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## Lung-anatomy: aid in Chameleon-taxonomy

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### ABSTRACT

*Chamaeleo pumilus* is often classified in a separate genus *Microsaura* or *Lophosaura*, partly because of differences in lung-structure as compared with a small number of other species. The validity of this assumption, that is questioned, is investigated by studying the lungs of 17 species. Apart from the two lung-types of *Chamaeleo chamaeleon* and *Chamaeleo pumilus* already known, many other clearly distinguishable lung-types were found. As similarities in lung-structure tend to coincide with the relationships distinguished by taxonomists, the lungs proved to be a useful character in this yet systematically difficult group.

The extensive variation is discussed in view of various processes in action during the evolution of lungs.

Thus it became possible to reconstruct two evolutionary lines, viz. a continental and a Malagasy one, within the genus *Chamaeleo*. The lung-types of the two species mentioned above represent respectively a primitive type in the one and an advanced type in the other line. Therefore the classification of *Chamaeleo pumilus* in a separate genus is not justified by the lung-anatomy.

### INTRODUCTION

In literature on chameleon-taxonomy, the South African *Chamaeleo pumilus* (Gmelin, 1789) and allies are sometimes classified in a separate genus *Lophosaura* or *Microsaura* (both by Gray, 1864). This separation is based on certain differences in lung- and skull-anatomy between these species and some others. In spite of these indeed striking differences, however, there are also taxonomists opposing this view and doubting the validity of another genus.

### HISTORICAL SURVEY

1864 J. E. Gray divides the family Chamaeleonidae into 14 genera, two of them being important here, viz. *Microsaura* and *Lophosaura*. The first one comprising only *Chamaeleo melanocephalus* (Gray, 1864), the

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- second *Chamaeleo pumilus*, *Chamaeleo ventralis* Gray, 1845, and *Chamaeleo tigris* Kuhl, 1820. This subdivision is based on external characters only.
- 1887 G. A. Boulenger publishes his "Catalogue of the Lizards in the British Museum" and in
- 1902 Fr. Werner gives a very comprehensive survey on chameleon-taxonomy. Both authors use external as well as anatomical characters, but, in contrast with Gray (1864) classify *Chamaeleo pumilus* and allies within the genus *Chamaeleo* Laurenti, 1768.
- 1914 P. A. Methuen & J. Hewitt restore the genus *Lophosaura* Gray, 1864, now comprising only all South African forms around *Chamaeleo pumilus*. They think the lungs and skull of these species to be basically different from other, mainly Malagasy species. They obtain additional anatomical data, concerning a few African and a Malagasy species from the paper of Beddard (1907).
- 1932 J. H. Power confirms the view of Methuen et al. (1914) in his brief examination of several specimens of *Chamaeleo quilensis* Bocage, 1866, and various species of the *Chamaeleo pumilus*-group.
- 1943 V. F. Fitzsimons also adopts the idea of a separate genus. However, he emphasizes that the name of that genus should be *Microsaura* Gray, 1864, instead of *Lophosaura* Gray, 1864, for Gray already used that name in 1852 for a genus of South American lizards, now known as *Basiliscus*.
- 1959 D. Hillenius considers *Chamaeleo pumilus* and allies to be one species comprising ten subspecies. He admits that the differences in lung- and skull-anatomy between *Chamaeleo pumilus* and *Chamaeleo dilepis* Leach, 1819, seem quite significant. In his opinion, however, too little is known about the variation of the characters in other groups of species. Therefore he thinks it to be undesirable to establish a separation between two species chosen at random.
- 1966 R. Mertens shares this last opinion as he states: "Ein derartiges Vorgehen wäre nur auf Grund einer morphologischen Untersuchung sämtlicher Chamäleon-Arten möglich." Considering *Chamaeleon pumilus* and allies to be one species, he also questions the validity of the name *Microsaura*, probably because the correct name of a separate genus around *Chamaeleo pumilus* is *Bradypodion* Fitzinger, 1843. After all, *Bradypodion* was the first name of a separate genus of which *Chamaeleo p. pumilus* was the type-species, whereas *Microsaura* is the name of the genus of which *Chamaeleo melanocephalus* (Gray, 1864) (now *Ch. pumilis melanocephalus*) is the type-species.

This study is an attempt to find an answer to the question of variation of one aspect, viz. the lungs within the genus *Chamaeleo*. Therefore, I dissected specimens of 17 species of nine different groups of species. Provenances are unknown. All specimens were kindly put at my disposal by Dr. D. Hillenius,

curator of the Herpetological Department of the Institute of Taxonomic Zoology (University of Amsterdam). To him I am also greatly indebted for his help and criticism, without which this study would not have been completed.

### THE LUNGS

The lungs of chameleons with their peculiar features are already known from descriptions of Meckel (1818), Owen (1832) and Cuvier (1840). These remarkable features are: the numerous tubular caecal outgrowths on the ventral and caudal margin of the lung and the two longitudinal septa, which divide the cavity of the lung into three chambers (see fig. 1). The greater part of the lung, including the septa, is covered with alveoles, which are small and deep in the anterior part of the lung, and which grow wider and shallower backwards. The caecal appendages and often the posterior part of the lung itself lack this alveolar network. This description applies to the lungs of *Ch. chamaeleon* (Linnaeus, 1758).

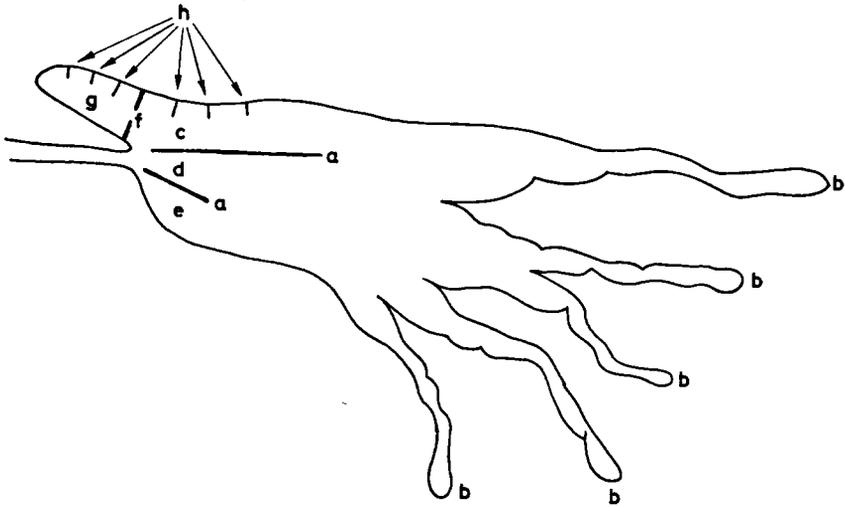


FIG. 1. *Chamaeleo basiliscus* (changed after Milani, 1894). a, longitudinal septa; b, diaphragm; c, dorsal chamber; d, middle chamber; e, ventral chamber; f, diaphragm; g, cranial chamber; h, small dorsal septa.

A second type of lung is found in *Ch. pumilus*. This lung looks like a simple sac without caecal appendages or septa, whereas the total inner surface is covered with alveoles.

In his study of the respiration-system of chameleons, comprising only *Ch. chamaeleon* and *Ch. monachus* Gray, 1864, Wiedersheim (1886) states that the situation in *Ch. monachus* resembles that of *Ch. chamaeleon*. The main difference between these two species consists of differences in number and shape of the appendages. Similar differences may also occur not only between

individuals of the same species, but even between the two sides of the body of the same specimen. He also describes an inflatable gular pouch connected with the trachea, just behind the larynx. Both species possess such a gular pouch.

Milani (1894) investigates the lungs of *Ch. basiliscus* Cope, 1868. In addition to the caecal outgrowth and the two septa, he finds out that the dorso-cranial top of the lung is separated from the dorsal chamber by means of a "diaphragm". In this diaphragm is an opening which connects both lung-sections. On the dorsal wall of the lung are also a few smaller septa, forming a kind of niches (see fig. 1). Milani (1894) also quotes Meckel (1818), who found similar caecal appendages in *Uroplates fimbriatus* and *Polychrus marmoratus*. So this feature is not as characteristic of chameleons as one tends to think and he therefore believes the septa to be more important — as they are constant — than the variable appearance of the caecal appendages.

Beddard (1907) describes the lungs of eight species, viz. *Ch. vulgaris* (= *Ch. chamaeleon*); *Ch. calcarifer* Peters, 1871 (probably *Ch. chamaeleon arabicus*, see Hillenius, 1966); *Ch. dilepis*; *Ch. pumilus*; *Ch. parvilobus* Boulenger, 1887 (= *Ch. dilepis quilensis* Bocage, 1866); *Ch. taeniabronchus* Smith, 1831 (= *Ch. pumilus taeniabronchus*); *Ch. basiliscus* and *Ch. verrucosus* Cuvier, 1829. In accordance with Wiedersheim (1886), Beddard (1907) states that the main differences between them are number and form of the caecal appendages, which they all have except *Ch. pumilus* and *Ch. taeniabronchus*. Considering the variation within the species and even in one individual, he thinks it hardly to be a useful character as distinctive of species unless large series are examined. He is vague about the subdivision of the lung-cavity, except *Ch. calcarifer* resembling *Ch. chamaeleon*, whereas *Ch. pumilus* and *Ch. taeniabronchus* resemble each other.

Methuen et al. (1914) describe only the exterior of the lungs of various, mainly Malagasy species. They call the caecal appendages "diverticula" and from now on I shall do the same. Although they describe lungs with very feebly developed diverticula, which apart from that are similar to those of *Ch. pumilus*, they use the absence of diverticula as an argument to classify *Ch. pumilus* and allies in a separate genus.

In his excellent account of the ontogeny of the lungs of *Ch. bitaeniatus* Fischer, 1884, Broman (1942) describes the development of an aberrant septa-arrangement. The two septa are connected with the ventral wall of the lung. So there is no posterior communication between the three chambers. Broman (1942) states, however, that caudal defects appear in the septa after birth, because of an extensive rise of pressure in the lung. Initially the septa become perforated and the caudal part will vanish ultimately. The result is a septa-arrangement as described by Milani c.s. No gular pouch was found in this species.

The following pages will give the results of my study on the lungs of 17 species. All descriptions fit to text-figures of the left lung only. Important differences between the left and the right lung will be dealt with separately.

**Chamaeleo basiliscus** Cope, 1868 (figs. 2 & 3)

The situation in this species fits exactly Milani's description (1894). There are two septa, of which the dorsal one is the largest. They divide the lung-cavity into three chambers, viz. a dorsal and a ventral one and a chamber in between, that is in a direct line with the bronchus. Caudally a perforation occurs in the septa, that increases and ultimately makes the septa disappear (this is not indicated in the text-figures). So the caudal part of the lung is constituted of one large cavity that terminates in diverticula. There is also a diaphragm that separates a cranial chamber from the dorsal one and moreover there are three small dorsal septa.

Contrary to Milani (1894) I did not find such small septa in the cranial chamber. Six diverticula are present, two of them bifid. Backwards the alveoles become wider and also less distinct because of a decrease in thickness of the alveolar wall. The alveoles in the cranial chamber are somewhat wider than the rest of them in the anterior part of the lung. The septa are also set with alveoles. This description also applies to the right lung except that here only one diverticulum is bifid. A large gular pouch is present <sup>1)</sup>.

**Chamaeleo gracilis** Hallowell, 1842 (figs. 4 & 5)

In this species the lungs show the same general structure as do those of *Ch. basiliscus*. The septa-arrangement is identical, except for the three small dorsal septa, that are absent. There are 12 rather slender diverticula, of which one is bifid. The right lung has ten simple diverticula. The alveolar network is somewhat wider in the cranial chamber and reaches not so far backwards as in the preceding species. The septa are also set with alveoles and a well-developed gular pouch is present.

**Chamaeleo senegalensis** Daudin, 1802 (figs. 6 & 7)

The same septa-arrangement as in *Ch. basiliscus*, viz. two longitudinal septa, a diaphragm and three small dorsal septa. There are 11 well-developed diverticula of different size and often with dilated termination. Four of them are bifid. The right lung has also 11 diverticula, two of them being bifid. The alveolar network is wider in the cranial chamber and extends not so far backwards, except for some scattered alveoles. The septa are also set with alveoles. A gular pouch is present.

**Chamaeleo dilepis quilensis** Bocage, 1866 (figs. 8 & 9)

The septa are arranged as in *Ch. gracilis*. Five diverticula are present, four of them being bifid. The most anterior diverticulum is a large bifid sac. Alveoles cover the greater part of the lung and are not distinctly wider in the cranial chamber. The septa are set with alveoles. The right lung has six diverticula, two of them bifid. A gular pouch is present.

<sup>1)</sup> This pouch occurs in both sexes. Also the absence of it in other species is not sex-linked.

**Chamaeleo dilepis dilepis** Leach, 1890 (figs. 10—13)

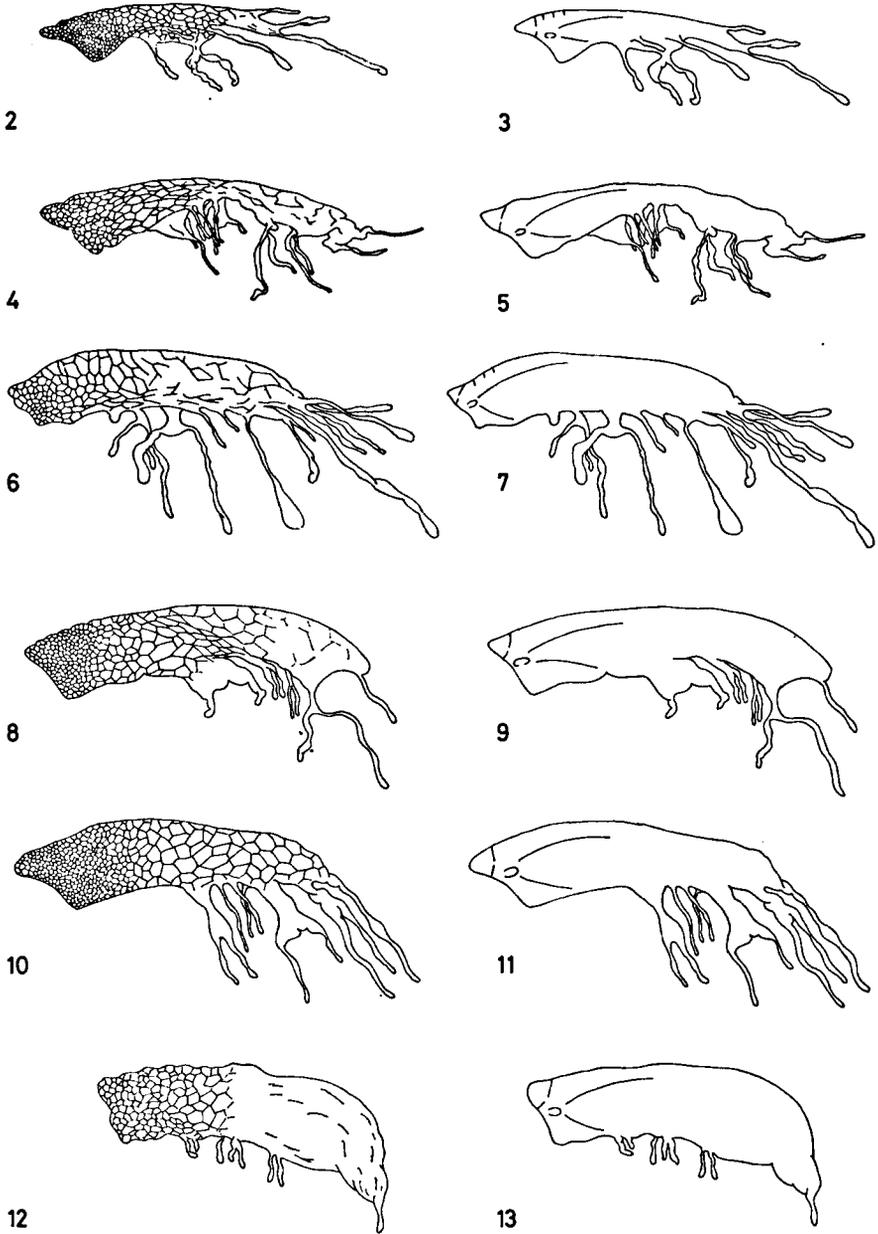
The septa are as in *Ch. d. quilensis*. Seven diverticula are present, three of them bifid and somewhat dilated at the base. The right lung has five simple and one bifid diverticulum. An alveolar network covers the entire lung, including the septa, and is also wider in the cranial chamber. Another specimen of the same species showed a quite aberrant lung-structure (see figs. 12 & 13). Although the septa-arrangement is identical, the lung itself terminates in a large sac without alveoles. The rather wide alveolar network is confined to the anterior part of the lung and is not wider in the cranial chamber. Alveoles are also present on the septa. The diverticula are very short and stout and are clearly different from the ones in preceding species. There are seven diverticula, one of them bifid and one at the end of the sac formed by the lung itself. The right lung has four diverticula, one being bifid. Beddard (1907) describes a similar lung in *Ch. dilepis* and thinks it to be quite different from the lungs he found in *Ch. parvilobus* showing a more current habitus with long clubbed diverticula. Apparently in this yet heterogeneous species there is also some variation to be found in lung-structure. A gular pouch is present in both specimens.

**Chamaeleo chamaeleon zeylanicus** Laurenti, 1786 (figs. 14 & 15)

The septa-arrangement resembles that of the preceding species. Contrary to *Ch. senegalensis* and *Ch. basiliscus*, however, there are four small dorsal septa. Five well-developed diverticula are present, two of them bifid. The right lung does also have three simple and two bifid diverticula. The alveoles in the cranial chamber are not distinctly wider than elsewhere in the anterior part of the lung. Almost all of the lung, including the septa, is covered with alveoles. A gular pouch is present too.

**Chamaeleo cristatus** Stutchbury, 1837 (figs. 16 & 17)

At first sight the lungs look quite like the ones of the species of the *Ch. chamaeleon*-group. Three large diverticula are present. The most anterior one has a small appendage and the middlemost is bifid. The right lung has three simple diverticula. The alveoles, also found on the septa, are rather wide and are not distinctly wider in the cranial chamber. A great difference is found in the septa, that show an aberrant pattern. A large and a small septum divide the lung-cavity into three chambers, of which the middlemost continues in the most anterior diverticulum. No trace of perforation was found in these septa. Anterior to the smaller septum is a very small chamber. Posterior to the larger septum is a chamber that takes up the greater part of the lung. There are also six small dorsal septa, one of them being V-shaped and another situated in the cranial chamber, that is limited by the diaphragm. In the right lung a V-shaped septum is absent. No gular pouch was found.



FIGS. 2-13. Fig. 2, *Ch. basiliscus*, outer aspect; fig. 3, *Ch. basiliscus*, subdivision of the lung-cavity; fig. 4, *Ch. gracilis*, outer aspect; fig. 5, *Ch. gracilis*, subdivision of the lung-cavity; fig. 6, *Ch. senegalensis*, outer aspect; fig. 7, *Ch. senegalensis*, subdivision of the lung-cavity; fig. 8, *Ch. dilepis quilensis*, outer aspect; fig. 9, *Ch. dilepis quilensis*, subdivision of the lung-cavity; fig. 10, *Ch. d. dilepis*, outer aspect; fig. 11, *Ch. d. dilepis*, subdivision of the lung-cavity; fig. 12, *Ch. d. dilepis*, outer aspect; fig. 13, *Ch. d. dilepis*, subdivision of the lung-cavity.

**Chamaeleo melleri** (Gray, 1864) (figs. 18 & 19)

The lung-structure of this species also deviates from the *Ch. chamaeleon*-type of lung.

The lung-cavity is divided by three septa into four successive chambers, which all have connection with one another by means of a dorsal aperture. The most anterior chamber is also limited by a little septum that arises from the cranial wall and it has no diverticula. The second lung-chamber terminates in a single short diverticulum, the third one has three, whereas the last one has five diverticula, two of them bifid. A diaphragm and consequently a cranial chamber are present.

In the right lung the first and the second chamber have no diverticula, whereas the third chamber has three bifid ones and the fourth chamber five diverticula, one of them bifid. Except for the caudal part of the last lung-chamber, the lung is set with alveoles. These alveoles are not wider in the cranial chamber and do appear on the septa. A gular pouch is present.

**Chamaeleo oweni** Gray, 1831 (figs. 20 & 21)

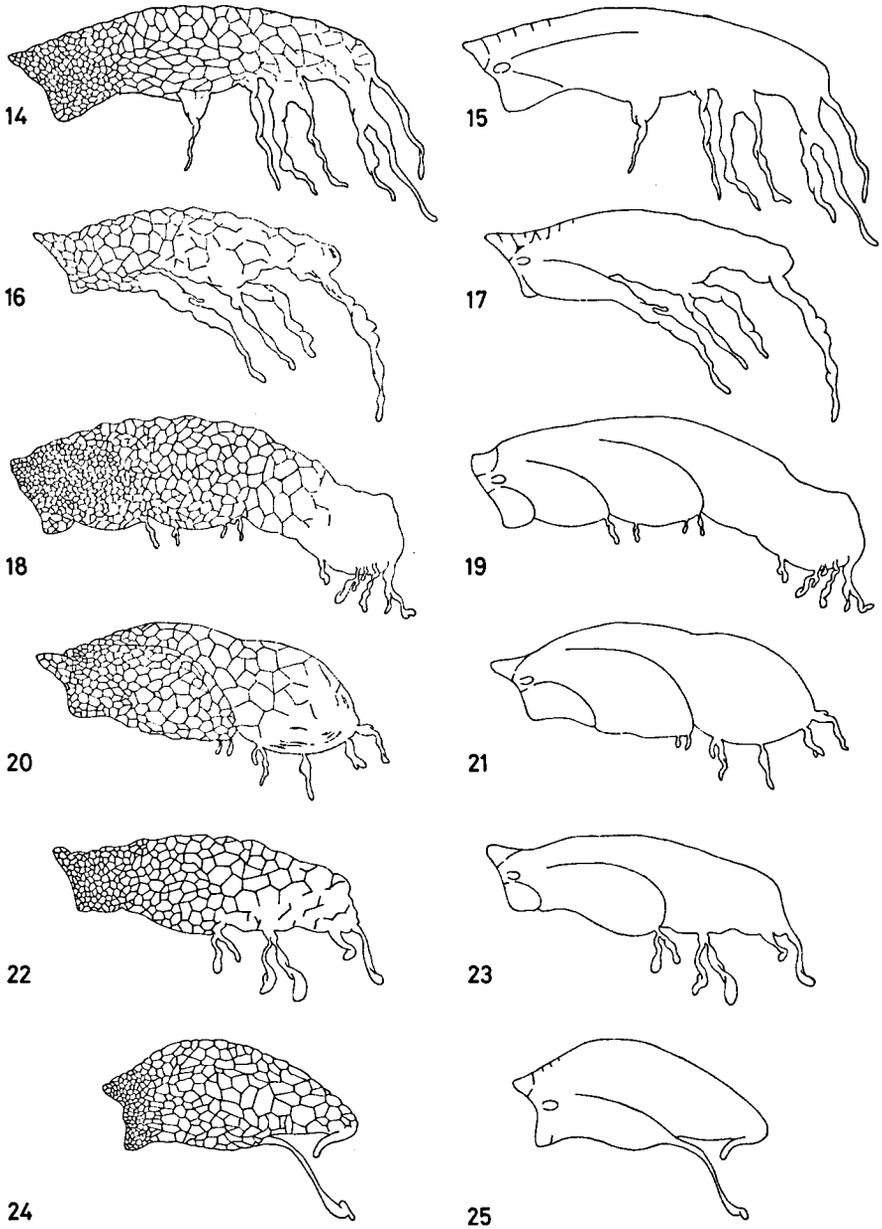
The lungs look much like the ones in *Ch. melleri*. Instead of three septa, however, two septa divide the lung-cavity into three successive chambers, that have also connection with each other by apertures on the dorsal side. The anterior lung-chamber is also limited by a little septum that arises from the anterior wall of the lung and has no diverticula. The middle chamber has two little diverticula, whereas the posterior one has four, two of them bifid. In the right lung only the posterior chamber has diverticula. The alveolar network extends all over the lung, but for the most caudal part of the last chamber. It also occurs on the septa and is distinctly wider in the cranial chamber. There is no gular pouch.

**Chamaeleo johnstoni** Boulenger, 1901 (figs. 22 & 23)

The lungs are almost identical to those of *Ch. oweni*. The lung-cavity is also divided by two uninterrupted septa into three successive chambers. The most anterior chamber is also limited by a small septum arising from the cranial wall of the lung. The second chamber terminates into one bifid diverticulum, whereas the third chamber has two simple and one bifid diverticulum. In the right lung the second chamber has two diverticula and the third chamber four, one of them bifid. A cranial chamber is separated from the rest of the lung by a diaphragm. The alveoles, also present on the septa, are hardly wider in this chamber. Also in this species the gular pouch is absent.

**Chamaeleo bitaeniatus** Fischer, 1884 (figs. 24 & 25)

The lungs differ from those of all species hitherto considered. One septum divides the lung-cavity into two chambers. The anterior chamber proceeds into the most anterior diverticulum. Cranially on the ventral wall of the lung



FIGS. 14-25. Fig. 14, *Ch. ch. zeylanicus*, outer aspect; fig. 15, *Ch. ch. zeylanicus*, subdivision of the lung-cavity; fig. 16, *Ch. cristatus*, outer aspect; fig. 17, *Ch. cristatus*, subdivision of the lung-cavity; fig. 18, *Ch. melleri*, outer aspect; fig. 19, *Ch. melleri*, subdivision of the lung-cavity; fig. 20, *Ch. oweni*, outer aspect; fig. 21, *Ch. oweni*, subdivision of the lung-cavity; fig. 22, *Ch. johnstoni*, outer aspect; fig. 23, *Ch. johnstoni*, subdivision of the lung-cavity; fig. 24, *Ch. bitaeniatus*, outer aspect; fig. 25, *Ch. bitaeniatus*, subdivision of the lung-cavity.

a much smaller septum is present that, however, is clearly distinguishable from the surrounding alveolar-walls.

The larger posterior chamber terminates in the second diverticulum. A diaphragm, a cranial chamber and three small dorsal septa are also present. The right lung is identical to the left one. The alveoles extend all over the lung and are also present on the septa. The alveoles in the cranial chamber are not wider.

The situation described here conforms to the embryonal lung-structure as described by Broman (1942). According to Broman the caudal ends of the septa are perforated at first after birth. The result would be a septa-arrangement as in *Ch. basiliscus*. In the adult specimen I examined, not a trace of perforation was found. The lung-shape and especially the septa also differ from those of *Ch. basiliscus*. I therefore question the statement of Broman about septa-perforation, that is probably due to poor preparation. For instance the septa could have been damaged by insufficient conservation, which brought Broman to consider the septa-arrangement in *Ch. bitaeniatus* to be identical to the apparently common type of lung described by Milani c.s. Apart from that it is also hard to imagine — considering the size of the anterior septum — how even a minor perforation could possibly leave some of the septum-tissue. In accordance to Broman no gular pouch was found.

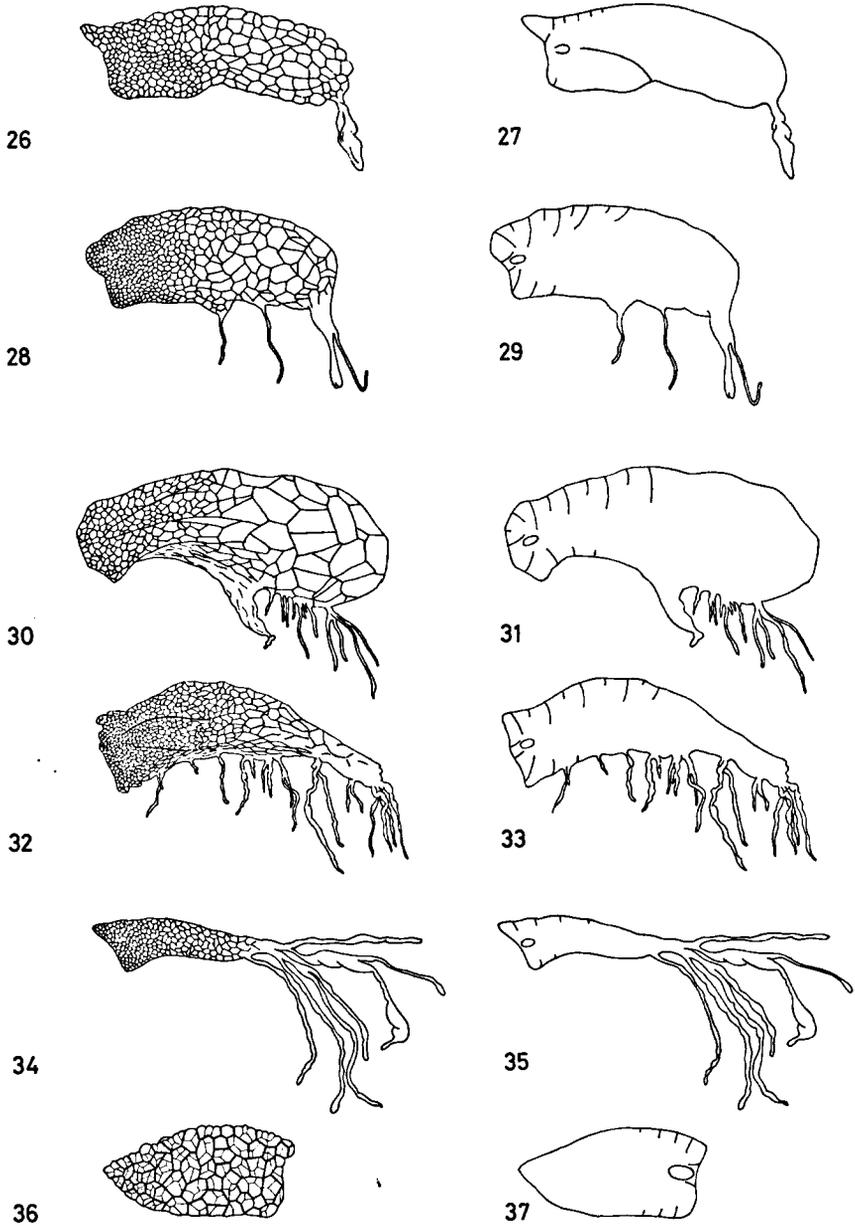
#### **Chamaeleo jacksoni** Boulenger, 1896 (figs. 26 & 27)

The septa-arrangement is much the same as the one in *Ch. bitaeniatus*. One septum divides the lung-cavity into two chambers. The anterior chamber does not terminate in a diverticulum as it does in *Ch. bitaeniatus*. Cranially on the ventral wall there is also a small but clearly distinguishable septum. The posterior chamber terminates in the only diverticulum.

A diaphragm, a cranial chamber and four small dorsal septa are present too. No difference exists between the right and the left lung. The alveolar network is distinctly wider in the cranial chamber and covers the total inner-surface of the lung, including the septa. No gular pouch was found.

#### **Chamaeleo lateralis** Gray, 1831 (figs. 28 & 29)

The septa-arrangement in this and following species is completely different from those of the species hitherto described. There are no longitudinal septa and the presence of a diaphragm is questionable. In the anterior part of the lung 14 septa project into the lung-cavity. Five larger and four smaller septa arise from the dorsal wall, three from the cranial and two from the ventral wall. Those on the dorsal and ventral wall are slightly curved in anterior direction. The size of these septa decreases in posterior direction. The most dorsal septum on the cranial wall and the first one on the dorsal wall form a kind of diaphragm. Three diverticula are present, two of them are quite slender whereas the third one is bifid with one stout and one slender branch. The right lung has six slender diverticula, two of them bifid. The alveolar



FIGS. 26-37. Fig. 26, *Ch. jacksoni*, outer aspect; fig. 27, *Ch. jacksoni*, subdivision of the lung-cavity; fig. 28, *Ch. lateralis*, outer aspect; fig. 29, *Ch. lateralis*, subdivision of the lung-cavity; fig. 30, *Ch. pardalis*, outer aspect; fig. 31, *Ch. pardalis*, subdivision of the lung-cavity; fig. 32, *Ch. oustaleti*, outer aspect; fig. 33, *Ch. oustaleti*, subdivision of the lung-cavity; fig. 34, *Ch. fischeri*, outer aspect; fig. 35, *Ch. fischeri*, subdivision of the lung-cavity; fig. 36, *Ch. p. pumilus*, outer aspect; fig. 37, *Ch. p. pumilus*, subdivision of the lung-cavity.

network extends all over the lung and is not wider in the dorso-cranial lung-top. It is also present on the septa. No gular pouch was found.

**Chamaeleo pardalis** G. Cuvier, 1829 (figs. 30 & 31)

The septa-arrangement is almost similar to that of the previous species. On the dorsal wall four large and three small septa are found, all curved in anterior direction. The size of these septa does not decrease in posterior direction. On the cranial wall three large and one small septum are present, whereas three septa, decreasing in size, are found on the ventral wall. The lung is covered with alveoles which are very wide in the posterior sac-shaped part of the lung. The right lung also terminates in a sac, although this is less extreme.

This difference is probably due to the extent of contraction or contents on the moment of preservation. The alveoles are not wider in the dorso-cranial lung-top and also occur on the septa. There are two muscular bands on the lateral wall of the lung. Furthermore nine diverticula were found, the most anterior one being much dilated and the most posterior one fourfold. There is no gular pouch.

**Chamaeleo oustaleti** Mocquard, 1894 (figs. 32 & 33)

On the dorsal wall five large and four small septa are found, which decrease in size. In accordance with both previous species the septa are curved in anterior direction. There is also a kind of diaphragm. Three septa are on the cranial wall and two on the ventral one. There are eight diverticula, four of them bifid. Two diverticula, including the most posterior one, are fourfold. The right lung has ten diverticula, of which three are bifid and even five fourfold. The lung terminates in a slender sac and is almost entirely covered with alveoles, that are also found on the septa. The alveoles are not wider in the dorso-cranial lung-top. There are two muscular bands on the lateral wall of the lung. A gular pouch is present.

**Chamaeleo fischeri** Reichenow, 1887 (figs. 34 & 35)

Four dorsal and two ventral septa were found. Septa on the cranial wall were not observed. The septa-arrangement described may be incomplete as the result of the rather bad condition of the contracted lung. The alveolar network extends all over the lung and also occurs on the septa. The lung itself is small compared with the well-developed diverticula. Three diverticula are present, two of them being forked in such a way that seven branches are constituted. The right lung has five diverticula, one of them bifid. No gular pouch was found.

**Chamaeleo pumilus pumilus** (Gmelin, 1789) (figs. 36 & 37)

At last the lung-structure of the species causing the controversy. As Beddard (1907) already stated the lungs are relatively as well as actually

smaller than those of other species and thus take up a smaller part of the coelom. The left lung is about half the size of the right one. Diverticula are not present. The alveolar network covers the entire lung and it is more complicated compared to that of other species. The network is formed by thick walls that enclose wide alveoles. These alveoles are subdivided by smaller and less thick walls into smaller alveoles. In their turn these last alveoles may also be subdivided.

The alveoles bounded by the thick walls are largest in the anterior part of the lung and get smaller posteriorly. This is in contradiction to Meckel (1818), who found the posterior alveoles the largest. Contrary to what is indicated in fig. 36, the posterior part of the alveolar network is hardly visible from the exterior. From earlier descriptions, except the one of Meckel perhaps, it is obvious that the lung-cavity is not subdivided by septa. The lung is a mere air-sac. I, however, distinguished various small septa, as is indicated in fig. 37. Four septa, decreasing in size, were found on the dorsal wall, two on the cranial and three on the ventral wall. So *Ch. p. pumilus* has a septa-arrangement that is not principally different from those of other chameleons. A gular pouch is present.

#### DISCUSSION

Apparently there is not only variation in number and shape of the diverticula but also in the shape of the lung itself and in the number and form of the septa. Similarities in lung-structure are not accidental, but coincide with the relationships distinguished by taxonomists.

At first we shall consider the group of *Ch. chamaeleon*. Wiedersheim c.s. already described the lung of this species extensively. This lung has a large number of diverticula, an alveolar network and two longitudinal septa. I myself also found a cranial chamber with a slightly wider alveolar network, separated from the dorsal chamber by a diaphragm. Distinct small dorsal septa were absent. The taxa with a similar lung-structure are: *Ch. basiliscus*, *Ch. gracilis*, *Ch. senegalensis*, *Ch. ch. zeylanicus*, *Ch. d. dilepis* and *Ch. d. quilensis*.

Differences within this group concerning the possible presence of the small dorsal septa and a wider alveolar network in the cranial chamber are probably irrelevant. These small structures might have got lost by respectively insufficient conservation and contraction of the lung-tissue. Thus it seems likely that these characters within this group are general and that the differences described are artefacts. Examination of more specimens of the species concerned might be decisive. An exception is the specimen of *Ch. d. dilepis* with its sac-shaped lung and small diverticula, being clearly distinguishable from the other species of this group, including its congener. The septa-arrangement, however, is corresponding. Another similarity between the species of the *Ch. chamaeleon*-group is the presence of a gular pouch.

The lungs of some other representatives of this group and more or less related species are known from previous publications. Wiedersheim (1886) describes the lungs of *Ch. monachus*, which are almost identical to those of

*Ch. chamaeleon*. Another similarity between these two species is the presence of a gular pouch. This confirms the relationship of both species as is assumed by Hillenius (1959 & 1963).

Beddard (1907) states about the lungs of *Ch. calcarifer*: "They show the same general structure as do those of *Ch. vulgaris*." As *Ch. calcarifer* is closely related to *Ch. chamaeleon* (see Hillenius, 1966), the anatomical and taxonomical data are also in accordance.

Methuen et al. (1914) give a description of the lungs of *Ch. namaquensis* Smith, 1831: "The lungs were found to have several long diverticula distally and ventrally, but they were not so numerous as in *Ch. dilepis*." As nothing is known about a possible septa-arrangement, this is only a partial and rather weak confirmation of the assumed relationship of this species with *Ch. chamaeleon* c.s.

Hillenius (1959 & 1963) classifies *Ch. melleri* together with *Ch. monachus* and *Ch. namaquensis* in a group of species which he thinks to be more or less related to the group of *Ch. chamaeleon*. As there are similarities as well as differences between *Ch. monachus* and *Ch. melleri*, he assumes that *Ch. melleri* can only be connected indirectly with the *Ch. chamaeleon*-group. The diverticula, the shape of the lung and especially the septa-arrangement in *Ch. melleri*, however, resemble by no means those of *Ch. chamaeleon* and *Ch. monachus* and thus do not support the classification of the species last mentioned and *Ch. melleri* in one group.

Considering the lung-structure *Ch. melleri* rather resembles *Ch. oweni* and *Ch. johnstoni*. The lungs of the last two species are — as far as the septa-arrangement is concerned — practically identical. Furthermore both species lack a gular pouch. Hillenius (1959 & 1963) regards them as very closely related as he classifies them into one group. So in this case the taxonomical data are confirmed by anatomical evidence too. Important differences between *Ch. oweni* and *Ch. johnstoni* on the one hand and *Ch. melleri* on the other, are the presence of a third septum and a gular pouch in *Ch. melleri*. I hope to demonstrate in the discussion of the lung-evolution, that in spite of the aberrant lung-structure *Ch. melleri* is related — although indirectly and probably not via *Ch. monachus* — to the *Ch. chamaeleon*-group and not to the *Ch. oweni*-group.

The relationship of *Ch. bitaeniatus* and *Ch. jacksoni* is confirmed too by the anatomy of the lungs. Except for one diverticulum the lungs are practically identical. As to the size of the alveoles in the cranial chamber, the same consideration can be hold as is pointed out above. Another similarity is the absence of a gular pouch in both species.

*Ch. cristatus* occupies a special position among the species I examined. The shape of the lung and the diverticula resemble those of *Ch. chamaeleon* c.s., whereas the septa-arrangement looks more like the one of *Ch. bitaeniatus*. The absence of a gular pouch in *Ch. cristatus* adds to the latter resemblance. Hillenius (1959 & 1963), however, mentions a possible relationship between the group of *Ch. cristatus* and that of *Ch. oweni* and although there

are great differences in lung-structure I hope to confirm hereafter this assumption to be correct.

Beddard (1907) gives a description of the lungs of *Ch. verrucosus* resembling those of *Ch. oustaleti* in more than one aspect. The "caecal outgrowth borne in tufts" and the "outgrowth of the lung itself" in *Ch. verrucosus* are undoubtedly comparable with respectively the fourfold diverticula and the narrow terminal sac in *Ch. oustaleti*. The shape of the lung in *Ch. pardalis* does not resemble those of the two preceding species to such an extent, but there is also a fourfold diverticulum. Just as *Ch. oustaleti*, *Ch. pardalis* has muscular bands on the lateral wall of the lung. So far the anatomy is more or less in accordance with the taxonomy, according to which these three species are closely related. A difference between *Ch. oustaleti* and *Ch. pardalis* however, is that a gular pouch was found in *Ch. pardalis* and not in *Ch. oustaleti*.

As to the habitus of the lungs of *Ch. fischeri*, classified in the *Ch. bifidus*-group it is similar to that of *Ch. bifidus*, known from the description of Methuen et al. (1914). These authors mention the lung of *Ch. bifidus* to be much contracted; a similar phenomena occurred in the specimen of *Ch. fischeri* I dissected. It is likely to expect, considering their relationship and similarity in shape of the lung, that the septa-arrangement in *Ch. bifidus* — and perhaps in the whole group — is of the same type as is the one of *Ch. fischeri*.

The differences and similarities in lung-structure as described above could develop by various processes in action during the evolution of lungs. According to Marcus (1937), Goodrich (1930), Moser (1902) and Wolf (1933) lungs have changed from large smoothly-walled air-sacs into small organs, complicated and effectuated by septa and alveoles. Respiration, originally dealt with by the total lung, gets confined to the most anterior part of the lung. In this section the lung becomes set with alveoles and also septa develop to conduct air over them. The caudal part of the lung thus becoming less important for respiration, remains functional as a mechanical or ventilating section. A similar process occurs in the cranial chamber (Wolf, 1933). The alveoles, if present at all, become wider and eventually may even disappear completely. As the total respiratory surface increases through the alveoles-development, it is possible for the lung to get smaller. This actually happens by degeneration of the caudal part of the lung. Through a more effective control of the air-currents in the lung by the septa, the caudal part also may loose its last function, thus facilitating further reduction. Various stadia of these processes can be distinguished in chameleon-lungs.

In *Ch. chamaeleon* and allies the lung is already divided into an anterior respiration-section with septa and alveoles, and a mechanical section consisting of the cranial chamber and the caudal part of the lung. The cranial chamber as well as the caudal part of the lung, except for the diverticula, are still set with an alveolar network, which, however, has become wider and diffuse as the result of reduction. The development of the anterior section

allows the lung to decrease, but a posterior mechanical section (still) is necessary. This results in a partial reduction of the caudal part of the lung. The vestiges are the diverticula reminding so strongly of the air-sacs in the lungs of birds <sup>2)</sup>).

According to Milani (1894) the diverticula were developed in a different way. He also starts from a lung originally lacking diverticula and septa. Two uninterrupted septa are developed on the caudal wall of the lung. Growing larger and forwards the septa divide the lung-cavity into three chambers and tend to stagnate the communication between them. In order to maintain the mutual communication and the communication with the bronchus, openings in the septa remained necessary. Milani (1894) presumes that the caudal parts of the septa are resorbed by the development of diverticula. The perforation of the septa would point in this direction. The diverticula might have developed from outgrown alveoles.

This process of diverticula-development is reversed to the more recent view described above. It implies, that a lung with two uninterrupted septa and without diverticula is resembling most the ancestral one with septa within the genus *Chamaeleo*. A lung of this structure is unknown and the ones which approximate this description most are those of *Ch. oweni* c.s. The septa are not perforated caudally, but small diverticula are already present. These diverticula still can be considered to be the initial phase, not yet resulted into perforation, but even then objections can be made. The lung of *Ch. oweni* c.s. then would be the most ancestral one within the genus *Chamaeleo* and that is in contradiction with Hillenius (1959), who demonstrates that *Ch. chamaeleon* s.l. resembles most the ancestral chameleon.

The ontogeny of the chameleon-lung also gives an indication that the diverticula cannot have been developed in the way described by Milani (1894) from "Nischen und Taschen", for in the embryo-lung first the diverticula are developed and thereafter the alveoles. A possible cause for the development of the septa and their function as described by Milani (1894) is obscure. This is not the case in the alternative hypothesis, in which the septa are developed to divide and conduct the air entering the lung. As to the posterior communications I do not see the necessity for their development as in all known septa-arrangements there are still large anterior communications.

So it seems more likely to me that diverticula are remains of an originally larger lung, the more so as the reduction of diverticula occurring within the genus *Chamaeleo* can be explained in terms of the logical continuation of the processes which gave rise to them, and also because the species lacking longitudinal septa do have diverticula. In this last case one can object that the septa already have completely disappeared. This implies, however, that there has been an unnecessary resorption of the septa, for a sufficient communication does not require a total absence of septa. Furthermore this assumed

<sup>2)</sup> Apart from the ventilating function, the diverticula are also used to inflate the animal impressively during threat-displays.

extensive resorption would have resulted in a proportional diverticula-development i.e. large and perhaps many diverticula. This is not the case in the species concerned here.

Considering the lungs of *Ch. chamaeleon* s.l. resembling most the one of the ancestral chameleon, we now can derive the other types from it. I want to start with the type of *Ch. oweni* and *Ch. johnstoni*. The septa have developed and are now connected with the ventral wall of the lung. The diverticula are small, which probably is not due to reduction but to little decrease of the lung itself. Indeed the lungs of these species are relatively large as compared to those of, for instance, *Ch. bitaeniatus* and *Ch. pumilus*, in which a considerable degeneration of the caudal part of the lung must have occurred. The similarity in shape of the lung and diverticula between *Ch. oweni* and *Ch. johnstoni* and the aberrant form of *Ch. d. dilepis* is striking. So it is likely that the lungs of *Ch. oweni* c.s. originate from a similar type of lung. Within the *Ch. chamaeleon*-group this aberrant type of lung of *Ch. d. dilepis* approximates the ancestral chameleon lung most. In *Ch. chamaeleon* c.s. the lungs have already decreased, hence larger diverticula developed. So the lungs of *Ch. oweni* and *Ch. johnstoni* are qua shape and diverticula primitive, but qua septa-arrangement advanced. Associated with the septa-development is the change in chamber-arrangement. The anterior chamber in *Ch. oweni* c.s. is homologous with the ventral one in *Ch. chamaeleon*, the most posterior chamber is homologous with the dorsal one and the chamber in between with the middle one.

The lungs of *Ch. melleri* have developed in a similar way as those of *Ch. oweni* c.s. The lungs are also still relatively large, have small diverticula, whereas the septa reach the ventral wall too. Because of the presence of a third septum, however, *Ch. melleri* occupies a unique position. Consequently nothing can be said of a possible homology of chambers and septa. In view of similarities between the *Ch. chamaeleon*-group and *Ch. melleri* in chromosome-pattern and external characters, the similarity in lung-shape and the superficial resemblance in septa-arrangement between *Ch. melleri* and *Ch. oweni* c.s. are probably due to convergence. So the lung-structure supports the idea of Hillenius (1959 & 1963), who considers *Ch. melleri* a rather isolated species, indirectly related with the *Ch. chamaeleon*-group.

In *Ch. cristatus* the two septa are also connected with the ventral wall of the lung. The lung has already decreased, whereas the diverticula increased. In a lung with a similar septa-arrangement the diverticula only have to ventilate a certain part of the lung, viz. the chamber which they are connected with. In *Ch. cristatus* the chamber, that is bounded by both septa and terminates in a single diverticulum, is responsible for a considerable part of the respiration. This particular chamber with its diverticulum is a functional unit, i.e. a kind of small lung within the lung itself. Apparently a more efficient ventilation of this chamber is achieved by one large diverticulum than by several small ones and this results in a numeral decrease and the development of one diverticulum. The small chamber, cranial to the smaller septum, is homologous with the ventral one in *Ch. chamaeleon* c.s. and with

the anterior one in *Ch. oweni* c.s. Just as in *Ch. oweni* c.s. it lacks diverticula. This chamber depends on other parts of the lung for its ventilation, especially on the chamber directly behind it. To utilise the ventilation of this chamber as efficiently as possible, the smaller septum, being an obstacle, has to disappear. In *Ch. cristatus* this septum is still quite large, but compared to that of *Ch. oweni* c.s., some reduction is obvious.

Further reduction of this septum has occurred in *Ch. bitaeniatus* and *Ch. jacksoni*, where it is no longer possible to distinguish an anterior chamber. Only two chambers are left, the anterior one being homologous with the middle one and the posterior one being homologous with the dorsal one in *Ch. chamaeleon* c.s. Two diverticula are left, each at the end of a chamber. More diverticula on the posterior chamber are developed in the embryo, but they disappear ultimately. The lungs have decreased and are now completely covered with alveoles.

In *Ch. jacksoni* the diverticulum of the anterior chamber is lost too. The reduction of this diverticulum was possible for the air that enters the lung is divided between both chambers by the only septum left. The presence of a diverticulum of its own is not an absolute necessity anymore and reduction could occur. It is possible that within the *Ch. bitaeniatus*-group there is a species that also lacks the last diverticulum. The ventilation then would be provided by the lung itself, a process which might be of some importance too in *Ch. bitaeniatus* and *Ch. jacksoni*, thus representing another factor reinforcing diverticula-reduction.

As *Ch. bitaeniatus* and *Ch. cristatus* differ in characters such as chromosome-pattern, o(vovi)viparity and external characters, the similarity in septa-arrangement and also the absence of a gular pouch is probably due to convergent evolution.

The assumed relationship of the groups of *Ch. oweni* and *Ch. cristatus* is not in contradiction with the lung-anatomy. Although the lungs do not resemble to such an extent, it is possible to derive the lungs of *Ch. cristatus* from those of *Ch. oweni*. The lungs have decreased and consequently the diverticula increased, but the number diminished. The septa-arrangement is almost identical except for the anterior septum that already is reduced somewhat in *Ch. cristatus*. Another similarity between the representatives of both groups is the absence of a gular pouch.

Finally we shall consider the type of lung with the small septa on the cranial, ventral and dorsal wall. As large diverticula may be present, we can assume, that also during the evolution of this type of lung, the lung has decreased and a separation occurred in a respiratory and a mechanical section. The septa-arrangement does not fit in the evolutionary line described above. It is possible that this type of lung has derived independently from a *Ch. chamaeleon*-type of lung. In that case the small dorsal septa, already present, would have shown further development. In addition similar septa would have developed on the cranial and ventral wall of the lung. As the septa grow larger onto the longitudinal septa, the niches bounded by them, tend to be

separated from the rest of the lung. This is prevented by an increasing perforation in the two longitudinal septa. This theory is supported by the fact that the line connecting the ends of the septa coincides more or less with the two longitudinal septa in species of the *Ch. chamaeleon*-group.

Another, and in my opinion a more acceptable possibility, is that this type of lung evolved independently from the lungs of the ancestral chameleon. In that case two independent evolutionary lines can be distinguished within the genus *Chamaeleo*: 1) the line described above leading from the *Ch. chamaeleon*-group to the groups of *Ch. oweni*, *Ch. cristatus* and *Ch. bitaeniatus*, and that seems to be confined to the species of continental Africa and adjacent countries. 2) the evolutionary line leading from the simple lung of the ancestral chameleon to the type of lung, which seems to occur only in Malagasy species and their continental relatives. The absence of a distinct diaphragm also suggests this last possibility.

The coincidence of the longitudinal septa with the line connecting the ends of the septa, can also be explained in this case. In the *Ch. chamaeleon*-type of lung two septa conduct a part of the air to the dorsal and ventral wall. These walls thus become more involved in respiration. A similar effect can be achieved with septa on the dorsal and ventral wall of the lung. These septa should extend so far into the lung-cavity, that they can intercept the air entering the lung. If these septa are also curved in the direction of the bronchus-aperture, the air still present in the niches will be refreshed adequately. Thus the coincidence of the longitudinal septa with the line that connects the ends of the septa, is not accidental but rather necessary to make the respiration as efficient as possible.

The septa-arrangement in various species is hardly different and therefore it is impossible to reconstruct an evolutionary line. The diverticula-reduction, that also occurs in this type of lung is not correlated with a development of septa and chambers as in the preceding one. The number of diverticula remains rather haphazard but is reduced as the lung decreases. The shape of the diverticula is characteristic as for instance in *Ch. oustaleti* and in *Ch. verrucosus*.

In view of the septa-arrangement I consider *Ch. pumilus* to be a representative of this last evolutionary line. Beddard (1907) as well as Methuen et al. (1914) describe lungs of which the diverticula are different in number and development. Therefore in both publications a reduction of the diverticula is mentioned. However, the authors do not conclude that the ultimate result of a reduction-tendency is the total absence of diverticula, hence a situation as is found in *Ch. pumilus*. Contrary to this opinion they consider the lungs of *Ch. pumilus* to be unique and use this character, together with some others, to classify *Ch. pumilus* in a separate genus.

In my opinion this proceeding is not correct. Indeed the lungs of *Ch. pumilus* are aberrant from the "typical" chameleon-lung, generalized until then, but the absence of diverticula is to be considered as a gradual difference. In this species the lungs have considerably decreased and all diverticula are reduced as well. To guarantee a sufficient respiration the alveolar network

got more complex. So the simplicity of structure, that is to say the absence of diverticula, is secondary instead of primary, as Methuen et al. (1914) want us to believe.

As I already mentioned in the introduction, Methuen et al. (1914) also described lungs that, apart from some underdeveloped sac-shaped diverticula, resemble the lungs of *Ch. pumilus* very much. There are similarities in shape of the lung and in alveolar network. The species concerned are *Ch. nasutus* Duméril & Bibron, 1836, and *Ch. gastrotaenia* Boulenger, 1888. As small species are concerned, Beddard (1907) assumes that the simplicity of structure is associated with the small body-size. At the most this is partially correct, because the evolution of the lungs does not primarily depend on a decreasing body-size, as also larger species like *Ch. tigris* seem to lack diverticula (Methuen et al., 1914).

According to Hillenius (1963) *Ch. nasutus* and *Ch. gastrotaenia* on the one hand and *Ch. pumilus* on the other are not closely related. Obviously the reduction-tendency within the genus *Chamaeleo* gave rise independently and several times to convergent lung-structures. Consider in this context also *Ch. bitaeniatus* and *Ch. jacksoni* in which the lungs are decreased too and the number of diverticula diminished, but which belong to another evolutionary line. This convergence in lung-shape between *Ch. pumilus* and *Ch. nasutus*, however, coincides with a convergence in chromosome-pattern of *Ch. pumilus* and a representative of the *Ch. nasutus*-group, viz. *Ch. gallus* Günther, 1877. As double convergences are unlikely, these resemblances perhaps do suggest some relationship between this South African group of chameleons and some of the species of Madagascar. The more so as the geographical distribution of the type of lung concerned demonstrates that — apart from the obviously related species as *Ch. fischeri* — *Ch. pumilus* seems to be the only continental species that is apparently not related to any Malagasy species, but does have a “Malagasy” type of lung.

As to the geographical distribution of the separate lung-types, this tends to coincide with the range of the species (*Ch. melleri*) or with the range of the groups of species (*Ch. chamaeleon* c.s., *Ch. oweni* c.s. etc.).

All lung-types are found in East Africa and their number gradually decreases from this area to the periphery of the distribution of the genus. So the lung-types also have a concentric distribution just as the external characters and the chromosome-pattern as was demonstrated by Hillenius (1959 & 1963), thus supporting his ideas about the origin and distribution of the genus *Chamaeleo*. It is, however, remarkable that the most general and widely distributed type of lung i.e. the *Ch. chamaeleon*-type, probably has failed to reach Madagascar. Only representatives of the evolutionary line that gave rise to the lungs with the dorsal, cranial and ventral septa seem to have managed to migrate to Madagascar.

Finally I may conclude that the morphology of the entire lung, and not for instance only that of the diverticula or the habitus, is of great importance to the taxonomy, especially when the external characters are inconclusive.

APPENDIX

In literature, very little is known about the pigmentation of the interior of the body. Beddard (1907) states, that among the species he examined there were only two, viz. *Ch. pumilus* and *Ch. taeniabronchus*, which had a totally black pigmented parietal peritoneum and mesenteries. In all other species examined the pigmentation was absent in the peritoneum and did only occur very slightly in the mesenteries.

In the introduction of his publication Beddard (1907) speaks of: "anatomical facts concerning the genus, which are also of classificatory importance." He concludes his remark about pigmentation with: "This peculiarity at once divides the two species mentioned from the rest, and other anatomical peculiarities in the present communication tend to show the separateness of these Chamaeleons from the others." It appears that Beddard is one of the first to classify these two species, if not in a separate genus, then at least in a clearly distinguishable group of species.

As I mentioned in the introduction, Methuen et al. (1914) actually re-established a separate genus *Lophosaura*. Although they mention the pigmentation to exist within this group of chameleons, they do not use this character in their argumentation! I found that black pigmented peritoneum and mesenteries are not only confined to *Ch. pumilus* and allies. It was also found in *Ch. bitaeniatus* and *Ch. jacksoni*. In the other species examined there was no peritoneum pigmentation and only a very slight pigmentation of the mesenteries.

Apparently this character tends to be confined to species that are ovoviviparous. This can be due to the fact, that the two groups of ovoviviparous chameleons distinguished by Hillenius (1959), viz. the *Ch. bitaeniatus*-group and *Ch. pumilus*-group, are more or less closely related. In my opinion, however, the similarity in pigmentation can be ascribed to a convergent evolution because of the presence of marked differences as well.

Just like ovoviviparity, pigmentation might be considered as an adaptation to life at high altitude. The function of the pigmented parietal peritoneum would be to protect the interior of the body — and in particular the gonads — against the harmful effects of the surplus of ultra-violet in the sunlight. Pigmentation is not in the first place a protection for the developing embryo's for it also occurs in males.

In accordance with Beddard (1907) the intestinal tract was deep black, without any variation. In general stomach and oesophagus were unpigmented except in *Ch. fischeri* and *Ch. melleri*. In both species the hinder part of the pharynx and the oesophagus were pigmented as deep black as the intestinal tract. The stomachs were not pigmented.

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