

THE RELATIONSHIP OF *BROOKESIA*, *RHAMPHOLEON* AND *CHAMAELEO* (*CHAMAELEONIDAE*, *REPTILIA*)

by

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ABSTRACT

Comparing the species of *Brookesia* and *Rhampholeon* with *Chamaeleo* it is concluded that *Brookesia* + *Rhampholeon* form a monophyletic group, arising from a branch of *Chamaeleo*, probably most related to the group around *Chamaeleo nasutus*. The separation between *Rhampholeon* and *Brookesia* is confirmed.

RÉSUMÉ

En comparant les espèces de *Brookesia* et de *Rhampholeon* avec *Chamaeleo*, on arrive à la conclusion que *Brookesia* + *Rhampholeon* constituent un groupe monophylétique, descendant d'une branche de *Chamaeleo*, probablement ayant des affinités accentuées avec le groupe autour de *Ch. nasutus*. La séparation de *Rhampholeon* et de *Brookesia* a été confirmée.

INTRODUCTION

The systematic position of the pygmy chameleons has been uncertain for more than a century. Although the genus *Brookesia* was described by Gray in 1864 and *Rhampholeon* in 1874 by Günther, several species that belong unmistakably to the pygmy chameleons were described later as belonging to *Chamaeleo*. For instance, in 1911 Werner regarded *temporalis* (Matschie) as a *Chamaeleo*. Even in Mertens' list of 1966 one of the pygmy chameleons (*marshalli* Boulenger) was included in *Chamaeleo*. A number of other genera will not be considered in this paper for reasons given by Klaver (1979).

Klaver (1979 and 1981) gives an excellent survey of the various opinions — sometimes of the same author in subsequent years — on the different genera that were proposed and after some time considered to be synonyms. Indeed,

Klaver himself provides an example of the changeable opinions inspired by these little lizards.

In 1979 he considered *Brookesia* s.l. to be derived from "a fully arboreal *Chamaeleo*-like ancestor". In 1981 he still considers *Brookesia* s.l. descendant of "a fully arboreal form" which, because of the "true chameleon feet" and other details (eyes, tongue), might be called at least *Chamaeleo*-like. Although the lungs of *Brookesia* s.l. are simpler than those of *Chamaeleo* this seems at first sight no problem; "This reversed evolutionary trend (viz. the return from arboreal life to ground dwelling) may also furnish an explanation for the simple lung structure of the *Brookesia* species". According to Klaver (1981) this secondarily simple lung structure includes only the reduction and, in most species, even the loss of the diverticula. However, one single character, the absence of lung septation, leads Klaver to the opposite conclusion: "I do not think that *Brookesia* lungs lost their septation secondarily, because there does not seem to be a correlation between septation and body form as in the case of diverticula".

Klaver's opinion of 1981 is best expressed in his diagram of a hypothesized phylogeny of chameleons based on lung septation (fig. 1). In that scheme *Brookesia* s.l. is closer to the original *Chamaeleonidae* than all the branches of *Chamaeleo*.

In this paper I want to discuss the following questions:

1. Is *Brookesia* s.l. more primitive than *Chamaeleo*, as Klaver (1981) suggested, or did *Brookesia* originate from a branch or branches of

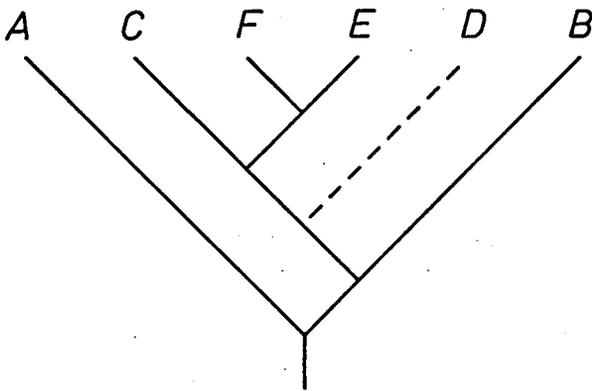


Fig. 1. Schema of hypothesized phylogeny of chameleons, based on lung septation. B, C, D, E and F represent groups of *Chamaeleo*, A is *Brookesia* (and *Rhampholeon*). After Klaver (1981).

Chamaeleo? In other words is *Brookesia* older or younger than *Chamaeleo*?

2. Is *Brookesia* s.l. (including all pygmy chameleons, *Rhampholeon* etc.) a monophyletic group?

3. How valid is the separation of *Brookesia* (Madagascar) and *Rhampholeon* (Africa)?

MATERIAL

All African species and all but four of the Madagascan species were examined. As far as possible I analyzed the four missing Madagascan species from literature. The following species are considered: *Rhampholeon brachyurus* Günther, 1892, *Rh. brevicaudatus* (Matschie, 1892), *Rh. kersteni* (Peters, 1866), *Rh. marshalli* Boulenger, 1906, *Rh. nchisiensis* (Loveridge, 1953), *Rh. platyceps* Günther, 1882, *Rh. spectrum* (Buchholz, 1874), *Rh. temporalis* (Matschie, 1892), *Brookesia antoetrae* Brygoo & Domergue, 1971, *Br. betschi* Brygoo, Blanc & Domergue, 1974, *Br. bonisi* Ramanantsoa, 1979, *Br. decaryi* Angel, 1938, *Br. dentata* Mocquard, 1900, *Br. ebenauai* (Boettger, 1880), *Br. griveaudi* Brygoo, Blanc & Domergue, 1974, *Br. karchei* Brygoo, Blanc & Domergue, 1970, *Br. lambertoni* Brygoo & Domergue, 1969, *Br. legendrei* Ramanantsoa, 1979, *Br. minima* Boettger, 1893, *Br. nasus* Boulenger, 1887, *Br. perarmata* (Angel, 1933), *Br. peyeri* Brygoo & Domergue, 1975, *Br. ramanantsoai* Brygoo & Domergue, 1975, *Br. stumpffi* Boettger, 1894, *Br. superciliosus* (Kuhl, 1820), *Br. therezieni* Brygoo & Domergue, 1970, *Br. thieli* Brygoo & Domergue, 1960, *Br. tuberculata* Mocquard, 1894, and *Br. vadoni* Brygoo & Domergue, 1968.

RESULTS

I took note of the following characters (see table I):

1. Length of head + body: from tip of snout to foremost border of the vent.
2. Length of tail: from the foremost border of the vent to tip of tail. Tail index expressed in percentage of the length of head + body.
3. Length of mouth cleft: from tip of snout to corner of mouth, index expressed in percentage of the length of head + body.
4. Width of mouth: measured at the corner of the mouth, index expressed in percentage of the length of mouth.
5. Height of head: measured in a vertical line at the corner of the mouth, from the underside of the jaws to the surface of the skull (see fig. 2), index expressed in percentage of the length of mouth.
6. Temporal crest: in accordance with Werner's (1911) use of this term in *Chamaeleo* I regard as temporal crest the one that "traverses the mid-lateral temporal region from the middle of the posterior border of the orbit horizontally to the posterior border of the skull" (Raw, 1976).

Klaver (1981) in his comment on the description of *Chamaeleo intermedius* Hillenius, 1978, made objections to my use of this term, as the homology of this character is uncertain. I will return to this problem more extensively elsewhere, but it may be stated here that the temporal crest in *Rhampholeon* is most probably homologous with the temporal crest in at least *Chamaeleo pumilus* s.l. and *Ch. tigris* since, in all these cases, the crest is based on the lateral ridges of the postorbital and the squamosal bones (see Engelbrecht, 1951; Frank, 1951; Siebenrock, 1893).

In *Brookesia* (the Madagascan species) the situation is more complicated. The fused postorbital and squamosal bones are rather broad (see Siebenrock, 1893), probably the temporal crest is based on the lower ridge of these bones (see fig. 2 and the next section).

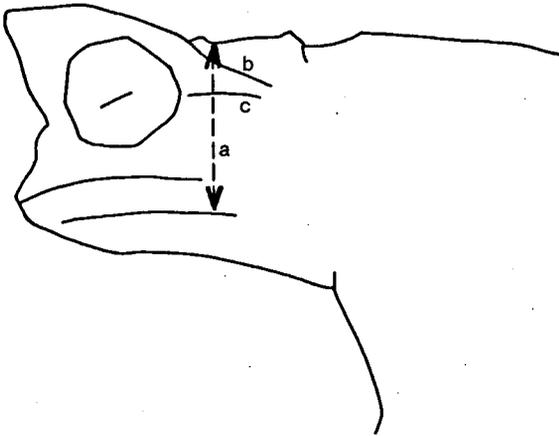


Fig. 2. Height of head measured in a vertical line at the corner of the mouth between the underside of the lower jaw and the surface of the skull (a); b, lateral crest; c, temporal crest. (Drawing Miss N. Pruim.)

7. Lateral crest: the continuation of the orbital crest backwards (see fig. 2). Werner (1911) calls this character in *Brookesia stumpffi* "Occipitalkante". Comparison with the skull of *Brookesia superciliaris* in the Paris Museum (see also Siebenrock, 1893) made it clear that the lateral crest coincides with the upper border of the fused postorbital and squamosal bones.

8. Parietal crest: in the mid-line of the broad parietal.

9. Form of the broad parietal: trigonal or trapezoid (see fig. 3).

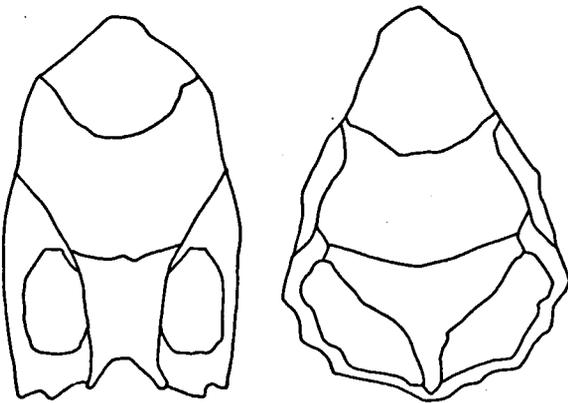


Fig. 3. Parietals, left: trapezoid in *Brookesia* (schematized after Siebenrock, 1893), right: trigonal in *Rhampholeon* (schematized after Frank, 1951). (Drawing Miss N. Pruim.)

10. Interorbital crest: from one orbital crest to the other, in front of the eyes, often accentuated on those crests with pointed excrescences.

11. Axillary pits: little pockets in the axillary region.

12. Inguinal pits: little pockets in the inguinal region.

13. Flexible excrescence on the tip of the snout.

14. Gular cones or 'tufts'; Loveridge, 1942: "beard-like 'tuft' of scales forming a flexible process on the chin".

15. Gular cones in a double row.

16. Form of the scales. In most pygmy chameleons I found scales with deeply indented borders (in table I indicated by 2, see figs. 4 to 7); sometimes the scales were polygonal (indicated by 1).

17. Lateral series of pointed excrescences or larger scales on the body. Parker (1942) described strong spines projecting laterally from the prezygapophysis of the dorsal vertebrae 3 to 9 and penetrating the skin. I do not doubt that most or all of the above-mentioned pointed excrescences are to be regarded as Parker's transverse processes, but indeed — as Klaver (1979) remarked — we do not know the skeleton of all *Brookesia* species, so I limit this character to its external manifestations.

18. Lung diverticula (after Klaver, 1979).

19. Lung septation (after Klaver, 1979).

20. Bicuspid claws.

21. Single spines at the base of the claws.

Werner (1911) called these "second claws".

22. Spiny cones on the soles of hands and feet.

In table II the average indices and the presence or absence of certain characters are compared in the African dwarf chameleons, the Madagascan dwarf chameleons, African *Chamaeleo* minus the representatives of the *nasutus*-group, Madagascan *Chamaeleo* minus the representatives of the *nasutus*-group and the group around *Ch. nasutus*, including *Ch. nasutus* (Duméril & Bibron), *Ch. fallax* (Mocquard), *Ch. gallus* (Günther), *Ch. linotus* (Müller), *Ch. boett-*

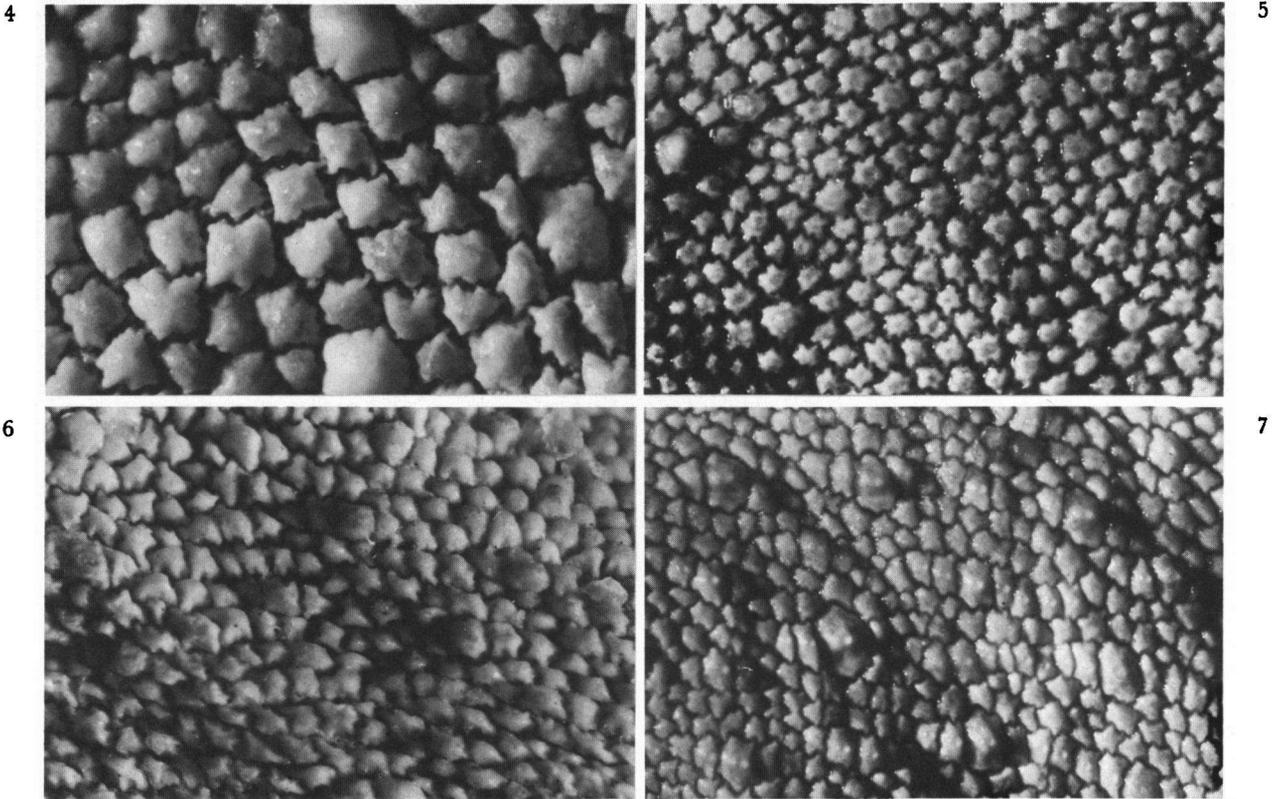


Fig. 4. Squamation of *Rhampholeon marshalli*.

Fig. 5. Squamation of *Rhampholeon spectrum*.

Fig. 6. Squamation of *Rhampholeon kersteni*.

Fig. 7. Squamation of *Brookesia stumpffi*. (Photographs by L. A. van der Laan, ZMA.)

geri (Boulenger), *Ch. guibei* Hillenius, *Ch. spinosus* (Matschie) and *Ch. tenuis* (Matschie).

The latter group was taken as a separate unit because of Klaver's remark (1979) that *Brookesia* s.l. has more characters in common with the group around *Ch. nasutus* than with any other group of chameleons. The measurements of head + body and the tail indices of *Chamaeleo* are computed from literature (Werner, 1911; Brygoo, 1971, 1978; De Witte, 1965). To get at least an indication of the indices of the length of mouth, the width of mouth, and the height of head, I took *Ch. chamaeleo* (Linnaeus) ♂ ZMA 14719 as an example for African *Chamaeleo*, *Ch. oustaleti* (Mocquard) ♂ ZMA 14302 for the Madagascan *Chamaeleo*, and *Ch. fallax* ♀ ZMA 15339 as a representative of the group around *Ch. nasutus*.

DISCUSSION AND CONCLUSIONS

1. Did *Brookesia* s.l. originate from a branch or branches of *Chamaeleo* or was it the reverse?

Table II shows that *Brookesia* s.l. and *Chamaeleo*, though not all species of these groups, have a number of characters in common: temporal crest, lateral crest (on the homology of these crests I hope to comment later on), a single parietal crest, a flexible rostral appendage, axillary pits, inguinal pits, gular cones in double rows, lung diverticula. These characters confirm the close relationship of *Chamaeleo* and *Brookesia* s.l., but do not indicate which group is the source of the other.

More important in this context are the characters which are not mentioned in table II because they are well known to belong to the

TABLE II

Comparison of *Rhampholeon*, *Brookesia*, African *Chamaeleo* (minus the species of the group around *Ch. nasutus*), Madagascan *Chamaeleo* (minus the species of the group around *Ch. nasutus*) and *Chamaeleo nasutus* c.s. For length of mouth, width of mouth, and height of head of the African chameleons *Ch. chamaeleo* is chosen as representative, of the Madagascan chameleons *Ch. oustaleti*, and of the group around *Ch. nasutus*, *Ch. fallax* is chosen. Squamation: 3 = not indented, not polygonal, like in *Chamaeleo*. Form parietal: 3 = narrow, as in *Ch. chamaeleo*, 4 = broad, as in *Ch. pumilus*. Other terms see table I.

	AFRICA (<i>Rhampholeon</i>)			MADAGASCAR (<i>Brookesia</i>)			AFRICA (<i>Chamaeleo</i>)			MADAGASCAR (<i>Chamaeleo</i>)			<i>Ch. nasutus</i> c.s.		
	av.	SD	n	av.	SD	n	av.	SD	n	av.	SD	n	av.	SD	n
head + body ♂	44	9.7	8	38	14.0	19	111	47	46	142	70	28	54	17	8
♀	54	8.5	8	43	12.4	17	117	53	37	107	50	26	53	8.3	6
tail index ♂	42	14.1	8	72	11.6	19	110	21.0	46	119	14.3	28	101	18.4	8
♀	36	13.0	8	64	10.9	17	100	22.1	37	104	18	26	102	6.5	6
mouth length index	19.3	2.5	8	18.4	2.8	17	24.8			18.5			19.2		
mouth width index	73.5	8.8	8	92.5	9.2	17	66.7			70.2			68.8		
head height index	81	7.3	8	93.7	9.0	17	114			130			82.3		
height : width	112	17.0	8	102	10.7	17	171			185			120		
temporal crest	1			1-0			1-0			1-0			1-0		
lateral crest	0			1-0			1-0			1-0			1		
parietal crest	1			0			1-0			1-0			1-0		
form parietal	2			1			3-4			4			?		
interorbital crest	1			1			0			0			0		
axillary pit	1-0			0			0			1-0			1-0		
inguinal pit	1-0			0			0			0			1-0		
rostral excrescence	1-0			0			0			0			1-0		
double gular crest	1-0			1-0			1-0			1-0			0		
squamation	2			1-2			3			3			3		
vertebral processus	0			1(0)			0			0			0		
lung diverticula	1-0			0			1-0			1-0			1-0		
lung alveoles/septa	1-0			1-0			2			2			2		
bicuspid claws	1-0			0(1)			0			0			0		
second claws	1-0			0			0			0			0		
spinose soles	1-0			1(0)			0			0			0		

common heritage of all Chamaeleonidae: the pincer shaped hands and feet, the independently movable eyes, the eyelids fused but for a small opening in front of the pupil, the projectile tongue, the prehensile tail (in most *Brookesia* s.l. too short to be effective, but even here one observes attempts to grip twigs or grass stems). It seems probable that these are arboreal adaptations which are retained in the secondarily ground-dwelling *Brookesia* s.l., most notably the highly modified hands and feet. The tail of *Brookesia*, more or less prehensile but too short to be of much use, is clearly derived from the functional *Chamaeleo* tail.

Other characters of which the derived status is clear are "the absence of Jacobson's organ, accessory transverse processes of the dorsal

vertebrae, pineal foramen situated in the frontal or absent, etc." (Klaver, 1981) and the low number of ribs. In table III I list numbers of ribs, as mentioned in the literature or observed personally in skeletons, in whole animals that have been opened or in X-ray photographs. The latter two sources are less accurate as the number of shorter ribs in the lumbar region is difficult to discern. It is clear that the number of ribs in *Brookesia* and in *Rhampholeon* is lower than in any species of *Chamaeleo*.

Methuen & Hewitt (1914) remark on this: "The smaller numbers most probably represent the more primitive conditions". But they do not give justification for this opinion. Most probably the smaller numbers are derived. In *Amblyrhynchus* (Iguanidae) I counted 19 ribs on

TABLE III

The number of ribs as found in literature (authors) or by myself on skeleton (s), in opened bodies (b) or on X-ray photographs (X). The two latter numbers are less accurate as the number of shorter ribs in the lumbar region is difficult to discern.

<i>Br. superciliaris</i>	11 (s)
<i>Br. stumpffi</i>	9 (Werner, 1911), 11 (X)
<i>Rh. spectrum</i>	12 (Werner, 1911), 12 (s)
<i>Rh. marshalli</i>	12 (X)
<i>Rh. temporalis</i>	12 (X)
<i>Ch. lateralis</i>	14 (b)
<i>Ch. oustaleti</i>	18 (X)
<i>Ch. verrucosus</i>	17 (X)
<i>Ch. chamaeleon</i>	16, 17 (s)
<i>Ch. jacksoni</i>	15 (X)
<i>Ch. bifidus</i>	16 (X)
<i>Ch. fischeri</i>	16, 17 (b)
<i>Ch. goetzei</i>	15 (X)
<i>Ch. fuelleborni</i>	14 (X)
<i>Ch. melleri</i>	17 (X)
<i>Ch. cristatus</i>	15 (X)
<i>Ch. johnstoni</i>	16 (b)
<i>Ch. pardalis</i>	16 (X)
<i>Ch. brevicornis</i>	14 (X)
<i>Ch. elliotti</i>	15 (s)
<i>Ch. pumilus</i>	14 (Methuen & Hewitt, 1914)
<i>Ch. dilepis (quilensis)</i>	16, 17 (Methuen & Hewitt, 1914)
<i>Ch. gastrotaenia</i>	13 (Methuen & Hewitt, 1914)
<i>Ch. nasutus</i>	13 (Methuen & Hewitt, 1914)

a skeleton and in *Amphibolurus* (Agamidae) 20. In Romer (1956) it is stated that the number of ribs in Squamata generally runs from 15 to 20. The number of ribs in *Chamaeleo* are closer to the general number in Squamata. It seems therefore that the low numbers in *Brookesia* and *Rhampholeon* must be derived.

Klaver (1981) mentions two character states in *Brookesia* s.l. which he considers plesiomorphic compared with the states in *Chamaeleo*: the broadened flat parietal and the lack of septa in the lungs. Consequently we have to assume that the ancestral chameleon looked like recent *Chamaeleo* but for the lack of septa in the lungs (which occur in all recent *Chamaeleo*) and the broad parietal (which occurs, in a different form, only in *Ch. pumilus* s.l.). The septal development and the narrowing of the parietal

would then have arisen in *Chamaeleo* only after *Brookesia* s.l. had split off.

In the Agamidae, one of the families most closely related to the Chamaeleonidae, we find: "The parietal consists of a flat, square to trapezoidal, anterior portion which roofs the cranial vault" (Moody, 1980). But in the Iguanidae, the other closely related family, both narrow and broad parietals are represented. Romer (1956) writes: "The parietal, often a broad plate, may be narrowed to a varied degree, sometimes — as in the iguanid *Conolophus* — developing a median sagittal crest". If there are no strong reasons for assuming monophyly for the character state narrow parietal, we might as well assume the possibility of reverse development. More important seems to me the state of the parietal in *Sphenodon punctatus*. The Rhynchocephalia are generally regarded as the sister group of the Squamata. The parietal in *Sphenodon* is quite narrow and Romer (1956) states: "modern *Sphenodon* appears to be of a persistently primitive type in most regards and may be considered as characteristic of the order".

As to the lung septation I do not understand why on this character alone — neglecting all the other characters mentioned above — we have to decide that *Brookesia* s.l. is the older group from which recent *Chamaeleo* stems. In the smaller species of *Chamaeleo* we observe a decrease in the number of septa (see *Ch. spinosus*, *Ch. guibei*, and *Ch. fallax*). It is striking that the lungs of *Ch. tenuis*, the largest representative of the *nasutus*-group, show a much more elaborate septation than the smaller species.

In 1979 Klaver was reminded by the enlarged alveolar walls found in the lungs of various *Brookesia* s.l. species of the small septa found in e.g. *Ch. fallax* and *Ch. guibei*. He writes: "The results of my studies on chameleon-lungs more or less support this view [Beddard's view "that the simplicity in lung-structure correlates with the small size of the animals"], as few or no diverticula and few or no septa are found in small to intermediate species. Theoretically this might have been expected, as small-sized animals have a relatively

large lung-surface area and probably can do without structures that increase the surface area further, such as septa.”

Klaver (1981) does not give reasons why his arguments of 1979 are not longer valid. So my conclusion is that *Brookesia* s.l. developed out of one or more branches of *Chamaeleo* and is therefore younger than *Chamaeleo*.

2. Is *Brookesia* s.l. monophyletic?

From table II we can see that a few characters which occur in all species of *Brookesia* s.l. are not known in *Chamaeleo*. These include the broad, flat parietal, quite different in form from the broad parietal of *Ch. pumilus*; the interorbital crest (absence or poor development in *Rh. brachyura* is probably secondary); the indented scales (the polygonal scales in *Br. decaryi* and *Br. ebenau* are probably derived from these, as *Br. thieli*, *Br. tuberculata* and *Br. vadoni* possess both polygonal and indented scales).

A number of characters occurs in some species of dwarf chameleons, both African (*Rhampholeon*) and Madagascar (*Brookesia* s.s.), but are unknown in *Chamaeleo*. Among these are bicuspid claws and spinose scales on the soles of hands and feet, and the great difference in average tail indices. It is true, as Klaver (1979) states, that a few chameleons have shorter tails than some *Brookesia*, but the overall difference is clear.

Brygoo (1971) mentions a particular kind of behaviour he observed in *Brookesia superciliaris*, *Br. thieli* and *Br. vadoni*: “une certaine vibration perceptible au toucher mais pratiquement inaudible. Cette vibration n’a jamais été constatée avec des *Chamaeleo*”. I observed this same vibration in *Rhampholeon kersteni*.

I conclude that the characters that differentiate *Brookesia* s.l. from *Chamaeleo* are autapomorphies and thus *Brookesia* s.l. has to be regarded as a monophyletic group.

3. Is the separation of *Brookesia* (Madagascar) and *Rhampholeon* (Africa) valid?

In table II we see that there are only a few characters that consistently differentiate

Madagascan and African species. The broad parietal is more or less trigonal in Africa, trapezoid in Madagascar. The transverse spines projecting laterally from the dorsal vertebrae and penetrating the skin, or at least the indications of these spines on the outside of the body in the form of enlarged scales, can only be found in Madagascan species. The only Madagascan species in which I could not discern it is *Brookesia nasus*.

Some other characters occur only in Africa or only in Madagascar but not in all species: the lateral crest is absent in Africa, present in most Madagascan species, the single parietal crest is only found in Africa, as are axillary and inguinal pits, flexible rostral processes and lung diverticula. To these may be added the differences in indices (table II): the tails in Madagascan species are relatively longer than in Africa, the heads of the Madagascan species are relatively higher and broader than those of Africa. Partial exceptions to this division are the African *Rh. kersteni* and the Madagascan *Br. nasus*. *Rh. kersteni* has the largest tail indices in Africa and it is the only species with gular cones in a pattern that is quite common in Madagascar. Moreover the body is much less flattened laterally than those of other African species and more like those of Madagascar. On the other hand it has a trigonal parietal. *Br. nasus* has a more or less flattened body (less so in the subspecies *pauliani*), no transverse processes on the vertebrae (so far as can be seen externally), a narrow head which is higher than broad, a somewhat flexible snout that is less developed but perhaps comparable with the rostral process in *Rh. temporalis*. However the parietal has a Madagascan form: trapezoid.

So with some hesitation I conclude that the division in *Brookesia* and *Rhampholeon* is valid. Even with a faint knowledge of the pygmy chameleons one might decide on appearance whether a specimen comes from Madagascar (*Brookesia*) or from Africa (*Rhampholeon*).

Of course, to strict cladists all these lizards have to be called *Chamaeleo* until eventually this genus is divided into a number of other genera. But, until much more is known about osteology

and other morphological characters, I do not feel inclined to subdivide it in this way.

4. To the above questions a last one may be added: what is the group of chameleons probably most closely related to *Brookesia* + *Rhampholeon*?

I referred already to Klaver's remark that *Brookesia* s.l. has more characters in common with the group around *Ch. nasutus* than with any other chameleon. In that same paper Klaver hoped to "demonstrate ... that similarity due to parallelism is the more acceptable proposition". However, I have not been able to find this demonstration in the succeeding paragraphs.

As shown in table II, *Brookesia* and *Rhampholeon* both have the following characters in common with *Ch. nasutus* c.s. whereas other African or Madagascan chameleons do not: size, relative height of head, height in relation to width of the head, axillary pits (also in other Madagascan chameleons), inguinal pits and flexible rostral protuberance. This leads me to regard *Ch. nasutus* c.s. as the group of chameleons most closely related to *Brookesia* and *Rhampholeon*.

Klaver (1979) considered the African *Rhampholeon* as intermediate between *Chamaeleo* and the Madagascan *Brookesia*. The only character in which *Brookesia* is closer to *Chamaeleo* than *Rhampholeon* is the tail index, in all other characters *Rhampholeon* is closer to *Chamaeleo*, or there is no difference between *Brookesia* and *Rhampholeon*. Probably *Brookesia* developed from a *Rhampholeon*-like stock.

In a forthcoming study on microcomplement fixation (Hofman et al., in prep.) my main conclusion about the relative age of *Brookesia* s.l. is confirmed. This study shows that the immunological distance between *Brookesia* and *Rhampholeon* on the one hand and *Ch. pardalis* on the other hand is clearly shorter than the distance between *Ch. pardalis* and *Ch. dilepis*, and between both these species and *Ch. montium*, *Ch. bitaeniatus* and *Ch. ellioti*. This means that *Brookesia* and *Rhampholeon* are younger than

the genus *Chamaeleo*, probably younger than the age of Madagascar as an island.

This suggests an invasion of Madagascar by a representative of *Rhampholeon*, perhaps — for reasons mentioned above — most closely resembling *Rh. kersteni*.

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