

Cladistic Relationships among Gekkonid Lizards

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A reevaluation of individual and interspecific variation in branchial arch osteology in gekkonid lizards and the use of the out-group criterion led to the conclusion that the continuous nature of the second ceratobranchial-epibranchial rod in *Anarbylus* and *Coleonyx* is an evolutionary reversal. An independently evolved autapomorphy is also proposed for the continuous second branchial arch in *Gonatodes vittatus*. The largest assemblage of gekkos currently recognized, the "Gekkoninae," is divided into two groups on the basis of the presence or absence of the second ceratobranchial. The absence of the second ceratobranchial, a synapomorphy in the Gekkonoidea, is diagnostic of the 35 genera referred to the Gekkonini, while the remaining genera are left *sedis mutabilis* in the "Gekkoninae." Two new genera are described and a third is resurrected from synonymy. Recognition of these three genera eliminates all known intrageneric variation in the second ceratobranchial, except for that observed in *Pristurus*. *Pristurus* appears to be a natural group, and those species without a second ceratobranchial belong to the most derived assemblage within the genus. Various corroborating synapomorphies suggest that the generic revisions are valid and that the Gekkonini is monophyletic.

RECENT advances in phylogenetic inference (Wiley, 1981) have forced systematists to reexamine previously published hypotheses of relationship and many of them have been rejected for lack of evidence. For example, not all of the major groups that I recognized in 1967, Eublepharinae, Diplodactylinae, Gekkoninae and Sphaerodactylinae, were diagnosed by one or more synapomorphies, and the present paper is one of a series devoted to the restudy of the genealogical relationships among those lizards and the closely related Pygopodidae (Kluge, 1976, 1982). My use of the paraphyletic assemblages "Eublepharinae" and "Gekkoninae" in this paper is for convenience of communication and for relating the new observations and conclusions to previous hypotheses.

The branchial arches of vertebrates have often served as sources of data for phylogenetic hypotheses, and I investigated the osteology of the hyoid apparatus in gekkonid lizards for that purpose in 1967. My review was brief, it focused on subfamilial relationships, and I did not report all of the observations I had accumulated. The following survey of the second branchial arch is based on this older research, as well as new findings, and it more fully exploits the available cladistic information.

The bilaterally symmetrical second branchial

arch in gekkonids (Fig. 1) consists of variously ossified ceratobranchial and epibranchial rods which are either separated or fused together (anatomical and taxonomic nomenclature follows Kluge, 1962, 1967). Further, the second ceratobranchial or the second epibranchial, or both, may be absent in gekkos.

CONTINUOUS SECOND BRANCHIAL ARCH

Cope (1892) appears to have been the first to identify a continuous second branchial arch, viz., an uninterrupted ceratobranchial and epibranchial rod, in a gekkonid. He described that condition in the eublepharine *Coleonyx elegans* (Cope, 1892: Pl. 3, Fig. 8, 1900; Furbringer, 1919), although he incorrectly illustrated a discontinuity in a congener, *C. variegatus*. Noble (1921) found no suture or break between the two parts in *C. variegatus*, and, following Furbringer (1919), asserted that such a condition is "the most primitive type of lacertilian hyoid apparatus." I reported on the uninterrupted nature of the arch in *C. brevis* and *C. mitratus* in 1962, and now document the same condition in *C. reticulatus*. Thus, all *Coleonyx* species exhibit the supposed primitive condition, as does the monotypic eublepharine genus, *Anarbylus* (USNM 211352). The arch is discontinuous, presum-

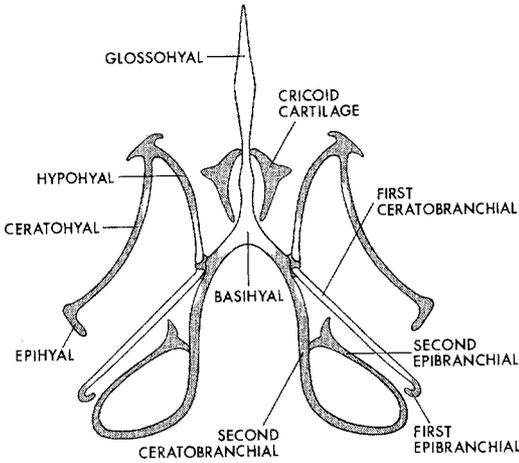


Fig. 1. Ventral view of the hyoid apparatus of *Coleonyx variegatus* (redrawn from Kluge, 1962) illustrating three continuous branchial arches.

ably at the junction of the ceratobranchial and epibranchial, in all other eublepharine gekkos, *Aeluroscalabotes*, *Eublepharis*, *Hemitheconyx* and *Holodactylus* (Kluge, 1967).

Camp (1923) attached considerable importance to a continuous second branchial arch in determining relative taxonomic primitiveness. He gave that state high "paleotelic weight," and it was largely on the basis of this condition that he claimed gekkos to be among the most primitive lizards. His position assumed, among other things, that the continuous arch evolved but once in saurian history, and, as I will argue below, this assumption has been violated, perhaps twice, in gekkos, with the *Anarblylus-Coleonyx* condition probably being an evolutionary reversal.

Stephenson and Stephenson (1956) reported a continuous second branchial arch in the diplodactyline gekko *Naultinus elegans*. In 1967, I stated that I was unable to confirm their observation with cleared and stained specimens (UMMZ 127576a-b), nor have I been able to do so more recently with dissections of fluid preserved material (FMNH 18179, UMMZ 129352). While Moffat (1973) considered *Naultinus* an example of "intrageneric variation," I am inclined to treat Stephenson and Stephenson's observation as simply erroneous. In my survey of all 13 diplodactyline genera (1967: 38), I stated that "the second visceral arch is invariably discontinuous . . . , and the long ceratobranchial and epibranchial parts are nor-

mally separated by moderate to large distances, with the exception of *Rhynchoedura*. The ceratobranchial and epibranchial overlap in the latter genus but do not come into contact."

Noble (1921) documented the interruption of the second branchial arch in *Gonatodes*, *Lepidoblepharis* and *Sphaerodactylus*, all members of the Sphaerodactylinae, and I found the same condition in the other genera (*Coleodactylus* and *Pseudogonatodes*) referred to that subfamily. I incorrectly stated (1967) that *Coleodactylus* had lost the epibranchial. It is present in *C. amazonicus* (UMMZ 127803a-b), *C. brachystoma* (UMMZ 144467) and *C. meridionalis* (UMMZ 103051a-b).

Both Noble (1921) and Camp (1923) emphasized the exceptional lengths of the second epibranchial and ceratobranchial rods in sphaerodactylines. In fact, in the single *Sphaerodactylus* species (*macrolepis*) studied by Noble (1921:3) the epibranchial had become "loosely attached to the second basibranchial some distance from the end." In 1967, I reported a case of second ceratobranchial-epibranchial overlap in *S. parkeri* and a definite fusion in one *Gonatodes vittatus*. I have since examined the second arch in many more cleared and stained sphaerodactylines (*Coleodactylus*—3 species, 5 specimens; *Gonatodes*—14 species, 35 specimens; *Lepidoblepharis*—5 species, 12 specimens; *Pseudogonatodes*—4 species, 9 specimens; *Sphaerodactylus*—51 species, 118 specimens), and all exhibited long second ceratobranchial and epibranchial rods. The species examined will be listed in a forthcoming publication on sphaerodactyline generic relationships. In situ, the second epibranchial almost always extended anteriorly beyond the caudal end of the second ceratobranchial, and frequently the two sections of the arch contacted one another at a right angle (Noble, 1921: Fig. 2A). No doubt, such contact led to the complete refusion of the two rods in the left arch of the only *S. rosaurae* studied by me (FSM 28557) and in all five *G. vittatus* examined, both right and left arches (UMMZ 54687, 54893, 127802a-b; CR 453). In fact, in one *G. vittatus* (UMMZ 127802a) the refusion between the second ceratobranchial and second epibranchial rods must have occurred at their free ends because there was no evidence of overlap. Such a condition is indistinguishable from that found in *Anarblylus* and *Coleonyx*, and the simplest interpretation is that an evolutionary reversal occurred in the lineage leading to *G. vittatus*. The likelihood that a com-

plete second branchial arch is not a uniquely evolved state, as exemplified by *G. vittatus*, is precedent for questioning the *Anarbylus* and *Coleonyx* state as primitive. Also, the possibility that the complete second branchial arch in *Anarbylus* and *Coleonyx* represents another evolutionary reversal, like the state in *G. vittatus*, seems especially reasonable when the other eublepharines are taken into consideration. For example, in *Eublepharis macularius* (UMMZ 127505), *E. hardwickii* (UMMZ 127503), *Hemitheconyx caudicinctus* (MCZ 21903; UMMZ 132006), and *Holodactylus africanus* (MCZ 21902), the free ends of the second ceratobranchial and second epibranchial extensively overlapped one another, and in *Aeluroscalabotes felinus* (MCZ 21665; UMMZ 127494a–b) the rods not only overlapped, but were in parallel and in such close contact throughout much of their length that one could not be moved without the other. While the elements of *Aeluroscalabotes* were not actually fused, they appeared to be tightly bound together with connective tissue. On the basis of these observations I hypothesize the continuous second ceratobranchial and epibranchial rod in *Anarbylus* and *Coleonyx* to be a synapomorphy within the "Eublepharinae," and the *G. vittatus* state to be an independently evolved autapomorphy in the Sphaerodactylinae. I prefer these interpretations, instead of plesiomorphy for each example of a continuous branchial arch in gekkonids, because they require fewer ad hoc hypotheses of character state evolution (Kluge, in press). Perhaps the most convincing support for my simpler hypotheses comes from the out-group comparison itself. While the sister lineage of gekkonids is not well documented, it seems eminently reasonable to conclude that it was another saurian, all of which have a discontinuous second branchial arch according to Camp (1923). Thus, the out-group criterion predicts the discontinuous second branchial arch is the plesiomorphic state in gekkonids. Pseudomorphosis cannot explain the origin of the continuous second arch in gekkos if refusion has occurred.

I consider a complete second branchial to be a synapomorphy within the "Eublepharinae," and it provides the basis for my placing the monotypic *Anarbylus* in the synonymy of *Coleonyx*. The numerous autapomorphies of *Anarbylus* (Murphy, 1974) are not sufficient to justify its continued recognition as a monotypic genus in a strictly monophyletic classification with minimum redundancy (Wiley, 1979).

SECOND CERATOBANCHIAL ABSENCE

Species previously referred to the subfamily "Gekkoninae" (Kluge, 1967) can be separated into two groups on the basis of the presence or absence of the second ceratobranchial. Many of the earlier students of gekkonid lizard branchial arch anatomy (Camp, 1923; Cope, 1892, 1900), were inconsistent in naming the various conditions of the first and second branchial arches (actually the second and third arches, the first being the hyoid), and this led to erroneous claims for various taxa and much confusion concerning phylogenetic relationships. In 1962, I reviewed the problem and attempted to standardize the anatomical nomenclature for gekkos (Fig. 1). In 1967, I reported the second ceratobranchial to be absent from 60% of the genera (the apomorphic state), and in the remaining 40% it ranged from being moderately long to very long. I continued my survey of gekkonine genera, and have found the second ceratobranchial invariably present or absent in all congeners examined, with the exception of *Cytodactylus*, *Phyllodactylus*, *Pristurus* and *Tropicolotes*. It was present in *Afroedura*, *Asaccus*, *Chondrodactylus*, *Colopus*, *Ebenavia*, *Geckonia*, *Homonota*, *Kaokogecko*, *Narudasia*, *Pachydactylus*, *Palmatogecko*, *Paroedura*, *Phelsuma*, *Ptenopus*, *Ptyodactylus*, *Quedenfeldtia*, *Rhothropus*, *Saurodactylus*, *Tarentola* and *Teratoscincus*; the second ceratobranchial is so thin in some species (e.g., *Phyllodactylus trachyrhinus*—BMNH 1967.496–497) that extreme care must be taken to avoid destroying it during dissection. Also, ossification of the gekkonid second branchial arch occurs relatively late during ontogeny, compared to the other arches, and adults must be examined if an unambiguous interpretation of the second ceratobranchial arch condition is desired. That portion of the second arch was definitely absent in *Agamura*, *Ailuronyx*, *Alsophylax*, *Aristelliger*, *Bogertia*, *Briba*, *Bunopus*, *Calodactylodes*, *Cnemaspis*, *Cosymbotus*, *Crossobamon*, *Dravidogecko*, *Geckolepis*, *Gehyra*, *Gekko*, *Gymnodactylus*, *Hemidactylus*, *Hemiphylloactylus*, *Heteronotia*, *Homopholis*, *Lepidodactylus*, *Luperosaurus*, *Lygodactylus*, *Milolissaurus*, *Perochirus*, *Phyllopezus*, *Pseudogecko*, *Ptychozoon*, *Stenodactylus*, *Teratolepis*, *Thecadactylus* and *Uroplatus*. In one specimen of *Aristelliger*, *Calodactylodes*, *Cnemaspis*, *Geckolepis*, *Gehyra*, *Homopholis* and *Lygodactylus* there was a tiny posterior bulge from the otherwise even margin of the basihyal, opposite the junction of the hyohyal and first ceratobranchial. I interpret

these to be remnants of the second ceratobranchial. In all such cases I had no difficulty in referring them to the "absent" character state. The only currently recognized gekkonine genera that I have not been able to examine are *Garzoniella*, *Microscalabotes* and *Paragehyra* (*Geisopristurus* is a synonym of *Pristurus* according to E. N. Arnold, pers. comm.). The fact that each genus shares some derived conditions with others that I have studied, *Garzoniella* with *Stenodactylus* (E. N. Arnold, pers. comm.), *Microscalabotes* with *Lygodactylus* (Pasteur, 1964), and *Paragehyra* with *Homopholis* (Russell, 1972), leads me to predict that the second ceratobranchial arch will be absent in the as yet unexamined taxa.

The second ceratobranchial is absent in all *Cyrtodactylus* species examined (Appendix 1), except *C. arnouxi*, *C. galgajuga*, *C. pelagicus*, *C. serpensinsula*, and *C. vankampeni*. The second ceratobranchial is present in all *Phyllodactylus* species examined (Appendix 2), except *P. inexpectatus*, *P. palmatus*, *P. weileri* and *P. wolterstorffi*. The second ceratobranchial is present in *Pristurus flavipunctatus*, *P. rupestris* and *P. sokotranus*, but absent in *P. carteri* and *P. crucifer*. In *Tropicolotes*, the second ceratobranchial is present in *T. helenae*, *T. latifi* and *T. persicus*, but absent in *T. depressus*, *T. heteropholis*, *T. scortecci*, *T. steudneri* and *T. tripolitanus*. The origins of these four examples of "intrageneric" variation are examined below under their respective generic headings.

I hypothesize the absence of the second ceratobranchial in the "Gekkoninae" to be a derived character state. The fact that the second ceratobranchial is well developed in all pygopodids (all cleared and stained taxa examined by me in 1976, in addition to *Delma torquatus*—UMMZ 137230, and *Paradelma orientalis*—CAS 77652), eublepharines, diplodactylines and sphaerodactylines suggests that its absence is a structural loss, and most probably represents a synapomorphy within the Gekkonioidea. I use this variation to justify the recognition of the tribe Gekkonini, which is diagnosed by the loss of the second ceratobranchial.

In the remainder of this paper, I find it convenient to refer to those gekkonines with a second ceratobranchial as "ptyodactylini" (incertae sedis in the "Gekkoninae"; Wiley, 1979). This usage must not be viewed as anything but a matter of convenience—no formal taxonomic statement of monophyly is implied—and it is equivalent to saying 'non-gekkonini gekko-

nines.' Haacke's (1976) excellent study provides evidence for the cladistic relationships of some African "ptyodactylini." He recognized *Colopus* and *Chondrodactylus* as sister taxa on the basis of a brachyphalangeal 4th finger, and *Kaoko-gecko* and *Palmatogecko* as monophyletic by reason of their webbed toes. According to Haacke, these four genera, plus *Pachydactylus*, *Rhoptropus* and *Tarentola* form a more inclusive natural assemblage, as deduced from their possessing an extra phalangeal bone in the 1st finger and toe. Russell (1972) also recognized this *Pachydactylus* Group as monophyletic, and added *Geckonia*, a genus not studied by Haacke, because it had the same hyperphalangeal state. Elaborate cloacal spurs may also corroborate the *Pachydactylus* Group as a natural assemblage (Russell, 1977).

Narudasia, *Pristurus*, *Quedenfeldtia* and *Saurodactylus* are all padless, more or less straight-toed, "ptyodactylini," and while they are rather different otherwise, they also share the absence of cloacal bones and sacs. The latter states appear to be derived (Kluge, 1982), and among the "ptyodactylini" those conditions are also found in *Asaccus* and the Socotra Island *Phyllodactylus riebeckii* and *P. trachyrhinus* (only females available). Relating the otherwise extremely different *Asaccus*, with its pair of leaf-like terminal scansors on all digits, reduced formula of the manus (2-3-4-4-3) and shortened transverse processes of the autotomic tail vertebrae (Arnold, 1977), to the three padless genera must be considered highly questionable. The two Socotra *Phyllodactylus* also have terminal scansors like *Asaccus* but they exhibit a primitive phalangeal formula. In addition, there has been considerable differentiation among the three padless genera (Haacke, 1976), and even this phylogenetic hypothesis based on the cloacal bone and sac synapomorphies requires further corroboration.

I am unaware of a synapomorphy diagnosing the "ptyodactylini" as monophyletic, and it is likely that those genera form a paraphyletic class, viz., a grade of evolution. Furthermore, other than the *Pachydactylus* Group, and perhaps *Narudasia* + *Pristurus* + *Quedenfeldtia* + *Saurodactylus* (Arnold, 1981) no other generic relationships have been discovered. Therefore, it seems only reasonable to classify each "ptyodactylini" genus, except those of the *Pachydactylus* Group, as sedis mutabilis (Wiley, 1979). The *Pachydactylus* Group, as well as the Gekkonini, should also be labeled sedis mutabilis within the Gekkonidae.

If the second ceratobranchial was lost but once in the "Gekkoninae," then all of the genera and species that unique synapomorphy characterizes form a monophyletic group. However, as noted above, the trait is variable in four genera, *Cyrtodactylus*, *Phyllodactylus*, *Pristurus* and *Tropicolotes*, each of which is currently treated as monophyletic, and thus both sets of claims for monophyly cannot be true. If the loss of the second ceratobranchial is a unique synapomorphy, then the diagnostic conditions linking the variant species to their respective genera cannot also be synapomorphies. I will approach a resolution of this contradiction in two ways. To attempt falsification of the generic synapomorphies for *Cyrtodactylus*, *Phyllodactylus*, *Pristurus*, and *Tropicolotes*, as they are presently constituted, I will reexamine their diagnostic characters for evidence of symplesiomorphy, and those characters being highly variable, or incorrectly observed. Also, dividing *Cyrtodactylus*, *Phyllodactylus*, *Pristurus* and *Tropicolotes* into those species with and those without a second ceratobranchial, I will search for synapomorphies corroborating each new, putative monophyletic, assemblage. If such corroboration cannot be found, then the second ceratobranchial synapomorphy—the loss of the rod—loses some credibility by virtue of its not being a unique evolutionary event. It is with this philosophical perspective that I review *Cyrtodactylus*, *Phyllodactylus*, *Pristurus* and *Tropicolotes*.

CYRTODACTYLUS

Seventy-six species are recognized in *Cyrtodactylus* Gray, type species *C. pulchellus* Gray (Appendix 1). Underwood (1954:475) reviewed the genus, and diagnosed it as "digits clawed slender, distal two or three phalanges make an angle with the proximal portion of the digits, row of transverse scales beneath digits; *Gekko*-type pupil; first pair of postmentals nearly always meet behind mental; generally three or more rows of lateral scales on digits, the scales on the underside of the tail are commonly not or but slightly enlarged transversely." Russell (1976) described some of the extensive variation in *Cyrtodactylus* digits, and Kluge (1967) discounted the pupil as a useful diagnostic character among the gekkos. The remaining characters set forth by Underwood also fail to diagnose *Cyrtodactylus*, either because of their individual and interspecific variation or because the common state is plesiomorphic. Thus, the

available evidence indicates that *Cyrtodactylus* cannot be diagnosed as it is presently constituted taxonomically, and, furthermore, the variation in the size and shape of the enlarged dorsal body tubercles and their keeling and the pre-anal pore arrangement suggest that the group may be polyphyletic. More importantly, Russell (1972, 1976) identified digital similarities relating various *Cyrtodactylus* species to as many as five other straight-toed genera, *Agamura*, *Asophylax*, *Bunopus*, *Cnemaspis* and *Crossobamon*, as well as to *Hemidactylus*, a genus with dilated toes. Five species, *C. arnouxi*, *C. galgajuga*, *C. pelagicus* (incl. subspecies *undulatus*), *C. serpensinsula* and *C. vankampeni*, in addition to being unique within *Cyrtodactylus* in possessing the second ceratobranchial, also exhibit the unique state of fused nasal bones. The fusion was found in both adults and subadults (e.g., *C. galgajuga*—23.0 mm SVL, AMNH 120271; *C. pelagicus*—22.0 mm SVL, AMNH 120275). If placed in the "ptyodactylini," this assemblage of five species can be distinguished from all other taxa without pads, except *Microgecko* (see below), in having fused nasal bones. The presence of enlarged dorsal body tubercles in *arnouxi*, *galgajuga*, *pelagicus*, *serpensinsula* and *vankampeni*, an apparent synapomorphy, is sufficient to distinguish them from *Microgecko*. Thus, to accommodate *arnouxi*, *galgajuga*, *pelagicus*, *serpensinsula* and *vankampeni*, as a monophyletic member of the "ptyodactylini," I refer them to:

NACTUS gen. nov.

type species *arnouxi* Dumeril (1851). *Nactus* is Latin for "stumbled upon," which alludes to my discovering by chance such a distinct assemblage of species in *Cyrtodactylus*. *N. arnouxi*, *N. pelagicus*, *N. serpensinsula* and *N. vankampeni* share cone-shaped dorsal body tubercles and small raised ventrals. Each tubercle and ventral has several minute ridges, apparently a unique form of keeling (Fig. 2). The conditions in *N. serpensinsula* are not as conspicuous as in *N. arnouxi*. In addition to these probable synapomorphies, the mental is greatly enlarged posteriorly, and the small paired postmentals (absent in *N. vankampeni*) do not meet on the midline (Fig. 3) in all but *N. serpensinsula*. These several corroborating synapomorphies give me confidence that both *Nactus* and the Gekkonini (the latter defined on the basis of the loss of the second ceratobranchial) are natural, monophyletic, groups (Arnold, 1980a; Kluge, in press). Russell (1972) also recognized the distinctness

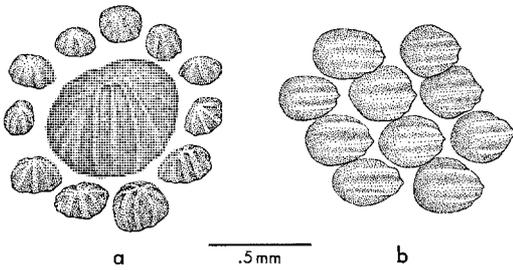


Fig. 2. *Nactus arnouxii* (UMMZ 131494). a) A representative cone-shaped and ridged dorsal body tubercle surrounded by smaller ridged scales. Dorsolateral view. b) Representative ventral body scales. Note the several minute ridges on these scales. Ventral view.

of *pelagicus* from all *Cyrtodactylus*; however, he thought it should be referred to *Heteronotia* (he did not examine other *Nactus*). *Heteronotia* and *Nactus* do not share the condition of the second ceratobranchial arch, and a synapomorphy hypothesis necessary to relate *N. pelagicus* to *Heteronotia* was not an obvious part of Russell's (1972) conclusion. Wermuth's (1965) placement of *N. vankampeni* in *Underwoodisaurus* (= *Phyllurus*), a member of the Diplodactylinae, is obviously in error (Kluge, 1967; Russell, 1972).

The cladistic relationships of *Nactus* to other "pyodactylini" are not clear, and its distribution outside the Ethiopian-southwestern Palearctic regions, along with that of the South American *Homonota*, is exceptional. The widespread and discontinuous geographic distribution of *Nactus* is also peculiar; *N. serpentsinsula* occurs only on Round and Serpent islands, Mascarene Islands in the Indian Ocean; *N. arnouxii* is found over a large area, from New Guinea to the south-central Pacific. The absence of *Nactus* species throughout the intervening western portion of the Indo-Australian Archipelago may be due to inadequate collecting, as inferred from the fact that the more common Pacific and Indo-Australian house geckos (*Gehyra mutilata*, *Hemidactylus frenatus*, *Hemiphyllodactylus typus* and *Lepidodactylus lugubris*) are found in the Mascarenes (Vinson and Vinson, 1969). *N. galgajuga* is restricted to the Trevethan Range, Queensland, Australia, and *N. vankampeni* is known only from a small area in northern New Guinea, specifically Aitape and the vicinity of Modderlust (Brown and Parker, 1973).

I have examined the holotype (MNHP 5210)

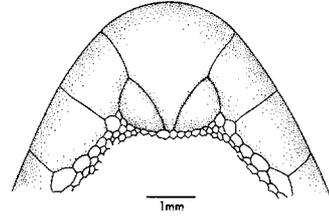


Fig. 3. The enlarged mental scale separating the small postmentals in *Nactus arnouxii* (UMMZ 131494). Ventral view.

of *N. arnouxii*, a species described by Dumeril (1851) from "Nouvelle-Zelande." The specimen is a subadult female (SVL = 45.4 mm), and it cannot be distinguished from the syntypes (USNM 5626a-b) of Girard's (1858) *N. pelagicus*. In addition to the fused nasals of *Nactus* (see above), it has the strongly keeled conical ventrals, regular rows of enlarged ridged dorsal body cone-shaped tubercles of *N. pelagicus*, and enlarged mental separating small postmentals. *N. vankampeni* is a much smaller species (adult SVL = 27.0-29.0 mm). In the original description by Dumeril, there is evidence, although now faint, that the holotype of *N. arnouxii* has irregular body and tail bands of dark brown like *N. pelagicus*. I was unable to discover a single major difference between the two named forms, and I consider *N. pelagicus* a junior synonym of *N. arnouxii*. While *N. pelagicus* has been far more frequently cited, *N. arnouxii* has appeared in recent literature (McCann, 1955; Wermuth, 1965), and I can find no justification for continuing to use the former name.

There remains the problem of the type locality of *N. arnouxii*. According to McCann (1955), *N. arnouxii* has not been recollected in New Zealand, and he doubted the given type locality, as do I. Dumeril (1851) described the species after the chief surgeon Arnoux, who accompanied the campaign of the Corvette le Rhin, 1842-1846 (J. Lescure, pers. comm.). Arnoux donated the specimen to the Paris Museum in 1846, and the localities of other specimens contributed by him include the Marquesas, Tasmania and Australia. *N. arnouxii* is unknown from the Marquesas Islands (W. Brown, pers. comm.) and Tasmania, and it is relatively rare, and restricted to the Cape York Peninsula, in Australia (Cogger, 1975). *N. arnouxii* (= *N. pelagicus* of previous authors) has been collected on many islands in the South

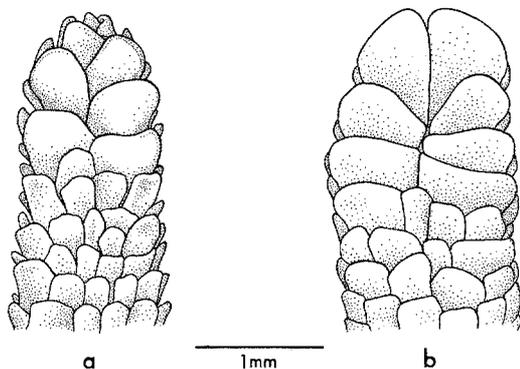


Fig. 4. Caudal scansorial pad in a) *Urocotyledon inexpectata* (UMMZ 168101) and b) *U. palmata* (MCZ 50240). Ventral view.

Pacific, from Kei Island off southwest New Guinea to Akiaki (Thrum Cap; 19°17'40"S, 138°42'W), Tuamotu Archipelago. Islands within this broad geographic range on which the species is known to be common (Roux, 1913), and where the Corvette le Rhin visited, includes New Caledonia (Jore, 1959). It seems likely that the type locality of New Zealand is in error, with the holotype having been collected on New Caledonia, and "Zelande" inadvertently substituted for "Caledonie" when the specimen was catalogued.

PHYLLODACTYLUS

Phyllodactylus, type species *P. pulcher* Gray, has undergone much revision in the last 20 years (Dixon, 1964; Dixon and Kluge, 1964; Dixon and Huey, 1970; Dixon and Anderson, 1973; Dixon and Kroll, 1974), and 63 congeners remain (Appendix 2). Its wide geographic range, United States through South America, including the Caribbean, Africa, Europe, the Near East, Australia and Southeast Asia, and considerable morphological variability imply that *Phyllodactylus* is still polyphyletic. In fact, I know of no single diagnostic character that would form the basis for claiming the group to be monophyletic. This is corroborated by Dixon's (pers. comm.) conclusion that several cladistically unrelated groups of Old World species are now referred to *Phyllodactylus*. Four species, *P. inexpectatus* (UMMZ 146733, 150988, 168094–106), *P. palmatus* (MCZ 50240–41), *P. weileri* (MW 491) and *P. wolterstorffi* (MCZ 54700) from Af-

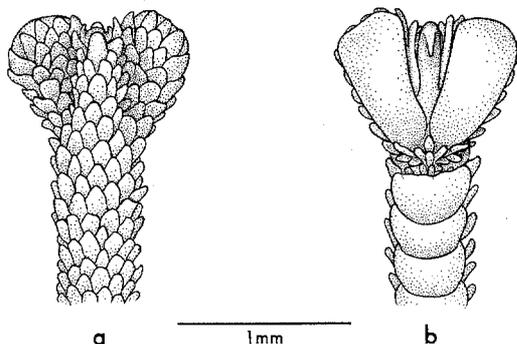


Fig. 5. Dorsal a) and ventral b) views of the apical portion of the fourth toe of *Urocotyledon inexpectata* (UMMZ 168101).

rica and the Seychelles Islands, in addition to being without the second ceratobranchial, possess a prehensile tail and a regularly arranged set of enlarged pilose scales on the ventral tip of the tail (Fig. 4). Only the holotype of *P. weileri* was examined, and while it has a regenerated tail, a scansorial pad was reproduced at the tip of the appendage. Doubtless, the prehensile nature of the tail and its scansorial pad aid these species in arboreal movement (Perret, 1963:Fig. 2). The caudal specialization is best developed in *P. palmatus* where the tail is also flattened, and in *P. palmatus*, *P. weileri* and *P. wolterstorffi* there exists extensive interdigital webbing, apparently another arboreal adaptation. *Phyllodactylus europaeus* has a prehensile tail; however, I have been unable to find any evidence of a caudal scansorial pad, viz., enlarged and flattened scales with pilosity (MCZ 5993, 27948; USNM 7466a–b, 14861a–b, 37216, 98959–62, 98964). The caudal scansorial pad is found elsewhere among the gekkos in *Lygodactylus* (Love-ridge, 1947:195) and *Pseudothecadactylus*, neither of which share any other derived states with *P. inexpectatus*, *P. palmatus*, *P. weileri* and *P. wolterstorffi*, not also exhibited by several other gekkos. The scalation of the digits themselves (Fig. 5) corroborate the apparent caudal synapomorphies diagnosing the four African-Seychelles species as a monophyletic group. The distal dilated portion of each digit is covered above with uniformly small scales. This state is closely approximated by some species of *Paroedura* (Dixon and Kroll, 1974), except for the enlarged mid-dorsal series found on each finger and toe. The casque headedness and fused nasal

bones of *Paroedura* serve to diagnose it as a monophyletic group distinct from the African-Seychelles taxon. Thus, I place *inexpectatus*, *palmatus*, *weileri*, and *wolterstorffi*, which lack a second ceratobranchial and possess the caudal and digital specializations noted above, in:

UROCOTYLEDON gen. nov.

type species *inexpectata* Stejneger (1893), and I refer that genus to the Gekkonini. *Uro* means tail and *cotyledon* refers to suckers, as on an octopus's tentacles. *Urocotyledon* is a Greek word which emphasizes one of the diagnostic characters, 'with a sucker on the tail,' of the four gekko species in question. *Urocotyledon* is feminine, and therefore the modified species names *U. inexpectata* and *U. palmata*.

PRISTURUS

Pristurus, type species *P. flavipunctatus* Ruppell (1835), consists of 10 species, *P. carteri*, *P. celerrimus*, *P. crucifer*, *P. flavipunctatus*, *P. insignis*, *P. minimus*, *P. phillipsii*, *P. rupestris*, *P. simonettai* and *P. sokotranus* (the genus is currently undergoing a revision by E. N. Arnold, pers. comm.). Unlike the other genera with second ceratobranchial variability examined herein, *Pristurus* can be diagnosed by several synapomorphies, and therefore is assumed to be monophyletic (Arnold, 1977). On the basis of the species that I have studied, *P. carteri*, *P. crucifer*, *P. flavipunctatus*, *P. rupestris* and *P. sokotranus*, the genus may be distinguished from all others by the loss of the splenial bone (also true for the Sphaerodactylinae), a tendency for extensive contact of the palatal portions of the maxillae behind the premaxilla (Haupt, 1980), and a failure of the lateral downgrowths of the frontal bone to meet on the midline and form a tube (the last two synapomorphies may not apply to *P. celerrimus* according to Arnold [1977]). Groups within *Pristurus* seem to be equally well defined, and the one that includes the species without the second ceratobranchial, *P. carteri*, *P. crucifer*, *P. minimus*, *P. phillipsii* and *P. simonettai*, is the most readily diagnosed and derived (Arnold, 1977; Russell, 1972). While I am forced to conclude that the loss of the second ceratobranchial is not unique within the Gekkonoidae, it does appear to have been independently lost in *Pristurus*. There is no evidence that the presence of the second ceratobranchial in *Pristurus* is an evolutionary reversal, and the genus

is therefore considered a *sedes mutabilis* "ptyodactylini."

TROPIOCOLOTES

Eight species are presently referred to *Tropiocolotes*, type species *T. tripolitanus* Peters (1880). As noted above, the second ceratobranchial is found only in *T. helenae*, *T. latifi* and *T. persicus*, and these three species are also unique within *Tropiocolotes* in sharing the derived condition of fused nasals. Even *T. latifi*, known only from the posthatchling holotype (SVL = 17.0 mm; CAS 134365), clearly exhibits the fused state. I have not examined representatives of all of the several subspecies of *T. helenae*, *T. persicus* and *T. tripolitanus*, and I assume that the branchial arch and nasal bone conditions are invariant within each species.

MICROGECKO

Microgecko, type species *helenae* Nikolskij (1907), is the oldest name available for those species with fused nasals and a persistent second ceratobranchial in *Tropiocolotes*, and I take this opportunity to resurrect that genus, and refer it to the "ptyodactylini" assemblage. Guibe (1966) discovered several scalational characters distinguishing *Microgecko* from *Tropiocolotes*, although shortly after he published, Minton et al. (1970) synonymized the two, with the caveat that further study might produce evidence that would reverse their action. I believe the presence of fused nasals and the character states emphasized by Guibe (1966) are sufficient corroboration to justify recognizing *Microgecko* as a distinct "ptyodactylini" genus (see also Tuck, 1971). Russell (1972; see also Leviton and Anderson, 1972) placed *helenae*, *latifi* and *persicus* in the same species group, but he did not provide a diagnostic character justifying his action. *Tropiocolotes*, restricted to *T. depressus*, *T. heteropholis*, *T. scortecci*, *T. studneri*, and *T. tripolitanus*, is placed in the Gekkonini. As in the reviews of *Cyrtodactylus* and *Phyllodactylus* above, I take the corroboration of the second branchial arch variation as additional evidence for the monophyly of the Gekkonini (Kluge, in press).

DISCUSSION

The cladistic methodology of phylogenetic systematics has once again demonstrated its use-

fulness in delimiting nested sets of putative monophyletic groups of gekkonid lizards (Kluge, 1976). The fact that one class of evidence, in this case the loss of the second ceratobranchial arch, coincides with inductions made from other different classes (fused nasal bones, caudal scansorial pad, etc.) is a test of the theory to which it applies (Kluge, in press). To be sure, the new taxonomic groupings recognized herein are not perfectly consistent with all phylogenetic hypotheses (e.g., *Pristurus*), and further testing is suggested.

Russell (1972:44) proposed several natural groups of genera, "based on overall functional foot structure, both internal and external." My division of the "Gekkoninae" into Gekkonini and other genera ("ptyodactylini") bears the following relationship to Russell's groups: *Afroedura* Group (*Afroedura*, *Calodactylodes*)—*Calodactylodes* is referred to the Gekkonini, *Afroedura* to the "ptyodactylini;" *Gekko* Group (*Gehyra*, *Gekko*, *Hemiphyllodactylus*, *Luperosaurus*, *Perochirus*, *Pseudogekko*)—all in the Gekkonini; *Hemidactylus* Group (*Briba*, *Cosymbotus*, *Dravidogekko*, *Hemidactylus*, *Teratolepis*)—all in the Gekkonini; *Homopholis* Group (*Blaesodactylus* [= *Homopholis*], *Geckolepis*, *Homopholis*, incertae sedis *Paragehyra*)—all in the Gekkonini; *Pachydactylus* Group (*Chondrodactylus*, *Colopus*, *Gekkonina*, *Kaokogekko*, *Pachydactylus*, *Palmatogekko*, *Rhoptropus*, *Tarentola*)—all in the "ptyodactylini;" *Phelsuma* Group (*Ailuronyx*, *Lygodactylus*, *Microscalabotes*, *Milotisaurus*, *Phelsuma*, *Rhoptropella* [= *Phelsuma*])—all in the Gekkonini, except for *Phelsuma*; *Phyllodactylus* Group (*Ebenavia*, *Phyllodactylus*, *Ptyodactylus*, *Uroplatus*)—*Uroplatus* is referred to the Gekkonini; *Stenodactylus* Group (*Stenodactylus*, *Teratoscincus*)—*Stenodactylus* is placed in the Gekkonini, *Teratoscincus* in the "ptyodactylini;" *Thecadactylus* Group (*Bogertia*, *Phyllopezus*, *Thecadactylus*)—all in the Gekkonini. Russell placed *Aristelliger* in its own group, and he did not recognize natural assemblages among the remaining straight-toed gekkos (*Agamura*, *Alsophylax*, *Ancylodactylus* [= *Cnemaspis*], *Bunopus*, *Cnemaspis*, *Crossobamon*, *Cyrtodactylus*, *Garthia* [= *Homonota*], *Geisopristurus* [= *Pristurus*], *Gymnodactylus*, *Heteronotia*, *Homonota*, *Microgekko*, *Narudasia*, *Pristurus*, *Ptenopus*, *Quedenfeldtia*, *Saurodactylus*, *Trachydactylus* [= *Bunopus*] and *Tropicolotes*). Thus, the differences between my classification and Russell's reduces most simply to the placement of only four genera, *Afroedura* (or *Calodactylodes*), *Phelsuma*, *Stenodactylus* (or *Teratoscin-*

cus) and *Uroplatus*, and further research should be devoted to choosing between the two sets of alternatives. This will necessitate re-examination of Russell's anatomical and functional evidence and the search for new synapomorphies corroborating one or the other hypothesis. One of the principal difficulties with evaluating Russell's observations will be discerning plesiomorphic and apomorphic states. He seems to have rarely applied the out-group comparison, and he based some of his hypotheses of relationships on primitive states and overall similarity. There will also be the added difficulty in determining how much Russell relied on questionable functional and geographic considerations, because they were usually only briefly acknowledged.

Some objection to the *Stenodactylus* + *Teratoscincus* assemblage (Group II of Kluge, 1967) has already been raised by two investigators. Russell's (1972:197) argument that the reduced phalangeal formula of *Stenodactylus* makes such a grouping impossible seems groundless; however, Arnold's (1980b) conclusion that the single putative synapomorphy of a large number of scleral ossicles may be a symplesiomorphy in *Teratoscincus* is a reasonable falsification.

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APPENDIX I

The following species of *Cyrtodactylus* were examined: *agusanensis*, *amictopholis*, *angularis*, *annulatus*, *arnouxii*, *baluensis*, *biordinis*, *brevipalmatus*, *caspicus*, *cavernicolus*, *collegalis*, *condorensis*, *consobrinus*, *darmadvillei*, *deccanensis*, *derongo*, *elongatus*, *frae*, *fedtschenkoi*, *fraenatus*, *fumosus*, *galgajuga*, *intermedius*, *irregularis*, *jellesmae*, *kachhensis*, *khasjensis*, *kirmanensis*, *kolschyi*, *laevigatus*, *lateralis*, *lawderanus*, *loriae*, *louisianensis*, *malayanus*, *malcolmsmithi*, *marmoratus*, *mimikanus*, *nebulosus*, *novaeguineae*, *oldhami*, *papuensis*, *pelagicus*, *peguensis*, *philippinicus*, *pubisulcus*, *pulchellus*, *quadrivirgatus*, *redimiculus*, *rubidus*, *russowii*, *sagittifer*, *scaber*, *sermo-waiensis*, *serpensinsula*, *stoliczkai*, *triedrus*, *vankampeni*, *watson* and *wetar-iensis*.

The following currently recognized *Cyrtodactylus* were not available for study: *agamuroides*, *brevipes*, *chitralensis*, *consobrinoides*, *deveti*, *fasciolatus*, *gastropholis*, *gubernatoris*, *heterocerus*, *himalayanus*, *jeyporensis*, *montiumsolorum*, *sworderi*, *turkmenicus*, *variegatus* and *yakhuna*.

APPENDIX 2

The following species of *Phyllodactylus* were examined: *angelenis*, *angustidigitus*, *barringtonensis*, *baurii*, *bordai*, *bugastrolepis*, *darwini*, *davisi*, *delcampi*, *dixonii*, *duellmani*, *europaeus*, *galapagensis*, *gerrhopygus*, *gilbertii*, *guentheri*, *homolepidurus*, *inaequalis*, *inexpectatus*, *insularis*, *interandinus*, *johnwrightii*, *julieni*, *kofordii*, *lanei*, *leei*, *lepidopygus*, *lineatus*, *marmoratus*, *martini*, *melanostictus*, *microphyllus*, *muralis*, *palmeus*, *palmatus*, *partidus*, *paucituberculatus*, *porphyreus*, *pulcher*, *pumilis*, *reissii*, *riebeckii*, *ruttieni*, *santacruzensis*, *siamensis*, *tinklei*, *trachyrhinus*, *transversalis*, *tuberculosus*, *unctus*, *ventralis*, *weileri*, *wirshingi*, *wolterstorffi* and *xanti*.

The following currently recognized *Phyllodactylus* were not available for study: *annulatus*, *ansorgii*, *apricus*, *clinatus*, *heterurus*, *microlepidotus*, *peringueyi* and *sentosus*.