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Generic relationships within Cordyliformes (Reptilia : Squamata)

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Abstract

Following demonstration of Cordyliformes (Cordylidae + Gerrhosauridae) monophyly, the proposed phylogenetic position within the Scincomorpha as the sister-taxon of Scincidae is accepted. A phylogenetic hypothesis of generic relationships is proposed based on 74 character complexes. Within Gerrhosauridae, the Madagascan clade *Tracheloptychus-Zonosaurus* represents a single speciation event coinciding with the separation of Madagascar from Africa. Within African gerrhosaurids, the monotypic *Angolosaurus* is regarded as the earliest diverging taxon. *Gerrhosaurus* is the sister-taxon to a *Cordylosaurus-Tetradactylus* clade. Within the purely African Cordylidae, the serpentine *Chamaesaura* is the earliest diverging taxon. *Cordylus* is the sister-taxon to a *Platysaurus-Pseudocordylus* clade. A new classification is proposed based on these phylogenetic patterns. This classification parallels taxonomic categories within the Scincomorpha. Biogeographical patterns are evaluated in light of the proposed phylogeny and compared with Chamaeleonidae, the only other squamate taxon showing a similar distribution. Cordylidae and Gerrhosauridae differentiated before the Madagascar-Africa separation. The latter coinciding with the divergence of subfamilies within Gerrhosauridae. Furthermore, diagnostic features (based on character states and other autapomorphies) are presented for each monophyletic taxon together with its content and geographical distribution.

Key words: Reptilia, Cordyliformes, Cordylidae, Gerrhosauridae, phylogeny, taxonomy, biogeography.

Zusammenfassung

Anhand von Sammlungsmaterial verschiedener Museen wurden 74 Beschuppungs-, Skelett- und Weichteilmerkmale nebst andere biologischer Daten Angehörigen aller Gattungen der Cordyliformes untersucht, um eine kladistische Merkmalsanalyse durchzuführen. Dazu wurden zunächst Merkmalszustände definiert und soweit möglich mit dem Außengruppen-Verfahren, Polaritäten geklärt. Um die Verwandtschaftsbeziehungen zwischen den Gattungen zu ermitteln wurde ein Computer Programm zur Aufstellung eines Kladogramms unter Annahme geringstmöglicher Schritte unabhängiger, gleichgestalteter Merkmalsübergänge benutzt. Danach sind die Cordyliden und Gerrhosauriden monophyletisch. Die Gerrhosauridae spalteten in einem ersten Schritt in die zwei Subfamilien die Zonosaurinae auf Madagaskar und die Gerrhosaurinae auf dem Afrikanischem Kontinent, auf. Innerhalb der afrikanischen Gerrhosaurinae ist die monotypische Gattung *Angolosaurus* als am frühesten abgespaltene Einheit anzusehen. *Gerrhosaurus* ist die Schwestergruppe von *Cordylosaurus* + *Tetradactylus*. Innerhalb der ausschlielich afrikanischen Cordylidae ist *Chamaesaura* die primitivste phylogenetische Einheit. *Cordylus* ist die Schwestergruppe von *Platysaurus* + *Pseudocordylus*. Eine neue Klassifikation der Cordyliformes wird vorgeschlagen, die dem Kladogramm Rechnung trägt.

Schlüßelwörter: Reptilia, Squamata, Cordyliformes, Cordylidae, Gerrhosauridae, Phylogenie, Taxonomie, Biogeographie.

Introduction

HISTORICAL REVIEW OF THE TAXONOMY AND PROPOSED AFFINITIES OF CORDYLIDAE + GERRHOSAURIDAE

The taxonomic history and proposed phylogenetic affinities of the herein recognized squamate families Cordylidae and Gerrhosauridae are rather complex.

COPE (1871) was the first to indicate affinities between cordylids and gerrhosaurids and erected the family Cordylidae to incorporate both taxa. BOULENGER (1884) later defined the family Zonuridae to incorporate the now recognized family Cordylidae and the family Gerrhosauridae. BOULENGER's "Zonuridae" furthermore contained members of the present day Anguidae. His catalogue (1885) is arranged such that taxa follow a probable line of evolution. The Zonuridae (= Cordylidae) are located between the Xenosauridae and Anguidae, whereas his Gerrhosauridae are situated between the Lacertidae and the Scincidae.

On the basis of hemipenial morphology the Zonuridae (= Cordylidae) were placed by COPE (1896) within a phylogenetic context close to the Iguanidae, rejecting his previous (1871) arrangement and separating them from Gerrhosauridae. GADOW (1901) further supported COPE's latter hypothesis and places the Zonuridae (= Cordylidae) together with the Iguanidae in his suborder Lacertae.

CAMP (1923) maintained the Gerrhosauridae as part of the Scincomorpha, more specifically as related to Lacertidae (see also skiogram in ESTES *et al.* 1988). This is slightly different from BOULENGER's (1887) notion that the gerrhosaurids occupy an intermediate position between Lacertidae and Scincidae. CAMP (1923) furthermore moved the Zonuridae from their ascalabotan affinities as proposed by COPE (1896) to the superfamily Zonuroidea within his section Anguimorpha as closely related to Helodermatidae + (Xenosauridae + Anguidae). This although he suggested that some derived characters such as the split of the geniohyoideus muscle are shared between Zonuridae (exclusive of *Chamaesaura*) and Iguanidae. STEJNEGER (1936) pointed out that *Zonurus* MERREM, 1820 is antedated by *Cordylus* LAURENTI, 1768 and BOULENGER's Zonuridae was therefore emendated to Cordylidae.

Cordylidae and Gerrhosauridae have thus been maintained as separate families since BOULENGER (1886) (see references above; as also (COPE (1900), FURBRINGER (1900), MALAN (1940), LOVERIDGE (1942, 1944), FITZSIMONS (1943), etc.) until the *formal* taxonomic reunification by ROMER (1956), reflecting COPE's (1871) original concept.

The main thrust of MCDOWELL and BOGERT's (1954 : 98-102) section on cordylids was to demonstrate that in contrast to CAMP's (1923) hypothesis, cordylids are not anguiomorphs but rather scincomorphs. This was demonstrated beyond reasonable doubt. It is only briefly that MCDOWELL and BOGERT (1954) state that gerrhosaurids and cordylids should be regarded as belonging to the same family : "It may therefore be wise to follow the course taken by COPE (1871) and include the gerrhosaurs with the zonures in a single family Cordylidae." This statement was based on the fact that : "(Cordylidae) ... resemblance to the gerrhosaurs is particularly close, even to such details as head squamation and the presence of post-cloacal spines." This is in stark contrast to statements by VAN PLETZEN (1946) who suggested that : "A careful comparison of the skulls of *Cordylus* and *Chamaesaura* with that of *Gerrhosaurus* investigated by MALAN (1940) affords no evidence of any striking morphological similarities between the families concerned." No alternative hypotheses of relationships were proposed by VAN PLETZEN (1946). As is also the case with MCDOWELL and BOGERT (1954), overall similarities are no indication of relationships.

In contrast to the similarities indicated by MCDOWELL and BOGERT (l.c.) shared by these two groups, various differences were enumerated such as the morphology of the clavicle and the well-developed lateral fold in gerrhosaurids and the total lack thereof in cordylids.

DOWLING and DUELLMAN (1978) further complicate the matter by statements suggesting that "(Cordylidae) (sensu lato) appear to be closely related to the lacertids, from which they may be derived or to which they may have given rise." These statements were not supported by any evidence. Furthermore, the proposed phylogenetic hypotheses of UNDERWOOD (1971), NORTHCUTT (1978) and PRESCH (1988) with respect to the phylogenetic position of Cordylidae + Gerrhosauridae are rejected (see section on preferred phylogenetic hypothesis below).

RIEPPEL's (1980) investigations on the jaw musculature of "lizards" was the first study using cladistic methodology of outgroup comparison to establish the Cordylidae (sensu lato) as a monophyletic unit (see section on monophyly). This was however based on but a single synapomorphy.

ESTES (1983) resurrected the superfamily Cordyloidea which included the fossil taxa Paramacellodidae, and the families Xantusiidae and Cordylidae.

ESTES *et al.*'s (1988) cladistic analysis of squamate families shows that in CAMP's (1923) arrangement, only two families were misplaced at the "section"-level [1]. One of these is Zonuridae (= Cordylinae), which is moved from Diploglossa within the Anguimorpha to the Scincoidea within the Scincomorpha. Gerrhosauridae is only shifted within the Scincomorpha from Lacertoidea to Scincoidea.

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[1] For convenience see CAMP's "skiogram" in ESTES *et al.* (1988).

McDowell and Bogert's (1954) suggestion that cordylids and gerrhosaurids share similarities was taxonomically formalized by Romer (1956), who separated the family Cordylidae into two subfamilies : Gerrhosaurinae and Cordylinae. Loveridge (1957), Wermuth (1968), Guibe (1970), Estes (1983), Brygoo (1985), Estes *et al.* (1988) and others all followed. In contrast, Hoffstetter (1962 : 254) reverted to the recognition of two separate families Cordylidae and Gerrhosauridae with the following statement : "Tout en reconnaissant les affinités réciproques des deux groupes j'estime qu'on ne doit pas minimiser à l'excès les différences reconnues par Cope, Furbringer et notamment par Camp." In any case the recognition of these taxa as subfamilies or families is subjective; rather the question of their monophyly and affinities is a more pressing issue.

Herein I recognize Cordylidae Gray (including : *Cordylus* Laurenti, *Chamaesaura* Schneider, *Platysaurus* A. Smith and *Pseudocordylus* A. Smith) and Gerrhosauridae Fitzinger (including : *Angolosaurus* Fitzsimons, *Cordylosaurus* Gray, *Gerrhosaurus* Wiegmann, *Tetradactylus* Merrem, *Tracheloptychus* Peters and *Zonosaurus* Boulenger [2]).

Monophyly of Cordylidae + Gerrhosauridae

Estes *et al.*'s (1988) phylogenetic analysis of squamate families supported Rieppel's (1980) hypothesis of a Cordylidae (sensu lato)-Scincidae clade. Estes *et al.*'s (1988) suggestion of splitting the single taxon Cordylidae within their character data matrix into component parts (genera) in order to substantiate the monophyly thereof has been taken to heart. In reevaluating Estes *et al.*'s hypothesis, the characters defining Iguania and Gekkota were omitted, reducing the initial character data set from 148 characters to 86. These 86 characters were reevaluated for each of the ten genera within the ingroup (Cordylidae + Gerrhosauridae). The resulting most parsimonious cladograms revealed that Gerrhosauridae was more closely related to Scincidae than to Cordylidae (238 steps; consistency index (C.I.) = 0.412). The Gerrhosauridae-Scincidae node however, was supported exclusively by homoplastic apomorphies (either reversals or convergences). In contrast, a cladogram indicating the monophyletic status of Cordylidae + Gerrhosauridae was only slightly longer (243 steps, C.I. = 0.403). In either case, there is no good evidence from the Estes *et al.* (1988) character data set to either reject or confirm the monophyly of Cordylidae + Gerrhosauridae.

A brief discussion of the seven characters listed by Estes *et al.* (1988) in support of the monophyletic status of Cordylidae + Gerrhosauridae is also warranted. The supratemporal fenestra closed primarily by the postorbital bone is convergent with Xantusiidae, Gymnophthalmidae and Anguidae. Symmetrical posterior skull epidermal scales surrounding a small interparietal is only applicable to the cordylids *Platysaurus*, *Pseudocordylus* and *Cordylus*. A relatively large and expanded coracoid is a subjective character and difficult to evaluate. The origin of the 3b head of the profundus layer of the m. adductor mandibulae externus from the mesial margin of the upper temporal fossa is convergent with some skinks (Rieppel, 1980). The attachment of some fibers of the 3c head of the profundus layer of the m. adductor mandibulae externus posteroventrally on the lateral surface of the bodenaponeurosis is convergent with Lacertidae (Rieppel, 1980). The osteoderms of cordylids and gerrhosaurids may in fact not be homologous as judged from Otto's (1909) and Schmidt's (1913) descriptions, but certainly need to be further investigated. Five attachment points for ribs on each side of the sternum is the plesiomorphic condition for Squamata and represents a reversal within Autarchoglossa, and is furthermore not present universally throughout Cordylidae + Gerrhosauridae.

The presence of cloacal spurs (Fig. 14) cited by McDowell and Bogert (1954), although universally present within Cordylidae + Gerrhosauridae, perhaps indicates an adaptation to a mode of copulation. Cloacal spurs are also found in *Kentropyx* and other teiids, in *Varanus storri* where it forms a comb-like structure, and in Gekkota.

The best evidence for the monophyly of Cordylidae + Gerrhosauridae comes from non-osteological structures; more specifically hemipenial morphology, myology of the trigeminal musculature and karyotype. Olmo and Odierna (1980) conclude that Cordylidae + Gerrhosauridae is a homogeneous and conservative group with respect to karyotype. Five of the ten ingroup genera were investigated and showed karyotypes consisting of 34 chromosomes (12 bi-armed macrochromosomes and 22 microchromosomes; FN = 46). This karyotype however is convergent with the karyotype of *Crocodilurus* (Gorman 1970; 1973). Rieppel (1980) offers the reduction (Cordylidae) and loss (Gerrhosauridae) of the insertional tendon of the pseudotemporalis superficialis muscle as a synapomorphy uniting these two clades. Böhme's (1988) investigation on genital morphology of squamates reveal three hemipenial structures that are found in Cordylidae + Gerrhosauridae and not in any other squamate taxa, and thus may serve as synapomorphies to indicate their monophyly. These are : 1) a thin, strongly folded apex; 2) irregularly arranged plicae with tendencies to slant, coalesce or be lost and 3) a strongly sigmoid sulcus spermaticus proximally with a hypertrophied lower (medial) sulcal lip (Böhme, 1988 : Fig. 29; Figs. 15 & 16). Also mentioned is an anchored internal tissue plate which functions as a support structure. Internal hemipenial support structures have also been

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[2] *Aspidosaurus* predates *Zonosaurus*. Brygoo ZN(S) 2465 has submitted a petition to have *Aspidosaurus* suppressed.

described in lacertids by Arnold (1973; 1983; 1986). It is not clear whether these structures are homologous or if a thin apex simply necessitates a rigid internal support structure.

Among Lepidosauromorphs the postfrontal bone is large, extending into the superior temporal fenestra (Estes *et al.*, 1988) in all taxa except those Iguanians that have a postfrontal bone (Etheridge and De Queiroz, 1988) and Cordylidae + Gerrhosauridae. The condition observed in lacertids and xantusiids is questionable (see Estes *et al.*, 1988 for discussion). It is clear that a reduced postfrontal bone, without a posterior flange, and not surrounding the superior temporal fossa can be regarded as further support for the monophyletic unity of Cordylidae + Gerrhosauridae. The condition observed in *Chamaesaura*, in which the postfrontal has a small posterior process, can be regarded as a consequence of the elongation of the skull in particular in the temporal region.

Although the monophyly of Cordylidae + Gerrhosauridae does not rest on overwhelming evidence, poly- or paraphyly at this point seems less likely. It is clear however that they are scincomorphs and together with Scincidae form the Scincoidea (Estes *et al.*, 1988). Parallel to these morphological further biochemical investigations should be probed to illuminate the systematic position and the monophyly question of Cordylidae + Gerrhosauridae.

Goals and problems of this study

The primary foci of this study are to investigate and establish the monophyletic status of the two families within the ingroup, and to postulate the phylogenetic affinities and monophyly of the ten genera therein. The assumption is made that the terminal taxa are monophyletic. Future investigations may reveal however that some of the genera are paraphyletic (Mouton, pers. comm.). The composition of the terminal taxa (i.e. genera) is defined by our knowledge at this moment (See diagnoses).

Furthermore, a diagnosis and description of the terminal taxa is sought. This diagnosis includes the monophyletic status as supported by synapomorphies, as well as distribution and possible autapomorphies.

An additional goal is to test the hypothesized phylogeny against proposed zoogeographic hypotheses of other squamate taxa as they relate to Madagascar and the African continent.

The hypothesized phylogeny is based on characters of pholidosis, osteology, characters from soft anatomy and characters of life history. Characters obtained from the literature such as modes of reproduction, karyotypes, genetic information, ecological data and physiological attributes are also listed, when a complete data set is available. Most of the latter characters, in addition to a few others could not be used as systematic characters because a complete data set for all in- and outgroup taxa was not obtainable and therefore an un-equivocal interpretation of the polarity of these characters states was not possible. These characters are listed in the section entitled "Characters not used in this study."

Material and Methods

SPECIMENS

Specimens used in this study were either preserved in alcohol, cleared and stained, or skeletons. Some of the skeletal material used was prepared from preserved specimens in order to obtain a satisfactorily large enough series for observing possible skeletal variation and ontogenetic changes. A list of specimens examined is in Appendix A.

OUTGROUP COMPARISON

Phylogenetic histories can only be constructed by synapomorphies (= shared derived characters) (Hennig, 1966). Synapomorphies contain information about the history of speciation of related entities and are indicators of monophyletic taxa, the only justifiably usable groups within a systematic or for that matter biological framework.

In order to discover synapomorphies, the polarity of character transformation series must be known. Methodologies for phylogenetic reconstruction have been reviewed by many authors such as Crisci and Steussy (1980), De Jong (1980), Stevens (1980), Arnold (1981), Nelson and Platnick (1981), Watrous and Wheeler (1981), Wiley (1981), Maddison *et al.* (1984), Ax (1984), Estes *et al.* (1988), Lang (1989), Lang (1990A) and others (see also literature cited therein). The ontogenetic and outgroup analysis methods have proven to be the most widely accepted and most logical methods.

Outgroup comparison ensures that ingroup relationships are not only parsimonious internally, but that they are also consistent when considered in the context of related groups (Engelmann and Wiley, 1977; Farris, 1982; Maddison *et al.* 1984).

Estes *et al.*'s (1988) analysis of squamate families has provided a framework for the choice of outgroup taxa to Cordylidae. The first taxonomic outgroup is Scincidae; the second Lacertoidea [Xantusiidae + (Lacertidae + (Gymnophthalmidae + Teiidae))] and the third is Anguimorpha (Estes *et al.*, 1988 : 140).

Maddison *et al.*'s (1984) methodology of outgroup analysis allows for easy determination of character states at any node within a cladogram. Interior nodes are determined by combining previously determined states at higher nodes. The following example pertains to a character having the binary states X and Y. If both higher nodes show state X then the interior node is assigned the state "X". If on the other hand one state has condition X and the other node exhibits the alternate character state Y, than an equivocal "X,Y" is assigned to the interior node. As defined, the equivocal "X,Y" indicates that it is equally parsimonious to assume that character states X or Y are plesiomorphic at that node. The polarity at the next inferior node is determined the same way as described above. For multistate characters the situation is more difficult and will be dealt with as it arises.

Maddison *et al.* (1984) indicate that a minimum of two operational taxonomic outgroups are required to assure accurate polarity assessment at the outgroup node. Only two outgroups are required if Maddison *et al.*'s (1984) "doublet rule" applies.

Table 1 summarizes the six possible distribution patterns of character states among the outgroup taxa and their subsequent polarity assessment at the outgroup node, following the methodology stipulated by Maddison *et al.* (1984). Only three of these (Cases I, III, IV) result in unequivocal polarity decisions. Characters showing a case II, V, or VI character state distribution pattern among outgroup taxa result in an equivocal polarity decision at the outgroup node. These latter character complexes will be left unpolarized within the character data matrix. (See also Fig. 41).

Estes *et al.* (1988) give an extensive discussion on the problems of variation involved in cladistic analyses. An important point made is that in previous systematic studies little or no comment on variation observed was reported. Therefore an adequate series of specimens for terminal taxa is necessary. Effort is made within this study to indicate observable variation within all terminal taxa. When variation occurs Kluge and Farris' (1969) suggestion of splitting that taxon into two "new" taxa in order to maintain information is used.

Table 1 :
Summary of character state distribution patterns among 3 outgroup taxa (OT) for binary characters with subsequent polarity assesment. See Appendix D for algorithm. 0 = plesiomorphic state.

CASE	OT1 Scincidae	OT2 & OT3 Anguiomorpha & Lacertoidea		Polarity Assesment
I	X	X	X Y X,Y	X = 0
II	X	Y	Y X,Y	EQUIVOCAL
III	X	X,Y	X,Y	X = 0
IV	X,Y	X	X X,Y	X = 0
V	X,Y	X	Y	EQUIVOCAL
VI	X,Y	X,Y	X,Y	EQUIVOCAL

Cladograms were constructed using the Paup (Phylogenetic Analysis using Parsimony) algorithm of Swofford (1985, version 2.4.1) based on the data matrix of 74 independently polarized and unpolarized character transformation series (Appendix B). Both the multiple parsimony and global swapping options for reading the input data matrix were used. The multiple parsimony option initiates the search for multiple equally parsimonious trees via branch-swapping, which often results in the discovery of shorter (more parsimonious) trees. Global swapping ensures overall global parsimony (Swofford, 1985). In addition, the Deltran (delayed transformation), which prefers convergences over reversals and the Farris optimization methods (Farris, 1970) were compared.

For unpolarized character transformation series, the "ancestor" line, upon which the remaining clades are rooted is coded as unknown ("9"), and the transformation series itself is coded as unordered. These unordered character transformations are polarized by the Paup algorithm by correlation with the most parsimonious trees generated by the independently polarized transformations.

Missing information for terminal taxa such as characters relating to the innervation of the appendages for limbless taxa are coded as "unknown" ("9") for that taxon.

Character weighting is rejected because of the inherent subjectivity (Patterson, 1982; Novacek, 1986). Rather, less parsimonious trees are compared with more parsimonious trees and criteria of biological importance and biogeography are used to evaluate the various hypotheses.

Systematic characters

Characters as defined in this study, represent evolutionary changes or modifications of existing structures. These characters differ absolutely between the terminal taxa. Examples of such are : the absence or presence of a structure; positional differences between structures that do not change during post-embryonic ontogeny; differences in shapes of structures; and variation in the number of serial structures to name a few.

Characters whose variation within a terminal taxon obscures the pattern of variation of that character between terminal taxa are excluded. Characters showing proportional differences can not be used, because they often reflect allometry. The exception here are characters that define structures that are under obvious ontogenetic control, versus homologous structures in other taxa that do not change during ontogeny (De Queiroz, 1985). These characters can only be defined providing that a sufficiently large ontogenetic series is examined in both in- and outgroups.

Autapomorphies of terminal taxa do not contain any information about relationships between taxa, but are informative as indicators for monophyletic clades and are cited in the diagnosis of taxa section.

Hypotheses of polarity are established for each character transformation series using the outgroup comparison method described above. Character states of a linear transformation series with a higher number indicate a direct transformation from a character state with the next lower number: 0 is used for the primitive state, 1 for the derived or intermediate state when a multi-state character is used, and 2 is the most derived state in a three state character transformation series, etc. A bidirectional transformation series on the other hand, implies a case of character evolution in two directions on either side of the plesiomorphic (ancestral) state. A bi- or multidirectional transformation series can be considered as two (or more) "uni-" directional transformation series in alternate directions and is coded as such.

Each of the defined character complexes is followed by a description of its condition in, and variation among the terminal taxa and outgroups together with the polarity decisions. Unpolarized character states are followed by an asterisk (*). Description of characters used from other studies are referenced followed by brief comments on discrepancies, ambiguities and/or conflicting ideas about polarity decisions as they arise. I do not consider it necessary to provide an elaborate discussion and description of the terminology used; for that, the reader is referred to the excellent anatomical descriptions of Siebenrock (1892, 1895), Camp (1923), Essex (1927), Malan (1941, 1946), Van Pletzen (1946), Mcdowell and Bogert (1954), Romer (1956), Rieppel (1980), Berger-Dell'Mour (1983) and Böhme (1988) for skeletal anatomy, hyoid apparatus, myology and hemipenial morphology. Scalation terminology follows Fitzsimons (1943) and Loveridge (1942 & 1944).

Information on the character states for the outgroup taxa was initially checked on specimens then compared to literature references. See Estes *et al.* (1988) for references providing information on outgroup taxa.

In the following section are descriptions of character complexes used in this analysis. The character complexes are divided into six sections and are for the most part arranged from anterior to posterior. The six defined sections are: 1) Scale characters; 2) Characters of Soft Anatomy; 3) Characters of Cranial Anatomy; 4) Characters of Postcranial Anatomy; 5) Characters of Life History and 6) Miscellaneous characters.

SCALE CHARACTERS

S1) *Position of nasal scales (N)*: 0) Nasal scales separated; 1) in contact. [Nasal scales separated in Scincidae (contact in *Riopa*), Gymnophthalmidae and Anguimorpha [3] as well as in *Holaspis guentheri* and some *Lacerta*. Xantusiidae, remaining Lacertidae and Teiidae have nasal scales in contact/CASE I].

In *Cordylus* all species except *giganteus*, *warreni* (Loveridge, 1944) and *lawrenci* the N scales are in contact. In *Platysaurus* considerable variation exists as shown by Broadley (1978). *Platysaurus imperator* has a 50-50 condition. In *Platysaurus maculatus* most specimens show N scales contacting each other, but with *P. maculatus lineicauda* showing complete separation of N scales (Broadley, 1978). Likewise, *Platysaurus fitzsimonsi* and *P. intermedius* have variable contact. On the other hand in *Platysaurus capensis* (Loveridge, 1944), *P. pungweensis* and *P. torquatus*, the N scales are consistently in contact. Nasal scales are consistently separated only in *Platysaurus relictus* (Broadley, 1978).

In *Chamaesaura* and *Pseudocordylus* the nasal scales are in contact.

In gerrhosaurids a more consistent pattern is observed. In *Angolosaurus*, *Tracheloptychus*, and in *Zonosaurus* the N scales are separated. In the other three genera: *Cordylosaurus*, *Gerrhosaurus* and *Tetradactylus* the N scales are in contact.

S2) *Condition of nostril*: (Bi-directional transformation series) 0) Nostril is surrounded entirely by the N or at the most by two scales: PN (postnasal) and N (0,0); 1A) Nostril is surrounded by only three scales: N, PN and first UL (upper labial) (1,0). In this condition the first UL is also in contact with the N scale; 1B) Nostril is bordered by 4 scales: the first UL, PN, N and R (rostral) (0,1). Fitzsimons (1943) described the two alternate apomorphic conditions. [Among outgroups examined only Xantusiidae and *Psammodromus* show condition 1A. The remaining taxa have at most 2 scales around the nostril/CASE I].

All cordylids exhibit the plesiomorphic character state in which the nostril is either entirely within the N scale or situated between the N and PN scale.

Character states 1A and 1B were identified in all gerrhosaurids, with the exception of *Tetradactylus breyeri* in which the nostril is located between the N and the PN scale. Character state 1A is typical of the african gerrhosaurids (*Angolosaurus*, *Cordylosaurus*, *Gerrhosaurus* and *Tetradactylus*) (Loveridge, 1944), whereas character state 1B (4 scales surrounding nostril) was identified in the malagasy gerrhosaurines (*Tracheloptychus* and *Zonosaurus*).

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[3] No homology is possibly with the head scales in Varanidae and Helodermatidae, which include most characters up to character S16.

S3) *Postnasal scale (PN)* : 0) PN distinct and separate from the N scale; 1) PN fused to N. [PN are distinct in all outgroup taxa except Gymnophthalmidae and Teiidae (fused with first loreal) and *Aniella* in which N-PN-1UL are fused into a single scale/CASE I].

All gerrhosaurids exhibit the plesiomorphic condition. Within Cordylidae the derived character state (lack of distinct PN) is identified only in *Chamaesaura*, in *Pseudocordylus spinosus*, and in the following *Cordylus* : *campbelli*, *coeruleopunctatus*, *mclachlani*, *namaquensis* and *warreni*.

S4) *Nasal(N)-prefrontal(PF) scales* : 0) N-PF separated (because of FN(frontonasal)-LO(loreal) contact); 1) N-PF in contact. [Among outgroup taxa examined all had a N-PF separation with the exception of *Typhlosaurus*, *Acontias* and *Panaspis* in which the PF are fused to the FN to form a large plate which contacts the N/CASE I]. The derived condition occurs exclusively in *Chamaesaura*, *Cordylus warreni*, *C. rhodesianus* and *Pseudocordylus spinosus*.

The situation in *Cordylosaurus* is unique because the PF scales are fused to the frontonasal scale to form a large shield. In *Tetradactylus* a variety of conditions occur. In the near-limbless *Tetradactylus africanus* and *T. tetradactylus* the PFs are fused with the FN to form a single large scale. In *Tetradactylus seps* either a single large (Berger-Dell'Mour, 1983) or two small scales are present (Fitzsimons, 1943; pers. observ.). The conditions in both *Tetradactylus* and *Cordylosaurus* are coded as missing information (9).

S5) *Prefrontal (PF) scales* : 0) distinct; 1) fused with the FN to form a large shield. [All outgroup taxa have distinct PF except *Typhlosaurus*, *Acontias*, *Panaspis* (see previous character) and *Diploglossus* (fused)/CASE I].

Among the ingroup taxa, the apomorphic character state is expressed in *Cordylosaurus* and *Tetradactylus* (see above). In all specimens of *Tetradactylus* examined, the PF scales are fused to the frontonasal scale. A drawing of Angel (1922 : 2) however illustrates *Tetradactylus ellenbergeri* in which the PF scales are distinct. Another variant is *Tetradactylus seps*. The illustration by Berger-Dell'Mour (1983 : 21) shows *Tetradactylus seps* with the 2 PFs fused together to form a single scale separate from the FN scale. Neither of these conditions were confirmed with available material.

S6) *Prefrontal (PF) scales*: [Character states unordered] 0*) PF in contact; 1*) PF separated (due to the contact between the Fj ♂and FN). [Scincidae and part of the Anguimorpha (*Anguis* and *Aniella*) have separated PF whereas some other taxa of the Anguimorpha (*Ophisaurus*, *Elgaria*, *Diploglossus*), lacertids, xantusiids, micro- and macroteiids have PF in contact/CASE II, polarity decision equivocal].

The distribution of the character states among the ingroup taxa does not show any consistent pattern. Within cordylids, the PF scales are in contact in *Chamaesaura aenea*, *Cordylus campbelli*, *C. cordylus*, *C. lawrenci*, *C. mclachlani*, *C. macropholis*, *C. namaquensis*, *C. polyzonus*, *C. pustulatus*, *C. rhodesianus* and *C. warreni*. They are also in contact in all *Platysaurus* and in *Pseudocordylus capensis* and *P. microlepidotus*. In gerrhosaurids, PFs are in contact in *Angolosaurus*, *Gerrhosaurus major*, *G. multilineatus*, *G. nigrolineatus*, *G. validus*, *Zonosaurus karsteni*, *Z. laticaudatus*, *Z. maximus*, *Z. quadrilineatus* and *Z. trilineatus* (Lang, 1990b). In all of the remaining ingroup taxa examined the PFs are separated by the F-FN scales. To be noted again is the fact that *Tracheloptychus* and *Cordylosaurus* lack PF scales and are coded as having missing data (9).

S7) *Subocular scale (SO)* : 0) SO not part of the upper labial margin; 1) part of the upper labial margin. [SO forming part of the upper labial margin was only observed in some skinks (*Mabuya*, *Sphenomorphus*, *Eumecia*, *Riopa* and *Panaspis*) and in some lacertids (except *Eremias* and *Acanthodactylus*). In all other outgroup taxa examined, the subocular scale did not form part of the upper labial margin/CASE I].

The apomorhic character state (a large subocular forming part of the upper labial margin) is present in *Chamaesaura*, *Cordylus coeruleopunctatus*, *C. peersi*, *C. polyzonus*, *C. warreni*, *Platysaurus*, *Pseudocordylus* and in all gerrhosaurids except *Angolosaurus*.

S8) *Supralabial scales (SL) anterior to subocular (SO)* : 0) 4 or more SL anterior to the SO forming part of the supralabial margin; 1) 3 supralabials; 2) only 2 supralabials anterior to the subocular scale that is part of the labial margin. [Among outgroups with a SO forming a part of the supralabial margin 5 SL are anterior to the SO in the scincids *Mabuya*, *Sphenomorphus* and in some lacertids. In *Eumecia* and other lacertids 4 SL are anterior to SO/CASE I]. This character is not a duplication of the previous character because some taxa have a SO forming part of the supralabial margin, but with 4 or more SL anterior to it. On the other hand those taxa that do not have a SO forming part of the supralabial margin also show the plesiomorphic condition for this character.

Within the ingroup, the plesiomorphic condition is present in all cordylids (with the exception of *Chamaesaura*) as also *Angolosaurus*, *Gerrhosaurus validus*, and in all *Zonosaurus* with the exception of the three species mentioned below.

The intermediate condition is present in *Chamaesaura* and the gerrhosaurids *Cordylosaurus*, *Gerrhosaurus* (with the exception of *validus*) *Tracheloptychus*, *Tetradactylus tetradactylus* and *T. seps*j ♂and in *Zonosaurus aeneus*, *Z. brygooi* and *Z. rufipes* (Lang, 1990b).

The derived character state with only 2 SL anterior to the SO that is part of the labial margin is only exemplified in *Tetradactylus africanus*, *T. breyeri*, *T. eastwoodae* and *T. ellenbergeri*. The derived character state (2) is found below the level of analysis (genera) of this study and is therefore left out of the character data matrix. *Tetradactylus* is coded as 1.

S9) *Frontoparietal scales (FP)* : 0) present; 1) present in juveniles, fused in adults; 2) absent. [FP present in most Scincidae (absent in *Acontias*, *Typhlosaurus*), Xantusiidae, most Lacertidae (fused to IP in *Holaspis guentheri*), Teiidae and Anguimorpha (not applicable to Varanidae and Helodermatidae). In Gymnophthalmidae the FP are fused with the IP (interparietal)/CASE IV]. All cordylids, *Angolosaurus*, *Gerrhosaurus* and *Tetradactylus* exhibit the plesiomorphic condition.

In *Cordylosaurus* the frontoparietal scales are distinct in juveniles but during ontogeny fuse with the median P and IP to form a single scale (intermediate condition) (Fitzsimons, 1943).

In the malagasy gerrhosaurines (*Tracheloptychus* and *Zonosaurus*) the derived character state is expressed in which there is a presumed embryonic fusion of the PF scales to the F. Both juveniles and adults have but a single scale located between the parietal and PF scales.

S10) *Number of parietal scales (P)* : 0) 2; 1) 4. [Scincidae, Lacertidae and Anguimorpha (not applicable to Varanidae and Helodermatidae) have 2 parietal scales; Xantusiidae, Gymnophthalmidae and Teiidae have 4 parietal scales/CASE I].

This character is consistent and shows a strict dichotomy between the 2 families. All cordylids have 4 parietal scales, whereas all gerrhosaurids have but 2.

S11) *Anterior parietal scales*: 0) separated; 1) in contact. [All outgroups have separated anterior parietal scales (not applicable in Varanidae & Helodermatidae)/ CASE I].

The anterior parietal scales are identified as those scales immediately posterior to the FP or F. In the case of cordylids these are the anterior pair of parietals. In gerrhosaurids they are the parietal scales.

In all gerrhosaurids with the exception of *Angolosaurus* the anterior parietal scales are in median contact posterior to the interparietal scale (1). In *Angolosaurus* they are completely separated by a rather prominent interparietal scale (0).

In cordylids the distribution of character states is not as clear-cut. Median contact is observed in most *Cordylus* (*campbelli*, *coeruleopunctatus*, *cordylus*, *lawrenci*, *mclachlani*, *peersi*, *polyzonus*, *pustulatus*, *tropidosternum* and in *warreni warreni*, *w. barbertonensis*, *w. vandami*), most *Platysaurus* (*capensis*, *guttatus guttatus*, *imperator*, *intermedius*, *maculatus*, *ocellatus*, *pungweensis* and *torquatus*) and in all *Pseudocordylus* examined. The anterior parietal scales are however separated in *Chamaesaura*, the remaining *Cordylus* (*cataphractus*, *giganteus*, *macropholis*, *namaquensis*, *rhodesianus*, *vittifer*, *warreni depressus*, *w. laevigatus*, *w. perkoensis*) and in *Platysaurus guttatus minor* and *mitchelli*.

S12) *Interparietal(IP)-frontoparietal(FP)* : 0) in contact; 1) separated. [All outgroups exhibit an IP-FP contact (not applicable to Varanidae & Helodermatidae, IP & FP fused in *Holaspis guentheri* and in Gymnophthalmidae/CASE I].

The interparietal is separated from the frontoparietal scale (derived condition) in the the following *Cordylus* : *campbelli*, *coeruleopunctatus*, *cordylus*, *lawrenci*, *mclachlani*, *peersi*, *pustulatus*, *polyzonus*, *tropidosternum*, *warreni warreni*, *w. barbertonensis*, *w. vandami*, in all *Platysaurus* except *Platysaurus guttatus minor* and in *Pseudocordylus*.

The plesiomorphic condition is found in the remaining cordylids as well as all gerrhosaurids. It should be noted that the madagascan gerrhosaurids are coded as unknown (9) because the FP are fused with the F (Lang, 1990b).

This character is different from the anterior parietal scale contact/separation character (S11) because in *Chamaesaura* and in some *Cordylus* the anterior parietal scales are separated by the IP-FP contact whereas in gerrhosaurids although there is a IP-FP contact the anterior parietal scales are still in contact posteriorly.

S13) *Interparietal(IP)-occipital(OC) scale* : 0) in contact; 1) separated. [IP-OC contact is exhibited in Lacertidae (not in *Eremias* in which the OC is missing), Gymnophthalmidae, Teiidae and Anguidae. In *Xantusia* the OC are present, but do not contact the IP. In Scincidae and *Lepidophyma* OC are absent/CASE I].

Those taxa that are lacking an occipital scale (see next character) are coded as "missing information".

The apomorphic character state (IP-OC separation) is exhibited in the following *Cordylus* : *campbelli*, *cataphractus*, *cordylus*, *giganteus*, *lawrenci*, *mclachlani*, *namaquensis*, *polyzonus*, *pustulatus*, *vittifer*, and *warreni*. This character state is also in the following *Platysaurus* : *imperator*, *maculatus*, *mitchelli*, and *pungweensis* (Broadley, 1978) as in *Pseudocordylus microlepidotus*.

Within gerrhosaurids the derived condition is only expressed in *Gerrhosaurus major* and in *Tracheloptychus*.

S14) *Median Occipital scale (OC)* : [Character states unordered] 0*) absent; 1*) present. [Scincidae and Xantusiidae (except *Xantusia henshawi*) lack a median OC, whereas Lacertidae, Teiidae, Gymnophthalmidae and Anguimorpha have a median OC/CASE II, polarity decision equivocal].

Among cordylids the characters states show no consis-

tent pattern. *Chamaesaura*, *Cordylus coeruleopunctatus*, *C. macropholis*, *C. peersi*, *C. rhodesianus*, *Platysaurus capensis* (70%), *Pseudocordylus capensis* and *P. spinosus* lack distinct occipital scales. This is also the case for all gerrhosaurids with the exception of *Angolosaurus*, *Gerrhosaurus major* and *Tracheloptychus*.
The remaining taxa exhibit the alternate condition. *Platysaurus ocellatus* and *Platysaurus pungweensis* are coded as having "missing information" because they have a 50-50 presence-absence ratio (Broadley, 1978).

S15) *Lower eyelids* : 0) either opaque or scaly; 1) with transparent disc; 2) brille. [The distribution of this character complex among outgroup taxa varies to a great degree and warrants some additional elaboration. In Xantusiidae as well as in Gymnophthalmidae, the gekkotan homolog is identified, in which the lower eyelid is completely transparent and is fused to the upper eyelid to form a brille. Most lacertids have scaly eyelids with a few notable exceptions. *Podarcis perspicillata* and *Lacerta cappadocia* both have transparent scales (1 large and 2 smaller ones respectively) within a scaly lower eyelid. The condition in *Cabrita* is curious in that the lower eyelid is completely transparent but not yet fused to the upper eyelid; i.e. a movable brille. In *Ophisops* a true brille is present. Nevertheless, Lacertidae is regarded as having a completely scaly lower eyelid plesiomorphically. In Scincidae the brille has evolved at least eight times (Greer, 1983). The ancestral condition then can only be regarded as equivocal. Of the skinks investigated, *Eumecia*, *Typhlosaurus*, *Panaspis* (with the exception of the subgenus *Afroablepharus*), *Acontias* and *Mabuya* for the most part have a transparent disc within the lower eyelid. *Riopa*, *Sphenomorphus* (those taxa examined) and *Scincus* have a scaly lower eyelid. The subgenus *Afroablepharus* of *Panaspis*, *Ablepharus* and *Cryptoblepharus* all have a true brille. Teiidae and anguimorphs universally have scaly lower eyelids. Although the distribution of character states among the outgroup taxa initially seems to be ambiguous it does show a CASE IV distribution pattern with a resulting unequivocal polarity decision].
The distribution of the character states of this transformation series among the ingroup is ambiguous. Transparent discs are present among gerrhosaurids only in *Cordylosaurus* (Loveridge, 1942; Fitzsimons, 1943). In cordylids a transparent disc within the lower eyelid is present in *Cordylus campbelli*, *C. namaquensis*, *C. polyzonus*, *Platysaurus guttatus* and *Platysaurus fitzsimonsi* (Broadley, 1978).
No brille was identified within the ingroup. The derived character state (2) is therefore not relevant for the ingroup analysis.
When confronted with a wide taxonomic distribution of derived character states the question of ecomorphological adaptations invariably arises. Greer (1983) indicates that the presence of a brille in members of Scincidae, Lacertidae and Gymnophthalmidae is associated with species of small size and diurnal habits inhabiting dry environments. The brille presumably prevents evaporative water loss from the eye. Greer (1983) furthermore suggests that a "windowed" lower eyelid is associated with intermediate size animals in intermediate (in terms of moisture) habitats. Scaly eyelids should be associated with large body size in mesic habitats.
In any case, for the purpose of this analysis, the presence of a "windowed" lower eyelid is an autapomorphy for *Cordylosaurus*.

S16) *Tympanum* : 0) exposed; 1) not exposed (covered by tympanic shield and/or lateral fold). [All outgroup taxa with the exception of *Scincus*, *Typhlosaurus*, *Anguis*, *Ophisaurus* and *Aniella* have an exposed tympanum/CASE I].
In all cordylids the tympanum is exposed. Within gerrhosaurids all *Zonosaurus* and *Gerrhosaurus* have an exposed tympanum. In *Angolosaurus* and *Tracheloptychus* the tympanum is covered by an enlarged tympanic shield. In the limbless *Tetradactylus* and *Cordylosaurus* the tympanum is covered by both the lateral body fold an enlarged tympanic shield. It is conceivable that this character reflects ecological correlations rather than genealogy, because the arenicolous and grass-swimmer ecomorphs for the most part posses a covered tympanum.

S17) *Posterior chin shields* : (Fig. 1) [Character states unordered] 0*) separated by first gular; 1*) in contact. [In Scincidae and Xantusiidae the posterior chin shields are separated. In Lacertidae, Gymnophthalmidae as in Anguimorpha the posterior chin shields are in contact/ CASE II, polarity decision equivocal].
All cordylids and madagascan gerrhosaurids (*Tracheloptychus* and *Zonosaurus*) have separated posterior chin shields (character state 0*) (Fig. 1B). The african gerrhosaurines have posterior chin shields in contact (character state 1*) (Fig. 1A).

S18) *Collar (antigular fold)* : (Fig. 2) 0) absent; 1) present, incomplete; 2) present, complete. [Scincidae, some Lacertidae, Teiidae, Anguidae and Helodermatidae, all lack a distinct collar. Varanidae have an incomplete collar. Xantusiidae (double in *Xantusia*, single in *Lepidophyma*), most Lacertidae and Gymnophthalmidae have a complete collar/CASE I].
Chamaesaura, *Cordylus* and all gerrhosaurids lack a collar (Fig. 2A). An incomplete collar is present in *Pseudocordylus*, *Platysaurus capensis*, *maculatus* and *mitchelli* (Fig. 2B). A complete collar is found in *Platysaurus imperator*, *intermedius*, *ocellatus*, *pungweensis* and *torquatus* (Figs. 2C & 3A).

S19) *Dorsal body scales* : 0) smooth; 1) keeled. [The outgroup taxa for the most part have smooth and tuber-

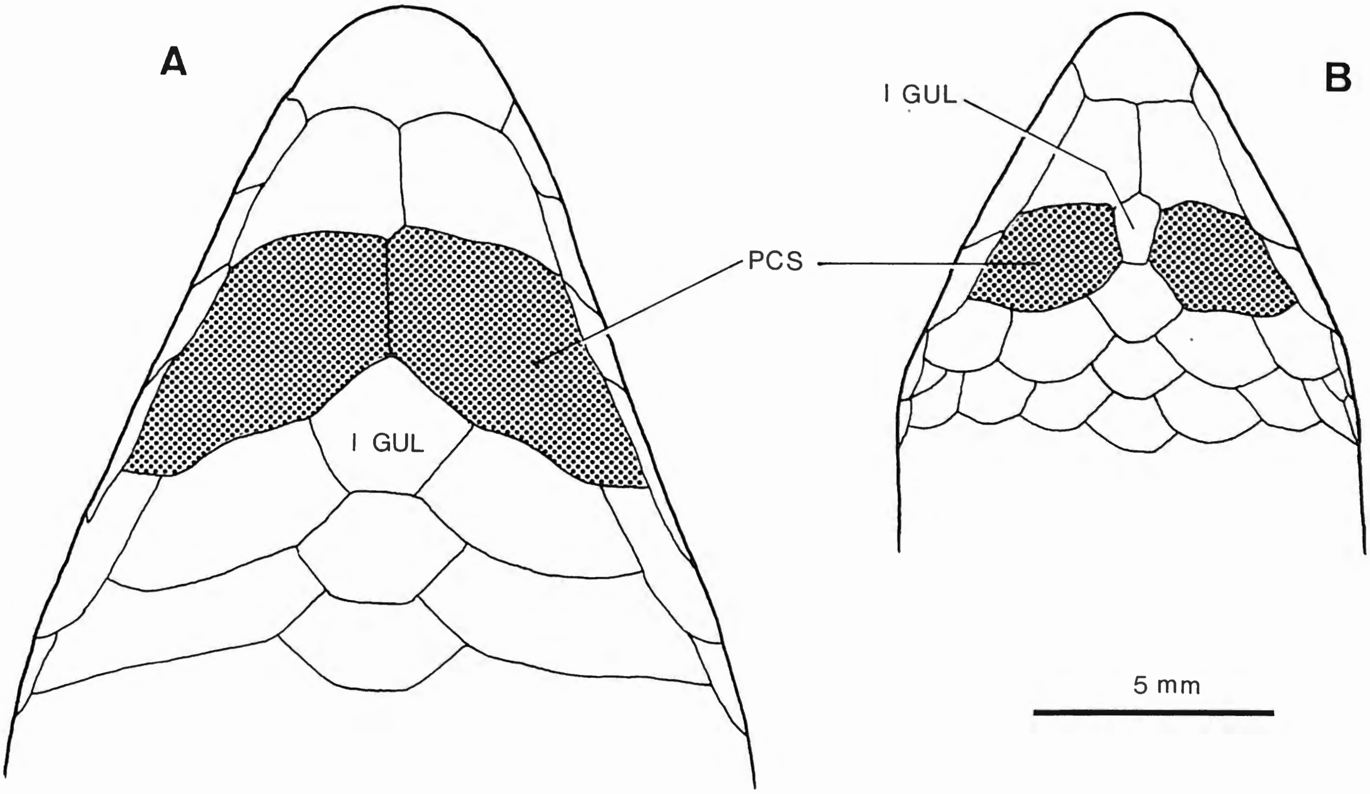

Figure 1 : *Patterns of posterior chin shields. A) Condition in which the two posterior chinshields are in contact (Gerrhosaurus* multilineatus*). B) Condition in which the 2 posterior chinshields are separated by the first gular (*Tracheloptychus madagascariensis*). Abbreviations : PCS = posterior chin shields; 1 GUL = first gular scale.*

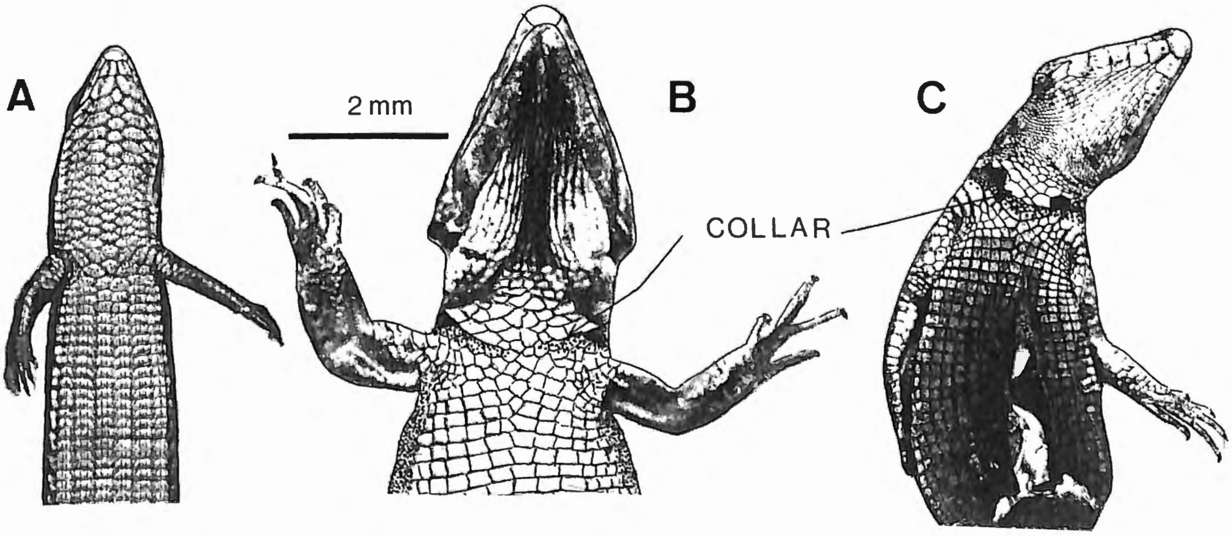

Figure 2 : *Character transformation series of collar (= antigular fold) within Cordyliformes. A) Absence of collar as seen in* Gerrhosaurus flavigularis. *(See also Fig. 3B & 3C). B) Incomplete collar as seen in* Pseudocordylus melanotus. *C) Complete collar as seen in* Platysaurus intermedius *(See also Fig. 3A).*

cular scales. Well-known exceptions are *Takydromus*, some *Psammodromus* (e.g. *algirus*), *Algyroides*, *Kentropyx*, *Tribolonotus*, *Tropidophorus*, *Echinosaura* and some *Elgaria* (e.g. *liocephalus*) /CASE I].

The apomorphic condition in cordylids is shown in *Chamaesaura* and all *Cordylus* examined except *C. polyzonus* and *C. pustulatus*. In gerrhosaurids the derived condition is expressed in all *Gerrhosaurus*, *Tetradactylus*, *Tracheloptychus* and some *Zonosaurus* (LANG, 1990b).

S20) *Ventral plates*: (Fig. 3) [Character states unordered] 0*) honeycomb pattern; 1*) ventral scales forming straight rows. [Among the outgroup taxa examined, Scincidae, *Psammodromus*, Gymnophthalmidae, and the Anguimorphs *Anguis*, *Ophisaurus*, *Aniella*, *Diploglossus* have ventral scales arranged in a honeycomb pattern. Xantusiidae, most Lacertidae, Teiidae, *Elgaria*, Varanidae and Helodermatidae by contrast have aligned ventral plates/CASE II, polarity decision equivocal].

All ingroup taxa, with the exception of *Chamaesaura* and the madagascan gerrhosaurids (*Tracheloptychus* and *Zonosaurus*) have aligned, straight ventral plates (Fig. 3A & 3B). *Tracheloptychus* and *Zonosaurus* have ventral plates arranged in a honeycomb pattern (Fig. 3C). In *Chamaesaura* dorsal and ventral scales can not be differentiated and are thus coded as "missing information".

S21) *Scales on sole of feet*: 0) round and tubercular; 1) flattened, oblique and keeled. [All outgroup taxa examined with the exception of *Mabuya sulcata* have round tubercular scales on the sole of their feet/CASE IV]. This character is subject to ontogenetic change in some skinks (e.g. *Mabuya brevicollis*, *M. perroteti*).

Within the ingroup the distribution of character states shows no distinct pattern. Within cordylids the apomorphic character state is expressed in *Cordylus*, *Platysaurus maculatus*, *P. mitchelli*, *P. torquatus*, *Pseudocordylus microlepidotus* and in *Pseudocordylus spinosus*. In gerrhosaurids the derived condition is present in *Angolosaurus*, *Cordylosaurus*, *Gerrhosaurus multilineatus*, *G. nigrolineatus*, *Tracheloptychus*, *Zonosaurus karsteni*, *Z. maximus* and *Z. ornatus* (Lang, 1990b). The remaining ingroup taxa examined have the plesiomorphic condition. The limbless *Chamaesaura* and *Tetradactylus* are coded as having "missing information".

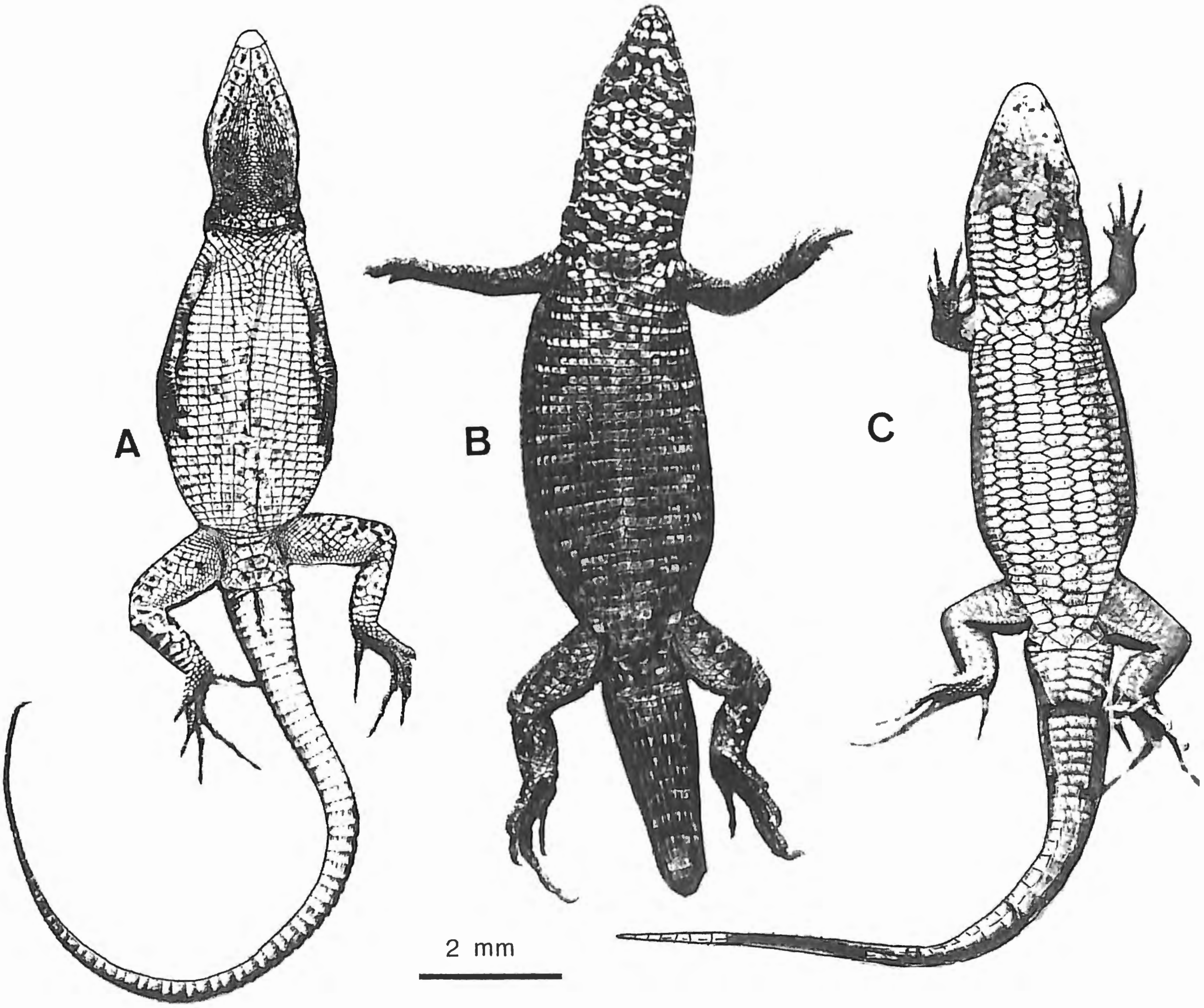

Figure 3 : *Patterns of ventral and throat scalation within Cordyliformes. A) Throat scales small and irregular, ventral scales rectangular, forming straight rows (illustrated here is* Platysaurus ocellatus*). B) Throat covered with cycloid scales, ventral scales rectangular, in straight transverse rows (Illustrated here is* Gerrhosaurus validus*). C) Throat covered with cycloid scales, ventral scales hexagonal, arranged in a honeycomb pattern (Illustrated here is* Zonosaurus rufipes*).*

S22) *Scales below forelimbs*: 0) smooth; 1) keeled. [Most outgroup taxa have smooth scales below forelimbs. In some *Psammodromus* and *Kentropyx* the scales below the forelimbs are slightly keeled/CASE I].
The apomorphic condition within cordylids is expressed in all *Cordylus* except *giganteus*, and in *Pseudocordylus microlepidotus* and *P. spinosus*. Within gerrhosaurids keeled scales below the forelimbs are present in *Angolosaurus*, *Gerrhosaurus nigrolineatus*, *G. validus*, *Tracheloptychus*, *Tetradactylus seps* and all *Zonosaurus* except *ornatus* (LANG, 1990b). Again the limbless forms are coded have "missing information", because the condition is umknown.

S23) *Scales below hind limbs*: 0) smooth; 1) keeled. [All outgroup taxa examined with the exception of *Kentropyx*, and those taxa that have keeled dorsal scales (see above) have smooth tubercular scales below the hind limbs/CASE I].
Within the cordylids the derived condition is present in *Cordylus mclachlani*, *C. namaquensis*, *C. peersi*, *C. polyzonus*, *C. rhodesianus*, *C. tropidosternum* and in *Pseudocordylus spinosus*. In gerrhosaurids the derived character state is not found. Limbless forms are again coded as unknown (9).

S24) *Subdigital lamellae*: [Character states unordered] 0*) smooth; 1*) keeled. [Some Scincidae and the remaining outgroup taxa for the most part have round tubercular subdigital lamellae. In *Riopa*, *Panaspis*, *Mabuya* and *Sphenomorphus* the subdigital scales are keeled. In *Lepidophyma* there is a small keel proximally/CASE II, polarity decision equivocal].*Platysaurus*, *Pseudocordylus microlepidotus*, *Gerrhosaurus*, *Tetradactylus seps* and all *Zonosaurus* have smooth subdigital lamellae. In contrast, *Cordylus*, *Pseudocordylus langi*, *P. spinosus*, *Angolosaurus*, *Cordylosaurus* and *Tracheloptychus* have keeled subdigital lamellae. The limbless forms are coded as missing data (9).

S25) *Cycloid scales*: (Fig. 3) 0) absent; 1) present on throat 2) present on throat and ventrum. [Cycloid scales consistently present only in Scincidae (with some noted exceptions as some species of *Tribolonotus* and *Tropidophorus*); some Gymnophthalmidae (PRESCH, 1980; *Anniella* and diploglossine anguids (HOFFSTETTER, 1962; STRAHM & SCHWARTZ, 1977)/CASE II]. At a higher phylogenetic level (Sclerroglossa) the absence of cycloid scales is the plesiomorphic condition. This character has been discussed by ESTES at al. (1988).
Cordylids have scales of variousmorphologies. However, no cycloid scales are present (Fig. 3A). The African gerrhosaurines exhibit the intermediate condition in which cycloid scales are present only in the throat region (Fig. 3B). The Madagascan gerrhosaurids by contrast have cycloid scales on the entire venter (Fig. 3C).

CHARACTERS OF SOFT ANATOMY

A1) *Tongue-covering*: (Fig. 4) 0) scale-like papillae covering entire or anterior 2/3 of tongue, with posterior 1/3 covered with oblique plicae (Fig. 4A & 4B); 1) scale-like papillae confined to anterior half, posterior half with oblique plicae (Fig. 4C); 2) scale-like papillae restricted to anterior tip, remaining portion of tongue covered with oblique plicae (Fig. 4D). [Scincidae, Anguimorpha, Gymnophthalmidae and Teiidae have a scale-like papillar covering of the tongue (ESTES *et al.* 1988; SCHWENK, 1988). Xantusiidae plus some Lacertidae (*Takydromus*, *Lacerta* and *Psammodromus*) have scale-like papillae restricted to the anterior half of the tongue, with the remaining being oblique plicae. In the remaining Lacertidae (*Acanthodactylus*, *Eremias*, *Algyroides* and *Holaspis*) the scale-like papillae are found only on the anterior tip of the tongue/CASE I]. This character corresponds to character number 139 of ESTES *et al.* (1988) with a slight variation of character states. Polaritities are congruent. The character states persented here are arranged in a linear transformation sequence showing a progression of oblique plicae within the ingroup.
The plesiomorphic condition is expressed in cordylids, *Angolosaurus* and *Gerrhosaurus*. The intermediate character state is restricted to the Malagasy gerrhosaurids *Tracheloptychus* and *Zonosaurus* (Fig. 4C). The most derived character state is noted in *Cordylosaurus* and *Tetradactylus* (Fig. 4D).

A2) *Tongue-pigmentation*: (Fig. 5) [Character states unordered] 0*) not pigmented or only faint lateral stripes at the anterior tip (Fig. 5A & 5B); 1*) anterior tip is pigmented; 2*) anterior 1/2 (+ in some posterior tips) pigmented (Fig. 5C); 3*) entire tongue is pigmented (Fig. 5D). [Character states vary widely among the outgroups with no consistent pattern. Scincidae: *Acontias plumbeus*, *Typhlosaurus lineatus* and *Scincus scincus* have unpigmented tongues. In *Riopa sundevalli*, *Panaspis dewittei*, *Eremias sulcata* and *Sphenomorphus ilanosi*, the anterior tip of the tongue is pigmented. Lacertidae: *Eremias*, *Lacerta bedriagae*, *Podarcis perspicillata*, *Psammodromus* and *Takydromus sexilineatus* have unpigmented tongues. In *Adolfus africanus*, *Acanthodactylus boskianus* and *Holaspis guentheri* the tongues are entirely pigmented. Xantusiidae: *Lepidophyma*, tongue unpigmented. *Xantusia*, tongue entirely pigmented. Teiidae: *Tupinambis teguixin* tongue entirely pigmented. *Kentropyx intermedius* tongue unpigmented. Gymnophthalmidae: *Gymnophthalmus quadrilineata* not pigmented. Anguidae: tip of tongue pigmented. The remaining anguimorphs also vary/CASE VI, polarity decision equivocal].
All cordylids except 3 species of *Cordylus* have unpigmented tongues. *Cordylus cataphractus* and *Cordylus*

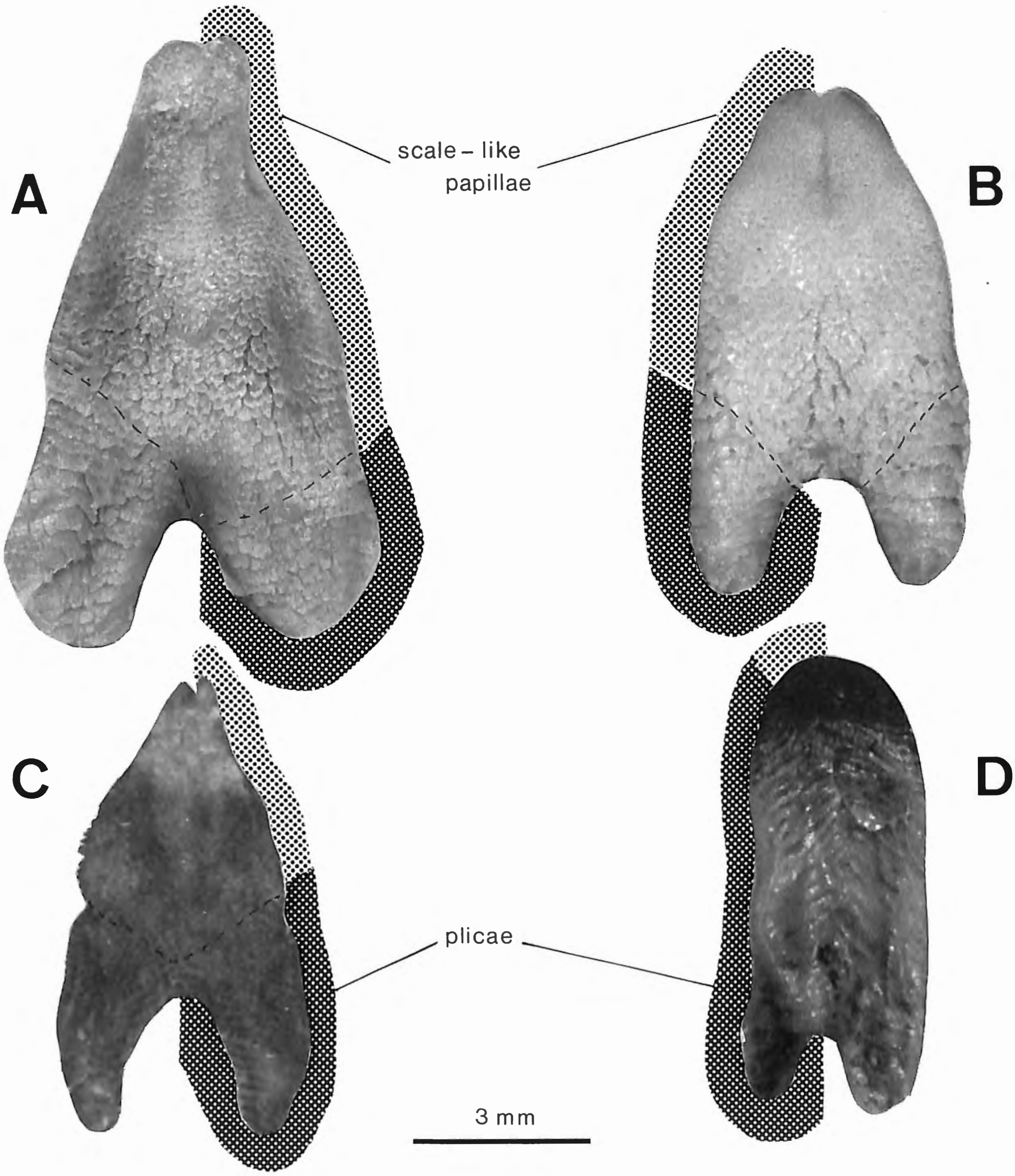

Figure 4 : *Gross morphology of tongue surface. A & B) Scale-like papillae cover the anterior 2/3 of the tongue, surface of hindtongue consisting of oblique plicae (A =* Cordylus cataphractus, *B =* Cordylus tropidosternum*). C) Anterior half of tongue with scale-like papillae, posterior portion of tongue with oblique plicae (C =* Tracheloptychus madagascariensis*). D) Anterior tip of tongue with scale-like papillae, remainder of tongue with distinct oblique plicae (D =* Tetradactylus seps*).*

warreni have entirely pigmented tongues (character state 3*). In addition, *Cordylus giganteus* is unique in that only the posterior half is pigmented.

Within gerrhosaurids non-pigmented tongues are present in *Angolosaurus*, *Cordylosaurus* and in *Gerrhosaurus major*. The remaining *Gerrhosaurus* as also *Tetradactylus* (no information available for *T. ellenbergeri*) and the single known specimen of *Zonosaurus boettgeri* have tongues in which the anterior tip is pigmented (character state 1*). *Tracheloptychus*, *Zonosaurus rufipes*, *Z. brygooi*, *Z. trilineatus* and *Z. quadrilineatus* all have entirely pigmented tongues (character state 3*) (Lang, 1990b). The remaining *Zonosaurus* have tongues in which the anterior portion of the tongue is pigmented (character state 2*).

Although the character states tend to vary among the outgroup taxa, the condition at the species-level of the ingroup is highly stable.

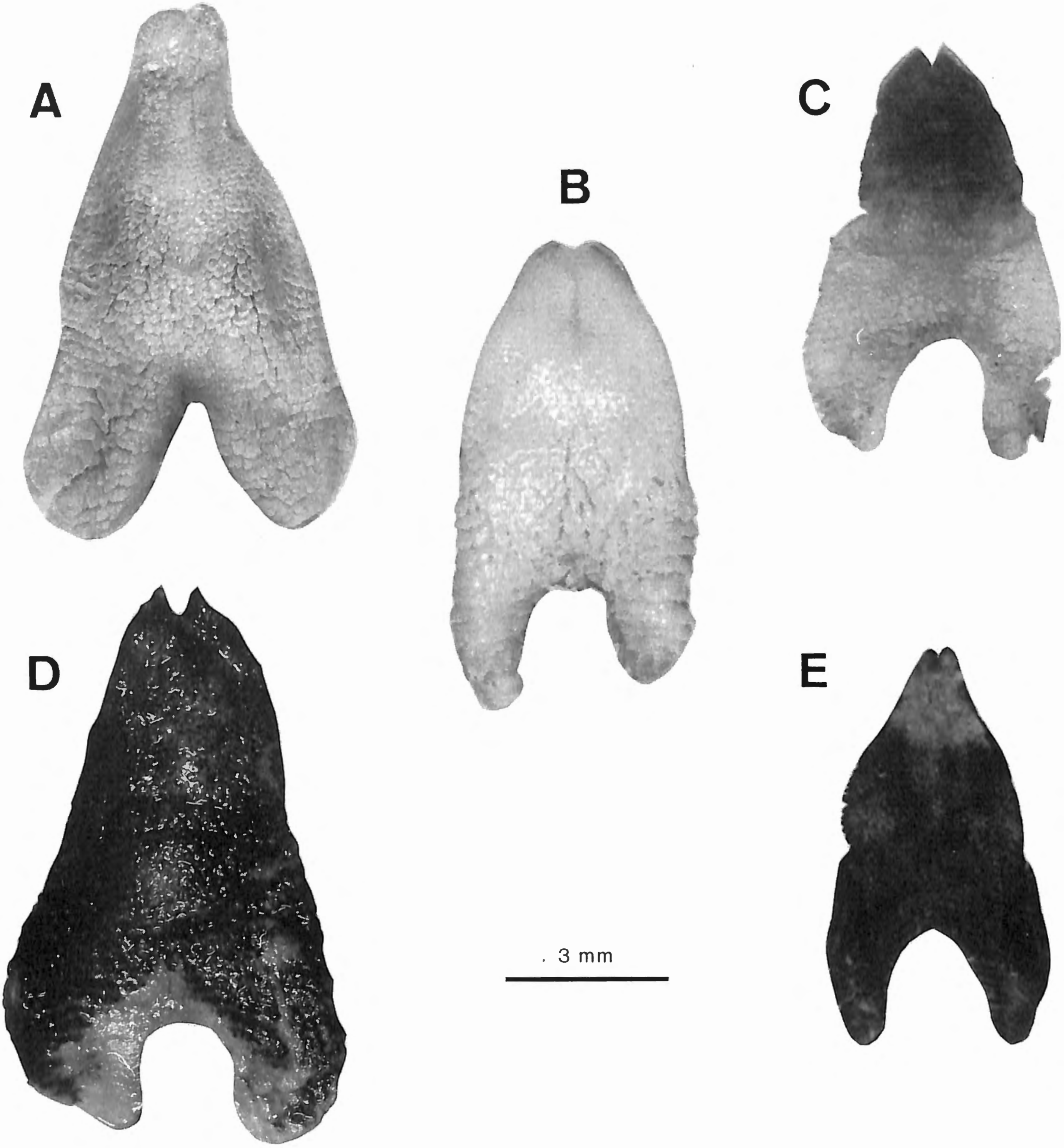

Figure 5 : *Pigmentation patterns of tongue in Cordyliformes. A) Tongue not pigmented (Illustrated here is* Cordylus cataphractus*). B) Dark pigmentation restricted to two discreet lines on foretongue (Illustrated here is* Cordylus tropidosternum*). C) Anterior half of tongue is pimented, posterior half devoid of pigment (Illustrated here is* Gerrhosaurus flavigularis*). D) Entire tongue is pigmented (Illustrated is* Zonosaurus maximus*). E) Anterior portion of tongue not pigmented, posterior half with pigment (Illustrated here is* Tracheloptychus madagascariensis*).*

A3) *Innervation of dorsal muscles of lower leg* : 0) Pattern A (peroneal N innervation); 1) Pattern B (interosseous N innervation). [All outgroups with the exception of Gymnophthalmidae + Teiidae show pattern A/ CASE I]. JULIEN and RENOUS-LECURU (1972) describe the variation of the nerves supplying the dorsal shank muscles in squamates. The results were used by ESTES *et al.* (1988) as a systematic character (# 143), the polarities of which are congruent with this study. The coding of character states for the ingroup is somewhat ambiguous. Although JULIEN and RENOUS-LECURU (1972) defined two distinct morphological patterns (A and B) some ingroup taxa were described as "not yet having achieved" either pattern. All cordylids have either a distinct A (*Cordylus* and *Pseudocordylus*) or distinct B (*Platysaurus*) pattern of innervation. In contrast, gerrhosaurids exhibit morphological states such as "approaching" B (*Gerrhosaurus nigrolineatus*), "approaching" A (*Tetradactylus tetradactylus* and *Zonosaurus madagascariensis*) or even intermediate between A and B (*Tracheloptychus madagascariensis*). The limbless *Chamaesaura* is coded as missing information (9). *Tetradactylus* is coded with the condition observed in the limbed *Tetradactylus seps*.

A4) *Insertional tendon of pseudotemporalis superficialis* : 0) present; 1) reduction of tendon; 2) loss of insertional tendon. [All outgroups have well-developed insertional tendons/CASE I]. RIEPPEL (1980) describes the condition of the insertional tendon of the pseudotemporalis superficialis in Scincomorpha. Cordylids have a reduced insertional tendon whereas gerrhosaurids have lost this tendon (See also section on the monophyly of Cordylidae + Gerrhosauridae).

CHARACTERS OF CRANIAL ANATOMY

C1) *Nasal-Prefrontal bones* : 0) narrow or no contact (separated by lateral processes of frontal contacting maxilla); 1) broad contact. [All outgroup taxa with the exception of some Gymnophthalmidae, Teiidae and Anguidae (ESTES *et al.*, 1988), and *Xantusia henshawi* and *arizonae* (RIEPPEL, 1984) have but a narrow or no contact zone between the nasal and prefrontal bones/ CASE I]. ESTES *et al.* (1988, character # 4) indicate that the contact between the nasal and prefrontal bones is an autapomorphy for Scincomorpha. At that level then, the contact between these two bones must therefore be regarded as plesiomorphic. This is supported by the character state distribution pattern among the outgroup taxa in this study. Within the ingroup the apomorphic character state is expressed in all gerrhosaurids exclusive of *Angolosaurus* in which the nasal and prefrontal bones are in very narrow contact (Figs. 28, 30, 32, 34, 36, 39).

C2) *Lacrimal bone* : 0) absent or prominent lateral exposure; 1) no lateral exposure (restricted to the lacrimal canal). [Lacrimal bone absent in Scincidae and Xantusiidae. Lacertidae, Teiidae and Anguimorpha have prominent lateral exposure of the lacrimal bone. Gymnophthalmidae has no lateral exposure of lacrimal/CASE I]. ROMER (1956) erroneously indicates that the lacrimal bone is absent in Cordylidae + Gerrhosauridae. In gerrhosaurids (exclusive of *Angolosaurus*) the lacrimal has a prominent lateral exposure, which is the plesiomorphic condition as observed in most squamates that have a lacrimal. In *Angolosaurus* and cordylids the lateral exposure as well as the lacrimal bone itself is severely reduced and this bone is restricted to lacrimal canal (Figs. 6A, 19, 21, 24, 26, 28).

C3) *Palatine-Jugal bones* : (Fig. 6) 0) separated; 1) in contact or overlaping at infraorbital foramen. [All outgroups except Anguimorpha have palatines and jugals that are separated/CASE I]. All gerrhosaurids, *Platysaurus* and *Pseudocordylus* exhibit the derived character state.

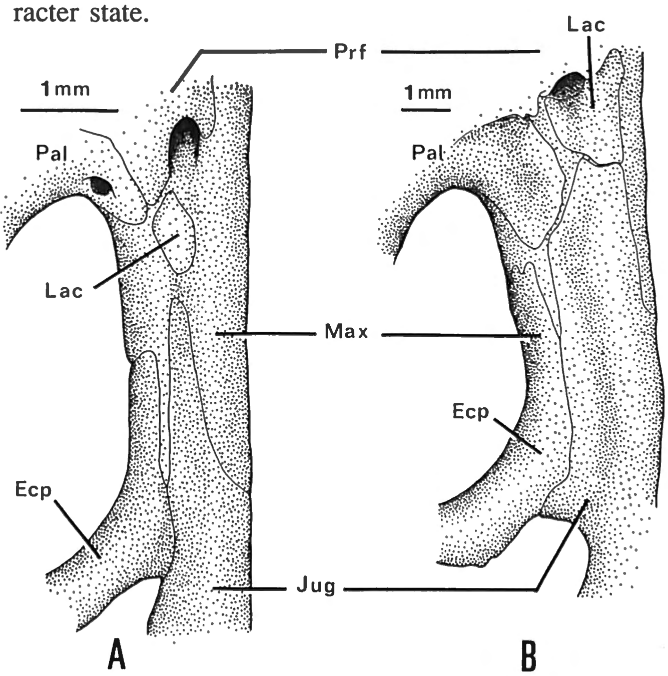

Figure 6 : *Contact patterns at infraorbital foramen. A)* Cordylus cordylus . *B)* Gerrhosaurus major. *Abbreviations : Ecp = ectopterygoid; Jug = jugal; Lac = lacrimal; Max = maxilla; Pal = palatine; Prf = prefrontal.*

C4) *Anteroventral border of orbit* : 0) formed by jugal; 1) formed by maxilla with anterior process of jugal confined to the medial surface of the maxilla. [Anteroventral orbit formed by jugal occurs in some Scincidae, Anguimorpha, Gymnophthalmidae, Teiidae and some Lacertidae. Remaining outgroups show alternate condition/CASE IV]. This character was defined by ESTES *et al.* (1988).
However, the polarities of the character states based on outgroup evidence are reversed at the ingroup node. All cordylids exhibit the apomorphic character state.

C5) *Postorbital contribution to posterior border of orbit*: 0) Postorbital bone forms less than 1/2 of the posterior orbital border (primarily a temporal bone); 1) forms about 1/2 of the posterior orbital rim (Postorbital bone with a strong ventral process). [Postorbital bone of all outgroups is primarily a temporal bone/CASE I]. This character complex was defined by ESTES *et al.* (1988). The character state distribution pattern among outgroup taxa at the scincomorpha level indicates that the polarities defined by ESTES *et al.* should be reversed. Within Autarchoglossa the apomorphic character state therefore forms an autapomorphy for Gerrhosauridae.

C6) *Frontal bone*: 0) paired; 1) embryonic fusion. [All outgroups with the except of Teiioidea have paired frontal bones postembryonically/CASE I]. Character previously defined by ESTES *et al.* (1988). *Cordylus*, *Chamaesaura* and *Pseudocordylus* all exhibit the derived condition (Figs. 19, 20, 24).

C7) *Postfrontal bone*: 0) forked medially, clasping the frontoparietal suture; 1) not forked medially. [All outgroup taxa have forked postfrontals/CASE I]. As defined by ESTES *et al.* (1988) a forked semilunate postfrontal bone clasping the frontoparietal suture is a synapomorphy for the Scleroglossa. This in part may be the result of a loss or reduction of this element in Iguania. Although the postfrontal bone is also reduced within the ingroup (see discussion of the monophyly of Cordylidae + Gerrhosauridae), both character states are observable. At the scleroglossan level then the non-forked postfrontal is to be regarded as apomorphic. All cordylids exhibit the plesiomorphic condition, whereas gerrhosaurids exhibit the derived character state.

C8) *Supratemporal fenestra*: 0) slit-like opening remains between frontal, postorbital and squamosal; 1) entirely closed by postfrontal and squamosal. [All outgroup taxa except Xantusiidae have either an open supratemporal fenestra or one that is closed by the postfrontal/CASE I]. Although not always evident from a dorsal view, all cordylids have an elongated supratemporal opening that is closed by both the postorbital and squamosal bones (Figs. 19, 21, 24, 26). The supratemporal opening is sometimes overlain by osteoderms, but can still be viewed dorsally. The derived condition is present in all gerrhosaurids in which there is a complete temporal closure due to the postorbital and squamosal (Figs. 28, 30, 32, 34, 36, 39). This condition is deemed convergent with xantusiids.

C9) *Ventral downgrowth of parietal*: [Character states unordered] 0*) absent; 1*) present, extending to (or just medial to) the epipterygoids. [Some Scincidae, Xantusiidae, Teiidae and Gymnophthalmidae have parietal downgrowths. Other Scincidae, Lacertidae and Anguimorpha lack parietal downgrowths/CASE IV, polarity decision equivocal]. ESTES *et al.* (1988) define the presence of parietal downgrowths as the derived condition for squamates. At the ingroup node the decision is equivocal and character states are left unordered. *Angolosaurus* and *Tracheloptychus* lack parietal downgrowths. Remaining gerrhosaurids and cordylids have ventral parietal downgrowths meeting the epipterygoids.

C10) *Parietal tabs*: [Character states unordered] 0*) absent; 1*) present. [Some Scincidae and Anguiomorphs lack parietal tabs. Some Scincidae and Lacertoidea have parietal tabs/CASE V, polarity decision equivocal] unordered character states]. As defined by ESTES *et al.* (1988) the parietal tabs are thin, triangular structures that extend anteriorly into shallow fossae on the ventral surface of the frontals. Although ESTES *et al.* (1988) defined the presence of ventral tabs as derived at the squamate level, the polarity decision at the Autarchoglossan node remains equivocal. Distinct parietal tabs are lacking in *Platysaurus*, *Angolosaurus* and *Cordylosaurus*. Parietal tabs are present in *Chamaesaura*, *Cordylus*, *Pseudocordylus*, *Gerrhosaurus*, *Tetradactylus*, *Tracheloptychus* and *Zonosaurus*.

C11) *Parietal bracing of supraoccipital ridge*: (Fig. 7) 0) median parietal process forked, ventral contact with supraoccipital ridge; 1) median parietal process deeply forked bracing the supraoccipital ridge. [All outgroups with the exception of Scincidae lack a median parietal process altogether]. Because there are no homologous structures in Lacertoidea[4] or Anguimorpha the condition observed in Scincidae is regarded as plesiomorphic within the ingroup.

In Scincidae the parietal has two ventrally projecting median processes. The two processes are highly variable and may be in close proximity as in *Trachydosaurus* or they may be widely separated as in *Chalcides*. In not a single case is there contact between the median parietal fork and the underlying supraoccipital ridge. Also, in contrast to Cordylidae the median parietal fork in Scincidae is directed ventrally.

The evolutionary trend of this character complex occurred hypothetically as follows: presence of a median parietal fork, widely separated, directed ventrally without contact to an undeveloped supraoccipital ridge (Scincidae); two median parietal processes in close proximity forming a parietal fork with a shallow notch that is only in ventral contact with a slightly expanded supraoccipital ridge (cordylids) (Fig. 7A); the two median processes of the parietal form a deeply-notched fork bracing an elongated supraoccipital ridge that projects slightly beyond the parietal table (gerrhosaurids) (Fig. 7B).

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[4] In Teiidae a prominent supraoccipital ridge (*sensu* VAN PLETZEN, 1946) is present but without a trace of median parietal processes.

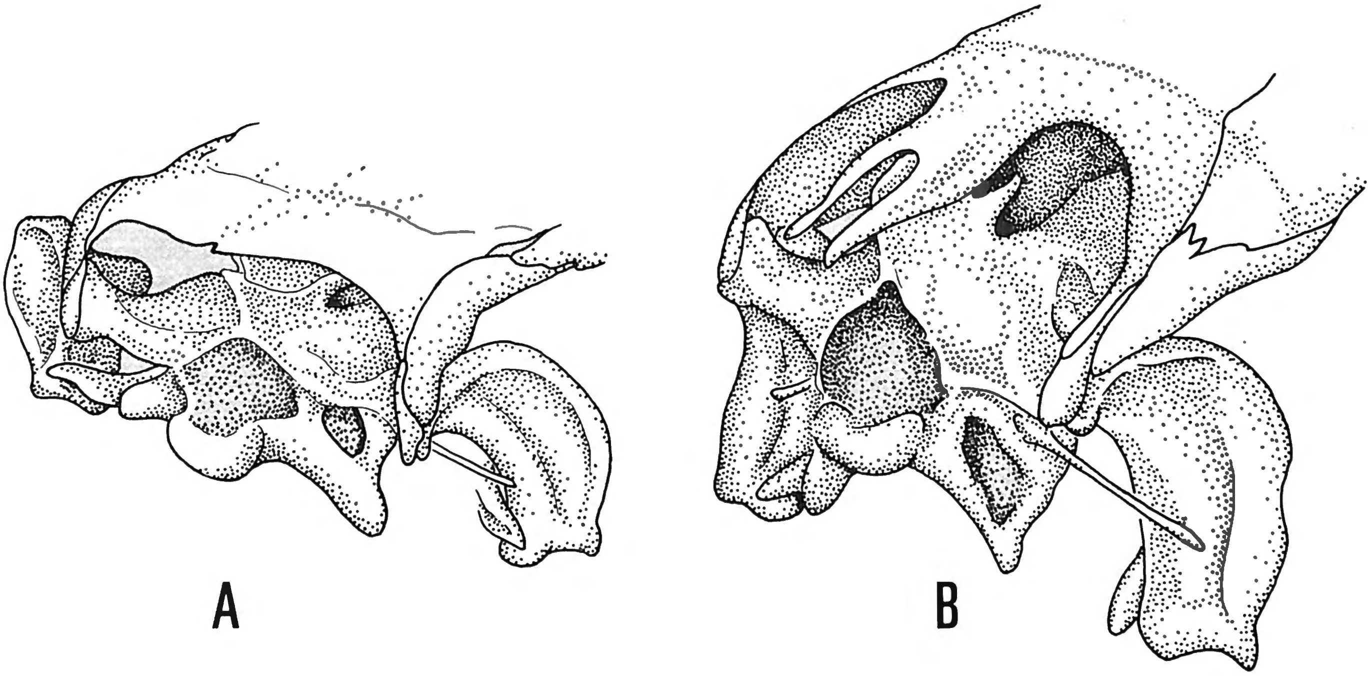

Figure 7 : *Articulation of supraoccipital ridge with parietal median processes. A) Condition as observed in* Cordylus, *with no contact. B) Condition observed in* Gerrhosaurus *with supraoccipital ridge being braced by forked median parietal process. Illustration redrawn from* McDowell *&* Bogert *(1954).*

The presence of median parietal processes may in fact be regarded as a synapomorphy for Scincidae + Cordylidae.

Three joints are the primary source of skull kinematics between the maxillary segment (= anterior portion of skull, as defined by Oelrich, 1956) and the occipital segment (= neurocranium) of the squamate skull. These three are : the joint between the paraocciptal process of the exocipital, the supratemporal and the parietal (syndesmosis); the basipterygoid-pterygoid joint (synovial); and the articulation of the median parietal processes and the supraoccipital ridge.

The major source of ventral kinesis between the maxillary and occipital segments of the skull is provided by the contact of the condyles of the basipterygoid processes with the pterygoid. The supraoccipital-parietal articulation is the site of metakinesis between the maxillary and occipital segments.

With respect to the ingroup taxa there is a clear distinction between Gerrhosauridae and Cordylidae. The rigid gerrhosaurid skull is characterized by a broad pterygoid joint (C16, Fig. 9B) and a forked bracing of the supraoccipital ridge (this character, Fig. 7B). The somewhat more kinetic cordylid skull has a narrow condylar surface of the basipterygoid processes (C16, Fig. 9A) allowing for more ventral kinesis and only a slight ventral contact between the supraoccipital ridge and the parietal (this character, Fig. 7A) permitting more metakinesis. It is possible then that gerrhosaurids have retained well-developed pterygoid teeth (C 15) to compensate for the loss in kinetic capabilities. Pterygoid teeth have been hypothesized to maximize the gripping capacity of the palate (Montanucci, 1968).

C12) *Parietal table* : 0) rounded; 1) flat. [Among the outgroup taxa flat parietal tables are observed in Xantusiidae and in Xenosauridae. Remaining taxa have rounded parietals/CASE III]. The derived condition is expressed in cordylids (Figs. 19, 21, 24, 26). This character could be regarded as an ecomorphological adaptation to crevice dwelling, but evidence to the contrary is based on the fact that *Chamaesaura* is a grass-swimmer with a flat skull. Either cordylids ancestrally were "flat-skulled," further facilitating a crevice habitus, or *Chamaesaura* is derived from a crevice dweller ancestor, secondarily becoming a grass-swimmer that retained a flat parietal table. Additional support for a phylogenetic linkage of a flat parietal table within the Scincomorpha at least is evidenced by the analogous post-cranial changes for grass-swimming between *Chamaesaura* on the one hand and *Tetradactylus* (Essex, 1927; Berger-Dell'Mour, 1983) as well as limbless Scincidae on the other, without analogous changes in skull morphology. The conditions in xantusiids and some lacertids must be regarded as ecomorphological convergence. It should be noted that *Gerrhosaurus validus* has strong tendencies, especially in older individuals, towards the development of a flattened posterior portion of the skull. This flattening seems to be associated with an exceptionally high number (11-12) of pterygoid teeth.

C13) *Pigmentation of skull*: (Fig. 8) 0) whitish, pigment lacking; 1) skull darkly pigmented. [All outgroups have unpigmented skulls/CASE I]. In all gerrhosaurids exclusive of *Cordylosaurus*, *Gerrhosaurus* and *Angolosaurus* the neurocranial elements are darkly pigmented. The composition of this pigment and its embryonic origin hasnot yet been determined. The pigment is more pronounced, in the neurocranial elements in particular the parietal.

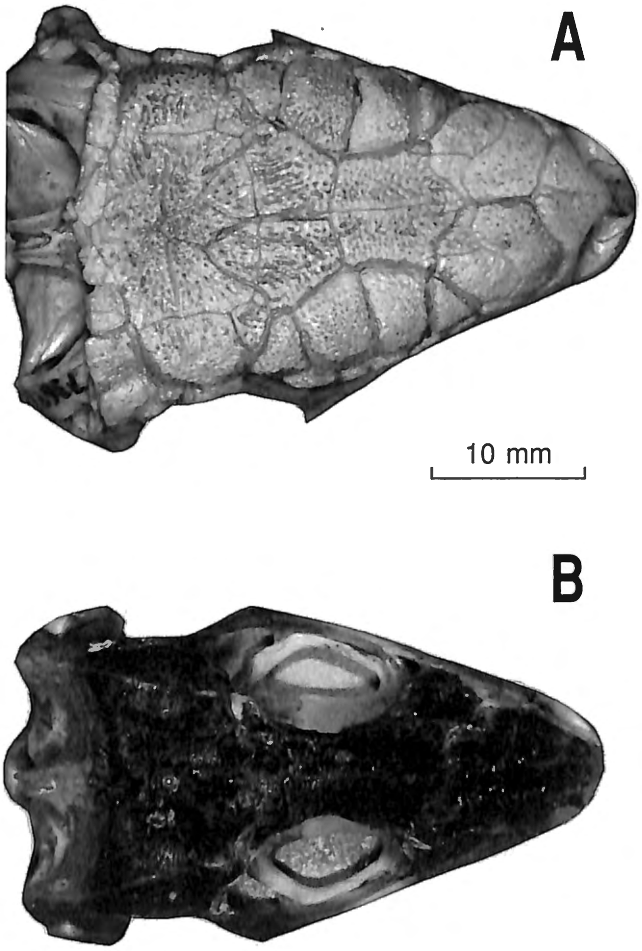

Figure 8 : *Top views of skulls of* Gerrhosaurus flavigularis *(A) and* Zonosaurus maximus *(B) showing differences in skull pigmentation.*

C14) *Vomers*: 0) ventromedial aspect of vomers without depression; 1) ventromedial heart-shaped depression within vomer. [All outgroups lack a ventromedial depression within the vomers/CASE I].
The ventral aspect of the vomer in *Cordylus*, *Platysaurus* and *Pseudocordylus* has a distinct heart shaped depression at the median contact zone of the two bones. The function of this depression if any, has not been determined but deserves further attention. The remaining ingroup taxa (*Chamaesaura* and gerrhosaurids) exhibit the outgroup condition of a smooth and even ventral surface of the vomers.

C15) *Pterygoid teeth*: 0) absent; 1) present. [All outgroup taxa have members who lack pterygoid teeth. Only some Scincidae, some lacertids, some microteiids and macroteiids as well as some anguids have pterygoid teeth/CASE I]. This character complex has been used by Estes *et al.* (1988) to resolve relationships among squamate families. The polarities of the character states are reversed with respect to Estes *et al.* (1988) because it is globally more parsimonious to assume that the absence of pterygoid teeth is the plesiomorphic condition for Autarchoglossans. Although extremely variable among squamate families, the absence or presence within the ingroup is consistent. Cordylids lack pterygoid teeth. Gerrhosaurids on average have five well-developed pterygoid teeth. See also character 11 for comments on the relationship of pterygoid teeth to skull kinetics and by consequence to diet.

C16) *Basipterygoid process*: (Fig. 9) 0) short, only slightly past base of parasphenoid process (X<Y) (Fig. 9B); 1) long, and elongated with smaller condylar surface (X>Y) (Fig. 9A). [All outgroup taxa show rather short basipterygoid processes/CASE I]. All cordylids, *Cordylosaurus*, *Tracheloptychus* and *Tetradactylus* show the derived condition. The condylar surface of the basipterygoid processes fits into a notch of the pterygoid an are the primary site of ventral skull kinesis (see character 11).

C17) *Spheno-occipital tubercle*: (Fig.9) 0) consisting of a basisphenoid flange and the basioccipital (Fig. 9A); 1) consists of basioccipital only (Fig. 9B). [All outgroup taxa with the exception of Teiidae and *Ophisaurus* have a spheno-occipital tubercle that is made up of basisphenoid and basioccipital components]. Within the ingroup the derived condition is expressed in *Chamaesaura*, *Pseudocordylus* and in *Tetradactylus*.

C18) *Posterior emargination of parietal*: 0) large semicircular posterior emargination of parietal table : supratemporal long, posterior braincase exposed; 1) posterior aspect of parietal not emarginated : parietal table long, supratemporal short, posterior braincase for the most part covered. [All outgroup taxa with the exception of Xantusiidae and some Lacertidae have a posteriorly emarginated parietal table/CASE I]. McDowell and Bogert (1954) indicated that one of the morphological differences between gerrhosaurids and cordylids is that in the former there is a large semi-circular posterior emargination of the parietal between the median (supraoccipital) and lateral (quadratic) process of the parietal, whereas in the latter no such emargination is present (Fig. 7). This is analogous to the character complex defined by Estes *et al.* (1988 : 148) with respect to the length of the parietal table. The polarity decision in this study based on the distribution of character states among the outgroup taxa, agrees with Estes *et al.*

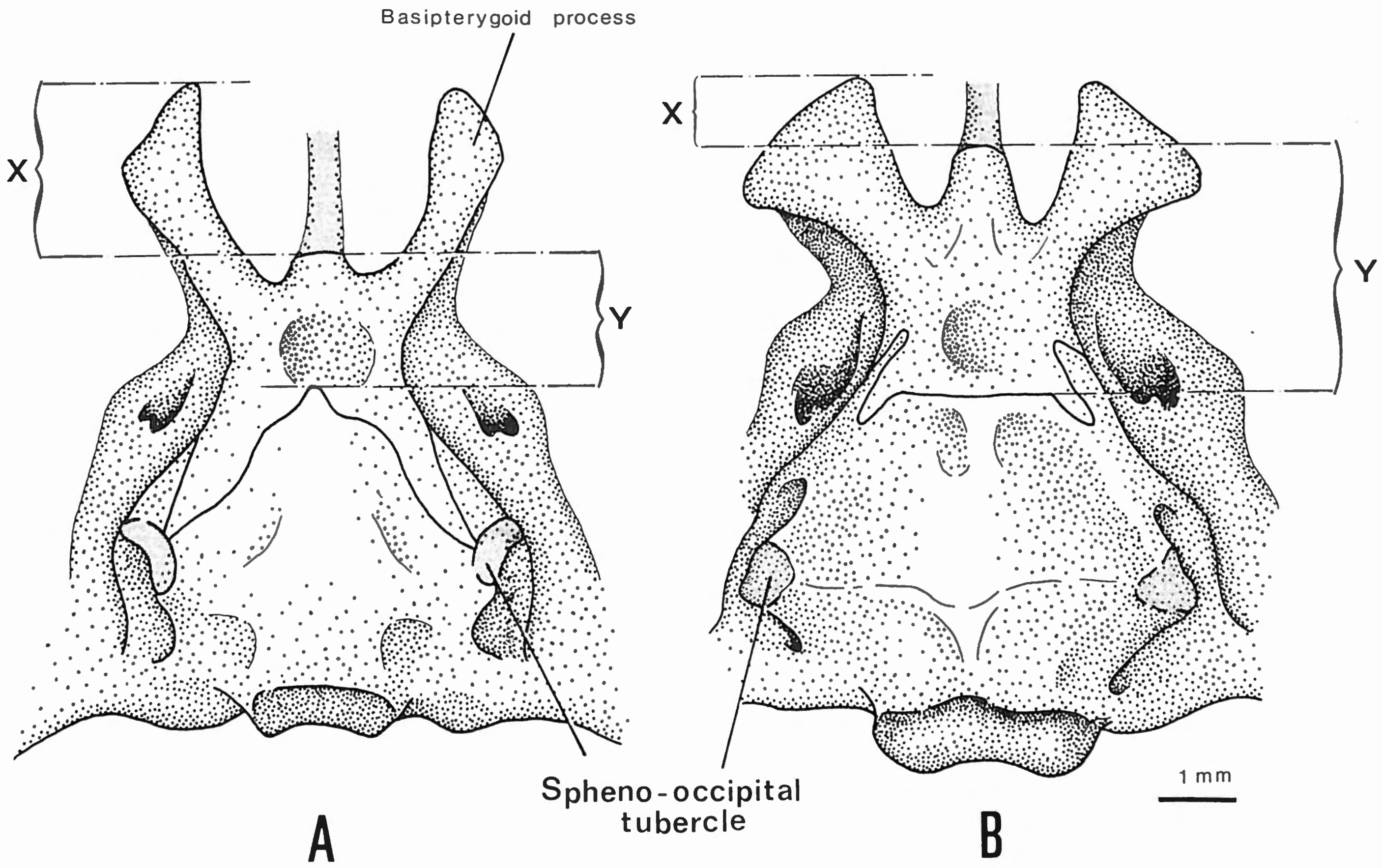

Figure 9 : *Ventral view of braincase in Cordyliformes with variation in length of basipterygoid process (X) and length of basipterygoid body (Y). Also note the composition of spheno-occipital tubercle. A)* Cordylus cordylus. *B)* Gerrhosaurus nigrolineatus.

(1988). Within the ingroup, *Cordylus*, *Platysaurus* and *Pseudocordylus* demonstrate the apomorphic condition (Figs. 21, 24, 26).

C19) *Depth of subdental shelf of maxilla* (crista dentalis) : (Fig. 10) 0) shallow; 1) deep. [All outgroup taxa either lack or have a rather shallow subdental shelf/ CASE I]. Within the ingroup taxa a deeply grooved subdental shelf of the maxilla just medial to the maxillary teeth is present in all cordylids and in *Angolosaurus* (Fig. 10). The function of a prominent subdental shelf is not known. This subdental shelf is deeper anteriorly in particular at the junction with the premaxilla and becomes somewhat more shallow posteriorly.

C20) *Second ceratobranchial* : (Fig. 11) [Character states unordered] 0*) absent; 1*) present. [For distribution of character states among outgroup taxa see Estes *et al.* (1988)/CASE V, polarity decision equivocal]. The distribution of character states among the outgroup taxa shows no consistent pattern that coincides with other character complexes defining phylogenetic units. The distribution of character states within the ingroup is therefore all the more surprising. All cordylids have a well-developed second ceratobranchial (Fig. 11A & 11B) whereas gerrhosaurids lack this structure (Fig. 11C).

C21) *Posterior extent of splenial* : 0) up to but not past apex of coronoid; 1) extends posteriorly beyond apex of coronoid. [All outgroup taxa examined with the exception of *Ameiva* have splenials extending posteriorly not past the apex of the coronoid/CASE I]. Cordylids and *Cordylosaurus* exhibit the derived character state (Figs. 19, 21, 24, 26, 34) whereas the remaining gerrhosaurids demonstrate the plesiomorphic condition (Figs. 28, 30, 32, 36, 39).
This character complex can be combined with character 66 of Estes *et al.* (1988) such that a bi-directional character complex can be hypothesized. The plesiomorphic condition would be a splenial that extends posteriorly to the apex of the coronoid. One transformation would be towards reduction of the posterior extent of the splenial as in some "iguanids", "agamids", xantusiids, *Heloderma* and *Varanus* (Estes *et al.*, 1988). The alternate transformation invokes a posterior elongation of the splenial in cordylids and *Cordylosaurus*.

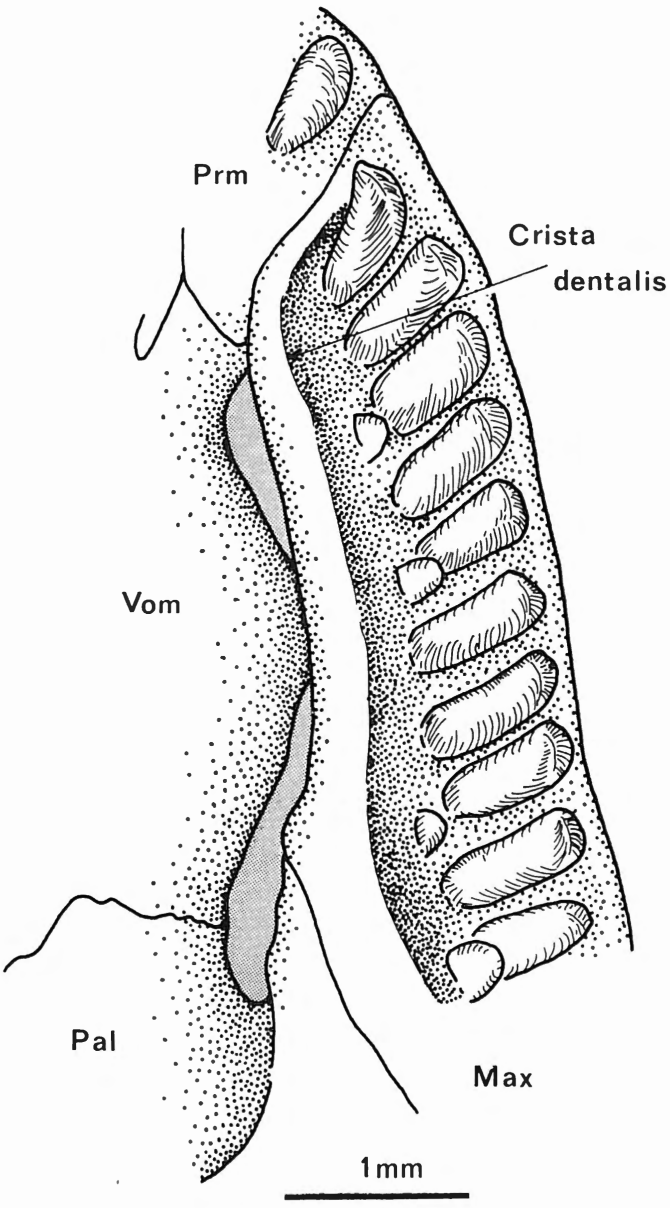

Figure 10: *Palatal view of* Cordylus cordylus *showing deeply grooved crista dentalis. Abbreviations: Max = maxilla; Pal = palatine; Prm = premaxilla; Vom = vomer.*

C22) *Coronoid lateral process*: 0) present as a lappet on the dentary; 1) absent or covered by postero-dorsal aspect of dentary. [All outgroup taxa with the exception of the Xantusiidae have a coronoid with lappet that projects anteriorly onto the dentary/CASE I]. This character has been used by Estes *et al.* (1988) to analyze phylogenetic relationships among squamate families. Within Squamata the presence of a coronoid lappet is the derived condition diagnosing the Autarchoglossa. At that level then, the presence of a lappet is plesiomorphic and Estes *et al.*'s (1988) polarities are reversed. Within the ingroup the derived condition is expressed in all taxa with the exclusion of *Chamaesaura* (Fig. 19).

C23) *Height of coronoid process*: 0) equal to the height of dentary; 1) shorter than the height of dentary. [Among outgroup taxa the distribution of character states is ambiguous. In Lacertidae, Gymnophthalmidae and Anguimorpha the height of the coronoid equals that of the body of the dentary. In Xantusiidae and Teiidae the coronoid process is distinctly shorter than the body of the coronoid. In Scincidae a variety of conditions occur. Some of the larger skinks such as *Tiliqua* and *Trachydosaurus* have short coronoid processes whereas the smaller skinks (e.g. *Chalcides* have longer coronoid processes/CASE I].
Within the ingroup the distribution of character states is clear. The presumed plesiomorphic condition is present in gerrhosaurids. Cordylids show the derived condition of a rather short coronoid process (Figs. 19, 21, 24, 26).

C24) *Lingual exposure of angular*: 0) present; 1) absent; i.e. angular restricted to labial surface. [All outgroup taxa examined have a lingual exposure of the angular bone. In Xantusiidae the condition is unique in that the surangular-articular and angular are fused to form a single compound bone (Rieppel, 1984). This compound bone however has a lingual exposure/CASE I].
Gerrhosaurids exhibit the plesiomorphic condition. In cordylids the angular bone is restricted exclusively to the labial surface of the lower jaw (Figs, 19, 21, 24, 26). In *Tracheloptychus* a homologous situation exists as in Xantusiidae, with the fusion of the surangular-angular bone with the angular to form a compound bone (Fig. 36). This compound bone has a distinct lingual exposure.

C25) *Ventral process of angular*: 0) extends anteriorly to the last marginal tooth; 1) extending anteriorly past apex of coronoid but does not reach the last marginal tooth; 2) does not extend anteriorly past the level of the apex of coronoid. [In all outgroup taxa with the exception of Xantusiidae, the ventral process of the angular reaches the level of the last marginal tooth. In Xantusiidae the anteroventral process of the surangular-articular-angular compound bone extends only slightly past the apex of the coronoid, but does not reach the level of the last marginal tooth/CASE I].
The plesiomorphic condition is expressed in all gerrhosaurids. *Chamaesaura* exhibits the intermediate condition. The remaining cordylids (*Cordylus*, *Platysaurus* and *Pseudocordylus*) show the apomorphic condition.

C26) *Adductor fossa size*: 0) small or moderate; 1) expanded fossa to accommodate the extension of the m. adductor mandibulae posterior into Meckel's canal. [Some Scincidae, Xantusiidae and all anguimorphans have a small or moderate adductor fossa/CASE IV]. Estes *et al.* (1988) defined an expanded adductor fossa

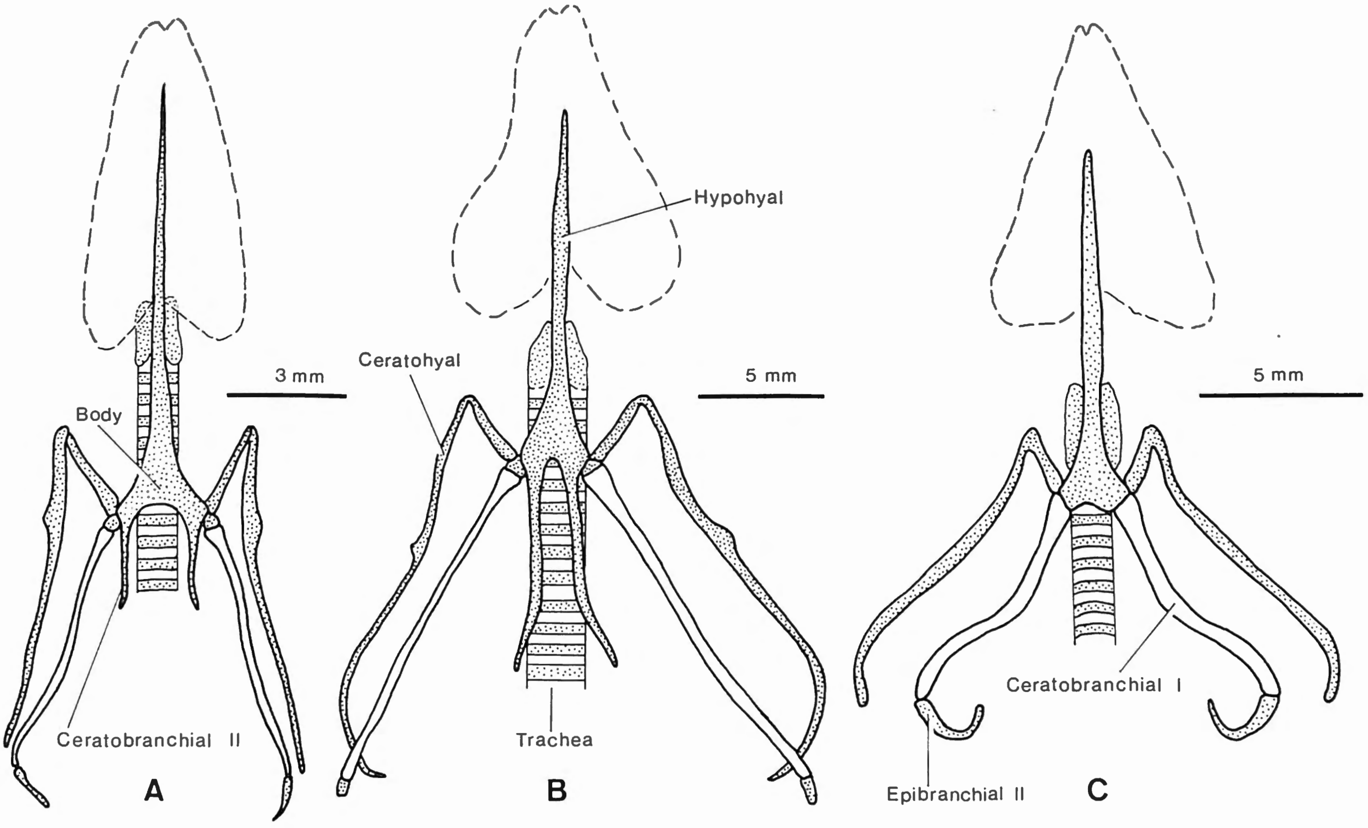

Figure 11 : *Variation in hyoid apparatus within ingroup A)* Platysaurus capensis. *B)* Pseudocordylus microlepidotus. *C)* Angolosaurus skoogi.

as a synapomorphy in support of the Lacertoidea with convergences being expressed in some Scincidae. Within the ingroup, the derived condition is also present in all cordylids and in *Cordylosaurus* (Figs. 19, 21, 24, 26, 32).

C27) *Dorsal surface of retroarticular process* : 0) dorsal surface without sulcus or pit; 1) deep pit present. [Outgroup taxa with the exception of Teiidae and Xantusiidae lack a prominent pit or sulcus on the dorsal aspect of the retroarticular process/CASE I]. The polarities at the Autarachoglossan level are reversed from the polarities as defined by Estes *et al.* (1988) for Squamata. Within the ingroup a deep pit on the dorsal aspect of the retroarticular process is present in *Chamaesaura* and all the gerrhosaurids.

C28) *Retroarticular process breadth posteriorly* : [Character states unordered] 0*) tapered or parallel-sided; 1*) broad posteriorly. [Scincidae and Anguidae have broad retroarticular processes. In the remaining outgroup taxa the retroarticular process is tapered/CASE II, polarity decision equivocal]. Estes *et al.* (1988) defined this character without suggesting any function or adaptation. Within the ingroup only *Cordylus* has a posteriorly tapering retroarticular process (Fig. 21).

C29) *Retroarticular process torsion* : 0) posterior border obliquely twisted; 1) not twisted posteriorly. [Anguimorphans and Scincidae have the posterior border of the retroarticular process twisted obliquely. Lacertidae, Xantusiidae and Gymnophthalmidae have a retroarticular process that is horizontal. In Teiidae the retroarticular process is vertical/CASE I]. Estes at al. (1988) indicate that a posteriorly twisted retroarticular process is a synapomorphy for the Scleroglossa. At this level the polarities are reversed from the squamate level as defined by Estes *et al.* (1988).
Chamaesaura, *Tetradactylus* and *Tracheloptychus* all show the derived condition. Remaining cordylids have the plesiomorphic character state.

CHARACTERS OF POSTCRANIAL ANATOMY

P1) *Cervical intercentral attachment* : 0) intervertebral; 1) sutured to anterior part of following centrum; 2) fused to anterior part of following centrum. [Both Scincidae and Anguimorphans have cervical intercentra connected to the preceding vertebra. Lacertidae and Xantusiidae are variable. In Teiidae and Gymnophthalmidae the cervical intercentra are associated with posterior vertebrae/ CASE I]. Estes *et al.* (1988) defined this character. At the Autarchoglossan level the polarities coincide with those at the squamate level. Although anterior and posterior associations of the cervical intercentra are possible, only the latter condition is expressed within the ingroup. Cervical intercentra located intervertebrally occur in all ingroup taxa with the exception of *Chamaesaura* and *Cordylus*. In *Chamaesaura* the cervical intercentra are consistently *sutured* to the following vertebrae. In *Cordylus* the intercentra are *fused* to the following vertebral bodies. In Autarchoglossa this latter condition is found only in some Gymnophthalmidae. *Tracheloptychus* has a unique condition in that the intercentra are not restricted to the cervical vertebrae only, but are also present on the anterior thoracic vertebrae. A total of 6 intercentra are present.

P2) *Zygosphene-zyganthra articulation* : [Character states unordered] 0*) absent or only weakly developed; 1*) strongly developed. [Scincidae, Lacertidae, Teiidae and Gymnophthalmidae have well-developed zygosphene-zyganthra articulations. In Xantusiidae and in Anguimorpha these processes are lacking/CASE II, polarity decision is equivocal].
This character complex has been used by various authors (e.g. ETHERIDGE & DE QUEIROZ, 1988; ESTES *et al.*, 1988). ESTES *et al.* (1988) discuses the problems associated with polarizing this character complex, but suggested that on the basis of parsimony and the distribution of other character complexes a weakly developed zygosphene-zyganthrum articulation is to be regarded as the plesiomorphic condition within Squamata[5]. The absence of, or strong development of the zygosphene-zyganthra articulation; are alternate apomorphies. At present this character complex will be left unpolarized. Within the ingroup, gerrhosaurids have a weakly developed zygosphene-zyganthra articulation at best. By contrast cordylids have a strongly developed zygosphene-zyganthra articulation. Within Scincoidea it is equally probable to postulate that a strongly developed zygosphene-zyganthra articulation has arisen once with subsequent loss in gerrhosaurids as it is to postulate a convergence between cordylids and skinks (ESTES *et al.*, 1988).

P3) *Clavicular angulation*: (Fig. 12) 0) strongly curved; 1) simple curved rods. [All outgroup taxa examined have strongly angulated anteriorly curving clavicles/CASE I]. ESTES *et al.* (1988) indicate that the strongly angulated clavicle is a synapomorphy for the Scleroglossa. At this level, and at the less-inclusive autarchoglossan node the polarities are reversed from the squamate node. Within the ingroup the derived condition is expressed in *Chamaesaura* (Fig. 12A) and *Platysaurus*. All of the remaining taxa have strongly angulated clavicles (Fig. 12B).

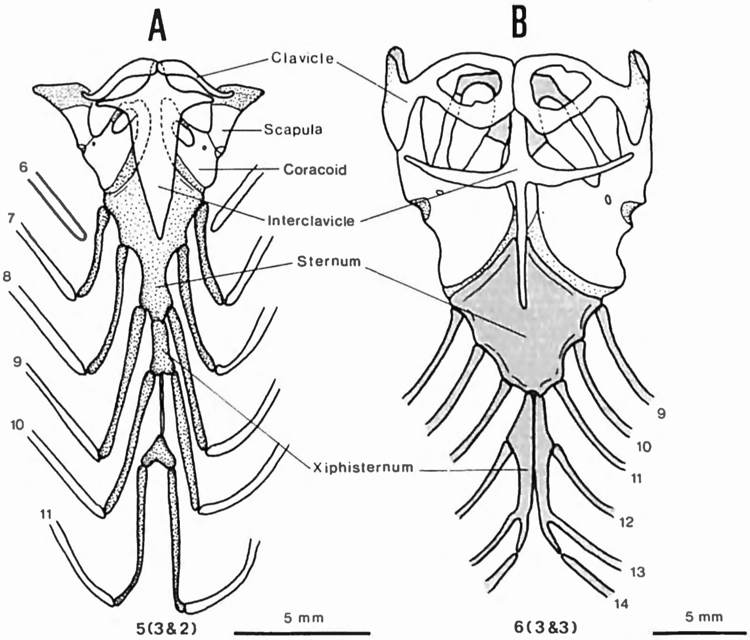

Figure 12 : *Ventral view of pectoral girdle of ingroup taxa with rib articulation patterns. A) 5(3&2) pattern as seen in* Chamaesaura anguina. *B) 6(3&3) pattern as seen in* Gerrhosaurus nigrolineatus. *The numbers next to the ribs indicate the vertebra with which they articulate.*

P4) *Interclavicle shape* : (Fig. 12) 0) cruciform; 1) T-shaped, with a small anterior process. [All outgroups (when the interclavicle is present) except some *Varanus* have cruciform interclavicles/CASE I]. The polarities are reversed from those defined by ESTES *et al.* (1988) at the squamate node. Within the ingroup the derived condition is found in all cordylids (Fig. 12A). By contrast, the gerrhosaurids have cruciform interclavicles (Fig. 12B).

P5) *Pubic tubercle* : 0) large, recurved medially; 1) absent or small. [All outgroup taxa examined have well-developed pubic tubercles, with the exception of Anguimorpha in which they are small but still present/CASE I].
The distribution of character states is split between the two ingroup families. Gerrhosaurids all have well developed medially recurved pubic tubercles. By contrast, cordylids for the most part have but small knobs. In the limbless species of *Tetradactylus* the pubic tubercles are lost (BERGER-DELL'MOUR, 1983). However, *Tetradactylus seps*, the presumed earliest diverging taxon, with fully developed limbs, has well-developed pubic tubercles. This genus is therefore coded as having the plesiomorphic condition.

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[5] This statement is deduced by combing characters 95 and 96 of ESTES *et al.* (1988) and hypothesizing a bi-directional transformation series.

P6) *Carpal intermedium* : 0) present; 1) absent. [All outgroup taxa with the exception of some teiids, some scincids and *Varanus* have a carpal intermedium/CASE IV]. Renous-Lecuru (1973) extensively investigated the carpal bones in Autarchoglossans, and noted the above listed taxa which lack a carpal intermedium. A reduced or absent intermedium itself is considered a synapomorphy of squamates (Gauthier *et al.*, 1988; Estes *et al.*, 1988). Within the ingroup *Chamaesaura*, *Platysaurus* and the madagascan gerrhosaurids each have a carpal intermedium whereas the remaining taxa lack a separate intermedium. The condition in *Zonosaurus* is peculiar in that the intermedium is relatively large for squamates and is wedged between the ulnare and radiale.

P7) *Phalangeal formula of manus* : 0) 2.3.4.5.3; 1) 2.3.4.4.3. [All limbed outgroup taxa have 5 phalangeal elements in the fourth finger/CASE I]. Romer (1956) indicates that "the formula established in the manus at an early stage in reptilian evolution was 2.3.4.5.3." Excluding limbless or reduced-limbed forms the primitive phalangeal formula is retained by most squamates as well as *Sphenodon.* As indicated by Romer (1956) numerous exceptions exist such as Chamaeleonidae, *Phrynosoma*, *Lanthanotus* (2.3.4.4.3) and *Molochus* (2.2.3.3.2). The loss of a phaLANGeal element in the fourth finger occurs also in some eublepharid geckos such as *Coleonyx brevis* and *Hemitheconyx taylori* (Grismer, 1988). In Scincidae with well-developed limbs such as *Mabuya*, *Scincus*, *Egernia*, *Eumeces*, *Euprepes*, *Ablepharus* and some *Lygosoma* the primitive phalangeal formula is present (Berger-Dell'Mour, 1983).

Within the ingroup a consistent pattern is observed. In *Chamaesaura anguina* and *C. macrolepis* the limbs are severely reduced with concordant reduction in phalangeal elements (Essex, 1927). The remaining cordylids with the inclusion of *Chamaesaura aenea* express the plesiomorphic phalangeal formula. In all gerrhosaurids exclusive of the limbless *Tetradactylus*, the phalangeal formula is 2.3.4.4.3. In *Tetradactylus seps*, the presumed earliest diverging taxon with normal limbs also has a derived phalangeal formula.

CHARACTERS OF LIFE HISTORY

L1) *Reproductive mode* : 0) oviparous; 1) viviparous. [All outgroup taxa at the familial level with the exception of Xantusiidae, *Xenosaurus* (but not *Shinisaurus* (Wilke, 1985)) and Aniellidae are oviparous/CASE III]. Blackburn's (1982) terminology of reproductive modes are used here in which oviparous means egg-laying and viviparous meaning live-bearing regardless of the form in which nutrients of development are supplied. Although oviparity is beyond doubt the plesiomorphic condition in squamates, the widespread independent acquisition of viviparity in a variety of taxa and the variability even within species (Fitch, 1970; Tinkle & Gibbons, 1977; Blackburn, 1982) makes this character complex difficult to apply within a systematic framework. Blackburn (1982) suggests that most of the subgeneric origins of viviparity within squamates have occurred in cold-climates, possibly to facilitate maternal thermoregulation of the developing embryos. In the case of Cordylidae + Gerrhosauridae, it seems that the timing of birth coinciding with the onset of the rainy season is a stronger ecological motivator. Tendencies towards egg retention are suggested to be a preadaptation towards viviparity, and demonstrates an analogous ecological strategy.

Although each species is influenced by external factors differentially, the close relationship between gerrhosaurids and cordylids, and the fact that they are sympatric over a wide area, postulates that ecological and physiological influences on reproductive modes are relatively similar. Therefore it is perhaps possible to regard this character complex as a systematic character, with the derived condition (viviparity) being prseent in *Chamaesaura*, *Cordylus* and *Pseudocordylus. Platysaurus* has a short gestation period with consistently only 2 relatively large eggs as and can be regarded as demonstrating an intermediate stadium between true oviparity and viviparity.

MISCELLANEOUS CHARACTERS

M1) *External limbs* : 0) well developed; 1) limbs reduced or absent. [Among the outgroup taxa, the presence of well developed limbs is the widespread condition. Limbless forms are present in Scincidae (e.g. *Eumecia*, *Panaspis*, *Acontias* and *Typhlosaurus*) and in Anguidae (e.g. *Aniella*, *Anguis* and *Ophisaurus*)/CASE IV].

Limb reduction is present in *Chamaesaura* and some species of *Tetradactylus*. This character most likely is independent from phylogeny and rather shows ecomorphological convergence.

M2) *Tail morphology* : 0) regular, no spines; 1) spinose whorls. [All outgroup taxa have regular tails with few exceptions (e.g. *Echinosaura*, some *Tribolonotus*, *Tropidophorus*). *Varanus storri* has a slightly spinose tail/ CASE I].

Pseudocordylus spinosus P. langi and all *Cordylus* except *coeruleopunctatus*, have tails with spinose whorls.

M3) *Osteoderm distribution* : (Fig. 13) 0) entire body covered with osteoderms; 1) dorsal aspect of head and tail covered with osteoderms; 2) osteoderms restricted to the dorsal aspect of head. [In Scincidae and Anguimorpha (with loss in Varanidae) the body is covered with osteoderms. In Lacertidae and Xantusiidae osteoderms are restricted to the dorsal aspect of the head.

Micro- and macroteiids completely lack osteoderms/ CASE I]. Although listed by various other authors as part of the osteology, this character complex is included here.

Granted that the presence of body osteoderms is derived within the context of Squamata, at the level of Autarchoglossa it is the plesiomorphic condition with subsequent loss in: Varanidae (sensu stricto); Lacertoidea sensu ESTES *et al.* (1988) and in the cordylid taxa listed below. All gerrhosaurids and *Cordylus* have the entire body covered with osteoderms (Fig. 13A). The intermediate character state in which osteoderms are restricted to the dorsal aspect of head and tail only is found in *Pseudocordylus* (Fig. 13B). The apomorphic condition (osteoderms only on dorsal aspect of head) is expressed in *Chamaesaura* and *Platysaurus* (Fig. 13C & 13D).

ESTES *et al.*'s (1988) character # 36 (palpebral ossifications present or absent) is incorporated into this character description. The absence of palpebral ossifications are in fact an adaptation to crevice dwelling, such that the eyes can be easily retracted into the head (BÖHME, pers. comm.). This is perhaps best illustrated in Lacertidae. ARNOLD (1973) postulates two principal skull types for lacertids. Most lacertids have skull type 1; a robust undepressed skull with a complete set of palpebral ossifications (= supraocular lamellae sensu ARNOLD). His skull type 2 is flattened with strongly fenestrated supraocular lamellae and is invariably present among crevice dwellers, such as the Yugoslavian rock lizards *Lacerta oxycephala*, *Lacerta horvathi* and *Lacerta mosorensis* (KLEMMER, 1957 : Taf. 1) or in extremely small lacertids such as *Algyroides fitzingeri* and *Lacerta andreanszkyi*. In the latter two, the absence of palpebral ossifications is presumably a paedomorphic retention or a function of small body size. Palpebral ossifications are also completely lacking in Xantusiidae.

It is also possible that the presence or absence of body osteoderms does not reflect phylogeny but rather ecomorphological adaptations. Evidence for this is the fact that cordylids which lack dorsal and ventral body osteoderms are rather flattened crevice ecomorphs. Although *Cordylus* for the most part is regarded as a rock crevice dweller, and is slightly depressed, both *Pseudocordylus* and *Platysaurus* are more highly specialized within this niche, penetrating deeper in the rock formations. The lack of osteoderms below the middle two supraocular scales are further crevice adaptations.

M4) *Lateral body fold* : 0) absent (i.e no zone of small lateral body scales); 1) present from corner of mouth to axilla; 2) corner of mouth to groin. [All outgroup taxa with the exception of Anguidae lack a lateral body fold/CASE I].

The intermediate character state is expressed exclusively in *Tracheloptychus*, with the remaining gerrhosaurids all having a lateral body fold extending the corner of the mouth to the groin.

Among cordylids, the apomorphic character state is present in all *Cordylus* examined except *tropidosternum*. The latter species exhibits the plesiomorphic condition.

M5) *Cross-sectional body form* : 0) ovid; 1) flattened. [All outgroup taxa with the exception of Xantusiidae and some lacertids (e.g. *Holaspis* and others) have round or oval bodies/CASE I].

All gerrhosaurids and *Chamaesaura* exhibit the plesiomorphic condition of a rounded cross-sectional body form. *Cordylus* and *Pseudocordylus* are somewhat flattened with *Platysaurus* being an extreme case.

M6) *Cloacal covering* : [Character states unordered]. 0*) absent; 1*) present, i.e. the preanal scales project past the cloaca. [A cloacal covering is present in Scincidae, but absent in the remaining outgroup taxa/CASE II, polarity decision equivocal]. Two options concerning the polarity of this character are possible. A cloacal covering can be regarded as an synapomorphy for Scincidae + [Cordylidae + Gerrhosauridae], with subsequent loss in cordylids; or the cloacal covering can be regarded as a convergence between gerrhosaurids and Scincidae. Both hypothesis require two evolutionary transformations.

As mentioned above the character states show a strict dichotomy between the two ingroup families : cordylids lack a cloacal covering, gerrhosaurids have a cloacal covering.

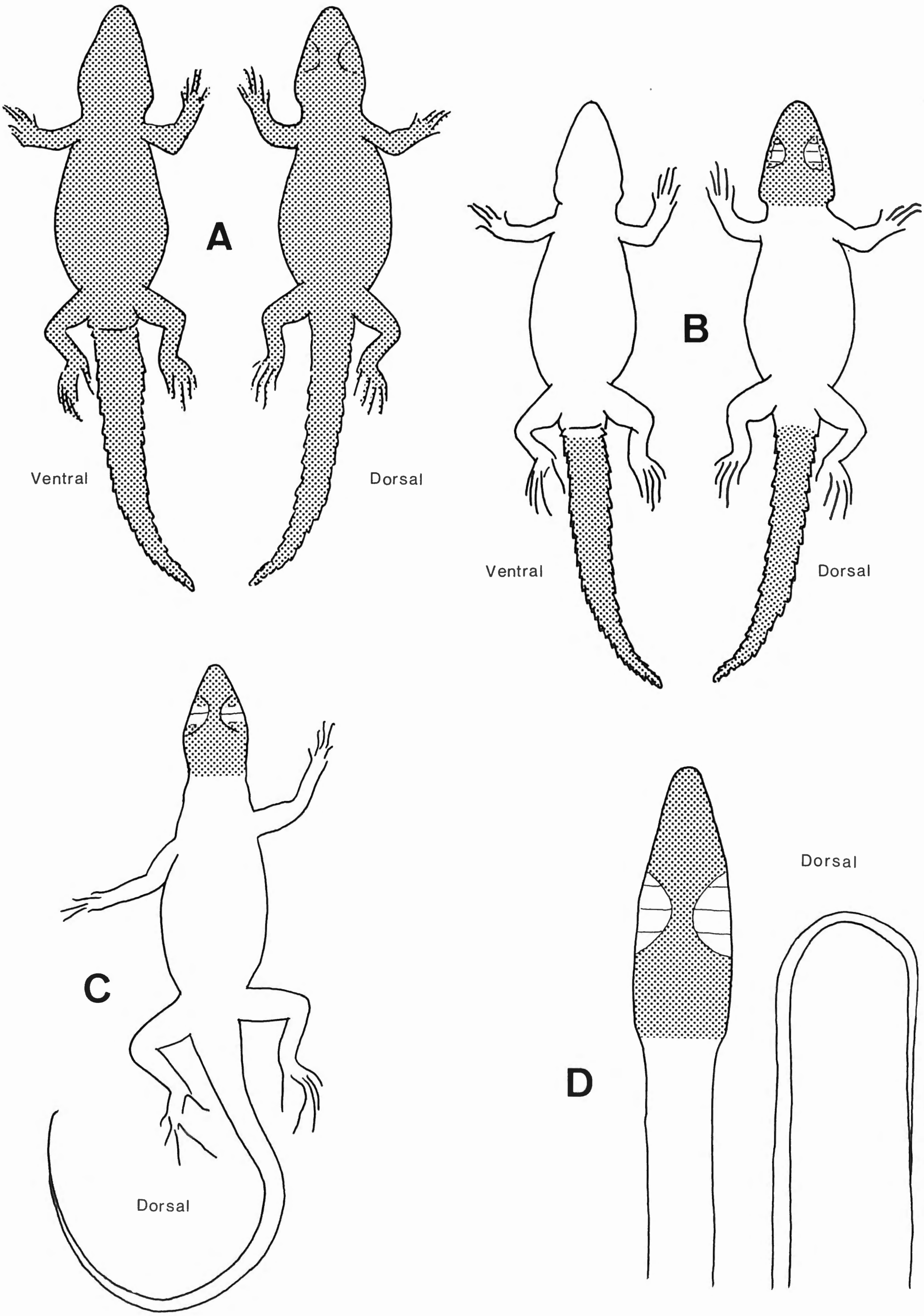
M7) *Cloacal pigmentation* : 0) absent; 1) present. [Outgroup taxa for the most part lack cloacal pigmentation/CASE I].

The distribution of character states among the ingroup taxa does not show any clear pattern. When present, cloacal pigmentation always occurs laterally at the junction of the anterior and posterior cloacal lips. Furthermore, either the anterior and/or posterior lip are partially or completely pigmented.

The character states are intraspecificaly stable, but vary in the degree of pigmentation. There also does not seem to be an age or sex dependant factor with respect to the amount of pigmentation.

Within cordylids; cloacal pigmentation around the inner cloacal margin is expressed in *Cordylus cataphractus*,

Figure 13 : *Schematic representation of distribution of osteoderms among the ingroup taxa. Shaded areas represent osteoderms. A) Whole body distribution of osteoderms as seen in* Cordylus *and Gerrhosauridae. B) Condition as observed within* Pseudocordylus. *C) Osteodermal distribution as observed in* Platysaurus. *D) Distribution of osteoderms as seen in* Chamaesaura. ▷


A
Ventral
Dorsal
B
Ventral
Dorsal
C
Dorsal
D
Dorsal

C. coeruleopunctatus, *C. rhodesianus* and *C. tropidosternum*. In *Cordylus macropholis* the entire cloacal region is pigmented. The remaining *Cordylus* investigated lacked cloacal pigmentation.

In *Platysaurus* cloacal pigmentation was identified in *capensis*, *pungweensis* and *torquatus* in which melanophores are primarily restricted to the junction of anterior and posterior cloacal lips. The remaining *Platysaurus* examined lacked such pigmentation.

Cloacal pigmentation is absent in *Chamaesaura* and *Pseudocordylus*.

In gerrhosaurids cloacal pigmentation primarily around the anterior cloacal lip was identified in *Tracheloptychus petersi* as in the following *Zonosaurus* : *aeneus* (patches on anterior lip); *karsteni* (entirely pigmented); *laticaudatus* (2 large patches on anterior lip); *maximus* (around cloacal margin) and *ornatus* (around cloacal margin). The remaining six species of *Zonosaurus* and *Tracheloptychus madagascariensis* lacked cloacal pigmentation.

M8) *Callous glands* : (Fig. 13) 0) absent; 1) present primarily on the ventral aspect of thighs anterior to femoral pores. [All outgroup taxa lack callous glands/ CASE I]. Within the ingroup, callous glands are identified on the ventral aspect of the thighs in limbed cordylids. *Chamaesaura* which for all purposes lacks hind limbs is coded as "missing data". In gerrhosaurids no such glands were identified.

Moody (1980) reviewed the composition of the epidermal holocrine glands, the terminology of which is used here. Callous glands have been identified within Squamata in some primitive agamids (Moody, 1980) and in sphaerodactyline and eublepharine gekkotans (Maderson, 1972). The homology of the callous glands in these two clades together with the ingroup taxa is questionable. In those agamids that have callous glands, they are present along the ventral surface of the femoral region, the inguinal and midline regions of the abdomen, the precloacal lip area, and an area between the posterior abdomen and the precloacal area. As mentioned above in cordylids the callous glands are found primarily along the ventral aspect of the thighs anterior to the femoral pores, although they can be found also around cloaca, on front legs and on back (Mouton, pers. comm.). The presence of callous glands may be correlated with the reduction in number of femoral pores in cordylids (see "femoral pores" below).

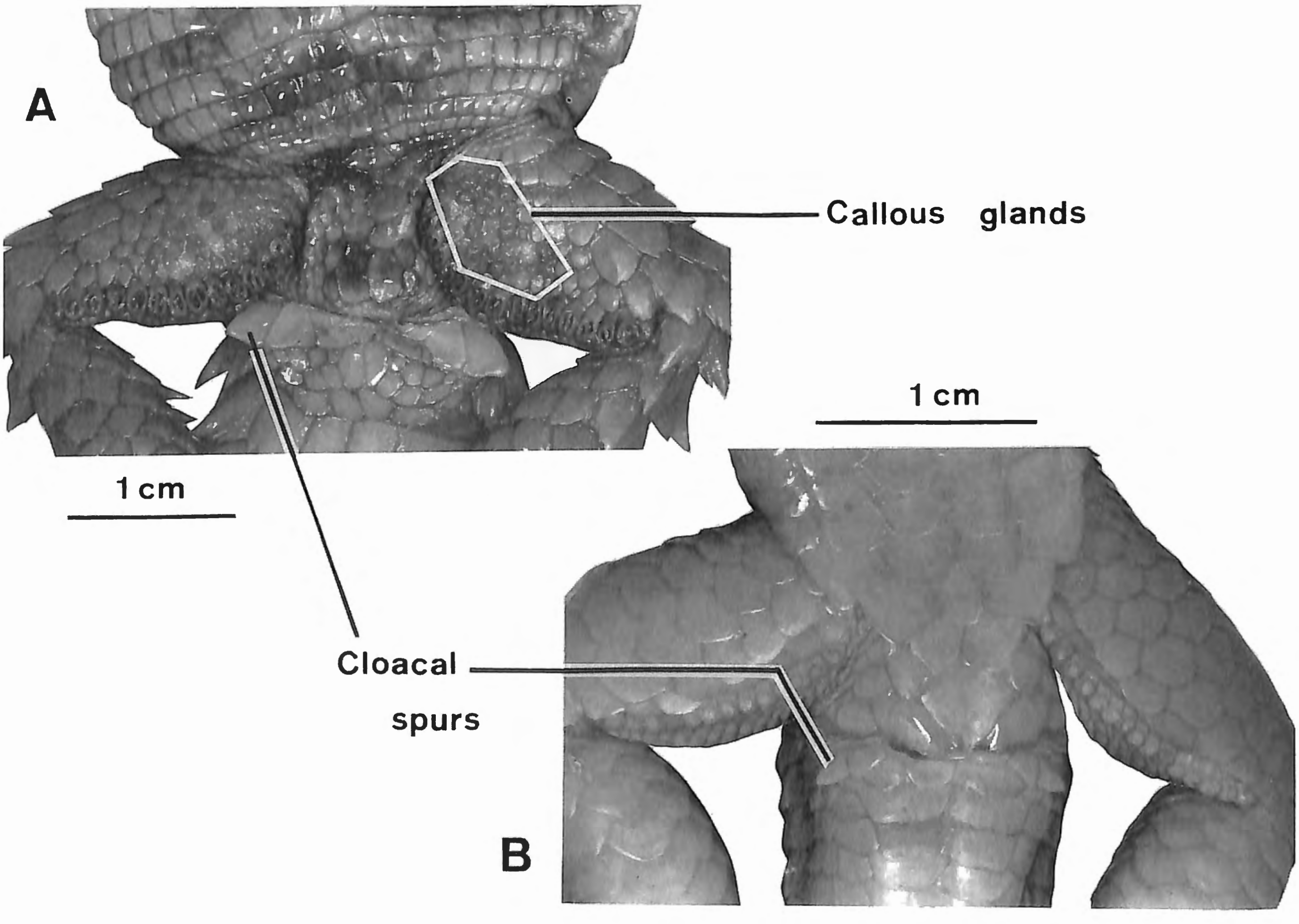


Figure 14 : *Cloacal region of ingroup taxa with the position of cloacal spurs and callous glands. A)* Cordylus cataphractus. *B)* Gerrhosaurus nigrolineatus.

Characters not used in this study

Although not definable as characters for reasons of in- or outgroup variability, ontogenetic shifts, information below the level of analysis or missing information, the following character complexes provide information that can perhaps be useful in the future.

Nasal scales (N) : Two distinct conditions of the nostril can be identified within the ingroup taxa : a flat and undifferentiated nostril or a distinctly inflated one. Most outgroup taxa have flat, undifferentiated nasal scales.
An expanded and inflated nasal region occur in a variety of taxa most of which are desert inhabitants such as *Agamura* (De Witte, 1973), *Ptyodactylus* (Heimes, 1982), *Eremias* and *Mesalina*. An expanded nasal capsule can prevent evaporative water loss in desert-dwelling species (Niethammer, pers. comm). A variety of adaptations of the nostril to loose sand habitats have been observed in squamates. Stebbins (1948) describes in detail the "sink-trap" nasal passage in desert iguanians. In the desert dwelling varanids the nostril is always a narrow slit and located close to the eyes. The nasal passage is elongated and initially proceeds anteriorly towards the snout then posteriorly (Mertens, 1942).
Undifferentiated nostrils are present in *Chamaesaura*, *Pseudocordylus* and all *Platysaurus* except *imperator*. *Platysaurus imperator* has an inflated nostril. In *Cordylus* both character states are observed. The following taxa have flat undifferentiated N scales : *coeruleopunctatus*, *cordylus*, *giganteus*, *macropholis*, *rhodesianus*, *tropidosternum*, *vittifer* and *warreni*. The nasal region immediately surrounding the external nasal passage is distinctly swollen in the following taxa of *Cordylus* : *campbelli*, *cataphractus*, *lawrenci*, *mclachlani*, *namaquensis*, *peersi* and *polyzonus*.

Upper labial margin : The postnasal scale (when present) may form part of the upper labial margin (condition A) or it may not (condition B). Among all Cordylidae condition A was found exclusively in *Pseudocordylus microlepidotus*, *robertsi* and *spinosus*. In *Pseudocordylus capensis* the PN is distinct, but does not form part of the upper labial margin.
Two hypothesis can be postulated. Either a PN forming part of the UL margin is a derived feature uniting the *microlepidotus-robertsi-spinosus* clade or it is an apomorphy for *Pseudocordylus* with a reversal in *capensis*. Because this is an analysis at the generic level this character is not relevant to this analysis but rather may be used to determine relationships within *Pseudocordylus*.

Interparietal scale : The interparietal scales is present in all Cordylidae and Gerrhosauridae with the exception of *Zonosaurus aeneus*, *rufipes* and *brygooi* (Lang, 1990b). In *Cordylosaurus* the interparietal scale is distinct in juveniles but tends to fuse with age with the frontoparietal scales and the anterior parietal scales to form a single large posterior head shield (Loveridge, 1942).
Because this character does not reveal any information concerning the relationships of the ingroup taxa at the generic level it is omitted from the character data set.

Occipital spines : Occipital spines are bony projections at the posterior aspect of the skull, and are found among in- and outgroup taxa only in *Cordylus giganteus* (4 very large) and *Cordylus warreni* (6 shorter). Because the presence of derived character states are below the level of analysis (genera) of this study it cannot be used to determine relationships between the genera.

Femoral pores. The number of femoral pores is quite variable within the ingroup with no consistent pattern observable. Cordylids have substantially fewer femoral pores than gerrhosaurids. In *Cordylus campbelli* 3 small pores are present. Other *Cordylus* such as *macropholis* have up to 7 pores, approximately the same as in *Platysaurus* and *Pseudocordylus*. In gerrhosaurids by contrast, the number of femoral pores ranges from 9-10 in *Cordylosaurus subtessellatus* to over 30 in *Zonosaurus maximus* (Brygoo, 1985). *Angolosaurus*, a dune-dweller is quite unique in having numerous well-developed femoral pores. All lacertids by contrast that lack femoral pores, that produce territorial markers are invariably loose sand ecomorphs (Cole, 1966).
The reduction in number of femoral pores in cordylids may be related to the fact that they are predominantly visually oriented (see M8; Fig. 14).

Hemipenes : Cope (1896) was the first to describe the hemipenes of a cordyliform (*Cordylus cordylus*). He indicated the presence of a rigid welt opposite the sulcus (Stutzsaum *sensu* Böhme, 1988). Furthermore, there is a triangular space at the medial side of the sulcus which is finely calcyculate. On the lateral side ia a wide space with radiating laminae. Böhme (1988) in his monographic study of the genital morphology in non-ophidian squamates examined and described the following ingroup taxa : *Cordylus tropidosternum*, *Platysaurus guttatus*, *Gerrhosaurus major* (both subspecies), *Gerrhosaurus flavigularis*, *Tracheloptychus petersi*, *Zonosaurus karsteni*, *Z. maximus*, *Z. madagascariensis* and *Z. quadrilineatus*.
Fig. 15 illustrates the hemipenis of the specimen of *Cordylus tropidosternum* investigated and described by Böhme (1988). The hemipenis of *Gerrhosaurus flavigularis* is illustrated as figure 16. The reader is referred to the descriptions of Böhme (1988) for the discussion of hemipenis morphology within the ingroup taxa (see also comments made in the monophyly section). The structure of the hemipenes could not be used as a character because of an incomplete data set.

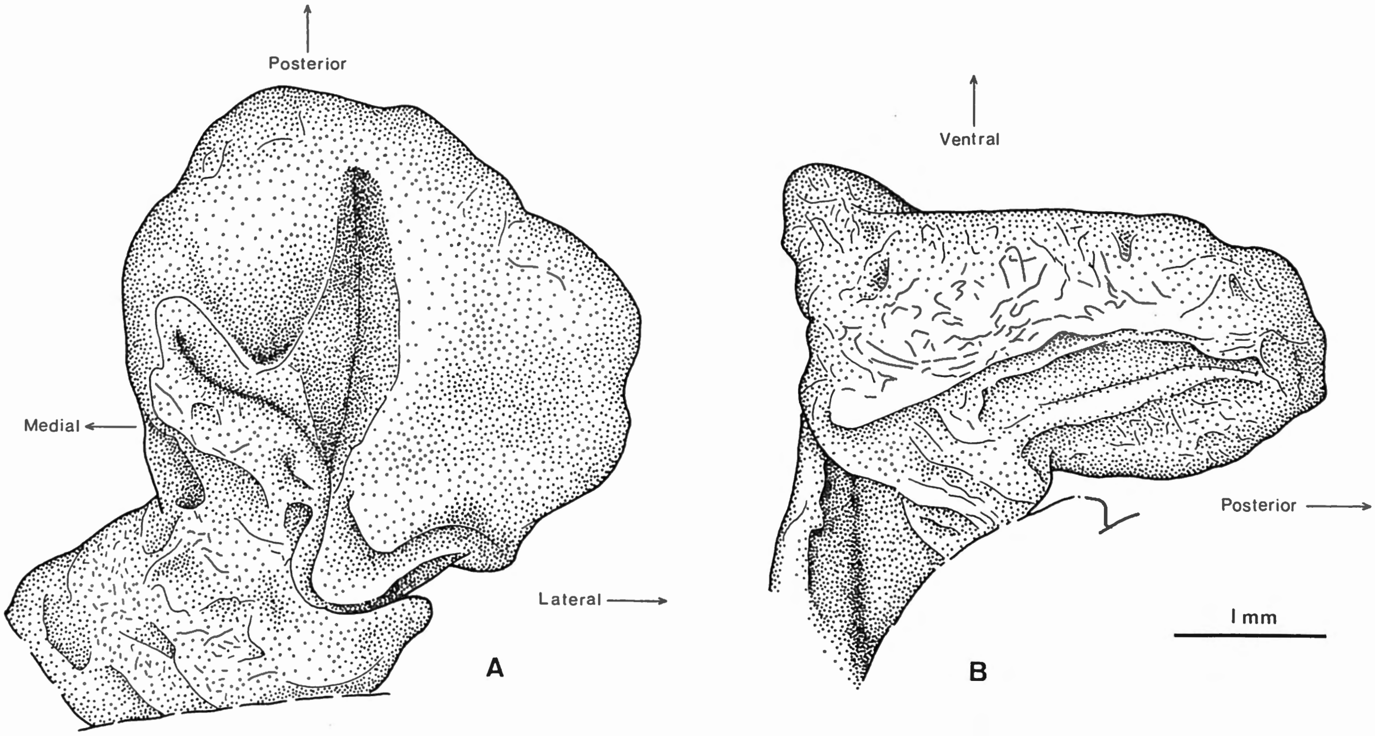
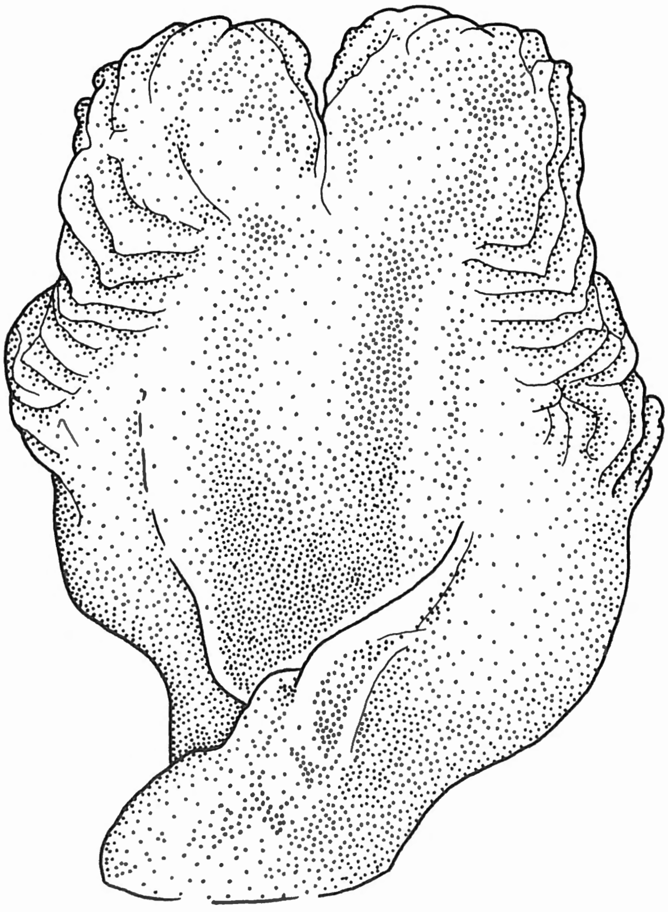


Figure 15 : *Ventral (sulcal) and lateral views of hemipenis of* Cordylus tropidosternum.

Figure 16 : *Sulcal view of hemipenis of* Gerrhosaurus flavigularis. *Illustration redrawn from* Dowling *&* Duellmann *(1978).*



Dermal rugosities on skull. As indicated by Estes *et al.* (1988) this character complex contains three character states : 0) absent; 1) present, non-vermiculite; 2) present, vermiculite. Although the distribution of character states within the ingroup is fairly consistent, in all outgroup at least two of the three character states are expressed. *Cordylus*, *Platysaurus* and *Pseudocordylus* have vermiculite dermal rugosities reflecting the cephalic scales with an extreme case in *Cordylus giganteus*. In *Platysaurus* the intermediate condition is often present. In *Chamaesaura* and gerrhosaurids no such vermiculite rugosities could be identified.

Vidian canal. The vidian canal is located within the basisphenoid and can be either open ventrally or covered by the crista ventrolateralis. The vidian canal is consistently uncovered in *Chamaesaura*, *Angolosaurus*, *Cordylosaurus* and *Tracheloptychus*. On the other hand, the vidian canal is covered in *Cordylus*, *Platysaurus* and in *Pseudocordylus*. In *Gerrhosaurus* and *Zonosaurus* considerable variation exists. For example in *Gerrhosaurus flavigularis*, *major* and *validus* the vidian canal is covered by the crista ventrolateral whereas in *multilineatus* and *nigrolineatus* the vidian canal is exposed. In *Zonosaurus*, an equal number of taxa show either condition, however, within a species the character states remain constant. The ingroup variability is deemed too great to formulate a systematic character complex.

Posterior opening of vidian canal. This character complex has been used as a systematic character by Estes *et al.* (1988) with the following defined character state polarities : 0) at basisphenoid-prootic suture; 1) within basisphenoid. Among the outgroup taxa the character states show no distinct distribution pattern. Some Scincidae, some Xantusiidae, Gymnophthalmidae, Teiidae and *Xenosaurus* all have the posterior opening of the vidian canal located within the basisphenoid. The remaining taxa show the alternative condition.

Within the ingroup all cordylids in addition to *Cordylosaurus*, *Tracheloptychus* and *Tetradactylus* exhibit the presumed derived condition. If the monophyly of the two families is to be maintained the vidian canal opening within the basisphenoid must have been derived within the Autarchoglossa, including the ingroup multiple times.

Presence or absence of parietal foramen : Although defined by Estes *et al.* (1988) as a systematic character, Degen (1910) and Gundy and Wurst (1975) indicate that the absence of a parietal foramen is frequently observed in tropical and subtropical squamates.

Within the ingroup a parietal foramen is present within the parietal bone in all taxa examined with the exception of *Cordylosaurus* and *Zonosaurus*. *Cordylosaurus* occurs throughout western Namibia and southwestern Cape Province certainly no tropical or subtropical region. *Zonosaurus* occurs throughout Madagascar, with those taxa living in the northern part of the island lacking an interparietal (e.g. *aeneus*, *madagascariensis*, some *rufipes*). Even if this character complex were to be regarded as a systematic character, it would suggest a convergence between *Cordylosaurus* and *Zonosaurus* within the ingroup and gekkonids, pygopodids, dibamids, gymnophthalmids, *Heloderma*, *Lanthanotus*, most amphisbaenians and snakes among other squamates (Estes *et al.*, 1988).

Scleral ossicles : The eye contains a sclerotic ring that is made up of overlapping thin bony platelets (scleral ossicles). The sclerotic ring is round, follows the contour of the eyeball and is imbedded within the sclera on the corneal side. Underwood (1970; 1984) defined scleral ossicles as either positive, negative or imbricating. Positive scleral ossicles are defined as overlapping both immediately adjacent ossicles. Negative ones are overlapped by both adjacent ossicles, whereas imbricating ossicles are those that are overlapped on one side and overlap on the other.

Not all ingroup taxa and enough outgroup taxa were investigated to permit a conclusive polarity decision for this character complex. Preliminary results of overlapping patterns for those ingroup taxa that were investigated is given in Table 2.

Meckel's groove. Estes *et al.* (1988) define three conditions of the Meckel's groove : open groove (0), Meckle's cartilage within a sutured tube (1), dentary tube closed and fused (2). Although the plesiomorphic and intermediate character states were reported to be present within the ingroup, only the plesiomorphic condition could be confirmed as being present in this study.

Number of presacral vertebrae : The number of presacral vertebrae in squamates have been extensively discussed by Hoffstetter and Gasc (1969) and has been used by Estes *et al.* (1988) as a systematic character. Because of inherent problems of variability in the in- and outgroups and the increase in number of presacral vertebrae in limbless forms; no compartimentalization of this character complex without significant overlap was possible. However the modal number of presacral vertebrae of cordylids (26) and gerrhosaurids (28) corresponds with those reported by Hoffstetter and Gasc (1969) in limbed forms. The obtainable information on Cordylidae and Gerrhosauridae is summarized in Table 3.

Symphysial process of pubis : Three different character states can be observed in the in- and outgroups with respect to the relative length of the symphysial process as defined by Estes *et al.* (1988). A) extremely elongated and anteriorly directed; B) relatively long, ven-

Table 2 :
Scleral ossicle patterns shown by ingroup taxa investigated. Symbols are explained in the text : + = positive, i = imbricating, – = negative. The # 1 ossicle is anteroventral.

CORDYLIDAE													
Cordylus cataphractus :	1+	2i	3i	4–	5+	6–	7+	8i	9–	10i	11i	12i	13i
Cordylus tropidosternum :	1+	2i	3i	4–	5i	6+	7i	8i	9–	10i	11i	12i	13i
Platysaurus intermedius :	1+	2i	3i	4–	5i	6+	7i	8i	9–	10i	11i	12i	
GERRHOSAURIDAE													
Gerrhosaurus flavigularis :	1+	2i	3i	4–	5i	6+	7i	8i	9–	10i	11i	12i	
Tracheloptychus :	1+	2i	3i	4–	5i	6+	7i	8i	9–	10i	11i	12i	
Zonosaurus haraldmeieri :	1+	2i	3i	4–	5i	6+	7–	8+	9–	10i	11i	12i	13i
Z. madagascariensis :	1+	2i	3i	4–	5i	6+	7i	8i	9–	10i	11i	12i	13i

trally directed and C) not elongated, directed ventrally. Outgroup comparison indicates that all Autarchoglossa with the exception of *Varanus* and Teiidae have extremely elongated anteriorly directed symphysial processes. The character state distribution among outgroup taxa demonstrate a CASE I for which the polarity decision is unequivocal at the outgroup node. The polarities would however be reversed from those of ESTES *et al.* (1988).

Table 3 :
*PRESACRAL FORMULAE. Numbers are as follows : 1°) # cervical vertebae without ribs, 2°) # vertebrae with ribs, but without sternal attachment, 3°) total # presacral vertebrae with sternal attachment, 4°) # true sternal ribs, 5°) # xiphisternal ribs, 6°) # presacral vertebrae posterior to last sternal attachment, 7°) total # presacral vertebrae. Refrences : * = CAMP (1923); ** = BERGER-DELL'MOUR (1983).*

CORDYLIDAE			
Chamaesaura anguina	*4(2+2)*	37	
Chamaesaura macrolepis	3+3+*4(2+2)*+27 =	37	
Cordylus cataphractus	2+6+*5(3+2)*+10 =	23	
Cordylus cordylus	3+5+*5(3+2)*+12 =	25	
Cordylus giganteus		24	
Cordylus peersi	3+5+*5(3+2)*+13 =	26	
Cordylus polyzonus	3+5+*5(3+2)*+13 =	26	
Cordylus tropidosternum	3+5+*5(3+2)*+13 =	26	
Cordylus vittifer	3+5+*5(3+2)*+11 =	24	
	3+5+*5(3+2)*+12 =	25	
Cordylus warreni	3+5+*5(3+2)*+13 =	26	
Platysaurus capensis	3+5+*5(3+2)*+13 =	26	
Platysaurus guttatus	3+5+*5(3+2)*+13 =	26	
Pseudocordylus microlepidotus	3+5+*5(3+2)*+13 =	26	
GERRHOSAURIDAE			
Angolosaurus skoogi	3+5+*5(3+2)*+15 =	28	
Cordylosaurus subtessellatus	3+5+*5(3+2)*+15 =	28	
Gerrhosaurus flavigularis	3+5+*5(3+2)*+15 =	28	
Gerrhosaurus major	*6(3+3)*	29	*
Gerrhosaurus nigrolineatus	3+5+*5(3+2)*+15 =	28	
Gerrhosaurus validus	3+5+*5(3+2)*+14 =	27	
Tetradactylus africanus	3+3+*3(3+0)*+25 =	34	**
	3+3+*3(3+0)*+26 =	35	**
	3+3+*3(3+0)*+27 =	36	**
	3+3+*3(2+1)*+28 =	37	**
	3+3+2*(2+0)*+30 =	38	**
	3+3+*3(3+0)*+29 =	38	**
Tetradactylus seps	3+5+*5(3+2)*+16 =	29	**
	3+5+*5(3+2)*+17 =	30	**
	3+5+*4(3+1)*+18 =	30	**
Tetradactylus tetradactylus	3+4+*5(3+2)*+19 =	31	**
	3+4+*4(3+1)*+20 =	31	**
	3+4+*4(3+1)*+21 =	32	**
	3+4+*4(2+2)*+21 =	32	**
	3+4+*5(3+2)*+21 =	33	**
	3+4+*4(3+1)*+22 =	33	**
	3+4+*4(2+2)*+22 =	33	**
Tracheloptychus madagascariensis	3+5+*5(3+2)*+14 =	27	
Tracheloptychus petersi	3+5+*5(3+2)*+14 =	27	
Zonosaurus madagascariensis	*5(3+2)*	28	
Zonosaurus maximus	2+5+*6(3+3)*+15 =	28	

In *Tetradactylus* all three character states are expressed. The limbless forms have a tendency to decrease the length of the symphysial process and to have the entire pelvic girdle oriented ventrally (ESSEX, 1927; BERGER-DELL'MOUR, 1983). This character complex is therefore regarded as an ecomorphological adaptation. Further support for this notion is evidenced by the condition observed in the limbless *Chamaesaura* which show similar conditions of the pelvic girdle as in the limbless *Tetradactylus*.

Additional pelvic characteristics of reduced limbed or legless forms is that the two pubic bones are rounded anteriorly with no pubic tubercles and are widely separated anteriorly by the epipubic cartilage (ESSEX, 1927; BERGER-DELL'MOUR, 1983). The epipubic cartilage itself does not extend too far anteriorly. The ischium is not well-developed and an ischial spine is completely lacking. The pelvic basin is slit shaped rather than heart shaped as in other tetrapodous squamates. The hypoischium extends as far back as the ilium. This latter case is observed in *Platysaurus capensis* but is not considered analogous because the ischium is shortened posteriorly rather than the elongation of the hypoischium.

Karyotypes : A complete set of karyotypes for ingroup and outgroup taxa was not available in order to define a systematic character complex. A list of the avilable data for the ingroup taxa is listed in Table 4.

Discussion of phylogenetic results

The data matrix of the 74 defined character transformation series was analyzed initially by the PAUP program (SWOFFORD, 1985, version 2.4.1) as described in the material and methods section.

Three equally parsimonious trees resulted with lengths of 140 steps and a consistency index of 0.579. These three trees differed only in the placement of the gerrhosaurid genera *Cordylosaurus*, *Tetradactylus* and *Gerrhosaurus*. Two of these trees placed *Tetradactylus* as the sister taxon of *Cordylosaurus*. The portion of the three most parsimonious cladograms outside of the three genera mentioned above were consistent which is reflected in both the ADAMS (1972) and Strict consensus trees with a MICKEVICH's consensus information factor of 0.750 (Fig. 17).

SANDERSON (1990) suggests that complex data sets with a high degree of homoplasy should be run on both the PAUP and the HENNIG86 algorithms. The data set was rerun with the HENNIG86 program (version 1.5) as defined by FARRIS (1988), using the implicit enumeration option. Two most parsimonious cladograms were found equalling the number of steps of the initial Paup cladograms. One of the Hennig86 trees is identical to one of the Paup trees. The second tree is regarded as the preferred phylogenetic hypothesis, in which *Angolosaurus* is placed with the other african gerrhosaurids to form an african radiation.

Angolosaurus, when placed as the earliest diverging gerrhosaurid taxon (in two of the four most parsimonious hypothesis) is defined entirely by homoplaseous characters (multiple convergences of S16, S21, S22; reversal of S7 and reversal of unpolarized S14, S24, C9 & C10). By contrast, placing *Angolosaurus* as the earliest diverging African gerrhosaurid is supported by 2 synapomorphies (C2, C19), that show convergence with but a single other clade each. Herein lies the major differences of the distribution of character states among the alternative hypotheses.

Within the african gerrhosaurid radiation *Cordylosaurus* is hypothesized to be the sister taxon of *Tetradactylus* because it appears so on two of the three most parsimonious trees. There is also good corroborating character evidence (S5 & A1) supporting this contention. *Gerrhosaurus* is hypothesized to be the sistertaxon to the *Cordylosaurus-Tetradactylus* clade. There is substantial evidence (see below) suggesting a malagasy gerrhosaurid clade consisting of *Tracheloptychus* and *Zonosaurus*.

Within the purely african Cordylidae, the serpentine *Chamaesaura* is regarded as the earliest diverging taxon and is the sistertaxon to the *Cordylus* + (*Pseudocordylus* + *Platysaurus*) primarily rock-crevice dwelling clade. Within the latter evolutionary unit, *Cordylus* is the earliest diverging taxon.

Definitions and diagnoses of taxa

In this section content, diagnoses and definitions are given for all branching nodes in the preferred hypothesis in addition to autapomorphies for terminal taxa when applicable. The list of diagnostic characters is taken directly from the Paup character analysis that is summarized in Appendix C. As a convention, convergences with other taxa are indicated by "C", reversals or retention of plesiomorphic conditions are indicated with a "R". The remaining characters are autapomorphic, meaning that they neither reverse at a less-inclusive level nor are convergent with other ingroup taxa.

In the comments section are additional autapomorphies not used in the analysis as well as some additional notes. A geographical range is given for each terminal taxon. A complete synonymy listing as well as ecological, physiological, reproductive and captive maintenance information forms part of a future publication.

Table 4 :
*Karyological data of various ingroup taxa. Abbreviations are : 2n = diploid chromosome #, V = # of bi-armed macrochromosomes; I = # of uni-armed macrochromosomes, m = # of microchromosomes, FN = fundamental #. References are : * = Olmo & Odierna (1980), = De Smet (1981).*

TAXON	2n	V	I	m	FN	Ref
CORDYLIDAE						
Cordylus cataphractus :	44	2	20	22	46	*
	45	1	22	22	46	*
Cordylus cordylus :	34	12	0	22	46	*
Cordylus giganteus :	44	2	0	22	46	*
Cordylus polyzonus :	34	12	0	22	46	*
Cordylus tropidosternum :	34	24	0	10	58	§
Cordylus vittifer :	34	12	0	22	46	*
	34	24	0	10	58	§
Cordylus warreni :	34	12	0	22	46	*
Platysaurus guttatus :	34	12	0	22	46	§
Platysaurus minor :	34	12	0	22	46	§
Pseudocordylus microlepidotus :	34	12	0	22	46	*
	32	28	0	4	60	§
GERRHOSAURIDAE						
Gerrhosaurus flavigularis :	34	12	0	22	46	§
Gerrhosaurus major :	34	12	0	22	46	*
	34	14	0	20	48	§
Gerrhosaurus validus :	34	12	0	22	46	*
Tetradactylus seps :	34	12	0	22	46	*

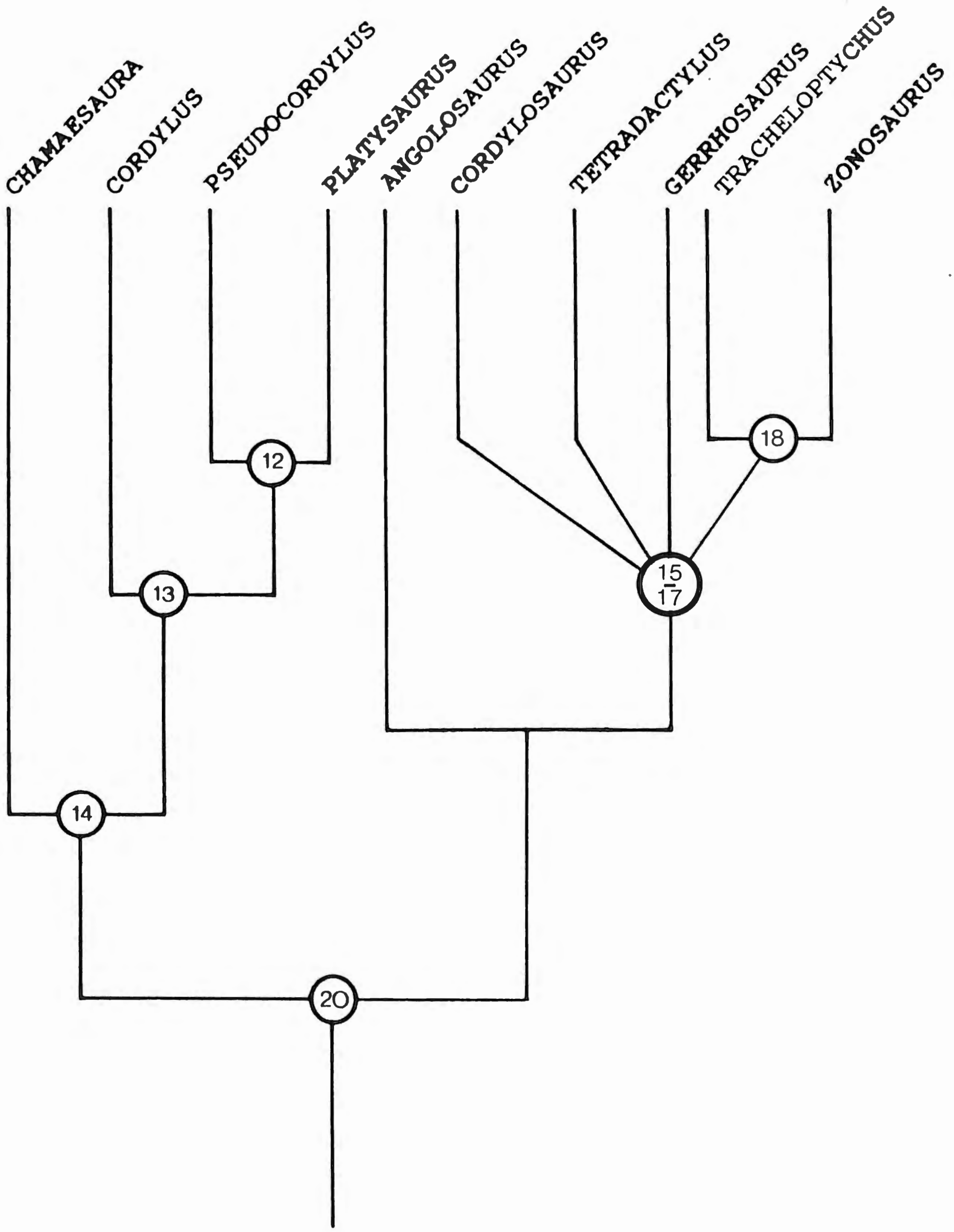


Figure 17 : *Adams and Strict consensus tree derived from the three most parsimonious trees of the* Paup *and* Hennig *86 analyses (See text for discussion).*

Some formal taxonomic changes are foreseen in this study (Fig.18). No objective methodology is available to define higher taxonomic categories, but three guidelines are followed here. First an attempt has been made to roughly equal taxonomic levels of other squamate clades. Secondly, maintenance of taxonomic stability has been sought after. Thirdly, the international code of zoological nomenclature is respected (see also Savage, 1990). Because there is good evidence of the monophyly of Cordylidae (sensu stricto) and Gerrhosauridae (sensu lato) these two clades are regarded as families. The evidence of monophyly is less convincing at the next

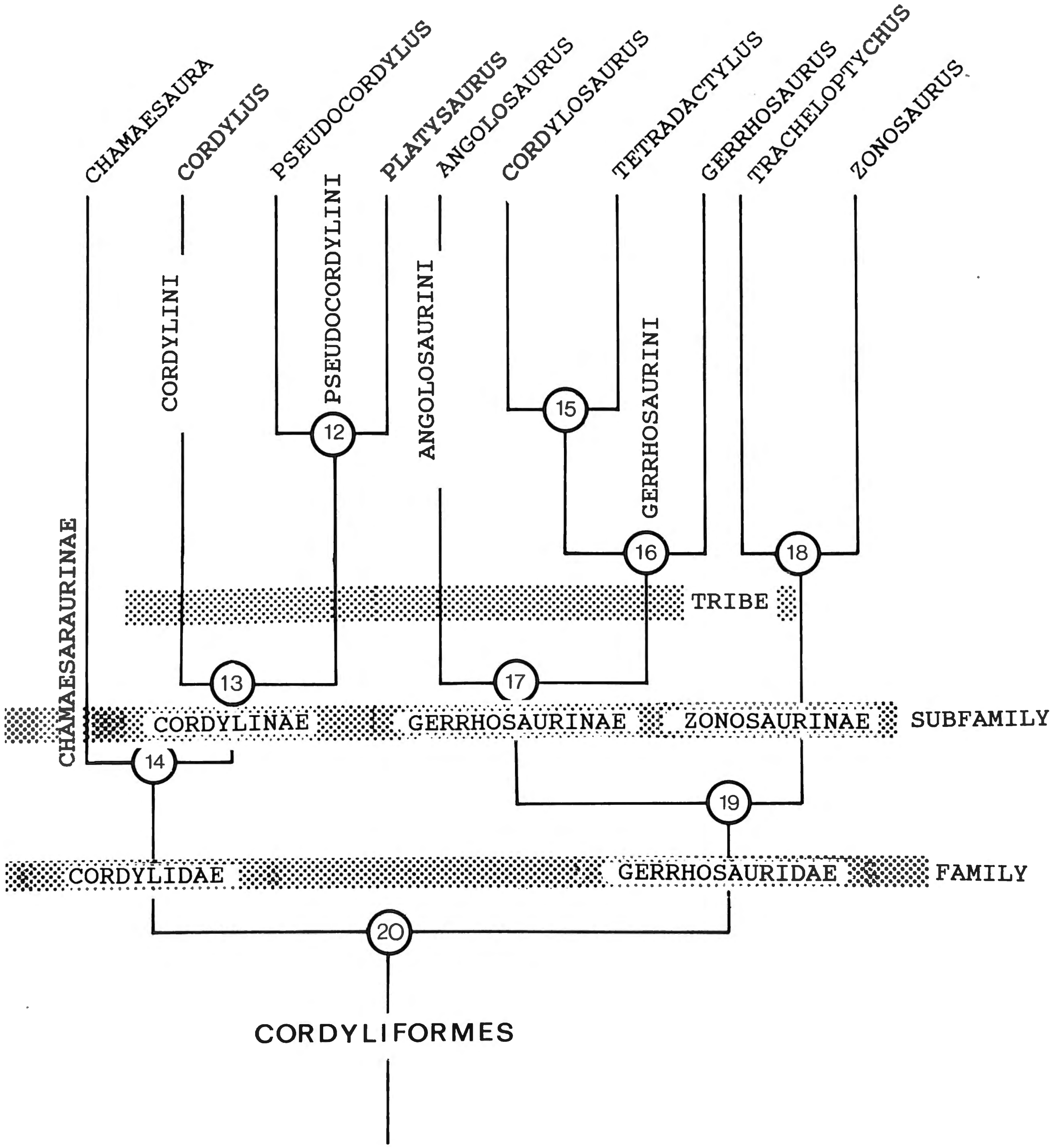


Figure 18 : *Preferred phylogenetic analysis of the Cordyliformes with taxonomic recommendations. The nodes are described in the definition and diagnosis of taxa section and summarized in Appendix C.*

higher level (see discussion of monophyly). In order to be consistent with the taxonomy within Squamata proposed by ESTES *et al.* (1988); Cordyliformes FITZINGER is defined to include both Cordylidae + Gerrhosauridae and together with Scincidae forms Scincoidea OPPEL as defined by ESTES *et al.* (1988).

Cordyliformes Fitzinger, 1826

1826 Cordyloidea Fitzinger, Neue Classific. : 11

Type genus :
Cordylus Linnaeus, 1758.

Content :
Two families CORDYLIDAE GRAY, 1837 & GERRHOSAURIDAE Fitzinger, 1843.

Diagnosis :
S7) Subocular scale forms part of the upper labial margin [R in *Angolosaurus* and in some *Cordylus*/ C with some skinks and some lacertids]. S13) Interparietal and occipital scales are separated [R is *Chamaesaura*, *Angolosaurus* and in some *Platysaurus*/ C with Xantusiidae]. S20*) Ventral scales arranged in straight rows [R in Zonosaurinae/ C with Xantusiidae, Lacertidae, Varanidae and Helodermatidae]. A4) Insertional tendon of pseudotemporalis superficialis reduced. C9*) Parietal downgrowths extend to epipterygoids [R in *Tracheloptychus* and *Angolosaurus*/ C with some Scincidae, Xantusiidae, Teiidae and Gymnophthalmidae]. C10) Parietal tabs present [R in *Platysaurus*, *Angolosaurus* and *Cordylosaurus*/ C in some Scincidae and Lacertiformes]. C22) Coronoid lateral process absent or covered by postero-dorsal aspect of dentary [R in *Chamaesaura*/ C with Xantusiidae]. C27) Dorsal surface of retroarticular process of coronoid deeply pitted [R in Cordylinae/ C with Teiidae and Xantusiidae]. C28*) Broad retroarticular process [R in *Cordylus*/ C with Scincidae and Anguidae].

Comments :
Additional derived characters (discussed in the section on monophyly) are : 1) 34 chromosomes (Gorman, 1970; 1973). 2) Hemipenial characters : thin strongly folded apex; irregularly arranged plicae; strongly sigmoid sulcus spermaticus proximally with a hypertrophied medial sulcal lip (Böhme, 1988) (Figs. 15 & 16). 3) large postfrontal bone extending to the supratemporal fenestra (Estes *et al.*, 1988). 4) cloacal spurs (Mcdowell & Bogert, 1954) (Fig. 13). 5) Derived morphology of caudal vertebrae (Etheridge, 1967 : 708).
Chamaesauri Wiegmann, 1834 predates Cordylidae Gray, 1837. From the original publication of Wiegmann it is not clear which taxa are included in this suprageneric taxon. Also Cordylidae is a well-established name and in order to maintain taxonomic stability Cordylidae Gray, 1837 is preferred over Chamaesauridae Wiegmann, 1834. Rather the latter is relegated to a subfamilial level as suggested by Camp (1923).
Bissinger and Simon (1979) investigated the correlation between rate of tongue extrusion and bifurcation in six families of squamates. An increase in the frequency of tongue extrusion seemed to be correlated with an increase in the bifurcation of the tongue. With respect to the ingroup; gerrhosaurids tongue touched significantly more often the substrate than cordylids. Gerrhosauridae is therefore more dependant on chemoreception whereas Cordylidae are primarily visually oriented. This is also reflected in the degree of tongue bifurcation (Fig. 5) with the notable exception of *Tetradactylus* (Fig. 4D).

Distribution :
Africa south of 5°N latitude but absent form the Zaire basin; Madagascar, Iles Glorieuses and Cosmoledo. Relictual populations are to be found in Eritrea, the Central African Republic, northern Cameroon and Nigeria, northern Benin, Togo and Ghana.

Cordylidae Gray, 1837

1837 Cordylidae Gray, Ann. natur. Hist., 1 : 388.

Type genus :
Cordylus Linnaeus, 1758.

Content :
Two subfamilies CHAMAESAURINAE Gray, 1834 & CORDYLINAE Camp, 1923.

Diagnosis :
S10) 4 parietal scales [C with Xantusiidae, Teiidae and Gymnophthalmidae]. C2) Lacrimal bone restricted to lacrimal canal with no lateral exposure [C with *Angolosaurus*/ C with Gymnophthalmidae]. C4) Anteroventral border of orbit formed by the maxilla, with the anterior process of the jugal restricted to the maxilla [C with some Scincidae, Xantusiidae and Lacertidae]. C6) Frontal bone fused embryonically [R in *Platysaurus*/ C with Teiioidea]. C12) Flat parietal table [C with Xantusiidae and Xenosauridae]. C16) Long basipterygoid process with small condylar surfaces. C19) Deep subdental shelf of maxilla [C with Clade : *Cordylosaurus*-*Tetradactylus* and *Tracheloptychus*]. C20*) Second ceratobranchial of hyoid present [C with a variety of outgroup taxa (see Estes *et al.*, 1988)]. C21) Splenial extends posteriorly beyond apex of coronoid. C23) Short coronoid process [C with some Scincidae, Xantusiidae and Teiidae]. C24) Angular bone restricted entirely to labial aspect of lower jaw [R in some *Pseudocordylus*]. C25) Ventral process of angular extends past the apex of the coronoid but does not reach the level of the last marginal tooth. C26) Adductor fossa expanded [C with *Cordylosaurus*/ C with Lacertiformes]. P1) Cervical intercentra sutured to anterior part of following centrum [R in Pseudocordylini/ C with Teiioidea]. P2*) Strongly developed zygosphene-zyganthrum articulation [C with Scincidae, Lacertidae, Teiidae and Gymnophthalmidae]. P4) Clavicles are simple curved rods. P5) Interclavicle T-shaped [C with *Varanus*]. L1) Viviparous [R in *Platysaurus*/ C with

Xantusiidae, *Xenosaurus* and Aniellidae]. M3) Dorsal aspect of head and tail covered with osteoderms [R in *Cordylus*]. M8) Callous gland present on thighs anterior to femoral pores.

Comments :

The subfamilial classification proposed here is identical to that proposed by Camp (1923) with Zonurinae being replaced by Cordylinae.

Very few comments are found in the literature concerning phylogenetic relationships within Cordylidae. One of the few is a statement by Essex (1927), suggesting (in parentheses are added comments) : "*Chamaesaura* can be undoubtedly looked upon as the most "primitive" of the Zonuridae (= Cordylidae), which at an early stage saved itself from extinction by becoming serpentiform, but keeping its primitive scaling (single row of scales per segment)."

Chamaesaurinae Wiegmann, 1834

1834 Chamaesauri Wiegmann, Herp. Mex. 11 : 29.

Type genus :

Chamaesaura Schneider, 1801.

Content :

Chamaesaura Schneider, 1801.

Comments :

Chamaesaurinae as defined here is identical to that proposed by Camp (1923 : 295).

Chamaesaura Schneider, 1801

1801 *Chamaesaura* Schneider, Hist. Amphib., 2 : 205, 210. - Type species (designated by Fitzinger 1826) : *Lacerta anguina* Linnaeus.

Content :

Chamaesaura aenea Wiegmann, 1834; *Chamaesaura anguina* (Linnaeus, 1758); *Chamaesaura maculatus* (Cope, 1862).

Diagnosis :

(For cranial characters see Fig. 19). S1) Nasal scales in contact [C with Gerrhosaurini, *Pseudocordylus*, some *Cordylus* and some *Platysaurus*/ C with Xantusiidae, some Lacertidae and Teiidae]. S3) Aberrant postnasal scales [C with some *Cordylus*/ C with Teiioidea]. S4) Nasal and prefrontal scales in contact [C with some *Cordylus* and some *Pseudocordylus*]. S8) 3 supralabial scales anterior to the subocular scale that forms part of the upper labial margin [C with Gerrhosaurini and *Tracheloptychus*]. S13) Interparietal and occipital scales separated [R from Cordyliformes]. S19) Dorsal body scales keeled [C with Gerrhosaurini, *Tracheloptychus*, some *Cordylus* and some *Zonosaurus*/ C with outgroup taxa listed in character description section]. C17) Spheno-occipital tubercle consisting exclusively of basioccipital [C with *Tetradactylus* and some *Pseudocordylus*/ C with Teiidae and *Ophisaurus*]. C22) Coronoid lateral process with a lappet on the dentary [R from Cordyliformes]. C29) Retroarticular process not twisted posteriorly [C with *Tetradactylus* and *Tracheloptychus*/ C with Xantusiidae, Lacertidae and Gymnophthalmidae]. P3) Clavicles are simple rods [C with *Platysaurus*]. M1) External limbs reduced [C with some *Tetradactylus*/ C with outgroup taxa listed in character description section]. M3-2) Osteoderms restricted to dorsal aspect

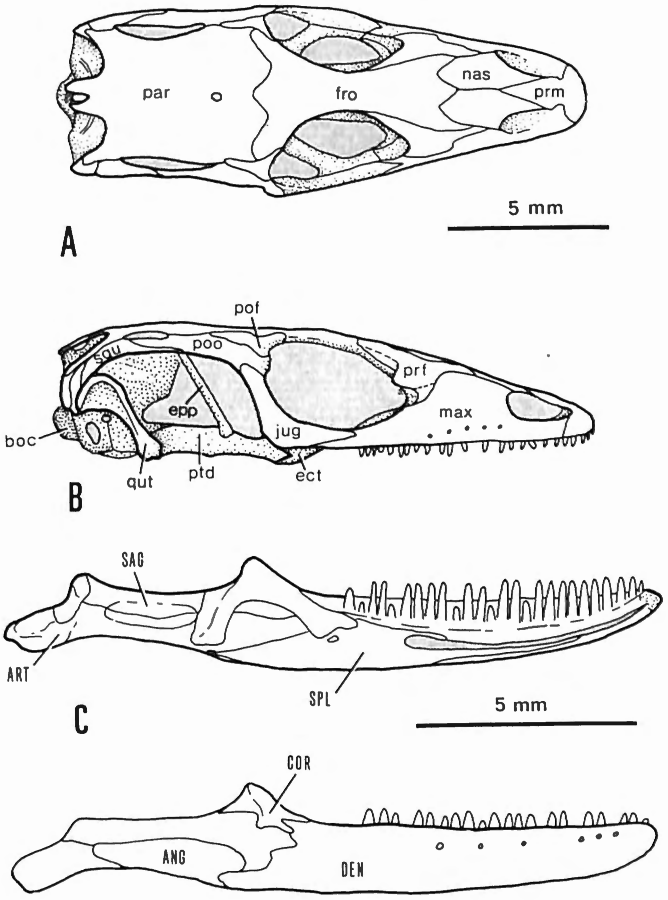


Figure 19 : *Dorsal & lateral views of skull and lingual & labial views of lower jaws of* Chamaesaura. *A)* Chamaesaura macrolepis. *B)* Chamaesaura anguina. *C)* Chamaesaura anguina. *Abbreviations of bones are : ang = angular; art = articular; bsp = basisphenoid; cor = coronoid; den = dentary; ect = ectopterygoid; epp = epipterygoid; fro = frontal; jug = jugal; lac = lacrimal; max = maxilla; nas = nasal; par = parietal; pof = postfronal; poo = postorbital; prf = prefrontal; prm = premaxilla; pro = prootic; ptd = pterygoid; qut = quadrate; sag = supra-angular; spl = splenial; squ = squamosal.*

of head [C with *Platysaurus*/ C with Xantusiidae and Lacertidae]. In some *Chamaesaura*: S6*) Prefrontal scales separated [C with *Tracheloptychus*, some *Cordylus*, some *Platysaurus*, some *Gerrhosaurus* and some *Zonosaurus*/ C with Scincidae and some Anguimorphans].

Comments:
Chamaesaura is without doubt monophyletic, supported by the following additional autapomorphies: 1) Evolutionary trends towards fore- and hindlimb reduction. (Convergent with some *Tetradactylus* within Cordyliformes.) This includes the reduction of pectoral and pelvic girdles. In *Chamaesaura macrolepis* a ligamentous posterior coracoid fenestra is present due to the reduction of the medial flange of the coracoid (ESSEX, 1927). The hypoischium is elongated and extends as far posterior as the ilium (ESSEX, 1927). The hypoischium in *Platysaurus capensis* also extends as far back as the ilium, but this is due to a reduction of the ilium. 2) Strongly keeled ventral scales. All autarchoglossans with a few noted exceptions such as the lacertid *Takydromus*, the scincids *Tribolonotus* and *Tropidophorus*, and in the teiid *Echinosaura* (some specimens) have smooth ventral scales. 3) Only 6 cervical vertebrae present (= vertebrae preceding the first vertebrae bearing a rib connecting to the sternum) (Table 2). As discussed by ESTES *et al.* (1988) 8 is the plesiomorphic number of cervical vertebrae with a bi-directional transformation towards reduction and increase. 4) Three rib attachment points on each side of the sternum (Table 2). Defined by ESTES *et al.* (1988) 5 attachment points is the plesiomorphic squamate condition, with evolutionary trends towards reduction of attachment points. Most cordyliformes have 4 attachment points. 5) Presence of inscriptional ribs in all three species (CAMP, 1923). This is convergent with limbless *Tetradactylus* within Cordyliformes, some Scincidae, some Gymnophthalmidae and some Lacertidae within Autarchoglossa. 6) Wide variation of foot structure with a predominance of a tibiale-fibulare foot structure rather than a tarsale proximale and occasional presence of 4 tarsalia in *Chamaesaura aenea* (ESSEX, 1927). An increased number of pedal phalangeal elements is also frequent in this taxon. In *Chamaesaura anguina* and more pronounced in *macrolepis* there is a reduction in the number of compositional elements of the foot (DUERDEN & ESSEX, 1922; ESSEX, 1927). A preliminary phylogenetic analysis indicates that *macrolepis* is more closely related to *anguina* than either is to *aenea*.

Distribution:
(Fig. 20). Coastal zone Republic of South Africa, Zimbabwe and E. Mozambique, NE Zambia. Malaŵi, Tanzania, S. Kenya, S. Uganda, Rwanda, Burundi, E. & S. Zaire and Angola.

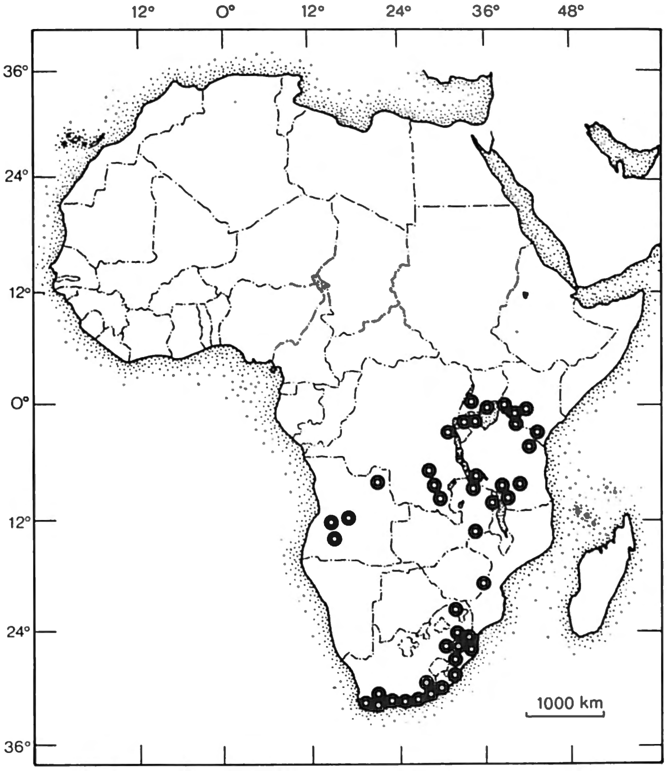


Figure 20: *Geographical distribution of* Chamaesaura *based on known collection localities. (Localities derived from* BRANCH, *1988;* DE WITTE, *1953;* HELLMICH, *1957b;* LAURENT, *1956a,b;* LOVERIDGE, *1929, 1944;* STEWART *&* WILSON, *1966).*

Cordylinae CAMP, 1923

1923 Zonurinae CAMP, Bull. Am. Mus. Nat. Hist., 48: 295. Name emendated to Cordylinae see STEJNEGER (1936).

Type genus:
Cordylus LAURENTI, 1768.

Content:
CORDYLINI new tribe & PSEUDOCORDYLINI new tribe.

Diagnosis:
C14) Vomers with a ventromedial heart-shaped depression. C18) Posterior aspect of parietal table not emarginated; supratemporal short and posterior braincase for the most part covered [C with Xantusiidae and some Lacertidae]. C25-2) Ventral process of angular does not extend anteriorly past the level of the apex of the coronoid. C27) Dorsal surface of retroarticular process without sulcus or pit [R from Cordyliformes]. P6) Carpal intermedium absent [C with Gerrhosaurinae and R in *Platysaurus*/ C with some Scincidae, some Lacertidae and *Varanus*]. M5) Flattened cross-sectional body form [C with Xantusiidae and some Lacertidae].

Cordylini New Tribe

Type genus :
Cordylus Laurenti 1768.

Content :
Cordylus Laurenti 1768.

Cordylus Laurenti, 1768

1768 *Cordylus* part., Laurenti, Synops. Rept. : 51. - Type species (by tautonomy) : *Lacerta cordylus* Linnaeus.

Content :
Cordylus Campbelli (Fitzsimons, 1938); *Cordylus cataphractus* Boie, 1828; *Cordylus coeruleopunctatus* (Hewitt & Methuen, 1913); *Cordylus cordylus* (Linnaeus, 1758); *Cordylus giganteus* Smith, 1844; *Cordylus lawrenci* (Fitzsimons, 1939); *Cordylus macropholis* (Boulenger, 1910); *Cordylus mclachlani* Mouton, 1986; *Cordylus minor* Fitzsimons, 1943; *Cordylus namaquensis* (Methuen & Hewitt, 1914); *Cordylus niger* Cuvier, 1829;*Cordylus oelofseni* Mouton & Van Wyk, 1990; *Cordylus peersi* (Hewitt, 1930); *Cordylus polyzonus* Smith, 1838; *Cordylus pustulatus* (Peters, 1862); *Cordylus rhodesianus* (Hewitt, 1933); *Cordylus rivae* (Boulenger, 1896); *Cordylus tasmani* (Power, 1930); *Cordylus tropidosternum* Cope, 1869; *Cordylus ukingensis* (Loveridge, 1932); *Cordylus vittifer* (Reichenow, 1887); *Cordylus warreni* (Boulenger, 1908).

Diagnosis :
(For cranial characters see Fig. 21). S21) Scales on sole of feet are flattened, oblique and keeled [C with *Tracheloptychus*, *Cordylosaurus*, *Angolosaurus*, some *Platysaurus*, some *Pseudocordylus*, some *Gerrhosaurus* and some *Zonosaurus*]. S24*) Keeled subdigital scales [C with *Tracheloptychus*, *Cordylosaurus*, *Angolosaurus* and some *Pseudocordylus*/ C with some Scincidae and some Xantusiidae]. C28*) Retroarticular process tapered posteriorly [R from Cordyliformes]. P1-2) Cervical intercentra fused to anterior part of following centrum [C with Teiioidea]. M3) Entire body covered with osteoderms [R from Cordylidae]. The following apomorphic conditions occur in some *Cordylus* : S1, S3, S6, S7[R], S11, S12, S14*, S15, S19, S22, S23, A2*[3*], M2, M4 and M7.

Comments :
In *Cordylus cataphractus* the fifth metacarpal is the same size as the fourth metacarpal and twice that of the first metacarpal (Fig. 22). In all other fully-limbed cordyliformes the first and fifth metacarpals are the same size and 1/2 the size of the fourth metacarpal.

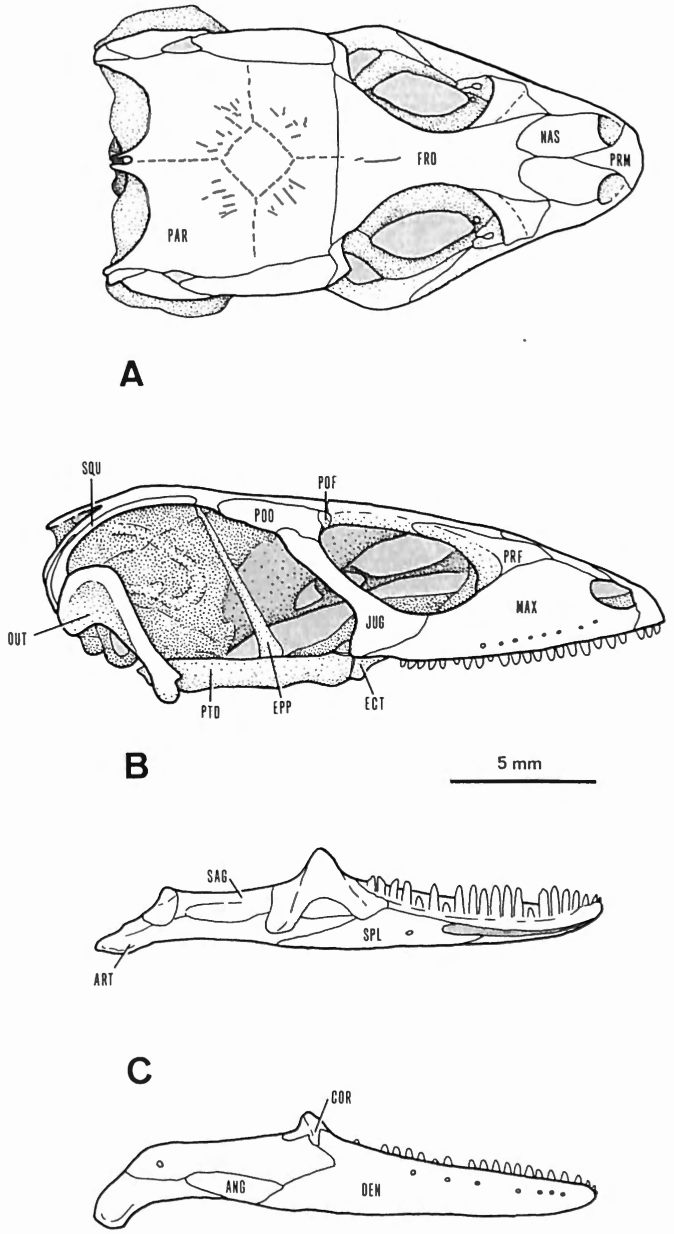


Figure 21 : *Dorsal & lateral views of skull and lingual & labial views of lower jaws of* Cordylus. *A)* Cordylus cordylus. *B)* Cordylus tropidosternum. *C)* Cordylus cordylus. *Abbreviations of bones are : ang = angular; art = articular; boc = basioccipital; cor = coronoid; den = dentary; ect = ectopterygoid; epp = epipterygoid; fro = frontal; jug = jugal; max = maxilla; nas = nasal; par = parietal; pof = postfronal; poo = postorbital; prf = prefrontal; prm = premaxilla; ptd = pterygoid; qut = quadrate; sag = supra-angular; spl = splenial; squ = squamosal.*

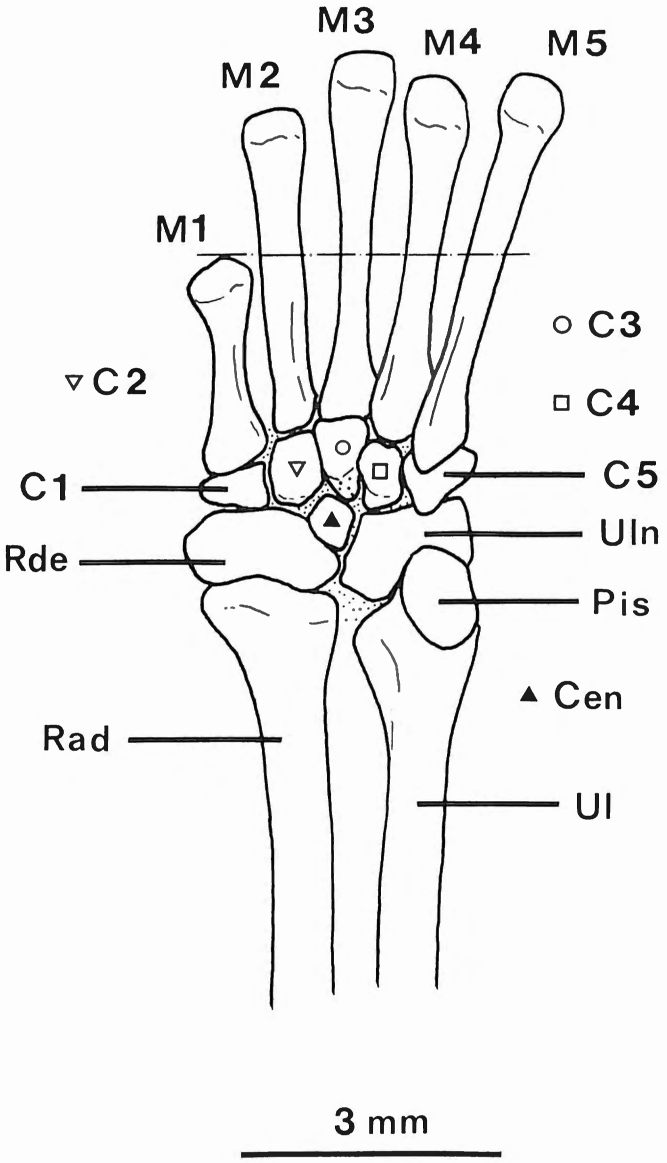


Figure 22 : *Palmar view of left manus of* Cordylus cataphractus. *Abbreviations : C1-C5 = Carpals 1-5 ; Cen = centrale ; M1-M5 = metacarpals 1-5 ; Pis = pisiforme ; Rad = radius ; Rde = radiale ; Ul = ulna ; Uln = ulnare.*

Distribution :
(Fig. 23). SE Kenya, E & S Tanzania, N. Zambia, SE Zaire, Central Mozambique, E & S Zimbabwe, E Botswana, Rep. S. Africa, Central Namibia. Relictual populations in S Ethiopia and SW Angola.

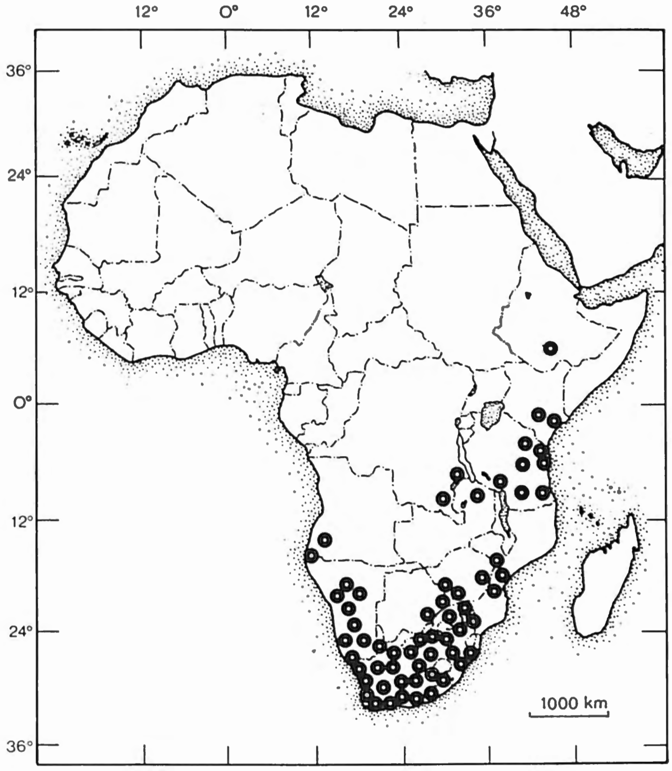


Figure 23 : *Geographical distribution of* Cordylus *based on known collection localities. (Localities derived from : Branch, 1988 ; Broadley, 1971 ; De Witte, 1942, 1953 ; Loveridge, 1944 ; Nieden, 1913).*

Pseudocordylini New Tribe

Type genus :
Pseudocordylus Smith, 1838.

Content :
Pseudocordylus Smith, 1838 & *Platysaurus* Smith, 1844.

Diagnosis : S12) Interparietal and frontoparietal scales separated [C with some *Cordylus*]. S18) Collar present but incomplete [C with Varanidae]. C3) Palatine and jugal bones in contact or overlapping at infraorbital foramen [C with Gerrhosauridae]. P1) Cervical intercentra attach intervertebrally [R from Cordylidae].

Comments :
An autapomorphy for this clade is the strong sexual dimorphism in body coloration. This condition was not observed in either *Chamaesaura* or *Cordylus*.
Broadley (1978 ;179) postulates that *Pseudocordylus* and *Platysaurus* appear to be independently derived from *Cordylus*. Within a cladistic framework, Broadley's comments would suggest that Pseudocordylini is a polyphyletic taxon.

Pseudocordylus Smith, 1838

1838 *Pseudocordylus* A. Smith, Mag. nat. Hist., London, (2) 2 : 32. - Type species : (Loveridge 1944) : *Pseudocordylus montanus* A. Smith = *Pseudocordylus microlepidotus* (Cuvier).

Content :
Pseudocordylus capensis Smith, 1838; *Pseudocordylus langi* Loveridge, 1944; *Pseudocordylus melanotus* Smith, 1838; *Pseudocordylus microlepidotus* (Cuvier, 1829); *Pseudocordylus spinosus* Fitzsimons, 1943.

Diagnosis :
(For cranial characters see Fig. 24). S1) Nasal scales in contact [C with Gerrhosaurini, *Chamaesaura*, some *Cordylus* and some *Platysaurus*/ C with Xantusiidae, some Lacertidae and Teiidae]. S11) Anterior parietal scales in contact [C with Gerrhosauridae, *Angolosaurus*, some *Cordylus* and *Platysaurus*]. C24) Lingual exposure of angular present [R from Cordylidae]. Apomorphies of the following character transformation series occur in some *Pseudocordylus* : S4) contact of nasal and prefrontal scales. S14*) presence of a median occipital scale. S21) scales on sole of feet flattened, oblique and keeled. S22) scales below forelimbs keeled. S23) scales below hindlimbs keeled. C17) spheno-occipital tubercle consisting only of the basioccipital. C24) lingual exposure of angular absent, and M2) tail with spinose whorles.

Comments :
In most *Pseudocordylus* the postnasal scale forms part of the upper labial margin. In all Autarchoglossa examined, the postnasal scale does not form part of the upper labial margin. *Pseudocordylus capensis* however retains the plesiomorphic condition in which the postnasal scales does not form part of the upper labial margin.

Distribution :
(Fig. 25) Republic of South Africa excluding most of the Kalahari and SE coastal zone.

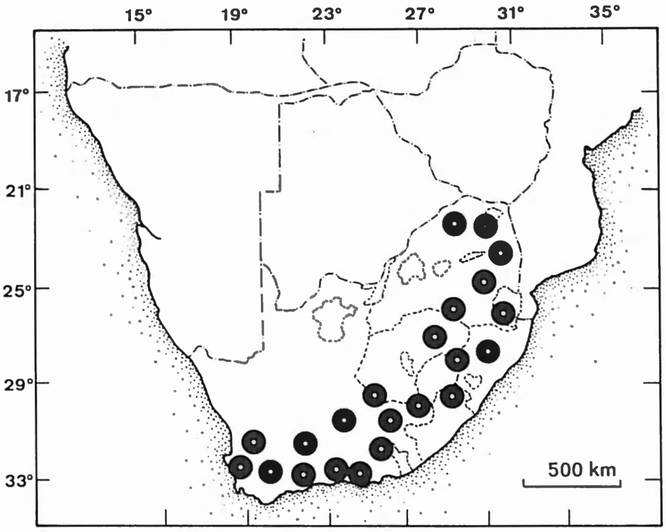


Figure 25 : *Geographical distribution of* Pseudocordylus *based on known locality data. (Modified from Branch, 1988).*

Platysaurus Smith, 1844

1844 *Platysaurus* A. Smith, Illustr. Zool. S. Afr., Rept. : Pl. 40 (Footnote). - Type species (by monotypy) : *Platysaurus capensis* A. Smith.

Content :
Platysaurus capensis Smith, 1844; *Platysaurus guttatus* Smith, 1849; *Platysaurus imperator* Broadley, 1962; *Platysaurus intermedius* Matschie, 1891; *Platysaurus maculatus* Broadley, 1965; *Platysaurus minor* Fitzsimons, 1930; *Platysaurus mitchelli* Loveridge, 1953; *Platysaurus ocellatus* Broadley, 1962; *Platysaurus orientalis* Fitzsimons, 1941; *Platysaurus pungweensis* Broadley, 1959; *Platysaurus relictus* Broadley, 1976; *Platysaurus torquatus* Peters, 1854.

Figure 24 (p. 160) : *Dorsal & lateral views of skull and labial & lingual views of lower jaws of* Pseudocordylus. *A)* Pseudocordylus microlepidotus. *B)* Pseudocordylus capensis. *C)* Pseudocordylus microlepidotus. *Abbreviations of bones are : ang = angular; art = articular; cor = coronoid; den = dentary; ect = ectopterygoid; epp = epipterygoid; fro = frontal; jug = jugal; max = maxilla; nas = nasal; par = parietal; pof = postfronal; poo = postorbital; prf = prefrontal; prm = premaxilla; ptd = pterygoid; qut = quadrate; sag = supra-angular; spl = splenial; squ = squamosal.*

▷

Figure 26 (p. 161) : *Dorsal & lateral views of skull and labial & lingual views of lower jaws of* Platysaurus. *A)* Platysaurus intermedius. *B)* Platysaurus imperator. *C)* Platysaurus imperator. *Abbreviations of bones are : ang = angular; art = articular; cor = coronoid; den = dentary; ect = ectopterygoid; epp = epipterygoid; fro = frontal; jug = jugal; max = maxilla; nas = nasal; par = parietal; pof = postfronal; poo = postorbital; prf = prefrontal; prm = premaxilla; ptd = pterygoid; qut = quadrate; sag = supra-angular; spl = splenial; squ = squamosal.*

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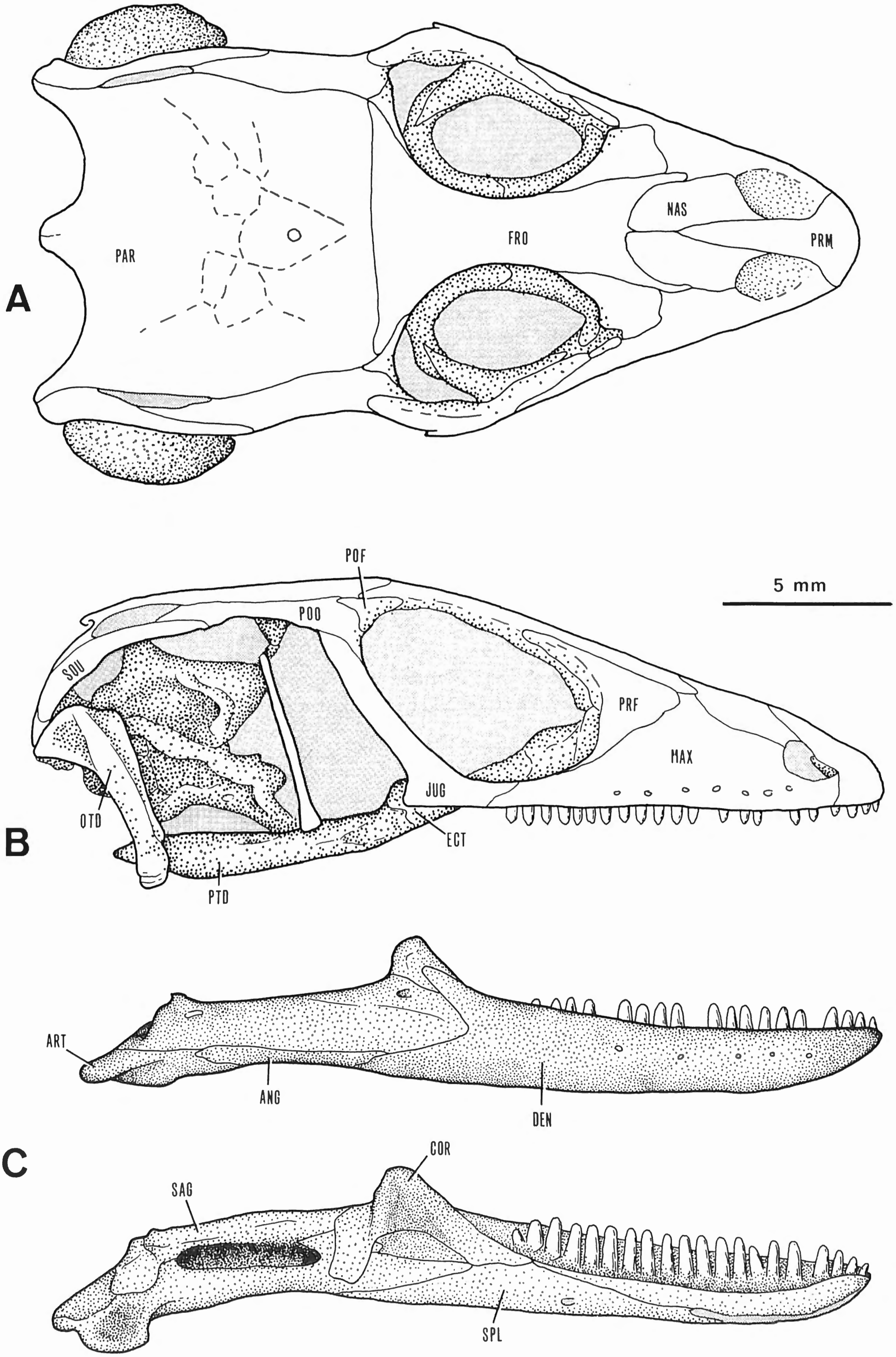
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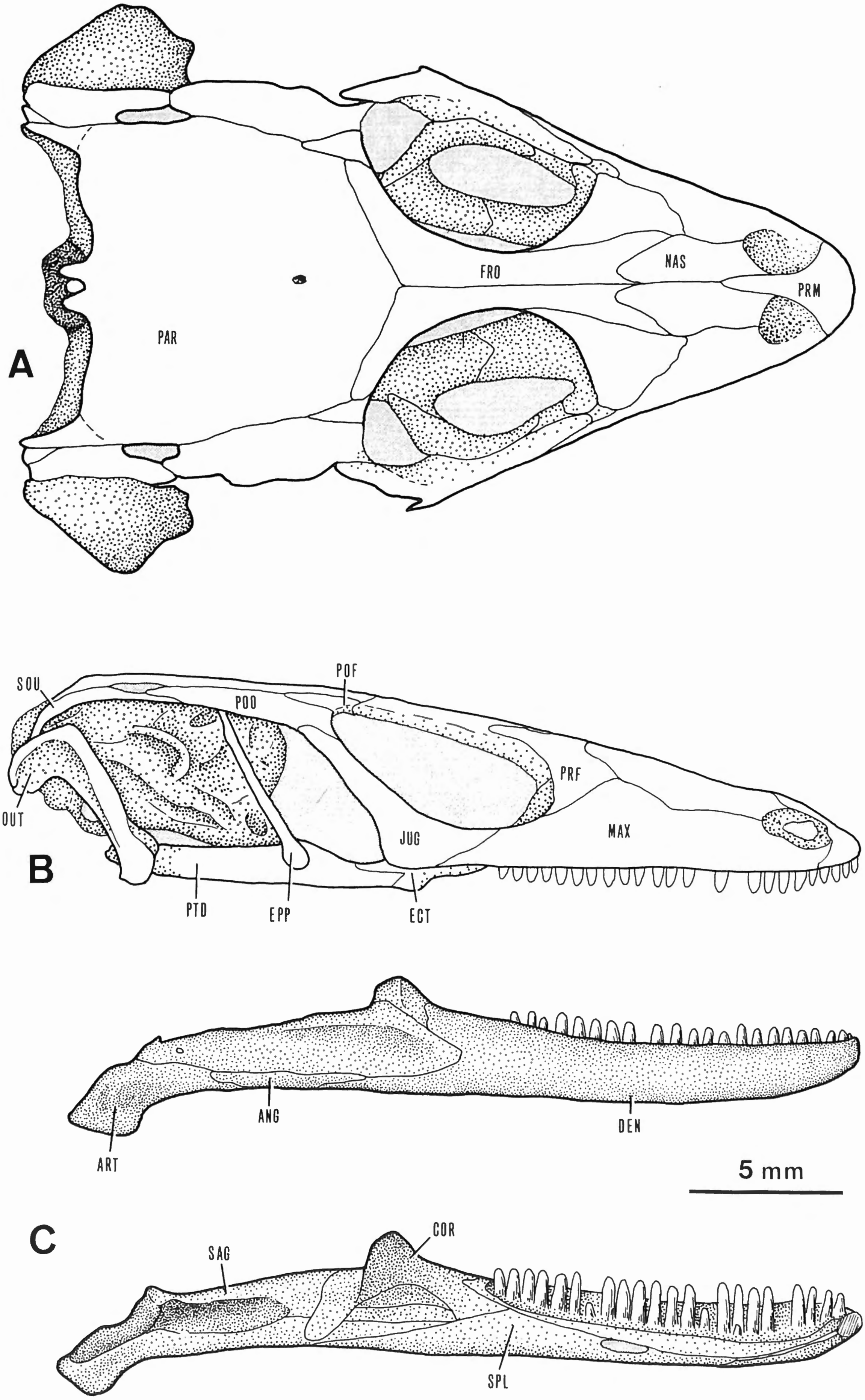
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Diagnosis :

(For cranial characters see Fig. 26). A3) Interosseous nerve innervation of dorsal muscles of lower leg [C with Gerrhosaurinae/ C with Teiioidea]. C6) Frontal bone unfused postembryonically [R from Cordylidae]. C10*) Parietal tab absent [R from Cordyliformes]. P3) Clavicles are simple curved rods [C with *Chamaesaura*]. P6) Carpal intermedium present [R from Cordylinae]. L1) Oviparous mode of reproduction [R from Cordylidae]. M3-2) osteoderms restricted to dorsal aspect of head [C with *Chamaesaura*]. Apomorphies of some of the following character transformation series also occur in some *Platysaurus* : S1) nasal scales in contact; S6*) prefrontal scales separated; S11) anterior parietal scales in contact and S13) interparietal and occipital scales separated.

Comments :

In *Platysaurus mitchelli* the nasal bones are separated medially by the contact of the premaxilla with the frontal. This condition is unique in Cordyliformes, but is present in some iguanians (Lang, 1989) and in Gymnophthalmidae (Maclean, 1974).

Broadley (1978) offers various comments on the phylogeny within *Platysaurus* and indicates that the Kalahari sand movement is the principal factor which has promoted speciation in this genus. His comments are reiterated here uncritically. *Platysaurus mitchelli* (with a lateral presentation display behavior pattern) and *P. maculatus* (with a unique dorsal pattern of stripes and spots) are regarded as the most "primitive" species and can be differentiated from the remaining species of *Platysaurus* by the retention of supranasal scales. Two other "primitive" forms are *P. ocellatus* (complete absence of longitudinal stripes) and *P. capensis*. Furthermore is the "*intermedius*" group which consists of *P. imperator*, *P. intermedius*, *P. torquatus*, *P. pungweensis*. Finally *Platysaurus guttatus*, *P. fitzsimonsi*, *P. minor*, *P. orientalis* and *P. relictus* are considered to form a unit by the presence of a brille in the lower eyelid which has secondarily been lost in *relictus*.

Distribution :

(Fig. 27) C & SW Mozambique, Zimbabwe, E. Botswana, N. Transvaal (Rep. S. Afr.). Isolated populations in the NW Cape Province (RSA) and S. Namibia.

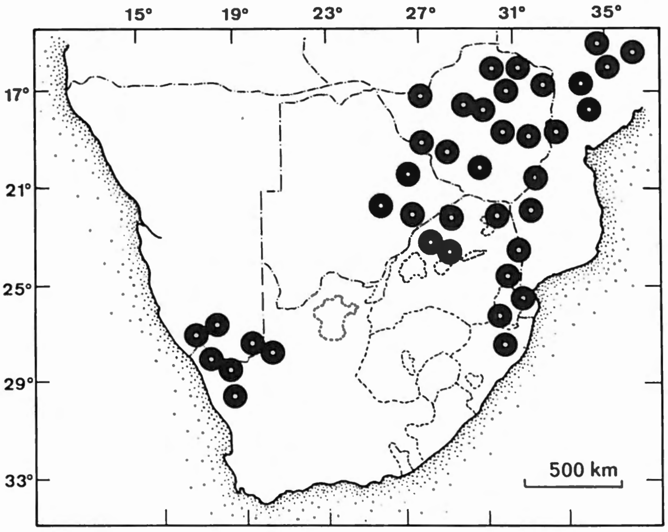


Figure 27 : *Geographical distribution of* Platysaurus *based on known locality data. (Modifed from Broadley, 1978 and Branch, 1988).*

Gerrhosauridae Fitzinger, 1843

1843 Gerrhosauri Fitzinger, Syst. Rept., 1 : 21.

Type genus :

Gerrhosaurus Wiegmann, 1828.

Content :

GERRHOSAURINAE new subfamily & ZONURINAE new subfamily.

Diagnosis :

S11) Anterior parietal scales in contact [R in *Angolosaurus*, C with *Pseudocordylus*, some *Cordylus* and some *Platysaurus*]. S25) Cycloid scales in throat region. A4-2) Insertional tendon of pseudotemporalis superficialis muscle lost. C1) Nasal and prefrontal bones in broad contact [R in *Angolosaurus*/ C with some Gymnophthalmidae Teiidae, Anguidae and *Xantusia*]. C3) Palatine and jugal bones in contact or overlap at the infraorbital foramen [C with Pseudocordylini/ C with Anguimorpha]. C5) The postorbital bone forms about half of the posterior orbital rim. C7) Postfrontal not forked medially. C8) Supratemporal fenestra entirely closed by postfrontal and squamosal [C with Xantusiidae]. C11) Median posterior processes of parietal bone deeply forked bracing the supraoccipital ridge. C13) Skull darkly pigmented [R in *Angolosaurus* and *Cordylosaurus*]. C15) Pterygoid teeth present [C; see character description]. P7) PhaLangeal formula of manus = 2.3.4.4.3. M4-2) Lateral body fold present from corner of mouth to groin [R to intermediate condition in *Tracheloptychus*, C with some *Cordylus*]. M6*) Preanal scales project past the cloaca forming a cloacal covering.

Gerrhosaurinae New Subfamily

Type genus :
Gerrhosaurus Wiegmann, 1828.

Content :
ANGOLOSAURINI new tribe & GERRHOSAURINI new tribe.

Diagnosis :
S2-1a) Nostril bordered by 3 scales. S17*) Posterior chin shields in contact [C with Lacertidae, Gymnophthalmidae and Anguimorpha]. A3) Interosseous nerve innervates the dorsal muscles of the lower leg [C with some *Platysaurus*]. P6) Carpal intermedium lost [C with Cordylinae/ C with some Scincidae, some Lacertidae and *Varanus*].

Angolosaurini New Tribe

Type genus :
Angolosaurus Fitzsimons, 1953.

Content :
Angolosaurus Fitzsimons, 1953.

Angolosaurus Fitzsimons, 1953

1953 *Angolosaurus* Fitzsimons, Ann. Transvaal Mus., Pretoria, 22 : 215. Type species (by original description) : *Gerrhosaurus skoogi* Andersson.

Content :
Angolosaurus skoogi Andersson, 1916.

Diagnosis :
(For cranial characters see Fig. 28). S7) Subocular scale does not form part of the upper labial margin [R from Cordyliformes]. S11) Anterior parietal scales separated [R from Gerrhosauridae]. S13) Interparietal and occipital scales in contact [R from Cordyliformes]. S14*) Median occipital scale absent [C with some *Cordylus*, *Platysaurus*, *Pseudocordylus* and *Gerrhosaurus*/ C with Lacertiformes and Anguimorpha]. S16) Tympanum covered by enlarged tympanic shield [C with *Tracheloptychus*, *Cordylosaurus* and some *Tetradactylus*/ C with outgroup taxa see character description]. S21) Scales on sole of feet flattened, oblique and keeled [C with *Tracheloptychus*, *Cordylosaurus*, *Cordylus*, some *Platysaurus*, some *Pseudocordylus*, some *Gerrhosaurus* and some *Zonosaurus*]. S22) Scales below forelimbs are keeled [C with *Tracheloptychus*, *Tetradactylus*, some *Cordylus*, some *Pseudocordylus*, some *Gerrhosaurus* and some *Zonosaurus*]. S24*) Subdigital lamellae keeled [C with *Tracheloptychus*, *Cordylosaurus*, *Cordylus* and some *Pseudocordylus*/ C with some Scincidae]. C1) Nasal and prefrontal bones in narrow contact [R from Gerrhosauridae]. C2) Lacrimal bone with no lateral exposure [C with Cordylidae/ C with Gymnophthalmidae]. C9*) Parietal downgrowth absent [R from Cordyliformes]. C10*) Parietal tabs [R from Cordyliformes]. C13) Skull unpigmented [R from Gerrhosauridae]. C19) Deep subdental shelf of maxilla [C with Cordylidae].

Comments :
In *Angolosaurus* the postorbital bone is enlarged and is in contact with the frontal bone (Fig. 28). Crown of marginal teeth are severely expanded as an adaptation to a vegetarian diet (Fig. 28) (autapomorphy).

Distribution :
Coastal zone of NW Namibia and SW Angola (Namib desert) (Fig.29).

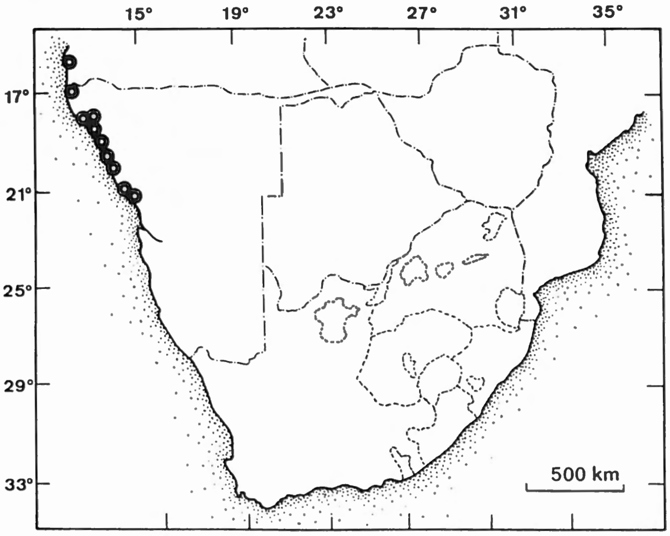
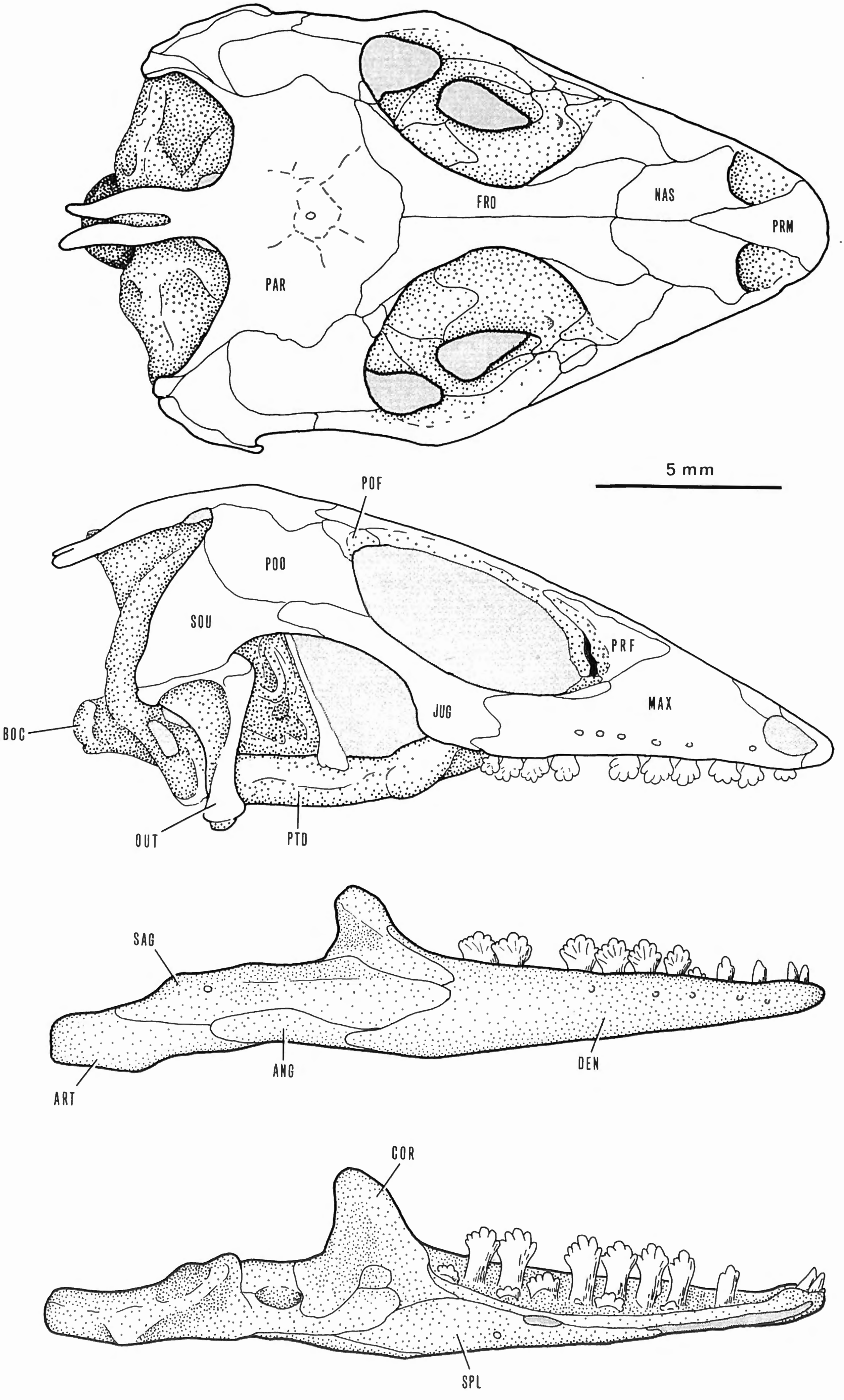


Figure 29 : *Geographical distribution of* Angolosaurus *based on known locality data . (Modified from* Visser, *1984 and* Branch, *1988).*

Figure 28 (p. 164) : *Dorsal & lateral views of skull and labial & lingual views of lower jaws of* Angolosaurus skoogi. *Abbreviations of bones are : ang = angular ; art = articular ; boc = basioccipital ; cor = coronoid ; den = dentary ; ect = ectopterygoid ; epp = epipterygoid ; fro = frontal ; jug = jugal ; lac = lacrimal ; max = maxilla ; nas = nasal ; par = parietal ; pof = postfronal ; poo = postorbital ; prf = prefrontal ; prm = premaxilla ; ptd = pterygoid ; qut = quadrate ; sag = supra-angular ; spl = splenial ; squ = squamosal.* ▷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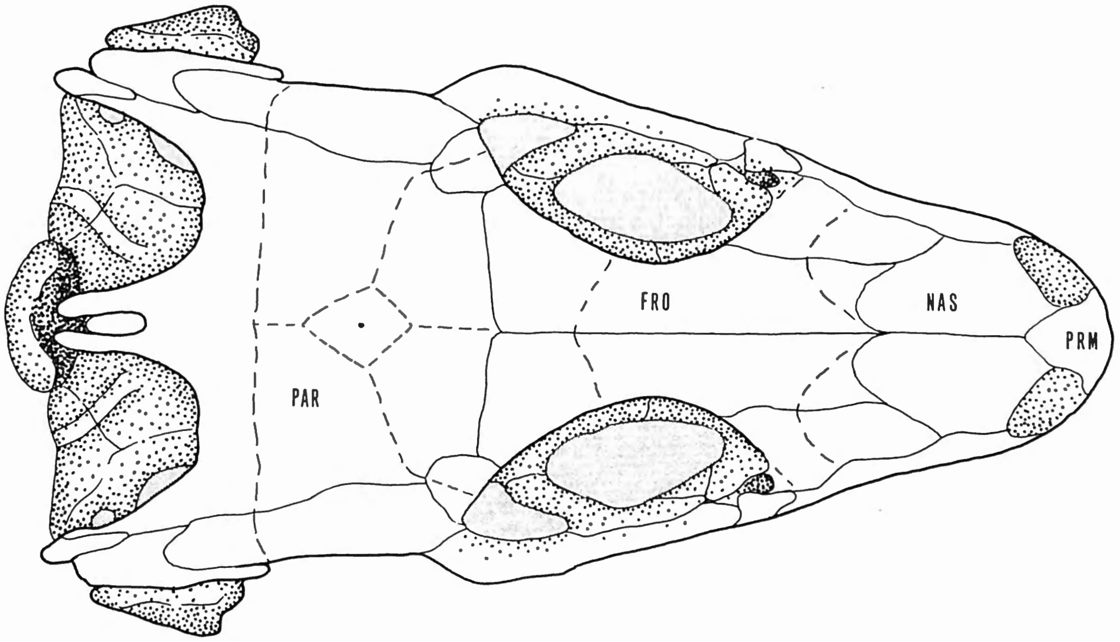
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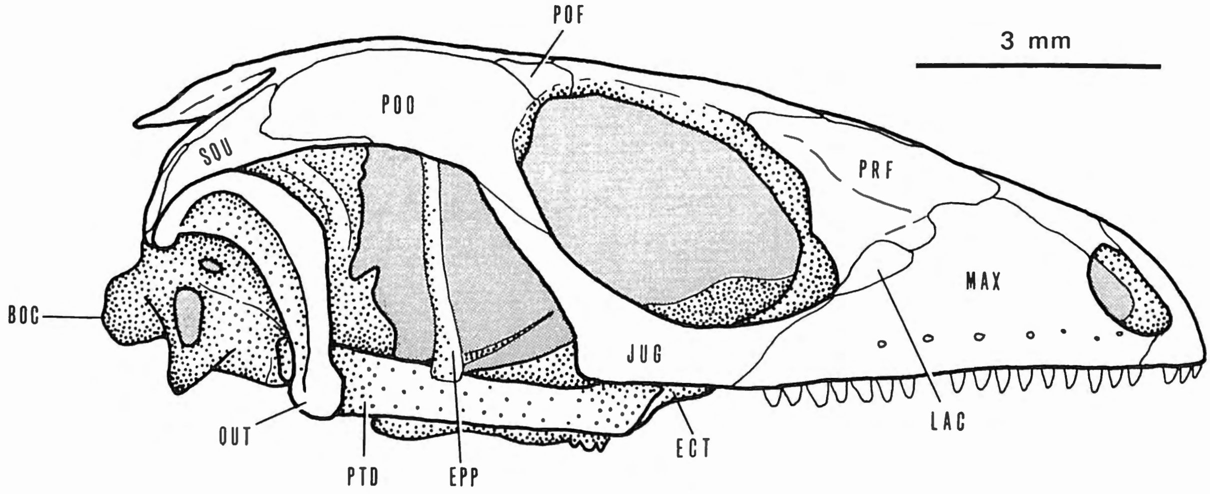
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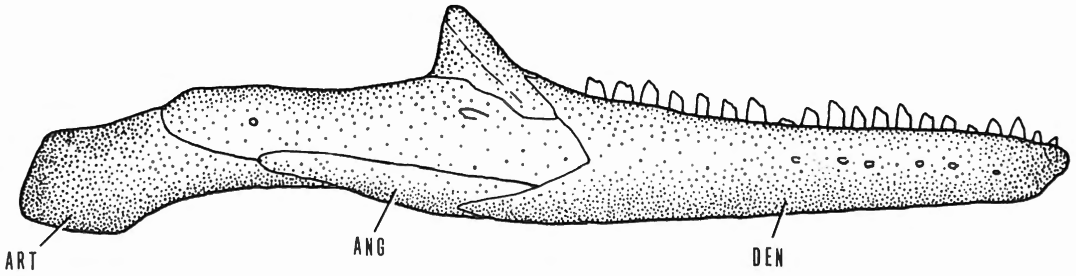
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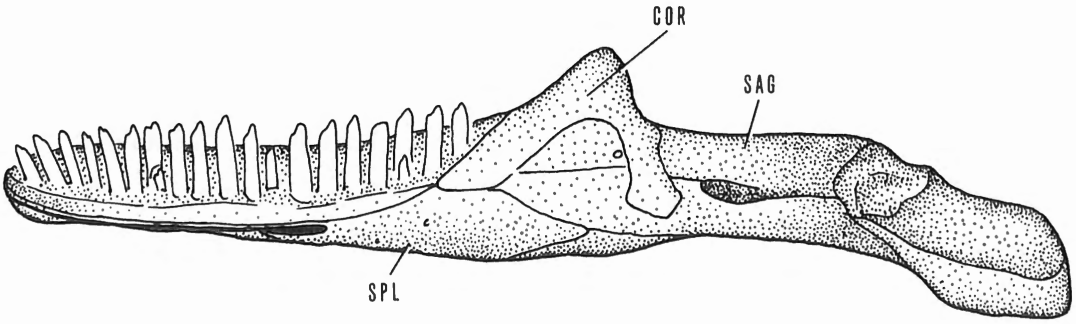
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Gerrhosaurini New Tribe

Type genus :
Gerrhosaurus Wiegmann, 1828.

Content :
Gerrhosaurus Wiegmann, 1828 & Clade : CORDYLOSAURUS - TETRADACTYLUS.

Diagnosis :
S1) Nasal scales in contact [C with *Pseudocordylus*, *Chamaesaura*, some *Cordylus* and some *Platysaurus*/ C with some Lacertidae, Xantusiidae and Teiidae]. S8) 3 supralabial scales anterior to subocular scale that forms part of the upper labial margin [C with *Tracheloptychus* and *Chamaesaura*]. S19) Dorsal body scales keeled [C with *Tracheloptychus*, *Chamaesaura*, some *Cordylus*, some *Zonosaurus*; R in *Cordylosaurus*/ C with outgroup taxa see character description].

Gerrhosaurus Wiegmann, 1828

1828 *Gerrhosaurus* Wiegmann, Isis (Oken), Leipzig, 21 : 378. - Type species (by monotypy) : *Gerrhosaurus flavigularis* Wiegmann.

Content :
Gerrhosaurus flavigularis Wiegmann, 1828; *Gerrhosaurus major* Duméril, 1851; *Gerrhosaurus multilineatus* Bocage, 1866; *Gerrhosaurus nigrolineatus* Hallowell, 1856; *Gerrhosaurus typicus* (Smith, 1836); *Gerrhosaurus validus* Smith, 1849.

Diagnosis :
(For cranial characters see Fig. 30). The following apomorphic character states are found in some *Gerrhosaurus* : S6*) Prefrontal scales separated [C with *Tracheloptychus*, some *Chamaesaura*, some *Cordylus*, some *Platysaurus*, some *Gerrhosaurus* and some *Zonosaurus*]. S14*) Median occipital scale present [C with *Angolosaurus*, some *Cordylus*, some *Platysaurus* and some *Pseudocordylus*/ C with Lacertidae, Teiioidea and Anguimorpha]. S21) Scales on sole of feet flattened, oblique and keeled [C with various ingroup and outgroup taxa, see character description]. S22) Scales below forelimbs smooth [C with various ingroup and outgroup taxa, see character description].

Distribution :
(Fig. 31). Africa, south of 5 deg. northern latitude except Zaire basin (i.e. forested areas) and Kalahari. Relictual populations found in Eritrea, Central African Republic, N. Cameroon, NE Nigeria, N. Benin, N. Togo and N. Ghana.

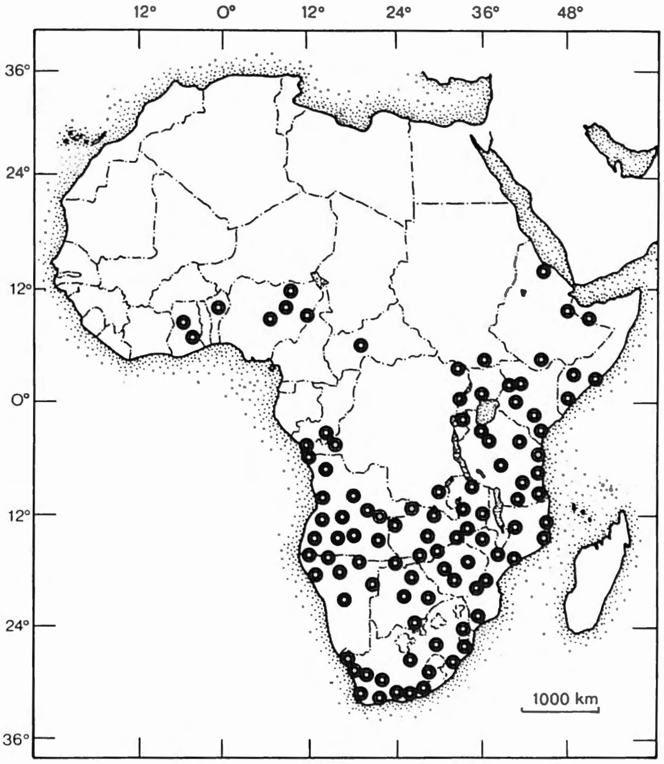


Figure 31 : *Geographical distribution of* Gerrhosaurus *based on known locality data. (Localities derived from* Branch*, 1988 ;* Broadley*, 1971, 1987 ;* De Witte*, 1953 ;* Mancas*, 1961, 1963 ;* Hellmich*, 1957a,b ;* Laurent *1956a, 1964 ;* Loveridge*, 1920, 1929, 1942 ;* Schmidt*, 1919).*

◁ Figure 30 (p 165) : *Dorsal & lateral views of skull and labial & lingual views of lower jaws of* Gerrhosaurus nigrolineatus. *Abbreviations of bones are : ang = angular ; art = articular ; boc = basioccipital ; cor = coronoid ; den = dentary ; ect = ectopterygoid ; epp = epipterygoid ; fro = frontal ; jug = jugal ; lac = lacrimal ; max = maxilla ; nas = nasal ; par = parietal ; pof = postfronal ; poo = postorbital ; prf = prefrontal ; prm = premaxilla ; ptd = pterygoid ; qut = quadrate ; sag = supra-angular ; spl = splenial ; squ = squamosal.*

Clade : **Cordylosaurus - Tetradactylus**

Type genus :
Tetradactylus Merrem, 1820.

Content :
Tetradactylus Merrem, 1820 & *Cordylosaurus* Gray, 1865.

Diagnosis :
S5) Prefrontal and frontonasal scales fused to form a large shield. A1-2) Scale-like papillae of tongue restricted to the anterior part of the tongue, posterior portion of the tongue covered with oblique plicae [C with some Lacertidae]. C16) Basipterygoid process long and elongated with small condylar surfaces [C with Cordylidae and *Tracheloptychus*].

Cordylosaurus Gray, 1865

1865 *Cordylosaurus* Gray, Proc. zool. Soc. London, 1865 : 641. - Type species (by monotypy) : *Cordylosaurus trivirgatus* Gray = *Cordylosaurus subtessellatus* (A. Smith).

Content :
Cordylosaurus subtessellatus (Smith, 1844).

Diagnosis :
(For cranial characters see Fig. 32). S9) Postfrontal scales distinct in juveniles but fuse during ontogeny with the median parietal and interparietal scales to form a single large scale. S15) Lower eyelid with transparent disc [C with some *Cordylus* and some *Platysaurus*/ C with some outgroup taxa; see character description]. S16) Tympanum covered by both a lateral fold and an enlarged tympanic shield [C with *Tracheloptychus*, *Angolosaurus* and some *Tetradactylus*/ C with some outgroup taxa; see character description]. S19) Dorsal body scales smooth [R from Gerrhosaurini]. S21) Scales on sole of feet flattened, oblique and keeled [C with *Tracheloptychus*, *Angolosaurus*, *Cordylus*, some *Platysaurus*, some *Pseudocordylus*, some *Gerrhosaurus* and some *Zonosaurus*]. S24) Subdigital lamellae keeled [C with *Tracheloptychus*, *Angolosaurus*, *Cordylus* and some *Pseudocordylus*/ C with some outgroup taxa; see character description]. C10*) Parietal tabs [R from Cordyliformes]. C13) Skull unpigmented [R from Gerrhosauridae]. C26) Expanded adductor fossa to accommodate the extension of the m. adductor mandibulae posterior into Meckel's canal [C with Cordylidae/ C with some Scincidae and Lacertiformes].

Distribution :
(Fig. 33). Southern Klein Karoo (from Matjesfontein northwards), Little and Big Namaqualand, northwestern Republic of South Africa and bordering area of Angola and Namibia.

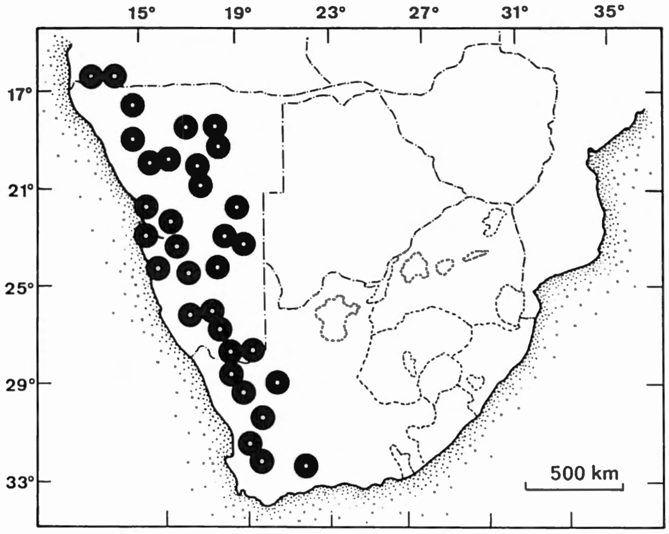


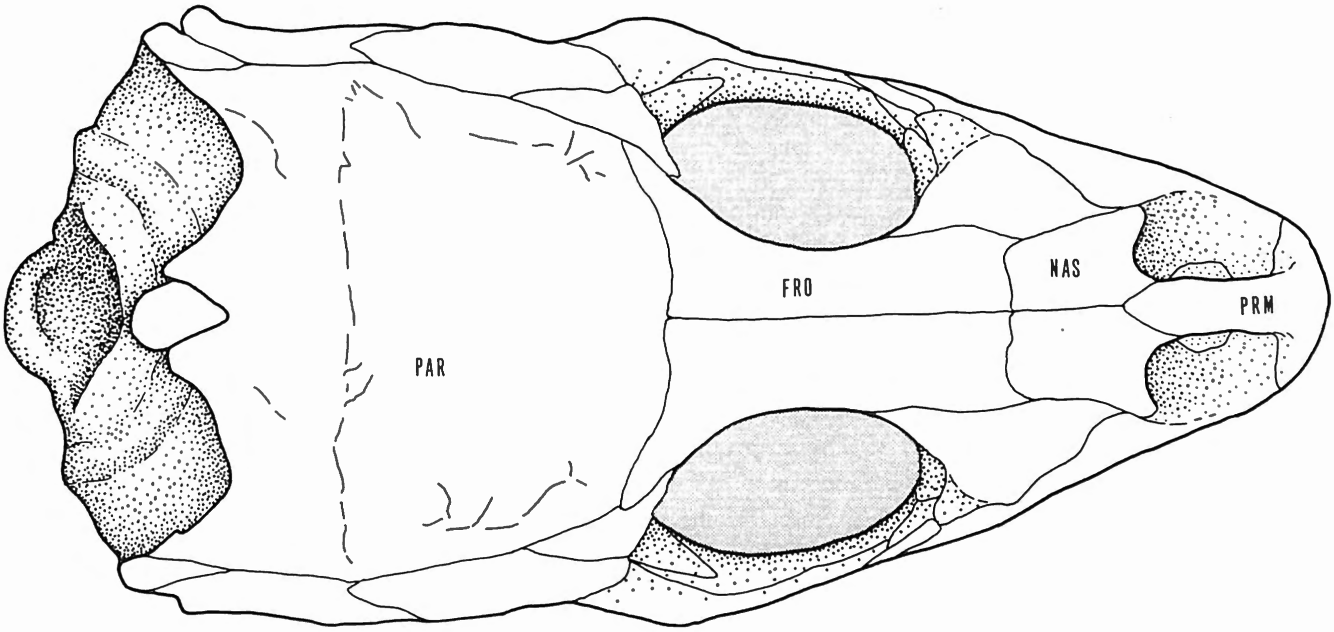
Figure 33 : *Geographical distribution of* Cordylosaurus *based on known locality data . (Modified from* *Visser, 1984 and Branch, 1988).*

Tetradactylus Merrem, 1820

1802 *Chalcides* part., Daudin, Rept., 4 : 359.
1820 *Tachydromus* part., Merrem, Tent. Syst. Amph. : 69.
1820 *Tetradactylus* Merrem, Tent. Syst. Amphib. : 13 : 75. - Type species (by monotypy) and later by tautonomy : *Tetradactylus chalcidicus* Merrem = *Tetradactylus tetradactylus* (Lacepede in Daudin).

Content :
Tetradactylus africanus (Gray, 1838); *Tetradactylus breyeri* Roux, 1907; *Tetradactylus eastwoodae* Methuen & Hewitt, 1913; *Tetradactylus ellenbergeri* (Angel, 1922); *Tetradactylus seps* (Linnaeus, 1758); *Tetradactylus tetradactylus* (Lacepede, 1802).

Figure 32 (p. 168) : *Dorsal & lateral views of skull and lingual & labial views of lower jaw of* Cordylosaurus subtesellatus. *Abbreviations of bones are : ect = ectopterygoid; epp = epipterygoid; fro = frontal; jug = jugal; lac = lacrimal; max = maxilla; nas = nasal; pal = palatine; par = parietal; pof = postfronal; poo = postorbital; prf = prefrontal; prm = premaxilla; ptd = pterygoid; qut = quadrate; squ = squamosal.* ▷


PAR
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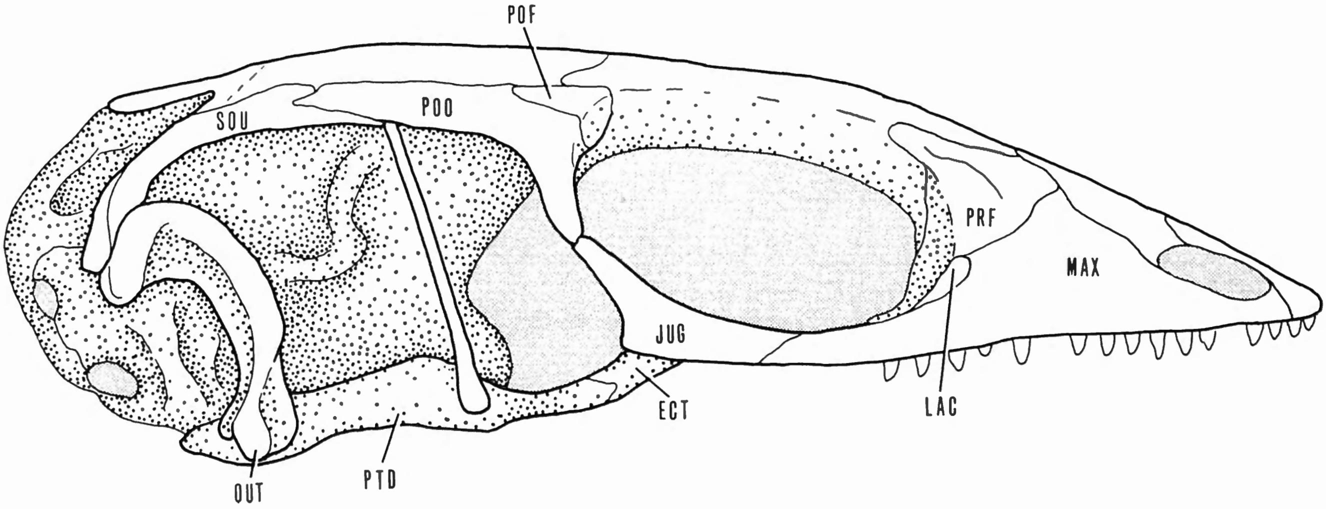
POF
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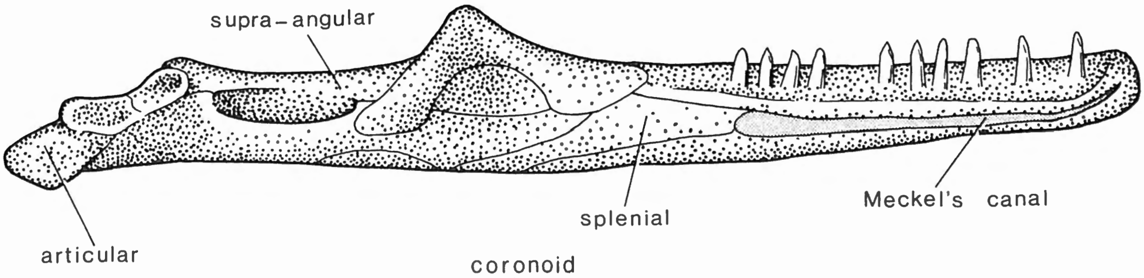
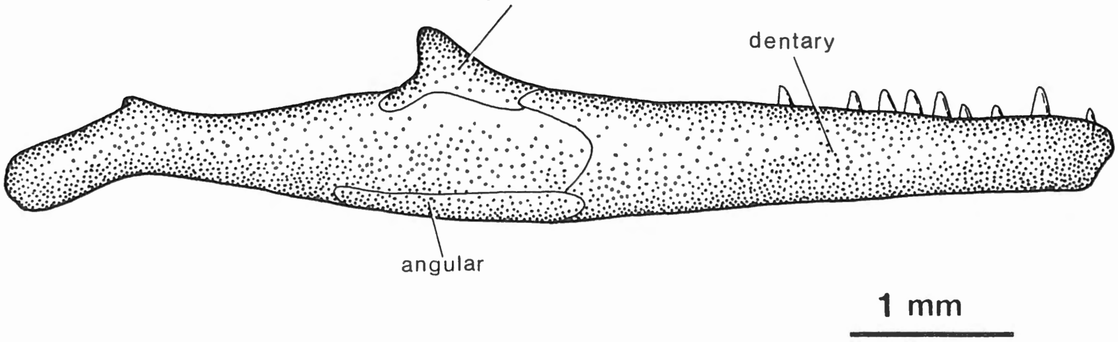

supra-angular
articular
splenial
Meckel's canal


coronoid
dentary
angular
1 mm

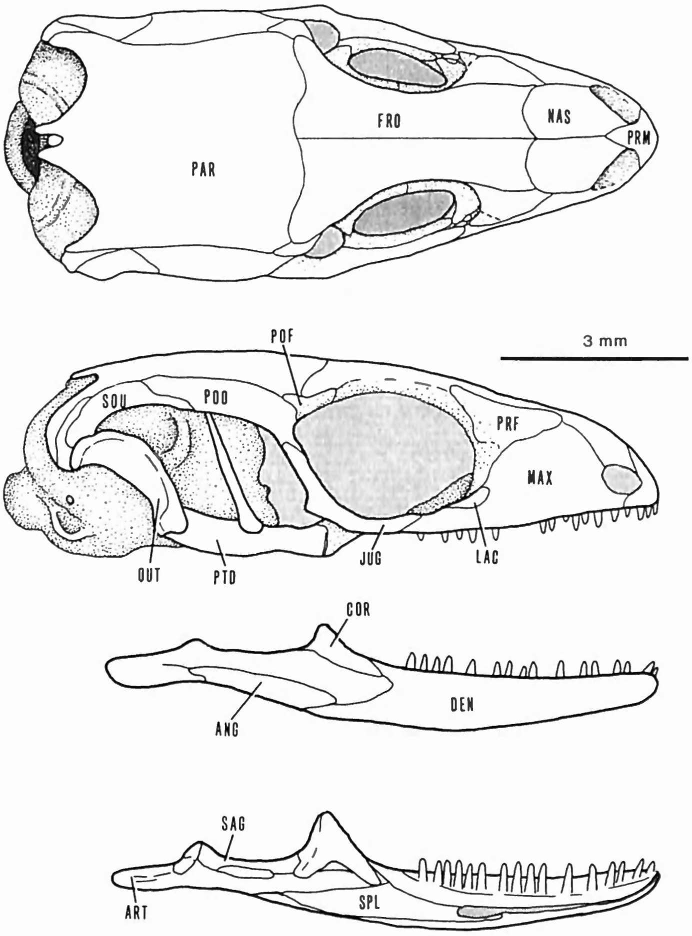


Figure 34 : *Dorsal & lateral views of skull and labial & lingual views of lower jaws of* Tetradactylus ellenbergeri. *Abbreviations of bones are : ang = angular ; art = articular ; cor = coronoid ; den = dentary ; ect = ectopterygoid ; epp = epipterygoid ; fro = frontal ; jug = jugal ; lac = lacrimal ; max = maxilla ; nas = nasal ; par = parietal ; pof = postfronal ; poo = postorbital ; prf = prefrontal ; prm = premaxilla ; ptd = pterygoid ; qut = quadrate ; sag = supra-angular ; spl = splenial ; squ = squamosal.*

Diagnosis :
(For cranial characters see Fig. 34). S22) Scales below forelimbs keeled in limbed species [C with *Tracheloptychus*, *Tetradactylus*, *Angolosaurus*, some *Cordylus*, some *Pseudocordylus*, some *Gerrhosaurus* and some *Zonosaurus*]. A2*) Anterior tip of tongue pigmented [C with some *Gerrhosaurus*/ C with some outgroup taxa; see character description]. C17) Spheno-occipital tubercle consisting exclusively of basioccipital bone [C with *Chamaesaura* and some *Pseudocordylus*]. C29) Retroarticular process with posterior border twisted obliquely [C with *Tracheloptychus*, *Tetradactylus* and *Chamaesaura*]. In some *Tetradactylus* the following apomorphies are also present : S16) Tympanum covered by lateral fold. M1) Limbs reduced or absent.

Comments :
In addition, *Tetradactylus* has several autapomorphies such as : 1) The separation of the frontoparietal scales by the contact of the interparietal and frontal scales in some *Tetradactylus* (e.g. *ellenbergeri* and *eastwoodae*) (Angel, 1922; Loveridge, 1942). In the remaining Cordyliformes as well as the remaining autarchoglossans, with the exception of Varanidae and Helodermatidae in which homologies of the cephalic scales is rather difficult to interpret, the interparietal and frontal scales are separated. 2) Presence of a large sternal fontanelle (Berger-Dell'Mour, 1983) (absent in *Tetradactylus africanus*). Although Siebenrock (1895) illustrates a sternal fontanelle in *Gerrhosaurus nigrolineatus*. This could not be confirmed in this study. 3) Within the genus there are tendencies towards serpentine locomotion and limb reduction with concordant morphological changes (Essex, 1927; Berger-Dell'Mour, 1983). This is convergent with *Chamaesaura*.

Distribution :
(Fig. 35). S & E Coastal zone and N Transvaal Province (Republic of Southern Africa), Central Zimbabwe, Central Zambia, SE Zaire and E Angola and S. Mozambique.

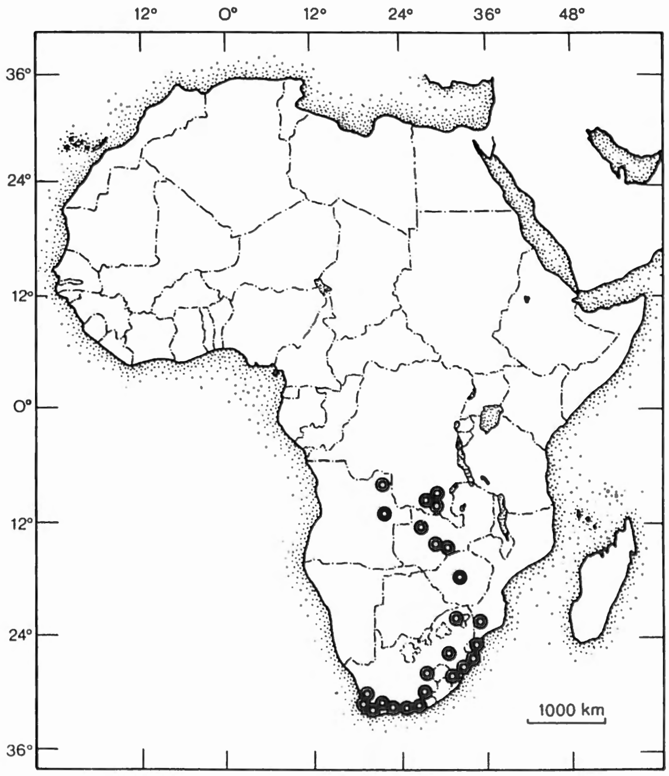


Figure 35 : *Geographical distribution of* Tetradactylus *based on known locality data. (Localities derived from Branch, 1988 ; Berger-Dell'Mour, 1983 ; Broadley, 1971 ; De Witte, 1933, 1942, 1953 ; Laurent, 1964).*

Zonosaurinae New Subfamily

Type genus :
Zonosaurus Boulenger, 1843.

Content :
Tracheloptychus Peters, 1854 & *Zonosaurus* Boulenger, 1843.

Diagnosis :
S2-1b) Nostril surrounded by 4 scales. S9-2) Frontoparietal scales absent [C with Gymnophthalmidae]. S20*) Ventral scales arranged in a honeycomb pattern [R from Cordyliformes]. S25-2) Cycloid scales present on throat and ventrum. A2*-3) Entire tongue pigmented [C with some *Cordylus*/ C with various outgroup taxa; see character description].

Tracheloptychus Peters, 1854

1854 *Tracheloptychus* Peters, M. Ber. k. preuss. Akad. Wiss. Berlin, 1854 : 617. - Type species (by monotypy) : *Tracheloptychus madagascariensis* Peters.

Content :
Tracheloptychus madagascariensis Peters, 1854 & *Tracheloptychus Petersi* Grandidier, 1869.

Diagnosis :
(For cranial characters see Fig. 36). S6*) Prefrontal scales separated [C with some *Chamaesaura*, some *Cordylus*, some *Platysaurus*, some *Gerrhosaurus* and some *Zonosaurus*/ C with some Scincidae and some Anguimorphs]. S8) 3 supralabial scales anterior to the subocular scale forming part of the upper labial margin [C with Gerrhosaurini and *Chamaesaura*]. S16) Tympanum covered by enlarged tympanic shield [C with *Cordylosaurus*, *Angolosaurus* and some *Tetradactylus*/ C with various outgroup taxa, see character description]. S19) Dorsal body scales keeled [C with Gerrhosaurini, *Cordylosaurus*, *Chamaesaura*, some *Cordylus* and some *Zonosaurus*/ C with various outgroup taxa, see character description]. S21) Scales on sole of feet oblique and keeled [C with *Cordylosaurus*, *Angolosaurus*, *Cordylus*, some *Platysaurus*, some *Pseudocordylus*, some *Gerrhosaurus* and some *Zonosaurus*]. S22) Scales below forelimbs keeled [C with *Tetradactylus*, *Angolosaurus*, some *Cordylus*, some *Pseudocordylus*, some *Gerrhosaurus* and some *Zonosaurus*]. S24*) Subdigital lamellae keeled [C with some *Cordylosaurus*, *Angolosaurus*, *Cordylus* and some *Pseudocordylus*/ C with some Scincidae]. A1) Scale-like papillae confined to the anterior half of the tongue, with the posterior half consisting of oblique plicae [C with Xantusiidae and some Lacertidae]. C9*) Parietal downgrowth absent [R from Cordyliformes]. C16) Basipterygoid process long and elongated with small condylar surfaces [C with Clade :*Cordylosaurus-Tetradactylus* and Cordylidae]. C29) Retroarticular process with posterior border twisted obliquely [C with *Chamaesaura* and *Tetradactylus*]. M4) Lateral body fold reaches from corner of mouth to axilla [R from Gerrhosauridae].

Comments :
A variety of derived characters are also found within *Tracheloptychus* such as : 1) Jugal and squamosal bones that are in narrow contact on the postorbital bar in *Tracheloptychus madagascariensis*. In all other Cordyliformes the jugal and squamosal are broadly separated.

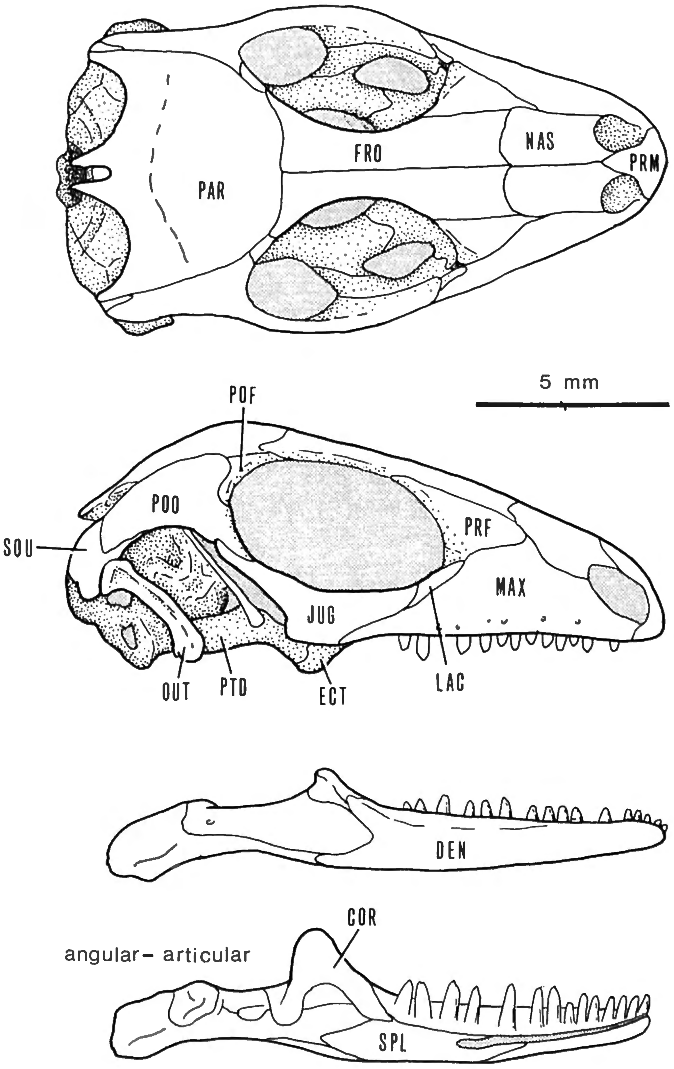


Figure 36 : *Dorsal & lateral views of skull and labial & lingual views of* Tracheloptychus petersi. *Abbreviations of bones are : cor = coronoid; den = dentary; ect = ectopterygoid; epp = epipterygoid; fro = frontal; jug = jugal; lac = lacrimal; max = maxilla; nas = nasal; par = parietal; pof = postfronal; poo = postorbital; prf = prefrontal; prm = premaxilla; ptd = pterygoid; qut = quadrate; spl = splenial; squ = squamosal.*

2) Cervical intercentra that are not restricted to the cervical vertebrae only, but are also present on the anterior thoracic vertebrae. A total of 6 intercentra that are attached intercalary (sutured in *T. madagascariensis*, fused in *T. Petersi*) are present. 3) Presence of an additional tarsal element. In all cordylids exclusive of *Tracheloptychus* the foot consists of a tarsale proximale (fusion of tibulare, fibulare and centrale), two tarsal elements (T3 & T4/5), 5 metatarsals and phalanges. *Tracheloptychus* however has retained the plesiomorphic condition and has a foot structure similar to that of *Sphenodon* with a tarsale proximale in addition to T1/2, T3, 4/5, 5 metatarsal and phalanges (Fig. 37). Within Cordyliformes this latter condition is derived.

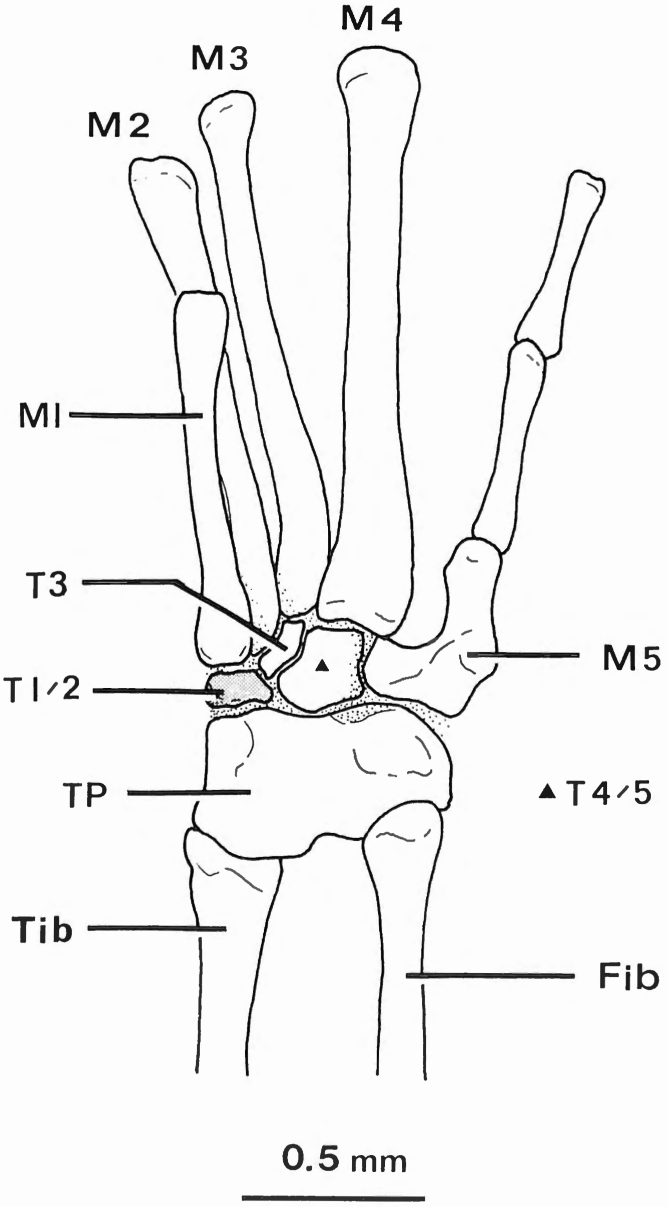


Figure 37 : *Plantar view of left pes of* Tracheloptychus petersi. *Abbreviations : Fib = fibula ; M1-M5 = metatarsals 1-5 ; T1/2-4/5 = tarsale 1/2 - 4/5 ; Tib = tibia ; TP = tibiale proximale.*

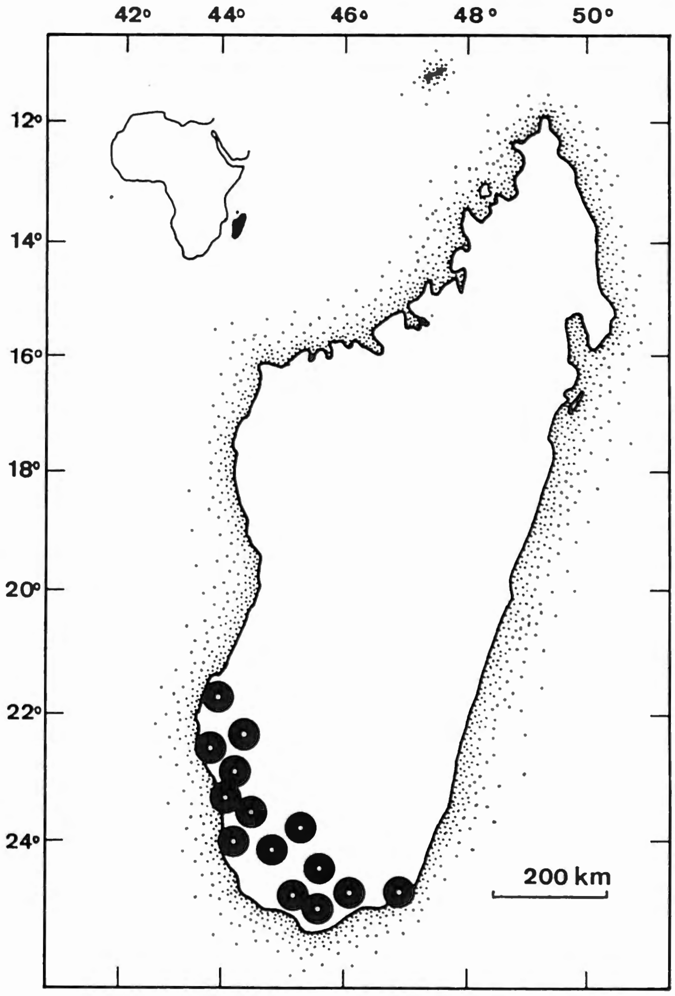


Figure 38 : *Geographical distribution of* Tracheloptychus *based on known locality data. (Modified from Brygoo, 1985).*

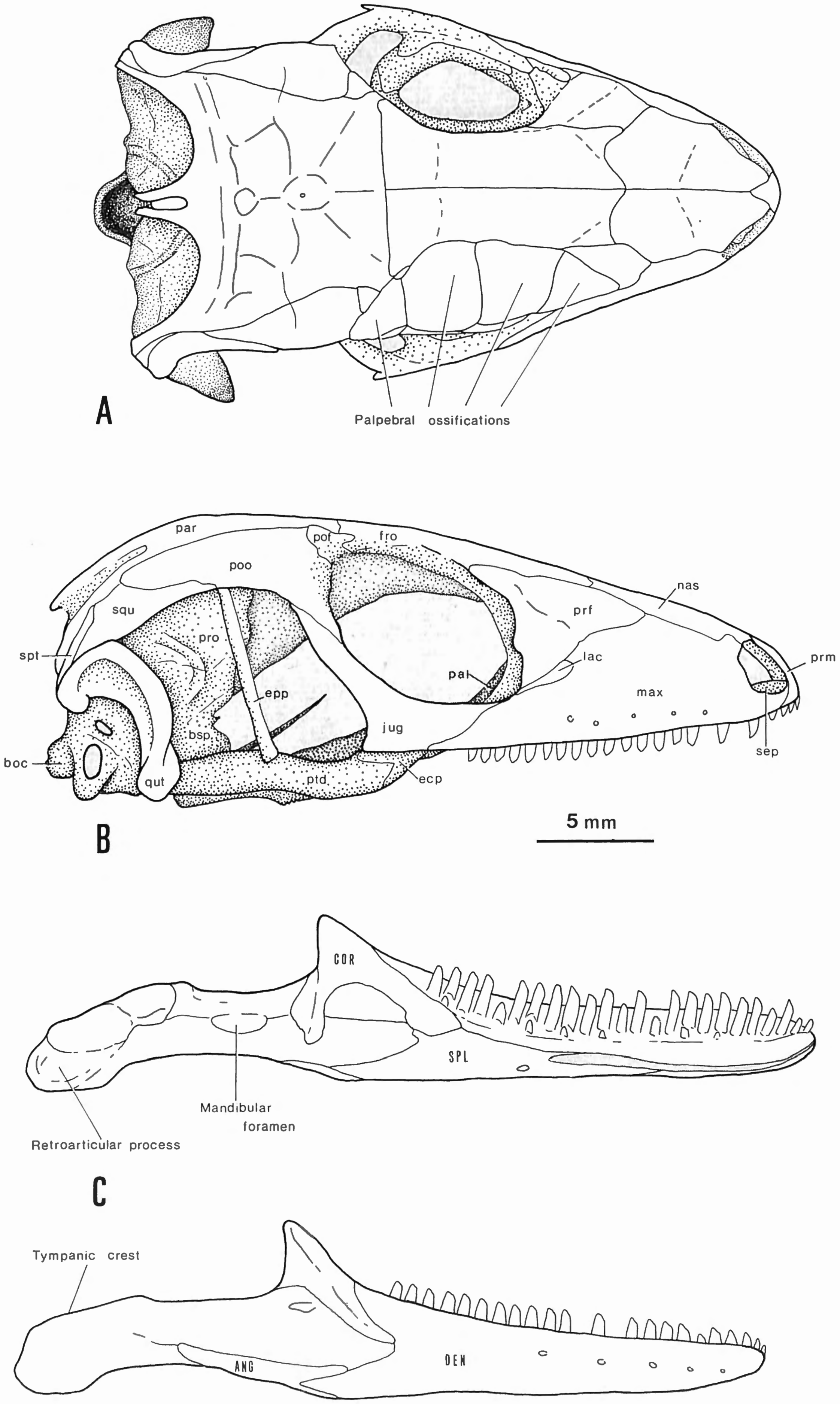
Distribution :

(Fig. 38). Southwestern Madagascar from Fort Dauphin to north of Tuléar.

Zonosaurus Boulenger, 1887

1843 *Aspidosaurus* Fitzinger, Syst. Rept. I : 21, Vindbonae. - Type species : *Gerrhosaurus bifasciatus* Dumeril and Bibron = *Zonosaurus madagascariensis* Gray, by synonymy. Suppression of this name by Brygoo ZN(S) 2465.

1887 *Zonosaurus* Boulenger, Cat. Liz. brit. Mus., 3 : 127. - Type species : *Cicigna madagascariensis* Gray, 1831, by subsequent designation of Savage, 1954, Trans. Kans. Acad. Sci., 57 : 332.


A
Palpebral ossifications
par
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pal
max
epp
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bsp
sep
boc
qut
ptd
ecp
5 mm
B
COR
SPL
Mandibular foramen
Retroarticular process
C
Tympanic crest
ANG
DEN

Content :

Zonosaurus aeneus (Grandidier, 1872); *Zonosaurus boettgeri* Steindachner, 1891; *Zonosaurus brygooi* Lang & Böhme, 1989; *Zonosaurus haraldmeieri* Brygoo & Böhme, 1985; *Zonosaurus karsteni* (Grandidier, 1869); *Zonosaurus laticaudatus* (Grandidier, 1869); *Zonosaurus madagascariensis* (Gray, 1831); *Zonosaurus maximus* Boulenger, 1896; *Zonosaurus ornatus* (Gray, 1831); *Zonosaurus quadrilineatus* (Grandidier, 1867); *Zonosaurus rufipes* (Boettger, 1881); *Zonosaurus trilineatus* Angel, 1939.

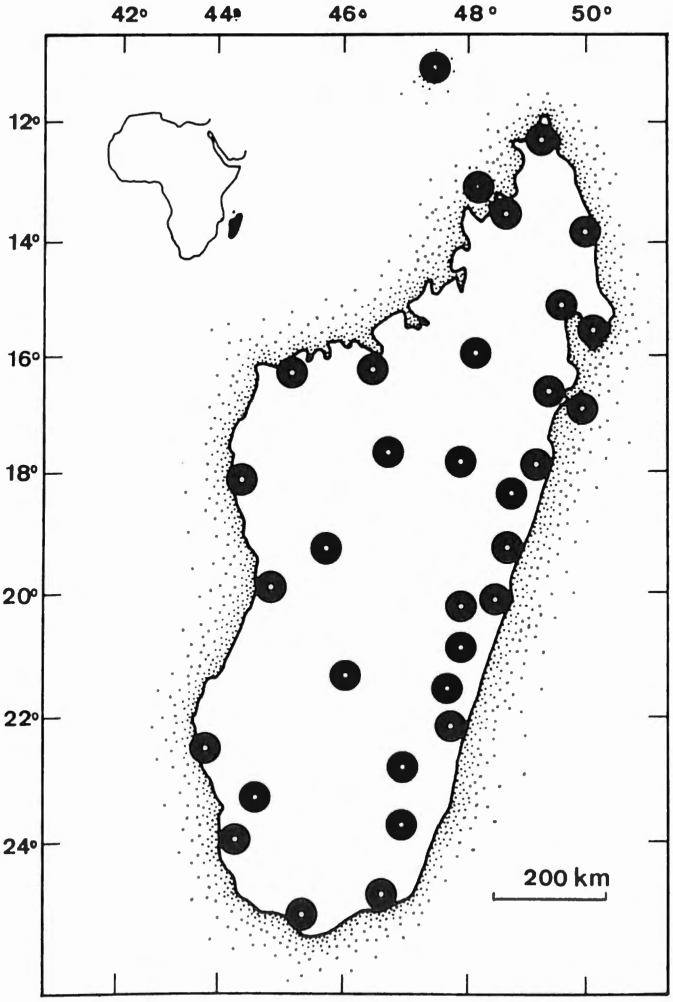
Diagnosis :

(For cranial characters see Fig. 39). In some *Zonosaurus* the following apomorphies are found : S6*) Prefrontal scales separated. S13)Interparietal and occipital scales are separated. S19) Dorsal body scales keeled. S21) Scales on the sole of feet are flattened, oblique and keeled. S22) Keeled scales below forelimbs. A2*) Anterior tip or anterior 1/2 of the tongue is pigmented [R from Zonosaurinae]. M7) Cloacal pigmentation.

Distribution :

(Fig. 40). Madagascar, adjacent islands, Iles Glorieuses and Cosmoledo.

Figure 40 : *Geographical distribution of* Zonosaurus *based on known locality data. (Modified from Brygoo (1985) and Meier (1989)).*



◁ Figure 39 : *Dorsal & lateral views of skull and lingual and labial views of lower jaws of* Zonosaurus. *A)* Zonosaurus maximus. *B)* Zonosaurus madagascariensis. *C)* Zonosaurus madagascariensis. *Abbreviations of bones are : ang = angular; art = articular; bsp = basisphenoid; boc = basioccipital; cor = coronoid; den = dentary; ecp = ectopterygoid; epp = epipterygoid; fro = frontal; jug = jugal; lac = lacrimal; max = maxilla; nas = nasal; pal = palatine; par = parietal; pof = postfronal; poo = postorbital; prf = prefrontal; prm = premaxilla; pro = prootic; ptd = pterygoid; qut = quadrate; sag = supra-angular; sep = septomaxilla; spl = splenial; spt = supratemporal; squ = squamosal.*

Biogeography

Vicariance biogeography supposes that congruence between observed phylogenetic and geographic patterns among monophyletic clades is evidence that they share a common history in space and time. The more such correlations are found, the greater the probability that the congruent patterns are due to common ancestry of the biotas (WILEY, 1988). This is in contrast to groups that have come to occupy their ranges through independent episodes of dispersal in response to different conditions.

In order to recapitulate the biogeographical history of Cordyliformes, other monophyletic taxa sharing similar distributional patterns should be investigated. As suggested by BÖHME (1988), Chamaeleonidae are, biogeographically, ideal candidates to compare with Cordyliformes. They occur throughout most of Africa, Madagascar and the Indian subcontinent. The only other squamates occurring in Africa and Madagascar are also widely distributed such as Gekkonidae, Scincidae, Typhlopidae, Boidae and Colubridae.

Biogeographical patterns of recent taxa must also be seen in light of their fossil relatives when known. Both *Pseudolacerta* DE STEFANO with two species and the monotypic *Palaeocordylus* ROCEK have been placed by ESTES (1983a) and ROCEK (1984) respectively within Cordyliformes. The phylogenetic position of these two taxa is not yet known. If in fact they are cordyliforms, then it may be concluded that Cordyliformes were represented in the herpetofauna of Europe from early Eocene to early Miocene. ESTES' (1983b) biogeographical scenario suggests an African origin of Cordyliformes. This is wholely supported by the phylogeny presented in this study, and would indicate that both *Pseudolacerta* and *Palaeocordylus* represent either a single or two separate (depending on their phylogenetic affinities) northward dispersals into Europe during peak Eocene tropicality. This time frame corresponds with the range extensions of other squamate taxa such as iguanids, agamids, gekkonids and varanids (ESTES, 1983b).

Early Eocene is regarded as the earliest occurrence of cordyliforms in Europe (AUGÉ, 1987). In addition, much of Europe was submerged during the Cretaceous (HALLAM, 1981). The latest occurrence of cordyliforms is the early Miocene of Bohemia (ROCEK, 1984), which corresponds with another wave of African immigrants such as *Chamaeleo caroliquarti* (MOODY & ROCEK, 1980), *C. pfeili* (SCHLEICH, 1983) and *C. bavaricus* (SCHLEICH, 1984). AUGÉ's (1987) statement that Cordyliformes may have been present in Europe from the Late Jurassic to the Miocene seems unlikely.

Concentrating on the recent Cordyliformes; only gross biogeographical events can be postulated. KLAVER and BÖHME's (1986) phylogeny of the Chamaeleonidae suggests that ancestrally chamaeleonids were distributed throughout Africa and Madagascar. This also appears true for Cordyliformes. During the Cretaceous prior to the Malagasy landmass separation from the Kenya-Tanzanian coast by sea-floor spreading (RABINOWITZ *et al.*, 1983) Chamaeleonidae had already diverged into the subfamilies Brookesiinae and Chamaeleoninae with both taxa having Madagascan representatives.

The Madagascar-Africa separation superimposed on the proposed phylogeny also suggests a Cordylidae-Gerrhosauridae split. Subsequently Cordylidae must have become extinct on Madagascar. The timing of separation of Cordylidae into subfamilies cannot be correlated with any geological event and occurred either before or after the Madagascar-Africa separation.

In Gerrhosauridae the divergence into two subfamilies coincides with the Madagascar-Africa separation, with the Madagascar clade further diverging into two extant genera; the African clade into four extant genera.

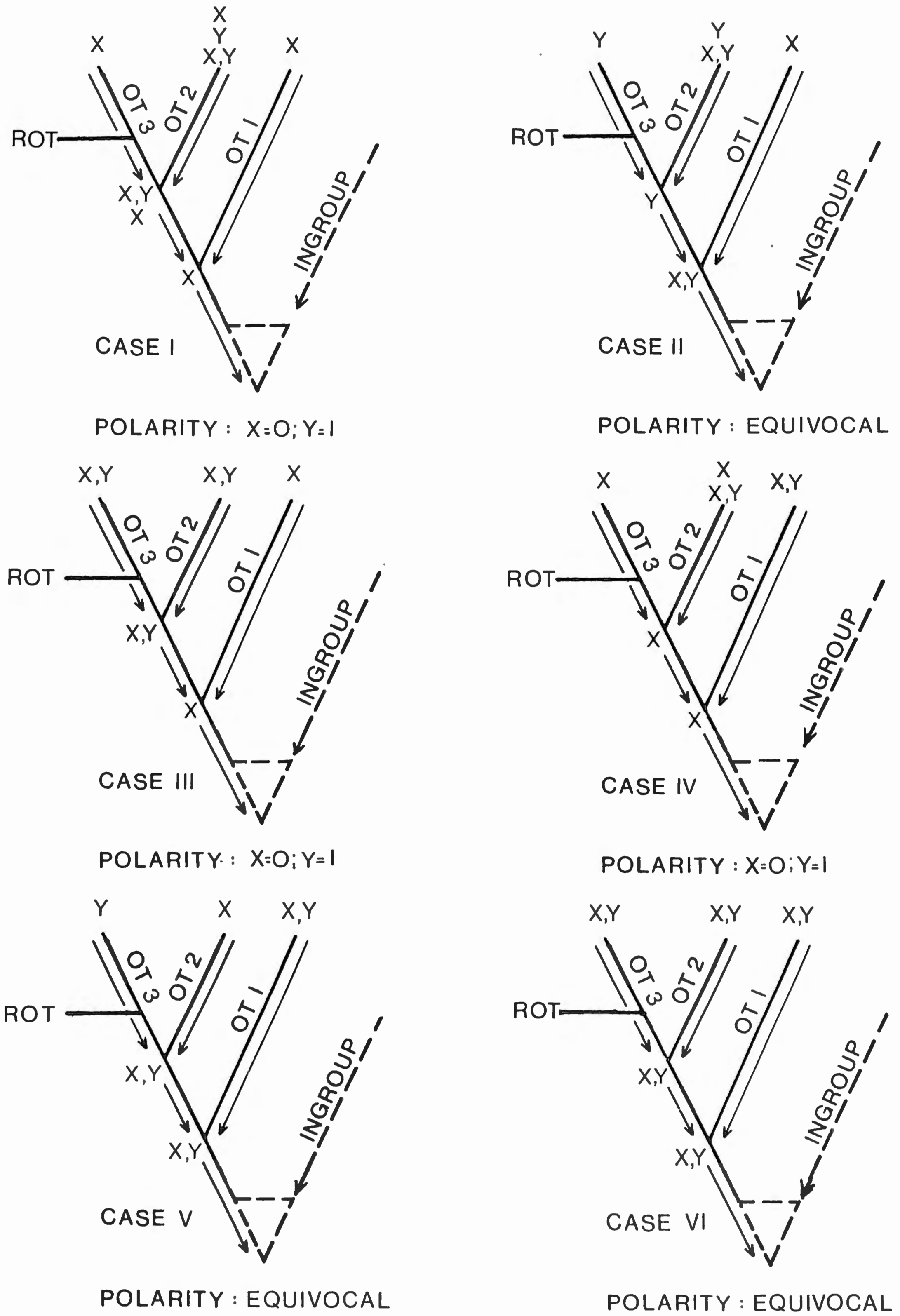


Figure 41 : *Distribution patterns for polarity decisions of character transformation series for an ingroup with 3 outgroups.*

Conclusions

An attempt has been made in this study to compile and describe characters in order to postulate phylogenetic relationships at the generic level within Cordyliformes (= Cordylidae + Gerrhosauridae). Following demonstration of cordyliform monophyly (see section on monophyly), Estes *et al.*'s (1988) hypothesis of a Scincidae-Cordyliformes relationship is reiterated, thereby rejecting the phylogenetic hypotheses of Underwood (1971), Northcutt (1978) and Presch (1988).

No attempt to date has been made to postulate relationships within Cordyliformes. The results of this study therefore, stand as hypotheses to be further tested against additional character data. A preferred cladoram is generated by the character data matrix of 74 character transformation series polarized by outgroup comparison.

The families Cordylidae and Gerrhosauridae form well-defined natural units, supported by a multitude of synapomorphies. Their relationship with one another is tentatively accepted although there is no overwhelming supporting evidence. Alternate hypotheses are less-likely.

Within Gerrhosauridae, the Madagascan clade *Tracheloptychus-Zonosaurus* represents a single speciation event coinciding with the separation of Madagascar from Africa during the Cretaceous. Within African gerrhosaurids, the monotypic *Angolosaurus* is the earliest diverging taxon. *Gerrhosaurus* is the sister-taxon to a *Cordylosaurus-Tetradactylus* clade.

Within the purely African Cordylidae the picture is also quite clear. The serpentine *Chamaesaura* is the earliest diverging taxon. *Cordylus* is the sister-taxon to a *Platysaurus-Pseudocordylus* clade.

A new classification is proposed based on the proposed phylogeny and an attempt is made to parallel taxonomic levels within Scincomorpha. Also presented are diagnoses (based on character states) for all monophyletic taxa of the ingroup.

Biogeographical patterns are evaluated in light of the proposed phylogeny and correlated to the Chamaeleonidae the only suitable squamate taxon with comparable distribution.

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I dedicate, with great pleasure, this study to my late father in recognition for all the things he has done for me.

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Appendix A : list of specimens examined

PRESERVED MATERIAL

Numerous preserved specimens of in- and outgroup taxa were examined in this study. Rather than to give a long list of numbers and localities of examined material, only a list of ingroup taxa examined is given together with the institutions and collections from which they originated.

CORDYLIDAE

Chamaesaura anguina; *macrolepis.*
Cordylus: *campbelli*; *cataphractus*; *coeruleopunctatus*; *cordylus*; *giganteus*; *lawrenci*; *macropholis*; *mclachlani*; *minor*; *namaquensis*; *peersi*; *polyzonus*; *pustulatus*; *rhodesianus*; *tropidosternum*; *vittifer*; *warreni.*
Platysaurus : *capensis*; *imperator*; *intermedius*; *maculatus*; *mitchelli*; *ocellatus*; *pungweensis*; *torquatus.*
Pseudocordylus : *microlepidotus*; *melanotus.*

GERRHOSAURIDAE

Angolosaurus skoogi.
Cordylosaurus subtessellatus.
Gerrhosaurus : *flavigularis*; *major*; *multilineatus*; *nigrolineatus*; *validus.*
Tetradactylus : *africanus*; *ellenbergeri*; *seps.*
Tracheloptychus : *madagascariensis*; *petersi.*
Zonosaurus: *aeneus*; *boettgeri*; *brygooi*; *karsteni*; *laticaudatus*; *madagascariensis*; *maximus*; *ornatus*; *quadrilineatus*; *rufipes*; *trilineatus.*

Origin of preserved materials :

Museum Alexander Koenig, Bonn [ZFMK]
Koninklijk Belgisch Instituut Voor Natuur Wetenschappen (Brussels) [IRSNB]
Koninklijk Museum voor Centraal Afrika, Tervuren [MRAC]
Staatliches Museum für Natuurkunde in Stuttgart [SMNS]
Forschungsinstitut Senckenberg, Frankfurt am Main [SMF]
British Museum (Natural History) [BMNH]
Zoologisches Museum an der Humboldt-Universität zu Berlin, Berlin [ZMB]
Naturhistorisches Museum Wien [NMW]
The National Histoy Museum of Zimbabwe, Bulawayo, Zimbabwe [NMZB/UM]
California Academy of Sciences [CAS]
Collection of John Visser (Durbanville, RSA)
Harvard University, Museum of Comparative Zoology [MCZ]
Field Museum of Natural History [FMNH]
Transvaal Museum, Pretoria, RSA [TM]
Staatsmuseum, Windhoek, Namibia [SMWN]
American Museum of Natural History, New York [AMNH]

SKELETAL MATERIAL

The following skeletal material was examined in this study. (See above section for museum acronyms).

CORDYLIDAE

Chamaesaura
- *anguina* IRSNB uncat.; MCZ 41101, 41104
- *macrolepis* IRSNB 8029; MCZ 47129; ZFMK 7822

Cordylus
- *cataphractus* ZFMK 7807, 7808, 7818
- *cordylus* IRSNB 914; MCZ 21567, 21570
- *giganteus* IRSNB 12301; AMNH 32577, MCZ 173137; ZFMK 7816, 7817
- *peersi* ZFMK 29406
- *polyzonus* MCZ 45443; ZFMK 7805
- *tropidosternum* IRSNB 7962; MCZ 52514; ZFMK 7803, 7810, 7811
- *vittifer* MCZ 13345, 21364
- *warreni* NMZB/UM 8970, 8971; MCZ 41881; ZFMK 7809

Platysaurus
- *capensis* ZFMK 7821
- *imperator* MCZ 67615 (Paratype)
- *intermedius* MCZ 44415, 44416, 44547
- *mitchelli* MCZ 87257

Pseudocordylus
- *microlepidotus* MCZ 21273, 52103; ZFMK 7806, 7820
- *robertsi* MCZ 41875

GERRHOSAURIDAE

Angolosaurus
- *skoogi* ZFMK 7819

Cordylosaurus
- *subtessellatus* MCZ 42695, ZFMK 7823

Gerrhosaurus
- *flavigularis* MCZ 41276 (Paratype); AMNH 73607; ZFMK 7813
- *major* NMZB/UM 25703, 32669; MCZ 147438; ZFMK 7815
- *multilineatus* IRSNB 8161
- *nigrolineatus* NMZB/UM 6613, IRSNB uncat.
- *validus* NMZB/UM 6741; FMNH 215858, 228400; MCZ 50973

Tetradactylus
- *ellenbergeri* IRSNB 10773; MCZ 52501

Tracheloptychus
- *madagascariensis* ZFMK 27678
- *petersi* ZFMK 8903

Zonosaurus
- *haraldmeieri* ZFMK 7824
- *laticaudatus* ZFMK 7256
- *madagascariensis* IRSNB 992, 12261; MCZ 20951
- *maximus* ZFMK 7802, 7812, 7825
- *ornatus* AMNH 47744
- *quadrilineatus* ZFMK 7804

SCINCIDAE

Chalcides ocellatus ZFMK 7837, 7850, 7851 / *Egernia cunninghami* ZFMK 21646 / *Tiliqua gigas* ZFMK 7852 / *Tiliqua scincoides* ZFMK 21645 / *Trachydosaurus rugosus* ZFMK 21642, 21643, 21644

XANTUSIIDAE

Xantusia henshawi ZFMK 7814

LACERTIDAE

Acanthodactylus erythrurus ZFMK 7873 / *Algyroides fitzingeri* ZFMK 7872 / *Gallotia atlantica* ZFMK 34964 / *Gallotia galloti* ZFMK 7826, 7832, 7834 / *Holaspis guentheri* ZFMK 7838, 7839 /*Lacerta agilis* ZFMK 7827 / *Lacerta laevis* ZFMK 7831, 7863 / *Lacerta lepida* ZFMK 7835, 7866 / *Lacerta monticola* ZFMK 7861, 7862 / *Lacerta pater* ZFMK 7870 / *Lacerta princeps* ZFMK 7877 / *Lacerta rudis* ZFMK 7830 / *Lacerta schreibersi* ZFMK 7836 / *Lacerta stehlini* ZFMK 7876 / *Lacerta trilineata* ZFMK 7869 / *Lacerta vivipara* ZFMK 7871 / *Podarcis erhardii* ZFMK 7868 / *Podarcis muralis* ZFMK 7874 / *Podarcis peloponnesiaca* ZFMK 7867 / *Podarcis pityusensis* ZFMK 7875 / *Podarcis taurica* ZFMK 7865 / *Psammodromus algirus* ZFMK 7864

TEIIDAE

Ameiva ameiva ZFMK 21640, 21641 / *Callopistes maculatus* ZFMK 7828, 7833, 7855, 7857, 7858 / *Callopistes sp.* ZFMK 7853, 7854 / *Echinosaura horrida* ZFMK 7856 / *Tupinambis rufescens* ZFMK 21639 / *Tupinambis teguixin* ZFMK 21638, 7859, 7860 ANGUIDAE*Anguis fragilis* ZFMK 7842 / *Gerrhonotus multicarinatus* ZFMK 7843 / *Ophisaurus apodus* ZFMK 7840, 7841, 7844

XENOSAURIDAE

Shinisaurus crocodilurus ZFMK 7849

HELODERMATIDAE

Heloderma suspectum ZFMK 21658, 7845*Heloderma horridum* ZFMK 7846

VARANIDAE

Varanus exanthematicus ZFMK 7847, 21652, 38432 / *Varanus flavescens* ZFMK 21653 / *Varanus griseus* ZFMK 7848 / *Varanus niloticus* ZFMK 21655 / *Varanus prasinus* ZFMK 7829 / *Varanus salvator* ZFMK 21651

Appendix B : character data matrix

Characters are described and defined in pp 15-74. Characters with an asterisk are unordered.

TAXON	CHARACTER						
	S1	S2	S3	S4	S5	S6*	S7
Chamaesaura	1	0/0	1	1	0	0,1	1
Cordylus	0,1	0/0	0,1	0,1	0	0,1	0,1
Platysaurus	0,1	0/0	0	0	0	0	1
Pseudocordylus	1	0/0	0	0,1	0	0,1	1
Angolosaurus	0	1/0	0	0	0	0	0
Cordylosaurus	1	1/0	0	?	1	?	1
Gerrhosaurus	1	1/0	0	0	0	0,1	1
Tetradactylus	1	1/0	0	?	1	?	1
Tracheloptychus	0	0/1	0	0	0	1	1
Zonosaurus	0	0/1	0	0	0	0,1	1

TAXON	CHARACTER						
	S8	S9	S10	S11	S12	S13	S14*
Chamaesaura	1	0	1	0	0	0	0
Cordylus	0	0	1	0,1	0,1	1	0,1
Platysaurus	0	0	1	0,1	1	0,1	0,1
Pseudocordylus	0	0	1	1	1	1	0,1
Angolosaurus	0	0	0	0	0	0	1
Cordylosaurus	1	1	0	1	0	1	0
Gerrhosaurus	1	0	0	1	0	1	0,1
Tetradactylus	1	0	0	1	0	1	0
Tracheloptychus	1	2	0	1	?	1	0
Zonosaurus	0	2	0	1	?	1,?	0

TAXON	CHARACTER						
	S15	S16	S17*	S18	S19	S20*	S21
Chamaesaura	0	0	0	0	1	?	?
Cordylus	0,1	0	0	0	0,1	1	1
Platysaurus	0,1	0	0	1,2	0	1	0,1
Pseudocordylus	0	0	0	1	0	1	0,1
Angolosaurus	0	1	1	0	0	1	1
Cordylosaurus	1	1	1	0	0	1	1
Gerrhosaurus	0	0	1	0	1	1	0,1
Tetradactylus	0	0,1	1	0	1	1	0,?
Tracheloptychus	0	1	0	0	1	0	1
Zonosaurus	0	0	0	0	0,1	0	0,1

TAXON	CHARACTER			
	S22	S23	S24*	S25
Chamaesaura	?	?	?	0
Cordylus	0,1	0,1	1	0
Platysaurus	0	0	0	0
Pseudocordylus	0,1	0,1	0,1	0
Angolosaurus	1	0	1	1
Cordylosaurus	0	0	1	1
Gerrhosaurus	0,1	0	0	1
Tetradactylus	1,?	0,?	0,?	1
Tracheloptychus	1	0	1	2
Zonosaurus	0,1	0	0	2

TAXON	CHARACTER			
	A1	A2*	A3	A4
Chamaesaura	0	0	?	1
Cordylus	0	0,3	0	1
Platysaurus	0	0	1	1
Pseudocordylus	0	0	0	1
Angolosaurus	0	0	?	2
Cordylosaurus	2	0	?	2
Gerrhosaurus	0	0,1	1	2
Tetradactylus	2	1	?	2
Tracheloptychus	1	3	0	2
Zonosaurus	0	1,2,3	0	2

TAXON	CHARACTER						
	C1	C2	C3	C4	C5	C6	C7
Chamaesaura	0	1	0	1	0	1	0
Cordylus	0	1	0	1	0	1	0
Platysaurus	0	1	1	1	0	0	0
Pseudocordylus	0	1	1	1	0	1	0
Angolosaurus	0	1	1	0	1	0	1
Cordylosaurus	1	0	1	0	1	0	1
Gerrhosaurus	1	0	1	0	1	0	1
Tetradactylus	1	0	1	0	1	0	1
Tracheloptychus	1	0	1	0	1	0	1
Zonosaurus	1	0	1	0	1	0	1

TAXON	CHARACTER						
	C8	C9*	C10*	C11	C12	C13	C14
Chamaesaura	0	1	1	0	1	0	0
Cordylus	0	1	1	0	1	0	1
Platysaurus	0	1	0	0	1	0	1
Pseudocordylus	0	1	1	0	1	0	1
Angolosaurus	1	0	0	1	0	0	0
Cordylosaurus	1	1	0	1	0	0	0
Gerrhosaurus	1	1	1	1	0	1	0
Tetradactylus	1	1	1	1	0	1	0
Tracheloptychus	1	0	1	1	0	1	0
Zonosaurus	1	1	1	1	0	1	0

TAXON	CHARACTER						
	C15	C16	C17	C18	C19	C20*	C21
Chamaesaura	0	1	1	0	1	1	1
Cordylus	0	1	0	1	1	1	1
Platysaurus	0	1	0	1	1	1	1
Pseudocordylus	0	1	0,1	1	1	1	1
Angolosaurus	?	0	0	0	1	0	0
Cordylosaurus	1	1	0	0	0	0	0
Gerrhosaurus	1	0	0	0	0	0	0
Tetradactylus	1	1	1	0	0	0	0
Tracheloptychus	1	1	0	0	0	0	0
Zonosaurus	1	0	0	0	0	0	0

TAXON	CHARACTER							
	C22	C23	C24	C25	C26	C27	C28*	C29
Chamaesaura	0	1	1	1	1	1	1	1
Cordylus	1	1	1	2	1	0	0	0
Platysaurus	1	1	1	2	1	0	1	0
Pseudocordylus	1	1	0,1	2	1	0	1	0
Angolosaurus	1	0	0	0	0	1	1	0
Cordylosaurus	1	0	0	0	1	1	1	0
Gerrhosaurus	1	0	0	0	0	1	1	0
Tetradactylus	1	0	0	0	0	1	1	1
Tracheloptychus	1	0	0	0	0	1	1	1
Zonosaurus	1	0	0	0	0	1	1	0

TAXON	CHARACTER							
	P1	P2*	P3	P4	P5	P6	P7	L1
Chamaesaura	1	1	1	1	1	0	0	1
Cordylus	2	1	0	1	1	1	0	1
Platysaurus	0	1	1	1	1	0	0	0
Pseudocordylus	0	1	0	1	1	1	0	1
Angolosaurus	0	0	0	0	0	1	1	0
Cordylosaurus	0	0	0	0	0	1	1	0
Gerrhosaurus	0	0	0	0	0	1	1	0
Tetradactylus	0	0	0	0	0	1	1	0
Tracheloptychus	0	0	0	0	0	0	1	0
Zonosaurus	0	0	0	0	0	0	1	0

TAXON	CHARACTER							
	M1	M2	M3	M4	M5	M6*	M7	M8
Chamaesaura	1	0	2	0	0	0	0	?
Cordylus	0	0,1	0	0,2	1	0	0,1	1
Platysaurus	0	0	2	0	1	0	0,1	1
Pseudocordylus	0	0,1	1	0	1	0	0	1
Angolosaurus	0	0	0	2	0	1	0	0
Cordylosaurus	0	0	0	2	0	1	0	0
Gerrhosaurus	0	0	0	2	0	1	0	0
Tetradactylus	0,1	0	0	2	0	1	0	0
Tracheloptychus	0	0	0	1	0	1	0	0
Zonosaurus	0	0	0	2	0	1	0,1	0

Appendix C : apomorphy and change list for preferred phylogenetic hypothesis.

In the first section of the following appendix is a list of the number of evolutionary changes at each node in the preferred hypothesis. Furthermore is a change list of the character transformation series and an apomorphy list for each node in the preferred hypothesis. The asterisk indicates unpolarized character transformations and charcter states. Nodes refer to cladogram of Fig. 18.

Node	Connected to node		Branch length
Chamaesaura	14	= Chamaesaurinae	13
Cordylus	13		6
Platysaurus	12		8
Pseudocordylus	12		3
Angolosaurus	17	= Angolosaurini	14
Cordylosaurus	15		9
Gerrhosaurus	16		0
Tetradactylus	15		4
Tracheloptychus	18		12
Zonosaurus	18		1
12	13	= Pseudocordylini	4
13	14	= Cordylinae	6
14	20	= Cordylidae	20
15	16	= Clade : *Cordylosaurus-Tetradactylus*	4
16	17	= Gerrhosaurini	3
17	19	= Gerrhosaurinae	4
18	19	= Zonosaurinae	7
19	20	= Gerrhosauridae	15
20 Outgroup		= Cordyliformes	9

Length = 141
Consistency index = 0.574

CHANGE LIST

Changed Character	From	To	Along branch
S1	0	1	17 → 16
	0	1	12 → *Pseudocordylus*
	0	1	14 → *Chamaesaura*
	0	1	in some *Cordylus* & *Platysaurus*
S2	0	1	19 → 18
S2(bis)	0	1	19 → 17

S3	0	1	14 → *Chamaesaura*
	0	1	in some *Cordylus*
S4	0	1	14 → *Chamaesaura*
	0	1	some *Cordylus* & *Pseudocordylus*
S5	0	1	16 → 15
S6*	0*	1*	18 → *Tracheloptychus*
	0*	1*	in some *Chamaesaura*, *Cordylus* *Platysaurus*, *Gerrhosaurus*, *Zonosaurus*
S7	0	1	Outgroup → 20
	1	0	17 → *Angolosaurus*
	1	0	13 → some *Cordylus*
S8	0	1	17 → 16
	0	1	18 → *Tracheloptychus*
	0	1	14 → *Chamaesaura*
S9	0	2	19 → 18
	0	1	15 → *Cordylosaurus*
S10	0	1	20 → 14
S11	0	1	20 → 19
	1	0	17 → *Angolosaurus*
	0	1	12 → *Pseudocordylus*
	0	1	in some *Cordylus* & *Platysaurus*
S12	0	1	13 → 12
	0	1	in some *Cordylus*
S13	0	1	Outgroup → 20
	1	0	17 → *Angolosaurus*
	1	0	12 → some *Platysaurus*
	1	0	14 → *Chamaesaura*
	?	?	in some *Zonosaurus*
S14*	0*	1*	17 → *Angolosaurus*
	0*	1*	in some *Cordylus*, *Platysaurus*, *Pseudocordylus*, *Gerrhosaurus*
S15	0	1	15 → *Cordylosaurus*
	0	1	in some *Cordylus* & *Platysaurus*
S16	0	1	18 → *Tracheloptychus*
	0	1	15 → *Cordylosaurus*
	0	1	17 → *Angolosaurus*
	0	1	in some *Tetradactylus*
S17*	0*	1*	19 → 17
S18	0	1	13 → 12
	1	2	in some *Platysaurus*
S19	0	1	17 → 16
	0	1	18 → *Tracheloptychus*
	1	0	15 → *Cordylosaurus*
	0	1	14 → *Chamaesaura*
	0	1	in some *Cordylus* & *Zonosaurus*
S20*	0*	1*	Outgroup → 20
	1*	0*	19 → 18
S21	0	1	18 → *Tracheloptychus*
	0	1	15 → *Cordylosaurus*
	0	1	17 → *Angolosaurus*
	0	1	13 → *Cordylus*
	0	1	in some *Platysaurus*, *Pseudocordylus*, *Gerrhosaurus*, *Zonosaurus*
	?	?	in some *Tetradactylus*
S22	0	1	18 → *Tracheloptychus*
	0	1	15 → *Tetradactylus*
	0	1	17 → *Angolosaurus*
	0	1	in some *Cordylus*, *Pseudocordylus*, *Gerrhosaurus*, *Zonosaurus*
S23	0	1	in some *Cordylus* & *Pseudocordylus*
	?	?	in some *Tetradactylus*
S24*	0*	1*	18 → *Tracheloptychus*
	0*	1*	15 → *Cordylosaurus*
	0*	1*	17 → *Angolosaurus*
	0*	1*	13 → *Cordylus*
	0*	1*	in some *Pseudocordylus*
	?	?	in some *Tetradactylus*
S25	0	1	20 → 19
	1	2	19 → 18
A1	0	1	18 → *Tracheloptychus*
	0	2	16 → 15
A2*	0*	3*	19 → 18
	3*	1*, 2*	18 → some *Zonosaurus*
	0*	1*	15 → *Tetradactylus*
	0*	3*	in some *Cordylus*
	0*	1*	in some *Gerrhosaurus*
A3	0	1	19 → 17
	0	1	12 → *Platysaurus*
A4	0	1	Outgroup → 20
	1	2	20 → 19
C1	0	1	20 → 19
	1	0	17 → *Angolosaurus*
C2	0	1	20 → 14
	0	1	17 → *Angolosaurus*
C3	0	1	20 → 19
	0	1	13 → 12
C4	0	1	20 → 14
C5	0	1	20 → 19
C6	0	1	20 → 14
	1	0	12 → *Platysaurus*
C7	0	1	20 → 19
C8	0	1	20 → 19
C9*	0*	1*	Outgroup → 20
	1*	0*	18 → *Tracheloptychus*
	1*	0*	17 → *Angolosaurus*
C10*	0*	1*	Outgroup → 20
	1*	0*	15 → *Cordylosaurus*
	1*	0*	17 → *Angolosaurus*
	1*	0*	12 → *Platysaurus*
C11	0	1	20 → 19
C12	0	1	20 → 14
C13	0	1	20 → 19
	1	0	15 → *Cordylosaurus*
	1	0	17 → *Angolosaurus*
C14	0	1	14 → 13
C15	0	1	20 → 19
C16	0	1	16 → 15
	0	1	20 → 14
	0	1	18 → *Tracheloptychus*
C17	0	1	15 → *Tetradactylus*
	0	1	14 → *Chamaesaura*
	0	1	in some *Pseudocordylus*
C18	0	1	14 → 13
C19	0	1	20 → 14
	0	1	17 → *Angolosaurus*
C20*	0*	1*	20 → 14
C21	0	1	20 → 14
	0	1	15 → *Cordylosaurus*
C22	0	1	Outgroup → 20
	1	0	14 → *Chamaesaura*
C23	0	1	20 → 14
C24	0	1	20 → 14
	1	0	12 → some *Pseudocordylus*

C25	0	1	20 → 14
	1	2	14 → 13
C26	0	1	20 → 14
	0	1	15 → *Cordylosaurus*
C27	0	1	Outgroup → 20
	1	0	14 → 13
C28*	0*	1*	Outgroup → 20
	1*	0*	13 → *Cordylus*
C29	0	1	18 → *Tracheloptychus*
	0	1	15 → *Tetradactylus*
	0	1	14 → *Chamaesaura*
P1	0	1	20 → 14
	1	0	13 → 12
	1	2	13 → *Cordylus*
P2*	0*	1*	20 → 14
P3	0	1	12 → *Platysaurus*
	0	1	14 → *Chamaesaura*
P4	0	1	20 → 14
P5	0	1	20 → 14
P6	0	1	19 → 17
	0	1	14 → 13
	1	0	12 → *Platysaurus*
P7	0	1	20 → 19
L1	0	1	20 → 14
	1	0	12 → *Platysaurus*
M1	0	1	14 → *Chamaesaura*
	0	1	in some *Tetradactylus*
M2	0	1	in some *Cordylus* & *Pseudocordylus*
M3	0	1	20 → 14
	1	2	12 → *Platysaurus*
	1	0	13 → *Cordylus*
	1	2	14 → *Chamaesaura*
M4	0	2	20 → 19
	2	1	18 → *Tracheloptychus*
	0	2	in some *Cordylus*
M5	0	1	14 → 13
M6*	0*	1*	20 → 19
M7	0	1	in some *Cordylus*, *Platysaurus* & *Zonosaurus*
M8	0	1	20 → 14

APOMORPHY LISTS

Node	Outgroup	Character	Ancestral state	Derived state
Chamaesaura	NODE 14	S1	0	1
		S3	0	1
		S4	0	1
		S8	0	1
		S13	1	0
		S19	0	1
		C17	0	1
		C22	1	0
		C29	0	1
		P3	0	1
		M1	0	1
		M3	1	2
In some :		S6*	0*	1*
Cordylus	NODE 13	S21	0	1
		S24*	0*	1*
		C28*	1*	0*
		P1	1	2
		M3	1	0
In some :		S1	0	1
		S3	0	1
		S6	0	1
		S7	1	0
		S11	0	1
		S12	0	1
		S14*	0*	1*
		S15	0	1
		S19	0	1
		S22	0	1
		S23	0	1
		A2*	0*	3*
		M2	0	1
		M4	0	2
		M7	0	1
Platysaurus	NODE 12	A3	0	1
		C6	1	0
		C10*	1*	0*
		P3	0	1
		P6	1	0
		L1	1	0
		M3	1	2
In some :		S1	0	1
		S6*	0	1
		S11	0	1
		S13	1	0
		S14*	0*	1*
		S15	0	1
		S18	1	2
		S21	0	1
		M7	0	1
Pseudocordylus	NODE 12	S1	0	1
		S11	0	1
		C24	1	0
In some :		S4	0	1
		S14*	0*	1*
		S21	0	1
		S22	0	1
		S23	0	1
		C17	0	1
		C24	1	0
		M2	0	1
Angolosaurus	NODE 17	S7	1	0
		S11	1	0
		S13	1	0
		S14*	0*	1*
		S16	0	1
		S21	0	1
		S22	0	1
		S24*	0*	1*
		C1	1	0
		C2	0	1
		C9*	1*	0*
		C10*	1*	0*
		C13	1	0
		C19	0	1
Cordylosaurus	NODE 15	S9	0	1
		S15	0	1

		S16	0	1
		S19	1	0
		S21	0	1
		S24	0	1
		C10*	1*	0*
		C13	1	0
		C21	0	1
		C26	0	1
Gerrhosaurus	NODE 16			
	Some :	S6*	0*	1*
		S14*	0*	1*
		S21	0	1
		S22	0	1
Tetradactylus	NODE 15	S22	0	1
		A2*	0*	1*
		C17	0	1
		C29	0	1
In some :		S16	0	1
		S21	?	?
		S22	?	?
		S23	?	?
		M1	0	1
Tracheloptychus	NODE 18	S6*	0*	1*
		S8	0	1
		S16	0	1
		S19	0	1
		S21	0	1
		S22	0	1
		S24*	0*	1*
		A1	0*	1*
		C9*	1*	0*
		C16	0	1
		C29	0	1
		M4	2	1
Zonosaurus	NODE 18			
In some :		S6*	0*	1*
		S13	0	1
		S19	0	1
		S21	0	1
		S22	0	1
		A2*	3*	1*,2*
		M7	0	1
NODE 12	NODE 13	S12	0	1
= Cordylini		S18	0	1
		C3	0	1
		P1	1	0
NODE 13	NODE 14	C14	0	1
= Cordylinae		C18	0	1
		C25	1	2
		C27	1	0
		P6	0	1
		M5	0	1
NODE 14	NODE 20	S10	0	1
= Cordylidae		C2	0	1
		C4	0	1
		C6	0	1
		C12	0	1
		C16	0	1
		C19	0	1
		C20*	0*	1*
		C21	0	1
		C23	0	1
		C24	0	1
		C25	0	1
		C26	0	1
		P1	0	1
		P2*	0*	1*
		P4	0	1
		P5	0	1
		L1	0	1
		M3	0	1
		M8	0	1
NODE 15	NODE 16	S5	0	1
= Clade : *Cordylosaurus-*		A1	0	2
Tetradactylus		C16	0	1
NODE 16	NODE 17	S1	0	1
= Gerrhosaurini		S8	0	1
		S19	0	1
NODE 17	NODE 19	S2(bis)	0	1
= Gerrhosaurinae		S17*	0*	1*
		A3	0	1
		P6	0	1
NODE 18	NODE 19	S2	0	1
= Zonosaurinae		S9	0	2
		S20*	1*	0*
		S25	1	2
		A1	0	1
		A2*	0*	3*
NODE 19	NODE 20	S11	0	1
= Gerrhosauridae		S25	0	1
		A4	1	2
		C1	0	1
		C3	0	1
		C5	0	1
		C7	0	1
		C8	0	1
		C11	0	1
		C13	0	1
		C15	0	1
		P7	0	1
		M4	0	2
		M6*	0*	1*
NODE 20	Outgroup	S7	0	1
= Cordyliformes		S13	0	1
		S20*	0*	1*
		A4	0	1
		C9*	0*	1*
		C10	0*	1*
		C22	0	1
		C27	0	1
		C28*	0*	1*

Appendix D : algorithm for outgroup comparison.

For an ingroup and 3 outgroups (OT), 6 distribution patterns of character states with subsequent polarity decisions are possible (Fig. 41). The methodology for the determination of polarities follows that of Maddison *et al.* (1984) and is further discussed in methods and materials section. The position of the remaining squamates is indicated by ROT (See also Table 1).