Chapter 7
Examples of Bioadhesives for Defence and Predation

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Abstract  Bioadhesives are widely used in nature, not only for settlement but also for defence, prey capture, nest construction or mobility. These glues are superbly adapted in terms of chemical composition and biomechanical properties to the requirements of those organisms producing them. More than 100 marine and terrestrial organisms are known to produce adhesives, some of them since 500 million years. However, only little is known about the composition, production, secretion mechanisms and mechanical properties of the vast majority of these glues.

Attaching to a substratum, as done by bacteria, plants and animals, surely is the most common function of bioadhesives and has been extensively described in various organisms such as mussels, acorn barnacles, sandcastle worms or slugs.

This chapter focuses on animals that use adhesive secretions for defence and predation, as these functions require specialized behaviours and adhesive properties, such as fast curing process in the millisecond range, squirting over distance, protection against own glue, or bonding to various sorts of substrata with varying
surface chemistry or texture. The depicted organisms cover a large environmental and phylogenetic diversity. In addition to marine animals such as hagfish and comb jellies, many terrestrial species like centipedes, salamanders, spitting spiders and velvet worms use adhesives for defence or prey capture. With its subterranean lifestyle, the glowworm exhibits a highly specialized adhesive system combined with prey-attracting bioluminescence.

Bioadhesion research is challenging but also offers understanding of bioadhesive evolution and mechanisms, and to identify commonalities and functional principles.

7.1 Introduction

The use of bioadhesives as means to cling to a support surface, be it a rock, a plant or another animal, is surely its most common function among bacteria, plants and animals. However, the sticky secretions also fulfil other purposes, such as defence, predation, locomotion or nest construction. Bioadhesives are perfectly adapted morphologically, biologically, chemically and physically to the needs and requirements of the organism. In particular those used for defence and predation exhibit a fast secretion and curing process, being swifter than that of any synthetic system, while others can be exposed for weeks in the environment without losing their bonding capability.

In the following chapter we shall describe some properties of the sticky secretions used for defence and predation, focusing on organisms that produce them. Major emphasis will be on gland morphology, release mechanisms, chemical composition and purpose. A detailed knowledge of these systems not only helps understanding their fast hardening process, but could also assist designing fast-reacting artificial systems in the future.

7.2 Defence

“The defensive form of war is in itself stronger than the offensive”. (Carl von Clausewitz, Selection from “On War”, Book 6, Chapter 1, Offence and Defence)

Animals have evolved a wide variety of antipredator mechanisms, such as camouflage, warning colouration, mimicry, immobile defensive structures including spines, hairs and bristles, unpalatability, the secretion of noxious chemicals, and various behavioural patterns. Although adhesives are rarely used as a weapon of defence, in contrast to other mechanisms listed in the chapters above, they still demonstrate a high degree of effectiveness against larger predators.

While some defence tools, such as the dorsal mucus of the slug Arion subfuscus (Draparnaud 1805), the Cuverian tubules in holothurians, and the epithelial secretions in the frog Notaden bennetti (Günther 1873), have recently been
described in detail elsewhere (see respective chapters in Smith (2016)), it is the goal of this review to provide a short description of some as yet incompletely characterised bioadhesive systems used as part of a defensive reaction.

### 7.2.1 Centipedes

Centipedes or Chilopoda are well known for their ability to capture a wide variety of prey, such as insects, spiders, amphibians, reptiles and even mammals, using lethal venoms (Undheim et al. 2015) secreted by aggregated epidermal glands located in the forcipules (maxillipeds). There are numerous observations, publications and medical reports on the composition of the different types of toxins (Undheim et al. 2015) and their venomous effect on invertebrates as well as vertebrates (for more details, see the related book chapters by Rosenberg (2009a) and Rosenberg et al. (2011)).

However, although some data are available regarding the offensive venom glands and the venoms’ chemical compositions, little is known about the adhesive secretions used for defence in some of the chilopods. Their milky-white sticky secretions are released from defence glands (named telopodal glands in Lithobiomorpha or sternal glands in Geophilomorpha) and harden immediately when the animal is, for example, attacked and bitten by a predator or irritated artificially (Fig. 7.1a, b).

At morphological level, the two glue-secreting glands (telopodal and sternal) share similar general cellular organisation with the venom glands. This type of gland, referred to as a recto-canal epidermal gland, as recently defined by Müller et al. (2014), consists of a multitude of closely packed (aggregated) morphological and functional modules, which contain a subset of four to five constitutive cells.

**Fig. 7.1** (a) Chilopods, such as *Haplophilus subterraneus* (Shaw 1794), release a milky-white glue droplet through the ventral sternal glands (see also Fig. 7.3 for details). (b) The secretion adheres to any material within seconds and exhibits a glossy surface (Images from Janek von Byern, Ludwig Boltzmann Institute for Experimental and Clinical Traumatology (Austria), and reproduced with his permission)
Among them are two secretory cells of unequal size, an intermediary cell of hitherto unknown function, and one or two canal cells making up the cuticle-lined duct (Fig. 7.2a–f).

The secretory cell is extremely elongated and surrounds a tubular, deep-reaching reservoir filled with fibrillous substance. Through the narrow passage the secretion is first squeezed into a widened, drop-shaped space, termed “atrium” (Rosenberg and Hilken 2006; Dugon and Arthur 2012). This structure is separated from more proximal parts of the conducting canal (= duct) by a conspicuous, valve-like structure (cf., Fig. 4.8D in Rosenberg et al. (2011)). The gland furthermore contains a cuticle-enforced duct (calyx) before it reaches particular surface areas of the body cuticle like, for instance, the sternal pore plates in case of geophilomorph sternal (defence) glands (Fig. 7.2) or the inner rim of the tarsungulum of the forcipule as in case of chilopod venom glands (Dugon and Arthur 2012; Dugon 2017).

Accompanying muscle fibres individually lining each gland module may support the release of the secretion. They are present in sternal glands of Geophilomorpha (see Fig. 4.10 in Rosenberg et al. (2011) and Fig. 7.2a in this review), but seem to be absent in lithobiomorph telopodal as well as venom glands (compare Rosenberg et al. (2011)).

Interestingly, the aggregated recto-canal epidermal glands reviewed in this chapter do not resemble each other at topological level; however they may share the same evolutionary origin. For instance, Dugon and Arthur (2012) assumed that the venom glands of Chilopoda might have derived from the internalisation of a formerly exposed glandular epithelium located at the inner rim of the tarsungulum or an appendage gradually transforming into proper forcipules. This assumption is based (a) on observations on early postembryonic stages in the development of the venom gland, namely the successive invagination of a grooved glandular epithelium and the final closure into a circular, internalised calyx (Dugon et al. 2012), and (b) the occurrence of a cuticular crest tying the calyx to the lateral cuticle of the tarsungulum (Dugon and Arthur 2012). Thus, it is perfectly possible that chilopod venom gland modules are homologous to telopodal-like glands present on the anterior trunk and/or head appendages.

7.2.1.1 Lithobiomorpha – Telopodal Glands

All species of Lithobiomorpha possess so-called telopodal glands (Keil 1975; = “periatral glands” sensu Carcupino (1996)), located on the inner face of the femur and tibia of the 14th pair of walking legs in addition to those of the 15th pair of legs, the ultimate or terminal legs, which are no longer used for locomotion (telopodites XII-XV sensu Rilling (1968) and Rosenberg et al. (2011)). Keil (1975) described solitary recto-canal epidermal glands from the antennae as showing an arrangement of cells similar to those of the modules of the aggregated telopodal glands. Either solitary or as modules in aggregated formation, each telopodal gland consists of either one secretory cell type (on the antennae) or two closely appended secretory
Fig. 7.2  General organization of aggregated modules in sternal (defensive) glands of geophilomorph centipedes using the example of *Himantarium gabrielis* (Linnaeus 1767). (a) Semischematic reconstruction of the cellular anatomy of a 4-cell sternal gland module (in mediolongitudinal view) comprising a canal cell (cc), an intermediary cell (ic), as well as two types of secretory cells, a short, granulated cell (sc1) and an extremely elongated, poorly granulated cell (sc2) forming the bulk of the repellent secretion (se) stored in a long tubular reservoir (res). A gland module is surrounded by longitudinal muscle fibres (gmu). (b–g) Module ultrastructure as revealed by TEM on selected section levels from distal to proximal gland areas, with section levels indicated in (a) by dashed, double-pointed arrows. (b) Gland pore (gp), note the secretion fixed in moment of discharge. (c) Longitudinal section of the two duct compartments formed by the canal cell, the distal, drop-shaped atrium (at) and the proximal part characterized by canal cell microvilli (mv) subjacent to duct wall cuticle (dcu). Note the cuticular valve structure (cv) preventing a secretion reflux during expulsion. (d) Proximal compartment of the gland duct (du) surrounded by microvilli with tips of microvilli are attached to the duct wall cuticle by a brush of filaments. (e) Apices of canal cell, intermediary cell and the elongated secretory cell; note that the duct wall cuticle covers only part of the apex of the intermediary cell (arrow). (f) Peripheral sector of the tubular reservoir and thin cytoplasmic sheath of the sc2 surrounding it. (g) The major part of the secretion is produced in the basal part of the sc2 indicated by numerous cisternae of the rough endoplasmatic reticulum (rER) and some secretory granules (gr). Further abbreviations: cu cuticle, ecm extracellular matrix, epc epidermal cell. Scale bars: 1 μm (d–e, g); 2 μm (b, c); 10 μm (f) (Image from Carsten Müller, University of Greifswald (Germany), and reproduced with his permission)
cells (on the posterior legs) as well as an intermediary cell (cf. Table 2 in Müller et al. (2014)). While their role in the production of pheromones had been discussed over 100 years ago (Verhoeff 1905), subsequent analyses have shown that the telopodal glands have a defensive function (Panic 1963; Simon 1964; Keil 1975; Rosenberg 2009b).

The species Lithobius forficatus (Linnaeus 1758) synthesizes and releases viscidous threads, which consist of proteins and lipids (positive reaction to Millon, Sudan black and ninhydrin; Rilling 1968). When attacked by a spider or an ant, this centipede lifts its most posterior leg pairs, catapulting the threads emanating from its telopodal glands against the predators and thus binding the offender to the ground, entangling or at least hampering the attacker severely (Rilling 1968). However, the definite mechanisms of secretion still remain unclear. A release by muscle contraction has been excluded, as the telopodal glands are not surrounded by muscles, and a release by haemolymph pressure remains uncertain, although it may play a role (Rilling 1968; Keil 1975). In addition, contracting microvilli projecting into the reservoir and the various levels of the highly diversified conducting canal may also create micro-currents propelling the secretion along the canal to the gland pore.

7.2.1.2 Geophilomorpha – Sternal (Defensive) Glands

Geophilomorph centipedes such as Henia vesuviana (Newport 1845) produce glowing and gluing substances in the so-called sternal glands (Rosenberg et al. 2011). These epidermal glands are also of the recto-canal type and are thus comparable to the telopodal glands of Lithobiomorpha and the venom glands of Chilopoda. Sternal glands include aggregated units comprising four to five cells: one or two type(s) of canal cells, eventually stacked onto each other (then termed distal and proximal canal cell), an intermediary cell, and two types of secretory cells, a “regular” but small secretory cell (termed type-1 secretory cell) containing many ER cisternae, Golgi stacks and secretory granules released into the gland duct at the microvilli-equipped apex (Fig. 7.2a) and an extremely elongated, poorly granulated secretory cell (type-2 secretory cell). The existence of a type-2 secretory cell in geophilomorph sternal glands is recorded here for the first time, using the example of Himantarium gabrielis (Fig. 7.2). Previous descriptions only documented type-2 secretory cells (Rosenberg et al. 2011). This failure may be easily explained by the small size of the type-1 secretory cells which can be easily overlooked, even during careful examination of related TEM section series.

Sternal glands are located on the ventral surface of each or only particular sternite(s) of a given geophilomorph species (Hopkin and Anger 1992). They are clearly identifiable by a large (2–4 μm) depressed pore patch (Fig. 7.3), also called ventral/sternal pore areas (Turcato and Minelli 1990; Turcato et al. 1995) or ventral pore fields (Bonato et al. 2010, Rosenberg et al. 2011). Up to 200 gland pores are found on each either circular or ovoid patch, coinciding with the occurrence of the same number of glandular units forming a connection to the related pores via a small duct to the ventral surface. Due to the extreme length of the secretory cell and
the tubular reservoir (Fig. 7.2), the glandular units reach deep into the perineural sinus, where they touch the ventral nerve cord at the centre of a trunk segment (cf. Fig. 4.10B in Rosenberg et al. (2011)). The secretory cell, or type-2 secretory cell, has been described as “a huge sac, surrounded by a thin layer of cytoplasm from which the glue is derived” (Hopkin and Anger 1992; Müller et al. 2014) (Fig. 7.4). Distal to the secretory cell there is a single intermediary cell, which presumably serves as an accessory secretory cell adding further components to an immature secretion discharged mainly by the type-2 secretory cell (cf. Rosenberg et al. 2011; Müller et al. 2014).

In the geophilomorph genus Henia, a distal, spacious, and slender-cylindrical compartment of the gland duct (atrium), close to the pore, includes a valve-like structure that may regulate the amount of secretion to be released from each unit (Hopkin and Anger 1992). In Pleurogeophilus mediterraneus (Meinert 1870), however, an internal plug of solidified glue in the duct serves to close the pore opening (Turcato and Minelli 1990; Turcato et al. 1995). In addition to the valve-based regulation of the amount of glue secreted, only those thoracic segments with legs that have been stimulated externally, either by a needle or a predator’s bite, show signs of glue secretion (Fig. 7.5). It is proposed that this stimulus results in a hydrostatic and/or muscular pressure on the glands of the respective segment and, thus, initiates a fast release of the glue. It remains an open question as to how geophilomorphs avoid being affected by their own glue. Hopkin and Anger (1992) assumed that additional, small solitary epidermal glands, located between the sternal glands (black arrows in Fig. 7.3), may produce an anti-adhesive secretion.
Fig. 7.4  Schematic drawing of the sternal gland system in the centipede *Henia vesuviana* with the glandular units (a) accumulating secretion or (b) exhausted after secretion (Hopkin and Read Hopkin and Anger 1992). Each glue-secretion glandular unit, and the dominant (type-2) secretory cell (sc) in particular, is embedded in a distinctive, sac-like structure (segg) containing associated muscle fibres, other glandular units, and the small, repellent-producing epidermal glands; the sac is lined by a basal matrix devoid of a basal labyrinth. Each cell secretes through a duct to the pore patch (pp), located on the sternite at the medial ventral surface (vs). According to the authors, secretion is effected by hydrostatic and/or muscular pressure (hmp), resulting in a hemispherical droplet of glue (hdg) (Image by Hopkin and Anger (1992) and republished with permission of the Naturwissenschaftlich-Medizinischer Verein in Innsbruck (Austria)).

Fig. 7.5  Stimulation of a leg (st) by a needle (n) in the centipede *Henia vesuviana* results in the secretion of a glue droplet (dg) in the corresponding segment, while the neighbouring segments remain unaffected (Image from Hopkin and Anger (1992) and republished with permission of the Naturwissenschaftlich-Medizinischer Verein in Innsbruck (Austria)).
Biochemical analyses of the adhesive secretion of *Henia* sp. indicate the presence of two major (12 kDa and 130 kDa) and several other minor proteins (molecular weight not specified) in the 1D–PAGE (Hopkin et al. 1990). Amino acid analyses of the glue secretion indicate that the glue protein content bears slightly more non-polar than polar or hydrophobic side groups (Hopkin et al. 1990), similar to the defensive glue secreted by salamanders (see the section Salamanders further below for details).

While *Henia vesuviana* is currently the only species known to contain only proteins in its sternal gland secretions (Hopkin et al. 1990), in three out of thirteen investigated geophilomorph centipedes (Linotaeniidae, Geophilidae and Himantartiidae) hydrogen cyanide (HCN) as well as other cyanogenic derivatives and precursors (benzoyl nitrile, benzaldehyde, mandelonitrile and others) may also be present in the viscid secretions (Schildknecht et al. 1968; Jones et al. 1976; Maschwitz et al. 1979; see also Table 2 in Vujisic et al. (2013)). However, while the protein composition has not yet been analysed for most geophilomorph centipedes, only in *Himantarium gabrielis* one major protein with a molecular weight of 55 kDa was detected (Vujisic et al. 2013) in contrast to the two proteins found in *Henia* sp. (Hopkin et al. 1990). This may raise the question if the constant part of the secretions consists of the cyanogenic components, while the proteomic content may vary among the geophilomorph subclades.

Apart from their chemical composition, the sternal secretions also differ in their pH values; for example, in *Pachymerium ferrugineum* (Koch 1835) the secretion has a low pH (3.5–4.0) (Schildknecht et al. 1968), while in *Geophilus vittatus* (Rafinesque 1820) it is almost neutral (pH 6.0–6.5) (Jones et al. 1976). Colour differences have also been observed; in *Geophilus carpophagus* (Leach 1815) the secretion fluid is “more watery and clear”, in *Himantarium gabrielis* it appears rose-red (Brade-Birks and Brade-Birks 1920), whereas in *Strigamia crassipes* (De Geer 1778) it looks milky white (Koch 1927). In several species, such as *Geophilus flavus* (De Geer 1778), *H. gabrielis*, *S. crassipes* and others, the secretions are furthermore bioluminescent (Koch 1927, Rosenberg and Meyer-Rochow 2009) and may be used as an aposematic defence strategy by these nocturnal centipedes.

In addition to the repellent effect of the cyanogenic components in the sternal glands of various geophilomorph centipedes (Schildknecht et al. 1968; Jones et al. 1976), the adhesive secretions also serve for defence against small arthropods such as ants and beetles (Hopkin and Gaywood 1987; Hopkin et al. 1990). The glue of representatives of *Henia* hardens within a few seconds when exposed to air and “physically immobilises large insects such as the Devil’s Coach Horse beetle (*Staphylinus olens* Müller 1764) for more than 20 minutes” (observation cited by Hopkin and Anger (1992)). However, this bonding ability of the secretion only occurs during direct and immediate contact with the substratum and is an irreversible process.
7.2.2 Salamanders

Amongst the amphibians, urodeles have evolved a wide variety of antipredator mechanisms (Brodie and Gibson 1969; Brodie 1977, 1983; Ducey and Brodie 1983; Ducey et al. 1993; Duellman and Trueb 1994). The most effective strategies are immobile posture, tail autotomy, colour patterns, various behavioural responses, and the release of toxic, noxious or adhesive skin secretions (Nowak and Brodie 1978; Brodie and Smatresk 1990; Heiss et al. 2010).

In addition to toxic or noxious secretions some salamanders also use adhesives to defend themselves (Arnold 1982; Evans and Brodie 1994); behavioural observations in the plethodontid salamander *Batrachoseps attenuatus* (Eschscholtz 1833) have demonstrated the effectiveness of its gluing strategy. Once attacked and grasped by a predator like, for example, a snake, the salamander loops its tail around the snake’s head and coats it with a sticky viscous fluid (Fig. 7.6a). The glue in the secretion hardens within seconds upon exposure to air (Brodie and Gibson 1969; Williams and Anthony 1994) and immobilizes the snake immediately (Fig. 7.6b). The salamander escapes, and the snake is unable to free itself for up to 48 h (Arnold 1982).

To date, this adhesive antipredator strategy has only been reported in a few North American (*Ambystoma* spp., *Plethodon* spp., *Batrachoseps* spp. and *Bolitoglossa* spp.; Brodie and Gibson 1969; Williams and Larsen 1986; Evans and Brodie 1994) and Japanese species (*Hynobius* spp.; Brodie 1977), and to some extent has been characterized in *Plethodon shermani* Stejneger 1906 (Largen and Woodley 2008; von Byern et al. 2015). Many of these species do not display obvious warning colours like, for example, *Salamandra salamandra* (Linnaeus 1758) or *Pseudotriton*

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**Fig. 7.6** Defence strategy of the salamander (*Batrachoseps* sp.) (*) towards a snake (+) attack using glue. (a) Typical defence reaction. Note the salamander’s tail wrapped around the snake’s neck. (b) In this case, the mouth of the snake has been glued open (Image from Arnold (1982) and reproduced with permission of the American Society of Ichthyologists and Herpetologists)**
ruber (Sonnini de Manoncourt and Latreille 1801) do (Mebs 2000; Mitchell and Gibbons 2010). They rather appear relatively dark, i.e. for Plethodon shermani, Plethodon glutinosus (Green 1818), Ambystoma opacum (Gravenhorst 1807), with a few yellowish-orange spots as Ambystoma maculatum (Shaw 1802) (Mitchell and Gibbons 2010), or are generally pale green as Hynobius dunni Tago 1931 (Brodie 1977), and secrete their adhesives only as a last resort of defence when provoked over a relatively long period of time (von Byern et al. 2015).

Morphological and histochemical studies of Plethodon shermani have shown that the adhesive glands are mainly distributed along the lateral edges of the tail ridge and in the parotid region. Two gland types occur in the dermal layer of the skin in Plethodon shermani (Fig. 7.7). The mucous glands are densely packed with flocculent material and contain mostly acidic glycoproteins (positive staining with Alcian blue, pH 2.5 as well as with Periodic acid-Schiff reaction - PAS) (von Byern et al. 2015). The granular glands secrete various granules of different sizes and densities that contain only basic proteinaceous material (strong staining with Biebrich scarlet at pH 6.0 and weakly at pH 8.5, but no reactivity at pH 9.5 and 10.5) and lack the glycan fraction (von Byern et al. 2015). Additionally, there is another glandular region named the granular gland area, which is adjacent to the granular gland and shows a similar composition to the mucous gland; however, its function remains as yet undetermined (von Byern et al. 2015).

Microanatomical analyses show that the secretory material of both gland types is not homogenous but varies considerably in size, density and content (Fig. 7.8). Some granules have up to three layers and contain small to large inclusions which appear electron-lucent, electron-dense or empty. This suggests that a “cocktail” of
substances is present even within one gland type, which is nevertheless able to form a rapid and highly stable glue seconds after being released. Unfortunately, due to the size differences of the glandular content a detailed characterisation of single granules could not be performed. Hence the acidic and basic protein contents remain uncertain (von Byern et al. 2015).

Protein identification strategies revealed proteins with pIs between 5.0 and 8.0 and molecular masses between 10 and 170 kDa from the glue of *Plethodon shermani* (von Byern et al. 2017a). As positive reactions for acidic and basic proteins are given in the isolated secretions, it can be concluded that both glands contribute to

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**Fig. 7.8** Semi-thin section of the granular gland (GG) and granular gland area (GGA) in the salamander *Plethodon shermani*. The GG and GGA share a secretion duct (d) and are commonly enclosed by a myoepithelium (red arrows) and connective tissue layer (red asterisks). However, the GG and GGA differ in view of their secretory content and chemical composition. Generally, the gland nucleus (n) in salamanders is a peripherally oriented nucleus; n-myo marks the nuclei of the myoepithelium layer. Scale bar: 10 μm (Image from von Byern et al. (2015) and reproduced with permission)
prominently express NADH dehydrogenase subunits. However, only short sequence tags were identified and homology with these proteins may not reflect the real function of the proteins.

Besides a high protein ratio (>70% of dry weight, based on amino acid analysis), the salamander glue also contains sugar moieties such as mannose (stained with lectin GNA), α-L-fucose (stained with lectin UEA) and N-acetyl-D-glucosamine (stained with lectin WGA) as well as lipids (von Byern et al. 2015). The glue of *Plethodon shermani* further exhibits only a relatively low water content of ~70% compared with other glue-producing animals, such as the Australian frog *Notaden bennetti* (water content 85–90%; Graham et al. 2005), the marine goose barnacle *Dosima fascicularis* (Ellis and Solander 1786) (water content 92%; Zheden et al. 2014), the terrestrial gastropod *Arion subfuscus* (water content 97%; Smith 2016) or the prey capture threads of the larvae of the New Zealand glowworm larvae *Arachnocampa luminosa* (Skuse 1890) (water content 99%; von Byern et al. 2016); see also the section Glowworm further below for more details). Upon release, the glue of *Plethodon shermani* cures immediately, enabling an irreversible and strong bonding of the adhesive to biological (human skin) and artificial (wood, glass, metal) but not hydrophobic surfaces.

Skin alkaloids present in many other amphibians (Daly et al. 2005; Mina et al. 2015; Jeckel et al. 2015) are lacking in the *Plethodon* skin (von Byern et al. 2017a); furthermore, the cured adhesives appear to be biocompatible in cell culture (von Byern et al. 2017b). Nevertheless, cell culture tests also show that the adhesive secretions of other glue-producing salamanders (e.g. *Ambystoma maculatum* and *Plethodon glutinosus*) are cytotoxic, as has been shown for toxin-producing species (von Byern et al. 2017b). This confirms that some glue-producing salamanders not only defend themselves exclusively through their sticky secretions (Fig. 7.6), but additionally use other approaches, mechanisms and strategies to survive an attack.

As was the case for the centipedes mentioned above, it remains unclear how salamanders avoid being glued by their own weapon. Unpublished data from *Plethodon shermani* indicate that the glue appears to be hydrophilic directly after secretion, but becomes hydrophobic during the curing stage. As the salamanders always have a moist skin, this water barrier may ensure that the glue cannot bond to the salamander’s skin, but rather adheres to the snake’s scaly and dry skin. Further studies are in progress to confirm this hypothesis. Such a wettability avoidance strategy is unlikely to exist in centipedes, as in contrast to salamanders these animals do not have a moist skin.

### 7.2.3 Hagfish

Hagfish (Myxinidae), also known as slime eels, are slender up to 60 cm long eel-shaped fish (Fig. 7.9). Their skin lacks scales and varies in colour from white or rose to darker reddish-brown and their tiny eyes appear unpigmented. As these fishes...
lack bones and instead possess cartilaginous skeletal elements, hagfishes are extremely flexible and can form a knot with their body, which works as a leverage mechanism for feeding or prey capture (Clark and Summers 2007; Zintzen et al. 2011). There are slime pores (around 150 in total) present prebranchially and caudally on the lateral body side (Weinrauch et al. 2017), which the animals use as part of a defence system (see below for details). Hagfishes are mostly demersal opportunistic scavengers (Martini 1998; Clark and Summers 2007), but myxine predatory behaviour has also been observed (Zintzen et al. 2011). Hagfishes are cosmopolitan and are found exclusively in marine waters at depths of 30–2000 m and even occur around hydrothermal vents (Martini 1998; Clark and Summers 2007).

Hagfishes are known to secrete large amounts of slime when threatened by predators, such as marine mammals, sharks and seabirds, or to deter feeding competitors (Lim et al. 2006; Zintzen et al. 2011). This slime is produced in specialised epidermally-derived slime glands (see below) and is instantaneously released (with a jet velocity of 0.18 ms⁻¹) (Lim et al. 2006) as milky droplets (in amounts of around 90 mg) (Fudge et al. 2005). The total content of the slime glands constitutes up to 3–4% of the hagfish body mass (Fudge et al. 2005). Once in contact with seawater, the droplets increase substantially in volume (up to around 900 ml) and form a large mucus-like cohesive mass, interspersed irregularly with threads.

Analyses have shown that this slime mass consists mostly of water (>99.9%) and a very low amount of exudate (mucin content 0.0015% and thread content 0.002%) (see below for details) (Fudge et al. 2005). Observations confirm that the slime is extruded when the animal has been directly threatened (bitten or engulfed) by the predator or stressed by nearby competitors (Martini 1998; Zintzen et al. 2011). The extruded slime does not show an adhesive effect as is given for the salamander secretion (see Fig. 7.6), but rather functions like a mesh, clogging the gills and mouths of the predators and thus impairing the flow of water (Lim et al. 2006).
The predator is only able to clear the slime from the mouth and gills by choking (Zintzen et al. 2011). There are no toxins in the slime and bitter substances also seem to be absent as the extruded slime is neutral (pH 7.3) when dissolved in water (Herr et al. 2010).

Unlike many other fish and lampreys, hagfish undergo direct development with no larval stages. The slime gland appears at a late embryonic stage (stage 14 of a total of 19) (Miyashita and Coates 2017), although it is not clear whether the gland is already functionally active at this early stage of development. Morphological studies indicate that the slime is produced by a deeply invaginated epithelial gland type (known as the slime gland, diameter up to 5 mm) (Terakado et al. 1975; Fudge et al. 2015), which contains two different cells: the gland thread cells (GTC) and the gland mucus cells (GMC) (Downing et al. 1981; Fudge and Schorno 2016). Each slime gland is connected to the epidermal surface by a short duct and the release occurs through a gland pore (Fig. 7.10).

The slime gland is surrounded by a connective tissue capsule and striated muscle, the musculus decussatus (Lametschwandtner et al. 1986), which affects the simultaneous release of the GTC and the GMC onto the epidermal surface. Both glands produce a different content, with a long coiled, proteinaceous thread from the GTC and mucin vesicles from the GMC (Fudge et al. 2015). During holocrine secretion, the content of both gland types becomes disrupted in the pore duct and is released as a large white droplet of mucus (Downing et al. 1981) on the epidermal surface. The intermediate filament unwinds itself and the mucin vesicles coalesce, rapidly forming a mass of viscous mucus (see below) (Koch et al. 1991).

The gland mucus cells (GMC) derive from stem cells in the gland epithelium and increase in size during maturation, finally reaching a diameter of up to 150 μm, with a centrally orientated, shrunken nucleus (Terakado et al. 1975). Within a slime gland there are numerous GMCs, each filled with vesicles, which stain slightly positive for PAS, Alcian blue at pH 2.5 and Gomori’s aldehyde fuchsin, confirming the presence of acidic sulphated glycoproteins (Terakado et al. 1975; Salo et al. 1983; Fudge et al. 2015). The gland thread cells (GTC) are oval-shaped, up to 180 μm × 80 μm in size (length × width), and embedded between the GMC within the slime gland (Fudge et al. 2015) (Fig. 7.10). Within a slime gland, both immature and mature GTCs can be found, with the immature ones being clustered at the periphery of the gland and the mature ones in the centre (Terakado et al. 1975). The round nucleus appears inconspicuous in the mature cells, but plays an important role during cell maturation (see below). As indicated by the name, each GTC is filled with a single coiled and densely packed intermediate filament (IF) (Fudge and Schorno 2016). This bi-directionally tapered thread, 150 mm in length and with a diameter of 2 μm (Terakado et al. 1975), stains positively with the Alloxan-Schiff reaction (Spitzer et al. 1984) and consists of three polypeptides (see below for details) (Terakado et al. 1975; Koch et al. 1991; Spitzer and Koch 1998).

In addition to the GMC and GTC, a third cell type, the gland interstitial cell (GIC), can be observed in the immature slime glands (Winegard 2012). This cell type completely occupies the spaces between the two gland types. The cells contain a large Golgi apparatus and a fusion of vesicles at the GTC and GMC membrane.
can be observed, suggesting a supportive function for both gland types. So far, no GIC has been observed in the expelled slime glands, but it cannot be excluded that the cells become damaged during the holocrine release (Winegard 2012).

While the slime glands are concentrated in specific regions and limited in number (see above), other gland cells dominate the hagfish integument, namely the small mucous cells (SMC) (91%) and, to a minor extent, the large mucous cells (LMC) (1%) as well as the epidermal thread cells (ETC) (7%) (Spitzer and Koch 1998). In comparison to the slime gland cells, the normal epidermal cells are smaller.
in size (SMC: 15 μm × 8 μm, LMC: 60 μm × 35 μm, ETC: 35–20 μm), isolated, and not encapsulated by connective tissue and muscle layers (Spitzer and Koch 1998). Nevertheless, each ETC is surrounded by SMCs and the two cell types interconnect via interdigitating plasma membranes, and the ETC thread binds with desmosome-like structures to these membranes (Whitear 1986). However, common properties of the content have not been described for the SMC and ETC as it has for the GMC and GTC of the slime gland. Mucous glands (SMC, LMC) and thread cells (ETC) are not limited to the hagfish integument but have also been found in other fishes such as the goblet cells (mucous cells) or the club cells (thread cells) in teleosts (Lane and Whitear 1980) or “skein cells” in lampreys (Leppi 1968; Rahemtulla et al. 1976).

Although the small and large mucous cells (SMC and LMC) also produce mucus and stain histochemically for acidic glycoproteins similar to the GMC (Subramanian et al. 2008), a higher enzyme activity (lysozyme, alkaline phosphatase, cathepsin B and proteases) and three additional proteins (13–16 kDa, matching haemoglobulin-3, histone H3 and H2B protein) can be observed in the extruded slime (Subramanian et al. 2008). In addition to the different mucous cells (GMC, SMC, LMC) to which they are associated in the hagfish integument, the thread cells of the normal epithelium (ETC) and those in the slime gland (GTC) also display differences. While the threads in the GTC are tightly wound and increase in thickness and length during gland maturation (Fig. 7.10), those of the ETC appear to be shorter and less organized. Radiolabelling tests furthermore support the assumption that more than one thread are produced in the different regions of the ETC, while there is only a single thread in the GTC.

While the predator-defensive function of the slime glands has been clearly documented (see above), the epithelial normal mucus is continuously released. It serves as a physical and biological barrier to the aquatic environment as well as pathogens (Lane and Whitear 1980) but does not contribute to slime production. The function of the threads from the ETC is unclear. Although also secreted, the threads do not participate in the slime formation; they may instead serve to “provide support against distortion in the soft mucigenic epidermis […]” (Fudge and Schorno 2016).

GMCs and GTCs are hypothesised to arise from a basal epithelial cell layer and form the slime gland as they grow and mature (Downing et al. 1984; Fudge et al. 2015). Further studies may be necessary to determine the stem cells and process of gland formation. Detailed studies are, however, available for the formation of the tightly coiled thread of the GTC. Initially, the nucleus of an immature GTC is roughly spherical and fills a large part of the cell. With further maturation, the cell becomes ellipsoidal in shape, with one end becoming pointed and the other more blunted. The nucleus also changes its shape, assuming a conical to elongate spindle form with a wide base at the blunt side of the cell (Downing et al. 1984). At this premature stage there is no thread formation, however, at this thread formation zone (also named the mitochondrial-rich zone – MRZ) (Downing et al. 1984) the cytoplasm is rich in mitochondria, ribosomes and polyribosomes. At maturation, the MRZ has disappeared and is occupied almost entirely by the formed thread, and the nucleus has retreated to the basal end of the cell (Fig. 7.11).
Images of the immature thread show that it is formed from a few (6–12) parallel bundled intermediate filaments (IF) (10–12 nm in diameter) of indeterminate length (Terakado et al. 1975), separated by an electron-lucent space and partly interconnected by fine fibrous structures associated with polyribosomes (Winegard et al. 2014). With maturation, the nucleus (darker area) shrinks in size and becomes slender, while in parallel the number of thread layers (light grey) increases. The centre and right column of the figure shows the maturation of the threads depending on the cell developmental stage. Initially, a cap-like thread coil (upper apricot-coloured thread) is formed in the mitochondria-rich zone, but with maturation the thread acquires a compact, ovoid form (lower green-coloured thread). Scale bar: 10 μm (Image from Winegard et al. (2014) and republished with permission)

Fig. 7.11 Growth of the gland thread cells (GTC) in the hagfish Myxine glutinosa. On the left column, the growth of the GTC is shown from an early stage to the full mature stage (upper to lower arrangement). With maturation, the nucleus (darker area) shrinks in size and becomes slender, while in parallel the number of thread layers (light grey) increases. The centre and right column of the figure shows the maturation of the threads depending on the cell developmental stage. Initially, a cap-like thread coil (upper apricot-coloured thread) is formed in the mitochondria-rich zone, but with maturation the thread acquires a compact, ovoid form (lower green-coloured thread). Scale bar: 10 μm (Image from Winegard et al. (2014) and republished with permission)
from the side (Fudge and Schorno 2016), either to deliver IFs and/or IF subunits, or to increase the thread’s girth (Terakado et al. 1975). Furthermore, in this intermediate stage the filament-to-filament spaces within the thread decrease, while in the filament-to-MT space, a zone of exclusion, named a halo, can be observed (Terakado et al. 1975; Downing et al. 1984; Fudge et al. 2015). Besides the addition of IF and MT to the thread, there is also a filamentous-like structure wrapped around the IF-MT bundle (Fudge et al. 2015) (Fig. 7.12).

With further development, the IFs are very tightly packed together and can hardly be separated visually, while a fluffy rind appears on the thread surface, where the filamentous-like structure is wrapped around the bundle (Fudge et al. 2015). In a fairly mature thread cell (fourth section from the left), the IFs condensate into a unitary superstructure; the MTs and their halos as well as the fluffy rind around the thread disappear and the superstructure eventually appears as a mature thread in the fifth section from the left (Images from Winegard et al. (2014) and republished with permission).

Spitzer et al. (1984) assumed that these processes might be triggered by chemical signalling. Besides the morphological changes of the IFs, the ratio of the three polypeptides (Spitzer et al. 1988) also changes and with the GTC maturation a progressive increase in the $\beta/\gamma$ value could be measured, while the $\alpha/(\beta + \gamma)$ ratios remain near 1 (Winegard et al. 2014). However, this IF condensation does not represent the final stage of thread maturation, as the thread continues to increase in diameter subsequently.
In addition to the aspect of thread maturation, questions remain as to how the coiling of the thread with about 500 thread loops is achieved. Fudge and Schorno (2016) have shown that the arrangement of thread loops is correlated with the changing morphology of the nucleus, whereby the oldest loops are located apically and the youngest ones basally (Fig. 7.11). As a specific wheel-like structure, which would enable the almost perfect coiling of the thread, has so far not been observed in the cytoplasm, it is hypothesized that the nucleus, with the thread attached to it, rotates around its own axis instead (Fig. 7.13) (Terakado et al. 1975).

Although the thread maturation of the GTC has quite extensively been described in the literature, no knowledge of its development period has so far been mentioned. Further open questions remain not only with regard to the mucin production in the GMC, but also more generally as to whether (and how fast) a re-synthesis of the slime gland takes place or if the gland actually degrades after having expelled its slimy content.

Chemical analyses of the extruded slime indicate a ratio of 77% protein, 12% carbohydrate, 5% lipid, and 6% sulphates (dry weight) (Salo et al. 1983). One part of this amount is surely produced by the GMC, whose mucin vesicles stain positively with Alcian blue and PAS (Salo et al. 1983; Spitzer et al. 1984), as well as for sugar moieties like $N$-acetylglalactosamine (lectin soybean agglutinin – SBA) (Winegard and Fudge 2010), indicating the presence of acidic sulphated glycoproteins in the slime. In the thread, three abundant IF proteins ($\alpha$, $\beta$, and $\gamma$) have been confirmed, with a similar molecular mass (63 kDa) but distinct pI values ($\alpha = $ pI 7.56, $\beta = $ pI 5.67, $\gamma = $ pI 5.31) (Spitzer et al. 1984; Schaffeld and Schultess 2006).
In earlier studies the hagfish thread was determined to be keratin-like, because of its low sequence identity with other IF proteins (Koch et al. 1991; Fudge et al. 2003) and mechanical properties different from mammalian hard α-keratins (Fudge and Gosline 2004). However, later genome analyses have confirmed that the γ thread protein is a member of the type I keratin family (although it shows structural congruence with the type III IF proteins), while the α thread protein appears to be homolog of the type II keratins (Schaffeld and Schultess 2006). Moreover, both hagfish IF proteins contain glycine-rich segments; these loops may contribute to the mechanical flexibility of the IFs (Schaffeld and Schultess 2006).

In addition to sugars and proteins, a substantial quantity of inorganic ions such as chloride (191 mmol l\(^{-1}\)), potassium (143 mmol l\(^{-1}\)) and, to a lower extent, sodium (41 mmol l\(^{-1}\)) could be confirmed in the slime in relation to its body fluid. The extruded slime furthermore contains organic osmolytes such as trimethylamine oxide (TMAO, 101.3 mmol l\(^{-1}\)), glycine (79.9 mmol l\(^{-1}\)) and others (Herr et al. 2010). However, it may be likely that these compounds serve mainly as osmoprotectants for the tissue. Hagfishes are osmoconformers, and their plasma, tissue and extruded slime (888 mOsm l\(^{-1}\)) have a similar osmolarity to that of sea water (1000 mOsm l\(^{-1}\)) (Herr et al. 2010).
This behaviour is caused by an irreversible transition of the $\alpha$-helices within the thread proteins towards a $\beta$-sheet confirmation (Fudge et al. 2003), effecting this high breaking stress value.

The hagfish slime itself is not adhesive, as is the case for the other animals described in this study. Nevertheless, the hagfish system provides a good basis for the study of food-relevant aspects (Bocker et al. 2016; Boni et al. 2016b) or the development of artificial protein-based fibres (Negishi et al. 2012; Dance 2016; Fu et al. 2017). Similarly, bioadhesives mostly also have a low sugar ratio (von Byern et al. 2017a), bind a high amount of water (von Byern et al. 2016), and assemble into fibrous 3D structures when released into sea water (Zheden et al. 2014, 2015). However, contrary to hagfish slime, these systems are currently far from being fully understood. Finally, characterizing the hagfish survival strategy may provide a new indication of how the animals avoid being trapped in their own slime, current data indicating that the elongational extrusion of the slime towards the predator causes a thickening of the slime, effective in clogging gills. On the other hand, shearing off the slime from its body by making a movable knot results in a slime thinning and by this the hagfish avoids being clogged by its own secretion (Boni et al. 2016a). Thus, hagfish slime could be a good model to understand the effects and mechanisms of a defensive system.

Fig. 7.14 Slime glands and slime formation in the hagfish *Myxine glutinosa*. (a) Photograph of slime gland pores and its isolated secretion. (b) Light micrograph of the two components. (c) Secreted mucin vesicles from the gland mucus cells. (d) Final slime (also named exudate) including mucin vesicles and threads from the gland thread cells. (e) Isolated threads (also named skeins) (Image from Boni et al. (2016a) and republished with permission)
7.3 Predation

“Invincibility lies in the defence; the possibility of victory in the attack”. (Sun Tzu, “The Art of War”)

Prey capture by adhesive secretion may take place passively through trap mechanism (e.g. silk web, mucus net or tentacle fan). Additionally a few species are known to directly attack and capture prey by their sticky secretion.
7.3.1 Trapping Approach

Orb-weaving spiders are quite possibly the model organism when discussing the use of adhesives to trap prey. With their large, impressive, highly structured webs and the different types of silk involved in building and maintaining these, while also enabling them to resist abiotic and biotic factors, these animals are highly specialised at prey capture. Studies on the viscid capture threads and the glue involved have recently been reviewed by Opell (2013). Therefore, we do not aim to provide a comprehensive summary of the review, but rather discuss and correlate the data given for orb-web spiders with an as yet poorly known web structure system, namely that of the New Zealand glowworm *Arachnocampa luminosa*.

7.3.1.1 Glowworm

Glowworms are the larval form of a fungus gnat of the Keroplatidae family (Matile 1981; Meyer-Rochow 2007; Baker et al. 2008). *Arachnocampa* (Edwards 1924) is a world-renowned glowworm genus, endemic to New Zealand and Australia (Merritt and Baker 2001; Evenhius 2006; Baker et al. 2008). Species of this genus are known for their ability to capture prey by means of adhesive droplets on vertical threads (Fig. 7.15) in combination with auto-bioluminescence (Richards 1960; Meyer-Rochow 2007; Willis et al. 2010). The habitat of this group of insects is limited to places with a high humidity and low air movement such as rainforest patches or tree fern-lined gullies, but the animals can also be found in wet boulder caves

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**Fig. 7.15** In situ image of a larva of the glowworm *Arachnocampa luminosa* and the curtain of fishing lines along its nest (Image from Janek von Byern, Ludwig Boltzmann Institute for Experimental and Clinical Traumatology (Austria), and reproduced with his permission)
Not all caves in New Zealand and Australia have glowworms, but in particular the world-famous Waitomo Cave (Humphries 1889) and Spellbound Cave on New Zealand’s North Island have populations of thousands of individuals, enabling a spectacular glowworm viewing experience at any time.

The larvae construct a nest composed of a mucous tube attached by a network of threads to the rocky substratum (Fig. 7.16) (Gatenby and Cotton 1960; Meyer-Rochow 2007). From this “hammock”, long fishing lines with evenly spaced adhesive droplets (von Byern et al. 2016) hang down, forming an adhesive curtain (Richards 1960) similar in function to orb-web spider webs (Meyer-Rochow 1990, 2007; Walker et al. 2012). The Arachnocampa larvae have adopted a “sit-and-lure” predatory strategy to catch phototropic flying insects.

To attract prey, bioluminescence (peak emission wavelength at 488 nm) (Lee 1976) is emitted from the larva’s posterior light organ, which is composed of several large modified Malpighian tubuli (Green 1978; Sivinski 1998; Willis et al. 2010; Merritt and Clarke 2011; Sharpe et al. 2015). With this blue light projecting downwards, the larva attracts potential prey, catching small flying (e.g., moths, gnats, sand- and stoneflies, or other Arachnocampa adults) or crawling animals (isopods, ants, amphipods, millipedes or even small land snails) (Richards 1960; Stringer 1967; Pugsley 1984; Broadley and Stringer 2001, 2009). In addition, larger insects such as Hymenoptera (bees and wasps) and Coleoptera (beetles) are also occasionally found within the fishing lines, but it is questionable whether these insect groups are actually and specifically attracted to the glowworms’ bioluminescence (Broadley and Stringer 2001).

The adhesive droplets are evenly spaced along a silk thread produced by Arachnocampa and are spindle shaped (Fig. 7.17) with a heavier double-sized droplet at the thread’s end (von Byern et al. 2016).

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**Fig. 7.16** Larva of the glowworm Arachnocampa luminosa within its tube, with its head (h) on the right figure side and its posterior light organ (LO) on the left side. The larva attracts the prey with its emitting bioluminescence and then catches it with adhesive threads made of silk (s) and adhesive vesicles (v) (Image originally by Gatenby (1959), modified by von Byern et al. (2016), and republished with permission by the Royal Society of New Zealand)
The droplets consist mostly of water (99%) and display hygroscopic properties at varying humidity levels (von Byern et al. 2016). So far, only free fatty acids (low concentration dodecanoic acid, tetracosanoic acid, pentadecanoic acid; higher concentration hexadecanoic acid, octadecanoic acid) and proteins (MW range of 58–62 kDa and a pI of 4.2–5.5) were investigated by GC-MS, 2D-PAGE while there is no indication for the presence of monosaccharides (unpubl. Data by V. Dorrer, J. von Byern and M. Marchetti-Deschmann). The glue furthermore appears weakly acidic (pH 4). The hygroscopic properties of the *Arachnocampa* glue indicate that additional compounds must be present. After drying, crystals appear in the droplet region, which attract water with increasing humidity (von Byern et al. 2016). In the past, it was assumed that glowworms use oxalic acid or barbiturate-like compounds in their adhesive droplets to kill and predigest their prey (Fulton 1941; Meyer-Rochow 2007). However, later analyses (Pugsley 1980; von Byern et al. 2016) rather speak against this; instead, the excretory products urea and/or uric acid (von Byern et al. 2016) may be present in the droplets and might be responsible for these hygroscopic properties.

Although it is named “*Arachno*” (“spider-like”), the prey capture system of *Arachnocampa* differs substantially in its origin, composition, strength and behaviour from the well-known orb-web spider system (Table 7.1). The glowworm thread is composed mainly of cross-β-sheet crystallites, as seen in other silks (Craig 1997; Walker et al. 2012, 2015) produced by paired labial glands (Gatenby 1960) and released through the mouth part. Orb-web spiders produce parallel-β-sheets to compose their silk threads (Craig 1997) with different mechanical properties and
molecular structures (Blackledge and Hayashi 2006) through a complex abdominal silk spinning organ named a spinneret (Vollrath 1999; Vollrath and Knight 2001). Besides the divergence in the silk structure, the *Arachnocampa* fishing lines and viscid threads of orb-web spiders also differ in their overall structure and adhesive droplet composition (Table 7.1).

In *Arachnocampa*, so far only a two-layered droplet could be confirmed, with a low number of components present. The droplets only show a bonding ability at humidity values higher than 80% (unpubl. data by von Byern). In contrast, a three-layered droplet model with quite a complex composition exists in spiders. Moreover, at low humidity (>20%; Opell and Hendricks, Opell et al. 2011, 2015; Stellwagen et al. 2014), the spiders’ droplets are still visible and adhesive.

The silk of spiders is known to show a high extensibility and tensile strength, comparable to artificial materials such as nylon (Gosline et al. 1999). The prey capture system of *Arachnocampa* lacks such strong mechanical properties (unpubl. data by von Byern). However, it should be noted that these animals live in a cave or forest throughout their life cycle. Hence, they have adapted to the very constant habitat conditions characterised by low turbidity and a lack of UV influence and humidity variation unlike spiders. The prey spectrum is also rather constant in size and impact force. Unpublished data may indicate that glowworms have developed a predetermined thread failure force limit. This would ensure that too many prey items or too heavy prey result in a breakage and loss of one fishing line, thus preventing the whole nest from being torn from the cave ceiling.

While some fungus gnats, such as *Arachnocampa*, have become a national and tourist celebrity and have been well described, the larval biology of most other fungus gnat species remains marginally investigated. South American *Neoditomyia* spp. (Sturm 1973) and the Jamaican species *Neoditomyia farri* (Coher 1996) likewise inhabits caves and captures prey by fishing lines (Stringer and Meyer-Rochow 1993, 1996) similar to *Arachnocampa*. However, *Neoditomyia* spp. appear to have longer fishing lines (of up to at least 17 cm) than *Arachnocampa* and these are coated with a thin layer of glue instead of distinct adhesive droplets (Stringer and Meyer-Rochow 1993, 1996; Meyer-Rochow 2007). Moreover, *Neoditomyia* spp. capture their prey “passively”, meaning that they do not attract prey through bioluminescence as do *Arachnocampa* spp. (Meyer-Rochow and Stringer 1998). Besides *Arachnocampa* and *Neoditomyia*, there are more carnivorous (Fulton 1939, 1941; Fisher (1940); Meyer-Rochow 2007) and non-carnivorous fungus gnats (Schmitz 1912; Sevcik et al. 2012; Osawa et al. 2014), whose adhesive and mucus secretions are currently far from being fully characterized.

### 7.3.1.2 Comb Jellies

The sea gooseberry *Pleurobrachia pileus* (Müller 1776) (Fig. 7.18) is a small (upto 4 cm) oval to ovoid ctenophore, occurring worldwide in the upper water column (Greve 1974, van Walraven et al. 2017). *Pleurobrachia* is a carnivorous species and catches actively swimming planktonic organisms, such as gammarid amphipods,
crab larvae, barnacle cyprids and copepods, with its two long tentacles. Unlike jellyfish of the phylum Cnidaria, the sea gooseberry does not use poisonous substances or nettle cells (cnidocytes) (Östman 2000), but instead uses an adhesive for prey capture (Bargmann et al. 1972). The two long retractable tentacles are branched into small thread-like filaments, so-called tentilla, which can fan out during swimming to spread over a large area (up to 400 cm²) for prey capture (Greve 1975). Both the tentacles and tentilla consist of central muscle cells surrounded by an outer epidermal layer. The latter comprises sensory cells and a large accumulation of fungiform-like secretory cells (the so-called “Lassozellen” or colloblasts) (Vences 1988), in which the glue is produced. Like the cnidarian cnidocystes (Anderson and Deban 2010, 2012; Anderson et al. 2012), the colloblasts in ctenophores are released and projected towards the external stimulus (Carré and Carré 1993) and bond to the prey at the moment of contact. This mechanism is comparable with the spin tongue of amphibians and some reptiles.

The size and morphology of the colloblasts vary between and within species (Benwitz 1978). In Pleurobrachia, they are about 10 μm long and 4 μm wide (Benwitz 1978), while in Eucharis multicornis (Eschscholtz 1928) the cells reach a size of 25 μm by 8–10 μm (length by width) (Franc 1978). Other species such as Minicetna luteola (Carré and Carré 1993) bear five different types of colloblasts, differing in size and cellular content, on a single tentillum (Benwitz 1978). As it could be excluded that these five colloblast types only represent different maturation phases, the functional significance of this high variability so far remains unclear (Benwitz 1978).

Colloblasts (Fig. 7.19) consist of a hemispherical head (the collosphere) and a helical filament (the collopod), which coils several times around the central stalk-like nucleus and is rooted in the mesoglea (Carré and Carré 1993). In Pleurobrachia, two types of granules can be distinguished: a layer of small osmiophilic external
granules (0.8–0.9 μm in diameter) located on the outer side of the collosphere (Benwitz 1978) and another layer of membrane-bound internal granules (“eosinophilic granules”, likewise around 0.8 μm in diameter) located inside the collosphere, enclosing a fine-grained content (von Byern et al. 2010). In the centre of the collosphere is the spheroidal body, a star-shaped structure from which up to 20 connecting strands (also called “radii”) radiate towards the internal granules. These strands, however, are not directly connected to the granules and end in a stamp-like plate from which tubular rods bind to the granules (Benwitz 1978). The function of this star-shaped body remains unclear. Carré and Carré 1993 assumed a nucleation centre for the spiral filament or an involvement in collosphere development. It is also conceivable that the strands determine the position of the internal vesicles and push them against the colloblast membrane.

Detailed descriptions of the development and differentiation of the colloblasts are given by Benwitz (1978) and Mackie et al. (1988). Based on their observations, colloblasts develop from choanocyte-like precursor cells through three intermediate stages. Moreover, the external granules are not formed by the colloblast itself but
rather by another cell type, namely the cap cells (Weill 1935; Hovasse and de Puytorac 1962, 1963; Bargmann 1972; Bargmann et al. 1972; Storch and Lehner-Moritz 1974; Benwitz 1978; Franc 1978; Emson and Whitfield 1991; Carré and Carré 1993). These cap cells appear at an early stage of the colloblast development and degenerate later, leaving the granules as “residual” droplets on the external membrane of the collosphere (von Byern et al. 2010). As a consequence, the mature external granules possess two membrane layers, an inner strongly osmiophilic vesicle membrane and the outer cap cell membrane (Moore 2001).

Although numerous studies are available on the anatomy of the colloblasts in different ctenophore species (McAlister 1960; Gilbert and Rayor 1983), many questions remain concerning glue synthesis and composition and its involvement in prey capture. Previous ultrastructural observations indicate that the external granules contain “osmiophilic lipoproteins” (Bargmann et al. 1972; preliminary studies by von Byern et al. (2010)) furthermore confirm the presence of neutral sugars (periodic acid-Schiff reaction) and proteins at pH 6.0–8.5 (Biebrich scarlet staining) in both the internal and/or external granules. Latest genome analyses identify a specific gene named “tentillin”, which exhibits cell-specific expression patterns in the tentacles, tentillae and mature colloblasts (Moroz et al. 2014).

Like the cnidarian cnidocytes, the colloblast in Ctenophora can only be used once as the spiral filament cannot be retracted and rewound. Also, the external granules are only synthesised by cap cells during colloblast development. In cnidarians, it is known that approximately 25% of the existing cnidocytes are used for prey capture. However the animals are able to replace and renew used cnidocytes within 48 h (von Byern et al. 2010). For ctenophores such as Pleurobrachia, there is as yet no information about the colloblast or tentilla replacement.

7.3.2 Direct Attack
7.3.2.1 Spitting Spider

In addition to the trapping mechanisms described for orb-web spiders, ground spiders (Gnaphosidae) (Wolff et al. 2017) or bolas spiders (Yeargan 1994) others like the so-called “spitting spiders” (Bürgis 1980, 1990) use another approach for prey capture. As its name suggests, Scytodes sp. (Scytodidae, Arachnida) does not produce adhesive webs but actively expels sticky silk onto its prey to ensnare it (Fig. 7.20) (Monterosso 1927, 1928; Kovoor and Zylberberg 1972). This system is also used as self-defence against predators (Bristowe 1931; Dabelow 1958; McAlister 1960; Valerio 1981; Jackson et al. 1998).

The genus Scytodes contains several species of small spiders, about 3–6 mm in length, whose females are slightly larger (4–6 mm) than the males (about 4 mm) (Robinson 2005). The animals are shiny and hairless but with short setae covering the body (Fig. 7.21). The body colour is mid-brown to pale yellow-reddish with black stripes on the cephalothorax that somewhat resemble a lyre (Jackson et al. 1998).
The legs, which slowly taper in size, are long and black banded. The abdomen, of roughly the same circular shape as the cephalothorax, slopes downwards towards the thin pedicel (waist-like connector) and bears paired black spots, of which the first pair is fused (Nentwig 1985). *Scytodes thoracica* (Latreille 1802) is the most prominent and best characterized species within the family Scytodidae. The animals prefer a concealed lifestyle and can commonly be found in shady areas in houses (cellars, dark areas, closets) and outside under bark, among tree leaves or beneath overhanging stones and slopes (Nentwig 1985; Suter and Stratton 2005). Although *Scytodes* spp. are ecribellate spiders and do not produce a dragnet as orb-web spiders do, they can be observed in a woven non-sticky web (Nentwig 1985).

The spitting spiders are solitary and actively hunt their prey at night by wandering around. During the day, the animals hide in a cryptic posture and avoid light (Nentwig 1985). The spiders are slow-moving and have extremely poor eyesight (Gilbert and Rayor 1985). Instead, they use their front legs, which are covered with sensory setae, to explore the environment and detect potential prey through vibrations or direct tactile sensation (Nentwig 1985). All types of prey, e.g. Formicidae, Lepidoptera, Diptera, Araneae, Heteroptera, Mantodea and others, are caught as long as they are within the same size range or slightly larger than the spider (Dabelow 1958; McAlister 1960; Nentwig 1985), but weakly chitinized prey seems to be preferred (Dabelow 1958).
In close proximity to a potential victim, the spider orients itself towards the prey (defined as an alert posture) and slowly taps its front legs until the prey is centred between the legs (Dabelow 1958; Gilbert and Rayor 1985; Bürgis 1990; Suter and Stratton 2010). Then the spider spits one (using only one chelicera) or two sticky threads in a zigzag pattern over the prey to trap it, moves forward, and wraps the prey in the drying threads with the first and second pair of legs.

This spitting process occurs within milliseconds (<35 ms) (Dabelow 1958), covering a distance of 5–20 mm (Suter and Stratton 2010). The zigzag pattern (Fig. 7.20) is controlled by a lateral-medial oscillation of the fangs with a ventral-to-dorsal extension of the chelicerae (Suter and Stratton 2010) and by this covers the prey completely with liquid (Fig. 7.22). Usually, the animals expel around 5–17 bands, whereas the right and left block contain an unequal number of bands (Gilbert and Rayor 1985) with a maximum length of up to 0.9 m (Suter and Stratton 2010). The animals are able to control the glue amount and only use more spit for prey that shows an increased “struggling intensity” (Clements and Li 2008). After being trapped by the silky bands, the prey is then paralysed with a venomous bite and wrapped in silk thread produced by the spinnerets (Dabelow 1958).

The glue glands are located in the cephalothorax (prosoma) and initially separated into three parts (Fig. 7.23), namely (1) a larger, posterior glue gland (defined as “fond séricigéne”) containing the adhesive components, (2) a smaller, anterior poison gland (defined as “ampoule”) containing the venom, and (3) the secreting canal in the chelicerae (Millot 1930). Later, Kovoor and Zylberberg (1972) furthermore separated the poison glands according to their gland cells and content and defined five distinct regions in total (Fig. 7.24):

I. The glue gland (defined as lobe I) synthesises the silk threads surrounded by glycoprotein microfibrils. The glands contain large nuclei and a high density of rough endoplasmatic reticulum. Gland cells, being closely related to lobe III of the poison gland (Fig. 7.24), furthermore contain small Golgi vesicles and are rich in proteins and acidic glycoproteins.
II. The posterior part of the poison gland is defined as lobe II and consists of gland cells with fibrillar, granular and paracristalline content, which stain for proteins and acidic glycoproteins. The glands contain organelles such as rER, Golgi vesicles and small mitochondria. Together with the anterior part (lobe III), these gland cells are thought to be responsible for the production of the toxic components.

III. The smaller lobe III, situated between the glue gland and lobe II, contains cells with electron-dense vesicles. However, these are located near the rER and Golgi apparatus and show no signs of contributing to the glue and/or toxin formation. Histochemically, these cells react to carboxylated glycoproteins.

IV. The content of lobe IV stains for neutral glycoproteins and, ultrastructurally, a “constant association of mitochondria with ER lamellae” can be detected in the gland cells. An involvement of this lobe in toxin production has not been determined, and its “functional role […] is not clear” (Kovoor and Zylberberg 1972).

V. The intracheliceral part (earlier defined as “canal”, labelled as Ca in Fig. 7.24) comprises different cell types: the canal itself is composed of muscle layers and its outer epithelium is covered by a cuticle. Internally, the ventral side of the canal is lined by a single epithelial cell layer, while the dorsal side is divided into the following different gland types (Fig. 7.24): (a) this gland type covers most parts and contains ergastoplasmic parasomes and glycogen accumulations; (b) these are neighbouring elongated cells, clearly distinguishable by their apical, club-shaped microvilli and the presence of microtubules in the cytoplasm. As some signs of pinocytosis activity can be observed, Kovoor and Zylberberg (1972) assume an involvement of this cell type in resorption, ionic...

Fig. 7.23  The gland system (highlighted in grey) of the spider *Scytodes thoracica* consists of into three parts: the posterior glue gland (GG), the anterior poison gland (PG), and the secretion channel (Ca) located in the chelicerae (Ch). The glands as well as the channel are enclosed by massive muscle fibres (Mu) (Image from Millot (1930) and republished with permission of the Société Zoologique de France)
regulation and transport of substances from the canal lumen to the cells and vice versa; (c) the last cell type connects the canal lumen with the outer cuticle; no information is given about any secretory activity for this cell (Kovoor and Zylberberg 1972).

So far it remains unclear whether Scytodes sp. spit already contains toxic components from lobes II and III or if they are released afterwards for the bite. Behavioural observation with prey covered with the glue of Scytodes sp. for a period of 24 h showed that it survived, and that the prey was also able to eat the hardened glue without any negative side effects (Clements and Li 2008).

Fig. 7.24 Anatomy of the spitting glands in the spider Scytodes thoracica. (a) Outer morphology of the isolated spitting gland. The glue gland is labelled as I, following the nomenclature of Kovoor and Zylberberg (1972), the poison gland is subdivided into the lobes II, III and IV. The glue is expelled through the channel (Ca) in the cheliceres. (b) Cross-section of the spitting gland; the gland cells mostly appear dorsally, while ventrally a non-secretory cell layer can be observed. The glue glands (marked as I*) neighbouring lobe III of the poison gland show a difference in secretory content compared to the remaining glue glands in lobe I. In the dorsal region of the channel (Ca), three different cells (a, b and c) can be distinguished based on their morphology and secretory content (Image from Kovoor and Zylberberg (1972) and republished with permission).
The latest chemical characterization of the poison/adhesive glands confirms a cocktail of toxins (35% of the proteome) present in this prey-capture system. Some of these components show a high homology to other spider toxins, e.g., those of *Phoneutria nigriventer* (Keyserling 1891), *Psalmopoeus cambridgei* (Pocock 1895), *Dysdera erythrina* (Walckenaer 1802) and others (Zobel-Thropp et al. 2014). The authors assume that the small (3.5–7 kDa) glycine-rich and diglutamine/dityrosine motif-containing peptides found by transcriptome and proteome analyses may contribute to the formation of the *Scytodes* glue. Unfortunately, Zobel-Thropp et al. (2014) characterized the complete gland system without separating the adhesive from the poison gland and without using the ejected spit for comparison. Therefore, it needs to be confirmed that toxins are absent from the spit and that the glue contains these small peptides found in the tissue samples (Zobel-Thropp et al. 2014).

Biomechanical data indicate that the *Scytodes* thread shortens by 40–60% directly after ejection, generating a force of 0.1–0.3 mN (Poinar 1996, Suter and Stratton 2010). As a consequence, the prey is not only arrested by the adhesive spit but is also immobilized onto the substratum by the contracting threads.

7.3.2.2 Velvet Worms

Onychophorans are carnivorous, exclusively terrestrial invertebrates that occur in tropical and temperate forests of the southern hemisphere and around the equator (Ruhberg 1985; Reid 1996; Mayer 2007; Oliveira et al. 2016). Their common name refers to the velvety appearance of their skin, which is water-repellent (Storch and Ruhberg 1993; Ruhberg and Mayer 2013). To date, 191 valid onychophoran species have been described, namely 76 peripatids from Central and South America, Western Africa and South-East Asia, and 115 peripatopsids from Chile, South Africa and Australasia (Mayer and Oliveira 2011; Oliveira et al. 2012; Oliveira and Mayer 2017). Representatives of most species do not exceed 5–6 cm in length, but some neotropical species reach body lengths of 20 cm or more (Morera-Brenes and Monge-Nájera 2010). Onychophorans possess a more or less cylindrical body with 13–43 pairs of unjointed legs called lobopods. At the anterior end, the lobopods have been modified to form three pairs of cephalic appendages, including the frontal antennae, the jaws located within the mouth cavity, and the slime papillae, which are used for slime ejection (Mayer et al. 2010, 2015).

The animals occur mostly in or under decaying logs and leaf litter of humid tropical and temperate forests, where they feed on small invertebrates such as termites, cockroaches, crickets and woodlice (Read and Hughes 1987; Barclay et al. 2000; Reinhard and Rowell 2005). Onychophorans are slow-moving animals and do not actively hunt their prey over a long distance or time, but instead localize their prey at a short distance using their sensory antennae (Read and Hughes 1987). In order to catch their potential prey, the animals typically eject two streams of a sticky secretion via the paired slime papillae (Fig. 7.25). The ideal distance for squirting and entangling the prey is 0.5–4.0 cm (Röper 1977; Read and Hughes 1987),
squirting distances of up to “almost a foot” (Sedgwick 1895), i.e. 30 cm, have also been reported.

Immediately after release, the slime hardens and entangles the prey in a net of sticky threads (Fig. 7.26). Read and Hughes (1987) observed that the animals direct additional focused slime squirts at the prey’s limbs and fangs if it is still violently struggling. The onychophoran glue-like slime lacks toxins or anaesthetics; instead, the velvet worm bites the immobilised prey and injects digestive saliva into its body (Heatley 1936; Storch et al. 1979; Nelson et al. 1980), leading to a rapid death and partial digestion of the victim (Read and Hughes 1987; Mayer et al. 2015). During the prey digestion process, the velvet worm also ingests its own squirted slime, often along with attached soil particles. In addition to prey capture, the glue-like slime is also used for defence against predators (Reinhard and Rowell 2005; Baer et al. 2014).

The slime is produced in long, slender, paired glands that are located within the main body cavity (central sinus) and extend along each side of the gut (Fig. 7.27). Each gland is subdivided into two major regions: the posterior glandular portion associated with numerous endpieces, in which the slime is produced, and the
anterior reservoir, from which the slime is released via the opening of the slime papilla (Baer and Mayer 2012). The slime gland opening is surrounded by denticle-like scales of an unknown function (Figs. 8D, F in Oliveira et al. (2012)). While the numerous endpieces of the slime gland directly open into the central secretory duct in representatives of Peripatopsidae, the endpieces are arranged in rosettes of four in Peripatidae, so that the slime is first collected in an atrium before being processed further into the central duct (Baer and Mayer 2012). The prismatic gland cells lining the cavity of the endpieces are densely packed with tubules of rough endoplasmic reticulum (rER) and Golgi vesicles (Ruhberg and Storch 1977). Furthermore, the nuclei and nucleoli of the gland cells are clearly larger than those of the surrounding tissue (Ruhberg and Storch 1977; Baer and Mayer 2012). The secretory vesicles in the glands are electron-dense (Ruhberg and Storch 1977) and either appear as an “usual granular structure” (Moseley 1874) or “are not concentrated in granules, rather they are released in a diffuse form” (Lavallard and Campiglia 1971). Also, there are differences between authors regarding their secretion into the cavity. According to Moseley (1874), the vesicles swell and finally burst the glandular content into the cavity, while Lavallard and Campiglia (1971) observed an apocrine
secretion. Transmission electron microscopy has revealed membrane residues and micellar particles in freshly secreted droplets, while such particles were absent in droplets fixed 12 min after secretion and these also lacked adhesiveness (Ruhberg and Storch 1977). The presence of micellar nanoglobules was indeed confirmed in a recent multiscale structural and compositional analysis of the onychophoran slime (Baer et al. 2017). Apart from this granular material, α-glycogen and lipid inclusions were observed within the glands, but not in the secreted droplets (Ruhberg and Storch 1977).

According to Ruhberg and Storch (1977), there are some differences between the adults and juveniles at the cellular level. Besides a higher amount of rER and free ribosomes, the young individuals apparently have a lower amount of Golgi vesicles and secretory inclusions in their glands. Also, species-related differences with respect to the number and length of the gland tubes and endpieces have been recorded, in addition to differences in protein band patterns (Baer and Mayer 2012; Baer et al. 2014). The glands are surrounded by an outer layer of connective tissue and muscle fibres; the latter, however, are lacking around the endpieces (Baer and Mayer 2012). The central secretory duct is formed by a single layer of epithelial cells that bear numerous apical microvilli. The duct is surrounded by a thick layer of collagen and muscle fibres towards the body cavity. In the transition area between the duct and the slime reservoir, a valve-like structure may be present, which might serve for preventing the backflow of the slime during the ejection event. Interestingly, this structure was only observed in the investigated representatives of Peripatopsidae, but not in the Peripatidae species (Baer and Mayer 2012).

The reservoir of the slime gland differs from the central secretory duct in that its lumen is lined by a thin cuticle, indicating an ectodermal origin (Ruhberg and Storch 1977). Only a few organelles are present in its cells, including a large nucleus and electron-lucent lipid inclusions. Additionally, the reservoir is enclosed by several layers of interlacing muscle and collagen fibres, most probably to facilitate a fast ejection of the slime (Baer and Mayer 2012). Further observations by the authors show that in dissected specimens kept in physiological saline, peristaltic contractions of the reservoir occur. The slime reservoir comprises around 11% of the entire body mass, but still contains slime even after several ejection events and is replenished within one day (Read and Hughes 1987).

The ejected slime consists of a small translucent thread (diameter 0.02 mm) along which clear and scentless droplets are aligned (Benkendorff et al. 1999) (Figs. 7.26 and 7.28). The droplets are similar in their appearance to those observed in orb-web spiders and glowworms (see sections above). However, in contrast to spiders and glowworms, the onychophoran thread consists of glue (Haritos et al. 2010) and does not contain silk (Craig 1997) or collagen (Benkendorff et al. 1999). The thread-like appearance of the slime is most likely a result of the jet-like propulsion during the ejection process and the re-arrangement and crosslinking of the proteins towards gelation (Haritos et al. 2010). Recent mechanoresponsive analyses of the onychophoran slime indeed suggest that the biopolymeric fibre assembly is facilitated via mono-disperse lipid-protein nanoglobules (Baer et al. 2017). These nanoglobules might self-assemble into nano- and microfibrils by shear forces,
which results in the formation of macroscopic fibres with a protein-enriched core and lipid-rich coating. This process seems to be reversible, as dissolution of dried fibres in water leads to re-formation of nanoglobules (Baer et al. 2017). Hence, the supramolecular assembly of proteins might be mediated by reversible non-covalent interactions within the slime.

Chemically, the onychophoran slime consists largely of water, around 84% (Röper 1977) in Peripatopsis moseleyi (Wood-Mason 1879) and up to 90% (Benkendorff et al. 1999) in Euperipatoides kanangrensis. There are also differences between the two species regarding the reported protein and sugar contents. However, it remains to be clarified whether these differences are species-specific, influenced by the prey items they consume or due to more sensitive analysis tools that were used in the study by Benkendorff et al. (1999). In P. moseleyi, a protein content of 16% (amino acids such as Gly = 41%, Glx = 11%, Lys = 1.3%) but no sugar was reported (Röper 1977). The slime of E. kanangrensis in contrast consists of 55% protein (amino acids such as Gly =27%, Glx = 5%, Pro =13%, Lys = 7%), lipids, nonylphenol and 1.3% glycan residues such as N-acetylgalactosamine (GalNAc), mannose and galactose (Benkendorff et al. 1999). In general, the onychophoran slime comprises proteins in a wide molecular mass range from 8 to 1300 kDa (Mora et al. 1996; Haritos et al. 2010; Baer et al. 2014). Benkendorff et al. (1999) classified the glue proteins into at least “two groups: high molecular weight (>600 kDa) monomers and low molecular weight dimers (25–28 kDa)” after gel electrophoretic separation. More detailed analyses of some major proteins (Er_P1 = 250, 350 kDa; Er_P2a and Er_P2b = 80 kDa) bear a high amount (>20%) of the amino acid proline. Both proteins are supposed to be responsible for the gelation of slime through cross-linking mechanisms involving covalent, ionic and/or hydrophobic bonds (Haritos et al. 2010). The low molecular weight proteins present in the onychophoran slime instead show a high homology to carbohydrate-binding proteins and protease inhibitors and are assumed to serve as antimicrobial agents within the slime glands (Haritos et al. 2010).

As stated above, the glandular systems of the two major onychophoran subgroups, the Peripatidae and Peripatopsidae, differ with respect to their structure. Also, on the proteomic level a clear species-related pattern can be observed, suitable
for species identification and phylogenetic evaluation (Mora et al. 1996; Baer et al. 2014). On the one hand, a high interspecific similarity has been detected for the high molecular weight proteins (350 kDa and ~ 780 kDa) maybe responsible for the formation and gelation of slime. On the other hand, in particular the low molecular weight (8–25 kDa) that have been proposed to serve as antimicrobial agents, allow a clear distinction at the species level (Baer et al. 2014). Slight differences in the gel electrophoretic protein pattern between specimens of the same species but from two neighbouring localities, albeit a similar habitat, could not yet be explained as an environmental adaptation (Baer et al. 2014).

Beyond species profiling, the major slime protein (Er_P1) of Euperipatoides rowelli (Reid 1996) also indicates a similarity to an amphibian glue protein (Nb-1R), namely that of the frog Notaden bennetti (Graham et al. 2013). According to the authors, Er_P1 and Nb-1R proteins are very large (260–500 kDa), rich in glycine (16–17 mol%), proline (7–12 mol%) and 4-hydroxyproline (4 mol%) and, beyond this, they have “oddly ‘turbulent’ bands” in gel electrophoretic separations (Graham et al. 2013). This proteinic congruence is interesting, in particular because the two glue-producing animals are not closely related to each other (a vertebrate versus a panarthropod/ecdyszoan). Also, in view of their glue gland locality and morphology as well as the usage of the adhesive, the animals clearly differ: the frog produces the defensive glue in its skin glands (Tyler 2010), as do the salamanders, while the onychophorans use their secretion for offence/defence and produce it in an internal gland system. Further studies would be necessary to confirm the hypothesis of a convergent evolution of adhesive components and common mechanisms of curing and adhesion and to compare this with the data given for other terrestrial, but also marine, glue-producing animals.

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References


Examples of Bioadhesives for Defence and Predation


