Lungs and mesopneumonia of scincomorph lizards (Reptilia: Squamata)

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Abstract

Mesopneumonia of 28 and lungs of 44 species of scincomorph lizards are described, representing mesopneumonia in six of the seven scincomorph families and lungs of all seven families of this taxon. Except for gymnophthalmids and scincids, a family typical organization of mesopneumonia occurs. In cordylids, gerrhosaurids, xantusiids and lacertids the complete right ventral mesopneumonium (VMp) inserts cranially on the posterior vena cava and caudally on the dorsal surface of the right liver lobe. The left VMp is attached to the ventrolateral body wall in cordylids and lacertids; in gerrhosaurids the left VMp is short and inserts on the pericardium and the posterior vena cava; in xantusiids the left VMp is reduced and the lungs are fused cranially with the pericardium. In scincids the VMp of both sides vary in length and insert on the ventral mesentery, or may be lacking completely. The visceral topology of the gymnophthalmids \textit{Calyptommatus} and \textit{Notobachia} differs from the general scincomorph pattern, with the liver and stomach elongated and situated on the right and left side of the body cavity, respectively. The left and the right VMp extend over the entire length of the lungs and insert on the ventral mesentery. All lungs examined in the study are single-chambered and show no major structural variability of the inner surfaces, except in lacertids, some gerrhosaurids, \textit{Cordylus}, and two genera of gymnophthalmids (\textit{Echinosaura} and \textit{Neusticurus}). In these groups, rows of dorsomedial niches are present.

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Introduction

Scincomorpha comprises seven families forming two clades. One group (Scincoidea) comprises Scincidae, Cordylidae and Gerrhosauridae, whereas the other (Lacertoidae) contains Xantusiidae, Lacertidae, Teiidae and Gymnophthalmidae (Fig. 1; Estes et al. 1988). The number of species exceeds 1900 for all scincomorph lizards, with approximately 1227 scincids (Greer 2001), 54 cordylids (Uetz 2004), 32 gerrhosaurids (Uetz 2004), 26 xantusiids (Uetz 2004), 264 lacertids (Uetz 2000), 117 teiids (Uetz 2000), and 182 gymnophthalmids (Uetz 2000).

The lungs of 13 and the mesopneumonia of 24 scincomorph species are described in detail, representing all or six of the seven scincomorph families, respectively (see Part 1 of the accompanying Organisms Diversity and Evolution Electronic Supplement at...
In most cases qualitative data for only one or two species per family is available (e.g. Milani 1894; Broman 1904; Becker 1993). However, within the Teiioidea the mesopneumonia (Klein et al. 2000), and within the Varanoidea the lung structure (Becker et al. 1989), comprise a useful character only at the family level. Therefore, description of a small number of species per family represents a meaningful contribution. The aim of the present paper is to describe the mesopneumonia and provide quantitative morphological data for the lungs of representatives of all families of scincomorph lizards, and thereby to develop some hypotheses about the functional and systematic value of the mesopneumonia–lung complex.

**Materials and methods**

Specimens from the Alexander Koenig Zoological Research Institute and Museum (ZFMK) in Bonn, Germany, and from the collection of P.L.B. Rocha (Universidade Federal da Bahia, Brazil) were used. Snout-vent length (SVL), total length (TL), and body mass ($M_B$) were recorded as reference data (see Electr. Suppl. 05-06, Pt. 2).

The visceral topology and location of mesos in each group are presented, followed by a description of the lungs. Definitions of the mesos and representation of the results follow Klein et al. (2000). Briefly, a standard schematic diagram, representing the parietal and visceral surfaces within a body cavity, is used to document the origin and insertion of the investigated mesos ($DM = $dorsal mesentery, $VM = $ventral mesentery; $DMp = $dorsal mesopneumonium, $VMp = $ventral mesopneumonium). The part of a meso attached to the organ is defined as its origin; the distal part as insertion.

To visualize the lungs, a combined toluidine blue-PAS (Periodic-Acid–Schiff reaction) en-bloc staining method was used. This method, which selectively stains tracheal cartilage and lung parenchyma, is as follows: (1) tap water, 6–8 h; (2) periodic acid (0.5%), 60 min; (3) Schiff’s reagent, 10 min; (4) tap water, 5 min; (5) acid ethanol (70%, 1% HCl conc.), 16 h; (6) toluidine blue (0.25%, pH<2), at least 4 h; (7) ethanol (70%), several repetitions to wash out superfluous toluidine blue; (8) ethanol (50%), 5 min; (9) clearing and storage of lungs in glycerol.

The following data for the respiratory system (glottis, trachea and lungs) were collected [units of measurement in square brackets]: length of respiratory system measured from cranial tip of glottis to most caudal end of lungs ($L_{RS}$ [mm]), length of lungs ($L_{Lu}$ [mm]), length of left lung ($L_{le}$ [mm]), length of right lung ($L_{ri}$ [mm]), length of trachea ($L_{Tr}$ [mm]), length of extrapulmonary bronchus ($L_{Br}$ [mm]), length of prehilar region ($L_{Ph}$ [mm]), number of niches ($N_N$), number of tracheal cartilages ($N_{TC}$), parenchymal type (ed $= $ediculae, fav $= $faveoli) and parenchymal distribution (het $= $heterogeneous, hom $= $homogeneous). $L_{RS}$, $L_{Lu}$ and $L_{Tr}$ were standardized to SVL, $L_{Tr}$ and $L_{Br}$ were standardized to $L_{RS}$, $L_{Ph}$ was standardized to $L_{Lu}$, and the quotients of lung length over tracheal length ($L_{Lu}/L_{Tr}$), and length of left lung over length of right lung ($L_{le}/L_{ri}$) were calculated.

**Results**

**Scincomorpha**

**General visceral topology**

The heart lies in its pericardial cavity at the level of the shoulder girdle, connected caudally via the vena cava to the liver. The latter is composed of two lobes, divided in the mediosagittal plane. The right lobe is larger than the left one and extends dorso-caudally, contacting the meso of the right gonad with its caudal end. The gall bladder is embedded in the ventro-caudal part of the right liver lobe and the stomach lies on the left side of the abdominal cavity. The lungs lie dorso-caudally to the heart and dorsally to the cranial parts of liver and stomach. No intrapulmonary bronchi are present and the extra-pulmonary bronchi, when present, are short. Intestine, gonads and fat bodies, whose presence and size vary according to the nutritional status of a specimen, fill the caudal part of the body cavity.

**Scincidae**

**Visceral topology and mesos**

The viscera of skinks show no deviation from the general scincomorph pattern. $DMp$ originate on the dorsal mid-line of the lungs and insert on the border alimentary canal-$DM$. The $VMp$ vary in their development.
on both sides. A cranial fusion of lungs with pericardium occurs in *Chalcides*, *Tiliqua* and *Tribolonotus* (Fig. 2a). *Novoeumeces* and *Mabuya* show a complete right VMp originating in the ventral mid-line of the lung and inserting at the border esophagus-VM. The left VMp of *Novoeumeces* extends from the cranial 1/4 of the lung and inserts at the base of the esophageal VM. In *Mabuya*, on the other hand, the left VMp is lacking and the left lung is fused cranially with the pericardium. The right VMp of *Scincus* originates in the cranial 3/4 of the lung and inserts on the VM. The left VMp, by contrast, originates only on the cranial 1/4 of the lung, also inserting on the VM (Fig. 2b).

**Respiratory system**

For results per species see Electr. Suppl. 05-06, Pt. 3. The $L_{RS}$ ranges from 36.3% SVL in *Chalcides* up to 56.7% SVL in *Tribolonotus*, with the mean at 45.3% SVL. The trachea averages 18.9% SVL (min. 15.5% in *Tiliqua*, max. 21.2% in *Scincus*), the extra-pulmonary bronchi 2.3% $L_{RS}$ (min. 1.6% in *Mabuya*, max. 3.2% in *Scincus*), the prehilus 6.2% $L_{Lu}$ (min. 2.5% in *Novoeumeces*, max. 12.3% in *Chalcides*), and the lungs 22.8% SVL (min. 13.2% in *Chalcides*, max. 32.3% in *Tribolonotus*). The lungs are of equal length, with $L_{Lu}/L_{Tr}$ 1.03 (min. 0.92 in *Mabuya*, max. 1.12 in *Scincus*). The $N_{TC}$ is 51.3 (min. 33.3 in *Tribolonotus*, max. 62.7 in *Mabuya*), and $L_{Lu}/L_{Tr}$ is 1.22 (min. 0.9 in *Chalcides*, max. 1.6 in *Tribolonotus*). The lungs are long and slender, show a slightly heterogeneous parenchymal distribution with faveoli in the cranial part of the lung and ediculae in the most caudal part. No niches are present (Fig. 2c).

**Cordylidae**

**Visceral topology and mesos**

The viscera show the general scincomorph pattern. The DMp are well developed, originate in the dorsal mid-line of each lung and insert cranially on the
esophagus. The insertion ends caudally on the DM. The complete right VMp originates in the ventral mid-line of the lung, inserts cranially on the posterior vena cava and caudally on the dorsal surface of the right liver lobe. The left VMp varies in length. It is shortest in *Pseudocordylus*, complete in *Platysaurus*. In general, it extends over the cranial half of the lung. The insertion begins cranially on the pericardium and extends caudally along the ventrolateral body wall (Fig. 3a).

Respiratory system

The dimensions of the respiratory system are similar to those of scincids, but the lungs appear more sac-like, except in *Chamaesaura anguina*, where they are long and slender. In *Platysaurus capensis* the right lung is slightly longer than the left one ($L_{lu}/L_{ri}$ 0.96), whereas in *C. anguina* the left lung is much longer than the right one ($L_{lu}/L_{ri}$ 1.20). *Cordylus giganteus* shows the longest trachea (26.5% SVL) together with the longest respiratory system (58.7% SVL), whereas *Chamaesaura macrolepis* shows the shortest trachea (10.6% SVL) and the shortest respiratory system (37.2% SVL). *Pseudocordylus melanotus* has the shortest lung (17.6% SVL), whereas *C. anguina* has the longest lung (33.8% SVL) but the shortest prehilus (4.4% $L_{lu}$). The longest prehilus (16.4% $L_{lu}$) occurs in *P. capensis*. Extra-pulmonary bronchi are shortest in *C. anguina* (1.5% $L_{RS}$) and *C. macrolepis* (2.8% $L_{RS}$), longest in *P. melanotus*, *P. capensis* and *P. microlepidotus* (8.2%, 7.9% and 7.8% $L_{RS}$, respectively). The $N_{TC}$ ranges from 32.7 in *C. anguina* and 39.0 in *C. macrolepis* up to 66.0 in *Platysaurus guttatus*. *Pseudocordylus melanotus* has the lowest $L_{lu}/L_{Tr}$ (0.68), *C. macrolepis* and *C. anguina* have the highest $L_{lu}/L_{Tr}$ (2.5 and 2.49, respectively). The parenchymal distribution is slightly heterogeneous, with faveoli cranially and ediculae caudally. *Chamaesaura anguina* and *C. macrolepis* display highly heterogeneous lungs, with ediculae cranially and trabecular parenchyma caudally.

Niches are present in *C. cordylus* (Fig. 3b).

Gerrhosauridae

Visceral topology and mesos

The viscera demonstrate the general scincomorph pattern. The DMp and the right VMp show the same pattern as in cordylids. The left VMp is short, being present only on the cranial half of the lung. It originates in the ventral mid-line and inserts on the pericardium and the vena cava (Fig. 4a).

Respiratory system

The $L_{RS}$ ranges from 37.2% SVL (*Tetradactylus*) to 50.8% SVL (*Gerrhosaurus*), $L_{lu}/L_{ri}$ ranges from 0.85 (*Gerrhosaurus*) to 1.13 (*Zonosaurus*). *Tetradactylus* displays the shortest lungs (20.3% SVL), the lowest $N_{TC}$ (46.7) and the lowest $L_{Br}$ (4.6% $L_{RS}$) and $L_{Ph}$ (10.4% $L_{RS}$). *Gerrhosaurus*, on the other hand, has the greatest $L_{lu}$ (29.0% SVL), $N_{TC}$ (52.5) and $L_{lu}/L_{Tr}$ (1.86), but the lowest $L_{Br}$ (3.5% $L_{RS}$) and $L_{Ph}$ (5.8% $L_{RS}$). The mean values are 43.0% SVL for $L_{RS}$, 23.1% SVL for $L_{lu}$, 8.5% $L_{RS}$ for $L_{Ph}$, 1.0 for $L_{lu}/L_{ri}$, and 1.3 for $L_{lu}/L_{Tr}$. The mean $L_{Tr}$, $L_{Br}$ and $N_{TC}$ are 17.4% SVL, 4.2% $L_{RS}$ and 50.0, respectively. The lungs show a homogeneous distribution of faveoli. Dorsal niches are present (Fig. 4b) in all genera except *Tetradactylus* (niches lacking). *Gerrhosaurus* having the most prominent niches connecting the left and right side of the lungs in a bridge-like structure. In *Tracheloptychus* and *Zonosaurus* the niches are generally small and composed of trabecular muscles which are lifted above the respiratory parenchyma. There are no faveoli or ediculae on the walls of the niches. *Zonosaurus* has the highest $N_{Ni}$ with 12.4.
Xantusiidae

Visceral topology and mesos
The viscera conform to the general scinciform pattern. The DMp of both lungs originate in the dorsal mid-line and insert at the border esophagus-DM. A complete VMp is present only on the right side, inserting cranially on the vena cava and caudally on the dorsal surface of the right liver lobe. On the left side the pericardium is fused with the lung (Fig. 5a).

Respiratory system
The $L_{RS}$ is 37.1% SVL, $L_{Lu}$ 16.5% SVL, $L_{Ph}$ 9.5% $L_{Lu}$, $L_{Tr}$ 17.0% SVL, $L_{Br}$ 5.0% $L_{RS}$, $L_{Lu}/L_{Tr}$ 0.97, $L_{le}/L_{i}$ 1.00, and $N_{TC}$ 44.5. The lungs are homogeneous, consisting entirely of faveoli. Niches are lacking (Fig. 5b).

Lacertidae

Visceral topology and mesos
The viscera do not differ from the general scinciform pattern. The DMp insert cranially on the esophagus and end caudally on the DM. The complete right VMp inserts cranially on the posterior vena cava and caudally on the dorsal surface of the right liver lobe. A left VMp has its origin only in the cranial 1/3 of the lung and inserts on the lateral body wall (Fig. 6a).

Respiratory system
The respiratory system is very similar in all investigated lacertids. There is little variation in $L_{RS}$ [42.3% SVL (Psammomimus) to 49.5% SVL (Lacerta viridis)], $L_{Lu}$ [16.8% SVL (Gallotia galloti) to 21.9% SVL (Psammomimus)], $L_{Ph}$ [0.0% $L_{Lu}$ (G. stehlini) to 9.4% $L_{Lu}$ (G. galloti)], $L_{le}/L_{i}$ [0.91 (G. stehlini) to 1.00 ($L_{ viridis}$ and Psammomimus)], $L_{Tr}$ [18.7% SVL]
Psammomuridus to 28.1% SVL (G. galloti), $L_{Br}$ [2.0% $L_{RS}$ (L. viridis), 2.1% $L_{RS}$ (T. lepida) to 5.5% $L_{RS}$ (Psammomuridus)]. The $N_{TC}$ ranges between 45.0 (Psammomuridus) and 60.0 (G. galloti), whereas $L_{Lu}/L_{Tr}$ ranges between 0.71 (G. galloti) and 1.18 (Psammomuridus). The parenchymal distribution is homogeneous, with faveoli covering all parts of the lung surface but with decreasing depth cranially to caudally. All lungs have small dorsomedial niches ($N_{Ni} = 9.3$; Fig. 6b).

Teiidae

Visceral topology and mesos

Visceral topology is the same as in scincomorphs. The mesos of this group have been described in detail (Klein et al. 2000).

Respiratory system

The $L_{RS}$ ranges from 38.4% SVL in Ameiva up to 50.1% SVL in Tupinambis, with the mean at 44.2% SVL. The $L_{Tr}$ averages 21.7% SVL (min. 17.2% in Ameiva, max. 27.0% in Callopistes), $L_{Br}$ 1.2% $L_{RS}$ (min. 0.0% in Dicrodon and Crocodilurus, max. 2.6% in A. undulata), $L_{Ph}$ 8.8% $L_{Lu}$ (min. 0.0% in Crocodilurus, max. 14.7% in Callopistes), $L_{Lu}$ 20.8% SVL (min. 17.6% in Cnemidophorus, max. 26.0% in Crocodilurus), and $L_{le}/L_{ri}$ 0.93 (min. 0.81 in Tupinambis, max. 1.04 in Crocodilurus). The $N_{TC}$ is 56.1 (min. 46.0 in Cnemidophorus, max. 72.0 in Tupinambis) and $L_{Lu}/L_{Tr}$ is 1.00 (min. 0.81 in Callopistes, max. 1.19 in A. undulata). All species display homogeneously distributed faveoli. Niches are never present (Fig. 7), and Ameiva, Crocodilurus, Teius and Tupinambis show a prominent muscular ridge on the lateral and medial internal surfaces of the lungs.

Gymnophthalmidae

Visceral topology and mesos

The visceral topology of Alopoglossus, Anadia, Echinosaura, Neusticurus, Pantodactylus, Pholidobolus, Prionodactylus, and Proctoporus has been described in a previous paper (Klein et al. 2000). Briefly, these genera do not differ from the general scincomorph pattern, nor do Psilophthalmus, Procellosaurus, and Vanzosaura (the latter has been separated from the
genus Gymnophthalmus by Rodrigues 1991; most authors, however, follow the old taxonomy and refer to Vanzosaura rubricauda as Gymnophthalmus rubricauda, e.g. Ziegler et al. 2002). In contrast to this, Calyptommatus and Notobachia show a smaller left liver lobe than the other gymnophthalmids, which is smallest in Calyptommatus and slightly larger in Notobachia (Fig. 8a). The right liver lobe is elongated and present only on the right side of the abdominal cavity. The stomach is relatively large and elongated, and lies on the left side of the abdominal cavity. The origin of the DMP is in the dorsal mid-line of the lungs, the insertion is at the border esophagus-DM. VMp are present along the entire length of both lungs, originating ventrolaterally on the lungs and inserting at the base of the esophageal VM. No post-hepatic septum (see Klein et al. 2000) was found (Fig. 8a).

**Respiratory system**

The mean $L_{RS}$ is 35.3% SVL, but values range from 16.8% SVL (Procellosaurinus) to 46.2% SVL (Neusticurus). Alapoglossus has the lowest $L_{Lu}$ (12.1% SVL), Neusticurus the greatest $L_{Lu}$ (18.7% SVL). The $L_{Lu}/L_{ri}$ varies between 0.88 (Neusticurus), 0.89 (Psilophthalmus) and 1.13 (Proctoporus). The $L_{Ri}$ ranges from 0.0% $L_{Lu}$ (Pantodactylus, Prionodactylus) up to 12.5% $L_{Lu}$ (Proctoporus) and 16.9% $L_{Lu}$ (Anadia). The $L_{TF}$ varies from 10.8% SVL (Notobachia) and 12.6% SVL (Calyptommatus) up to 24.9% SVL (Neusticurus), whereas $L_{Br}$ varies from 0.7% $L_{RS}$ (Calyptommatus) and 0.8% $L_{RS}$ (Notobachia) up to 5.9% $L_{RS}$ (Procellosaurinus) and 7.0% $L_{RS}$ (Proctoporus). The $N_{TC}$ is lowest in Alapoglossus (36.0) and highest in Neusticurus (55.5). The $L_{Lu}/L_{TF}$ varies from 0.63 (Pantodactylus) up to 1.12 (Calyptommatus) and 1.28 (Notobachia). The parenchymal distribution is homogeneous, with faveoli in all investigated genera (Fig. 8b) except Echinosaura, which has ediculae homogeneously distributed in the lungs. Neusticurus and Echinosaura display small dorsomedial niches.

**Discussion**

The following morphological features characterize the respiratory system in scincomorph lizards (as defined by Estes et al. 1988) and, taken together, distinguish it from that of other major saurian clades: (1) scincomorph lungs are single-chambered, (2) of equal size in the plesiomorphic state, and (3) the parenchyma tends to be distributed homogeneously. Furthermore, (4) the left and right lungs tend to be mirror images of each other, distinguishing them from those of iguanian and anguimorphian lizards, which characteristically differ in length or structure (Milani 1894; Perry 1998). As in the Gekkota, (5) dorsomedial niches appear to be ancestral but are lost in highly derived forms. (6) The internal septation into chambers and lobes that characterizes the transitional lung structure of many Iguania is lacking, (7) as are fused bronchi, which are present in many geckos (Mauelshagen 1997; Perry 1998). (8) The trachea and the bronchi (when present) are reinforced by cartilaginous rings. (9) The lungs in all scincomorph groups retain complete mobility and are fused with surrounding structures only at the apex. (10) The complete right VMp inserts in the plesiomorphic state on the dorsal liver surface.

Moreover, a set of apomorphies can be ascribed to some groups of scincomorph lizards. (A) In scincids the VMp of the right and left side insert on the ventral mesentery or may be lacking completely. Niches are lacking, and parenchymal distribution tends to be heterogeneous. (B) Cordylids show an insertion of the left VMp on the lateral body wall, and lost niches in most groups. (C) Gerrhosaurids show no apomorphy,
except that in *T. seps seps* no niches have been found. (D) In lizards the left VMp inserts on the lateral body wall. (E) Both teiid families lack niches and show no left VMp. In teiids the right VMp is also completely reduced. Some of these characters, however, may be reversed secondarily in advanced gymnophthalmids, especially in fossorial species.

A comparison of the phylogenetic relationships of squamates based on the hypotheses of Estes et al. (1988) and Lee (1998) reveals a fundamental difference: the clade Scincomorpha as defined by Estes et al. (1988) has been revised by Lee (1998), who suggests that xantusiids are the sister group of a clade ((Pygopodidae: Geckonidae) (Amphisbaenidae: Dibamidae)), and furthermore that (scincids; cordyliforms) are sister to all anguimorphans including snakes. Based on characters of squamate soft anatomy, Lee (2000) places scincids and cordyliforms within the scincomorphan clade, but not xantusiid lizards who remain in a sister-group relationship to pygopodids, geckonids, amphisbaenians and dibamids. In both studies (Lee 1998, 2000), however, the phylogenetic relationships of the Scincoides are only weakly supported. Based on the limited set of characters examined in the present study, neither of the two suggested phylogenies can be supported or refused. Some Anguidae show short bronchi and small, single-chambered lungs of equal size, containing homogeneously distributed parenchyma (Perry 1998). They thus resemble the lungs of scincids and cordylids, which is consistent with the hypothesis of Lee (1998). Quantitative data on the respiratory system from all families of squamate lizards are needed to develop hypotheses about the evolution of this complex organ system.

**Lung structure**

Within the Scincomorpha, numerous apomorphic traits distinguish individual taxa with respect to lung structure. *Chamaesaura*, for example, shows a heterogeneous parenchymal distribution, with the caudal region of the lung containing a small number of trabeculae that lie directly on the lung floor (trabecular parenchyma; Perry 1998). However, the lungs are not elongated (*L_{lu} 33.84% SVL*, compared to 32.30% SVL in *Tribolonotus*) as could be expected from the serpentine body form. Lacertids, gerrhosaurids, some cordylids, and the gymnophthalmid genera *Echinosaura* and *Neusticus*, on the other hand, display dorsomedial intrapulmonary niches. These niches generally are small and composed of muscular trabeculae, which are raised above the respiratory parenchyma. However, because they lack faveoli or ediculae on their walls, it is questionable if these niches are homologous to those found in iguanids or chameleons. In *Gerrhosaurus* the niches are even more prominent and connect the medial and lateral sides of the lungs in a suspension bridge-like fashion.

Interestingly, *Echinosaura* and *Neusticus* – the only gymnophthalmids that possess dorsomedial niches – also lack a post-hepatic septum (Klein et al. 2000). Others that lack a post-hepatic septum (*Calyptommatus, Notobachia, Psilophthalmus, Procelsolaurus, Van佐saira*) are distinguished by their extremely small size, and thus the lack of a post-hepatic septum could be attributed to a distribution of mechanical forces (see below) different from that in genera like *Echinosaura* and *Neusticus* with larger body size. The raised trabeculae of the niches may also help preserve the equilibrium of the lungs in spite of their angular external contour. In addition, niche structure, as opposed to faveoli or ediculae, results in a more efficient use of the low degree of air movement likely to be present during breath-hold periods (Perry 1992). Alternatively, the present systematic position of *Echinosaura* and *Neusticus* could be in error, and presence of dorsomedial niches is a symplesiomorphic trait, common to these and other basal lizards. Böhme (1988), using hemipenal morphology, showed that *Neusticus* possesses teiid as well as lacertid characters, making the position of this genus within gymnophthalmids questionable.

The quantitative proportions of the respiratory system are more or less uniform throughout the Scincomorpha, except for the gymnophthalmids. Their *L_{RS} is about 10% SVL lower than that of the other families, even when the extreme values of *Neusticus, Pholidobolus* and *Procelsolaurus* are disregarded (new mean *L_{RS}: 35.1% ± 6.2%*). This difference is almost completely attributable to the lungs, which are 5–10% shorter than in the other groups. The trachea, on the other hand, displays the same proportions as in other scincomorphs, but with fewer tracheal cartilages (*N_{TC} = 43.2*). The lungs generally are of equal length, with *L_{le}/L_{lu} between 0.97 and 1.03*. A notable exception is *Bachia cophias* Cunha, 1958, in which the right lung is reduced significantly, thereby resembling the amphisbaenian (rather than serpentian) pattern of one-sided lung reduction (Böhme 1989). On the family level, only teiids show a slight tendency to reduce the right lung, with *L_{le}/L_{lu} at 0.93 ± 0.07*.

*Ameiva, Crocodilurus, Teius and Tupinambis* show a muscular ridge on the inner lateral surfaces of the lungs. The trabecular muscle is presumed to support gas exchange by contracting and therefore moving oxygen-poor air out of the faveoli to the central lumen of the lung (Perry 1992). For highly aerobic animals, active contraction of the faveoli could help maintain a given level of oxygenated blood during rest, since near the faveoli oxygen is extracted much more rapidly than from the central lung lumen (diffusion-dominated gas exchange model; Perry 1992). In general, teiids are
highly active, whereas gymnophthalmids are mostly secretive, sit-and-wait predators (Urban 1965; MacLean 1974). On the other hand, the muscular ridge may stabilize the lungs and provide a large surface area of ciliated epithelium for transport of mucus from the large faveolar lung surface.

With regard to external airways, the values for $L_{\text{Lu}}/L_{\text{Te}}$ appear to conform with the systematic position within the Scincidea (Scincidae 1.22, Cordylidae 1.35, Gerrhosauridae 1.35) and Lacertidea (Xantusiidae 0.97, Lacertidae 1.00, Teiidae 1.00, Gymnophthalmidae 0.81). However, after removing the extreme values of Chamaesaura macrolepis (2.50), C. anguia tenuior (2.49), Gerrhosaurus (1.86), and Tribolonotus (1.62), the corresponding means for the remaining scincids (1.13), cordylids (0.92), and gerrhosaurids (1.11) are similar to the values found in lacertoids. Therefore, all values are comparable, with gymnophthalmids showing the shortest trachea in relation to the lungs.

Mesopneumonia

The mesopneumonia of most scincomorph taxa are conservative. Both lungs always have complete dorsal mesopneumonia, and a well-developed right VMp is also present in most groups. The insertion of the dorsal and ventral mesopneumonia on or near the respective dorsal and ventral mesenteries is also generally conservative.

Within the Teiioidea the position of intracoelomic ligaments, in particular the development of the post-hepatic septum, correlates well with the systematic position of species determined according to skeletal and external morphological characters (Estes et al. 1988; Klein et al. 2000). The lack of a post-hepatic septum in very small and/or elongate gymnophthalmids (Klein et al. 2000), the corresponding means for the remaining scincids (1.13), cordylids (0.92), and gerrhosaurids (1.11) are similar to the values found in lacertoids. Therefore, all values are comparable, with gymnophthalmids showing the shortest trachea in relation to the lungs.

Regarding the degree of expression of the mesopneumonia in non-teioid scincomorphs, gerrhosaurids can be grouped with the xantusiids, whereas the picture is more diverse among scincid lizards. Here, Chalcides, Tiliqua, and Tribolonotus resemble teiids in lacking right and left Vmp, but Novoeneuces, “Mabuya” (sensu lato, but see Hausfeld 2003) and Scincus resemble certain gymnophthalmids (Allopoglossus, Anadua, Echinosaura, Neusticosaurus, Pantodactylus, Pholidobolus, and Priodontactylus) in showing Vmp (Klein et al. 2000). Interestingly, this arrangement of mesopneumonia is in contradiction to the lifestyle of the animal. Chalcides, Tiliqua and Tribolonotus are characterized as slow-moving lizards (Zug et al. 2001), and therefore resemble ‘sit-and-wait’ gymnophthalmids, whereas Novoeneuces, “Mabuya” and Scincus are fast-moving lizards, resembling the highly active teiids (Zug et al. 2001). The possible correlation of mesopneumonium expression with the systematics of gymnophthalmids and scincids is uncertain, as the systematics is not yet fully resolved.
sufficiently resolved to allow a comparison within these two groups. The variation observed here within the Scincidae – a group comprising more than 1200 species – also merits further study. The Gekkota – also with more than 1000 species – show much less variation in the expression of the VMp than do scincids (Becker 1993; Mauelshagen 1997).

Serpentine body form and topology of internal organs

Most scincomorph lizards display similar general visceral topology: the lungs overlap caudally with the cranial parts of liver and stomach. In Calyptommatus and Notobachia, however, the short lungs lie anterior to the liver and stomach, which are on the right or left side of the body cavity, respectively (Fig. 8a). These two genera, together with Chamaesaura, have a very short trachea (LT, 10.6% SVL in Chamaesaura macrolepis, 10.8% SVL in Notobachia, 12.5% SVL in Chamaesaura anguina, and 12.6% SVL in Calyptommatus). All of these genera have reduced limbs, but only Calyptommatus and Notobachia show an elongation of the trunk. Since Chamaesaura obtains a serpentine form to a great extent by elongation of the tail and exhibits only moderate elongation of the trunk, the proportions of lungs and viscera conform to the general scincomorph pattern. Thus, with regard to internal topology there are at least three possibilities that result in serpentine body form and limb reduction: (1) the snake/amphisbaenian/Bachia cophias pattern, characterized by elongation of the trunk, reduction or elimination of one lung and elongation of the remaining one, together with the liver and the stomach, and by asymmetry of the elongated kidneys (Gans 1975; Böhme 1989); (2) the pattern shown by Calyptommatus and Notobachia, which is characterized by elongation of the trunk, while the lungs remain of equal size and occupy the cranial part of the body cavity, with no overlapping with the elongated liver and stomach; and (3) the cordylid pattern, showing elongation of the tail with no change in general visceral topology (Chamaesaura).

Camp (1923) distinguished two ecomorphs of snake-like squamates: small, short-tailed burrowers versus large, long-tailed grass-swimmers. The first type can be found in amphisbaenians (Pough et al. 1998), primitive snakes (Pough et al. 1998), and in many groups of burrowing skinks (Caputo et al. 1995), whereas the second one is present in cordylids (Chamaesaura), Gerrhosauridae (Tetractylus) and lacertids (Takydromus), as well as in the Mahuya megakura-huettneri group. Recently, this dichotomy was supported by Wiens and Slingluff (2001), who studied the evolution of serpentine body form in anguids and found both ecomorphs within the family.

For the gymnophthalmids Calyptommatus and Notobachia, however, classification into the two ecomorphs described above remains questionable, as the animals are small but have long tails. These two genera are closely related but differ in their ecology. Whereas Calyptommatus is strictly nocturnal and fossorial, Notobachia can be active during the day or night, and forages mainly in leaf litter (Rodrigues 1996). Further studies of visceral morphology, locomotor mechanisms and respiration in scincomorph lizards may help to explain the complex structure-function relationship among these features and the role it may play in the evolution of squamates.

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