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Investigation of various ontogenetic stages of *Raillietiella* sp. (Pentastomida: Cephalobaenida): Survey of gland systems[1]

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Abstract: This study presents a survey of the gland systems occurring during the development of the pentastomid *Raillietiella* sp. in small lizards (*Hemidactylus frenatus*). For the first time, a general outlook of all glands of a pentastomid genus is presented. Ten different gland systems, including three new ones and one that has been redetected, are reported. The glands consist of cells belonging to class one and three according to the classification of NOIROT & QUENNEDY (1974). Class three gland cells show significant similarities. A comparison of the complete glandular equipment of *Raillietiella* sp. with other pentastomid species has revealed a fundamental conformity and a generalized gland equipment of extant pentastomids is proposed. Furthermore, the hypothetical gland equipment of a pentastomid archetype has been deduced.

Key words: gland systems, Pentastomida, development, dorsal organ, *Raillietiella*, ultrastructure, ontogeny.

Introduction

The Pentastomids (tongue-worms), a poorly defined taxon, include about 120 species. All recent species are vermiform parasites and obtain nourishment by injesting blood from the respiratory systems and air sacs of sea birds and reptiles or by feeding on mucus and sloughed cells in the nasopharyngeal cavity of mammals. The length of the females range from 20 to 160 mm (e.g. *Armillifer armillatus*) and thus Pentastomids belong to the largest endo-parasites within the arthropods. Definitive hosts of Pentastomida are usually reptiles, about 70 % of which are snakes. Intermediate hosts here are invertebrates (e.g. in *Raillietiella*) and vertebrates of all classes, except birds. Within the intermediate host, larvae become encapsulated and, after moulting, develop into the infective 4th larval stage.

Pentastomids are devoid of a circulatory system and of pronounced excretory organs. However, their secretory system is characterized by the number and size of glands in all developmental stages and is regarded as a fundamental feature of this animal group (LEUCKART 1860, STORCH 1993).

The porocephalid studies of BANAJA et al. 1977, AMBROSE & RILEY 1988, 1989, JONES & RILEY 1991, RILEY 1992 supply us with important information concerning the ultra structure and function of some of these glands. Investigations on the ontogeny of single glands from porocephalids are very rare. STILES (1891) has investigated various larval stages and adults from *Porocephalus clavatus*. AMBROSE & RILEY (1988) have studied the development of single glands from *Porocephalus crotali*.

The anatomy of the glands of cephalobaenids is obscure, although some studies have been published (DOUCET 1965, BÖCKELER 1982, 1984a, b, BANAJA et al. 1977, RILEY et al. 1973a, 1979). The total number of glands, their position and the time of their development during ontogeny remains unknown.

Nevertheless, these publications make clear that we can expect the development of the glandular system to be complex. The dynamics of their equipment and position during ontogenesis is not well understood and demands thorough investigation. A complete survey of the gland ontogeny of *Raillietiella* sp. is therefore presented here for the first time and is based on the thesis of STENDER-SEIDEL 1995. Furthermore, investigations on *Raillietiella boulengeri*, *Reighardia sternae*, *Cephalobaena tetrapoda*, *Sutriquetra subtriquetra* and *Porocephalus crotali* are included. The introduction of a defined topographical outline and the comparison of previous results demands a

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[1] Herrn Professor Dr. Horst Aspöck mit innigem Dank und großer Hochachtung zu seinem 65. Geburtstag gewidmet! Herrn Aspöck schätzen wir als „Seele" und Garant eines hohen wissenschaftlichen Niveaus, sei es als Autor, als Präsident einer Gesellschaft, als eloquenter Vortragender oder als anregender Diskussionspartner. Seine offiziellen und spontanen, mit Humor gewürzten und sehr herzlichen Reden inspirierten so manchen Zuhörer. Mit seinen hervorragenden Kenntnissen auf den Gebieten der Parasitologie, der Zoologie und der Musik sind Gespräche zwischen uns nie langweilig geworden. Der wienerische Charme ist geprägt von menschlicher Wärme und Zuverlässigkeit. Mein Geburtstagswunsch: Möge ihm der „Unruhestand" viel Kraft und Zeit für seine Bücher sowie Hobbys geben und uns die Möglichkeit, ihm hier und da zu begegnen!

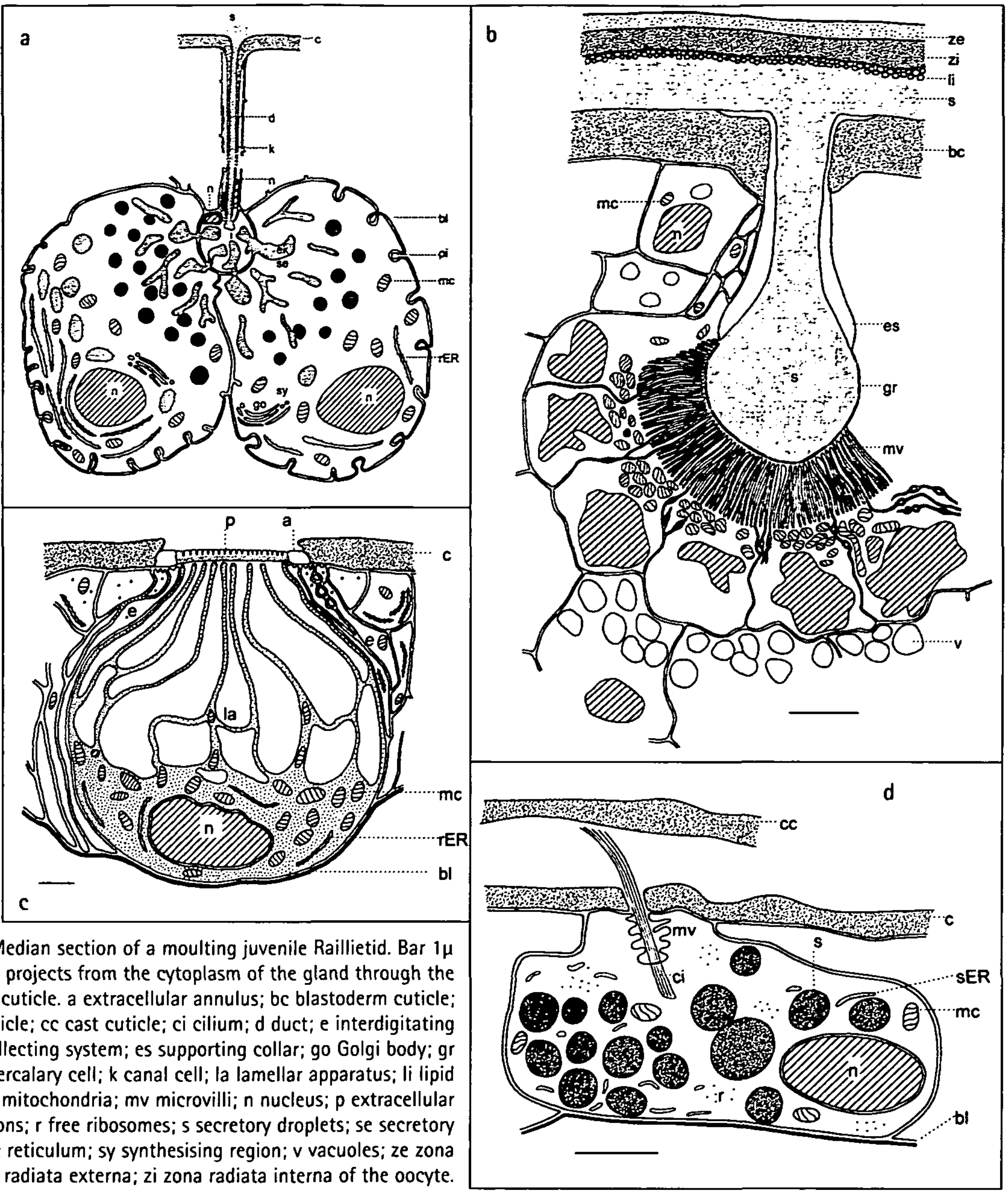

Fig. 1 a–d: a: Schematical drawing of a single secretory lobule consisting of class three (simplified and not to scale). Several gland types of Raillietiella sp. Consist of numerous lobules. The number of lobules and the number of secretory cells varies according to age and gland type. b: Embryonic gland: Median section of embryo, stage 4; gland cells surround a pear shaped hollow. The apical neck region has a circular, extra cellular supporting collar, secreted by the embryonic gland cell. The basal cells with numerous microvilli secrete the second layer of the embryonic envelope. The electron dense secretion (s) containing lipid droplets at the zona radiata interna are shed between the blastoderm cuticle and the zi. The beginning disintegration of the embryonic gland is marked by an extracellular layer on the micrivilli. Cells with numerous vacuoles surround the secretory cells of the embryonic gland. Bar 2 µm. c: Ionical gland. Median section of an adult Raillietid, typically existing of several modified epidermal cells. Bar 1 µm; see text. d: Hypodermal gland Median section of a moulting juvenile Raillietid. Bar 1µ During the molt a cilium projects from the cytoplasm of the gland through the extracellular space beneath the cuticle. a extracellular annulus; bc blastoderm cuticle; bl basement membrane; c cuticle; cc cast cuticle; ci cilium; d duct; e interdigitating cells; ek extracellular collecting system; es supporting collar; go Golgi body; gr extracellular layer; i intercalary cell; k canal cell; la lamellar apparatus; li lipid droplets; m mitichondria; mc mitochondria; mv microvilli; n nucleus; p extracellular porecap; pi periphery invaginations; r free ribosomes; s secretory droplets; se secretory region; sER smooth endoplasmic reticulum; sy synthesising region; v vacuoles; ze zona radiata externa; zi zona radiata interna of the oocyte.

new nomenclature of the glands. Single definitions of gland names, the integration of synonyms, the ultra structural description of single glands, a comparison with glands from various species and the material and methods are as published in STENDER-SEIDEL & THOMAS 1997; STENDER-SEIDEL et al. 1997a, b, 1999 and 2000.

Material and methods

The various ontogenetic stages were obtained by means of a laboratory model (BOSCH 1985, THOMAS & STENDER-SEIDEL 1996). They were studied by light- and electron microscopy (for further details, see STENDER-SEIDEL et al. 1997a).

Results

During ontogeny, the gland systems change continuously according to their tasks: these changes involve the equipment with glands, the number of gland cells belonging to one gland, and their size and physiology. The position of the glands in the organism likewise changes.

One characteristic of the gland systems of *Raillietiella* is that glands, once having arisen in one stage, remain during the following stages. Exceptions are the embryonic dorsal organ and, possibly, the hypodermal gland cells and suboral gland. Consequently, the number of glands increases during ontogeny.

Glands consist of gland cells belonging to class one or class three (Fig. 1) according to the classification of NOIROT & QUENNEDEY (1974).

The dorsal organ, ionical glands and hypodermal gland cells are composed of class one gland cells. The ultra structure of these glands is unique (STENDER-SEIDEL 1995, STENDER-SEIDEL et al. 1997a; 1999).

The frontal gland, suboral gland, tongue gland, hook glands, buccal gland, subparietal glands and accessory genital glands are composed of class three gland cells (STENDER-SEIDEL et al. 2000). Generally, class three glands exhibit a large variation in structure (NOIROT & QUENNEDEY 1974, 1991). However, the investigated *Raillietiella* glands show significant conformity: one or more terminal cells are connected with one intercalary cell to which the canal cell(s) are linked. This structure is preserved during ontogeny. The ultrastructure of the canal cells and intercalary cells of the different glands is uniform. Terminal gland cells differ in the form and structure of their secretory droplets and maturation. Usually, they are divided into a synthe- sizing and a secreting region. The gland products are stored in vacuoles and exocytotically secreted into an extra cellular collecting system formed by terminal cell(s) and an intercalary cell, which is continuous with the gland duct. Mitochondria and r-ER are typical cell organelles.

Embryo, stage 3-4 (Fig. 2a)

The **dorsal organ** is the first gland system to arise during the development of *Raillietiella*. It emerges from a dorsal infolding of the blastoderm before the limbs, gut or nerve system develop. Its formation and function are closely connected to the development of the embryonic envelope. The product of the dorsal organ extends between the blastoderm and zona radiata interna. When this viscous layer has reached a certain size, the blastoderm cuticle is produced. The dorsal organ disintegrates when the embryonic cuticle is formed and the blastoderm cuticle is shed.

Embryo, stage 5 (Fig. 2b)

The four dorsal terminal gland cells, which belong to class three, are **frontal and/or suboral gland** cells. They are characterized by their enormous size. Apically, they contact the dorsal organ, dorsally the blastodermis. They have a uniform ultra structure. At least two cranial **tongue gland** cells also contact the blastodermis dorsally. Their ultra structure differs little from the frontal/ suboral gland cells. Paired **ionical glands** are located dorsolaterally and cranially of the dorsal organ.

Embryo, stage 6 (Fig. 2c)

Embryos at stage six contain all the glands of primary larvae. Differences are observed in the ultra structure of the glands. The **dorsal organ** has disintegrated. Its secretory cells have degenerated. The porus is closed by a bordering structure of extra cellular material. Epidermal cell branches, which secrete the cuticle at the next moult, extend under the bordering structure.

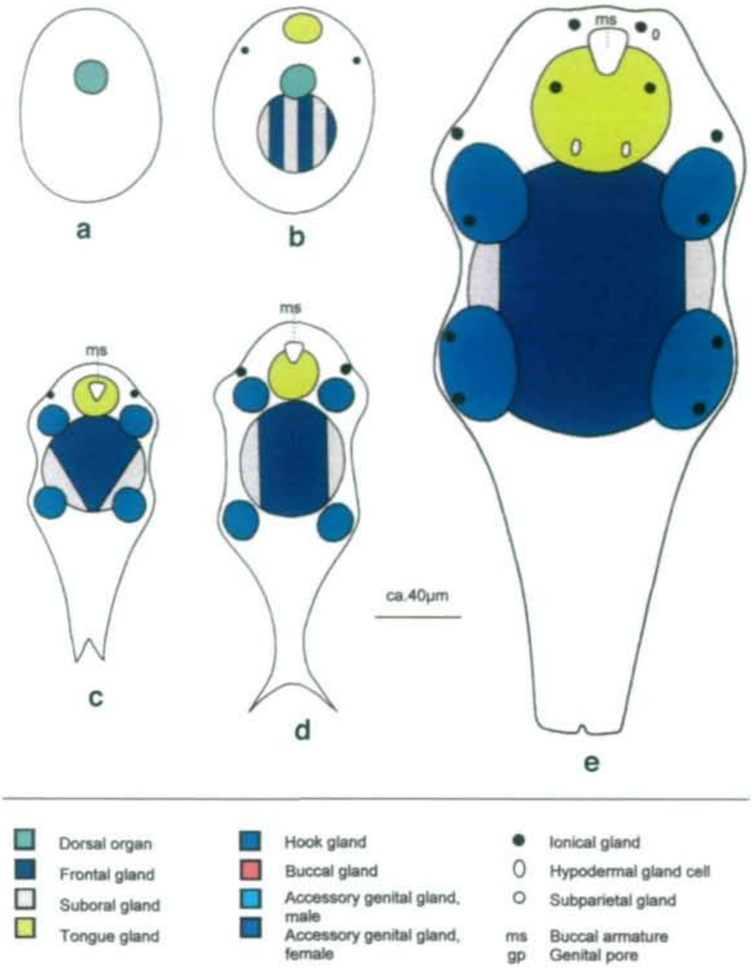

Fig. 2a–e: Glandular equipment of *Raillietiella sp.* **a:** Embryo stage 3-4. **b:** Embryo stage 5. **c:** Embryo stage 6. **d:** First larva. **e:** Infective larva.

Changes in the embryonic envelopes are not observed following the loss of the blastoderm cuticle. The **frontal gland** lies dorsal to the distal pharynx and consists of four terminal gland cells. Each pair is connected to one intercalary cell (Fig. 3, 4). One duct originates at each intercalary cell and proceeds to the anteriorly located penetration apparatus. The **suboral gland** contains two terminal cells lateral of the frontal gland. Each cell transports the gland product via an intercalary cell into the duct, which empties caudally of the mouth. The **tongue gland**, which lies dorsal of the mouth, is bordered by the dorsolateral muscles. At least four terminal cells, two intercalary cells and two ducts, which empty onto the tongue, are present in this gland. The **hook glands** are located at the base of the hook-bearing limbs. They each consist of one large terminal gland cell, one intercalary cell and a duct that empties ventrally at each limb base.

Paired **ionical glands** are found dorsolaterally at the base of the first limb. They are located between the hook glands of the first hooks and the frontal gland. Laterally, they are bordered by dorsolateral muscles. The typical three elements of the central cell, an extra cellular pore

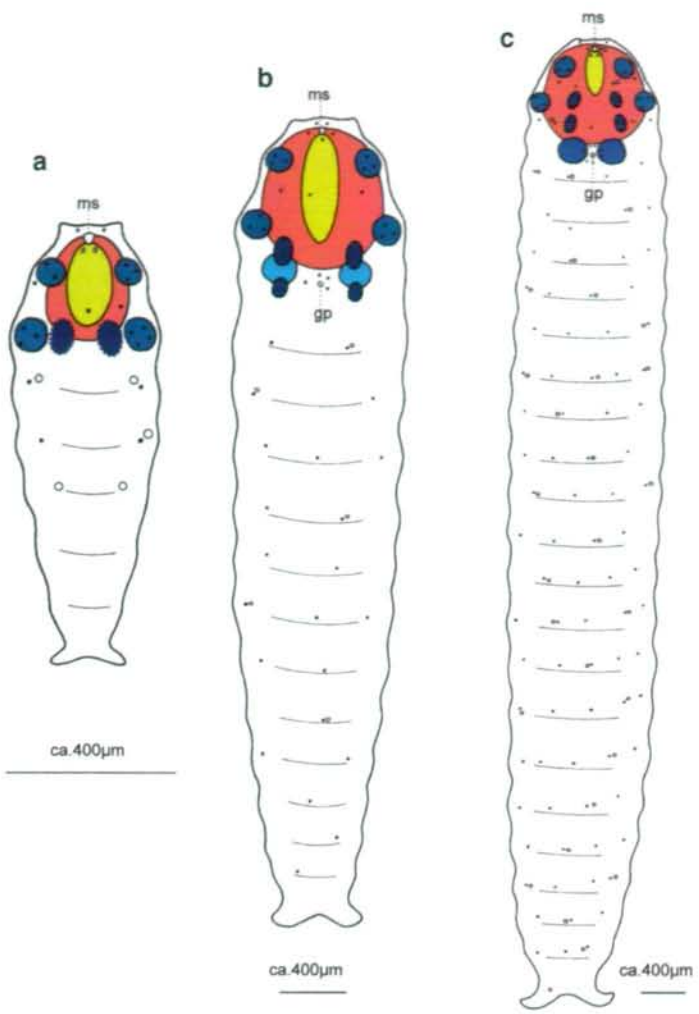

Fig. 3: **a:** Juvenile of *Raillietiella* sp., distribution of gland cells, and intercalary cells; position and course of gland ducts. The gland duct is connected via one intercalary cell (circle) with one or more secreting cells. Adult: **b:** Male of *Raillietiella* sp., distribution of gland cells, and intercalary cells; position and course of gland ducts. The gland duct is connected via one intercalary cell (circle) with one or more secreting cells. **c:** Female. **F** frontal gland cell; **H** hook gland cell; **Io** ionical gland; **S** suboral gland cell; **Z** tongue gland cell; ***** hypodermal gland cell; **h** hook; **ms** midgut; **m** buccal armature; **pa** penetration apparatus; Bar: 50µm.

cap with annulus, the lamellar apparatus and perinuclear region, are recognizable. However, ultra-structural investigations show that they are not yet mature at this ontogenetic stage.

First (= Primary) larvae (L_I) (Fig. 2d, 3a)

Primary larvae infest the arthropod intermediate host. They migrate and penetrate host tissue by means of their penetration apparatus.

The **dorsal organ** has disintegrated. Only the position of the characteristic cells in connection with a significant dorsal border structure near the first hooks is reminiscent of the former dorsal organ. The **frontal gland** includes four significant large gland cells, which are arranged with bilateral symmetry. They are located dorsally between the hook pairs. Each pair is connected to an intercalary cell. One duct originates at each intercalary cell and proceeds to the anteriorly located penetration apparatus. The **suboral gland** consists of two terminal gland cells, localized lateral to the frontal gland. They are arranged with bilateral symmetry. Each cell is linked to an intercalary cell. The ducts proceed close to the frontal gland ducts up to the first hooks. There, they bend ventrally and discharge into the mouth caudally. The **tongue gland** is located dorsal of the mouth, the pharynx and the oesophagus and contacts the frontal gland. The dorsoventral muscles and hook glands of the first hooks lie laterally, whereas the haemolymph and epidermal cells are found dorsally. The gland consists of six uniform terminal cells, grouped into threes connected by an intercalary cell. At this stage, the intercalary cells are located with bilateral symmetry next to the pharynx. Two ducts proceed between the tongue gland and foregut. At the mouth ring, the ducts bend ventrally and approach each other. They proceed side by side to the tip of the tongue, separate again and empty laterally into an opening at the base of a sensillum. The **hook glands** of the first and second hooks lie at the base of the hook-bearing limbs. They can be recognised as being associated with the hooks even at the light-microscopic level. In each of them one terminal cell encloses one intercalary sac-like cell, which is connected with the duct cell(s). The ducts empty ventral to each limb base. The **ionical glands** mature during this stage. Whereas specimens possessing embryonic central cells without distinct microvilli can be observed, specimens possessing ionical glands with microvilli have also been found. The two ionical glands lie dorsolateral of the first hook base. They contact the hook glands.

Infective (= L IV) Larvae (Fig. 2e, 3b)

Infective larvae infest the final host. They are tissue-migrating stages. Their gland systems resemble those of embryos at stage six and primary larvae. Additionally, they have hypodermal gland cells.

The gland cells grow concurrently with the intense extension of the larvae. In some glands, the number of terminal cells increases. Fragments of the dorsal organ are no longer observed. The **frontal gland** dominates with respect to cell number and size. The number of apical-emptying ducts doubles to four. The **suboral gland** cells increase in size. Compared with L_I, the number of terminal cells and ducts remains constant. The **tongue gland** increases in volume remarkably. Although the cell number is constant, the terminal cells grow in size. One subunit of three terminal cells with one intercalary cell occupies the cranial region, while the second subunit shifts caudally. The **hook gland** ducts empty into the newly developed hook pits. The number of subunits and the size of the terminal gland cells increase. Two terminal cells are now connected with one intercalary cell. The number of **ionical glands** increases. They are distributed with bilateral symmetry. Their ultra structure resembles the mature ionical glands of the primary larvae. Embryonic structures are not observed. The **hypodermal gland cells** may be overlooked, even by electron-microscopic investigation, because of their relatively small size. In this study, they have been observed near the frontal papillae and lie apically of the first ganglion, caudally of the mouth. Associations with other cell types or structures have not been seen. The hypodermal cell is connected via a small collar to the cuticle. Basally, it lies beneath the hypodermal cells. The cytoplasm contains many secretory vacuoles.

Juvenile raillietiellids (Fig. 3a)

In juvenile and even in adult Raillietiellids, the identification of gland cells is extremely difficult because of the large number of different terminal gland cells, which are closely packed. Only the combination of light- and electron-microscopic investigation in connection with the knowledge of the larval gland systems has allowed the definitive identification of the gland cells.

Juvenile Raillietiellids are characterized by growth and moults. Their altered life conditions and the start of their development into the sexually mature stage result in complex modifications of the gland systems. The **frontal gland** empties with four ducts near the frontal papilla. The terminal cells cannot be identified. The **suboral gland** cannot be identified. Its existence remains obscure. The **tongue gland** is unchanged in its position and cell number. The course of the ducts between the tongue muscles is constant but the pore of the ducts shifts caudally to the distal pharynx. The **hook glands** retain their position at the hook base. The number of subunits increases. Each subunit consists of at least two terminal gland cells, which are connected to an intercalary cell. Single ducts empty into the hook pits; common collecting ducts are not observed. **Ionical glands** occur in a large number at the apical region, near the mouth and the lobi parapodiales. The abdomen is divided into two regions: the cranial region is equipped with annular ionical glands, which are associated with subparietal glands. The caudal region shows no ionical glands. The connecting region is divided into two parts: caudally, we have observed subparietal glands only, whereas cranially, we have found subparietal glands and immature ionical glands. As a rule, ionical glands develop near to the duct pores of the subparietal glands. The **hypodermal gland cells** are paired. Two cells lie close to each other, ventrally near the middle, caudally of the mouth and cranially of the first ganglion. The existence of further cells in the anterior region, as observed in the infective larvae, is highly likely. The **buccal gland** develops in these blood-sucking stages. It consists of a number of sub-units, in which three terminal cells are linked to one intercalary cell. The size of the terminal cells, the number of the subunits and consequently the number of ducts increase during ontogeny. The single ducts proceed dorsolaterally in two bands to the buccal cavity and empty anteriorly of the dorsally inserted tongue. The **subparietal glands** are present in small numbers. They are located laterally in the anterior trunk between the longitudinal muscles and muscles surrounding the gut. Immature subparietal glands do not contain secretion vacuoles. Ducts and intercalary cells continue to develop. Mature subparietal cells are characterized by lamellar secretion.

Adults

The gland equipment of males and females is similar. Differences are however observed in the sizes of the various glands and in the structure of the genital glands.

Males (Fig. 3b)

The **frontal gland** is divided into two pairs of gland subunits. One pair lies laterally of the cardia, the other pair is found dorsally of the accessory genital gland. Each part consists of two uniform terminal cells, which are linked to an intercalary cell. The four ducts proceed in part next to the ducts of the hook glands of the first hooks to the anterior margin of the head and empty near the frontal papillae. The **suboral gland** has not been observed. The **tongue gland** lies dorsally of the pharynx and oesophagus. It consists of two separated subunits that lie trifoliately one after the other. The units are composed of three terminal cells connected to one intercalary cell.

The two ducts empty onto the tongue close to the pharyngeal ring. The cell number and arrangement are identical with the juvenile stages, although the size of the terminal cells has increased. The **hook glands** lie at the base of the limbs. They consist of a number of subunits with a uniform structure. At least two identical terminal cells are linked with one intercalary cell. The ducts proceed in bundles to the particular hook pits and empty onto the intern lobe. The surroundings of the hook and buccal gland cells do not allow an identification of the glands at the light-microscopic level. **Ionical glands** are irregularly distributed in the head. Numerous ionical glands lie next to the frontal papillae, the mouth, the genital pore and the lobi parapodiales. On the trunk, they are distributed annularly in smaller numbers than those observed in females. The **buccal gland** is the most extensive gland. It lies cranially of the second hooks, contacts other glands and consists of at least 15 subunits with a characteristic structure. Three terminal cells are connected to an intercalary cell. One of these cells differs from the other two. Ducts proceed into the buccal cavity and empty anteriorly of the dorsally inserted tongue. The **subparietal glands** are present in small numbers. Histological stains (Alcianblue, pH 1.0) show irregularly distributed glands, each consisting of two terminal cells connected to one intercalary cell. The **accessory genital glands**, which appear ventrolaterally of the vasa deferentia, form two compact cell groups. Their relatively small size distinguishes them from other glands. Their subunits consist of three terminal cells linked to one intercalary cell. The ducts empty into the genital atrium.

Females (Fig. 3c)

The **frontal gland** consists of two pairs of gland subunits. Two subunits lie laterally of the cardia and two laterally of the proximal midgut. Two identical terminal cells are linked to one intercalary cell. The four single ducts proceed cranially in two lateral strands. At the mouth ring, they fuse into two common collecting ducts. The **suboral gland** is not observed. The **tongue gland** is formed of two subunits lying one after the other dorsally of oesophagus and pharynx and ventrally of numerous buccal gland cells. The subunit consists of three terminal cells linked to one intercalary cell. The ducts empty onto the tongue near the pharynx. The **hook glands** lie at the base of each limb and each consist of numerous subunits that contain two identical terminal cells connected to an intercalary cell. Single ducts proceed in bundles to the hook pits and empty on the internal lobe. **Ionical glands** exist in large numbers in females. They are distributed over the whole body surface. They occur irregularly in the head region. The lateral lobi parapodiales bear numerous glands, whereas none are observed on the median lobes. Rows of regularly arranged glands are observed at the annuli. They are usually associated with subparietal glands. Various physiological stages can be observed. Different types of ionical glands on the head and trunk have not been observed. Ionical glands occur in ectodermic tissue of the genital system between the pores of the accessory genital glands. Their ultra structure resembles the ionical glands of the body surface. The **buccal gland** extends from the second hooks to the anterior region. At least 20 subunits empty into the buccal cavity. The subunits consist of two identical and one different terminal cell connected to one intercalary cell. The **subparietal glands** exist in large numbers. Although being distributed annularly in the trunk, they are spread irregularly in the head. Two identical terminal cells are connected to one intercalary cell. They are associated with ionical glands. The **accessory genital glands** can be identified by light- and electron-microscopic means because subunits are concentrated in two distinct complexes lateral to the vagina and uterus. Additionally, the gland cells are of a relatively small size and have a characteristic ultrastructure. At least three terminal cells are connected to one intercalary cell. Single ducts empty into the genital system.

Nomenclature and synonyms

The assignment of gland types that change their topography during onto-genesis and their homologisation with those in different pentastomid species is only possible if the discharging position of their ductules is definitively known.

Other kinds of characterization, e.g. position (Hett 1924) and function (Banaja et al. 1977), has in the past led to misinterpretations.

In the following, the complete glandular equipment of *Raillietiella* sp. taken from the house gecko *Hemidactylus frenatus* will be typified. Each gland will be briefly characterized; the new nomenclature („original“) is introduced and compared with earlier names. A list of synonyms is added.

The Dorsal organ

Names:	
Glandula embryonalis	Original
Dorsalorgan	Heymons 1926
Dorsal organ	Esslinger 1968

Characterization: the dorsal organ, a dorsal invagination of the blastodermis, appears only during embryogenesis. Its mucous product, discharged at a dorsal pore, bursts the blastoderm cuticle and embeds the growing eggs within the uterus. Noirot & Quennedy (1974): Class one.

Synonyms:	
Rückenorgan	Schubaert 1852 (nach Stiles 1891)
Rückenkreuz und Facette	Leuckart 1860, Stiles 1891
Rückenring	Heymons 1926
Dorsalorgan	Heymons 1926
dorsale organ	Doucet 1965
dorsal organ	Esslinger 1968

The frontal gland

Names:	
Glandula frontalis	Original
Frontaldrüse	Heymons 1935
Frontal gland	Riley 1973a

Characterization: The frontal gland discharges during larval periods at the anterior region of the head and in adults near the frontal papillae. Noirot & Quennedey (1974): Class three.

Synonyms:	
Hakendrüsen	Lohrmann 1889
Kopfdrüsen	Stiles 1891, Von Haffner 1924, Böckeler 1982
head-glands	Spencer 1893, Hett 1915
hook-glands	Giglioli 1923
lateral glands	Hett 1924
Frontaldrüse	Heymons 1935
glandulas cefálicas	Motta 1963a, b; Motta C.S. & D.C. Gomes, 1968
glandes latérales	Doucet 1965
glandes cephaliques	Doucet 1965
cephalic glands	Ambrose & Riley 1988

frontal glands	Riley 1973a,b, 1992, Riley, James & Banaja 1979, Ambrose & Riley 1988, Jones & Riley 1991

Suboral gland (new)

Names:	
Glandula suboralis	Original
Suboraldrüse	Original
Suboral gland	Original

Characterization: In larvae, it discharges caudally of the mouth. In juveniles and adults, its existence is obscure. Noirot & Quennedey (1974): Class three.

Synonyms: none

Tongue gland (new)

Names:	
Glandula lingualis	Original
Zungendrüse	Original
Tongue gland	Original

Characterization: The tongue gland complex is located dorsally of the pharynx and oesophagus. Gland cells and ductules are found in pairs and emerge directly on the tongue. Noirot & Quennedey (1974): Class three.

Synonyms: none

Hook glands

Names:	
Glandulae onychiales	Original
Hakendrüse	Leuckart 1860
Hook glands	Spencer 1893

Characterization: Hook glands are complexes, associated in pairs, each unit discharging by means of one or several efferent ductules near the corresponding hook. The number of the glands increases during ontogenesis. Noirot & Quennedey (1974): Class three.

Synonyms:

Hakendrüse	Leuckart 1860, Hoyle 1883, Lohrmann 1889, Kulagin 1898, Stiles 1891, Giglioli 1923, Von Haffner 1924, Heymons 1935
Hook-gland	Spencer 1893, Hett 1915, Riley 1973a, Riley, James & Banaja 1979, Ambrose & Riley 1988
digestive gland	Giglioli 1923
head gland	Hett 1924

Ionical glands

Names:	
Glandulae ionorum	Original
Ionendrüsen	Original
Ionical glands	Original

Characterization: A fuctional complex of several modified epidermal cells. One or more central cells are surrounded by several small peripheral cells. Each central cell is divided into three regions: the basal region, containing the nucleus and numerous mitochondria; the apical region with deep foldings of the plasma membrane forming the lamellar apparatus; and the end apparatus, composed of an extracellular matrix. The number increases during ontogeny. Noirot & Quennedey (1974): Class one.

Synonyms:

Stigmata	Diesing 1835, Leuckart 1860, Esslinger 1962
Stigmendrüsen	Lohrmann 1889, Spencer 1893, Von Haffner 1924, Von Haffner & Rack 1971, Heymons 1935
Drüsenstigmen	Stiles 1891, Heymons 1926
epidermal glands	Hett 1924
Hautdrüsen	Bovien 1927, Heymons 1935, Von Haffner 1964
Frontalporen	Bovien 1927
Boviensche Zellen	Heymons 1935
glandes cutanées	Doucet 1965
glandes cuticulaires	Doucet 1965
cellules des Bovien	Doucet 1965
cuticular glands	Riley 1973a,
chloride cells	Banaja, James & Riley 1977, Riley 1988, Ambrose & Riley 1988, Storch 1993
ionocytes	Storch 1993

Hypodermal gland cells (new)

Names:	
Glandulae hypodermales	Original
Hypodermale Drüsenzellen	Original
Hypodermal gland cells	Original

Characterization: Hypodermal gland cells, which occur in infective larvae and juveniles, are modified hypodermal cells. They open at a pore on the cuticle. Noirot & Quennedey (1974): Class one.

Synonyms: none

Buccal gland

Names:	
Glandula buccalis	Original
Buccaldrüse	Original
Buccal gland	Original

Characterization: A glandular complex, the ductules of which empty into the buccal cavity. The ductules might be arranged in bilaterally. It has not been established whether the glands also follow this bilateral arrangement. Noirot & Quennedey (1974): Class three.

Synonyms:

glandes antérieur coelomique	Doucet 1965
frontal glands	Riley 1973b

Subparietal gland

Names:	
Glandulae subparietales	Original
Subparietaldrüsen	Original
Subparietal gland	Riley 1973a

Characterization: Single glands that directly open near the surface of the body. They are annularly distributed and can also be found in the head region. Noirot & Quennedey (1974): Class three.

Synonyms:	
Parietalzellen	Hoyle 1883
Parietaldrüsen	Stiles 1891, Heymons 1935
parietal cells	Spencer 1893
parietal glands	Hett 1915, 1924
parietal gland cells	Giglioli 1923
glandes sous-cuticulaires	Doucet 1965
glandes parietales	Doucet 1965
sub-parietal glands	Riley 1973a, Riley, James & Banaja 1979, Ambrose & Riley 1988
SPC	Ambrose 1989

Accessory genital glands

Names:	
Glandulae accessoriae genitales	Original
Akzessorische Genitaldrüsen	Böckeler 1984b (for females)
Accessory genital glands	Riley 1988 (for males)

Characterization: The accessory genital glands are paired complexes found in both males and females and consist of bi- and tricellular gland units. In females, the ductules empty into the transversal canal or the oviduct. Noirot & Quennedy (1974). Class three

Synonyms:	
tubular accessory glands	Spencer 1893
akzessorische Genitaldrüse	Böckeler 1984b
accessory genital gland	Riley 1988
ductual gland	Riley 1988

In males, they discharge into the vasa deferentia or genital atrium either via single ductules or common collecting ductules. Noirot & Quennedey (1974): Class three.

Synonyms:	
accessory sex glands	Riley 1988
ductual glands	Riley 1988
genital glands	Böckeler & Storch 1990

Discussion

The results of this study show that ten different gland types occur in *Raillietiella* sp. The detection of the suboral gland, tongue gland and hypodermal gland cells, as the redetection of the buccal gland enlarges our knowledge of the gland systems in pentastomids with respect to four important functional units. The diversity of glands in *Raillietiella* suggests an equal functional diversity. The term „cephalic glands" or „head glands" used for the class three anterior glands of cephalobaenids (Riley et al. 1979, Storch 1993) should no longer be used because this term does not distinguish such different glands as the frontal gland, suboral gland, tongue gland, hook gland and buccal gland.

The identification of the glands is extremely difficult: The terminal cells of these glands lie close to each other. The glands are similar in their structure. Histological stains aid identification only to a limited degree. The position of the gland cells and their ultra structure change during ontogeny. The only significant feature that is consistant is the pore of the gland ducts. Pores of gland ducts appear at a constant position in different species of porocephalids and cephalobaenids. In this study, the pore of the gland ducts has turned out to be the defining character regarding which cells belong to a specified gland.

Hypothetical gland equipment of extant pentastomids

The comparision of the gland systems of *Raillietiella* sp. with other cephalobaenid or porocephalid species has shown a remarkable conformity. A hypothetical gland equipment of extant pentastomids may be deduced but should be confirmed by further investigations.

Dorsal organ, frontal gland, suboral gland, hook glands, ionical glands, subparietal glands and accessory genital glands exist in cephalobaenids and porocephalids.

Hypodermal gland cells are not observed in other pentastomid species but Raillietiellids to date but their possible function as pheromone glands points to their existence in further pentastomid species.

The tongue gland occurs in *Raillietiella* sp., in *Reighardia sternae* and *Cephalobaena tetrapoda*. Cell complexes exist in identical positions (own unpublished observations). Their existence in all cephalobaenids is probable but is obscure in porocephalids. Since, in *Raillietiella* sp., the tongue gland exists consistently in invertebrate and vertebrate hosts without significant modification, its existence in porocephalids can be supposed.

The buccal gland has been observed in *Raillietiella* sp. and *Reighardia sternae* and probably exists in all cephalobaenids. It has also been seen in *Subtriquetra subtriquetra*, a porocephalid, during this study and hence its existence in other porocephalids is likely.

The gland equipment of *Raillietiella* sp. at a defined ontogenetic stage depends on the current host type. In

Porocephalus clavatus (STILES 1891) and *Porocephalus crotali* (AMBROSE & RILEY 1988) changes in the gland equipment are observed that are synchronous with the host change. The dependence of the current gland equipment on the host type appears to be a general phenomenon.

Hypothetical gland equipment of a pentastomid archetype

The remarkable correspondence of glands in embryos of extant pentastomids points to the early existence of these glands in phylogeny. Frontal, suboral and hook glands are present in all embryos investigated to date, independently of their further development. Therefore, they can be regarded as plesiomorphous glands.

In *Raillietiella* sp., the tongue gland belongs to the embryonic glands. However, evidence for its existence in porocephalids is absent. Whether it was also an „original" gland cannot be decided without further research.

Based on the embryological investigation of *Reighardia sternae*, BÖCKELER (1982) presented a hypothetical model of a pentastomid archetype. The position of the gland duct pores allows the integration of those glands that are considered as plesiomorphous glands into BÖCKELER's hypothetical model:

1. head-segment	frontal gland
2. head-segment	suboral gland
3. head-segment	hook gland of first hooks
4. head-segment	hook glands of second hooks

Gland pores at the limbs are also found in the fossils *Heymonsicambria scandica* and *Boeckelericambria pelturae* (WALOSSEK & MÜLLER 1994).

In the fossils and in the *Reighardia sternae* larvae, which have been used for comparision by WALOSSEK & MÜLLER, they describe two pores on each limb. The pore of numerous hook gland units is typical for juveniles and adults of *Raillietiella* sp. The segmental arrangement of nephridia or their derivatives is an articulate feature. Originally, they existed in all somites. In Euarthropods, they are usually reduced to a few somites and are modified. Only in Onychophorans (Protarthropoda) they can be found in all somites; they partly exist in original form. The segmental glands of pentastomids can be derived from articulate nephridia. The specialisation of a limited number of serial excretory organs might be an adaption to parasitic life.

Zusammenfassung

Die vorliegende Studie lässt erstmalig einen Gesamtüberblick über den dynamischen Prozess der Drüsenentwicklung zu, der sich während der Ontogenese bei dem Pentastomiden *Raillietiella* sp. (Cephalobaenida) aus dem Hausgecko (*Hemidactylus* sp.) abspielt. Das Drüsensystem von Raillietiella sp. besteht aus 10 ultrastrukturell und funktionell verschiedenen Drüsentypen. Sie lassen sich nach NOIROT & QUENNEDY (1974) in die Klassen eins und drei einordnen. Auf der Basis der fundamentalen Übereinstimmung zahlreicher überprüfter anderer Pentastomidenarten hinsichtlich Ausstattung und Anordnung der Drüsentypen wird eine hypothetische Drüsenausstattung rezenter Pentastomiden entwickelt. Aufgrund der heterogenen und sich überschneidenden Benennungen wird eine neue Nomenklatur vorgestellt.

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