This is a facsimile of


translated into English.

I tried to retain the feel of Wolf’s language. That combines with the need to put accuracy before literary smoothness of the translation to make for awkward grammar and odd wordings.

All text and figures, the latter at the exact print size of the original, can be found on the correct page numbers, so that this translation can be cited just like the original text.

Heinrich Mallison, Jan 14, 2014.
On the construction and function of the reptilian lung

By
Siegfried Wolf (Dresden)
(from the Zoological Institute of the Saxonian Technical University at Dresden.)

With 45 text figures.
Table of Content.

I. Introduction ................................................................. 139
II. Problem statement ...................................................... 142
III. Findings on lacertilian lungs ......................................... 144
IV. Findings on chelonian lungs ......................................... 152
V. Findings on ophidian lungs ........................................... 157
VI. Comparisons ............................................................. 168
Appendix (periodic breathing in Emys) ............................ 177
Summary ................................................................. 188
Reference list ............................................................. 189

I. Introduction

The work presented here sets out to investigate certain relationships between reptile and bird lung and if possible to resolve them. It is based on the study of many reptile lungs and observations on living animals. In order to present a more or less complete overview some findings already known had to be presented again, which could previously not be sorted under encompassing aspects and analysed for general insights.
The Appendix reports on a test series on *Emys europaea*, the results of which illuminate and confirm the finding of the main part from a different aspect.

The richness of variations of the reptile lung drew interest early on. During comparative morphological studies there was no avoiding the recognition that the lungs of some chamaeleonts showed appendices reminiscent of corresponding parts of bird lungs.

As is generally known, the breathing apparatus of birds differs totally from the rank of lung types usual in vertebrates by the possession of air sacs.

The lungs of some chamaeleonts now possess similar membranous appendices. In fact, they do not show such a significant size as the air sacs of birds, but present only as air-conducting lobes of varying number and expression at the caudal end of the lung. At least the external similarity to air sacs of the bird lung is big enough that once they became known one was inclined to view the chamaeleont lung form as a predecessor of the bird lung.

In 1894 Milani became convinced that such a conclusion went too far. To wit, he found corresponding membranous appendices of the lung also in *Uroplatus fimbriatus* and *Polychrus marmoratus*. However, because he found on the lungs of *Chamaeleon*, *Uroplatus* and *Polychrus*, except for the air sac like shapes, no other reminiscences to the bird lung, and because these lacertilians are not closely related by the construction of the breathing organs otherwise or in other respects, he did not assign their abnormal lungs any special importance. Based on his morphological study he assumed that such protrusions may theoretically appear on any lacertilian lung. This assumption was confirmed 10 years later by Fanny Moser (1902) via ontogenetic studies.

Such considerations could back then have been taken as cause for an investigation into the diverse relations between reptile and bird lungs. The impulse had to proceed without result, as two important factors opposed a clarification. Firstly, the reptile lung was not placed at its proper place in the suspected course of development.
Generally, it was in the past assumed that the lungs of vertebrates had a quite uniform developmental path. MECKEL (1818), F.E. SCHULZE (1871) and MILANI (1894, 1897) argue thus in their works. To them the simple lung sac of lower amphibians as the starting point of the development of all complex lungs. However hard one tried to illustrate the increasing complexity of lung construction in a series of systematic steps is especially shown by the large-scale studies of Milani (1894, 1897).  

Aside from an erroneous equation of the nooks, pockets and cells of the reptile lung with the alveoli of the mammalian lung such an approach is necessarily based on the hypothesis that the differentiation of simply lung sacs occurs via the ingrowth of septa. In 1902 FANNY MOSER flawlessly showed the indefensibility of this view. Sadly, she committed the error of falling for the opposite extreme in her interpretation of her own lung studies. Embryonic states of mammals seem to her the norm, original state example and basis for comparison. Because the bronchial tree of very young mammalian embryos with its formation of buds at the end of the tracheal duct externally is similar to the lungs of reptiles and birds, she let herself be misled to ascribe this principle of budding and branching to the latter as well.

Against this obvious exaggeration of developmental thinking FLEISCHMANN spoke out in 1914. Studies stimulated by him and performed by BOEKH, MANTEL and HEILMANN showed that a bronchial tree is limited to mammals, and is alien to reptiles.

The really crucial step that helps us with the present case is only done in 1924 by BRANDES. His studies bring the erection of two separate developmental sequences, the first of which runs from the amphibians to the mammals (alveolar lung type), whereas the second begins the the reptile group and leads to the birds (organ type).

---

1 A quite similar point of view, which however is quite defensible, as it is based on different issues, was taken by HILBER in his study “Der formative Einfluß der Luft auf die Atemorgane” [The formative influence of air on the breathing organs] (Comparative study on construction and development of reptile and mammalian lungs) (1932, Morphol. Jahrb., Vol. 71, Issue ½), which appeared while this study was in press, and to which here I can thus only point. Hilber investigates the influence of moving air on the shaping of the lung, a factor that is of importance for the breathing organs of all vertebrates and shows comprehensive principles.
The second factor hindering the resolution of our problem was that the finer details of the work paths of the bird lung, especially the paths of the air in it, were unclear. This was also explained plausibly by BRANDES (1924). Sadly, his remarks did not find the deserved attention, as they lacked direct, provable experiments. Only in 1930 did DOTTERWEICH in his experiments “Versuche über den Weg der Atemluft in der Vogellunge” [Experiments on the paths of air in the bird lung], which were reinforced again the same year (1930a), bring BRANDES’ view to common acceptance. The scheme reproduced in Fig. 1 illustrates the path of the air within the bird lung. The freshly inhaled air first reaches the caudal air sacs via trachea, bronchus and mesobronchus. Only from there it finds its way through saccobronchi (Bronchi recurrentes F.E. SCHULZE) and the dorsobronchi to the respiratory tissue, i.e. the walls of the bronchioli extending from the parabronchi. The used air is then emitted into the oral air sacs via the ventrobronchi, and from there to the outside via bronchus and trachea.

**II. Problem statement**

Obviously it can’t be the task to find “precursors” to the bird lung within the group of the reptiles. The special and extremely complicated construction of the bird lung must appear within the extant animals as isolated without proper intermediates as flight itself, the large, uninterrupted energy need of which makes this lung necessary. Rather, the question is to be focused on if the increase of complexity of the lung for improved exploitation of the air is achieved in the
reptile in principally the same way that ultimately leads to the bird lung. In order to answer this question a comparison of the reptile lung with the bird lung is needed.

If one wanted to start the comparison with the reptile lung, the incredible variation in forms would initially confuse. It seems almost impossible to abstract a lung bauplan from the plethora of these expressions that in a sense portrays the basic form of the reptile lung.\(^1\) The comparison, however, is much easier, if we initially look at the bird lung, as the lungs of various birds differ from each other only in minute detail. Thus, a common bauplan can easily be recognized.

If one takes into account the short description of the construction and functionality of the bird lung, the following points appear as the essence of this complicated breathing apparatus:

1. The respiratory tissue is limited in its extent to only part of the entire breathing apparatus. The visible partitioning of the breathing apparatus into air sac and proper lung results in a clear separation of a mechanical (ventilating) part from a respiratory part. Whereas the mechanical part (the air sacs) has a smooth inner surface, the respiratory part (the lung proper) shows an imaginable advantageous surface design. Also, the respiratory tissue does not, as in the alveolar lung type, form the walls of dead-end sacs, but the walls of fine canals, through which the air flows.

2. To allow this unique steering of the air the bronchus has grown deep into the lung as a mesobronchium, so that the freshly inhaled air initially reaches the caudal air sacs, i.e. a not respiratory but purely mechanical (ventilating) part of the lung.

3. From there it can reach the respiratory tissue via special canals, the saccobronchi (Bronchi recurrentes), pass by it and then on through the ventrorbronchi into the oral air sacs and from there via bronchus and trachea back outside.

In order to show up the functional connection of the reptile lung to the bird lung, our attention must be directed at

---

\(^1\) This variance of the reptile lungs is founded not only in the much varying body shape and mode of life within the group. At least reality exceeds all expectations based on these considerations. Thus the lungs of ophidian show significant differences for nearly equal body shape. Even within the same species I repeatedly found notable divergence from the norm. In my opinion this variability of the reptile lung is a sign of it being an intermediate area.
screening the lungs of reptiles for similar conditions as the ones just mentioned or their initiation. If such connections really exist, one can expect for the lungs of reptiles the following features:

A. The beginning separation of the lung into a mainly mechanical and a mainly respiratory part.
B. The presence of an interpulmonary bronchus, that like the mesobronchus of the bird leads the inhaled air first to the caudal mechanical part.
C. The formation of communications that, like the saccobronchi, let the air of the caudal mechanical part flow as a special path back to the respiratory parts.

The ingenious construction and the special functionality of the bird lung guarantees that the oxygen is so efficiently exploited as is mandatory mainly for flying in birds. Reptile lungs with far-reaching reminiscences to the bird lung should thus only be suspected where similarly high demands are put on respiration. Such conditions may be given by a number of circumstances, such as large size or special performance (diving etc.).

To what extent these expectations will be fulfilled will be shown below. The lungs of the three main stems of reptiles will be treated separately, to avoid repetition, by means of the aspects described above.

The animals I studied usually were dead when they reached my hands, usually without having been conserved in any way. Preparation of the lungs occurred after previous inflation with air or injection of Formol 1:20, in special cases also without any such measures. If necessary, the lungs were hardened and made translucent by transfer and long residence in xylol.

**III. Findings on lacertilian lungs.**

_General remarks:_ The lungs of lacertilians lie as relatively large, membranous sacs in the dorsal part of the body cavity. They always exist as a pair. Even in those lacertilians built, like _Anguis_ and _Pseudopus_, very elongated and resembling snakes in their external appearance, they are present as a pair. The external shape of the animal seems only to have an influence on the
shape of the lung in so far as that it sometimes is more cylindrical round in cross section, sometimes flatter.

In some lacertilians one lung is stronger and bigger expressed than the other. According to my observations the size difference only appears during growth, and is thus probably caused by lack of space in the body cavity. Very young animals show equally sized lungs (cf. Fig. 2, 3 and 4).

The trachea splits into two longer or shorter branches, which normally do not attach at the oral-most end of the lung, but below a longer or shorter cusp-shaped extension of the lung. Whereas the presence of such an oral cusp is the rule a few lacertilians show the exception to form similar but more narrow, finger-like extension on the caudal end of the lung (*Chamaeleon, Uroplates, Polychrus*).

The respiratory capillaries run in a simple lung in a coarser or finder net- or strut-work of the
lung walls. In complex lung forms the lumen of the lung is also more or less chambered or fanned.

A. If one prepares a lacertilian lung from a fresh, just-killed animal, the usually locally differently strong perfusion with blood is visible. Almost without exception one finds the caudal section of the lung less strongly reddened than the rest of the lung. When opening the organ becomes evident that the differing perfusion is related to a differing of the inside of the walls. The lungs of all lacertilians, especially however those of the larger and higher organised ones, are in their oral parts richly equipped with respiratory ridge-work etc. than the caudal parts, where compartments and chambers, if present, are larger and coarser. At the caudal end the lung wall often appears thin, translucent, membranous, and only relatively low ridges cover in a wide mesh the inside wall, or are lacking entirely.

Sadly, MECKEL (1818) as well as MILANI (1894, 1897) in their classic investigations of many reptile lungs did not pay special attention to these circumstances. This is, aside from the previously described inner reasons, which resulted in a totally different direction of study, certainly also caused in part by the external reason that they mostly had specimens available that were conserved in spirit. Lung conserved this way do not show the natural differences in perfusion anymore. Still, one can gather by thorough inspection read from the statements of both authors, especially taking into account the

Fig. 4. Lungs of *Tiliqua scincoides*. Total length of the young animal was 12.5 cm, both lungs were of the same size (ca. 3.3 cm).
figures, that they also met with the above described conditions.

In the entire literature available to me, however, the fact has been ignored that in wide distribution among lacertilians quite analogue conditions exist in the extreme oral cusp of the lung. In this cusp-shaped extension, below which normally the bronchus enters, also the decoration of the wall aimed at increasing of the surface decreases towards the extreme oral end, and thus the density and extent of respiratory tissue. Although some drawings and photographs of MILANI (20) depict these remarkable conditions clearly, the text does not address them at all. All other authors who later noted or copied the splendid schemata and photos of MILANI in manuscripts, textbooks etc., passed them by.

The locally differing extent and density of respiratory tissue and the varying amount of perfusion are especially marked on certain dry lung preparations. If one creates them in the simple way of inflating with air, extraction and drying, membranous and little blood perfused parts will dry first and harden in tautly convex shape. The spongy respiratory tissue moistened by blood in contrast takes much longer to harden, and sinks down according to the air slowly diffusing out through the lung wall. This way preparations are created the grotesque form of which inform quite vividly on the differences in the detailed construction, which are otherwise visible only in sections.

Fig. 5 shows as an example the thus dried lung of a common iguana. Both on the right and the left lung the caudal sections and the oral cornet are fully convex. Here, the lung wall has membranous properties. The regions in between, however, have collapsed into folds while drying, as they distinguish themselves by dense and strongly perfused respiratory tissue.

\footnote{MECKEL in Lacerta ameria, jamaicensis, turcica; Anguis fragilis; Cordylus; Agama marmorata; Chamaeleon pumilis; Stellio brevicaudatus; Tupinambis americanus, maculatus. MILANI in Eumeces; Tiliqua; Lygosoma verreauxi; Ophisaurus opus.}
The locally variable expression of the respiratory tissue within the lung and the difference in perfusion of the lung caused by it allow a special interpretation. With ease it can be concluded that the lung areas with only weakly expressed respiratory tissue also have only a low suitability for respiration, and thus play a minor role only in gas exchange. The zig-zag arrangement of internal ridges seen in such areas in contrast indicates a large mechanical load (see also ROTHLEY (1939). One can therefore assume that already within the lung of lacertilians a separation between the respiratory and the mechanical parts is beginning. It is of interest that the position of the mechanical part is the same as in the breathing apparatus of birds, i.e. caudal and oral of the respiratory part of the lung proper.

In the lacertilian lung the spatial separation of the parts with differing functions is never sudden. Always the transition is gradual and is evident in the increasing width of the respiratory mesh and finally the total lack thereof. Only in some cases is the small oral mechanical part separated from the remaining lung by an incomplete partition (Lacerta, Anguis, Pseudopus apus, Stellio vulgaris, Iguana tuberculata, Chamaeleon)\textsuperscript{1}.

In one Tiliqua I found air sacs conforming fully those of a bird, suddenly separated from the lung proper. The animal was delivered as Tiliqua scincoides by the animal dealership SCHOLZE & POESCHKE, but rather seemed to be Tiliqua nigrolutea. The species could not, however, be determined with certainty. As during later study of three specimens

\textsuperscript{1} In the definition of the oral mechanical part considerable individual differences can be seen (e.g. Pseudopus, Iguana).
doubt came to me if these conditions of the first Tiliqua were the norm I asked the Berlin importer for the locality. Sadly, I could only find out that the Tiliqua came from a transport from Sidney. Ecological clues and explanations are thus impossible, if the lungs of this Tiliqua, as I assume, were not normal, but a transitional form.

At any rate, for the present study knowledge of an abnormity can be valuable, especially if it is a question of such remarkable circumstances as those dealt with in the following.

The just-deceased Tiliqua was roughly 50 cm long. During section it became immediately obvious that during insufflation of air into the trachea not only the two roughly equally sized lungs swelled up, but also two thin-walled colourless air sacs resting between them (Fig. 6). These two air sacs communicated with the lung of their respective side very close to the short, only implied bronchi. They had a cylindrical form and reached with their caudal ends the pelvic girdle. Their walls were membranous and extremely delicate. The blood supply was served by a single caudally directed vessel stem, which branched only little. The construction of the proper lung fit the description that MILANI (1894, p. 554) gave of the lung of Tiliqua scincioïds. Solely, the oral cusps shaped extension shows a nearly smooth inner wall with very little perfusion, unmentioned by MILANI. Whereas the lung proper was bright red the cusp was only weakly yellow: an excellent example for the formation of a small oral mechanical part. Surprisingly, the insufflated air remained in the lung and air sacs without the use of binding screws etc. This

![Fig. 6. Air sac lung of a Tiliqua. T trachea. L lung. OMT oral mechanical part (cornute extension). LS air sacs.](image-url)
make the presence of valves likely. The air only escaped from the lungs and air sacs when the latter were destroyed.

B. Within the lacertilians a factor takes shape with increasing complexity that is of importance for our study, which is the creation of an intrapulmonary bronchus.

Already in relatively simple lungs the bronchial path continues as a cartilaginous or fibrous ribbon into the lung (e.g. Lacerta ocellata). In some cases this appearance is further emphasized by the inner wall of the lung showing noticeably enlarges meshes along this band (e.g. Scincus officinalis).

In the complex lungs of varanids and crocodiles things don’t stop at such an allusion. Here, the bronchus sinks deep into the lung, in the shape of a long, closed canal. This pipe-shaped air way is rather wide and strengthened by cartilaginous braces. In the oral part of its path it shows a double row of openings, the first and largest of which connects with the extreme oral cusp of the lung (the oral mechanical part). By its entire path, its cartilaginous bracing and its ostia it suggests a comparison to the mesobronchium of the bird lung. As it extends to the large caudal final chamber (the caudal mechanical part) it is likely that also in these lungs the inhaled air entirely or at least in large parts first passes to the caudal mechanical part.

C. In the lungs of the monitor lizard one finds air passages that can be compared functionally to the saccobronchi. Here communications appear that allow the air to pass directly from the caudal mechanical final chamber to the respiratory part of the lung without first flowing back into the intrapulmonary bronchus.

Based on my findings the scheme given by MILANI of the lung of the monitor lizard (Fig. 7) is erroneous. The longitudinal section is places through the lung so that one has to assume

\[1\] F. E. SCHULZE showed that in certain locations of the air-conduction canals in the bird lung there are rings of muscle well suitable to serve as valves. BETHE, BRANDES and DOTTERWEICH traced the steering of the air in the bird lung to the presence of such valves.
that the individual chambers are blind sacs and only accessible via the intrapulmonary bronchus. One can easily convince oneself that this is wrong by injecting a bit of fluid into a lung inflated with air. If now the lung is held with the caudal end down the fluid gathers in the terminal sac. During lateral tilting one can then follow the path of the fluid through the translucent lung walls. One can see that the lateral chambers communicate all the way to the oral end of the lung with one another.

Also, again unregarded by MILANI, the diverting parts of the lateral chambers communicate through a large number of fine, short connections, so that a maze of narrow chambers is created, which, judging from the strong perfusion, are the main location of respiration. Thus, the respiratory tissue forms here not the walls of blind sacs, but the walls of passages open at both ends, through which the air can flow. Fig. 8 attempts to depict the complex conditions for a...
Part of the lung in a simplified and schematic way. In this construction it is possible that the air is shunted exactly like in the bird lung.

**IV. Findings on chelonian lungs.**

**General remarks:** The lungs of chelonians known to me do not differ from one another as much as this is the case in other reptilians. The respiratory organs appear to only present minor variations of a general bauplan.

Always the lungs are present in paired state. As oval, somewhat flattened sacs of at least significant size they fill the entire dorsal part of the body cavity between shoulder and pelvic girdle. Right and left lung are usually equally well developed and of equal size. Among the many animals I studied there was only one in which one lung, the right, was retarded in its development.

The trachea is rather short and rapidly splits into two bronchi, which in contrast are relatively long. Unlike in lacertilians, they do not end in the extreme oral part of the lung, rather, the mouth has shifted quite far caudally.

The lumen of the lung is split by projecting horizontal and vertical walls. Thus more or less large and numerous chambers are created, the largest of which is the caudal final chamber (see Fig. 9).

The respiratory capillaries run along the inner walls of the individual chambers.

A. The lungs of chelonians also show a locally varying supply of respiratory capillaries. On

---

1 The inner layout of the entire lung fits scheme Fig. 43.
injected material of *Emys* one can easily see that the large caudal final chamber is only very little perfused with blood. From this an only minor respiratory function of this lung section can be deduced. As additionally there is a layer of striated muscle surrounding the anterior 2/3 of the lung, whereas the caudal part, said final chamber, remains free, the assumption is further supported than the final chamber has a different function from the rest of the lung.¹

For the present study the turtle lung becomes remarkable by its bronchus clearly continuing as an intrapulmonary cartilage-supported channel. As in the mesobronchium of the bird lung it leads straight to a part not significant for respiration, the caudal chamber, and shows along its path a number of further openings that are reverse connections to the respiratory part of the lung.

Here, proof is lacking that also in this construction the air first reaches the final chamber. But this path of the air is likely, as it can be shown that the expired air form the lung does not stem from the final chamber, but from the respiratory part. Already when sectioning a dead turtle one notes that on opening of the body cavity the lung does not collapse; the final chamber rather always remains partly filled with air. The construction of the lung is therefore so that even during purly mechanical deflation of the lung the air is expelled not from the final chamber, but from the other parts.

The same was illustrated by experiments on living animals. Test specimen of *Emys europaea* were clamped by the dorsal shield immersed into an eosin solution so that all extremities remains fully mobile.² After the death of the animal the lungs were immediately excised. It became apparent then that the coloured solution never reached the final chamber, but always others, mainly the lateral and dorsal

¹ The lung of *Trionyx* seems to be an exception. According to Rothley (1930) the striated muscle layer, that apparently acts as expirator, covers the entire lung, thus also across the caudal section. This special case, however, immediately becomes an exception if one keeps in mind that in *Trionyx* the final chamber is strongly perfused and thus shows ist respiratory use.

² It is known that in chelonians the mobility of the girdles is of great importance for breathing mechanics.
chambers. In order to not get confused by gravity the experiment was repeated with varying positions of the animals: ventral or dorsal position, vertically rotated up or down (head down or up), and obliquely inclined. For section the animal was if possible not removed from its position. Always the results agreed in that the colour did not reach the final chamber. The two Figures 10 and 11 report the distribution of the coloured solution for different experimental setups.

As one has to assume that the coloured solution enters purely mechanically in place of the used-up air ejected under threat of asphyxiation, these experiments seem well-suited to characterize the deep-reaching difference in function between final chamber (mechanical part) and the other chambers (respiratory part).

For the success of this experiment an important issue must be respected. The eosin solution used must be created with freshly cooked water. If this procedure is forgotten death of the animal occurs only after days.
In these cases there is no coloured fluid in the lung. In water containing air lung breathing thus doesn’t even seem to be attempted.

The exceptional diving capabilities demand the assumption of an accessory breathing method. Various specimens of *Emy europaea* could be kept under water for 17-19 days in an aquarium through which per minute ca. 1 l of tap water at 12° C was flowing before death occurred.

The ability to remain submerged for weeks on end unharmed is amazing even for an aquatic turtle like *Emys*. The capacity of the large lungs, their internal architecture and the low oxygen use rate of the animal are not a sufficient explanation.

Repeatedly it has been suspected that the large anal sacs, present in some chelonians as dorsolateral protuberances of the wall of the urodaeum, serve respiratory functions (see BABAK, 1921, p. 864). This assumption I find, at least for *Emys*, for baseless, as injected material shows that here the walls of the sacs are only little perfused. However, a potential function of the sacs was experimentally prevented by suturing the anal orifice. As was to be expected no adverse effect on diving duration occurred.

During the first few hours of diving it rather seems to be the oral cavity that is active in respiration. By rhythmically lifting and lowering the lower jaw it is vigorously flushed about 20 times per minute. The richly branching network of fine capillaries that characterizes the mucosa of the oral cavity, well visible on injected preparation, makes a respiratory function possible and likely.¹

During the later hours of diving the flushing of the oral cavity becomes rare, though. Finally, it only sets in during vigorous motion of the entire animal. The gas exchange necessary for maintaining life now appears to be performed by cutaneous respiration. The cutaneous respiration of turtles has usually been neglected.

¹ Of two soft-shelled American turtles bucco-pharyngeal respiration is known. In these animals the mucosa of the pharynx is characterised by villous extensions which are supplied with breathing water by rhythmic motions of the hyoid apparatus (see WINTERSTEIN (1921) p. 128 and BABAK (1921) p. 845 and 864). *Emys* does not have any such villi.
in studies. In view of the strong plating it was a priori deemed very small (see Winterstein (1929) p. 204). But its relevance seems – at least in Emys – to be quite important. Viz, the potential diving time was immediately reduced to only a few days when the non-plated parts of the animal were covered thoroughly with collodion. It sank even further if the entire epidermis including the plates was in this was bereaved of its respiratory function.

C. The important role of cutaneous and oral cavity breathing in chelonians may have resulted in the complexity of their lungs not being as high as in those of lacertilians, which in other respects resemble those of chelonians. In the lungs of the monitor lizard we saw special communications that could be compared functionally to the saccobronchi of the bird lung. In the lungs of Emys and Testudo such communications are missing, which would create a special path into the respiratory part for the air by letting it pass directly into the caudal mechanical part. As can be seen from Fig. 9 the chambers communicate with each other only to a limited degree. Both in Emys and in Testudo the final chamber (the caudal mechanical part) can only be reached via the stem bronchus, whereas 5 times two chambers each are connected to each other. The individual chambers or chamber pairs, respectively, thus form blind sacs the supply path of which is solely the stem bronchus with its openings. But based on the observations described above it also seems to be fundamentally true for the chelonian lungs that the air in large parts first reaches the final chamber, the caudal mechanical part, and then from there by and by is guided to the chambers which are better supplied with capillaries.

It is not impossible that saccobronchial communications occur in the large and complicated lungs of the giant and marine tortoises. The fact that in previous published descriptions of such lungs such conditions have not been pointed out only serves to show that no attention has been paid.

\footnote{1 A dry preparation of a chelonian lung in possession of Prof. Brandes does show such communications clearly, though.}
V. Findings on ophidian lungs.

General remarks: The lungs of ophidians are elongate tubes, fitting the body shape. In some cases the caudal end of the lung reaches the anal region.

Lungs are present either as a pair or unpaired. Never, however, are both lungs of the same size and strength. In some ophidians the left, in some the right lung is vestigial.

The respiratory tissue forms the walls of a meshwork which in many cases can become so dense and thick that it appears as a fabric of repeatedly anastomosing tubes.

A. Whereas the locally variably strong expression of respiratory tissues in lungs of lacertilians and chelonians has only very rarely seen attention so far – and even then not under our angles – the very aspect was so generally known in ophidians that it was seen as a characteristic of the snake lung. This is caused by the snake lung’s caudal mechanical part calls for attention by its little perfused, thin walls and its large size. After all, the respiratory part normally makes up little more than one third of the entire lung. Only in the oral and medial part, respectively, of the lung one can find thick, spongy respiratory tissue. The caudal part of the lung is on its inner wall nearly or fully smooth and appears as a thin-walled, transparent sac. It is well known that this part is supplied by systemic circulation.

Such a conspicuous air sac caused assumptions about its function. Usually it was seen as an air reservoir, like the air sacs of the bird lung.¹ The air stored in it was supposed to serve the oxygen demand at times where normal working of the lung was hampered (entangling the prey, large content of oesophagus and stomach).

¹ Leaving aside assumptions that refer to a totally different effect of the air sac, e.g. ist hydrostatic function in swimming. See also PAGENSTECHER (1875).
In the course of our observations such a well-expressed air sac does not form a fundamental novelty. After all the ophidian lung shows only the general – as we saw – feature of the reptile lung, a separation of a mainly mechanical part from a mainly respiratory part, stretched far apart because of the elongate shape and thus very noticeable.

With regards to our special interest three basic construction forms of the ophidian lung can be found based on the distribution of mainly respiratory and mainly mechanical parts of the lung (Fig. 12 and Table p. 159).

The 1. Lung type is found e.g. in Boa and Eunectes. The relatively long trachea splits near the heart into two short bronchi, which lead into two unequally shaped lung tubes. Unlike in the lacertilian or chelonian lungs the mouth is not located at the oral-most point, but shifted slightly distally (see Fig. 15, 20, 21). The respiratory main part forms the oral third of the lung. Versus the caudal end the meshwork and tubing becomes coarser and shallower, and finally transitions into the membranous caudal air sac. Here, there are only low ridges woven into a large-meshes network, the alignment of which suggests strong mechanical loading (extension without strain via the principle of “Venetian scissors”, see Fig. 13, 14).

Whereas in the just-described 1. Lung type the reduction of one lung rarely leads to complete atrophy\(^1\), the 2. and 3. Lung type only know one single lung\(^2\). Therefore the trachea does not split into two bronchi, but leads directly to the lung, namely to its extreme oral point. A clearly defined insertion can’t be named here, though, as the trachea widens considerably and thus transitions into the lung. This occurs by the filling membrane, which which [sic] in Ophidians connects the never fully closed cartilage straps of the trachea, closing them to a tube, distally increasing in width.

---

\(^1\) One *Boa constrictor* (see Fig. 23, 24) shows one lung atrophied to a few millimetres.

\(^2\) The second lung may be present as a rudiment. In one specimen of *Naja tripudians* the rudimentary lung presented as a pointed protrusion of a few centimetres length. Its lumen was connected to the lumen of the lung via an opening that broke through the cartilaginous bronchial channel just before its entry into the respiratory part.
In the 2. Lung type (e.g. *Vipera ammodytes*) respiratory meshwork appears on the inside with increasing width of this filling membrane, so that the lung appears as a widening of the trachea, which on its dorsal inner wall is already furnished with respiratory tissue. The respiratory meshwork reaches its highest development already in front of the heart, the respiratory part is thus located orally relative to the heart. Therefore, the lung artery turns proximad. The mechanical part (the air sac) has a nearly or fully smooth inner wall and forms the caudal final part of the lung.

The 3. Lung type (e.g. *Naja tripudians*) is characterized mainly the presence of an oral mechanical part in addition to the caudal mechanical part. The trachea widens a lot here, too, but without forming respiratory recesses or meshes to a significant degree. Thus, an elongate, membranous bubble with longitudinal folds is created as the oral part of the breathing apparatus, through which a strongly hollowed-out tube made from tracheal cartilage (Fig. 27, 30; 28, 31). Only at the level of the heart there is respiratory meshwork, which further distally makes room for smooth-walled caudal mechanical part (Fig. 29). The respiratory part of the lung thus forms the medial part of the tubular lung, and is flanked orally and caudally by an air sac (mechanical part). As the respiratory part is located caudally of the heart the lung artery turns caudad.

The manner of how the two parts of different function in snake lungs, namely the respiratory part and the mechanical part,
can be distinguished from each other is remarkable.

In the 1. Lung type the respiratory part transitions gradually by enlargement and levelling of its structure into the caudal mechanical part, which still carries on its inner surface a wide-meshed lattice-work of shallow ridges (Fig. 13, 14; 17, 18).

In the 2. and especially the 3. Lung types, the air sacs of which are extremely delicate and on the inside usually completely smooth, but form longitudinal folds when collapsing, the separation becomes much more obvious and sudden (Fig. 29).

The oral mechanical part is always strictly separated from the respiratory part (Fig. 28, 31).

An external constriction of the caudal mechanical part from the respiratory part was also found on the lung of Phyton molurus (1. Lung type). Even taught inflation a constriction at the transition point remained.

More commonly an inner constriction is found, a narrowing of the lumen at the transition point. (Especially in the 2. lung type, e.g. in Coluber quattuorlineatus, Lachesis lanceolatus, etc.) See Fig. 25 ¹).

B. Of special importance for our studies is the fact that in the elongated lung of Ophidians bronchial

---

¹ On Pelamys similar conditions seems to have been observed. PAGENSTECHER (1875, Part 3, p. 314) remarks that „Pelamys bicolor has separated an anterior from a posterior wideing of the lung by a very narrow channel in the area of the heart“.
paths can be followed that lead, as in the lungs of higher lacertilians and chelonians, often
directly to the caudal mechanical part. They usually run down the ventral side of the lung, but in
some cases turn lateral (Fig. 34) or dorsal. In the lungs available to be the following constructions
could be distinguished:

I. The intrapulmonary bronchial
paths are more rigid than the
remaining lung tissue (Fully or
partly cartilaginous.)

  a) The trachea, resp. the
bronchus, reaches only a
short distance into the
respiratory part of the
lung, as a cartilaginous
channel, but can be
followed to the caudal
mechanical part of the
lung as a cartilaginous or
fibrous band, which
repeatedly emits lateral
strips. Next to the
cartilaginous or fibrous
band there is on various
occasions a clearly
excised groove, the V-
shaped cross section of
which is also supported by the mentioned lateral strips of the band.

    In the 1. Lung type; e.g. in Tropidonotus natrix (Fig. 36).

  b) The trachea, resp. the bronchus, the cross section of which displays a
semi- or three-quarter-circle, reaches through the entire respiratory part
to the caudal mechanical part, in the shape of a cartilaginous channel. The
intrapulmonary bronchus thus presents here the likeness of a
longitudinally slotted tube.

    In the 2. and 3. Lung type; e.g. Lachesis etc. (Fig. 25, 26, 33,
34, 35, also 23).

  c) From the only shallowly convex cartilaginous bronchial channel a sieve-
like perforated cartilaginous mantle spreads bilaterally, which covers the
entire axial main lumen of the oral respiratory part 1.

---

1 The presence of cartilage in the snake lung seems to be relatively rare. In the
literature available to me there was a single reference to Acrochodus (Siebold and Stannius, 1848,
p. 232). Rothley (30, p. 19) even opined that the cartilaginous support in snake lungs was „not
present and also not required“.
This way the axial main volume is stiffened and forms a permanently open air passage to the caudal mechanical part. Here, therefore, the entire axial main lumen of the respiratory part must be regarded as part of the intrapulmonary bronchus. In the caudal part the cartilage does not form a continuous context anymore, but appears only at certain places.

II. The intrapulmonary bronchial paths are less rigid than the remaining lung tissue (membranous).

Fig. 15. Right, larger lung of *Eunectes murinus* (1. Lung type). Cut open from the insertion point of the trachea to show the cartilaginous bronchial channel and the thick cartilaginous sheathing extending from it.

Fig. 16. Left, smaller lung of of *Eunectes murinus* (1. Lung type). The oral part of the lung has been opened and spread out.

This construction was found only in very large lungs, in which ventilation of the respiratory part is difficult due to its great length. In the 1. Lung type; especially in *Eunectes murinus* (Fig. 15, 16), also in *Phyton molurus* (Fig. 21, 22).
In *Naja tripudians*, for example, a broad, folded, very stretchable, very conspicuously longitudinally folded and striated membrane without any respiratory meshes appears in the region of the heart in place of the dorsal cartilaginous bronchial channel. Stretchability and the conspicuous striation hint at mechanical loading. This membranous channel reaches all the way through the respiratory part to the caudal air sac.

In the 3. Lung type, e.g. *Naja tripudians* (Fig. 28, 29), similar in *Bits gabonica* (Fig. 36).

The real character of the intrapulmonary bronchus of the snake lung therefore is that it does not, like the lungs of higher lacertilians and chelonians, have only a few openings, but that it is along its entire extent, either via a very large number of openings (*lc*) or via a longitudinal slit (*lb*, pot. also *la* and *ll*), reconnected with the surrounding lung part.¹

---

¹ This construction is necessary for the continuation of internal ventilation during feeding and digestion. If only few ostiae were present the passage of food could easily compress important air passages or otherwise block them.
The air-conducting effect of the longitudinally slotted bronchial tube is sustained by it always either being either more or less rigidly built than the neighbouring lung tissue, so that the remaining lung tissue supplies the part that is necessary for the completion of the tube.

This assumption is reinforced by the shape of the cross section of the snake lung. The snake lung shows, unless it is artificially, on the oral half not a circular, but a flat-oval cross section (Fig. 32-36). Among other things this results in the gaping longitudinal slit of the cartilaginous intrapulmonary bronchial tube has always a closing cover available, so to speak, of easily mobile tissue 1.

In the lungs described above as 2. Type and 3. Type the cross section in this region sometimes even dumbbell or lemniscate-shaped. As this longitudinal fold reaches all the way to the caudal air sac the lung is thus split into three separate longitudinal hollows. The smaller the space available in the body cavity for the lung, the sharper will these

---

1 The lung tissue is usually thinnest directly vis-a-vis the bronchial channel.
volumes be separated\(^1\). It is entirely possible that the medial volume forms the forward run of the air to the caudal air sac, whereas the two lateral spaces perform the backflow of the air, as the respiratory meshwork is always most prominently expressed on the lateral walls of the lung (Fig. 35, 36).

The bronchial channel is also located so that can work as a cohesive airway to the caudal mechanical part when the lungs are under pressure, or especially then, in lungs in which such a longitudinal fold is not expressed: the bronchial channel of e.g. *Viperus berus* (Fig. 26, 34) run all the way on the right lateral side, effectively passing by the respiratory part to the caudal air sac.

C. Aside from the conditions usually present in ophidians: separation of a mainly mechanical lung part from mainly respiratory one and occurrence of intrapulmonary bronchial paths I found in *Eunectes murinus* a construction that shows further relations to the bird lung.

Because the lungs of *Anaconda* certainly are rarely studied a more detailed description of its construction may be interpolated.

---

\(^1\) E.g. in the expired position of the ribs or during feeding and digestion.
The still young animal measured from head to tail tip 2.75 m. The extremely sturdy trachea shows a cross section of ca. 6 mm. The giant lung tubes fused for 2 cm were dorsally of the outlet of the extremely short bronchi. 1 The length of the right, larger lung as 67 cm, that of the left 50 cm, of which roughly 30 cm each being strong, spongy, well perfused respiratory tissue. The respiratory tubing transitioned near the middle of the lung sac into the only shallowly and roughly meshes folding of the mechanical part (the air sac). The lumen of the lung was lined cartilaginous (Fig. 15, 16). In the oral half the cartilage was so strong that it quasi formed a millimetre thick sieve-like perforated sheathing, from which 10 cm from the tip of the lung the two merged cartilaginous segments of the trachea constituted themselves as cartilaginous channel (Fig. 15). In the caudal section cartilage could in contrast only be found as globular rises on the crossing points of the net-like ridging that covers the inner side of the lung wall of this section (Fig. 18). The cross section and the lumen of the lung were not circular, but rather flattened. The laterally located respiratory tube network reached a considerable thickness, the ventral and lateral networks, however, remained thin and transparent. Even in the spot where the respiratory part transitions into the mechanical part the differences in thickness of the tissues remained, made especially noticeable by pointed growths of the respiratory meshwork into the air sac.

At this place also elongate canals started, which ran all the way on the periphery and could be followed to the oral part.

1 An equivalent fusion was also found in Python molurus (Fig. 21, 22) and Tropidonotus natrix.
of the lung. The enclosed photos (Fig. 19, 19a) were taken in strong light directed at
the outer wall of the lung, and show in the mentioned canals air glossy bubbles
straining forward. In cross sections these relatively wide air corridors

can also be seen clearly. Functionally they are the equivalent of the saccobronchi of
the bird lung, because the air in the air sac can reach the respiratory tissue through
them, without having to pass into the main lumen again.

The respiratory tissue in *Eunectes murinus* forms the walls of a dense
fabric of multiplicative anastomosing tubes,
reminiscent of the parabronchi of the bird lung. At the base they are connected to the mentioned longitudinal channels and open on the other end into the main lumen of the lung. In such a construction a circulation of air as in the bird lung is possible (Fig. 19).

VI. Comparisons.

The discussions given above show that the issues defined from the study of the bird lung can be fruitful used for the comparative study of the reptile lungs.

A similar saccobronchial-like channel system also occurs in *Naja tripudians*, but is less clearly expressed.
It follows that the complexities of the reptile lung constructions is reached via basically the same constructive means,

Fig. 25. Lung of *Lachesis lanceolatus* (2. Lung type). The intrapulmonary bronchus runs through the respiratory part to the caudal mechanical part as a longitudinally slotted, cartilaginous channel. Just before entering the latter part it narrows a bit and incises especially deeply. *H* heart.

Fig. 26. View into the body cavity of *Vipera berus* (2. Lung type). The body cavity has been opened. One can see how the cartilaginous intrapulmonary bronchus runs laterally past the oral respiratory part as a lightly-coloured, translucent tube to the caudal mechanical part. The respiratory part shows dark in the photo, due to its strong perfusion, the mechanical part lightly coloured. *IB* intrapulmonary bronchus. *ORT* oral respiratory part. *CMT* caudal mechanical part. *H* heart. *L* liver.

Compare to Fig. 34

which in their highest expression can be found in the bird lung, and in the past seemed to be the characteristics of the bird lung, to viz.:
A. Separation of the lung into a mainly mechanical and a mainly respiratory part.

Fig. 27. Oral mechanical part of the lung of *Naja tripudians* (3. Lung type). The wall of the mechanical part is membraneous, longitudinally striated and longitudinally folded. (Stretchability!) The cartilaginous bronchial channel lead all through the oral mechanical part to the respiratory part (comp. to Fig. 28.)

Fig. 28. Border area between the oral mechanical part and the respiratory part in the lung of *Naja tripudians* (3. Lung type). The cartilaginous bronchial channel flattens and ends in a tip. (The circular opening leads to the rudimentary lung, compare to p. 158, footnote 2.) The folded, longitudinally striated membrane of the oral mechanical part, in contrast, leads throught the entire respiratory part and to the caudal mechanical part (Fig. 29).

The initiation of such properties can also be found more or less strongly expressed in all reptile lungs. It shows itself firstly by the locally differing tendency to increase the inner surface area of the lung and, secondly, by locally differently strong perfusion with blood. In the mainly respiratory part there is ample mesh and recess creation, tight chambering or fanning and extensive supply with respiratory capillaries. In the mechanical part the perfusion is low and the inner wall without respiratory meshing. In contrast, it shows signs of strong mechanical use.
The alignment of the ribs and muscle groups that extend and compress the lung during respiration makes these different modes of operation clear.

In the higher lacertilians the oral rib pairs are integrated to a common but not very extensive work. The caudal ribs, in contrast, are free and very mobile, as is necessary for the mainly mechanical work of the caudal part of the lung.

Fig. 29. Border area between the respiratory part and the caudal mechanical part in the lung of *Naja tripudians* (3. Lung type). The respiratory meshwork suddenly stops, and the delicate, membranous wall caudal mechanical part steps into its place.

Fig. 30. Oral mechanical part of the lung of *Bitis gabonica* (3. Lung type). The membranous wall has folded (stretchability!). As opposed to Fig. 27, here the cartilaginous bronchial channel, not the membranous part, has been cut open, so that one half can be seen all the way on the left, the other all the way on the right. Compare to Fig. 31.
In the chelonia there are no mobile ribs. The motion of breathing of the oral part of the lung occurs with the aid of a striated muscle that surrounds this part of the lung. The filling and emptying of the mechanical final chamber is achieved in a totally different way, viz., by the motion of the muscles of the pelvic girdle.

Fig. 32. Schematic cross section through the oral part of the lung of *Eunectes murinus* (1. Lung type). The axial main lumen is stiffened by a cartilage sheathing. Compare to Fig. 15, 16.

In the ophidians the up and down of individual rib pairs can be achieved separately. This guarantees a separate ventilation of locally separated lung parts.

The larger mechanical part usually forms the caudal part of the breathing apparatus. In some lacertilians and ophidians there is a somewhat smaller mechanical part also in the extreme oral part of the lung. This latter arrangement

Fig. 33. Schematic cross section of the lung of *Lachesis lanceolatus* (2. Lung type). The intrapulmonary bronchus leads, as a longitudinally slotted tube, to the caudal mechanical part of the lung. The lung tissue is most mobile where it faces the slot.

Fig. 34. Schematic cross section of the lung of *Vipera berus* (2. Lung type). Compare to Fig. 26.
is remarkable because it matches exactly the grouping of the functionally different parts of the bird lung and thus hints at an identical or similar functionality. In the breathing apparatus of birds, as is generally known, the proper lung, the respiratory part, is centrally located, whereas orally and caudally the air sacs, the mechanical parts, are placed. With this placement the mechanical parts can act as bellows and partly lead air to the respiratory parts via pressure, partly pull it out via suction.

**B. Initiation of an intrapulmonary bronchus that leads the freshly inhaled air directly to the caudal mechanical part.**

The bronchus continues as a cartilaginous or fibrous ribbon deep into the lung, already in relatively simple lacertilian lungs, and in complex lacertilian lungs as a tube\(^(*)\). The intrapulmonary bronchus of varanids, crocodilians and chelonians shows far-reaching similarity with the mesobronchium of the bird lung. Like the latter, it leads directly to the caudal mechanical part.

In the ophidians the analogue conditions are more complex. The intrapulmonary bronchial paths here form either a cartilaginous or fibrous ribbon or a channel. In the lungs of very large animals a perforated cartilage mantle extends from both sides of the channel, which covers the axial lumen of the respiratory part of the lung completely and

\(^(*)\) **NOTE:** the German word “Kanal” does not necessarily mean a closed tube, but can also refer to an open channel. However, below Wolf uses the term “Rinne” for such a shape, so that here it is likely that “Kanal” means a closed tube.
thus stiffens it. Then, the axial lumen of the respiratory part can be seen as the analogue of the mesobronchium of the bird lung.

C. The formation of communications that pass the air from the caudal mechanical part to the respiratory parts without it having to flow back into the pulmonary stem bronchus.

Such communications were found among the reptile lungs at my disposition in the monitor lizard and some snakes. It is however likely that similar conditions exist also in other larger and higher organized reptile lungs.

From the summary of the morphological findings one can conclude that the pathways of the air within the lung typical for birds have been initiated in the group of the reptiles. Because, however, the expression of the intrapulmonary airways is as clear as in the bird lung in none of the reptile lungs studied by me, I assume that in the reptile lung not the entire air but only a larger or smaller part of it circulates in the manner of the bird lung.\(^1\) The separation of the heart into left and right halves that begins and increases within the reptile group is likely connected and will give a scale.\(^2\)

These insights can be used to bring a clear and understandable overview into the so far difficult to survey richness of forms of reptile lungs. Such an overview has so far only been given for a partial area, the lacertilians, by Milani. A description of Milani’s (1897) lung types is, however, unnecessary, as they are a product of later disproven assumptions, according to which the increase of complexity of simple lung sacs occurs only via the ingrowth of septae.

---

\(^1\) An inner ventilation is certainly taking place. Compare Pagenstecher (1875); according to him there are up to 30 rib breathing motions between two breaths in ophidians, during which apparently the air is moved within the breathing apparatus. Kahn (1902) reports on corresponding observations in lacertilians.

\(^2\) In crocodilians it is generally known that right and left ventricle are fully separate. However, a certain degree of mixing of arterial and venous blood is possible via the foramen panizzae.
The basic bauplans shown by me below refer, in contrast, to the entire subject of reptile lungs. However, I refrain right from the start from picking out a uniform series of development of the reptile lung. This is in my opinion not possible. As we have seen, the increase in complexity follows three tendencies, viz.

A. the separation of the lung into a mainly respiratory and a mainly mechanical part,
B. the formation of an intrapulmonary bronchus leading to the caudal mechanical part, and
C. the initiation of communications connecting the caudal mechanical part directly to the respiratory part.

According to the variably high expression of these specialties that are important for the function of the lung I differentiate the following main stops of the development:

---

1 The external shape of my schematics in Figs. 37-43 is based on the shape of the lacertilian and chelonian lun. However, the schemes are essentially also valid for the lungs of ophidians, as these are usually only externally different from those of the remaining reptiles. For clarification the basic schemas were drawn with straight lines crossing at right angles.
Fig. 39. Grundbauplan 3.
Fig. 40. Grundbauplan 4.
Fig. 41. Grundbauplan 5.
Fig. 42. Grundbauplan 6.
a) Basic bauplan 1 (Fig. 37). A simple lung sac, which in a way represents the touching point between the reptile lung and that of the amphibs.
b) Basic bauplan 2 (Fig. 38). The lung is split into a mechanical and a respiratory part. (In lacertilians, e.g. *Anguis*).
c) Basic bauplan 3 (Fig. 39). A respiratory part, a caudal and an oral mechanical part. (In ohpids and lacertilians, e.g. *Typhobis; Iguana; Pseudopus*.)
d) Basic bauplan 4 (Fig. 40). A caudal mechanical part, a respiratory part, an intrapulmonary bronchus. (In chelonians and ophidians, e.g. *Emys; Vipera berus*.)
e) Basic bauplan 5 (Fig. 41). A caudal and an oral mechanical part, a respiratory part, an intrapulmonary bronchus. (In ophidians.)
f) Basic bauplan 6 (Fig. 42). A caudal mechanical part, a respiratory part, intrapulmonary bronchus, saccobranchi-like communications. (In lacertilians and ophidians, e.g., *Eunectes*.)
g) Basic bauplan 7 (Fig. 43). A caudal and an oral mechanical part, a respiratory part, intrapulmonary bronchus, saccobranchi-like communications. (In varanids.) This construction is closest to the bird lung. Naturally, the analogy of the construction reaches only so far as the much more contractile construction of the reptile lung allows. A comparison of Fig. 43 and Fig. 1 informs on commonalities and differences.

**Appendix**

1. Introduction

In the following a test series is followed the description of which in the main text would have disrupted the uniform, straightforward line of thought chosen there.

The experiments on *Emys europaea* hint at a regulated sequence of breathing of this animal, at a certain periodicity.

2. General remarks on the breathing of chelonians

The proper mode of respiration in chelonians is, as in all other reptiles, *inspiration via suction*. Normally, the air flows passively into the extending lung volume. Because of the lack of mobile ribs, this is achieved mainly via the muscles.
the muscles of the girdles under cooperation of accessory motions of extremities and head.

In addition to this thoracic intake air can be swallowed under special circumstances, in which strong motions of the throat press the air into the lungs (HEINEMANN, 1877).

These strong motions of the throat must not be mixed up with slight motions of the throat that accompany regular breathing, or throat oscillations, the significance of which probably is on another aspect altogether.

According to the general scheme of reptilian breathing the individual breath is tri-phased, i.e. there is in addition to inspiration and expiration also a phase of respite of shorter or longer duration. The position of the hiatus seems to be variable. According to BERT (1869) it splits expiration, according to COUVREUR (1898, 1904) inspiration into two halves, according to CHARBONNEL-SALLE (1883) it occurs after completion of inspiration, according to DUBJAGA (1882) after completion of expiration.

Aside from a miniature rhythm that guides the individual breath another breathing rhythm has been observed in turtles, which becomes apparent only over the course of several breaths. FANO (1893, 1893a) observed in hibernating turtles a large, variable number of breaths alternate with a lengthy stand-still of breathing. As the breathing of chelonians is described as very irregular by all authors in agreement this result deserves special attention.

### 3. Preconsiderations with regards to methodology

During my work on *Emys europaea* I noted several side issues that caused me to follow the trail discovered by FANO (1893, 1893a) and search for a periodicity of breathing also under differing circumstances than those offered* by hibernation.

The differences, yes contradictions of the above-mentioned findings on the position of the breathing hiatus are not only an expression of the variability and lability of breathing, but also a strong criticism on the insufficiency of artificial recording method. Although the use of recording devices

(*)note: in High German the original text seems to read that the “circumstances of hibernation”, not those “differing from hibernation”, are meant. However, the use of the wrong preposition that reverts the meaning is typical in the Saxonian idiom that Wolf either spoke or at least was exposed to during his time in Dresden. As the interpretation “differing conditions” makes sense, the reverse however does not, I here chose to assume that Wolf’s grammar was not perfect, and translate accordingly. H.M.
promises, aside from convenience, also the advantage of strictest objectivity, in truth it only leads to sources of error that are hard to eliminate, and makes it hard to distinguish the norm from its exceptions.

Because the respiratory centre of turtles can be influenced by external stimuli extremely easily, it should be of advantage especially in our case to remove irritating apparatus wherever possible.

If one wishes to attempt to get by without recording devices the external signs of respiration must be known exactly. In *Emy europaea*, used in most of the experiments below, in dorsal position the breathing action is very easily tracked by the convex and concave flexing of the crinkly skin areas in front of the hind limbs. If one fixes a rubber finger, punctured at the tip, on the head of *Emys*, one will easily see that inspiration, visible as the deflation of the rubber finger, coincides with a convex bending of said skin area. However, further work with such a rubber finger is not be recommenced. The negative or positive pressure occurring with each inspiration or expiration, respectively, and the hindrance or suppression of throat motions would make the breathing irregular, even erratic. After application of a rubber cap Kahn (1929) observed breathing pauses of over 20 minutes.

Also, one can fix a thin strip of wrapping tissue in front of nose and mouth, which by its motions indicates the direction of the present air flow.

Strong breathing makes itself also known by a small divergence of the angle at which the oral and caudal part of the abdominals touch like a flap.

4. Experiments

A. Surprisingly, a dorsal position of the test animal already showed remarkable results, if it was performed under certain conditions.

If one supports an *Emys* on the dorsal shell so that the extremities are completely free to move, i.e. so that the animal cannot free itself out of the dorsal position, then after the animal has calmed down a phase of breathing alternates periodically with a phase of apnoea. Most assiduous
Avoidance of motions, sounds, light and temperature stimuli etc. is, however, a precondition for success.

In Table 1 I report 12 consecutive breathing periods, which were observed in an *Emys* positioned in the mentioned manner. As can be seen the duration of the breathing phase is 1-2 minutes, on average 1.3 minutes. In this time interval there are 13-28 inspirations, on average 20. The hiatus, which here will be called “apnoea phase” [Atemstille] to distinguish it from the “breathing pause” [Atempause] that interrupts the individual breath, last somewhat longer, viz. 1-2.7 minutes, on average 1.9 minutes.

The phase of breathing activity coincides in dorsal position usually with phases of strong motions of the extremities. After 12-28 breaths the motion of legs and the head ceases, the extremities straighten and quasi freeze (Fig. 44, 45). During this apnoea phase the animal’s ability to react is remarkably reduced. Stimuli by touch etc. that normally lead immediately to retraction of the extremities are either not answered at all, or only by a defensive
closings of the eyes. Only very strong stimuli cause low interim breathing, which however ceases again immediately. The respiratory centre and the sensory and motor centres coupled with it appear now to be in a “refractory state”. This is a parallel to BABEK’s results (1914), who observed the occurrence of such a refractory state in crocodiles, which also show periodicity of breathing (BERT, 1869), after each apnoea phase.

<table>
<thead>
<tr>
<th>After a breathing phase of min.</th>
<th>with breaths</th>
<th>followed a phase of apnoea von min.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td>16</td>
<td>1.5</td>
</tr>
<tr>
<td>1.7</td>
<td>24</td>
<td>2.2</td>
</tr>
<tr>
<td>1.8</td>
<td>32</td>
<td>2.2</td>
</tr>
<tr>
<td>1.2</td>
<td>14</td>
<td>1.8</td>
</tr>
<tr>
<td>1.5</td>
<td>23</td>
<td>2.0</td>
</tr>
<tr>
<td>2.0</td>
<td>28</td>
<td>2.0</td>
</tr>
<tr>
<td>1.0</td>
<td>13</td>
<td>1.0</td>
</tr>
<tr>
<td>1.1</td>
<td>15</td>
<td>1.5</td>
</tr>
<tr>
<td>1.1</td>
<td>16</td>
<td>1.8</td>
</tr>
<tr>
<td>1.3</td>
<td>18</td>
<td>2.7</td>
</tr>
<tr>
<td>1.0</td>
<td>13</td>
<td>2.5</td>
</tr>
<tr>
<td>1.0</td>
<td>22</td>
<td>1.2</td>
</tr>
<tr>
<td>On average: 1.3 minutes</td>
<td>On average: 20 breaths</td>
<td>On average: 1.9 minutes</td>
</tr>
</tbody>
</table>

During the apnoea phase in Emys the crinkly skin area in front of the hind limbs is more or less deeply concave or sinks in during this time. The apnoea does therefore not occur during inspiration position. More cannot be said with certainty based on these external characteristics, as it only informs on the filling of the caudal end chamber.

At the end of the apnoea phase slight throat motions set in, and slow breathing starts, which later becomes stronger and combines with strong motions of the extremities. Then, head and leg motions cease first, the extremities sink down like frozen, and the breaths become weaker and finally stop completely. Before each apnoea phase expiration usually occurs, and after apnoea inspiration.

Repetition of the experiment with different individuals delivered basically the same results. Always a periodic alteration of a phase of
breathing, combined with strong motions of the extremities, and a phase of apnoea, combined with a freezing-like state of the limbs could be observed. Obviously, small individual variance was noticeable, on which size and age seemed to be of influence. Young animals (length of shell 5 cm) showed shorter and less regular periods. Specimens of roughly 20 cm shell length were best suited. But even in these the periods are irregular shortly after feeding. The constant series of breathing and apnoea emerges the most markedly after a starvation period of several days, which slows the metabolism. The initially mentioned periodicity of breathing in hibernating turtles (FANO 1893, 1893a) may potentially be tightly connected to the starvation metabolism.

B. The performance of the same experiment at increased temperature did not give quite unambiguous results. Some of the test animals showed an increased frequency of the individual phases, whereas others appeared to be hindered in their breathing by the influence of high, dry heat. The former was to be expected; as the latter case is interesting as a deviation from the norm I give the data in detail (see Tab. 2).

<table>
<thead>
<tr>
<th>The breathing phase lastet min.</th>
<th>The following apnoea phase min.</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.3</td>
<td>1.0</td>
</tr>
<tr>
<td>0.8</td>
<td>3.5</td>
</tr>
<tr>
<td>0.2</td>
<td>6.5</td>
</tr>
<tr>
<td>0.8</td>
<td>3.5</td>
</tr>
<tr>
<td>0.5</td>
<td>3.0</td>
</tr>
<tr>
<td>0.8</td>
<td>2.0</td>
</tr>
<tr>
<td>0.9</td>
<td>6.0</td>
</tr>
<tr>
<td>and so on</td>
<td>and so on</td>
</tr>
<tr>
<td>On average: 0.6 minutes</td>
<td>On average: 3.6 minutes</td>
</tr>
</tbody>
</table>

C. As reported before in chelonians breathing occurs with the aid of the muscles of the shoulder and pelvic girdles, because of the lack of mobile ribs. Therefore, muscles are active that also serve the motion of the extremities. Between motion and breathing there therefore exist an important relationships.

---

1 The other experiments were conducted by room temperature of 18° C.
According to CHARBONNEL-SALLE (1883) the normal miniature rhythm of the
individual breath taking was destroyed by immobilisation of the girdles in tortoises,
whereas it remained intact in aquatic turtles under the same treatment.

CHARBONNEL-SALLE ascribes to the muscles of the pectoral girdle a higher
impact than those of the pelvic girdle. My own experiments led to different results:
First, the test animal was fixated in dorsal position so that the forelimbs were pulled
forward, the hind limbs tightly backwards, while a block placed under [the turtle]
supported the dorsal shell. After about 10 minutes recording can start. Table 3

<table>
<thead>
<tr>
<th>After a breathing phase of min.</th>
<th>with breaths</th>
<th>followed a phase of apnoea von min.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td>3</td>
<td>1.8</td>
</tr>
<tr>
<td>2.0</td>
<td>2</td>
<td>1.5</td>
</tr>
<tr>
<td>1.4</td>
<td>4</td>
<td>2.0</td>
</tr>
<tr>
<td>1.6</td>
<td>2</td>
<td>1.0</td>
</tr>
<tr>
<td>1.5</td>
<td>3</td>
<td>2.0</td>
</tr>
<tr>
<td>1.7</td>
<td>3</td>
<td>1.3</td>
</tr>
<tr>
<td>1.3</td>
<td>6</td>
<td>3.0</td>
</tr>
<tr>
<td>1.5</td>
<td>5</td>
<td>1.3</td>
</tr>
<tr>
<td>1.4</td>
<td>6</td>
<td>4.5</td>
</tr>
<tr>
<td>1.2</td>
<td>4</td>
<td>1.0</td>
</tr>
<tr>
<td>1.3</td>
<td>2</td>
<td>1.0</td>
</tr>
<tr>
<td>1.7</td>
<td>6</td>
<td>4.0</td>
</tr>
<tr>
<td>On average: 1.7 minutes</td>
<td>On average: 4 breaths</td>
<td>On average: 2 minutes</td>
</tr>
</tbody>
</table>

Gives the results of an experiment of 40 min. duration. It shows that even
with fixated extremities the periodicity of breathing with its regular alternation of
breathing and apnoea remains intact. The average duration of the phases also
changes relatively little. A comparison of Tables 1 and 3 shows that during an
observation time of each ca. 40 minutes

without fixation of the extremities 16 min. were spent breathing and 23 min. pausing,
with " " 17 min. " " 23 min. " .

As reactions to the aggravated breathing due to the fixation of the extremities one
sees larger fluctuations of the phases, an elongation of individual phases and
especially the enormously (to ca. 1/5) reduced number of breaths.
D. Fixation of the posterior extremities alone already had similar success. There is vigorous rowing with the freely mobile front limbs, and the head stretches forward and backward with the exhalation and inhalation. During apnoea the forelimbs are stiffly extended, and the head is back down. Before breathing is resumes, the head is incorporated (start of breathing with inspiration). Table 4 shows

<table>
<thead>
<tr>
<th>After a breathing phase of min.</th>
<th>with breaths</th>
<th>followed a phase of apnoea von min.</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.3</td>
<td>13</td>
<td>1.5</td>
</tr>
<tr>
<td>1.8</td>
<td>5</td>
<td>3.8</td>
</tr>
<tr>
<td>2.9</td>
<td>9</td>
<td>2.5</td>
</tr>
<tr>
<td>2.6</td>
<td>7</td>
<td>2.3</td>
</tr>
<tr>
<td>2.3</td>
<td>6</td>
<td>3.0</td>
</tr>
<tr>
<td>2.5</td>
<td>7</td>
<td>2.7</td>
</tr>
<tr>
<td>On average: 2.4 minutes</td>
<td>On average: 8 breaths</td>
<td>On average: 2.6 minutes</td>
</tr>
</tbody>
</table>

as an example an observation of 30 min. duration. It shows that already by fixation of the hind limbs breathing is significantly influenced: the number of breaths is greatly reduced. The spasmodical working with the forelimbs increases the impression of respiratory distress. The head motions seems to indicate gullar pumping, which occurs only under strong impediment.

E. Even more effective than the simple backward stretching of the hind limbs is a crossing of them, which nearly totally fixates the pelvic girdle. The right leg was tightly clamped to the left, the left to the right. This method of fixation of the hind limbs has a more drastic effect than simply fixation. The number of inspirations during a breathing phase decreases down to two, whereas the duration of apnoea can increase to up to 7 min. (For an example Tab. 5).

From the given numbers it shows that the mobility of the pelvic girdle, at least in *Emys*, has a larger influence on breathing mechanics than was assumed according to Charbonnel-Salle (1883).
After a very short breathing phase with breaths

<table>
<thead>
<tr>
<th></th>
<th>Followed an apnoea phase of min.</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.3</td>
<td>1.0</td>
</tr>
<tr>
<td>0.8</td>
<td>3.5</td>
</tr>
<tr>
<td>0.2</td>
<td>6.5</td>
</tr>
<tr>
<td>0.8</td>
<td>3.5</td>
</tr>
<tr>
<td>0.5</td>
<td>3.0</td>
</tr>
<tr>
<td>0.8</td>
<td>2.0</td>
</tr>
<tr>
<td>0.9</td>
<td>6.0</td>
</tr>
<tr>
<td>and so on</td>
<td>and so on</td>
</tr>
<tr>
<td>On average: 0.6 minutes</td>
<td>On average: 3.6 minutes</td>
</tr>
</tbody>
</table>

F. Comparative studies I undertook on other species of turtles showed that the described periodicity in similarly easy way can be observed only in aquatic turtles. This suggests that the periodicity in them will make itself known by some signs also under water.

If a trained diver wants to stay under water for an extended period of time he will not fill his lung all too full. *Emys* behaves similarly. Brought under water it will emit a part of the air in the lung again and thus reach the optimal lung filling for diving. If one has previously brought an *Emys* into the previously described dorsal position and noted the average periods of the breathing pattern, one will now note that the excess air is immediately emitted, if the animal is dumped into water during the breathing phase. If one brings it under water during the apnoea phase, however, the regulation of the lung filling state occurs later, i.e. after the end of the apnoea phase. For submersion the animal was kept in dorsal position. Submersion obviously has to be performed very carefully, in order not to disturb the development of the phases by external stimuli.

Occasionally it could be observed that the experimental animal remained in its quasi frozen state when it was placed very carefully with its back on the water. Only after the roughly predicted conclusion
of this phase, which runs parallel with the refractory period of the sensory and motor centres, it [the animal] made efforts to exchange its unnatural position with the regular one.

During a longer diving period (45-60 minutes) the refractory stadium also appears, perhaps as an expression of the still working periodicity that underlies breathing. If a test animal is submerged, it is only natural that it tried to free itself from its involuntary position. It must attract even more attention that even not clearly enough phases of desire for air, recognizable by intense attempts to surface, alternate with phases of apathetic immobility. For the duration of such a phase quite some animals remained motionless submerged, even if they had full freedom of motion.

A small *Emys caspica*, which was unable to bring itself back to normal position from dorsal position by swimming, was placed in the water with the ventral shell up. It showed for 4 minutes a periodic alternation of rest and motion, with the head all the time bent backwards and under the surface of the water. Each phase lasted roughly 1 minute.

Under water the motion of the extremities gains a new meaning. Even though it can now in diving position not serve to bring fresh air to the lung, each motion, especially of the hind limbs, leads to a mixing of the air content of the lung. Such an internal ventilation of the lung can occur under water even with fixated extremities. Often, a repetitive swelling and depression of the crinkly skin area in front of the posterior extremities happens already after a few minutes of diving, from which the charge of the caudal final chamber of the lung can be seen.

5. Application of the experiments

So far I have done little more than give a pure report of facts, now the possible interpretations of the experiment results are to be considered.

As the most important results the following circumstances appeared:

1. **Under certain circumstances a periodicity of breathing was observed in *Emys europaea*. Regularly, a phase of breathing activity, combined with strong motions of the extremities, alternates with a phase of apnoea with quasi frozen limbs.
2. In animals of medium size the duration of a breathing phase with 13-28 breaths (on average 20) was ca. 1-2 minutes (on average 1.3). The duration of apnoea was somewhat longer, viz. 1-2.7 minutes (on average 1.9).

3. Fixation of the limbs does not break the periodicity, but the number of breaths in a breathing phase is reduced, whereas the average duration of apnoea increases somewhat.

4. The pelvic girdle has an especially high importance for the mechanics of breathing.

5. Signs of periodicity can be recognized also during diving.

The periodicity of breathing shown here can be interpreted in two ways. Firstly, one could assume the alternation of breathing activity and apnoea to be a secondary phenomenon, which is based on the periodic motion of the extremities. In dorsal position the animal would aim to achieve normal position. After strong but useless muscular effort that uses a lot of oxygen exhaustion would set in. This results in the ensuing rest period. After the rest motion with breathing again sets in, etc.

It seems to me that this explanation does not hit the mark. If exhaustion only was the cause, the hindrance of breathing by fixation of the extremities would have to influence the duration of the phases much more. In my opinion the breathing and the motion of the extremities connected to it is not suspended or started anew because of external but internal causes. The periodicity of breathing must be seen as a consequence of construction and working mechanism of the lung, because crocodilians, the lungs of which resemble those of chelonians to some degree, show a quite corresponding periodicity of breathing (BERT 1869, BABAK 1914)\(^1\).

Subsequent to the considerations of the main part of the present work some aspects are of interest that are to be discussed in more detail here.

As opposed to the general opinion it became apparent during the course of the experiments described above that the muscles of the pelvic girdle have a larger role in the mechanics of breathing than those of the shoulder girdle. Such a determination would be highly unbelievable if the less well perfused

\(^1\) Breathing rhythm and breathing periodicity are closely connected. External stimuli can cause one mode of breathing to be replaced by the other. It can be assumed that in our case the pressure of the innards on the lung (dorsal position!) is the causing stimulus.
caudal part of the turtle lung was only used as an air reservoir. It becomes immediately understandable, however, if one concludes on a special air flow pattern in the turtle lung based on its special construction. Then the caudal final chamber can be compared functionally to the caudal air sac of birds, and plays like the latter an important mechanical role in the ventilation of the lung. Only if this is really the case will the obstruction of muscle effort in the pelvic girdle block hinder breathing so much, as the experiments in question show. That only the muscles of the pelvic girdle fill and empty the caudal final chamber of *Emys* is visible from the earlier mentioned fact that precisely the caudal part of the lung remains free of the expiratory muscle cover that surrounds all the rest of the lung.

Additionally, it seems unique that signs of periodicity of breathing can be shown to exist also in the diving animal. This aspect can also only be explained with the aid of the results won in the main part of this work. It was pointed out that the periodic alteration of motion and stillness of the extremities that can be observed in animals in diving position hints at a periodically occurring internal ventilation of the lung (with closed glottis). This inner ventilation of the lung occurs always during the breathing phases (the phases of air hunger) and seems to satisfy the animal’s demand for oxygen temporarily. A satisfaction of the demand for oxygen is however only possible, if there is air richer in oxygen in the caudal final chamber than in the other chambers, i.e. if the freshly inhaled air first is led to the caudal air chamber and only from there reaches the respiratory parts of the lung.

**Summary**

The present work delivered a comparative look at the most varied reptile lungs. Special attention was paid to the relations between the reptile and the bird lung, which are suited to deliver on the one hand parallels on the most important specialties of construction of the bird lung, and on the other hand explain the confusing diversity and richness of forms of the reptile lung.
It was found that the complication [increased complexity] of the reptile lung for the more effective use of the air mainly is achieved by the same specialties of construction which in higher expression and completeness characterize the breathing apparatus of birds. The insights resulting from this were used to trace back the polymorphy of the reptile lung to a few basic bauplans.

The inspiration to this work I received from my revered teacher, Prof. Dr. BRANDES. Sincere heartfelt thanks in this place also to him for his help and for making available the in part very rare and valuable material. Also I do not wish to forget to thank private lecturer Dr. DOTTERWEICH, who aided me in especially in practical matters with advise and deeds.

Reference list


→, 1897, Beiträge zur Kenntnis der Reptilienlunge, 2. Teil (Chelonier), in: ibid., Vol. 10, Heft 1.


