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Morphology in Chilopoda – a survey

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A survey of what is known about chilopod morphology: status and needs

The knowledge on morphology in Chilopoda was published in a huge number of different scientific periodicals. Surveys and critical reviews on morphological and physiological studies in Chilopoda were carried out by Verhoeff (1920–25), Attems (1929, 1926–1930, 1930), Kaestner (1963), Lewis (1981), Minelli (1993), Dunger (1993), and most recently by Rosenberg (2009). In the following, a survey on morphological investigations in light and electron microscopy of different organs and organ systems in Chilopoda will be presented. Scientific names of species varied. To assign the species given by the authors in the original publication, the original species name cited by authors was always used. Both fundamental and partial gaps of knowledge are noticeable in almost every field/organ system reviewed and listed up below. This compilation should be seen as a guideline for prospective researchers where to fit in with their project, hopefully by integrating 'modern' techniques. It is believed that filling those gaps is essential for evolutionary morphology. Progresses are necessary, because in the case of failure comparative, functional and phylogenetic conclusions will permanently remain difficult and preliminary.

1. Integument

1.1 General structure

In Chilopoda, similar as in all Arthropoda, the integument consists of a single layered epidermis and the cuticle, which is secreted by the epidermal cells. At their base the cells secrete a basal lamina of different width. The cuticle serves as an exoskeleton and covers the surface of the body completely. Invaginations of the integument are lined by a cuticle, as tracheae, the conducting canals of glands, the reproductive system, the fore and the hind gut. The cuticle gives physical and mechanical protection, is the insertion for muscles and is the most important barrier between the environmental influence and the inner milieu of the animals. The cuticle is important to protect the animals against evaporation and intrusion of water. The cuticle has to moult periodically, even in adult in Chilopoda.

- **LM investigations**

The cuticle of Chilopoda is hitherto mostly investigated by light microscopy and is characterised according to the different colours of their layers (see Tab. 1). It was Duboscq (1898a) who differentiate between strongly sclerotised ('sclérites') and lesser sclerotised ('chitine des articulations') areas. He first observed that in Geophilomorpha the cuticle exhibit several strongly stainable conical inclusions ('cône chromophile'). In *Lithobius forficatus* and *Haplophilus subterraneus* Blower (1950, 1951) described an optically distinguishable endo- and exocuticle, both containing chitin. The exocuticle varies in its form and thickness in different regions of the body (sclerite, arthropodial membrane, intermediate sclerite). The cuticle is covered by a thin colourless membrane, thought to be a lipoid material secreted by epidermal glands. The chilopod cuticle seems to characterised by the absence of an outer resistant and non-chitinous layer. The characterisation of the different cuticular layers by light microscopical investigation is given in Tab. 1.

Tab. 1 Terminology of the different cuticular layers by light microscopical investigations after different authors.

author	**species**	**epidermis**	**cuticle**		
Passerini (1884a,b)	different Chilopoda	ipoderma (cellular)	epidermide (cellular)		
Duboscq (1898a)	different Chilopoda	épithélium proprement	couche lamelleuse acidophile	couche basophile	chitin achromatique
Fuhrmann (1922)	different Chilopoda	Epidermis + Basalmembran	Innenlage der Cuticula	Außenlage der Cuticula	Grenzhäut-chen der Cuticula
Verhoeff (1902–1925)	different Chilopoda	Epidermis ('Hypodermis')	Lamellen-schicht (mehr-schichtig)	Farbschicht	Oberflächen-schicht
Fahlander (1938)	different Chilopoda	Epidermis + Basalmembran	Lamellen-schicht	Pigment-schicht	Grenzlamelle
Blower (1951)	*Lithobius forficatus, Himantarium subterraneus*	epidermis + basement membrane	endocuticle	exocuticle	lipoid-layer
Krishnan (1956)	*Scolopendra subspinipes*	epidermis	inner + outer endocuticle	tanned exocuticle	inner + outer epicuticle
Füller (1963)	different Chilopoda	Epidermis	Endo- + Mesocuticula	Exocuticula	Epicuticula
Manton (1965)	different Chilopoda	ectoderm	endocuticle	exocuticle	outer non-staining exocuticle

Tab. 1 cont.

author	species	epidermis	cuticle		
Jangi (1966)	*Scolopendra morsitans*	hypodermis + basement membrane	inner + outer endocuticle	exocuticle	(-)
Rilling (1968)	*Lithobius forficatus*	Epidermis	Endokutikula	Mesokutikula	Exo- + Epikutikula
Shrivastava (1971)	*Scolopendra morsitans*	hypodermis + basement membrane	inner endo- + mesocuticle	outer endocuticle	exocuticle

- **TEM investigations**

Only few, but no comparative electron microscopical investigations exist on the cuticle of Chilopoda. Scheffel (1987) characterised the cuticular layers as endo-, exo- and epicuticle. On the top of the tergite of Lithobiomorpha, the epicuticle is about 0.1 µm, the lamellated exocuticle about 0.8 µm and the lamellated endocuticle is about 5–6 µm in height. The epicuticle is rather faint (10–20 nm) (Fusco et al. 2000). Several specialised epithelia secrete a more of widened subcuticle which underlayed the cuticular layers: Coxal and anal organs (e.g. Rosenberg 1985) or the maxillary organ (Hilken & Rosenberg 2005a). It is conspicuous that the cuticle is only rarely traversed by pore canals from the epidermis up to the epicuticle, in contrast to the cuticle of insects.

In Chilopoda the surface of the epicuticle often display a polygonal pattern. In former times it was supposed that the patterns correspond to the underlying epidermal cells (e.g. Fuhrmann 1922, Fahlander 1938, Blower 1951, Füller 1963, Rilling 1968). In lithobiomorph centipedes the individual polygonal fields (= scutes) forming this pattern are generally regarded as corresponding to the outer faces of the epidermal cells. The scutes can record the geometry of the external face of epidermal cells at the stage of deposition of the very first layers of the cuticle, the epicuticle (Fusco et al. 2000).

1.2 Chemical composition of the cuticle

Up to now investigations on the chemical composition of the cuticle are rare and often contradictory. Proteins and chitin were detected histologically in the endo- and epicuticle (Blower 1950, 1951, Shrivastava 1970, 1971). In *Scolopendra* resilin was demonstrated within the arthropodial membrane between prefemur and femur (Sundara Rajulu 1971c). Since Semenova (1961) it is thought that a special feature of chilopod cuticle is the absence of a wax layer, but this is hitherto only proved experimentally (Joly 1962), not by histochemical and electron microscopical methods.

2. Epidermal glands

2.1 General structure

- **LM investigations**

In Chilopoda the integument is pierced by numerous ducts arising from epidermal glands within the epidermis. The ducts pass through the cuticle and open to the exterior. The epidermal glands were mostly described by light microscopy as unicellular glands (Duboscq 1898a, Brade-Birks & Brade-Birks 1920, Fuhrmann 1922, Koch 1927, Fahlander 1938, Blower 1950, 1951, Rilling 1968, Maschwitz et al. 1979, Desbalmes 1992). Additionally, Rilling (1968) described in *Lithobius* bipartite epidermal glands which consist of one or two secretory cell(s) and a canal cell. There are more glands in the sclerites than elsewhere. It is most likely that those regions of the animal that come into contact with the environment are well supplied with epidermal glands (Blower 1951, Desbalmes 1992).

- **TEM investigations**

The first description of the fine structure of an epidermal gland is given by Tichy (1973a, b). These bipartite glands surround the Tömösváry organs of *Lithobius* (but see tab. 2). Keil (1975) described in *Lithobius* bipartite epidermal glands ('kleine Epidermisdrüsen') near sensilla trichodea, between the antennal 'telopodal glands' and the telopodal glands itself, which are composed of 1–2 secretory cells and 2 sheath cells ('Hüllzellen'). Comparative investigations reveal that epidermal glands are composed of more than two cell types, the secretory cell and the canal cell. It can be shown that between secretory cell(s) and the cell(s) of the conducting canal an intermediary cell exists (Hilken et al. 2003b, 2005, Rosenberg & Hilken 2006, Müller et al. 2003, 2006, 2009). The secretory cell discharges their content into an extracellular reservoir, lined by a microvillar border. Intermediary and canal cell(s) form the conduction canal that passes through the cuticle and drains the secretion outside. Generally, the intermediary cell is lined only in its most distal part by a cuticle, whereas in its proximal part, the apex forms a circular fringe of microvilli. In the area of the canal cell(s), the conducting canal is completely covered by a cuticle. As the conducting canal is differently structured, two different types of epidermal glands are to distinguish: glands with a straight (recto-canal epidermal gland) and a contorted conducting canal (flexo-canal epidermal gland) (Müller et al. 2006, 2009). In Chilopoda epidermal glands show a conspicuous structural diversity. Beside isolated epidermal glands multicellular compound glandular organs exist, which consist of many glandular units.

Four types of epidermal glands with different cell types are hitherto known (see also Tab. 1 in Müller et al. 2009): i) Two-cell-glands (including one secretory cell + one canal cell), ii) Three-cell-glands (secretory cell + intermediary cell + canal cell), iii) Four-cell-glands (secretory cell + intermediary cell + proximal + distal canal cells), and iv) Five-cell-glands (2 secretory cells + intermediary cell + proximal + distal canal cell).

2.2 Poison glands

The modification of the legs of the first trunk segment into maxillipeds (forcipules) with its characteristic poison claws is the most prominent autapomorphy of the Chilopoda. Each maxilliped contains a large poison gland that surrounds the proximal and median part of the common poison duct and opens on the inner side of the tarsungulum. Length and shape of the poison ducts varied among species (Chao & Chang 2006). Light and first electron-microscopical studies (see above) described the glands as unicellular, recent studies reveal that the poison gland of *Lithobius forficatus* is composed of hundreds of multicellular epidermal gland units. Each of them consists of three different cell types, a secretory cell, an intermediary cell, and two different canal cells (4-cell epidermal gland) (Rosenberg & Hilken (2006).

- **LM investigations**

  Newport (1845), Müller (1829), Kutorga (1834): *Scolopendra morsitans*,

  Leon-Dufour (1823): *Lithobius forficatus*,

  Mac Leod (1878): *Scutigera coleoptrata*, *Lithobius forficatus*, *Scolopendra gigantea*, *Scolopendra horrida*, *Cryptops savignyi*, *Himantarium gervaisii*, *Geophilus flavus*,

  Herbst (1891): *Scutigera coleoptrata*, *L. forficatus*, *Lithobius grossipes*, *Scolopendra cingulata*,

  Karlinski (1883): *L. forficatus*, *Lithobius piceus*, *Lithobius nigrifrons*,

  Sograff (1880): *L. forficatus*,

  Duboscq (1894, 1895, 1896b, 1898a, c): *S. coleoptrata*, *L. forficatus*, *Lithobius calcaratus*, *S. cingulata*, *Cryptops hortensis*, *Geophilus flavus*, *Geophilus sodalis*, *Chaetechelyne vesuviana*,

  Pawlowsky (1912, 1913, 1927): *Scolopendra morsitans*,

  Cornwell (1916): *Ethmostigmus spinosus*, *Rhysida* spec., *Otostigmus* nov. sp.,

  Bücherl (1946, 1971): *Scolopendra viridicornis*, *Scolopendra subspinipes*, *Otostigmus scabricauda*, *Cryptops iheringi*, *Otocryptops ferrugineus*,

  Barth (1967): *S. viridicornis*,

  Nagpal & Kanwar (1981): *Otostigmus ceylonicus*.

- **TEM investigations**

  Dass & Jangi (1978): *S. morsitans*,

  Ménez et al. (1990): *Ethmostigmus rubripes*,

  Rosenberg & Hilken (2006): *L. forficatus*,

  Antoniazzi et al. 2009: *Cryptops iheringi*, *Otostigmus pradoi*, *Scolopendra viridicornis* (LM/TEM).

2.3 Defence glands

Defence glands in Chilopoda are hitherto known as telopodal glands (Lithobiomorpha), sternal glands (Geophilomorpha), and hydrogen-cyanide-producing glands (Scolopendromorpha). The telopodal glands are situated at the inner (posterior) borders of the telopodites on the twelfth to fifteenth pairs of legs, where they open on the femur, tibia, tarsus, and metatarsus. They produce a sticky, string-like secretion. Most Geophilomorpha have voluminous clusters of sternal glands which open into in sternal pore areas. The sternal glands produce a sticky fluid in response to attack from predatory arthropods. The glue hardens within a few seconds. The hydrogen-cyanide-producing glands are spread all over the body from the second to the next to the last body segment and over the legs. The defensive secretion contains hydrogen cyanide and protein.

2.3.1 Telopodal glands

- **LM**

  Vogt & Yung (1883) ('glandes cutanées'), Verhoeff (1905, 1902–1925) ('Telopoditdrüsen'): *Lithobius*.

- **TEM**

  Keil (1975): *Lithobius forficatus*.

2.3.2 Sternal glands

- **LM investigation**

  Meinert (1870), Verhoeff (1902-1925) ('Bauchplattendrüsen'), Brade-Birks & Brade-Birks (1920): *Geophilus carpophagus*,

  Koch (1927): *Scolioplanes crassipes*, *Geophilus linearis*.

- **TEM investigation**

  Hopkin & Anger (1992), Hopkin & Gaywood (1990): *Henia vesuviana*,

  Turcato et al. (1990): *Pleurogeophilus mediterraneus*.

2.3.3 Hydrogen cyanide-producing glands

- **LM investigation**

  Maschwitz et al. (1979): *Asanada* n. sp.

3. Head and vesicular glands

- **LM investigation**

First anatomical and histological investigations on glands in the head of Chilopoda were done by Müller (1829) (*Scolopendra morsitans*), Léon-Dufour (1824) (*Scutigera coleoptrata*, *Lithobius forficatus*), Plateau (1878) (*L. forficatus*, *Cryptops* spec., *Geophilus flavus*, *Stigmatogaster subterraneus*), Herbst (1889, 1891) (*S. coleoptrata*, *L. forficatus*, *Eupolybothrus grossipes*, *Scolopendra cingulata*); Duboscq (1895, 1898a) (*S. cingulata* – 'glandes de la tête'), Chalande (1905) (*G. flavus*), Fahlander (1938) (*S. coleoptrata*, *Thereuopoda clunifera*, *Thereuonema tuberculata*, *L. forficatus*, *Archilithobius erythrocephalus*, *Bothropolys asperatus*, *Polybothrus fasciatus*, *Paralamyctes spenceri*, *S. cingulata*, *S. morsitans*, *Scolopendra subspinipes*, *Cormocephalus rubriceps*, *Otocryptops rubiginosus*, *Cryptops hortensis*, *G. proximus*, *Pachymerium ferrugineum*, *Scolioplanes hirtipes*, *Mecistocephalus smithii*), Manton (1965) (*Scutigera coleoptrata*, *Lithobius forficatus*, *Craterostigmus tasmanianus*), Jangi (1966) (*Scolopendra morsitans*), Rilling (1968) (*L. forficatus*), Borucki (1996) (*Craterostigmus tasmanianus*), Desbalmes (1992) (*Theatops erythrocephalus*).

Fahlander distinguished between maximally 5 pairs of head glands (‘Kopfdrüsen’) with their conducting canal in the head region (2 buccal glands, 1 mandibular gland, 1 maxilla I gland, 1 maxilla II gland) and maximally 2 pairs of vesicular glands (‘vesikulöse Drüsen’) within the first trunk segments. In most cases head glands function as salivary glands, the function of vesicular glands is hitherto unknown.

- **TEM investigation**

  Only a few fine structural investigations of head and vesicular glands exist. Comparative studies on fine structure and function are completely absent.

  Rosenberg & Seifert (1975a): *Lithobius forficatus* (maxilla II-gland),

  Hilken & Rosenberg (2006a): *Scutigera coleoptrata* (maxilla I-gland),

  Hilken & Rosenberg (2009): *Scutigera coleoptrata* (vesicular glands).

4. Maxillary organ of *Scutigera*

In Notostigmophora, the maxillary organ is located inside the posterior coxal lobes of the first maxillae and extends posteriorly as sac-like pouches, lined by a cuticle. The maxillary organ is probably not evertable. The epithelium consists mainly of a specialised pseudostratified columnar epithelium, covered by a highly folded cuticle. Hundreds of setae (fusiform and filiform) extend from the cuticle into the cavity of the maxillary organ. The two sac-like pouches are joined dorsomedially by the glandular epithelium of the maxillary organ gland. The maxillary organ communicates with the maxillary organ gland, the maxillary nephridium by a dorso-ventral part of the labyrinth canal, and the oral cavity. Additionally a large number of epidermal glands secrete into the maxillary organ. In the past, the maxillary organ was thought to be a sense organ (Latzel 1880), an auditory organ (Haase 1884b, Heathcote 1885, Verhoeff 1902–25), an organ of gas exchange (Borucki 1996), or as an evertable cleaning organ (Verhoeff 1902–1925, Manton 1965, Desbalmes 1987, Borucki 1996). It is now clear the maxillary organ acts primarily as a reservoir, storing probably parts of the excretion fluid from the maxillary nephridium and the secretion of the maxillary organ gland and other epidermal glands. The pseudostratified epithelium and the folded cuticle can probably be stretched considerably and than becomes flattened. It is thought that the fluid is primarily used as preening fluid. During preening with the aid of the moveable telopodites of the first maxilla, the maxillary organ was never observed to be everted (Rosenberg et al. 2004, 2006).

- **LM investigations:**

  Latzel 1880, Haase (1884b), Heathcote (1885), Verhoeff (1902–1925), Manton (1965), Borucki (1996), Desbalmes (1987, 1992). Koch & Edgecombe (2009)

- **TEM investigation:**

  Hilken & Rosenberg (2005a).

5. Alimentary system

The knowledge on the alimentary system is rather fragmentary. Only Plateau (1878) (different Lithobiomorpha, Scolopendromorpha, Geophilomorpha), Kaufman (1961c) (*Scutigera coleoptrata*), and Rilling (1968) (*Lithobius forficatus*) made anatomical and first histological studies on the alimentary system. Takakuwa (1955) gave a short description of the alimentary system of a scutigeromorph species. The alimentary system of the Scutigeromorpha was not described as a whole. Other investigations were done on particular characteristics within the fore and the hind gut.

5.1 General structure

5.1.1 Scutigeromorpha

- **LM investigations**

  Takakuwa (1955) (in Japanese), Kaufman (1961c) (in Russian), Seifert (1967c) ('Pharynxapparat').

- **SEM/TEM investigations**

  Koch & Edgecombe (2006): different Scutigeromorpha (peristomatic structures),

  Hilken & Rosenberg (2009) (pharynx apparatus).

5.1.2 Lithobiomorpha

- **LM investigations**

  Plateau (1878), Gibson-Carmichael (1885), Kaufman (1961a), Manton & Heatley (1937), Léger & Duboscq (1902d), Rilling (1968): *Lithobius forficatus*,

  Gibson-Carmichael (1883–1885): *Lithobius forficatus*, *Lithobius grossipes*, *Lithobius variegatus*.

- **TEM/SEM investigations**

  Koch & Edgecombe (2008): different Lithobiidae and Henicopidae (peristomatic structures),

  Vandenbulcke et al. 1998: *Lithobius forficatus* (midgut),

  Wenning (1977, 1978, 1979): *L. forficatus* (hind gut).

5.1.3 Scolopendromorpha

- **LM investigations**

  Plateau (1878): *Cryptops savignyi*, *Cryptops agilis*, *Cryptops hortensis*,

  Willem (1889): *Cryptops punctatus*, *C. hortensis*, *Scolopocryptops* sp., *Scolopendra heros*, *Scolopendra hispanica*, *Scolopendra cingulata*, *Scolopendra subspinipes*,

  Balbiani (1890): *C. hortensis*, *C. punctatus,*

  de Serres (1813), Verhoeff (1902–1925), Kaufman (1962a): *S. cingulata*,

  Shukla (1962, 1964), Jangi (1966), Sundara Rajulu (1970a, 1971a): *Scolopendra morsitans*.

- **SEM investigation**

  Edgecombe & Koch (2008): different Cryptopidae, Scolopocryptopidae and Scolopendridae (peristomatic structures).

  Koch et al. (2009): different Scolopendromorpha (gizzard),

  Edgecombe & Koch: different Scolopendromorpha (2009) (peristomatic structures, gizzard).

5.1.4 Geophilomorpha

- **LM investigations**

Plateau (1878): *Haplophilus subterraneus*, *Geophilus flavus*,

Gibson-Carmichael (1883–1885): *Geophilus longicornis*, *Himantarium gabrielis*,

Verhoeff (1902–1925), Kaufman (1960c): *Geophilus proximus*,

Lewis 1981: *Strigamia maritima*.

5.2 Peritrophic membrane

- **LM investigation**

Plateau (1878): *Lithobius forficatus*, *Cryptops savignyi*, *Cryptops agilis*, *Cryptops hortensis*, *Haplophilus subterraneus*, *Geophilus flavus*,

Gibson-Carmichael (1883–1885): *Lithobius forficatus*, *Lithobius grossipes*, *Lithobius variegatus*.

Balbiani (1890): *Cryptops hortensis*, *C. punctatus*.

- **TEM investigation**

Sundara Rajulu (1971b): *Ethmostigmus spinosus*.

6. Excretory system

6.1 Maxillary nephridia

In *Scutigera coleoptrata* Herbst (1889) described two glandular systems in the region of maxilla I and II. System I opens between the maxillae I, system II opens laterally on the head. In *Lithobius forficatus*, Herbst (1891) described a paired glandular system (system II), connected among each other. The system II has two openings ventrally of the maxilla I and the maxilla II respectively. Fahlander was the first (1938) who identified these structures as nephridia, the maxillary nephridia. This was confirmed later on by light and electron microscopical studies (see above).

- **LM investigations**

Fahlander (1938): *Thereuopoda clunifera*, *Lithobius forficatus*,
Palm (1954): *L. forficatus*,
Gabe (1967, 1972): *S. coleoptrata*, *L. forficatus*,
Rilling (1968): *L. forficatus*.

- **TEM investigations**

Rosenberg (1979b): *Scutigera coleoptrata*,
Rosenberg et al. (2009): *L. forficatus*.

6.2 Malpighian tubules

In general, all centipedes have one pair of Malpighian tubules (except for *Craterostigmus* see below). The tubules run through nearly the whole trunk and enter via an ampulla the digestive tract between the midgut and the hindgut. Comparative studies by light microscope were only done by Bertheau (1971).

6.2.1 Scutigeromorpha

- **LM investigation**

Léon-Dufour (1824): *S. coleoptrata* ('vaisseau hépatique'),
Kowalevsky (1892/1893): *Scutigera*.

6.2.2 Lithobiomorpha

- **LM investigation**

Léon-Dufour (1824): *L. forficatus* ('vaisseau hépatique'),
Plateau (1878), Kowalevsky (1892/1893), Palm (1954), Rilling (1968): *L. forficatus*,
Bertheau (1971): *L. tricuspis*.

- **TEM investigation**

Füller (1966): *L. forficatus*.

6.2.3 Craterostigmomorpha

- **LM investigation**

Prunesco & Prunesco (1996a): *Craterostigmus tasmanianus* (3 Malpighian tubules).

6.2.4 Scolopendromorpha

- **LM investigation**

Müller (1829), Shukla (1964), Jangi (1966): *SScolopendra morsitans*,
Bertheau (1971): *S. cingulata*,
Wang & Wu (1947): *Scolopendra subspinipes*,
Plateau (1878), Balbiani (1890): *Cryptops*,
Bertheau (1971): *C. hortensis*.

6.2.5 Geophilomorpha

- **LM investigation**

Plateau (1878): *Himantarium*, *Scolopendra*,
Kowalevsky (1892/1893): *Geophilus*,
Palm (1954): *Geophilus linearis*, *Geophilus flavus*, *Pachymerium ferrugineum*,
Bertheau (1971): *Clinopodes linearis*.

6.3 Nephrocytes

It falls under oblivion that nephrocytes in Arthropoda were first detected in Myriapoda at the end of the 19th century.

- **LM investigations**

Nephrocytes were first detected in *Lithobius forficatus* by Plateau (1878) as 'cellules spéciales à pigment'. These cells are recognised by selective uptake of vital dyes like ammonium carmine. Later on these cells were described by Herbst (1891), Kowalevsky (1892, 1892/1893, 1895), and Duboscq (1896a, 1898a) (*Scolopendra cingulata*, different Geophilomorpha). In *Scutigera* they surround the maxillary nephridium (Duboscq 1896a). The cells are described under various names (Herbst 1891: Fettkörperregenrationsketten;

Kowalevsky 1892/1892, 1893: filaments acides, réseau acide; Duboscq 1896a, 1898a: cellules à carminate). In insects similar cells, capable to absorb specific dyes, are termed 'nephrocytes' by Ribaucourt (1901). In Diplopoda and Chilopoda these cells are termed as 'néphrocyte à carminate' (Bruntz 1904, 1906). Palm (1954) described these cells in different Diplopoda (*Polydesmus*, *Craspedosoma*, *Glomeris*, *Julus*, *Schizophyllum*) and Chilopoda (Lithobiomorpha, Geophilomorpha). In 1963 Scheffel described 'lymphatic strands' around the Glandulae mandibulares in *L. forficatus* as an ecdysial organ; these cells were characterised later on as nephrocytes (Seifert & Rosenberg 1974).

- **TEM investigations**

As shown by TEM-investigations, nephrocytes in Chilopoda are specialised cells formed always as podocytes with deeply folded plasma membranes (foot processes or pedicels), bridged by diaphragms. In *Scutigera coleoptrata* they form a compact endocrine gland (Glandula capitis) in the head (Rosenberg & Seifert 1973, Rosenberg 1974), in *Lithobius forficatus* they form an endocrine gland (Glandula ecdysialis) in the head, surrounding the Glandulae mandibulares (Seifert & Rosenberg 1974), in *Cryptops hortensis* and in different Geophilomorpha (*Haplophilus subterraneus*, *Clinopodes linearis*, *G. flavus*) they form cell strands around the Malpighian tubules within the fat body and around the ventral blood vessel (Rosenberg et al. 1997, Rosenberg 1978, 1979a).

7. Coxal and anal organs

Different- sized pore openings on the coxae of the last 2–5 extremities (Lithobiomorpha) or the hind extremities (Scolopendromorpha, Geophilomorpha) display a conspicuous and early described morphological character. These so-called coxal pores are the openings of huge multicellular organs that surround at its base a more or less deeply invaginated pore canal.

In different anamorphic Lithobiomorpha and adult Geophilomorpha paired anal pores on the anal segment (= 2. genital segment) are developed. The inward leading canal is at its base surrounded by a huge epithelium that corresponds to that of the coxal organs. In Lithobiomorpha, the anal segment of anamorphic larval stadia ventrally bears an unpaired anal pore. The pore is reduced in the following epimorphic stadia and is replaced by the coxal organs (Rosenberg 1984). In adult Geophilomorpha anal pores are only developed in some classes, their presence can vary within the families. In Craterostigmomorpha the inner ventral side of each anal valve displays four pairs of pore fields, each separated from the other by broad cuticular bars. Each field bears several deeply invaginated openings of anal pores, surrounded by the huge epithelium of the anal organs.

Comparative fine-structural investigations clearly reveal that the epithelia of the coxal and anal organs are not glandular as described in light microscopical studies, but are formed as typical transporting epithelia. Therefore, they are named coxal and anal organs, respectively (Rosenberg 1985). As comparative organs are lacking in Notostigmophora, it is postulated that the development of coxal and anal organs is an autapomorphy of pleurostigmophoran centipedes. The coxal and anal organs seem to be the site of water vapour uptake (Rosenberg & Bajorat 1984).

7.1 Coxal organs

- **LM investigations**

Latzel 1880, Herbst (1891): *Lithobius crossipes*, *Scolopendra cingulata*, *Himantarium* ('Coxaldrüsen', 'Pleuraldrüsen'),
Verhoeff (1892, 1902–1925, 1931): *Scolopendra*, *Otostigmus*, *Heterostoma* ('Analpleuren', 'Pleuraldrüsen', 'Coxopleurendrüsen'),
Tömösváry (1883-1884): Geophilidae ('Spinndrüsen'),
Willem (1897): *Lithobius*: ('glandes filiaires'),
Duboscq (1898a): *Scolopendra cingulata* ('glandes coxal'),
Attems (1929): ('Hüftdrüsen'),
Rilling (1968): *Lithobius forficatus* ('Coxaldrüsen').

- **TEM investigations**

– **Lithobiomorpha:**
Littlewood (1983): *Lithobius forficatus*, *Lithobius crassipes*,
Rosenberg (1983a), Rosenberg & Greven (1996), Greven et al. (1997): *Lithobius forficatus*,
– **Geophilomorpha:**
Rosenberg & Seifert (1977), Rosenberg (1982): *Geophilus flavus*, *Haplophilus subterraneus*, *Clinopodes linearis*, *Strigamia maritima*.

7.2 Anal organs

- **LM investigations**

Tömösváry (1883–1884): Geophilidae ('Spinndrüsen'),
Verhoeff (1905): different *Lithobius* species ('Analdrüsen'),
Biegel (1922): *Lithobius forficatus* ('Analdrüsen'),
Archey (1916, 1937): *Craterostigmus tasmanianus* ('gland-like bodies').

- **TEM investigations**

– **Lithobiomorpha:**
Rosenberg (1984): *Lithobius forficatus* (anamorphic larvae),
– **Craterostigmomorpha:**
Borucki & Rosenberg (1997), Rosenberg et al. (2006),
– **Scolopendromorpha:**
Rosenberg (1983b): *Scolopendra cingulata*, *Cryptops hortensis*,
– **Geophilomorpha:**
Rosenberg (1989): different Geophilidae.

8. Nervous system

The nervous system of Chilopoda consists of the brain with proto-, deuto-, and tritocerebrum, and the paired ganglia of the ventral nerve chain. A comparative topography of the brain and the stomatogastric nerve system of Chilopoda (except Craterostigmomorpha) is given by Seifert (1967a). The topography of the nerve system with its arising nerves and innervating organs is thoroughly described by Rilling (1960, 1968) in *Lithobius forficatus*. A review is given by Joly & Descamps (1987).

8.1 Topography and brain structure

8.1.1 Scutigeromorpha

- **Topography (LM investigations)**

Newport (1843), Adensamer (1894b), Saint-Rémy (1887, 1889), Herbst (1891), Chatin (1893), Duboscq (1898a), Hilton (1930), Seifert (1967a): *Scutigera coleoptrata*,
Fahlander (1938): *Thereuopoda clunifera*.

- **Brain structure (LM investigations)**

Saint-Rémy (1887, 1889), Holmgren (1916), Hanström (1926, 1928), Hörberg (1931): *Scutigera coleoptrata*,
Fahlander (1938): *Thereuopoda clunifera*,
Saint-Rémy (1888): *Scolopendra morsitans*,
Sombke et al. (2009): *Scutigera coleoptrata*.

- **Brain structure (TEM investigations)**

Strausfeld (1998, 2005): *Scutigera coleoptrata*.

8.1.2 Lithobiomorpha

- **Topography (LM investigations)**

Treviranus & Treviranus (1817), Léon-Dufour (1824), Saint-Remy (1887), Chatin (1893), Haller (1905), Jawlowski (1929), Hanström (1928), Hilton (1930), Fahlander (1938), Rilling (1960, 1968), Seifert (1967a): *Lithobius forficatus*,
Duboscq (1898a): *Lithobius. piceus*, *Lithobius hexodus*,
Henry (1948), Applegarth (1952): *Pseudolithobius megaloporus*.

- **Stomatogastric nerve system (LM investigations)**

Seifert (1967a, b): *L. forficatus*, *L. piceus*.

- **Neurilemm (LM/TEM investigations)**

Füller (1964), Füller & Ude (1969), Joly & Descamps (1987): *L. forficatus*,

- **Brain structure (LM investigations)**

Holmgren (1916), Fahlander (1938), (Melzer et al. 1996/1997): *L. forficatus*, *Lithobius* sp.

- **Innervation patterns (LM investigations)**

Kutsch & Breidbach (1994), Kutsch & Heckmann (1995), Heckmann & Kutsch (1995): *L. forficatus*.

- **Axo- and neurogenesis (LM investigations)**

Kadner & Stollewerk (2004): *L. forficatus*.

8.1.3 Scolopendromorpha:

- **Topography (LM investigations)**

Saint-Rémy (1887, 1888): *Cryptops hortensis*, *Cryptops savignyi*, *Scolopendra morsitans*,
Herbst (1891): *Scolopendra cingulata*,
Chatin (1893): *S. morsitans*,
Campbell (1920): *Scolopendra polymorpha*,
Hilton (1930): *Scolopendra* sp.,

Fahlander (1938): *S. cingulata*,
Shukla (1960, 1968): *Scolopendra amazonica*, *S. morsitans*,
Jangi (1966): *S. morsitans*,
Seifert (1967a): *Cryptops hortensis*, *S. cingulata*, *Rhysida atra*,
Joshi et al. (1977): *S. morsitans*.

- **Innervation of antennal muscles (LM investigations)**

  Changulani (1969): *S. morsitans*.

- **Brain structure (LM investigations)**

  Saint-Rémy (1887, 1889): *Cryptops hortensis*, *Cryptops savignyi*, *S. morsitans*,
  Loesel et al. (2002): *Scolopendra polymorpha*, *Scolopendra subspinipes*, *Scolopendra alternans*.

- **Embryonic development of nerve system (LM investigations)**

  Heymons (1901): *S. cingulata*, *Scolopendra dalmatica*.

- **Axo- and neurogenesis (LM investigations)**

  Whitington (1995, 2006), Whitington & Bacon (1998), Whitington et al. (1991): *Ethmostigmus rubripes*.

- **Glial blood-brain-barrier (TEM investigations)**

  Lane (1989, 1991): *Scolopendra* sp. ('linker junctions').

8.1.4 Geophilomorpha

- **Topography (LM investigations)**

  Newport (1843): *Geophilus flavus, Haplophilus subterraneus*,
  Saint-Rémy (1887): *G. flavus*, *H. subterraneus*,
  Duboscq (1898a): *G. flavus*, *Clinopodes linearis*,
  Hilton (1930): *Geophilus* sp.,
  Fahlander (1938): *Scolioplanes hirtipes* (= *Strigamia hirsutipes*),
  Lorenzo (1960): *Arenophilus bipuncticeps*,
  Seifert (1967a): *Geophilus* sp., *G. flavus*, *Strigamia acuminatus*,
  Ernst (1971): *G. flavus*.

- **Brain structure (LM investigations)**

  Saint-Rémy (1887, 1889): *G. flavus*, *H. subterraneus*.

- **Myelinised outer neural lamella (TEM investigations)**

  Rosenberg & Seifert (1978): *C. linearis*, *G. flavus*, *H. subterraneus*,

- **Axo- and neurogenesis (LM investigations)**

  Chipman & Stollewerk (2006), Stollewerk & Chipman (2006): *Strigamia maritima*.

8.2 Neuroendocrine glands (cerebral glands)

- **LM investigations**

Heymons (1901): *Scolopendra cingulata* (‘Tömösvárysches Organ’),
Fahlander (1938): Scutigeromorpha, Lithobiomorpha, Scolopendromorpha, Geophilomorpha (‘Glandula cerebralis’),
Hanström (1940): *Scutigera coleoptrata*, *Cormocephalus rubriceps*, different Geophilomorpha,
De Lerma (1951): *S. cingulata*,
Gabe (1952, 1953a, b, 1956): different Scutigeromorpha, Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha, Geophilomorpha,
Palm (1956): *Lithobius forficatus*, *Lithobius curtipes*, *Lithobius crassipes*, *Geophilus flavus*, *Pachymerium ferrugineum*,
Rilling (1960, 1968), Scheffel (1961): *L. forficatus*,
Descamps & Joly (1985): *Scolopendra cingulata*, *Cryptops savignyi*, *Cryptops hortensis*,
Joly & Descamps (1968): *L. forficatus*, *Lithobius calceratus*, *Lithobius melanops*, *C. savignyi*, *C. hortensis*, *Haplophilus subterraneus*, *Geophilus flavus*, *Geophilus carpophagus*, *Scolioplanes acuminatus*.

- **TEM investigations**

Scheffel (1965), Joly (1966): *Lithobius forficatus*,
Ernst (1971): *Geophilus flavus*,
Rosenberg (1976): *Scutigera coleoptrata* (‘organe de Gabe’).
Review: Juberthie-Jupeau (1983), Descamps et al. (1990).

8.3 Neurosecretory areas

- **LM/TEM investigations**

Gabe (1952, 1953a, 1956, 1966): Scutigeromorpha, Lithobiomorpha, Scolopendromorpha, Craterostigmomorpha, Geophilomorpha,
Palm (1956), Scheffel (1961), Joly (1966), Joly & Descamps (1968), Prunesco (1970a), Jamault-Navarro & Joly (1977), Jamault (1981): *Lithobius forficatus*,
Prunesco (1970a): *Scutigera coleoptrata*,
Prunesco (1970b): *Scolopendra cingulata*, *Plutonium zwierleinii*, *Dicellophilus carniolensis*,
Ernst (1971): *Geophilus flavus*.
Review: Juberthie-Jupeau (1983).

9. Sensory organs

Whereas in insects a high number of studies on fine structure and function of sense organs is counted, there is comparatively little knowledge in Chilopoda. Comparable and fine structural studies on compound eyes and lateral ocelli were done, but the understanding of structural organisation and function of cuticular sensilla is still poor.

9.1 Photoreceptors

9.1.1 Intracerebrale photoreceptors

- **TEM investigation**

Jamault-Navarro (1992): *Lithobius forficatus.*

9.1.2 Compound eyes and lateral ocelli

According to Müller & Rosenberg (2006) and Müller (2008), the eyes of Chilopoda can be divided in two different groups (Müller et al. 2003b): Compound eyes with a crystalline cone (Scutigeromorpha) and lateral ocelli with cornea lenses, but without crystalline cones (Lithobiomorpha, Scolopendromorpha, Craterostigmomorpha). The retina always consists of two different types of retinula cells.

9.1.2.1 Scutigeromorpha

- **LM investigations**

The compound eyes of the Scutigeromorpha have been the topic of numerous light microscopic investigations, involving the genera *Scutigera* and *Thereuopoda*.
Grenacher (1880), Packard (1880). Rosenstadt (1896), Adensamer (1894a, b), Hemenway (1900), Hesse (1901): *Scutigera coleoptrata*,
Hanström (1934): *Thereuonema tuberculata*, *Thereuonema clunifera*.

- **TEM investigations**

Paulus (1979, 1986) ('pseudocompound eyes'), Müller et al. (2003b) ('compound eyes'): *S. coleoptrata*.

9.1.2.2. Lithobiomorpha

- **LM investigations**

Graber (1880), Grenacher (1880), Willem (1891a, b, 1892a), Hesse (1901): *Lithobius forficatus*.

- **TEM investigations**

Joly & Herbaut (1968), Joly (1969), Bähr (1971, 1972, 1974): *L. forficatus*,
Bedini (1968): *Polybothrus fasciatus*,
Müller & Rosenberg (2006c): *L. forficatus*, *Lithobius dentatus*, *Lithobius mutabilis*, *Ethmostigmus fasciatus*.

9.1.2.3. Craterostigmomorpha

- **TEM investigation**

Müller & Meyer-Rochow (2006b): *Craterostigmus tasmanianus*.

9.1.2.4 Scolopendromorpha

- **LM investigations**

Graber (1880): *Scolopendra cingulata*,
Grenacher (1880): *Heterostoma australicum*, *Branchiostoma australicum*, *Cormocephalus foecundus*, *Cormocephalus gracilis*, *Scolopendra morsitans*, *Scolopendra cingulata*, *Scolopendra tahitiana*, different *Scolopendra* species,

Hesse (1901): *Scolopendra morsitans*,
Heymons (1901): *S. cingulata*, *S. dalmatica*.

- **TEM investigation**

Müller & Meyer-Rochow (2006a): *S. cingulata*, *Scolopendra oraniensis*.

9.2 Tömösváry organ

This sensory organ is only developed in Scutigeromorpha, Lithobiomorpha, and Craterostigmomorpha.

- **LM investigations**

Latzel (1884), Tömösváry (1882–1883), Willem (1892b), Vogt & Yung (1883), Pflugfelder (1933): *L. forficatus*,
Pflugfelder (1933), Knoll (1974): *Scolopendra coleoptrata*.

- **TEM investigations**

Tichy & Barth (1992): *S. coleoptrata*,
Tichy (1972, 1973a, b), Tichy & Barth (1992): *Lithobius forficatus*,
Yamana & Toh (1990): *Thereuonema hilgendorfi*.

- **Function (carbon-dioxide sensing structure)**

Yamana et al. (1986), Yamana & Toh (1987), Yamana et al. (1998): *Th. hilgendorfi*.
Review: Stange & Stowe (1999).

9.3 Cuticular or hair sensilla

According to their outer appearance different types of antennal cuticular sensilla are distinguishable as e.g. sensilla trichodea, s. microtrichodea, s. basiconica, s. coeloconica, and s. brachyconica. In Chilopoda comparative fine structural and electrophysiological studies are rare, the sensilla are classified only to their outer appearance and not on functional reasons.

- **LM investigations**

Leydig (1860): *Lithobius*, *Scolopendra morsitans* ('Geruchszapfen'),
Fuhrmann (1922): *Scutigera coleoptrata*, *Lithobius forficatus*, *Scolopendra morsitans*, *Geophilus* species ('Schaftorgan', 'Borsten', 'kleine blasse Borsten', 'dünnwandige Zapfen', 'herzförmige Sinneskegel', 'kegelförmige Sinnesorgane'),
Duboscq (1897a, b, 1898a): *Scolopendra cingulata*,
Rilling (1960, 1968): *Lithobius forficatus* ('Sinneshaare', 'Sinneszapfen', 'Sinneskegel').

9.3.1 Sensilla trichodea

- **LM investigations**

Antennal sensilla: Fuhrmann (1922): ('haar- bis borstenförmige Sensillen'),
Rilling (1960, 1968): *L. forficatus* ('Sinneshaare').

- **TEM investigations**

Keil (1975, 1976): *Lithobius forficatus* (Antennal sensilla; possible function: contact-chemoreceptors),
Ernst (1976, 1994, 1996, 1999, 2000a, b): *Geophilus flavus* (sensilla on antennae, maxilla I, II; possible function: contact-chemoreceptor).

- **SEM investigations**

  Ernst et al. (2009): *Cryptops hortensis* (possible function: contact-chemoreceptor).

9.3.2 Sensilla microtrichodea

- **LM investigations**

  Antennal sensilla: Fuhrmann (1922) ('kleine blasse Borsten'),
  Rilling (1960, 1968): *Lithobius forficatus* ('Sinneskegel', 'Stellungshaare').

- **TEM investigations**

  Antennal sensilla: Keil (1975): *L. forficatus* ('kleine Borsten')
  Ernst (1983, 1996, 1997, 2000b): *Geophilus flavus* (possible function: proprioreceptor),

- **SEM investigations**

  Antennal sensilla: Ernst et al. (2006, 2009): *Craterostigmus tasmanianus*, *Cryptops hortensis* (with terminal pore; possible function: contact-chemoreceptor).

9.3.3 Sensilla basiconica

- **LM investigations**

  Antennal sensilla: Fuhrmann (1922) ('Sinneszapfen', 'Sinneskegel').

- **TEM investigations**

  Antennal sensilla: Keil (1975): *Lithobius forficatus* (two types: 'short peg sensilla' and 'long cone sensilla'; possible function: thermo and/or hygroreceptor),
  Ernst (1979, 2000a, b): *Geophilus flavus* (possible function: olfactoric receptor).

- **SEM investigations**

  Antennal sensilla: Ernst et al. (2006, 2009): *Craterostigmus tasmanianus*, *Cryptops hortensis* (possible function: olfactoric receptor).

9.3.4 Sensilla coeloconica

- **TEM investigations**

  Ernst (1995), Ernst & Rosenberg (2003): *Geophilus. flavus* (three types of sensilla coeloconica on the poison claw of the maxillipedes; possible function: thermo- and hygroreception), Ernst & Rosenberg (2003): *Lithobius forficatus* (three types of sensilla basiconica on the poison claw of the maxillipedes; possible function: type I + III chemoreceptors (thermo- and hygroreception), type II contact-chemoreceptor).

- **SEM investigations**

  Ernst & Rosenberg (2003), Ernst et al. (2002): *Scutigera coleoptrata*, *Craterostigmus tasmanianus, Cryptops hortensis* (three types of s. coeloconica on the maxillipedes); *Lithobius mutabilis*, *Lithobius dentatus* (maxilliped of larval stages I and II; possible function: chemoreceptors).

9.3.5 Sensilla brachyconica

- **TEM investigations**

Antennal sensilla: Ernst (1981, 1996, 2000b): *Geophilus flavus* (possible function: thermo- and/or hygroreceptor).

- **SEM investigations**

Antennal sensilla: Ernst et al. (2009): *Cryptops hortensis* (possible function: olfactory receptor).

9.3.6 Sensilla basiconica

- **SEM investigations**

Antennal sensilla: Ernst et al. (2009): *Cryptops hortensis* (possible function: chemoreceptor).

9.3.7 Club-shaped sensilla

- **SEM investigations**

Antennal sensilla: Ernst et al. (2009): *Cryptops hortensis* (possible function: chemoreceptor).

9.3.8 Collared sensilla

- **SEM investigations**

Antennal sensilla: Ernst et al. (2006): *Craterostigmus tasmanianus* ('collared tube-like' and 'collared bottle-like sensilla' on different antennal articles; function is unclear),
Edgecombe & Giribet (2004): *Craterostigmus tasmanianus*, *Scolopocryptops sexspinosus* (collared antennal sensilla; function is unclear),
Sensilla on epipharynx: Koch & Edgecombe (2006, 2008): different Scutigeromorpha and Lithobiomorpha ('bottle-shaped sensilla'; function is unclear).

9.3.9 Button-shaped, rimmed sensilla

- **SEM investigations**

Sensilla on hypopharynx: Koch & Edgecombe (2006): different Scutigeromorpha (sensilla with terminal pore; possible function: chemoreceptor).

9.3.10 Hat-like sensilla

- **SEM investigations**

Antennal sensilla: Ernst et al. (2009): *Cryptops hortensis* (antennal sensilla; possible function: chemoreceptor).

9.3.11 Schaftorgan on base of antennae

- **LM investigations**

Fuhrmann (1922): *Scutigera coleoptrata.*

10. Respiratory system

The tracheal system is developed differently in Notostigmophora and Pleurostigmophora. In Notostigmophora short tracheal tubuli are situated on the tergites. The tracheal tubules are closed at their end. In all Pleurostigmophora, the whole body is crossed by long tracheae in different arrangements. A comparative morphological study on tracheal systems and its phylogenetic implications are given by Hilken (1998).

10.1 Notostigmophora

- **LM investigations**

  Pagenstecher (1878), Tömösváry (1881, 1883a, b), Sinclair (1881, 1892), Voges (1882, 1916), Haase (1884a, 1885), Chalande (1885), Dubuisson (1928), Hilken (1997).

- **TEM investigations**

  Hilken (1997, 1998), Prunesco & Prunesco (1996b).

10.2 Pleurostigmophora

10.2.1 Lithobiomorpha

- **LM investigation**

  Sograff (1880), Haase (1884a), Chalande (1885), Verhoeff (1902–1925, 1905, 1941): *Lithobius*,
  Voges (1916), Ripper (1931), Kaufman (1961b), Rilling (1968), Hilken (1998): *Lithobius forficatus*.

- **TEM investigations**

  Hilken (1998): *L. forficatus*.

10.2.2 Craterostigmomorpha

- **LM investigations**

  Manton (1965), Prunesco (1965d), Hilken (1997, 1998).

10.2.3 Scolopendromorpha

- **LM investigations**

  Müller (1829): *Scolopendra morsitans*,
  Kohlrausch (1879): different Scolopendridae,
  Chalande (1885): *Scolopendra hispanica*,
  Haase (1884a): *Cryptops hortensis*, *Scolopendra cingulata*,
  Verhoeff (1902–1925): different Scolopendromorpha,
  Dubuisson (1928): *C. hortensis*, *S. cingulata*,
  Kaufman (1962b, 1964): *Cryptops* sp., *S. cingulata*,
  Manton (1965): *S. cingulata*, *Scolopendra anomalans*,
  Jangi (1966): *S. morsitans*,
  Hilken (1997, 1998): *S. cingulata*, *C. hortensis*.

- **TEM investigations**

Hilken (1997, 1998): *S. cingulata*, *C. hortensis*.

10.2.4 Geophilomorpha

- **LM investigations**

Palmén (1877): *Geophilus* sp.,
Haase (1884a): *Clinopodes linearis*, *Geophilus electricus*, *Geophilus ferrugineus*, *Geophilus proximus*, *Himantarium gabrielis*, *Strigamia acuminatus*, *Strigamia crassipes*, *Schendyla nemorensis*,
Chalande (1885): *Geophilus electricus*, *H. gabrielis*,
Dubuisson (1928): *G. carpophagus*,
Chartschewa (1949): *Geophilus* sp.,
Demange (1942): Geophilidae, Himantariidae, Mecistocephalidae, Oryidae,
Kaufman (1959, 1960a, b): *Geophilus proximus*,
Manton (1965): *Haplophilus subterraneus*, *Orya barbarica*,
Füller (1960): *Geophilus carpophagus*, *Geophilus flavus*, *S. acuminatus*,
Hilken (1998): *G. carpophagus*, *H. gabrielis*.

- **TEM investigations**

Hilken (1998): *G. carpophagus*, *H. gabrielis*.

11. Circulatory system

The cardiovascular system in Chilopoda is one of the most complex circulatory systems among arthropods. The vascular system consists of two longitudinal central vessels, the dorsal and the ventral vessel. Both are connected by a vessel ring, the maxilliped arch, situated in the first trunk segment. Dorsal and ventral vessels can be divided into two regions lying anteriorly and posteriorly of the maxilliped arch. The dorsal vessel is divided in the anterior cephalic aorta and the following heart, the ventral vessel consists of the ventral cephalic vessel and the supraneural vessel. From the central vessels numerous peripheral vessels branch off. They posses open endings through which the haemolymph enters into the haemocoel. The main pumping structure is the heart, which is enclosed in a pericardium, attached to the tergal cuticle by the dorsal diaphragm. In the heart a pair of ostia is located in each leg-bearing segment. The cephalic aorta lacks ostia. A comparative study is given by Wirkner & Pass (2000, 2002).

11.1 Structure

- **LM investigations**

Straus-Durckheim (1828): *Scolopendra* sp.,
Lord (1838): *Scolopendra* sp.,
Newport (1838, 1843): *Scutigera* sp., *Lithobius* sp., *Scolopendra alternans*, *S. hardwickei*, *Mecistocephalus maxillaris*, *Gonibregmatus* sp.,
Herbst (1889, 1891): *Scutigera coleoptrata*, *Lithobius forficatus*, *Lithobius grossipes*, *Henicops* sp., *Scolopendra cingulata*,
Duboscq (1896a, 1898a): *Cryptops* sp., *Lithobius* sp., different Geophilomorpha,
Biegel (1922): *L. forficatus*,

Dubuisson (1928): *Scutigera coleoptrata*,
Fahlander (1938): *S. coleoptrata*, *Thereuopoda clunifera*, *Thereuonema tuberculata*, *Lithobius forficatus*, *Scolopendra cingulata*,
Rilling (1968): *Lithobius forficatus*,
Ernst (1971): *Geophilus flavus*,
Wirkner & Pass (2000, 2002): *S. coleoptrata*, *Thereuopoda longicornis*, *L. forficatus*, *Craterostigmus tasmanianus, S. cingulata*, *Orya barbarica*, *G. flavus*.

- **TEM investigations**

Seifert & Rosenberg (1973, 1978): *Scutigera coleoptrata*, *L. forficatus*, *Geophilus flavus*,
Rosenberg & Seifert (1975b): *S. coleoptrata*,
Økland et al. (1982): *L. forficatus*,
Økland (1984): *Strigamia maritima*,
Jamault-Navarro (1984): *L. forficatus*,
Wirkner & Pass (2002): *S. coleoptrata*,
Hilken et al. (2006): *S. coleoptrata* ('aortic diverticles').

11.2 Innervation of the dorsal vessel

- **LM investigations**

Herbst (1891): *Scutigera coleoptrata*, *Scolopendra* sp., *Lithobius* sp.,
Fahlander (1938: different Scolopendromorpha, Lithobiomorpha, Scutigeromorpha,
Seifert (1967a, b): *Lithobius forficatus*, *Lithobius piceus*,
Scheffel (1961): *L. forficatus*,
Sundara Rajulu (1967): *Scolopendra morsitans*,
Ernst (1971): *Geophilus flavus*,
Varma (1971): *S. morsitans*.

- **TEM investigations**

Ernst (1971): *G. flavus*,
Økland et al. (1982): *L. forficatus*,
Økland (1984): *Strigamia maritima*,
Jamault-Navarro (1984): *L. forficatus*.

11.3 Perivascular cells/Pericardial cells/ Kowalevsky bodies

Perivascular cells surround the dorsal vessel of *Scutigera coleoptrata*. Their function is unclear. Pericardial cells surround the dorsal vessel in other Chilopoda. Only perivascular cells are described ultrastructurally. Pericardial cells were hitherto described only by light microscopy, it remains unclear if their fine structure is similar to those of the perivascular cells. The endings of peripheral vessels are surrounded by Kowalevsky bodies, which are able to absorb vital dyes. Their fine structure and function remain unclear.

- **LM investigation**

  Cuénot (1891, 1897): *Scutigera coleoptrata*, *Scolopendra cingulata* ('glandes lymphatiques'),
  Herbst (1891): *S. coleoptrata*, *S. cingulata* ('Perikardialzellen'),
  Duboscq (1896a, 1898 a, b): *S. cingulata* ('cellules péricardiales', 'corpuscules de Kowalevsky'),
  Kowalevsky (1892–93, 1895): *Lithobius*, *Scolopendra* ('glandes lymphatique'),
  Rilling (1968): *Lithobius forficatus*,
  Palm (1954): *L. forficatus*.

- **TEM investigations**

  Hilken & Rosenberg (2005b): *Scutigera coleoptrata* ('Perivascular cells').

11.4 Haemocytes

The knowledge about haemocytes in Chilopoda is fragmentary. The results of light and electron microscopical investigations are contradictory. The most elaborate investigation is given by Nevermann et al. (1991) and Nevermann (1996).

- **LM investigations**

  Vogt & Yung (1883): *Lithobius forficatus*,
  Cattaneo (1889): *Scutigera* sp. ('leucocytes'),
  Cuénot (1891, 1897): *Scolopendra cingulata* ('amibocytes'),
  Duboscq (1898b): *S. cingulata* ('globules du sang'),
  Review by Kollmann (1908).

- **TEM investigations**

  Hilken et al. (2003a): *Scutigera coleoptrata*,
  Nevermann et al. (1991), Nevermann (1996): *Lithobius forficatus*,
  Ravindranath (1981), Sundara Rajulu (1971d): *Scolopendra morsitans*,
  Sarojini & Gowri (1981): *Otostigmus* sp.,
  Nevermann (1996): *S. cingulata*,
  Sundara Rajulu (1970b): *Ethmostigmus spinosus*.

12. Reproductive system

In female Chilopoda, the unpaired ovary leads to a short paired oviduct that opens into the genital atrium on the anal segment. Two pairs of accessory glands and a seminal receptacle opens into the genital atrium. The reproductive organs of male Chilopoda vary more. The testis are paired (Scutigeromorpha, Geophilomorpha), unpaired (Lithobiomorpha) or are arranged in pairs behind each other. They are connected by an anterior and posterior vas efferens that join the common vas deferens (Scolopendromorpha, Craterostigmomorpha). The reproductive products were transferred via vas deferens and vesicula seminalis into the ductus ejaculatorius. At least two pairs of accessory glands are developed. A survey on the anatomical circumstances of accessory glands is given by Demange (1988). In most cases, fine-structural studies on the female and male reproductive system are missing.

12.1. Structure

12.1.1 Scutigeromorpha

- **Female reproductive system (LM investigations)**

Fabre (1855), Chalande (1905), Knoll (1974), Prunesco (1965b, 1967b): *Scutigera coleoptrata*.

- **Male reproductive system (LM investigations)**

Fabre (1855), Leon-Dufour (1824), Chalande (1905), Prunesco (1969), Prunesco & Prunesco (2000): *Scutigera coleoptrata*,
Fahlander (1938): *Thereuonema tuberculata*.

12.1.2 Lithobiomorpha

- **Larval stages (TEM investigations)**

Camatini & Franchi (1975): *Lithobius forficatus*.

- **Female reproductive system (LM investigations)**

– **Lithobiidae:**

Fabre (1855), Sograff (1880), Schaufler (1889), Prunesco (1965a), Rilling (1968): *Lithobius forficatus*,
Prunesco (1965a): *Lithobius bulgaricus*, *Lithobius muticus*, *Lithobius burzenlandicus*, *Harpolithobius banaticus*, *Eupolybothrus transsylvanicus*, *Eupolybothrus leptopus*,
Carcupino (1996): *Eupolybothrus fasciatus*.

– **Henicopidae:**

Prunesco & Prunesco (1999): *Lamyctes anderis*.

- **Male reproductive system (LM investigations)**

– **Lithobiidae:**

Leon-Dufour (1824), Fabre (1855), Sograff (1880), Schaufler (1889), Fahlander (1938), Prunesco (1963, 1964, 1965b), Rilling (1968): *Lithobius forficatus*,
Tuzet & Manier (1953): *Lithobius duboscqui*,
Prunesco (1963, 1964, 1965b): different Lithobiidae, Harpolithobius, *Eupolybothrus*,
Prunesco et al. (1996): *Esastigmatobius longitarsis*.

– **Henicopidae:**

Prunesco & Johns (1969), Prunesco (1969/1970, 1992a), Prunesco & Prunesco (2000): *Anopsobius neozelandicus*, *Dichelobius bicuspis*,
Prunesco & Prunesco (1999): *Lamyctes anderis*.

- **Accessory sex glands (LM/TEM investigations)**

Fahlander (1938), Rilling (1968): *Lithobius forficatus* (LM),
Carcupino (1996): *Eupolybothrus fasciatus* (TEM).

12.1.3 Craterostigmomorpha

- **Female reproductive system (LM investigations)**

Prunesco (1965d).

- **Male reproductive system (LM investigations)**

Prunesco et al. (1996).

- **Accessory sex glands (LM/TEM investigations)**
  Prunesco (1965d) (LM),
  Carcupino et al. (1996) (TEM).

12.1.4 Scolopendromorpha

- **Female reproductive system (LM investigations)**

– **Cryptopidae:**

Fabre (1855): *Cryptops savignyi*, *Cryptops hortensis*,
Prunesco (1965c, 1997): *Cryptops anomalans*, *Cryptops parisi*, *Theatops erythrocephalus*,
Schaufler (1889): *Cryptops hortensis*, *C. punctatus*.

– **Scolopendridae:**

Fabre (1855): *Scolopendra complanata*,
Jangi (1957): *Scolopendra morsitans*,
Prunesco (1965e, 1997): *Ethmostigmus trigonopodus*, *Scolopendra cingulata*,
Brunhuber & Hall (1970): *Cormocephalus anceps anceps*,
Sareen (1982), Sareen & Rajyana (1982): *Otostigmus aculatus*,
Radl (1993): *Scolopendra cingulata*.
Review: Sareen (1983).

- **Male reproductive system (LM investigations)**

– **Cryptopidae:**

Fabre (1855): *Cryptops hortensis*, *Cryptops savignyi*,
Tuzet & Manier (1953): *Cryptops trisulcatus*,
Demange & Richard (1969): *C. hortensis*,
Prunesco (1997): *Cryptops parisi*,
Prunesco (1997): *C. parisi*, *Theatops erythrocephalus*, *Plutonium zwierleinii*.

– **Scolopendridae:**

Fabre (1855): *Scolopendra complanata*,
Heymons (1901): *Scolopendra cingulata*,
Jangi (1956): *Scolopendra morsitans*,
Demange & Richard (1969): *Scolopendra valida*,
Brunhuber & Hall (1970): *Cormocephalus anceps anceps*,
Radl (1993): *S. cingulata*,
Prunesco (1997): *S. cingulata*, *Asanada brevicornis*,
Demange (1946), Demange & Richard (1969): comparative studies on Cryptodinae, Scolopendrinae, Otostigminae.

- **Accessory sex glands (LM investigations)**
  Jangi (1957): *Scolopendra morsitans*,
  Demange & Richard (1969): *Scolopendra valida*,
  Prunesco (1997): *Scolopendra cingulata*.

12.1.5 Geophilomorpha

- **Female reproductive system (LM investigations)**

Fabre (1855): *Himantarium gabrielis*, *Geophilus ilicis*, *Geophilus convolvens*,
Schaufler (1889): different Geophilomorpha,
Tuzet & Manier (1953): *Schendyla nemorensis*, *Chaetechelyne vesuviana*, *Geophilus osquidatum*,
Lewis (1961): *Strigamia maritima*,
Prunesco (1967a): *Dicellophilus carniolensis*, *Pachymerium ferrugineum*, *Pachymerium tristanicus*, *Strigamia acuminata*, *Himantarium gabrielis*,
Prunesco & Capuse (1971): *P. ferrugineum*,
Sareen (1982): *Lamnonyx cephalotes*.

- **Male reproductive system**

– **LM investigations**

Fabre (1855): *Himantarium gabrielis*, *Geophilus electricus*, *G. ilicis*, *G. convolvens*,
Schaufler (1889): *Scotophilus illyricus*, *Scolioplanes crassipes*, *Geophilus flavidus*,
Tuzet & Manier (1953): *Schendyla nemorensis*, *Chaetechelyne vesuviana*, *Geophilus osquidatum*,
Lewis (1961): *Strigamia maritima*,
Prunesco (1967 a, 1968): *Dicellophilus carniolensis*, *Scolioplanes crassipes*, *Pachymerium ferrugineum*, *Himantarium gabrielis*,
Prunesco & Capuse (1971): *P. ferrugineum*.

– **TEM investigations**

Breucker (1970): *Geophilus linearis*.

- **Accessory sex glands (LM investigations)**

Prunesco (1967a): *Dicellophilus carniolensis*, *Pachymerium ferrugineum, Pachymerium tristanicus*, *Strigamia acuminata, Himantarium gabrielis*.

13. Gametogenesis

13.1 Oogenesis and oocytes

The main recent investigations on oogenesis and oocytes were done in *Lithobius forficatus* by LM and TEM studies.

- **LM investigations**

Knoll (1974b): *Scutigera coleoptrata*,
Tönniges (1902), King (1924), Nath (1924), Zerbib (1966), Rilling (1968), Herbaut (1976, 1977a, b): *Lithobius forficatus*,
Leydig (1889): *Lithobius*, *Geophilus*,
Nath & Husain (1926): *Scolopendra*,
Nath & Husain (1929): *Otostigmus feae*,
Sareen (1982), Sareen & Rajyana (1982): *Otostigmus aculeatus*, *Lamnonyx cephalotes*,
Lubbock (1861), Balbiani (1883, 1864, 1865): *Geophilus flavus*.

- **TEM investigations**

Herbaut & Joly (1972), Herbaut (1972a, 1974): *Lithobius forficatus*,
Beams & Sekhon (1967, 1968): *Scolopendra* sp.
Review: Sareen (1983), Sareen & Adiyodi (1983), Descamps (1990).

13.2 Spermatogenesis

- **LM investigations**

Carnoy (1884), Medes (1905), Bouin (1922a, 1934), Bouin & Ancel (1911): *Scutigera coleoptrata*,
Carnoy (1884), Prenant (1887, 1892), Bouin & Bouin (1901a, b, 1902), Bouin (1900, 1901, 1903b), Meves & v. Korff (1901), Tönniges (1902), Bouin (1903b), Blackman (1907), Nath (1925), Golanski (1929), Zerbib (1966), Descamps (1969a–c), Joly & Descamps (1969): *Lithobius forficatus*,
Tuzet & Manier (1951): *Lithobius calcaratus*,
Gilson (1884, 1886, 1887): *Lithobius* sp.,
Blackman (1901, 1903, 1905a, b, 1910): *Scolopendra cingulata, Scolopendra heros*, *Scolopendra subspinipes*,
Bouin (1903b, c, 1905, 1922a, b): *S. cingulata*,
Bouin (1920): *Scolopendra* sp.,
Gilson (1884, 1886, 1887), Carnoy (1884): *Scolopendra. dalmatica*,
Ram (1937), Nath & Gupta (1957): *Rhysida longipes*,
Bouin (1904), Bouin & Bouin (1902, 1903), Bouin & Collin (1901): *Geophilus linearis*,
Carnoy (1884), Bouin & Bouin (1902): *Geophilus* sp.

- **TEM investigations**

Descamps (1971a–d, 1972), Joly & Descamps (1969), Camatini et al. (1974), Saita et al. (1978, 1979): *L. forficatus*.

13.3 Sperm structure

The structure of chilopod sperm has been described by light- and electron microscopy. Reviews are given by Jamieson (1986) and Mazzini et al. (1991a).

13.3.1 Scutigeromorpha

- **LM investigations**

Medes (1905), Ansley (1954): *Scutigera coleoptrata*.

- **TEM investigations**

Camatini et al. (1977), Franchi et al. (1978), Mazzini et al. (1992), Prunesco et al. (1995): *S. coleoptrata*.

13.3.2 Lithobiomorpha

- **LM investigations**

Prenant (1887), Tönniges (1902), Blackman (1907), Nath (1925), Tuzet & Manier (1953a), Descamps (1969a, b, c, 1971a–d, 1972): *Lithobius forficatus*,
Tuzet & Manier (1953a): *Lithobius microps*.

- **TEM investigations**

Camatini et al. (1974), Franchi et al. (1978), Saita et al. (1979), Castellani-Ceresa et al. (1979), Reger et al. (1980), Beniouri et al. (1985): *Lithobius forficatus*,
Mazzini et al. (1991a): *Lithobius castaneus*, *Eupolybothrus grossipes*.

13.3.3 Craterostigmomorpha

- **TEM investigations**

Carcupino et al. (1996).

13.3.4 Scolopendromorpha

- **LM investigations**

Prenant (1887, 1892): *Scolopendra morsitans*,
Blackman (1901, 1903, 1905a, b, 1910): *Scolopendra heros*, *Scolopendra subspinipes*,
Tuzet & Manier (1953a): *Cryptops trisulcatus*.

- **TEM investigations**

Beniouri & Descamps (1985): *Cryptops hortensis*,
Jamieson (1986): *Ethmostigmus rubripes*,
Castellani-Ceresa et al. (1979), Mazzini et al. (1993), Carcupino et al. (1999): *Scolopendra cingulata*,
Mazzini et al. (1991a): *Scolopendra oraniensis*,
Mazzini et al. (1993): *Scolopendra cingulata*, *Scolopendra clavipes*,
Camatini & Franchi (1979), Saita et al. (1979): *Scolopendra morsitans*.

13.3.5 Geophilomorpha

- **LM investigations**

Tuzet & Manier (1953a): *Chaetechelyne vesuviana, Geophilus carpophagus*, *Geophilus osquidatum, Schendyla nemorensis*,
Tuzet & Manier (1953b): *Himantarium gabrielis*,
Beniouri (1985): *Geophilus flavus*, *Haplophilus subterraneus*, *Scolioplanes acuminata*.

- **TEM investigations**

Horstmann (1968): *Clinopodes linearis*,
Cotelli et al. (1978): Carcupino et al. (1999), Saita et al. (1979): *Himantarium gabrielis*,
Saita et al. (1978): *Geophilus* sp.,
Mazzini et al. (1991a): *Clinopodes flavidus*, *Clinopodes poseidonis*, *Henia vesuviana*.

13.4 Double spermatogenesis

Chilopoda have two types of sperms: macrosperms and microsperms. The filiform macrosperms are the longest sperms within the animal kingdom, with a maximum length of 3 mm (Jamieson 1986). The length of microsperms is about 200 µm. A review is given by Jamieson (1986). Already by light microscopy spermatozoa of two sizes have been demonstrated in Scutigeromorpha, Lithobiomorpha, Scolopendromorpha, and Geophilomorpha.

By electron microscopy sperm dimorphism has only been observed in *Ethmostigmus rubripes* (Jamieson 1986), in *Scutigera coleoptrata* (Prunesco et al. 1995), and in *Scolopendra cingulata* (Carcupino et al. 1999). Other fine-structural investigations resulted in description of only one of the two types or of a ‘chimaera’ consisting of parts of the two types (Jamieson 1986). No sperm dimorphisms could be recognised for Geophilomorpha by electron microscopy (Jamieson 1986; Carcupino et al. 1999: *Himantarium gabrielis*).

13.4.1 Scutigeromorpha

- **LM investigations**

  Bouin (1903a, 1922a, 1934), Ancel & Bouin (1908), Bouin & Ancel (1911), Ansley (1954), Prunesco (1992b), Prunesco & Prunesco (2000): *Scutigera coleoptrata*.

- **TEM investigations**

  Prunesco et al. (1995): *Scutigera coleoptrata*.

13.4.2 Lithobiomorpha

- **LM investigations**

  Tuzet & Manier (1953a): *Lithobius calcaratus*, *Lithobius forficatus*,
  Prunesco & Prunesco (2000): *Anopsobius neozelandicus*.

13.4.3 Scolopendromorpha

- **LM investigations**

  Bouin (1903a): *Scolopendra morsitans*,
  Bouin (1920, 1925): *Scolopendra cingulata*,
  Blackman (1905a): *Scolopendra heros*,
  Aron (1920): *Cryptops* sp.

- **TEM investigations**

  Carcupino et al. (1999): *S. cingulata*,
  Jamieson (1986): *Ethmostigmus rubripes*.

13.4.4 Geophilomorpha

- **LM investigations**

  Tuzet & Manier (1953a): *Chaetechelyne vesuviana*.

- **TEM investigations**

  Carcupino et al. 1999: *Himantarium gabrielis* (no sperm dimorphism).

14. Embryonic development

Comparative embryonic studies in Chilopoda are rare. For long time the comprehensive study of Heymons (1901) on the embryonic development of *Scolopendra* has been the only source of information. Aspects of embryonic development of different Chilopoda are investigated by Metschnikoff (1875), Sograff (1882, 1883), Ivanov (1940), and Dawydoff (1943, 1957). Summarising articles are given by Johansen & Butt (1941), Anderson (1973) and Gilbert (1997) referring mostly to Heymon's investigations. Dohle (1969), Knoll (1974) and Hertzel (1983, 1984, 1986) investigated the embryonic development of anamorphic Chilopoda. With the aid of modern techniques Whitington et al. (1991), Whitington (1995, 2006), Hughes & Kaufman (2002), Kadner & Stollewerk (2004), Kettle et al. (2003), and Chipman et al. (2004a, b) investigated embryonic stadia, segmentation and neurogenesis in different Chilopoda. In Chilopoda, the cleavage of the egg cells results in a blastoderm that forms an ectodermal germ band (superficial cleavage).

14.1 Scutigeromorpha

Dohle (1969), Knoll (1974, 1975): *Scutigera coleoptrata.*

14.2 Lithobiomorpha

Hertzel (1983, 1984, 1986): *Lithobius forficatus*,
Whitington & Bacon (1998) Kadner & Stollewerk (2004): *Lithobius forficatus* (neurogenesis),
Hughes & Kaufman (2002a, b, c): *Lithobius atkinsoni* (embryonic stadia, segmentation genes).

14.3 Scolopendromorpha

Heymons (1897, 1898, 1901): *Scolopendra cingulata*, *Scolopendra dalmatica*,
Dawydoff (1943, 1957): *Scolopendra*, *Rhysida*,
Whitington et al. 1991), Grenier et al. (1997): *Ethmostigmus rubripes* (embryonic stadia, segmentation genes).

14.4 Geophilomorpha

Metschnikoff (1875), Dawydoff (1943, 1957): *Geophilus* sp.,
Sograff (1882, 1883): *Geophilus ferrugineus*, *Geophilus proximus*,
Kettle et al. (2003), Chipman et al. (2004a), Chipman & Stollewerk (2006): *Strigamia maritima* (embryonic stadia, segmentation genes),
Bastianello et al. (2002): *Pachymerium ferrugineum* (segmentation genes).

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