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COMPARATIVE MORPHOLOGY AND KARYOLOGY OF THE AUSTRALIAN MEMBERS OF THE FAMILY AGAMIDAE AND THEIR PHYLOGENETIC IMPLICATIONS

by

Geoffrey James Witten

A thesis submitted in fulfilment of
the requirements for the degree of
Doctor of Philosophy

Department of Anatomy
University of Sydney

May, 1982

ABSTRACT

The comparative morphology of the Australian agamids is investigated, and morphometric analyses performed to compare growth patterns. The karyotypes of representatives of most Australian genera and species-groups are presented. These studies confirm that the Australian agamids belong to one of two groups. The larger group has few congeneric species outside Australia, and none outside the Australian region. The smaller group has congeners in Asia and in the Indo-Australian archipelago. Within the larger, and presumably older, Australian group four supra-generic groups are recognised, with a total of 13 species-groups of generic status. Karyotypic variation within the Australian radiation is limited, with only one genus, Lophognathus, with a karyotype differing from the other endemic groups.

The morphological divergence within the Australian radiation suggests a long period of separate evolution. It seems unlikely that ancestors of the Australian radiation arrived on the continent by over-water dispersal. The possibility of a Gondwanan origin for the Australian agamids is therefore suggested. All current fossil evidence is consistent with such an hypothesis. Agamids may have been restricted to East Gondwanaland. It is suggested that the basically arid-adapted Australian radiation may have been restricted to arid refugia during the long periods of relatively high rainfall in Australia.

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I. Introduction.

The family Agamidae forms a prominent part of the lizard fauna in much of the Old World. Agamids occur throughout Australia, Africa, southern Asia, and extend into southern Europe.

Camp (1923) divided the Sauria (Lacertilia) into two divisions, the Ascalabota and Autarchoglossa. Within the Ascalabota he recognised three sections, the Gekkota, the Iguania, and the Rhiptoglossa. Section Iguania included the Iguanidae and the Agamidae. Most lizards were included in the Autarchoglossa.

The Ascalabota were considered the more primitive division by Camp (1923), yet contained some of the most specialised of all lizards. The chameleons (Rhiptoglossa) show a number of peculiar specialisations, including an extensile tongue and an acrodont, heterodont dentition. Camp went so far as to say "there is scarcely anything primitive in the structure of the chameleons" (p. 364).

The Rhiptoglossa probably arose from the Agamidae, with which family they share their acrodont, heterodont dentition, as well as a number of other features (Camp, 1923). This dentition has apparently evolved with precise occlusion of the jaws, allowing the development of a precise shearing mechanism (Robinson, 1976). This presumably endows the animal with a more effective chewing mechanism than is possessed by most other lizards. A similar dentition and shearing arrangement evolved in the non-streptostylic skull of the sphenodontids (Robinson, 1976). The shearing action is more simply achieved here because of the single mandibular joint on either side. The streptostylic skull of the squamates involves two jaw articulations, one at either end of the mobile quadrate. The precise occlusion and chewing mechanism of the agamids and chameleons therefore represents a complex evolutionary achievement.

Acrodont teeth occur also in some amphisbaenids. In the agamids teeth are added to each jaw quadrant posteriorly, and these later teeth are larger (Cooper, Poole and Lawson, 1970). In the amphisbaenids, by contrast, the first or second of only three or four teeth is the largest (Gans, 1960), suggesting that tooth growth is quite dissimilar. Gans (1960) suggested that foramina on the lingual aspect of the mandibles of the acrodont amphisbaenids represented "a temporary stage in the replacement cycle". This implies a close similarity between the amphisbaenid condition and the pleurodont, successional teeth of the majority of lizards. The acrodont dentition of the agamids and chameleons appears to be peculiar to that group alone.

Agamids are considered more advanced than the iguanids, apparently replacing them in most of the Old World (Camp, 1923; Darlington, 1948). They are a large and diverse group and include four of the most spectacular living lizard forms. The species of Draco have evolved a gliding habit, using a flap of skin supported by elongated ribs. Hydrosaurus has a large dorsal 'sail' reminiscent of some of the Pelecosaurs. The Australian Chlamydosaurus has a quite different dermal fold in the form of a spectacular 'frill'. Moloch, also of Australia, is highly specialised, with a peculiarly modified dentition and a remarkably spinose skin.

Two hundred and ninety species were recognised in the family Agamidae by Wermuth (1967), who placed them in 34 genera. He listed a further 96 subspecies, giving a total of 386 taxa in the family. Using Darlington's (1948) estimate of 300 lizard genera with nearly 3,000 species, the Agamidae constitute about one tenth of all lizards. Of the 34 genera recognised by Wermuth, nine occur in Australia. According to his list, these genera include 43 Australian species and a total of 58 taxa if subspecies are included. Only two genera had species in both

Asia and the Australian region.

Currently nine Australian genera are recognised (Houston, 1978). The number of recognised species has increased to 56 since Wermuth's (1967) publication, and a total of 76 species and subspecies are known.

The family Agamidae represents a considerable part of the Australian lizard fauna. Of the five families present in Australia the agamids are second in terms of diversity, with more taxa than all except the Scincidae (Table 1). The largest lizards in Australia belong to the family Varanidae, but the Agamidae includes the next largest species. All agamids are diurnal, and many species are particularly obvious to human observers because of the perching behaviour of territorial males. At least one species of agamid occurs in most districts of Australia, and most Australians are aware of their existence. The frilled lizard, Chlamydosaurus, appears on Australian coins.

Table 1. Species Diversity of Australian Lizard Families.

Family	Genera	Species	Subspecies	Total Taxa
Scincidae	20	193	27	220
Agamidae	10	53	18	71
Gekkonidae	16	63	3	66
Pygopodidae	8	29	1	30
Varanidae	1	21	7	28

A considerable literature dealing with the thermal ecology of Australian lizards has built up over the past decade and a half. Warburg (1965a, 1965b, 1966) worked on water balance and thermal requirements of many Australian lizards, including members of the Agamidae, Scincidae and

Gekkonidae. Licht *et al* (1966a, 1966b) used representatives of the same families. Lee and Badham (1963) worked on one agamid, *Amphibolurus barbatus*, and much of the more recent literature (Heatwole, 1970; Bradshaw and Main, 1968; Cogger, 1974; Witten and Heatwole, 1978) has been on members of the Agamidae.

Three major ecological studies on Australian lizards have been carried out on agamid species (Bradshaw, 1971: *Ctenophorus ornatus*; Heatwole, 1970: *Amphibolurus nuchalis*; Cogger, 1978: *A. fordi*). Many other shorter papers have also reported on their ecology (e.g. Pianka, 1971a, 1971b, 1971c; Witten, 1974). Similar papers have been published on representatives of the other Australian lizard families (e.g. Bustard, 1968a, 1968b, 1969; Pianka, 1968, 1969, 1970), but the other four families have not attracted the detailed attention received by the agamids.

Considerable work has been done on the physiology of Australian agamids. Bartholomew and Tucker (1963) used *A. barbatus* in what was virtually the first modern physiological paper on Australian lizards. Grigg, Drane and Courtice (1979) did similar work on *Physignathus lesueurii*. Much work has also been published by Heatwole and his associates (Firth and Heatwole, 1976; Heatwole, Firth and Webb, 1973; Heatwole, Firth and Stoddart, 1975; Chong, Heatwole and Firth, 1973; Parmenter and Heatwole, 1975).

Carpenter, Badham and Kimble (1970) and Gibbons (1979) have published reports on the territorial displays of various agamids. These complex, species-specific displays are known only in the Agamidae and the Iguanidae.

In the period when this considerable literature on agamid physiology, ecology and behaviour appeared there was no corresponding advance in agamid taxonomy above the species level. Storr (1964, 1965, 1966, 1967, 1974, 1977), Witten (1972), Houston (1974a, 1974b, 1977) and Badham (1976) described new species of agamids. However, only Mitchell (1965), Storr (1974, 1977), Cogger and Lindner (1974) and Houston (1978) have suggested changes at the generic level. These changes involved a total of only six species. Apart from *Caimanops* Storr 1974 the most recently described Australian agamid genera are *Tympanocryptis* Peters 1863, *Calotella* Steindachner 1867 and *Redtenbacheria* Steindachner 1869. Only the first of these three names is still in use.

The Agamidae have received less attention from taxonomists than other Australian lizards. Kluge (1967a, 1967b) has provided recent revisions of the Australian Gekkonidae. Kluge (1974) revised all members of the Pygopodidae. Mertens (1958, 1959) has done considerable work on the Varanidae. The largest family in Australia, the Scincidae, has been the subject of many taxonomic studies recently, of which papers by Greer (1970, 1974, 1979) are representative.

Considering the diversity and prominence of the Australian agamids the lack of recent general taxonomic or phylogenetic publications dealing with the group is remarkable. This apparent lack prompted the present study.

The need for revision of the Australian agamids has been recognised by several recent workers. Cogger and Lindner (1974) referred to the "present unsatisfactory generic arrangement of Australian agamid lizards". The main feature of this problem is that *Amphibolurus* is a large genus which is "almost certainly composite and polyphyletic" (Cogger, 1975). Houston (1974b) has also commented on the problem, stating that the species of *Amphibolurus* "cohere more by the lack of specialised features characterising other genera than by the possesssion of features unique to them as a group". Gray (1845) was probably the first to express doubt about the validity of the genus. His decision to "reduce" *Grammatophora* and *Amphibolurus* to one genus was apparently based on the occurrence of an intermediate species, and not on the lack of variation at the generic level. Recently this variation within *Amphibolurus* has been recognised by a number of workers, who have described species-groups within the genus (Storr, 1965, 1966, 1977; Humphries, 1972; Houston, 1974a, 1978; Badham, 1976), but no genera have been erected to accommodate these groups.

Clearly an investigation of the phylogenetic relationships of the Australian agamids is overdue. Such an investigation should not only be useful to taxonomists, but also may assist in the interpretation of results obtained by workers in the fields of ecology, physiology and behaviour. Information useful in forming phylogenetic hypotheses may also provide clues to the biological and geological history of Australia.

Before the taxonomic relationships of Australian agamids can be adequately discussed decisions need to be made on some points of nomenclature. Table 2 presents the nomenclature to be adopted in the present dissertation. The major changes made to recent published lists of the species of Australian agamids (Cogger, 1975) have been in dividing *Amphibolurus* into a number of species-groups. Each of these species-groups should be regarded as being of generic rank, but new names for these groups have not been employed to avoid the possible creation of *nomina nuda*. The only generic name available for any of these groups is *Ctenophorus* Fitzinger 1843. *Ctenophorus* is here applied to the *A. decresii* species-group (Houston, 1974a). Further, two recommendations that species not previously in *Amphibolurus* be transferred to that genus have not been accepted. The species concerned are *Tympanocryptis parviceps* (Storr, 1977), and the three species of *Lophognathus* (Houston, 1978).

Table 2. Nomenclature Adopted for the Present Study.*

Genus or Sp-gp.	Species.
Australian Endemic Genera	
Tympanocryptis Group	
Tympanocryptis	T. cephalus T. intima T. lineata T. parviceps T. tetraporophora T. uniformis
A. adelaidensis Species-group	A. adelaidensis A. diemensis
Chlamydosaurus Group	
A. muricatus Species-group	A. muricatus A. nobbi
Caimanops	C. amphiboluroides
Chlamydosaurus	C. kingii
Diporiphora	D. albilabris D. australis D. bennettii D. bilineata D. convergens D. lalliae D. linga D. magna D. reginae D. superba D. winneckei
Lophognathus	L. gilberti L. longirostris L. temporalis
Ctenophorus Group	
Ctenophorus	C. decresii C. fionni C. ornatus C. pictus C. rufescens C. vadnappa
A. maculatus Species-group	A. maculatus A. femoralis A. fordi A. isolepis A. scutulatus
A. cristatus Species-group	A. cristatus A. caudicinctus
A. reticulatus Species-group	A. reticulatus A. clayi A. gibba A. maculosus A. nuchalis
A. barbatus Species-group	A. barbatus A. microlepidotus A. minimus A. minor A. mitchelli A. nullarbor A. vitticeps
Moloch Group	
Moloch	M. horridus
Asian-derived Genera	
Chelosania	C. brunnea
Physignathus	P. lesueurii
Gonocephalus	G. boydii G. spinipes

A number of species of *Amphibolurus* have not previously been assigned to species-groups. *A. diemensis* has been included in the *A.*

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* For ready reference a copy of this table is included in the cover pocket.

adelaidensis species-group (Storr, 1977). *A. pictus* has been assigned by others to the *A. reticulatus* species-group (Storr, 1966; Humphries, 1972), but is here placed in *Ctenophorus*. Houston (1974a) noted that *A. pictus* resembled the *A. decresii* species-group (= *Ctenophorus*). Storr (1966) included *A. decresii* in the *A. reticulatus* species-group, although this has not been accepted by subsequent authors. *A. scutulatus* has been included in the *A. maculatus* species-group (Storr, 1965). *A. cristatus* and *A. caudicinctus* have been placed in a new species-group, the *A. cristatus* species-group. Three groups above generic rank have also been defined in Table 2: the *Chlamydosaurus* group, the *Tympanocryptis* group and the *Ctenophorus* group. The justification of these groupings will be found in the following dissertation.

II. Historical Review

The first Australian agamid to be formally named was *Lacerta muricata* Shaw 1790. Kaup (1827) described the genus *Gemmatophora* to accommodate this species. He had earlier (1825) described *Gonocephalus*, in which genus some Australian species were later placed. The first Australian genus in the Agamidae was *Chlamydosaurus* Gray 1825 (published as *Clamydosaurus*, due to a typographical error, *fide* Wermuth, 1967).

Cuvier (1829) described another Australian agamid species in *Agama barbata*. He also described *Physignathus cocincinus* from Cochin China, which genus later had an Australian species assigned to it.

Wagler (1830) provided two generic names as substitutes for names coined by Kaup in 1825 and 1827. These were *Gonyocephalus* for *Gonocephalus*, and *Amphibolurus* for *Gemmatophora*. Both names eventually became widely accepted.

Dumeril and Bibron (1837) also provided a *nomen substitutum* for *Gemmatophora* Kaup, *Grammatophora*. In *Grammatophora* they placed *Lacerta muricata*, *G. decresii* sp. nov. and *G. gaimardii*, a synonym for *Uromastyx maculatus* Gray 1831.

Gray described the distinctive *Moloch horridus* in 1841. In 1842 he added two more Australian agamids, and accorded each its own genus. These were *Lophognathus gilberti* and *Diporiphora bilineata*. In the same paper he provided, possibly in error, an alternative name for *Chlamydosaurus* by describing specimens of *Chlamydophorus kingii*.

Fitzinger (1843) provided two more generic names for Australian agamids. The first of these, *Homalonotus*, was created to accommodate *Grammatophora gaimardii* Dumeril and Bibron. This was not a valid genus, as the name was preoccupied (*Homalonotus* Koenig 1825 = Trilobita;

Homalonotus Schoenherr 1836 = Coleoptera). Fitzinger's second genus, *Ctenophorus*, contained only *Grammatophora decresii* Dumeril and Bibron, and is still available. Among his other changes Fitzinger adopted Wagler's *nomen substitutum* of *Gonyocephalus* instead of the original *Gonocephalus* Kaup. He attempted to split *Amphibolurus* and *Grammatophora*. *Amphibolurus* he restricted to *A. muricatus*, including the synonym *Agama jacksoniensis* Peron 1820. In *Grammatophora* he included *G. barbata*.

Gray (1845) also sought to split *Amphibolurus* and *Grammatophora* along similar lines. In his key he characterised *Amphibolurus* as "back crested, with longitudinal series of larger keeled scales. Femoral pores numerous". *Grammatophora* was distinguished from *Amphibolurus* by "back not crested, with cross rows of enlarged scales". However, Gray changed his mind between writing the key and his description of individual species, stating later "but on consideration, I have thought it better to reduce it again". It seems that his original plan was to include *Grammatophora cristata* and *G. muricata* in *Amphibolurus* and to relegate *G. barbata*, *G. angulifera* (= *diemensis*), *G. maculata*, *G. decresii* and *G. ornata* to *Grammatophora*. Perhaps the reason for Gray's failure to persevere with this division was *Grammatophora reticulata*, which cuts across his 'generic' key characters, with his own description "back with a central series of keeled scales, and with cross rows of larger keeled scales on each side".

The attempts by both Fitzinger and Gray to separate and retain both *Amphibolurus* and *Grammatophora* could not succeed, as the genera share the same type species, *Lacerta muricata* Shaw 1790.

Gray's catalogue (1845) saw the description of two more agamid genera from Australia, with the description of *Chelosania brunnea* and

Gindalia bennettii. Gray reverted to *Chlamydosaurus* in this work, but created *Diporophora* as a *nomen substitutum* for *Diporiphora*, possibly unintentionally. Gray also adopted Wagler's *Gonyocephalus* for *Gonocephalus* Kaup (Table 3).

In 1851 A. Dumeril described the first Australian species of *Gonocephalus* Kaup as *Lophyrus spinipes*.

Girard (1857) described *Oreodeira gracilipes*, a new genus and species from Australia. The single female specimen caused some confusion in later publications. Boulenger (1885) does not include the species in his key, commenting that "its place in the system can hardly be assigned unless it be known whether or not preanal or femoral pores exist in the male". Moody (pers. comm.) has located the type specimen and suggests that it is a female *Agama sp*. from southern Africa. This explanation is accepted here.

The genus *Tympanocryptis* Peters 1863 was described to accommodate *Tympanocryptis lineata*. Peters also described a number of other Australian agamids (1863, 1866, 1867), and adopted Wagler's *Amphibolurus* for these species. Gray (1845) had inexplicably preferred *Grammatophora* Dumeril & Bibron 1837 to *Amphibolurus* Wagler 1830 when "reducing" them to one genus, although he may have failed to note that Dumeril & Bibron's *Grammatophora* differed from Kaup's *Gemmatophora* (1827). Certainly he listed "*Grammatophora* Kaup" as his genus 24. Other authors of the same era as Peters followed Gray in describing new Australian agamids in the genus *Grammatophora* (Gunther, 1867, 1875; Fischer, 1881; Table 3).

Steindachner (1867) described new genera with two species of Australian dragons. These were *Calotella australis* and *Redtenbacheria fasciata*. The first was later placed in *Diporophora* (Boulenger, 1885), and the latter synonymised with *Physignathus gilberti* (Boulenger, 1885).

Table 3. Summary of History of Australian Agamid Nomenclature.

Species	Gray (1845)	Boulenger (1885)	Loveridge (1934)	Cogger (1975)
Lacerta muricata Shaw 1790	Grammatophora muricata	Amphibolurus muricatus	Amphibolurus muricatus	Amphibolurus muricatus
Chlamydosaurus kingii Gray 1825	Chlamydosaurus kingii	Chlamydosaurus kingii	Chlamydosaurus kingii	Chlamydosaurus kingii
Agama barbata Cuvier 1829	Grammatophora barbata	Amphibolurus barbatus	Amphibolurus barbatus	Amphibolurus barbatus
Lophura lesueurii Gray 1831	Physignathus lesueurii	Physignathus lesueurii	Physignathus lesueurii	Physignathus lesueurii
Uromastyx maculata Gray 1831	Grammatophora maculata	Amphibolurus maculatus	Amphibolurus maculatus	Amphibolurus maculatus
Grammatophora decresii Dumeril & Bibron 1837	Grammatophora decresii	Amphibolurus decresii	Amphibolurus decresii	Amphibolurus decresii
Gindalia bennettii Gray 1841	Gindalia bennettii	Diporophora bennettii	-	Diporiphora bennettii
Grammatophora cristata Gray 1841	Grammatophora cristata	Amphibolurus cristatus	-	Amphibolurus cristatus

Table 3. (cont.)

Species	Gray (1845)	Boulenger (1885)	Loveridge (1934)	Cogger (1975)
Grammatophora muricata var.diemensis Gray 1841	(?)Grammatophora angulifera	Amphibolurus angulifera	Amphibolurus diemensis	Amphibolurus diemensis
Grammatophora adelaidensis Gray 1841	Grammatophora angulifera var.2	Amphibolurus adelaidensis	Amphibolurus adelaidensis	Amphibolurus adelaidensis
Moloch horridus Gray 1841	Moloch horridus	Moloch horridus	Moloch horridus	Moloch horridus
Lophognathus gilberti Gray 1842	Lophognathus gilberti	Physignathus gilberti	Physignathus gilberti	Lophognathus gilberti
Diporiphora bilineata Gray 1842	Diporophora bilineata	Diporophora bilineata	Diporiphora bilineata	Diporiphora bilineata
Grammatophora ornata Gray 1844	Grammatophora ornata	Amphibolurus ornatus	Amphibolurus ornatus	Amphibolurus ornatus
Chelosania brunnea Gray 1845	Chelosania brunnea	Chelosania brunnea	-	Chelosania brunnea
Grammatophora reticulata Gray 1845	Grammatophora reticulata	Amphibolurus reticulatus	Amphibolurus reticulatus	Amphibolurus reticulatus
Lophyrus spinipes A. Dumeril 1851	-	Gonyocephalus spinipes	Gonyocephalus spinipes	Gonocephalus spinipes

Table 3. (cont.)

Species	Gray (1845)	Boulenger (1885)	Loveridge (1934)	Cogger (1975)
Tympanocryptis lineata Peters 1863	-	Tympanocryptis lineata	Tympanocryptis lineata	Tympanocryptis lineata
Amphibolurus pictus Peters 1866	-	Amphibolurus pictus	Amphibolurus pictus	Amphibolurus pictus
Calotella australis Steindachner 1867	-	Diporophora australis	Diporiphora australis	Diporiphora australis
Tympanocryptis cephalus Gunther 1867	-	Tympanocryptis cephalus	Tympanocryptis cephalus	Tympanocryptis cephalus
Grammatophora temporalis Gunther 1867	-	Physignathus temporalis	*Physignathus temporalis	Lophognathus temporalis
Grammatophora caudicincta Gunther 1875	-	Amphibolurus caudicinctus	Amphibolurus caudicinctus	Amphibolurus caudicinctus
Grammatophora isolepis Fischer 1881	-	Amphibolurus maculatus	-	Amphibolurus isolepis
Lophognathus longirostris Boulenger 1883	-	Physignathus longirostris	Physignathus longirostris	Lophognathus longirostris
Tiaris boydii Macleay 1884	-	Gonyocephalus boydii	Gonyocephalus boydii	Gonocephalus boydii

Table 3. (cont.)

Species	Gray (1845)	Boulenger (1885)	Loveridge (1934)	Cogger (1975)
Macrops nuchalis De Vis 1884	-	-	(?) Amphibolurus reticulatus inermis	Amphibolurus nuchalis
Amphibolurus scutulatus Stirling & Zietz 1893	-	-	Amphibolurus scutulatus	Amphibolurus scutulatus
Amphibolurus rufescens Stirling & Zietz 1893	-	-	*Amphibolurus rufescens	Amphibolurus rufescens
Tympanocryptis tetraporophora Lucas & Frost 1895	-	-	Tympanocryptis cephalus	Tympanocryptis tetraporophora
Diporiphora winneckei Lucas & Frost 1896	-	-	Diporiphora winneckei	Diporiphora winneckei

* No specimens, but mentioned in discussion.

Boulenger catalogued the specimens in the British Museum during the latter part of the nineteenth century. As a small part of this massive undertaking he was faced with 35 described Australian agamid species in possibly 15 genera. Boulenger (1885) followed Peters (1863, 1866, 1867) in preferring *Amphibolurus* Wagler to *Grammatophora* Dumeril & Bibron (Table 3). All species placed in *Grammatophora* by Gray (1845) were formally placed in *Amphibolurus* by Boulenger. *Lophyrus spinipes* A. Dumeril and *Tiaris boydii* Macleay were both placed in *Gonyocephalus*. *Calotella* and *Gindalia* were placed in synonymy with *Diporophora*. *Lophognathus*, including new species described by himself two years earlier (1883), was placed in synonymy with *Physignathus*. In all, Boulenger synonymised a number of species and genera, described two new species, and ended with 30 species in 9 genera.

From the time of Boulenger's major revision until 1934 most contributions to Australian agamid taxonomy were in the form of descriptions of individual species. Loveridge (1934) presented the next major review of Australian agamids (Table 3). His main contribution was in synonymising many of the species described after Boulenger's revision. Loveridge referred to Gray's original description of *Diporiphora* (1842) and reverted to the original spelling, correcting the 'error' of Gray's (1845) catalogue and all subsequent publications.

Loveridge recognised *Grammatophora inermis* De Vis 1888 as a subspecies of *Amphibolurus reticulatus*. De Vis had earlier described the same taxon as *Macrops nuchalis* De Vis 1884. This earlier description was apparently available to Loveridge, as he synonymised four species of *Diporophora* described by De Vis in the same paper. Cogger (1975) has recognised the earlier description as valid and used *Amphibolurus nuchalis* instead of *Amphibolurus reticulatus inermis* of Loveridge and others. This recognition has been accepted here, there being no question of priority between the two available names.

Loveridge's paper was not intended as a complete revision of the Australian agamids, but almost achieved this. There were only five species of agamid described from Australia which were not mentioned by Loveridge. With these species included there was a total of 32 species in 9 genera at the time of his publication. This total included *Oreodeira gracilipes* Girard, which does not deserve continued recognition.

The next Australian agamids described were three new species of *Tympanocryptis* by Mitchell (1948). Mitchell also resurrected *T. tetraporophora* and described new subspecies of *T. lineata* and *T. cephalus*. He later (1965) examined the relationships of *T. maculosa* Mitchell and transferred it to *Amphibolurus*.

Storr (1974) described the genus *Caimanops* to accommodate the distinctive *Diporiphora amphiboluroides*. Apart from this action he has concentrated his work at the species and subspecies level, having described a total of 25 taxa in little more than a decade.

Cogger and Lindner (1974) resurrected *Lophognathus* Gray. Boulenger's placement of *Lophognathus* within *Physignathus* was puzzling, as the two genera are not very similar. Cogger and Lindner noted that the species of *Lophognathus* "are extremely close, in their morphology and osteology, to *Amphibolurus muricatus* (the type species of the genus)". However, they declined to place *Lophognathus* within *Amphibolurus* due to the "present unsatisfactory generic arrangement of Australian agamid lizards". Houston (1978) included *Lophognathus* within *Amphibolurus* for the first time. To facilitate discussion of this group of species his action has not been adopted in the present study.

Storr (1977), following a pattern set by Mitchell (1948, 1965), referred *Tympanocryptis parviceps* Storr to *Amphibolurus* on the basis of its close similarity in many characters to *A. adelaidensis*. He considered these two species as constituting the *A. adelaidensis* species-group.

Storr (1965, 1966) named species-groups within the genus *Amphibolurus*. These were apparently not intended as subgenera, but rather to define the area covered by individual publications. Storr's papers have concentrated heavily on Western Australian species, and he has neglected some eastern species.

Humphries (1972) attempted to group all species of *Amphibolurus* into species-groups (Table 4). This unpublished Honours thesis remains the only such attempt. Humphries, like Storr, was based in Western Australia, and his placement of some eastern species reflected his limited knowledge of them. He depended heavily on ecological characters, which cuts across normal taxonomic practice. Such a bias towards ecological types would presumably increase the chance of creating polyphyletic groups. Species in a similar ecological niche but evolving from distantly related ancestors might easily be grouped together in such a system.

Houston (1974a) described the *A. decresii* species-group. This group was essentially the same as Humphries' *A. ornatus* species-group. The "type species" of their respective groups reflects the areas in which they worked. Both authors included *A. rufescens* in this group, recognising Storr's (1967) error of regarding this species as a subspecies of *A. caudicinctus*. Storr's (1966) inclusion of *A. decresii* in the *A. reticulatus* species-group was apparently overlooked by both Humphries (1972) and Houston (1974a). However, Houston (1974b) suggested that both *A. decresii* and *A. pictus* should not be included within the *A. reticulatus* species-group. Houston (1974b) and Humphries (1972) both placed the "earless" *A. maculosus* in the *A. reticulatus* species-group.

Table 4. Species-groups of Amphibolurus According to Humphries (1972)

A. barbatus species-group
A. barbatus
A. minor
A. minimus
A. microlepidotus
A. muricatus
A. diemensis
A. adelaidensis
A. parviceps

A. reticulatus species-group
A. reticulatus
A. inermis (= nuchalis)
A. pictus
A. clayi
A. maculosus

A. maculatus species-group
A. maculatus
A. fordi
A. femoralis

A. isolepis species-group
A. isolepis
A. scutulatus
A. cristatus

A. ornatus species-group
A. ornatus
A. decresii
A. fionni
A. rufescens

A. caudicinctus was placed in its own group.

Badham (1976) published the first attempt at an Australia-wide revision of a single species-group within *Amphibolurus*. Her work suffered from an eastern bias, contrasting with the work of Storr and Humphries.

Houston (1978) produced the most complete list of species-groups within *Amphibolurus*. However, he used these species-groups only as a device to shorten individual species descriptions. He did not mention Storr's (1965) *A. maculatus* species-group. The group, as Storr defined it, has only two species occurring in South Australia. Houston presumably saw little economy in introducing another species-group for the sake of reducing the length of two species descriptions. Similarly the *A. adelaidensis* species-group (Storr, 1977) was not described. Houston (1978) did not assign *A. diemensis*, *A. cristatus*, *A. scutulatus*, *A. caudicinctus* or *A. pictus* to any species-group.

The knowledge of the relationships between the species of Amphibolurus, and between other Australian agamid genera is seriously inadequate. An investigation into these relationships was therefore initiated, using the traditional methods of gross morphology and morphometrics, and the more modern techniques of karyology.

III. MATERIALS AND METHODS

Materials:

Specimens representing all genera and species-groups occurring in Australia were examined. These were mostly preserved museum specimens, the majority lodged in the Australian Museum, Sydney. A large number of specimens were collected by the author, used for experimental purposes, and will be donated to the Australian Museum. These are identified individually in the present study by Australian Museum field tag numbers. Further specimens were borrowed from the Western Australian Museum and the South Australian Museum. The late Peter Rankin and Dr. W.E. Duellman loaned specimens in their personal collections.

The number of specimens of each species examined in each section of the study is listed in Table 5. The actual specimens examined are listed in Appendix A.

Methods:

A. Comparative Morphology.

Data for this section were recorded from specimens directly or with the assistance of a binocular dissecting microscope. Most data were first recorded on a cassette recorder and later transcribed to data sheets.

I. Repeatability of Measurement.

A pilot study was conducted using a sample of 13 lizards, following the methods of Kluge (1974). For this analysis 57 characters were recorded twice from each lizard. The characters were divisible into two categories; ordered or unordered character states. Values assigned to ordered character states vary according to the magnitude of the feature

Table 5. Specimens Examined.

Species	Pilot Study	Comp Morph	Pore Arr	Cav.Tiss		Morph Mtrcs	Kary type
				Mal	Fem		
Chelosania		6				6	
Gonocephalus		3			1	3	1
Physignathus		12	3	2	1	14	1
Moloch		10		1		12	
T. cephalus		8				12	
T. intima		12				12	
T. lineata		3				3	
T. parviceps		4	1			4	
T. tetraporophora	2	16	2	3	3	17	5
T. uniformis		1				1	
A. adelaidensis		16	5			16	
A. diemensis		46	8	3	2	49	7
A. muricatus		12	11	3	2	57	8
A. nobbi		16	11	3	1	20	7
Caimanops		23	1			22	
Chlamydosaurus		14	4			14	1
D. albilabris		14				14	
D. australis		11	2	1	1	15	2
D. bennettii		13	1	1		13	1
D. bilineata	3	28	10	1	3	29	3
D. lalliae		10				10	
D. linga		1				1	
D. magna		12	3	1		14	2
D. superba		1				1	
D. winneckei		13				13	
L. gilberti		15	6			14	1
L. g. centralis		19		3	2	61	9
L. longirostris		12	3			12	
L. temporalis		12	2			12	
C. decresii		14	10	3	2	14	7
C. fionni		13	11			19	
C. ornatus		10	11	1		10	
C. pictus		21	8	3	2	23	11
C. rufescens		2	2			2	
C. vadnappa		3	3			3	
A. maculatus		5	3			4	
A. femoralis							1
A. fordi		12	8	4	1	31	6
A. isolepis	3	62	1	1		62	1
A. scutulatus	1	4	7			4	
A. cristatus		19	10		1	18	1
A. caudicinctus	3	30	5	1		32	
A. reticulatus		8	7			20	
A. clayi		6	1	1		6	1
A. gibba		12	10			17	
A. maculosus		10	11			28	
A. nuchalis		40	7	3	2	52	2
A. barbatus	1	21	9	2	3	21	6
A. minor		5				5	
A. mitchelli		1	1			1	
A. vitticeps		16	6	2		16	6

in question (e.g. scale counts). For ordered character states the correlation coefficient (r) was calculated, comparing the first and second recording of each character, and using the formula (from Zar, 1974):

$$r = \frac{\Sigma (x - \bar{x})(y - \bar{y})}{\sqrt{\Sigma (x - \bar{x})^2 \; \Sigma (y - \bar{y})^2}}$$

Where x = character value at first recording,

y = character value at second recording,

$\bar{x}$ = mean of first recording for all lizards,

and $\bar{y}$ = mean of second recording for all lizards.

In unordered character states the value assigned to a character bears no relation to the size of the feature measured (e.g. colour patterns, presence/absence records). The application of the correlation coefficient to such characters is therefore inappropriate. An estimate of the reliability of these characters was obtained by calculating the proportion of identical records from the first and second recordings, expressed as a part of unity. For example, a character recorded differently in three of thirteen second recordings will be scored as 10/13 = 0.769.

On the basis of these measures of reliability, characters were retained, altered or discarded.

II. Character Descriptions.

The characters are listed below in the order in which they were recorded throughout the study. Counts were recorded first, followed by character states.

Some characters were modified after the pilot study to improve their reliability. For such characters the modified form is described below. The original form, and the reasons for its modification, will be presented with the results of the pilot study (p. 43).

The 43 characters retained throughout the study are listed below. The characters rejected after the pilot study are described subsequently.

Counts.

1. Pre-nasal scales (PNS, Fig. 1).

2. Sub-nasal scales (SNS, Fig. 1).

3. Inter-nasal scales (INS, Fig. 2).

4. Snout-parietal scales (SPS, Fig. 2).

5. Sub-orbital scales (SOS, Fig. 1). The upper scale of this count was either part of the loreal scale row or, where the loreal scale row was not apparent, the uppermost of the longitudinally keeled, elongate scales beneath the orbit.

6. Supralabial scales (SLS, Fig. 1).

7. Infralabial scales (ILS, Fig. 1).

8. Nuchal scale count (NS, Fig. 1).

9. Gular scale count (GS, Fig. 1).

10. Mid-body scale count (MBS). Number of scales around the body at a point midway between axilla and groin.

11. Interpore scale count (IPS, Fig. 3). Number of scales separating the most medial pore on either side of the midline.

12. Inguinal scale count (IS, Fig. 3).

13. Femoral scale count (FMS, Fig. 3). Number of scales from the most distal femoral pore to the scale overlying the condyle of the femur palpable ventrally.

14. Preanal pores (PP, Fig. 3). Number of preanal pores in a series distinct from any femoral pores.

15. Femoral pores (FP, Fig. 3). Number of pores in series extending along the ventral surface of the thigh and, where there is no

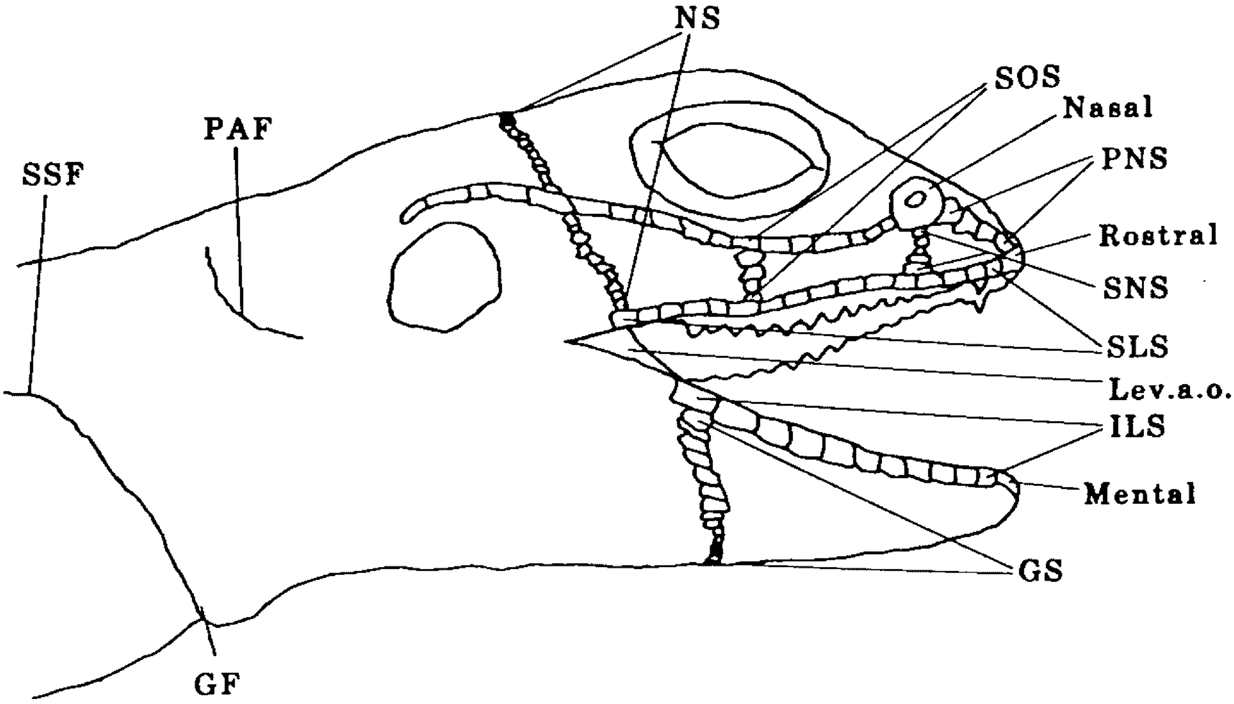


Figure 1. Characters from Lateral Aspect of Head. SSF = Scapular fold; PAF = Postauricular fold; NS = Nuchal scale count; SOS = Sub-orbital scales; PNS = Pre-nasal scales; SNS = Sub-nasal scales; SLS = Supralabial scales; Lev. a. o. = Fold indicating M. levator anguli oris; ILS = Infralabial scales; GS = Gular scale count; GF = Gular fold. NS and GS were counted to the corresponding point on the other side. Posterior scale of SLS and ILS was taken as the scale overlying the fold of levator anguli oris.

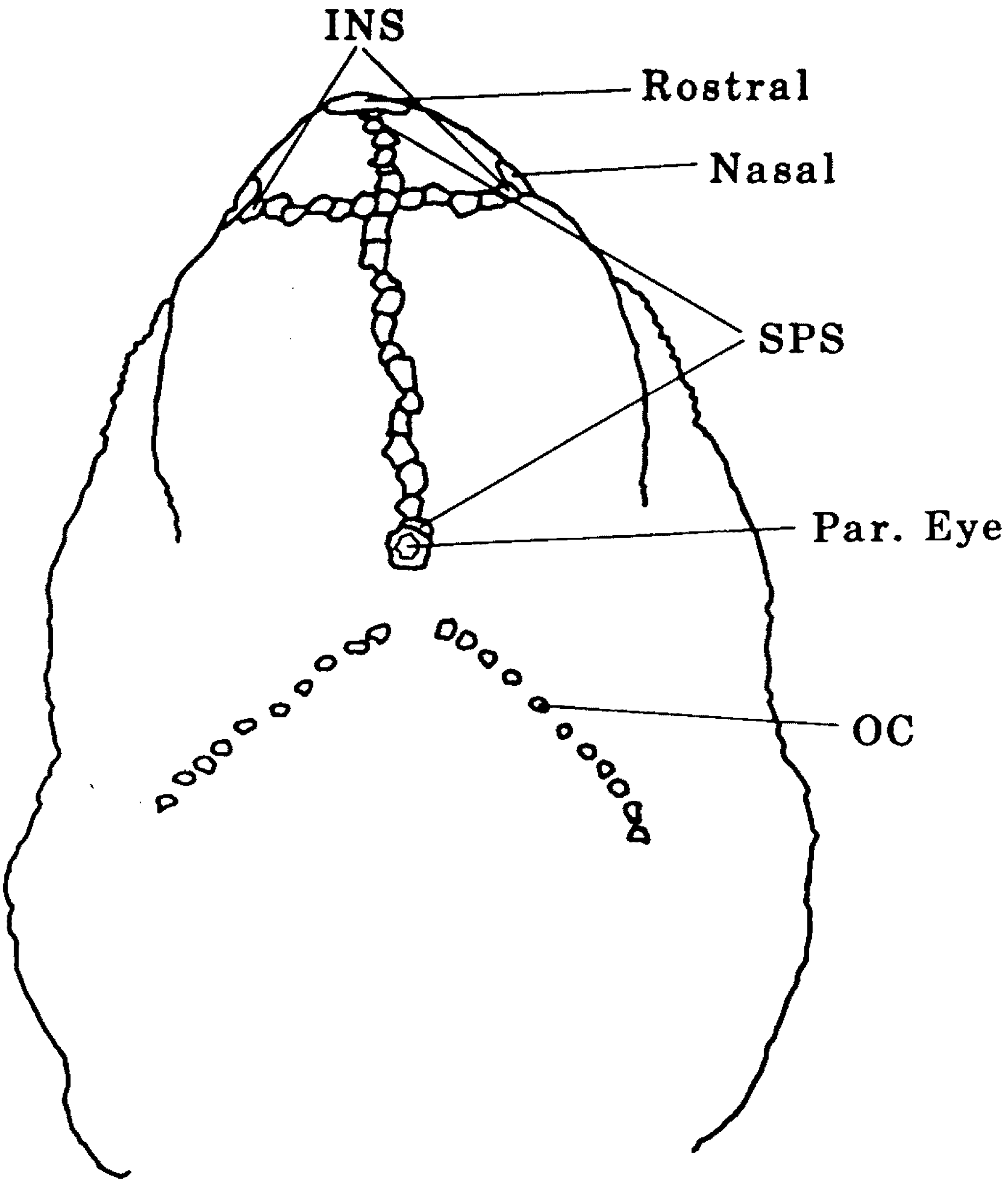


Figure 2. Characters from Dorsal Aspect of Head. INS = Internasal scales; SPS = Snout-parietal scales; Par. Eye = Parietal eye in interparietal scale; OC = Occipital crest.

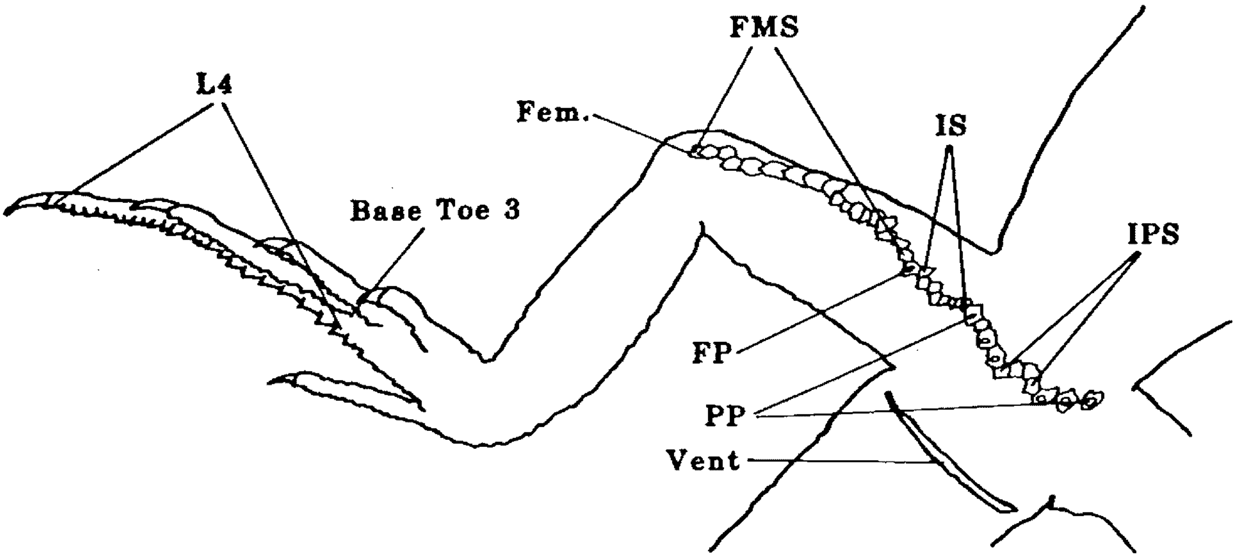


Figure 3. Characters from Ventral Aspect of Hind Limb Region. L4 = Lamellae under fourth toe; Fem. = Position of femoral condyle; FMS = Femoral scale count; IS = Inguinal scale count; IPS = Interpore scale count; PP = Preanal pores; FP = Femoral pore.

distinct inguinal interruption of the series, into the preanal region.

16. Lamellae under the fourth toe (L4, Fig. 3).

17. Paravertebral scale length (PVS10). Number of scales in a longitudinal interval one tenth of the snout-vent length, counted two or three scales lateral to the vertebral line midway between axilla and groin. This character, and the scale length characters below, were counted between the arms of dial calipers fixed at the required interval. When enlarged tubercles or spines were present they were included within the count. This may have lowered the value of the record for those species with strongly heterogeneous dorsal scalation (see DH, below). This was also a factor in LS10 and BTS10, but ventral and gular scales were usually regular in size.

18. Ventral scale length (VS10). Similar to PVS10, counted near the mid-ventral line at mid-body.

19. Gular scale length (GS10). Similar to PVS10, counted along the median line, with the interval midway between the mental scale and the gular fold (when present).

20. Lateral scale length (LS10). Similar to PVS10, counted near the mid-lateral level at mid-body.

21. Scale length on the base of the tail (BTS10). Similar to PVS10, counted along the tail from the first row of scales on the base of the tail which are clearly larger than the scales of the groin.

22. Premaxillary teeth (PMX). Number of teeth on the premaxilla.

Character States.

23. Dorsal scale keeling (DSK). Most dorsal scales smooth - (0); keeled - (1).

24. Ventral scale keeling (VSK). As for DSK.

25. Gular scale keeling (GSK). As for DSK.

26. Direction of dorsal scale series (DIPV). Dorsal scales granular, not forming series either by aligned keels or direction of overlapping - (0); forming series running in different directions - (1); forming posteromedial series - (2); forming series which run parallel with the midline - (3); forming posterolateral series - (4).

27. Direction of ventral scale series (DIV). Scored as for DIPV.

28. Enlarged dorsal scale rows (DESR). No discernible series of scales on the dorsum larger than the majority of scales - (0); longitudinal rows of scales distinctly larger than surrounding scales - (1); enlarged scales arranged in longitudinal and transverse series - (2); enlarged scales arranged in transverse series - (3).

29. Nuchal scale ridge (NC). No distinct nuchal scale ridge of enlarged scales - (0); a distinct nuchal series of enlarged, keeled scales - (1).

30. Vertebral scale ridge (VC). No median series of keeled scales extending posteriorly to the level of the hindlimbs - (0); a median series of keeled scales extending at least to the level of the hindlimbs - (1).

31. Occipital crest (OC, Fig. 2). Scales of the occipital region regular, or with scattered tubercles - (0); a transverse series of enlarged spinous tubercles across the occipital region - (1).

32. Spinose gular scale row (GSR). Scales of throat subequal - (0); enlarged spinose scales forming a short transverse series at or near the angle of the mouth - (1); enlarged spinose scales forming a complete transverse row across the throat - (2).

33. Dorsal scale heterogeneity (DH). Dorsal scales homogeneous or subequal - (0); some dorsal scales more than twice the width of others - (1). (When larger scales were present in orderly rows the

scales were not scored as heterogeneous; see DESR above).

34. Thigh scale heterogeneity (TH). Scored as for DH.

35. Postauricular scale row (PAS). Area behind tympanum with no distinctly enlarged scales - (0); with an enlarged tubercle, or a few scattered tubercles - (1); with a contiguous series of enlarged tubercles - (2).

36. Upper eyelid fringe (UELD). Upper eyelid covered entirely with smooth scales - (0); a row of keeled scales forming a ridge parallel with the margin - (1); a fringe composed of triangular or conical projections from scales, each projection being longer than wide - (2).

37. Lower eyelid fringe (LELD). Scored as for UELD.

38. Nostril shape (SN). Opening of nostril circular or almost so - (0); elliptical or slit-like - (1).

39. Supra-auricular fold (SAF). No skin fold above tympanum - (0); tympanic membrane beneath overhanging fold of skin - (1).

40. Postauricular fold (PAF). Skin behind tympanum smooth - (0); with a distinct fold of skin bilaterally - (1).

41. Gular fold (GF). No skin fold crossing midline of throat - (0); a distinct skin fold across throat - (1).

42. Scapular fold (SSF). Skin on side of neck smooth - (0); a distinct fold passing between the side of the neck and the insertion of the forelimb - (1).

43. Tympanum exposed (EAM). No visible tympanic membrane - (0); at least part of tympanic membrane exposed - (1).

The characters described below were discarded after the pilot study. The reasons for their rejection are presented with the results of the pilot study (Ch. IV: 1, p. 44).

Counts.

44. Loreal scales (LS). Number of scales between the nasal and most anterior small scale in the orbit.

45. Interorbital scales (IOS). Number of scales across the bone separating the orbits.

Character States.

46. Direction of gular scale series (DIG). Scored as for DIPV.

47. Lateral scale heterogeneity (LH). Scored as for DH.

48. Heterogeneity of scales on the base of the tail (BTH). Scored as for DH.

49. Supra-auricular scale row (SAS). Scored as for PAS, above the tympanum.

50. Nostril position relative to canthus rostralis (PNC). Nostril below canthus rostralis - (0); on canthus rostralis - (1); above canthus rostralis - (2).

51. Nostril position relative to the snout-eye interval (NSE). Scored as an estimate of the distance between the tip of the snout and the centre of the eye, out of 10.

52. Shape of canthus rostralis (CR). No distinct canthal ridge - (0); a distinct canthal ridge from snout to above orbit - (1); an acute canthus rostralis, so that lips are not visible from directly above the head - (2).

53. Ventral colour pattern (VCP). Ventral surface a uniform light colour - (0); uniform dark colour - (1); with longitudinal stripes - (2); with pattern of stripes combined with blotches or spots - (3); with pattern of blotches or spots - (4); with transverse stripes - (5).

54. Dorsal colour pattern (DCP). Scored as for VCP.

55. Gular colour pattern (GCP). Scored as for VCP.

56. Eye stripe (ES). No indication of a stripe behind the eye - (0); stripe running posteriorly from behind the eye - (1); stripe running posteroinferiorly from behind the eye - (2).

57. Tail colour pattern (TCP). Scored as for VCP.

Some other characters were scored on a few animals, but were abandoned as impractical before the completion of the pilot study. These characters are mentioned with the results of the pilot study.

III. Pore Type and Arrangement.

The characters described above relating to the arrangement of pores (IPS, IS, FMS) were not as effective as hoped in quantifying the clear taxonomic significance of these features. A representative sample of specimens was examined more critically for the arrangement of pores and the relationship between pores and scales, and written descriptions made. These descriptions were then compared and the significant trends and differences reported with the results. The species examined and the numbers of each are listed in Table 5.

IV. Deep Features of Dorsal Crest.

Structures deep to the dorsal crest were investigated. Exploratory dissections of species known to raise a crest revealed two possible means of crest erection. One was a longitudinal midline tissue block which may have been erectile. The other structures of interest were the attachments between the skin and the superficial dorsolateral muscles.

To examine the above structures transverse blocks of tissue were removed from preserved lizards. Usually two blocks were removed from each specimen, one from the neck and another from the trunk at a level near the elbow of the adpressed forelimb. Each block was approximately 5 mm in length, 10 mm in width, and deep enough to include several layers of muscle and fascia. The blocks were removed by making two parallel transverse scalpel cuts, then removing the intervening tissue with fine scissors. Each block was mounted and sectioned transversely using standard histological techniques. Sections of 7-10 μ were stained in Haematoxolin and Eosin and in Masson's Trichrome. These sections were examined to investigate the type of tissue in the central fascial block.

The relationship of muscles, fascia and skin was examined on either side of the depressions created by the removal of the blocks of tissue for sectioning. Notes were made on the relative strength of the fascia, and the positions of attachment to the overlying skin, particularly in positions likely to cause the erection of a vertebral crest.

V. Other Features.

Data were accumulated on a number of characters over the course of this study. Although these data were not sought systematically, many of them were of interest, and were thus included. The more important of these characters, and the manner in which data were collected, are described below.

Many animals changed colour from the time of collection to the time of sacrifice for experiments. Observations of colour changes were made also on specimens in the field and in cages. These observations have been recorded in the results.

Hemipenes were examined in most male specimens preserved by the author. This was done by the injection of preservative into the base of the tail, so that the hemipenes were extruded. This procedure had been followed in some museum specimens, but the form of these hemipenes was often altered, by crushing during fixation, or partial retraction, or both. Extruded hemipenes were examined under a dissecting microscope, and notes made of the observed structure.

Specimens of *Tympanocryptis parviceps* were examined to establish the number of phalanges. This was achieved simply by bending the digits and counting the joints. *T. parviceps* was described subsequent to the studies of Cogger (1961) and Mitchell (1965) who examined representatives of all endemic Australian agamid groups for this character. *T. parviceps* was compared with specimens of other species of *Tympanocryptis* and of the *A. adelaidensis* species-group.

B. Morphometrics.

I. Measurements.

Head measurements were made to the nearest 0.05 mm using dial calipers. Larger measurements were made using a perspex-mounted plastic ruler, checked against the dial calipers for accuracy. Limb measurements were made with the perspex board pressed into the groin or axilla, and the limb stretched along the scale. Measurements were made to the base of the claw on the fourth digit. These larger measurements were estimated to the nearest half mm.

Measurements were made on preserved specimens. As with the other characters recorded from museum specimens the measurements were recorded first and later transcribed to data sheets. Eleven measurements, where possible, were recorded for each specimen. These were:

1. Snout-vent length (SV, Fig. 4).
2. Tail length (TL, Fig. 4)
3. Head width (HW, Fig. 4). Measured at the broadest part of the head.
4. Snout-parietal distance (SP, Fig. 4).
5. Snout-ear distance (HLE, Fig. 5). Recorded from either side of the head and the mean used in analysis. This procedure was followed

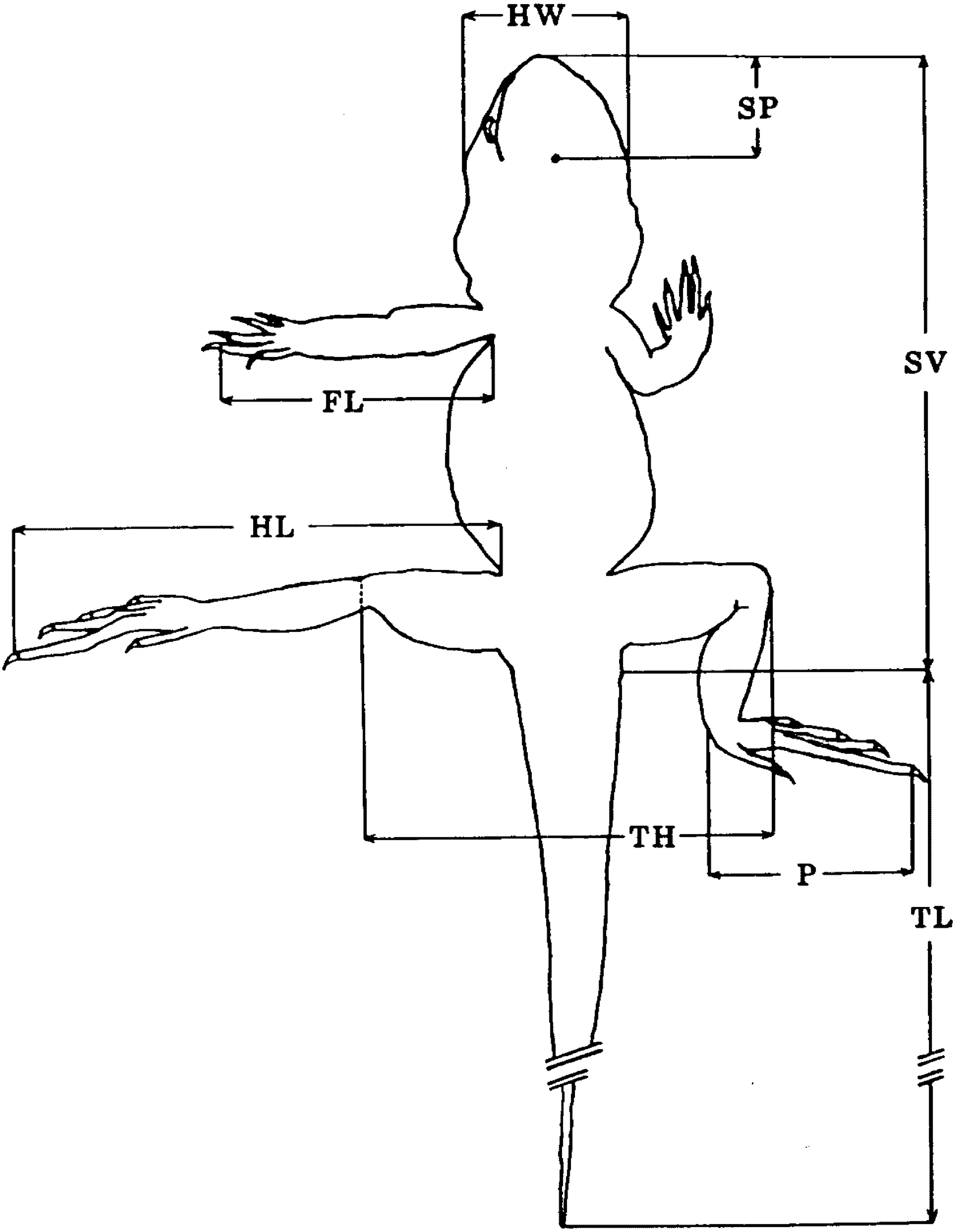


Figure 4. Measurements. HW = Head width; SP = Snout-parietal distance; SV = Snout-vent length; TL = Tail length; P = Pes length; TH = Thigh measurement; HL = Hind limb length; FL = Fore limb length.

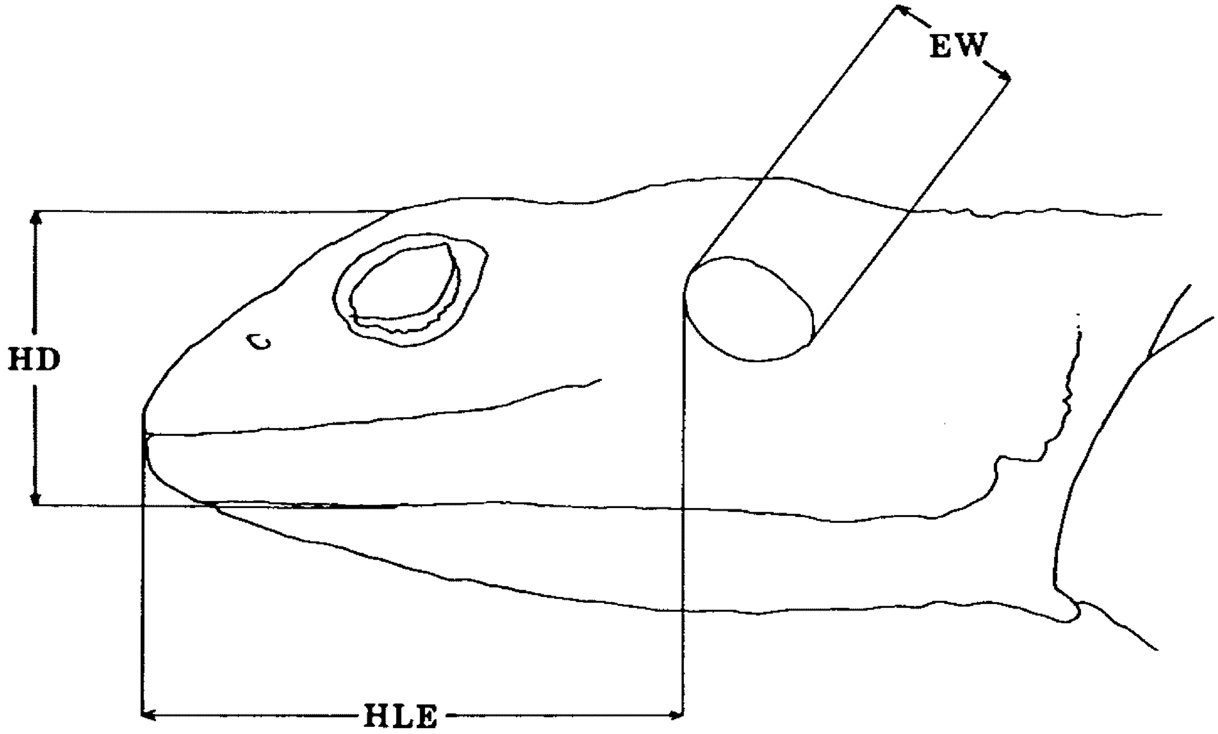


Figure 5. Measurements from Lateral Aspect of Head. HD = Head depth; EW = Ear width; HLE = Snout-ear distance.

with the other bilateral measurements (EW, HL, P, FL).

6. Head depth (HD, Fig. 5).

7. Ear width (EW, Fig. 5). Measured at the widest part of the tympanum.

8. Thigh measurement (TH, Fig. 4).

9. Hind limb length (HL, Fig. 4).

10. Pes length (P, Fig. 4).

11. Fore limb length (FL, Fig. 4).

Some other measurements were attempted, but abandoned as impractical after a short trial period. Attempts to measure the length of the head were abandoned mainly because large males of many species develop "jowls", which make locating the posterior limit of the jaw almost impossible. Other posterior features of the skull were even less prominent. Other intervals which were measured initially were the snout-orbit, snout-nostril, and the orbit-angle of mouth.

II. Analysis.

All analyses of data were carried out using the facilities of the Computing Centre at the University of Sydney.

Data from a representative group of lizards were analysed to determine which of the eleven measurements recorded was the best indicator of size. A principal components analysis of variance was performed using the FACTOR subprogram from SPSS (Statistical Package for the Social Sciences; Nie et al, 1975), following the procedures of Dodson (1975a). The results of this program suggested that the snout-vent measurement accounted for most variability, and was thus chosen as the best indicator of size. Further analyses were carried out using the snout-vent measurement as the basis of size estimation.

Another set of analyses was performed to study changes in head shape. Relative head size in most vertebrates decreases markedly after birth or hatching. The best indicator of head size taken from the results of the same FACTOR analysis proved to be the snout-ear measurement. However, Tympanocryptis data did not contain this measure, so the second best indicator of head size, the snout-parietal measurement, was used as the standard for studying changes in head shape.

The SCATTERGRAM subprogram of SPSS (Nie et al, 1975) was used to perform analysis of the data. For each species each measurement was plotted against the snout-vent length, and regression lines calculated. To allow for comparison with previous studies, and to test for allometric growth, all data were converted to natural logarithms and regressed a second time. This second regression allowed the calculation of Huxley's formula. A comparison between linear and logarithmic regressions was made.

Dodson (1975a, b) preferred Bartlett's best fit to the least squares regression calculation. His reason for this was that the least squares method assumes that all measurement error occurs in one parameter (the dependent variable) and none in the other (the independent variable). This is not usually true for biological material. However, Bartlett's best fit is calculated using only the upper and lower thirds of the data matrix, as measured by the dependent variable, and ignores the middle third of the data. This also appears biased, as there is undue emphasis placed on the data from the largest and smallest specimens. Indeed, as Dodson (1975b) himself states, "for a continuously growing species, individuals of maximum size are less important to the population than are smaller, sexually mature stages". In this study specimens were selected with a view towards examining an ontogenetic series as wide as possible. Where very large and very small specimens were available these were selected in preference to lizards in the medium-sized range. This bias in the selection of specimens makes the use of Bartlett's best fit even more inappropriate, concentrating as it does on the extremes of the range of data.

Allometric coefficients were considered statistically different from unity if they differed from one by more than two standard errors (1.96 SE's on either side of the estimate represent the 20% confidence limits; Zar, 1974). Coefficients below 0.9 or above 1.1 were considered to represent strong negative and positive allometry respectively.

C. KARYOLOGY

I. Methods.

Most karyotypes were prepared using an *in vivo* technique modified from the methods employed by Baker, Bull and Mengden (1971). The modified technique was as follows:-

1. Blood was removed from the animal, by means of a capillary tube inserted into the posterior angle of the eyelids, and pushed posteriorly into an orbital blood sinus.

2. An intraperitoneal injection of 0.1% colchicine was administered with a dosage rate of 0.05 ml/g body weight (dosage rate from Stephenson, Robinson and Stephenson, 1974).

3. The animal was sacrificed 5 hours after the colchicine injection by intracranial injection of 95% ethanol.

4. The spleen, and in males a testis, was removed, cut into small pieces and placed in 0.9% sodium citrate solution for 10 minutes.

5. A suspension of cells was pipetted off the sodium citrate solution and centrifuged for 3 minutes at approximately 1500 g's.

6. The supernatant was removed and a freshly made up mixture of 3

parts methanol/1 part acetic acid was added as a fixative, and the cells shaken into suspension. This was left to fix for 10 minutes.

7. The suspension was centrifuged as in step 5, and the supernatant removed. Fresh fixative was added, but the cells were not re-suspended. This was left for a further 10 minutes.

8. Step 7 was repeated.

9. After further centrifuging the supernatant was removed and the cell button re-suspended in fresh fixative.

10. Three drops were pipetted onto a microscope slide and ignited. After allowing the suspension to burn the residue was slung off.

11. The slide was stained in an aqueous solution of Gurr's improved Giemsa stain for 10-15 minutes. The slide was again slung dry.

12. Slides were mounted with Canada Balsam after drying for at least an hour on a hot plate at 40-45°C.

Some early results were obtained using a method similar to that of Baker _et al_ (1971). Bone marrow from the femur was flushed out using 1% sodium citrate solution, after bleeding the animal and treating it with phytohaemagglutanin for two days. Results from this method were poor with the exception of _Physignathus lesueurii_, and the method described above was developed in subsequent work.

Tissue from the duodenal walls was also taken in many of the early animals, but proved less than satisfactory.

II. Analysis.

At least ten cells were examined from each preparation. The clearer of these preparations were photographed under oil immersion using a Leitz Orthomat camera mounted on a Leitz Orthoplan microscope. The photomicrographs were printed on 10 X 8 paper and the lengths of the chromosomes measured using Mitutoyo dial calipers. The pointed arms designed for measuring internal diameters were used in a step-wise fashion, beginning at the centromere. Straight sections of the chromosome were measured and the calipers rotated around the axis of the pointed arm where the chromosome changed direction. The calipers were then further extended along the length of the chromosome. The total length of each chromosome arm was recorded, and the percentage of total macrochromosome length and centromeric indices were then calculated for each cell. Where possible somatic preparations were used for analysis, but many second meiotic divisions were also used. Some Meiosis I cells were used to obtain estimates of relative chromosome lengths, although the centromeres were not observable on such preparations.

IV. COMPARATIVE MORPHOLOGY

1. Repeatability of Measurement.

A pilot study was performed at the beginning of the study of comparative morphology. This study was designed to examine the reliability of the recording of possible characters. Thirteen lizards were drawn at random from the limited number of preserved specimens available early in this study. Six species of three genera were represented in the sample (Table 5). Each character was recorded twice from each lizard, and either the correlation coefficient (r) or the proportion of identical records between first and second recordings calculated (Table 6).

Table 6. A. Correlation Coefficients for Ordered Character States.

Character	r	Character	r	Character	r
PNS	0.955	NS	0.945	L4	0.986
SNS	0.940	ILS	0.981	PVS10	0.951
LS	0.745**	GS	0.955	VS10	0.954
INS	0.988	MBS	0.971	GS10	0.926
SPS	0.984	IPS	0.983	LS10	0.918
IOS	0.706**	IS	0.942	BTS10	0.953
SOS*	0.482	FMS	0.930	PMX	1.000
SOS	1.000	PP	1.000	NSE	0.796**
SLS	0.988	FP	0.999		

B. Proportion Repeated for Unordered Character States.

Character	PR	Character	PR	Character	PR
DSK	1.000	LH	1.000**	SAF	1.000
VSK	0.923	TH	1.000	PAF*	0.615
GSK	1.000	BTH	1.000**	PAF	0.846
DIPV	0.923	SAS	0.615**	GF	1.000
DIV	1.000	PAS*	0.769	SSF	1.000
DIG	0.539**	PAS	0.923	DCP	0.615**
DESR	0.846	UELD	0.917	VCP	0.692**
NC	1.000	LELD	0.917	GCP	0.385**
VC	1.000	PNC	0.769**	ES	0.615**
OC	1.000	SN	0.923	TCP	0.615**
GSR	1.000	CR	0.923**	EAM	1.000
DH	1.000				

* Unmodified character state. ** Discarded.

Those characters with a high level of reliability (> 0.85) were retained throughout the study. Some characters were discarded as unreliable. Several characters were modified and scored again on the animals where most variation had occurred in the original two recordings. Three such modifications were apparently successful, and the modified characters were retained. These characters and their modifications are described below.

The suborbital scale count (SOS) was originally scored as the number of scales from the supralabials to the lowest point of the orbit, excluding the small scales of the lower eyelid. This was modified so that the uppermost scale counted was either the scale in the 'loreal scale row' immediately below the orbit, or, where the loreal scale row was not evident, the scale beneath the eye forming part of a series of keeled, elongate scales running longitudinally. This modification raised the value of 'r' to unity.

The postauricular scale row (PAS) was originally scored using five character states, three of which indicated the direction of the scale series if present. Simplification to three character states recording the presence of continuous, interrupted, or no scale series resulted in the proportion repeated being raised from 0.769 to 0.923.

Attempts to record the direction of the postauricular fold (PAF) were also abandoned. When the different directions of this fold were disregarded the proportion of repeated records rose to 0.846.

Several characters retained after the pilot study were later discarded. The shape of the canthus rostralis (CR) was difficult to record in some species (e.g. *A. nuchalis*) because of swelling associated with the nostril.

Two "heterogeneity" scale characters, on the side of the body (LH) and tail (BTH) were later discarded. Both characters paralleled the dorsal scale character (DH), and little advantage was seen in their continuation.

All colour characters were discarded. Most preserved dragons tend to fade in spirits, and colour patterns were often difficult to discern. What pattern remained in preserved specimens also tended to vary with the degree of desiccation of the specimen being examined.

Several other characters were discarded as impractical before the completion of the pilot study. The direction of scale series in the loreal and temporal regions was not recorded as these scales do not imbricate in most species. The number of scales across the snout, along the snout to a point between the orbits, and across the anterior margin of the vent all proved difficult to record.

2. Arrangement of Preanal and Femoral Pores.

Preanal and femoral glands occur in several families of lizards, and are very similar in at least five of them (Cole, 1966b). Pores in some *Agama* and some geckoes may represent separate evolutionary developments with a similar function (Camp, 1923). Australian agamids have pores of a type and arrangement similar to those of most other lizards. The independent evolution of these glands in several groups is generally considered less likely than the retention of an ancestral trait. The presence of preanal and femoral glands and pores is therefore considered a conservative character above the familial level. Many non-Australian agamids have lost these pores which, however, the majority of Australian agamids retain. A comparison of pore-related characters in Australian species is consequently worthwhile.

The femoral pores in *Physignathus* were arranged in a closely spaced line running along the posteroventral margin of the thigh. The pore series of either side were widely separated in the preanal region (Fig. 6A). Because of this wide separation the alignment of the preanal pore series relative to the vent was difficult to determine, but the pore series usually inclined slightly anteriorly.

Many Australian endemic agamids had pores arranged in a manner essentially similar to *Physignathus*. These species, listed in Table 7, differed in that the preanal separation was usually not so wide. These species all lacked an inguinal interruption to the pore series. In most of these species the pores anterior to the vent formed a slight arch forward. There were, however, several exceptions to this generalisation.

Some specimens of *A. diemensis* had the more medial preanal pores more posteriorly placed. The preanal pores in most *A. diemensis*, and in *A. caudicinctus*, formed series parallel with the vent, with no distinct

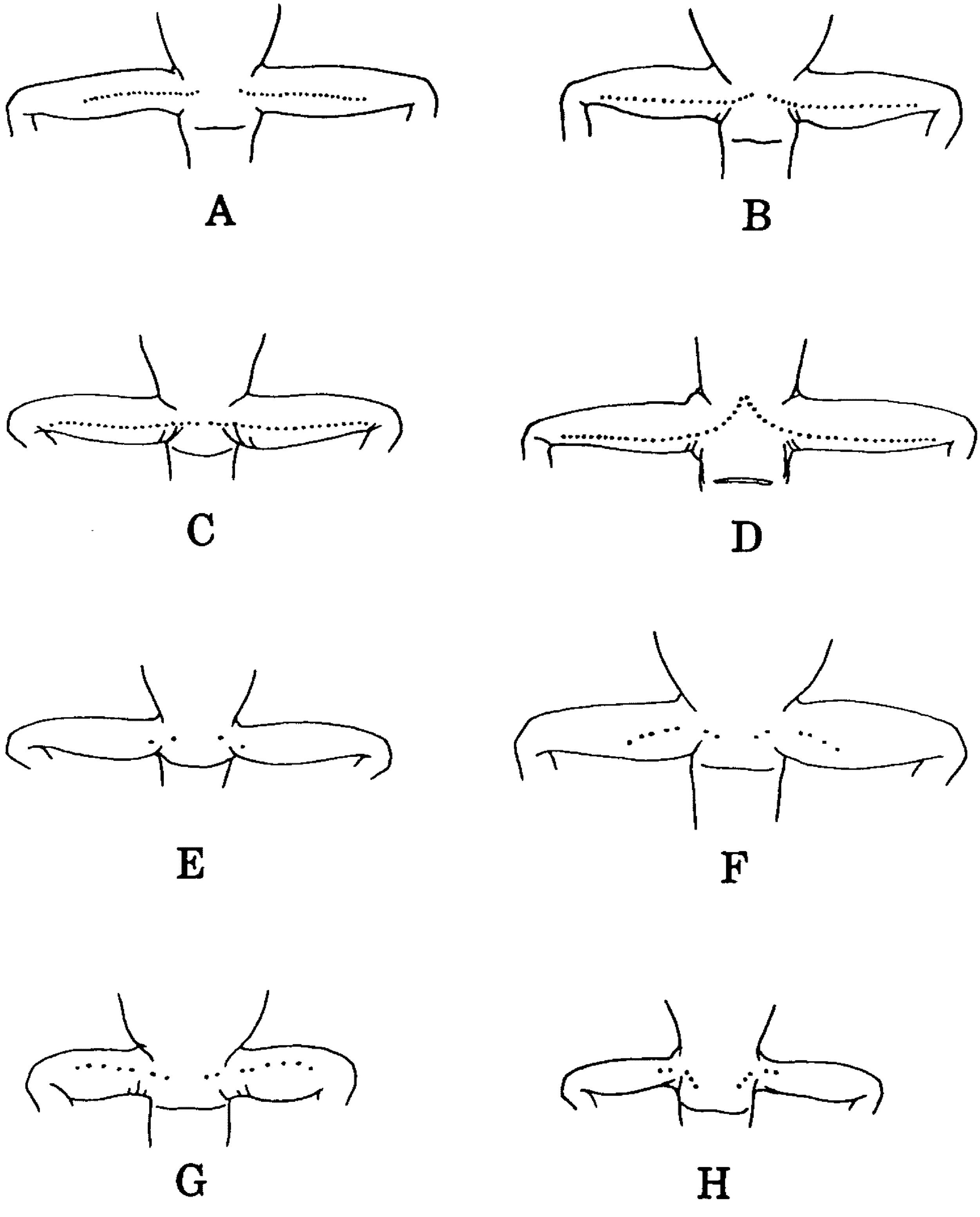


Figure 6. Arrangement of Pores. A = *Physignathus lesueurii*; B = *Ctenophorus decresii*; C = *Amphibolurus caudicinctus*; D = *A. isolepis*; E = *Tympanocryptis tetraporophora*; F = *Chlamydosaurus kingii*; G = *A. nuchalis*; H = A. *nobbi*.

forward arch (Fig. 6C).

Table 7. Australian Endemic Species with Pore Arrangement similar to *Physignathus*.

Tympanocryptis:	T. parviceps	A. maculatus species-group	A. femoralis A. fordi A. isolepis A. maculatus A. scutulatus
A. adelaidensis species-group	A. adelaidensis A. diemensis		
Ctenophorus	C. decresii C. fionni C. ornatus C. pictus C. rufescens C. vadnappa	A. cristatus species-group	A. cristatus A. caudicinctus
		A. reticulatus species-group	A. gibba A. reticulatus

In specimens of *C. pictus* examined the anterior arch of the preanal pores was found to be quite variable. Some specimens showed an acute angle, while others had a weak forward deviation similar to other species of *Ctenophorus* (Fig. 6B).

A. isolepis and *A. scutulatus* both possessed preanal pore series which arched very strongly forward in the preanal region (Fig. 6D).

The pore arrangement in two species of the *A. reticulatus* species-group was dramatically different. *A. nuchalis* differed from *A. reticulatus* in that the femoral pores were on the anterior edge of the ventral surface of the thigh (Fig. 6G). This was exaggerated towards the centre of the thigh, so that the femoral pore series described a curve convex forward. In the preanal region there was a wide interruption between the pore series from either side, and the few preanal pores were variable in their orientation. The reduced number of pores in *A. clayi* made any determination of the orientation of the preanal pore series impossible. The femoral pores were also widely spaced and difficult to visualise as a series. Most femoral pores presented on the anteroventral aspect of the thigh, and so the pore arrangement in *A. clayi* was considered similar to that of *A. nuchalis*.

All species in the *A. barbatus* species-group had widely spaced pores extending at least half the length of the thigh from the preanal region. There was no distinct break of the pore series in the inguinal region, so that distinct groups of preanal and femoral pores were not formed. Very often there was a pore in the inguinal fold. This arrangement was essentially identical to the arrangement in *A. nuchalis*.

The *A. muricatus* species-group typically had the preanal pores arranged on scales which formed posteromedial series. The preanal pores therefore formed a series arching strongly posteriorly (Fig. 6H). Preanal and femoral pores were normally widely separated in the inguinal region, and the two pore series tended to be differently spaced. Preanal pores were usually on adjacent scales, or on scales separated from each other by one other. Femoral pores were usually on scales separated from one another by at least two or three scales.

The arrangement of the preanal pores described for *A. muricatus* was typical of those species of *Caimanops*, *Diporiphora* and *Lophognathus* which possessed pores. Femoral pores were normally absent from *Diporiphora* and *Caimanops*. However, a single femoral pore was present on either side in one specimen of *Caimanops*, and a number of *Diporiphora* also had a pair of femoral pores. These femoral pores all presented at a point approximately equivalent to the proximal end of the femoral pore series in *A. muricatus* (see IS, Fig. 8). The arrangement of femoral pores in *Lophognathus* was essentially identical to that of *A. muricatus*, except in *L. longirostris*. In that species the femoral pores were larger, and the series extended further laterally. However, there was still a distinct inguinal interruption to the pore series.

Chlamydosaurus resembled *A. muricatus* in having the preanal and femoral pores in distinct series . The preanal pores were not so regularly arranged as in *A. muricatus*, and the posterior curve in the preanal pore series was not so consistently present, nor was it as sharp. However, the arrangement of pores in *Chlamydosaurus* was more similar to *A. muricatus* and its relatives than to other Australian agamids (Fig. 6F).

No species of *Tympanocryptis* apart from *T. parviceps* had more than four pores. When four pores were present they were arranged with one preanal and one femoral pore on either side (Fig. 6E). Often there were only two preanal pores present.

Three scale counts were made in an attempt to quantify differences between taxa in the arrangement of pores. These counts were (a) interpore scales, (b) inguinal scales and (c) femoral scales.

a. Interpore Scales (IPS).

Interpore scales were counted as the number of scales separating the innermost pores from either side of the midline. The results are summarised in Figure 7.

A. maculosus differed from all other endemic dragons by having the pore series shortened from the medial end. The resulting high number of interpore scales could be used as a diagnostic character. The pores were otherwise arranged in a manner similar to *A. gibba*.

Physignathus, *Chlamydosaurus* and *Lophognathus* had a higher interpore scale count than most other species.

Counting of scales and pores was possible in only one of the four *T. parviceps* examined owing to fixation in strong formalin solution of the other three specimens which, however, had the same pore arrangement.

b. Inguinal Scales (IS).

This character was designed to quantify the difference between those species with separate preanal and femoral pore series and those in

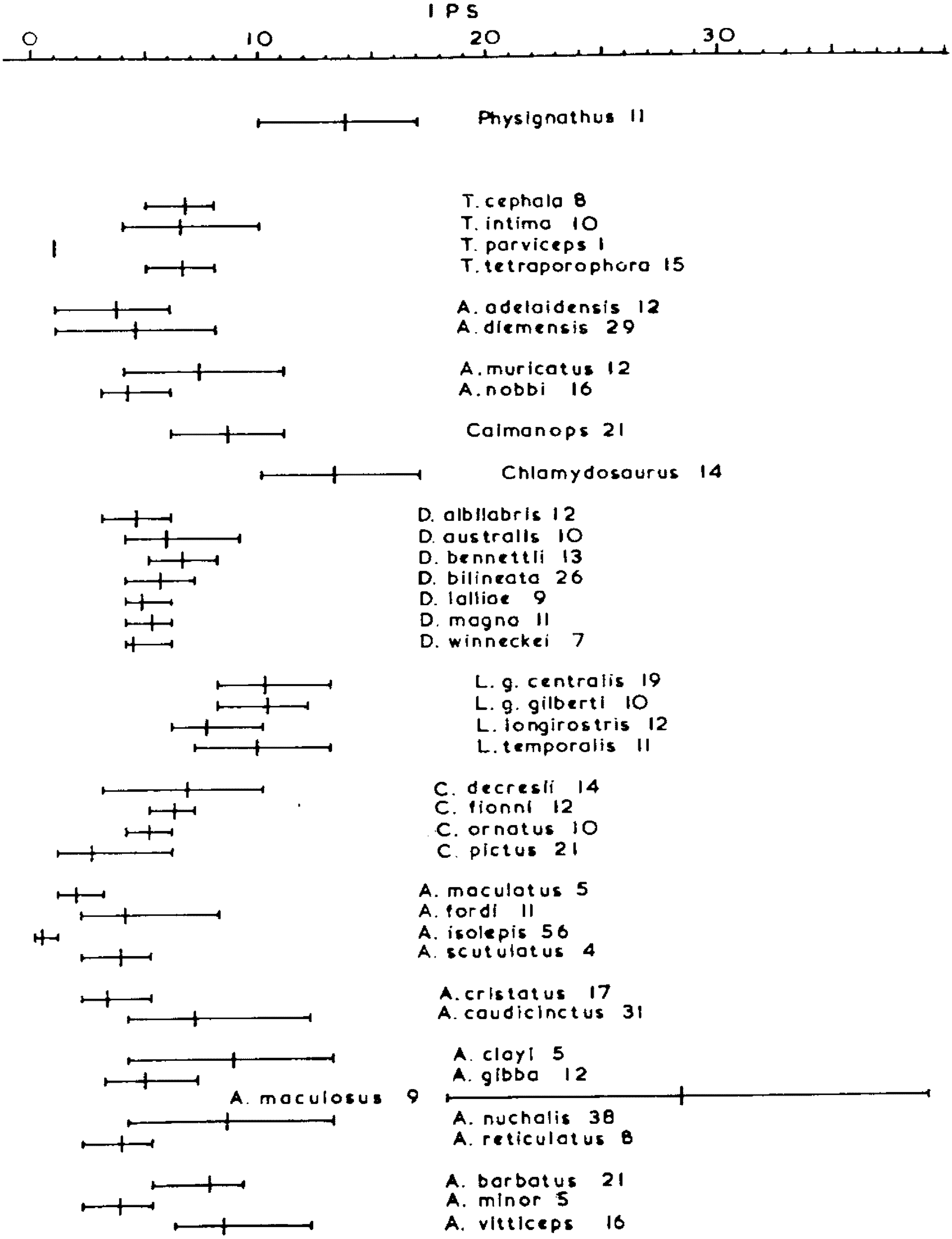


Figure 7. Interpore Scale Counts. Horizontal line = range; Vertical cross-bar = mean; Number following species name = number of specimens. Species are grouped according to genera or species-groups.

which the pores form a single series on either side. Figure 8 summarises the results.

Species examined could be placed in one of two groups on the basis of the inguinal scale count. One group had up to four inguinal scales. This group includes *Physignathus*, *Ctenophorus*, the *A. maculatus* species-group, 3 members of the *A. reticulatus* species-group, and *Tympanocryptis parviceps*. Members of the *A. adelaidensis* and *A. cristatus* species-groups, and *A. nuchalis*, often had four or fewer inguinal scales, but often had higher counts. The other species examined had consistently higher inguinal scale counts.

c. Femoral Scales (FMS).

This character was chosen in an attempt to quantify the distal extent of the femoral pore series. The count was made from the most distal femoral pore to the scale overlying the condyle of the femur palpable on the ventral surface of the knee.

Results of femoral scale counts are summarised in Figure 9. This character defined two groups of Australian agamids. *Physignathus*, the *A. muricatus* species-group, *Caimanops*, *Chlamydosaurus*, *Diporiphora*, *Lophognathus* and two species of *Tympanocryptis* differed clearly from all other species examined in possessing a high femoral scale count. *T. parviceps* had a very much lower femoral scale count than other species examined.

Discussion.

Gray (1845) subdivided some agamid genera by using the presence of preanal pores to distinguish one group of genera, the presence of femoral pores a second, and the absence of pores a third. This was probably the first use of the arrangement of pores as a taxonomic character. Boulenger (1885) retained the same characters for some of the same genera.

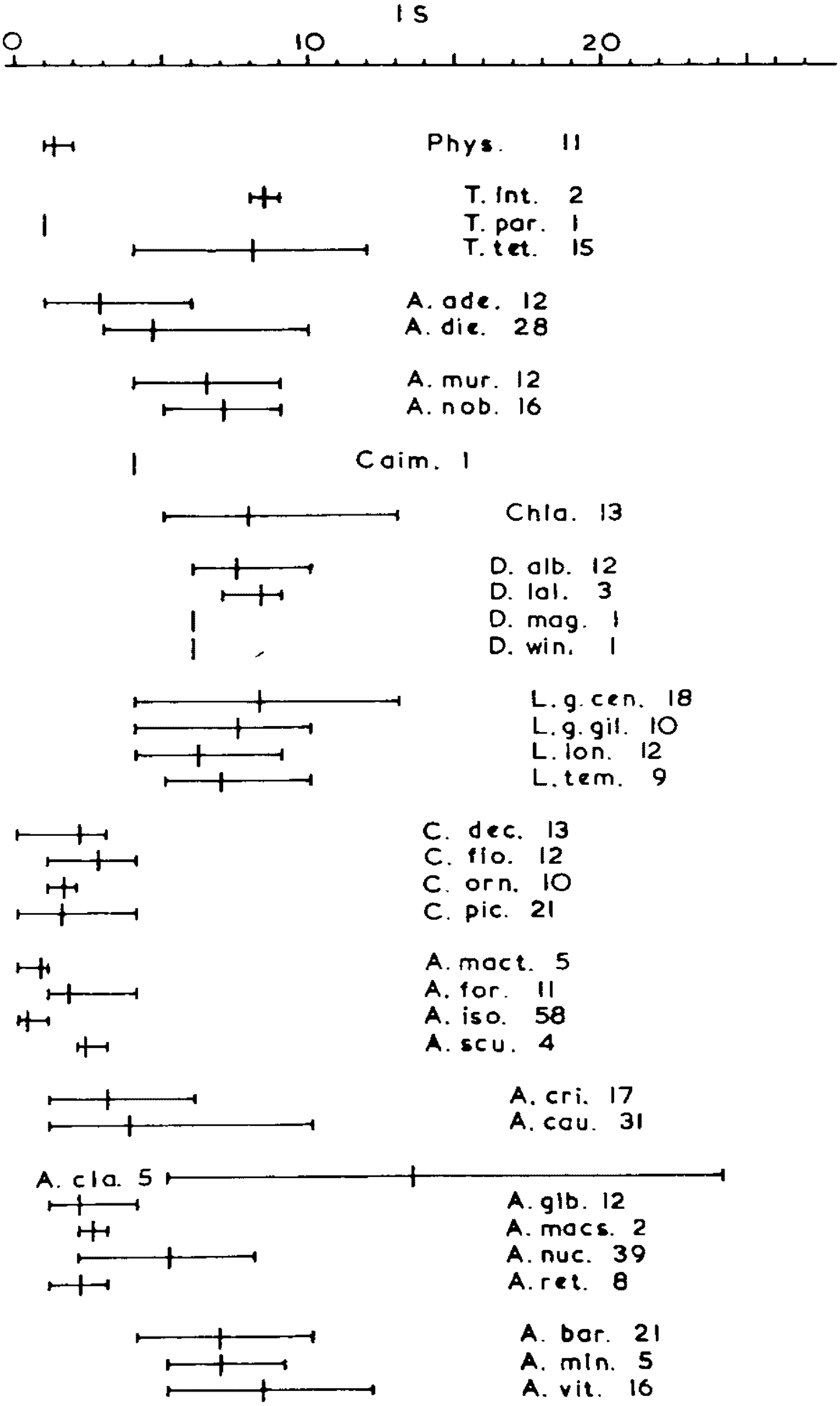


Figure 8. Inguinal Scale Counts. Symbols as for Fig. 7. Species in the same order as in Fig. 7. Most *Diporiphora* and *Caimanops* lacked femoral pores. The few specimens with femoral pores are included to allow a more complete comparison.

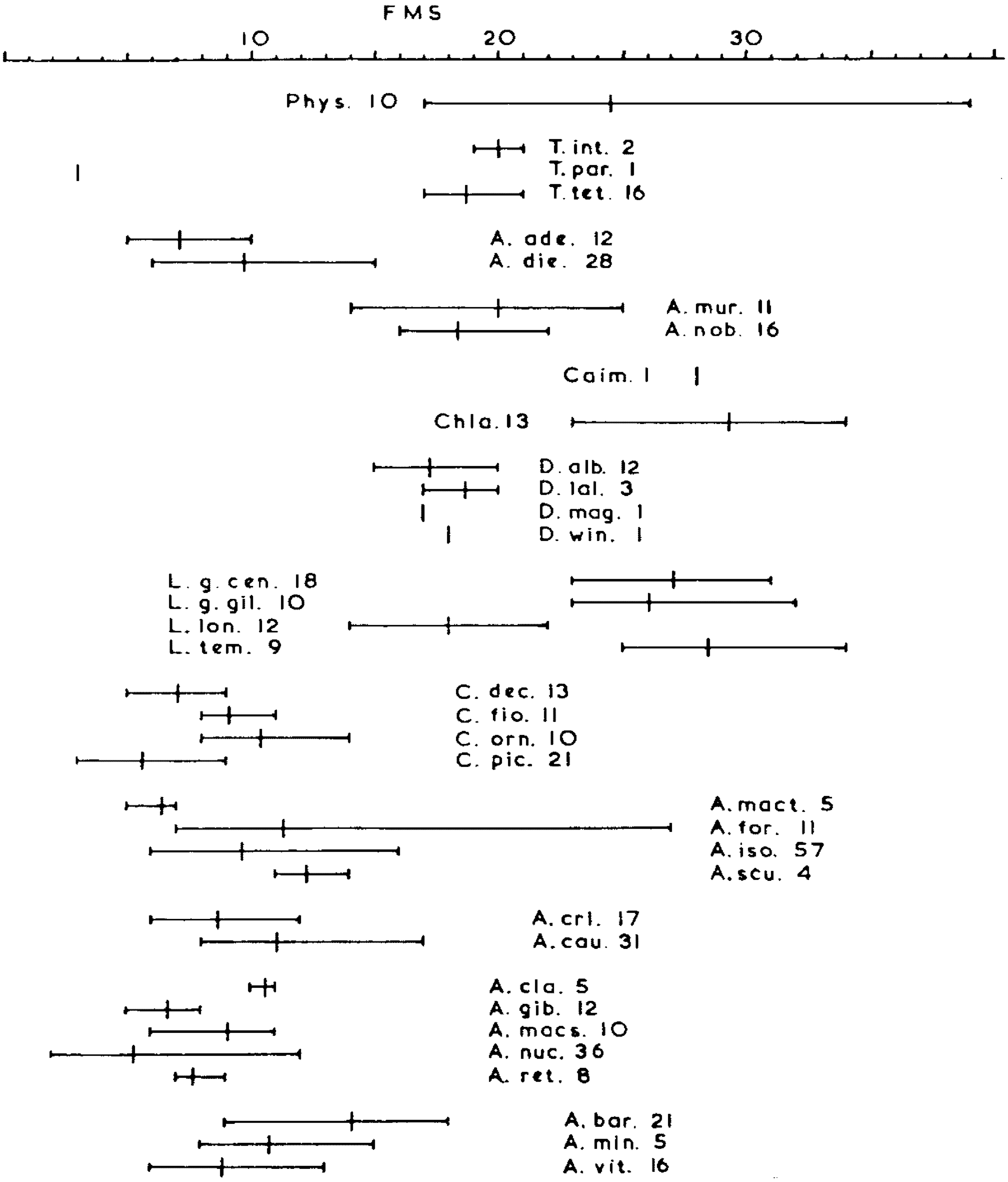


Figure 9. Femoral Scale Counts. Symbols as for Fig. 7. Species in the same order as in Fig. 7.

Storr (1965, 1966) used the distribution and arrangement of preanal and femoral pores to help distinguish between species of the A. maculatus and A. reticulatus species-groups. Apart from the distinction between preanal and femoral pores, remarkably little had been reported on the differences in pore arrangements prior to Storr's papers. Humphries (1972) and Houston (1978) have since expanded the use of these characteristics to other species-groups, but have not based taxonomic decisions upon them.

The function of preanal and femoral glands remains open to debate. Cole (1966a) investigated the morphology of the glands in Crotaphytus collaris, an American iguanid. His data suggested a relationship with sexual behaviour, as they were found to be larger in males than females, and larger in the breeding season than at other times of the year.

While the function of preanal and femoral glands remains uncertain the selective pressures acting to produce change in the form and arrangement of pores will also remain unknown. However, as will be shown, taxonomic groups formed on the basis of other characters tend to share similar pore arrangements and form. On this basis pore morphology has been accorded considerable importance in this study.

The most complete arrangement of pores encountered in the present study was a series on the posteroventral aspect of the thigh running medially in an unbroken line to the preanal ventral skin. This condition is shared by Physignathus (Fig. 6A), Leiolepis (an Asian genus), Ctenophorus and several species-groups of Amphibolurus. The Australian endemic species have probably been evolving separately from other members of the family for a very considerable period (Cogger, 1961). The occurrence of a similar pore arrangement in both Asian and Australian radiations may have arisen from the two lineages evolving the arrangement independently, or have been retained from a common ancestor. The latter is the favoured hypothesis. The arrangement of pores seen in *Physignathus* and many endemic Australian agamids has therefore been designated the primitive condition.

Of the non-Australian agamids *Uromastyx* has an arrangement of pores different from the primitive condition. The femoral pores present upon the posteroventral aspect of the thigh, but curve posteriorly in the preanal region, an arrangement resembling that found in the *A. barbatus* species-group and *A. nuchalis*. The arrangement differs in that the pores are not on the anteroventral part of the thigh.

There are three quite different pore arrangements among the Australian agamids, presumably derived from the primitive condition. The first of these is that described for the *A. muricatus* species-group. This pore arrangement is shared by *Caimanops*, *Chlamydosaurus*, *Diporiphora* and *Lophognathus*, all members of the *Chlamydosaurus* group. *Chlamydosaurus* is not considered the most typical, but it is the most distinctive and probably the best known member of the group. The arrangement of pores typical of the *Chlamydosaurus* group consists of preanal pores in posteromedial series separated from any femoral pores by an area without pores in the inguinal region.

Humphries (1972) made the point that *Lophognathus* (his *Physignathus*(?) spp.) possessed a "pore line curving towards the tail in the preanal region". This condition, he stated, was restricted to *Lophognathus*, *Diporiphora* and some members of the *A. barbatus* species-group. He included *A. muricatus* in the *A. barbatus* species-group, although apparently not examining specimens of that species. Houston (1978) used this character in his diagnosis for the *A. muricatus* species-group, in which he placed Lophognathus. Houston also noted the character in his comments on Diporiphora, and suggested that "future taxonomic studies, then, may result in the merging of Diporiphora with Amphibolurus".

The posterior curve of the pore series toward the midline in some A. barbatus and A. nuchalis differs from the condition in the Chlamydosaurus group in which the preanal pore series is discrete and forms a relatively straight line towards the vent.

No species outside the Chlamydosaurus group has a consistent break in the pore series in the inguinal region. Tympanocryptis tetraporophora may be considered an exception, but the consistent "interruption" in the inguinal region is caused by the pore number being fixed at four. This condition is almost certainly unrelated to the condition seen in the Chlamydosaurus group.

The arrangement of pores in A. nuchalis, A. clayi and the A. barbatus species-group is distinctive. This condition probably represents a second pore arrangement derived from the primitive condition. There are two ways in which the arrangement of pores in these species differs from the primitive condition. Firstly, the pores are more widely spaced, with from five to ten scales separating adjacent pores. Secondly, the pores present on the anteroventral aspect of the thigh, at least near the centre of the thigh. This second difference is unique among the Australian dragons.

The presence of this presumably derived pore arrangement and the presumed primitive condition in other members of the A. reticulatus species-group is interesting. If this pore arrangement has evolved only once, then A. nuchalis (of the A. reticulatus species-group) would logically be close to the ancestor of the A. barbatus species-group. Alternatively, a derived arrangement of pores may have evolved independently within the *A. reticulatus* species-group and in an ancestor of the *A. barbatus* species-group (see below). If the species-groups are related the evidence favours the *A. reticulatus* species-group as the more primitive because all members of the *A. barbatus* species-group possess the derived condition and would therefore be expected to have evolved from a species similar to *A. nuchalis* in pore arrangement. The reverse hypothesis, that the *A. reticulatus* species-group descended from a species ancestral to *A. barbatus*, would require the reversion to the primitive pore arrangement by some of its members. This appears less likely than the former hypothesis.

The two species-groups may be unrelated and have developed derived pore arrangements independently. This does not seem likely. However, the possibility that similar selective pressure has acted on the two groups cannot be excluded while the function of the pores remains unclear. This argument gains support from the examination of the pore arrangement in *Uromastyx*, which shares the wide spacing of the pores seen in the *A. barbatus* species-group.

A further presumably derived arrangement of pores is seen in the genus *Tympanocryptis*. In all species of *Tympanocryptis*, except *T. parviceps*, the remaining two or four pores are arranged in a distinctive manner. *T. parviceps* retains the primitive pore arrangement, indistinguishable from that of *A. adelaidensis*. The existence of *T. parviceps* (with about 30 pores) suggests strongly that the condition of only two preanal and two femoral pores has evolved since the loss of the tympanic membrane and one phalanx of the pes. The possibility that *T. parviceps*, a rare species with a peripheral distribution, has evolved the primitive pore arrangement *de novo* seems remote. *T. parviceps* is therefore considered primitive within *Tympanocryptis*.

The similarity between *T. parviceps* and *A. adelaidensis* is remarkable. Humphries (1972) did not distinguish between the arrangement of pores in *A. adelaidensis* and *T. parviceps*. Storr (1977) placed *T. parviceps* in *Amphibolurus*. He implied that only the fact that *T. parviceps* and *A. adelaidensis* were sympatric prevented him from lowering *T. parviceps* to subspecific level. The similarity is here taken to indicate that the two species are, in fact, related. As *A. adelaidensis* has not lost the tympanum and a phalanx of the pes (see below), it is considered the more primitive. *T. parviceps* has probably evolved from *A. adelaidensis* or a species closely related to it.

A variation in arrangement of pores occurs within the *A. maculatus* species-group. This involves a sharp forward arch in the preanal region. Storr (1965) used this character to distinguish between species of the group. As Storr defined the group only *A. isolepis* had this sharp forward deviation. Humphries (1972) split the *A. maculatus* species-group, preferring to place *A. isolepis* with *A. scutulatus* and *A. cristatus* in a group of their own. Humphries (pers. comm.) based this decision mainly on the ecology of the species. Part of his justification for this decision, however, was apparently in the shape of the pore line. He illustrated the three species as identical in the arrangement of pores. On the basis of specimens examined by the author this was true for *A. scutulatus*, but was clearly not the case for *A. cristatus*. The preanal pores in the latter species do form an anterior arch towards the midline, but there is no acute anterior angle like that of *A. isolepis*. This feature suggests that *A. scutulatus* should be placed with *A. isolepis* in the *A. maculatus* species-group. Humphries' decision to place *A. cristatus* and *A. scutulatus* together is justified on ecological grounds (Pianka, 1971b), but little morphological justification is evident.

C. pictus was illustrated by Humphries (1972) as possessing a sharp forward arch in the preanal pore series. Examination of specimens showed that this varied intraspecifically. No specimen had an anterior angle as acute as the normal in *A. isolepis*. Little phylogenetic significance is attached to this character here.

Scale counts taken to quantify differences in the arrangement of pores met with mixed success. Generally larger species tend to have relatively smaller scales (see Scale Size, pp. 119-134). For this reason scale size was often not a good indicator of pore arrangement. For example, the species of *Lophognathus* had higher femoral scale counts than the generally much smaller *Diporiphora*, despite the fact that the femoral pores extended further distally in *Lophognathus*.

The inguinal scale count proved useful in distinguishing those species retaining the primitive pore arrangement from those with a derived arrangement. In animals with the primitive arrangement there was no inguinal interruption to the series so the inguinal scale count recorded the number of scales between two pores of an apparently evenly spaced series. Within this group the *A. adelaidensis* and *A. cristatus* species-groups appear to be evolving wider spacing of the pores, as evidenced by many specimens scoring higher inguinal scale counts. This fact is not readily apparent from qualitative examination.

3. Pore Type.

Boulenger (1885) refined the use of pores as a taxonomic character in agamids by recognising a difference in kind between the pores of some African genera. Pore type was neglected as a character in Australian agamids until Humphries (1972), in an unpublished thesis, used the morphological relationship of pores to scales. This relationship has since been mentioned in publications by Storr (1977) and Houston (1978), but no systematic use of the character has been made in a published work.

Humphries illustrated three pore types, interpreted here as:

I) Interscalar; the pore penetrating the skin between scales,

II) Posterior intrascalar; the pore penetrating the posterior margin of a scale, and

III) Ventral intrascalar; the pore penetrating the ventral aspect of a scale.

Examination of a representative group of specimens (see Table 5) produced the results summarised in Table 8.

Physignathus possessed intrascalar pores. Pores in juveniles appeared on the visible surface of a scale close to, but clearly in front of, the posterior margin. In large adults the scales bearing pores were greatly increased in size, and the pore penetrated the posterior margin of the scale.

All members of the *Tympanocryptis* group examined had pores between scales. In the species with a more imbricate ventral scalation the pore was often concealed beneath the free posterior edge of a scale. In *A. diemensis* this was particularly common. *T. cephalus* and *T. intima*, which possess the smoothest and least imbricate scalation of the group, never exhibited this condition.

All members of the *Chlamydosaurus* group had intrascalar pores, usually presenting on the ventral surface of a keeled scale. Pores of Diporiphora were generally nearer the posterior margin of the pore-bearing scale, and several posterior intrascalar pores were recorded in D. bilineata and D. magna. Pores of this type were also recorded in some Lophognathus longirostris and one individual L. gilberti. These specimens also possessed ventral intrascalar pores.

Table 8. Pore Type.

Species	N	Interscalar	Posterior Intrascalar	Ventral Intrascalar
Physignathus	3		+	+
T. cephalus		+		
T. parviceps	1	+		
T. tetraporophora	2	+		
A. adelaidensis	5	+		
A. diemensis	8	+		
A. muricatus	11			+
A. nobbi	11			+
Caimanops	1			+
Chlamydosaurus	4			+
D. australis	2			+
D. bilineata	10		+	+
D. magna	3		+	+
L. gilberti	6		+	+
L. longirostris	3		+	+
L. temporalis	2			+
C. decresii	10	+	+	
C. fionni	11	+	+	
C. ornatus	11	+	+	
C. pictus	8	+	+	
C. rufescens	2	+	+	
C. vadnappa	3	+	+	
A. maculatus	3		+	
A. fordi	8	+	+	
A. isolepis	1		+	
A. scutulatus	6	+	+	
A. cristatus	10	+	+	
A. caudicinctus	5	+		
A. reticulatus	7		+	+
A. clayi	1	+	+	
A. gibba	10	+	+	
A. maculosus	11	+	+	
A. nuchalis	7	+	+	+
A. barbatus	9	+	+	
A. mitchelli	1	+	+	
A. vitticeps	6	+	+	

+ = at least some pores of that type.

Most *Ctenophorus* examined had at least some posterior intrascalar pores. However, many pores were interscalar, particularly in the preanal region, and both types were recorded from all species of *Ctenophorus* (Table 8).

Members of the *A. maculatus* species-group had mainly posterior intrascalar pores, with only a few interscalar pores in some specimens.

Some individual *A. cristatus* possessed only interscalar pores, while others possessed mainly posterior intrascalar pores. *A. caudicinctus* possessed only interscalar pores.

Posterior intrascalar pores were recorded in all species of the *A. reticulatus* species-group, and only *A. reticulatus* did not possess some interscalar pores. In some *A. nuchalis* and *A. reticulatus* the intrascalar pores were clearly forward of the posterior margin of the scale, and were therefore scored as ventral intrascalar.

Pores of the *A. barbatus* species-group were most often interscalar. Posterior intrascalar pores were often present toward the lateral extreme of the femoral pore series.

Discussion.

Early in this study pore type was considered of major taxonomic significance. Humphries (1972) had made some use of the character in separating species-groups of *Amphibolurus*, and a wider application than that of Humphries was anticipated. Variation between individuals of single species, and between the medial and lateral pores of the same specimen were discouraging. However, enough consistent variation exists between groups to corroborate conclusions drawn from other information.

Interscalar pores have been reported for *A. adelaidensis* (Humphries, 1972; Houston, 1978) and *T. parviceps* (Humphries, 1972). These reports have been confirmed by the present study, and extended to all members of the *Tympanocryptis* group examined.

In the *Chlamydosaurus* group all species examined have at least some ventral intrascalar pores. Outside the group these pores occur only in juvenile *Physignathus* and in some members of the *A. reticulatus* species-group.

Some specimens of all species of the *Ctenophorus* group except *A. caudicinctus* have posterior intrascalar pores. However, most species also have interscalar pores. There is thus no single pore type which may be considered typical of the group.

Designation of a pore type as primitive is difficult. At least two different pore types occur in agamids outside the Australian endemic radiation. *Leiolepis* and juvenile *Physignathus* have ventral intrascalar pores, which develop ontogenetically in *Physignathus* to become posterior intrascalar. *Uromastyx* has interscalar pores presenting behind an enlarged, notched scale. All these pore types can be found in *A. nuchalis*, and the latter two pore types (of adult *Physignathus* and *Uromastyx*) are found in most species of the *Ctenophorus* group. It is thus more likely that the pore types typical of the *Chlamydosaurus* and *Tympanocryptis* groups represent derived states.

4. Number of Pores.

a. Preanal pores.

Preanal pores were scored as present only in members of the *Chlamydosaurus* group and in the advanced species of *Tympanocryptis* (Table 9). These two groups contain all species which have a distinct preanal group of pores, separated from any pores on the ventral surface of the thigh by an absence of pores in the inguinal region.

Most specimens of the advanced *Tympanocryptis* (species other than *T. parviceps*) had two preanal pores. One *T. intima* had only one pore, and two of the three *T. lineata* examined lacked pores.

The most common number of preanal pores in members of the *Chlamydosaurus* group was four. *A. nobbi* and *L. longirostris* usually had six, *L. temporalis* two and *D. winneckei* none (see Mode, Table 9). Otherwise all species most commonly had four preanal pores.

b. Femoral pores.

Each of the four pore arrangements described earlier could be said to have a typical number of femoral pores. Those species with a primitive arrangement (Table 7) had a total of from 15 to 60 femoral pores. The number was generally lower in all the derived pore arrangements.

Three of the five genera of the *Chlamydosaurus* group had from four to eight femoral pores. Femoral pores were absent in most *Diporiphora* and *Caimanops*. However, *D. albilabris* usually had one femoral pore on either side. One *Caimanops* and occasional other *Diporiphora* also had femoral pores (Table 10).

Only *T. tetraporophora* of the advanced *Tympanocryptis* normally had femoral pores. Two of the 11 *T. intima* examined also had femoral pores (Table 10).

A. nuchalis and members of the *A. barbatus* species-group had a

Table 9. Preanal Pores (Bilateral).

Species	Mean	Min	Max	SD	N	Mode
Chelosania	0	0	0	0	6	0
Gonocephalus	0	0	0	0	3	0
Physignathus	0	0	0	0	10	0
Moloch	0	0	0	0	10	0
T. cephalus	2.00	2	2	0	8	2
T. intima	1.91	1	2	0.30	11	2
T. lineata	0.67	0	2	1.16	3	0
T. parviceps	0	0	0	0	2	0
T. tetraporophora	2.00	2	2	0	16	2
A. adelaidensis	0	0	0	0	12	0
A. diemensis	0	0	0	0	28	0
A. muricatus	4.08	3	6	0.79	12	4
A. nobbi	5.44	4	6	0.89	16	6
Caimanops	3.81	2	6	1.12	21	4
Chlamydosaurus	3.08	0	5	1.61	13	4
D. albilabris	3.58	2	4	0.79	12	4
D. australis	3.60	2	4	0.70	10	4
D. bennettii	3.23	2	4	0.93	13	4
D. bilineata	2.93	0	6	1.49	29	4
D. lalliae	4.11	2	6	1.05	9	4
D. linga	4	-	-	-	1	-
D. magna	4.00	4	4	0	11	4
D. superba	4	-	-	-	1	-
D. winneckei	1.69	0	4	1.69	13	0
L. gilberti	4.60	4	6	0.84	10	4
L. g. centralis	3.68	2	4	0.67	19	4
L. longirostris	5.42	4	6	0.67	12	6
L. temporalis	1.83	0	2	0.58	12	2
C. decresii	0	0	0	0	13	0
C. fionni	0	0	0	0	12	0
C. ornatus	0	0	0	0	10	0
C. pictus	0	0	0	0	21	0
C. rufescens	0	-	-	-	1	-
C. vadnappa	0	0	0	0	3	0
A. maculatus	0	0	0	0	5	0
A. fordi	0	0	0	0	11	0
A. isolepis	0	0	0	0	58	0
A. scutulatus	0	0	0	0	4	0
A. cristatus	0	0	0	0	18	0
A. caudicinctus	0	0	0	0	31	0
A. reticulatus	0	0	0	0	8	0
A. clayi	0	0	0	0	5	0
A. gibba	0	0	0	0	12	0
A. maculosus	0	0	0	0	10	0
A. nuchalis	0	0	0	0	38	0
A. barbatus	0	0	0	0	21	0
A. minor	0	0	0	0	5	0
A. mitchelli	0	-	-	-	1	-
A. vitticeps	0	0	0	0	16	0

Table 10. Femoral Pores (Bilateral).

Species	Mean	Min	Max	SD	N	Mode
Chelosania	0	0	0	0	6	0
Gonocephalus	0	0	0	0	3	0
Physignathus	39.3	32	43	4.03	10	43
Moloch	0	0	0	0	10	0
T. cephalus	0	0	0	0	8	0
T. intima	0.36	0	2	0.81	11	0
T. lineata	0	0	0	0	3	0
T. parviceps	33	-	-	-	1	-
T. tetraporophora	2.00	2	2	0	16	2
A. adelaidensis	22.0	14	27	3.62	12	24
A. diemensis	19.6	13	26	3.68	27	15,18
A. muricatus	5.83	4	7	1.12	12	6,7
A. nobbi	2.75	2	4	0.93	16	2
Caimanops	0.10	0	2	0.44	21	0
Chlamydosaurus	8.46	6	12	2.03	13	7,8
D. albilabris	1.92	1	2	0.29	12	2
D. australis	0	0	0	0	10	0
D. bennettii	0	0	0	0	13	0
D. bilineata	0	0	0	0	29	0
D. lalliae	1.11	0	4	1.76	9	0
D. linga	0	-	-	-	1	-
D. magna	0.18	0	2	0.60	11	0
D. superba	0	-	-	-	1	-
D. winneckei	0.15	0	2	0.56	13	0
L. gilberti	5.50	4	7	0.97	10	6
L. g. centralis	3.68	0	6	1.34	19	4
L. longirostris	17.0	13	21	2.42	12	18
L. temporalis	2.25	0	4	1.60	12	2,4
C. decresii	39.2	35	42	2.33	12	41
C. fionni	38.0	33	46	3.90	11	36
C. ornatus	57.2	51	72	6.29	10	51
C. pictus	40.7	37	47	2.60	20	39
C. rufescens	35	-	-	-	1	-
C. vadnappa	39.7	38	41	1.53	3	-
A. maculatus	53.6	50	58	3.58	5	50
A. fordi	33.7	27	40	4.05	11	-
A. isolepis	53.8	41	64	4.01	53	57
A. scutulatus	49.8	43	56	5.32	4	50
A. cristatus	57.3	51	62	3.15	15	56
A. caudicinctus	27.2	18	35	4.04	30	26
A. reticulatus	40.8	34	49	5.90	8	37
A. clayi	5.20	4	7	1.10	5	5
A. gibba	31.2	28	34	2.21	12	33
A. maculosus	10.0	5	14	2.49	10	10
A. nuchalis	18.9	14	27	2.69	36	19
A. barbatus	14.2	11	19	1.97	21	14
A. minor	13.2	12	16	1.79	5	12
A. mitchelli	11	-	-	-	1	-
A. vitticeps	13.6	9	16	2.19	16	13

reduced number of femoral pores relative to those species with the primitive pore arrangement. *A. clayi* had a very low pore count (Table 10).

Discussion.

The three derived pore arrangements of the endemic Australian agamids all involve a reduced number of pores. The advanced *Tympanocryptis* have the least pores (a maximum of 4), the *Chlamydosaurus* group are intermediate (from 0 to 27), and those species with the pores arranged as in *A. nuchalis* (including the *A. barbatus* species-group) have usually retained more (from 5 to 27). However, there are several considerable differences between closely related species. For example, *Lophognathus longirostris* has more pores than any other member of the *Chlamydosaurus* group while the congeneric *L. temporalis* has some individuals which lack pores entirely. Variation such as this suggests that the number of pores should not be accorded much importance above the species level.

5. Exposed Tympanum.

Many genera of agamids have the tympanic membrane hidden or covered by scales. Both Gray (1845) and Boulenger (1885) used the character extensively in their synopses. However, the Australian genus *Tympanocryptis* Peters 1863 was not known at the time of Gray's catalogue. The only other Australian dragon with a concealed tympanum, *Amphibolurus maculosus*, was not described until well after Boulenger's catalogue.

An exposed tympanum was recorded as absent from all specimens of all species of *Tympanocryptis* (n = 44) and from all specimens of *A. maculosus* (n = 10), but was present in all other species examined.

Dissection of the head of *T. tetraporophora* (Fig. 10) revealed that the depressor mandibulae muscle rested on the posterosuperior aspect of the quadrate bone with only a fascial compartment separating these two structures which normally surround the tympanic cavity. This anatomical arrangement was easily detected in undissected specimens by palpation. No specimen of any species of *Tympanocryptis* retained any evidence of a tympanic membrane.

The tympanum of *A. maculosus* was completely covered by scales. The tympanic membrane was still obvious, to the extent that measurements of the ear width were still possible in the species.

No systematic attempt was made to record the presence of scales on the tympanum. However, the ear width of all specimens was measured, and notes made of the few specimens which had such a feature. Two of the 16 *A. adelaidensis* examined had some scales on the tympanum. These were on the upper posterior aspect of the tympanum. The three *Gonocephalus spinipes* examined had a similar condition.

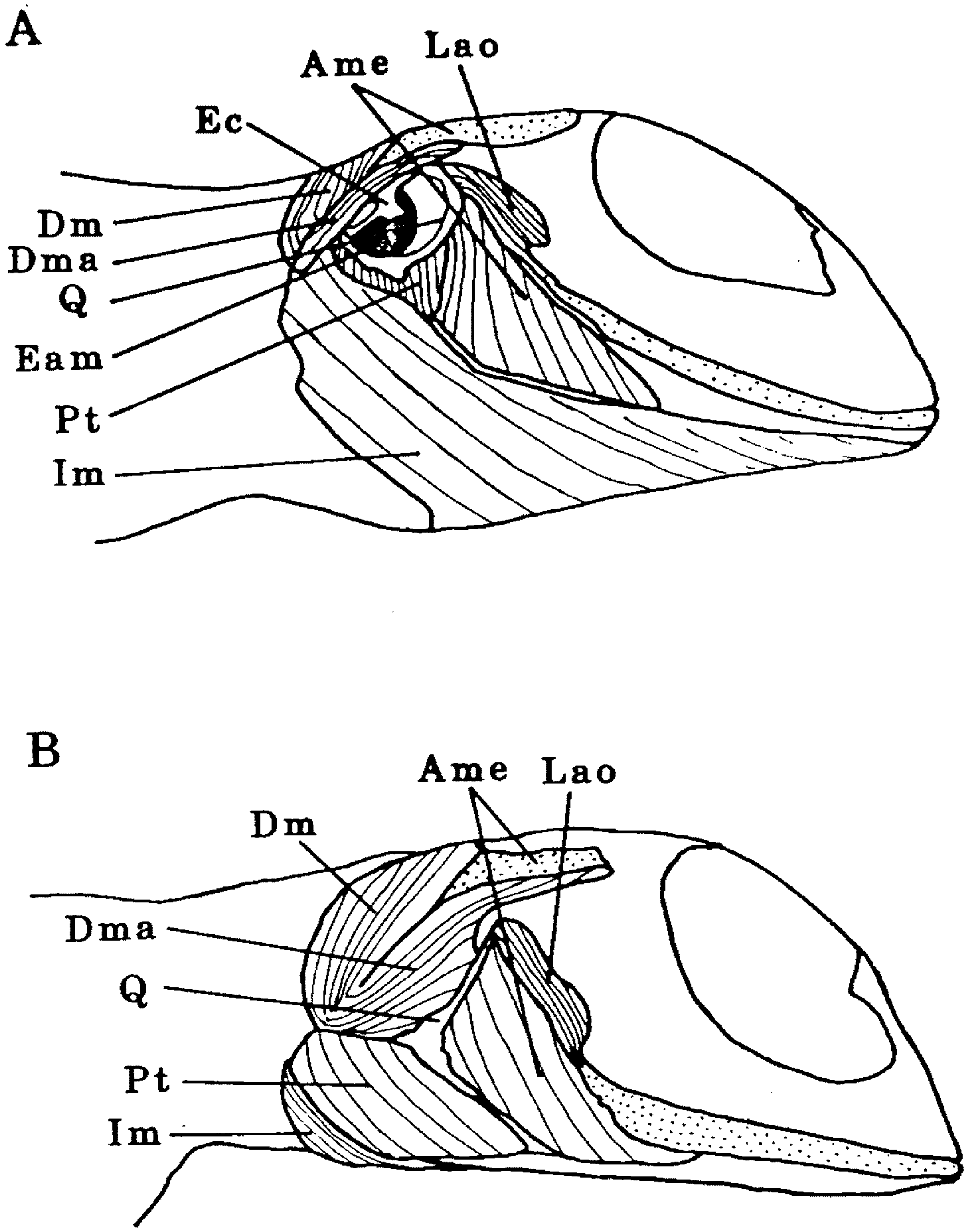


Figure 10. Dissections of the Posterior Jaw Muscles. A = *Diporiphora bilineata*; B = *Tympanocryptis tetraporophora*. Key: Ame = Adductor mandibulae externus; Dm = Depressor mandibulae; Dma = Depressor mandibulae, accessory head; Eam = External auditory meatus; Ec = Extracolumella; Im = Intermandibularis; Lao = Levator anguli oris; Pt = Pterygoideus; Q = Quadrate. Note that the quadrate bone in *Diporiphora* (A) forms the anterior boundary of the external auditory meatus while in *Tympanocryptis* (B) it forms part of the attachment of the accessory head of Depressor mandibulae muscle (terminology after Haas, 1973).

Discussion.

The character of an exposed or scale-covered tympanum has been used extensively in agamid taxonomy since Gray (1845) published his catalogue. However, the character received little attention with regard to the Australian species before Mitchell (1948) described *Tympanocryptis maculosa*. Until the description of this species all "earless" Australian dragons formed a discrete group of small, depressed species with strongly heterogeneous dorsal scalation. Mitchell (1965) investigated the relationships of the distinctive *T. maculosa* and recommended that it be considered a "specialised member" of the genus *Amphibolurus*. Mitchell concluded that "closure of the tympanic membrane" was a "secondary character", and that true members of the genus *Tympanocryptis* should be distinguished by the "reduction of one phalanx of the fifth digit of the pes". Mitchell showed no knowledge of the complete loss of the tympanum in true *Tympanocryptis*. This was despite making alizarin preparations, which normally require the skinning of specimens before clearing. Cogger (1961) did not emphasise the loss of the tympanic membrane, though he was aware of the change.

Mitchell (1965) mentioned a lizard from the Grampians in Victoria which had a partially scale covered tympanum. This was almost certainly an *A. diemensis*. No *A. diemensis* (of the 46 examined) in the present study were recorded as possessing a scaly tympanum. However, the feature was observed in the closely related *A. adelaidensis*, so it would not be surprising to find this character occasionally in *A. diemensis*.

Storr's (1977) attempt to move *T. parviceps* into *Amphibolurus* is remarkable in view of Mitchell's (1965) recommendations. Since he did not examine phalangeal formulae it seems probable that he was not aware of Mitchell's (1965) paper.

The adaptive significance of a concealed tympanum probably lies in a more effective camouflage. The presence of both the eye and the tympanum on the side of the head of most lizards is a feature by which predators might recognise the whole animal. The loss of one of these features would presumably improve a lizard's camouflage.

6. Phalangeal Formula.

Mitchell (1965) compared a number of Australian agamid species specifically to elucidate the relationships of *Tympanocryptis maculosa* Mitchell. He examined a limited number of specimens for skeletal features, and concluded "the only clearly defined dichotomy evident from this study" was the variation in the phalangeal formula of the pes. True *Tympanocryptis* exhibit a reduction in the pes phalangeal formula to 2.3.4.5.3. Other species examined by Mitchell, including *T. maculosa*, had a formula of 2.3.4.5.4. On this basis *maculosa* was transferred to *Amphibolurus*. Cogger (1961) had earlier discovered this, and had also noted a variation in the phalangeal formula for *Moloch*, the formula for both manus and pes being 2.2.3.3.2.

In this study the phalangeal formula was examined in those species related to *Tympanocryptis*. The phalangeal formula for the pes of *Tympanocryptis* was confirmed as 2.3.4.5.3. Specimens of *T. cephalus*, *T. tetraporophora*, *T. intima* and *T. parviceps* were examined.

A. adelaidensis and *A. diemensis* both possessed a phalangeal formula for the pes of 2.3.4.5.4.

The reduced phalangeal formula of *T. parviceps* agrees with that of the genus. This, and the apparent loss of the tympanic membrane suggest that the species should remain in the genus *Tympanocryptis*. The action of Storr (1977) in including *T. parviceps* in the *A. adelaidensis* species-group is understandable on the basis of pore arrangement and some scale characters. His apparent ignorance of Mitchell's (1965) paper is less explicable.

The greatly reduced phalangeal formulae of *Moloch* (Cogger, 1961) emphasise the great divergence of that genus.

7. Crested Back.

Many agamids have dorsal series of enlarged, mucronate scales. These are restricted to the neck region in many species, and are absent in some. This feature was recorded from Australian agamids in two parts; as a nuchal scale ridge (NC) and a vertebral scale ridge (VC).

a. Nuchal Scale Ridge.

Tables 11 and 12 summarise the results obtained from recording the presence of a nuchal scale ridge. There was considerable variation in the development of the ridge when present, and descriptions of these variations are presented below.

All three Asian-derived genera possessed a nuchal scale ridge. In *Chelosania* the scales making up the ridge were spinose and compressed, but were not greatly enlarged. In *Gonocephalus* the scales of the nuchal ridge were much larger than the adjacent scales, and formed a large serrated nuchal crest. The nuchal ridge in *Physignathus* was intermediate in development.

Generally in species where only some specimens had a nuchal ridge the ridge was weakly developed. The ridge consisted of slightly enlarged mucronate scales forming a discontinuous series for a short distance behind the occiput. Exceptions to this generalisation were *Diporiphora* and the *A. adelaidensis* species-group. Some specimens of these groups did possess weak scale ridges, but others possessed a contiguous series of strongly keeled mucronate scales extending well onto the trunk. This condition was similar to that in most species which usually possessed a nuchal scale ridge.

In large males of *Caimanops*, *L. longirostris* and *L. temporalis* the scales of the nuchal ridge became greatly enlarged and laterally compressed to form a distinct nuchal crest. This crest was weakly developed

Table 11. Median Scale Ridges.

Species	NC		VC	
	0	1	0	1
Chelosania	0	6	0	6
Gonocephalus	0	3	0	3
Physignathus	0	12	0	12
Moloch	10	0	10	0
T. cephalus	7	1	8	0
T. intima	12	0	12	0
T. lineata	2	1	3	0
T. parviceps	2	2	4	0
T. tetraporophora	15	1	16	0
T. uniformis	1	0	1	0
A. adelaidensis	8	8	12	4
A. diemensis	19	27	38	8
A. muricatus	0	12	0	12
A. nobbi	0	16	0	16
Caimanops	0	23	17	6
Chlamydosaurus	4	10	14	0
D. albilabris	6	8	14	0
D. australis	2	9	11	0
D. bennettii	3	10	13	0
D. bilineata	11	18	29	0
D. lalliae	4	6	9	1
D. linga	1	0	1	0
D. magna	7	5	12	0
D. superba	1	0	1	0
D. winneckei	13	0	13	0
L. gilberti	0	34	0	34
L. longirostris	0	12	0	12
L. temporalis	0	12	0	12
C. decresii	0	14	13	1
C. fionni	1	12	13	0
C. ornatus	0	10	7	3
C. pictus	0	21	4	17
C. rufescens	0	2	2	0
C. vadnappa	0	3	2	1
A. maculatus	1	4	1	4
A. fordi	11	1	12	0
A. isolepis	62	0	62	0
A. scutulatus	0	4	0	4
A. cristatus	0	19	0	19
A. caudicinctus	0	31	2	29
A. reticulatus	0	8	8	0
A. clayi	5	1	6	0
A. gibba	0	12	12	0
A. maculosus	1	9	10	0
A. nuchalis	2	38	35	5
A. barbatus	11	10	21	0
A. minor	2	3	5	0
A. mitchelli	1	0	1	0
A. vitticeps	3	13	16	0

0 = absent. 1 = present

in large male L. gilberti and A. muricatus.

The nuchal scale ridge of A. cristatus was unusual in being invariably present, but usually composed of an interrupted series of enlarged spinose scales. These scales became very large in adults, and then formed a distinctive nuchal crest.

Table 12. Summary of Presence of Median Scale Ridges.

Taxon	Always Present	Usually Present	Variable	Usually Absent	Always Absent
Asian-derived genera	NC, VC				
Moloch					NC, VC
Tympanocryptis				NC	VC
A. adelaidensis species-group			NC	VC	
A. muricatus species-group	NC, VC				
Chlamydosaurus		NC			VC
Caimanops	NC			VC	
Diporiphora			NC		VC
Lophognathus	NC, VC				
Ctenophorus	NC		VC		
A. maculatus species-group			NC, VC		
A. cristatus species-group	NC	VC			
A. reticulatus species-group	NC			VC	
A. barbatus species-group			NC		VC

NC = Nuchal scale ridge. VC = Vertebral scale ridge.
Always = 95-100%. Usually = 66-95%.
Variable = 33-66%, or some species with, some without (see Table 11).

Of the species where more than ten specimens were examined only four species invariably lacked a nuchal scale ridge. These were Moloch, D. winneckei, T. intima and A. isolepis. The eastern A. fordi examined lacked a nuchal ridge, but one of the two Western Australian specimens examined had a weak nuchal scale ridge. A. fordi, A. isolepis and D.

winneckei are ecologically associated with *Triodia* grass tussocks.

b. Vertebral Scale Ridge.

Results of scoring the presence or absence of a vertebral scale ridge are presented in Table 11, and the main points are summarised in Table 12.

The vertebral scale ridge in most of the endemic Australian dragons consisted of a contiguous series of mucronate to weakly spinose scales. In general the development of the vertebral series paraleled the prominence of the nuchal scale ridge. Those species with a more prominent nuchal ridge usually possessed a more spinose and prominent vertebral scale ridge. The exception to this generalisation was *Caimanops*. Only 6 of the 23 specimens examined were recorded as possessing a vertebral ridge. In all specimens a series of enlarged mucronate scales extended along the vertebral line from the nuchal crest or ridge, but in only 6 specimens did this extend to the level of the groin.

In all species of *Ctenophorus* the nuchal scale ridge extended back onto the trunk to some extent. However, no specimen of *C. fionni* was scored as possessing a vertebral scale ridge.

Of the 5 *A. maculatus* examined 4 were scored as possessing a vertebral scale ridge. The one specimen without did possess a nuchal scale ridge, but the vertebral continuation of this did not extend as far as the level of the groin.

Discussion

A median scale ridge is a very common character in both families of the Iguania. This, and the almost universal occurrence of the feature in Australian agamids means the feature should be regarded as primitive. Reduction of the median scale ridge usually begins posteriorly; no group has lost the nuchal scale ridge while retaining a vertebral scale ridge

(Table 12).

Moloch is the only Australian genus with no specimen exhibiting any sign of a nuchal scale ridge. In view of the highly specialised nature of the genus this is not surprising.

Selective pressures acting on the degree of development of the median scale ridge are not clear. However, strong circumstantial evidence exists which suggests that an arboreal habit is consistent with a better developed median scale ridge.

The three Asian-derived genera are arboreal or semi-arboreal. All retain a vertebral scale ridge. Among the Australian endemics only *Lophognathus* and the *A. muricatus* species-group invariably possess a vertebral scale ridge. Both are semi-arboreal. Of the terrestrial endemic groups only the *A. cristatus* species-group normally possesses a vertebral scale ridge (Table 12).

In the *Tympanocryptis* group the presumed more primitive *A. adelaidensis* and *A. diemensis* have some specimens retaining a vertebral scale ridge, and about half retain a nuchal scale ridge (Table 11). *Tympanocryptis* has lost the vertebral scale ridge entirely. One of the advanced species, *T. intima*, may have lost the nuchal series as well; no specimens examined had one.

The retention of the vertebral scale ridge in *Lophognathus* and the *A. muricatus* species-group is probably related to their semi-arboreal habit (see above). The semi-arboreal *Caimanops* also retains prominent nuchal and vertebral crests, but the vertebral scale ridge often does not extend to the level of the groin. The more terrestrial *Diporiphora* has lost the feature entirely, as has the specialised *Chlamydosaurus*.

Triodia-associated species of both the *Chlamydosaurus* and the *Ctenophorus* groups have progressed furthest towards the loss of the nuchal scale ridge. *A. isolepis* and *A. fordi* of the *A. maculatus* species-group (*Ctenophorus* group), and *Diporiphora linga* and *D. winneckei* (*Chlamydosaurus* group) have reduced or absent nuchal ridges. These species also share the characters of small adult size and small homogeneous dorsal scales. Some selective advantage is inferred for this combination of characters. Small size presumably facilitates movement among the network formed by *Triodia* tussocks. The small reddish dorsal scales give better camouflage against the sandy soils often associated with *Triodia*. The selective advantage of no median scale ridge is more obscure. However, the two species from each radiation probably represent a case of parallelism. The fact that all four species have lost or almost lost the median scale ridge suggests a strong selective pressure against its retention.

Most members of the *Ctenophorus* group retain a nuchal scale ridge, and some members of all species-groups except the *A. barbatus* species-group retain a vertebral series.

The *A. reticulatus* species-group, if considered ancestral to the *A. barbatus* species-group, might be expected to retain a better developed median scale ridge. This is the case. Within the *A. barbatus* species-group a nuchal scale ridge is more common in *A. vitticeps* than *A. barbatus*. This suggests the former is the more primitive, a suggestion corroborated by evidence from Badham (1976)(see Frill, pp. 176-177).

A. maculatus, the first species listed in Boulenger's (1885) synopsis of the genus, was diagnosed by the description: "no nuchal crest; nostril below the canthus rostralis". Boulenger included *Grammatophora isolepis* Fischer 1881 in this species, and may have checked specimens of that species for this character. Gray (1845) described a "rudimentary scaly crest" for *A. maculatus*. Gray's description was confirmed by this study. Storr (1965) did not mention the character in his resurrection of *A. isolepis*. Cogger (1975) included in his description of *A. maculatus* the clause: "without distinct nuchal or vertebral series". Cogger may have simply followed Boulenger, or relied on material not seen by the author. Storr (1965) described four subspecies of *A. maculatus*. It is possible that the character varies among these taxa. Only *A. maculatus griseus* were examined in this study.

Within groups whose species share a similar ecological niche the median scale ridge appears to be a good indicator of phylogenetic position. However, the character is apparently altered quite rapidly under strong selective pressure, having been lost independently within two generic groups with *Triodea*-associated species. Major taxonomic changes on the basis of this character should not be made before there is a clearer understanding of its ecological significance.

c. Deep Structures of the Median Crests.

Several agamid species were seen raising median skin folds to form nuchal and vertebral crests. An investigation was performed to establish the morphological basis for crest erection. Observation of animals erecting crests led the author to expect one of two mechanisms, or a combination of both, to be responsible. The two expected mechanisms were (i) an attachment of the skin to underlying muscles, or (ii) a block of "erectile" tissue.

i. Muscle Attachments.

Crest erection involved the medial movement of skin on the side of the neck and anterior part of the trunk. This movement could have been produced by a muscle attached to the vertebrae medially and the skin laterally. The margins of some of the muscles of the forelimb could act in this manner, and were examined closely. However, no lateral skin attachments were found, nor was there any separate muscle capable of producing the observed skin movements.

ii. Erectile Tissue.

In all species examined except *Moloch* a median connective tissue block connected the midline skin with vertebral neural spines. This tissue block was thicker about half way between skin and spines, and at this level received attachment from the medial aponeuroses of some fore-limb muscles. In many species the tissue of this central thickening was highly vascular.

In the species where this vascular tissue was most highly developed there was a thick connective tissue sheath surrounding the vascular tissue (Fig. 11). Within the sheath relatively loose connective tissue predominated, and there were numerous veins and some arteries. Where large veins were present the lumina were flattened horizontally (Fig. 12), and most venules were also wider than deep (Fig. 11). There were comparatively few arteries, and these were surrounded by thicker connective tissue (Fig. 13).

Animals with a smaller vascular tissue block retained the sheath, but the tissue within the block was more diffuse (Fig. 14). In some specimens the block was reduced to a connective tissue envelope with a few contained vessels (Fig. 15).

The results of a preliminary survey into the occurrence of this vascular tissue block are summarised in Table 13. The feature was scored as present whenever vessels invaded the central connective tissue block. The number of specimens examined for each species is given in Table 5.

The vascular tissue block was relatively largest in males of *Lophognathus*, *Diporiphora* and the *A. muricatus* species-group. The females of these genera had little or no vascular tissue. Sexual

Figure 11. Transverse Section of Mid-dorsal Region of *A. muricatus*. Ap = central aponeurosis of forelimb muscle; D = dermis; Sh = dense connective tissue sheath; M = paravertebral muscle. Rectangles A and B represent Figures 12 and 13 respectively. Most dark areas within central vascular tissue block are venules. Note that these are generally wider than deep. Masson's trichrome.

Figure 12. Detail from Vascular Tissue in Mid-dorsal Region of A. muricatus. Note three large veins with flattened lumina, filled with nucleated blood cells (arrow). The veins are accompanied by a small artery (a).

Figure 13. Detail from Vascular Tissue in Mid-dorsal Region of *A. muricatus*. Note two arteries (A) surrounded by more densely packed connective tissue.

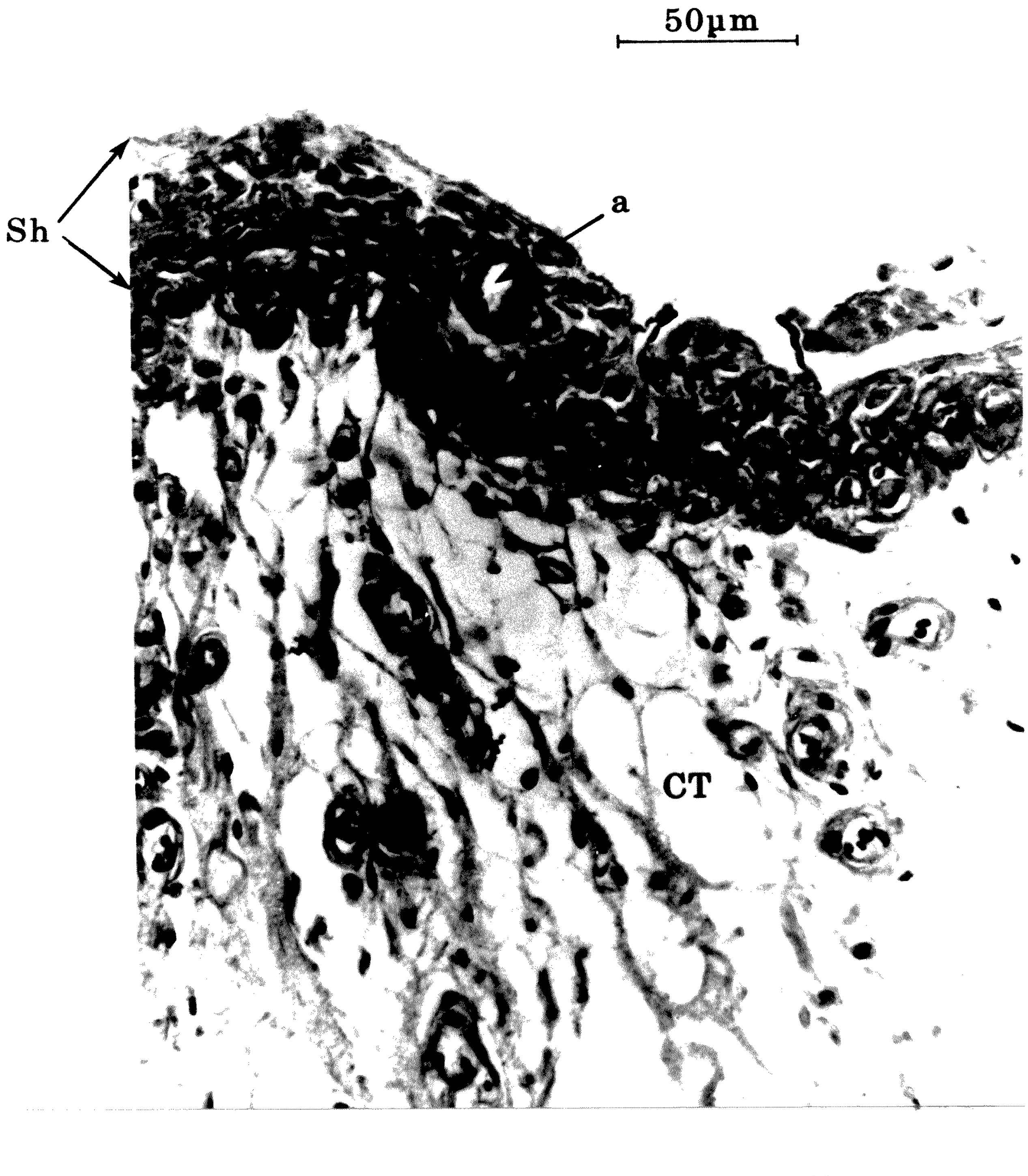


Figure 14. Connective Tissue Sheath of C. decresii. Wall of central vascular tissue block showing an arteriole (a) within the sheath (Sh) surrounding venules and loose connective tissue (CT). Note that connective tissue is less densely packed than in A. muricatus (Figs. 12, 13). Masson's trichrome.

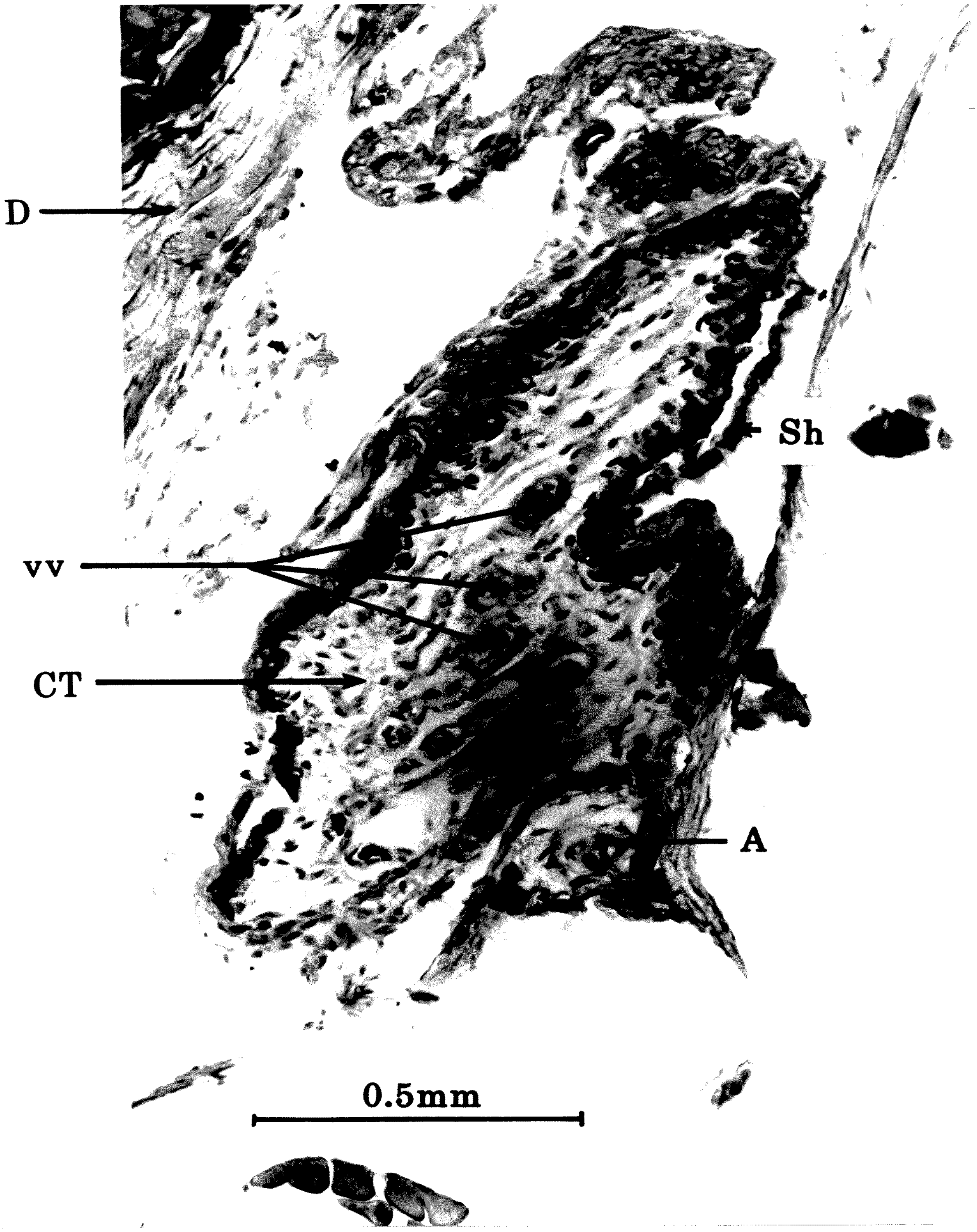


Figure 15. Complete Vascular Tissue Block of *C. pictus*. A = artery; CT = connective tissue; D = dermis; Sh = sheath; vv = venules. Masson's trichrome.

dimorphism was observed also in Tympanocryptis and Ctenophorus pictus, but the males of these species had relatively little vascular tissue. There was a large vascular tissue block in the single A. cristatus examined, a female.

Table 13. Median Dorsal Vascular Tissue Block.

Species	Males	Females	Juveniles	Crest#
G. spinipes		-		
Physignathus	-	-	+	
Moloch	+			
T. tetraporophora	-	-		
A. diemensis	+	-		
A. muricatus	+	+/-		+
A. nobbi	-	-		+
Chlamydosaurus	+	-		
D. australis	+	-		+
D. bennettii	+			
D. bilineata	+	-		
D. magna	+			
L. gilberti	+	-	+	+
C. decresii	+	+		+*
C. ornatus	+			
C. pictus	-	-		+**
A. fordi	-	-		
A. isolepis				
A. cristatus	+	+		
A. caudicinctus	+			
A. clayi	+			
A. nuchalis	-	+/-		
A. barbatus	-	-		
A. vitticeps	-			

Crest = observed to raise a median skin fold.
* Gibbons (1979). ** Hudson (1979).
+ = present. - = absent. +/- = variable.

Two juveniles, one Physignathus and a female L. gilberti, were sectioned. Both had some vascular tissue. Adult Physignathus and adult female Lophognathus did not.

Discussion.

The vascular tissue reported here in agamids might function as erectile tissue. Three pieces of evidence support this contention. Engorgement of the large veins (Fig. 12) would presumably increase the dorsoventral diameter of the tissue block, helping to raise a median crest. The thick connective tissue envelope surrounding the vascular tissue resembles the tunica albuginea of the erectile bodies of the mammalian penis. Thirdly, the vascular tissue was best developed in those species which commonly erect median crests (Table 13).

Winokur (1977) described erectile tissue in the "tentacles" of the snake *Erpeton tentaculatum*. Cavernous tissue occurs in the paranasal region of many reptiles, and has been the subject of many studies and functional hypotheses (see Winokur, 1977, for discussion). The development of erectile tissue in the tentacles of *Erpeton* is readily explained as deriving from this tissue.

The vascular tissue of agamids does not closely resemble the paranasal cavernous tissue of other reptiles, and is not typical erectile tissue. However, the vascular tissue is remarkable and present in several common agamids. It is therefore surprising to find no record of the structure in the literature. Winokur (pers. comm.) was not aware of any report of vascular tissue in this region of any reptile.

Some members of the *Chlamydosaurus*, *Tympanocryptis* and *Ctenophorus* groups possess dorsal vascular tissue. *Physignathus* has a similar structure, if only as a juvenile trait. The common occurrence of this vascular tissue in the Australian radiation and its presence in *Physignathus* is best explained by considering it a primitive feature.

Several members of the *Chlamydosaurus* group were observed raising a dorsal crest. In these species, *L. gilberti*, *A. muricatus*, *A. nobbi* and *D. australis*, the crest was raised for extended periods, and the erection of the crest took several minutes. Gibbons (1979) reported crest erection in the rock-dwelling *Ctenophorus* of South Australia (*C. decresii*, *C. fionni* and *C. vadnappa*). Hudson (1979) reported similar behaviour in *C. pictus*. Crest erection in *Ctenophorus* appears, from their descriptions, to be a more transitory phenomenon than in members of the *Chlamydosaurus* group. No morphological evidence was found to support this distinction between the two groups.

Several Australian genera appear to have lost the vascular tissue block. *Moloch* and *Chlamydosaurus* have no evidence of the feature. Species examined in the *A. barbatus*, *A. adelaidensis* and *A. maculatus* species-groups did not have any vascular tissue. However, *A. scutulatus* (of the *A. maculatus* species-group) retains the ability to raise nuchal and dorsal crests (Peterson, pers. comm.) and probably retains the tissue block. Vascular tissue in juveniles of animals which do not possess the structure as adults suggests that juveniles should be examined before drawing conclusions on the basis of this feature.

The vascular tissue block is subject to sexual dimorphism in all species where both sexes were examined, the structure being better developed in the male. The degree of dimorphism varies considerably. *Lophognathus* males have a very large vascular tissue block while adult females apparently have none. By contrast, both sexes of *C. decresii* have a small block. More work is needed before much taxonomic significance can be attached to these differences, but sexual dimorphism of the structure appears to be weaker in the *Ctenophorus* group.

The female *A. cristatus* examined had a far larger vascular tissue block than any other female examined. This feature helps to distinguish this species from all other Australian agamids.

The ontogenetic disappearance of vascular tissue in *Physignathus* may be related to a modification of the trunk vertebrae. The large male examined had greatly elongated neural spines, and these were closely adherent to the subdermal fascia. This elongation had the external effect of compressing the body form by raising a permanent vertebral crest. Internally the longer spines had the effect of reducing the height of the central connective tissue block, and the vascular tissue of juveniles was apparently lost in the adult.

8. Skin Folds.

The presence of a gular fold has been used in agamid taxonomy at least since Boulenger (1885), who used the presence of a gular fold to distinguish *Gonocephalus* from *Acanthosaura*, *Salea*, *Calotes* and *Chelosania*. Gray (1845) had earlier noted the presence of a gular fold in several higher categories of his synopsis, but did not use the feature diagnostically. Loveridge (1934) noted the absence of a gular fold in *Diporiphora bilineata*, which helped to distinguish the species from *D. australis*. More recently Storr (1974) expanded the use of skin folds in *Diporiphora* taxonomy by introducing the presence of postauricular and scapular folds as diagnostic characters.

a. Postauricular Fold (Fig. 1).

Chelosania possessed five or six deep furrows in the skin of the postauricular area. The uppermost of these ran from the posterior limit of the characteristically triangular ear aperture. *Chelosania* had a sunken tympanum, with a large skin fold both above and below the tympanum. These skin folds contacted each other near the posterior limit of the tympanum and continued posterosuperiorly into the neck region as a distinctive furrow. Beneath this groove four or five similar furrows ran in parallel, separated from each other by a series of skin folds each of which presented a row of squarish, tubercular scales. The skin of this area was mobile, and the furrows could be opened widely with the application of relatively light pressure.

The other Australian agamids examined were divisible into two groups on the basis of the skin in the postauricular region. In the *Chlamydosaurus* group the skin was relatively immobile, and postauricular folds, when present, were distinct. In other groups the skin of this area was loose. In life this skin allowed lateral movement of the head, and was often without folds. In preserved specimens, however, the skin was often thrown into folds which then appeared as distinct structures. A postauricular fold was commonly recorded as absent in only three groups; *Diporiphora*, and the *A. maculatus* and *A. cristatus* species-groups. Only postauricular folds consistently present are described below.

A distinctive postauricular fold occurred in *A. muricatus*, *A. nobbi*, *Caimanops*, and those specimens of *Diporiphora* scored as possessing one. This fold ran posterosuperiorly from near the posterior limit of the mandibular musculature. The fold did not extend ventrally below the level of the mouth. This fold was weakly developed in many *Diporiphora*, and absent in most *D. bilineata*. *Lophognathus* possessed a similar fold, but this was more posteriorly placed, and usually continued into the lateral part of the gular region as a small fold anterior to the prominent transverse gular fold.

A postauricular fold of the type seen in the other members of the *Chlamydosaurus* group was entirely absent in *Chlamydosaurus*. The fold may have been incorporated into the lateral part of the frill, which extended to above the level of the tympanum. This lateral extension of the frill was scored as a postauricular fold, as this skin fold separated the tympanum and scapular fold, the position occupied by other postauricular folds.

A postauricular fold was recorded in all members of *Ctenophorus*. This fold was associated with a roughly vertically aligned group of tubercles. The postauricular folds and tubercles were less distinct in *C. pictus*.

Members of the *A. barbatus* species-group possessed a distinct posterosuperior skin fold behind the tympanum. This was the lateral continuation of the "beard", and bore a series of scales modified as elongate spines in some species.

b. Gular and Scapular Folds.

The gular and scapular folds were continuous when both were present, and are therefore considered together. The results of scoring the presence of these folds are tabulated in Table 14.

Chelosania possessed strong scapular folds on either side, but ventrally these folds extended posteriorly in the gular region and did not meet in the midline. The laterally compressed dewlap, or gular pouch, raised a longitudinal fold of skin which ended posteriorly at the same point.

In *Gonocephalus spinipes* the gular fold was present, but was narrowest at the mid-ventral point, and in this respect was similar to *Chelosania*.

Among the endemic Australian agamids only *Diporiphora* showed any significant variation in the development of the gular and scapular folds. *D. bilineata* and *D. magna* entirely lacked a gular fold. Both these species retained a scapular fold to some extent. *D. magna* characteristically had a prominent scapular fold, but only occasional specimens of *D. bilineata* retained a distinct scapular fold. In *D. winneckei* two individuals were recorded as lacking a gular fold, but all 13 individuals possessed a scapular fold.

A. barbatus possessed a modification of the scapular fold. In large specimens a group of spines at the uppermost limit of the scapular fold became raised by a fatty deposit. This elevation became quite prominent in aged specimens of most species of the species-group. No effort was made to compare the varying degree of development between species of the group. The tissue raising the tubercle was identified as fat by dis-

Table 14. Skin Folds.

Species	GF		SSF		SAF	
	0	1	0	1	0	1
Chelosania	6	-	-	6	-	6
Gonocephalus	1	2	-	3	2	1
Physignathus	1	11	1	11	9	3
Moloch	-	10	3	7	10	-
T. cephalus	-	8	-	8	8	-
T. intima	-	12	-	12	10	2
T. lineata	1	2	1	2	3	-
T. parviceps	-	4	-	4	4	-
T. tetraporophora	-	16	-	16	16	-
A. adelaidensis	-	16	-	16	11	5
A. diemensis	-	46	1	45	22	24
A. muricatus	-	12	-	12	-	12
A. nobbi	-	16	1	15	4	12
Caimanops	-	23	-	23	1	22
Chlamydosaurus	-	14	-	14	2	12
D. albilabris	-	14	-	14	2	12
D. australis	-	11	-	11	9	2
D. bennettii	-	13	1	12	8	5
D. bilineata	29	-	25	3	29	-
D. lalliae	-	10	-	10	8	2
D. linga	-	1	-	1	-	1
D. magna	12	-	-	12	8	4
D. superba	1	-	1	-	-	1
D. winneckei	2	11	-	13	6	7
L. gilberti	-	34	-	34	5	29
L. longirostris	-	12	-	12	3	9
L. temporalis	-	12	-	12	4	8
C. decresii	-	14	-	14	4	10
C. fionni	-	13	-	13	5	8
C. ornatus	-	10	-	10	5	5
C. pictus	-	21	-	21	1	20
C. rufescens	-	2	-	2	1	1
C. vadnappa	-	3	-	3	-	3
A. maculatus	-	5	-	5	4	1
A. fordi	-	12	-	12	12	-
A. isolepis	-	62	-	62	58	4
A. scutulatus	-	4	-	4	2	2
A. cristatus	-	19	-	19	12	7
A. caudicinctus	-	31	-	31	31	-
A. reticulatus	-	8	-	8	-	8
A. clayi	-	6	-	6	1	5
A. gibba	-	12	-	12	-	12
A. maculosus	-	10	-	10	10	-
A. nuchalis	2	38	-	39	5	35
A. barbatus	-	21	-	21	1	20
A. minor	-	5	-	5	-	5
A. mitchelli	-	1	-	1	-	1
A. vitticeps	-	16	-	16	5	11

0 = absent. 1 = present.

section. Fat in the abdominal cavity agreed closely in appearance to the tissue within the tubercle, although the latter possibly contained more fibrous tissue.

c. Supra-auricular Fold.

The results of scoring the presence of a supra-auricular fold are summarised in Table 14. There was considerable intraspecific variation in this feature.

Only four species were recorded as never possessing a supra-auricular fold. These were *Diporiphora bilineata*, *A. fordi*, *Moloch horridus* and *A. caudicinctus*.

Juveniles of almost all species were recorded as lacking a supra-auricular fold. Large specimens of most species developed a sunken tympanum, with the result that they were scored as possessing a supra-auricular fold.

Only three species had all specimens examined scored as possessing a supra-auricular fold. These were *A. muricatus*, *A. gibba* and *A. reticulatus*.

Discussion.

The postauricular furrows of *Chelosania* are both distinctive and unique. They serve to distinguish *Chelosania* from all other agamids.

The *Chlamydosaurus* group differs from the other endemic Australian groups in having distinct postauricular folds in some species of most genera. The postauricular scales in members of the *Chlamydosaurus* group are relatively larger than in most other endemic agamids. This could cause the more rigid skin of the group, and the more consistent recording of postauricular folds.

In some other groups consistent arrangements of spines in the postauricular area raise skin folds in otherwise loose skin (see PAS, pp. 97-102). All members of the A. barbatus species-group possess spines in this area. The interspecific variation in the arrangement of these spines has been used by Badham (1976) in her revision of the group.

Ctenophorus possesses a distinctive series of tubercles raising a postauricular fold. This character is shared by C. pictus, helping to confirm the placement of that species in Ctenophorus.

Boulenger (1885) used the lack of a gular fold in Chelosania as a diagnostic character in separating it from Gonocephalus. Gray (1845) attributed "a slight cross fold behind" to the throat of Chelosania. The strong scapular folds of each side approach each other closely, and Gray apparently failed to notice the interruption between the folds of either side. The fact that one of three Gonocephalus examined in this study had a similar condition to Chelosania suggests that the gular fold is not a good distinguishing feature between the genera.

The A. barbatus species-group has a further distinctive character in the spinose tubercle of the shoulder. The fatty deposit raising the tubercle at this point in adults is shared by no other Australian species. The character develops ontogenetically and is barely noticeable in hatchlings. It is therefore not a good diagnostic character. It does add to the weight of evidence suggesting that the A. barbatus species-group has diverged quite remarkably from the other endemic agamids.

The character of a supra-auricular fold in fact recorded whether the tympanum was superficial or sunken. The character is of doubtful taxonomic significance, as in most species-groups the tympanum is superficial in hatchlings but becomes more deeply placed during ontogeny.

Diporiphora bilineata was the smallest member of the Chlamydosaurus group examined. A. fordi was the smallest species of the A. maculatus species-group. Neither exhibited a supra-auricular fold.

Cogger (1961) established that *A. fordi* was a neotenic form derived from a species similar to *A. maculatus*. As mentioned above, hatchlings of most species normally have a superficial tympanum. The complete absence of a supra-auricular fold in *A. fordi* is probably an indication of its neotenic nature. It is quite likely that the evolution of small size in *D. bilineata* has also resulted in the retention of the same juvenile characteristic in the adult.

The other two species recorded as always lacking a supra-auricular fold were *Moloch* and *A. caudicinctus*. The latter is considerably smaller than the closely related *A. cristatus*. Storr (1967) suggested that at least some populations of *A. caudicinctus* had a normal life span of only slightly more than a year. The development of this "annual" life cycle and a smaller adult size may have resulted in the retention of some juvenile characters in the adult of the species.

The absence of a supra-auricular fold in *Moloch* is most likely another indication of the extraordinary divergence of the genus from other agamids.

9. Enlarged Scale Rows of Head.

Badham (1976) used several scale characters to distinguish between members of the *A. barbatus* species-group. These characters included a transverse row of spinous scales in the gular region, and a series of spines on the occipital region, here termed an occipital crest (Fig. 2). Both these features varied in the degree of development between members of the species-group. A further character, a postauricular scale row, is introduced in this study.

a. Postauricular Scale Row.

The results of scoring the presence of a postauricular scale row are presented in Table 15. Consistent and distinctive postauricular scale rows typified relatively few groups of species.

Chelosania and *Chlamydosaurus* lacked any enlarged tubercles or spines in the postauricular area.

Physignathus possessed a distinct horizontal scale row running posteriorly from the upper margin of the tympanum. A further series of enlarged tubercles was arranged in a posterosuperior direction below and behind the tympanum. Both series were normally interrupted by smaller scales.

In *Ctenophorus* a vertical row of enlarged tubercles presented on the postauricular fold. These scales were not prominently enlarged, but were often paler than the surrounding scales and were therefore conspicuous. *C. pictus* had less conspicuous tubercles; most specimens examined were scored as possessing a discontinuous scale row.

Members of the *A. barbatus* species-group possessed a continuous scale row in the postauricular region. This presented on the lateral continuation of the beard, and ran in a posterosuperior direction. As with the fold, the development of the spinous scale series varied among

Table 15. Enlarged Scale Rows of Head.

Species	PAS			OC		GSR		
	0	1	2	0	1	0	1	2
Chelosania	6	0	0	6	0	6	0	0
Gonocephalus	0	3	0	3	0	3	0	0
Physignathus	0	2	10	12	0	12	0	0
Moloch	0	0	10	0	10	6	4	0
T. cephalus	0	2	6	8	0	8	0	0
T. intima	0	6	6	10	2	12	0	0
T. lineata	0	2	0	3	0	3	0	0
T. parviceps	0	0	4	4	0	4	0	0
T. tetraporophora	0	7	9	16	0	16	0	0
T. uniformis	1	0	0	1	0	1	0	0
A. adelaidensis	0	10	6	14	2	16	0	0
A. diemensis	0	22	24	31	15	42	4	0
A. muricatus	0	0	11	12	0	12	0	0
A. nobbi	0	5	11	16	0	16	0	0
Caimanops	0	14	9	23	0	23	0	0
Chlamydosaurus	14	0	0	13	1	14	0	0
D. albilabris	1	9	4	14	0	14	0	0
D. australis	1	7	3	11	0	11	0	0
D. bennettii	5	8	0	13	0	13	0	0
D. bilineata	9	20	0	29	0	29	0	0
D. lalliae	7	3	0	10	0	10	0	0
D. linga	1	0	0	1	0	1	0	0
D. magna	5	7	0	12	0	12	0	0
D. superba	1	0	0	1	0	1	0	0
D. winneckei	12	1	0	13	0	13	0	0
L. gilberti	0	7	27	34	0	34	0	0
L. longirostris	0	4	8	12	0	12	0	0
L. temporalis	0	2	10	12	0	12	0	0
C. decresii	0	4	10	14	0	14	0	0
C. fionni	0	4	9	13	0	13	0	0
C. ornatus	0	3	7	10	0	10	0	0
C. pictus	0	16	5	21	0	21	0	0
C. rufescens	0	1	1	2	0	2	0	0
C. vadnappa	0	3	0	3	0	3	0	0
A. maculatus	0	4	1	5	0	5	0	0
A. fordi	0	10	2	12	0	12	0	0
A. isolepis	56	5	1	62	0	62	0	0
A. scutulatus	0	2	2	3	1	4	0	0
A. cristatus	0	19	0	19	0	19	0	0
A. caudicinctus	11	20	0	31	0	31	0	0
A. reticulatus	0	5	3	8	0	8	0	0
A. clayi	3	3	0	6	0	6	0	0
A. gibba	0	12	0	12	0	12	0	0
A. maculosus	0	9	1	10	0	10	0	0
A. nuchalis	1	23	16	39	1	40	0	0
A. barbatus	0	1	20	0	21	1	2	18
A. minor	0	0	5	0	5	0	5	0
A. mitchelli	0	0	1	0	1	1	0	0
A. vitticeps	0	0	16	0	16	0	7	9

the members of the species-group.

All *Moloch* were scored as possessing a continuous postauricular scale row. In fact this was a reflection of the extreme development of spines in this genus, rather than the possession of a distinct scale row comparable with any other dragon.

All other species had at least some individuals with scattered tubercles or spines in the postauricular region. The number and size of these enlarged scales varied intraspecifically.

b. Gular Scale Row.

All species of the *A. barbatus* species-group possessed a gular scale row, except possibly *A. mitchelli* (Table 15), of which only one specimen was examined. In a similar undescribed species the spiny gular scale row was almost lost, but at least some specimens retained an incomplete row. This species was able to erect a small "beard" like that of *A. barbatus*.

An incomplete gular scale row was scored as present in four of the 46 *A. diemensis* examined. In these specimens a few spinous scales were present immediately below the angle of the jaw. Four *Moloch* had some spines in the same area. These records represented the only occurrence of the gular scale row outside the *A. barbatus* species-group.

c. Occipital Crest.

An occipital crest is a characteristic of the *A. barbatus* species-group, and was scored as present in all specimens of the group examined (Table 15). All *Moloch* were also scored as possessing an occipital crest. Apart from these, no species invariably possessed an occipital crest. Both species of the *A. adelaidensis* species-group and *T. intima* had some individuals with an occipital crest. In these species the crest was formed by a series of mucronate to weakly spinose scales, arranged in a series near the posteromedial margin of the parietal bone.

d. Loreal Scale Row.

The loreal scale row was a characteristic series of elongate scales running from behind the nostril, beneath the eye, and then back and upwards to above the ear (Fig. 1). These scales were enlarged and strongly keeled, but did not imbricate. The keels of contiguous scales were aligned to form a ridge running the course of the series.

No systematic attempt was made to record the presence of a loreal scale row from all specimens examined. However, the scale of this series directly beneath the orbit was included in the suborbital scale count (see p. 24). The comparative development of the scale series was therefore noted from most specimens.

The loreal scale row was characteristic of *Ctenophorus*, the *A. maculatus*, *A. cristatus* and *A. reticulatus* species-groups. Juvenile *A. barbatus* possessed the feature, but differential growth of scales during development obscured the scale row as an adult character. No adult of the *A. barbatus* species-group was observed to possess a loreal scale row, but the feature was still distinguishable in some subadults.

Chlamydosaurus lacked a loreal scale row. In other members of the *Chlamydosaurus* group, and in all members of the *Tympanocryptis* group the loreal scale row was obscure. In most of these species there was a series of scales similar to the anterior half of the row, but these scales were not strongly differentiated in size or form from other scales in the area. In occasional specimens of *L. gilberti* and *A. muricatus* a number of larger scales were present along the expected course of the loreal scale row above the ear, perhaps representing the posterior part of a discontinuous loreal scale row. In most specimens the row did not continue behind the posterior margin of the eye.

Discussion.

Many agamids possess spinous scales in the postauricular region. This probably has the effect of breaking up the regular outline of a lizard's head. Only a few genera possess a regular series of scales in the postauricular region.

In the *Chlamydosaurus* group a postauricular scale row is prominent only in *A. muricatus*. The same structure is evident, but weakly developed in *A. nobbi* and *Caimanops*. The postauricular tubercle used by Storr (1974) to distinguish *D. bilineata* is probably homologous with this scale series. Some other species of *Diporiphora* possess a more distinct series, but most have lost it. The series in *Lophognathus* differs mainly in being more posteriorly placed than in the other members of this group (see PAF, p. 91).

The vertical scale row of *Ctenophorus* is distinctive and useful diagnostically. This character is useful in demonstrating the relationships of *C. pictus*. The scale row is relatively weaker in *C. pictus*, but is recognisably similar to the same feature in other *Ctenophorus*.

Members of the *A. barbatus* species-group normally possess a gular scale row which continues laterally into the postauricular region. This row of spines is probably best considered as part of the gular scale row.

The gular scale row is a characteristic of the *A. barbatus* species-group. Those records of its occurrence outside the group were from a few *A. diemensis* and *Moloch*. These species both possess very heterogeneous spiny scales, and these records are probably best interpreted as an extension of that condition to the gular region. The few scattered spines in this area are almost certainly not homologous with the well developed transverse row of spines in the *A. barbatus* species-group.

The scattered spines of the postauricular region, presumed to act as camouflage in breaking up the regular outline of the head, often extend onto the dorsum of the head. These scattered scales were sometimes scored as an occipital crest in species where the crest was usually absent, and probably resemble the type of structure from which the occipital crest developed.

The occipital crest in *A. diemensis*, *A. adelaidensis* and *Tympanocryptis* is probably not homologous with that of the *A. barbatus* species-group. In the *A. barbatus* species-group the crest approximates the posterior limit of the skull, but the scales forming the crest are not closely related to any feature of the skull. In the *Tympanocryptis* group the crest runs along the posteromedial margin of the parietal bone, and the scales forming the crest are much less spinose than those of the *A. barbatus* species-group. *T. intima* was the only species of *Tympanocryptis* recorded with an occipital crest in this study, but Houston (1978) illustrated the closely related *T. cephalus* with a specimen exhibiting a prominent occipital crest.

The structure of the occipital crest within the *A. barbatus* species-group was used by Badham (1976) as an important diagnostic character in her revision of the group. The occipital crest probably evolved from scattered spinous scales on the back of the head, not unlike the condition persisting in *A. minimus*. If this hypothesis is true, then *A. minimus* should be considered the most primitive species of the group. The other species of the species-group all have well defined occipital crests, but any attempt to attribute "advanced" status to a particular type of crest would require some evidence of the adaptive significance of different crests. Such data are wanting.

The loreal scale row occurs in most agamids. It is therefore probably best considered a primitive feature. The loss or reduction of the loreal scale row reported in the results might be better described as a modification of the other scales of the side of the head. Those species with a reduced loreal scale row have developed cheek scales which are more or less indistinguishable from those normally constituting the row. The loreal scale row is thus only obvious in species with smaller, more circular scales on the side of the head. This description fits most members of _Ctenophorus_ and the _A_. _maculatus_, _A_. _cristatus_ and _A_. _reticulatus_ species-groups, which are the groups with the most obvious loreal scale rows. Juveniles of most species have smoother scales than adults, and in consequence the loreal scale row is more obvious in juveniles.

10. Eyelid Border.

There is a prominent eyelid "fringe" in several common Australian agamids. However, Cogger (1975) appears to be the first author to mention the feature. Houston (1978) also described the fringe in a couple of species. Neither author used the character as a key character.

The eyelids of all Australian dragons were bordered by a row of modified scales. The row nearest the margin of the eyelid was formed of flattened quadrangular scales similar to other scales of the eyelid. The row of scales abutting these was modified in one of three ways. In most species this row of scales formed a ridge parallel with the margin of the eyelid. This ridge was more or less continuous, with the keels of contiguous scales abutting one another. In some species the keel of each scale was triangular, giving a serrated appearance to the eyelid. In still other species the projection of each scale was extended in an elongate spine, forming a distinct fringe.

The results of scoring the presence of a fringe on both upper and lower eyelids are presented in Table 16. The original method of scoring did not differentiate between fringes formed by a discontinuous ridge or by a series of spines. There were also apparent ontogenetic differences which are described below.

In all species examined the ridge or fringe on the eyelid became relatively larger during growth. The two A. diemensis and single A. nobbi scored as having no ridge on the upper eyelid (Table 16) were hatchlings.

Species which typically had continuous eyelid ridges sometimes developed discontinuities of the ridge in large individuals. This phenomenon resulted in some Physignathus and some members of both the Chlamydosaurus and Tympanocryptis groups being scored as possessing a

Table 16. Eyelid Fringe.

Species	UELD			LELD		
	0	1	2	0	1	2
Chelosania	0	6	0	0	6	0
Gonocephalus	0	3	0	0	3	0
Physignathus	0	10	2	0	11	1
Moloch	0	10	0	0	10	0
T. cephalus	0	8	0	0	6	2
T. intima	0	12	0	0	11	1
T. lineata	0	3	0	0	3	0
T. parviceps	0	4	0	0	4	0
T. tetraporophora	0	16	0	0	15	1
T. uniformis	0	1	0	0	1	0
A. adelaidensis	0	16	0	0	16	0
A. diemensis	2	44	0	0	46	0
A. muricatus	0	12	0	0	12	0
A. nobbi	1	15	0	0	16	0
Caimanops	0	23	0	0	22	1
Chlamydosaurus	0	14	0	0	12	2
D. albilabris	0	14	0	0	14	0
D. australis	0	11	0	0	11	0
D. bennettii	0	13	0	0	13	0
D. bilineata	0	29	0	0	29	0
D. lalliae	0	10	0	0	10	0
D. linga	0	1	0	0	1	0
D. magna	0	12	0	0	12	0
D. superba	0	1	0	0	1	0
D. winneckei	0	13	0	0	13	0
L. gilberti	0	34	0	0	33	1
L. longirostris	0	12	0	0	11	1
L. temporalis	0	12	0	0	12	0
C. decresii	0	11	3	0	3	11
C. fionni	0	11	2	0	4	9
C. ornatus	0	4	6	0	0	10
C. pictus	0	21	0	0	2	19
C. rufescens	0	2	0	0	0	2
C. vadnappa	0	2	1	0	0	3
A. maculatus	0	5	0	0	5	0
A. fordi	0	12	0	0	12	0
A. isolepis	0	59	3	0	47	15
A. scutulatus	0	2	2	0	0	4
A. cristatus	0	14	5	0	2	17
A. caudicinctus	0	21	10	0	4	27
A. reticulatus	0	8	0	0	0	8
A. clayi	0	6	0	0	2	4
A. gibba	0	12	0	0	0	12
A. maculosus	0	10	0	0	0	10
A. nuchalis	0	38	1	0	0	39
A. barbatus	0	20	0	0	1	19
A. minor	0	5	0	0	1	4
A. mitchelli	0	1	0	0	0	1
A. vitticeps	0	16	0	0	0	16

marginal fringe. In fact no member of these groups possessed pointed processes on the eyelid margin.

Those specimens scored as possessing a fringe on the upper eyelid in fact possessed an interrupted ridge. All such specimens were adults. Only C. ornatus had more specimens with an upper eyelid fringe than without (Table 16).

The modified scales of the lower eyelid of some species possessed triangular keels forming a serrated fringe. This feature was present in all species of Ctenophorus and in A. cristatus and A. caudicinctus. The triangular keels became larger ontogenetically, and some juveniles of these species were scored as not possessing a fringe.

The A. reticulatus and A. barbatus species-groups had a series of spines on the lower eyelid. These spines, like the ridges of other species, became relatively larger ontogenetically. The few individuals scored as not possessing a fringe were hatchlings, where the spines were shorter than the width of the scale (see LELD, p. 30).

Discussion.

The borders of the lower eyelid of all Australian agamids may be categorised into two distinct types. Most species possess a scale ridge on the row of scales one removed from the margin of the eyelid. This ridge becomes wider and less continuous with increasing size, and occasional specimens of all species greater than about 60 or 70 mm in snout-vent length tend to have an interrupted scale ridge. Those species with triangular keels may be included in this first group (e.g. C. decresii). The second type of lower eyelid border consists of a series of distinct, slender, conical spines on the corresponding scale row. These also become better developed as the animal increases in size.

The more common type of eyelid border occurs in both Asian and most Australian endemic species. This condition should therefore be considered primitive. The derived condition of conical spines is restricted to the *A. reticulatus* species-group and the *A. barbatus* species-group. This character strongly supports the theory that the *A. barbatus* and *A. reticulatus* species-groups are related. The lower eyelid border in the *A. barbatus* species-group is prominent and characteristic. It is therefore surprising to find no mention of the character in the literature.

The literature relating to eyelid borders is fragmentary. Cogger (1975) noted the type of eyelid fringe in a large number of species, but his reports were included in individual species descriptions, and no comparative statements were made. Houston (1978) mentioned a lower eyelid fringe for *A. nuchalis* and *A. reticulatus*, but did not for the other members of the *A. reticulatus* species-group. No author has noted or attempted to use the clear dichotomy found in the present study as a taxonomic character.

Most species with a lower eyelid fringe of triangular keels had some specimens with a discontinuous upper eyelid ridge. Those species with a fringe of spinous processes, however, had almost no specimens with such a ridge. This was true also for *C. pictus*, a burrowing species. It is possible that a more prominent lower eyelid fringe and a narrow upper eyelid scale ridge are an adaptation to burrowing. This would be consistent with the condition seen in the predominantly burrowing *A. reticulatus* species-group, and would suggest that *C. pictus* is beginning a parallel development. The *A. barbatus* species-group are not habitual burrowers, and so the same selective pressures cannot be invoked to explain the condition seen in the group. The fringe is better explained as a legacy of its relationship with the *A. reticulatus* species-group.

11. Head Scale Counts.

In squamates with large head shields the number and arrangement of these scales provide convenient and widely accepted taxonomic characters. In families with small, irregular scales these characters are largely irrelevant. The use of similar characters has, therefore, been neglected in the agamids.

Storr (1964) appears to be the first to use a head scale count in Australian agamid taxonomy. He distinguished Tympanocryptis parviceps from others in the genus by the lower number of scales separating the nasal from the labial scales. This character was adopted by Cogger (1975). Storr (1964, 1965, 1966, 1967, 1974, 1977) has also reported the number of supralabial scales for many species, but has not used these as key characters. Witten (1972) also reported numbers of supralabial scales.

a. Prenasal Scale Count (PNS)(Figs. 1, 16).

All Moloch possessed more prenasal scales than any other specimen of any other species. Chelosania also had a high PNS score.

The PNS was low in Physignathus and in Lophognathus temporalis.

A. nuchalis and A. clayi had a higher PNS than other members of the A. reticulatus species-group.

b. Subnasal Scale Count (SNS)(Figs. 1, 17).

Moloch had a remarkably high SNS count. Only A. nuchalis approached the same high scores.

Two species had distinctly fewer subnasal scales. T. parviceps usually had a lower SNS score than its near relatives in Tympanocryptis and the A. adelaidensis species-group. A. maculosus had a distinctly reduced SNS score when compared with other members of the A. reticulatus species-group.

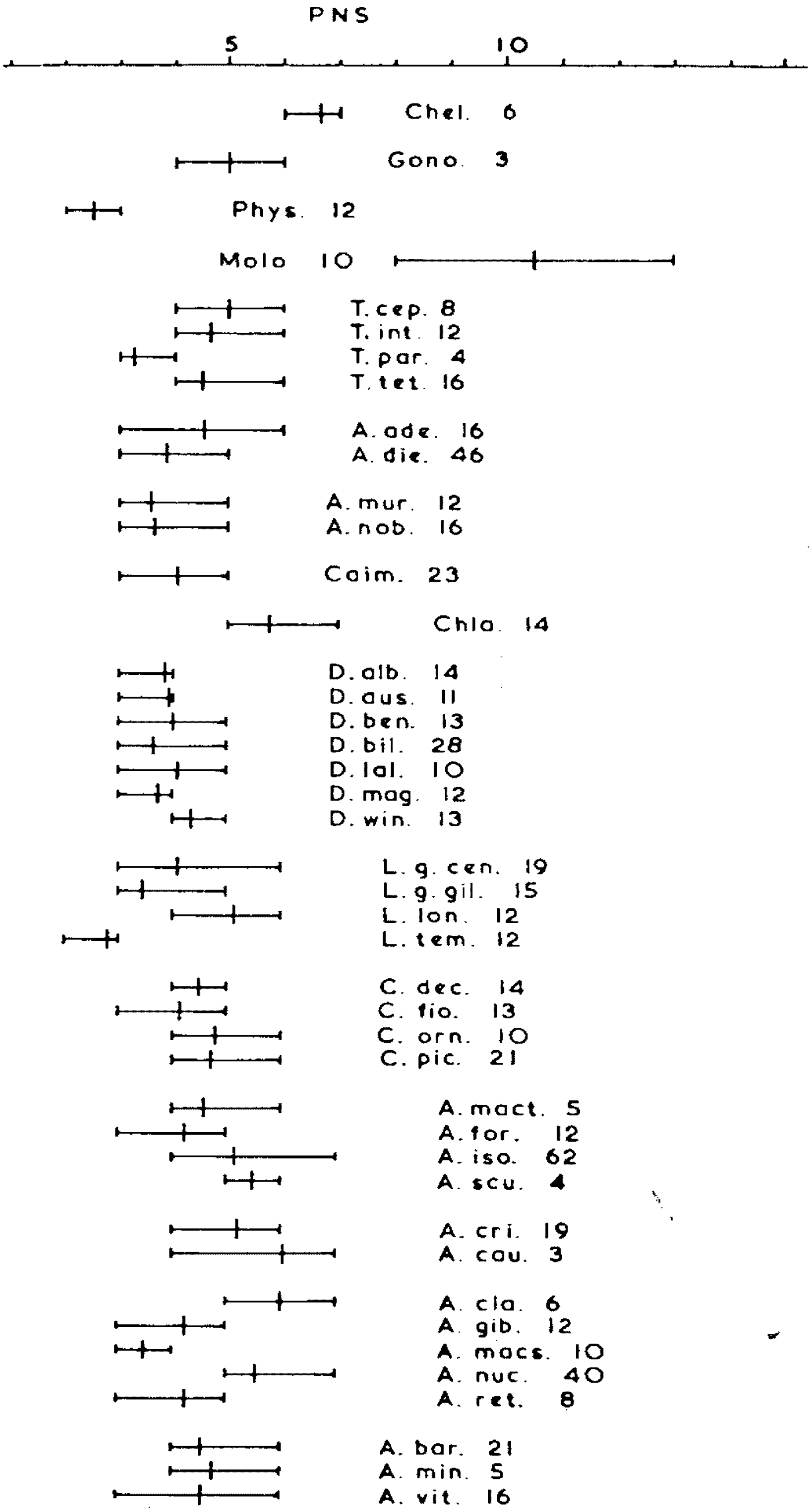


Figure 16. Prenasal Scale Counts. Symbols as for Figure 7. Chel. = *Chelosania*; Gono. = *Gonocephalus spinipes*; Molo. = *Moloch*. Other abbreviations as for Figure 7.

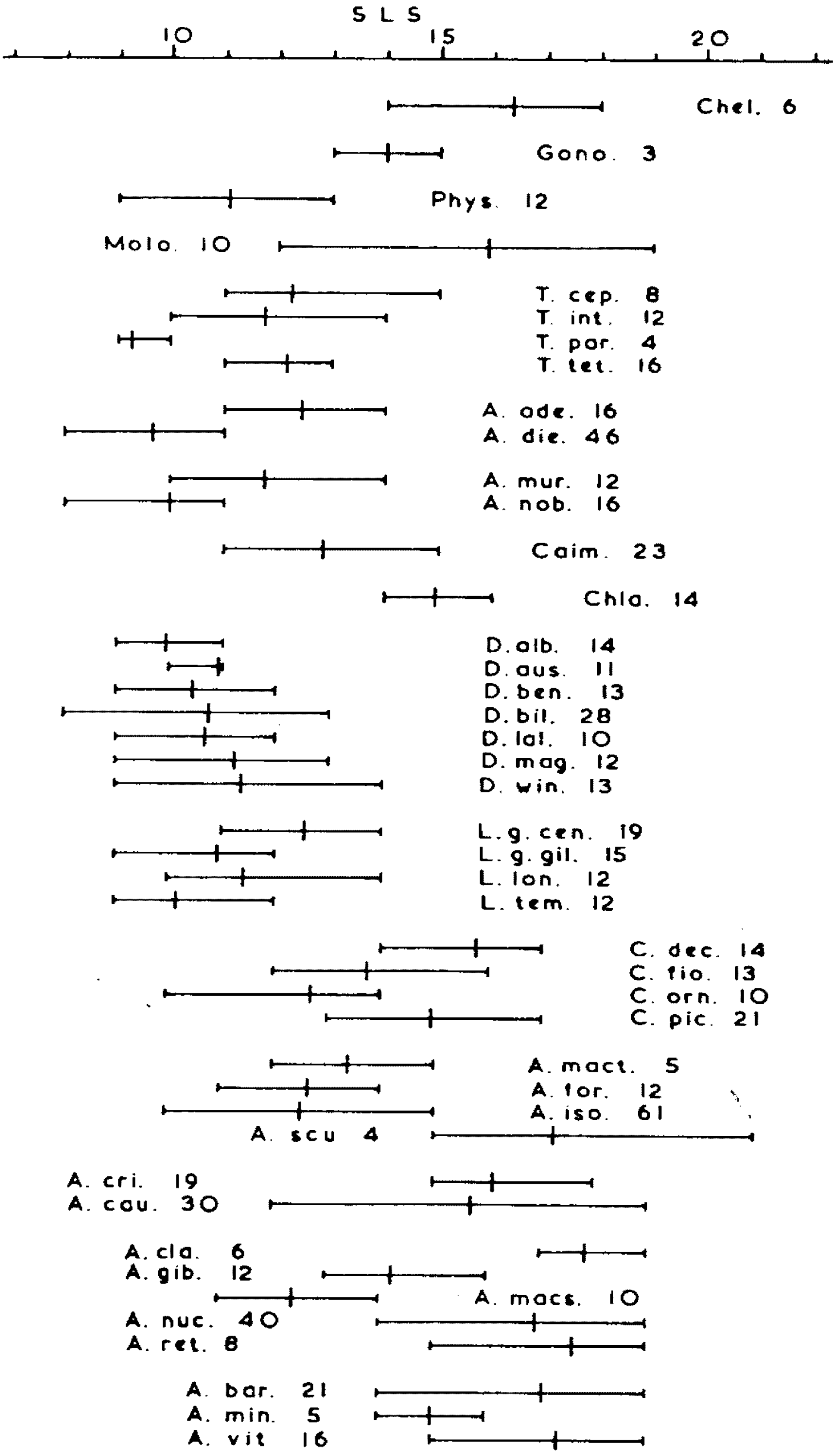


Figure 17. Subnasal Scale Counts. Symbols and abbreviations as for Figure 16.

In general Caimanops, Chlamydosaurus, Diporiphora, Lophognathus and the A. muricatus and A. barbatus species-groups had a lower SNS than other Australian agamids.

c. Inter-nasal Scales (INS)(Figs. 2, 18).

Caimanops and Moloch had relatively low INS counts. Chlamydosaurus had a very high INS count.

Great variation occurred within two groups. In the Tympanocryptis group T. parviceps had a relatively high and T. cephalus a relatively low INS count. In the A. reticulatus species-group A. clayi had high and A. maculosus and A. reticulatus low INS scores.

d. Snout-parietal Scale Count (SPS)(Figs. 2, 19).

Physignathus and Chlamydosaurus had very high SPS counts. Gonocephalus also had an SPS count higher than most agamids, but not as high as the former two genera. The only other outstanding result was that A. clayi had a much higher SPS count than other members of the A. reticulatus species-group.

e. Suborbital Scale Count (SOS)(Figs. 1, 20).

A. maculosus had a lower number of scales beneath the orbit than other members of the A. reticulatus species-group. T. parviceps had a lower SOS score than most members of the Tympanocryptis group, with only A. diemensis of that group having any specimens with an SOS count as low. T. parviceps usually had only two suborbital scales. The suborbital scale count was also low in Caimanops and D. winneckei, but was not of diagnostic use in these cases.

f. Supralabial Scale Count (SLS)(Figs. 1, 21).

Diporiphora, Lophognathus, and the A. muricatus species-group had generally lower supralabial counts than other Australian dragons. This correlated with the enlarged, elongate supralabials in these animals.

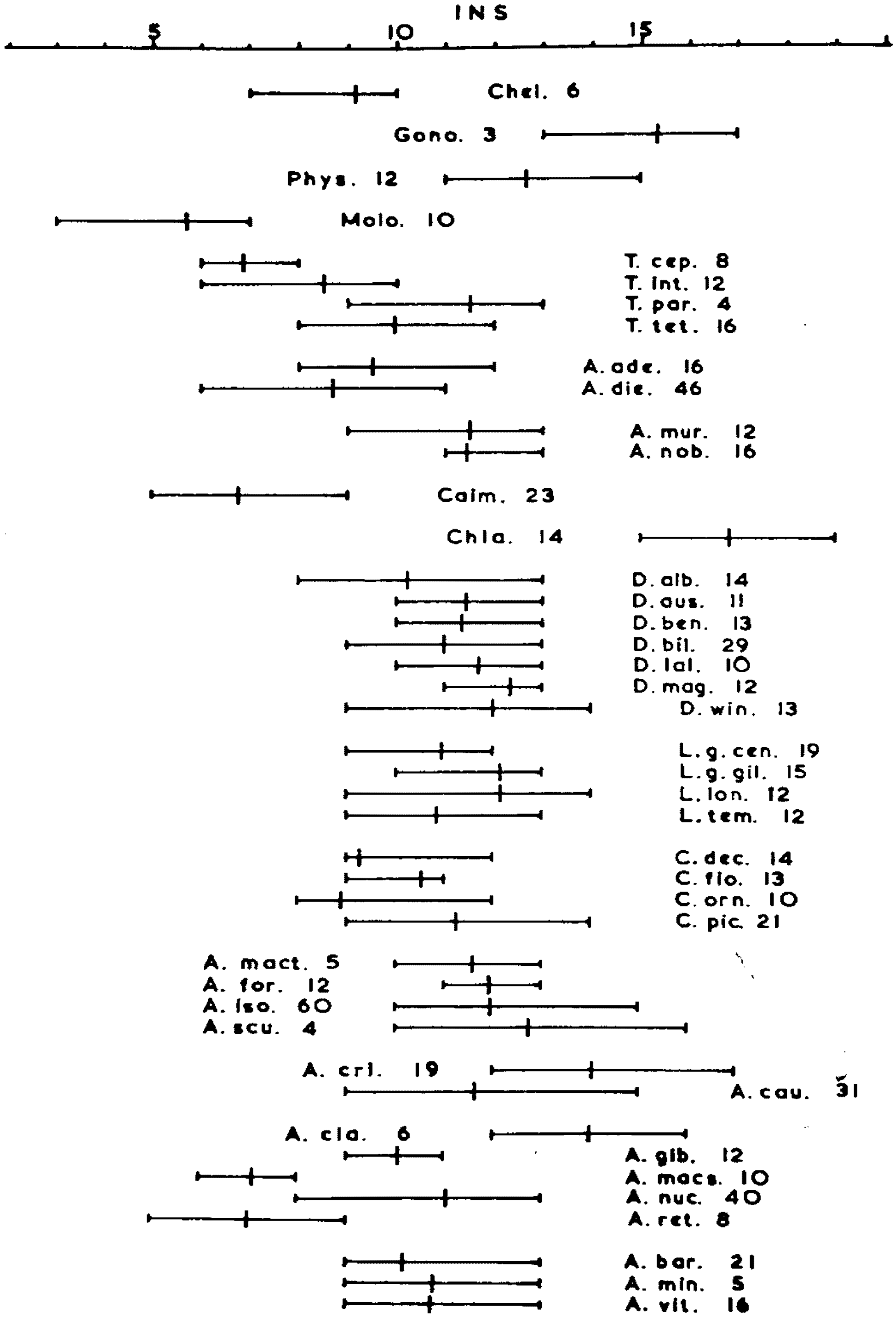


Figure 18. Inter-nasal Scale Counts. Symbols and abbreviations as for Figure 16.

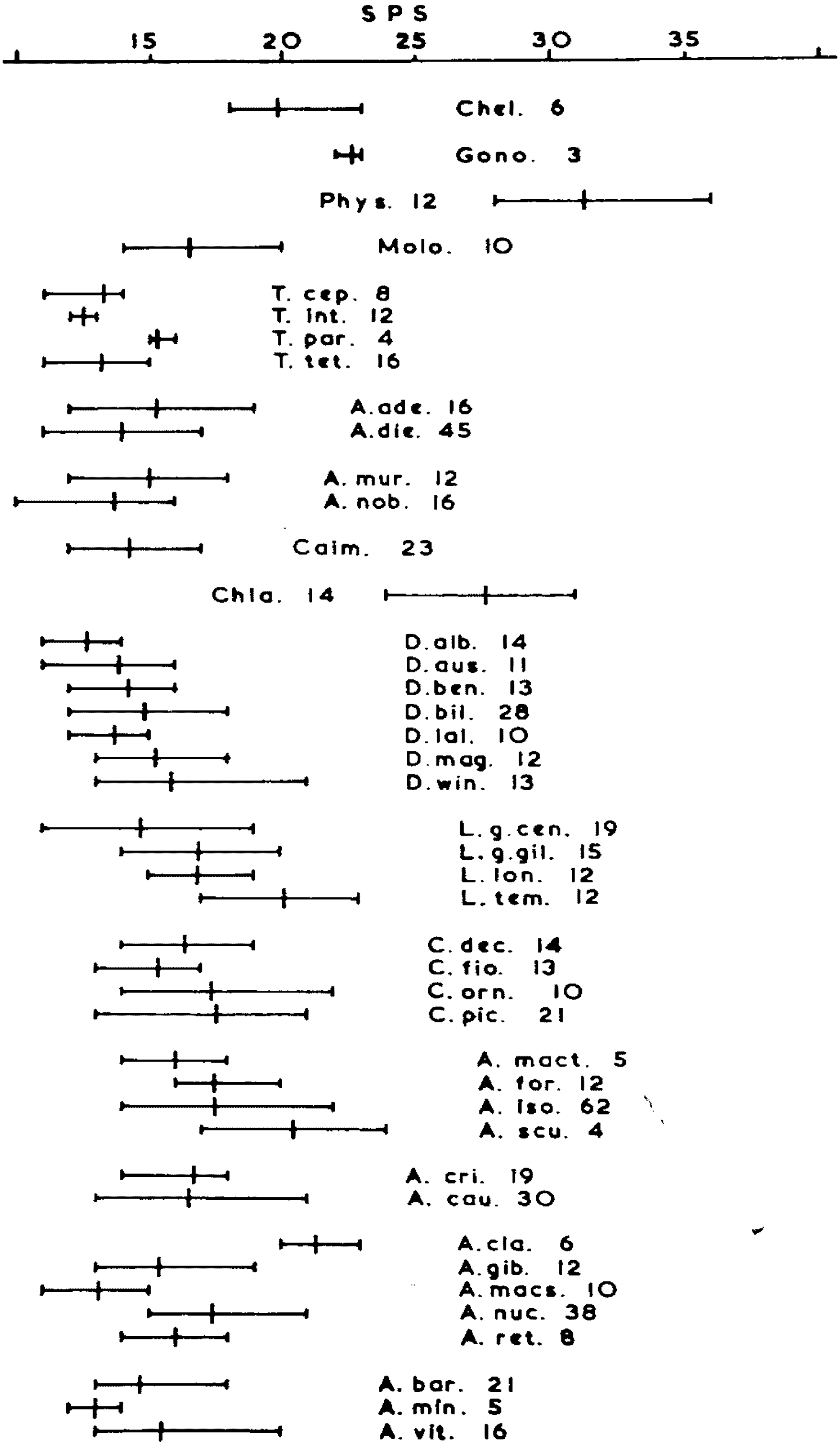


Figure 19. Snout-parietal Scale Counts. Symbols and abbreviations as for Figure 16.

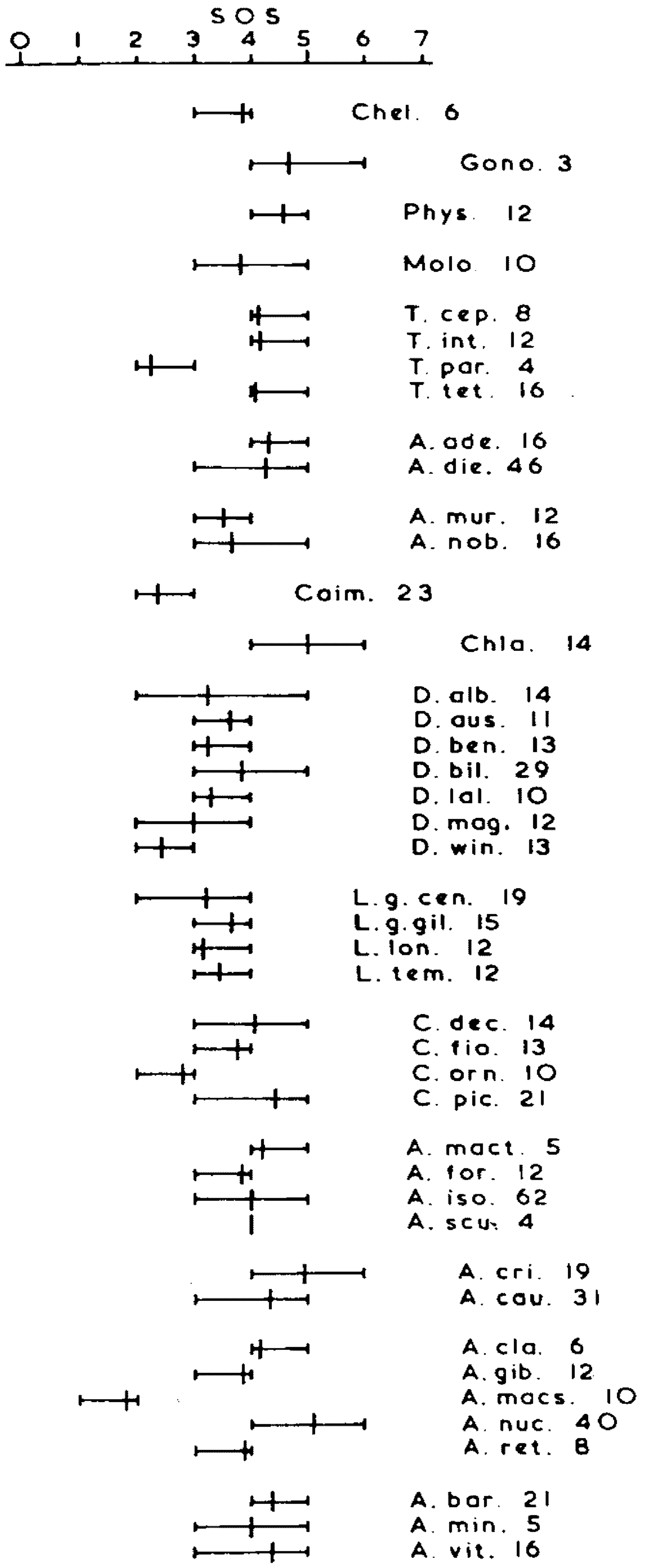


Figure 20. Suborbital Scale Counts. Symbols and abbreviations as for Figure 16.

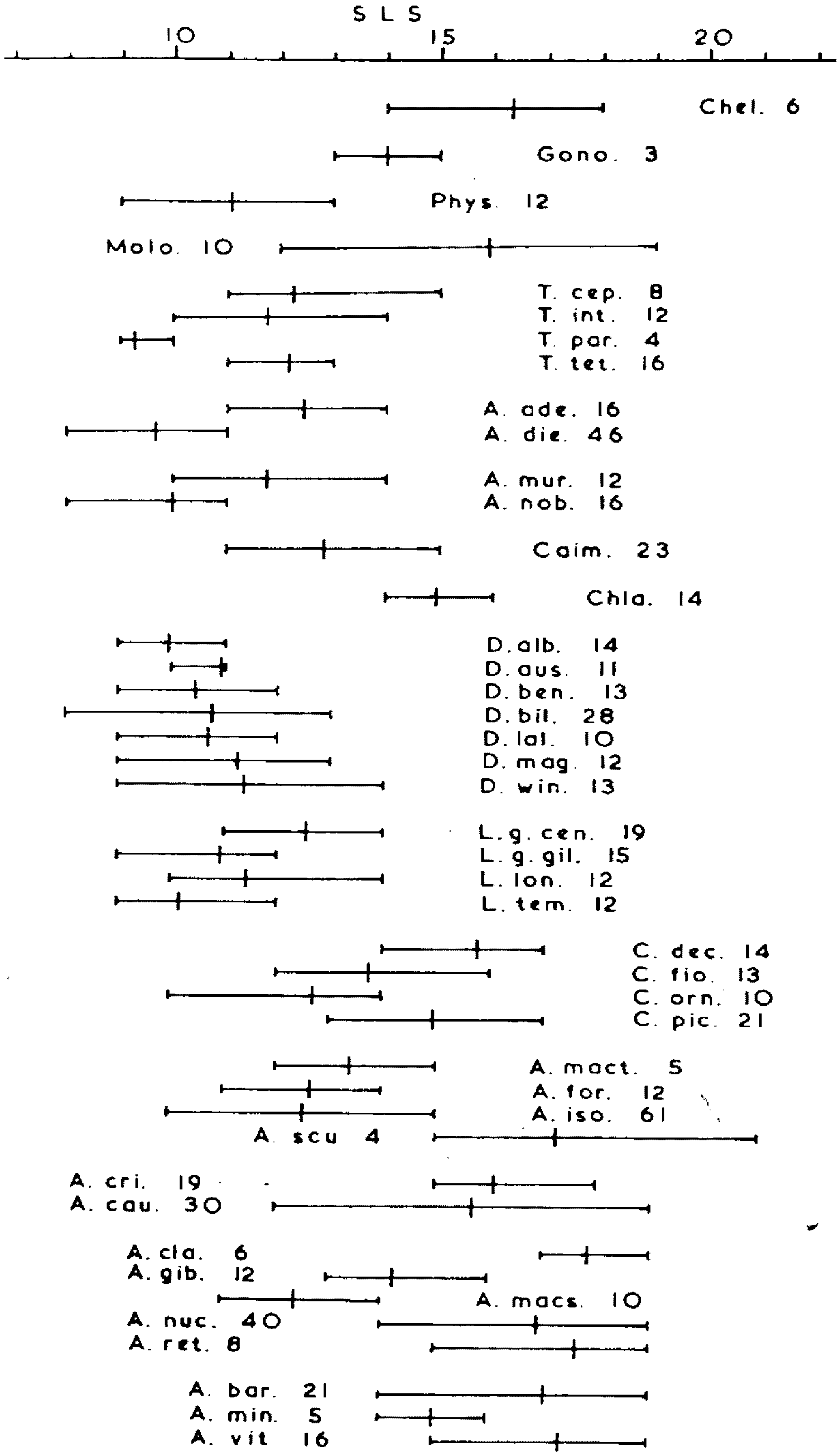


Figure 21. Supralabial Scale Counts. Symbols and abbreviations as for Figure 16.

The supralabials in Ctenophorus and in the A. maculatus, A. cristatus A. reticulatus and A. barbatus species-groups were similar in length to the adjacent loreal scales. Consequently the number of supralabial scales in these groups was generally higher.

g. Infralabial Scale Count (ILS)(Figs. 1, 22).

The differences apparent from the supralabial scale counts were paralleled by the infralabial scale counts. The general trends outlined above were usually clearer in the infralabial scale counts.

Discussion.

Many observed differences in head scale counts were between closely related species. Such differences are of limited value in phylogenetic reconstructions. Only trends apparent at the generic level and above are discussed below.

The prenasal scale count depends heavily on the position of the nostril as well as on scale size. The nostrils in Moloch are on the dorsum of the snout, well away from the rostral, leading to the exceptionally high PNS score. This modification of the nostrils in Moloch is also revealed in a high subnasal scale count and a low inter-nasal scale count for the genus.

The dorsum of the snout in Caimanops is covered with enlarged scales. In large males the central row of scales becomes strongly keeled, forming a "rostral crest" unique to the genus. The low inter-nasal scale count recorded for Caimanops is probably related to this feature.

Generally, the Chlamydosaurus group has a lower subnasal scale count than other Australian agamids. This is probably related to the enlarged lateral head scales of the group, the apparent reason for the loss of the loreal scale row (see pp. 102-103).

Physignathus and Chlamydosaurus are the two largest agamids in

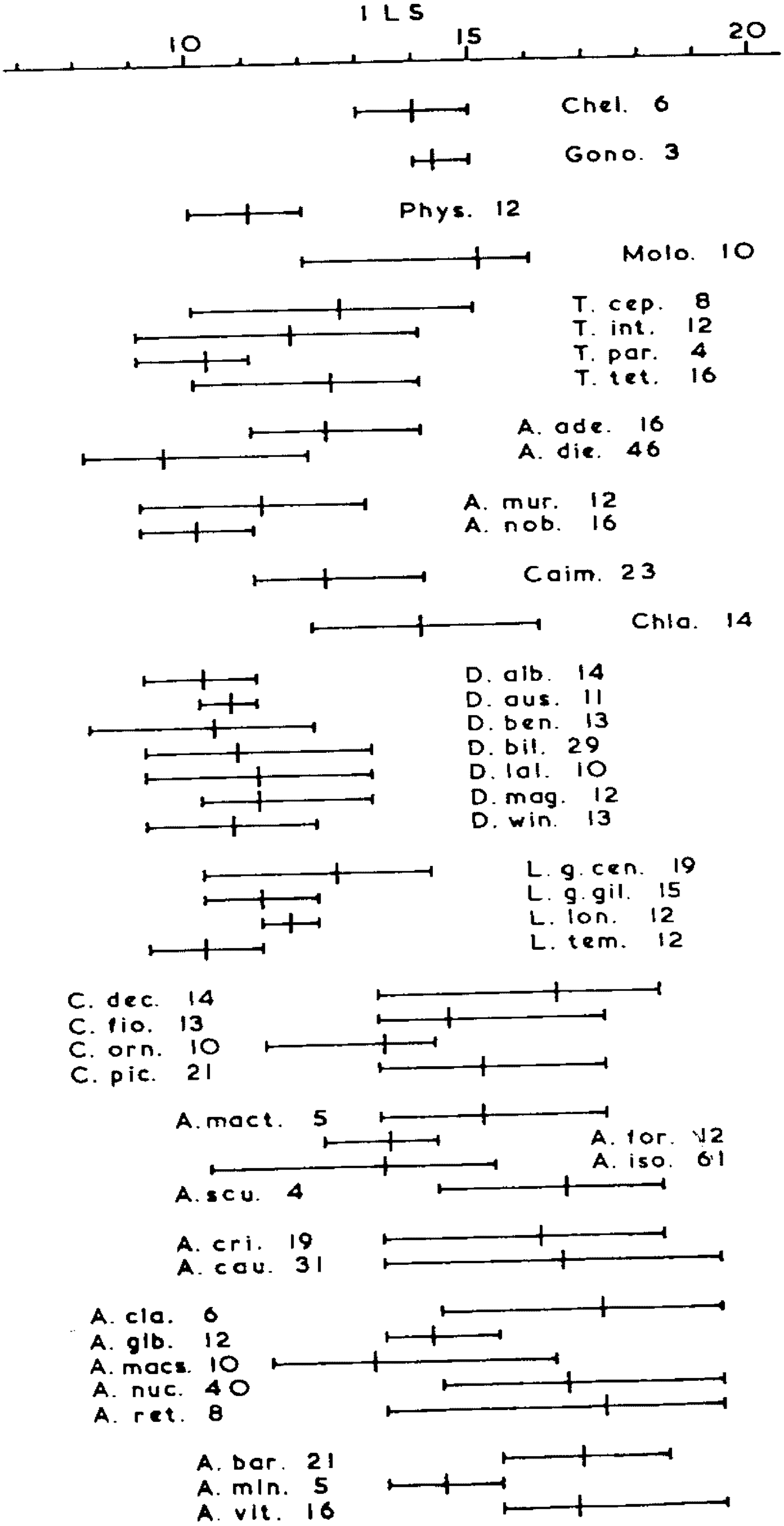


Figure 22. Infralabial Scale Counts. Symbols and abbreviations as for Figure 16.

Australia. As larger species tend to have more scales (see below) the high SPS counts for these genera are not surprising. The high INS count for *Chlamydosaurus* is probably also related to this factor.

Chelosania, *Moloch*, *Chlamydosaurus*, *Ctenophorus*, and members of the *A. maculatus*, *A. cristatus*, *A. reticulatus* and *A. barbatus* species-groups have high supralabial scale counts. Of these, *Chlamydosaurus* is a very large genus with relatively small scales. All the others have relatively unmodified supralabials, about as long as the adjacent scales. Apart from *Moloch* and *Chelosania* these species constitute the *Ctenophorus* group. The relatively unmodified supralabials shared by all species of the group help to characterise the group.

Those species with elongate supralabials and a resultant reduced supralabial count constitute the *Chlamydosaurus* and *Tympanocryptis* groups. In the latter group *A. diemensis* and *T. parviceps* have particularly low supralabial scale counts. Both species are considered primitive, suggesting at least for the *Tympanocryptis* group that the more advanced species may be developing shorter supralabials. These advanced species inhabit arid areas and form part of a general trend for more arid-adapted species to have a higher number of supralabials. Any adaptive significance of this trend is unclear, and the data are far from conclusive.

The reduced number of infralabial scales in the *Chlamydosaurus* and *Tympanocryptis* groups is more distinct than the reduction in the number of supralabials. The apparent conservatism of this character is surprising, particularly in view of the wide variation within species-groups of some other head scale counts.

12. Scale Size.

Scale size is one of the main diagnostic characters in use in herpetology. The use of the number of mid-body scale rows, an inverse measure of scale width, is an almost universal descriptive character for squamate species. It is therefore surprising that, with the exception of Witten (1972), no such character has been applied to the Australian agamids. The relatively small scales and correspondingly high counts have doubtless discouraged the use of the character. The irregularity of the scales of most Australian species may also have discouraged the use of scale counts. Witten (1972) used the number of scale rows between outer enlarged dorsal scale rows as a diagnostic character in his description of A. nobbi. This count has a limited application, being relevant to only a few closely related genera.

While scale size is accepted as a good diagnostic taxonomic tool, the adaptive significance of scale size has been the subject of several recent publications. Soule (1966) and Soule and Kerfoot (1972) claimed that larger scales were an advantage for species inhabiting hot areas. This claim was based upon statistical correlations between climate and scale counts within populations of two single species. Their argument rests on the fact that larger scales in the iguanids they studied tend to be more strongly keeled and to imbricate more widely. Both these trends result in an increase in the surface area of the lizard. They then argued that this increased surface area would allow greater heat loss in areas of "chronic" heat load. The natural corollary that greater heat uptake would also occur seems to have escaped them. This fault in logic was pointed out by Regal (1975).

Soule and Kerfoot (1972) also claimed a correlation between areas of regular drought and scale size of the lizard populations of these areas. The reduced size of keels and reduced imbrication of the smaller scales would result in an effectively smaller surface area. On the basis that a significant proportion of water loss occurs through the scales, a case was made for small scales being an advantage.

Horton (1972) disputed the conclusions of Soule and Kerfoot (1972). He presented data from Australian skinks which demonstrated trends opposite to those reported by Soule and Kerfoot in iguanids. However, Horton appears to have missed the point that keel size increases with scale size. This feature was not relevant to the skinks he worked on, possibly accounting for his conflicting evidence.

Regal (1975) criticised both Soule and Kerfoot (1972) and Horton (1972). The former he attacked on the basis that provision for greater heat loss would open the possibility of greater uptake. Horton was attacked for his "excessively rigid" stance. Regal quoted Horton's statement; "if Soule and Kerfoot's hypothesis is correct it should apply to all lizards", as an example of this rigidity. In fact both Horton and Soule and Kerfoot appear to be too dogmatic on the basis of their presented data. Soule and Kerfoot presented some data which ran counter to their heat loss hypothesis. Also, the retention of data from an isolated population in Yellowstone National Park because of "clear affinities to the western group based on scatter diagrams of mean dorsal scale counts and climatic variables" suggests an element of circular reasoning in their case. This data was apparently retained only because it supported an hypothesis which was formulated at least in part on the basis of the same data. Further doubt is cast on this set of data by Mueller (1969). He presented data on the isolated Yellowstone population which suggest that the lizards survive in that area because of the microclimate provided by thermal springs. Any climatic data recorded by standard techniques would probably be largely irrelevant to the adaptation of this population. The use of data from this population and standard climatic data casts some doubt on the validity of all Soule and Kerfoot's hypotheses.

Regal (1975) provided a theoretical argument for selection towards elongate scales as a heat shield. His data and argument appear sound, but the absence of extant species with this type of adaptation render his arguments academic.

No general selective trend is obvious in scale size. This is demonstrated by the conflicting views of workers commenting on scale size and adaptation. In the absence of strong unequivocal data to the contrary, scale size might be considered a reasonable taxonomic character, useful in phylogenetic consideratons.

A number of scale counts were made which were designed to give an inverse measure of scale size. Three of these (NS, GS, MBS) gave an inverse measure of scale width, and five characters (PVS10, VS10, GS10, LS10, BTS10) gave an inverse indication of length.

a. Nuchal Scale Count (NS)(Figs. 1, 23).

The nuchal scale count was high in *Gonocephalus*, *Physignathus* and *Chlamydosaurus*. *Tympanocryptis* had a low nuchal scale count.

L. temporalis had a higher mean nuchal scale count than other *Lophognathus*. *A. gibba* and *A. maculosus* had a much lower nuchal scale count than other members of the *A. reticulatus* species-group.

b. Gular Scale Count (GS)(Figs. 1, 24).

The gular scale count of *Moloch* was low. *Diporiphora* also had a relatively low gular scale count. Variation between members of other genera and species-groups masked any taxonomic significance beyond these observations.

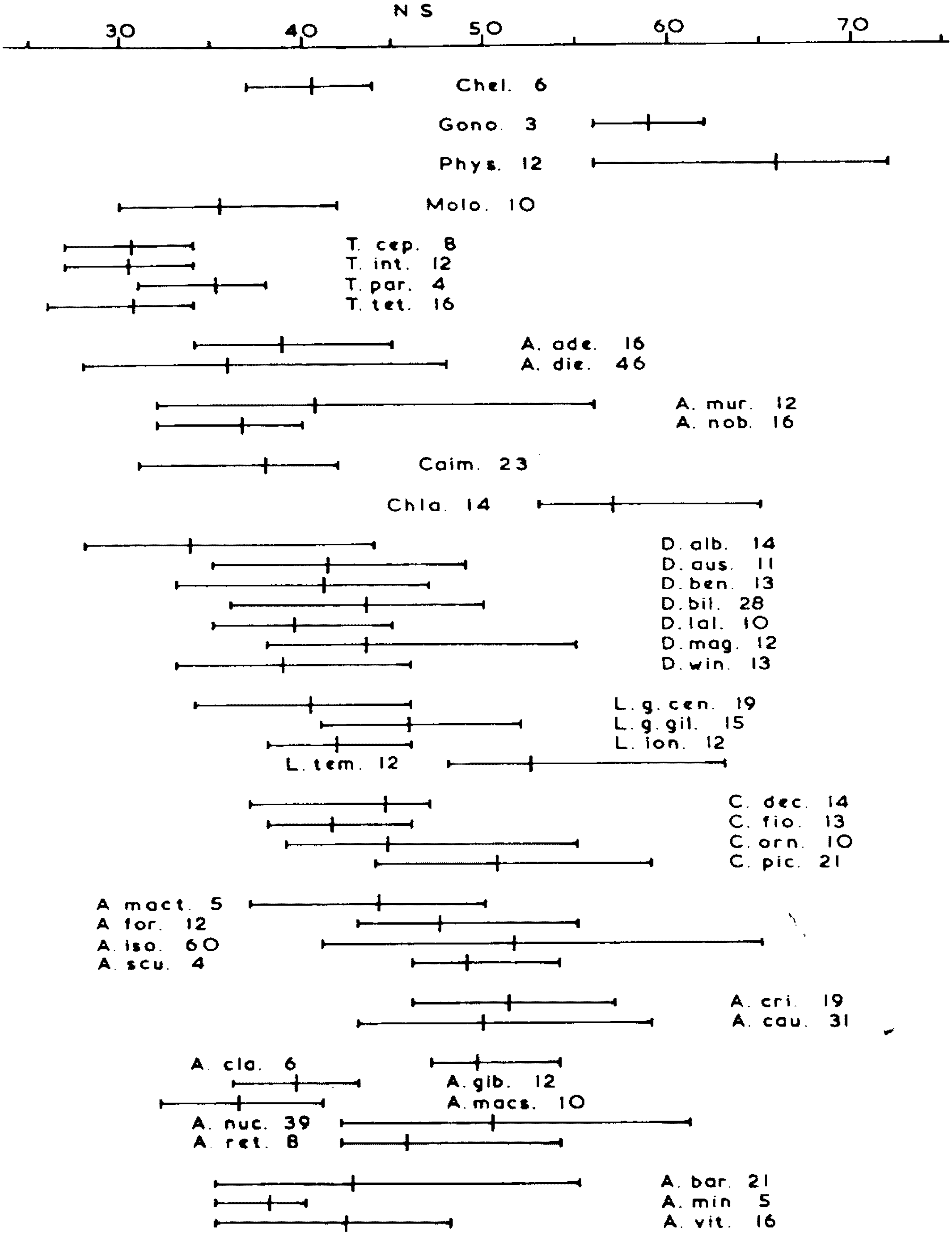


Figure 23. Nuchal Scale Counts. Symbols and abbreviations as for Figure 16.

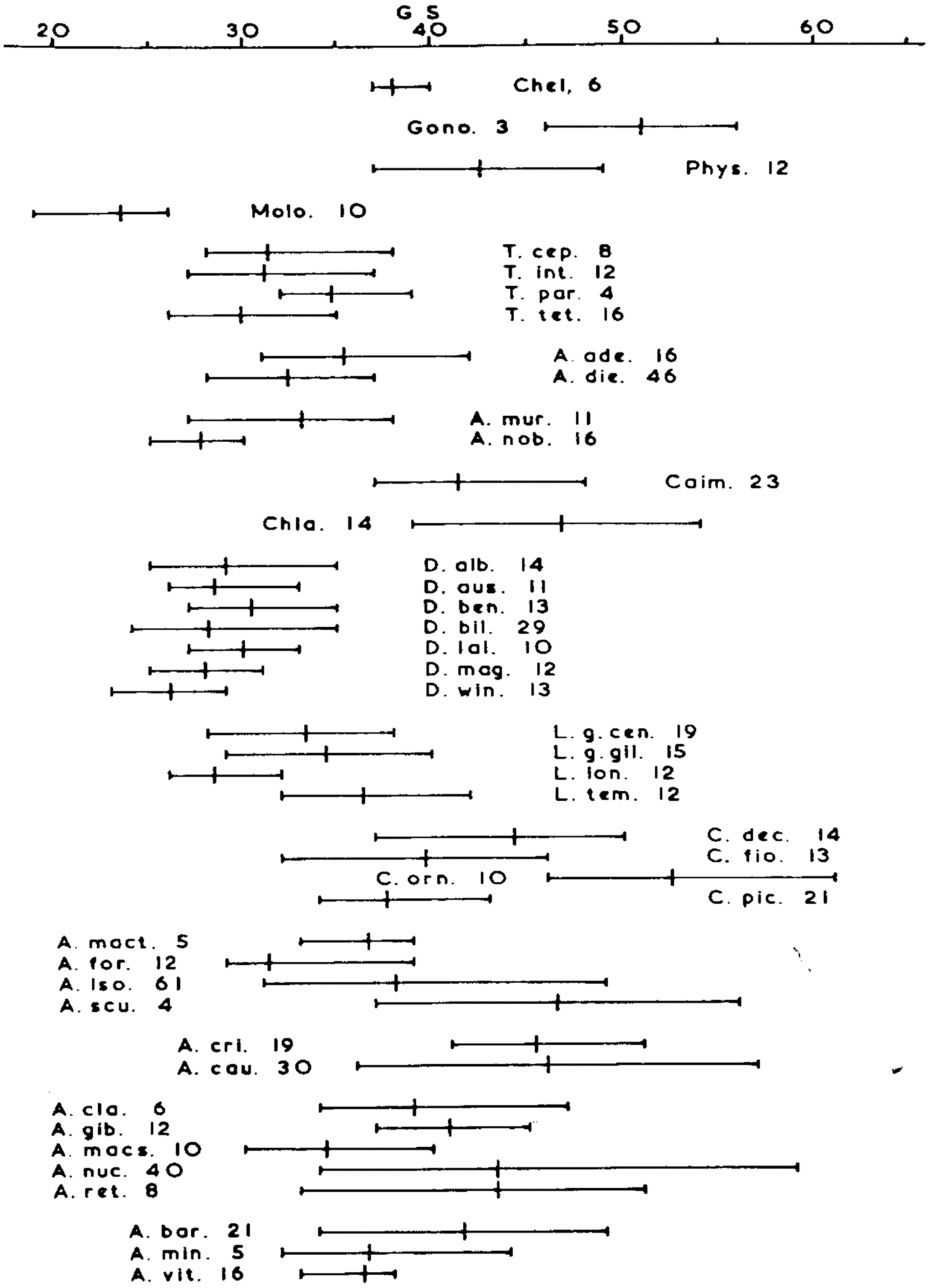


Figure 24. Gular Scale Counts. Symbols and abbreviations as for Figure 16.

c. Mid-body Scale Count (MBS)(Fig. 25).

The number of mid-body scale rows varied little between the species within *Lophognathus* and *Diporiphora*, although the counts of the former genus were much higher. *Chelosania*, *Tympanocryptis* and the *A. muricatus* species-group had low mid-body scale counts, while *Caimanops* and *Chlamydosaurus* had higher counts. *Moloch* and *Physignathus* had very high counts.

There was considerable variation within the other species-groups. Generally the larger species of these groups had a higher scale count. The variation in size within these species-groups was much greater than for the genera mentioned above.

d. Paravertebral Scale Count (PVS10)(Fig. 26, Table 17).

Physignathus had relatively short paravertebral scales, exhibiting a PVS10 score higher than other genera. *Ctenophorus* varied little among the species, and had a relatively high PVS10 count. The paravertebral scales were relatively longer in *Tympanocryptis* and *Diporiphora* than in other groups.

e. Ventral Scale Count (VS10)(Table 17).

The ventral scales were relatively longer in *Diporiphora*, *Tympanocryptis* and the *A. adelaidensis* species-group.

f. Gular Scale Count, Length (GS10)(Table 17).

Caimanops had smaller gular scales than most of the other members of the *Chlamydosaurus* group. The gular scales of *Chlamydosaurus* and the *A. barbatus* species-group were relatively longer than scales of these taxa in other areas. The comparative scale size of other groups was similar in the gular region to other areas.

g. Lateral Scale Count (LS10)(Table 17).

Lateral scales were generally smaller than the scales of other

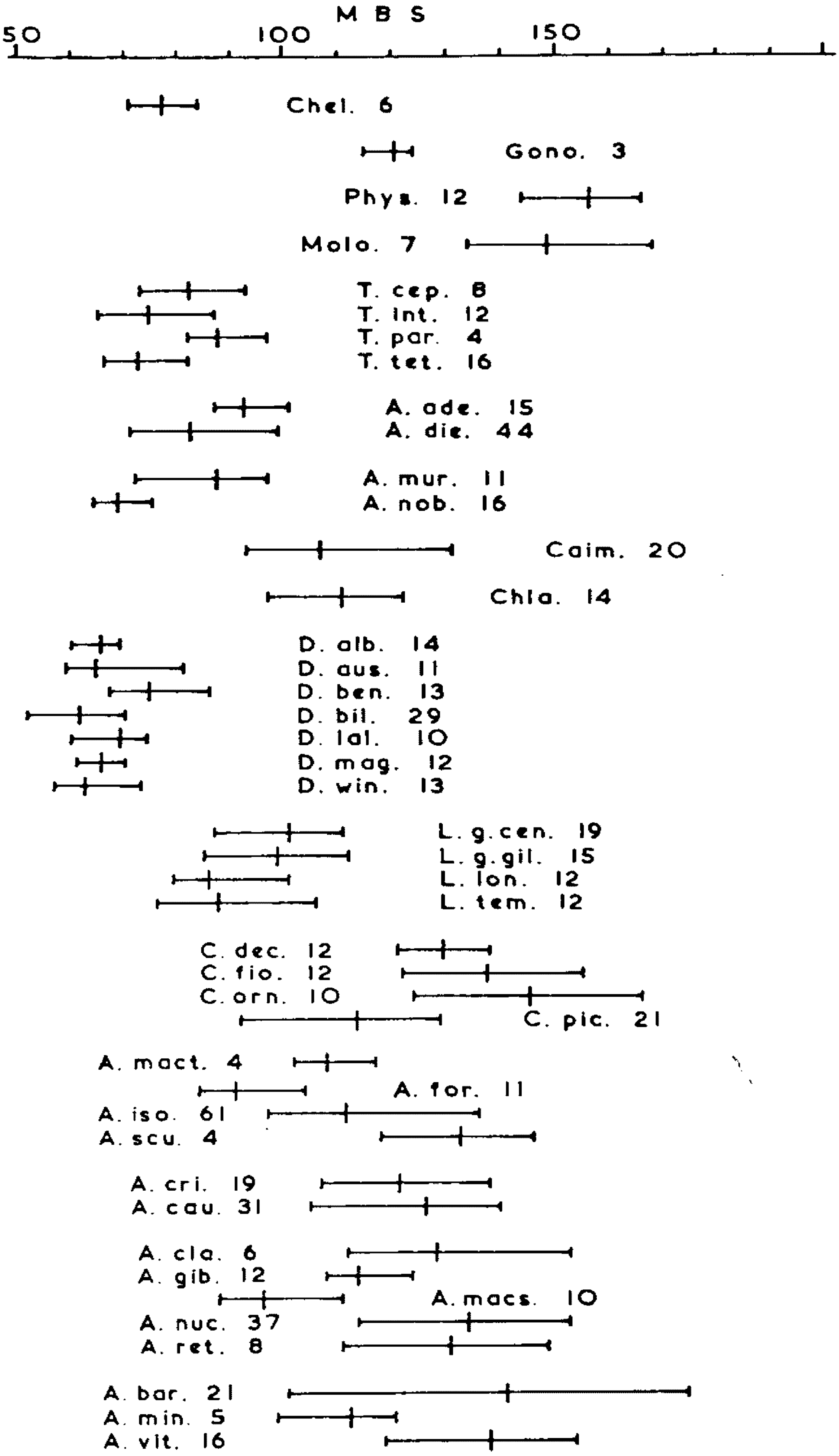


Figure 25. Midbody Scale Counts. Symbols and abbreviations as for Figure 16.

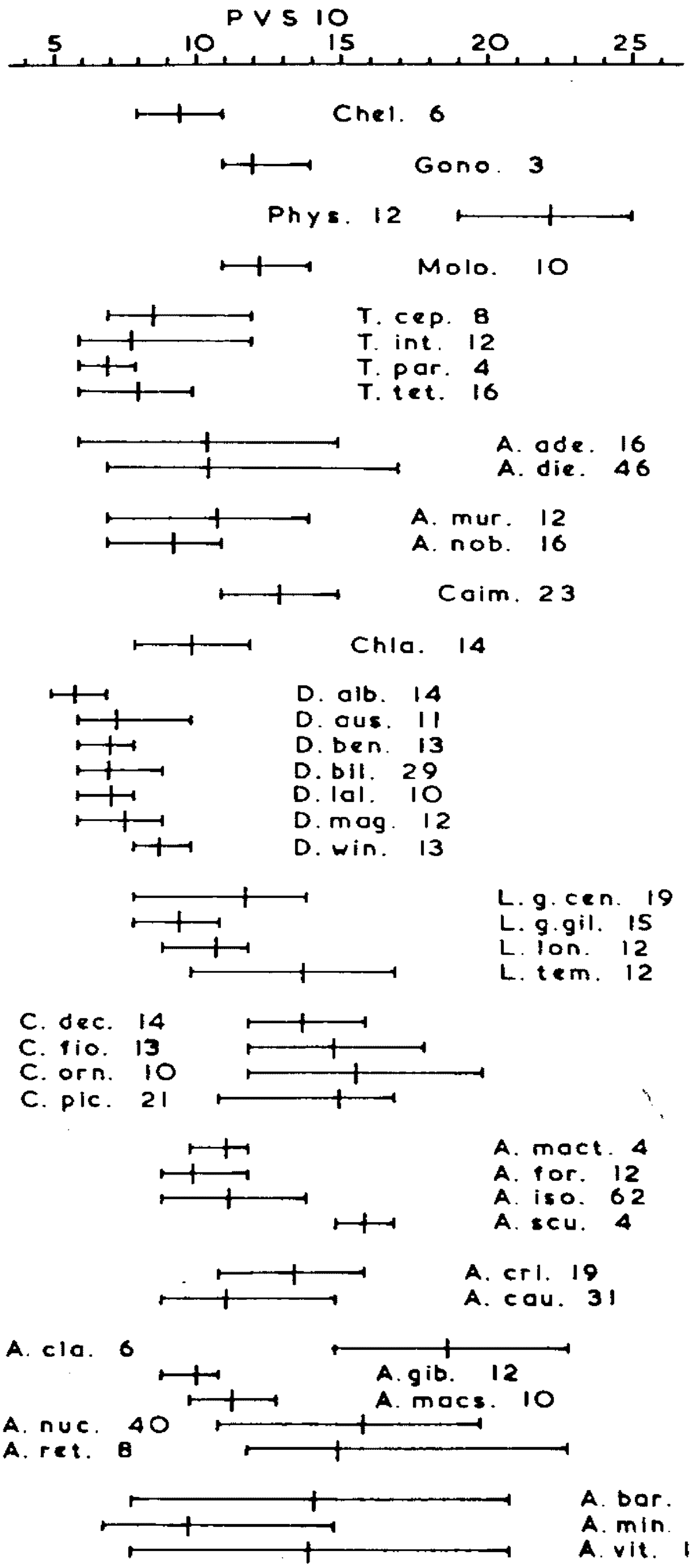


Figure 26. Paravertebral Scale Counts. Symbols and abbreviations as for Figure 16.

Table 17. Relative Scale Lengths.

Species	N	PVS10			VS10			GS10			LS10			BTS10		
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Chelosania	6	9.5	1.0	8-11	11.8	1.3	10-14	18.2	3.0	14-23	10.3	1.4	9-12	9.5	0.8	8-10
Gonocephalus	3	12.0	1.7	11-14	11.7	0.6	11-12	15.0	2.6	12-17	15.7	1.5	14-17	7.7	1.2	7-9
Physignathus	12	22.2	1.7	19-25	14.2	2.0	10-18	18.3	2.2	15-22	21.4	2.6	16-26	18.4	2.5	14-22
Moloch	10	12.3	1.1	11-14	14.4	2.1	10-17	20.0	5.2	11-27	12.8	3.6	7-18	15.1	2.7	11-19
T. cephalus	8	8.6	1.6	7-12	7.9	1.1	6-9	10.9	1.0	10-13	9.6	1.5	7-12	9.1	1.0	8-11
T. intima	12	7.8	1.9	6-12	8.4	2.0	6-12	11.2	2.4	8-16	8.6	1.5	6-12	8.2	0.9	7-10
T. parviceps	4	7.0	0.8	6-8	7.8	1.0	7-9	10.5	1.7	9-13	10.0	1.2	9-11	6.8	1.0	6-8
T. tetra-porophora	16	8.1	1.1	6-10	7.8	1.2	6-11	10.7	1.4	8-13	8.9	1.1	7-11	7.7	1.0	6-9
A. adelaidensis	16	10.5	2.5	6-15	9.0	1.7	6-12	10.8	1.8	8-15	13.1	2.3	10-17	9.5	1.7	7-13
A. diemensis	46	10.6	2.0	7-17	7.9	1.4	6-11	9.2	1.3	7-13	11.3	2.6	7-16	8.1	1.6	6-13
A. muricatus	11	10.8	2.2	7-14	9.5	0.8	8-11	12.5	0.9	11-14	12.0	1.4	10-14	9.1	1.1	8-11
A. nobbi	16	9.4	1.1	7-11	8.4	0.6	8-10	9.4	1.5	7-12	10.6	1.8	8-15	8.2	1.2	7-10
Caimanops	23	13.0	1.3	11-15	12.4	2.0	9-17	18.0	2.7	14-25	15.1	2.0	12-20	10.1	1.7	7-13
Chlamydosaurus	14	10.0	1.0	8-12	8.9	1.3	7-12	9.8	1.1	8-12	14.2	3.0	10-20	10.5	0.8	9-12
D. albilabris	14	5.9	0.7	5-7	7.0	0.8	6-9	8.6	0.6	8-10	8.6	1.3	6-12	6.7	0.8	5-8
D. australis	11	7.4	1.3	6-10	7.0	0.9	6-8	9.0	1.0	8-11	8.7	1.5	7-12	7.5	1.0	6-9
D. bennettii	13	7.2	0.7	6-8	7.0	0.8	6-9	10.0	1.2	8-12	9.7	0.8	8-12	7.3	0.6	6-8
D. bilineata	29	7.1	1.1	6-9	6.8	1.0	5-9	8.0	1.1	6-10	8.3	1.4	6-12	7.2	0.8	5-9
D. lalliae	10	7.2	0.8	6-8	8.0	1.2	6-10	10.2	1.3	9-13	9.5	1.3	8-11	8.1	1.0	7-10
D. magna	12	7.7	0.9	6-9	6.6	0.5	6-7	8.8	1.4	7-12	9.0	1.5	7-13	7.7	0.7	7-9
D. winneckei	13	8.9	0.6	8-10	7.5	0.8	6-9	9.2	1.2	7-11	9.5	1.3	8-12	7.8	1.0	6-9
L. gilberti	15	9.6	0.9	8-11	9.2	1.1	7-11	15.0	2.5	10-18	15.2	2.0	12-19	10.7	1.3	9-13
L. g. centralis	19	11.9	1.6	8-14	10.4	1.6	7-13	15.9	1.7	13-19	14.9	2.2	10-19	10.4	1.2	9-13
L. longirostris	12	10.9	1.2	9-12	10.8	1.2	9-13	11.9	2.2	9-17	15.6	1.0	14-17	11.8	0.9	10-13
L. temporalis	12	13.8	1.7	10-17	8.7	1.0	7-10	15.8	2.9	12-21	14.5	2.9	10-21	11.7	1.6	9-15

C. decresii	14	13.9	1.3	12-16	12.1	1.6	10-16	16.4	1.6	15-19	17.4	2.6	14-22	12.8	0.9	11-14
C. fionni	13	14.9	1.6	12-18	11.7	1.0	10-14	15.7	2.1	13-20	19.3	2.2	16-24	13.5	1.9	11-18
C. ornatus	10	15.7	2.8	12-20	13.7	1.2	12-15	23.0	1.2	18-26	21.6	2.5	16-25	9.8	0.8	9-11
C. pictus	21	15.1	1.8	11-17	9.8	1.2	8-12	13.8	1.5	11-17	16.6	2.2	13-20	12.2	1.4	10-15
A. maculatus	4	11.3	1.0	10-12	10.0	1.4	9-12	15.5	1.9	14-18	17.5	0.6	17-18	14.5	1.3	13-16
A. fordi	12	10.1	1.1	9-12	9.3	0.8	8-11	12.3	1.6	10-16	14.3	2.3	11-18	11.3	1.4	9-14
A. isolepis	62	11.4	1.2	9-14	10.6	1.2	8-13	14.8	1.5	11-18	16.9	2.5	11-24	12.6	1.3	10-16
A. scutulatus	4	16.0	0.8	15-17	11.8	1.3	10-13	18.3	1.0	17-19	20.3	2.6	18-24	15.3	2.1	13-17
A. cristatus	19	13.6	1.4	11-16	11.9	1.2	10-14	18.7	1.9	15-22	19.5	2.7	14-25	15.1	1.6	13-19
A. caudicinctus	31	11.3	1.3	9-15	12.3	1.2	10-15	16.1	2.5	12-23	19.0	2.2	16-24	11.4	1.5	9-14
A. reticulatus	8	15.1	3.4	12-23	11.1	1.1	10-13	16.9	3.6	13-24	18.4	1.3	16-20	12.8	2.0	10-16
A. clayi	6	18.8	3.7	15-23	10.7	1.2	10-13	17.7	2.7	15-22	18.8	2.4	15-22	14.2	2.1	12-18
A. gibba	12	10.3	0.8	9-11	9.7	1.2	7-11	16.8	1.8	13-19	20.3	2.7	17-24	11.7	1.0	10-14
A. maculosus	10	11.5	0.9	10-13	7.9	1.1	7-10	14.2	0.9	13-16	15.4	1.4	14-18	9.0	0.5	8-10
A. nuchalis	40	16.0	2.1	11-20	12.1	1.8	9-18	17.3	2.4	13-23	20.4	2.8	16-26	16.0	2.6	11-22
A. barbatus	21	14.3	3.1	8-21	11.0	1.6	7-13	9.8	1.4	8-13	13.0	3.1	8-22	9.4	1.4	7-13
A. minor	5	10.0	3.2	7-15	9.4	1.5	8-12	10.8	0.8	10-12	11.4	2.9	9-16	8.8	0.4	8-9
A. vitticeps	16	14.2	3.5	8-21	10.8	1.3	9-13	9.7	1.4	7-13	14.4	3.5	11-23	9.6	1.7	7-13

areas. The comparative size of scales was similar for the laterals as for other areas.

h. Base of Tail Scale Count (BTS10)(Table 17).

The scales on the base of the tail, like the laterals, showed interspecific variation in size similar to the scales of other areas.

Maximum Body Size.

It became apparent during analysis of the data presented above that the maximum body size of a species and scale number were directly related. The maximum size attained by each species and the various scale size parameters were compared (Table 18). An index of scale size was calculated for each species. This index was simply the sum of scale counts giving an inverse measure of width (MBS, NS, GS) and those giving an inverse measure of length (PVS10, VS10, GS10, LS10, BTS10). A least squares regression calculation performed for members of the *Chlamydosaurus* group found a highly significant correlation between this index and size ($P < 0.0005$; Fig. 27). A similar regression for members of the *A. cristatus*, *A. maculatus* and *A. reticulatus* species-groups and *Ctenophorus* (Fig. 28) also found a significant correlation between body size and scale number, but the trend was not as strong ($P < 0.01$). Figure 29 presents graphically the data for the species not included in Figures 27 and 28. The calculated regression lines from those figures have been superimposed on Figure 29 to allow graphic comparison of all taxa.

Discussion.

The most significant result from measuring scale size is the strong correlation between the size of the species and scale size. This correlation has not been reported previously. Most of the recent literature on this subject has concentrated heavily on physiological adaptations of scale size (see introduction to this section). These authors

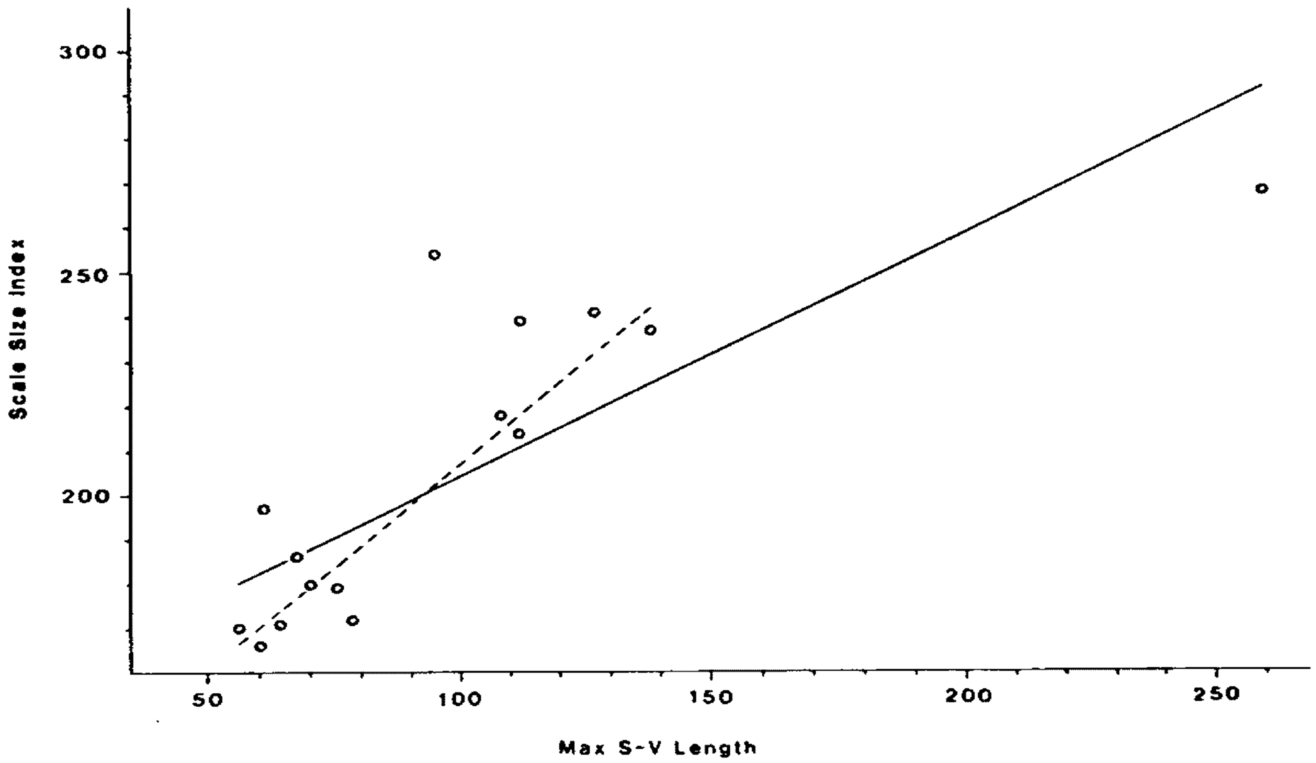


Figure 27. Maximum Body Size and Scale Size Index, Chlamydosaurus Group. Unbroken line represents least squares regression for whole group. Slope is significantly different from zero (F = 24.25 (DF 1/15), $P < 0.0005$). Broken line represents least squares regression with Chlamydosaurus and Caimanops excluded (F = 46.98 (DF 1/13), $P \ll 0.0005$).

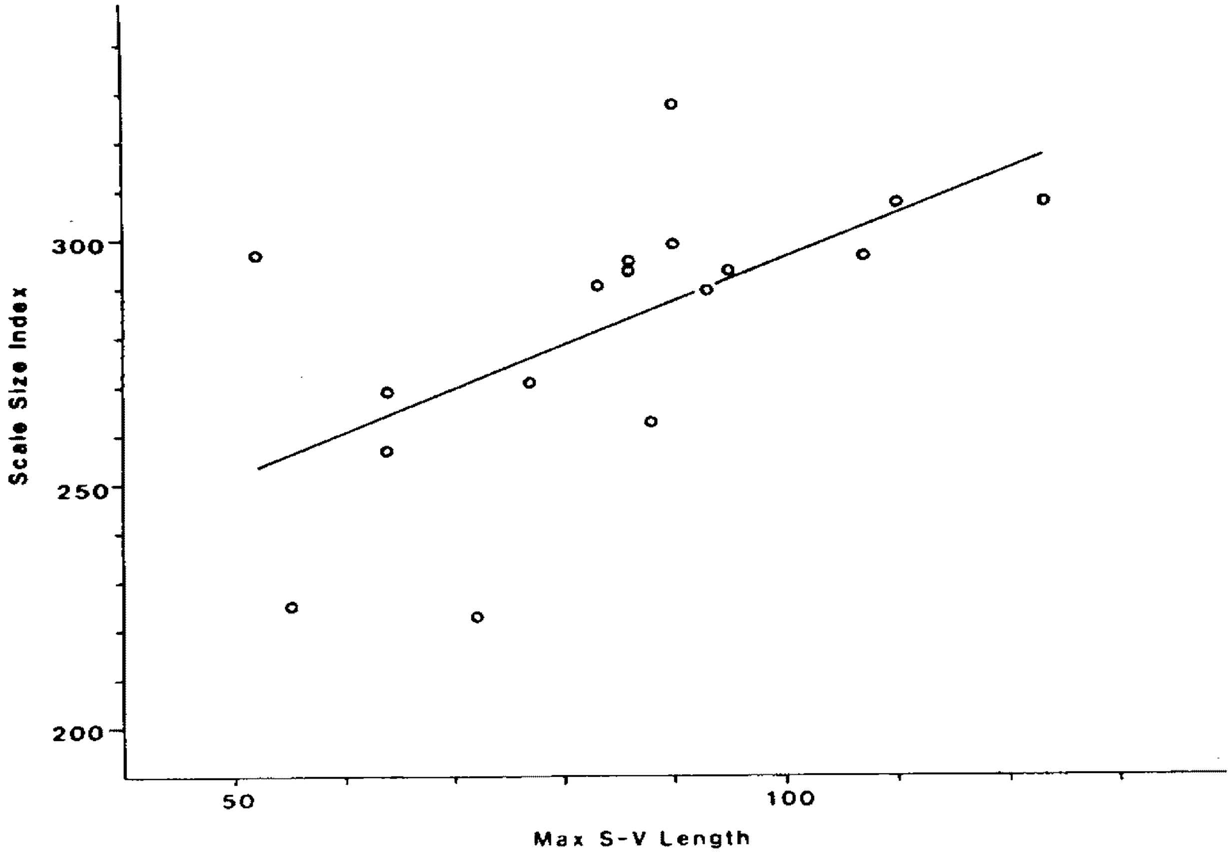


Figure 28. Maximum Body Size and Scale Size Index, Ctenophorus Group (A. barbatus species-group excluded). Line represents least squares regression. Slope is significantly different from zero (F = 8.87 (DF 1/15), P < 0.01).

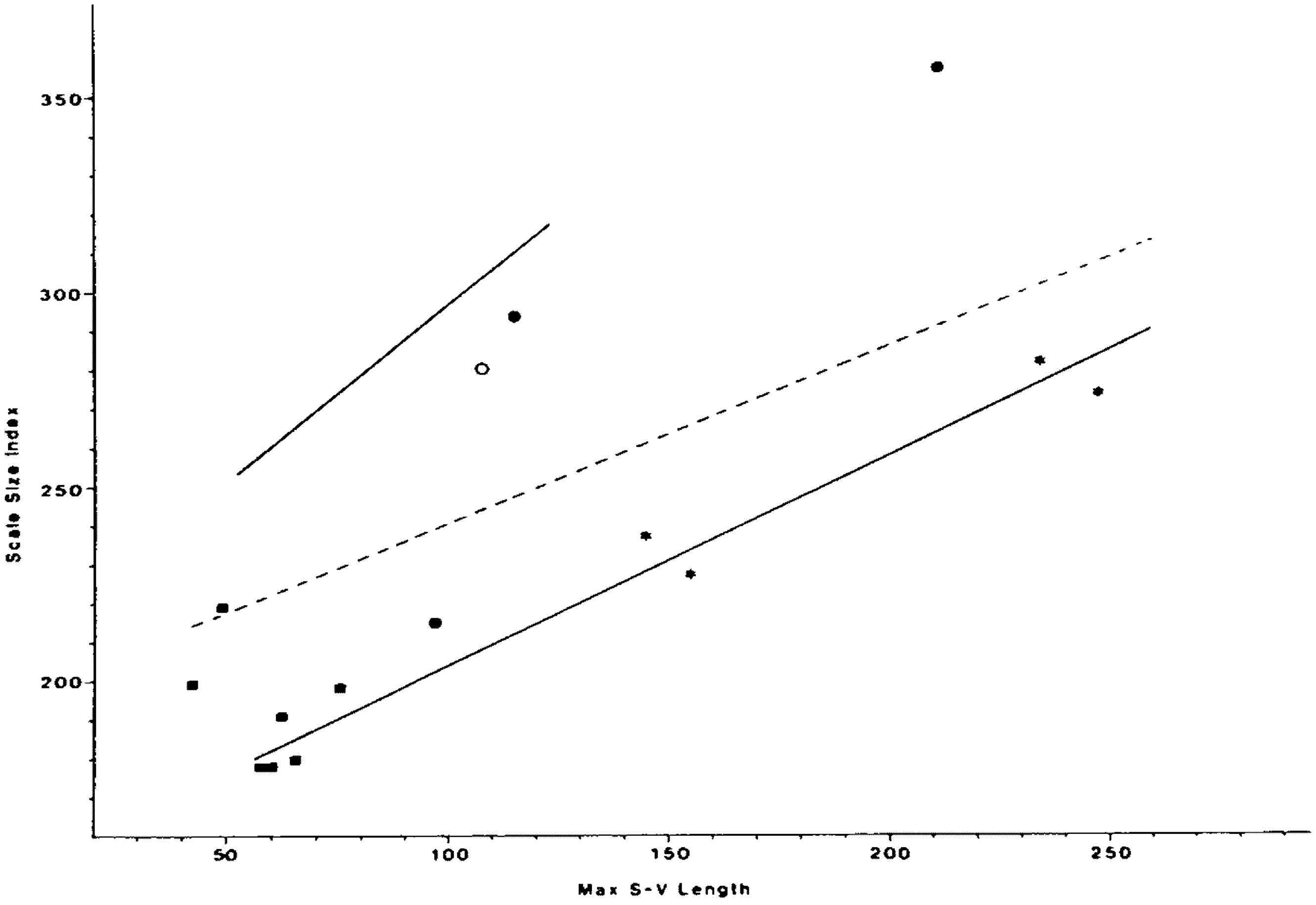


Figure 29. Maximum Body Size and Scale Size Index, All Taxa. Upper line represents regression from Figure 28 (Ctenophorus group), lower line is unbroken line of Fig. 27 (Chlamydosaurus group). Broken line represents least squares regression for all taxa. Slope of this line is significantly different from zero ($F = 11.59$ (DF 1/47), $P < 0.0025$). Open circles = Asian-derived genera; Closed circle = Moloch; Squares = Tympanocryptis group; Stars = A. barbatus species-group.

Table 18. Relative Scale Size.

Species	Max Siz	MBS	NS	GS	PVS 10	VS 10	GS 10	LS 10	BTS 10	N	Scale Index
Chelosania	97	77	41	38	9	12	18	10	10	6	215
Gonocephalus	115	121	59	51	12	12	15	16	8	3	294
Physignathus	210	156	66	43	22	14	18	21	18	12	358
Moloch	108	149	35	23	12	14	20	13	15	10	281
T. cephalus	62	82	31	31	9	8	11	10	9	8	191
T. intima	65	75	30	31	8	8	11	9	8	12	180
T. lineata	58	75	31	31	8	8	10	8	7	3	178
T. parviceps	42	87	35	35	7	8	10	10	7	4	199
T. tetraporophora	60	73	31	30	8	8	11	9	8	16	178
A. adelaidensis	49	93	39	35	10	9	11	13	9	16	219
A. diemensis	75	83	36	32	11	8	9	11	8	46	198
A. muricatus	112	87	41	33	11	9	12	12	9	12	214
A. nobbi	75	69	37	28	9	8	9	11	8	16	179
Caimanops	95	107	38	41	13	12	18	15	10	23	254
Chlamydosaurus	259	111	57	47	10	9	10	14	10	14	268
D. albilabris	60	65	34	29	6	7	9	9	7	14	166
D. australis	78	64	41	28	7	7	9	9	7	11	172
D. bennettii	67	74	41	30	7	70	10	10	73	13	186
D. bilineata	56	61	44	28	7	7	8	8	7	29	170
D. lalliae	70	69	39	30	7	8	10	9	8	10	180
D. linga	61	78	45	30	10	8	9	10	7	1	197
D. magna	86	66	43	28	8	7	9	9	8	12	178
D. superba	88	60	44	27	8	9	9	12	7	1	176
D. winneckei	64	63	39	26	10	7	9	9	8	13	171
L. gilberti	112	99	46	34	10	9	15	15	11	15	239
L. g. centralis	138	101	40	33	12	10	16	15	10	19	237
L. longirostris	108	86	42	28	11	11	12	16	12	12	218
L. temporalis	127	88	52	36	14	9	16	14	12	12	241

C. decresii	93	129	45	44	14	12	16	17	13	14	290
C. fionni	86	137	42	40	15	12	16	19	13	13	294
C. ornatus	90	146	45	52	16	14	23	22	10	10	328
C. pictus	77	114	51	38	15	10	14	17	12	21	271
C. rufescens	90	137	45	42	15	12	18	17	14	2	300
C. vadnappa	86	134	45	44	15	10	16	19	13	3	296
A. maculatus	64	108	44	37	11	10	16	17	14	4	257
A. fordi	55	91	47	31	10	9	12	14	11	12	225
A. isolepis	64	112	52	38	11	11	15	17	13	62	269
A. scutulatus	110	132	49	46	16	12	18	20	15	4	308
A. cristatus	107	121	51	45	14	12	19	20	15	19	297
A. caudicinctus	83	126	50	46	11	12	16	19	11	31	291
A. reticulatus	95	131	46	43	15	11	17	18	13	8	294
A. clayi	52	128	49	39	19	11	18	19	14	6	297
A. gibba	88	114	39	41	10	10	17	20	12	12	263
A. maculosus	72	96	36	34	11	8	14	15	9	10	223
A. nuchalis	123	134	50	43	16	12	17	20	16	40	308
A. barbatus	234	141	43	42	14	11	10	13	9	21	283
A. minor	145	113	38	37	10	9	11	11	9	5	238
A. mitchelli	155	106	40	34	8	9	11	11	9	1	228
A. vitticeps	247	138	42	36	14	11	10	14	10	16	275

have assumed that a higher scale count has indicated smaller scales, without taking into account the maximum size, or the usual adult size, attained by the populations under consideration.

The data presented here would suggest that scale size may be extraordinarily conservative. The fact that larger species have more scales could indicate that scales of a certain absolute size are typical of a taxonomic group. Thus a species attaining a larger size will require more of these scales at full adult body size to cover the body. Conversely, a smaller species could reduce the number of scales.

The retention of scales of the same absolute size has a number of attractive properties as a theory. Soule and Kerfoot (1972) commented that larger scales in sceloporine iguanids tend to be more strongly keeled and more spinose. This occurs whether the scale increases in size ontogenetically or phylogenetically. The same is apparently true of Australian dragons. In both cases the scales probably develop under the control of similar "rate control" genes. Based on this assumption one could postulate that a species phylogenetically increasing in size without increasing the number of scales would develop heavily keeled and spinose scales. This may not be selectively advantageous, and a similar species increasing the number of scales would then be favoured.

An increase in the absolute size of a scale may involve a more complex scale structure for a number of reasons. Diffusion rates in the larger scale may require an increased number of blood vessels to supply each scale, or changes in relative thickness to facilitate diffusion. A wider, longer scale may become more prone to buckling or tearing under pressure without becoming disproportionately thick. Such changes as may be required to overcome these problems would presumably involve some "phylogenetic expense".

Many of the differences noted between species in the scale size index can be attributed to differences in size. After size has been taken into account some generalisations are, however, possible. *Moloch*, *Ctenophorus*, and members of the *A. cristatus*, *A. maculatus* and *A. reticulatus* species-groups have smaller scales than other endemic agamids (Fig. 29).

Two genera of the *Chlamydosaurus* group differ in scale size from the other three genera. *Chlamydosaurus* grows to a much greater size than other members of the group, yet has only slightly more scales. *Caimanops* has relatively small scales considering it attains a maximum recorded snout-vent length of only 97 mm.

A. clayi has remarkably small scales. The species is the smallest member of the *A. reticulatus* species-group, yet has a very high mid-body scale count. This may be a development to camouflage the species against the sandy soils on which it lives. Storr (1966) suggested that the species was exceptionally difficult to observe. The hypothesis that the small scales are a cryptic adaptation is supported by the fact that the ventral and gular scales are relatively much larger in *A. clayi*. These scales would not be a factor in normal camouflage, and would not be subject to the same selective pressure from predators.

13. Scale Characters.

Several features of scales have been used diagnostically in agamid taxonomy. These characters were recorded in the present study to examine their validity.

a. Heterogeneity.

Gray (1845) considered the imbricate, irregular nature of the scales of most Australian dragons as an important diagnostic character. He used this feature in his synopsis to identify a group of genera including *Chlamydosaurus*, *Lophognathus*, *Diporiphora* and *Amphibolurus*. Boulenger (1885) did not use the same character to distinguish these genera. However, he discriminated between the Asian genera *Acanthosaura* ("dorsal scales unequal") and *Calotes* ("equal") with a similar character. Witten (1972) used the homogeneity of dorsal scales as one of the main distinguishing characters of *Amphibolurus nobbi*, contrasting this species with the closely related *A. muricatus*, which has very heterogeneous scales. Houston (1978) used the regularity of scales on the dorsal surface of the thigh to distinguish *A. nobbi coggeri* from *A. muricatus*. This character was included in the present study.

Strongly heterogeneous scales were characteristic of the *A. barbatus* and *A. adelaidensis* species-groups, *Tympanocryptis*, *Moloch* and *A. muricatus*. The *A. maculatus* species-group and *Chelosania* invariably had small, regular scales. Members of most other groups varied in both body and thigh scale heterogeneity (Table 19). Scattered tubercles among otherwise homogeneous scalation was responsible for *A. reticulatus*, *A. maculosus*, *A. nuchalis*, *A. cristatus*, *G. spinipes* and *Physignathus* being scored as possessing heterogeneous scalation.

b. Direction of Scale Series.

Gray (1845) used the direction of dorsal scale series to

Table 19. Scale Heterogeneity.

Species	Dorsum		Thigh	
	0	1	0	1
Chelosania	6	-	6	-
Gonocephalus	-	3	-	3
Physignathus	1	11	-	12
Moloch	-	10	-	10
T. cephalus	-	8	-	8
T. intima	-	12	-	12
T. lineata	1	2	1	2
T. parviceps	-	4	-	4
T. tetraporophora	-	16	-	16
T. uniformis	-	1	1	-
A. adelaidensis	-	16	-	16
A. diemensis	-	46	-	46
A. muricatus	-	12	-	12
A. nobbi	11	5	15	1
Caimanops	-	23	4	19
Chlamydosaurus	7	7	14	-
D. albilabris	6	8	14	-
D. australis	7	4	11	-
D. bennettii	13	-	13	-
D. bilineata	27	2	29	-
D. lalliae	9	1	9	1
D. linga	1	-	1	-
D. magna	11	1	12	-
D. superba	1	-	1	-
D. winneckei	13	-	13	-
L. gilberti	6	9	15	-
L. g. centralis	5	14	6	13
L. longirostris	12	-	12	-
L. temporalis	12	-	12	-
C. decresii	13	1	14	-
C. fionni	10	3	13	-
C. ornatus	3	7	8	2
C. pictus	20	1	21	-
C. rufescens	2	-	2	-
C. vadnappa	3	-	3	-
A. maculatus	5	-	5	-
A. fordi	12	-	12	-
A. isolepis	62	-	62	-
A. scutulatus	4	-	4	-
A. cristatus	7	12	14	5
A. caudicinctus	31	-	31	-
A. reticulatus	-	8	1	7
A. clayi	6	-	6	-
A. gibba	12	-	12	-
A. maculosus	1	9	9	1
A. nuchalis	-	40	23	17
A. barbatus	-	21	-	21
A. minor	-	5	-	5
A. mitchelli	-	1	-	1
A. vitticeps	-	16	-	16

0 = homogeneous. 1 = heterogeneous

distinguish three genera. *Calotes* was typified by "ascending series", *Salea* by "longitudinal series" and *Bronchocela* by "descending series". Boulenger (1885) apparently considered the character less important. He synonymised *Bronchocela* with *Calotes*.

Boulenger (1883) distinguished *Lophognathus gilberti* from other species in the genus with the character "upper dorsal scales horizontal, forming parallel rows with the vertebral crest". This contradicted Gray's original (1842) description where the back was described as covered by scales "placed in oblique ascending series". Boulenger (1885) decided that both Gray's type series of *L. gilberti* and Gunther's (1867) type series of *Grammatophora temporalis* in fact included specimens of both species. Boulenger proposed that *L. gilberti* be distinguished by the possession of parallel scale series. This has been accepted, and both *L. gilberti* and *L. temporalis* are currently recognised.

Storr (1974) used the direction of the keels of scales in a similar manner to that of Boulenger (1883) to distinguish *L. gilberti*. He further distinguished *L. gilberti centralis* from the nominate subspecies on the basis of the direction of keel lines of dorsolateral scales. Storr also applied the direction of lateral scale keel lines to distinguish two species of *Diporiphora*.

The direction of scale series or keel lines has thus come to be considered most suited to species distinctions since the publication of Boulenger's catalogue.

Chelosania was outstanding in possessing paravertebral scale rows diverging from the midline. Two *Chelosania* were the only specimens with converging ventrals (Table 20).

Scale series were difficult to discern in those species with extremely heterogeneous dorsal scalation. Thus most members of the *A.*

Table 20. Direction of Scale Series.

Species	Paravertebrals					Ventrals				
	0	1	2	3	4	0	1	2	3	4
Chelosania	-	-	-	-	6	-	-	2	3	1
Gonocephalus	-	-	3	-	-	-	-	-	1	2
Physignathus	-	1	11	-	-	-	-	-	4	8
Moloch	5	5	-	-	-	2	7	-	-	1
T. cephalus	-	8	-	-	-	-	-	-	-	8
T. intima	-	12	-	-	-	-	-	-	-	12
T. lineata	-	3	-	-	-	-	-	-	-	3
T. parviceps	-	3	1	-	-	-	-	-	-	4
T. tetraporophora	-	11	3	2	-	-	-	-	-	16
T. uniformis	-	1	-	-	-	-	-	-	-	1
A. adelaidensis	-	15	-	1	-	-	-	-	-	16
A. diemensis	-	42	2	1	-	-	2	-	5	37
A. muricatus	-	3	8	1	-	-	-	-	1	11
A. nobbi	-	1	4	11	-	-	-	-	5	11
Caimanops	-	18	1	4	-	-	17	-	1	5
Chlamydosaurus	-	1	2	9	1	-	-	-	8	6
D. albilabris	-	-	-	14	-	-	-	-	8	6
D. australis	-	-	-	11	-	-	-	-	10	1
D. bennettii	-	-	1	12	-	-	-	-	7	6
D. bilineata	-	-	-	29	-	-	-	-	26	3
D. lalliae	-	-	-	10	-	-	-	-	6	4
D. linga	-	-	-	1	-	-	-	-	1	-
D. magna	-	-	-	12	-	-	-	-	10	2
D. superba	-	-	1	-	-	-	-	-	1	-
D. winneckei	-	-	7	6	-	-	-	-	1	12
L. gilberti	-	-	-	15	-	-	-	-	4	11
L. g. centralis	-	-	16	3	-	-	-	-	-	19
L. longirostris	-	-	12	-	-	-	-	-	2	10
L. temporalis	-	-	12	-	-	-	1	-	1	10
C. decresii	-	-	14	-	-	-	-	-	-	14
C. fionni	-	-	13	-	-	-	-	-	-	13
C. ornatus	-	-	10	-	-	-	-	-	-	10
C. pictus	-	-	21	-	-	-	-	-	-	21
C. rufescens	-	-	2	-	-	-	-	-	-	2
C. vadnappa	-	-	3	-	-	-	-	-	-	3
A. maculatus	-	-	5	-	-	-	-	-	-	5
A. fordi	-	-	12	-	-	-	-	-	-	11
A. isolepis	-	-	60	2	-	-	-	-	-	62
A. scutulatus	-	-	4	-	-	-	-	-	-	4
A. cristatus	-	-	19	-	-	-	-	-	-	19
A. caudicinctus	-	-	31	-	-	-	-	-	-	31
A. reticulatus	-	1	6	1	-	-	-	-	-	8
A. clayi	-	-	6	-	-	-	-	-	-	6
A. gibba	-	-	11	1	-	-	-	-	-	12
A. maculosus	-	-	10	-	-	-	-	-	-	10
A. nuchalis	-	1	39	-	-	-	-	-	-	38
A. barbatus	-	17	4	-	-	-	-	-	2	19
A. minor	-	5	-	-	-	-	-	-	-	5
A. mitchelli	-	1	-	-	-	-	-	-	-	1
A. vitticeps	-	15	1	-	-	-	-	-	-	16

0 = no discernible scale rows. 1 = scale rows haphazard. 2 = posteromedial scale rows. 3 = scale rows parallel with long axis of body. 4 = posterolateral scale rows.

barbatus and *A. adelaidensis* species-groups and *Tympanocryptis* were scored as possessing random dorsal scale rows (Table 20). These species normally possessed ventrals diverging from the midline. *Caimanops* had heterogeneous paravertebral scales, but in both the paravertebrals and ventrals there was a tendency for short, irregular scale rows to form, running in no consistent direction relative to the long axis of the body. The scales of *Moloch* did not imbricate widely, if at all. The scales also lacked a keel, so keel lines were not discernible.

Most species with clear scale rows had paravertebral scale rows converging on and ventral scale rows diverging from the midline. Most *Diporiphora* were exceptions, with most scale rows parallel with the midline (Table 20). This feature occurred in some members of all genera in the *Chlamydosaurus* group.

c. Scale Keeling.

Cogger (1975) used the degree of development of keels on ventral scales to separate the *A. maculatus* species-group from *Ctenophorus*. He used a similar character of the gular scales to distinguish *A. adelaidensis* from *A. diemensis*. The presence of keeled scales was recorded in the present study in the dorsal, ventral and gular regions.

Smooth dorsals occurred commonly only in members of the *A. reticulatus* species-group. Occasional specimens of *T. cephalus*, *T. intima*, *C. pictus* and *A. caudicinctus* were also scored as possessing smooth dorsals (Table 21).

Strongly keeled ventrals were typical of all members of the *Chlamydosaurus* group. *Chelosania*, *G. spinipes* and the *A. barbatus* species-group also invariably had keeled ventrals (Table 21). Smooth ventrals were typical only of *Ctenophorus*. The gular scales closely paralleled the ventrals, but were more often smooth in most groups (Table

Table 21. Scale Keeling.

Species	Dorsals		Ventrals		Gulars	
	Smth	Kld	Smth	Kld	Smth	Kld
Chelosania	-	6	-	6	-	6
Gonocephalus	-	3	-	3	-	3
Physignathus	-	12	1	11	3	9
Moloch	-	10	-	10	-	10
T. cephalus	3	5	3	5	2	6
T. intima	2	10	1	11	1	11
T. lineata	-	3	1	2	1	2
T. parviceps	-	4	-	4	-	4
T. tetraporophora	-	16	2	14	6	10
T. uniformis	-	1	-	1	-	1
A. adelaidensis	-	16	2	14	2	14
A. diemensis	-	46	-	46	-	46
A. muricatus	-	12	-	12	1	11
A. nobbi	-	16	-	16	-	16
Caimanops	-	23	1	22	6	17
Chlamydosaurus	-	14	-	14	-	14
D. albilabris	-	14	-	14	-	14
D. australis	-	11	-	11	-	11
D. bennettii	-	13	-	13	-	13
D. bilineata	-	29	-	29	-	29
D. lalliae	-	10	-	10	-	10
D. linga	-	1	-	1	1	-
D. magna	-	12	-	12	-	12
D. superba	-	1	-	1	-	1
D. winneckei	-	13	-	13	9	4
L. gilberti	-	15	-	15	9	6
L. g. centralis	-	19	-	19	18	1
L. longirostris	-	12	-	12	8	4
L. temporalis	-	12	-	12	2	10
C. decresii	1	13	14	-	14	-
C. fionni	-	13	13	-	13	-
C. ornatus	-	10	10	-	10	-
C. pictus	2	19	14	7	21	-
C. rufescens	-	2	2	-	2	-
C. vadnappa	-	3	3	-	3	-
A. maculatus	-	5	2	3	3	2
A. fordi	-	12	1	11	11	1
A. isolepis	-	62	1	61	14	48
A. scutulatus	-	4	1	3	2	2
A. cristatus	-	19	8	11	15	4
A. caudicinctus	3	31	30	1	31	-
A. reticulatus	7	1	8	-	7	1
A. clayi	1	5	3	3	6	-
A. gibba	12	-	10	2	12	-
A. maculosus	7	3	9	1	10	-
A. nuchalis	16	24	26	14	32	8
A. barbatus	-	21	-	21	-	21
A. minor	-	5	-	5	2	3
A. mitchelli	-	1	-	1	-	1
A. vitticeps	-	16	-	16	-	16

Smth = Smooth. Kld = Keeled.

21).

d. Enlarged Dorsal Scale Rows.

Enlarged dorsal scale rows have been reported in many agamids, but little systematic use has been made of the character. The presence of enlarged scales arranged in either longitudinal or transverse series was recorded in this study to establish whether these features might be useful taxonomically.

Species with strongly heterogeneous dorsal scalation often had some spines arranged in irregular, interrupted transverse or longitudinal series. This type of condition accounted for all individuals scored as possessing both longitudinal and transverse series (Table 22). *Physignathus* was the only genus where tubercles were arranged in regular transverse series.

Regular longitudinal enlarged scale series were present in *A. muricatus*, *A. nobbi*, *Caimanops* and some species of *Diporiphora* and *Lophognathus*. In these species there were usually two enlarged scale rows on either side of the midline, the more lateral being near the dorsolateral skin fold. The longitudinal scale series of *A. cristatus* consisted of spinose scales arranged at irregular intervals along this fold. In *Chlamydosaurus* the more medial scales were much larger than the laterals, and formed short series of from 5 to 10 scales. These rather irregular scale rows account for the large proportion of *Chlamydosaurus* recorded as possessing enlarged dorsal scale rows (Table 22).

e. General Remarks.

Members of the *A. barbatus* species-group had an arrangement of dorsal scales unique to the group. There was an area close to the vertebral line in which the scales were distinctly larger than elsewhere on the dorsal surface (Fig. 30). These scales were deep posteriorly, and

Figure 30. Dorsum of *A. barbatus*. Note large medial scales forming a series of rasp-like corrugations. Note also that scales away from the central area are smaller, with many spinose tubercles.

Table 22. Enlarged Dorsal Scale Rows.

Species	Abst	Long	Long Trns	Trns
Chelosania	6	-	-	-
Gonocephalus	2	-	-	1
Physignathus	-	-	-	12
Moloch	-	9	1	-
T. cephalus	5	1	1	1
T. intima	7	5	-	-
T. lineata	1	1	1	-
T. parviceps	-	4	-	-
T. tetraporophora	10	3	3	-
T. uniformis	-	1	-	-
A. adelaidensis	2	11	3	-
A. diemensis	3	16	26	1
A. muricatus	-	12	-	-
A. nobbi	-	16	-	-
Caimanops	-	23	-	-
Chlamydosaurus	1	13	-	-
D. albilabris	2	12	-	-
D. australis	1	10	-	-
D. bennettii	13	-	-	-
D. bilineata	7	22	-	-
D. lalliae	10	-	-	-
D. linga	1	-	-	-
D. magna	7	5	-	-
D. superba	1	-	-	-
D. winneckei	13	-	-	-
L. gilberti	-	34	-	-
L. longirostris	12	-	-	-
L. temporalis	12	-	-	-
C. decresii	14	-	-	-
C. fionni	13	-	-	-
C. ornatus	9	-	-	1
C. pictus	21	-	-	-
C. rufescens	2	-	-	-
C. vadnappa	3	-	-	-
A. maculatus	5	-	-	-
A. fordi	12	-	-	-
A. isolepis	62	-	-	-
A. scutulatus	4	-	-	-
A. cristatus	1	15	3	-
A. caudicinctus	31	-	-	-
A. reticulatus	6	-	-	2
A. clayi	6	-	-	-
A. gibba	12	-	-	-
A. maculosus	10	-	-	-
A. nuchalis	35	-	4	1
A. barbatus	2	-	18	1
A. minor	1	3	1	-
A. mitchelli	1	-	-	-
A. vitticeps	-	1	14	1

Abst = Absent. Long = Longitudinal.
Trns = Transverse.

the posterior surface of each scale rose to a sharp angled border. These scales together created a surface remarkably similar to a farrier's rasp. Lateral to these enlarged scales there was a broad area of heterogeneous spinose scales with scattered enlarged tubercles. These enlarged spines were almost circular, and therefore nearer the condition of spines in Moloch than any other scales of Australian agamids. On the lateral margin of the trunk was a series of very elongate spinous processes. Some species of the group possessed a single row of these spines while others had several rows.

Discussion.

The dorsal scales of a lizard cover the surface most often exposed to potential predators. In a group of lizards which contains a number of cryptic species the dorsal scalation might be expected to change rapidly as species adapt to new niches. The evidence gathered in the present study, however, suggests that scalation features are reasonably reliable taxonomic indicators.

Gray (1845) recognised that most Australian agamids have irregular scutellation. As this is an almost universal character, it should be regarded as a primitive feature of the endemic radiation. Those species with regular scales might be expected to have developed this character in response to selective pressure acting upon them.

The regular scalation of the Triodia-associated species has already been mentioned (p. 77-78). The development of small, regular scales in A. isolepis, A. fordi, D. linga and, to a lesser extent, D. winneckei produces an appearance not unlike the sand on which these species live. This explanation supports the assumption that the character has been developed independently as a camouflage within the A. maculatus species-group and Diporiphora.

Lophognathus temporalis, L. longirostris and northwestern populations of L. gilberti have developed relatively smooth, regular scalation. No explanation is readily available. The character is helpful in distinguishing the genus from other members of the Chlamydosaurus group.

One of the most distinctive external characters setting Chelosania apart from the other Australian agamids is the alignment of the keels of the paravertebral scales in rows diverging from the midline. This character has not been noted by previous workers. Gray (1845) noted that the ventral scales were "keeled obliquely", but described the dorsals as "placed in cross rings". Boulenger (1885) noted "regular transverse series" of body scales. Of the non-Australian agamids Calotes cristatellus was placed in the genus Bronchocela by Gray (1845) on the basis of this character ("descending series"). Superficial examination of specimens of the species supports Boulenger's (1885) placement of the species in Calotes. The presence of the character in a lizard occurring in Timor and New Guinea is of interest in phylogentetic speculation. There is no question of Chelosania brunnea being transferred to Calotes, but the possibility exists that Chelosania and Calotes cristatellus share a common ancestor.

At least some specimens of Chelosania, Physignathus, Gonocephalus and all genera of the Chlamydosaurus group have keeled ventrals parallel with the midline. All other Australian species have ventrals which diverge from the midline. All the former genera are arboreal, semi-arboreal, or have semi-arboreal members. There is probably a selective advantage in possessing keeled parallel ventrals for arboreal species. These could be important in preventing lateral slipping while climbing, while allowing easy forward progress. This argument is supported by data from the genus Diporiphora, where the more terrestrial species have a higher proportion of individuals with diverging ventral scale rows. The ventrals of these more terrestrial species also tend to be smoother.

Scale rows parallel with the midline have been used to distinguish species within *Lophognathus* (Boulenger, 1883) and *Diporiphora* (Storr, 1974). Among the endemic Australian radiation only members of the *Chlamydosaurus* group usually have parallel scale rows.

The orientation of ventrals and dorsals appears related. *Chelosania* has scale rows continuing from the dorsum onto the venter in a direction peculiar to that genus. All members of the *A. maculatus*, *A. cristatus* and *A. reticulatus* species-groups and *Ctenophorus* have dorsal scale rows converging on the midline and ventrals which diverge from the midline. A species developing ventral scale rows parallel with the midline might be expected to also develop dorsal scale rows parallel with the midline. This expectation is fulfilled in *Diporiphora*, where most scale rows are parallel.

The *A. barbatus* species-group and the *Tympanocryptis* group lack organised dorsal scale rows. Both groups contain mainly cryptic, terrestrial species. Both groups also invariably have ventral scales in rows which diverge from the midline. This is taken to indicate that both groups were derived from species which had the dorsals in rows converging upon the midline.

The condition of dorsal scale heterogeneity of the *Tympanocryptis* group and the *A. barbatus* species-group probably represents another case of parallelism. A third parallel may exist in the condition of the dorsal scales in *A. muricatus*. Here the dorsal scales are less heterogeneous, and scale rows are still discernible, particularly in juveniles. This type of scalation provides excellent camouflage against a background of rough bark or leaf litter. The cryptic geckoes of the genus *Phyllurus* have also developed heterogeneous dorsal scalation. The obvious selective pressure acting to produce this type of scalation, and the general possession of irregular scales in the Australian radiation both suggest that the evolution of this type of scalation three times is not very unlikely.

The distinctive "farrier's rasp" condition of the medial dorsal scales in the *A. barbatus* species-group is a further distinguishing character of the group. No similar condition occurs outside the species-group. *Chlamydosaurus* has a condition nearest that of *A. barbatus*, with larger scales nearer the midline. However, there is a general trend among all Australian endemic agamids for the medial dorsal scales to be larger. *Chlamydosaurus* has probably the largest scales in absolute terms of all the endemic species, and any similarity to the *A. barbatus* species-group is probably because of this fact, rather than any phylogenetic relationship.

14. Premaxillary Teeth.

Boulenger (1885) introduced the use of some features of dentition to the identification of agamids. Moloch constituted one "half" of the first dichotomy of his key. Part of the description for Moloch was "teeth in the upper jaw horizontal, directed inwards". This condition is sufficient to separate Moloch from all other agamids, described by Boulenger as "mouth large; teeth erect in both jaws". Boulenger also used the specialised incisors of Uromastyx to distinguish that genus and Aporoscelis (= Uromastyx, part) from other agamids. This character is not relevant to any Australian species.

The number of premaxillary teeth was not constant for any species where more than 5 specimens were examined (Table 23). The variation in most species appeared to be related to size, with larger specimens having a higher number of teeth. Teeth acquired with increasing size were not obvious by their greater size, suggesting that the original median or medial teeth had been replaced by successively larger teeth. This process of replacement was apparently taking place in many specimens. For example, a large median tooth was often flanked by one tooth on one side and two on the other. The smaller of the two lateral teeth on such specimens was often loose.

Most specimens of most species had an odd number of premaxillary teeth, suggesting there was a median tooth. The exceptions to this generalisation were C. decresii, C. fionni, A. fordi, A. isolepis and A. caudicinctus. Most specimens of these species had 4 premaxillary teeth (Table 23).

All species of Lophognathus normally had 5 premaxillary teeth. This was true also for Diporiphora bennettii. Other species with some specimens with 5 symmetrically arranged teeth were A. muricatus, A.

Table 23. Number of Premaxillary Teeth.

Species	0	1	2	3	4	5	6
Chelosania	-	1	1	4	-	-	-
Gonocephalus	-	1	-	1	-	1	-
Physignathus	-	-	4	1	3	4	-
Moloch	-	-	2	5	-	-	-
T. cephalus	-	-	2	6	-	-	-
T. intima	-	1	4	7	-	-	-
T. lineata	-	-	-	3	-	-	-
T. parviceps	-	-	-	4	-	-	-
T. tetraporophora	-	-	1	15	-	-	-
T. uniformis	-	-	1	-	-	-	-
A. adelaidensis	-	-	4	12	-	-	-
A. diemensis	4	3	10	24	3	-	1
A. muricatus	-	-	-	4	5	2	-
A. nobbi	-	-	-	9	4	3	-
Caimanops	-	1	9	12	1	-	-
Chlamydosaurus	-	1	2	11	-	-	-
D. albilabris	-	-	1	10	3	-	-
D. australis	-	1	-	5	3	2	-
D. bennettii	-	1	-	1	1	10	-
D. bilineata	-	1	2	20	3	2	1
D. lalliae	-	1	-	5	4	-	-
D. linga	-	-	-	1	-	-	-
D. magna	-	-	-	11	-	-	-
D. superba	-	-	-	-	-	1	-
D. winneckei	-	-	-	12	1	-	-
L. gilberti	-	-	1	2	-	12	-
L. g. centralis	-	-	-	3	3	12	-
L. longirostris	-	-	-	-	2	10	-
L. temporalis	-	-	1	-	1	10	-
C. decresii	-	-	-	4	10	-	-
C. fionni	1	-	2	3	7	-	-
C. ornatus	-	1	1	4	3	1	-
C. pictus	-	-	2	19	-	-	-
C. rufescens	-	-	-	-	1	-	-
C. vadnappa	-	-	-	1	2	-	-
A. maculatus	-	-	-	1	3	1	-
A. fordi	-	-	-	4	7	1	-
A. isolepis	-	1	3	17	36	1	-
A. scutulatus	-	-	1	2	1	-	-
A. cristatus	-	-	-	13	6	-	-
A. caudicinctus	1	-	2	4	21	-	-
A. reticulatus	1	1	1	5	-	-	-
A. clayi	-	-	1	5	-	-	-
A. gibba	-	1	-	9	2	-	-
A. maculosus	-	1	1	8	-	-	-
A. nuchalis	3	2	4	30	-	-	-
A. barbatus	1	-	4	13	1	-	-
A. minor	-	-	-	5	-	-	-
A. mitchelli	-	-	-	-	1	-	-
A. vitticeps	1	1	1	13	-	-	-

nobbi, *D. australis* and *D. bilineata* (Table 23). In these species the larger specimens tended to have 5 premaxillary teeth while the smaller individuals had only 3.

With the exception of 2 specimens of *A. gibba* (PMX = 4) no member of the *A. reticulatus* species-group had in excess of 3 premaxillary teeth. One specimen of *A. barbatus*, and the single *A. mitchelli* examined were the only representatives of the *A. barbatus* species-group with more than 3 premaxillary teeth. *Chlamydosaurus* also had 3 or fewer premaxillary teeth.

Discussion.

The modified dentition of *Moloch*, noted by Boulenger (1885) has not resulted in a markedly different number of premaxillary teeth. However, Robinson (1976) claimed that *Moloch*, and some *Uromastyx*, lack pleurodont successional teeth in the anterior part of the jaws. She considered this due to the fact that *Moloch* uses the tongue for prey capture, rendering the caniniform pleurodont teeth of most agamids redundant.

Cooper, Poole and Lawson (1970) decribed the anterior caniniform teeth of agamids as pleurodont. They did not emphasise the distinction between premaxillary and maxillary teeth. They did, however, compare the width of the premaxillae of different genera. *Agama* has a narrow premaxilla with only one tooth. The Australian genera examined by Cooper *et al* included *Amphibolurus* (represented by *A. barbatus* and *A. reticulatus*), which had 3 premaxillary teeth and *Gonocephalus* and *Physignathus* with 4 premaxillary teeth. Cooper *et al* did not appear greatly impressed by the occurrence of a tooth in the median plane, although this was apparently considered normal for *Agama* (1), *Calotes*, *Draco*, *Amphibolurus* (3), and *Japalura* (5). Cogger (1961) noted that the single premaxilla is derived from the fusion of a paired bone, and the possession of a median tooth is therefore surprising. Cogger suggested that the egg-tooth might be retained. Cooper *et al* (1970) noted that the egg-tooth of *A. agama* was lost during the day after hatching, and the median premaxillary tooth was "the first replacement tooth to erupt". This perhaps supports Cogger's suggestion, although Cogger did not seem aware that the premaxillary teeth were replaced. Cogger apparently considered a median tooth normal for all Australian agamids. He noted that *Chlamydosaurus* had a median tooth, and did not mention differences in his comparative osteology section.

Uromastyx apparently does not possess a median tooth. Cooper and Poole (1973) described paired premaxillary teeth in *U. hardwicki*. This was expanded upon by Robinson (1976), who described paired replacement teeth on the premaxilla of four different species of *Uromastyx*, while confirming Cooper and Poole's earlier observation. A detailed study of the premaxillae of all agamids might be rewarding. The possibility exists, however, that *Uromastyx* has lost the median replacement tooth as part of its adaptation to a shearing premaxilla.

Mitchell (1965) noted the premaxilla was reduced in size in *A. reticulatus inermis* (= *nuchalis*). This correlated well with the low number of premaxillary teeth observed in that species. The same may be said for *A. barbatus*, which Mitchell described as atypical of *Amphibolurus* for two reasons, the second being the failure of the premaxilla to "reach beyond the posterior margin of the external nares". Badham (1976) figured the premaxilla as smaller in *A. vitticeps* than in *A. barbatus*. This information is consistent with the theory that *A. nuchalis* may resemble the ancestor of the *A. barbatus* species-group. *A. vitticeps* is considered more primitive than *A. barbatus*, and the smaller premaxilla of

A. vitticeps is nearer the condition of *A. nuchalis*.

The low number of premaxillary teeth of *Chlamydosaurus* does not seem related to a reduced premaxillary bone. Cogger (1961) figured *Chlamydosaurus* with a premaxilla extending well posterior to the external nares. The bone is, however, quite narrow.

The presence of four premaxillary teeth in most specimens of *C. decresii*, *C. fionni*, *A. fordi*, *A. isolepis* and *A. caudicinctus* deserves comment. The premaxillary teeth of these species, and other members of their species-groups, were relatively even in size. Adults had larger teeth than juveniles, indicating that the premaxillary teeth had been replaced. These species may replace the premaxillary teeth more often than most other agamids. This would help to explain the evenness of size. This explanation is supported by the fact that many individuals of these species had teeth apparently in the process of moving onto the premaxilla. A more detailed study is required to establish whether these species have lost the median tooth of the premaxilla. The data collected in this study are not conclusive in this respect.

15. Nostril Shape and Position.

The shape of the nostril has only recently been introduced as a taxonomic character in Australian agamids. Storr (1966) used the "slit-like or narrowly elliptical" nostrils of *A. clayi* to distinguish it from *C. pictus* in his key to the "*A. reticulatus*" species-group. Cogger (1975) used a combination of characters to identify *C. ornatus* from among other *Ctenophorus*. One of these characters was "nostril elliptical".

The position of the nostril relative both to the snout-eye interval and the canthus rostralis has been used several times in Australian agamid taxonomy. Neither character was systematically recorded in the present study as both proved unreliable in the pilot study.

The single *Diporiphora superba* and all individuals of *D. albilabris* and *Tympanocryptis parviceps* were scored as possessing elliptical nostrils (Table 24). Several other species of *Diporiphora*, and *Lophognathus longirostris*, usually had an elongate nostril opening. A substantial minority of *Caimanops* also had elliptical nostrils.

Other species in which a majority of specimens were scored as having elliptical nostrils were *A. gibba* and *A. maculosus*. In *A. maculosus* this was associated with the development of a valve in the nostril. This valve was formed by what appeared to be a shed scale, and was removable.

Most other species usually had circular nostrils, but a few specimens of many species had elliptical nostrils (Table 24).

Discussion.

Elliptical nostrils have been used to characterise *A. clayi* (Storr, 1966) and *C. ornatus* (Cogger, 1975). In neither species were the majority of specimens examined scored as agreeing with these descriptions. Both species possess nasal passages which open at an upward

Table 24. Nostril Shape.

Species	Circular	Elliptic
Chelosania	4	2
Gonocephalus	-	3
Physignathus	12	-
Moloch	5	5
T. cephalus	7	1
T. intima	9	3
T. lineata	2	1
T. parviceps	-	4
T. tetraporophora	16	-
T. uniformis	1	-
A. adelaidensis	14	2
A. diemensis	46	-
A. muricatus	12	-
A. nobbi	15	1
Caimanops	15	8
Chlamydosaurus	13	1
D. albilabris	-	14
D. australis	8	3
D. bennettii	2	11
D. bilineata	27	2
D. lalliae	3	7
D. linga	1	-
D. magna	6	6
D. superba	-	1
D. winneckei	2	11
L. gilberti	34	-
L. longirostris	1	11
L. temporalis	12	-
C. decresii	14	-
C. fionni	10	3
C. ornatus	8	2
C. pictus	20	1
C. rufescens	2	-
C. vadnappa	3	-
A. maculatus	4	1
A. fordi	12	-
A. isolepis	54	8
A. scutulatus	3	1
A. cristatus	19	-
A. caudicinctus	31	-
A. reticulatus	8	-
A. clayi	4	2
A. gibba	4	8
A. maculosus	4	6
A. nuchalis	38	2
A. barbatus	20	1
A. minor	3	2
A. mitchelli	1	-
A. vitticeps	13	3

angle, so that a circular nostril viewed laterally appears elliptical. The degree of intraspecific variation recorded in the present study suggests that nostril shape is not a good diagnostic character.

The direction of opening of nostrils shows more consistent variation than any variation in shape. Most Australian dragons have nasal passages which emerge in a posterior direction. Often there is an upward inclination as well, as mentioned in Storr's (1964) description of *T. parviceps*; "nostril which enters downwards and forwards". Paradoxically, *Tympanocryptis* and the *A. adelaidensis* species-group possess nostrils which enter more nearly perpendicularly to the skin than most other endemic Australian agamids. *Chelosania*, *Gonocephalus* and *Physignathus* have nasal passages which also emerge at a posterior angle, although slight in the latter two genera.

Moloch has distinctive, punctiform nostrils on the dorsal aspect of the head, resulting in high prenostril and subnostril scale counts (see Discussion, Head Scale Counts, p. 116).

Members of the *A. reticulatus* species-group, *A. caudicinctus* and *C. ornatus* possess nostrils which open more nearly vertically than most other species examined. There may be internal modifications of the nasal passages associated with this external feature. A more detailed study of this structure could be rewarding.

The development of a valvular structure in the nostril of *A. clayi* and *A. maculosus* of the *A. reticulatus* species-group is interesting, and probably highly adaptive. Mitchell (1973) described an ability of *A. maculosus* to "swim" in the loose sand beneath the salt crust of its normal habitat, and a valvular nostril would surely be useful in those circumstances. However, the structure is delicate, and often lacking in preserved specimens. The structure of the valve has not been investigated closely, but observations in this study suggest that it may be the remnant of a shed scale. Such "valvular" obstructions of the nostril were not infrequently observed in a wide range of species.

16. Ventral Colour Pattern.

Storr (1965) used the extent of the black ventral markings of members of the *A. maculatus* species-group to assist in the definition of species. The ventral colour pattern has also been used in the definition of a subspecies of *A. adelaidensis* (Storr, 1977) and a race of *Diporiphora winneckei* (Houston, 1977). Humphries (1972) considered the ventral colour patterns important in differentiating species-groups, but did not treat the subject extensively. The ventral colour patterns of some other species have been well illustrated (Houston, 1978), but no taxonomic use above the species level has been attempted in published literature.

Colour characters proved to be difficult to record in preserved specimens and a systematic attempt to record colour patterns was abandoned after the initial pilot study. However, some species had permanent black ventral markings which faded little if at all in preserved specimens. The taxonomic occurrence of these markings is presented below.

Permanent black ventral markings were characteristic of males of a number of species. *A. caudicinctus*, *A. cristatus*, and all species of *Ctenophorus* had a rhomboidal black chest patch. The development of this marking varied, but the widest portion corresponded with the base of the forelimbs, and the patch was usually longer than wide. A similar marking was typical of *A. isolepis* and *A. scutulatus*. *A. maculatus* had a chevron-shaped chest pattern, and *A. femoralis* a transverse bar across the chest. *A. fordi* possessed only a few spots on the anterior part of the chest and on the gular region.

In the *A. reticulatus* species-group *A. nuchalis* and *A. reticulatus* lacked black chest and throat markings. *A. gibba* possessed a series of three spots in the ventral midline, the first in the mental region, the second on the throat and the third on the chest. *A. maculosus* had a median stripe from the chin to the throat. *A. clayi* had a dark collar near the gular fold.

No other Australian agamid possessed these permanent chest markings. The *A. muricatus* species-group and *Lophognathus* were able to change the colour of the chest to black, but this was not permanent.

Discussion.

The presence of permanent black ventral markings in males is a character useful in distinguishing three species-groups of Australian agamids. Thus the *A. cristatus*, *A. maculatus* and *A. reticulatus* species-groups are characterised by most species possessing the feature, as is *Ctenophorus*. This character, and a combination of other features, suggests that this group is monophyletic. Only three species of the group do not have distinct black ventral markings. *A. fordi* has a few dark spots on the chest and throat, but has lost any distinctive black area. The black neck or chest patch in other species is a male feature, probably used in territorial displays. The loss of the black patch in *A. fordi* may be related to the less dominant role played by the male in the mating behaviour of that species (Cogger, 1978). The complete loss of black ventral markings is less explicable in *A. nuchalis* and *A. reticulatus*.

The dark ventral markings of *A. adelaidensis* (Storr, 1977) and of some *Tympanocryptis lineata* (Houston, 1978) are in the form of reticulations, and are not similar to the markings of *Ctenophorus*. The ventral stripes of *D. winneckei* (Houston, 1977) are not permanent. No member of the *Chlamydosaurus* group possesses permanent black ventral markings.

17. Colour Change.

The ability of lizards to change colour has not been used taxonomically, at least in the Australian agamids. The present investigation sought taxonomic correlations with the differing ability of species to change colour.

No term is in wide use to describe colour change of whole animals. Bradshaw and Main (1968) used the term "metachromatism" to describe colour change in "Amphibolurus" lizards. This term is defined in current dictionaries as a synonym of metachromasia. Metachromasia is the property of some tissues which can change the colour of certain vital dyes in the process of staining. It is suggested here that "metachromatism" should be restricted to the description of the ability of some animals to change their colour over a brief period. Colour changes over a more prolonged period, such as seasonal breeding plumage in birds or the successive instars in insects, are not comparable processes.

Bradshaw and Main (1968) defined two types of metachromatism. One they called "pattern changes". They associated these changes with the cryptic species they studied and presumed this ability constituted an attempted camouflage. The other mode of colour change they called "albedo changes" or "blanching". This mode of colour change was associated with raised body temperatures.

Blanching of lizards at high temperatures has been recognised by many other investigators. Krehl and Soetbeer (1899) were probably the first to record the phenomenon, reporting that it occurred at body temperatures of 41°C in the agamid Uromastyx (from Hamilton, 1973). Others to report blanching at elevated temperatures have been Norris and Lowe (1964), Norris (1967), and Pearson (1977), all of whom worked on iguanids.

Remarkably little has been published on the use of colour change in lizard display behaviour. Gibbons (1979), however, noted that species of Ctenophorus possessed the ability to "intensify markedly" the colour of a red or orange area on the underside of the tail during territorial displays.

The observations of Bradshaw and Main (1968) and Gibbons (1979) suggest the Australian dragons utilise metachromatism in three functions. These functions of camouflage, temperature regulation and territorial display have not been correlated taxonomically. An investigation into the distribution of these abilities among taxonomic groups could provide evidence of phylogenetic importance.

Colour changes which caused a change in pattern were observed in a number of species. These species, and others observed in the field for some time without such changes being observed are listed in Table 25. Descriptions of the observed pattern changes are presented below.

Female and non-breeding male A. muricatus were normally light grey in colour, with darker reticulations, blotches and stripes. Males in breeding colouration were mainly black. The throat and anterior part of the ventral surface became intensely black. The dorsum of the head, the vertebral strip, and the sides of the trunk became very much darker than their usual shade of grey, leaving two stripes of a much lighter colour dorsolaterally. These pale stripes appeared white by contrast, and were certainly paler than the same areas in the "cryptic" colour pattern. Captured males in these breeding colours returned to the cryptic colour phase over a period of one or two hours. The darker pattern in these animals was restored within minutes of physiological stress being applied, such as an intraperitoneal injection of cold fluid.

A. nobbi closely resembled A. muricatus in metachromatic ability.

Breeding males of *A. nobbi* were capable of becoming black on the throat and chest. Both lips were considerably paler, and appeared white by contrast. A yellow flush covered much of the trunk, and the pale dorsolateral stripes of the breeding colour phase were bright yellow. Unlike *A. muricatus*, the dorsal surface did not darken markedly, but became more brownish and the pattern became less distinct.

Table 25. Metachromatism.

Metachromatic Species	Non-metachromatic Species
Results of Present Study	
A. muricatus	Physignathus lesueurii
A. nobbi	T. tetraporophora
D. albilabris	A. diemensis
D. australis	C. decresii
D. bennettii	C. pictus
D. bilineata	A. fordi
L. gilberti centralis	A. nuchalis
A. barbatus	
A. vitticeps	
Literature Records	
Gonocephalus sp.[1]	C. ornatus[5]
Chelosania[2]	A. caudicinctus[4,5]
A. adelaidensis[3]	T. cephalus[4]
Chlamydosaurus[4]	A. nuchalis[4,5]
Diporiphora sp.[4]	
A. minor[5]	
A. minimus[5]	

1. McCoy (1978). 2. Greer (Pers. Comm.).
3. Tyler (1960). 4. Stammer (1976).
5. Bradshaw & Main (1968)

Many species of *Diporiphora* possessed a black "shoulder patch". This patch showed a remarkable ability to appear and disappear. A rather plain lizard when killed often developed the black patch during fixation and appeared quite different post mortem. Other colour changes normally accompanied the appearance of the black shoulder patch. In most species two dorsolateral light lines became more prominent in the "patch" colour phase, and the pattern between these lines became less distinct. Colour changes of this type were observed in D. bilineata and D. australis during the present study.

The shoulder patch of D. australis was more anteriorly placed than in most Diporiphora, forming a 7-shaped mark on the left side of the neck. The more vertical stroke ran upwards behind the scapular fold, and the horizontal bar ran anteriorly across this fold. The dark area in D. albilabris was similar. D. bennettii, D. lalliae, D. magna and D. bilineata had more circular black areas on or behind the scapular fold. In view of the similar nature of these dark areas, and the close relationship of the species possessing them, it was considered probable that all these species were able to change their colour pattern.

Shoulder patches were not observed in D. winneckei, D. linga or D. superba. Only one specimen each of the latter two species was seen. The apparent absence of a shoulder patch from D. winneckei was not considered evidence against the possibility of the species being metachromatic. Living specimens were not available for study.

Lophognathus gilberti centralis in its cryptic colour phase was very similar to A. muricatus. However, a lighter area was present on the lower lip, continuing back below the tympanum to the angular fold of skin covering the posterior jaw muscles. This area in the darkened individuals of both sexes became tinted with purple, but otherwise matched the surrounding grey colouration, so as to be indistinguishable in a monochrome photograph. At most times the area was very light grey to white in colour. In males in the breeding season this pale area became brilliant white. At the same time much of the rest of the anterior half of the body became black. The pale dorsolateral stripes appeared white by contrast, particularly anteriorly, and may have become paler, but were not the same brilliant colour of the white lip area. Colour change on the tail and hind limbs was not so pronounced.

Living specimens of the other species of *Lophognathus* were not observed. All taxa in *Lophognathus* possessed the distinctive white area on the lower jaw. Observed variation in the colour of this area in preserved *Lophognathus* of all taxa suggested that the metachromatic abilities observed in *L. g. centralis* are shared by the other species of the genus.

Sections of the skin from the lower jaw of *L. gilberti* were made and examined without staining. The pigment of the chromatophores of the jaw stripe area transmitted more red light than the pigment of chromatophores at other parts of the section. This difference in the pigment might explain the difference in the colour of the area in living specimens.

The dorsal surface of *A. barbatus* was normally patterned in light and dark grey. The pattern was recognisable while the colour shade changed from nearly black to light grey. Under physiological stress the dorsal colour pattern was lost, the whole dorsum becoming light brown. At the same time the legs, normally barred light and dark grey, became pale yellow. This colour pattern could be induced by raising the animal's temperature to very high levels, or by the administration of an intraperitoneal injection of cold fluid. In territorial and defence displays *A. barbatus* was capable of darkening the skin of the transverse gular pouch. This colour change could be made independently of the colour of the rest of the body.

A. vitticeps was capable of a similar range of colour change as that observed in *A. barbatus*.

Chromatophores were observed in the skin of all specimens sectioned to examine the dorsal median vascular tissue (see Table 5). These cells differed very little in form in different species. A quantitative assessment was not attempted. The only sections prepared specifically to examine chromatophores were those of the jaw area in *L. gilberti* discussed above, and "control" sections of the same area in *A. muricatus*.

Discussion.

The ability to change colour has attracted considerable comment in the literature. Much of this comment has been of a fragmentary nature. An attempt has been made here to bring the data relevant to the Australian agamids together to add to the information reported in the results (Table 25).

The Australian members of *Gonocephalus* have not been studied extensively, and have not been reported to change colour. *G. godeffroyi* in the Solomon Islands was reported to change colour "dependent upon the lizard's mood" (McCoy, 1978). McCoy referred specifically to the "ground colour" as being changeable, noting that the animal darkened considerably at night and when alarmed. There may, therefore, be both temperature-dependent (night) and territorial ("mood") colour changes. As there is little doubt that the Australian *Gonocephalus* are congeners of *G. godeffroyi* the genus should be considered metachromatic.

Little is known about the biology of *Chelosania*. Greer (pers. comm.) noted that a specimen observed over a number of days changed from light to dark phases. In the dark phase a black spot appeared on the neck anterior to the forelimb, and the bands on the tail became more prominent. These observations suggest the genus is capable of both an "albedo" and a "pattern" change of colour.

Tyler (1960) noted rapid colour changes in specimens of *A. adelaidensis* moved from dark to light surfaces and vice versa. His comment that "a pattern of markings appeared that had not been observed in the field" appears to place these colour changes in the "pattern" category.

The identification of Tyler's specimens has been questioned by Houston (1978). He noted that no specimens of *A. adelaidensis* were available to him from Tyler's study area, and that some of Tyler's specimens exceeded all other known *A. adelaidensis* in size. Houston's suggestion that these specimens were *Tympanocryptis lineata* is dismissed, as three strong characters were included in Tyler's descriptions of his specimens. Hind limb lengths were measured relative to the tympanum (absent in *Tympanocryptis*), pores varied in number from 20 to 30 (up to 2, or at most 4, in *T. lineata*), and "outwardly projecting spines" were present on the base of the tail (absent in *Tympanocryptis*). It is possible that Tyler's specimens represent an otherwise undescribed taxon closely related to *A. adelaidensis*.

Tyler's report conflicts with the information gathered in the present study. No other species of the *Tympanocryptis* group exhibits obvious metachromatism. In fact Stammer (1976) claimed that *T. cephalus* lacks the ability to change colour. Tyler performed experiments specifically designed to elicit camouflage-related colour change. This type of work has not been reported for any other species of Australian agamid. It is possible that Tyler has subjected his animals to the one set of conditions which maximise the metachromatic response. Similar experiments using other members of the *Tympanocryptis* group may prove interesting. However, the identification of Tyler's specimens should precede further speculation on the subject.

Changes in colour pattern have been described in *Chlamydosaurus*. Stammer (1976) described a "large, bold network pattern" of dark grey superimposed over a "medium-grey body colour" which could fade "in minutes to an all-over putty colour". Stammer suggested that the more pronounced colour pattern was effective as camouflage when the lizard was at rest in a tree. The reason for the other colour pattern was not suggested. Other authors have not described these colour changes. Cogger (1975) described a number of colour patterns, but implied that these occur in different individuals. Stammer is one of the few herpetologists who has observed *Chlamydosaurus* for prolonged periods in the field, including periods over the breeding season. It is possible that *Chlamydosaurus*, like *Lophognathus* and *Amphibolurus*, changes colour in a more spectacular manner during the breeding season.

Stammer (1976) reported colour changes in *Diporiphora* in the Mount Isa area. He mentioned a transient black mark "behind and below each shoulder" on each side of the chest. His descriptions agree closely with the reports in the present study of colour change in *D. bilineata*.

Cogger (1975) described a "pale cream or white dorso-lateral stripe" in *Lophognathus gilberti* and a "broad, pale dorso-lateral stripe" in *L. temporalis* and commented that the "intensity" of these stripes was "subject to rapid changes" in both species. Observations of *L. gilberti* by the author suggested that these stripes changed little in colour, but the surrounding darker areas changed colour rapidly, altering the degree to which the stripes contrast with their boundaries. Cogger's comments clearly refer to this phenomenon. Houston (1978) noted the ventral surface of *L. longirostris* was "white dappled or variegated with grey (possibly becoming black at times in males)". Houston mentioned that *L. gilberti* males "may become black laterally and ventrally". Houston evidently suspected that both these *Lophognathus* were metachromatic.

Ctenophorus decresii, *C. fionni* and *C. vadnappa* were recently studied by Gibbons (1979). He reported that the red or orange colour on the ventral surface of the tail of these species "intensified markedly" during displays. He made no other specific reference to colour change. *C. ornatus* was studied very extensively by Bradshaw (1971), yet Bradshaw and Main (1968) specifically denied that *C. ornatus* possessed any metachromatic ability. *C. ornatus* males possess a red flush on the ventral surface of the tail, and it seems likely that a study of territorial displays similar to Gibbons' (1979) work might reveal a limited metachromatism. Bradshaw and Main concentrated heavily on thermal behaviour, and a strictly communicative metachromatism might easily have been overlooked. The author's limited field observations of *C. decresii* detected no metachromatic ability.

No metachromatism was observed in this study for any member of the *A. maculatus*, *A. reticulatus* or *A. cristatus* species-groups. Temperature related blanching has been reported for *A. fordi* of the *A. maculatus* species-group (Cogger, 1974), *A. nuchalis* of the *A. reticulatus* species-group (Heatwole, 1970; Bradshaw and Main, 1968; Stammer, 1976), and in *A. caudicinctus* of the *A. cristatus* species-group (Bradshaw and Main, 1968; Stammer, 1976). Each of these species has been the subject of considerable research, and the failure of any report to mention display or camouflage related colour changes in them suggests strongly that these types of colour change are at least not obvious. This is particularly true of *A. nuchalis* and *A. caudicinctus* which both Bradshaw and Main (1968) and Stammer (1976) specifically deny are capable of pattern changes.

Mitchell (1973) reported a colour change in *A. maculosus* following flooding of their normal habitat, forcing a shift to nearby sand areas. He described the "background colour" darkening and the normal spots typical of the species becoming "more numerous and intense". Unfortunately no time scale for these changes was given, although one may infer a relatively slow change as the changes were for periods of weeks to months.

Houston (1978) reported that brightly coloured individuals of *A. cristatus* lost their yellow or orange tints within minutes of capture. This account contrasts with the character of the yellow and red colours of *A. nobbi*. In that species the yellow and red colouration intensifies seasonally, and is more or less prominent when the animal is light or dark respectively. It is possible that this occurs also in *A. cristatus* and Houston has not recognised the general darkening of the animal to obscure the bright colours. More observation of this phenomenon is needed.

Bradshaw and Main (1968) reported "pattern" changes in *A. minor* and *A. minimus*. These observations agree with pattern changes reported in the present study for other members of the *A. barbatus* species-group.

Some broad generalisations are possible with reference to the development of metachromatism. The *A. muricatus* species-group, *Lophognathus* and *Diporiphora* share the ability to change areas to a solid black colour from a light grey or brown. This ability appears better developed or more obvious in males, but is possessed by the females of at least some *Diporiphora*. These genera, *Chlamydosaurus* and the *A. barbatus* species-group are the only groups which definitely show "pattern" changes. In this assemblage only the *A. barbatus* species-group is not within the *Chlamydosaurus* group. The *A. barbatus* species-group differs in that the sexual differences in the development of metachromatism are weak or absent, although this may also be true of *Chlamydosaurus*. The report of Tyler (1960) on *A. adelaidensis* must await positive identification of his material before that species could be added to the group.

Other endemic Australian species lack the ability to change colour patterns rapidly. Stammer (1976) commented on this phenomenon, suggesting that the species unable to change pattern were the "most heat tolerant of all dragons". The species included in this group by Stammer were *A. nuchalis*, *A. caudicinctus* and *T. cephalus*. However, Bradshaw and Main (1968) considered *D. bilineata* the most heat-resistant species they examined, yet Stammer stated that *D. bilineata* underwent "the greatest colour and pattern changes among the dragons of the Mount Isa area". The species grouped by Stammer might better be described as desert-adapted. The reasons for these species losing the ability to change pattern remain open to question. There are, however, broad taxonomic correlations with the ability to change colour. No members of *Ctenophorus*, the *A. maculatus*, *A. reticulatus* or *A. cristatus* species-groups can change pattern. These species-groups are considered more closely related to one another than to other species. Similarly, no member of the *Tympanocryptis* group has been confirmed as capable of pattern changes.

All species of *Lophognathus* share the character of a white lip area. From examination of preserved specimens and photographs it appears that all species are capable of making this area brilliant white in colour. The sections of skin examined in this study suggest that this ability may be due to the development of a different pigment carried in the chromatophores. While many pigments apart from melanin occur in a number of diverse taxonomic groups (Bagnara *et al*, 1979), this pigment appears to be unique among Australian agamids. As such it constitutes a good character supporting the continued recognition of the genus *Lophognathus*.

18. Subdigital Lamellae (L4)(Figs. 3, 31).

The number of lamellae under the fourth toe is a standard taxonomic character in use on lizards. Storr (1964) introduced the character to Australian agamid taxonomy, and continued to use it in his later papers. However, he used it to support only subspecific separations, and even then only on the basis of averaged data. The feature would thus seem to be of limited taxonomic use.

The number of lamellae under the fourth toe of *Moloch* reached a maximum of 6, less than half the number of the next lowest count from an Australian agamid (Fig. 31). *Physignathus* had at least 36 lamellae. Variation within other species-groups prevented the use of the character to distinguish taxa above the species level. However, some general trends were apparent.

The advanced *Tympanocryptis* had a low number of lamellae, up to a maximum of 22 in *T. tetraporophora*. The count was higher in the *A. adelaidensis* species-group and *T. parviceps*, with both *T. parviceps* and *A. diemensis* having a mean number of lamellae in excess of 22 (Fig. 31).

Lophognathus had a relatively high number of lamellae. *L. longirostris* in particular had a high count, with a recorded maximum of 46.

In the *Ctenophorus* group the *A. maculatus* and *A. cristatus* species-groups had a high number of lamellae. By comparison *Ctenophorus*, and particularly the *A. reticulatus* and *A. barbatus* species-groups had low lamellar counts.

Discussion.

The number of lamellae under the fourth toe is likely to be heavily dependent upon toe length. It is therefore not surprising to find the two genera with a reduced phalangeal formula, *Moloch* and *Tympanocryptis*, have the lowest numbers of lamellae. The number of

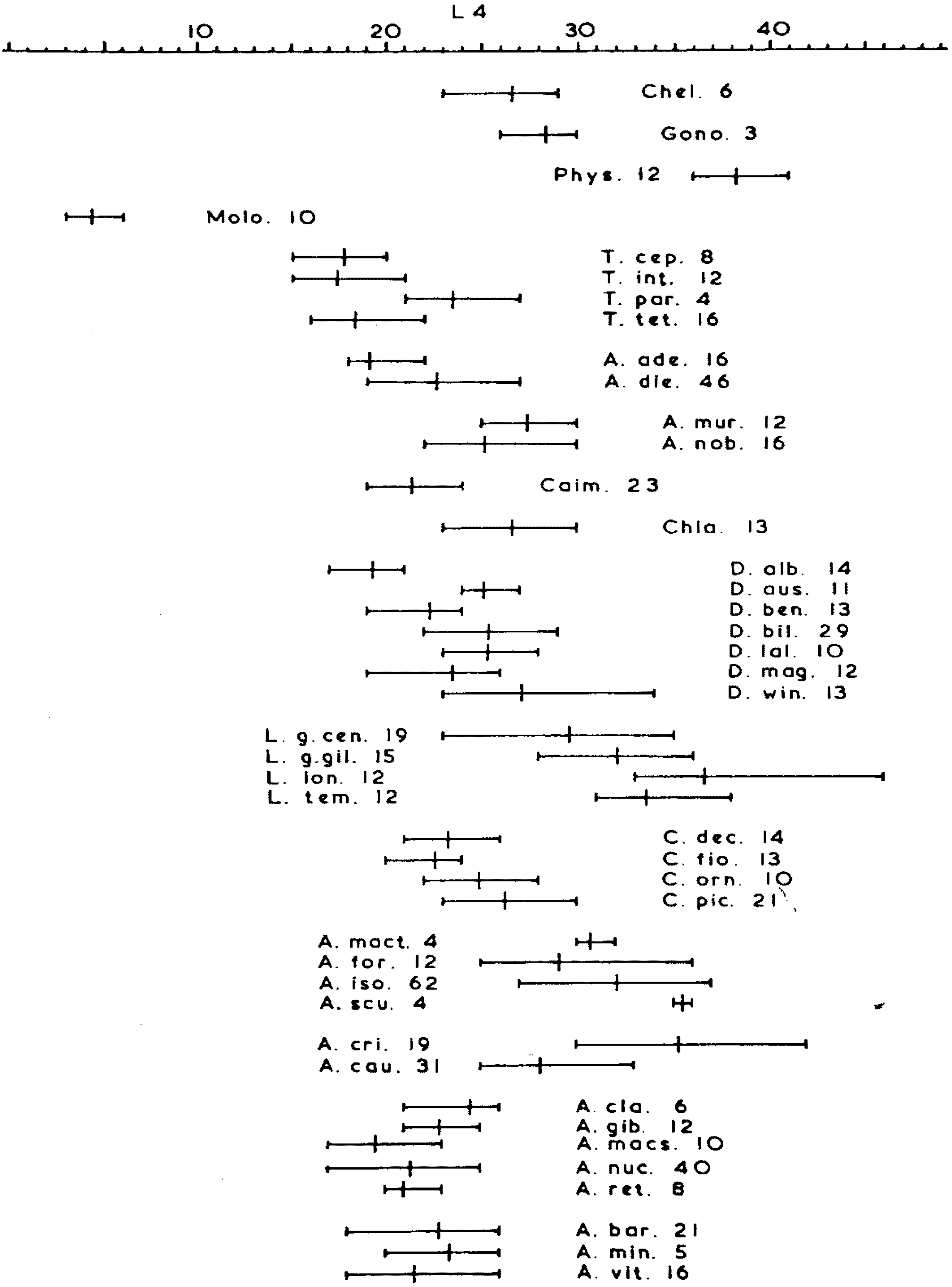


Figure 31. Subdigital Lamellar Counts. Symbols and abbreviations as for Figure 16.

lamellae in *Moloch* is, however, exceptionally low.

Physignathus is ecologically similar in some respects to the American iguanid *Basiliscus*. Both genera are capable of running for a short distance on the surface of the water. While this ability is only weakly developed in *Physignathus*, it is interesting to speculate that the very high lamellar count in *Physignathus* might reflect the beginning of the development of very long toes similar to those possessed by *Basiliscus*.

Terrestrial, cryptic species such as those in *Tympanocryptis* and the *A. barbatus* species-group tend to have fewer lamellae. Fast moving species, such as *A. cristatus* and members of the *A. maculatus* species-group, have long slender toes and correspondingly high lamellar counts. Lamellar counts are probably better ecological indicators than phylogenetic tools.

19. Hemipenes.

Hemipenes are often described and compared taxonomically, particularly in reptiles with a reduced number of external features. Thus the hemipenial morphology of snakes has received much more attention than the same topic in lizards. No data have been published on the hemipenial morphology of Australian agamids.

The hemipenes of Australian agamids were remarkably conservative in structure. Examination of species representing most groups showed almost no variation in hemipenial morphology. Most endemic agamids possessed hemipenes similar to the structure illustrated in Figure 32A. The head of this "typical" hemipenis was somewhat kidney-shaped, with two ornamental whorls surrounding a double depression.

One species, *Diporiphora australis*, possessed different hemipenes (Fig. 32B). The basal structure was similar to other Australian agamids, and the ornamentation of the crown appeared similar. However, the head was bifurcate, and the ornamentation of the two horns was separated by a smooth area between their bases. Bifurcate hemipenes were clearly seen only in *D. australis*, but partially extruded hemipenes approaching this condition were observed in preserved specimens of *D. winneckei* and *D. magna*.

Discussion

Reliable observations of hemipenial morphology could be made easily only on fresh material. Hemipenes extruded at the time of fixation usually invaginated to some extent during fixation, making accurate comparisons of preserved material difficult. Despite this, some taxonomic conclusions may be drawn from the observed variation in hemipenial morphology.

Diporiphora australis has distinctly different hemipenes from all

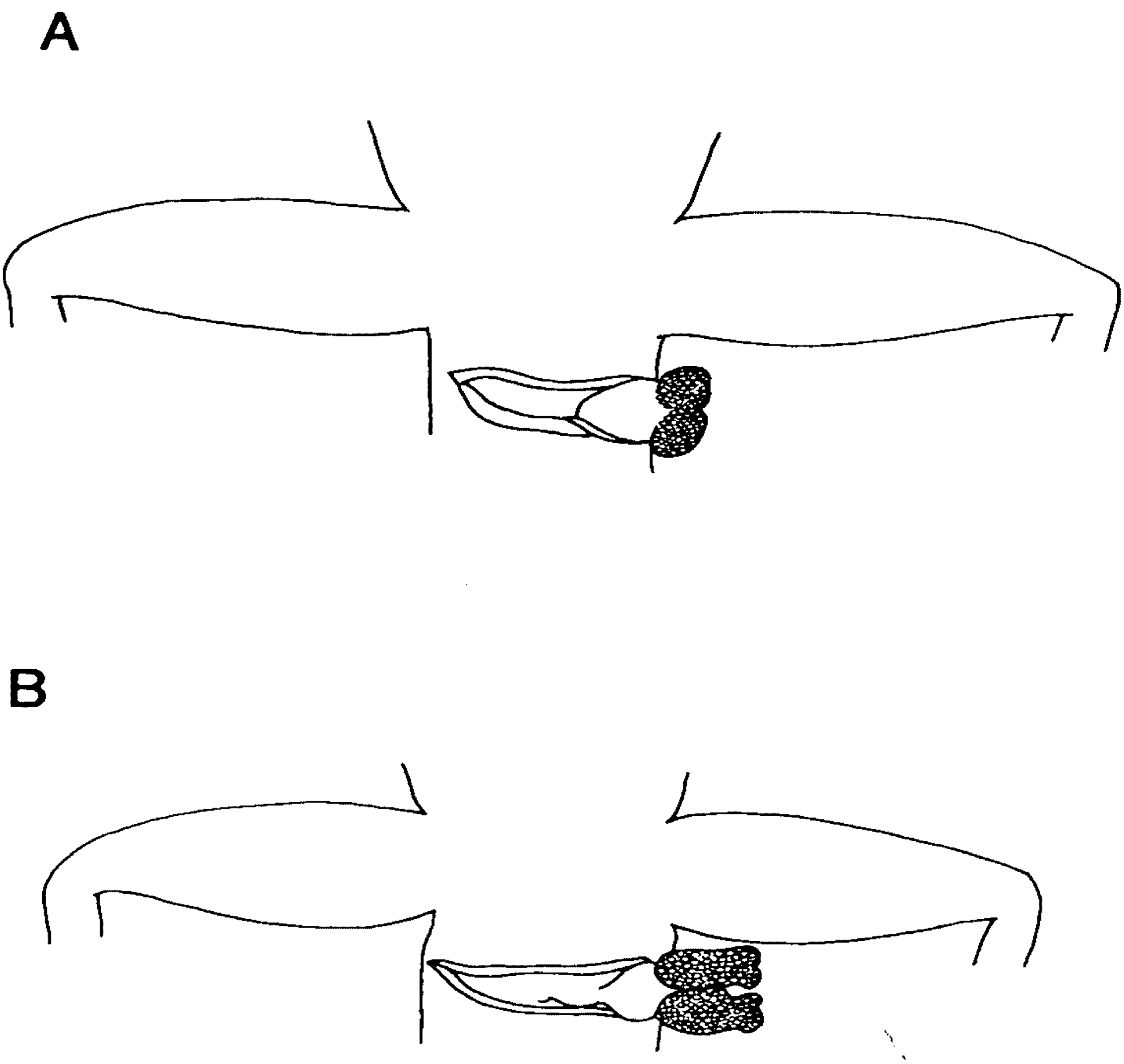


Figure 32. Ventral Aspect of Extruded Hemipenes. A = *Amphibolurus nobbi*; B = *Diporiphora australis*. Note that ornamentation in A is continuous between the two whorls of the hemipenial head. The ornamentation of the two horns of the bifurcate hemipenis of B is separated by a smooth area at their bases. (A drawn from AMF 11386, B from 13665).

species of other genera. *D. australis* closely resembles *A. nobbi* in a number of features, but the latter species does not possess bifurcate hemipenes. The possibility that bifurcate hemipenes are possessed by all *Diporiphora* has some foundation in the observation of at least partially divided hemipenes in *D. winneckei* and *D. magna*. If further work established this as a consistent character for all species of *Diporiphora*, this single character would probably justify the continued recognition of the genus.

The selective pressures acting on hemipenial morphology are largely unknown. It has generally been assumed, however, that the structure of these organs is important at only one point in the life history of each generation, and would not be subject to rapid evolutionary change. It is possible that the ornamentation and variation of the hemipenes of many squamate reptiles may represent reproductive isolating mechanisms. However, data supporting this idea are lacking. Until such data are gathered, the morphology of the hemipenes is probably best considered a conservative character.

20. Other Features.

A number of characters mentioned extensively in the literature of Australian agamids were not systematically recorded in the present study. These features are discussed briefly below.

a. Dermal Frill and Hyoid Apparatus.

Gray (1845) used the possession of a "frill-like expansion" as the distinguishing character for Chlamydosaurus. Although the genus possesses other unique combinations of characters, this one outstanding feature was used in the most recent published key to the genera of Australian dragons (Cogger, 1975).

The frill of Chlamydosaurus consists of a large dermal fold attached across the gular region anterior to the transverse gular fold. On either side of the head the attachment of the frill extends into the temporal region posteromedial to the tympana. The frill is thus discontinuous only across the occipital region, and here the margins of the frill overlap when the frill is folded. In adults the frill extends back to the forelimbs, abutting the chest ventrally and overlapping the upper parts of the arm laterally. In hatchlings and juveniles the frill is relatively smaller, a fact noted by Gray (1842). There is no apparent sexual dimorphism in the development of the frill.

South of the range of Chlamydosaurus, A. barbatus is frequently referred to as the "frilled lizard". The structure causing this name is a transverse gular pouch. It is marked externally by a transverse row of spinose scales.

The frill of Chlamydosaurus and the beard of A. barbatus share some characteristics. Both structures are supported by the first ceratobranchials of the hyoid apparatus (Cogger, 1961). The second ceratobranchial has been lost in both species (Cogger, 1961). However, only

A. barbatus and *A. nullarbor* of the *A. barbatus* species-group have lost the second ceratobranchial. All other species of the group retain this element (Badham, 1976). Both structures are used behaviourly in defence displays, and may have developed for that purpose.

The beard of *A. barbatus* and the frill of *Chlamydosaurus* differ in their basic structure. The beard is an expanded gular pouch, and is only evident when distended. At other times the loose skin of the beard folds onto the posterior part of the throat, forming a second gular fold anterior to the permanent fold. The frill, by contrast, is a dermal fold attached along a relatively immobile line across the throat. The gular pouch of *Chlamydosaurus* is not enlarged, and does not extend into the frill. There is no fringe of spinose scales on the frill. These differences suggest that the two structures probably developed independently. The many other features separating the two groups add weight to this argument.

The similarities between the beard and the frill are not of a nature suggesting close phylogenetic links. Most Australian dragons are capable of distending the gular pouch to some extent. The hyoid apparatus supporting this distension does so transversely in all endemics. An enlarged gular fold developed by any endemic Australian agamid might reasonably be expected to be supported by the outer elements of this hyoid apparatus. Such is the case, as both the beard of the *A. barbatus* species-group, and the frill of *Chlamydosaurus* are supported by the first ceratobranchials (Cogger, 1961; Badham, 1976). In contrast to the Australian endemic agamids all three Asian-derived genera have a median longitudinal gular fold. Distension of this fold might be expected to be supported by the more medial parts of the hyoid apparatus. The second ceratobranchial is much longer in *Gonocephalus* than in the endemic

Australian genera (Cogger, 1961), strongly supporting this idea.

b. Nuchal Hump.

The nuchal hump of *Moloch* was described by Gray (1845) as a "convex tubercle". The feature is quite unique. Cogger (1975) included its presence as one of several features identifying the genus in his key to the genera of Australian dragons.

It has been suggested that the hump functions to deter predators (Pianka and Pianka, 1970), but evidence is lacking. Cogger (1967) noted that *Moloch* "pulls its head protectively down between its front legs, leaving the head-like hump in the position normally occupied by the head itself". This "false head" function for the hump appears plausible, but Cogger also notes that it is rare to find a specimen with a damaged hump, and concluded that the "primary function" of the hump "is still unknown".

c. Body Form.

Body form was accorded considerable importance by early workers on the agamids. Gray (1845) and Boulenger (1885) both used differences in body form to separate groups above the generic level.

In more recent studies body form has been dropped as a diagnostic character. While consistent differences occur, particularly between arboreal and terrestrial genera, these differences are seldom found between closely related genera, and are therefore seldom diagnostically useful. Differences also occur during ontogeny. Storr (1967) noted that body form changes quite markedly during ontogeny in *A. caudicinctus caudicinctus*: "As males mature, tail and (to smaller extent) body become laterally compressed". Storr claimed that this ontogenetic change was responsible for the failure of earlier workers to recognise specimens of *Amphibolurus imbricatus* Peters as juvenile *A. caudicinctus*.

All Australian agamids possess some ability to alter their body shape with rib movements. This ability is best developed in the *A. barbatus* species-group. *A. barbatus* is capable of depressing the trunk so that it appears almost circular from above and is about five times as wide as deep. This behaviour is associated with both defence and thermoregulation. At other times the body is moderately depressed, about one and a half times to twice as wide as deep.

The ability to change body shape makes comparisons of body form difficult. In general terrestrial species are more depressed, and arboreal and semi-arboreal species more compressed, a trend noted by Gray (1845). With the exception of the *A. barbatus* species-group, there is not a great variety in this character in Australian agamids. *Gonocephalus*, which is a little deeper than broad, represents one extreme. *Tympanocryptis* is probably the most depressed genus, but is at most about twice as wide as deep.

Little phylogenetic weight has been attached to body form in the present study because of the difficulty in quantifying the character. Also, apart from the extreme ability of the *A. barbatus* species-group to flatten the trunk, no species greatly departed from a roughly cylindrical body form.

21. General Discussion.

The function of preanal and femoral pores is still open to question, but the most favoured hypothesis is that they function in marking territories (Cole, 1966b). The secretion of the glands does not have a strong characteristic odour, and so would seem unlikely to function as do the musk secretions of many mammals. However, many lizards, including agamids, protrude the tongue at regular intervals. These lizards have been presumed to transfer minute particles from the substrate to their Jacobson's organ (Gravelle and Simon, 1980). This habit may enable the preanal and femoral gland secretion to act as a "taste" territorial marker.

Pore number, arrangement and type are useful characters in distinguishing the Chlamydosaurus group as a taxonomic unit. This group contains mainly "perching" species, males of which defend territories by visual means from an elevated site. The importance of preanal and femoral pores is likely to be diminished in such semi-arboreal species. The reduction in number of pores in most members of the group is circumstantial evidence supporting this idea. Further support is derived from the fact that L. longirostris and D. albilabris, the most terrestrial species in their respective genera, also have more pores than their congeners.

Gravelle and Simon (1980) have presented further circumstantial evidence to support this theory. They noted that a terrestrial iguanid species protruded the tongue far more frequently than an arboreal species.

The type of visual display used in territorial defence is also likely to be affected by the assumption of a semi-arboreal habit. A terrestrial species may display ventral markings by performing headbobbing and push-up displays. These ventral markings would be effectively hidden by flattening against the substrate. A perching lizard would be unable to conceal ventral markings as easily. The development of transient display markings in the *Chlamydosaurus* group might also be an adaptation to a perching habit. The other group with highly developed metachromatic ability, the *A. barbatus* species-group, also defends territories from a perching site.

Many members of the *Chlamydosaurus* group possess other adaptations to an arboreal existence, such as the possession of keeled, parallel ventral scale rows. It is therefore remarkable to find that only one species of the group, *Diporiphora superba*, appears to have become entirely arboreal.

Within the *Chlamydosaurus* group *Chlamydosaurus* and *Caimanops* stand out as the two most distinctive species. *Chlamydosaurus* possesses the distinctive frill, but also has evolved a number of features distinguishing it from other members of the group. *Caimanops* is not so dramatically different as is *Chlamydosaurus*, but still possesses a number of distinctive features. There is the small "rostral crest" of strongly keeled scales on the snout, and the scales are much smaller than other genera of the *Chlamydosaurus* group.

The more terrestrial Australian agamids include three distinctive groups. *Moloch* is one of the most distinctive lizards of the world. Its nuchal hump, modified dentition, reduced phalangeal formula and lack of pores set this genus far from any other endemic agamid.

The *A. adelaidensis* species-group and *Tympanocryptis* form another discrete, distinct group. All species in this group are small, cryptic and terrestrial. Their relationships to other species-groups are not clear. The *A. adelaidensis* species-group retains the primitive pore arrangement, so the group may be considered more closely related to the *Ctenophorus* group than to members of the *Chlamydosaurus* group.

The other terrestrial species show clear relationships to each other. The most distinctive species-group is that of *A. barbatus*. This species-group has diverged markedly from all other endemic agamids, but three apparently conservative characters point to the group being related to *A. nuchalis* of the *A. reticulatus* species-group. *A. nuchalis* and all members of the *A. barbatus* species-group share a peculiar derived pore arrangement. The *A. barbatus* and *A. reticulatus* species-groups are the only Australian agamids with a spinous row of scales on the lower eyelid. A premaxilla reduced in size also suggests that these species-groups are related.

The *A. reticulatus* species-group provides a link between the *A. barbatus* species-group and other terrestrial Australian agamids. *Ctenophorus*, the *A. maculatus* and the *A. cristatus* species-groups share the character of a permanent black ventral marking with some members of the *A. reticulatus* species-group. The latter species-groups lack the regular postauricular scale row of *Ctenophorus*, and tend to have longer digits. The *A. maculatus* species-group is distinguished by its development of relatively homogeneous dorsal scalation. The *A. cristatus* species-group exhibits the best developed vertebral scale ridge of the *Ctenophorus* group, and often has interscalar pores.

22. Summary

Phylogenetic polarity has been assigned to many characters. These are summarised in Table 26 below.

Table 26. Phylogenetic Polarity of Morphological Characters.

Character	Primtve	Unknown	Derived
Lacrymal bone present	+		
Preanal or femoral pores present	+		
Pore arrangement similar to *Physignathus*	+		
Pore arrangement similar to *A. nuchalis*			+
Pore arrangement similar to *Tympanocryptis*			+
Pore arrangement similar to *Chlamydosaurus*			+
Interscalar pores			+
Posterior intrascalar pores	+		
Ventral intrascalar pores			+
Tympanum absent			+
Scale-covered tympanum			+
Reduced phalangeal formula			+
Median dorsal scale ridges	+		
Dorsal vascular tissue	+		
Postauricular furrows (*Chelosania*)			+
Gular and scapular folds	+		
Postauricular folds		+	
Scapular tubercle			+
Postauricular scale row		+	
Gular scale row			+
Occipital crest			+
Loreal scale row	+		
Eyelid fringe			+
Rostral crest			+
Elongate labials		+	
Scale heterogeneity (Australian endemics)	+		
Enlarged dorsal scale rows		+	
Medial scales forming "farrier's rasp"			+
Low number of premaxillary teeth		+	
Metachromatism	+		
White lip stripe (*Lophognathus*)			+
Bifurcate hemipenes			+
Dermal frill			+
Second ceratobranchial absent			+
Gular pouch longitudinal		+	
Nuchal hump			+

Australian agamids are divisible into two major groups:

I. Asian-derived Genera, characterised by:

a. Lacrymal bone present.

b. Gular pouch longitudinal, with a relatively long hyoid apparatus.

and:

II. Endemic Australian Genera, characterised by:

a. Lacrymal bone absent.

b. Gular pouch transverse, with a relatively short hyoid apparatus.

c. Preanal and femoral pores present (except *Moloch*).

There are three Asian-derived genera in Australia. These are listed below with their distinguishing characters.

1. *Chelosania*.

a. Five or six deep postauricular furrows.

b. Gular fold incomplete mid-ventrally.

c. Paravertebral scales in posterolateral rows.

d. Labial scales not elongate.

e. Preanal and femoral pores absent.

2. *Gonocephalus*.

a. Labial scales not elongate.

b. Preanal and femoral pores absent.

3. *Physignathus*.

a. Preanal and femoral pores in primitive arrangement.

b. Labial scales elongate.

c. Loreal scale row present.

d. Regular transverse rows of enlarged scales.

The endemic Australian genera can be placed into four supra-generic groups, listed below.

A. Moloch Group.

a. Preanal and femoral pores absent.

b. Phalangeal formula of both manus and pes reduced to 2.2.3.3.2.

c. Median dorsal scale ridges absent.

d. Labial scales not elongate.

e. A prominent nuchal hump.

f. Nostrils on dorsum of snout.

g. Modified dentition.

h. Loreal scale row absent.

i. Scales relatively small.

j. Tympanum superficial.

B. Tympanocryptis Group.

a. Interscalar pores.

b. Pores relatively widely spaced.

c. Loreal scale row reduced or obscure.

d. Labial scales elongate.

e. Ventral scales always in posterolateral rows.

f. Dorsal scales strongly heterogeneous.

C. Chlamydosaurus Group.

a. Derived pore arrangement.

b. Ventral intrascalar pores.

c. Distinct preanal and femoral pore series.

d. Postauricular skin relatively immobile.

e. Loreal scale row absent or obscure.

f. Labial scales elongate.

g. Scale rows often parallel with midline.

h. Ventral scales keeled.

i. Scales relatively large.

j. Median premaxillary tooth usually present.

k. Permanent black ventral markings absent.

l. Metachromatic.

D. Ctenophorus Group.

a. Pores interscalar or posterior intrascalar.

b. Inguinal interruption to pore series absent.

c. Postauricular skin relatively loose.

d. Labial scales not elongate.

e. Scales relatively small (except *A. barbatus* species-group).

f. Ventral scales always in posterolateral rows.

There are 13 Australian endemic genera or generic groups. These are listed below with their distinguishing features.

1. Moloch (Moloch Group).

Distinguishing features as for group.

2. A. adelaidensis Species-group (Tympanocryptis Group).

a. Primitive pore arrangement.

b. Group of spinose tubercles on base of tail.

c. Nuchal scale ridge often present.

3. Tympanocryptis (Tympanocryptis Group).

a. Tympanum absent.

b. Pes phalangeal formula of 2.3.4.5.3.

c. Derived pore arrangement (except *T. parviceps*).

d. Nuchal scale ridge reduced or absent.

e. Vertebral scale ridge absent.

f. Not metachromatic.

4. A. muricatus Species-group (Chlamydosaurus Group).

a. Nuchal and vertebral scale ridge present.

b. Posterosuperior postauricular skin fold.

5. Caimanops (Chlamydosaurus Group).

a. Nuchal and vertebral crests in adult males.

b. Femoral pores usually absent.

c. Posterosuperior postauricular skin fold.

d. Rostral crest present in adult males.

e. Relatively small scales.

6. Chlamydosaurus (Chlamydosaurus Group).

a. Vertebral scale ridge absent.

b. Postauricular skin smooth.

c. Relatively large scales.

d. Premaxilla narrow.

e. Large dermal frill.

7. Diporiphora (Chlamydosaurus Group).

a. Vertebral scale ridge absent.

b. Femoral pores reduced in number or absent.

c. Gular fold present or absent.

d. Body scales usually in rows parallel with midline.

e. Hemipenes bifurcate.

8. Lophognathus (Chlamydosaurus Group).

a. Nuchal and vertebral scale ridge present.

b. Posterosuperior postauricular skin fold often extending into gular region.

c. Brilliant white lower lip.

d. Dorsal scales usually relatively homogeneous.

9. Ctenophorus (Ctenophorus Group).

a. Primitive pore arrangement.

b. Nuchal scale ridge present.

c. Vertical postauricular skin fold with series of tubercles present.

d. Loreal scale row present.

e. Ventral scales smooth.

f. Often with 4 premaxillary teeth.

g. Permanent black ventral marking.

h. Not strongly metachromatic.

10. A. maculatus Species-group (Ctenophorus Group).

a. Primitive pore arrangement.

b. Pores usually posterior intrascalar.

c. Loreal scale row present.

d. Ventrals usually keeled.

e. Often with 4 premaxillary teeth.

f. Permanent black ventral marking usually present.

g. Not strongly metachromatic.

11. A. cristatus Species-group (Ctenophorus Group).

a. Primitive pore arrangement.

b. Pores relatively widely spaced.

c. Pores usually interscalar.

d. Nuchal scale ridge present.

e. Vertebral scale ridge usually present.

f. Loreal scale row present.

g. Ventral scales often smooth.

h. Often with 4 premaxillary teeth.

i. Permanent black ventral marking present.

j. Not strongly metachromatic.

12. A. reticulatus Species-group (Ctenophorus Group).

a. Primitive and derived pore arrangement.

b. Nuchal scale ridge present.

c. Loreal scale row present.

d. Series of spines on lower eyelid.

e. Ventrals usually smooth.

f. Three or fewer premaxillary teeth.

g. Permanent black ventral markings present or absent.

h. Not strongly metachromatic.

13. A. barbatus Species-group (Ctenophorus Group).

a. Derived pore arrangement.

b. Pores usually interscalar.

c. Vertebral scale ridge absent.

d. Scapular tubercle present.

e. Gular scale row present.

f. Occipital crest present.

g. Loreal scale row obscure in adults.

h. Series of spines on lower eyelid.

i. Ventral scales keeled.

j. Medial dorsal scales forming "farrier's rasp".

k. Series of spines on lateral margin of trunk.

l. Three or fewer premaxillary teeth.

m. Permanent black ventral markings absent.

n. Metachromatic.

o. Enlarged gular pouch.

V. Morphometrics

Introduction.

Cogger (1961) compared the osteology of many Australian agamids. His work centred on a neotenic form of *Amphibolurus maculatus* (= *A. fordi*), which retains an essentially juvenile skull as an adult. In order to illustrate this point Cogger compared adult and juvenile skulls of several other species. In most species examined the skull changes considerably in shape during growth. However, there is some variation in the degree of change between species examined, and in *Moloch* "all regions of the skull grow more or less isometrically during ontogeny". This variation in growth patterns suggested that the study of relative growth might be a fruitful area of research.

The term "relative growth" was introduced by Julian Huxley in "Problems of Relative Growth" (1932). Huxley covered many aspects of the problem, from physical ones such as changing length, surface area and volume, to neoteny and evolution. He proposed an equation to describe the growth of part of an organism:

$$Y = bX^k$$

Where: Y = size of the part,

X = a measure of the size of the animal,

b = a constant, the "fractional coefficient",

and k = the "growth coefficient".

When the growth coefficient was above one, the part was said to be growing with positive heterogony; at unity, growth was isogonic; for values of k less than unity, growth was with negative heterogony. Huxley touched on taxonomic and phylogenetic considerations in his concluding chapter. Here he suggested that growth-constants would make good taxonomic characters.

Huxley's terms have been modified in subsequent publications. The more euphonious "allometry" has been substituted for his "heterogony". Huxley's "growth coefficient", "k", is now more usually referred to as the "allometric coefficient", "a" (see Gould, 1977, for review).

Huxley (1932) wrote at a time when, according to Gould (1977), the theory of recapitulation had recently fallen out of favour due to the reappearance of Mendelian genetics. Gould argued that the "biogenetic law" of Haeckel which stated "ontogeny is the short and rapid recapitulation of phylogeny" was heavily dependent upon the acceptance of Lamarckian inheritance. The denial of the possible inheritance of acquired characters which was inherent in Mendelian genetics refuted the accepted explanation for recapitulation. Recapitulation was thus "abandoned as a universal proposition and displayed as but one possible result of a more general process - evolutionary alteration of times and rates to produce acceleration and retardation in the ontogenetic development of specific characters" (Gould, 1977).

Gould sought to rekindle interest in ontogeny as a phylogenetic tool. He pointed out that the very considerable body of data assembled to prove the "biogenetic law" should not simply be abandoned with the law for which it was gathered. The explanation for this data, Gould argued, lies in the conservatism of early development. Related forms are more likely to resemble one another as embryos than as adults.

The conservatism of earlier developmental stages was also noted by Huxley (1932) as the basis for "von Baer's law" (= "biogenetic law"). However, while clearly aware of this conservatism, he chose to play it down as a possible phylogenetic tool. He considered rate genes, and their expression as growth-constants, to be more important. Gould (1977), however, emphasised the phylogenetic importance of early conservatism, for which Dodson (1975b) provided a possible explanation. He found lower variability of measurements in the larger of two species of *Sceloporus* which he compared morphometrically. He suggested that this is due to the need for "narrower canalization of the developmental pattern necessary to produce a larger animal...; projection of a variant individual to large size would form a relatively grotesque adult".

Storr (1964, 1965, 1966, 1967, 1974, 1977) has presented morphometric data with all his contributions to agamid taxonomy. In none of these papers, however, has he considered absolute size or relative growth as a factor, preferring to propose ecological adaptations to explain differences in relative proportions between taxa.

Morphometric data were used by Badham (1976) to distinguish *A. barbatus* from *A. vitticeps*. She noted differences in the allometric coefficient for tail length between the species, and between the sexes of each species.

The establishment of differences between sexes and closely related species was not considered an important aspect of the present study. The main objective here was to examine broadly whether relationships inferred from other data were supported by morphometric analyses.

Results.

Linear and logarithmic regressions produced similar results (e.g. Fig. 33). Correlation coefficients were similar for all sets of data, although usually slightly higher for the logarithmic regression. Almost all recent studies of growth patterns have used logarithmic regressions to calculate Huxley's formula. Thus both the literature and comparisons between linear and logarithmic regressions indicate the latter should be preferred. Consequently only the results of the logarithmic regressions are presented below.

1. Tail Length (Table 27).

General.

Most species for which sufficient data were collected showed a trend towards positive allometry of tail length. Only *L. longirostris* and *A. vitticeps* had significant negative allometry.

Asian-derived Genera.

Physignathus had a high juvenile tail length. *Chelosania*, by contrast, had a relatively short tail as a juvenile (Table 27).

Moloch.

Moloch had a very short tail relative to all other species examined.

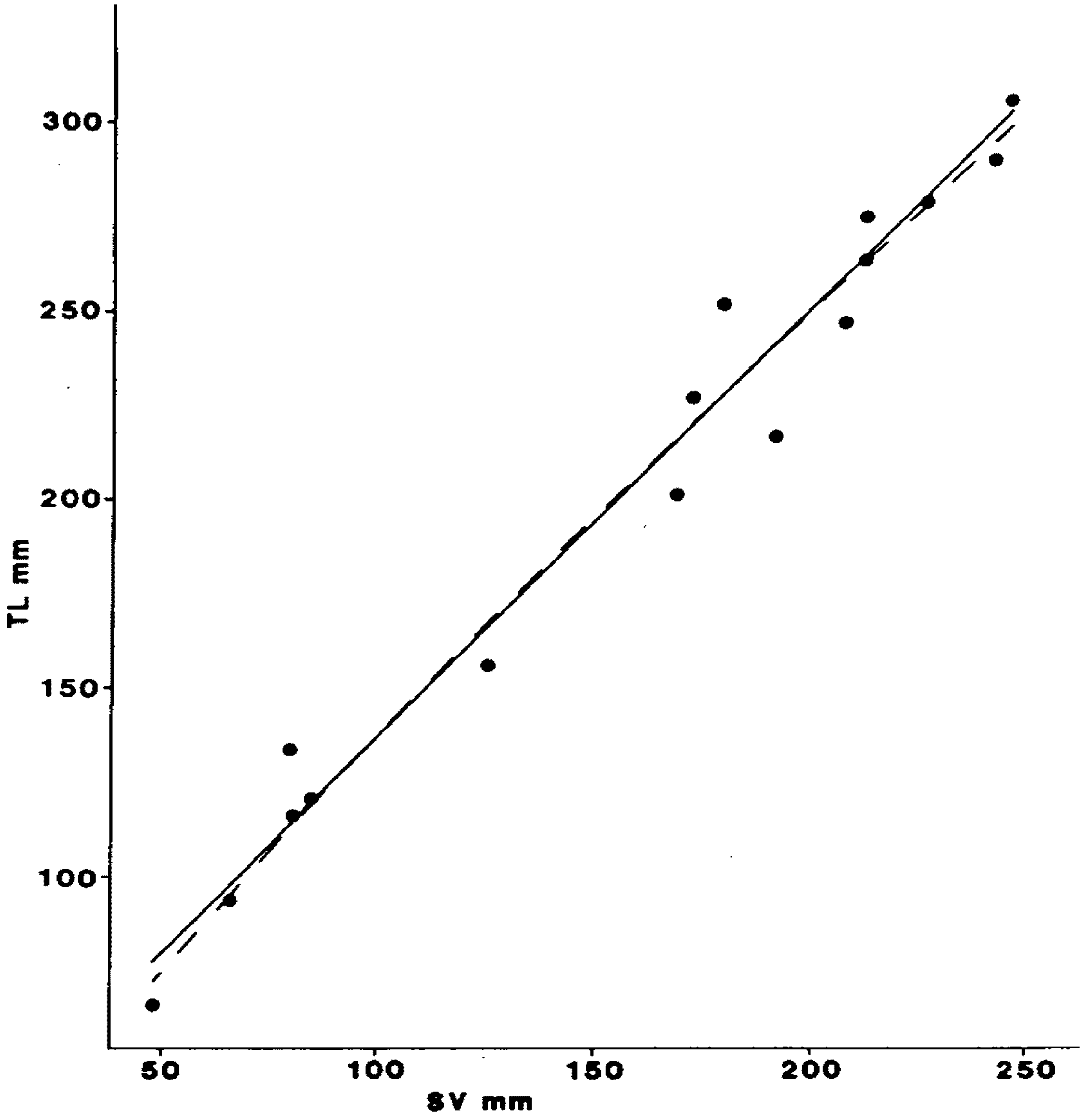
Tympanocryptis Group.

All members of the *Tympanocryptis* group showed a tendency towards positive allometry of tail growth, although this was significant only in *T. cephalus* and *T. intima*. *A. diemensis* had a relatively longer tail, and a higher TL30 figure (Table 27).

Chlamydosaurus Group.

Both species of the *A. muricatus* species-group and most species of *Diporiphora* exhibited positive allometry of the tail. Only *D. albilabris*

Figure 33. Comparison of Linear and Logarithmic Regressions (Facing page). Unbroken line represents linear regression from raw data, broken line represents regression fitted to data converted to natural logarithms. Upper graph shows tail length (TL) regressed against snout-vent length (SV) for *A. vitticeps*. Correlation coefficient (r) for linear regression = 0.9863; r for logarithmic regression = 0.9881. Lower graph shows snout-parietal distance (SP) regressed against snout-vent length (SV) for *A. caudicinctus*. Correlation coefficient (r) for linear regression = 0.9876; r for logarithmic regression = 0.9885.


300
250
200
150
100
TL mm
50
100
150
200
250
SV mm

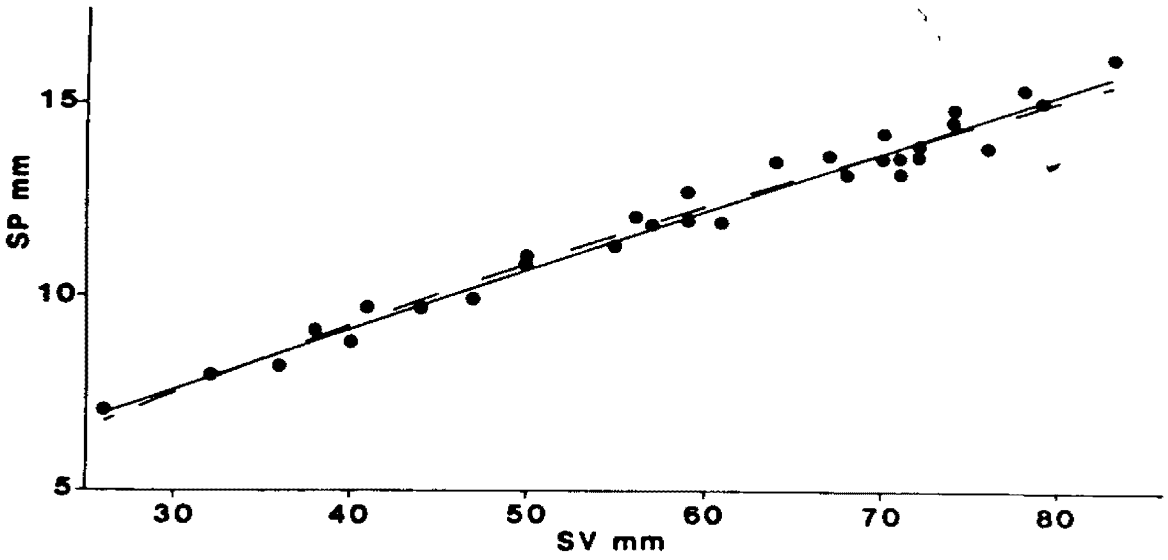

15
10
5
SP mm
30
40
50
60
70
80
SV mm

Table 27. Tail Length Regressed against Snout-vent Length.

Species	Allometric Coeff. (a)	Standard Error a	n	TL30	Significance of Allometry
Chelosania	1.186	0.071	6	37.6*	+
Physignathus	0.962	0.030	13	72.0**	0
Moloch	0.892	0.070	12	23.5*	0
T. cephalus	1.369	0.048	12	33.2	+
T. intima	1.337	0.116	12	33.3	+
T. tetraporophora	1.194	0.123	17	41.4	0
A. adelaidensis	1.087	0.160	16	38.4	0
A. diemensis	1.107	0.059	48	49.9	0
A. muricatus	1.137	0.030	53	57.8*	+
A. nobbi	1.374	0.065	19	52.2	+
Caimanops	0.964	0.064	22	50.9**	0
Chlamydosaurus	1.058	0.035	14	54.2**	0
D. albilabris	0.836	0.132	14	58.7*	0
D. australis	1.245	0.066	15	58.3	+
D. bennettii	1.325	0.079	13	54.7*	+
D. bilineata	1.321	0.125	27	58.0*	+
D. lalliae	1.374	0.123	9	64.0*	+
D. magna	1.157	0.077	12	64.6*	+
D. winneckei	1.036	0.185	13	71.7*	0
L. g. gilberti	1.026	0.041	14	87.6*	0
L. g. centralis	0.983	0.024	52	76.6**	0
L. longirostris	0.791	0.094	12	122.1**	-
L. temporalis	1.127	0.046	12	78.1*	+
C. decresii	1.037	0.037	10	54.6*	0
C. fionni	1.197	0.052	17	49.0	+
C. ornatus	1.056	0.054	10	56.2*	0
C. pictus	1.051	0.086	22	53.8*	0
A. fordi	1.457	0.053	31	54.3	+
A. isolepis	0.943	0.068	49	71.7*	0
A. cristatus	1.190	0.053	14	55.0*	+
A. caudicinctus	1.123	0.034	25	57.7	+
A. reticulatus	1.166	0.164	20	35.1**	0
A. gibba	1.004	0.042	16	43.9*	0
A. maculosus	1.131	0.031	28	37.2	+
A. nuchalis	1.045	0.039	48	36.6*	0
A. barbatus	0.970	0.031	20	43.4**	0
A. vitticeps	0.866	0.036	16	48.2**	-

TL30 = Calculated tail length at snout-vent length of 30 mm. This figure was chosen to represent small juvenile size: most species are about this size or smaller when hatched.

* Involves extrapolation below observed size range.

** Smallest individual more than 40 mm snout-vent length.

"a" considered significantly different from 1 when more than 2SE's above or below 1.

displayed a trend towards negative allometry, but this was not significant. The tail of neither *Caimanops* nor *Chlamydosaurus* grew at a rate significantly different from isometry.

Lophognathus temporalis had positive allometry of tail length, contrasting with *L. longirostris* which had negative allometry. All four taxa within *Lophognathus* have limited ability to regenerate their tails when broken. Regrown tails were difficult to detect without the use of X-rays, and the results for *L. longirostris* may reflect common undetected tail breakage in the species. There were no very small juveniles of this species available for study (Fig. 34), which might also contribute to a misleading result. Certainly there was considerable variation in the measurements of tail length in *L. longirostris*.

Lophognathus differed from the other members of the *Chlamydosaurus* group in possessing much longer tails as juveniles. The calculated tail lengths at a snout-vent length of 30 mm (TL30) for *Lophognathus* were much higher than for other genera (Table 27). The figures for *L. gilberti centralis* and *L. longirostris* involved extrapolation below the observed size range, but the observations on small *L. g. gilberti* and *L. temporalis* confirmed that very small juveniles of *Lophognathus* did possess relatively long tails.

Ctenophorus Group.

Members of the *Ctenophorus* group fell into two distinct groups on the basis of tail length. The *A. reticulatus* and *A. barbatus* species-groups had relatively short tails. *Ctenophorus* and members of the *A. maculatus* and *A. cristatus* species-groups had relatively longer tails. The data for *A. isolepis* were heavily biased towards adults and subadults, with no small juveniles being examined (Fig. 34). Allometric coefficients for this species are therefore probably not comparable with

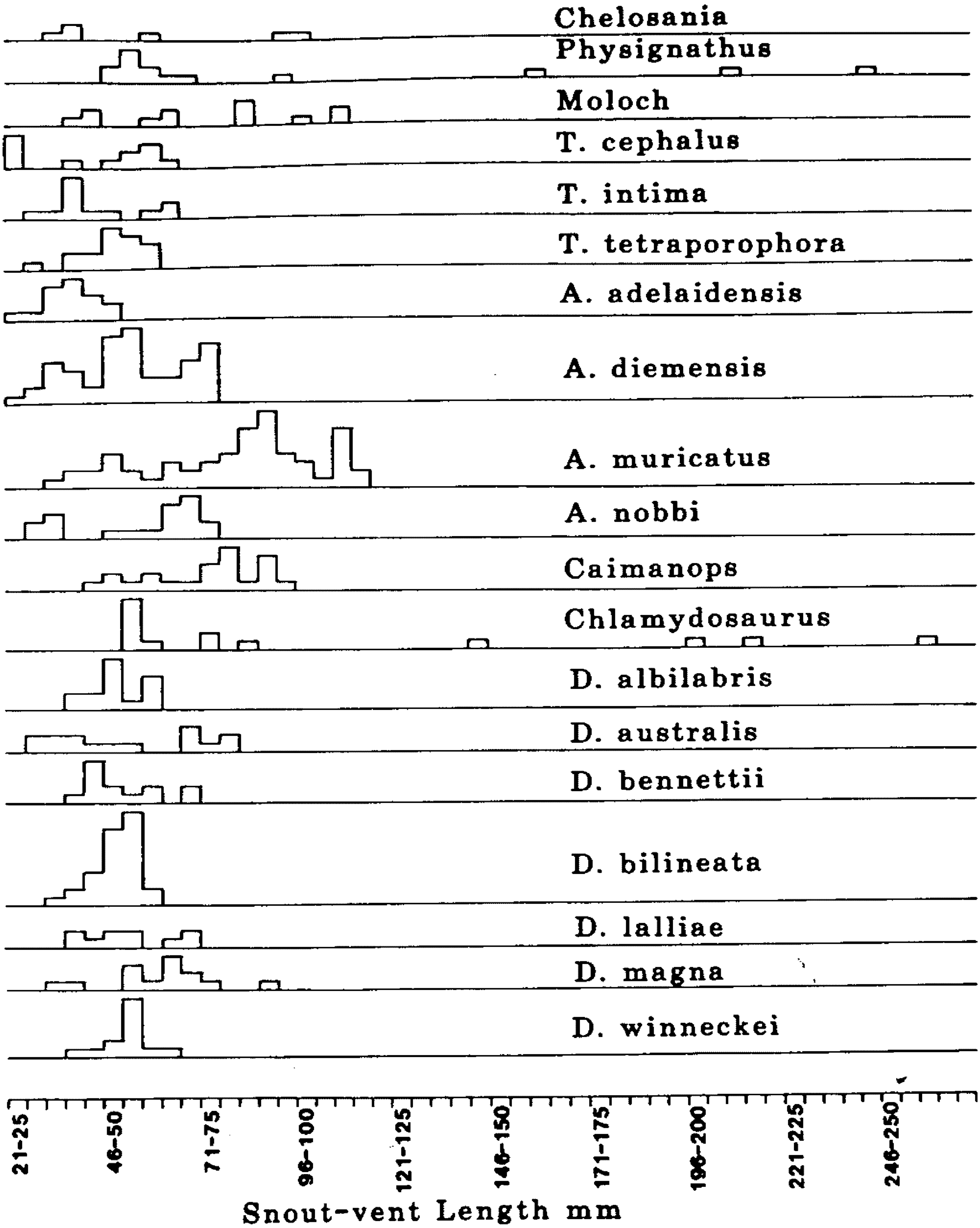


Figure 34. Histogram Showing Size Range and Distribution of Specimens Examined. Each specimen represented by a block about 1.5 mm in height (continued next page).

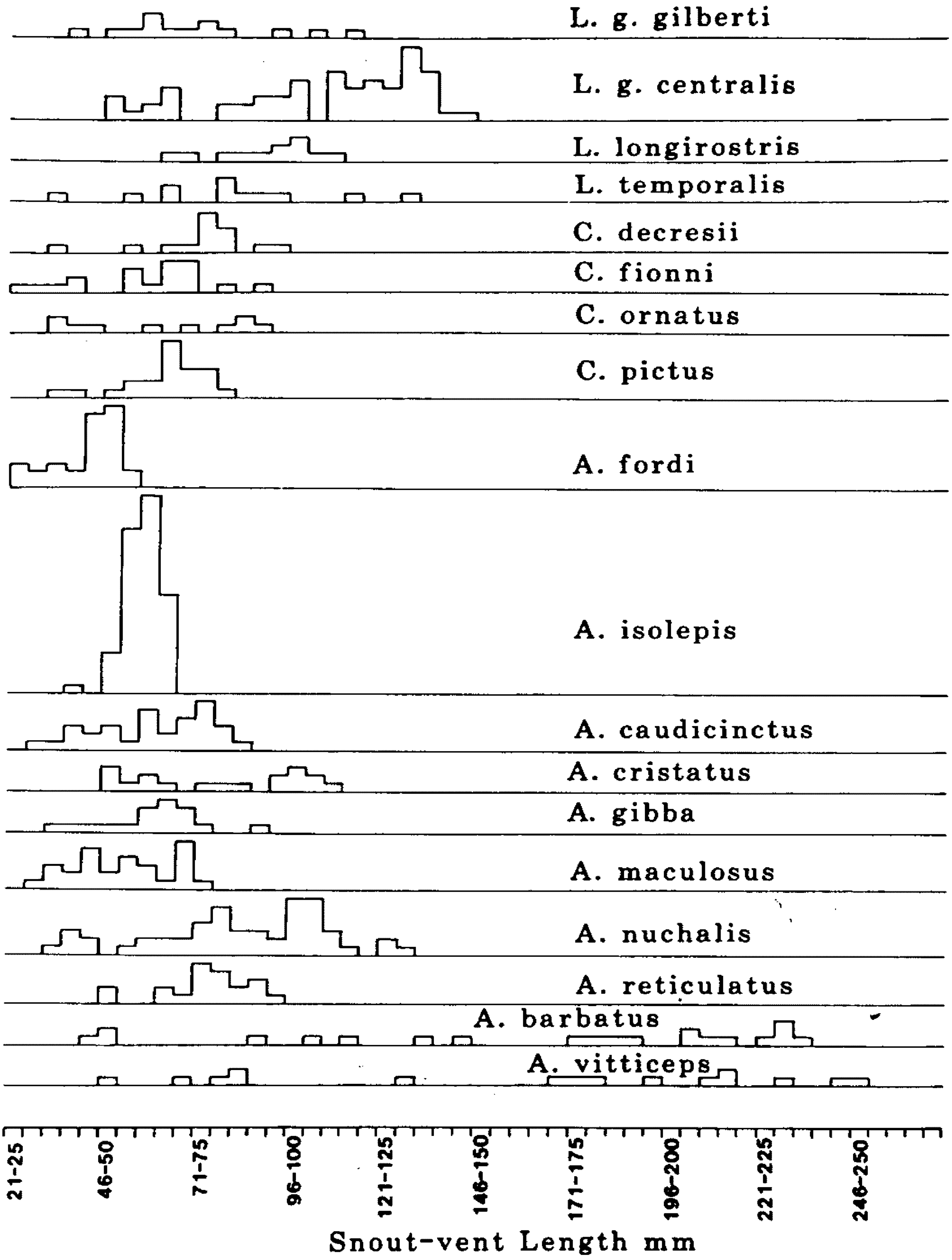


Figure 34 (Continued).

those obtained for most other species.

2. Hind Limb (Table 28).

General.

There was a trend in most species for the hind limb to grow with negative allometry. Only *A. nobbi* and *D. bennettii* went against this trend, and had significant positive allometry.

Moloch and *Chelosania* both had remarkably short hind limbs relative to other genera examined.

Chlamydosaurus Group.

Two genera within the *Chlamydosaurus* group were distinctive by virtue of the calculated length of the hind limb at a snout-vent length of 30 mm (HL30). *Caimanops* had a much lower value for this figure. The four taxa in *Lophognathus* had much longer hind limbs as juveniles than the other members of the *Chlamydosaurus* group.

Although *D. bennettii* displayed positive allometry and *D. albilabris* negative allometry of the hind limb, there was remarkably little variation between the species of *Diporiphora* in the HL30 figures.

Ctenophorus Group.

Most burrowing species studied had strong negative allometry of hind limb growth. This ecological group includes *C. pictus* as well as members of the *A. reticulatus* species-group. *A. gibba* and *A. maculosus* had relatively longer limbs and weaker negative allometry than the other members of the *A. reticulatus* species-group (Table 28).

A. caudicinctus and *A. cristatus* were very similar in both the allometric coefficient and the HL30 figure. *A. barbatus* and *A. vitticeps* were also very similar to each other in these figures (Table 28).

Table 28. Hind Limb Length Regressed against Snout-vent Length.

Species	Allometric Coeff. (a)	Standard Error a	n	HL30	Significance of Allometry
Chelosania	1.052	0.038	6	14.9*	0
Physignathus	0.941	0.012	13	26.1**	-
Moloch	0.999	0.063	12	15.2*	0
T. cephalus	1.052	0.040	12	20.0	0
T. intima	1.007	0.086	12	19.6	0
T. tetraporophora	1.016	0.094	17	20.7	0
A. adelaidensis	0.833	0.105	16	20.9	0
A. diemensis	0.958	0.041	48	21.7	0
A. muricatus	0.958	0.023	56	23.7*	0
A. nobbi	1.101	0.027	19	21.7	+
Caimanops	1.016	0.043	22	16.2**	0
Chlamydosaurus	0.977	0.014	13	22.6**	0
D. albilabris	0.741	0.101	14	23.8*	-
D. australis	0.950	0.045	15	22.3	0
D. bennettii	1.133	0.055	13	21.2*	+
D. bilineata	0.955	0.088	29	23.3*	0
D. lalliae	0.826	0.088	10	25.3*	0
D. magna	0.934	0.070	14	21.6*	0
D. winneckei	0.835	0.109	13	22.2*	0
L. g. gilberti	0.995	0.052	14	26.7*	0
L. g. centralis	0.893	0.018	60	27.7**	-
L. longirostris	0.866	0.104	12	29.6**	0
L. temporalis	0.944	0.035	12	27.8*	0
C. decresii	0.907	0.042	14	26.8*	-
C. fionni	0.980	0.026	19	24.5	0
C. ornatus	0.959	0.034	10	26.1*	0
C. pictus	0.837	0.052	23	25.3*	-
A. fordi	1.065	0.038	31	26.0	0
A. isolepis	0.695	0.071	62	34.3*	-
A. cristatus	1.025	0.016	18	27.9*	0
A. caudicinctus	1.016	0.031	31	27.3	0
A. reticulatus	0.816	0.072	20	21.1**	-
A. gibba	0.940	0.030	17	26.6*	-
A. maculosus	0.914	0.022	28	21.5	-
A. nuchalis	0.891	0.020	49	19.8*	-
A. barbatus	0.883	0.020	21	19.3**	-
A. vitticeps	0.909	0.016	16	19.2**	-

HL30 = Calculated hind limb length at snout-vent length of 30 mm.
* Involves extrapolation below observed size range.
** Smallest individual more than 40 mm snout-vent length.
"a" considered significantly different from 1 when more than 2SE's above or below 1.

3. Thigh (Table 29).

Moloch.

Moloch had a Th30 value similar to most other genera examined. The relatively short hind limbs of the genus may be due largely to the abbreviated digits of the genus (see Pes, below).

Chlamydosaurus Group.

The thigh measurement of *Caimanops* was remarkably low. The calculated thigh measurement for juveniles (Th30) was lower than for any other endemic species (Table 29). Only *Chelosania*, an Asian-derived genus, had a lower Th30 figure. *Lophognathus* had a higher Th30 value than other members of the *Chlamydosaurus* group (Table 29).

Ctenophorus Group.

Both members of the *A. barbatus* species-group studied had a low Th30 value. Most members of the *A. reticulatus* species-group also had a low Th30 value, but *A. gibba* had a higher value. *A. gibba* and *A. maculosus* differed from the other burrowing species studied in not possessing negative allometry of thigh length. *A. nuchalis*, *A. reticulatus* and *C. pictus* all had significant negative allometry of thigh length. *C. pictus*, however, had a higher Th30 value than the former two species (Table 29).

A. caudicinctus and *A. cristatus* both had high Th30 values and similar allometric coefficients.

4. Pes (Table 30).

General.

There was a strong general trend towards negative allometry of pes growth. In a majority of species for which data were analysed this negative allometry was significant.

Moloch and *Chelosania* had relatively low pes measurements,

Table 29. Thigh Measurement Regressed against Snout-vent Length.

Species	Allometric Coeff. (a)	Standard Error a	n	Th30	Significance of Allometry
Chelosania	1.068	0.033	6	12.8*	+
Physignathus	0.995	0.011	13	18.2**	0
Moloch	1.089	0.046	12	16.6*	0
T. cephalus	1.084	0.028	12	17.0	+
T. intima	1.079	0.083	12	16.3	0
T. tetraporophora	1.007	0.047	17	17.2	0
A. adelaidensis	1.073	0.103	16	16.4	0
A. diemensis	0.993	0.029	49	16.7	0
A. muricatus	1.017	0.018	56	17.1*	0
A. nobbi	1.114	0.029	19	15.9	+
Caimanops	1.019	0.039	22	13.9**	0
Chlamydosaurus	1.036	0.012	14	16.4**	+
D. albilabris	0.911	0.097	14	17.0*	0
D. australis	1.069	0.032	15	15.8	+
D. bennettii	1.119	0.058	13	15.9*	+
D. bilineata	0.961	0.053	29	16.5*	0
D. lalliae	0.923	0.071	10	17.2*	0
D. magna	1.046	0.054	14	15.0*	0
D. winneckei	0.966	0.116	13	14.8*	0
L. g. gilberti	1.075	0.054	12	17.5*	0
L. g. centralis	0.979	0.019	60	18.8**	0
L. longirostris	0.999	0.079	12	17.7**	0
L. temporalis	1.040	0.044	12	17.6*	0
C. decresii	1.002	0.030	12	19.4*	0
C. fionni	1.108	0.033	19	17.3	+
C. ornatus	1.039	0.023	10	19.2*	0
C. pictus	0.913	0.042	23	18.8*	-
A. fordi	1.127	0.035	31	17.5	+
A. isolepis	0.770	0.058	61	22.4*	-
A. cristatus	1.043	0.018	18	19.5*	+
A. caudicinctus	1.021	0.027	31	20.0	0
A. reticulatus	0.913	0.042	20	16.4**	-
A. gibba	1.033	0.032	17	19.5*	0
A. maculosus	1.012	0.020	28	17.3	0
A. nuchalis	0.953	0.016	49	15.6*	-
A. barbatus	0.970	0.019	19	14.8**	0
A. vitticeps	0.983	0.014	15	15.2**	0

Th30 = Calculated thigh length at snout-vent length of 30 mm.
* Involves extrapolation below observed size range.
** Smallest individual more than 40 mm snout-vent length.
"a" considered significantly different from 1 when more than 2SE's above or below 1.

Table 30. Pes Length Regressed against Snout-vent Length.

Species	Allometric Coeff. (a)	Standard Error a	n	P30	Significance of Allometry
Chelosania	0.845	0.039	6	7.4*	-
Physignathus	0.895	0.018	14	12.4**	-
Moloch	0.868	0.054	12	4.6*	-
T. cephalus	0.932	0.039	12	8.4	0
T. intima	0.846	0.092	12	8.3	0
T. tetraporophora	0.938	0.105	17	8.5	0
A. adelaidensis	0.604	0.122	16	9.3	-
A. diemensis	0.881	0.044	49	10.2	-
A. muricatus	0.877	0.035	57	11.4*	-
A. nobbi	1.050	0.031	19	10.2	0
Caimanops	0.963	0.050	22	7.0**	0
Chlamydosaurus	0.915	0.024	13	10.0**	-
D. albilabris	0.636	0.114	14	10.7*	-
D. australis	0.872	0.040	15	10.3	-
D. bennettii	1.130	0.077	13	9.3*	0
D. bilineata	0.830	0.107	29	11.0*	0
D. lalliae	0.793	0.087	10	11.4*	-
D. magna	0.873	0.068	14	9.9*	0
D. winneckei	0.764	0.109	13	10.2*	-
L. g. gilberti	0.955	0.050	14	12.7*	0
L. g. centralis	0.823	0.021	61	13.1**	-
L. longirostris	0.800	0.130	12	14.1**	0
L. temporalis	0.891	0.040	12	13.4*	-
C. decresii	0.823	0.050	14	12.0*	-
C. fionni	0.881	0.034	19	11.1	-
C. ornatus	0.887	0.034	10	11.7*	-
C. pictus	0.750	0.055	23	11.2*	-
A. fordi	0.985	0.051	31	11.9	0
A. isolepis	0.543	0.082	62	16.3*	-
A. cristatus	0.951	0.030	18	13.0*	0
A. caudicinctus	0.979	0.035	31	11.6	0
A. reticulatus	0.726	0.086	20	9.2**	-
A. gibba	0.858	0.045	17	11.4*	-
A. maculosus	0.862	0.031	28	8.9	-
A. nuchalis	0.802	0.023	52	8.5*	-
A. barbatus	0.800	0.026	21	8.6**	-
A. vitticeps	0.848	0.018	16	8.1**	-

P30 = Calculated pes length at snout-vent length of 30 mm.
* Involves extrapolation below observed size range.
** Smallest individual more than 40 mm snout-vent length.
"a" considered significantly different from 1 when more than 2SE's above or below 1.

particularly the former.

Tympanocryptis Group.

A. diemensis and *A. adelaidensis* had more pronounced negative allometry of the pes than *Tympanocryptis*, but their P30 values were higher (Table 30).

Chlamydosaurus Group.

Caimanops had less pronounced negative allometry of pes growth, but a calculated pes length at 30 mm snout-vent length much lower than any other member of the group (Table 30). The four taxa in *Lophognathus* had the four highest P30 values for the *Chlamydosaurus* group.

Ctenophorus Group.

The *A. barbatus* and *A. reticulatus* species-groups generally had low P30 values relative to most other species. *A. gibba* was an exception to this generalisation, with a P30 value similar to the species of *Ctenophorus* (Table 30).

4. Forelimb (Table 31).

General.

There was a general trend towards negative allometry of forelimb growth. This was particularly pronounced in *Ctenophorus* and members of the *A. reticulatus* and *A. barbatus* species-groups.

Tympanocryptis Group.

A. adelaidensis and *A. diemensis* differed strongly from *Tympanocryptis* in possessing strong negative allometry of forelimb growth (Table 31). No species of *Tympanocryptis* had significant negative allometry.

Chlamydosaurus Group.

Diporiphora bennettii differed from all other species analysed in exhibiting strong positive allometry of forelimb growth. By contrast, the allometric coefficient was low for *D. albilabris* and *L. longirostris*,

Table 31. Fore Limb Length Regressed against Snout-vent Length.

Species	Allometric Coeff. (a)	Standard Error a	n	FL30	Significance of Allometry
Chelosania	0.965	0.033	6	12.3*	0
Physignathus	0.964	0.011	14	13.7**	-
Moloch	1.004	0.060	12	12.5*	0
T. cephalus	0.984	0.043	12	14.0	0
T. intima	0.980	0.066	12	13.1	0
T. tetraporophora	0.927	0.091	17	14.2	0
A. adelaidensis	0.777	0.098	16	13.7	-
A. diemensis	0.887	0.026	49	13.4	-
A. muricatus	0.945	0.024	57	12.8*	-
A. nobbi	0.979	0.029	19	12.8	0
Caimanops	0.956	0.048	22	11.8**	0
Chlamydosaurus	0.923	0.017	13	14.8**	-
D. albilabris	0.788	0.115	14	13.8*	0
D. australis	0.931	0.045	15	13.3	0
D. bennettii	1.125	0.055	13	11.9*	+
D. bilineata	0.917	0.061	29	14.1*	0
D. lalliae	0.932	0.046	10	13.3*	0
D. magna	0.940	0.062	14	12.9*	0
D. winneckei	0.902	0.086	13	12.6*	0
L. g. gilberti	1.001	0.044	14	12.8*	0
L. g. centralis	0.903	0.020	60	13.8**	-
L. longirostris	0.779	0.070	12	15.6**	-
L. temporalis	0.978	0.050	12	13.2*	0
C. decresii	0.803	0.044	14	14.3*	-
C. fionni	0.861	0.021	19	13.5	-
C. ornatus	0.880	0.034	10	14.1*	-
C. pictus	0.810	0.054	23	13.6*	-
A. fordi	0.964	0.029	31	13.1	0
A. isolepis	0.758	0.057	62	14.7*	-
A. cristatus	0.987	0.026	18	12.6*	0
A. caudicinctus	0.962	0.028	31	13.9	0
A. reticulatus	0.722	0.058	20	14.0**	-
A. gibba	0.821	0.031	17	15.3*	-
A. maculosus	0.839	0.023	28	14.2	-
A. nuchalis	0.843	0.016	52	13.6*	-
A. barbatus	0.887	0.020	21	14.2**	-
A. vitticeps	0.911	0.024	16	14.0**	-

FL30 = Calculated fore limb length at snout-vent length of 30 mm.
* Involves extrapolation below observed size range.
** Smallest individual more than 40 mm snout-vent length.
"a" considered significantly different from 1 when more than 2SE's above or below 1.

but all other species of the *Chlamydosaurus* group showed remarkably little variation. *Caimanops* and *D. bennettii* had a lower calculated forelimb length in juveniles (FL30, Table 31). *Chlamydosaurus* and *L. longirostris* had higher FL30 values.

Ctenophorus Group.

A. caudicinctus and *A. cristatus* differed from *Ctenophorus* and the *A. reticulatus* and *A. barbatus* species-groups by virtue of almost isometric growth of the forelimb (Table 31). *A. fordi* also had a relatively high allometric coefficient. There was otherwise little variation among members of the *Ctenophorus* group.

5. Head Size.

As with most vertebrates, the head grew with strong negative allometry in all species of agamids studied. Analysis of the five head measurements using the snout-vent length as the standard revealed little in the way of meaningful comparison. These data were also regressed against the snout-parietal distance, which method emphasised differences in head shape. However, some results from the regressions against snout-vent length deserve comment.

Moloch had by far the most pronounced negative allometry of head size. Of the five head measurements analysed with reference to the snout-vent length, only the allometric coefficient for ear width exceeded 0.6 (Table 32).

The snout-ear interval for *Lophognathus* grew almost isometrically when compared with the snout-vent length. The allometric coefficients for the snout-ear interval were generally higher for the *Chlamydosaurus* group than for the other Australian agamids (Table 32).

A. vitticeps grew with positive allometry of head width. *A. barbatus*, *L. gilberti centralis* and *L. longirostris* also had allometric

Table 32. Head Measurements Regressed against Snout-vent Length.

Species	HW / SV		SP / SV		HLE / SV		HD / SV		EW / SV		SP30
	a	SE	a	SE	a	SE	a	SE	a	SE	
Chelosania	0.784	0.066	0.666	0.043	0.831	0.063	0.818	0.071	0.869	0.150	7.48
Physignathus	0.887	0.026	0.758	0.012	0.911	0.015	0.851	0.027	0.867	0.033	7.80
Moloch	0.595	0.041	0.567	0.041	0.575	0.041	0.540	0.060	0.639	0.070	6.05
T. cephalus	0.763	0.041	0.748	0.035	-	-	0.798	0.029	-	-	7.07
T. intima	0.704	0.058	0.565	0.060	-	-	0.803	0.083	-	-	7.78
T. tetraporophora	0.740	0.042	0.716	0.044	-	-	0.841	0.074	-	-	7.21
A. adelaidensis	0.890	0.068	0.739	0.048	0.800	0.032	1.020	0.094	1.121	0.135	6.98
A. diemensis	0.802	0.017	0.733	0.021	0.839	0.020	0.797	0.023	1.086	0.060	7.77
A. muricatus	0.860	0.019	0.774	0.013	0.900	0.014	0.856	0.019	1.020	0.038	7.99
A. nobbi	0.827	0.021	0.752	0.022	0.905	0.020	0.788	0.042	1.046	0.041	7.71
Caimanops	0.794	0.060	0.833	0.041	0.934	0.051	1.003	0.069	0.914	0.081	6.69
Chlamydosaurus	0.911	0.039	0.711	0.023	0.857	0.028	0.746	0.030	0.848	0.037	8.72
D. albilabris	0.675	0.115	0.662	0.090	0.766	0.089	0.635	0.094	0.902	0.188	7.79
D. australis	0.728	0.039	0.754	0.038	0.849	0.034	0.791	0.049	0.852	0.042	7.23
D. bennettii	0.978	0.076	0.892	0.068	1.047	0.067	0.938	0.075	1.171	0.109	7.15
D. bilineata	0.808	0.048	0.767	0.062	0.910	0.042	0.960	0.072	0.863	0.157	7.19
D. lalliae	0.658	0.084	0.655	0.065	0.760	0.069	0.821	0.119	0.872	0.122	7.37
D. magna	0.912	0.057	0.810	0.023	0.982	0.046	0.914	0.059	1.076	0.095	7.10
D. winneckei	0.632	0.107	0.815	0.047	0.795	0.066	0.713	0.063	0.878	0.147	6.01
L. g. gilberti	0.924	0.039	0.746	0.021	0.939	0.022	0.800	0.046	0.975	0.051	8.13
L. g. centralis	1.049	0.036	0.814	0.018	0.985	0.021	0.940	0.023	0.926	0.031	7.78
L. longirostris	1.128	0.143	0.924	0.082	1.019	0.081	1.081	0.126	0.957	0.110	6.53
L. temporalis	0.853	0.059	0.803	0.048	0.958	0.056	0.851	0.066	0.925	0.076	7.45

C. decresii	0.829	0.067	0.686	0.027	0.827	0.043	0.765	0.106	0.871	0.153	7.76
C. fionni	0.861	0.026	0.724	0.021	0.864	0.019	0.839	0.043	1.004	0.025	7.67
C. ornatus	0.808	0.082	0.719	0.037	0.859	0.038	0.765	0.076	0.937	0.078	7.19
C. pictus	0.988	0.060	0.778	0.046	0.919	0.048	0.992	0.049	1.139	0.091	7.05
A. fordi	0.802	0.023	0.698	0.022	0.816	0.025	0.922	0.032	0.809	0.044	6.92
A. isolepis	0.792	0.047	0.796	0.052	0.903	0.044	0.983	0.061	0.963	0.091	7.00
A. cristatus	0.647	0.032	0.693	0.032	0.798	0.032	0.737	0.031	0.957	0.035	7.76
A. caudicinctus	0.895	0.025	0.714	0.020	0.874	0.024	0.884	0.042	0.898	0.057	7.51
A. reticulatus	0.906	0.068	0.670	0.040	0.820	0.059	0.801	0.059	1.097	0.121	6.98
A. gibba	0.903	0.049	0.749	0.028	0.859	0.030	0.895	0.033	1.130	0.108	7.21
A. maculosus	0.796	0.025	0.672	0.024	0.836	0.028	0.778	0.041	0.979	0.072	7.09
A. nuchalis	0.827	0.019	0.630	0.013	0.783	0.015	0.813	0.021	0.886	0.030	7.53
A. barbatus	1.039	0.058	0.693	0.014	0.874	0.018	0.842	0.034	1.048	0.030	8.19
A. vitticeps	1.160	0.049	0.699	0.021	0.909	0.023	0.906	0.031	1.011	0.057	7.97

SP30 = Calculated snout-parietal distance at snout-vent length of 30 mm.
HW = Head Width, SV = Snout-vent length, SP = Snout-parietal distance,
HLE = Snout-ear distance, HD = Head depth, EW = Ear width.
"a" considered significantly different from 1 when more than 2SE's above or below 1.

coefficients greater than one, but not significantly so.

6. Head Width (Table 33).

A. cristatus was the only species with negative allometry of head width when this measurement was regressed against the snout-parietal distance (Table 33).

The calculated head width for juveniles (HW7.4) was relatively low in three groups. These were the *A. barbatus* species-group, *Chlamydosaurus* and *Lophognathus* (Table 33). The result for the first two of these groups may have been due to extrapolation below the limits of the real data. *Lophognathus*, however, do have narrower heads as juveniles.

7. Snout-ear Distance (Table 34).

In almost all species analysed there was positive allometry of this measurement. There was remarkably little variation, both in the calculated allometric coefficients and in the calculated length of the interval in juveniles (Table 34).

8. Head Depth (Table 35).

Generally head depth increased more rapidly than the snout-parietal interval. *Moloch*, *D. albilabris* and *D. winneckei* had allometric coefficients less than one, but none had significant negative allometry. *A. cristatus* and *C. ornatus* had lower allometric coefficients than their closer relatives (Table 35).

9. Ear Width (Table 36).

The tympanum generally grew with positive allometry relative to the snout-parietal distance (Table 36).

Most members of the *Chlamydosaurus* group had less pronounced positive allometry than other Australian agamids. The exceptions to this generalisation were *A. muricatus* and *A. nobbi*. These species, and *Caimanops*, also had a lower calculated value for ear width in juveniles

Table 33. Head Width Regressed against Snout-parietal Distance.

Species	Allometric Coeff. (a)	Standard Error a	n	HW7.4	Significance of Allometry
Chelosania	1.173	0.075	6	6.17*	+
Physignathus	1.166	0.039	14	6.20**	+
Moloch	1.037	0.047	12	8.88*	0
T. cephalus	1.019	0.028	12	8.43	0
T. intima	1.155	0.125	12	7.93	0
T. tetraporophora	1.013	0.048	17	7.98	0
A. adelaidensis	1.160	0.098	16	8.16	0
A. diemensis	1.062	0.031	49	7.43	+
A. muricatus	1.106	0.022	57	6.91*	+
A. nobbi	1.084	0.045	19	7.01	0
Caimanops	0.951	0.055	22	7.00**	0
Chlamydosaurus	1.284	0.035	13	5.70**	+
D. albilabris	1.033	0.082	14	7.46*	0
D. australis	0.956	0.042	15	7.39	0
D. bennettii	1.070	0.074	13	6.99*	0
D. bilineata	0.927	0.073	28	7.25*	0
D. lalliae	1.003	0.081	10	7.20*	0
D. magna	1.131	0.055	14	6.35*	+
D. winneckei	0.768	0.126	13	7.19*	0
L. g. gilberti	1.229	0.058	14	5.71*	+
L. g. centralis	1.292	0.032	60	5.55**	+
L. longirostris	1.210	0.118	12	5.06**	0
L. temporalis	1.063	0.033	12	5.87*	0
C. decresii	1.221	0.069	14	7.20*	+
C. fionni	1.182	0.035	19	7.39	+
C. ornatus	1.109	0.115	10	7.41*	0
C. pictus	1.256	0.046	23	7.31*	+
A. fordi	1.129	0.037	31	7.16	+
A. isolepis	0.907	0.047	62	7.55*	0
A. cristatus	0.931	0.026	18	7.86*	–
A. caudicinctus	1.238	0.038	32	7.19	+
A. reticulatus	1.348	0.064	20	7.22**	+
A. gibba	1.210	0.041	17	7.54*	+
A. maculosus	1.170	0.031	28	8.11	+
A. nuchalis	1.302	0.027	52	7.34*	+
A. barbatus	1.502	0.077	21	5.38**	+
A. vitticeps	1.656	0.058	16	5.21**	+

HW7.4 = Calculated head width at snout-parietal distance of 7.4 mm. The mean of SP30 figures for all species was approximately 7.4 mm. This figure was then used to allow comparisons of juvenile head shape to be made.

* Involves extrapolation below observed size range.

** Smallest individual more than 40 mm snout-vent length.

"a" considered significantly different from 1 when more than 2SE's above or below 1.

Table 34. Snout-ear Distance Regressed against Snout-parietal Distance.

Species	Allometric Coeff. (a)	Standard Error a	n	SE7.4	Significance of Allometry
Chelosania	1.251	0.017	6	7.81*	+
Physignathus	1.199	0.025	14	7.46**	+
Moloch	1.005	0.038	12	8.86*	0
A. adelaidensis	1.044	0.053	16	8.86	0
A. diemensis	1.128	0.021	49	8.08	+
A. muricatus	1.160	0.010	57	7.94*	+
A. nobbi	1.196	0.027	19	7.87	+
Caimanops	1.123	0.022	22	8.37**	+
Chlamydosaurus	1.205	0.015	14	7.08**	+
D. albilabris	1.108	0.064	14	8.70*	0
D. australis	1.114	0.029	15	8.26	+
D. bennettii	1.157	0.037	13	8.23*	+
D. bilineata	1.065	0.064	28	8.63*	0
D. lalliae	1.146	0.050	10	8.41*	+
D. magna	1.216	0.037	14	7.84*	+
D. winneckei	0.973	0.061	13	8.95*	0
L. g. gilberti	1.254	0.029	14	7.31*	+
L. g. centralis	1.208	0.012	61	7.48**	+
L. longirostris	1.085	0.048	12	8.42**	0
L. temporalis	1.187	0.033	12	7.41*	+
C. decresii	1.206	0.042	14	8.05*	+
C. fionni	1.187	0.021	19	8.21	+
C. ornatus	1.187	0.033	10	8.25*	+
C. pictus	1.164	0.033	23	8.27*	+
A. fordi	1.156	0.032	31	8.02	+
A. isolepis	1.037	0.039	62	8.24*	0
A. cristatus	1.145	0.020	18	7.71*	+
A. caudicinctus	1.209	0.035	32	7.96	+
A. reticulatus	1.231	0.036	20	7.92**	+
A. gibba	1.139	0.033	17	8.34*	+
A. maculosus	1.234	0.027	28	8.33	+
A. nuchalis	1.236	0.015	52	7.80*	+
A. barbatus	1.261	0.015	21	7.34**	+
A. vitticeps	1.295	0.025	16	7.20**	+

SE7.4 = Calculated snout-ear distance at snout-parietal distance of 7.4 mm.

* Involves extrapolation below observed size range.

** Smallest individual more than 40 mm snout-vent length.

"a" considered significantly different from 1 when more than 2SE's above or below 1.

Table 35. Head Depth Regressed against Snout-parietal Distance.

Species	Allometric Coeff. (a)	Standard Error a	n	HD7.4	Significance of Allometry
Chelosania	1.221	0.096	6	4.99*	+
Physignathus	1.121	0.034	14	4.98**	+
Moloch	0.895	0.129	12	7.11*	0
T. cephalus	1.057	0.033	12	5.30	0
T. intima	1.380	0.104	12	4.62	+
T. tetraporophora	1.165	0.082	17	4.83	+
A. adelaidensis	1.327	0.133	16	5.08	+
A. diemensis	1.059	0.035	49	4.89	0
A. muricatus	1.102	0.020	57	4.67*	+
A. nobbi	1.029	0.068	19	4.98	0
Caimanops	1.203	0.058	22	4.39**	+
Chlamydosaurus	1.050	0.031	13	5.40**	0
D. albilabris	0.961	0.050	14	5.19*	0
D. australis	1.043	0.050	15	5.10	0
D. bennettii	1.031	0.067	13	4.92*	0
D. bilineata	1.088	0.106	28	4.87*	0
D. lalliae	1.261	0.118	10	4.50*	+
D. magna	1.132	0.060	14	4.66*	+
D. winneckei	0.861	0.074	13	5.15*	0
L. g. gilberti	1.071	0.056	14	4.66*	0
L. g. centralis	1.151	0.021	59	4.35**	+
L. longirostris	1.171	0.083	12	3.91**	+
L. temporalis	1.063	0.043	12	4.85*	0
C. decresii	1.161	0.115	14	4.12*	0
C. fionni	1.156	0.053	19	4.28	+
C. ornatus	1.075	0.072	10	3.92*	0
C. pictus	1.233	0.059	23	4.92*	+
A. fordi	1.280	0.064	31	4.25	+
A. isolepis	1.114	0.064	62	4.37*	0
A. cristatus	1.052	0.033	18	5.24*	0
A. caudicinctus	1.237	0.048	32	4.65	+
A. reticulatus	1.180	0.067	20	5.37**	+
A. gibba	1.189	0.033	17	5.32*	+
A. maculosus	1.151	0.051	28	5.41	+
A. nuchalis	1.280	0.030	52	5.13*	+
A. barbatus	1.214	0.044	21	4.46**	+
A. vitticeps	1.293	0.033	16	4.44**	+

HD7.4 = Calculated head depth at snout-parietal distance of 7.4 mm.
* Involves extrapolation below observed size range.
** Smallest individual more than 40 mm snout-vent length.
"a" considered significantly different from 1 when more than 2SE's above or below 1.

Table 36. Ear Width Regressed against Snout-parietal Distance.

Species	Allometric Coeff. (a)	Standard Error a	n	EW7.4	Significance of Allometry
Chelosania	1.294	0.223	6	1.46*	0
Physignathus	1.143	0.041	14	1.34**	+
Moloch	1.077	0.138	12	2.03*	0
A. adelaidensis	1.490	0.168	16	1.43	+
A. diemensis	1.450	0.081	49	1.26	+
A. muricatus	1.308	0.048	57	1.21*	+
A. nobbi	1.370	0.070	19	1.35	+
Caimanops	1.079	0.091	22	1.34**	0
Chlamydosaurus	1.181	0.061	14	1.55**	+
D. albilabris	1.222	0.262	14	1.65*	0
D. australis	1.094	0.079	15	1.56	0
D. bennettii	1.292	0.098	13	1.59*	+
D. bilineata	1.133	0.182	28	1.58*	0
D. lalliae	1.282	0.180	10	1.60*	0
D. magna	1.329	0.110	14	1.43*	+
D. winneckei	1.036	0.188	13	1.42*	0
L. g. gilberti	1.299	0.070	14	1.56*	+
L. g. centralis	1.120	0.038	61	1.58**	+
L. longirostris	0.978	0.130	12	1.83**	0
L. temporalis	1.133	0.090	12	1.66*	0
C. decresii	1.309	0.195	14	1.48*	0
C. fionni	1.367	0.055	19	1.49	+
C. ornatus	1.271	0.132	10	1.69*	+
C. pictus	1.370	0.136	23	1.57*	+
A. fordi	1.124	0.073	31	1.75	0
A. isolepis	1.016	0.112	62	2.04*	0
A. cristatus	1.352	0.060	18	1.65*	+
A. caudicinctus	1.230	0.085	32	1.77	+
A. reticulatus	1.657	0.135	20	1.37**	+
A. gibba	1.531	0.114	17	1.35*	+
A. maculosus	1.424	0.110	28	0.919	+
A. nuchalis	1.377	0.056	52	1.78*	+
A. barbatus	1.511	0.036	21	1.07**	+
A. vitticeps	1.441	0.077	16	1.05**	+

EW7.4 = Calculated ear width at snout-parietal distance of 7.4 mm.
* Involves extrapolation below observed size range.
** Smallest individual more than 40 mm snout-vent length.
"a" considered significantly different from 1 when more than 2SE's above or below 1.

(EW7.4, Table 36).

A. fordi and A. isolepis had comparatively weak positive allometry of ear width. These two species, A. caudicinctus and A. cristatus had high EW7.4 values (Table 36).

The scale covered tympanum of A. maculosus grew at a similar rate to the tympana of other members of the A. reticulatus species-group, but A. maculosus had a much lower EW7.4 value (Table 36).

Discussion.

Several points of interest have emerged from the analysis of morphometric data in this study. Probably the most dramatic finding is the extraordinarily rapid rates of change shown by some species. These rapid rates of change demonstrate the danger of using simple arithmetic analyses of data for taxonomic purposes. These dangers are differing adult size and sampling bias.

The comparison of adults from populations attaining different sizes yet retaining similar growth patterns could give apparently significant morphometric differences. Taxonomic decisions based on such differences might not be justifiable on other grounds.

Any sampling bias could also give quite misleading results. This danger is high with many Australian agamids, as many species appear to be "annual" Storr (1965, 1967). Samples of these species collected between April and December are likely to contain individuals of only one year-class. Comparison between populations of the same species collected at two different times of the year would probably yield significant morphometric differences. This problem is illustrated by the sampling bias of _A. isolepis_ in the present study. Museum collections of this species have been collected at times corresponding to the long vacation of Australian universities. At this time of year (December-January) there are very few hatchlings (Storr, 1965). The smallest _A. isolepis_ in the Australian Museum is 38 mm in snout-vent length, much larger than the smallest individual reported by Storr (1965, 22 mm). As a consequence of this sampling error the results obtained for _A. isolepis_ in the present section are largely meaningless.

The literature provides two basic suggestions as to how the study of morphometric changes in ontogeny may be useful in the interpretation of phylogeny. Huxley (1932) suggested that "growth-constants" may be useful taxonomically. Gould (1977), by contrast, suggested that similar juvenile proportions are more likely to indicate phylogenetic relationships. The latter suggestion appears to be more favoured by the data collected in this study.

Three examples supporting Gould's suggestion are presented here. In *D. bennettii* the hind limb grows with positive allometry, contrasting with the negative allometric coefficients of all other *Diporiphora*. Head width within the *A. cristatus* species-group grows with positive allometry in *A. caudicinctus* and negative allometry in *A. cristatus*. The thigh of *C. pictus* grows with negative allometry, in contrast with the positive allometry of *C. fionni*. In all three examples the relevant measurements are similar in juveniles, but quite dissimilar in adults. Thus, relationships established on other grounds are supported by similar juvenile proportions but "growth-constants" may be dramatically different.

Further evidence supporting Gould may be taken from species occupying a similar ecological niche, but from different species-groups or genera. *Lophognathus gilberti centralis* and *Amphibolurus muricatus* occupy almost identical ecological niches. The two species are parapatric on the western side of the Great Dividing Range in northern New South Wales, and occur in apparently identical habitats within a few kilometres of one another. The relative proportions of the two species as adults are almost identical, yet the juveniles differ greatly. Similarly, *C. pictus* is related to the rock-dwelling *Ctenophorus*, but has developed a burrowing habit. Adult *C. pictus* have limb lengths similar to the burrowing *A. reticulatus* species-group, but the juveniles retain limbs proportionately similar to juveniles of *Ctenophorus*.

Changes in body proportions have not been achieved solely by alteration of allometric coefficients. *D. lalliae* has a longer tail than most *Diporiphora*, and has both a high positive allometric coefficient and a relatively long tail as a juvenile. Thus, selective pressure evidently may produce changes in juvenile proportions. However, rate genes appear to be more commonly affected.

There is a strong general trend towards more closely related species having similar juvenile proportions. Selective pressure acting to alter some part of the body appears to act more readily on the rate of allometric change than on the size of the part at hatching. Presumably continued selective pressure would be likely also to produce changes in the juvenile ratios. If this hypothesis is true, then phylogenetic relationships may be inferred by the degree of similarity of juveniles of two taxa.

The main results of morphometric analysis are summarised in Table 37. It can be seen that most genera and species-groups are distinguishable as juveniles by one or more morphometric features. Only *Diporiphora* and *Amphibolurus* are not.

The extent to which growth departs from isometry seems, at least in part, to vary with the size of a species. Smaller species tend to change proportions more rapidly. The highest allometric coefficient for tail growth was for *A. fordi* (1.457), the smallest species for which sufficient data were collected. Larger species tend to have allometric coefficients nearer to one.

A good example of this size difference is provided by the data for *A. nuchalis* and *A. reticulatus*. These species are related and occupy an almost identical ecological niche. Growth for all limb segments measured is further from isometry in the smaller *A. reticulatus*.

Table 37. Summary of Morphometric Data

Tympanocryptis Group

Measurement	A. adelaidensis species-group		Tympanocryptis	
	Juvenile Proportions	Allometry	Juvenile Proportions	Allometry
Pes	long*	–	short*	0
Forelimb		–		0

Chlamydosaurus Group

Measurement	A. muricat species-gp		Caimanops		Chlamydos		Diporiphor		Lophognath	
	JP	All	JP	All	JP	All	JP	All	JP	All
Tail		+		0		0			long	V
Hind Limb			short	0		0		V	long	–
Thigh		+	short	0		+			long	0
Pes			short	0		–			long	–
Fore Limb		–	short	0	long	–				
Head Width		+		0	short	+			short	+
Head Depth		+		+	long	0				+
Ear Width		+		0		+		+	long	

Ctenophorus Group

Measurement	Ctenophorus		A. maculat. species-gp		A. cristat. species-gp		A. reticul. species-gp		A. barbatus species-gp	
	JP	All	JP	All	JP	All	JP	All	JP	All
Tail						+	short	+		–
Hind Limb		–				0	short	–	short	–
Thigh		V		V	long	+			short	0
Pes		–		–		0	short	–	short	–
Fore Limb		–		–	short	0		–		–
Head Width		+				V		+	short	+
Head Depth		+		+	long	+	long	+		+
Ear Width		+	long	0		+		+		+

* All juvenile proportions expressed as relative to other members of the group.

V = some species with significant positive allometry, others with significant negative allometry.

\+ = all species with significant positive allometry or allometric coefficient above one.

0 = no species with significant allometry.

– = all species with significant negative allometry or allometric coefficient below one.

Dodson's (1975b) suggestion that larger animals are more stringently selected as juveniles (see introduction) may be relevant to this observation. His suggestion that a "variant individual" would produce a "relatively grotesque adult" in large species would be even further exaggerated if there were strong allometric changes during growth. This may help to explain the relative isometry for most measurements of Chlamydosaurus, the largest species for which adequate data were collected.

The functional significance of most allometric change is obscure. Two problems of interpretation are present. The first involves general trends in development, such as the almost universal negative allometry in limb growth. The second problem lies in the sometimes quite strong differences in growth patterns between closely related species. An explanation for the former problem might be found with a better understanding of the mechanical problems involved with locomotion during development. A more complete knowledge of comparative ecology than is presently available for Australian agamids should provide at least some explanations for the second problem.

The aim of the present work has been to establish broad trends, rather than the detailed comparison of closely related species. Consequently the data collected are not directly comparable with the one published account using this type of analysis (Badham, 1976). Badham (1976) compared tail growth in A. barbatus and A. vitticeps, demonstrating clear differences between the sexes of each species and between each sex of the different species. Her results suggest that more detailed analysis than that attempted here may prove useful in the comparison of closely related species.

Several strong trends have become apparent in the present study which help to establish taxonomic groupings within the Australian agamids (Table 37). Most of these strong differences correspond with groups which are easily defined on other morphological features, but some differences occur between groups which are not thus clearly defined.

VI. Karyology

Introduction.

The study of taxonomy in recent literature has become very much concerned with measuring the degree of genetic similarity between taxa. The structural bases for genetic transmission, the chromosomes, have received increasing attention in a taxonomic context over the past twenty years.

Before the 1950's the study of karyology was a tedious and painstaking task. It relied on the examination of standard histological sections of tissues with many dividing cells, such as testicular tissue, or the gonads of embryos (e.g. Makino and Asana, 1948). This method relied heavily on chance both to find nuclei in the metaphase stage of division which also had been sectioned without damage.

In the 1950's two advances in technique greatly increased the ability of researchers to find suitable nuclei for study. The use of hypotonic suspensions allowed the easy preparation of a single-cell layer for microscopic examination, and avoided the problems inherent in sectioned material. The use of colchicine prevented the continuation of the division process beyond metaphase (Ford and Hamerton, 1956), greatly increasing the number of mitotic nuclei suitable for study.

Comparative work on lizard karyotypes before the 1950's had been pioneered by relatively few researchers. Matthey (1931) was probably the major contributor to the field, but much work was carried out in Japan. During the 1960's and 1970's the amount of information available on lizard karyotypes has expanded rapidly, and much of this information has proved useful taxonomically.

The amount of variation in lizard karyotypes varies between the families so far studied. Some families appear to have a remarkably conservative karyotype, with little or no variation among its members, while others are apparently prone to rapid chromosomal evolution (Gorman, 1973). Within the Gekkonidae, for example, some species-groups consist of a number of different chromosome races which are difficult to distinguish morphologically (King, 1977).

Remarkably little has been published on the karyology of the agamids. Matthey (1931) described the karyotype of two species. Since then major contributions have appeared from Sokolovsky (1974, 1975) and Gorman and Shochat (1972). However, karyotypes have been described for only 35 species of agamids belonging to 11 genera. The only published karyotype for an Australian agamid has arisen from the present study (Witten, 1978).

Results.

Karyotypes of 90 individuals of 18 species were obtained. Three distinct karyotypes were encountered.

Physignathus lesueurii and *Gonocephalus spinipes* possessed the presumed primitive lizard karyotype (Gorman, 1973) of 12 metacentric macrochromosomes and 24 microchromosomes (2n = 36; 12M 24m), with a distinct break in size between the larger and smaller chromosomes (Fig. 35). The second largest pair of macrochromosomes was submetacentric.

The great majority of endemic Australian species karyotyped possessed a karyotype similar to that of *Physignathus*, but with four fewer microchromosomes (2n = 32; 12M 20m; Fig. 35). This karyotype was present in *Amphibolurus*, *Diporiphora*, *Chlamydosaurus*, *Tympanocryptis* and *Ctenophorus* (Table 38).

Lophognathus gilberti centralis possessed a karyotype with a haploid complement of 20 (2n = 40). There was a less distinct break in

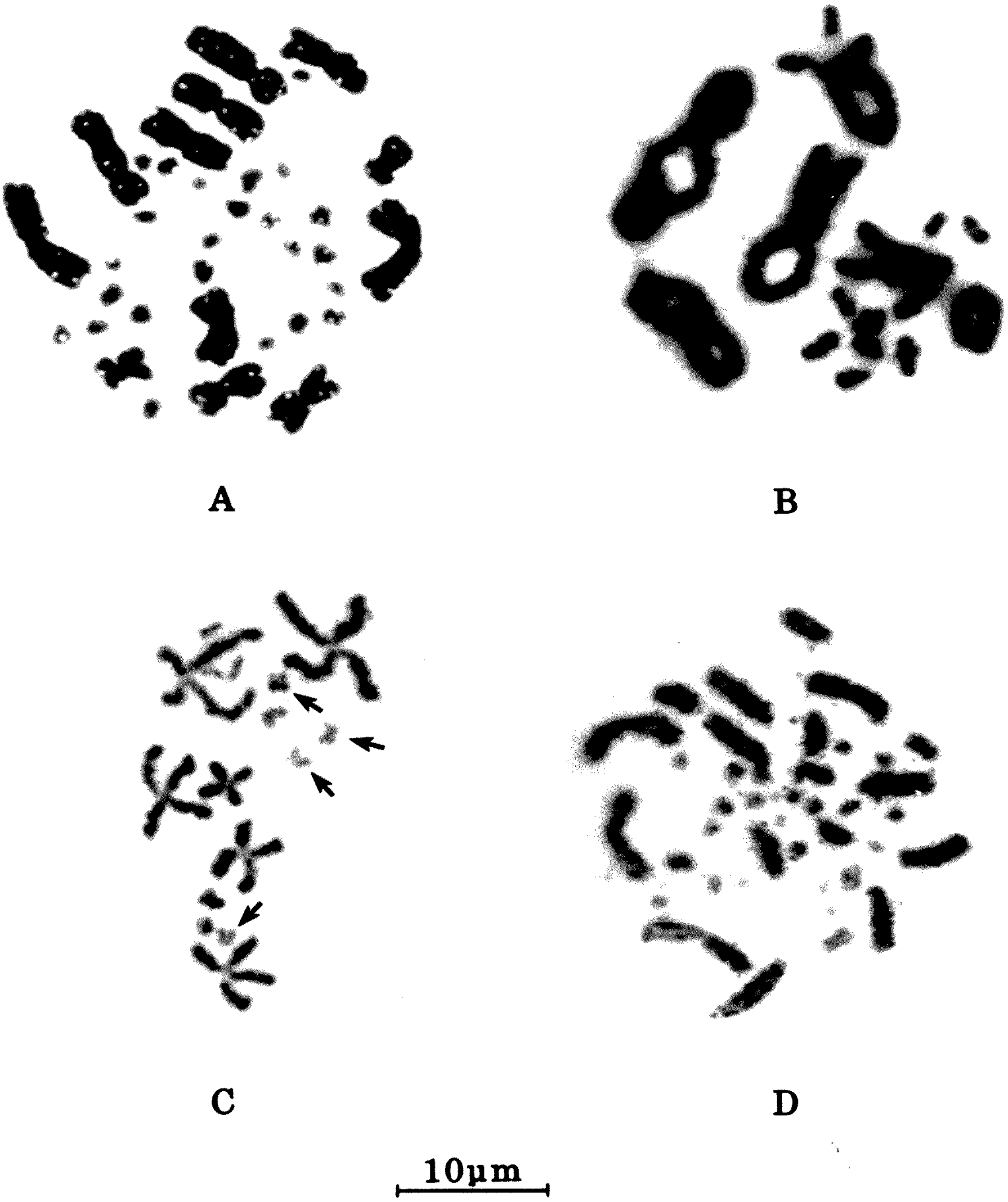


Figure 35. Chromosome Figures. A = Somatic complement from bone marrow of Physignathus lesueurii; B = First meiotic division from testis of Amphibolurus barbatus; C = Second meiotic division from testis of Amphibolurus muricatus; D = Somatic division from testis of Lophognathus gilberti. Note that there are 24 microchromosomes in A, but only 10 in B and C. The four largest microchromosomes in C appear to be metacentric (arrowed). Note the less distinct break in size between macro- and microchromosomes in D.

size between macrochromosomes and microchromosomes (Fig. 35), but there appeared to be 20 macrochromosomes and 20 microchromosomes. Most macrochromosomes were telocentric or subtelocentric, with only three pairs metacentric. Some of the larger microchromosomes also appeared to be metacentric.

Table 38. Karyotypes of Australian Agamids.

Species	Number (Animals)	Somatic Cells (No. Animals)	Meiotic Cells (No. Animals)	2n	Description
Gonocephalus	1	1	-	36	12M 24m
Physignathus	1	1	-	36	12M 24m
T. tetraporophora	5	2	5	32	12M 20m
A. diemensis	7	7	4	32	12M 20m
A. muricatus	8	5	6	32	12M 20m
A. nobbi	7	6	7	32	12M 20m
Chlamydosaurus	1	1	-	32	12M 20m
D. australis	2	2	2	32	12M 20m
D. bennettii	1	1	1	32	12M 20m
D. bilineata	3	3	1	32	12M 20m
D. magna	2	1	2	32	12M 20m
L. g. gilberti	1	1	-	?	? *
L. g. centralis	9	7	5	40	20M 20m
C. decresii	7	6	6	32	12M 20m
C. pictus	11	6	10	32	12M 20m
A. fordi	6	4	4	32	12M 20m
A. femoralis	1	1	1	32	12M 20m
A. isolepis	1	1	1	32	12M 20m
A. cristatus	1	1	-	32	12M 20m
A. clayi	1	1	1	32	12M 20m
A. nuchalis	2	2	1	32	12M 20m
A. barbatus	6	5	5	32	12M 20m
A. vitticeps	6	6	6	32	12M 20m

* One L. g. gilberti was studied. The few cells on the preparation showed a number of telocentric chromosomes, which were seen in the above species only in this specimen and in L. g. centralis. An accurate count was not possible.

Analysis of chromosome lengths did not reveal consistent differences between those taxa with twelve macrochromosomes (Table 39). In all such species analysed the second largest pair of chromosomes was submetacentric (Table 40). All other macrochromosomes were metacentric. At

Table 39. Relative Macrochromosome Lengths.

Species	n	I		II		III		IV		V		VI	
		%	SD	%	SD	%	SD	%	SD	%	SD	%	SD
Physignathus	6	11.42	0.40	10.45	0.53	8.77	0.35	7.83	0.52	6.65	0.36	4.88	0.25
A. diemensis	13	11.47	0.74	10.39	0.64	8.77	0.48	8.00	0.62	6.73	0.34	4.64	0.37
A. muricatus	10	11.31	0.83	10.35	0.54	8.61	0.43	8.18	0.49	6.84	0.72	4.71	0.36
A. nobbi	19	11.95	0.82	10.71	0.90	8.49	0.43	8.08	0.58	6.47	0.34	4.29	0.43
C. decresii	13	11.74	0.84	10.59	1.10	8.89	0.53	7.83	0.67	6.54	0.50	4.41	0.38
C. pictus	10	11.41	0.47	10.77	0.94	8.84	0.61	7.98	0.37	6.58	0.43	4.43	0.46
A. fordi	10	12.52	0.86	10.00	0.69	8.78	0.63	7.83	0.39	6.60	0.22	4.27	0.30
A. barbatus	13	12.17	0.75	10.25	0.71	8.45	0.67	8.01	0.70	6.63	0.37	4.49	0.41
A. vitticeps	10	12.02	0.63	10.40	0.65	8.74	0.48	8.04	0.48	6.41	0.37	4.39	0.34

(Lengths expressed as percentage of total macrochromosome lengths).
n = number of cells analysed.

Table 40. Centromeric Indices.

Species	n	I		II		III		IV		V		VI	
		Ic	SD	Ic	SD	Ic	SD	Ic	SD	Ic	SD	Ic	SD
Physignathus	6	47.0	1.3	31.3	1.5	48.7	1.1	46.8	2.3	47.5	1.8	47.4	2.7
A. diemensis	12	48.3	1.7	29.7	2.6	46.3	1.8	46.8	2.2	46.8	2.6	47.7	2.1
A. muricatus	8	46.8	1.8	29.4	3.1	47.0	2.9	47.3	2.2	46.2	1.6	44.8	2.7
A. nobbi	17	46.5	1.6	29.9	3.1	47.0	1.8	47.7	1.4	46.8	2.2	47.3	2.5
C. decresii	12	46.7	3.0	30.3	4.1	47.0	2.1	46.7	3.7	47.3	2.8	46.2	3.5
C. pictus	10	46.6	2.1	30.0	3.9	48.6	1.5	48.8	1.0	46.8	1.9	47.1	3.7
A. fordi	8	47.2	1.8	30.6	3.0	48.0	2.3	48.0	1.0	46.6	2.4	46.5	2.9
A. barbatus	10	46.1	2.7	27.8	2.2	48.2	2.0	47.1	1.7	44.3	4.6	45.7	2.8
A. vitticeps	8	46.7	2.5	32.6	3.7	47.4	3.3	47.9	2.3	45.8	3.2	45.4	3.3

Ic = Centromeric Index.

least the larger microchromosomes appeared to be metacentric in those species with only 20 microchromosomes.

The Lophognathus karyotype was more difficult to analyse. The larger number of chromosomes meant that fewer cells were suitable for measurement, as chromosomes were more often superimposed on one another. The telocentric chromosomes made determination of the centromere position more difficult. The larger two chromosomes represent a similar proportion of the total macrochromosome length to pairs III and IV in the other agamid species analysed (Table 41).

Table 41. Lophognathus gilberti centralis Chromosome Data.

Chromosome Number	Relative Length %	SD	Centromeric Index Ic	SD
I	7.82	0.52	47.6	0.92
II	7.33	0.33	40.9	3.19
III	7.12	0.82	20.8	2.01
IV	5.88	0.40	19.8	5.36
V	5.29	0.28	3.63	5.65
VI	4.44	0.43	23.1	6.77
VII	3.82	0.43	25.0	4.25
VIII	3.40	0.30	7.24	11.5
IX	2.86	0.30	40.7	4.76
X	2.07	0.47	0	0

% = Percentage of total macrochromosome length.
Ic = Centromeric Index.

Discussion.

Humphries (1972) described the karyotype of 25 species of 6 genera of Australian agamids. All of these species, he reported, had a karyotype of 2n = 36 (12M, 24m). About ten of the species studied by Humphries have also been examined in this study. Only Physignathus lesueurii has been confirmed as agreeing with Humphries' results. Most of the other species have a karyotype of 2n = 32 (12M, 20m), but Lophognathus gilberti has a very different karyotype of 2n = 40 (20M, 20m). Humphries (pers. comm.) was confident only of his *Physignathus* karyotype, and his other results are therefore suspect.

Data have been published for 35 agamid species in 11 genera (Table 42). Many agamids possess the karyotype suggested by Gorman (1973) to be primitive, with 12 metacentric macrochromosomes and 24 microchromosomes.

The form of the macrochromosomes appears to be remarkably similar in all those agamids retaining six pairs. The second largest pair is submetacentric and the other five pairs are metacentric. A comparison between the analyses of Krishna Rao and Aswathanarayana (1979) for two Indian agamids and the Australian species with twelve macrochromosomes (Table 43) reveals few differences. The centromeric indices for the Australian species are lower for the second pair, but the absence of statistical data for the Indian species means that no meaningful comparison is possible. The general description of the form of the macrochromosomes is apparently applicable to most other agamids with six pairs of macrochromosomes. Figures in Moody and Hutterer (1978: *Lyriocephalus*), Sokolovsky (1975: *Agama*) and Hall (1970: *Leiolepis*) all show the second largest macrochromosome as submetacentric. The same basic structure occurs also in at least some iguanids (Gorman, 1973).

Most agamids with more than twelve macrochromosomes have largely telocentric or submetacentric chromosomes. Most of these karyotypes are at least theoretically derivable from the primitive arrangement by centric fission, the primitive complement of 24 macrochromosome arms being retained in most species. For example, *Japalura* (Makino and Momma, 1949) and most *Phrynocephalus* (Sokolovsky, 1974) have 24 telocentric macrochromosomes. Changes in the number of macrochromosome arms have more often been reductions. Gorman and Shochat (1972) reported reductions in some species of *Agama* (22: *A. agama*, *A. sanguinolenta*, *A.*

Table 42. Published Karyotype Data on the Family Agamidae.

Species	2n	Description*	Source
Agama agama	42-44	2V+18I+22-24m	Gorman & Shochat, 1972
Agama atricollis	34-36	8V+2I+24-26m	Gorman & Shochat, 1972
Agama caucasica	34	12V + 22m	Arronet, 1965 (*fide* Gorman, 1973)
Agama caucasica	36	12V + 24m	Sokolovsky, 1975
Agama erythrogastra	36	12V + 24m	Sokolovsky, 1975
Agama hymalayana	36	12V + 24m	Sokolovsky, 1975
Agama lehmanni	36	12V + 24m	Sokolovsky, 1975
Agama planiceps	48	24I + 24m	Gorman & Shochat, 1972
Agama pallida	46	24I + 22m	Gorman, 1973;Gorman & Shochat,1972
Agama ruderata	46	24I + 22m	Bhatnagar & Yoniss, 1977
Agama sanguinolenta	46	22I + 24m	Sokolovsky, 1975
Agama savignii	46	24I + 22m	Gorman, 1973;Gorman & Shochat,1972
Agama sinaita	44	22I + 22m	Gorman, 1973;Gorman & Shochat,1972
Agama stellio	36	12V + 24m	Matthey, 1931 (*fide* Gorman, 1973)
Agama stellio	34-36	12V+22-24m	Gorman & Shochat, 1972
Agama tuberculata	34	12V + 22m	Dutt, 1969 (*fide* Gorman, 1973)
Amphibolurus nobbi	32	12V + 20m	Witten, 1978
Calotes versicolor	34	12V + 22m	Makino & Asana, 1948 #
Calotes jerdoni	34	12V + 22m	Sharma & Nakhasi, 1980
Japalura swinhonis	46	24I + 22m	Nakamura, 1935 (*fide* Gorman, 1973)
Japalura polygonata	46	24I + 22m	Makino & Momma, 1949
Leiolepis belliana	36	12V + 24m	Hall, 1970
Lyriocephalus scutatus	30	12V + 18m	Moody & Hutterer, 1978

Phrynocephalus guttatus	46	24I + 22m	Sokolovsky, 1974
Phrynocephalus helioscopus	44	2V+18I+24m	Arronet, 1965 (*fide* Gorman, 1973)
Phrynocephalus helioscopus	46	2V+18I+26m	Sokolovsky, 1974
Phrynocephalus interscapularis	48	24I + 24m	Sokolovsky, 1974
Phrynocephalus mystaceus	48	22I+2V+24m	Sokolovsky, 1974
Phrynocephalus raddei	48	24I + 24m	Sokolovsky, 1974
Phrynocephalus reticulatus	48	24I + 24m	Sokolovsky, 1974
Phrynocephalus rossikowi	48	24I + 24m	Sokolovsky, 1974
Phrynocephalus versicolor	48	24I + 24m	Sokolovsky, 1974
Psammophilus dorsalis	32	12V + 20m	Krishna Rao & Aswathanarayana,1979
Ptyctolaemus gularis	34	12V + 22m	Sharma & Nakhasi, 1980
Sitana ponticeriana	46	24I + 22m	Makino & Asana, 1948
Uromastyx aegyptius	?	12V + ?	Gorman & Shochat, 1972
Uromastyx hardwickei	36	12V + 24m	Matthey, 1931 (*fide* Gorman, 1973); Sharma & Nakhasi, 1980
Uromastyx hardwickei	34	12V + 22m	Makino & Asana, 1948
Uromastyx ornatus	?	12V + ?	Gorman & Shochat, 1972

* V = Metacentric or submetacentric macrochromosomes,
I = Telocentric or subtelocentric macrochromosomes,
m = microchromosomes.

\# Confirmed by Singh et al, 1970 (fide Gorman, 1973); Krishna Rao & Aswathanarayana, 1979; Sharma & Nakhasi, 1980.

Table 43. Comparative Chromosome Data from Australian and Asian Agamids.

Species	I		II		III		IV		V		VI	
	%M	Ic	%M	Ic	%M	Ic	%M	Ic	%M	Ic	%M	Ic
Psammophilus *	12.3	46.4	10.5	36.0	8.3	46.2	7.9	47.8	6.6	46.1	4.3	44.3
Calotes *	11.8	44.3	11.1	36.0	8.3	49.1	7.9	48.1	6.6	46.9	4.3	47.5
Physignathus	11.4	47.0	10.5	31.3	8.8	48.7	7.8	46.8	6.7	47.5	4.9	47.4
A. diemensis	11.5	48.3	10.4	29.7	8.8	46.3	8.0	46.8	6.7	46.8	4.6	47.7
A. muricatus	11.3	46.8	10.4	29.4	8.6	47.0	8.2	47.3	6.8	46.2	4.7	44.8
A. nobbi	12.0	46.5	10.7	29.9	8.5	47.0	8.1	47.7	6.5	46.8	4.3	47.3
C. decresii	11.7	46.7	10.6	30.3	8.9	47.0	7.8	46.7	6.5	47.3	4.4	46.2
C. pictus	11.4	46.6	10.8	30.0	8.8	48.6	8.0	48.8	6.6	46.8	4.4	47.1
A. fordi	12.5	47.2	10.0	30.6	8.8	48.0	7.8	48.0	6.6	46.6	4.3	46.5
A. barbatus	12.2	46.1	10.3	27.8	8.5	48.2	8.0	47.1	6.6	44.3	4.5	45.7
A. vitticeps	12.0	46.7	10.4	32.6	8.7	47.4	8.0	47.9	6.4	45.8	4.4	45.4

* Data from Krishna Rao and Aswathanarayana, 1979.

sinaita; 18: A. atricollis)(A. sanguinolenta from Sokolovsky, 1975). Phrynocephalus contains the other two species which depart from the normal number of macrochromosomal arms; P. helioscopus with a reduced number of 22 (Arronet, 1965 [fide Gorman, 1973]; Sokolovsky, 1974) and P. mystaceus with an increased number of 26 (Sokolovsky, 1974). Lophognathus thus represents the only other species with an increased number of macrochromosomal arms (26). Although P. mystaceus and Lophognathus share the same number of arms, the karyotypes are quite different (P. mystaceus: 2V+22I+24m; Lophognathus: 6V+14I+20m).

The Lophognathus karyotype could have been derived from the primitive karyotype with centric fissions in 4 of the 6 pairs of chromosomes. A pericentric inversion could subsequently have caused the ninth pair to become metacentric.

Almost all agamid species previously studied have 24 microchromosomes. A significant minority have a reduced microchromosome complement of 22 (Table 42). Only Lyriocephalus and Psammophilus had previously been reported to possess fewer than 22 microchromosomes. In the case of Lyriocephalus, Moody and Hutterer (1978) suggested that several telocentric microchromosomes may have fused to form the larger, apparently metacentric chromosomes of that genus. This explanation is apparently not applicable to Psammophilus, where all microchromosomes are telocentric (Krishna Rao and Aswathanarayana, 1979). Krishna Rao and Aswathanarayana (1979) suggested that the extra two or four microchromosomes may have fused with the macrochromosomes, although they presented no data to substantiate this claim.

Of the Australian species karyotyped Physignathus and Gonocephalus possess a "full" complement of 24 apparently telocentric microchromosomes. Of the endemic species karyotyped, including Lophognathus, all possess 20 microchromosomes, the largest pair of which are apparently metacentric. It therefore appears likely that the reduced complement of the Australian endemics is due to the fusion of four pairs of telocentric microchromosomes to form two pairs of slightly larger metacentric microchromosomes.

Centric fission appears to be a common phenomenon in agamid karyotypes. There are at least three different karyotypes reported in the literature which apparently represent the results of centric fission (Table 42). The different degrees of fission within *Phrynocephalus* (Sokolovsky, 1974) and *Agama* (Gorman and Shochat, 1972) probably represent separate evolutionary events, demonstrating a predisposition in at least these genera towards centric fission. The centric fissions presumed to have occurred in the evolution of the *Lophognathus* karyotype are therefore not unusual for the family. However, the form and reduced number of microchromosomes in the *Lophognathus* karyotype indicate a close relationship with the other endemic Australian agamids.

The reduced number of microchromosomes in all Australian agamids except *Physignathus* and *Gonocephalus* suggests that these species represent a single radiation. The karyotypes of *Moloch* and *Chelosania* have not been studied, and other features have been used to place these genera phylogenetically. The only other species with a karyotype of 2n = 34, *Psammophilus dorsalis* (Krishna Rao and Aswathanarayana, 1979), differs from the Australian radiation in the possession of telocentric microchromosomes. The other karyotype which resembles that of the Australian radiation, *Lyriocephalus* (Moody and Hutterer, 1978), does not correspond exactly with the most common Australian configuration. There is a strong possibility that the reduction in the number of microchromosomes occurred in a similar way in the two groups, but the reduction has been greater in

Lyriocephalus. The differing karyotypes increase the probability that they represent completely separate but parallel evolutionary events. There is little other information which suggests that _Lyriocephalus_ and the Australian radiation are related.

VII. Conclusions and Discussion.

Phylogenetic Groups.

A. Major Divisions.

Australian agamid lizards may be assigned to one of two groups. There is one large radiation of species belonging to genera confined to the Australian region. Only three genera do not belong to this large "endemic" group: *Gonocephalus*, *Physignathus* and *Chelosania*. The first two of these have species in southeastern Asia, and were distinguished from other Australian agamids by their retention of the lacrymal bone (Cogger, 1961). *Chelosania* also retains the lacrymal bone (Cogger, pers. comm.) and is included with the other two genera to form an "Asian-derived" group.

The results of this study have confirmed this division of the Australian agamids. *Gonocephalus* and *Physignathus* retain the primitive lizard karyotype of 2n = 36 (12M, 24m). All endemic species karyotyped have only 20 microchromosomes, setting them apart from almost all other agamids.

The Asian-derived genera also differ strongly from the endemic species by virtue of their climatic preference. *Gonocephalus* is restricted to high-rainfall forests, *Physignathus* occupies riparian habitats and *Chelosania* occurs in seasonally wet areas in the north of the continent. All the endemic Australian agamids are restricted to arid habitats or belong to genera with many arid-adapted species.

B. Intergeneric Relationships.

i. Asian-derived Genera.

Chelosania does not have obvious affinities with any other extant agamid. The genus is restricted to northern Australia, west of the Gulf of Carpentaria. It is unique among Australian agamids in possessing posteromedial dorsal scale rows, a feature also present in *Calotes cristatellus* of Timor and New Guinea. The two taxa are not otherwise very similar, but the possibility of their being related cannot be dismissed.

Gonocephalus and *Physignathus* are superficially similar. The two genera have several similar scale characters and share the same karyotype. *Physignathus* differs in the possession of pores. *Hydrosaurus* of New Guinea and other islands of the Indo-Australian archipelago shares the possession of pores and several other features with *Physignathus*.

ii. Endemic Genera.

The endemic species are divisible into four groups. One of these groups contains the single monotypic genus *Moloch*. Each of the other three groups contains species which are clearly related to one another, but at a level often higher than generic rank. The *Tympanocryptis* group has two generic groups, the *Chlamydosaurus* group and the *Ctenophorus* group five each. The intergeneric relationships within these groups are discussed below. Affinities between the four different groups are obscure. The species exhibiting the greatest number of primitive features are within the *Tympanocryptis* and *Ctenophorus* groups. However, a number of features separate the groups and the phylogenetic polarities of these characters are unknown. *Moloch* and the *Chlamydosaurus* group exhibit a number of derived character states, so would be less likely to resemble a hypothetical ancestral species. Any further attempt to relate these groups phylogenetically would be very speculative.

1. Moloch.

Moloch is an extraordinary genus, divergent not only from other endemic agamids, but from all other lizards. The genus lacks a lacrymal

(Cogger, 1961), and thus probably belongs with the other endemic agamids. Any attempt to hypothesise closer relationships would be premature.

Moloch has a large number of unique and divergent characters (see p. 185). The degree and diversity of these features suggest that *Moloch* has had a long separate evolutionary history.

2. *Tympanocryptis* Group.

All members of the *Tympanocryptis* group are small (less than 80 mm snout-vent), terrestrial, cryptic species. *Tympanocryptis* has a reduced phalangeal formula and has lost the tympanic membrane. Both these are clearly derived features. *T. parviceps* so closely resembles *Amphibolurus adelaidensis* in other features, however, that Storr (1977) suggested that *parviceps* belongs in *Amphibolurus*. These taxa possess the primitive pore arrangement, contrasting with the reduced number of pores typical of the other species of *Tympanocryptis*.* A combination of these features and the current distribution of species within the group provide a good foundation for speculation on the patterns of evolution within the group.

Tympanocryptis almost certainly arose from a species similar to *A. adelaidensis*. The tympanic membrane and fourth phalanx of the fifth toe were probably lost at about the same time. Subsequently more advanced species have reduced the number of preanal and femoral pores, leaving *T. parviceps* as a link between the advanced *Tympanocryptis* and the *A. adelaidensis* species-group.

The more primitive members of the *Tympanocryptis* group occur

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* During the final preparation of this thesis Storr (1981) described *Tympanocryptis aurita*, a species of *Tympanocryptis* which possesses an exposed tympanum. However, the holotype has 17 preanal and femoral pores, and the phalangeal formula was not given. Clearly further work on the relationships of this species is needed.

peripherally on the Australian continent. *A. diemensis* is the single species of agamid in Tasmania, and has a disjunct mainland distribution. The species occurs in localised populations in heath communities on very porous soils. These areas drain rapidly following rain and become effective semi-arid areas with a few days of dry weather. These restricted habitats may represent "dry refugia" where more primitive arid-adapted species are protected from competition from more modern species by large "barriers" of more mesic habitats. Such an hypothesis may also be applicable to the peripheral distributions of *A. adelaidensis* and *T. parviceps* in the west of the continent (Fig. 36).

The highest species diversity of the *Tympanocryptis* group is in central Australia (Fig. 36). All species in this area are advanced *Tympanocryptis*. Thus the modern distribution of the *Tympanocryptis* group is consistent with the hypothesis of a central "centre of evolution" where the more primitive species have been replaced.

3. Chlamydosaurus Group.

Chlamydosaurus is the most distinctive genus of this group. A number of features combine to suggest that it is related to the other four genera of the group, but it is not obviously more closely related to any one of them. Its phylogeny therefore remains obscure.

Amphibolurus, *Diporiphora*, *Lophognathus* and *Caimanops* are apparently closely related. *Caimanops* is quite divergent from the other three in morphometric features, but retains many of the morphological features typical of the other three genera. *Lophognathus* also differs morphometrically, and also has a derived karyotype. Either character would support the continued recognition of the genus. *Amphibolurus* and *Diporiphora* are extremely similar. The loss of a vertebral scale ridge in *Diporiphora* is one of the few definite features distinguishing the

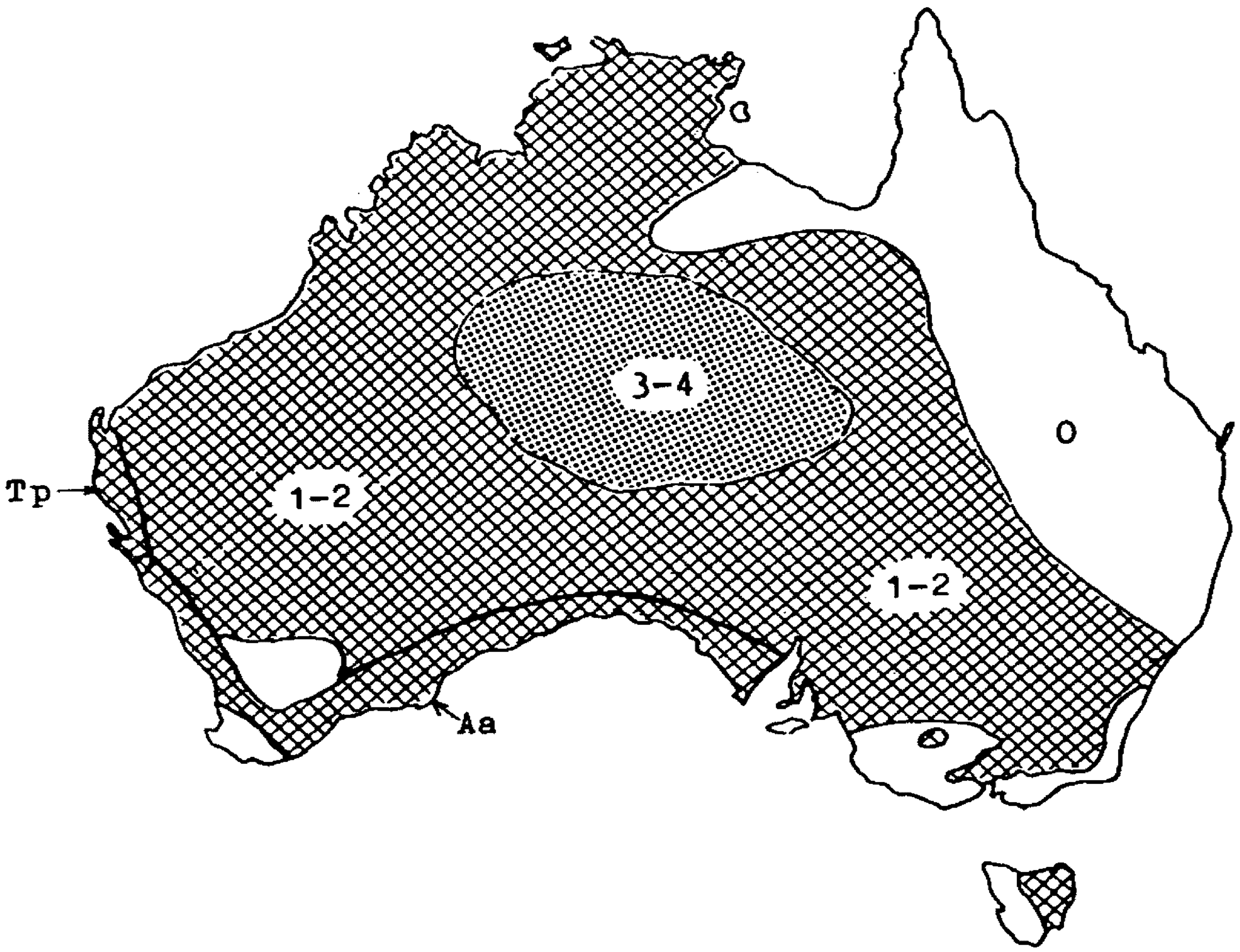

Figure 36. Species Diversity of the Tympanocryptis Group. Outlined area indicated Tp = distribution of T. parviceps; area Aa = distribution of A. adelaidensis. Numbers indicate number of species in each area. Data from Cogger (1975) and Storr (1964, 1977).

genus from *Amphibolurus*. The possibility that all *Diporiphora* possess bifurcate hemipenes, however, suggests that *Diporiphora* should be retained.

Darlington (1948) suggested that ectotherms would be more likely to undergo rapid evolution in tropical areas. Several factors support this reasoning. Growth rates are likely to be more rapid in tropical climates, allowing more rapid maturation and reduced generation times. These trends are accentuated by the absence of periods of dormancy, and the possibility of breeding throughout the year. Tropical areas are also likely to support a greater diversity of ectotherms. Both of these factors increase the probability of new forms evolving more often in tropical rather than temperate areas.

Faster generation times and greater competition would tend to produce more rapid evolution in the tropical north. Where the same ecological niche is occupied by different taxa in the north and south, the northern taxon might be expected to have evolved further from a common ancestor.

Lophognathus, *Caimanops*, and the *Amphibolurus muricatus* species-group occupy similar ecological niches. *Lophognathus* has a derived karyotype and a northern distribution. These two facts suggest that *Lophognathus* has evolved more recently than *Caimanops* and *Amphibolurus*, which are more southern in their distributions. *Diporiphora* has a northern Australian distribution, although some species have penetrated far to the south. *Caimanops* resembles *Lophognathus* in its elongate form and prominent nuchal and vertebral crests. It is likely that *Lophognathus* arose from a species resembling *Caimanops*. *Amphibolurus* and *Diporiphora* are extremely similar, and it seems likely that *Diporiphora* arose from a species very similar to *A. nobbi*. The probable intergeneric relationships of the *Chlamydosaurus* group are represented in Figure 37.

The greatest species diversity of the *Chlamydosaurus* group occurs in northern Australia (Fig. 38). Three of the five genera in the group occur in this area. The presumed more primitive *Caimanops* and *Amphibolurus* are more southerly in distribution. As the more advanced genera are more prominent in the north it seems probable that much of the evolution of the *Chlamydosaurus* group occurs in or near these areas of greatest species diversity. This is similar to the situation in the *Tympanocryptis* group.

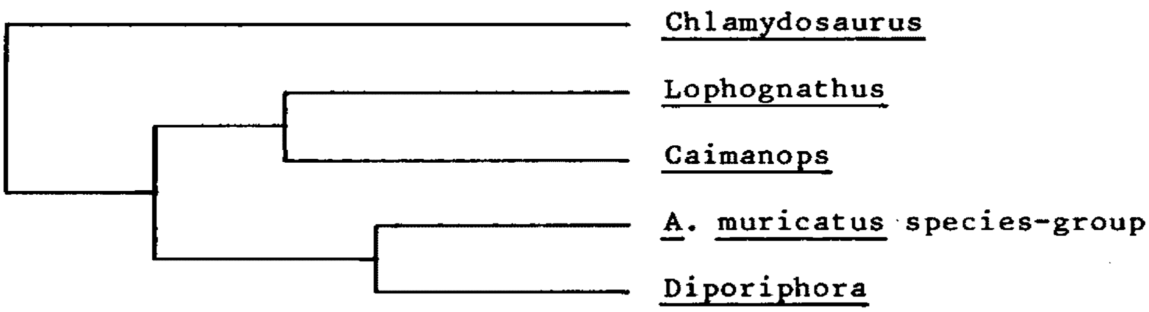

Figure 37. Probable Intergeneric Relationships of the *Chlamydosaurus* Group. Dendrograph illustrating the relationships of the genera in the group. The level of branching is based on a subjective assessment of the degree of similarity between genera.

4. *Ctenophorus Group*.

Five groups make up the fourth Australian radiation. These are *Ctenophorus*, the *Amphibolurus cristatus*, *A. maculatus*, *A. reticulatus* and *A. barbatus* species-groups. Each warrants generic recognition.

The *Ctenophorus* group is generally restricted to the more arid areas of the continent, with the exception of some species of the *A. barbatus* species-group. The areas of greatest species diversity are in the north-west and central-west of the continent (Fig. 39). The centre

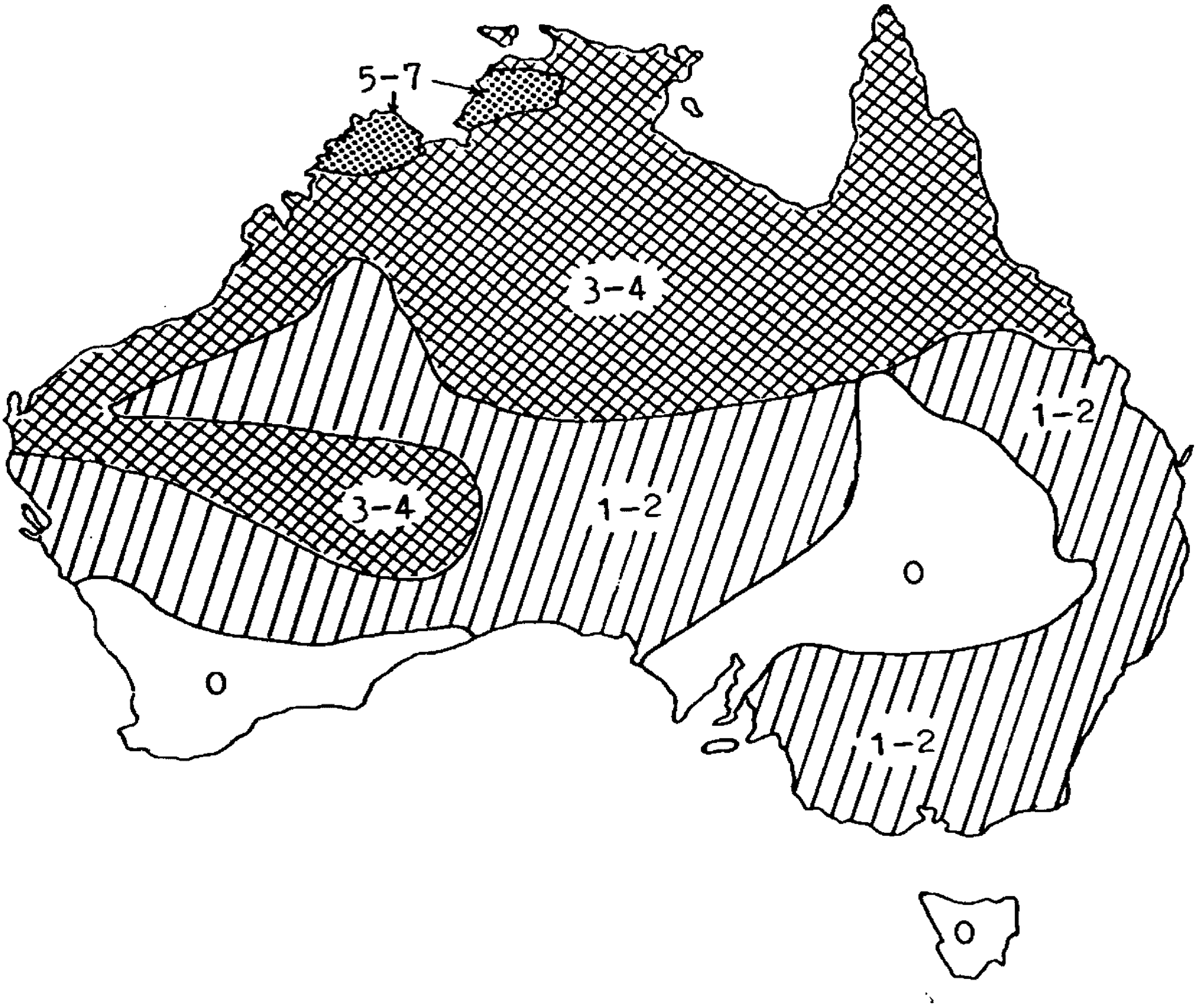

Figure 38. Species Diversity of the *Chlamydosaurus* Group. Numbers indicate number of species in each area. Data from Cogger (1975).

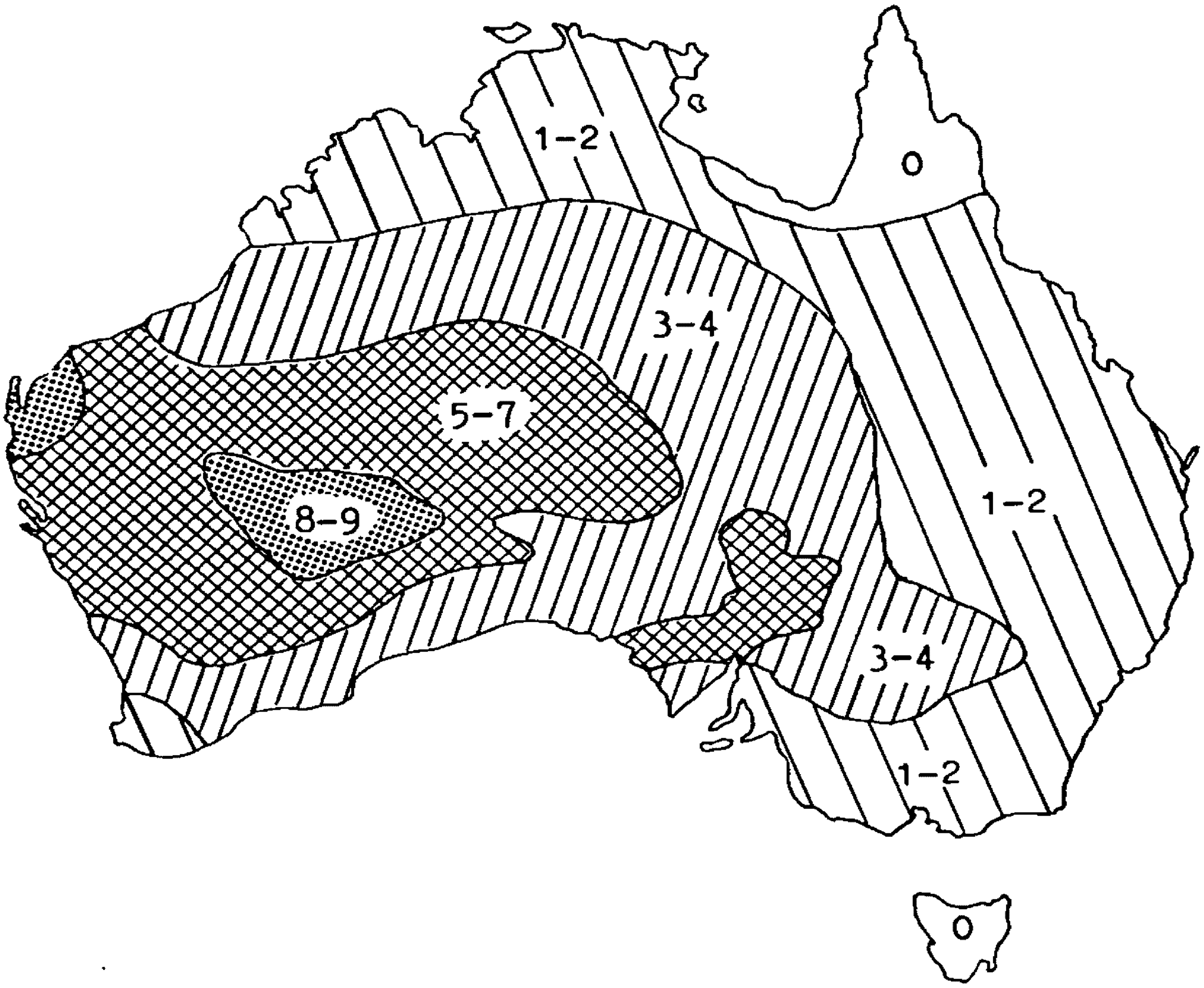

Figure 39. Species Diversity of the Ctenophorus Group. Numbers indicate number of species in each area. Data from Cogger (1975).

of evolution of the group probably lies in one of these areas. Using data from the *Tympanocryptis* and *Chlamydosaurus* groups as a guide, the more primitive members of the group might be expected to occur away from these centres.

Ctenophorus is restricted to the southern half of the continent, and is not represented in either area of greatest species diversity. Most features considered primitive may be found in this genus, including the vertebral scale ridge and the primitive pore arrangement. One species, *C. pictus*, is a burrower, but all other members of *Ctenophorus* are rock-dwellers. The genus is probably nearest the ancestral form of this radiation.

The *A. cristatus* species-group has only two species, *A. cristatus* and *A. caudicinctus*. The two species are remarkably similar in morphometric ratios. These same ratios serve to distinguish the species-group from all other members of this radiation. These species retain some characters presumed to be primitive, including a well-developed scale ridge, but there are two factors suggesting that the group is more advanced than *Ctenophorus*. The species-group exhibits wider spacing of the pores, a derived character. Also, *A. caudicinctus* is a common, widespread species occurring in both centres of evolution, and extending further north than any other species of the *Ctenophorus* group. *A. caudicinctus* is a rock-dweller, and may have replaced *Ctenophorus* in the north. Thus the *A. cristatus* species-group is probably best considered as more advanced than *Ctenophorus*, but more primitive than the other species-groups of the *Ctenophorus* group. The distinctive nuchal crest of *A. cristatus*, and some less important features, might justify placing the two species of this group in separate genera. The recognition of a relationship between the two species has been considered more important than the creation of new generic groups.

Morphometric analysis revealed that members of the *A. maculatus* species-group are rather depressed in form, particularly as juveniles. This observation is consistent with the group having evolved from a species of *Ctenophorus*. Most *Ctenophorus* are depressed in form as an adaptation for living in rock crevices. No such ecological adaptive significance is apparent for the *A. maculatus* species-group, and the depressed form of the group is best explained as a legacy of its descent from *Ctenophorus*.

The presence of three derived character states within the *A. maculatus* species-group makes reconstruction of speciation within the group possible (Fig. 40). Retention of a vertebral scale ridge and the ventral colour pattern typical of *Ctenophorus* suggest that *A. scutulatus* is the most primitive member of the group. *A. isolepis* has retained the ventral pattern and pore arrangement of *A. scutulatus*, and probably evolved from a species similar to it. *A. maculatus* also retains the vertebral scale ridge, but has evolved a derived ventral colour pattern and pore arrangement similar to those of *A. fordi* and *A. femoralis*. The loss of the nuchal and vertebral scale ridges in the latter two species has probably occurred independently from *A. isolepis*. This loss has also occurred in *Diporiphora linga* and *D. winneckei* as an adaptation to living in grass tussocks. There is apparently strong selective pressure against the retention of a nuchal scale ridge in this ecological group (see pp. 77-78).

The *A. reticulatus* species-group has one feature which is almost certainly derived. The series of spines on the lower eyelid is seen in this and the *A. barbatus* species-group and no other. The pore arrangement of *A. nuchalis* and *A. clayi* represents a derived character occurring within the group. The scale-covered tympanum of *A. maculosus* represents another such feature. The group retains many of the features of *Ctenophorus*, at least in some species. Juvenile *A. gibba* resemble juvenile *Ctenophorus* morphometrically, although adult ratios differ widely between the two groups. There is enough evidence, therefore, to suggest that the *A. reticulatus* species-group evolved from a species similar to those of *Ctenophorus*. The presence of three important derived character states within the group suggest that it has probably had a long separate evolutionary history.

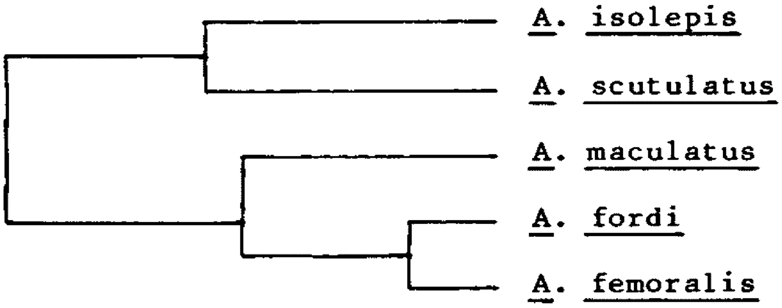

Figure 40. Probable Relationships between Species of the *A. maculatus* Species-group. Dendrograph illustrating the relationships of the species in the group. The level of branching is based on a subjective assessment of the degree of similarity between species.

Evolution within the *A. reticulatus* species-group is difficult to reconstruct. *A. gibba* almost certainly represents the most primitive species of the group. *A. maculosus* has probably evolved from a species similar to *A. gibba*, as suggested by Houston (1974b). *A. reticulatus* probably represents another relatively primitive member of the group. Its close similarity to *A. nuchalis* almost certainly represents the continued occupation of a similar ecological niche rather than a close phylogenetic relationship. *A. clayi* and *A. nuchalis*, with their peculiar pore arrangement, represent another line of evolution within the group. The retention of some black ventral colouration in *A. clayi* (lost in *A. nuchalis*) suggests that it may be the more primitive, but this is highly speculative. The probable phylogenetic relationships of this group are shown in Figure 41.

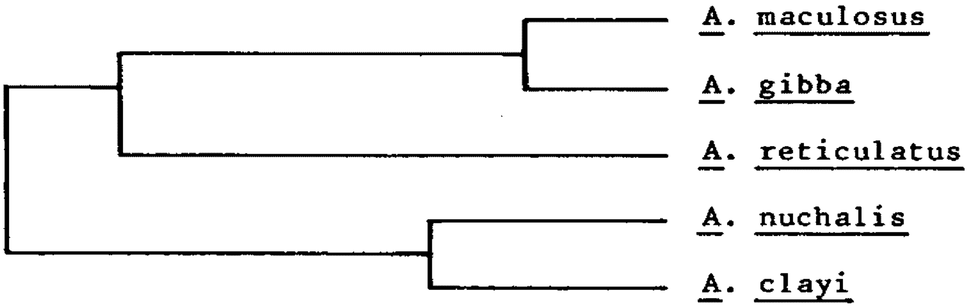

Figure 41. Probable Relationships between Species of the *A. reticulatus* Species-group. Dendrograph illustrating the relationships of the species in the group. The level of branching is based on a subjective assessment of the degree of similarity between species.

The *A. barbatus* species-group probably evolved from a species similar to *A. nuchalis*. Both taxa have a series of spines on the lower eyelid, a similar derived pore arrangement, and a narrow premaxilla. They are also similar morphometrically. The lower eyelid marginal fringe is probably an adaptation to burrowing. Its presence in the *A. barbatus* species-group, which do not habitually burrow, is best explained by a phylogenetic relationship to the *A. reticulatus* species-group.

Explaining speciation within the *A. barbatus* species-group is difficult. Those species with a better developed beard have lost the second ceratobranchial (Badham, 1976), an apparently derived character.

These more advanced species, *A. barbatus* and *A. nullarbor*, occur in more mesic habitats in the east and south respectively. *A. minimus* probably represents the least specialised member of the group, and occurs in the south-west of the continent and islands off that coast. The peripheral species of the group thus include the most advanced and the most primitive.

The probable phylogenetic relationships of the species-groups within the *Ctenophorus* group are summarised in Figure 42.

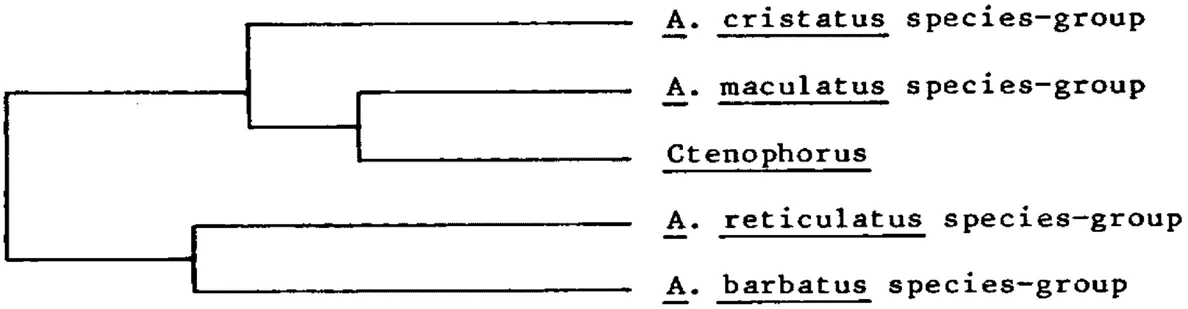

Figure 42. Probable Phylogenetic Relationships within the *Ctenophorus* Group. Dendrograph illustrating the relationships of the species-groups in the *Ctenophorus* group. The level of branching is based on a subjective assessment of the degree of similarity between species-groups.

Phylogeny and History.

Australian Geological History.

Australia was once part of the southern supercontinent Gondwanaland. Gondwanaland broke up in the late Jurassic (about 150 million years Before Present) to form East (India, Australia and Antarctica) and West (South America and Africa) Gondwanaland (Fig. 43). Subsequently Australia and Greater India began to separate at about 125 m.y.B.P., but may have remained in contact until about 115 m.y.B.P. Australia and Antarctica began spreading about 53 m.y.B.P. (Powell, Johnson and Veevers, 1980; Johnson, Powell and Veevers, 1980; Johnson, Powell and Veevers, 1976).

Greater India moved north from Australia throughout the late Cretaceous, colliding with Eurasia approximately 55 m.y.B.P. in the Palaeocene (Powell, 1979). During Greater India's northward "flight" another continental plate, Sundaland, was swinging behind India and to the north of Australia. This plate made its nearest approach to Australia some 15 m.y.B.P. (Powell and Johnson, 1980).

Origin of Australian Agamids.

The family Agamidae has been regarded as centred in Asia, and the Australian species derived from invading Asian species (Cogger, 1961; Tyler, 1979). In view of the world distribution of the family such an interpretation is quite reasonable. Tyler (1979), in designating the agamids as an "Oriental element", stated that the Agamidae had a "virtually continuous range from Africa to Australia". The family is absent from South America, and this led Tyler to the conclusion that agamids were not part of the fauna when Gondwanaland split in the late Jurassic.

The presence of agamids in Australia may be explained in one of two ways. Either (a) the family evolved in Asia and has spread into

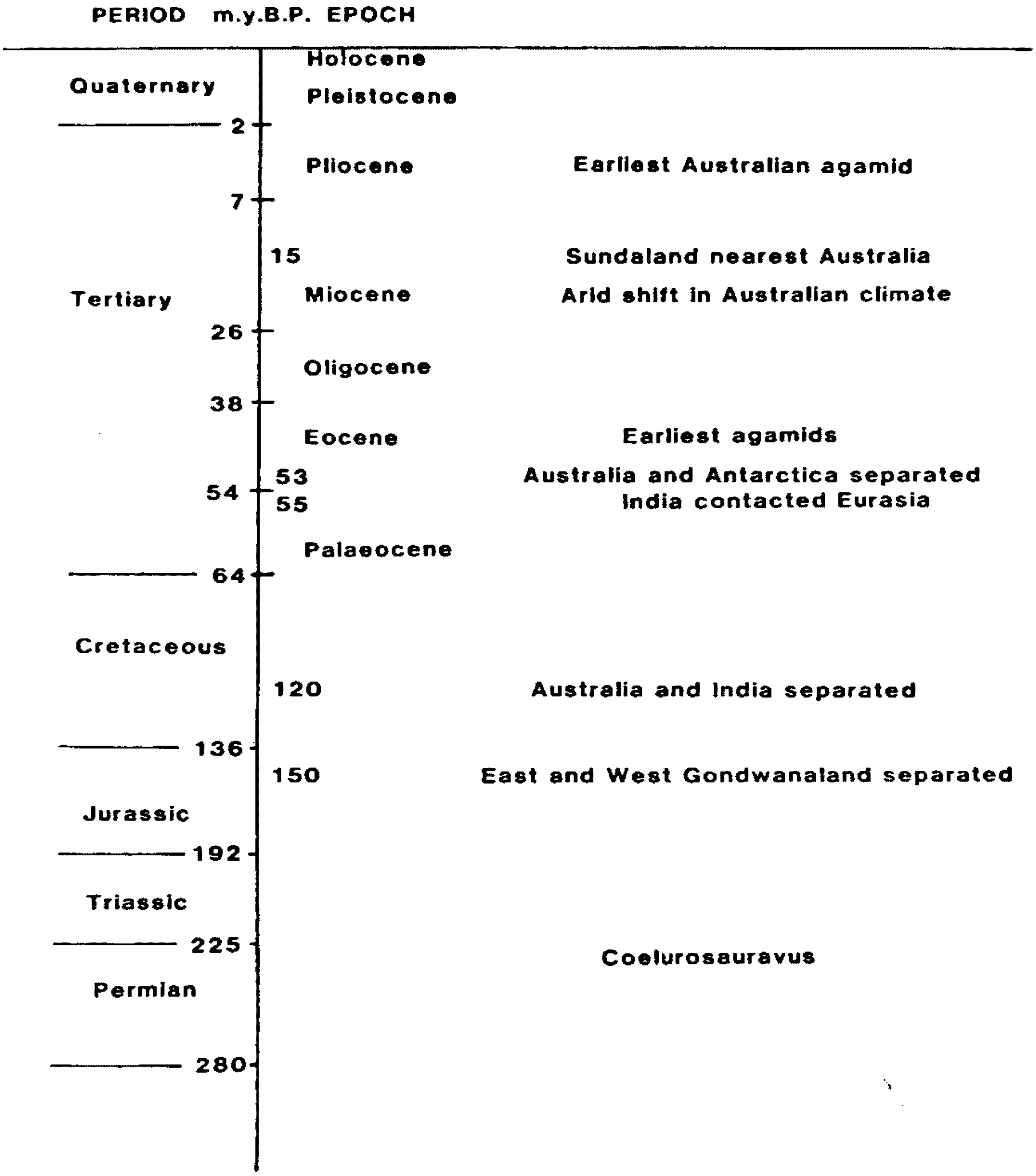

Figure 43. Summary of Events Important in Australian Agamid Phylogeny. Numbers to the left of vertical line indicate approximate limits of periods and epochs; numbers to the right indicate times of events listed to the right. Sources of data are acknowledged in text.

Africa and Australia, or (b) the family evolved in Gondwanaland, parts of which now make up Australia, Africa and the Indian subcontinent.

a. The Agamidae as an Asian Family.

A recent (post-Cretaceous) Asian origin for the Australian agamids assumes that over-water dispersal has occurred. If this were true, then species with a predisposition towards over-water dispersal might be expected among the Australian agamids.

Agamids are likely to cross sea barriers only by "rafting". The chance of an agamid swimming in sea water for more than a couple of hours seems remote. Animals likely to be transported by flotsam should be abundant in coastal or riparian habitats and be associated with vegetation in their normal habitat (Levins and Heatwole, 1963; *fide* Heatwole and Levins, 1972). Agamid genera approaching these prerequisites in Australia are *Gonocephalus*, *Chelosania* and *Physignathus*. Of the endemic agamids only *Lophognathus temporalis* and *Diporiphora superba* seem close to fulfilling these requirements. Both species belong to genera with a number of derived features, and so would be unlikely to represent ancestral stock. *L. temporalis* has apparently reached Timor and New Guinea recently, where it is the only representative of its genus. *D. superba* is very poorly known, but is apparently the only arboreal species of the endemic genera.

The fact that all three Asian-derived genera are predisposed towards over-water dispersal emphasises the probability that the other Australian agamids are derived from an Australian radiation which is basically arid-adapted.

It is generally accepted that the climate of Australia during the major part of the Tertiary was much wetter than at present. The presence of pollen from rainforest trees in central Australia from the Palaeocene to the Miocene supports this contention (Kemp and Harris, 1980). The possibility of an arid-adapted family surviving these mesic climates deserves comment.

Kemp and Harris (1980) point out that the palaeobotanical record is "undoubtedly biased towards preservation in wet environments". The absence of arid-adapted species in the fossil record is therefore not strong evidence of a lack of arid habitats. "Dry refugia" in wet areas of modern Australia (see _Tympanocryptis_ group discussion, pp. 234-235) demonstrate how arid-adapted plants and animals might survive in high rainfall areas. The presence of sclerophyllous plants in the Eocene of Australia (Martin, 1980) may indicate the presence of such dry refugia.

b. The Agamidae as a Gondwanan Family.

The alternative to Australian agamids being Asian in origin is that they represent a Gondwanan element. This hypothesis deserves further comment.

Most modern agamid genera are represented either in India and South-east Asia or in Australia. This distribution is consistent with the hypothesis that agamids, or their predecessors, were present on East Gondwanaland. Lizard fossils from before the Upper Cretaceous are not assignable to modern families (Camp, 1923). It is therefore possible that acrodont lizards of West Gondwanaland gave rise to the Chameleonidae (Africa and Madagascar) while those in East Gondwanaland became the Agamidae. The chameleons apparently arose from the agamids, or from a similar ancestor (Camp, 1923).

The break up of East Gondwanaland would have resulted in the separation of the early agamids into two or three groups. Any agamids on Antarctica presumably became extinct. Those on Greater India would have travelled north to colonise Eurasia in the Palaeocene. This radiation has apparently evolved species capable of over-water dispersal which have since spread southward into Sundaland and Australia.

Very few lizard fossils from the southern hemisphere have been described. The oldest known agamid fossils from Australia are from the Pliocene (Fig. 43) and at least resemble extant genera (Archer and Wade, 1976). These fossils are therefore of limited value in phylogenetic reconstruction.

The paucity of described agamid fossils from Australia is readily explicable. Most work on Australian fossils has concentrated on the larger and more spectacular groups, leaving the possibility that many agamid remains await description. Secondly, and probably much more importantly, there is a distinct bias towards preservation of biological material in wet climates (Kemp and Harris, 1980). There is a tendency for soils to be laid down rapidly in rainforests and eroded away in deserts. Thus, the likelihood of finding fossils of an arid-adapted family are greatly reduced.

Fossil agamids were reported from the upper Cretaceous of Mongolia by Gilmore (1943, *fide* Sulimski, 1972) and Sulimski (1972). These fossils have since been placed in different families (Sulimski, 1978), following the observation that their dentition was not truly acrodont. The most ancient agamid fossil now known is *Thinosaurus* from the Eocene of North America and Europe (Hecht, 1959; Hoffstetter, 1962). This genus post-dates the collision of Greater India with Eurasia (Powell, 1979; Fig. 43), and its existence is consistent with a Gondwanan origin for the Agamidae.

Fossils of reptiles possibly ancestral to the lizards have been reported from the upper Permian of Madagascar (Carroll, 1978). One of these genera, *Coelurosauravus*, has a dentition "strikingly close to the pattern common among living agamid lizards". The dentition of this animal consisted of an anterior "socketed" maxillary tooth and posterior acrodont teeth. These acrodont teeth, judging from Carroll's figures, were quite different from modern agamids, being widely spaced with narrow bases. Modern agamid teeth are usually closely spaced with wide bases. As with modern agamids, the premaxillary teeth differed in form from those of the maxilla, described by Carroll as "peg-like". The other genus described by Carroll had pleurodont teeth.

Coelurosauravus elivensis may be similar to the ancestors of the squamates (Carroll, 1977). It is therefore possible that the modern agamids derived their dentition directly from this group, and not as a modification of the more common pleurodont dentition of other lizards.

Madagascar was part of Gondwanaland during the Permian (Powell, Johnson and Veevers, 1980). The existence of *Coelurosauravus* in Gondwanaland is consistent with a Gondwanan origin for the Agamidae.

Asian-derived Agamids in Australia.

The arrival of the three Asian-derived genera in Australia can be correlated with plate movements in the Australian region. Sundaland made its closest approach to the Australian continental plate between ten and twenty million years ago (Powell and Johnson, 1980). As Sundaland consists of a series of islands its agamid fauna would probably be predisposed towards over-water dispersal. Broad contact need not have occurred for agamid species to have transferred to Australia. However, the chances of such a transfer occurring would be enhanced by reductions in the distances involved. It is therefore most likely that Asian-derived agamid species first arrived in Australia between 10 and 20 m.y.B.P.

Chelosania could very well represent the descendant of such an invasion. The genus is apparently unrelated to Australian endemics, but also lacks clear relatives among Asian or Asian-derived agamids. *Calotes cristatellus* of Timor and New Guinea has dorsal scales forming postero-lateral rows, a feature it shares with *Chelosania* and few other agamids. *C. cristatellus* may resemble the ancestor of *Chelosania*, but they are clearly no longer congeneric and have presumably been evolving separately for a considerable period of time.

Physignathus appears to be a more recent Australian arrival than *Chelosania*. It resembles *Hydrosaurus* in some aspects of its ecology and morphology, including the possession of elongate neural spines of the trunk vertebrae. *Hydrosaurus* is endemic to Sundaland (Darlington, 1957). The riparian semi-arboreal niche occupied by *Physignathus* strongly predisposes the genus to over-water dispersal, a contention supported by the presence of another species in South-east Asia. *Hydrosaurus* may have displaced *Physignathus* in much of the Indo-Australian archipelago leading to the modern disjunct distribution.

Gonocephalus also appears to be a recent arrival in Australia. The genus is well established and diverse in New Guinea, but is also common in South-east Asia.

Evolution within Australia.

Phylogenetic links between the four major groups of endemic agamids are obscure. However, some groups possess more derived characters than others, and it is possible to speculate which group most nearly resembles a hypothetical ancestral agamid.

An examination of primitive characters should allow a description of the hypothetical ancestor of the Australian agamids. This animal would presumably have the primitive pore arrangement. There would probably be a nuchal and vertebral scale ridge. As most endemic Australian species have irregular scales the ancestral species was probably cryptic, with irregular scales helping to break up the outline of the animal. Most semi-arboreal or perching species appear to be more advanced, so the ancestral species might be expected to be terrestrial.

Moloch has so many specialised features that the possibility of it being ancestral to the more generalised species seems remote.

All members of the *Chlamydosaurus* group possess a derived pore arrangement. Most are also semi-arboreal in habit. The group is probably best regarded as being more advanced than the groups discussed below.

The more primitive members of the *Tympanocryptis* group satisfy all requirements for the ancestral animal. Both members of the *A. adelaidensis* species-group are terrestrial, cryptic, have the primitive pore arrangement and at least occasionally possess a nuchal and vertebral scale ridge.

The other group which satisfies most of the requirements for an ancestral agamid is *Ctenophorus*. This genus is apparently the most primitive of the *Ctenophorus* group. However, *Ctenophorus* does not have strongly heterogeneous scales. The *A. adelaidensis* species-group should therefore tentatively be considered the most primitive of the Australian agamid radiation.

Taxonomic Conclusion.

The Australian agamids have probably been evolving independently since the middle Cretaceous. Although the morphological divergence between the Australian and Asian agamids is not great, recognition of this long period of separate evolution would support the erection of a subfamily to accommodate the endemic Australian radiation.

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APPENDIX A

Specimens Examined.

Museum specimens examined in this study are listed below, using the following abbreviations: AM = Australian Museum, Sydney; AMF = Australian Museum Field Tag; SM = Shellshear Museum, University of Sydney; SAM = South Australian Museum; WAM = Western Australian Museum; WED = Duellman Collection.

Chelosania brunnea: AM R39097, R40445, R40810, R40909, R41647, R43535.

Gonocephalus spinipes: AMF 13664; AM R7307; WED (Field series) 051094.

Physignathus lesueurii: AMF 11219, 11326, 13657; AM R19406, R40658, R52727, R71217, R71721, R71727, R73769, R73772-3, R74028-9.

Moloch horridus: AM R73, R1115, R2468, R4773, R11182, R17611, R18677, R25792-3, R25886, R67999.

Tympanocryptis cephalus: AM R13935, R20372-5, R20825-6, R49629, R60224, R65070, R65072, R66228.

Tympanocryptis intima: AM R17181, R17725, R17727, R20823, R49976, R63637-40, R65071, R74756, R75090.

Tympanocryptis lineata: AMF 11244; AM R49748, R49964.

Tympanocryptis parviceps: AM R40427-9, R81395.

Tympanocryptis tetraporophora: AMF 11241-3, 11249-50, 11262, 11282, 11346, 13600, 13605-7, 13613-5, 13656; AM R49668.

Tympanocryptis uniformis: AM R55098.

Amphibolurus adelaidensis: AM R4936, R7732, R7734, R9125, R61522, R64984, R86489; WAM R12427, R24165, R48426, R49895, R58801-2, R59773-4, R59773-4, R59868, R59870.

Amphibolurus diemensis: AMF 11334-5, 11371-4, 11377-81, 13637; AM A6766, A11096, 32966, R1134, R1904, R1906, R2051, R2697, R2867, R3529, R4353-5, R4477, R4876-7, R4879, R8558-61, R10039, R10044, R10447, R10490, R10987, R11664, R12281, R12786, R17076, R20965, R20981, R41176, R46049, R55666.

Amphibolurus muricatus: AMF 11294-5, 11305, 11308-10, 11328, 11370, 11375-6, 11382, 13638-41; AM R57583.

Amphibolurus nobbi: AMF 11299, 11302, 11304, 11324-5, 11385-6, 11392, 13604, 13643-8; AM R40119, R41155-7, R64965.

Caimanops amphiboluroides: AM R3373; WAM R544, R5297, R10612, R12034, R14367, R14464-6, R16954, R17686, R19779-80, R24010, R25154, R28286, R28849, R30929, R39044, R40636, R45619, R53062, R54387.

Chlamydosaurus kingii: AMF 13642, 13658; AM R1582, R2257, R3955, R10249, R13472, R13590-1, R15126, R16468, R16506, R30384, R75843-4.

Diporiphora albilabris: AM R12696, R52185-8, R60226-8, R75383-7, R75443.

Diporiphora australis: AMF 11204-5, 13661-2, 13665-6; AM R6009, R9618, R47873-4, R47510, R63489, R63619-20, R63632.

Diporiphora bennettii: AMF 11367; AM R59895, R72499-501, R72503, R72661, R72665, R72990, R73011, R73027, R73068, R73075.

Diporiphora bilineata: AMF 11206-8, 11210-1, 11213-8, 11220-2, 11336-7; AM R9711-4, R41916, R41938, R57071-4.

Diporiphora lalliae: AM R39719-20, R40307, R48103, R49080, R59601, R70077, R72991, R73033-4.

Diporiphora linga: AM R7681.

Diporiphora magna: AMF 11368-9, 13659-60; AM R20324, R21086, R53445, R53526, R59897, R60229-31, R62667, R75453.

Diporiphora superba: AM R74772.

Diporiphora winneckei: AM R2144-5, R17736, R49711, R50535, R59746, R60972-6, R64297, R71187.

Lophognathus gilberti: AMF 11225-7, 11231-2, 11234-5, 11237, 11245, 11258-9, 11263-75, 11277-81, 11283-6, 11289-93, 11296-8, 11300-1, 11303, 11306-7, 11320-2, 11332-3, 11351-2, 11384, 11387-8, 11391, 11397, 13649-52, 13655; AM R12451, R40008, R40217-8, R40220-1, R40243, R40337, R40339, R40531, R40534, R41270, R48647.

Lophognathus longirostris: AM R10867, R25998, R40294, R41087, R41263, R41270, R49283, R49557, R51394, R65085-6, R65088-9, R73909.

Lophognathus temporalis: AM R14086-7, R14101, R14139, R15177, R23902-4, R38500-1, R41207, R41263.

Ctenophorus decresii: AMF 11344-5, 13601, 13609-10, 13612, 13617-9, 13621-2; AM R47294-5, R47298.

Ctenophorus fionni: AM R5672, R5676, R5682, R7166, R7169-72, R7174-5, R14661, R20968-9, R20971-8, R20980, R73510-1.

Ctenophorus ornatus: AMF 6574, 13663; AM R4933, R7719, R11746, R12348, R29535, R57068-70, R70144-5, R75861, R81413-4, R86424, R86478-80.

Ctenophorus pictus: AMF 13602-3, 13616, 13623-27, 13629-34; AM R13933, R26576, R42757, R55097, R60235, R64010, R64017.

Ctenophorus rufescens: AM R5642, R20573.

Ctenophorus vadnappa: AM R64981-3.

Amphibolurus femoralis: AMF 13667.

Amphibolurus fordi: AMF 11353-7, 11361-4; AM R49578-9, R49679, R75757, R75762, R75781, R75796-7, R75805-6, R75812.

Amphibolurus isolepis: AMF 6549; AM R14120, R49264, R49379-85, R49401-7, R49412-3, R49416, R49420, R49508-22, R49548-56, R49565-6, R49570, R49572, R49574-7, R52167-72.

Amphibolurus maculatus: AM R73512-4; WAM R21743-4.

Amphibolurus scutulatus: AM R2959, R3178, R4060, R8381, R11376, R40318, R65201.

Amphibolurus caudicinctus: SM 119.5-119.9; AM R2098, R4874-5, R12008-9, R14129, R15424, R18623, R18661, R20519, R49314-6, R49341-4, R49669, R52173-81, R57255-8.

Amphibolurus cristatus: AMF 6561; AM R2620, R2958, R3083, R3111, R7661-5, R8380, R9134, R13694, R67962-70.

Amphibolurus clayi: AMF 6519-23; AM R9541.

Amphibolurus gibba: SAM R13893, R14051, R14136A, R14406A-C, R14408, R14411, R14412A-D, R14413-4, R14799, R15031A-B.

Amphibolurus maculosus: SAM R3409B, R3430, R3621A, R3627, R6081, R6084, R6550, R7610-1, R7737, R8154, R8442, R8805, R9136A, R9136E-F, R9332A, R9334B-C, R9415A, R11163, R11377, R13683A, R13895A-B, R13895F-G, R13895J.

Amphibolurus nuchalis: AMF 11228-30, 11327, 11329-31, 11365-6, 13620; AM R0542, R2113-4, R4892, R7024, R9540, R10873-5, R11924, R11928-30, R11936, R11938, R11943, R11946, R11954-5, R11981, R11983, R13911-3, R13918, R13920, R13925, R17260, R17610, R21466-9.

Amphibolurus reticulatus: AM R2966, R3061, R3089, R3175, R3368-9, R9982-3.

Amphibolurus barbatus: AMF11201-3, 11223, 11236, 11338-9, 11342, 11347-9, 11360, 11398-400, 13608; AM R17904, R20987, R21578, R25789.

Amphibolurus minor: AM R4930, R5660-1, R7658, R15182.

Amphibolurus mitchelli: AM R38712.

Amphibolurus mitchelli (?): AMF 11238, 11240.

Amphibolurus vitticeps: AMF 11248, 11252, 11264, 11340-1, 11343, 11350, 11358-9, 13635-6; AM R13904-5, R15295, R17122-3, R21077, R47319.

Table 2. Nomenclature Adopted for the Present Study.

Australian Endemic Genera

Genus or Sp-gp.	Species.
Tympanocryptis Group	
Tympanocryptis	T. cephalus T. intima T. lineata T. parviceps T. tetraporophora T. uniformis
A. adelaidensis Species-group	A. adelaidensis A. diemensis

Genus or Sp-gp.	Species.
Chlamydosaurus Group	
A. muricatus Species-group	A. muricatus A. nobbi
Caimanops	C. amphiboluroides
Chlamydosaurus	C. kingii
Diporiphora	D. albilabris D. australis D. bennettii D. bilineata D. convergens D. lalliae D. linga D. magna D. reginae D. superba D. winneckei
Lophognathus	L. gilberti L. longirostris L. temporalis

Genus or Sp-gp.	Species.
Ctenophorus Group	
Ctenophorus	C. decresii C. fionni C. ornatus C. pictus C. rufescens C. vadnappa
A. maculatus Species-group	A. maculatus A. femoralis A. fordi A. isolepis A. scutulatus
A. cristatus Species-group	A. cristatus A. caudicinctus
A. reticulatus Species-group	A. reticulatus A. clayi A. gibba A. maculosus A. nuchalis
A. barbatus Species-group	A. barbatus A. microlepidotus A. minimus A. minor A. mitchelli A. nullarbor A. vitticeps

Genus or Sp-gp.	Species.
Moloch Group	
Moloch	M. horridus

Asian-derived Genera

Genus or Sp-gp.	Species.	Genus or Sp-gp.	Species.
Chelosania	C. brunnea	Gonocephalus	G. boydii G. spinipes
Physignathus	P. lesueurii		