The jumping spider mouth (Araneae: Salticidae)[1]

David Edwin Hill [2]

Abstract

Behind the chelicerae, and between the *endites* (coxae of the pedipalps) of a salticid, are two laterally articulated, median appendages surrounding a flattened, procurved *mouth cavity*: the anterior *rostrum* and the posterior *labium*. Both appear to develop initially as 'lips' around the embryonic mouth (segment 1), before the chelicerae (segment 2) and pedipalps (segment 3) migrate to the front. The distal, anterior surface of the rostrum bears a rostral organ, where the rostral gland is discharged. The floor of the mouth (*labial plate*) is relatively smooth but bears many fine, transverse bands of projecting microfilaments, corresponding to the microfilament bands of the roof of the mouth (*rostral plate*). The rostral plate is a sponge-like microfilter, bearing an array of transverse or lateral channels under microfilament bands, leading to a median *rostral duct*, which in turn conducts liquid to and from the anterior digestive tract, comprised (from front to rear) of a flexible, muscular *pharynx* (connecting the rostral duct to the esophagus), a rigid *esophagus* passing through the central nervous system, and a muscular *stomach* (sucking stomach). When the spider molts, the entire cuticular lining of this tract, from the plates of the mouth to the stomach, is shed in one piece. Feeding by a salticid is a cyclic behavior including alternation of rapid disgorging (regurgitation) from the digestive tract, powered by contraction of opisthosomal muscles, and much slower engorging (ingestion), associated with negative pressure created by powerful dilators of the sucking stomach. Disgorging of digestive juice (kime) may be expedited as microfilament bands are pushed away from the rostral plate during each regurgitation phase, whereas engorging may be constrained as liquid is forced to pass through these microfilament bands before it can reach the transverse channels leading to a postero-median entry slot into the rostral duct. Thus the rostral plate appears to be a sophisticated *directional microfilter*. A broad longitudinal muscle inserted distally in the labium has been associated with dilation of the pharynx, but may also support posterior rotation of the labium and mouth floor during feeding. The rostrum is also associated with muscles that should allow it to change shape in association with feeding activity. A hypothesis for the coordinated dilation of the pharynx and sucking stomach of a feeding spider is presented, based on behavioral and anatomic observations. Studies that can measure movement of the rostrum, labium, pharynx and sucking stomach by the feeding spider are needed.

Introduction

English language descriptions related to the arrangement of spider mouthparts and related feeding behavior are often incomplete or inaccurate, and related nomenclature is inconsistent. This inconsistency is greatest when it comes to the *rostrum*, which bears the roof of the mouth (*rostral plate*) on its posterior surface. Most often (e. g., Bristowe 1971, Kaston 1978, Gertsch 1979, Barnes 1980, Preston-Mafham and Preston-Mafham 1984, 1996, Dalton 2008), the rostrum is neither named nor diagrammed in a tally of spider mouthparts. In other accounts (Levi and Levi 1968, Kosloff 1990, Ubick et al. 2005), it receives minor treatment as a *labrum* or *upper lip*. Main (1972) briefly described an *oral cone formed by the labrum and lower lip*. Liu et al. (2009) referred to the rostrum as the *hypostome*.

Although the rostrum is well-known in other arachnids (*e.g.,* the Solifugae; Pocock 1909, Punzo 1998), it is difficult to observe in spiders unless they are dissected. Thus the image presented in Figure 1 is quite remarkable.

Figure 1. Face view of an adult male *Mopsus mormon* (Karsch 1878) from Cairns, Queensland, Australia. Note the rostrum in its median ventral position, visible to the rear of the chelicerae, between the endites. The coloration of this spider, diffuse illumination, and its position, with chelicerae and endites separated, all made this image possible. Photograph Copyright © Vesselin Petkov, used with permission.

There is a great deal to be learned about the most basic feeding processes of spiders, and here again published accounts are often less than satisfactory. Bristowe (1971) diagrammed taste glands associated with much of the *gullet* (here termed the *mouth*), and the presence of *tiny teeth* (the serrula) of the maxillae (the *endites*) sometimes *used in mashing up the food*. Gertsch (1979) also described this use of *the sharp edges of the endites*, also claiming that prey is *bathed with quantities of digestive fluid from the maxillary glands*. Kozloff (1990) reported that *glands in the labrum* (rostrum) *and coxae of the pedipalps* (endites) *secrete saliva*, but he also mentioned the discharge of midgut fluid bearing digestive enzymes. Foelix (2011; also see Foelix and Erb 2011) wrote that the serrula of the endites is *used as a saw for cutting into prey*, but questioned Millot's report (Millot 1936) that a taste sense is associated with the lateral walls of the *pharynx* (the mouth), since this conjecture was based solely on histological evidence. Foelix also cited Nawabi's (1974) pertinent finding that secretory cells of the intestinal epithelium immediately began to release enzymatic granules into the intestinal lumen after prey was captured.

Based on the spacing of teeth and position of the serrula, it may play a role in the collection of silk by a spider climbing up its dragline. I agree with Foelix that the presence of chemosensory setae (spondylae) provides a worthy alternative explanation for the presence of a taste sense in spiders, and there is also ample evidence that digestive liquid (kime) is moved forward out of the opisthosoma during the disgorging cycle of a feeding spider, to support the injection of this enzyme-rich liquid into the prey or feeding mass. The same liquid, enriched with the products of digestion, is moved back toward the opisthosoma during each of a series of engorging cycles.

There are two good reasons to review Comstock's descriptions (1913, pages 102, 104). First, his summary of spider mouthparts still stands as one of the most complete *English* accounts. Second, some of the points that he makes with respect to the homology of respective body segments with those of insects can now be addressed with more certainty:

> THE ROSTRUM.— The *rostrum* or upper lip is a single, median, appendage-like part of the head, which resembles in form and position the labrum of an insect; and it is quite probable that the two are homologous. The rostrum is situated below or behind the chelicerae and between the second pair of appendages, the pedipalps.

> By removing the chelicerae, the rostrum can be seen lying between and upon the endites of the pedipalps. On the dorsal surface of the rostrum there is a longitudinal, median keel, which is clothed with a band of hairs.

> THE EPIPHARYNX.— On the ventral surface of the rostrum there is a plate which may be termed by analogy the *epipharynx*. This plate is strongly chitinized, and is marked by many transverse striae, which lead to a central longitudinal slit, opening into a longitudinal tube within the rostrum.

> As the tube in the rostrum extends back to the beginning of the oesophagus, the function of these striae in the epipharynx is, evidently, to collect the fluid pressed from the spider's victim and to conduct this fluid to the tube, from which it can flow to the oesophagus.

> THE LABIUM (la'bi-um).— The ventral wall of the head is formed of a single sclerite, which is usually more or less movable, and which on account of its position has been termed the lower lip or *labium*. Like the rostrum, the labium is situated between the second pair of appendages, the pedipalps, the rostrum occupying a more dorsal position, and the labium, a more ventral one.

> The labium of a spider is not homologous with the labium of an insect, which is formed of a pair of united appendages.

> THE MOUTH.— The mouth cavity is situated between the base of the pedipalps, which form the sides of this cavity. The roof of the mouth is formed by the epipharynx; and the floor by a sclerite, the tip of which lies upon the labium.

> The mouth is fitted for the reception of only liquid food. The spider cuts and presses its victim; and when it is sucked dry, the hard parts are thrown away.

Less accessible to the English reader, but much more useful, is the more extensive collection of early papers dealing with the anatomy of spider mouthparts in French and German (*e.g.,* Wasmann 1846, Kessler 1849, Plateau 1877, Schimkewitsch 1884, Bertkau 1884, Zimmerman 1934, Gerhardt and Kaestner 1938). Foelix (2011) provides a valuable introduction to some of this work.

Schimkewitsch (1884) divided the anterior digestive tract of spiders into three parts: the *pharynx*, the *esophagus*, and the *sucking stomach*. Most authors have followed this approach, portraying the *rostral plate* (Foelix 2011) as either an *epipharynx* (Comstock 1913), or as one of the components of the pharynx. This structure that has been called the pharynx includes not only the two plates that surround the mouth cavity, but also also the curved, connecting tube that links the duct in the rostral plate to the esophagus. In this account, I will refer to the lower portion of the pharynx as the *mouth* (by analogy to the vertebrate

mouth) and will order structures associated with this mouth from front to back (anterior to posterior), using descriptive terminology close to that used by Comstock as follows:

ROSTRUM.— (*labrum, upper lip, hypostome*) Structure that includes the rostral plate to the rear, and all associated structures to the front of this, between the endites and behind the chelicerae, anterior to the mouth cavity. This includes contained rostral muscles (see Schimkewitsch 1884), and the *rostral organ*. The rostrum is also associated with an unpaired *rostral ganglion* situated above the anterior esophagus, and it is innervated by the anteriorly directed *rostral nerve* (Hill 2022).

ROSTRAL PLATE.— (*epipharynx, roof of the mouth, palate*) The spoon-shaped (truncated at top) chitinous plate at the rear of the rostrum, laterally broad, tapering and procurved distally, and containing the median rostral duct, under a postero-median *rostral keel*. This is joined flexibly to the labial plate dorsally, and along the sides, except for the distal part associated with the mouth opening.

ROSTRAL DUCT.— The distally tapering median tube that runs along the length of the rostral plate, joined at the top to the pharynx. A median slot in this tube opens into the mouth.

MOUTH.— (*lower pharynx, oral pharynx*) Flattened (front to back) chamber containing the mouth cavity, including the chitinous rostral and labial plates, and the flexible, lateral connections between the two plates.

MOUTH OPENING.— (*pharygeal orifice, orifice*) The small, laterally wide slit between the distal rostral plate and distal labial plate through which liquid passes into and out of the mouth; part of the mouth.

MOUTH CAVITY.— (*mouth cavity, oral cavity, pharyngeal lumen*) The space or lumen contained within the mouth, bounded anteriorly by the rostral plate, and posteriorly by the labial plate; part of the mouth.

LABIAL PLATE.— (*floor of the mouth*). Chitinous anterior wall of the labium, spoon-shaped (truncated at top), laterally broad but tapering and procurved distally, flexibly articulated to the rostral plate at its widest place (dorsally), and laterally except for the distal part associated with the mouth opening. This is relatively thin when compared to the rostral plate.

LABIUM.— (*lower lip*) Structure that includes the labial plate to the front, the labial sternite to the rear, and all associated tissue including labial muscles in-between. The labium is posterior to the mouth cavity.

PHARYNX.— (*upper pharynx, sucking pharynx*) Curved section of the digestive tube, or tract, that connects the rostral duct at the top of the mouth to the thick chitinous tube of the esophagus. Attached muscles can expand the lumen of the pharynx, but no constrictor muscles are known (Schimkewitsch 1884).

ESOPHAGUS.— Relatively thick and rigid, chitinous tube that connects the pharynx (anterior) to the sucking stomach (posterior), and passes through the central nervous system.

STOMACH.— (*sucking stomach*) Structure joined anteriorly to the esophagus, and posteriorly to the midgut, situated above the endosternite (internal skeletal component of the prosoma), and lined with cuticle. The plates of the stomach are pulled apart to expand the stomach cavity by the insertion of powerful muscles that originate with either the dorsal wall of the prosoma, or with the endosternite.

With respect to the homologies advanced by Comstock, recent study of the pattern of Hox genes associated with the body segments of insects and spiders now gives us a slightly different story (Damen *et al.* 1998, Hass *et al.* 2001, Angelini *et al.* 2005, Schwager 2008). First, the insect labrum is now associated with the insect intercalary segment, which would make it homologous to the segment containing the pedipalps (*Pp*, segment 3) of a spider, not with the rostrum of a spider, which is pre-oral and originates from cells associated with the first segment (*Oc*, ocular or cephalic lobe), in front of the chelicerae (*Ch*, segment 2) and the pedipalps (Figure 2). Comstock was correct with respect to the lack of homology of the labium of insects with that of spiders. The insect labium originates with a pair of appendages that are actually homologous with the second pair of legs of a spider (*L2*, segment 6).
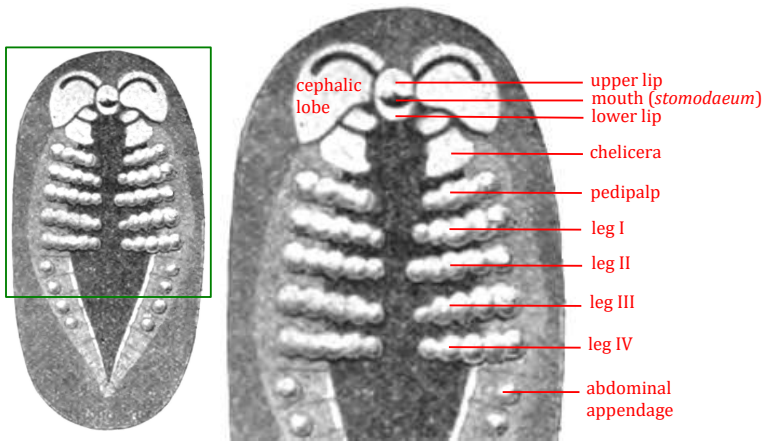
cephalic lobe

upper lip
mouth (*stomodaeum*)
lower lip

chelicera

pedipalp

leg I

leg II

leg III

leg IV

abdominal appendage

Figure 2. Schematic view of 'unrolled' embryo of *Agelena labyrinthica* (Clerck 1757), based on Korschelt *et al.* 1899 (fig. 28, p. 52; also see Liu *et al.* 2009). In real life, this embryo would be wrapped around a ball of yolk. As the embryo develops, the right and left appendages that you see here continue to separate, and the dark area at center in this diagram becomes the dorsum of the spider. At the same time, the chelicerae and pedipalps move forward, relative to the mouth. The *upper lip* here corresponds to the rostrum. It appears that the *lower lip*, which also represents a thicker band of cells, may become the labium, but this is not known for certain. Some authors (*e.g.*, Kozloff 1990) view the labium as the *sternum* (or sternite) of the pedipalpal segment.

This paper will be concerned primarily with the structure and function of the mouth (including the rostral and labial plates). For an overview of the structure and function of chelicerae and pedipalps (including endites) of salticids and other spiders, see Hill (1977a), Foelix (2011), and Foelix and Erb (2011).

Photographic study of salticid mouthparts

Observation of living spiders. From below, only the posterior wall of the labium, the endites, and the chelicerae are visible (Figure 3).
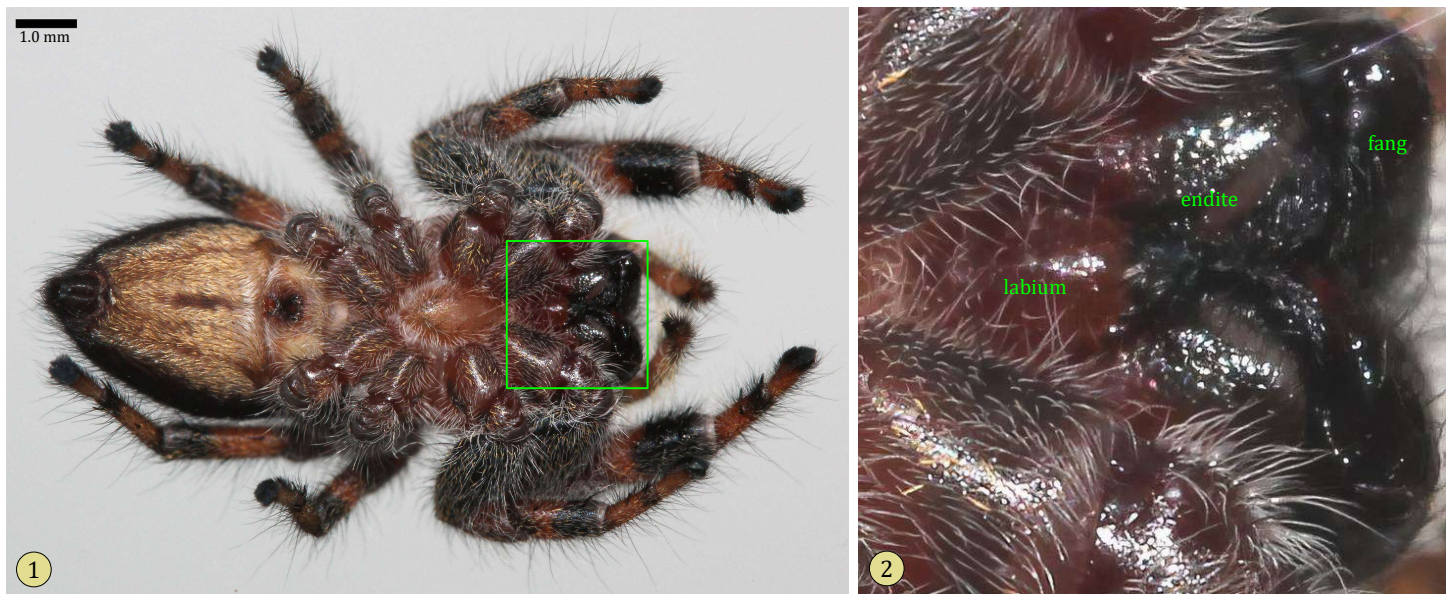

Figure 3. Adult female *Phidippus cardinalis* (Hentz 1845), from Greenville County, South Carolina. **1,** View of entire spider. **2,** Detail of inset in (1), showing visible mouth parts. The anterior labial plate (floor of the mouth), the mouth, and the rostrum are concealed, and dense, black medial brushes of the endites dominate the area in front of the mouth.

Observation of exuviae. As shown here (Figure 4), the cuticular lining of the mouth, pharynx, esophagus, and stomach are shed as a single unit, and they can be teased apart to reveal more detail. The *rostral organ* (Figure 4, 4) includes an external pocket associated with the antero-distal rostrum, linked to an internal *rostral gland* (Lopez 1984, Juberthie and Lopez 1993). The function of this organ and its secretion is not known. Foelix and Erb (2011) also provide some excellent views of exuvial mouthparts,

including an SEM view of the mouth-to-stomach assembly. One must always remember that exuviae consist only of dried cuticle that has been shed, and not the structures that these may represent. In some cases this can be misleading. For example, the pharynx (connecting esophagus to the rostral duct) is thin-walled, flexible, and muscular, and the exuvial remains of this structure are minimal. One can tease apart the rostral plate to view not only the posterior side (roof of mouth) of this plate, but also the anterior. Unlike the posterior side, which borders the mouth cavity, the anterior side of this plate is connected to soft tissue in the living animal (Figure 5.1). Recognizable in the exuvia, the anterior face of the rostrum is relatively thin-walled and its appearance in the living animal can be quite different. Although it is procurved, much of the detail of the rear of the rostral plate can be seen if flattened under a microscope cover glass (Figure 5.2).
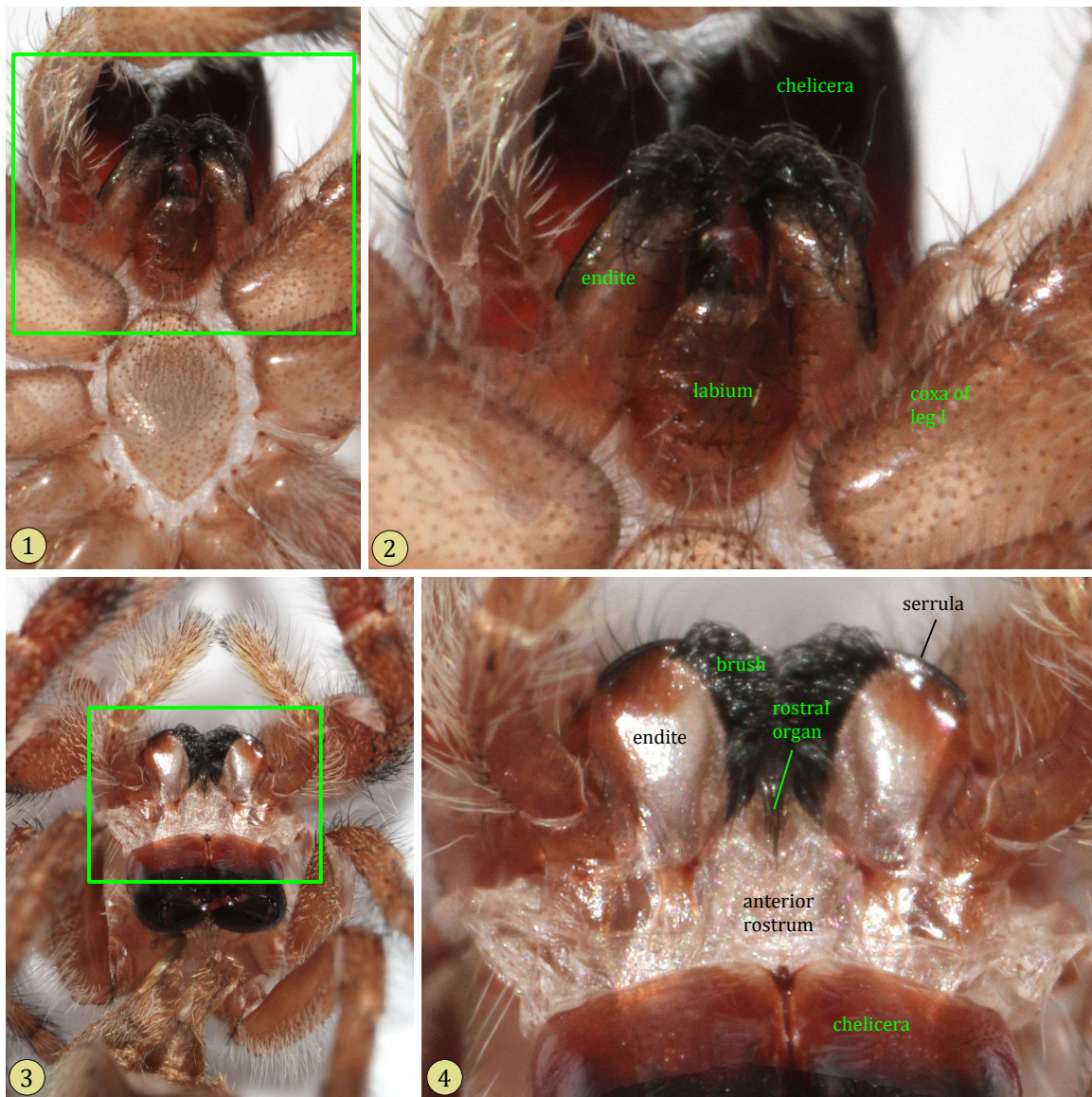

Figure 4 (continued on next page). Images of exuviae from *Phidippus princeps* Peckham and Peckham 1883. **1—2,** View from below. **3—4,** View from above, with chelicerae flipped to the rear to reveal the rostrum at the center.
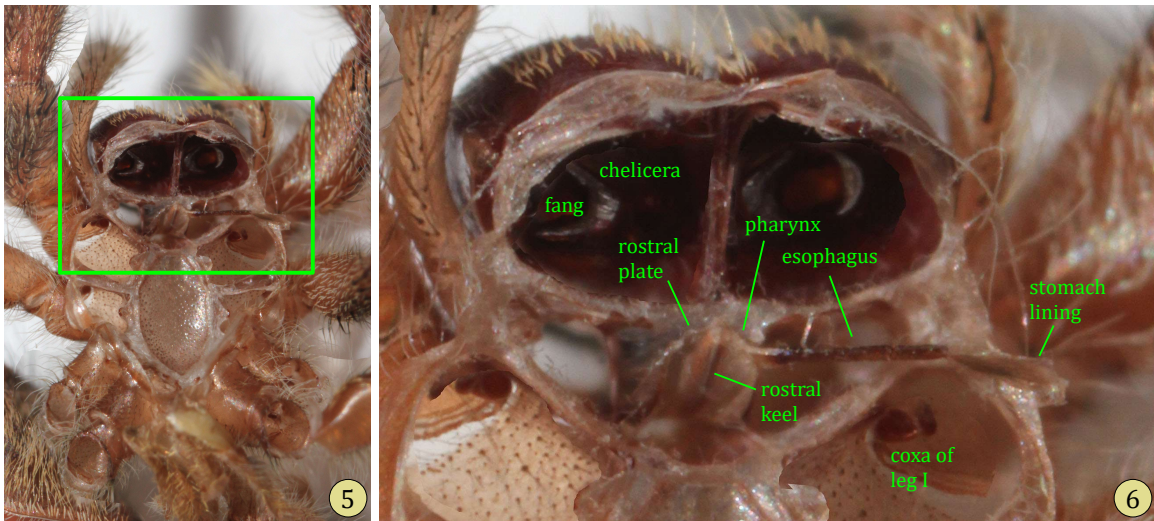
Figure 4 (continued from previous page). Images of exuviae from *Phidippus princeps* Peckham and Peckham 1883. **5—6,** View from above showing connected tube assembly from the mouth (rostrum) to the stomach.
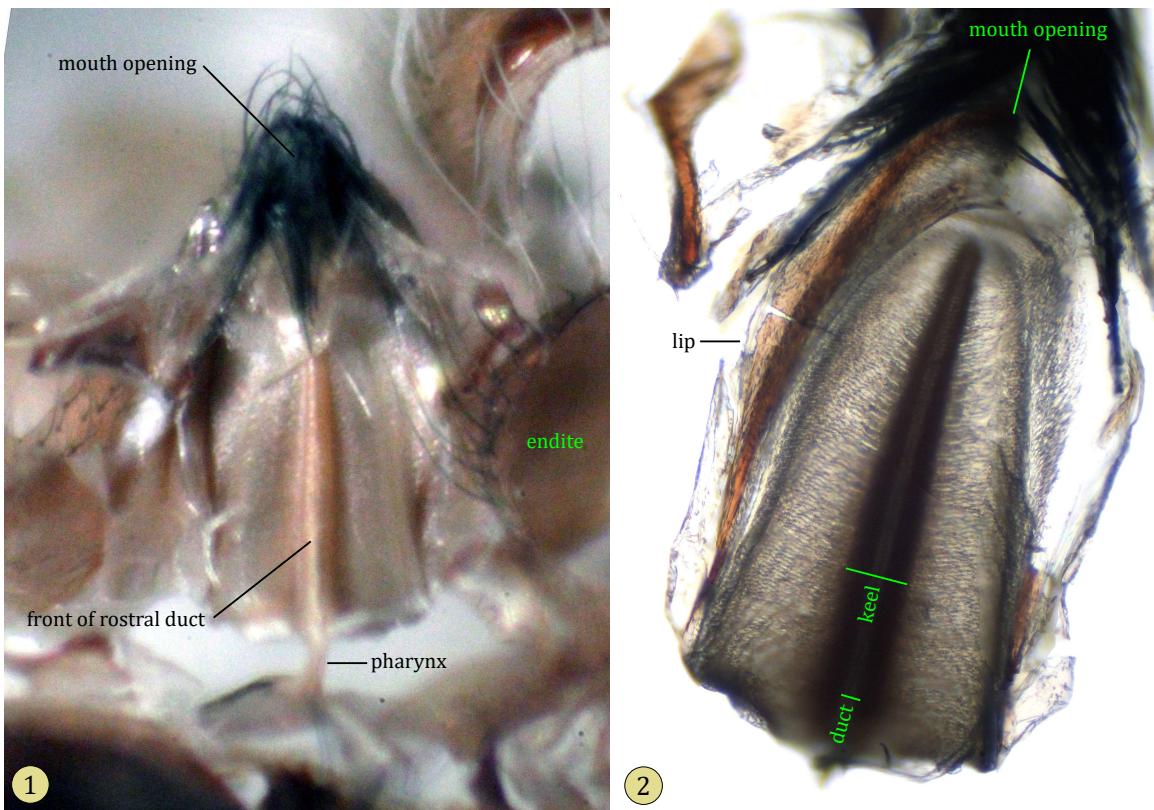

Figure 5. Rostral plates from exuviae of *Phidippus princeps*. **1,** Antero-dorsal view of dissected rostral plate, as seen in reflected light. The tapering vertical tube, at center, contains the rostral duct. This plate tapers distally, and is procurved (bends anteriorly, toward the top of this image). At the bottom you can make out its connection with the pharynx, which appears as a thinner tube. In an intact animal, this face of the rostrum is connected to soft tissue. **2,** Posterior (mouth) view of the dissected rostral plate as viewed with transmitted light. Many fine, transverse channels radiate in either direction from the distally tapering rostral keel (center), which contains the rostral duct. It is difficult to see the 3-D effect in this composite image, but distally the *lip* or margin of the rostrum is thicker, and there are many dark setae surrounding the mouth opening.

Observation of histological sections. I prepared a series of sections of jumping spiders some years ago as part of a project on the structure of the central nervous system of *Phidippus*, and techniques related to the preparation and staining of these sections can be found in a related paper (Hill 2006). There are several limitations to this approach. First, a series of sections must be examined to reconstruct a 3-D structure. Second, techniques of fixation, clearing, embedding, and sectioning have a tendency to pull epithelia apart from associated cuticle, and to otherwise shrink soft tissue. Nonetheless, the technique is key to histological examination of the relationship of individual cells to tissues and structures. Several sections that depict internal structures associated with the salticid mouth are presented here (Figure 6). The labium is filled with longitudinal muscle that appears to originate below the pharynx and insert on the distal wall of the labium. These have been associated with depression of the pharynx (*ventral dilator of the pharynx* according to Hill 2006, 2022; Foelix 2011, p. 38, Figure 2.23). Schimkewitsch (1884) described the attachments of these muscles without reference to their function. Based on their position, contraction of these muscles may be associated with posterior movement of the labium and the associated labial plate (floor of the mouth), or some combination of dilation of the pharynx and movement of the labium. Schimkewitsch also described the two horizontal muscles that connect the right and left sides of the rostrum, both shown in Figure 6 (3—4). These appear to play a role in expanding the mouth cavity, suggesting a more active role of the rostrum during the feeding process.
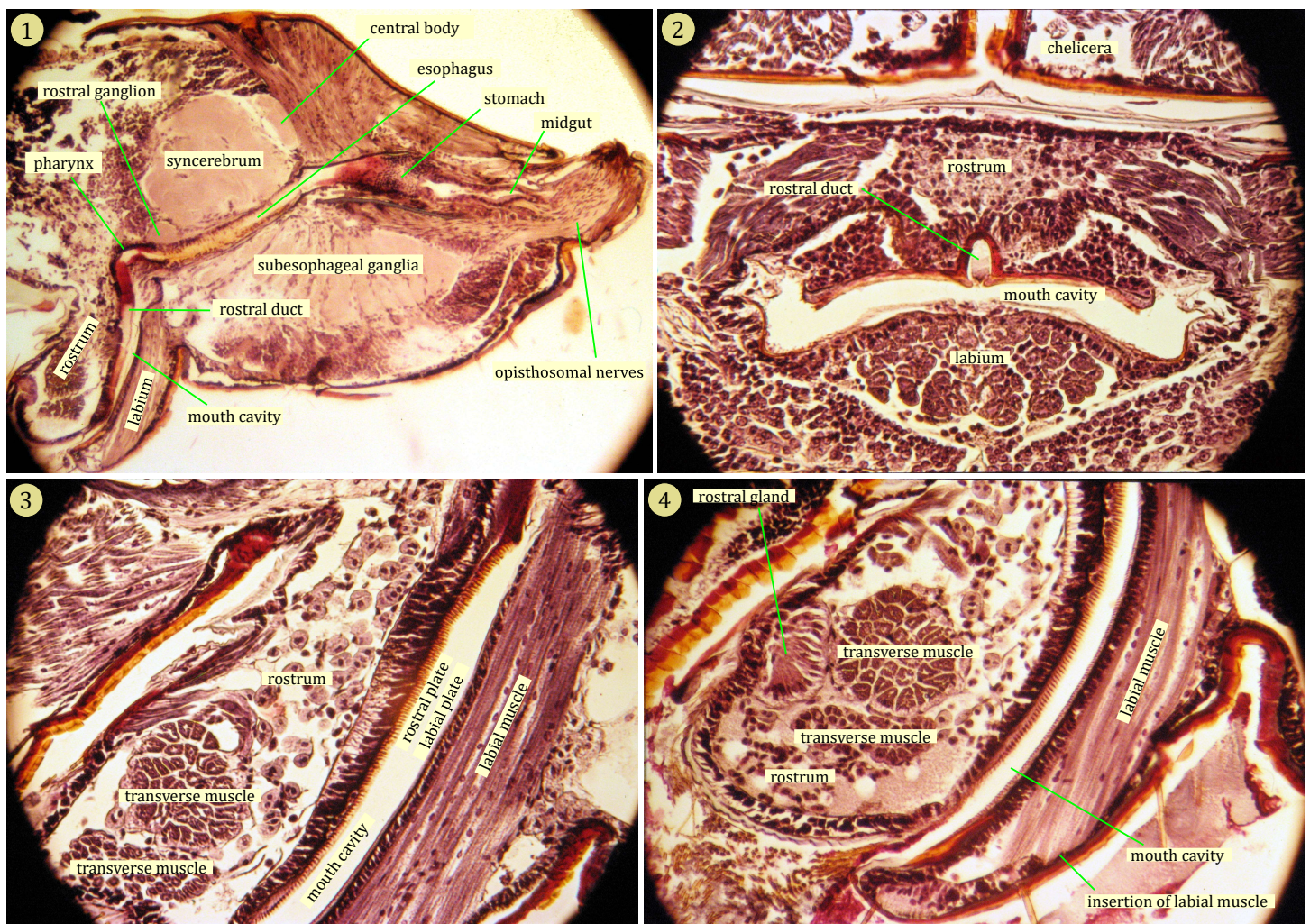

Figure 6. Stained near-sagittal (1, 3—4) and horizontal (2) sections of the prosoma of fifth instar *Phidippus clarus* Keyserling 1885. **1,** Sagittal section showing the procurved mouth extending down and forward (left) between the rostrum and labium. **2,** Horizontal section (anterior at top) below the level of the pharynx, showing (cross section, center) the thick-walled rostral duct that runs along the length of the rostral plate, with its median opening into the mouth cavity. At this level, the labium is

filled with dorso-ventral muscles (shown here in cross section) that insert on the wall of the lower labium.   **3—4,** Detail of near-sagittal sections through the mouth corresponding to the orientation of (1). Note the cross section of the two transverse muscles associated with the distal rostrum, and (4) the long secretory epithelial cells of the rostral gland. The transverse muscles were described by Schimkewitsch (1884), and must allow the spider to compress the rostrum laterally. Some of the detail of the regular channels associated with the rostral plate can also be seen in the orange cuticle that lines the mouth. Behind this (to the left), the thickness of the associated tissue is related to the fact that these sections cut through the length of the rostral keel. The labium is filled with dorso-ventral muscle, the distal insertion of which can be seen in (4). These muscles run dorsally to attach below the pharynx. Sections shown here and in Figure 7 were stained with a modified version of the *Masson Trichrome* stain; see Hill (2006) for details.

A transverse section of the stomach is compared with a transverse section of the pharynx in Figure 7. Although it is clear that the stomach is much more important as a generator of suction due to its larger size and the greater extent of associated dilator muscles, the role of the pharynx must also be significant. The coordination and respective roles of these two structures during the feeding process is unknown, however. One reasonable hypothesis is that the pharynx acts as more of a flexible valve or regulator for the regurgitation (disgorging) process, a process powered by an array of opisthosomal muscles, wheras the powerful suction of the stomach would be needed to pull fluid back into the body in opposition to internal fluid pressure, and also through the filter resistance of the rostral plate. These considerations will be addressed in more detail later in this paper.
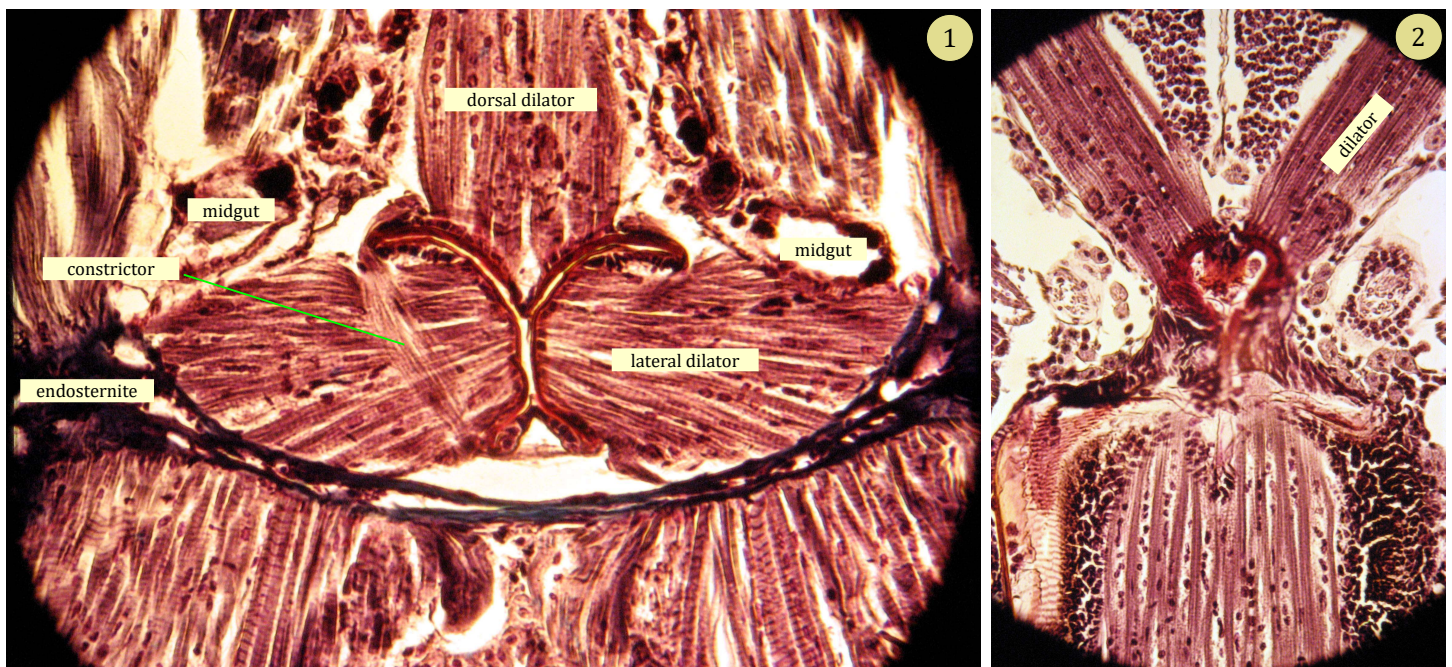

Figure 7. Stained transverse sections of the prosoma of fifth instar *Phidippus clarus*, at the level of the *stomach* (1, center) and the *pharynx* (2). **1,** The stomach (or *sucking stomach*), situated to the rear of the central nervous system (CNS), is expanded through the action of powerful dilators originating with the carapace dorsally, and with the endosternite (an internal skeletal element) as shown. **2,** At the anterior end of the rigid esophagus that passes through the CNS lies the pharynx, also connected to dilator muscles. Between the dilators, at top, can be seen darkly-stained unipolar neuron somata associated with the front of the CNS. Just how these two pump or valve systems are coordinated during feeding is not known (see Figure 15). The dorsal direction is at the top in both images.

Structure revealed by SEM and cryofracture technique. SEM images presented here were produced in the 1975—1976 time frame, in the SEM laboratory at the University of Iowa in Iowa City, following procedures described by Hill (1977b). The image presented in Figure 8.1 shows the general arrangement of mouth parts as viewed from below, in a second instar *Phidippus clarus*. The distally situated rostral organ (Figure 8.1) is associated with the rostral gland, and is bounded by a curiously thin anterior flap

(see also Juberthie & Lopez 1993). The function of this organ is not known, but its position near the distal mouth opening suggests that it produces some substance that facilitates the feeding process of the spider.
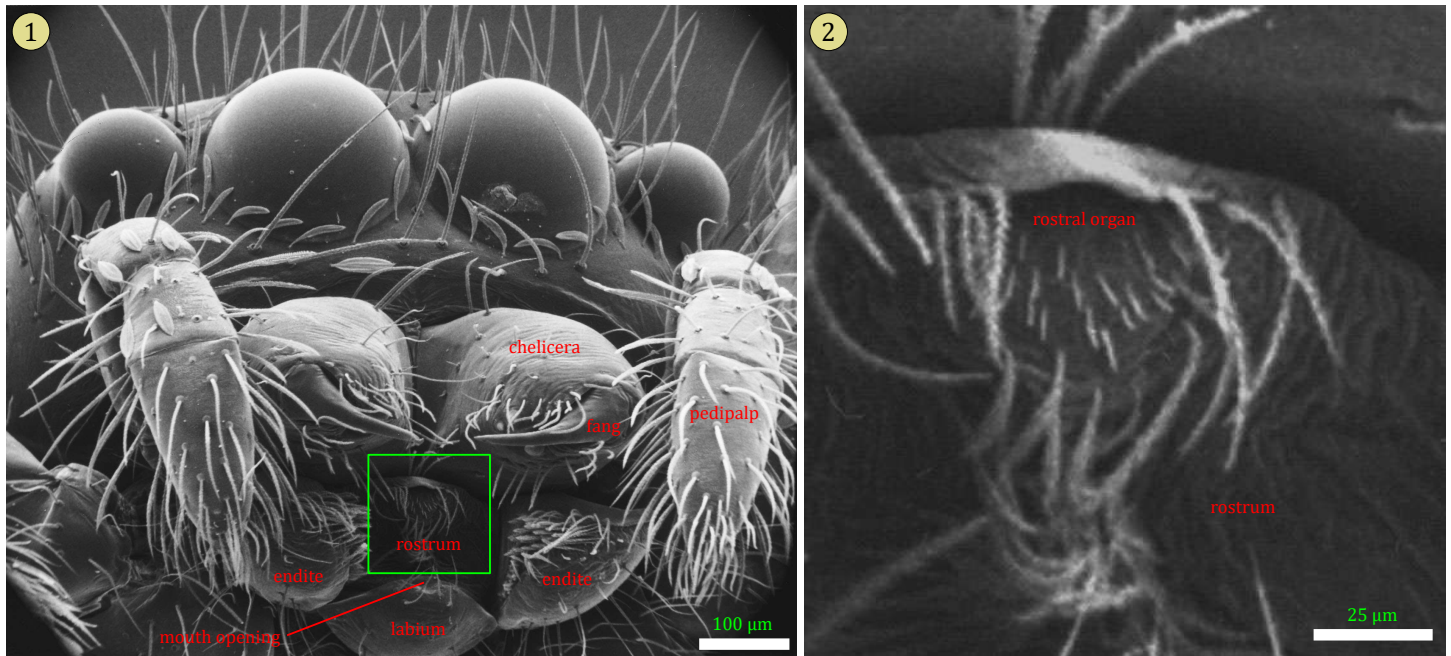

Figure 8. Mouth parts of second instar *Phidippus clarus* viewed from below. **1,** With few setae to obscure the view, the relationship of mouth parts to the mouth opening (mouth cavity bordered by rostrum and labium) can be seen clearly. **2,** Detail of inset from (1), showing the rostral organ with its thin anterior flap.

Some adult male *Phidippus audax* (Hentz 1845) were frozen in liquid nitrogen (LN_2) and cryofractured with a sharp razor, prior to dehydration and treatment for SEM viewing (as described in Hill 1977b). Cryofracture is a particularly valuable technique for the study of arthropod structure, as it tends to maintain the structural relationships of both hard and soft tissues, even at the level of individual cells. Near-sagittal fracture of the prosoma (Figure 9) revealed the detailed structure of the rostral plate.

Figure 9.3 is particularly revealing, as it shows the open channels underlying the lateral *microfilament bands* of the rostrum, as well as the lateral ridges that divide to support multiple bands. By overlapping, these fringes can effectively close off these channels, creating a microfilter barrier between the mouth cavity and the collecting channels. At the same time, when disgorged digestive fluid is pushed out of the rostral duct into the mouth, these fringes are arranged so that they would open up to expedite this flow. Thus, there is good reason to believe that the rostral plate is a *sieve plate*, effectively a *directional microfilter*, allowing the passage of liquid through its entire area into collecting channels.
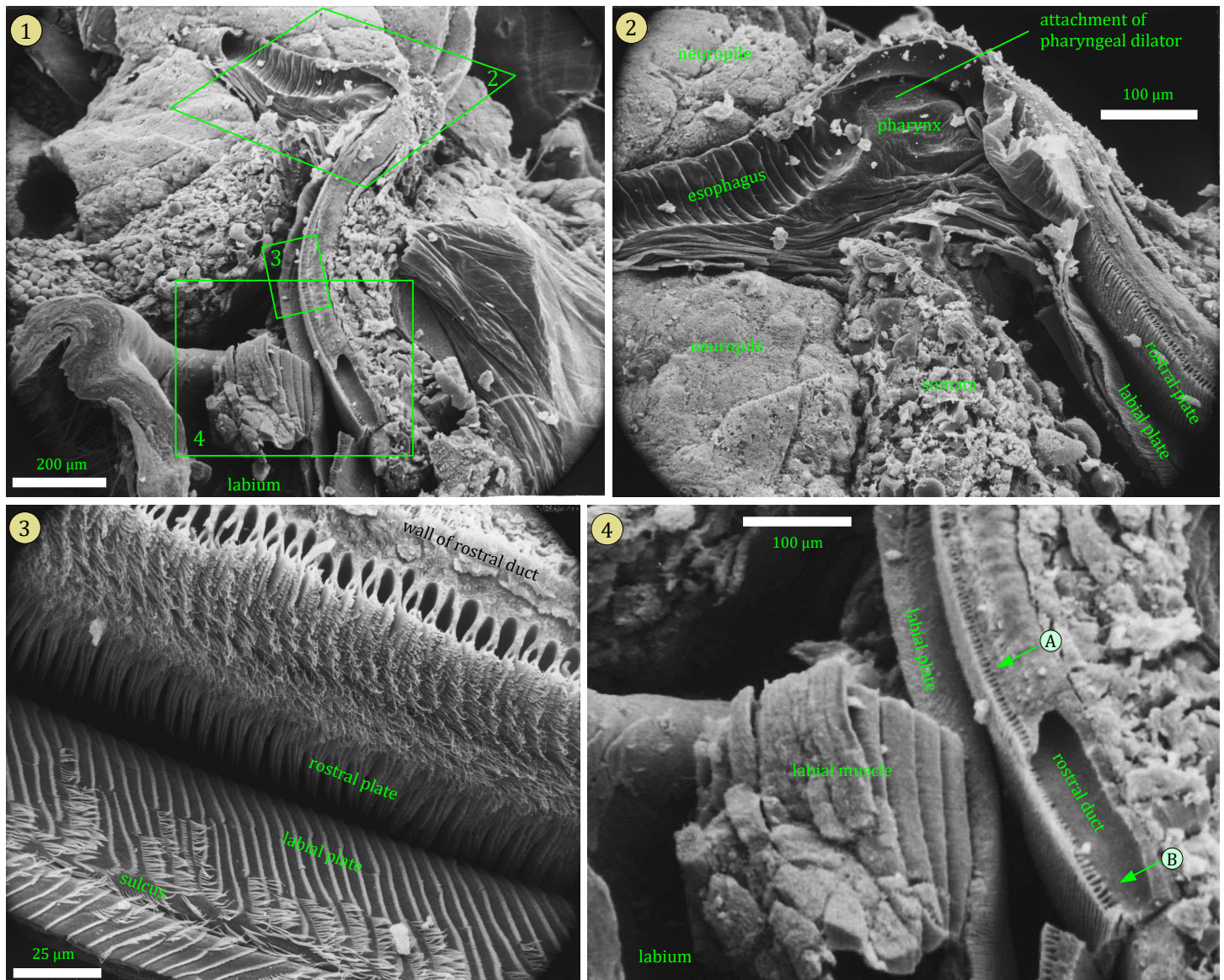
Figure 9. Sagittal cryofracture of the prosoma of an adult male *Phidippus audax* from the vicinity of Iowa City, Iowa. **1,** Overview, with relative positions of detailed views showin in insets (2—4). The dorsal direction is at the top, and the anterior is to the right. **2,** Detail of transition from mouth (space between rostral and labial plates) to pharyx, and then to the rigid esophagus passing through the CNS. **3,** Detail of mouth structure, showing relationship of the rostral and labial plates. Because this is a near-sagittal fracture, the median *sulcus* (or depression) of the labial plate can be seen at bottom, left, and the rostral plate is fractured (upper right) through the rostral keel. The spacing of microfilament rows on the labial plate agrees with the spacing of the more elaborate microfilament bands and underlying channels of the rostrum. Foelix (2011) referred to these microfilament bands as *cuticular platelets arranged like shingles*. This fracture reveals the branching of the lateral ridges, each of which supports multiple microfilament bands above an open channel. **4,** Detail near the end of the rostral duct (lower right). Note the separation of the duct from the lateral channels under the filamentous bands (A), and the limited connection of these channels along the midline of the rostral duct that is exposed at (B). This connection corresponds to the narrow postero-median opening of the rostral duct into the mouth cavity (Figure 6, 2), a feature that runs along the length of this duct, connecting that duct to the network of lateral channels.

In Figure 10, surface views of the rostral and labial plates, exposed in other cryofractured specimens, are shown. These illustrate the regular spacing of these features.
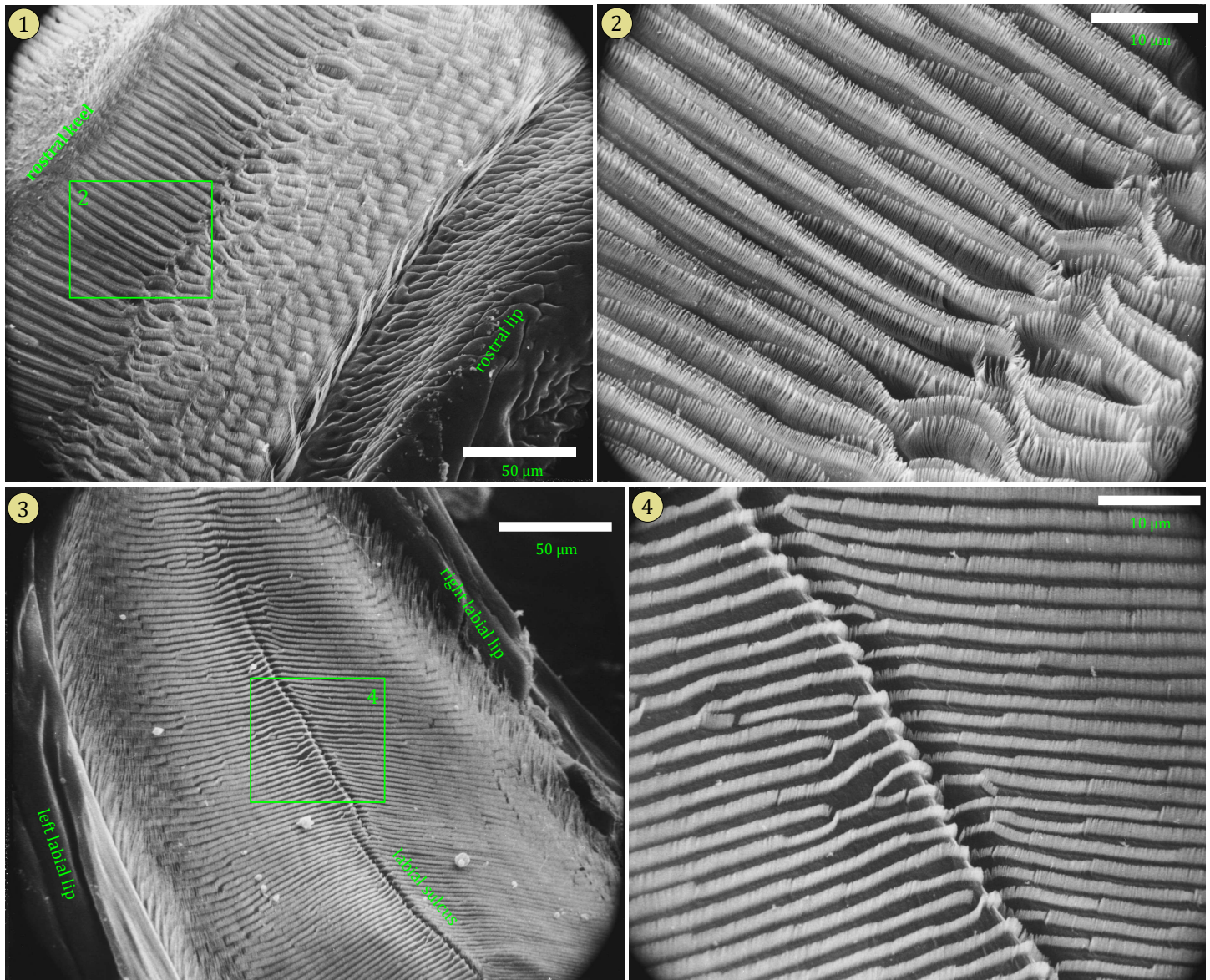
Figure 10. Views of rostral and labial plates from cryofractured adult male *Phidippus audax*. **1,** Lateral ridges and associated microfilament bands are more regular on the slope approaching the median rostral keel (upper left), where a denser array of overlapping microfilament bands covers the entry to the rostral duct along the length of the keel. **2,** Detail of (1). **3,** View of the labial plate or floor of the mouth, showing regular bands of cuticular filaments corresponding to the rostral bands. **4,** Detail of (3). Note the median sulcus or depression, opposing the rostral keel. Although the floor and roof of the mouth do not fit together tightly, the arrangement of microfilaments on the labial plate may facilitate the channeling of fluid in a lateral direction, into (or out of) the corresponding lateral channels of the rostrum.

Observation of feeding behavior

Salticid feeding behavior is a cyclic activity, involving alternation of disgorging (*egestion*) and engorging (ingestion) of fluid (Figures 11—13). At times, and particularly when feeding on soft-bodied prey, this also involves active maceration of prey with the chelicerae. Salticids disgorge (regurgitate or inject) digestive fluid into or onto their prey (or, in some cases, onto a plant exudate or other substance that they encounter). This is generally a rapid process, requiring only a few seconds to complete. If the prey is relatively large, this is associated with a noticeable reduction in the size of the opisthosoma, as digestive juice (kime) is forced forward as a result of the contraction of opisthosomal muscles. It is often possible to observe the inflation of prey as the spider injects fluid. Even though spiders are relatively soft-bodied, I

have often observed salticids such as *Thiodina sylvana* (Hentz 1846) using a leg as a 'straw' (Figure 14), and the alternating processes of disgorging and engorging are particularly easy to observe in these cases. Engorging is a much slower process, involving a visible vibration of the spider as it pumps. The degree to which prey is macerated by a salticid (between the fangs and teeth of the chelicerae) depends in part on whether the prey is 'hard-shelled' or 'soft-shelled' and in part on the size of the spider. Soft prey, such as a small spider, may be macerated and eaten completely, with no remains.
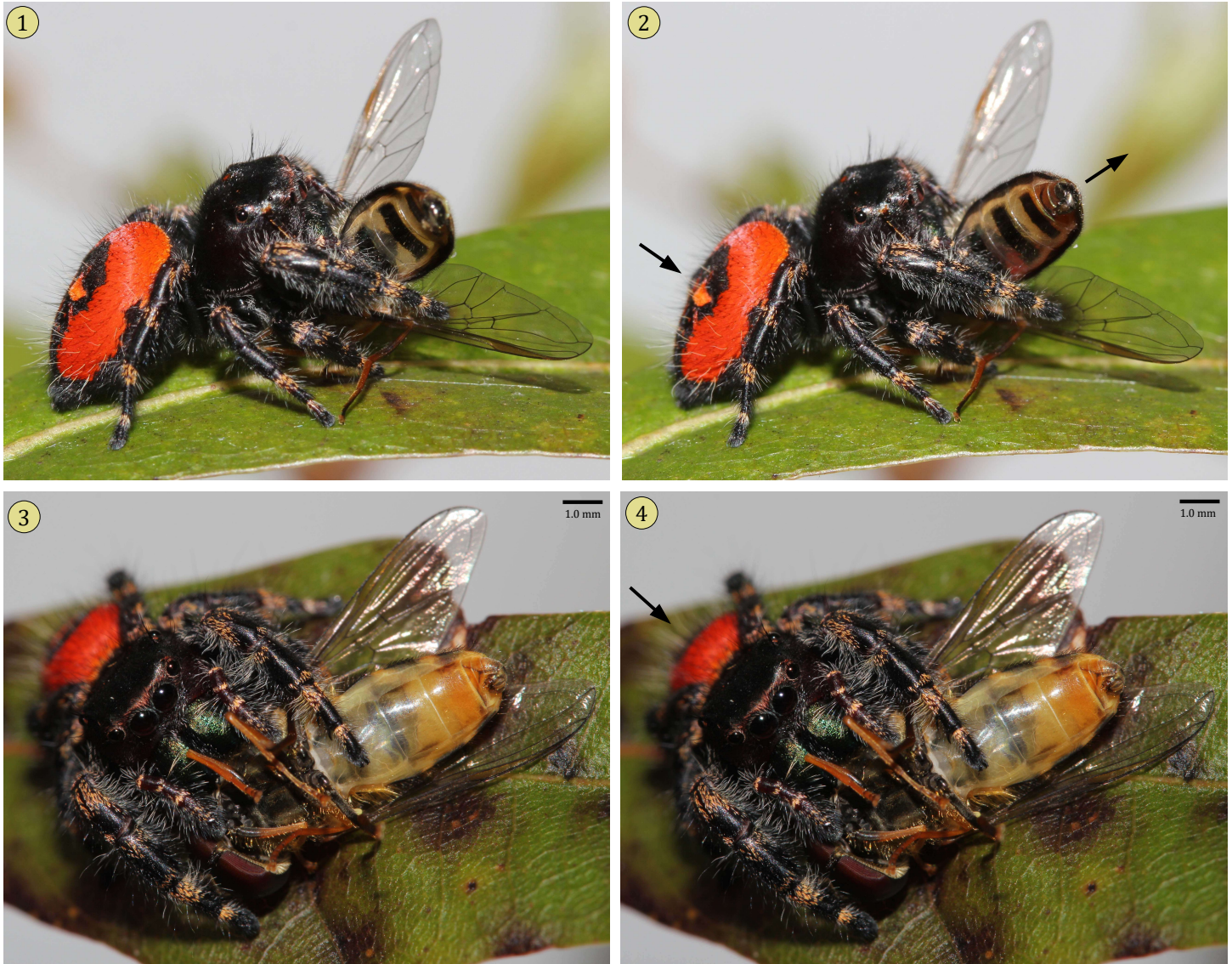

Figure 11. Images from two sequences showing an adult female *Phidippus pulcherrimus* Keyserling 1885, from Tavares, Florida, feeding on a large fly. **1—2,** Note (2) depression of the opisthosoma and inflation of the abdomen of the fly (arrows) as kime was disgorged (injected) by the spider. **3—4,** Depression of the opisthosoma (4, arrow) as disgorged kime was injected into the prey. Compared to engorging, which involved a series of cycles, disgorging was a relatively rapid process, accompanied by some cheliceral movement.
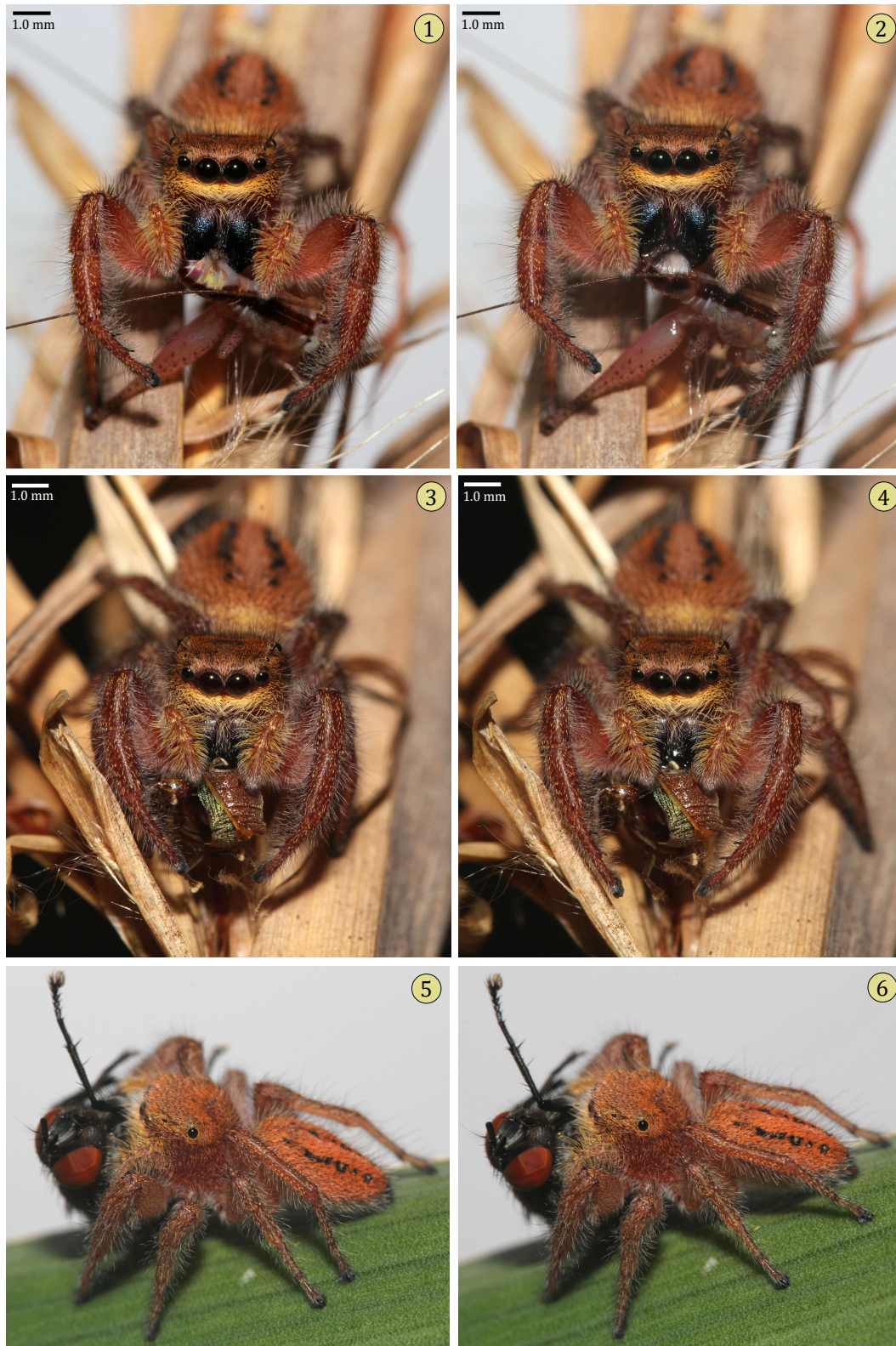
Figure 12. Three sequences (1—2, 3—4, 5—6) depicting a feeding adult female *Phidippus pius* Scheffer 1905, from Greenville County, South Carolina.　**1—2,** Engorging (1), then disgorging and macerating (2), while feeding on a soft-bodied field cricket (Tettigonidae). **3—4,** Engorging (3), then disgorging, while feeding on a hard-bodied weevil (Cuculionidae). **5—6,** Disgorging (5) and then engorging liquid out of a large brachyceran fly (6). Note the expansion of the opisthosoma in (6).

Figure 13. Feeding *Phidippus*. **1,** Adult male *P. audax* feeding on a captured heteropteran. Many heteroptera release a characteristic mix of chemicals including pungent aldehydes ('bug odor') when they are threatened (Aldrich 1988). This spider was holding a 'bug' in its chelicerae until these volatile chemicals dissipated. Since no digestive liquid had been disgorged at this point, the anterior rostrum (arrow) could be seen between the chelicerae. The anterior rostrum of *P. audax* has a dark mid-line and is otherwise uniform light grey in color, different from that of *Mopsus mormon* (Figure 1). **2,** Adult male *P. cardinalis* feeding on a small captured spider. A gelatinous, liquid mass obscured the rostrum as this *P. cardinalis* macerated its prey after disgorging kime. Both spiders were from southern Greenville County, South Carolina.
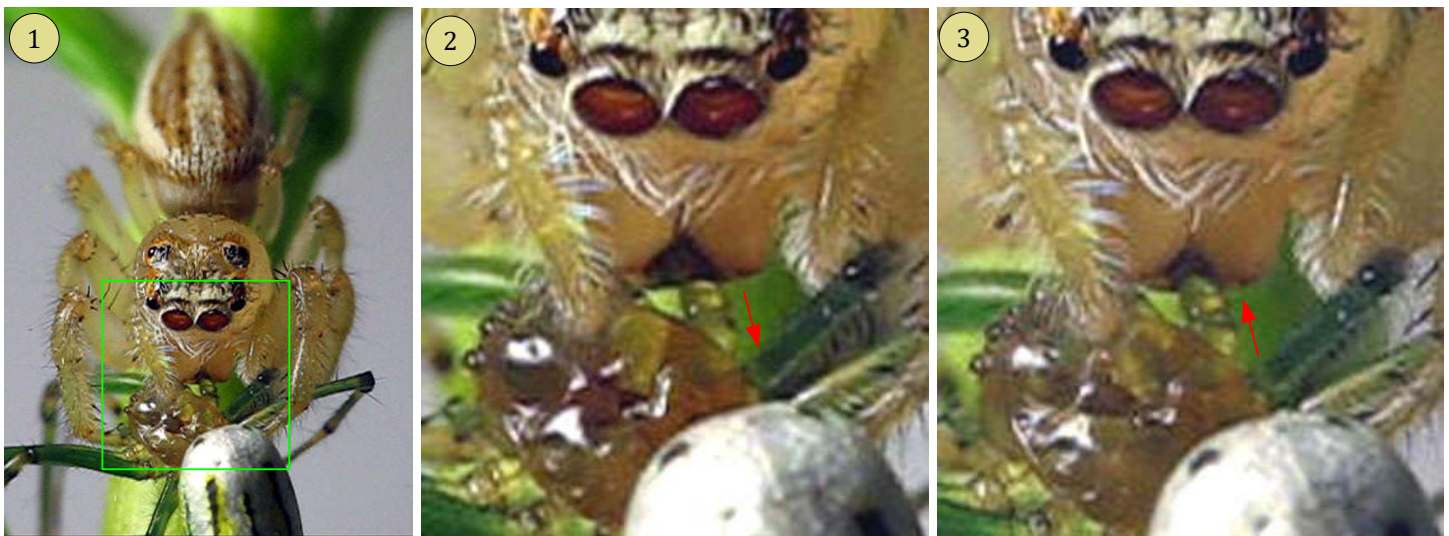

Figure 14. Frames from a video (Hill 2007d) showing an adult female *Thiodina sylvana* (Hentz 1846) feeding on the tetragnathid orb-weaver *Leucauge venusta* (Walckenaer 1841). **1,** After capturing this prey with a bite to the carapace, the *Thiodina* moved to a leg to feed as shown here. Later, the soft opisthosoma was also macerated with the chelicerae. **2,** Movement of digestive liquid into the prey through the leg, as well as the filling of the prosoma of the prey, could be observed directly. Note the accumulation of kime between the fangs (dark area) as it was disgorged. **3,** Movement of kime back into the spider as it engorged, and the emptying of the prosoma of this prey, could also be observed directly. Note the relative lack of kime between the fangs during ingestion.

A number of videos documenting the feeding behavior of various salticids can be accessed online (Hill 2007a—d, 2008, 2009a—e), but they should be downloaded to view them in full resolution. These videos depict feeding on both insects and spiders, and clearly illustrate the alternating cycles of disgorging (*egestion*) and rhythmic engorging, as well as maceration in association with disgorging.

Discussion

Based on *English language* publications, the structure and function of the spider mouth is a little-studied subject.   The details of feeding behavior have also received little attention, and fluid flow during feeding has seldom been described as a cyclical process involving movement of fluid in two directions (*disgorging* and *engorging*). Figure 15 describes a hypothesis of how dilation of the stomach and pharynx work together to support feeding by spiders.
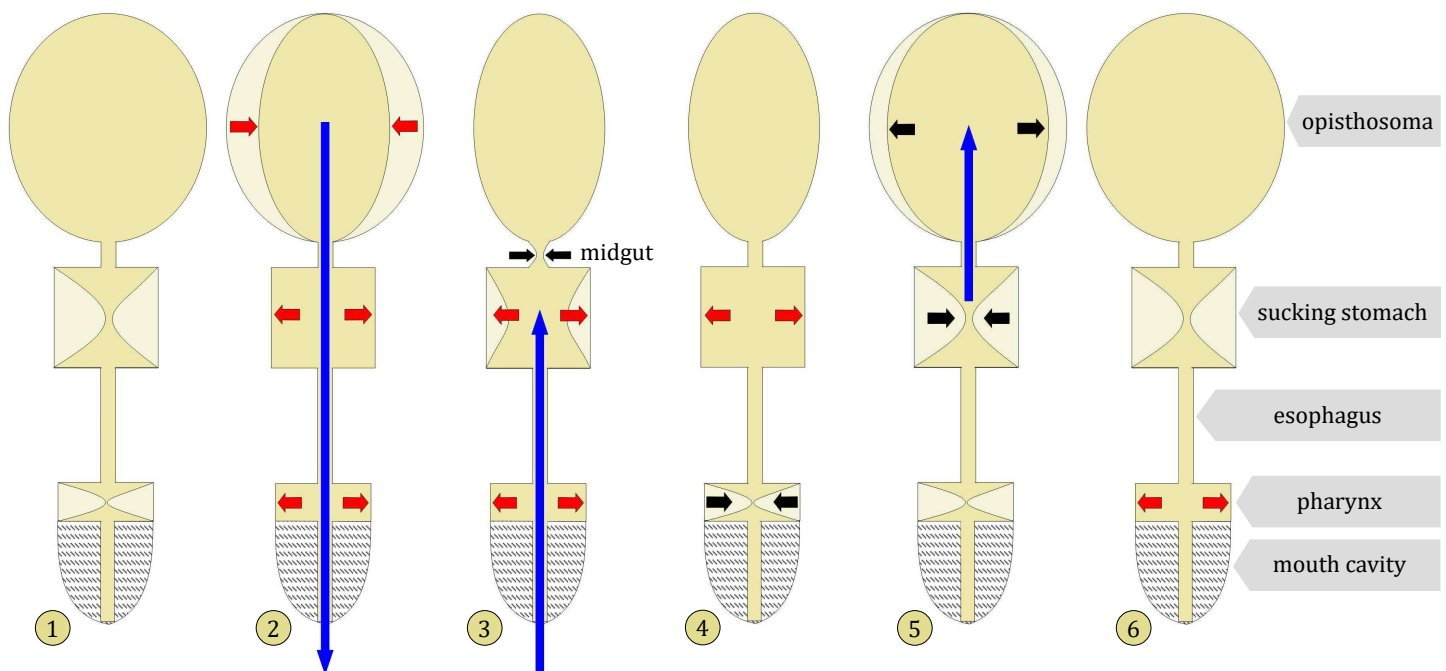

Figure 15.   Hypothetical coordination of muscles associated with the feeding process of spiders. **1,** Resting state, with the dilators of the stomach and pharynx are relaxed to close the foregut. **2,** Digestive liquid (*kime*) is disgorged by contraction of the opisthosoma when both the stomach and pharynx are dilated. This is a slower process, alternating with a series of rapid or rhythmic cycles associated with engorging (3-6). **3,** With the pharynx dilated, dilation of the stomach pulls in liquid from the mouth. Rigidity of the foregut supports this process, and the flexible walls of the midgut may be pulled together to restrict movement of digestive liquid from the midgut into the stomach. **4,** With the stomach full, relaxation of pharyngeal dilators prevents disgorging. **5,** Relaxation of stomach dilators, with contraction of several small muscles, constricts the stomach to drive liquid into the midgut and the distensible opisthosoma. **6,** Contraction of pharyngeal dilators opens up the pharynx to prepare for the next cycle of engorging.

As mentioned in the introduction, there are a number of significant publications dealing with the anterior digestive tract of the Araneae, in French and German. For the most part these were written in the 1800's, when the study of functional morphology received much more support and interest than it does today. Even the best summaries of this early work date back more than 70 years. Some of the earlier papers were very descriptive, and clearly written. With respect to the mouth cavity (*Mundhöhle*) of *Lycosa*, for example, Kessler (1849, p. 509) wrote: *Die innere Wandung der Mundhöhle wird von längliche-ovalen, vornen zugerundeten, dünnen, hornigen Platten, einer oberen und einer unteren, gebildet*.   Wasmann (1846), another early student of the *Anatomie der Spinnen*, also wrote with a keen eye for details (Figure

16). After Plateau's later work (1877, including new views of agelenid anatomy), Schimkewitsch (1884, with respect to an araneid) and Bertkau (1885, dealing with several different families of Araneae) published important descriptions of the anterior digestive tract, including summaries of earlier work. It is unfortunate that many of the detailed drawings of these earlier observers, collected into crowded plates at the end of their respective volumes, have deteriorated to the point where in some cases (*e. g.*, Bertkau 1884) I have found them to be totally unreadable. Much more recent reviews and compilations on the subject were published by Zimmerman (1934) and Gerhardt & Kaestner (1938), and these documents are still in good condition. Zimmerman published a very nice schematic of the mouthparts of the lycosid *Tarantula* as 'viewed' from the front, and also drew a detailed section of the many ridges and channels of the posterior rostral plate. Gerhardt & Kaestner, based in part on the earlier work of Plateau and Wasmann, published some very nice perspective drawings of the anterior digestive tract of the Agelenidae and Theraphosidae. None of these published descriptions differ in any major way from my limited observations of salticids, although the mouth of lycosids and agelenids appears to taper more acutely toward the distal end, when compared to the salticid.
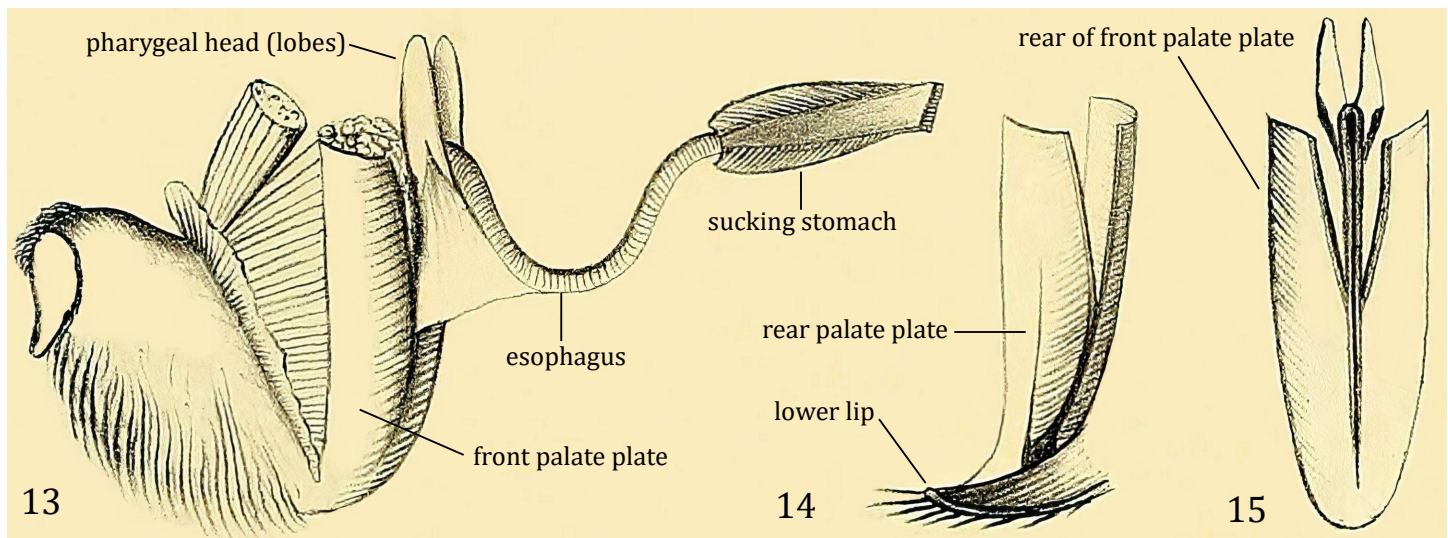

Figure 16. Drawings of the spider foregut (Wasmann 1846, pl. XIII, figs. 13-15).

There are several reports relating the ability of spiders to filter out small particulate solids, such as the pigment particles in India ink, and to collect and dispose of these as a mass (*e. g.*, Breene 2002, Foelix 2011). Given the fact that the linear dimensions (length or width) of bacteria range generally from 0.3—5.0 µm, it is reasonable to expect that the rostral plate is a good filter for even small bacteria, or other microorganisms, which might include pathogens resistant to the digestive enzymes of a spider. This compares favorably with the ability of the commercial microfilters used by back-country hikers to screen out particles of a similar size. As noted above, the detailed structure of the rostral plate supports the hypothesis that the filaments associated with each transverse row are pulled down to close the filter tightly during ingestion, and that they are pushed out to open this filter during regurgitation. This can be characterized as a *directional microfilter*.

Movement of the labium and rostrum during feeding is a subject that needs more study. As noted above, labial muscles may be associated with expansion of the pharynx, movement of the labium to expand the mouth cavity, or both. Rostral muscles (Schimkewitsch 1884) may also be used bend the rostral plate, thus changing the shape of the mouth cavity. Any movement that could expand the mouth cavity would also produce negative fluid pressure, pulling liquid into the mouth. In conjunction with coordinated movements of the pharyx and stomach, these movements may contribute to the rhythmic pulses (~2/s)

associated with the engorging (ingestion) process. One thinks of the manner in which the mouth of a baleen whale opens to capture plankton, then closes to force that plankton into a sieve of baleen plates (Fudge et al. 2009).

It appears that muscles associated with the pharynx and sucking stomach are coordinated by the *rostral ganglion* (Figure 6.1), which is situated above the anterior end of the esophagus. The recurrent nerve (above the esophagus) and two lateral esophageal nerves lead to the rear, and a rostral nerve leads forward to the rostrum, from this ganglion (Hill 2022). The *buccal ganglion* of mollusks (Rosen et al. 1991) and the insect *frontal ganglion* (Ayali 2004) occupy a similar position, as in other protostomes.

Acknowledgments

References

Aldrich 1988. Jeffrey R. Aldrich. Chemical ecology of the Heteroptera. Annual Review of Entomology 33: 211—238.

Angelini et al. 2005. David R. Angelini, Paul Z. Liu, Cynthia L. Hughes and Thomas C. Kaufman. 15 NOV 2005. Hox gene function and interaction in the milkweed bug *Oncopeltus fasciatus* (Hemiptera). Developmental Biology 287 (2): 440—455.

Ayali 2004. Amir Ayali. JAN—APR 2004. The insect frontal ganglion and stomatogastric pattern generator networks. Neurosignals 13 (1—2): 20-36.

Barnes 1980. Robert D. Barnes. Invertebrate Zoology. Fourth Edition. Saunders College, Philadelphia. i—xv, 1—1089.

Bertkau 1884. Ph. Bertkau. DEC 1884. Über den Verdauungsapparat der Spinnen. Archiv für mikroskopische Anatomie 24: 398—451, pl. XX—XXI.

Breene 2002. Robert Gale Breene III. Spider digestion and food storage. Posted online at http://atshq.org/articles/Digestion.pdf 1—6.

Bristowe 1971. W. S. Bristowe. The World of Spiders. Revised Edition. Collins, London. i—xvi, 1—304.

Comstock 1913. John Henry Comstock. The Spider Book. Doubleday, Page and Company, New York. i—xv, 1—721.

Dalton 2008. Stephen Dalton. Spiders: The Ultimate Predators. Firefly Books, Richmond Hill. 1—208.

Damen et al. 1998. Wim G. M. Damen, Monika Hausdorf, Ernst-August Seyfarth and Diethard Tautz. SEP 1998. A conserved mode of head segmentation in arthropods revealed by the expression pattern of Hox genes in a spider. Proceedings of the National Academy of Science, USA 95: 10665—10670.

Foelix 2011. Rainer F. Foelix. Biology of Spiders. Third Edition. Oxford University Press, New York. i—viii, 1—419.

Foelix & Erb 2011. Rainer F. foelix and Bruno Erb. 8 MAY 2011. Microscopical studies on exuviae of the jumping spider *Phidippus regius*. Peckhamia 90.1: 1—15.

Fudge et al. 2009. Douglas S. Fudge, Lawrence J. Szewciu and Astrid N. Schwalb. Morphology and development of blue whale baleen: an annotated translation of Tycho Tullberg's classic 1883 paper. Aquatic Mammals 35 (2): 226—252.

Gerhardt & Kaestner 1938. U. Gerhardt and A. Kaestner. 8. Ordnung der Arachnida: Araneae=Echte Spinnen=Webspinnen. In: *Handbuch der Zoologie*, ed. W. Kükenthal and T. Krumbach, DeGruyter, Berlin. 394—656.

Gertsch 1979. Willis J. Gertsch. American Spiders. Second Edition. Van Nostrand Reinhold Company, New York. i—xiii, 1—274.

Hass et al. 2001. M. Susan Haas, Susan J. Brown and Richard Beeman. MAR 2001. Pondering the procephalon: the segmental origin of the labrum. Development Genes and Evolution 211 (2): 89—95.

Hill 1977a. David E. Hill. MAY 1977 The salticid fang. Peckhamia 1 (2): 24—26, republished 14 AUG 2008 as Peckhamia 11.1: 24—26. *online at* http://www.peckhamia.com/peckhamia/PECKHAMIA 11.1.pdf

Hill 1977b. David E. Hill. The pretarsus of salticid spiders. Zoological Journal of the Linnean Society 60: 319—338.

Hill 2006. David E. Hill. 31 OCT 2006. The structure of the central nervous system of jumping spiders of the genus *Phidippus* (Araneae: Salticidae). Republication Version 1. Peckhamia Epublications. 1—46. *online at* http://www.peckhamia.com/ epublications/Hill 2006 Central nervous system of Phidippus RV1 EB PDF.pdf

Hill 2007a. David E. Hill. Feeding *Lyssomanes viridis* (Araneae: Salticidae). Internet Archive 481 MB, 1:01:22. *online at* http://www.archive.org/details/FeedingLyssomanesviridis

Hill 2007b. David E. Hill. Male jumping spider *Thiodina sylvana* (Araneae: Salticidae) feeding on *Oxyopes salticus* (Araneae: Oxyopidae). Internet Archive 231 MB, 35:39. *online at* http://www.archive.org/details/MaleThiodinasylvana feedingonOxyopessalticus

Hill 2007c. David E. Hill. Portrait of feeding female *Phidippus audax* jumping spiders (Araneae: Salticidae). Internet Archive 358 MB, 55:20. *online at* http://www.archive.org/details/PortraitoffeedingfemalePhidippusaudax

Hill 2007d. David E. Hill. *Thiodina sylvana* (Araneae: Salticidae) feeding on *Leucauge venusta* (Araneae: Araneidae). Internet Archive 112 MB, 17:17. *online at* http://www.archive.org/details/Thiodina_feeding_on_Leucage

Hill 2008. David E. Hill. Feeding and pursuit behavior of *Anasaitis canosa* jumping spiders in Greenville County, SC, USA. Internet Archive 302 MB, 46:16. *online at* http://www.archive.org/details/DavidEdwinHillFeedingandpursuitbehaviorofAnasaitiscanosajumping spidersinGreenvilleCountySC_0

Hill 2009a. David E. Hill. Feeding female *Phidippus princeps* jumping spider (Araneae: Salticidae). Internet Archive 492 MB, 1:20:08. *online at* http://www.archive.org/details/feeding_female_Phidippus_princeps_1

Hill 2009b. David E. Hill. Female *Phidippus audax* feeding on lycosid spiders, part 1. Internet Archive 386 MB, 1:03:05. *online at* http://www.archive.org/details/female_Phidippus_audax_feeding_1

Hill 2009c. David E. Hill. Female *Phidippus audax* feeding on lycosid spiders, part 2. Internet Archive 382 MB, 1:01:58. *online at* http://www.archive.org/details/female_Phidippus_audax_feeding_2

Hill 2009d. David E. Hill. Female *Phidippus audax* feeding on brachyceran flies. Internet Archive 128 MB, 21:00. *online at* http://www.archive.org/details/female_Phidippus_audax_feeding_3

Hill 2009e. David E. Hill. Large adult female *Phidippus clarus* (Araneae: Salticidae) feeding on *Acacesia hamata* (Araneidae) in Greenville County, SC, USA. Internet Archive 330 MB, 54:00. *online at* http://www.archive.org/details/Phidippus_clarus_feeding_Acasesia_hamata

Hill 2022. David E. Hill. 12 FEB 2022. Neurobiology and vision of jumping spiders (Araneae: Salticidae). Peckhamia 255.1: 1-81.

Juberthie & Lopez 1993. J. L. Juberthie and A. Lopez. L'organe du rostre chez les *Argyrodes* (Araneae: Theridiidae); confirmation ultrastructurale de la nature glandulaire. Memoires de Biospeologie 20: 125—130.

Kaston 1978. B. j. Kaston. How to Know the Spiders. Third Edition. Wm. C. Brown Company, Dubuque. i—vii, 1—272.

Kessler 1849. Beiträge zur Naturgeschichte und Anatomie der Gattung *Lycosa*. Bulletin de la Société Impériale des Naturalistes de Moscou 22, Number IV: 480—523, plate IX.

Korschelt et al. 1899. E. Korschelt, K. Heider, E. L. Mark, W. M. Woodworth, M. Bernard and M. F. Woodward. Textbook of the embryology of invertebrates. Vol III. Arachnida, Pentastomidae, Pantopoda, Tardigrada, Onychophora, Myriapoda, Insecta. Swan Sonnenschein and Company, Ltd., London. i—xii, 1—441.

Kozleff 1990. E. N. Kozloff. Invertebrates. Saunders College Publishing, a division of Holt, Rinehart and Winston, Inc., United States of America. i—xiv, 1—866, front and rear end-papers.

Levi & Levi 1968. Herbert W. Levi and Lorna R. Levi. Spiders and their Kin. Western Publishing Company, New York. 1—160.

Liu et al. 2009. Yu Liu, Andreas Maas and Dieter Waloszek. SEP 2009. Early development of the anterior body region of the grey widow spider *Latrodectus geometricus* Koch, 1841 (Theridiidae, Araneae). Arthropod Structure & Development 38: 401—416.

Lopez 1984. Andre Lopez. Some observations on the internal anatomy of *Diguetia canities* (McCook, 1890) (Araneae, Diguetidae). The Journal of Arachnology 11: 377—384.

Main 1972. Barbara Y. Main. Sub-phylum Chelicerata. In: *Textbook of Zoology. Invertebrates*, ed. A. J. Marshall and W. D. Williams, American Elsevier Publishing Company, Inc., New York. 411—480.

Millot 1936. Jacques Millot. Le sens du goût chez les araignées. Bulletin de la Société Zoologique de France 61: 27—38.

Nawabi 1974. Storai Nawabi. Histologische Untersuchungen an der Mitteldarmdrüse von *Stegodyphus pacificus* (Pockock 1900) (Araneae, Eresidae). M. S. Thesis, Universität Bonn.

Plateau 1877. Félix Auguste Joseph Plateau. Recherches sur la structure de l'appareil digestif et sur les phénomènes de la digestion chez les Aranéides dipneumones. Bulletins de l'Acadèmie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique, 2me Sér. 44: 129—181.

Pocock 1909. Reginald Innes Pocock. Arachnida. In: *The Fauna of British India, including Ceylon and Burma*, ed. W. T. Blanford, Taylor and Francis, London. i—xii, 1—279.

Preston-Mafham& Preston-Mafham 1984. Ken Preston Mafham and Rod Preston Mafham. Spiders of the World. Facts on File Publications, New York. 1—191.

Preston-Mafham& Preston-Mafham 1996. Ken Preston Mafham and Rod Preston Mafham. The Natural History of Spiders. The Crowood Press Ltd., Ramsbury. 1—160.

Punzo 1998. Fred Punzo. The Biology of Camel-spiders. Kluwer Academic Publishers, Norwell, Massachusetts. 1—301.

Rosen et al. 1991. Steven C. Rosen, Thomas Teyke, Mark W. miller, Klaudiusz R. Weiss and Irving Kupfermann. NOV 1991. Identification and characterization of cerebral-to-buccal interneurons implicated in the control of motor programs associated with feeding in *Aplysia*. The Journal of Neuroscience 11 (11): 3630-3655.

Schimkewitsch 1884. W. Schimkewitsch. Etude sur l'anatomie de l'Epeire. Annales des Sciences Naturelles. Zoologie et Paléontologie. Sixième Série 17: 1—94, Planche 1—8.

Schwager 2008. Evelyn Schwager. Segmentation of the spider *Achaearanea tepidariorum* investigated by gene expression and functional analysis of the gap gene *hunchback*. Ph. D. thesis, Universität zu Köln. i—viii, 1—181.

Ubick et al. 2005. D. Ubick, P. Paquin, Paula E. Cushing and V. Roth, eds. Spiders of North America: an identification manual. American Arachnological Society. i—v, 1—377.

Wasmann 1846. A. Wasmann. Beiträge zur Anatomie der Spinnen. Abhandlungen aus dem Gebiete der Naturwissenschaften herausgegeben von dem naturwissenschaftlichen Verein in Hamburg. 1: 131—161, Tafel XII—XIV.

Zimmerman 1934. E. W. Zimmerman. Untersuchungen über den Bau des Mundhöhlendaches der Gewebespinnen. Revue Suisse Zoologie 41: 149—176.