Are pygopods just legless geckos? Evidence from retinal structures

BEATE RÖLL & F. WILHELM HENKEL

Abstract

The retinae of pygopods contain two types of single visual cells (types A1 and A2), while the retinae of geckos conatin only one type of single visual cell (type A). On the other hand, pygopods lack a specialized type of visual cell (type C double visual cell), which is present in the retinae of all geckos. The visual system of geckos and its history is well understood, and the evolutionary course of aquisition and loss of retinal characters is discussed.

The case of the type C visual cell in particular clearly points to geckos and pygopods to have evolved independently from common ancestral stock. Therefore, we suggest to retain the 'traditional' arrangement of pygopods as sister group of all geckos and to regard pygopods as distinct family Pygopodidae next to geckos Gekkonidae.

Key words: Sauria: Gekkonidae, Pygopodidae; diplodactyline geckos; sister group; visual cells; double visual cell of type C.

Zusammenfassung

Sind Pygopoden tatsächlich beinlose Geckos? Auswertung von Retinastrukturen.

Aufgrund zahlreicher Synapomorphien wurden Geckos (Gekkonidae) und Pygopoden (Pygopodidae, Flossenfüße) als Schwestergruppen innerhalb der Gekkota angesehen. Die Gekkonidae wurden dabei in vier Unterfamilien unterteilt (Eublepharinae, Gekkoninae, Sphaerodactylinae, Diplodactylinae). Neuere systematische Gliederungsversuche der Geckos führten einerseits zur Höhergruppierung verschiedener Gecko-Taxa und andererseits zur Aufnahme der Pygopoden in die Gruppe der Geckos als monophyletisches Schwestertaxon der Diplodactylinae. Diese nicht allgemein akzeptierte systematische Einteilung basiert auf einem einzigen Merkmal, welches als Synapomorphie diplodactyline Geckos und Pygopoden kennzeichnen soll. Hierbei handelt es sich um die morphologische Ausprägung des Muskels, der den äußeren Gehörgang schließt. Sowohl bei diplodactylinen Geckos als auch bei Pygopoden wird er als O-förmig beschrieben, bei den meisten gekkoninen Geckos dagegen als L-förmig. Da aber sowohl Vorkommen als auch Form dieses Muskels sich bei Geckos als sehr variabel erweisen, erscheint die Plazierung der Pygopoden in die Gruppe der diplodactylinen Geckos nicht überzeugend.

Aus diesem Grund wird hier ein anderes Merkmalssystem zur Klärung der verwandtschaftlichen Beziehungen von Geckos und Pygopoden herangezogen: das visuelle System. Das visuelle System der Geckos und seine phylogenetische Entwicklung sind aufgrund elektronenmikroskopischer und biochemischer Arbeiten sehr gut bekannt; ausgehend von dieser Grundlage können Erwerb sowie Verlust von retinalen Kennzeichen während der Evolution diskutiert werden.

Die Retinae aller bisher untersuchten squamaten Echsen aus den verschiedensten Familien (ohne Gekkonidae) enthalten Einzelsehzellen, und zwar - soweit bekannt - zwei Typen (Typ A1 und Typ A2) sowie einen Typ einer Doppelsehzelle (Typ B). In den Retinae aller bisher untersuchten Geckos findet sich jedoch nur ein Typ von Einzelsehzelle (Typ A), dagegen zwei Typen von Doppelsehzellen (Typ B und Typ C). Die Doppelsehzelle vom Typ C kommt ausschließlich in den Retinae von Geckos vor und fehlt in den Retinae der Pygopoden. Die Retinae der Pygopoden enthalten Typen von Sehzellen (Einzelsehzellen der Typen A1 und A2, Doppelsehzelle vom Typ B), die denen anderer squamater Echsen entsprechen. Insbesondere das Fehlen der Doppelsehzelle vom Typ C in den Retinae der Pygopoden wird im Zusammenhang mit der Evolution der Nacht- und Tagaktivität der Geckos diskutiert. Es wird dargestellt, dass das Fehlen dieser Doppelsehzelle nicht als Apomorphie allein der Pygopoden angesehen werden kann, sondern dass Geckos und Pygopoden sich unabhängig voneinander aus einem

Salamandra, Rheinbach, 30.06.2002, **38**(2): 73-84.

gemeinsamen Vorfahren entwickelt haben müssen. Wir schlagen vor, die traditionelle Einordnung der Pygopoden (Pygopodidae) als Schwestergruppe aller Geckos (Gekkonidae) beizubehalten.

Schlagwörter: Sauria: Gekkonidae, Pygopodidae; diplodactyline Geckos; Schwestergruppen; Sehzellen; Doppelsehzelle vom Typ C.

Based on numerous synapomorphies, gekkonid and pygopodid lizards were usually treated as sister taxa Gekkonidae and Pygopodidae within the Gekkota (e. g. UNDERWOOD 1957, KLUGE 1967, MOFFAT 1973, RIEPPEL 1984) (Fig. 1a). Gekkonidae were further divided into subfamilies Eublepharinae, Gekkoninae, Sphaerodactylinae and Diplodactylinae, while Pygopodidae usually remained undivided.

More recently, KLUGE (1987) raised Eublepharinae to family level. Furthermore, he included pygopods in geckos, forming a monophyletic sister lineage to the subfamily Diplodactylinae only (Fig. 1b). The two superfamilies Eublepharoidea and Gekkonoidea form the microorder Gekkota (infraorder Gekkonomorpha).

However, the inclusion of pygopods within geckos has not been generally accepted (e. g. ESTES et al. 1988, SCHWENK 1988, COGGER 1992, SHEA 1993, KING and HORNER 1993, HUTCHINSON & DONNELLAN 1993, BAUER 1994). Some of the reasons for this reluctance are obvious. Geckos, occurring circumtropically on all continents and on most oceanic islands, always have well-developed limbs, and there is no tendency

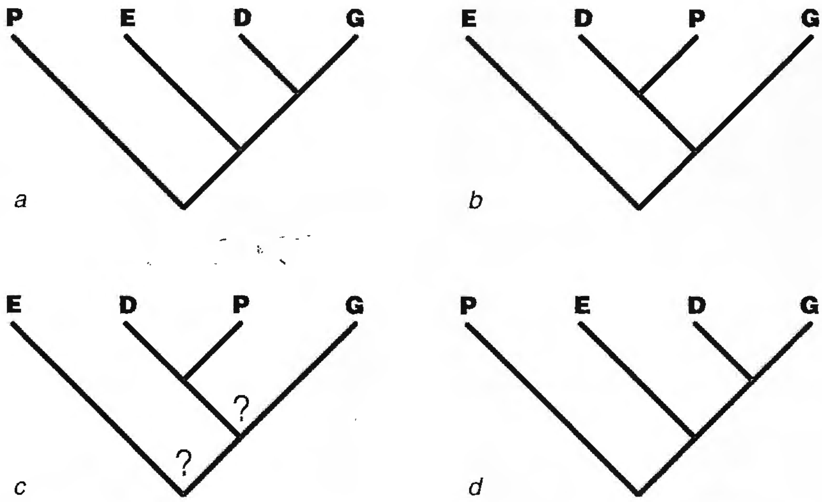


Fig. 1. Cladograms of four major groups of gekkotans. D = diplodactylines, E = eublepharines, G = gekkonines, P = pygopods. a) after UNDERWOOD 1954, 1957, KLUGE 1967; b) after KLUGE 1987; c) after ZUG et al. 2001; d) this paper.
N.B.: It should be kept in mind that the taxonomic rank of the taxa differs between authors. Nevertheless, the phylogenetic relations between them are comparable.

Kladogramme von vier wichtigen Gruppen der Gekkota. D = diplodactyline Geckos, E = eublepharine Geckos, G = gekkonine Geckos, P = Pygopoden. a) nach UNDERWOOD 1954, 1957, KLUGE 1967; b) nach KLUGE 1987; c) nach ZUG et al. 2001; d) diese Arbeit.
N.B.: Der taxonomische Rang der verschiedenen Gruppen ist bei den Autoren durchaus unterschiedlich. Die phylogenetischen Beziehungen sind jedoch vergleichbar.

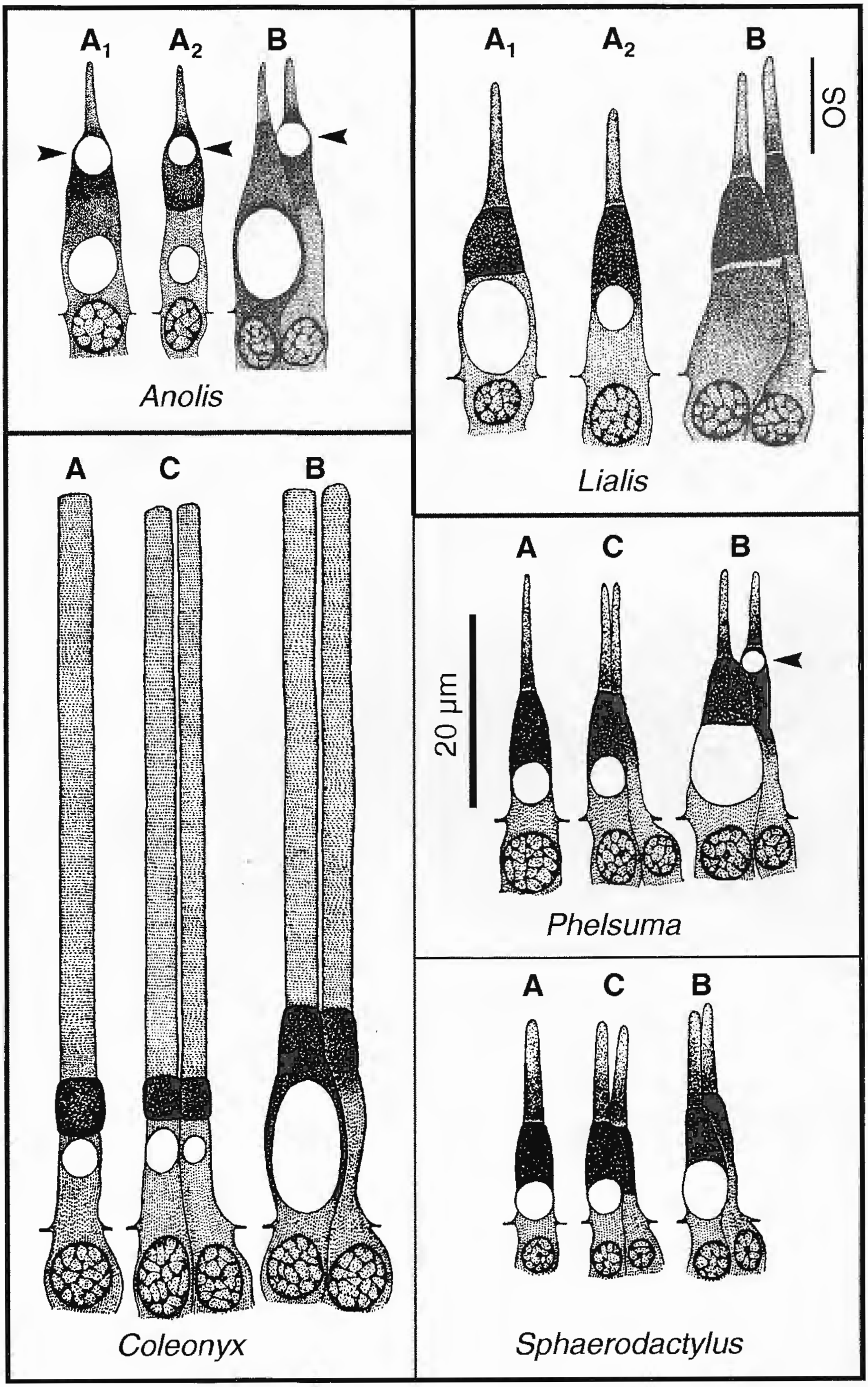
of their reduction in any clade (Fig. 2a). On the contrary, the toes of many geckos are the most specialized of all squamates as regards their specializations for adhesion to smooth surfaces.

Fig. 2. a) *Oedura coggeri* BUSTARD, 1966, a diplodactyline gecko occurring on Cape York Peninsula, Australia.

Oedura coggeri BUSTARD, 1966, ein diplodactyliner Gecko von der Halbinsel Cape York, Australien.

b) *Lialis burtonis* GRAY, 1835, a pygopodid lizard widely distributed in Australia and New Guinea.

Lialis burtonis GRAY, 1835, eine pygopodide Echse, die in Australien und Neuguinea weit verbreitet ist.


A1
A2
B
Anolis
A1
A2
B
OS
Lialis
A
C
B
Coleonyx
A
C
B
20 µm
Phelsuma
A
C
B
Sphaerodactylus

In contrast, the Pygopodidae, which are strictly confined to Australia and New Guinea, are virtually limbless: forelimbs are completely absent and hindlimbs are reduced to small flaps on each side of the vent, which gave rise to their vernacular names "flat-footed lizards" or "legless lizards" (Fig. 2b).

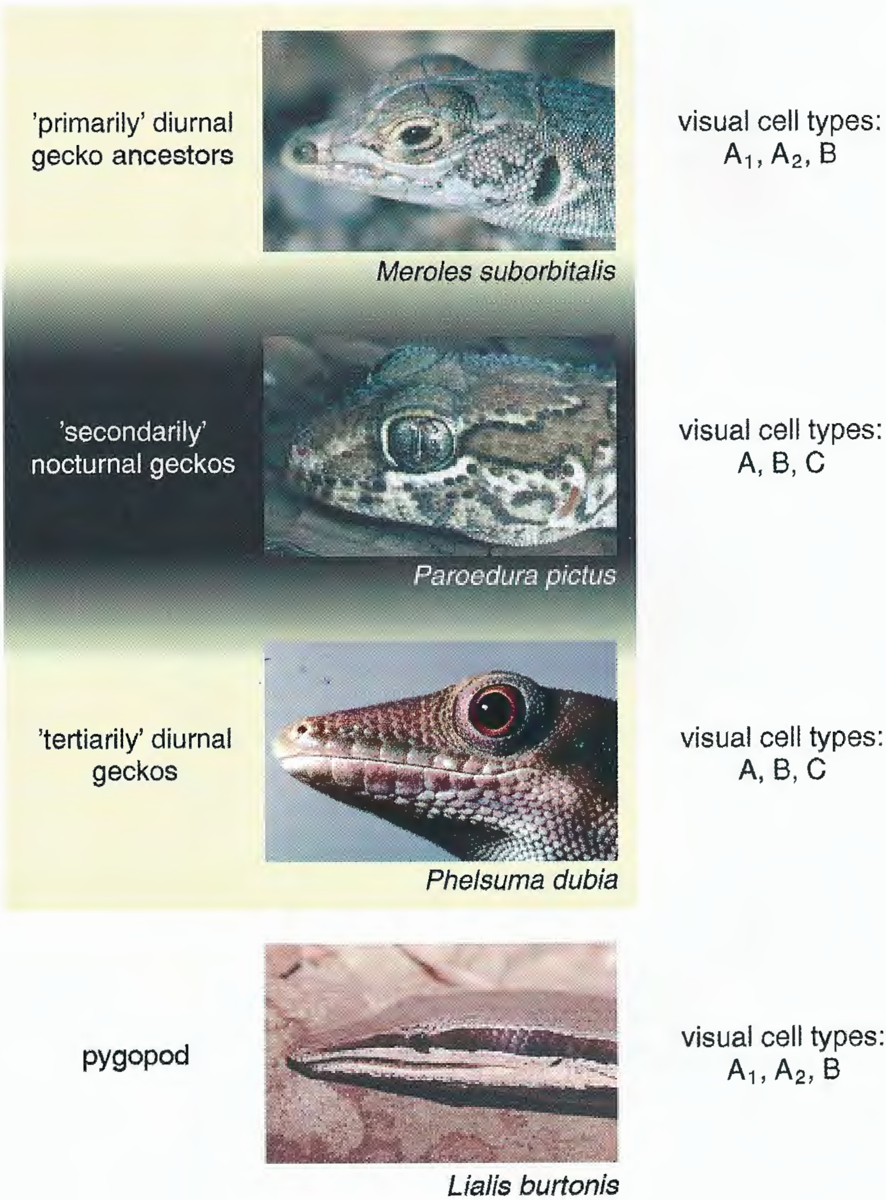
There is no overlap between the morphological and ecological "types" of geckos and pygopods. In an evolutionary context, the proposed relationship requires a complete reversal of the evolutionary locomotory trends within geckos from perfection of adhesive structures to almost complete loss of legs. Additionally, the latter would have to have taken place in a comparatively very short time (i. e., after separation of the Pygopodinae sensu KLUGE 1987 from the rest of diplodactyline geckos), while other geckos retained their various adhesive devices. The proposed nesting of pygopods next to diplodactyline geckos within the Gekkonidae therefore seems rather strange and certainly requires good evidence.

In fact, while KLUGE (1987) summarized many data from external and internal anatomy, physiology and behaviour, he placed pygopods as a sister lineage of

Fig. 3 (left page). Types of visual cells of several squamate retinae.
Iguanid lizard (*Anolis lineatopus*): Two types of single visual cells (types A1 and A2) and one type of double visual cell (type B). The single visual cells and the minor (smaller) members of the double visual cells contain yellow or – more rarely – colourless oil droplets.
Pygopodid lizard (*Lialis burtonis*): Two types of single visual cells (types A1 and A2) and one type of double visual cell (type B). All visual cells lack oil droplets.
Nocturnal gekkonid lizard (*Coleonyx variegatus*): One type of single visual cell (type A) and two types of double visual cells (types B and C). All visual cells lack oil droplets.
Diurnal gekkonid lizards (*Phelsuma cepediana*, *Sphaerodactylus argus*): One type of single visual cell (type A) and two types of double visual cells (types B and C). Oil droplets are usually lacking, e. g. in visual cells of *Sphaerodactylus*; they are present only in the minor members of type B double visual cells of a few genera, e. g. in the retina of *Phelsuma*.
OS: outer segment of the visual cell. Arrowheads indicate oil droplets located in front of the outer segments (note that light would enter the visual cells from the bottom of the page).
All figures adapted from CRESCITELLI 1972 and 1977 (after WALLS 1942 and UNDERWOOD 1957 1970). Scale bar (for all drawings): 20 µm.

linke Seite: Sehzell-Typen der Retinae einiger Squamaten.
Leguan (*Anolis lineatopus*): Zwei Typen von Einzelsehzellen (Typ A1 und A2) und ein Typ von Doppelsehzelle (Typ B). Die Einzelsehzellen und das schmalere Mitglied der Doppelsehzelle enthalten eine gelbe oder – seltener – eine farblose Ölkugel.
Pygopodide Echse (*Lialis burtonis*): Zwei Typen von Einzelsehzellen (Typ A1 und A2) und ein Typ von Doppelsehzelle (Typ B). Allen Sehzellen fehlen Ölkugeln.
Nachtaktiver Gecko (*Coleonyx variegatus*): Ein Typ von Einzelsehzelle (Typ A) und zwei Typen von Doppelsehzellen (Typ B und C). Allen Sehzellen fehlen Ölkugeln.
Tagaktive Geckos (*Phelsuma cepediana, Sphaerodactylus argus*): Ein Typ von Einzelsehzelle (Typ A) und zwei Typen von Doppelsehzellen (Typ B und C). Bei den meisten Gattungen fehlen den Sehzellen Ölkugeln, wie z. B. bei *Sphaerodactylus*. Nur bei einigen wenigen Gattungen, z. B. bei *Phelsuma*, enthalten die schmalen Mitglieder der Doppelsehzellen des Typs B farblose Ölkugeln.
OS: Außensegmente der Sehzellen. Die Pfeilköpfe weisen auf Ölkugeln, die im Lichtweg vor den Außensegmenten liegen (Licht würde die Sehzellen von unten erreichen). Maßstab (gilt für alle Einzelabbildungen): 20 µm.
Alle Abbildungen modifiziert aus CRESCITELLI 1972, 1977 (nach WALLS 1942 und UNDERWOOD 1970).

diplodactyline geckos solely on the basis of their shared possession of an O-shaped muscle closing the external auditory meatus. This meatal muscle occurs in two forms. The L-shaped form borders the posterior and ventral meatal margins, whereas the O-shaped form encircles the meatus completely or nearly so. The L-shaped form is considered plesiomorphic, as it resembles the supposedly primitive ventral position of the muscle. It is found in all eublepharines investigated and all gekkonines, except



a few diurnal genera where the meatal muscle is completely absent. The O-shaped form is assumed to represent the apomorphic condition. It characterizes diplodactyline geckos and pygopods.

However, very few if any pygopods apart from *Lialis burtonis* (Wever 1974, 1978) seem to have been examined in this context. Additionally, the O-shaped muscle of diplodactyline geckos seems to be quite variable; e. g. it entirely or nearly completely encircles the meatus in the ear of *Pseudothecadactylus* or *Hoplodactylus*, while it is more open, "C-shaped", in *Naultinus* (Kluge 1987). In *Carphodactylus laevis* the muscle seems to be confined to the posterior meatal margin. Similarly, the L-shaped form appears to vary even intraspecifically as has been shown for the ear of the gekkonine species *Cyrtopodion kotschyi* (Kluge 1987). As occurrence and form of the meatal muscle are far from constant in the species investigated, the inclusion of pygopods in diplodactyline geckos based on this single presumed synapomorphy seems not convincing.

A recent molecular study of partial sequences of a mitochondrial gene and of a nuclear oncogene (Donnellan et al. 1999) confirmed Kluge's arrangement: Two pygopod species clustered next to eight diplodactyline gecko species, while two gekkonine and one eublepharine species were grouped more distantly. However, as in parsimony studies the selection of taxa included is crucial (cf. Tyler et al. 1994, Lee 2001), this evidence is regarded here as preliminary.

There is, however, a character set that gives some definite information: the visual system. The eyes of geckos have received considerable attention (reviews in Walls 1942, Underwood 1970, Röll 2001a). In this context, the following parameters are of importance: the arrangement of the visual cells in the retina, the ocurrence or lack of oil droplets in the ellipsoids of the visual cells, the occurrence or lack of double visual cells of type C and the relative position of geckos and pygopods in the "transmutation" cycle (Walls 1942, Underwood 1970, Röll 2000a, b, 2001b, c).

The visual cells of reptiles may be arranged in a seemingly random manner or they may show a clear, well-ordered mosaic of cells. The latter is more obvious and

Fig. 4 (left page). Transmutation theory (Walls 1942) (adapted from Röll 2001c).
Geckos evolved from "primarily" diurnal lizard ancestors (here the extant *Meroles suborbitalis* for illustration). In "secondarily" nocturnal geckos the visual cells, which had been cones, are modified ("transmuted") to "rods" (actually rod-like cones) for night vision. In "tertiarily" diurnal geckos the visual cells are "transmuted" back to "normal" cones. There are no extant "primarily" diurnal geckos (see text). Pygopods do not fit among nocturnal or diurnal geckos, but have the visual cell set typical of "primarily" diurnal squamates.

linke Seite: Transmutationstheorie (Walls 1942) (verändert nach Röll 2001c).
Geckos evolvierten aus "primär" diurnalen Echsenvorfahren (hier die rezente *Meroles suborbitalis* zur Veranschaulichung). Bei "sekundär" nocturnalen Geckos sind die Sehzellen, ehemals Zapfen, zu "Stäbchen" (tatsächlich stäbchenartigen Zapfen) "transmutiert", um die Lichtempfindlichkeit zu erhöhen. Bei "tertiär" diurnalen Geckos sind die Sehzellen zu "normalen" Zapfen zurück-"transmutiert". Rezent gibt es keine "primär" diurnalen Geckos mehr (siehe Text). Pygopoden lassen sich in dieser Hinsicht weder bei nocturnalen noch bei diurnalen Geckos einfügen; sie besitzen den "Standard-Sehzellensatz" "primär" diurnaler Squamaten.

definitely rarer. It occurs in all geckos examined and in pygopods (Underwood 1970, Röll 2000b). However, it also occurs in *Anolis* (Iguanidae; Underwood 1970) and probably also in *Cryptoblepharus* (Scincidae; Röll, unpubl.). Apart from Reptilia, it also occurs in the eyes of many fishes, and its occurrence seems to be linked to sight hunting and motion detection (Engström 1963, Wagner 1978).

Oil droplets – highly refractive spherical organelles – occur in the retinae of most reptiles (and other vertebrates, except of mammals). They are often brightly coloured because of high concentrations of stored carotenoids and supposed to aid in some kind of colour vision. In geckos, their ultrastructure and their spectral characteristics have been examined recently (Röll 2000b), and their occurrence or lack has been discussed with respect to Walls' (1942) "transmutation theory" (Röll 2001a; see next paragraph). Pygopods do not possess oil droplets. They share this character with virtually all nocturnal geckos and many diurnal geckos living in or under leaf litter (e. g., *Sphaerodactylus*) or in rock crevices (e. g., *Narudasia, Rhoptropus*). However, as there is a clear tendency for loss of the colour of oil droplets or for the complete loss of oil droplets in secretive, crepuscular and nocturnal species of various reptile groups, this character cannot be used in this phylogenetic context.

Interest has, for several reasons, focused on the visual cells themselves. In squamates several types of them have been described (Fig. 3). In all retinae of squamates studied, there are single visual cells (type A) and double visual cells (type B). Where the retinae have been studied in greater detail, two subtypes of single visual cells have been found (A1 and A2), which differ markedly in size and in other characters. E. g., if there are oil droplets in the visual cells, A1 contains a coloured (usually yellow) oil droplet, while A2 contains a colourless one. Double visual cells of type B consist of two members of very unequal sizes, where the major member never contains an oil droplet.

This set of visual cell types (A1, A2 and B) is regarded as the plesiomorphic state. This assumption seems fair enough, although a direct proof of homology of the subtypes A1 and A2 in different families of squamates has not yet been attempted. Visual cells of type C are composed of two members of virtually identical sizes and are dealt with later.

The differences in the visual cells of nocturnal and diurnal geckos led Walls (1942) to erect his "transmutation theory" (Fig. 4). According to Walls, nocturnal geckos are supposed to have descended from primarily diurnal lizard ancestors whose visual cells had been cones. Thus, the "rods" of extant nocturnal geckos have "transmuted" from cones. Regarding nocturnality as a derived character, Walls designated geckos as "secondarily" nocturnal. Furthermore, he suggested that those gekkonid species that are now diurnal are derived from nocturnal gecko ancestors and therefore are "tertiarily" diurnal. Their visual cells have undergone a second "transmutation" from "rods" back to cones.

The visual cells of geckos have been re-examined ultrastructurally (Röll 2000a). While the visual cells of both nocturnal and diurnal species were shown to be in fact all cones modified for vision at high or low light intensities, Walls' "transmutation theory" was confirmed in other aspects. Most important here was the finding that there are no extant "primarily" diurnal geckos; all diurnal species are "tertiarily" diurnal (Röll 2001a, b, c).

In geckos, there is a specialized visual cell: the type C double visual cell (Fig. 3). Here, two visual cells of about equal sizes are combined to form a morphological, and presumably also functional, unit. While double visual cells with two very unequal members, the so-called type B, are widespread among the Squamata, type C is confined to geckos only and is considered as a synapomorphy of these lizards (Underwood 1970, Peterson 1991, Röll 2001a). It can be speculated that it must have some kind of advantage for nocturnal vision, perhaps by enhancing visual sensitivity by adding the effective photon-capturing cross sections of two photoreceptors. It is important to note that all diurnal geckos studied (about 22 species from nine genera including the diplodactyline genus *Naultinus*) retained type C double visual cells. Nocturnal as well as diurnal geckos are mainly sight hunters. As both groups heavily depend on their visual sense for foraging, there is no selective pressure to secondarily lose visual cell type C as long as it does not interfere with or perhaps even enhances vision in some way.

On the contrary, pygopods, which also rely on vision for prey capture, lack type C double visual cells. The composition of their visual cell types more closely resembles that of other diurnal lizards than that of geckos (Fig. 3). The retinae of pygopods contain two types of single visual cells (types A1 and A2) and type B double visual cells as do the retinae of "primarily" diurnal squamates. Kluge (1987) rejected the absence of the double visual of type C as a phylogenetical important character on the grounds that only two genera (*Lialis*, *Aprasia*) had been examined. He especially stressed that the visual cell status of *Delma* must be known. However, the visual cells of *Delma* were described as being similar to *Aprasia* confirming the lack of type C double visual cells in the retinae of pygopods (Underwood 1970, Crescitelli 1972).

As stated earlier, there are no extant "primarily" diurnal geckos (Röll 2001a). All diplodactyline geckos, except of the genus *Naultinus,* are "secondarily" nocturnal. Pygopods are largely diurnal, tending to crepuscular, and many species have a secretive or burrowing lifestyle (Cogger 1992, Zug et al. 2001). The question then is: are pygopods "tertiarily" diurnal, respectively "quarterily" crepuscular, or are they "primarily" diurnal, respectively "secondarily" crepuscular sensu Walls (1942)?

There are two possibilities (Fig. 5): First, if pygopods ever had type C double visual cells, they could have lost them after divergence from their nearest gecko relatives (Fig. 5b, d). This would be an apomorphy of pygopods, while all geckos would be plesiomorphic in this respect. However, as pointed out earlier, all diurnal geckos are "tertiarily" diurnal and have retained type C double visual cells. Therefore, there is obviously no selective pressure for removal of these cells; on the contrary, they may still be positively selected.

Alternatively, pygopods never had type C double visual cells (Fig. 5a, c). In this case, they are either "primarily" diurnal or have separated from gecko ancestral stock before invention of type C double visual cells. As they possess – in contrast to all

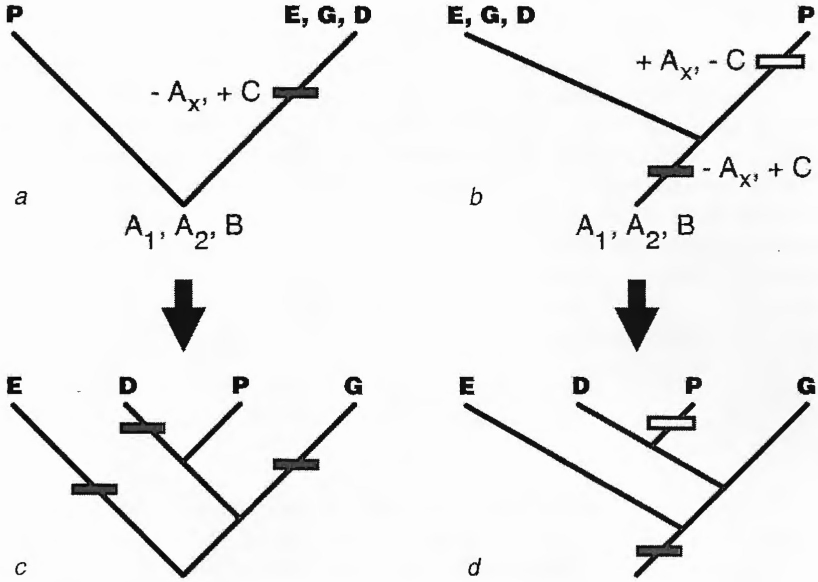


Fig. 5. Application of retinal structure dendrograms (a, b) to KLUGE's (1987) cladogram (c, d). D = diplodactylines, E = eublepharines, G = gekkonines, P = pygopods; A1, A2, B: standard set of squamate visual cells, -Ax+C: loss of one type of single visual cell, acquisition of double visual cell of type C, +Ax-C: re-acquisition of second type of single visual cell, loss of double visual cell of type C.
a, c) If pygopods alone retained the ancestral set of visual cell types, i. e. if the pygopods character is plesiomorphic, the loss of one type of single visual cell (Ax) and the acquisition of type C double visual cell would have to have occurred three times independently (black bars).
b, d) If the loss of one type of single visual cell (Ax) and the acquisition of type C double visual cell occurred early in gekkotan evolutionary history, it would be an apomorphy of pygopods to have reverted to the ancestral situation again (white bar). However, this would also be an highly unlikely assumption.
Instead, both possibilities are much more consistent with sister status of pygopods and (all) geckos (Fig. 1d).

Anwendung der Retinastruktur-Dendrogramme (a, b) auf KLUGES (1987) Kladogramm (c, d). D = diplodactyline Geckos, E = eublepharine Geckos, G = gekkonine Geckos, P = Pygopoden; A1, A2, B: Standardsatz der Sehzellen von Squamaten, -Ax+C: Verlust eines Typs von Einzelsehzelle, Erwerb der Doppelsehzelle vom Typ C, +Ax-C: Wieder-Erwerb des zweiten Typs von Einzelsehzelle, Verlust der Doppelsehzelle vom Typ C.
a, c) Falls Pygopoden den ursprünglichen Sehzell-Satz als plesiomorphes Merkmal beibehalten hätten, müsste der Verlust eines Typs von Einzelsehzelle (Ax) und der Erwerb der Doppelsehzelle vom Typ C drei Mal unabhängig eingetreten sein (schwarze Balken).
b, d) Falls der Verlust eines Typs von Einzelsehzelle (Ax) und der Erwerb der Doppelsehzelle vom Typ C bereits früh in der Evolution der Gekkota stattfanden, hätten die Pygopoden den ursprünglichen Zustand als Apomorphie wieder neu "erfunden" (weißer Balken). Auch dies ist jedoch eine sehr unwahrscheinliche Annahme.
Beide Möglichkeiten sind wesentlich besser damit vereinbar, Pygopoden und (alle) Geckos als Schwestergruppen zu betrachten (Fig. 1d).

geckos – two types of single visual cells, this alternative definitely seems more likely. However, it is irreconcilable with sister group status of pygopods to diplodactyline geckos only.

Especially the case of the type C double visual cell clearly points to geckos and pygopods to have evolved independently from common ancestral stock. Therefore, we suggest to retain the "traditional" arrangement of pygopods as sister group of all geckos. To minimize modification of the current taxonomic arrangement of these lizards as given in ZUG et al. (2001) (Fig. 1c), where all four taxa are treated as subfamilies, pygopods have to be regarded as distinct family Pygopodidae (one subfamily) next to geckos Gekkonidae (three subfamilies) (Fig. 1d).

References

BAUER, A.M. (1994): Familia Gekkonidae (Reptilia, Sauria). Part I. Australia and Oceania. – Das Tierreich, **109**, xiii + 306 pp.

COGGER, H.G. (1992): Reptiles and amphibians of Australia (fifth edition). – Chatswood (Reed International Books), 775 pp.

CRESCITELLI, F. (1972): The visual cells and the visual pigments of the vertebrate eye. – pp. 245-363 in: H.J.A. DARTNALL (ed.): Handbook of Sensory Physiology, Vol. VII/I. – Heidelberg (Springer-Verlag).

— (1977): The visual pigments of geckos and other vertebrates: an essay in comparative biology. – pp. 391-449 in: F. CRESCITELLI (ed.): Handbook of Sensory Physiology, VII/5. – Heidelberg etc. (Springer-Verlag).

DONNELLAN, S.C., M.N. HUTCHINSON & K.M. SAINT (1999): Molecular evidence for the phylogeny of Australian gekkonid lizards. – Biol. J. Linn. Soc., **67**: 97-118.

ENGSTRÖM, K. (1963): Structure, organization and ultrastructure of the visual cells in the teleost family Labridae. – Acta Zool., **44**: 1-41.

ESTES, R., K. DE QUEIROZ & J. GAUTHIER (1988): Phylogenetic relationships within Squamata. – pp. 119-281 in: ESTES, R. & G. PREGILL (eds.): Phylogenetic relationship of the lizard families. – Palo Alto (Stanford University Press).

HUTCHINSON, M.N. & S.C. DONNELLAN (1993): Biogeography and phylogeny of the Squamata. – pp. 210-220 in: GLASBY, C.J., B.J.B. ROSS & P.L. BEESLEY (eds.): Fauna of Australia, Vol. 2A. – Canberra (Australian Government Publishing Service).

KING, M. & P. HORNER (1993): Family Gekkonidae. – pp. 221-233 in: GLASBY, C.J., B.J.B. ROSS & P.L. BEESLEY (eds.): Fauna of Australia, Vol. 2A. – Canberra (Australian Government Publishing Service).

KLUGE, A.G. (1967): Higher taxonomic categories of gekkonid lizards and their evolution. – Bull. Am. Mus. Nat. Hist., **135**: 1-59.

— (1987): Cladistic relationships in the Gekkonoidea (Squamata, Sauria). – Misc. Pub. Mus. Zool., **173**: 1-54.

LEE, M.S.Y. (2001): Molecules, morphology, and the monophyly of diapsid reptiles. – Contrib. Zool., **70**: 1-22.

MOFFAT, L.A. (1973): The concept of primitiveness and its bearing on the phylogenetic classification of the Gekkota. – Proc. Linn. Soc. New South Wales, **97**: 275-301.

PETERSON, E.H. (1991): Retinal structure. – pp. 1-135 in: GANS, C.C. (ed.): Biology of the Reptilia, Vol. 17. – London (University of Chicago Press).

RIEPPEL, O. (1984): The structure of the skull and jaw adductor musculature in the Gekkota, with comments on the phylogenetic relationships of the Xantusiidae (Reptilia: Lacertilia). – Zool. J. Linn. Soc., **82**: 291-318.

Röll, B. (2000a): Gecko vision – visual cells, evolution, and ecological constraints. – J. Neurocytol., **29**: 471-484.

— (2000b): Characterization of retinal oil droplets in diurnal geckos (Reptilia, Gekkonidae). – J. Exp. Zool., **287**: 467-476.

— (2001a): Multiple origin of diurnality in geckos – evidence from eye lens crystallins. – Naturwissenschaften, **88**: 293-296.

— (2001b): Gecko vision – retinal organization, foveae and implications for binocular vision. – Vision Res., **41**: 2043-2056.

— (2001c): Visuelle Ökologie des Reptilienauges am Beispiel der Echsenfamilie der Geckos (Reptilia: Gekkonidae). – Habilitation thesis, Bochum, 75 pp.

Schwenk, K. (1988): Comparative morphology of the lepidosaur tongue and its relevance to the squamate phylogeny. – pp. 571-598 in: Estes, R. & G. Pregill (eds.): Phylogenetic relationship of the lizard families. – Palo Alto (Stanford University Press).

Shea, G.M. (1993): Family Pygopodidae. – pp. 234-239 in: Glasby, C.J., B.J.B. Ross & P.L. Beesley (eds.): Fauna of Australia, Vol. 2A. – Canberra (Australian Government Publishing Service).

Tyler, H.A, K.S. Brown & K.H. Wilson (1994): Swallowtail butterflies of the Americas. – Gainesville (Scientific Publishers), 376 pp.

Underwood, G. (1957): On lizards of the family Pygopodidae. – J. Morph., **100**: 207-268.

— (1970): The eye. – pp. 1-97 in: Gans, C. (ed.): Biology of the Reptilia, Vol. 2. - New York (Academic Press).

Wagner, H.-J. (1978): Cell types and connectivity patterns in mosaic retinas. – Adv. Anat. Embryol. Cell Biol., **55**: 1-81.

Walls, G.L. (1942): The Vertebrate Eye and its Adaptive Radiation. – Bloomfield Hills (Cranbrook Institute of Science), 785 pp.

Wever, E.G. (1974): The ear of *Lialis burtonis* (Sauria: Pygopodidae); its structure and function. – Copeia, **1974**(2): 297-305.

Manuscript received: 2. Februar 2002

Authors: Beate Röll, Lehrstuhl für Allgemeine Zoologie und Neurobiologie, Fakultät für Biologie, Ruhr-Universität Bochum, D-44780 Bochum; F. Wilhelm Henkel, Alfred-Döblin-Straße 80, D-59192 Bergkamen.