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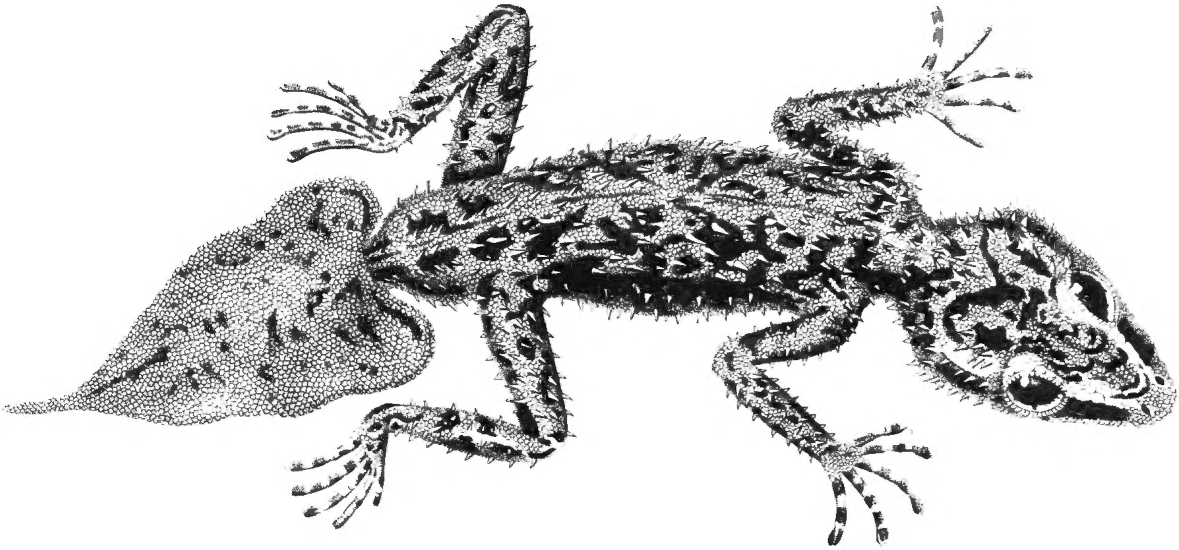

BRISBANE
20 SEPTEMBER, 1990

MEMOIRS OF THE
QUEENSLAND MUSEUM

VOLUME 29
PART 2

Preface

Most of these papers and notes were presented at the Australian Bicentennial Herpetological Conference held at the Queensland Museum, Brisbane, on 17–20 August, 1988. A handful were received subsequently and judged suitable for inclusion in the proceedings.

Publication costs have been borne by the conference participants, the Australian Society of Herpetologists and the Board of Trustees of the Queensland Museum. The Queensland Museum generously supported the conference from concept to conclusion, so it is especially appropriate that the conference papers be published in a special issue of the *Memoirs of the Queensland Museum*.

Production headaches and the attendant effort, and anxiety were cheerfully and willingly borne by Glen Ingram, Editor, and Neale Hall, Typesetter. Their diligence and patience have ensured the highest standards of presentation throughout.

Peter Jell, Wayne Longmore, Peter Davie, Patrick Couper, Kim Easterbrook and Liza Hug also assisted in either running the conference successfully, or in the production of this memoir, or both.

This is a fine collection of papers, clearly and concisely presented. A wealth of interesting and important new information is contained in these pages, all devoted to what are, without any doubt, the most fascinating elements of the Australian fauna.

Without wishing to reveal my further bias, may I commend it to you?

Jeanette Covacevich,
President,
Australian Society of Herpetologists Inc.,
Senior Curator (Vertebrates),
Queensland Museum.
22 August, 1990.

Delegates to the Australian Bicentennial Herpetological Conference, 17-20 August, 1988, assembled in the Dinosaur Garden of the Queensland Museum with Bette the giant Cane Toad.

MEMOIRS
OF THE
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ALTERNATIVE DIGITAL SCANSOR DESIGN IN THE NEW CALEDONIAN GEKKONID GENERA *BAVAYIA* AND *EURYDACTYLODES*

AARON M. BAUER AND ANTHONY P. RUSSELL

Bauer, A.M. and Russell, A.P. 1990 09 20: Alternative digital scansor design in the New Caledonian gekkonid genera *Bavayia* and *Eurydactylodes*. *Memoirs of the Queensland Museum* **29**(2): 299-310. Brisbane. ISSN 0079-8835.

Gekkonid feet are complex and highly integrated functional units. Convergence and parallelism are common themes in gecko digital design. Alternatively, closely related geckos may exhibit widely differing toe morphologies within a framework of phylogenetic constraint.

The New Caledonian carphodactyline geckos *Bavayia* and *Eurydactylodes* are closely related to one another yet they exhibit marked differences in external digital form. *Bavayia* possesses divided scansors and a highly arcuate penultimate phalanx. In *Eurydactylodes* the scansors are undivided and the penultimate phalanx is not raised. Internally *Bavayia* has a divided vascular sinus and a region of adipose tissue which helps to distribute forces laterally in conjunction with the divided pad. Proximally the digits of *Bavayia* are filled with adipose tissue which provides passive support and conformation for the non-scansorial friction pads. In *Eurydactylodes* a huge vascular sinus transduces forces directly from the penultimate phalanx.

Differences in scansor morphology between the taxa are related to the differences in control mechanisms of single versus divided pads. The functional significance of the alternative scansor designs is unclear, but the divided scansors of *Bavayia* may have played a role in the relative success of the genus in New Caledonia. ☐ *Gekkonidae, Carphodactylinae, Bavayia, Eurydactylodes, digits, scansors, functional morphology, evolutionary constraint.*

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The scansors of the gekkonid foot are extremely complex and highly integrated functional units (Dellit, 1934; Russell, 1972, 1975, 1976, 1979, 1981, 1986). The adhesive ability of geckos is dependent not only upon the setal microstructures that interact with the substrate (Hiller, 1968, 1969, 1975), but also upon internal features of the scansors that transmit forces to the seta-bearing surfaces (Russell, 1975, 1981) and permit the distribution of forces associated with weight-bearing (Russell, 1986).

The precise nature of the organisation of components of the musculo-skeletal and circulatory systems, as well as connective and adipose tissues varies among the taxa studied to date. Distantly related taxa, however, often cope with similar locomotory demands (frequently substrate related) in near identical fashion. This has been well-documented in the case of ecologically equivalent members of the subfamilies Gekkoninae and Diplodactylinae (Russell, 1979) and has even resulted in parallel radiations of geckos in these groups on the basis of key innovations (sensu Liem and Osse, 1975) in pedal structure and scansor architecture. Within a single subfamily, similar convergences have also been noted in genera occupying similar spatial niches or exploiting particular substrates (e.g. Russell, 1976). Indeed, a particular morphology, such as that characterising 'leaf-toed' geckos, may have been independently derived in many lineages (Russell and Bauer, 1989).

Conversely, even closely related taxa may exhibit a diversity of digital forms within the constraints of shared descent (see Brundin, 1968). Russell (1976), for example, demonstrated a morphotypic series in digital design and complexity in the gekkonine genera *Pachydactylus* and *Hemidactylus*. Both of these genera are speciose and ecologically diverse and exhibit variations in both external and internal digital design.

The subfamily Diplodactylinae is less speciose than the Gekkoninae and much more geographically circumscribed, with all taxa occurring in the Southwest Pacific (Australia, New Zealand and New Caledonia). None the less, there is great ecological diversity in the group, which includes burrowers, terrestrial forms and arboreal species. Like marsupials, the diplodactylines represent an ancient independent lineage which includes major radiations to some extent comparable to those of their more widespread relatives.

The parallels between the Diplodactylinae and Gekkoninae are striking (Russell, 1979) but the analysis of the diplodactyline radiations is interesting in its own right. Unfortunately, few studies have examined diplodactyline morphology to date. Russell (1972, 1979) examined the pedal morphology of several species in the Diplodactylinae, but his data were derived almost exclusively from gross dissection. Further, Russell lacked an explicit hypothesis of relationship among the diplodactylines upon which he could interpret the observed anatomy. Such an hypothesis is essential if the evolutionary and ecological significance of morphologies are to be evaluated in a phylogenetic context (Lauder, 1981, 1982).

In this paper we examine aspects of digital scansor morphology in representatives of the New Caledonian genera *Bavayia* and *Eurydactylodes*, two closely related diplodactyline geckos in the tribe Carphodactylini. Although Underwood (1954) initially placed the two genera in different subfamilies, he later (Underwood, 1955) reconsidered the affinities of *Eurydactylodes* and placed both genera in his Diplodactylinae. Kluge (1965, 1967) accepted the affinities of these taxa and their close relationship to a third New Caledonian genus, *Rhacodactylus* and included all three in the tribe Carphodactylini. Bauer (1986), on the basis of a morphologically- based cladistic analysis, proposed a specific pattern of relationships among these three taxa (Fig. 1). Although a characteristic previously thought to be diagnostic of the Gekkoninae (sensu Kluge, 1987), the presence of extracranial endolymphatic calcium deposits, has since been identified in *Eurydactylodes* (Bauer, 1989), the overwhelming evidence of other characters suggests that the New Caledonian endemic geckos are indeed closely related. Despite this affinity, the external digital morphology of *Bavayia* and *Eurydactylodes* is markedly different. *Bavayia* is characterised by divided scansors and highly arcuate distal phalanges while the latter possesses single

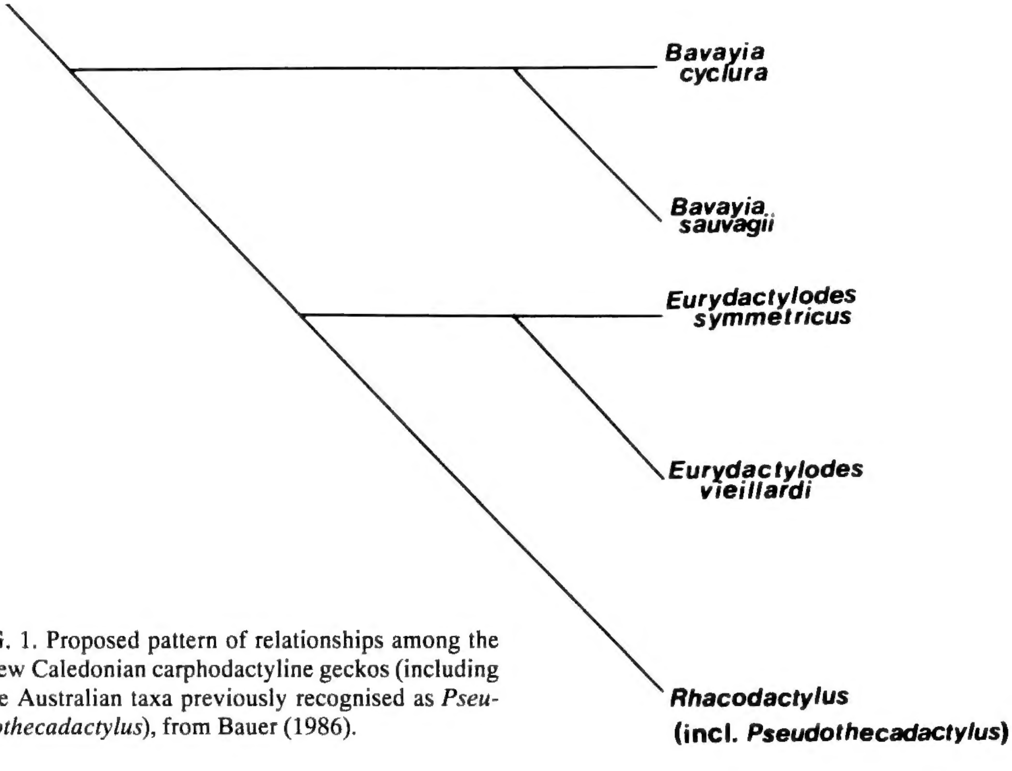

FIG. 1. Proposed pattern of relationships among the New Caledonian carphodactyline geckos (including the Australian taxa previously recognised as *Pseudothecadactylus*), from Bauer (1986).

subdigital plates and a less markedly raised penultimate phalanx. Outward variation of this nature in the Gekkoninae is generally indicative of major design differences in internal anatomy and consequent functional differences (see Russell, 1972, 1976, 1979). We here assess the specific anatomical differences exhibited by *Bavayia* and *Eurydactylodes* and evaluate significance (if any) of alternative digital designs within the well circumscribed New Caledonian carphodactyline lineage.

MATERIALS AND METHODS

Specimens examined in this study were collected by the senior author in New Caledonia under the authority of the Service des Eaux et Forêts and have been deposited in the California Academy of Sciences (CAS). In addition, specimens were also examined in the collections of several museums, most notably, the Australian Museum (AMS), the Naturhistorisches Museum Basel (NHMB), the Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK), and the British Museum (Natural History) (BMNH).

Gross external observations and dissections were carried out on formalin-fixed, alcohol preserved museum specimens of *Bavayia* and *Eurydactylodes*. Radiographs of selected specimens were prepared using a self-contained x-ray unit.

Cleared-and-stained preparations were made following a modification of the protocol of Wassersug (1976). Specimens for light microscopy were decalcified, dehydrated, cleared and embedded in paraffin. Sections were cut on a rotary microtome at thicknesses of 8–12μm and stained according to the protocol for Mallory's azan trichrome stain (Humason, 1979). Photomicrographs were prepared with a Wild compound microscope with 35 mm photo attachment. Specimens for scanning electron microscopy were dehydrated through a graded alcohol series, critical point dried and sputter-coated to a thickness of 30nm with gold-palladium alloy before examination with an ISI-DS 130 microscope.

RESULTS

EXTERNAL ANATOMY OF THE DIGITS

Eurydactylodes

The digits of *Eurydactylodes symmetricus* and *E. vieillardi* are essentially identical in form. The following description is based primarily upon specimens of the latter taxon. The digits are short and broadly dilated. Small fleshy webs are present between digits II and III and III and IV. The penultimate phalanges of digits II -V are mostly subsumed within their respective pads and the claw is carried only a short distance beyond the distal margin of the scansors. The ungual phalanx is firmly connected to the dorsum of the pad by a fleshy sheath. Digits II -V of the manus fan out broadly whereas the first four of the pes are bound together at the level of the metatarsals, restricting the spread of the digits.

The ventral surface of the pads of digits II - IV bear a series of broad scansorial plates that are generally straight proximally and somewhat chevron-shaped distally (Fig. 2A). Proximally, the scansors grade into enlarged subdigital scales that terminate at the level of the proximal portion of the first phalanx and are replaced by small non-setose scales similar to those of the palms. The proximalmost plates are generally non scansorial (sensu Russell, 1975) but do bear setae. There are typically 10 - 12 expanded plates under the fourth (longest) toe in both species.

Digit one is small and bears a series of about five small friction pads proximal to the minute claw. The claw itself is sheathed and is bordered both laterally and medially by small terminal plates. Unlike all other New Caledonian and New Zealand carphodactylines (Bauer, 1986) these plates are completely separated from one another. The medial plate is substantially larger than the lateral (Fig. 2D).

Bavayia

The digits of *Bavayia cyclura* are moderately elongate and broadly dilated distally. As in *Eurydactylodes* the claws of digits II - V extend beyond their respective pads, but are firmly anchored to them by cutaneous sheaths. The penultimate phalanx is very strongly arcuate and rises well above the plantar surface of the pad. Small webs connect the bases of digits II and III, III and IV and IV and V. As in all New Caledonian and New Zealand carphodactylines, metatarsals of digits I - IV are joined, reducing the digital spread of the pes (Fig. 3).

All enlarged subdigital plates except the distalmost are divided and the pairs are strongly angled so that the medial ends meet at the midline far proximal to the lateral termini (Fig. 2B). At about the level of the antepenultimate phalanx the more distal true scansors (defined on their internal morphology - see below) give way to

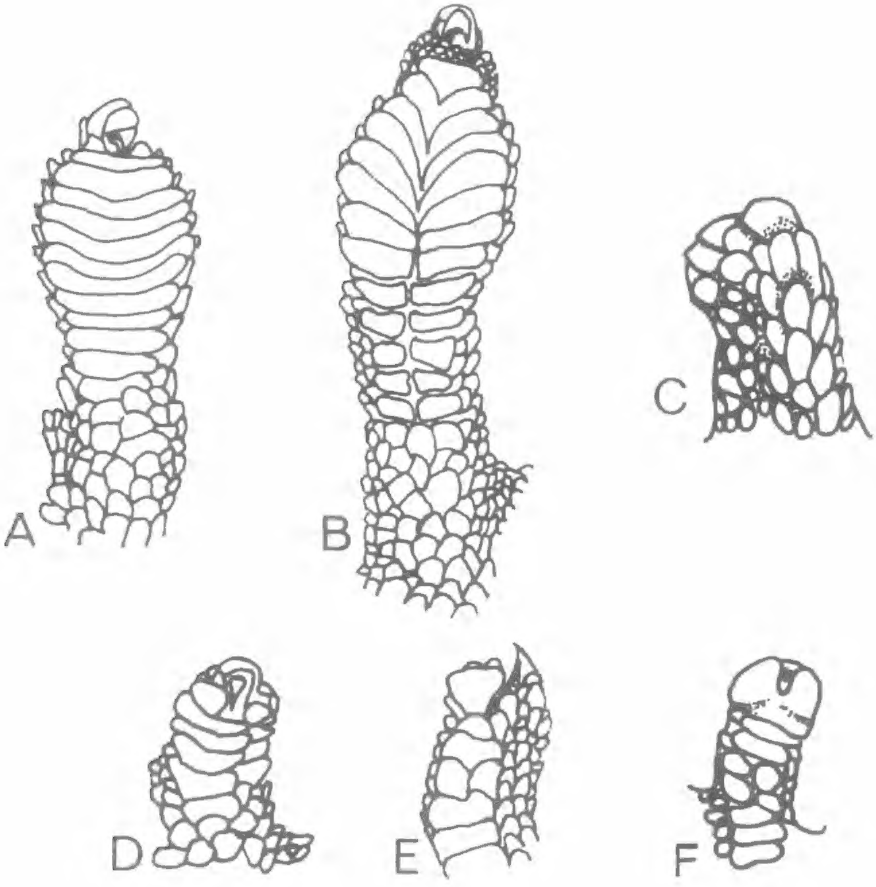

FIG. 2.A. *Eurydactylodes vieillardi* (BMNH 1926.9.17.7), digit III, right pes. B. *Bavayia sauvagii* (BMNH 1926.9.17.25), digit IV, left pes. C. *Bavayia sauvagii* (CAS 159532), digit I, right pes, dorsal view. D. *Eurydactylodes vieillardi* (BMNH 1926.9.17.7), digit I, right pes. E. *Bavayia sauvagii* (BMNH 1926.9.17.25), digit I, left pes. F. *Bavayia cyclura* (CAS 159550), digit I, right pes. Note the architecture of the subdigital plates in A and B and the disposition of the terminal plates in D - F.

simple friction pads. At the metapodial/phalangeal joints the friction pads grade into irregular smaller scales which, in turn, grade into the palmar scales.

Digit I of both manus and pes is reduced and carries a series of undivided friction plates, but no expanded pad. In contrast to those of the remaining digits, the claw of digit I is minute. It is bordered by a large, cleft terminal plate which is asymmetrical, bearing a larger medial pad (Fig. 2F). A diastema separates the terminal plates from the basal friction plates, which extend well onto the palmar surface.

The digits of *Bavayia sauvagii* are similar in most respects to those of their congeners but are somewhat more elongate and less broad. The scansor pairs of digits II - V are separated by a somewhat broader gap than are those of *B. cyclura* and break up into small scales somewhat more distally. Digital setae are longest at the free margins of the lamellae and appear to be better developed on the true scansors than on the friction plates (Fig. 4). Most notably, the terminal plate of digit I is entirely medial to the claw (Fig. 2E). In dorsal view the claw of this digit appears completely sheathed (Fig. 2C).

INTERNAL ANATOMY OF THE DIGITS

Eurydactylodes

The musculo-skeletal system of *Eurydactylodes* and *Bavayia* are essentially identical to that described by Russell (1972, 1979) for the

FIG. 3. Ventral view of the left pes of *Bavayia sauvagii* (CAS 159532) showing the metatarsal binding of the first four digits. Scale bar = 1mm.

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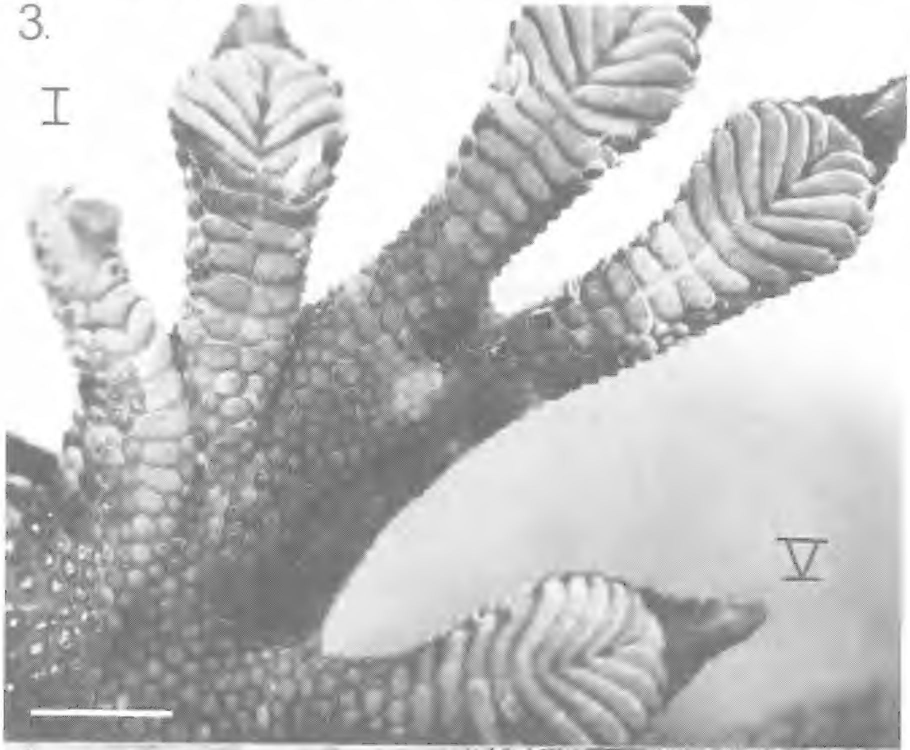

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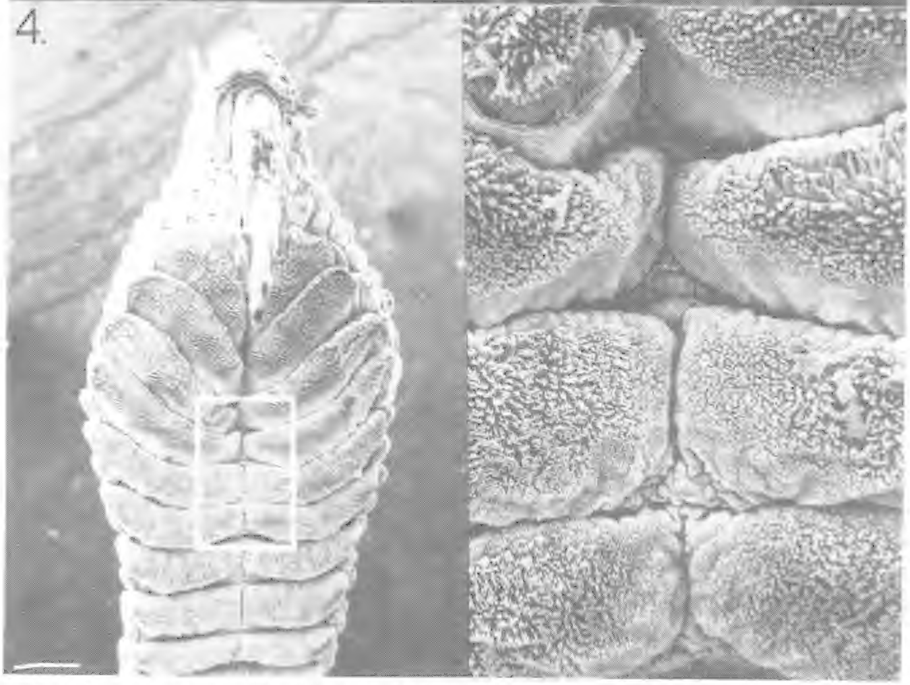

FIG. 4. Scanning electron micrograph of digit IV, right pes of *Bavayia cyclura* (no catalogue number) illustrating the median scansor cleft and the relative decrease in the depth of setal pile near the midline of the toe. Scale bar = 300μm (right side shows 5 X enlargement of box on left).

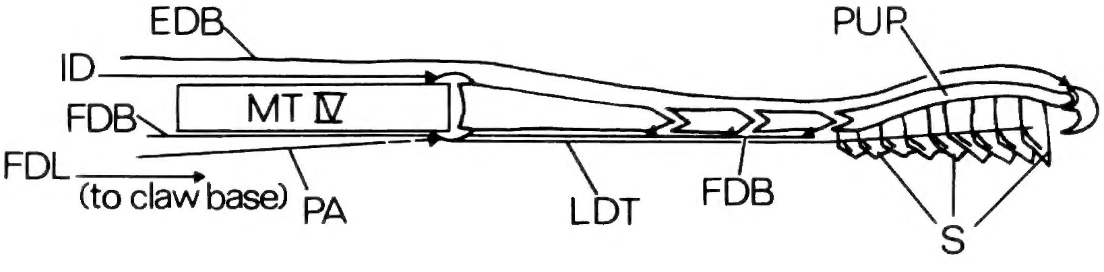

FIG. 5. Diagrammatic representation of the musculo-tendinous system of digit IV of a generalised New Caledonian carphodactyline gecko. EDB = extensor digitorum brevis, FDB = flexor digitorum brevis, FDL = flexor digitorum longus, ID = interossei dorsales, LDT = lateral digital tendon, MT IV = fourth metatarsal, PA = plantar aponeurosis, PUP = penultimate phalanx, S = scansors. Arrows indicate points of attachment of muscles and tendons.

closely related genus *Rhacodactylus*. The phalangeal formulae are unreduced (2-3- 4-5-3 manus, 2-3-4-5-4 pes). The penultimate phalanx is cylindrical in section and arches over the broadest part of the pad. The first phalanx is generally also cylindrical. Intermediate phalanges are strongly depressed and barbell-shaped, with broad epiphyseal surfaces.

The dorsal extensor musculature consists of two asymmetrically developed bellies for each digit. Each pair of bellies sends a tendon to the middorsal region of its respective ungual phalanx. The dorsal interossei muscles reach only the level of the metapodial elements and do not send out tendons to the phalanges. Ventrally, lateral digital tendons extend from the metapodial- phalangeal joint capsule to the proximal borders of each of the true scansors. Digital flexor muscles run in parallel with the lateral digital tendons and insert on the distal ends of the phalanges (except the ungual and penultimate phalanges; the long flexor muscle inserts on the lower part of the base of the ungual phalanx). In addition, the base of the digits receive slips from the femorotibial gastrocnemius (see Fig. 5 for a diagrammatic summary of the muscular and tendinous components of the digit).

Internally, the scansor-bearing digits (II - V) of *Eurydactylodes vieillardi* are typified by the presence of an extensive digital sinus system consisting of a large central sinus and a reticular network (Figs. 6, 7) supplying both the medial and lateral portions of the scansors with vascularization in association with scansorial control (see Russell, 1981). True scansors are present beneath the penultimate phalanx as well as the more proximal phalanges. There is a minimal amount of loose connective tissue in the toe, and no adipose deposits were evident in histological sections.

Bavayia

The external differences between *Bavayia cyclura* and *B. sauvagii* are not manifested in the internal structure of the digits. In both taxa the proximal portion of the digit is largely filled with connective tissue invested with adipose cells (Fig. 8). This condition extends as far distally as the level of the penultimate phalanx where true scansors are located. In the region of the scansors lies a central blood sinus which has two lateral chambers, one on either side of the midline scansor cleft (Fig. 9). In all areas of the toe connective tissue, usually containing adipose deposits, occupies the dorsal portion of the pad and the lateral portions of the scansorial plates themselves.

DISCUSSION

PHYLOGENETIC CONSTRAINTS

The observable morphologies of living organisms are strongly influenced by the history of the taxa that possess them (Lauder, 1982). The influence of past environmental factors on form and function of organ systems should thus be reflected in descendent taxa, and taxa with shared descent should exhibit certain such historical features, or constraints, in common.

Eurydactylodes and *Bavayia* appear to share a number of digital features as a result of common descent. In common with *Rhacodactylus* (including *Pseudothecadactylus*), *Hoplodactylus* and *Naultinus*, metatarsals I - IV, especially III and IV are parallel to one another, thus reducing digital spread (Russell, 1972; Bauer, 1986). These genera also share a 'simplified' muscular system in which the distal phalanges are free of the fleshy portions of the flexor and extensor muscles. Likewise, the digits receive no direct

FIG. 6. Cross-section through the fourth digit, right pes of *Eurydactylodes vieillardi* (ZFMK 16113) under the anterior portion of the penultimate phalanx. Note the many vascular lacunae (marked with X's) that are components of the reticular network of vessels that regulates and transduces pressure within the scansors. Abbreviations as in Figure 5. Scale bar = 250μm.

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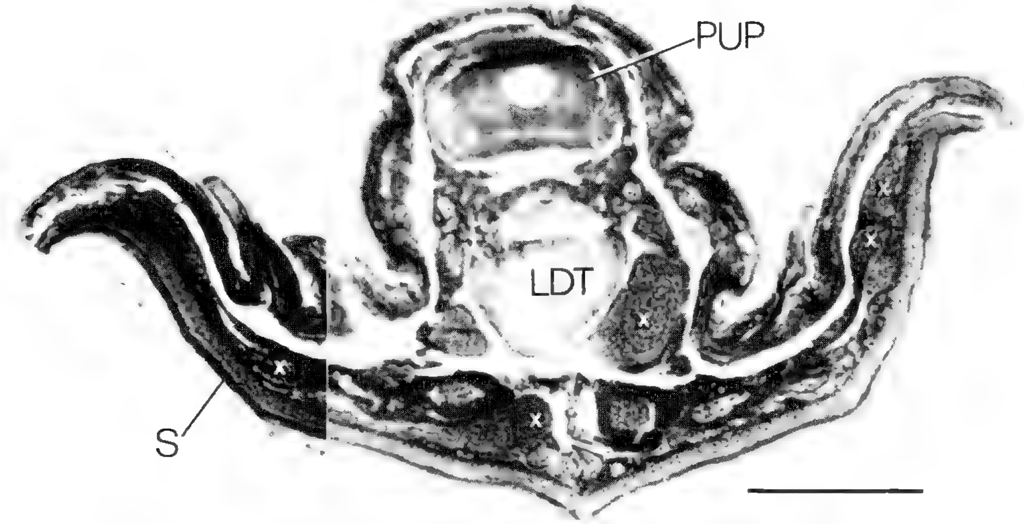

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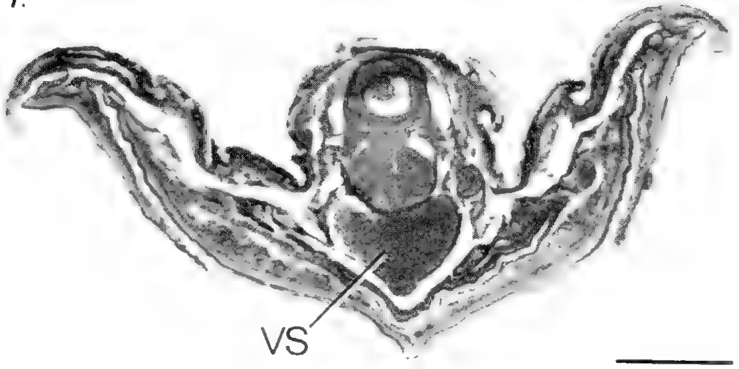

FIG. 7. Cross-section slightly proximal to Figure 6 showing the large central vascular sinus (VS) typical of *Eurydactylodes*. Note the absence of adipose tissue. Scale bar = 250μm.

tendinous slips from the dorsal interossei muscles. The presence of small, asymmetrical terminal plates on digit I is also a synapomorphy of the padded genera of carphodactylines (Bauer, 1986). At a more restrictive level, that of the broader padded carphodactylines, *Bavayia* and *Eurydactylodes* share the extreme flattening of intermediate phalanges.

ALTERNATIVE DESIGNS

The major differences in the digital morphology of *Bavayia* and *Eurydactylodes* are directly related to the scansors themselves, namely external scansor form and the internal support system of the scansors and friction pads. The autapomorphic condition of the completely divided apical plates of *Eurydactylodes* (Fig. 2D) seems unlikely to be of functional significance.

Russell (1979) associated scansor division with the dissociation of the penultimate phalanx from the pad of the toe. In gekkonines scansor division is associated with the division of the blood sinus into two large lateral branches (Dellit, 1934; Russell, 1976, 1979), ensuring intimate contact despite the lessening of the direct pressure link through the penultimate phalanx. Russell and Bauer (1988) have demonstrated that this pattern is also generally associated with the inception of some sort of paraphalangeal support for the lateral regions of the pad, probably associated with the transmission of force to the sinus in the absence of a direct phalangeal transmission system. Scansors directly beneath the midline are subsequently lost with the absence of an effective scansor control mechanism in that region. The highly arcuate penultimate phalanx of *Bavayia* spp. seems to function to some degree in this manner, although here the sinus is only truly divided dorsal to the distalmost scansors. More proximally the central sinus sends two subdivisions out to the scansor pairs (Fig. 9). Although somewhat free of the pad, the penultimate phalanges of *Bavayia* are much less independent than in some gekkonines such as *Gehyra*. *Eurydactylodes*, on the other hand, with its undivided scansors possesses an undivided central sinus and the penultimate phalanx, although arcuate, is not strongly so.

In addition to the subdivision of the scansors the two genera also differ in the distribution of adipose tissue in the digit and the extent of the vascular network. In *Eurydactylodes* there is very little adipose tissue, and the posterior expansion of large blood lacunae is suggestive of a posterior extension of the scansors (sensu Russell, 1975). In *Bavayia*, on the other hand, the scansors are limited to the area under the penultimate phalanx and the remainder of the expanded plates are filled with adipose tissue as is the entire dorsal surface of the toe. A subdigital adipose zone has been reported in the other New Caledonian genus, *Rhacodactylus* (Russell, 1972, 1979; Bauer, 1986) where it runs in the midline of the toe, the area equivalent to the scansorial cleft in *Bavayia*. Adipose cells also fill the posterior portion of the pad in *Rhacodactylus*. In *Rhacodactylus*, however, adipose tissue has not been associated with regions dorsal to the scansors in the lateral regions of the pad. The fat channel in *Rhacodactylus* appears to be a semi-controllable mechanism for the conformation of the pad to the substrate in the midline. The combination of vascular and adipose tissue as a means of control and/or mechanism of conformity of the scansors thus appears to be a general feature of the New Caledonian carphodactylines (it may be independently derived in *Bavayia* and *Rhacodactylus*, or lost in *Eurydactylodes*). The combination of the two systems (vascular and adipose) deep to the scansors of *Rhacodactylus* may be a solution to the problem of support in extremely wide (in both relative and absolute terms) digits. The problem of support in the much smaller digits of *Bavayia* and *Eurydactylodes* has been solved in different ways.

In *Eurydactylodes* the digits, though wide relative to the animal's size, are tiny in absolute terms. Here the sinus is so large in relation to the pad that it is able to provide active control of the scansors in the absence of adipose deposits. The less arcuate penultimate phalanx of this taxon retains the ability to efficiently transduce forces onto a single, central vascular sinus (see Fig. 10A) which regulates pressure throughout the scansors by way of a reticular vascular network.

In *Bavayia* pad control is achieved by pad division and concomitant vascular modification (Fig. 10B). The high arch of the penultimate phalanx probably precludes the direct use of a central adipose core as seen in *Rhacodactylus*, and the median scansors are lost in favour of the dual scansor control mechanism. With the divisions of the subdigital plates and the elevated penultimate phalanx comes the requirement for lateral support of the pad, as the control mechanisms become at least partly restricted to one side of the digit or the other. Among divided-scansored gekkonines the position dorsal to the divided sinuses may be filled with adipose tissue, as in *Thecadactylus* or with incipient paraphalanges, as in *Homopholis* (Russell and Bauer, 1988). Clearly, a number of solutions to the problem of transducing pressure onto the lateral scansors are possible. *Bavayia*, starting with a diplodactyline or, more specifically, a carphodactyline heritage (and its concomitant constraints) has solved the problem by maintaining a partially undivided sinus (thus allowing some central transduction of force from the penultimate phalanx) and by utilising a dorsal adipose zone to distribute pressure laterally. Basally in the digits, proximal to the scansors, extensive fat deposits are also present (Fig. 9) and *Bavayia* thus maintains at least some passive control of the mechanism of substrate conformation in the series of friction plates.

FUNCTION

There is little information available about the biology of New Caledonian geckos, especially those of the genus *Eurydactylodes*. As far as is known, both *Eurydactylodes* species are exclusively arboreal (Roux, 1913; Meier, 1979) and seem to prefer branches of small diameter. *Bavayia cyclura* dwells primarily on trees or in

FIG. 8. Cross-section through the proximal portion of digit IV, right pes of *Bavayia sauvagii* (author's collection, AMB 267) showing the adipose zone (AZ) beneath the phalanx and above the friction plates (FP). Adipose invested connective tissue also fills much of the remainder of the digit. Scale bar = 250μm.

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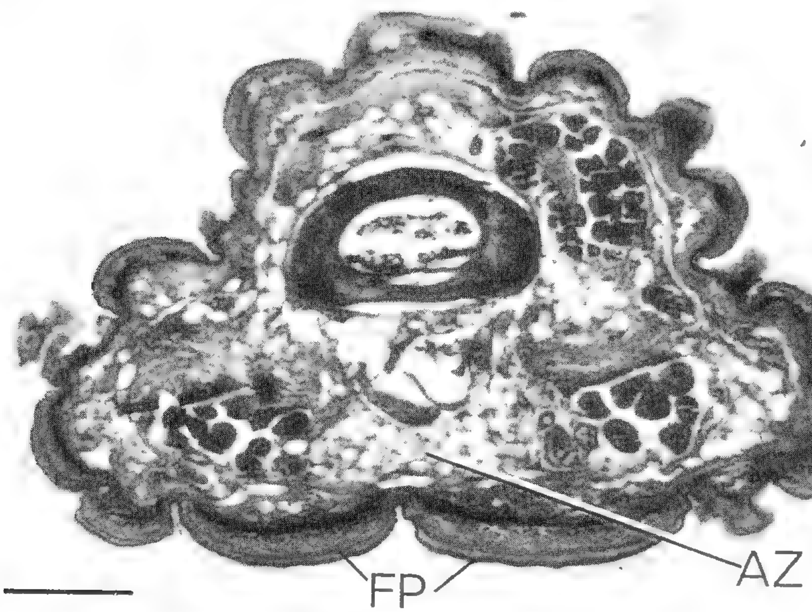

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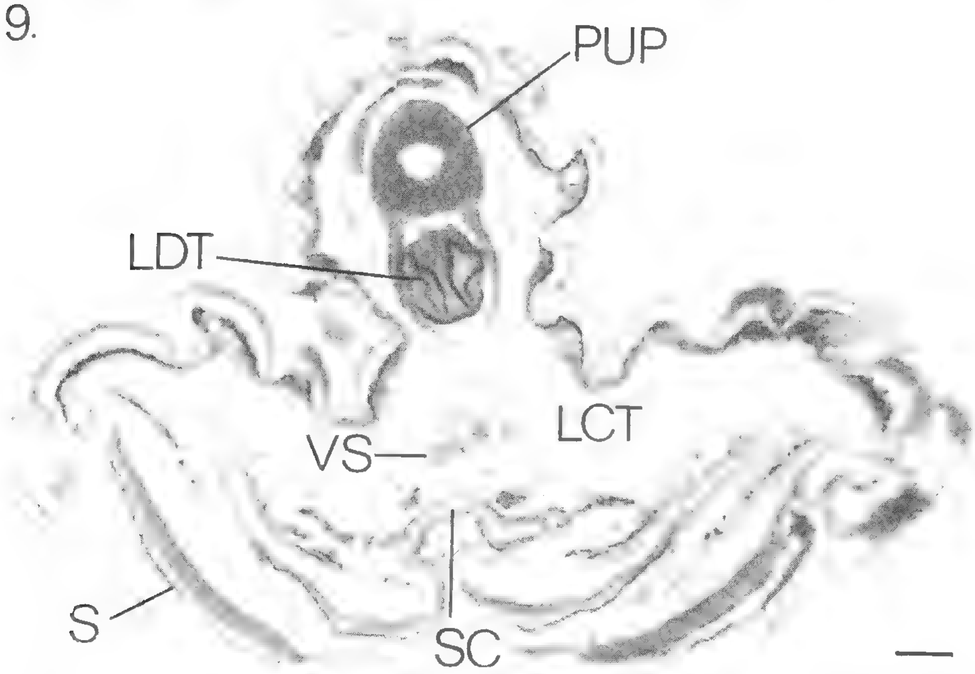

FIG. 9. Cross-section through digit IV, right pes of *Bavayia sauvagii* (AMB 506) at the level of the penultimate phalanx. Note the division of the vascular sinus into two lateral branches on either side of the scansor cleft (SC) and the presence of loose connective tissue (LCT) containing adipose deposits above the branches of the sinus. Other abbreviations as in Figure 5. Scale bar = 250μm.

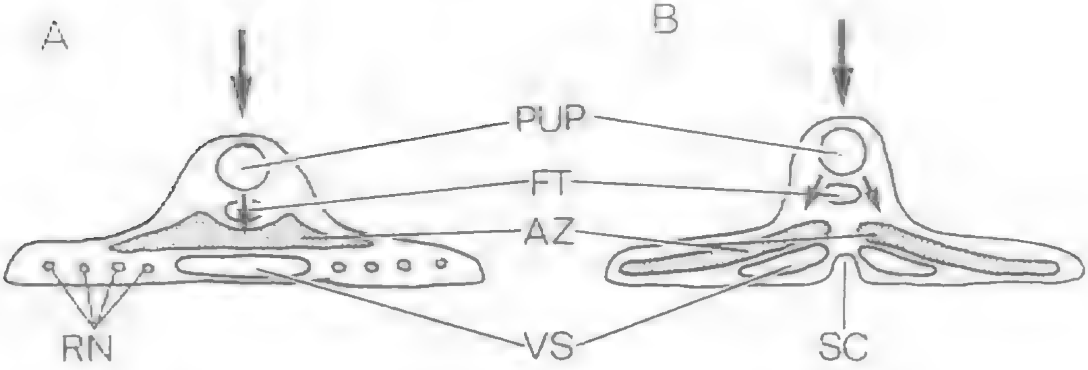

FIG. 10. Diagrammatic sections through the distal portions of the digits of A. *Rhacodactylus/Eurydactylodes* (adipose zone would be lacking in the latter) type toe and B. *Bavayia* type toe. In A forces are transduced directly to the sinus or through the adipose zone to the sinus through the midline of the toe. An extensive reticular network of blood vessels (RN) is present. In B some transduction of pressure is direct while the remainder is spread through the adipose zone. FT = flexor tendon. Other abbreviations as in previous figures.

logs and stumps (Roux, 1913; Meier, 1979; Bauer, 1986). *Bavayia sauvagii*, although generally perceived as arboreal, spends much of its time under rocks in terrestrial microhabitats, although animals may also live in tree holes or climb saplings at night to feed (Bauer and DeVaney, 1987). Unfortunately our knowledge of the pedal performance requirements of scansors on different substrates is rudimentary. Further, the relative importance of claws versus scansors on substrates such as wood is unknown. Indeed, factors of safety (sensu Alexander, 1981) in digital design (with respect to both claws and scansors) appear to vary greatly among even closely related geckos (Bauer and Good, 1986) and parts of the scansorial apparatus may be 'overdesigned' by more than an order of magnitude.

Despite our ignorance, however, it is probable that divided scansors as seen in *Bavayia* do offer some advantage in terms of control. By possessing independently functioning halves of each subdigital plate, the animal is able to exert finer tendinous and vascular control over the scansor and the scansor pairs themselves are freer to deform to substrate irregularities. None the less, finer control of the scansors is also associated with a less direct transduction of forces onto the blood sinus and the 'advantage' (if any) of the divided scansor design of *Bavayia* over the single scansor of *Eurydactylodes* or *Rhacodactylus* is difficult to determine. The only valid assessment of the efficiency of these alternative designs would be one which was based upon performance of the morphologies in direct competition. Although many alternative solutions may suffice for a given problem of locomotor performance, some may be more effective than others under competitive circumstances (Russell, 1976). Such situations are rare in nature but the exclusion of certain native geckos from human-commensal habitats by the introduced divided-scansored gekkonine *Hemidactylus frenatus* in both Hawaii (Hunsaker and Breese, 1967; McKeown, 1978) and New Caledonia (Bauer and Vindum, unpublished) may be indicative of the advantages of a particular digital design under certain circumstances. No such head-to-head competition appears to occur between *Bavayia* and *Eurydactylodes* but it may be valid to evaluate the relative 'success' of the two forms by means of their geographic distribution and abundance. The species of *Bavayia* (actually species complexes, Ross Sadlier, pers. comm.) are distributed across all of New Caledonia and the Loyalty Islands and occupy habitats from houses and beach wrack to rainforest and savanna, from sea level to over 1000m (Bauer, 1986). In contrast, the species of *Eurydactylodes* are known from scattered localities on the New Caledonian mainland and may be limited to regions of the edaphic vegetation of lateritic soils (Bauer, 1986; Bauer and Vindum, unpublished). Likewise, *Bavayia* is generally encountered in large numbers in the field, while *Eurydactylodes* is rarely found and has never been reported in high densities. Of course the patterns of species density and distribution are more than simple reflections of digital design. All other attributes of the animals' biology, as well as the complexity of habitat type, and the vagaries of the search images of human collectors all combine to yield these patterns. None the less, the divided scansors of *Bavayia* may have played a role in the spread and habitat diversification of the genus.

For the time being it seems prudent to regard the differences observed between *Bavayia* and *Eurydactylodes* as merely alternative designs for arboreal or semi-arboreal pedal function rather than specific adaptations for particular microhabitats or surface features. It is clear that both morphologies suffice for their possessors and it is likely that many other designs could also perform effectively in the same habitats. Optimality may be a useful concept in theoretical considerations of biological phenomena but to our knowledge, animal morphologies are not, nor should they be expected to be, optimally constructed. Adaptation of the organism to its environment at this level is trivial (see Gould and Lewontin, 1979). The most (or only?) valid assessment of the 'adaptation' of alternative scansor designs is that which incorporates both biotic and abiotic features of the environment into the determination of selective value. Unfortunately, in the study of gekkonid morphology we are only at the stage that we can identify differences and suggest reasons (phylogenetic, functional, structural or stochastic) for their existence. A complete analysis of the 'meaning' of alternative scansor design in *Bavayia* and *Eurydactylodes* must await a more detailed and fine-grained understanding of the biology of these taxa.

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DENTITIONAL DIVERSITY IN *RHACODACTYLUS* (REPTILIA: GEKKONIDAE)

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The teeth of gekkonid lizards have long (and erroneously) been considered to be simple, homodont, isodont and conical. Although some previously held beliefs about gecko dentition are largely true, the immense variability expressed among the approximately 900 species precludes the applicability of most generalities. A particularly wide range of tooth types is seen in the carphodactyline gecko genus *Rhacodactylus* (including those Australian forms previously assigned to the genus *Pseudothecadactylus*).

Rhacodactylus auriculatus is characterised by huge caniniform teeth that are few in number and widely-spaced. There is a steady increase with body size in the number of tooth loci in juveniles of this species (after the loss of the egg teeth). The pointed uni- or bicuspid teeth in this taxon are only slightly recurved and are constricted at the crown base. In *R. leachianus* and *R. trachyrhynchus* the teeth are decidedly recurved and present a long, blade-like occlusal surface. The teeth of other members of the genus are smaller and much more numerous (up to 180+ marginal tooth loci). Teeth in these forms may be uni- or bicuspid and typically have short crowns, either conical or with moderately pronounced occlusal ridges.

Dental anatomy in *Rhacodactylus* appears largely unrelated to phylogeny. Rather, the teeth correspond to dietary preferences. Many tooth designs are capable of processing insect prey but the caniniform teeth of *R. auriculatus* and the recurved teeth of some of its congeners seem to be specialisations for feeding on vertebrates and other soft-bodied prey. Dietary data, though fragmentary, supports this interpretation. ☐ *Gekkonidae, Rhacodactylus, dentition, diet, phylogeny, functional morphology.*

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The teeth of gekkonid lizards have been characterised as small, numerous, pleurodont, homodont, and pointed (Kluge, 1967). This generalisation has, however, not withstood the input of new data gained through more detailed analyses of dental morphology. Variation in tooth structure among the approximately 900 species of geckos is marked and has most recently been evaluated by Sumida and Murphy (1987) who identified several morphologies, including both bicuspid and quadricuspid tooth crowns.

Among the generalisations about gekkonid dentition that do hold true are that the teeth are pleurodont and, relative to most lizards, very numerous (see Edmund, 1969; Vorobyeva and Chugunova, 1986 for representative tooth counts for selected lizard groups). One species of gekkonine gecko, *Uroplatus fimbriatus*, may have more marginal teeth than any other living amniote (Bauer and Russell, 1989). Tooth number in geckos increases with age and the concomitant increase in the length of the germinal tooth bed or dental lamina (Kluge, 1962; Edmund, 1969). Like most lizards with determinate growth, adult tooth number in geckos stabilises around a particular species mode (Owen, 1866) although variance may be quite high.

All geckos bear teeth only on the maxillae, premaxillae and dentaries (Sumida and Murphy, 1987). Tooth size generally increases from posterior to anterior within a tooth-bearing element, but in at least one species, *Teratoscincus scincus*, the largest teeth are in the middle of the tooth rows (Edmund, 1969). Tooth replacement and addition of new loci is believed to proceed from back to front in waves affecting alternating positions in accordance with Edmund's Zahnreihen theory (Edmund 1960, 1969; Osborn, 1973, 1975; Kline 1983; Kline and Cullum, 1984, 1985), although most evidence for this pattern comes from other lizard groups. In addition to the typical adult dentition, all oviparous geckos also exhibit embryonic egg teeth (Kluge, 1967) which drop out shortly after hatching (Ananjeva and Orlov, 1986). The paired condition of gekkonid (including pygopodid) egg teeth appears to be a uniquely derived condition for the group (Kluge, 1967, 1987; Ananjeva and Orlov, 1986).

During the course of revision of the carphodactyline geckos of the Southwest Pacific (Bauer, 1986) we noted a unique dental morphology characterising the New Caledonian forest gecko, *Rhacodactylus auriculatus* - the possession of enlarged, pointed caniniform 'fangs'. This taxon is one of 44 in the tribe Carphodactylini, a monophyletic group of poorly known geckos endemic to Australia, New Zealand and New Caledonia. *Rhacodactylus* is of particular interest because the genus consists of moderately to very large species that are capable of taking prey types outside of the range normally available to other geckos. Further, *Rhacodactylus* (including the Australian geckos previously assigned to the genus *Pseudothecadactylus*) occupies a fairly wide range of habitat types, from the Arnhem Land escarpment to the rainforests of eastern New Caledonia. In New Caledonia, in particular, members of the genus have few competitors and may be considered the primary non-volant predators. In light of the implications of *Rhacodactylus* biology for dental form and a renewed interest in gekkonoid tooth form and function in general (e.g. Patchell and Shine 1986a,b; Sumida and Murphy, 1987) we take this opportunity to present an analysis of the descriptive and functional anatomy of the teeth in the genus *Rhacodactylus*.

MATERIALS AND METHODS

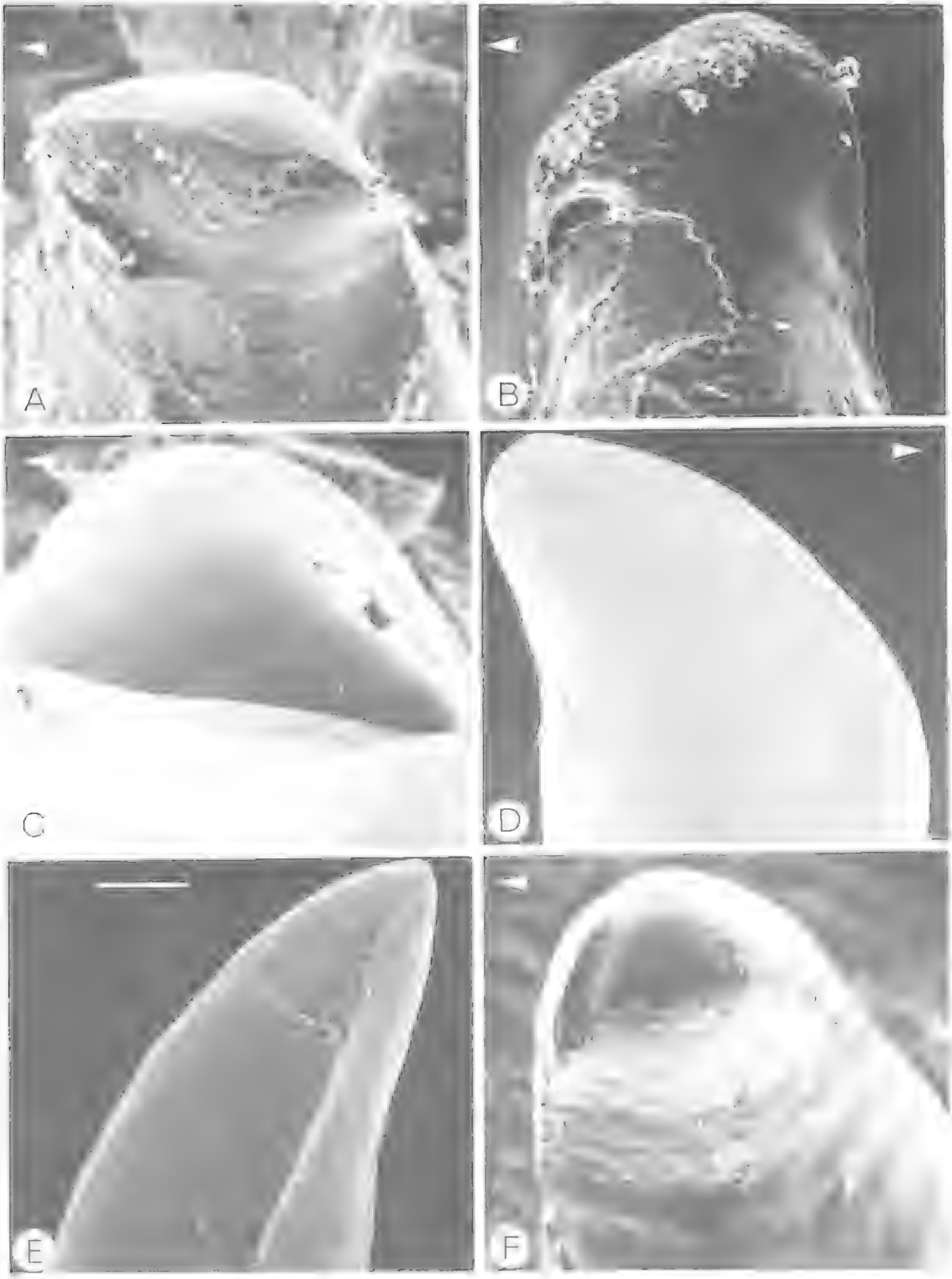
Dentition was examined in adult skeletal and cleared-and-stained specimens of five of the six recognised species of New Caledonian *Rhacodactylus* as follows: *R. auriculatus* (10 specimens), *R. chahoua* (1 specimen). *R. ciliatus* (1 specimen), *R. leachianus* (1 specimen), *R. trachyrhynchus* (1 specimen). In addition, one cleared and stained pre-hatchling of *R. auriculatus* was also examined. Vascularization of the dental lamina was also observed in a number of cleared and stained adult *R. auriculatus* which had been injected with Microfil^{TM} medium (see Russell et al., 1987, 1988). Radiographs of all of the above-mentioned taxa, as well as *R. sarasinorum* and the Australian members of the genus, *Rhacodactylus* (*Pseudothecadactylus*) *australis* and *R.* (*P.*) *lindneri*, were examined and spirit-preserved specimens of most taxa were also consulted. Specimens were borrowed from the collections of the California Academy of Sciences (CAS), the British Museum (Natural History) (BM(NH)), the Australian Museum (AMS) and the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). Tooth counts for these taxa are expressed in terms of tooth loci, since teeth themselves may be lost or damaged post mortem. For comparative purposes reference was made to dry skeletal, cleared-and-stained and radiographic material representing all gekkonid genera except *Microscalabotes* and *Paragehyra*. Skeletal material was examined under a binocular microscope and individual teeth were removed, sputter- coated with gold-palladium alloy and examined with an Hitachi S–450 scanning electron microscope. Photomicrographs were taken on a Wild stereo dissecting microscope with camera mount or with a 35mm camera with macro lens.

RESULTS

TOOTH MORPHOLOGY

In *Rhacodactylus chahoua*, *R. ciliatus*, *R. sarasinorum* and the Australian species *R.* (*Pseudothecadactylus*) *australis* and *R.* (*P.*) *lindneri*, the tooth crowns are short, relatively blunt, and generally peg-like. All teeth are somewhat labio- lingually compressed, with the labial face of each tooth exhibiting a marked convex bowing. The lingual surface is somewhat more perpendicular with respect to the tooth-bearing bone. In *R. ciliatus* the crown is distinctly

FIG. 1.A. Maxillary tooth of *Rhacodactylus chahoua* (CAS 167764), occlusal view. Arrow in this and subsequent figures represents anterior direction. B. Same specimen as A, labial view showing asymmetrical crown height. C. Maxillary tooth of *Rhacodactylus leachianus* (CAS 167890), occlusal view showing elongate narrow cutting ridge. D. Same specimen, labial view showing pronounced recurvature of the tooth crown. E. Oblique view of maxillary tooth of *Rhacodactylus auriculatus* (CAS 165891) illustrating pointed tooth crown and lateral extension of single cusp. F. Same specimen as E, occlusal view showing the dorsally directed single cusp and general smoothness of the tooth. Scale bars for all figures = 100µm.


A
B
C
D
E
F

bicuspid, with a shallow trough separating the higher and more pronounced labial cusp from its lingual counterpart. In *R. chahoua* the tooth crown is basically unicuspid (Fig. 1A), although older, more worn teeth may exhibit a weakly demarcated lingual 'shoulder'. In the remaining taxa the teeth have weakly developed cusps or are conical with a rather blunt point. The latter condition is especially true of younger teeth at the posteriormost loci. In all taxa, but most notably in *Rhacodactylus chahoua*, the tooth crowns are directed somewhat posteriorly (Fig. 1B) and the posterior portion of the cusp(s) rise(s) slightly higher above the gum line. In *R. chahoua* the largest teeth are at the level of the posterior border of the nostril, in the anterior portion of the maxillae. The premaxillary teeth are uniformly small, but similar in morphology to those of the maxillae and dentaries. *Rhacodactylus sarasinorum*, *R. ciliatus* and the *Pseudothecadactylus* species are characterised by isodonty.

In the largest species of *Rhacodactylus*, *R. leachianus* and *R. trachyrhynchus*, teeth at the posterior (younger) loci are generally similar in appearance to those of *R. chahoua*. Anteriorly, however, the teeth are elongate and their crowns are decidedly angled. In *R. leachianus* the crown presents a very long and narrow occlusal blade (Fig. 1C). The highest (posteriormost) point of the crown projects backwards beyond the plane of the crown base as a rounded hook (Fig. 1D). There are no multicuspid teeth in this taxon. In *R. trachyrhynchus* the anterior teeth are only slightly curved and do exhibit a lingual 'shoulder' or weak cusp. As in *R. chahoua* the largest teeth in both *R. trachyrhynchus* and *R. leachianus* are in the anterior part of the maxillae but in the former species, the premaxillary teeth are also quite large.

A third type of morphology is exhibited by *Rhacodactylus auriculatus*. In this taxon all of the teeth are elongate and sharply pointed (Fig. 1E). The crown is only slightly inflected. Although most teeth appear to be unicuspid (Fig. 1F), a faint lingual cusp characterises some of the teeth in anterior loci of all tooth-bearing bones. Unlike other *Rhacodactylus* species, some of the teeth of *R. auriculatus* are constricted at the junction of root and crown (Fig. 2). This condition does not occur in the premaxillary teeth and is most evident in the teeth occupying older, anterior maxillary and dentary loci.

FIG. 2. Anterior portion of left maxilla of *Rhacodactylus auriculatus* (CAS 165891) showing the constriction (c) of the teeth at the junction of crown and root.

No surface microstructures, such as grooves or serrations, were located on the teeth of any species *Rhacodactylus*. Likewise, the teeth of upper and lower jaws do not normally contact one another in occlusion.

TOOTH SIZE, NUMBER AND REPLACEMENT

There is a two-fold difference in marginal tooth locus number in mature individuals of *Rhacodactylus* spp. Total locus number ranges from a mean of 105.5 in *R. auriculatus* to over 180 in *R. sarasinorum*. Figure 3 shows the distribution of marginal tooth loci versus skull length for mature specimens for which total counts could be made umambiguously. Although sample sizes for all taxa except *R. auriculatus* are very small, qualitative differences among species are evident. (Unfortunately the two specimens of *R. trachyrhynchus* examined were sub-adults and thus the data for this taxon are not strictly comparable to those derived from other specimens.) *Rhacodactylus sarasinorum*, *R. ciliatus* (Fig. 4A) and the two *Pseudothecadactylus* have the smallest skull (and body) size, yet they exhibit the greatest tooth number. The remaining, larger New Caledonian *Rhacodactylus* exhibit much lower tooth locus numbers (see Fig. 4B, C).

In interspecific comparisons tooth size is inversely correlated with tooth number (see Table 1). This is due in part to packing constraints, but also results from the relatively large diastimae that characterise the larger species, and *Rhacodactylus auriculatus* in particular (Fig. 4D).

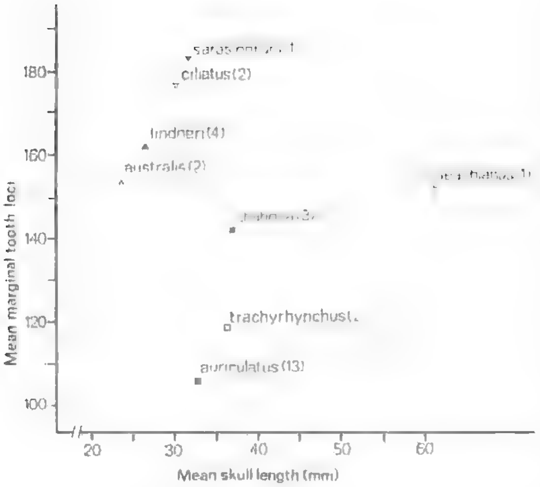


FIG. 3. Graph of mean marginal tooth loci versus mean skull length for eight *Rhacodactylus* species. Number of specimens of each taxon examined is listed parenthetically. Only adult specimens for which accurate tooth locus counts could be made are included (see text for exception of *R. trachyrhynchus*).

In all species, tooth replacement patterns leave at least some loci without functional marginal teeth. In these instances small replacement teeth of the next generation may be seen attached to the alveolar locus. Precise counts of the number of loci undergoing replacement at any time were not possible in the material available, as museum material, especially dry skeletal specimens, may lose teeth through the skeletonization process, storage or shipping. It is noteworthy, however, that premaxillary teeth were rarely absent and that maxillary and dentary tooth rows lacked approximately 20 - 25% of teeth in all taxa except *Rhacodactylus auriculatus*, in which 25 - 30% were lacking.

Within a single species, such as *Rhacodactylus auriculatus*, tooth number increases ontogenetically (Fig. 5) at least until sexual maturity. A more or less steady addition of tooth loci begins during prenatal life and continues until a body size of approximately 95mm SVL (skull length 26mm) is reached. This corresponds roughly to minimal breeding size. Other than absolute size, no differences in juvenile and adult dental morphology were noted in *R. auriculatus*. No sexually related differences in either tooth size or number were noted in this, or any other *Rhacodactylus* species.

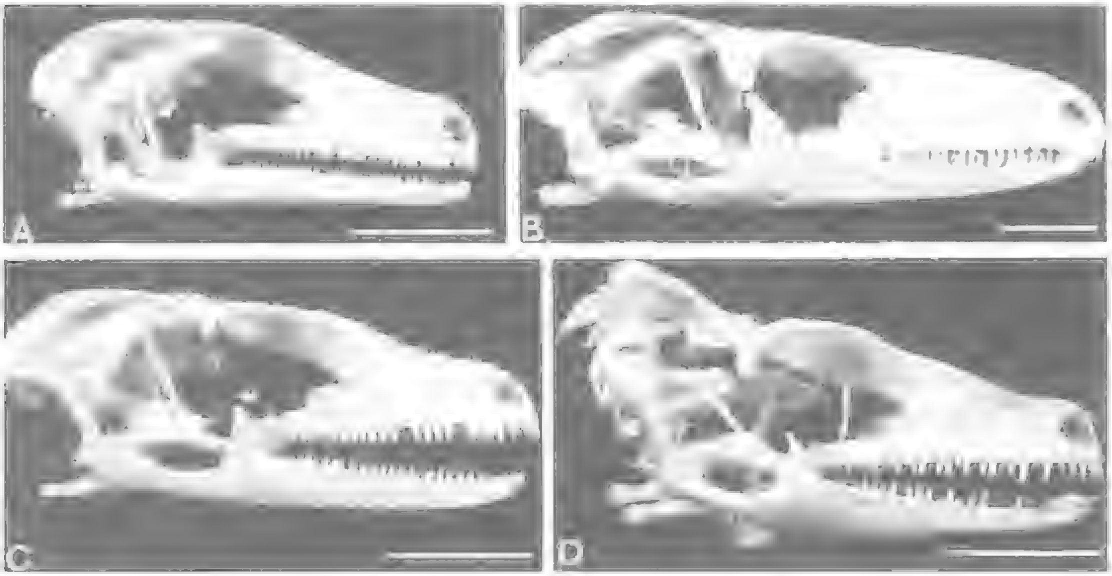


FIG. 4. Right lateral views of the skulls of *Rhacodactylus* spp. illustrating variation in tooth size, number and shape. A. *R. ciliatus* (BM(NH) 86.3.11.4), B. *R. leachianus* (CAS 165890), C. *R. trachyrhynchus* (BM(NH) 85.11.16.7), D. *R. auriculatus* (CAS 165891). In D. the posterior end of the skull is somewhat distorted by the separation of the quadrate, squamosal and parietal bones. Scale bars for all figures = 10mm.

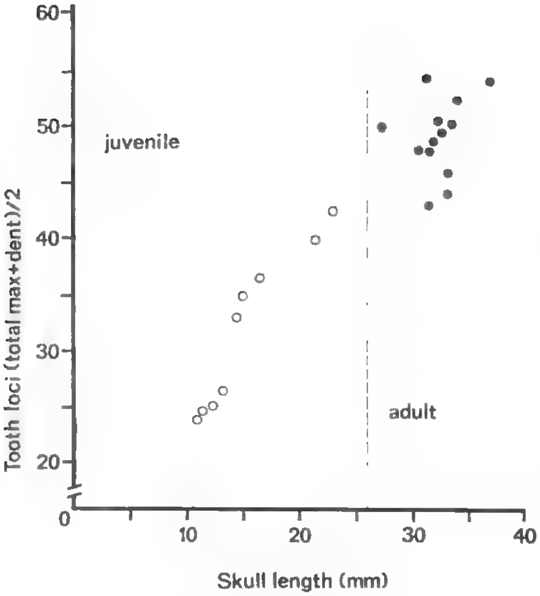


FIG. 5. Graph of mean unilateral tooth loci (maxillary and dentary) versus skull length (measured from tip of snout to occipital condyle) for specimens of *Rhacodactylus auriculatus*. Premaxillary teeth were excluded because of the relative constancy of their number after hatching and subsequent loss of the egg teeth. Dashed line separates juveniles (including pre-hatchlings) (open circles) from adults (closed circles).

EGG TEETH

In all *Rhacodactylus* the number of premaxillary teeth is small and relatively stable. In the largest species and those species with high total tooth counts there are generally nine to eleven premaxillary loci while in *R. auriculatus* seven is the modal number. As in all oviparous geckos, embryos and hatchling *Rhacodactylus* possess only deciduous egg teeth in the premaxillae. These are shed within a few days of eclosion and replaced shortly thereafter by premaxillary teeth essentially identical to those of the adult. Egg teeth were examined in *R. auriculatus* and *R. chahoua*. These structures are about twice the size of the dentary or maxillary teeth. The egg teeth are broad and flattened and project anteriorly (Fig. 6). The presence of egg teeth in the viviparous species *Rhacodactylus trachyrhynchus* has not been confirmed.

TOOTH VASCULARIZATION

A gross examination of vascularization of the mouth cavity of *Rhacodactylus auriculatus* revealed that the entire oral mucosa is supplied by a dense network of blood vessels (Fig. 7). Individual tooth roots are invested with capillary cores which take their origin from the dental branches of the maxillary and mandibular arteries (vessel terminology follows O'Donoghue, 1921, and Oelrich, 1956). These arteries in turn arise from the stapedial artery which ultimately takes its origin from the internal carotid.

DISCUSSION

PHYLOGENETIC IMPLICATIONS

Gecko tooth form (Bauer, 1986) and cuspation (Grismer, 1986, 1987; Sumida and Murphy, 1987) have been employed to a limited extent in phylogenetic analysis. Unfortunately, many of the details of dental structure are difficult to examine without removing teeth for electron microscopy, and as a result only very few taxa have been adequately investigated. Relationships within *Rhacodactylus* proposed by Bauer (1986), largely on the basis of non-dental characters, are not strongly reflected in the evidence from tooth morphology. The sister group status of the *Pseudothecadactylus* species may be confirmed by the similarity of their tooth morphology, but in the absence of comparable data from other carphodactyline geckos their shared features cannot be assumed to be apomorphic. The

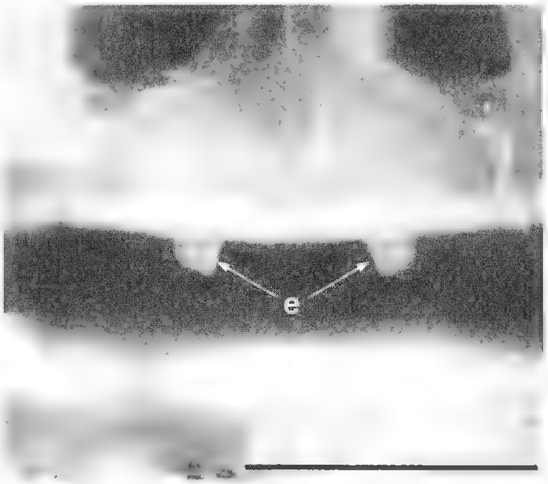


FIG. 6. Egg teeth of a cleared-and-stained pre-hatchling of *Rhacodactylus auriculatus* (AMB, personal collection). Note the orientation and large size of the egg teeth (e) relative to the maxillary and dentary dentition. Scale bar = 1mm.

FIG. 7. Palatal view of a cleared-and-stained Microfil^{TM}-injected *Rhacodactylus auriculatus* (CAS 165897) showing the dense vascularization of the oral mucosa. Tooth roots are served by dental branches of the maxillary and mandibular arteries. Scale bar = 5mm.

autapomorphic elongate caniniform teeth of *Rhacodactylus auriculatus* would appear to be unique among the Diplodactylinae, but provide no clues to affinity. *Rhacodactylus leachianus* and *R. trachyrhynchus* share some features, such as moderately great crown height and recurved crown tips, but differences in cuspation and a lack of corroboration from other characters renders these features of little systematic value. Indeed, the diversity of tooth form among the eight taxa examined is unexpected and, if the monophyly of the *Rhacodactylus/Pseudothecadactylus* lineage is accepted, then function rather than phylogeny may be supposed to play the greatest role in the determination of tooth form.

FUNCTION

Dietary correlates of dental morphology have long been presented as evidence of a tightly coupled form-function complex. Mammals, including bats (Freeman, 1979, 1981, 1988) and sabre-toothed cats (Akersten, 1985), among many others, have been the subject of intensive analysis. Lizards, largely because of the mistaken belief that their dentitions are simple, homodont and isodont have received less attention (Edmund, 1969; Vorobyeva and Chugunova, 1986). None the less, iguanids (Hot-

FIG. 8. Radiograph of an adult female *Rhacodactylus auriculatus* (AMS R 78121) illustrating the presence of a whole snail shell (s) as well as chitinous arthropod debris (d) in the digestive tract. Scale bar = 10mm.

ton, 1955; Montanucci, 1968) macroteids (Presch, 1974; Dalrymple, 1979; Dessem, 1985), agamids (Cooper et al., 1970; Chugunova et al., 1987) and varanids (Lönnberg, 1903; Cowles, 1930) have received some attention in this regard. Among gekkotans functional dental morphology has only recently begun to be explored (Sumida and Murphy, 1987; Patchell and Shine 1986a,b - pygopodids).

The diversity of dental form found within *Rhacodactylus* provides the opportunity to make predictions about dietary preferences on the basis of data from other lizard groups. The elongate caniniform teeth of *R. auriculatus* are typical of tetrapods that feed primarily on soft-bodied prey items. Such pointed, elongate 'fangs' have been reported elsewhere in the teiid *Callopistes flavipunctatus* (Presch, 1974) and the iguanid *Gambelia wislizenii* (Hotton, 1955), both of which feed on vertebrate prey. Among other geckos Sumida and Murphy (1987) reported that *Gekko* and *Chondrodactylus*, again vertebrate predators, possessed upright, partly developed cusps implying that penetration rather than crushing or restraining functions are paramount in these forms. A similar morphology is seen in moth-feeding molossid bats (Freeman, 1979). The constricted 'neck' of *Rhacodactylus auriculatus* teeth (Fig. 2) may represent a preformed zone of weakness at which breakage may occur during excessive prey movement. Gecko teeth in general have been characterised as brittle (Vorobyeva and Chugunova, 1986) and high replacement rates (Edmund, 1969) have been interpreted as a compensation for this. In *R. auriculatus* facilitated crown loss may insure that the dental lamina itself is not damaged by trauma resulting from rapid root movement. Such breakage phenomena may be akin to the dietary-related ones evident in predatory mammals (Van Valkenburgh, 1988), where dental fracture is associated with occasional, unpredictable high stresses.

Available information on diet confirms that *Rhacodactylus auriculatus* feeds, at least in part, on soft-bodied prey. Bauer and DeVaney (1987) recorded the remains of the small carphodactyline *Bavayia sauvagii* from the stomach of this species. The species is also known to eat insects (Bauer and DeVaney, 1987) and snails (Fig. 8) as well as flowers (Bavay, 1869) but there are no obvious dental correlates of these foods, suggesting that vertebrate prey (and perhaps large, soft-bodied insects) comprise the bulk of the diet. This prediction may be evaluated by analysing the gut contents of the many specimens available in museum collections. Alternatively, however, a preformed zone of weakness may be associated with rare (Gretener 1984) but significant events and may represent an example of what may initially appear to be an 'excessive construction' (Gans, 1979).

The recurved teeth of *Rhacodactylus trachyrhynchus* and especially *R. leachianus* are rare among geckos. Sumida and Murphy (1987) did not acknowledge their existence, while Grismer (1986) reported them only in *Hemidactylus flaviviridis*, *Hemitheconyx* spp. *Phelsuma sundbergi* and *Tarentola americana*. Normally, recurved teeth are associated with grasping or holding prey during the ingestion cycle (see Wake and Wurst, 1977). However, such teeth are also believed to concentrate bite force at the recurved point (Gans 1974) and in non-geckos are frequently associated with multiple cuspation (see Sumida and Murphy, 1987). In *Rhacodactylus leachianus* there is but a single cusp (Fig. 1C) and this is parallel to the tooth row. In this species the teeth appear best suited to piercing and shearing motions, again probably associated with soft-bodied prey. The large size of this gecko and its ability to overpower prey may obviate the need for the more piercing/holding dentition of *R. auriculatus*, or alternatively it may permit finer intraoral processing of very large prey items. Little is known of the diet of this species in the wild, although small birds are known to be taken (Roux, 1913). In captivity mice (Bauer and DeVaney, 1987) and fruit (Mertens, 1964) are accepted. Small vertebrates, insects and fruit (Bauer, 1986) have been proposed as the food of *Rhacodactylus trachyrhynchus* but the native diet remains unconfirmed. Tooth morphology and the apparent ecological position of this, and other large *Rhacodactylus* species as dominant predators in New Caledonia, however, strongly suggest that this species could exploit saurian or avian prey.

The teeth of the remaining species of *Rhacodactylus*, although varying in cuspation, are very small and tightly packed (Fig. 4A). Bicuspid teeth in particular, such as those of *R. ciliatus*, have been associated with a crushing function useful for hard bodied insects. Small blunt teeth, as in *Pseudothecadactylus* spp. have also been associated with insectivory, especially in regard to smaller, softer taxa (Hotton, 1955). A somewhat similar morphology characterises *Coleonyx* spp. (Kluge, 1962) which are known insectivores. Comparable analogues also occur

TABLE 1. Tooth number and size in adult *Rhacodactylus*.

Taxon (n)	Total tooth Loci ($\bar{x}$)	Maximum Crown height (mm)	Maximum Crown width (mm)
NEW CALEDONIAN			
R. auriculatus (13)	105.5	1.55	0.71
R. chahoua (3)	142	0.75	0.45
R. ciliatus (2)	177	0.50	0.40
R. leachianus (1)	153	1.60	0.70
R. sarasinorum (1)[1]	183	0.45	0.40
R. trachyrhynchus (2)[2]	119.5	1.00	0.43
AUSTRALIAN			
R. (*Pseudothecadactylus*) *australis* (2)[1]	153.5	0.40	0.37
R. (*P.*) *lindneri* (4)[1]	162	0.45	0.40

[1] Tooth dimensions estimated from radiographs. [2] Data come from sub-adult specimens.

in mammalian insectivores (see Freeman, 1979, 1988).

Little is known of the diet of the smaller species of *Rhacodactylus* (including *Pseudothecadactylus*), but it is likely that all consume insects. In captivity *Rhacodactylus chahoua* accepts both fruit and insects (Bauer, 1985). *Rhacodactylus* (*Pseudothecadactylus*) *lindneri* includes at least some vertebrates in its diet and has been observed to feed on *Gehyra* species in Kakadu National Park (Bauer, 1986).

Although well-defined characteristic dentitions appear to typify durophagous (Lönnberg, 1903; Dalrymple, 1979; Vorobyeva and Chugunova, 1986) and herbivorous (Hotton, 1955; Montanucci, 1968; Cooper et al., 1970; DeQueiroz, 1987) lizards, mechanical constraints on the processing of other food types, including insects and vertebrates seem to be less restrictive. Thus dietary preference may be reflected in dentition, but, depending on size and phylogenetic limitations, several tooth morphologies may be equally efficacious in processing the same prey type (Chugunova et al., 1987). Much of the difficulty in understanding the correlation of diet and dentition stems from the fact that little is really known of the properties of different food types (Freeman, 1988) or of the dietary scope of most lizards. Indeed, most geckos, and certainly all *Rhacodactylus*, take a variety of prey types. Dentitions must not, therefore, be expected to be optimally constructed to deal with single prey types. Rather they may be predicted to present a compromise solution to the problem of a varied diet, with an emphasis on those features most suited to the processing of food items that comprise the greatest bulk of the consumed prey, or those imposing the greatest mechanical stress (Gans, 1979; Van Valkenburgh and Ruff, 1987). Future additions to our knowledge of the diet of *Rhacodactylus* spp. may confirm or clarify the predictions stemming from the details of morphology discussed here.

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WALUNARRA, BUNGARRA MALI AND THE GANGALIDDA AT OLD DOOMADGEE: – Near Old Doomadgee (16°57'S, 138°49'E), the country of the Gangalidda people, in the monsoon tropics, there are two species of freshwater turtles: walunarra, the 'mud turtle', is a species of *Chelodina* (possibly *C. rugosa*, possibly an undescribed species) and bungarra mali, the 'stinking turtle', is *Chelodina novaeguineae.*

In the area, there is no permanent freshwater although lagoons provide plentiful surface water for much of the year. At varying times during the dry season, which usually begins in June-July, the lagoons become rock-hard clay beds. The rate of drying depends on size, shape, depth, substrate, vegetation, previous rains and temperatures. Within a radius of 30km of Old Doomadgee, there are some ten lagoons. Both walunarra and bungarra mali occur in all of these waters and they have been collected as a prized food source by the Gangalidda for as long as is remembered. As the waters of the lagoons recede during 'the dry', walunarra digs into the mud to aestivate and bungarra mali migrates to other longer-lasting lagoons.

At an unnamed lagoon 3km SW of Old Doomadgee, three of us (JC, PC, KM) recently accompanied Major Walden, a senior Gangalidda, while he collected a specimen of walnunarra from its aestivation site. The site was well concealed both by the low, thick, sharp foliage and by the tangled root system of *Melaleuca acacioides*, which fringes many of the lagoons in the area. To the untrained eye, surface evidence of an aestivating turtle is difficult to find. The mound of mud above the site is some 60-70mm high. It is a whorl and resembles those made by freshwater crabs. However, they are much less common and they lack the central hole (diameter 20-30mm) of those made by crabs. As well, at the base of the turtle's mud-whorl is a small air hole (diameter about 3- 5mm), used by the turtle for breathing.

As Major Walden dug into the rock-hard mud below the whorl, the digging disturbed the aestivating turtle and it emitted a sudden 'whoosh' of air; this is characteristic behaviour. The turtle was located, head down, eyes-closed (they appeared 'sealed' against desiccation) at a depth, from rear of shell to ground surface, of approximately 120mm. The turtle was not vertically aligned. Rather, it rested on the diagonal at an angle of about 30°. A second specimen was located in the same way, under very similar conditions between the surface roots of a large *Melaleuca leucodendra* close to the lagoon edge.

When we visited the area (June, 1990) water levels were still high in the lagoons, although they were drying up quite rapidly. In the previous weeks, bungarra mali had been found, apparently moving to new, temporary lagoons – something that has been observed in the area for many years (Alice Ned, pers. comm.) at roughly the same time each year.

Both species of turtles are utilised as food by the Gangalidda. Major Walden and others have supplied us with details of the method of cooking walunarra. (We have no data on whether the same procedure is followed for bungarra mali). The turtle is killed by ringing its neck. The neck is then cut to expose its wind pipe into which air is blown. (In early times, the live turtle was held so air could be blown into its mouth and nose). The wind pipe is then tied to keep the air in so a 'cushion' exists to separate internal organs from the shell to prevent their becoming stuck to the shell during cooking. If air is not blown into the turtle, the carapace and plastron are cracked to ensure successful cooking.

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MOLECULAR EVOLUTION IN AUSTRALIAN DRAGONS AND SKINKS: A PROGRESS REPORT

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We have been using microcomplement fixation of albumin to assess the evolutionary relationships of the dragons and skinks of Australia, and to provide approximate dates of divergence of extant taxa. The results are preliminary, but suggest the following salient features. For the dragons: (1) The amphibolurid radiation is very recent, less than 20 MYBP; (2) *Moloch* is a part of the amphibolurid radiation; (3) the Australasian *Gonocephalus* are much more closely related to the amphibolurids and *Physignathus* than to Asian *Gonocephalus*; (4) the divergence of the amphibolurids, *Physignathus* and Australasian *Gonocephalus* occured in the mid-Miocene; (5) The Australasian agamids (including *Gonocephalus* and *Physignathus*) are closer to the African *Agama* than any Asian dragon so far tested. For the skinks: (1) The data are in accord with Greer's (1979) recognition of three groups of skinks in Australia, diverging about 60 MYBP; (2) The genus *Leiolopisma* is paraphyletic with the genera *Lampropholis, Carlia, Menetia* and *Morethia*; (3) The New Zealand *Leiolopisma* fall within the Australian *Leiolopisma* with a divergence time of about 20 MYBP. ☐ *Dragon, skink, microcomplement fixation, molecular clock, biogeography.*

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Five families of lizards occur in Australia - the Agamidae (dragons), Scincidae (skinks), Varanidae (goannas), Gekkonidae (geckos), and Pygopodidae (legless lizards). Of these, only the Pygopodidae are endemic to Australasia.

The last 15 years have seen enormous changes in our understanding of the generic and specific limits of Australian lizards, as a comparison of Worrell's (1963) book with Cogger's (1986) book reveals. Despite this work, the evolutionary origins and relationships among genera are often poorly known, and subject to very varied opinions (e.g. Tyler, 1979; Greer, 1979; Cogger and Heatwole, 1981; Witten, 1982). This uncertainty results from paucity of suitable morphological characters, high level of homoplasy in some groups, use of principally non-cladistic analyses, and paucity of fossils. It is in such areas that molecular genetic techniques can prove extremely valuable.

The molecular genetic approach to systematics and biogeography has two major contributions to make. Firstly, it provides a view of the evolutionary relationships of a group that is totally independent of that provided by morphology. This does not mean that it is the panacea for all problems in systematics. Rather, molecular genetic data should be seen as challenging established ideas about the evolution of a group, and highlighting areas of discrepancy. Secondly, there is mounting evidence that molecular genetic techniques can be used to provide a time-frame, albeit approximate, for the cladistic events in the evolution of a group (Wilson et al., 1977; Thorpe, 1982; Ayala, 1986).

Over the past several years, we have been using the molecular genetic technique of microcomplement fixation (Champion et al., 1974) to assess molecular evolution in the Australian lizards. The study of the Varanidae with D. King and M. King is completed and will be published separately, while our work on the Gekkonidae and Pygopodidae has barely begun. However, our data on the Agamidae and Scincidae, although incomplete, are sufficiently extensive to provide a rough picture of their evolution in Australasia. We have taken the opportunity of the Bicentennial Herpetology Conference to present our preliminary data on these groups. Some aspects of the work we report here on the Scincidae has involved S. Burgin, M. Hutchinson and C. Daugherty.

MATERIALS AND METHODS

Albumin was purified from plasma by disc electrophoresis and injected into rabbits (three per antigen) over a period of three months according to the schedule of Champion et al. (1974). Purity of antisera was checked by immunoelectrophoresis. The microcomplement fixation procedure followed the protocol of Champion et al., (1974). The results of cross-reactions are reported as Albumin Immunologic Distances (AIDs). One AID is roughly equivalent to one amino-acid substitution (Maxson and Wilson, 1974).

RESULTS

THE AGAMIDAE

Antisera were raised to six species of Australian agamids - *Ctenophorus vadnappa, Pogona barbata, Lophognathus gilberti, Moloch horridus, Gonocephalus bruynii* and *Physignathus lesueurii.* The full reciprocal matrix for these six taxa was corrected for reciprocity by the method of Cronin and Sarich (1975). The standard deviation for reciprocity (Maxson and Wilson, 1974) was 21.8% before correction and 8.2% after correction. The corrected reciprocal matrix is shown in Table 1. Also shown in Table 1 are the results of the one-way reactions to a range of other agamids from Australia, New Guinea, Asia, and Africa and two iguanids from North America.

The reciprocal data were used to produce an unrooted tree by the Fitch-Margoliash method (Fitch and Margoliash, 1967), using the PHYLIP 2.7 package written and kindly supplied by J. Felsenstein. To root this tree, an outgroup is needed. The outgroup must be close enough to be able to detect differential rates of evolution in the ingroup, but far enough away to be sure that it is an outgroup. The taxa tested for suitability as outgroups were *Agama aculeata, Calotes tympanostriga, Dipsosaurus dorsalis* and *Iguana iguana* (Table 1). Of these, only *Agama aculeata* was close enough to be useful as an outgroup.

Because we do not have immunological distances of all antisera to *A. aculeata*, it was not possible to produce a rooted tree for the Australian agamids using the Fitch-Margoliash criterion. However, we added *A. aculeata* to the tree by optimising the four distances available (Table 1). The resulting rooted tree for the Australasian agamids is shown in Fig. 1. This tree should be treated as provisional since it is based on incomplete data for *A. aculeata*, and has not been tested for robustness by jackknifing (Lanyon, 1985) . On the tree in Fig. 1, *Moloch* stands apart from the amphibolurids represented (*Pogona, Ctenophorus* and *Lophognathus*). However, the one-way reactions to other amphibolurids (*Chlamydosaurus* and *Diporiphora*) suggest that these genera fall outside a *Moloch/Pogona/Ctenophorus/Lophognathus* clade (Table 1). If this is true (and it needs to be tested by antisera to *Chlamydosaurus* and *Diporiphora*), then *Moloch* may in fact be part of the amphibolurid radiation. Moreover, again based on the one-way distance to *Chlamydosaurus* and *Diporiphora, Physignathus lesueurii* may be closely related to this clade.

A second feature of the one-way cross-reactions shown in Table 2 are the albumin distances to non-Australasian taxa. Of all the taxa tested, the African *Agama* is much closer to the Australasian agamids than are the Asian agamids, including, significantly, *Gonocephalus kuhli.*

THE SCINCIDAE

Antisera have been raised to 10 species of Australian skinks. A partial reciprocal matrix for these 10 species is shown in Table 2. Table 2 also shows the results of cross-reactions of these 10 antisera to a range of other skinks. Because the reciprocal matrix is as yet incomplete, it is not possible to correct for reciprocity by the method of Cronin and Sarich (1975), nor to construct phylogenetic trees by the Fitch-Margoliash method. Nevertheless, a number of perhaps unexpected features emerge from the limited data available. They are:

(1) The genus *Lampropholis* is highly diverse at the albumin level. AIDs among members of the genus range up to 29, which is as high as that characterising the entire amphibolurid radiation (see Table 2). Indeed, the species separated by 29 AIDs are *La. basiliscus* and *La. challengeri*, which are sibling species.

(2) The genus *Leiolopisma* is even more diverse at the molecular level, with AIDs up to 40! Indeed it is clear that the genus is not monophyletic. Some species of *Leiolopisma (entrecasteauxii, pretiosum, palfreymani* and *metallicum*) are closer to *Lampropholis* and *Carlia* than to other *Leiolopisma*, while *Le. duper-*

TABLE 1. Albumin immunologic distances (corrected for reciprocity) of antisera to six species of Australian agamids to a range of other agamids and iguanids. The standard deviation for reciprocity was 21.8% before correction and 8.2% after correction. CF is the correction factor.

	Antibody						Geographic origin
	Cv	Pb	Lg	Mh	Gb	Pl	
Antigen CF	0.70	0.79	0.98	1.64	1.03	0.89	
Ctenophorus vadnappa (Cv)	0	14	18	19	47	23	Australia
Pogona barbata (Pb)	10	0	18	21	42	21	Australia
Lophognathus gilberti (Lg)	24	14	0	23	39	26	Australia
Moloch horridus (Mh)	19	18	26	0	29	17	Australia
Gonocephalus bruynii (Gb)	43	42	40	27	0	33	New Guinea
Physignathus lesueurii (Pl)	26	25	23	19	29	0	Australia
Antigens only							
Tympanocryptis intima	17	14	20	23	48	35	Australia
Chlamydosaurus kingii	24	25	15	21	44	31	Australia
Diporiphora bilineata	31	33	30	26	50	33	Australia
Gonocephalus modestus	36	—	38	—	16	38	New Guinea
Gonocephalus kuhli	136	—	117	—	134	108	Asia
Calotes tympanostriga	169	—	157	—	139	—	Asia
Agama aculeata	71	—	68	56	71	—	Africa
Dipsosaurus dorsalis	163	—	—	—	141	—	North America
Iguana iguana	210	—	—	—	—	—	North America

reyi is closer to *Menetia* and *Morethia* than to other *Leiolopisma*. The New Zealand *Le. grande* forms a third group.

(3) The *Eugongylus* group of Greer (1979), here represented by *Eugongylus, Carlia, Lampropholis, Leiolopisma, Menetia, Morethia, Cryptoblepharus* and *Emoia*, appears to form a monophyletic group to the exclusion of *Egernia, Tiliqua, Sphenomorphus, Ctenotus, Mabuya, Lamprolepis, Tribolonotus* and, perhaps, *Mabuya*.

(4) Of the non-*Eugongylus* group species, *Egernia* and *Tiliqua* are close, but we have no data yet on possible relationships among other species.

DISCUSSION

THE AGAMIDAE

Current views of the biogeographical history of Australian and New Guinean agamids are highly disparate in some areas (cf. Tyler, 1979; Cogger and Heatwole, 1981; Witten, 1982). Briefly summarised, all schemes agree that there is an endemic component which is referred to as the amphibolurid radiation but whose composition varies between authors, and a group of genera (*Physignathus, Gonocephalus* and *Chelosonia*) which arose from Asian ancestors and have entered Australia recently from New Guinea.

The phylogenetic relationships of *Moloch* are not known with certainty, due to its highly autapomorphic morphology. *Moloch* has been considered as either the first agamid to have entered Australia and hence phylogenetically outside the amphibolurid radiation (Cogger and Heatwole, 1981), or as an embedded member of the endemic radiation (Witten, 1982). The albumin data support the latter, and moreover suggest that *Moloch* is well embedded in the amphibolurid radiation. Thus the hypothesis of a separate entry into Australia by *Moloch* is not supported by our data.

The origin of the supposedly Asian-derived species of *Gonocephalus* and *Physignathus* is also questioned by the albumin data. Most proposals in this area appear to have been strongly influenced by the current taxonomy. The albumin data suggest that the current taxonomy does not reflect the phylogenetic relationships of species in these genera. The New Guinean *Gonocephalus* available to us are *much* more closely related to the amphibolurids than to the Asian *Gonocephalus kuhli*. Similarly, *Physignathus lesueurii* is much more closely related to

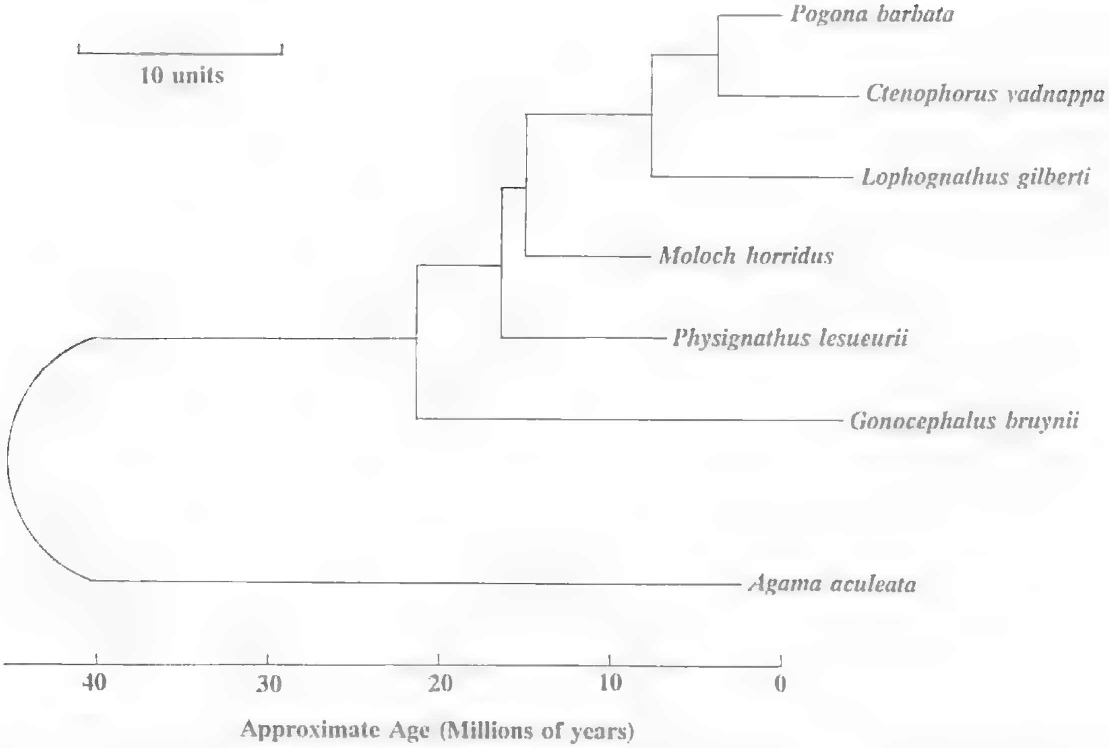


FIG.1. Phylogenetic tree, constructed by the Fitch-Margoliash method, among the six species of agamids to which antisera were raised. The tree was rooted using *Agama aculeata* as an outgroup. Branch lengths shown are proportional to the proposed amount of albumin change along each branch. An approximate time scale is given assuming T=0.6D.

the amphibolurids than to the available Asian genera. The only other member of the genus, *P. cocincinus*, is found in Indochina, and may not be very closely related to *P. lesueurii* (Witten, 1982). Hence the proposed recent Asian origin for these genera must be questioned critically in the light of the albumin data.

Taken at face value the tree in Fig.1 shows clear evidence that rates of albumin evolution within the Australasian agamids have been reasonably uniform among lineages. From the node common to all Australasian agamids, the range in amounts of albumin evolution vary from 12 units to *Moloch horridus* to 22 units to *Ctenophorus vadnappa*, a less than two-fold range. It is therefore appropriate to use a molecular clock for this data set. However, we need to calibrate the clock for agamids. Usually, such a calibration relies on obtaining from fossils an estimate of the age of at least one and preferably two cladogenic events in the history of the group. In order to date cladogenic events from fossil data, three requirements must be met. Firstly, the fossil must be well-dated, secondly, the fossil must be sufficiently well-preserved to be placed in a phylogenetic framework; thirdly, and most importantly, the systematics of extant forms must be well-established. Unfortunately, none of these requirements can be met for Australian agamids (Molnar, 1984).

The relationship T=0.6D (where T=time in millions of years and D=albumin immunologic distance) has been used frequently in the literature for a wide range of vertebrates including eutherians (Sarich, 1985), marsupials (Maxson et al., 1975), lizards and crocodiles (Gorman et al., 1971) and snakes (Cadle and Sarich, 1981), although usually without specifically calibrating the clock for the group in question. In the majority of cases, such a calibration has proved to be compatible with what limited available data there are for the group in question. Recently, however, Sarich (1985) has suggested that a relationship of T=0.37D is more appropriate for

TABLE 2. Albumin immunologic distances of antisera to 10 species of Australian skinks cross-reacted to a range of other skink species. The data are uncorrected.

				Antibody							Geographic
	Lac	Lag	Lab	Lad	Ma	Lep	Lea	Lee	Led	Ef	origin
Antigen											
Lampropholis challengeri (Lac)	0	17	29	23	45	14	17	30	40	–	Australia
Lampropholis guichenoti (Lag)	20	0	18	20	32	13	16	29	46	105	Australia
Lampropholis basiliscus (Lab)	17	13	0	12	–	–	–	–	–	–	Australia
Lampropholis cf. *delicata* (Lad)	21	19	25	0	–	–	–	–	–	–	Australia
Morethia adelaidensis (Ma)	59	62	49	46	0	36	46	28	29	–	Australia
Leiolopisma pretiosum (Lep)	–	–	–	–	30	0	6	18	37	–	Australia
Leiolopisma palfreymani (Lea)	20	16	23	12	–	5	0	17	35	–	Australia
Leiolopisma entrecasteauxii (Lee)	36	28	–	26	21	23	0	28	–	–	Australia
Leiolopisma duperreyi (Led)	67	51	49	47	22	35	40	26	0	–	Australia
Egernia frerei (Ef)	110	126	98	100	–	–	129	–	–	0	Australia
Antigens only											
Leiolopisma metallicum	17	16	24	21	–	4	9	–	–	–	Australia
Leiolopisma zia	24	22	29	14	–	14	13	25	47	–	Australia
Leiolopisma grande	45	41	44	35	–	29	–	–	34	–	New Zealand
Cryptoblepharus plagiocephalus	–	–	–	–	31	–	–	22	–	–	Australia
Carlia rostralis	28	21	26	24	–	27	22	38	39	–	Australia
Menetia greyi	60	50	48	46	21	38	41	35	10	–	Australia
Emoia longicauda	58	61	57	50	54	37	41	40	–	–	Australia/ New Guinea
Eugongylus rufescens	53	54	60	55	–	–	–	36	–	–	New Guinea
Sphenomorphus murrayi	94	104	85	–	–	–	–	–	–	–	Australia
Ctenotus grandis	110	117	94	96	–	–	103	–	–	–	Australia
Mabuya multifasciata	–	60	–	–	–	–	126	–	–	–	Indonesia
Lamprolepis smaragdina	114	120	90	–	–	–	–	–	–	–	New Guinea
Tribolonotus gracilis	–	120	140	–	–	–	–	–	–	–	New Guinea
Egernia kingii	–	–	–	–	–	–	–	–	–	17	Australia
Tiliqua rugosa	–	–	–	–	–	–	–	–	–	20	Australia

eutherian mammals, although Baverstock et al. (1989) have shown that such a relationship is not appropriate for marsupials. We herein use T=0.6D, although this relationship may need to be adjusted if and when relevant fossil data come to hand.

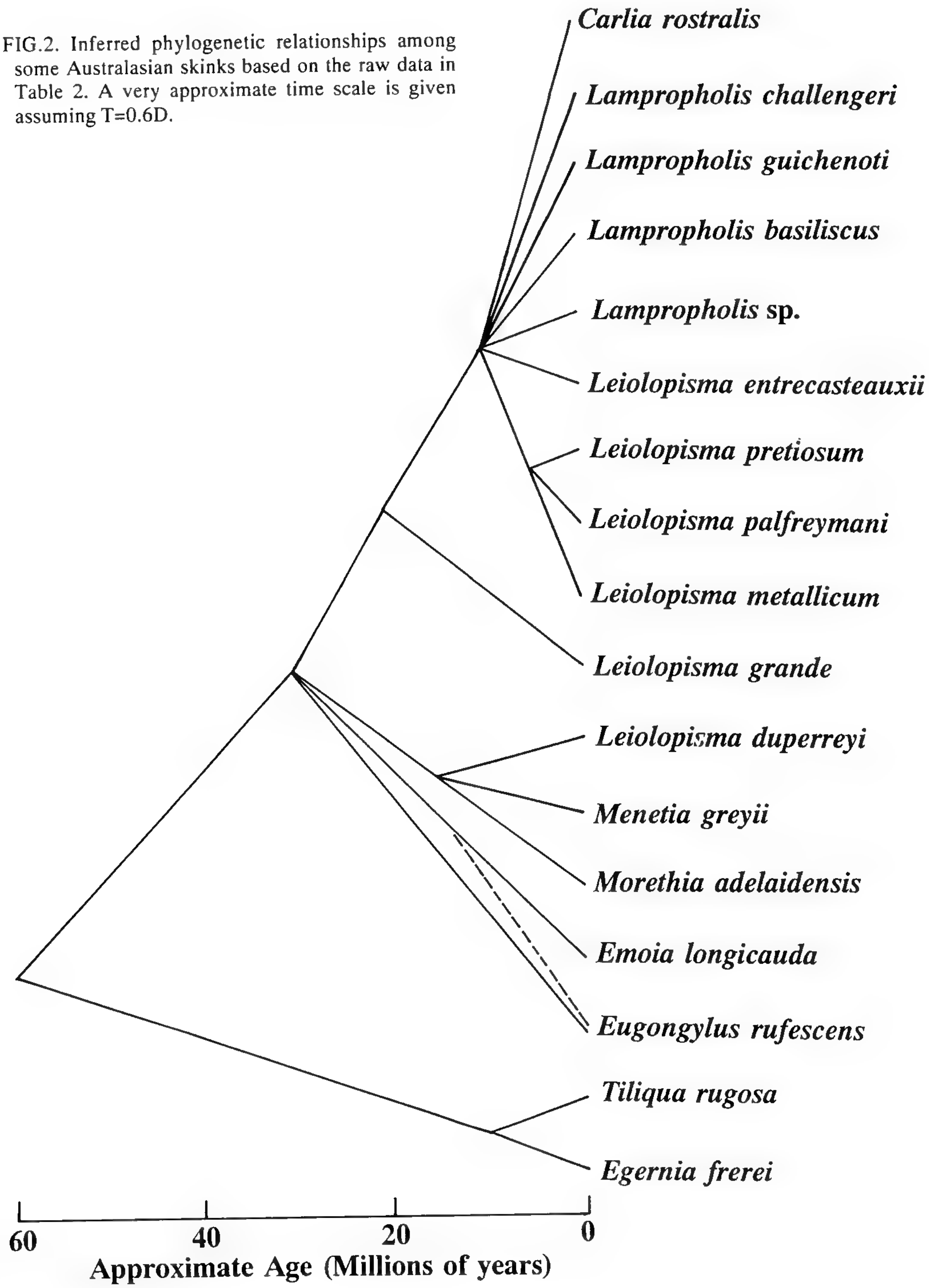
Fig. 1. shows an approximate time-scale for the Australasian agamid radiation, using T=0.6D. On this analysis, the three amphibolurids represented form a monophyletic group, radiating in the late Miocene-early Pliocene. However, the one-way data (Table 1) suggest that the radiation involving other amphibolurids (and *Moloch*) occurred a little earlier, perhaps mid-Miocene, and that the Australian *Physignathus* and *Gonocephalus* also diverged about this time.

Based on the phylogenetic relationships indicated by Fig.1 and Table 1, it is tempting to speculate that the Australasian agamids do indeed have a Gondwanan origin. On this scenario, the Australasian component gave rise to radiations in two land masses, Australia and what was to become New Guinea. The first gave the amphibolurid radiation (including *Moloch*) and the second to New Guinean *Gonocephalus* and *Physignathus*, which recently entered Australia. The morphological similarity of Asian and New Guinean *Gonocephalus* and *Physignathus* is then seen to be due to convergence. Using T=0.6D gives a divergence time of *Agama* from Australasian agamids of 40MY. This is much too short for a Gondwanan connection, but it is based on only one species of African agamid, one-way cross- reactions, and an untested calibration of T=0.6D. If the Australasian agamids do have an Asian origin, then the possible sister taxa are not Asian *Gonocephalus* and Asian *Physignathus*, and have not been included in our analyses.

THE SCINCIDAE

Most inferences of the biogeographic history of Australian skinks are based on the distribution of extant forms (the fossil record is virtually non-existent) and estimates of the time scale of cladistic events from comparisons of levels of faunal diversity (Greer, 1979; Tyler, 1979; Cogger and Heatwole, 1981). It has been amply

FIG.2. Inferred phylogenetic relationships among some Australasian skinks based on the raw data in Table 2. A very approximate time scale is given assuming T=0.6D.



demonstrated that speciation and morphological clocks do not exist (Baverstock and Adams, 1987) and hence estimates of time based on these are purely speculative. Additionally, if the current systematics does not accurately reflect the phylogenetic relationships then inferences based on the distribution of such groups can be erroneous. Greer (1979), Tyler (1979) and Cogger and Heatwole (1981) concur that skinks arose north of Australia's present day position and Greer (1979) and Cogger and Heatwole (1981) propose that the ancestors of the scincid radiation entered Australia at least twice. Cogger and Heatwole (1981) suggest that the earliest invaders were here by at least the mid-Tertiary. The finding of fossil cranial elements from the mid-Miocene referable to the extant genus *Egernia* (Estes, 1984) at least gives a minimum age of entry which is compatible with this view.

The microcomplement fixation data suggest some anomalies in the current systematics and provide a rough estimate of the timing of evolutionary events. However, our data are as yet not extensive enough at the suprageneric level to provide information relevant to the evolutionary origins of the skink fauna of Australia. Fig.2 is summary cladogram of the relationships among some Australian skinks that seem to be indicated by the data in Table 2. We do stress however that these proposed relationships are very tentative, and will undoubtedly be refined as additional antigens and antisera are added to the data set. We have also added a very approximate time scale assuming T=0.6D is an appropriate calibration for the Australian skinks.

While our data provide strong support for a monophyletic *Eugongylus* group, they are at odds with Greer's (1979) concept of two subgroups within the *Eugongylus* group. If indeed there are two subgroups present then their compositions are vastly different from those conceived by Greer (1979). Several authors concur that the genus *Leiolopisma* is composite (Rawlinson, 1974; Greer, 1982). Our data demonstrate that this is so, but the groups delineated do not agree with previous schemes. *L. duperreyi* is more closely related to *Morethia* and *Menetia* than to other *Leiolopisma*. Greer (1980) had previously suggested such a relationship but later included *L. duperreyi* in his *L. baudini* species group which included *L. entrecasteauxii* and *L. metallicum*, species not especially related by the microcomplement fixation data.

Hutchinson (1980) from immunoelectrophoretic comparisons and a reappraisal of Greer's (1979) morphological assessment suggested that the spiney skinks of the genus *Tribolonotus* are probably closest to the *Eugongylus* group. While our data on *Tribolonotus* are based at this stage on one-way comparisons, they do not provide strong support for such a view, and instead suggest that *Tribolonotus* is at least as divergent from the *Eugongylus* group as *Egernia* and *Lamprolepis*.

While the present study shows that the genus *Leiolopisma* is at least paraphyletic, nevertheless the New Zealand representative of the genus available to us (*Le. grande*) is clearly a member of the *Eugongylus* group, with a divergence time from its nearest Australian relatives of about 20 MYBP. Thus a Gondwanan origin for New Zealand *Leiolopisma* is clearly rejected by the albumin data, which support Hardy's (1977) view of a more recent invasion of New Zealand from Australia.

CONCLUDING REMARKS

We have been struck by the highly disparate pattern of morphological and molecular genetic evolution in the Australian skinks and agamids. In the skinks, morphologically similar species are nevertheless highly divergent at the molecular level. This feature is emphasised in the genus *Lampropholis*, where sibling species have albumins that differ by up to 20 amino-acids. By contrast, the agamids show morphological diversity in the face of relative uniformity at the albumin level. Species as diverse at the morphological level as bearded dragons (*Pogona*), thorny devil (*Moloch*), and frilled-neck lizard (*Chlamydosaurus*) are nevertheless as similar at the molecular level as sibling species of *Lampropholis*.

These contrasts highlight the vast disparity between morphological evolution and molecular evolution, a feature which has been noted in other groups (e.g. Maxson and Wilson, 1974; Wilson et al., 1977; Baverstock and Adams, 1987). While rates of molecular evolution may vary a little between different groups (perhaps two- or threefold; see Brownell, 1983; Wu and Li, 1985), it is apparent that rates of morphological evolution can vary enormously between groups. Thus estimates of divergence times and biogeographic reconstructions that rely upon considerations of morphological diversity alone are unlikely to be valid.

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FURTHER EVIDENCE OF OPHIOPHAGY IN AN AUSTRALIAN FALCON: Australia, despite the presence of a rich terrestrial snake fauna, does not support a specialised predator of snakes among its raptors. One species, the Brown Falcon *Falco berigora* Vigors and Horsfield, does possess certain morphological features - densely feathered breast, thick toes, and coarsely scaled legs and feet - that are usually associated with specialised snake-eating raptors such as the Old World snake eagles, *Circaetus* and *Spilornis*, and New World Laughing Falcon, *Herpetotheres cachinnans*.

Although there are a number of records of Brown Falcons preying on snakes in the older literature (Shea, 1987), these do not provide identifications of the snakes involved. Recent reports (see Sonter and Debus, 1985; Shea, 1987 and citations therein) provide evidence that these raptors may be important predators of snakes in some areas (if not the greater part of the falcon's range). The following contribution provides evidence based on field observations of Brown Falcons as predators of both elapid and colubrid snakes. The observations reported were made during general surveys of raptors. Each record is summarised in the anecdotal list below. Lengths of snakes given are estimates and are only provided for complete specimens.

Brown Tree Snake *Boiga irregularis*: single record of 1.0m specimen being carried in flight, Maleny, SEQ (October 1971).

Green Tree Snake *Dendrelaphis punctulatus*: one partially eaten specimen brought to nest, Woodford, SEQ (November 1986); one being carried in flight, 0.8–1.0m, over Bruce Highway near Nambour, SEQ (August 1990).

Keelback *Tropidonotus mairii*: two partially eaten specimens observed in nest, Woodford, SEQ (November 1986).

Yellow-faced Whip Snake *Demansia psammophis*: one 0.5m specimen being carried in flight, near Townsville, NEQ (July 1979); one specimen being eaten on roadside post, Bundaberg, SEQ (August 1979); one specimen, 0.6-0.8m, being carried in flight, Yarraman, SEQ (April 1987).

Whip Snake *Demansia* sp.: partially eaten specimen being carried in flight, Richmond, CQ (May 1984)

Marsh Snake *Hemiaspis signata*: one specimen being eaten at perch, near Kenilworth, SEQ (December 1976).

Red-bellied Black Snake *Pseudechis porphyriacus*: single partially eaten specimen being carried in flight, Maleny, SEQ (June 1978).

Eastern Brown Snake *Pseudonaja textilis*: one specimen carried in flight, 0.9–1.1m, near Rockhampton, CEQ (May 1985); one specimen being carried in flight, 1.1-1.2m, near Gladstone, SEQ (April 1981); one partially eaten specimen being carried in flight near West Wyalong, SCNSW (December 1984).

Brown Snake *Pseudonaja* sp.: (possibly *P.guttata*) being carried in flight, 0.5–0.6m, near Richmond, CQ (August 1983).

These observations provide further evidence that the Brown Falcon, although a generalist predator, is an accomplished predator of snakes. Not only are non-venomous and mildly venomous species taken, highly dangerous species of the genera *Austrelaps*, *Notechis*, *Pseudechis* and *Pseudonaja* are also successfully preyed upon (see also Sonter and Debus, 1985; Shea (1987). It would also appear from the above observations and the records published to date, that there is no tendency on the part of these raptors to select smaller sized elapids relative to colubrids.

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G.V. Czechura, Queensland Museum, PO Box 300, South Brisbane, Queensalnd 4101, Australia; 17 August, 1990.

COURTSHIP AND MATING IN WILD *VARANUS VARIUS*(VARANIDAE: AUSTRALIA)

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Carter, D.B. 1990 09 20: Courtship and mating in wild *Varanus varius* (Varanidae: Australia).*Memoirs of the Queensland Museum* **29**(2): 333-338.Brisbane. ISSN 0079-8835

Observations of wild *Varanus varius* in southern New South Wales indicate that mating takes place between mid-November and early January; that communication between individuals is by means of olfactory, visual and tactile cues; that females mate with several males, including subordinates; and that pairs mate frequently using hemipenes alternately.☐ *Varanidae, mating, reproduction, behaviour, Varanus varius.*

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Goannas are wary lizards. Their behaviour in the wild is rarely documented although there are a number of published accounts of reproductive behaviour in captive varanids (Auffenberg, 1983; Moehn, 1984). The published records of mating in wild varanids include King and Green (1979), Tasoulis (1983), Wilson (1987) and Auffenberg (1978, 1981) but apart from Auffenberg's studies of *Varanus komodoensis* these provide little detail. This paper reports the results of observations on courtship and mating obtained as part of a wider study of reproduction in wild lace monitors.

MATERIALS AND METHODS

This work was undertaken in the valley of the Deua River, Deua National Park in southeastern New South Wales (35°46' S, 149°56' E). The country is steep and rugged with rocky soils covered by an open forest dominated by *Eucalyptus globoidea*. The study site is in the southern temperate part of the range of *Varanus varius*, which is the only varanid known to occur in the area (Cogger, 1986). Goannas were captured with a pole and noose, measured, weighed and marked and released at the place of capture usually within 24h. They were individually marked, temporarily with bands of acrylic paint around the tail and permanently by excising a combination of scales from the prominent fringe of scales under the rear fourth toes. The latter method was preferred to toe clipping because it did not deprive these arboreal lizards of one or more of their strongly clawed digits.

Males were sexed when seen mating, when they fully everted their hemipenes during capture or handling, or by radioxerography of the base of the tail showing the hemipenes which are partly ossified (Shea and Reddacliff, 1986). Animals were classified as females only when they were seen mating or by the absence of hemipene ossification in radioxerographs. Probing at the base of the tail was considered an unreliable method of sexing (Weavers, 1983; King and Green, 1979). A selection of animals were fitted with radiotransmitters (tracking only), which were attached with glue and stainless steel sutures to the side of the tail just behind the rear leg (method of Weavers, 1983). Complete transmitter packages weighed between 19 and 22g (<1.5 % body weight).

On the evening preceding a planned period of observation a telemetered animal was located in its roost. The next morning before 0730h I would take up a suitable position about 5 -15m from the roost before the animal emerged. I was equipped with binoculars and radio receiver and was concealed under a frameless canvas hide which allowed me to move to keep animals in view (Carter, 1988). Although these lizards are usually very wary of humans and typically respond by climbing the nearest large tree, I was ignored by most animals whenever I wore the hide.

A total of 37 hours of observations from within the hide were made between 17 November, 1987 and 8 January, 1988. During the period from September, 1987 to March, 1988 a total of 81 days were spent at the study site and information on location and activity was recorded whenever individuals, pairs and groups of goannas were encountered. Events were timed to the nearest minute, Eastern Standard Time. Because it was impracticable to use video or still cameras, diagrams of behaviour were drawn from photographs of dead goannas arranged in accordance with detailed field notes

RESULTS

Ten marked animals and another five unmarked were observed either mating or in what were presumed to be mating groups. Table 1 summarises data about the marked animals observed; Table 2 provides details of the groups seen.

Mating Season

Throughout most of the year lace monitors were found to be solitary (174 solitary individuals were recorded). However between 18 November and 2 January, I saw 11 groups of goannas; some of which were mating, some fighting, some roosting together, and some that were surprised on the ground and climbed into trees before I could see what they were doing.These observations indicate that the mating season extends from about mid-November to early January.

Id No.	Sex (method)	SVL (cm)	Weight (kg)	Date (1st Capt.)
1	M(h)	65.0	6.30	10.09.87
3*	F(x)	49.0	2.10	18.09.87
7	U	43.5	1.16	06.10.87
11*	M(m)	78.0	7.00	21.10.87
14*	F(m)	46.5	2.06	22.10.87
18*	M(?)	58.5	3.75	18.11.87
19*	M(?)	73.0	7.25	18.11.87
22*	M(?)	61.5	4.65	18.11.87
26	M(h)	66.0	5.40	24.11.87
32*	F(m)	47.5	1.85	20.12.87

TABLE 1. Data concerning marked individuals found in mating/courting groups. Sex is followed in brackets by method of sexing, U = unknown sex, h = everted hemipenes, x = radioxerograph, m = mating, ? = probably male because of behaviour towards known males and females. Asterix indicates animals which were carrying a transmitter during observations.

TABLE 2. Dates, activities and composition of mating groups observed November 87 to January 88. F=female, M=male, n=not marked, U=unknown sex, a= unmarked but recognisable individual.

Date	No of goannas	Activity	Individuals
18.11.87	3	on ground	14(F), 18(M), 19(M)
20.11.87	2	roosting in mound	(F), 18(M)
21.11.87	2	mating	14(F), n(M)a
22.11.87	3	roosting in mound	14(F), 11(M), n(U)
23.11.87	2	fighting	n(M)a, 11(M)
23.11.87	6	fighting/ mating	11(M), 14(F), 18(M), n(M), n(M), n(F)
24.11.87	3	on ground	7(U), n(U), n(U)
20.12.87	2	on ground	32(F), 22(M)
23.12.87	2	mating	32(F), n(M)
26.12.87	2	on ground	32(F), 26(M)
02.01.88	2	on ground	3(F), 1(M)

Mating System

Females mated with several males over a period of days. Female 14 was seen to mate with two different males and over a period of 6 days associated with at least six different males. Female 32 was found on three separate days with three different males and was observed mating with one of them. Mating/courting groups varied from just the pair to as many as six individuals. If females were accompanied by more than one male the largest would chase other males that approached the females.

Communication and Courtship

Lace monitors appear to use three forms of communication - olfactory, visual and tactile. Scent trails and marking of particular sites are used to communicate over long distances or periods of time whereas body position and head movements are used to communicate directly when animals can see each other. Tactile cues become important as the male comes close to the female and attempts to straddle and mount her.

Male 11 was seen to follow, for about 20m, the exact pathway taken by another male 10min earlier. Male 11 moved slowly with wide sweeps of the head and rapid flicking of the tongue consistent with detecting and following a scent trail (Auffenberg, 1982). On another occasion an unmarked male approached a tree where male 18 had basked 80min previously. After flicking his tongue around the base of the tree for about 1min the unmarked male carefully wiped both sides of his head on the tree trunk and then repeated this action before moving away. Another unmarked male was observed for 1h as he located the overnight roost (hollow log) of female 32 and then followed her exact path to the nearby tree where she had moved to bask 2h 18min earlier. While he was locating her he stopped twice to vigorously rub his cloacal region against the ground and twice to rub his head, neck and throat on a tree and a log near her roost. During his approach to her roost, he moved very slowly over a distance of about 100m and appeared to be carefully scenting the ground with rapid flicks of his tongue. He also seemed to be pressing his cloaca to the ground as he walked.

One large termite mound appeared to be an important focus of breeding activity for animals 11, 14, 18, 19 and at least 5 unmarked goannas. The mound had a large hole dug into the side. Over one week of observations several of these goannas roosted in the hole overnight and during the day there were frequent skirmishes between males that tried to approach the mound. Two males, which were seen mating or attempting to mate with females, had both visited the mound less than thirty minutes before they were seen with the females and may have picked up the female scent trail at the mound.

Goannas, which were close enough to see each other, adopted distinctive posture and head movements according to their sex (Fig. 1.). Females remained still or moved slowly, always with their bodies flat on the ground and necks extended along the ground. Females were inconspicuous. In contrast, the movements of males were rapid and exaggerated, making them conspicuous. Males held their bodies raised from the ground, the neck usually vertical and the head

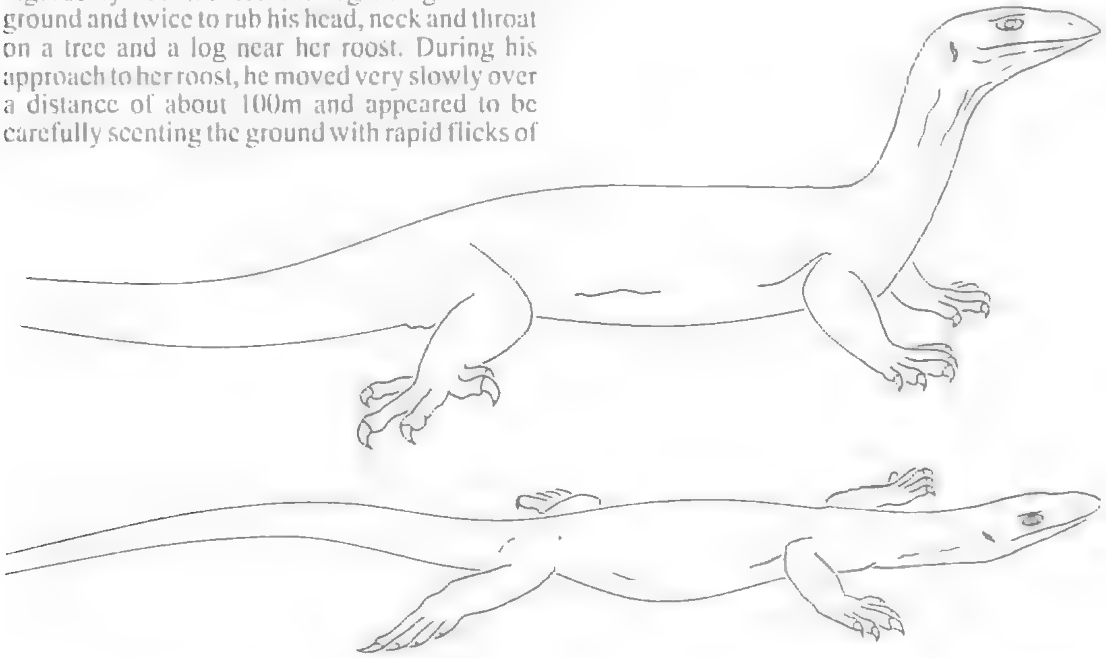

FIG. 1. Demeanour of male (top) and female (below) when they can see each other The female remains still or crawls slowly but always with body and neck flattened to the ground. The male moves rapidly, with head raised and often makes spasmodic shuddering movements of the head as he approaches the female. His behaviour towards other males is similar.

held high and frequently jerked from side to side in a spasmodic, shuddering fashion. This head shuddering became more frequent and pronounced when closely approaching a female. The unmarked male which spent at least an hour locating female 32 used this head shuddering signal when he looked up from the base of her tree and first saw her looking down at him from a height of about 5m. She immediately descended and they mated several times during the next hour. On another occasion when an unmarked female in a mating group was alarmed by my approach and climbed a tree, male 11 who was trying to mate with her climbed up after her and repeatedly gave the head shuddering signal. She ignored him and remained in the tree for the next 2h while I continued to watch the remaining animals, which appeared unconcerned by my presence. Head shuddering was also employed by males approaching each other - most vigorously by the largest of the males.

MATING

Twenty four acts of mating were observed. Female 14 and an unmarked male, with no other animals present, mated 16 times over a period of 3h. Another pair consisting of female 32 and an unmarked male mated 7 times over a period of 1h. In both these cases the unmarked males were relatively small - about 60cm snout-vent length - and certainly smaller than other males seen in the vicinity. Female 14 and the large male 11 were in a group with another female and 3 other males and, over a period of 2h, mated only once although male11 spent much of the time circling, hissing and chasing other males.

From these observations, mating behaviour can be summarised as follows. The female lies still and flat on the ground with neck fully extended and head on the ground (Fig. 1). The male approaches from the rear and to one side with body raised clear of the ground. The head is raised with the snout markedly tilted down towards the female and darts rapidly from side to side as he flicks his tongue over her back and neck (Fig 2). Sometimes the male's head movements appear to be an involuntary spasm or shudder. He brings his head up to the right of hers, his body lying diagonally across hers and his vent adjacent to the left side of her tail. He then reaches over the base of her tail with his right hind foot and scrabbles at the right side of her tail with his claws apparently to stimulate her to raise the base of her tail. She recurves her back, lifts her hindquarters off the ground and raises her tail in a high arch. With his right hind foot still over the top of her tail and holding it firmly, he curves the base of his tail under hers to insert the right hemipenis (Fig. 3).

Events so far have taken about half a minute and the pair may lie still in this position for a further half minute or so. Both may look around; the female with neck extended horizontally and head tilted up, the male with neck vertical and head horizontal. He may open his mouth slightly and pump the gular region presumably to cool. Then he begins vigorous thrusting, powered primarily by the left hind leg. Twenty or 30 thrusts may be made over about one minute with the last one or two being slower and much less vigorous. The muscle tension in both animals then subsides, the arched tails relax and they uncouple. The time taken from the initial approach by the male to uncoupling is two to three minutes.

The next copulation may commence within two or three minutes and in most cases the male approaches from the other side and uses the other hemipenis. After several copulations the male may retire to the shade to cool for a few minutes

FIG. 2. Courtship. The male begins to straddle the female, rapidly flicking his tongue over her back, neck and head. He may rake the claws of one front leg down her back. She remains flattened.

before returning to mate again. The female may terminate a period of mating by climbing a tree or may prevent the male from mounting by continually crawling forwards. During the last few matings between 14 and the unmarked male there was no vigorous thrusting as the male appeared to tire. On one occasion during mating between female 32 and the unmarked male, he raked his front claws several times along her back.

DISCUSSION

A comparison of my observations with those of Moehn (1984) for captive *V. timorensis*, Auffenberg (1978, 1981) for wild *V. komodoensis* and Auffenberg (1983) for captive *V. bengalensis* reveals differences in behaviour and timing of courtship events. None of these papers report head shuddering or jerking behaviour by males in courtship although Davis et al. (1986) report such behaviour by male *V. dumerili* prior to combat. Neither Moehn nor Auffenberg emphasise distinctive demeanours for males and females early in courtship although Auffenberg (1983) reports 'do nothing' behaviour by female *V. bengalensis* which seems to encourage courtship by males and Moehn mentions that female *V. timorensis* are 'passive' during courtship. Mating of *V. timorensis* was markedly prolonged compared to *V. varius*. Whereas *V. timorensis* were coupled for up to 47min and pelvic thrusting occurred at intervals of 5 to 22s, *V. varius* coupled for no more than four minutes and executed 20 or 30 pelvic thrusts within about one minute. *V. bengalensis* completed courtship and intromission in a maximum of 123s.

In both *V. komodoensis* and *V. bengalensis* Auffenberg emphasises the aggressive nature of females which he regards as a danger to males attempting to mate. He regards the pacifying and immobilising of females as an important part of courtship behaviour in these species and he interprets the mating success of large males as largely due to their ability to restrain females. I observed no aggressive behaviour by *V. varius* females towards males or other females. In general, females appeared to be cooperative until they terminated a period of mating by climbing a tree. During mating males did not restrain the forelegs of the female as Auffenberg reports for *V. bengalensis* although male *V. varius* maintained a firm grip on the female's tail with his hind leg during intromission. In this species males grow much larger than females (Carter, unpubl. obs.) and in all cases I observed the males were at least twice the mass of their partners. The initial approach by a male *V. varius* with raised body and conspicuous head movements may advertise his size and strength, as well as communicate his sex, and inhibit aggressive behaviour in females.

A prolonged period during which a pair mate frequently, as in *V. varius*, has not been reported for other species of varanids.

Several communication and courtship acts of *V. varius* coincide with the behaviour of other varanids. Tongue flicking over the female's back and neck, scratching upwards with the hind leg at the base of the female's tail, scratching the female's back with the foreleg and the position for mating are similar in *V. komodoensis*, *V. bengalensis*, *V. timorensis* and *V. varius*. Also, Auffenberg (1981) describes the importance of

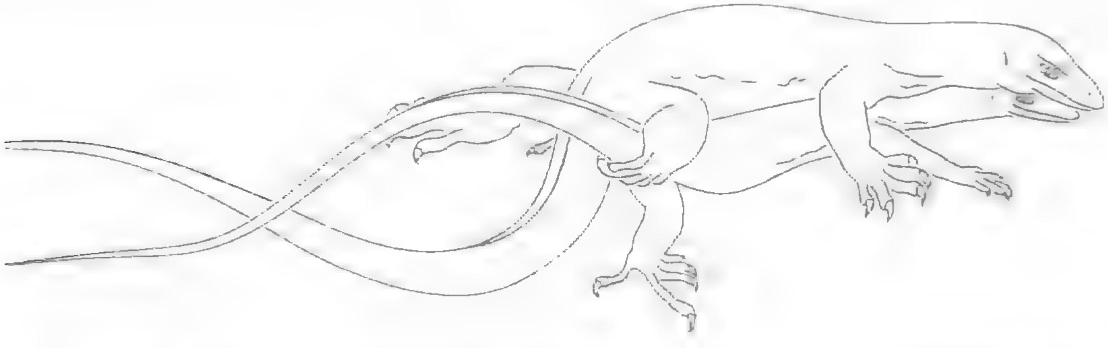

FIG. 3. Mating. The male has reached over her tail with his hind leg, scrabbling upwards on the side of her tail with his claws. She has responded by recurving her back, raising her hindquarters and arching her tail. With his hind foot gripping her tail he has then been able to curve his tail under hers and insert his right hemipenis.

scent marking in the behaviour of *V. komodoensis* and reports behaviour such as 'head scraping', 'cloaca scraping' and deposition of faeces.

That females are so readily able to mate with smaller males even though a dominant male may be in the vicinity is puzzling. The fierce fighting between males during the mating season, often resulting in large wounds (Carter, unpub. obs.), suggests that there is strong competition for mates. Yet females are left unattended by dominant males for long periods when they may mate with subordinate males. There may be mechanisms related to sperm competition or timing of fertilisation which would confer some advantage to dominant males.

ACKNOWLEDGEMENTS

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MIOCENE DRAGONS FROM RIVERSLEIGH : NEW DATA ON THE HISTORY OF THE FAMILY AGAMIDAE (REPTILIA: SQUAMATA) IN AUSTRALIA

J. COVACEVICH, P. COUPER, R.E. MOLNAR, G. WITTEN AND W. YOUNG

Covacevich, J., Couper, P., Molnar, R.E., Witten, G. and Young, W. 1990 09 20: Miocene dragons from Riversleigh: new data on the history of the family Agamidae (Reptilia: Squamata) in Australia. *Memoirs of the Queensland Museum* **29**(2): 339-360. Brisbane. ISSN 0079-8835.

Physignathus sp. and *Sulcatidens quadratus* gen. et. sp. nov. have been identified from a series of some 30 agamid jaw fragments recovered from the Riversleigh fossil beds. One specimen (dentary QM F18004) has a healed fracture.
The presence of *Physignathus* confirms a strong Asian influence in the composition of the Australian lepidosaur fauna as early as the Miocene. It also suggests that the Riversleigh area was well-watered at that time. Of the eight Australian Miocene lepidosaur genera, six survive. *Sulcatidens* and *Montypythonoides* are extinct.
Examination of the type specimens of the extant *Physignathus cocincinus* of Southeast Asia confirms that the Australia- ?Papua New Guinean *P. lesueurii* is properly assigned to the genus *Physignathus*. ☐ *Sulcatidens, Physignathus, Riversleigh, Agamidae, Miocene.*

J. Covacevich, P. Couper, R. Molnar, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101; G. Witten, Phillip Institute of Technology, Bundoora, Victoria 3083; W. Young, Department of Oral Biology, University of Queensland, St Lucia, Queensland 4067; 21 January, 1990.

Fossils from freshwater limestones of Riversleigh Station, northwestern Queensland (c.19°02'S,138°45'E) were first reported near the turn of the century, but no serious work on them was undertaken until the 1960s. Intensive collection of this deposit began in the late 1970s with team work led by Dr Michael Archer (of the University of New South Wales; Archer, Hand and Godthelp, 1986). What is known of the Riversleigh stratigraphy and palaeoecology is summarized by Archer, Godthelp, Hand and Megirian (1989).

The rich fossil fauna includes fish, frog, reptile (crocodile, turtle, lizard, python), bird, marsupial (bandicoot, dasyurid, potoroid, phalangerid) and placental (bat, rodent) remains (Flannery, Archer and Plane, 1983; Hand, 1982, 1985). Studies of the fauna continue in many groups, including arthropods and snakes (typhlopids, elapids). Reviews and descriptions of some of these groups have been published (e.g. Smith and Plane, 1985; Hand, 1985; Archer and Flannery, 1985; and references therein). From comparisons with other fossil faunas of known age, it has been suggested that the Riversleigh deposit yielding the material described herein is of Miocene age (Archer and Bartholomai, 1978; Archer, 1981; Godthelp, pers. comm.).

Amongst material recovered are some 30 fragments of agamid skulls. Agamids are readily distinguished in having fixed, acrodont teeth which can be differentiated into 'incisors, canines and molars' (Boulenger, 1885). Agamid dentition and other distinctive characters are ably summarized by Boulenger (1885) and Estes (1983b). Modern Australian agamid maxillae and dentaries are illustrated in Fig. 1. The Riversleigh agamid material is small sized and in delicate condition. These fragments have been compared with small samples of all but one of the extant Australian genera of agamids. Not available to us is *Cryptagama* Witten 1984. (*Cryptagama aurita*, the type and only species, most closely resembles *Ctenophorus clayi*, another small cryptic dragon (Witten, unpublished data)). The fossils have also been compared with a range of agamids from other continents, either through the literature (e.g.

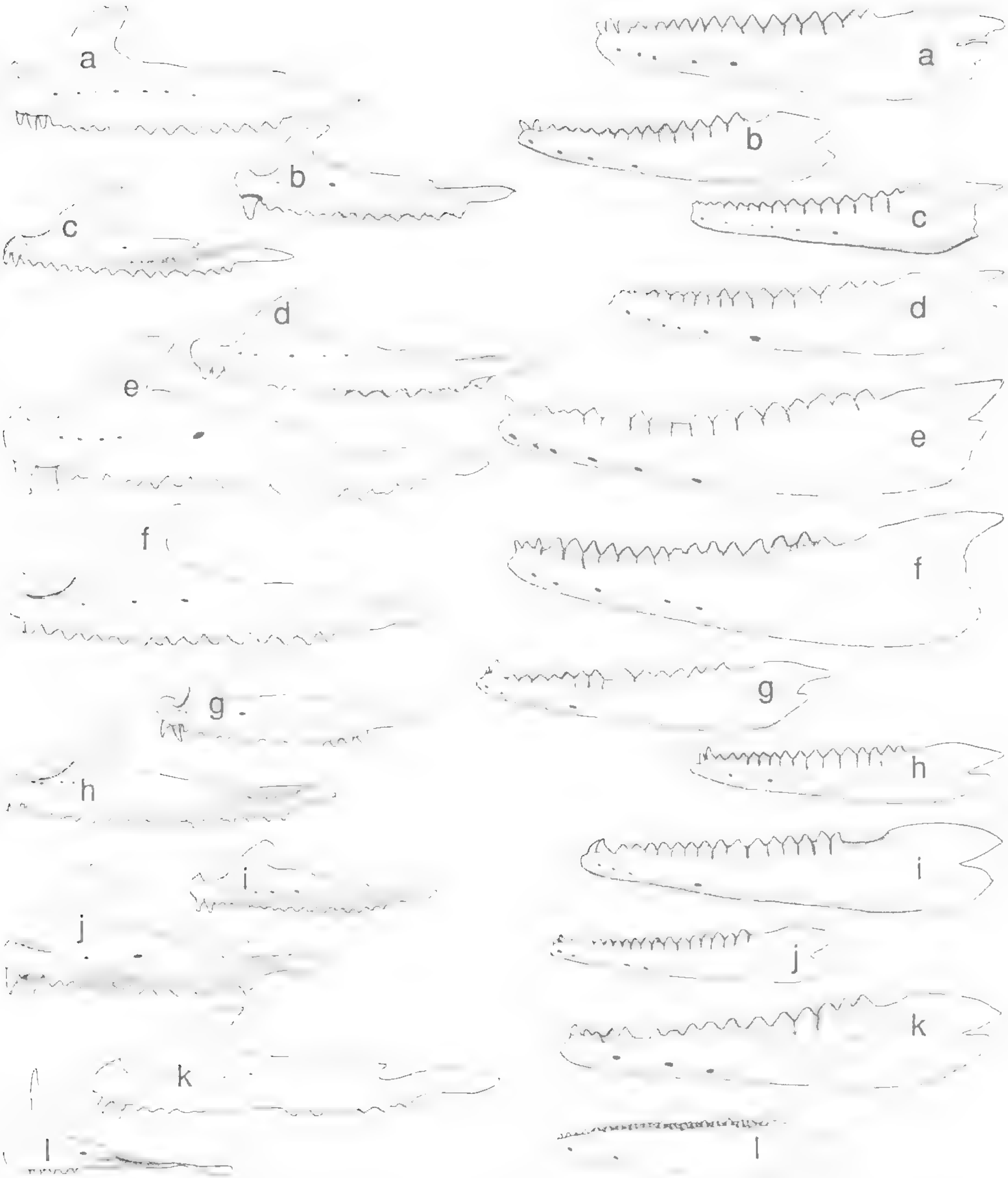


FIG. 1. Maxillae (left) and dentaries (right) from modern Australian agamids. (a) *Physignathus lesueurii* x1.5 (QM J26671); (b) *Diporiphora bilineata* x3, (QM J11141); (c) *Hypsilurus spinipes* x1.5 (QM J45306); (d) *Pogona barbata* x1.5 (QM J23950); (e) *Chamydosaurus kingii* x1.5 (QM J45307); (f) *Chelosania brunnea* x3 (WAM R41565); (g) *Caimanops amphiboluroides* x3 (WAM R15564); (h) *Tympanocryptis tetraporophora* x3 (QM J34580); (i) *Ctenophorus caudicinctus* x3 (QM J21654); (j) *Lophognathus gilberti* x1.5 (QM J39042); (k) *Gemmatophora nobbi* x3 (QM J38738); (l) *Moloch horridus* x3 (QM J11492).

Cooper and Poole, 1973; Cooper, Poole and Lawson, 1970) or with specimens (e.g. Chamaelonidae, Sphenodontidae).

Collection designations: AMNH, American Museum of Natural History, New York; MNHN, Musée Nationale d'Histoire Naturelle, Paris; QM, Queensland Museum, Brisbane, WAM, Western Australian Museum, Perth.

COMPARATIVE MATERIAL EXAMINED

RECENT AUSTRALIAN AGAMIDAE

Amphibolurus nobbi ♂. QM J38748, Mt Windsor Tableland, NEQ.

Caimanops amphiboluroides ♀. WAM R14464, 34km S of Warrorra, WA.

Chelosania brunnea. WAM R41565, Mitchell Plateau, WA.

Chlamydosaurus kingii. QM J3718, Zillmere, Brisbane, SEQ; QM J5707, Gulf Country; QM J19707, Rockhampton, MEQ. (dentary and maxillary fragments); QM J21929, Darwin area, NT; QM J45307, Cooktown area, NEQ; QM J47642, (juv) Wenlock, Pascoe River, Cape York, NEQ.

Ctenophorus caudicinctus ♂. QM J21654, Black Mountain, Warenda Station, WCQ.

Diporiphora bilineata ♀. QM J11141, Endeavour R., near Cooktown, NEQ.

Lophognathus gilberti ♀. QM J39042, 56.3km E of Camooweal, NWQ.

Gonocephalus boydii ♂. QM J17799, Mt Bellenden Ker, NEQ.

G. spinipes, QM J8330, Coomera Gorge, Lamington National Park, SEQ; ?. QM J45306,Richmond Range, via Bonalbo, NENSW.

Moloch horridus ♂.QM J11492, Giles, WA.

Physignathus lesueurii. QM J3865, Bellevue Station, via Coominya, SEQ; QM J5449, Brisbane, SEQ; QM J26671, Caboolture, SEQ; QM J35270, Ferguson SF, Saltwater Ck tributary, via Maryborough, SEQ. (left dentary only); QM J38108, Cobble Ck. via Samford, SEQ; QM J47339, Mt Nebo area, SEQ. (right dentary only); QM J47973, SEQ.

Pogona barbata. QM J4141, Brookstead, Darling Downs, SEQ; QM J14402, Wacol, Brisbane, SEQ; QM J23950, Everton Park, Brisbane, SEQ; QM J45852, no locality; QM J47070, Banyo, Brisbane, SEQ; QM J47077, Brisbane, SEQ.

Tympanocryptis tetraporophora ♂. QM J34580, Cuddapan Station, via Windorah, SWQ.

RECENT FOREIGN AGAMIDAE

Uromastyx aegypticus. AMNH 73160, Saudi Arabia; AMNH 74816, Saudi Arabia.

Physignathus cocincinus. MNHN Ag82, MNHN 2537, MNHN 1856, MNHN 2536.

CHAMAELEONIDAE

Chameleo (?) *basiliscus*. QM J45322, no data.

IGUANIDAE

Iguana sp. QM J49263, no data.

SPHENODONTIDAE

Sphenodon punctatus. QM J1046, New Zealand.

FOSSIL AGAMIDAE

Middle to late Miocene specimens, Gag Site. QM F18031-F18033.

Early Miocene specimens, Godthelp Hills and Hal's Hill sequence. QM F18004-F18011, QM F18014-F18030.

?, Inabayance Site, QM F18012-F18013.

FOSSIL AGAMIDS FROM RIVERSLEIGH

Identification of this material has been confounded by the small size and fragility of the fragments and by the fact that they are all from only dentaries or maxillae. Not one piece of cranium has yet been found. The studies by Cooper and Poole (1973) and Cooper et al. (1970) have been very useful in regard to cranial and dental anatomy comparisons and in recognising ontogenetic changes. Despite this, however, distinguishing juveniles from adults and making identifications from only a few characters has been difficult. In the descriptions which follow, the extent of our material is shown in accompanying diagrams. The material present is shaded on stylized agamid skulls or jaws, based on those of *Diporiphora bilineata*. The descriptions concentrate on features of potential taxonomic significance.

In an effort to refine the process of identification of these small fragments, epoxy resin replicas of QM J5449, J47339 (*Physignathus lesueurii*) and of fossil specimens QM F18024, F18011, F18018 and F18015 were made for comparisons of microwear patterns. The replicas were sputter coated with gold and examined under a Phillips 505 scanning electron microscope to compare anatomical features with those produced by wear. However, there are few microwear features on the specimens and, consequently, they are of no diagnostic significance.

Family AGAMIDAE Gray, 1827
Physignathus Cuvier, 1829
Physignathus sp.

QM F18004

LOCALITY

Camel Sputum Site (Camel Sputum local fauna).

DESCRIPTION

A portion of left dentary which bears 12 acrodont teeth and a trace of the 13th acrodont tooth. Length 17.38mm, maximum depth (excluding tooth row) 3.71mm. There is a healed fracture in the mid tooth row. The fracture has healed out of alignment, displacing the anterior half of the dentary towards the labial.

The labial surface of the dentary is vertically notched between the tooth bases. Three foramina are present close to the ventral surface, below the third, fifth and seventh acrodont teeth. The anterior ventral surface of the dentary is badly weathered, so it is impossible to determine whether more foramina were present. On the lingual surface a longitudinal groove runs beneath the tooth bases. This groove shallows posteriorly. It is not continuous, having been displaced by the mid-dentary fracture. A large foramen is present in the roof of the Meckelian Groove, below the third posteriormost acrodont tooth. When viewed occlusally, the displacement of the tooth row is obvious. Both tooth surfaces are rounded, but the lingual is slightly flattened. An inward curve can be detected towards the anterior tip of the dentary.

QM F18007

LOCALITY

Camel Sputum Site (Camel Sputum local fauna).

DESCRIPTION

Right dentary; length 17.67mm; maximum depth (excluding teeth 4.96mm). No pleurodont teeth are present, although one empty 'socket' is visible in occlusal aspect. The first and third acrodont teeth are damaged.

In a labial view, only one foramen is visible, situated below the eighth acrodont tooth. The labial surface is pitted and there are deep notches at the bases of the acrodont teeth.

Viewed occlusally the acrodont teeth are rounded on both lingual and labial surfaces. The posterior three acrodont teeth are weakly cusped. The lingual faces are slightly flattened. The anterior tip of the dentary curves inward. On the lingual face of the dentary a deep groove runs below and parallel to the acrodont tooth row. The Meckelian Groove is clearly visible, but badly chipped anteriorly.

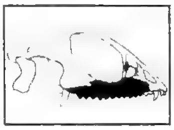
QM F18008

LOCALITY

Wayne's Wok (Wayne's Wok Site local fauna).

DESCRIPTION

Right, worn maxilla bearing 11 acrodont teeth, with a flattened labial aspect. Length 16.25mm; maximum depth (excluding teeth) 4.01mm. The posterior three acrodont teeth are weakly cusped.



On the labial surface, there is a slight inward curve of the maxilla, tilting the tooth row lingually. High on the labial face, below the posterior margin of the nasal process, are two foramina. Further foramina are present in the groove parallelling the maxillary/jugal/lacrimal suture. The largest of the foramina lies directly behind the nasal process. Posterior to this are four small foramina. A small process projecting towards the rear of the maxilla is situated posteriorly on the maxillary/jugal suture. This is located above the third acrodont tooth from the posterior margin of the tooth row. There is a broad palatal process that reaches its widest point towards the middle of the tooth row, then rapidly tapers off, becoming almost non-existent posteriorly.

QM F18012

LOCALITY

Wayne's Wok (Wayne's Wok Site local fauna).

DESCRIPTION

Portion of right maxilla bearing complete acrodont tooth row. Length 19.67mm, maximum depth (excluding teeth) 3.81mm (Fig. 2).

The first four acrodont teeth are damaged, but

the rest of the acrodont tooth row has a flattened labial aspect and the teeth are slightly cusped. The acrodont teeth are moderately 'shouldered'. The maxilla has a

FIG. 2. Occlusal view of QM F18012 x3.

slight inward curve tilting the acrodont teeth lingually. Three foramina are present on the labial surface above the third acrodont tooth; and a further two above the sixth and eighth acrodont teeth. Three foramina are present in the groove which runs parallel to the jugal/maxilla/lacrimal suture. A small process projecting towards the rear of the maxilla is situated posteriorly on the maxillary/jugal suture. This is located above the third acrodont tooth from the posterior margin of the tooth row. On the lingual surface, the palatal process is moderately developed anteriorly, broadening to its widest point half way along the acrodont tooth row, then narrowing posteriorly.

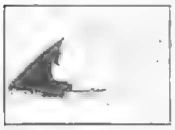
QM F18013

LOCALITY

Inabayance Site.

DESCRIPTION

Almost complete left side of snout, including the premaxilla. Length 18.13mm; maximum depth (excluding teeth) 14.07mm. Perfect suture definition is present between the premaxilla, nasal, maxilla and prefrontal (Fig. 3). The pleurodont teeth of the premaxilla and maxilla have not been preserved. The anterior four acrodont teeth are reduced from wear, each tooth being difficult to distinguish from those adjoining it. The posterior four acrodont teeth are intact, their broad triangular form being well preserved.



QM F18014

LOCALITY

RSO Site.

DESCRIPTION

Specimen F18014 is a fragment of the left dentary, bearing eight acrodont teeth. Length 11.24mm, maximum depth (excluding teeth) 3.66mm.

The labial surface of the dentary is deeply notched vertically between the tooth bases. Also clearly visible is a single foramen placed close to the ventral surface of the dentary, below the third acrodont tooth. The lingual surface bears a distinct longitudinal groove immediately below the tooth row. This groove shallows posteriorly. In the roof of the Meckelian Groove is a large foramen below the fifth acrodont tooth. Occlusally viewed, both tooth surfaces are gently rounded, but slightly flattened labially.

QM F18016

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Damaged right dentary, bearing two pleurodont and eight acrodont teeth. Behind the eighth acrodont tooth the fragment is damaged, revealing two internal longitudinal cavities, one above, and the other below, the Meckelian groove. Length 14.60mm, maximum depth (excluding teeth) 3.28mm. The labial face of the dentary bears four foramina, one below each of the pleurodont teeth and one below the second and sixth acrodont teeth. Strong vertical notch-

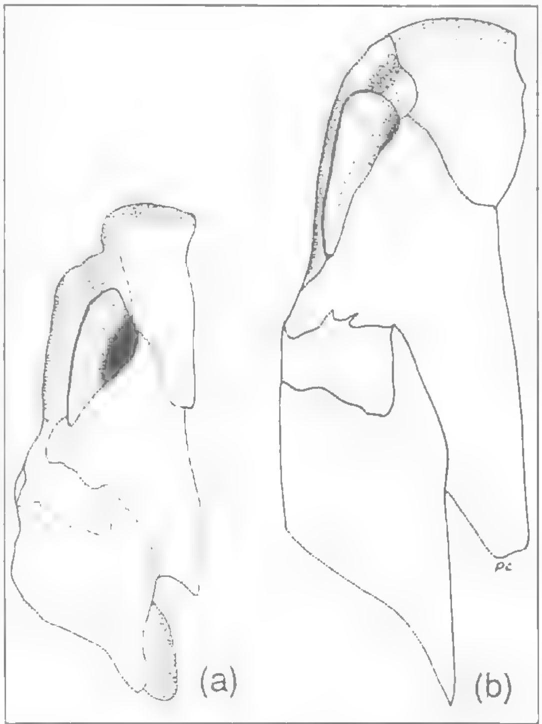


FIG. 3. Dorsal view of snout, illustrating variation in sutures between (a) *Physignathus* sp. x3 (QM F18013) and (b) *Physignathus lesueurii* x3 (QM J5449).

ing is evident at the bases of the acrodont teeth. The occlusal aspect shows a distinct inward curve of the dentary anteriorly. Both lingual and labial faces of each acrodont tooth are rounded, the tooth margin being centrally positioned. On the lingual surface of the dentary a distinct groove runs below the tooth row. The Meckelian Groove is clearly defined and has a distinct foramen posteriorly on the upper surface.

QM F18017

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Specimen F18017 is the upper anterior portion of the left dentary. Eight acrodont teeth are present on this fragment, the first and third broken at the base. Length 9.64mm, maximum depth (excluding teeth) 2.17mm.

The labial surface exhibits deep vertical notching between the tooth bases and, on the lingual surface, the only distinctive feature preserved is a longitudinal groove below the tooth bases. Viewed occlusally, both tooth surfaces are rounded but the labial is more strongly convex. A slight curvature of the jaw line is evident.

QM F18018

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

An almost complete left dentary with 14 acrodont teeth and three pleurodont teeth. Acrodont teeth two, three, four and seven are damaged. Length 24.38mm; depth (including tooth row) 4.76mm (Fig. 4).

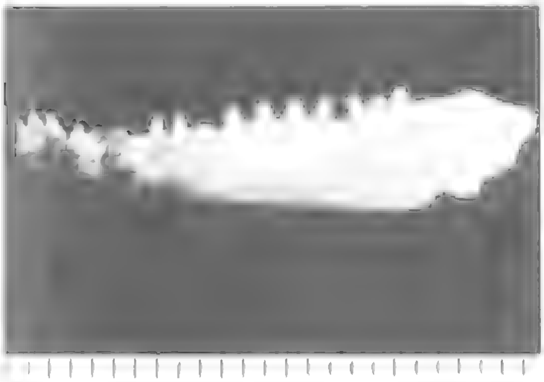
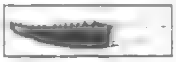


FIG. 4. *Physignathus* sp. (QM F18018).

Below the tooth row there is a distinct longitudinal groove lingually which shallows posteriorly.



QM F18019

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Anterior half of left dentary, bearing three forwardly inclined pleurodont teeth and eight acrodont teeth; length 12.64mm, maximum depth (excluding teeth) 2.67mm.

The second tooth is the larger. The acrodont teeth are sharply tipped and distinctly grooved at their bases labially along most of the tooth row. There are six foramina on the labial surface; one below each of the pleurodont teeth, and one below the second, fourth and seventh acrodont teeth. When viewed occlusally the acrodont teeth are rounded both lingually and labially and the dentary has a distinct inward curve anteriorly. On the lingual surface beneath the tooth row is a distinct longitudinal groove, which shallows posteriorly.

QM F18020

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Specimen F18020 is a portion of mid to anterior right dentary, bearing eight acrodont teeth. Length 9.09mm; maximum depth (excluding teeth) 3.27mm.

The labial face of the dentary is deeply notched vertically at the tooth bases. Three foramina are present towards the ventral surface, one each below the second, third, and sixth acrodont teeth. On the lingual surface a longitudinal groove runs beneath the tooth bases. The Meckelian Groove is clearly defined. Occlusally viewed both tooth surfaces are rounded but the lingual face is less convex. Anteriorly the tooth row curves medially.

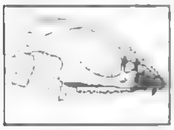
QM F18021

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Tip of right maxilla. Length 9.10mm, maximum depth (excluding teeth) 4.54mm. This fragment bears one complete acrodont tooth, followed by three damaged teeth. There are two pleurodont teeth, posteriorly inclined, and one empty socket.



A ridge is present on the labial surface of the maxilla. This originates at the base of the third pleurodont tooth and runs parallel to the acrodont tooth row. Below this ridge the maxilla is flexed lingually. Six foramina are present, three on the labial surface, one in the ventral margin of the naris and two in a groove where the maxilla joins the jugal behind the nasal process. The position of these foramina corresponds closely to those of F18024.

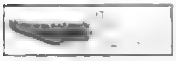
QM F18022

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Damaged left dentary. The anterior tip of the dentary is also damaged behind the second acrodont tooth. Two (possibly three) acrodont teeth are missing. All but the anterior six acrodont teeth are weakly cusped. Length 18.31mm; maximum depth (excluding teeth) 3.01mm (Fig. 5).



Anteriorly three pleurodont teeth, which incline slightly anteriorly, are present. Three prominent foramina are present labially, one each below both the second and third pleurodont teeth, and one below the second acrodont tooth.

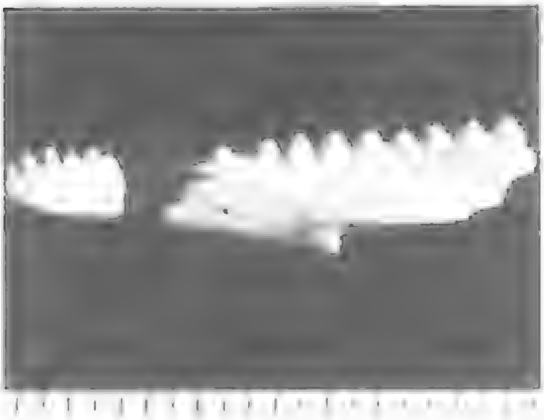


FIG. 5. *Physignathus* sp. (QM F18022).

The body of the dentary bears nine acrodont teeth, the first of which is damaged. There is a foramen below this first damaged tooth. The acrodont teeth have rounded labial and lingual surfaces, and deep vertical grooves at the bases on the labial aspect. On the lingual surface a distinct longitudinal groove runs beneath the tooth row. This groove shallows posteriorly. The Meckelian Groove is distinct and contains a foramen, situated below the fourth acrodont tooth from the posterior margin of the tooth row.

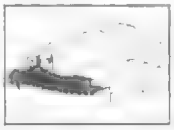
QM F18024

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Left maxilla, bearing complete tooth row. Length 18.5mm, maximum depth (excluding teeth) 5.44mm. There are 13 acrodont teeth, and two pleurodont teeth. Anterior to these is an empty 'socket' of a third pleurodont tooth.



A distinct ridge is present on the labial surface. This rises at the base of the third pleurodont tooth and runs parallel to the acrodont tooth row. Below this ridge, the maxilla inclines inwards. Five foramina are present on the labial face of the maxilla, beginning above the third pleurodont tooth and running back to the seventh acrodont tooth. Viewed from above the teeth are worn labially and rounded lingually. The acrodont teeth are weakly cusped. A distinct groove is present, running parallel to the maxillary/jugal/lacrimal suture just above the palatal process. This groove contains five foramina, two of which lie behind the nasal process. The second foramen is the largest. The remaining three are of equal size and are situated above the seventh and eighth acrodont teeth. On the lingual surface of the maxilla a distinct palatal process is present above the acrodont tooth row. This process is moderate anteriorly, broadening to its widest point half way along the acrodont tooth row. It then narrows and is only barely visible below the posterior acrodont teeth.

QM F18025

LOCALITY

Upper Site (Upper site local fauna).

DESCRIPTION

Right maxilla bearing a complete acrodont tooth row of 14 teeth and 1 pleurodont tooth.

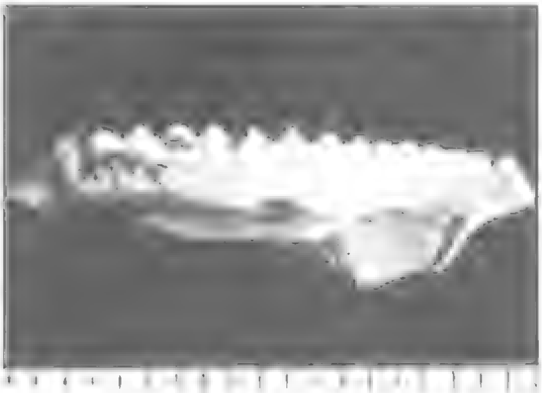
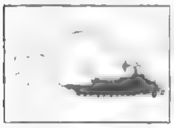


FIG. 6. *Physignathus* sp. (QM F18025).

Length 19.31mm; maximum depth (excluding teeth) 4.93mm. Just posterior to the anterior tip a ridge of enamel is preserved, indicating the presence of at least one other pleurodont tooth. The nasal process, the palatal process and the posterior tip of the maxilla are slightly damaged (Fig. 6).



Three foramina are present on the labial surface; one above the second acrodont tooth; and one each above the sixth and eighth acrodont teeth. Three additional foramina are present in the groove which parallels the jugal/maxilla/lacrimal suture; the anterior (below the nasal process) is the largest. The remaining two foramina are slightly smaller and lie above the eighth and ninth acrodont teeth. There are also four small foramina in this groove and one lies on the floor of the naris. A small process projecting towards the rear of the maxilla is situated posteriorly on the maxillary/jugal suture. This is located above the third acrodont tooth from the posterior margin of the tooth row. The rear six acrodont teeth are weakly cusped ('shouldered').

On the lingual face of the maxilla, there is a broad palatal process which reaches its widest point opposite the eighth and ninth acrodont teeth and is only barely discernable at the 11th acrodont tooth. A small secondary flange is present opposite the 13th and 14th acrodont teeth. The acrodont tooth row, occlusally viewed, has a flattened labial aspect. The pleurodont tooth is strongly inclined outwards.

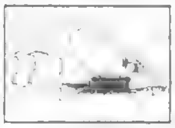
QM F18026

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Portion of the right maxilla bearing eight acrodont teeth. Three of these (the posterior two and the fifth from the posterior margin) are damaged. Length 9.98mm, maximum depth (excluding teeth) 3.93mm.



The labial face of the maxilla has a distinct longitudinal ridge about halfway down. Below this ridge, the maxilla and tooth row slope inwards. Two foramina are present, the first and larger is situated above the second anterior most tooth, and above the longitudinal ridge. The second foramen is much smaller, situated above the third tooth, and below the longitudinal ridge. A further three foramina are present in the groove running parallel to the maxillary/jugal/lacrimal suture. These lie close together and are situated anteriorly. The anteriormost foramen is the smallest and the posteriormost is the largest. Viewed laterally, the acrodont teeth are 'shouldered'.

On the lingual face of the maxilla is a broad palatal process which tapers posteriorly on the tooth row. Posteriorly, near the dorsal edge of the medial surface of the labial face there is a deep notch positioned posteriorly in the groove running parallel to the maxillary/jugal suture. This notch is normally associated with the posterior process of the maxillary/jugal suture. On specimen F18026 the process has not been preserved, but the position of the groove indicates that the process was positioned anterior to the end of the tooth row.

Viewed occlusally, the teeth have a flattened labial face and the lingual surface is distinctly rounded. Posteriorly in the tooth row the teeth have a distinct wear facet on the anterior face.

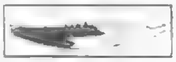
QM F18027

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Left dentary bearing complete tooth row. The two anterior-most acrodont teeth are damaged and the three pleurodont teeth are represented by broken stumps. Length 18.96mm, maximum depth (excluding teeth) 3.81mm.



The labial face of the dentary bears four foramina; one below both the second and third pleurodont teeth, and one below both the second and fifth acrodont teeth. When viewed occlusally the acrodont teeth are rounded on both the lingual and labial surfaces and the dentary exhibits a distinct inward curve anteriorly. On the lingual surface beneath the tooth row is a distinct longitudinal groove which shallows posteriorly.

QM F18028

Locality

Upper Site (Upper Site local fauna).

Description

Right dentary bearing 12 acrodont teeth; length 16.38mm, maximum depth (excluding teeth) 3.55mm. The acrodont tooth row is almost complete.

The labial surface of the dentary is pitted. Nonetheless two foramina are clearly visible below both the third and fifth anterior-most acrodont teeth. Deep notching is visible between the acrodont tooth bases, except on the two posterior acrodont teeth. On the lingual surface of the dentary, a distinct longitudinal groove shallowing posteriorly runs immediately below the tooth bases. There is a large foramen on the roof of the Meckelian Groove, below the sixth and seventh anterior-most acrodont teeth. Occlusally viewed both surfaces of the teeth are rounded, but the lingual is slightly flattened. A slight inward curve of the dentary is detectable anteriorly.

QM F18029

Locality

Upper Site (Upper Site local fauna).

Description

Anterior fragment of left dentary bearing one pleurodont and several acrodont teeth. There are two empty 'sockets' of pleurodont teeth, one on either side of the tooth. The first two of the acrodont teeth are in good condition. Length 9.45mm; maximum depth (excluding teeth) 2.52mm.

Occusally viewed, the dentary anteriorly displays a distinct inward curve. The pleurodont tooth is slightly procumbent. Four foramina are present on the labial surface of the dentary; one below both the second and third pleurodont teeth; one below both the third and sixth acrodont teeth.

QM F18030

Locality

Upper Site (Upper Site local fauna).

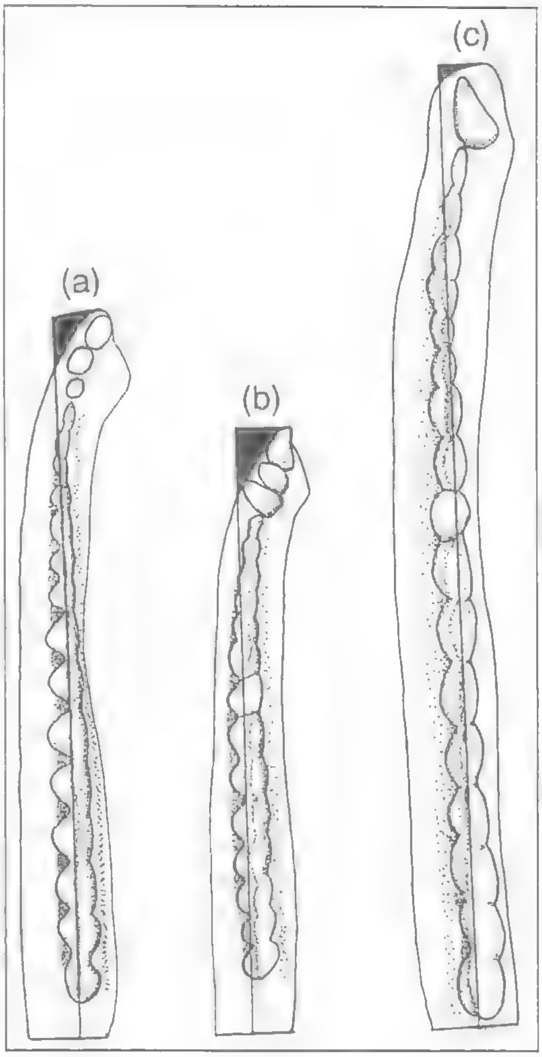


FIG. 7. Occlusal view of dentaries illustrating the varying degrees of dentary curvature between (a) *Physignathus lesueurii* x3 (QM J26671), (b) *Physignathus* sp. x3 (QM F18018) and (c) *Chlamydosaurus kingii* x3 (QM J45307).

Description

Fragment of right anterior maxilla bearing seven acrodont teeth. The 3rd anteriormost is damaged, broken off at the base. Length 9.54mm; maximum depth (excluding teeth) 3.15mm.

In a labial view, the lower edge of the maxilla curves inward. Four well-spaced foramina are present on the labial face, above the first, third, fifth and sixth acrodont teeth. The acrodont teeth have well rounded tips. The teeth are not cusped. Viewed occlusally, the labial tooth surface is flattened. The lingual surface is very angular, with both the anterior and posterior faces flattened, giving the teeth a three sided appearance. On the lingual face of the maxilla there is a broad palatal process. Four foramina are situated in the groove in the base of the nasal process, the anteriormost above the third acrodont tooth. The remaining three are above the fifth and sixth acrodont teeth.

IDENTIFICATION

The specimens F18004, F18007-8, F18012-14, F18016-22, F18024-30 are all referred to *Physignathus* sp. Dentary F18018 is one of the best preserved in the sample and, although the numbers of and wear pattern on agamid teeth vary greatly (Cooper and Poole, 1973), it shows similarity to the dentary of *Chlamydosaurus*, *Lophognathus*, *Amphibolurus*, *Physignathus*, *Ctenophorus*, *Pogona* and *Diporiphora*. This specimen is easily distinguished from *Chlamydosaurus kingii* by number of acrodont teeth (19-20 in *C. kingii* vs 14 in F18018); number of pleurodont teeth (1-2 vs 3); shape and size of pleurodont teeth (one very large caniniform tooth, with one smaller tooth on right ramus vs three teeth, with the first the smallest, followed by two teeth of almost equal size). Further, the upper edge of Meckel's Groove in *C. kingii* lacks the slight upward curve present in F18018, and the mid-line (occlusally viewed) of the dentary in *C. kingii* is almost straight, whilst in F18018 this curves markedly inward anteriorly. The dentaries of *Ctenophorus*, *Pogona*, *Lophognathus*, *Amphibolurus*, *Diporiphora* and *Physignathus* have the distinct medial anterior curve of specimen F18018. However, *Lophognathus*, *Amphibolurus*, *Ctenophorus* and *Pogona* specimens lack the enlarged forward projecting teeth of F18018 and *Pogona* has only two pleurodont teeth (vs three in F18018).

Specimen F18018 and the dentary QM J26671 (*Physignathus lesueurii*) are very close (Fig. 7). Table 1 summarizes these comparisons.

F18018 does not differ in any substantial degree from specimens of the extant *P. lesueurii* (Gray 1831), but, from only this dentary we cannot assign it to this species with any certainty.

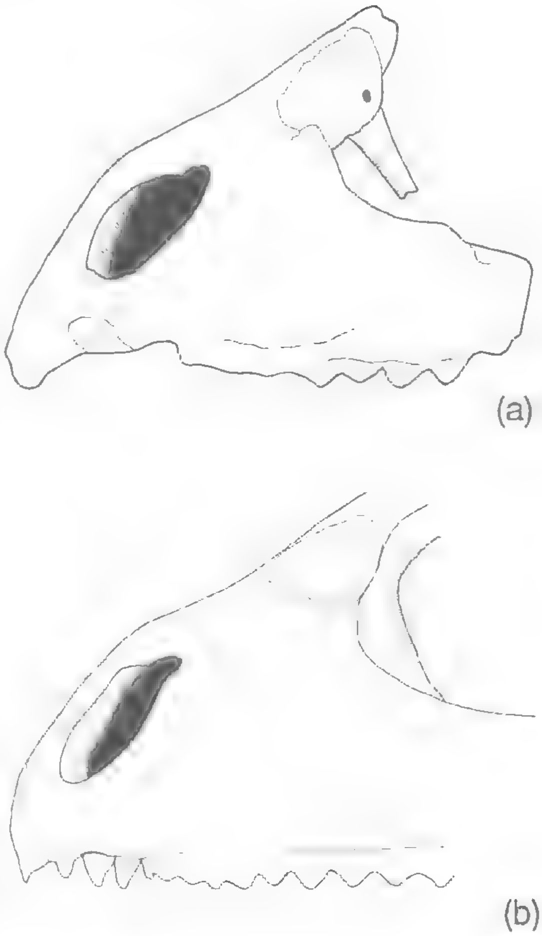


FIG. 8. Lateral view of snout, illustrating the distinct 'Roman nose' profile shared by (a) *Physignathus* sp. x3 (QM F18013) and (b) *Physignathus lesueurii* x1.5 (QM J5449).

The following characters, found only in *Physignathus*, have formed the basis of the remaining identifications: the form of the inward curve on the dentary (F18004, F18007, F18019, F18022, F18027, F18028, F18029); the lingual longitudinal groove below the bases of the dentary teeth (F18004, F18007, F18014, F18016, F18019, F18022, F18027, F18028); the number, shape, size and cusping of the acrodont dentary teeth (F18004, F18007, F18014, F18016, F18019, F18022, F18027, F18028); the number, shape, and size of the pleurodont dentary teeth (F18016[1], F18019, F18022, F18029); the degree

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[1] F18016 has only two pleurodont teeth, while three are present in other complete material in the sample. Examination of modern *Physignathus* confirms that this character varies between two (QM J35270) and three (other material examined).

TABLE 1. A comparison of the dentaries of F18018 (Riversleigh fossil agamid) with J26671 (*Physignathus lesueurii*).

CHARACTER	F18018	J26671
acrodont tooth number	14	15
pleurodont tooth number	3	3
angle of projection of pleurodont teeth	1, anteriorly; 2,3 upward and anteriorly	1, anteriorly; 2,3 upward and anteriorly
curvature of midline of jaw (occlusal view)	marked	marked
pattern of tooth wear	lingual face flattened; labial face rounded	lingual face flattened; labial face rounded

of flattening of the labial aspect of the acrodont teeth (F18012, F18024, F18025, F18030); the number, shape, size and cusping of the acrodont maxillary teeth (F18008, F18012, F18025, F18026); the number, shape and size of the pleurodont teeth on the premaxilla-maxilla (F18021, F18024, F18025); proportions of the palatal process (F18008, F18012, F18024, F18025, F18026); the steeply-sloped posterior edge of the narial opening (F18012, F18024, F18025); the 'Roman-nose' profile (F18013) (Fig. 8); shape and position of the nares (F18013); the form of the small posterior maxillary process (F18008)(Fig. 9).

Family Agamidae Gray 1827

Sulcatidens gen. nov.

TYPE AND ONLY SPECIES

Sulcatidens quadratus gen. nov. and sp. nov.

FIG. 9. Maxilla from *Physignathus lesueurii* x1.5 (QM J26671), showing the position of the posterior maxillary process. Similar processes are present in many of the modern agamid maxillae examined (Fig. 1) and in fossil maxillae where they are complete enough (e.g. F18008). This feature has not been used previously to help identify agamid fragments.

FIG. 10. Occlusal view of the holotype of *Sulcatidens quadratus* gen. et sp. nov. QM F18010 x3.

GENERIC DIAGNOSIS

Sulcatidens is distinguished from all other agamids in having the distal margins of the posterior maxillary teeth set in a notch in the mesial margin of the adjacent posterior crown.

ETYMOLOGY

From the Latin *sulcare*, to furrow, in reference to the notches or furrows in the mesial margins of the posterior maxillary teeth. The gender is masculine.

Sulcatidens quadratus sp. nov.

HOLOTYPE

QM F18010, an incomplete right maxilla bearing 11 acrodont teeth (Fig. 10).

TYPE LOCALITY

Wayne's Wok Site, Riversleigh Station, NW Queensland. Miocene.

SPECIFIC DIAGNOSIS

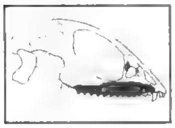
As for the genus.

ETYMOLOGY

From the Latin *quadratus*, from *quadrare*, to make square. Named in reference to the nearly quadrate profile of the posterior maxillary teeth.

DESCRIPTION

Right maxilla bearing 11 acrodont teeth, length 18.28mm, maximum depth (excluding teeth) 3.92mm. On the lingual face of the maxilla, some of the bases of the teeth are corroded. In labial view the maxillary face is rounded, tilting the acrodont tooth row lingually. The acrodont teeth are cusped, and their tips are directed posteriorly. The four posteriormost acrodont teeth are unusual, distinct from the typical triangular agamid dentition. In profile, these teeth are almost quadrate and are very closely spaced. Viewed occlusally the acrodont teeth are flattened on the labial face. The four posterior acrodont teeth are very distinct in form from those situated more anteriorly in the toothrow. In most agamids the posterior acrodont teeth slightly overlap, as a result of rotation about their vertical axes (Cooper and Poole, 1973). This is not the case with F18010. On this specimen the posterior five acrodont teeth tightly abut. The distal edge of each tooth is notched into the mesial edge of the posteriorly adjacent tooth. We have not seen this character in any other agamid.



DISCUSSION

Although anteriorly F18010 shows some similarity (a broad palatal process and the form of the acrodont teeth) to fossils assigned to the extant genus, *Physignathus* in this study, posteriorly the differences from *Physignathus* are marked. The tightly abutting posterior acrodont teeth are unique, and this state is not found in any other genera of Australian agamids examined. Even in genera where tooth wear plays an important role in shaping the posterior acrodont teeth (e.g. *Pogona*, *Chlamydosaurus* and *Physignathus*), the teeth remain broadly triangular in profile, rather than nearly quadrate as in F18010.

REFERRED SPECIMEN

QM F18015, fragment of right maxilla with four acrodont teeth (Fig. 11).

LOCALITY

?

DESCRIPTION

Fragment of right maxilla with four acrodont teeth. Maximum length 4.95mm; maximum depth (excluding teeth) 1.08mm.

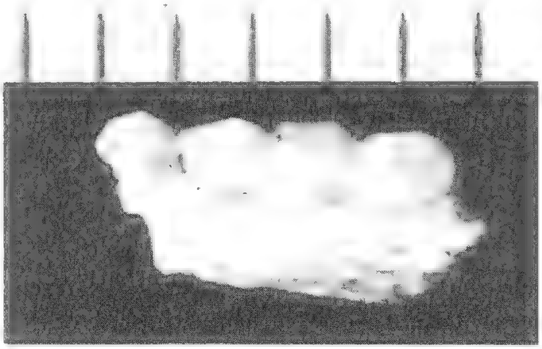
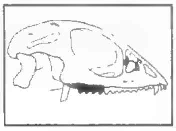


FIG. 11. *Sulcatidens quadratus* (QM F18015).

In both labial and lingual view, no distinguishing features have been preserved on the maxilla. However, the acrodont teeth have a distinct chisel-like form. Viewed occlusally, the acrodont teeth are somewhat flattened on the labial face. The lingual face is gently rounded, and the teeth abut tightly. There is slight development of the 'tongue-in-groove' contact of the teeth seen in QM F18010.



DISCUSSION

F18015 shares with F18010 similar form of the posterior maxillary dentition. In F18010, each of the posterior five teeth is notched into the adjoining tooth. This is evident in F18015, but less pronounced. It may be that F18015 preserves the more anterior of the teeth showing this feature, or it may have derived from a younger individual that had not yet developed the notching to the extent seen in F18010. F18015 is referred to *Sulcatidens quadratus* gen. et sp. nov. because it has the distinctive notching in the posterior five teeth.

Family AGAMIDAE Gray, 1827
Unidentified Material

QM F18005

LOCALITY

Camel Sputum Site (Camel Sputum local fauna).

DESCRIPTION

Portion of left dentary bearing 6 posterior acrodont teeth. The anterior tooth row is badly

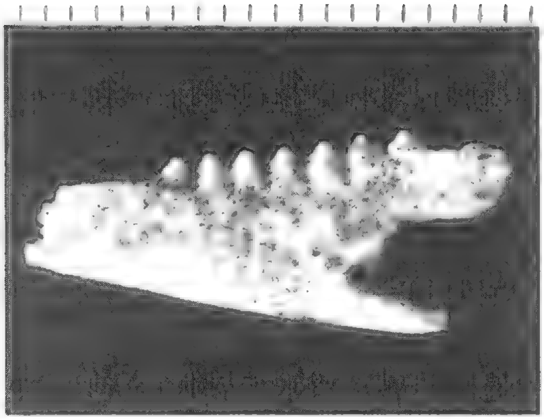
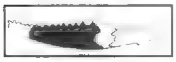


FIG. 12. Unidentified agamid (QM F18005).



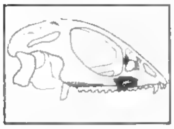
worn so several acrodont teeth are missing. Length 19.75mm; maximum depth (excluding teeth) 7.40mm. The labial face of the dentary is badly eroded and it bears little surface detail (Fig. 12). Posteriorly the acrodont teeth are weakly cusped, and there is deep vertical notching between the tooth bases labially. On the lingual surface a longitudinal groove, which shallows posteriorly, runs beneath the tooth bases. A large foramen is present in the roof of the Meckelian Groove below the acrodont tooth fourth from the posterior end. In occlusal view the tooth ridges are displaced towards the lingual surface.

QM F18006

LOCALITY

Camel Sputum Site (Camel Sputum local fauna).

DESCRIPTION



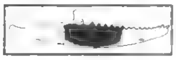
A small fragment from the middle of the right maxilla. It bears two undamaged acrodont teeth and anteriorly the bases of three fragmentary acrodont teeth. Length 8.48mm; maximum depth (excluding teeth) 2.58mm. On the labial face of the maxilla are three foramina, one below each of the broken acrodont teeth. The labial surface is curved in cross-section. On the lingual surface a groove runs above the acrodont tooth bases. The palatal process is broad. Viewed occlusally, the acrodont teeth have a flattened labial surface. The posterior acrodont tooth is very slightly tricuspid. Three foramina are present in a groove which parallels the maxilla/jugal/lacrimal suture medially. These foramina are tightly clustered, the posterior being the largest, and the anterior smallest.

QM F18009

LOCALITY

Wayne's Wok (Wayne's Wok local fauna).

DESCRIPTION



Posterior fragment of right dentary, bearing one damaged and five complete acrodont teeth. Length 12.82mm; maximum depth (excluding teeth) 4.01mm. Few distinguishing features are preserved on the labial surface. The posterior teeth are 'shouldered' and broadly triangular. Vertical notching is present at the tooth bases, except on the two posteriormost teeth. Viewed occlusally, both the lingual and labial tooth surfaces are well-rounded. The lingual surface of the dentary clearly displays a longitudinal groove running parallel to the tooth bases. At the posterior margin of the tooth row is a distinct depression in the surface, once carrying an additional acrodont tooth. The Meckelian Groove is clearly visible and contains a large foramen close to the anterior fracture.

QM F18011

LOCALITY

Wayne's Wok (Wayne's Wok site local fauna).

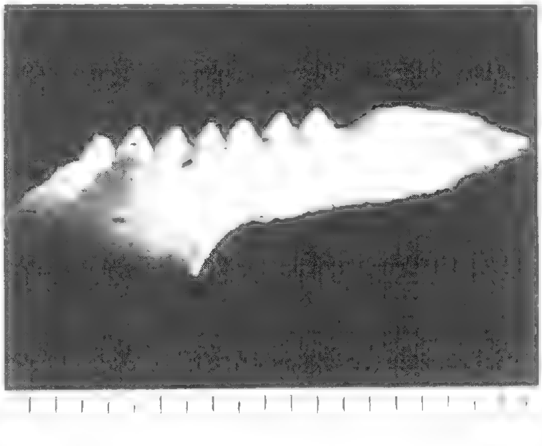


FIG. 13. Unidentified agamid (QM F18011).

Description

Damaged left dentary bearing seven acrodont teeth. The anterior one is damaged near the tip. Length 20.83mm, maximum depth (excluding teeth) 4.43mm. Viewed in labial aspect, the margin of the dentary/coronoid suture is well preserved (Fig. 13).

Two foramina are present on the labial face. One lies on the anterior fracture line. The other is immediately behind the damaged anterior acrodont tooth. Both foramina are displaced towards the ventral surface. The acrodont teeth are sharply pointed and inclined slightly back. The two hind-most teeth have a small cusp on the posterior edge. Deep vertical grooving is present between most of the tooth bases on the labial face of the dentary. However, the four posterior teeth do not show this. Viewed occlusally, the tooth ridge is slightly off-set labially and both tooth surfaces are gently rounded. The teeth curve slightly inwards, toward the lingual face. On the lingual surface of the dentary a well defined groove runs parallel to the tooth row, immediately below the tooth bases. A shallow cavity behind the posteriormost tooth has held a tooth. The damaged ventral surface of the dentary clearly exposes the Meckelian Groove in which there are two foramina, situated in the roof. The first and largest lies below the second acrodont tooth. The second is below the fourth acrodont tooth.

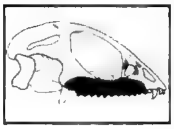
QM F18023

Locality

Upper Site (Upper Site local fauna).

Description

Right maxilla bearing 12 acrodont teeth. Length 15.30mm, maximum depth (excluding teeth) 2.83mm. The posterior margin of the maxilla is well preserved.



Labially two foramina are present above the third and fifth acrodont teeth. Anteriorly a distinct ridge is present on the labial face, giving the lower labial surface a distinct inward curve. The acrodont teeth are not cusped and the tooth tips are well rounded. The two posteriormost teeth have a broader profile than the rest of the tooth row. Occlusally, most of the acrodont teeth are flattened on the labial face, and well rounded on the lingual face. The posteriormost tooth differs in being gently rounded on both faces and almost chisel-shaped with a distinct ridge at its tip. The second posteriormost tooth, although similar, has a flattened anterior face, giving the tooth three faces. The lingual face of the maxilla has a deep vertical notch along the tooth bases. A distinct groove runs parallel to the tooth row terminating before the posterior two acrodont teeth. The palatal process is widest towards the middle of the tooth row. From this point it slopes back towards the tooth row and reaches its narrowest point level with the fourth posteriormost acrodont tooth. From here, it broadens to form a distinct posterior flange level with the end of the acrodont tooth row. Above the palatal process is a deep groove at the base of the nasal process. This groove contains two closely-spaced, large foramina, which are situated above the fifth and sixth acrodont teeth.

FIG. 14. Occlusal view of QM F18031 x3.

QM F18031

Locality

Gag Site (Dwornamor local fauna).

Description

Right maxilla bearing 11 acrodont teeth (Fig. 14). Length 13.97mm; maximum depth (excluding teeth) 3.60mm. Labially three foramina are present, situated above the second, fourth and fifth acrodont teeth. The teeth are broadly triangular, and cusped particularly on the posterior edge. Occlusally for most of the tooth row the labial face is flattened and the lingual face well rounded. The three posterior acrodont teeth are gently rounded on both faces. Their broad form and pronounced central ridge, give an almost chisel-like appearance. The lingual face of the dentary shows broad vertical grooving at the tooth bases, each groove located between adjacent teeth. As in fossil QM F18023 the palatal process is widest towards the middle of the tooth row. This tapers and then gives rise to a small posterior medial flange, level with the end of the tooth row. A deep groove at the base of the nasal process, contains three foramina, situated above the fourth and sixth acrodont teeth.

QM F18032

LOCALITY

Gag Site (Dwornamor local fauna).

DESCRIPTION

Left dentary fragment bearing three posterior acrodont teeth and a fragment of a fourth. Length 5.02mm; maximum depth (excluding teeth) 1.25mm. The only distinguishing feature on this fragment is the nature of the acrodont teeth. These are broadly triangular and tricuspid. Both the lingual and labial surface of the acrodont teeth are rounded when viewed occlusally. The tooth margin is displaced slightly toward the labial side. Slight rotation of the vertical axes gives the acrodont teeth some degree of overlap.

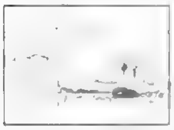
QM F18033

LOCALITY

Gag Site (Dwornamor local fauna).

DESCRIPTION

Right maxillary fragment bearing four acrodont teeth, probably originating from the mid-posterior maxilla. Length 4.66mm; maximum depth (excluding teeth) 2.15mm. The only possibly distinguishing feature is one foramen on the labial surface. The teeth are broadly triangular and one is slightly shouldered. Viewed occlusally the teeth have a flattened labial face.



IDENTIFICATION

The specimens F18005-6, F18009, F18011, F18023, F18031-3 can easily be assigned to the Agamidae. All have fixed acrodont teeth, a major character of the family. However, the specimens are generally small and have worn or damaged teeth, or are otherwise damaged. They thus lack other characters useful in identification. One specimen (F18032) has distinctly triangular, tricuspid teeth. This is seen in *Physignathus*, *Chelosania*, *Caimanops*, *Gonocephalus*, and *Diporiphora* but, as no other useful characters are preserved on the specimen, it is impossible to refine its identification.

THE FAMILY AGAMIDAE, EXTINCT AND EXTANT

Fossil agamids are known from China, Mongolia, the Middle East, Belgium, France, southeastern Europe (including Crete), north-eastern Africa, Wyoming (USA) and Australia (Estes 1983b). The oldest material is from the Cretaceous of China and Mongolia. Many taxa have been described from this region (Estes, 1983a; Holman, 1981; Hou, 1976). Estes (1983a) has reviewed the fossil record and early distribution patterns of lizards and concluded that agamids originated in the Late Cretaceous in southern 'Eurasia', the area which conforms today with South-east Asia and India, including part of Australia. This view is supported by both early and recent reports of Cretaceous agamids from Mongolia and China. *Anhuisaurus hauinanensis*, *Tinosaurus doumuensis*, and *Agama sinensis* (all of Hou, 1976) are agamids from the Palaeocene of China. Agamids are not present in North America (Estes, 1964; Holman, 1981), South America, or Europe. And fossils of appropriate age in Africa are so poorly known that it is impossible to comment on the presence of the group in Africa. The remaining material is more recent, from the Eocene, or, like that from Palestine and Australia (excluding the Riversleigh material), from the Pleistocene. The Australian fossil record of agamids is extremely poor. Estes (1984) describes, briefly, 'an acrodont lizard (presumably an agamid) from localities in the Wipajiri Formation ... Etadunna Formation ... South Australia.' This Middle Miocene fragment presents the first evidence of a possible agamid presence here. There is a gap in the record (prior to the discovery of the Riversleigh deposits) until the Pliocene. Archer and Wade (1976) report an agamid lizard similar to some species of *Amphibolurus* and Estes (1983a,b) reports part of a skull of *Chlamydosaurus kingii*. The only other agamid material is from the Pleistocene (Bennett, 1876; Smith, 1976, 1982).

The occurrence of modern agamids reflects this fossil record. Agamids are strongly represented in both Asia and Australia, which are widely regarded as centres of diversity for the group. The group is most diverse at both specific and generic levels on the Indian subcontinent. Dragons occur in Africa, southern Europe, and some Pacific islands. Species from Africa and southern Europe are not numerous, and belong to genera from India or the Middle East.

In Australia, 60–70 species are probably present, although not all are yet described. There is general agreement about species boundaries, but no such accord in regard to generic definition and allocation. Thus, there are several recent proposals regarding generic divisions (e.g. Witten, 1982a; Cogger, et al., 1983; Storr, et al. 1983; Wilson and Knowles, 1988). Here, we follow Storr et al. (1983), and Wilson and Knowles (1988), with minor modification.

THE AUSTRALIAN LEPIDOSAUR FOSSIL RECORD

In order to provide a perspective on the agamids from Riversleigh, we briefly review the history of the lepidosaurs in Australia. Molnar (1982, 1984a,b, 1985) summarized what is known from the fossil record here. The earliest remains are a Triassic (c.240 my) specimen identified as *Kudnu mackinlayi*. (*Kadimakara australiensis*, previously regarded as the oldest Australian lepidosaur, is referred to the sister group of the archosaurs, Molnar, 1990). Estes (pers. comm.) notes further that this species is not a 'lizard' and that no Triassic forms have the squamate synapomorphies. Some lacertilian fragments are known from the Lower Cretaceous (100my) of Victoria and a mosasaur has been recorded from the Upper Cretaceous of Western Australia. None of these have descendants amongst our modern fauna. Molnar (1985) describes 'a yawning gap' in the record and notes elsewhere (1982), that the bulk of Australian fossil lepidosaur material is of Pleistocene age. The Pleistocene remains belong either to essentially modern taxa or to extinct, related fossil taxa (e.g. *Varanus* vs *Megalania*).

PRE-RIVERSLEIGH HYPOTHESES

Despite a scant fossil record, a plethora of theories about the evolution of agamids in Australia has emerged (Heatwole, 1987).

1. Harrison (1928) noted three elements in Australia's fauna: A. Autochthonian which 'must have had its origins at a time when Australia was in connection with other land masses...'; B. Euronotian, '... which has reached Australia from elsewhere, and undergone radiation ... a bone of contention for a long time ... derived chiefly from South America, by means of antarctic connections...'; C. Papuan, '... not well-named since it came from further afield than New Guinea, through which is merely passed....' From his discussion of the occurrence of 'The Agamidae' (pp. 378-380) it can reasonably be inferred that he regarded the group as having fundamentally Asian origins (i.e. forming part of his Papuan element).

2. Cogger (1961) suggested '... there were 4 agamid invasions of Australia beginning some time in the early to mid Tertiary, all of which entered Australia via New Guinea. The earliest invasion was by the ancestor of *Moloch horridus*, the second one arrived probably in the Pliocene and gave rise to the amphiboluroid radiation.... The final two, *Physignathus lesueurii* followed by *Gonocephalus* species are little differentiated from their New Guinea relatives and are probably of recent origin. These two are found only in the wet, forested part of eastern Australia, whereas the older elements are primarily adapted to semi-arid regions....' This approach has been reiterated by Cogger and Heatwole (1984).

3. Witten (1982a) observed two possible explanations for the occurrence of agamids in Australia. 'Either (a) the family evolved in Asia and has spread into Africa and Australia, or (b) the family evolved in Gondwanaland, part of which now makes up Australia, Africa and the Indian subcontinent....' He regards *Physignathus* as one of the Asian-derived agamids in Australia, 'a more recent Australian arrival than *Chelosania*...' i.e. more recent than 10-20mya when he suggested the first Asian-derived agamid species invaded.

4. Estes (1983a,b) has a world view of the agamid fossil record and has commented in detail on origin and early distributions of the family. He described a Middle-Late Jurassic (190-145my) '... more northern Gondwanan acrodont iguanian group (which) underwent vicariance as the Asia-Southeast Asia-Australia-India blocks separated from Africa ...' and resulted in the agamids (in Asia and Australia) and in the chameleonids (in Africa). He notes elsewhere (p. 392) the centre of origin for the agamids (along with geckos, skinks, and varanids) during the Early Cretaceous (i.e. about 120my) as 'the conjoined area' of what is today India, Australia and Southeast Asia. Tyler (1979) has also contributed to this interpretation.

5. Greer (1990) contends that '... agamids evolved initially on the northern landmass and entered the southern continents, including Australia, only relatively late in their history,...'

MODERN *PHYSIGNATHUS* SPECIES

The affinities of the bulk of the agamid fossils from Riversleigh lie with the extant genus *Physignathus*, the water dragons. Three species of *Physignathus* are currently recognised – *P. lesueurii*, *P. cocincinus* and *P. mentager*.

P. lesueurii occurs in coastal Australia from southern Victoria (Gippsland) to northeastern Queensland (Cooktown area), and in Papua New Guinea (Wilson and Knowles, 1988; de Rooij, 1915). That many species are shared between Papua New Guinea and Australia is the well documented result of several recent land links that have favoured the exchange of both open and rain forest faunas (de Rooij, 1915; Tyler, 1972; Storr, 1964; Covacevich and Ingram, 1980; Kikkawa, et al., 1981; Covacevich and McDonald, in press). That *Physignathus lesueurii* should have colonised Papua New Guinea from Australia (or vice versa) sometime in the last 100,000 years is not a matter for comment, as such colonisations are entirely consistent with patterns for other taxa. However, the Australo-New Guinean distribution of *P. lesueurii* presents a paradox. It seems reasonable to suggest that a non-specialised, reptile which could colonise an area that is now two separate land masses, should be rather 'evenly' distributed throughout its range. Such is not the case. *P. lesueurii* is listed from only the Western and Gulf Provinces (Whitaker et al., 1982) and from the Arfak Mts of Irian Jaya (de Rooij, 1915). In Australia, it ranges from the banks of the Endeavour River, Cooktown, NEQ to Victoria, some 2500km. A distribution including New Guinea and most of coastal, eastern Australia, but excluding Cape York Peninsula north of Cooktown, is unique amongst the vertebrates. This appears anomalous in the light of the generalised habits of *P. lesueurii*, which occurs in a wide variety of riparian habitats and is a catholic feeder. There are two possible explanations. 1. *P. lesueurii* occurred, and has, become secondarily extinct, on Cape York Peninsula north of Cooktown. 2. *P. lesueurii* occurs only in Australia and 'P. lesueurii' from Papua New Guinea is in fact another taxon whose status and affinities are not known.

P. cocincinus occurs on mainland southeast Asia, in Indochina and Thailand (Boulenger, 1885; specimens in the Musée National d'Histoire Naturelle, Paris). Very little has been written about this species since Boulenger's (1885) work.

As the affinities of the bulk of the fossil material lie with *Physignathus*, any attempt at interpretation of the data presented by the fossils makes desirable an assessment of the relationship between the modern Australo-New Guinean representative of the group (i.e. *P. lesueurii*) and the Asian *P. cocincinus*. However, assessment of the status of the New Guinean taxon is not possible because of the lack of accessible material.

Skulls of *P. cocincinus* (MNHN, two specimens Ag8, here termed Ag81 and Ag82) and of *P. lesueurii* (several specimens, see specimens examined) are available to us. *P. cocincinus* and *P. lesueurii* resemble each other in general skull form, form of cusps on the teeth, the labial aspect of the teeth, position and size of maxillary foramina, and numbers of both acrodont and pleurodont teeth. In both species the maxillae are inflexed just above the tooth row. There is no discernable groove at the maxillary-jugal-lacrimal suture. In both, also, there is a marked longitudinal groove shallowing posteriorly below the tooth row of the dentary, although the degree of grooving varies slightly from side to side in Ag82 and also between the two specimens.

They differ in size, but there is only slight difference in proportion.

The shape of the parietal and frontal bones is distinct. In *P. cocincinus* these bones are broadly flattened, while in *P. lesueurii* they are more gracile and the occipital processes of the parietal are narrower. The posterior maxillary process in Ag82 lies above the second last maxillary tooth, while in J47973 it is just posterior to the last maxillary tooth. Further, the snout profile of *P. cocincinus* is acute rather than 'Roman', almost truncate, like that of *P. lesueurii*.

Notwithstanding the differences, the skulls of *P. cocincinus* and *P. lesueurii* are closer to each other than either is to skulls of any of the other genera examined by us or illustrated by Cooper, Poole and Lawson (1970). Skull sizes, shapes, and dentition, particularly the pleurodont teeth, distinguish the genera. Table 2 summarizes the results of our examination and that by Cooper, Poole and Lawson (1970) of the skulls of a wide range of agamid genera. *Physignathus* (including *P. cocincinus*) has 15 or more pleurodont teeth in total, made up of a maximum of 6 on the maxillae, 6 on the dentaries and up to 5 on the premaxilla. The presence of 3 caniniform pleurodont teeth on each dentary and each maxilla sets *Physignathus* apart from all other Australian and Asian agamids examined for this study.

The three spirit syntypes of *P. cocincinus* (MNHN 2537, 1856, 2536) have been examined by one of us (RM). They have no external features which suggest separation at the generic level from *P. lesueurii*. Because the specimens

TABLE 2. Numbers and sizes of pleurodont teeth in selected agamid taxa.

TAXA	PLEURODONT TEETH			
	PREMAXILLA * MAXILLARIES	DENTARIES *	TOTAL NUMBER	SIZE#
Physignathus lesueurii (QM specimens)	9–11	6	15–17	medium
+ *Physignathus lesueurii*	?	?	15	?
Physignathus cocincinus	10	6	16	medium
+ *Agama*	?	?	9, 9<15	?
Amphibolurus	5	3	8	large
Caimanops	8	4	12	large
+ *Calotes*	?	?	9 <15	?
Chelosania	7	4	11	small
Chlamydosaurus	3-7	0–3	3–10	large
Ctenophorus	7	4	11	medium
Diporiphora	3	3	6	large
+ *Draco*	?	?	9<15	?
Lophognathus	8	4	12	large
Hypsilurus	4–5	0	4–5	small
+ *Japalura*	?	?	9<15	?
+ *Liolepis*	?	?	9<15	?
Moloch	7	3	10	small
+ *Phrynocephalus*	?	?	9<15	?
Pogona	4–8	0–4	4–11	small
* *Uromastix*	?	?	9< 15	large

* based on actual teeth . # of largest teeth. + after Cooper, Poole and Lawson,(1970).

are old and faded, colour and pattern can not be assessed confidently. However, Taylor and Elbel (1958) describe distinct banding on the tail of *P. cocincinus* specimens from Thailand. Tails of *P. lesueurii* are also distinctly banded. Differences in size, degree of nuchal cresting, colour pattern, and head scalation, along with skeletal differences, warrant maintenance of the two species.

The status of *Physignathus mentager* Günther 1861 remains unresolved, but is inconsequential in a study of the Miocene *Physignathus* and their broad relationships. It was described by Boulenger (1885) from 'Siam' (= Thailand). Information on this taxon is scant, but comparisons between descriptions of *P. cocincinus* and of *P. mentager* suggest the latter could be a junior synonym of *P. cocincinus*. The authors of recent reviews of the reptiles of southeast Asia have not used the name *P. mentager*.

GENERA SHARED BETWEEN AUSTRALIA AND MAINLAND SOUTHEAST ASIA

Affinities between the faunas and floras of south-east Asia (including the archipelagos), Australia and New Guinea have long been the subject of observation and discussion. Among the modern lizard genera there is an easily demonstrated affinity. The following genera occur in both Australia and south-east Asia: *Cyrtodactylus*, *Hemidactylus*, *Gehyra*, *Lepidodactylus*, *Gonocephalus*, *Physignathus*, *Cryptoblepharus*, *Emoia*, *Sphenomorphus*, *Tropidophorus* and *Varanus*. It seems reasonable to suggest that this results from a combination of past continetal connections and recent migrations, either across the sea, or via land bridges at times of lowered sea levels. (New Guinea and the islands between it, and the Indonesian archipelago, abound with endemic genera which complicate the clear pattern evident at the Australia-Southeast Asian poles of the continuum of the Australasian region).

Notwithstanding the fact that close examination of the taxa shared between Australia and South-east Asia will undoubtedly bring about new allocations, and the recognition of new species and generic definitions, there are strong associations between the two continents.

DISCUSSION

> '. . The Water Dragons are so conspicuous that it cannot be supposed that they have been overlooked. Since they are aquatic and freely enter the sea, their distribution becomes even more remarkable and beggars explanation....'
>
> Harrison 1928, p. 380.

The following Miocene agamids are now known from Australia:

Physignathus sp. (QM F18004, 18007-8, 18012-14, 18016-22, 18024-30); *Sulcatidens quadratus* gen. et. sp. nov. (QM F18010 holotype; 18015); unidentified (QM F18005-6, 18009, 18011, 18023, 18031-33).

In assessing the significance of the Riversleigh agamid material, we know that:

1. *Physignathus* sp. was present in Australia in the Miocene. *Physignathus* remains dominate the sample which also includes a taxon quite distinct from any extant form, *Sulcatidens quadratus* gen. et. sp. nov. The Riversleigh material establishes that agamids have had a much longer history here than has generally been supposed. Agamids have been here for at least 15-20my and the *Physignathus* represented appear to have changed little in that time.

2. Australia was separated by water from lands to the north until the late Miocene. This has been illustrated by Archer et al. (1989) at 40, 30, and 10mya. Despite the controversy about the exact details of the timing of fracturing of the continents and fluctuating sea levels, it is apparent that sea separated Australia from the archipelago to its north throughout the Eocene, and Oligocene and into the late Miocene. Thus, any dragons moving between Southeast Asia and Australia would have required high salt tolerance.

3. *P. lesueurii* lives in large numbers on the banks of the Brisbane River where salinity is of the order of 20 parts per 1000. The dragons, although terrestrial, use the water as a refuge. They readily enter the water and are capable of spending long periods submerged. This suggests a level of salt tolerance unusual in other Australo/New Guinean lizards observed. (Covacevich, pers. obs.)

4. *Physignathus* species occur coastally in both Australia (*P. lesueurii*) and SE Asia (*P. cocincinus*), and in the intervening area, New Guinea. Comparison of *P. lesueurii* and *P. cocincinus* indicates a close phylogenetic relationship.

5. Modern Australian agamids can be placed in two groups. *Physignathus*, *Gonocephalus* and possibly *Chelosania* form one group. The remaining genera all have a reduced number of microchromosomes, lack lacrimal bones, and are

adapted to arid or semi-arid conditions (Witten, 1983). It is not certain that these both represent monophyletic groups.

This evidence can be used to support two hypotheses about the origins of agamids in Australia. Either they have evolved from Asian stock that entered Australia across the seas or via land bridges about 20mybp. (An obvious corollary of this hypothosis is that they may have originated in Australia and colonized Asia), or the agamids had earlier origins in Gondwanaland. They are, today, conspicuous in some of the the southern continents.

Witten (1982) surmised that *Physignathus* was Asian and that the first of the Asian-derived agamids 'arrived' in Australia between 10 and 20mybp. He postulated that *Chelosania* was the most likely direct descendant of such an invasion and that *Physignathus* appeared '... to be a more recent arrival....'

The evidence presented here, coupled with the well-documented, long history of the Agamidae (at least from the Cretaceous) in China and near regions, most strongly support the suggestion that *Physignathus* is Asian-derived and that *P. lesueurii* and *P. cocincinus* are the direct and similar descendants of the Asian ancestral *Physignathus*.

It seems reasonable to infer from the agamid remains identified, that the Riversleigh environment in the Miocene may have resembled (in climate and forest profile, at least) present day coastal Queensland. If present requirements for *Physignathus* are relevant the area must have been well-watered. As *Sulcatidens quadratus* gen. et. sp. nov. is based on an incomplete maxilla and appears to have no obvious close relationships to any modern agamid genus, it reveals nothing of the palaeoecology of Riversleigh. Lepidosaurs are poorly known from the Miocene in Australia. *Egernia*, *Tiliqua*, *Varanus*, *Ramphotyphlops*?, *Morelia* (= *Python*), and *Montypythonoides*, have been reported (Molnar, 1990). In addition, we here report *Physignathus* and *Sulcatidens* gen. nov. Six of these eight genera are represented in the modern fauna. The extinction of *Sulcatidens* and *Montypythonoides* does not conform to this pattern of general conservatism in the Australia lepidosaurs.

NOTED ADDED IN PRESS

Since the review work for this paper was completed, 38 further agamid jaw fragments have been extracted from the Riversleigh matrix. The specimens have been registered into the Queensland Museum reference collection (F18044-F18081). There are no taxa represented in these fragments that differ from those already identified. All compare well with the initial sample. These specimens do not, therefore, alter the conclusions already drawn.

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TAUDACTYLUS DIURNUS AND THE CASE OF THE DISAPPEARING FROGS

GREGORY V. CZECHURA AND GLEN J. INGRAM

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The southernmost representatives of the myobatrachid genus *Taudactylus* is the Southern Dayfrog (*T. diurnus*). This frog has been recorded from only the subcoastal ranges near Brisbane in southeastern Queensland. *T. diurnus* inhabits creeks and their edges in rainforest and tall open forest communities at elevations in the 300-850m range. It is diurnal, terrestrial, and easily observed and most commonly encountered during the summer months. Breeding is restricted to the spring-summer wet season. *T. diurnus* has not been recorded in the wild since early 1979. It is possible it is now extinct. *T. diurnus* and *Rheobatrachus silus* are apparently linked by similar fates. They were closely associated in the wild and both were last seen in 1979. As well, their related species, *T. eungellensis* and *R. vitellinus* have not been seen since 1985. If these missing frogs are exinct, their passing was not a slow process. Rather it appears to have been a catastrophic event that could not have been anticipated or prevented. There may be reasons to fear for the other species of *Taudactylus*. These species should be studied and monitored. ☐ *Taudactylus diurnus, biology, Rheobatrachus, extinction.*

Gregory V. Czechura and Glen J. Ingram, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101, Australia; 20 June, 1990.

Taudactylus diurnus and *Rheobatrachus silus* are two very different frogs that are linked by similar fates (Ingram, 1990). Both species apparently disappeared in the same year and neither have been seen in the wild since 1979. While *R. silus* is a well- studied frog, (see Tyler, 1983, for an overview, and papers therein), no overview is available for *T. diurnus*.

Myobatrachid frogs of the genus *Taudactylus* occur in association with upland and montane rainforests of high rainfall in eastern Queensland (Ingram, 1980; Czechura, 1986a; Winter and McDonald, 1986). Of the six species of *Taudactylus*, only two occur south of the Tropic of Capricorn. These are the Kroombit Tops Dayfrog (*T. pleione*) and the Southern Dayfrog (*T. diurnus*). The former species is restricted to a small area of Kroombit Tops near Gladstone (Czechura, 1986a). *T. diurnus* is found near Brisbane in the south of the region (Ingram, 1980). No detailed field investigations of the biology of either species have been conducted. Czechura (1986b), however, summarised what was known of *T. pleione*. Aspects of the biology of *T. diurnus* have been reported by Straughan and Lee (1966), Johnson (1971), Liem and Hosmer (1973), Czechura (1975), Corben (1977), Ingram (1980) and Czechura (in press). In this review, we detail field observations made during general and specific investigations of the vertebrates found in the Blackall-Conondale Ranges of southeastern Queensland. The general results of these investigations have been reported elsewhere (Czechura, 1974, 1975, 1976, 1978, 1983, 1985, in press; Roberts, 1977; Ingram, 1983). We also incorporate information about *T. diurnus* in the D'Aguilar Range. Unless otherwise stated, all reports are based on the authors' observations.

Vegetation types follow Webb (1978) for rainforests and Specht (1970) and Groves (1981) for other vegetation types, and Stanton and Morgan (1977) provide a broad view of the area. Young and McDonald (1987) describe rainforests of southern Queensland.

Taudactylus diurnus

GENERAL

T. diurnus has been recorded from three subcoastal mountain ranges (Blackall, Conondale, and D'Aguilar Ranges) near Brisbane (26° 30'-27°23'S). The species occurs over a relatively narrow altitudinal range of 350-800m, with most records falling in the 500-800m range. The lowest altitudinal records were all attained on the southern and southeastern slopes of the Blackall Range near Maleny (Mooloola and Stanley

River drainages).

These frogs are found in association with permanent and temporary watercourses in extensive forests or gallery forests of the following types: Notophyll Vine Forest (NVF), Tall Open Forest (TOF), NVF-TOF transitions, and Sclerophyll Fern Forest. In addition, they have been found along watercourses in pure stands of the palm *Archontophoenix cunninghamiana*, in exposed rocky areas, in gorges, in dense non-forest riparian vegetation (*Lomandra longifolia, Carex neuroclamys, Elastostems reticulatum* and *Blechnum nudum* with or without a shrub story of *Callistemon* sp.), and where these have been lightly infested with exotic *Lantana camara*. *T. diurnus* have not been found where such areas have been heavily infested with *Lantana*, where weed infestations of *Baccharis halimifilia* and *Eupatorium riparium* occur. The frogs are also absent from streams that have very muddy waters and seem to prefer clear or 'black-water' conditions.

Permanent streams with rocky substrates are favoured, but *T. diurnus* also occurs in permanent and ephemeral streams on gravel, clay, sand and soil substrates. Active *T. diurnus* are found in and along the margins of watercourses and leaf-litter within 10m of water. The greatest distance that any *T. diurnus* has been recorded beyond a watercourse was about 22m in wet weather. Individuals are usually very active, moving or swimming about the stream and environs, but they will remain rather motionless at times on stones, debris or low vegetation in or near the watercourse. At night individuals have been located in rock crevices, under stones at the water's edge, under debris, in fallen palm fronds, in old burrows or clinging to broad-leafed riparian vegetation.

These frogs avoid danger by diving into fast-flowing water and allowing themselves to be carried downstream, swimming across still or slow-flowing water, or hiding among submerged stones, debris, in rock crevices or in leaf-litter (Straughan and Lee, 1966; Liem and Hosmer, 1973; Corben, 1977). In watercourses with muddy substrates, the frogs have been observed diving into the loose upper mud layers and then remaining motionless on the bottom partially covered with mud.

DAILY AND SEASONAL ACTIVITY PATTERNS

Active *T. diurnus* have been observed throughout the year, although they were encountered less frequently during the generally colder winter months (e.g. this is the period when minimum activity temperatures are likely to be reached; Johnson, 1971). During periods of prolonged inactivity individual frogs and small groups of frogs (6-13) have been found under stones, in boulder piles, deep stone beds, streamside rocks and stones, fallen logs, deep soil crevices and rock shelves , often near waterfalls. Shelter sites in rock crevices and under stones are often shared with other species such as *Litoria barringtonensis* and *L. lesueurii*.

T. diurnus is diurnal. Activity begins at or soon after sunrise, peaks at full light, and rapidly declines with the onset of evening. Most foraging occurs during the day, but may extend into the evening (Ingram, 1980). Captive individuals often remain active until late at night, although this has not been observed in the wild.

These frogs appear to engage in basking behaviour; individuals have been observed sitting motionless in patches of sunlight before moving away into leaf-litter or along stream edges. Other individuals have been noted sitting on warm rocks for lengthy periods, possibly absorbing heat from the substrate, which in mid-summer remains warm until late at night. Regular movement between patches of sunlight and shade was also observed.

Individuals regularly move between land and water by swimming from one point to another. They also cling to rocks, debris or vegetation, with most of their bodies submerged or sit in shallow water.

The thermal relations and water balance of *T. diurnus* were studied by Johnson (1971), who found the body temperatures of *T. diurnus* ranged from 13.6-22.8°C (mean 18.4). The critical thermal maximum was 31.1°C (range 28.4-33.7). It was found that *T. diurnus* shows little tolerance to desiccation despite an ability to rehydrate rapidly.

Breeding occurs in warm weather after or during heavy rain commencing in late October, November or early December. Straughan and Lee (1966) reported finding gravid females between November and May, with a January-March peak. The eggs are deposited in gelatinous clumps under rocks in water. The tadpoles are bottom-dwellers that feed by scraping food from the substrate with their umbrella-shaped lips. Liem and Hosmer (1973, fig.6) illustrated the tadpole.

Males call despite the absence of vocal sacs (Liem and Hosmer, 1973; Corben, 1977; Ingram, 1980). Calls are barely audible in the field, although they are obvious in captivity and are uttered in response to disturbance (Corben, 1977), male-male interactions (Ingram, 1980) or advertisement calls. There is no evidence that breeding choruses are formed. Very little courtship and territorial behaviour has been reported. However, some interactions have been observed: male-male interactions involving head to head encounters while 'eek-eek' were uttered (Ingram, 1980); males making soft clucking calls from leaf-litter along stream margins or from rocks in stream; amplectant pairs (amplexus is inguinal) in water-filled rock crevice during day and under stone in afternoon: and male in amplexus with male *L. barringtonensis* during late morning (amplexus inguinal).

Food

Straughan and Lee (1966) analysed gut contents and showed these frogs to be opportunistic feeders of the forest floor. Amphipods, hymenopterans and lepidopteran larvae were the most commonly recorded prey in their sample. Captive *T. diurnus* take a variety of small soft-bodied insects such as immature cockroaches, moths, winged termites and flies. In the wild, feeding frogs have been observed taking small insects along or near streams. There are no observations to suggest that prey is taken from the water.

THE CASE OF THE DISAPPEARING FROGS

For *T. diurnus*, there are no quantitative estimates of population density. However, the general impression is that most observers thought *T. diurnus* was an abundant frog where it occurred. For example, McEvoy et al. (1979) reported them to be abundant along streams in NVF in the Kilcoy Creek drainage of Conondale Range. Nevertheless, surveys (G.V. Czechura and G.F. Maywald, pers. obs.) of several streams in the Blackall Range (Obi Obi Creek drainage, Stanley River headwaters) and Conondale Range (Booloumba Creek drainage) indicated that the density varied along a given watercourse. In addition, changes in numbers sometimes occurred in a particular area between successive visits (i.e. weekly to monthly variation) and was sometimes maintained across one or two seasons (e.g. streams in the Narrows National Park area, Blackall Range, 1973-1975).

No one expected *T. diurnus* to disappear: the last sightings had to be reconstructed. It seems it has not been met in the field since possibly late 1975 on the D'Aguilar Range (C. Corben pers. comm.), early November 1978 on the Blackall Range (G. Czechura, pers. obs.) and January 1979 on the Conondale Range (K. McDonald pers. comm.). The significance of these last sightings of *T. diurnus* have taken sometime to emerge. However, at present all that can be stated with certainty is that during late 1978-early 1979 on the Blackall-Conondale Ranges and possibly as early as 1975 on the D'Aguilar Range (the time of disappearance here is unknown) the last encounters with this frog occurred, and for the last decade attempts to locate them have failed.

Like *T. diurnus*, *Rheobatrachus silus* also appears to have vanished. Both species were closely associated in the wild, although *R. silus* was never recorded from the D'Aguilar Range. There are some data from Ingram's (1983) study for the disappearance of *R. silus*. He worked with wild populations of the frog in the Conondale Range between October, 1976, and December, 1981. During his study, they disappeared and the study had to be placed in limbo. The last frogs captured by Ingram were two juveniles on 18 October, 1979. Apparently, the last wild frog seen was a juvenile at Ingram's study site on 8 December, 1979, by Gregory Czechura. (However, Tyler and Davies (1985) reported that the last known frog died in captivity on 5 November, 1983, in Adelaide, presumably in their laboratory). Ingram (loc. cit.) had noticed that *R. silus* had declined before 1979 and said the number of captures in 1978 had decreased. He presumed that this was related to late rains. His actual numbers for the years 1976-1981 for the number of individuals captured (not counting recaptures) were: 1976, 59; 1977, 35; 1978, 24; 1979, 2; 1980, 0; 1981, 0 (Ingram unpubl. data). *R. silus* was never a common frog. Ingram (1983) calculated there were 1.11 frogs/are on his study site. Barinaga's (1990) estimate of commonness appears to be journalistic licence.

Both *R. silus* and *T. diurnus* were last seen in 1979 - but what makes 1979 a special year for disappearing frogs in Australia? The report of Heyer et al. (1988) of population reductions and extinctions of frogs in southeastern Brazil in 1979 adds to the intrigue. Is this coincidence? Maybe the question should be rephrased to 'What makes 1979 special for the disappearance of frogs on two large, but remote southern continents?' Ingram (1990) argued that the disappearances in southeast Queensland were probably due to late rains falling in cooler months. Heyer et al. (1988) argued that unusually heavy frosts were responsible in southeast Brazil. If the disappearances are related, it is likely that Osborne (1989) is correct. He conjectured the cause to be deterioration in climate affecting both continents.

However, if climate did change, there is evidence that it might still be changing. Winter and McDonald (1986) noted the sudden disappearance of Eungella Gastric Brooding Frog (*R. vitellinus*) and Eungella Dayfrog (*T. eungellensis*) in 1985. These species still had not been located in early 1990 (K. McDonald, pers. comm). There disappearances illustrate another coincidence. Their sister species are respectively the vanished frogs, *R. silus* and *T. diurnus* (see Ingram, 1980; Mahony et al., 1984). For wildlife conservation, this subsequent disappearance of closely related species illustrates the wisdom of one of the Berne Criteria for CITES, that '...the listing of one Linnean species on Appendix I of CITES means that other species in the genus must be listed on Appendix II unless there is a reason for listing them otherwise' (Holt, 1987, p.20). In fact, the warning signs are there for the safety of the other species of *Taudactylus*. A project should be commenced to monitor their numbers and study their biology.

However, it is very difficult to decide whether or not the missing frogs are extinct. Extinction is not easy to prove. If the missing frogs *are* extinct, their passing was not a slow process. Rather it appears to have been a catastrophic event that could not have been anticipated or prevented.

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NOTES ON THE DISTRIBUTION AND OCCURRENCE OF SOME STRIPED SKINKS (GENUS *CTENOTUS*) IN QUEENSLAND: The following provides details on the occurrence and distribution of some species of *Ctenotus* in northern and western Queensland.

Ctenotus piankai Storr has been included in the Queensland herpetofauna (e.g. Cogger, 1986) on the basis of a specimen in the South Australian Museum (SAM 5387, Doomadgee Mission) reported in Storr (1970). G.M. Storr (pers. comm.) has informed us that this specimen is referable to *Ctenotus striaticeps* Storr, a species that has since been found throughout the area of north-western Queensland and adjacent parts of the Northern Territory. On this basis, *Ctenotus piankai* should be deleted from lists of the Queensland herpetofauna.

Ctenotus decaneurus Storr has been included in the Queensland herpetofauna by Wilson and Knowles (1988), who figure a specimen from 'Muellers Range, Winton District, Queensland' (Photograph 343, p.264). This view of the distribution of *Ctenotus decaneurus* contrasts with that provided by both Cogger (1986) and Rankin (1978) who indicate that this skink is more-or-less restricted to the area between the northern Kimberley region of Western Australia and western Arnhem Land. Wilson and Knowles' identification is correct and a relatively extensive distribution of the species through western Queensland is confirmed by reference to material in the Queensland Museum herpetological collection (QMJ). Three specimens, all clearly referable to *Ctenotus decaneurus*, indicate that this skink occurs through hummock grass habitats on extensive stony substrates in the arid western half of the State. (QMJ30430 'Cloncurry'; QMJ43244 'Mica Creek via Mt Isa'; QMJ43267 '88km south west of Winton', the latter specimen is the one figured by Wilson and Knowles, 1988).

Ctenotus inornatus (Gray) has been reported to occur on eastern Cape York Peninsula in the vicinity of Iron Range (Wilson and Knowles, 1988). This population is apparently isolated from its conspecifics in subhumid and semi-arid northern Australia (between Broome and the southern Gulf of Carpentaria). The occurrence of this skink in what is a humid, wet region appears problematical and requires some explanation. The presence of *Ctenotus inornatus* on eastern Cape York is based on two specimens collected by Donald Thomson from 'Near Lockhart River' and held in the Museum of Victoria (MV DT-D273-4). Both specimens are referable to *Ctenotus inornatus* (Gray). Although Thomson collected extensively in Arnhem Land, NT, and at Aurukun, W Cape York Peninsula (Dixon and Huxley, 1985), there appears to be no reason to doubt the provenance of these two specimens (A.J. Coventry, pers. comm.). However, the locality given is sufficiently vague in that the specimens may have actually been taken some distance from Lockhart River. Further comment on the range of *Ctenotus inornatus* in eastern Cape York must await collection of additional specimens.

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THE RELATIVE IMPORTANCE OF HOST BEHAVIOUR, METHOD OF TRANSMISSION AND LONGEVITY ON THE ESTABLISHMENT OF AN ACANTHOCEPHALAN POPULATION IN TWO REPTILIAN HOSTS.

CHRISTOPHER B. DANIELS

Daniels, C.B. 1990 09 20: The relative importance of host behaviour, method of transmission and longevity on the establishment of an acanthocephalan population in two reptilian hosts. *Memoirs of the Queensland Museum* **29**(2): 367-374. Brisbane. ISSN 0079-8835.

The acanthocephalan parasite *Sphaerechinorhynchus rotundocapitatus* occupies the rectum and large intestine of the riparian Australian snake, *Pseudechis porphyriacus*. Eggs are released into water to be consumed by an aquatic arthropod (intermediate host) which in turn is captured by the eastern water skink, *Eulamprus quoyii* (transport host). The parasite adopts a resting, encysted stage in both hosts until the lizard falls prey to the snake. *Pseudechis porphyriacus* exhibits a relatively high frequency of infection but *E. quoyii* comprises only 2% of prey items. Aquatic prey also represent only a small proportion of the diet of *E. quoyii*. Unlike all other acanthocephalans so far examined, there is no evidence that the parasite alters intermediate host behaviour or physiology to increase the chance of capture by the next host in the life cycle. Rather, the operation of the food web appears to provide sufficient momentum to transfer the parasite from one stage to the next, provided both the hosts and the parasite are long lived. Transfer mechanisms involving parasite mediated alterations in host behaviour can be termed 'active' while those which do not significantly affect a host are termed 'passive'. The advantages of passive transfer mechanisms are discussed. ☐ *Parasite, lizard, snake, invertebrate, Acanthocephala, life cycle, passive transport, mathematical model.*

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Almost all parasites with multistage lifecycles often rely for transmission on the predation of their intermediate host by their final host. However, usually only a small proportion of intermediate hosts (infected or otherwise) are captured by predators. Thus, sometimes natural selection influences parasites to alter intermediate host behaviour to increase the chance of capture by the final host. Many such parasites produce extreme and often spectacular alterations in intermediate host behaviour to move the prey into the feeding niche of the final host and/or decrease the frequency of predation by other inappropriate carnivores (e.g. Holmes, 1976; Moore, 1984). Holmes (1976) suggested that if the final host is an efficient predator, the strategy of the parasite should be to make the prey more conspicuous, and when the predator is inefficient the parasite should make the prey more conspicuous and easier to catch. In both cases the parasite may either institute novel behaviour patterns or simply elicit pre-existing host behaviours under inappropriate conditions (Moore, 1984).

In cases where the parasite interacts with, and influences, host behaviour to promote transmission, the methods employed can be termed 'active'. Mechanisms whereby parasites promote their own transmission without influencing host behaviour or physiology can be termed 'passive'. Thus, increasing parasite longevity and reproductive output may 'passively' promote transmission by increasing the number of infective individuals which can contact hosts. Digeneans amplify their numbers in intermediate hosts by producing cercariae highly adapted for transmission. Active interactions between parasites and their hosts have received considerable attention recently from behavioural, physiological, evolutionary and genetic viewpoints (Holmes and Bethel, 1972; Bethel and Holmes, 1973,1974,1977; Clarke, 1979; Smith-Trail, 1980; Brassard et al. 1982; Rand et al. 1983, Schall, 1983) as well as in studies of population dynamics (Holmes, 1982). However, this study will show: (1) the importance of passive forces in influencing a parasite life cycle; (2) present a simple model to illustrate how selection can act on passive mechanisms to increase the probability of parasite transmission from one host to the next; (3) present an example where an apparently active interaction between a parasite and its host in fact represents a method of passive transmission; (4) discuss the advantages and disadvantages of active and passive transmission techniques.

The system examined involves an acanthocephalan parasite of a snake. The parasite has two sequential intermediate hosts: an aquatic invertebrate and a riparian lizard. Because I have been unable to identify the invertebrate host and in order to test the 'worst case scenario', I will ignore any possible differences between the first and second intermediate hosts in the acanthocephalan life cycle. Behavioural changes in the first intermediate host are well documented but are relatively uncommon in the second host, possibly because parasites are usually associated with the first host for a longer period. However, in this system it will be demonstrated that while behavioural transformations in a host may improve the probability of transmission, such changes are not necessary for the successful establishment of the parasitic life cycle.

MATERIALS AND METHODS

This study applies aspects of the ecology of the acanthocephalan parasite *Sphaerechinorhynchus rotundocapitatus*, the eastern water skink *Eulamprus quoyii* and the red-bellied black snake *Pseudechis porphyriacus* to a simple probability model to test whether the parasite is utilising active or passive transfer mechanisms. More complex ecological and physiological studies of these animals are documented elsewhere (Shine 1975; Daniels, 1984; Daniels and Simbotwe, 1984) and only the salient characteristics will be present here.

Sphaerechinorhynchus rotundocapitatus

Sphaerechinorhynchus belongs to the order Palaeacanthocephala and contains two species both of which probably utilise snakes as final hosts (Schmidt and Kunz, 1966; Morris and Crompton, 1982). Palaeacanthocephala occupy the intestine of aquatic or semiaquatic vertebrates and their intermediate hosts are usually aquatic crustaceans, especially ostracods, amphipods or isopods (Crompton, 1970, 1975; Morris and Crompton, 1982). Palaeacanthocephalans sometimes utilise a second intermediate host, often a vertebrate (Morris and Crompton, 1982). The second intermediate host of *S. rotundocapitatus* is the Australian skink *Eulamprus quoyii* which consumes infected intermediate hosts (currently unknown) and the lizards in turn are eaten by the final host (Daniels and Simbotwe, 1984).

The fully embryonated eggs of *S. rotundocapitatus* measure 0.07-0.09 x 0.025mm. These are released into water in the faeces of the snake, and are immediately infective and retain their infectivity for many months (Johnston and Deland, 1929a,b; Crompton, 1970, 1975). In most acanthocephalan life cycles the eggs are consumed by the correct arthropod host, hatch in the gut and the larval stage (acanthor) burrows through the intestinal wall to reach the haemocoel. The acanthor then develops into an acanthella and encysts. The encapsulated acanthella is termed a cystacanth (Crompton, 1970,1975). Most of the cystacanths so far examined alter intermediate host behaviour which increase the likelihood of consumption by the final host (Holmes, 1976; Moore, 1984).

Infected arthropods are consumed by *E. quoyii*. The cystacanths hatch and the acanthellae again burrow into the peritoneum and encyst. Thirty four percent of 53 *E. quoyii* contained worms (X = 2.0, S.D. = 2.2, range 1-8), which measured up to 26mm long (Daniels and Simbotwe, 1984). Cystacanths were removed from the peritoneal wall, liver, outer gut wall, and sperm ducts. These can survive in the lizard for at least 6 months (Daniels and Simbotwe, 1984). Only 8% of juvenile *E. quoyii* were infected compared to 41.5% of adults (Daniels and Simbotwe, 1984). A few cystacanths have been recovered from other species of small lizard but not, to date, from frogs (Johnston, 1911, 1913; Johnston and Deland, 1929a; Daniels and Simbotwe, 1984).

Infected *E. quoyii* exhibited a mean voluntary diving time of nearly 8 minutes, while uninfected ones dived for an average of 4.5 minutes (Daniels, 1985a). Altering the voluntary diving time of *E. quoyii* may represent an active strategy promoting parasite transport because the red bellied black snake forages underwater and thus contacts more infected *E. quoyii* (Gilbert, 1935; Fleay, 1937; Shine, 1975). Twenty three percent of 22 *P. porphyriacus* contained adult *S. rotundocapitatus* in their rectum and lower large intestine (X = 2.3; S.D. = 2.3; range 1-7). Female worms measured up to 37mm while males exhibited a maximum length of 23mm (Johnston and Deland, 1929b).

Eulamprus quoyii

The eastern water skink, *Eulamprus quoyii*, is a common inhabitant of creek banks in eastern Australia (Veron and Heatwole, 1970; Spellerberg, 1972; Daniels, 1984). This lizard is territorial and intraspecifically aggressive (Done and Heatwole, 1977) often existing in dense populations. In the New England region of northern New South Wales, *E. quoyii* is active from September to May, and hibernates during the winter (Veron 1968, 1969b). Water skinks are viviparous, mate in October and the young are born in January/February (Veron, 1969b). Hatchlings are 35mm SVL (snout to vent length) and occupy fossorial habitats until they reach 55-80mm SVL. The juveniles then emerge and occupy suboptimal habitats, which are more exposed regions often some distance from water. Adults measure 80-110mm SVL and prefer rocky regions near expanses of water. Water skinks become sexually mature in their third year and live for 6-10 years (Veron, 1968, 1969b; Daniels, 1984).

Water skinks consume at least 25 taxa of prey including insects, worms, frogs, crustaceans, mammals, spiders, myriapods, snails, lizards and fish (Veron 1968, 1969a; Daniels, 1987). Approximately 25% of prey taxa are aquatic (Daniels, 1987). Of the aquatic prey items, the possible intermediate hosts of *S. rotundocapitatus* could be; Coleoptra (7.1% of the prey of *E. quoyii*), Hemiptera (2.9%), Odonata (3.8%), Plecoptera (2.2%), Crustacea (2.2%), Gastropoda (0.7%) or perhaps Anura (0.9% of prey taken by water skinks). Thus, whatever the immediate host, it must comprise less than 7% of the prey items of the transport hosts. A more realistic estimate is probably 1-2%. The most important prey items for *E. quoyii* are terrestrial Coleoptra (15% of prey) and ants which vary from 2% to 95% of the prey consumed depending on the season (Veron, 1969a; Daniels, 1987).

Water skinks can avoid predators by practising tail autotomy, with 49% of 110 New England lizards possessing regenerated tails (Daniels, 1985b). These lizards also exhibit a diverse range of escape tactics. Of 698 lizards chased by me around streams in New England, 32% escaped by swimming across open water to cover (rocks or reeds), 5% dived to the bottom of ponds and remained submerged and motionless for at least 2 minutes, while 61% ran to cover and 2% remained motionless (Daniels, 1984; Daniels and Heatwole, 1990).

Pseudechis porphyriacus

The red-bellied black snake *Pseudechis porphyriacus* is a large riparian elapid common in stream habitats in eastern Australia. In New England the snake is active from September to May with 5-8 young born alive in January/February (Shine, 1975, 1978). Hatchlings measure 24cm SVL and reach sexual maturity in their third year (Shine, 1978). Large snakes are 150cm SVL and at least 10 years old (Shine, 1975, 1978; Daniels, 1984). Red-bellied black snakes consume 34 types of prey including lizards, frogs, mammals, snakes and fish. Invertebrates are almost non-existent dietary items (Shine, 1977). Frogs comprise 82.4% of prey with *Limnodynastes tasmaniensis* the most common (16.9%). Water skinks are only 2% of the prey of *P. porphyriacus* (Shine, 1977). *P. porphyriacus* is an active forager and can capture prey on land or in water. The snakes will swim underwater for considerable periods in search of tadpoles, fish and other animals hiding amongst litter on the pond bottom (Gilbert, 1935; Fleay, 1937).

RESULTS AND DISCUSSION

If intermediate hosts comprise less than 7% of the diet of *E. quoyii* but 34% of *E. quoyii* are infected with cysts of *S. rotundocapitatus* and if *E. quoyii* comprise 2% of the diet of P. porphyriacus but 23% of *P. porphyriacus* are infected, then how can infection occur? One alternative is for the parasite to employ an active transfer mechanism. Some aspects of the behaviour of the transport host indicate this possibility. Parasitised lizards possessed much longer voluntary diving times than unparasitised ones and may be more likely to be captured by *P. porphyriacus* foraging underwater (Daniels and Simbotwe, 1984). However, it is unlikely that the parasite is exerting an active effect on the behaviour or physiology of *E. quoyii*, for a number of reasons. Firstly, an enhanced voluntary diving time may not necessarily indicate an increased tendency to use diving as the predominant escape method. Moreover, lizards rarely dived, with only 5% of individuals diving to avoid me (Daniels, 1984). Secondly, neither body mass nor swimming stamina were affected by parasitism (Daniels, 1985a). If the parasite exerted some physiological, behavioural or metabolic effect on the lizard to promote diving, it is surprising that the other parameters remained unaffected. Swimming was the predominant aquatic escape tactic employed by *E. quoyii* and therefore seems a much more suitable mechanism for the parasite to exploit. Acanthocephalans alter the swimming behaviour of many invertebrate intermediate hosts (Holmes and Bethel, 1972; Bethel and Holmes, 1973, 1974, 1977). Parasites also often interfere with the stamina of many vertebrate hosts (Rau and Caron, 1979). Aberrant swimming behaviour may still confer protection from many terrestrial predators while reducing the ability of the lizard to escape from *P. porphyriacus*. Diving is so infrequently practised that even if all the divers I observed were parasitised they represent a barely significant proportion of the total population. In addition, if 5% of the lizard population were divers and all were parasitised, then 85% of the parasitised individuals did not dive.

Thirdly, if *S. rotundocapitatus* actively influences diving, which increases the likelihood of infected lizards being consumed by the snake, then the proportion of the diet of *P. porphyriacus* comprised of parasitised lizards must increase from that predicted by random collection, i.e. from 34% of all *E. quoyii* captured, to a maximum of 100% of the water skink component of the snake diet. However, infected lizards can only increase from 0.68% to 2% of the dietary items of red-bellied black snakes. The snakes do most of their foraging on land, collecting frogs and lizards from holes or undercover on the stream banks (Shine, 1975, 1977). Comparatively few of the prey species of the snake are completely aquatic (Shine, 1977). Hence any parasitic alterations to skink behaviour which promote water utilisation may neither increase nor decrease the likelihood of consumption by the snake.

However, some selective advantages for an active strategy can still exist if the increased utilisation of aquatic escape tactics confers protection from all predators except *P. porphyriacus*. This does not appear likely. Water skinks in the New England region are potential prey items for 101 species of predator (Daniels and Heatwole, 1984). Fifty species are known to consume lizards and include mammals, birds, reptiles, fish and invertebrates. An additional 51 species have been reported to capture other similar sized vertebrates. Of the total 101 potential predators, 27.7% are most likely to capture *E. quoyii* only in water, 11.9% can capture lizards on land or in water, 54.5% are purely terrestrial predators while 5.9% of predators are fossorial (Daniels and Heatwole, 1984). Thus the use of water as an escape medium still exposes *E. quoyii* to attack from 39 predatory species, several of which are as important, if not more so, than *P. porphyriacus* (e.g. kingfishers and herons).

It seems unlikely therefore that *S. rotundocapitatus* is using active mechanisms to promote the consumption of the transport host by the final host. The only behavioural aberration so far observed in infected lizards is unlikely to affect capture frequency, particularly as the lizards are so rarely eaten by snakes. In addition, as a consequence of any active changes, natural selection may promote host resistance either to the parasite or to the behavioural change. There is always the risk that the response of the host may outweigh any advantage of the changed behaviour, to the detriment of the parasite. All my examinations to date have failed to isolate the intermediate host. However, it is possible that the parasite does not employ any active transfer mechanisms in that host either or that employing active transport mechanisms may not be necessary. I do not know that the parasite affects the first host in the same manner as the second. Many other acanthocephalans influence the behaviour of the first host but are benign in the second. However it is reasonable to hypothesise that passive strategies are the primitive ones from which time and natural selection develop more active methods in some species. As I wish to examine the primitive 'worst case' situation I will assume that in this system transition through the first host is also passive.

Holmes (1976) observed that once in an intermediate host the normal operation of the food web will greatly enhance the probabilities of reaching some potential final host. In the case of *S. rotundocapitatus*, it is possible that the operation of the food web will passively support parasite transfer and enable the establishment of a viable parasite population, provided both the hosts and the worms are long lived. Utilising the knowledge of the ecology of the two vertebrate hosts and the parasite, it is possible to calculate the time required for a parasite population to become established. Assume an infected *P. porphyriacus* enters a riparian habitat previously free of the acanthocephalan. Then *S. rotundocapitatus* eggs become abundant and can retain their infectivity for very long periods until consumed by the intermediate host. Assuming that the abundance of eggs result in the very rapid infection of a substantial proportion of the intermediate host population then there are two crucial periods in the parasite lifecycle. Firstly, the infection of 34% of the *E. quoyii* with cystacanths and then the infection of 23% of the *P. porphyriacus*.

To calculate the time for the passive transfer of the parasite from the intermediate host to the lizard, six assumptions are made: (1) As aquatic prey comprise 1-7% of prey items, we assume 1% of food items are the intermediate hosts; (2) 33% of intermediate hosts are infected; (3) Lizards eat every day; (4) Lizards eat two types of prey/day; (5) Lizards are active 6 months/year; (6) 20% of cystacanths hatch in the lizard and survive to again form a cystacanth. The predicted proportion of infected arthropods is unsubstantiated because the intermediate host is unknown. However, the proportion is similar to the levels of infection observed in the other hosts. Both Daniels (1984, 1987) and Veron (1969a) observed virtually all *E. quoyii* to contain fresh prey. Half of Veron's lizards contained prey from more than five taxa while most of mine had more than two prey items. The value of 20% of cystacanth viability is an estimate, probably an underestimate. About 20% of cystacanths removed from *E. quoyii* and fed to *P. porphyriacus* developed into adults (Daniels, pers. obs.). Thus the time for 34% of *E. quoyii* to become infected with *S. rotundocapitatus*:

= (% of prey infected)x(% of prey in diet)x(no. prey items/day)x(% of lizards infected)x(viability of cystacanths)

= (100/33)x(100/1)x(1/2)x(34/100)x(100/20)

= 258 days or approximately one year

Because lizards are only active 6 months/year, it takes about 1.5-2 years for 34% of *E. quoyii* to become infected.

To calculate the time for 23% of *P. porphyriacus* to become infected it is necessary to make five assumptions; (1) Snakes eat one prey item at a time; (2) Snakes eat once every three days; (3) 34% of *E. quoyii* contain cystacanths; (4) 20% of cystacanths exsheath and survive to reproduce in *P. porphyriacus*; (5) Snakes are active 6 months/year. A third of 22 *P. porphyriacus* I examined had prey in their stomachs, although Shine observed that a greater percentage of his snakes had fed recently (Shine, 1977). I usually found one prey item/snake although the average in Shines' was nearly three (Shine, 1977). *P. porphyriacus* probably feed more often than assumed here. Thus the time for 23% of *P. porphyriacus* to become infected is:

= (no. of prey eaten/feed)x(frequency of eating)x(% of snakes infected) x(viability of cystacanths)x(% of lizards infected)

= (1)x(3)x(100/2)x(23/100)x(100/20)x(100/34)

= 507 days

Snakes are active for only half of the year so it takes approximately 3 years for 23% of the snake population to become infected. The total time for a parasite population to become established in all hosts is therefore 5-6 years, well within the lifespan of both the lizard and the snake, the more so considering the conservative nature of the calculations.

However, can the parasites maintain their numbers in two reptilian hosts in the face of natural mortality and the short activity period? Assuming lizards live 6 years then 17% of the population die each year. On third of that, or 6% of the total lizard population die containing parasites. (This is probably an overestimate because during any year, most mortality within the *E. quoyii* population occurs amongst the juveniles, which are not parasitised (Veron, 1969a; Daniels, 1984). Thus, to maintain the population stability *S. rotundocapitatus* must infect 6% of the uninfected lizards/year:

= (% of prey in diet)x(% of prey infected)x(prey items eaten/day) x(% of lizards infected)x(viability of cystacanths)

= (100/1)x(100/33)x(1/2)x(6/100) x(100/20)

= 45 days

But 28% of the surviving population is already infected. Thus, the time for infection:

= 45x c. 125/100

= 56 days or approximately 2 months

Similarly if snakes live 10 years then the population turnover is 10%/year with approximately 2.5% of the population dying while containing parasites (again an overestimate because the greatest mortality occurs amongst juveniles which are relatively unparasitised (Shine, 1978; Daniels, 1984). Therefore, for population stability, approximately 2.5% of the uninfected snakes must collect a parasite/year. Thus the time for infection:

= (% of prey in diet)x(prey eaten at a time)x(no. days between feeding)x(% of snakes infected)x(viability of cystacanths)x(% of lizards infected)

= (100/2)x(1)x(3)x(2.5/100)x(100/20) x(100/34)

= 55 days

However, 20% of the surviving population is already infected. Therefore the tine for infection:

= 55x120/100

= 66 days or approximately 2 months

Hence it takes approximately 4 months for the parasite to replace individuals lost when their hosts die. Four months is well within the yearly activity period of the reptiles, the more so considering the conservative nature of the calculations.

This study supports the hypothesis that the operation of the food web will passively transport the parasite from one stage in its life cycle to the next. The time predicted is probably an overestimate. However, as acanthocephalans have separate sexes, it is crucial for at least 2 worms to reach each snake. The number of cystacanths per lizard is not important. The conservative basis within the calculations provides excess time which may be important for allowing extra parasites to infect hosts. Moreover, the great longevity of *P. porphyriacus* may compensate for the low rate of consumption of *E. quoyii* and enable populations of *S. rotundocapitatus* to become established in each infected snake.

Perhaps the most convincing evidence for the utilised of the passive transfer mechanism involves the very low numbers of parasite/host. It is possible that the low numbers of parasites per host represent a truncated negative binomial distribution because host mortality may be associated with increasing intensity of infection. However, no pathological effects were observed in either host, even in the skink with 8 parasites (Daniels and Simbotwe, 1984). Other animals appear to be capable of supporting large numbers of acanthocephalans without discernible effect (Holmes, 1982). Hence, parasites practising passive strategies rely on time and the laws of probability to promote infection. As each infection is an independent event, then the structure of the parasite population should be characterised by many infected hosts containing relatively few individuals. The distribution of *S. rotundocapitatus* in both *E. quoyii* and *P. porphyriacus* clearly falls into the passive type.

Parasites can increased the probability of transfer and promote the success of the passive mechanism in three ways. Firstly, by prolonging the survival time and viability of the eggs, cystacanths and adults. In some acanthocephalan species the eggs retain their infectivity for more than 3 years (Crompton, 1975) while acanthellae at least 6 months old have been removed from cystacanths in *E. quoyii* (Daniels and Simbotwe, 1984). Longevity is crucial because of the slow rate of transfer between hosts. However, a prolonged survival time is especially important for cystacanths and adult worms because of the long hibernation periods of their hosts. Host hibernation results in long periods of food unavailability for adult *S. rotundocapitatus* and reduces mating opportunities because of the delay in the rate of acquisition of more parasites.

Hibernation also affects reproduction because it stops the release of eggs into the correct aquatic habitats. Adult worms must either live a long time and be capable of producing large numbers of eggs or live a short time and produce very large numbers of long lived eggs in order to maximise reproductive output and compensate for the high attrition rate in this type of life cycle.

It is also crucial for cystacanths to be capable of exsheathing, transferring and establishing themselves in the next host when the opportunity arises. The value of 20% used in my calculations may be unrealistically low. A doubling of this percentage incurs a major reduction in the time necessary to establish a parasite population. Cystacanth viability is probably the most important variable in the population dynamics of the parasite because it is the most malleable. Without a high cystacanth viability it is unlikely that enough cystacanths would reach the final host in time to develop into adults, mate and maintain egg production.

Secondly, the passive transfer mechanism could be promoted if the parasite was not specific to one intermediate or transport host. In situations where both the transport host and the final host consume a wide range of prey items all at a low frequency, parasites will transfer more rapidly from one host to the next by using many host species rather than by increasing the level of infection within one specific host. Therefore, cystacanths should tolerate a relatively broad range of physiological conditions in order to survive in many different types of host. Cystacanths of *S. rotundocapitatus* have been extracted from two other small skinks, *Hemiergis decresiensis* and *Lampropholis guichenoti* but in both cases the level of infection was less than 6% (Daniels and Simbotwe, 1984). Undescribed acanthocephalan cystacanths have also been extracted from other snakes and lizards (Johnston and Deland, 1929a). However, somewhat surprisingly, cystacanths have not been collected from frogs. From a transfer viewpoint, frogs would be better transport hosts than lizards because they are more important dietary items for *P. porphyriacus*. However, its appears either that *S. rotundocapitatus* cystacanths cannot survive in other animals, or the consumption of infected *E. quoyii* is sufficient to maintain the parasite population.

The third mechanism available to *S. rotundocapitatus* to promote the passive transfer mechanism involves exploiting behavioural variability within the host population. The presence of parasites in water skinks with extended voluntary diving times may reflect such an exploitation. The tendency to dive may vary greatly between animals within a population. Long dives might be characteristic of lizards which use the water most frequently as an escape medium and also as a food source. These more aquatic lizards may be more likely to feed at the waters' edge, capture aquatic prey and thus become infected with *S. rotundocapitatus*. When attacked, the more aquatic lizards may exhibit a greater tendency to swim or dive, conferring a degree of protection from terrestrial predators but not from *P. porphyriacus* (Daniels, 1985a). Thus the parasite can exploit a polytheism within the host population to increase the chance of reaching the final host. The presence of *S. rotundocapitatus* correlates with, rather than causes, a behavioural or physiological difference and is therefore less likely to stimulate host resistance.

Active transfer mechanisms can be disadvantageous when the intermediate host represents a small proportion of the diet of the final host, the final host consumes a wide variety of prey and the intermediate host is a prey item for a large range of different predators. This type of food web is common in Australian ecosystems and specialist systems involving one predator and one prey are rare (although there are a number of vertebrates which specialise on ants or termites). The relative absence of simple food webs, especially amongst the vertebrates may be a result of the low vertebrate biomass. It may be impossible for one carnivore to specialise on one, or a few, prey species because the densities of the latter are too low. The optimal transport strategies for parasites in diffuse and complex food webs are often passive rather than active, provided reproductive output remains high enough to compensate for the attrition.

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FACTORS AFFECTING THE ESCAPE BEHAVIOUR OF A RIPARIAN LIZARD

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The escape tactics employed by water skinks, *Eulamprus quoyii*, are determined by their immediate location and orientation and by the physical characteristics of the habitat. Running was the most frequently practised type of escape, with rocks the preferred form of cover. Swimming and diving were employed to a lesser extent. Juvenile water skinks did not differ in escape behaviour from adults.

Water skinks use only a small proportion of their maximal locomotor and diving abilities during escape. Short dives and/or short bursts of swimming or running enable escape from a predator and still allow the individual to resume normal activities almost immediately (or execute more evasive manoeuvres). Juveniles are poorer swimmers and divers but only slightly poorer runners than adults.☐ *Eulamprus quoyii, escape diversity, running, swimming, diving, micohabitat.*

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The selection of an appropriate escape response is a critical factor in survival, and recently has been analysed using lizards as model animals (Jaksic and Núñez, 1979; Simbotwe, 1983; Schall and Pianka, 1980). The latter found that lizards alternated among various methods of escape, and predicted that prey populations faced with higher per capita predation pressure should evolve more diverse escape tactics than less heavily predated conspecific populations. The present paper deals with the more proximate nature of diversity and escape tactics, by asking the following question: When a lizard is threatened, what factors determine which of the escape tactics in its repertory it will use? The subject of the study was the water skink *Eulamprus quoyii* (formerly *Sphenomorphus quoyii*), a riparian lizard that eludes predators by running to terrestrial cover, and/or by swimming or diving (Veron and Heatwole, 1970).

STUDY AREAS

The study was undertaken at three locations near Armidale, NSW, Australia, in summer (January and February) 1983. Each site comprised 1.5km of stream bank. They were structurally different but all supported large populations of water skinks. The heterogeneity of each habitat was determined by quantifying the emergent ground cover in 10 m^2 sections every 100m along the stream bank. The percentage of each section covered with small rocks (surface area<15cm^2), medium-sized rocks (15-100cm^2), large rocks (>100cm^2), vegetation and fallen timber, and bare ground, was recorded. Rocks 15-100cm^2 seemed to be optimal basking sites. Stream speed was measured at each section by timing the rate of passage of a floating ball down the fastest flowing 10m. The characteristics of the three sites are presented in Table 1.

Boorolong Creek, 26km southwest of Armidale, was a wide, slowly flowing stream usually divided into very large pools by granite outcrops or fallen trees; the banks were densely lined with reeds, grasses, blackberries (*Rubus* sp.) and *Casuarina*. The Gara River, 15km north of Armidale, was a narrow, rapid stream with many small pools located at the periphery. The stream contained many large rock outcrops but small rocks were comparatively scarce. The banks were densely lined with reeds, grasses and bottlebrushes (*Callistemon* sp.). Blue Hole was located 15km downstream from the Gara River study site and 15km northwest of Armidale. The banks were thickly covered with granite boulders of a variety of sizes with a corresponding reduction in streamside vegetation. Although

TABLE 1. Characteristics of the three streams used as study sites expressed as $\bar{x}\%$ ± S.E. (n).

MICROHABITAT	BLUE HOLE	GARA RIVER	BOOROLONG CREEK
Open Bank	13.1± 3.6 (12)	31.3± 6.4 (10)	33.9± 6.5 (15)
Small rocks	9.4± 2.2 (12)	1.5± 1.1 (10)	19.3± 4.4 (15)
Medium sized rocks	15.8± 2.3 (12)	6.5± 1.5 (10)	10.0± 3.7 (15)
Large rocks	53.3± 5.0 (12)	5.7± 2.2 (10)	6.9± 2.2 (15)
Vegetation	7.5± 1.4 (12)	55.0± 6.8 (10)	30.3± 6.4 (15)
Flow rate (ms^{-1})	1.3± 1.8 (12)	0.73± 0.19(10)	0.10± 0.05(15)

midstream flow is rapid, the rocks allow the formation of numerous small, quiet pools. The vegetation consisted primarily of grasses, blackberries and casuarinas. All sites were located in dry sclerophyll forest or open woodlands. In summary, Blue Hole was much rockier, more open and less vegetated than the other two sites, and Gara River had a higher rate of stream flow than the other two.

MATERIAL AND METHODS

ECOLOGICAL FACTORS

Observations were undertaken only on fine sunny days with little or no wind and air temperature of 25-30°C. Light falls of rain occurred intermittently during the study period but were not sufficient to greatly alter stream morphology or rate of flow.

The stimulus used to induce escape was a person approaching on foot at a moderate speed from the landward side. The same person was used throughout. For each escape event the following data were recorded: (1) initial microhabitats and body orientation of the lizard with respect to the water and to bank cover, (2) execution of changes in direction from the initial orientation, but prior to fleeing, (3) microhabitat selected for escape and (4) escape tactic employed. Data from adults and juveniles were recorded separately; juveniles were defined as water skinks shorter than 85 mm snout to vent (Veron, 1969).

The categories of initial microhabitat were: (1) water, (2) on a rock surrounded by water, (3) on a rock on the bank and (4) on the bank.

A lizard's initial orientation was tallied as (1) facing the water, (2) facing the bank or (3) parallel with both. Alteration in orientation prior to fleeing was listed as nearest to 0°, 45°, 90°, 135°, or 180° from original orientation.

The covers selected for protection were classed as (1) reeds, (2) rocks, (3) the bank or (4) open water.

Water skinks utilised terrestrial (running), or aquatic (swimming and/or diving) escape tactics. Swimming was always undertaken on the surface with the head above water, while diving was defined as a descent to the bottom of a pond and remaining motionless there in leaf litter or rock crevices, usually for several minutes. Occasionally lizards did not move when approached and were easily caught. Another escape response, active surface swimming followed by a dive, was only occasionally observed and represents the only overlapping of categories of escape tactics.

Values for the breadth of each habitat niche were calculated using Simpson's (1949) diversity index (DS). Microhabitat niche overlap and escape behaviour overlap were calculated using Pianka's (1973) index. Statistical analyses employed the chi-squared goodness of fit and the G test for independent samples (Sokal and Rohlf, 1969; Snedecor and Cochrane, 1978).

Since observations were made at different times of day, a test was made to see whether there was a temporal effect. Morning and afternoon values were not significantly different for microhabitats prior to escape (G = 0.86; P>0.05; niche overlap between morning and afternoon = 0.999), escape tactic (G = 4.26; P>0.05), original orientation (G=1.24; P> 0.05) and degree change in orientation (G = 4.10; P>0.05). Consequently, data from both periods of the day were pooled for subsequent analyses.

Data on microhabitat prior to escape were also pooled for juvenile and adult lizards as at all sites there were no significant differences between the age classes (G = 1.94, 5.40, and 6.80 for Blue Hole, Gara River and Boorolong Creek respectively; P>0.05 in all cases; niche overlap between juveniles and adults in the three respective areas were 0.988, 0.922 and 0.938). There were too few juveniles for testing the other results for Gara River. However, there were no significant differences between adults and juveniles in escape tactics (G = 5.12 and 5.64 for Blue Hole and Boorolong Creek respectively, $P>0.05$ in both cases) original orientation (G = 1.96 and 0.94; $P>0.05$) and degree change in orientation (G = 2.28, 4.34; $P>0.05$), and data were pooled for these as well.

PHYSIOLOGICAL FACTORS

Eulamprus quoyii were tested to determine voluntary diving time, swimming speed, stamina, running speed and running stamina according to methods already described (Daniels, 1984b, 1985). Lizards were collected by hand from Tea Tree Creek and Boorolong Creek between February 1982 and December 1983. Adults and juveniles were both maintained as previously described (Daniels, 1984b, 1985). In the experiments, unless otherwise stated, air temperatures of 30-32° and water temperatures of 19-20°C were used. These temperatures approximate air and water temperatures during summer at creeks inhabited by the species (Pidgeon, 1978) and straddle its mean preferred body temperature of 29.6°C (Spellerberg, 1972a,c).

Diving time determined by timing 30 dives for each of 21 lizards at a water temperature (mean ± S.D.) of 19.1° ± 1.7°C and an air temperature of 31.6° ± 1.1°C. Swimming stamina was examined by maximally exercising 16 lizards until exhaustion (trial 1). The time taken before the lizard stopped swimming was recorded. A second swimming trial (trial 2) was conducted on the same lizard 20 minutes later to determine recovery capacity. Two trials per lizard were conducted every day for 10 days. Running speeds were determined by stimulating 17 lizards to run the length of a 161 x 40 x 50cm glass tank with a sand substrate at Ta = 31.6° ± 1.1° C. Ten trials were conducted for each lizard with 20 minutes rest between trials. Juvenile *E. quoyii* were timed while running a distance of 68cm. Running stamina was also determined at an ambient temperature of 18.1° ± 0.8°C in a tank (24.5 x 38.5 x 37.5cm) with a dirt substrate. Nine lizards were chased, one at a time, around the periphery of the tank until they refused to move after five consecutive taps on the base of the tail. A low ambient temperature was chosen to match that of the water temperature during the swimming stamina experiments, so as to make direct comparisons between the two types of stamina possible. A second running endurance trial was conducted for each lizard 20 minutes after the first; two such trials were conducted each day for 10 days.

All times were recorded using a Lauris Stopwatch accurate to 0.02 seconds. From the repetitions of all experiments mean values were calculated for each individual; the maximum value was also analysed. All results were expressed as means ± standard errors (S.E.) except air and water temperatures which were expressed as means ± standard deviations (S.D.). Statistical analysis employed Student t-test and paired t-tests (Sokal and Rohlf, 1969). Speeds were expressed in metres per second (ms^{-1}), and stamina and diving times were expressed in seconds (s). In addition to these laboratory studies, voluntary diving, swimming and running times were determined in the field. Water skinks were chased into the water at Blue Hole and Boorolong Creek and timed till they swam to cover or, if they dived, until re-emergence. Air and water temperatures were recorded at the site of entry into the water. Running times were recorded at Blue Hole and Boorolong Creek for lizards chased from their basking sites towards rocks or reeds. Air temperatures were recorded at the basking sites.

RESULTS

MICROHABITAT

Undisturbed water skinks were usually at sunlit sites, particularly on rocks near the water (Table 2). The second highest usage was of the stream bank. Only occasionally were lizards in the water, floating or resting on algal mats. Thus, there seems to be a clear preference for emergent streamside sites rather than for the water itself. There were three major terrestrial microhabitats available, rocks, open banks and vegetation (Table 1). When the observed frequencies of their use by lizards were tested by Chi-square analysis against the values expected on the basis of their relative cover, the observed values departed significantly from the expected ones (X^2, Blue Hole 54.1, Gara River 298.0, Boorolong Creek 86.4; $P<<0.005$ in all cases), indicating the lizards were not randomly associated with substrate type. No lizards were found in the vegetation at any locality despite it having mean cover values in the three areas of 7.5-55.0% but rocks and open habitats had rather high frequencies of usage. Thus, the lizards seemed to select non-vegetated microhabitats.

TABLE 2. Microhabitat preferences (frequency of use) of *Eulamprus quoyii* prior to escape.

MICROHABITAT	BLUE HOLE	GARA RIVER	BOOROLONG CREEK
In water	0.015	0.048	0.039
On rock in water	0.111	0.136	0.196
On rock on bank	0.637	0.552	0.324
On bank	0.237	0.264	0.441
n	333	124	204
X^2 (df)	1.62 (1)	188.86 (1)	2.19 (1)
P	>0.05	<0.05	>0.05
Niche breadth	0.369	0.510	0.649

To test whether rock or open banks were favoured, a second Chi-square analysis was performed testing observed frequencies of use of these microhabitats relative to their proportional representation in non-vegetated stream sides. At Blue Hole where rocky habitat was abundant and bare bank relatively rare (Table 1) the lizards inhabited banks more often than expected by its relative cover ($X^2 = 25.4$; $P << 0.005$). At the Gara River where open bank was well represented and rocks less common, the lizards favoured rocks ($X^2 = 96.0$, $P << 0.005$).

At Boorolong Creek where the two microhabitats were represented in about equal proportions, use of rocks and banks did not differ significantly from expected values ($X^2 = 0.51$; $0.50 > P > 0.025$). It may be that the lizards tend to preferentially use whichever is the rarer of these two microhabitats. Niche breadth was greatest at Boorolong Creek, the locality with the most even coverage of habitat types, and least at Blue Hole where habitat diversity was lowest, rocks accounting for over 78% of total microhabitat (Tables 1, 2).

Overlap in microhabitat niche was high among sites (Table 2). Gara River and Boorolong Creek, the two sites most similar in habitat characteristics (Table 1), did not differ significantly in the frequency of use of different microhabitats by the lizards (Table 3). The greater dissimilarity in habitat characteristics of Boorolong Creek was reflected in a significant difference in frequency of microhabitat use by lizards there in comparison to the other two places (Table 3).

ESCAPE BEHAVIOUR

When approached, lizards usually escaped significantly more often by running rather than by swimming or diving. Rocks were the preferred cover sought regardless of the escape route or mode of locomotion employed (Table 4). The diversity of escape responses was lowest at Blue Hole, which had the greatest uniformity of microhabitat and the greatest proportion of rocks, the preferred escape cover (Tables 1, 4).

Although the overlap in escape tactics was high among areas, each area differed significantly from every other in the frequency with which different tactics were employed, and with one exception (Gara River vs Boorolong Creek), in the frequency with which different modes of locomotion were used (Table 3). The most notable differences were that in the rockiest area (Blue Hole) lizards ran to rocks more often for escape than at the other localities, and employed aquatic escape less frequently (Table 4). In the terrestrial situation water skinks at Blue Hole employed terrestrial escape tactics significantly more often than did those from Boorolong Creek ($G_{(1)} = 11.26$; $P < 0.05$); those that originally faced parallel to or toward the banks escaped less frequently to water at Blue Hole than did those with similar initial orientation at Boorolong Creek ($G_{(1)} = 4.96$; $P < 0.05$). It would seem that when rocks are abundant they are preferentially used for escape, but when they are less abundant, escape by diving or swimming increases in frequency.

Rate of stream flow also may be a factor. Blue Hole, where aquatic escape was lowest, had the swiftest current (Table 1).

Unmolested water skinks most frequently faced the water, and once disturbed, they tended to move away in the direction they were originally facing, usually to the nearest rock (Table 5). Thus, either the lizards tended to face toward predetermined escape routes or perhaps merely

TABLE 3. Comparison among localities of the microhabitat selection and escape tactics of *Eulamprus quoyii*.

	GARA RIVER VS BOOROLONG CREEK	BOOROLONG CREEK VS BLUE HOLE	BLUE HOLE VS GARA RIVER
MICROHABITAT			
Niche overlap	0.884	0.830	0.993
G (df)	20.18 (3)	50.92 (3)	5.38 (3)
P	<0.05	<0.05	>0.05
ESCAPE TACTICS			
Overlap	0.933	0.693	0.893
G (df)	17.76 (9)	111.06 (9)	43.88 (9)
P	<0.05	<0.05	<0.05
ESCAPE TACTIC SUBTOTALS			
G (df)	3.16 (3)	20.60 (3)	10.78 (3)
P	>0.05	<0.05	<0.05

fled in whatever direction they happened to facing.

Approach was from the landward side and that may have influenced direction of escape. The 90° and 180° turns occurred most often when the lizard was initially facing the direction from which the person approached. However, a landward approach would be expected to drive the lizards into the water, rather than along terrestrial escape routes. Such did not occur and direction of approach did not seem to be an overriding factor.

Unfortunately, data on original orientation and degree change of direction are available only for two sites (Blue Hole and Boorolong Creek). These two areas did not differ in regard to the direction undisturbed lizards faced (Table 5). By contrast, those from Boorolong Creek tended to alter their original orientation in order to escape, significantly more often than did those from Blue Hole (Table 5). This is probably because the abundance of rocks at Blue Hole provided escape avenues in almost all directions, but at Boorolong Creek where rocks were less than half as abundant, a lizard would more often have to change direction in order to head for rocky cover.

Comparison of the antecedent behaviour of lizards escaping aquatically with those escaping terrestrially, revealed a number of important differences. For example, at all study sites lizards that were already in the water or on rocks surrounded by water used an aquatic avenue of escape more often than a landward escape; those initially located on land escaped significantly more often to the land than to water (Table 6). Thus, the microhabitat occupied at the time of disturbance influences the avenue of escape that is adopted.

At Boorolong Creek, lizards parallel to the shore or facing the water initially showed no significant preference for escape to any particular medium, but those facing the land effected a terrestrial escape significantly more often than they fled to water (Table 6). At Blue Hole most animals in all categories escaped to land. For those parallel to the shore or initially facing land selection for a landward escape was significant; for those originally facing water it was not (Table 6). Thus, initial orientation may influence direction of escape.

Finally, there was no significant correlation between the degree of change in direction and the proportion of escapes that were toward the water (Spearman Rank Test: Boorolong Creek $r_s = -0.6$, $P>0.10$; Blue Hole $r_s = -0.4$, $P>0.10$). The data (Table 6) again confirmed the greater tendency toward terrestrial escapes at Blue Hole compared to Boorolong Creek. In neither area, however, are lizards that escaped in the direction they initially faced more (or less) prone to escape toward a particular medium than are those which showed greater amounts of turning after disturbance.

LOCOMOTOR PERFORMANCE

Adult and juvenile *Eulamprus quoyii* both exhibited similar diving behaviours. Lizards often submerged vertically in a crevice in the diving tank, and remained motionless with eyes closed throughout the dive. Both size groups exhibited a mean voluntary diving time in the laboratory

TABLE 4. Escape tactics of *Eulamprus quoyii* at three sites.

ESCAPE TACTIC	BLUE HOLE	GARA RIVER	BOOROLONG CREEK
Swim : to Reeds	0.034	0.134	0.188
: to Rocks	0.197	0.119	0.127
: to Bank	0.040	0.060	0.075
: then Dive	0.003	0.022	0
Dive : in Open Water	0.003	0.007	0.014
: in Reeds	0.009	0.015	0.028
: in Rocks	0.017	0.045	0.042
Run : to Rocks	0.519	0.299	0.174
: to Reeds	0.165	0.254	0.333
Remain Motionless	0.014	0.045	0.019
n	351	134	213
X^2 (df)	137.74(9)	165.50(9)	157.82(9)
P	<0.05	<0.05	<0.05
Escape Diversity	2.95	5.14	4.97
ESCAPE TACTIC SUBTOTALS			
Swim	0.274	0.336	0.390
Dive	0.028	0.067	0.085
Run	0.684	0.552	0.507
Remain Motionless	0.014	0.045	0.019

of between 5 and 6 minutes (Table 7), and the difference between the two groups was not significant ($t_{(19)} = 0.65$, $P>0.05$). However, the adults did have significantly longer maximum dives ($t_{(19)} = 1.86$, $P<0.05$). The longest dive for an adult *E. quoyii* was 35.4 minutes and the longest dive by a juvenile was 15.1 minutes. There was a significant trend in both groups for mean voluntary dive time to decrease as the number of completed dives increased (Daniels, 1984a,b, 1985). In the field, water skinks dived for only short periods. Mean voluntary diving time was 2.5 ± 2.00 minutes (n = 12) with the longest dive being 12.5 minutes (water temperature 24.1°+ 0.51°C; air temperature 28.2° ± 0.87°C).

The skinks usually swam in an anguilliform manner (Batholomew et al., 1976). The legs were held laterally against the side of the body and thrust was developed by lateral undulations of the body and tail. As the lizards became exhausted, tail undulations became weaker and propulsion was maintained by body movements and, prior to complete exhaustion, with flipper-like actions of the forelegs. The size groups exhibited significantly different mean speeds ($t_{(13)} = 85.37$, $P<0.05$) and maximum speeds ($t_{(15)} = 122.77$, $P<0.05$) (Table 11). The fastest adult *S. quoyii* swam at 1.34ms^{-1} and the fastest juvenile at 0.4ms^{-1}. In the first swimming trial, lizards continued swimming for more than two minutes. Juveniles had slightly less stamina (mean swimming stamina: $t_{(14)} = 1.10$, $P>0.05$). The longest endurance for an adult in trial 1 was 181s and for a juvenile 163s.

If adult water skinks could sustain a mean swimming speed of 0.64ms^{-1} for two minutes, then they could swim up to 80m before becoming exhausted. However, 124 adults and juveniles inhabiting New England creeks and chased into water of 21.0 ± 0.86°C (air temperature 23.5 + 1.09°C) swam for 2.19 ± 0.15s, with the maximum swimming period being 79.5s. There was no significant difference in these swimming times between adults and juveniles(adults: 3.69 ± 0.96s, n = 88; juveniles: 1.65 ± 0.19s, n = 36; Student t- test: $t_{(122)} = 1.37$, $P>0.05$). Lizards rarely swam more than 2-3m before emerging onto rocks or the bank.

Twenty minutes after being exercised maximally, lizards could only sustain short bursts of swimming (Table 7). Mean swimming stamina was significantly less in trial 2 than in trial 1 for both groups (adults: $t_{(205)}= 20.73$, $P<0.05$; juveniles: $t_{(101)} = 13.39$, $P<0.05$). The greatest stamina for an adult in trial 2 was 121s and for a juvenile 100s. Adults swam for significantly longer than juveniles in trial 2 (mean stamina:

TABLE 5. Original orientation and degree change in direction by *Eulamprus quoyii* from Blue Hole and Boorolong Creek.

	Blue Hole	Boorolong Creek
Original Orientation		
Facing Water	0.407	0.354
Parallel to Water/Bank	0.258	0.323
Facing Bank	0.335	0.323
n	248	201
X^2 (df)	38.15(2)	25.44(2)
P	<0.05	<0.05
G (df)	2.54(2)	
P	>0.05	
Degree Change in Direction		
0°	0.421	o 373
45°	0.109	0.070
90°	0.239	0.294
135°	0.065	0.080
180°	0.166	0.184
n	247	201
X^2 (df)	91.802(4)	73.654(4)
P	<0.05	<0.05
G (df)	4.4(4)	
P	<0.05	

$t_{(14)} = 2.28$, $P<0.05$; maximum stamina: $t_{(14)} = 2.78$, $P<0.05$).

The intraspecific differences observed for swimming stamina were not observed for running stamina (Table 7). Juveniles could sustain activity for as long as adults in trial 1 (mean running stamina: $t_{(7)} = 0.45$, $P> 0.05$; maximum stamina : $t_{(7)} = 0.21$, $P>0.05$). Maximum running endurance for an adult in trial 1 was 142s and for a juvenile 144s. Adults and juveniles also possessed similar recovery capacities (Table 7) (mean running stamina in trial 2: $t_{(7)} = 1.05$, $P>0.05$; maximum stamina $t_{(7)} = 0.42$, $P> 0.05$). During trial 2 the longest endurance of an adult was 103s and that for a juvenile was 108s. As in the swimming stamina trials, the mean exercise times in trial 2 were significantly shorter than those of trial 1 (adults, $t_{(43)} = 12.47$, $P<0.05$; juveniles, $t_{(38)} = 13.00$, $P<0.05$). No significant differences existed between the mean running and swimming stamina of adults (trial 1: $t_{(151)} = 1.65$; $P>0.05$; trial 2: $t_{(140)} = 1.66$; $P>0.05$). Juveniles swam longer than they ran in trial 1 ($t_{(98)} = 2.56$, $P<0.05$).

Adults ran faster than hatchlings (Table 7), (mean speed: $t_{(15)} = 27.89$, $P<0.05$; maximum speed $t_{(15)} = 34.78$, $P<0.05$). The fastest speed for an adult was 1.52ms^{-1} and that for a juvenile was 0.76ms^{-1}. When approached in the field, lizards utilised only short bursts of running. The mean time it took lizards to reach cover, once disturbed, was 1.90 ± 0.80s (n = 56) (air temperature = 28.2° ± 0.87°C.

DISCUSSION

Diversity of Escape Tactics

Water skinks are potential prey for over 100 different species of vertebrate predators (Daniels and Heatwole, 1984), yet they exhibited a relatively low index of escape diversity. The values of 2.95-5.14 (Table 4) rank in the bottom third of the 14 species of lizards so far studied (Table 8). The small diversity value reflects the high proportion of individuals that retreated to a single type of cover (rocks). It may be that such a tactic is effective against a wide range of the common predators of water skinks. Another pos-

TABLE 6.Percentage of aquatic and terrestial escapes of *Eulamprus quoyii* to microhabitat selection, original orientation and degree change in direction.

	BLUE HOLE			GARA RIVER			BOOROLONG CREEK		
	AQUATIC	TERRESTRIAL	N	AQUATIC	TERRESTRIAL	N	AQUATIC	TERRESTRIAL	N
MICROHABITAT									
In water	80	20	10*	83	17	6	100	0	8*
On Rock in Water	92	8	37**	94	6	17**	93	7	41**
On Rock on Bank	27	73	214**	34	66	67*	34	66	66*
On Bank	13	87	80**	30	70	31*	34	66	90*
ORIGINAL ORIENTATION									
Facing Water	43	56	99	–	–	–	60	40	69
Parallel with Shore	35	65	63**	–	–	–	46	54	61
Facing Bank	14	86	82**		–	–	36	64	61*
DEGREE CHANGE IN ORIENTATION									
0°	25	75	107	–	–	–	48	52	56
45°	39	61	28	–	–	–	57	43	14
90°	34	66	61	–	–	–	53	47	59
135°	31	69	18	–	–	–	33	67	16
180°	19	81	43	–	–	–	39	61	37

An asterisk at N values for Microhabitat and Original Orientation categories indicates a chi-square test on the actual numbers gave a P of<0.05 (significant). Two asterisks indicate P< 0.001 (highly significant). No asterisks indicate P>0.05 (not significant).

TABLE 7. The exercise capacities of adult and juvenile *Eulamprus quoyii*.

EXERCISE	UNITS	TEMPERATURE (°C)		ADULTS				JUVENILES			
		Air	Medium	Mass (g)	Snout-vent length (mm)	n	Time	Mass (g)	Snout-vent length (mm)	n	Time
DIVING											
Mean	s	31.6±1.1	19.1±0.7	24.6±1.5	102.9±1.5	14	360.5±17.3	7.3±0.6	69.7±1.6	7	312.7±11.0
Max.	s						1075.1± 182.5			6	83.9±59.8
SWIMMING SPEED											
Mean	ms^{-1}	31.6±1.1	22.1±1.4	23.4±1.5	102.0±1.9	12	0.64±0.01	0.8±0.1	34.4±1.0	5	0.29±0.01
Max.	ms^{-1}						0.85±0.07				0.36±0.02
SWIMMING STAMINA											
Trial 1											
Mean	s	31.6±1.1	19.8±2.1	25.9±1.7	103.0±1.8	10	130.1±2.0	7.3±0.6	69.7±1.7	6	118.7±3.8
Max.	s						155.8±0.1				154.3±6.5
Trial 2											
Mean	s	31.6±1.1	19.8±2.1			10	74.6±1.8			6	59.0±2.4
Max.	s						93.9±0.1				70.0±10.7
RUNNING SPEED											
Mean	ms^{-1}	31.6±1.1	31.6±1.1	23.4±1.5	102.0±1.9	12	0.96±0.01	0.8±0.1	34.4±1.0	5	0.39±0.02
Max.	ms^{-1}						1.17±0.05				0.54±0.06
RUNNING STAMINA											
Trial 1											
Mean	s	31.0±1.0	18.1±0.8	25.8±2.8	105.0±3.0	5	114.5±2.3	7.3±1.0	67.8±1.9	4	106.2±2.6
Max.	s						129.4±5.0				125.0±9.2
Trial 2											
Mean	s	31.0±1.0	18.1±0.8			5	79.5±1.9			4	67.5±.2.0
Max.	s						93.6±2.9				86.8±7.1

sibility is that this species adjusts its escape tactic to a particular kind of potential predator, e.g. using different tactics for snakes than for birds, or for humans. By using only one stimulus (humans) we may have observed only the subset of escape tactics given to large land animals. Analysis of predator-specific escape responses might be a fruitful line of research.

We would like to caution against over-interpretation of such diversity indices. The index is influenced by the number of categories of escape response. Had we used each of our rock sizes as a separate category (Table 1) rather than 'rocks' as a single one, the diversity index would have been altered. We suggest that some of the variation in escape diversity may merely reflect differences in investigator's classifications of escape tactics.

The utilisation of water by primarily terrestrial lizards for predator avoidance is not uncommon, being practised by over 50 species from 10 families (Daniels, 1984a). Most of these lizards swim across open water to avoid terrestrial predators. A number submerge and rest on the bottom until a predator departs. Water skinks utilise short aerobically sustained dives (Daniels, 1984a). The predator may still be in the vicinity when the lizard emerges, but because the skink is not exhausted it can submerge again if threatened. Moreover, because anaerobiosis has not been extensively employed, the skinks are still capable of rapid swimming to avoid predators. Thus, short dives keep all escape options open. In addition, the use of swimming, diving and/or running in sequence has the advantage of providing flexibility if one method of escape is suddenly unavailable. For example, if disturbance of rock cover removes running or other terrestrial tactics as a viable escape method, swimming or diving still remain.

The second major tactical advantage concerns locomotor capacity. Water skinks can dive for up to 35 minutes and swim or run continuously for over 2 minutes. However, in natural situations, these lizards either do not, or do not have to, perform at these maximal capacities. By exhibiting dives of 2-5 minutes and sprints of 2 seconds in the field, water skinks are utilising only a small proportion of their maximal escape capability. Such behaviour enables the lizards to avoid a potential predator in a given encounter and still be able to resume normal daily activities (or flee from other predators) almost immediately. These lizards have flexibility in escape tactics and the behavioural and locomotor capacity to maximise the effectiveness of any of the escape tactics selected.

Intraspecific Differences

Ontogenetic changes in diving performance have been observed in several ectotherms and Butler and Jones (1982) suggested that dive duration should be proportional to (body mass)$^{0.75}$ for ectotherms. The values obtained on water skinks in the present study are consistent with that view. Ontogenetic increases in swimming speed have been observed for *Amblyrhynchus cristatus* (Bartholomew et al., 1976) and some anurans (Taigen and Pough, 1979; Miller, 1983). Running speed increases ontogenetically for several African lizards (Huey, 1982; Huey and Hertz, 1982). The swimming stamina and recovery capacity of juvenile water skinks was much lower than that of adults, although the running stamina of the two size groups were similar.

In view of the lower capabilities of juveniles for aquatic life it is surprising that their escape responses did not differ significantly from those of adults. However, use of water for escape is low in all age groups, and even the adults have not developed unusual physiological adaptations for diving (Daniels, Oakes and Heatwole, 1987).

Effect of Habitat on Escape Tactics

E. quoyii is a territorial, solitary heliotherm. Sunlit rocks, especially those on a soil substrate suitable for burrowing, are the preferred microhabitat for basking and other activities (Spellerberg, 1972a,b,c,d, 1974; Done and Heatwole, 1977). Because of their close proximity to rocks and their use of them for other activities, it is not surprising that water skinks also use rocks as a primary shelter during escape.

Schall and Pianka (1980) observed that the escape diversity of *Cnemidophorus* was not correlated with environmental heterogeneity (plant volume diversity or percent vegetative cover) but rather with presumed predation pressure (high incidence of tail breaks). Aside from the doubtfulness of incidence of broken tails as an indicator of predation pressure (e.g. intraspecific fighting also may injure tails), such an explanation cannot be used to explain the differences in escape diversity between Blue Hole and Boorolong Creek lizards in the present study. Samples from both sites had similar frequencies of animals with regenerated tails; Blue Hole, original tails 54%, regenerated tails 46% (N = 15); Boorolong Creek, original tails 55%,

TABLE 8. Diversity of escape tactics and the practice of immobility by lizards.

Species	Habitat	Escape Tactic Diversity	Techniques for Predator Avoidance	Number of Classes	n	Frequency of Remaining Motionless	References
*Anolis aeneus** juveniles	Terrestrial	2.80	MR	3	23	0.44	Stamps (1983)
Cnemidophorus (overall)	Terrestrial	9.04	MR	12	–	–	Schall & Pianka (1980)
C. exsanguis	Terrestrial	7.2	MR	12	155	0.15	Schall & Pianka (1980)
C. gularis	Terrestrial	8.2	MR	12	169	0.05	Schall & Pianka (1980)
C. inornatus	Terrestrial	6.5	MR	12	268	0.16	Schall & Pianka (1980)
C. tesselatus	Terrestrial	6.5	MR	12	143	0.15	Schall & Pianka (1980)
C. tigris	Terrestrial	4.4	MR	12	288	0.03	Schall & Pianka (1980)
Eulamprus quoyii	Aquatic Terrestrial	4.31	MRSD	10	698	0.07	This Study
*Lacerta vivipara**							
males	Terrestrial	3.14	MR	6	401	0.01	Bauwens & Thoen (1981)
females	Terrestrial	3.12	MR	6	475	0.01	Bauwens & Thoen (1981)
Liolaemus fuscus	Terrestrial	1.32	R	2	297	–	Jaksic & Núñez (1979)
L. lemniscatus	Terrestrial	1.39	R	2	148	–	Jaksic & Núñez (1979)
Lygodactylus capensis	Arboreal	7.91	MRJ	10	100	0.07	Simbotwe (1983)
L. chobiensis	Arboreal	8.27	MRJ	10	100	0.07	Simbotwe (1983)
Physignathus lesueurii	Terrestrial/ Aquatic	4.42	RSD	10	870		Daniels (1984a)

M = remain motionless. J =jump (from tree to tree). R = run. S = swim. D = dive. * = values calculated from data presented in the paper.

regenerated tails 45% (N = 22). These frequencies are not significantly different ($G_{(1)} = 0.04$, $P > 0.05$) between the two areas.

Contrary to the prediction of Schall and Pianka (1980), mode of escape was related to the physical characteristics of the habitat. Blue Hole was the rockiest site and a greater proportion of water skinks there escaped to rocks than at any other locality. There was a significant increase in the utilisation of aquatic escape tactics from the rocky to the vegetated sites and from the fast-flowing to the slow-flowing sites. It appears that if rock cover is available, then lizards prefer to run to it rather than utilise aquatic escape behaviours. Running to rocks may represent the energetically least expensive form of escape because the sprint distance is frequently short and rocks represent a secure form of protection. Moreover, diving into cold water results in decrease in body temperature which may retard locomotor capacity (Hertz et al., 1982; Daniels, Heatwole and Oakes, 1987). Fast stream flow may pose the threat of sweeping the lizard away and probably requires greater energy expenditure during swimming.

In conclusion, water skinks alter their escape tactics depending on their immediate location and orientation and the physical characteristics of the habitat, and seem to select the energetically least demanding option. As a result they use only a small part of their capacity in a given escape attempt, leaving sufficient reserves for repeated attempts, or for other activities.

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AN INEXPENSIVE FORCE PLATFORM FOR USE WITH SMALL ANIMALS DESIGN AND APPLICATION

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A force platform was designed and manufactured to meet the following criteria: 1. be inexpensive and able to be constructed from readily available components. 2. be suitable for use with animals of less than 1kg and able to to provide an indication of the direction and timing of the forces produced by a lizard during locomotion. 3. be small enough to record forces from a pair of ipsilateral feet only, but large enough to allow a reasonable chance for a running lizard to place its feet on the platform.

A force analysis of Bearded Dragons (*Amphibolurus barbatus*) and Water Dragons (*Physignathus lesueurii*) indicated that unlike the more erect mammals, the legs of lizards apply no forward force to the ground during the limb cycle. Instead of the acceleration/deceleration cycle that occurs in the limbs of erect mammals, the lizards apparently apply a 'rotational' force that simply alters the angular momentum of the limb. These findings are discussed. ☐ *Lizards, locomotion, force platform.*

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The locomotor performance of animals can be investigated in a number of different ways: trackway analysis, for example, can provide estimates of speed, stride length, animal size etc. even for animals that have long been extinct (Thulborn, 1982; Thulborn and Wade, 1984); anatomical studies can elucidate certain locomotor constraints (e.g. Russell and Rewcastle, 1979); and kinematic analysis has been used to provide comparative data useful in understanding locomotor abnormalities (Parker and Bronks, 1980). However, none of these methods can provide more than an estimate of the way in which forces are transmitted to the ground during locomotion; to measure these ground reaction forces, a force platform is required. Unfortunately, force platforms are not always readily available, are often complicated, sometimes not completely suitable and usually extremely expensive. In this paper I describe a force platform that was used as part of a larger study of the locomotion of two species of agamid lizard. The platform is cheap, simple to construct and suitable for use with small animals.

THE FORCE PLATFORM

DESIGN CRITERIA

To produce an inexpensive force platform that could be constructed from readily available components, was suitable for animals less than 1kg, and would provide an indication of the direction and timing of the typical forces produced during the locomotion of the lizards used in this study. The platform was to be small enough to record forces from a pair of ipsilateral feet only, but big enough to allow a reasonable chance for a running lizard to place its feet on the platform.

TRANSDUCER ELEMENTS

The most expensive components of a force platform are the transducer elements used to convert variations in the applied forces into signals that can be recorded and analysed. In the system described here, inexpensive, commercially-available crystal microphone elements were modified (Fig. 1 and see below) to act as force tranducers. The output from these crystal elements varies with the rate of change of the force (i.e. the first derivative of the force, Fig. 2) thereby making an estimation of the actual value of applied forces an integrating process (either electrical or mathematical). However, as the primary purpose of the force platform was to provide an indication of the direction and timing of the forces applied to the ground by a moving lizard, actual values of the forces were not required and integration of the crystal output was considered unnecessary.

CONSTRUCTION (Fig. 3)

The surface plate for the force platform was

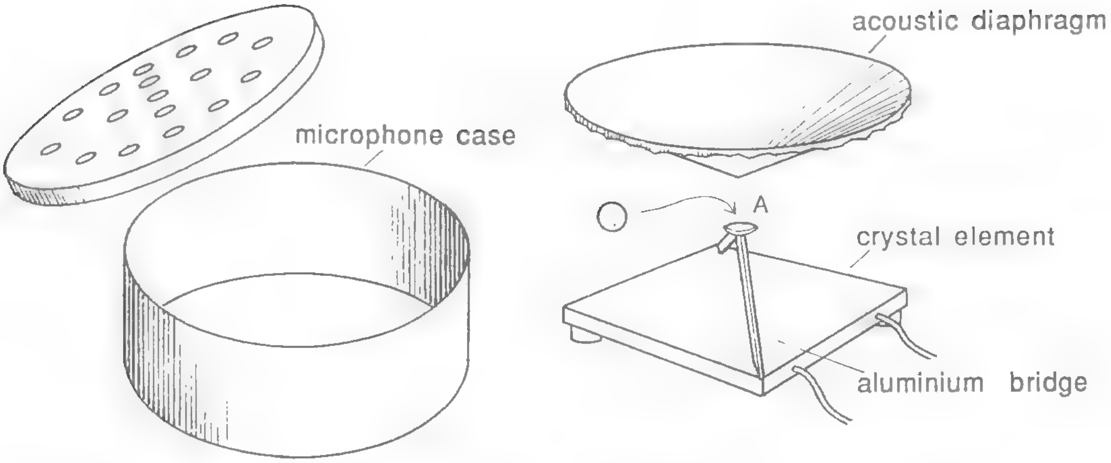


FIG. 1. Exploded view of the crystal microphone element used to provide the force transducers. A: shows the position of attachment of the glass bead.

provided by a piece of aluminium plate 10cm square and 3mm thick. An aluminium cube 25mm to a side was cemented to the centre of the plate and a transducer element was attached to each of the five remaining surfaces of the cube. The transducer element, when removed from the microphone case and acoustic diaphragm, consisted of a peizo- electric crystal wafer with two small rubber 'feet' mounted on diagonally opposite corners of one side. On the other side an aluminium bridge spanned the two remaining corners. Before fitting the transducer elements to

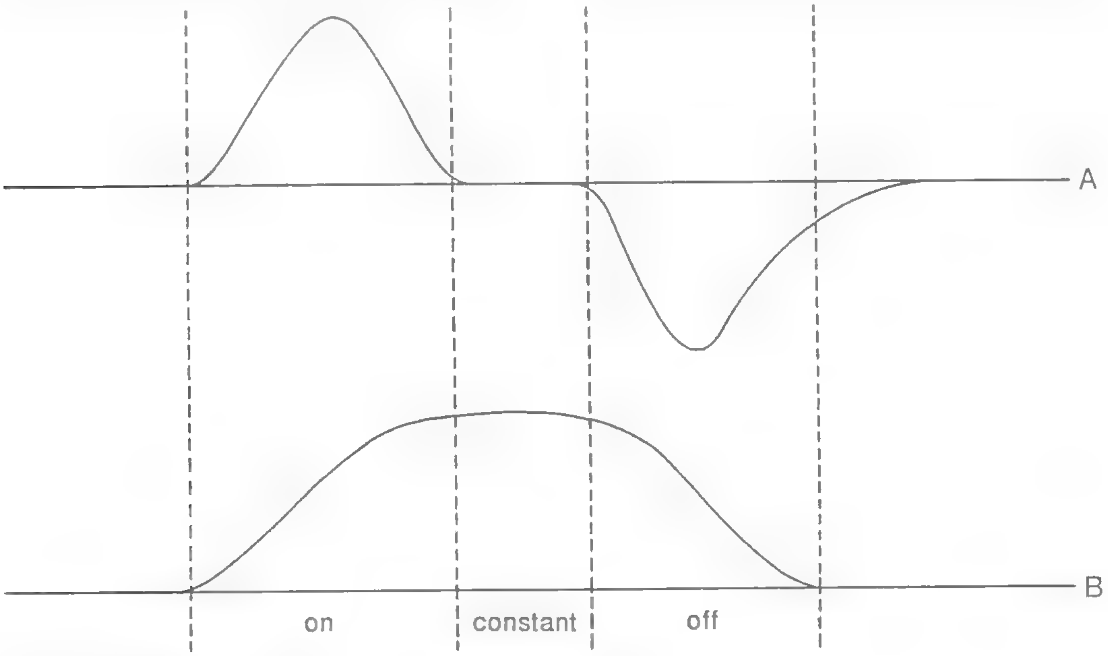


FIG. 2. Force diagrams: Transducer output, the first derivative of the force (A), compared with the actual force (B) its integral.

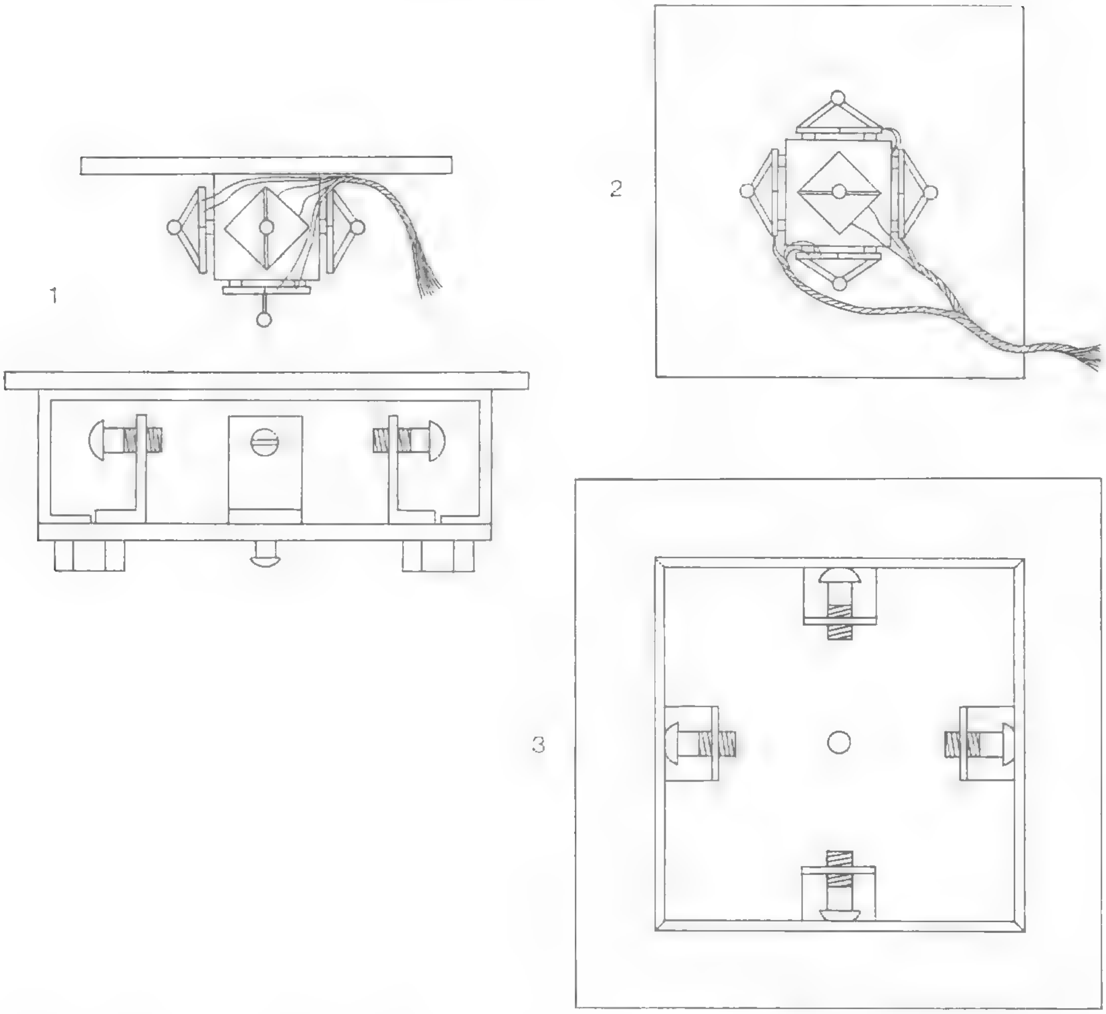


FIG. 3. Exploded view of force platform. 1: Lateral view of plate and base; 2: Ventral view of plate (note the arrangement of transducer elements); 3: Dorsal view of base.

the surface plate, a 3mm diameter glass bead was cemented at the apex of the bridge of each element. The surface plate was recessed into and supported by the body of the force platform which was also made from aluminium. Initially the surface plate was separated from the body of the force platform by a thin layer of low density foam but this arrangement was found to be overly sensitive and a more rigid, silicone jointing compound (silastic) was later used. The silastic effectively damped the plate and the amount used was varied, in conjunction with the degree of signal amplification, to suit the size of the lizard that was running over the platform during any particular set of trials. Five fine-thread brass screws were mounted in the body of the platform in such a way that they could be screwed up until just touching the glass bead of the transducer element. To reduce friction, and hence 'crosstalk' between the transducers, the ends of the screws were machined and polished and coated with teflon grease. Coarse grade sandpaper was glued to the top of the force plate which was recessed into the floor on one side of the runway. Electrical leads from each of the transducers were connected to a Grass 79D four-pen chart-recorder and the force platform was calibrated in situ before and after a set of trials for each lizard. As there were five transducers, but only four recorder pens, the output from lateral and medial transducers was duplexed to a single chart-recorder pen so that a laterally

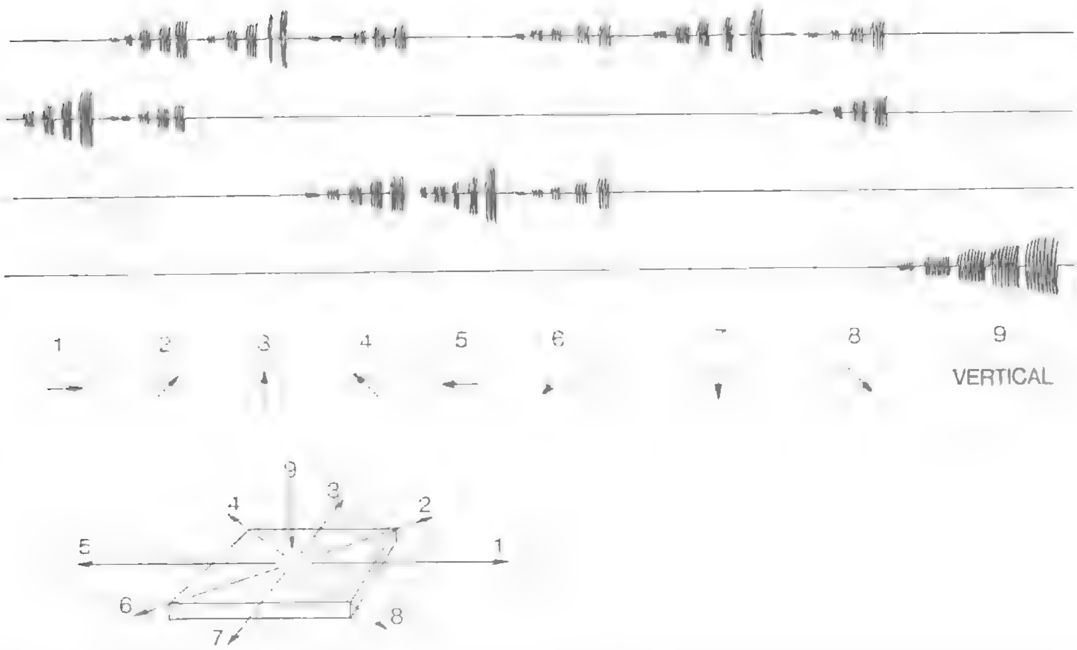


FIG. 4. Calibration of the force platform. A,B,C,: Horizontal transducer outputs; D: Vertical transducer outputs. 1-9 directions of application of force to the plate.

directed force resulted in an initial pen displacement in one direction and a medially directed force in the other.

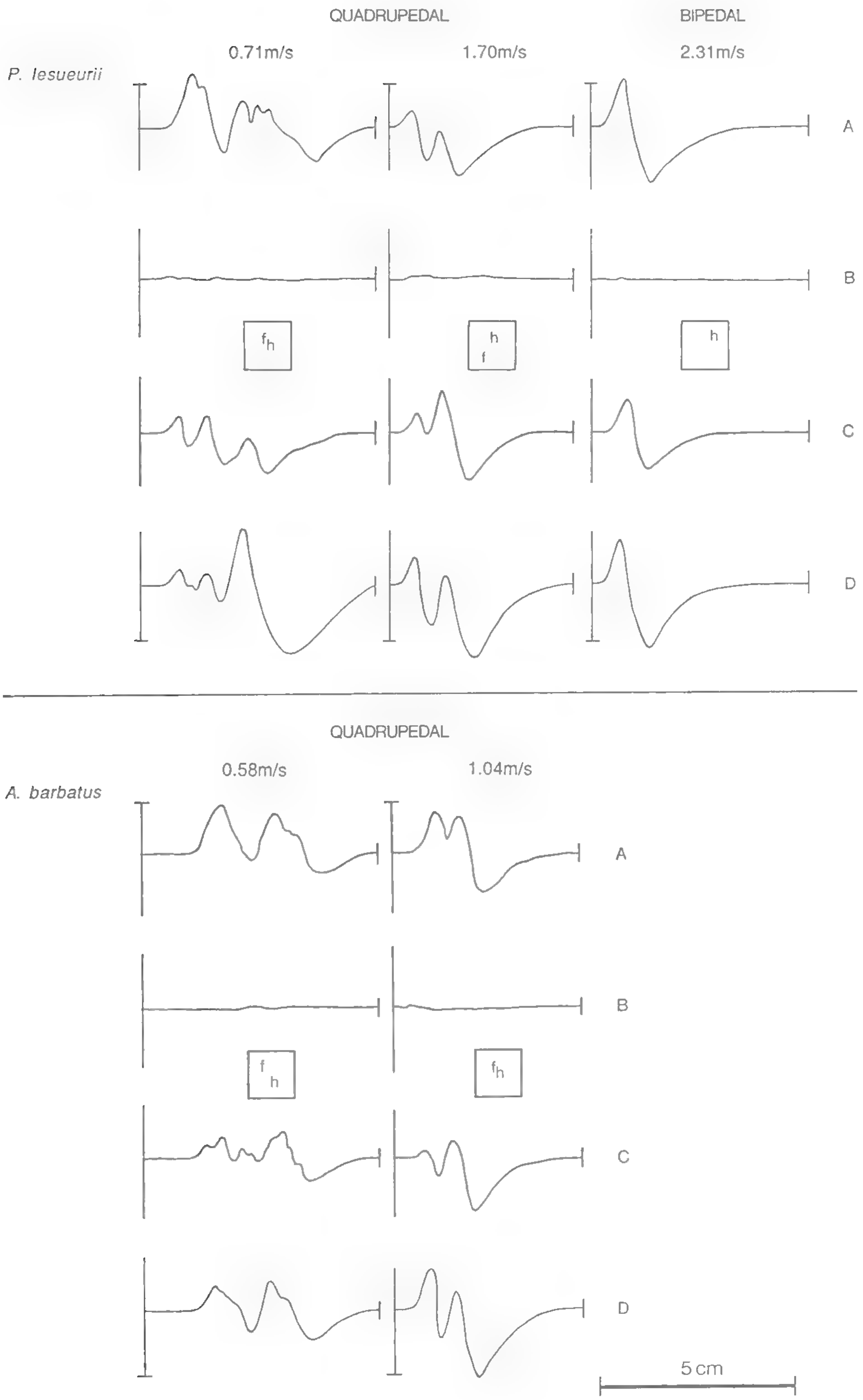
CALIBRATION

Fig.4 is an example of the calibration record obtained from the force platform before and after each set of trials for a particular lizard. As shown, repetitive sequences of force were applied at 45° angles through 360° of a horizontal plane and vertically downwards. Force increments in each series were 50g and the forces applied ranged from 50g to 250g. As nearly as could be determined: 1. each of the transducers reacted instantaneously to the application a force; 2. each transducer reacted if a component of the applied force acted on it, and; 3. 'crosstalk' from transducers that had no component of the force acting on them was minimal.

PERFORMANCE

Hegland (1981, p.333) has listed eight attributes of an ideal force platform. It should ' (1) be able to resolve the vertical, forward and lateral components of the force; (2) have low "crosstalk" between the measured components of the force, (3) have sufficient sensitivity and resolution for the subject of interest; (4) have a linear response; (5) have a response independant of where on the plate surface the force is exerted; (6) have a high natural frequency of oscillation; (7) have sufficient safety margin to protect both the plate and subject from damage due to failure; and (8) be simple and inexpensive.' The force platform described here meets most of these requirements but is perhaps questionable in three of them: (a) Linearity of response (no.4) - this was not critically assessed but is, to a large extent, dependent on the transducer elements. Improvement in this area would require better, hence more expensive, crystal elements, which is not necessary under the stated design criteria. (b) Response independent of position on the plate (no.5) - the response of this plate was found to vary slightly the farthur a foot was placed from

FIG. 5. Derivatives of the components of the ground reaction forces: (As applied by the lizard). A: Lateral force component; B: Forward component; C. Backward component; D: Vertical (downward) component. f and h are the points at which fore and hind feet respectively were placed on the force platform.


QUADRUPEDAL
BIPEDAL
0.71m/s
1.70m/s
2.31m/s
P. lesueurii
A
B
f h
h f
h
C
D
QUADRUPEDAL
0.58m/s
1.04m/s
A. barbatus
A
B
f h
f h
C
D
5 cm

the centre of the plate. This factor was controlled during the study by only using records where the foot or feet had been placed centrally on the plate. (c) Frequency of oscillation (no.6) - the frequency of oscillation is a function of the jointing compound used to damp the plate and can be controlled only marginally. However, in terms of the design criteria of the platform, this is relatively unimportant. In general, the force platform described here was found to fulfill the design criteria adequately and be capable of providing records of the direction and timing of the components of the ground reaction forces produced by a running lizard.

METHODS

Two Bearded Dragons (*Amphibolurus barbatus*: snout-vent lengths of 180mm and 239mm and weights of 148.5g and 403.5g respectively), and two Water Dragons (*Physignathus lesueurii*: snout-vent lengths of 172mm and 212mm and weights of 180.9g and 337.5g respectively) were used in the trials. Each lizard was encouraged to run in either direction along the runway as often as was necessary to produce acceptable force records for right and left ipsilateral feet. Trials were extended to obtain force records for the hind feet of Water Dragons moving bipedally.

RESULTS

Fig.5 shows typical records of the forces exerted by both species of lizard during quadrupedal locomotion and by Water Dragons during bipedal locomotion. Force records for left and right feet were essentially the same and only records from right feet are presented here for comparison. All records exhibit three distinct components of the force: a lateral component, a backward component and a vertical component. None of the records gave any indication that there was a forward component to the force exerted by a lizard during locomotion. Two major peaks are evident in each of the force components for all animals during quadrupedal locomotion and these correspond to the rates of force application by a front foot followed by a hind foot. At lower speeds, minor peaks can be seen within the major peaks for each foot, but as speed increases the minor peaks in the profiles become less obvious. All three components of the force for each foot were initiated at the same time and, at lower speeds, have approximately the same rate and duration of application. At higher speeds, however, the rate of application of the backward force, by a front foot, was less than that for the vertical and lateral components of the same foot. As is to be expected, the duration of the power stroke at higher speeds was considerably less than it was for lower speeds. Force records for bipedal locomotion are similar to records for hind feet during fast quadrupedal locomotion - each component of the force consisting of only one major peak with a relatively smooth profile. The initiation and duration of all three force components was the same but the maximum rate of application of the backward component was consistently less than that for the other two components. The duration of the power stroke during bipedal locomotion varied only slightly with speed and was similar to the duration of the power stroke during fast quadrupedal locomotion.

DISCUSSION

Because the force platform had to be preloaded to different degrees during each trial, the force records presented in Figure 5 can not be used to provide estimates of the absolute magnitudes of the forces applied to the plate by a running lizard. However, the components of the force can be compared within each trial to provide an indication of their relative importance. For convenience, forces are discussed here in terms of 'as applied by the lizard'; for example, a backward force means the force, or force component, applied by the lizard in a caudal direction resulting in the animal moving forwards.

Perhaps the most surprising result of the force analysis in this investigation is the lack of any indication of a forward component to the horizontal force exerted on the ground. The alternation of forward and backward forces during a locomotor cycle is responsible for the fluctuation in kinetic energy and consequently for a large part of the energy cost of locomotion. Yet Alexander (1977) showed mathematically that for a range of bipedal and quadrupedal animals it is energetically more efficient to incorporate both backward and forward components of force into the locomotor cycle. It would seem from Alexander's (1977) formulation that the locomotion of lizards is energetically inefficient and yet Bakker's (1972) investigations give evidence to the contrary. Although a mathematical analysis of the forces applied during lizard locomotion is beyond the scope of this investigation there may be a simple solution to this apparent conflict.

Alexander's model of applied forces relies (as he points out) on the height at the hip being greater than half the step length (step length = distance the animal moves while a foot is on the ground), which it apparently is for most animals (Alexander, 1977). Hip height in a lizard, however is less than 30% of total step length.

In fact, the way lizards apply force to the ground may even be the reason for their slightly greater locomotor efficiency (Bakker, 1972) than mammals of a similar size. Although Jenkins (1971) has shown that significant femoral abduction occurs in many species of small mammals, the movement of their limbs is still essentially forwards and backwards: energy must be expended to accelerate and decelerate the limb in both directions. By comparison, the movement of the limb of a lizard during locomotion is essentially rotatory: energy need be applied only to change its angular momentum. Although this may be an oversimplification, work by Fedak et al. (1982) has shown that the energetic cost of the changes in the potential energy of the limbs of some bipeds and quadrupeds during locomotion was not as high as expected because the essentially parasagittal movement of the limb in these animals also included a slight rotatory component. Further investigation in this area should prove instructive.

ACKNOWLEDGEMENTS

I am indebted to Dr Neil Gribble for his contribution to the design and operation of the force platform, and to Dr Tony Thulborn for his encouragement and assistance through all stages of the project from which this work was taken.

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***TROPIDONOTUS MAIRII* VS *BUFO MARINUS*:** – *Bufo marinus* was released in sugar-growing districts of eastern Queensland in 1935–6 and now occurs widely in that State and in northeast New South Wales. It is a highly toxic species (Meyer and Linde, 1971, p.522). The bulk of the venom is contained in the parotid glands. Venom is also secreted by smaller glands that cover the whole animal and toxins have been identified in other parts of the body, e.g. blood and ovaries (Meyer and Linde, 1971). The eggs also contain toxins (Licht, 1967) and, although there are no data on toxicity of the larvae, it does not seem unreasonable to assume they are also toxic.

Several native vertebrates can utilise *B. marinus* as a food source by eating eggs, larvae, newly metamorphosed young (e.g. Jungle Perch, *Kuhlia rupestris*;Snapping Tortoise, *Elseya latisternum*; Green Tree Snake, *Dendrelaphis punctulatus*; Common Keelback, *Tropidonotus mairii*) and selected body organs (e.g. Crow, *Corvus* sp.; Swamp Hen, *Porphyrio porphyrio*; White Ibis, *Thresikiornis mollucca*; Water Rat, *Hydromys chrysogaster*); or by 'washing' adults prior to ingestion (captive Estuarine Crocodiles, *Crocodylus porosus* have been observed washing *B. marinus* by shaking them vigorously in water for several minutes prior to successful ingestion) (Covacevich and Archer, 1975;Hamley and Georges, 1985; G. Ingram, pers. obs.).

Australian frog-eating snakes are known to be particularly susceptible to the toxin of *B. marinus* with one exception. This species the Common Keelback Snake (*Tropidonotus mairii*) has been regarded as the most successful and only regular native predator of *B. marinus*. It is known to consume large numbers of eggs, larvae, and newly metamorphosed young (Lyon, 1973; Covacevich and Archer, 1975; C. Tanner pers. comm.). *T. mairii*, a colubrid snake (subfamily Natricinae), is closely related to other natricine species occurring in North and South America, Asia and Europe (Malnate, 1960) where *Bufo* spp. also occur naturally. Its apparent high tolerance of *Bufo marinus* venom was attributed to the long evolutionary association of natricines and bufonids in these areas.

In December, 1976 a dead specimen of *Tropidonotus mairii* (total length 85cm) with a young adult *Bufo marinus* (head width 2.5 cm), one third ingested from the vent (rather than the head as is usual with snakes), was found in the dry bed of Richter's Creek, 10km north of Cairns, NEQ (Queensland Museum registration no. J 28417). There were no marks on the snake to suggest death from an encounter with a possible predator, and the toad is no larger than other frogs or small mammals commonly consumed by snakes of comparable size. Death from toad toxin is the only apparent explanation.

The discovery of this single known unsuccessful encounter between *T. mairii* and *B. marinus* is not conclusive evidence that larger *B. marinus* are invariably toxic to *T. mairii*, but this species is apparently more susceptible to *B. marinus* toxins than was supposed, particularly because in the case reported here, the snake had begun to ingest the toad from the rear, thus avoiding toxin concentrations in the parotid glands immediately behind the head.

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G.J. Ingram and J. Covacevich, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101, Australia; 16 August, 1990.

THE GENERIC CLASSIFICATION OF THE AUSTRALIAN TERRESTRIAL ELAPID SNAKES

M. N. HUTCHINSON

Hutchinson, M. N. 1990 09 20: The generic classification of the Australian terrestrial elapid snakes. *Memoirs of the Queensland Museum* 29(2): 397-405. Brisbane. ISSN 0079-8835.

The generic arrangement for the Australian elapid snakes has been unstable because, in part, of a lack of phylogenetic data by which monophyletic taxa could be recognised. Recently there have been advances in our understanding of Australian elapid phylogeny. These are summarised and a revised classification is proposed. This is based, as far as the data will allow, on monophyletic units. Evidence for monophyly is drawn from karyotypic, electrophoretic, immunological and internal and external anatomical data. ☐ *Serpentes, Elapidae, taxonomy, phylogeny, Australia.*

M. N. Hutchinson, South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia ; 1 June 1990.

The Australian terrestrial elapid genera have had an unstable recent taxonomic history. Mengden (1983) thoroughly reviewed the history of Australian elapid snake nomenclature, pointing out the conflicting views of the workers who have tackled this problem, and also noting areas where lack of data inhibited resolution of taxonomic problems. Cogger (1985) also reviewed elapid taxonomy, concluding that its history of largely intuitive analysis of morphological variation was responsible both for the prolonged instability of elapid systematics and the present disagreements over generic boundaries. He anticipated that an objective, biologically well-based taxonomy would only be achieved following a clear understanding of phylogenetic relationships.

For much of the twentieth century snake workers (including Kinghorn [1929; 1956] in his influential guides) followed Boulenger's (1896) arrangement, with relatively few genera diagnosed by features of anal and subcaudal scalation, head shield modification, number of maxillary teeth and general appearance. Worrell (1961; 1963) expressed his conviction that the fauna was more diverse by proposing several new genera, although his views were ignored until McDowell's (1967; 1969a; 1970) studies supported some of Worrell's suggestions. McDowell's comparative anatomical data led him to identify what he called 'natural groups', implying monophyly. Instead, some of his own analysis indicated that he formed some groups based on their *lack* of the derived character state for a feature, so that some, but not all, of his groups are grades, not clades. It is not surprising therefore, that his different data sets did not always coincide, resulting in a partially inconclusive revision of elapid taxonomy. Cogger (1975 et seq.) adopted a highly subdivided generic arrangement where most diagnosable groups were accorded generic status. Storr (Storr, 1985; Storr et al., 1986), however, has resisted this generic subdivision and has clustered together groups of species which have several external morphological features in common.

Typological thinking has thus led to the definition of diagnosable units (e.g. McDowell's 'natural groups') whose monophyly is assumed but untested. Clearly, as long as genera are defined in this way, classifications will continue to be accepted - or not - on the basis of authority or 'gut feeling', making discussion of the merits or biological validity of competing classifications very difficult.

Recently, data on elapid phylogeny became available in the series of articles forming part of the symposium volume edited by Grigg et al. (1985). These articles presented phylogenetic hypotheses based on karyology and allozyme electrophoresis (Mengden, 1985a; 1985b), immunological comparison of serum proteins (Schwaner, et al. 1985) and soft anatomy (Wallach, 1985). None of these studies was complete, in that, for each, certain taxa were unavailable or their relationships were not clearly indicated, and the individual authors were not in a position to benefit from the others' insights. Nevertheless, the different data sets corroborate one another on several points and, more importantly, there are no obvious discordances among the conclusions arrived at by the different authors. Thus, while a fully resolved, highly corroborated phylogeny for the Australian elapids has not yet been achieved, sufficient data are now available to set up a taxonomic scheme in which the included genera can be defined so as to be monophyletic as well as morphologically cohesive.

For the remainder of this paper I set out the genera which I propose should be recognised, with annotations concerning the evidence for monophyly and the reasons, where appropriate, for the points at which this generic arrangement differs from those accepted by Storr or Cogger. One of the problem areas discussed by Mengden (1983), namely whether 'Elapidae' is the appropriate family name for the Australian proteroglyphs, will not be discussed here. Although biochemical (Mao et al., 1983; Schwaner et al., 1985) and morphological (McDowell, 1967) evidence suggests that the Australian region proteroglyphs (including sea snakes) are monophyletic, suprageneric taxonomy will not be finalised until relationships to exotic proteroglyphs, and other colubroids, are better known. Through this article, 'elapid' is used as a convenient adjective, rather than as a position statement on higher taxonomy.

In arriving at a generic scheme I have used the following guidelines:

1. Genera must be truly monophyletic (holophyletic). Paraphyletic groups have been avoided by making genera either more inclusive or by complete splitting of terminal taxa. Monophyly has been based on the data in Grigg et al. (1985) and on McDowell's data on the derived states of adaptive complexes in venom gland musculature, palatal morphology and hemipenial structure.

2. Apart from the restrictions imposed by (1), genera are composed of species with strong phenetic similarities and ecologies.

3. Where a choice has been possible, genera have been inclusive ('lumped') rather than subdivided ('split') in order to show where species groups have clear sister-groups.

4. Aside from (1)-(3), at least one generic decision (concerning *Notechis, Austrelaps, Tropidechis*) has been taken (pro tem) to maintain usage of medically significant generic names.

The generic scheme adopted here is summarised in Table 1 and compared to those of Cogger (1986) and Storr (1985; Storr et al., 1986). For generic synonymies see Cogger et al. (1983).

Acanthophis Daudin, 1803

REMARKS

A chromosomally conservative but morphologically highly derived genus, biochemically well-separated from its nearest relatives, the other viviparous species with entire anal and subcaudal scales.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

antarcticus (Shaw and Nodder, 1802); *praelongus* Ramsay, 1877; *pyrrhus* Boulenger, 1896.

Austrelaps Worrell, 1963

REMARKS

See remarks for *Notechis*.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

superbus (Günther, 1858). As presently defined, this is a species-complex (Rawlinson and Hutchinson, in prep.)

Cacophis Günther, 1863

REMARKS

A genus of small cryptozoic snakes associated by most workers with the species here included in *Furina*. Its species retain the primitive *Glyphodon* type of venom gland musculature and (apart from the autapomorphic *squamulosus*) the primitive karyotype. Features which argue for their monophyly with respect to *Furina* are the hemipenis, which is of the derived single type (fide Wallach, 1985) and the characteristic (probably derived) colour pattern of a nuchal pale blotch extending forward over the lores while *Furina* species are possibly monophyletic with respect to *Cacophis* based on their uniformly dark eyes (iris paler than pupil in *Cacophis*). Thus I tentatively support separate recognition of *Cacophis* pending more thorough phylogenetic study.

TABLE 1. Correspondence between generic classification proposed and the generic schemes of Cogger (1985) and Storr (Storr, 1985; Storr et al., 1986).

Cogger	Present Work	Storr
Acanthophis	*Acanthophis*	*Acanthophis*
Austrelaps	*Austrelaps* ← part	
Drysdalia	*Drysdalia* ← part	
Echiopsis	*Echiopsis* ← part	*Notechis*
Elapognathus	*Elapognathus* ← part	
Notechis	*Notechis*	
Demansia	*Demansia*	*Demansia*
Cacophis	*Cacophis*	*Cacophis*
Furina	→ *Furina*	*Furina*
Glyphodon →		
Hemiaspis	*Hemiaspis*	*Hemiaspis*
Hoplocephalus	*Hoplocephalus*	*Hoplocephalus*
Denisonia → part	*Denisonia*	part ← *Denisonia*
Suta	→ *Suta* ←	
Unechis → part		
Rhinoplocephalus	→ *Rhinoplocephalus*	part ← *Rhinoplocephalus*
Cryptophis →		*Cryptophis*
Oxyuranus	→ *Oxyuranus*	*Oxyuranus*
Parademansia →		
Pseudechis	*Pseudechis*	*Pseudechis*
Pseudonaja	*Pseudonaja*	*Pseudonaja*
Tropidechis	*Tropidechis*	*Tropidechis*
Neelaps →		
Simoselaps	→ *Simoselaps* ←	part
Vermicella	*Vermicella*	*Vermicella*

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

harriettae Krefft, 1869; *krefftii* Günther, 1863; *squamulosus* (Duméril, Bibron and Duméril, 1854).

Demansia Günther, 1858

REMARKS

A chromosomally unique genus whose members have a derived morphology (convergent on Holarctic racers) for highly active diurnal foraging. Biochemical evidence indicates wide divergence from its nearest relatives (*Pseudechis* and *Pseudonaja*).

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

calodera Storr, 1978; *olivacea* (Gray, 1842); *papuensis* (Macleay, 1877); *psammophis* (Schlegel, 1837); *reticulata* (Gray, 1842); *rufescens* Storr, 1978; *simplex* Storr, 1978; *torquata* (Günther, 1862); *vestigiata* (de Vis, 1884) (from Storr et al., 1986; Ingram, 1990; and pers. obs.).

Denisonia Krefft, 1869

REMARKS

It is clear from all of the studies in Grigg et al. (1985) that this genus, even in the restricted sense of Cogger (1986), is polyphyletic. The type (*maculata*) and *devisi* are sister species, but more closely related to *Drysdalia* than to the other species retained in *Denisonia* by Cogger (*fasciata* and *punctata*) or the species placed by Storr in his expanded *Denisonia*. The pronounced difference in morphology and ecology between the two species retained here in *Denisonia* and their nearest relatives, *Drysdalia* (nocturnal, broad head-and-body species with glossy scales, elliptical pupils, versus diurnal, gracile species with matt scales and round pupils) argues for separate generic status for these two groups.

AMENDED DIAGNOSIS

As in Cogger (1985) with the following additions: Pupil vertically elliptic, iris of eye pale.

Distinguished from some superficially similar species of *Suta* by venom gland musculature of the *Oxyuranus* type (versus the *Pseudechis* type), retention of the deeply forked hemipenis (simple in *Suta*), diploid number of 34 with pair 5 sex chromosomes (versus 30 with pair 4 sex chromosomes) and upper labials strongly barred with white and dark brown.

INCLUDED SPECIES

devisi Waite and Longman, 1920; *maculata* (Steindachner, 1867).

Drysdalia Worrell, 1961

REMARKS

The distinctive pair 5 (rather than pair 4) sex chromosomes (shared with *Denisonia* s.s.) separate this morphologically cohesive group of small diurnal skink predators from *Notechis* and its relatives. *D. coronata*, which lacks the chromosomal synapomorphy, is nevertheless close to the other three species based on anatomical features (Wallach, 1985). On biochemical evidence (Schwaner et al., 1985; Mengden, 1985a) these snakes are less closely related to *Notechis* than are several morphologically divergent genera, notably *Hoplocephalus* and *Tropidechis*.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

coronata (Schlegel, 1837); *coronoides* (Günther, 1858); *mastersii* (Krefft, 1866); *rhodogaster* (Jan, 1873).

Echiopsis Fitzinger, 1843

REMARKS

Undoubtedly a close relative of *Notechis* on the basis of strong internal anatomical (Wallach, 1985) and biochemical similarities (Schwaner et al., 1985; Mengden, 1985b), as well as the phenetic similarities noted by Storr (1982). However, its derived *Acanthophis*-like habitus, including the subdivided temporal scalation noted by Mengden (1985a) and vertically elliptical pupil, and the absence of the derived *Notechis* karyotype, support separate generic status for at least *curta*. Mengden (1985a) also reported that *curta* showed venom properties with *Acanthophis*, adding to the list of features suggesting a possible sister-group relationship between these two taxa, rather than between *curta* and *Notechis scutatus*. *Brachyaspis atriceps* Storr, 1980, has not been studied and may, as Storr suggests, be closer to his *Denisonia* (*Suta* in my sense) than to *curta*.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

curta (Schlegel, 1837).

Elapognathus Boulenger, 1896

REMARKS

The general relationships of this monotypic genus clearly lie with the large group of viviparous species having entire anal and subcaudal scales. Storr (1982) partly expressed this in synonymising *Elapognathus* with *Notechis*. However, the precise sister species of *E. minor* is not identified by the available data. It retains the primitive 2n = 36 karyotype and is biochemically rather divergent from its relatives. Wallach's analysis fails to consistently identify a sister taxon. In 'gestalt', *E. minor* is most similar to juvenile copperheads (esp. *superbus*, s.s.) and Storr placed it in his *Notechis* on the basis of shared similarities with *scutatus*, *superbus* and *Drysdalia*. Storr dismissed the single generic character (no post-fang maxillary teeth) by making a general statement about the cautious use of dental characters in snakes. Nevertheless, his taxonomic characters for *Notechis* (s.l.) define a paraphyletic taxon (*Tropidechis, Hoplocephalus, Denisonia* s.s., and possibly even *Acanthophis*, should all be included) so that his data have defined only a grade of organisation (the primitive morphology for this group of genera?) rather than a strictly monophyletic taxon. My conclusion is that *Elapognathus* is, like *Echiopsis*, morphologically distinct (fang only on the maxilla, a derived character state) and lacks the apomorphic chromosomal feature of either *Notechis* or *Drysdalia*. Its single species, *E. minor*, is, on the basis of biochemical data, a very distinct species with no obvious sister taxon, and I favour its recognition.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

minor (Günther, 1863)

Furina Duméril, 1853

REMARKS

Furina and *Glyphodon* are similar small snakes characterised by divided anal and subcaudal scales, a cryptozoic way of life and, in most species, white to red nuchal patches. This pair has been least studied chromosomally and biochemically, so that there is rather little well-constructed phylogenetic data available. The genera are separated by features (presence/absence of a divided nasal) of unknown phylogenetic significance. In Wallach's analysis, the species included in the two genera tend to fall out as each-other's closest relatives, but do not form sub-groups matching the current generic boundaries; indeed, with every alteration in algorithm, the branching order changes. Mengden, on the basis of unspecified data, groups the pair as a monophyletic cluster of early divergence, with *Cacophis* the sister group of *Furina* (*diadema* only) plus *Glyphodon* (including *F. ornata*). The boundary between *Furina* and *Glyphodon* seems tenuous, especially the intermediacy of *F. ornata* with respect to *F. diadema* (generotype) on one hand and *G. tristis* (generotype) on the other. This lineage needs more study, pending which I feel there is insufficient data of phylogenetic significance by which the two genera can be justified. Uniting them under the oldest available name does, with seeming reliability, give rise to a monophyletic unit, which is moreover, relatively cohesive in ecology.

DIAGNOSIS

A genus of glossy-scaled (15-21 rows at midbody), snakes with a divided anal and divided subcaudals. Often (not *F. barnardi* or *F. dunmalli*) with a pale (white to red) nuchal blotch. Five or more teeth on each maxilla behind the fang. Head somewhat to markedly wider than neck and lacking a canthus rostralis.

INCLUDED SPECIES

barnardi (Kinghorn, 1929); *diadema* (Schlegel, 1837); *dunmalli* (Worrell, 1955); *ornata* (Gray, 1842); *tristis* (Günther, 1858).

Hemiaspis Fitzinger, 1860

REMARKS

A karyotypically unique pair of species, showing the unusual combination of divided anal, entire subcaudals and viviparity. Electrophoretic (? and chromosomal) data of Mengden suggested a very close relationship between the two species, as did Wallach's morphological data. The sister group of these two is not well established, but it seems a well-defined taxon.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

damelii (Günther, 1876); *signata* (Jan, 1859).

Hoplocephalus Wagler, 1830

REMARKS

Another chromosomally unique and morphologically well-defined genus, whose members possess the arboreal adaptation of angular ventrals and have markedly broad heads distinct from the narrow neck. Very closely related, on immunological (Schwaner et al., 1985) and morphological (Wallach, 1985) data to *Notechis* and *Tropidechis*. The phylogenetic position of this genus gives one of the strongest indications that Storr's concept of *Notechis* is paraphyletic, implying that his generic diagnosis is based at least in part on symplesiomorphies.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

bitorquatus (Jan, 1859); *bungaroides* (Schlegel, 1837). *stephensii* Krefft, 1869.

Notechis Boulenger, 1896

REMARKS

At present a controversial genus containing either two or a single species (Cogger, 1986; Schwaner pers. comm.), or a cluster of species which are surface-dwelling, viviparous, have entire anal and subcaudal scales and are otherwise morphologically conservative (Storr, 1982). Immunological, chromosomal and morphological studies all indicate that Storr's concept is paraphyletic.*

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*And nomenclaturally invalid. Storr (1982) dismissed *Echiopsis* Fitzinger as a nomen oblitum although declaration of a name as 'forgotten' could no longer be made after 1 January 1973. Fitzinger's (1843) names are widely regarded as available and are in wide use (including *Echiopsis*, see Cogger et al., 1983). Thus the correct name for Storr's genus should have been *Echiopsis* Fitzinger, 1843, not *Notechis* Boulenger, 1896.

However, there is a strong indication that *scutatus* is very closely related to the *Austrelaps superbus* complex, the two sharing (with *Tropidechis*) a uniquely derived karyotype and being very similar biochemically, anatomically and ecologically. Accordingly, I would favour the elimination of *Austrelaps* and the transferral of the *superbus* complex to *Notechis*. However, the precise relationships of *scutatus*, the *superbus* complex and *Tropidechis carinatus* are not yet established. The three taxa differ in minor features of proportions and scalation and are, based on the chromosomal synapomorphy, each-other's closest relatives. Amalgamation of the three would be a simple answer, except for the nomenclatural problem of the synonymisation of *Notechis* under the older *Tropidechis*. Because of the widespread use of the junior name, phylogenetic data would need to be compelling before such a destabilising revision of the existing taxonomy would be justified - in fact it could well lead to appeals to the ICZN to suppress *Tropidechis* in favour of *Notechis*. Pending detailed phylogenetic knowledge, *Tropidechis* and *Notechis*, and therefore *Austrelaps* should remain separate genera, although the close relationship between them should be borne in mind. *Tropidechis* is derived with respect to *Notechis* (s.s.) in its keeled scalation and increased midbody scale count, while *Austrelaps* differs in its derived *Pseudechis* type (rather than *Oxyuranus* type) of venom gland musculature.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

scutatus (Peters, 1861).

Oxyuranus Kinghorn, 1923

REMARKS

Covacevich et al. (1981) set out a range of characteristics which argued for sister-species relationship and congeneric status of *Pseudechis scutellatus* Peters, 1868 and *Diemenia microlepidota* McCoy, 1879. Cogger preferred to continue recognition of a monotypic *Parademansia* for *microlepidota*, but the additional data from the 1985 symposium reinforce the close relationship of these two species and further argue for their inclusion in a single genus.

DIAGNOSIS

See Covacevich et al. (1981).

INCLUDED SPECIES

microlepidotus (McCoy, 1879); *scutellatus* (Peters, 1868).

Pseudechis Wagler, 1830

REMARKS

A morphologically cohesive group retaining a primitive karyotype, but closely-related on the basis of immunological data (Schwaner et al., 1985) and monophyletic based on morphology (Wallach, 1985) and allozyme comparisons (Mengden et al., 1986).

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

australis (Gray, 1842); *butleri* Smith, 1982; *colletti* Boulenger, 1902; *guttatus* de Vis, 1905; *papuanus* Peters and Doria, 1878; *porphyriacus* (Shaw, 1794).

Pseudonaja Günther, 1858

REMARKS

Another well defined and monophyletic genus, although its alpha taxonomy is presently very unsatisfactory. Wallach's (1985) contention that *modesta* was not allied to the other species in this genus was refuted on several ground by Mengden (1985b).

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

affinis Günther, 1872; *guttata* (Parker, 1926); *ingrami* (Boulenger, 1908); *modesta* (Günther, 1872); *nuchalis* Günther, 1858; *textilis* (Duméril, Bibron and Duméril, 1854).

Rhinoplocephalus Müller, 1885

REMARKS

Another genus treated discordantly by Cogger and Storr. Long regarded as a monotypic genus (on the strength of the fused internasals and nasals) Storr greatly expanded the genus to include the other small, pale-bellied and dark-eyed semi-fossorial/nocturnal species placed by Cogger in *Unechis*. Mengden's and Wallach's studies partially support Storr, in that they indicate that some other species are closely related to *bicolor*, the type of *Rhinoplocephalus*, these being the two species of *Cryptophis* plus the type species of *Unechis*, *U. boschmai* (formerly *U. carpentariae*) and possibly *U. nigrostriatus*. However, the other small black-headed snakes (the *gouldii* complex) show a closer relationship to *Suta* and 'Denisonia' *punctata* and 'D.' *fasciata* than they do to *bicolor*. Thus I favour expanding *Rhinoplocephalus* to include the four close relatives mentioned above (including the types of *Cryptophis* and *Unechis*), but transferring the remaining species of Storr's *Rhinoplocephalus* to *Suta* (see below).

Revised Diagnosis

A group of small to moderate-sized species lacking contrasting dark head colouring (apart from *R. nigrostriatus*), with glossy midbody scales in 15 rows, anal and subcaudals entire, eye small with black iris, indistinguishable from pupil. Head slightly to moderately depressed, no canthus. Distinguished externally from some superficially similar species of *Suta* by deeper, blunter head, absence of contrasting colour pattern (except black-headed *R. nigrostriatus*) and/or longer tails (subcaudal counts exceed 40 in most species [not *boschmai*], versus 40 or fewer in most *Suta*). Further distinguished from other genera by the unique karyotypes (not present in *bicolor*), 2n = 36 (20 M, 16 M) or 40.

Included Species

bicolor Müller, 1885; *boschmai* (Brongersma and Knaap-Van Meeuwen, 1961); *nigrescens* (Günther, 1862); *nigrostriatus* (Krefft, 1864); *pallidiceps* (Günther, 1858).

Simoselaps Jan, 1859

Remarks

Storr and Cogger both noted that the small, mostly cross-banded fossorial snakes of arid Australia fall into several distinct subgroups, based on body, head and head-shield proportions which reflect ecological specialisation (Shine, 1984). Cogger separated some of these as distinct genera, but Storr united all in *Vermicella*, while identifying subgeneric groups having similar morphologies. Karyotypic data show that at least two of Cogger's genera (*Neelaps* and *Vermicella* s.s.) retain the primitive karyotype, while the types of two other genera or sub-genera (*Simoselaps* and *Brachyurophis*) have derived karyotypes. Of the latter pair, Mengden (1985a) derived the karyotype of (*Brachyurophis*) *semifasciatus* from that of (*Simoselaps*) *bertholdi*, implying a phylogenetic relationship between these taxa. Wallach's (1985) analysis shows all of the burrowing group consistently forming a monophyletic lineage, but the branching order within the group is not unequivocal. Only *Cacophis warro* de Vis, 1884, fails to fall out with the other burrowers, but Mengden's report of its showing the uniquely derived karyotype of *bertholdi* would argue for retention in the same genus as this species at least. No authors seem to have taken account of McDowell's (1969a) report of the distinctive biting apparatus present in all but *annulata* (and presumably *multifasciata*). This functional complex argues strongly for monophyly of at least all of the species except the type of *Vermicella*. *Furina annulata* Gray, 1841 is a remarkably primitive species, retaining the plesiomorphic state of the karyotype, venom gland musculature, hemipenis and palatine bone. As the true bandy-bandys (*Vermicella* s.s.) show none of the synapomorphies which unite some or all of the remaining species, there are no strong grounds, as McDowell (1969a) pointed out, for placing *annulata* with the other burrowers grouped together here as an expanded *Simoselaps*. Although morphological subgroups certainly exist within *Simoselaps*, relationships among them are obscure, and I prefer to recognise the probable monophyly of this group rather than itemising variation of uncertain phylogenetic significance.

Diagnosis

A group of small (less than 0.6 m total length), glossy scaled semi-fossorial snakes with anal divided, short tails with 35 or fewer paired subcaudals and showing variation in snout shape and body proportions analogous to those seen in *Ramphotyphlops*. Rostral always projecting but varying in profile from bulbous (e.g. *bimaculatus*) to wedge-shaped (e.g. *fasciolatus*) to upturned and angular (e.g. *semifasciatus*). No canthus rostralis. Body short and dumpy to elongate, but ventrals fewer than 230. Dark parietal and nuchal blotches always present, body usually yellow, orange or reddish, generally with darker reticulated or cross-banded pattern.

Included Species

anomala (Sternfeld, 1919); *approximans* (Glauert, 1954); *australis* (Krefft, 1864); *bertholdi* (Jan, 1859); *bimaculata* (Duméril, Bibron and Duméril, 1854); *calonota* (Duméril, Bibron and Duméril, 1854); *fasciolatus* (Günther, 1872); *incincta* Storr, 1968; *littoralis* Storr, 1968; *minima* (Worrell, 1960); *roperi* (Kinghorn, 1931); *semifasciatus* (Günther, 1863); *warro* (de Vis, 1884).

Suta Worrell, 1961

REMARKS

Preceding discussion on *Denisonia* and *Rhinoplocephalus* has alluded to the fact that several species share a close relationship with the type species of *Suta* (*Hoplocephalus sutus* Peters, 1863). The most compelling evidence is the uniquely shared 2n = 30 karyomorph, present in *Suta*, 'Denisonia' *fasciata* and 'D.' *punctata*, and the 'Unechis' *gouldii* species group. All are morphologically similar in being, like *Rhinoplocephalus*, small, glossy scaled cryptozoic species with entire anal and subcaudal scales. All species tested by Schwaner et al. (1985) also proved to be close to the *Notechis* group, and all of these species fall out as each other's closest relatives in Wallach's analysis. All have the derived *Pseudechis* type of venom gland musculature (McDowell, 1970). Storr et al. (1986) separated the three species with pale iris colour (*suta, ordensis* and *fasciata*) from the remainder, and place them with superficially similar species in his *Denisonia*. However, the pale iris is evidently a retained primitive feature, and eye colour is known to be intraspecifically variable in *ordensis* (Storr et al., 1986, p. 75).

REVISED DIAGNOSIS

A group of small to moderate-sized snakes with a consistent colour pattern of dark head markings (often a black to brown cap) and lighter brown body (cross-banded in *fasciata*), midbody scales very glossy, in 15-21 rows, anal and subcaudal scales entire. Head slightly to markedly depressed; no canthus rostralis. Eye uniformly black in most species, but paler than pupil, which contracts to a vertical ellipse, in *suta, fasciata* and most *ordensis*. Further distinguished by unique 2n = 30 karyomorph. (See also *Rhinoplocephalus*.)

INCLUDED SPECIES

dwyeri (Worrell, 1956); *fasciata* (Rosén, 1905); *flagellum* (McCoy, 1878); *gouldii* (Gray, 1841); *monachus* (Storr, 1964), *nigriceps* (Günther, 1863); *ordensis* (Storr, 1984); *punctata* (Boulenger, 1896); *spectabilis* (Krefft, 1869); *suta* (Peters, 1863). Probably *Brachyaspis atriceps* Storr, 1980, belongs here as well.

Tropidechis Günther, 1863

REMARKS

See remarks for *Notechis*.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

carinatus (Krefft, 1863).

Vermicella Günther, 1858

REMARKS

See remarks for *Simoselaps*. Aside from the unique colour pattern of black and white bands, the two species of *Vermicella* share a very to extremely attenuate body. Ventral counts in *V. annulata* range as high as 243 (Storr et al., 1986) (250 or fewer, generally less then 200, in other Australian elapid taxa) while in *V. multifasciata* counts range up to 290 (Cogger, 1986). Western populations of this genus have been described as a subspecies, *snelli* Storr, 1968, which Cogger (1986) placed with *annulata* but Storr et al. (1986) placed with *multifasciata*. The very high ventral count of *snelli* (to 318 ; Storr et al., 1986) indicates a closer relationship to *multifasciata*, although it lacks the latter's derived fusion of internasal and prefrontal shields.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

annulata (Gray, 1841); *multifasciata* (Longman, 1915).

ACKNOWLEDGEMENTS

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HERPETOLOGISTS AND SNAKE-BITE:– Snake-bite is an occupational hazard for professional and amateur herpetologists alike. A series of clinical case studies of reptile keepers bitten by snakes has revealed several 'at risk' themes. This note documents these in the hope that the frequency and morbidity of bites might be reduced, and convalescence hastened.

Snake-bite involving experts can happen at any time, including while attempting to catch snakes. The majority of clinical cases, however, occur during cleaning of vivaria or during other husbandry activities. Many cases occur at night. Unlike other syndromes of human snake-bite (the 'Big Game Hunter' scenario, for example, where an amateur, often intoxicated, tries to catch a snake for an audience), the victim is often working alone. The victim, despite experience in handling reptiles, sometimes is unsure whether a strike has actually occurred. A snake can strike a hand in a cage and recoil with lightning speed. As well, the skin lesions caused by the majority of Australian elapid snakes are trivial. Often no lesions or blood specks are visible in the first few minutes after strikes.

Many reptile fanciers who are bitten are envenomed by dangerous Australian species. A significant proportion of the very severe clinical envenomations seen in practice results from the bites of *Oxyuranus*, *Pseudonaja* and *Tropidechis*. A special potential medical problem that involves herpetologists is the scenario of envenomation by exotic snakes. It is essential that specific antivenom to African, Asian and American species is held at the national reference antivenom facility (Commonwealth Serum Laboratories, Parkville, Melbourne) if one is keeping such imported species.

Another medical problem for herpetologists is the multiple (serial) bite syndrome. Snake venom is highly allergenic and many reptile fanciers become sensitised to the venom. Insofar as the initial (transient) collapse of some victims is thought to be due to hypotension, this problem may be of particular relevance to the serial victim. Secondly, the risk of anaphylaxis rises with repeated (serial) injections of horse serum (antivenom) and the risk of such reactions probably rises above ten percent in those who have had several lifesaving infusions following previous bites. One problem encountered in practice is the fear of such reactions in an experienced herpetologist - sweating, tachycardia and faintness can be signs of true envenomation or incipient allergic reactions, or can be those simply of apprehension itself.

The skin lesions of elapid snakes are pleomorphic - typical two fang punctures (often with oozing blood specks) occur in 60 percent of cases only. Single punctures, multiple fang marks, and combined fang and teeth (both maxillary and palatine) lesions are common. If multiple strikes have occurred - a not uncommon scenario for both herpetologists and toddler children (both tend to hang on to the snake) - the potential for severe envenomation is greatly increased.

It is essential that all herpetologists should be trained in first aid, and have a compressive bandage (preferably an Esmarch bandage) and splint handy when they are working. With proper first aid treatment, elapid snakebite does not necessarily mean severe envenomation and severe envenomation does not mean morbidity or death.

John Pearn, Director of Training, St John Ambulance Australia, c/- Department of Child Health, Royal Children's Hospital, Brisbane, Queensland 4029, Australia; 17 August, 1990.

FOUR NEW SPECIES OF STRIPED SKINKS FROM QUEENSLAND

G.J. INGRAM AND G.V. CZECHURA

Ingram, G.J. and Czechura, G.V. 1990 09 20: Four new species of striped skinks from Queensland. *Memoirs of the Queensland Museum* 29(2): 407-410. Brisbane. ISSN 0079-8835.

Ctenotus nullum sp. nov., *C. hypatia* sp. nov. and *C. terrareginae* sp. nov. are skinks of rocky substrates from northeast Queensalnd. *C. aphrodite* sp. nov. is found in the arid country of the southwest of the State. ☐ *Ctenotus, skinks, new species, Queensland.*

Glen J. Ingram and Gregory V. Czechura, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101, Australia; 17 August, 1990.

Ctenotus is a very speciose genus of skinks. Wilson and Knowles (1988) listed 81 species and illustrated several additional new species. In this paper, we describe four new species from Queensland. *Ctenotus* was described in 1964 by Dr Glen Storr of Perth, Western Australia, and most of the species of the genus were subsequently described by him (see Wilson and Knowles, loc. cit., for a list of papers). Sadly, Glen Storr recently passed away. Australians owe him a debt for his thirty years of ceaseless work towards elucidating the species of reptiles of this continent. He will be sorely missed by his colleagues. Our paper is dedicated to his memory.

In the following, pattern nomenclature is of Wilson and Knowles (1988). Abbreviations are: SV, distance from snout to vent in mm; HW, head width at widest part as % SV; HL, length of hindlimb as % SV; TL, tail length as % SV; QM, Queensland Museum; AM, Australian Museum.

Ctenotus nullum sp. nov.

Ctenotus sp. (4). Wilson and Knowles, 1988, p.278.

MATERIAL EXAMINED

HOLOTYPE: QM J32424, sandstone escarpment, 2 km W of McIvor River Crossing, Cape York Peninsula, (15°07'S 145°04'E), Queensland, collected by G.J. Ingram on 15 July, 1976.

PARATYPES: nr Isabella Falls (QM J41023-5, J42768-9); Finch Bay, 1.7 km SE of Cooktown (AM R71031); ESE side of Mt Simon (AM R71033); Black Mountain, S of Cooktown (QM 24647); Shiptons Flat (QM J42736); Split Rock Gallery, S of Laura (QM J37999-38001); Quinkan, S of Laura (QM J24705).

DIAGNOSIS

A moderately large (maximum SV 79) *Ctenotus* with a pattern of stripes and an upper lateral row of pale squarish blotches which are usually confluent with the midlateral stripe; a black vertebral stripe begins on the nuchals and always extends to at least the fore back; a brow that does not conceal the supraciliaries; supralabials usually 8; subdigital lamellae widely calloused, 25-28 on fourth toe; four supraoculars; 4-6 ear lobules; and 26-28 midbody scales.

For an illustration of the species see Wilson and Knowles (1988, p.278, photo no. 424).

DISTRIBUTION

Sandstone areas around Laura and those to the near north of Cooktown; also at the base of the boulder mountains of Trevethan Range; and Shiptons Flat south of Cooktown.

DESCRIPTION

SV: 45-79 (N = 9, mean 62.2). HW: 13-17 (N = 9, mean 14.8). HL: 46-55 (N = 9, mean 51.2). TL: 245-257 (N = 4, mean 251.8).

Snout sloping, slightly rounded in profile. Nasals separated. Nasal groove absent. Rostral and frontonasal in narrow contact. Prefrontals large, separated or contacting and forming a short suture along the midline. Frontal long and narrow, contacting the prefrontals (and the frontonasal in 66% of specimens), the first three supraoculars, and the frontoparietals. 2-4 enlarged nuchals on either side (N = 18, mean 2.7). Four supraoculars, second much the larger. Supraciliaries 9-11 (N = 18, mean 9.5), first largest. Supralabials 8, uncommonly 9 (N = 18, mean 8.1); sixth under the eye and enters the orbit. Ear aperture large, 4-6 (N = 8, mean 4.8) pointed lobules on anterior border. Midbody scale rows 26-28 (N = 9, mean 27.8). Number of scales from chin to vent 60-66 (N = 9, mean

62.4). Toes long, compressed; subdigital lamellae widely calloused, 25-28 (N = 9, mean 26.4) under fourth toe.

Upperparts olive to reddish brown with a narrow black vertebral stripe edged with white paravertebral stripes continuing for varying distances down back or tail. There are 2 to 4 white-lined black dashes on the hind edge of the parietals. A white dorsolateral stripe begins at the last supraocular and continues down back and along tail. This is edged broadly (sometimes narrowly) by a black laterodorsal stripe at least as far as the base of the tail. Upper lateral zone black with squarish white, or fawn with white centres, spots that are usually confluent with the midlateral stripe (in life, the upper lateral spots are usually red). The white midlateral stripe begins behind the nostril and continues back through ear, along the body and tail. This stripe is lined darkly below, with white blotches against a greyish background on the lower lateral surface. Sometimes there is a suggestion of a white ventrolateral stripe. Limbs with three black stripes. Ventrally cream to white.

ETYMOLOGY

'Nullum' is a patronym from the Ko-ko-ya-o language of eastern Cape York Peninsula, Queensland.

REMARKS

On specimens from the coast near Cooktown, the black vertebral stripe extends from the nuchals to the hind back or base of the tail. On specimens from the sandstones near Laura, this stripe only extends to the fore-back.

The range and habitat of *C. nullum* is similar to that of *C. quinkan*, except the latter has only been collected on sandstone (Ingram, 1979).

Ctenotus hypatia sp. nov.

Ctenotus sp. (3). Wilson and Knowles, 1988, p.278.

MATERIAL EXAMINED

HOLOTYPE: QM J42092, granite gorge, 15km W of Mareeba, (17°00'S, 145°17'E), NEQ, by D. Knowles on 17 October, 1983.

DIAGNOSIS

A medium sized (SV 54) *Ctenotus* with a pattern of stripes and an upper lateral zone of tan or white blotches on chocolate-brown; supralabials 7; subdigital lamellae keeled, 20 on fourth toe; four supraoculars; 3-4 ear lobules; and 28 midbody scales.

For an illustration of the species see Wilson and Knowles (1988, p.278, photo no. 423).

DISTRIBUTION

Known only from the holotype, which was taken in a granite gorge.

DESCRIPTION

SV: 54. HW: 12. HL: 44. TL: 215.

Snout sloping, slightly pointed in profile. Nasals separated. Nasal groove absent. Rostral and frontonasal in narrow contact. Prefrontals large, separated. Frontal long and narrow, contacting the prefrontals, the frontonasal, the first three supraoculars, and the frontoparietals. 4-5 enlarged nuchals. Four supraoculars, second much the larger. Supraciliaries 9, first largest. Supralabials 7, fifth under the eye and enters the orbit. Ear aperture large, 3-4 pointed lobules on anterior border. Midbody scale rows 28. Number of scales from chin to vent 75. Toes long, compressed; subdigital lamellae keeled, 20 under fourth toe.

Dorsal ground colour orange-brown. Black vertebral stripe begins at nuchals and continues onto tail for about 15mm. White paravertebral stripes begin at nuchals and fade out at base of tail. Black laterodorsal and white dorsolateral stripes begin above and behind the eye; laterodorsal fades out at fore back while dorsolateral breaks up at mid back but continues as white dashes onto the base of the tail. Upper lateral zone chocolate-brown with tan or white blotches that give the effect of barring but breaks up into speckling on the tail. White midlateral stripe begins in front of ear and ends at hindlimb. Lower lateral zone grey with white blotching. Side of head blotched with chocolate-brown stripes. Ventrally white.

ETYMOLOGY

Named for Hypatia of Alexandria who occupied the chair of Platonic philosophy. She was murdered in 415AD by a Christian mob.

Ctenotus terrareginae sp. nov.

Ctenotus sp. (6). Wilson and Knowles, 1988, p.278.

MATERIAL EXAMINED

HOLOTYPE: QM J41996, Warrawilla Ck, Hinchinbrook Is, (18°22'S 146°15'E), NEQ, collected by D. Milton on 14 July, 1983.

Diagnosis

A large (SV 91) *Ctenotus* with a pattern of stripes and an upper lateral zone of white blotching on black; supralabials 7; subdigital lamellae widely calloused, 28 on fourth toe; four supraoculars; 3 ear lobules; and 28 midbody scales.

For an illustration of the species see Wilson and Knowles (1988, p.278, photo no. 426).

Distribution

Known from Hinchinbrook Island and about 60km south of the island by the turnoff to Paluma on the Bruce Highway, on the coast. (GVC, pers. obs.).

Description

SV: 91. HW: 11. HL: 44. TL: 227.

Snout sloping, slightly rounded in profile. Nasals separated. Nasal groove present. Rostral and frontonasal in narrow contact. Divided prefrontals large, separated. Frontal long and narrow, contacting the prefrontals, the frontonasal, the first three supraoculars, and the frontoparietals. 3-4 enlarged nuchals. Four supraoculars, second much the larger. Supraciliaries 10, first largest. Supralabials 7; fifth under the eye and enters the orbit. Ear aperture large, 3 pointed lobules on anterior border. Midbody scale rows 28. Number of scales from chin to vent 74. Toes long, compressed; subdigital lamellae widely calloused, 28 under fourth toe.

Dorsal ground colour dark brown. Short black vertebral stripe begins at nuchals and terminates on upper back. Head scales marbled with black. Black laterodorsal and white dorsolateral stripes begin above and in front of eye and continue along nearly the full length of the tail. Black upper lateral stripe begins in front of eye and continues to beyond base of tail where it becomes divided into two black stripes by a brown mid-stripe. White midlateral stripe begins behind nasals and continues back to and along length of tail. Lower lateral zone black with white blotching from head to midlateral area (white blotches sometimes coalesce with midlateral stripe to give an effect of black barring) where blotches merge to form a black lower lateral stripe that continues along the tail. Limbs reddish brown with black and white stripes. Ventrally white.

Remarks

The holotype was found under rock exfoliation amongst shrubs along a creek.

Etymology

Named for Queensland.

Ctenotus aphrodite sp. nov.

Material Examined

HOLOTYPE: QM J41814, Oorida area, Diamantina Lakes, ($23^{\circ}46'$S $141^{\circ}08'$E), SWQ, collected by R. Atherton and G. Porter on 12 March, 1983.

Diagnosis

A moderately large (SV 72) *Ctenotus* with a pattern of stripes (five black and four white dorsal stripes between the dorsolateral stripes) and an upper lateral zone of white blotches on black; supralabials 8; subdigital lamellae narrowly calloused, 34 on fourth toe; four supraoculars; 3-4 ear lobules; and 31 midbody scales.

Distribution

Known only from the type locality.

Description

SV: 72. HW: 12. HL: 53. TL: 229.

Snout sloping, pointed in profile. Nasals separated. Nasal groove absent. Rostral and frontonasal in narrow contact. Prefrontals large, widely separated. Frontal broad, contacting the prefrontals, the frontonasal, the first three supraoculars, and the frontoparietals. Two enlarged nuchals on either side. Four supraoculars, second much the larger. Supraciliaries 8, first largest. Supralabials 8; sixth under the eye and enters the orbit. Ear aperture large, 3-4 pointed lobules on anterior border. Midbody scale rows 31. Number of scales from chin to vent 76. Toes long, compressed; subdigital lamellae narrowly calloused, 34 under fourth toe.

Dorsal ground colour coppery brown. Top of head marbled with black. There are five black and four white dorsal stripes between the dorsolateral stripes. Black vertebral and white paravertebral stripes fade out above hindlegs. Other dorsal stripes break up just beyond mid back. In alcohol, the pale dorsal stripes can appear to be coloured bluish-white or copper depending upon the angle of the light. Upper lateral zone black with distinct white blotches but, from hindlegs to along tail, the blotches are absent. White, wavy midlateral stripe sometimes broken with black. Lower lateral zone grey to black with white blotching; continues as a grey lower lateral stripe outlining below the white midlateral stripe along the tail. Limbs light brown with black stripes. Ventrally pinkish white.

ETYMOLOGY

Named for Aphrodite, the Greek Goddess of love.

ACKNOWLEDGEMENTS

We thank Stephen Wilson, Queensland Museum, for his kind help.

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ELEMENTS IN THE PROCESS OF RECOVERY BY *CROCODYLUS POROSUS* (REPTILIA : CROCODILIDAE) IN THE EAST ALLIGATOR RIVER AND ASSOCIATED WETLANDS

ROBERT W.G. JENKINS AND MALCOLM A. FORBES

Jenkins, R.W.G. and Forbes, M.A. 1990 09 20: Elements in the process of recovery by *Crocodylus porosus* (Reptilia : Crocodilidae) in the East Alligator River and associated wetlands. *Memoirs of the Queensland Museum* **29**(2): 411-420. Brisbane. ISSN 0079-8835.

This paper reports the results of spotlight surveys from 1977 to 1987 of *Crocodylus porosus* populations in the tidal East Alligator River and its associated freshwater wetlands. Comparative data on the size and structure of the tidal and freshwater 'subpopulations' are analysed and recovery assessed since protection of the species in 1971.

The population in the tidal river has increased significantly at an annual rate of 0.06. Hatchling production in the tidal river has increased significantly at an annual rate of 0.14. In contrast to the absence of any significant long term increase in the numbers of non-hatchling crocodiles in the mid and downstream sections of the tidal river, non-hatchling crocodiles in the upstream section (>55km) have increased significantly at an annual rate of 0.14. This increase in the number of crocodiles in the upstream section is largely accounted for by animals >1.2m in length which have increased significantly at an annual rate of 0.11.

The data reveal major differences in the population structure between the tidal river and freshwater wetlands. Recruitment into the population is essentially confined to the tidal subpopulation, and is concentrated in the midsection of the river. The absence of suitable nesting habitat severely limits successful nesting in freshwater.

The tidal and freshwater subpopulations do not appear to be mutually exclusive. Increases observed in the freshwater subpopulation although not statistically significant, are surmised to have been derived from the tidal subpopulation. Regular seasonal movement of non-breeding crocodiles >1.2m in length between the tidal and freshwater habitat occurs during the wet season and following dry season. This movement is localised in the upstream section of the river and is thought to be the principal mechanism by which animals enter freshwater habitat.

Crocodylus porosus populations in the East Alligator River System have responded positively to protection and the amelioration of habitat degradation that has resulted from the active control of feral Asiatic water buffalo *Bubalus bubalis* in Kakadu National Park by the Australian National Parks and Wildlife Service. ☐ *Crocodiles, Crocodylus porosus, East Alligator River, survey.*

Robert W.G. Jenkins and Malcolm A. Forbes, Australian National Parks and Wildlife Service, PO Box 636, Canberra City, Australian Capital City 2601, Australia; 20 August, 1988.

Crocodylus porosus populations inhabiting the tidal rivers of northern Australia have been described by Messel et al (1979, 1981) as a result of comprehensive spotlight surveys. In that work the authors indicated that saltwater crocodile populations, despite a number of years of protection, were still in a depleted state. They suggested, however, that the extensive freshwater swamps associated with the tidal rivers that comprise the Alligator Rivers Region may act as important recruitment centres or rearing stockyards for sub-adult crocodiles and hence the rate of recovery in these rivers could be expected to be more rapid relative to most other tidal rivers in northern Australia.

STUDY AREA

The East Alligator River drains the escarpment country of western Arnhem Land and flows in a generally northerly direction through extensive sub-coastal floodplains into Van Diemens Gulf. The river is tidal for a distance of 84.5km upstream from its mouth (Fig. 1). The influence of all tides in the extreme upstream sections of the East Alligator River except those associated with full and new moon phases is largely impeded by the presence of a concrete causeway at Cahills Crossing (84.5km). Fringing vegetation, salinity and temperature profiles for the East Alligator River are described by Messel et al. (1979).

Magela Creek traverses subcoastal floodplains and enters the East Alligator River 49.7km upstream from the mouth. It is characterised as a series of discrete fresh waterbodies (billabongs) of varying size and depth in the late dry season (October - November). During the wet season when rainfall and run-off substantially increase water levels,individual billabongs become connected and inundate adjacent low-lying countryside forming extensive areas of fresh water with emergent vegetation.

Mean annual rainfall in the study area is 1556mm, 82% of which occurs between December and March (Bureau of Meteorology - Jabiru Recording Station). The result of this rainfall pattern is a distinctive wet summer and dry winter.

SURVEYS

Tidal River

Surveys were conducted from 1980-1985 under varying seasonal conditions. However, greatest effort was concentrated in the early (April-May) and late (October-November) dry seasons to coincide with hatchling recruitment and minimum discharge of freshwater from the catchment respectively. No survey was undertaken when the volume of fresh water discharge was sufficient to breach the banks of the river.

Crocodiles inhabiting the tidal section were counted at night from a boat using a 12 volt/100 watt sealed beam spotlight. The survey area extended from the confluence with Cooper Creek (13km from the mouth) to Cahills Crossing (84.5km from the mouth). Cooper Creek was not surveyed, however, two tidal creeks intersecting the west bank of the river (Creek A at 32.9km and Magela Creek at 49.7km) were included in the surveys (see Fig. 1). Survey procedure described by Messel et al. (1981) was adopted with the following modification. The east and west banks of the East Alligator River between Cooper Creek and the 50km mark were surveyed on consecutive nights. Because of the extreme width of the river below 50km and limitations in personnel and equipment both banks could not be surveyed simultaneously. Most *C. porosus* are sighted at the water's edge; we assumed that movement between banks was minimal and, if it does occur, movement east would be the same as movement west.

Surveys were carried out in the East Alligator River from Cooper Creek in an upstream direction on a half rising tide during periods coinciding with high tides in excess of 6 metres (i.e. full or new moon phases). The extreme upstream section (74km–84.5km) of the river is not navigable on tides <5.5 metres because of sand and rock bars.

Each crocodile located in the spotlight beam was approached and its total length estimated in one foot categories. Animals greater than 10ft in length were assigned to the one category (>10ft). For analyses, size class data were grouped into the following categories; hatchling, 2-3 ft (0.6-0.9m), 3-4 ft (0.9-1.2m), 4-6 ft (1.2-1.8m) and >6 ft (>1.8m). Animals that could not be approached were scored as 'eyes only'. Animals in the 'eyes only' category were allocated to the >1.8m size class if they were sighted in midstream, or if the spacing between the eyes indicated a large animal. This category represented on average approximately 23 per cent of observations. The 'eyes only' component of the population that could not be ascribed with certainty to the >1.8 m category was treated in the following manner. The size frequency composition of crocodiles for each 5 km length of the river was determined and the remaining 'eyes only' component for each section was allocated proportionately among size classes >0.9m. Experience has shown that crocodiles <0.9m are easily approached and sized. If these crocodiles submerge on being approached, they surface nearby almost immediately and their size can be estimated. The location of each animal sighted was plotted onto a calibrated river map compiled by Messel et al.(1982).

Freshwater Wetlands

On the basis of broad vegetation type the area was stratified into the following three zones: (a) floodplain; (b) woodland; and (c) *Melaleuca* corridor separating the first two zones. Sample billabongs (see Fig. 1) were selected randomly from a pool of accessible billabongs in each stratum. This paper deals only with those situated in strata (a) and (c). Each billabong was surveyed during October or November prior to the onset of the monsoonal wet season when the area of surface water was at its minimum.

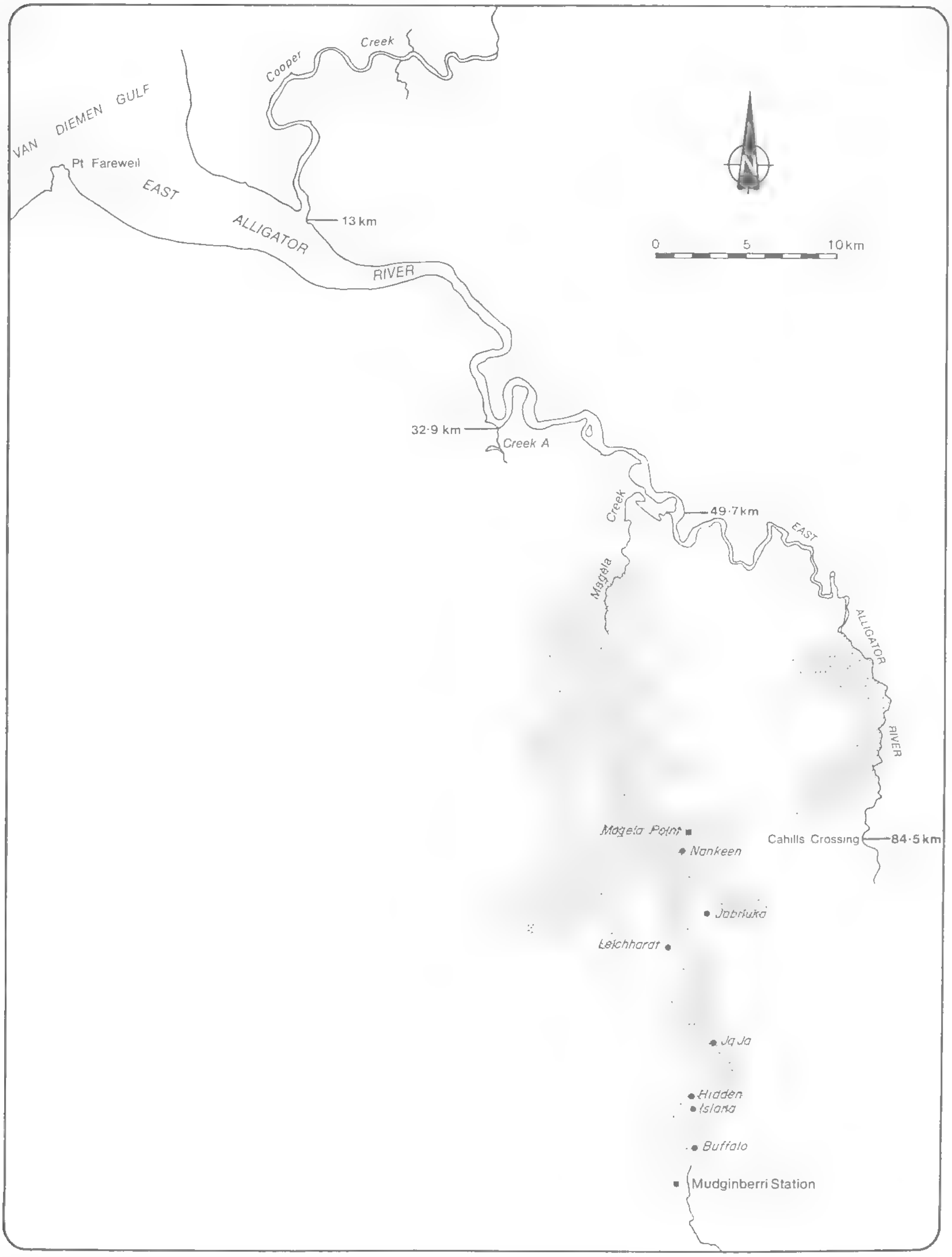

FIG. 1. The study area within Kakadu National Park showing the location of survey billabongs on Magela Creek in relation to the East Alligator River.

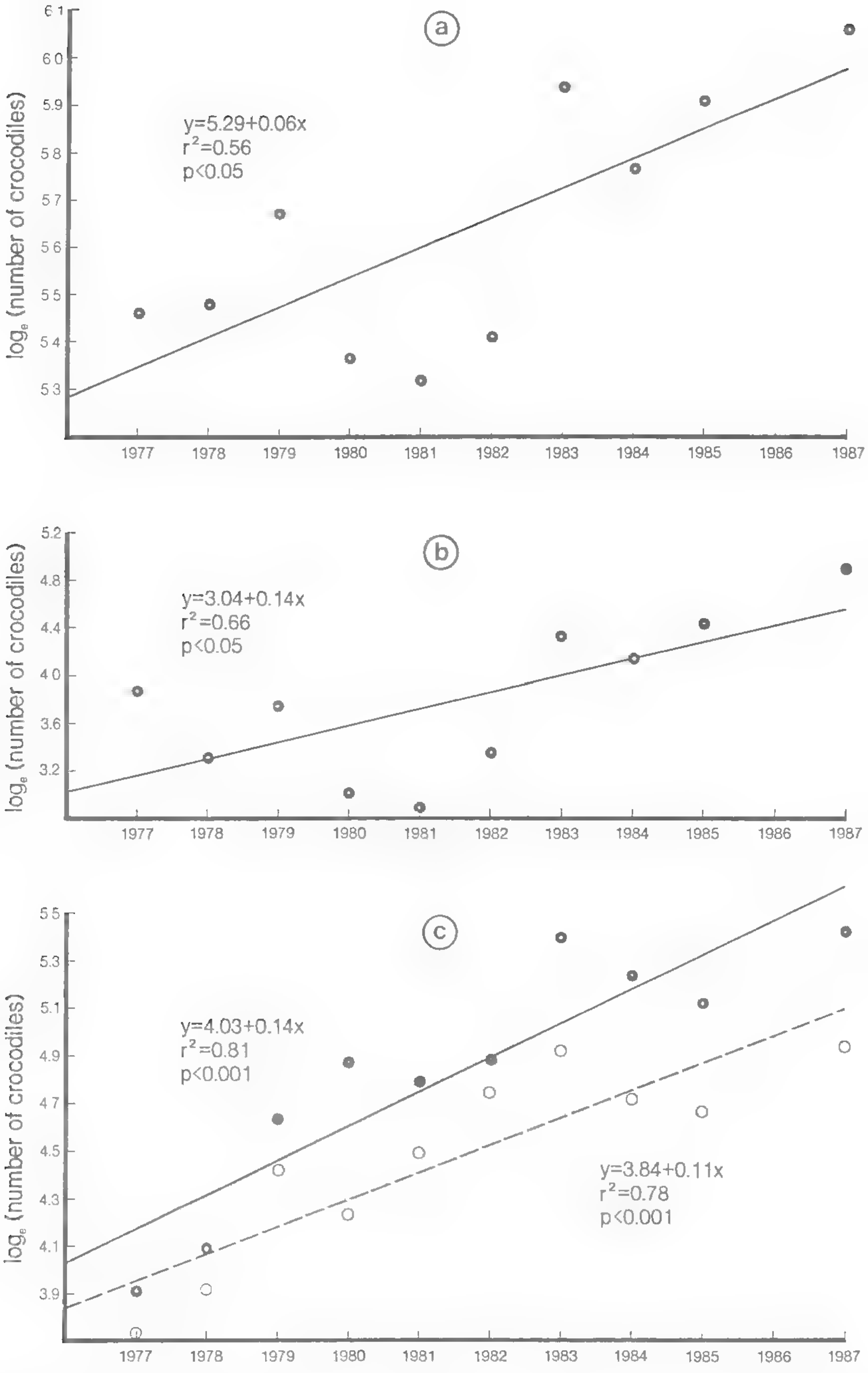

FIG. 2. Regression line relationships between late dry season numbers of crocodiles (natural logarithms) sighted in the tidal East Alligator River and year. (a) Total number of crocodiles in the river. (b) Total number of hatchling crocodiles in the river. (c) Total number of crocodiles in the river (solid datum points and line) and number of animals > 1.2m in length (hollow datum points and dashed line) upstream of 55km. Regression formulae apply x=1,2,3 etc. where 1=1977,2=1978 etc.

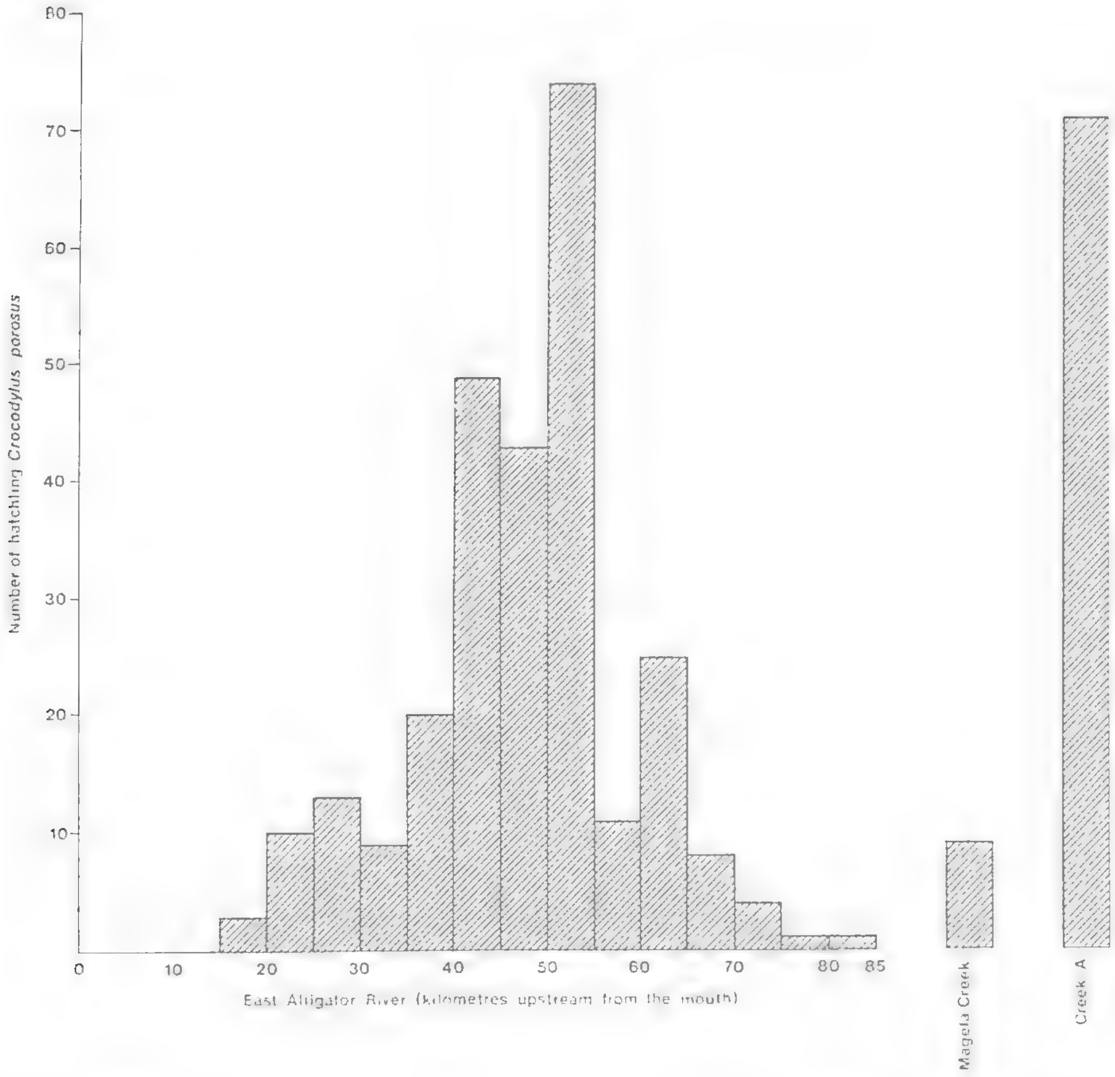

FIG. 3. Distribution of hatchling *C. porosus* in the East Alligator River, 1977–83. (N=351 where N represents the sum of maximum number recorded annually).

Crocodiles were counted with a spotlight from a boat or from the edge of the billabong on foot. Species identification and size, where possible, were recorded for each crocodile observed. In the billabongs sampled *C. porosus* was invariably the only species of crocodile sighted.

RESULTS

TIDAL RIVER

The numbers of *C. porosus* sighted during spotlight surveys in the tidal East Alligator River are presented in Table 1. A linear regression analysis of the transformed late dry season data (ln of the total number of crocodiles sighted in the river) against year for the period 1977-1987 (Fig. 2a) indicates a significant relationship ($r^2 = 0.56$, $p < 0.05$). The slope of this relationship is 0.06.

A significant relationship was found to exist when a similar analysis was performed (Fig. 2b) on the late dry season data on the total number of hatchling crocodiles sighted in the river against year ($r^2 = 0.66$, $p<0.05$, slope = 0.14)

The rate of increase in the number of hatchling crocodiles in the river does not reflect a uniform distribution of this age class in the river. Maximum numbers of hatchling *C. porosus* recorded each year from 1977 to 1979 (Messel et al., 1979, 1980) and 1980 to 1983 have been pooled for 5 km segments and presented in Fig. 3. Survey data for 1985 and 1987 were gathered in a manner that did not facilitate this form of analysis. Regular annual recruitment during this period has been generally restricted to the mid-section of the river (30km-55km) and Creek A.

In comparing the 1977 late dry season data (Messel et al., 1979) with those for November 1983 (Fig. 4), the distribution of crocodiles in the river has changed significantly (X^2=58.423, p<0.001). This difference has resulted from a highly significant increase in the abundance of >1.2m long crocodiles in the upstream section of the river above 55km(t=9.771, p<0.001). Linear regression analyses performed on the transformed late dry season data (ln of the total number of crocodiles sighted) for this section of the river against year for the period 1977-1987 (Fig. 2c) show the annual rate of increase (slope = 0.14) to be highly significant (r^2=0.81, p<0.001) and that it largely comprises crocodiles >1.2m long (Fig. 2c) which have been increasing annually in this section of the river at 11 percent (r^2=0.78,p<0.001).

Although the slopes of regression lines for crocodiles >1.2m in length elsewhere in the river for the period 1977-1987 are positive, the relationships are not significant.

FRESHWATER WETLANDS

The number and sizes of *C. porosus* recorded in freshwater billabongs which characterise Magela Creek in the late dry season are summarised in Table 2. There is some difficulty in interpreting crocodiles recorded as 'eyes only' in freshwater habitat. The 'eyes only' category in freshwater habitats constitutes a greater component of the sightable population than in tidal rivers. It is not possible to approach animals in shallow water, very often located amongst fallen timber and/or grasses, to determine a size. We assumed that the frequency distribution of animals able to be sized is a reflection of the entire population and apportioned the 'eyes only' component among the size classes recorded.

The size structure of the freshwater population differs from that inhabiting the tidal East Alligator River in that there is an almost total absence of hatchling and yearling (0.6–0.9m) crocodiles (Table 2). These data suggest that recruitment within the freshwater populations of *C. porosus* is absent or at best minimal.

No statistically significant increase in numbers of crocodiles in comparable billabongs was detected for the period 1980 to 1985 (Table 3). Whilst there has been an increase in the number of *C. porosus* in some of the sampled billabongs, there has been little change in others. Comparisons with surveys of a small series of Magela Creek billabongs undertaken in 1977 (Messel, pers. comm.) indicate an obvious increase in abundance of crocodiles between 1977 and 1980. However, the increase is not statistically significant. This may in part be explained by the inability to sight crocodiles in some billabongs in the latter stages of the study and the small sample size. Surveys of Leichhardt Billabong could not be conducted in 1984 and 1985 because the entire surface of this waterbody was covered with the introduced aquatic plant *Salvinia molesta*. This plant was also present on Jabiluka and Nankeen Billabongs during the 1985 surveys and severely hindered progress on the water and the ability to locate crocodiles in previously accessible areas.

DISCUSSION

Messel et al. (1981) modelled the dynamics of *C. porosus* in tidal rivers of northern Australia based on (a) the suitability of a river for crocodile breeding being determined by its salinity characteristics and (b) movement of non-reproductive animals from breeding rivers into non-breeding areas. In considering the East Alligator River system, Messel et al. (1981) recognised the potential importance of the freshwater swamps but were unable to quantify it.

Jenkins and Forbes (1985) found that for the East Alligator River the distribution as well as the size class structure of *C. porosus* inhabiting the tidal river in the late dry season (October - November) differed significantly from that during the early dry season (April - May). They also found that generally *C. porosus* abundance in the river was greatest at the end of the dry season.

Analysis of the total numbers of crocodiles sighted in the river during the late dry season for the period 1977-1987 indicates an annual rate of increase of 0.06 (Fig. 2a). This rate is marginally lower than the annual rate of increase of 0.07 derived by Bayliss (1987) and Webb et al. (1989)

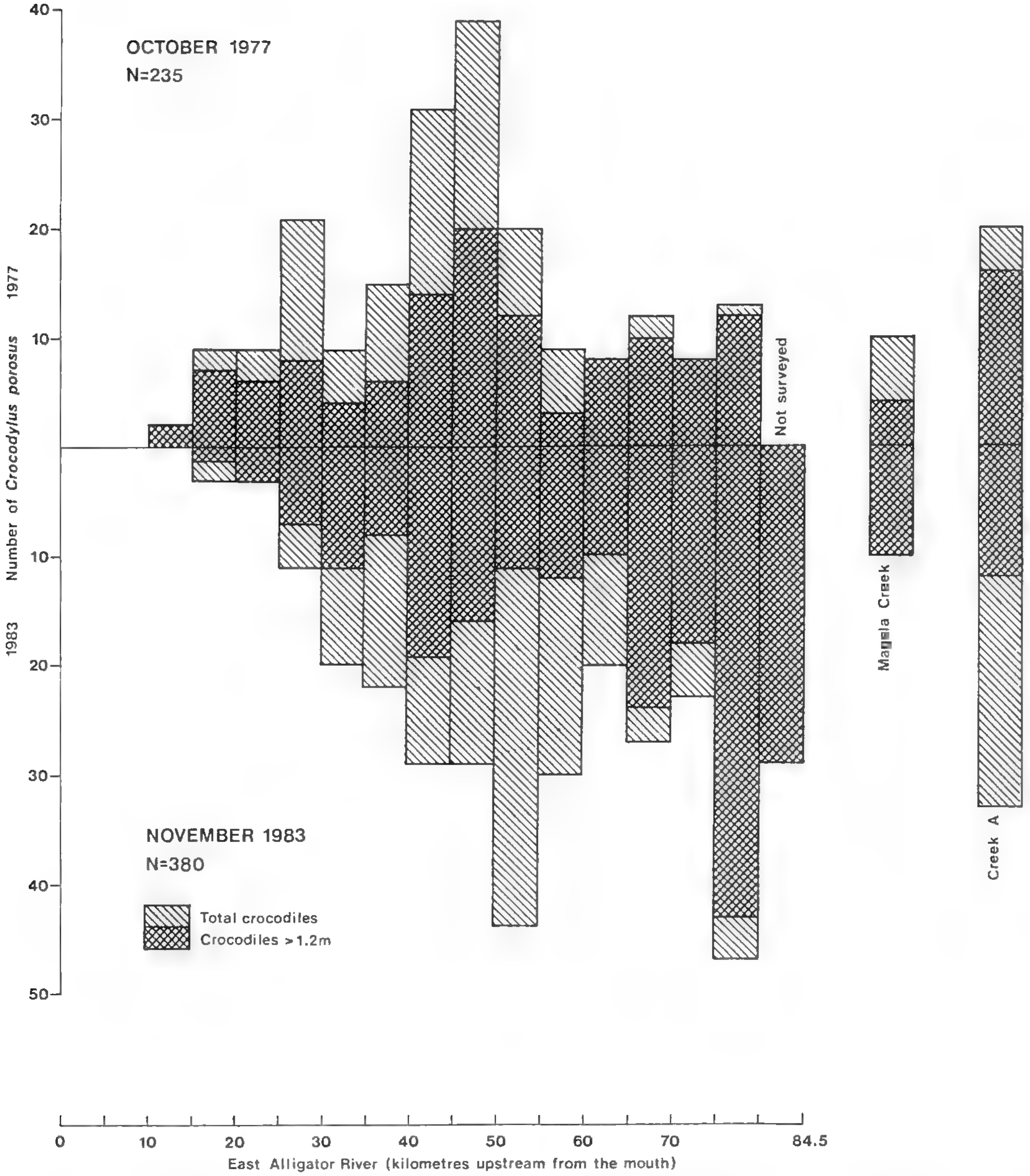

FIG. 4.Distribution of *C. porosus* sighted during late dry season spotlight surveys in the East Alligator River system in 1977 (above line) and 1983 (below line). 1977 data from Messel et al. (1979).

for the period 1977- 1985. This difference in the rates of increase may be due to the two additional years recovery and the omission from this study of (a) Cooper Creek - a major tributary of the East Alligator River, and (b) results of surveys undertaken during the early dry season to avoid incorporating in the regression analysis large numbers of hatchling crocodiles that enter the population during the period but are subject to high mortalities between the early and late dry season (Jenkins and Forbes, 1985). Notwithstanding, it is to be expected that the rate of

TABLE 1. Numbers of *C. porosus* in various size classes sighted in the tidal East Alligator River system during spotlight surveys

	Hatchlings	2-3ft (0.6-0.9m)	3-4ft (0.9-1.2m)	4-6ft (1.2-1.8m)	>6ft (>1.8m)	Eyes only	N
June 1980	26	29	29	39	30	45	198
October 1980	21	16	41	51	41	43	213
July 1981	23	18	24	56	46	34	201
November 1981	17	20	19	58	54	36	204
April 1982	89	26	12	20	28	32	207
November 1982*	29	11	11	49	79	44	223
June 1983	52	47	22	19	81	39	260
November 1983	78	50	20	60	142	30	380
May 1984	34	34	7	19	45	21	160
November 1984	65	34	22	57	74	68	320
November 1985	83	34	28	64	110	48	367
October 1987**	134	20	13	28	159	74	428

*partial survey (13-30km not surveyed). ** ex–Conservation Commission of the Northern Territory

increase in a recovering population will tend towards zero in the long term. It is therefore of interest that the rate of increase in the East Alligator River is lower than the mean annual rate of increase of 0.08 for all crocodiles calculated by Webb et al. (1989) for 26 tidal rivers in the Northern Territory.

Hatchling production has been variable in the East Alligator River. When initial mortalities have been discounted through regression analysis of late dry season sightings, the annual rate of increase for the period 1977-1987 has been significant at a rate of 0.14 (Fig. 2b). Nesting activity has generally been restricted to the mid section of the East Alligator River (30km-55km) including Creek A and Magela Creek although in later years there has been increased nesting activity in the upstream sections above 55km.

Recruitment to the population is essentially confined to the tidal East Alligator River. Hatchling production in freshwater is minimal or absent because of the limited availability of suitable nesting habitat (Wells, 1980). In the absence of such habitat nesting effort in freshwater is generally unsuccessful as nests are subject to inundation with concomitant high egg mortality.

The size structure and distribution of the population inhabiting the river have changed significantly since 1977. This study demonstrates a highly significant increase in upstream numbers of crocodiles at an annual rate of 0.14 (Fig. 2c) has occurred in the period 1977-1987. When the size structure of this segment of the population is examined, animals >1.2m in length largely account for the overall increase in the upstream section increasing at an annual rate of 0.11 (Fig. 2c).

The marked seasonal difference in the numbers of crocodiles inhabiting the upstream section of the river results from a significant reduction in the abundance of >1.2m long crocodiles in the early dry season. Jenkins and Forbes (1985) attributed this difference to wet season movement of animals out of the river into adjacent freshwater habitat being facilitated by the flooding characteristics of the East Alligator River. These animals can be considered to be non-breeding as limited nesting activity occurs in this section of the tidal river. The observed increase in the freshwater population can thus be explained as having been derived from wet season movement from the breached upstream sections of the river. In the absence of any significant long-term increase in abundance of non-hatchling crocodiles elsewhere in the river and the virtual absence of hatchling crocodiles in freshwater habitat, the upstream section of the river may be considered the major dispersal corridor to freshwater habitat for animals derived from downstream breeding and nursery areas. The annual concentration and movement of crocodiles >1.2m in length from the upstream section of the tidal river into adjacent freshwater wetlands may also explain the lower annual rate of increase in overall numbers of crocodiles in the East Alligator River relative to the mean rate

	No. of billabongs	Hatchlings	2-3ft (0.6-0.9m)	3-4ft (0.9-1.2m)	4-6ft (1.2-1.8m)	>6ft >1.8m	Eyes only	N
October 1980	4	–	–	3	22	10	22	57
November 1981	6	–	–	4	19	19	26	68
November 1982	6	2	–	2	17	25	31	77
November 1983	8	–	–	1	26	64	22	113
November 1984	7	6	2	10	31	63	35	147

TABLE 2. Numbers of *C. porosus* in various size classes sighted in freshwater billabongs of Magela Creek during spotlight surveys

calculated by Webb et al. (1989) for 26 tidal rivers in the Northern Territory. Movement of *C. porosus* from the East Alligator River to adjacent freshwater swamps was also suggested by Messel et al. (1980) to explain differences observed in the population in 1977 to 1979. Webb et al. (1983) also recorded marked differences in the number of *C. porosus* sighted during wet season surveys in the Adelaide River compared with surveys undertaken in the dry season. This behaviour is consistent with movement documented for other crocodilians in response to rainfall and flooding in Uganda and Northern Rhodesia (Cott, 1961), Louisiana (Chabreck, 1965) and Venezuela (Gorzula, 1978).

The restriction of regular recruitment to the mid-section of the East Alligator River suggests that recovery by the population in the tidal system and associated freshwater wetlands since protection has been derived principally from this area. The most important agent responsible for the destruction of *C. porosus* nesting habitat is the Asian water buffalo *Bubalus bubalis* (Letts et al., 1979, Fogarty, 1982). Excessive numbers of this large feral herbivore have been a major constraint to the rate of recovery of *C. porosus* by limiting available nesting habitat. The appearance of creches of hatchlings in the upstream section of the tidal East Alligator River in later years has accompanied the re-establishment of suitable riverside nesting vegetation following the removal of large numbers of water buffalo by the Australian National Parks and Wildlife Service under the Plan of Management for Kakadu National Park. Similarly, it has been demonstrated elsewhere in Kakadu National Park that floating grass mats become re-established in the freshwater wetlands following the removal of significant numbers of water buffalo (Jenkins, unpubl. data). The increasing stability of these vegetation platforms with time may result in successful breeding by saltwater crocodiles in freshwater habitat.

The results of this study confirm the ability of *C. porosus* to exhibit a rapid response to habitat and harvest protection similar to that reported for other crocodilians, viz. *Crocodylus niloticus* (Blomberg, 1976, Graham, 1976) and *Alligator mississippiensis* (Campbell, 1978). The continuing recovery of the East Alligator River population of *C. porosus* together with those inhabiting the other rivers and associated wetlands of Kakadu National Park that are managed under a regime of national park legislative protection

TABLE 3. Numbers of *C. porosus* recorded in freshwater billabongs of Magela Creekin 1977 (Messel pers. comm.) and 1980-1983 n.s.= not surveyed

	1977	1980	1981	1982	1983	1984	1985
Buffalo	ns	2	1	1	1	4	2
Island	8	11	14	14	11	18	11
Hidden	ns	ns	4	4	1	7	7
JaJa	ns	15	10	14	18	23	18
Jabiluka	1	ns	9	11	9	17	9**
Nankeen	8	28	30	23	20	18	14**
Magela Point	ns	ns	ns	ns	43	56	30
Leichhardt	5	ns	ns	ns	10	ns*	ns*

*100% surface coverage of *Salvinia* sp. **Substantial coverage (>30%) of surface with *Salvinia* sp.

provide a sound basis for continued commercial ranching outside of the conservation reserve network. It also demonstrates the need for management policies for the *C. porosus* resource to be cognizant of and responsive to the increasing potential for interaction between visitors to Kakadu National Park and *C. porosus*.

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GROWTH AND CALCIUM METABOLISM OF EMBRYOS OF THE LONG-NECKED TORTOISE, *CHELODINA LONGICOLLIS* (SHAW).

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Miller, J and Jones, M. 1990 09 20: Growth and calcium metabolism of embryos of the long-necked tortoise, *Chelodina longicollis* (Shaw). *Memoirs of the Queensland Museum* 29(2): 421-436. Brisbane. ISSN 0070-8835.

Growth (change in mass) and calcium metabolism of embryonic turtles have received little attention. The present study extends this small data set to include the long-necked tortoise, *Chelodina longicollis*, Shaw (Testudinata: Chelidae). Eggs were 3/4 buried in vermiculite and incubated under controlled moisture (-200kPa) and temperature (30°C) conditions. Embryonic growth was described by the regression of log dry mass on log day of incubation. Total calcium in the egg did not change but was redistributed. The demand for calcium during embryogenesis exceeded the amount available from the yolk and albumen; the additional calcium required for osteogenesis was supplied by the shell. ☐ *Growth, calcium metabolism, tortoise embryos.*

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The few studies that have considered growth (change in mass) of embryonic turtles have been restricted to cryptodires (Ackerman, 1980, 1981, Cheloniidae: *Caretta, Chelonia*; Miller, 1982, Cheloniidae: *Caretta, Chelonia, Eretmochelys, Natator*; Morris et al., 1983, Chelydridae, *Chelydra serpentina*; G. Packard et al., 1983, Emydidae, *Chrysemys picta*). Growth of these embryos follows an exponential or logistic form. There are no published data on the growth of embryonic pleurodiran turtles.

Four studies have considered the pattern of calcium metabolism within incubating eggs of oviparous reptiles (Packard et al., 1984a, Chelydridae: *Chelydra serpentina*; Packard et al., 1984b, Colubridae: *Coluber constrictor*; Packard et al., 1985, Agamidae: *Amphibolurus barbatus*; Packard and Packard, 1986, Emydidae, *Chrysemys picta*). Other studies concerning the utilization of calcium in reptilian eggs only identified that the shell was the primary source (Simkiss, 1962, 1967; Bustard et al., 1969: Dermochelyidae, Cheloniidae). In eggs of the American snapping turtle, *Chelydra serpentina*, about 56% of the calcium for embryogenesis originates in the shell (Packard et al., 1984a); embryos of sea turtles obtain between 60 and 80% of the required calcium from the shell (Simkiss, 1962, 1967; Bustard et al., 1969).

The present study was designed to extend the knowledge of growth and calcium metabolism in reptilian embryos to include the long-necked tortoise, *Chelodina longicollis* (Shaw, 1794) (Testudinata: Chelidae). The specific objectives were (a) to describe the pattern of embryonic growth, (b) to determine the amount of calcium in each of the compartments of the egg (yolk, albumen, shell) at oviposition and (c) to describe the pattern of calcium utilization and the relative contribution from these sources during development of the embryo. Preovulatory follicles were also analyzed for calcium content.

METHODS

Gravid tortoises were collected by netting dams between 13 November and 7 December, 1983 at Herbert Park (30°27'S, 151°50'E), approximately 25 km northeast of Armidale, NSW. Tortoises were housed in individual aquaria at ambient temperature (18-25°C). No tortoise was retained longer than 10 days.

The straight carapace length (SCL) of each tortoise was measured to the nearest 0.01cm with calipers from the anterior edge of the nuchal (cervical) scute to the posterior edge of the postcentrals (12th marginals). Each tortoise was weighed to the nearest 5 grams using a Pesola spring balance.

Tortoises were palpated in the inguinal area to determine if eggs were present. Oviposition was induced by intracoelomic injection of oxytocin at a dosage of 1 iu/100g of total body mass (Ewert and Legler, 1978). If the first injection did not produce eggs within one hour, a second injection was given. If no eggs were expelled, a third injection was given. No more than three injections were given to any tortoise; all eggs were laid in water.

Within 2 minutes of egg laying, eggs were removed from the water, wiped dry, and numbered using permanent ink. Eggs were weighed to the nearest 0.01 gram on a Bosch p115 top pan balance and measured (length and width) to the nearest 0.01cm with calipers.

Eggs were incubated in 2.5 litre plastic containers sealed with tight-fitting lids. Eggs were 3/4 buried in vermiculite moistened to 15 % water by weight (approximately -200kpa). The moisture level was maintained by adding 3-8ml distilled water every 7-10 days during incubation. The temperature was maintained at 30$^+$/- 0.7°C throughout incubation. The position of each container was regularly shifted within the incubator to minimize the potential effects of temperature gradients (Bull et al., 1982).

If most eggs in a clutch did not exhibit a white area on the uppermost part of the shell (an indication of viability) within 7 days of oviposition, the clutch was not used for the calcium metabolism experiments.

One egg from each clutch was collected at predetermined times during incubation (0, 20, 30, 35, 40, 45, 50, 55, 60 days, and hatching). Each egg was re-weighed and re-measured at the time of sampling then opened and the contents were separated into embryo, yolk, membranes and fluids, and shell. The fresh mass of each component was obtained to the nearest milligram. The embryos were staged according to Yntema (1968). To determine hatching success, it was assumed that normal embryos obtained from eggs sampled during incubation would have developed into normal hatchlings and it was assumed that abnormal embryos would not have produced hatchlings.

Follicles (n=66) of different measured diameters (±0.01cm) were removed from the ovaries of four decapitated tortoises and weighed (± 0.01g).

Each egg component and follicle was dried to constant mass at 60°C. Embryos were ground in a mill into fine particles; yolks and follicles were homogenized by hand using a mortar and pestle. Subsamples of 300mg or entire samples were digested in boiling, concentrated nitric acid aided by 30 % hydrogen peroxide (both reagent grade). Samples were brought to 100ml volume with distilled water. Further dilutions of digestate were made using 0.02 % strontium chloride (1ml sample + 9ml dilutent) dispensed through an auto-dilution system (Hook and Tucker Instruments, New Addington, England). Five samples of water from vermiculite that had been soaked for 20 days in distilled water were also analyzed for calcium.

The calcium content of each sample was determined using a Pye Unicam SP 190 single-beam Atomic Absorption Spectrophotometer (using an air/acetylene flame) coordinated with an SP 450 automatic sample changer following standard procedures.

The data were analyzed using one-way analysis of variance with the initial egg mass as the potential covariate (programme BMDP2V, Dixon et al., 1981). Further examination of the data for calcium in yolks and embryos was done by comparing the regressions for the variables among the clutches. This approach was taken because only one egg was collected from each clutch at the sampling times which precluded use of analysis of co-variance with groupings by clutch and day of sampling. Data for the regression analysis were truncated to eliminate time zero because preliminary analysis demonstrated no significant differences occurred between data at time zero and day 20. Truncation simplified the curvilinear nature of the remaining data and allowed better comparison on a linear basis. Because of this, however, these regression lines do not fully describe the entire data set. Sample sizes vary among the treatments; P = 0.05 was used to establish significance. Least Significant Difference (LSD) values were calculated using Statistix (Analytical Software, St Paul, MN, USA) computer program; calculation of other statistical tests followed Zar (1974).

RESULTS

A total of 64 female tortoises were captured and injected with oxytocin; only 16 (25%) produced eggs (Table 1), usually after a third injection. The general effectiveness of oxytocin on the tortoises was low. The time interval between injection and oviposition was variable. The shortest period was 1.5 hours and the longest was nearly 15 hours. All tortoises required at least two injections before oviposition was induced. Most tortoises were not obviously distressed by handling or injection; all animals

TABLE 1. Summary on tortoises, clutches, incubation period, and hatching success.

FEMALE NUMBER	WEIGHT (g)	SCL (cm)	NUMBER OF EGGS	TOTAL CLUTCH WEIGHT (g)	PERCENT CLUTCH WEIGHT (g)	INCUBATION PERIOD (days)	HATCHING SUCCESS (%)
USED IN CALCIUM DETERMINATION							
6A	1020	19.34	14	74.68	7.32	81	92.8
11	1020	19.97	12	94.01	9.02	75.5	91.6
16	750	17.94	8	38.76	5.16	64	100
27	1010	19.15	17	84.17	8.33	80	70.5
41	790		9	55.69	7.05	74	100
61	1060		11	74.68	7.05	67	100
82			11	62.08		71.5	100
89	780		9	49.51	6.35	66.5	100
122	914	19.43	11	79.59	8.71	70	100
MEAN	918	19.17	11.33	68.13	7.37	72.17	94.99
STD DEV	118.9	0.671	2.624	16.815	1.203	5.622	9.229
MINIMUM	750	17.94	8	38.76	5.16	64	70.5
MAXIMUM	1060	19.97	17	94.01	9.02	81	100
NUMBER	8	5	9	9	8	9	9
NOT USED IN CALCIUM DETERMINATION							
6B	940	19.34	15	67.5	7.18	0	0
15	720	17.84	9	45.28	6.28	0	0
78	980	19.81	4	34.2	3.48	0	0
99			13	89.93		0	0
102	750	17.72	9	62.49	8.33	74.5	22.2
103	1080	20.18	11	66.95	6.2	0	0
118	930	19.25	12	60.89	6.54	0	0
MEAN	900	19.023	10.43	61.034	6.33		
STD DEV	126.62	0.932	3.288	16.397	1.466		
MINIMUM	720	17.72	4	34.2	3.48		
MAXIMUM	1080	20.18	15	89.93	8.33		
NUMBER	6	6	7	7	6		

remained watchful and active during their captivity. Oviposition was usually preceded by a slight increase in activity.

In total, 175 eggs were induced from 16 tortoises giving a mean clutch size of 10.93 eggs (sd=3.47, range=4-17) (Table 1). Non-viable eggs were found in 7 clutches containing 73 eggs.

SIZE AND WEIGHT OF FEMALE TORTOISES

The mean straight carapace length (SCL) of female tortoises captured during the study was 19.1cm (sd=2.229, Range=14.1-26.5, n=59). There was no significant difference between the mean SCL of tortoises that laid eggs (19.1cm, sd=0.867, range=17.72-20.18, n=11) and the mean SCL of those that did not (19.1cm, sd=2.411, range=14.12-26.5, n=48) (t=0.0831, df=57). In the group of tortoises that yielded eggs, there was no significant difference between the SCL measurements of those tortoises whose eggs were used in the calcium experiment and the others (t=0.254, df=10).

The mean mass of all female tortoises was 855.4g (sd=229.7, range= 364-1440, n=62). There was no significant difference between the mean mass of the tortoises which yielded eggs (909g, sd=130.2g, range=720-1080, n=14) and the mean mass of those that did not (824.5g (sd=266.1, range=364-1440, n=48) (t=1.162, df=61). There was no significant difference between the masses of those females whose eggs were used in the calcium experiment and the others (t=0.252, df=12).

Further comparisons between the tortoises used in the calcium experiment and the others that oviposited revealed no significant differences in the number of eggs (t=1.344, df=14), total clutch weight (t= 1.5889, df=14), or in the percentage of the female weight represented by the total clutch weight (t=1.346, df=12).

The relationship between the straight carapace length and mass of all female tortoises was described by the equation: SCL = 0.00835 female mass + 11.983, R^2=0.86 where SCL is in cm and weight is in grams. The relationship between SCL and log of the mass for the tortoises which yielded eggs was described by the equation: SCL (cm) = 21.597-0.3572 log female mass (g), R^2=0.26.

SIZE, AND WEIGHT OF EGGS

Based on the 102 viable eggs which were used in the study of calcium metabolism, the mean mass of freshly oviposited eggs grouped by clutch was 6.0g (sd=1.04, range=4.85-7.83, n=9 clutches). The mean length of these eggs was 3.09cm (sd=0.1824, range=2.81-3.38, n=9 clutches); the mean width was 1.82cm (sd=0.16, range=1.51-2.04, n=9 clutches).

The relationships between egg length, width and mass were described best by the equations:

Mean Egg Width = -0.31621 (Mean Egg Length) + 2.7797,

R^2=0.074, P>0.05:

Mean Egg Width = 0.14245 (Mean Egg Fresh Mass) + 0.9742,

R^2=0.725, P<0.01

Mean Egg Length = 0.03018 (Mean Egg Fresh Mass) + 2.8811,

R^2=0.037, P>0.05.

There was a tendency for the width of eggs to increase as mass increased, but the mean egg length did not increase proportionally.

Female mass was not correlated with the number of eggs produced (R^2= 0.099, P>0.05) but was slightly correlated with mean egg mass (R^2= 0.247, P<0.05) (Fig. 1). The poor correlation between egg mass and female mass is partially explained by the ineffectiveness of the oxytocin on the tortoises; it is possible that some females were induced to oviposit incomplete clutches. The correlation between female SCL and total clutch mass was also poor (R^2=0.269) and so was that between female mass and total clutch mass (R^2=0.512). The mass of clutches that contained viable eggs represented an average of 7.4 % (range= 5.16-9.02, n=9) of the female mass.

There was a slight decrease in the mass of all eggs during incubation (egg mass = -0.042 + 6.863 days, n=102). The slopes of the regressions of the change in egg mass grouped by clutch were not significantly different (F 0.05 [8,62]=1.123); however the elevations were (F 0.05 [8,70]=56.64). Analysis of variance among the initial masses of the eggs from different clutches showed that significant differences occurred between clutches (Table 2).

Among the 102 eggs used in the calcium study, 95 eggs (93.1 %) produced normal embryos or hatchlings (given the assumptions above); only 6.9 % of these eggs failed to develop normally.

The mean duration of incubation at 30°+/- 0.7°C was 70.41 days (sd=5.85, range=63-82, n=12 eggs from 7 clutches) when averaged from the clutch averages. When considered independently of clutch, the mean was 69.2 days (sd=5.25, range 63-82, n=12).

WET AND DRY MASS

The relation between wet mass and dry mass of follicles followed the power curve (log dry mass = 0.9608 + 0.6693 log wet mass, R^2=0.993). The diameter and wet mass of follicles were related according to the equation: log wet mass = 2.896 + 0.4514 log diameter, R^2=0.671.

There was no significant difference between the mean mass of the 15 largest follicles and the mean mass of yolks of ovipositional eggs (wet mass: t=1.13, df=22, P>0.05). However, there was a significant difference between the dry masses (t=3.71, df=22, P<0.05). The mean dry mass of the follicles was heavier than that of the ovipositional egg yolks; this may have resulted from differences between clutches.

At oviposition, a turtle egg is comprised of shell, albumen, yolk and embryo. However, the embryo is at the early gastrula stage (Yntema, 1968; Cunningham, 1922; Lynn and von Brand, 1945; Miller, 1985) and contributes little to the total mass. Because of the difficulty of removing the blastodisc from the yolk, its actual contribution was ignored until it could be retrieved (about Stage 10, Yntema, 1968). The proportions of the egg components changed little during the first third of incubation but thereafter the amount of yolk and albumen decreased and the amount of embryo increased (Table 3).

The mass of the fresh egg shell decreased significantly during incubation (F 0.05[10,57] =3.885) but the dry mass of the shells did not decrease significantly (F 0.05[6,28] = 0.186).

Although there was a significant decrease in

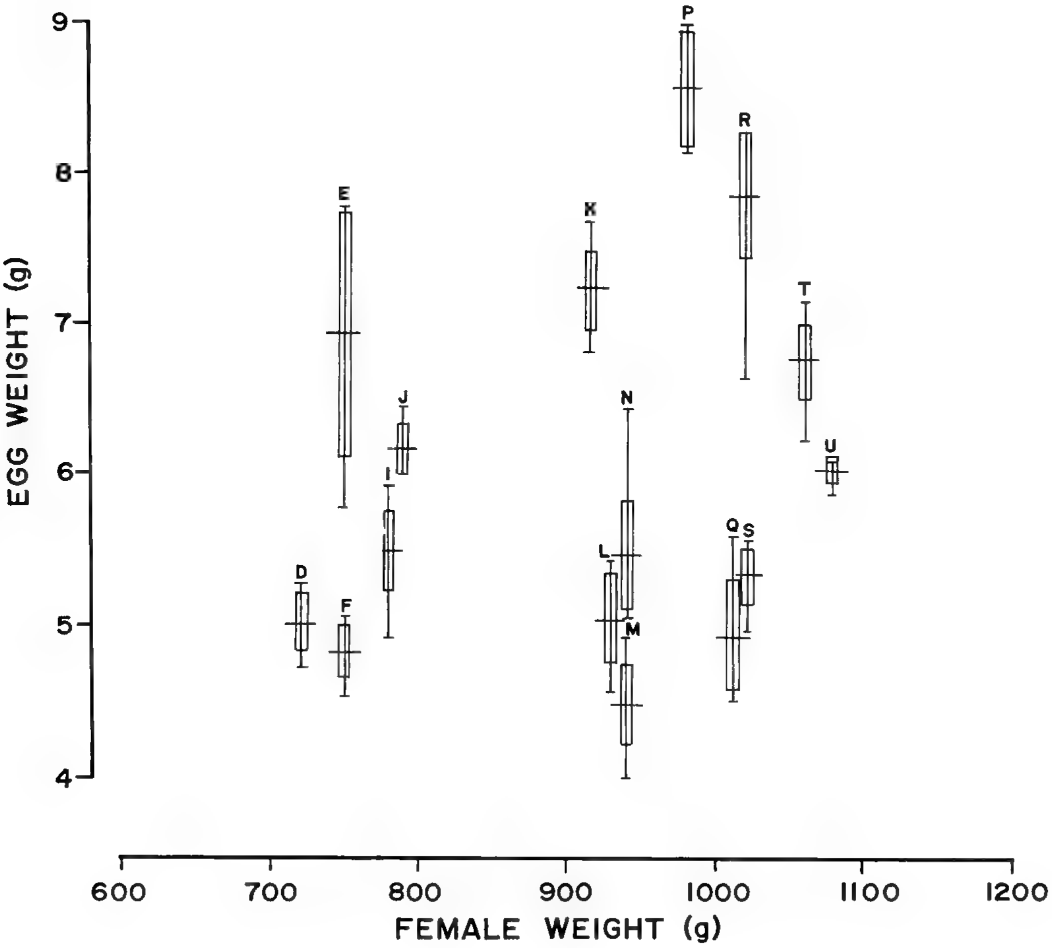

FIG. 1. The relation between female body weight and mean egg weight grouped by clutch. Letters identify clutches: D=15, E=102, F=16, H=82, I=89, J=41, K=122, L=118, M=6b, P=78, Q=27, R=11, S=6a, T=61, U=103.

the wet mass of the albumen beginning at about one-third of the incubation period (F 0.05[8,29] = 6.265), there was not a significant decrease in the dry mass of the solid material of the albumen during incubation (F 0.05[8,29] = 2.201).

The wet mass of the yolk decreased significantly during incubation (F 0.05[10,55] = 22.866). This was mirrored by the decrease in dry mass of the yolks (F 0.05[10,55] = 13.277) (Fig. 3).

The combined mass of the fresh yolk and albumen decreased significantly during incubation (F 0.05[9,42] = 15.464). The combined mass of dry yolk and albumen exhibited a significant decrease (F 0.05[9,42] = 26.416).

The mass of water in the albumen, yolk and combined yolk and albumen decreased during incubation in concert with the decrease in the total mass of each. However, the percentage of water in the albumen and yolk remained relatively constant (Table 4). Water comprised approximately 95.3% of the mass of fresh albumen throughout incubation. Water contributed approximately 69.3 % of the total mass of the yolk at the beginning of incubation but only 56.3 % at hatching. There appeared to be little change in the proportion of water in the yolk during the first

TABLE 2. Results of analysis of variance between clutches for ovipositional weight, length, and width of eggs.

	SUM OF SQUARES	DEGREES FREEDOM	MEAN SQUARE	F	P
OVIPOSITIONAL EGG WEIGHT					
REGRESSION	103.561	8	12.945	154.597	0.001
RESIDUAL	7.787	93	0.984		
OVIPOSITIONAL EGG LENGTH					
REGRESSION	3.115	8	0.389	53.943	0.001
RESIDUAL	0.671	93	0.007		
OVIPOSITIONAL EGG WIDTH					
REGRESSION	2.097	8	0.262	15.821	0.001
RESIDUAL	1.541	93	0.017		

one-half of incubation but during the last half, the proportion of water decreased. Even though there was a nett decrease in the solid material in the yolk, the percentage of solids increased because, proportionally more water than solids was removed.

The fresh mass of the embryos increased significantly (F 0.05[9,61] = 24.157) during incubation. In embryos, as the amount (mass) of water increased, the percentage of water decreased (Table 4). The dry mass of embryos increased significantly during incubation (F 0.05[9,60] = 20.588).

STAGE OF DEVELOPMENT

The stage of development reached by the embryos at any given time during incubation at 30°C was described by the equation: log stage = 1.448 + 0.4325 log days, R^2=0.651. The stages of development increased rapidly during the first half of incubation and began to plateau shortly thereafter (Fig 2). This is predictable because more stages are defined to occur during this

TABLE 3. Percent composition of fresh egg components at selected times during incubation. ND=not determined.

	DAY OF INCUBATION				
	0	20	35	50	70
PERCENT ALBUMEN	42.8	45.9	48.2	23.5	25.3
WEIGHT OF ALBUMEN					
MEAN	2.26	2.85	2.8	1.32	1.19
STD DEV	0.457	0.965	0.359	0.196	0.499
NUMBER	6	3	3	3	2
PERCENT YOLK	57.2	52.3	38.2	29.2	2.6
WEIGHT OF YOLK					
MEAN	3.02	3.25	2.22	1.65	0.12
STD DEV	1.678	0.703	1.16	1.192	0.176
NUMBER	9	3	2	6	11
PERCENT EMBRYO	ND	1.78	13.6	47.3	72.1
WEIGHT OF EMBRYO					
MEAN	ND	0.11	0.79	2.65	3.37
STD DEV		0.060	0.179	0.596	1.037
NUMBER		5	6	7	12

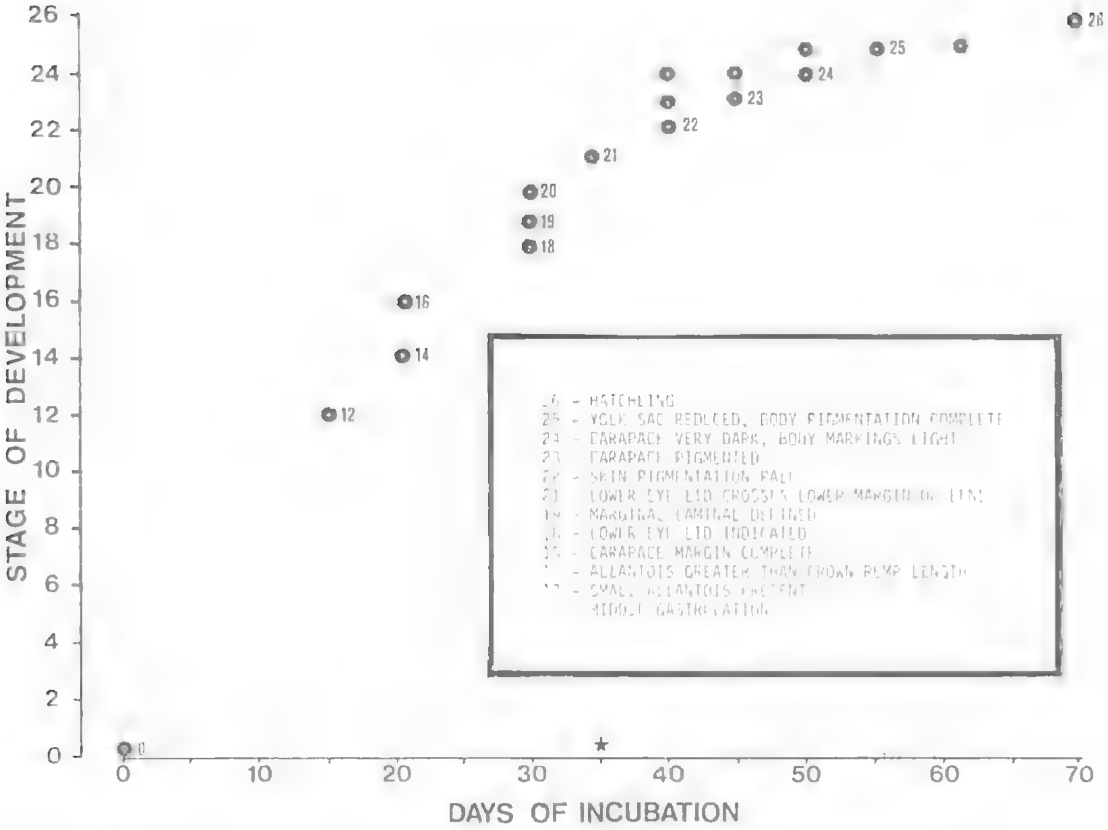

FIG. 2. Stages of development of *Chelodina longicollis* based on the table of normal development for *Chelydra serpentina* (Yntema, 1968). The box provides some of the characteristics for determining the stage.

period when differentiation is occurring rapidly (see Yntema, 1968). Development of the allantois began before the mid-point of incubation. As the membrane grew into position to participate fully in metabolic activity, embryonic growth accelerated.

CALCIUM IN FOLLICLES AND EGGS

The calcium available from the incubation medium (vermiculite + distilled water) averaged 0.019mg (range=0.025-0.015, n=5). The pattern of increase in calcium in follicles of increasing dry mass followed the formula: $\log Ca = 1.3483 + 1.2086 \log$ dry follicle mass ($R^2=0.792$). The amount of calcium contained in the 15 largest follicles did not differ significantly from that in ovipositional yolks ($t = 0.268$, $P > 0.05$).

Twelve samples of shell were analyzed to provide an estimate of total calcium available for translocation into the developing embryo. Shells were collected from early in incubation because later shells tended to fragment. The mean of the samples was 184.9mg Ca (sd=41.054, range=135.6-248.7).

Eighteen samples of albumen were analyzed to determine calcium content. The mean was 0.6252mg Ca (sd=0.4422, range=0.119-1.637). The samples were accepted only as an indication and were not subjected to further analysis because of the potential of contamination by other materials (e.g. blood, extra-embryonic fluids and granules of shell) during preparation.

The amount of calcium in the yolk did not change significantly during the first 30 days of incubation, then it declined rapidly for about 20 days after which it leveled off at about 2% of the mean starting value (Fig. 4; Table 5). Analysis of variance with initial egg mass as the potential covariate showed there was significant decrease in the amount of calcium in the yolk ($F_{0.05[9,69]} = 135.40$). Comparison of the slopes of regression lines of the amount of calcium in the yolk against time for each clutch were not

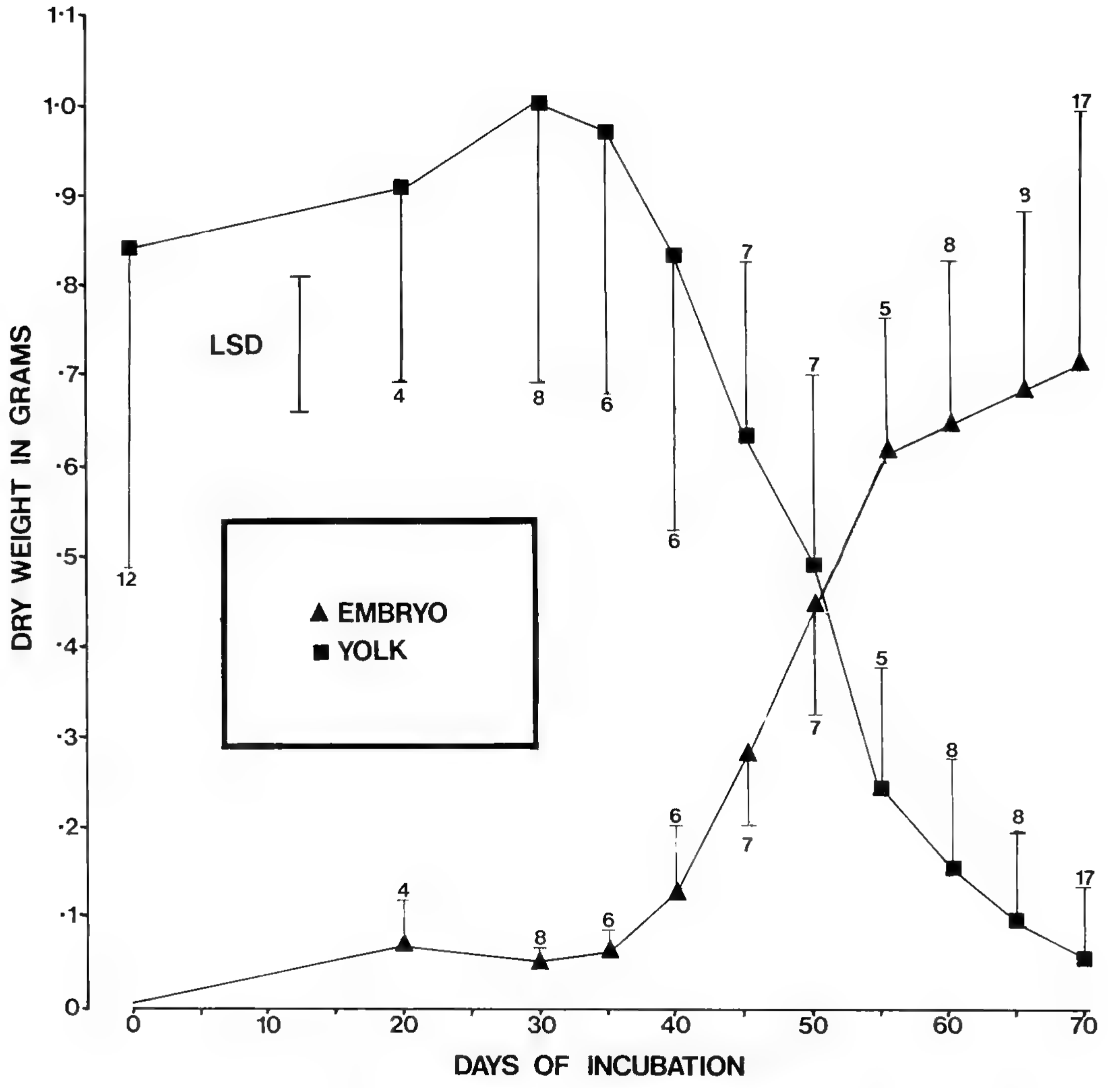

FIG. 3. The change in dry mass of embryos and yolks during incubation of *Chelodina longicollis* eggs. Vertical lines indicate one standard deviation; numbers are sample sizes. Means that are separated by at least one LSD bar are significantly different at the 0.05 level.

significantly different (F 0.05[8,50] = 1.594) but the elevations were (F 0.05[8,58] = 3.058).

The concentration of calcium in the yolk remained relatively stable for the first half of incubation but decreased thereafter to hatching (Fig. 5). Analysis of variance with initial egg mass as the potential covariate revealed that the concentration of calcium in the yolk decreased significantly during incubation (Table 6). Different clutches displayed significantly different slopes indicating that the concentration of calcium during incubation was significantly different (Table 6).

The amount of calcium in the embryos did not increase significantly until after 30 days of development. The rate of change was slow at first then increased rapidly until just before hatching. The amount of calcium in the embryo of ovipositional eggs was assumed to be negligible; this was confirmed by analysis of slightly older embryos (Table 5). Analysis of variance with initial egg mass as the potential covariate demonstrated that significant differences oc-

TABLE 4. Percentage of water and solids in egg components at selected times during incubation. ND= not determined.

	DAY OF INCUBATION				
	0	20	35	50	70
PERCENT WATER					
ALBUMEN MEAN	95.3	95.4	96.1	96.4	95.3
STD DEV	7.46	1.12		1.34	0.65
NUMBER	6	3	1	3	4
YOLK MEAN	69.3	78.6	79.6	63.4	56.3
STD DEV	7.38	3.93		12.3	8.52
NUMBER	9	3	1	6	11
EMBRYO MEAN	ND	94.8	90.1	82.8	78.8
STD DEV		2.8	0.85	1.38	1.62
NUMBER		4	6	7	12
PERCENT SOLIDS					
ALBUMEN MEAN	4.6	4.3	3.9	3.6	4.7
STD DEV	0.746	1.25		1.345	0.65
NUMBER	6	3	1	3	4
YOLK MEAN	30.4	21.4	20.4	36.6	43.7
STD DEV	7.375	4.05		12.32	8.532
NUMBER	6	3	1	6	11
EMBRYO MEAN	ND	6.6	9.7	17.1	20.8
STD DEV		0.495	0.854	1.384	1.798
NUMBER		2	6	7	13

curred in the amount of calcium in the embryos during incubation (Table 6).

The concentration of calcium in the embryos increased steadily from about 20-30 days until hatching (Fig. 5). The increased variance following 60 days of incubation resulted from either of two sources: (1) contamination by extra-embryonic fluids, blood, or granules of shell or (2) non-discrimination between late stage embryos and hatchlings. Analysis of variance with initial egg mass as the potential covariate substantiated that the concentration of calcium increased significantly during incubation (Table 6).

The total amount of calcium in the egg, excluding the shell, increased significantly during incubation (Table 6). The pattern of change in the total calcium followed that of the yolk for slightly more than the first half of incubation and followed the increase in the embryo thereafter (Fig. 5). The demand for calcium by the embryo for osteogenesis exceeded the amount available from the yolk and albumen combined. Because only a low concentration of calcium was available from the incubation medium and because eggs showed a net loss of water during incubation, it is assumed that the extra requirement was supplied by the shell.

DISCUSSION

References to studies of the ecology and general biology of *Chelodina longicollis* are provided by Cogger et al. (1983); Parmenter (1976) studied the ecology of this tortoise in the Armidale region and provided a comparative review of the older literature.

Parmenter (1976, 1985) found that larger females tended to lay more eggs than smaller ones. The average number of eggs reported was 13.9 (sd=4.29, range 6-23, n=74). The average clutch size in the present study was 10.93 (range 4-17) eggs. Both of these values are consistent with other reports on the number of eggs per clutch (Harrington, 1933: n=up to 20; Goode, 1967: n=10-15; Krefft, 1865: n=15-20; McCooey: 1887, n=15-36; Lucus and Le Souef, 1909: n=7-21; Vestjens, 1969: n=13-24).

At an incubation temperature of 30°C, incubation requires 60-69 days (Parmenter, 1976, 1985), 73-78 days (Goode and Russell, 1968), 53-76.5 days (Legler, 1985) and 63-82 (this

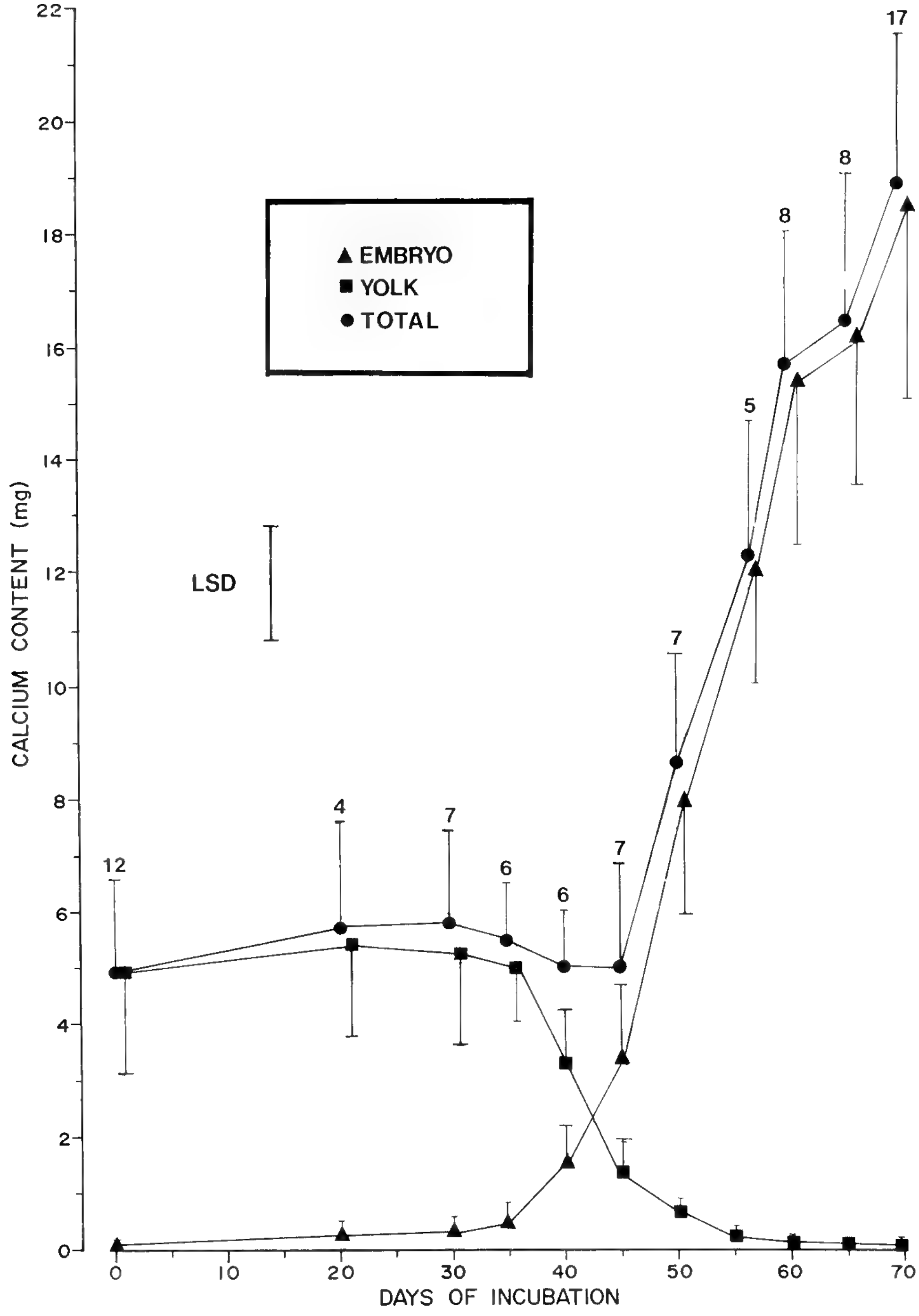

FIG. 4. The content of calcium in embryos, yolks and total egg (excluding the egg shell) during incubation of *Chelodina longicollis* eggs. Vertical lines indicate one standard deviation; numbers are sample sizes. Means that are separated by at least one LSD bar are significantly different at the 0.05 level.

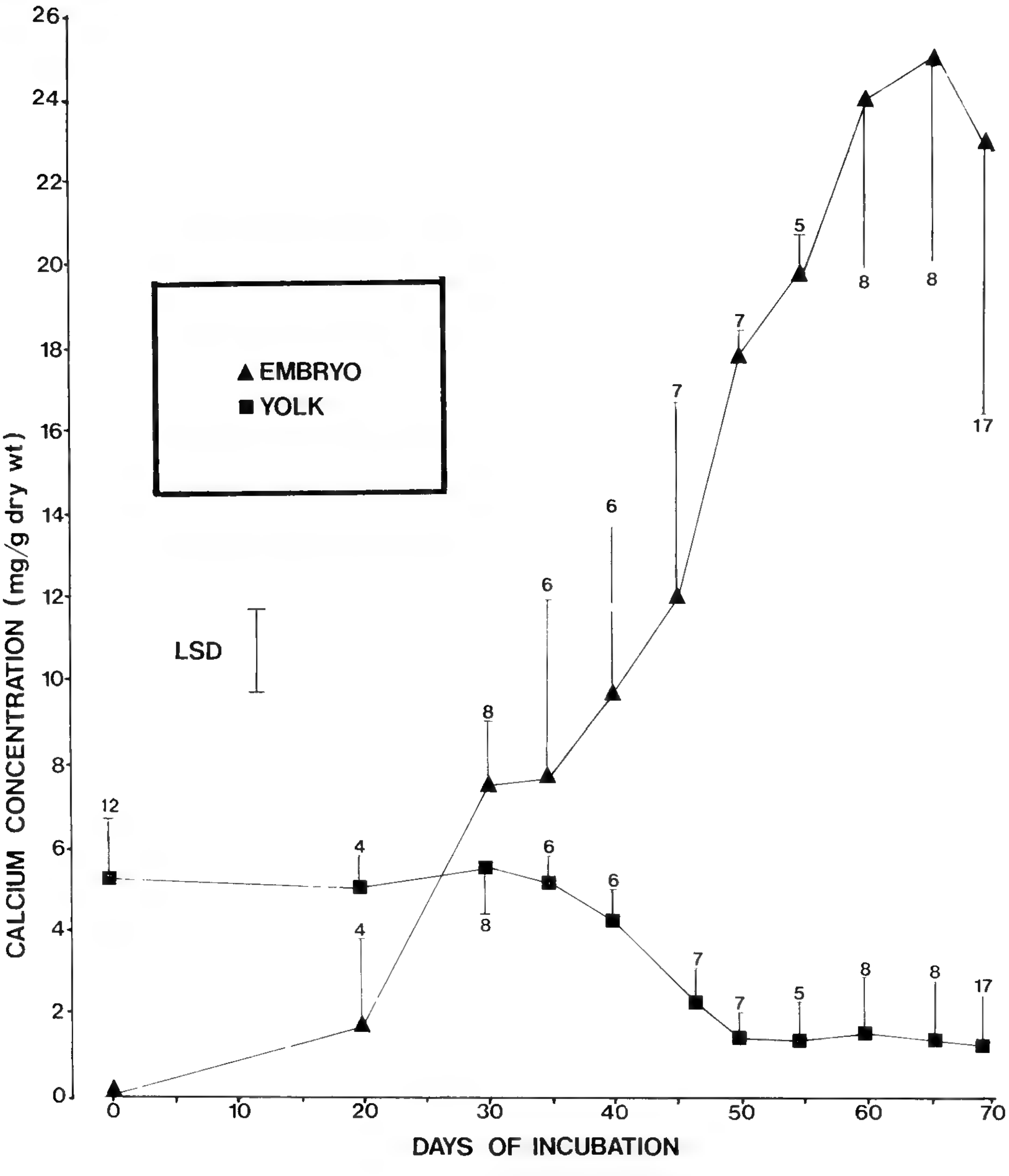

FIG. 5. The concentration of calcium in embryos and yolks during incubation of *Chelodina longicollis* eggs. Vertical lines indicate one standard deviation; numbers are sample sizes. Means that are separated by at least one LSD bar are significantly different at the 0.05 level.

study). Because the duration of incubation varies inversely with temperature, eggs incubated under natural conditions require longer to hatch (Goode, 1967: 130-137d; Goode and Russell, 1968: 131-145d; Vestjens, 1969: 118-150d; Parmenter, 1976: 105-123d).

Parmenter (1976) reported a very strong correlation between the log of female mass and straight carapace length (SCL) (R^2=0.97). In the present study, the linear regression had the best correlation between female mass and SCL. Parmenter (1976) also found a significant, positive

TABLE 5. Amounts of calcium (mg) in egg components at selected times during incubation. ND=not determined.

	Day of Incubation				
	0	20	35	50	70
Albumen Mean	0.625	0.205	0.394	0.227	0.412
Std Dev	0.442		0.321	0.152	0.132
Number	4	1	2	2	5
Yolk Mean	5.232	5.395	5.134	0.758	0.126
Std Dev	1.889	2.246	1.679	0.405	0.128
Number	12	4	6	7	12
Embryo Mean	ND	0.343	0.657	8.192	18.45
Std Dev		0.589	0.117	2.196	3.918
Number		3	5	7	13
Shell Mean	189.66	179.9	160.59		
Std dev	49.59	37.47	30.34		
Number	4	2	4		

Albumen Groups not Significantly Different
Anova: F 0.05 [4,9]=0.5819

Yolk Groups Significantly Different
Anova: F0.001 [4,36] =28.311

Embryo Groups Significantly Different
Anova: F0.001[3,24]=60.284

shell groups not Significantly Different
Anova: F 0.005[2,7]=0.3705

correlation between the size of the female and the total number of eggs in the clutch. This was not supported in the present study but may simply reflect differences in sample sizes. Although there was a reasonable correlation ($R^2=0.77$) between egg diameter and the SCL of the female, the correlation between egg length and SCL was poor ($R^2=0.18$) (Parmenter, 1976). The generalization that egg length does not increase substantially with SCL but that egg diameter does was supported by the present results. The correlation between mean egg width and mean egg mass is associated with an increase in follicle diameter in larger females. Although not demonstrated in the present study, the increase in follicle diameter affects the diameter and increase in mass of the eggs in marine turtles (Miller, 1982). Because the eggs are oval and the yolks are round, there is little albumen between the vitelline membrane of the yolk and the inner portion of the shell membrane. The albumen is situated primarily towards the ends of the egg.

Embryonic growth in *Chelodina longicollis* as indicated by the change in dry mass of embryos and yolks is similar to that reported for *Chelydra serpentina* (Morris et al., 1983) and follows the general pattern of embryonic growth in marine turtles (Ackerman, 1981; Miller, 1982).

The distribution of calcium in fresh eggs of *Chelodina longicollis* is similar to that reported for other species of oviparous reptiles (see Packard and Packard, 1984). At oviposition the albumen contained only a small quantity of calcium. The yolk contained more, but less than the egg shell (Table 5). At the end of incubation, calcium reserves in the albumen had not been significantly reduced. Those of the yolk were reduced and calcium in the embryo had increased significantly.

The yolk contributed about 30% of the total calcium required by the developing embryo; the remaining 70% of the embryonic requirement was derived from the shell. This compares favorably with the contribution (% Ca) made by the egg shells of sea turtles (Cheloniidae and Dermochelyidae) of between 60 and 80 % (Simkiss, 1962, 1967; Bustard et al., 1969; Miller and Jones, unpub data). The contribution made by the egg shell of *Chelodina longicollis* is about 15 % higher than occurs in *Chelydra serpentina* (56%, M. Packard et al., 1984b) and is much higher than the contribution made by the poorly calcified egg shell of the snake *Coluber constrictor* (21 %, M. Packard et al., 1984a) and the lizard *Amphibolurus barbatus* (40 % M. Packard et al., 1985).

TABLE 6. Analysis of variance tables for calcium content and concentration in embryos, yolks, and the total egg (excluding shell) with initial egg weight as the potential covariate based on log (value + 1) NS=Not Significant.

SOURCE	SUM OF SQUARES	DEGREES FREEDOM	MEAN SQUARE	F	P
YOLK DRY WEIGHT (g)					
Day of incubation	4.841	9	0.538	33.92	0.01
Initial egg weight	0.809	1	0.809	51.04	0.01
Error	1.094	69	0.015		
EMBRYO DRY WEIGHT (g)					
Day of incubation	2.719	9	0.302	14.44	0.01
Initial egg weight	0.226	1	0.226	10.02	0.01
Error	1.444	69	0.021		
YOLK CA CONCENTRATION (mg/g)					
Day of incubation	18.563	9	2.063	11.84	0.01
Initial egg weight	0.0188	1	0.0188	0.11	NS
Error	12.022	69	0.174		
EMBRYO CA CONCENTRATION (mg/g)					
Day of incubation	75.607	9	8.401	9.64	0.01
Initial egg weight	0.955	1	0.955	1.1	NS
Error	60.124	69	0.871		
YOLK CA (mg)					
Day of incubation	44.307	9	4.923	135.4	0.01
Initial egg weight	1.830	1	1.830	50.34	0.01
Error	2.508	69	0.036		
EMBRYO CA (mg)					
Day of incubation	112.512	9	12.501	184.17	0.01
Initial egg weight	0.625	1	0.625	9.21	0.01
Error	4.683	69	0.067		
TOTAL CA (mg) IN EGG EXCLUDING SHELL					
Day of incubation	19.451	9	2.161	40.81	0.01
Initial egg weight	2.778	1	2.778	52.46	0.01
Error	3.654	69	0.053		

The total calcium in the entire egg (shell, albumen, yolk, embryo) apparently does not change but is redistributed. The total egg contains enough calcium for embryogenesis without obtaining any from the environment. However, the combined yolk and albumen cannot supply the requirements for embryogenesis without augmentation from the shell. The pattern of embryonic growth and incorporation of calcium indicates that the two sources (yolk, shell) are utilized more or less sequentially. More calcium is derived from the shell later in incubation as reserves in the yolk decline. This is consistent with the pattern of development of the allantois and indicates that extraction from the egg shell is by the chorioallontic membrane. Further, the two sources of calcium are not utilized equally by the embryo. By the end of incubation the calcium in the yolk was nearly exhausted; whereas the shell contained sufficient calcium to supply all the embryonic demand (based on samples taken early in incubation, Table 5).

The pattern of calcium utilization by embryonic *Chelodina longicollis* is similar to that reported for *Chelydra serpentina* (Packard et al., 1984a) and *Chrysemys picta* (Packard and Packard, 1986). The amount of calcium in the yolk is at first relatively stable suggesting little use of calcium by the embryo. However, the amount of yolk declines sharply after about 50

% of incubation. Similarly, there is no detectable change in calcium during the early stages of embryonic differentiation. However, the amount of calcium increases rapidly after the embryo begins the growth phase of development. The only noticeable variation in the two patterns occurs late in incubation of *Chelodina longicollis* when the rates of calcium uptake in the embryo and loss by the yolk is slow. This may be the case in reptilian eggs when the incubation period is variable. The incubation ranged between 63 and 82 days under constant conditions. This range is equal to one-third of the fastest developmental time and one-quarter of the slowest. At present the variation cannot be evaluated because few clutches were incubated, and the possibility of a subtle influence by minor temperature gradients cannot be discounted. There may also have been a minor influence resulting from forced oviposition, as has been shown in lizards (Jones, 1983).

Rapid mobilization of calcium into the embryo in the latter half of incubation coincides with the osteogenic phase of development. The primary use of calcium by the embryo is in the building of bones (Simkiss, 1967).

Embryonic calcium levels increase in concert with the decrease in yolk calcium. The yolk supplies the calcium necessary for the initiation of the embryonic growth phase. The somatic development of the embryo requires calcium (albeit small quantities) at a time when the allantois has not developed sufficiently to give ready access to the reserves in the shell. As the vitelline membrane extends around the yolk, the area between the sinus terminalis and the embryo becomes vascularised. This occurs close enough to the inner part of the shell membrane to allow the necessary respiratory exchange; only a thin layer of albumen and the chorion lie between them. This degree of apposition may allow some translocation of calcium. Certainly, as the area vasculosa of the vitelline increases, before the allantois extrudes between it and the chorion, some calcium may be acquired from the shell. However, at this time the demand is small and the vascularised surface of the vitelline is actively interacting with the yolk for the general nutrition of the embryo and apparently selectively removes calcium (see Packard et al., 1984a; Packard and Packard, 1984). The development of the allantois prior to (or simultaneously with) the increase in demand for oxygen and calcium ensures support for the growth phase.

The role of respiratory exchange in the translocation of calcium in reptilian eggs has not been demonstrated but gas exchange plays an important role in translocation during avian development (Crooks and Simkiss, 1974). Packard and Packard (1984) provide critical speculation about the function of the chorioallantois in translocation of calcium but no experimental data are available.

During incubation, embryos of domestic fowl (*Gallus domesticus*) store calcium derived from the shell in the yolk to such an extent that by hatching the yolk contains more calcium (50-75 %) and at a higher concentration than at oviposition (Johnston and Comar, 1955; Romanoff, 1967; Simkiss, 1967; Crooks and Simkiss, 1974). In contrast, the amount of calcium in yolks of *Chelydra serpentina* (Packard et al, 1984a), *Chrysemys picta* (Packard and Packard, 1986) and *Chelodina longicollis* decrease during incubation. The decrease in concentration of calcium in the yolk indicates that these embryos selectively remove calcium from the yolk. Simkiss (1967) reported a decline in the amount of calcium in yolks of *Caretta caretta* during incubation, although the temporal changes in the quantity and concentration were not determined; he also reported that the 'calcium in the egg contents increases rapidly in the latter part of incubation and is five times greater at hatching than in the fresh egg' (Simkiss, 1967, p.229). Earlier, Simkiss (1962) demonstrated a fourfold increase of calcium within the egg of *Dermochelys coriacea*. Clearly these oviparous reptiles follow a similar pattern of utilization of calcium that is quite different from the pattern followed by birds.

Although all the calcium for embryogenesis is available from the yolk and shell, the ultimate source of calcium is the female who secretes both of these structures. Very little work has focused on this aspect of the overall role of calcium in reproduction. Data derived from a number of different reptiles (see review by Simkiss, 1967) provides only a partial picture. Reproduction by an oviparous reptile can be subdivided into two phases. The first phase includes the preparation of the follicles prior to ovulation. This may require only a month or so in some lizards or as long as two years or more (e.g. *Vipera berus*). The second phase is the deposition of the shell around the ovulated ova. The process of vitellogenesis provides the yolk proteins containing calcium over a period of time that is typically longer than the period required for deposition of the shell. The former does not put as much stress on the calcium budget of the female as does the latter. The proximal source of calcium for vitellogenesis and shell deposition is bone (Dessauer and Fox, 1959) but the ultimate source is the diet of the female.

ACKNOWLEDGEMENTS

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NEW CRANIAL ELEMENTS OF A GIANT VARANID FROM QUEENSLAND

R. E. MOLNAR

Molnar, R.E. 1990 09 20: New cranial elements of a giant varanid from Queensland. *Memoirs of the Queensland Museum* 29(2): 437-444. Brisbane. ISSN 0079-8835.

Two massive varanid frontals and matching parietal from the eastern Darling Downs (Queensland) Pleistocene derive from a large varanid, probably *Megalania prisca* . The frontal is characterised by a sagittal crest and low ornamentation on the dorsal surface. The parietal has relatively longer lateral and supratemporal processes than in modern varanids, and a relatively smaller area roofing the braincase. Confluent contacts on the frontal for the prefrontal and postfrontal-postorbital and the encroachment of the supratemporal fossa onto the dorsal surface of the parietal suggest that *M. prisca* was a more derived varanid than any now existing in Australia. The frontal appears quite thick and the endocranial cavity small; these both are probably allometric effects. ☐ *Queensland, Australia, Pleistocene, Varanidae, Megalania, sagittal crest*

R. E. Molnar, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101, Australia; 19 December, 1988.

The giant varanid, *Megalania prisca* (Owen, 1859), is among the most distinctive Australian fossil tetrapods, as well as the largest known terrestrial lepidosaur. It is known from the remains of one skeleton, or possibly two, (Rich, 1985) from the eastern Darling Downs of Queensland, and isolated remains from there and other localities in the eastern half of Australia (Lydekker, 1888; Hecht, 1975). Fossils of *M. prisca* are known only from the Pleistocene. Smaller vertebrae attributed to *Megalania* sp. are known from the Pliocene of Chinchilla, western Darling Downs, Queensland (Hecht, 1975). Recently discovered or recognised material sheds new light, and raises new questions, regarding this animal. The material described here suggests that the skull of *M. prisca* was unusual in its construction.

Specimen numbers prefixed with 'J' or 'F' are held in the Queensland Museum, that prefixed with 'V' in the Ian Sobbe collection and that prefixed by 'BMNH' in the British Museum (Natural History).

DESCRIPTION

In about 1984, Mr Ian Sobbe recovered an unusual bone (F16783) from the Pleistocene deposits at Pearson's Locality, King Creek, eastern Darling Downs, Queensland. In August of 1985 a second, worn specimen (V0033), was recovered, also by Mr Sobbe, from the 'Sutton Bed', King Creek west of Clifton. Both elements are left frontals, approximately equal in size (Table 1). During preparation of this paper, Mr Sobbe donated a large lacertilian right parietal (F16792), collected from King Creek about ten years ago.

In form the frontals are basically like those of *Varanus salvadorii* (Figs 1,2). In dorsal view the element resembles a reversed L, the stem representing the body of the frontal and the lower bar, the lateral process that contacts the fused postfrontal-postorbital distally and the parietal posteriorly. The nasal contact is like that of *Varanus varius*, with the dorsal surface of the frontal projecting anteriorly along the midline. This would give the frontonasal contact a V-shape, with the apex anteriorly directed. A shallow horizontal flange dorsally limits the prefrontal contact: there is no such flange in either *V. salvadorii* or *V. varius*. The lateral process of the frontal is anteroposteriorly nar-

	F 16783	V0033
Midline length	89.2	74.3
Maximum length	93.0	85.6
Maximum width	57.2	48.5
Minimum width at orbit	25.4	25.6
Maximum thickness	25.2	19.8

TABLE 1. Giant varanid frontals (mm).

FIG. 1. Left frontals of a large varanid, probably *Megalania prisca* . Unworn frontal (F16783) in dorsal (A) and lateral (C) views. Worn frontal (V0033) in dorsal (B) and lateral (D) views. Scale bar 1cm.

rower, relative to its length, than in the modern species examined (in addition to those noted, *Varanus gouldii* and *Varanus mertensi* were seen) The contact surface for the prefrontal meets that for the postfrontal-postorbital, with no indication of a free orbital margin on the frontal, as there is in modern varanid skulls. F16783 is shorter than the frontal of *V. salvadorii*, more similar in its proportions to that of *V. varius*. However the orbital emargination is placed relatively further back. Ventrally, the frontals are similar in form to those of the modern species. The subolfactory processes are well developed and extend to the midline, hence would be in contact medially. A small foramen penetrates the processes along the midline contact.

The Pleistocene frontals differ from those of modern varanids in three particulars. A distinct sagittal crest is present (Fig. 1C), which terminates posteriorly in front of the parietal contact. This indicates that the crest was limited to the frontal. Lateral to the crest the dorsal face of the frontal is ornamented with low, rounded, mostly parallel ridges (Fig. 1A). Low parallel ridges are often found on vertebrae of *M. prisca*, abutting articular surfaces, but I know of no other varanid with such ornament or, for that matter, any other reptile. However, a low dorsal ridge at the frontal symphysis is apparent in the skulls of several varanids, including *Varanus indicus* (J11017 and J11018), *Varanus spenceri* (J42022 and J47915), *Varanus tristis* (J50726) and *V. varius* (J15361, J16156 and J47065) It is absent in *V. gouldii* (J16135) and *V. mertensi* (J46280). Finally, and most obviously, the King Creek frontal is massive. At the parietal contact the depth of the frontal is 1/4 its midline length; in *V. salvadorii* this ratio is less than 1/10.

The parietal (F16792) is worn, although less than V0033. However the anterior suture pattern is lost. It is a crescentic element (Fig. 2). Apparently both parietals were fused medially, as in modern varanids, but this specimen is broken along the midline. Anteriorly the lateral process projects perpendicular to the longitudinal axis, and posteriorly a longer supratemporal process projects posterolaterally at an angle of 35 degrees to the longitudinal axis. In proportions the parietal is basically similar to those of *V. salvadorii* and *V. varius*, but differs in having a proportionately shorter body. In conjunction with this the supratemporal process of the parietal, which distally contacts the paroccipital process, is relatively longer. At the anterior termination of the mediolaterally compressed supratemporal process a prominent horizontal pit penetrates the body of the parietal. Such a pit is also present in at least *V. varius*.

Although in form basically similar to those of modern varanids, this parietal differs in several points. A large parietal foramen is present, 1cm in diameter, but set less than 1cm back from the frontal contact. Thus it is more anterior than in the modern varanids seen. The supratemporal process is horizontal and not declined posteriorly as in living varanids. The dorsal margin of this process is distinctly elevated from the dorsal face of the body. This, together with the extension of the supratemporal fenestra over the top of the parietal to the midline, suggests powerful development of the jaw adductors. Correlated with these differences, the flat dorsal face of the parietal extends posteriorly from the frontal contact only to the parietal foramen, unlike the modern varanids available where this surface extends from frontal margin to occipital face. The mediolaterally compressed supratemporal process bears a distinct medial shelf along its entire length but less prominent distally. Such a shelf was not seen on any of the modern varanid material available. Ventrally the area of the parietal roofing the endocranial cavity is strongly reduced compared to the condition in *V. varius* (J47065) and *V. salvadorii* (J14498). The linear dimensions of the endocranial roof are twice those of J47065 (*V. varius*), but the lengths of the lateral and supratemporal processes are three to four times those of that specimen. This reduction of amount of the parietal forming the endocranial roof is reflected in the extension of the parietal laterally beyond the lateral walls of the braincase.

The broken face of the parietal shows a depth of 2.5cm of which the top 0.5cm is compact bone and most of the remainder is spongy bone. A thin (0.2cm) layer of compact bone forms the ventral surface.

SCALING

The large size of the King Creek varanid cranial material leads to questions of its scaling. This is relevant to the following taxonomic discussion and interesting in its own right. Two issues will be raised: whether the apparent thickness of the frontals results only from their large size and the relative size of the endocranial cavity.

Could the appearance of thickness of the frontals and parietal from King Creek simply be the result of scaling? McMahon's elastic scaling

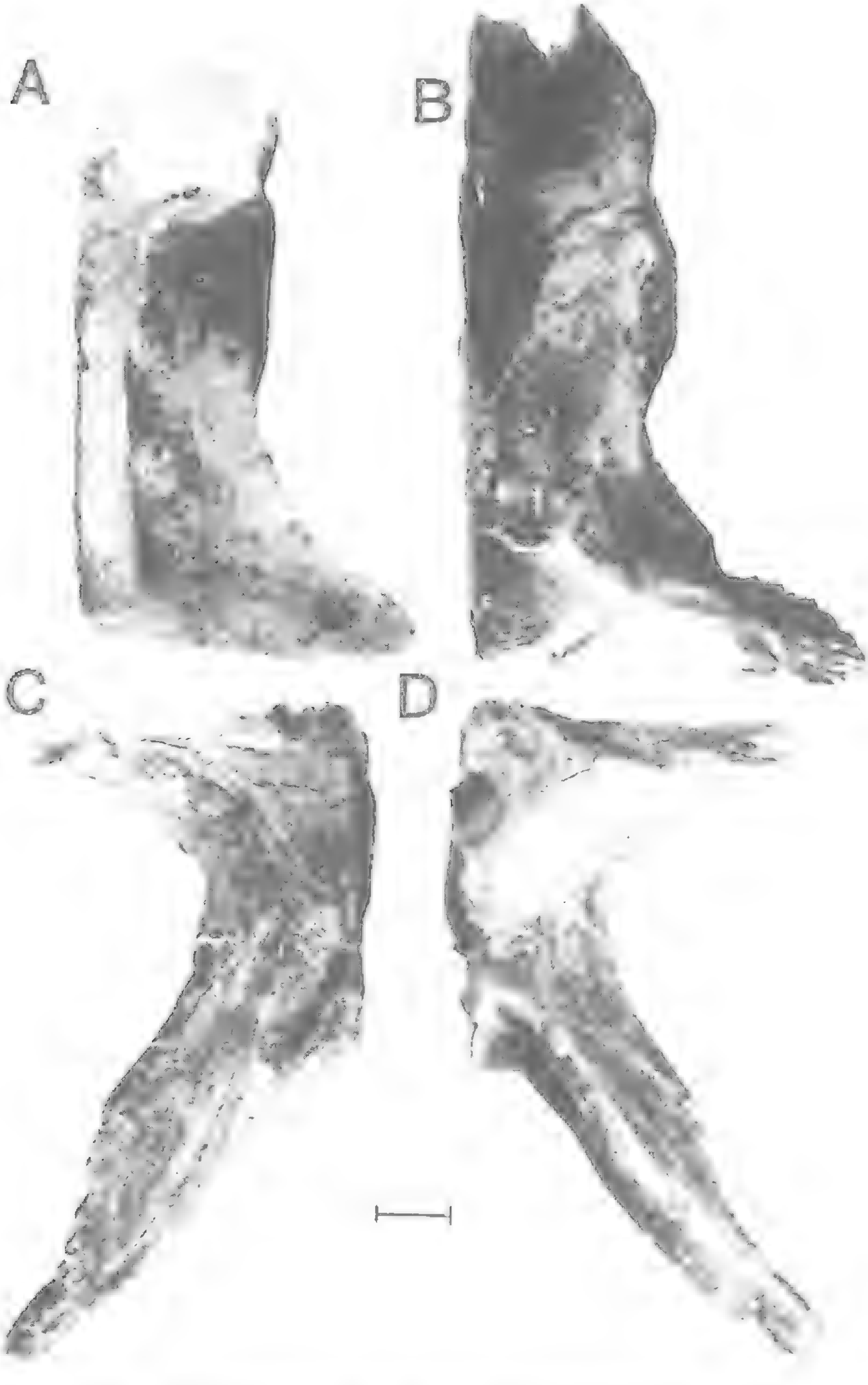

FIG. 2. Left frontals and right parietal of a large varanid, probably *Megalania prisca* . Worn frontal (V0033)

(McMahon, 1973; McMahon and Bonner, 1983), for which there is some evidence when applied to the anatomical analogues of columns (Hamley, 1990; McMahon, 1975), recognises that transverse linear dimensions scale as the 3/2 power of longitudinal linear dimensions. McMahon assumes that the orthogonal transverse dimensions will be equal, that is $D^2 = L^3$ where D is the transverse dimension and L the length. However if the two orthogonal transverse dimensions were not equal, as is here the case, then it would follow from the derivation that $D1 \times D2 = L^3$. In this case if D1 is the width of the frontal and D2 its thickness, we wish to find the value of D2 expected from knowing L and D1, if the large frontal were to have the same resistance to bending as the frontals of smaller modern varanids (here *V. salvadorii* and *V. varius*). This analysis treats the frontals as a plate principally resisting bending stresses imposed in biting, and transmitting the forces then impressed to the parietal and occipital regions of the skull. It also assumes that the frontals can be regarded as simple plates with resistance to bending proportional only to the cross-sectional area. It ignores any possible role in stiffening the frontals of the subolfactory processes, which in varanids make the posterior part of the frontals into a flattened tube. It also ignores the role of the sagittal crest of the King Creek frontals. However these effects will be ignored here for two reasons, first they are technically difficult to treat, and second both considerations would act to increase the resistance to bending of the frontals. Thus consideration of both factors would tend to decrease the estimate of thickness for scaled up frontals. I wish to determine if the King Creek frontals are thicker than expected from arguments of scaling and hence wish to err (if at all) on the side of estimating too thick rather than too thin.

Working with the dimensions of the two available skulls, J14498 (*V. salvadorii*) and J47065 (*V. varius*), it appears that the thickness of the King Creek frontals is such as would be predicted from elastic scaling. Scaling up the skull of *V. salvadorii* would give a frontal about 20 mm thick, which is close to the thickness of the F16783 (19.8 mm), while scaling up that of *V. varius* would predict frontals even thicker, about 45 mm thick. In view of the approximations used in making these calculations, this is viewed as reasonable agreement (i.e. within one order of magnitude), providing no evidence that the frontals from King Creek are unusually thick.

For purposes of an order of magnitude calculation the endocranial cast of a varanid may be approximated by a six-faced irregular but bilaterally symmetric polyhedron that approximates the endocranial cavity. The ventral surface of the parietals forms the upper face of the polyhedron. This polyhedron was defined from examination of the figures 10, 17 and 18 of Starck (1979) and of a skull of *V. varius* (J1656) that retains some of the soft connective tissue walling the endocranial cavity. The figures of Starck (1979) indicate that in *V. salvator* at least virtually all of the brain is included within this volume, although not filling it. The similarity in form of the parietals of *V. varius* to that from King Creek, suggests that this polyhedron may be used to approximate the endocranial cavity of that form as well. Because the same polyhedron is used in both instances, if the ratio of the areas of the corresponding face of each of the two polyhedra is known, the ratio of the volumes can be calculated.

The endocranial surface of the parietals of F16792 is about 5 times greater than that of *V. varius* (J47065). Using the relationship that volume is proportional to the 3/2 power of area, this gives a ratio of volumes of about 11 to 1. This result gives no indication that the endocranial cavity of the King Creek varanid was relatively smaller than in the modern *V. varius* in spite of the fact that relatively less of the ventral face of the parietal roofs the endocranial cavity in the fossil form than in the living one. In modern varanids the brain is substantially smaller than the endocranial cavity and so does not closely conform to the endocranial surfaces (Starck, 1979, figs 17 and 18). Thus no inferences regarding relative brain size will be essayed here.

TAXONOMIC IDENTIFICATION

Varanoid frontals are characterised by the structure of the subolfactory processes (Pregill et al., 1986), which are well developed and come in contact medially. Thus the King Creek frontals are varanoid. Pregill et al. (1986) cite a mediolaterally compressed supratemporal process of the parietal as characteristic of varanids, hence this parietal derives from a varanid.

The parietal matches in the size the two frontals, suggesting that both elements derive from the same species. Unfortunately the anterior suture pattern on the parietal has been worn, so direct comparison of their forms is not possible. However, some similarity is evident. The parietal contact face of the frontal is stepped, its medial centimetre situated slightly forward of the lateral portion. The anterior face of the parietal shows a corresponding step, with its medial centimetre set slightly forward. The dorsoventral thickness of the lateral process (2.1cm) matches that of the frontal (2.0cm), so that the two elements could have derived from the same individual. The parietal is also consistent in size with the occipital segment of Owen (1880), although that comes from Gowrie, not King Creek. The similar thickness and form of the frontal-parietal contact indicates that the frontals and parietal probably derive from the same species.

Further evidence for common derivation could be given if the parietal had a similar pattern of ornament. Unfortunately there is no indication on the dorsal face of the parietal of the unique sculpture or the sagittal crest seen on the frontal. Because the dorsal face of the parietal has been worn and the sculpture of the frontal is very subdued at its posterior margin, sculpture may have been present and lost from wear. A sagittal crest, however, should have been sufficiently marked to have survived this degree of wear, were any crest present on the parietal.

Presumably this material pertains to *Megalania prisca*. The holotype of *M. prisca* consists of two and half dorsal vertebrae (BMNH 32908a, 32908b and 32908c: Lydekker, 1888), and so reference to this species must depend on comparison with associated material. No frontals or parietals of *M. prisca* were previously known (Rich, 1985, figure on p. 154). However both King Creek frontals were found in association with material of *M. prisca*, vertebrae and teeth at Pearson's locality and vertebrae and a tibia at Sutton's bed. But much other tetrapod material has also been found at these localities, so no firm conclusion may be drawn from this. However *M. prisca* is the only large varanid known from Pleistocene Australia, and since these skull roof elements derive from a large varanid, reference to *M. prisca* is reasonable.

Further conclusions may be drawn regarding the evolutionary position of the beast from which these elements derived. A close approach of the prefrontal to the postfrontal above the orbit is a derived feature (Pregill et al., 1986). Thus confluent contact surfaces for the prefrontal and postfrontal-postorbital is a derived feature. So these frontals represent a more derived condition than any surviving Australian varanids examined. The parietal appears less derived, in that it retains the parietal foramen (Pregill et al., 1986), and a large one at that. However I would suggest, by analogy with the evolution of the cranial roof in large theropod dinosaurs (Walker, 1964), that reduction of the flat dorsal surface of the parietal by encroachment of the supratemporal fenestrae is also a derived feature in varanoids. This suggests that *Megalania* represents a more derived varanid than now exists in Australia.

DISCUSSION WITH SPECULATIONS

The frontals and parietal from King Creek appear obviously thicker than the maxillae and dentary attributed to *Megalania prisca* . Either the skull roof was considerably thicker than the trophic apparatus, or the roof elements derive from an individual larger than those from which the jaws are known, or there was variation, such as sexual dimorphism, in thickness of the skull elements.

A dentary, F6562, from an animal presumably approximately equal in size to that from which the cranial roof elements derive, is at the base of the teeth (where it is thickest) only 60% as thick as the frontal F16783. A maxilla (F12370), also apparently from an animal of this size, is equally thin compared to the frontal. This is not the case in the skulls of living varanids, where the frontal and dentary are approximately equally thick. The only other amniotes known to me with the skull roof significantly more massive than the trophic apparatus are the herbivorous pachycephalosaurian dinosaurs (Maryanska and Osmolska, 1974). These are quite different in cranial form. The tooth form of *M. prisca* implies that it was most likely either a predator or scavenger. In neither case is the braincase expected to be more robust than the trophic apparatus; such construction is unknown among living predators and scavengers.

The frontal and parietal appear to be approximately of the size expected to match the known maxillae and dentary, to judge from comparison with living varanids. Unless its cranial proportions were very different from modern varanids they would not derive from an individual 30% larger than those from which the jaws come. So the possibility that they derive from individuals of different sizes seems remote.

Possibly one sex, presumably the male, had a more robust skull, or at least skull roof, than the other. There is at present no way of testing this possibility. Sexual dimorphism is unknown in living varanids, but the environmental circumstances of *Megalania* were doubtless different and sexual dimorphism is known in some mammalian top carnivores, e.g. lions.

The frontal crest suggests habits different from those of living varanids. It may have been a weapon, or display (species recognition) structure. *M. prisca* would presumably have been a top carnivore of the Australian Pleistocene (cf. Rich, 1985) and thus, at least in some respects, analogous to the large theropod dinosaurs of the Mesozoic. Large theropods bore cranial ornament, usually horns or crests (Molnar, 1977; Kurzanov, 1976; Welles, 1984; Bonaparte, 1985), thus it is not unreasonable to suggest that *M. prisca* too might have had cranial ornament. The frontal crest may have been used in head to head shoving contests, as among the marine iguana *Amblyrhynchus cristatus* (Carpenter, 1978). Living varanids are not known to engage in such contests (Stamps, 1977; Carpenter, 1978), but the circumstances of the life of *M. prisca*, as a large terrestrial top carnivore were unlike those of modern varanids.

A different speculative significance of the crest has also been suggested. It is well known that aquatic lizards (including some varanids) usually show lateral compression of the tail and sometimes the trunk. Furthermore many show some development of a dorsal ridge or crest along the back and tail, as in *Hydrosaurus amboinensis* (although rarely so prominent). In some species of *Basiliscus* these crests are complemented by a crest on the skull roof. Possibly the sagittal crest of the King Creek frontal indicates aquatic or amphibious habits. A cranial crest is found in some arboreal lizards, such as *Corythophanes*. We seem safe in presuming, however, that the giant King Creek varanid was not arboreal.

If the King Creek varanid was amphibious or aquatic, one might expect that crocodiles would have been rare in its habitat. Indeed, crocodile remains are rare (Pearson's locality) or absent (Sutton's bed) from the localities and levels at which the frontals were found (Sobbe, pers. comm., 1988; also cf. Bartholomai, 1976). This suggests that competition for the niche of a large aquatic predator would have been weak or absent. It also suggests that predation on a large aquatic lizard would have been weak or absent.

CONCLUSIONS

Two frontals and a parietal from King Creek, eastern Darling Downs, Queensland, indicate the presence of a giant varanid. This form, presumably *Megalania* , was more derived than living varanids in two features: the contact of the articular surfaces for prefrontal and postfrontal-postorbital and the encroachment of the supratemporal fenestra over the top of the parietals. Both the appearance of unusually thick frontals and of a relatively small endocranial cavity seem to result from scaling effects.

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The persistence and acute eye of Mr Ian Sobbe in finding the cranial material and his kindness in donating it made this paper possible. Two of the speculations discussed in above - sexual dimorphism and aquatic habitus - were suggested by Tony Thulborn and Greg Czechura, respectively. They are not, of course, responsible for my treatment of their suggestions. Valuable assistance was also given by Drs M. Borsuk-Bialynicka (Warsaw), R. Estes and G. K. Pregill (both in San Diego).

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PUTATIVE LOWER CRETACEOUS AUSTRALIAN LIZARD JAW LIKELY A FISH

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A jaw fragment from Lower Cretaceous beds of Victoria has been identified as that of a lacertilian. If correct this would be the oldest known lacertilian cranial material from Australia. The acrodont, transversely broadened teeth of uniform size lack cusps and are well separated from one another in the tooth row. We have not been able to match these features in any Mesozoic reptile. Thus we conclude that the jaw fragment probably derives from a large teleost fish. ☐ *Early Cretaceous, Victoria, Australia, Koonwarra, teeth, lizard.*

R.E. Molnar, and G.V. Czechura, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101, Australia; 20 February, 1989.

A fragmentary jaw from the Lower Cretaceous of Victoria has been labelled as lizard. The jaw was collected by a Field Museum of Natural History field party, probably in 1964. According to a letter from W. Turnbull (Chicago) to J. Warren (Melbourne), the locality is uncertain. Collecting at that time was carried out at the Koonwarra pond deposits and at coastal deposits at Cape Paterson. Comparison of the matrix in which the fragment was found with samples from both Koonwarra and Cape Paterson was inconclusive. An impressive fauna of fishes (Waldman, 1971), mostly teleosts, but with some dipnoans and invertebrates (Jell and Duncan, 1986), has been recovered from Koonwarra. These rocks are assigned to the Strzelecki Gr., of Valagianian to Aptian age (approximately 113-138 million years ago: Dettman, 1986). The Cape Paterson deposits also are the Strzelecki Gr., and have been studied extensively by T. and P. Rich. They have yielded a fauna of fish, turtles, dinosaurs (Rich and Rich, 1989) and a single humerus probably from a lizard (Molnar, 1980).

FIG. 1. The jaw fragment (PR1425) from the early Cretaceous of Victoria labelled as lizard. The teeth are visible toward the top: the bevelled appearance may be seen of the second and third from the right: the first and fourth are clearly broken. Scale in mm.

If the identification of the jaw is correct, it is the oldest known Australian lizard material identifiable to a level below suborder. Molnar's (1980) likely lizard humerus - from the Strzelecki Gr. at Eagles Nest, on the Gippsland coast - lacked the articular ends and thus is not identifiable more precisely than as 'lacertilian'.

The oldest Australian lacertilian material identifiable to familial level or below is of Miocene age (Estes, 1984; Molnar, 1985, and references cited therein; Covacevich et al., 1990). Since lizards were present in the Jurassic, potentially a very substantial portion of lacertilian history in Australia is completely unknown. Thus study of the Victorian fragment is potentially very significant for understanding the evolution of Australian lepidosaurs. We here describe this specimen and show that it seems, after all, not to be a lizard but is most likely a teleost fish. (The reference of Molnar (1985) to lepidosaur

FIG. 2. Occlusal view of the teeth of PR1425: the gaps between successive teeth can be seen at the arrow. Scale in mm

material from the Lower Cretaceous Toolebuc Fm. of Queensland, is also incorrect: this vertebra appears to derive from a diminutive archosaur).

The specimen is catalogued as Field Museum of Natural History (Chicago) PR1425: it consists of a fragment of jaw 16mm long, 5mm in maximum thickness and 7mm in maximum depth (Fig. 1). The entire edge opposite the dentigerous margin is broken. The fragment is now embedded in transparent resin to reinforce the fragile bone. Six teeth are preserved, three apparently complete, and three broken apically, with spaces for four more present. Each crown is separated from its neighbours by a distinct gap, apparently of uniform width along the series. The blunt teeth are acrodont, and triangular in anterior aspect. They are anteroposteriorly compressed (Fig. 2). In lateral view the basal half of the crown has almost parallel margins, but in the apical half one margin becomes inclined so as to intersect the other (Fig. 1), giving the crown a bevelled or chisel-like appearance. The teeth are set at a very slight inclination to the dentigerous margin and are uniform in size. None show cusps, striae, denticles or other such structures. There are no resorption pits or other indication of tooth replacement. The bone of the jaw is not sculptured, and lacks foramina. One face of the jaw fragment is slightly convex, while the other (the embedded face) is concave, so that the bone thins away from the dentigerous edge, and apparently broadens abruptly to form that margin. It is unfortunately impossible to be certain of this because of the resin. Because of the fragmentary nature of the specimen, it is also impossible to determine if this fragment derives from the upper or lower jaw.

The acrodont tooth emplacement contraindicates reference to such Cretaceous reptiles as have thecodont (archosaurs) or pleurodont teeth. Most modern lepidosaurs have pleurodont teeth: acrodont dentitions are found among agamids and chamaeleonids (Edmund, 1969). Acrodonty is also found in amphisbaenians (Gans, 1960) - which may be eliminated because of their quite different tooth form - and sphenodontians. Tranversely broadened teeth are found in some sphenodontians (Throckmorton et al., 1981; Fraser, 1986) and trilophosaurs (Gregory, 1945; Robinson, 1957). Trilophosaurs have tricuspate, wedge-shaped, often dilated crowns, distinct from those of the Victorian fragment. Most of the few sphenodontians with transversely widened teeth have teeth that noticeably increase in size posteriorly (Throckmorton et al., 1981, fig. 5; Fraser, 1986, fig. 5). The most similar dentition is that of the sphenodontian *Eilenodon robustus* (Rasmussen and Callison, 1981) from the Upper Jurassic Morrison Fm. of Colorado. Its teeth are transversely broadened pyramids, showing considerable wear. They are placed in the jaw very close to one another, without the distinct separation shown in the Victorian fragment. Sphenodontians seem either to lack transversely broadened teeth, or where such teeth are present, to lack teeth that are distinctly separated. Thus neither trilophosaurs nor sphenodontians seem sufficiently similar to the Victorian fragment for reference.

Comparison was carried out with a variety of Australian modern and Miocene (Riversleigh) lacertilian material. Overseas material, both modern and fossil, was compared using the literature. Lacertilian teeth, when compressed, are almost always longitudinally rather than transversely compressed: one of the few exceptions is *Polyglyphanodon sternbergi* (Gilmore 1942). This longitudinal compression is especially obvious for acrodont lacertilians, such as agamids and chamaeleontids. The lacertilian (and sphenodont) teeth examined by us uniformly taper toward the tip and do not show bevelled form of the Victorian crowns (including those of *Polyglyphanodon*). The only reported bevelled lacertilian crowns are those of the teiid *Macrocephalosaurus ferrugenous* (Gilmore, 1943). Only a single crown, however, was considered, with some doubt, to be unworn and this exhibited low cusps.

We have been unable to find any convincing match between the crowns of the Victorian fragment and the teeth of known Mesozoic or later reptiles. Thus we conclude that this jaw fragment is not demonstrably reptilian: it is clearly not referable to any of the (few) known Lower Cretaceous Australian reptiles (mostly archosaurs). Presumably it derives from one of the many teleost taxa known from this deposit.

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SPIDER PREDATORS OF REPTILES AND AMPHIBIA:—Predation of vertebrates by spiders in not uncommon. In Australia, Whisting Spiders (*Selenotypus plumipes*, Theraphosidae) have been reported dragging a young chicken 50 feet from its enclosure and then attemping to drag it into a small burrow 1.25 inches in diameter (Chisholm, 1919).

Predation of reptiles is less known. Two cases reported from Australia are that of the Whistling Spiders (*Selenocosmia* and *Selenotypus* spp.) feeding on the frog *Helioporus centralis* (Main and Main, 1956) and the Funnel-web spider (*Atrax formidabilis*) feeding on *Hyla* (=*Litoria*) *caerulea* (McKeown, 1952). Those predators, however, are large powerful trapdoor spiders that would seize prey on the ground. Predation of vertebrates by web building spiders is also known. Best known are the very strong webs of Golden Orb-Weavers (*Nephila*) that snare and kill small birds but evidently do not consume them.

McKeown (1952) shows a mouse caught and hoisted in the web of a Redback Spider (*Latrodectus hasseltii*). He also reported cases of a Funnel-web spider (*Atrax robustus*) taking a chicken, Water spiders (*Dolomedes*) taking fish, and web-building spiders taking small native birds, bats, and reptiles. A skink, *Lygosoma*, had also been taken by a Redback. One account discussed a black snake that had been tied head to tail and killed by an adult Redback spider. The spider's young were evidently feeding on the snake.

Two cases of Redback Spider predation on reptiles have been noted in our collections. A female Redback spider had built a web in the fold of a blanket left hanging on a clothes line to dry, presumably for some days. On removing the blanket, two Wall Skinks (*Cryptobelpharus virgatus*) were found dead and partially consumed in the web. (My nomenclature for reptiles and amphibians follows Cogger, 1983) In the second case (Fig. 1), the web of the female Redback had been built close to the ground and it had snared a Verreaux's Skink (*Anomalopus verreauxii*). Apparently, the very sticky lower vertical lines of the Redback had trapped the skink and lifted its head high off the ground. The spider then moved repeatedly to the underside of the skink to inflict its bite (arrow shows blood stained scar). The spider did not consume the lizard but merely immobilised it. Raven and Gallon (1987) suggested that the Redback is an introduced spider and hence may rank along with *Bufo marinus* in its effects on native vertebrates.

A third instance, observed personally, was that of a Wolf Spider and a young frog (*Litoria lesueuri*). I had caught, identified and placed the frog back on the rocks of a creek bed. Immediately, a large female *Lycosa lapidosa* jumped onto the frog, impaling it on its fangs. The live spider and its prey were taken in a vial back to camp where the vial was opened. Only a grey liquid mound remained of the frog, no hard tissue could be felt with a wooden probe. Little more than five minutes had passed since the spider had seized the frog.

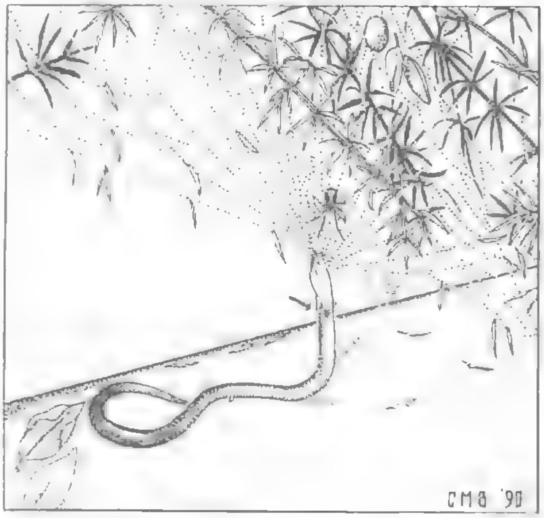

FIG. 1. Redback and snared Verreaux's Skink.

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Robert J. Raven, Queensland Museum, P.O. Box 300, South Brisbane, Queensland, 4101, Australia.; 20 August, 1990.

TREATMENT OF CLOACAL PROLAPSE IN THE ESTUARINE CROCODILE

LYALL NAYLOR

Naylor, L. 1990 09 20: Treatment of cloacal prolapse in the Estuarine Crocodile. *Memoirs of the Queensland Museum* 29(2): 449-451. Brisbane. ISSN 0078-8835.

The prolapsed and inflamed genitalia of two captive male specimens of *Crocodylus porosus* were successfully repaired following sedation of the specimen; cleansing and replacement of the genitalia and surrounding tissues; and suturing of the vent to prevent repetition of the prolapse. ☐ *Treatment, cloacal prolapse, Crocodylus porosus.*

Lyall Naylor, C/- Wild World, Palm Cove, Queensland 4879, Australia; 18 August, 1988.

The Estuarine Crocodile, *Crocodylus porosus* is a species which is kept frequently in, and generally adapts well to, captivity. Many specimens are held in zoological collections and farms in Australia. One potentially serious problem with captive crocodiles results from territorial conflicts between males, even between individuals who have shared ponds harmonious-

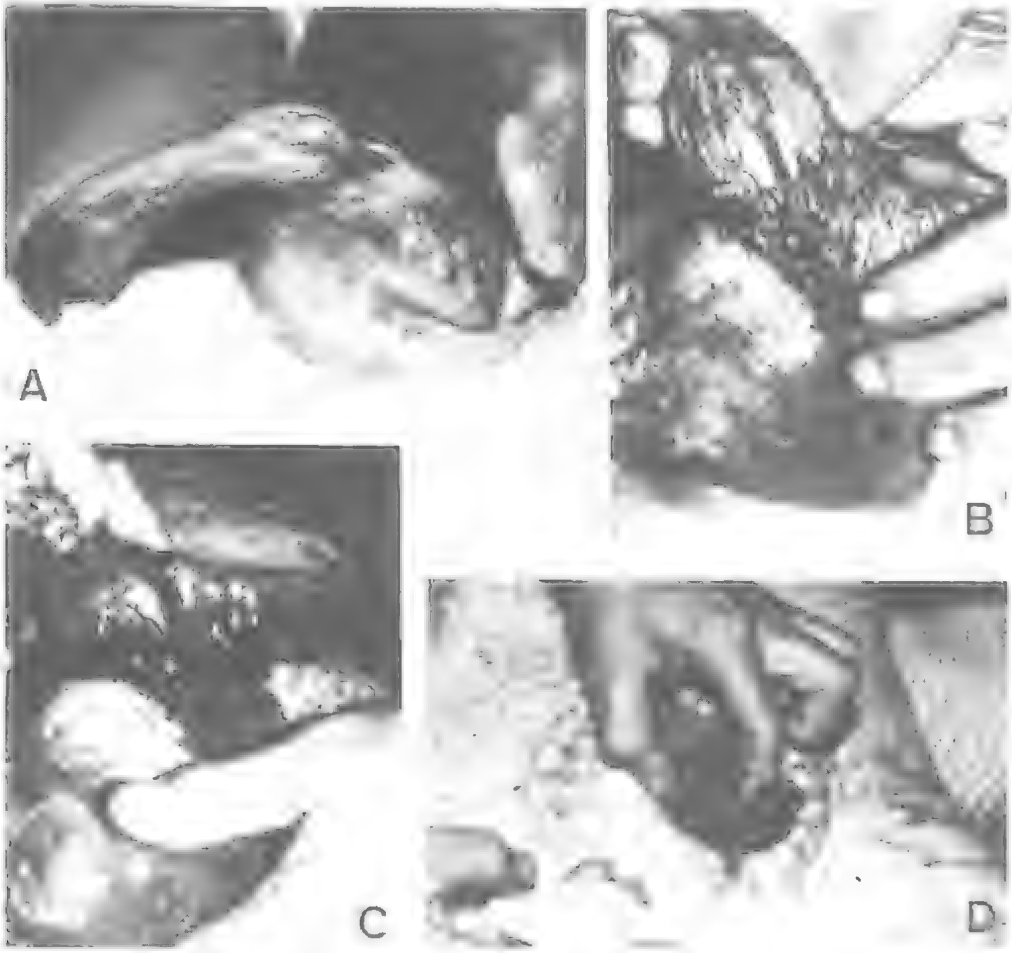


FIG. 1. A. Prolapsed and inflamed genitalia of *C. porosus.* B. Abraded tissue. C. Cleaning method. D. Replacement of genital tissue.

TABLE 1. Doses of Flaxedil and Valium required to sedate *Crocodylus porosus* specimens.

TL(m)	Drug Dose (mls)	
	Flaxedil	Valium
2.1–2.7	1–2	2–4
2.7–3.3	2–4	4–8
3.3–3.9	4–8	8–10

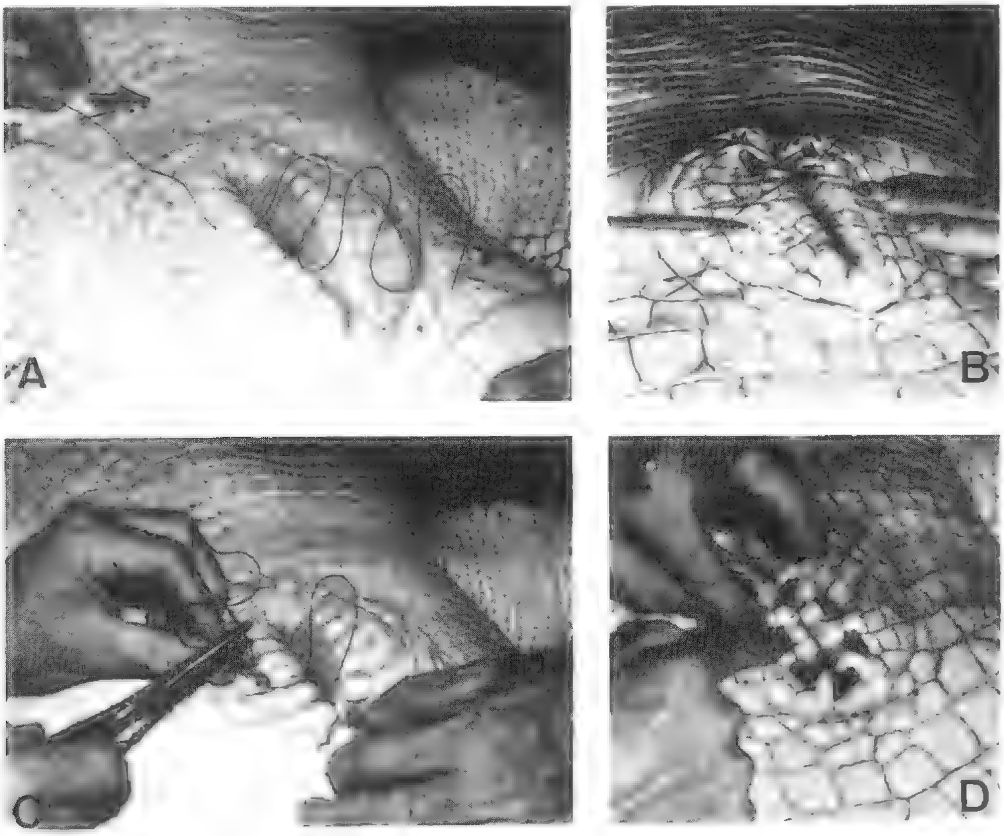
ly for long periods. Here, the circumstances leading to cloacal prolapse with subsequent irritation of the genital organs and successful treatment of this problem are reported for two specimens.

When two males fight, displaced sexual arousal can expose their genital organs. These can be severely injured, either by abrasive contact with concrete (most battles take place in concrete-lined ponds) or by an opponent (Fig. 1A,B). The prolapse can be aggravated by sand and debris. Captive crocodiles bask in favoured sites that become denuded of grass cover and sand quickly enters the genital area and exacerbates the problem. Abrasion of the hemipenis, testicles, and surrounding soft tissue results in a serious discomfort. Crocodiles suffering from the combination of prolapse and inflamed, abraded genitalia walk with their hind legs fully extended to help hold the injured tissue above the ground to avoid further discomfort. Even at rest, they favour elevating their hindquarters.

REPAIR PROCEDURE

The crocodiles were sedated prior to surgery with Valium and Flaxedil-Gallamine (Table 1). These were administered via a syringe attached to a suitably modified 2m aluminium pole. Sedatives were injected via the neck, hind legs or butt of the tail depending on the animal's position and disposition. Once the specimens were sedated, their jaws were bound and their eyes covered.

FIG. 2. A-C. Suturing of cloacal opening. Note plastic tubing to prevent tearing. D. Completed repair.



Then the animals were positioned dorsum down on a hessian mattress.

With the specimens 'safe' and in position for surgery, Betadine surgical scrub solution (7.5% uv povidone-iodine) was applied liberally to the whole area affected. This was then rinsed with tap water (Fig. 1C). (With hindsight it is now felt that sterile saline — 0.9% sodium chloride solution — would be a more appropriate rinse). To ensure removal of all foreign bodies and cleanse the wounds this procedure was repeated several times.

The genitalia and exposed tissues were replaced in the cloaca (Fig. 1D) after the application of 50gms of socatyl-sulphonamide paste (active constituent formosulphathiazole) to facilitate placement and reduce the risk of infection.

The vent of crocodiles has an elliptical shape and this, sutured to reduce its size dramatically, assisted prevention of repeated prolapse until healing was complete. To prevent tearing of sutures small sections of plastic tubing were affixed to entry and exit points (Fig. 2). Finally, after suturing, the whole area was washed with Betadine.

The animals were isolated during the recovery period and were not fed until the sutures were removed some six weeks after the repair. Both crocodiles have made uneventful recoveries, though the ability of these animals to breed is doubtful and, as yet, untested.

ACKNOWLEDGEMENTS

Dr D.A. Johnson, Veterinary Surgeon to Wild World via Cairns, supervised this procedure. I am also indebted to K. Day, M. O'Brien, C. Shaw and S. Wallis for advice and assistance.

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DIGIT I IN PAD-BEARING GEKKONINE GECKOS: ALTERNATE DESIGNS AND THE POTENTIAL CONSTRAINTS OF PHALANGEAL NUMBER

ANTHONY P. RUSSELL AND AARON M. BAUER

Russell, A.P. and Bauer, A.M. 1990 09 20: Digit I in pad-bearing gekkonine geckos: alternate designs and the potential constraints of phalangeal number. *Memoirs of the Queensland Museum* 29(2): 453-472. Brisbane. ISSN 0079-8835.

Sprawling locomotion is typical of lizards and dictates the kinematics of locomotion. While lateral undulation of the body is still an important component in the production of locomotor thrust, the kinematics of the limb joints coupled with the marked asymmetry of foot structure result in most of the thrust being directed posteriorly and little of it being oriented laterally. The asymmetry of pedal design, however, leaves digit I with only two phalanges. With the independent acquisition, in many lineages, of subdigital adhesive pads in gekkonine geckos there is a potential 'problem' in incorporating a pad into digit I and enabling it to operate effectively. All other digits have three or more phalanges, but the first lacks the fundamental prerequisites to permit hyperextension of the digit and the deployment of subdigital setae.

Such inherent limitations have resulted in a variety of solutions of this problem and there is great variance in the structure of digit I of pad-bearing gekkonines. Some lineages have reduced the first digit and abandoned it as an effective locomotor device, while others have modified it in a variety of ways in order to permit the functioning of an adhesive apparatus. This paper documents the alternate designs that have evolved in the various lineages of gekkonine geckos and relates them to perceived phylogenetic and functional design constraints. Comparison with diplodactyline geckos and anoline iguanids further exemplify the fundamental constraints involved. ☐ *Gekkonidae, Gekkoninae, first digit, adhesive pads, functional morphology, evolutionary constraint.*

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The pedal asymmetry that is associated with the three-dimensional kinematics of sprawling locomotion in lizards (Rewcastle, 1983) places constraints upon the morphological potential of foot structure. In both the forelimb (Renous and Gasc, 1977) and hindlimb (Rewcastle, 1983) the complex, three-dimensional movements of the components of the limb skeleton during the limb cycle dictate that a line of contact perpendicular to the body long axis must be made by the foot in question for posteriorly- directed thrust to be developed. In the pes this line of contact is delineated by the metatarsophalangeal line, which connects the distal ends of the first three or four metatarsals (Fig. 1). The asymmetry of the pes is emphasised by the unequal lengths of the digits, with the first being primitively the shortest and the fourth the longest (Fig. 1).

This asymmetry in digital length is important in the maintenance of contact with the substratum as the locomotor thrust is delivered (Brinkman, 1980, 1981). Ultimately the foot rolls onto its mesial border as the proximal end of the fifth metatarsal is raised. This is determined by the geometry of the knee and mesotarsal joints (Rewcastle, 1980, 1981, 1983) and results in complex and controlled movements and deformations in the pes (Rewcastle, 1983). Similar deformations occur in the manus (Landsmeer, 1981, 1984).

In terms of digital structure, asymmetry is reflected not only in the relative lengths of the digits, but also in phalangeal formulae. The primitive manual phalangeal formula for lizards is 2-3-4-5-3, and that for the pes is 2-3-4-5-4 (Romer, 1956). The ventral surfaces of the feet and digits are subjected to tractive and torsional forces as the powerstroke of the limb is delivered (Landsmeer, 1981, 1984). This is correlated with the presence of friction pads (Figs. 2, 3) and enlarged plates in these regions. Friction pads may be defined as enlarged scales that are

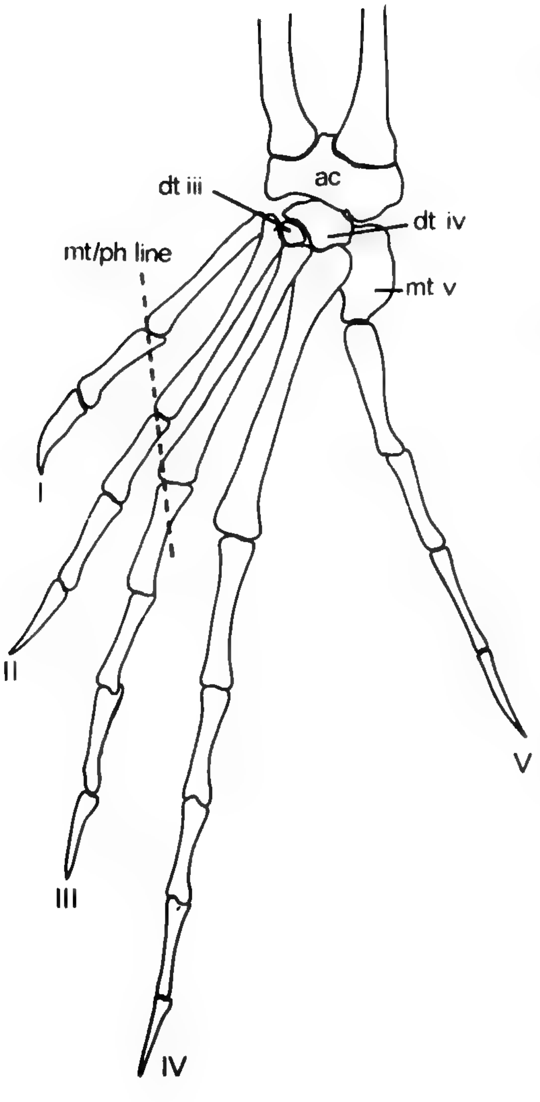


FIG. 1. Dorsal view of the left pes of *Iguana iguana*. Note the asymmetry of the foot, the sub-parallel disposition of the first four digits and the offset nature of the fifth. The dashed line is the metatarsophalangeal line and represents the line of contact of the foot towards the end of the power stroke. This line connects the distal ends of the first three metatarsals and is normal to the body long axis. The foot rolls of the substrate such that the fifth metatarsal is raised,the fourth distal tarsal pivots about the astragalocalcaneum and the mesial border of the first digit is pressed into contact with the substratum. Abbreviations: ac, astragalocalcaneum; dt iii, dt iv, third and fourth distal tarsals; mt/ph line, metatarsophalangeal line; I - V, digits one to five.

present in areas of potentially intensive loading that are thickened and robust. They have sometimes, in pad-bearing forms, been included in a count of total lamellae, but they differ from true scansors (Russell, 1975) in that they are not controlled by the lateral digital tendon system (Russell, 1986) and lack an internal hydrostatic (Russell, 1981) or similar support system. Such friction pads contribute to the minimisation of rotational slippage (Padian and Olsen, 1984) and are arranged in association with the fundamental asymmetry of the foot (Schaeffer, 1941; Snyder, 1952; Robinson, 1975). This asymmetry is of long standing in tetrapod reptiles and is found in a variety of fossil forms, including thecodonts such as *Euparkeria* (Ewer, 1965), *Chasmatosaurus* (Cruickshank, 1972) and many pelycosaurs (Romer, 1956). Charig (1972) noted that the development of a symmetrical foot, as seen in crocodilians, dinosaurs and mammals, is correlated with erect limb posture and two-dimensional limb kinematics. Thus, asymmetry of the manus and pes is a primitive lacertilian characteristic and is inherently associated with the normal sprawling locomotor mode of lizards.

While the basic characteristics of sprawling locomotion and pedal asymmetry are typical of lizards in general, there have been significant departures from this pattern. In chamaeleons, for example, semi-erect posture is correlated with a zygodactylous grasping foot (Gasc, 1963; Peterson, 1984). Limb reduction coupled with body elongation is associated with simplification and ultimate loss of the feet and ultimately the appendages (Essex, 1927; Lande, 1978; Raynaud, 1985; Greer, 1987). Perhaps one of the most remarkable examples of pedal redesign is seen in those lizards bearing a subdigital adhesive apparatus. Variations on this theme are evident in a wide variety of gekkonid lizards (Solano G., 1964; Russell, 1976), as well as in the anoline iguanid radiation (Peterson, 1983a, b), and in an incipient form in some scincids (Smith, 1935; Williams and Peterson, 1982). Modifications associated with the operation of these adhesive systems (Dellit, 1934; Russell, 1975) place further constraints on digital and pedal design. The adhesive pads are placed into contact with and removed from the substrate by way of digital hyperextension (Russell, 1975). Here the limitation of the number of phalanges primitively present in the first digit of both manus and pes renders problematic the incorporation of a fully-developed subdigital pad into digit I. Thus, in pad-bearing geckos there is a wide array of varia-

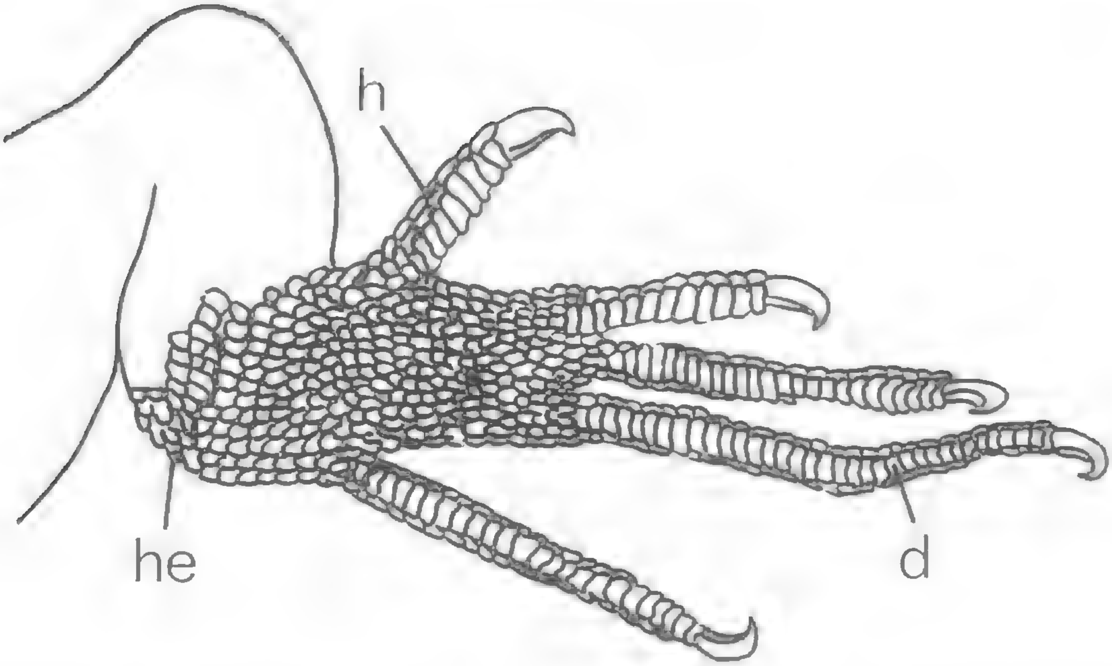


FIG. 2. Ventral surface of the left pes of *Varanus prasinus* indicating the enlarged friction plates on the ventral surfaces of the digits (d), the mesial border of the hallux (h), and the heel region (he). Drawn from a photograph in Greene (1986).

tion in the structure of the first digit and even a tendency to its reduction in some lineages. Such trends are not seen elsewhere among lizards and reflect the compromise of either modifying the first digit into an effective adhesive device or abandoning it as such a structure.

We here survey the subfamily Gekkoninae and document the variation in form of the first digit. We attempt to correlate certain design constraints and modifications with the construction of an adhesive apparatus in general. Numerous adaptive radiations are evident within the widespread and diverse Gekkoninae (Russell, 1976) and each of these serves as a test of ideas put forward for other radiations. Additionally, the situation found in the subfamily Diplodactylinae acts as another independent test, as does that found in the iguanid anoline radiation.

MATERIALS AND METHODS

The structure of the first digit of gekkonine geckos was surveyed by examination of museum specimens. The chief collections employed were those of the British Museum (Natural History) (BMNH), the California Academy of Sciences (CAS), the Transvaal Museum, Pretoria (TM) and the University of Calgary Museum of Zoology (UCMZ). Additionally specimens in the collection of the senior author were also used (APR). Russell's (1972) groupings were employed as the units of comparison, with comparison being carried out both within and between groups. Specimens were examined by one or more of a combination of approaches - a survey of overall external morphology; a survey of skeletal preparations; a survey of cleared-and-stained preparations; radiography; and histology.

RESULTS

For completeness and to establish certain parameters of baseline information some non-gekkonids and primitively padless gekkonines were examined. This permitted the plesiomorphic state of the first digit of lacertilians to be established. Following this, a group by group survey of pad-bearing gekkonines was made in order to document the structure of the pollex and hallux. Finally, for the sake of comparison, the structure of the first digit in the iguanid *Anolis* is examined. While not wanting to presuppose the discussion, the sequence of presentation of the basic data is given in the same order as it is considered in the discussion. In such a broad survey some order must be imposed in order to ensure a logical discussion of the results.

PADLESS NON-GEKKONIDS.

A variety of non-gekkonid taxa, in addition to *Iguana iguana* (Fig. 1), was examined to establish the basic parameters of the form of digit I. In none of these was the pollex or hallux found to be reduced in size. For the purpose of discussion, the first digit of *Lacerta dugesii* will serve as an example (Fig. 3). In both the manus and pes digit I is considerably shorter than the second, bears a strongly-developed claw and has contact points with the substrate at the claw tip and the base of the digit. There are two phalanges present but there is no inflection between them. The most extensively- developed area of friction plates occurs at the base of the digit, beneath the metacarpophalangeal and metatarsophalangeal joints (Fig. 3). The scales beneath the free part of the digit are plate-like and transversely widened, but are not the main load/friction-bearing areas of the digit during normal terrestrial locomotion. The remaining digits of *Lacerta dugesii* also lack marked inflections and their subdigital scale architecture is similar to that of digit I.

In this type of foot design the first four digits are sub- parallel, with the fifth markedly divergent in the pes (Fig. 1). The metatarsophalangeal line connects the distal ends of the first three metatarsals.

NAKED-TOED GEKKONINES.

Many genera of gekkonine geckos primitively lack subdigital pads (Russell, 1976). Of these, two examples have been chosen as extremes. One of these bears digits without inflections, the other with.

The genus *Teratoscincus* may be taken as an example of the situation in primitively padless gekkonines in which purely terrestrial locomotion is practised and in which the digits are not inflected. [Indeed, they are modified for sand-walking and burrowing - Luke, 1986]. As with *Lacerta dugesii* (above) the first digit is considerably shorter than the second, bears a strongly-developed although somewhat less curved claw, and has normal contact points with the substrate at the claw tip and base of the digit (Fig. 4). In *Teratoscincus* there are no friction plates at the base of the digits or enlarged plates beneath the free phalanx, but such situations do exist in other primitively padless gekkonines, such as *Bunopus* and *Agamura* (Fig. 5). Contact with the substrate may be made with the entire ventral surface of the digits and foot (*Teratoscincus*) or with more restricted areas (*Agamura*), this being determined by locomotor substrate preference and by the condition of the skin of the plantar surface of the foot ('puffy' in *Teratoscincus* and taut in *Agamura*).

The first four digits are sub-parallel (Figs. 4, 5) and the metatarsophalangeal line is similar to that for *Lacerta dugesii* and *Iguana iguana* (Fig. 1).

In contrast to the straight, uninflected digits described above, those of many species of the (probably paraphyletic) genus *Cyrtodactylus* are strongly inflected (Fig. 6). Some species of *Cyr-*

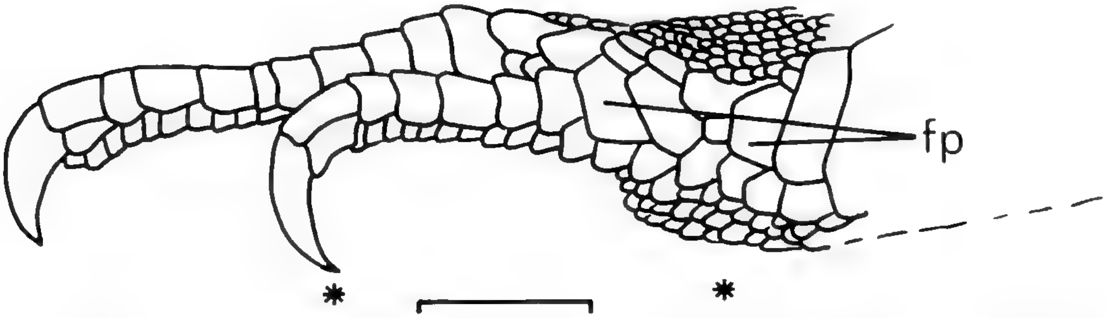


FIG. 3. Mesial view of the first and second digits, right pes of *Lacerta dugesii*. The enlarged friction plates (fp) at the base of the first digit are evident, representing the area of contact as the foot rolls off the substratum during normal terrestrial locomotion. The contact points of the first digit during normal resting posture are marked with asterisks (*). Scale bar = 2mm.

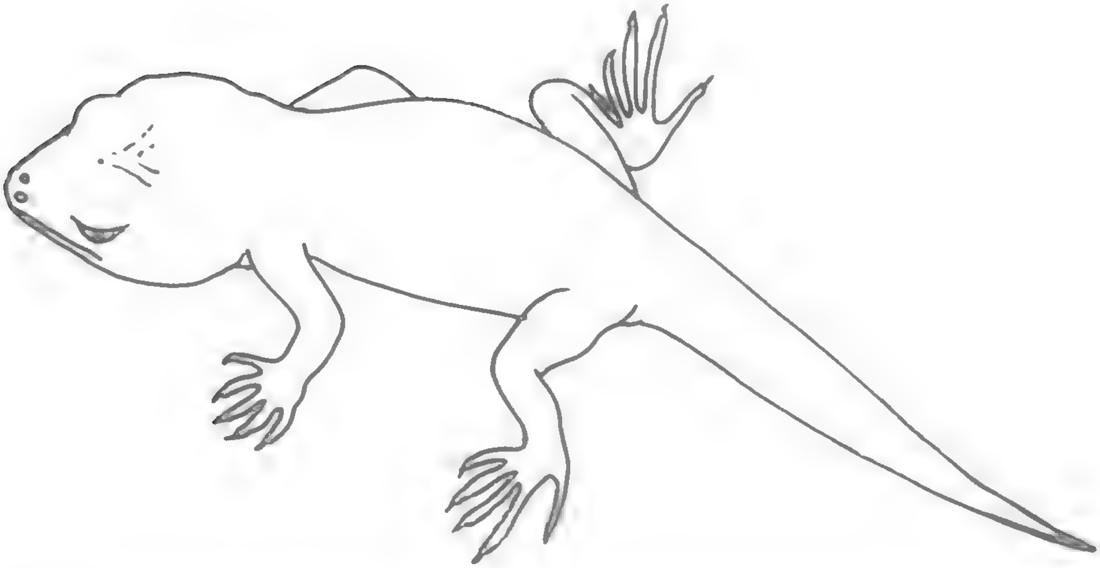


FIG. 4. Outline of *Teratoscincus scincus* illustrating the asymmetry of the pes and the essentially flat digits. Redrawn from Lanza (1972).

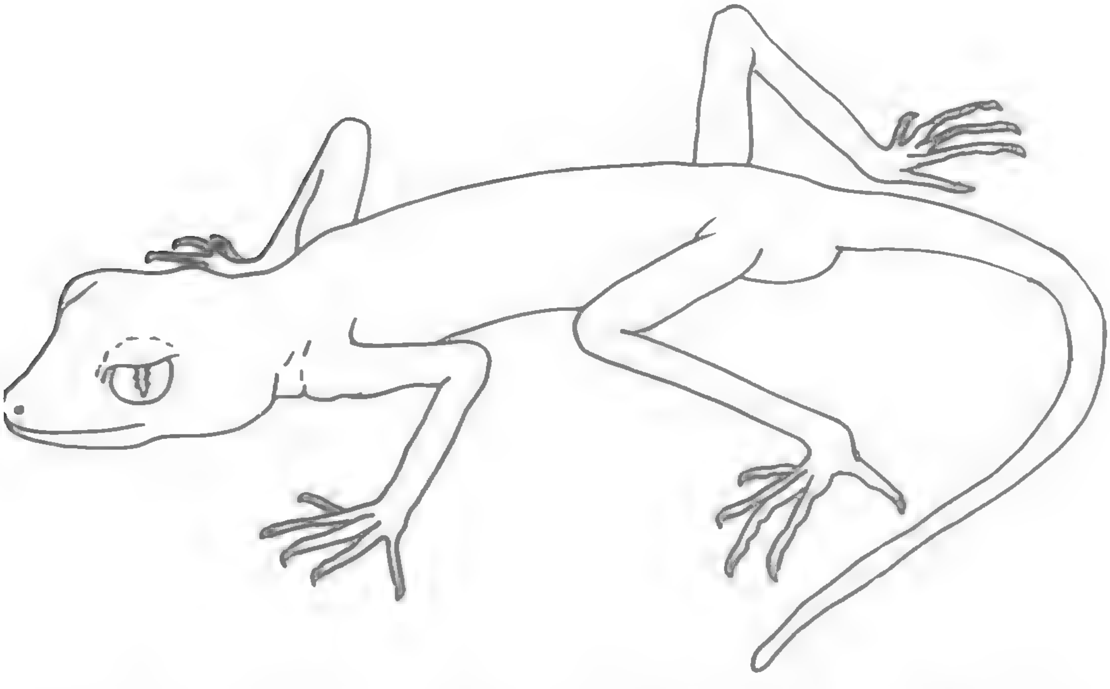


FIG. 5. Outline of *Agamura persica* illustrating the asymmetry of the pes and the essentially flat digits. This species bears friction plates on the ventral surface of the digits and soles of the feet. Redrawn from Lanza (1972).

todactylus (sensu lato) even bear incipient pads (Russell, 1976, 1977). In general, enlarged friction pads occur at the metacarpophalangeal/metatarsophalangeal joints and beneath the inflections (Fig. 6). Transversely widened plates are evident between these points. Beyond the inflection the distal phalanges are held above the substratum and are clad ventrally in smaller scales. All digits are strongly clawed.

Digit I bears no enlarged plates beneath its proximal phalanx, but enlarged friction plates occur at the base of the digit (Fig. 6), while the digit proper is clad ventrally in smaller scales. The enlarged plates at the base of digit I are similar in position and form to those seen in *Lacerta dugesii* (Fig. 3).

PAD-BEARING GEKKONINES

Within the radiations of pad-bearing gekkonines there have been lineages that have developed pads from the base of the digits that have spread distally, and lineages that have developed pads distally that have spread proximally (Russell, 1976). As a result of this, not all groups can be considered in a single linear sequence or as part of a single morphotypic series. We have chosen examples that appear to exemplify evolutionary trends in pad structure and in the form of digit I, but the sequences we have chosen should be treated as being illustrative of morphological rather than phylogenetic trends. We begin by considering forms that are believed to have developed pads from the basal portions of the digits, and then consider assemblages where pads appear to have begun distally. Both of these have had different influences on the first digit, but there are also parallels between the two types.

Genera with basally-derived pads

Working on the premise established by Russell (1976, 1977) that the pedal structure seen in the genus *Cyrtodactylus* could be, morphologically, a precursor of the *Hemidactylus* pattern, we begin here with a consideration of the *Hemidactylus* group. Here the digits bear basal pads (Fig. 7) in which the scansors are borne beneath the modified digital inflection (Russell, 1977, Fig. 3) similar to that seen in *Cyrtodactylus* (Fig. 6). The scansors of *Hemidactylus* grade into friction plates at the bases of the digits (Fig. 7). The distal phalanges are free of the pad and there is no evidence that they have ever been included within its confines. As with other pad-bearing geckos the disposition of the digits is more symmetrical than in padless forms (Figs. 6, 7), this symmetry being brought about largely by a greater divergence of digit IV from digit III.

The first digit still possesses only two phalanges and hence the pad borne on this digit is relatively small (Figs. 7, 8). The ability to hyperextend (Russell, 1975) the pad is rather limited and occurs at the junction of the first metacarpal/metatarsal and the first phalanx (Fig. 9). In all other digits hyperextension occurs between two phalanges rather than between the basal phalanx and a metapodial. The size of the pad in digit I is thus restricted by the dimensions of this digit and the absence of a free basal portion (Figs. 7, 8).

Although there is a great deal of variation within the genus *Hemidactylus*, the situation described above prevails in all species. Similar arrangements are encountered in the satellite genera *Cosymbotus* (=*Platyurus*) and *Teratolepis*, while *Dravidogecko* (Fig. 10) exhibits what may essentially be taken to be a stage morphologically intermediate between *Hemidactylus* and the digitally more derived species of *Cyrtodactylus* (Russell, 1976). Here again, however, digit I exhibits only incipient pad development.

The most marked departure from the basic '*Hemidactylus*' condition is seen in the monotypic genus *Briba*. Here both the pollex and hallux are small (Vanzolini, 1968a, b), and both are clawless (Amaral, 1937, Fig. 2). The distalmost phalanx (ungual phalanx) in each is somewhat elongated and supports the distal extremity of the pad (Fig. 11), rather than being extended beyond it (Figs. 7, 8). Thus, both phalanges in digit I support the pad and are involved in hyperextension of the pad. While the first digit is relatively small in size it is more fully committed to involvement in the operation of the pad.

Genera with distally-derived pads.

The complex of generic groupings to be considered here represents the result of multiple evolutionary pathways (Bock, 1959) rather than a single morphotypic sequence. The basic assumption made is that adhesive pads in all of these assemblages arose distally and that in some lineages they subsequently spread towards the base of each digit. Data derived from internal morphology of the digits is consistent with this interpretation (Russell, 1976).

In this context the structurally simplest case within the Gekkoninae is exemplified by *Phyllodactylus* (sensu lato) and its putative allies. The

FIG. 6. Ventral aspect of the right pes of *Cyrtodactylus peguensis*. Note the digital inflections, the friction plates at the bases of the digits and those beneath the first metatarsal (far right). Specimen UCMZ (R) 1981.3.

FIG. 7. Ventral view of the right pes of *Hemidactylus brookii*. Note the free distal portions of the digits, the basal pads and the relative symmetry of the foot. Uncatalogued specimen.

FIG. 8. Ventral view of the scansors of digit I, right pes of *Hemidactylus brookii*. Note the relative lack of expansion of the pad and its relatively small size. The scansors grade into the friction plates at the base of the digit. Uncatalogued specimen.

basic morphological pattern is apparent in such forms as *Phyllodactylus porphyreus* (Fig. 12), although there is much variation within this genus and its allies (*Asaccus, Ebenavia, Paroedura* and *Urocotyledon*). Typically in *Phyllodactylus* the adhesive plates are present as paired, leaf-like structures at the distal extremity of each digit (Fig. 12), with the claw being disposed between them. The proximal end of each plate is located adjacent to the joint between the penultimate and ungual phalanx. Proximal to this the ventral surface of each digit is clad in expanded, plate-like scales that merge gradually into the scales of the palm/sole (Fig. 12). There are no enlarged friction plates in the palm/sole area. Although radiation of the digits is somewhat pronounced, digit IV is not markedly divergent from digit III (Fig. 12).

Digit I again contains two phalanges and is relatively short (Fig. 12). The distal, leaf-like pads (Fig. 13) are strongly developed, however, and may be raised from the substratum by hyperextension of the distalmost digital joint and the metacarpophalangeal/metatarsophalangeal joint.

The genera *Ptyodactylus* and *Uroplatus* were included within the *Phyllodactylus* group by Russell (1972), based upon certain morphological similarities of digital structure. From a functional viewpoint the replacement of a terminal single pair of leaves by a subdivided, radiating, fan-like array of scansors has had little impact on the disposition of other digital components. The first digit remains strongly developed, the scansor area is still confined to the extreme distal end of the digit, and the basal components of the digits are still devoid of any scansor-like structures (see Smith, 1935, Fig. 24 for *Ptyodactylus* and Duméril and Bibron, 1836, plate 31 for *Uroplatus*).

In all members of the putative *Phyllodactylus* group (Russell, 1972) the digits are flat and lack inflections. Thus, while the adhesive pads are situated distally the majority of the ventral sur-

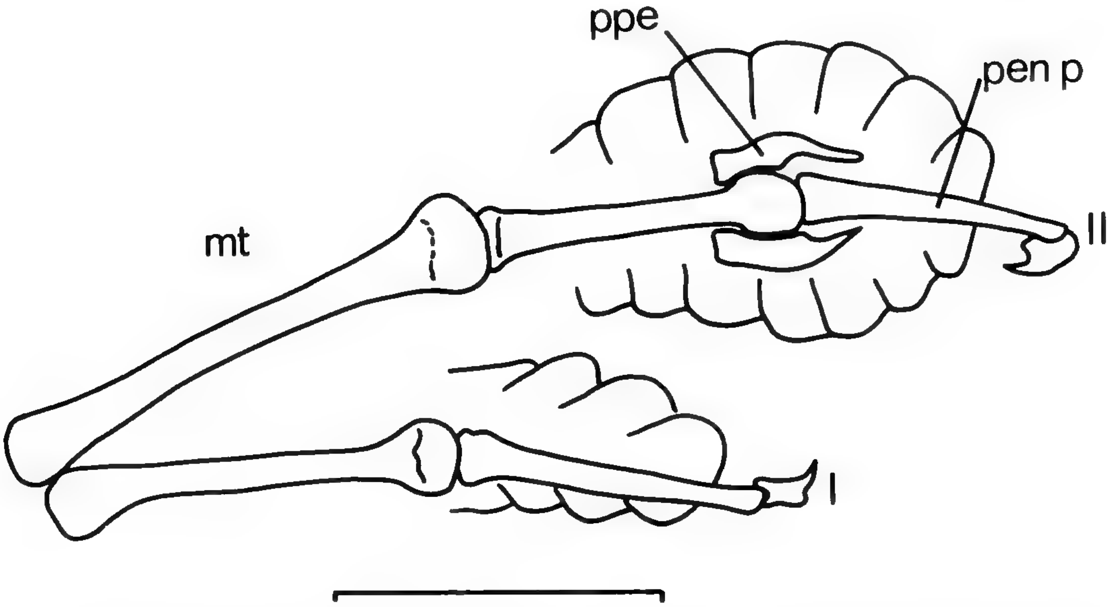


FIG. 9. Dorsal view of the skeletons and pad outlines of the first and second digits, left pes of *Cosymbotus platyurus*. In the second digit the greatest expansion of the pad occurs beneath the penultimate phalanx and this can be hyperextended on the first phalanx. In the first digit hyperextension is limited to the metatarsophalangeal joint. Drawn from a cleared-and- stained specimen - CAS 18565. Scale bar = 2mm. Abbreviations: mt, metatarsal; pen.p, penultimate phalanx; ppe, paraphalangeal element; I, II, digits one and two.

face of each digit is free to contact the locomotor substratum.

The gekkonine genera *Afroedura* and *Calodactylodes* represent a continuation of a morphotypic series begun by *Phyllodactylus* (Russell and Bauer, 1989). Here the scansors are more elaborate. The terminal pair of leaf-like scansors has been augmented by more proximal plates. While these plates are not as fully demarcated as the distalmost pair, they are quite distinct from the more proximal scales and bear distinct fields of setae (Fig. 14). Digits II - V exhibit this proximal encroachment of the adhesive apparatus. The digits are without inflection and digit IV is considerably divergent from digit III. As has been pointed out elsewhere (Russell, 1979), the proximal sets of scansors are controlled by a different musculotendinous complex than the distalmost ones.

Digit I has much less scope for the proximal elaboration of scansors (Fig. 15). The terminal pair of scansors is still well- developed, but the more proximal ones are much less prominent than those of the other digits (Figs. 14, 15). The more proximal scansors of digit I are present beneath the raised component of the first phalanx, but there is little in the way of a free portion of the digit for the incorporation of a more elaborate pad. The claw is still prominent on digit I (Fig. 15) and in all digits the more proximal scansors are located proximal to the ungual joint, beneath the raised portion of the penultimate phalanx.

Based upon the scenario outlined by Russell (1979) which suggests that distally originating scansors migrate proximally in their extent, the next example in the proposed morphotypic series can be taken from *Aristelliger*. Here the second to fifth digits have broadly expanded series of scansors beneath the proximal part of the penultimate phalanx and the distal part of the next most proximal one (Fig. 16). More proximal still there is a free basal portion to each digit, and the penultimate phalanx and claw are carried free beyond the distal end of the pad (Fig. 16). In digit I, however, the more proximal part of the pad is only incipiently developed (Fig. 17), while a single, asymmetrically disposed leaf-like plate remains present distally. Digit I remains clawed but has no free distal portion and remains much less distinctly pad-bearing than the other digits

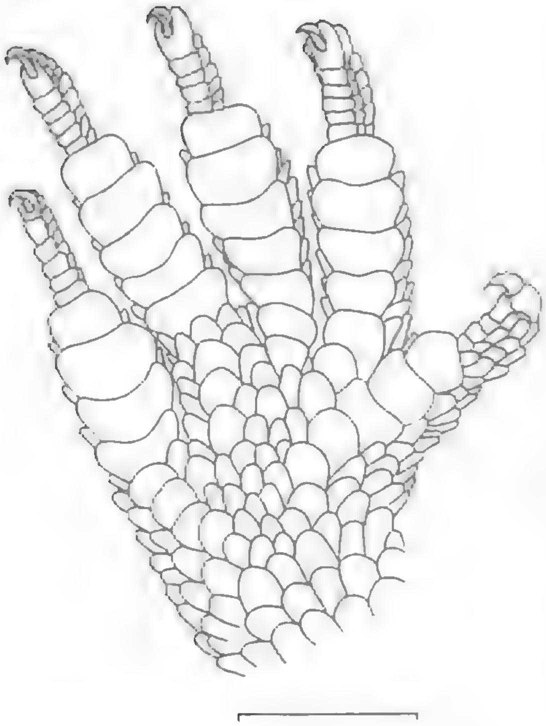


FIG. 10. Ventral aspect of the right pes of *Dravidogecko anamallensis* (BM(NH) 82.5.22.79). Note the undivided nature of the scansors and the basal friction plates/scansors on digit I. Scale bar = 2mm.

(Fig. 16). Terminal, leaf-like pads are no longer evident on digits II - V.

Beyond this situation a number of groups have modified the first digit in a variety of ways. In the *Gekko* group the nominal genus bears a strongly padded first digit, the pad being expanded in the same manner as that of the other digits (Fig. 18). Examination of foot structure reveals, however, that digits II - V are strongly clawed while digit I is clawless. Internally digit I can be seen to possess an elongate distalmost phalanx, and it is beneath this that the pad is positioned (Fig. 19). Thus, the distalmost phalanx may be hyperextended on the first phalanx of this digit, and the internal control mechanism is the same as that for the other digits (Russell, 1975).

Within the genus *Gehyra* a similar situation obtains in some cases, with divided scansors being borne on the first digit (Figs. 20, 21). Some species of *Gehyra* exhibit a somewhat intermediate stage in which the claw is still evident but small and needle-like (Fig. 22). The distalmost phalanx is somewhat elongate and the pad is partially expanded. Other genera in this assemblage that exhibit a clawless or minutely clawed first digit with an expanded pad are *Lepidodactylus*, *Luperosaurus*, *Pseudogekko* and *Ptychozoon*.

Some genera belonging to the *Gekko* group (sensu Russell, 1972) do not, however, exhibit elongation of the distalmost phalanx and loss of the functional claw in digit I. In both *Hemiphyllodactylus* and *Perochirus* the first digit remains small and unexpanded. In *Hemiphyllodactylus* the first digit of both the manus and pes is minute but clawed, and pads are not evident. In *Perochirus* the pollex is rudimentary and clawless (Fig. 23), while the hallux is rudimentary but bears a claw (Fig. 24). The digits of *Perochirus*, except for the first, are widely expanded (Figs. 23, 24). The first digit has essentially been suppressed by the second and does not form a functional pad.

The *Ailuronyx* group includes the nominal genus plus *Phelsuma*, *Lygodactylus*, *Microscalabotes* and *Millotisaurus*. Only in *Ailuronyx* is the first digit expanded and pad-bearing. There are relatively few scansors but the digit is

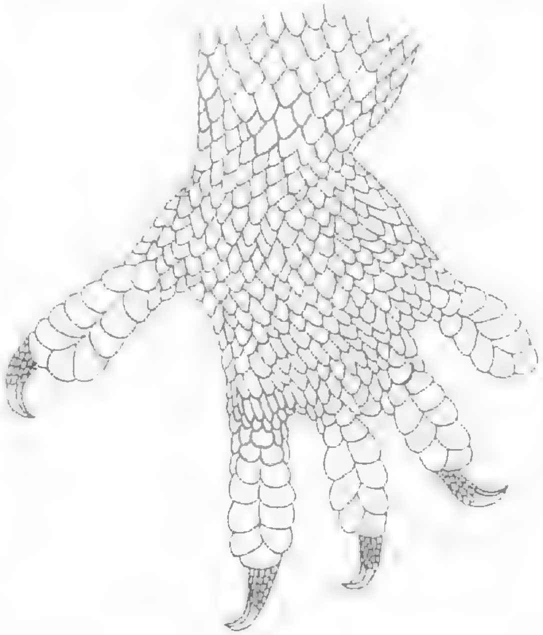


FIG. 11. Ventral view of the pes of *Briba brasiliana*. Redrawn from Amaral (1937). The first digit lacks a claw and the free portion of the pad is enhanced by incorporation of the ungual phalanx into it.

FIG. 12. Ventral view of the left pes of *Phyllodactylus porphyreus*. CAS 167593. Note the terminal, leaf-like scansors on each digit and the broad plates borne more proximally.

FIG. 13. Ventral aspect of digit I, left pes of *Phyllodactylus porphyreus*. CAS 167593.

FIG. 14. Ventral view of the left pes of *Afroedura hawaquensis*. CAS 167638. Proximal encroachment of scansors on digits II - V is evident.

FIG. 15. Ventral aspect of the left hallux of *Afroeaura hawaquensis*. CAS 167638. The proximal setose plates remain poorly differentiated.

FIG. 16. The left pes of *Aristelliger praesignis* in ventral view. The adhesive pads on digits II - V are well-developed, but digit I lacks this differentiation. Uncatalogued specimen.

FIG. 17. Ventral view of the left hallux of *Aristelliger praesignis*. The single, terminal leaf-like scansor is evident distally (demarcated by an asterisk - *). The claw (arrow) lies to the medial side of the terminal plate.

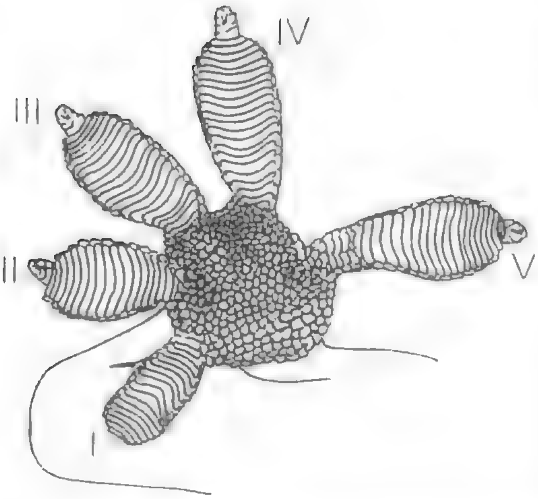


FIG. 18. Ventral view of the left pes of *Gekko gecko*. Note the broadly expanded pad on digit I and the absence of a claw from this digit. Abbreviations: I - V, digits one to five.

clawed, although the penultimate phalanx is not raised. The pad on digit I of the manus is relatively narrow, while that on the pes is slightly wider but still considerably narrower than the pads on the other digits. The entire padded portion of digit I is free.

In all other genera of this putative assemblage the first digit is greatly reduced in size. In *Phelsuma* it is minutely clawed, and only friction plates are present ventrally (Figs. 25, 26). The other digits bear widely expanded pads and the claws are reduced (Fig. 25). Functionally and proportionally digit I is similar to the pollex of *Perochirus* (Fig. 23). Similarly, in *Lygodactylus* and *Microscalabotes* (Fig. 27) the first digit is markedly reduced in size, although here it remains prominently clawed. In *Millotisaurus* the pollex is essentially absent (Pasteur, 1964, Plate 1) and the distalmost (ungual) phalanx is absent. The hallux is small, clawed and of much the same form as that of *Microscalabotes* (Fig. 27).

In contrast to the cases of reduction in size of the first digit or expansion of the pad by virtue of elongation of the distalmost phalanx, as outlined above, the *Pachydactylus* group is characterised by a rather prominent digit I. Here there is a relatively long free basal portion capped, in those species not showing reduction of the adhesive apparatus, with an expanded pad. In all genera included within the *Pachydactylus* group (*Pachydactylus, Rhoptropus, Colopus, Chondrodactylus, Kaokogecko, Palmatogecko, Tarentola* and *Geckonia*) there is a hyperphalangy of the first digit, with the phalangeal formula being 3-3-4-5-3/3-3-4-5-4. Thus, in combination with clawlessness of the first digit (or the possession of needle-like elongate claws) the distal two phalanges of the pollex and hallux may be hyperextended while the stoutly developed proximalmost phalanx remains as a stable base for the digit, with friction plates beneath (Fig. 28). Friction plates are also present at the bases of the other digits (Fig. 28). When not climbing, members of the *Pachydactylus* group walk on the bases of their digits with the distal ends held in a permanently hyperextended position. Even in situations where the pads are reduced in size (Figs. 29, 30, 31) the first digit remains relatively long, with the remnant of the pad being displaced distally.

In the genus *Homopholis* (Fig. 32) the claw of digit I is needle-like and elongate and the pad is relatively strongly dilated. The condition in the manus and pes is not identical, however. The pollex (Fig. 32) exhibits hyperphalangy similar to the situation outlined for the *Pachydactylus* group (above) while the hallux has the normal compliment of two phalanges, but with the distal one being elongated to support the pad. The latter condition is similar to that found in *Gekko* (see above). Thus in *Homopholis* two independent

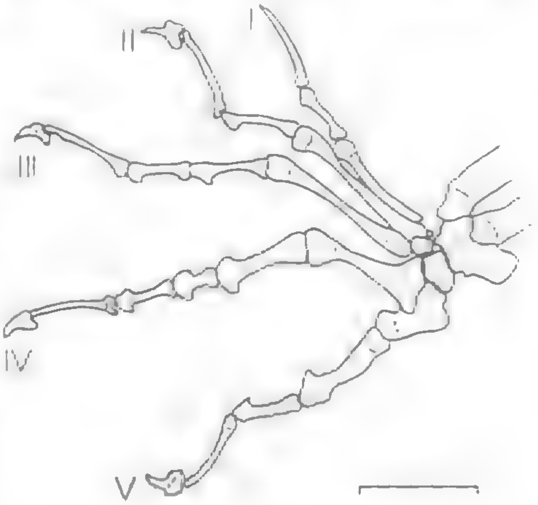
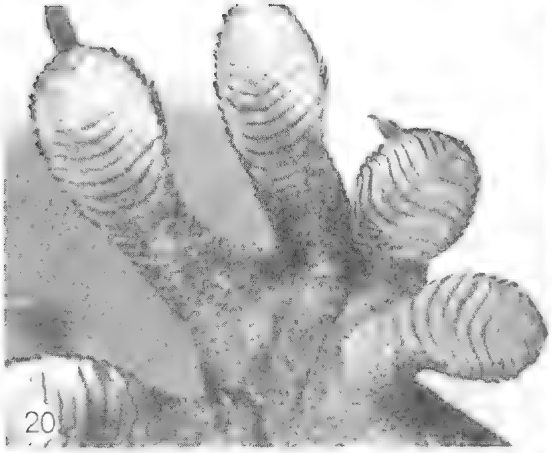
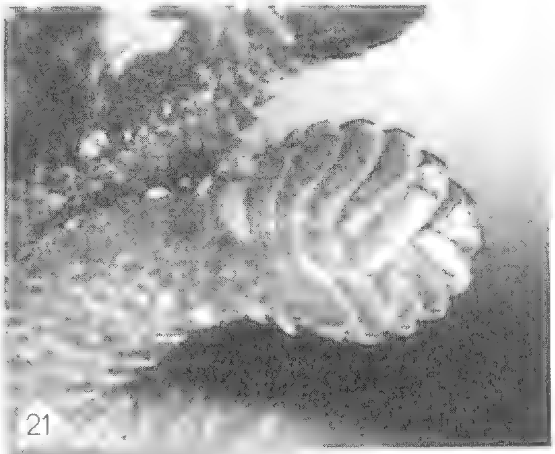
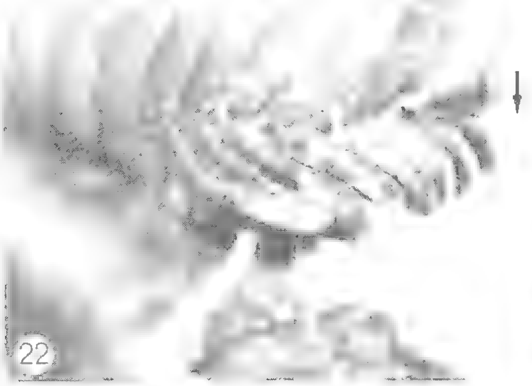


FIG. 19. Dorsal view of the skeleton of the right pes of *Gekko gecko*. Note the elongated terminal phalanx on digit I. Compare this figure to Fig. 1. Abbreviations: I - V, digits one to five.







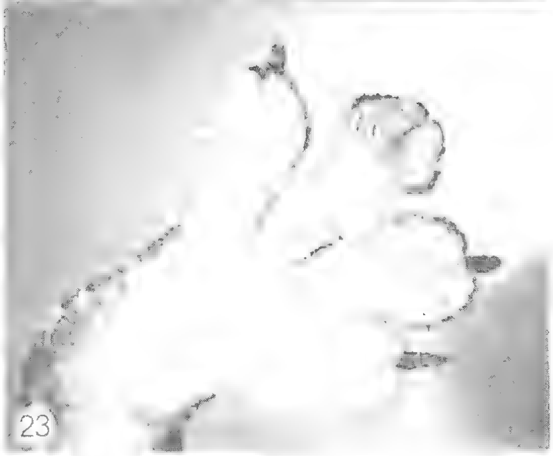


FIG. 20. Ventral view of the right pes of *Gehyra oceanica* (CAS 159706).

Fig. 21. Ventral view of the left hallux of *Gehyra punctata* (APR 48).

FIG. 22. Ventral aspect of digit I, left pes of *Gehyra interstitialis* (CAS 89686). Note the minute claw visible distally (arrow).

FIG. 23. Ventral view of the right manus of *Perochirus ateles* (CAS 159768). The pollex lacks a claw.

FIG. 24. Ventral view of the left pes of *Perochirus ateles* (CAS 159768). The hallux bears a claw.

solutions to the operation of a functional pad on the first digit have occurred, one in the manus and one in the pes. The genus *Geckolepis* was included within the *Homopholis* group by Russell (1972). Members of this taxon bear a needle-like claw on both the pollex and hallux, associated with a distally elaborated pad (Figs. 33, 34). In this genus both the manus and pes exhibit elongation of the terminal phalanx of digit I, similar to that found in the hallux of *Homopholis*.

The final group to be considered is the

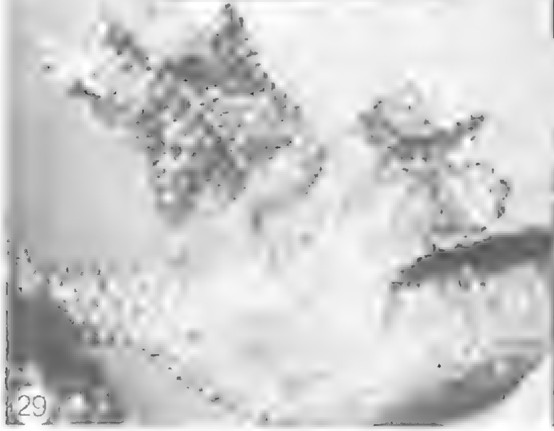


FIG. 25. The left pes of *Phelsuma sundbergi* (CAS 167553) in ventral view. Note the small size of digit I and the friction plates at its base.

FIG. 26. The hallux of *Phelsuma sundbergi* (CAS 167553) in ventral view. A minute claw is still evident.

FIG. 27. The first and second digits of the left pes of *Microscalabotes bivittis* (CAS 126289) in ventral view. The hallux is extremely small.

FIG. 28. Ventral view of the right pes of *Rhoptropus bradfieldi* (CAS167673). The pad on digit I is prominent.

FIG. 29. Ventral aspect of the right pes of *Pachydactylus maculatus* (CAS 167613).

FIG. 30. The hallux of *Geckonia chazaliae* (CAS 134579) in ventral view. Although the pad is reduced this digit is still relatively long.

FIG. 31. Ventral aspect of the right pes of *Pachydactylus kochi* (CAS 126170). The pads are greatly reduced but all digits remain long.

FIG. 32. Ventral view of the right manus of *Homopholis wahlbergi* (TM 57464).

FIG. 33. The right pes of *Geckolepis maculatus* (CAS 156886) in ventral view. The hallux is to the extreme right.

FIG. 34. Ventral aspect of the right hallux of *Geckolepis maculatus* (CAS 156886).

Thecadactylus group (*Thecadactylus*, *Bogertia* and *Phyllopezus*) of South America. In *Phyllopezus* digit I has a prominent claw and a free terminal phalanx, but only unexpanded friction plates at the base of the digit. In appearance the pollex and hallux are similar to those of *Aristelliger* (Fig. 16), but without the asymmetrically placed terminal leaf-like scansor. The remaining digits bear broadly expanded pads. In the closely related *Bogertia* the first digit is minute and the claw small (Fig. 35), while the remainder of the digits are broadly expanded. In *Thecadactylus* the claw on digit I, as on all other digits, is drawn up into a sulcus and scansors are present in two distinct rows. Digit I is strongly developed, broadly expanded and the penultimate phalanx is long and permits hyperextension at the metacarpophalangeal/metatarsophalangeal joint. The incorporation of a sulcus for the claw of digit I has permitted distal extension of the pad on this digit.

THE GENUS *ANOLIS* – AN INDEPENDENT TEST CASE

Other than gekkonid lizards, the group that exhibits the greatest development of a subdigital adhesive apparatus is the iguanid *Anolis* and its immediate allies (Peterson, 1983a,b). Here pads appear to have been developed beneath digital inflections, with the scansors being derived from friction plates beneath the digital inflections (see Peterson, 1983a, fig. 5 for a comparative illustration of this between the primitive anoline

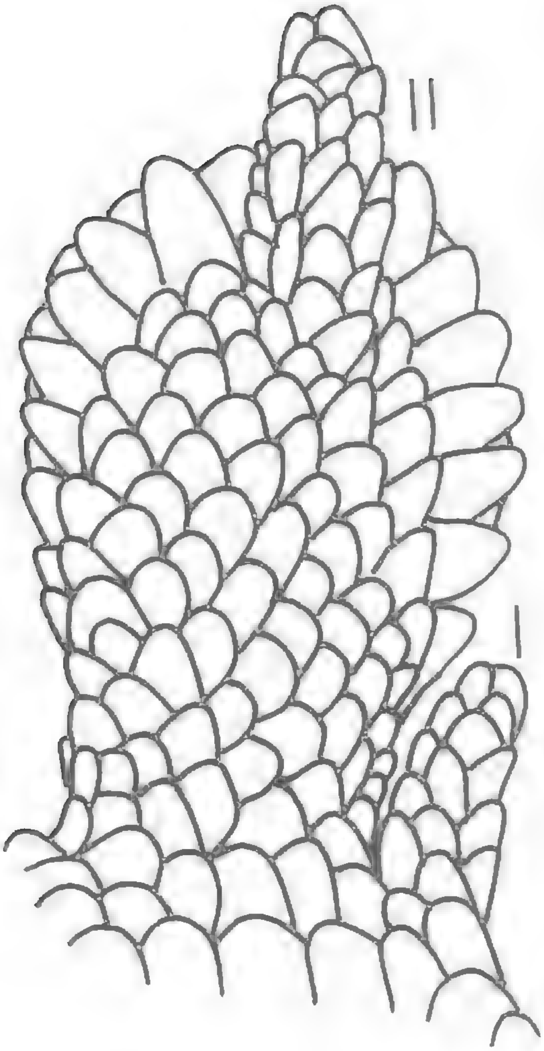


FIG. 35. Dorsal view of digits I and II of *Bogertia lutzae*. Redrawn from Vanzolini (1968b).

Chamaelinorops and the pedally derived *Anolis occultus*). An examination of digit I in this assemblage will be instructive in placing the observations on gekkonines into perspective.

In *Anolis* (Fig. 36) digit I lacks a pad but bears enlarged friction plates basally. The remainder of the digit is held out of contact with the substrate and the claw contacts the locomotor surface distally. All other digits bear similar friction plates proximally but have adhesive pads located more distally at the region of the junction of the penultimate and antepenultimate phalanges. Thus, as in many gekkonine geckos, the first digit lacks a pad and is not functionally a part of the adhesive apparatus.

DISCUSSION

The results presented above indicate a great deal of variability in the structure of the first digit of gekkonine geckos. Such variability may be correlated with functional constraints. With the inception of the hyperextension mechanism of pad control (Russell, 1975) the mode of operation of the feet during locomotion changed. No longer is the majority of locomotor thrust developed as the foot rolls onto its mesial border and makes contact at the metatarsophalangeal line. The adhesive apparatus has brought along with it a re-establishment of pedal symmetry in many groups of gekkonines and has dictated that thrust is generated in a different way (Russell, 1975). The metatarsophalangeal/metacarpophalangeal area is no longer the primary site

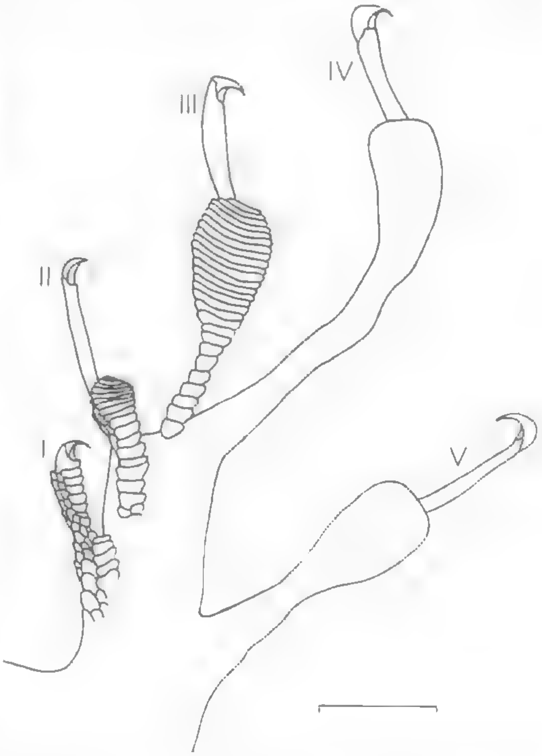


FIG. 36. Ventral view of the left pes of *Anolis garmani* (APR 257) showing the digital proportions and the pads on digits II - V. Digit I bears only friction plates at its base, similar to those at the bases of the other digits (illustrated for digits II and III). Scale bar = 5mm.

of application of thrust to the substratum in pad-bearing gekkonines and the digits play a greater role in providing fixed areas of attachment over which the body moves. Protection of the adhesive apparatus also dictates the way in which locomotion can be brought about (Russell, 1975).

The fundamental asymmetry of the lizard foot resulted in only two phalanges being incorporated into the first digit. This condition is retained in pad-bearing gekkonines and thus places restrictions on the incorporation of an adhesive pad into this digit. This has resulted in either the omission of an adhesive system from this digit, or modifications of it such that an adhesive apparatus can be incorporated.

The perceived possibilities of digit I evolution in gekkonines are outlined in Fig. 57. Beginning from the primitively padless condition digits may remain flat or may develop inflections to assist in climbing. In either of these circumstances pads may develop. In the case of the former they initially develop distally, while in inflected digits they develop basally. The *Hemidactylus* group appears to have developed pads in a basal position from a morphotypic ancestral state such as that exemplified in the genus *Cyrtodactylus*. As digit I bears only two phalanges, no inflection is present within the digit. Hence, any enlarged scansor-like plates that develop do so beneath the distal portion of the penultimate phalanx. Constraints of digital form dictate that the pad remains relatively rudimentary. The alternate solution is to elongate the pad by losing the claw and elongating the distalmost phalanx. This provides more support to the pad and permits it to extend distally. This condition is found in *Briba*, although the pollex and hallux are not greatly elaborated in this genus.

The simplest situation found in distally derived pads is that exemplified by the genus *Phyllodactylus*. Here each digit bears a single pair of terminal, leaf-like scansors that are associated with the distalmost digital joint. The plates on each pair of digits are equally developed and the digits remain essentially flat. One form of elaboration of this pattern is to subdivide the distal plates but to not extend the adhesive apparatus any further proximally along the digit. Such a situation is seen in the genera *Ptyodactylus* and *Uroplatus* and the adhesive apparatus on digit I is as well-developed as it is on the other digits.

The other means of elaborating the adhesive apparatus that is seen in the Gekkoninae is to permit it to encroach onto the proximal regions of the digit. This is more feasible for digits II - V than it is for digit I. Thus in genera such as *Afroedura*, where this occurs, the pads become further elaborated on all but the pollex and hallux where they remain essentially terminal. This trend is continued in genera such as *Aristelliger* where digits II - V develop elaborate, multiscansorial pads. In this genus, however, pad development on digit I is suppressed and proximal elaboration does not occur.

The internal digital structure in the *Gekko* group is more complex than that in *Aristelliger*, but if the claw is retained on digit I as a free and independently controllable structure, then elaboration of a pad on digit I is suppressed. Such a situation is seen in genera such as *Hemiphyllodactylus* and *Perochirus*. Some members of the *Gekko* group have developed an enlarged pad on digit I, but this has come at the cost of a freely controllable claw on this digit. Thus, in *Gekko* the distalmost phalanx of digit I has become elongate and supports the elaborated and enlarged pad. In essence these two choices have been adopted by members of the *Ailuronyx* group also. In *Ailuronyx* the first digit is moderately well padded and retains its claw although this is not held free of the pad. In *Phelsuma* and *Lygodactylus* and its relatives the pad on the first digit is suppressed.

An alternative solution to the maintenance of a well-developed pad on digit I is found in the *Pachydactylus* group. Here, instead of the distalmost phalanx becoming elongated, an additional phalanx has been incorporated resulting in hyperphalangy in digit I. The genus *Homopholis* has employed both solutions, being hyperphalangic in the pollex and having an elongate distalmost phalanx in the hallux.

Yet another solution is seen in the genus *Thecadactylus*. Here the claw is retracted into a sulcus, in digit I as well as the other digits, allowing the pad to become elaborated distally without hindrance from the claw.

The situation seen in *Anolis* illustrates that the problem of elaborating a pad on the first digit exists outside of the family Gekkonidae. Here the constraints of only two phalanges have resulted in this digit lacking the development of a subdigital adhesive pad. Thus, although theoretically all digits may be thought of as possessing approximately the same potential in terms of evolutionary modification, limitations occur that are imposed by functional demands. The same problem has manifested itself in essentially the same way in the Gekkonidae and the

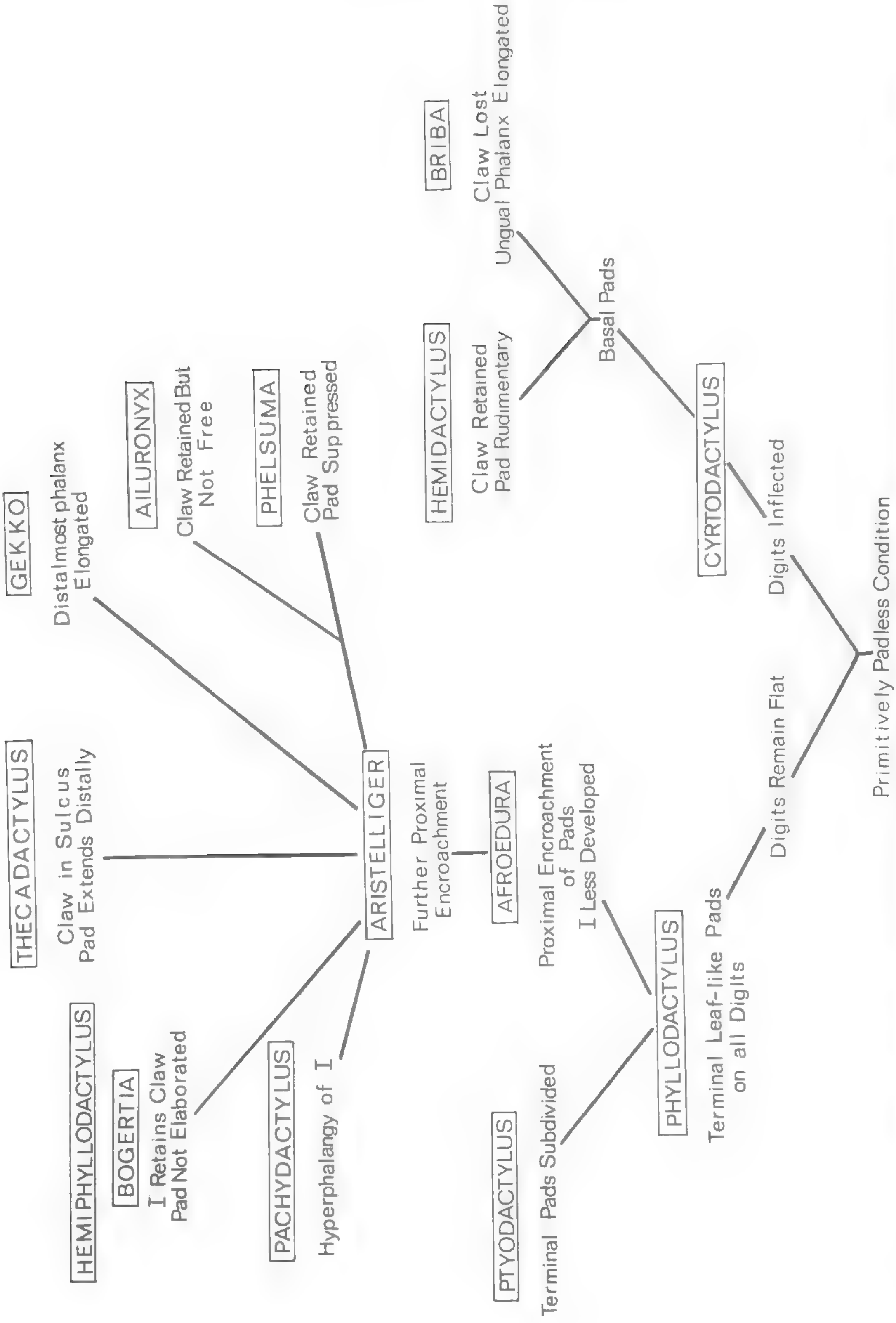


FIG. 37. Summary diagram of perceived trends in the evolution of digit I in gekkonine geckos. The genera indicated are used as examples of particular morphotypes and the scheme should not be interpreted as a phylogeny.

Iguanidae. Within the Gekkonidae similar trends are seen in the diplodactyline geckos, a radiation parallel to that of the Gekkoninae but restricted to the Australasian region (Kluge, 1967a,b; Bauer, 1986). In *Diplodactylus* digits morphologically very similar to those of *Phyllodactylus* (see above) are present and a single pair of terminal leaf-like plates is present on all digits. Modifications of this pattern are also evident in the satellite genera *Crenadactylus* and *Rhynchoedura*. In the closely related *Oedura* proximal elaboration of the pads is seen in digits II - V in a fashion very similar to that seen in *Afroedura* (see above). In digit I, however, proximal encroachment of scansors is much less marked, again paralleling the situation seen in *Afroedura*. In the tribe Carphodactylini the simplest pads are seen in the genus *Naultinus*. Here digits II - V bear pads consisting of multiple scansors beyond which is a free, clawed distal portion of the digit. Digit I retains its claw and lacks a definitive pad, there being only friction pads at the base of this digit. Distally there is an asymmetrical, leaf-like pad similar to that seen in *Aristelliger* (see above). A similar situation obtains in *Hoplodactylus* although the pads on digits II - V are somewhat broader. Digit I bears an asymmetrical, leaf-like pad very much like that of *Naultinus*. The genera *Rhacodactylus, Bavayia* and *Eurydactylodes* bear more elaborate pads on digits II -V but digit I remains much less expanded and again retains the terminal, leaf-like plate (Bauer, 1986). In all of these genera the claw is retained on the pollex and hallux, and the incipient pad at the base of digit I is not expanded. Thus again, although those digits with a free basal portion have elaborated substantial pads, the inherent limitations in the design of digit I have suppressed such an expression here. The genus *Pseudothecadactylus*, now subsumed as part of *Rhacodactylus* (Bauer, 1986) has divided scansors on digits II - V somewhat reminiscent of those of *Thecadactylus*, with the claw at least partially recessed into a sulcus between the rows of scansorial plates. Digit I lacks a claw and the possession of a sulcus has permitted distal extension of the pad, again similar to the situation seen in *Thecadactylus*. Thus *Pseudothecadactylus* has a pad on digit I that is much more extensively elaborated than that in any other carphodactylines and is constructed on similar lines to the first digit of the gekkonine *Thecadactylus*.

The discovery of constraints and limitations in morphology (Zweers, 1979) gives us some insight into why things are the way they are (Seilacher, 1970). The repetition of pattern in different evolutionary lineages serves to reciprocally illuminate the concepts being postulated. In the above example the constraints placed upon the first digit of lizards by virtue of its inherent design have had a strong influence in the elaboration of the adhesive apparatus in gekkonid lizards. This in turn has had, presumably, some effect on the locomotor mechanics of pad-bearing geckos, ,with different selective factors being influential in the particular outcome in a given set of ecological circumstances. In questions such as this, however, our background information is still woefully inadequate to attempt to assess what these influences might be.

In almost all groups of lizards trends towards limb reduction are evident (Gasc and Renous, 1976), and in these cases digital reduction is a progressive and essentially symmetrical event (Lande, 1978; Raynaud, 1985). In some lacertilians, however, there are patterns of digital reduction that occur independently of those of entire limb reduction and that are associated with quite different locomotor modifications. In the agamid genus *Sitana*, for example, the fifth digit of the pes is lost (Russell and Rewcastle, 1979) while the other digits remain seemingly unaffected. A similar reduction is present in the teiid *Teius* (Presch, 1970). The standard models that have been proposed to account for digital reduction (Raynaud, 1977; Lande, 1978) have assumed an equal functional importance for all digits. In both *Sitana* (Russell and Rewcastle, 1979) and in a variety of gekkonine geckos this cannot be assumed to be the case, however. Indeed, the various trends towards simplification and reduction of the pollex and hallux in gekkonine geckos, as outlined above, can be directly associated with proposed functional constraints that place a different set of selective pressures on digit I than they do on the other digits.

Thus in gekkonines there are trends to both elaboration and reduction of the first digit in association with the acquisition of a setal adhesive apparatus. This in itself is instructive as it indicates to us that there are a variety of ways to achieve a functional adhesive system. In the case of the lack of incorporation of digit I into this system one can invoke Underwood's (1976) distinction between simplification (reduction in the complexity of structure without loss of full anatomical and histological differentiation) and degeneration (reduction with loss of precise differentiation). The distinction is not always sharp, but Underwood (1976) stated further that simplification is involved with modification of function without a break in continuity of function, while degeneration is associated with reduction or loss of original function. In this context the reduction of digit I in a variety of gekkonines is probably best categorised as simplification, with sufficient of its structure remaining to permit a variety of already extant anatomical relationships to persist. In no case is the entire complement of components of digit I lost, even if its external manifestation becomes negligible.

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OEDURA AND *AFROEDURA* (REPTILIA: GEKKONIDAE) REVISITED. SIMILARITIES OF DIGITAL DESIGN, AND CONSTRAINTS ON THE DEVELOPMENT OF MULTISCANSORIAL SUBDIGITAL PADS?

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The gekkonid genera *Oedura* (Diplodactylinae) and *Afroedura* (Gekkoninae) possess digits that are very similar in external morphology. These are characterised by the possession of a large, terminal pair of leaf-like scansors and a series of scansor-like plates that gradually grade into the scales of the digital bases. Such genera appear to have developed an elaborate subdigital adhesive system by encroachment of the scansorial system proximally. The genera *Diplodactylus* and *Phyllodactylus* provide potential morphotypic precursors of the digital form seen in *Oedura* and *Afroedura* respectively.

Proximal encroachment of the adhesive system involves changes in external morphology, the internal muscular and tendon systems and the integument. In both *Afroedura* and *Oedura* the perceived elaboration of the adhesive system from an external perspective is not tracked exactly by internal changes. Not all of the plates that become enlarged and hypertrophied are converted into true scansors — structures that possess some form of internal hydraulic support system in association with musculotendinous control systems and a seta-bearing integument. Only those plates that occur beneath the arcuate penultimate phalanx become elaborated into true scansors.

The genera *Oedura* and *Afroedura* may both represent independent trends towards the elaboration of multiscansorial pads. They can be employed to represent a stage in a morphotypic series towards this end, but lack the features found in multiscansorial systems, such as subdivision of both the scansors and associated sinus system beneath the penultimate phalanx, overlap of scansors, and the development of a free margin on the scansors. The development of such features may operate as constraints on the evolutionary elaboration of multiscansorial pads. ☐ *Gekkonidae, Oedura, Afroedura, digits, scansors, functional morphology, evolutionary constraint.*

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The similarity of digital form in the diplodactyline genus *Oedura* and the gekkonine genus *Afroedura* was at one time thought to be of sufficient significance to unite these taxa in a single genus (Boulenger, 1888), notwithstanding their great geographic separation. Not until much later (Loveridge, 1944) was this congeneric status seriously questioned, and here certain external digital features were employed to advocate separation. Further credence was given to the separation of these two taxa as the systematics of gekkonid lizards became better known (Underwood, 1954) and different sets of characters became employed. This led to a further evaluation of their status (Cogger, 1964) and the examination of a wide array of anatomical systems. Thus, Cogger (1964) ably demonstrated that similarities between *Oedura* and *Afroedura* were due to convergence and brought into focus questions about why such overt similarities should be so. Despite the subsequent unequivocal systematic separation of gekkonine and diplodactyline geckos (Kluge, 1967a, b), however, the basis for such similarity has remained largely unstudied. A brief attempt at addressing this question was made by Russell (1979), but the consequences of particular digital design in these two genera were only partially pursued, and the potential constraints on further elaboration of this particular design remained largely unaddressed.

It was proposed by Russell (1979) that the digital pattern seen in *Oedura* has been developed from a condition similar to that seen in the ostensibly closely related genus *Diplodactylus* and its satellite genera *Crenadactylus* and *Rhynchoedura*. (see King, 1987, however, for an alternative but less traditional view that *Oedura* is a carphodactyline). The basis of this proposed evolutionary trend was that the simple, single pair of terminal, leaf-like scansors of *Diplodactylus* and its satellite genera had become modified into a more elaborate system by proximal recruitment of additional adhesive plates. Some species of *Diplodactylus*, such as *D. strophurus* and *D. ciliaris* possess what appear to be more proximally located incipient scansors on digits two to five, and it was proposed (Russell, 1979) that such structures were the morphological precursors of the more proximal enlarged plates in *Oedura*. Only the latter genus within the Diplodactylini possesses an adhesive system incorporating more than a single pair of scansors per digit.

Within the Gekkoninae the genus *Afroedura* possesses digits that are externally similar in form to those of *Oedura*. Given what is known about the phylogeny of the Diplodactylinae (Bauer, 1986) and Gekkoninae (Kluge, 1967b, 1983) the digital patterns of these two genera appear to have been independently evolved, with that of *Afroedura* being derived from a *Phyllodactylus*-like ancestor (Russell, 1972; Russell and Bauer, 1989). The similarity is not merely superficial, however, but also involves certain aspects of the internal control mechanisms of the seta-bearing plates (Russell, 1979). Such similarity is worthy of further scrutiny, as the independent development of very similar systems by distantly related taxa is indicative not only of similar selective pressures but also of the constraints that potentially govern the final form that systems will take. In this context we may initially assume that the behavioural component of the organism - environment interaction (Bock and von Wahlert, 1965) has played a major role in influencing the morphological parameters of the system, the major dictates being the way in which subdigital setae can be employed as effective agents of adhesion (Russell, 1975).

Morphological systems consist of integrated sets of components that must operate together if the entire system is to function (Alexander, 1975; Zweers, 1979). In the case of subdigital adhesive systems, a variety of functional and control criteria appear to be directly correlated with the evolution of such systems in gekkonids (Russell 1975, 1976, 1981, 1986). The genera *Oedura* and *Afroedura* provide an instructive example of how canalisation (sensu Brundin, 1968) of the evolution of morphological features is involved in the elaboration of a system. Given a particular basic morphology and a particular 'problem' to be 'solved', there is only a limited amount of scope available within a given phylogenetic lineage.

The recognition of such a great degree of digital similarity between *Oedura* and *Afroedura* gives cause to pose questions about the functional reasons for such convergence. It also prompts investigation about the evolution of the system in each lineage and the potential that the increased complexity of the system has. Thus, we have here employed these two genera in order to analyse the basic features of the mechanical components (Gans, 1969) employed by each and to attempt to make some predictions about the integration of components in the evolution of digital adhesive mechanisms in gekkonids.

Taking the digits of *Oedura* and *Afroedura* as examples, we initially postulate that the adhesive systems evolved from conditions similar to those in the supposed outgroups, *Diplodactylus* and *Phyllodactylus* respectively. Here a single pair of leaf-like scansors, a means of hyperextension of the digits and the possession of a device for conforming the existing scansors to the substratum is present. Assuming that more proximal scansors are evolutionarily governed by the same functional concerns, the following predictions can be made about their elaboration from ancestrally simpler structures (subdigital scales).

(i) More scales will be added to the system in a sequential manner, from distal to proximal, and these will become modified into scansors. Thus, the distalmost of the newly acquired plates will be the most elaborate and will grade into more proximal plates that are barely distinguishable from scales, and finally into scales themselves. True scansors will be recognisable by a combination of discrete characteristics.

(ii)The elaboration of additional scansors will be associated with the elaboration of a muscular control system. Means of application of the scansors to the substratum and removal of the scansors therefrom will be associated with specific musculotendinous networks. There may not, however, be a direct and exact correlation of the recruitment of true scansors, the elaboration of setal fields, and the differentiation of the muscular control systems and their tendinous networks. Thus, true scansors and subdigital lamellae should be distinguishable from each other on anatomical and histological grounds.

MATERIALS AND METHODS

Gross morphological, internal anatomical and histological features of digits of the genera *Oedura* and *Afroedura* were examined and compared with each other and with similar features of *Diplodactylus* and *Phyllodactylus*. Dissection material and that for histological investigation was obtained from collections housed at the Australian Museum, British Museum (Natural History), California Academy of Sciences and the Transvaal Museum. The chief histological procedures employed were haematoxylin and eosin, Milligan's trichrome and Mallory's azan, protocols for which may be found in Humason (1979). Dissection and external examination was carried out on *Oedura castelnaui*, *O. coggeri*, *O lesueurii*, *O. marmorata*, *O. ocellata*. *O. robusta*. *O. tryoni*, *Afroedura karroica*, *A. hawaquensis*. *A. nivaria*, *A. pondolia*, *A. tembulica* and *A. transvaalica*, as well as on a variety of species of *Diplodactylus* and *Phyllodactylus*. Histological examination was conducted on *Oedura marmorata*. *O. monilis*, *O. tryoni*, *Afroedura africana*, *Diplodactylus strophurus* and *Ebenavia inunguis* (a satellite genus of *Phyllodactylus*).

RESULTS

GROSS EXTERNAL MORPHOLOGY

The digits of both *Phyllodactylus porphyreus* (Fig. 1) and *Diplodactylus strophurus* (Fig. 2) are similar in external form in that they are free, relatively flat throughout their length and bear a pair of expanded, leaf-like plates at the distal end. These plates are disposed symmetrically about the claw and their bases are coincident with the articulation between the ungual and penultimate phalanx. The scales on the ventral surface of the digit are broadly expanded and extend back far proximally on the digit, but show no tendency to division or to becoming setose in any macroscopically visible sense.

In both *Afroedura* (Fig. 3) and *Oedura* (Fig. 4) the digits are also essentially flat and they each bear a pair of enlarged terminal, leaf-like plates similar to those of *Phyllodactylus* and *Diplodactylus* (Figs. 1,2). More proximally, however, further series of enlarged plates are present that are both divided and setose (Figs. 3,4,5,6). These plates are borne proximal to the distalmost digital joint and are, therefore placed beneath the penultimate and preceding phalanges. Their number varies from digit to digit in *Oedura* (Fig. 4), with the longer digits having the greater number of elaborated plates. In *Oedura marmorata*, for example, there are three pairs of more proximal divided plates on digit two of the pes, four pairs on digits three and four, and three pairs on digit five. Digit one bears no additional divided plates (Fig. 4). Proximal to the divided plates a short series of gradually diminishing undivided plates merges with the plantar scales. The extent of the setose, more proximal divided plates is less marked in *Afroedura* in general (Fig. 3), with an additional one or two plates located on digits two to five (Onderstall, 1984). The basic arrangement is very similar to that found in *Oedura*, however, including a lack of elaboration of further divided plates on the first digit. As in *Oedura*, the more proximal scales of the digits gradually diminish in size (Fig. 3) and merge with the plantar scales (Onderstall, 1984: Fig. 6).

In both *Afroedura* (Fig. 3) and *Oedura* (Fig. 4) there is a tendency for the second pair (counting from distal to proximal) of additional divided plates to be more broadly expanded and to exhibit greater lateromesial separation than the others. This is consistent in all digits and represents a position at the base of the penultimate phalanx (see below).

INTERNAL GROSS ANATOMY OF THE DIGITS.

In both *Phyllodactylus* (Fig. 7) and *Diplodactylus* (Fig. 8), the internal morphology of the digits is relatively simple. In both, the intermediate phalanges are short, depressed and crescentic distally, this being associated with the process of hyperextension (Russell 1975, 1976) In *Phyllodactylus* (Fig. 7) the dorsal interossei muscles do not traverse any of the phalanges fleshily and do not anastomose, but instead insert mainly at the level of the metapodial-phalangeal joint capsule of each digit. The short digital extensor muscles control the claw and the scansors, but their bellies do not extend fleshily to cross any of the phalanges (Fig. 7). At the distal end of the penultimate phalanx the tendon of each short digital extensor divides into three, with one branch continuing to insert mid-dorsally on the claw and the other two diverging to insert distally on each scansorial plate. On the flexor surface the plantar aponeurosis sends

FIG. 1. Ventral view of the left pes of *Phyllodactylus porphyreus* (California Academy of Sciences - CAS 167593). Note the terminal, leaf-like scansors and the more proximal transversely expanded plates.

FIG. 2. Ventral aspect of the left pes of *Diplodactylus strophurus*. (Uncatalogued specimen). Note the leaf-like scansors and the more proximal expanded plates. The dashed lines and the numbers 11-15 represent the planes of the sections depicted in Figs. 11-15.

FIG. 3. Ventral view of the left pes of *Afroedura hawaquensis* (CAS 167638). Note the distal, leaf-like scansors and the more proximal expanded plates.

FIG. 4. Ventral view of the left pes of *Oedura marmorata* (CAS 75405). Note the terminal, leaf-like scansors and the more proximal expanded and divided plates.

FIG. 5. Ventral aspect of digit IV, left pes of *Oedura marmorata* (CAS 75405), showing the relative sizes of the distal scansor pair and the more proximal plates.

FIG. 6. Ventral aspect of digit V, left pes of *Oedura robusta* (CAS 75671), showing the setal fields on the distalmost three pairs of plates.

branches to each of the synovial metapodial-phalangeal joint capsules. Lateral digital tendons arise at these joint capsules and insert at the distal end of the antepenultimate phalanx. The lateral digital tendons thus have no contact with the scansors. The long flexor tendon extends the entire length of the digit mid-ventrally and divides distally in the manner of the short extensor tendon, to serve the claw mid- ventrally and the proximal borders of the scansors (Fig. 7). Interdigital tendinous webs are present but relatively weak, while transverse intermetatarsal and intermetacarpal ligaments are strongly developed.

The internal structure of the digits of *Diplodactylus* (Fig. 8) is architecturally very similar to that of *Phyllodactylus* described above. The short digital extensors give rise to tendons at the level of the metapodial-phalangeal joint capsules, and these traverse the phalanges (which are of the same basic form as those of *Phyllodactylus*) to insert on the claw and distal ends of the scansors. Ventrally the long flexor tendon controls the claw and the scansor pair in the same manner as that of *Phyllodactylus*, and the more proximal ventral plates are not connected with this system. The lateral digital tendons extend as far distally as the distal extremity of the antepenultimate phalanx.

In *Afroedura* (Fig. 9) the internal anatomy of the digits is somewhat more complex. The dorsal interossei muscles extend fleshily to the penultimate phalanx, and from here send a tendinous sheet to the distal extremity of the distalmost scansor pair. The more proximal pair of scansors also receives a tendinous sheet from the dorsal interossei muscles. The claw receives its extensor control from the tendon of the short digital extensor, arising from the belly of this muscle at the base of the digit.

Ventrally the branches of the plantar aponeurosis insert at the synovial metapodial-phalangeal joint capsules. These capsules are also linked by the interdigital tendinous webs and the transverse intermetacarpal and intermetatarsal ligaments. The lateral digital tendons arise from the synovial joint capsules and insert on the proximal borders of the more proximal scansor pairs. The long flexor tendon is strongly developed and serves the claw and the distalmost scansor pair, as in *Phyllodactylus*. Thus, the distalmost and more proximal scansors are controlled by different components of the flexor system. The phalanges have the same basic form as those of *Phyllodactylus*, but the penultimate phalanx is slightly more arcuate.

Comparing the internal anatomy of the digits of *Oedura* with those of *Diplodactylus* again reveals major differences (Figs. 8,10). Here the short digital extensors have anastomosed mid-dorsally and extended fleshily as far as the proximal end of the penultimate phalanx (Russell, 1979). The architecture of the modified short digital extensors (Fig. 10) is similar to that of the dorsal interossei of *Afroedura* (Fig. 9). Here, however, the mid-dorsal tendinous raphe gives rise to individual tendons that insert distally on each of the scansor pairs, including the distalmost. A mid-dorsal tendon also continues distally to insert on the claw. The plantar aponeurosis and associated ligamentous strands are similar to those of *Afroedura*. The long flexor tendon splits distally to serve the claw and the distalmost scansor pair, as in *Diplodactylus*, while the lateral digital tendons serve the more proximal scansor pairs in a manner similar to that in *Afroedura* (Figs. 9,10). The phalanges of *Oedura* are similar to those of *Diplodactylus*, but the penultimate phalanx is more arcuate.

HISTOLOGICAL DETAILS

Gross dissection of the digits of all four genera in question reveals that blood sinuses are present in the digits. The extent of these and their tributaries is only evident, however, if sections of the digits are examined.

In *Phyllodactylus* (Dellit, 1934:Fig. 13) and *Diplodactylus* (Fig. 11) a sinus is present but is restricted to the distalmost part of the digit and is associated with the penultimate and ungual phalanges. The sinus is a paired structure distally, with the ungual phalanx intervening between its two halves (Fig. 11). Immediately proximal to the distal scansor pair the sinus diminishes in size (Fig. 12) and finally disappears as a discrete structure in the hinge region between the scansor bases and the next most proximal plate (Fig. 13). The next most proximal plate is undivided and bears a smaller, but none the less distinct, expanded sinus that is mostly concentrated over the central part of the plate (Fig. 14). This plate resides beneath the penultimate phalanx. The next more proximal plate is borne beneath the antepenultimate phalanx. It is single but shows some sign of incipient division centrally (Fig. 15). This plate bears setae but appears to be cushioned primarily by vacuolar adipose tissue (Fig. 15). The difference in size of the sinuses of the distalmost and next more proximal plates can be more fully appreciated in longitudinal section

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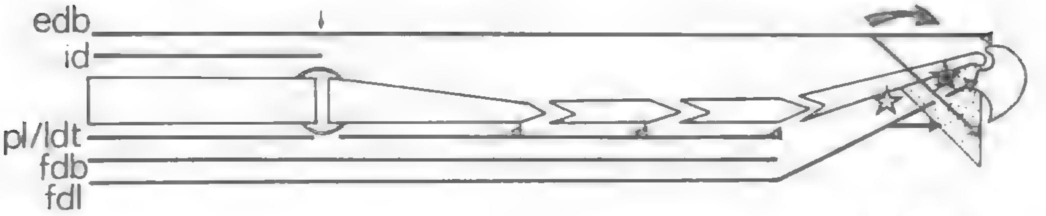

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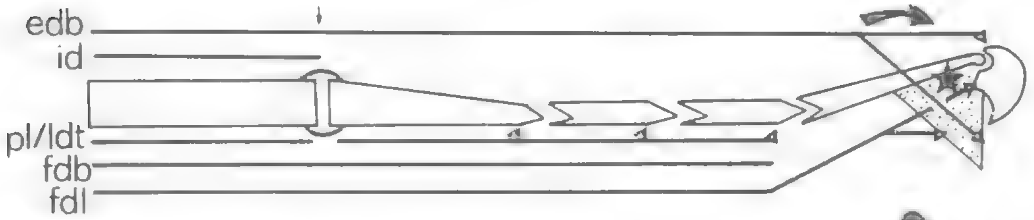

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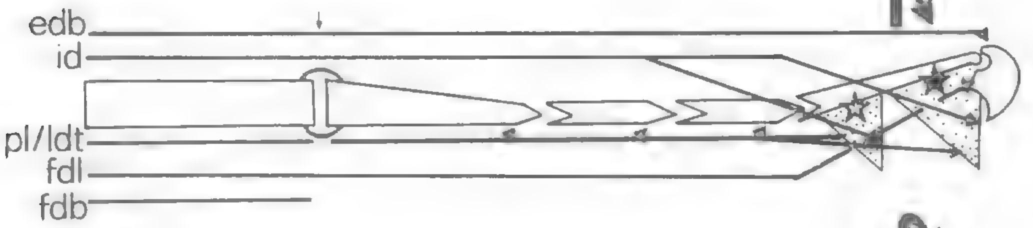

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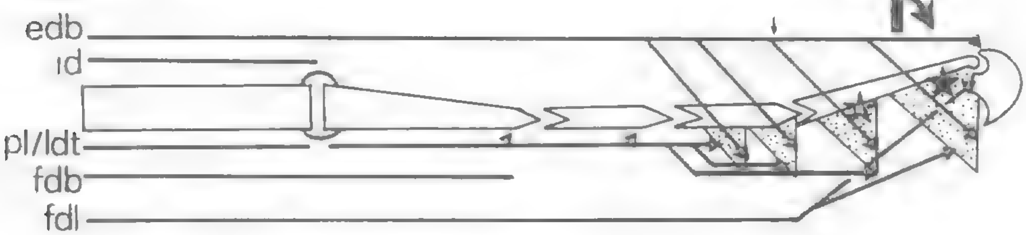


FIG. 7. Diagrammatic representation of the musculoskeletal system of digit IV of the pes of *Diplodactylus*. The block-like structures represent the metatarsal and the phalanges, those with chevron-shaped ends being the phalanges involved in hyperextension. The muscles are represented by black lines, with arrow heads indicating their insertions. The large, black arrow represents the relatively mild curvature of the penultimate phalanx. Blood sinuses are represented by stars, the primary one being solid and the secondary one open. The scansors are stippled. The hoop-like structure connecting the metatarsal (the large block to the far left) with the first phalanx (the block to the immediate right of this) represents the metatarsophalangeal joint capsule. Abbreviations: edb, extensor digitorum brevis; fdb, flexor digitorum brevis; fdl, flexor digitorum longus; id, interossei dorsales; pl/ldt, plantar aponeurosis/lateral digital tendon continuum. The small, vertical arrow represents the distal extent of the fleshy belly of the extensor digitorum brevis.

FIG. 8. Diagrammatic representation of the musculoskeletal system of digit IV of the pes of *Phyllodactylus*. The symbolism and abbreviations are as for those of Fig. 7.

FIG. 9. Diagrammatic representation of the musculoskeletal system of digit IV of the pes of *Afroedura*. The symbolism and abbreviations are as for those of Fig. 7 except for the large, black arrow that represents a greater curvature of the penultimate phalanx.

FIG. 10. Diagrammatic representation of the musculoskeletal system of digit IV of the pes of *Oedura*. The symbolism and abbreviations are as for those of Fig. 9. Note that in *Oedura* the extensor digitorum brevis controls the hyperextension of the scansors, while in *Afroedura* this is achieved by the interossei dorsales.

(Fig. 16), together with the absence of any appreciable sinus development in the most distal of the plates beneath the antepenultimate phalanx. The penultimate plate may be considered as an incipient scansor.

The stratum compactum of the dermis of the distalmost plates is strongly developed at their bases (Fig. 17). This is associated with the long flexor tendon. In the more proximal plates there is incipient development of a strong basal stratum compactum, especially in the most distal of the single plates. As one passes proximally the plates become less well-developed in this regard (Fig. 17), although they are cushioned by adipose-like tissue. The more proximal manifestations of the stratum compactum may be associated with the lateral digital tendons.

In *Oedura* and *Afroedura* the extent of the setal fields is greater than it is in *Phyllodactylus* and *Diplodactylus*, and to some extent this is reflected in the internal anatomy. In *Oedura monilis* the sinus associated with the distalmost pair of plates is massive and single, but sends branches into both sides of the terminal pad (Fig. 18). This is associated with what appears to be vertically stacked columns of smooth muscle associated with the walls of the sinuses (Fig. 18). Further proximally the sinus diminishes in size and then appears again as an appreciable expansion in the next most proximal, and divided, plate. This pair is borne beneath the penultimate phalanx. Here, however, the sinus is somewhat smaller, more diffuse and more markedly paired (Fig. 19). A large amount of fibrous connective tissue is present centrally, above the division between the two halves of the penultimate plate. As in *Diplodactylus*, only the distalmost and the next most proximal plates are housed ventral to the penultimate phalanx. The next more proximal pair of plates is present beneath the antepenultimate phalanx (Fig. 20), and here the involvement of the vascular system is minimal. In longitudinal section the diminution in extent of involvement of the vascular system in the plates is evident (Fig. 21), as is the arcuate nature of the penultimate phalanx and the basal development of the stratum compactum in the scansors proper and the more proximal plates. More laterally the association of the columns of smooth muscle cells with the sinus in the distalmost scansor pair, the extent of the sinus system in the next most proximal scansor pair and the sharp demarcation between these and the more proximal plates can be seen (Fig. 22).

Setal Differentiation.

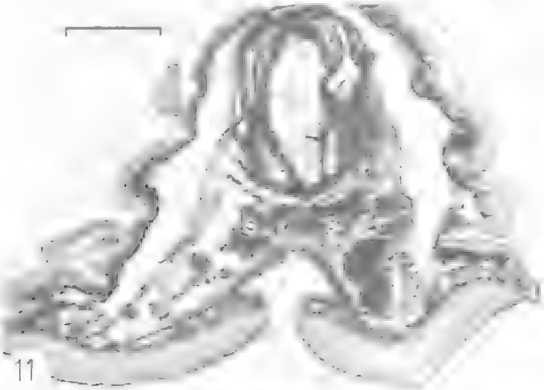
Comparing *Diploductylus* with *Oedura* (and *Phyllodactylus* with *Afroedura*) it can be seen that setae are associated with subdigital plates that exhibit a hypertrophied epidermis (Figs. 16,21). There is a sharp demarcation between these plates and more proximal, typical scales. Viewed with the light microscope there does not appear to be a significant diminution in size of the setae from distal to proximal, even though the internal structure of the plates that bear them differs considerably. The more distal plates are associated with the blood sinus system while the more proximal ones have little or no such association and are instead filled with vacuolar, adipose-type tissue. Those plates exhibiting the seta-bearing (Schleich and Kästle, 1986: plate 6, fig. 3), hypertrophied epidermis occur beneath the hyperextensible phalanges (phalanges two to five in digit four) (Figs. 16,21). A comparative survey of the potential differentiation of spines, spikes, prongs and setae on the various subdigital scales and plates, similar to that performed by Peterson (1983) for anoline iguanids, remains to be carried out.

DISCUSSION

The data outlined above make it possible to make some deductions about the development of a subdigital, adhesive apparatus and about the distinction between scansors and 'lamellae'. The scenario outlined by Russell (1976) that lineages that initially develop distal scansors may expand the subdigital pads by extending the scansor series proximally is the premise upon which the deductions below are based.

Comparisons of *Phyllodactylus* and *Afroedura* from the Gekkoninae and *Diplodactylus* and *Oedura* from the Diplodactylinae provide two independent morphotypic series in which trends can be compared. In both there is a tendency to elaborate the size of the proximal plates on digits two to five, to divide them and to increase the seta-bearing surface area. This may be postulated to be a means of increasing adhesive efficiency, although empirical tests of this in standardised conditions, or rigorous comparisons of the details and physical properties of preferred locomotor substrata are not available (Bauer and Good, 1986). In both putative lineages an adhesive system is primitively present, relying on the employment of a pair of distinct and enlarged distal leaves. These are morphologically sharply demarcated from the more proximal digital plates. The digits of both *Phyllodactylus* and *Diplodactylus* are capable of hyperextension (Russell, pers. obs.) and this activity is practised during normal locomotion. The musculotendinous systems that bring these movements about are relatively simple, but possess all of the basic requisites deemed to be necessary for such activity (Russell 1975, 1976). The distal plates are true scansors (Russell 1981), as adjudged by their possession of setae, a mechanism enabling them to be hyperextended, and an internal hydraulic device that permits these plates to conform to irregularities of the substratum and thus make optimal contact (Russell, 1981). In this case the hydraulic device is present as a vascular sinus system, but other mechanisms also exist (Russell, 1972, 1979).

More proximally the next plate may be categorised as an incipient scansor. It bears setae, may be hyperextended, but possesses only a relatively small sinus system, making conformation with the substratum potentially less effective. This more proximal plate is borne beneath the penultimate phalanx, which arches away from the substratum and permits the housing of the central component of the sinus system



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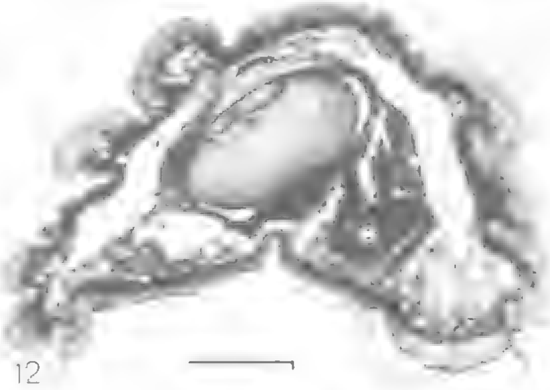

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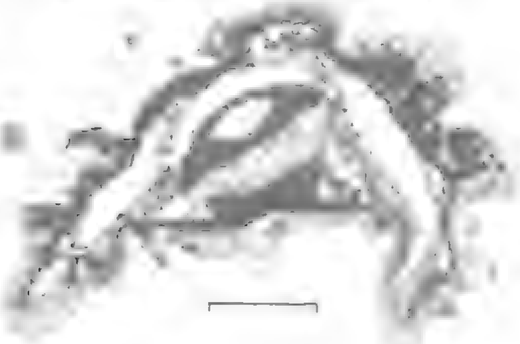

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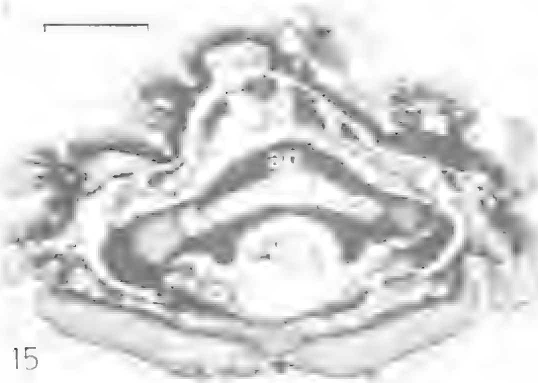

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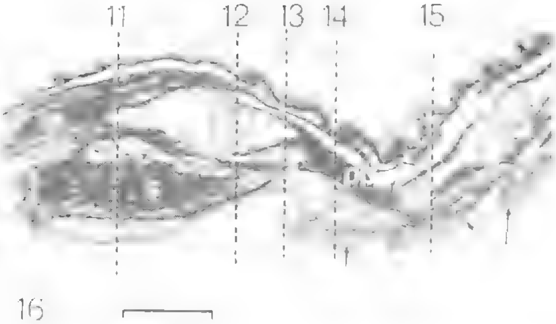

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beneath it (Russell, 1981). Proximal to this the plates do not possess the properties of true scansors in as much as the sinus system, or some other hydrostatic device that can be pressurised, is not incorporated. This appears to be due largely to the morphology of the intermediate phalanges (phalanges two and three in digit four) that are associated with hyperextension. Typically these are depressed and wide (Russell, 1975) and remain firmly adpressed to the substratum (Russell, 1976). Their morphology precludes the incorporation of a centralised sinus or similar device beneath them. The presence of such phalanges in forms that develop distal scansors may later act as a constraint on the potential for further digital modification as they may preclude the development of true scansors beneath them (see below). Forms that have developed scansors from the base of the digits distally have a different constructional arrangement of the intermediate phalanges (Russell, 1977).

Further elaboration of the control systems of the digits in *Afroedura* and *Oedura*, as compared to their putative morphotypic precursors, has not brought about a concomitant increase in the number of scansors, if the criteria for their recognition, as outlined above, are applied. Here the mechanisms of application of the subdigital plates to the substratum and their removal from it can apparently be more precisely controlled, as deduced from the increased complexity of the musculotendinous features of the digits. Examination of histological detail reveals, however, that although the sinus system remains elaborate in the distal pair of plates and has become more elaborate in the next most proximal pair, it is not evident proximal to this. Thus, although externally the yet more proximal plates have become more prominent and more scansor-like (more so in *Oedura* than *Afroedura*) in appearance, their internal differentiation is not so marked. Thus, in the proximal encroachment of subdigital pads from a distal beginning, more than external elaboration is required to convert these structures into fully-differentiated scansors. It appears that one constraining parameter is the ability to incorporate a sinus system into a pad consisting of multiple scansors. Here, the incorporation of scansors beneath the penultimate phalanx becomes critical. This phenomenon was noted for the tokay (*Gekko gecko*) by Russell (1981: Fig. 7). Here, multiple scansors are present beneath the penultimate phalanx and these possess branches of an elaborate sinus system. Proximal to this the lamellae bear setae but are morphologically

FIG. 11. Cross section of digit IV, left pes of *Diplodactylus strophurus* through the terminal, leaf-like scansors at the base of the claw. See Figs. 2 and 16 for position of section. The sinus (s) is large and is positioned ventral to the ungual phalanx (up). At this point the sinus is paired, one half being associated with each leaf of the scansor (scan). The scale bar = 0.25mm. Mallory's azan stain.

FIG. 12. Cross section of digit IV, left pes of *Diplodactylus strophurus* through the base of the distal scansor pair. See Figs. 2 and 16 for position of the section. At this point the sinus (s) is paired but smaller and lies beneath the distal cartilaginous epiphysis (ep) of the penultimate phalanx. The section is somewhat oblique, with the right leaf and sinus being represented more proximally than the left, where the scansor base (scan) is still visible. The scale bar = 0.25mm. Mallory's azan stain.

FIG. 13. Cross section of digit IV, left pes of *Diplodactylus strophurus* through the hinge region between the distal scansor pair and the next most proximal plate. See Figs. 2 and 16 for position of the section. The sinus (s) is much reduced at this point and is present only as a connecting channel between the scansors and the penultimate plate. The penultimate phalanx (pp) is depressed and transversely widened at this point. The scale bar = 0.25mm. Mallory's azan stain.

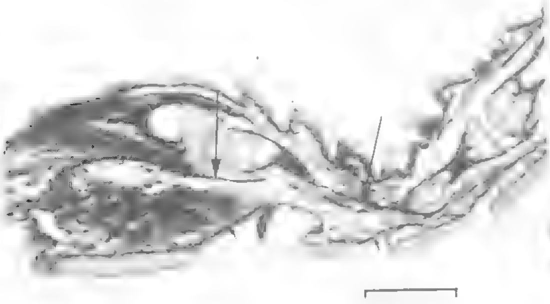
FIG. 14. Cross section of digit IV, left pes of *Diplodactylus strophurus* through the undivided penultimate plate. See Figs. 2 and 16 for position of the section. The sinus (s) is expanded again and is present beneath the penultimate phalanx (pp) and associated tendon of the flexor digitorum longus (fdl). The incipient scansor (incip. scan) bears no central thinned area. The scale bar = 0.25mm. Mallory's azan stain.

FIG. 15. Cross section of digit IV, left pes of *Diplodactylus strophurus* through the antepenultimate plate, beneath the antepenultimate phalanx (ap). See Figs. 2 and 16 for position of the section. The sinus is not evident and the lamella (lam) is cushioned by vacuolar adipose tissue (at). The tunnel for the tendon of the flexor digitorum longus (fdl) is evident. The scale bar = 0.25mm. Mallory's azan stain.

FIG. 16. Longitudinal section of digit IV, left pes of *Diplodactylus strophurus* showing the relationships of the sinus (s), scansors (scan), incipient scansor (incip. scan), lamellae (lam), ungual (up), penultimate (pp) and antepenultimate (ap) phalanges. The dashed lines and the numbers 11-15 represent the planes of the sections depicted in Figs. 11-15. The scale bar = 0.5mm. Mallory's azan stain

much less elaborate, bearing a closer resemblance to true scales than do the scansors. Again there is probably a functional correlate of this differentiation, as the scansors are more likely to be able to maximise contact with the substratum (on at least some locomotor surfaces) due to their additional compliance. In the tokay (and many other geckos having multiple scansors) the adhesive properties are probably further enhanced by the overlapping nature of the scansors (Fig. 23) and the sequential effect of the reticular network of the sinus system of one scansor on the setae of the next most proximal scansor (Russell, 1981). In *Oedura* and *Afroedura* the scansors do not overlap and do not have the free border typical of those of the tokay (Fig. 23), so again the adhesive efficiency is potentially limited.

The digital conditions in *Oedura* and *Afroedura* appear to be indicative of a transitional phase (in the sense of evolutionary morphology rather than phylogeny) between a single scansor system and a multiscansorial system. These taxa do, therefore, provide us with some insight as to how the latter may have evolved from a morphologically less complex condition.



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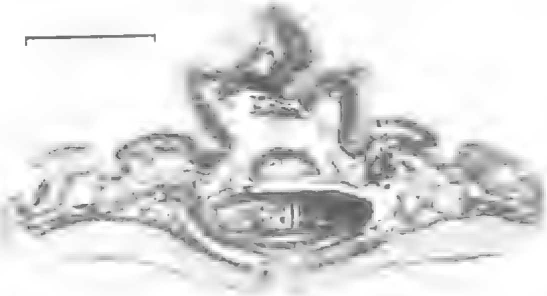

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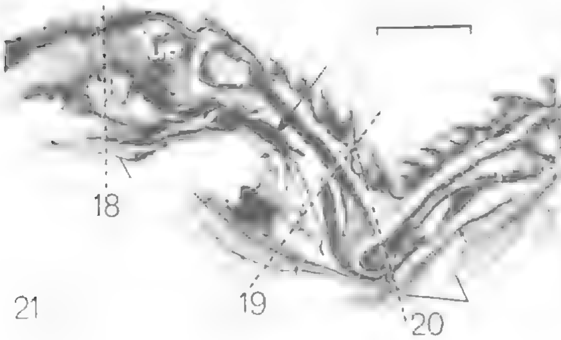

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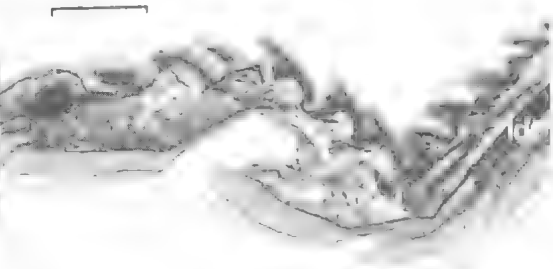

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The transition as visualised in a morphotypic sequence is not smooth, however, and the differences between the *Gekko* system (typifying multiscansorial pads) and the *Oedura* and *Afroedura* systems are quite marked. The differences seen may be indicative of a syndrome of characters that are synonymous with the evolution of a multiscansorial system, and functional constraints may operate either to govern the potential transition or to prevent it. The sequence by which multiscansorial pads arose is not known, but examination of the condition of the digits in *Oedura* and *Afroedura* provides one means of attempting to understand how this may have come about. Further anatomical and histological investigations of other genera will be helpful in attempting to assess the feasibility of the proposed scheme. A similar scheme erected for anoline iguanids (Peterson, 1983) suggests a similar set of related morphological events, although her assessment was based entirely on external features.

Given what can be potentially deduced about digital form and evolution in the *Diplodactylus* - *Oedura* and *Phyllodactylus* - *Afroedura* morphotypic sequences, the following represents a relative chronology of changes in the adhesive system based upon the constraints as outlined. This chronology attempts to firstly account for the transition from a single pair of terminal, leaf-like scansors to the elaboration of more proximal pairs, as exemplified by *Oedura* and *Afroedura*. Secondly it attempts to explain how the latter conformation may be morphologically extended into a multiscansorial system (or alternatively how it may be limited by the magnitude of the morphological gaps that are evident).

1.The pattern begins with a pair of terminal, leaf-like scansors with extensive setal fields and a well-developed blood sinus system. The digit is able to be hyperextended. The proximal part of the digit is flat and the transversely widened plates beneath are endowed with setae as far proximally as the distal end of the first phalanx. The most distal widened plate is positioned ventral to the penultimate phalanx and possesses an incipient sinus. This is the condition exemplified by *Phyllodactylus* and *Diplodactylus*. This stage suggests that seta-bearing lamellae precede the development of true scansors both

FIG. 17. Longitudinal section of digit IV, left pes of *Diplodactylus strophurus* showing the stratum compactum of the dermis of the scansors and penultimate plate (small arrows), this being associated with the long flexor tendon (large arrows). The scale bar = 0.5mm. Mallory's azan stain.

FIG. 18. Cross section of digit IV, left pes of *Oedura monilis* through the terminal, leaf-like scansor pair. See Fig. 21 for position of the section. The large central sinus (s) is evident, together with its associated smooth muscle columns (sm). The sinus resides beneath the ungual phalanx (up) and cushions the scansors (scan). The scale bar = 0.5mm. Mallory's azan stain.

FIG. 19. Cross section of digit IV, left pes of *Oedura monilis* through the penultimate scansor pair. See Fig. 21 for position of the section. The sinus (s) is paired and smaller than that of the distalmost scansor pair. The penultimate scansor pair (scan) resides beneath the penultimate phalanx (pp). Fibrous connective tissue (fct) fills the space above the cleft between the leaves of the scansor pair. The scale bar = 0.5mm. Mallory's azan stain.

FIG. 20. Cross section of digit IV, left pes of *Oedura monilis* through the antepenultimate pair of plates. See Fig. 21 for position of the section. The lamellae (lam) are cushioned only by adipose tissue (at) and reside beneath the antepenultimate phalanx (ap) and its associated tendon of the flexor digitorum longus (fdl). The scale bar = 0.5mm. Mallory's azan stain.

FIG. 21. Longitudinal section of digit IV, left pes of *Oedura monilis* showing the relationships of the sinus (s), scansors (scan), lamellae (lam), ungual (up), penultimate (pp) and antepenultimate (ap) phalanges. The stratum compactum of the dermis of the scansors (small arrows) is evident. That of the distal scansor pair is associated with the tendon of the flexor digitorum longus (large arrow), while that of the penultimate scansor pair is associated with the lateral digital tendon (out of the plane of the section, but see Fig. 22). The dashed lines and the numbers 18-20 represent the planes of the sections depicted in Figs. 18-20. The scale bar = 0.5mm. Mallory's azan stain.

FIG. 22. Parasagittal section of digit IV, left pes of *Oedura monilis*, showing the columns of smooth muscle (sm) associated with the distal scansor pair and the extent of the sinus (s) of the penultimate scansor pair. The lateral digital tendon (ldt) and its association with the stratum compactum of the penultimate scansor pair is evident. Note the absence of a free distal margin on the scansors (compare with Fig. 23) and the sharp demarcation between the scansors and the more proximal lamellae. The scale bar = 0.5mm. Mallory's azan stain.

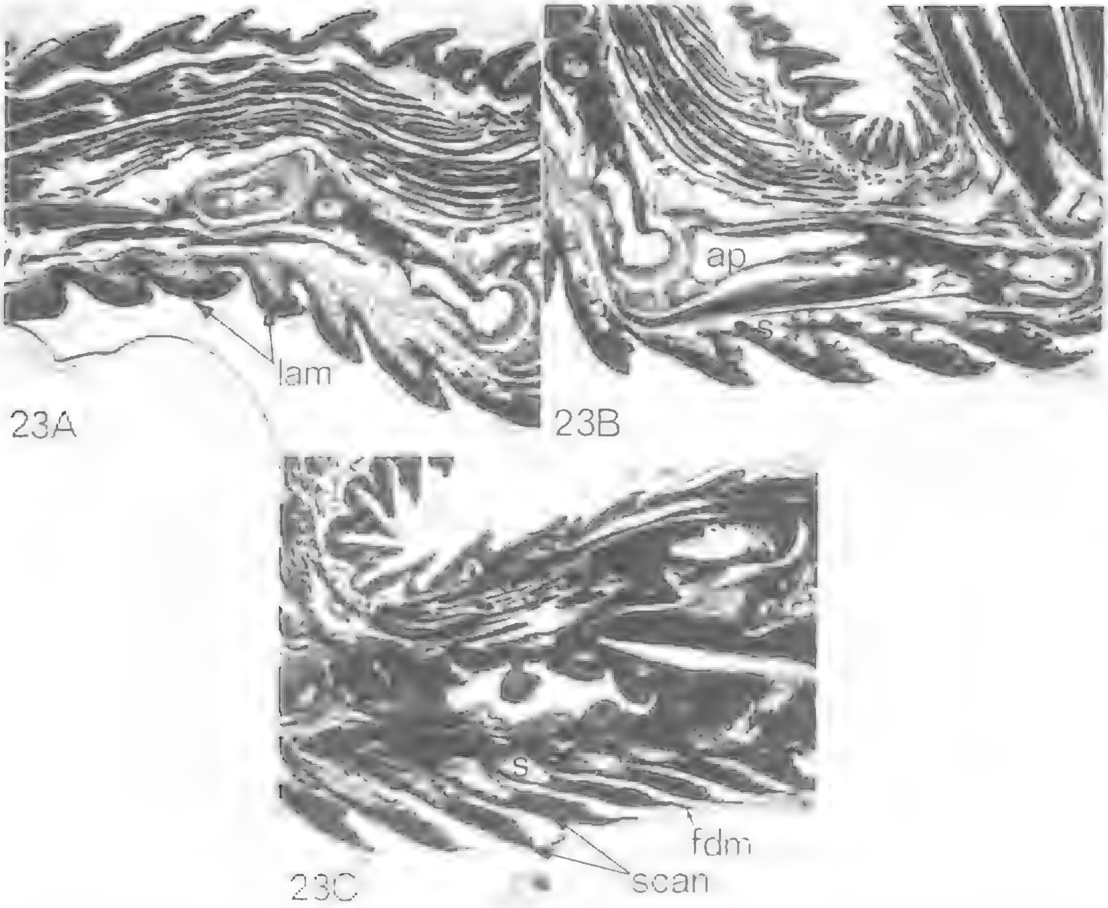

FIG. 23. Scansor and lamellar differentiation in *Gekko gecko*. A. represents a longitudinal section through the proximal region of digit IV, left pes. Here the subdigital plates bear short setae but lack a free distal margin and an involvement of the sinus system. B. represents a longitudinal section through the region of the antepenultimate phalanx. Here the free distal margin is slightly developed and the sinus system is partially involved. C. represents the region of fully differentiated scansors beneath the penultimate phalanx. Note the multiple scansors in this region, the extensive involvement of the sinus system, the extensive overlap of the scansors and the extensive free distal margin on each scansor. Abbreviations: ap, antepenultimate phalanx; fdm, free distal margin; lam, lamellae; pp, penultimate phalanx; s, sinus; scan, scansors.

evolutionarily and positionally. This suggests that adhesive systems begin by employing expanded plates with setose surfaces (lamellae). Subsequently these may be modified to become true scansors, and this may increase adhesive efficiency.

2. The adhesive system is elaborated by a proximal encroachment of scansor-like plates, enhancing the possibility of surface contact by elaborating the core of the plate by the development of vacuolar, adipose-like tissue. The distal scansors remain well-developed and the next most proximal plate gives rise to leaves that possess a greater elaboration of the sinus system. The penultimate phalanx is more arcuate and true scansors reside beneath this. Proximal to this the scansor-like plates are enlarged and prominent but lack branches of the sinus system. The proximal plates may thus increase the adhesive power of the digits, but they do not have the flexibility for conformity with the locomotor substratum that the true scansors do, with their sinus systems. The distal scansor pair is controlled in its flexor aspect in the same way as in

Diplodactylus and *Phyllodactylus*, while the more proximal plates receive their flexor control from the lateral digital tendons. Only the most distal of these is a true scansor. The extensor control of the plates has been taken over by the distal migration of muscle bellies into the digit proper, and these traverse all but the penultimate and distalmost phalanges. The scansors and more proximal plates are controlled on the extensor surface in essentially the same way. This is essentially the condition in *Afroedura* and *Oedura*, although in the former the plates have not progressed as far proximally as they have in the latter.

3.The trend so far outlined appears to be one that is leading towards the elaboration of multiscansorial pads, but both *Afroedura* and *Oedura* lack certain features that are typical of a multiscansorial system. In order to continue the trend to give rise to such a pad the following changes would be predicted to take place (based on a comparative survey of scansor and pad design in general): The distal scansor pair would become reduced in size, giving the claw a greater degree of freedom from the pad. In association with this the scansor pair beneath the penultimate phalanx would become subdivided as the penultimate phalanx became more arcuate (This is seen also in the gekkonine genus *Calodactylodes*). The sinus system would become subdivided, with the reticular networks of the scansors being confined to their bases. As the scansors subdivided there would be a trend to the elaboration of a free, distal, seta-bearing margin that would become overlain by the reticular network of the next most distal scansor. True scansors would be restricted to the area beneath the penultimate phalanx. Proximal to this, enlarged plates would bear fields of setae but would not possess branches of the sinus system. These plates would lack the free margin and would remain essentially similar to the more proximal plates seen in *Diplodactylus* and *Oedura*. The constraints of the incorporation of components of the venous sinus system and the restriction to elaboration of scansors to the region immediately below or adjacent to the penultimate phalanx dictate to a large degree how the system as seen in *Oedura* and *Afroedura* may be further elaborated.

Cogger (1964) was intrigued with the phenetic similarity of, but apparent lack of phylogenetic affinity between, *Oedura* and *Afroedura*. He carefully documented the similarities and differences between these two taxa and correctly surmised that the similarities were due to convergence. Although Cogger (1964) indicated that similarities of foot structure were superficial, they are, in fact, quite extensive. The arrangement of components and their integration indicate that the independent acquisition of this basic pattern has been governed by very similar selective factors relating to the functional control of the scansor system. Both genera appear to exhibit a morphologically intermediate condition between a relatively simple adhesive system and one that is considerably more complex. The potential limits and constraints on both genera, in terms of further elaboration of their subdigital adhesive apparatus, appear to be rather similar and represent an example of how functional demands can potentially canalise (Brundin, 1968) an evolving system.

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THE SCINCID LIZARD GENUS *NANNOSCINCUS* GÜNTHER: A REVALUATION

R.A. SADLIER

Sadlier, R.A. 1990 09 20: The scincid lizard genus *Nannoscincus* Günther: a revaluation. *Memoirs of the Queensland Museum* 29(2): 487-494. Brisbane. ISSN 0079-8835.

A combination of skeletal, scalation, coloration and reproductive characteristics are used to analyse the intrageneric relationships of the species included in *Nannoscincus* (Sadlier, 1987), which is here shown to comprise 2 subgenera. Proposed is a monotypic subgenus *Nannoseps* n. subgen. for the Australian species *N. maccoyi* (Lucas and Frost). The New Caledonian species *N. mariei* (Bavay), *N. gracilis* (Bavay), *N. sleveni* (Loveridge), *N. rankini* Sadlier and *N. greeri* Sadlier comprise the nominate subgenus. Within the subgenus *Nannoscincus* there appear to be 2 distinct species groups, the *N. mariei* species group (including *N. mariei*, *N. greeri* and tentatively *N. rankini*) and the *N. gracilis* species group (including *N. gracilis* and *N. sleveni*). ☐ *Scincidae, Nannoscincus, phylogeny, Australia, New Caledonia*

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Greer (1979) diagnosed 3 major lineages for the Australian scincid lizard fauna, the *Egernia*, *Sphenomorphus* and *Eugongylus* groups. These groups are widespread within Australia and also include most scincid genera in the Pacific region. Outside Australia, the *Egernia* and *Sphenomorphus* groups are distributed mainly over the Indonesian archipelago east to the Solomon Islands; members of the *Sphenomorphus* group in particular are prominent in closed forest habitats. By contrast, the distribution of the *Eugongylus* group outside of Australia is mainly over the Pacific islands to the east of Australia (including New Guinea) and is poorly represented in the Indonesian archipelago.

Within the *Eugongylus* group (Greer, 1990) there is a distinct subgroup of species that share a derived character state unique within lygosomine skinks. This subgroup is diagnosed by having the atlantal arches of the first cervical vertebrae fused to the intercentrum. Within this subgroup a subset of species share a pattern of phalangeal reduction on the 4th digit of the manus not observed in other *Eugongylus* group members. This subset of species comprises the genus *Nannoscincus* and includes: *Anotis mariei* Bavay, 1869; *Lygosoma gracilis* Bavay, 1869; *Saiphos maccoyi* Lucas and Frost, 1894; *Lygosoma sleveni* Loveridge, 1941; *Nannoscincus rankini* Sadlier, 1987; *Nannoscincus greeri* Sadlier, 1987. In addition to the pattern of phalangeal loss all members of this subgroup are small (maximum snout to vent length of 50mm in *maccoyi* the largest species) with elongate bodies and reduced limbs which fail to meet when adpressed to the body. They generally occur in closed forest or montane habitats, sheltering beneath and within rotting logs or under stones, or within the fine, loose superficial substrate beneath these sheltering sites.

SYSTEMATICS

Greer (1974) in reviewing *Leiolopisma* and associated species identified 2 groups (Groups II and III of that work) which essentially comprise what is now regarded as the *Eugongylus* group (Greer,1979). Greer (1974) was however unclear as to whether *Anotis* Bavay (a Group II member at that time comprising the Australian species *A. maccoyi* (Lucas and Frost), *A. graciloides* (Lönnberg and Anderson), and the New Caledonian species *A. mariei* Bavay, *A. gracilis* (Bavay), and *A. sleveni* (Loveridge)) was monophyletic or polyphyletic.

Czechura (1981) noted that *Anotis* Bavay was preoccupied, and resurrected *Nannoscincus* Günther to replace it.

A review of the New Caledonian scincids by Sadlier (1987) redefined *Nannoscincus* largely on the basis of the pattern of phalange reduction in the 4th digit of the manus. *Lygosoma graciloides* with a pattern of phalange reduction in the 1st digit only was removed, and the genus then comprised the species *N. gracilis, N. mariei, N. sleveni, N. rankini, N. greeri* and *N. maccoyi*. Note that Greer (1982) further defined *Geomyersia* when describing a second species in the genus, *G. coggeri;* he listed as one of the diagnostic features a phalangeal formula similar to *Nannoscincus.* Re-examination of *Geomyersia* shows it to have a primitive phalangeal formula and is for this reason not considered further here.

Subsequent research on the species of *Nannoscincus*, particularly osteology and soft morphology, has established the Australian species *Saiphos maccoyi* Lucas and Frost as a sister group warranting subgeneric recognition within a redefined *Nannoscincus* that also recognises the New Caledonian species as a monophyletic subgenus.

METHODS AND MATERIALS

Scalation and reproductive characteristics were assessed on whole alcoholic specimens. Phalange and presacral vertebrae condition were assessed from x-rays of selected samples. Vertebral and sternal characters were assessed from a combination of cleared and stained and whole alcoholic specimens, and skull characters from a combination of cleared and stained and skeletal preparations. Coloration characteristics were determined from my field observations. Polarities for characters, unless otherwise stated, are those used by Greer in determining relationships between lygosomine skinks, otherwise the primitive state is considered the widespread condition in the primitive *Eugongylus* group species. Sources used in assigning character polarities are as follows: character state A, Greer (1974); character state B, this work; character state C, Greer (1974); character state D, Greer (1983); character state E, this work; character state F, this work and Greer (1974); character state G, Lecuru (1968 :524, fig. 8a and 8b); character states H and I, Romer (1956) as cited in Greer (1983); character state J, Hoffstetter and Gasc as cited in Greer (1983); character state K, Romer (1956); character state L, Greer (1987).

EVALUATION AND DISTRIBUTION OF CHARACTERS

The following 13 characters were used in inferring relationships between species of *Nannoscincus*.

A. Prefrontal scales. Primitively the prefrontals of lygosomine skinks are moderately large and either in contact medially or narrowly-moderately separated (A). From this primitive condition the prefrontals can be lost in 2 ways, either through fusion to the frontonasal (a1) or through diminution (a2).

In *N. maccoyi* the prefrontals are absent. Loss of the prefrontal scales through fusion (a1) in *N. maccoyi* is indicated by a single 'anomalous' specimen from Bendigo, Victoria (Fig. 1a) in which the prefrontals are distinct and in broad contact, whereas in all other *N. maccoyi* examined the prefrontals are absent (Fig. 1b) but retain an undulating shape to the frontonasal-

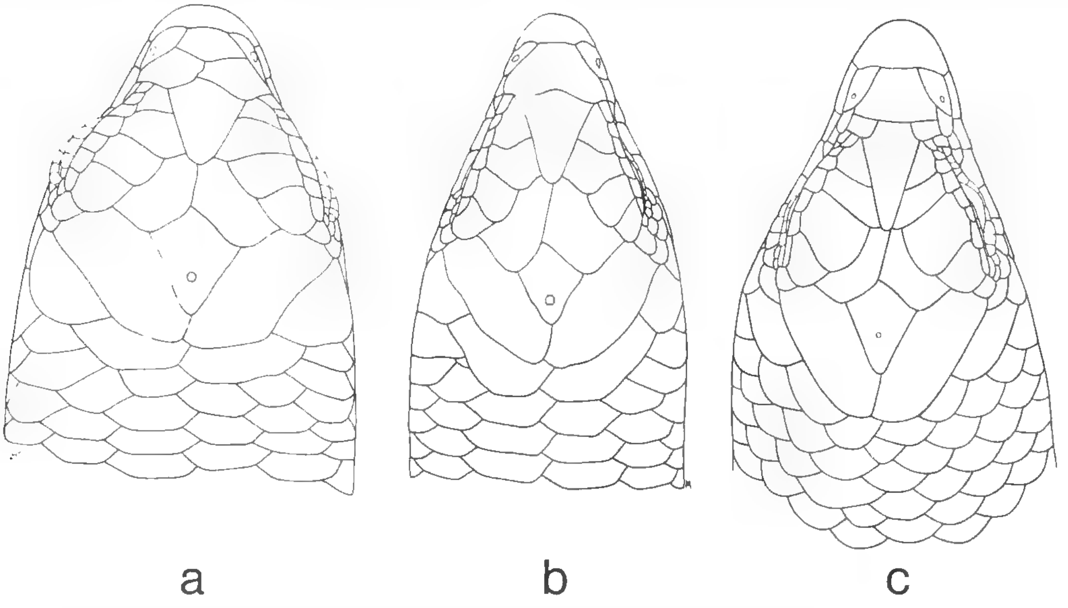

FIG. 1. Dorsal views of the head scalation of: (a) aberrant *N. maccoyi* (note broadly contacting prefrontal scales); (b) lectotype of *Saiphos maccoyi* Lucas and Frost (NMV D1851); (c) *N. mariei.*

frontal suture characteristic of species with well developed prefrontals (and also in the specimen of *N. maccoyi* from Bendigo mentioned above). The prefrontals in the remaining species of *Nannoscincus* appear to have been reduced by diminution (Fig. 1c) as indicated by their small size and obvious separation.

B. Contact between the 1st supraciliary and frontal scales. Contact between the prefrontal and 1st supraocular scales is considered the primitive (B) condition. Contact between the 1st supraciliary and frontal scale, thereby excluding contact between the prefrontal and 1st supraocular is considered derived (b).

Contact between the prefrontal and 1st supraocular occurs in *N. maccoyi*, and *N. mariei*, while *N. gracilis*, *N. sleveni*, *N. greeri* and *N. rankini* generally have the derived condition.

C. Frontoparietal scales. In the primitive condition the frontoparietals are present as 2 distinct scales (C). Fusion of these scales along the midline to form a single scale is considered to be derived (c).

The primitive condition occurs in *N. maccoyi*, *N. mariei*, *N. gracilis*, and *N. sleveni*, while the derived condition occurs in *N. greeri* and *N. rankini*.

D. Loreal scales. The presence of 2 distinct loreal scales between the nasal and preocular scales is considered to be the primitive condition for lygosomine skinks (D). In most primitive lygosomine skinks the anterior loreal is either square or slightly higher than wide, while the posterior loreal is either square or slightly wider than high.

The primitive loreal condition in *Nannoscincus* occurs in *N. gracilis* and *N. sleveni* which have 2 reduced loreal scales (D), the anterior usually present as a semilunar scale positioned on the posterodorsal margin of the nasal and failing to contact the labials, and the posterior usually as high as the nasal but noticeably wider dorsally than basally. *N. maccoyi*, *N. mariei*, *N. greeri* and *N. rankini* all have a single loreal scale which is considered to be derived (d).

E. Lower labial scales. Most generally primitive *Eugongylus* group species have 6 lower labials which is considered the primitive condition (E). Reduction in the number of lower labials, is considered to be derived (e).

N. maccoyi, *N. gracilis* , and *N. sleveni* have the primitive condition of 6 lower labial scales, while *N. mariei*, *N. greeri* and *N. rankini* have 5 lower labials (e).

F. Lower eyelid morphology. A scaled lower eyelid is considered primitive for lygosomine skinks, and derivations from this condition derived.

The lower eyelid of *N. maccoyi*, *N. greeri* (Fig. 2b) and *N. rankini* has a semi-transparent disc below a distinct palpebral rim. *N. mariei*, *N. gracilis* and *N.sleveni* (Fig. 2a and 2c) lack sutures defining the palpebral rim and have the opaque central area of the lower eyelid divided by fine transverse sutures only ('scaled').

It is however unclear whether these conditions

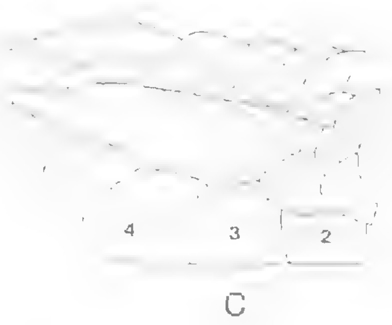

FIG. 2. Lateral view of the head of: (a) *N. sleveni* with the lower eyelid in the raised position showing the 'scaled' lower eyelid typical of *N. gracilis*, *N. sleveni* and *N. mariei*; (b) *N. greeri* with the lower eyelid in the raised position showing the windowed condition typical of *N. maccoyi*, *N. greeri*, and *N. rankini*; (c) detail of the scalation of (a) above.

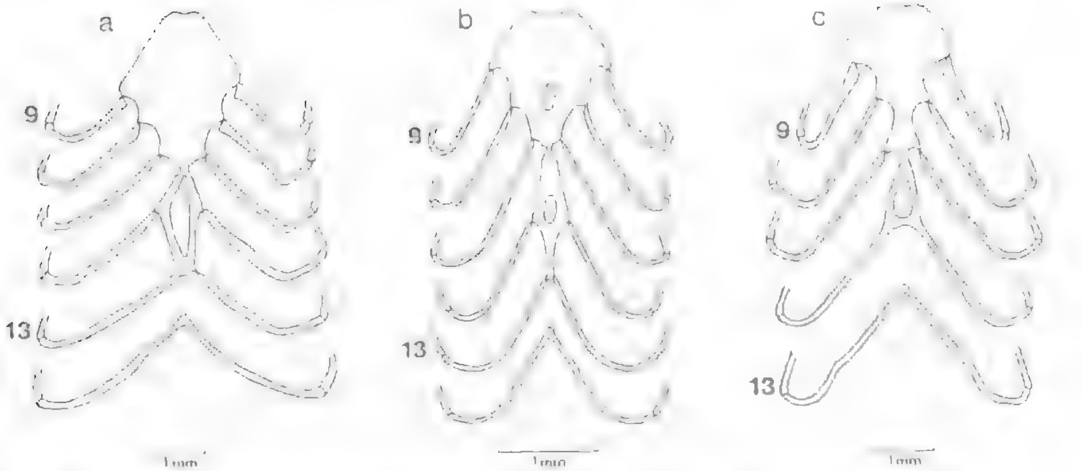

FIG. 3. The various types of mesosternal rib attachment found in the *Nannoscincus* subgroup: (a) *N. maccoyi*; (b) *N. mariei*, typical of *N. mariei* and *N. greeri*; (c) *N. gracilis*, typical of *N. gracilis*, *N. sleveni*, and *N. rankini*.

(above) for *Nannoscincus* represent: 1) 2 independent patterns of evolution from an ancestor with the scaled condition, 2) the 'scaled' condition is secondarily derived from an ancestor having a semi-transparent disc in the lower eyelid, 3) the lower eyelid with a semi-transparent disc is derived from an ancestor with a 'scaled' lower eyelid. For this reason polarities have not here been assigned to either of the conditions.

Of the above possibilities the most parsimonious would be the 2nd, with the apparent loss of the palpebral sutures defining the palpebral rim and reaquisition of fine, widely spaced, transverse sutures possibly the result of an extension of the palpebral rim down over the centre of the eye to its lower margin, from an ancestor with a semi-transparent disc.

G. Mesosternal rib attachment. Contact of the 12th and 13th ribs with the mesosternum is considered the primitive condition (G). Loss of the 13th rib attachment to the mesosternum (g) is considered to be the derived condition.

The primitive condition exists in *N. maccoyi* (Fig. 3a) and in a slightly modified form in *N. mariei* and *N. greeri* (Fig. 3b), whereas *N. rankini*, *N. gracilis* and *N. sleveni* have the 12th rib only contacting the mesosternum (g) (Fig. 3c), and the 13th rib lying posterior and separate to the mesosternum.

H. Phalangeal formula of the manus. The primitive phalangeal formula for the manus is 2.3.4.5.3. Loss of phalanges on the manus is a derived condition. The phalangeal formula for the manus of the ancestor of *Nannoscincus* is considered to be 2.3.4.4.3 (H), and is the condition occurring in *N. maccoyi*, *N. greeri*, *N. rankini* and *N. mariei*. Loss of an additional phalange on the 3rd and 4th digits of the manus of *N. gracilis* (2.3.3.3.2) and *N. sleveni* (2.3.3.3.0) is considered derived (h) within the genus. Note the phalangeal formula for *N. sleveni* given previously by Sadlier (1987) was incorrect (read in reverse off x-ray plate) and is here corrected to a loss of the 5th (rather than 1st) digit - a condition unique within the Eugongylus group.

I. Phalangeal formula of the pes. The primitive phalangeal formula for the pes is 2.3.4.5.4. (I), and reduction in phalange number derived (i).

N. greeri, has the primitive phalangeal formula. The phalangeal formula for the remaining species of *Nannoscincus* is 2.3.4.4.3. Loss of a phalange on the 4th and 5th digits of the pes of these species is considered derived within the genus.

J. Presacral vertebrae. In skinks the modal number of presacral vertebrae is 26, any deviations from this can be taken as progressive derivations. The species with the lowest number of vertebrae above 26 will be primitive for this condition, and those with a higher number of vertebrae derived.

In *Nannoscincus* presacral vertebrae number is variable but falls roughly into 2 groups: *N. mariei* (31-32, mode 31), *N. greeri* (29) and *N. rankini* (29-30) with generally 31 or fewer presacral vertebrae which is considered primitive (J) for the genus; and *N. maccoyi* (34-37), *N.*

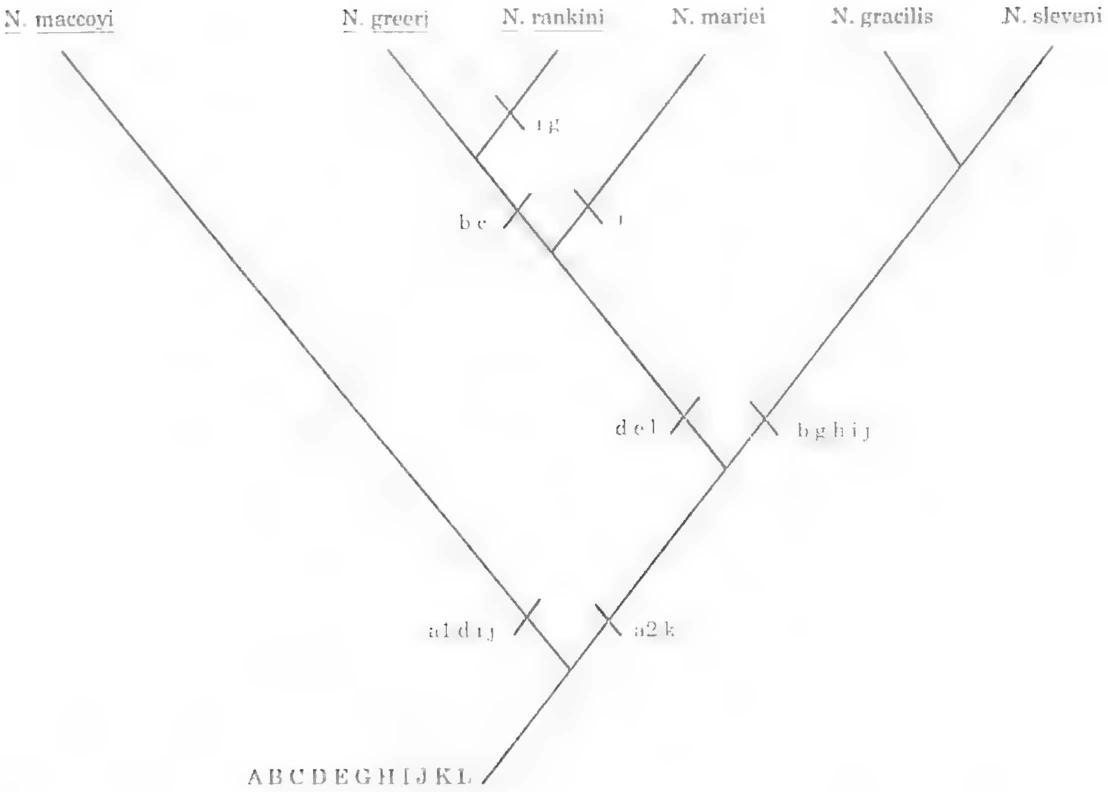

FIG. 4. Phylogeny of the genus *Nannoscincus* subgroup.

sleveni (31-34, mode 32) and *N. gracilis* (33-34) with generally 32 or more presacral vertebrae which is derived (j) within the genus.

K. Atlantal vertebrae. In most generally primitive lygosomine skinks the atlas consists of 3 distinct elements, the 2 atlantal arches and the intercentrum.

All species of *Nannoscincus* have the atlantal arches fused to the intercentrum. *N. maccoyi* has the atlantal arches distinct dorsally where they abut, this is considered the primitive condition (K) within the genus. The remaining species of *Nannoscincus* have undergone further fusion of the atlantal vertebrae, the atlantal arches being fused to one another dorsally, this is derived (k) for the genus.

L. Oviduct. The presence of a pair of oviducts in females is considered the primitive condition (L) and occurs in *N. maccoyi*, *N. gracilis* (*bar 1 specimen see below), and *N. sleveni*. A single oviduct only occurs on the right side of the body in *N. mariei* and *N. greeri*, and is the derived condition (l).

N. rankini is known only from 2 adult male specimens, the female reproductive trait for this species is therefore unknown.

A single female *N. gracilis* examined had a single oviduct on the right side of the body containing a single enlarged yolked ovarian follicle. This individual is unusual in 2 other respects. Firstly it is the smallest reproductively active female *N. gracilis* examined, and secondly it is from a geographically disjunct point in the species range. At this stage it is unclear as to whether this specimen represents an aberrant individual of *N. gracilis*, or a sibling species to *N. gracilis* distinguished solely on the oviduct condition. If the latter it would represent another case of loss of the left oviduct.

M. Ventral coloration. The polarity of features of coloration are uncertain, however they may in the future add to our knowledge of relationships.

The venter of *N. maccoyi* in life has an orange flush predominantly in males and a yellow flush in females. No orange or yellow flush to the venter was observed in live (breeding and non-breeding) *N. mariei, N. gracilis, N. sleveni* or *N. rankini* I have observed.

TABLE 1. Summary of distribution of character states within *Nannoscincus*. Polarities are denoted by capital letters for the primitive condition and lower case for the derived condition.

Character States	*N. maccoyi*	*N. greeri*	*N. mariei*	*N. rankini*	*N. gracilis*	*N. sleveni*
a1 prefrontals fused a2 prefrontals diminutive	a1	a2	a2	a2	a2	a2
B frontal not contacting 1st supraciliary b frontal contacting 1st supraciliary	B	b	B	b	b	b
C frontoparietal scales paired c frontoparietal scales fused	C	c	C	c	C	C
D loreal scales 2 d loreal scales 1	d	d	d	d	D	D
E lower labial scales 6 e lower labial scales 5	E	e	e	e	E	E
F? lower eyelid ‘scaled’ lower eyelid windowed	window	window	‘scaled’	window	‘scaled’	‘scaled’
G mesosternal ribs 12 + 13th g mesosternal ribs 12th only	G	G	G	g	g	g
H phalanges of manus 2.3.4.4.3 h phalanges of manus 2.3.4.4.2	H	H	H	H	h	h
I phalanges of pes 2.3.4.5.4 i phalanges of pes 2.3.4.4.3	i	I	i	i	i	i
J presacral vertebrae 31 or less j presacral vertebrae 32 or more	j	J	J	J	j	j
K atlantal arches distinct k atlantal arches fused	K	k	k	k	k	k
L oviducts paired l oviduct single	L	l	l	?	L	L
M? ventral colouration present ventral colouration absent	present	?	absent	absent	absent	absent

RELATIONSHIPS WITHIN *NANNOSCINCUS*

The most parsimonious phylogenetic interpretation drawn from these characters proposes an initial dichotomy between the Australian species *N. maccoyi* and the remaining New Caledonian species of *Nannoscincus*. The New Caledonian *Nannoscincus* are diagnosed by the derived character state (k) atlantal arches fused dorsally; while the Australian species *N. maccoyi* is diagnosed by the unique contact between the frontal and premaxilliary bones given in the subgeneric diagnosis below. Interpreting loss of prefrontals in *N. maccoyi* (a1), and the diminutation of prefrontals in the New Caledonian *Nannoscincus* (a2) as 2 independently derived patterns of reduction would further identify this basic dichotomy in *Nannoscincus*. Similarly presence or absence of ventral coloration, depending on the polarity of the character states, would further diagnose either *N. maccoyi* or the New Caledonian *Nannoscincus* as monophyletic subgenera.

Between these proposed subgenera is inferred parallel evolution in the following characters: (d) reduction to a single loreal in that region between *N. maccoyi* and *N. mariei* + *N. rankini* + *N. greeri*; (i) loss of a phalange on the 4th and 5th digits of the pes between *N. maccoyi*, and *N. mariei*, *N. rankini*, and *N. gracilis* + *N. sleveni* to infer 4 independent occurrences of this character evolving; (j) increased number of presacral vertebrae between *N. maccoyi*, and *N. gracilis* + *N. sleveni*; and the windowed lower eyelid between *N. maccoyi* and, *N. greeri* + *N. rankini*, if it is considered to have evolved from a primitively scaled or 'scaled' lower eyelid.

Diagnosis for the proposed subgenera within *Nannoscincus* are given below.

Subgenus **Nannoscincus** Günther

Anotis Bavay, 1869: 29 (type species *Anotis mariei*, Bavay, 1869).

Nannoscincus Günther, 1872: 421 (type species *Nannoscincus fuscus*, Günther, 1872 = *Nannoscincus mariei*).

Type Species

As for genus.

Diagnosis

The species here included in the subgenus *Nannoscincus* can be distinguished from other *Eugongylus* group genera by sharing the following combination of derived characters : atlantal arches fused dorsally; loss of a single phalange in the 4th digit of the manus (2.3.4.4.3 for *N. greeri*, *N. rankini* and *N. mariei*, further reduced to 2.3.3.3.2 in *N. gracilis* and 2.3.3.3.0 in *N. sleveni*); ear opening reduced or completely scaled over; supranasals absent; prefrontals small to diminutive and widely separated, or absent; upper labials 6; single pair of enlarged nuchals.

Distribution

New Caledonia.

Subgenus **Nannoseps** n. subgen.

Type Species

Saiphos maccoyi, Lucas and Frost, 1894).

Diagnosis

The monotypic subgenus *Nannoseps* can be distinguished from other *Eugongylus* group genera by the following combination of derived characters: frontal bone contacting premaxilliary thereby excluding contact between nasals; loss of a single phalange in the 4th digit of the manus (2.3.4.4.3); loss of a single phalange in the 4th and 5th digits of the pes (2.3.4.4.3); ear opening reduced; supranasals absent; prefrontals absent; upper labials 6; single pair of enlarged nuchals.

Distribution

Southeastern Australia.

Etymology

Nannoseps is derived from the Greek 'nannos' meaning dwarf or little, and the Latin 'seps' for lizard.

RELATIONSHIPS WITHIN THE SUBGENUS *NANNOSCINCUS*

Within the subgenus *Nannoscincus* the most parsimonious interpretation proposes an initial dichotomy between the species *N. mariei* + *N. rankini* + *N. greeri* (the *N. mariei* species group), and the species *N. gracilis* + *N. sleveni* (the *N. gracilis* species group).

The *N. mariei* species group is diagnosed by the derived characters: (d) a single loreal scale; (e) reduction to 5 lower labials; and tentatively (l) loss of the left oviduct. The *N. gracilis* species group is diagnosed by the derived characters: (h) loss of an additional phalange on the 3rd and 4th digits of the manus; (j) a presacral vertebrae number of generally 32 or more.

This initial subdivision infers parallel evolution of character states in: (b) the 1st supraciliary scale contacting the frontal between *N. greeri* + *N. rankini*, and *N. gracilis* + *N. sleveni*; (g) the 12th rib only contacting the mesosternum between *N. rankini*, and *N. gracilis* + *N. sleveni*; (i) loss of a phalange on the 4th and 5th digits of the pes between *N. mariei*, *N. rankini*, and *N. gracilis* + *N. sleveni*; and the 'scaled' lower eyelid between *N. mariei* and the *N. gracilis* species group if it is considered to have evolved from an ancestor with a primitively scaled or windowed lower eyelid.

COMMENTS

The majority of scincid genera (ie. 7 of 10 recognised by Sadlier, 1987) occurring in New Caledonia are either endemic to the main island (*Geoscincus*, *Graciliscincus*, *Marmorosphax*, *Tropidoscincus*, *Sigaloseps*) or only extend outside the main island east to the nearby Loyalty Islands (*Phoboscincus*, *Caledoniscincus*). Those species restricted to mainland New Caledonia usually occur in moist closed forest habitats (only the species of *Tropidoscincus* occur in open habitat), while the endemic New Caledonian genera with representatives on the Loyalty Islands tend to be habitat generalists. Species assigned to *Leiolopisma* by Sadlier (1987) comprise a residue of essentially primitive *Eugongylus* group species whose relationships are obscure. While they cannot at present be placed with certainty within existing monophyletic genera they may eventually be diagnosed as endemic New Caledonian taxa. The strength of the context within which *Nannoscincus* is placed, i.e. within a subgroup of *Eugongylus* group species having the atlantal arches fused to the intercentrum, lies in the occurrence of this character in both surface active and semifossorial or burrowing species. Its presence in the former infers it evolved other than as a modification to a subsurface mode of existence, unlike phalange reduction and/or increase in presacral vertebrae number which have evolved a number of times and are variably expressed in burrowing lineages of skinks. The phylogeny here proposed for the species of *Nannoscincus* presents a scheme of relationships inferring the least number of cases of parallel evolution of characters, and identifies the New Caledonia *Nannoscincus* as a discrete geographical unit. However, these groups or lineages so far defined within *Nannoscincus*, are based on two or less derived characters for which no instance of parallel evolution is inferred, and usually a further 1-4 characters for which one or more instance of parallel evolution is inferred.

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THE GENERA *TILIQUA* AND *CYCLODOMORPHUS* (LACERTILIA: SCINCIDAE): GENERIC DIAGNOSES AND SYSTEMATIC RELATIONSHIPS

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A suite of morphological synapomorphies diagnoses a *Tiliqua* lineage in the subfamily Lygosominae. Two sister genera, *Tiliqua* and *Cyclodomorphus*, are diagnosed in this lineage. On the basis of the available evidence, *Trachydosaurus* is highly derived within *Tiliqua*, and is synonymised with it, while *Hemisphaeriodon* is synonymised with *Cyclodomorphus*. ☐*Scincidae, Tiliqua, Cyclodomorphus, taxonomy, osteology, morphology.*

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The Scincidae has traditionally been considered to be systematically amongst the most complex and refractory of the lizard families. There are a very large number of species, a great morphological diversity with subtle differences between many of the species and frequent convergent evolution. Within this family, the large bluetongue skinks of Australia and New Guinea are amongst the most familiar and recognisable. Yet, even they have been the subject of debate regarding generic boundaries for over a century and a half. Six species, *Lacerta scincoides* Shaw, 1790, *Scincus gigas* Boddaert, 1783, *Scincus nigroluteus* Quoy and Gaimard, 1824, *Cyclodus adelaidensis* Peters, 1864, *Cyclodus occipitalis* Peters, 1864 and *Tiliqua occipitalis multifasciata* Sternfeld, 1919, have consistently been grouped together, either as *Tiliqua* Gray, 1825, or *Cyclodus* Wagler, 1828, a junior synonym. Associated with this core at various times have been four other groups of species.

The first of these associated groups, consisting only of *Trachydosaurus rugosus* Gray, 1825, was considered distinct from *Tiliqua*, though frequently closely allied to it, by all authors up until 1950, when Mitchell (1950) synonymised it with *Tiliqua*. Since that time, the generic status of *Trachydosaurus* has varied, being regarded as distinct by Copland (1953), Mertens (1958), Glauert (1960), Worrell (1963), Cogger (1975, 1983) and Wells and Wellington (1984, 1985) or synonymous with *Tiliqua* by Storr (1965), Rawlinson (1966), Greer (1979a) and Hutchinson (1981). In the first half of this paper, I refer to this group as *Trachydosaurus*.

The second group, also monotypic, consists of *Hemisphaeriodon gerrardii* (Gray, 1845). First described as a *Hinulia*, which was a predecessor of Boulenger's (1887) enormous polyphyletic assemblage *Lygosoma*, *gerrardii* was placed in a new genus, *Hemisphaeriodon*, by Peters (1867). Boulenger (1887) and Cope (1892a) accepted the generic status of *Hemisphaeriodon*, placing it alongside *Tiliqua* in their classifications. Mitchell (1950) synonymised it with *Tiliqua*, where it has largely remained to the present time, although Wells and Wellington (1984, 1985) resurrected the genus without discussion, and Czechura (1986) placed *gerrardii* with the next group. In the first half of this paper, I refer to this group as *Hemisphaeriodon*.

The third group, currently consisting of *Cyclodus casuarinae* Duméril and Bibron, 1839, *Hinulia branchialis* Günther, 1867 (unpublished work by the author and B. Miller indicates that five taxa are recognisable in this 'species') and *Omolepida maxima* Storr, 1976, has had a more varied history. Although originally described as a *Cyclodus*, *casuarinae* was subsequently removed to the monotypic genera, *Cyclodomorphus* Fitzinger, 1843 and *Omolepida* Gray, 1845. Duméril and Duméril (1851) returned *Omolepida* to the synonymy of *Cyclodus*, while Strauch (1866) recognised it as a subgenus of *Cyclodus*. Boulenger (1887) placed *casuarinae* and *branchialis* together in *Homolepida* (an emendation of *Omolepida*) as a subgenus of *Lygosoma*, an arrangement foreshadowed by Günther's (1867) description of *branchialis* in *Hinulia*. Frost and Lucas (1894) recognised a relationship between this group and *Hemisphaeriodon* when they described *Hemisphaeriodon tasmanicum*, a synonym of *casuarinae*. Cope (1892a) elevated *Homolepida* to generic level, while Smith (1937) returned *Omolepida* to the synonymy of *Tiliqua*. Mitchell (1950) accepted Smith's synonymy, while Storr (1964, 1976) resurrected *Omolepida* as a genus. More recently, Greer (1979a), Hutchinson (1981) and Cogger (1983) have returned *Omolepida* to the synonymy of *Tiliqua*, while Wells and Wellington (1984, 1985) resurrect *Cyclodomorphus* as a genus. In the first half of this paper, I refer to this group as *Cyclodomorphus*.

The final group, the *Egernia luctuosa* species group, comprising *E. luctuosa* (Peters, 1866) and *E. coventryi* Storr, 1978, has generally been placed in *Egernia*. However, Peters (1866) and Mitchell (1950) placed *E. luctuosa* in *Tiliqua*. Peters assigned it to the then subgenus *Omolepida*, although he subsequently (Peters, 1872) placed it in a monotypic genus, *Lissolepis*. Mitchell's placement was accepted by Glauert (1960) and Worrell (1963).

It is clear that consensus has not yet been reached regarding the generic boundaries of *Tiliqua*. This paper begins the taxonomic revision of *Tiliqua* (sensu lato) by redefining what I believe to be the genera within this group, and critically reviewing the evidence for alternative classifications. I base my diagnoses on a range of characters, including scalation, cranial and post-cranial osteology, and coloration. I have not considered soft-tissue characters at this time, as there is insufficient comparative data for other skinks. Character polarity is determined by outgroup comparison (Arnold, 1981) and only derived states used in the diagnoses.

OUTGROUP SELECTION

For the purpose of determining character polarity, I have used three successively more distant outgroups:

1. the genus *Egernia*
2. other non-attenuate skinks of the subfamily Lygosominae, especially *Mabuya*
3. non-attenuate scincine skinks, with emphasis on *Eumeces*

My rationale for the selection of these outgroups is explained below.

Egernia has consistently been considered the genus closest to *Tiliqua* (s.l.) by most authors from Gray (1845) on. Although Boulenger (1887) and Cope (1892a) separated *Tiliqua* and *Egernia* on the basis of separation or contact of palatine bones, Waite (1929) noted that this character was invalid in the form expressed by Boulenger. In both genera, the palatine bones are usually separated on the midline. Mitchell (1950) believed that the two genera 'separated relatively recently from a common stock and have developed along two monophyletic lines', although no characters of any utility were advanced to define this relationship. The two genera were separated on the basis of the presence or absence of contact of a medial palatine process of the ectopterygoid with the palatines, and tooth shape, but difficulty was experienced in assigning the *Egernia whitii* group, which has narrow contact between palatine and ectopterygoid process.

A close relationship between *Egernia* and *Tiliqua* was also implicit in the classifications proposed and argued by other workers in subsequent years (for review, see Hutchinson, 1981). Greer (1979a) considered the two genera, along with the monotypic *Corucia*, a lineage (the *Egernia* group) within the subfamily Lygosominae, diagnosed on the basis of a single character: a reduced modal number of premaxillary teeth (7-8 vs the primitive 9). Three other synapomorphies were employed in inferring a sister-group relationship between the *Egernia* and *Eugongylus* groups: closure of Meckel's groove in the dentary, loss of pterygoid teeth and loss of a distinct postorbital, although the latter two characters were not employed in diagnosing lineages as they 'were not completely diagnostic for all groups'. However, if the loss of pterygoid teeth and loss of a distinct postorbital be considered less than diagnostic, so too must the sole synapomorphy for the *Egernia* group, as three species of *Egernia*, *E. coventryi*, *E. luctuosa* and *E. major*, have a mode of 9 premaxillary teeth (Greer, 1979a; pers. obs.). Further, loss of pterygoid teeth is not a synapomorphy for the combined *Egernia*/*Eugongylus* group lineage, as they are present in both *Leiolopisma telfairii* and *L. mauritianus* of the *Eugongylus* group (Arnold, 1980) and in *Corucia zebrata* in the *Egernia* group (pers. obs.).

Despite this, there remain three fairly clear lines of evidence for the monophyly of Greer's *Egernia* group. *Tiliqua*, *Egernia* and *Corucia* share a distinctive karyotype, with diploid number 2n=32, nine pairs of macrochromosomes, six pairs of microchromosomes, and pair six smaller than pair five (King, 1973a,b; Donnellan, 1985).

This karyotype is not known from any other lygosomine, scincid or scincomorph group. While it is not possible to determine the direction of karyotypic evolution within the Scincidae, as no group has a demonstrably primitive karyotype as determined by outgroup comparison, each karyomorph may be uniquely derived (Donnellan, 1985). Secondly, immunoelectrophoretic studies (Hutchinson, 1981) have indicated that *Egernia* and *Tiliqua* are each other's closest relatives, with *Corucia* slightly more distant. Finally, intergeneric hybridisation has been reported between captive *E. cunninghami* and *T. gigas* (Rose, 1985), further suggesting that the genetic distance between the two genera is not great.

Although *Corucia* is a member of this lineage, I have not included it with *Egernia* in the first outgroup. *Corucia* displays a combination of recognisably very primitive characters (e.g., pterygoid teeth, double row of supradigital scales) with a number of bizarre autapomorphies (e.g., loss of central supraciliaries, extremely elongate last supralabial, separation of first pair of chin shields, grossly enlarged frontonasal scale, cuspidate teeth, distal end of tail forming a slight hook), at least some recognisably the result of a unique ecology (arboreal herbivory) amongst skinks. Immunological evidence has suggested that it is more distantly related to *Tiliqua* than is *Egernia* (Hutchinson, 1981), and I have consequently relegated it to the second outgroup, where its influence on determination of polarities is diluted.

The *Egernia* lineage has been placed in the subfamily Lygosominae (Greer, 1970a). This assignment has withstood critical evaluation, and the monophyly of the subfamily successfully defended (Donnellan, 1985; Greer, 1986a) against criticism (King, 1973b; Rawlinson, 1974; Hutchinson, 1981). Within the Lygosominae, many lineages have undergone convergent evolution towards a fossorial lifestyle (Greer and Cogger, 1985; Heyer, 1972), with a number of derived characters, especially those associated with burrowing, having evolved a number of times. Complete loss of limbs has evolved at least five times within the subfamily (Greer and Cogger, 1985) with some loss of phalanges and an increase in the number of presacral vertebrae occurring in many other genera. The resulting 'noise' hampers use of a uniform outgroup composed of all non-*Tiliqua* lygosomines. Greer (1977, 1979a, 1983) has attempted to block this 'noise' by placing emphasis on character states in *Mabuya*, as 'the genus that seems to comprise the most generally structurally primitive species among the lygosomines...' (Greer, 1979a: 340). However, of the many plesiomorphies advanced in support of this view (Greer, 1979a), most are also present in *Tiliqua*, *Egernia* and most other non-attenuate lygosomines. Only in the presence of supranasal scales, postorbital bones, and pterygoid teeth is *Mabuya* as a whole notably more primitive than *Egernia* and many other lygosomines. Consequently, I have not placed as much emphasis on character states in *Mabuya* as Greer, but instead have filtered out the influence of convergence in fossorial and cryptozoic species by only considering those lygosomine genera which possess the primitive number of presacral vertebrae (n = 26; Hoffstetter and Gasc, 1969), or only a slight elevation above this (n≤30). Fifty-eight genera or species groups are in this category (*Eugongylus* group: *Caledoniscincus*, *Carlia*, *Cophoscincopus*, *Cryptoblepharus*, *Cyclodina*, *Emoia*, *Eroticoscincus*, *Eugongylus*, *Geomyersia*, *Geoscincus*, *Lampropholis*, '*Leiolopisma*' *entrecasteauxii* species group, '*Leiolopisma*' *nigrofasciolatum* species group, Tasmanian '*Leiolopisma*', New Zealand '*Leiolopisma*', Mascarene Island *Leiolopisma*, other Australian '*Leiolopisma*' (*coventryi*, *jigurru*, *zia*), other Pacific '*Leiolopisma*' (*alazon*, *steindachneri*), *Lygisaurus*, *Marmorosphax*, *Menetia*, *Morethia*, *Nannoscincus* (part: *greeri*, *maccoyi*, *mariei*, *rankini*), *Panaspis*, *Phoboscincus*, *Proablepharus*, *Ristella*, *Saproscincus*, *Sigaloseps*, *Tachygyia*, *Tropidoscincus*, *Tribolonotus*: *Sphenomorphus* group: *Ablepharus*, *Asymblepharus*, *Ateuchosaurus*, *Calyptotis*, *Ctenotus*, *Eremiascincus*, *Eulamprus*, *Fojia*, *Glaphyromorphus* (non *crassicaudis* group), *Gnypetoscincus*, *Lipinia*, *Lobulia*, *Notoscincus*, *Papuascincus*, *Prasinohaema*, *Scincella*, *Sphenomorphus fasciatus* species group, *Sphenomorphus variegatus* species group, *Tropidophorus*; '*Mabuya* group': *Apterygodon*, *Dasia*, *Lamprolepis*, *Mabuya*, *Macroscincus*; *Egernia* group: *Corucia*; data from Greer, 1982, 1983, 1985, 1986b, pers. comm., Greer and Cogger, 1985, Sadlier, 1987 and pers. obs.; species groups in '*Leiolopisma*' follow Sadlier (1987) and M. Hutchinson, pers. comm.) and these are used as the second outgroup.

Three other subfamilies of the Scincidae have been proposed by Greer (1970a). Two of these, the Acontinae and the Feyliniinae are composed of attenuate burrowing species with markedly

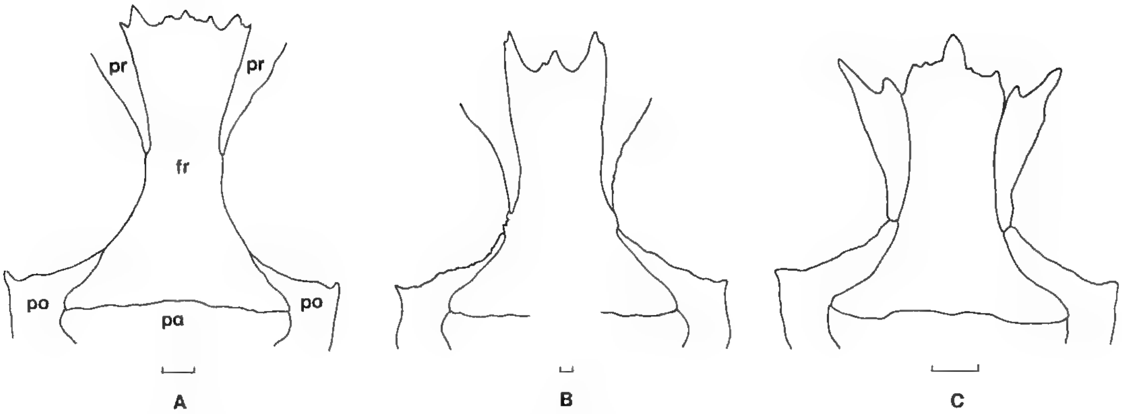

FIG. 1. Dorsal view of interorbital area of skull of A. *Egernia modesta* (Australian Museum (AM) R106893), B. *Tiliqua gigas* (AM R93222) and C. *Cyclodomorphus casuarinae* (AM R127932). Fr = frontal; po = postfrontal; pr = prefrontal. Scale bar = 1mm.

elevated numbers of presacral vertebrae. The remaining subfamily, the Scincinae, is plesiomorphic vis-à-vis the Lygosominae (Greer, 1970a, 1986a; Hutchinson, 1981; Estes, 1983). Within the Scincinae, most genera show marked limb reduction and body elongation, and I have excluded these from the third outgroup, for the same reason as given above. Six scincine genera or subgenera (*Amphiglossus* (*Madascincus*), *Eumeces, Janetaescincus, Pamelaescincus, Scincus* and *Scincopus*), however, have a primitive or near-primitive number of presacral vertebrae (El-Toubi, 1938; Brygoo, 1981; A.E. Greer, pers. comm.), and this group is used as the third outgroup. Brygoo (1981) also lists *Gongylomorphus* as having 26 presacral vertebrae, but two Australian Museum specimens of *G. b. bojeri* (R73340-41) have 32, and I have therefore not included *Gongylomorphus* in this outgroup. Within the Scincinae, *Eumeces* is recognisably the most primitive genus (Greer, 1970a, 1974, 1979a), as well as the largest. Fortuitously, it is also the genus for which the greatest body of literature on scalation and osteology exists (Taylor, 1935; Kingman, 1932; Nash and Tanner, 1970; Hikida, 1978), and I have consequently placed most emphasis on this genus within the third outgroup.

DETERMINATION OF CHARACTER POLARITIES

1. Presacral vertebrae. The primitive number of presacral vertebrae in skinks is 26 (Hoffstetter and Gasc, 1969). All *Egernia* and *Corucia* have a mode of 26 presacral vertebrae, while the range for *Cyclodomorphus, Hemisphaeriodon, Tiliqua* and *Trachydosaurus* is 32-44 (Siebenrock, 1895; pers. obs.).

2. Phalangeal formula of manus. A phalangeal formula of 2.3.4.5.3 is considered primitive for lepidosaurs (Romer, 1956; Greer, 1983, 1987). All *Egernia* species and 44 of 53 genera and species groups in the next two outgroups have this configuration, while only 9 genera have a different formula, involving loss of phalanges in all but *Scincus* (El-Toubi, 1938). *Cyclodomorphus, Hemisphaeriodon* and *Tiliqua* have a manus formula of 2.3.4.4.3 (i.e., loss of one phalanx in the fourth finger), while *Trachydosaurus* has 2.3.3.3.2 (loss of a further three phalanges). These are assumed to be successive derivations from the primitive condition.

3. Phalangeal formula of pes. A phalangeal formula of 2.3.4.5.4 is considered primitive for lepidosaurs. All *Egernia* species and 50 of 53 genera and species groups in the next two outgroups have this configuration. *Cyclodomorphus, Hemisphaeriodon* and *Tiliqua* have a pes formula of 2.3.4.4.3 (i.e., loss of one phalanx in each of the fourth and fifth toes) while *Trachydosaurus* has 2.2.3.3.2 (loss of a further four phalanges). These are assumed to be successive derivations from the primitive condition.

4. Medial margin of orbit. In most skinks the prefrontal and postfrontal bones are widely separated along the lateral margin of the frontal, the separation generally equal to or greater than the smallest width of the frontal. Within *Egernia*, a slightly narrower separation occurs in *E.*

major, while in the members of the second and third outgroups examined, only in *Corucia*, *Macroscincus*, the Mauritian *Leiolopisma* and the *Sphenomorphus fasciatus* species group is the separation narrower. Broad separation of pre- and postfrontal bones is considered primitive, and the narrow separation to broad contact seen in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* (Fig. 1) derived. In *T. adelaidensis*, the separation is greater than in other species, but this is most likely to be a reversal.

5. Upper temporal arch. In most skinks the jugal and squamosal are narrowly to moderately separated along the lateral edge of the postorbital or postfrontal, while in only a few is there direct contact between jugal and squamosal. Within *Egernia*, distinct contact occurs only in most members of the *E. whitii* species group. In other non-attenuate lygosomines examined, the two bones are separated. In scincines, separation occurs in *Scincus* (El-Toubi, 1938) and moderate separation to variable point contact in 11 of the 13 *Eumeces* species for which data is available, while narrow to moderate contact has been reported for two *Eumeces* species (Kingman, 1932). Separation of the jugal and squamosal is assumed primitive for skinks, and the consistent narrow to broad contact seen in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* (Fig. 2) derived.

6. Coronoid process of dentary. In the majority of skinks examined, the coronoid process of the dentary articulates with only the rostral margin of the dorsal process of the coronoid, although in most *Egernia* species the articulation also extends slightly over the rostrolateral face of the coronoid. In *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus*, the coronoid process of the dentary largely covers or completely overlaps the dorsal process of the coronoid laterally (Hoffstetter, 1949). Articulation of the coronoid process of the dentary with only the rostral or rostrolateral margin of the coronoid is considered primitive, and extended lateral overlap of the coronoid (Fig. 3) derived.

7. Lacrimal bone. A distinct lacrimal forming the lateral margin of the lacrimal foramen is present in most skinks, though often very reduced in size and thickness in very small species. Despite a claim of absence in *E. whitii* (Siebenrock, 1892), a well- developed lacrimal was seen in all *Egernia* species examined (n = 20), including *E. whitii* and covering all species groups within the genus. Within the other outgroups, a distinct lacrimal was not found only in *Geomyersia* (Greer, 1982), *Ristella* (A. Greer, pers. comm.), *Menetia* and one species of *Lobulia* (pers. obs.). The presence of a lacrimal is considered primitive, and the loss of the lacrimal seen in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* (Fig. 4) derived.

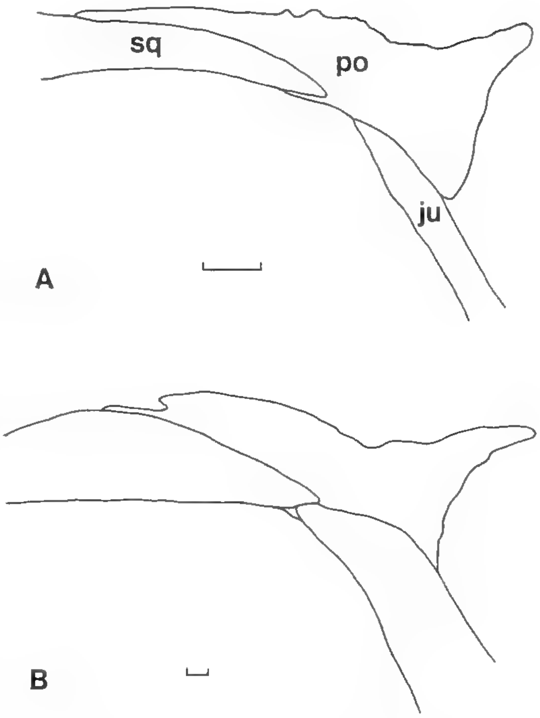

FIG. 2. Right oblique view of upper temporal arch in A. *Egernia saxatilis* (AM R122135) and B. *Tiliqua gigas* (AM R93222). Ju = jugal; po = postfrontal; sq = squamosal. Scale bar = 1mm.

8. Palatine process of ectopterygoid. A medial palatine process of the ectopterygoid, bordering the medial margin of the infraorbital fenestra, has been considered a derived character amongst skinks (Fuhn, 1969; Greer, 1970a,b, 1976; Greer and Cogger, 1985). Within *Egernia*, a long palatine process of the ectopterygoid reaching the palatine was seen in nine of the 20 species examined. However, these nine species comprised only three of nine recognisable species groups within the genus (Shea, in prep.). In the second outgroup, the process is lacking in 23 genera and species groups, present but not contacting the palatine in three, present and contacting the palatine in nine, and variably present (i.e.,

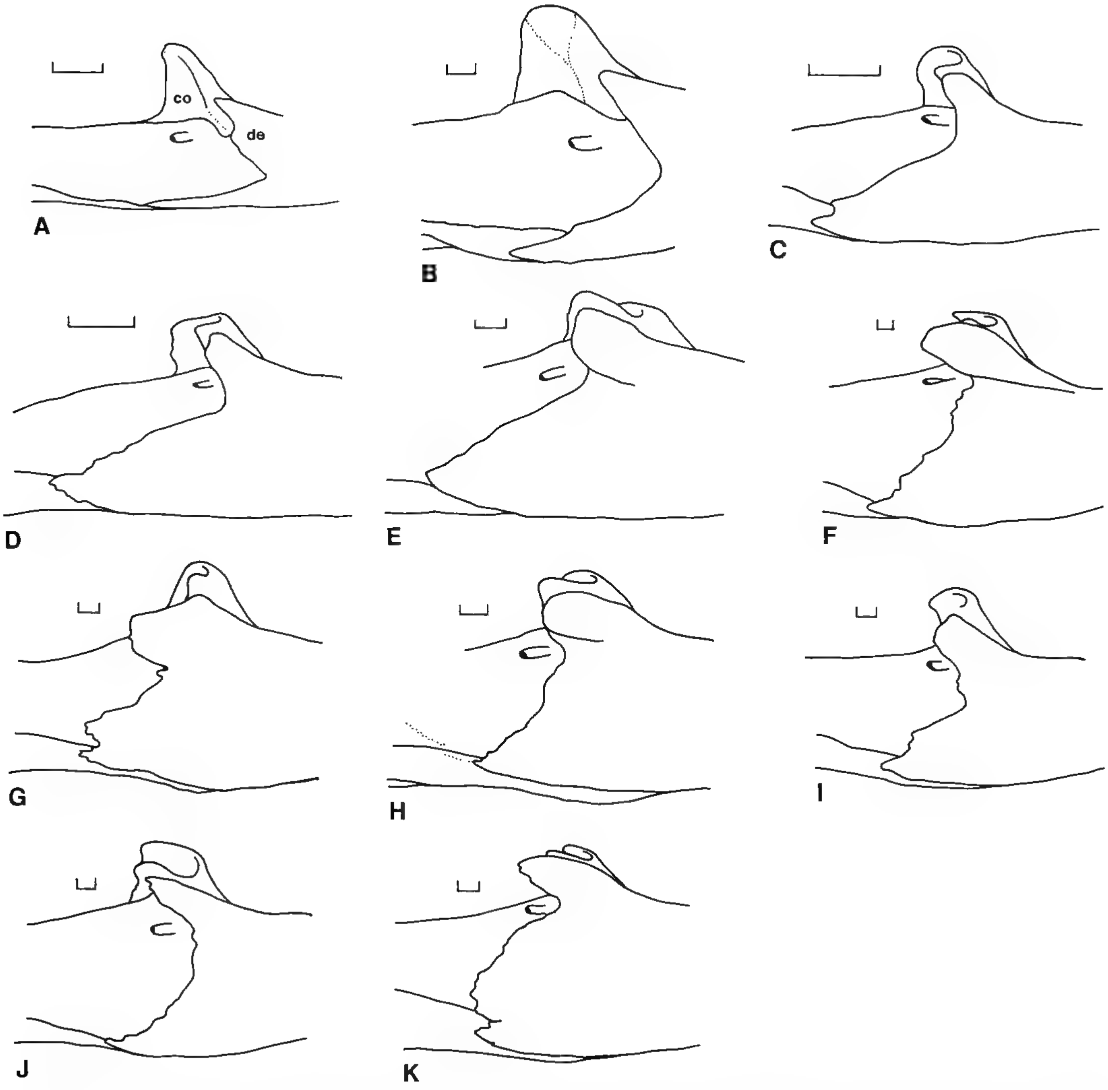

FIG. 3. Right lateral view of coronoid region of mandible of A. *Mabuya multifasciata* (AM R92623), B. *Egernia cunninghami* (AM R66018), C. *Cyclodomorphus branchialis* (AM R127930), D. *C. casuarinae* (AM R37706), E. *C. gerrardii* (AM R127926), F. *Tiliqua gigas* (AM R93222), G. *T. multifasciata* (AM R127920), H. *T. nigrolutea* (AM R106842), I. *T. occipitalis* (AM R127925), J. *T. rugosa* (AM R95260), K. *T. scincoides* (AM R127901). Co = coronoid; de = dentary. Scale bar = 1mm.

present in only some species) in three. Within *Mabuya*, the process has only been seen in five species (Greer, 1976; pers. obs.). In the third outgroup, the process is lacking in all genera. Absence of a medial palatine process of ectopterygoid is considered primitive, and its presence in *Cyclodomorphus, Hemisphaeriodon, Tiliqua* and *Trachydosaurus* (Fig. 5) derived.

9. Heterodonty. Most skinks have a homodont dentition, with marked heterodonty only reported in *Cyclodomorphus, Hemisphaeriodon, Tiliqua, Trachydosaurus* and one species each of *Eumeces* and *Lerista* (Estes and Williams, 1984). *Egernia, Mabuya*, other *Eumeces* species, and all other species examined within the outgroups have homodont dentition. Although there is variation in the degree of heterodonty in adults, juveniles of all *Cyclodomorphus, Hemisphaeriodon, Tiliqua* and *Trachydosaurus* species have a single markedly enlarged tooth in

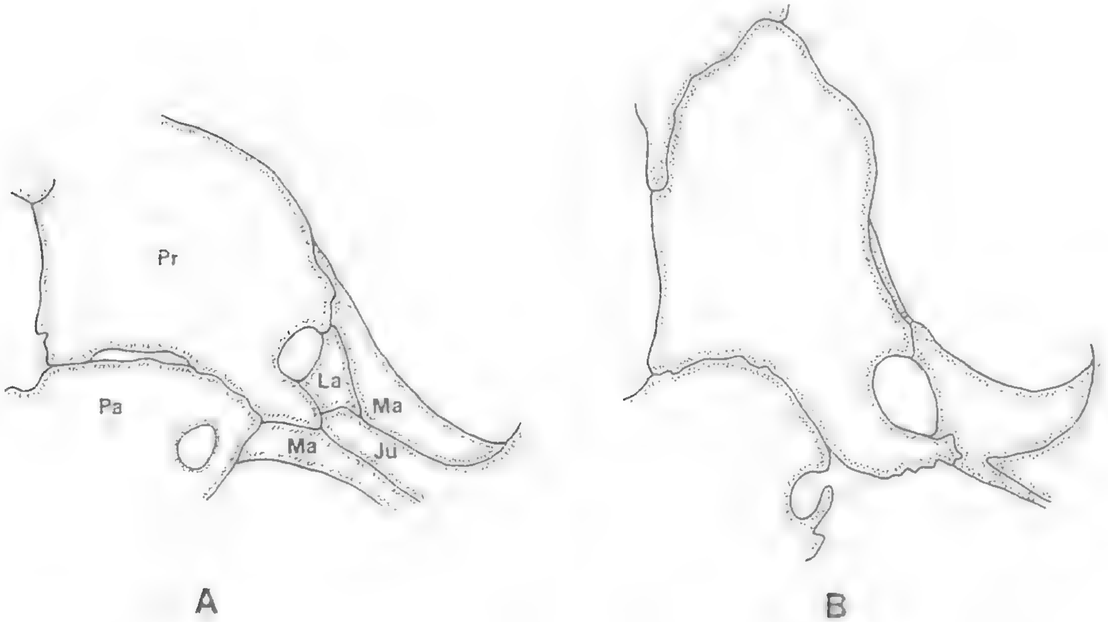

FIG. 4. Right caudal view of rostral margin of orbit of A. *Egernia carinata* (Western Australian Museum (WAM) R37926) and B. *Tiliqua nigrolutea* (AM R106842). Ju = jugal; La = lacrimal; Ma = maxilla; Pa = palatine; Pr = prefrontal. Scale bar = 1mm.

the maxillary (position number 7 or 8) and dentary (position number 10) arcades (Shea, pers. obs.). Homodonty is considered primitive and juvenile heterodonty derived (Estes and Williams, 1984).

10. Scales over temporal region. The majority of skinks have two supralabials caudal to the subocular supralabial, a single primary temporal dorsally between these, a single lower secondary temporal caudodorsal to the last supralabial, and a single upper secondary temporal dorsally, bordering parietal, primary temporal and lower secondary temporal, overlapping the latter scale. Generally, the last two supralabials are subequal in height, and both higher than the preceding supralabials (Fig. 6). This is assumed to be the primitive temporal configuration. All *Egernia* species, over two-thirds of the genera and species groups in the second outgroup, and *Eumeces, Scincus* and *Scincopus* in the third outgroup show this arrangement, although some genera in the *Sphenomorphus* group and a few *Eumeces* species have reversed the overlap of upper and lower secondary temporals. Other genera in the second and third outgroups show a variety of modifications to this pattern, mostly apparently involving subdivision of scales, particularly the lower secondary temporal and last supralabial scales. In *Cyclodomorphus, Hemisphaeriodon* and *Tiliqua*, the last supralabial is divided into an upper and a lower scale by a suture, leaving a single low 'last supralabial' bordering the lip. Most *Tiliqua* species additionally show further divisions of the primary and lower secondary temporal scales. In *Trachydosaurus*, the number and pattern of division of the supralabial and temporal scales is variable. However, the consistently low last two supralabials, frequent irregularity of the caudal margin of the 'lower secondary temporal' and the number and pattern of overlap of surrounding scales suggests that the two parts of the lower secondary temporal, and sometimes the upper part of the last supralabial, have fused again, as part of a general reduction of number of scales in this species (see below).

11. Supraciliary scales. Most species in the first two outgroups modally have eight or more supraciliaries, although most *Mabuya* have 5-6 supraciliaries. In the third outgroup, *Amphiglossus* (*Madascincus*), *Janetaescincus, Pamelaescincus* and over 70% of *Eumeces* species have modes of 7 or more supraciliaries. Seven to nine supraciliaries is considered primitive for skinks,

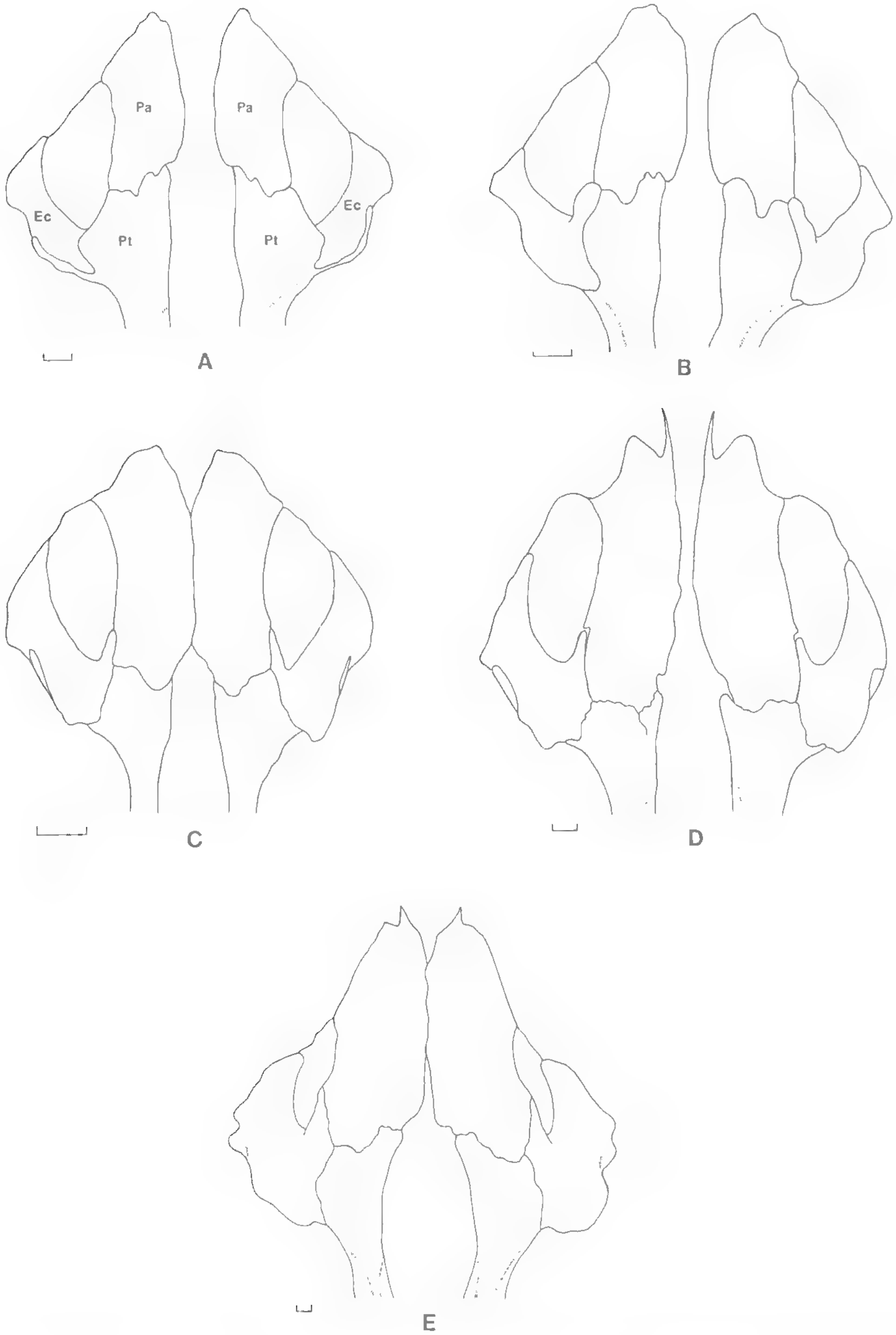

FIG. 5. Ventral view of palate of A. *Egernia mcpheei* (AM R127936), B. *E. pulchra* (WAM R47386), C. *Cyclodomorphus casuarinae* (AM R37706), D. *C. gerrardii* (AM R13084) and E. *Tiliqua scincoides* (AM R96439). Ec = ectopterygoid; Pa = palatine; Pt = pterygoid. Scale bar = 1mm.

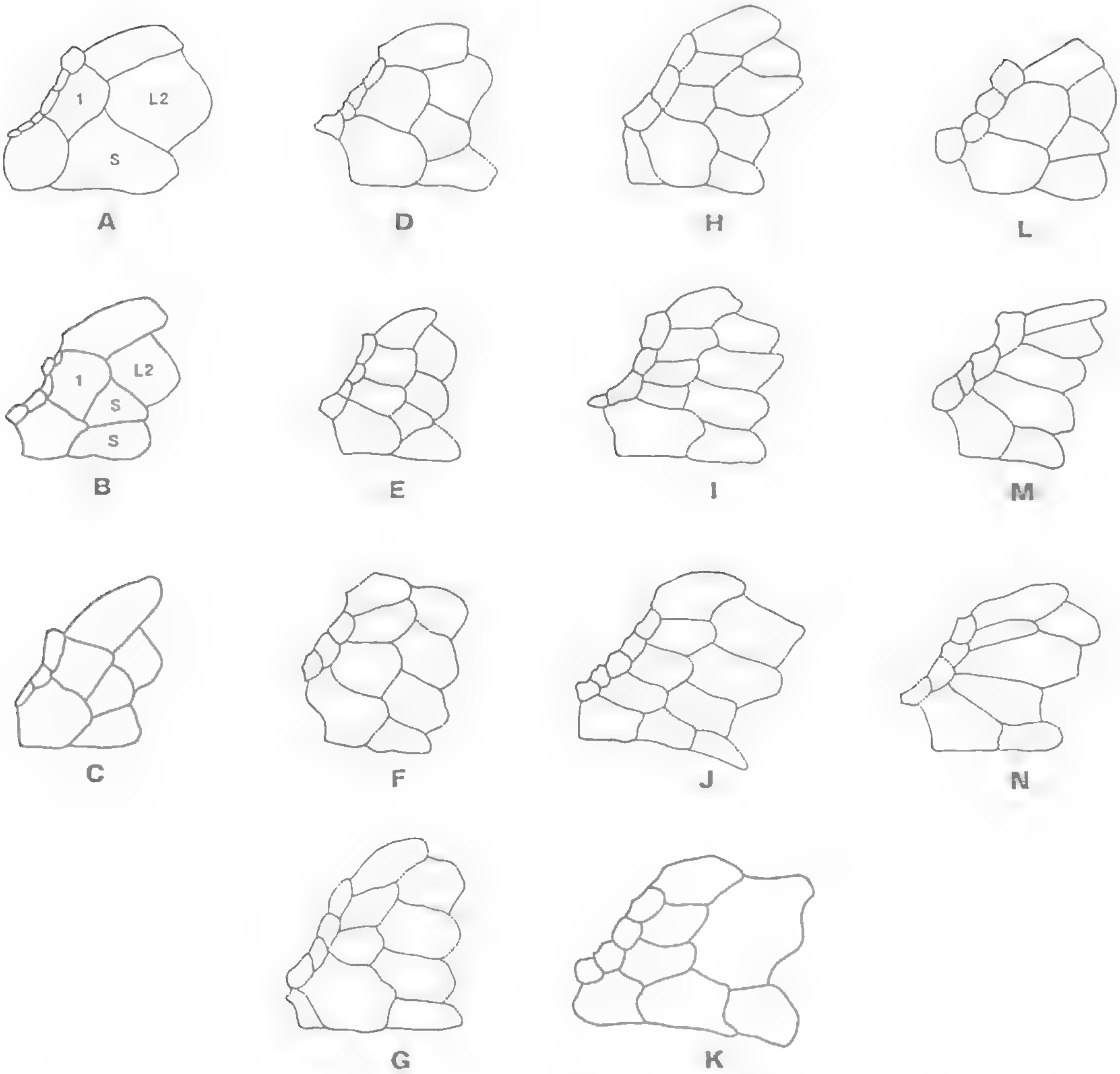

FIG. 6. Scales of temporal region of A. *Egernia saxatilis* (AM R15273), B. *Cyclodomorphus casuarinae* (AM R107594), C. *C. branchialis* (AM R102728), D. *C. gerrardii* (AM R47341), E. *C. gerrardii* (AM R47876), F. *Tiliqua multifasciata* (AM R10080), G. *T. occipitalis* (AM R123943), H. *T. nigrolutea* (AM R28494), I. *T. nigrolutea* (AM R106903), J. *T. rugosa* (AM R105622), K. *T. rugosa* (AM R102594), L. *T. adelaidensis* (Naturhistorisches Museum Vienna 20472.2), M. *T. scincoides* (AM R123927), N. *T. gigas* (Naturhistorisches Museum Basel 6218). 1 = primary temporal; L2 = lower secondary temporal; S = last supralabial.

and modes of six or fewer derived. *Cyclodomorphus, Hemisphaeriodon, T. gigas* and *T. scincoides* usually have six supraciliaries while other *Tiliqua* and *Trachydosaurus* usually have five or fewer supraciliaries (Fig. 7).

12. Tongue colour. Although this character has been relatively little studied in skinks, most Australian lygosomines I have examined in life (including 14 species of *Egernia*) have pink to light grey tongues. *Corucia* also has a pink tongue. Consequently, I believe that a pink or only lightly melanised tongue is primitive and the dark blue-black to bright blue tongues of *Cyclodomorphus, Hemisphaeriodon, Tiliqua* and *Trachydosaurus* are derived. Although *Hemisphaeriodon* variably has a pink or blue tongue as an adult, the tongue is dark blue-black in juveniles. Tongue colour in life is not known

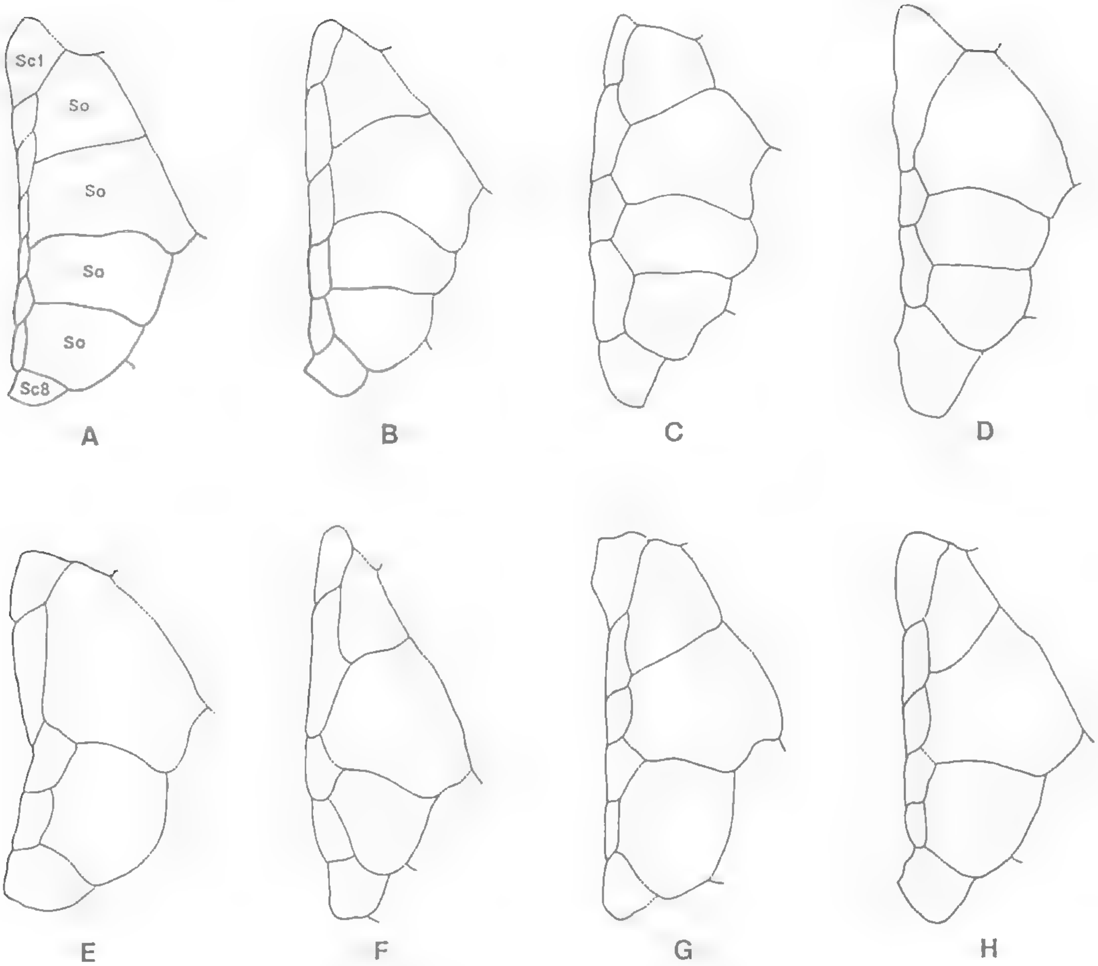

FIG. 7. Supraocular and supraciliary scales of A. *Egernia whitii* (AM R125299), B. *Tiliqua scincoides* (AM R123923), C. *T. nigrolutea* (AM R111500), D. *T. rugosa* (AM R102594), E. *T. multifasciata* (AM R10080), F. *T. adelaidensis* (South Australian Museum (SAM) R2227), G. *Cyclodomorphus gerrardii* (AM R50219), H. *C. casuarinae* (AM R112395). Sc1 = first supraciliary; Sc8 = eighth (last) supraciliary; So = supraoculars.

for *T. adelaidensis*, although long-preserved material shows no pigmentation on the tongue.

13. Colour pattern. Broad patterns of dorsal and lateral coloration have been frequently used in skink systematics at the generic level (Greer, 1970b, 1974, 1979b). The majority of taxa within the outgroups, including most *Eumeces*, *Mabuya* and *Egernia* species, show strong indications of a longitudinally striped pattern dorsally and laterally, generally with some or all of the following elements: continuous dark dorsal stripes, longitudinally aligned dark dorsal streaks, a broad dark upper lateral stripe and a pale midlateral stripe. In contrast, strongly banded colour patterns are uncommon in all outgroups (Greer, 1970b, 1979b). A dominance of longitudinal elements of pattern is considered primitive, and strongly banded patterns derived. Most *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* have a dorsal and lateral body and tail pattern of strongly contrasting light and dark bands. Two species (*T. nigrolutea*, some *Trachydosaurus*) have the transverse elements obscured by expansion of the dark-pigmented areas, while *T. adelaidensis* has a back pattern of broken narrow dark vermiculations on a light background. *Cyclodomorphus* species have either narrow alternating light and dark bands

(most *C. casuarinae*) or a pattern of dark and light spots (*C. branchialis*, *C. maximus*), which in all species are most prominent in juveniles. However, even in *Cyclodomorphus* and *T. adelaidensis*, the dark markings are transversely aligned rather than longitudinal, and I believe that the pattern in these cases is most simply explained as a secondary reduction of the broad-banded motif.

14. Subocular scale row. The presence of a complete row of enlarged subocular scales, separating the lower eyelid from the supralabials, has variously been considered primitive (Fuhn, 1969; Greer and Cogger, 1985) or derived (Greer, 1982; Sadlier, 1987). In attempting to survey this character, I have experienced occasional difficulties in differentiating subocular scales from enlarged granules on the ventral margin of the lower eyelid. In these instances, I have defined a complete subocular scale row as existing only when fewer than three moderate to large scales border the subocular supralabial between presubocular and postsubocular series. Within *Egernia*, a complete subocular row is present only in the *E. luctuosa* species group, *E. major*, *E. rugosa* and a few members of the *E. whitii* species group. In the second and third outgroups, a complete subocular row is consistently present in 16 genera or species groups, variably present in four (and then only in a few species), and absent in 39 genera or species groups. Most *Eumeces* and *Mabuya* species have an incomplete subocular row. The incomplete subocular scale row seen in *Cyclodomorphus* and *Hemisphaeriodon* is primitive and the complete, even subocular row, with 0-1 scales interposed between presubocular and postsubocular series, seen in *Tiliqua* and *Trachydosaurus* (Fig. 8) is derived.

15. Nuchal scales. In general, transversely enlarged nuchal scales exhibit three patterns in skinks: absent (i.e., scales bordering the caudal margin of parietals not noticeably wider than succeeding scales, each scale overlapping three scales caudally), a single pair present (each nuchal overlapping four or more scales caudally), or a variable number of multiple pairs present (Fig. 9). The first condition is rare in the first three outgroups, and is considered derived. However, it is more difficult to determine the relative polarities of the other two conditions. In *Egernia*, a single pair of nuchals is characteristic of the *E. whitii* species group, while most other groups have multiple pairs of nuchal scales. Within the second outgroup, a single pair of nuchals characterises most members of the *Eugongylus* group, *Mabuya*, *Macroscincus* and *Dasia*, while multiple pairs of nuchals are characteristic of most members of the *Sphenomorphus* group and *Lamprolepis*. Within the third outgroup, *Eumeces*, *Scincus* and *Scincopus* have multiple pairs of nuchals, while *Janetaescincus* and *Pamelaescincus* lack nuchals. Because of the more widespread occurrence of multiple nuchals in *Egernia*, I am inclined to consider multiple nuchals primitive within the *Tiliqua* lineage. *Cyclodomorphus* and *Hemisphaeriodon* have multiple pairs of nuchals, while most *Tiliqua* and *Trachydosaurus* lack nuchals (Fig. 9). The exception, *T. adelaidensis*, has a variably expressed single pair of slightly enlarged nuchals generally separated by an internuchal.

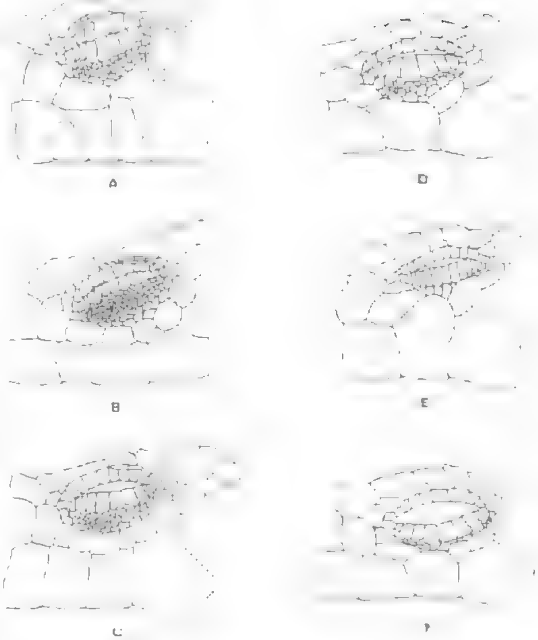

FIG. 8. Periorbital scalation of A. *T. nigrolutea* (AM R28494), B. *T. rugosa* (AM R102594), C. *T. multifasciata* (AM R123942), D. *C. branchialis* (AM R101805), E. *C. gerrardii* (AM R50219), F. *C. casuarinae* (AM R107594).

16. Jugal bone. The dorsal process of the jugal is long and slender in all of the outgroups, generally much narrower than the adjoining jugal process of the maxilla, although in some *Egernia* species and a few other skinks the caudoventral angle bears a narrow spur to support the quadratojugal ligament. A narrow dorsal process, rounded in cross-section, as occurs in

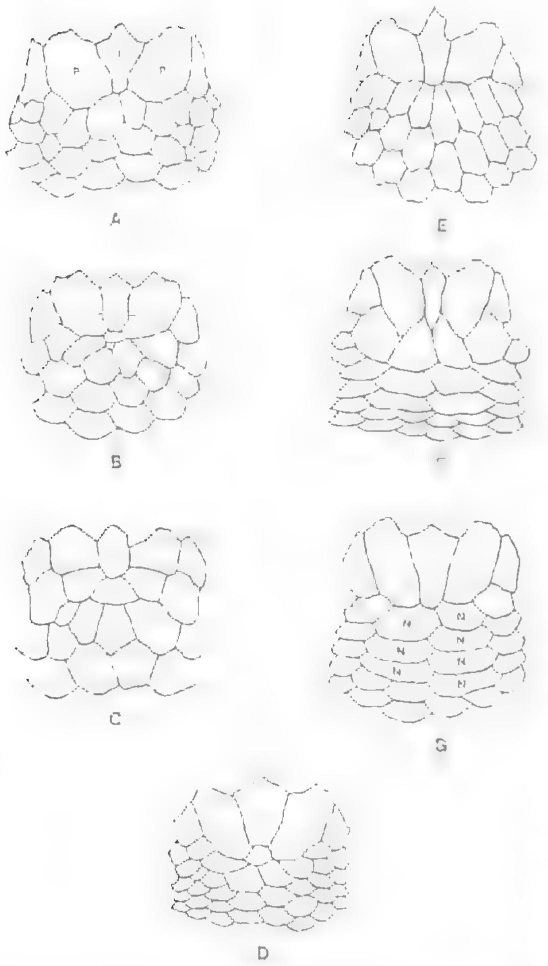

FIG. 9. Scales of nuchal region of A. *Tiliqua gigas* (United States National Museum 195733), B. *T. nigrolutea* (AM R111500), C. *T. rugosa* (AM R105622), D. *T. adelaidensis* (SAM R2227), E. *T. multifasciata* (AM R123942), F. *Cyclodomorphus gerrardii* (AM R47341), G. *C. casuarinae* (AM R112395). P = parietal; I = interparietal, N = nuchal.

Hemisphaeriodon and most *Cyclodomorphus*, is considered primitive. In *Tiliqua* and *Trachydosaurus*, the dorsal process is much more robust (Fig. 10), apparently largely due to expansion of its caudal free margin, producing a flattened cross-section. This expansion of the caudal margin is particularly evident at the dorsal and ventral extremities, which are expanded into two caudally-directed flanges. *C. branchialis* and *Hemisphaeriodon* show some trend in this direction, but in both the expansion is less than in *Tiliqua* and *Trachydosaurus*, as is evidenced by the the lack of expansion of the caudoventral angle beyond the maxilla, and in *Hemisphaeriodon* by the rounded cross-section and the very narrow, straight dorsal extremity.

17. Rostral margin of frontal bone. In most skinks the frontal extends superficially a variable distance laterally along the nasals, forming lateral frontal processes between nasals, prefrontals and often the maxillae. These processes are consistently present, and usually long in the outgroups, and in *Tiliqua* and *Trachydosaurus*, although in *Eugongylus* they extend into the nasals rather than along their lateral border. In *Cyclodomorphus* and *Hemisphaeriodon* they are either completely absent, or when present in some individuals, short and less developed than the opposing caudomedial frontal processes of the maxillae. Consequently, I believe that the presence of superficial lateral rostral frontal processes, forming a W-shaped rostral frontal margin, is primitive, and their absence, replaced by caudomedial processes from the maxillae, and leaving a Λ-shaped frontal margin (Fig. 11), is derived.

18. Supraocular scales. Four supraoculars, the first two contacting the frontal, has been considered the primitive condition for skinks (Greer, 1974; Perret, 1975; Greer and Cogger, 1985). This configuration occurs in all *Egernia* species, and in at least some species in 46 of 51 genera and species groups in the second outgroup, although most *Mabuya* species have the first three supraoculars contacting the frontal. In the third outgroup, *Amphiglossus* (*Madascincus*), *Janetaescincus* and *Pamelaescincus* have four supraoculars (although fusion of frontoparietals and frontal makes it impossible to determine the pattern of frontal contact), *Scincus* and *Scincopus* have multiple supraoculars, and most *Eumeces* have four supraoculars with the first three contacting the frontal, although some species have the four-two configuration. The evidence suggests that the four-two configuration is primitive for lygosomines at least, and reduction either in total number or number contacting the frontal is derived. In *Tiliqua*, *T. gigas*, *T. nigrolutea* and *T. scincoides* usually have the primitive condition, while *T. multifasciata*, *T. occipitalis* and *T. rugosa* usually have the first and second supraoculars fused, leaving only a single supraocular contacting the frontal. *T. adelaidensis*, *Cyclodomorphus* and *Hemisphaeriodon* have only three supraoculars, but two contacting the frontal (Fig. 7). On the basis

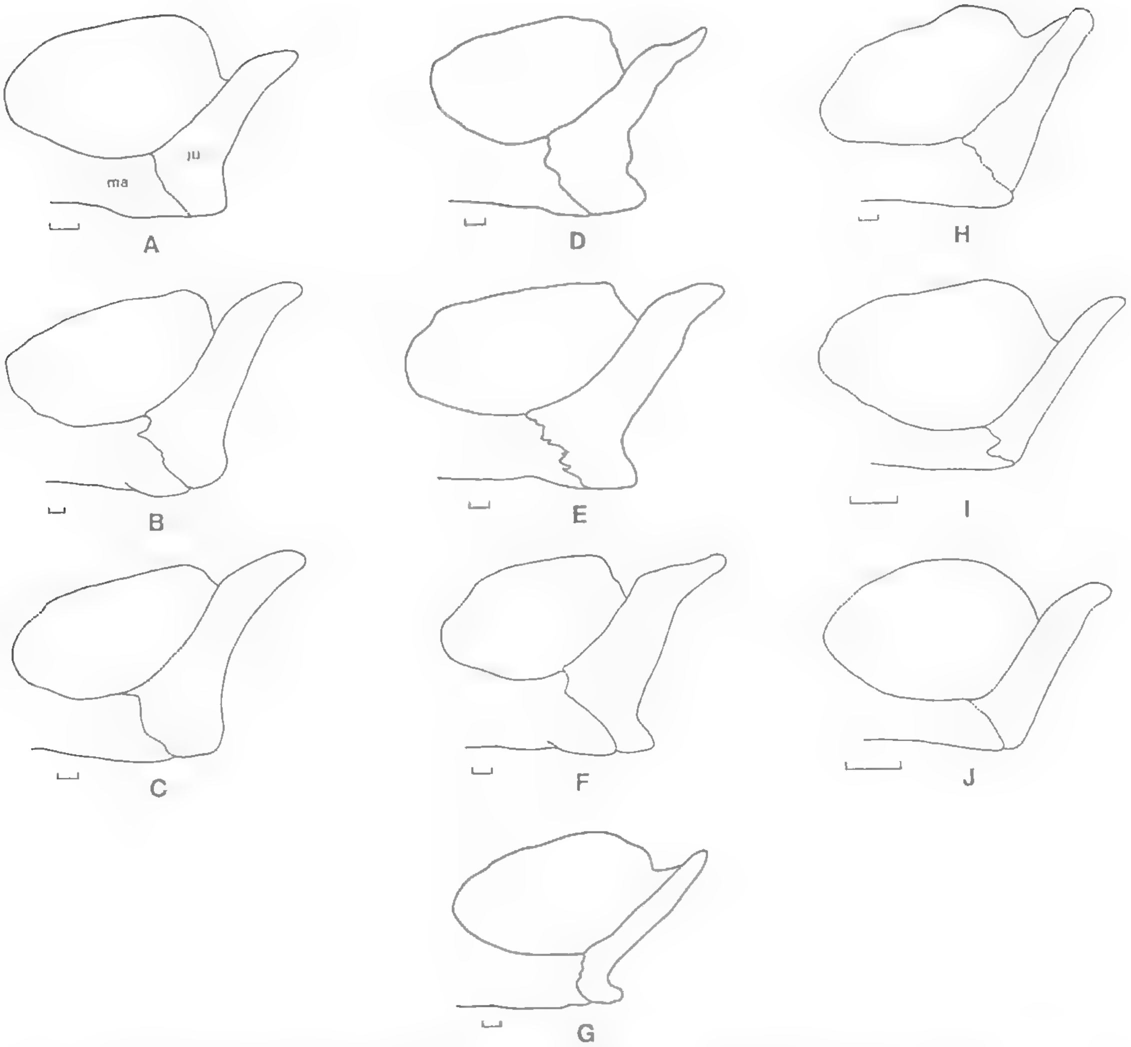

FIG. 10. Lateral view of jugal of A. *Tiliqua scincoides* (AM R127904; SVL = 95mm), B. *T. gigas* (AM R93222), C. *T. rugosa* (WAM R13162), D. *T. nigrolutea* (AM R127909), E. *T. occipitalis* (AM R127925), F. *T. multifasciata* (AM R100984), G. *Egernia cunninghami* (AM R66018), H. *Cyclodomorphus gerrardii* (AM R13084), I. *C. casuarinae* (AM R37706), J. *C. branchialis* (AM R127930). Ju = jugal; Ma = maxilla. Scale bar = 1mm.

of the supraciliary contact pattern, it appears that the second and third supraoculars have fused in these taxa. However, in that *T. adelaidensis* modally has only five supraciliaries, like most *Tiliqua*, while *Cyclodomorphus* and *Hemisphaeriodon* have the more primitive six, I believe that fusion of the second and third supraoculars has occurred independently in this species.

19. Ear lobules. Most generally primitive skinks have a moderate to large external ear, with several rounded to acute lobules along the rostral margin (Perret, 1975; Greer, 1982), although lobules are generally lacking in those taxa which have a greatly reduced external ear. Of those taxa which have a moderate to large ear, several moderate to large lobules are present in all *Egernia* species and consistently present in half (24 of 48) of the genera and species groups in the second outgroup (including *Corucia*, most *Mabuya*, and most members of the *Eugongylus* group). In the third outgroup, ear lobules are

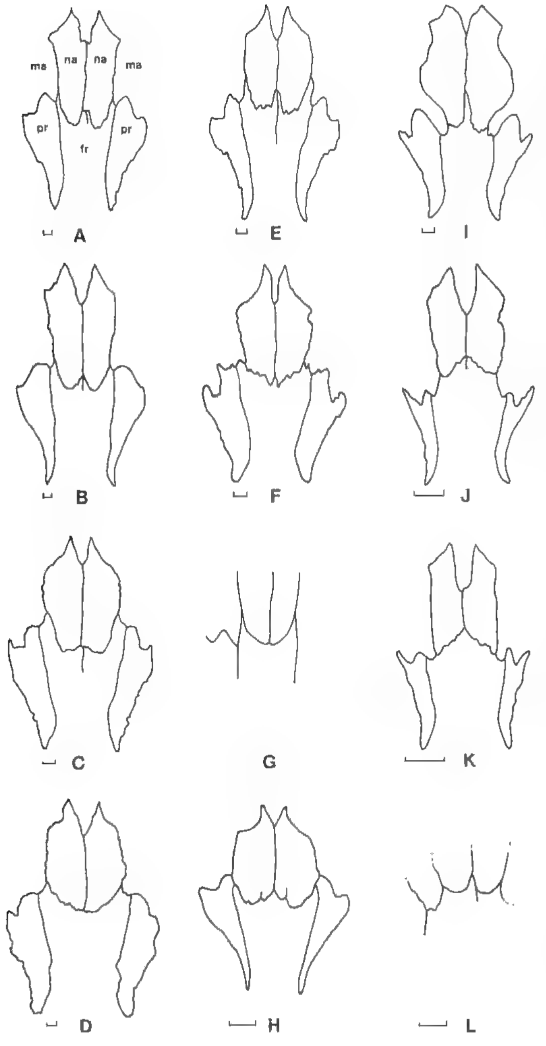

FIG. 11. Dorsal view of fronto-nasal region of skulls of A. *Tiliqua scincoides* (AM R127901), B. *T. gigas* (AM R93222), C. *T. nigrolutea* (AM R127911), D. *T. rugosa* (AM R127916), E. *T. occipitalis* (AM R127925), F. *T. multifasciata* (AM R100984), G. *T. adelaidensis* (SAM R4307A), H. *Egernia striata* (WAM R25402), I. *Cyclodomorphus gerrardii* (AM R13084), J. *C. casuarinae* (AM R37706), K. *C. branchialis* (AM R127930), L. *C. maximus* (WAM R77042). Fr = frontal; ma = maxilla; na = nasal; pr = prefrontal. Scale bar = 1mm.

generally present in *Eumeces* and *Scincopus*, but absent in *Janetaescincus* and *Pamelaescincus*. Although the evidence is not conclusive, the condition shown by *Egernia, Corucia, Mabuya* and *Eumeces*, several moderate to large lobules along the rostral margin of the ear, is considered primitive, and the 0-2 small rounded lobules seen in *Cyclodomorphus, Hemisphaeriodon* and *T. adelaidensis*, derived. It is difficult to assess the condition of the rostral margin of the ear in *Trachydosaurus*, as the scales are thick and bony, and evenly grade into smaller bony scales deep within the external auditory meatus, but these thickened bony scales may be derived from the lobules of other *Tiliqua* species.

THE *TILIQUA* LINEAGE

The species variously assigned to *Cyclodomorphus, Hemisphaeriodon, Tiliqua* and *Trachydosaurus* share the derived condition in characters 1-13, and constitute a lineage, which may be defined as follows:

Osteology: Prefrontal and postfrontal narrowly separated or in contact; jugal and squamosal in contact; lacrimal absent; medial palatine process of ectopterygoid strong, broadly contacting palatine; coronoid process of dentary laterally overlapping coronoid; single grossly enlarged tooth in maxilla (position 7 or 8) and dentary (position 10) in juveniles; presacral vertebrae 32-44; phalangeal formulae of manus and pes 2.3.4.4.3/2.3.4.4.3 or fewer.

Scalation: Caudalmost supralabial divided into an upper and a lower scale; supraciliaries modally six or fewer.

Coloration: tongue deeply pigmented, at least in juveniles, blue- black to bright blue; dorsal and lateral pattern on body and tail predominantly consists of narrow to broad bands or transversely aligned vermiculations or spots, at least in juveniles.

THE HOLOPHYLY AND RELATIONSHIPS OF THE *TILIQUA* LINEAGE

There seems little doubt that the *Tiliqua* lineage is holophyletic. Two characters seem particularly telling in this regard: the increase in number of presacral vertebrae and the pattern of phalangeal loss. Within the *Egernia* group, these characters readily separate the *Tiliqua* lineage from both *Egernia* and *Corucia*, with no evidence of intermediacy. The *Egernia luctuosa* species group is clearly not a member of the *Tiliqua* lineage on both characters, having the primitive number of presacral vertebrae and phalanges.

No skinks currently outside of the *Egernia* group appear to be members of the *Tiliqua* lineage or likely close relatives. The cluster of genera closest to the *Egernia* group, the *Eugongylus* group, rarely show marked increases in number of presacral vertebrae or phalangeal loss, apart from the loss of the first finger in *Carlia*, *Lygisaurus*, *Menetia*, *Ristella* and *Saproscincus tetradactyla* (Greer, 1974, 1979a; pers. obs.), a derived state that does not occur within the *Egernia* group. The only two exceptions to this pattern are *Graciliscincus*, which has a similar number of presacral vertebrae to the *Tiliqua* lineage while still retaining the primitive phalangeal configuration, and *Nannoscincus*, in which there is a mosaic of taxa with elevated numbers of presacral vertebrae and phalangeal loss (Sadlier, 1987, pers. comm.), including the combination seen in the *Tiliqua* lineage. However, it is apparent that this similarity between *Nannoscincus* and the *Tiliqua* lineage is due to convergence, as *Nannoscincus* is both monophyletic and clearly a member of the *Eugongylus* group rather than the *Egernia* group (Greer, 1974; Sadlier, 1987), and otherwise shows little resemblance to *Tiliqua*.

Although *Egernia* has been shown to be the genetically closest genus to the *Tiliqua* lineage (Hutchinson, 1981), the nature of the relationship has not previously been determined. Three types of relationship are possible: *Egernia* and the *Tiliqua* lineage are sister-groups; *Egernia* is primitive, possibly ancestral to the *Tiliqua* lineage, or the *Tiliqua* lineage is primitive, possibly ancestral to *Egernia*. The latter hypothesis was favoured by Horton (1972). At first glance, the third hypothesis seems untenable, given the above argument for the holophyly of the *Tiliqua* lineage. However, given the high frequency of parallel evolution and character reversal within the Scincidae, if the third alternative were the case, use of *Egernia* as the primary outgroup would be inappropriate, potentially assigning erroneous character polarities. This is worrying, when it is remembered that in almost all characters used to define the *Tiliqua* lineage, either *Egernia* uniformly shows the 'primitive' condition, or only a few *Egernia* species show the 'derived' condition. However, exclusion of the first outgroup does not reverse the inferred polarity of any character, and hence confirms the highly derived nature of the *Tiliqua* lineage.

In contrast, I have been unable to identify any synapomorphies with which to diagnose *Egernia* vis-à-vis the *Tiliqua* lineage. Previous diagnoses have also failed to demonstrate a sister-group relationship between the two groups. The modern concept of *Egernia* is derived from Boulenger (1887), who placed in one genus a range of species formerly spread over at least five genera. Boulenger's diagnosis utilises only two derived characters compared to generally primitive lygosomine skinks: pterygoid teeth 'few or absent' and lack of supranasal scales. Although Hoffstetter (1949) also records pterygoid teeth in *Egernia*, I have been able to identify them only in one specimen of *E. cunninghami*. Both characters are shared with *Tiliqua*, and the second also with *Corucia*. At best, the second character merely supports the monophyly of the *Egernia* group, and the first the monophyly of *Egernia* + *Tiliqua*. Mitchell (1950), Cogger (1975) and Storr (1978) have subsequently attempted to diagnose *Egernia*. However, none of these diagnoses offer any additional synapomorphies for *Egernia*.

On present knowledge, therefore, the second hypothesis, that *Egernia* is primitive, possibly ancestral to the *Tiliqua* lineage, and potentially a paraphyletic assemblage, seems to be the most likely. Although there are arguments for not recognising paraphyletic taxa (recently discussed by Hutchinson and Maxson, 1987), the interrelationships of the recognisable lineages within *Egernia* remain obscure (Horton, 1972; Storr, 1978; Wells and Wellington, 1984, 1985; Shea, in prep.) and in the absence of firm evidence relating the *Tiliqua* lineage to any one of these other lineages, I prefer to retain the *Egernia* assemblage as a generic unit distinct from the *Tiliqua* lineage.

GENERA WITHIN THE *TILIQUA* LINEAGE

On the basis of characters 14-19, I believe that two sister-taxa can be recognised within the *Tiliqua* lineage. The first of these, comprising the species formerly placed in *Tiliqua* (s.s.) and *Trachydosaurus* and for which the name *Tiliqua* is available, may be diagnosed as follows:

Tiliqua Gray, 1825

Tiliqua Gray, 1825: 201. Type species *Lacerta scincoides* Shaw, 1790, by subsequent designation (Cogger et al., 1983).

Trachydosaurus Gray, 1825: 201. Type species, by monotypy, *Trachydosaurus rugosus* Gray, 1825.

Trachysaurus Gray, 1827: 430. Unjustified emendation pro. *Trachydosaurus*.

Cyclodus Wagler, 1828: pl. 6. Type species, by monotypy, *Cyclodus flavigularis* Wagler, 1828 [= *T. gigas*].

Brachydactylus Smith, 1834: 144. Type species, by monotypy, *Brachydactylus typicus* Smith, 1834 [= *T. rugosa*].

Tiligua Duméril, 1837: 16. Lapsus pro. *Tiliqua.*

Keneaux Duméril, 1837: 16. Nomen nudum. Originally proposed without included species, ex Cocteau MS.

Tachydosaurus Gray, 1838: 288. Lapsus pro. *Trachydosaurus.*

DIAGNOSIS

Moderate to very large skinks, with a complete subocular row of evenly enlarged scales separating supralabials from lower eyelid, nuchals either a single variably expressed pair or absent, and a broad, winglike jugal.

CONTENT

Cyclodus adelaidensis Peters, 1864, *Scincus gigas* Boddaert, 1783, *Tiliqua occipitalis multifasciata* Sternfeld, 1919, *Scincus nigroluteus* Quoy and Gaimard, 1824, *Cyclodus occipitalis* Peters, 1864, *Trachydosaurus rugosus* Gray, 1825, *Lacerta scincoides* Shaw, 1790. See Boulenger (1887) and Cogger et al. (1983) for species synonymies.

NOMENCLATURE

Although *Tiliqua* and *Trachydosaurus* were both erected by Gray (1825), Mitchell (1950), acting as first reviser in the sense of Article 24(b) of the Code of Zoological Nomenclature, selected *Tiliqua* to have precedence over *Trachydosaurus.*

The second taxon, comprising the species variably placed in *Omolepida, Cyclodomorphus* and *Hemisphaeriodon*, for which *Cyclodomorphus* is the earliest available name, may be diagnosed as:

Cyclodomorphus Fitzinger, 1843.

Cyclodomorphus Fitzinger, 1843: 23. Type species, by original designation, *Cyclodus casuarinae* Duméril and Bibron, 1839.

Omolepida Gray, 1845: 71, 87. Type species, by monotypy, *Cyclodus casuarinae* Duméril and Bibron, 1839.

Hemisphaeriodon Peters, 1867: 24. Type species, by monotypy, *Hinulia gerrardii* Gray, 1845.

Homolepida Lütken, 1863: 294. Lapsus pro. *Omolepida.*

Omolepidota Frost and Lucas, 1894: 227. Lapsus pro. *Omolepida.*

DIAGNOSIS

Small to moderately large skinks lacking lateral rostral projections of frontal bone, or with them very reduced, leaving a Λ-shaped frontal margin; second and third supraoculars fused, leaving only three supraoculars, first two contacting the frontal; lobules along rostral margin of ear very reduced (both in size and number) or absent.

CONTENT

Hinulia branchialis Günther, 1867, *Cyclodus casuarinae* Duméril and Bibron, 1839, *Hinulia gerrardii* Gray, 1845, *Omolepida maxima* Storr, 1976. See Cogger et al. (1983) for species synonymies.

NOMENCLATURE

Although *Cyclodomorphus*, a senior objective synonym of *Omolepida*, has been formally used only six times in the 145 years since its erection (Fitzinger, 1860; Wells and Wellington, 1984, 1985; Shea and Wells, 1985; Czechura, 1986; Shea, 1988), while *Omolepida* (or its emendation *Homolepida*) has been frequently used as an available generic or subgeneric name over the same period, I do not believe that recognition of the priority of *Cyclodomorphus* over *Omolepida* disturbs stability or causes confusion (Articles 23(b) and 79(c) of the Code). Mitchell (1950), Hutchinson (1981) and Cogger (1983), while placing both names into the synonymy of *Tiliqua*, clearly recognised the priority of *Cyclodomorphus*. In the previous fifty years, *Omolepida* has been formally used only once in combination with the type species (Storr, 1976), although frequently used as the generic name for the *C. branchialis* complex and *C. maximus* in Western Australia. Use of *Cyclodomorphus* here recognises the rather different concept of the genus I have proposed, and clearly distinguishes this version from that to which the name *Omolepida* had formerly been applied.

Romer (1956) and Cogger et al. (1983) list three additional names in the synonymy of *Tiliqua* and *Trachydosaurus*: *Rachites, Homolepides* and *Silubolepis*. All are apparently derived from an unpublished manuscript, *Tabulae synopticae Scincoideorum*, by J.-T. Cocteau, submitted to the Académie des Sciences in Paris, and described by Duméril (1837). All three names appear to be unavailable. *Rachites* was published without any included species or description (Duméril, 1837; Duméril and Bibron, 1839: 523). There appears to be no justification for associating *Rachites* with *Tiliqua* other than the inclusion of both, along with *Euprepis* Wagler, 1830, *Keneaux*, *Psammites*, *Heremites* and *Arne* (the latter four similarly nomina nuda) as subgenera of the vernacular Sclérobléphárides by Duméril (1837). *Keneaux* Duméril, 1837 was subsequently associated with *Tiliqua* by the inclusion of two of Cocteau's vernacular names, Kéneaux de l'Uranie and Kéneaux de Boddaert, in the synonymy of *Cyclodus nigroluteus* and *C. boddaertii* (Duméril and Bibron, 1839). *Homolepides* Agassiz, 1846 was based, again without included species, on Cocteau's vernacular Omolépides. There is no indication provided by Duméril (1837) as to the status assigned to this name, other than that it was six divisions below a tribe and, in turn, three divisions above *Tiliqua*. Consequently, there appears to be no basis for associating *Homolepides* with the *Tiliqua* lineage. *Silubolepis* Duméril and Bibron, 1839, a name assigned to Cocteau, appears only in the synonymy of *Trachysaurus*, and is not therefore available (Article 11(c)).

An alternative classification reflecting the same relationships as defined here would be to recognise *Tiliqua* and *Cyclodomorphus* as subgenera within an expanded *Tiliqua*. This would emphasise the sister-group relationship between the two taxa. However, I prefer generic separation for three reasons. Firstly the larger *Tiliqua* are frequently used as experimental subjects in comparative physiological and biochemical research. Generic separation simplifies a nomenclature frequently used by non-taxonomists. Secondly, with the generic status of *Egernia* still undetermined, generic status adds two well-defined monophyletic groups to an *Egernia* group otherwise having *Corucia* as its only other definable genus. Finally, the two genera are also ecologically distinct. With the exception of *T. adelaidensis*, a small, probably extinct species of largely unknown habits (Ehmann, 1983), *Tiliqua* comprises large, mostly diurnally active species that forage widely in largely open habitats, while *Cyclodomorphus* species are mostly of small to moderate size and secretive habits in generally 'closed' habitats and microhabitats, from closed forest (*C. gerrardii*) to *Triodia* tussocks (*C. branchialis*).

PREVIOUS ARGUMENTS FOR THE SYNONYMY OF *CYCLODOMORPHUS* WITH *TILIQUA*

Arguments for the synonymy of *Cyclodomorphus* with *Tiliqua* are based on two lines of evidence: morphology (Duméril and Bibron, 1839; Duméril and Duméril, 1851; Strauch, 1866; Smith, 1937; Mitchell, 1950; Cogger, 1983) and immunology (Hutchinson, 1981).

Hutchinson (1981), using serum immunoelectrophoresis with a single *T. rugosa* antiserum, found little antigenic difference between *T. rugosa* and *T. scincoides*, a greater divergence between *T. rugosa* and *C. casuarinae*, and *C. gerrardii* the most divergent. Hence, he concluded, 'to separate *T. rugosa* or *T. casuarinae* [from *Tiliqua*], and not *T. gerrardii*, as has been suggested [by Storr, 1976], is quite inconsistent with the IEP results' (Hutchinson, 1981: 188). By comparison with *Egernia*, which showed greater intrageneric variation to *E. cunninghami* antiserum than occurred between *T. rugosa* and *C. gerrardii*, yet was still treated as a monophyletic unit, *Cyclodomorphus* was regarded as synonymous with *Tiliqua*.

However, as noted above, evidence for the monophyly of *Egernia* is wanting, and hence the comparison used by Hutchinson (1981) is invalid. The classification proposed here satisfies Hutchinson's other major criticism by separating both *C. gerrardii* and *C. casuarinae* from *Tiliqua*. Indeed, Hutchinson's criticism of Storr's (1976) concept of *Omolepida* is flawed. Although Storr did not specifically include *gerrardii* in *Omolepida* (perhaps due to lack of familiarity with the species), it possesses all of the diagnostic characters Storr proposed for the genus, and clearly should have been included.

Of the morphological arguments for the synonymy of *Cyclodomorphus* and *Tiliqua*, those of Duméril and Duméril (1851) and Strauch (1866) are not explicit, but appear to be largely based on a combination of overall phenetic similarity and the synapomorphy of enlarged, molariform teeth, while one of the two characters employed by Smith (1937), complete separation of the parietals by the interparietal, is a symplesiomorphy (Greer, 1979a) and hence of no use in inferring relationships. Most authors advocating synonymy on morphological grounds have recognised a basic division within *Tiliqua* (s.l.). Duméril and Bibron (1839) and Duméril and Duméril (1851) separated *C. casuarinae* from the two other *Cyclodus* species then recognised in the first couplet of their keys, on the basis of lack of ear lobules. Strauch (1866) separated the subgenus *Omolepida* on the basis of lack of a postnarial groove. Smith (1937) and Mitchell (1950) separated *casuarinae* and the *branchialis* complex from other *Tiliqua* on the basis of a longer tail and incomplete subocular scale row. Using these criteria, *C. gerrardii* comes out with *C. casuarinae* (Mitchell, 1950). The generic separation advocated here does not contradict any of these proposed taxonomies, apart from the level at which the distinction is made.

Cogger (1983:8) introduced a more serious objection to the recognition of *Cyclodomorphus* by stating 'there is a continuum of character states linking the extreme expression of *Tiliqua* via *Hemisphaeriodon* with that of *Omolepida* (=*Cyclodomorphus*)'. I do not believe this to be the case. *Hemisphaeriodon* shows all of the synapomorphies used to diagnose *Cyclodomorphus* vis-à-vis *Tiliqua*, most notably the supraocular pattern and the shape of the suture between frontal, nasals, maxillae and prefrontals, and is plesiomorphic vis-à-vis *Tiliqua* in all diagnostic characters. Within *Cyclodomorphus*, *gerrardii* shares with *casuarinae* one synapomorphy unique within the *Tiliqua* lineage, loss of the postnarial groove, and another synapomorphy rare in other taxa, extreme reduction of the single ear lobule. A derived behavioural pattern also links the two species: tongue-flickering, used in both food location and defence (Shea, 1988, pers. obs.), in contrast to simple tongue protrusion in other species. Both species are primitive within the *Tiliqua* lineage in possessing a mode of eight premaxillary teeth (Greer, 1979a; Shea, pers. obs.). These characters in combination suggest to me that *C. casuarinae* and *C. gerrardii* are each other's closest relatives, and that any apparent phenetic similarity between *C. gerrardii* and *Tiliqua* is due to a position for *C. gerrardii* close to the basal stock of the lineage.

PREVIOUS ARGUMENTS FOR THE RECOGNITION OF *TRACHYDOSAURUS*

Trachydosaurus rugosus possesses all of the diagnostic characters listed above for *Tiliqua*, or further derivations from these, and is clearly a member of the *Tiliqua* (s.s.) radiation. *Trachydosaurus* has previously been differentiated from *Tiliqua* by only a few characters.

Gray (1825), in describing *Trachydosaurus*, used two characters: thick, bony scales on head and body, and a short, depressed tail. Wagler (1830) added to these a difference in dentition: conical teeth in *Trachydosaurus* vs rounded, obtuse crowns in *Cyclodus*. These three characters were employed by all authors for over sixty years (Gray, 1827, 1831, 1838, 1845; Wiegmann, 1834; Duméril and Bibron, 1839; Duméril and Duméril, 1851; McCoy, 1885), although Peters (1864) noted that the teeth of *T. adelaidensis* had conical rather than rounded crowns. Boulenger (1887) recognised all three characters, and added a further two: the presence of an azygous occipital scale and mostly divided subdigital lamellae. Mitchell (1950), in synonymising *Trachydosaurus* with *Tiliqua*, considered only the difference in tail morphology to be of potential value for generic separation, stating 'the general scalation, dentition and osteology are identical with those typifying *Tiliqua*' (Mitchell, 1950: 277). The tail shape he dismissed as a character by using as a parallel the placement of the similarly short-tailed *depressa* and *stokesii* in *Egernia*. However, as noted above, this argument is invalid, as *Egernia* is plesiomorphic and may only be an assemblage. Copland (1953: xxi) wished to retain *Trachydosaurus* 'if only on the grounds of its gross scalation'. Mertens (1958) resurrected *Trachydosaurus* in describing the insular race *T. r. konowi*, but reserved his reasons for publication in a report on his 1957 Australian expedition. This appears not to have been published. Glauert (1960) used the blunt tail as a diagnosis for *Trachydosaurus*, while Worrell (1963) used both the tail and the rugose scalation. Cogger (1975) noted the short tail, rugose scalation, and mostly divided subdigital lamellae. Cogger (1983: 8) justified his continued recognition of *Trachydosaurus*, stating 'I believe ... that the available morphological, biological and geographic evidence suggests that the shingle-back/blue-tongue divergence was earlier than, rather than approximately contemporaneous with, the radiation of the blue-tongued lizards in Australia', apparently hypothesising a sister-group relationship with *Tiliqua* (inclusive of *Cyclodomorphus*). However, no evidence was advanced in support of this hypothesis.

In summary, previous arguments for the recognition of *Trachydosaurus* have rested on five morphological characters: a short, blunt tail, thickened, rugose scalation, divided subdigital lamellae, conical teeth and an azygous occipital scale.

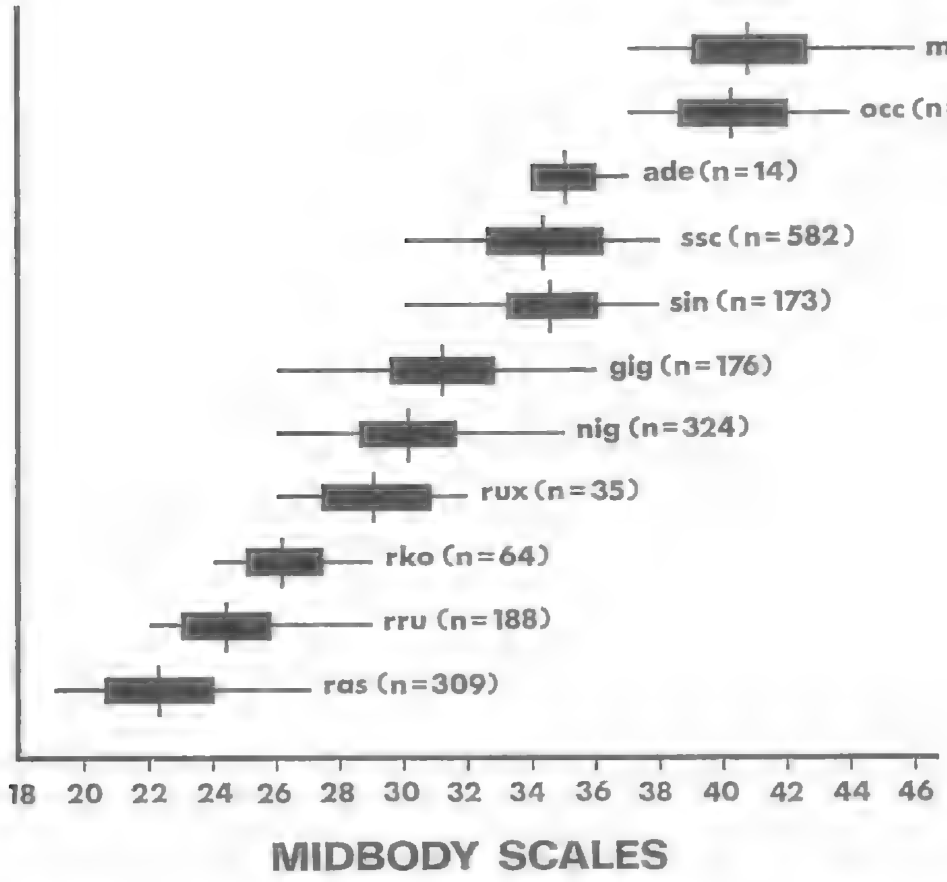

FIG. 12. Variation in number of midbody scales in *Tiliqua* species. Vertical bar is mean, solid rectangle is one standard deviation on each side of mean, horizontal line is range. Ade = *T. adelaidensis*, gig = *T. gigas*, mul = *T. multifasciata*, nig = *T. nigrolutea*, occ = *T. occipitalis*, ras = *T. rugosa asper*, rko = *T. r. konowi*, rru = *T. r. rugosa*, rux = *T. r.* subsp. nov., sin = *T. scincoides intermedia*, ssc = *T. s. scincoides*.

The latter two characters are of no use in diagnosing *Trachydosaurus*, as they also occur in *Tiliqua* species. Within *Tiliqua*, there is marked interspecific and ontogenetic variation in tooth shape (Shea, pers obs.). Only *T. gigas* and *T. scincoides*, the first two described species, have the rounded tooth crowns noted by Wagler (1830). The other species have more conical crowns, those of *T. nigrolutea* being more conical than in *Trachydosaurus*.

The presence of a median occipital is variable in *Trachydosaurus*, although it is present in most individuals. A median scale caudal to the interparietal is a derived character in skinks (Greer, 1968), and has been previously used as a major diagnostic character in one genus, *Geomyersia*. However, the median occipital of *Trachydosaurus* also occurs in *T. adelaidensis* (Fig. 9D), and is frequently present in *T. nigrolutea*, occurring in 42.1% (n = 321) of specimens examined. Asymmetry in the scales bordering the caudal margin of the parietal/interparietal complex, a possible precursor to the differentiation of a median occipital, is common in other *Tiliqua* species.

Similarly, although the grossly enlarged, thickened osteoderms characteristic of *Trachydosaurus* are unique within the Scincidae, *T. nigrolutea* also displays a trend in this direction. Enlargement of body scales can also be expressed as a reduction in number of scales. If number of midbody scales, paravertebral scales and ventral scales are compared (Figs. 12-14), it can be seen that the values for *T. rugosa* overlap with *T. nigrolutea* in two cases (midbody and ventral scales) while *T. nigrolutea* also

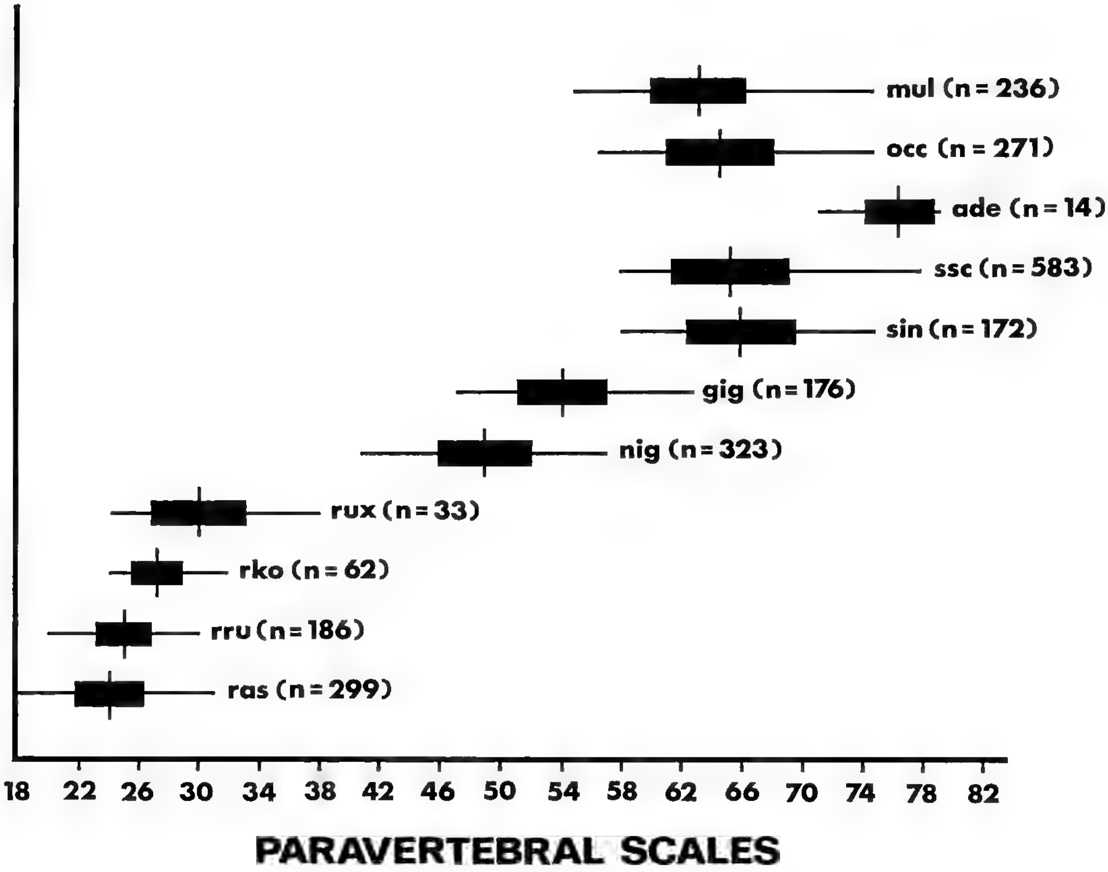

FIG. 13. Variation in number of paravertebral scales in *Tiliqua* species. Conventions as in Fig 12.

shows a trend towards *T. rugosa* in number of paravertebral scales.

The short, depressed, blunt-tipped tail of *Trachydosaurus* is also derived. However, there is geographic variation in tail length in *Trachydosaurus*, with the longest tails occurring in the south-west of Western Australia. Moreover, some Western Australian individuals have a distinctly conical tail tip (Fig. 15). *T. nigrolutea* again shows some trend in the direction of *Trachydosaurus*, having a short, thick tail which becomes depressed in emaciated individuals, in contrast to the compressed tail seen in *T. multifasciata* and *T. occipitalis*.

The division of subdigital lamellae seen in *Trachydosaurus* is uniquely derived within the *Egernia* group, with no trend in this direction, such as a median groove, seen in any other *Tiliqua* species.

A number of other differences between *T. rugosa* and other *Tiliqua* (usually as represented by *T. scincoides*) have been noted in the course of more general comparative studies, though not previously utilised for formal taxonomic separation (Arnold, 1984; Camp, 1923; Cope, 1892b; Greer, 1979a; Hoffstetter, 1949; Lécuru, 1968; Parker, 1868; Renous-Lécuru, 1973; Siebenrock, 1892, 1895; Smith, 1976, 1982). I have reexamined all of these characters. In almost all cases, I find the purported differences to be less than diagnostic, either due to variation within *T. rugosa*, or *Tiliqua* species not previously examined having the condition reported for *T. rugosa*. Only in the further reduction of phalangeal formula (Siebenrock, 1895; Hoffstetter, 1949) is the difference clear-cut and consistent.

In summary, *T. rugosa* differs markedly and consistently from other *Tiliqua* species in having some subdigital lamellae divided and in further reduction in phalangeal formula. In two other

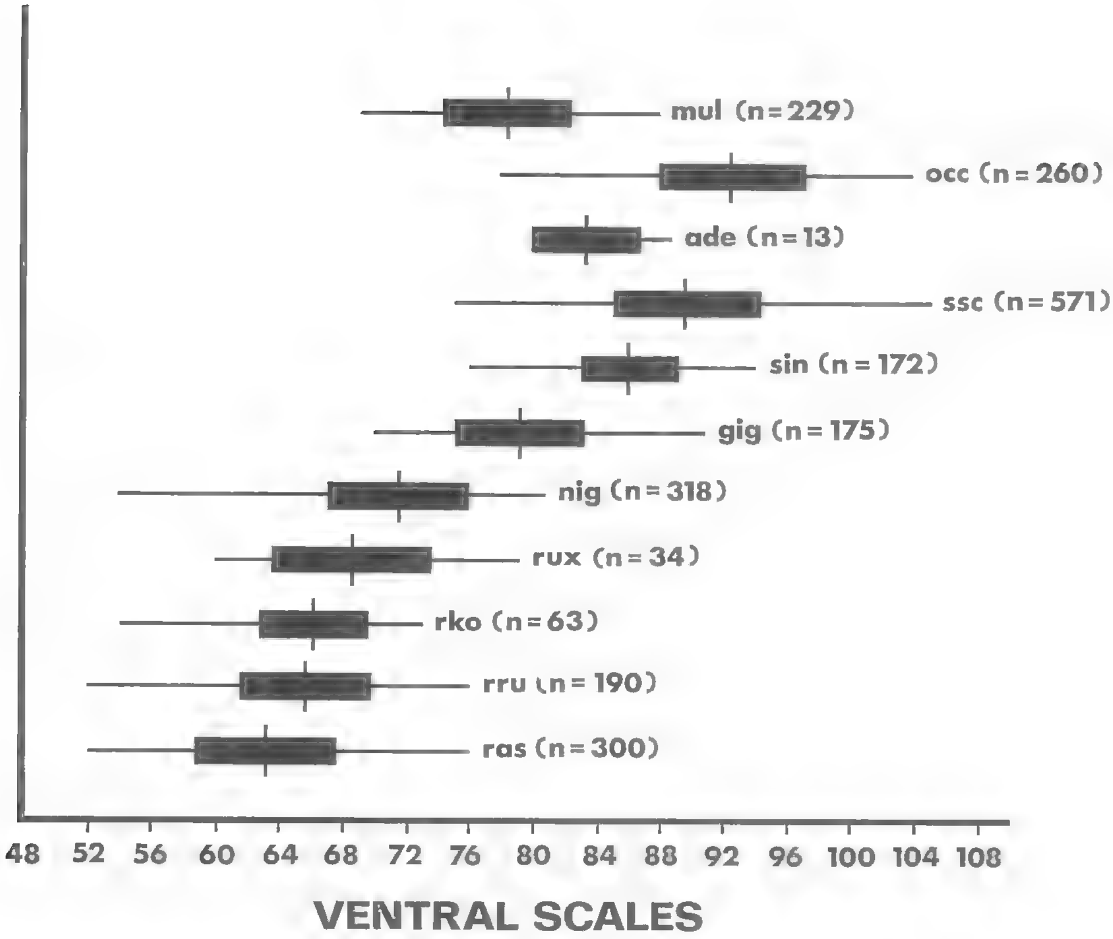

FIG. 14. Variation in number of ventral scales in *Tiliqua* species. Conventions as in Fig 12.

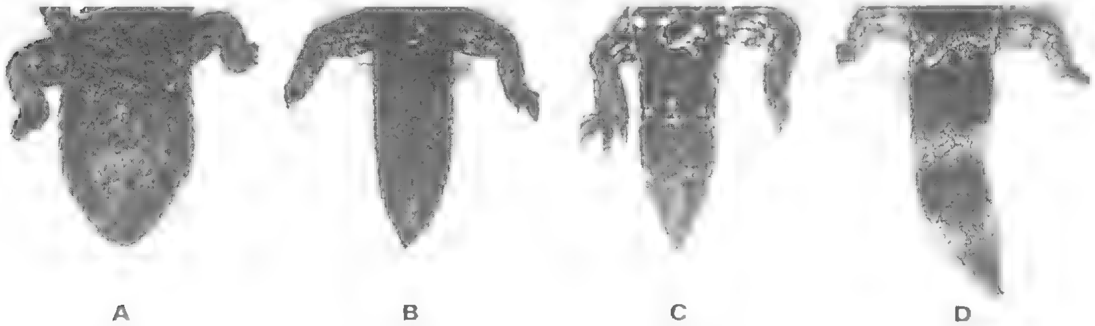

FIG. 15. Dorsal view of tails of A. *Tiliqua rugosa asper* (AM R123583), B. *T. rugosa* subsp. nov. (AM field series 15164), C. *T. rugosa* subsp. nov. (AM R102711), D. *T. r. rugosa* (AM R102594).

characters, tail shape and rugosity of body scalation, variation is largely non-overlapping with other *Tiliqua* species, although in both cases *T. nigrolutea* displays a trend in the direction of *T. rugosa*. In all of these characters, the state present in *T. rugosa* is derived. However, to generically separate *Trachydosaurus* on these characters would leave *Tiliqua* an undiagnosable entity vis-à-vis *Trachydosaurus*, as there are as yet no identifiable synapomorphies to link the remaining *Tiliqua* species independent of *T. rugosa*. On the available data, *T. rugosa* is merely a highly derived member of the genus, phenetically most similar to *T. nigrolutea*, and *Tiliqua* without *T. rugosa* is paraphyletic. Consequently, I retain *Trachydosaurus* in the synonymy of *Tiliqua*.

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BARU DARROWI GEN. ET SP. NOV., A LARGE, BROAD-SNOUTED CROCODYLINE (EUSUCHIA: CROCODYLIDAE) FROM MID-TERTIARY FRESHWATER LIMESTONES IN NORTHERN AUSTRALIA

PAUL WILLIS, PETER MURRAY AND DIRK MEGIRIAN

Willis, P., Murray, P. and Megirian, D. 1990 09 20: *Baru darrowi* gen. et sp. nov., a large, broad-snouted crocodyline (Eusuchia: Crocodylidae) from mid-Tertiary freshwater limestones in Northern Australia. *Memoirs of the Queensland Museum* **29**(2): 521-540. Brisbane. ISSN 0079-8835.

Baru darrowi gen. et sp. nov., is a common element in limestones of late Oligocene to late Miocene age on Riversleigh Station in northwestern Queensland and at Bullock Creek in the Northern Territory. Although *Baru* is a member of the Crocodylinae and appears to have many features in common with certain early Tertiary crocodiles such as the North American *Brachyuranochampsa eversolei* Zangerl, it also resembles sebecosuchian and pristichampsine crocodiles in having ziphodont (serrated, laterally compressed) teeth similar to those of flesh-eating dinosaurs. The Australian ziphodont crocodile *Quinkana fortirostrum* Molnar, was previously considered to be closely related to the Pristichampsinae on the basis of its cranial profile and highly developed ziphodonty. *Quinkana fortirostrum* and *Baru darrowi* share characters not present in pristichampsine crocodiles and they appear to be more closely related to one another than to any other ziphodont taxa. Because *Baru darrowi* is clearly a member of the Crocodylinae, we propose that *Quinkana* and *Baru* represent a new crocodyline ziphodont clade and that these two forms, together with *Pallimnarchus pollens*, form a monophyletic endemic Australian radiation. ☐ *Crocodylidae, Eusuchia, systematics, Tertiary, Ziphodont, Baru.*

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An unusually complete assemblage of fossil crocodile material has been recovered from fluviolacustrine sediments of middle to late Miocene age at Bullock Creek in the Northern Territory and late Oligocene to early Miocene age on Riversleigh Station, Queensland. The material provides clear evidence of a member of the subfamily Crocodylinae possessing ziphodont teeth. Previous finds of Australian ziphodont crocodiles have not been complete enough to determine their subfamilial affinity with confidence (Hecht and Archer, 1977; Molnar, 1981, 1982). The material described here is referred to the new genus and species *Baru darrowi*, a large crocodilian with many distinctive features. Its broad, short snout, robust proportions and deeply festooned jaws set it apart from any living *Crocodylus* species. Its dentition consists of posteriorly inclined, slightly recurved, laterally compressed crowns of greatly varying dimensions, bearing well-developed anterior and posterior crests (carinae). In some Northern Territory specimens, these carinae are finely serrated like the teeth of South American sebecosuchian and Northern Hemisphere early Tertiary pristichampsine crocodiles. Oddly, no specimens of *Baru* from the Riversleigh deposits have serrated carinae. Large, slightly compressed carinate teeth with fine serrations are also known from the Alcoota Local Fauna of the Northern Territory (P.M., pers. obs.) and from other middle to late Tertiary localities throughout the interior of Australia. These have been variously assigned to the genus *Pallimnarchus* (Molnar, 1982) or to unidentified sebecosuchians (Hecht and Archer, 1977). It can now be demonstrated that at least some of the ziphodont crocodile teeth found in Australia belong to a crocodyline genus. The proposition that pristichampsine and sebecosuchian ziphodont crocodiles may have been present in Australia is therefore re-examined.

Quinkana fortirostrum (Molnar, 1981), the first Australian crocodile formally described as a ziphodont, is known primarily from a snout. Although sufficiently well represented to suggest a closer affinity with *Baru darrowi* than with *Pristichampsus*, its principle features are dominated by trophic specialisations. Because crocodilians are otherwise structurally conservative, there are few character states suitable for a cladistic evaluation. We are therefore confined to a few observations strongly supporting the more parsimonious hypothesis that Australian ziphodont crocodiles represent a monophyletic radiation with Gondwana as its likely origin.

Interpretation of the polarity of character states, and basic concepts of crocodilian phylogeny used in this study, are based on Molnar (1981), Benton and Clark (1988) and Langston (1973); nomenclature follows Steel (1973) and Iordansky (1973). Prefixes used to indicate the source of specimens are as follows: NTM P, Northern Territory Museum, Palaeontological Collections; NTM R, Northern Territory Museum, Reptile Collections; QM F, Queensland Museum, Fossil Collections; SAM P, South Australian Museum, Palaeontological Collections.

Order CROCODILIA Gmelin, 1700
Suborder EUSUCHIA Huxley, 1875
Family CROCODYLIDAE Cuvier, 1807
Subfamily CROCODYLINAE Cuvier, 1807

Baru darrowi gen. et sp. nov.

GENOTYPIC SPECIES

Baru darrowi sp. nov. (Fig. 1a-c).

DIAGNOSIS

Species of *Baru* differ from all other crocodylines in the following combination of features: Broad moderately deep snout containing thirteen maxillary teeth; five premaxillary teeth present in juveniles and four in adults owing to loss of the second tooth; premaxillary and anterior six maxillary teeth directed posteriorly; tooth crowns moderately compressed bucco-lingually with carinae on the anterior and posterior margins; tooth crown and socket dimensions highly differentiated along both upper and lower tooth rows with correspondingly wide, deep alveolar processes; conspicuous maxillary reception pits, corresponding to dentary tooth crowns, situated lingual to the upper tooth row; anterior margin of the palatal fenestrae extending to the level of the seventh maxillary tooth; anterior palatine process absent; mandibular symphysis extends posteriorly to between the sixth and seventh dentary teeth; splenial terminates anteriorly at the level of the seventh dentary tooth and does not enter symphysis; internal nares with raised rim; external nares terminal; distinctive bony crest arches posteriorly from the maxillae and jugals, extending to the quadratojugals.

ETYMOLOGY

'Baru' is the Dreamtime Crocodile Man from the Aboriginal mythological lore of Eastern Arnhem Land (Groger-Wurm, 1973). The specific name honours British actor Paul Darrow, best known for his role in the television series 'Blake's Seven', in recognition of his support of continuing palaeontological investigations of the Riversleigh deposits.

SPECIFIC DIAGNOSIS

That of the genus until additional species are known.

MATERIAL EXAMINED

HOLOTYPE. NTM P8695-8, a nearly complete cranium missing the skull roof (frontals, parietals, postorbitals and squamosals) and basicranium posterior to the orbits.

PARATYPES. From D-Site, Riversleigh: NTM P8778-(1-5), right posterior mandible fragment, right posterior skull fragment preserving the lateral temporal fenestra, right pterygoid, ectopterygoid and posterior region of the maxilla; NTM P8681-14, left mandible lacking the articular and adjacent angular and surangular posterior to the lateral foramen and a small portion of the dentary at the level of the third tooth; NTM P8738-1, right jugal, pterygoid, ectopterygoid and posterior maxilla and an associated dentary fragment; QM F16822, premaxilla and anterior portion of left maxilla retaining fourteen teeth; from Pancake Site, Riversleigh: SAM P27866, right premaxilla; from Blast Site, Bullock Creek, NTM P87103-11, left squamosal, quadrate and opisthotic (juvenile).

REFERRED SPECIMENS. From D-Site, Riversleigh: QM F16823, jugal fragment; QM F16824, premaxillary fragments; QM F16825, right dentary; QM F16826, right dentary; From Site Y, Bullock Creek, NTM P87105-1, right mandible fragments. From Blast Site, Bullock Creek, NTM P87103-12, juvenile right maxilla; NTM P8697-2, right jugal.

TYPE LOCALITY.

Blast Site, Camfield Beds, located '16 miles southeast of Camfield Homestead in north central Northern Territory' (Plane and Gatehouse, 1968).

AGE

Late Oligocene to mid Miocene.

TABLE 1. Snout proportions of *Baru* and other crocodilians.

Taxon	H/L	H/W	W/L
Brachyuranochampsa eversolei	–	–	0.40
Sebecus icaeorhinus	0.39	.37	0.28
Pristichampsus vorax	0.24	0.51	0.48
Quinkana fortirostrum	0.36	0.51	0.70
Osteolaemus tetraspis tetraspis	0.35	0.35	1.00
Osteolaemus tetraspis osborni	0.31	0.41	0.74
Paleosuchus palpebrosus	0.29	0.48	0.60
Crocodylus porosus	0.21	0.37	0.57
Alligator mississippiensis	0.26	0.28	0.93
Gavialis gangeticus	0.09	0.54	0.16
Baru darrowi	0.68	0.94	0.72

L is the distance from the anterior extremity of the orbit to the posterior extremity of the external nares, H is the maximum depth of the snout at the fifth alveolus, and W is the maximum breadth of the snout at the fifth alveolus. Values for the first seven taxa are from Molnar (1981,p.809). Values for *Crocodylus*, *Alligator* and *Gavialis* are from Australian Museum Specimens (AM R32646, AM R130772 and AM R131340 respectively). Values for Baru are from NTM P8695-8.

STRATIGRAPHY

Vertebrate thanatocoenoses often occur as geographically or stratigraphically discrete assemblages in the middle Tertiary limestones of northern Australia. Because of uncertainty about the relationships (temporal and ecological) of these assemblages, it has become common practice to treat each as a separate local fauna (sensu Tedford, 1970).

Archer et al (1989) suggest three significant time periods are represented at Riversleigh between the Oligocene and the Miocene. Woodburne et al. (1985) suggest a mid to late Miocene age for the Bullock Creek Local Fauna. However, if the more derived Alcoota Local Fauna is also considered late Miocene, the Bullock Creek Local Fauna is more appropriately designated as mid Miocene.

The specimens of *Baru darrowi* from Bullock Creek were collected from the Blast Site and nearby Site Y, approximately 17°S, 131°30'E. It is not yet clear that any particular Bullock Creek site assemblage is significantly different from any other and all have been tentatively referred to the Bullock Creek Local Fauna (Murray et al., in prep.).

Consequently, the age range of *Baru darrowi* probably extends from late Oligocene (Riversleigh) to mid Miocene (Bullock Creek).

DESCRIPTION

Because of the limited comparative material available, *Baru darrowi* is compared with the living saltwater crocodile, *Crocodylus porosus*. However, *Baru* has much in common with more archaic crocodylines (e.g. a wide incisive foramen and overlapping bite (Langston, 1973)), conditions apparently lost among the more derived living genera. Large triangular palatal fenestrae were also characteristic of many early Tertiary crocodylines. A comparison of the snout proportions of *Baru darrowi* with other crocodilians is given in Table 1. Table 2 provides a classification of snout proportions according to Molnar (1981). Table 3 lists specific features of *Baru darrowi* and compares them with other crocodilians.

Cranium. The cranium of *Baru darrowi* is triangular in dorsal profile and trapezoidal in section at the level of the maxillo-jugal suture. Compared to *C. porosus* the cranium of *Baru* is much deeper and broader in proportion to its length (Table 1). In lateral profile (Fig. 1A) the cranium is deep, slightly wedge-shaped and nearly as high immediately posterior to the narial aperture as it is just anterior to the orbits. The dorsal outline of the snout is concave. The profile of the premaxilla is distinctive in its shortness and depth. The anterior margin is a vertical surface, rounded ventrally and demarcated posteriorly by a wide notch for the caniniform fourth mandibular tooth. In dorsal view (Fig. 1B) the premaxillae describe a broad, D-shaped surface immediately anterior to the tooth notches. Posterior to the constriction, the maxillae widen over laterally swollen alveolar festoons. Posteriorly the maxillae become more steep sided, slab-like and shallowly concave. Dorsally the nasomaxillary junction is accentuated by a low crest. The alveolar process (sensu Molnar, 1981) is a wall of interconnected, buttressed alveoli. Anteriorly the alveolar process is strongly festooned but posteriorly it is more uniform.

The jugal extends deeper ventrally and the maxillo-jugal suture is longer than in *C. porosus* of comparable size. The subtemporal ramus of the jugal widens laterally. Lateral to the lateral temporal fenestra this process is dorsoventrally flattened gradually becoming more rounded in cross section lateral to the quadratojugal. The lateral edge of the subtemporal ramus extends anteriorly as a ridge onto the broad anterior face of the jugal. In lateral view, the shape and size of the orbit is similar to and no less dorsally situated than in *C. porosus*. A well preserved

TABLE 2. Classification of snout proportions.

A. SNOUT DEPTH (H/W)		B. SNOUT BREADTH (W/L)*	
Low	x<0.5	Broad	x≥ 0.66
Moderately deep,	0.5≤ x<1.0	Moderately Narrow	0.66> x>0.33
Deep	x ≥1.0	Narrow	x≤0.33

* Molnar (1981,p.817) states that this ratio is L/W. This contradicts discussion of snout width ratios elsewhere in that paper. Molnar (pers. comm.) reveals that this ratio was intended to be W/L (not L/W). Classification of values for snout depth and snout breadth ratios according to Molnar (1981,p.817).

portion of the jugal and quadratojugal indicates that the lateral temporal fenestra was both longer and wider than in any living crocodyline species.

In dorsal aspect, the posterior of the cranium is about one-third broader than a *C. porosus* of equivalent length and the anterior is broader by a quarter. The premaxillae are wider relative to their length than in the Saltwater Crocodile and the narial aperture is shorter and broader. It extends to the anterior margin of the premaxillae. Reception sockets for the first dentary teeth do not breach the outer surface of the snout as in *C. porosus*.

Sutural relations on the dorsal surface of the cranium are essentially like those of *C. porosus* (Fig. 2). Well-developed dorsal processes of the premaxillae project posteriorly alongside the nasals. The premaxillae join in the midline anterior to the nasals, excluding them from the external nares. The paired nasals are elliptical in shape and slightly expanded posteriorly, shorter and less wedge-like than in *C. porosus*. The maxillae are greatly expanded laterally into deep, steep-sided lobes, which flatten out posteriorly before expanding outwards again at the base of the jugals.

In the large mature specimen, the sutural pattern of the upper facial region is party obscured by age-related fusion and elaborate bony ornamentation. The basic pattern is like that of *Crocodylus* spp. The lachrymal extends anteriorly to meet the nasal bone, so excluding the prefrontal from contacting the maxilla. The prefrontal forms the anteromedial orbital margin. The posteromedial half of the orbit is formed by the orbital process of the frontal (Fig. 2). The position of the orbits, their shape and the morphology of the interorbital area are essentially the same as in *C. porosus*. The shape of the orbits of *Baru* differ from those of *C. porosus* only in being slightly longer, wider posteriorly and also more pointed anteriorly (Fig. 1B). The quadratojugals and jugals form a wide shelf bounding the comparatively large, triangular lateral temporal fenestra (approximately 52.0mm wide by 86.0mm long in NTM P8778-4). This opening is about twice the length of that of a *C. porosus* of equivalent size. A portion of the superior temporal fenestra is also preserved on that fragment and on a fragment of the skull roof of a much smaller individual, NTM P87103-11. These indicate that the proportions of the superior temporal fenestrae were similar to those of *C. porosus*. The auditory meatus is more anteriorly placed in *Baru* than it is in *C. porosus*. The portion of squamosal preserved on NTM P87103-11 indicates that the skull roof of *Baru* was flat and wider posteriorly than in *C. porosus*.

The ventral surface of the cranium is dominated by the broad, flat maxillary palate with its wide alveolar processes and by the large triangular, anteriorly located palatal fenestrae (Fig. 1C). The premaxillae are penetrated by a large, oval incisive foramen recessed within a deep fossa, the anterior portion of which is confluent with a pair of reception pits for the first dentary teeth. In combination with the wide, deep alveolar process containing four large tooth sockets on each side, the premaxillary palate is distinctly vaulted in contrast to the relatively flat premaxillary palate of *C. porosus*. The maxillary palate is broad and short and is elevated above the alveolar margins. A row of small nutrient foramina clearly define the maxillary palate. The maxillary alveolar process is greatly expanded to accommodate the enlarged fourth and fifth maxillary caniniform teeth. Like *Caiman* and *Osteolaemus*, *Baru darrowi* has fewer maxillary teeth than *C. porosus* and the size range of the tooth sockets and their corresponding teeth is greater than in any living crocodile. *Baru* specimens have a consistent number of thirteen maxillary teeth, as in the broad-snouted caimans. The moderate lateral compression of the tooth crowns of *Baru* is not clearly reflected in the shape of the alveoli which are predominantly round (Figs 1C,2,5A). The anterior maxillary teeth are posteriorly directed. The genus also

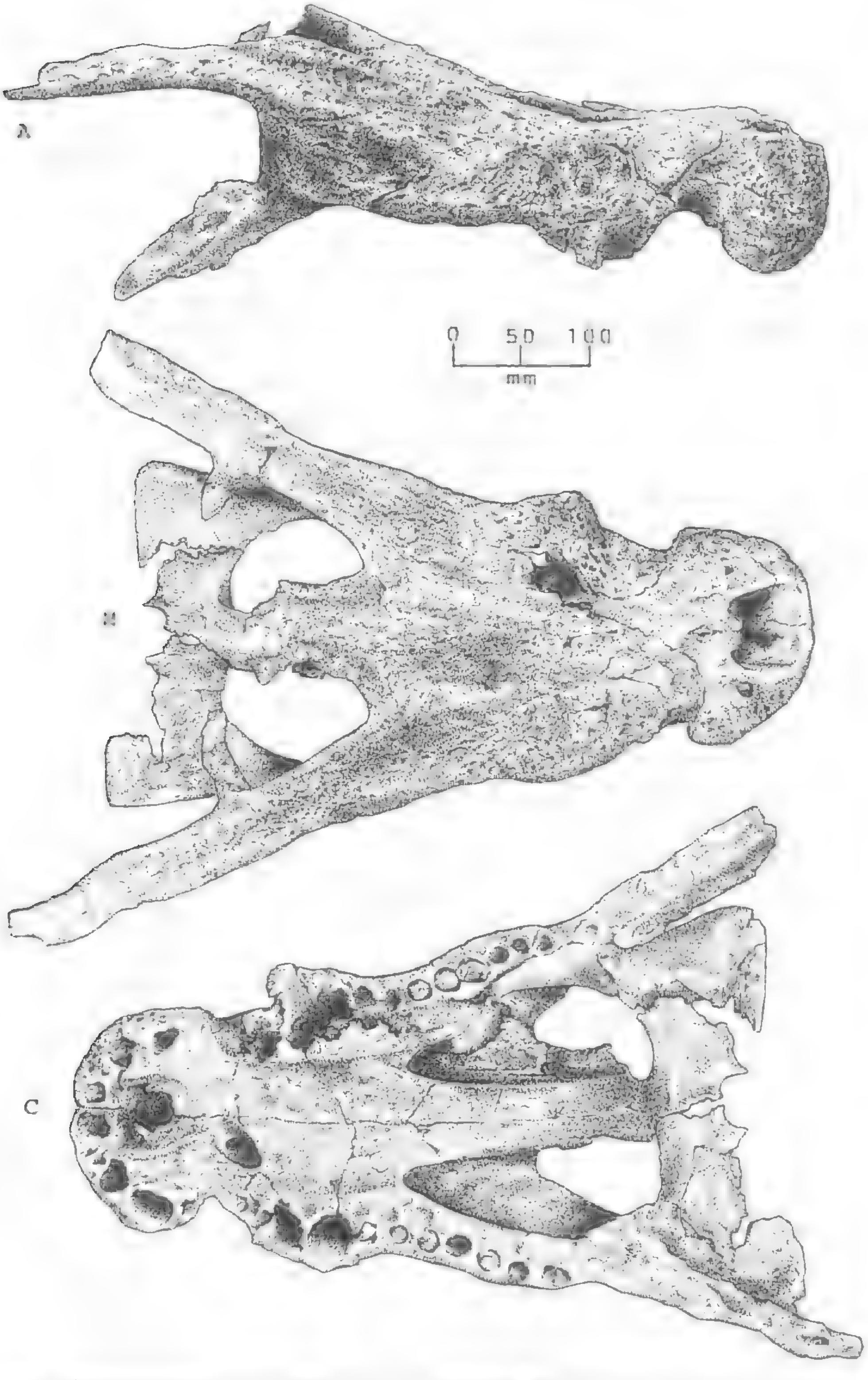


FIG. 1. *Baru darrowi* holotype, NTM P8695-8: (A) lateral view; (B) dorsal view; (C) ventral view.

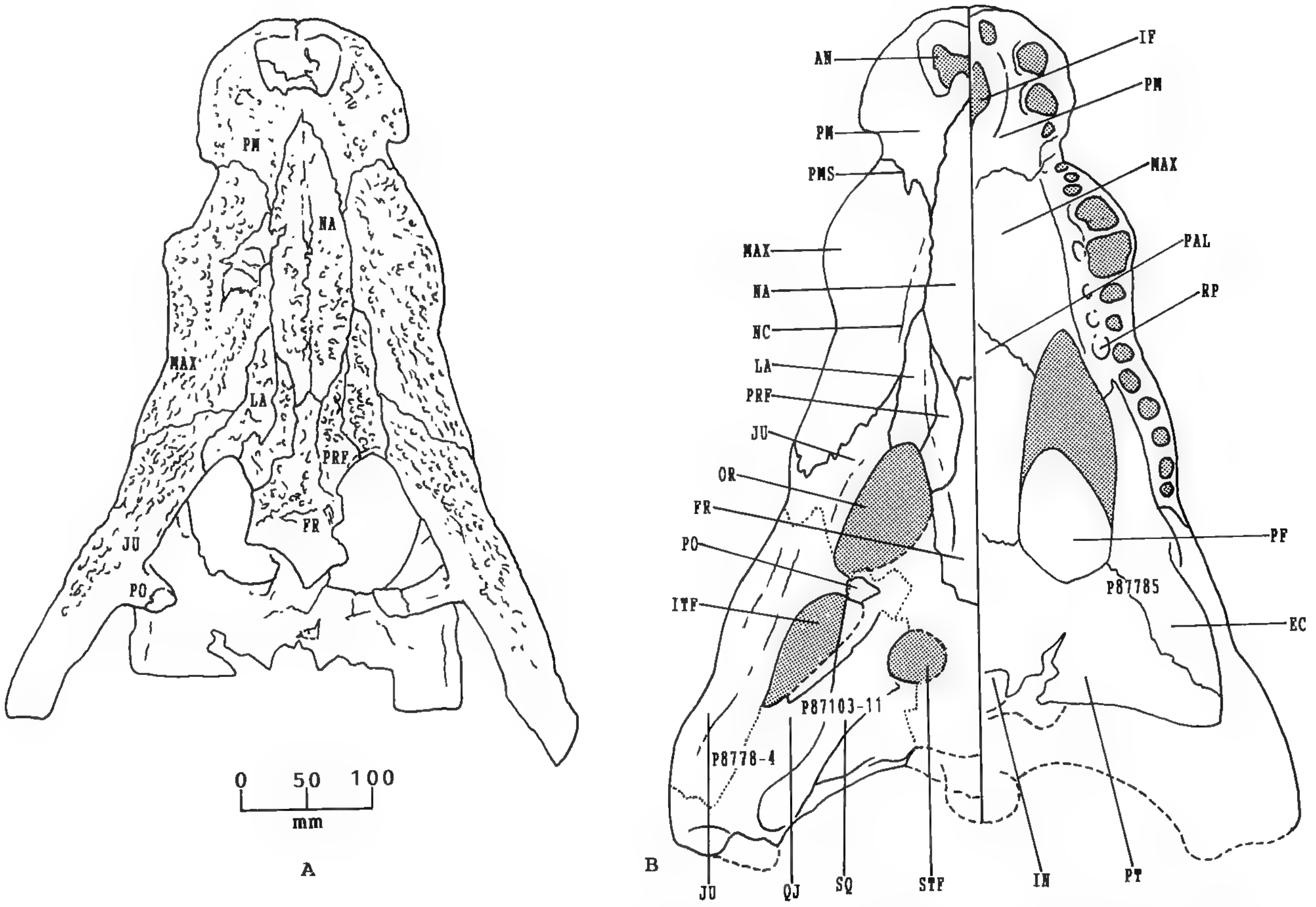


FIG. 2. (A) Interpretation of the dorsal sutures of the *Baru darrowi* holotype, NTM P8695-8. In this specimen many of the dorsal sutures are partially obscured by age obliteration and ornamentation. (B) Composite restoration, dorsal and ventral views, of Baru darrowi showing structures. Catalogue numbers (all with NTM prefix) indicate portions of the skull not represented, or poorly represented, on the holotype NTM P8695-8. Abbreviations: AN, narial aperture; EC, ectopterygoid; FR, frontal,; IF, incisive foramen; IN, internal nares; ITF, lateral temporal fenestra; JU, jugal; LA, lachrymal; MAX, maxilla; NA, nasal; NC, nasal crest; OR, orbit; PAL, palatine; PF, palatine fenestra; PM, premaxilla; PMS, premaxillo-maxillary suture; PO, postorbital; PRF, prefrontal; PT, pterygoid; QJ, quadratojugal; RP, reception pit for mandibular tooth; SQ, squamosal; STF, superior temporal fenestra.

differs from *Crocodylus* in that the crowns of the lower dentition occlude inside the upper tooth row, the longer dentary teeth having reception pits between and mesial to maxillary teeth four through eight.

The palatal fenestrae of *Baru darrowi*, in addition to their large size and distinctive shape, invade the maxillary palate anteriorly to the level of the seventh maxillary tooth (Figs 1C,2B). In *C. porosus* the fenestrae extend only to the ninth maxillary tooth. In this respect also, *Baru* is similar to short-faced crocodyline *Osteolaemus tetraspis* and the equally short-faced alligatorine, *Paleosuchus trigonatus*. It differs from all living and most extinct crocodylids in lacking anterior palatine processes. The course of the maxillo-palatine is a wide chevron between the anteromedial margins of the palatal fenestrae. The palatine bones are concave medially to accommodate the long, posteriorly wide palatal fenestrae. In contrast to *C. porosus* but like *C. novaeguineae*, the posterior margins of the palatal fenestrae are formed mainly by the pterygoids.

In keeping with the width of the back of the cranium, the pterygoids are broad. In lateral profile, the ectopterygoids are longer and project ventrally at a somewhat different angle than in *C. porosus*. The posteroventral process of the ectopterygoids appears to be slightly longer than that of *C. porosus* and the anterior (palatal) process is decidedly more robust. Overall dimensions of the holotype are given in Figs 3A-C.

Mandible. NTM P8681-14 comprises an almost complete left mandible lacking only surangular posterior to the external fenestra, the coronoid, and a short length of the dentary bearing the third tooth. The first, second, fourth, fifth, sixth, fourteenth and fifteenth teeth are preserved. In general proportions the mandible is slightly larger than that of an approximately four-metre-long *C. porosus* (NTM R13748). In occlusal view (Fig. 4a) the symphysis extends posteriorly to just beyond the level of the sixth tooth. In *C. porosus* it ends level with the fifth tooth. The angle between the axis of the mandibular ramus and the symphyseal plane is similar to that of *C. porosus*. The lateral surface of the mandible and the tooth row are concave laterally in contrast to a gentle convexity in *C. porosus* (Fig. 4a). The caniniform fourth tooth and its broad alveolus protrude laterally. NTM P8681-14 shows a slightly greater variation in alveolar size than *C. porosus* although the pattern of tooth differentiation is basically the same. A pronounced difference in alveolus shape is exhibited by the confluence of the tenth and eleventh, whereas in *C. porosus* the alveoli are usually separated by between five and ten millimetres of bone.

The greater degree of festooning in *Baru* reflects the enlargement of the caniniform fourth tooth and the laterally compressed tenth and eleventh teeth. As in *C. porosus*, *Baru* has a conspicuous excavation on the lateral surface of the dentary to accommodate the upper fourth and fifth maxillary teeth (Fig. 4b).

The coronoid is not preserved on any specimen nor are there any examples of a complete Meckelian fossa. Incomplete specimens indicate that the Meckelian fossa was similar in size to *C. porosus*. In the Bullock Creek specimen NTM P87105-1, the long axis of the Meckelian fossa is aligned at a relatively high angle (c. 25°) to the inferior border of the mandibular ramus; in Riversleigh specimens and *C. porosus* it is nearly parallel to the inferior border (Figs. 4b, 5c).

The lateral mandibular ramus is more heavily sculptured than that of *C. porosus*. In NTM P8779-2 and NTM P87105-1, the sculptured region on the angular and surangular is delineated from the adjacent smooth bone by a prominent margin. In *C. porosus*, the two surface textures in this region grade into each other. The external mandibular fenestra is narrower dorsoventrally and the posterior upward inflection of the inferior border of the mandibular ramus is greater in *Baru darrowi* (Figs 4b, 5b-c). On NTM P8681-14, a 5.0mm wide longitudinal sulcus originates from a small foramen located about 45.0mm from the last tooth. A similar sulcus is not evident on any *Crocodylus* specimens in our possession. A damaged articular is preserved on NTM P8778-2 (Fig. 4b). It has a somewhat longer anterior process entering the adductor fossa than that of *C. porosus*, thus providing a relatively larger sutural contact with the angular.

Sutural relations between the mandibular elements show only minor differences from those of *C. porosus*. In NTM P87105-1 and NTM P8778-2 the angular and surangular butt against each other within the adductor fossa and terminate anteriorly high on the posteroventral margin of the external fenestra. In *C. porosus* they meet at a lap joint and the suture contacts the external fenestra in the mid-region of the posteroventral border.

VARIABILITY

On the basis of a limited selection of material, *Baru darrowi* has been described as a variable species that existed over a considerable span of geological time. The possibility that more than one *Baru* species was present between Riversleigh and Bullock Creek times has been considered. At present, there is insufficient evidence to support a specific separation of the two populations due to lack of information about sexual dimorphism, ontogenetic changes and allometry in these extinct crocodiles. By analogy with living crocodiles, at least some observed differences between the Riversleigh and Bullock Creek specimens could be attributed to these factors.

One of the more intriguing differences between the two populations is the absence of serrations on the carinae of the teeth in the Riversleigh *Baru* sample. Riversleigh *Baru* specimens also have a more pointed premaxilla when viewed from the dorsal aspect. This may also relate to the apparently longer span between the fourth and the first dentary teeth observed in Riversleigh mandibles. While attempting to reconstruct *Baru* for an illustration, one of us (P.M.) was unable to match the length of the Riversleigh symphysis to the Bullock Creek premaxilla, although the remainder of the mandible seemed to fit reasonably well in terms of size and shape. A single specimen of the dentary symphysis from Bullock Creek is proportionally shorter and fits the contours of the premaxilla of the holotype. Differences in the angle of the long axis of the mandibular fenestra to the inferior border of the mandibular ramus are noted above. Given the current state of resolution, we consider the definition of a single chronospecies subsuming these variations to be adequate for the time being.

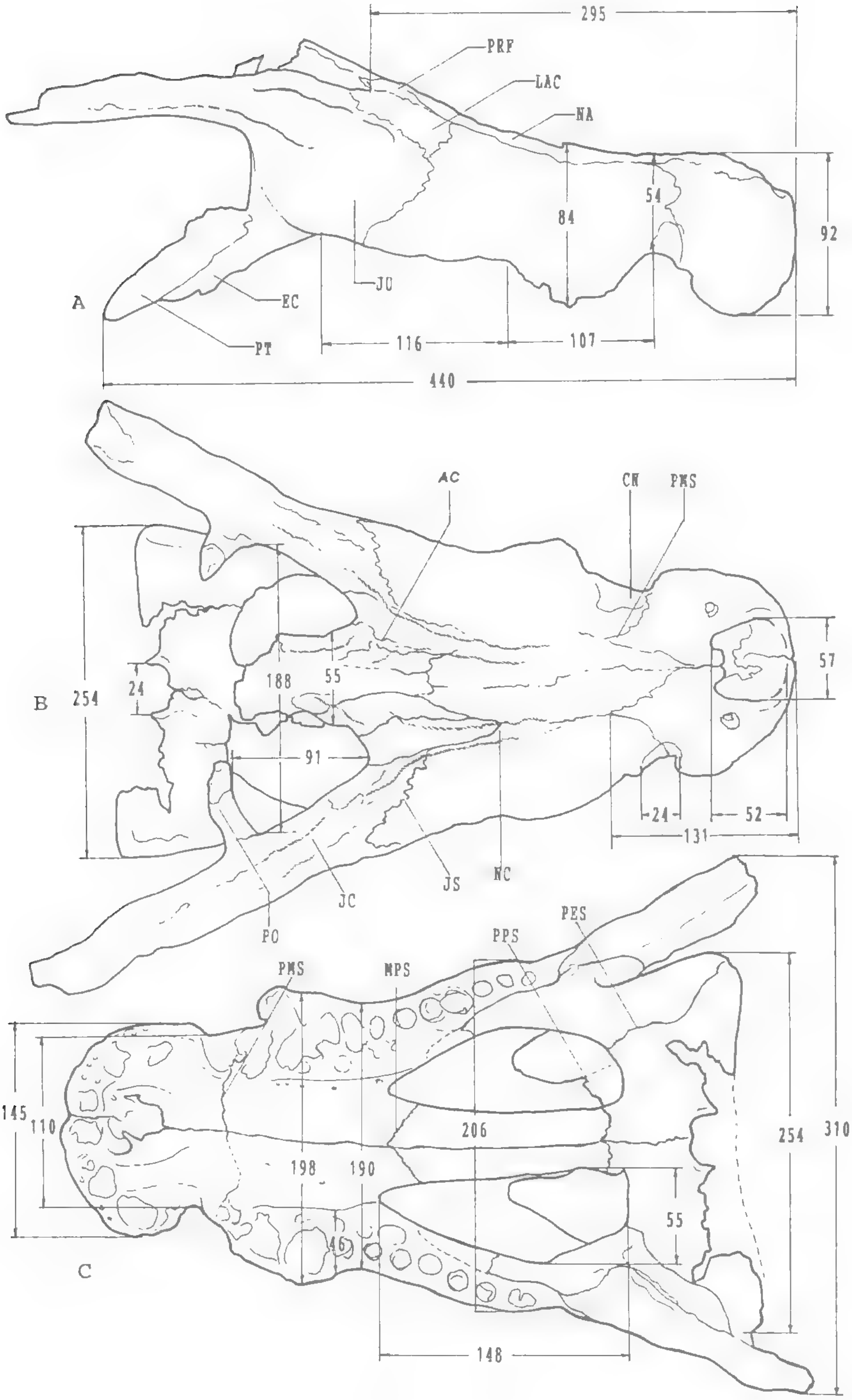
COMPARISONS WITH OTHER CROCODYLIDS

Wider comparison of *Baru darrowi* emphasises some of its more unusual features. This comparison is unavoidably brief and incomplete due to our limited comparative material. We confine our observations to crocodilians which have certain obvious similarities to *B. darrowi* either in terms of the dentition or cranial morphology.

Living Crocodylids. Of living crocodylid species, *Baru darrowi* most closely resembles such broad-snouted forms as *Osteolaemus tetraspis* among the crocodylines and *Paleosuchus trigonatus* among the alligatorines (Table 1). Similarities include the number of maxillary teeth (13) and the size and position of the palatal fenestrae (Table 3). *Paleosuchus* spp. also possesses the alligatorine overbite which is similar to the condition in *B. darrowi.* Some caiman species have marked differences in tooth size, festooning and large caniniforms, whereas *Osteolaemus tetraspis* appears to have mildly durophagous specialisations. Although the palatal fenestrae of both forms are very large and end at the level of the seventh maxillary tooth, as in *B. darrowi,* they are differently shaped and have somewhat different proportional contributions to their margins from the surrounding palatal complex. A conspicuous difference is the presence in both living forms of a well defined anterior palatine process, absent in *B. darrowi.* These striking proportional similarities indicate that a substantial portion of *Baru*'s rostral morphology is trophically dedicated, derived and the result of parallel evolution. Similar remarkable parallel developments within various crocodilian lineages are discussed by Langston (1973).

The extent to which *B. darrowi*'s rostral proportions differ from *Crocodylus porosus* depends largely upon the state of maturity of the specimens compared. The holotype is obviously an adult and bears little resemblance to young specimens of *C. porosus.* However, when compared to a very large *C. porosus,* the width to length proportions (Webb and Messel, 1978) of *Baru* appear to differ very little (Fig. 6). This brings us to the peculiar case of the 'Lansdowne snout' (QM F1752), a Pliocene crocodile rostrum recovered from Lansdowne Station, Queensland. It was originally described as *Pallimnarchus pollens* (Longman, 1925) but was

FIG. 3. (A) Lateral view of *Baru darrowi* holotype NTM P8695-8 showing structures and dimensions. All measurements in millimetres. Abbreviations: EC, ectopterygoid; JU, jugal; LAC, lachrymal; NA, nasal; PRF, prefrontal; PT, pterygoid. (B) Dorsal view of the *Baru darrowi* holotype NTM P8695-8 showing structures and dimensions. The two circular structures on the premaxilla are artefacts produced by the breaching of the dorsal surface by the alveoli of the upper teeth. All measurements in millimetres. Abbreviations: AC, antorbital crest; CN, canine notch; JS, jugal sulcus; JU, jugal; NC, nasal crest; PMS, premaxillo-maxillary suture; PO, postorbital. (C) Ventral view of the *Baru darrowi* holotype NTM P8695-8 showing structures and dimensions. Abbreviations: MPS, maxillo-palatine suture; PES, pterygoid-ectopterygoid suture; PMS, premaxillo-maxillary suture; PPS, palatine-pterygoid suture.


A
295
PRF
LAC
NA
84
54
92
JU
EC
PT
116
107
440
B
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188
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57
91
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52
131
JS
NC
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145
110
198
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206
254
310
46
55
148

later assigned to *C. porosus* (Molnar, 1982). The Lansdowne snout is proportionally shorter and broader than that of the *B. darrowi* holotype. Its ventral profile, moreover, closely resembles that of *B. darrowi* in its exaggerated maxillary swellings, short, broad premaxillary outline, its overbite, and, so far as can be determined from illustrations (viz Molnar, 1982; fig. 5), its large and anteriorly positioned palatal fenestrae. Work in preparation by one of us (P.W.) and Molnar suggests that the Lansdowne snout should be referred to *Pallimnarchus* after all, but perhaps not *P. pollens*.

Fossil Crocodylines. In addition to its short

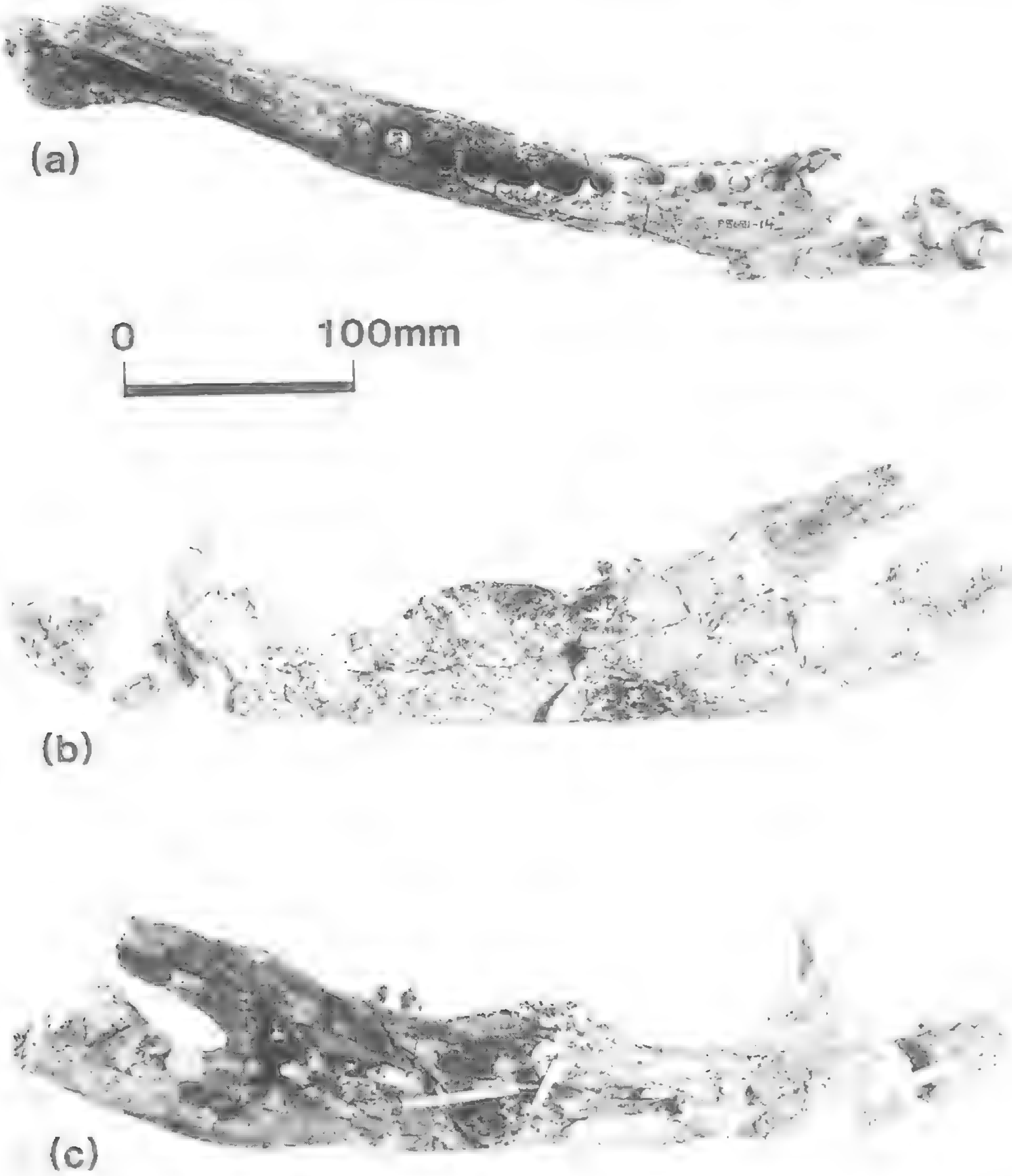

FIG. 4. *Baru darrowi*, NTM P8681-14, left mandible from 'D-Site', Riversleigh: (a) occlusal view; (b) lateral view; (c) medial view.

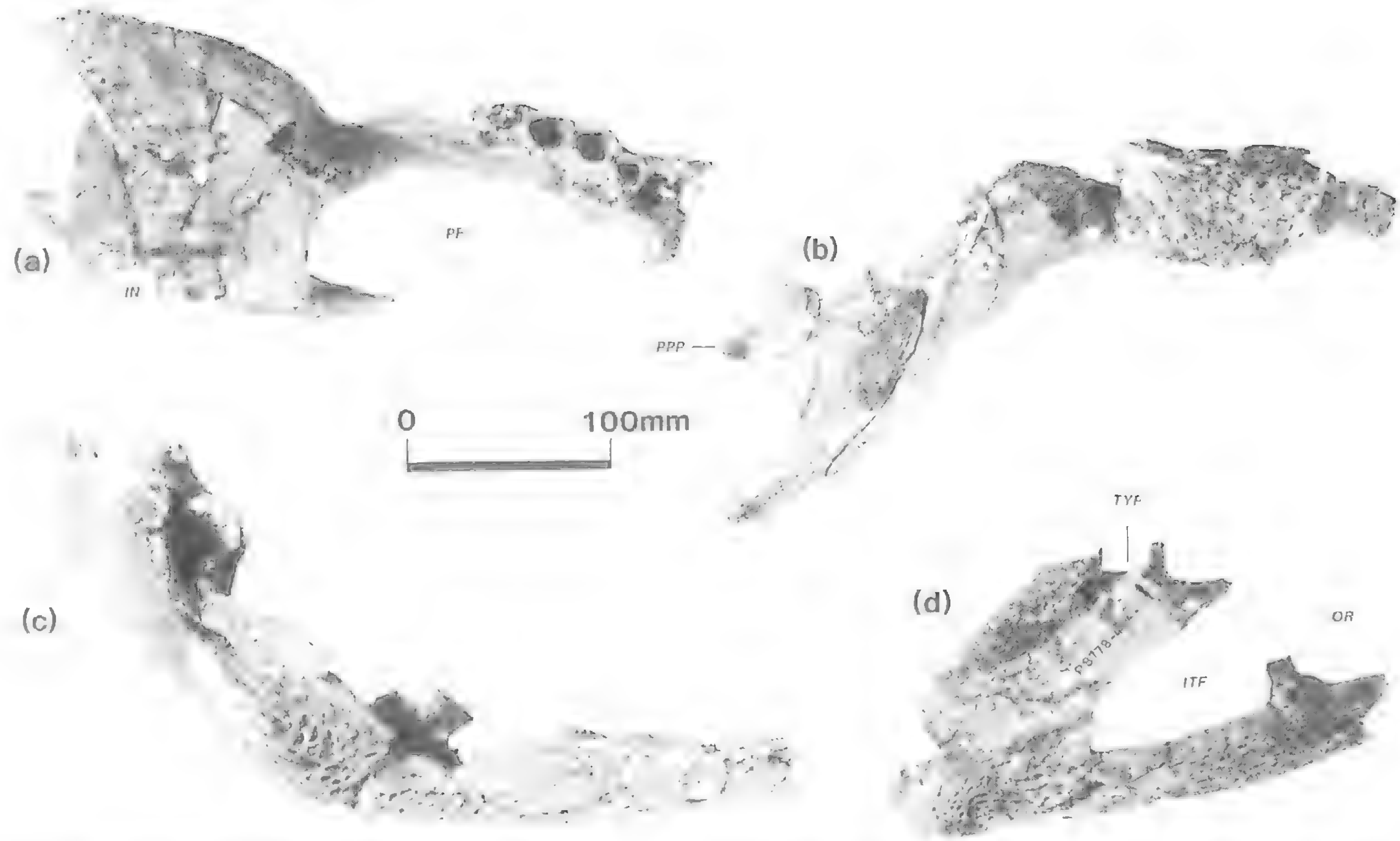

FIG. 5. *Baru darrowi*, NTM P8778 individual from 'D-Site', Riversleigh: (a) ventral view; (b) lateral view, NTM P8778-5, right pterygoid, ectopterygoid and posterior region of maxilla: (c) NTM P8778-2, right posterior mandibular fragment, lateral view; (d) NTM P8778-4, right posterolateral skull fragment, dorsal view. Abbreviations: IN, internal nares; ITF, lateral temporal fossa; OR, orbit; PF, palatine fenestra; PPP, posterior pterygoid process; TYF, tympanic fenestra.

TABLE 3. Characters of *Baru darrowi* and their distribution.

CHARACTER	A	B	C	D	E	F	G	H	I	J
1. Procoelous vertebrae	p	?	?p	a	p	p	p	p	p	p
2. Internal nares	Pt	?	?Pt	Pt/P	Pt	Pt	Pt	Pt	Pt	Pt
3. Tooth enlargement sequence	c	c	c	–	c	c	al	c	c	c
4. Tooth notch	p	p	p	p	p	p	a	p	p	p
5. Lacrymal/nasal contact	p	p	p	p	p	p	a	p	p	p
6. Palatal fenestrae position (Mx. tooth number)	7-8	7	7	10	10	9	12	7-8	7	8-9
7. Palatal process	a	a	a	p	p	p	p	a/p	a/p	a
8. Occlusion	o	o	o	o	o	i	o	o	i	o
9. Jugal ridge	a	p	p	?p	?p	p	p	?p	?p	?p
10. Pseudoheterodonty	p	a	p	a	a	p	p	p	p	p
11. Festooning	p	a	p	a	a	p	p	p	p	p
12. Snout width	b	b	?	n	m	b	b	b	b	m
13. Snout depth	md	md	?	d	md	l	l	md	l	?
14. Tooth compression	p	p	a	p	p	a	a	a	a	?
15. Serrated carinae	p	p	p	p	p	a	a	a	a	?
16. Teeth inclined to posterior	p	a	a	a	a	a	a	a	a	?

Key to species: A, *Baru darrowi*; B, *Quinkana fortirostrum*; C, *Pallimnarchus pollens*; D, *Sebecus icaeorhinus*; E *Pristichampsus vorax*; F, *Crocodylus porosus*; G, *Alligator mississippiensis*; H, *Paleosuchus osborni*; I, *Osteolaemus tetraspis*; J, *Brachyuranochampsa eversolei*. Key to character states: a, absent; al, alligatorine; b, broad; c, crocodyline; d, deep; i, interlocking; l, low; m, moderately narrow; md, moderately deep; n, narrow; o, overbite; p, present; Pt, pterygoid only; Pt/P, palatine and pterygoid contact. Interpretations from the following sources: A, B, C, F and G from specimens; D from Colbert (1946); E from Langston (1975); H and I from Mook (1921); J from Zangerl (1944); all interpretations were compared and completed from Molnar (1981).

snout, *Baru darrowi* has a distinctive broadly triangular cranium, great width of the jugals lateral to the orbits, elongation of the inferior temporal fenestra, large triangular palatal fenestrae that constrict the palatines posteriorly, absence of the anterior palatine processes and the elliptical shape of the nasal bones.

Crocodylines with similar features were widespread in North America in the early Tertiary. One of the best preserved of these crocodilians is *Brachyuranochampsa eversolei* Zangerl, 1944, from the Washakie Eocene of Wyoming, U.S.A. Like *Baru*, *Brachyuranochampsa* combines the presence of a crocodyline notch for the fourth dentary tooth with an alligatorine-like overbite denoted by a series of reception pits medial to the upper tooth row. Although *Brachyuranochampsa* is a moderately narrow-snouted crocodyline (Table 1) it is heterodont and the alveoli are closely approximated. The jugals are broad and everted, nasals are elliptical, inferior temporal fenestra are large, the quadrates and quadratojugals are broad. The nasal aperture, although damaged anteriorly appears to have been terminal or nearly so and trapezoidal in shape, like that of *Baru*, in contrast to the elliptical nares of *Crocodylus* spp. The palatal structure resembles *Baru* in its lack of an anterior palatine process and large, triangular palatal fenestrae and palatines that narrow posteriorly rather than widen as in *Crocodylus*. However, unlike *Baru* its dentition is not ziphodont and fourteen rather than thirteen maxillary teeth are present. The palatal fenestrae extend anteriorly only to a level between the eighth and ninth maxillary teeth. This is consistent with the observation that short-snouted crocodylines have more anteriorly-positioned palatal fenestrae. With our present state of knowledge it would be imprudent to force *Baru* into a phyletic relationship with this particular American genus, which may be expressing a symplesiomorphic character complex widely distributed among primitive early Tertiary crocodylines. However, given the dearth of other living and fossil forms that lack the anterior palatine processes combined with the broad similarities previously mentioned, the likelihood of an entirely parallel development of these features seems fairly remote.

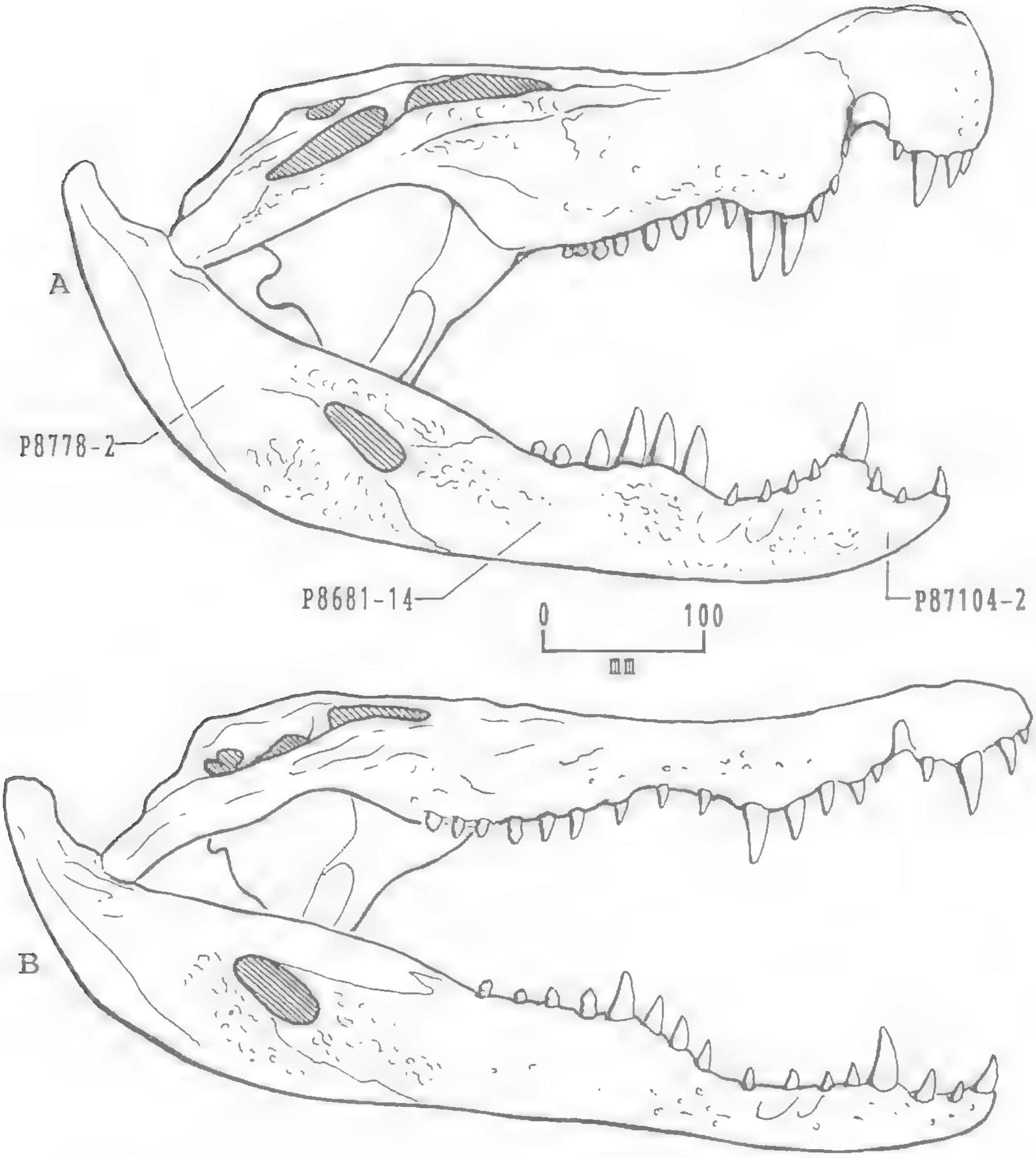

FIG. 6. Comparison of the lateral profiles of the skulls of (A) *Baru darrowi* and (B) an extant saltwater crocodile, *Crocodylus porosus*, of approximately the same length. Among the contrasts with *Crocodylus porosus, Baru* posses deeper jaws with correspondingly exaggerated festoons, more anteriorly situated external nares, a conspicuous jugal crest and posteriorly slanted pseudoheterodont teeth. These features reflect significant differences in the manner of dispatching, and perhaps in its preference of, prey animals.

Sebecosuchian Ziphodonts. Although clearly eusuchian, *Baru* is compared to sebecosuchian crocodiles because of its convergent ziphodont features. With the exception of its laterally compressed, serrated dentition, *Sebecus* shows few similarities with *Baru.* This is of some importance because the concept of ziphodonty is often broadened to imply a specialised terrestrial predatory complex. The laterally directed orbits, high, narrow, convex snout profile and modifica-

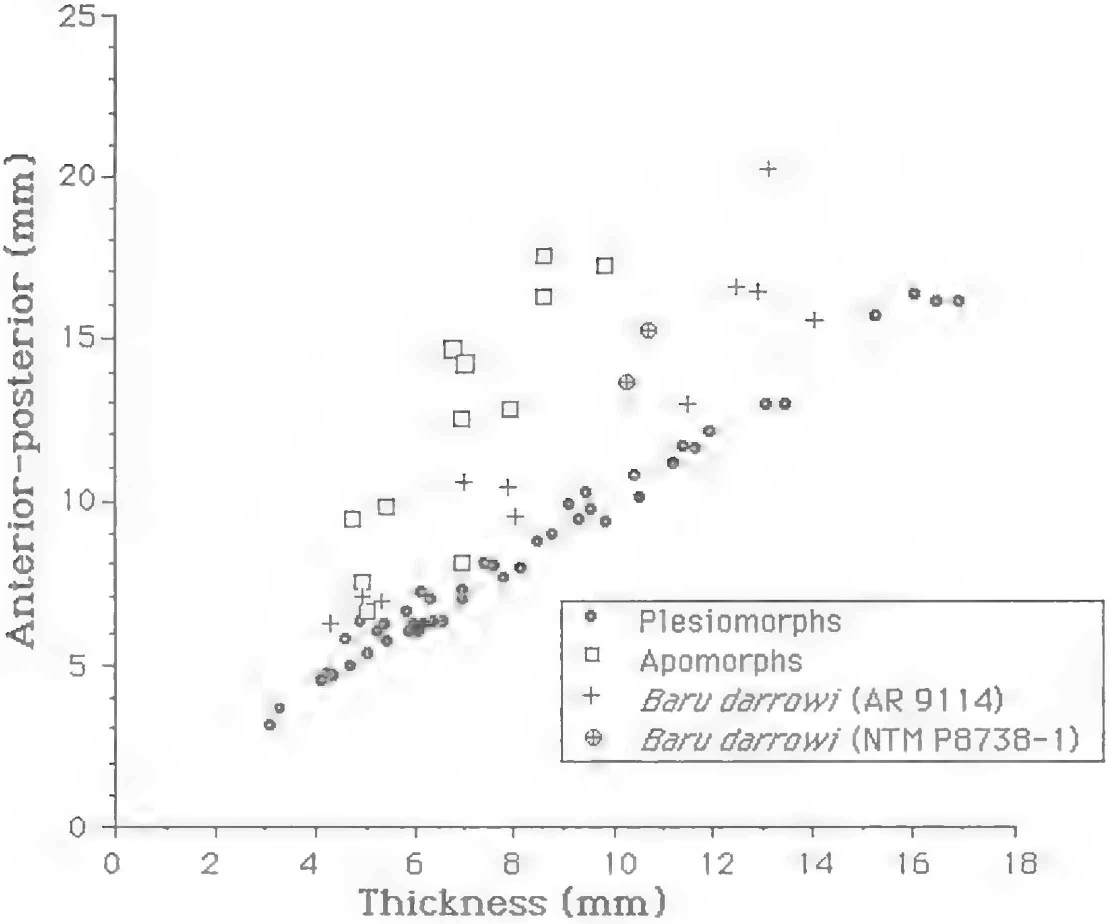

FIG 7. Scatter diagram showing tooth compression in various crocodilians. This shows the teeth of *Baru darrowi* to be more compressed than those of *Crocodylus porosus* and *Alligator mississippiensis* but not as compressed as in the ziphodont forms *Pristichampsus rollinati, Sebecus icaeorhinus* and *Sebecus* sp. Measurements for ziphodont forms from Langston (1956). Measurements for *C. porosus* and *A. mississippiensis* from unnumbered specimens in the Australian Museum reptile collection.

tions of the trochlear surface of the quadrate in relation to specialised jaw mechanics (Colbert, 1946; Langston, 1973) suggest that *Sebecus* was an active predaceous carnivore capable of pursing prey on land. Although the depth of *Baru*'s snout appears to most closely approach that of *Sebecus* (Table 1) this is a somewhat misleading comparison because the convention of measuring the depth of the snout at the level of the fifth tooth includes the marked alveolar festoon. The proportions of the snouts of the two forms are actually very different; that of *Sebecus* is high and narrow and virtually triangular in section. *Baru*'s snout has a broad-based trapezoidal cross-section and is short and broad. Its lateral profile is strongly concave as opposed to the convex, narrow bridge of *Sebecus*. More importantly, however, is the typical crocodyline dorsal orientation of *Baru*'s orbits and its nares being sufficiently elevated, despite their terminal position, to allow the head to lie cryptically submerged.

Pristichampsine Ziphodonts. *Baru darrowi* shows a greater degree of overall similarity with the early Tertiary Eurasian eusuchian ziphodonts of the subfamily Pristichampsinae than to the sebecosuchians. However, Pristichampsine crocodiles, known from several species of the genus *Pristichampsus*, are strikingly convergent with the sebecosuchians, not only in their possession of double-serrated and compressed teeth, but in the lateral position of the orbits, the narrow snout and the similarly specialised craniomandibular joint (Langston, 1973). Although the trochlear surface of *Baru*'s quadrate is imperfectly known, the shape of the quadratojugal and the distal surface immediately preceding the jaw joint are more reminiscent of *Pristichampsus* than *Crocodylus*. The articular of *Baru* indicates that its craniomandibular joint could be modified along the lines of the sebecosuchian and pristichampsine ziphodonts. *Pristichampsus* has a vaulted palate and the skull is narrow, as opposed to broad, across the base of the jugals and through the orbital region. The primary resemblance between *Baru* and *Pristichampsus* is in the lateral view of the snout where the dorsal outline is deeply concave, although the premaxilla of *Pristichampsus* is less bulbous. The teeth are moderately differentiated, at least in some species of *Pristichampsus*, closely approximated and are directed slightly backwards from the maxillary festoon (see Langston, 1973, fig. 4d). The notch for the fourth dentary tooth is weakly developed, particularly when viewed from below and the dentition is considerably less robust than in *Baru*. The teeth of *Baru* are moderately compressed, not as compressed as in the ziphodont crocodilians (i.e. *Pristichampsus* and *Sebecus*) but more so than in less derived crocodilians (Fig. 7).

The palatal morphology of *Pristichampsus* differs from that of *Baru* in possessing well-developed anterior palatine processes, proportionately similar to those of *Crocodylus*. The anterior palatine processes persist among the living short-snouted crocodylids and therefore their presence or absence does not appear to be conditioned by the relative anteroposterior length of the palatal fenestrae. Apparently the resemblances between *Baru* and *Pristichampsus* are largely plesiomorphic for crocodylids but include some elements of the ziphodont trophic complex.

Australasian Endemic Crocodilians. The two endemic *Crocodylus* species, *C. johnsoni* and *C. novaeguineae* are subsumed under the remarks previously made for *Crocodylus*. Besides the formally described endemically Australian genera, *Pallimnarchus* and *Quinkana*, there are other extinct species that are too poorly represented to merit systematic designation. The apparent distinction of the Australian *Crocodylus* species and the remaining known Australian genera makes it improbable that a direct ancestor-descendant relationship between them will be found on this continent. A compelling alternative, therefore, is to consider the possibility of a close relationship among the endemic genera not affiliated with *Crocodylus*.

Quinkana fortirostrum Molnar, 1981, is a highly distinctive crocodilian characterised by a broad, short snout with a deep, convex profile, large anteriorly positioned palatal fenestrae and doubly-serrated laterally compressed teeth showing only moderate differentiation along the tooth row. Its short snout and palatal morphology is unlike that of either sebecosuchian or pristichampsine ziphodonts (Table 1), but its dentition is morphologically similar to members of those groups.

The type specimen, AM F.57844, is a fragment of the snout broken immediately anterior to the orbits, but including the anterior margins of the palatal fenestrae and the anterior palatine suture. In section, the rostrum is trapezoidal, with well developed alveolar processes. Due to the position of the break, Molnar (1981) was able to examine the internal structure of the snout cavity. He observed that "A high, posteriorly concave partition dorsally bounds the anterior margin of the palatal fenestra. A similar but less developed partition is found in *Crocodylus johnsoni*, *C. novaeguineae* and *C. porosus*, where, however, it is placed well anterior to the margin of the fenestra, and is restricted to the lateral portion of the snout cavity. In *Q. fortirostrum* the maxilla is excavated anterior to this partition, forming lateral chambers that open posteriorly. Above the junction of the palatal processes of the two maxillae rise two thin, nearly vertical flanges, which together form a narrow trough along the floor of the snout cavity" (Molnar, 1981). It is therefore of some importance to note that a similar arrangement occurs in *Baru*. However, as this condition is regarded only in contrast to the typical *Crocodylus* condition, we are unsure of the morphology of the same region in other short snouted crocodylids such as *Osteolaemus* and *Paleosuchus* in which the more anterior position of the palatal fenestrae might also determine similar relations. Although described by Iordansky (1973), he does not compare this region in various genera. *Quinkana* and *Baru* lack the anterior palatine processes, which is unusual among crocodilians and apparently not conditioned by the anterior disposition of the palatal fenestrae, or by the proportions of the interfenestral laminae of the palatines. *Quinkana* is otherwise very different from *Baru*, but has few specific similarities with any other group of crocodilians. Thus *Quinkana* has a combination of characters; some ziphodont features (implying a terrestrial or semi-terrestrial predaceous existence) others unique and a few, very specific and rather compelling features, suggestive of a close relationship with *Baru*.

To date, specimens of *Pallimnarchus pollens* have been fragments and no complete skulls are known (Molnar, 1982). However, nearly complete snouts referable to *Pallimnarchus* have recently become available for study (Willis and Molnar, in prep.). This more complete material reveals that *Pallimnarchus* has anteriorly located palatal fenestrae (anterior level with the seventh alveoli) and lack anterior palatine processes. Teeth referred to *Pallimnarchus* (Molnar, 1982) are distinguished by serrate carinae on a broadly conical form. A more complete comparison with *Baru* will have to wait until the new *Pallimnarchus* material is properly described.

We are unable to fully support the hypothesis that the three known Australian endemic crocodiles represent a monophyletic group because of limited comparative material and incomplete fossils. There is, however, sufficient evidence to indicate that this is a solid alternative to the notion of sebecosuchian and/or pristichampsine ancestry of the group. The possible relationship between these forms are considered in the following section.

CHARACTER ANALYSIS

The following examination of crocodilian character states is based on Molnar (1981), Norell (1989) and Benton and Clark (1988). Molnar used character frequency to determine character polarities where as Benton and Clark, and Norell, used the outgroup method proposed by Maddison et al. (1984). We have accepted the polarity of characters as determined by Molnar, Benton and Clark, and Norell. The polarity of new characters introduced into this study have been determined by their distribution among the ten taxa indicated in Table 3.

SUBORDINAL CHARACTERS

1) Procoelous vertebrae have been found with specimens attributed to *B. darrowi*. No amphicoelous vertebrae are known from deposits from which *B. darrowi* has been found. It is therefore a reasonable assumption that *Baru* had procoelous vertebrae, which is recognised as a eusuchian character (Steel, 1973; Kuhn, 1968). Benton and Clark (1988) recognise procoelous vertebrae as an apomorphy of a group that includes Eusuchia and an undescribed early Cretaceous crocodile from North America.

2) The movement of the internal nares posteriorly in advanced crocodiles was recognised by Huxley (1875). The internal nares are completely surrounded by the pterygoids in *Baru*. This is regarded as a eusuchian character state (Steel, 1973; Kuhn, 1968; Benton and Clark, 1988).

SUBFAMILIAL CHARACTERS

3) The pattern of tooth enlargement in the crocodilian skull has been used to distinguish members of the Alligatorinae from the Crocodylinae (e.g. Steel, 1973). In alligatorines the fourth maxillary tooth is usually the largest; in crocodylines it is the fifth. In *Baru* the fifth tooth is largest.

4) The presence of a notch between the premaxilla and maxilla can be used to distinguish alligatorines from other crocodilians (Steel, 1973). In crocodilians the fourth dentary tooth fits into this notch when the jaws are closed. In alligatorines this tooth usually fits into a pit in the palate medial to the upper tooth row. *Baru* conforms to the plesiomorphic condition.

5) In *Alligator* and many fossil alligatorines the lachrymal is separated from the nasal bone by the maxilla (a derived condition), whereas in crocodylines and the caimanoid alligatorines the lachrymal contacts the nasals. This may also be expressed as the prefrontals lacking any contact with the maxilla in crocodylines. *Baru* is crocodyline in this respect.

FEATURES OF AUSTRALIAN FORMS

6) *Baru*, *Quinkana* and *Pallimnarchus* have large anteriorly placed palatal fenestrae. This condition appears to be part of a functional complex related to short, broad snouts.

7) Most crocodiles possess an anterior palatine process. *Baru*, *Quinkana* and *Pallimnarchus* lack this process. The only other eusuchian crocodiles for which descriptions are available that lack these structures are those of the American Eocene genus *Brachyuranochampsa*. This is a moderately narrow snouted form with more posteriorly situated palatal fenestrae. Therefore it appears that the lack of the anterior palatine processes is independent of the position of the palatal fenestrae.

8) Molnar (1981) determined interlocking teeth to be a derived crocodilian state. However, Norell (1989) determined that an overbite, as seen in *Baru* and *Quinkana*, is the derived state.

Norell's determination is accepted here because of his use of the outgroup method of Maddison et al. (1984).

9) The conspicuous jugal ridge observed in *Baru* appears to be an unique feature among crocodiles. Its presence in *Baru* is taken to be autapomorphic.

Ziphodont Characters

10) Molnar (1981) considers highly differentiated crocodyline dentitions to be plesiomorphic and more uniform dentitions of longirostrine and ziphodont crocodiles to be derived.

11) Festooning is a plesiomorphic feature. The derived condition is a straight tooth row (Molnar, 1981). These conditions are clearly associated with the degree of size differentiation of the dentition.

12) Extremely narrow snouted eusuchians are derived. Moderately narrow to moderately broad snouts are plesiomorphic. Extremely broad, short snouts are also derived (Molnar, 1981). *Quinkana* and *Baru* are unusual ziphodonts in having short, broad snouts. *Peirosaurus* (Gasparini, 1982) appears to be a ziphodont with a moderately broad or broad snout.

13) According to Molnar's classification, ziphodont crocodilians have deep to moderately deep snouts. He proposes that this is a derived state. Both *Baru* and *Quinkana* have moderately deep snouts. The plesiomorphic condition is a low snout form.

14) Laterally compressed teeth are considered to be derived. The plesiomorphic condition is a tooth of circular or broadly oval cross section. The teeth of *Quinkana* are decidedly compressed whereas those of *Baru* retain the plesiomorphic conical shape towards the base, becoming progressively flattened on the lingual side towards the tip of the crown.

15) Serrations are not known to occur on any round conical crocodilian teeth (with the exception of some teeth attributed to *Pallimnarchus*, Molnar, 1982), they are invariably associated with some degree of transverse compression of the crown. Laterally compressed teeth with serrated edges are termed ziphodont. The ziphodont condition is a derived character state.

16) Posterior inclination of the teeth appears to be an unusual feature in crocodilians. The condition may be present in the sebecosuchian *Baurusuchus* and perhaps to some extent in *Pristichampsus*. The condition is probably a derived one.

Discussion

The most complete cladistic analysis of the Crocodilia is that of Benton and Clark (1988). They left the crocodylids (including gavials, alligators and crocodylines) as an unresolved crown group. Norell (1989) analysed this crown group based on twelve characters and defined the relationship between the gavialinae, crocodylids and alligatorids. Unfortunately, Norell's work was published after this paper had been reviewed and his characters have not been fully incorporated in this analysis. However, *Baru* has all three apomorphies that Norell has used to separate crocodylids from gavials and alligators.

Baru retains many plesiomorphic crocodyline features. Its principle derivations are related to a specialised trophic complex which involves some elements of the so-called ziphodont condition. As is often the case with ancient surviving groups, they are exceptionally conservative in their basic morphology and many lineages have paralleled and converged in their trophic mechanisms. It is under these circumstances that the phylogenetic methodology becomes severely strained. Most apomorphic features are dedicated to trophic adaptations and the field of relevant character states (discrete or exclusive characters independent of functional requirements) are few and difficult to substantiate. In terms of phylogenetics, therefore, we are confined to a single possible synapomorphy, the absence of the anterior palatine process, in uniting the three extinct Australian genera under consideration. Ziphodont teeth have evolved convergently and in parallel, and anteriorly placed palatal fenestrae have evolved independently in the caiman and *Osteolaemus*. We are unable to verify the uniqueness of the similarity of the internal rostral partitioning in *Baru* and *Quinkana* at this time due to lack of the necessary specimens. The absence of the anterior palatine processes appears to be the least trophically related apomorphic character uniting *Baru*, *Quinkana* and *Pallimnarchus* with another group (e.g. *Brachyuranochampsa*). We consider this possible relationship to be a more parsimonious one than basing a relationship with the Pristichampsinae, on the assumption that the anterior palatine process was lost in parallel.

The ingroup interrelationship of *Baru*, *Pallimnarchus* and *Quinkana* are little closer to resolution. *Baru* and *Pallimnarchus* are more plesiomorphic than *Quinkana* according to the character polarities used here. However, *Pallimnarchus* is not sufficiently well known to determine its phyletic position relative to *Baru*. It appears, however, that *Baru darrowi* is too specialised to have given rise to *Quinkana*. We are therefore unable to build a connected sequence and must assume that another clade for which we have no information is involved.

PALAEOBIOLOGY

A detailed functional analysis of *Baru*'s cranial anatomy must preclude any definite conclusions as to the nature of its trophic specialisations. However, its distinctive dentition and robust proportions justify some speculation on the nature of its habits.

The prominent upper and lower festoons bearing large, posteriorly-directed and closely spaced teeth constitute a specialised cleaver-like biting mechanism, designed to deliver an immediate incapacitating blow to its prey. The upper and lower festoons and their dentitions complement one another so as to produce a fulcrum above which the lower caniniforms drive into the prey. The resultant is a combined shearing and tissue deforming (tearing and breaking) action capable of breaching tough, flexible material (thick hides, as well as more durable materials such as armoured skin and perhaps bony carapaces). Because of the fulcrum-like structure of the interposed maxillary festoon, tissues are stretched against and severely deformed by a triangle of forces. The large posteriorly-angled teeth restrain the prey-object during the early phases of jaw closure, when resultant forces exerted by the jaw tend to drive the object forward.

The purpose of the serrations in *Baru* appears to be a secondary refinement in which the struggling movements of the prey combined with small movements of the jaws and perhaps equally importantly, elevation and depression of the head at the craniocervical joint can continue to sever tissues in the grasping period during which the adducted jaws are restricted in their movement.

Baru's dental specialisations are therefore interpreted as a mechanism for rapid immobilisation of relatively large prey. Judging from the dimensions of the type, *Baru* was capable of killing animals up to 300 kg in weight based on analogous feats by the saltwater crocodile. *Baru* would therefore have been a likely predator of mammals and other large crocodiles, as its dental complex and powerful adductor mass was capable of breaching armoured hides.

The remains of *Baru* are consistently associated with fluvio-lacustrine sediments. Its short, broad heavy cranium and the morphology of its atlas-axis complex indicate that it had no greater head mobility than *C. porosus*, which would have limited an active terrestrial predator. Unlike sebecosuchians, pristichampsines and Australia's ziphodont *Quinkana*, *Baru* has dorsally oriented orbits like aquatic crocodiles which spend the majority of their lives partially submerged. We conclude that *Baru* was an aquatic crocodile adapted to shallow, inland freshwater lakes and small streams in which the saltwater crocodile habit of dragging its larger prey into deep water may not have been possible. In shallow water and narrow streams the prey has an opportunity to continue to struggle, whereas the saltwater crocodile is often able to release its half-drowned prey to effect a new grasp. *Baru* probably ambushed large mammals from the edge of streams and shallow lakes relying on its powerful bite to incapacitate its prey through shock-inducing trauma. If *Baru* were a terrestrial or semi-terrestrial form, the risky and energy-consuming action of immediately immobilising its prey would be unnecessary. Large terrestrial reptiles, best known from the studies of the Komodo Dragon by Auffenberg (1982), initially injure large prey by hamstringing it from behind, then follow it until it expires from exhaustion and bleeding. This pattern appears more appropriate to species of *Pristichampsus* and *Quinkana*.

The postulated predatory behaviour of *Baru* is too specialised to suggest a preadaptation to terrestriality for *Quinkana*. However, terrestrial predation in crocodiles probably had its roots in behaviour in which prey was ambushed from the water, then followed onto the land.

CONCLUSIONS

Functional complexes reflecting trophic adaptations, superimposed on a general morphological conservatism have produced numerous convergences within the Crocodilia. Consequently, taxonomic relationships are difficult to unravel.

The contribution of the pterygoids to the secondary palate, posterior intra-pterygoidal position of the internal nares, confluent external nares, subdermal postorbital bar, small superior temporal fenestra, well developed mandibular fenestra and associated procoelous, keeled cervical vertebrae (NTM P9778) place *Baru* in the Eusuchia, Family Crocodylidae (sensu Romer, 1956). The diagnostic enlarged fifth maxillary tooth and the lateral notch at the maxillo-premaxillary suture to accommodate the fourth mandibular tooth align *Baru* with the Crocodylinae.

Baru shares a number of character states with two other Australian endemic fossil genera. Its incipient ziphodonty, broad snout, presence of a similar arrangement of the internal partition of the maxilla and similar palatal proportions may support a phylogenetic relationship with *Quinkana* and *Pallimnarchus*. The absence of the anterior palatine process in all three of these genera may link them to the Eocene North American taxon *Brachyuranochampsa*, and distinguishes the Australian crocodiles from the pristichampsine ziphodonts.

In *Baru*, the shorter, wider and deeper rostrum, hypertrophied festooning, greatly differentiated tooth size and laterally compressed serrated teeth are a functionally related complex and as such are not reliable taxonomic indicators. Ziphodont teeth have evolved independently in several crocodilian lineages and have been associated with highly specialised, perhaps terrestrial predatory habits. Adaptations apparently suited to a terrestrial predatory mode include a convex deep, dorsal snout profile and dorsolaterally directed orbits and external nares. In contrast, *Baru* has elevated premaxillae, high anterodorsal placement of the external nares, concave dorsal snout profile and dorsally oriented orbits. These features indicate that *Baru* was an aquatic crocodile.

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