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Underwood's classification of the geckos: a 21st century appreciation

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SYNOPSIS. The publication in 1954 of Underwood's **'**On the classification and evolution of geckos**'** was the first comprehensive attempt to understand the systematics, evolution and biogeography of this group of lizards. Combining the use of the exploration of novel characters with a global overview of geckos, Underwood erected hypotheses of relationship and patterns of distribution. In the 48 years since that landmark publication much has changed, but much has stayed the same. Underwood's division of geckos into four major clusters is still recognised today, although the sphaerodactyls are now regarded as a group derived from within the gekkonines, and the diplodactylines have been diminished by the removal of several genera and their placement in the gekkonines. The framework that Underwood established has resulted in generic and/or species level phylogenies being generated for the eublepharids, some sphaerodactyls, the carphodactyline diplodactylines and some clusters within the gekkonines. The latter group, because of its size, has remained intractable to detailed systematic analysis at the generic level, although the recognition of many discrete monophyletic clusters within the Gekkonidae (the Gekkoninae of Underwood) holds out the possibility that greater levels of intergeneric resolution are close to realisation.

Underwood's initial approach to the systematic analysis of geckos was distinguished by its use of novel characters of the visual system that led to new insights. It is possible that the next breakthrough in higher level systematic analysis of geckos may again come from the exploitation of new character sources. Some examples of these possibilities are discussed.

INTRODUCTION

'[We] would like to make a distinction between *how* [Dr. Underwood] thought about the classification of [gekkotans] and *what* he thought, since in [our] view how a man thinks is far more important than what he thinks … [we] suggest that *how* [Underwood] thought about classification survives untarnished to this day. Does *what* he thought about it bear critical scrutiny nearly fifty years later?**'** With these words (bracketed modifications aside) Garth Underwood (1971a) began his *A Modern Appreciation of Camp's* **'***Classification of the Lizards.***'** Nearly 50 years after its publication we here consider Underwood's classification of the Gekkota, its central position in the study of these lizards, its influence on subsequent work in the field and how its conclusions have been modified over the intervening decades. This work was Underwood's first substantial contribution to squamate evolution, preceding other major contributions to the systematics of pygopods (Underwood, 1957) and snakes (Underwood, 1967) and establishing the way he was to think about and employ character analysis in approaches to what had previously been regarded as rather intractable problems.

Garth Underwood was interested in both the theory and practice of systematics and also in the evolutionary morphology of the organisms that he chose as the subjects of his systematic analyses. He was bold in embracing novel sources of data for his systematic analyses, put forward hypotheses of relationship in the hopes that they would be scrutinised and evaluated by others, and frequently returned to systematic problems that he had already published some years earlier to bring fresh insights and approaches. Specimens always figured prominently as a primary source of inspiration and new data.

A comparison of the lizard families recognised by Boulenger (1885), Camp (1923), and most modern workers (e.g., Macey *et al.*, 1997; Harris *et al.*, 1999) reveals almost no discrepancies. The gekkotan lizards, however, are an exception. Until the middle of the 20th century, lizard systematists variously recognised the Eublepharidae and Uroplatidae as entities distinct from the Gekkonidae. Different classificatory schemes reflected not only different interpretations of characters, but alternative views of the systematic meaning of novel morphologies. For most of the time after the description of the first gecko genera by Laurenti (1768), gecko systematics was dominated by alpha systematic treatments and the allocation of newly discovered species to an ever growing number of genera, defined chiefly by externally discernible digital features. This reliance on digital characters as almost the sole determinant of affinity resulted in the widespread recognition of composite genera constituted by digitally convergent taxa. Further, the focus on foot structure did little to resolve higher order relationships among gekkotans, as the digital characters then recognised suggested many discrete clusterings of species, but provided few putative links between them.

Garth Underwood was led to the topic of gecko classification, which he (1954:469) characterised as **'**far from stable**'**, through his research on the reptilian eye. His earlier work on retinal morphology (Underwood 1951a) and pupil shape (Underwood 1951b) had both highlighted the distinctiveness of the gecko eye and suggested that ophthamological characters could be of use in the resolution of higher order relationships among the many gecko genera. Underwood's optimism that the eye could provide useful characters was bolstered by the then recent work of Bellairs (1948), who had conclusively demonstrated that the true eyelids of the eublepharid geckos were primitive to the derived condition of a well-developed brille and lack of moveable lids typical of other geckos. Further, Walls (1942) and Prince (1949) had examined the eyes of some geckos in their broader ophthamological treatments, suggesting avenues for further research.

Walls' (1942) comprehensive treatment of the vertebrate eye led Underwood to hypothesise that this organ system could yield useful and stable associations of characters. The general recognition of the retinal characteristics of the eyes of geckos as evidence of secondary nocturnality, and a preliminary survey (Underwood 1951b) of the form of the pupil suggested that a more intensive survey of pupil form may provide a means by which gekkonids could be subdivided into more manageable and meaningful subsets reflective of their evolutionary history. Underwood (1954) set himself the task of surveying a moderately comprehensive collection of preserved geckos at the Museum of Comparative Zoology, Harvard University, and to analyse the resulting data. He used these data to erect the first modern generic level analysis of gekkotan relationships. He recognised potential problems with character state interpretation caused by state of preservation and the limitations of a single-character classification, but nonetheless regarded pupil character states to be sufficiently discrete for the purpose of establishing a workable classification of geckos, which would be subject to modification as additional data became available. Werner (1977) later demonstrated that pupil shape and dilation change with differing light levels, and these observations have helped refine Underwood's (1954) initial conclusions (see below).

UNDERWOOD'S CLASSIFICATION OF THE GECKOS

Underwood (1954) recognised three families of gekkotan lizards. The Eublepharidae was characterised by true eyelids, the lack of a spectacle and vertical pupils reflective of the nocturnal adaptations of the family. The five genera he included were those subsequently placed by Kluge (1967a) in his Eublepharinae, and by Kluge (1987) and Grismer (1988) in the Eublepharidae. [Note: The current allocation of taxa employed in this article is based upon Kluge, 2001]. Underwood (1954) considered *Aeluroscalabotes* as the most primitive member of the family. It has subsequently been regarded as the sister group of all remaining eublepharids (Grismer, 1988).

Underwood's Sphaerodactylidae was supported by the presence of a round, diurnal-type pupil (or eliptical or straight vertical pupil in some cases), the existence of a fovea, and the presence of a spectacle. He included five genera therein, corresponding to Kluge's (1967a) Sphaerodactylinae and later Sphaerodactylini (Kluge 1987, 1995).

All remaining genera were placed in the Gekkonidae, characterised by a spectacle and lack of a fovea. Pupil shape was variable. Within the Gekkonidae he recognised two subfamilies, the Diplodactylinae and the Gekkoninae. The former had vertical pupils with straight margins, or circular pupils. He included 22 genera in this group. Among them are all of the genera now assigned to the Diplodactylinae by Kluge (1967a) except for *Eurydactylodes*, *Pseudothecadactylus*, and *Crenadactylus*. Underwood had doubts about the placement of the first of these genera (see below), specimens of which he had not examined himself, and changed its allocation the following year (Underwood 1955). *Crenadactylus ocellatus* was examined but was included with *Phyllodactylus* in the Gekkoninae by Underwood (1954). The Diplodactylinae was subsequently retained by Kluge (1987) and Bauer (1990a), although its affinities with the Pygopodidae were uncertain (see below). Stephenson and Stephenson (1956) regarded New Zealand geckos (*Hoplodactylus* and *Naultinus*) as the most primitive forms on the basis of Underwood's (1955) revised view that amphicoelous vertebral centra are primitive within lizards and within the Gekkota. Furthermore, Stephenson (1960) rejected Underwood's (1954) ophthamalogical division of the Gekkonidae into two subfamilies as it was inconsistent with osteological characters, but neither Underwood nor Stephenson 'correctly' placed all Australian genera.

Also included in Underwood's Diplodactylinae were several genera not now regarded as closely allied to the Australo-Pacific diplodactylines: *Aristelliger, Chondrodactylus, Colopus, Gymnodactylus, Palmatogecko, Phelsuma, Ptenopus, Rhoptropella, Rhoptropus, Saurodactylus,* and *Teratoscincus*. Four of these, *Chondrodactylus*, *Colopus*, *Rhoptropus*, and *Palmatogecko*, share many features in common with each other and with *Pachydactylus* (placed by Underwood [1954] in the Gekkoninae). Kluge (1967a) moved these taxa to the Gekkoninae, and Russell (1972) and Haacke (1976) established the affinities of these forms as part of the *Pachydactylus* group (see below).

Two other taxa, *Rhoptropella* and *Phelsuma*, have also been regarded as being closely related to one another (see below). Both of these genera, as well as all remaining ones, were moved to the Gekkoninae by Kluge (1967a) and have remained there since, with *Teratoscincus* as the sister group of all other gekkonines. The affinities of *Gymnodactylus* have remained problematic (Abdala 1988, 1996; Abdala and Moro 1996), as have those of *Aristelliger* (Russell and Bauer 1993), and *Ptenopus* (Bauer 1990b), whereas *Saurodactylus* has been considered allied to the sphaerodactyline lineage (Kluge 1995). Underwood's *Phyllurus* also included within it a species now assigned to the gekkonine genus *Nactus*.

The Gekkoninae were characterised by *Gekko*-type pupils or secondarily circular pupils. Underwood's (1954) Gekkoninae, although lacking the taxa mentioned above (and with the addition of *Eurydactylodes*, and *Crenadactylus* as *Phyllodactylus ocellatus*) otherwise included all of the genera placed in the group by Kluge (1967a). This grouping also included *Uroplatus*, which by virtue of a large suite of autapomorphic features had been accorded separate familial status by many previous workers (see Bauer and Russell 1989 for a review). In this regard, Underwood's (1954) results were similar to those of Wellborn (1933), who had based her conclusions on osteological data. Underwood did not rely entirely on the pupil character, however, as *Lygodactylus*, with round pupils, was placed in the Gekkoninae on the basis of other (digital) similarities with *Hemidactylus*.

Nine genera were not assigned to family or subfamily by Underwood. Five of these were unplaced due to lack of material. The remaining four were taxa with round pupils that were regarded as secondarily diurnal gekkonids, but which Underwood considered, on the basis of existing data, could not be allocated to one or the other of his two subfamilies. Of the latter, one genus, *Ancylodactylus*, has been synonymized with another, *Cnemaspis*. The other two were *Quedenfeldtia* and *Pristurus*. Of the genera not examined, *Ceramodactylus* has since been subsumed in *Stenodactylus*, and *Dravidogecko* has been synonymized with *Hemidactylus*.

Underwood also recognised some instances of convergence among geckos. Specifically he addressed the allocation of species of leaf-toed geckos (then chiefly distributed in *Diplodactylus* and *Phyllodactylus*), and bent-toed geckos (then mostly placed in *Gymnodactylus*). Among the leaf-toed geckos, pupil shape suggested the transfer of several species of African *Diplodactylus* to *Phyllodactylus*. These geckos are now regarded as members of the genus *Urocotyledon* (Kluge, 1983) and are, as Underwood indicated, correctly assigned to the Gekkonidae rather than the Diplodactylidae.

Diplodactylyus, as recognised by Underwood, corresponds to two currently recognised genera, *Diplodactylus* and *Strophurus*. His reconstituted *Phyllodactylus* included forms now placed in that genus as well as *Asaccus, Afrogecko, Euleptes, Christinus, Crenadactylus, Paroedura* and *Urocotyledon* (based on his list of specimens examined). He also separated *Narudasia* from *Quedenfeldtia*, and divided the then cosmopolitan *Gymnodactylus* into four genera: *Gymnodactylus* (restricted to South America), *Phyllurus* (corresponding to the current *Phyllurus* and *Saltuarius*, but also including the species *vankampeni*, now allocated to the gekkonine genus *Nactus*), *Cyrtodactylus* (including representatives of *Cyrtodactylus, Geckoella, Tenuidactylus, Mediodactylus, Nactus*), and *Wallsaurus* (the latter now synonymized with *Homonota*, a genus listed as unexamined by Underwood).

STEPS TOWARDS FURTHER SYSTEMATIC RESOLUTION

Underwood's (1954) classification provided a springboard for subsequent systematic work on geckos. The four large units he established were **'**corrected**'** by Kluge (1967a), but remained as the chief elements in Kluge's higher order treatment of the group. Moffat (1973) generally accepted Kluge's (1967a) allocation of genera to subfamilies but disagreed with his methodology and his pattern of subfamilial relationships.

Eublepharidae

The most stable unit has been the Eublepharidae. This group was retained intact by Kluge (1967a), although reduced to subfamilial rank. All subsequent researchers have accepted the monophyly of this group and more recent treatments have reflected the phylogenetic position of the Eublepharidae as the sister-group of all other gekkotans by again according it familial rank (e.g. Grismer 1988). Further, patterns of relationship within the eublepharids have been established at the generic and species levels (Grismer, 1988, 1991, 1994; Grismer *et al.*, 1999; Ota *et al.*, 1999). In this instance, Underwood (1954) chiefly used primitive features in diagnosing the family (e.g. true eyelids present, etc.) but subsequent research has identified numerous synapomorphies that support the reality of this monophyletic unit (Grismer, 1988; Ota *et al.*, 1999).

Sphaerodactylidae

The Sphaerodactylidae of Underwood has remained unchanged in terms of generic content. Kluge (1967a) recognised the group as a subfamily and considered it to be highly derived, in contrast to Underwood (1954), who interpreted it as a primitively diurnal group and a relatively early offshoot of the gekkotan lineage. Subsequently Kluge (1987) demonstrated that sphaerodactyls are derived from within gekkonines, confirming their monophyly while obviating their recognition as a higher order group, as such recognition would render the Gekkoninae paraphyletic. This arrangement also received support from reproductive characters including the restriction of the calcareous eggshell to gekkonines and sphaerodactylines (Bustard 1968; Werner 1972). Kluge (1995) later conducted an explicit investigation of the phylogeny of the sphaerodactyls, yielding a fully resolved generic level pattern for the group. Kluge (1995) regarded the gekkonine *Pristurus* as the immediate sister group of the sphaerodactyls and considered *Quedenfeldtia, Cnemaspis, Narudasia* and *Saurodactylus* as other appropriate outgroup taxa for his analysis (see below). Of these outgroup genera, Underwood examined material of only *Narudasia* and *Saurodactylus*. Species level analyses within individual sphaerodactyl genera are ongoing and have been attempted for the largest genus, *Sphaerodactylus* (Hass 1991, 1996).

Diplodactylinae

The composition of the Diplodactylinae has changed most significantly. Kluge (1967a, b) removed a large number of genera from this group to the Gekkoninae, leaving only forms with parchment-shelled eggs in his Diplodactylinae, and provided a generic level hypothesis of relationships among the remaining forms. Bauer (1990a) erected a species level hypothesis of relationships among the Carphodactylini, one of two tribal groups established by Kluge (1967a). Additional hypotheses at the species level have been presented by Good *et al.* (1997) and Vences *et al.* (2001). The Diplodactylini, also established by Kluge (1967a), has yet to be investigated phylogenetically at the species level, although Kluge (1967b) erected a generic level hypothesis of relationships and King (1987b) suggested a species level phylogeny of *Diplodactylus* based on several karyotypic characters. Underwood (1954) had purged the genus *Diplodactylus* of two taxa with *Gekko*-type pupils, rendering a cluster of taxa still accepted as monophyletic. However, he retained in *Phyllodactylus* the species *ocellatus*, which has since been recognised as a diplodactyline and placed in the genus *Crenadactylus.*

Although the content of Underwood's (1954) Diplodactylinae as a whole has changed little, argument persists over patterns of internal relationship. In particular, the monophyly of the Carphodactylini has been called into question (Donnellan *et al.* 1999) and the relationship of New Zealand taxa has also been reevaluated (Chambers *et al.* 2001). King (1987b) and King and Mengden (1990), based on chromosomal data, argued that *Oedura* was more closely allied to the Carphodactylini than to other Diplodactylini, and that pygopods are also allied to the carphodactylines. Donnellan *et al.* (1999), based on molecular data (12SRNA, c-mos), regarded the Diplodactylini , including *Oedura*, as monophyletic, but suggested that the Carphodactylini is paraphyletic. They found pygopods to be the sister group of all Diplodactylines.

Patterns of relationship within the Diplodactylinae have further been complicated by the recognition that pygopods are more closely related to this group (or some component thereof) than to other gekkotans (Kluge 1987). On this basis, Kluge (1987) recognised a redefined Pygopodidae for the group that includes diplodactyline geckos plus pygopods. Good *et al.* (1997), based in part on arguments presented by Bauer (1990a), proposed an alternative higher level scheme, recognising the Diplodactylidae as a family level group. Based on the patterns of relationship retrieved by Donnellan *et al.* (1999), the Diplodactylidae and Pygopodidae are sister taxa.

As mentioned above, the genus *Eurydactylodes* proved particularly problematic to Underwood (1954) and he only included it in his Diplodactylinae in the following year (Underwood, 1955). For a variety of reasons, this genus has continued to be enigmatic, exhibiting an odd mosaic of characteristics. Although *Eurydactylodes* appears to be a member of a monophyletic New Caledonian carphodactyline radiation (Bauer 1990a), it possesses a number of features that are problematic and, at least superficially, link it to other groups of geckos. One such feature is the tail-squirting apparatus. Members of this genus have caudal glands that secrete a sticky substance as a defensive mechanism. Such mechanisms have been widely reported in arthropods (Deslippe *et al.* 1996), and amphibians (Arnold 1982), but among amniotes have been noted only for geckos of the Australian diplodactyline genus *Strophurus* (Rosenberg and Russell 1980) and *Eurydactylodes* (Böhme and Sering 1997). Although the secretion has not been characterised, it is likely similar to that of *Strophurus* spp., which is proteinaceous (Rosenberg *et al.* 1984) and is effective in detering at least some small predators, such as spiders, which become entangled in the secretion (Minton 1982). However, both the anatomy of the gland and the ejection mechanism of secretion differ between the two gecko genera, suggesting that the apparatus in convergent (Böhme and Sering 1997). *Eurydactylodes* is also convergent with *Strophurus* in its bright yellow-orange mouth coloration. Most geckos have unpigmented buccal linings.

Eurydactylodes also shares some features with gekkonid geckos. Most notable is the presence of extracranial endolymphatic sacs in the neck region, especially in juveniles and reproductive females. These calcium-storing structures frequently form conspicuous bulges on the necks of gekkonids, but in diplodactylids are intracranial and contain little calcium. *Eurydactylodes* is an exception in that very large sacs are often present, in some individuals artificially increasing the apparent size of the head (Bauer 1989). Perhaps related to this, the eggshells of *Eurydactylodes*, although similar in most regards to those of typical carphodactylines, are covered by a calcified outer surface (Bauer and Sadlier 2000), which otherwise typifies gekkonids (Bustard, 1968; Werner, 1972).

Gekkoninae

The Gekkoninae was the most heterogeneous and unwieldy of Underwood's higher order groups and it has remained largely intractable to this day. Indeed, as a result of the resolution of the content of the Diplodactyinae, the Gekkoninae has grown significantly. Further, the vast majority of all new or resurrected genera since 1954 are gekkonines. Underwood (1954) initiated the process of dismantling some of the larger gekkonid genera that he recognised as polyphyletic assemblages of digitally convergent taxa. In particular he addressed the composition of *Phyllodactylus* and *Gymnodactylus*, two of the largest and most cosmopolitan taxa.

Subsequent reduction of *Phyllodactylus* occurred with the removal of *Crenadactylus* and its shift to the Diplodactylinae (Dixon and Kluge 1964), and the placement of several geographically coherent gekkonine leaf-toed forms into *Paroedura* (Dixon and Kroll 1974), *Asaccus* (Dixon and Anderson 1973), *Urocotyledon* (Kluge 1983), and *Christinus* (Wells and Wellington 1983). All remaining Old World leaf-toed geckos were removed from the now strictly American *Phyllodactylus* by Bauer *et al.* (1997), who erected *Haemodracon, Dixonius, Afrogecko*, *Cryptactites* and *Goggia*, and resurrected *Euleptes*. Nussbaum *et al.* (1998) further provided a new generic name for the elongate-bodied leaf-toed geckos of Madagascar, *Matoatoa*. Arnold and Gardner (1994) also provided a species level phylogeny for *Asaccus*, using a variety of Old and New World leaf-toed geckos as outgroup taxa, but without explicit justification. Both these authors and Nussbaum *et al.* (1998) suggested that at least some phyllodactyl taxa might be closely related.

A similar dismantling of *Gymnodactylus* was begun by Underwood (1954), who removed *Phyllurus* to the Diplodactylinae and recognised the genera *Gymnodactylus*, *Cyrtodactylus* and *Wallsaurus* for a subset of the naked-toed geckos. Subsequently Golubev and Szczerbak (1981) and Szczerbak and Golubev (1984) divided the Old World forms placed by Underwood in *Cyrtodactylus*, which they regarded as polyphyletic, into several genera, including the Palearctic *Tenuidactylus*, *Cyrtopodion*, *Mesodactylus*, *Carinatogecko, Mediodactylus* and *Asiocolotes*. Tropical forms were divided into *Cyrtodactylus, Geckoella* and *Nactus* (Kluge 1983).

The effect of these actions has been to dismantle several larger, clearly polyphyletic groups and to instead recognise a larger number of smaller, but putatively monophyletic, genera. The problem remains, however, that relationships among these genera are poorly resolved. While the identification of monophyletic units is a necessary first step in the resolution of gekkotan relationships, the increase in the number of such units increases the sampling required in order to erect a hypothesis of relationship across all members of the group. This has been the major stumbling block in the phylogenetic interpretation of the Gekkoninae: any attempt to resolve relationships among some subset of genera of necessity requires an analysis of virtually all other genera. The sheer diversity of the group has been an impediment to its resolution.

Despite the difficulty of determining relationships among gekkonines, some clusters of genera that appear to be monophyletic have been identified. These groups are chiefly those that share highly distinctive and generally restricted derived conditions. Thus, such groups have typically been identified on the basis of information intrinsic to themselves rather than on the basis of outgroup comparison. Indeed, when outgroup analysis has been attempted, the choice of outgroup has been based on geography (e.g., Joger 1985; Bauer 1990b; Abdala 1996; Macey *et al.* 2000) or on some preconceived notion of similarity, usually based on digital anatomy (e.g., Arnold and Gardner 1994; Macey *et al.* 2000). Chromosomal characteristics of gekkonids are highly heterogeneous (King 1987c), but such variation may occur within genera and thus has contributed little to the resolution of higher order relationships.

One of the most substantially supported subgroups of gekkonines is the *Pachydactylus* group. This is a cluster of genera sharing the unique feature of hyperphalangy of digit I of both the manus and pes. The group includes the chiefly Mediterranean genera *Tarentola* and *Geckonia* and the southern Africa forms *Pachydactylus, Rhoptropus, Chondrodactylus*, *Colopus*, and *Palmatogecko*. Underwood (1954) recognised the relationship of all of these except *Pachydactylus* itself, placing them in the Diplodactylinae and identifying a peculiar pupil shape, the *Rhoptropus*-type, that all shared. Several species of *Pachydactylus* (e.g., *P. austeni*, *P. kochi*) are strikingly similar, even in external appearance, to *Colopus* and *Palmatogecko*. By chance, however, Underwood's (1954) list of taxa examined reveals that he did not examine any of these species. Hyperphalangy had previously been identified in some members of the group by Wellborn (1933), but her sampling was inadequate to highlight the potential phylogenetic value of the feature. Russell (1972, 1976) and Haacke (1976) recognised the significance of hyperphalangy and argued convincingly that this was evidence of the relatedness of these taxa. Virtually all subsequent workers (Bauer 1990b, 2000; Kluge and Nussbaum 1995; Lamb and Bauer 2002; but see Joger 1985) have agreed that these seven genera (including collectively approximately 80 species) form a monophyletic group. With closely related taxa thus identified, species level phylogenies have been possible within constituent genera (e.g., *Rhoptropus*: Bauer and Good 1996, Lamb and Bauer 2001; *Pachydactylus*: Lamb and Bauer 2000, 2002).

Other clusterings, although less well investigated, have also been proposed, although not necessarily tested. The *Gekko* group, consisting of *Gekko*, *Gehyra*, *Hemiphyllodactylus*, *Lepidodactylus*, *Luperosaurus*, *Perochirus*, *Pseudogekko,* and *Ptychozoon*, all share similarities of digital structure (Kluge 1968; Russell 1972, 1976) and are probably a monophyletic group, although particular patterns of intergeneric relationship remain untested.

The large and heterogeneous genus *Hemidactylus* seems to be related to a number of much smaller genera that are also similar digitally, and are united by synapomorphies of size and shape of the intermediate phalanges (Russell, 1977a). *Dravidogecko,* for example, has been synonymized with *Hemidactylus* on the basis of digital morphology (Bauer and Russell 1995). In addition, *Cosymbotus*, *Briba* and *Teratolepis* are also very similar and are almost certainly share a common ancestry with *Hemidactylus*, or are derived from within it.

Bauer (1990b) found some evidence for the recognition of a Madagascan radiation including several genera of leaf and fan-toed geckos including *Uroplatus*, *Ebenavia* and *Paroedura*. Kluge and Nussbaum (1995) did not retrieve identical patterns of relationship, but these genera nonetheless grouped closely when only Afro-Malagasy geckos were included in the analysis. An expanded Indian Ocean lineage, including these taxa plus *Ailuronyx*, *Blaesodactylus*, *Homopholis*, and *Geckolepis* was retrieved by Bauer (1990b), although not by Kluge and Nussbaum (1995).

Another putatively monophyletic group is the *Lygodactylus* complex (Pasteur 1964), which includes two additional genera, at least one of which, *Millotisaurus*, is probably derived from within *Lygodactylus* (Pasteur, 1995; Krüger, 2001). *Lygodactylus* itself clustered with *Phelsuma* in analyses constrained to include only Afro-Malagasy genera (Bauer 1990b; Kluge and Nussbaum 1995). Krüger (2001) also clustered *Lygodactylus* and *Phelsuma* together.

Although some genera have been revised at the alpha level, and numerous new taxa have been erected, most revisions have merely proposed species groups, without providing explicit hypotheses of relationship (e.g. Pasteur 1964; Brown and Parker 1977; Nussbaum and Raxworthy 2000). These, like many of the other groups, share digital similarities and geographic cohesiveness. Among those genera for which some idea of relationships exist, there are several for which species level phylogenies have been proposed, including *Uroplatus* (Bauer and Russell 1989) and *Gehyra* (selected species only; King 1979, 1983).

Rhoptropella has been associated with several different genera by different authors. Russell (1977b) used digital morphology to argue that it was in fact a *Phelsuma*, with no direct affinities to *Rhoptropus*, with which it had previously been associated (e.g. Boulenger 1885). Russell and Bauer (1990) found additional support for this from histological investigations and Good and Bauer (1995) presented allozyme evidence for *Rhoptropella*'s links to *Phelsuma*. Both Bauer (1990b) and Kluge and Nussbaum (1995) found the two genera to be sister taxa when a generic analysis was conducted. Rösler (2001), discussing pholidosis, also concluded that *Phelsuma* and *Rhoptropella* are sister taxa. Röll (1999), however, using ophthalmological and digital surface data, interpreted it as displaying features of both *Rhoptropus* and *Phelsuma*, which, if true, could suggest affinities between the chiefly African *Pachydactylus* group and the putatively monophyletic Indian Ocean complex. A variety of character types also suggest that *Bogertia* and *Thecadactylus* may be allied (Russell and Bauer 1988; Abdala and Moro 1996).

Cnemaspis, Narudasia, Quedenfeldtia, Saurodactylus and *Pristurus* have been proposed as gekkonine taxa basal to the sphaerodactyl lineage (Arnold 1993; Kluge 1995), demonstrating the paraphyly of the Gekkoninae. Although Kluge (1995) did not claim any specific relationships among these taxa, his analysis did yield patterns in which *Pristurus* was the sister group of the sphaerodactyls, and *Narudasia, Saurodactylus* and *Cnemaspis* formed a clade. Arnold (1993) advocated the pattern ((((*Pristurus*, *Quedenfeldtia*) sphaerodactyls) *Saurodactylus*) *Narudasia*). Behavioural apomorphies unique to this cluster were documented by Rösler and Wranik (2001), who noted reproductive morphological apomorphies shared by *Quedenfeldtia* and the sphaerodactyls to the exclusion of *Pristurus.* Arnold (1993) provided a species level phylogeny for *Pristurus*. The African members of this group were also clustered together in an anlysis of Afro-Malagasy taxa by Kluge and Nussbaum (1995). Röll and Schwemer (1999) identified a unique crystallin ligand common to several of these taxa (plus *Lygodactylus*), that they interpreted as synapomorphic. This was subsequently found in *Cnemaspis* (Röll, in press), but whether this indicates affinity or convergence among secondarily diurnal forms remains to be determined.

The naked-toed geckos have proved especially difficult to deal with. Szczerbak and Golubev (1984, 1986) provided evidence of relationship among some Palearctic forms, such as *Tenuidactylus*, *Mediodactylus*, *Asiocolotes*, and *Cyrtopodion*. Macey *et al.* (2000) found evidence for the monphyly of *Cyrtopodion* and *Mediodactylus* and hypothesized relationships among a small number of species in each group. The generic allocation of certain Himalayan members of the group has proved especially problematic (Khan 1993; Khan and Rösler 1999).

Another group of naked-toed geckos including *Agamura*, *Bunopus*, *Alsophylax*, *Crossobamon*, *Microgecko*, and *Tropiocolotes* has been even less well investigated (Leviton and Anderson 1972; Szczerbak and Golubev 1977; Golubev 1984; Golubev and Szczerbak 1985). The New World naked toed forms, *Gymnodactylus* and *Homonota*, have been included in analyses by Abdala (1996) and Abdala and Moro (1996) but these investigations included only South American gekkonines. Abdala (1988) also provided a species level phylogeny for *Homonota* (see also Vanzolini 1968).

While some degree of resolution for the gekkonine taxa outlined above has been reached, certain other gekkonines remain enigmatic and without any sound indication of affinities. *Teratoscincus* is highly unusual in its morphology, and appears to be the sister group of all remaining gekkonines (Kluge 1987). A species level phylogeny for this group has been generated (Macey *et al*. 1999). *Stenodactylus* has sometimes been considered to be allied to *Teratoscincus* (Kluge 1967a; Kluge and Nussbaum 1995), but its position remains equivocal (Arnold 1980).

Another perplexing padless genus is *Ptenopus*, a southern African endemic. Both Bauer (1990b) and Kluge and Nussbaum (1995) found little evidence for particular affinities, and constrained or retrieved a basal placement among African gekkonines. *Ptenopus* possesses a large number of autapomorphic traits (Haacke 1975; Rittenhouse *et al*. 1998; Russell *et al.* 2000). This mirrors the situation that plagued analyses of *Uroplatus* in that many features segregate these geckos from other taxa, but those traits that are shared are chiefly primitive ones.

Four pad-bearing genera, which appear unrelated to one another and have no obvious affinities to previously discussed groups, are also problematic. These are *Afroedura, Aristelliger, Calodactylodes*, and *Paragehyra*. *Paragehyra* was long known from a single specimen of a single species, but a second species was recently discovered (Nussbaum and Raxworthy 1994). The availability of additional material allowed the relationships of the genus to be investigated in more detail, but this has not yielded any definitive statements about its position within the Gekkoninae (Kluge and Nussbaum 1995), although Nussbaum and Raxworthy (1994) noted the similarity of the digits of this form to those of another enigmatic taxon, the West Indian *Aristelliger*.

Russell (1972) grouped *Afroedura* and *Calodactylodes* in the same digitally defined cluster. Loveridge (1944) had initially segregated *Afroedura* from the Australian *Oedura*, and this was reflected in Underwood's (1954) placement of the genera in different subfamilies. Some question as to the distinctiveness of these taxa remained, however, until Cogger (1964) conducted detailed osteological comparisons. Despite some similarities in digital design, Russell and Bauer (1989) concluded that *Calodactylodes* and *Afroedura* were more likely convergent than related. Bauer and Das (2000) noted some superficial similarity and geographic proximity to *Asaccus*, but again concluded that the relationships of *Calodactylodes* were obscure.

Aristelliger was one of the taxa regarded as enigmatic by Underwood (1954). He placed it in the Diplodactylinae and regarded it as an archaic form, possibly unable to compete with the gekkonines, which he regarded as more derived. Indeed, he regarded it as being a basal gekkonnid, retaining oil droplets in the eyes and displaying vertebral amphicoely. In part, Underwood's (1954) assessment of this genus may have been influenced by the fact that he was, at the time, based in the West Indies and had more information about it than most other geckos, and certainly more than any that he also placed in the Dioplodactylinae. *Aristelliger* has been employed in a variety of evolutionary (Hecht 1952) and morphological (Ruibal and Ernst 1965) studies, probably because of ease of availability. These studies, however, have helped little to clarify the position of the taxon. Although it has rather complex external digital structure, anatomically it reveals a quite simple architecture. Thus more detailed studies of the digits (Russell 1976, 1979; Russell and Bauer 1990, 1993) have not assisted in placing it with other genera that typically show a more complex anatomy.

BIOGEOGRAPHIC AND EVOLUTIONARY IMPLICATIONS OF UNDERWOOD'S CLASSIFICATION OF THE GECKOS

Underwood (1954) pioneered a comprehensive approach to gecko systematics. As a result of this, he was faced with issues of biogeography and evolution that begged an explanation. For geckos, this was essentially uncharted territory and the recognition of clusters, especially within his Gekkoninae, generated new biogeographic and evolutionary problems. Chief among these was the need to explain the biogeography and evolution of his Diplodactylinae. This proved especially challenging because, as noted above, this cluster of taxa later proved to be the least stable of Underwood's (1954) proposed units.

Underwood (1954) interpreted eublepharids, with their scattered distribution, as an ancient radiation with its own specialisations, chiefly to arid conditions, rather than as a cluster of relicts. He viewed the eublepharids as the primary, ancient Northern Hemisphere radiation of the Gekkota.

The sphaerodactylids were biogeographically non-problematic as all occur in the New World. Underwood (1954) viewed them as an early New World offshoot of the Gekkota, based on his belief that they were primitively diurnal, retaining certain plesiomorphic lacertilian ophthalmological features. Kluge's (1967) demonstration that the sphaerodactyls are derived from within the gekkonines, and subsequent recognition of secondary diurnality in the sphaerodactylines (Röll, in press) has resulted in a reinterpretation of sphaerodactyl biogeography and evolutionary history, with north African affinities being supported by more recent systematic investigations (Arnold, 1993; Kluge, 1995).

Underwood (1954) undertook to explain the distribution of the Diplodactylinae which, in his view, included a large core of Australo-Pacific taxa, but also genera from Africa and the Americas. He noted that no genus occupied more than one continent and that most genera had rather limited or patchy distributions. Only *Aristelliger* and the New Zealand taxa did not co-occur with Gekkonines. He felt that ovoviviparity might explain their ability to survive in New Zealand. In the case of *Aristelliger*, he noted that its occurrence was basically complementary to that of gekkonines, and suggested that it may have formerly had a broader distribution but had subsequently withdrawn in the face of competition with gekkonine geckos. He viewed the gekkonines as a more modern, expanding group that was displacing diplodactylines from areas of previous occupancy. He regarded New Caledonia as marking the periphery of the range of the gekkonines, with *Lepidodactylus* and *Eurydactylodes* being relatively recent invaders into diplodactyline (*Rhacodactylus* and *Bavayia*) territory. He believed that *Phelsuma*, being chiefly insular, diurnal, and arboreal, was ecologically segregated from the gekkonines with which it co-occurs. He regarded its occurrence in mainland East Africa as a recent event. Its arrival on islands of the Indian Ocean was hypothesised to be as a nocturnal stock, an offshoot of the southern African cluster of diplodactylines, with a subsequent change in life style enabling it to coexist with gekkonines. He regarded most continental diplodactylines as being terrestrial, with arboreal forms being peripheral.

The foregoing rather tortuous scenario developed by Underwood (1954) to account for diplodactyline biogeography and evolution was the direct result of the recognition of, as it was formulated at the time, a polyphyletic assemblage. Removal of *Aristelliger, Phelsuma* and a variety of other taxa (see above) from the Diplodactylinae (Kluge, 1967) and inclusion of *Eurydactylodes* within it (Underwood, 1955) rendered biogeographic and evolutionary consideration of the remaining diplodactylids more tractable (Bauer, 1990a), but left the Gekkonidae (Underwood's Gekkoninae) yet more unwieldy. That some gekkonine genera were present on multiple continents suggested to Underwood (1954) that this was the dominant group. He recognised four major digital morphologies among gekkonines, and believed that each had reached most areas of the world and that most had radiated in situ in each area, giving rise to numerous regionally endemic genera. Thus, while expansion was an important theme in the evolution of gekkonines, there was significant within-region evolution as well. These ideas were obviously heavily influenced by those of Darlington (1948) and by the idea of competitive exclusion (a more ecological than historical view). He noted the waif dispersal capabilities of some geckos and opined that this complicated the picture of dispersal via land bridges that served as his main paradigm. The issue of waif dispersal, though recognised as being restricted to certain taxa, remains to this day as a confounding factor in the interpretation of the evolution of gekkonid spatial patterns.

Further systematic consideration (see above) has resulted in an increased complement of gekkonid genera, but has also resulted in some level of internal resolution, which, in turn, has influenced some aspects of biogeographic interpretation. For many regions, local radiations of monophyletic clusters of genera have been recognised, but resolution of pattern between these clusters remains poorly understood.

CONCLUSIONS

Underwood's (1954) systematic, biogeographic and evolutionary considerations of geckos marked the first attempt to comprehensively assess this circumglobal and highly diverse cluster. His analyses brought some degree of order to a previously very poorly understood set of problems, and his choice of ophthalmological characters as those of primary consideration resulted in the establishment of a basic pattern that has survived to the present in modified form. Although Underwood (1968, 1970, 1971b, 1977a ,b) revisited the gekkotan eye repeatedly, the promise of phylogenetic utility originally held out by ophthalmolgical data has not, until recently, been pursued. Röll (1995, 1997, 1999) and Röll and Schwemer (1999) have demonstrated that many diurnal geckos are unable to modify pupil shape and instead regulate light through absorbance by crystallins in the lens. Although Röll and Schwemer (1999) assumed that the use of particular crystallins was likely to have evolved only once, there is no evidence that all diurnal gekkonids are allied (e.g. *Phelsuma* + *Lygodactylus* and *Sphaerodactylus* + *Quedenfeltia* + *Narudasia* + *Saurodactylus*; Kluge and Nussbaum 1995). This avenue of approach, however, suggests that at the anatomical and molecular level, data from the visual system may yet be of significance in assisting in the resolution of pattern between nocturnal and secondarily diurnal clusters of gekkonids (including sphaerodactyls).

Despite attempts to move away from digital architecture as a primary means of identifying suprageneric clusters, this has continued to play a role and has been instrumental, by way of examination of internal architecture, in assisting in the circumscription of a number of apparently monophyletic assemblages (Russell, 1976). Pedal anatomy remains a primary determinant of generic allocation and a major clue to potential higher order relationships (e.g., Nussbaum and Raxworthy 1994).

Changes in generic alignment and more modern views of plate tectonics have necessitated a rethinking of Underwood's (1954) biogeographic hypotheses. Essentially the eublepharids appear to represent an ancient Laurasian radiation, in keeping with Underwood's (1954) ideas. The remaining gekkotans are now regarded as being of Gondwanan origin and to consist of an essentially east Gondwanan diplodactylid radiation and a west Gondwanan gekkonid radiation, with the latter having given rise, in turn, to the New World sphaerodactyls.

Interpretation of patterns of relationship must now deal with the recognition that the age of the Gekkota is much greater than was believed in 1954 and that many genera might be quite ancient. Hence, generic body plans may have been established for very long periods, making them rather discrete from one another and rendering it difficult to erect hypotheses of relationship. Even among the sphaerodacyls, generic differentiation is estimated to have occurred as much as 40 million years ago (Hass 1991). King (1987a, 1987b), on the basis of chromosomal and immunological data correlated with tectonic history of the Australian region, estimated a minimum divergence of 66 my between the two major clades of diplodactylines, and at least 120 my for the origin of the gekkotans.

Despite the magnitude of the problem, only patterns of relationship within the rather amorphous Gekkonidae (Underwood's Gekkoninae) remain relatively unassailed. Even here, however, large, circumglobal unwieldy genera have been broken into smaller, more geographically circumscribed taxa and there is now an opportunity to begin to make inroads into the determination of the patterns of interrelationship of suprageneric clusters of gekkonid taxa. This may best be broached by taking exemplars, appropriately selected (Bininda-Emonds *et al.* 1998) from the putative clusters and the enigmatic genera, and investigating a combination of morphological and molecular data. Given the magnitude of the problem, this will be an iterative process and will necessitate frequent cross-checking within and between clusters. The boldness of Garth Underwood's approach will have to be adopted in selecting novel sources of data to allow new approaches to be taken and insights to be revealed.

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