminarily discussed in the cited paper.

Now we will go on with the inferior row of Figure 22 and Figure 23, illustrating characteristic features of the African and Euro-Asiatic great family Lacertidae, with more than 220 species and 25 genera. That is our last information about Lacertoidea of the Scincomorpha embranchment. The striking morphological affinities in supraocular lepidosis between Lacertidae and their counterpart Teiioidea from the American

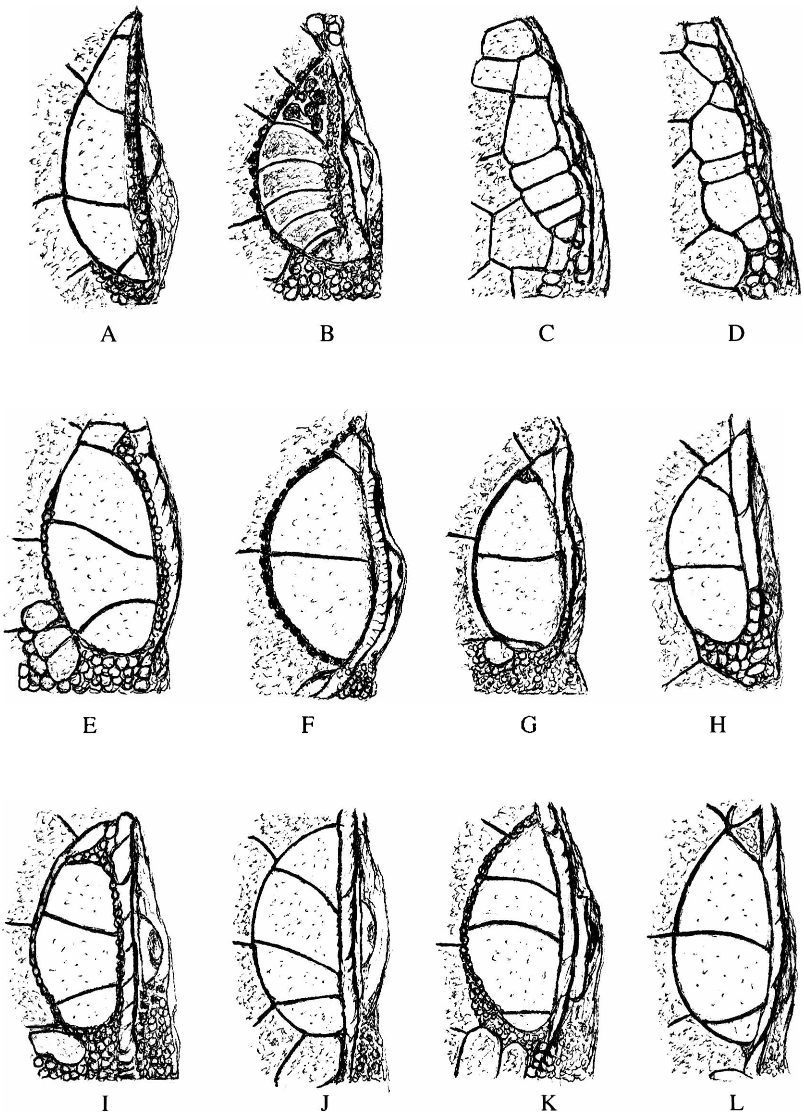

Figure 20. TEIIDAE. A. *Ameiva ameiva* (French Guyana); B. *Callopistes palluma* (Chile); C. *Dracaena paraguayensis* (Mato Grosso, Brazil); D. *D. guianensis* (Guyana); E. *Dicrodon guttulatus* (Ecuador); F. *Kentropyx viridistriga* (Corrientes, Argentina); G. *Kentropyx lagartica* (Tucuman, Argentina); H. *K. pelviceps* (Amazonia, Ecuador); I. *Teius oculatus* (Cordoba, Argentina); J. *Cnemidophorus lemniscatus* (Yaracui, Venezuela); K. *C. ocellifer* (Chaco, Argentina); L. *C. lacertoides* (Jujuy, Argentina)

Figura 20. TEIIDAE. A. Ameiva ameiva (French Guyana); B. Callopistes palluma (Chile); C. Dracaena paraguayensis (Mato Grosso, Brazil); D. D. guianensis (Guyana); E. Dicrodon guttulatus (Ecuador); F. Kentropyx viridistriga (Corrientes, Argentina); G. Kentropyx lagartica (Tucuman, Argentina); H. K. pelviceps (Amazonia, Ecuador); I. Teius oculatus (Cordoba, Argentina); J. Cnemidophorus lemniscatus (Yaracui, Venezuela); K. C. ocellifer (Chaco, Argentina); L. C. lacertoides (Jujuy, Argentina)

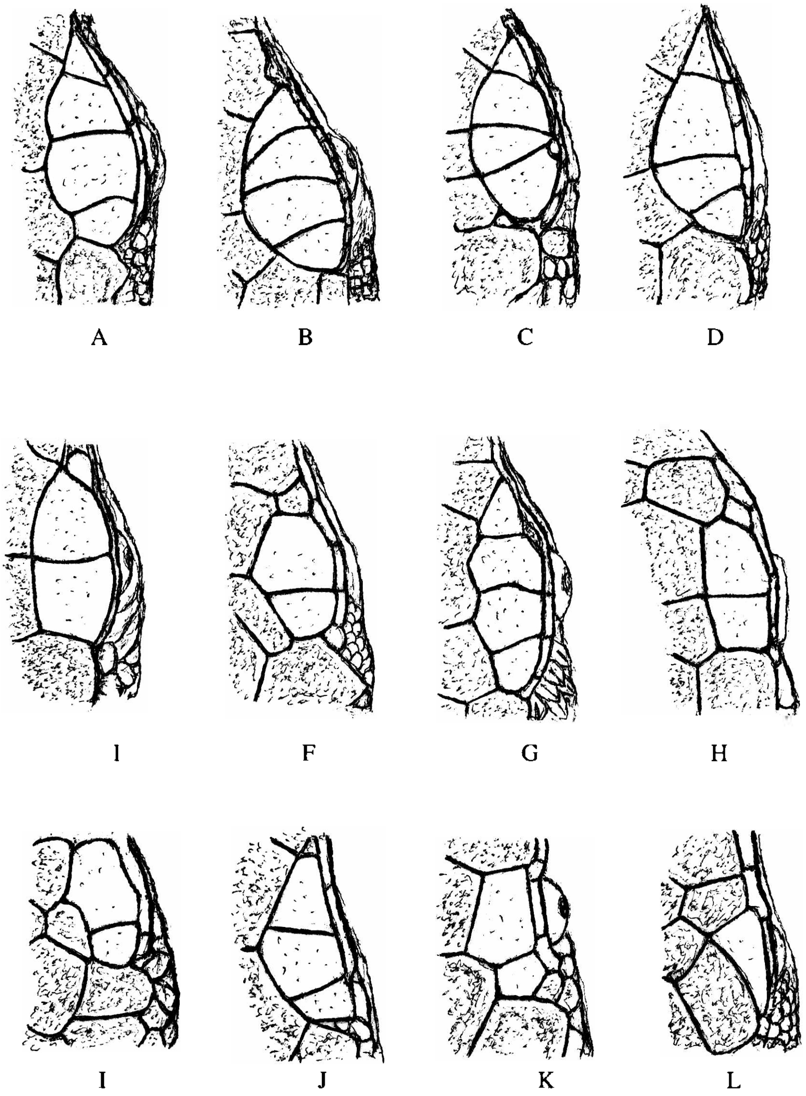

Figure 21. GYMNOPHTHALMIDAE. A. *Alopoglossus angulatus* (Northern South America); B. *Neusticurus bicarinatus* (Brasil, Guyana); C. *Pantodactylus schreibersi* (Cordoba, Argentina); D. *Arthrosaura kockii* (Surinam, N Brazil); E. *Anadia bipunctata* (Merida, Venezuela); F. *Tretioscincus agilis* (Guyana, N Brazil); G. *Leposoma guianense* (Guyana, N Brazil); H. *Iphisa elegans* (Northern South America); I. *Microblepharus maximiliani* (NE Brazil, Paraguay); J. *Prionodactylus argulus* (Ecuador, Guyana); K. *Gymnophthalmus multiscutatus* (NE Brazil); L. *Gymnophthalmus underwoodi* (Surinam, Tobago Is.)

Figura 21. GYMNOPHTHALMIDAE. A. Alopoglossus angulatus (Northern South America); B. Neusticurus bicarinatus (Brasil, Guyana); C. Pantodactylus schreibersi (Cordoba, Argentina); D. Arthrosaura kockii (Surinam, N Brazil); E. Anadia bipunctata (Merida, Venezuela); F. Tretioscincus agilis (Guyana, N Brazil); G. Leposoma guianense (Guyana, N Brazil); H. Iphisa elegans (Northern South America); I. Microblepharus maximiliani (NE Brazil, Paraguay); J. Prionodactylus argulus (Ecuador, Guyana); K. Gymnophthalmus multiscutatus (NE Brazil); L. Gymnophthalmus underwoodi (Surinam, Tobago Is.)

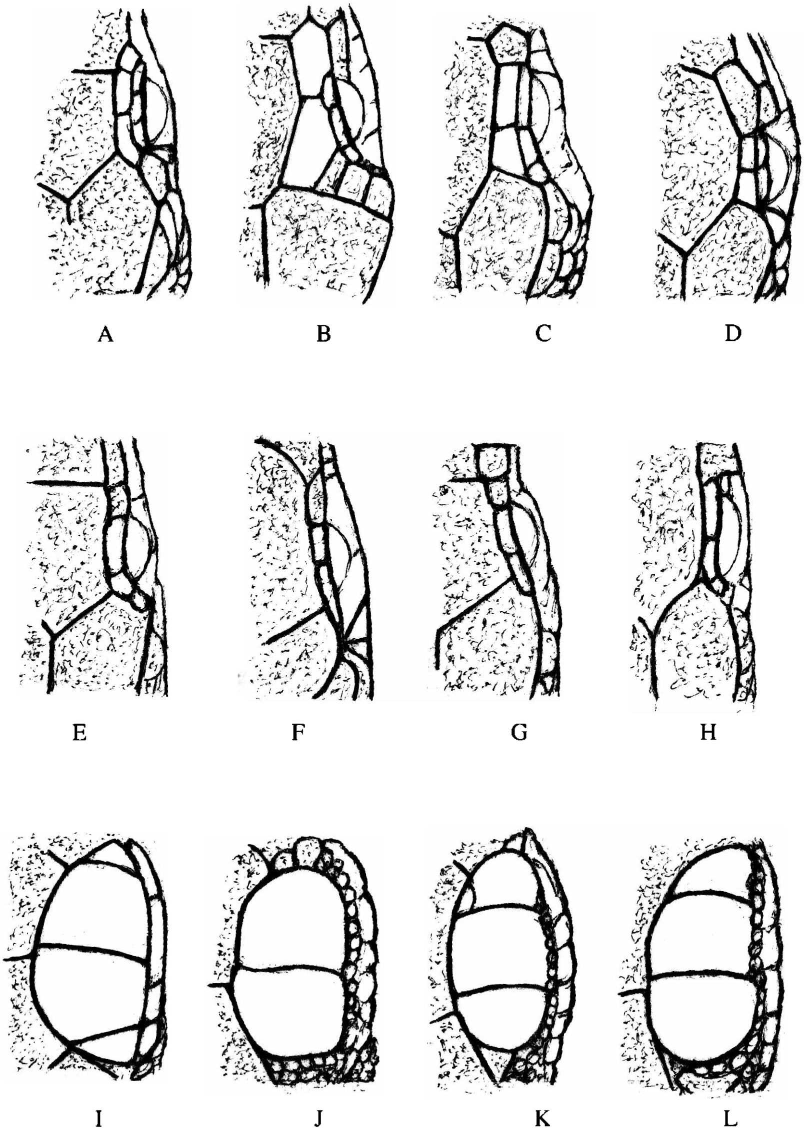

Figure 22. GYMNOPHTHALMIDAE. A. *Heterodactylus imbricatus* (SE Brazil); B. *Bachia heteropa* (Venezuela); C. *Bachia flavescens* (Guyana); D. *B. pellidiceps* (Panama, Colombia); E. *B. talpa* (Colombia); F. *B. trisanale* (Peru, Ecuador); G. *B. huallagana* (Peru); H. *B. intermedia* (Peru). LACERTIDAE. I. *Psammodromus algirus* (SW Europe, NW Africa); J. *Acanthodactylus erytrurus* (SW Europe); K. *A. pardalis* (Maroc, Marruecos); L. *A. boskianus* (NW Africa)

Figura 22. GYMNOPHTHALMIDAE. A. Heterodactylus imbricatus (SE Brazil); B. Bachia heteropa (Venezuela); C. Bachia flavescens (Guyana); D. B. pellidiceps (Panama, Colombia); E. B. talpa (Colombia); F. B. trisanale (Peru, Ecuador); G. B. huallagana (Peru); H. B. intermedia (Peru). LACERTIDAE. I. Psammodromus algirus (SW Europe, NW Africa); J. Acanthodactylus erytrurus (SW Europe); K. A. pardalis (Maroc, Marruecos); L. A. boskianus (NW Africa)

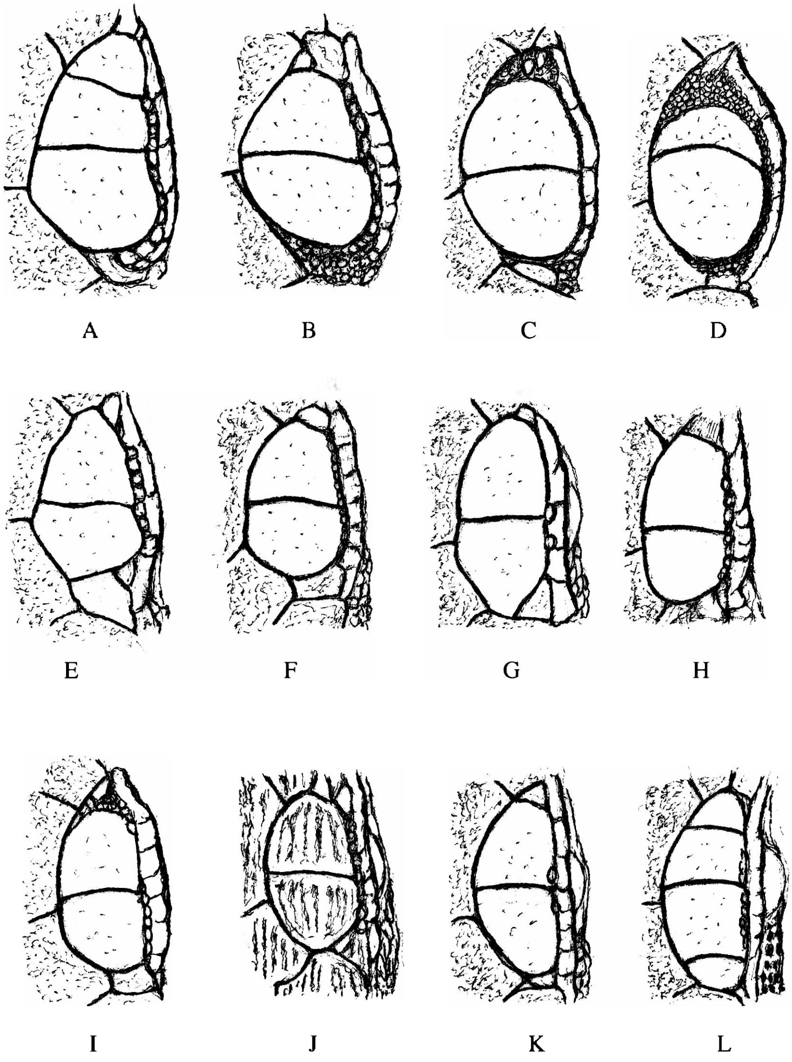

Figure 23. *LACERTIDAE*. A. *Acanthodactylus blanfordi* (Afghanistan); B. *A. grandis* (Siria); C. *Eremias strauchi* (Armenia, Iran); D. *Eremias arguta* (Iran, Central Asia); E. *Lacerta lepida* (SW Europe); F. *Lacerta defilippi* (Iran); G. *L. vivipara* (Northern Eurasia); H. *Gallotia atlantica* (Canary Isl.); I. *Mesalina brevirostris* (Middle East); J. *Ichnotropis bivittata* (Angola); K. *Nucras scalaris* (Angola); L. *Nucras taeniolata* (SW Africa)

Figura 23. LACERTIDAE. A. Acanthodactylus blanfordi (Afghanistan); B. A. grandis (Siria); C. Eremias strauchi (Armenia, Iran); D. Eremias arguta (Iran, Central Asia); E. Lacerta lepida (SW Europe); F. Lacerta defilippi (Iran); G. L. vivipara (Northern Eurasia); H. Gallotia atlantica (Canary Isl.); I. Mesalina brevirostris (Middle East); J. Ichnotropis bivittata (Angola); K. Nucras scalaris (Angola); L. Nucras taeniolata (SW Africa)

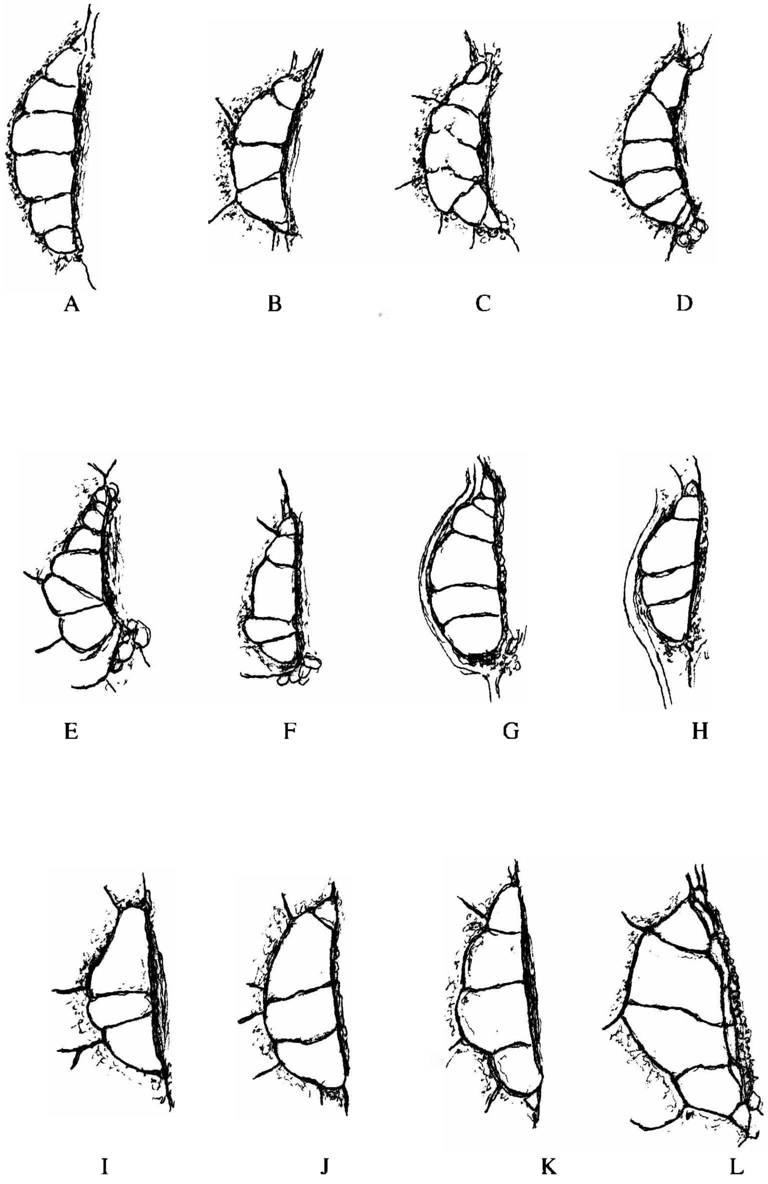

Figure 24. SCINCIDAE. A. *Leiolopisma coventryi* (S Australia); B. *Emoia nativitatis* (Christmas Is., W Australia); C. *Egernia striolata* (E Australia); D. *Egernia coventryi* (S Australia); E. *Ctenotus inornatus* (N Australia); F. *C. helenae* (W Central Australia); G. *Ctenotus dux* (Central Australia); H. *C. allotropis* (SE Australia); I. *Mabuya dorsivittata* (Cordoba, Argentina); J. *Mabuya frenata* (Brazil); K. *Mabuya aurata* (Lebanon, Syria); L. *Mabuya maculilabris* (Ghana, W Africa)

Figura 24. SCINCIDAE. A. Leiolopisma coventryi (S Australia); B. Emoia nativitatis (Christmas Is., W Australia); C. Egernia striolata (E Australia); D. Egernia coventryi (S Australia); E. Ctenotus inornatus (N Australia); F. C. helenae (W Central Australia); G. Ctenotus dux (Central Australia); H. C. allotropis (SE Australia); I. Mabuya dorsivittata (Cordoba, Argentina); J. Mabuya frenata (Brazil); K. Mabuya aurata (Lebanon, Syria); L. Mabuya maculilabris (Ghana, W Africa) continent sound suggestive. The sixteen species and eight genera represented may be a sufficient sample, given our multiple controls carried out on a remarkable number of additional specimens. In the well known genus *Acanthodactylus* 3-2 broad supraocular scales are the rule, without apparent circumorbital semicircles, pronounced supraciliaries being instead separated or not from supraoculars by a narrow row of diminutive scales. Comparing this pattern with the other drawn supraocular patterns of Lacertidae, such as *Psammodromus*, *Eremias*, *Lacerta*, *Mesalina*, *Ichnotropis*, *Nucras* or *Gallotia*, their fundamental trends of similarity are recognizable at first sight. However, a diligent comparison of the supraocular lepidosis in Lacertidae with the above reported supraocular lepidosis in Teiioidea (Figures 19, 20 and 21) may point out the independent systematic identity of both these major taxa, surely in accordance with different evolutionary lines, in spite of any indubitable morphological convergence of their supraocular scutellar patterns.

It is now the turn of our comments on supraocular lepidosis in Scincoidea families, Scincidae and Cordylidae - Gerrhosauridae, thus completing our analytical relation as regards (regarding) the Scincomorpha branch of Autarchoglossa. The general homogeneity and shape uniformity of supraorbital scales, before revised, are again almost the same in Scincoidea, such as an authentic "Autarchoglossa band".

In all subfamilies of Scincidae (Greer, 1970) the supraocular pattern exposed in Figures 24-25 reveals no noticeable variations for either the 6, 5, 4, 3 broad longitudinal scales, or the reduced supraciliaries known for *Leiolapisma*, *Emoia*, *Egernia*, *Ctenotus* from Australia, *Mabuya* from middle East Africa and South America, *Eumeces taeniolatus* from Pakistan, *Eumeces obsoletus* from Kansas, USA, *Scincus scincus* from Irak, or *Scincus mitranus* from Saudi Arabia.

The scarce exceptions, registered in Figure 25, were drawn for *Sepsina* (Angola), *Chalcides* (South Europe, Canary Islands), *Malaconthas holomelas*, *Typhlosaurus lineatus* (S. Africa), *Tiliqua occipitalis* (Australia), *Ablepharus kitaibelii* (SE Europe). All the evolutionary diversifications (scale reduction, shape, etc.) likely originated from some primitive common strain under adaptive environmental push (ecological, climate changes, fossorial life, etc.).

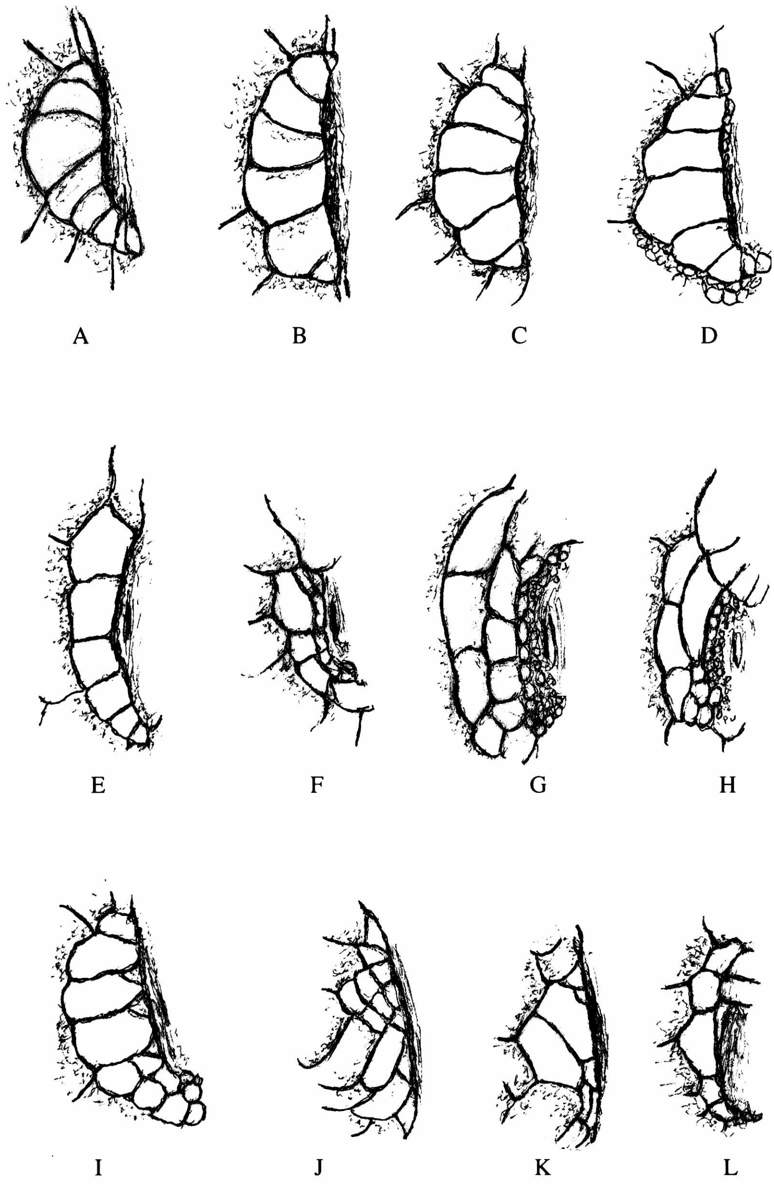

Figure 25. SCINCIDAE. A. *Eumeces taeniolatus* (Pakistan); B. *Eumeces obsoletus* (Kansas, USA); C. *Scincus scincus* (Irak, Arabia); D. *Scincus mitranus* (Saudi Arabia); E. *Sepsina copei* (Angola, W Africa); F. *Sepsina bayonii* (Angola, W Africa); G. *Chalcides chalcides* (S Italy); H. *Chalcides viridens* (Canary Isl.); I. *Malacontias holomelas* (Madagascar); J. *Typhlosaurus lineatus* (S Africa); K. *Tiliqua occipitalis* (Australia); L. *Ablepharus kitaibelii* (SE Europe, Turkey)

Figura 25. SCINCIDAE. A. Eumeces taeniolatus (Pakistan); B. Eumeces obsoletus (Kansas, USA); C. Scincus scincus (Irak, Arabia); D. Scincus mitranus (Saudi Arabia); E. Sepsina copei (Angola, W Africa); F. Sepsina bayonii (Angola, W Africa); G. Chalcides chalcides (S Italy); H. Chalcides viridens (Canary Isl.); I. Malacontias holomelas (Madagascar); J. Typhlosaurus lineatus (S Africa); K. Tiliqua occipitalis (Australia); L. Ablepharus kitaibelii (SE Europe, Turkey)

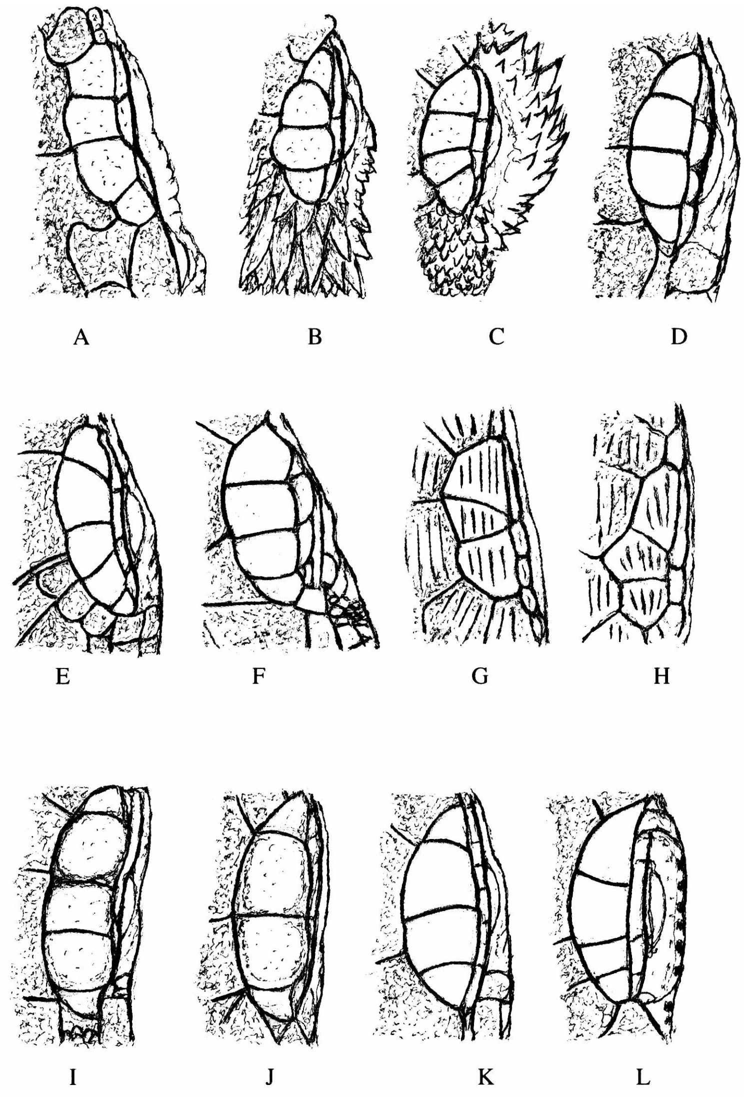

Figure 26. CORDYLIDAE. A. *Cordylus vittifer* (Angola); B. *Cordylus giganteus* (S Africa) ; C. *Cordylus polyzonus* (S Africa); D. *Pseudocordylus microlepidotus* (Cape Prov., S Africa); E. *Platysaurus guttatus* (S Africa); F. *Platysaurus capensis* (S Africa); G. *Chamaesaura aenea* (Transvaal, S Africa); H. *Chamaesaura anguina* (Cape Prov., S Africa).

GERRHOSAURIDAE. I. *Gerrhosaurus major* (S Africa); J. *G. nigrolineatus* (S Africa); K. *Zonosaurus maximus* (Madagascar); L. *Tetradactylus tetradactylus* (S Africa)

Figura 26. CORDYLIDAE. A. Cordylus vittifer (Angola); B. Cordylus giganteus (S Africa); C. Cordylus polyzonus (S Africa); D. Pseudocordylus microlepidotus (Cape Prov., S Africa); E. Platysaurus guttatus (S Africa); F. Platysaurus capensis (S Africa); G. Chamaesaura aenea (Transvaal, S Africa); H. Chamaesaura anguina (Cape Prov., S Africa).

GERRHOSAURIDAE. I. Gerrhosaurus major (S Africa); J. G. nigrolineatus (S Africa); K. Zonosaurus maximus (Madagascar); L. Tetradactylus tetradactylus (S Africa)

Cordylidae and Gerrhosauridae, considered as separate families in recent classifications, are lizards living in African and Madagascar territories. Exemplified in Figure 26, we remark the impressive similarity between their supraocular lepidosis and the above analysed scincid pattern. The supraciliary borders of these Scincomorpha are wider and more developed than supraciliaries of Scincidae. In the large, armoured *Cordylus* species, such as *C. giganteus*, *C. cataphractus*, *C. warreni*, *C. polyzonus*, the supraocular region is subject to sourrounding quills, horns, sharp-points of a strong dermal sclerosis. The broad longitudinal scales of so peculiar reptiles differ from 6 to 4 in number (mostly 4). An analogous remark can be made for other genera of Cordylidae and Gerrhosauridae, such as *Platysaurus*, *Gerrhosaurus*, *Zonosaurus, Tetradactylus* or the unusual snake-like *Chamaesaura* whose residual legged species exhibit deeply keeled scales.

To all appearance the "scincoid" model of supraocular scutellation is a prevalent one in the Scleroglossa taxon. Indeed, if we examine a sample of Squamata Anguimorpha, the great family Anguidae, i.e., with its more than 100 species and 13 genera, we get back to the kind of supraocular pattern we were reporting before for scincids as some *Eumeces*, *Scincus* or *Chalcides*, all lizards showing a tendency to minimization of legs and to having snake-like features. Of course, some adaptive Anguid characters are recognizable in drawings of Figure 27, as the strengthening of supraciliaries or the 7, 6, 5, 4 broad supraocular scales. A snake-like form is besides visible in the Euro-Asiatic *Anguis*, in *Ophisaurus gracilis* or *O. apodus* from SE Asia, in the several *Diploglossus* and *Ophiodes* from South America and West Indies.

In Estes *et al.*'s indented taxonomy, Xenosauridae, Anguidae and Varanoidea are included under the taxon Anguimorpha. But, as these authors stated, "the Xenosauridae and Anguidae cannot be demonstrated to be more closely related to each other than either is to Varanoids". Therefore, the authors placed xenosaurs, anguids and varanoids in an unresolved triatomy, and they mentioned that a metataxon Anguioidea wants sufficient reason for being formally recognized.

The impoverished family Xenosauridae adds to its strange, disjoint distribution (China, Mexico) some peculiarities of its supraocular scutellation, being thus in accordance with the sentence not long ago stated here on the

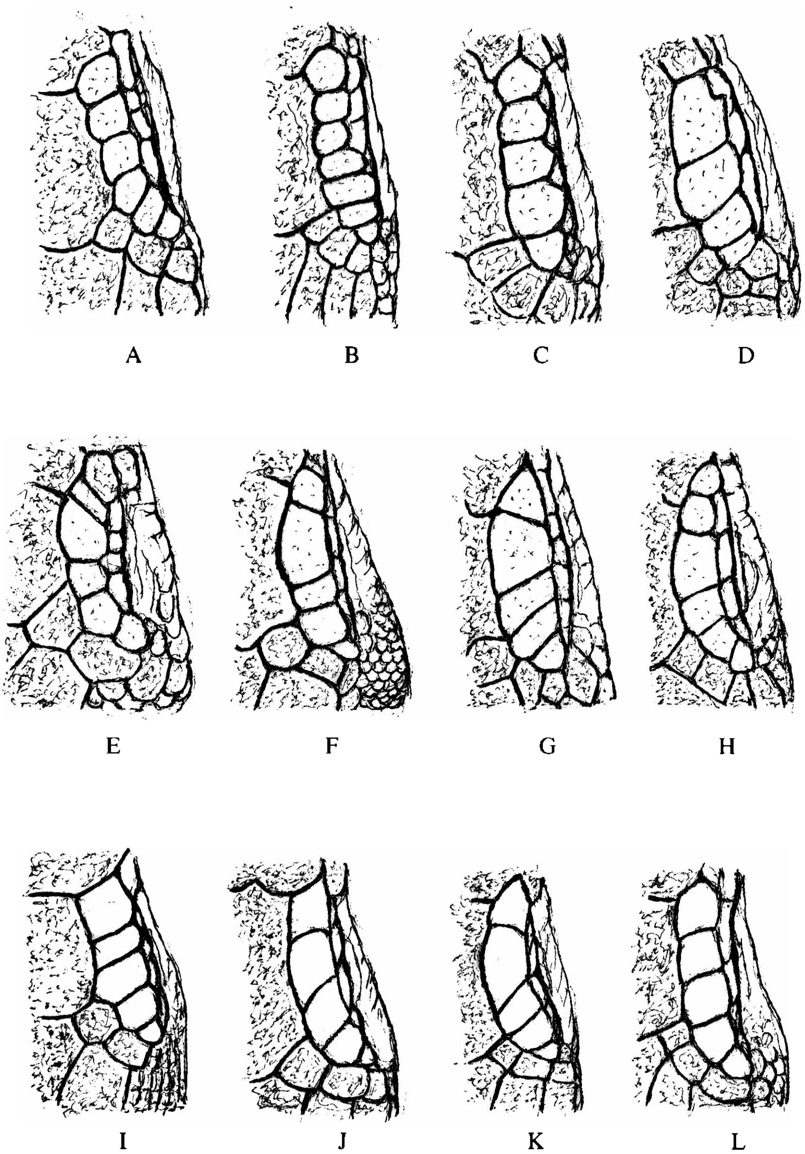

Figure 27. ANGUIDAE. A. *Anguis fragilis* (SE Europe); B. *A. fragilis* (N Europe); C. *Ophisaurus gracilis* (Hymalayas, Burma); D. *Elgaria coerulea* (Pacific coast USA, Costa Rica); E. *Diploglossus lessonae* (NE Brazil); F. *D. hewardii* (Jamaica, West Indies); G. *D. monotropis* (Costa Rica); H. *D. warreni* (Hispaniola, West Indies); I. *Ophiodes yacupoi* (Misiones, Argentina); J. *O. striatus* (S. Paulo, Brazil); K. *Ophiodes intermedius* (Entre Ríos, Argentina); L. *O. vertebralis* (Buenos Aires, Argentina)

Figura 27. ANGUIDAE. A. Anguis fragilis (SE Europe); B. A. fragilis (N Europe); C. Ophisaurus gracilis (Hymalayas, Burma); D. Elgaria coerulea (Pacific coast USA, Costa Rica); E. Diploglossus lessonae (NE Brasil); F. D. hewardii (Jamaica, West Indies); G. D. monotropis (Costa Rica); H. D. warreni (Hispaniola, West Indies); I. Ophiodes yacupoi (Misiones, Argentina); J. O. striatus (S. Paulo, Brasil); K. Ophiodes intermedius (Entre Ríos, Argentina); L. O. vertebralis (Buenos Aires, Argentina) precariousness of systematic categories such as Anguimorpha or Anguioidea. In fact, the Chinese monotypic *Shinisaurus* (*S. crocodilurus*, Figure 28) displays a supraocular bare covering with particular circumorbital semicircles and supraciliaries, round a somewhat eccentric relief more related to a Chinese decoration than to cephalic lepidosis. The few *Xenosaurus* species from Mexico, on the contrary, exhibit a very regular Squamata supraocular pattern with some Pleurodontid reminiscences, affording complete, evident circumorbital semicircles, opposed to moderate supraciliaries and, within their boundaries, a longitudinal row of broader scales, 4-5 in number, having some rows of irregular smaller scales on both sides.

In this same Figure 28, taxa belonging to the heterogeneous Varanoidea assemblage are presented. It is about two small, probably primitive families, as Lanthanotidae with only one species from Borneo, or Helodermatidae with two species from Mexico and SW United States, besides the remarkable Varanidae, whose more than 55 species of the unique genus *Varanus* spread from Africa and SE Asia to Australia and New Guinea. In *Lanthanotus borneensis*, the supraocular region is uniquely covered by dense, irregular small scales, without circumorbital semicircles but bordered by overlapping ciliaries. Somewhat similar is the pattern of *Heloderma suspectum* and *H. horridum*, the robust venomous lizards from sandy American deserts, even though size and distribution of their prominent round scales are distinct. In Figure 28, inferior row, the supraocular covering of the African *Varanus niloticus* and *V. exanthematicus* is drawn, together with that of the South Asiatic *Varanus monitor*. The uncertain boundaries of reduced supraocular semicircles, the absence of broad scales and the very narrow ciliaries of the African forms can be pointed out, contrasting with the more regular small supraocular scales of *Varanus monitor*, whose supraciliaries are reduced in the extreme. In Figure 29, a selection of supraocular coverings in several species from the extensive distribution of the genus is provided, from the gigantic *Varanus komodensis* or the differentiated scales of *Varanus grayi* from Philippines, where circumorbital semicircles are identifiable, to the very variable patterns of Australian taxa, where only the minimized scales of supraocular coverings and the utmost restricted space of supraciliaries are common characters.

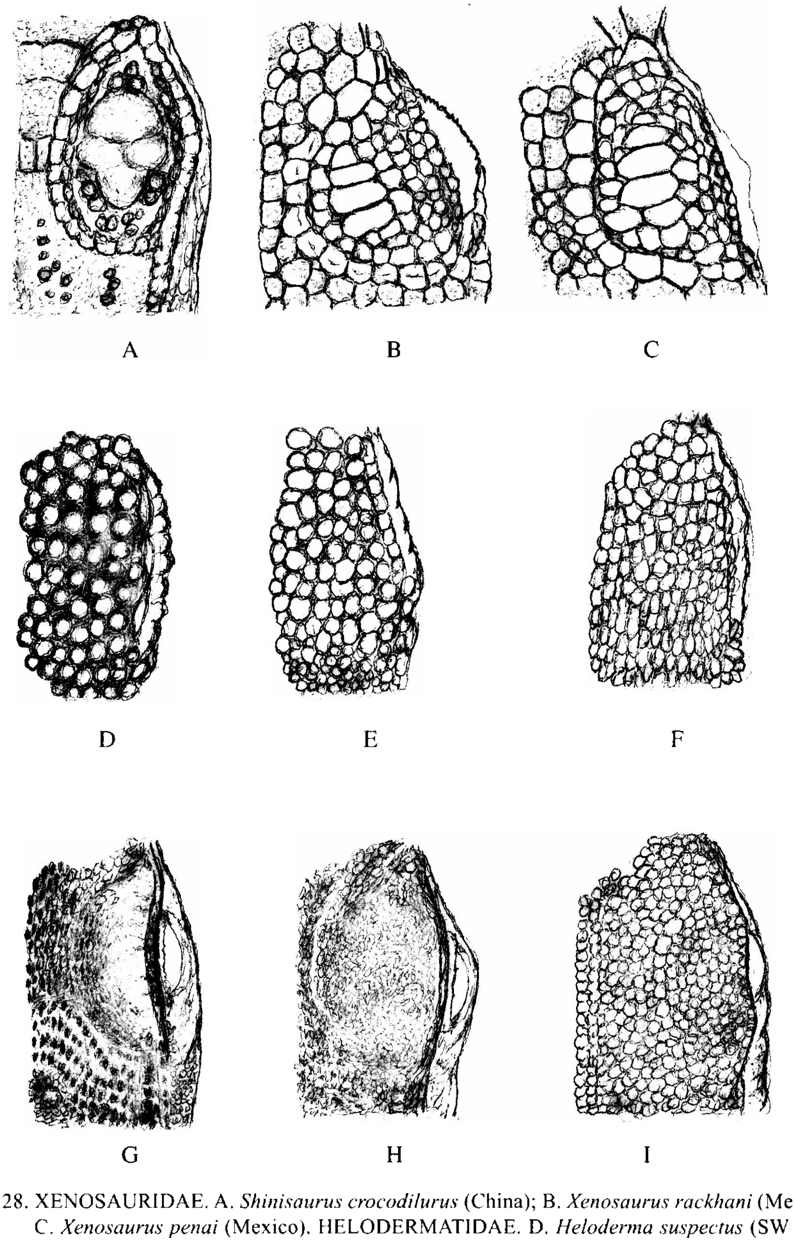

Figure 28. XENOSAURIDAE. A. *Shinisaurus crocodilurus* (China); B. *Xenosaurus rackhani* (Mexico); C. *Xenosaurus penai* (Mexico). HELODERMATIDAE. D. *Heloderma suspectus* (SW USA, N Mexico); E. *Heloderma horridum* (Tehuantepec, Mexico). LANTHANOTIDAE. F. *Lanthanotus borneensis* (Borneo). VARANIDAE. G. *Varanus niloticus* (E Africa); H. *V. exanthematicus* (S Africa); I. *V. monitor* (S Asia)

Figura 28. XENOSAURIDAE. A. Shinisaurus crocodilurus (China); B. Xenosaurus rackhani (Mexico); C. Xenosaurus penai (Mexico). HELODERMATIDAE. D. Heloderma suspectus (SW USA, N Mexico); E. Heloderma horridum (Tehuantepec, Mexico). LANTHANOTIDAE. F. Lanthanotus borneensis (Borneo). VARANIDAE. G. Varanus niloticus (E Africa); H. V. exanthematicus (S Africa); I. V. monitor (S Asia)

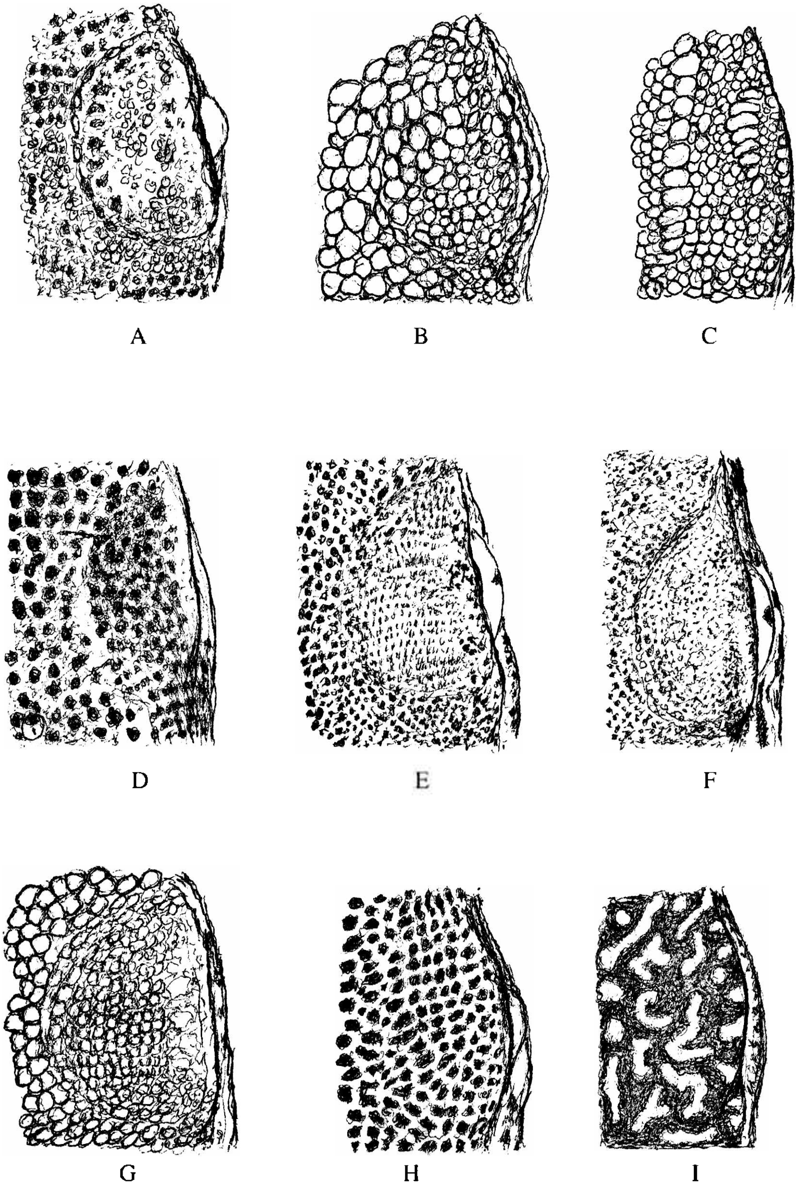

Figure 29. VARANIDAE. A. *Varanus komodoensis* (Komodo Isl. Indonesia); B. *Varanus grayi* (Philippine Isls.); C. *V. nebulorus* (Burma, Malasia); D. *V. mitchelli* (N Australia); E. *V. giganteus* (N Australia); F. *V. gouldii* (N Australia); G. *V. spenceri* (N Australia); H. *V. mertensi* (SW Australia); I. *V. timorensis* (Timor Isls., Australasia)

Figura 29. VARANIDAE. A. Varanus komodoensis (Komodo Isl. Indonesia); B. Varanus grayi (Philippine Isls.); C. V. nebulorus (Burma, Malasia); D. V. mitchelli (N Australia); E. V. giganteus (N Australia); F. V. gouldii (N Australia); G. V. spenceri (N Australia); H. V. mertensi (SW Australia); I. V. timorensis (Timor Isls., Australasia)

DISCUSSION

We must apologize for so long, often monotonous descriptive reports despite their unavoidable documentary essence. As first sentence, we can now state that a postulated relationship between the many morphological trends of Lacertilian supraocular lepidosis and a taxonomic evolutionary system is a reality. That is supported by drawings of our 27 Figures and their joined analytical comparative comments. We would like to add that the chosen indented taxonomy from the thought over treatise by Estes *et al.* (1988) was a very congruent one with the peculiar features and the systematic distribution of the many taxa examined in this paper. A still more convincing observation can be emphasized here with the undoubted affinity of our results with the reclassification of the Iguania by Frost *et al.* (2001). The families proposed in such a reclassification are well individualized by their supraocular scale patterns, thus a first distinction between Acrodonta and Pleurodonta is possible on these lepidosis characters. The almost uniform supraocular lepidosis of Agamid or Chamaeleonid taxa, with their more or less rounded or squared moderate scales, is in fact at first sight dissimilar from the well differentiated supraocular scales in Pleurodontid families as Leiocephalidae, Phrynosomatidae, Polychrotidae and Tropiduridae. Impressive is the family Leiosauridae, whose supraocular scutellation is unmistakable, of course taking generic and specific variations into account. But even more remarkable is its partition into two subfamilies, Leiosaurinae and Enyaliinae, proposed by Frost *et al.* (2001) and reproduced in the differentiation of supraocular scales in their respective taxa. Generic and specific variations occur in other families such as Hoplocercidae, Corytophanidae, Iguanidae, Liolaemidae, already with a recognizable Pleurodont brand, however with some primitive characters as in Opluridae, and exceptional divergence perhaps adaptive as in Crotaphytidae.

The great Squamata division into Iguania and Scleroglossa appears fully in accordance with the evolutionary morphological status of the supraocular lepidosis in lizards. A first separation between Gekkota and Autarchoglossa is also justified. In the cosmopolitan Gekkota stem, the families Gekkonidae, Diplodactylidae, Eublepharidae are distinguished by a variable expression of their scantily differentiated supraocular lepidosis, wanting recognizable circumorbital semicircles, showing moderate supraciliaries exceptionally prominent or sharp-pointed, and having a very heterogeneous layer of moderate roundish scales, frequently rarefied. Striking is a comparison with the joined snake-like family, the Australian Pygopodidae, whose adaptive modifications of the cephalic lepidosis, formerly studied by Kluge (1974), reaffirm the importance of supraocular scales as a discriminating taxonomic character.

Autarchoglossa and its subdivisions exhibit the most clear-cut difference from Iguania because of the supraocular lepidosis of all its numerous taxa, either Scincomorpha or Anguimorpha. A general pattern of some wide scales (2 to 7) longitudinally disposed along the ciliary border is repeated either in Lacertoidea or Scincoidea, as well as in Anguidae. A somewhat discordant supraocular scale reduction of the family Xantusiidae is unusual and takes us back to its probably uncertain taxonomic position invoked in a past careful Savage's research (1963).

The two major branches of Lacertiformes, Lacertidae from Africa and Eurasia, Teiioidea from the American continents, put in evidence a clear-cut example of parallel evolution, with their almost similar supraocular lepidosis patterns illustrated in our Figures 19-23. Some minor features attain to highlight the natural characteristics of an African or European lacertilid as well as those of a South American Teiid or Gimnophthalmid.

Gymnophthalmidae and Teiidae, formerly considered as microteiids or macroteiids are moreover distinguished now at family level also by their significant supraocular morphology. The peculiar case of the evolutionary modification of supraocular scales until their disappearance in the Gymnophthalmid genus *Bachia* has been reported. Scincoidea is still more respectful of the mentioned Autarchoglossa model of supraocular scutellation, either in its cosmopolitan family Scincidae or in its related African family Cordylidae, now divided by the creation of the related taxon Gerrhosauridae. With unavoidably distinct morphological features, also Anguidae, South American and Euro-Asiatic lizards appear not to deviate from the just commented morphological expression of supraocular lepidosis in Scincoidea. But the other taxon placed in Anguimorpha in our chosen indented taxonomy, the family

Xenosauridae, is the rarest finding in the whole Scleroglossa embranchment, either for its disjoint distribution (China, Mexico) or for the unusual supraocular scales. The probable artificiality of the taxon Anguimorpha was considered by the same authors of the indented taxonomy.

We reach the end of a simple, objective discussion of data from our patient comparative checking of hundreds of Squamata lizards. The last scanty families Helodermatidae and Lanthanotidae show a quite uniform, likely primitive, supraocular lepidosis, with roundish scales, evident supraciliaries but indistinct circumorbital semicircles. The extensive family Varanidae, unknown in the American continents, assembles a very variable set of supraocular coverings, from scales distinctly arranged to almost naked surfaces, mottled or variegated. A typical Varanid supraocular pattern is thus indefinable.

CONCLUSIONS

Conclusions of a scientific paper are the summarized exposition of every confirmed novelty or improvement concerning the original status or condition of morphological or biological systems that are the subject of research. Thus, in a synthetic sequence, the first conclusion of the present study is that the supraocular lepidosis in the Squamata taxa is not a structure at random, but a constant, defined scale arrangement, different in shape and size, in accordance with the species or other taxa considered and their evolutionary systematic position. Second conclusion is the significant agreement observed between a classificatory system, as the indented taxonomy elicited by Estes *et al.* (1988), and the results of our comparative research, leading to establishing defined supraocular lepidosis patterns as comparable morphological characters of every taxon. Third conclusion is that a reassessment of the Iguanian Pleurodonta taxon of Estes *et al.*'s indented taxonomy, as in the reclassification proposed by Frost *et al.* (2001), is also in agreement with morphological results on the supraocular scutellation of Squamata, shown in our comparative review.

A final conclusive remark is the repeated application of the pointed out relationships between indented phylogenetic taxonomy and differentiated supraocular lepidosis, such as in the case of several systematic new proposals.

The new Pleurodont family Leiosauridae and its two subfamilies must be here remembered, according to Frost *et al.* (2001). Other significant systematic agreements in relation to supraocular lepidosis can be cited for the families Scincoidea, Scincidae and Cordylidae and for the families Teiioidea, Teiidae and Gymnophthalmidae (macroteiids and microteiids).

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NOTE: This manuscript was still on his desk when unfortunately Dr. Cei died. He was internationally recognized and his work will remain indelible for future generations of herpetologists, because of his profuse and invaluable scientific contribution and proposal of new ideas for the biological sciences and evolution.

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