# Phylogenetic Systematics and Biogeography of the Carphodactylini (Reptilia: Gekkonidae)

by

AARON M. BAUER

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## ABSTRACT

The tribe Carphodactylini is composed of 49 species of geckos of the subfamily Diplodactylinae that are endemic to the regions of Australia, New Caledonia and New Zealand. The systematics of the group is approached through the methodology of phylogenetic systematics and a hypothesis of genealogical relationship is presented. The padless Australian genera *Nephrurus* (including *Underwoodisaurus*), *Phyllurus*, and *Carphodactylus* are the sister group of the New Caledonian and New Zealand carphodactylines. The New Zealand genus *Hoplodactylus* is paraphyletic. The New Caledonian taxa (*Bavayia, Eurydactylodes*, and *Rhacodactylus*) form a monophyletic unit if the northern Australian genus *Pseudothecadactylus* is regarded as a subgenus of *Rhacodactylus*. Systematic accounts and summaries of all biological literature relating to each species are presented.

The tectonic history of the southwest Pacific region is in harmony with the hypothesis of carphodactyline relationships. The primary division of the tribe into Australian and Tasmantis lineages was probably brought about by the opening of the Tasman Sea about 80 mybp. By the Oligocene marine ingressions isolated New Caledonia from northern New Zealand, thus splitting *Hoplodactylus*. Carphodactyline geckos highlight the antiquity, endemism and biogeographic significance of the herpetofauna of the southwest Pacific, and New Caledonia in particular.

## INTRODUCTION

Although a great deal of systematic work has dealt with the place of gekkonids among squamates and with higher order relationships among geckos, little has been produced with respect to inter- and intrageneric relationships within the tribe Carphodactylini. The carphodactylines as currently construed include the Australian genera *Nephrurus, Phyllurus, Carphodactylus* and *Pseudothecadactylus*, the New Zealand genera *Naultinus* and *Hoplodactylus*, and the genera *Bavayia, Eurydactylodes* and *Rhacodactylus* from New Caledonia and the Loyalty Islands. In addition, *Underwoodisaurus* (Australia) and *Heteropholis* (New Zealand) are also occasionally recognized as distinct taxa at a generic level. The present work is an attempt to summarize that which is known about carphodactyline biology and to erect a hypothesis of relationship upon which subsequent evolutionary morphological studies may be based. (In the pages that follow, in order to avoid confusion, nomenclatural changes implemented as a result of this study are used consistently from the start — e.g., *Nephrurus milii* instead of *Phyllurus milii* or *Underwoodisaurus milii*).

The earliest reviewers of lizard taxonomy were perplexed by the taxonomic affinities of the first described carphodactyline, *Phyllurus platurus* (White 1790). Schneider (1797), Daudin (1802), La Cépède (1804), and Merrem (1820) all placed the species in an agamid genus, either *Agama* or *Stellio*. Gray (1825) was uncertain as to its affinities, but suggested links with either the agamids or gekkonids. Bory de Saint-Vincent (1825) described a second species, *P. milii* (= *Nephrurus milii*), recognized its similarity to *P. platurus*, and assigned both to the Gekkonidae.

Fitzinger (1843) distributed the four species known to him into three genera in two families of the Ordo Ascalabotae. The family Stenodactyli, essentially containing all geckos without dilated scansorial subdigital pads, included *Gymnodactylus miliusii* and *Gonyodactylus platurus*, the latter genus being distinguished by a prominent kink in the digits. The remaining taxa, *Hoplodactylus duvaucelii* and *Hoplodactylus (Rhacodactylus) leachianus*, were included among the Platydactyli, a mixture of all of the padded geckos without divided or lobed scansors. This classification system, like most of those which followed for over one hundred years, made no attempt at phylogenetic analysis but rather pigeon-holed species primarily on the basis of external digital characters.

Gray (1845) keyed *Phyllurus* and *Naultinus* to the same first subdivision of geckos while separating *Platydactylus* (including *Rhacodactylus* and *Hoplodactylus duvaucelii*). Girard (1858) relied on artificial divisions to yield information about natural groups ("the genus *Naultinus* is a Stenodactylian: hence widely distinct from *Hoplodactylus*, which . . . is a Platydactylian").

Boulenger (1885a) accorded no special recognition to the group now regarded as the Carphodactylini. His division in the "Catalogue of Lizards" was based on the order in which genera fell out in the family keys. Nevertheless, the structure of the keys, while largely artificial, may imply some phylogenetic information (Russell 1976). Boulenger's primary divisions were based upon pedal structure and the carphodactylines known at the time were distributed among five different major groups of geckos. Notably, division VII lists the genera *Naultinus, Hoplodactylus* and *Rhacodactylus* in sequence. These are immediately preceded by *Lepidodactylus* which at the time included the species later transferred to *Bavayia*. Although clustered together because of digital similarities, the particular order of these genera may reflect Boulenger's belief in some sort of close relationship among these taxa, a belief that would have been supported by biogeographical data.

Gadow (1901), Werner (1912), Camp (1923) and Smith (1933a), while shuffling the taxonomic rank of the eublepharine geckos and the Madagascan *Uroplatus*, made no distinction as to the taxonomic subdivision of the majority of the Gekkonidae. Roux (1913), however, did suggest that the New Caledonian genera *Rhacodactylus, Eurydactylus (= Eurydactylodes)* and *Bavayia* might share affinities with *Hoplodactylus*, based upon their possession of an offset terminal pad on digit one.

Underwood (1954) provided the first attempt at a reexamination of the higher systematics of geckos. His division of the Gekkonidae into the subfamilies Diplodactylinae and Gekkoninae was based primarily on the structure of the pupil in life; straight-edged in the former and a series of pinholes ("*Gekko*-type") in the latter. This distinction, while later challenged (Kluge 1964, 1967a; Cogger 1964), was effective in delineating the patterns of subfamilial affinities that have since been vindicated by the work of Kluge (1967a, 1967b, 1982, 1983a, 1987) and others. Using the pupil-shape criterion Underwood successfully removed the ambiguity then present as to the distinction between species of *Diplodactylus* and *Phyllodactylus*. It also clarified the position of *Phyllurus* as distinct from other Old World *Gymnodactylus* (= *Cyrtodactylus* sensu Underwood). Underwood (1954) included within *Phyllurus*, in addition to *P. cornutus, P. milii* and *P. platurus*, the New Guinean *P. vankampeni*, which has since been identified as a gekkonine (Kluge 1967a).

Table 1. Components of the Diplodactylinae (Underwood 1954) with corresponding tribal (Kluge 1967b for Diplodactylinae; Kluge 1983a for Gekkoninae) and generic group (Russel 1972) placements. AUS = Australia, NZ = New Zealand, NC = New Caledonia, SAF = Southern Africa, NAF = North Africa, ASI = Asia, WI = West Indes, SAM = South America. R = *Rhoptropus*-type pupil (sensu Underwood 1954).

| Genus | Region | Tribe (Kluge 1967b, 1983a) | Generic group (Russel 1972) |
|---|---|---|---|
| *Carphodactylus* | AUS | Carphodactylini | |
| *Nephrurus* | AUS | Carphodactylini | |
| *Phyllurus** | AUS | Carphodactylini | |
| *Diplodactylus* | AUS | Diplodactylini | |
| *Lucasius* | AUS | Diplodactylini | |
| *Oedura* | AUS | Diplodactylini | |
| *Rhynchoedura* | AUS | Diplodactylini | |
| *Hoplodactylus* | NZ | Carphodactylini | |
| *Naultinus* | NZ | Carphodactylini | |
| *Bavayia* | NC | Carphodactylini | |
| *Rhacodactylus* | NC | Carphodactylini | |
| *Chondrodactylus (R)* | SAF | Ptyodactylini | *Pachydactylus*[1] |
| *Colopus (R)* | SAF | Ptyodactylini | *Pachydactylus* |
| *Palmatogecko (R)* | SAF | Ptyodactylini | *Pachydactylus* |
| *Rhoptropus (R)* | SAF | Ptyodactylini | *Pachydactylus* |
| *Phelsuma (R)* | SAF | Ptyodactylini | *Lygodactylus*[2] |
| *Rhotropella** (R)* | SAF | Ptyodactylini | *Lygodactylus* |
| *Ptenopus (R)* | SAF | Ptyodactylini | not placed |
| *Saurodactylus* | NAF | Ptyodactylini | not placed |
| *Teratoscincus* | ASI | Ptyodactylini | *Stenodactylus*[3] |
| *Aristelliger* | WI | Gekkonini | *Aristelliger*[4] |
| *Gymnodactylus* | SAM | Gekkonini | not placed |

* Includes *Cyrtodactylus vankampeni*

** Synonomized with *Phelsuma* by Russel (1977a)

[1] Also includes *Geckonia*, *Tarentola*, and *Kaokogecko* (not known to Underwood). Haacke (1976), Russel (1977a) and Kluge (1983a) found evidence for the monophyly of this generic group. Joger (1985) provided immunological support for the group as well, although he indicated that *Pachydactylus* itself is polyphyletic.

[2] Also includes *Ailuronyx*, *Microscalabotes*, *Millotisaurus*. Kluge (1983a) placed all members of this group, except *Phelsuma* in the Gekkonini.

[3] Includes only *Stenodactylus* and *Teratoscincus*.

[4] Placed in own species group.

In all, Underwood's (1954) Diplodactylinae included 22 genera (see Table 1), incorporating all but two of the genera now accepted as well as some members of a (probably monophyletic) group of South African gekkonines, *Saurodactylus*, the South American *Gymnodactylus* and two particularly odd gekkonines, *Teratoscincus* and *Aristelliger*. The last has been noted for its many convergent characters with diplodactylines (Russell 1979a; A. E. Greer pers. comm.) and its distinctive autapomorphies (Kluge 1982). A number of the remaining taxa possessed what Underwood referred to as the "*Rhoptropus*-type" pupil (Table 1). The removal of these taxa, now recognized as African gekkonines, would have left Underwood's Diplodactylinae slightly less polyphyletic.

Within the Diplodactylinae Underwood (1954) noted the similarities in the pollex among *Aristelliger, Bavayia* and *Rhacodactylus*. His views on the affinities of this group were strengthened by his contention that the three shared primitive features of the digits and eyes and that all "occupy peripheral positions in the total world range of geckos". This last statement is difficult to interpret given that geckos are pan-tropical and occur with great species diversity both in the West Indies and the Southwest Pacific.

Underwood (1954) ascribed two genera now recognized as carphodactylines to the Gekkoninae (*Pseudothecadactylus* = *Rhacodactylus* (part) and *Eurydactylus* = *Eurydactylodes*). While no particular mention is made of the former genus, the latter was discussed at some length. While placing this form in the Gekkoninae, Underwood indicated that it, along with *Oedura* and *Rhynchoedura*, required examination of living material as pseudo-"*Gekko*-type" pupil lobulation was suspected. Subsequently Underwood (1955, 1957) indicated that *Eurydactylus* was indeed a diplodactyline and that *Rhynchoedura* should be treated as a gekkonine. His statement "the six Australian, three New Caledonian, and two New Zealand diplodactyline genera form a well-defined tribe within the subfamily on osteological characters" (criteria unstated) essentially recognized a monophyletic Diplodactylinae (sensu Kluge 1967a, 1967b) with the exception of *Pseudothecadactylus* and *Rhynchoedura* and the retention of *Phyllurus (= Cyrtodactylus) vankampeni*.

Stephenson (1960), endorsed no particular theory of relationships, but criticized Underwood's single character methods and suggested that the use of another randomly chosen character might yield a different subdivision of the Australian geckos.

Werner (1961a, 1961b) accepted Underwood's scheme but drew rather different conclusions about evolution within the family. He stated that the New Zealand Diplodactylinae were the most primitive of the living geckos and derived the remaining three subfamilies from the diplodactylines. There are many inconsistencies within this scheme and the hypothesis of relationships it implies is supported by few synapomorphies. Werner based his hypothesis on the assumptions that the vertical pupil (present in *Naultinus*) is primitive, that the New Zealand diplodactylines have "a most primitive skeleton" (based on the claims of Stephenson & Stephenson 1956), and that narrow, padded toes are primitive for the family. Werner (1961b) further suggested that ovoviviparity might be primitive for geckos, having been lost in all non-New Zealand forms. These assumptions also require the independent evolution of eyelids in the

Eublepharinae and imply that eublepharines are secondarily padless (see discussion below). Further, procoely must evolve at least three times from an amphicoelous diplodactyline ancestor. This last character state transformation was apparently based on acceptance of Underwood's (1955) reversal of his previous, supported (see character analysis of axial skeleton) view (Underwood 1954) that procoely was primitive for the Gekkonidae. Werner's views were never published in their full form consequently not gaining wide acceptance. Werner's more recent work reflects a general acceptance of the hypotheses of relationship developed by Kluge (1967a).

Kluge (1965a, 1967a, 1967b), based on a wide variety of both osteological and soft characters, provided stability to the subfamilial divisions of the Gekkonidae and removed the African and New World components of Underwood's (1954) Diplodactylinae. He also provided the first explicit hypotheses of carphodactyline generic relationships. Based on the distribution of preanal pores and features of the nasal process of the premaxilla, Kluge (1965a, 1967b) divided the diplodactylines into two tribes, the Carphodactylini and the Diplodactylini.

Kluge (1967b) diagnosed the Carphodactylini on the presence of numerous rows of preanal pores arranged in a large, irregularly- shaped patch (Fig. 1), although *Bavayia sauvagii*, as well as the Australian genera *Nephrurus* and *Phyllurus*, show secondary modifications of this condition. Carphodactylines also possess a short, wide nasal process of the maxilla, but this character is plesiomorphic for the Diplodactylinae. Further, the presence of paired premaxillae throughout life is characteristic of the carphodac-

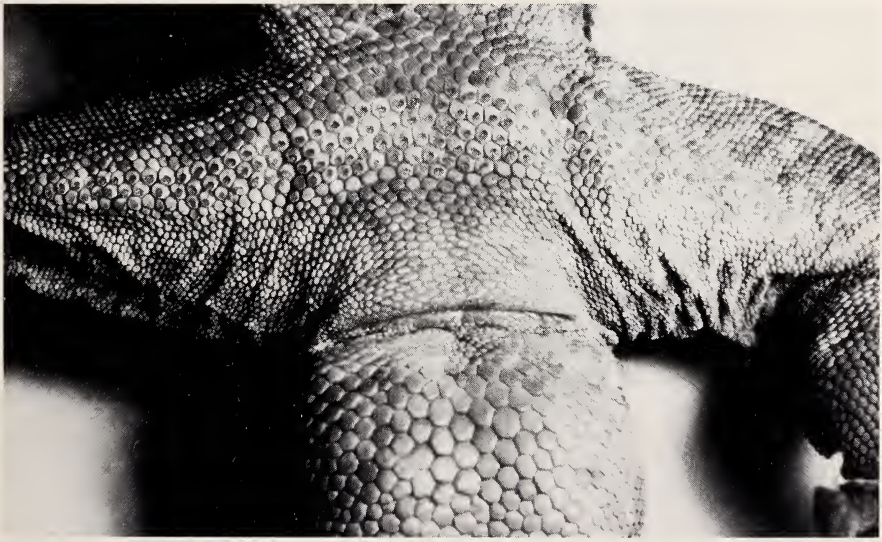

Fig.1: Ventral view of cloacal region of adult male *Hoplodactylus duvaucelii* showing the large patch of preanal organs, a synapomorphy of the Carphodactylini. (Photo courtesy of B.W. Thomas)

tyline genera (a reduced split, or partial fusion is seen in the New Zealand genera, *Rhacodactylus* and *Bavayia*).

The Diplodactylini, as well, were diagnosed by a series of synapomorphies by Kluge (1967b). The shared presence of the plesiomorphic condition for each of the characters used to diagnose the Diplodactylini was then used by Kluge as further evidence of carphodactyline relationships. Recent work by Kluge (1983a, 1987) employing the method of phylogenetic systematics has used only synapomorphies as evidence of shared ancestry.

Kluge (1965a, 1967b) believed that the tribe Carphodactylini possessed more primitive features than the Diplodactylini. Within carphodactylines he considered *Carphodactylus, Nephrurus* and *Phyllurus* to be most similar to the ancestral stock of the subfamily, with the latter two genera more closely related to each other than either is to *Carphodactylus*. Kluge also considered all three of the New Caledonian genera to be closely related, although he was uncertain of the relationship of *Bavayia* to the other genera. *Pseudothecadactylus* was considered to be more closely related to the New Caledonian radiation than to the main Australian radiation despite certain osteological similarities shared with the latter. Kluge accepted viviparity as evidence for the close phylogenetic relationship of the three New Zealand genera he recognized, and within this group considered *Hoplodactylus* and *Heteropholis* to be more closely related to each other than either was to *Naultinus*. The reason for this view, given the fact that *Naultinus* and *Heteropholis* cannot be diagnosed from one another, is unclear but probably results from Kluge's acceptance of the authority of McCann's (1955) "Lizards of New Zealand". This scheme of relationships is shown in Fig. 2.

It is unclear from Kluge's early work whether he accepted a monophyletic Carphodactylini. While he did provide a synapomorphy for the group he stressed the primitive aspects of the tribe and did not address the issue of padlessness in the Australian radiation. If it is accepted that this group is primitively padless (Russell 1972, 1979a) then pads must have evolved at least twice within the Diplodactylinae (and no padless Diplodactylini survived), or the Carphodactylini is paraphyletic, having given rise to the Diplodactylini.

Russell (1972), accepting the phylogeny of Kluge (1967a, 1967b), found that digital characters supported the unit *Carphodactylus* + *Nephrurus* + *Phyllurus* + *Underwoodisaurus* as a "compact group" and agreed with Kluge (1967b) that *Carphodactylus* was probably the most primitive extant member of the tribe (presumably because of the overall similarity to the eublepharine *Aeluroscalobotes*). Russell found no morphological intermediates between the primitively padless Australian genera and the padded forms of New Zealand and New Caledonia. He described a morphological series of increasing complexity in digital structure from *Heteropholis* through *Naultinus* to *Hoplodactylus*. Russell further considered the digital structure of the New Caledonian forms to be more advanced than that of their New Zealand relatives, and suggested that *Rhacodactylus* and *Eurydactylodes* were sister-taxa. *Pseudothecadactylus* was considered to be the most advanced genus in terms of pedal morphology and to share some similarities with *Rhacodactylus*.

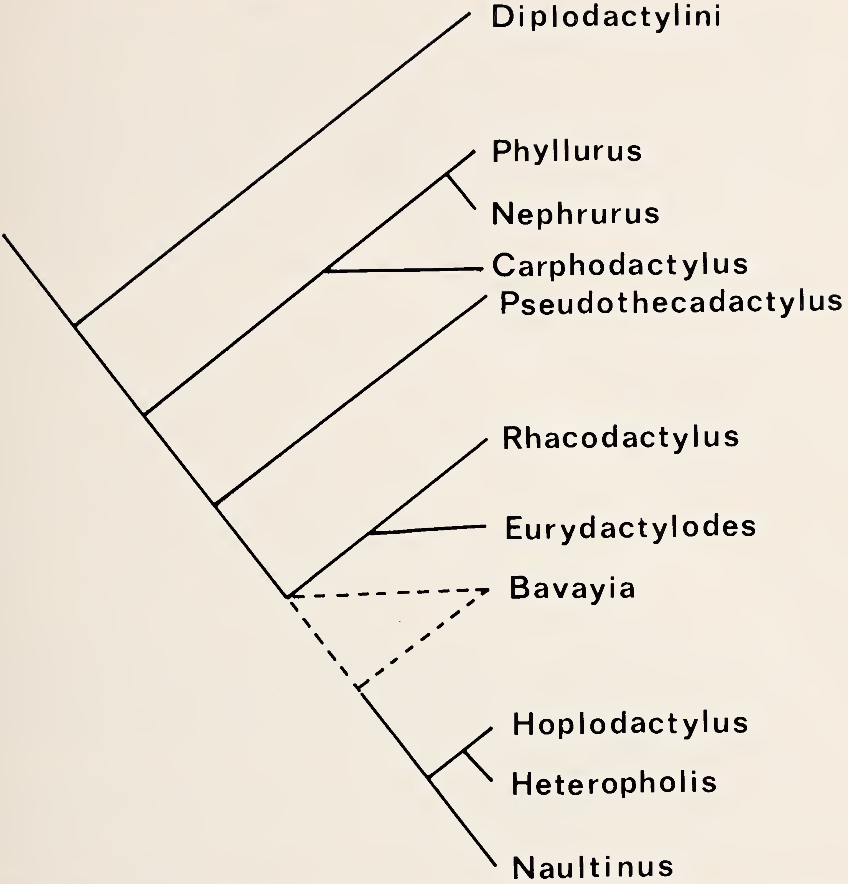

Fig.2: Tree diagram of hypothesized diplodactyline relations redrawn as a cladogram after Kluge (1965a, plate VI, Fig. 11).

Russell (1979a) later addressed the question of carphodactyline monophyly. He stated "the most parsimonious argument is that pads were acquired only once within this subfamily (the Diplodactylinae) . . . The basal stock of the Carphodactylini . . . was padless but it would appear that the Diplodactylini arose from an ancestor which possessed terminal subdigital pads". The acquisition of terminal pads is thus postulated as occurring before the separation of the Diplodactylini and the pad-bearing Carphodactylini. While this implies support for a polyphyletic Carphodactylini, Russell (pers. comm.) accepts the possibility that pads might have evolved twice within the Diplodactylinae — with a primarily distal enlargement in the Diplodactylini and a primarily basal enlargement in the padded carphodactylines. The existence of a well defined and supported Diplodactylinae and Gekkoninae + Sphaerodactylinae (Kluge

1987) necessitates parallel development of pads within geckos, even if the Carphodactylini is polyphyletic. Thus, convergent evolution of scansorial pads should not be ruled out within the Diplodactylinae on the grounds of parsimony.

Moffat (1973a) rejected Kluge's conclusions regarding subfamilial evolution but did not herself address the question of generic relationships within the subfamilies. Bull and Whitaker (1975), apparently without supporting data, suggested that the New Zealand genera of carphodactylines were directly derived from one or more New Caledonian genera. Hecht (1976) and Hecht & Edwards (1977) reevaluated the phylogenetic hypotheses of Underwood (1954), Kluge (1967a) and Moffat (1973a) but added little to the knowledge of intergeneric relationships.

Kluge (1987) revised his interpretations of diplodactyline phylogeny and biogeography. He provided explicit synapomorphies for the Diplodactylinae and demonstrated a sister-group relationship with the Pygopodidae. Although Kluge (1987) did not specifically address the question of carphodactyline monophyly he did continue to list the tribe Carphodactylini as a (presumably natural) unit in the classification scheme isomorphic with his phylogenetic hypothesis. Although I accept Kluge's (1987) phylogenetic hypothesis I disagree with the ranks proposed for the clades in his classification. Specifically the inclusion of the subfamily Diplodactylinae with the Pygopodinae within the Pygopodidae disrupts the taxonomic stability of a large number of geckos and suggests a fundamental shift in the conception of both the Gekkonidae and the Pygopodidae. The relegation of pygopodids to subfamilial rank within the Gekkonidae would retain the current meaning of the two groups as well as maintain isomorphy. Kluge's (1987) statement that pygopodids may share additional derived characters with the Diplodactylini suggests that the rank of the flap-footed lizards may yet be even further reduced to that of a tribe.

King (1987a, 1987b, 1988) has used karyological and albumin immunological data to support the monophyly of the Diplodactylinae, but has proposed that the Carphodactylini should include the genus *Oedura*, which shares a derived karyomorph with the carphodactylines as presently construed. However, at least two species of *Oedura* as well as some *Nephrurus* and *Phyllurus* do not share the derived pattern and the basis for recognizing specific karyomorphic features as synapomorphies is not altogether clear.

I accept, for the present, the monophyly of the Carphodactylini on the basis of the preanal organ character proposed by Kluge (1967b) and accordingly base the determination of polarity by outgroup method on the hypothesis of higher order gekkotan relationships derived by Kluge (1967a, 1983a, 1987) and summarized in Fig. 3.

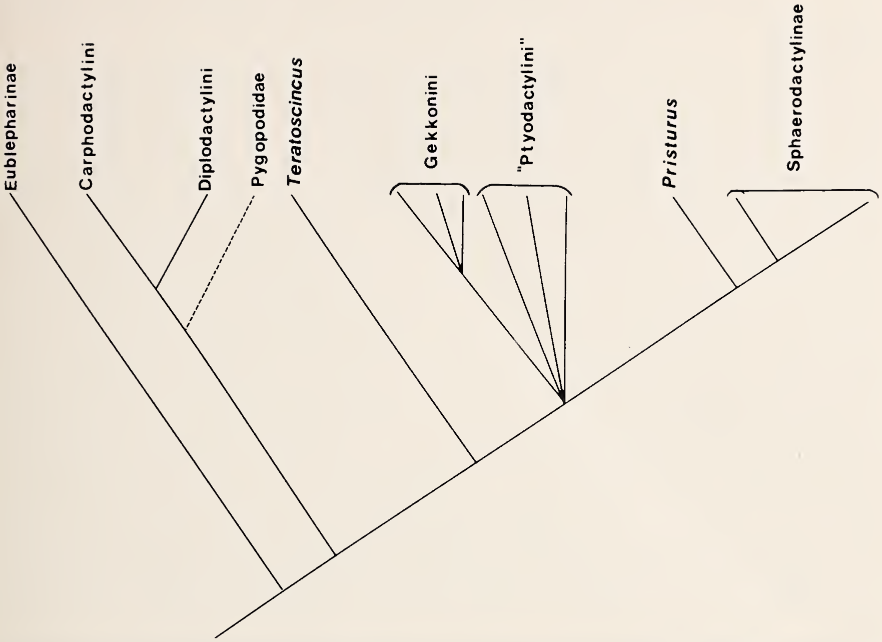

Fig.3: Hypothesis of higher order gekkonid relationships (after Kluge 1967a, 1967b, 1987) used in this analysis for the purpose of selecting outgroups. Dashed line indicates tentative placement of the Pygopodidae. For the purposes of this study all taxa from *Teratoscincus* to the right of the cladogram are considered to be Gekkonine geckos. Quotation marks around the Ptyodactylini indicate the recognized paraphyly of this taxon. The most commonly used taxonomic group names are used although these are not necessarily isomorphic with respect to the phylogeny.

## MATERIALS AND METHODS

More than 3000 specimens (see Appendix B), representing all but one of the species of carphodactyline geckos, were examined including living and preserved material from major museums and a few private collections (see Appendix A for collection acronyms). Formalin or alcohol fixed specimens stored in 65-75% ethanol provided the basis for external character analysis. Many of these specimens, particularly those from New Caledonia, were collected during the course of the study. These animals were killed by intraperitoneal injection with T-61 euthanasia solution or by freezing before standard fixation with 10% neutral buffered formalin. Osteological information was obtained from dermestid beetle prepared dry skeletons or from specimens cleared and stained following a modification of the methods of Wassersug (1976), Dingerkus & Uhler (1977), and Hanken & Wassersug (1981). In addition, whole body radiographs of representatives of most species were prepared for use in the study of post-cranial characters.

I employed the method of Hennig (1966) (= phylogenetic systematics) in order to deduce patterns of genealogical relationship among the carphodactyline geckos. The polarity of characters was generally assessed by outgroup comparison (Watrous & Wheeler 1981; Farris 1982; Maddison et al. 1984; Brooks & Wiley 1985) which appears to be the most philosophically robust and generally applicable method (P.F. Stevens 1980). In the case of several digital characters, however, an argument based on the internal consistency of functional units has been invoked, even though its results conflict with those of the outgroup method. It is crucial to recall that polarity assessment in outgroup analysis invokes parsimony; that is, the character state(s) present at the ingroup node, or first outgroup node (Maddison et al. 1984) is determined based on the minimization of steps to that node. This type of parsimony (descriptive parsimony, sensu Johnson 1982; methodological parsimony, sensu Kluge 1984) does not have logical hegemony in this (or any?) biological instance. It is, rather, an objective criterion for assessing character state polarities, or more generally for choosing among hypotheses.

When employed in this study, outgroups were chosen on the basis of the extensive work on the higher systematics of gekkotans carried out by Kluge (1967a, 1967b, 1974, 1983a, 1987). Specifically, the outgroups used, in order of decreasing proximity to the Carphodactylini, were the members of the tribe Diplodactylini, the members of the subfamily Gekkoninae (including the species currently placed in the Sphaerodactylinae), and the members of the subfamily Eublepharinae. While relationships within these groups are not necessarily well established (see Kluge 1983a; Joger 1985), their placement relative to one another is now generally accepted (Fig. 3).

Despite irrefutable evidence for the close relationship of geckos and pygopodids (Underwood 1957; Kluge 1976, 1987) these latter lizards were not used as outgroup taxa. One reason is the absence in these limbless forms of many of the characters which are variable among the carphodactylines. Missing data can be accomodated by most computer-based phylogenetic analysis programs, however, pygopodids are so aberrant (in many of the characters used in this study) as to shed little light on intra-tribal affinities. More importantly, however, is the question of their phylogenetic relationship to the other taxa. Since the work of Underwood (1957), pygopodids have generally been regarded as the sister group of geckos, but more recent work suggests that they are the sister group to all, or part of, the Diplodactylinae (Kluge 1987).

Character state polarities were assessed according to the guidelines of Maddison et al. (1984), and in order to insure global parsimony in the subsequent analysis the primitive states for each character were determined at the first outgroup node rather than at the ingroup node. Under the algorithm of Maddison et al. (1984), a single state at the outgroup node may be determined if the two most proximal branches share a common state (Fig. 4b), or if the first and third taxa relative to the ingroup share the same state (Fig. 4c) (or, of course, if the character state does not vary in the outgroup members). However, in cases where the first sister taxon differs in state from the next two distally (Fig. 4d), no polarity can be assigned. These characters were retained in the analysis

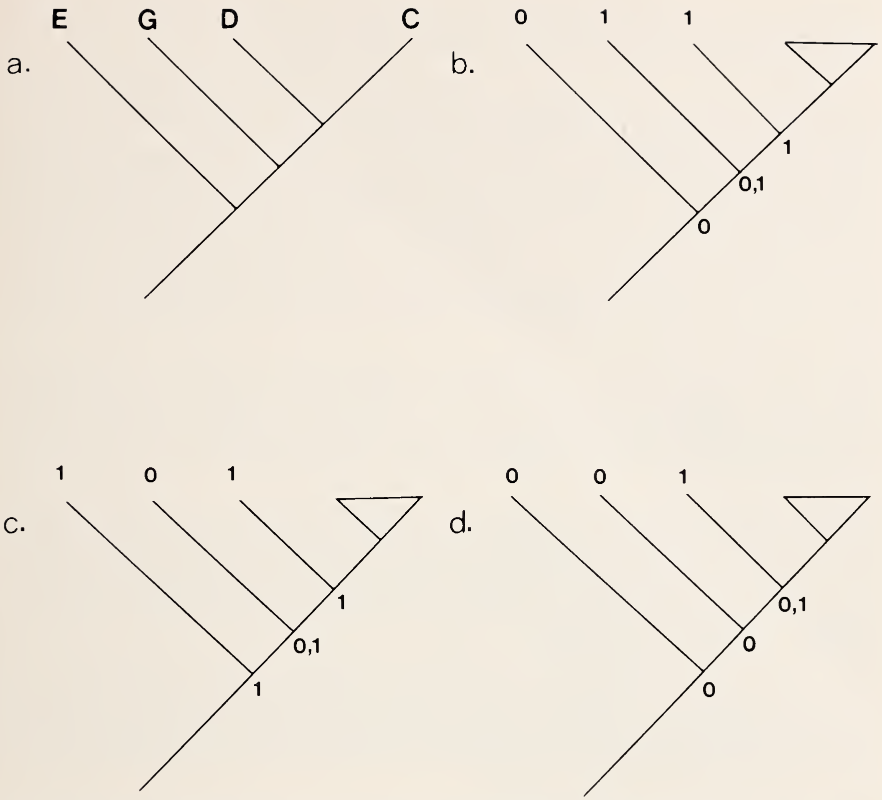

Fig.4: Method of assigning polarity by outgroup comparison (after Maddison et al. 1984).
a. Simplified cladogram of higher order gekkonid relationships (E= Eublepharinae, G= Gekkoninae, D= Diplodactylini, C= Carphodactylini).
b—d. Derivation of polarity at the outgroup (terminal) node resulting from the possible distribution of character states (0 or 1) in three successive outgroup taxa. See text for discussion.

but were entered as "missing" for the ancestor in the PAUP (Swofford 1985) analysis (see below) and were not, therefore, assigned polarity before the analysis. For the purposes of the analysis a hypothetical ancestral carphodactyline possessing the character states present at the outgroup node was assumed.

For the Diplodactylini and Eublepharinae, representatives of each genus were examined in order to supplement literature records for certain characters. The huge number of taxa in the Gekkoninae made a comprehensive survey impractical, but specimens of representatives of most major lineages as well as literature reports were used to determine the condition of this taxon.

Most species currently recognized as belonging to the carphodactylini were analysed (see species accounts). While some homogeneous subgroups exist, for example

*Naultinus*, generic monophyly has not been established for all carphodactylines and it was thus inappropriate to carry out a generic level analysis.

Procedurally I have assumed both the monophyly of the Carphodactylini as a whole and that of the OTU's, the individual species. The former requirement is, of course, necessary for the application of outgroup criterion. Thus, polarity determinants may shift in some characters if the ingroup is not monophyletic or if some members of the outgroup are actually members of the ingroup. The evidence for carphodactyline monophyly is admittedly weak. Kluge's (1967b) division of the Diplodactylinae is supported by several derived characters, most diagnosing the Diplodactylini, not the Carphodactylini. Nonetheless, Kluge's preanal organ patch character remains a putative synapomorphy for the tribe.

Some of the taxa analysed were actually complexes of several species — for example, *Bavayia cyclura* and *B. sauvagii* as run in the analysis each consist of several discrete biological entities. However, the complexes themselves are assumed to be monophyletic, thus there should be no affect on the results of the analysis.

Variation within single OTU's occurred in a number of presumptive characters. When this could not be attributed to pathology, sexual dimorphism or ontogeny, or when polarity could not be assessed within the taxon concerned, the character was discarded for the purposes of the analysis. Overall, few characters were involved, and most of these were variable for many taxa.

The character state distribution data were used to construct patterns of nested sets of taxa. Basal branches of these cladograms were initially constructed without computer aid, but the large number of taxa and degree of homoplasy in the data prevented resolution of distal branches by this method.

The patterns presented as cladograms were generated by the PAUP (Phylogenetic Analysis Using Parsimony) version 2.4 (Swofford 1985) on an IBM AT computer. This program uses the Wagner method (Kluge & Farris 1969; Farris 1970) to produce branching diagrams of minimal length.

A variety of options was used on the data set with varying degrees of success (both in terms of time to run and tree length). In general, however, the options MULPARS and SWAP = ALT with the default ROOT = ANCESTOR (refer to Swofford 1985) were most effective. Two data sets were run with this program. In both, taxa with a great deal of missing data were omitted. The taxa affected were *Rhacodactylus cavaticus, Hoplodactylus delcourti, H. kahutarae, H. chrysosireticus, Naultinus manukanus* and *N. tuberculatus*. The first species was not examined. The second is known only from a single mounted specimen. The remainder have been examined, but I lack skeletal information or have been unable to examine specimens in conjunction with comparative material. PAUP performs "Fitch optimization" (Fitch 1971) which treats missing data as "all possible states" and places the taxa on the tree in the most parsimonious way. Although the resulting placement of these taxa is probably little biased by the missing data, I chose to add these taxa (in tentative positions) after the initial analysis. The exclusion of these taxa does not result in distortion of the interpretation of relationships among the remaining species (contra Arnold 1981). *Eurydactylodes symmetricus* was also excluded from the initial analysis as it shared the same character states for all characters with *E. vieillardi*.

The larger of the two sets run included all of the species level taxa except those listed above. A smaller data set was also run in which well supported, and largely homogeneous groups of taxa were reduced to a single "consensus" OTU. The collapsed taxa included all of the knob-tailed *Nephrurus*, all *Naultinus*, and all *Phyllurus*. The polarity of variable characters in the collapsed groups was reassessed on the basis of initial runs of the complete data set according to the algorithm of Maddison et al. (1984). Unpolarizable character states were rescored as missing in the "consensus" OTU.

In association with the reduced data set, each collapsed set of three or more taxa was reanalyzed by PAUP using the branch and bound method, with the ancestor designated as possessing the character states present at the outgroup node relative to the group. In the case of *Naultinus*, in which very few characters were variable, the run was aborted after more than 200 equally parsimonious trees (all of branch length 6) had been generated.

Finally, a consensus tree (Rohlf 1982) was prepared by hand from all of the trees generated. This process essentially involved the collapsing of conflicting branching patterns into polychotomies at the nodes in question. The resulting cladogram was ultimately used as a hypothesis of relationship within the Carphodactylini. Although this compromise tree is less explanatory than any of the original trees from which it is derived (Mickevich & Farris 1981; Farris 1983; Carpenter 1988) it does serve to highlight weak areas of the analysis and is here used in preference to other methods (e.g. Carpenter 1988) of choosing among multiple equally parsimonious cladograms.

## CHARACTER ANALYSIS

A large number of skeletal characters was evaluated for all carphodactyline species available. When possible, character state distributions were supplemented by information from the literature. In addition to osteological characters, 46 characters of coloration and external anatomy and one character each dealing with reproductive mode and behavior were employed in the phylogenetic analysis. Each character is described in general for the Carphodactylini and variation within the tribe is assessed. Determination of character state polarities, if possible, is indicated. Character states are listed as 0 (primitive) or 1 (derived) based upon the condition possessed by the "ancestor" — i.e. the outgroup node (Maddison et al. 1984). Characters for which polarities could not be assessed initially are listed as A or B. The polarity of some of these characters was determined using the preliminary results of the PAUP analysis. Only when one or more successively nearer outgroups (relative to the taxa having the putatively apomorphic character state) were identified as a result of the primary analysis was this procedure employed. Thus, the polarity a character having the distribution illustrated in Fig. 4d, which could not be assessed initially on the basis of the outgroup method (Maddison et al. 1984) could be determined by the addition of an additional, proximal sister taxon from within the Carphodactylini. In practice, this was possible when the character in question varied only within one of the two major lineages resulting from the analysis (see "Results"). The polarities of characters 9, 13, 16, 24, 29, 32, 33, 50, 54, 66, 79, 83 and 101 ultimately could not be determined. Historical and functional aspects of particular characters are presented when appropriate. A full character matrix is provided in Appendix C.

## Cranial Osteology

Though lizard cranial osteology has been well studied in some forms (e.g. the Lacertidae, Parker 1880; Gaupp 1906; Brock 1935; DeBeer 1930, 1937; Bellairs & Kamal 1981), relatively little attention has been focussed on the gecko skull. Even this work, in general, has been restricted to the analysis of the elements of the skull in one or a few species. Wellborn (1933), in her review of comparative osteology, considered 20 species, but no carphodactylines were among them, and Grismer (1988) analysed cranial characters in the eublepharines. Other studies which compared several taxa include those of Häupl (1980) on five gekkonines, Stephenson & Stephenson (1956), and Stephenson (1960) on New Zealand and Australian forms respectively (the latter also includes information on New Guinea and Caribbean gekkonine species), and Cope (1892), Camp (1923), and Rieppel (1984a) on representatives of all four subfamilies. Kluge (1967a, 1967b, 1987) and Moffat (1973a) also discussed some cranial characters but made no attempt at complete descriptions of the skull. Descriptive works exist for *Coleonyx* (Kluge 1962), *Palmatogecko* (Webb 1951), *Afroedura* (Webb 1951; Cogger 1964), *Homonota* (Fabián-Beurmann et al. 1980), *Hemidactylus* (Mahendra 1949; Liang & Wang 1973; Fabián-Beurmann et al. 1980), *Uroplatus* (Siebenrock 1893) and *Oedura* (Cogger 1964). Aspects of developmental osteology and of the chondrocranium have been considered by Brock (1932), Kamal (1960, 1961a, 1961b, 1961c, 1965a, 1965b), El-Toubi & Kamal (1961a, 1961b, 1961c), Sewertzoff (1900) and Häfferl (1921). Pratt (1948) and Underwood (1957), among others, have discussed the gekkonid skull in papers dealing primarily with other lepidosaur groups.

The carphodactyline skull exhibits no major modifications or structural innovations relative to those of other gekkonids. It shows the typical gekkonid condition of the loss of the supratemporal arch. This feature has been considered a gekkotan synapomorphy by Kluge (1967a, 1987) as has the reduction of the jugal, which is responsible for the incomplete postorbital arch in this group (Underwood 1957; Kluge 1967a, 1987). The reduction of bracing structures in the gekkonid skull contributes to the internal mobility of the skull as a whole. The skulls of carphodactylines and all other geckos studied to date are amphikinetic (Webb 1951; Frazzetta 1962). Rieppel (1984a) discussed a number of trends in cranial anatomy associated with kineticism.

A basic description of each cranial element used in the analysis is given and specific characteristics that vary within the group are described for individual taxa. Many elements are similar in shape and position throughout all geckos and, to avoid repetition, the reader is directed to Kluge (1962) and Grismer (1988) for descriptions of certain morphologically complex elements.

I have made no attempt to be exhaustive in the analysis of cranial features and their variation. Those of the neurocranium and occipital region, in particular, could not be examined in detail in many of the taxa due to a lack of disarticulated material. I examined, but found no significant or consistent variation in the following cranial elements of the species examined: maxilla, septomaxilla, prefrontal, vomer, palatine, pterygoid, epipterygoid, ectopterygoid, sphenoid, prootic, opisthotic, exoccipital, supraoccipital, basioccipital and stapes. Bauer (1986) provides detailed discussions of the shape and position of these bones among the carphodactylines.

**Cranium** — (Cranial features are illustrated by the skulls of *Nephrurus deleani*; *Rhacodactylus ciliatus* and *R. leachianus* in Figs. 5—7).

Co-ossification

Character 1: Dorsal skin of head free of skull (0) or co-ossified (1).

Co-ossification (character 1) involves the direct application of the dermis to the underlying bone. This condition is derived for carphodactylines as it is lacking in all species of the Diplodactylini. It was first noted in *Nephrurus* by Boulenger (1885a). Stephenson (1960) recorded co-ossification of the skull and skin in *Nephrurus* (except *N. milii*), *Phyllurus* and *Carphodactylus*. Kluge (1967b) recorded the trait as present in the last of these genera and in *Pseudothecadactylus* and scored it as variably present in *Nephrurus*, *Phyllurus* and *Rhacodactylus*. He also considered the likelihood of co-ossification in *Heteropholis* to be high, but did not record the condition in any of the specimens he examined. I have found co-ossification in specimens of the following taxa: *Nephrurus levis* (frontals — also reported for prefrontals, postfrontals and parietals, Stephenson 1960), *N. asper* (frontals, prefrontals, parietals, postfrontals, squamosals), *Rhacodactylus australis, R. leachianus* and *R. trachyrhynchus* (nasal process of premaxillae, nasals, maxillae, prefrontals, frontals, parietals), *Phyllurus cornutus, P. salebrosus* and *Carphodactylus laevis* (nasals, maxillae, prefrontals, frontals, postfrontals, parietals, squamosals), and *P. platurus* and *P. caudiannulatus* (all of the above mentioned elements except the squamosal). Cogger (1975a) stated that the skull of *Pseudothecadactylus lindneri* "is distinctly ornamented on the snout" but this was not confirmed by the specimens I examined. The distribution of co-ossification varies ontogenetically (Stephenson 1960) and neonates of all species (except perhaps *R. trachyrhynchus*) have unornamented skulls.

Premaxilla

Character 2: Premaxillae fused along midline with partial trace of suture (0) or with no remaining suture (1).

The premaxillae are dermal bones at the anteriormost extent of the snout. The body of each premaxilla forms the ventral or anterior border of the external naris and the

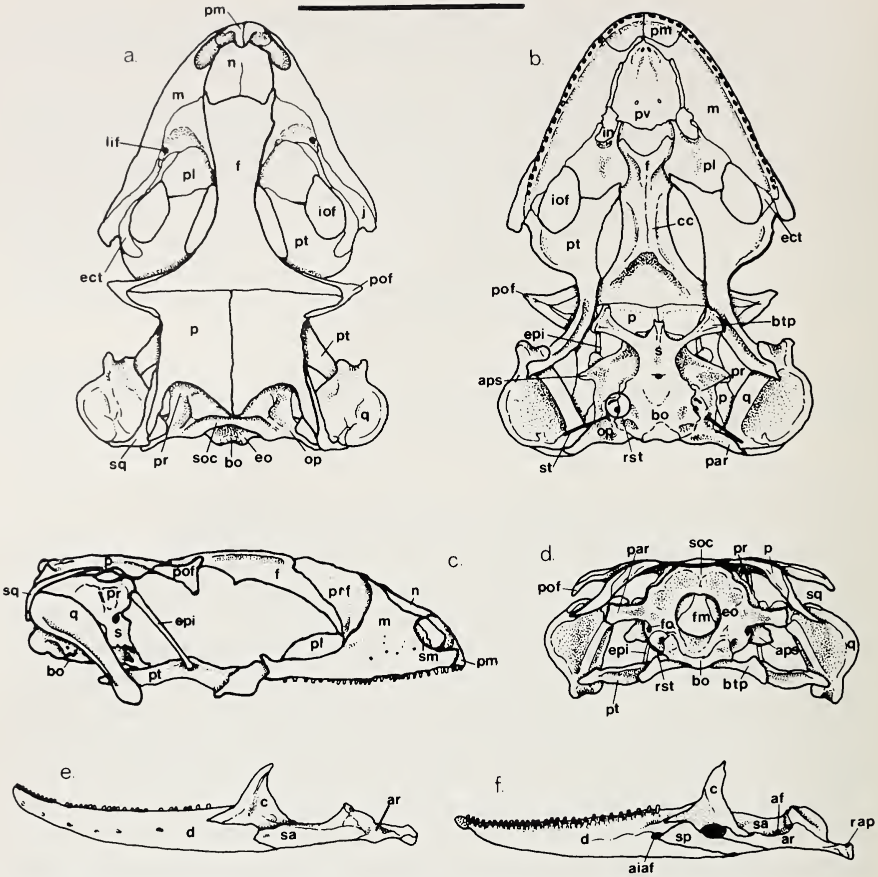

Fig.5: Views of the skull of *Nephrurus deleani* (AMB 46). a. dorsal, b. ventral, c. lateral, d. posterior, e. lateral view of mandible, f. medial view of mandible. Scale bar = 10 mm. The following list of abbreviations applies to Figs. 5—7.

af — adductor fossa
aiaf — anterior inferior alveolar foramen
amf — anterior mylchyoid foramen
aps — alar process of sphenoid
ar — articular
bo — basioccipital
btp — basitrabecular process
c — coronoid
cc — crista cranii
d — dentary
ect — ectopterygoid
eo — exoccipital
epi — epipterygoid
f — frontal
fo — fenestra ovalis
in — internal naris
iof — infraorbital fenestra
j — jugal
lif — lateral infraorbital foramen
m — maxilla
n — nasal
op — opisthotic
p — parietal
par — paroccipital process
pl — palatine
pm — premaxilla
pof — postfrontal
pr — prootic
prf — prefrontal
pt — pterygoid
pv — prevomer
q — quadrate
rap — retroarticular process
rst — recessus scalae tympanii
s — sphenoid
sa — surangular
sm — septomaxilla
soc — supraoccipital
sot — spheno-occipital tubercle
sp — splenial
sq — squamosal
st — stapes
tc — trabeculae communis

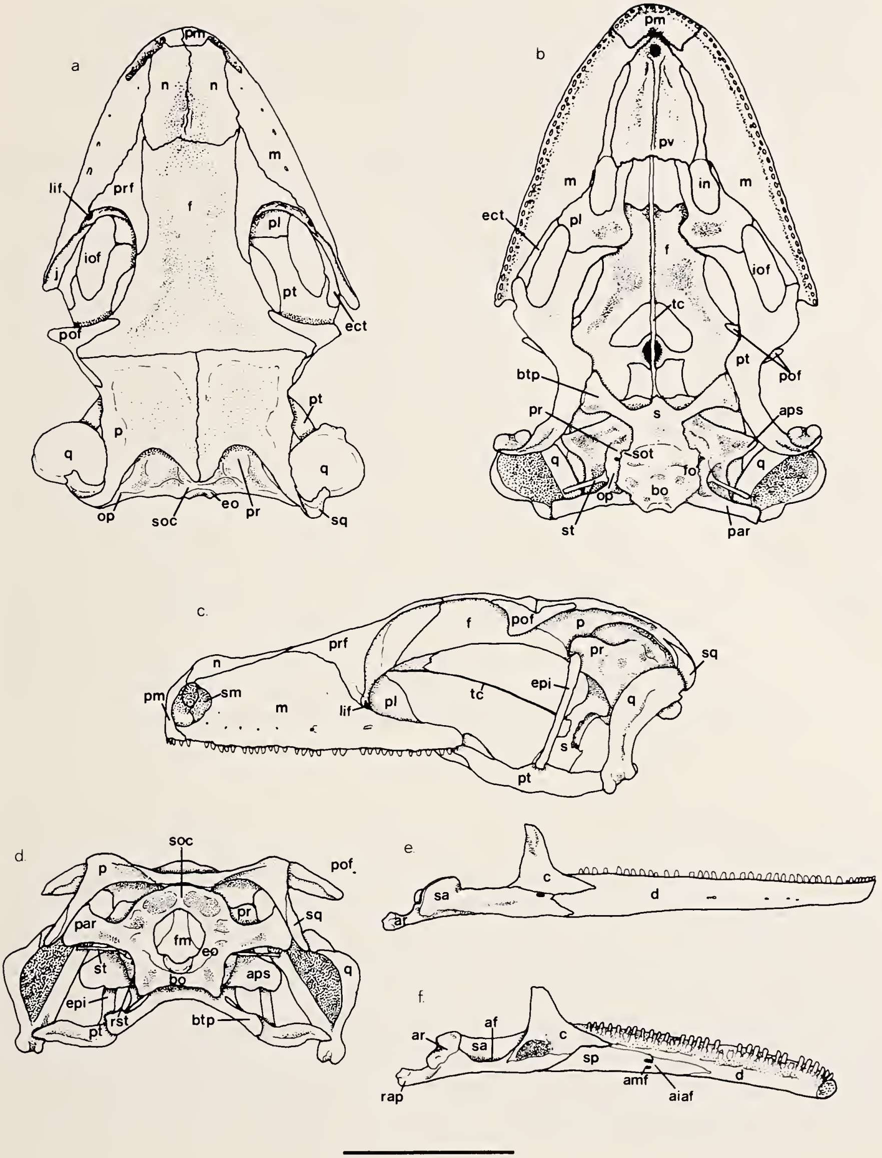

Fig.6: Views of the skull of *Rhacodactylus ciliatus* (BMNH 85.11.16.7). a. dorsal, b. palatal, c. lateral, d. posterior, e. lateral view of mandible, f. medial view of mandible. Scale bar = 10 mm. For abbreviations see Fig. 5.

nasal process of the premaxilla contributes to the medial border of the naris. A short, wide basal process is symplesiomorphic for the Carphodactylini (Kluge 1967b). Laterally and ventrally the body and pars dentalis of the premaxilla, respectively, contact the maxilla. Posteriorly the nasal process overlaps the paired nasals. The small septomaxilla abuts the pars dentalis dorsal to the palate.

The partially paired condition of the premaxillae observed in the Eublepharinae and Diplodactylinae is primitive for the family (Camp 1923; Kluge 1967a). In all carphodactylines the bones remain paired early in ontogeny (Kluge 1967a) although partial fusion occurs at the midline in species of *Hoplodactylus, Rhacodactylus, Bavayia, Naultinus* and *Eurydactylodes* by the time of parturition or hatching. Stephenson (1960) stated that the premaxillae were distinctly paired in the New Zealand taxa, but partial fusion characterized all of the postnatal specimens examined in this study; Kluge (1967b) stated that the premaxillae remained paired in *Eurydactylodes* and in *Pseudothecadactylus*, but this could not be confirmed. The bones remain paired throughout life with no fusion in the remaining Australian genera (character 2). Prehatchlings typically bear a single large deciduous egg-tooth on each premaxilla, as in the Diplodactylini and Eublepharinae. This condition is primitive for the Carphodactylini. However, as noted by Kluge (1967a), the live-bearing species of New Zealand geckos show no such structures and the adult-type dentition is present on the pars dentalis at birth. The condition in the live-bearing New Caledonian species *Rhacodactylus trachyrhynchus* requires study. In the youngest specimen available to me (less than one month post-natal), adult dentition is present. Hatchlings of *R. auriculatus, R. chahoua* and *R. leachianus* all conform to the typical, plesiomorphic condition. The states of this character are thus coincident with those for reproductive mode (see character 106).

### Nasal

Character 3: Nasal bones short and relatively broad (0) or elongate and narrow (1).

The nasals are roofing bones lying just dorsal and posterior to the external nares. The nasals are paired in all carphodactylines and are azygous only in a small number of gekkonines (Kluge 1967a). Anteriorly they are partially covered by the overlapping nasal processes of the premaxillae. Laterally they border the ascending plates of the maxillae to the border of these elements with the frontal, which is overlapped by the posterior portion of the nasal. The nasals are generally similar amongst all geckos. In most species they are relatively short and wide; however, an apomorphic condition of elongate, somewhat narrowed nasal bones is typical of *Carphodactylus laevis* and the species of *Phyllurus* (character 3).

### Frontal

Character 4: Frontal bone much longer than wide (0) or approximately as wide as long (1).

Character 5: Supraocular portion of frontal generally flat (0) or deeply furrowed or concave (1).

The frontal is the most extensive dermal roofing bone. It is invariably azygous in diplodactylines. It is bounded anteromedially by the overlapping nasals and anterolaterally by the prefrontal. Kluge (1967b) recorded a variety of character states for maxilla/frontal contact within the Carphodactylini. Based on the condition seen in the Diplodactylini (Kluge 1967b; Cogger 1964), contact would appear to be derived. However, in the secondary outgroup, the Gekkoninae, this state appears to be general (Wellborn 1933; Häupl 1980) as it does in the Eublepharinae (Kluge 1962). Extensive contact is rare among the carphodactylines and has been reported only for *Carphodactylus, Pseudothecadactylus* and *Bavayia* (Kluge 1967b). Contrary to these reports I found that maxilla/frontal contact was typical only of *Nephrurus sphyrurus*. In other species a narrow anterior process of the prefrontal or the body of the prefrontal itself provides a narrow separation between the two elements. In several other species contact was variable among specimens, and in *Hoplodactylus duvaucelii* contact appears to increase with body size. Given the extreme variability of this character within the basic taxa of this study I consider it uninformative at this level of analysis.

The frontal forms the dorsal ridge of the orbit and runs posteriorly to the transverse frontoparietal border where it contacts the small postfrontals laterally. Ventrally the thickened supraorbital ridges form an enclosed passage (the crista cranii) through which cranial nerve I passes on its way to the telencephalon. Rieppel (1984c) indicated that these processes fuse without a trace of a suture in all gekkonids. The complete closure of this canal has been recognized as a synapomorphy of the Gekkota (Kluge 1967a, 1987).

On the basis of the condition in Diplodactylini, Gekkoninae and Eublepharinae, the frontal is primitively somewhat hour-glass shaped — longer than wide, with the widest point at the parietal suture. This condition obtains in all taxa except the knob-tailed *Nephrurus*. In this group the posterior portion of the frontal is widened to almost the length of the element (character 4).

In the smooth knob-tail geckos, the midportion of the frontal is greatly narrowed, enhancing the apparent size of the orbits. This supraocular portion of the frontal is flat or nearly so in the Diplodactylini and the successively more distant sister taxa and is thus regarded as primitive for the Carphodactylini. This is the condition seen in *Naultinus, Nephrurus, Bavayia, Eurydactylodes, Hoplodactylus* (except in adult *H. duvaucelii*), *Phyllurus platurus* and *P. caudiannulatus*. A distinctive median groove or furrow is located medially in the frontal bones of *P. cornutus* and *P. salebrosus* as well as in *Carphodactylus* and *Rhacodactylus* (including *Pseudothecadactylus*) (character 5). The condition is most pronounced in *R. auriculatus* and is least developed in *R. trachyrhynchus* and the species of the subgenus *Pseudothecadactylus*.

### Postfrontal

Character 6: Lateral prong of postfrontal extends horizontally or only slightly downcurved (0), or distinctly ventrally curved (1).

The postfrontal in carphodactylines is stirrup-shaped and articulates with the frontal and parietal. Although Camp (1923) and most subsequent workers have regarded the bone as simple, some authors (e.g. Stephenson & Stephenson 1956; Rieppel 1984a) maintain that it contains both postfrontal and postorbital components. According to Rieppel (1984c) the postfrontal acts as a lateral brace for the otherwise highly kinetic frontoparietal joint. An elongate, blunt-ended process projects ventrolaterally to form the posterodorsal border of the orbit. The shape of the postfrontal is general for carphodactylines but also occurs in several other gekkonid lineages (Häupl 1980). In *Uroplatus fimbriatus* the lateral prong of the element is extremely elongate and, as in some carphodactylines, it is connected to the mandible by a calcified postorbital ligament. In most species the element changes shape ontogenetically. Initially the limbs of the postfrontal are narrow and the bone as a whole is "y"-shaped. With age the limbs thicken and broaden and the element becomes more "v"-shaped. Primitively in the Carphodactylini the lateral limb of the postfrontal curves somewhat downward as it does in many of the members of the outgroups. In *Rhacodactylus auriculatus* and *R. leachianus*, however, the process is so downcurved as to be oriented nearly vertically (Fig. 7) (character 6).

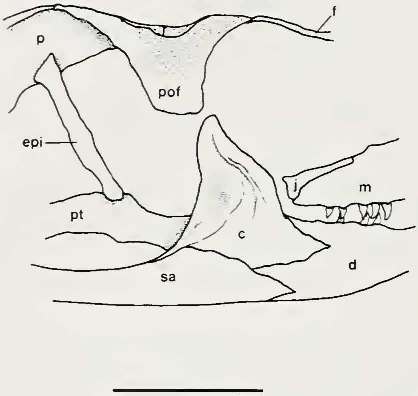

Fig.7: Lateral view of the postorbital region of the skull of *Rhacodactylus leachianus* (CAS 165890) showing greatly downturned postfrontal approaching the coronoid (character 6). Scale bar = 10 mm. For abbreviations see Fig. 5.

### Parietal

Character 7: Posterior border of parietals distinctly emarginate (0), or complete — roofing entire occipital region (1).

Character 8: Parietals as a unit approximately as long as wide (0), or short and very wide (1).

Character 9: Frontoparietal suture straight (A), or curved (B).

Character 10: Parietal crest at mid-dorsal suture absent (0), or present (1).

The parietals are the posteriormost roofing bones of the skull. The paired condition shared by all diplodactylines has been considered both primitive (Moffat 1973a) and derived (Kluge 1967a) for gekkonids, although there seems little support from outgroup comparison for the former view. Stephenson (1960) reported partial fusion of the parietals in *Carphodactylus laevis*. While I could not confirm this observation, I did find that virtually complete fusion of the parietals had occurred in adult *Rhacodactylus leachianus* and in both adult and juvenile *R. trachyrhynchus*. Similarly, the radiographs of *Hoplodactylus delcourti* show no sutures. This character is taken to be uninformative in terms of phylogenetic reconstruction; it is regarded as a byproduct of the gigantic size attained by all of these species of geckos.

Anteriorly, the parietal contacts the frontal and the posterior limb of the postfrontal. Posteriorly, lateral processes of the parietals contact the squamosal ventrolaterally. Ventrally, the parietals abut the supraoccipital at the midline. In the primitive condition the lateral posterior processes of the parietal curve anteromedially, producing an emargination bounded medially by the supraoccipital tubercle. A caudal extension of the parietal plate has reduced or eliminated this emargination in *Phyllurus, Carphodactylus* and in *Nephrurus asper* and *N. levis* (character 7). In all members of these genera the parietal is greatly broadened and shortened as compared with the primitive state (character 8). These genera also share with *Rhacodactylus* and *Pseudothecadactylus* a straight, rather than curved, frontal suture (character 9). The polarity of this trait cannot be assessed on the basis of available evidence. A small median parietal crest is a derived feature typical of *R. auriculatus* and *R. ciliatus* (character 10). *Rhacodactylus trachyrhynchus* is autapomorphic in its possession of an extremely elongate parietal.

### Squamosal

Character 11: Squamosal small and splint-like (0), or large and relatively broad (1).

The squamosal is typically a relatively small element lateral to the parotic process and parietal and in contact with the postero-medial aspect of the quadrate. Camp (1923) considered the element the tabulare (= supratemporal bone), based on analogy with *Heloderma*. Brock (1935) also supported this view and Bellairs & Kamal (1981) considered it the prevailing interpretation through the 1950s. Underwood (1957), however, located a tiny supratemporal element between the so-called tabulare and parietal in the Eublepharinae and thus established the element in question as the squamosal. Kluge (1962, 1967a) provided additional evidence for this interpretation that has led to its subsequent widespread acceptance (Rieppel 1984b), although Häupl (1980) referred to the element simply as the "Temporalknochen".

Dorsally the thin, laterally-oriented blades of the squamosal articulate with the posterior process of the parietal. Posteriorly and ventrally it curves to lie medial to the dorsal portion of the quadrate conch and lateral to the anterolateral face of the paroccipital process. The squamosal is greatly expanded in *Nephrurus asper, Carphodactylus laevis* and *Phyllurus* (character 11) and participates in the formation of the dorsal skull roof. This expansion represents a derived condition.

### Quadrate

Character 12: Lateral lip of quadrate narrow (0), or expanded as a lateral flange (1).

The quadrate is a large bone lying lateral to the brain case and participating in the jaw articulation. Dorsomedially, the quadrate contacts the squamosal and the paroccipital process of the opisthotic. Ventrally, the quadrate condyle articulates with a groove in the articular bone of the mandible. The posterior projection of the pterygoid contacts the medial portion of the condyle above the jaw articulation. In posterior view, the quadrate above the condyle is greatly concave, forming the quadrate conch. The medial edge of the conch is thickened and more or less straight. The lateral border of the conch is generally curved or slightly flared. A derived condition in which the lateral borders are broadly flared is seen in *Rhacodactylus ciliatus* and *R. auriculatus* (character 12) (see Fig. 6).

### Jugal

Character 13: Overlap of jugal and lateral infraorbital process of prefrontal extensive A) (0), or narrow or excluded B) (1).

The jugal in carphodactylines is a bony splint dorsal to the maxillary shelf, which lies between the lateral wall of the maxilla and the ectopterygoid. Anteriorly, within the border of the orbit, the jugal contacts the infraorbital process of the prefrontal. Kluge (1967b) considered the jugal long and wide in all carphodactyline genera except *Bavayia* (moderately long and narrow) and *Eurydactylodes* (not recorded). However, I found variations within taxa to be great in the present study and no discrete character states could be assigned. Extensive overlap of the jugal by the lateral infraorbital process of the prefrontal (Kluge 1967b) is seen in *Hoplodactylus* and *Rhacodactylus*, whereas the remaining genera show degrees of lesser contact from "nearly touching" *(Bavayia)* to "some overlap" (Kluge 1967b) (character 13).

### Basioccipital

Character 14: Recessus scalae tympani exposed ventrally A) (0), or at least partially obscured in ventral view by lateral process of the basioccipital B) (1).

The basioccipital forms the posterior portion of the floor of the brain case. Anteriorly, it contacts the sphenoid. Posteriorly the basioccipital narrows to form the thickened, u-shaped lip of the ventral border of the foramen magnum. Laterally it contacts the prootics, opisthotics and, posterolaterally, the exoccipital. Anterolaterally the basioccipital contributes to the ventrally inflected spheno-occipital tubercle. Dorsal to the tubercle lies the recessus scalae tympani. In all *Rhacodactylus* there is a prominent lateral process of the basioccipital which, in ventral view, hides the recessus. This is a derived condition that is also present, though variably developed, in *Eurydactylodes* and *Bavayia* (character 14).

### Scleral Ossicles

Character 15: 30 or more scleral ossicles (0), or fewer than 30 scleral ossicles (1).

Scleral ossicles are small plates of ossified cartilage that lie within the sclera of the eyeball in many amniotes, as well as certain anamniotes (Edinger 1929). It is generally thought that the ossicles maintain the shape of the eyeball (Walls 1942; de Queiroz 1982) although it is unclear how they function in this capacity given that they are absent in many major amniote groups, e.g. mammals, snakes and modern crocodilians. Underwood (1954) suggested that the reduction of the scleral sulcus in nocturnal geckos might reduce the functional significance of scleral ossicles even further.

Kluge (1967a) recorded scleral ossicle number for approximately 250 species of geckos, including members of most recognized genera. Outgroup information within the Gekkonidae for this character is derived chiefly from this data set. While the pattern of ossicle overlap may be of phylogenetic significance in some groups (de Queiroz 1982), it varies widely and may be difficult to score accurately in geckos (Underwood 1970, 1977a). Consequently only scleral ossicle number is considered here. It is problematical whether the mean species values or ranges should be used as character states. For the sake of convenience I have chosen to use mean values, although ranges are also reported. Eyes were removed from the sockets and manually cleared of the conjunctiva before counting. No stains were used.

Gugg (1939) and Underwood (1954) stated that 14 is the "standard" number of ossicles for amniotes. The view that 14 ossicles is also primitive for lepidosaurians and gekkotans was also espoused by Underwood (1954) and later endorsed by Moffat (1973a). Kluge (1967a), however, rejected 14 scleral ossicles as being primitive for geckos, citing the higher number found in eublepharines, especially *Aeluroscalobotes*, which he considered to be the most primitive living gecko. Data from outgroups provided by Underwood (1970) and de Queiroz (1982) clearly demonstrate that the former opinion is correct, and this view has since been accepted by Kluge (1987). The primitive condition for carphodactylines, however, would appear, on the basis of immediate outgroup analysis, to be the presence of a high number of scleral ossicles. Among the Diplodactylini Kluge (1967a) reported mean ossicle numbers of less than 30 in only two of 25 species and the overall species mean for this group is 32.7, ranging as high as individual counts of 40 in *Diplodactylus conspicillatus* (the highest number known for any vertebrate). This character is scored as derived for the Carphodactylini if mean species ossicle number is less than 30 (character 15).

The scleral ossicle counts for all carphodactylines examined are presented in Table 2. Means range from 20.5 to 35.3. Variation is high in most species with high sample size, but no sexual or ontogenetic trends in variation have been noted. My data do not support Stephenson's (1960) claim that ossicle number decreases with age in *Nephrurus*.

## Mandible

The lower jaw consists of five discrete elements in the Carphodactylini. Features of the mandible are illustrated in Figs. 5 and 6 for *Nephrurus deleani* and *Rhacodactylus ciliatus*. No consistent patterns of variation were noted in the dentary splenial, coronoid, or articular bones.

### Surangular

Character 16: Surangular dentary suture at the same antero-posterior position as coronoid-dentary suture A), or posterior to coronoid-dentary suture B).

Much of the posterior portion of the mandible, including both medial and lateral faces, is formed by the surangular. Laterally it is overlapped by the posterior processes of the

Table 2. Scleral Ossicle Counts for Species of Carphodactyline Geckos.

| Taxon | n (eyeballs) | No. of Ossicles Range (Mean) | Source |
|---|---|---|---|
| *Bavayia cyclura* | 8 | 29—33 (31.7) | B, K, U3 |
| *Bavayia sauvagii* | 18 | 30—34 (32.0) | B, K |
| *Carphodactylus laevis* | 6 | 30—33 (31.2) | K, S |
| *Eurydactylodes vieillardi* | 3 | 26—27 (26.7) | B, K, K2 |
| *Hoplodactylus duvaucelii* | 8 | 24—26 (25.0) | B, K, (SS) |
| *Hoplodactylus granulatus* | 10 | 23—27 (25.4) | B, K |
| *Hoplodactylus maculatus* | 4 | 26—28 (27.0) | B, (K*) |
| *Hoplodactylus pacificus* | ? | 25** | (U, SS) |
| *Hoplodactylus stephensi* | 1 | 24 | B |
| *Nephrurus asper* | 8 | 28—33 (30.4) | B, K, (S) |
| *Nephrurus deleani* | 4 | 32—33 (31.8) | B |
| *Nephrurus laevissimus* | 6 | 31—35 (32.7) | B, K |
| *Nephrurus levis* | 18 | 32—39 (34.3) | B, K, (S) |
| *Nephrurus milii* | 20 | 28—31 (29.4) | K, (S) |
| *Nephrurus sphyrurus* | 4 | 27—29 (29.4) | B, K |
| *Nephrurus stellatus* | 1 | 29 | B |
| *Nephrurus vertebralis* | 1 | 31 | B |
| *Nephrurus wheeleri* | 2 | 32—33 (32.5) | K |
| *Phyllurus caudiannulatus* | 1 | 26 | B |
| *Phyllurus cornutus* | 4 | 25—27 (26.0) | K |
| *Phyllurus platurus* | 12 | 24—28 (26.0) | B, K, (S, SS) |
| *Phyllurus salebrosus* | 2 | 28—30 (29.0) | B |
| *Naultinus elegans* | 10 | 18—23 (20.9) | B, K, U, (SS) |
| *Naultinus grayii* | 2 | 20—21 (20.5) | B |
| *Naultinus tuberculatus* | 2 | 21—22 (21.5) | K |
| *Rhacodactylus auriculatus* | 16 | 27—31 (28.8) | B, K, (U2+) |
| *Rhacodactylus australis* | 2 | 31—32 (31.5) | K |
| *Rhacodactylus chahoua* | 4 | 33—36 (34.0) | B |
| *Rhacodactylus ciliatus* | 1 | 32 | B |
| *Rhacodactylus leachianus* | 3 | 28—29 (28.6) | B |
| *Rhacodactylus lindneri* | 3 | 35—36 (35.3) | B |
| *Rhacodactylus sarasinorum* | 1 | 35 | B |
| *Rhacodactylus trachyrhynchus* | 1 | 33 | B |

References: B — Bauer, this study; K — Kluge (1967a); K2 — Kluge (1967b); S — Stephenson (1960); SS — Stephenson & Stephenson (1956); U — Underwood (1954); U2 — Underwood (1970); U3 — Underwood (1977a). Sources appearing in parentheses provided ossicle numbers but not sample sizes and consequently are not represented in the ranges or means.

* — Kluge (1967a, 1967b) did not recognize the species *H. maculatus*, therefore his values for *H. pacificus* may include (or consist entirely of) *H. maculatus*. For this reason the figures reported by Kluge have not been included in the table.

** — Neither source provides a sample size.

\+ — Underwood (1970) reported counts of 26 and 27 for *Rhacodactylus*, but did not specify the species. It is likely that these figures refer to *R. auriculatus*.

dentary and coronoid, while medially it contacts the dentary and coronoid anteriorly and the articular ventrally and posteriorly, enclosing the mandibular fossa. Two patterns of surangular position are seen on the lateral face of the mandible in carphodactylines. In *Nephrurus, Carphodactylus* and *Phyllurus* the anterior-most border of the surangular lies posterior to the anterior-most lateral border of the coronoid. In all other species the borders of the two elements lie approximately at the same level (character 16). This character varies in the outgroups and no assessment of polarity could be made.

## Teeth

Character 17: Teeth moderate to small (0), or extremely minute (1).

Adult gekkonid teeth are generally conical, homodont and pleurodont and are borne on the lingual faces of the dentary, maxilla and premaxilla. The number of teeth in post-hatchlings has been demonstrated to vary greatly within species (Kluge 1962; Bauer & Russell in press). An increase of tooth number with age corresponds to an increase length of the germinal tooth region. In adult geckos, as in other lizards, the number of teeth tends to vary around a particular species mode (Owen 1866). Except for *Teratoscincus*, in which teeth in the middle of the tooth rows are the longest (Edmund 1969), teeth tend to increase in size anteriorly in geckos. Among eublepharines and diplodactylines, and primitively in gekkonines, teeth are of moderate size and are relatively blunt and somewhat compressed distally. This morphology is characteristic of most carphodactylines (Fig. 8b). However, all *Nephrurus, Carphodactylus* and *Phyllurus* possess tiny, extremely numerous teeth similar in shape to those of other geckos (Fig. 8c) (character 17). Elsewhere amongst geckos this morphology appears in *Uroplatus*. Interestingly, *Hoplodactylus delcourti* and *Rhacodactylus leachianus*, which share gigantic size with *Uroplatus fimbriatus*, show rather typical tooth counts for their respective genera. There are no obvious functional correlates of this derived morphology. These geckos are more or less typical in their diet, except that *Nephrurus* frequently take vertebrate prey items (Pianka & Pianka 1976; Pianka 1986). A second derived morphology occurs in *Rhacodactylus auriculatus*. This gecko possesses elongate, slender, pointed teeth (Fig. 8a). Again the significance of this morphology is unclear but may be related to the vertebrate prey taken by this species (Bauer & DeVaney 1987; Bauer & Russell in press). Cuspation patterns vary with some phylogenetically

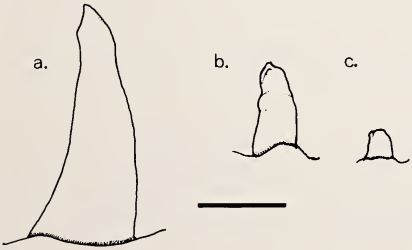

Fig.8: Anterior maxillary teeth of (a) *Rhacodactylus auriculatus* (CAS 165891), (b) *Hoplodactylus duvaucelii*, juvenile (AMB 455) and (c) *Nephrurus deleani* (AMB 46). Note the small size of tooth c (character 17) and the elongate fanglike structure of a. Scale bar = 0.5 mm.

significant patterns amongst other gekkonids (Sumida & Murphy 1987) and may be expected to do so in the Carphodactylini, although this type of variation was not assessed in the present study.

## Hyobranchial Apparatus

Character 18: Hyoid cornu with both anteromedial and posterolateral processes well developed (0), or with anteromedial process reduced and posterolateral process large, hooked (1).

Character 19: Inner promixal ceratohyal process absent (0), or present (1).

Character 20: Second epibranchial short, moderately to widely separated from second ceratobranchial (0), or long and recurred, nearly in contact with cerabranchial (1).

Camp (1923) emphasized the importance of the hyobranchial apparatus by assigning the greatest "paleotelic" weight (i.e. indication of primitiveness) to a character of this

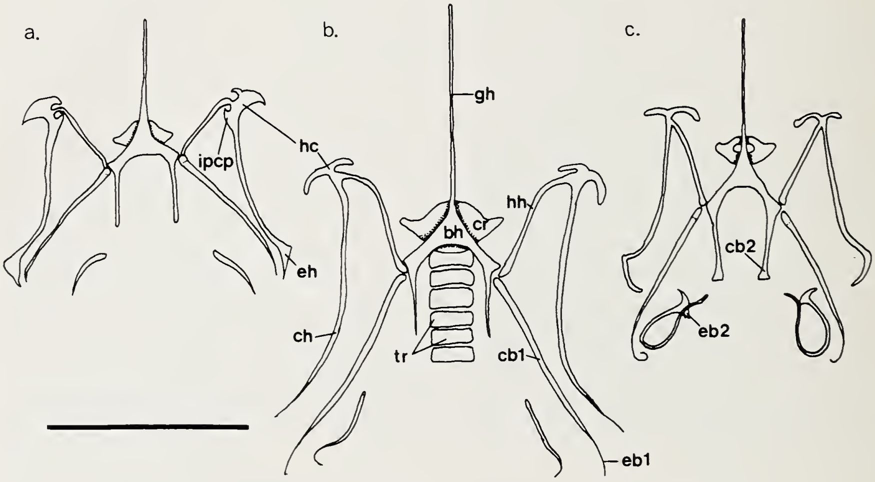

Fig.9: Hyoid apparati of representative carphodactyline geckos. (a) *Nephrurus laevissimus* (LACM 57101), (b) *Rhacodactylus auriculatus* (CAS 165895) and (c) *Bavayia sauvagii* (CAS 165905). Note the overlap of the second epibranchials in c (character 20), the shape of the hyoid cornu (character 18) and the presence of the inner proximal ceratohyal process in a. Scale bar = 10 mm. Abbreviations are as follows:

bh — basihyal
cb1 — first ceratobranchial
cb2 — second ceratobranchial
ch — ceratohyal
cr — cricoid cartilage
eb1 — first epibranchial
eb2 — second epibranchial
eh — epihyal
gh — glossohyal process
hc — hyoid cornu
hh — hypohyal
ipcp — inner proximal ceratohyal process
tr — tracheal cartilages

structure (the number of complete branchial arches). Following Fürbringer (1919) and Noble (1921), Camp and later authors (e.g. Stephenson & Stephenson 1956; Kluge 1967a) accepted that the complete arch arrangement first illustrated in *Coleonyx* by Cope (1892) was plesiomorphic. Kluge (1983a), however has demonstrated that the presence of three uninterrupted arches (the hyoid plus branchial arches I and II) are derived reversals occurring in *Coleonyx* spp. among eublepharines and *Gonatodes vittatus* in the sphaerodactylines. Stephenson & Stephenson (1956) reported the same condition in the carphodactyline *Naultinus elegans*. However, I was unable to confirm this observation in any of the *Naultinus* examined in the course of this study.

The typical carphodactyline hyobranchial apparatus (Fig. 9) consists of a central tripartate basihyal extending anteriorly into a narrow glossohyal process, lying ventral to the cricoid cartilage of the larynx. The hypohyals run anterolaterally from the dorsal margin of the posterior apices of the basihyal and fuse with the posterolaterally-directed ceratohyals at the hyoid cornu, a wing-like process lateral and just anterior to the level of the cricoid. The cornu varies in form among gekkonines (Wellborn 1933) but is relatively uniform in the Carphodactylini. However, all *Carphodactylus, Nephrurus* and *Phyllurus* exhibit a uniquely derived morphology of the cornu in which the anteromedial prong is reduced and the posteriolateral prong is drawn out into a broad, blade-like process (Fig. 9a) (character 18). An inner proximal ceratohyal projection was reported by Kluge (1967a) in *Carphodactylus, Nephrurus, Phyllurus* and *Naultinus* (character 19). This feature is absent in the Diplodactylini and the Eublepharinae and variable present in the Gekkoninae (including the Sphaerodactylinae). Its presence in certain carphodactylines is interpreted as being derived. A small, medially curving epihyal is fused to the posterior tip of the ceratohyal and abuts the paroccipital process of the cranium. The fusion of the distal portion of the ceratohyal with the crista parotica of the auditory bulla recorded in certain geckos (Versluys 1903; Brock 1932) is not seen in any carphodactyline.

The first ceratobranchial extends posterolaterally from the basihyal and terminates in a small hooked epibranchial. This arch is not associated with the cranium and may continue posteriorly for a considerable distance in the throat musculature. It is exceedingly elongate in *Rhacodactylus leachianus* where it may extend past the level of the fourth cervical vertebra. The second branchial arch (visceral arch four) consists of paired posteriorly projecting ceratobranchials fused to the basihyal and medially-looping epibranchials. As previously mentioned, there is a definite break between these elements in all carphodactylines, although both elements are invariably present. However, in gekkonines, the second ceratobranchial is variably present, and Kluge (1983a) has used the presumed synapomorphy of the loss of the second ceratobranchial as the sole character supporting his division of that subfamily into two tribes. While no carphodactyline shows the complete arch, the gap between the epi- and ceratobranchials is very small in *Bavayia* (Fig. 9c). Members of this genus also show another condition interpreted as derived on the basis of outgroup comparison; the second epibranchial curves in a circle, terminating in a flanged tip just dorsal to the gap separating its proximal end from the ceratobranchial (character 20).

Generally only the basihyal, glossohyal (or entoglossal) process, first and second ceratobranchials and part of the hypohyals ossify in adults. Additional ossification is seen in larger, older specimens of the larger species and, as in many osteological characters, *Naultinus* shows relatively little ossification in the hypobranchial apparatus.

Variation in the larynx and tracheal rings was not assessed but the basic morphology generally follows that reported by Kluge (1962) for *Coleonyx* and Mahendra (1947) for *Hemidactylus flaviviridis*.

## Axial Skeleton

### Vertebral Shape

Character 21: Trunk vertebrae amphicoelous (0), or procoelous (1).

Noble (1921) and Camp (1923) accepted amphicoely as primitive for lizards on "comparative grounds". Camp (1923) provided a discourse on the differences between procoely and amphicoely but no justification for his determination of polarity. Underwood (1954) and Romer (1956) considered the amphicoelous condition of gekkonid vertebrae to be secondarily derived although Underwood (1955) later reversed the polarity of this character on the evidence of amphicoely in kuehneosaurs, which he accepted as early lizards. Holder (1960) also accepted evidence from kuehneosaurs as supportive of primitive amphicoely in gekkotans. Her support from Mahendra's (1950) comparison of amphicoely in *Sphenodon* is uninformative with respect to the condition in geckos. Although she stressed the simplicity of a morphological transformation between the two types, Holder (1960) seems to have ruled out, a priori, the occurrence of paedomorphosis (in what she recognized as a generally paedomorphic group) to account for the amphicoelous condition in geckos. She also accepted Camp's (1923) relative assessments of paleotelic weight as inviolate; thus her arguments regarding the polarity of this character are circular.

Kluge (1967a) interpreted amphicoely as derived within gekkonids, citing the procoelous ardeosaurs as potential gekkotan ancestors. He also pointed out that kuehneosaurs, so important for the arguments of Underwood (1955) and Holder (1960), were not early lizards (see Evans 1982; Estes 1983). He further advocated a paedomorphic origin for the derived condition on gekkotan amphicoely. This is supported by the presence of persistent, and often unconstricted, notochord in the centra of adult geckos (Holder 1960; Moffat 1973a, 1973b; Werner 1961a, 1967, 1971; Hoffstetter & Gasc 1969). I accept this hypothesis as the most plausible explanation of the origin of this character state.

Procoely has apparently been derived independently in a number of gekkotan lineages including the Sphaerodactylinae (Noble 1921) and the Pygopodidae (Camp 1923; Stokley 1947), as well as in certain carphodactylines (Holder 1960; Kluge 1967a; Moffat 1973a). Kluge (1987), following Winchester & Bellairs (1977), stressed that condylar formation is essentially the same in geckos as in other squamates (contra Hoffstetter & Gasc 1969 and Werner 1971). Hecht (1976) and Hecht & Edwards (1977) interpreted Moffat's (1973a, 1973b) work on joint capsules as implying four character states of "coely" and came to the conclusion that procoely was primitive for gekkotans. Based on parsimony arguments, Underwood (1977b) also returned to his 1954 stance on the question.

Despite his criticisms of Moffat (née Holder) (Holder 1960; Moffat 1973a), Kluge (1987) has recently accepted her assessment of amphicoely as primitive for gekkonids. In Kluge's scheme it would be equally parsimonious on other grounds to accept either state as primitive. His decision thus seems predicated on his acceptance of the Bavarisauridae (but not the Ardeosauridae) as the sister group of the living gekkotans. I disagree with this interpretation on the grounds that these groups are neither diagnosable nor share any derived features with living gekkotans and I accept procoely as primitive in the Eublepharinae and some ardeosaurs. Secondary procoely is characteristic of the pygopodids and sphaerodactylines. It is interesting to note that both lineages are typified by miniaturization (Rieppel 1984a) and it seems possible that acceleration (Gould 1977; Alberch et al. 1979), which has been suggested as being responsible for a number of skull features, may account for this condition.

Within the Carphodactylinae it is most parsimonious to view amphicoely as primitive. Thus procoely in *Carphodactylus laevis* and *Phyllurus milii* (Holder 1960; Kluge 1967a) is a derived condition (character 21).

## Vertebrae and Ribs

The typical gekkonid presacral vertebra is relatively short and broad. This is generally true of all of the carphodactyline species. Twenty-four presacral vertebrae appears to be the primitive number for lizards as a whole and this number is frequently encountered in non-chameleontid iguanians (Romer 1956; Hoffstetter & Gasc 1969). The total number of presacral vertebrae varies between 23 and 29 within the gekkonids (Wellborn 1933; Hoffstetter & Gasc 1969), with 26 as à mode. Hoffstetter & Gasc (1969) remark on the "stabilization" at this number in most non- anguimorph scleroglossans. Members of the Diplodactylini have between 25 and 27 presacrals (Holder 1960), again with a mode at 26.

Among the species examined, presacral counts ranged from 24 to 27 (see Tab. 3). Holder (1960) examined a number of carphodactyline species and obtained similar results, although I found 26 rather than 27 vertebrae in all of the fifteen *Carphodactylus laevis* examined. Holder (1960) also found more variation in presacral vertebral number than I did, although her sample sizes, except for *Phyllurus platurus*, were smaller.

## Cervical Vertebrae

There are generally eight cervical vertebrae in lizards (Romer 1956; Hoffstetter & Gasc 1969) and this is invariant in the Carphodactylini. The general morphology of the atlas and axis is not significantly different from the condition detailed in the eublepharine *Coleonyx* (Kluge 1962). Other detailed observations on the morphology of the adult gekkonid vertebrae are provided by Ganguly & Mitra (1958) and Werner (1961a). The cervical vertebrae, like all gecko vertebrae, are associated with small persistent intercentra that lie ventral to the intervertebral discs, or persistent notochord. In association

Table 3. Attributes of the axial skeletons of carphodactyline geckos (data this study, sample size = 5 for all species, unless otherwise noted. For species for which PV = ? no skeletons were examined). PV = presacral vertebrae (modal); FC = rib-free cervicals; SR = sternal ribs (range); MS = mesosternal ribs (range); IR = inscriptional ribs (range, mode underlined); ME = mesosternal extention; RR = vertebrae bearing reduced ribs (abdominal vertebrae); LV = lumbar vertebrae; SV = sacral vertebrae; CV = caudal vertebrae (range); SP = autotomy septum-bearing vertebrae; AS = first caudal vertebra bearing autotomy septum; red = reduced number.

| Taxon (N if not 5) | PV | FC | SR | MS | IR | ME | RR | LV | SV | CV | SP | AS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Bavayia cyclura* | 26 | 3 | 2 | 2 | 0 | + | 6 | 1 | 2 | 26 | all | 6 |
| *B. sauvagii* | 26 | 3 | 2 | 2 | 0 | + | 6 | 1 | 2 | 30 | all | 6 |
| *Carphodactylus laevis* | 26 | 2-3 | 2 | 3 | 3 | — | 3 | 2-3 | 2 | 47 | 1-2 | 5 |
| *Eurodactylodes symmetricus* | 26 | 3 | 2 | 2 | 6 | — | 5 | 1 | 2 | 35 | all | 6 |
| *E. vieillardi* | 26 | 3 | 2 | 2 | 6-7 | — | 6 | 1 | 2 | 31 | all | 6 |
| *Hoplodactylus chrysosireticus* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | all | ? |
| *H. duvaucelii* | 26 | 3 | 2-3 | 2-3 | 0-1 | + | 6 | 1 | 2 | 32 | all | 6 |
| *H. granulatus* | 25 | 3 | 2 | 2 | 2 | — | 5 | 1 | 2 | 31 | all | 6 |
| *H. maculatus* | 26 | 3 | 2 | 2 | 0-1 | + | 5 | 1 | 2 | 29 | all | 6 |
| *H. pacificus* | 26 | 3 | 2 | 2 | 0 | + | 4-5 | 1 | 2 | 29 | all | 6 |
| *H. rakiurae* (1) | 26 | 3 | 2 | 2 | 0 | — | 4 | 1 | 2 | 28 | all | 6 |
| *H. stephensi* (3) | 26 | 3 | 2 | 2 | 0-1 | + | 5 | 1 | 2 | 32 | all | 6 |
| *Naultinus elegans* | 27 | 3 | 2-3 | 2-3 | 2-4 | — | 5 | 1-2 | 2 | 33 | red | 6 |
| *N. gemmeus* | 25 | 3 | 2-3 | 2-3 | 2-3 | — | 4 | 1 | 2 | 32 | red | 6 |
| *N. grayii* | 27 | 3 | 3 | 2 | 3-4 | — | 4 | 1 | 2 | 36 | red | 6 |
| *N. manukanus* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | red | ? |
| *N. poecilochlorus* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | red | ? |
| *N. rudis* (3) | 26 | 2-3 | 2 | 3 | 2 | — | 5 | 1 | 2 | 30 | red | 6 |
| *N. stellatus* (1) | 27 | 3 | 2 | 3 | 2 | — | 4 | 2 | 2 | 30 | red | 6 |
| *N. tuberculatus* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | red | ? |
| *Nephrurus asper* | 26 | 3 | 3 | 2-3 | 1 | — | 3 | 2 | 2-3 | 23 | none | — |
| *N. deleani* (3) | 25 | 3 | 3 | 2 | 1 | — | 4 | 1 | 2-3 | 26 | 1-2 | 6 |
| *N. laevissimus* | 26 | 2-3 | 3 | 2-3 | 0-2 | — | 3 | 2 | 2-3 | 25 | 1-2 | 6-7 |
| *N. levis* | 26 | 3 | 3 | 2 | 1 | — | 3 | 2 | 2-3 | 27 | 1-2 | 6-7 |
| *N. milii* | 26 | 3 | 3 | 2 | 0-1 | — | 3 | 2 | 2 | 35 | 1-2 | 6 |
| *N. sphyrurus* (4) | 26 | 3 | 3 | 2-3 | 1 | — | 3 | 2-3 | 2 | 22 | 1-2 | 6 |
| *N. stellatus* (2) | 24-25 | 2-3 | 3 | 2 | 0-1 | — | 4 | 1 | 2-3 | 24 | 1-2 | 6 |
| *N. vertebralis* | 26 | 3 | 3 | 2 | 0 | — | 3 | 2 | 2 | 32 | 1-2 | 6 |
| *N. wheeleri* | 26 | 3 | 3 | 2 | 0-1 | — | 3 | 2 | 2-3 | ? | 1-2 | 6 |
| *Phyllurus caudiannulatus* | 26 | 3 | 2-3 | 3 | 1-2 | — | 4 | 2 | 2 | 30 | 1-2 | 5 |
| *P. cornutus* | 25 | 3 | 2-3 | 2-3 | 3-4 | — | 4 | 2 | 2 | 30 | 1-2 | 6 |
| *P. platurus* | 25 | 3 | 3 | 2 | 1 | — | 3 | 2 | 2 | 31 | 1-2 | 6 |
| *P. salebrosus* | 25 | 3 | 3 | 2 | 2-4 | — | 3-4 | 1-2 | 2 | 27 | 1-2 | 6 |
| *Rhacodactylus auriculatus* | 26 | 3 | 3 | 2-3 | 2-3 | — | 4-5 | 1 | 2 | 28 | all | 6 |
| *R. australis* | 27 | 3 | 2 | 2 | 3-4 | — | 4 | 1 | 2 | 29 | all | 6 |
| *R. cavaticus* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | all | ? |
| *R. chahoua* | 26 | 3 | 3 | 2 | 1 | — | 5 | 1 | 2 | 31 | all | 5 |
| *R. ciliatus* | 26 | 3 | 2 | 2 | 0-1 | — | 6 | 1 | 2 | 30 | all | 5 |
| *R. leachianus* | 26 | 3 | 3 | 2 | 3-4 | — | 4 | 1 | 2 | 22 | all | 7 |
| *R. lindneri* | 26 | 3 | 3 | 2 | 0 | — | 4 | 1 | 2 | 28 | all | 6 |
| *R. sarasinorum* (4) | 26 | 3 | 3 | 2 | 1 | — | 5 | 1 | ? | ? | all | 6 |
| *R. trachyrhynchus* | 26 | 3 | 2-3 | 2 | 0-2 | — | 5 | 1 | 2 | 30 | all | 6 |

with the cervical vertebrae these intercentra are somewhat enlarged and form hypapophyses ventrally. Typically the cervical intercentra are relatively narrow; however, in *Rhacodactylus trachyrhynchus* (Hoffstetter & Gasc 1969) and perhaps other members of this genus, the intercentra are broad and bear posteriorly-directed hypapophyses.

Hoffstetter & Gasc (1969) listed formulae for the cervical vertebral series and suggested that some were primitive. This determination seems to have been based on the assumption that gekkonids tend to show the primitive condition. Their pattern "a" (three ribless vertebrae, three with short ribs and two with long, slender ribs) is widespread among the outgroups (Wellborn 1933) and appears to be plesiomorphic for carphodactylines. A reduced number of rib-free cervicals consisting solely of the atlas and axis is seen in some individuals of *Naultinus rudis, Nephrurus laevissimus, Nephrurus stellatus* and *Carphodactylus laevis* (see Tab. 3). Ribs attach to the vertebral centra at the parapophyses (synapophyses). In all carphodactylines the anterior cervical ribs are simple in structure, consisting of a short bony vertebro-costal element and occasionally a very small distal cartilaginous segment. The posterior cervical ribs bear elongate, somewhat posteriorly curving cartilaginous processes.

### Trunk Vertebrae

Character 22: Neural spines of trunk vertebrae low, less than half of total vertebral height (0), or high, contributing to compressed appearance of animal (1).

The vertebrae of the trunk region consist of the sternal, mesosternal, interthoracolumbar and lumbar series (Kluge 1962). All of these designations are based on features of rib attachment rather than on vertebral morphology per se. Little variation in trunk vertebrae was noted among the taxa examined, however, *Carphodactylus* and *Eurydactylodes* have extremely high neural spines on all of the presacral vertebrae adding to the overall appearance of compression of the body (character 22). High neural spines occur only in a few species among the outgroup taxa and are interpreted as derived within the Carphodactylini.

### Lumbar Vertebrae

Character 23: Two (or three) lumbar vertebrae present (0), or one lumbar vertebra present (1).

Lumbar vertebrae are defined as non-rib-bearing vertebrae immediately anterior to the sacrum. One to three lumbar vertebrae are typical for carphodactylines; two appear to be primitive for the tribe. This is the typical condition in the Diplodactylini, although a single lumbar vertebra is said to be the most common occurrence among gekkonines (Wellborn 1933). One lumbar is found in all species in New Caledonian carphodactylines, *Hoplodactylus, Rhacodactylus (Pseudothecadactylus)*, and in some *Naultinus, Nephrurus* and *Phyllurus*. Other members of these genera have two lumbar vertebrae. Three lumbar vertebrae were found in some specimens of *Carphodactylus laevis* and *Nephrurus sphyrurus* (character 23). This condition has been scored as a variant of the primitive state.

Romer (1956) stated that all fully limbed lizards have two sacral vertebrae. This is generally true of geckos, but three and even four sacral vertebrae occur in some carphodactylines. *Hemitheconyx* is also reported as having three sacral vertebrae (Wellborn 1933) as are certain other eublepharines (Kluge 1962). The condition results from the inclusion of the first pygal vertebra into the sacral complex (Holder 1960; Kluge 1962). The condition is variable among species of both *Nephrurus* and *Phyllurus* (Holder 1960).

Holder (1960; Moffat 1973a) regarded the loss of a sacral pleurapophyseal process in the Diplodactylinae as a putative synapomorphy. I have not located this structure in any carphodactyline. Moffat (1973a) stated that the process is present in all eublepharines and gekkonines. Kluge (1987) has indicated that it is present only in some diplodactylines and pygopodids. It thus seems unlikely that the reduction is a synapomorphy of the Diplodactylinae as a whole.

### Caudal Vertebrae

Character 24: Pygal pleurapophyses decrease in size markedly distally A), or broadly expanded on all pygal vertebrae B).

Character 25: 30 or more caudal vertebrae (0), or fewer than 30 caudal vertebrae (1).

Character 26: Centra of caudal vertebrae elongate (0), or very short (sometimes shorter than wide) (1).

Character 27: Post-pygal pleurapophyses present (0), or absent or greatly reduced (1).

Character 28: Autotomy planes present in all post-pygal vertebrae (0), or absent in some or all post-pygal vertebrae (1).

Character 29: Autotomy planes absent from posterior half of tail A), or absent from all but one to three anterior vertebrae B).

Character 30: Anteriormost autotomy septum in sixth (or seventh) caudal vertebra A) (0), or in fifth caudal vertebra B) (1).

The anterior caudal vertebrae are generally similar in form to the posterior sacral but rapidly change shape posteriorly. Modified intercentra are present as haemapophyses (chevron bones) from about the third postsacral intervertebral region to almost the tip of the tail in most species. This appears to be the primitive condition for the group and is the norm in the outgroups (Wellborn 1933). The first haemapophysis may remain unfused throughout life in certain individuals. Holder (1960) reports fusion of anterior haemapophyses in some *Phyllurus* and *Nephrurus*. Like the centra, the smaller, more posterior haemapophyses may be somewhat irregular, and in those species with reduced tails the haemapophyses may be entirely lacking in the posterior-most quarter to half of the tail.

The caudal vertebrae may be divided into pygal and post-pygal series. The first post-pygal is reckoned as the anteriormost vertebra bearing an autotomy septum. The ability to autotomize the tail is primitive for the Carphodactylini and for the family as a whole. The septa of all carphodactylines corresponds to Etheridge's (1967) type 4 which lies posterior to the relatively short, posteriorly directed transverse process. The transverse processes of the pygal series in the Eublepharinae, Gekkoninae and Diplodactylini generally decrease posteriorly and are substantially narrower than those of the posterior interthoracolumbar. This condition occurs in *Pseudothecadactylus* and all of the New Zealand and New Caledonian carphodactylines. The derived condition of extremely broad pygal transverse processes is found in all species of the remaining Australian genera (character 24). Caudal ribs (El-Toubi & Khalil 1950) are never present, although Stephenson & Stephenson (1956) reported them in unspecified New Zealand species.

The number of caudal vertebrae varies greatly among carphodactylines. The ancestral condition for lizards as a whole was probably high (50 or more) (Romer 1956), but it is difficult to assess the primitive condition for gekkotans, although this too was probably reasonably high. Wellborn (1933) cites approximately 40 caudals as the most common condition among Gekkonines although Werner (1965) found a range of 18-35 (mode 25) in Israeli geckos. As a whole, geckos have relatively short tails that account for roughly one half of the total length. Extremely short tails, however, are rare. Among the Diplodactylini they occur in the *Diplodactylus conspicilatus* and *D. elderi* groups. Postsacral vertebral counts do not always reflect tail length however; the knob-tailed gecko *Nephrurus vertebralis* has more than thirty caudals, more than many species with tails of "normal" length. I accept the number of approximately thirty as the primitive number of carphodactyline caudal vertebrae. Alternative derived states are seen in *Carphodactylus laevis* which averages 47 caudals and in several species with reduced counts — *Rhacodactylus leachianus* (22), *Nephrurus sphyrurus* (22) and some species of knob-tailed *Nephrurus* (see Tab. 3) (character 25). Werner (1961a, 1964) noted geographic and temperature related variation in vertebral number, but no intraspecific trends were noted in the species examined in this study.

All species of *Phyllurus, Nephrurus* and *Carphodactylus* possess greatly shortened caudal centra relative to the other carphodactyline genera and the outgroups (character 26). This is interpreted as a derived state within the tribe. In some specimens of *Nephrurus asper* even the anteriormost post-pygals (see below) may be shorter than wide. Fusions are frequent in the caudal vertebrae of this species and in large specimens, the entire tail may be ankylosed. All of these species except *N. sphyrurus* also exhibit the derived feature of reduced (usually absent) transverse processes on the post-pygal caudal vertebrae (character 27). Etheridge (1967) reported that a similar loss was independently derived in many lizard lineages. In general the processes occur on no more than two or three post-pygals. In *Nephrurus sphyrurus* the transverse processes are present for about half the length of the tail.

As discussed, autotomy is primitive for the tribe. Among the outgroups, autotomy is generally possible through any post-pygal vertebrae except the very smallest irregular posterior elements. In cases such as *Uroplatus* (Siebenrock 1893; Wellborn 1933) and *Stenodactylus* (Werner 1965, 1968) the site of autotomy is restricted to one or several planes. Among carphodactylines the primitive condition (all post-pygals autotomic) is found in most *Hoplodactylus*, all *Rhacodactylus (Pseudothecadactylus)* and all New Caledonian species. Site restriction to one or two vertebrae is typical of all species of the remaining Australian genera. *Nephrurus asper* is unique among gekkonids in lacking autotomy septa entirely. A second derived condition is shared by all *Naultinus* and *Hoplodactylus granulatus*. This involves the restriction of autotomy to the first five to twelve post-pygal vertebrae (characters 28, 29). It is not clear that one condition is derived from the other; therefore each is regarded as a separately evolved apomorphy. It is noteworthy that, with the exception of *Nephrurus sphyrurus*, the feature of a reduced number of autotomy sites is coincident with the loss of transverse processes. The same phenomenon is also reported for *Uroplatus* (Siebenrock 1893; Wellborn 1933). Thus it appears that the lack of transverse processes may preclude autotomy although the reverse is generally, though not necessarily, so.

The site of the first autotomy plane also varies among members of the group. The first septum passing through the sixth caudal vertebra is the most common condition in the diplodactylines and probably for the gekkonines as well. Some intraspecific variation has been noted (Holder 1960), but I have found this to be minimal. I am in agreement with Holder on the presence of the rarer condition (first septum in fifth caudal vertebra) in *Carphodactylus laevis* but cannot confirm her report of a similar state in *Nephrurus milii*. Holder's (1960) variable states in *P. platurus* may in fact represent the inclusion of two taxa, *P. platurus* and *P. caudiannulatus*, in her sample. I have found that the former typically displays the more common condition while the latter invariably exhibits the rare condition. In this species pair the total number of pre-autotomic vertebrae is equal at 32. The former species, however, possesses one fewer presacral and one more pygal vertebra than the latter. Because it appears likely that both counts are the result of a single shift in sacral placement, only the derived state of the autotomy site shift in *P. caudiannulatus* was considered in the phylogenetic analysis. Werner (1965) reported a similar situation in specimens of *Tropiocolotes steudneri* in which a shift in the first autotomy site was accompanied by a complementary change in the number of presacral vertebrae. Among the non-Australian taxa, the more anterior first autotomy septa was also found in *Rhacodactylus chahoua* and *R. ciliatus* (character 30). A second apomorphic state is seen in *Rhacodactylus leachianus*, in which the seventh caudal vertebra always contains the first autotomy septum.

### Ribs

Character 31: Mesosternal extension absent A)(0), or present B)(1).

Character 32: Inscriptional ribs generally absent or one A), two, three, or four B), or five, six, or seven C).

Character 33: Abdominal ribs five or six (modal number) A), or three or four (modal number) B).

The sternal ribs (Fig. 10) of carphodactylines, like all gekkonid ribs, are holocephalous and originate on the parapophyseal facet on the lateral face of the centrum. Thoracic ribs are generally divisible into three segments: a bony vertebro-costal element (always present), a cartilaginous intermediate element, and a sterno- (or mesosterno-) costal element.

Sternal ribs attach directly to the sternum. Mesosternal ribs connect to the sternum via a mesosternum or "xiphisternum" (Fig. 11). In carphodactylines this structure consists of narrow, paired bands of cartilage running posterior from the sternum along the midventral line of the body. It forms as the result of the fusion of the cartilaginous portions of the adjoining ribs. A small mesosternal extension may continue posteriorly from the junction of the mesosternum and posteriormost mesosternal rib. Sternal ribs and mesosternal ribs number between two and three in the carphodactylines and the number of either may vary within a single species (Tab. 3).

*Bavayia* (Fig. 10b) and some species of *Hoplodactylus* have mesosternal extensions (character 31). In contrast to Kluge's (1967b) observations, I saw only small extensions in these forms and none in *Naultinus, Carphodactylus* or *Nephrurus*.

Parathoracic ribs (Weber 1835; Hoffstetter & Gasc 1969) or inscriptional ribs (sensu Kluge 1967b) are those that lie caudad to the mesosternal ribs and curve anteriorly to approach the mesosternum along the midline. In many cases these paired elements fuse at the midline, forming a chevron. Free chevrons (parasternalia sensu Remane 1936) are absent in carphodactylines and in most geckos in general. *Uroplatus fimbriatus*, a gekkonine, is unique in its possession of 13 fused inscriptional ribs including three free parasternalia (Siebenrock 1893; Wellborn 1933). Among members of the tribe Carphodactylini, between zero and seven inscriptional ribs were recorded. The number frequently varies by one or (rarely) two within a species. It appears that the same rib in different animals may or may not fuse to the mesosternum. Thus, the sum of mesosternal and inscriptional ribs within a species is usually constant. Kluge (1967b) provides generic summaries of rib counts, but because this lumps species it is not particularly useful for my analysis.

Species of both *Nephrurus* and *Hoplodactylus* typically bore two to three inscriptional ribs. Three were recorded in *Carphodactylus* and zero to four were found in *Phyllurus* and *Rhacodactylus*. A minimum of six sets of inscriptional ribs, most fused, were found in both species of *Eurydactylodes* (Tab. 3) (character 32). Kluge (1967b) summarized inscriptional rib counts within the species groups of *Diplodactylus* and determined that an increased number of inscriptional ribs characterizes primarily arboreal taxa. This was hypothesized as being an adaptation to prevent visceral sagging and to increase the area for muscle attachment. A similar trend was seen when comparing the primarily arboreal species of carphodactylines with the terrestrial *Nephrurus*. Conflicting evidence from the successive outgroups prevented assessment of the polarity of this character.

"Abdominal" ribs lacking intermediate and mesosternal elements typically number four to six in the New Caledonian and New Zealand taxa as well as in *Rhacodactylus (Pseudothecadactylus)*. Three to four are found in the remaining Australian genera (character 33).

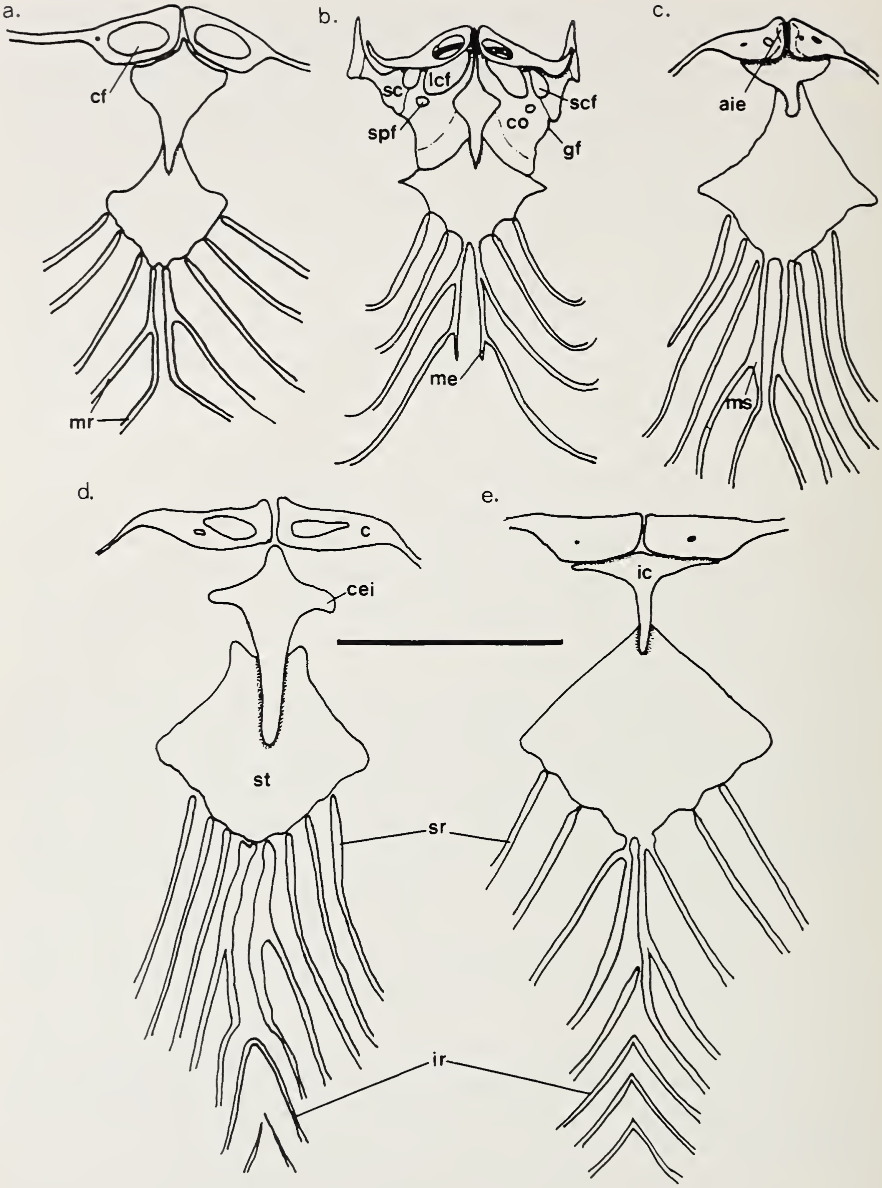

Fig.10: Sternum, pectoral girdle and ribs of selected carphodactyline geckos. (a) *Nephrurus levis* (AMS R20451), (b) *Bavayia sauvagii* (CAS 165905), (c) *Phyllurus platurus* (AMB, no number), (d) *Rhacodactylus auriculatus* (CAS 165895) and (e) *Phyllurus cornutus* (AMS R20477). Scapulocoracoid shown in b only. Note the differences in mesosternum (character 31), ribs (character 32),

## Sternum, Pectoral Girdle and Forelimb

### Sternum

Character 34: Sternum long and broad (0), or short and narrow (1).

Character 35: Sternum ossified in adult (0), or cartilagionous (1).

The sternum in all carphodactylines is a rhomboidal plate straddling the ventral midline of the trunk. Primitively it is both broad and long relative to the interclavicle and medial portion of the clavicle. In all species of *Nephrurus*, especially *N. sphyrurus*, the sternum, although maintaining the same shape and position, is relatively much smaller than in other species (character 34) (Fig. 10). This condition does not occur in examined species of the outgroup taxa and is interpreted as being derived. Primitively in each of the successive outgroup taxa the sternum ossifies more or less completely through pre- and early post-natal ontogeny. As noted by Stephenson & Stephenson (1956), in *Naultinus* the sternum shows the apomorphic and paedomorphic condition of remaining unossified throughout post-natal ontogeny (character 35). No trace of an enclosed sternal fontanel (see Camp 1923) was found in any of the carphodactyline specimens examined. However, an emargination open posteriorly between the mesosternal rods (as reported by Kluge 1962, in *Coleonyx*) was found to occur in some *Phyllurus caudiannulatus* and *P. cornutus* (Fig. 10). This character was not scored because it was variable within these taxa and depends largely on the extent of mesosternal fusion.

### Interclavicle

Character 36: Interclavicle imperforate (0), or perforate (1).

Character 37: Anterior process of interclavicle (if present) narrow and splint-like (0), or terminating in a broadened disk (1).

Character 38: Anterior process of interclavicle present (0), or absent (1).

Character 39: Coracoid processes of interclavicle anteriorly located A)(0), or located posteriorly along interclavicular body B)(1).

Character 40: Coracoid process of interclavicle distinctly narrowed and elongate (0), or broad and indistinct (1).

Character 41: Coracoid process of interclavicle does not contact clavicle (0), or does contact clavicle (1).

sternum and interclavicle (characters 34, 36—41), clavicle (characters 42—43). Scale bar = 10 mm. Abbreviations are as follows:

aie — anterior interclavicular extension
cei — coracoid extension of interclavicle
cf — clavicular fenestra
co — coracoid
gf — glenoid fossa
ic — interclavicle
ir — inscriptional ribs
lcf — lateral coracoid fenestra
me — mesosternal extension
mr — mesosternal ribs
ms — mesosternum
sc — scapula
scf — scapulocoracoid fenestra
spf — supracoracoid foramen
sr — sternal ribs
st — sternum

Immediately anterior to the sternum, and also in the ventral midline, lies the interclavicle, a dermal bony element present in all geckos, although greatly reduced in the aberrant gekkonine *Uroplatus* (Siebenrock 1893). Even in highly circumscribed groups the shape of the interclavicle may vary widely (Noble 1921; Kluge 1967b). In the primitive condition within carphodactylines the interclavicle is considerably longer than wide and bears a pair of laterally directed coracoid extensions just posterior to the clavicles. Posteriorly the interclavicle inserts into a depression of the sternal apex. The cartilaginous epicoracoids support the interclavicle and bridge the gap between this element and the scapulocoracoid proper. A small anterior extension of the interclavicle sometimes runs deep to the clavicles. The interclavicle is primitively imperforate in the outgroups to the Carphodactylini. However, fenestrations sometimes occur in the widest part of the bone in *Carphodactylus* (Kluge 1967b) and *Nephrurus* (excluding *N. sphyrurus*) (character 36). This condition is interpreted as apomorphic. A unique broadened disk is present at the terminus of the anterior interclavicular extension in *Phyllurus caudiannulatus* and *P. platurus* (character 37). In the remaining two species of leaf-tails the anterior extension has been completely lost, yielding in a T-shaped interclavicle (character 38) (Fig. 10). In all other species the primitive condition of a narrow, tapering splint characterizes the anterior interclavicular process as it does in the outgroups.

In members of the outgroups, and primitively in the carphodactylines, the coracoid extensions of the interclavicle, which may project slightly anteriorly or posteriorly, are placed far anteriorly on the element, just posterior to the clavicles. Exceptions are seen in *Bavayia* and *Rhacodactylus (Pseudothecadactylus)* in which the extensions originate far posteriorly on the interclavicular body (character 39). As noted by Kluge (1967b), *Carphodactylus* and *Nephrurus* are characterized by the apomorphic condition of a greatly expanded interclavicle (character 40). In *N. asper* and *N. deleani* the anterolaterally projecting coracoid extensions remain as distinct, though short processes. In the remainder of these forms the interclavicle anterior to the sternal extention is broadly expanded, resembling a rhomboid, but variation is more or less continuous. In all species of *Naultinus* a reduction of the element is seen. Stephenson & Stephenson (1956) referred to the interclavicle in this taxon as a splint. However, I have found that this bone generally has at least weakly developed coracoid extensions. The small size and somewhat irregular shape of this element probably reflects its truncated development. It appears to form late in pre-natal ontogeny. The coracoid extensions of the interclavicle do not touch the clavicles except in *Carphodactylus, Nephrurus* and *Phyllurus* (Fig. 10) (the latter two variably within species) (character 41).

### Clavicle

Character 42: Clavicular fenestrae present (0), or absent (rarely present as minute openings) (1).

Character 43: Clavicular fenestrae small to moderate in size A)(0), or very large B)(1).

Anterior to the interclavicle are the paired dermal clavicles, which meet at the midline deep to the anterior extension of the interclavicle (if present). For carphodactylines a broadly expanded and fenestrated medial portion is primitive. The lateral portions of the clavicles extend dorsally along the curve of the coracoid border, terminating deep to the antero-ventral border of the suprascapula. As described for *Hemidactylus flaviviridis* (Mahendra 1950), there is a small depression in the suprascapula that receives this process. Stephenson & Stephenson (1956) reported the clavicles as imperforate in *Naultinus elegans*, although Kluge (1967b) found minute fenestrae in this species and large fenestrae in *"Heteropholis"*. I found generally small to minute fenestrae in *Naultinus*. Although there is generally one fenestra per clavicle, there may be as many as three, and fenestral number may be asymmetrical. Fenestral size varies widely in the group and is highly variable within genera (Kluge 1967b). Fenestrae are generally absent in *Carphodactylus* and *Phyllurus* (Stephenson 1960; Kluge 1967b) (character 42). Exceptionally large fenestrae may be present in *Nephrurus* (Fig. 10) (variable in *N. asper* and *N. wheeleri*) (character 43). Based on comparisons with outgroup taxa both the enlarged and reduced fenestral conditions are derived.

### Scapula

Character 44: Scapula possesses a short, stout blade (0), or scapular blade elongate with narrow shaft (1).

The primary paired lateral components of the pectoral girdle are in the scapulocoracoids. Each of these compound elements is highly complex and is oriented with the flat coracoid plate at approximately right angles to the dorsally projecting scapula. The suture between these elements is visible only in some *Naultinus elegans* (Stephenson & Stephenson 1956), perhaps another indication of the paedomorphic nature of this genus. The scapulo-coracoid fenestrae perforate the element in the region of the embryonic suture, just anterior to the glenoid fossa. A large lateral coracoid fenestra occurs just medial to this. Finally a supracoracoid foramen penetrates the plate posterior to the lateral coracoid fenestra and anteromedially to the glenoid. The foramen is always contained entirely within the coracoid. The fenestrae, however, in some individuals of most species are emarginate anteriorly and may be closed by a union with the epicoracoid cartilage (see Romer 1956 for a discussion of this term). Similarly the epicoracoids may form the medial border of the medial coracoid fenestra, represented by an emargination of the adjacent coracoid. In all species the epicoracoids overlap in the midline dorsal to the interclavicle.

The scapula is primitively broad dorsally at its border with the suprascapula, slightly narrower near its midpoint, and expanded again ventrally at the coracoid suture. All of the knob-tailed *Nephrurus* plus *N. sphyrurus* depart from this morphology and display an apomorphic condition of an elongate and narrow shafted scapula that flares rather abruptly both proximally and distally (character 44). In all species of carphodactylines the supracoracoids remain largely uncalcified and extend posteriorly in a broad plate.

The proximal elements of the forelimb (the humerus, ulna and radius) are largely invariant, except for size and proportion, among the carphodactyline genera. The individual elements are basically in agreement with descriptions of appendicular osteology in other gekkonid taxa (Mahendra 1950; Wellborn 1933; Siebenrock 1893; Kluge 1962). A single brachial sesamoid, the patella ulnaris, is generally present in the tendon of the triceps in mature specimens of all species.

Generally the carpal series consists of a large proximal radiale and ulnare articulating with the epiphyses of the long bones. A small centrale is situated between these two elements and a pisiform of variable size articulates with the postaxial border of the distal epiphysis of the ulna. Distal carpals I—V are small, somewhat rounded elements basal to the metacarpals. This basic structure is maintained in many lineages and is primitive for the family as a whole (Kluge 1962; Mahendra 1950; Siebenrock 1893; Khalil & Sabri 1977a).

### Metacarpals

Character 45: Metacarpal V shortest with I and IV subequal (0), or metacarpals IV and V subequal, shortest (1).

The metacarpals are splayed widely, V is the shortest. Metacarpals I and IV are next in size, and both are distinctly longer less robus V in the majority of carphodactylines. This condition is assessed as primitive on the basis of its distribution in the outgroups. In *Phyllurus* and *Carphodactylus*, however, metacarpals IV and V are similar in size and shape and both are distinctly shorter than metacarpal I (character 45). The structure of individual phalangeal elements is similar to that described below for the phalanges of the pes. Paraphalangeal elements are lacking in both the manus and pes of all carphodactylines.

### Phalanges

Character 46: Phalangeal formulae 2-3-4-5-3 (manus) and 2-3-4-5-4 (pes) (0), or 2-3-4-4-3 (manus) and 2-3-4-4-4 (pes) (1), or 2-3-3-3-3 (manus and pes) (2).

The primitive phalangeal formulae for the Lacertilia are 2-3-4-5-3 (manus) and 2-3-4-5-4 (pes) (Romer 1956). The same formulae are plesiomorphic at the level of the Carphodactylini. Within the tribe variation is seen only among knob-tailed members of the genus *Nephrurus* (Stephenson 1960; Kluge 1967a). All species have been examined and found to conform to one of two patterns first delineated by Stephenson (1960). *Nephrurus asper* and *N. wheeleri*, the spiny knob-tails, show a single reduction in digit IV of the manus (2-3-4-4-3) and pes (2-3-4-4-4). The remaining five taxa show further reduction in digits III and IV of the manus and III, IV and V of the pes, yielding the formula 2-3-3-3-3 for both manus and pes (character 46). These two conditions are regarded as successive apomorphic states relative to an unreduced phalangeal complement. Among the Diplodactylini reduction occurs in *Diplodactylus stenodactylus* and *Rhynchoedura ornata* (manus only). Parellel reduction has taken place many times in other gekkonid lineages (Russell 1972, 1979a).

## Pelvic Girdle and Hindlimb

The pelvic girdle is entirely endochrondral in origin. It consists of two tripartate innominate bones, each composed of a pubis, ischium and ilium. The pubis is the anteriormost element and lies ventrally in the body in a horizontal plane. Anteriorly the pubis contacts an epipubic cartilage in the midline. Near its posterior border it is pierced by the obturator foramen for the passage of the obturator nerve. It meets the other elements at the acetabulum, the receptacle for the femoral head. The sutures at the acetabulum are generally obscured although they are rarely visible early in postnatal ontogeny (Stephenson 1960) and in some adult *Naultinus* (Stephenson & Stephenson 1956).

The ischium runs as a horizontal plate postero-medially from the acetabulum to the ventral midline, where it contacts the medial ligamentum hypoischium and os hypoischium. The elongate ilium passes posterodorsally to lie just lateral to the sacrum. The space enclosed by the ventral portion of the innominate bones is the ischiopubic fenestra or cordiform foramen. In many lizards a medial ligament, which sometimes calcifies (Khalil & Sabri 1977b), bisects the ischiopubic fenestra (Mehnert 1891; Mahendra 1950). Such a structure has been reported in *Gonatodes, Sphaerodactylus* and *Aristelliger* (Noble 1921; Stephenson 1960), but may simply refer to an anterior extension of the hypoischium as reported in *Gonatodes* by Wellborn (1933). No medial ligament was observed in any of the carphodactyline geckos.

### Epipubic Cartilage

Character 47: Epipubic cartilage small and wedge-shaped (0), or greatly expanded anteriorly to form a broad, thick pad (1).

The pubic bones of carphodactylines never directly contact one another at the pubic symphysis, but are separated by an epipubic cartilage. The primitive condition of a narrow, triangular epipubic cartilage with its apex directed posteriorly is shared by most carphodactylines, the Diplodactylini and most other geckos. In *Phyllurus cornutus* and *P. salebrosus*, however, the epipubis forms a greatly expanded wedge which may be as much as one half the size of a single pubic bone (Fig. 11) (character 47).

### Pubis

Character 48: Pectineal process of pubis small and ventrally directed (0), or large and domed (1).

The primary plate of the pubis is relatively narrow, particularly anteriorly in most carphodactylines and their outgroups. In all species of *Phyllurus*, however, the pubis is broad and robust (Fig. 11). A pectineal tubercle or process is present anterior to the obturator foramen in all species. Curiously, Romer (1956) reported the structure absent in all geckos. However, it has been identified in all geckos examined to date (Noble 1921; Wellborn 1933; Stephenson 1960; Stephenson & Stephenson 1956; Kluge 1962; Mahendra 1950; Siebenrock 1893; Cogger 1964). The pectineal process is primitively weakly

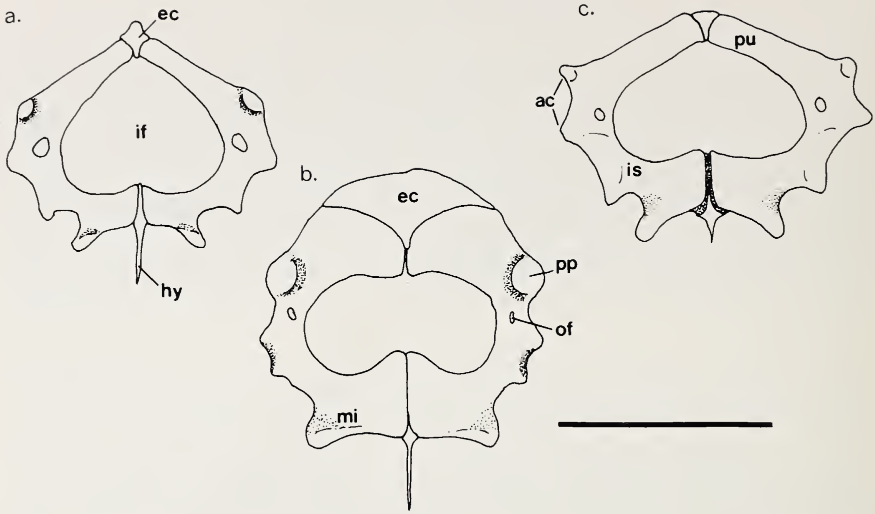

Fig.11: Ventral views of pelvis in (a) *Bavayia sauvagii* (CAS 165906), (b) *Phyllurus cornutus* (AMS R20447) and (c) *Naultinus elegans* (AMB 395). Note the differences in the size and shape of the epipubic cartilage (character 47), the pectineal processes of the pubis (character 48), the metischium (character 49) and the hypoischium (characters 50—51). Scale bar = 10 mm (b), 5 mm (a, c). Abbreviations are as follows:

ac — acetabulum
ec — epipubic cartilage
hy — hypoischium
if — ischiopubic fenestra
is — ischium
mi — metischial process
of — obdurator foramen
pp — pectineal process
pu — pubis

developed but projects ventrally in carphodactylines. A derived condition is seen in *Phyllurus*, in which the process is robust and domed (character 48).

### Ischium

Character 49: Metischial processes narrowly separated from one another posteriorly (0), or expanded posterolaterally, widely separated from one another (1).

The posterior portion of the ischium bears a large, blade-like metischial process. The distance between the two metischial processes is generally small — less than the width of the ischiopubic fenestra in the Diplodactylini and the New Zealand and New Caledonian species of the carphodactylines (Fig. 11), as well as in *Rhacodactylus (Pseudothecadactylus)*. The remaining carphodactylines share the synapomorphy of a much broadened and expanded ischium and metischial process (character 49).

### Hypoischium

Character 50: Hypoischium slender and narrow A), or short and dagger-shaped B).

Character 51: Hypoischium short (0), or extending posteriorly almost to level of vent (1).

A prominent hypoischium is present in all species (contra Arnold 1984, who reported this element as reduced or absent in *Hoplodactylus pacificus* and *Rhacodactylus trachyrhynchus* as well as in other diplodactylines and eublepharines). This feature was discussed by Camp (1923), who presented evidence against the hypothesis of Mehnert (1891), who believed that the hypoischium was an ancient portion of the ischial plate. Rather, the free hypoischium appears to be a continuation of the ligamentum hypoischium, which serves as the ischial symphyseal pad. Among eublepharines there appaers to be little posterior projection of the hypoischium (Kluge 1962; Khalil & Sabri 1977b) and in the Diplodactylini and many gekkonines the hypoischium is splint- or dagger-shaped and extends posteriorly a short distance posterior to the metischial process. Among carphodactylines the hypoischium is slender and elongate in *Carphodactylus, Phyllurus* and *Nephrurus*. A shorter, dagger-shaped process occurs in all of the New Zealand and New Caledonian forms as well as in *Pseudothecadactylus* (character 50). The polarity of these character states cannot be assessed by use of the outgroup method. The hypoischium is generally calcified, but is never so in *Naultinus*, in which the hypoischium resembles the diamond-shaped element figured in adult *Uroplatus fimbriatus* (Siebenrock 1893; Camp 1923). All of the knob-tailed *Nephrurus* share the apomorphic condition of an extremely elongate, slender hypoischium, extending posteriorly to the level of the medial cloacal bones (character 51).

No consistent variation was noted in the ilium. The overall shape of the ischiopubic fenestra varies greatly within the Carphodactylini. The Australian padless genera show a relatively smaller angle between the pubis and ischium, yielding a compressed oval foramen. In other genera the fenestra is more strictly cordiform. This is particularly so in *Naultinus*.

Little information of systematic value was obtained from the proximal elements of the hindlimb. The morphology of the femur, tibia and fibula is adequately described in other geckos (Mahendra 1950; Wellborn 1933; Siebenrock 1893; Kluge 1962). A patella tibialis is generally present on the preaxial face of the femoral-tibial joint in the tendon of the quadriceps group. A parafibula is rarely ossified. Lunulae are present as tiny sesamoid ossifications in the knee capsule of some particularly large specimens. These are most evident in the immense *Hoplodactylus delcourti* (Bauer & Russell 1986). Like all sesamoids, the presence of these bones is highly variable and is generally unreliable for systematic uses (Fürbringer 1900; Kluge 1962).

### Metatarsals

Character 52: Metatarsals I and V shortest (0), or metatarsals IV and V shortest (1).

Character 53: Increasing order of metatarsal length V-I-IV-II-III A), or V-I-II-IV-III B).

Character 54: Metatarsal V slightly hooked A), or greatly hooked B).

Character 55: Digits of pes all splayed due to metatarsal position (0), or digit V almost opposable to I—IV (1).

Character 56: Metatarsals I—IV $\leqq$ 150% length of longest phalanx (0), or approximately twice length of longest phalanx (1).

Character 57: Metatarsals III and IV diverging (0), or parallel (1).

The structure of the gekkonid tarsus, as well as that of the pes proper, has been considered by numerous authors (Russell 1972, 1975; Haacke 1976; Khalil & Sabri 1977a). Russell (1972) surveyed the majority of genera in the family and provided osteological information, especially for the metatarsals and pedal phalanges, for many carphodactyline species.

Primitively for the tribe, a basal tibiofibulare or fused astragalus and calcaneum but (see Broom 1921 for a different interpretation) articulates with both the tibia and the smaller fibula. As described by Kluge (1962) for *Coleonyx*, a large cuboid lies basal to metatarsal IV. Smaller distal tarsals are basal to metatarsals I and III, and sometimes II (Stephenson 1960). Metatarsal V also articulates with the tibiofibulare and the cuboid as well as with its associated proximal phalanx. Three patterns of metatarsal length (from shortest to longest) are seen among carphodactylines. The pattern V-I-IV-II-III characterizes *Nephrurus* and *Naultinus*; V-IV-I-II-III is typical for the leaf-tailed *Phyllurus* and for *Carphodactylus laevis*; V-I-II-IV-III is typical for the remaining species in the tribe. Among the outgroups metatarsals V and I are the shortest in the Diplodactylini and in Eublepharinae (the character is variable among gekkonines). On this basis the pattern involving metatarsals V and IV as the shorter elements are regarded as derived (character 52). However, no a priori polarity of the remaining two patterns is suggested.

Metatarsal V is generally hooked in lepidosaurs (Robinson 1975) and serves as a site of attachment for most of the crural musculature. In general the structure of this element permits the foot to grip the substrate and to serve as a heel-analogue (Vialleton 1924; Schaeffer 1941; Robinson 1975; Russell & Rewcastle 1979; Brinkman 1980). In all of the padded genera metatarsal V is strongly hooked, while in the padless Australian genera, there is only a slight hooking (character 54). The polarity of this character could not be assessed on the basis of outgroup comparison.

The placement of metatarsal V generally causes digit V to splay away from the remaining digits in geckos. This is further accentuated in the knob-tailed *Nephrurus*, in which the remaining four digits are tightly bound together by connective tissue to yield an almost opposable digit V (character 55). Further, all knob-tails except *N. asper* and *N. wheeleri* share the derived condition of having metatarsals I through IV approximately twice the length of the longest phalanx of their respective digits (character 56). A similar condition has been reported in the gekkonine *Rhoptropus afer* (Haacke 1976; Wellborn 1933).

In the outgroups and carphodactylines, metatarsals I—IV diverge distally. This pattern is typical in *Phyllurus* and *Carphodactylus* and in *Nephrurus milii* and *N. sphyrurus*, although in some specimens metatarsals I and II, or II and III may be more or less parallel to one another. All remaining members of the tribe show the derived condition of parallel metatarsals III and IV (character 57).

### Phalanges

Character 58: Metatarsal-phalangeal joint and first interphalangeal joint with little or no inflection (0), or strongly kinked (1).

Many features of internal digital structure vary within the carphodactylines, but most appear to be coincident with other osteological or external features. Russell (1972) discussed the pes of several species in detail, including *Rhacodactylus auriculatus* and *Carphodactylus laevis*. In general, the internal features, which include the presence of subdigital adipose pads and blood sinuses, are characterized by Russell (1972) as morphological transition series within the padded carphodactylines, from *Heteropholis* through *Naultinus* to *Hoplodactylus*, the New Caledonian species and eventually to the most pedally complex group, *Pseudothecadactylus*.

The phalanges are generally relatively wide, depressed and crescentic distally in padded forms and stout and deep in padless forms. Slight kinks are present in the digits of all species as a result of angulation between the proximal phalangeal elements and the metatarsals. However, a prominent kink is a derived condition for *Phyllurus* (character 58). This is achieved by the strong angulation of the joints between the metatarsal and phalanx one and between the proximal two phalanges. Elsewhere among geckos, the condition is paralleled in members of the genus *Cyrtodactylus* (Russell 1972, 1976, 1979a).

A strongly arcuate and slender penultimate phalanx is typical of many pad-bearing geckos (Russell 1972, 1979a) but is not universal. The function of the arcuate phalanx was discussed by Russell (1975). This condition is derived relative to the short, generally straight penultimate phalanx found in the Diplodactylini, Eublepharinae and many gekkonines. Among carphodactylines, the apomorphic condition is seen in all species of pad-bearers, although it is only weakly developed in *Naultinus* and in some *Hoplodactylus*. It has not been scored separately because its distribution is identical to that of certain functionally coupled external features treated later.

## Cloacal Bones

Character 59: Lateral pair of cloacal bones absent (0), or present (1).

One or two pairs of small bones are typically present in association with the pygal region of male gekkonids. The medial pair of bones is present in all diplodactylines. These are slender semi-lunate or "J"-shaped bones lying along the anterior margins of the cloacal sac apertures. The lateral bones, which are variably present, are generally flattened and irregularly shaped and lie along the ventro-lateral aspect of the tail base in association with the cloacal spurs. An additional ossification, a hemipenial bone has been found in at least some species of the aberrant gekkonine genus *Aristelliger* (Russell 1977b; Kluge 1982). Cloacal bones were first noted by Schlegel (1838) in *Gekko japonicus* and have since been reported in most species of non-sphaerodactyline geckos (Wellborn 1933; Brongersma 1934; Underwood 1954; Kluge 1967a, 1982; Russell 1977b; Bastinck 1986) as well as pygopodids (Kluge 1967a, 1974, 1982). Somewhat similar elements are also found in the Xantusiidae (Savage 1957; Rieppel 1976a) and in the "prolacertilians" *Tanystropheus longobardicus* (Wild 1973) and *Tanytrachelos ahynis* (Olsen 1979). Kluge (1982) has argued that these elements in non-gekkonids are not homologous. This view has received support from the recent reassignment of the fossil taxa from the Lepidosauria to the Archosauromorpha (Gauthier 1984; Benton 1984, 1985). Thus Rieppel's (1976a) claim that cloacal bones are primitive among the Lacertilia is based solely upon the presumed overall primitiveness of the taxa exhibiting cloacal ossifications. The bones and their associated cloacal sacs thus appear to be gekkonid synapomorphies (Kluge 1967a, 1982).

While the presence of bones and sacs may be regarded as apomorphic for the Gekkonoidea as a whole, the polarity of the presence of one versus two pairs of bones is more equivocal. Within the Diplodactylini, the immediate sister group of the Carphodactylini, both conditions occur. *Rhynchoedura* and most *Diplodactylus* have both medial and lateral cloacal bones, but the remaining taxa have only the medial elements (Kluge 1967b). The character is again variable in the Gekkoninae (excluding the sphaerodactylines and several other groups that lack the bones). In the tertiary outgroup, the Eublepharinae, however, all taxa have both sets of bones (Kluge 1962, 1967a). Kluge (1967b) considered two sets of cloacal bones as the derived condition within *Diplodactylus* and within the Diplodactylinae as a whole.

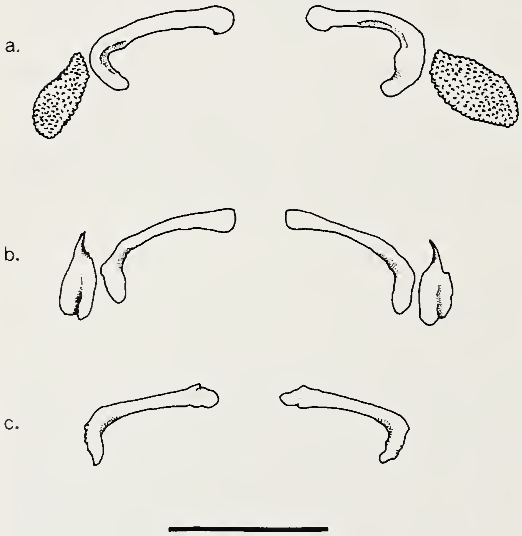

Fig.12: Cloacal bones in ventral view. (a) *Nephrurus milii* (NHMW 17424:1) — medial bones with lateral calcifications, (b) *Naultinus gemmeus* (MHNG 653.83) — lateral and medial bones present and (c) *Hoplodactylus maculatus* (MHNG 678.304) — medial bones only present. See character 59. Scale bar = 3 mm.

Both sets of bones are found in all species of *Naultinus* examined *(N. elegans, N. gemmeus, N. grayi, N. stellatus)* (Fig. 12b). Only the medial pair is present in the species of *Bavayia, Rhacodactylus, Eurydactylodes, Carphodactylus, Nephrurus, Phyllurus* and *Pseudothecadactylus*. Lateral calcium accretions were identified in two of seven adult male *Nephrurus milii* (Fig. 12a). These irregular accretions were found only in the largest specimens. I concur with Kluge (1967b) that these masses are not true cloacal bones. Members of the genus *Hoplodactylus* varied in this character, both among and within species. Both pairs of bones were present in all *H. granulatus, H. rakiurae* and *H. stephensi* examined. The single known specimen of *H. delcourti* lacked the lateral bone as did 67% of *H. maculatus* (Fig. 12c), 33% of *H. pacificus*, and 25% of *H. duvaucelii*. *Hoplodactylus chrysosireticus* and *H. kahutarae* were not scored for this character (character 59).

Kluge (1967a, 1967b) considered the lateral cloacal bones to be highly variable in form and presence and recently postulated as many as six independent losses of the entire cloacal bone/sac system within the Gekkonoidea (Kluge 1982, 1987). The function of the system is still unclear but it appears that the medial bones are intimately related to the cloacal sacs (Smith 1933a) and perhaps to hemipenial stability (Wiedersheim 1876). The lateral bones have long been associated with the external cloacal spurs and the physical enlargement of the female's cloaca during copulation (Noble & Bradley 1933; Greenberg 1943; Russell 1977b).

## Coloration

Character 60: Color pattern not primarily green (0), or color pattern predominantly green, fading to red or pink in preservative (1).

Character 61: Dorsal color pattern of head and nape unicolored or bearing a single band of color (0), or with three dark bards (1).

Character 62: Juvenile color pattern as adult or with dorso-lateral longitudinal markings A)(0), or with parvavertebral rows of light spots B)(1).

Green coloration is relatively rare among the Gekkonidae, in which it is primarily associated with diurnal forms. Among the sister-taxa to the Carphodactylini, this character state is lacking in all of the Diplodactylini and pygopodids. It occurs among certain gekkonines (sensu lato), most notably in *Phelsuma* (Schmidt 1912), certain *Lygodactylus*, and in numerous sphaerodactylines. Green coloration is absent in the Eublepharinae.

Among the carphodactylines, green coloration is seen in life among members of the genera *Naultinus, Hoplodactylus* and *Rhacodactylus*. A pale lime color is also present in some *Eurydactylodes vieillardi* and perhaps in *E. symmetricus*, and in some *Hoplodactylus rakiurae*. Olive green hues are sometimes seen in the background coloration of *H. maculatus, H. pacificus* and *H. chrysosireticus*. Yellow-green markings may also be present on some *H. granulatus*. Individuals of all species of the genus *Naultinus* may be primarily green, although male Banks Peninsula *N. gemmeus* and some *N. rudis* may be entirely brown and/or gray (Thomas 1982a; Robb 1980a) and some species, especially North Island forms, may be bluish or yellow instead of green. Among *Rhacodactylus* all *R. chahoua* and some *R. leachianus* exhibit green coloration. This is particularly striking in female *R. chahoua* (Bauer 1985a). No fresh specimens of *R. ciliatus* have been examined but Guichenot (1866) did not mention a green pattern in his color notes. Of the above mentioned taxa, only members of the genus *Naultinus* exhibit a fading to pink or violet (or occasionally blue or yellow) in preservative (Hutton 1872; Fischer 1882; Robb & Hitchmough 1980). This fading has been observed in all species. In contrast, members of the other genera eventually fade to brown, gray or white. This difference in fading suggests that different mechanisms may produce the green coloration in life. Thus it seems prudent to regard the green coloration of *Naultinus* and *Rhacodactylus* as homoplastic. The fading condition found among the members of the genus *Naultinus* is here regarded as an apomorphic condition (character 60).

A unique barred pattern is characteristic of certain *Nephrurus* (character 61). Most specimens of *N. stellatus, N. laevissimus, N. levis* and *N. deleani* bear a pattern of three dark, dorsal bands across the head, nape and shoulders. This pattern is present, although obscured by the dorsal stripe, in *N. vertebralis. Nephrurus asper* and *N. wheeleri* frequently have dark markings on the nape and shoulders but usually in the form of a single broad band. The condition seen in the smooth knob-tails is regarded as derived.

Paravertebral stripes and spots are common in many species in the Carphodactylini, including specimens of most *Naultinus*, some *Hoplodactylus, Rhacodactylus auriculatus* and *Bavayia cyclura*. Variation within single taxa for this character was great, and at least in *Rhacodactylus auriculatus* individuals from the same locality varied from completely barred to completely striped. As a result this character was not used in the analysis. However, more stable taxon-specific patterns in juvenile coloring were noted and this character was used (character 62). Two character states were recognized: one in which juvenile pattern is simlar to that of the adult or in which markings are mid-dorsal, and one in which juvenile markings consisted of longitudinal rows of paravertebral light-colored spots. Most *Rhacodactylus* and *Hoplodactylus duvaucelii* showed the latter condition.

## Membrane Pigmentation

Character 63: Tongue pinkish (unpigmented) (0), or distinctly pigmented (1).

Character 64: Mouth lining pinkish (unpigmented) (0), or distinctly pigmented (blue, black, yellow, or orange) (1).

Character 65: Parietal peritoneum unpigmented (0), or pigmented (1).

Character 66: Peritoneal pigmentaiton scattered (brown) A), or dense (jet black) B).

Besides variation in external coloration, several patterns of membrane pigmentation occur among carphodactylines. The first involve the coloration of the tongue (character 63) and the lining of the mouth (character 64). Based on outgroup comparison, the polarity of neither of these characters could be determined. Most geckos have pinkish or reddish mouths and tongues, reflecting a lack of pigmentation — the coloration being provided by the underlying blood vessels. Some gekkonines and many species of the genus *Diplodactylus*, however, have darkly pigmented mouths and tongues. Blue, black, yellow or orange tongues and/or mouths are present in at least some specimens of all species of *Naultinus*, in *Rhacodactylus australis* and in *Hoplodactylus* *granulatus, kahutarae* and *stephensi* (see Appendix C for precise character state distribution). The primitive gekkonid unpigmented condition pertains in the case of the remaining carphodactyline taxa.

The absence of chromatophores in the lining of the parietal peritoneal membrane is taken to be plesiomorphic for carphodactylines and geckos as a whole and is probably associated with the primitive nocturnality of the Gekkota. The apomorphic condition of a darkly pigmented membrane is found in all *Hoplodactylus* and *Naultinus* examined (character 65). All Australian and New Caledonian species lack peritoneal pigmentation. In all *Naultinus* examined, and in *Hoplodactylus granulatus, H. rakiurae, H. kahutarae, H. duvaucelii* and *H. chrysosireticus* the peritoneum is jet black, while in the remaining *Hoplodactylus* there is a varying amount of scattered brown pigment (characters 66). Pigmentation of the bones (Greer 1967), meninges, and nervous and circulatory epithelia (Martinez Rica 1974) was not examined.

## Eye

### Pupil

Character 67: Pupil vertical with crenelated margins (0), or pupil vertical with smooth margins (1).

Pupil shape was the primary criterion used by Underwood (1954) in his division of the Gekkonidae into subfamilies. The usefulness of this character was subsequently questioned (Cogger 1964; Kluge 1964, 1967a) and the use of pupil shape in delineating relationships has since been generally abandoned. Kluge (1967a) argued that the condition of specimens (living, freshly killed, or preserved) influenced the apparent shape of the pupil and that within taxa there was considerable variation in pupil shape. Further, he identified and figured types intermediate between Underwood's straight vertical (diplodactyline) and "*Gekko*-type" pupil shapes. Other authors (Mann 1931; McCann 1955; Cogger 1964; Mertens 1972) have also discussed variation in pupil shape among geckos.

However, it appears that the character of pupil shape may indeed be useful. Greer (pers.comm.) has found, using uniform lighting on living specimens, that five major patterns of pupil shape may be identified. A crenelated margin, closing to a series of pin-holes ("*Gekko*-type"), occurs in most members of the Diplodactylinae and the Gekkoninae. A crenelate margin closing to four pin-holes is a gekkonine type pupil, while one closing to six-holes is characteristic of diplodactylines. Each subfamily, in turn, seems to demonstrate a peculiar pupil form among diurnal taxa. In the case of gekkonines, this is generally a circular pupil corresponding to Underwood's *Rhoptropus*-type. In the Diplodactylinae diurnal forms (i.e. *Naultinus*) exhibits a straight-edged, vertical pupil (character 67). All of the Diplodactylini possess the six-lobed pupil type and this is interpreted as primitive for the Carphodactylini. The derived pupil shape is shared by all *Naultinus*. This character needs to be verified in living *Hoplodactylus kahutarae* and in several of the South Island green geckos. However, I have had no trouble identifying the pupil types in formalin fixed specimens and tentatively accept the results of examinations of preserved material.

### Extra-brillar Fringe

Character 68: Extrabrillar fringe weakly developed (0), or larger, thick and prominent (1).

Non-eublepharine geckos share the derived condition of lidlessness and have a spectacle (Kluge 1967a). Within this monophyletic group, a lid-like extra-brillar fringe (Bellairs 1948) has evolved several times. The gekkonine *Ptenopus* has been identified as one form in which these structures are particularly highly developed and even moveable (Bellairs 1948; Kluge 1967a). These fringes, or folds, supposedly act to protect the eye and its spectacle from damage due to abrasion by wind-blown sand or soil encountered in burrowing (Bellairs 1948; Brain 1962; Kluge 1967a). They may also act as sun shield in those species that are partially active by day (Brain 1962).

Extra-brillar folds are well developed in all species of *Nephrurus* and in *Carphodactylus* (character 68). They are developed only weakly, or not at all, in the remaining carphodactyline taxa. Morphological information, as well as outgroup analysis, suggests that the extra-brillar folds are part of a transformation series including the simple brillar fringes present in many geckos (Smith 1935, 1939; Bellairs 1948). Among the lidless outgroups, prominent extra-brillar fringes are absent in the Diplodactylini and in pygopodids and occur only in phylogenetically scattered groups of gekkonines that are presumed to be derived with respect to this feature. An additional feature that is invariably coincident with the prominent fringes is the presence of a small patch of dark pigment on the inner lining of the extra-brillar fold. The function, if any, of this spot is unknown.

## Ear

Character 69: External ear aperture small, oval (0), or large, vertically oriented (1).

Character 70: Aural opening free of skin folds (0), or partially occluded by flaps of loose skin (1).

Features of the inner ear have been used recently in a subfamilial level analysis of the Gekkonidae (Kluge 1987) and one character in particular, an "O"-shaped meatal closure muscle, appears to be a synapomorphy of the Diplodactylinae + Pygopodidae. Only external features of the ear were examined in the present study.

Among carphodactylines external ear size varies greatly. The auditory opening varies widely in size, but is generally oval in shape (the condition cannot be assessed in *Hoplodactylus delcourti* because this region of the specimen is distorted). This is similar to the condition seen in all examined species of the Diplodactylini, Eublepharinae and Gekkoninae. Members of the genera *Nephrurus, Phyllurus* and *Carphodactylus*, however, exhibit a generally vertically oriented ear opening, although in *P. platurus* the opening may be only slightly higher than wide. This shape of the ear is interpreted as apomorphic (character 69).

Within the New Caledonian species of carphodactylines two additional derived aural features are seen. In all New Caledonian *Rhacodactylus* except *R. auriculatus* the ear is partially occluded by horizontal folds of skin, yielding a very narrow, slit-like aural opening (character 70). Within *Eurydactylodes* another feature, unique among geckos, is seen. Andersson (1908) first noted that a shallow groove runs from the angle of the mouth to the ear in *Eurydactylodes symmetricus*. The groove is lined with unscaled skin that merges imperceptably with the oral epithelium. Its function is unknown. The condition is slightly different in *E. vieillardi*, in which a narrow band of skin interrupts the groove immediately anterior to the ear.

## Endolymphatic System

The endolymphatic system of tetrapods consists of bilateral endolymphatic ducts which originate from the sacculus of the inner ear and may expand into endolymphatic sacs in the cranial vault after passing through endolymphatic foramina (Whiteside 1922). In certain iguanians, e.g. anolines, *Polychrus* (Etheridge 1959), *Cophotis ceylanica* and *Brookesia* (Moody 1983) and many geckos (Wiedersheim 1876; Kluge 1967a), the endolymphatic sacs are expanded extra-cranially and lie along the surface of the dorsal neck musculature. Frequently the sacs are filled with a calcium carbonate solution (Ruth 1918). This material, which generally solidifies in preserved specimens, has been identified as aragonite (Camp 1923; Kluge 1987).

The presence of enlarged endolymphatic sacs and "calcium-milk" has been interpreted as a synapomorphy of the Gekkoninae plus Sphaerodactylinae (Kluge 1967a, 1987). The plesiomorphic condition was believed to have been shared by all eublepharines, diplodactylines and pygopodids. Radiographs of preserved specimens show, however, that aragonite accretions are present in sacs in the nuchal region of both species of the New Caledonian genus *Eurydactylodes* (Bauer 1989b). Such sacs were not located in any other diplodactylines, nor in members of the Eublepharinae or Pygopodidae. The presence of these sacs is an independently derived synapomorphy of the species of *Eurydactylodes*. Bauer (1989b) reviewed hypotheses of endolymphatic calcium function and concluded that it is related to calcium stress in reproductive females. This feature is autapomorphic for *Eurydactylodes* and has not been included in the character analysis.

## External Digital Characters

Character 71: Ventral digital scalation lamellate (0), or spinose (1).

Character 72: Digital lamellae without scansorial setae (0), or with scansorial setae (1).

Character 73: Scansorial pad narrow (0), or broadly dilated (1).

Character 74: Scansorial plates single (0), or divided (1).

Character 75: Apical plates of digit I single, medial A) (1); or cleft, asymmetrical with larger medial portion B) (0).

Lamellae, the rectangular subdigital scales present in many lizard groups, are universally present in eublepharines. They are present in most gekkonines and Diplodactylini except certain species of burrowing or sand-dwelling geckos including representatives of the genera *Chondrodactylus* (Haacke 1976) and *Stenodactylus* (Arnold 1980). Within the Carphodactylini the knob-tailed *Nephrurus* share the derived condition of a non-lamellate subdigital surface (character 71). In these forms the surface of the toes is spinose (Fig. 13a). The frequent association of this type of subdigital scalation with phalangeal reduction deserves further investigation.

Underwood (1954) stated that the Eublepharinae primitively lacked subdigital pads but did not provide explicit evidence for this belief. Russell (1972, 1976, 1979a) outlined the morphological features associated with primitive padlessness. His arguments are based primarily upon the absence of features permitting hyperextension — an ability necessary for the operation of the gekkonid scansorial apparatus. Among these features are the extensive overlapping of the dorsal and ventral regions of the interphalangeal

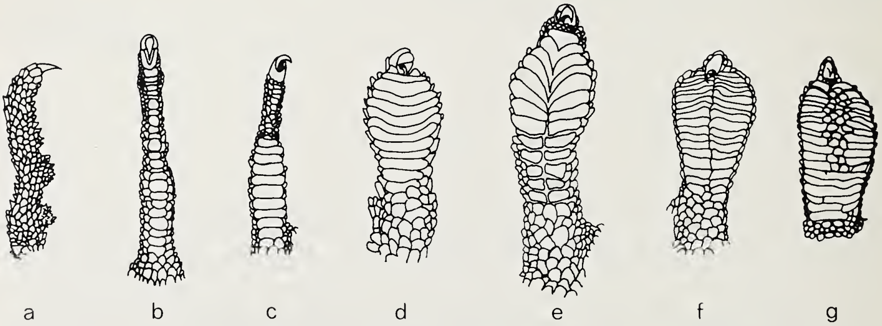

Fig.13: Toes of carphodactyline geckos. (a) Lateral view of digit I, right pes of *Nephrurus asper* (BMNH 1926.2.25.20) note spinose ventral scales (character 71). (b—g) ventral views: (b) *Phyllurus cornutus* (MNHN 1963.593) digit IV, left pes, (c) *Hoplodactylus granulatus* (BMNH 1946.8.22.71), digit IV, right pes, (d) *Eurydactylodes vieillardi* (BMNH (1926.9.17.7), digit II, right pes, (e) *Bavayia sauvagii* (BMNH 1926.9.17.25), digit IV, left pes, (f) *Pseudothecadactylus australis* (BMNH 77.3.3.12), digit IV, left pes and (g) *Rhacodactylus trachyrhynchus* (ZFMK 31809), digit IV, right pes (Figures a—f after Russell 1972). Note the differences in scansorial pad width and in scansor division (characters 72—74). *Rhacodactylus trachyrhynchus* possesses a unique lamellar pattern in which the scansors are fragmented medially (g).

joints and a relatively "simple" flexor musculature and tendonous system. Modifications of the digital units associated with hyperextension are present even in secondarily padless geckos (Russell 1976, 1979a) and determination of the primary padless condition is unambiguous. Using the outgroup comparison to assess polarity would result in determination of the padded condition as primitive for the Carphodactylini. However, examination of the digital structure reveals that the padless carphodactylines *Nephrurus, Phyllurus* and *Carphodactylus* (Fig. 13) are primitively so. This evidence is considered sufficient to establish the polarity of the character and the presence of pads in the Carphodactylini is interpreted as apomorphic (character 72). Secondary padlessness does not occur in any carphodactyline genera. Scansorial pads, when present, may be either narrow or broadly dilated. Again, based on Russell's (1972) arguments for a transformation series in digital structure, I accept as plesiomorphic the narrow condition, with the simpler musculo-tendonous structure. This condition pertains in all members of the genus *Naultinus* and in *Hoplodactylus granulatus, H. kahutarae* and *H. rakiurae*. The derived condition is seen in *Rhacodactylus (Pseudothecadactylus)*, the New Caledonian taxa and the remaining *Hoplodactylus* (character 73).

This determination of polarity for the presence of scansorial lamellae raises the question of the origin of pads. If we accept the preceding argument, then either all of the Diplodactylini are more closely related to some carphodactylines (i.e. to the padded species) than they are to others, or the padded conditions seen in the Carphodactylini and Diplodactylini (and the Gekkoninae) are independently derived. I believe the latter to be the case as presented in the "Introduction". Russell (1979a) discussed the spinose Oberhäutchen layer of the epidermis as a "universal primitive feature" from which the parallel, or shared but non-homologous, subdigital pads of the Gekkoninae and Diplodactylinae were derived. Yet he did not extend this concept to his analysis of pad evolution within the Diplodactylinae. I agree with Russell's (1979a) assessment that the Diplodactylini primitively bore terminal pads, yet there is little evidence to suggest that these share a common ancestry with the basal pads borne by the padded carphodactylines.

The acceptance of this hypothesis has some important ramifications for the polarity of other digital characters because homologies of character states cannot be inferred between the outgroups and the ingroup.

In those species with scansors, the pads may be either single or divided (character 74). Among the Carphodactylini the former condition pertains in all cases except *Bavayia* (Fig. 13e) and *Rhacodactylus (Pseudothecadactylus*, Fig. 13f) (Russell 1972, 1979a, considered *Bavayia* to possess truly divided scansors while those of the latter genus, except for the distalmost, were merely hinged as in *Hemidactylus*). Divided scansors have been considered as responses to functional demands and, as such, not valuable for assessing relationships (Vanzolini 1968; Russell 1979a). This position is clearly untenable, as the functional demand also has a history and reflects phylogeny at some level. Divided scansors function to maintain intimate surface contact when the penultimate phalanx becomes so arcuate as to lose its effective association with the underlying blood sinus (Russell 1975). In these instances a separate branch of the sinus supplies each of the scansor rows (Dellit 1934; Russell 1976). In many specimens of typically single-scansored geckos, proximal scansors may be somewhat irregular and divided. A unique, regular division of the scansors, however, is seen only in *Rhacodactylus trachyrhynchus* (Fig. 13g). The functional significance of these median divisions of the scansors is unknown.

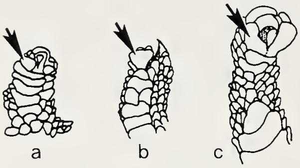

Fig.14: Terminal scansor (arrows) morphology of digit I in (a) *Eurydactylodes vieillardi* (BMNH 1926.9.17.7), right pes (completely divided terminal scansor), (b) *Bavayia sauvagii* (BMNH 1926.9.17.25), left pes (single scansor offset medially) and (c) *Hoplodactylus duvaucelii* (BMNH 54.11.6.4), left pes (single scansor, partially divided). See character 75.

Terminal scansors are present in the East Tasman genera of the Carphodactylini (Fig. 14). These structures do not resemble the apical plates of the Diplodactylini and are not considered strictly homologous to them. These are typically restricted to digit I of the manus and pes, and are absent in *Rhacodactylus (Pseudothecadactylus)*, which has lost the claw on these digits (see below). *Hoplodactylus rakiurae*, however, lacks this terminal scansor and *H. kahutarae* possesses scansors around the claws of all digits. The terminal plates are variously developed in the constituent taxa with the narrow-padded *Hoplodactylus* and *Naultinus* bearing smaller plates than the new Caledonian genera. *Eurydactylodes* may be distinguished from all other genera by its autapomorphic possession of two terminal plates, completely divided, on either side of the claw (Fig. 14a). All other species show either a single, medial scansorial plate or a single cleft plate, assymmetrical, with a large medial portion (character 75). The former condition is seen in all *Rhacodactylus* and in *Bavayia sauvagii* and *B. ornata* (Fig. 14b), the latter in *B. cyclura, B. crassicollis, B. montana, B. septuiclavis, B. validiclavis* and in the New Zealand species (Fig. 14c). The polarity of these character states could not be assessed and were entered into the analysis as missing for the ancestor.

## Claws

Character 76: Claws present on all digits (0), or digit I clawless (1).

Character 77: Claws deep at base, moderately to strongly decurved (0), or slender at base, straight or only slightly decurved (1).

All carphodactyline geckos have claws on all digits with the exception of the species of *Rhacodactylus (Pseudothecadactylus)*, which lack claws (but retain the ultimate phalanx) on digit I of both manus and pes (character 76). In general, claws are high at the base, compressed, robust, and distinctly decurved. All Diplodactylini except the monotypic *Crenadactylus* (which is completely clawless) bear a total of 20 claws. This is the most widespread condition and would also appear to be plesiomorphic for the Gekkoninae (Bastinck 1981) as well as the Diplodactylinae.

The plesiomorphic claw shape occurs in most carphodactyline taxa, including *Pseudothecadactylus*. In all knob-tailed geckos of the genus *Nephrurus*, however, the claws are slender and narrow at their bases, and the curve of the claw, is slight (character 77). This unique morphology may relate to the completely terrestrial habits of *Nephrurus*, which would not require the robust, strongly decurved claws of those forms that are primary or occasional climbers. Invariably associated with the slender claws of *Nephrurus* are keeled periungulate scales, which may also be related to terrestrial locomotion.

## Scalation Characters

Character 78: Dorsal body scalation heterogeneous A)(0), or homogeneous B)(1).

Character 79: Nostril contacts rostral scale A), or excluded from rostral scale B).

Character 80: First infralabials do not contact behind mental scale A)(0), or do contact behind mental scale B)(1).

Character 81: Postmental scales enlarged anteriorly A)(0), or subequal B)(1).

Character 82: Dorsal body scales without rosettes of surrounding scales (0), or tubercular with surrounding rosettes (1).

Character 83: Scales of rosettes not spinose A), or spinose B).

Character 84: Palmar scales only slightly smaller than scales on lower limbs (0), or sharply reduced in size relative to limb scales (1).

Character 85: Labial scales much larger than neighboring A)(0), or only slightly larger than neighboring scales B)(1).

Character 86: Infralabial scales broader than deep (0), or deeper than broad (1).

Character 87: Anterior loreal scales only slightly smaller than posterior loreals (0), or minute (1).

Many scalation features vary among carphodactyline species; few with any obvious functional correlates. For most such characters polarity cannot be reliably assessed by the outgroup method, so most were entered as unpolarized in the phylogenetic analysis. Those characters for which polarities could not be determined included: heterogeneous vs. homogeneous dorsal trunk scalation (character 78), rostral scale contacting or excluded from nostril (character 79), first infralabials contacting or not behind mental scale (character 80), and postmental scales enlarged anteriorly vs. uniform in size (character 81). These particular scale characters tended to show little relationship to presumed generic-level groupings, but were associated with lower level groupings of taxa (see Appendix C for the distribution of the states of these characters).

Atuberculate or simple tuberculate dorsal scales represent the primitive condition in the Carphodactylinae relative to the rosette-surrounded tubercles found in the species of the *Nephrurus* and *Phyllurus* (character 82). The rosette scales in turn may be either granular or spinose (character 83) but the polarity of this character could not be assessed. Another character that could be assessed was the size of the palmar scales. In the primitive condition, the scales of the palmar surfaces are the same size or only slightly smaller than those of the wrist and post-axial forearm. Much smaller palmar scales characterize *Nephrurus milii* and *N. sphyrurus* (character 84).

Among the head scales, the labials may be much deeper than the surrounding scales (most carphodactylines) or they may be only slightly larger than their neighbors (character 85). The latter condition is found in the knob-tailed *Nephrurus*. Although the former condition is the most generally common among geckos, the latter is prevalent in certain of the Diplodactylini and the character polarity is ambiguous. Within the more common condition a further refinement in character state is possible. Some taxa, notably *Rhacodactylus* and *Eurydactylodes*, display the derived condition of the infralabials being deeper than broad (character 86). This is particularly notable in *Rhacodactylus trachyrhynchus*, in which all of the labial scales are extremely elongate.

Loreal scales are those relatively unspecialized scales occupying the region above the labials and between the eye and the nostril. In most geckos the anterior loreals are slightly smaller to slightly larger than the posterior loreals. This condition appears to be primitive for each of the outgroups and is interpreted as being plesiomorphic at the first outgroup node. Minute anterior loreals (character 87) occur in *Carphodactylus laevis, Nephrurus asper, N. levis* and *N. milii*, in which they are interpreted as a derived state.

## Skin Folds and Webs

Character 88: Webbing absent between digits II, III, and IV (0), or webbing present between digits II, III, and IV (1).

Character 89: Webbing absent between digits IV and V (0), or webbing present between digits IV and V (1).

Character 90: No loose skin on posterior face of hindlimb (0), or folds of loose skin present on posterior face of hindlimb (1).

Character 91: Folds of loose skin around mandibular margins absent (0), or present (1).

Digital webbing is dependent on the presence of subdigital pads. Webbing between digits II and III and II and IV (character 88) is considered derived for carphodactylines and is found in the Tasmantis genera exclusive of *Naultinus*. Webbing between digits IV and V is less common (character 89) and is found only in *Rhacodactylus chahoua, R. ciliatus* and *R. leachianus*.

Body webbing or folds also occurs in some of the padded carphodactylines. Ventrolateral folds are common in most species of carphodactylines and in many other geckos. This may involve large margins around the body as in *Ptychozoon* (Russell 1979b), but more typically consists only of a slightly loose area between the axilla and groin. The fold is generally lined with adipose tissue and its size is, to some extent, a measure of the nutritional state of the animal. Besides these folds, which are considered plesiomorphic, certain carphodactylines possess loose folds of skin on the posterior face of the hindlimb (character 90), frequently forming a mite pocket (Smith 1933a). This feature is shared by the species of *Eurydactylodes* and by *Rhacodactylus auriculatus, R. chahoua, R. ciliatus* and *R. leachianus*. The function of mite pockets has been considered by Arnold (1986). Loose skin folds along the margins of the mandible are further restricted (character 91) to *R. chahoua* and *R. leachianus*.

## Preanal Organs

Character 92: Preanal organs present (0), or absent (1).

Character 93: Preanal organs extend onto thighs A)(0), or limited to preanal region only B)(1).

Two major epidermal gland types, generation glands and preanal organs, are found among the Gekkonidae (Maderson & Chiu 1970; Maderson 1972; Kluge 1983b). Among carphodactylines both preanal organs and beta-type generation glands occur (Bons & Pasteur 1977). Both are involved in holocrine secretion but the former is independent of the generation patterns of the remainder of the epidermis (Maderson 1970; Maderson & Chiu 1970). The function of both gland types is problematic (Cole 1966; Maderson 1985) but a role in reproduction (Greenberg 1943; Chiu & Maderson 1975; Menchel & Maderson 1975; Forbes 1941) or pheromone production (Maderson & Chiu 1984) has been implied.

Maderson (1970; Maderson & Chiu 1970) has considered the gland types as a transformation series with the following polarity: generation gland → preanal organ. Kluge (1983b) has correctly argued that this polarity, based upon current knowledge of gland distribution in lizards as a whole, should be reversed. Indeed, the ubiquity of preanal glands among lizards has long been recognized (Schaefer 1902).

Preanal organs are present in males of all carphodactylines except *Pseudothecadactylus cavaticus* (Cogger 1975a), all species of *Nephrurus* and most *Phyllurus*. Maderson & Chiu's (1970) reference to preanal organs in *P. cornutus* was not confirmed. However, male *P. salebrosus* do have small to moderate sized preanal organs and the specimens upon which Maderson & Chiu's comments were based may have been representatives of this species, which was undescribed at the time. Rösler (1985) also identified pores in *P. cornutus*, but again, the specimens may have been *P. salebrosus*. Preanal organs are present but reduced in size in *Carphodactylus* and *Rhacodactylus lindneri*. Pore patches are generally uninterrupted but may have a median gap of one to several scales in some species (e.g. some *Bavayia*, see Roux 1913). Absence of preanal organs is interpreted as a derived condition within the Carphodactylini (character 92).

Kluge (1967a, 1967b) used the character of a large median patch of preanal pores (Fig. 1) as diagnostic for the Carphodactylini. This condition is uniquely derived among geckos and is accepted as a synapomorphy of the tribe as a whole. Within the group, reduction to a single row of pores occurs only in members of the *Bavayia sauvagii* complex. All preanal pore-bearing species have pores in the trunk region just anterior to the cloaca. Extension of pore rows onto the thighs (= femoral pores) occurs in most species but not in *Hoplodactylus pacificus, H. kahutarae, Rhacodactylus auriculatus, R. trachyrhynchus*, or in either species of the pore-bearing Australian *Rhacodactylus* (character 93). In several other New Caledonian taxa a somewhat intermediate condition (scored as "pores extend onto thighs") may occur. The polarity of this character could not be assessed.

## Cloacal spurs

Character 94: Cloacal spurs few, flattened against tail base (0), or consisting of a cluster of six or more dorsolaterally directed scales (1)

Character 95: Scales of flattened cloacal spurs rounded, one to five in number A) (1), or pointed, two or more in number B) (0).

The cloacal spurs are sets of scales located at the postero-lateral margin of the vent, often associated with the lateral cloacal bones (if present). The spurs are frequently found in both sexes, but are particularly prominent in adult males. Three basic morphologies are represented among the Carphodactylini. In all species of *Nephrurus,*

Fig.15: Cloacal spurs (characters 94—95). (a) *Naultinus stellatus*, (b) *Hoplodactylus stephensi*, (c) *Naultinus grayii*, (d) *Rhacodactylus lindneri*, (e) *Bavayia sauvagii*, (f) *Rhacodactylus chahoua*, (g) *Nephrurus wheeleri*, (h) *Nephrurus levis*, (i) *Phyllurus platurus* (a—c are left spurs — anterior to left; d—i are right spurs — anterior to right).

*Phyllurus* and in *Carphodactylus laevis* the entire spur cluster is inflated and directed dorsolaterally (Fig. 15g—i). The clusters consist of an oblong *(P. platurus, C. laevis)* to rounded (all other species) unit of six or more enlarged scales, usually conical and tuberculate. *Rhacodactylus, Eurydactylodes, Bavayia, Hoplodactylus duvaucelii, H. delcourti, H. maculatus, H. pacificus* and *H. chrysosireticus* (Robb 1980b) exhibit a second type of spur consisting of a single row of one to five enlarged, smooth tubercles that lie flat against the tail base and project posterodorsally (Fig. 15d—f). *Hoplodactylus stephensi, H. granulatus, H. rakiurae, N. grayii, N. stellatus, N. elegans* and *N. poecilochloris* (Robb 1980b) present a third pattern with a series of two or more flattened, pointed scales lying more or less flat against the tail base and projecting posterodorsally (Fig. 15a—c) (characters 94, 95).

The last two conditions are present in members of the Diplodactylini and superficially similar situations are seen among the members of the subsequent outgroups. It is not possible to determine the polarity of these two character states using outgroup comparison but the first condition described is unique among geckos and is apomorphic relative to other cloacal spur morphologies. *Carphodactylus* is further distinguished by a unique patch of dark pigmentation on the proximal portion of the spur.

## Tail

Character 96: Tail elongate, tapering (0), or short, pyramidal (1).

Character 97: Tail with smooth margins (0), or leaf-shaped with ragged, flattened margins (1).

Character 98: Regenerated tail similar in shape to original (0), or short and bulbous (1).

Character 99: Cartilaginous rod of regenerated tail present, cylindrical (0), or absent or amorphous (1).

Character 100: Tail terminates in a conical point (0), or in a small knob (1).

Character 101: Dorsal scales of tail granular or tubercular A), or spinose B).

Character 102: Pygal region of tail tapers into post-pygal region (0), or abruptly decreases in diameter at pygal/post-pygal boundary (1).

Character 103: Scale rows on original tails at level of autotomy septa undifferentiated (0), or slightly smaller than neighboring rows (1).

Character 104: Ventral tail sulcus absent (0), or present (1).

Character 105: Subcaudal lamellae absent (0), or present (1).

Immediately posterior to the vent lies the pygal or pre-autotomic portion of the tail. Typically, ventral scales of this region are similar to those of the trunk venter, or only slightly larger. An autapomorphic condition seen in *Rhacodactylus australis* is the presence of enlarged hexagonal to octagonal scales in the subpygal region. This condition is evident in all specimens but is most pronounced in adult males.

Kluge (1967a) remarked on the extreme variability seen in gecko tails. Tail morphology seems to have been a primary component in the adaptive radiations of a number of gekkonid groups (Russell & Rosenberg 1981; Vitt & Ballinger 1982). Several researchers have used characters of the tail in taxonomic studies of diplodactylines (Storr 1963; Covacevich 1975; Russell & Rosenberg 1981).

Tail shape in geckos, in general, may be described as elongate and cylindrical or subcylindrical. This form is characteristic of all of the Diplodactylini and most of the Eublepharinae and Gekkoninae. Among the Carphodactylini a highly modified form is seen in a number of groups. *Carphodactylus laevis* differs from all other geckos in its autapomorphic possession of a compressed tail. The remaining Australian padless species have another derived condition, a relatively short, pyramidal tail shape (character 96). In *Phyllurus* the tail ranges from unmodified (some *P. caudiannulatus*) to extremely broad and leaf-shaped. Leaf-shaped tails, typified by a thin fringed margin of skin, occur elsewhere among geckos only in the Madagascan *Uroplatus* and to some extent in species of *Ptychozoon*. This condition is considered derived for *Phyllurus* (character 97). Covacevich (1975) stated that the regenerated tail of *P. caudiannulatus* is always cylindrical. However, a number of specimens with typical, leaf-shaped regenerates were examined in this study.

In the knob-tailed *Nephrurus* the tail is always moderately broad and short (see also character 25). In all *Nephrurus* except some *N. milii*, the tail does not taper evenly but rather has an abrupt constriction one third to three-quarters along its length. In *N. levis, N. milii* and *N. sphyrurus* the proximal, enlarged portion of the tail is quite extensive relative to the narrow terminal portion. All *Nephrurus* (except *N. asper*, which lacks autotomy septa) produce relatively amorphous regenerated tails that are short and bear none of the features characteristic of the original appendages (character 98). Furthermore, in all autotomizing knob-tailed species the cartilaginous rod that typifies lizard regenerates also may be lacking (character 99). Both of these characters are lacking in the outgroups and are deemed derived.

A cartilaginous terminal knob occurs in all species of *Nephrurus* except *N. milii* and *N. sphyrurus*, as well as in *Carphodactylus laevis* (character 100). The presence of this condition in the latter genus has not been previously noted, perhaps because the knob is tiny and few original-tailed specimens have been collected. The knob is best developed in *Nephrurus asper*, in which it is somewhat bilobed (hence the generic name). The function of the knob, if any, remains unknown, although plugging burrow entrances, monitoring mechanical stimuli, and thermoregulation have been suggested (Russell & Bauer 1988). All *Nephrurus* and *Phyllurus* share a further character in the presence of spinose scales on the dorsal surface of the tail (character 101). The primitive condition of smooth or granular scaled tails is seen in all of the East Tasman padded carphodactylines and in *Carphodactylus*, in which the smoothness of the caudal appendage contrasts with the heterogeneous scales of the trunk dorsum.

Several caudal characters also show derived conditions among the padded Carphodactylini. In most gekkonids, and primitively for all tribal and subfamilial groups, the pygal region of the tail tapers gradually into the elongate post-pygal region. This is true of most carphodactylines but in some species a distinct decrease in tail diameter occurs at the pygal/post-pygal border (character 102). This derived state is seen in *Bavayia* *cyclura*, in most of the *Rhacodactylus*, and sometimes in *Hoplodactylus chrysosireticus, H. maculatus, H. pacificus, H. stephensi* and *H. delcourti*.

Another character limited to these three genera plus *Eurydactylodes* is the presence of slightly smaller scale rows on original tails that correspond to the level of autotomy septa (character 103). This feature is lacking in *Naultinus* and in *Hoplodactylus rakiurae*.

Kluge (1967b) included tail prehensility as a character in his analysis and reported it present for all of the padded Carphodactylini. He also evaluated the presence of subcaudal lamellae. Prehensility involves a suite of features, some of which have already been discussed. Two further features include the presence of a ventral tail sulcus (character 104), associated with the increase in contralateral muscle bundle mass, and the development of subcaudal lamellae, similar in structure to those under the toes (character 105). The first character is found in *Eurydactylodes* and in *Rhacodactylus leachianus*. Subcaudal scansors were first noted in *Phyllodactylus europaeus* (Fitzinger 1843). The function of these structures has been studied both from the perspective of behavior (van Eijsden 1983) and ecology (Vitt & Ballinger 1982). Subcaudal lamellae occur in all *Rhacodactylus, Eurydactylodes, Bavayia* and *Pseudothecadactylus*. The primitive padless condition occurs in all other carphodactylines. A unique, paddle-shaped tail-tip, perhaps also associated with prehensility (Guichenot 1866), occurs in *Rhacodactylus ciliatus*.

## Reproductive Mode

Character 106: Reproductive mode oviparous (0) or ovoviviparous (1).

Although widespread in squamates as a whole, viviparity is very rare among gekkonids (Kluge 1967a). It occurs only among certain carphodactyline taxa. The plesiomorphic reproductive mode for the Gekkonidae as a whole and more specifically for the Carphodactylini is oviparity, in which two leathery-shelled eggs are laid (Werner 1972; Bustard 1965, 1967a, 1968, 1970). Viviparity has been reported only in the New Zealand genera *Naultinus* and *Hoplodactylus* and in the New Caledonian species *Rhacodactylus trachyrhynchus* (Bartmann & Minuth 1979) (character 106).

Colenso (1880, 1887) first reported viviparity in *Naultinus elegans*. Subsequently all members of this genus have been demonstrated to be live-bearing. Similarly, all *Hoplodactylus* for which reproductive data are available are also viviparous. Reproductive mode is unknown in *H. kahutarae*. Bauer & Russell (1986) postulated that the extinct giant *Hoplodactylus delcourti* was also viviparous. Shine (1985a, 1985b) stated that the reproductive mode of many New Caledonian carphodactylines was unknown. However, literature records exist for egg-laying in *Rhacodactylus chahoua* (Henkel 1981), *R. auriculatus* (Böhme & Henkel 1985), *R. sarasinorum* (Henkel 1986a, 1987, 1988) and *R. leachianus* (Roux 1913; Mertens 1964a). Thus, among *Rhacodactylus*, reproductive mode remains unknown only for *Rhacodactylus ciliatus*. Among the other New Caledonian carphodactylines, all *Bavayia* are oviparous as is *Eurydactylodes vieillardi* (Sauvage 1878), and probably its congener *E. symmetricus*.

The extent of maternal dependence in lizards is difficult to determine. Although much fetal nourishment in live-bearing carphodactylines is derived from yolk, Boyd (1942) reported that the choriovitelline placenta of *Hoplodactylus maculatus* functions "to some extent for food absorption". The ubiquity of viviparity among the New Zealand taxa has lent support to the theory that live-bearing is an adaptation to cold or unfavourable climates. The recent discovery of a tropical live-bearer has shown the need for reconsideration of this hypothesis (see Wake 1977, 1980, 1982 for alternative suggestions about the evolution of viviparity in the Amphibia). Initially proposed by Gadow (1910) and Weekes (1935), this notion has been promoted by most subsequent workers (Neill 1964; Fitch 1970 inter alia). Recently the importance of intermediate stages in the evolution of viviparity has been emphasized (Tinkle & Gibbons 1977; Shine & Bull 1979). Blackburn (1982), Shine (1983a), Shine & Berry (1978) and Shine & Bull (1979) have demonstrated that there are indeed, many more instances of viviparous lizards in cold regions but indicate that this result may primarily reflect differential survival rather than origin of live-bearing under such circumstances. Thus, viviparity might have been a more widespread trait in Eastern Tasman carphodactylines that have survived chiefly in the harsher climatic regime of New Zealand. Despite this possibility, both Blackburn (1982) and Shine (1985a) regarded the distribution of live-bearing among the Carphodactylini to represent a minimum of two independent origins of viviparity.

Fitch (1970), Shine & Bull (1979) and Shine (1985a) have outlined features of biology and ecology that should promote the evolution of live-bearing. Although most of these features are not found in the viviparous carphodactylines (i.e. high demand for nest sites), one is of particular note. Because the female will be burdened by carrying young for a long period of time (up to eleven months in some species), it is essential that she can "afford" not to be exceptionally mobile. Among geckos, most live- bearers, especially *Rhacodactylus trachyrhynchus* and the species of *Naultinus*, are quite slow and deliberate in their movements and both have evolved on land masses free of potential terrestrial mammalian predators.

## Defensive Behavior

Character 107: Defensive behavior incorporates back arching and leg extension (0), or lacks these elements (1).

Two states of interspecific defense behavior are seen among members of the Carphodactylini. In some forms the limbs are straightened and extended, the back arched, the tail erected and waved or twitched and the mouth is opened. Frequently this is associated with hissing or vocalizing and may culminate in a lunge at the antagonist. This behavior has been detailed in *Phyllurus platurus* (Mertens 1946; Mebs 1973; Green 1973), *Nephrurus milii* (Bustard 1967b), *N. asper* (Longman 1918; Mertens 1946; Bustard 1967b, 1979; Gow 1979), *N. deleani* (Delean 1982) and *N. levis* (Waite 1929; Bustard 1965) and appears to be typical for all members of these genera. Tail twitching under unspecified conditions has been seen in *Phyllurus cornutus* (Bustard 1965). Similar actions are performed by members of the genus *Naultinus* (Robb 1980a). *Hoplodactylus granulatus* juveniles may tail-twitch (Angelus 1988), and vocalize, but back arching and leg straightening have not been reported. Rieppel (1973) reported back arching and leg extension in *H. maculatus*, but only during bouts of intraspecific antagonism. Similar patterns of male—male displays have been reported for *Oedura* (Bustard 1965), *Diplodactylus (Lucasium)* (Bustard 1965), *Lygodactylus* (Greer 1967; Kästle 1964), *Phelsuma* (Kästle 1964) and *Coleonyx* (Greenberg 1943).

This set of action patterns has not been reported in connection with interspecific behavior by any of the New Caledonian carphodactylines or by *Hoplodactylus*. Typically, when approached, these taxa will 1) flatten their bodies against the substrate, 2) flee, 3) hiss, growl or croak without a physical display (or with tail waving only), or 4) bite without a preceding display. The defensive behavior of *Carphodactylus* is unknown. The more complex pattern of defense responses is taken to be primitive because it occurs in a variety of gekkonines and, more informatively, is common among the tail-squirting *Diplodactylus* (Bustard 1964, 1969).

## RESULTS

Three levels of analysis of the phylogenetic data are presented. The first, which follows here presents the outcome of the PAUP analysis and identifies those derived characters supporting relationships among taxa. The second, an interpretation of these results appears in the discussion. Finally, geological events and a timetable are associated with the phylogeny to yield a scenario of the evolution of the Carphodactylini.

The results of the phylogenetic analysis for full set of taxa and that including the collapsed knob-tailed *Nephrurus* and *Naultinus* (see "Materials and Methods" for a discussion of collapsing these taxa) were similar. The most parsimonious trees generated were 209 steps (consistency index = 0.522) and 186 steps (c.i. = 0.586), respectively. A minimum of 50 most parsimonious trees was generated in each case. Exhaustive searches within the collapsed *Nephrurus* taxa, using the branch and bound option of PAUP, located ten equally parsimonious trees of length 20 and c.i. = 0.650. Use of this option with *Naultinus* yielded more than 200 trees (operation terminated due to limited storage space) of length 6 and c.i. = 0.833.

An Adams (1972) consensus tree, in which competing patterns of branching are represented as unresolved polychotomies, was constructed from the trees generated by PAUP. Twenty subterminal nodes result from the analysis of 38 terminal taxa (Figs. 16-19). Diagnoses of terminal taxa (species) and nodes of "generic" or less inclusive rank are presented under "Systematic Accounts". Basal (suprageneric) nodes are discussed on the following pages.

Two major branches result from the analysis. In the first of these *Phyllurus* was found to be the sister taxon of *Carphodactylus*. These taxa together form the sister group to *Nephrurus* (including those species formerly assigned to the genus *Underwoodisaurus*).

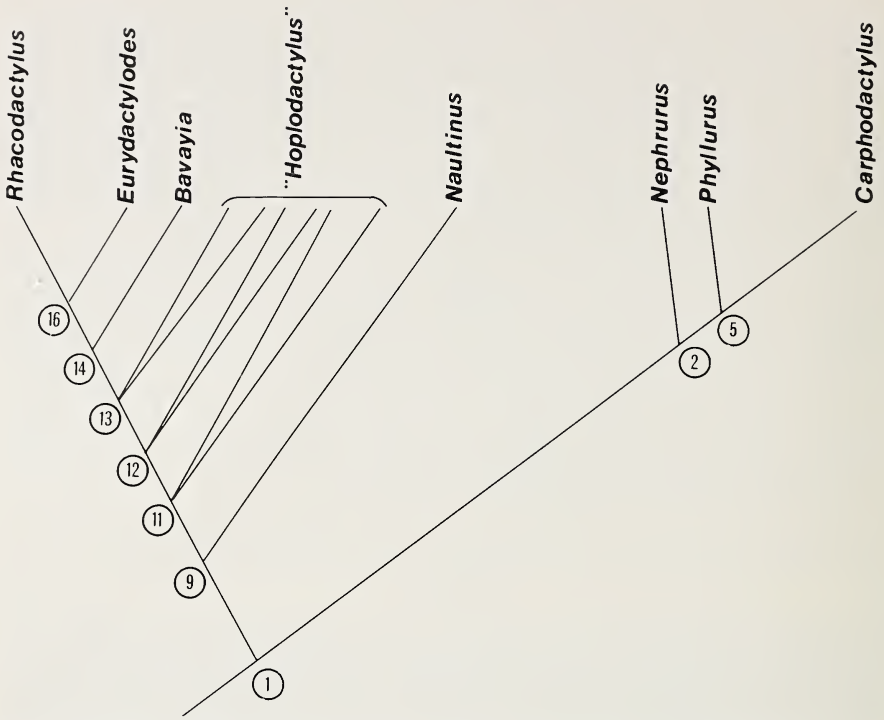

Fig.16: Consensus cladogram of carphodactyline genera. The subgenus *Pseudothecadactylus* is included within *Rhacodactylus*. Numbers of nodes referred to in the text are circled in this and subsequent figures.

In the second major clade *Pseudothecadactylus* forms part of *Rhacodactylus*, which is the sister taxon of *Eurydactylodes*. *Bavayia* is the sister taxon of this group. Subsequent outgroups include three pairs of species of *"Hoplodactylus"*, each forming a trichotomy (Fig. 18). *Naultinus* is the sister taxon of *"Hoplodactylus"* plus the New Caledonian carphodactylines (and *Pseudothecadactylus*) (Fig. 16).

Diagnoses of the suprageneric nodes are in telegraphic form and include all of the changes of character state that occur at a given node as supported by the consensus cladogram. The numbers of the characters applicable at each node follows parenthetically. Character state reversals may be distributed in several different patterns on the cladogram and such characters may be more inclusive than indicated by the diagnoses. Reversals between nodes are indicated by semi-bold figures. Uniquely derived character states are followed by an asterisk (*). Autapomorphic characters not included in the analysis are also included in the diagnoses and external characters are stressed over osteological features.

**Node 1**

This grouping corresponds to the Carphodactylini in its entirety (Fig. 16). Taxa united at this node share the following character states derived relative to the outgroup node: extreme overlap of jugal and lateral infraorbital process of prefrontal; inner ceratohyal process present; autotomy planes absent in at least some pygal vertebrae; preanal organs in a triangular patch*. (13, 18, 28).

**Node 2**

The taxa united at Node 2 (Fig. 17), correspond to the group of padless Australian carphodactylines *(Carphodactylus, Nephrurus, Phyllurus)* and primitively share the following derived character states: premaxillae completely unfused; parietal short and very broad; coronoid-dentary suture anterior to dentary-surangular suture; teeth minute and extremely numerous; hyoid cornu with antero-medial process reduced and postero-lateral process large and hooked; lumbar vertebrae two (rarely three) in number; caudal vertebral centra extremely short; post-pygal pleurapophyses absent or greatly reduced; metischial process expanded; hypoischium slender and elongate; metatarsal V only slightly hooked; extra-brillar fringe large, thick, with brown spot on internal face; external ear aperture large and vertical; dorsal trunk scalation consisting

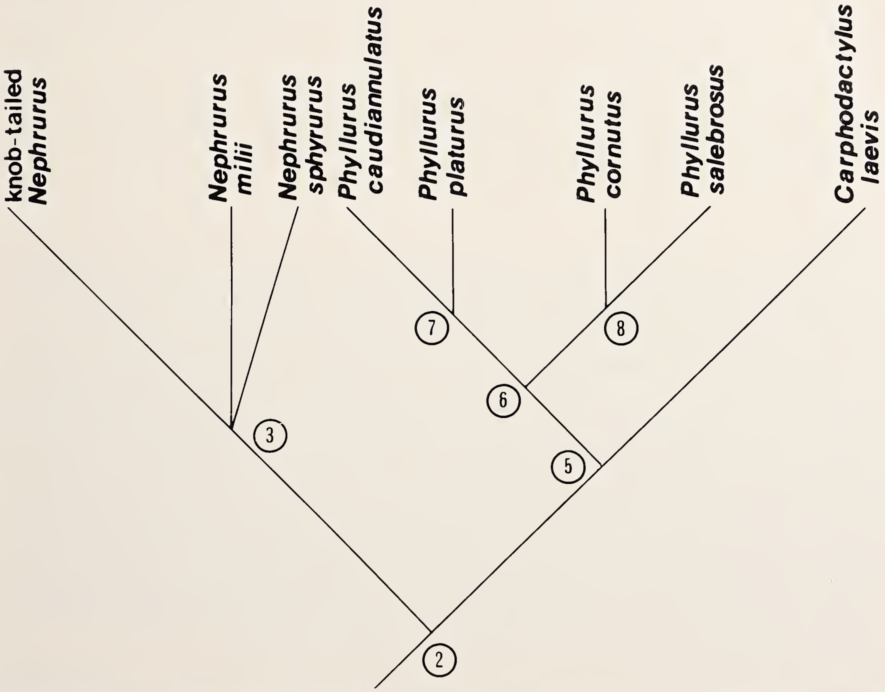

Fig.17: Consensus cladogram of the Australian padless carphodactyline genera. See text for characters at each node.

of tubercles surrounded by rosettes of scales; preanal organs absent; cloacal spurs consisting of clusters of conical scales; tail short and pyramidal; dorsal tail scalation spinose. The polarity of the states of characters 16, 50 and 54 could not be assessed, but among the Carphodactylini occur in all species united at Node 2 and in no others. Character 96 undergoes one reversal and characters 92 and 101 undergo at least two reversals or may have evolved independently outside of node 2 (in *Rhacodactylus cavaticus*). (2, 8*, 16-B, 17*, 18*, 26*, 27*, 49*, 50-A, 54-A, 68*, 69*, 92*, 94*, 96*, 101-B).

**Nodes 3 and 4**

See *Nephrurus* in systematic accounts.

**Node 5**

The taxa united at Node 5 correspond to the group including *Carphodactylus laevis* and all the species of *Phyllurus* and form a monophyletic group, the members of which primitively share the following set of characters: dorsal skin of head co-ossified with skull; nasal bones elongate and narrow; supraoccular portion of frontal deeply furrowed or concave; posterior border of parietals complete, roofing entire occipital region of skull; squamosal large and relatively broad; clavicular fenestrae minute or absent; metatarsals V and IV shortest. Characters 1, 7 and 11 arise in parallel in several other carphodactyline lineages. Characters 5 and 7 undergo reversals at less inclusive nodes. (1, 3*, 5, 7, 11, 42*, 52*).

**Nodes 6—8**

See *Phyllurus* in systematic accounts.

**Node 9**

The taxa united at Node 9 correspond to the East Tasman group of padded carphodactylines (*Naultinus, Hoplodactylus, Bavayia, Eurydactylodes* and *Rhacodactylus* including *Pseudothecadactylus*) and primitively share the following character states: fronto-parietal suture curved; scleral ossicles fewer than 30; coronoid dentary suture at same level as dentary-surangular suture; one lumbar vertebra; pygal pleurapophyses markedly decreasing in size distally; metatarsals III and IV parallel; lateral pair of cloacal bones present; tongue and lining of mouth distinctly pigmented; peritoneum pigmented jet black; digital lamellae with scansorial setae; scales of cloacal spurs pointed, two or more in number; dorsal tail scales granular; live-bearing. Reversals occur in characters 9, 15, 59, 63—66, 95 and 106. The derived character state 15 also appear independently at several places within the padless lineage. Character 59 is variable in the taxa *Hoplodactylus duvaucelii, H. maculatus* and *H. pacificus*. (9-B, 15, 16-A, 23, 24-A, 57*, 59, 63, 64, 65, 66-B, 72*, 101-A, 95, 106).

**Node 10**

See *Naultinus* in systematic accounts.

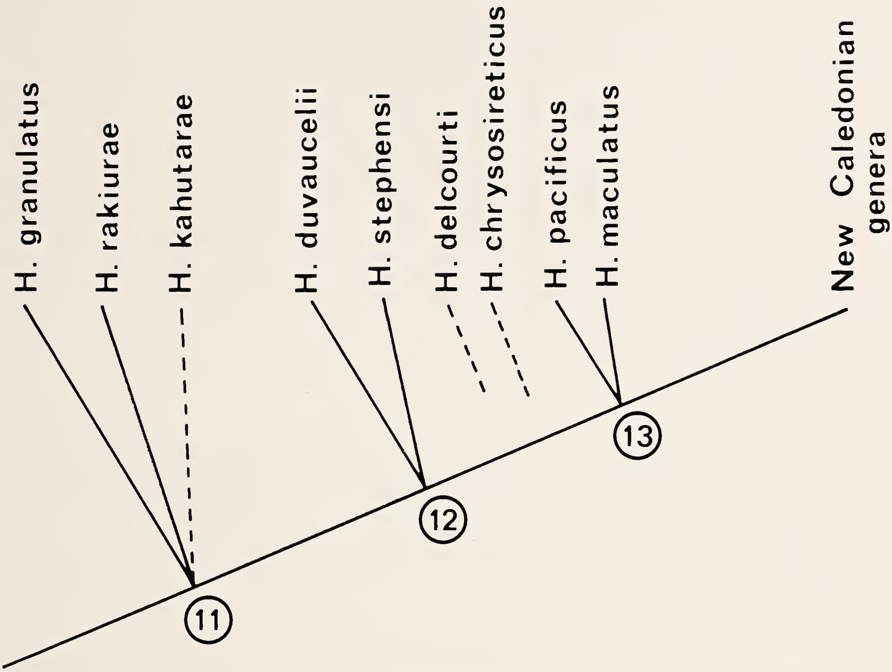

Fig.18: Consensus cladogram of the species of the paraphyletic metataxon *Hoplodactylus*. Species connected by dashed lines were not included in the initial phylogenetic analysis.

**Node 11**

The taxa united at this node correspond to the group of padded carphodactylines exclusive of *Naultinus* (Fig. 18) and primitively share the following character states: overlap of jugal and lateral infraorbital process of prefrontal narrow or excluded; inner proximal ceratohyal process absent; zero or one inscriptional ribs; three to four abdominal ribs; autotomy planes present in all post-pygal vertebrae; metatarsal length (shortest to longest) V-I-II-IV-III; dorsal body scalation homogeneous; webbing between digits II-III-IV; smaller scale rows on tail corresponding to level of autotomy septa; defensive behavior without sterotyped tail wave and lunge. Characters 13, 19 and 28 all undergo reversals at this node. Character 78 appears in parallel in two species of *Naultinus* and undergoes later reversals within node 18. (**13**, **19**, **28**, 32-A, 33-B, 53*, 78, 88*, 103, 107*).

**Node 12**

The New Caledonian carphodactylines, *Rhacodactylus (Pseudothecadactylus)* and *Hoplodactylus* exclusive of *H. rakiurae, H. granulatus* and probably *H. kahutarae* are united by the following characters: mesosternal extension present, color of mouth lining pale pinkish, scansorial pads broadly dilated. Character 31 undergoes a reversal at node 16. (31, **64**, 73*).

### Node 13

The taxa at node 12 exclusive of *Hoplodactylus stephensi* and *H. duvaucelii* and perhaps *H. chrysosireticus* and *H. delcourti* (the latter two taxa may be diagnosed at node 14), are united at Node 13 and primitively share the following characters: color of tongue pale pinkish; peritoneal pigmentation present, scattered; pygal region of tail abruptly decreasing in diameter to that of pygal region; scales of cloacal spurs rounded, 1—5 in number. Character 102 undergoes several subsequent reversals and character 63 may apply at the more inclusive node 12. (**63**, 66-A, 95, 102).

### Node 14

The New Caledonian taxa plus *Pseudothecadactylus*, united at Node 14 (Fig. 19), primitively share the following characters: overlap of jugal and lateral infraorbital process of prefrontal extensive; recessus scalae tympanii at least partially hidden ventrally by lateral process of basioccipital; scleral ossicles 30 or more in number; peritoneum unpigmented; subcaudal scansors present; oviparous. (**13**, 14*, **15**, **65**, 105*, **106**).

### Node 15

See *Bavayia* in systematic accounts.

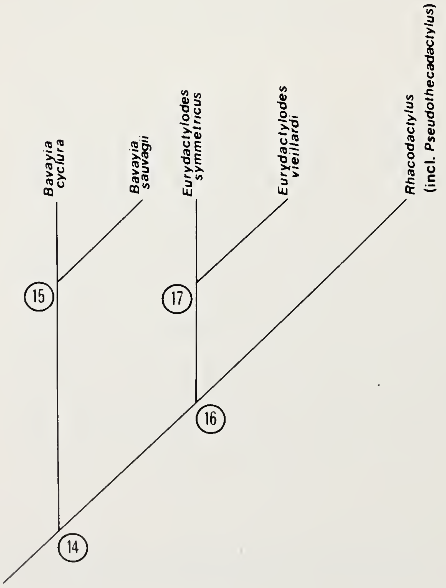

Fig.19: Consensus cladogram of the New Caledonian carphodactyline geckos. See text for characters at each node.

### Node 16

This node unites the group including *Eurydactylodes, Rhacodactylus* and *Pseudothecadactylus*, the members of which primitively share the following characters: mesosternal extension absent; infralabial scales deeper than broad; folds of loose skin on posterior face of hindlimb. Character 90 undergoes two reversals in species of *Rhacodactylus*. (**31**, 86*, 90).

### Node 17

See *Eurydactylodes* in systematic accounts.

### Nodes 18 and 19

See *Rhacodactylus* in systematic accounts.

### Node 20

See *Rhacodactylus (Pseudothecadactylus)* in systematic accounts.

## DISCUSSION

The phylogenetic analysis supports a primary division of the Carphodactylini into a primitively padless Australian clade (Node 2) and a padded Tasmantis clade (Node 9). This division is supported by pedal characters, cranial and axial skeletal features and characters of scalation. The padless lineage is especially well-supported with eleven uniquely derived features. An additional character not included in the analysis — the presence of setules on cutaneous sensilla (Bauer & Russell 1988) — also appear to support this group. Fifteen shared character states support the padded group but only ten of these are known to be derived and only two are synapomorphies unique to all members of the clade.

Within the padless lineage the consensus tree yields a secondary division into the *Nephrurus* clade (Node 3) and the *Phyllurus—Carphodactylus* clade (Node 5). A number of characters are shared among some members of the two clades but the dichotomy is unequivocal and both lineages are supported by three uniquely derived states. Three additional characters support each of the subdivisions of the latter group. *Phyllurus* is divided into two clades of two species each. The first contains the smaller "leaf-tails" *(P. caudiannulatus* and *P. platurus)* (Node 7) and the second, the larger forms *P. cornutus* and *P. salebrosus* (Node 8). Both clades are supported by osteological synapomorphies.

The genus *Nephrurus* (Node 3) is reduced into three unresolved branches (Fig. 17): the knob-tailed species (Node 4), *N. milii* and *N. sphyrurus*. The last two species were formerly placed in the genus *Phyllurus* (Kluge 1967b; Russell 1980) or were accorded generic rank as representatives of *Underwoodisaurus* (Wermuth 1965; Cogger 1975b, 1979, 1983) (see synonymy), which was assumed to have close affinities with *Phyllurus*. The results of the analysis, however, support the association of these two species with *Nephrurus*, rather than with the leaf-tails. This relationship is also supported by the fine structure of integumentary mechanoreceptors not dealt with in this analysis (Bauer & Russell 1988). It appears that Waite (1929) was among the only workers to recognize the similarity between *milii* and the knob-tailed geckos and to hint at some relationship. This relationship is supported by features such as an expanded brillar fringe and a short, pyramidal tail. *Nephrurus milii* and *N. sphyrurus* lack the knob- tail, spinose toe surfaces and reduced phalangeal formulae of their congeners, but these are plesiomorphic features. Further, microcomplement fixation work by Baverstock (King 1987a, 1987b) also supports this affinity, suggesting an approximate divergence time of 7 my between *N. milii* and *N. laevis* versus 23—26 my between *N. milii* and *Phyllurus* spp.

Although the consensus cladogram (Fig. 17) depicts a trichotomy above Node 3, it is possible that future work will indicate that *N. milii* and *N. sphyrurus* are each others closest relatives, forming a monophyletic group with the knob-tailed geckos as their immediate sister group. In this case the retention of the generic name *Underwoodisaurus* would be recommended. As a phylogenetically conservative measure I have included all of the taxa in the genus *Nephrurus*, pending more detailed analysis of relationships within the clade. Regardless, the generic name *Phyllurus* should not be used for the species *milii* and *sphyrurus* as this would make *Phyllurus* polyphyletic. Within the knob-tailed *Nephrurus* (Node 4), no resolution was possible, although some patterns of relationship were suggested by particular sets of the original cladograms generated. In particular, the "spiny" knob-tails, *Nephrurus asper* and *N. wheeleri*, are probably each others closest relatives and represent the sister taxon of the "smooth" knob-tails, which are united by a further digital reduction and many other characters. Similarity of scalation suggests affinities between *N. levis* and *N. vertebralis* and between *N. stellatus* and *N. deleani*. The consensus resolution into a polychotomy is primarily based on several homoplastic features, such as co-ossification, which tend to unite the larger species *N. asper* and *N. levis*.

The first division within the Tasmantis lineage (Node 9) suggests the divergence of the members of the genus *Naultinus* (Node 10) from the remaining taxa. The eight species of *Naultinus* are morphologically similar and share the uniquely derived character states of weakly ossified girdles, green pigmentation and smooth-sided, vertical pupils and diurnality. No resolution within the genus was suggested by the analysis although each species may be diagnosed using a variety of external characters. The genus *Heteropholis*, resurrected by McCann (1955) for the South Island green geckos, appears to have no genealogical reality. No division into North and South Island components is suggested and it seems unlikely that the addition of the taxa not included in the initial analysis, *N. manukanus, N. tuberculatus* and *N. poecilochloris*, would provide any additional resolution.

Bull & Whitaker (1975) and Thomas (1982b) suggested that *Naultinus manukanus* and *N. rudis* are sister taxa and that *N. tuberculatus* and *N. stellatus* perhaps also form a species pair. In turn *N. poecilochloris* has been regarded as intermediate between the other forms that surround its geographical range. Rare wild hybrids of some of the adjacent species pairs are known (Bull & Whitaker 1975) and all of the species will freely interbreed in captivity (Meads 1982). However, breeding seasons in the wild are generally somewhat asynchronous, suggesting some degree of premating isolation. In addition, the species are largely allopatric, although in the northern South Island, the ranges of several species approach one another or overlap slightly.

The overall patterns suggest a recent radiation of the genus *Naultinus*, with some behavioral but little morphological divergence. Electrophoretic analysis might be useful in elucidating relationships within the group, for few morphological features of determinable polarity were discerned. I accept the validity of all of the generally recognizable species, largely on the grounds of coloration differences and reproductive timing, but many or all of the species may be involved in a Rassenkreis, similar to that of the plethodontid salamander *Ensatina eschscholtzii* (Stebbins 1949, 1957; Brown 1974; Wake & Yanev 1986; Wake et al. 1986).

The taxon *Hoplodactylus*, consisting of nine species (one believed to be extinct), is paraphyletic, with some members more closely related to the New Caledonian carphodactylines (Node 14) than to other *Hoplodactylus*. With three taxa excluded from the analysis *(H. chrysosireticus, H. delcourti* and *H. kahutarae)*, three levels of polychotomous branching within the genus were identified and the resultant patterns of relationship are tentative at best. The group as a whole (Node 11), including the New Caledonian genera, is supported by ten characters, three of which are uniquely derived: relative metatarsal length, digital webbing, and absence of a stereotyped defensive behavior. *Hoplodactylus rakiurae* and *H. granulatus*, and probably *H. kahutarae*, are sister taxa to Node 12, which is supported by the single uniquely derived feature of broadened scansorial pads. The consensus cladogram also suggests that *H. duvaucelii* and *H. stephensi* are sister taxa to the remaining species (Node 13) and that *H. maculatus* and *H. pacificus* are part of a trichotomy also involving the monophyletic New Caledonian group. No uniquely derived characters support the relationship of *Hoplodactylus maculatus* and *H. pacificus* to the New Caledonian carphodactylines. Rather, I consider it likely that all of the species which branch at nodes 12 and 13 plus *H. chrysosireticus* and *H. delcourti* form a monophyletic group of broaded-padded *Hoplodactylus* which, as a whole, forms the sister taxon of the New Caledonian species. On the basis of external characters of unknown polarity *H. pacificus* and *H. stephensi*, and *H. maculatus* and *H. chrysosireticus* appear to be affiliated, although it is possible that *Hoplodactylus maculatus* as now construed is a paraphyletic species complex. *Hoplodactylus* thus is holophyletic but not monophyletic. I propose that use of the name be maintained until relationships within the subgroupings are resolved and two or more natural groups may be demonstrated.

It is somewhat surprising that the New Caledonian species appear to have arisen from within the New Zealand stock, as this would suggest that live-bearing has been evolved and subsequently lost (and regained in *Rhacodactylus trachyrhynchus*). Although there is no reason to assume that live-bearing, especially ovoviviparity, cannot undergo a character state change to oviparity, the current dogma would not seem to allow it (see **reproductive mode** in character analysis).

Node 15 diagnoses the genus *Bavayia* with five characters, among them uniquely derived, long, nearly complete second ceratobranchial arches. Node 16 diagnoses the remaining carphodactylines, which are supported by three characters, including the uniquely derived condition of infralabials deeper than broad. The two major divisions within this clade are the genera *Eurydactylodes* (Node 17) and *Rhacodactylus* (Node 18). *Eurydactylodes* possesses many apomorphic characters and is one of the most morphologically distinct of all gekkonid lizards. *Rhacodactylus* includes both, the giant New Caledonian forest geckos and the Australian geckos formerly referred to the genus *Pseudothecadactylus* (Node 20).

*"Pseudothecadactylus"* is diagnosed from other *Rhacodactylus* by the absence of a claw on digit one and by divided subdigital scansors. Although it was not entered into the analysis, *"P". cavaticus*, based on external morphology, is assumed to be most closely related to *"P." lindneri*. These species in turn form the sister group of *P. australis*. Among the New Caledonian species only one subgrouping was supported by the consensus tree, that uniting *R. ciliatus* and *R. chahoua*. Nevertheless, the majority of the original trees produced suggested that *Rhacodactylus auriculatus* is the sister taxon of all other members of the genus and that *R. leachianus* is the sister taxon to the *R. ciliatus/chahoua* group. *Rhacodactylus sarasinorum, R. trachyrhynchus* and the Australian species are successively remote sister groups of these taxa. As used throughout this paper, the name *Pseudothecadactylus* should be relegated to subgeneric status in order to maintain the monophyly of *Rhacodactylus*. In addition to the morphological evidence supporting this suggestion, King (1987a) found that *Pseudothecadactylus* shares a derived chromosomal morphology with *Rhacodactylus*. These results contradict Cogger's (1975a) conclusions that *Pseudothecadactylus* is an ancient group with relict distribution in northern Australia.

With the exception of the segments of the cladogram dealing with the species currently assigned to *Hoplodactylus*, the hypothesis of relationship among the carphodactylines is moderately robust and provides resolution at least at the generic level. These results differ in several ways from the hypothesis put forward by Kluge (1965a, 1967a, 1967b). Although Kluge recognized the unity of padless forms, he suggested that *Nephrurus* and *Phyllurus* were sister taxa and that *Carphodactylus* was the sister taxon of these two genera combined. He also placed both *Nephrurus milii* and *N. sphyrurus* in the genus *Phyllurus*.

Kluge's (1965a, 1967b) placement of *Pseudothecadactylus* as the immediate sister group to the remaining padded taxa is also contradicted. My hypothesis is, however, in accord with Russell's (1972) views of *Pseudothecadactylus*, in part because the polarity of some toe characters was established on the basis of Russell's work. Other intra-Caledonian relationships are similar to those proposed by Kluge. On the other hand, Kluge (1965a, 1967b) regarded the New Caledonian group as a whole paraphyletic because it gave rise to the New Zealand species. The reverse has been found in this study, and the genus *Hoplodactylus* is seen as a paraphyletic group. It is probable that

Kluge's views were in part due to the belief that ovoviviparity had only arisen once in the Gekkonidae and that a reversal to oviparity was unlikely. Kluge (1967b) also considered *Hoplodactylus* and *Heteropholis* to be each other's closest relatives. It has since been demonstrated that *Naultinus* and *Heteropholis* should be synonymized (Meads 1982; Thomas 1982b; this study), and the synonymy of all species of *Heteropholis* and *Naultinus* has even been proposed (Meads 1982; Gill 1986).

Aspects of the phylogenetic hypothesis are also supported by independent sets of data from other sources. Recent studies of karyology by King (1987a, 1987b, 1988) suggest that the Carphodactylini plus *Oedura* form a monophyletic group. The placement of *Oedura* has not been addressed in this study but again raises persistent questions about carphodactyline monophyly that need to be addressed in the context of a broader systematic work. Immunological work in progress (Rainey & Bauer, in prep.) also provides some support for the hypothesis, but this is too tentative at present to serve as a test of the hypothesis. Data regarding the geological history of the southwest Pacific, however, are plentiful and internally corroborated, and should serve as a means to evaluate, if not test, the phylogenetic hypothesis.

## BIOGEOGRAPHY OF THE CARPHODACTYLINI

The modern approach of biogeographical analysis has been (or should be) characterized as a mixture of vicariant and dispersalist philosophies (McDowall 1980; Murphy 1983). Dispersal and equilibrium faunal exchange have historically been regarded as the prime determinants of species number and diversity of islands (MacArthur & Wilson 1963, 1967). It now appears that paleogeographical legacy is more important in determining faunal composition in at least some situations (e.g. Lawlor 1986 for Indo-Australian mammals and Gardner 1986 for lizards of the Seychelles). The importance of paleogeographical factors increases with island age and isolation, and is greatest for groups of organisms with low vagility. Furthermore, the effects of paleogeological events on the compositions of island faunas should be reflected in the phylogenies of many groups of organisms (Nelson & Platnick 1981). Dispersal events can and do occur in nature, they are difficult to corroborate with independent sources of data (although Murphy 1983 has applied genetic distance techniques to this question). The ad hoc nature of most dispersalist arguments does not affect the likelihood that such events are responsible for the distribution of animal groups, but it does make such arguments difficult to support. For this reason I have used vicariance biogeography as my initial method of evaluating the phylogeny of the Carphodactylini hypothesized in the preceeding section.

I use two approaches of paleobiogeography which may be useful in examining the phylogenetic hypothesis of carphodactyline relationships. The first is the search for reciprocal illumination between phylogenetic and geological hypothesis. Congruence of implied biogeographical pattern (e.g. of taxon-area cladogram and geological-area cladogram) supports both hypotheses (but is not testable). The second approach is that of "cladistic biogeography" (Humphries & Parenti 1986) in which patterns of phylogeny of many groups or organisms yield hypotheses of common biogeographical pattern. Again, corroboration of a given phylogeny may be obtained by congruence of implied biogeographical relationships to that of the generalized hypothesis. Although the general hypothesis is perhaps falsifiable (Kirsch 1984), individual phylogenies cannot be falsified by non-congruence with the general pattern. Rosen's (1976) arguments regarding falsifiability of biogeographic hypotheses are circular. If neither the phylogenies of the organisms nor the geological histories of the areas involved in a particular distributional track are "known", non-congruence is at best a falsification of one (but which?) of the biological or geological hypotheses.

Despite certain limitations of the method, I accept the logical hegemony of vicariance over ad hoc dispersalist hypotheses and propose that for the southwest Pacific, where geological data are abundant and largely verified by numerous techniques, a meaningful evaluation of the phylogenetic hypothesis can be made by

1) an examination of the degree of reciprocal illumination provided by the phylogenetic and geological data sets and

2) the application of the cladistic biogeographic method.

Unfortunately the number of taxa inhabiting the region for which phylogenetic hypotheses exist is small. I shall therefore concentrate on the comparison of phylogenetic and geological data sets.

My interpretation of the major events in the history of the southwest Pacific region is largely derived from recent general works on the Pacific Basin, as well as more technical regional geological studies. The following works have been particularly useful: Keast 1981; Packham 1973; Lewis 1980; G.R. Stevens 1977, 1980a, 1980b; Lillie & Brothers 1970; Griffiths & Varne 1972; Hayes & Ringis 1973; Smith et al. 1973; Paris 1981; Archer & Clayton 1984; Holloway 1979; Coleman 1980; Raven & Axelrod 1972; Recy & Dupont 1982; Briggs 1987.

## Evaluation of the Phylogenetic Hypothesis

The hypothesis of carphodactyline relationships based on morphological synapomorphies is evaluated by comparison to the presumed geological history of the regions associated with the distribution of the taxa. A simplified consensus cladogram depicting the hypothesis of relationships, is shown in (Fig. 20a). This, in turn is translated into a taxon-area cladogram by substituting the regions occupied for each taxon (Fig. 20b). Some of the ranges have been simplified and represent the distribution of each taxon as a whole, excluding parts of the ranges of single species if they fall far outside the primary distribution of the higher order taxon. Thus, although *Nephrurus milii* and *N. sphyrurus* occur (in part) in eastern Australia, the genus *Nephrurus* has been replaced by the area "Western Australia". Similarly, in New Zealand, the wide-ranging *Hoplodactylus granulatus* and *Hoplodactylus maculatus* have been assigned to the

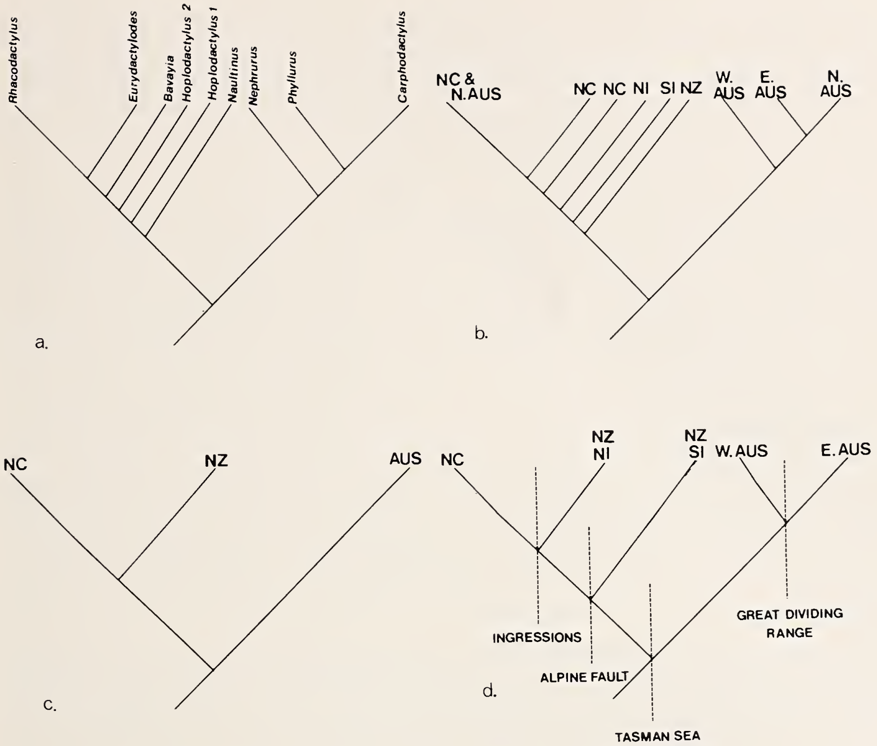

Fig.20: Test of the phylogenetic hypothesis. (a) Simplified consensus cladogram of the Carphodactylini. (b) Area cladogram derived from A (NC = New Caledonia, AUS = Australia, NI = North Island, New Zealand, SI = South Island, New Zealand, NZ = New Zealand). (c) Simplified pattern of geographical relationships derived from geological data. (d) Modified geographical pattern of relationships derived from geological data. Note the similarities between b and d.

South Island and North Island respectively, on the basis of the distribution of the other members of the clades of which they are a part.

A simplified tree of geological relationship for the areas involved is presented in Fig. 20c. In this diagram New Caledonia and New Zealand are shown as sister areas. This primary division from Australia is the result of the opening of the Tasman Sea while the division between the two island groups is the result of the sinking of the Lord Howe Rise and subsequent marine ingressions. The first event is conclusively dated to 80 mybp, but the second is less accurate, because effective contact may have been lost at any time before the Oligocene. At least sporadic contact was probably likely until that time (Dawson 1986), although a date as early as 65 mybp is possible.

This reconstruction, however, treats New Zealand as a single entity. In fact, New Zealand seems to have been divided since at least the time of the Tasman split, except for brief periods during the Pleistocene glaciations. It is unclear exactly which areas of New Zealand were emergent during the entire period of time since the opening of the Tasman barrier, but the components of both the Pacific and Australo—Indican plate blocks of New Zealand were relatively distant during much of the period between the initiation of movement along the Alpine Fault and the Miocene. The earlier event corresponds to the earliest Paleocene.

A more accurate reconstruction of the relationships among land masses in the southwest Pacific may be made based upon the composite structure of New Zealand (Fig. 20d). The first split in this figure corresponds to the opening of the Tasman Sea and the separation of Australia from the Tasmantis block. Within Australia an orogenic event, the raising of the Great Dividing Range, occurred in the Paleocene, coincident with the subduction of the Pacific Plate under the Australian crust as a result of the counter-clockwise rotation of New Zealand. Concurrently in New Zealand, movement was initiated along the Alpine Fault, and emergent portions of the southern block (= Torlesse terrane) began a long period of isolation from the northern, Australian Plate terranes of New Zealand. The latter retained sporadic northern contacts along the Inner Melanesian Arc. Later, probably as a result of Oligocene marine ingressions, New Zealand and New Caledonia lost the contact that had previously been provided by emergent land and narrow water gaps along the Lord Howe Rise and/or the Norfolk Ridge.

This reconstruction corroborates the phylogenetic hypothesis of relationships among the Carphodactylini in its broad outline, especially with regard to the nodes corresponding to the Australian padless genera (Node 2, Fig. 16), the genus *Nephrurus*, the genera *Phyllurus* and *Carphodactylus* (5), the Tasmantis (padded) genera (9), the New Caledonian genera plus the northern *Hoplodactylus* (12), and the New Caledonian genera alone (14). In each of these cases, a known vicariant event corresponds to a cladogenic event and provides a putative explanation for the origins of allopatry and subsequent divergence of the lineages involved. Each case is discussed in more detail in the scenario for the evolution of the Carphodactylini that follows. Other portions of the phylogenetic hypothesis, including division between *Phyllurus* and *Carphodactylus* and the distribution of *Pseudothecadactylus* (i.e. some *Rhacodactylus*) in Australia, are not corroborated by this geologically-derived geographical pattern of relationships. In these instances, more detailed geographical hypotheses should be examined.

When geographical hypotheses are lacking it may be possible to obtain corroboration (although not falsification) of the phylogenetic hypothesis by referring to taxon-area relationships in other, unrelated organisms. Unfortunately, this method can rarely be applied with success because it is only useful when genealogical relationships within these other taxa are known. However, the congruency of several taxon-area relationships suggests a generalized track (sensu Croizat 1958, 1964) which in turn implies commonality of distributional cause, i.e. a pattern reflecting vicariance. Repeated generalized tracks thus indicate that geological data may support paleogeographical reconstructions which are consistent with hypothesized patterns of cladogenesis. Certain patterns of carphodactyline relationships not addressed by the coarse-grained geological comparison are supported by the corroboration of congruent patterns of taxon-area relationships in other taxa. In particular, Cracraft (1986) demonstrated that a clade of northern Australian chestnut-shouldered wrens *(Malurus)* share the same pattern of species-area relationships as *Rhacodactylus* (subgenus *Pseudothecadactylus*), i.e. northern Cape York Peninsula + (Arnhem Land + Kimberley Plateau). The same pattern is also found in the finch *Poephila personata* (Arnhem Land + Kimberley Plateau) and its sister species *P. leucotis* (Cape York) and in many other bird groups (Ford 1978; Cracraft 1986). Similarly, the association of the Atherton Plateau with the eastern forest belt of coastal Queensland and New South Wales, as suggested by the relationship of *Carphodactylus* and *Phyllurus*, is corroborated by the distributions of sister taxa within the avian genera *Tregellasia* and *Ptiloris* (Cracraft 1986).

Details of the phylogenetic hypothesis dealing specifically with the carphodactylines of New Zealand require more attention. The ranges of many of the 17 gecko species that occur there are complex. Furthermore, the phylogenetic hypothesis within *Hoplodactylus* is weak. The geology of the areas involved is well studied but the correlation of paleoposition with emergent land is not exact enough to provide a sound basis for corroboration of any but the primary north/south division following the initiation of plate rotation. Corroboration of the hypothesis of carphodactyline relationships by taxon-area congruence must also await phylogenetic analyses of other New Zealand groups.

Details of the phylogenetic hypothesis as they relate to intra-island distributions remain untested by geological data, but division of the Carphodactylini into regional groupings receives support from paleogeography and suggests that cladogenesis within the group is associated with vicariant events in the Late Mesozoic or Early Tertiary.

## The Traditional View of Carphodactyline Evolution and Biogeography

Underwood (1957) proposed a scenario for the arrival in Australia of the various gekkotan groups, but did not deal with the events in Tasmantis. He suggested that pygopodids were the first invaders of Australia, with diplodactylines following shortly thereafter. *Phyllodactylus* (recognized by Underwood to be worldwide in its distribution) was the next to enter, followed finally by the ancestors of the remaining Australian gekkonines. Kluge (1965a, 1967a, 1967b) first proposed a scenario for the evolution of the Carphodactylinae as a whole. Like Underwood, Kluge worked in a pre-tectonic, dispersalist framework; thus he did not consider the theory of continental drift "germane to a discussion of the zoogeography of the Gekkonidae, particularly the Diplodactylinae". Furthermore, Kluge's hypotheses of relationship were pre-Hennigian — based not upon shared derived features, but on the percentage of primitive relative to derived features, with primitiveness not always demonstrated. (It should be noted that Kluge (1987) has revised his evaluation of the evolution of higher order gekkonid taxa using plate tectonics as a basis, although he does not provide a new scenario for the evolution of the Carphodactylini.)

Kluge (1967a) stated that geckos arose in the Upper Jurassic or Lower Cretaceous (based upon the dating of *Ardeosaurus*, now rejected by Kluge 1987 as not demonstrably gekkotan). The Eublepharinae, circum-global in distribution, were considered to show a relict pattern of extant forms, of which the most primitive genus was *Aeluroscalobotes*. By virtue of its occurrence in Borneo and South East Asia, *Aeluroscalobotes* fits well with Darlington's (1948, 1957) views of the Old World tropics as the center of reptilian origins. By the Tertiary, proto-*Coleonyx* had entered the Americas via the Bering Land Bridge. Kluge proposed that diplodactyline ancestors evolved in southeast Asia during the late Mesozoic and dispersed through the Indo—Australian Archipelago to Australia, where they subsequently replaced any pre-existing eublepharines. By the end of the Maestrichtian, the diplodactyline stock had crossed a broad land connection south into Australia (the Sumatran migration tract of van Steenis 1934a, 1934b, 1936), where they continued to evolve in isolation. Rising sea levels in the upper Eocene and later in the Pliocene cut off Australia from New Guinea, where diplodactylines were replaced by gekkonines. These had probably evolved at the same time as diplodactylines, and first radiated westward into Africa. New World gekkonines and the Sphaerodactylinae reached America by rafting; the latter stemmed from a *Lygodactylus*-like ancestor in the early Tertiary.

Kluge's (1967b) more detailed scenario for the evolution of the Carphodactylini was based largely upon prevailing views that there had never been any trans-Tasman land connections (Flemming 1962), although he did accept links from Australia to New Caledonia. Kluge considered the center of the Carphodactyline radiation to be in northeastern Australia and New Guinea in the paleotropical Tertiary flora (Burbidge 1960). Major radiations within the Carphodactylini occurred along the New Zealand migration tract (Burbidge 1960) from the center in Queensland to New Caledonia and the Loyalty Islands and thence to New Zealand. Kluge proposed that the New Zealand species were derived from near the basal stock of the New Caledonian species and that they reached New Zealand in the Miocene. Thus ultimately, Kluge (1967a, 1967b) accepted a Malaysian origin for the Diplodactylinae, similar to that proposed for most of the principal plant groups.

The carphodactyline/diplodactyline split was associated with the Tropical and Eremean floral zones, respectively (or Toressian and Eyrean zones) (Kluge 1967b). The Diplodactylinae evolved primarily in association with arid regions and later invaded the Toressian and Bassian mesic zones. Likewise, the Carphodactylini in Australia remained in association with the eastern forests, with some *Nephrurus* invading the Eyrean deserts. Neither group successfully invaded the cooler southeastern Bassian region of Victoria or Tasmania.

Kluge's scenario was a reasonable reconstruction, given the geological knowledge available and accepted by mainstream biologists (Darlington 1957, Solem 1959 and Caughley 1964 had earlier suggested similar dispersal routes). Unfortunately, as the reality of the tectonic development of the region became known, few workers abandoned this analysis. Cogger & Heatwole (1981) provided a tectonic overview by way of introduction, but retained Kluge's biogeographical hypothesis even though the paleopositions of Asia and Australia in the late Mesozoic would have precluded the type of dispersal that Kluge advocated (Cracraft 1975).

Bull & Whitaker (1975) also maintained Kluge's Miocene date for the entry of geckos into New Zealand, and as recently as 1986 Robb (1986) maintained that "lizards evolved much more recently than *Leiopelma* and *Sphenodon*, and would not have spread to Gondwanaland before it broke up". Robb (1986) further contended, as Kluge did, that the geckos arrived from the north, via New Caledonia. Thus, while she acknowledged the tectonic framework of the southern continents, she favored a scenario based on pretectonic geology. Acceptance of the ramifications of tectonics would also solve the problem of the absence of snakes in New Zealand and New Caledonia (Robb 1973) because they imply that the Tasman Sea opened long before snakes appeared in Australia (Smith 1973).

Recently, however, many workers (Tyler 1979a; Cracraft 1980; Flannery 1984; Gibbons 1985; Kluge 1987) have recognized the inconsistencies of maintaining Kluge's (1967b) scenario in light of current geological knowledge and have proposed a Cretaceous spread of the Diplodactylinae in the southwest Pacific before the isolation and breakup of Tasmantis. Tyler (1979) went as far as to suggest that the Diplodactylines may have been the only squamates in Australia in the Eocene. In New Zealand, Towns et al. (1985) have also questioned the proposed age of the scincid fauna and have advocated biochemical methods as a means of gauging approximate ages of lineages. King (1987a, 1987b) has proposed a detailed scenario for the biogeographic history of the Diplodactylinae on the basis of karyological and immunological evidence. In general, the application of such techniques to phylogenetic problems in Australia and the Pacific has pushed back divergence times from the Pleistocene to the mid-Tertiary (e.g. Maxson et al. 1982; Maxson & Roberts 1985), in accordance with known geological events. The following reconstruction of the evolution of the Carphodactylini is based on the historical geological reconstruction of the southwest Pacific as outlined above and suggests a possible scenario for the evolution of the group as a whole.

## A Scenario for the Evolution of the Carphodactylini

The primary division of the Diplodactylinae into the Diplodactylini and Carphodactylini cannot be clearly related to a single vicariant event. The period 140—120 mybp was a time of continental lake systems in Australia. These lake systems, along with occasional marine ingressions from the east, may have been associated with this division. Likewise, the origin of the Pygopodidae probably dates from the Mid-Cretaceous and cannot be associated with a particular tectonic event.

By the close of the Rangitata Orogeny, the eastern margin of Gondwana (the incipient Tasmantis) had been raised and remained near or in contact with Australia until 90—80 mybp. In the intervening 30—40 my a subset of the Carphodactylini — one that had perhaps already evolved padded toes independently — migrated into this marginal continental area, probably from the south. Here contact with the mainland near the Australo—Antarctic boundary was more extensive.

The subsequent opening of the Tasman Sea isolated the two divisions of the Carphodactylini and by 80 mybp the production of new sea floor between Australia and Tasmantis would have prevented interchange of most non-vagile animals. Spread of the two stocks probably proceeded rapidly. In Australia, the Late Cretaceous regression of epeiric seas was likely followed by westward expansion of the padless carphodactyline ancestors. In Tasmantis, carphodactylines had probably reached New Caledonia by the time of the Tasman rifting, and were certainly there by 65 mybp when the Lord Howe Rise sank and the New Caledonian Basin formed. Movement into New Guinea was blocked by the discontinuity in the Inner Melanesian Arc resulting from the formation of the Coral Sea. Interchange to parts of Northern New Zealand were probably possible as late as the Oligocene, at which time marine ingressions resulted in a large deep water gap along this portion of the Inner Melanesian Arc. The proximity of New Caledonia to Australia had ended with the formation of the Coral Sea as an extension of the Tasman, but contact was unlikely even before this.

In the Paleocene the initiation of movement along the Alpine Fault in New Zealand probably separated the variably emergent northern Australian Plate regions, with their connections to New Caledonia, from the southern Pacific Plate parts of New Zealand. The counter-clockwise rotation of the Pacific Plate caused subduction of its western margin under the Australian plate, resulting in the orogenic event that produced the Great Dividing Range in eastern Australia (53 mybp). These events isolated the ancestors of *Naultinus* and the southern species of *Hoplodactylus* from the northern *Hoplodactylus* and New Caledonian ancestors. In Australia, they divided the *Nephrurus* and *Phyllurus* + *Carphodactylus*.

In Australia during the Eocene, the opening of the Southern Ocean initiated the modern weather system patterns in the Southern Hemisphere. Members of both the Diplodactylini, probably long present in western Australia, and the padless carphodactylines moved with the continent into more northern latitudes, where desertification of much of the central and western parts of the continent occurred. The *"Underwoodisaurus" (Nephrurus milii* and *N. sphyrurus)* remained in association with coastal regions and with the western flanks of the Dividing Range, while the ancestors of the knob-tailed geckos evolved in the more xeric, sandy areas of the interior. *Nephrurus milii* has probably achieved its huge range only since the Late Miocene, when a coastal route around the western side of Australia would have been possible. Inland spread is probably still more recent and may have followed the drying of the lake systems. The isolated records of *N. milii* in Northern Territory, Australia may represent an introduction, or may be the result of a successful invasion via rocky corridors to the McDonnell Ranges.

Following the appearance of those characters shared by the knob-tailed group (Node 4), such as spinose subdigital scales and the knob itself, *Nephrurus* evolved into two lineages on either side of the central Australian continental lake system: a northern lineage, resulting in *N. asper* in the Northern Territory and Queensland and *N. wheeleri* in Western Australia, and a southern lineage, the smooth knob-tails. Subsequent to the drying of the lake system since the Miocene, *Nephrurus* has invaded the entire arid region and has undergone species specific habitat specialization (Pianka 1972).

In eastern Australia the division of the *Phyllurus* and *Carphodactylus* lineages is obscure, but habitat barriers of savannah vegetation have existed in coastal Queensland at least since the Pleistocene (Kikkawa et al. 1981) and remnants of the continental lake system in northern Queensland may have been responsible for the division of these groups. Today *Carphodactylus* is found only in the region of the Atherton Tablelands. *Phyllurus* occurs from northern Queensland south to the sandstone area of the Sydney—Hawkesbury drainage. It is possible that a smaller, southern rupicolous form *(P. platurus)* and a larger, northern arboreal form *(P. cornutus)* have each given rise to a sister species with different habitat preferences. Separation of populations leading to speciation may have been a recent result of rising post-Pleistocene sea levels, and it continues as rainforest fragmentation separates populations of the arboreal forms, particularly *P. cornutus*.

Parts of Tasmania remained submerged for most of the early part of the Tertiary. If Tasmania was not colonized by geckos before the Early Miocene, when Australia moved into its present latitude, it is likely that colder Bassian climates and occasional ocean barriers would have prevented subsequent movement into this region. Thus, no geckos are present in Tasmania today.

In New Zealand, the initiation of movement along the Alpine Fault some 50 mybp isolated the two groups of padded carphodactyline geckos. Both groups primitively had the features of a pigmented mouth, tongue and peritoneum, ovoviviparity, and tail prehensility. In the Pacific Plate region (Torlesse terrane and others) of New Zealand, a prior (unknown) event was associated with the division of the ancestral *Naultinus* stock from the ancestral *Hoplodactylus* (sensu lato) that had probably spread northward prior to the opening of the Tasman. From the Paleocene through the Miocene, the two portions of New Zealand were variably emergent, but were not close.

Within the southern terranes, Oligocene ingressions probably greatly reduced the available land area. Not until the Pliocene Kaikoura Orogeny did the present rugged topography of the region appear. Associated with these movements, *Hoplodactylus granulatus* was probably isolated in the Kaikouras themselves, and eventually evolved into the modern sub-alpine species *H. kahutarae*. At the same time, or perhaps earlier, a similar event in the far south led to the eventual evolution of *Hoplodactylus rakiurae* on Stewart Island. Until the early Pleistocene, the ancestors of modern *Naultinus* remained in the South Island where they evolved diurnality, perhaps in association with the low temperatures of the region and the absence of predators and competitors. With the Kaikoura Orogeny and the Pleistocene glaciations, the range of *Naultinus* became fragmented, and this led to their present degree of differentiation. In the north geckos similar to *N. manukanus* invaded the North Island where they successfully established very recently. In the northern South Island, the retreat of the glaciers opened up corridors between formerly isolated populations that had become behaviorally, and somewhat morphologically distinct. In some regions in Nelson, rather distinct forms occur in near sympatry.

Following their isolation from narrow-padded forms in the Paleocene, the ancestors of the broad-padded *Hoplodactylus* had spread northward into New Caledonia before the onset of peak Oligocene ingressions. Northland, which has a long emergent history, may have been the site of early divergence within the broad-padded *Hoplodactylus. Hoplodactylus pacificus* is currently limited to the North Island north of the line of an early Miocene seaway from Taranaki to Hawkes Bay. On the other hand, *H. maculatus* is distributed throughout New Zealand and, like *H. granulatus*, may have invaded the other island during the latest Tertiary or Quaternary. *Hoplodactylus chrysosireticus, H. stephensi* and probably *H. delcourti* have (or had) restricted ranges and at least the former two may be relatively recent derivatives of ancestors shared with *H. maculatus* or *H. pacificus. Hoplodactylus chrysosireticus* may have been isolated in Taranaki by the rising of Mt. Egmont (G.R. Stevens 1980b) subsequently arriving on Mana Island and in the northwest coastal islands via dispersal in the very recent past; alternatively, it may have once enjoyed a wider range, disrupted by the Taranaki vulcanism and the rising post-Pleistocene sea levels. The origin of *H. stephensi* is problematical, as is the origin of certain other Stephens Island endemics, but probably relatively recent.

*Hoplodactylus duvaucelii* once had a much wider range than it has today; it was widespread on the mainland in pre-human times (Worthy 1987). Today, along with the tuatara and the skinks *Cyclodina macgregori* and *C. whitakeri*, it is limited in its distribution to the northern offshore islands of New Zealand and the islands of Cook Strait. The extermination of these species on the mainland, and the extinction of *Hoplodactylus delcourti* is related to the simultaneous arrival of man and the kiore *(Rattus exulans)*. Large, nocturnal reptiles are particularly vulnerable to rats (Thomas 1982a; Whitaker 1973, 1978) and *H. duvaucelii*, for example, occurs on rat inhabited islands only in rocky cliff areas. Its present distribution on islands is also limited by island size and habitat diversity (Towns & Robb 1986; Towns et al. 1985).

The carphodactylines of New Caledonia may have arrived in that region even before the opening of the Tasman Sea, but certainly no later than the Oligocene. A time prior to the sinking of the Lord Howe Rise (65 mybp) seems likely. In many ways *Bavayia* resembles the smaller North Island species of *Hoplodactylus* except for the presence of divided subdigital scansors and a subcaudal scansorial pad. *Bavayia* also differs from the New Zealand species in that it is oviparous rather than viviparous. No vicariant event appears to account for the division of the species complexes of *Bavayia* in New Caledonia. Both groups probably invaded the Loyalty Islands in the Quaternary. It is possible that *B. sauvagii* was established first on Maré, which has risen the greatest amount and was the first of the islands to rise. A subsequent *B. cyclura/B. crassicollis* dispersal event (or events) may have resulted in the population of all three islands by this form. *Bavayia sauvagii* may be habitat-limited or may be unable to compete with its larger congeners in the simpler habitats of Lifou and Ouvéa.

*Eurydactylodes* and *Rhacodactylus* are among the most bizarre of living geckos. Both genera are associated largely with regions of ultrabasic rocks resulting from the Eocene overthrusting of peridotite sheets (Dubois et al. 1973; Avias 1973). These rocks have greatly affected the evolution of the highly endemic flora of New Caledonia (Guillaumin 1921, 1964; Virot 1956; Schmid 1981; Morat et al. 1986; Jaffré et al. 1987). These two gekkonid genera may have evolved in the late Eocene or slightly later in association with the edaphic plants of the ultramafic formations and their associated arthropods.

*Eurydactylodes* occurs in association with scrub vegetation in areas of both high and low rainfall. *Rhacodactylus* is primarily found in very wet areas. Both genera occur in southern, central and northeastern New Caledonia. No records exist from the northwestern parts of New Caledonia or from non-ultramafic areas, although there are indications that *R. leachianus* once occurred in the Belep Islands in the far north, but even these are covered in peridotite sheets. Distributions of individual species are discussed in the species accounts. *Rhacodactylus auriculatus* and *R. sarasinorum* are found only in association with the southern third of New Caledonia, the area of the largest single mass of ultrabasics in the territory. Most of the other species are found chiefly in the central region of the island or in coastal forest regions of the northeast.

The species of the subgenus *Pseudothecadactylus* are highly modified *Rhacodactylus* distributed in three isolated populations in northern Australia. If the phylogenetic and geological hypotheses are accepted, it is inconceivable that these species were in Australia before the opening of the Tasman Sea. Despite the low vagility of carphodactylines (Bauer 1989a), it appears necessary to evoke a dispersal event for the arrival of *Pseudothecadactylus* in Australia. The PAUP analysis suggested that these animals were most closely related to *R. trachyrhynchus* and *R. sarasinorum*, to which they bear some general resemblance. Cogger & Heatwole (1981) suggested that a tropical dispersal route linked northeastern Queensland with Arnhem Land along the Gulf of Carpentaria or further north during a period of marine regression. They also indicated that additional corridors led to the Kimberleys in Western Australia and suggested that the distribution of *Pseudothecadactylus* and the *Carlia fusca* complex might be explained by such a series of pathways. Pleistocene sea level drops also exposed several large areas between Australia and New Caledonia, including the Queensland Plateau and the Chesterfield Reefs (Holloway 1979; Gibbons 1985). It is unclear, however, whether this route across the Coral Sea would account for the extremely limited range of *Rhacodactylus australis* in Queensland today. Although the minor differences between *R. lindneri* and *R. cavaticus* are consistent with Pleistocene divergence, the large morphological gaps between *R. australis* and the more western species are difficult to reconcile with a Pleistocene arrival in Australia. It seems most probable that the ancestor of *R. australis* arrived over water from New Caledonia sometime in the late Tertiary and that habitat restrictions limited it from passing into New Guinea, which would have been connected by land to Queensland at the same time. Evolution of the *Rhacodactylus lindneri-cavaticus* form must have occurred shortly thereafter. The subsequent division of these species may have occurred as a result of migration over an Arafura Land bridge during periods of glaciation, with subsequent independent evolution following marine ingressions in the post-Pleistocene. However, Cracraft (1986) proposed climatic ecological factors as the likely cause of the separation of the avifauna of Arnhem Land and the Kimberley Plateau. He also suggested that the arid region at the head of the Gulf of Carpentaria may have served to divide the biotas of Arnhem Land and the Cape York Peninsula. Either interpretation is consistent with the congruent patterns of species-area relationships in these three regions.

The absence of carphodactylines elsewhere in the southwest Pacific seems related largely to the low vagility of the species. Norfolk island and Lord Howe Island, which have been emergent only since the late Tertiary, and would have had to be colonized over water therefore lack these geckos.

The corroboration of the phylogenetic hypothesis by geological data in no way "proves" that the phylogeny is correct (Arnold 1981), but is does support its robustness by independent evidence. Further resolution within *Hoplodactylus* and an ecological analysis of *Rhacodactylus* may allow a far more detailed comparison with paleogeography. It may also further strengthen and confirm or improve parts of the preceding scenario. Analysis by karyological and immunological methods would also provide an independent test of the phylogenetic hypothesis and perhaps suggest particular dates of divergence for comparison with supposed vicariant events. The discovery of fossil material from New Caledonia or New Zealand would also do much to bolster the scenario, but unfortunately only Pleistocene and recent material are currently available.

## CARPHODACTYLINE SPECIES ACCOUNTS

The following accounts present diagnoses and complete synonymies for all genera and species of carphodactyline geckos. The nomenclature employed is consistent with the preceding phylogenetic analysis in that only convex (sensu Meacham & Duncan 1987) genera are recognized. Species epithets follow the spelling of the original descriptions.

All known published variants of names are included in the synonymies. Names appear more than once in a synonymy when an existing name, after a period of disuse, was employed again at a later date. Thus the synonymies reflect the complete history of the nomenclature of each taxon. Popular and semi-popular works are also included in some cases. For example, the works of Cogger (1975b, 1979, 1983, 1986) are the general references for the use of names of Australian reptiles and have as much, if not more, widespread influence than technical works dealing with the systematics of particular groups of taxa. Name changes proposed by Wells & Wellington (1984, 1985a, 1985b) are considered invalid and unsupported (see Thulborn 1986) and suppression of these works has been proposed (Anonymous 1987; Shea 1987). They are therefore excluded from the synonyms.

Keys are provided to the genera and species (see each generic account) of the Carphodactylini. A variety of keys is available for species of genera in the tribe. These include Roux (1913) and Sadlier (1989) for New Caledonian species, McCann (1955), Towns (1985), and Gill (1986) for New Zealand species, and Cogger (1986), Storr (1963), and Covacevich (1975) for Australian carphodactylines. Boulenger (1885a) provided keys for the species known to him. Although exsting keys are sufficient for some genera (e.g. *Rhacodactylus*), many other keys require that determination be made from living specimens, adult males, original-tailed individuals or animals of known provenance; conditions that are not universally applicable. For this reason, new keys based on characters clearly visible on almost any museum specimen have been provided. In some circumstances the pre-existing keys should be consulted first since determination based on color or locality (if known) may be accomplished more rapidly. Members of the genus *Naultinus* as well as some *Nephrurus, Phyllurus* and *Hoplodactylus* may be particularly difficult to distinguish from one another.

A "Comments" section follows the synonymy and diagnosis of each species and genus. Because the biology of all carphodactylines is poorly known and the literature is scattered and often obscure, I present a summary of all known aspects of the biology of each taxon. All major references to size, distribution, taxonomy, ecology, behavior and reproduction are cited in these "Comments" sections. Unpublished accounts of the biology of some New Caledonian taxa gathered during this study are also included. Plotted distributions based on specimens examined and literature records are provided.

### Key to the genera of carphodactyline geckos

1a. Subdigital scansorial lamellae absent .......... 2
b. Subdigital scansorial lamellae present .......... 4
2a. Middorsal row of enlarged body scales, body compressed ..... *Carphodactylus*
b. No enlarged middorsal scale row, body depressed .......... 3
3a. Enlarged extra-brillar fringe, digits not kinked .......... *Nephrurus*
b. Extra-brillar fringes not enlarged, digits kinked .......... *Phyllurus*
4a. Lamellae divided .......... 5
b. Lamellae undivided .......... 6
5a. Digit I of manus clawless .......... *Rhacodactylus (Pseudothecadactylus)*
b. All digits clawed .......... *Bavayia*
6a. Penultimate phalanx of some digits partially subsumed in pad .......... 7
b. Penultimate phalanx of all digits free of pad .......... 8
7a. Body scales greatly enlarged, body compressed .......... *Eurydactylodes*
b. Body scales small and granular or tubercular, body depressed ... *Rhacodactylus*
8a. Dorsal scales of snout and body subequal, pupil margins crenelated *Hoplodactylus*
b. Dorsal scales of snout enlarged, pupil margins smooth .......... *Naultinus*

### *Bavayia* **Roux, 1913**

1913 *Bavayia* Roux. Nova Caledonia, Zoologie, I(II): 85.

Type species: *Peripia cyclura* Günther, 1872 by original designation.

1954 *Bavaya* Underwood. Proc.Zool.Soc.London 124: 471 (lapsus pro *Bavayia* Roux, 1913).

1983 *Bavaia* Rösler. Salamandra 19: 223 (ex errore pro *Bavayia* Roux, 1913).

Species referred: *Bavayia crassicollis* Roux, 1913, *B. cyclura* (Günther, 1872), *B. montana* Roux, 1913, *B. ornata* Roux, 1913, *B. sauvagii* (Boulenger, 1883), *B. septuiclavis* Sadlier, 1989, *B. validiclavis* Sadlier, 1989.

Diagnosis: A monophyletic genus diagnosed by the following characters: second epibranchial long and recurved, nearly contacting ceratobranchial; coracoid process of interclavicle posteriorly placed; digits scansorial, broadly dilated; scansors divided; assymmetrical terminal scansors on digit one; first infralabials (sometimes) contact behind mental; webbing between digits II-III-IV; tail relatively short, sub-cylindrical with subcaudal scansors (**15**, 20*, 39, 74, 80).

Comments: Because of the superficial resemblance of these geckos to certain gekkonine genera, the special status of this endemic New Caledonian group was not recognized until Roux's (1913) review of the New Caledonian herpetofauna. Roux (1913) recognized a number of subspecies but these do not correspond exactly to the distinct (species level) populations now recognized (Sadlier 1989). In this paper *Bavayia* was reduced to two species complexes in the phylogenetic analysis, *B. sauvagii* (also incorporating *B. ornata*), *B. cyclura* (incorporating the remaining taxa). The key provided by Roux (1913) is sufficient to differentiate the two species complexes. Sadlier (1989) provides a key to species. A thorough revision of the genus is needed. *Bavayia* occurs throughout New Caledonia and the Loyalty Islands. It is probable that the Belep Isles and other smaller islands also support one or more species. These are by far the most widely distributed and ecologically generalized of the New Caledonian geckos. Forest habitats in New Caledonia represent one of the only cases in which co-occurring diplodactylines (*Bavayia* spp.) occur in greater density than sympatric gekkonines *(Nactus pelagicus)* to a significant degree. Typically throughout Australia the gekkonines *Heteronota binoei, Phyllodactylus (= Christinus) marmoratus* and *Gehyra* spp. rival or outnumber diplodactyline species.

### Key to the Species of *Bavayia*

1a. Claw of thumb situated between the halves of cleft terminal scansor ........ 2
b. Claw of thumb situated medial to a single terminal scansor ................. 6
2a. Dorsal pattern with pale, broad vertebral stripe .......................... 3
b. Dorsal pattern composed of pale, transversely oriented blotches ............. 4
3a. Preanal pores in two rows; supranasals generally separated by a single internasal scale .............................................. *B. validiclavis*
b. Preanal pores in a single row; internasal region fragmented ...... *B. septuiclavis*
4a. First pair of infralabials usually contacting medially ............. *B. montana*
b. First pair of infralabials usually separated ............................... 5
5a. Distinct, bold, dark transverse bands bordering pale dorsal blotches . *B. cyclura*
b. Pale, dorsal blotches and dark bands obscure and poorly defined . *B. crassicollis*
6a. Lateral surface of hindlimb with distinct, contrasting pale spots on a dark background .................................................... *B. ornata*
b. Lateral surface of hindlimb without pale spots, or spots indistinct .. *B. sauvagii*

**_Bavayia crassicollis_ Roux, 1913**

1913 *Bavayia cyclura crassicollis* Roux. Nova Caledonia, Zoologie I(II): 89.
Type locality: (hoc loco restricta — Kramer 1979) Maré, Iles Loyalty.
Lectotype: NMBA 6931 (designated by Kramer 1979).
1954 *Bavayia cyclura crassicollis* Underwood. Proc.Zool.Soc. London 124: 477.
1989 *Bavayia crassicollis* Sadlier. Rec.Aust.Mus. 40: 366.

Diagnosis: Terminal scansor of digit I cleft; first infralabials generally separated from one another; more than one row of preanal pores in males, fewer than 20 pores in anterior row; pygal region of tail abruptly decreases in diameter at post-pygal border; dorsum with poorly defined blotches, no vertebral stripe; venter often yellowish in life.

Comments: *Bavayia crassicollis* was first described as a subspecies of *B. cyclura* by Roux (1913) who considered it restricted to the Loyalty Islands. The species as presently conceived (Sadlier 1989) occurs both in the Loyalties and the New Caledonian mainland. It has also been taken of several smaller offshore islands, including the Ilot de Hienghéne, a tiny coralline satellite.

In most respects the biology of *B. crassicollis* appears to be similar to that of *B. cyclura*, although the former is somewhat larger (maximum 86 mm SVL — AMS R78349). The species has been found in association with dead trees, bark and mangrove vegetation. It occupies one of the widest ranges of any *Bavayia* species and seems to have a broad tolerance of habitat types.

**_Bavayia cyclura_ (Günther, 1872) (Fig. 21)**

1869 *Platydactylus pacificus* Bavay. Mém.Soc.Linn.Normandie 15: 8 (nec Gray, 1842).

1872 *Peripia cyclura* Günther. Ann.Mag.Nat.Hist. (4)10: 422.
Type locality: New Caledonia.
Syntypes: BMNH 71.4.16.30 (A—B), 71.4.16.31 (A—C). (71.4.16.31 (A—C) are *B. sauvagii*).
1873 *Lepidodactylus neocaledonicus* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 4: 206.
Type locality: Nouvelle Calédonie.
Syntypes: MLI (specimen number unknown) destroyed by fire.
1878 *Hemidactylus (Peripia) bavayi* Sauvage. Bull.Soc.Philomat., Paris (7)3: 71.
Type locality: Nouvelle-Calédonie.
Syntypes: MNHN 5311-2. (5312 is a *B. sauvagii*).
1883 *Lepidodactylus cyclurus* Boulenger. Proc.Zool.Soc. London 1883: 121; pl. XXII (fig. 4).
1913 *Bavayia cyclura* Roux. Nova Caledonia, Zoologie I(II): 88.
1932 *Bavayia cyclura cyclura* Burt & Burt. Bull.Amer.Mus.Nat.Hist. 63: 497.
1965 *Bavayia cyclura* Wermuth. Das Tierreich 80: 9.

Diagnosis: Terminal scansor of digit I cleft; first infralabials generally separated from one another; preanal pores of males in more than one row, fewer than 20 pores in anterior row; pygal region of tail abruptly decreases in diameter at post-pygal border; dorsum generally without vertebral stripe; venter yellowish in life.

Fig.21: a. Syntype of *Peripia cyclura* Günther, 1872 (= *Bavayia cyclura*). BMNH 71.4.16.30B. b. Syntype of *Hemidactylus (Peripia) bavayi* Sauvage, 1878 (= *Bavayia cyclura*). MNHN 5312. This specimen is referable to *Bavayia sauvagii*. c. Holotype of *Lepidodactylus sauvagii* Boulenger, 1883 (= *Bavayia sauvagii*). MNHN 5790. Although the type description matches the species associated with this name, the holotype is referable to the species now regarded as *Bavayia cyclura*. (Photos courtesy of Ross Sadlier, The Australian Museum)

Comments: *Bavayia cyclura* was first noted by Bavay (1869) as *Platydactylus pacificus*. Günther's (1872) description is inadequate to differentiate *cyclura* from other species and probably inadequate to identify the genus. The species is known from all areas of New Caledonia as well as the three Loyalty Islands and the Isle of Pines (Fig. 22). (Pending a thorough review of the *B. cyclura* complex *(B. crassicollis, B. cyclura, B. montana, B. septuiclavis)* no distinction between taxa is made on the distribution map).

Bavay (1869) found the species common throughout New Caledonia except in association with houses. He stated that 15—20 could be found under bark associated with small grey scorpions. Roux (1913) stated that *B. cyclura* could be found under bark or in rotten wood. I have collected this species in houses and under debris (rarely) and in rotten trees and stumps as well as under bark. The species is more common than most of its congeners in drier parts of the island, e.g. the west coast and at middle elevations. In natural situations it is almost invariably associated with dead wood. These geckos apparently spend daylight hours under bark and emerge after sunset to forage on the ground and on tree trunks. This species is of moderate size, the largest specimen

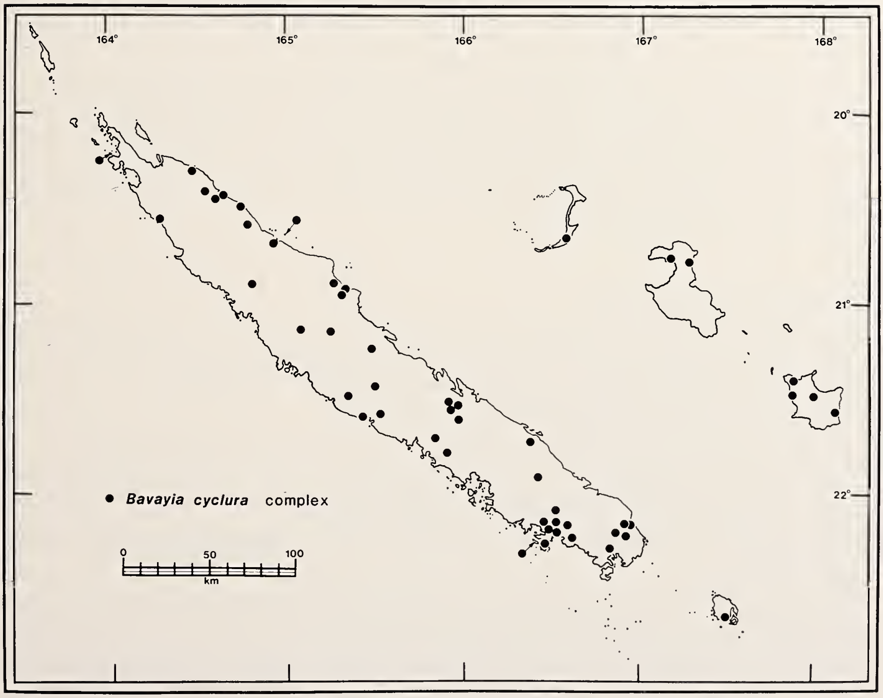

Fig.22: Distribution of the *Bavayia cyclura* complex in New Caledonia and the Loyalty Islands.

reaching 72 mm SVL (Bauer & Vindum, in press). Natural diet appears to consist chiefly of arthropods (Bauer & DeVaney 1987). Members of the *B. cyclura* complex display greater aggressive behavior than those of the *sauvagii* group and frequently bite when captured. The two eggs are relatively large and breeding apparently takes place, at least in the range as a whole, all year. This species may be found in association with *Rhacodactylus* in tree holes (Meier 1979). Russell (1972, 1979a) has examined the foot morphology of members of the *B. cyclura* complex.

### *Bavayia montana* Roux, 1913

1913 *Bavayia cyclura montana* Roux. Nova Caledonia, Zoologie I(II): 88.
Type locality: (hoc loco restricta — Kramer 1979) Mount Ignambi, 700-800 m, Nouvelle-Calédonie.
Lectotype: NMBA 6954 (designated by Kramer 1979).
1989 *Bavayia montana*. Sadlier. Rec.Aust.Mus. 40: 366.

Diagnosis: Terminal scansor of digit I cleft; first infralabials generally contact one another medially; preanal pores in males in more than one row, typically 20 or more pores in anterior row; pygal region of tail abruptly decreases in diameter at post-pygal border; dorsum generally dark with transverse blotches, no vertebral stripe; venter yellowish in life.

Comments: *Bavayia montana* is restricted to the mountains of the east coast chain of New Caledonia (Roux 1913). This species is relatively large (maximum 76 mm SVL — NMBA 6942) and thick bodied. It prefers more mesic environments than most of its congeners and has been found in tree fern fronds and on *Pandanus* (Roux 1913) as well as under moist rotten logs and within rotted tree stumps. Although it occurs at elevations of up to 930 m, it has also been collected at 80 m on Mt. Koyaboa, near Poindimié, just upslope from *B. sauvagii*.

### *Bavayia ornata* Roux, 1913

1913 *Bavayia sauvagei ornata* Roux. Nova Caledonia, Zoologie I(II): 92; pl. IV (fig. 3).
Type locality: Forêt du Mont Panié, altit. 500 m, Nouvelle-Calédonie.
Lectotype: NMBA 7025 (designated by Kramer 1979).
1989 *Bavayia ornata*. Sadlier. Rec.Aust.Mus. 40: 366.

Diagnosis: Terminal scansor of digit single, medial; cloacal spurs in males rounded; pygal region of tail tapers into post-pygal; preanal pores in male, in a single transverse row; lateral surface of hindlimbs with distinct pale spots; venter whitish in life. (75, **102**).

Comments: This species appears to be restricted in distribution to the lower slopes of Mt. Panié in northeastern New Caledonia (Fig. 23). This relatively small (maximum 69 mm SVL — NMBA 7023) species is extremely gracile and is found in closed forest (Sadlier 1989) beneath bark or in rotten stumps. Nothing is known of the biology of *B. ornata*.

***Bavayia sauvagii* (Boulenger, 1883) (Fig. 21)**

1878 *Hemidactylus cyclura* Sauvage. Bull.Soc.Philomat., Paris (7)3: 72 (nec Günther, 1872).

1883 *Lepidodactylus sauvagii* Boulenger. Proc.Zool.Soc. London 1883: 122; pl. XXII (figs. 5,5a).

Type locality: New Caledonia.

Holotype: MNHN 5790. (The type description is clearly that of the species now recognized as *Bavayia sauvagii*, however, the specimen now labeled as the holotype itself is conspecific with *B. cyclura*).

1913 *Bavayia sauvagei* Roux. Nova Caledonia, Zoologie I(II): 91; pl. IV (figs. 2,2a) (nomen emendatum pro *Bavayia sauvagii* Boulenger, 1883).

1932 *Bavayia sauvagii sauvagii* Burt & Burt. Bull.Amer.Mus.Nat.Hist. 63: 497.

1954 *Bavaya sauvagei* Underwood. Proc.Zool.Soc. London 124: 477.

1965 *Bavayia sauvagii* Wermuth. Das Tierreich 80: 9.

Diagnosis: Terminal scansor of digit I single, medial; cloacal spurs in males somewhat pointed; pygal region of tail tapers into post-pygal; preanal pores in a single transverse row; lateral surface of hindlimbs without distinct pale spots; venter whitish in life. (75, **102**).

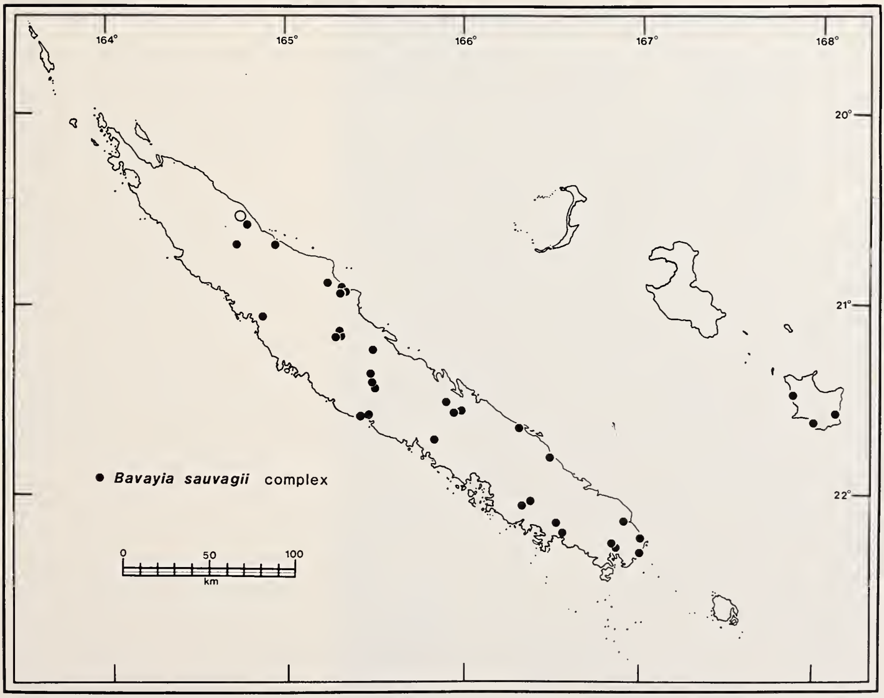

Fig.23: Distribution of the *Bavayia sauvagii* complex in New Caledonia and the Loyalty Islands. *B. sauvagii* (closed circles), *B. ornata* (open circles).

Comments: This species was not initially recognized as being distinct from *Bavayia cyclura*. Perhaps because of the partial division of some distal scansors, Sauvage (1878) placed this form in the genus *Hemidactylus*, although he believed that he was examining *B. cyclura*. The range of the species as a whole encompasses the whole of the mainland (except for the far north), and Maré (Fig. 23). It is likely that this species is also present on the Isle of Pines and perhaps on the other Loyalty Islands and in northern New Caledonia. Alternatively, the species may be restricted in its distribution by low rainfall and unsuitable cover in the aforementioned areas.

Roux found *B. sauvagii* under rocks and logs in forested areas. I have collected it primarily under rocks by day in areas of high to very high rainfall (Bauer & DeVaney 1987) (Fig. 24). At night these geckos may be found climbing on the trunks of saplings and smaller trees. *Bavayia sauvagii* appears to be partially active under stones all day, although peak activity is several hours after sunset. At Poindimié this small species (maximum 62 mm SVL — CAS 162184) may be found in association with a variety of terrestrial lizards — *Nactus pelagicus, Marmorosphax tricolor, Nannoscincus mariae, N. gracilis* as well as with scorpions and large millipedes. Two or three individuals may be found under a single stone. These animals frequently occupy crevices in loose rock banks. At Mt. Koyaboa this species occurs only at lower elevations (<50 m). *Bavayia*

Fig.24: Typical secondary forest habitat of *Bavayia sauvagii* at low elevation on Mt. Koyaboa, Poindimié, New Caledonia.

*montana* is found in low numbers above 80 m on the same slopes. Like *B. cyclura*, this species apparently breeds all year long. The diet is varied and consists chiefly of arthropods, particularly crickets and isopods. Ants, though very abundant are only rarely taken (Bauer & DeVaney 1987). Remains of *Bavayia sauvagii* have been found in the stomach of *Rhacodactylus auriculatus.*

### *Bavayia septuiclavis* Sadlier, 1989

1989 *Bavayia septuiclavis* Sadlier. Rec.Aust.Mus. 40: 367.

Type locality: 4 km along Mt. Gouemba road from turnoff on Yate-Goro road (300—350 m), 22°09'S x 166°54'E, New Caledonia.

Holotype: AMS R78139.

Diagnosis: Terminal scansor of digit I cleft; scales of internasal region fragmented; infralabials generally separated from one another; preanal pores in males in a single row; pygal region of tail abruptly decreases in diameter at post-pygal border, tail slender; dorsum with a broad, light colored vertebral stripe.

Comments: *Bavayia septuiclavis* is known from only two localities in southern New Caledonia. It has similar habitat preferences to *B. sauvagii* and has been found sheltering under stones by day and active on tree trunks and branches by night (Sadlier 1989), Maximum 50 mm SVL (Sadlier 1989).

### *Bavayia validiclavis* Sadlier, 1989

1989 *Bavayia validiclavis* Sadlier. Rec.Aust.Mus. 40: 367.

Type locality: Mt. Panie (500—600 m), 20°33'S x 164°45'E, New Caledonia.

Holotype: AMS R77855.

Diagnosis: Terminal scansor of digit I cleft; supranasal scales generally separated by a single internasal; first infralabials generally separated from one another; preanal pores in males in more than one row; pygal region of tail abruptly decreased in diameter at post-pygal border; dorsum with a broad, light colored vertebral stripe.

Comments: *Bavayia validiclavis* is restricted to the northeastern mountains of mainland New Caledonia. This is the smallest species of the genus and the smallest carphodactyline with a maximum SVL of 45 mm (Sadlier 1989). Little is known of its biology but it appears to be similar to *B. sauvagii* and *B. septuiclavis* (Sadlier 1989).

## *Carphodactylus* Günther, 1897

1897 *Carphodactylus* Günther. Novit.Zool. 4: 403.

Type species: *Carphodactylus laevis* Günther, 1897 by monotypy.

Species referred: *Carphodactylus laevis* Günther, 1897.

Diagnosis: A monotypic taxon diagnosed by the following characters: Trunk vertebrae somewhat procoelous; two ribless cervical vertebrae; neural spines of trunk high — giving the body a compressed appearance; first autotomy septum in fifth caudal vertebra; coracoid process of interclavicle indistinct; anterior loreal scales minute; middorsal scales enlarged to form a low crest; preanal organs present but weakly developed; tail elongate, compressed, without spinose scales, terminating in a tiny knob; cloacal spurs bear a darkly pigmented spot; toes bear non-scansorial lamellae; extra-brillar fringes prominent; canthus prominent. (15, 48*, 58*, **68**, 97*).

Comments: This little-known monotypic genus was the last of the carphodactyline genera to be discovered. Kluge's (1967b) choice of the tribal name Carphodactylini derives from his belief that this genus exhibited the greatest number of primitive traits.

### *Carphodactylus laevis* Günther, 1897 (Fig. 25)

1897 *Carphodactylus laevis* Günther. Novit.Zool. 4: 403, pl.XI.
Type locality: Mt. Bartle Frere, Queensland.
Holotype: presumed lost (fide Cogger et al. 1983).

Diagnosis: As for genus.

Comments: Günther's (1897) description of *Carphodactylus laevis* is adequate and appears to describe an individual with a regenerated tail, since no mention of the caudal knob characteristic of original tails is made. Cogger (1986) reported a maximum SVL of 130 mm. The species is distributed within the area 15°49'—17°23'S by 145°17'—145°49'E, a small patch of coastal mountainous terrain running from about Tully north to Cooktown, Queensland (Fig. 26). This southern Cape York endemic occurs in rainforest areas and has been claimed to be both arboreal (Worrell 1963) and terrestrial (Loveridge 1934), although an intermediate ecology appears most likely (Cogger 1983; Wilson & Knowles 1988). *Carphodactylus laevis* is primarily insectivorous. This is the only Australian carphodactyline proposed for international protection (Ehmann & Cogger 1985), and Czechura & Covacevich (1985) considered it to be at indeterminate risk due to its patchy distribution within the range.

Fig.25: *Carphodactylus laevis* Günther, 1897 AMS R10838. SVL = 92 mm. (Scientific Photography Laboratory, U.C. Berkeley)

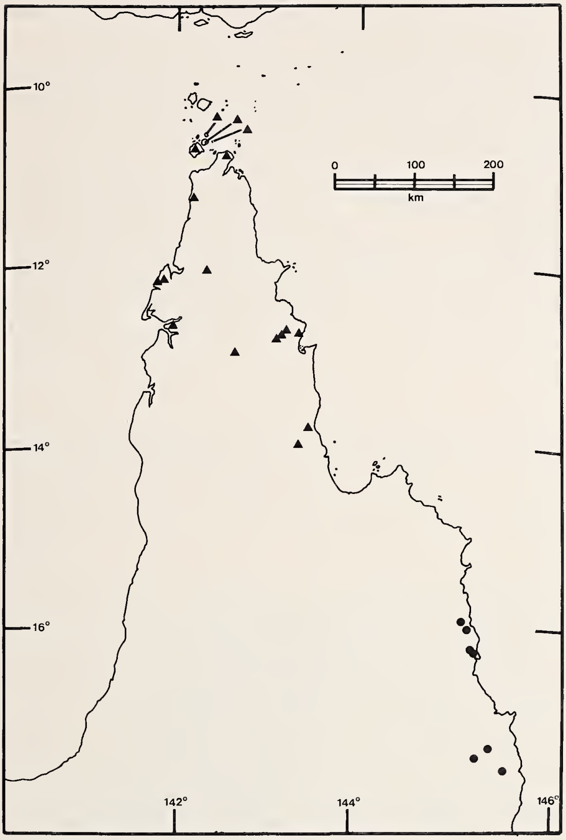

Fig.26: Distribution of *Rhacodactylus australis* (triangles) and *Carphodactylus laevis* (circles) in northern Queensland.

## *Eurydactylodes* Wermuth, 1965

1878 *Eurydactylus* Sauvage. Bull.Soc.Philomat., Paris (7)3: 70 (non *Eurydactylus* Laferte, 1851 = Coleoptera; non *Eurydactylus* Hagedorn, 1909 = Coleoptera).
Type species: *Platydactylus vieillardi* Bavay, 1869 by monotypy.
1883 *Eurydectylus* Boulenger. Proc.Zool.Soc. London 1883: 129. (error typographicus (in synonymy) pro *Eurydactylus* Sauvage, 1878).
1965 *Eurydactylodes* Wermuth. Das Tierreich 80: IX (nomen novum pro *Eurydactylus* Sauvage, 1878).

Species referred: *Eurydactylodes symmetricus* (Andersson, 1908); *E. vieillardi* (Bavay, 1869).

Diagnosis: (Node 17) A monophyletic taxon diagnosed by the following characters: Fewer than 30 scleral ossicles; neural spines of trunk vertebrae very high, giving body a compressed appearance; six or seven inscriptional ribs; dorsal body scalation heterogeneous, consisting of enlarged, smooth, flat scales; claw lies between two separate terminal scansors*; folds of loose skin on posterior face of hind limb; tail with subcaudal lamellae and ventral sulcus; slit from angle of mouth to ear*; endolymphatic sacs expanded extra-cranially*. (15, 22, 32-C, **74**, 90, **102**, 104, 105).

Comments: This small genus is among the least well known of the carphodactyline groups. Underwood (1954) initially placed this genus in the Gekkoninae but later (1955) moved it to the Diplodactylinae. *Eurydactylodes* is limited in its distribution to the main island of New Caledonia and appears to be fairly widely distributed except on the dry west coast of the island (Fig. 27). Both species may be locally abundant; the few specimens in collections probably reflect the difficulty in spotting these small cryptic geckos.

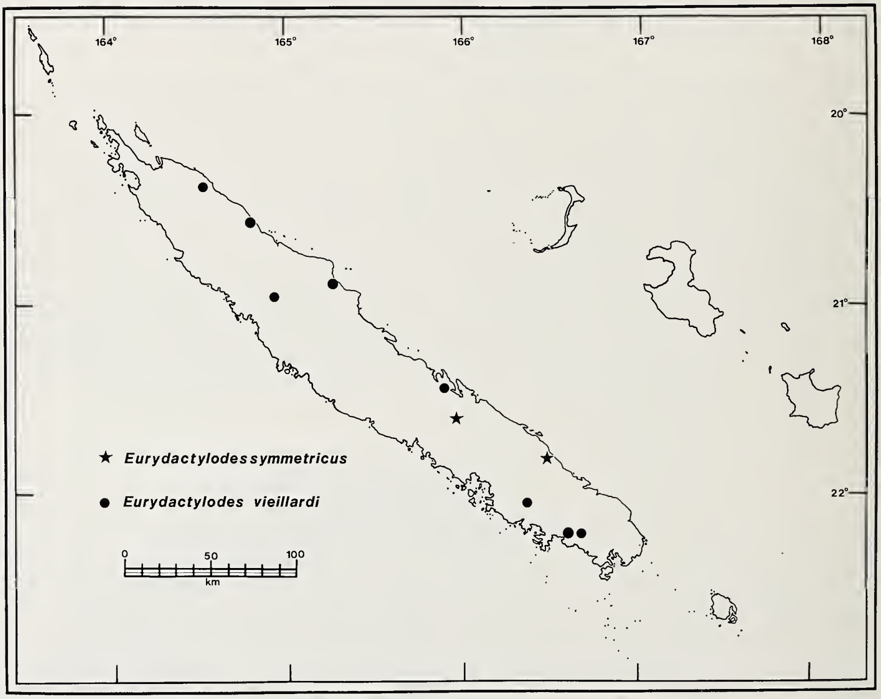

Fig.27: Distribution of *Eurydactylodes symmetricus* (stars) and *E. vieillardi* (circles) in New Caledonia.

## Key to the Species of *Eurydactylodes*

1a. Cruciform patch of raised, rounded scales on nape. Dorsal head scales enlarged, regularly arranged and generally in contact ..................... *E. symmetricus*
b. No raised scales on nape. Enlarged dorsal head scales usually irregularly arranged, separated by smaller interscales .................................... *E. vieillardi*

### *Eurydactylodes symmetricus* (Andersson, 1908) (Fig. 28)

1908 *Eurydactylus symmetricus* Andersson. Ark.Zool. 4(14): 1, fig. 1a-1d.
Type locality: New Caledonia.
Holotype: NHMG 651.
1965 *Eurydactylodes symmetricus* Wermuth. Das Tierreich 80: 30.

Diagnosis: Nape with cruciform patch of raised tubercles; head scales generally large; symmetrical without small interscales; slit from mouth to ear continuous.

Comments: Andersson's (1908) description is detailed, as is his re-diagnosis of the genus. However, the characters proposed by Andersson (1908) and Roux (1913) to separate this species from *E. vieillardi* are too variable to be reliable.

Fig.28: Holotype of *Eurydactylus symmetricus* Anderson, 1980 (= *Eurydactylodes symmetricus*). NHMG 651. Total length = 93 mm. (Photo courtesy of Ross Sadlier, The Australian Museum)

*Eurydactylodes symmetricus* reaches a SVL of 69 mm (Andersson 1908) and has been collected in forest at 200 m (Roux 1913) and 510 m altitude (MNHN 1985-123). Nothing is known of its biology.

### *Eurydactylodes vieillardi* (Bavay, 1869) (Fig. 29)

1869 *Platydactylus vieillardi* Bavay. Mém.Soc.Linn. Normandie 15: 10.
Type locality: Canala, Neu Kaledonien. (Type locality of Bavay (1869) = Houagape (= Wagap), Nouvelle-Calédonie).
Holotype: EMNB (specimen number unknown), presumed lost.
Neotype: ZFMK 46981, here designated.
1878 *Eurydactylus viellardi* Sauvage. Bull.Soc.Philomat., Paris (7)3: 70 (lapsus pro *Platydactylus vieillardi* Bavay, 1869).
1883 *Eurydectylus viellardi* Boulenger. Proc.Zool.Soc. London 1883: 129; pl. XXII (figs. 7,7a,7b) (error typographicus).
1885 *Eurydactylus vieillardi* Boulenger. Catalogue of Lizards in the British Museum vol.1: 192.
1932 *Eurydactylus viellardi* Burt & Burt. Bull.Amer.Mus.Nat.Hist. 63: 479.
1934 *Eurydactylus vieillardi* Brongersma. Zool.Meded. 17: 166.
1965 *Eurydactylodes vieillardi* Wermuth. Das Tierreich 80: 30.

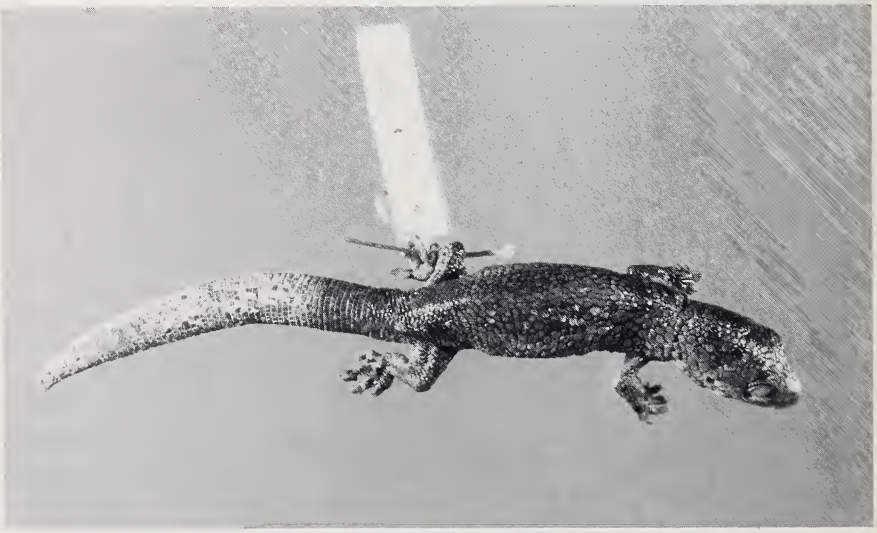

Fig.29: Neotype of *Eurydactylodes vieillardi* (Bavay, 1869). ZFMK 46981. (Photo courtesy of J. Schicke, Zoologisches Forschungsinstitut und Museum A. Koenig)

Fig.30: Carénage River, southern ultramafic region of New Caledonia. Typical peridotite habitat of *Eurydactylodes vieillardi* and *Rhacodactylus auriculatus*.

Diagnosis: Scales of nape similar those of dorsum; head scales irregular, separated by small interscales; slit from mouth to ear interrupted anterior to meatus.

Comments: The description of *Eurydactylodes vieillardi* (Bavay, 1869) is complete and sufficient to diagnose the genus.

Like its congener, this species is widely distributed in central and eastern New Caledonia (Figs. 27,30). It has been collected from the branches of bushes (Roux 1913; Meier 1979). Sauvage (1878) describes the eggs of this species, which appear to be among the largest in the family in relative size. Maximum adult SVL is 57 mm (MNHN 699-1863).

### *Hoplodactylus* Fitzinger, 1843

1842 *Naultinus* (part) Gray. Zool.Misc.: 58.
Type species: *Naultinus pacificus* Gray, 1842 by original designation.
1843 *Hoplodactylus* Fitzinger. Systema Reptilium: 100 (non *Hoplodactylus* Agassiz,

1845 = Echinodermata; non *Hoplodactylus* Chaudoir, 1878 = Coleoptera).
Type species: *Platydactylus duvaucelii* Duméril & Bibron, 1836 by original designation.
1845 *Pentadactylus* Gray. Catalogue of the Specimens of Lizards in the British Museum: 160.
Type species: *Platydactylus duvaucelii* Duméril & Bibron, 1836 by monotypy.
1867 *Dactylocnemis* Steindachner. Reptilien. Reise der Fregatte Novara: 11.
Type species: *Naultinus pacificus* Gray, 1842 by monotypy.
1901 *Woodworthia* Garman. Bull.Mus.Comp.Zool. 39: 4.
Type species: *Woodworthia digitata* Garman, 1901 by monotypy.
1913 *Woodwarthia* Roux. Nova Caledonia, Zoologie I(II): 86 (lapsus pro *Woodworthia* Garman, 1901).

Species referred: *Hoplodactylus chrysosireticus* Robb, 1980; *H. delcourti* Bauer & Russell, 1986; *H. duvaucelii* (Duméril & Bibron, 1836); *H. granulatus* (Gray, 1845); *H. kahutarae* Whitaker, 1985; *H. maculatus* (Gray, 1845); *H. pacificus* (Gray, 1842); *H. rakiurae* Thomas, 1981; *H. stephensi* Robb, 1980.

Diagnosis: This is a paraphyletic group and as such cannot be diagnosed. The species included in *Hoplodactylus* are those which share the characters present at Node 11 but none of those present at or above Node 14 (Fig. 18).

Comments: The history of the genus *Hoplodactylus* is intimately interwoven with that of *Naultinus*. The genus was erected by Fitzinger (1843) to accomodate *Platydactylus duvaucelii* Duméril & Bibron, 1836. Instability at the generic level has occurred in several instances. Steindachner (1867) erected *Dactylocnemis* to accommodate Gray's (non-diurnal) *Naultinus*, believing these forms to be substantially distinct from *Hoplodactylus duvaucelii*, at that time believed confined to Bengal. Garman (1901), apparently lacking comparative *Hoplodactylus* material, introduced another genus, *Woodworthia*. Smith (1933a) settled the generic synonomies which are accepted here, although Chrapliwy et al. (1961) detected the historical error in the application of the names *Hoplodactylus* and *Naultinus* and proposed the use of *Naultinus* solely for the New Zealand "brown" geckos. Myers (1961) successfully argued for the retention of the names as currently used.

There are nine species in the genus, many of which have been only recently described. These geckos are typically terrestrial or saxicolous, although some, especially *H. granulatus*, may be more arboreal. The genus is distributed throughout New Zealand and its offshore islands (Pickard & Towns 1988). It includes the most southerly gecko in the world, *H. rakiurae* (Thomas 1981) and the largest gecko in the world, *H. delcourti* (Bauer & Russell 1986). All species are ovoviviparous and typically give birth to two young at a time. Although primarily insectivorous, several species are known to eat fruits and seeds (Whitaker 1968, 1982, 1987; Barwick 1982). A number of detailed ecological studies have been performed on species of *Hoplodactylus* (Whitaker 1968, 1982; Barwick 1982). Hardy (1972) and Allison (1982) reviewed the extensive literature on the parasites of the genus. Millener (1981) recorded the presence of fossils from a number of sites in New Zealand, some of which have since been referred to *Hoplodactylus* (Worthy 1987).

## Key to the Species of *Hoplodactylus*

1a. Apical terminal scansors absent or present on all digits .................. 2
b. Apical terminal scansors on digit I only .................................. 3
2a. No apical scansors on digits (gray with faint transverse bars — Seaward Kaikouras) ........................................................ *H. kahutarae*
b. Apical scansors on all digits (harlequin pattern — Stewart Island) .. *H. rakiurae*
3a. Rostral contacts nostril ................................................ 4
b. Rostral excluded from nostril by anterior nasal ............................ 8
4a. Proximal portion of toe two or more times width of distal portion, penultimate phalanx strongly arched, clearly arising from within expanded pad ............. 5
b. Proximal portion of toe less than twice width of distal portion ............. 6
5a. 25 or more lamellae under fourth toe (longitudinally striped pattern — unknown locality) .................................................... *H. delcourti*
b. 20 or fewer lamellae under fourth toe (pattern of transverse chevrons, invariably with light markings on nape — offshore islands of the North Island and Cook Strait) ........................................................ *H. duvaucelii*
6a. Penultimate phalanx does not arise from within pad (pattern variable, invariably with a white mark between eye and ear) ........................ *H. granulatus*
b. Penultimate phalanx arises from within pad ................................ 7
7a*. Approx. 7 scale rows on free portion of digit IV of pes, 6—9 rows of preanal pores in males .................................................. *H. stephensi*
b. Approx. 12 scale rows on free portion of digit IV of pes, 1—4 rows of preanal pores in males .................................................. *H. pacificus*
8a.** Rostral 2 times broader than deep .......................... *H. maculatus*
b. Rostral 2.5—3 times broader than deep .................... *H. chrysosireticus*

* Striped specimens of *H. pacificus* are extremely difficult to distinguish from *H. stephensi*. Because the ranges of these two species are non-overlapping, locality, if known, should be accepted as supplemental evidence of identity.

** This species pair is even more difficult to distinguish than the previous as ranges overlap. Robb's (1980b) color description may be the only way to distinguish *H. chrysosireticus* from striped *H. maculatus* with certainty. I have seen too few specimens of the former animal to judge the validity of her pattern criteria.

### *Hoplodactylus chrysosireticus* Robb, 1980 (Fig. 31)

1980 *Hoplodactylus chrysosireticus* Robb. New Zealand Amphibians and Reptiles in Colour: 57; pl. 12 (upper left and middle).
1980 *Hoplodactylus chrysosireticus* Robb. Rec.Natl.Mus. New Zealand 1: 306; fig. 1A. Type locality: Taranaki, North Island, New Zealand).
Holotype: NMNZ R25.

Diagnosis: Digits broadly expanded, bearing scansors; terminal scansors present on digit one only; rostral excluded from nostril; rostral 2.5-3.0 times broader than deep; tail prehensile; mouth and tongue not distinctly pigmented; peritoneum black; dorsum bears a pattern of longitudinal stripes.

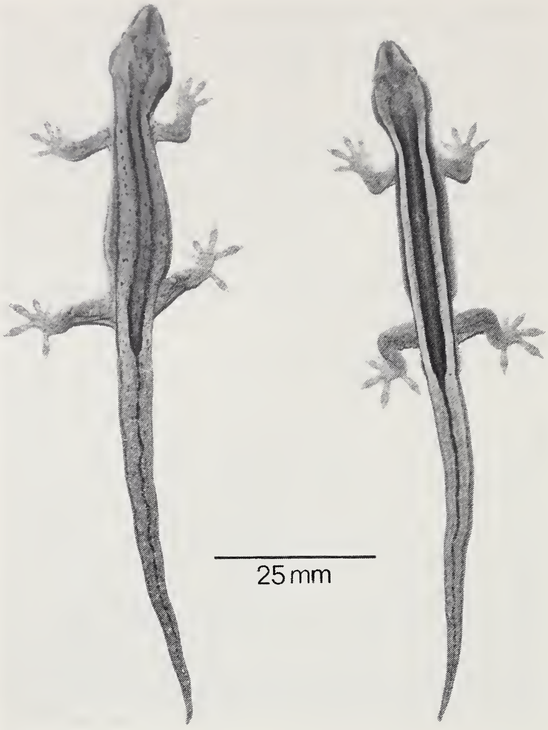

Fig.31: Two specimens of *Hoplodactylus chrysosireticus* Robb, 1980 showing variation in dorsal patterns. (Photo courtesy of B.W. Thomas)

Comments: *Hoplodactylus chrysosireticus* was only recently recognized as a taxon distinct from *H. pacificus*. Although morphological differences between the taxa are minor, they appear to be consistent and thus warrant separation.

Newman (1980) considered the names *Hoplodactylus chrysosireticus, H. stephensi* and *Heteropholis poecilochlorus* as used by Robb (1980a) as nomina nuda. McDowall (1981), however, correctly showed that the usage of the names in Robb constitute valid descriptions. This species is distributed in coastal and central Taranaki (North Island) from Waitara to just north of Paitea and Mana Island (near Titahi Bay). It has also reportedly been discovered several hundred kilometers to the north on Motupia Island (Pickard & Towns 1988, see Fig. 34) but this record may be false (A.H. Whitaker pers. comm.). It is primarily terrestrial and nocturnal, although it frequently basks during daylight hours (Wilkinson 1981). Robb (1980a) reported that it was associated with human structures and had not been found in native bush. It has also been found in *Kniphólia* and flax (Robb 1980b; Wilkinson 1981). Maximum size is 70 mm SVL (Robb 1980a). Diet consists of flies, moths, earwigs, spiders and woodlice (Robb 1980a; Wilkinson 1981). Like all *Hoplodactylus*, the species is viviparous. Mating takes place in April and young are born February—March (Wilkinson 1977; Rowlands 1981a). The species is listed in the New Zealand Red Data Book (Williams & Given 1981) as being of indeterminate status.

### *Hoplodactylus delcourti* Bauer & Russell, 1986 (Fig. 32)

1986 *Hoplodactylus delcourti* Bauer & Russell. New Zealand J.Zool. 13:(141).
Type locality: "possibly the North Island, New Zealand".
Holotype: MMNH 1985-38.
1988 *Hoplodactylus delcorti* Towns. A Field Guide to the Lizards of New Zealand: 6 (lapsus pro *Hoplodactylus delcourti* Bauer & Russell, 1986).

Diagnosis: Digits broadly dilated, scansorial; terminal scansors present on digit one only; rostral contacts nostril; proximal portion of toe approximately three times width of distal portion; penultimate phalanx strongly arcuate; 25 or more lamellae under fourth toe; body striped longitudinally; huge size.

Fig.32: Ventral and dorsal views of the Holotype of *Hoplodactylus delcourti* Bauer & Russell, 1986. MMNH 1985-38 (rule = 30 cm).

Comments: This species is known from a single, partial specimen. Its provenance is unknown, but it has been suggested that the specimen originated from Northland (Bauer & Russell 1986, 1987). The animal has been associated with the kawekaweau, a reptile of Maori legend (Bauer & Russell 1987). Russell & Bauer (1986) hypothesized that the biology of this species was probably similar to that of *H. duvaucelii* and Whitaker (1987) suggested that it may also have been a nectivore or frugivore. The single extant specimen has a SVL of 370 mm, making it by far the largest species of gekkonid ever to have lived. The species is probably extinct (Bauer & Russell 1986) but might still occur in rocky, forested regions in the northern North Island. Recent searches in the area have not located evidence for the continued existance of *H. delcourti* (Clark 1985).

### *Hoplodactylus duvaucelii* (Duméril & Bibron, 1836) (Fig. 33)

1836 *Platydactylus duvaucelii* Duméril & Bibron. Erpétologie Géneralé vol. 3: 312.
Type locality: Bengal (Terra typica designata — Smith 1933a: "Island of Hen and Chickens, east coast of the North Island of New Zealand").
Lectotype: MNHN 5977, here designated.
Paralectotypes: MNHN 6680-1; RMNH 2722.
1843 *Hoplodactylus duvaucelii* Fitzinger. Systema Reptilium: 19,100.
1856 *Platydactylus duvaucelii* Lichtenstein. Nomenclator Reptilium et Amphibiorum Musei Zoologici Berolinensis: 4.
1859 *Naultinus pacificus* Blyth. J.Asiatic Soc. Bengal 28: 279 (nec *Naultinus pacificus* Gray, 1842)
1864 *Pentadactylus duvaucelii* Günther. The Reptiles of British India: 118.
1885 *Hoplodactylus duvaucelii* Boulenger. Catalogue of Lizards in the British Museum, vol. 1: 172.
1897 *Hoplodactylus granulatus* (part) Lucas & Frost. Trans. New Zealand Inst. 1896 29: 265.
1902 *Hoplodactylus duvancellii* Schaefer. Arch. Naturgesch. 68: 35.
1954 *Rhacodactylus trachyrhynchus* Guibé. Catalogues des Types des Lézards: 16 (ex errore pro *Hoplodactylus duvaucelii* (Duméril & Bibron, 1836); non *Rhacodactylus trachyrhynchus* Bocage, 1873).
1954 *Hoplodactylus duvaucellii* (part) Hard. Tane 6: 143.

Fig.33: Lectotype of *Platydactylus duvaucelii* Duméril & Bibron, 1836 (= *Hoplodactylus duvaucelii*). MNHN 5977. (Photo courtesy of Muséum National d'Histoire Naturelle, Paris)

1955 *Hoplodactylus duvauceli* McCann. Dominion Mus.Bull. 17: 39; pl. 3 (figs. 1—7); fig. 3. (nomen emendatum pro *Hoplodactylus duvaucelii* (Duméril & Bibron, 1836)).
1956 *Hoplodactylus duvaucelii* Stephenson & Stephenson. Trans.Roy.Soc. New Zealand 84: 341; figs. 1B,C, 2B,C, 3B, 6A,D,E.
1961 *Naultinus duvauceli* Chrapliwy et al. Herpetologica 17: 7.
1961 *Hoplodactylus duvaucelii* Myers. Herpetologica 17: 171.
1966 *Hoplodactylus duvauceli* Sharell. The Tuatara, Lizards and Frogs of New Zealand: 49; pls. 28, 29, 30, 31.
1967 *Hoplodactylus duvaucelii* Kluge. Bull.Amer.Mus.Nat.Hist. 135: 25.
1970 *Hoplodactylus duvaucelii* Forster & Forster. Small Land Animals of New Zealand: 16; 2 figs. (p. 16).
1988 *Hoplodactylus duvaucelii* Bauer. New Zealand J.Zool. 14 (1987): 593.

Diagnosis: Supraocular portion of frontal deeply furrowed (in adults); juvenile color pattern with paravertebral longitudinal rows of light spots; cloacal spurs rounded, 1—5 in number; terminal scansors on digit one only; rostral contacts nostril; proximal portion of toe approximately three times width of distal portion; penultimate phalanx

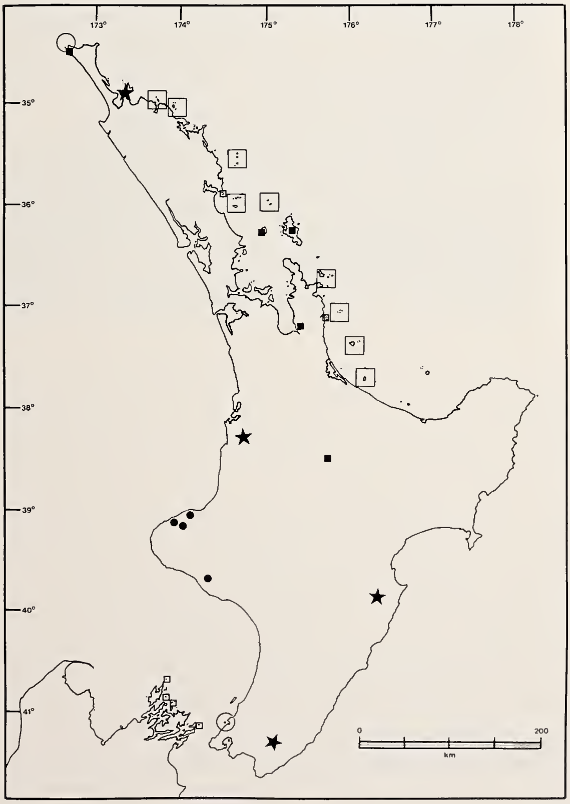

Fig.34: Distribution of *Hoplodactylus duvaucelii* (squares — modern localities, stars — subfossil sites) and *H. chrysosireticus* (closed circles) in northern New Zealand.

strongly arcuate; twenty or fewer lamellae under fourth toe; adult pattern of chevrons on dorsum. (5, 62, 95-A).

Comments: The history of the problem of the provenance of *H. duvaucellii* was reviewed by Smith (1933a, 1933b), Stephenson (1948) and Bauer (1988). The species currently has a disjunct range including most of the northern offshore islands (summaries of distribution by island group are provided by McCallum 1982a, Bauer 1986, Towns & Robb 1986, Pickard & Towns 1988) as well as the islands of Cook Strait — Brothers (McCann 1955; Barwick 1982), Chetwode Islands (Meads 1976; McCallum 1984) and Trios Island (Werner 1901; McCann 1955; Meads 1976) (Fig 34). McCann (1955) reports a single specimen from Stephen (= Stephens) Island, but *Hoplodactylus duvaucelii* is not currently present there. It is likely that this species was once more widely distributed on the mainland of the North Island. Recent subfossil material confirms this (Worthy 1987). There is also an old, but doubtful record from Cape Maria van Diemen (McCallum 1981). The current disjunct distribution pattern is shared by *Cyclodina whitakeri* and *C. macgregori* as well as the tuatara (Towns et al. 1985).

*Hoplodactylus duvaucelii* has a broad range of habitats and retreats (Whitaker 1968) and has been found under ground cover and debris (Werner & Whitaker 1978; Miller 1978), in flax (Whitaker 1968; Miller 1978), *Leptospermum* (Hard 1954; Towns 1971a), under the bark of *Meterosideros excelsa* (Hard 1954), in *Macropiper excelsum* (Hard 1954), on boulder beaches and cliffs (Porter 1982), and in forest fringe vegetation (Whitaker 1968). It has also been reported from the burrows of petrels (Whitaker 1968) and tuataras (McCann 1955; Forster & Forster 1970). Subfossil evidence, however, suggests that forested habitats were occupied by *H. duvaucelii* 3000—4000 ybp (Worthy 1987). Whitaker (1973, 1978) indicates that this species is particularly vulnerable to the effects of the introduced kiore *(Rattus exulans)* and, on islands with kiore, is usually only found in crevices on cliff faces (Fig. 35). It is generally rare or absent on islands of less than one hectare in area (Whitaker 1973; McCallum 1982b).

This is the largest living New Zealand gecko with a maximum SVL of 160 mm (Whitaker 1968). Specimens from the northern islands are generally larger than those from Cook Strait (Whitaker 1968; Barwick 1982). Animals in the Poor Knights generally became active about 30 minutes after sunset, reached peak activity at about 21:00 and began retiring by 3:30 (Whitaker 1968). The diet consists of flies, moths, grubs (Hard 1954), orthopterans, beetles (Porter 1981; Barwick 1982), small crustaceans, the fruit of kawakawa trees and pohutukawa, ngaio, and flax nectar (Whitaker 1968, 1987), a variety of plant parts and young *Hoplodactylus maculatus* (Barwick 1982). *Hoplodactylus duvaucelii* is known to forage on beaches down to the splash zone (Whitaker 1968). Both males and females on the Brothers (Cook Strait) become mature at about 95—100 mm SVL, or after about seven years (Barwick 1982). Breeding takes place in September or October and young are born between February and May (Rowlands 1981a). Whitaker's (1968) detailed ecological work demonstrated that individuals range widely and that population densities may reach 75—125/acre on Aorangi. Heavy mite infestations are common (McCann 1955; Whitaker 1968; Porter 1981; Allison 1982). Population dynamics and tail break data are discussed by Barwick

Fig.35: Typical rocky coastal cliff habitat of *Hoplodactylus duvaucelii* on Lady Alice Island, Hen and Chickens Group, Hauraki Gulf, New Zealand.

(1982) for the Brothers Islands populations of *H. duvaucelii*. McCann (1955) and Robb (1980a) discussed agressive behavior and possible family groups in the species. Protest calls of this gecko are discussed by McCann (1955).

### *Hoplodactylus granulatus* (Gray, 1845) (Fig. 36)

1843 *Naultinus pacificus* (part) Gray. Travels in New Zealand, vol. 2: 203.
1845 *Naultinus granulatus* Gray. Catalogue of the Specimens of Lizards in the Collection of the British Museum: 273.
Type locality: New Zealand.
Lectotype: BMNH 1946.8.22.71, here designated.
Paralectotypes: BMNH 1947.8.22.70, 1946.8.22.72, 1946.9.8.13.
1863 *Hoplodactylus (Naultinus) granulatus* Hochstetter. Neu-Seeland: 429.
1870 *Naultinus greyii* Knox. Trans. New Zealand Inst. 2: 20. (lapsus pro *Naultinus grayii* Bell, 1843; nec *Naultinus grayii* Bell, 1843).

1871 *Naultinus granulatus* Buller. Trans. New Zealand Inst. 3: 9.
1872 *Naultinus pacificus* (part) Hutton. Trans. New Zealand Inst. 4: 172.
1875 *Naultinus granulatus* Günther. The Zoology of the Voyage of H.M.S. Erebus and Terror, vol.2: 17.
1881 *Naultinus sylvestris* Buller. Trans. New Zealand Inst. 13: 419.
Type locality: Wooded country of the Wanganui District, North Island (New Zealand).
Holotype: not located.
1885 *Naultinus versicolor* Colenso. Trans. New Zealand Inst. 17: 149.
Type locality: Forests near Norsewood, County of Waipawa and Glenross, County of Hawke's Bay (New Zealand).
Syntypes: CMC ; NMNZ (specimens not located).
1885 *Naultinus elegans* (part) Boulenger. Catalogue of Lizards in the British Museum, vol.1: 169.
1885 *Naultinus silvestris* Boulenger. Ibid., vol. 1: 169 (ex errore in synonomy of *Naultinus elegans* Gray, 1842 pro *Naultinus sylvestris* Buller, 1881).
1885 *Hoplodactylus granulatus* Boulenger. Ibid., vol.1: 171; pl. XV (fig. 1).
1895 *Naultinus sylvestris* Buller. Trans. New Zealand Inst. 27: 93.
1904 *Dactylocnemis granulatus* Hutton & Drummond. The Animals of New Zealand: 439.
1904 *Hoplodactylus granulatus* Hutton. Index Faunae Novae Zelandiae: 39.
1905 *Naultinus sylvestris* Buller. Supplement to Birds of New Zealand: xx.
1919 *Dactylocnemis granulatus* Dore. New Zealand J.Sci. and Technol. (2)3: 164.
1929 *Naultinus elegans* (part) Martin. The New Zealand Nature Book: fig. 41 (p. 160).
1929 *Hoplodactylus granulatus* Martin. Ibid.: 162.
1936 *Haplodactylus granulatus* Falla. The Weekly News, 3 June, 1936: 57. (error typographicus pro *Hoplodactylus granulatus* (Gray, 1845)).
1948 *Hoplodactylus granulatus* Stephenson. Rec. Auckland Inst. and Mus. 3: 339.
1955 *Heteropholis nebulosus* McCann. Dominion Mus.Bull. 17: 69; pl. 7 (figs. 8—11).
Type locality: Cundy (= Kundy) Island, off (western coast of) Stewart Island (New Zealand (47°07'S, 167°33'E)).
Holotype: NMNZ R93.
1961 *Naultinus granulatus* Chrapliwy et al. Herpetologica 17: 7.
1961 *Naultinus grayi* Chrapliwy et al. Ibid.: 7. (lapsus pro *Naultinus greyii* (Knox, 1870); nec *Naultinus grayii* Bell, 1843).
1961 *Naultinus brevidactylus* Chrapliwy et al. Ibid.: 7. (nec *Naultinus brevidactylus* Grey, 1845).
1961 *Naultinus maculatus* Chrapliwy et al. Ibid.: 7. (ex errore).
1961 *Hoplodactylus granulatus* Myers. Herpetologica 17: 169.
1980 *Hoplodactylus nebulosus* Robb. New Zealand Amphibians and Reptiles in Colour: 60.

Diagnosis: 2—4 inscriptional ribs; apical scansors on digit one only; digits scansorial, narrow; rostral contacts nostril; penultimate phalanx not strongly arcuate; juvenile pattern as adult; white patch between eye and ear; tail without small scale rows at autotomy septa. (32-B).

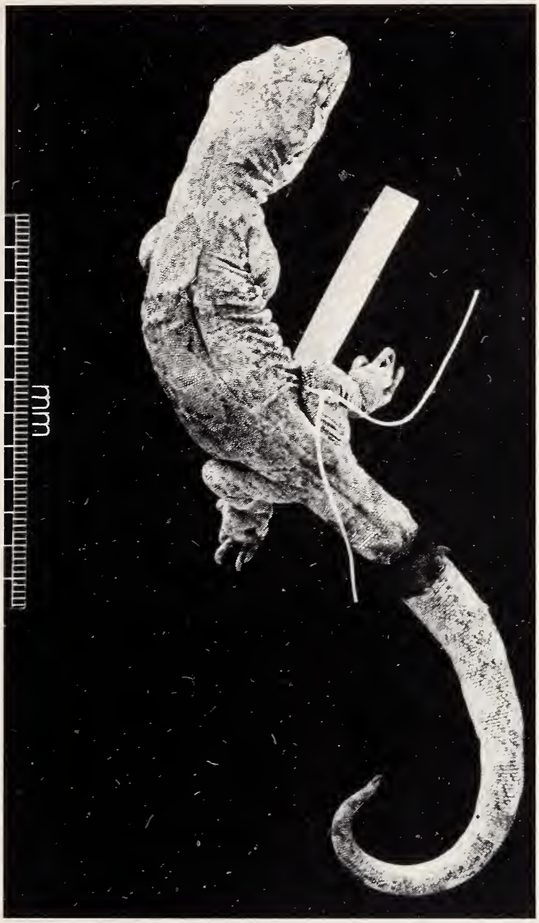

Fig.36: Lectotype of *Naultinus granulatus* Gray, 1845 (= *Hoplodactylus granulatus*). BMNH 1946.8.22.71. (Photo courtesy of British Museum (Natural History))

Comments: The taxonomic history of this species is the most confused for any in the tribe Carphodactylini. Fifteen different names or combinations have been used since the description of the species by Gray (1845). Thomas (1981), in synonymizing *Heteropholis nebulosus* with *Hoplodactylus granulatus*, presented a summary of the history of the former name and an exhaustive synonomy of the taxon. McCann (1955) explained some of the taxonomic problems of this taxon while creating additional ones himself. Despite its unique coloration, its more slender toes and tail, and generally *Naultinus*-like post-cranial morphology, many workers have doubted the distinctness of *H. granulatus* and relegated it to the synonomy of *H. pacificus*. Others (Buller 1881; Colenso 1885) were unaware that their new taxa had been described, albeit poorly, forty years earlier. It is unclear what prompted McCann (1955) to erect *Heteropholis nebulosus* for two Stewart Island specimens of *H. granulatus*.

The species is distributed throughout most of New Zealand, with the exception of the extreme north of the North Island and the south central South Island (Pickard & Towns 1988) (McCann 1956 mistakingly believed this taxon to be limited in distribution to the North Island) (Fig. 37). Northern offshore island records include Great Barrier (Newman & Towns 1985), Little Barrier and Waiheke Island (McCallum & Harker 1982). (A doubtful record exists from Middle Island in the Mercury group, Atkinson 1964). Towns & Robb (1986) considered that this restricted distribution, like that of *Naultinus elegans*, probably reflects the requirements of this species for larger islands, capable of supporting sufficient forest growth. In the south *Hoplodactylus granulatus* occurs at elevations of up to 1700 m (Bull & Whitaker 1975) and is widely distributed on the mainland and on the islands of Cook Strait — Maud Island (Meads 1976); Chetwode Islands (McCallum 1984) and Foveaux Strait — Zero Rock, Women Island, Herekopane Island, Big Island and Kundy Island (Adams & Cheyne 1968; Thomas 1981, 1982a). Lucas & Frost (1897) cited the species as occurring on Stephens Island, but this is probably incorrect.

*Hoplodactylus granulatus* is regarded as primarily a forest dweller and has been found in beech forest *(Nothofagus)* (Thomas 1976), bush and shrubland (Miller & Miller 1981), and manuka (Buller 1896). Although often active at night, it may be found by

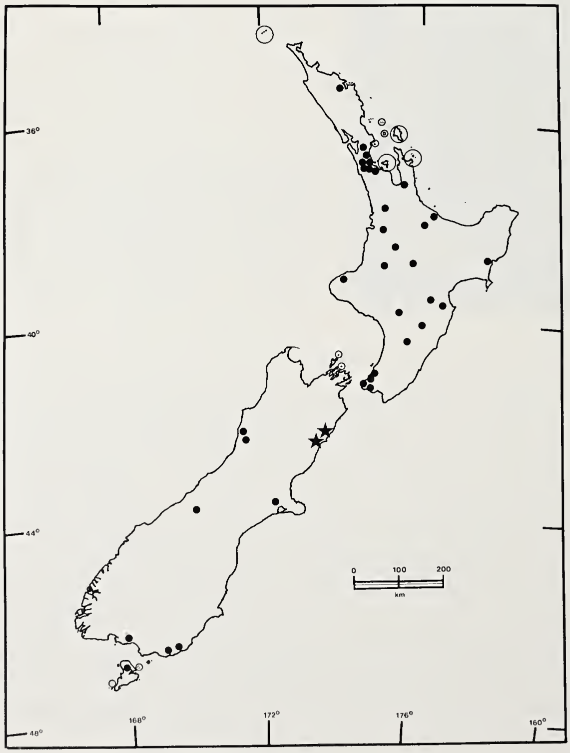

Fig.37: Distribution of *Hoplodactylus granulatus* (circles) and *H. kahutarae* (stars) in New Zealand.

day in hollows of trees (McCann 1955) or basking (Robb 1980a). Rowlands (1975a) stated that the species is crepuscular. Maximum size is 89 mm SVL (ZMH R02821). The diet consists mainly of insects. McCann (1955) and Rowlands (1981a) have discussed captive feeding habits. This species is taken by kingfishers *(Halcyon sancta)* among other predators (Fitzgerald et al. 1986). Rowlands (1981a) reported bimodal mating periods in captivity and young are generally born in mid- to late summer (Robb 1980a; Rowlands 1981a). Copulation was described by Edney (1970). Mites are common parasites on this species (Buller 1880; Colenso 1880). This species is not currently protected under the New Zealand Wildlife Act.

### ***Hoplodactylus kahutarae*** **Whitaker, 1985 (Fig. 38)**

1985 *Hoplodactylus kahutarae* Whitaker. New Zealand J.Zool. 11 (1984): 260; figs. 2—4.
Type locality: 1380 m, on west side of Kahutara Saddle, Seaward Kaikoura Range (42°19'22"S, 173°26'06"E) South Island, New Zealand.
Holotype: NMNZ R1980.

Fig.38: Living female *Hoplodactylus kahutarae* Whitaker, 1985. SVL = 85 mm.

Diagnosis: Limbs and toes elongate; no terminal scansors on any digits; digits scansorial, narrow; prominent supraciliary scales; mouth lining yellowish; peritoneum black; eye black; preanal pores not extending onto thighs.

Comments: This species, first discovered in 1970 (Whitaker 1985), is, in many respects, atypical of members of the genus. *Hoplodactylus kahutarae* is known only from Mt. Tarahaka and Kahutara Saddle in the Seaward Kaikoura Range on the east coast of the South Island (Fig. 37). The habitat is described in detail by Whitaker (1985). Specimens have been found at altitudes of 1300 m in sub-alpine habitats of solid rock bluffs (Fig. 39). Animals are active at temperatures as low as 7 °C (Whitaker 1985) and bask frequently at temperatures above 13 °C. Nothing is known of its biology in the wild, although in captivity this species feeds on a variety of small arthropods (B.W. Thomas pers. comm.). Newman (1982) listed the species as having a high conservation priority largely because of its restricted range.

Fig.39: Subalpine habitat of *Hoplodactylus kahutarae* in the Seaward Kaikoura Range, South Island, New Zealand (elevation approx. 1300 m). (Photo courtesy of A.H. Whitaker)

***Hoplodactylus maculatus* (Gray, 1845) (Figs. 40,41)**

1845 *Naultinus maculatus* Gray. Catalogue of the Specimens of Lizards in the British Museum: 273.
Type locality: New Zealand.
Lectotype: BMNH 1946.9.8.14, here designated.
Paralectotype: BMNH 1946.9.8.15.
1871 *Naultinus pacificus* (part) Buller. Trans.New Zealand Inst. 3: 7.
1871 *Naultinus granulatus* (?) Buller. Ibid.: 9. (fide Robb & Rowlands 1977).
1872 *Naultinus pacificus* (part) Hutton. Trans.New Zealand Inst. 4: 172.
1885 *Hoplodactylus maculatus* Boulenger. Catalogue of the Lizards in the British Museum, vol.1: 171; pl. XIV (fig. 1).
1901 *Woodworthia digitata* Garman. Bull.Mus.Comp.Zool. 39: 4; pl. 1 (figs. 2, 2a—f).
Type locality: New Zealand.

Fig.40: Lectotype of *Naultinus maculatus* Gray, 1845 (= *Hoplodactylus maculatus*). BMNH 1946.9.8.14. (Photo courtesy of British Museum (Natural History))

Syntypes: MCZ 6153, 152218.
1955 *Hoplodactylus pacificus* (part) McCann. Dominion Mus.Bull. 17: 44; fig. 6.
1961 *Naultinus pacificus* (part) Chrapliwy et al. Herpetologica 17: 7.
1961 *Hoplodactylus pacificus* (part) Myers. Herpetologica 17: 169.
1965 *Hoplodactylus digitatus* Wermuth. Das Tierreich 80: 94.
1965 *Hoplodactylus pacificus* (part) Wermuth. Ibid.: 95.
1977 *Hoplodactylus maculatus* Robb & Rowlands. Rec.Auckland Inst.Mus. 14: 139; figs. 2,4,6,8,10.

Diagnosis: Terminal scansors on digit one only; rostral excluded from nostril; rostral 2 times broader than deep; digits scansorial, broadly expanded; peritoneum lightly pigmented; mouth lining and tongue pinkish; juvenile pattern as adult; preanal organs extending on to thighs. **(79)**.

Comments: This species has only recently been resurected from the synonymy of *Hoplodactylus pacificus* (Rowlands 1977; Robb & Rowlands 1977). It is now generally recognized that *H. maculatus* as now construed is actually a species complex (B.W. Thomas pers. comm.) with perhaps three or more specific level subunits. Although differentiated little in morphology, these forms have distinct size, breeding and behavioral peculiarities. Because the revision of the complex is incomplete I have treated all of these forms as a single species because all members of the complex appear, on preliminary morphological and biochemical grounds, to form a monophyletic group.

Fig.41: Large group of *Hoplodactylus maculatus* under communal cover in the Keeper's Bush, Stephens Island, Cook Strait, New Zealand.

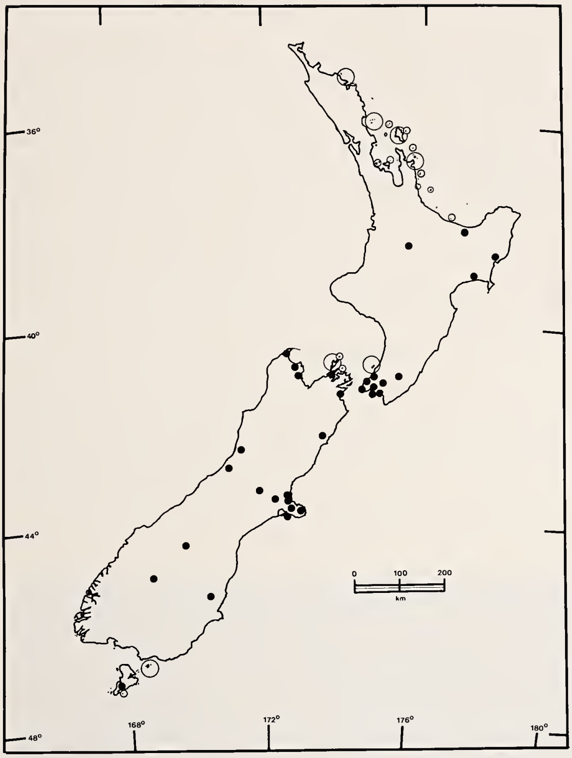

Fig.42: Distribution of *Hoplodactylus maculatus* in New Zealand.

It should be noted that the confusion of this species with *H. pacificus* has caused some problems with the interpretation of biological data. In many cases in which specimens are not available to confirm species identification, the name *pacificus* may refer to *maculatus*. When only the latter occurs the interpretation is obvious, but in areas of sympatry (most of the North Island) this determination cannot be made. Such references are discussed in the comments for *H. pacificus*. In most cases statements apply to both species.

*H. maculatus* is distributed throughout New Zealand with the possible exception of the North Cape region (McCallum 1981, but see Pickard & Towns 1988) and a number of offshore islands (Fig. 42). Known island localities include D'Urville Island (Buckingham & Elliott 1979), Stephens Island (Werner 1901; Walls 1983), Trios Island (Werner 1901) and the Stephenson Island group (McCallum 1982b) in Cook Strait, Bird Island and Green Island (Foveaux Strait) (Thomas 1982a) and many northern islands (McCallum 1982a; Bauer 1986; Towns & Robb 1986). Notable island groups lacking this species are the Poor Knights, Three Kings, Mokohinaus and Stewart Island proper (there is a single, doubtful record from Stewart Island — SMI E81.3/1—3). On all northern island groups except Whale Island, *H. maculatus* is sympatric with *H. pacificus*.

Everywhere it occurs, *H. maculatus* is the most plentiful gecko. It is not protected under the New Zealand Wildlife Act. The species is found from sea-level to 1700 m (Bull & Whitaker 1975). It lives a wide variety of habitats and has been found in association with exfoliating rocks (Miller & Miller 1981; McCallum 1982b), under stones (Thomas 1976; Werner & Whitaker 1978; Buckingham & Elliott 1979; Walls 1983), in tree hollows and under bark (Towns 1971b; Walls 1983) on steep rock faces and road cuttings (Buckingham & Elliot 1979; Walls 1983) and in flax (Cawthorn 1972). It is sometimes active in the splash zone on the coast (Cawthorn 1972; Robb & Rowlands 1977). It is somewhat less arboreal than *H. pacificus* (Robb & Rowlands 1977; Robb 1980a). During daylight hours this gecko usually remains concealed, heating indirectly from its cover (Werner & Whitaker 1978), although direct basking is known (Cawthorn 1972; Robb 1980a). Frequently many individuals may be found together under a piece of bark, rock or debris. I have seen as many as 200 individuals under a single tin sheet on Stephens Island (Fig. 41). Whitaker (1982) estimated mainland (Turakirae Head) populations at approximately 4000 individuals/hectare. This species reaches a maximum size of 82 mm SVL (Towns 1971b). The diet is composed largely of arthropods, with spiders and mites being the most important items (Martin 1929; Whitaker 1982). The fruits of *Coprosma* and *Muehlenbeckia* also are eaten and flax nectar may be taken as well (Whitaker 1982).

Breathing and activity pattern have been studied by McIvor (1973). Walls (1983) reported activity on nights as cold as 7°C. This may be facilitated by a temperature compensation mechanism based on variable oxygen consumption rates (Grimmond & Evetts 1981). Werner & Whitaker (1978) also reported on temperature relations. Winter and possibly summer lows in activity are seen in the species (Whitaker 1982). The biochemistry of "hibernating" *H. maculatus* has also been examined (Pollock & MacAvoy 1973). This species reaches sexual maturity in about the fourth year at Wellington (Whitaker 1982). Mating occurs in April or May and young are born February — May (Rowlands 1981a). Aspects of reproduction and the sexual cycle have been examined by Fawcett (1972) and Boyd (1940, 1942). Mating behavior has been outlined by Rieppel (1973, 1976b). Individuals may live up to 17 or more years (Anastasiadis & Whitaker 1987). Predators include rats, mice, hedgehogs, cats, gulls, kingfishers, harriers, moreporks, herons (Whitaker 1982), *H. duvaucelii* (Barwick 1982) and tuataras (Crook 1975; Walls 1981). Benson (1976) used circadian rhythms to suggest the separation of *maculatus* from *pacificus*. Hardy (1975) discussed the karyotype of *H. maculatus*.

### *Hoplodactylus pacificus* (Gray, 1842) (Fig. 43)

1842 *Naultinus pacificus* Gray. Zool.Misc.: 58.
Type locality: South Sea Islands.
Lectotype: BMNH 1946.8.22.67, here designated.
Paralectotype: BMNH 1946.8.22.65.
1842 *Naultinus pacifica* Gray. Ibid.: 72.
1843 *Naultinus pacificus* (part) Gray. Travels in New Zealand: 203.

1843 *Platydactylus duvaucelii* Gray. Ibid.: 203. (nec *Platydactylus duvaucelii* Duméril & Bibron, 1836).

1845 *Naultinus pacificus* (part) Gray. Catalogue of the Specimens of Lizards in the British Museum: 169.

1851 *Platydactylus pacificus* Duméril. Catalogue Méthodique de la Collection des Reptiles: 35 (nec *Platydactylus pacificus* Duméril, 1851 ad Bavay 1869).

1857 *Hoplodactylus pomarii* Girard. Proc.Acad.Nat.Sci. Philadelphia 8: 197.

Type locality: New Zealand.

Holotype: USNM 5690.

1858 *Gehyra oceanica* (part) Girard. Herpetology of the United States Exploring Expedition: 273.

1861 *Dactylocnemis wüllerstorfii* Fitzinger. Österr.Akad.Wissensch. Math.-nat. Klasse 42: 400. (nomen nudum).

1867 *Dactylocnemis pacificus* Steindachner. Reptilien. Reise der Fregatte Novara: 11.

1868 *Pentadactylus brunneus* Cope. Proc.Acad.Nat.Sci. Philadelphia 20: 320 (synonymy fide Kluge 1965b).

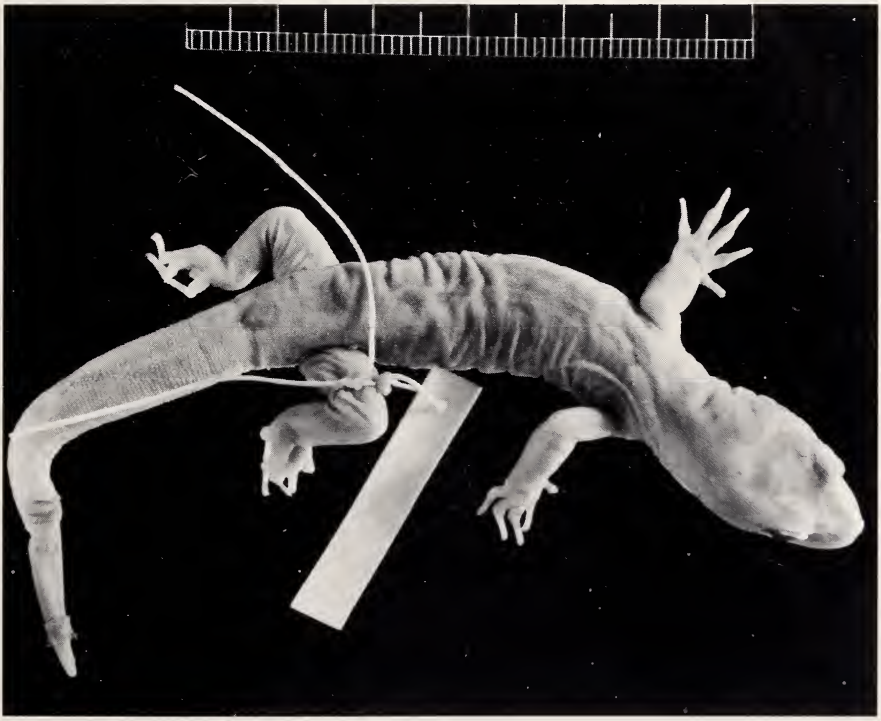

Fig.43: Lectotype of *Naultinus pacificus* Gray, 1842 (= *Hoplodactylus pacificus*). BMNH 1946.8.22.67. (Photo courtesy of British Museum (Natural History))

1871 *Naultinus pacificus* (part) Buller. Trans. New Zealand Inst. 3: 7.
1872 *Naultinus pacificus* Hutton. Trans. New Zealand Inst. 4: 172.
1885 *Aelurosaurus brunneus* Boulenger. Catalogue of Lizards in the British Museum, vol. 1: 74.
1885 *Hoplodactylus pacificus* Boulenger. Ibid.: 173.
1885 *Aeluroscalobotes brunneus* Boulenger. Ann.Mag.Nat.Hist. (5)16: 387.
1924 *Hoplodaetylus pacificus* Lord & Scott. Animals of Tasmania: 109 (lapsus pro *Hoplodactylus pacificus* (Gray, 1842)).
1954 *Hoplodactylus duvaucellii* (part) Hard. Tane 6: 143.
1955 *Hoplodactylus pacificus* (part) McCann. Dominion Mus.Bull. 17: 44; figs. 4—5.
1961 *Naultinus pacificus* (part) Chrapliwy et al. Herpetologica 17: 7.
1961 *Hoplodactylus pacificus* (part) Myers. Herpetologica 17: 169.
1977 *Hoplodactylus pacificus* (part) Robb & Rowlands. Rec. Auckland Inst.Mus. 14: 137; figs. 1,3,5,7,9.
1980 *Hoplodactylus pacificus* Robb. Rec.Natl.Mus. New Zealand 1: 308.

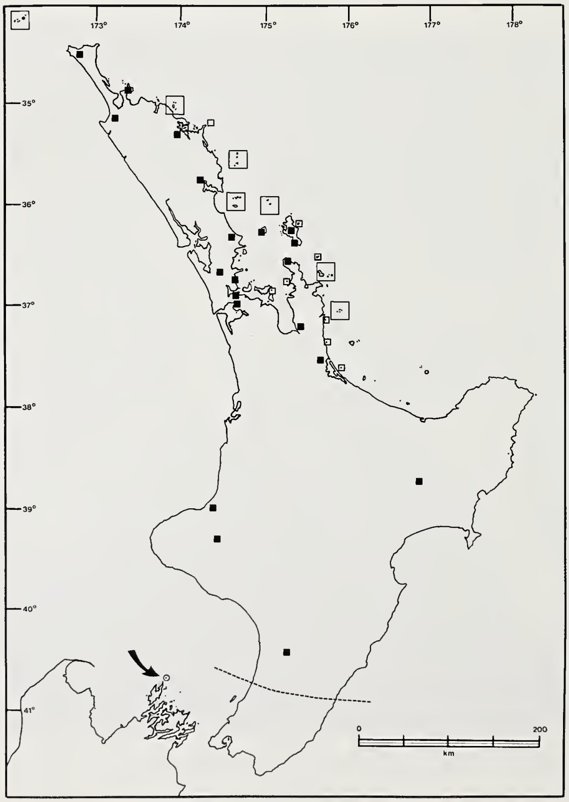

Fig.44: Distribution of *Hoplodactylus pacificus* (squares) and *H. stephensi* (circle indicated by arrow) in the North Island of New Zealand. Dashed line represents the southern extent of the range of *H. pacificus* according to Robb (1980a).

Diagnosis: Digits scansorial, broadly dilated, proximal portion approximately twice width of distal; penultimate phalanx arises from within pad; approximately 12 scale rows on free portion of digit IV of pes; mouth lining and tongue pinkish; juvenile pattern as adult; preanal pores do not extend on to thighs. (93).

Comments: The systematic confusion surrounding this species and *H. maculatus* has already been discussed. The naming of *H. pomarii* Girard, 1857 seems to have resulted from the uncertainty of the identity of *H. pacificus* as the original description was very sketchy. Fitzinger's (1861) *Dactylocnemis wüllerstorfii* is a nomen nudum; his reference to this animal as a house gecko is certainly incorrect. The systematic status and redescription are provided by Robb & Rowlands (1977). At various times *H. maculatus, H. chrysosireticus* and *H. stephensi* were all subsumed under this name as well.

The species is distributed over most of the North Island as far south as Palmerston North — 40°40'S (but see Pickard & Towns 1988 for a Wellington locality) and occurs on most of the northern offshore islands (Towns & Robb 1986; Bauer 1986) (Fig. 44). It is not known from any South Island localities or any of the islands of Cook Strait. The Stephens Island specimens mentioned by Sharell (1966) and Robb & Rowlands (1977) have since been referred to *H. stephensi*.

Like *H. maculatus*, this species occurs in a wide range of habitat types including beach rocks, wrack or driftwood (McCann 1955; Miller 1978; pers. obs.), in cliff crevices (McCallum 1980) or in forested or scrub situations, either on trees, under bark or under ground debris (Whitaker 1968; Robb & Rowlands 1977; McCallum & Harker 1982). Whitaker (1968) also found this species in petrel burrows and occasionally found this species sharing a retreat with *H. duvaucelii*. The "oceanic" gecko from North Cape that was reported to run from beach wrack into the ocean to avoid capture (Browne 1946) is probably this species. Whitaker (1968, 1973) found this species rare or absent on islands with kiore. If present, populations were small and were found only in association with steep rocky cliffs. This species is generally larger (maximum SVL 94 mm — Whitaker 1968), but more gracile than *H. maculatus*. On Aorangi, *H. pacificus* occasionally basks during daylight hours and forages at dusk, at which time they frequently climbed pohutukawa trees (Whitaker 1968). Animals remain active until about 4:30. Dietary items include a variety of insects and arthropods (Rowlands 1975b), crustaceans (McCann 1955; Whitaker 1968), kawakawa fruit and pohutukawa, ngaio and flax nectar (Whitaker 1968, 1987). Whitaker (1968) reported 50 individuals in a single pohutukawa feeding on nectar. In turn, this species is preyed upon by tuataras, kingfishers, harriers and cats (McCann 1955; Whitaker 1968; Gibb et al. 1969). The preadators listed for *H. maculatus* probably all are potential predators of this species as well. This species mates March — May and gives birth to two young in February — March (McCann 1955; Robb 1980a; Rowlands 1981a). Whitaker (1968), in his superb ecological study, relates an escape behavior in which an individual dove into a pool of water and remained submerged for more than 14 minutes while holding on to a rock; other aspects of ecology and behavior are covered in this paper as well.

### *Hoplodactylus rakiurae* Thomas, 1981 (Fig. 45)

1981 *Hoplodactylus rakiurae* Thomas. New Zealand J.Zool. 8: 33; figs. 2—4.

Type locality: Southern Tin Range, Stewart Island (47°08'30"S 167°44'30"E), New Zealand.

Holotype: NMNZ R1825.

Diagnosis: Abdominal ribs 5—6; terminal scansors present on all digits; digits scansorial, narrow; dorsal scales conical; tail short; juvenile and adult pattern of complex harlequin design; mouth, tongue and peritoneum darkly pigmented. (33-A).

Fig.45: Living specimen of *Hoplodactylus rakiurae* from Stewart Island, New Zealand. Note the unique coloration pattern. SVL = 60 mm. (Photo courtesy of B.W. Thomas)

Comments: This striking species was first collected in 1969 (Thomas 1981). Thomas' (1981) description is excellent and is a good general statement of all that is known about the biology of this species. *Hoplodactylus rakiurae* is known only from the southern part of Stewart Island (Fig. 46). The species has been found under rocks and basking on moss but in captivity is active at night in foliage (Thomas 1981). In general, vegetation near known localities is composed of a variety of windshorn scrub plants, including manuka and other divaricating shrubs (Thomas 1981). At SVL 64 mm (Thomas 1981) this is the smallest species of New Zealand carphodactyline. Thomas (1981) lists a variety of insects and amphipods as well as nectar as potential food for *H. rakiurae*. Introduced rats and cats have been cited as possible predators (Thomas 1982a). The species is classified as rare (Williams & Given 1981).

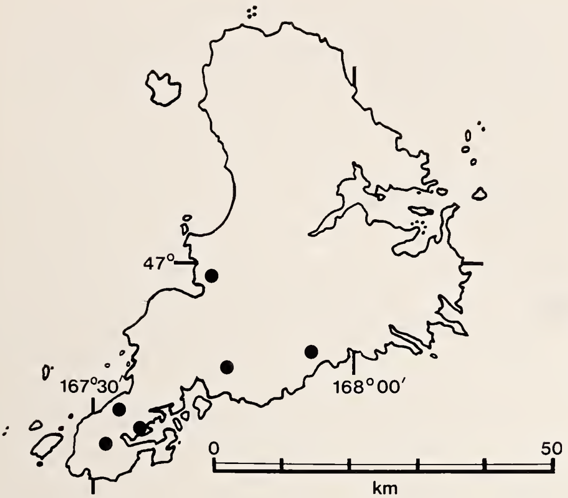

Fig.46: Distribution of *Hoplodactylus rakiurae* on Stewart Island, New Zealand.

*Hoplodactylus stephensi* **Robb, 1980**

1977 *Holplodactylus pacificus* (part) Robb & Rowlands. Rec. Auckland Inst. Mus. 14: 137.

1980 *Hoplodactylus stephensi* Robb. New Zealand Amphibians and Reptiles in Colour: 60; pl.12 (lower left and right).

1980 *Hoplodactylus stephensi* Robb. Rec.Natl.Mus. New Zealand 1: 308, fig. 1B.

Type locality: Stephens Island, New Zealand.

Holotype: NMNZ R1858.

Diagnosis: Digits scansorial, broadened, proximal portion approximately twice width of distal portion; penultimate phalanx arises from within pad; 7 rows on free portion of digit IV of pes; 6—9 rows of preanal pores in males; peritoneum brown; tongue pink; mouth lining distinctly pigmented. (**63**, 64, 66-A).

Comments: This species was previously considered to be part of *H. pacificus. Hoplodactylus stephensi* occurs only on Stephens Island in Cook Strait (Fig. 44) and thus has perhaps the most limited distribution of any gekkonid species in the world, and is considered rare and vulnerable (Williams & Given 1981). Towns et al. (1985) consider the existing population to represent a relict population. It would, however, seem more plausible that the species represents a recent offshoot from *pacificus-maculatus* stock.

Robb (1980a) stated that this species was strongly nocturnal and that its daytime retreats were in hollows or under bark in or near forested areas of the island. I have observed the species, however, active on an overcast day in divaricating shrubs on an exposed hillside on Stephens Island. Maximum SVL is 80 mm (Robb 1980b). Nothing is known of the natural diet of this species but it is probably similar to *H. maculatus* in similar regions of New Zealand. Mating takes place in spring and two live young are born in late summer or early autumn (Robb 1980b). Sharell (1966) stated that the "Stephens Island *H. pacificus*" was a prey item in the diet of *Sphenodon punctatus*, although it is unclear whether this is in reference to *H. stephensi* or sympatric *H. maculatus.*

## *Naultinus* Gray, 1842

1842 *Naultinus* (part) Gray. Zool. Misc.: 72.
Type species: *Naultinus elegans* Gray, 1842 (fide Myers 1961).
1882 *Heteropholis* Fischer. Abh.Naturwiss.Ver. Bremen 7: 236. (nomen novum pro *Naultinus* (part) Gray, 1842).
Type species: *Heteropholis rudis* Fischer, 1882 by monotypy.
1961 *Naultinulus* Chrapliwy et al. Herpetologica 17: 7. (nomen novum pro *Naultinus* Gray, 1842 (part)).
1961 *Naultinus* Myers. Herpetologica 17: 169.

Species referred: *Naultinus elegans* Gray, 1842; *N. gemmeus* (McCann, 1955); *N. grayii* Bell, 1843; *N. manukanus* (McCann, 1955); *N. poecilochloris* (Robb, 1980); *N. rudis* (Fischer, 1882); *N. stellatus* Hutton, 1872; *N. tuberculatus* (McCann, 1955).

Diagnosis: (Node 10) A monophyletic taxon diagnosed by the following characters: pectoral girdle largely cartilaginous; green pigmentation present; metatarsals II and IV parallel; metatarsal length (shortest to longest) V-I-IV-II-III; lateral pair of cloacal bones present; mouth lining and tongue distinctly pigmented; peritoneum jet black; pupil vertical with smooth margins; diurnal; external ear generally minute; digits narrow with scansorial pads; terminal scansor single, cleft; webbing between toes absent; preanal pores present, extend on to thighs; autotomy limited to anterior post-pygal vertebrae; tail elongate and prehensile, without scansors; live bearing. (29-A, 35*, 60*, 67*).

Comments: Great controversy has surrounded this genus since its erection by Gray (1842a, 1842b). Initially the genus included both the New Zealand green and brown geckos. Subsequent usage has restricted the name *Naultinus* to the green geckos. Chrapliwy et al. (1961), Myers (1961), Robb & Hitchmough (1980) and Whitaker (1982) have reviewed the history of the taxonomy of this genus in detail. Primary confusion has resulted from the fact that the first species in the genus *Naultinus* was in fact the brown gecko *Hoplodactylus pacificus*. Chrapliwy et al. (1961) attempted to substitute the new name *Naultinulus* for the green geckos and reinstate *Naultinus* for the members currently in *Hoplodactylus*. This was rejected both on the grounds of nomenclatural stability and adherence to the International Code of Zoological Nomenclature (Myers 1961). Thomas (1982b) listed reliable characters for separating *Naultinus* (sensu lato) and *Hoplodactylus.*

A second point of contention has been the use of the name *Heteropholis* for the South Island green geckos. First proposed by Fischer (1882), this name was largely in disuse until resurrected by McCann (1955). Traditionally, all South Island day geckos were referred to *N. elegans*. Since 1955, the use of *Heteropholis* for South Island species has been more or less universal. Robb (1982) suggested that this usage be maintained, while Thomas (1982b), citing a lack of diagnostic characters to separate the genera, synonymized *Heteropholis* with *Naultinus*. Meads (1982), taking a more extreme view, indicated the captive production of fertile offspring from a variety of mixed crossings and advocated synonymizing all New Zealand green geckos with *N. elegans*. The latter view appears to be unwarranted because the taxa involved, although potentially interbreeding, are spatially, and in some cases, temporally separated. Thomas' (1982b) generic synonymy, however, is consistent with the results of this study and should be adopted. Robb & Hitchmough (1980) provided a systematic review of the North Island species including partial synonomies and new diagnoses and descriptions. Hitchmough (1982a) also presented a summary of morphological and distributional data for the members of the genus. McCann's (1955) "The Lizards of New Zealand" is the most recent systematic treatment of the South Island species.

The genus as a whole ranges from the North Cape region to Southland and perhaps to Stewart Island. No species occur on the northern offshore islands (except Great and Little Barrier Islands) or on large portions of the South Island, notably Fiordland and the Southern Alps (Pickard & Towns 1988). In general, all species are diurnal and are associated with a variety of bushes and small trees. McCann (1955), Sharell (1966) and Robb (1980a) reviewed the biology of the constituent species. Captive care, including information on feeding, reproduction and parasites, has also been discussed (Rowlands 1981b; Hume 1974, 1976; Hardy 1972; Allison 1982). All *Naultinus* are ovoviviparous and typically give birth to two young. All species in the genus are protected by the New Zealand Wildlife Act of 1983.

## Key to the Species of *Naultinus*

1a. Scalation of dorsal body surface homogeneous .......................... 2
b. Scalation of dorsal body surface heterogeneous .......................... 3
2a. Dome shaped scales on snout, 3 or more post-mental scales ....... *N. elegans*
b. Scales of snout flat, usually 2 post-mentals .......................... *N. grayii*
3a. Scales heterogeneous on body and head .................................. 4
b. Head and nape only with heterogeneous conical scales ..................... 5
4a. Entire body covered by enlarged, conical scales ................... *N. rudis*
b. Enlarged scales only on head and along mid-dorsal line (nape and sacrum only in Stephens Island specimens) ........................................ *N. manukanus*
5a. Scales of body generally granular ........................................ 6
b. Scales of body generally conical or tuberculate ............................ 7
6a. Supraciliary scales conical (Fig. 47) ........................... *N. gemmeus*
b. Supraciliary scales granular ...................................... *N. stellatus*
7a. Scales of body flat .............................................. *N. tuberculatus*
b. Scales of body pointed ........................................ *N. poecilochloris*

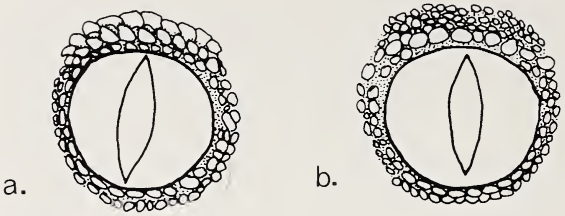

Fig.47: Circumorbital scalation of (a) *Naultinus gemmeus* and (b) *Naultinus stellatus* showing conical and granular supraciliaries, respectively (couplet 6 of *Naultinus* key).

### *Naultinus elegans* Gray, 1842 (Fig. 48)

1842 *Naultinus elegans* Gray. Zool. Misc.: 72.
Type locality: Auckland, New Zealand.
Holotype: BMNH 1946.8.22.36.
1843 *Naultinus punctatus* Gray. Travels in New Zealand, 2. The Fauna of New Zealand: 204.
Type locality: New Zealand.
Holotype: BMNH 1946.8.22.38.
1851 *Gymnodactylus elegans* Duméril. Catalogue Méthodique de la Collection des Reptiles: 43.
1861 *Hoplodactylus elegans* Fitzinger. Österr.Akad.Wissensch. Math.-nat. Klasse 42: 400.
1861 *Hoplodactylus punctatus* Fitzinger. Ibid.: 400.
1867 *Naultinus elegans* (part) Steindachner. Reptilien. Reise der Fregatte Novara: 19.
1867 *Naultinus punctatus* Steindachner. Ibid.: 20.
1871 *Naultinus sulphureus* Buller. Trans.Proc. New Zealand Inst. 3: 8.
Type locality: Rotorua, North Island, New Zealand. (Hutton 1872 stated that the true type locality was Maketu, Buller 1872 maintained that the "Hot Springs" (= Rotorua) was correct).
Holotype: NMNZ (specimen number unknown).
1880 *Naultinus pentagonalis* Colenso. Trans.Proc. New Zealand Inst. 12: 262.
Type locality: Hampden, North Island, New Zealand.
Syntypes: repository unknown.
1885 *Naultinus elegans* Boulenger. Catalogue of Lizards in the British Museum, vol. 1: 168; pl. XIV (fig. 3).
1955 *Naultinus elegans* form *elegans* (part) McCann. Dominion Mus.Bull. 17: 31, pl. II (figs. 8—14).
1955 *Naultinus elegans* form *punctatus* McCann. Ibid.: 31.
1955 *Naultinus elegans* form *sulphureus* McCann. Ibid.: 31.
1955 *Naultinus elegans* form *occelatus* McCann. Ibid.: 31.
1961 *Naultinulus elegans* (part) Chrapliwy et al. Herpetologica 17: 7.
1961 *Naultinus elegans* (part) Myers. Herpetologica 17: 169.
1966 *Naultinus sulphureus* Sharell. The Tuatara, Lizards and Frogs of New Zealand: 48; pls. 26, 27.

1980 *Naultinus elegans elegans* Robb. New Zealand Amphibians and Reptiles in Colour: 61; pls. 11 (bottom left), 13 (top and middle).
1980 *Naultinus elegans pentagonalis* Robb. Ibid.: 62; pl. 13 (bottom).
1980 *Naultinus elegans punctatus* Robb & Hitchmough. Rec. Auckland Mus. 16: 193.

Diagnosis: Generally three or four abdominal ribs; dorsal scalation homogeneous; scales on snout dome shaped; three or more postmental scales. (33-B, 78).

Comments: Gray's descriptions (1842b, 1843) are too vague to be usefull. Girard (1857) presented a good redescription of *N. punctatus*. The great variety of color patterns exhibited by members of this species resulted in numerous new taxa as seen in the synonymy above. Buller's (1871) *sulphureus*, in particular, has had a continued reappearance as amateur naturalists have continued to accord specific rank to this color phase. Robb & Hitchmough (1980) recognized two subspecies, *N. e. elegans* and *N. e. punctatus*, the former distributed from Dargaville and Whangarei south to the northern Bay of Plenty and northern Taranaki and the latter in the remaining southern parts of the North Island (Pickard & Towns 1988). Morphological differences are minor and in-

Fig.48: a. Holotype of *Naultinus elegans* Gray, 1842. BMNH 1946.8.22.36. b. Holotype of *Naultinus punctatus* Gray, 1843 (= *Naultinus elegans*). BMNH 1946.8.22.38. (Photos courtesy of British Museum (Natural History))

consistent, although differences in reproductive timing (Rowlands 1981a) suggest that the populations may warrant taxonomic distinction.

In addition to the North Island, populations (nominate subspecies) exist on Great and Little Barrier Islands in the Hauraki Gulf (Robb & Hitchmough 1980; Dick 1981; Ogle 1981) (Fig. 49). McCallum & Harker (1982) also reported *N. elegans* from inner islands of the Gulf. Gray (1843) described the habitat of *Naultinus elegans* as "amongst decayed trees and running about between the fern". Hutton (1872) recorded open fernland as the habitat. This species and its congeners are often found in manuka *(Leptospermum scoparium)* and kanuka *(L. ericoides)* (Sharell 1966; Taylor 1976; Robb 1980a). This species overwinters among roots of *Phormium* (flax) (McCann 1955) and shelters under bark or stones (Robb 1980a). The maximum size recorded for this taxon is SVL 95 mm (Robb & Hitchmough 1980). Northern individuals mate in September—November and give birth to two live young between April and September. The southern form mates and gives birth several months earlier (Rowlands 1981). Colenso (1880, 1887) was apparently the first to confirm live birth in this species and stated that gestation was five and a half months, although in reality it lasts approximately nine to eleven months (Rowlands 1979; Robb 1980a). Diet consists primarily of insects (McCann

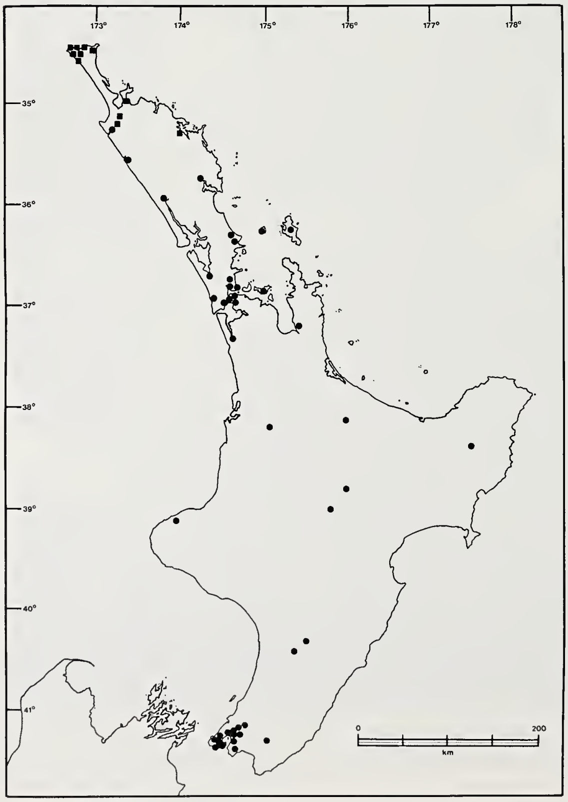

Fig.49: Distribution of members of genus *Naultinus* in the North Island of New Zealand. *Naultinus elegans* (circles), *N. grayii* (squares).

1955; Bull & Whitaker 1975) but nectar may also form part of the wild diet, McCann (1955). The call and threat display of *N. elegans* is described by McCann (1955). The Maori name for this animal is "kakariki" and like most lizards, this species was feared by the early Maori (Best 1923; Downes 1937).

### *Naultinus gemmeus* (McCann, 1955)

1869 *Naultinus lineatus* Gray. Ann.Mag.Nat.Hist. (4)3: 243.
Type locality: Otraroa (= Akaroa) in Canterbury (South Island) New Zealand.
Holotype: BMNH (specimen number unknown).
1955 *Heteropholis gemmeus* McCann. Dominion Mus.Bull. 17: 63; figs. 9,10.
Type locality: Rangiora, South Island, New Zealand.
Holotype: CMC (specimen number unknown).
1982 *Naultinus elegans gemmeus* Meads. New Zealand Herpetology: 324.
1982 *Naultinus gemmeus* Thomas. New Zealand Herpetology: 336.
1986 *Naultinus elegans gemmeus* Gill. Collins Handguide to the Frogs and Reptiles of New Zealand: 48.

Diagnosis: Dorsal scalation heterogeneous, granular; supraciliary scales conical.

Comments: This is the most widespread of the South Island *Naultinus*. Three distinct populations exist, one on the Banks Peninsula and the Canterbury Plains, a second on the Otago Peninsula and coastal southeast and a third, isolated form from Mt. Cook (Fig. 51). Geckos from extreme southern New Zealand (Invercargill, Bluff, Green Island and Stewart Island) have been reported (Thomas 1982a) and may be referable to this species.

In general, these geckos are found in forest or scrub areas, typically on the outer foliage of divaricating shrubs two to four meters above the ground (Thomas 1982a). In Otago this species has been found in *Coprosma areolata* (Miller & Miller 1981). Henle (1981) reported on both native plants and on introduced *Pinus radiata*. Although generally assumed to be diurnal (Robb 1980a), McCann (1955) reports that captives were generally inactive during the day except for periods of basking. Maximum size is SVL 80 mm (Robb 1980a). The species mates in September—October and gives birth between February and May (Robb 1980a; Rowlands 1981a). Specimens from the Banks Peninsula are sexually dichromatic, with females being green and males brown or gray in background coloration (Thomas 1982a). There is no dichromatism among the Otago specimens. Offspring of a *N. gemmeus x N. rudis* cross showed dichromatism (Meads 1982). Wild diet is similar to that reported for the previous species (Robb 1980a).

### *Naultinus grayii* Bell, 1843 (Fig. 50)

1843 *Naultinus grayii* Bell. The Zoology of the Voyages of H.M.S. Beagle. 27; pl.16 (fig. 2).
Type locality: Bay of Islands, North Island, New Zealand.
Holotype: BMNH 1946.9.8.16.
1858 *Naultinus graii* Girard. Herpetology of the United States Exploring Expedition: 309. (lapsus pro *Naultinus grayii* Bell, 1843).

1861 *Hoplodactylus grayi* Fitzinger. Österr.Akad.Wissensch. Math.-nat. Klasse 42: 400. (lapsus pro *Naultinus grayii* Bell, 1843).
1871 *Naultinus grayii* Buller. Trans.Proc. New Zealand Inst. 3: 7.
1885 *Naultinus elegans* (part) Boulenger. Catalogue of Lizards in the British Museum, vol. 1: 168.
1899 *Naultinus grayi* Dendy. Trans. New Zealand Inst. 31: 730.
1955 *Naultinus elegans* form *elegans* (part) McCann. Dominion Mus.Bull. 17: 31.
1961 *Naultinulus elegans* (part) Chrapliwy et al. Herpetologica 17: 7.
1961 *Naultinus elegans* (part) Myers. Herpetologica 17: 169.
1980 *Naultinus simpsoni* Robb. New Zealand Amphibians and Reptiles in Colour: 62; pls. 14, 15 (top) (nomen nudum pro *Naultinus grayii* Bell, 1843).
1980 *Naultinus grayi* Robb & Hitchmough. Rec. Auckland Mus. 16: 195; figs. 3,4,6.
1982 *Naultinus elegans grayi* Meads. New Zealand Herpetology: 324.
1982 *Naultinus grayi* Thomas. New Zealand Herpetology: 336.
1986 *Naultinus elegans grayi* Gill. Collins Handguide to the Frogs and Reptiles of New Zealand: 46.
1988 *Naultinus grayii* Bauer. New Zealand J.Zool. 14 (1987): 593.

Diagnosis: Dorsal scalation homogeneous; scales on snout flat; usually two postmental scales. (78).

Comments: This species is similar in most respects to *N. elegans*, with which it has been frequently confused. Robb & Hitchmough (1980) resurrected this name for the green geckos of Northland, north of Whangaroa (Fig. 49). *Naultinus grayii* is unknown from offshore islands (Towns & Robb 1986). Bell (1843), whose description is adequate,

Fig.50: Holotype of *Naultinus grayii* Bell, 1843. BMNH 1946.9.8.16. (Photo courtesy of British Museum (Natural History))

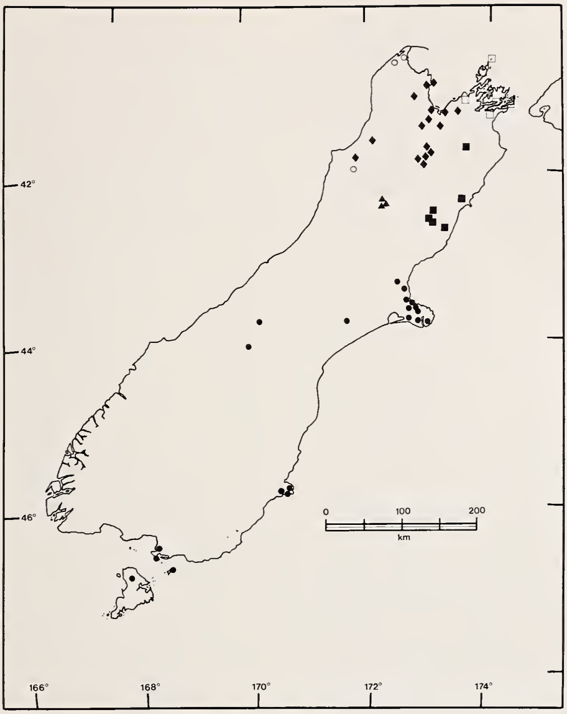

Fig.51: Distribution of members of the genus *Naultinus* in the South Island of New Zealand. *Naultinus gemmeus* (closed circles), *N. manukanus* (open squares), *N. poecilochloris* (closed triangles), *N. rudis* (closed squares), *N. stellatus* (closed diamonds), *N. tuberculatus* (open circle).

stated that this gecko lives in trees. Like most other *Naultinus*, this species typically inhabits *Leptospermum* (Robb 1980a; McCallum 1981; Hitchmough 1982b). Population density on the Karikari Peninsula was estimated at 55 individuals/hectare (Hitchmough 1982b). Maximum SVL is 95 mm (Robb & Hitchmough 1980). Food consists of a variety of insects and other arthropods (Sharell 1966). Births occur from March to June following August—September matings (Dendy 1899; Rowlands 1981a; Hitchmough 1982b). Maturity is reached after 16—17 months and females give birth at about two years (Robb & Hitchmough 1980). Ontogenetic color changes have been noted in *N. grayii* (Hitchmough 1982b). Robb (1980a) reported parental defense of young.

### *Naultinus manukanus* (McCann, 1955) (Fig. 52)

1955 *Heteropholis manukanus* McCann. Dominion Mus.Bull. 17: 59; pl. 4 (figs. 7—11).
Type locality: Marlborough Sounds, South Island, New Zealand.
Holotype: NMNZ R238.
1955 *Naultinus elegans* (part) McCann. Dominion Mus.Bull. 17: 29.
1982 *Naultinus elegans manukanus* Meads. New Zealand Herpetology: 324.
1982 *Naultinus rudis* (part) Thomas. New Zealand Herpetology: 336.
1986 *Naultinus elegans manukanus* Gill. Collins Handguide to the Frogs and Lizards of New Zealand: 48.

Fig.52: *Naultinus manukanus* (McCann, 1955) exhibiting tail prehension, Stephens Island, Cook Strait, New Zealand. SVL = 62 mm.

Diagnosis: Dorsal scalation heterogeneous, at least on head, nape and sacral region, but never on entire body; rostral contacts nostril. (79).

Comments: Thomas (1982b) considered this species to be conspecific with *N. rudis* and indicated that the morphocline first reported by Bull & Whitaker (1975) was indeed present. I have examined only specimens from Stephens Island which are quite distinct from *N. rudis* and therefore favor the specific distinction of the two taxa.

*Naultinus manukanus* is distributed throughout the Marlborough Sounds and on Stephens Island and D'Urville Island (Buckingham & Elliott 1979) (Fig. 51). The species is found chiefly in manuka and kanuka (Robb 1980a) but I have observed them on a variety of small divaricating shrubs on Stephens Island (Fig. 53). They are also known from heights of 0.5 to 1.5 m in taupata *(Coprosma repens)* (Werner & Whitaker 1978). Walls (1983) reported that the species was fairly common on Stephens Island and that specimens there showed summer peaks and winter troughs of activity. The maximum SVL is 68 mm (Robb 1980a). The diet consists of insects and other small invertebrates (Robb 1980a). *Naultinus manukanus* mates from June to October and gives birth in March or April (Rowlands 1981a). Habitat destruction in the Marlborough Sounds appears to be having a negative effect on the populations there (Robb 1980a).

Fig.53: Stands of native vegetation, Stephens Island, Cook Strait, New Zealand. Habitat of *Hoplodactylus stephensi, Naultinus manukanus* and *Sphenodon punctatus*.

### *Naultinus poecilochlorus* (Robb, 1980)

1980 *Heteropholis poecilochloris* Robb. New Zealand Amphibians and Reptiles in Colour: 67; pl. 19.

1980 *Heteropholis poecilochlorus* Robb. Rec.Natl.Mus. New Zealand 1: 309; fig. 1C.

Type locality: Lewis Pass, South Island, New Zealand.

Holotype: NMNZ R1862.

1982 *Naultinus elegans poecilochlorus* Meads. New Zealand Herpetology: 324.

Diagnosis: Dorsal scalation of head and nape heterogeneous; scales conical, pointed.

Comments: This species is restricted to a small area in south Nelson — north Canterbury centered around Lewis Pass from Rahu to Reefton (Robb 1980b) (Fig. 51). It is separated from the range of *N. stellatus* by a mountainous region. It is associated with shrubs in and around *Nothofagus* forests (Robb 1980b; Henle 1981). *Naultinus poecilochloris* has been found in *Leptospermum scoparium, Discaria toumatou, Rubus* spp. and *Gahnia* sp. (Robb 1980b). The species occurs above the winter snow line and apparently utilizes rocks and other ground cover as winter retreats (Robb 1980b). Maximum SVL is 85 mm (Robb 1980a). Mating in captivity occurs in September or October and young are born in late Autumn (April—May) (Robb 1980b; Rowlands 1981a). Robb (1980a, 1980b) describes threat posturing and barking in the male.

*Naultinus rudis* **(Fischer, 1882) (Fig. 54)**

1882 *Heteropholis rudis* Fischer. Abh.Naturwiss.Ver. Bremen 7: 236; pl. 16, figs. 1—5.
Type locality: Neuseeland.
Holotype: BMNH 1946.8.22.37.
1885 *Naultinus rudis* Boulenger. Catalogue of Lizards in the British Museum, vol. 1: 170.
1955 *Heteropholis rudis* McCann. Dominion Mus.Bull. 17: 57; pls. 4 (figs. 1—6), 4,5.
1982 *Naultinus elegans rudis* Meads. New Zealand Herpetology: 324.
1982 *Naultinus rudis* (part) Thomas. New Zealand Herpetology: 336.
1986 *Naultinus elegans rudis* Gill. Collins Handguide to the Frogs and Reptiles of New Zealand: 48.

Diagnosis: Two ribless cervical vertebrae; five—six abdominal ribs; rostral contacts nostril; dorsal scalation heterogeneous, entire body covered with irregular conical scales. (33, 79).

Fig.54: Holotype of *Heteropholis rudis* Fischer, 1882 (= *Naultinus rudis*). BMNH 1946.8.22.37. (Photo courtesy of British Museum (Natural History))

Comments: Fischer's (1882) description is detailed and accurate. Thomas (1982a) suggested synonymizing *N. manukanus* with *N. rudis* and described variation throughout the range of the two taxa. *Naultinus rudis* is distributed in patches in the northeastern part of the South Island in parts of Nelson, Marlborough and Canterbury (Fig. 51). In the Kaikoura Ranges it occurs at elevations of up to 400 m (Robb 1980b) and is most often found in manuka or kanuka (Werner & Whitaker 1978), although it has also been reported from a variety of other plants including *Pseudopanax* (Robb 1980b). Maximum size is 72 mm SVL (NMNZ G855). Mating takes place in September—October (June—October in captivity) and young are born in March or April (Robb 1980b; Rowlands 1981a).

### *Naultinus stellatus* Hutton, 1872 (Fig. 55)

1872 *Naultinus elegans stellatus* Hutton. Trans.Proc. New Zealand Inst. (1871) 4:(171).
Type locality: Lake Rotoiti, Nelson District, South Island, New Zealand (type locality of Hutton 1872 = near the top of Mount Arthur, New Zealand).
Holotype: MNNZ (specimen "not available" fide McCann 1955).
Neotype: NMNZ R458.

Fig.55: *Naultinus stellatus* male from Station Creek, Upper Buller Valley, South Island, New Zealand. SVL = 75 mm. (Photo courtesy of B.W. Thomas)

1877 *Naultinus pulcherrimus* Buller. Trans.Proc. New Zealand Inst. 9: 326; pl. 17 top and middle.
Type locality: One of the Nelson and Foxhill railway stations, in the Waimea District, South Island, New Zealand.
Holotype: NMNZ (specimen "not available" fide McCann 1955).
1955 *Hetropholis stellatus* McCann. Dominion Mus.Bull. 17: 66; pl. 7 (figs. 1—7).
1982 *Naultinus elegans stellatus* Meads. New Zealand Herpetology: 324.
1982 *Naultinus stellatus* Thomas. New Zealand Herpetology: 336.
1986 *Naultinus elegans stellatus* Gill. Collins Handguide to the Frogs and Reptiles of New Zealand: 48.

Diagnosis: Lumbar vertebrae generally two; dorsal scalation of head and nape heterogeneous, granular; supraciliary scales granular.

Comments: *Naultinus stellatus* is distributed through the Nelson Lakes district and in the Maitai Valley in Nelson Province (Fig. 51). Mainwaring (1979) and Robb (1980b) described geographical variation in the species. Specimens have been found on red beech (Robb 1980b) as well as *Coprosma* and *Rubus* at a height of 1.2 to 1.5 m (Werner & Whitaker 1978). Hutton (1872) reports finding a specimen under a stone in the snow on Mt. Arthur. Maximum size is 79 mm SVL (UMMZ 132102). There is a distinct reduction of activity in winter (May—July) (Mainwaring 1979; Robb 1980b). Mating occurs in late winter or spring and young are born in autumn or early winter (Robb 1980b; Rowlands 1979, 1981a). Rowlands (1981b) reports blowfly *(Calliphora)* infestations in *N. stellatus* in captivity. Buller (1877) described a tail-coiling behavior.

### *Naultinus tuberculatus* **(McCann, 1955)**

1955 *Heteropholis tuberculatus* McCann. Dominion Mus.Bull. 17: 61.
Type locality: Westland, South Island.
Holotype: CMC (specimen number unknown).
1982 *Naultinus elegans tuberculatus* Meads. New Zealand Herpetology: 324.
1982 *Naultinus tuberculatus* Thomas. New Zealand Herpetology: 336.
1986 *Naultinus elegans tuberculatus* Gill. Collins Handguide to the Frogs and Reptiles of New Zealand: 48.

Diagnosis: Dorsal scales of head and nape heterogeneous, conical, flattened; rostral contacts nostril. (79).

Comments: *Naultinus tuberculatus* occurs in the extreme northwestern parts of the South Island in parts of Nelson Province and Westland (Fig. 51). It reaches a maximum size of 77 mm SVL (McCann 1955). This species, found in manuka and kanuka (Robb 1980b), feeds on moths, flies and other invertebrates (Robb 1980b). Mating occurs in September—October and young are born in March—May (Robb 1980b; Rowlands 1981a). Robb (1980b) described male aggressiveness.

## *Nephrurus* Günther, 1876

1876 *Nephrurus* Günther. J.Mus. Godeffroy 5: 46.
Type species: *Nephrurus asper* Günther 1876 by monotypy.
1965 *Underwoodisaurus* Wermuth. Das Tierreich 80: IX (nomen substitutum pro *Phyllurus* Schinz, 1822 (part)).

Species referred: *Nephrurus asper* Günther, 1876; *N. deleani* Harvey, 1983; *N. laevissimus* Mertens, 1958; *N. levis* De Vis, 1886; *N. milii* (Bory de Saint-Vincent, 1825); *N. sphyrurus* (Ogilby, 1892); *N. stellatus* Storr, 1968; *N. vertebralis* Storr, 1963; *N. wheeleri* Loveridge, 1932.

Diagnosis: Node 3 (Fig. 17) corresponds to a monophyletic taxon including the knob-tailed species of *Nephrurus* and the two species of *Nephrurus* formerly assigned to the genus *Phyllurus*, *N. milii* and *N. sphyrurus*. This grouping is diagnosed by the following characters: zero or one inscriptional ribs; sternum short and narrow; clavicular fenestrae very large; head large; skin bearing rosettes around tubercles; digits generally short; regenerated tail short and bulbous. (32-A, 34*, 43*, 81, 98*).

Within the genus a further monophyletic grouping (Node 4) exists, uniting the species *N. asper, deleani, laevissimus, levis, stellatus, vertebralis* and *wheeleri*. This node, corresponding to the knob-tailed *Nephrurus*, is diagnosed by the following characters: frontal bone approximately as wide as long; caudal vertebrae fewer than 30; coracoid processes of interclavicle indistinct; phalangeal formula reduced; hypoischium extending posteriorly to the level of the vent; metatarsal length (shortest to longest) V-I-IV-III-II; metatarsals I—IV greater than two times length of longest respective phalanges; digit V of pes offset from others; dorsal color pattern of three dark bands on head, nape and shoulders; ventral toe scalation spinose; claws slender at base, slightly decurved; labial scales only slightly larger than neighboring scales; cartilagenous rod of regenerated tail lacking or amorphous; tail terminating in a small knob. (4*, 25, 40, 46*, 51*, 55*, 56, 61, 71*, 77*, 85*, 99*, 100).

Comments: Because the distribution of *Nephrurus* is chiefly to the west of the Great Dividing Range in the more arid regions of the Australian continent, many of the species have only recently been described. Keys for the species are provided by Cogger (1986) but rely on variable characters. Storr (1963) provided a phenetic catalogue and key to the Western Australian species. Delean (1982) gave diagnoses and descriptions for the species of South Australia and the Northern Territory and also provides notes on biology. Cogger et al. (1983) presented a partial synonymy of all species as well as a summary of distribution and habitat.

Pianka & Pianka (1976) presented detailed findings on the ecology of three Western Australian species *(N. laevissimus, levis* and *vertebralis).* Members of the genus are entirely terrestrial. The knob-tailed species burrow or utilize the burrows of other animals as daytime refuges. The odd tail may be used in thermoregulation and/or monitoring mechanical stimuli (Russell & Bauer 1988). Most are associated with sandplains or sandridges, although *N. asper* uses a broader range of habitats and *N. milii* and especially *N. sphyrurus* are typically associated with more mesic habitats. Barrett (1950) reported

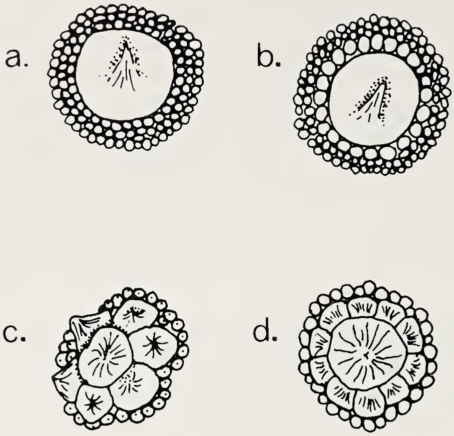

Fig.56: Dorsal body tubercles of (a) *Nephrurus deleani*, (b) *N. stellatus*, (c) *N. asper*, (d) *N. wheeleri* (see *Nephrurus* key couplet 3) (a and b redrawn from Harvey 1983).

the occurrence of unspecified *Nephrurus* in caves and mines. All species lay two eggs and feed primarily on a variety of arthropods and small nocturnal vertebrates (mostly other geckos).

## Key to the Species of *Nephrurus*

1a. Subdigital surface lamellate ........................................ 2
b. Subdigital surface spinose ........................................ 3
2a. Anterior loreals minute ........................................ *N. milii*
b. Anterior loreals only slightly smaller than posterior ............ *N. sphyrurus*
3a. Entire dorsum covered by sets of conical scales surrounded by rosettes of smaller conical scales (Fig. 56) ........................................ 4
b. Body without conical tubercles and rosettes ............................ 5
4a. 8 interorbital scales, preocular scales not enlarged ................. *N. asper*
b. 6 or fewer interorbital scales, vertical series of enlarged, tubercular preocular scales ........................................ *N. wheeleri*
5a. Flanks (and most of dorsum) smooth ...................... *N. laevissimus*
b. Flanks and dorsum with scattered small tubercles ........................ 6
6a. Anterior face of forearm with scattered, enlarged conical tubercles (≈ 2x neighboring scales) (Fig. 57) ........................................ 7
b. Anterior face of forearm with small, flattened tubercles .................. 8

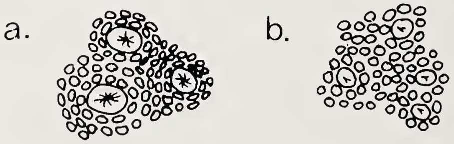

Fig.57: Scalation of the anterior face of the forearm of (a) *Nephrurus levis* and (b) *N. stellatus* showing relative size of tubercles (*Nephrurus* key couplet 6).

7a. Mental rectangular, posterior dorsal tubercles surrounded by rosettes of slightly enlarged scales ........................................................ *N. deleani*
b. Mental hemispherical, scales of rosettes not enlarged .............. *N. stellatus*
8a. Skin of ventral surface of articular region of jaw with scattered, enlarged tubercles ........................................................................ *N. levis*
b. Skin of ventral surface of articular region of jaw with few or no enlarged tubercles ........................................................................ *N. vertebralis*

### *Nephrurus asper* Günther, 1876 (Fig. 58)

1876 *Nephrurus asper* Günther. J.Mus. Godeffroy 5: 46.
Type locality: Peak Downs, Queensland.
Holotype: BMNH 1946.8.23.34.

Diagnosis: Dorsal skin of head co-ossified with skull; posterior border of parietals complete; roofing entire occipital region; squamosal large and broad; metatarsals I—IV one and a half or fewer times the length of corresponding phalanges; phalangeal formulae 2-3-4-4-3 (manus), 2-3-4-4-4 (pes); dorsal pattern of head and nape without three dark bands; eight or more interorbital scales; preocular sclaes not enlarged; rosettes around dorsal tubercles spinose; anterior loreal scales minute; tail extremely short; 4—5 longitudinal rows of caudal tubercles; 8—12 caudal annuli. (1, 7, 11, **56**, **61**, 83-B, 87).

Comments: This is the largest species in the genus (maximum SVL 136 mm, AMS R104458) (McPhee 1979 attributed the unlikely total length of 200 mm to this species).

Fig.58: Holotype of *Nephrurus asper* Günther, 1876. BMNH 1946.8.23.34. (Photo courtesy of British Museum (Natural History))

For some reason much confusion seems to have surrounded the size and distribution of this species. For example, Worrell (1963) gives inland Queensland for the range and lists this species size as being second in diminutiveness only to *N. laevissimus*. Specimens from the south-central Northern Territory appear to attain larger sizes than those in other parts of the range.

*Nephrurus asper* ranges across most of northern Australia from the Kimberleys to the central Queensland coast and as far south as the South Australian border and south-central Queensland. In the Northern Territory it ranges from the arid regions of the central desert to the moist tropical rock outcrops of the Alligator Rivers drainages (Fig. 59). The ecology of *N. asper* is atypical for the genus as a whole. It occurs in rocky areas and may excavate burrows under logs, rocks, bark or other debris (Delean 1982). In Arnhem Land (N.T.), it is found in association with sandstone caves, cliffs and outcrops (Cogger 1981). Longman (1918), Bustard (1967b) and Gow (1979) have reported on the typical defensive behavior and vocalization of this species and Gow (1979) documented aspects of egg-laying and burrowing. There are no autotomy septa in *N. asper* — an autapomorphy for this taxon. The natural diet of the species includes small insects and spiders (Broom 1897; Gow 1979). Skinks are also taken in captivity and it is likely that small lizards in general may be important prey items.

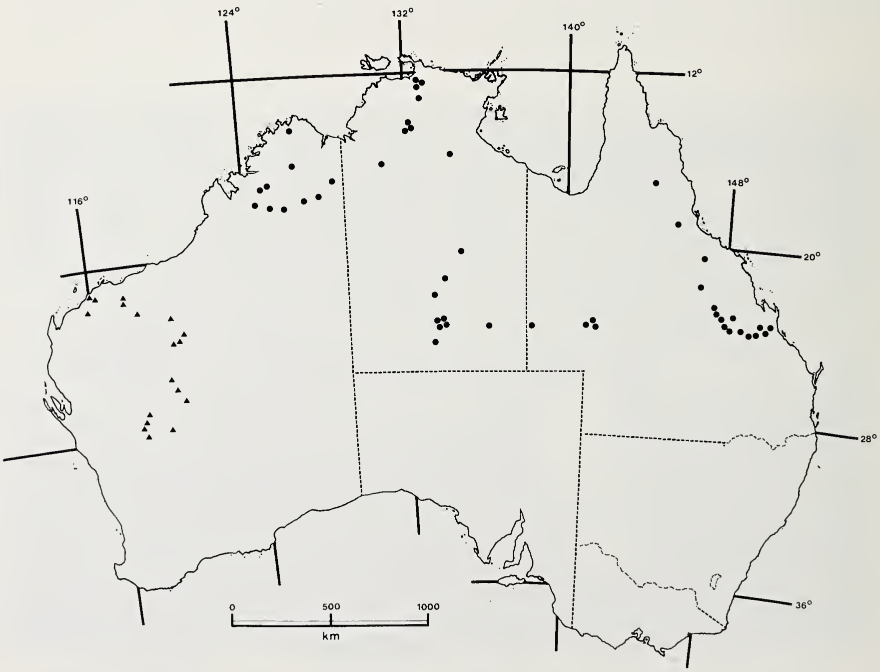

Fig.59: Distribution of *Nephrurus asper* (circles) and *N. wheeleri* (triangles) in Australia.

**Nephrurus deleani Harvey, 1983 (Fig. 60)**

1979 *Nephrurus vertebralis* (part) Cogger. Reptiles and Amphibians of Australia, 2nd ed.: 166.
1983 *Nephrurus deleani* Harvey. Trans.Roy.Soc.S.Aust. 107: 232; figs. 2,3.
Type locality: 44 km SE of Pimba, South Australia (31°31'S 137°08'E).
Holotype: SAMA R21868.

Diagnosis: Single lumbar vertebra; phalangeal formulae 2-3-3-3-3 (manus and pes); metatarsals two or more times length of corresponding phalanges; anterior face of forelimb with scattered enlarged conical tubercles; flanks with scattered tubercles;

Fig.60: Holotype of *Nephrurus deleani* Harvey, 1983. SAMA R21868. SVL 79.3 mm. (Photo courtesy of South Australian Museum)

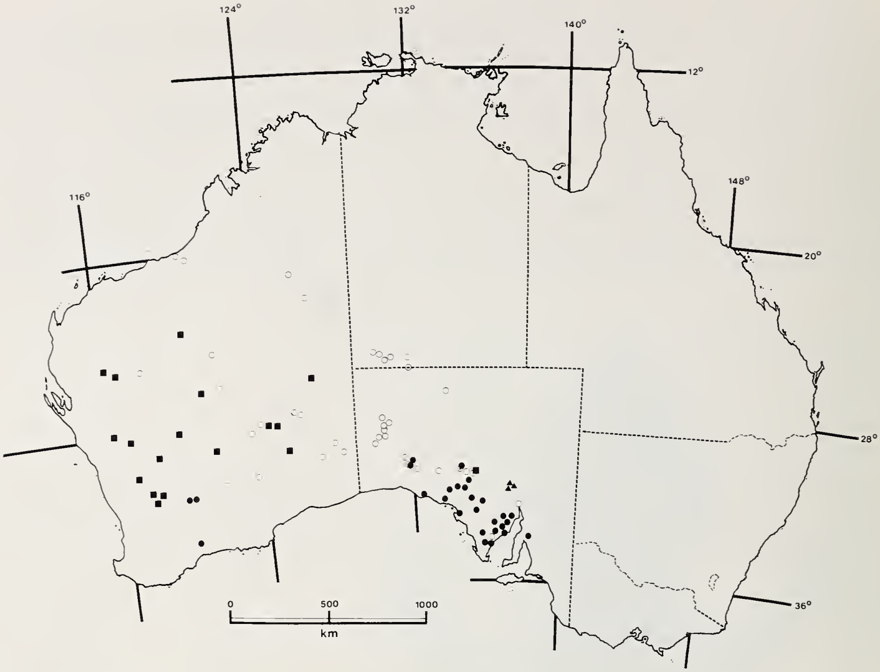

Fig.61: Distribution of *Nephrurus deleani* (closed triangles), *N. laevissimus* (open circles), *N. stellatus* (closed circles) and *N. vertebralis* (closed squares) in Australia.

mental rectangular; posterior dorsal tubercles surrounded by rosettes of slightly enlarged scales; tail moderate, with 9—10 rows of tubercles and 15—17 caudal annuli. (23).

Comments: This species, first discovered in 1971, was believed to represent a disjunct population of *N. vertebralis*, otherwise known only from Western Australia. The type description of Harvey (1983) is detailed and useful. Maximum size recorded for *N. deleani* is 98 mm SVL (Delean 1982). As in all its congeners, females are generally larger than males. Maturity is reached at about 55 mm (Delean 1982). The species is endemic to the region of Pernatty Lagoon in south-central South Australia (Figs. 61,62). It is associated with the sand hills to the north and west of the lagoon (a dry salt lake bed) which are dominated by *Acacia aneura* and *A. ligulata* (Harvey 1983). Surrounding salt lakes and the Gawler Ranges to the south west apparently present a barrier to contact with *N. levis* and *N. laevissimus* (Harvey 1983). *Nephrurus deleani* inhabits the crests of red dunes in this area of low rainfall (< 175 mm/yr) and feeds on moths, spiders, scorpions and several sympatric geckos *(Diplodactylus damaeus, Gehyra variegata* and *Rhynchoedura ornata)* as well as other small nocturnal animals (Delean 1982). Delean (1982) presented additional information on population structure, tail-break frequency and behavior (including a description of scorpion feeding in this species).

Fig.62: Red sand desert with dry lake in background right, vicinity of Birthday, South Australia — near region of greatest sympatry or near-sympatry of species of *Nephrurus*.

### *Nephrurus laevissimus* Mertens, 1958

1924 *Nephrurus levis* (part) Kinghorn. Rec.Aust.Mus. 14: 166.
1958 *Nephrurus laevissimus* Mertens. Senckenberg.Biol. 39: 51; pl. 3 (fig. 4).
Type locality: Dünen etwa 2 km NW des Ayers Rock, Northern Territory, Zentral-Australien.
Holotype: SMF 53201.

Diagnosis: Two ribless cervical vertebrae; phalangeal formulae 2-3-3-3-3 (manus and pes); metatarsals two or more times length of corresponding phalanges; flanks smooth; tail moderate, with 5—7 rows of caudal tubercles and 13—19 caudal annuli.

Comments: Mertens' (1958) description is adequate. *Nephrurus laevissimus* occurs in sandridge regions throughout the arid zone (Fig. 61) and is in sympatry with *N. asper* in the southern Northern Territory, with *N. levis* across northern South Australia, with *N. vertebralis* in eastern Western Australia and with *N. stellatus* in a narrow band across the Nularbor Plain. It reaches a maximum SVL of 87 mm (Delean & Harvey 1981). Pianka & Pianka (1976) and Delean & Harvey (1981), in Western and South Australia respectively, found *N. laevissimus* in association with *Triodia* dominated sandridges where populations may be locally very dense. It feeds primarily on spiders, coleopterans and a variety of other arthropods, and on the diplodactyline gecko *Rhynchoedura ornata* (Pianka & Pianka 1976). Delean & Harvey (1981) provided further information on population structure and Pianka & Pianka (1976) gave a detailed analysis of diet, activity period, temperatures and morphometrics. Tail break frequencies in this species are the lowest known for any autotomizing gecko (0.6%) (Pianka & Pianka 1976). Jones (1985) recorded nematode parasites.

### *Nephrurus levis* De Vis, 1886 (Fig. 63)

1886 *Nephrurus levis* De Vis. Proc.Linn.Soc. New South Wales (2)1: 168.
Type locality: not given (Chinchilla, SE Queensland — fide Covacevich 1971).
Holotype: QM J246.
1886 *Nephrurus platyurus* Boulenger. Ann.Mag.Nat.Hist. (5)18: 91.
Type locality: Adelaide, South Australia.
Holotype: BMNH 1946.8.23.42.
1887 *Nephrurus laevis* Boulenger. Catalogue of Lizards in the British Museum (Natural History), vol. 3: 477 (nomen emendatum pro *Nephrurus levis* De Vis, 1886).
1910 *Nephrurus platyurus* Werner. Die Fauna Südwest-Australiens II: 451.
1929 *Nephrurus levis* Waite. The Reptiles and Amphibians of South Australia: 69; fig. 36.
1961 *Nephrurus laevis* Glauert. A Handbook of the Lizards of Western Australia: 10; fig. 3(2).

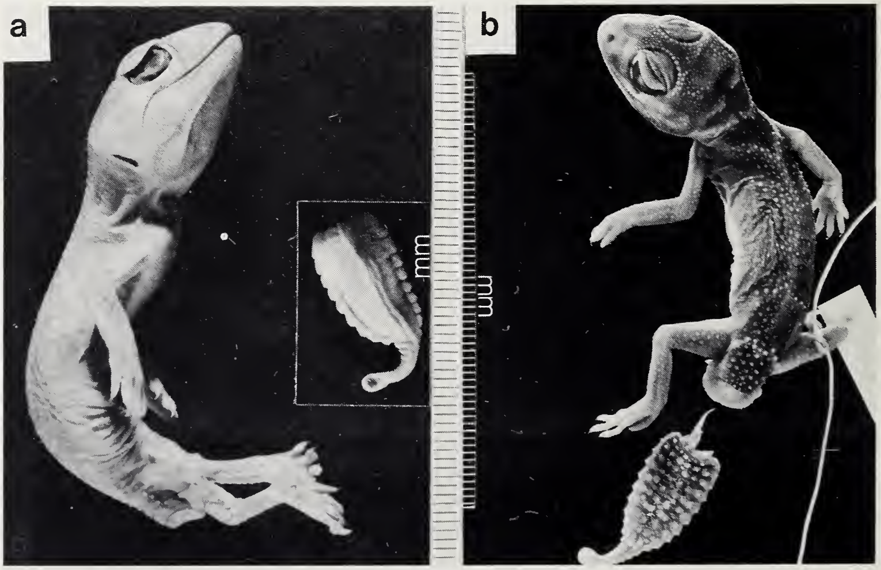

Fig.63: a. Holotype of *Nephrurus levis* De Vis, 1886. QM J246. (Photo courtesy of Jeanette Covacevich, Queensland Museum) b. Holotype of *Nephrurus platyurus* Boulenger, 1886 (= *Nephrurus levis*). BMNH 1946.8.23.42. (Photo courtesy British Museum (Natural History))

1963 *Nephrurus levis levis* Storr. J.Roy.Soc.W.Aust. 46: 87; fig. 2, middle right.
1963 *Nephrurus levis occidentalis* Storr. Ibid.: 88.
Type locality: Narryer, Western Australia, (26°34'S, 115°56'E).
Holotype: WAM R13918.
1963 *Nephrurus levis pilbarensis* Storr. Ibid.: 88.
Type locality: 12 miles E of Mundabullangana, Western Australia, (20°31'S, 118°13'E).
Holotype: WAM R14835.
1970 *Nephrurus laevis* Davey. Australian Lizards: 35.
1975 *Nephrurus levis* Cogger. Amphibians and Reptiles of Australia: 165; figs. 75,408.

Diagnosis: Skin of head co-ossified with skull; posterior border of parietal complete; 30 or more caudal vertebrae; metatarsals two or more times longer than corresponding phalanges; phalangeal formulae 2-3-3-3-3 (manus and pes); anterior loreal scales minute; flanks and dorsum with small scattered tubercles; anterior face of forelimb with small flattened tubercles; skin of ventral surface of articular region of jaw with scattered, enlarged tubercles; tail long, broad, with 6—10 rows of caudal tubercles and 12—21 caudal annuli. (1, 7, **25**, 87).

Comments: De Vis (1886) provided an excellent decription of this species. Systematic confusion has occasionally resulted from the inclusion of other taxa into this taxon and there have been repeated shifts in the spelling of the specific epithet as zoologists trained in Latin have unconsciously rectified De Vis's spelling error. *Nephrurus levis* is the most widespread and variable member of the genus. Its range includes most of arid and semi-arid central Australia west from the Great Dividing Range to the coast of central Western Australia (Fig. 64). *Nephrurus levis* is common both on inland red dunes and coastal white dunes in the regions of Shark Bay (Storr & Harold 1978) and Exmouth (Storr & Hanlon 1980), but rarer near Geraldton to the south (Storr et al. 1983). In the Western Australian wheatbelt *N. levis* occurs exclusively on sandy loams in shrubland (Chapman & Dell 1985). It has also been recorded from Bernier, Dorre and Dirk Hartog Islands near the Peron Peninsula (Storr & Harold 1978). It occurs in all mainland states except Victoria. Storr (1963) divided this species into three subspecific forms in Western Australia.

The maximum known SVL is 94 mm (Waite 1929), Swanson (1976) credits this species with a total length of up to 150 mm. Like most of its congeners it burrows in areas of sandy soil associated with *Triodia*. It feeds on a very wide range of arthropods (especially spiders, beetles, locusts and scorpions) as well as *Rhynchoedura ornata* (Pianka & Pianka 1976). Waite (1929) cited the association of this species with logs and stones but this would appear to be an atypical habitat and, like his description of defensive behavior, be in reference to *N. asper*. Like all diplodactylines it lays two eggs. A photograph by Greer (1981) illustrates a mating pair of *N. levis* with the smaller male biting the nape of the female as he mounts. My observations condtradict Bustard's (1967b) claim that this species does not exhibit a defensive display. Pianka & Pianka (1976) gave detailed information on many aspects of the ecology of this species. Heatwole (1976) reports a particular resistance to cold in this taxon.

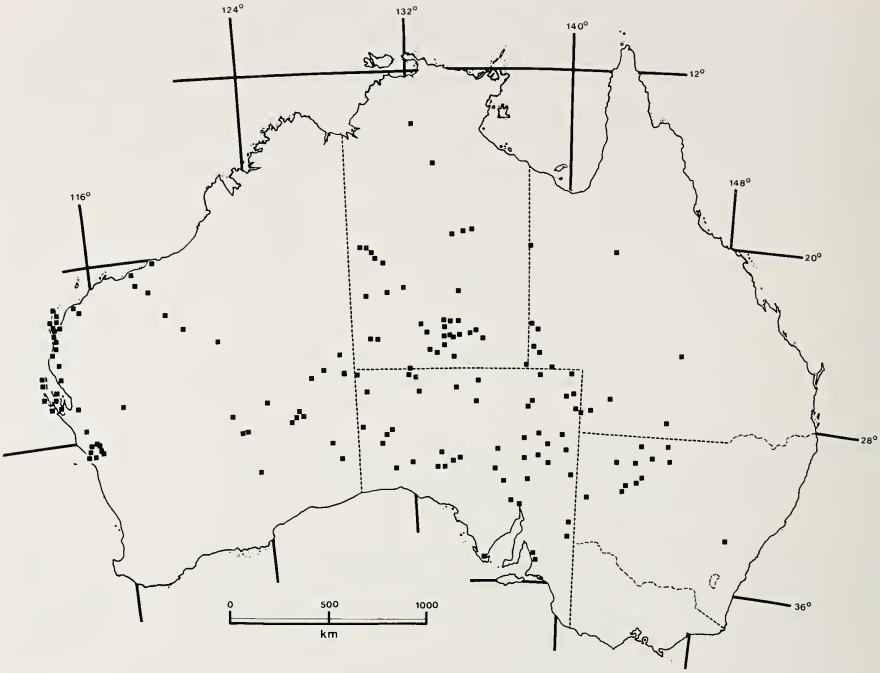

Fig.64: Distribution of *Nephrurus levis* in Australia.

***Nephrurus milii* (Bory de Saint-Vincent, 1825) (Fig. 65)**

1825 *Phyllurus milii* Bory de Saint-Vincent. Dictionnaire Classique d'Histoire Naturelle, vol. 7: 183.

Type locality: Rives de la baie des Chiens-Marins, Australasie (= Shark Bay, Western Australia).

Holotype: presumed lost.

1831 *Cyrtodactylus milii* Gray. The Animal Kingdom Arranged in Conformity with its Organization by the Baron Cuvier, vol. 9: 52 (lapsus pro *Phyllurus milii* Bory de Saint-Vincent, 1825).

1836 *Gymnodactylus miliusii* Duméril & Bibron. Erpétologie Générale, vol. 3: 430; pl. 33 (fig. 1) (nomen substitutum pro *Phyllurus milii* Bory de Saint-Vincent, 1825).

1843 *Gymnodactylus (Anomalurus) miliusii* Fitzinger. Systema Reptilium: 90.

1845 *Phyllurus miliusii* Gray. Catalogue of the Specimens of Lizards in the Collection of the British Museum: 176.

1857 *Gymnodactylus vittatus* Anonymous. Storia Naturale Illustrata del Regno Animale, vol. 3: 61; fig. 2160 (lapsus pro *Gymnodactylus miliusii* ad Duméril & Bibron, 1836; non *Gymnodactylus vitattus* Lichtenstein, 1856).

1867 *Phyllurus myliusii* Gray. The Lizards of Australia and New Zealand in the Collection of the British Museum: 6; pl. 17 (fig. 2) (ex errore pro *Phyllurus miliusii* ad Duméril & Bibron, 1836).
1885 *Gymnodactylus miliusii* Boulenger. Catalogue of the Lizards in the British Museum, vol.1: 48.
1913 *Gymnodactylus asper* Boulenger. Ann.Mag.Nat.Hist. (8)12: 563.
Type locality: Milparinha (= Milparinka), western New South Wales.
Holotype: BMNH 1913.7.28.1.
1934 *Gymnodactylus milii* Loveridge. Bull.Mus.Comp.Zool. 77: 299.
1950 *Gymnodactylus milusii* Barrett. Reptiles of Australia: 30 (ex errore pro *Phyllurus miliusii* ad Duméril & Bibron, 1836).
1954 *Phyllurus milii* Underwood. Proc.Zool.Soc. London 124: 474.
1961 *Gymnodactylus milii* Glauert. A Handbook of the Lizards of Western Australia: 12; fig. 3(5).
1964 *Phyllurus miliusii* Dixon & Kluge. Copeia 1964: 180.
1965 *Gymnodactylus (Underwoodisaurus) milii* Wermuth. Das Tierreich 80: IX.
1967 *Phyllurus milii* Kluge. Aust.J.Zool. 15: 1017.
1967 *Gymnodactylus milii* Cogger. Australian Reptiles in Colour: 25; pl. 8.
1967 *Phyllurus mili* Bustard. Herpetologica 23: 128.
1970 *Underwoodisaurus milii* Bustard. Australian Lizards: 58; pl. 27.
1978 *Phyllurus milii* Storr & Harold. Rec.West.Aust.Mus. 6: 455.
1979 *Underwoodisaurus milii* Cogger. Reptiles and Amphibians of Australia, revised (2nd) ed: 178.
1980 *Phyllurus milii* Russell. J.Herpetol. 14: 415.
1983 *Phyllurus milii* Storr et al. Rec.West.Aust.Mus. 10: 221.

Fig.65: *Gymnodactylus asper* Boulenger, 1913 (= *Nephrurus milii*). BMNH 1913.7.28.1. SVL = 105 mm. (Photo courtesy of British Museum (Natural History))

1983 *Underwoodisaurus milii* Cogger. Reptiles and Amphibians of Australia, 3rd ed: 198; fig. 479.
1987 *Phyllurus milii* King. Aust.J.Zool. 35: 510.

Diagnosis: Trunk vertebrae "procoelous"; anterior loreal scales minute; postmental scales enlarged anteriorly; digits with subdigital lamellae; tail elongate; phalangeal formula unreduced; dorsal pattern of three bands on head and nape absent; labial scales much larger than neighboring scales; claws deep, recurved; no terminal knob on tail. (21, **81**, 87).

Comments: The placement of this species has, in the past, been the major instability in the composition of *Phyllurus*, to which it appears only distantly related. Otherwise there has been little confusion over the identity of this gecko, although at least five different spellings of its specific epithet have been employed. Bory de Saint-Vincent (1825) described an animal from the north-western extreme of the range. Although incomplete, it is sufficient to identify the species without question. *Gymnodactylus asper* Boulenger, 1913 is an extremely large (105 mm SVL), faded *N. milii* with a regenerated tail. An anonymous (1857) Italian distillation of Duméril & Bibron (1836) inexplicably uses the name *Gymnodactylus vittatus* for this species, but this is definitely an error in copying rather than an attempted revision of the specific epithet.

Maximum total lengths of 200 mm have been reported (McPhee 1979) but are probably extremely rare. Specimens from western New South Wales and some offshore islands (Bush 1981) tend to be larger than those from elsewhere in the range, which includes extreme southern Queensland, most of New South Wales and northern Victoria and sweeps across South and Western Australia, intermittantly penetrating several hundred miles inland (Fig. 66). Two records from Northern Queensland are probably in error although there are two reliable records from the southern part of the Northern Territory (Strong & Gillam 1983; R.W. Murphy pers. comm.). North of Perth, *N. milii* is restricted to a narrow coastal belt stretching almost as far north as Exmouth. A single specimen is recorded from Onslow. *Nephrurus milii* is widely distributed on islands off the west and south coasts of the continent, including Bernier, Dorre and Dirk Hartog Islands (near Shark Bay, W.A.) (Storr & Harold 1978), the Houtman Abrolhos (Alexander 1921; Loveridge 1934; Storr et al. 1983) Kangaroo and St. Francis Islands (Waite 1929), Franklin Islands (Schwaner 1985) and the Recherche Archipelago (Kinghorn 1924; Bush 1981).

In coastal Western Australia *Nephrurus milii* is found in association with limestone caves and cliffs (Storr & Harold 1978; Storr et al. 1983). Barrett (1950) refers to this terrestrial species as a house gecko, although this, in the standard use of the phrase, is incorrect. In the eastern parts of its range *N. milii* is known from red sand plains, mallee heath and sclerophyll forest in granite, sandstone and limestone areas (Wells & Wellington 1984). In the Western Australian wheatbelt it is primarily associated with rocky outcrops and woodlands (Chapman & Dell 1985). Over most of its range it is found during the day under logs, rocks and other debris and among exfoliating granite outcrops. Swanson (1976) states that it may also be found in burrows. Communal egg-laying (McPhee 1979; pers. obs.) and over-wintering aggregations in rock crevices (Wells

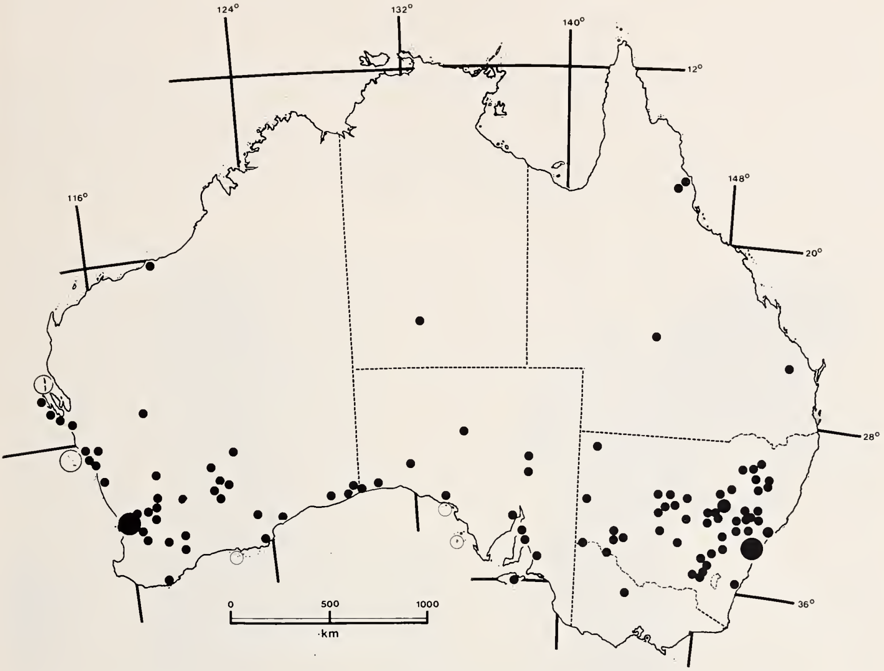

Fig.66: Distribution of *Nephrurus milii* in Australia. Large circles represent 5 or 10 (largest circles) localities in close proximity.

& Wellington 1983) have been reported. Defensive behavior (Bustard 1967b) and tail autotomy and function (Waite 1929) have been considered. Diet includes small lizards (McPhee 1979) as well as many insects and arachnids. *Nephrurus milii* is known to be prey to tiger snakes *Notechis ater niger* (Schwaner 1985) and feral cats (Strong & Gillam 1983).

***Nephrurus sphyrurus*** **(Ogilby, 1892) (Fig. 67)**

1892 *Gymnodactylus sphyrurus* Ogilby. Rec.Aust.Mus. 2: 6.
Type locality: interior of New South Wales (Tumut? — sic!).
Holotype: AMS R3800.
1931 *Heteronota walshi* Kinghorn. Rec.Aust.Mus. 18: 268; fig. 2.
Type locality: Boggabri, on the northern tablelands of New South Wales.
Holotype: AMS R10266.
1965 *Gymnodactylus sphyrurus* Wermuth. Das Tierreich 80: 67.
1967 *Phyllurus sphyrurus* Kluge. Aust.J.Zool. 15: 1017.
1975 *Underwoodisaurus sphyrurus* Cogger. Reptiles and Amphibians of Australia: 179; fig. 80.
1980 *Phyllurus sphyrurus* Russell. J. Herpetol. 14: 415.

1983 *Underwoodisaurus sphyrurus* Cogger. Reptiles and Amphibians of Australia, 3rd ed: 198; fig. 88.

Diagnosis: Caudal vertebrae fewer than 30; post-pygal pleurapophyses well developed; no enlarged post-mental scales; anterior loreal only slightly smaller than posterior; tail short, very wide, without knob at terminus; non-scansorial subdigital lamellae present; phalangeal formula unreduced; without dorsal patterns of three dark bands on head and nape. (25, **27**, 81).

Fig.67: a. Holotype of *Gymnodactylus sphyrurus* Ogilby, 1892 (= *Nephrurus sphyrurus*). AMS R3800. b. Holotype of *Heteronota walshi* Kinghorn, 1931 (= *Nephrurus sphyrurus*). AMS R10266. (Photos courtesy of The Australian Museum)

Comments: Ogilby's (1892) description is adequate, but not completely useful for differentiating all specimens of this species from *N. milii*, with which he suggested close alliance. Kinghorn (1931) placed a specimen from Boggabri, N.S.W. in the genus *Heteronota (= Heteronotia)*. Maximum SVL is 81 mm (AMS R4880). Little is known of the ecology of this species. It is known only from the cool granitic highland areas of the Murray-Darling Basin (Fig. 72). Czechura & Covacevich (1985) considered this species to be at indeterminate risk owing to its patchy distribution in an area of great human impact.

### *Nephrurus stellatus* Storr, 1968

1968 *Nephrurus stellatus* Storr. W.Aust.Nat. 10: 180; fig. 1.
Type locality: 41 miles E of Southern Cross, Western Australia, (31°25'S, 120°00'E).
Holotype: WAM R28363.

Diagnosis: Two ribless cervical vertebrae; lumbar vertebrae two in number; metatarsal two or more times length of corresponding phalanges; phalangeal formulae 2-3-3-3-3 (manus and pes); flanks and dorsum with scattered small tubercles; anterior face of forelimb with scattered, enlarged conical tubercles; mental hemispherical; rosette scales not enlarged; dorsal pattern of distinct white spots; tail moderate, with 5—7 caudal tubercle rows, 9—14 caudal annuli.

Comments: *Nephrurus stellatus* is distributed in a narrow belt across the southern part of Australia from the Eyre Peninsula to central Western Australia (Fig. 61). It reaches a maximum size of 84 mm SVL (Delean 1982). This species is associated with sandy soils dominated by *Eucalyptus* and *Triodia* (Delean 1982) or *Eucalyptus* and *Maleleuca* (Galliford 1981). Burrows are often constructed at the base of *Triodia* bushes. The diet consists of small nocturnal arthropods and perhaps other geckos.

### *Nephrurus vertebralis* Storr, 1963

1961 *Nephrurus laevis* (form 2) Glauert. A Handbook of the Lizards of Western Australia: 10.
1963 *Nephrurus vertebralis* Storr. J.Roy.Soc.W.Aust. 46: 88; fig. 2 top right.
Type locality: Jibberding, Western Australia (29°58'S, 116°51'E).
Holotype: WAM R5231.

Diagnosis: Scleral ossicles fewer than 30; caudal vertebrae greater than 30 in number; metatarsals two or more times length of corresponding phalanges; phalangeal formulae 2-3-3-3-3 (manus and pes); flanks and dorsum with small scattered tubercles, anterior face of forearm with small, flattened tubercles, ventral surface of articular region of jaw smooth, white mid-dorsal stripe extending on to tail; tail moderate, with 7—8 rows of caudal tubercles, 17—19 caudal annuli. (15, 25).

Comments: This species reaches a maximum SVL of 92 mm (Storr 1963) and is distributed throughout the central portion of Western Australia as far south as the northeastern Wheat Belt (Fig. 61). Storr's (1963) description is largely uninformative. Pianka & Pianka (1976) reported that the species is associated with shrub *Acacia* and that it uses the abandoned burrows of other animals. Spiders and a wide range of other arthropods make up the majority of the food items in the diet although, by bulk, lizards *(Rhynchoedura ornata* and *Diplodactylus conspicillatus)* are one of the most important prey items. Further ecological details were provided by Pianka & Pianka (1976).

### *Nephrurus wheeleri* Loveridge, 1932 (Fig. 68)

1909 *Nephrurus laevis* (part) Lucas & Le Souef. The Animals of Australia, Mammals, Reptiles and Amphibians: fig. p. 206.
1932 *Nephrurus wheeleri* Loveridge. Proc. New England Zool.Club 13: 31.

Type locality: Yandil, 30 miles NW of Wiluna, Western Australia.
Holotype: MCZ 32590.
1963 *Nephrurus wheeleri wheeleri* Storr. J.Roy.Soc.West.Aust. 46: 86; fig. 2 top left.
1963 *Nephrurus wheeleri cinctus* Storr. Ibid.: 86; fig. 2 middle left.
Type locality: Tambrey, Western Australia, (21°38'S, 117°37'E).
Holotype: WAM R4284.

Diagnosis: Metatarsals I—IV one and a half or fewer times length of corresponding phalanges; phalangeal formulae 2-3-4-4-3 (manus), 2-3-4-4-4 (pes); dorsal pattern of head and nape without three dark bands; postmental scales enlarged anteriorly; dorsum covered by conical scales surrounded by conical rosette scales; six or fewer interorbital scales; vertical series of enlarged, tuberculate preocular scales; tail moderate. (**56, 61, 81**).

Comments: Loveridge's (1932) description and diagnosis are thorough. *Nephrurus wheeleri* reaches a maximum SVL of 92 mm (Thomson & Hosmer 1963). This species, which resembles *N. asper*, is found only in the Murchison and Fortescue River districts of Western Australia (Fig. 59). *Nephrurus wheeleri* has been recorded from shrubland and open grassland in arid and semi-arid regions where it has a diet similar to that of its congeners (Pianka & Pianka 1976; Cogger et al. 1983).

Fig.68: Holotype of *Nephrurus wheeleri* Loveridge, 1932. MCZ 32950. SVL = 87 mm. (Scientific Photography Laboratory, U.C. Berkeley)

## *Phyllurus* Goldfuss, 1820

1807 *Geckoides* Péron. Voyage de Découvertes aux Terres Australes, vol. 1: 450 (nomen oblitum).
Type species: "*Gecko platurus* Shaw" (= *Lacerta platura* White, 1790) by original designation.
1817 *Phyllurus* Oken. Isis von Oken, Jena 2(8): 1183 (nomen nudum).
1820 *Phyllurus* Goldfuss. Handbuch der Zoologie, vol. 3: 156.
Type species: *Phyllurus spinosus* Goldfuss, 1820 (pro vernacular of La Cépède, 1788, vol. 2: pl. 23, fig. 1) by monotypy.
1827 *Phyllura* Kaup. Isis von Oken, Jena 20: (nomen substitutum pro *Phyllurus* Oken, 1817).

Species referred: *Phyllurus caudiannulatus* Covacevich, 1975, *P. cornutus* (Ogilby, 1892), *P. platurus* (White, 1790), *P. salebrosus* Covacevich, 1975.

Diagnosis: (Node 6) A monophyletic taxon diagnosed by the following characters: scleral ossicles fewer than 30; clavicular fenestrae tiny or absent; pectineal process of pubis enlarged; proximal joints of manus and pes kinked; tail depressed, leaf-shaped; limbs long and slender; head flattened, distinctly triangular; toes bear non-scansorial lamellae; skin of head co-ossified with skull; dorsum of body and tail bears spinose scales surrounded by rosettes. (15, 48*, 58*, **68**, 97*).

Within *Phyllurus* there are two diagnosable subgroups (Nodes 7 and 8) (see Fig. 17). Node 7, consisting of *P. caudiannulatus* and *P. platurus* is diagnosed by the following characters: Supraocular portion of frontal flattened; zero or one inscriptional ribs; anterior process of interclavicle terminates in a broadened disk; metacarpals V and IV shortest; no enlarged post-mental scales; rostral excluded from nostril; flank tubercles small. (5, 32-A, 37*, 45*, 81).

Node 8, including *Phyllurus cornutus* and *P. salebrosus*, is diagnosed by the following characters: Anterior process of interclavicle absent; epipubic cartilage greatly expanded; rosettes surrounding dorsal spines and tubercles also spinose; rostral contacts nostril; flank tubercles elongate, hooked. (38*, 47*, 83-B).

Comments: *Phyllurus* was the first genus of carphodactylines to be discovered and described. The characteristic flattened leaf-shaped tail of the type species, *P. platurus* gave the name to the taxon. Péron (1807) used the name *Geckoides* but subsequent disuse has rendered this a nomen oblitum. The term "phyllure" was first used by Cuvier, but not as a binomial. Oken (1817) used the latinized *Phyllurus*, but as a nomen nudum. The first recognized acceptable usage of this generic name had long thought to be that of Schinz (1822), but Goldfuss (1820) used the combination *Phyllurus spinosus* and thus should be credited with authorship of the taxon. The absence of scansorial pads and the spiny skin of these geckos led a number of early workers to place members of this group in the Agamidae. Although Wagler (1830) clearly indicated their proper inclusion as gekkonids, Swainson (1839) wrote that the leaf-tailed lizard of New Holland served as a link to connect the geckos to *Stellio*.

The contents of the genus have been in flux since the description of the second species, *N. milii*, which has been variously assigned to the polyphyletic *Gymnodactylus* and to its own genus (along with *P. sphyrurus*), *Underwoodisaurus*. The results of this study do not concur with the views of Kluge (1967b) and Russell (1980) in their inclusion of these forms in *Phyllurus*. Rather, *milii* and *sphyrurus* should be considered members of the genus *Nephrurus* or perhaps members of a distinct genus, *Underwoodisaurus* (although this group is not diagnosable at present). The retention of these taxa in *Phyllurus* would leave this genus polyphyletic (see Fig. 17). Kluge (1967b) removed *P. vankampeni* from the genus, otherwise leaving Underwood's (1954) redefined *Phyllurus* intact. Kluge's (1967b) diagnosis of the genus is no longer adequate because some of the taxa he included have been removed. Covacevich (1975) provided good descriptions of all species but her key is not generally workable. The genus as a whole is distributed along the eastern coast of Australia from the northern Cape York Peninsula south to the area of Sydney. Members of the genus are by far the most well known Australian carphodactylines.

## Key to the Species of *Phyllurus*

1a. Rostral contacts nostril .................................................. 2
b. Rostral excluded from nostril .................................................. 3
2a. Throat tuberculate .................................................. *P. salebrosus*
b. Throat smooth .................................................. *P. cornutus*
3a. Scales at metatarsal-phalangeal joint tuberculate (Fig. 69) ......... *P. platurus*
b. Scales at metatarsal-phalangeal joint spinose ............... *P. caudiannulatus*

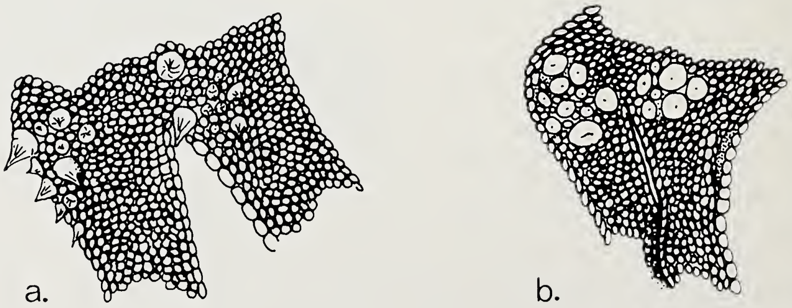

Fig.69: Metatarsal-phalangeal joint region of digits III and IV of (a) *Phyllurus caudiannulatus* and (b) *P. platurus*. Note the spinose tubercles in a (*Phyllurus* key character 3).

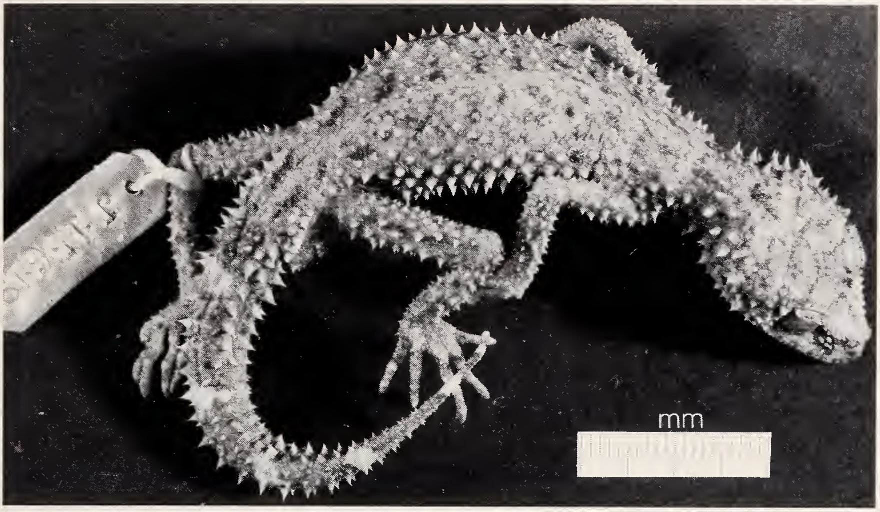

Fig.70: Holotype of *Phyllurus caudiannulatus* Covacevich, 1975. QM J15619. (Photo courtesy of Jeanette Covacevich, Queensland Museum)

***Phyllurus caudiannulatus*** **Covacevich, 1975 (Fig. 70)**

1975 *Phyllurus caudiannulatus* Covacevich. Mem.Qld.Mus. 17: 297; figs. 2—4; pls. 36a, 37c, 38a, 39a, 40a.
Type locality: Bulburin State Forest, via Many Peaks, Queensland.
Holotype: QM J15619.

Diagnosis: First autotomy plane in fifth caudal vertebra; flank tubercles small; preanal organs lacking; scales at metatarsal-phalangeal joint spinose; dorsal scales of body generally spinose; tail rounded or leaf-shaped; original tail bearing white bands.

Comments: The description of *P. caudiannulatus* (Covacevich 1975) is detailed and useful. This small (maximum SVL 112 mm — AMNH 27326) species is known from Bulburin State Forest, to the south and west of Brisbane, and from Eungella National Park, all in south-eastern Queensland (Fig. 72). It has been collected under bark and on tree trunks and branches in cloud forest, primarily 350—950 m elevation. It has been reported from heights of 12 m in trees (Covacevich 1975). At Bulburin it is sympatric with *P. salebrosus*. Coleopterans have been recorded as natural dietary items (Rose 1974).

***Phyllurus cornutus*** **(Ogilby, 1892) (Fig. 71)**

1892 *Gymnodactylus cornutus* Ogilby. Rec.Aust.Mus. 2: 8.
Type locality: Bellenden—Ker Ranges, NE Queensland. (A note with the specimen reads "Herbert River, Q. 13/10/91 Ogilby").
Holotype: AMS R749.

1897 *Phyllurus lichenosus* Günther. Novit.Zool. 4: 404; pl. XII.
Type locality: Mount Bartle Frere, Queensland.
Holotype: presumed lost.
1901 *Phyllurus cornutus* Garman. Bull.Mus.Comp.Zool. 39: 2.
1909 *Gymnodactylus cornutus* Lucas & Le Souef. The Animals of Australia, Mammals, Reptiles and Amphibians: 209.
1950 *Gymnodactylus spyrurus* Barrett. Reptiles of Australia: 31 (non *Gymnodactylus sphyrurus* Ogilby, 1892; lapsus pro *Gymnodactylus cornutus* Ogilby, 1892).
1954 *Phyllurus cornutus* Underwood. Proc.Zool.Soc. London 124: 474.
1976 *Phyllurus cornutum* Swanson. Lizards of Australia: 18; pl. 29.
1979 *Phyllurus cornutus* Cogger. Reptiles and Amphibians of Australia, revised (2nd) ed.: 174; figs. 78, 423, 424.

Diagnosis: Rostral contacts nostril, preanal pores absent, throat smooth, flank tubercles enlarged and hooked; attenuated tail tip > 1/3 total tail length.

Comments: Ogilby's (1892) description is adequate, although a variable feature — a spinate knob on the brillar flap — is stressed as the diagnostic character. Günther (1897) described *P. lichenosus* based on his specimen's variance from *P. cornutus* in this character. This is one of the largest Australian geckos, reaching 144 mm SVL (AMS

Fig.71: Holotype of *Gymnodactylus cornutus* Ogilby, 1892 (= *Phyllurus cornutus*). AMS R749. (Photo courtesy of The Australian Museum)

42163). Populations in the southern parts of the range tend to be of smaller size than those from the Cape York Peninsula. There are three disjunct populations of *Phyllurus cornutus*, all to the east of the Great Dividing Range, located in the northern Cape York near Coen, in the area between Townsville and Cooktown, and in a strip from extreme south-eastern Queensland through central coastal New South Wales (Fig. 72). Most known localities are above 300 m elevation. A population near Stanthorpe (Qld.) is recognized as distinct (Covacevich 1975) and may warrant specific recognition (J. Covacevich pers. comm.). Covacevich (1975) stated that similarly disjunct patterns are

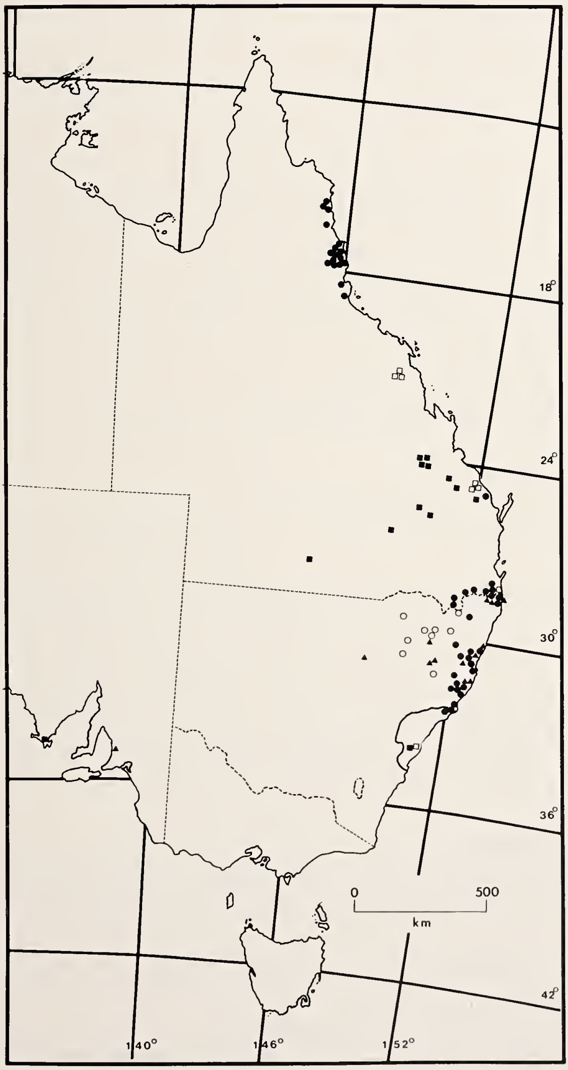

Fig.72: Distribution of *Phyllurus cornutus* (closed circles), *P. caudiannulatus* (open squares), *P. salebrosus* (closed squares), *Nephrurus sphyrurus* (open circles) and *Phyllurus platurus* (area bounded by dark line in the region of Sydney, N.S.W.). Closed triangles represent records of *P. platurus* probably referable to *P. caudiannulatus*.

seen in the distribution of *Tropidechis carinatus, Leiolopisma challengeri, Lechriodus fletcheri* and *Litoria chloris.*

This species occurs in virgin and disturbed areas of cloud forest and adjacent sclerophyll forests, usually found on trees, to a height of 10 m (Loveridge 1934). At Stanthorpe it is found in a granite boulder area with relatively open vegetation (Covacevich 1975). Bustard (1965) recorded this species from cave mouths and the trunks of *Laportea gigas* in northern New South Wales. Bustard (1965) and Rösler (1981) discussed behavior and feeding in captivity. *Phyllurus cornutus* is chiefly an arthropod feeder in the wild. The species is a known prey item in the diet of the elapid *Demansia psammophis* (see Shine 1980).

***Phyllurus platurus* (White, 1790) (Figs. 73,74)**

1790 *Lacerta platura* White. Journal of a Voyage to New South Wales: 246; pl. 32 (fig. 2).
Type locality: New South Wales.
Holotype: probably BMNH xxii.98.a (cleared and stained specimen) (fide Covacevich 1975).
1797 *Stellio phyllurus* Schneider. Amphibiorum Physiologiae Specimen Secundeum. 2nd ed.: 31 (nomen substitutum pro *Lacerta platura* White, 1790).
1802 *Stellio platurus* Daudin. Histoire Naturelle Générale et Particulière des Reptiles, vol. 4: 24.
1802 *Lacerta platura* Shaw. General Zoology, vol III, pt. I: 247.
1804 *Agama grandoculis* La Cépède. Ann.Mus.Natl.Hist.Nat. Paris 4: 191.
Type locality: Nouvelle-Hollande.
Holotype: MNHN (specimen number unknown).
1804 *Lacerta platura* Hammer. Observationes Zoologicae: 266.
1807 *Geckoides platurus* Péron. Voyage de Découvertes aux Terres Australes, vol. 1: 450.
1820 *Phyllurus spinosus* Goldfuss. Handbuch der Zoologie, vol. 3: 156 (nomen substitutum pro *Lacerta platura* White, 1790; pro vernacular of La Cépède 1788, vol. 2: pl. 23, fig. 1).
1820 *Agama platyura* Merrem. Versuch eines Systems der Amphibien: 51 (nomen substitutum pro *Lacerta platura* White, 1790).
1820 *Agama discosura* Merrem. Ibid.: 51 (pro vernacular "lézard discosure" of La Cépède 1804).
Type locality: Nova Hollandia.
Holotype: MNHN (specimen not located).
1822 *Phyll(urus) novaehollandiae* Schinz. Das Thierreich eingetheilt nach dem Bau der Thiere von Cuvier: 79 (ex Cuvier manuscript; nomen substitutum pro *Lacerta platura* White, 1790).
1825 *Phyllurus cuvieri* Bory de Saint-Vincent. Dictionnaire Classique d'Histoire Naturelle, vol.7: 183.
Type locality: environs de Port Jackson, New South Wales.
Holotype: MNHN (presumed lost).

1825 *P(hyllurus) whitii* Gray. Ann.Phil. (2)10: 198.
Type locality: not given.
Holotype: BMNH, specimen not located.
1826 *Phyllurus platurus* Fitzinger. Neue Classification der Reptilien nach ihren natürlichen Verwandschaften: 47.
1827 *Phyllura discosura* Kaup. Isis von Oken, Jena 20: 613 (nomen substitutum pro *Phyllurus* Oken, 1817).
1827 *Phyllura grandoculis* Kaup. Ibid.: 613 (nomen substitutum pro *Phyllurus* Oken, 1817).
1830 *Gymnodactylus platyurus* Wagler. Natürliches System der Amphibien: 144.
1831 *Cyrtodactylus platura* Gray. In: The Animal Kingdom Arranged in Conformity with its Organization by the Baron Cuvier, vol. 9: 52.
1833 *Gecko platycaudus* Schinz. Naturgeschichte und Abbildungen der Reptilien: 75; pl.17 (fig. 3) (nomen substitutum pro *Stellio phyllurus* Schneider, 1797).
1834 *Gymnodactylus (Phyllurus) phyllurus* Wiegmann. Herpetologia Mexicana: 19.
1836 *Gymnodactylus phyllurus* Duméril & Bibron. Erpétologie Générale, vol. 3: 428.
1839 *Phyllurus australis* Swainson. The Natural History of Fishes, Amphibians, and Reptiles, vol.2: 370 (fig. 123a) (nomen substitutum pro *Phyllurus platurus* (White, 1790)).
1842 *Phyllurus cuvierii* Bory de Saint-Vincent. Traité Elementaire d'Erpétologie ou l'Histoire Naturelle des Reptiles: 130 (lapsus pro *Phyllurus cuvieri* Bory de Saint-Vincent, 1825).
1843 *Gymnodactylus (Phyllurus) platurus* Fitzinger. Systema Reptilium: 92.
1845 *Phyllurus platurus* Gray. Catalogue of the Specimens of Lizards in the Collection of the British Museum: 176.
1845 *Phyllurus inermis* Gray. Ibid.: 176.
Type locality: Australia.
Holotype: BMNH xxii.100.a.
1885 *Gymnodactylus platurus* Boulenger. Catalogue of Lizards in the British Museum, vol. 1: 49.
1909 *Gymnodactylus phyllurus* Lucas & LeSouef. The Animals of Australia, Mammals, Reptiles, and Amphibians: 209.
1910 *G(ymnodactylus) platyurus* Werner. Die Fauna Südwest- Australiens, II: 453.
1934 *Phyllurus platurus* Loveridge. Bull.Mus.Comp.Zool. 77: 298.
1950 *Gymnodactylus platurus* Barrett. Reptiles of Australia: 31.
1954 *Phyllurus platurus* Underwood. Proc.Zool.Soc. London 124: 474.

Diagnosis: Rostral excluded from nostril; scales at metatarsal-phalangeal joint flat, tuberculate; preanal organs absent; flank tubercles small; original tail without bands; first autotomy plane in sixth caudal vertebra.

Comments: *Phyllurus platurus* was the first species of carphodactyline gecko to be described. Its distinct morphology, coupled with its abundance in and around Sydney, Australia's oldest and largest population center, has been responsible for the many references relating to this animal. White's (1790) description is short but, with the ac-

Fig.73: Presumed holotype of *Lacerta platura* White, 1790 (= *Phyllurus platurus*). BMNH xxii.98.a. (Photo courtesy British Museum (Natural History))

companying illustration, is sufficient to diagnose the species from other congeners except *P. caudiannulatus*. Numerous names have been substituted for *platurus*. This was especially true during the first half of the nineteenth century. Gray's (1845) *P. inermis* is based on a *P. platurus* with a typical smooth-scaled regenerated tail.

Girard (1857: 303) wrote "this species, owing to its uncommon aspect, has often attracted the attention of naturalists and iconographists, so that we may say that it is pretty generally well known". Unfortunately this is not true. As for most carphodactylines, little is known of the biology of this species. Swanson (1976) reports a maximum total length of 150 mm. The largest individual museum specimen measures 95.9 mm SVL (Covacevich 1975). The southern leaf-tailed gecko is distributed in a small area of coastal south-central New South Wales (Fig. 72). This range corresponds to the Sydney-Hawkesbury Sandstone (Breeden & Breeden 1972). It is likely that specimens reported from Queensland localities are either *P. cornutus*, or more likely *P. caudiannulatus*. It occurs in forests, in association with rocks (Cogger et al. 1983), in small wind-blown caves and in houses and garages (Cogger 1967). It is chiefly saxicolous and spends the daylight hours partially active in deep rock crevices. Bory de Saint-Vincent (1825) gave the earliest information on carphodactyline biology and stated that *P. cuvieri (= P. platurus)* feeds on insects and aquatic larvae in the rocky areas around Port Jackson (= Sydney). The reference to aquatic larvae is doubtful but the species is chiefly insec-

Fig.74: Holotype of *Phyllurus inermis* Gray, 1845 (= *Phyllurus platurus*). BMNH xxii.100.a. (Photo courtesy British Museum (Natural History))

tivorous. Green (1973) reported spiders *(Hemidoea)*, coleopterans, lepidopterans and acridids in the diet. Eggs are laid in rock crevices and deposition sites may be communal and up to 16 individuals have been found in a single rock crevice (Green 1973). Embryos are at stage 29 of development at the time of ovoposition (Shine 1983b). Covacevich (1975) gave information on tail break frequencies in this species as well as bivariate plots of several body size parameters for this and other *Phyllurus*. Mebs (1973) and Green (1973) described the defensive response of this species. Red mite infestations are common and cats, rodents, owls, bats and *Antichinus stuartii* (a marsupial mouse) are probable predators (Green 1973).

***Phyllurus salebrosus* Covacevich, 1975 (Fig. 75)**

1975 *Phyllurus salebrosus* Covacevich. Mem.Qld.Mus. 17: 300; figs. 3—4; pls. 36c, 37a, 38b, 39b, 40b.
Type locality: Monto, SE Queensland.
Holotype: QM J8142.

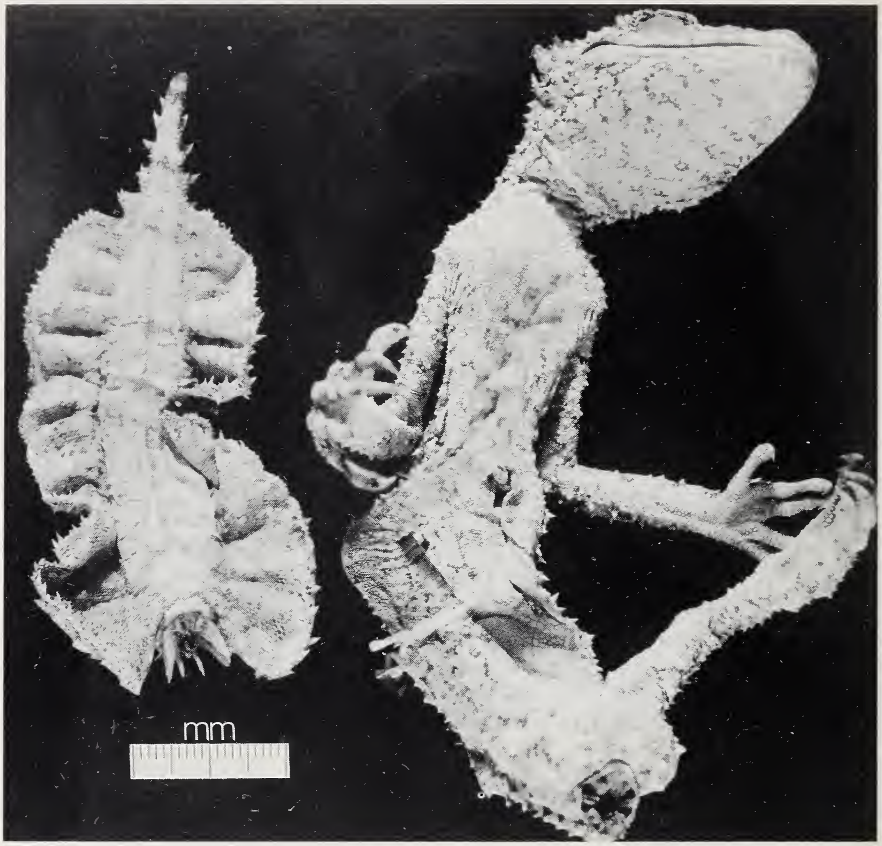

Fig.75: Holotype of *Phyllurus salebrosus* Covacevich, 1975. QM J8142. (Photo courtesy of Jeanette Covacevich, Queensland Museum)

Diagnosis: Rostral contacts nostril; throat tuberculate; flanks with enlarged tubercles; preanal pores present; attenuated tail tip < 1/3 total tail length. **(92)**.

Comments: *Phyllurus salebrosus* is among the largest Australian carphodactylines at 143 mm SVL (QM J33732). It is rare throughout its range which extends over parts of coastal and mid southern Queensland (Fig. 72). Records of specimens from Sydney (N.S.W.) and Port Lincoln (S.A.) are surely in error. It has been collected from areas of granite rocks, sandstone and on a cave roof (Covacevich 1975). It may be arboreal, saxicolous or cavernicolous in different areas and generally occurs in more open habitats than its morphologically similar, but allopatric congener *P. cornutus*. It is primarily insectivorous.

## *Rhacodactylus* Fitzinger, 1843

(Note: Members of the subgenus *Pseudothecadactylus* follow other *Rhacodactylus* spp.)

1843 *Rhacodactylus* Fitzinger. Systema Reptilium: 90.
Type species: *A(scalabotes) leachianus* Cuvier, 1829 by original designation.
1866 *Correlophus* Guichenot. Mém.Soc.Hist.Nat. Cherbourg 12: 249.
Type species: *Correlophus ciliatus* Guichenot, 1866 by monotypy.
1873 *Ceratolophus* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 4: 204 (non *Ceratolophus* Kieffer, 1899 = Diptera).
Type species: *Ceratolophus hexaceros* Bocage, 1873 by monotypy.
1878 *Chameleonurus* Boulenger. Bull.Soc.Zool. France 3: 68.
Type species: *Chameleonurus trachycephalus* Boulenger, 1878 by monotypy.
1889 *Chamaeleonurus* Carus. Zool.Anz., Leipzig: 83 (ex errore pro *Chameleonurus* Boulenger, 1878).
1972 *Ceratophus* Mufti & Hafiz. Biologia (Lahore) 18: 191 (lapsus pro *Ceratolophus* Bocage, 1873).

Species referred: *Rhacodactylus auriculatus* (Bavay, 1869); *R. chahoua* (Bavay, 1869); *R. ciliatus* (Guichenot, 1866); *R. leachianus* (Cuvier, 1829); *R. sarasinorum* Roux, 1913; *R. trachyrhynchus* Bocage, 1873; *R. (Pseudothecadactylus) australis* (Günther, 1877); *R.(P.) cavaticus* Cogger, 1975; *R.(P.) lindneri* Cogger, 1975.

Diagnosis: *Rhacodactylus*, as previously construed was a metataxon, a paraphyletic grouping which excludes some members of the natural group united by a suite of characters at Node 18. Thus, the traditional New Caledonian group of *Rhacodactylus* consists of the taxa sharing the character states present at Node 18 but lacking those at Node 20. The following characters diagnose the species of *Rhacodactylus* including those of the subgenus *Pseudothecadactylus*: Supraocular portion of frontal deeply furrowed or concave; fronto-parietal suture straight; overlap of jugal and infraorbital process of prefrontal extensive; metatarsals III and IV parallel; lateral pair of cloacal bones absent; juvenile color pattern with paravertebral rows of light-colored spots; aural opening partially occluded by skin folds; digital scansors broadly dilated; apical pads single, medial; tail with subcaudal lamellae. (5, **9**, 13, **59**, 62, 70, 7

Within *Rhacodactylus* (sensu stricto) a single resolvable subgrouping occurs (apart from those characters diagnosing *Pseudothecadactylus*). Represented by Node 19 on the cladogram this unites *R. chahoua* and *R. ciliatus*. This clade is diagnosed by the following characters: anteriormost autotomy septum in fifth caudal vertebra; webbing between digits IV and V present; folds of loose skin on face of hindlimbs. (30, 89, 90).

Comments: (comments for *Pseudothecadactylus* follow subgeneric synonymy): The genus *Rhacodactylus* includes some of the largest geckos in the world (Bauer & Russell 1986; Russell & Bauer 1986). Because of this size there have been a great many references to the taxon (see Bauer 1985b), although few have made substantial additions to the knowledge of *Rhacodactylus*. Cuvier described *R. leachianus* in 1829 as a member of the genus *Ascalobotes*. This generic designation was uniformly miscited as *Platydactylus*. The species remained in this genus until Fitzinger (1843) erected the subgenus *Rhacodactylus* within *Hoplodactylus*. The outlandish morphologies of several of the species resulted in the erection of new genera based solely on these autapomorphic charaters. Nomenclature stabilized after the review of New Caledonian geckos by Boulenger (1883). *Rhacodactylus* occurs over much of New Caledonia, although no reliable records exist from the west coastal plains areas. Records from the Loyalty Islands are all anecdotal. Records from the Isle of Pines and the Belep Isles may be valid, although Roux (1913) considered the genus as being restricted to New Caledonia proper. All species are primarily arboreal and as many as four species may occur in sympatry. Remarks on the biology and systematics of the species may be found in Boulenger (1883), Roux (1913), Mertens (1964a) and Meier (1979). Jouan (1863) and Bavay (1869) report that the indigenous people of New Caledonia, the Kanaks, have a variety of superstitions regarding members of the genus. This is still true to some extent and most people will avoid these animals, which are known by the vernacular "cameleons".

### Key to the Species of *Rhacodactylus*

1a. All digits clawed ................................................ 2
b. Digit I of manus clawless .................... subgenus *Pseudothecadactylus*
2a. Body with loose folds of skin along throat and flanks, digits half-webbed ... 3
b. Body without lateral folds, digits less than one third webbed ................ 4
3a. Rostral contacts nostril ........................................ *R. chahoua*
b. Rostral excluded from nostril ................................. *R. leachianus*
4a. Pair of posteriorly converging ciliated crests on dorsum ........... *R. ciliatus*
b. Dorsal scales generally homogeneous ................................ 5
5a. Head with raised bosses or rugosities .............................. 6
b. Head smooth, no bosses or rugosities ...................... *R. sarasinorum*
6a. Snout rugose ........................................ *R. trachyrhynchus*
b. Raised orbital and aural bosses present, snout smooth .......... *R. auriculatus*

***Rhacodactylus auriculatus* (Bavay, 1869) (Fig. 76)**

1869 *Platydactylus auriculatus* Bavay. Mém.Soc.Linn. Normandie 15: 6.
Type locality: Mont d'Or (= Mont Dore), Nouvelle-Calédonie.
Holotype: EMNB (presumed lost).
1873 *Ceratolophus hexaceros* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 4: 205.
Type locality: Nouvelle Calédonie.
Syntypes: MLI (specimen number unknown, destroyed by fire).
1878 *Platydactylus (Ceratolophus) auriculatus* Sauvage. Bull.Soc.Philomat., Paris (7)3: 67.
1881 *Ceratolophus auriculatus* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 8: 130.
1883 *Rhacodactylus auriculatus* Boulenger. Proc.Zool.Soc. London 1883: 127.
1920 *Ceratolophus auriculatus* Woodland. Q.J.Microscop.Sci. 65: 63.
1932 *Rhacodactylus auriculatus* Burt & Burt. Bull.Amer.Mus.Nat.Hist. 63: 479.

Fig.76: Two color phases of *Rhacodactylus auriculatus* (Bavay, 1869) from Touaourou, New Caledonia. (Scientific Photography Laboratory, U.C. Berkeley)

1949 *Gecko ceratolophus* Boring et al. Peking Nat.Hist.Bull. 17: 85 (lapsus pro *Ceratolophus auriculatus* (Bavay, 1869) ad Woodland (1920)).
1964 *Rhacodactylus auriculatus* Mertens. Zool.Garten, Leipzig, N.F. 29: 52.
1972 *Ceratophus auriculatus* Mufti & Hafiz. Biologia (Lahore) 18: 191 (lapsus pro *Ceratolophus auriculatus* (Bavay, 1869) ad Woodland (1920)).
1979 *Rhacodactylus auriculatus* Meier. Salamandra 15: 113.

Diagnosis: This species is diagnosed by the following characters: lateral prong of postfrontal distinctly ventrally curved; parietal crest present; lateral lip of quadrate extended in a flange; fewer than 30 scleral ossicles; two to four inscriptional ribs; juvenile color pattern as adult; aural opening free of skin folds; first infralabials may contact behind mental; folds of loose skin on posterior face of hindlimb present; preanal organs extend onto thighs; pygal region tapers into post-pygal region. (6, 10, 12, 15, 32B, **62**, **70**, 80, 90, 93, **102**).

Comments: The large knobs on the skull of this species make it difficult to confuse with any other. It is unclear how Bocage (1873) could have failed to recognized his *Ceratolophus hexaceros* from Bavay's (1869) superb description of *Platydactylus auriculatus*. This is the most well known of the members of the genus and over 100 specimens exist in museum collections.

*Rhacodactylus auriculatus* is one of the smallest members of the genus with a maximum SVL of 125 mm (Boulenger 1883; MNHN 1974-805). It is distributed over much of southern and south-central New Caledonia (Fig. 77), chiefly in association with ultramafic soils and their associated vegetation (Figs. 30,84). Concentrations within the range of the species probably reflect ease of access and collection concentration in these areas. It has been collected from a variety of shrubs and smaller trees (Bavay 1869; Meier 1979; Böhme & Henkel 1985; pers. obs.).

While Bavay (1869) found the species in montaine forest I have collected it at sea level all along the south-east coast of New Caledonia and it seems likely that lower elevation, drier forests are more typical habitats for this gecko. One individual was collected on a tree trunk 3 m from high tide. Individuals may also spend substantial periods of time on the ground as they are frequently seen crossing dirt roads between forest stands south of Yaté. This species is occasionally encountered basking on tree trunks 1—3 m above the ground during daylight hours (Meier 1979; pers. obs.). Sameit (1985) and Böhme & Henkel (1985) included additional information about the habitat of *R. auriculatus*. Reported dietary items include flowers of the *Geiossois*, snails (Bavay 1869), crickets and *Bavayia sauvagii* (Bauer & DeVaney 1987). It is probable that spiders

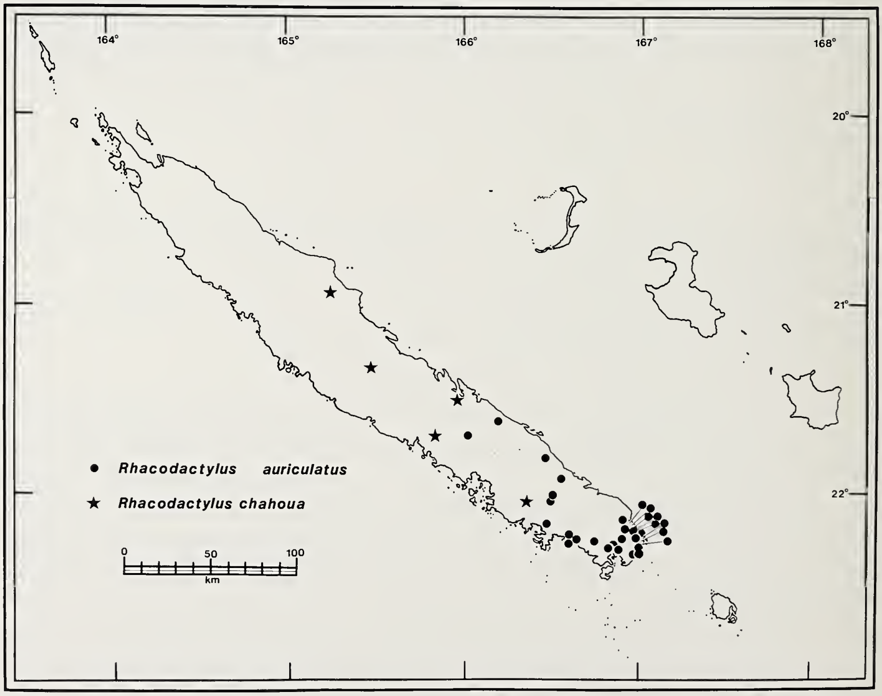

Fig.77: Distribution of *Rhacodactylus auriculatus* (circles) and *R. chahoua* (stars) in New Caledonia.

and a wide variety of other arthropods are also important in the diet of this species. Mertens (1964a) reported on the frugivorous habits of this species in captivity. *Rhacodactylus auriculatus* is highly variable in color and a wide range of pattern phases may be found at one locality (Böhme & Henkel 1985). The species is oviparous and lays two eggs (approximately 25 x 11 mm). Repeated copulations are common in captivity (K. McCloud pers. comm.). No laying sites have been found in New Caledonia and it is possible that the species can breed all year. Incubation period ranges from 42—48 days (Henkel 1986a) to about 60 days (K. McCloud pers. comm.). Mites are frequently present in mite-pockets on the hindlimbs (Böhme & Henkel 1985; pers. obs.).

Fig.78: Neotype of *Rhacodactylus chahoua* (Bavay, 1869). CAS 156692 (SVL = 136 mm).

*Rhacodactylus chahoua* **(Bavay, 1869) (Fig. 78)**

1869 *Platydactylus chahoua* Bavay. Mém.Soc.Linn. Normandie 15: 3.
Type locality: Vallée d'Amoa, near St. Thérèse, approx. 15 km NW of Poindimié, New Caledonia. (Type locality of Bavay (1869) = Kanala, Lifou (sic!, probably Canala, New Caledonia)).
Holotype: EMNB (presumed lost).
Neotype: CAS 156692 (designated by Bauer 1985a).
1878 *Platydactylus (Rhacodactylus) chahoua* (part) Sauvage. Bull.Soc.Philomat., Paris (7)3: 66.
1879 *Chameleonurus chahoua* (part) Boulenger. Bull.Soc.Zool. France 4: 142.
1883 *Rhacodactylus chahoua* Boulenger. Proc.Zool.Soc. London 1883: 125; pl. XXI (figs. 1,1a—1d).

Diagnosis: This species is diagnosed from its congeners by the characters at Node 19 and from *R. ciliatus* by the presence of mandibular folds of skin, absence of ciliated dorsal crests, non-expanded lateral quadrate conch flange, small superciliary scales and homogeneous dorsal scalation. (91).

Comments: Bavay (1869) provided a detailed diagnosis and description for this species. The specific epithet, *chahoua*, is suppossed to be derived from a Kanak word for the devil, with which the giant forest geckos were associated by the natives (Bavay 1869). Bauer (1985a) provides a brief summary of the taxonomic confusion surrounding this animal and its congener *R. trachyrhynchus*. This species, as well as several other carphodactylines named by Bavay, has been the source of numerous taxonomic debates. The types of Bavay were deposited in the Musée de l'Ecole de Médecine Navale in Brest (Roux 1913) but are now presumed lost. Bauer (1985a) designated a neotype in an effort to permanently stabilize the name.

This species, which grows to a maximum SVL of 147 mm (CAS 156691) is known from five localities in south and central New Caledonia. Bavay's (1869) type locality (Kanala, Lifou) is assumed to be an error for Canala, New Caledonia. All localities are on or very near large rivers and are associated with primary forest patches with relatively high rainfall. Bauer (1985a) discussed ontogenetic and sexual variation in *R. chahoua* as well as feeding and courtship behavior in captivity. Incubation (approximately 85 days) is described by Henkel (1981, 1986a) along with other aspects of husbandry. A large number of this species have now been bred and raised in captivity (pers. comm. H. Meier, F.W. Henkel). It is probable that this species is associated with larger trees (Bauer 1985a; Sameit 1985; Henkel 1986b) and that it only rarely descends trunks below the level of the lowest branches.

*Rhacodactylus ciliatus* **(Guichenot, 1866) (Fig. 79)**

1866 *Correlophus ciliatus* Guichenot. Mém.Soc.Hist.Nat. Cherbourg 12: 249; pl. VIII.
Type locality: Nouvelle-Calédonie.
Lectotype: MNHN 701a, here designated.
Paralectotype: MNHN 701
1883 *Rhacodactylus ciliatus* Boulenger. Proc.Zool.Soc., London 1883: 128.

Fig.79: Lectotype of *Correlophus ciliatus* Guichenot, 1866 (= *Rhacodactylus ciliatus*). MNHN 701a. (Photo courtesy of Muséum National d'Histoire Naturelle, Paris)

1934 *Correlophus ciliatus* Brongersma. Zool.Meded. 17: 165.
1964 *Rhacodactylus ciliatus* Mertens. Zool.Garten, Leipzig, N.F. 29: 52.

Diagnosis: This species is diagnosed from its congeners by the characters at node 19 and from *R. chahoua* by the presence of a parietal crest; expanded lateral lip of the quadrate; dorsal body scalation heterogeneous, with paired ciliated crests from temporal region converging at shoulders; nostril excluded from rostral; enlarged supracilliary scales; original tail tip oar-shaped. (10, 12, **78**, **79**).

Comments: *Rhacodactylus ciliatus* is the least well known of the New Caledonian geckos because all of the numerous specimens were collected in the nineteenth century and few have associated data. Guichenot (1866) created the genus *Correlophus* for the species. His description is adequate and is accompanied by an engraving. Bavay (1869) believed that it should be relegated to a subgenus of *Platydactylus* but did not make the taxonomic shift himself.

The only known localities are Ciu and Noumea (Fig. 86), although it is probable that the later is in reality the place of shipment of the specimen rather than of collection. Bavay (1869) stated that this species lived in montaine forests and that it was only to be seen during rains. *Rhacodactylus ciliatus* attains a maximum SVL of 106 mm (NHW 17927-1) and is probably similar to its closest relative, *R. chahoua*, in its biology. Mites are common on this species. This is the only member of the genus for which reproductive mode is unknown.

***Rhacodactylus leachianus* (Cuvier, 1829) (Fig. 80)**

1829 *A(scalabotes) leachianus* Cuvier. Le Règne Animal, vol.2: 54.
Type locality: not given.
Holotype : MNHN 6687
1831 *Pteroplura (Gecko) leachianus* Gray. The Animal Kingdom Arranged in Conformity with its Organization by the Baron Cuvier, vol. 9: 49.
1833 *Gecko leachii* Schinz. Naturgeschichte und Abbildungen der Reptilien: 73 (nomen emendatum pro *Gecko leachianus* (Cuvier, 1829)).
1836 *Platydactylus leachianus* Duméril & Bibron. Erpétologie Générale, vol.3: 315.
1843 *Hoplodactylus (Rhacodactylus) leachianus* Fitzinger. Systema Reptilia: 90.
1869 *Platydactylus leachianus* Bavay. Mém.Soc.Linn. Normandie 15: 3.
1873 *Rhacodactylus leachianus* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 4: 201.
1873 *Rhacodactylus aubrianus* Bocage. Ibid.: 202.
Type locality: Nouvelle Calédonie.
Syntypes: MLI (specimen number unknown, destroyed by fire).
1881 *Rhacodactylus aubryanus* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 8: 127 (ex errore pro *Rhacodactylus aubrianus* Bocage, 1873).
1913 *Rhacodactylus leachianus aubryanus* Roux. Nova Caledonia, Zoologie I(II): 96.
1932 *Rhacodactylus leachianus* Burt & Burt. Bull.Amer.Mus.Nat.Hist. 63: 479.

Diagnosis: This species is diagnosed by the following characters: Skin of head co-ossified with skull; lateral prong of postfrontal distinctly downcurved; scleral ossicles fewer than thirty in number; two to four inscriptional ribs present; three to four abdominal ribs present; fewer than thirty caudal vertebrae; rostral scales excluded from nostril; webbing between digits IV and V present; folds of loose skin on posterior face of hindlimb; folds of skin at mandibular margins; ventral tail sulcus present. (1, 6, 15, 25, 32B, **33**, **79**, 89, 90, 91, 104).

Comments: This is the largest extant species of gecko (Bauer & Russell 1986; Russell & Bauer 1986) reaching a maximum SVL of 245 mm (CAS 165890). Cuvier's (1829) description is woefully inadequate. It follows in its entirety: "Nous en avons une espèce lisse, à pieds palmés (*A. leachianus* Nob.)". Duméril & Bibron (1836) provided an adequate description of the species and illustrated the digits. *Rhacodactylus aubrianus* Bocage, 1873 would appear to be merely a particular ontogenetic phase or aberant form. Unfortunately, the only known specimens bearing this name, along with other rare New Caledonian carphodactylines, were destroyed by fire in the Lisbon Museum. There is a wide range of variability, particularly in coloration, within this

Fig.80: Holotype of *A(scalabotes) leachianus* Cuvier, 1829 (= *Rhacodactylus leachianus*). MNHN 6687. (Photo courtesy of Muséum National d'Histoire Naturelle, Paris)

species. Typically, juveniles have distinct whitish spots, sub-adults have large pinkish lateral bands and adults assume a more uniform drab dorsal pattern. However, some animals remain more or less reticulate throughout life. Although the possibility that two species are present is unlikely, there may be some populational variation.

The provenance of *R. leachianus* was unknown until 1869, when Bavay confirmed its presence in New Caledonia. The species is distributed over most of the east coast of

Fig.81: Primary rainforest on the slopes of the Massif de Panié, northeast coastal New Caledonia — habitat of *Rhacodactylus leachianus*.

the island as well as in mountainous areas in the southern half of the island (Figs. 81,82). Most localities appear to be associated with rivers and humid forest vegetation from sea-level to 1100 m (Mertens 1964a), although individuals have been collected in slightly drier regions in the far south in association with ultramafic soils and edaphic vegetation (Fig. 82). Boulenger (1885a) recorded a specimen from the Isle of Pines off the southern tip of New Caledonia. This may be a legitimate record, given the similarity in paleogeography and geological structure of the Isle of Pines to the mainland of New Caledonia. Jouan (1864) reported that there was a giant gecko called "paït" by the natives at Hienghène (a known *R. leachianus* locality) and "tint" by those at Belep, the island group to the north of New Caledonia. It too shares certain features with the mainland, which would suggest that this record may have some validity, although no specimens exist from this area.

Bocage (1881) stated that *R. leachianus* was common in New Caledonia, my observations would tend to support that statement today, although habitat alteration threatens this and other forest geckos in New Caledonia (Meier 1979; Bauer 1985a; Bauer in press). Jouan (1863) described a 400 mm gecko from Hienghène which is found under bark and in the forks of rotten trees. Bavay (1869) also reported this species from boulder areas and permanently dispelled the belief that webbed feet in gekkonids were associated with aquatic habits. I have frequently seen this species climbing on the

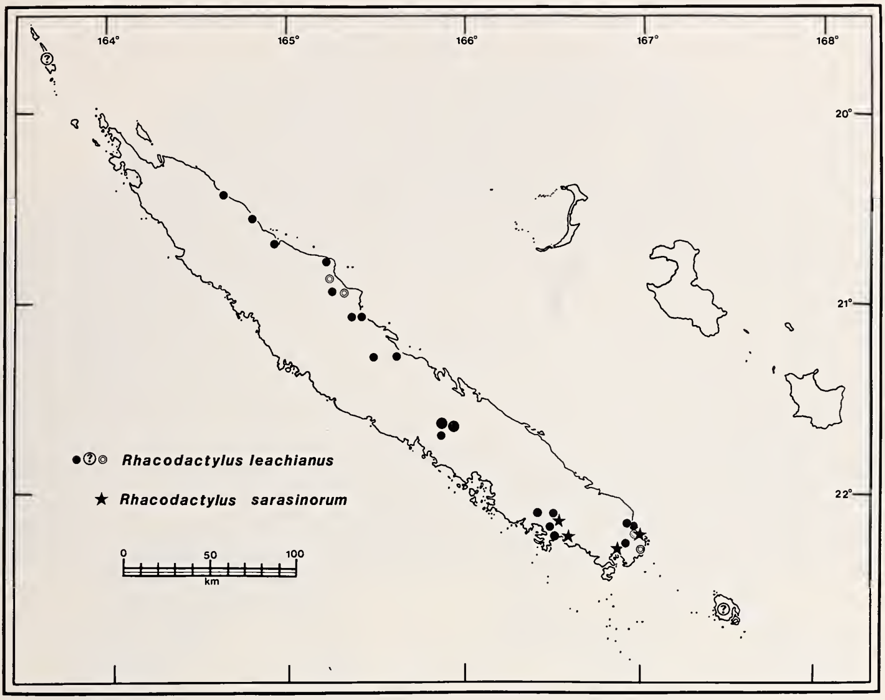

Fig.82: Distribution of *Rhacodactylus leachianus* (circles) and *R. sarasinorum* (stars) in New Caledonia. Question marks indicate doubtful island localities of *R. leachianus*. Circles within circles represent sight records of *R. leachianus*.

trunks of large trees at night, usually at 10—20 m. It has a prehensile tail (Mertens 1964a, 1964b; Meier 1979). Near Poindimié and Ponerihouen it occurs in sympatry with *R. chahoua* and with *R. auriculatus, R. sarasinorum* and *R. trachyrhynchus* in southeastern New Caledonia and probably at Mt. Koghis. In all cases except the last it appears that *R. leachianus* is associated with larger trees and higher zones of activity than its congeners. Meier (1979) reported that this species was found most frequently in very large trees which provided numerous holes which provided daytime retreats. Unlike *R. auriculatus*, this species is rather clumsy on the ground, but is a very rapid climber.

Roux (1913) reported that the diet of this species included *Glyciphila (= Lichmera) incana*, a meliphagid bird, one of the only records of a bird as a natural gekkonid prey item. Mertens (1964a) discussed feeding in captivity, emphasizing frugivory and Mitchell (1986) reported captive cannibalism. Nothing is known of courtship in the species but eggs are described by Roux (1913) and Mertens (1964a). *Rhacodactylus leachianus* can inflict a painful bite and when threatened inflates its lungs with air and emits a loud hiss or croak (Bavay 1869; Mertens 1964a).

### *Rhacodactylus sarasinorum* **Roux, 1913 (Fig. 83)**

1913 *Rhacodactylus sarasinorum* Roux. Nova Caledonia, Zoologie I(II): 99; pl. IV (figs. 6,6a).
Type locality: Forêt de Prony (env. 100 m d'altitude), New Caledonia.
Holotype: NMBA 7246.

Diagnosis: No derived character states were found for this taxon in the phylogenetic analysis. However, it may be distinguished from congeners by its gracile form and by the contrasting dark dorsum and cream venter and by its general lack of fleshy folds, digital webbing and bony protruberences.

Fig.83: Holotype of *Rhacodactylus sarasinorum* Roux, 1913. NMBA 7246 (SVL = 110 mm).

Comments: All specimens of this species are from extreme southern New Caledonia and are associated with the southern ultramafic formation or outlying areas (Figs. 82,84). This is by far the most gracile New Caledonian *Rhacodactylus* and reaches a SVL of 125 mm (CAS 157675). The specimens examined vary considerably in color pattern and body proportion. Roux (1913) reported the species from leaf litter in a fork of *Pandanus*. I have collected this species 3 m above the ground in a small shrub, approximately two meters away from *R. auriculatus* and within 50 m of a tree containing *R. leachianus*. Böhme & Henkel (1985), Sameit (1985), and Henkel (1987, 1988) described the collection of this species in primary forest and discuss captive care. These publications also present color photographs of the species. Insects and arachnids are the probable wild food of this species (Roux 1913). Mite-pockets have been reported for *R. sarasinorum* (Böhme & Henkel 1985). Infertile eggs have been laid in captivity (Henkel 1986a) and successful capture reproduction has been discussed by Henkel (1987).

Fig.84: Abandoned mining site 8 km south of Goro, New Caledonia. Forest in foreground is typical habitat of *Rhacodactylus sarasinorum, R. auriculatus* and *R. leachianus* (in larger trees). *Bavayia sauvagii* occurs under rocks in adjacent coastal forest. *R. trachyrhynchus* has been collected from similar mountain forest at Gouemba, about 20 km to the north of this site.

***Rhacodactylus trachyrhynchus* Bocage, 1873 (Fig. 85)**

1869 *Platydactylus duvaucelii* Bavay. Mém.Soc.Linn. Normandie 15: 6 (nec Duméril & Bibron, 1836 — fide Boulenger 1883).
1873 *Rhacodactylus trachyrhynchus* Bocage. J.Sci.Mat.Phys.Nat. Lisboa 4: 203.
Type locality: Nouvelle Calédonie.
Holotype: MLI (specimen number unknown, destroyed by fire).
1878 *Platydactylus (Rhacodactylus) chahoua* (part) Sauvage. Bull.Soc.Philomat. Paris (7)3: 66.
1878 *Chameleonurus trachycephalus* Boulenger. Bull.Soc.Zool. France 3: 68; pl.2.
Type locality: Ile des Pins (Nouvelle-Calédonie).
Lectotype: IRSNB 2.5 32, here designated.
1879 *Chameleonurus chahoua* (part) Boulenger. Bull.Soc.Zool. France 4: 142.
1883 *Rhacodactylus trachyrhynchus* Boulenger. Proc.Zool.Soc. London 1883: 126; pl. XXI (figs. 2,2a—2d).
1889 *Chamaeleonurus trachycephalus* Carus. Reg.Zool.Anz. 1889: 83.
1913 *Rhacodactylus trachyrhynchus* Roux. Nova Caledonia, Zoologie I(II): 98.

Diagnosis: This species may be diagnosed by the following characters: skin of head co-ossified with skull; two to four inscriptional ribs; rostral excluded from nostril; in-

Fig.85. Juvenile *Rhacodactylus trachyrhynchus* Bocage, 1873. ZFMK 31806. (Photo courtesy of E. Schmidt, Zoologisches Forschungsinstitut und Museum A. Koenig)

fralabials extremely large; first infralabials contact behind mental; digital scansors divided by small central plates; preanal organs do not extend onto thighs; tail long and thick; livebearing; newborns lack egg-teeth. (1, 32-B, **79**, 80, 93-B, 106).

Comments: This species was first recorded as *Platydactylus duvaucelii* by Bavay (1869). Bocage's (1873) description is adequate but too brief to be useful. During the subsequent decade Boulenger (1878, 1879), Sauvage (1878), and Bocage (1881) confused this species with *R. chahoua* (Bauer 1985a). The taxonomy of *R. trachyrhynchus* stabilized in 1883 with Boulenger's review of New Caledonian geckos.

This species is currently known from only five confirmed localities, all in central or southern New Caledonia (Fig. 86). An additional record from the Isle of Pines is based on the types of *Chameleonurus trachycephalus* Boulenger, 1878. *Rhacodactylus trachyrhynchus* has been found on bark (Mertens 1964a) and is generally associated with large trees in primary humid forest (Meier 1979; Böhme & Henkel 1985; Sameit 1985). Henkel (1986a) stated that it is a crown-dwelling species, occurring at heights of 20 m or more. The interesting habit of hiding in water-filled bromeliads has been noted in juveniles (Henkel 1986a). Unlike *R. leachianus* this species has a long, stout, prehensile tail. Tail break frequencies are high and may be attributed to predation attempts by raptors, particularly *Accipiter haplochrous* and *A. fasciatus* (Meier 1979). This species reaches a maximum SVL of 170 mm (ZFMK 25398) and in many respects resemble *R. leachianus* in its biology. Wild diet is unknown but probably consists of lizards

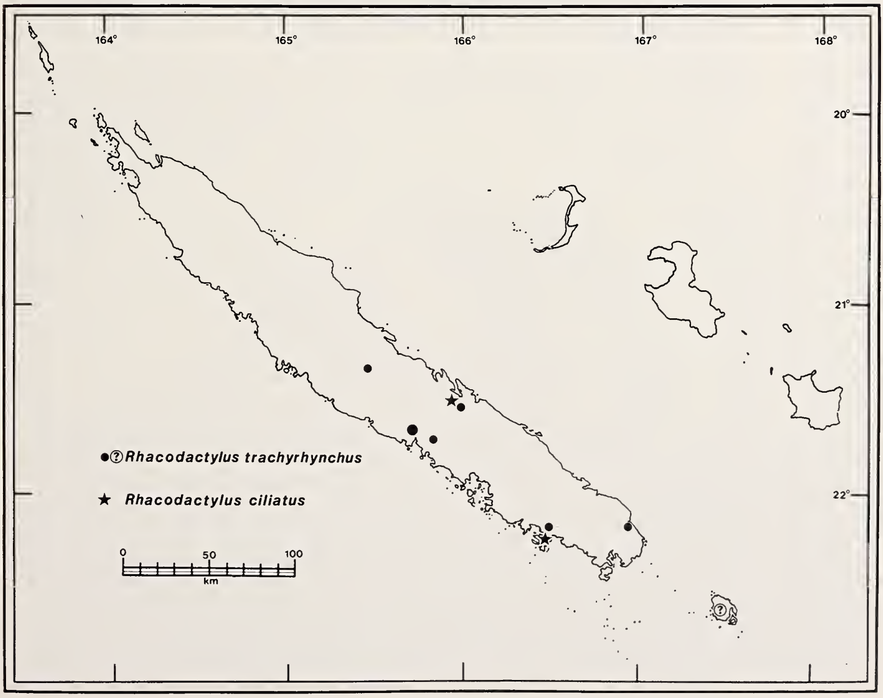

Fig.86: Distribution of *Rhacodactylus trachyrhynchus* and *R. ciliatus* in New Caledonia. Question mark indicates a doubtful record of *R. trachyrhynchus* from the Isles of Pines.

and arthropods. *Rhacodactylus trachyrhynchus* is unique among New Caledonian carphodactylines in being viviparous (Bartmann & Minuth 1979; Meier 1979). The two young are roughly half the total length of the adult and weigh approximately four grams each (Bartmann & Minuth 1979).

### *Rhacodactylus* (subgenus *Pseudothecadactylus*) (Brongersma, 1936)

1934 *Torresia* Brongersma. Zool.Meded. 17: 176. (non *Torresia* Castelnau, 1875 = Pisces).
Type species: *Thecadactylus australis* Günther, 1877 by original designation.
1936 *Pseudothecadactylus* Brongersma. Zool.Meded. 19:136 (nomen novum pro *Torresia* Brongersma, 1934).

Species referred: *Rhacodactylus (Pseudothecadactylus) australis* (Günther, 1877); *R.(P). cavaticus* (Cogger, 1975); *R.(P). lindneri* (Cogger, 1975).

Diagnosis: (Node 20) A monophyletic subgeneric taxon diagnosed by the following characters: Five or more abdominal ribs; coracoid process placed posteriorly along interclavicular body; digital scansors present, broadened and divided; digit one of manus and pes clawless; preanal organs (if present) do not extend onto thighs; tail bearing subcaudal lamellae. (33, 39, **70**, 74, 76*, **86**, 93-B, 107).

Comments: This subgenus is confined to areas of relatively high rainfall in extreme northern Australia. Günther (1877) described *Thecadactylus australis* as the second member of that genus, the only other representative being the neotropical *T. rapicauda*. Although he remarked on the significance of such a disjunct distribution, it was more than sixty years before the two were separated at the generic level. Brongersma (1934) errected *Torresia* for the Australian form and shortly there after replaced this preoccupied name with *Pseudothecadactylus* (Brongersma 1936). *Pseudothecadactylus* was placed by Underwood (1954) in the Gekkoninae.

### Key to the species of *Rhacodactylus (Pseudothecadactylus)*

1a.Rostral scales approximately as broad as high; ear opening approximately same size as nostril ........................................................ *R. australis*
b. Rostral much broader than high; ear opening at least five times size of nostril 2
2a. Rostral excluded from nostril; dorsal body scalation homogeneous . *R. lindneri*
b. Rostral narrowly contacts nostril; dorsal body scalation heterogeneous *R. cavaticus*

### *Rhacodactylus (Pseudothecadactylus) australis* (Günther, 1877) (Fig. 87)

1877 *Thecadactylus australis* Günther. Ann.Mag.Nat.Hist. (4)19: 414.
Type locality: Islands of Torres Strait, Queensland.
Holotype: BMNH 77.3.3.12.
1934 *Torresia australis* Brongersma. Zool.Meded. 17: 176; figs. 5—7.

1936 *Pseudothecadactylus australis* Brongersma. Zool.Meded. 19: 136.
1963 *Thecadactylus australis* Worrell. Reptiles of Australia: 30.
1965 *Pseudothecadactylus australis* Wermuth. Das Tierreich 80: 153.

Diagnosis: 3—4 inscriptional ribs; skin of head co-ossified with skull; lining of mouth and tongue navy to black; first infralabials may contact behind mental; subpygal scales enlarged, hexagonal to octagonal; preanal organs present; ear opening minute; usually one cloacal spur; juvenile color pattern as adult. (1, **62**, 63, 64, 80).

Comments: Günther's (1877) description is sketchy. The holotype is from an unspecified island in Torres Strait. Brongersma (1934) provided an excellent redescription and clearly diagnosed *Pseudothecadactylus* as distinct from *Thecadactylus*. The species was known only from the holotype until the discovery of a single individual from the McIlwraith Ranges (Loveridge 1934). The species is now known to range throughout the northern Cape York Peninsula and Islands of Torres Straits (Fig. 25) and it possibly occurs on the mainland of New Guinea. Worrell (1963), in his discussion of *"Thecadactylus australis"*, seems to have confused this species with its ex-congener *(T. rapicauda)*, including tropical America as well as northern Queensland in its range.

Fig.87: Holotype of *Thecadactylus australis* Günther, 1877 (= *Rhacodactylus australis*). BMNH 77.3.3.12. (Photo courtesy British Museum (Natural History))

*Rhacodactylus australis* reaches a maximum SVL of 120 mm (Cogger 1986 — largest specimen measured by author 112 mm QM J38327). It is chiefly arboreal and its habitat has been described as woodland and open forest (Cogger et al. 1983) heaths, monsoon forest, woodland and mangrove (Covacevich & Ingram 1980). Specimens have been collected in hollows of *Melaleuca cajuputi* (Cogger 1975). It is primarily an arthropod feeder.

### *Rhacodactylus (Pseudothecadactylus) cavaticus* Cogger, 1975

1975 *Pseudothecadactylus lindneri cavaticus* Cogger. Rec.Aust.Mus. 30: 93; figs. 5—6.
Type locality: near Mitchell River Falls, approx. 25 km SW of Crystal Head, Port Warrender (approx. 14°40'S, 125°42'E), Western Australia.
Holotype: WAM R43176.

Diagnosis: No inscriptional ribs; no co-ossification of skull; mouth and tongue pink in life; ear opening large; dorsal scalation heterogeneous; preanal pores absent; dorsum with broad light bands with lighter centers. (**78**, 92).

Comments: *Rhacodactylus cavaticus* is known only from the coastal region of the Kimberleys, W.A. (Fig. 89) where it occurs in association with caves and crevices of sandstone formations (Cogger 1983). I have not examined specimens of this form but consistent differences in morphology suggested by the description (Cogger 1975a) seem to warrent the recognition of this taxon at the specific level.

### *Rhacodactylus (Pseudothecadactylus) lindneri* Cogger, 1975 (Fig. 88)

1975 *Pseudothecadactylus lindneri* Cogger. Rec.Aust.Mus. 30: 89; figs. 1—5.
Type locality: Deaf Adder Gorge, Arnhem Land, Northern Territory.
Holotype: AMS R38734.

Fig.88: Holotype of *Pseudothecadactylus lindneri* Cogger, 1975 (= *Rhacodactylus lindneri*). AMS R38734. (Photo courtesy of The Australian Museum)

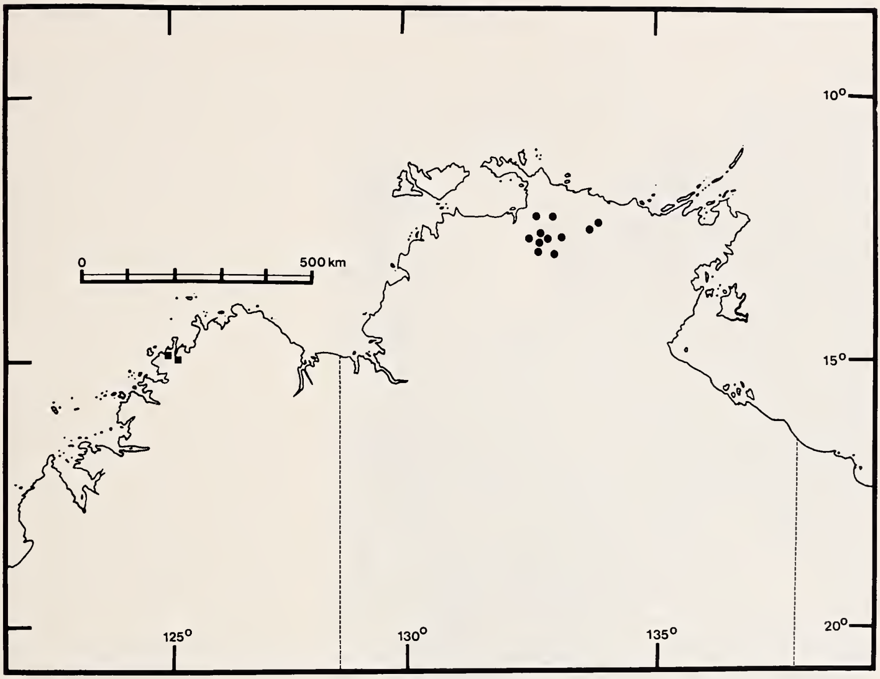

Fig.89: Distribution of *Rhacodactylus lindneri* (circles) and *R. cavaticus* (squares) in northern Australia.

Diagnosis: No inscriptional ribs; no co-ossification of skull; mouth and tongue pink in life; ear opening large; dorsal scalation homogeneous; preanal pores greatly reduced; dorsum with narrow light bands, fading laterally to spots.

Comments: *Rhacodactylus lindneri* is a large gecko (maximum SVL 107 — Cogger 1975a) which went undiscovered until 1972. Cogger's (1975a) description and diagnosis of the species is complete and informative. It is endemic to western Arnhem Land, N.T. (Fig. 89) where it is found in association with sandstone formations (Cogger 1975a, 1981) (Fig. 90). Cogger (1975a) discussed and illustrated the moderately prehensile scansorial caudal pad of *R. lindneri*. It feeds on spiders and insects as well as members of the genus *Gehyra* which co-occur on sandstone faces. This species at East Alligator typically becomes active about three hours after sunset and will frequently leap from the rock faces of the sandstone escarpments to nearby trees where they will forage for several hours before returning to refuges in the rock walls (pers. obs.).

Fig.90: Sandstone outliers at the western edge of the Arnhem Land Escarpment, Ngarragji Warde Djobkeng, near East Alligator Station, Kakadu National Park, Northern Territory, Australia — typical habitat of *Rhacodactylus lindneri.*

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## APPENDIX A

**Collection Acronyms.** Alcoholic, skeletal or living specimens from the following gekkonid collections have been examined or referenced in this study. For complete addresses of most institutions see Leviton et al. (1985). Institutions marked with an asterisk no longer exist.

**AIM** — Auckland Institute and Museum (Auckland, New Zealand)

**AMB** — Aaron M. Bauer, personal collection (Villanova, U.S.A.) (to be deposited in the collections of CAS and MVZ)

**AMNH** — American Museum of Natural History (New York, U.S.A.)

**AMS** — The Australian Museum (Sydney, Australia)
**ANWC** — Australian National Wildlife Collection (Canberra, Australia)
**BMNH** — British Museum (Natural History) (London, England)
**CAS** — California Academy of Sciences (San Francisco, U.S.A.)
**CAS/SU** — California Academy of Sciences/Stanford University Collection (San Francisco, U.S.A.)
**CMC** — Canterbury Museum (Christchurch, New Zealand)
**EMNB*** — Musée de l'école de Médecine Navale (Brest, France)
**FMNH** — Field Museum of Natural History (Chicago, U.S.A.)
**IRSNB** — Institut Royal des Sciences Naturelles de Belgique (Brussels, Belgium)
**LACM** — Los Angeles County Museum of Natural History (Los Angeles, U.S.A.)
**MCZ** — Museum of Comparative Zoology, Harvard University (Cambridge, U.S.A.)
**MHNG** — Muséum d'Histoire Naturelle (Génève, Switzerland)
**MLI*** — Museu de Lisboa (Lisbon, Portugal)
**MMNH** — Musée d'Histoire Naturelle (Marseille, France)
**MNHN** — Muséum National d'Histoire Naturelle (Paris, France)
**MNNZ** — Nelson Museum (Nelson, New Zealand)
**MVZ** — Museum of Vertebrate Zoology, University of California (Berkeley, U.S.A.)
**NHMG** — Naturhistoriska Riksmuseet (Göteborg, Sweden)
**NHRM** — Naturhistoriska Riksmuseet (Stockholm, Sweden)
**NHW** — Naturhistorisches Museum (Wien, Austria)
**NMBA** — Naturhistorisches Museum Basel (Basel, Switzerland)
**NMNZ** — National Museum of New Zealand (Wellington, New Zealand)
**NTM** — Northern Territory Museum of Arts and Sciences (Darwin, Australia)
**PFN** — Parc Forestier (Nouméa, New Caledonia)
**QM** — Queensland Museum (Brisbane, Australia)
**RMNH** — Rijksmuseum van Natuurlijke Historie (Leiden, The Netherlands)
**SAMA** — South Australian Museum (Adelaide, Australia)
**SMF** — Natur-Museum und Forschungs-Institut Senckenberg (Frankfurt-am-Main, Federal Republic of Germany)
**SMNS** — Staatliche Museum für Naturkunde in Stuttgart (Ludwigsburg, Federal Republic of Germany)
**UMMZ** — University of Michigan Museum of Zoology (Ann Arbor, U.S.A.)
**USNM** — United States National Museum of Natural History (Washington, U.S.A.)
**WAM** — Western Australian Museum (Perth, Australia)
**ZFMK** — Zoologisches Forschungsinstitut und Museum Alexander Koenig (Bonn, Federal Republic of Germany)
**ZMA** — Universiteit van Amsterdam (Amsterdam, The Netherlands)
**ZMB** — Universität Humboldt (East Berlin, German Democratic Republic)
**ZMH** — Universität Hamburg (Hamburg, Federal Republic of Germany)
**ZMUC** — Kobenhavns Universitet (Copenhagen, Denmark)
**ZMUZ** — Universität Zürich (Zurich, Switzerland)
**ZSM** — Zoologische Sammlung der Bayerischen Staates (München, Federal Republic of Germany)

## APPENDIX B

**Specimens Examined** (for acronyms see Appendix A). An asterisk following a specimen indicates a holotype, neotype or lectotype. Type specimens associated with junior synonyms are not indicated here but are listed under the appropriate species in the species accounts. Unless otherwise indicated all specimens are alcohol preserved. (s) = dry skeletal preparation, (c+s) = cleared and stained preparation. In addition to specimens listed most taxa have been observed alive.

*Bavayia crassicollis* (17 specimens):
CAS 157695; MCZ 19633, 27935; NMBA 6931*, 6933-41; USNM 146331-2; ZFMK 30548, 32652.

*Bavayia cyclura* (200 specimens):
AMNH 24681-83, 60472, 61683-7, 61689-91, 81758, 81768, 81772; BMNH 71.4.16.30* (A-B), 85.11.16.15-16, 86.3.11.11-15, 1926.9.17.8-19; CAS 80864-8, 80869 (s), 80870-71, 157696-704, 158548-50, 159546, 159550-1, 162203-9, 162219-21, 162237-9; 165861-74; 165877-79; 165884-7; FMNH 25921, 105666-7, 105710, 170762; MCZ 6209, 9293-4, 29935, 162911; MNHN 703 (A-E), 5310-1, 5790, 85.24, 85.755, 88.82, 1980.977-9, 1980.1063-6, 1981.172-3, 1985.112-19; NMBA 2901-4, 6894-6, 6898-912, 6915, 6917-21, 6923, 6925-6, 6929-30; NMW 19362 (2-5); RMNH 6788-9; SMF 9029, 9121; UMMZ 64306, 93830 (1-9), 93831, 93832 (0-10), 93833, 127507(c+s), 174097; ZFMK 15895, 25404-5, 25448.

*Bavayia montana* (23 specimens):
CAS 157694; MCZ 19634; NMBA 6942-45, 6946*, 6948-56, 6959; USNM 267840-1; ZFMK 25402-3, 25447, 48663.

*Bavayia ornata* (15 specimens):
AMS R77843, R77870-4, R77888, R77892-3; NMBA 7023, 7024*, 7025-8.

*Bavayia sauvagii* (418 specimens):
AMNH 24689-90, 60469-71, 61589, 81769-71; AMS R6678, R64917, R77543-4, R77660-4, R77687, R77721, R77782, R77801-4, R77815-6, R77844-6, R77859, R78350-2; BMNH 71.4.16.31* (A-C), 1926.9.17.2; CAS 38826, 80823(s), 80824-63, 157705-10, 157711-8, 157914-70, 158321-32, 158378-83, 158386-8, 158430-508, 15913-25, 159528-43, 159552-3, 159555-61, 159566-7, 162184-200, 162213-8, 162225, 162228-32, 162235, 162240-3, 165875-6, 165880-83, 165888-9, 165893-4 (s), 165903-10 (c+s); FMNH 62804-5, 106963-4; MCZ 19635, 27938, 46171; MNHN 5312; NHRM AAA/1912809.3733; NMBA 6981-5, 6987-99, 7001-7, 7009-10, 7012, 7014-6, 7018-22; NMW 14754, 19362 (1), 19363 (1-2), 19366 (1-2), 19672 (1-2); RMNH 6787; SMF 9030; UMMZ 64307-8, 174469; USNM 59008-9, 267842, 268761; ZFMK 16102-12.

*Bavayia septuiclavis* (16 specimens):
AMS R78139*-41, R782346, R78339, R90193, R125888, R125291-3; MNHN 1985-120, 1985-121; ZFMK 25400, 45032-4.

*Bavayia validiclavis* (10 specimens):
AMS R77353, R77847, R77853-4, R77855*, R77856-8, R77895; MNHN 1980-1067.

*Carphodactylus laevis* (38 specimens examined):
AMNH 69530, 83857; AMS R2252, R10095, R10835-46, R10847(c+s), R11377-81, R55938, R56335-6, R58304, R64914; BMNH 1960.1.5.70; FMNH 57492; MCZ 35109-12, 35114-5; RMNH 6407(1-2); SMF 22504.

***Eurydactylodes symmetricus*** (6 specimens):
MNHN 94.453, 94.454, 94.454a, 1985.123; NHMG 651*; NMBA 7072.

***Eurydactylodes vieillardi*** (22 specimens):
BMNH 90.7.26.1, 1926.4.17.7, 1927.11.22.1; CAS 158556; MNHN 5313, 699-1863; NHMG 605; NMBA 7068-71, 9703; UMMZ 174095-6; USNM 267843; ZFMK 16113, 46981*, 48259-62, 48981.

***Hoplodactylus chrysosireticus*** (13 specimens):
AIM J257-8, J779-81, 841(s); CMC 512, 543; NMNZ R25*, R1857, R1867, G559, G923.

***Hoplodactylus delcourti*** (1 specimen):
MMNH 1985-38* (skin and partial skeleton).

***Hoplodactylus duvaucelii*** (138 specimens):
AIM 162-9, 666-7, 717, 884(s); AMB 455(s); AMS R114880; BMNH 45.2.15.81, 61.3.20.11(s); CMC 180, 224; FMNH 207824, 210144; MCZ 18413; MHNG 653.82(1-2); MNHN 5977*, 6680*-1*; NMNZ G4-6, G91-2, G118, G128, G134-6, G141-4, G147-50, G219, G358-9, G366-71, G384, G476, G505, G569-70, G581, G583-6, G597-600, G606-7, G609-10, G624-5, G627, G631-2, G641, G643, G651, G654-5, G667-8, G705-6, G708-9, G712, G719, G723, G731, G747, G753-6, G761, G794, G808-9, G850-3, G860-1, G895, G966-72, G1009-12, G1088-9; NMW 20808(1-7); RMNH 2722*; SMF 9036-7; SMNS 184a-b; UMMZ 127158(1-2), 129351; USNM 209587; ZMH R02822-3.

***Hoplodactylus granulatus*** (104 specimens):
AIM 235-49, 668, 673(s), 703-14, 735-741, 754, 888(s), 919-20(s); AMB 450, 451(s); AMNH 22407, 68920; AMS R427, R1320, R1660, R4458-9, R5216, R5233; BMNH 1946.8.22.71*; CAS 47982-3, 47984(s), 47985, 47987; CMC 160, 182-3, 185-7, 189-91, 205, 208, 219, 256; FMNH 18180; MNHN 33:131-3; NMNZ R51-2, R56-9, R93, R459, R1047, R1752; NMW 17920; RMNH 2500; SMF 9038; SMI E81.4; SMNS 186a-b, 187; USNM 209588-9; ZFMK 30055, 37310-1, 40177; ZMH R02821; ZMK R34729-33.

***Hoplodactylus kahutarae*** (4 specimens):
NMNZ R1980*-2, G345.

***Hoplodactylus maculatus*** (151 specimens):
AIM 545-9, 745-60, 842; 928, 935(s), 938(s), 944(s), 952(s), 960(s), 990(s); AMB 88(s), 89-90, 91(s), 92,93(living), 94-5; AMNH 22408-16, 23058, 31547(s), 65539; AMS R3820, R4460-2, R5578, R12073 (1-4); BMNH 1946.9.8.14-15*; CAS/SU 12211-15; CMC 172, 176, 179, 184, 200-4, 206, 212, 216-8, 225-6, 228, 233, 257, 260, 262-3, (two specimens - no catalogue number); MCZ 6153, 28653, 126223-6, 152218; MHNG 653.84(A-B), 661.80(A-B), 678.30(A-B); MNHN 6684; MVZ 187689; NMBA 2906-8, 21324; NMW 17921 (1-4), 20762; RMNH 4442(1-2);SMF 9034-5, 50612-5; UMMZ 127126-7, 129366; USNM 209590-1; ZFMK 26270-1, 37305-9; ZIH 4778, 6341, 6391, 10380(1-2), 29025(1-3); ZMH R02819-20; ZMK R34219-22; R34725-8.

***Hoplodactylus pacificus*** (229 specimens):
AIM 188-234, 615, 676-7(s), 734, 761-72, 774-5, 777, 785, 795-6, 803-5, 808, 838, 846-8, 933(s), 939(s), 942(s), 946-7(s), 956(s); AMB 481(s), 482 (c+s); AMNH 31536-50; AMS R4457; BMNH 62.9.2.18(s), 1946.8.22.64*, 1946.8.22.65-6; CAS 47975, 47978-81; CMC 181; FMNH 58146-87; MCZ (three specimens - no catalogue number); MNHN 33:13h, 6465, 6682-3, 6685-6; NMW 14750(1-2)(?), 14751, 17922(1-14), 17923(1-19), 17924(1-6), 17925(1-22), 20416; 4442(1-2), 4443(2); UMMZ 54110(1-2), 60483; USNM 5690; ZFMK 30056-7; ZIH 7621(1-2), 13839, 18762-3.

*Hoplodactylus rakiurae* (6 specimens):
NMNZ R1823-5*, R2014, R2043, G236.

*Hoplodactylus stephensi* (9 specimens):
CAS 47986; NMNZ 163-4, R1061, R1857-1858*, R1859-61.

*Naultinus elegans* (131 specimens examined):
AIM 360-74, 742-7, 791-2, 890(s), 912(s), 929(s), 934(s), 940(s), 943(s), 949, 992; AMB 394-395(c+s), 480; AMS R4454, R4456, R5239, R5378; BMNH 1975.854(s); CAS 47776-7; CMC 174, 178, 181A, 188, 192, 198, 244, 277, 534-6, 541-2, 557, 560; FMNH 18179; MNHN 5007, 6750-2 NHNG 661.78(A-B), 661.79; NMBA 231-2, 2905, 19650, 21325; NMNZ R75-6, R78-81, R915; NMW 14980, 17918(1-8), 17919(1-13); RMNH 4445; SMF 9031-3, 69410, 69416, 69419; SMNS 175; SNMR NNN/1928989.6451; UMMZ 127576(1-2), 142536(c+s) 192352(1-2); ZFMK 37313-6; ZIH 5188, 7832, 8195, 10381, 15557, 18764-5; ZMH R02824; ZMK R34120-3, R34734, R34736-7.

*Naultinus gemmeus* (80 specimens examined):
AIM 719-22; AMNH 22406, 23059-60; AMS R4455, R12264; BMNH 72.10.14.8-10; CMC 173, 175, 177, 213, 250, 276, 339, 523-6, 527(1-4), 528-30, 531(1-2), 532, 538, 540, 545, 550; MHNG 653.83; NMNZ R1870-2, R1875-6, G129-30, G233-5, G413-6, G516, G790, G857, G879, G896, G898, G902, G905, G936, G1070, G1092, G1098-103; SMF 69414; SMI E81.5, 83.3356; SMNS 174a-b; UMMZ 129356-7, 142538(s); ZIH 7875, 13838; ZMH R02825.

*Naultinus grayii* (24 specimens examined):
AIM 551-2, 786-7, 789(1-2), 889, 891(s), 892(s), 893(s), 894(s), 937(s); CMC 514(1-2), 537, 554-6, 558-9(s), 561; ZIH 8195; ZMH R02826; ZMK 34735.

*Naultinus manukanus* (22 specimens):
AIM 725-7; NMNZ R238*, R448, R2008, R2012-3,G2, G54, G99, G122, G125, G127, G137, G312-3, G437, G517, G528, G798, G939.

*Naultinus poecilochloris* (6 specimens):
NMNZ R1863-6, R1992, G1064.

*Naultinus rudis* (18 specimens examined):
BMNH 86.5.15.40 (1946.8.22.37)*; CMC 513, 515; NMNZ R1817, G485, G791, G799, G854-6, G900-1, G1057-62.

*Naultinus stellatus* (67 specimens examined):
AIM 723-4; AMB 483; BMNH 1905.11.30.9; CMC 518-22, 539; NMNZ R2002-4, R2006, G12-8, G33, G346, G421, G429, G440, G442, G471, G504, G509-10, G529-30, G792, G796, G800, G858, G878, G903, 1056, G1067-9, G1071, G1079-83, G1091, G1093-7; SMF 69411-13; UMMZ 129353-5, 132102, 142539(1-5)(c+s).

*Naultinus tuberculatus* (8 specimens examined):
AIM 718; CMC 171, 199, 516-7; NMNZ G208, G1072; UMMZ 127571 (c+s).

*Nephrurus asper* (68 specimens examined):
AMNH 5086, 27317, 27324, 86395-7; AMS R1131(c+s), R1883, R1925(1-2), R10371, R10905(c+s), R11965, R12876, R13403, R14183, R15107, R20449-50(c+s), R31773, R40070, R42760, R49716, R50542, R55786, R63065, R72980, R88668, R90198, R93181-2, R104458, R107165, R107703, R110544, R110562, R113116, R113852, R120094, (one specimen, no number) ; BMNH 76.3.4.5, 1926.2.25.20, 1946.8.23.34*; CAS 74732-5, 76250, 77509; MCZ 13961-2, 83257; NMW 17267; SMF 8139, 61685, 61745, 69297-9; SMNH MJO/1910484.5978; ZFMK 42040, 42506, 44665, 46992-4; ZIH 10773-4.

*Nephrurus deleani* (10 specimens examined):
AMB 45, 46(s), 47-8, 49(s); SAM R21864-8*.

*Nephrurus laevissimus* (50 specimens examined):
AMS R17585, R49672, R49680, R49730, R49736, R86506-7, R91077-81, R100910; BMNH 1957.1.10.34, 1969.2403-10; FMNH 97652; LACM 57065, 57071, 57080, 57086, 57090, 57092(c+s), 57101(c+s), 57117, 57120, 57140; MCZ 158551-2; SAM R665(c+s), R15566B, R18221; SMF 53201*; ZFMK 42036-9, 42511-2, 43678, 45955-7; 46420.

*Nephrurus levis* (189 specimens examined):
AMNH 24922-5, 62882, 86393, 86394(c+s); AMS R2039, R2105(c+s), R2407, R5397, R6754, R6917, R7672, R7693, R10905-6, R11400(c+s), R11966-7, R13028, R13403, R13941-2, R14338, R16471, R17741, R20451-2(c+s), R20845, R21217, R27936, R31593-4, R31648, R31774, R32397, R32909, R40457, R41674, R47529, R49084, R49091, R49801, R49529, R49581, R49673, R49681, R49692-3, R49718-9,R49735, R50666, R50674-6, R52138-41, R55787, R55992, R56949, R57097-8, R60282, R65100, R65287, R66651, R70039, R70049-50, R73915, R76644, R83250-72, R86499, R93002, R95426, R96111-3, R96126, R96130-1, R96160, R101551-2, R101580, R101785-7, R101981, R102446-58, R102519, R102546-7, R102599-610, R105641, R105700, R105729, R105762, R110578, R110594, R113264-73, R114829-30; CAS/SU 12610; FMNH 95840, 202409; LACM 57010, 57019, 57035-6; MCZ 28654, 43113, 74997, 78673-4, 79447, 163948; MVZ 78122, 78827; NMW 17263-5, 17266 (1-2); SMF 8140-2, 69306-7, 70181; SMNH MJO/1911809.5979; ZFMK 25380-1, 42035, 45024, 45380, 45952-53, 46419; ZIH 29655; ZMH R02829.

*Nephrurus milii* (338 specimens examined):
AMB 460(s), 499; AMNH 50585(c+s); AMS R44, R53, R97, R231, R254, R1047, R1942, R1969, R2426, R2465, R2481, R2691, R2951, R3115, R3409, R3412, R3417, R3427, R3435, R3595-6, R3868, R3875, R4412, R4566 (1-2), R4567, R4584-5, R4923-4, R5293, R5310, R6089-90, R6116, R6259, R7144, R7177 (1-3), R7670-1, R7725, R8375-6, R9136, R9448, R10033, R10059, R10465, R10550, R10986, R11149, R11718 (1-2), R12205-6, R12413, R12577, R13128, R14642, R14993-4, R15104, R15206, R15577, R15862-3, R16118, R16972, R17187, R17856-61, R18479, R18645, R18662, R18681-3, R18732, R18777, R19259, R20353, R20534, R20561, R26031, R26187, R26504-5, R27327-8, R27348, R27799, R28066, R28546, R29702-3, R39505-6, R40118, R40422, R41201, R42716, R44721, R45328-62, R50672-3, R54079-80, R55812-20, R61518-21, R64942, R66243, R67656-8, R68315, R69205-6, R69718, R69841-62, R70038, R70042, R70130, R76711-2, R81385, R81540-2, R81763, R86212-3, R86332-7, R86491-2, R89140, R89219-21, R93815, R93922, R93924, R93929-31, R94644, R94833, R94837, R95851, R97919, R99367, R101967-8, R102611-9, R103560, R103717, R104822, R105614, R105788, R106612-3, R106940, R107697, R107914, R107919-22, R108909, R111051, R111952, R113125, R114262, R114479, R114553, R115227, R115667, R115740-3, R115788, R120572; BMNH 55.10.16.106(s), 1913.7.28.1, sixteen specimens (no numbers); CAS 74743-5, 83634(c+s), 83635, 94188-9, 100887-90, 100923-4; MNHN 2334-5, 5318, 5601; NMBA 2665, 18104-5; NMW 17423(1-2), 17424(1-2), 17425-7, 17428(1-4); RMNH 2636(1-3), 2637; RSW (2 specimens, no numbers); SMF 21667, 40008, 45418, 66197; USNM 6479, 58909, 62732-3, 63126, 63167-9.

*Nephrurus sphyrurus* (23 specimens):
AMS R1818, R2766, R2768, R3800*, R4880, R5617, R6770, R6771(c+s), R6772-3, R10266, R10532, R12571, R15195, R15642, R35188, R51688-9, R69717, R106935; BMNH 1912.11.1.89; QM J3859, J4342.

*Nephrurus stellatus* (4 specimens examined):
SAM R18515; ZFMK 48263-4; ZIH 02828.

*Nephrurus vertebralis* (5 specimens examined):
AMS R96161-2; LACM 57044, 57048; RMNH one specimen (no number).

*Nephrurus wheeleri* (12 specimens examined):
AMS R100897, R100899; BMNH 1932.7.13.1, 1946.8.23.52; MCZ 32950*3; RMNH 6406; SAM R222, R4485; ZMH R02827.

*Phyllurus caudianulatus* (100 specimens examined):
AMNH 27326; AMS R20427(c+s), R47521, R47551-6, R47641, R47654-7, R47738-62, R47836-49, R47888, R47896, R47901-14, R47956-7, R47959, R57782, R57912, R61473, R76186, R90205, (19 specimens, no numbers); QM J15619*, J22286-7, J24132, J25411.

*Phyllurus cornutus* (112 specimens):
AMNH 20876, 27261, 27302, 27325, 69534-5, 120292-3; AMS A233, R748, R749*, R750, R752-3, R1094, R2315, R2409, R3795, R3799, R4769, R5839, R6247, R6284, R6792, R6915, R8103, R8253, R11160, R11375, R11553, R11621, R11844, R12935, R15412, R16905, R16989, R17008, R20447-8(c+s), R26117-23, R41148, R42163, R43870-7, R47494, R54071, R55810-1, R59313-4, R65251-2, R69866-7, R70058-9, R71372-3, R81921, R92119-23, R97670-2, R97823, R98332-3, R101338, R103031, R106749, R110510, R116978; BMNH 1963.592-3; CAS 44119, 44120(s), 44121-23, 44135; FMNH 29046, 35237, 37495-503, 97699; NMW 17440; SMF 22502; USNM 64947-9; ZFMK 29114.

*Phyllurus platurus* (288 specimens examined):
AMB 42(s), 43-44, 1453(s), 1454 (c+s), one specimen, (no number) (c+s); AMNH 12858(c+s), 20875, 32873-4, 44940, 97748, 121268; AMS A1237, A9615, 4942, 5241, R959, R966, R992, R1124, R1550, R1575, R2306, R2531, R3134, R3182, R3392, R3582-3, R3585, R3588, R3601, R3666, R3793, R4396, R4404, R4814, R5181-2, R5520, R6141, R6728, R7189, R7194, R7294, R7747, R7987, R8018, R8037, R8087, R8125-6, R8271, R8277, R8595, R8980, R9274, R9305, R9826, R10051, R10066, R10068, R10220, R10374, R10377, R10384, R10387, R10412, R10429, R10482, R10504, R10761, R11587, R11701, R11753, R12209, R12907, R13105, R16117, R19084, R20381, R20419-20(c+s), R21047, R25891, R25912, R26208, R27324-5, R27330, R27334, R27740, R28308, R32613, R47958, R49185, R51776, R55802-9, R58269, R60995, R61097, R68314, R68342, R69814-40, R69865, R69870-94, R70051-4, R70128-9, R74914, R76444, R80742, R81912-20, R81922, R92870, R93900, R93997-8, R97261-2, R103126-8, R106491-9, R106601-11, R106801, R107089, R110651, R110701, R110762, R110889, R121020, nineteen specimens (no numbers); FMNH 29047, 75163-4, 97697-8, 207638, 207821, 213244; NMBA 2666-7, 8001-3; NMK R34118, R34740-1; NMW 14737(1-6), 14739(1-3); SMF 61215, 61216(1-10), 65242, 68269; SMNS 4466; USNM 5679, 5890-1; ZFMK 20560-2, 30903, 38646; ZIH 5127, 5204, 8530, 46662.

*Phyllurus salebrosus* (33 specimens):
AMS R300, R5586, R5838, R47884; CAS 74737-42; QM J2879, J8142, J4474, J4897, J5390, J6198, J6382, J8377, J9770, J22288 J25360, J28741, J28802, J29778, J33700, J33730-2, J33744, J35400, J35448, J36114, J36116.

*Rhacodactylus auriculatus* (137 specimens):
AIM 926; AMS R78113-25, R78126-7, R78232-8, R78304-8, R90186-7, R93711; BMNH 85.11.16.2-4, 86.3.11.5-9, 1926.9.17.5; CAS 157676-84, 158389-90, 158919-25, 159512, 162178-83, 165858-60, 165891-2(s), 165895-902(c+s); MCZ 15968; MNHN 5305, 5305a, 86.393-5, 87.272-5,

94.450-1, 1974.804-5, 1985.108-9; NHMG 874 (1-3), 658 (1-11); NMBA 2909, 7047-8, 7050-2; NMW 17926 (1-4), 18609; RMNH 5451; SMF 61778, 64806, 71024; UMMZ 127599(c+s), 174094; ZFMK 29111, 38940, 43584, 43685-9, 45036, 45384, 46119; ZMH R02830.

*Rhacodactylus australis* (39 specimens examined):
AMS R38502, R46293-6, R46415, R48089, R57783, R59951, R61974-5, R62332, R64236-7, R76618, R82597, R91493-4, R91496, R93651, R94466, R99835, R99973, R106907; BMNH 77.3.3.12*; MCZ 35162, 45502; NMW 17426; QM J6433, J8164, J28785, J29126, J30064, J31823, J38220, J38327, J38332, UMMZ 127150, 127598(c+s).

*Rhacodactylus chahoua* (13 specimens examined):
CAS 156691-2*(neotype), 162177, 167764(s); NMBA 9702; SMF 61779; ZFMK 27653, 30549, 38631-4, 42410.

*Rhacodactylus ciliatus* (16 specimens examined):
BMNH 85.11.16.5-6, 85.11.16.7(s), 90.7.26.2-3,3a-b; IRSNB 797; MNHN 701*, 701a*, 1312, 1755, 4213, 1974.802; NMW 17927 (1-2).

*Rhacodactylus leachianus* (47 specimens examined):
AMNH 62686; AMS R90386; BMNH 53.8.16.13, 85.11.16.1, 86.3.17.1, 1926.9.17.6; CAS 80879-81, 156690, 159510, 165857, 165890(s); IRSNB 806; MCZ 15967; MMNH (1 spec. no number); MNHN 702, 1483, 4210, 6687*, 86.24; NHMG 657 (1-2); NMBA 7053, 7057-60, 7062, 7064-7, 7095; NMW 17668, 17928; SMF 59030-1, 60655, 65887; USNM 267945; ZFMK 2539, 36270, 45845, 46983; ZMH R02831.

*Rhacodactylus lindneri* (42 specimens examined):
AMS R37128(c+s), R37129-33, R38730-3, R38734*, R38735, R38945-6, R39493, R39496-7, R39520-2, R39895, R39975, R39992, R40283, R41843-4(c+s), R42123, R75697-700, R76506, R88616, R90194-5, R97346; MVZ 99554; ZFMK 25506-9, 38640.

*Rhacodactylus sarasinorum* (8 specimens examined):
AMS R90188; CAS 157675; MNHN 94.452*; NMBA 7246*; ZFMK 46408, 46984-6.

*Rhacodactylus trachyrhynchus* (31 specimens examined):
Alcoholic specimens - AMS R78129-32, R90185; BMNH 80.6.17.5a-b, 86.3.11.2-3, 86.3.11.4(s), 1920.1.20.305; IRSNB 2.532, 786s; MCZ 19647; MNHN 700, 5789, 85.756, 86.271-2, 1974.803; NMBA 7039-42, 7044, 7046; ZFMK 25398; 29112, 31806, 46106, 46982.

# APPENDIX C

**Character Matrix** (all characters for all carphodactyline taxa). Missing data are represented by a 9. Character numbers refer to the character state descriptions in the text. Character states entered as unpolarized are listed as letters. Polarized characters are listed as numbers.

| Taxon | Characters<br>11111111<br>11111111112222222222333333333344444444445555555555666666666677777777778888888888999999999900000000<br>12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567 |
|---|---|
| *Bavayia cyclura* | 00000000B000AB0A0001001A00009ABAB00000B000A000000B00BB0010A00AAA0900000111B00BABA090A0010000A0A00000A1B0101 |
| *Bavayia sauvagii* | 00000000B000AB0A0001001A00009ABAB00000B000A000000B00BB0010A00AAA0900000111A00BABA090A0010000A0A00000A0B0101 |
| *Carphodactylus laevis* | 11101011A010AA0B1110110A1011BBABA00100A111A010001A019A0000A00AAA0901100099900ABAA1A0A0100000A1900001A0A0009 |
| *Eurydactylodes symmetricus* | 00000000B000AB1A0000011A00009AACB00000A000A000000B00BB0010A00AAA0900000110900AAAA090A1010100A0A00000A0B1101 |
| *Eurydactylodes vieillardii* | 00000000B000AB1A0000011A00009AACB00000A000A000000B00BB0010A00AAA0900000110900AAAA090A1010100A0A00000A0B1101 |
| *Hoplodactylus chrysosireticus* | 09999999999999999999909999999999999999999999990999999990910900AAA1B00000110B00BBAA090A0010000A0A00000A0B0011 |
| *Hoplodactylus delcourti* | 00009000B0999A9909999999999999999999999999999990999990BB0010A009999990990110B00BAAA090A0010000A0A00000A0B0099 |
| *Hoplodactylus duvaucelii* | 00001000B000BA1A0000001A00009ABAB00000A000A000000B00BB0010B00BAA1B00000110B00BAAA090A0010000A0A00000A0B0011 |
| *Hoplodactylus granulatus* | 00000000B000BA1A0000001A00009AABB00000A000A000000B00BB0010B00ABB1B00000100B00BAAA090A0010000A0B00000A0B0011 |
| *Hoplodactylus kahutarae* | 09999999999999990999909999999999999999999999990999999990910900 9BB1B00000100900BAAA090A0010000B0B00000A0B0011 |
| *Hoplodactylus maculatus* | 00000000B000BA1A0000001A00009ABAB00000A000A000000B00BB0010B00AAA1A00000110B00BBAA090A0010000A0A00000A1B0011 |
| *Hoplodactylus pacificus* | 00000000B000BA1A0000001A00009ABAB00000A000A000000B00BB0010B00AAA1A00000110B00BAAA090A0010000B0A00000A1B0011 |
| *Hoplodactylus rakiurae* | 00000000B000BA9A0000001A00009AAAA00000A000A000000B00BB0010B00ABB1B00000100B00BAAA090A0010000A0B00000A0B0011 |
| *Hoplodactylus stephensi* | 00000000B000BA1A0000001A00009ABAB00000A000A000000B00BB0010B00AAB1A00000110B00BAAA090A0010000A0B00000A0B0011 |
| *Naultinus elegans* | 00000000B000AA1A0010001A0001AAABB01000A000A000000B00AB0010B10ABB1B10000100B00BBAA090A0000000A0B00000A0A0010 |
| *Naultinus gemmeus* | 00000000B000AA9A0010001A0001AAABA01000A000A000000B00AB0010B10ABB1B10000100B00ABAA090A0000000A0B00000A0A0010 |
| *Naultinus grayii* | 00000000B000AA1A0010001A0001AAABA01000A000A000000B00AB0010B10ABB1B10000100B00BBAA090A0000000A0B00000A0A0010 |
| *Naultinus manukanus* | 09999999999999990999909999999999999999999999900999999990910910AAB1B10000100B00AAAA090A0000000A0B00000A0A0010 |
| *Naultinus poecilochloris* | 09999999999999990999909999999999999999999999900999999990910910ABB1B10000100B00ABAA090A0000000A0B00000A0A0010 |
| *Naultinus rudis* | 00000000B000AA9A0010001A0001AAABB01000A000A000000B00AB0010910ABB1B10000100B00AAAA090A0000000A0B00000A0A0010 |
| *Naultinus stellatus* | 00000000B000AA9A0010000A0001AAABA01000A000A000000B00AB0010B10ABB1B10000100B00ABAA090A0000000A0B00000A0A0010 |
| *Naultinus tuberculatus* | 0999999999999919099990999991AA9999999999999900999B00AB0010910ABB1B10000100B00ABAA090A0000000A0B00000A0A0010 |
| *Nephrurus asper* | 11010011A010AA0B1110000B1111BAAAA10100A110B101001A10AA1000A10AAA0901101999901AAAA1B0A01000019191099 1B0A0000 |
| *Nephrurus deleani* | 01010001A000AA0B1110001B1111BAAAA10100A110B102001A10AA1100A01AAA0A01101999901ABAB1A0B000000191910111B0A0000 |
| *Nephrurus laevissimus* | 01010001A000AA0B1110000B1111BAAAA10100A110B102001A10AA1100A01AAA0A01101999901ABAB1A0B000000191910111B0A0000 |
| *Nephrurus levis* | 11010011A000AA0B1110000B0111BAAAA10100A110B102001A10AA1100A01AAA0A01101999901ABAB1A0B010000191910111B0A0000 |
| *Nephrurus milii* | 01000001A000AA1B1110100B0111BAAAA10100A010B000001A00AA0000A00AAA0901100099900AAAA1A1A010000191910100B0A0000 |
| *Nephrurus sphyrurus* | 01000001A000AA1B1110000B1101BAAAA10000A010B100001A00AA0000A00AAA0901100099900ABAB1A1A000000191910100B0A0000 |
| *Nephrurus stellatus* | 01010001A000AA1B1110001B1111BAAAA10100A110B102001A10AA1100A01AAA0901101999901ABAB1A0B000000191910111B0A0000 |
| *Nephrurus vertebralis* | 01010001A000AA0B1110000B0111BAAAA10100A110B102001A10AA1100A01AAA0901101999901ABAB1A0B000000191910111B0A0000 |
| *Nephrurus wheeleri* | 91010001A000AA0B1110000B9991BAAAA10100A110B101001A10AA1000A00AAA0901101999901ABAA1A0B000000191910111B0A0000 |
| *Phyllurus caudiannulatus* | 11100011A010AA1B1110000B0111BAAAA00010A011A010011A019A0001A00AAA0900100099900ABAB1A0A000000191911000B0A0000 |
| *Phyllurus cornutus* | 11101011A010AA1B1110000B0111BAABA00091A011A010111A019A0001A00AAA0900100099000ABAA1B0A000000191911000B0A0000 |
| *Phyllurus platurus* | 11100011A010AA1B1110000B0111BAAAA00010A011A010011A019A0001A00AAA0900100099900ABAB1A0A000000191911000B0A0000 |
| *Phyllurus salebrosus* | 11101011A010AA1B1110000B0111BAABA00091A011A010111A019A0001A00AAA0900100099900AAAA1B0A0000000A1911000B0A0000 |
| *Rhacodactylus auriculatus* | 00001100A101BB1A0000001A00009AABB00000A000A000000B00BB0010A00AAA0900000110A00BABA090A1010100B0A00000A0B0101 |
| *Rhacodactylus australis* | 10001000A000BB0A0000001A00009AABA00000B000A000000B00BB0010A00ABB0900000111910BBBA090A0010000B0A00000A1A0101 |
| *Rhacodactylus cavaticus* | 0999999999999999099990999999A999999999999999009999999990910A009AA0900000111910ABAA090A001000190A00000A1A0109 |
| *Rhacodactylus chahoua* | 00001000A000BB0A0000001A00009BAAB00000A000A000000B00BB0010A00BAA0900010110A00BAAA090A1011110A0A00000A190101 |
| *Rhacodactylus ciliatus* | 00001000A101BB0A0000001A00009BAAB00000A000A000000B00BB0010A00BAA0900010110A00ABAA090A1011100A0A00000A1B0109 |
| *Rhacodactylus leachianus* | 10001100A000BB1A0000001A10009AABA00000A000A000000B00BB0010A00BAA0900010110A00BBAA090A1011110A0A00000A1B1101 |
| *Rhacodactylus lindneri* | 00001000A000BB0A0000001A00009AAAA00000B000A000000B00BB0010A00BAA0900000111910BBAA090A0010000B0A00000A1A0101 |
| *Rhacodactylus sarasinorum* | 00001000A000BB0A0000001A00009AAAB00000A000A000000B00BB0010A00BAA0900010110A00BAAA090A1010000A0A00000A190901 |
| *Rhacodactylus trachyrhynchus* | 10001000A000BB0A0000001A00009AABB00000A000A000000B00BB0010A00BAA0900010110A00BBBA090A1010000B0A00000A1B0111 |

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