

## From four- to three-segmented labium in Reduviidae (Hemiptera: Heteroptera)\*)

Christiane WEIRAUCH

Department of Entomology, University of California Riverside, CA, 92521, USA;  
e-mail: [christiane.weirauch@ucr.edu](mailto:christiane.weirauch@ucr.edu)

**Abstract.** The majority of Reduviidae – unlike most other Heteroptera – has a labium that consists of only three segments. The first segment is said to be either lost or fused to the head capsule. Cladistic analysis shows that this loss or fusion occurred once or twice among basal Reduviidae and that the four-segmented labium in Hammacerinae is plesiomorphic and homologous to the one in non-reduviid Cimicomorpha. In the present contribution, extrinsic labial muscles and sclerites associated with the base of the labium are documented (micro-dissections, histology) for *Himacerus apterus* (Fabricius, 1789) (Nabidae), *Microtomus purcis* (Drury, 1782) (Reduviidae: Hammacerinae) and *Rhynocoris erythropus* (Linnaeus, 1767) (Reduviidae: Harpactorinae). Primary homology hypotheses are proposed on lever, depressor, and transverse muscles among the examined taxa and previously published descriptions of Nepomorpha and Leptopodomorpha. The two Reduviidae are unique in having a large portion of the *Musculus levator labii* (muscle A) originating from the first labial segment (*M. purcis*) or the gena (*R. erythropus*). This may indicate that part of the gena is homologous to part of the first labial segment, i.e. the proximal portion of the first labial segment may be fused to the gena, but migration of the muscle origin may also account for this condition. The insertion of *M. transversalis labii* has shifted from the dorsal surface of the first labial segment to the anterior portion of the suspensory plate, possibly indicating that this structure may include part of the first labial segment. Even though the first labial segment is not visible externally in the majority of Reduviidae, two muscles that were originally associated with it are thus retained. Mapped on a phylogeny of Reduivoidea it seems evident that in a first step the levator muscle became larger at the base of the Reduviidae. In a second step the first labial segment fused to the head capsule, possibly providing this enlarged muscle with a more solid origin.

**Key words.** Reduviidae, morphology, labium, histology, muscle, phylogeny

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\*) This paper is dedicated to Prof. Pavel Štys, one of the most influential heteropterists and great morphologist, on the occasion of his 75th birthday. I am very grateful for his continued encouragement and support.

## Introduction

Reduviidae or assassin bugs are frequently diagnosed by a short, stout and three-segmented labium (ARNETT 1993, TRIPLEHORN & JOHNSON 2005). Most other Heteroptera (PARSONS 1959, RIEGER 1976) including Cimicomorpha (SCHUH & ŠTYS 1991) have four labial segments and this condition is also found in Pachynomidae, the sistergroup of Reduviidae (CARAYON & VILLIERS 1968; SCHUH & ŠTYS 1991). However, two small subfamilies of Reduviidae, the Southeast Asian Centrocneminae and the Neotropical and Nearctic Hammacerinae have four labial segments (MILLER 1956, SCHUH & ŠTYS 1991, PUTSHKOV 1993). PUTSHKOV (1993) proposed that the visible segments 1-4 in Centrocneminae correspond to those observed in other True Bugs. He also pointed out that the visible segments 1-3 in non-centrocnemine Reduviidae are homologous to segments 2-4 of other Heteroptera. PUTSHKOV (1993) further assumed that the first labial segment had not simply vanished within Reduviidae, but had gradually fused to the head capsule. He subdivided this process into four stages of gradual fusion (free, semi-free, quasi-integrated, and integrated) and proposed that the four steps can be observed in different subfamilies. PUTSHKOV (1993) finally pointed out that the integration of the first labial segment evolved independently multiple times within Reduviidae, but did not base this statement on a formal cladistic analysis. WEIRAUCH (2008) re-examined head capsules in a comprehensive sample covering most subfamilies of Reduviidae, did not find evidence for PUTSHKOV's (1993) two intermediate stages, and treated the conditions in Reduviidae as two distinct character states, i.e. labial segment 1 free and labial segment 1 fused [to the head capsule] or reduced. In that analysis, the four-segmented condition in Centrocneminae, which are part of a monophyletic Phymatine Complex, is ambiguous and either treated as plesiomorphic or as a reversal. However, Hammacerinae is the sistergroup of all remaining Reduviidae, its four-segmented labium is plesiomorphic, and the first labial segment is treated as being homologous to that segment in non-reduviid Cimicomorpha.

Both, Putshkov's and Weirauch's studies, focused on head sclerites and neither documented internal head characters or muscles. Among the papers on head muscles in Heteroptera (e.g., WEBER 1930; BARTH 1952, 1953; PARSONS 1959, 1962; RIEGER 1976), Parson's and Rieger's works on Nepomorpha and Leptopodomorpha (both with four segmented labium) stand out as being comprehensive, well illustrated, and consistent in their terminology. According to their studies, three muscles (lever, depressor, and transverse; sometimes split into subsets) are associated with the base of the labium and the distal parts of the head capsule including suspensory plate and hypopharyngeal wings. Origins and insertions of these muscles are relatively conserved and primary homology hypotheses between the nepomorphan and leptopodomorphan taxa studied seem mostly straightforward. Documenting extrinsic labial muscles in Reduviidae with three and four labial segments and establishing their homology with those of non-reduviid Heteroptera might therefore provide insights into the transition from four to three segmented labium.

In the present contribution, one non-reduviid representative of Cimicomorpha (*Himacerus apterus* (Fabricius, 1789) – Nabidae), one reduviid with four-segmented labium (*Microtomus purcis* (Drury, 1782) – Hammacerinae) and one reduviid with three-segmented labium (*Rhynocoris erythropus* (Linnaeus, 1767) – Harpactorinae) were examined using micro-dissections

and histology and results were compared with extrinsic labial muscles as described by PARSONS (1959, 1962) and RIEGER (1976). These observations were supplemented with examination of head capsule sclerites for Pachynomidae, for which no fresh specimens were available. In particular, this study aims on describing sclerites associated with the base of the labium in *H. apterus*, *M. purcis*, and *R. erythropus* and on describing and documenting origins and insertions of *Musculus levator labii*, *M. depressor labii primus*, and *M. transversalis labii* in the three taxa. This documentation then might allow insights into the whereabouts of muscles that once were associated with the first labial segment and might provide evidence on the fate of the first segment in Reduviidae with three-segmented labium.

## Material and methods

**Specimens examined.** Only external examination (\*), micro-dissections of muscles, but no histology (°); external, dissections, and histology (^). **Nabidae:** Nabinae: ^*Himacerus apterus*. **Pachynomidae:** Pachynominae: \**Pachynomus picipes* Klug, 1830. **Reduviidae:** Centrocneminae: \**Neocentrocnemis* sp. Ectrichodiinae: \**Zirta limbata* Breddin, 1901. Hammacerinae: °*Microtomus purcis*. Harpactorinae: Harpactorini: \**Pristhesancus plagipennis* Walker, 1873; ^*Rhynocoris erythropus*. Holoptilinae: Holoptilini: \**Ptilocnemus lemur* (Westwood, 1840). Reduviinae: \**Neivacoris steini* (Stål, 1859). Triatominae: Rhodniini: \**Rhodnius prolixus* Stål, 1859.

**Dissections.** The heads of 70% ethanol-preserved specimens of *H. apterus*, *M. purcis*, and *R. erythropus* were removed. The cuticle of the left gena was lifted with fine forceps to expose the outer layers of muscles (e.g., head muscles 1 and A in *R. erythropus*). The dissections were stained with eosin to increase contrast between individual muscles. Muscles were illustrated, removed, and the next layer was stained and documented (e.g., muscle 2a and 2b in *R. erythropus*).

**Histology.** For semi-thin sections of head sclerites, internal cuticular structures, and muscles, adult specimens of *H. apterus* and fifth-instar immatures of *R. erythropus* were fixed in Bouion's fixative (*R. erythropus*) or 70% ethanol (*H. apterus*). The head was removed, dehydrated (alcohol series), and embedded in Kulzers Technovit 7100. Two µm sections were cut on a R. Jung microtome, transferred to slides, stained with eosin and toluidine blue, and covered using Eukitt and cover slips dipped in Rotihistol (Roth, Karlsruhe, Germany).

**Observation and documentation.** External observation of head sclerites were made on a Leitz Diaplan dissection microscope. Drawings were made using a camera lucida on the Leitz Diaplan microscope. Photographs of histological sections were taken with a Fujifilm FinePix S1 Pro digital camera mounted on the Zeiss Axioplan, using differential interference contrast (DIC).

**Terminology.** I am following the nomenclature for head muscles used by PARSONS (1962) and RIEGER (1979). Only three groups of muscles are relevant for the purposes of this paper, namely the *Musculus levator labii* (1 and derivations), the *Musculus depressor labii* (2 and derivations), and *Musculus transversalis labii* (3), but the *Musculus protractor setae maxillaris* (12) is shown in some illustrations. The *M. transversalis labii* does not show much variation among previously examined taxa (PARSONS 1962, RIEGER 1976), but the levator and

depressor muscles may differ with respect to origin, insertion and number of subsets. The table provided (Table 1) allows a synoptic view of proposed homology hypotheses among previously examined taxa and those studied in the present paper.

**Abbreviations used in the figures.** 1, muscle 1, i.e. portion of the *Musculus levator labii*; 2, muscle 2, i.e. *Musculus depressor labii*, sometimes divided into portions 2a and 2b; 3, muscle 3, i.e. *Musculus transversali labii*; 4, *Musculus depressor labii secundus*; 12, *Musculus protractor setae maxillaris*; A, muscle A, i.e. portion of the *Musculus levator labii*; ant, antenna; antf, antennifer; apo, apodeme; cly, clypeus; ge, gena; hyp, hypopharyngeal wing; lbr, labrum; mdp, mandibular plate; mxp, maxillary plate; op, oblique plate; sd, salivary duct; st, stylets; su, suspensory plate; vsc, ventral sclerite in the membrane between labial segment 2 and 1 (or head capsule).

## Results

### The head capsule and proximal labial segments in *Himacerus apterus*, *Pachynomus picipes*, *Microtomus purcis*, and *Rhynocoris erythropus*

Exterior structures of head capsule and proximal labial segments. The antecular portion of the head consists laterally (posterior to anterior) of mandibular plate, maxillary plate, and gena as documented for *Himacerus apterus* (Fig. 1A), *Pachynomus picipes* (Fig. 1B), *Microtomus purcis* (Fig. 1C), and *Rhynocoris erythropus* (Fig. 1D). The medial portion is formed by frons, clypeus, and labrum (Fig. 1). The portion of the gena anterior to the maxillary plate is relatively large in *Himacerus* (Fig. 1A) and *Rhynocoris* (Fig. 1D), but very short in *Pachynomus* (Fig. 1B), and short and partially covered by the large lobe of the maxillary plate in *Microtomus* (Fig. 1C). The three- (Fig. 1D) or four-segmented labium (Fig. 1A-C) attaches to the head capsule through a membrane. The first labial segment in *Himacerus* and *Pachynomus* is stout and relatively short (Fig. 1A-B) and has a truncate anterior margin. This segment in *Himacerus* is not distinctly drawn into the head capsule (Fig. 1A), whereas the first segment in *Microtomus* has a ventrolateral process and extends far into the head capsule when the labium is at rest (Fig. 1C). The ventral membrane between first and second labial segments (Fig. 2A) or the first visible segment (= second segment) and the head capsule (Fig. 2D-E) carries a sclerite that may be horseshoe shaped as here documented for *R. erythropus* (Fig. 2E, inset).

Interior sclerotized structures of the head capsule. Internal head structures are best documented using the histological cross sections for *Himacerus* and *Rhynocoris* (Figs. 3-4) in concert with the semi-schematic representation of the dissected heads of *Himacerus*, *Microtomus*, and *Rhynocoris* (Fig. 2A-E). The position of the sections of the head of *Rhynocoris* (Fig. 3) is indicated in Fig. 2C. The most prominent internal sclerotized structures are the hypopharynx including the paired hypopharyngeal wings (e.g., Fig. 3D) and the median salivary duct (Fig. 3D). More anteriorly, but connected to the hypopharyngeal wings, the suspensory plate forms the dorsal surface of the head capsule beneath the clypeus and the stylet bundle (Fig. 3B). Associated with the second labial segment (= first visible segment) in *Rhynocoris* is the oblique plate, which forms a triangular lobe with a pointed tip that is facing into the head cavity (Figs. 2A,D, 3A).

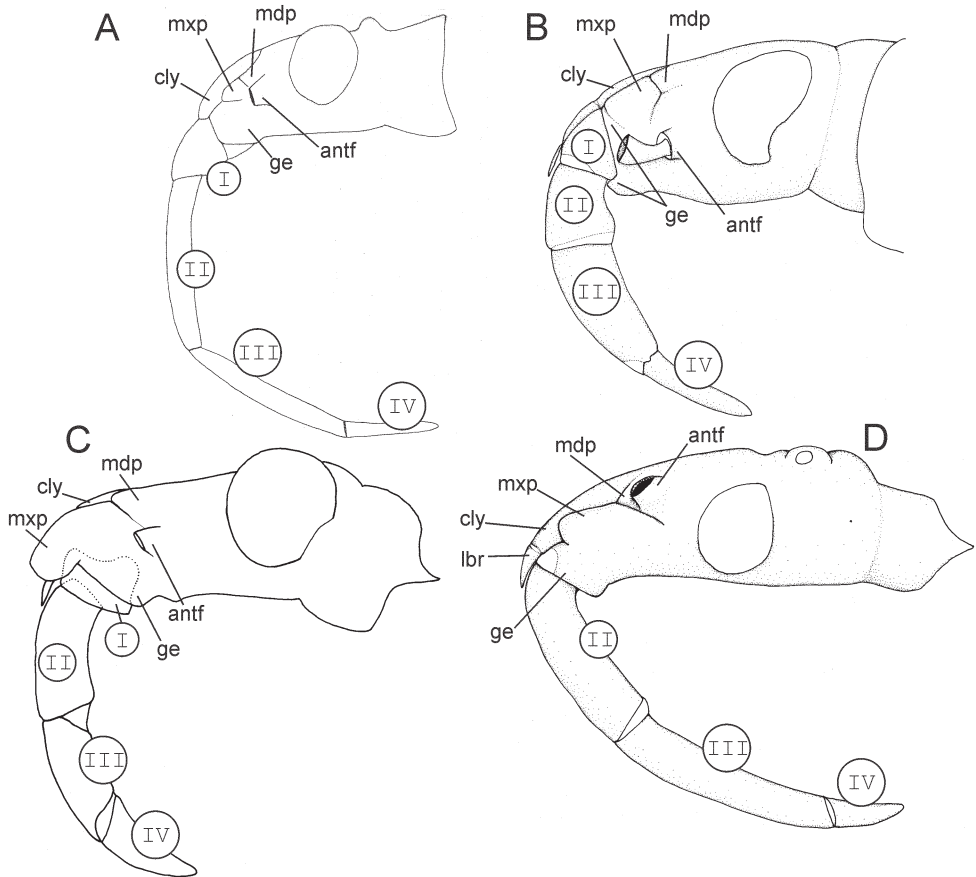


Fig. 1. Lateral view of the head. A – *Himacerus apterus* (Fabricius, 1789) (Nabidae: Nabinae); B – *Pachynomus picipes* Klug, 1830 (Pachynomidae: Pachynominae); C – *Microtomus purcis* (Drury, 1782) (Reduviidae: Hamma-cerinae); D – *Rhynocoris erythropus* (Linnaeus, 1767) (Reduviidae: Harpactorinae).

### Extrinsic labial muscles in *Himacerus apterus*, *Microtomus purcis*, and *Rhynocoris erythropus* (Tab. 1, Figs. 2-4)

The head muscles relevant for this project are extrinsic muscles associated with the anterior part of the head capsule and labial segments 1 and 2, i.e. muscles that lift the labium (*Musculus levator labii*, 1 and A), lower the labium (*Musculus depressor labii primus*, 2), and flex the second segment versus the first segment or the head capsule (*Musculus transversalis labii*, 3). Origin and insertion of the three muscles, which are sometimes divided into distinct portions, are provided in Table 1 for *Himacerus*, *Microtomus*, and *Rhynocoris* and are homologized with extrinsic labial muscles in *Gelastocoris oculatus* (Fabricius, 1798) (PARSONS 1959), *Ochterus marginatus* (Latreille, 1804) (RIEGER 1976), and *Saldula pallipes* (Fabricius, 1794)

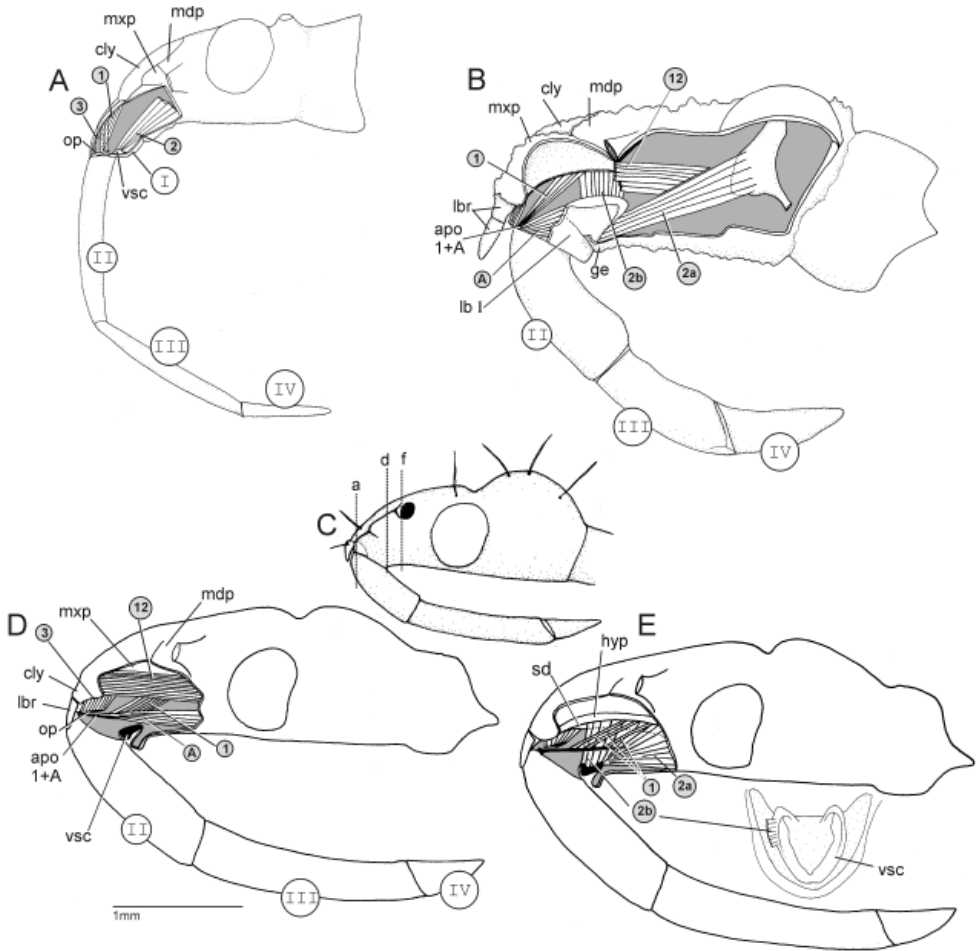


Fig. 2. Documentation of dissections of extrinsic labial muscles. A – *Himacerus apterus* (Fabricius, 1789) (Nabidae); B – *Microtomus purcis* (Drury, 1782) (Reduviidae: Hammacerinae); C–E – *Rhynocoris erythropus* (Linnaeus, 1767) (Reduviidae: Harpactorinae). Fig. 2C shows the head in lateral view of one of the specimens that were used for histology, the lines labeled a, d, and f correspond to the sections A, D, and F shown in Fig. 3.

(PARSONS 1962). The two Reduviidae examined differ from the nabid and from the previously documented *Nepomorpha* and *Leptopodomorpha* in having the *Musculus levator labii* formed by two distinct portions with different origin, but joint insertion, here termed muscle 1 and muscle A (Tab. 1, Figs. 2B,D,E, 3B-E). The levator muscles insert via an apodeme (Fig. 3A,B) on the dorsolateral surface of the second labial segment in all examined and previously documented taxa. In non-reduviids, this muscle originates from the suspensory

plate or the hypopharyngeal wings (Tab. 1). In reduviids, only muscle 1 originates from the hypopharyngeal wings. The second portion of the *M. levator labii*, is here referred to as muscle A. It is relatively large (Fig. 3D) and originates either on the ventrolateral surface of the first labial segment (*Microtomus*; Fig. 2B) or on the gena in the reduviid with reduced first labial segment (*Rhynocoris*; Figs. 2D, 3E). The two Reduviidae examined further differ from the

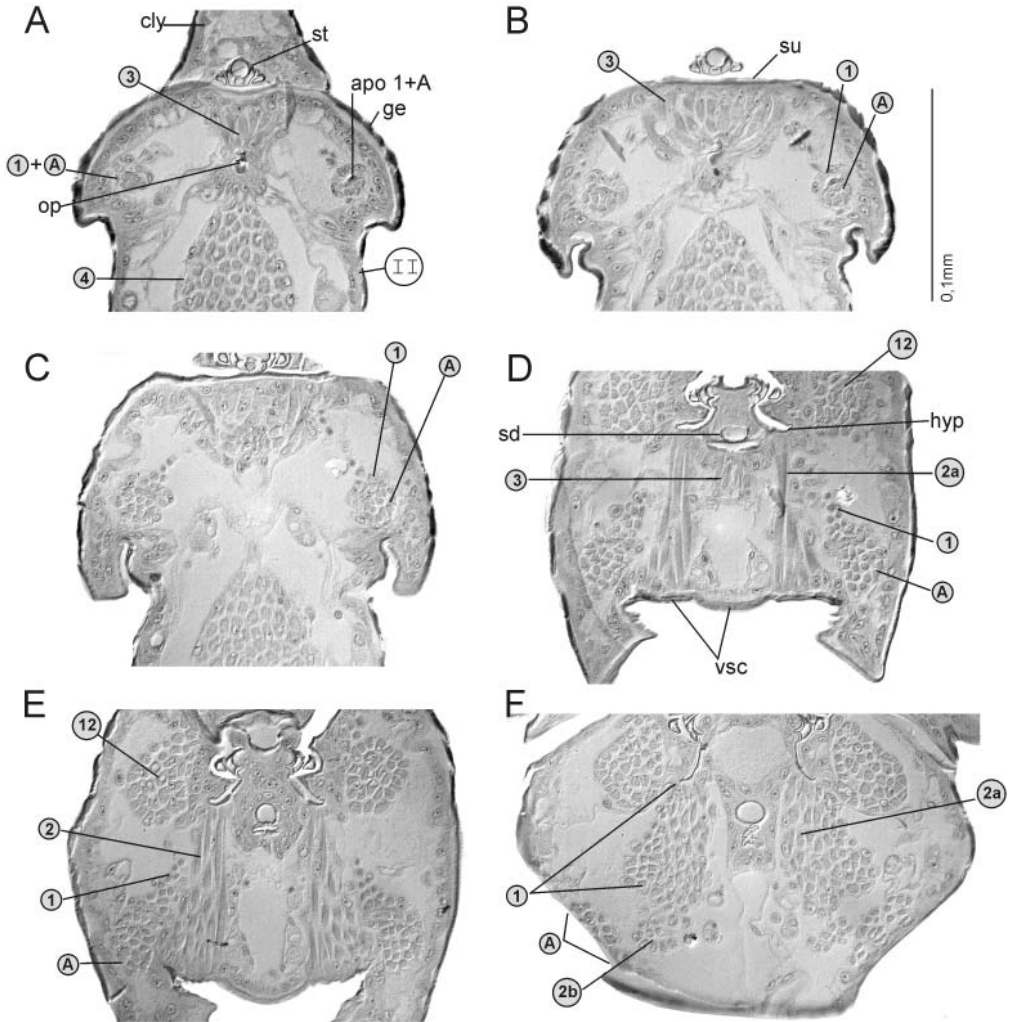


Fig. 3. Histological sections showing internal head structures and muscles of *Rhynocoris erythropus* (Linnaeus, 1767), fifth-instar larva. The sections progress from the anterior tip of the head (A) to the level of the antennifers (F); the exact location of sections A, D, F is also shown in Fig. 2C.

nabid (Fig. 4B), the saldid, and the nepomorphan taxa in having the *Musculus transversalis labii*, or muscles 3, inserting on the suspensory plate rather than the dorsal surface of the first labial segment (Tab. 1, Figs. 2B,D,E, 3A,B). The suspensory plate is the insertion in both, the reduviid with (*Microtomus*) and without (*Rhynocoris*) the first labial segment. The *Musculus depressor labii*, or muscle 2, consists of two portions in most taxa examined and previously documented and Reduviidae are no exception (Tab.1). Both portions are well developed in Reduviidae, originate on the hypopharyngeal wings and insert either lateroventrally on segment 2 or on the ventral sclerite (Figs. 2D,E, 3D-F, 4C-F).

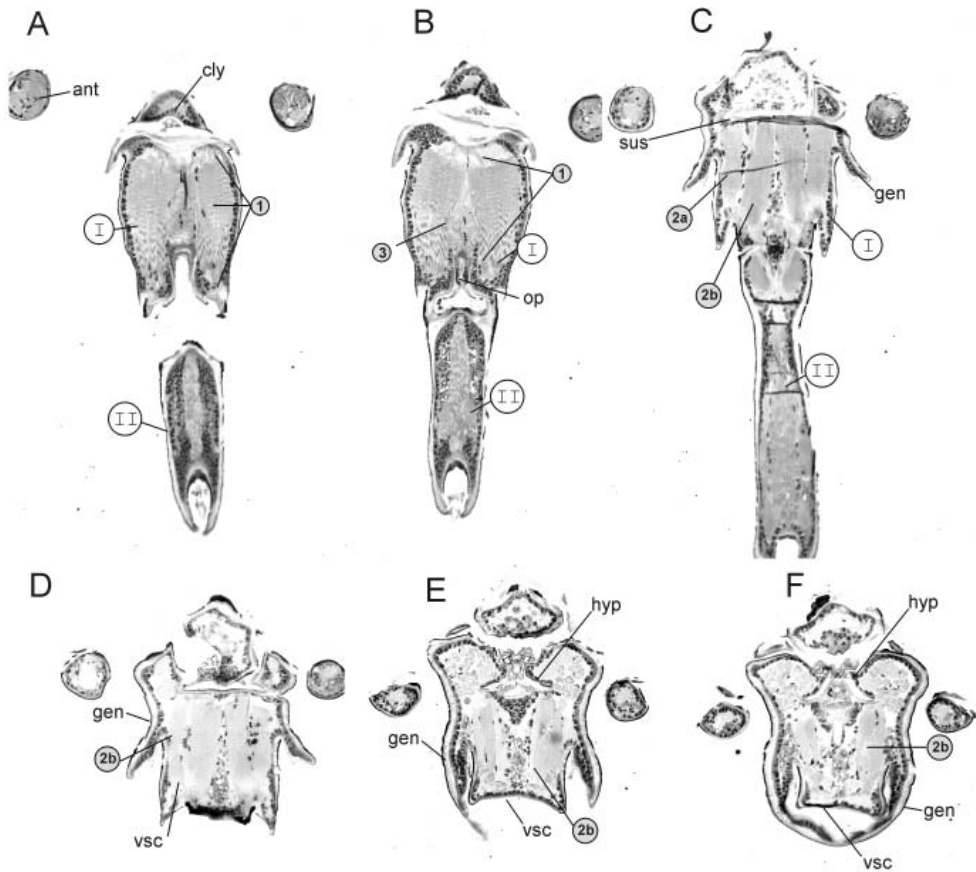


Fig. 4. Histological sections showing internal head structures and muscles of *Himacerus apterus* (Fabricius, 1789), adult. As in Fig. 3, the sections progress from the anterior tip of the head (A) to the anterior margin of the maxillary plate (F).



Table 1. Synopsis of extrinsic labial muscles and proposed homology of species examined during this study (taxa in bold) and previously documented species (PARSONS 1959, 1962; RIEGER 1976). [Nepo. = Nepomorpha, Lepto. = Leptopodomorpha, Cimico. = Cimicomorpha]

Muscle / taxon	<b>M. levator labii (1)</b>		<b>M. depressor labii (2)</b>		<b>M. transversalis labii (3)</b>	
	origin	insertion	origin	insertion	origin	insertion
<i>Gelastocoris</i> (Nepo.)	suspensory plate	posterior margin of 2nd segment	hypopharyngeal wing	posterior margin of 2nd segment and on intersegmental sclerite 1/2	dorsal surface of oblique plate, 2nd segment	floor of stylet groove, 1st segment
<i>Ochterus</i> (Nepo.)	suspensory plate	dorsally on 1st segment, ventro-lateral apodeme of 2nd segment	<b>2a:</b> hypopharyngeal wing (anterior) <b>2b:</b> hypopharyngeal wing (posterior)	<b>2a:</b> ventro-lateral apodeme of 2nd segment <b>2b:</b> medio-ventral apodeme of 2nd segment	dorsal surface of oblique plate, 2nd segment	floor of stylet groove, 1st segment
<i>Saldula</i> (Lepto.)	<b>1a:</b> suspensory plate <b>1b:</b> hypopharyngeal wing	<b>1a:</b> dorsolateral margin of base of 2nd segment <b>1b:</b> basal margin of 2nd segment	hypopharyngeal wing	ventrolateral margin of base of 2nd segment	dorsal surface of oblique plate, 2nd segment	dorsal surface of 1st segment
<i>Himacerus</i> (Cimico.)	suspensory plate	dorsally on posterior margin of 2nd segment	<b>2a:</b> hypopharyngeal wing (ant.) <b>2b:</b> hypopharyngeal wing (post.)	<b>2a:</b> lateroventrally on 2nd segment <b>2b:</b> intersegmental sclerite 1/2	dorsal surface of oblique plate, 2nd segment	dorsal surface of 1st segment
<i>Microtomus</i> (Cimico.)	1: on hypopharyngeal wing A: laterally on proximal lobes of 1st segment	1 and A: on joint apodeme that inserts dorsally on posterior margin of 2nd segment	<b>2a:</b> hypopharyngeal wing (post.) <b>2b:</b> hypopharyngeal wing (ant.)	<b>2a:</b> lateroventrally on 2nd segment <b>2b:</b> intersegmental sclerite 1/2	dorsal surface of oblique plate, 2nd segment	suspensorium
<i>Rhynocoris</i> (Cimico.)	1: on hypopharyngeal wing A: laterally on gena	1 and A: on joint apodeme that inserts dorsally on posterior margin of 2nd segment	<b>2a:</b> hypopharyngeal wing (post.) <b>2b:</b> hypopharyngeal wing (ant.)	<b>2a:</b> lateroventrally on 2nd segment <b>2b:</b> intersegmental sclerite 1/2	dorsal surface of oblique plate, 2nd segment	suspensorium

## Discussion

**Homologies of extrinsic labial muscles.** Even though studies on head muscles in Heteroptera are rare, representatives of four infraorders have been documented to date, namely Gerromorpha, Nepomorpha (Fig. 5), Leptopodomorpha (Fig. 5), and Cimicomorpha (e.g., ANDERSON 1982; PARSONS 1959, 1962; RIEGER 1976; Figs. 2-4). Comparison between some of these taxa shows that the general scheme of extrinsic labial muscles is relatively conserved within Heteroptera (Figs. 2-5), such that hypotheses on primary homology (sensu DE PINNA 1991) seem straightforward. This also applies to muscles in Reduviidae with three-segmented and four-segmented labium as documented in Table 1. The two remarkable features in Reduviidae are the additional portion of the levator muscles (M. levator labii, muscle A) that was not observed in any non-reduviid and the fact that the transverse muscle of the second labial segment does not insert within the first labial segment, but on the suspensory plate and therefore on the head capsule. The most interesting difference between *Microtomus* and *Rhynocoris* is the origin of muscle A, i.e. part of the levator muscle, on either the first labial segment or the gena.

**The remains of the first labial segment.** Even though an externally visible and sclerotized first labial segment has disappeared in the majority of Reduviidae, i.e. *Ptilocnemus lemur* (Westwood, 1840), *Pristhesancus plagipennis* Walker, 1873, *Zirta limbata* Breddin, 1901, *Neivacoris steini* (Stål, 1859), and *Rhodnius prolixus* Stål, 1859 (Fig. 6), the muscles that most likely were once associated with it are still present. In the four-segmented labium of *Microtomus*, muscle A originates on the lateral surface of the first labial segment. However, muscle A is associated with the gena in *Rhynocoris*, a reduviid with three-segmented labium. Given the systematic position of *Microtomus* at the base of the Reduviidae (PUTSHKOV 1987, CLAYTON 1990, WEIRAUCH 2008; Fig. 6) and the fact that muscle A seems to be restricted to Reduviidae (Pachynomidae not studied), the situation seen in *Microtomus* might represent the ancestral condition in Reduviidae. Muscle A could therefore be referred to as being part of the first labial segment, even in Reduviidae such as *Rhynocoris*, which have lost the corresponding sclerotized portion of the segment. The same argument is valid for muscle 3, which once inserted on the first labial segment, but in the two Reduviidae examined inserts on the head capsule.

**Fusion or loss.** Do the insertions of muscle A in Reduviidae on the gena and muscle 3 on the suspensory plate infer that these parts of the head capsule correspond to the first labial segment? Has the first labial segment fused to the head capsule? Origin and insertion of a muscle apparently may migrate (e.g. SNODGRASS 1935), even though evidence for such migration is limited. Migration seems a possible explanation for the situation seen in the transverse muscles, where the dorsal surface of the first labial segment and the suspensory plate are separated by no more than a very narrow membrane in *Himacerus* and *Microtomus*. Migration of the origin of muscle A from the ventral surface of the first labial segment onto the head capsule would require more extensive reorganizations, but does not seem impossible. Neither hypothesis – migration of the muscles or fusion of the first labial segment with the head capsule – can be ruled out at the moment to explain the different arrangements seen in the outgroups, in *Microtomus*, and in *Rhynocoris*.

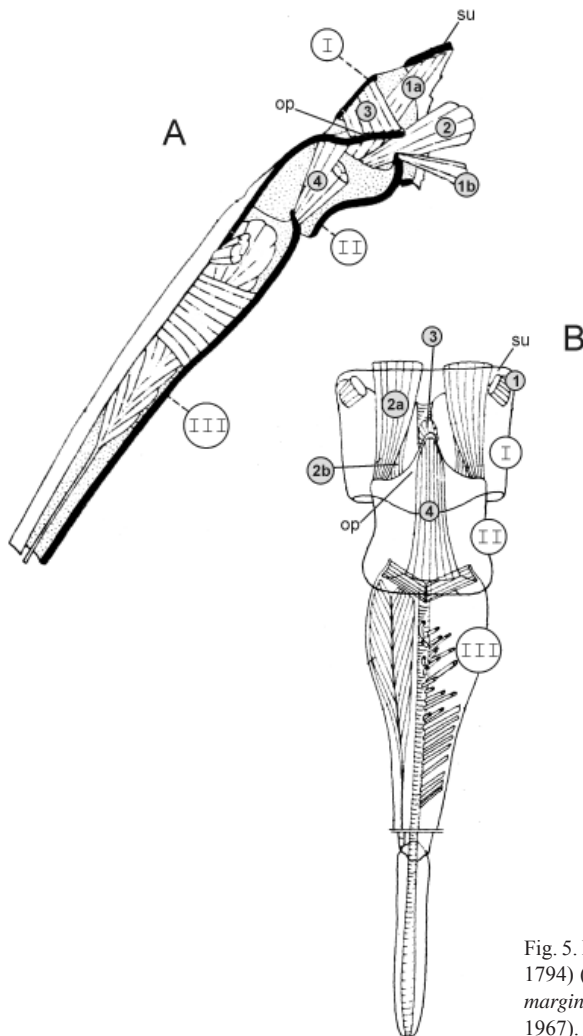


Fig. 5. Labial muscles. A – *Saldula pallipes* (Fabricius, 1794) (Saldidae) (after PARSONS 1962); B – *Ochterus marginatus* (Latreille, 1804) (Ochteridae) (after RIEGER 1967).

**First the muscle, then the fusion or reduction.** Even though a conclusive answer on fusion or loss of the sclerotized parts of the first labial segment in Reduviidae with three-segmented labium seems impossible at this stage, we can speculate on factors that might have driven the transition from four- to three-segmented labium.

Mapped on a recent phylogeny of Reduviidae by WEIRAUCH (2008) the following picture emerges for the origin of muscle A and the fusion or loss of segment 1 (Fig. 6): the evolution of muscle A at either the base of Reduvidae or Reduviidae is ambiguous since data for Pachynomidae are lacking. A larger sample of Reduviidae with three-segmented labium should be checked to verify the existence of muscle A. Another problem arises from the

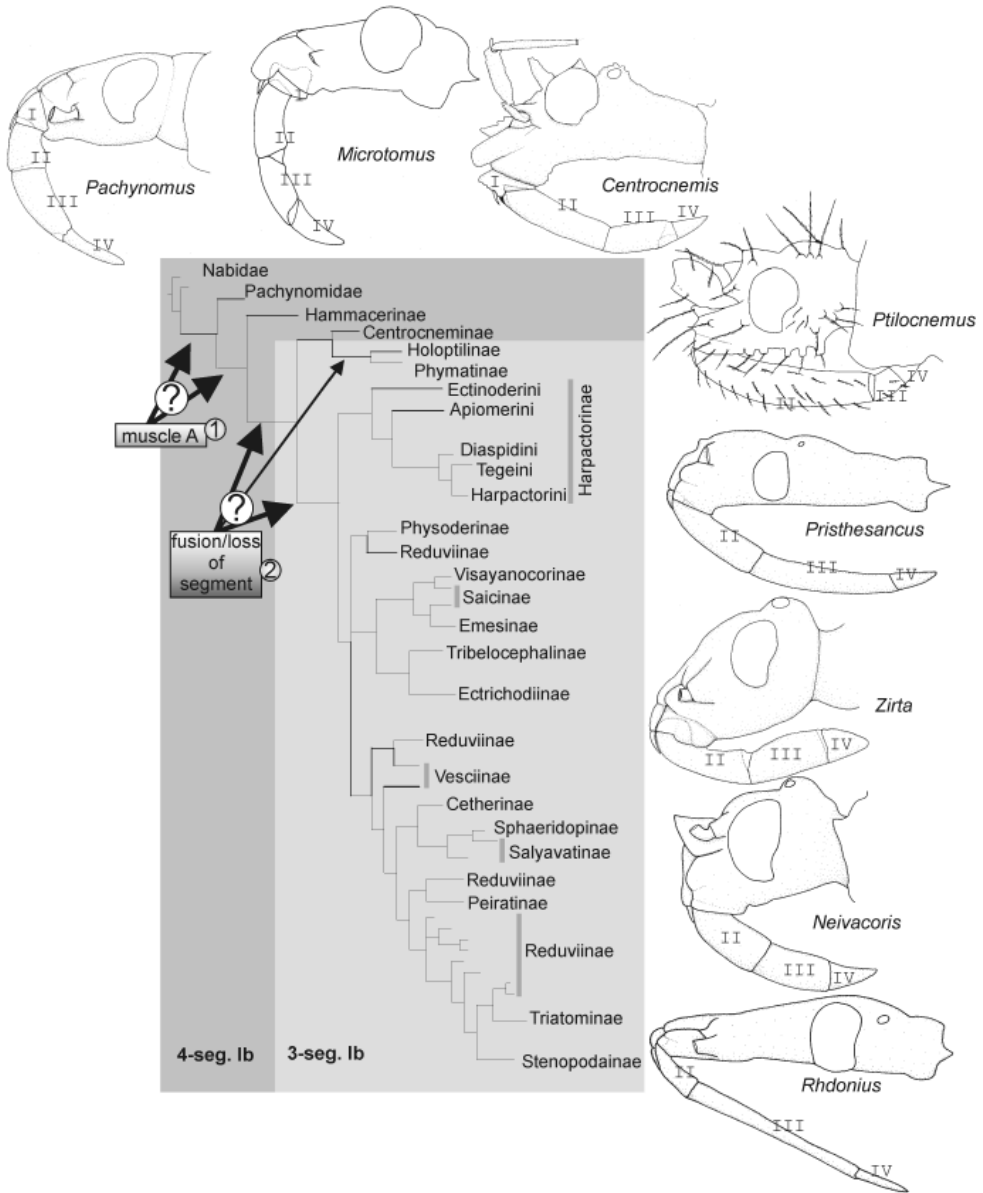


Fig. 6. Labial condition (three and four segmented) mapped on the phylogeny of Reduviidae by WEIRAUCH (2008) and possible line of events in the transition from four to three-segmented labium at the base of the group. The exact position of the origin of muscle A and of the fusion/loss of segment 1 is unclear, but the origin of the muscle predates the loss/fusion of the segment.

lack of specimens of Centrocneminae for comparative study of extrinsic labial muscles and the fact that the analysis of WEIRAUCH (2008) does not resolve the ambiguous condition of the four-segmented labium in Centrocneminae: the first labial segment in Centrocneminae might be plesiomorphic and we then would assume two independent losses of the first labial segment within the Phymatine Complex and at the base of the remaining Reduviidae (Fig. 6). The first labial segment in *Neocentrocnemis* sp. (Centrocneminae) and allies could however also be a secondary gain, with the initial loss or fusion taking place immediately after the Hammacerinae branched off (Fig. 6).

Despite these drawbacks, we can still pinpoint a hypothesis on the evolution of the three-segmented labium in Reduviidae. The phylogeny together with the results presented in this paper show that the origin of muscle A at the base of the Reduviidae predates the fusion or loss of the first segment. Muscle A originated on the movable labial segment 1, which might not have provided an optimal counter bearing for a relatively strong muscle that in Reduviidae is responsible for lifting the labium before striking out for a prey insect. Migration onto the head capsule and subsequent loss of segment 1 or fusion of the segment with the head capsule might have provide this muscle with a much more solid support.

### Acknowledgements

For the loan and donation of specimens, I thank R. Britz (The Natural History Museum, London, UK); the Insect Collection of the 'Universidade Federal do Rio Grande do Sul' (UFRGS; Jocelia Grazia, Porto Alegre, Brazil); and the American Museum of Natural History (AMNH; Randall T. Schuh, New York, USA). The results presented here are derived from my Ph.D. dissertation project (Freie Universität Berlin, FU), even though they were analyzed and written up while working in my current position at the University of California, Riverside. I thank Walter Sudhaus for supervising my dissertation and the 'AG Evolutionsbiologie' at FU for discussions and help with various technical aspects, especially Peter Lederer for introducing me to the secrets of histology. For financial support I acknowledge the 'Nachwuchsförderungsgesetz des Landes Berlin' (NaFöG), Anette Kade Graduate Student Fellowship Program at the AMNH, and the 'Berliner Programm zur Förderung der Chancengleichheit für Frauen in Forschung und Lehre'.

Dimitri Forero and Dominique Pluot-Sigwalt critically read the manuscript and I am grateful for their comments.

### References

- ANDERSEN N. M. 1982: The semiaquatic bugs (Hemiptera, Gerromorpha). Phylogeny, adaptations, biogeography, and classification. *Entomograph* **3**: 1-455.
- ARNETT R. H. Jr. 1993: *American insects: A handbook of the insects of America north of Mexico*. CRC Press LLC, Boca Raton, Florida, i-xiii + 1-1003 pp.
- BARTH R. 1952: Estudos anatômicos e histológicos sobre a subfamília Triatominae (Heteroptera, Reduviidae). I. Parte: A cabeça do Triatoma infestans. *Memorias do Instituto Oswaldo Cruz* **50**: 156-196.
- BARTH R. 1953: Anatomische und histologische Studien über die Unterfamilie Triatominae (Heteroptera, Reduviidae). III. Untersuchungen über den Stechvorgang bei Triatominae. *Memorias do Instituto Oswaldo Cruz* **51**: 11-94.

- CARAYON J. & VILLIERS A. 1968: Étude sur les Hémiptères Pachynomidae. *Annales de la Société Entomologique de France*, N. S. **4**: 703-739.
- CLAYTON R. A. 1990. *A Phylogenetic analysis of the Reduviidae (Hemiptera: Heteroptera) with redescription of the Subfamilies and Tribes*. Dissertation, The George Washington University, Washington D.C., 191 pp (unpublished).
- DE PINNA M. C. C. 1991: Concepts and tests of homology in the cladistic paradigm. *Cladistics* **7**: 367-394.
- MILLER N. C. E. 1956: *Biology of the Heteroptera*. Leonard Hill Books, London, 162 pp.
- PARSONS M. C. 1959: Skeleton and musculature of the head of *Gelastocoris oculatus* (Fabricius) (Hemiptera-Heteroptera). *Bulletin of the Museum of Comparative Zoology* **122**: 1-53.
- PARSONS M. C. 1962: Skeleton and musculature of the head of *Saldula pallipes* (F.) (Heteroptera: Saldidae). *Transactions of the Royal Entomological Society London* **114**: 97-130.
- PUTSHKOV P. V. 1993: The submental rostral segment of assassin bugs. *Journal of the Ukrainian Entomological Society* **1**: 3-8.
- PUTSHKOV P. V. 1987: *Poluzhestkokrylye. Khishchnetsy. [True bugs. Reduviidae]. Fauna Ukrainy. Vol. 21(5)*. Naukova Dumka, Kiiiv, 247 pp (in Russian).
- RIEGER C. 1976: Skelett und Muskulatur des Kopfes und Prothorax von *Ochterus marginatus* Latreille. Beitrag zur Klärung der phylogenetischen Verwandtschaftsbeziehungen der Ochteridae (Insecta, Heteroptera). *Zoomorphologie* **83**: 109-191.
- SCHUH R. T. & ŠTYS P. 1991: Phylogenetic analysis of cimicomorphan family relationships (Heteroptera). *Journal of the New York Entomological Society* **99**: 298-350.
- SNODGRASS R. E. 1935: *Principles of Insect Morphology*. McGraw-Hill, New York, 667 pp.
- TRIPLEHORN C. A. & JOHNSON N. F. 2005: *Borror and DeLong's Introduction to the Study of Insects*. Thomson Brooks/Cole, Belmont, 864 pp.
- WEBER H. 1930. *Biologie der Hemipteren*. Julius Springer, Berlin, 543 pp.
- WEIRAUCH C. 2008: Cladistic analysis of Reduviidae (Insecta: Heteroptera) based on morphological characters. *Systematic Entomology* **33**: 229-274