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## Comparative lung-morphology in the genus *Chamaeleo* Laurenti, 1768 (Sauria: Chamaeleonidae) with a discussion of taxonomic and zoogeographic implications

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### ABSTRACT

In this paper the lung-morphology of a large number of chameleons is described. Various characters can be distinguished, e.g. the septa-arrangement and the caecal outgrowths or "diverticula" on the ventral and caudal margin of the lungs. These characters are variable, but their shape often is characteristic of the species or the group of species. Next to *C. pumilus* (Gmelin, 1789), the only species known to lack diverticula so far, various other species without diverticula were found. Various lung-types, i.e. lungs with a similar combination of characters can be distinguished. Similarities in lung-structure tend to coincide with established affinities between species, but may also affirm assumed ones or even indicate new affinities. The geographical distribution of the lung-types is in accordance with the prevalent theory about the origin of chameleons. Some alternative hypotheses are formulated concerning the evolution and dispersion of chameleons.

### INTRODUCTION

Most of the literature on the lung-anatomy of chameleons dates back to the first part of this century. In spite of the rather fragmentary character of these descriptions, far-reaching decisions were based on them, e.g. the splitting of the genus *Chamaeleo* into various genera. For a historical survey of this literature, see the paper of Klaver (1973). In this paper the existence of an extensive variation in lung-structure was demonstrated, which indeed did not justify the splitting. Moreover, as similarities in lung-structure coincided with the relationships established by taxonomists, the lungs proved to be a useful taxonomic character. On account of the similarities and variation it was possible to reconstruct two evolutionary lines, viz. a continental and a Malagasy one.

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As the study of Klaver (1973) had the drawback of being founded on a limited number of specimens and species, and thus being in danger to commit the same error as the earlier authors, a more comprehensive study was undertaken, of which this paper is the result. I dissected 79 specimens of 46 different species, amongst which many types. Part of this material was put at my disposal by Dr. D. Broadley of the Umtali Museum (UM), Rhodesia, Dr. A. Jarret of the Seychelles College (SC), Mahé, Seychelles, Dr. D. Thijs van den Audenaerde of the Musée Royale de l'Afrique Centrale (MRAC), Belgium, and Dr. R. Zweifel of the American Museum of Natural History (AMNH), U.S.A., to whom I am most grateful. Special thanks are due to Dr. J. Guibé for his hospitality during my stay at the Muséum National d'Histoire Naturelle (MNHN), France, and to the Institute of Taxonomic Zoology (University of Amsterdam) for providing financial aid for my stay in Paris. Finally I want to thank Dr. D. Hillenius for his help and for critically reading my type-script.

#### THE LUNGS

Naturally, curators of taxonomic collections feel quite uneasy about dissection of their valuable specimens. In order to remove both lungs, however, the only necessary damage done to the taxonomic important "outside" are three incisions. The first one lateral of the midventral line from the neck to the inguinal region, the second one vertically just in front of the foreleg, starting lateral of the dorsal crest and joining the former incision ventrally, and the last one in front of the hind-leg, running in a similar way as the previous one. Hereafter the skin with the foreleg attached to it is detached from the body wall and turned over dorsad. Next we remove the body wall by cutting the ribs, thus gaining access to the general body cavity. With some care the lungs can be removed without damaging the other internal organs too much. As Wiedersheim (1886) already demonstrated, chameleons may have a so-called gular pouch connected with the trachea, just behind the larynx. Its presence can be established by cutting the sternohyoid muscle and pulling the hyoid downwards, thus enabling the inspection of the trachea.

Hereafter we can close up the animal by putting back the part of the body wall removed, returning the skin and foreleg into their normal position and finally securing this with some thread. In this way important characters e.g. dorsal and ventral crests, axillary pits a.o. remain intact and the animal will not fall apart during normal taxonomic examinations to follow.

As to the lungs, some characters e.g. the number and sometimes the shape of the diverticula, are often quite variable within one species and even within one specimen (see Beddard, 1907 and Klaver, 1973). Therefore it is omitted to give an extensive list of the number of diverticula in the various specimens of one species. Instead, one general description is given that fits to text-figures of one lung only and that is to be considered representative for the

species concerned. Notable aberrations e.g. absence of diverticula or typically branched diverticula will be dealt with separately. It must be noted that the text-figures are not to scale. The sequence in which the species are described is such that related species, often with a similar lung-structure, are next to each other. For this purpose the subdivision of the genus *Chamaeleo* into groups of species as established by Hillenius (1959 & 1963) and Brygoo (1971) is used. Finally the observed characteristics in lung-structure of the species described, including those of the species whose lung-structure is already known (see Klaver, 1973), are summarized in table 1.

*Chamaeleo calyptratus* A. Dumeril, 1851 (Figs. 1—2)  
MNHN 87—224 ♂, De Ibb et Taz, Yemen.

The lung has seven diverticula, two of them bifid. Apart from the caudal part, the entire inner-surface of the lung is set with alveoles that are small and deep anteriorly. Backwards the alveoles become wider and shallower. Two large longitudinal septa divide the anterior part of the lung-cavity into three chambers, viz. a dorsal and a ventral one and a chamber in between. The septa are also set with alveoles. A diaphragm separates a cranial chamber from the dorsal one and, moreover, there are three small dorsal septa. A gular pouch is present.

*Chamaeleo dilepis dilepis* Leach, 1819

UM 8147 ♀, Monapo, N. Mozambique; UM 16244 ♂, Tsodilo Hills, Botswana; UM 28635 ♀, Umtali, Rhodesia.

The lungs of these specimens all correspond to the description of the lungs of *C. d. dilepis* already given by Klaver (1973). They only differ in the number of diverticula and the presence of three small dorsal septa.

*Chamaeleo dilepis isabellinus* Günther, 1893

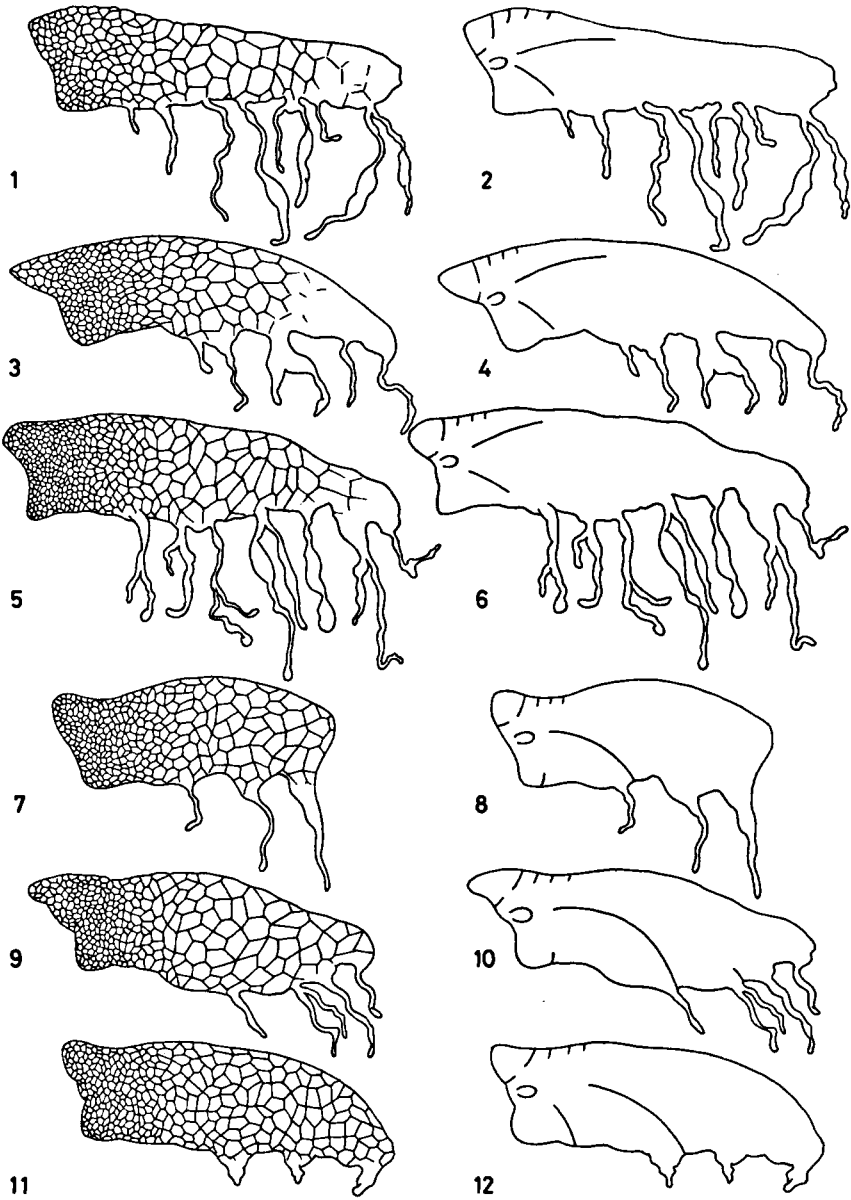
UM 4276 ♀, Lujeri Estate, Mlanje, Malawi.

The lungs of this specimen resemble the baglike lungs with the stout diverticula of the "aberrant" *C. d. dilepis* described by Klaver (*op. cit.*). They only differ in a more posterior extending alveolar network and the presence of various longer caudal diverticula. In all four specimens of *C. dilepis* a gular pouch is present.

*Chamaeleo laeyigatus* Gray, 1863 (Figs. 3—4)

MRAC 10446 and 10447 ♂♂, Iswa, Mahagi Terr., Zaire.

The same septa-arrangement as in the preceding species, viz. two longitudinal septa, a diaphragm and three small dorsal septa. There are five diverticula, one of them bifid. The alveoles are somewhat wider in the cranial chamber as compared to the other anterior alveoles. The caudal part of the lung lacks alveoles. A gular pouch is present.



Figs. 1—12. In the left column the habitus of the lung, in the right column the septa-arrangement (except for *C. tigris* and *C. isaratananensis*).  
Figs. 1—2, *C. calyptratus*; figs. 3—4, *C. laevigatus*; figs. 5—6, *C. namaquensis*; figs. 7—8, *C. rudis*; figs. 9—10, *C. ellioti*; figs. 11—12, *C. fuelleborni*.

*Chamaeleo namaquensis* Smith, 1831 (Figs. 5—6)

AMNH 32800 ♀, 70 km East of Mossamedes, Pico Azevedo, Angola.

The lungs of this species show the same general structure as do those of the previous species. Two large septa, a diaphragm and three small dorsal septa are present. The alveoles cover the greater part of the lung and are somewhat wider in the cranial chamber. There are seven diverticula, five of them bifid. A gular pouch is present.

*Chamaeleo melleri* (Gray, 1864)

UM 3932 ♂, Blantyre, Malawi.

The lungs of this specimen correspond in detail to the description given by Klaver (1973). Three large septa connected with the ventral wall of the lung, divide the lung-cavity into four successive chambers. The chambers communicate with one another by means of dorsal apertures. The number of diverticula also corresponds, viz. nine in both lungs. Except for the caudal part the entire lung is set with alveoles. Contrary to the former description, two small dorsal septa were found just behind the diaphragm. A gular pouch is present.

*Chamaeleo rudis rudis* Boulenger, 1906 (Figs. 7—8)

MRAC 26119 and 26120 ♂♂, Talya (900 m alt.), Kivu, Zaire.

A large and a small septum are present, both connected with the ventral wall of the lung. There are three diverticula, a diaphragm and three small dorsal septa. The alveoles extend all over the lung. The lungs of *C. r. sternfeldi* Rand, 1963, MNHN 23—103 ♀ (paratype), Kilimanjaro (2740 m alt.), Tanzania, only differ from those of *C. r. rudis* by a second diverticulum between the small and the large ventral septum. All three specimens of *C. rudis* lack a gular pouch.

*Chamaeleo elliotti* Günther, 1895 (Figs. 9—10)

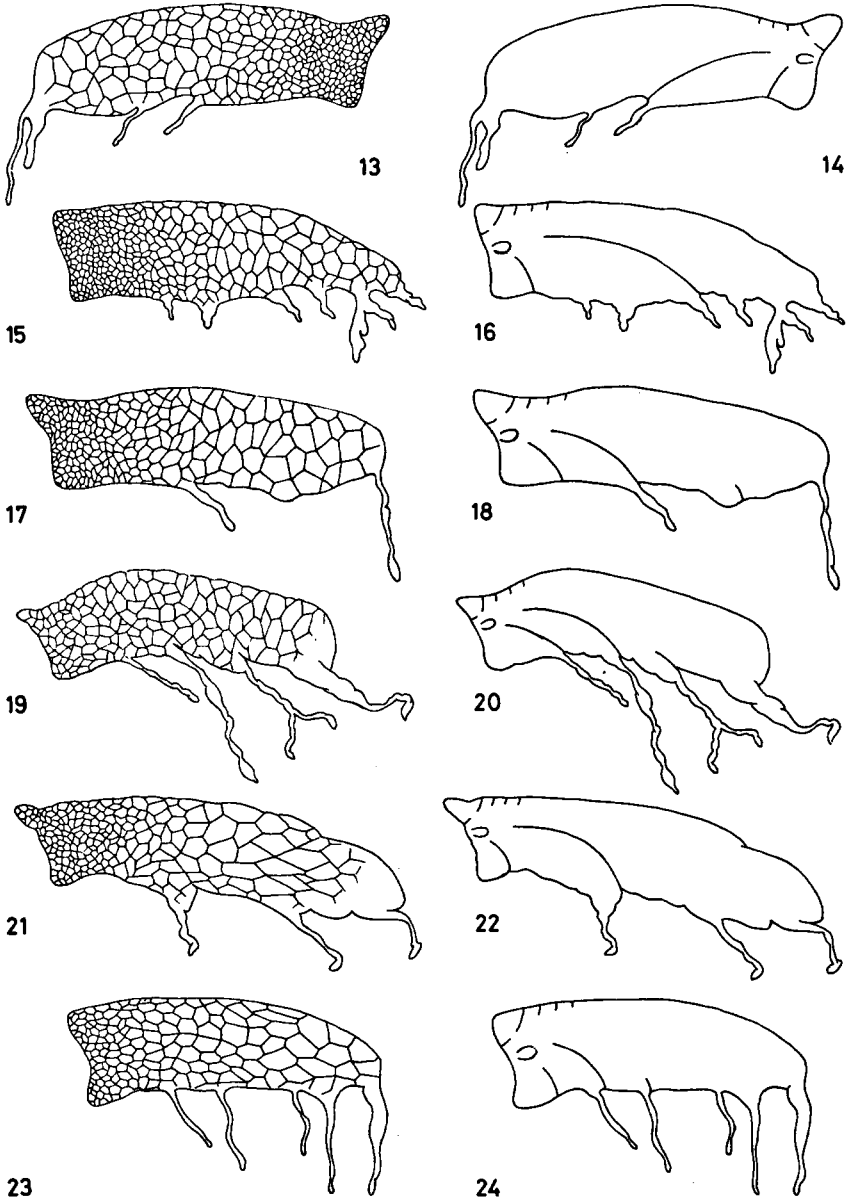
MRAC 23894 and 23895 ♀♀, Astrida (1750 m alt.), Rwanda.

The septa-arrangement is much the same as in *C. rudis*. A large and a small ventral septum are present next to a diaphragm and three small dorsal septa. In front of the large septum there is one diverticulum, whereas posterior to it there are three, one forked. In one of the four lungs studied a third small, but clearly distinguishable septum was present caudally on the ventral wall of the lung (see fig. 10). The alveolar network is distinctly wider in the cranial chamber and covers the entire inner-surface of the lung, including the septa. A gular pouch is absent.

*Chamaeleo fuelleborni* Tornier, 1900 (Figs. 11—12)

AMNH 49909 ♀, Nyamwanga, Poroto Mts., Tanzania.

Two large septa of unequal size arise from the ventral wall of the lung and divide the lung-cavity into three successive chambers. A diaphragm and



Figs. 13—24. Figs. 13—14, *C. weneri*; figs. 15—16, *C. tempeli*; figs. 17—18, *C. affinis*; figs. 19—20, *C. wiedersheimi*; figs. 21—22, *C. montium*; figs. 23—24, *C. goetzei nyikae*.

three small dorsal septa are present too. The diverticula consist of swollen sacs. In the right lung the middle chamber does not have a diverticulum. Alveoles cover the entire lung. There is no gular pouch.

*Chamaeleo weneri* Tornier, 1899 (Figs. 13—14)  
MNHN 31—55 ♀ (holotype), Tanganyika Territory.

Only the right lung was sufficiently preserved. It looks very much like the lung of the previous species. The only differences consist of the shape of the diverticula and a wider alveolar network in the cranial chamber. There is no gular pouch.

*Chamaeleo tempeli* Tornier, 1899 (Figs. 15—16)  
AMNH 47460 ♀, Ukinja Mts., Madehami, Tanzania

The lungs show the same general structure as do those of the two preceding species. The differences consist of the number and shape of the diverticula. A gular pouch is absent.

*Chamaeleo affinis* Rüppell, 1845 (Figs. 17—18)  
MNHN 1974—410 ♂, 1974—412 ♀ and 1974—413 ♀, Koffole, Arussi, Ethiopia; AMNH 20011 ♀, Dakyou, Harrar Prov., Ethiopia.

Of the previous three species, the lung of *C. weneri* resembles that of *C. affinis* most. Next to the same septa-arrangement and alveolar network, especially the shape of the diverticula adds to their resemblance. In one specimen, however, any trace of diverticula is absent. The lungs of the other specimens all at least have one and at the most two diverticula. In one lung in three different specimens there is a small third ventral septum. A gular pouch is absent.

*Chamaeleo wiedersheimi* Nieden, 1910 (Figs. 19—20)  
MNHN 39—86 and 39—87 ♂♂, Djuttitsa, Bamboutos Mts. (2000 m alt.), Cameroon; AMNH 101038 ♂, Nguroji, Mambilla Plateau (170 m alt.), Nigeria.

Considering the outer aspect, especially the large diverticula, the lungs of this species hardly resemble those of the latter species described. As to the septa-arrangement, however, there is an obvious resemblance. Moreover, in all three specimens a small third ventral septum is found (cf. *C. ellioti* and *C. affinis*). The alveoles, which are rather wide anteriorly, are absent at the most posterior part of the lung. A gular pouch is absent.

*Chamaeleo montium* Buchholz, 1874 (Figs. 21—22)  
MNHN 39—90 and 39—91 ♂♂, Buéa (1000 m alt.), Cameroon.

In this species there also are two large ventral septa, a diaphragm and three small dorsal septa. Three simple diverticula are present and alveoles cover almost the entire inner-surface of the lung. There is no gular pouch.

*Chamaeleo johnstoni ituriensis* Schmidt, 1919

MRAC 26539 and 26540 ♀ ♀, Lutunguru (1500 m alt.), Kivu, Zaire.

The lungs of these specimens correspond to the description of those of *C. j. johnstoni* given by Klaver (1973). The only difference consists of the presence of three small dorsal septa in this subspecies. There is no gular pouch.

*Chamaeleo goetzei nyikae* Loveridge, 1953 (Figs. 23—24)

UM 7023 ♂, Nyikae Plateau, Zambia.

Also in this species two septa arise from the ventral wall of the lung. A diaphragm and three small dorsal septa are present, next to five long and slender diverticula. Furthermore a third small septum is found on the ventral wall of the lung. The alveoles cover the entire lung. A gular pouch is present.

The lungs, the septa in particular, of the following species differ completely from those of the species hitherto described. Contrary to the types of septa-arrangement as in *C. calyptratus*, *C. ellioti* and *C. fuellborni*, a number of septa project from the dorsal, cranial and ventral wall of the lung into the anterior part of the lung-cavity. Normally five large and four small septa arise from the dorsal wall, two from the cranial and three from the ventral wall. Especially the septa on the dorsal wall are curved in anterior direction. The size of the septa on both the dorsal and ventral wall diminishes in posterior direction. A distinct diaphragm is not present. As to the alveolar network, it normally covers the entire inner-surface of the lung. Hereafter only notable exceptions to this scheme will be mentioned.

*Chamaeleo mlanjensis* Broadley, 1965 (Figs. 25—26)

UM 17597 ♀, Mulezi River, S.E. Mlanje, Malawi.

Two large forked diverticula are present. The septa-arrangement conforms exactly to the general description given above. There is no gular pouch.

*Chamaeleo pumilus* (Gmelin, 1789)

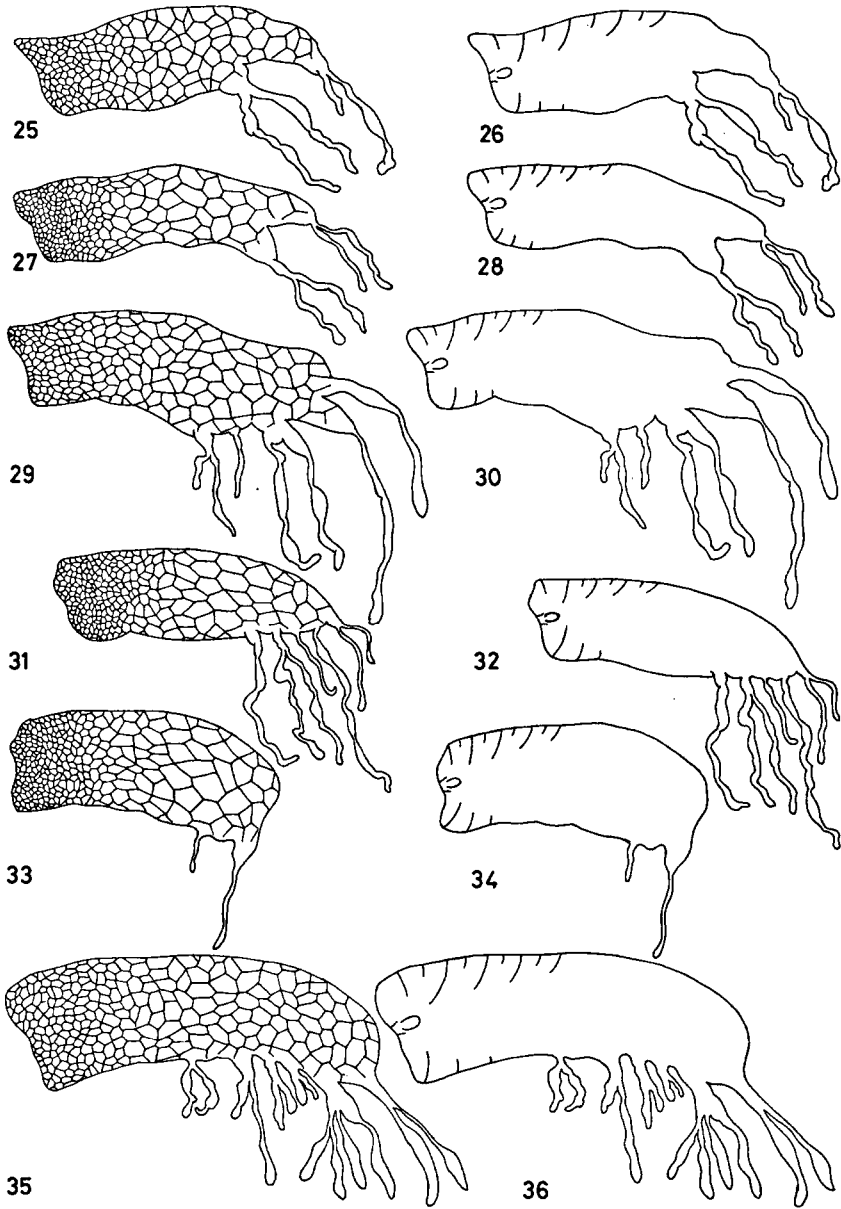
MNHN 381 ♂, Great Namaqualand, S. Africa.

The lungs of this specimen correspond to the description given by Klaver (1973). Both lungs lack diverticula, whereas the left lung is about half the size of the right one. Contrary to the former description, the septa are more pronounced and the alveolar network is not more complicated as compared with that of other species. Four septa, decreasing in size, are present on the dorsal wall, two on the cranial and three on the ventral wall. A gular pouch is present.

*Chamaeleo tavetanus* Steindachner, 1891 (Figs. 27—28)

MNHN 04—258 and 04—259 ♂ ♂, between Taita and the Kilimanjaro, Kenya-Tanzania.





Figs. 25—36. Figs. 25—26, *C. mlanjensis*; figs. 27—28, *C. tavetanus*; figs. 29—30, *C. bifidus*; figs. 31—32, *C. minor*; figs. 33—34, *C. willsii*; figs. 35—36, *C. parsonii*.

The septa-arrangement is in accordance with the general description given above. Two forked diverticula are present, whereas in the second specimen one lung has three diverticula, two of them triple. A gular pouch is absent.

*Chamaeleo bifidus* Brongniart, 1800 (Figs. 29—30)

MNHN 55—40 ♂, Madagascar; AMNH 71463 ♂, Tampina, Madagascar.

Five diverticula are present, two of them bifid and the terminal ones quite long. No gular pouch is found.

*Chamaeleo minor* Günther, 1879 (Figs. 31—32)

MNHN 5474 ♂, Madagascar; MNHN 06—165 ♀, Bétafo, Bestileo Prov., Madagascar.

The lung has five long diverticula, two of them bifid, and looks like the lung of the previous species. Instead of four, three small dorsal septa are present. There is no gular pouch.

*Chamaeleo willsii* Günther, 1890 (Figs. 33—34)

MNHN 57—114 ♂, Ankarafantsika, Madagascar; MNHN 29—51 ♂, Rogez Region, Madagascar.

Only two slender diverticula are present, whereas there is no gular pouch.

*Chamaeleo parsonii* G. Cuvier, 1824 (Figs. 35—36)

MNHN 6659 2 ♂♂, Nossi Bé, Madagascar.

Five diverticula are present, viz. four bifid and one quadruple. The remaining three lungs miss such a quadruple diverticulum. The septa-arrangement conforms to the general description. There is no gular pouch.

*Chamaeleo oshaughnessyi oshaughnessyi* Günther, 1881 (Figs. 37—38)

MNHN 01—380 ♂, between Fort Dauphin and Fianarantsoa, Madagascar.

Five simple, stout diverticula are present. No gular pouch is found. This description also fits the lungs of *C. o. ambreensis* Ramanantsoa, 1974, MNHN 1974—9 ♀ and 1974—10 ♂ (paratypes), Station forestières des Roussettes, Mt. d'Ambre, Madagascar.

*Chamaeleo globifer* Günther, 1879 (Figs. 39—40)

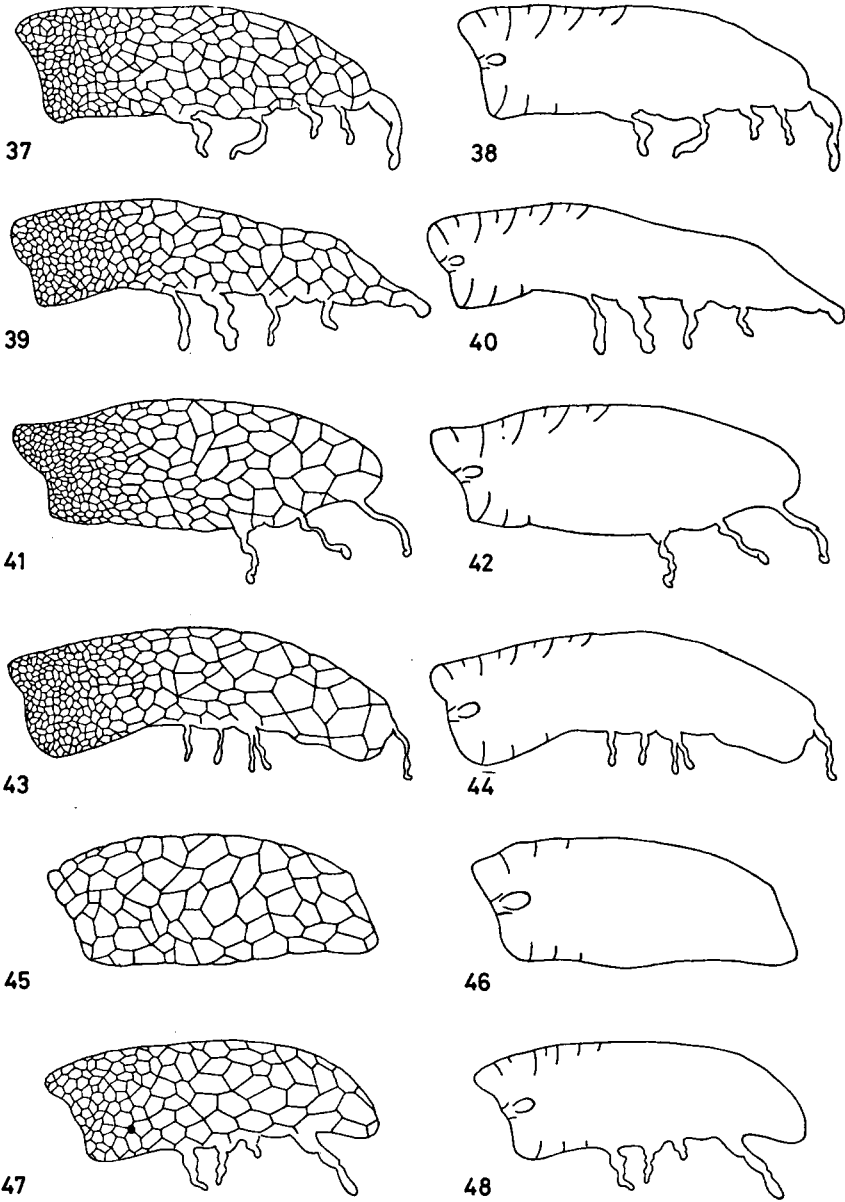
MNHN 57—214 and 57—215 ♂♂, Mt. d'Ambre, Madagascar.

The lung resembles that of the previous species. There are five simple diverticula. A gular pouch is absent.

*Chamaeleo capuroni* Brygoo, Blanc & Domergue, 1972 (Figs. 41—42)

MNHN A-333 ♀ and A-338 ♂ (paratypes), Anosyennes (1900 m alt.), Madagascar.

The lung has three slender diverticula, whereas only three small dorsal septa are present. There is no gular pouch.



Figs. 37—48. Figs. 37—38, *C. oshaughnessyi*; figs. 39—40, *C. globifer*; figs. 41—42, *C. capuroni*; figs. 43—44, *C. nasutus*; figs. 45—46, *C. fallax*; figs. 47—48, *C. gallus*.

*Chamaeleo nasutus* Duméril & Bibron, 1836 (Figs. 43—44)

MNHN 21—268 ♀, Fito Region, Madagascar; MNHN 8906 ♂, Ankara-fantsika and Ampijoroa, Madagascar; AMNH 32880 ♀, Antsihanako, Madagascar.

Four diverticula are present, one of them bifid. One of the six lungs examined has a triple diverticulum. There is no gular pouch.

*Chamaeleo fallax* Mocquard, 1900 (Figs. 45—46)

MNHN 02—94 and 02—95 ♂♂, Ikongo, Madagascar.

No diverticula are found in the lungs of both specimens. As to the septa, there only are three of them on the dorsal wall. A gular pouch is absent.

*Chamaeleo gallus* Günther, 1877 (Figs. 47—48)

MNHN 54—71 2 ♂♂, Madagascar.

There are four simple diverticula and two small dorsal septa are absent. There is no gular pouch.

*Chamaeleo boettgeri* Boulenger, 1888 (Figs. 49—50)

MNHN 93170 ♂ and 93—171 ♀, Diégo-Suarez, Madagascar.

There are four diverticula, one being bifid. Except for one small dorsal septum, the septa-arrangement is in accordance with the general description. There is no gular pouch.

*Chamaeleo guibei* Hillenius, 1959 (Figs. 51—52)

MNHN 50—354 ♀ (holotype), Mt. Tsaratanana (1800 m alt.), Madagascar; MNHN 57—115 ♀ (paratype), Sihanaka, Madagascar.

Diverticula are not present in the lungs of both specimens. There are only three septa on the dorsal wall of the lung. A gular pouch is absent.

*Chamaeleo cucullatus* Gray, 1831 (Figs. 53—54)

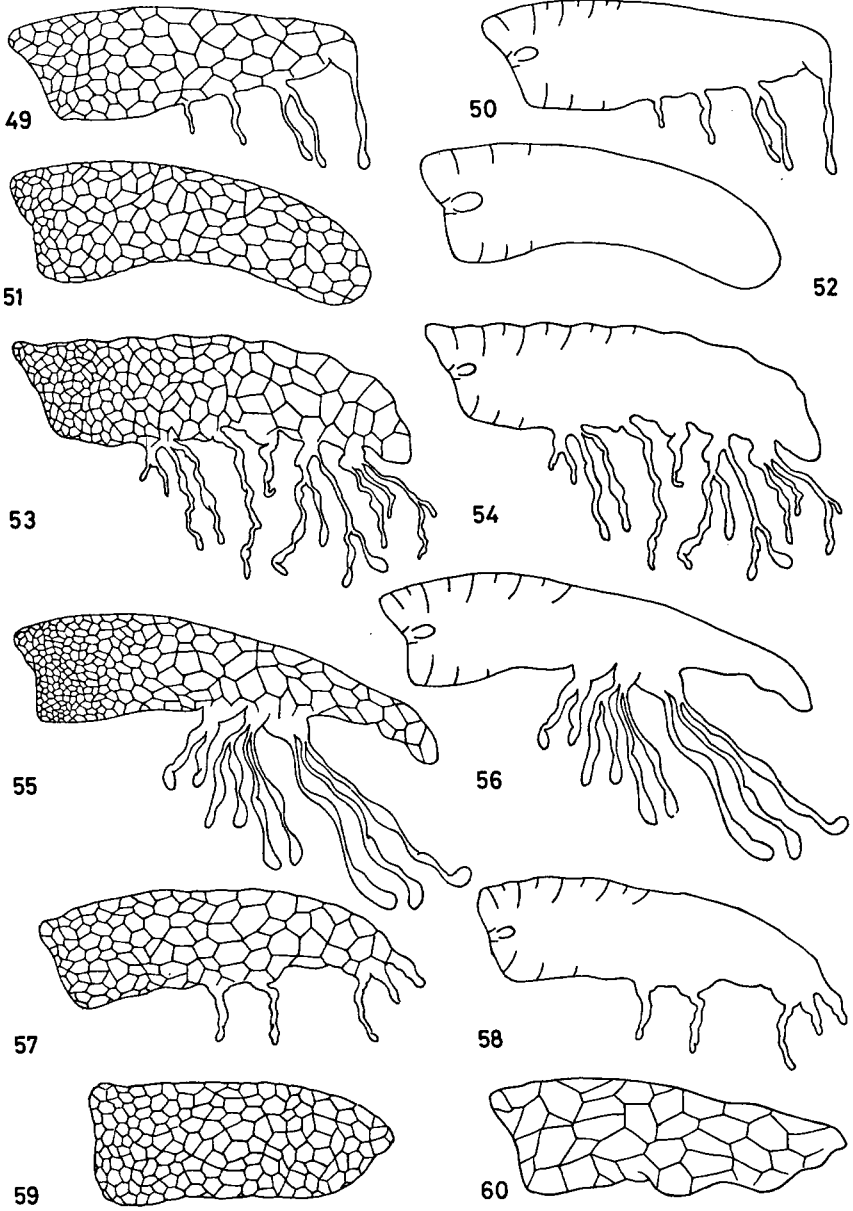
MNHN 83—570 ♂ and 83—572 ♀, Madagascar.

Five diverticula are present, three of them being forked in such a way that four branches are constituted. The septa-arrangement conforms to the general description. A gular pouch is present.

*Chamaeleo brevicornis brevicornis* Günther, 1879 (Figs. 55—56)

MNHN A-103 ♂, Madagascar; MNHN 1965—135 ♂, Perinet, Madagascar; AMNH 12823 ♂, Amatbondrazaka, Madagascar.

A bifid, a triple and quadruple diverticulum are present, the latter being of considerable length. The lung also has a saccular termination. There is no gular pouch. The lungs of *C. b. hilleniusi* Brygoo, Blanc & Domergue, 1973, MNHN 1972—50 ♀ and 1972—54 ♂ (paratypes), Ankaratra, Madagascar, correspond to this description as well.



Figs. 49—60. Figs. 49—50, *C. boettgeri*; figs. 51—52, *C. guibei*; figs. 53—54, *C. cucullatus*; figs. 55—56, *C. brevicornis*; figs. 57—58, *C. malthe*; fig. 59, *C. tsaratananensis*; fig. 60, *C. tigris*.

*Chamaeleo malthe* Günther, 1879 (Figs. 57—58)

MNHN 21—257 ♀, Fito Region, W. of Sihanaka, Madagascar; MNHN 35—142 ♀, Isaka-Ivondro (700 m alt.), Madagascar; MNHN 1973—453 and 1973—454 ♀ ♀, Massif du Marojezy, Madagascar.

The status of the two specimens last mentioned is uncertain. They might prove to belong to a separate subspecies (cf. Brygoo, Blanc & Domergue, 1974). In spite of this the lungs do not differ significantly from those of the other specimens. Four diverticula are present, one of them bifid. A gular pouch is absent.

*Chamaeleo tsaratananensis* Brygoo & Domergue, 1968 (Fig. 59)

MNHN A-59 ♀ (holotype), Massif du Tsaratanana (2500 m alt.), Madagascar.

Both lungs lack diverticula. As the result of poor conservation, there are only traces of dorsal and ventral septa. There is no gular pouch.

*Chamaeleo verrucosus* G. Cuvier, 1829 (Figs. 61—62)

MNHN 8914 ♂, Majunga, Madagascar.

The lung is almost completely covered with alveoles and only three small dorsal septa are present. There are twelve diverticula, viz. two simple, three bifid, four triple and three quadruple ones. A gular pouch is present.

*Chamaeleo tuzetae* Brygoo, Bourgat & Domergue, 1972 (Figs. 63—64)

MNHN A-258 ♂ (holotype), Andrenalamivola, Canton Befandriana, Madagascar.

There are two simple, one bifid and one triple diverticulum. The lung itself terminates in a slender sac. A gular pouch is present.

*Chamaeleo belalandaensis* Brygoo & Domergue, 1970 (Figs. 65—66)

MNHN 1969—114 ♂ (holotype), Belalanda, Madagascar.

The lung, with a saccular termination as in *C. tuzetae*, has three simple and two triple diverticula. A gular pouch is absent.

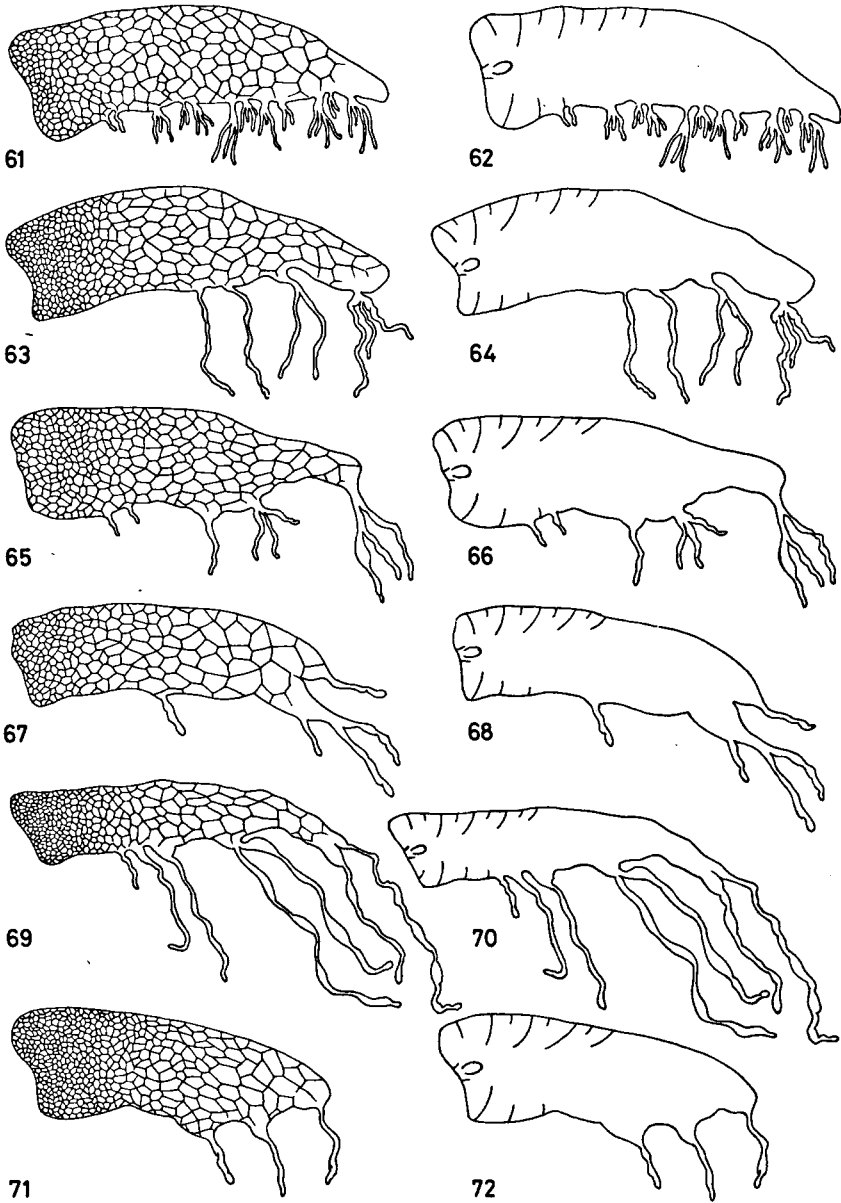
*Chamaeleo rhinoceratus* Gray, 1845 (Figs. 67—68)

MNHN 1967—175 and 1967—176 ♂ ♂, Ampijora, Madagascar.

The lung has two simple and one complex diverticulum, the last one could be considered triple. The lungs of the second specimen resemble more those of *C. labordi*, although the diverticula do not meet the same extreme length (see below). There is no gular pouch, but only an indication of it on the ventral side of the trachea. This situation is to be distinguished from the one found in other species which do not have a gular pouch.

*Chamaeleo labordi* A. Grandidier, 1872 (Figs. 69—70)

MNHN 1967—178 ♂ and 1967—179 ♀, Ihotry, between Befandria and Morombe, Madagascar.



Figs. 61—72. Figs. 61—62, *C. verrucosus*; figs. 63—64, *C. tuzetae*; figs. 65—66, *C. belalandaensis*; figs. 67—68, *C. rhinocerotus*; figs. 69—70, *C. labordi*; figs. 71—72, *C. antimena*.

The lung is characterized by the extremely developed diverticula, three of them being simple and two forked. Once a third cranial septum was found, next to the regular septa, as is indicated in figure 70. There is no gular pouch, but a situation as found in *C. rhinocerotus*.

*Chamaeleo antimena* A. Grandidier, 1872 (Figs. 71—72)

MNHN 1970—288 ♀ and 1970—289 ♂, Tsungurita, Madagascar.

In one specimen both lungs have three simple diverticula. In the other specimen the left lung fits this description, but the right lung has a simple, a bifid and a triple diverticulum. Besides, the diverticula of this last specimen are longer, thus resembling more those of *C. labordi*. Only three small dorsal septa are present. There is no gular pouch, but a situation as found in the two previous species.

*Chamaeleo campani* A. Grandidier, 1872 (Figs. 73—74)

MNHN 57—222 ♂, Tsiafajarona, Massif de l'Ankaratra, Madagascar; MNHN 29—47 ♀, Tananarive, Madagascar.

Three slender diverticula are present, whereas the septa do not depart from the general scheme. A gular pouch is absent.

*Chamaeleo polleni* Peters, 1873 (Figs. 75—76)

MNHN 0—148 ♂, locality unknown; 84—463 ♂, Batraieus de Mayotte, Comoro Islands.

The lungs of one specimen bear one terminal diverticulum each, whereas both lungs of the second specimen lack any diverticula. Thus the lungs of this last specimen look very much like those of *C. cephalolepis*, although the septa are somewhat more pronounced. There is no gular pouch.

*Chamaeleo cephalolepis* Günther, 1880 (Figs. 77—78)

MNHN 89—367 ♀ and 89—372 ♂, probably Comoro Islands; UM 29231 ♀, Moroni, Comoro Islands.

The lungs of this species are very much like those of *C. pumilus*. There are no diverticula. The septa-arrangement, however, differs from that of *C. pumilus*, as it conforms the previously given general description. A gular pouch is absent.

*Chamaeleo gastrotaenia gastrotaenia* Boulenger, 1888 (Figs. 79—80)

MNHN 07—65 ♀, Tanamala, Madagascar; MNHN 21—274 ♂, Fito Region, W. of Sihanaka, Madagascar.

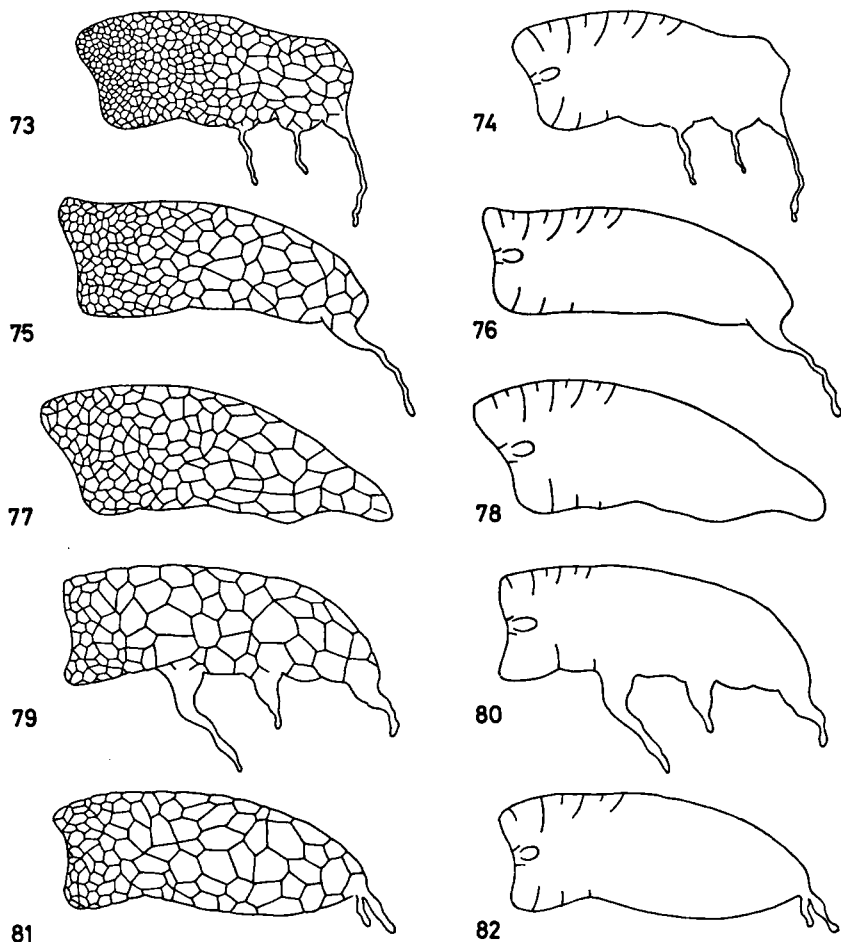
Three relatively large diverticula are present. As to the septa, three large and two small septa are present on the dorsal wall of the lung, two on the cranial and also two on the ventral wall. There is no gular pouch. The lungs of the following subspecies correspond to this description as well: *C. g. marojezensis* Brygoo, Blanc & Domergue, 1970, MNHN A-160 ♂ (holotype),



Massif du Marojezy, Madagascar; *C. g. andringitraensis* Brygoo, Blanc & Domergue, 1972, MNHN A-330 ♂ (holotype), Ambalamarovandana, Massif de l'Andringitra (1500 m alt.), Madagascar and *C. g. guillaumeti* Brygoo, Blanc & Domergue, 1973, MNHN 1973—447 ♀ (paratype), Massif du Marojezy, Madagascar.

*Chamaeleo peyrierasi* Brygoo, Blanc & Domergue, 1974 (Figs. 81—82)  
MNHN 1973—440 ♂ (holotype) and 1973—441 ♀ (paratype), Massif du Majorezy, Madagascar.

The lungs of the first specimen show no sign of diverticula, whereas those of the second specimen have a terminal diverticulum each, which is bifid in one of them. The septa-arrangement more or less resembles that of the



Figs. 73—82. Figs. 73—74, *C. campani*; figs. 75—76, *C. polleni*; figs. 77—78, *C. cephalolepis*; figs. 79—80, *C. gastrotaenia*; figs. 81—82, *C. peyrierasi*.

Table 1. A synopsis of lung-characters in chameleons. Species grouped according to Hillenius (1959, 1963). The lungs of the species followed by the author name are known from previous descriptions (cf. Klaver, 1973).

Symbols used:

Septa-arrangement:

a = a diaphragm, small dorsal septa and two large longitudinal septa; b = a diaphragm, small dorsal septa and three large septa connected with the ventral wall of the lung; c = a diaphragm, small dorsal septa and one small and one large septum connected with the ventral wall of the lung; d = a diaphragm, small dorsal septa and two large septa connected with the ventral wall of the lung; e = no diaphragm, numerous septa on the dorsal, cranial and ventral wall of the lung; + = extra small septum ventrally.

Diverticula:

+ = present; ± = may be present or absent; — = absent; a = triple and b = quadruple diverticula.

Alveolar network:

+ = covers the entire lung; — = does not cover the entire lung.

Terminal sac:

+ = present; — = absent.

Gular pouch:

+ = present; ± = indicated only; — = absent.

	septa- arrangement	diverti- cula	alveolar network	terminal sac	gular pouch
<b>C. chamaeleon-group:</b>					
<i>C. chamaeleon</i> (Linnaeus, 1758)	a	+	—	—	+
<i>C. c. zeylanicus</i> Laurenti, 1786	a	+	—	—	+
<i>C. basiliscus</i> Cope, 1868	a	+	—	—	+
<i>C. senegalensis</i> Daudin, 1802	a	+	—	—	+
<i>C. gracilis</i> Hallowell, 1842	a	+	—	—	+
<i>C. d. dilepis</i> Leach, 1890	a	+	—	—	+
<i>C. d. quilensis</i> Bocage, 1866	a	+	—	—	+
<i>C. d. isabellinus</i>	a	+	—	—	+
<i>C. calyptratus</i>	a	+	—	—	+
<i>C. laevigatus</i>	a	+	—	—	+
<b>More or less related to the former group:</b>					
<i>C. monachus</i> Gray, 1864	a	+	—	—	+
<i>C. namaquensis</i>	a	+	—	—	+
<i>C. melleri</i>	b	+	—	—	+
<b>C. bitaeniatus-group:</b>					
<i>C. bitaeniatus</i> Fischer, 1884	c	+	+	—	—
<i>C. jacksoni</i> Boulenger, 1896	c	+	+	—	—
<i>C. ellioti</i>	c+	+	+	—	—
<i>C. r. rudis</i>	c	+	+	—	—
<i>C. r. sternfeldi</i>	c	+	+	—	—
<i>C. fuelleborni</i>	d	+	+	—	—
<i>C. tempeli</i>	d	+	+	—	—
<i>C. weneri</i>	d	+	+	—	—
<b>C. cristatus-group:</b>					
<i>C. cristatus</i> Stutchbury, 1837	d	+	—	—	—
<i>C. montium</i>	d	+	—	—	—
<i>C. wiedersheimi</i>	d+	+	—	—	—
<b>C. oweni-group:</b>					
<i>C. oweni</i> Gray, 1831	d	+	—	—	—
<i>C. j. johnstoni</i> Boulenger, 1901	d	+	—	—	—
<i>C. j. ituriensis</i>	d	+	—	—	—

	septa- arrangement	diverti- cula	alveolar network	terminal sac	gular pouch
Miscellaneous					
<i>C. affinis</i>	d+	±	+	—	—
<i>C. goetzei nyikae</i>	d+	+	+	—	+
<i>C. mlanjensis</i>	e	+	+	—	—
<i>C. tigris</i>	e	—	+	—	—
<i>C. pumilus</i> -group:					
<i>C. p. pumilus</i>	e	—	+	—	+
<i>C. bifidus</i> -group:					
<i>C. fischeri</i> Reichenow, 1887	e	+a	+	—	—
<i>C. tavetanus</i>	e	+a	+	—	—
<i>C. bifidus</i>	e	+	+	—	—
<i>C. minor</i>	e	+	+	—	—
<i>C. willsii</i>	e	+	+	—	—
<i>C. parsonii</i> -group:					
<i>C. parsonii</i>	e	+b	+	—	—
<i>C. o. oshaughnessyi</i>	e	+	+	—	—
<i>C. o. ambreensis</i>	e	+	+	—	—
<i>C. globifer</i>	e	+	+	—	—
<i>C. capuroni</i>	e	+	+	—	—
<i>C. nasutus</i> -group:					
<i>C. nasutus</i>	e	+a	+	—	—
<i>C. fallax</i>	e	—	+	—	—
<i>C. gallus</i>	e	+	+	—	—
<i>C. boettgeri</i>	e	+	+	—	—
<i>C. guibei</i>	e	—	+	—	—
<i>C. cucullatus</i> -group:					
<i>C. cucullatus</i>	e	+b	+	—	+
<i>C. b. brevicornis</i>	e	+ab	+	+	—
<i>C. b. hilleniusi</i>	e	+ab	+	+	—
<i>C. malthe</i>	e	+	+	—	—
<i>C. tsaratananensis</i>	e	—	+	—	—
<i>C. oustaleti</i> -group:					
<i>C. oustaleti</i> Mocquard, 1894	e	+b	—	+	+
<i>C. pardalis</i> G. Cuvier, 1829	e	+b	+	—	—
<i>C. verrucosus</i>	e	+ab	—	+	+
Probably related to the former as well as the next group:					
<i>C. tuzetae</i>	e	+a	+	+	+
<i>C. belalandaensis</i>	e	+a	+	+	—
<i>C. rhinoceratus</i> -group:					
<i>C. rhinoceratus</i>	e	+a	+	—	±
<i>C. labordi</i>	e	+	+	—	±
<i>C. antimena</i>	e	+a	+	—	±
<i>C. lateralis</i> -group:					
<i>C. lateralis</i> Gray, 1831	e	+	+	—	—
<i>C. campani</i>	e	+	+	—	—
<i>C. polleni</i> -group:					
<i>C. polleni</i>	e	±	+	—	—
<i>C. cephalolepis</i>	e	—	+	—	—
<i>C. gastrotaenia</i> -group:					
<i>C. g. gastrotaenia</i>	e	+	+	—	—
<i>C. g. marojezensis</i>	e	+	+	—	—
<i>C. g. andringitraensis</i>	e	+	+	—	—
<i>C. g. guillaumeti</i>	e	+	+	—	—
<i>C. peyrierasi</i>	e	±	+	—	—

previous species, viz. four large and two small dorsal septa, two cranial and three ventral septa. There is no gular pouch.

*Chamaeleo tigris* Kuhl, 1820 (Fig. 60)

MNHN 664 2 ♀ ♀, Seychelles; SC-FMC 81349 ♂, Seychelles.

Unfortunately the lungs of all specimens were rather badly preserved, so the description is incomplete. Diverticula are absent. The alveolar network also is rather wide in the anterior part of the lung. Possibly the smaller and thinner alveolar walls have disappeared as the result of insufficient conservation. In one lung only one septum is present on the dorsal wall. This probably implies a similar septa-arrangement as in the species last considered, but future examination must be awaited. A gular pouch is absent.

## DISCUSSION

### *Lung-morphology and taxonomy*

Similarities in lung-structure generally confirm the relationships established by taxonomists like Hillenius (1959, 1963) and Brygoo (1971). Especially in the African forms the anatomical data support the morphological and cytological evidence quite well.

The large but homogeneous group of *C. chamaeleon* is characterized by one type of lung and the presence of a gular pouch (see table 1). In my first paper differences concerning the presence of the small dorsal septa and a wider alveolar network in the cranial chamber already were supposed to be due to insufficient conservation and contraction of lung-tissue respectively. This view is confirmed by the observation of these characters in *C. d. dilepis* (but see also *C. melleri* and *C. johnstoni*). The sac-shaped type of lung found in *C. d. dilepis* (see Klaver, 1973) probably is the result of a similar process, i.e. contraction of lung-tissue, as the lungs of *C. d. isabellinus* are more or less intermediate between this sac-shaped form and the "normal" one.

Hillenius (1959, 1963) classified *C. namaquensis* together with *C. anchietae* Bocage, 1872, *C. monachus* and *C. melleri* into a group more or less related to *C. chamaeleon* c.s. Considering the lungs and the presence of a gular pouch, however, *C. monachus* and *C. namaquensis* cannot be distinguished from *C. chamaeleon* c.s. Therefore I propose to class them within the *C. chamaeleon*-group, the more so as there only is little difference in external morphology. Another reason to split up this group is that the lungs of *C. melleri* in no way resemble those found in the *C. chamaeleon*-group, including *C. monachus* and *C. namaquensis*. On the other hand the relation of *C. melleri* to the *C. chamaeleon*-group is obvious from similarities in external morphology, the same karyotype and the presence of a gular pouch. Therefore an isolated position, although indirectly linked with the *C. chamaeleon*-group, as proposed by Hillenius (1959, 1963), is plausible.

In the *C. cristatus*-group there is some variability in lung-structure. The

lungs of *C. cristatus* and *C. wiedersheimi* have much in common, viz. few but large diverticula, the septa-arrangement and a rather wide alveolar network anteriorly. A notable difference is the presence of a diverticulum, connected with the first chamber of the lung in *C. wiedersheimi*. Although the lungs of *C. montium* have a similar septa-arrangement as those of the previous species, the shape of the lung itself and of the diverticula are clearly different. Hillenius (1959, 1963) supposed that the *C. cristatus*-group and the *C. oweni*-group may perhaps be joined in one group. Their external morphology and especially their cytology would not contradict this. Indeed *C. montium* seems to be the link between these groups. Its lungs resemble most those of *C. oweni* and *C. johnstoni*, whereas its external morphology approximates that of *C. wiedersheimi*. Next to this Klaver (1973) already demonstrated that the differences in lung-structure are gradual and probably representing subsequent stages in lung-evolution. I, therefore, think it is justified to combine the species concerned into one group of West and Central African chameleons.

The *C. bitaeniatus*-group can be divided into two subgroups, comprising a.o. *C. bitaeniatus*, *C. rudis*, *C. ellioti* and *C. jacksoni* on the one hand and *C. tempeli*, *C. weneri* and *fuelleborni* on the other. The lungs of the species of the first subgroup are characterized by a septa-arrangement with one small and one large septum. The species of the second subgroup have two large septa instead. Thus the lung-morphology acknowledges the established classification. The lungs of the species of the second subgroup resemble those of *C. oweni* c.s. quite well. Another similarity is the absence of a gular pouch. However, there also are slight differences in e.g. shape of the septa. Besides representatives of these groups also differ markedly in karyotype, external morphology and are either oviparous or ovoviviparous. Therefore the similarities are most probably due to convergent evolution (see also Klaver, 1973).

The lungs of *C. affinis* resemble those of *C. weneri* to a great extent, i.e. have a similar septa-arrangement and a complete alveolar network. Hillenius (1959) mentions a more or less corresponding gular squamation pattern in both species, but he demonstrates *C. affinis* has much more in common with *C. wiedersheimi*. Differences in shape of the lungs do not have to contradict this affinity, because the same view concerning lung-evolution can be hold as was mentioned above in case with *C. montium*. This would lead to the conclusion that the affinity of *C. affinis* and *C. wiedersheimi* is confirmed by the lung-anatomy, whereas the similarities in lung-structure between *C. affinis* and *C. weneri* are to be ascribed to convergence. However, the observed similarities between *C. affinis* and *C. weneri* on the one hand and between *C. affinis* and *C. wiedersheimi* on the other hand, and especially the geographical distribution of these three species, also suggest another possibility. It is likely that the African chameleons originally are descendants from an ancestral East African form (Hillenius, 1959). From East Africa the chameleons have spread over the African continent. I, therefore, wonder if *C. affinis* and *C.*

*wiedersheimi* cannot be considered derived from the same East African stock by way of the *C. werneri*-subgroup and the *C. oweni*-group (or their forbears) respectively. Similarities in lung-structure between *C. affinis* and *C. werneri* then do not have to be ascribed to convergence, but are due to their common origin. The same reasoning applies to the two groups mentioned. At the same time it explains the similarities in external morphology and lung-structure and thus the inferred relationship of *C. affinis* and *C. wiedersheimi*, despite their discontinuous geographical distribution. Consequently differences between representatives of the two groups in external morphology and cytology are the result of more recent evolutionary processes in the various localities reached. In favor of this hypothesis are the similarities already mentioned, the absence of a gular pouch in all species involved and also the occasional appearance of a small third ventral septum in *C. wiedersheimi*, *C. ellioti* and *C. affinis*.

A similar septum is found in *C. goetzei nyikae*. Hillenius (1959) demonstrated this species has characters in common with both *C. wiedersheimi* and *C. affinis*. The lungs of *C. goetzei nyikae* can be considered of the same type as those of *C. affinis*, although the septa are smaller. However, the presence of a gular pouch distinguishes *C. goetzei nyikae* from all other species concerned. In connection with this another anatomical character may be mentioned. In my former paper on chameleonlungs, I described a pigmentation of the parietal peritoneum and the mesenteries in *C. bitaeniatus*, *C. jacksoni* and *C. pumilus*. A similar pigmentation is found in *C. ellioti*, *C. r. rudis*, *C. r. sternfeldi*, *C. werneri*, *C. fuelleborni* and *C. goetzei nyikae*. This pigmentation is absent in *C. tempeli*, *C. affinis* and *C. oweni* c.s.<sup>1)</sup> Apparently the various characters are not strictly limited to a certain group. Therefore I conclude, that, as only a limited number of specimens were examined by Hillenius as well as by myself, the groups of chameleons concerned deserve more attention to clarify the variability and to verify the hypothesis sketched above.

A differentiation in septa-arrangement as found in the continental species does not occur in the mainly Malagasy species to be discussed next. The only difference consists of less pronounced septa in some species. As to the absence of one or more dorsal septa, I hold the same view as was expressed above, i.e. insufficient conservation, although a reduction of septa might have occurred in *C. fallax* for instance. Consequently we must rely on other, unfortunately more variable characters for comparison, that may exceed the group-boundaries distinguished by taxonomists.

According to Hillenius (1959) the continental *C. fischeri* and *C. tavetanus* constitute one group with *C. bifidus*, *C. minor* and *C. willsii* from Madagascar.

<sup>1)</sup> Moreover, a similar pigmentation is found in *C. marshalli* Boulenger, 1906, but is absent in the approximately 20 species of dwarf chameleons I examined. So the presence of this character does not support the decision of Broadley (1973), who, contrary to Mertens (1966), transfers *C. marshalli* to the genus *Rhampholeon* Günther, 1874.

Except for the last species, the shape of the lungs and the large diverticula do not contradict this. Considering the external morphology, any affinity between *C. willsii*, *C. campani* and *C. lateralis* is unlikely, despite the resemblance in lung-habitus. The karyotype of *C. willsii*, however, resembles more that of *C. campani* than that of *C. fischeri*. The karyotype of *C. fischeri* is identical to the one of *C. parsonii*, *C. oshaughnessyi* and *C. globifer* (cf. Bourgat, 1973). This is in accordance with the affinity of the *C. parsonii*-group (to which the three species last mentioned belong) with the *C. bifidus*-group, as was assumed by Hillenius on account of morphological considerations. As to the lungs of *C. parsonii* c.s. there is little resemblance compared to those of *C. bifidus* c.s., except perhaps for *C. parsonii* with its large diverticula. The lungs of *C. o. oshaughnessyi*, *C. o. ambreensis*, *C. globifer* and the more recently described member of this group *C. capuroni*, do resemble each other, i.e. bearing few and short diverticula <sup>1)</sup>.

The lungs of the members of the *C. nasutus*-group, comprising *C. nasutus*, *C. fallax*, *C. gallus*, *C. boettgeri* and *C. guibei* a.o. have a comparable shape. Diverticula are absent in *C. guibei* and *C. fallax* and not in *C. gallus*. Owing to this and to the absence of diverticula in various unrelated species, viz. *C. tsaratananensis*, *C. cephalolepis* and *C. affinis*, the affinity of *C. gallus* and *C. pumilus* as suggested by Klaver (1973) is unlikely. Similarity in septa-arrangement does not change this view, for other continental species possess such a septa-arrangement as well. The fact that other species without diverticula were found refutes the often advocated classification of *C. pumilus* in a separate genus (cf. Methuen et al., 1914). Lastly the validity of *C. fallax*, discussed by Brygoo (1971), is confirmed by the lung-anatomy. The diverticulate lungs of *C. nasutus* can easily be distinguished from the lungs of *C. fallax*, that do not have diverticula.

The lungs of *C. nasutus* and *C. malthe* have a more or less similar habitus. This may be ascribed to convergence, as significant differences in external morphology are present and the lungs of their respective groupmembers also differ markedly. On the other hand, however, the karyotype of a groupmember of *C. malthe*, viz. *C. brevicornis*, can easily be derived via robertsonian fusion from the one of *C. nasutus* (see Matthey, 1961). Moreover, in both species the lungs may bear triple diverticula. Perhaps this indicates some relationship after all.

Within the *C. cucullatus*-group there is much variation in lung-structure. *C. cucullatus*, *C. b. brevicornis* and *C. b. hilleniusi* have well-developed and triple as well as quadruple diverticula, *C. malthe* has small simple diverticula, whereas *C. tsaratananensis* does not have any at all. Thus the validity of *C. tsaratananensis*, discussed by Brygoo (1971), is confirmed, as the absence of diverticula clearly distinguishes this species from *C. malthe*.

<sup>1)</sup> In the original description of *C. capuroni*, Brygoo, Blanc & Domergue (1972) consider the remarkable V-shaped gular crest unique within the genus *Chamaeleo*. This is, however, incorrect, for a similar gular crest already was described in *C. tempeli* by Tornier (1899).

As to *C. brevicornis* and *C. cucullatus*, they have various characters in common with *C. oustaleti* and *C. verrucosus*, which may be an indication of affinity. *C. brevicornis* possesses triple diverticula as does *C. verrucosus*. Moreover it has quadruple diverticula and a terminal sac, which was observed previously in both *C. oustaleti* and *C. verrucosus*. Quadruple diverticula are found in *C. cucullatus* as well and, notably, this species has a gular pouch, a character that is only shared with *C. oustaleti*, *C. verrucosus* and *C. tuzetae* on Madagascar. Although the lungs of *C. cucullatus* do not have a terminal sac, I would not be surprised when this character would be found in this species after all, for the situation might be the same as in *C. verrucosus*. In the specimen of this last species, described in this paper, no terminal sac was found either, whereas it has been reported to exist by Beddard (1907). For the rest the description by Beddard fits the present one exceptionally well.

Both *C. tuzetae* and *C. belalandaensis* have characters in common with species of the *C. oustaleti*-group and with species of the *C. rhinoceratus*-group (see Brygoo, Bourgat & Domergue, 1972 and Brygoo & Domergue, 1970 respectively). As to the lung-morphology we find a similar resemblance. The lungs with their terminal sac in both species strongly resemble those of *C. oustaleti*. Moreover *C. tuzetae* has, as we have seen, a gular pouch as well. On the other hand their lungs only bear triple diverticula (next to simple and/or forked ones of course) and no quadruple ones, just like those of *C. rhinoceratus* and *C. antimena*. Within the *C. rhinoceratus*-group there is little variation in lung-structure, except for the length of the diverticula. Next to the triple diverticula, already mentioned above and also found in *C. verrucosus* there are some striking similarities between members of the *C. oustaleti*-group and the *C. rhinoceratus*-group concerning the karyotype and external morphology. The karyotypes of *C. oustaleti*, *C. verrucosus*, *C. angeli* and *C. rhinoceratus* are identical, whereas those of *C. antimena* and *C. labordi* only differ in one chromosome. Hillenius (pers. commun.) pointed out to me the close resemblance of the dorsal crest, the casque and the squamation in *C. verrucosus* and *C. antimena*. Moreover there is the indication of the gular pouch in the species of the *C. rhinoceratus*-group. So in my opinion these inter-group similarities and the intermediate position of *C. tuzetae* and *C. belalandaensis* justifies the assumption of the affinity of the two groups concerned.

This reasoning is also supported when we consider *C. pardalis*. Originally classed within the *C. oustaleti*-group (Hillenius, 1959) but later by Brygoo (1971) in a separate group with *C. belalandaensis* a.o., *C. pardalis* has characters in common with the *C. rhinoceratus*-group as well. For instance Brygoo (1971) states about the hemipenis of *C. pardalis*: "Sa forme se rapproche de celui de *C. oustaleti* avec néanmoins une différenciation apicale et se rattacherait à celle des *C. lateralis* et *C. rhinoceratus*." Moreover the hemipenis of *C. belalandaensis* resembles those of *C. pardalis*, *C. oustaleti*, *C. verrucosus* and *C. lateralis*. The karyotype of *C. pardalis* is identical to the one



of *C. oustaleti* and *C. verrucosus* as described by Bourgat (1973). Previously, in these last two species a slightly different karyotype was described (same number of chromosomes but of different shape). This karyotype is identical to that of *C. rhinoceratus* and *C. angeli*. As to the lungs, *C. pardalis* resembles *C. oustaleti* more than *C. rhinoceratus*, but like the latter species it does not have a gular pouch.

The lung-characters of *C. lateralis* hardly support the other available evidence concerning its affinity. Although the hemipenis of *C. pardalis* and *C. belalandaensis* resembles those of *C. lateralis*, the hemipenis of this last species looks most like that of *C. rhinoceratus* (cf. Brygoo, 1971). The karyotype of *C. lateralis* (24 chromosomes and not 22 as is often stated) is identical to that of *C. antimena*. Thus there is some indication of affinity between *C. lateralis* and the *C. rhinoceratus*-group. However, this view is only supported by the slight resemblance in lung-shape between *C. lateralis* and *C. antimena*.

The lungs of *C. campani*, often classed in one group with *C. lateralis*, resemble those of *C. lateralis*. However, the hemipenis and especially the karyotype of *C. campani* are very different from those of *C. lateralis* (cf. Brygoo, 1971). Therefore the conclusion of Hillenius (1963) to split up this group seems plausible, as the similarities in external morphology are not very convincing either. Contrary to *C. lateralis*, however, the affinity of *C. campani* is obscure. Its lungs and karyotype might suggest some affinity to *C. willsii*, but as their external morphology does not support this, this similarity probably is a coincidence.

Brygoo (1971) classed the related *C. polleni* and *C. cephalolepis* in one group with *C. pardalis* and *C. belalandaensis*, although they only have few characters in common with these latter species. This taxonomical conclusion is not in contradiction with the cytological evidence. All species concerned possess a "continuous" karyotype, that seems to be characteristic of the species of what one might call by now the *C. oustaleti-rhinoceratus*-complex. Actually the karyotype of *C. polleni* is identical to that of *C. antimena* and *C. lateralis* (cf. Bourgat, 1973). However, Brygoo's decision appears a little rash to me, the more so as the lungs of *C. pardalis* and *C. belalandaensis* are absolutely different from those of *C. cephalolepis* and *C. polleni*. The shape of the diverticulate lung of *C. polleni* may remind us a little of the lungs of *C. antimena*. Mostly, however, diverticula are absent and as in various clearly unrelated species the diverticula may be absent as well, the lungs do not provide a decisive answer as to affinity.

The lungs of *C. gastrotaenia* and its subspecies and *C. peyrierasi* do not clear up the still unknown affinity of these species either. The lungs more or less resemble those of *C. polleni* and *C. gallus* for instance, but this similarity is not supported by any other evidence.

The same reasoning applies to *C. tigris*. This species was supposed to be related to *C. pumilus* (cf. Gray, 1864), however, they really have very little in common. *C. tigris* and *C. pumilus* do have the same type of lung, but so do *C.*

*tigris* and *C. cephalolepis* and all other species that do not have diverticula. Moreover the geographical distribution of *C. tigris* and *C. pumilus* is highly discontinuous.

The lungs of *C. mlanjensis* resemble those of *C. tavetanus*. Any close affinity between these two species, however, seems dubious as other characters relate them to quite different species, viz. to *C. adolfifriderici* Sternfeld, 1912 (see Broadley, 1965) and *C. bifidus* respectively.

Lastly the lungs of six Malagasy species are known already from descriptions of Methuen et al. (1914). In case of *C. bifidus* the present description is in accordance with the previous one. As to the lungs of *C. parsonii* var. *crisifer* Methuen & Hewitt, 1913, no obvious resemblance exists as compared with those of *C. parsonii*. The lungs of *C. malthe* also differ from the present description, as they only bear three swollen outgrowths. Contrary to the reduction of outgrowths in *C. brevicornis* mentioned by Methuen et al., various well-developed diverticula were found. Their position, however, is the same, i.e. attached to the ventral wall of the lung. Finally Methuen et al. describe the lungs of *C. nasutus* and *C. gastrotaenia* with few saccular outgrowths, looking very much alike. The lungs of *C. nasutus* as described above do not fit this description, whereas at the most a superficial resemblance exists in the case of *C. gastrotaenia*. On the whole the descriptions and figures presented by Methuen et al. are rather sketchy as compared with those of e.g. Wiedersheim (1886) and Klaver (1973). Therefore I do not consider these differences very important, the more so as only the variable habitus of the lungs is concerned.

### *Geography and evolution*

The fact that *C. mlanjensis* and *C. tavetanus* have a type of lung with septa on the dorsal and ventral wall of the lung entails that, at the present, four continental species are known to have a "Malagasy" type of lung, viz. *C. mlanjensis*, *C. tavetanus*, *C. fischeri* and *C. pumilus*. The expression "Malagasy type of lung" was used for the first time by Klaver (1973). In this paper I distinguished two evolutionary lines within the genus *Chamaeleo*, which I indicated as "continental" and "Malagasy". I still think this distinction to be correct, but to refer to these lines in terms of "continental" or "Malagasy" is not correct. Although probably all Malagasy species belong to the "Malagasy" line, this line is not exclusively confined to Madagascar. We already saw four continental species to have this type of lung as well. Moreover, considering the affinity of the species whose lung-structure is still unknown, I expect the lungs of several other continental species to have a similar septa-arrangement. These species are: *C. adolfifriderici*, probably closely related to *C. mlanjensis*, but it also shows resemblance to *C. polleni* (cf. Hillenius, 1959, 1963); *C. chapini* Witte, 1964 probably related to the previous species (cf. Witte, 1964); *C. carpenteri* Parker, 1929 and *C. xenorhinus* Boulenger, 1901 both included in the *C. rhinocerotus*-group (cf. Hillenius, 1959, 1963); *C.*

*tenuis* Matschie, 1892 and *C. spinosus* Matschie, 1892 both related to *C. nasutus* c.s. (cf. Hillenius, 1959, 1963) and *C. uthmoelleri* Müller, 1938 probably related to *C. tavetanus* (cf. Mertens, 1955).

To be complete I shall also list the remaining species and indicate their (probable) affinity as well as the type of lung I expect them to have.

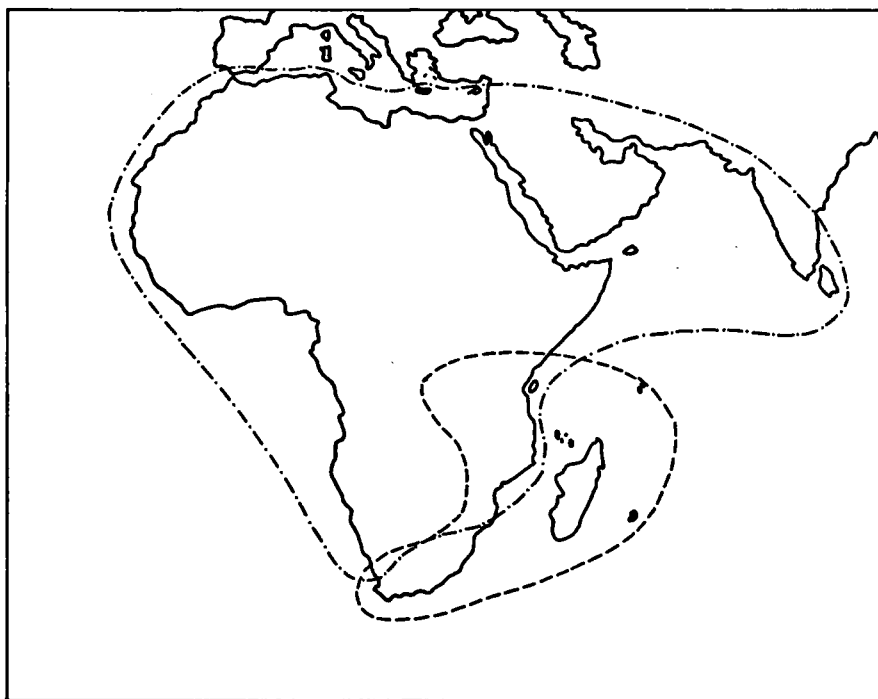
First of all there are five species from Madagascar of which I am convinced they have a similar type of lung as is found in all other Malagasy species, i.e. with various septa on the dorsal and ventral wall of the lung. These species are: *C. angeli* Brygoo & Domergue, 1968 and *C. monoceras* Boettger, 1913 both included in the *C. rhinocerus*-group (cf. Brygoo, 1971); *C. balteatus* Duméril & Bibron, 1851 included in the *C. parsonii*-group (cf. Brygoo, 1971); *C. furcifer* Vaillant & Grandidier, 1880 related to *C. gastrotaenia* (cf. Hillenius, 1959) and *C. linotus* Müller, 1924 included in the *C. nasutus*-group (cf. Hillenius, 1959).

Secondly there are several continental species related to different groups. Consequently they will have a different lung-structure. *C. anchietae* probably has a *C. chamaeleon*-type of lung, for it seems to be related to this species. *C. hoehnelii* Steindachner, 1891, *C. kinetensis* Schmidt, 1943 and *C. schubotzi* Sternfeld, 1912 belong to the *C. bitaeniatus*-group (see Rand, 1963). In all probability their lungs will prove to be similar to those of *C. bitaeniatus* and *C. jacksoni* and perhaps even miss diverticula. According to Hillenius (1959, 1963) *C. incornutus* Loveridge, 1932 and *C. laterispinis* Loveridge, 1932 are closely related to *C. tempeli* a.o. Therefore a septa-arrangement consisting of two large septa connected with the ventral wall of the lung can be expected.

At last six species that are clearly related to members of the *C. cristatus*-group. Hillenius (1963) includes in this group: *C. camerunensis* Müller, 1909; *C. feae* Boulenger, 1906; *C. pfefferi* Tornier, 1900; *C. quadricornis* Tornier, 1899 and *C. deremensis* Matschie, 1892. Mertens (1968) described the remarkable *C. eisentrauti*, which he considers most closely related to *C. quadricornis*.

It is important to notice that the East African *C. deremensis* (locality: Usambara, Tanzania) is included in the mainly West African *C. cristatus*-group. Despite similarities in external morphology this discontinuous geographical distribution of the species makes any affinity unlikely. However, a similar reasoning may apply as was expressed above with relation to the affinity of *C. affinis* and *C. widdersheimi*.

A supplementary remark concerning the lung-evolution is appropriate in this context. In considering the combination of the *C. cristatus*- and the *C. oweni*-group into one group of West and Central African chameleons, I already stated that the differences in lung-structure are gradual and probably representing subsequent stages in lung-evolution (see Klaver, 1973). I still think this is correct, but my ideas about the origin of diverticula probably were faulty. In my former paper the diverticula were supposed to be the remains of an originally larger lung. Indeed, the size of the lungs may have diminished in combination with the development of the anterior respiratory



Map 1. The joint geographical distribution of the species representing two evolutionary lines.  
-.-.-.- = lung-types with 1—3 large septa.  
----- = lung-types with several small dorsal and ventral septa.

part of the lung. However, an active development of diverticula, serving the thermoregulation of the animals a.o., seems to be more plausible than an inactive one (see George & Shah, 1965 and Burrage, 1973). Thus the diverticula function as a ventilating device. Their subsequent evolution is probably linked with the development of the septa and lung-chambers as was exemplified with *C. cristatus* and *C. bitaeniatus* (cf. Klaver, 1973).

To return to the proper subject, some variation in lung-habitus may be found in the remaining species of the *C. cristatus*-group. The septa-arrangement probably will be the same in all species and resembling the one found in e.g. *C. montium*.

Assuming the above considerations to be correct, we now can establish a joint distribution of the species that represent the two evolutionary lines (see map 1). The type of lung with septa on the dorsal and ventral wall of the lung is found in species from East, South East and South Africa, Madagascar, Réunion, the Comoro Islands and the Seychelles. The types of lung of the other evolutionary line (leading from the *C. chamaeleon*-group to the groups of *C. oweni*, *C. cristatus* and *C. bitaeniatus*, see Klaver, 1973) are mainly found in species from North, North East, West, South West and Central Africa and

adjacent countries and islands. Of course there is some overlap. For instance *C. dilepis* is distributed in the east as far as Zanzibar and in the south as far as Natal and Transvaal. As a matter of fact most overlap occurs in East Africa, i.e. overlap with most species involved. Apart from the species, East Africa is the only place where five different basic lung-types (i.e. septa-arrangements) are found, viz. the *C. chamaeleon*-type, the *C. bitaeniatus*-type, the *C. tempeli*-type, the *C. melleri*-type and the *C. fischeri*-type. These facts support the theory of Hillenius (1959), concerning the origin and distribution of the genus *Chamaeleo* from East Africa. According to this theory not the number of species but the number of characters that can be distinguished is largest in East Africa, gradually decreasing from this area to the periphery of the distribution of the genus.

The distribution as sketched in map 1 can be explained very well with the help of Hillenius' theory. East Africa is considered the centre where both evolutionary lines originated. Species of the *C. chamaeleon*-line mainly dispersed to North, West and South West Africa and subsequently gave rise to species such as *C. cristatus*, *C. namaquensis* etc. Species of the other evolutionary line dispersed to the south (*C. mlanjensis* and *C. pumilus*) and especially to the east to Madagascar and adjacent islands. Various factors, viz. the distribution of the species on the continent, the course of the East African rivers such as the Ruvuma and Ruvu and the sea-currents all were in favor of the dispersion to Madagascar by means of rafting. Moreover the composition of the Malagasy fauna corresponds perfectly to an immigration across the Mozambique Channel of African animals brought over at various periods on rough natural rafts (see Millot, 1972 and Blanc, 1972).

As we noted above various continental species still show a close relationship to Malagasy species. Most species of *Chamaeleo* of Madagascar, however, do not show a striking, closer resemblance to any of the species of the continent. Hillenius (1959) therefore assumes two main periods of immigration: "A first period, so long ago that the species that have evolved from it have lost any close resemblance to continental species and a second, more recent period, in which at least three different groups came to Madagascar, viz. *rhinoceratus*-like specimens, *nasutus*-like specimens and *bifidus*-like specimens". He even mentions a later migration in the opposite direction to explain the origin of *C. tenuis*. In my opinion, however, these assumptions are in contradiction with the present knowledge about island biology and the assumed affinity between the *C. rhinoceratus*-group and the *C. oustaleti*-group. Although it is possible that there have been several migrations from the mainland, I do not think it necessary, that the species that still show some resemblance with continental species arrived later than the species lacking any resemblance. On the contrary, the reverse may be true. The congeners, already established on the island and adapted to the local opportunities, force the later immigrants to change dramatically or forestall a successful immigration altogether. This may well be the reason that the later immigrants rapidly lost the resemblance with their continental

relatives, whereas for their predecessors there was no such compulsory reason to do so (see Williams, 1969 and Carlquist, 1974).

Moreover, the hypothesis of Hillenius is invalidated in still another way. According to Hillenius *C. oustaleti* c.s. that do not resemble any continental species, should have arrived on Madagascar before *C. rhinocerotus* c.s. Considering the affinity of the *C. rhinocerotus*-group and the *C. oustaleti*-group it is more likely that the one group evolved from the other on Madagascar. Of course one can hardly expect the species of the "new" group to resemble some continental species. Notice that the lungs of *C. rhinocerotus* c.s. are not principally different from those of, for instance, *C. fischeri*, whereas *C. oustaleti* c.s. have characters that seem to be exclusive for Madagascar, viz. quadruple diverticula and terminal sacs. On the other hand *C. oustaleti* a.o. retained its gular pouch, whereas *C. rhinocerotus* c.s. probably lost it. The relative scarcity of related species in the original source area and the multitude of endemic species on Madagascar also points to autochthonous diversification on Madagascar. The fact that probably all Malagasy chameleons have a similar type of lung, i.e. septa-arrangement, suggests that the number of immigrations was limited indeed. Moreover, various apparently unrelated species do have some characters in common. For instance, both *C. cucullatus* and *C. oustaleti* have quadruple diverticula and a gular pouch. The lungs of *C. cucullatus* and *C. parsonii* have a similar habitus and quadruple diverticula as well. It is tempting to assume that these similarities reflect some affinity and thus autochthonous speciation. The absence of other characters in common does not necessarily contradict this, as "There is a strong implication in the concept of adaptive radiation that products are strikingly different, often exceptional" (Carlquist, 1974). However, whether all this is true or not remains to be seen and certainly requires a better understanding of the Malagasy chameleon fauna.

A reverse migration of *nasutus*-like specimens to explain the existence of *C. tenuis* in East Africa appears unlikely to me. *C. tenuis* has a mountainous distribution which is so characteristic of many other East African chameleons. Moreover, the Ruvu-river and its tributaries almost "drain" potential emigrants from the Usambara Mountains to the Mozambique Channel.

Another striking phenomenon is the apparent inability of *C. dilepis* and the like, to reach or establish on Madagascar. They occur in East Africa as well and species of the same group did not fail to reach other islands, for instance *C. monachus* on Sokotra. It is possible that the ecological requirements of *C. dilepis* are such that the chances to be rafted out to the sea are minimal. Another possibility is that once *C. dilepis* did reach Madagascar he was unable to face the existing ecological conditions and/or the competition already present. It is obvious, that if we want to study the population of Madagascar in depth, ecological studies on chameleons are a prerequisite.

A difficulty that remains to be solved is the inability to link the two evolutionary lines. Perhaps a division of the genus *Chamaeleo* took place

early in its history. Consequently the type of lung with the septa on the dorsal and ventral wall of the lung evolved independently from the lungs of some ancestral chameleon. This is the point of view I favoured in my first paper (Klaver, 1973). However, the absence of striking differences in other characters between the chameleons of the two evolutionary lines do not support such an early splitting and subsequent long and separate evolution. The lungs with the septa on the dorsal and ventral wall of the lung could just as well have been derived from the *C. chamaeleon*-type of lung, just like all other lung-types. Although I still do not see an answer to the question as to how (if at all) this was established, there are some indications.

First of all the vast number of species on Madagascar suggests that their type of lung represents a separate evolutionary line. If Madagascar had not existed, we probably would consider similar lungs in continental species as "just another type of lung", that at the most was hard to link with the other ones. Therefore map 1 gives us a false picture. This type of lung is to be incorporated with the other lung-types, which results in a map that indicates the total distribution of all lung-types, hence the total range of the genus or, if not, the other lung-types have to be mapped separately as well.

Next, the lung-structure of several species from East and Central Africa is still unknown. Especially in these species we might expect to find some intermediate type of lung.

Lastly *C. goetzei* has some remarkable characters, viz. lungs with rather small septa, including a third ventral septum, a gular pouch and pigmented peritoneum and mesenteries. The only species to combine the last two characters is *C. pumilus*. I therefore wonder if some reduction-tendency, affecting the septa-arrangement, could not have altered a *C. goetzei*-type of lung into a *C. pumilus*-type of lung. Of course *C. goetzei* itself does not have to represent the link. As the South East African region with respect to the chameleon fauna is still quite unknown (see Hillenius, 1959, map 20 and 21), one or more species probably are to be discovered yet. Their lung-structure could be decisive in this matter.

Finally I cannot omit to compare the extra small ventral septum found in *C. goetzei*, *C. widdersheimi*, *C. affinis* and *C. ellioti* with the third large ventral septum of *C. melleri*. Perhaps these septa are homologous, which would imply still another possibility in lung-evolution.

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