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Review

Form, function and evolution of the mouthparts of blood-feeding Arthropoda☆

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ABSTRACT

This review compares the mouthparts and their modes of operation in blood-feeding Arthropoda which have medical relevance to humans. All possess piercing blood-sucking proboscides which exhibit thin stylet-shaped structures to puncture the host's skin. The tips of the piercing structures are serrated to provide anchorage. Usually, the piercing organs are enveloped by a soft sheath-like part which is not inserted. The piercing process includes either back and forth movements of the piercing structures, or sideways cutting motions, or the apex of the proboscis bears teeth-like structures which execute drilling movements. Most piercing-proboscides have a food-canal which is separate from a salivary canal. The food-canal is functionally connected to a suction pump in the head that transports blood into the alimentary tract. The salivary canal conducts saliva to the tip of the proboscis, from where it is discharged into the host. Piercing blood-sucking proboscides evolved either from (1) generalized biting-chewing mouthparts, (2) from piercing mouthparts of predators, or plant sap or seed feeders, (3) from lapping or sponging mouthparts. Representatives of one taxon of Acari liquefy skin tissue by enzymatic action. During feeding, many blood-feeding arthropods inadvertently transmit pathogens, which mostly are transported through the discharged saliva into the host.

1. Introduction

Among the Arthropoda there is a variety of Insecta and Acari (ticks and mites) which nourish themselves from human blood and which are significant carriers of, pathogens. The biology of blood-feeding insects and their importance as vectors of pathogens have been well-studied for numerous examples (summaries are given in Mehlhorn and Piekarski (2002), Mullen and Durden (2002), Wenk and Renz (2003), Lehane, (2005), and Aspöck (2010)). All blood-feeding arthropods use modified extremities of the head and extensions of the head capsule or the prosoma as piercing-sucking mouthparts to obtain and feed on blood. A suction pump in the head or anterior body generates the pressure necessary to suck blood through the food tube, into the mouth and the alimentary tract. Simultaneously, a salivary pump injects saliva into the stab wound. Bioactive components of the saliva prevent blood clotting and reduce the host's sensitivity to pain (Lehane, 2005). In many species the deposition of saliva is responsible for the transmission of pathogens (Table 1), which can substantially reduce the life expectancy of infected individuals. The diseases are responsible for enormous humanitarian problems and cause exorbitant medical costs, which can decisively influence the potential economic and social development of large regions, particularly in the tropics. Blood-feeding insects, mites and ticks are thus a global problem; and it is their mouthparts which are the main organs by which these animals transfer pathogens and parasites.

The enormous morphological diversity of insect mouthparts is reflective of the many and precise adaptations to the respective diets. Despite this evolutionary diversity, the mouthparts of insects are always composed of the same set of structures (i.e., labrum, mandibles, maxillae, labium) and show a strong correspondence to the specific food preferences. The evolutionary starting point for these developments is the functional biting-chewing kind of mouthparts (Snodgrass, 1935), which are adapted to receive solid foods. To a certain extent, liquids can also be ingested by licking movements of the mouthparts. The generalized biting-chewing mouthparts enclose a preoral cavity, adjacent the actual mouth and the duct opening of the salivary glands. The preoral cavity is closed anteriorly by the labrum, and the inner side is usually lined by the epipharynx. The mandibles are the biting structures which shred the food. These paired tong-like organs bear frontally a sharpened edge and in the posterior section a chewing surface.

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Table 1
Medical significance of blood-feeding arthropods. Relevant taxa, their distribution, pathogens transmitted, and diseases caused. References after the diseases refer predominantly to Aspöck (2010).

Blood-feeding taxa (distribution) (references)	Blood-feeding on humans	Hematophagous stages	Pathogens	Major diseases caused (references)
Insecta: Heteroptera/True Bugs				
Reduviidae: Triatominae/ Assassin bugs (Southern parts of N. America, central and S. America) (Krinsky, 2002a)	ca. 100 species of *Triatoma, Rhodnius, Dipetalogaster, Panstrongylus*	Nymphs, adults	*Trypanosoma cruzi*	Chagas disease (Walochnik and Aspöck, 2010b)
Cimicidae/Bed Bugs (worldwide) (Krinsky, 2002a)	*Cimex lectularius, C. hemipterus, C. columbarius, C. pipistrelli, Oeciacus hirundinis*	Nymphs, adults	Hepatitis B Virus (?), occasionally other viruses and bacteria (?)	No regularities (Pospischil, 2010)
Phthiraptera/Lice				
Pthiridae/Crab Lice (worldwide) (Durden, 2002)	*Pthirus pubis*	Nymphs, adults	No evidence	No evidence (Habedank, 2010)
Pediculidae/Pediculid Lice (worldwide) (Durden, 2002)	*Pediculus capitis*	Nymphs, adults	No evidence	No evidence (Habedank, 2010)
	Pediculus humanus	Nymphs, adults	*Rickettsia prowazekii, Bartonella quintana, Borrelia recurrentis*	Epidemic Typhus (Dobler, 2010). Trench Fever, Wolhynia Fever, Bacillary Angiomatosis. Louse-Borne (Epidemic) Relapsing Fever (Stanek, 2010)
Diptera/Flies				
Culicidae/Mosquitoes (worldwide) (Foster and Walker, 2002)	Numerous species of Anophelinae (*Anopheles*) and Culicinae (*Aedes, Ochlerotatus, Culex, Culiseta, Mansonia,* etc.)	Female imagines	Numerous arboviruses, particularly of Togaviridae (Alphavirus), Flaviviridae (Flavivirus), Bunyaviridae (Orthobunyavirus, Phlebovirus)	Numerous arbovirus infections associated with (acute) febrile illness, arthralgia, skin rash, hemorrhagic fever, and/or affliction of CNS (meningitis, encephalitis): Western, Eastern, Venezuelan Equine Encephalitis, Chikungunya; Dengue, Yellow Fever, Japanese Encephalitis, West Nile, Murray Valley Encephalitis, St. Louis Encephalitis; California Encephalitis, Rift Valley Fever etc. (Aspöck and Dobler, 2010; Dobler and Aspöck, 2010b)
			Plasmodium falciparum, P. vivax, P. ovale, P. malariae, P. knowlesi and other species	Malaria tropica, Malaria tertiana, Malaria quartana, Malaria quotidiana (Wernsdorfer and Wernsdorfer, 2010; Löscher et al., 2010)
			Wuchereria bancrofti, Brugia malayi, B. timori	Lymphatic Filariosis, Elephantiasis (Auer and Aspöck, 2010a)
			Dirofilaria immitis, D. repens	Dirofilarioses (Auer and Aspöck, 2010c)
Simuliidae/Black Flies (worldwide) (Adler and McCreadie, 2002)	Numerous species of *Simulium, Prosimulium, Austrosimulium*	Female imagines	*Onchocerca volvulus*	Onchocercosis/River Blindness (Auer and Aspöck, 2010e)
			Mansonella streptocerca	Subcutaneous Mansonellosis (Auer and Aspöck, 2010b)
Ceratopogonidae/Biting Midges (worldwide) (Mullen, 2002a)	Numerous species of *Culicoides*, one species of *Leptoconops*	Female imagines	*Mansonella ozzardi, M. perstans, M. streptocerca*	Mansonellosis of connective tissues or serous cavities (Auer and Aspöck, 2010b)
Psychodidae: Phlebotominae/ Sandflies (tropics, subtropics, warm temperate regions) (Rutledge and Gupta, 2002)	Numerous species of *Phlebotomus* and *Lutzomyia*	Female imagines	Numerous arboviruses of Bunyaviridae (Phlebovirus)	Pappataci Fever, Toscana Sandfly Fever (Dobler and Aspöck, 2010c)
			Bartonella bacilliformis	Oroya Fever, Verruga peruana (Carrion's Disease) (Löscher 2010)
			Leishmania spp.	Various forms of Visceral and Cutaneous Leishmanioses (Walochnik and Aspöck, 2010c)
Rhagionidae/Snipe Flies (Australia, North America) (Hall and Gerhardt, 2002)	Several species of *Spaniopsis, Symphoromya*	Female imagines	No evidence	No evidence (Kerr, 2010)
Tabanidae/Horse Flies (worldwide) (Mullens, 2002)	Numerous species of *Tabanus, Chrysops, Hybomitra, Philoliche, Haematopota,* etc.	Female imagines	*Bacillus anthracis*	Anthrax (Fleischer and Frangoulidis, 2010)
			Francisella tularensis	Tularemia (Grassberger, 2010)
			Loa loa	Loaosis (Auer and Aspöck, 2010d)
Glossinidae/Tsetse Flies (Africa, Arabian Peninsula) (Krinsky, 2002b)	Several species of *Glossina*	Imagines (both sexes)	*Trypanosoma brucei gambiense, T.b. rhodesiense*	African Sleeping Sickness (Walochnik and Aspöck, 2010a)

Table 1 (*continued*)

Blood-feeding taxa (distribution) (references)	Blood-feeding on humans	Hematophagous stages	Pathogens	Major diseases caused (references)
Muscidae (worldwide) (Moon, 2002)	Several species of *Stomoxys*, *Hydrotaea*, *Haematobia*, etc.	Imagines (both sexes)	No regularities	No confirmed cases
Siphonaptera/Fleas				
Pulicidae, Tungidae, etc. (worldwide) (Durden and Traub, 2002)	*Pulex irritans*, *Ctenocephalides canis*, *C. felis*, *Xenopsylla cheopis*, *Tunga penetrans*, etc.	Imagines (both sexes)	*Yersinis pestis*	Plague (Pfeffer, 2010; Schmiedel, 2010)
			Rickettsia typhi	Endemic Typhus (Dobler, 2010)
			Rickettsia felis	Cat-Flea Typhus (Beck and Prosl, 2010b; Dobler, 2010)
Lepidoptera/Butterflies and Moths				
Noctuidae/Owlet Moths (Southeast Asia) (Mullen, 2002b)	Several species of *Calyptra*	Male imagines	No evidence	No evidence (Büttiker et al., 1996; Bänziger, 1980; Bänziger, 1989; Zaspel et al., 2011)
Arachnida: *Acari/Ticks and Mites*				
Ixodidae/Ticks (worldwide) (Sonenshine et al., 2002)	Numerous species of *Ixodes*, *Amblyomma*, *Haemaphysalis*, *Hyalomma*, *Dermacentor*, *Rhipicephalus*	Larvae, nymphs, adults of both sexes	Numerous arboviruses of Flaviviridae (Flavivirus), Bunyaviridae (Nairovirus), Reoviridae (Coltivirus)	Numerous arbovirus infections associated with acute febrile illness, frequently with hemorrhagic fever and/or affliction of CNS (Meningitis, encephalitis): Tick-Borne Encephalitis (TBE), Omsk Hemorrhagic Fever (OHF), Kyasanur Forest Disease (KFD); Crimean Congo Hemorrhagic Fever (CCHF); Colorado Tick Fever (Aspöck and Dobler, 2010; Dobler and Aspöck, 2010a)
			Rickettsia rickettsii	Rocky Mountain Spotted Fever (Dobler, 2010)
			Rickettsia conorii	Boutoneuse Fever (Mediterranean Spotted Fever) (Dobler, 2010)
			Rickettsia africae	African Tick Bite Fever (Dobler, 2010)
			Rickettsia helvetica	Uneruptive Tick Bite Fever (Dobler, 2010)
			Rickettsia slovaca	TIBOLA (Dobler, 2010)
			Ehrlichia chaffeensis	Human Monocytic Ehrlichiosis (Dobler, 2010)
			Anaplasma phagocytophilum	Human Granulocytic Anaplasmosis (Dobler, 2010)
			Coxiella burnetii	Q-Fever (Kimmig, 2010)
			Borrelia burgdorferi, *B. afzelii*, *B. garinii* and other species	Various forms of Lyme Borreliosis (Stanek, 2010)
			Francisella tularensis	Tularemia (Schmiedel, 2010)
			Babesia spp.	Babesiosis (Walochnik and Aspöck, 2010d)
Argasidae/Soft Ticks (tropics, subtropics, temperate regions) (Sonenshine et al., 2002)	Several species of *Argas* and *Ornithodoros*	Larvae, nymphs, adults of both sexes	*Borrelia duttonii* and other species	Endemic Relapsing Fever (Stanek, 2010)
Dermanyssidae (worldwide) (Mullen and Oconnor, 2002)	*Lyponyssoides sanguineus*	Adults of both sexes, nymphs (partially)	*Rickettsia akari*	Rickettsial Pox (Beck and Prosl, 2010a; Dobler, 2010)
Trombiculidae/Harvest Mites (worldwide) (Mullen and Oconnor, 2002)	*Leptotrombidium* spp.	Larvae/chiggers	*Orientia tsutsugamushi*	Scrub Typhus (Dobler, 2010; Kampen, 2010)

Each mandible is connected to the head capsule by two points of articulation. Abductor muscles that open the mandibles are attached by tendons to the inner base, while the large and powerful adductor muscles on the outer base close the mandibles. The maxillae are paired and contain the two basic components (cardo and stipes) which articulate with the head capsule and which bear an appendage-like, segmented palp (maxillary palp), as well as sensory organs. The stipes gives rise to two apical parts, the lacinia and galea. The lacinia lies medially and serves to transfer pieces of food bitten off by the mandibles into the mouth opening. The laterally positioned galea overlaps the lacinia, is membranous and bears many sensory organs. The labium consists of several sclerites (submentum, mentum, prementum) and bears the appendage-like segmented palps (labial palps). Arising between the labial palps are two pairs of lobes, the median glossae and the lateral paraglossae. The tongue-like hypopharynx is situated in the posterior preoral cavity. The opening to the salivary glands is located beneath the hypopharynx and the anterior surface of the labium, called the salivarium (Grimaldi and Engel, 2005).

All blood-feeding insects possess piercing-sucking mouthparts modified from the basic pattern. Convergent paths of evolution have led in various groups of insects to the construction of different piercing-proboscides which are able to pierce the skin of vertebrates and extract blood from deeper lying tissues. Despite the different structural and functional mechanisms in the mouthparts, several characteristic similarities are common to the piercing-proboscides of blood-feeding arthropods. These include structures for puncturing, penetration and anchoring of the mouthparts, as well as a sheath-like covering, a food-canal and almost always a separate canal for saliva (Table 2).

Like all Arachnida, ticks and mites have no head, rather the anterior body section which is distinguished from the posterior body section, is referred to as the capitulum or gnathosoma. It contains two paired extremities, the chelicerae and pedipalps, both of which contribute to the uptake of food. The construction and function of the feeding organs will be discussed for two groups of Acari, Ixodidae and Trombiculidae. Representatives of both regularly suck blood from humans. They are vectors of diseases and thus are of medical importance (Table 1). Ticks of the family Argasidae only rarely transmit pathogens, however persons sensitive to the toxic components of the saliva may react symptomatically and experience tachycardia or breathing difficulties (Sonenshine et al., 2002; Kleine-Tebbe et al., 2006).

The goal of this review is to comparatively analyze the structures and function of the mouthparts of arthropods which regularly feed on human blood and which, therefore, play an important role as vectors of pathogens. The similarities, differences and characteristics of various blood-feeding organs are presented that allow arthropods in a relatively short period of time to draw blood, while remaining largely unnoticed. An extended version of this review was first published in German by Krenn and Aspöck (2010) as a chapter in the book "Krank durch Arthropoden" (Aspöck, 2010).

2. Material and methods

2.1. Studied species

The mouthparts of the following species were investigated as exemplary for the various groups of blood-feeding arthropods.

Hexapoda/Insecta: *Triatoma infestans* (Klug, 1834) (Reduviidae, Heteroptera), *Cimex lectularis* (Linnaeus, 1758) (Cimicidae, Heteroptera); *Pediculus humanus capitis* (De Geer, 1778) (Pediculidae, Phthiraptera); *Anopheles stephensi* (Liston, 1901) (Culicidae, Diptera), *Simulium* sp. (Simuliidae, Diptera), *Phlebotomus duboscqi* (Neveu-Lemaire, 1906) (Psychodidae, Diptera), *Tabanus bromius* (Linnaeus, 1758) (Tabanidae, Diptera), *Glossina* sp. (Glossinidae, Diptera), *Stomoxys* sp. (Muscidae, Diptera); *Ctenocephalides* sp. (Pulicidae, Siphonaptera); Arachnida/Acari: *Ixodes ricinus* (Linnaeus, 1758) (Ixodidae, Acari).

2.2. Scanning electron microscopy

Scanning electron microscopy was used for illustration of the external morphology. Ethanol-fixed specimens were dehydrated in absolute ethanol, submersed in Hexamethyldisilazane, air-dried, sputter-coated with gold and examined in a Jeol JSM-35 CF scanning electron microscope at 10–12 kV.

2.3. Section technique

To elucidate the anatomy of the mouthparts the semi-thin section technique was used. The specimens were fixed in 70% ethanol or in alcoholic Bouin solution and were stored in 70% ethanol. The bodies were dehydrated in ascending series of ethanol (80%, 90% and 3 times 100%), 3 times 100% acetone and embedded in ERL-4206 epoxy resin or Agar Low Viscosity Resin under vacuum impregnation. Polymerization was achieved at 65–70 °C within 24 h (procedure see Pernstich et al., 2003). Semi-thin section (1 µm thickness) were cut using diamond knives and subsequently stained using a mixture of methylene blue and Azure blue.

2.4. Micrographs

Digital photos of the section were taken with a Nikon FXA light microscope. The photos were optimized using Adobe Photoshop CS

Table 2
Construction of the piercing-proboscis and function of individual parts in blood-feeding insects and mites; compiled and updated from Babos (1964), Smith (1985), Nagatomi and Soroida (1985), McKeever et al. (1988), Chaudonneret (1990), Tröster (1990), Büttiker et al. (1996), Lehane (2005) and own investigations.

	Proboscis formation			Function during feeding		
	Proboscis sheath	Food-canal	Salivary canal	Puncturing organ	Anchorage	Piercing organ
Insecta: Hemiptera						
Reduviidae	Labium	Laciniae	Laciniae	Mandible	Mandibular teeth	Lacinia
Cimicidae	Labium	Laciniae	Laciniae	Mandible	?	Lacinia, Mandible
Phthiraptera						
Phthiridae, Pediculidae	Evagination of labium	Hypopharynx	Hypopharynx, Prementum	Epipharyngeal teeth	Epipharyngeal teeth	Hypopharynx, Prementum
Diptera						
Culicidae	Labium	Labrum, Hypopharynx	Hypopharynx	Labrum, Mandible, Laciniae	Lacinial teeth	Lacinia
Simuliidae	Labium	Labrum, Mandible	Hypopharnyx, Mandible	Labrum, Mandible	Lacinial teeth	Mandible, Lacinia
Ceratopogonidae	Labium	Labrum, Mandible	Mandible, Hypopharynx	Mandible	Lacinia	Mandible
Psychodidae: Phlebotominae	Labium	Labrum, Mandible, Laciniae, Hypopharynx	Mandible, Hypopharynx	Mandible	Lacinia	Mandible
Rhagionidae	Detailed studies absent			Mandible, Lacinia (?)	?	Mandible, Lacinia (?)
Tabanidae	Labium	Labrum, Mandibles	Hypopharynx	Mandible, Lacinia	Lacinial teeth	Mandible, Lacinia
Glossinidae	Maxillary palps	Labrum, Labium	Hypopharynx	Prestomal-teeth	Prestomal-teeth	Prestomal-teeth
Muscidae: Stomoxinae	Absent	Labrum, Labium	Hypopharynx	Prestomal-teeth	Prestomal-teeth	Prestomal-teeth
Siphonaptera	Labium, Labial palps	Labrum/Epipharynx, Laciniae	Laciniae	Lacinia	Lacinial teeth	Lacinia
Lepidoptera						
Noctuidae: *Calyptra*	Absent	Galeae	Galeae	Galeal apex	Galeal sensillae	Galea
Arachnida: Acari						
Ixodidae Argasidae	Pedipalps	Base of chelicera, Hypostome	Base of chelicera, Hypostome	Hypostome	Hypostomal teeth	Chelicerae

4 to improve brightness and contrast as well as to prepare the micrographs.

3. Results

3.1. Diversity of blood-feeding mouthparts of insects

3.1.1. Heteroptera (true bugs)

All true bugs have an elongated piercing-proboscis, which is basically identical in all species and in all developmental stages. This applies, as well, to bugs that do not feed on blood, but which pierce and suck fluids, for example, from seeds and fruits. One group, the assassin bugs (Reduviidae), contains large tropical species which regularly suck blood from humans. All of the approximately 70 species of bed bugs (Cimicidae) are blood-feeding ectoparasites; some species prey on humans.

3.1.1.1. Reduviidae (assassin bugs). The function and morphology of the proboscis of assassin bugs of the genera *Triatoma* and *Rhodnius* are well-studied (e.g., Barth, 1952; Smith, 1985; Wenk et al., 2010) since these insects, in comparison to other blood-feeders, attain a body size of several centimeters. Their piercing-proboscis is about 5–6 mm long and is normally folded under the body when not in use (Fig. 1A). The labrum is a narrow plate, which together with parts of the head capsule forms the frontal base of the proboscis. The proboscis consists of a sheath and piercing stylets. The latter are formed by the mandibles and the laciniae of the maxillae, which are entirely covered by the sheath and are usually not visible from the outside (Fig. 1B). Frontally the labium forms a deep groove that completely surrounds the stylets which can be projected outward (Fig. 1B and C). The paired mandibles are trough-like in cross-section, with a diameter of about 20 μm and are dentate at the apex. The paired laciniae, which lie between them, are elongate, very thin (with a diameter of about 10 μm) and lack teeth. The laciniae are well-connected to each other through grooves and folds anteriorly and posteriorly; they form the broad food-canal, in addition to the narrower salivary canal (Fig. 1B).

The process of feeding was described in detail for species of *Triatoma* and *Rhodnius* (Friend and Smith, 1971; Smith, 1985; Wirtz, 1987). The proboscis folds outward between 90° and 180° and may even point forward (Wenk et al., 2010). The apex of the labium presses against the host's skin, and sensory hairs serve to locate which body part is suitable for piercing. The mandibles are then moved alternatively in rapid succession by protractor and retractor muscles in the head and plunge deep into the skin of the host. The labium does not penetrate the skin but bends backward. Each mandible bears backward-directed teeth that sink into the skin enabling the other mandible to advance. To anchor the proboscis, the mandibles need to only superficially penetrate the skin. The laciniae, located between the mandibles, however, project deeply into the wound due to their quiver-like movements, which are more rapid than the movements of the mandibles. During this process, the laciniae may bend and thus change the course of penetration, resulting in a curved route. Experiments with penetrable membranes show that each lacinia can be projected to a different length. When a blood vessel is tapped, the left lacinia retreats slightly; the connection between the two maxillary parts opens, and the tip of the left lacinia bends back during intake of the blood. This position presumably facilitates the uptake of blood along the food-canal, while the slightly bent tip serves to brace the mouthparts in the tissue (Wirtz, 1987). Proximally, the hypopharynx extends into the food tube like a wide tongue. The distal region of the hypopharynx is acute and x-shaped in cross-section. It interlocks with the laciniae in the same manner as a fixed slider of a zip-lock (Wenk et al., 2010).

The salivary duct extends through the hypopharynx and emerges at the base of laciniae. Saliva is forced by action of the salivary pump through the salivary canal between the laciniae. The salivarium is located under the food-canal in the head. It consists of a salivary pump formed by a cavity and with a moveable part which forces saliva into the salivary duct (Wenk et al., 2010). Muscles pull this process upward, thereby increasing the volume of the pump's cavity and saliva can be sucked in. The elasticity of the wall returns the process back to its original position and presses saliva into the salivary canal of the mouthparts. There are two separate efferent ducts, i.e., the dorsal duct which conducts saliva directly between the laciniae and the ventral duct which extends into a bag which can be closed by a cuticle and opened by muscles (Wenk et al., 2010). At the apex of the mouthparts, the saliva flows out of the opening on the base of the foldable section of the lacinia into the pierced wound. Saliva is not exclusively discharged into the maxillary salivary duct but flows also directly into the tube of the labium which encloses the piercing structures (Wenk et al., 2010).

The food-canal is directly connected to the suction pump in the oral cavity, and the pumping action draws blood into the space between the laciniae (Wenk et al., 2010). Large quantities of blood can be rapidly extracted by the efficient suction pump, which occupies a large part of the head. *Rhodnius* can ingest, for example, up to 300 mg of blood in about 15 min. The floor of the pump consists of a U-shaped plate which is elastically connected to the

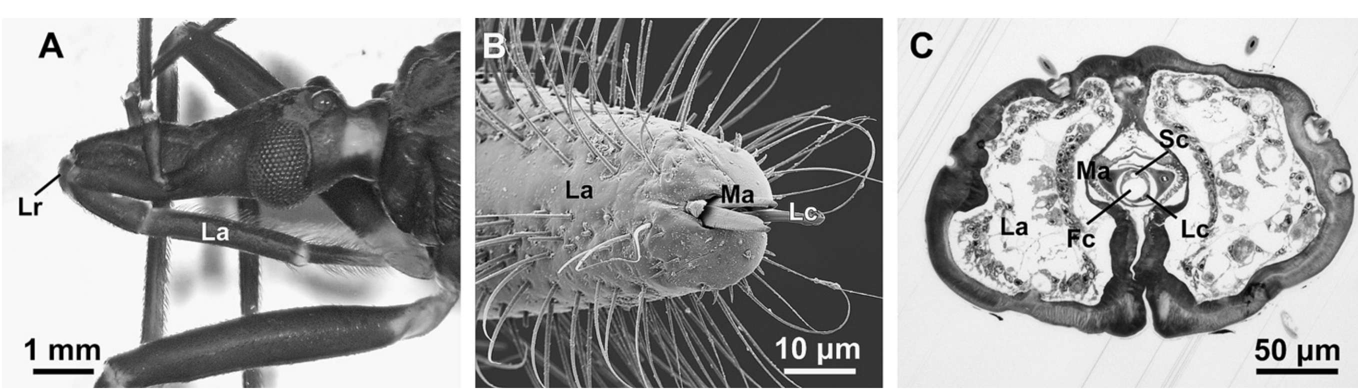

Fig. 1. The head and mouthparts of the blood-feeding assassin bug *Triatoma infestans* (Reduviidae, Heteroptera). A. Piercing-proboscis folded under the head. The labrum (Lr) covers the base of the proboscis; the labium (La) is a threefold covering sheath the piercing structures. B. Apex of the labium (La). The mandible (Ma) and lacinia (Lc) form the piercing structures, which can be projected beyond the sheath covering. C. Cross-section of proboscis. The laciniae (Lc) form the food-canal (Fc) and the very thin salivary canal (Sc). The mandibles (Ma) are laterally positioned, the labium (La) surrounds the piercing structures.

flexible roof. From there, large muscles extend to the head capsule and cause the cavity to expand. The suction pump probably produces a strong negative pressure in the order of 1–2 atm. The pumping rate is approximately 7 cycles per second, each cycle draws about 0.06–0.07 µl of blood (Kingsolver and Daniel, 1995). Immature assassin bugs are capable of ingesting up to 12 times their weight in blood during a single meal. They require at least one meal of blood for each larval stage of development. The imagines can consume a volume of blood three times their body weight. A person can be bitten up to 25 times in a night (Lehane, 2005).

3.1.1.2. Cimicidae (bed bugs). All species of bed bugs are wingless and have a flattened, light brown body about 4–7 mm in size. They feed exclusively on blood. Two species are synanthropic and attack humans. A third species only occasionally parasitizes humans; it is tropical and normally feeds on blood from bats (Lehane, 2005).

The basic construction of the mouthparts in Cimicidae is identical to that in Reduviidae. However in contrast to the assassin bugs, which can extend their proboscis forward, the proboscis of bed bugs can only be extended downward (Usinger 1966). The piercing structures are formed by the mandibles and laciniae, and when not in use they are normally enclosed in a large central groove of the labium (Fig. 2A and B). The proximal base of the proboscis is developed by the labrum (Fig. 2A). The laciniae build both the food-canal and the salivary canal. These structures are extremely thin hollow tubes that are tightly connected to each other (Fig. 2C). The labium is not the piercing organ; rather it bends back and partly telescopes together (Weber, 1933). The apex of the mandibles first punctures the skin. In contrast to the Reduviidae, both the thin mandibles and the laciniae are used to penetrate deep into the host's skin (Smith, 1985). The behavior of bed bugs, when localizing the host and when selecting a suitable injection site, as well as regarding the frequency and amount of blood taken, are summarized in Reinhardt and Siva-Jothy (2007). A hungry bed bug can consume a volume of blood between 130% and 200% of its body weight.

3.1.2. Phthiraptera (animal lice): Anoplura (sucking lice)

The Phthiraptera comprise various groups of wingless ectoparasites which live on vertebrates. These are the Amblycera (bird lice) and Ischnocera (chewing lice), which possess biting-chewing mouthparts to feed on the skin, hair and feathers of their hosts, as well as the Rhynchophthirina (elephant lice) and the Anoplura (sucking lice) which possess a piercing-proboscis to suck blood. The representatives of the Anoplura are hematophagous in all stages of development and usually remain on their hosts for their entire life. Three species from the genera *Pediculus* and *Phthirus* parasitize humans; they are a few millimeters long and equipped with hook-like claws on their legs (Fig. 3A).

The essential parts of the piercing apparatus in *Pediculus* consist of the labium and hypopharynx, which lie on top of each other. The dorsal tube is an extension of the hypopharynx, and the ventral piercing stylet emerges from the prementum of the labium. Remnants of the mandibles and maxillae located in the head contribute only to the formation of the base of the piercing-proboscis (Tröster, 1990). At rest, the mouthparts are normally not visible from the outside but are retracted into the head (Fig. 3A). They retreat into a sac-like structure (i.e., the proboscis sheath) in the oral/preoral cavity (Fig. 3B).

The head terminates in a short and extendable tube, known as the buccal funnel ("Mundkegel", Weber, 1933). It corresponds to the labrum. The opening of the buccal funnel is set in an invagination of the epipharynx which bears backward-pointing teeth that allow the insect to retain its grip in the host's skin at the beginning of the piercing process (Wenk and Renz, 2003). The buccal funnel is pressed against the skin of the host. Due to an increase in hemolymphic pressure, the funnel evaginates and stretches the skin of the host to permit the tips of the ventral stylets to cut into it. The fork-like proximal ends of the hypopharynx serve as long muscle attachment sites (Fig. 3B) for the protractor muscles which originate on the front of the proboscis sheath. Contraction of these muscles forces the piercing stylets out of the proboscis sheath. The dorsal stylet forms the food-canal (Fig. 3C). The ventral stylet constitutes the actual piercing organ, and it bears pointed teeth at the apex. The sclerotized prementum is rod-shaped and forms the salivary canal which opens apically to allow the release of saliva directly into the wound (Tröster, 1990).

The dorsal and the ventral stylet penetrate the skin of the host by alternating movements of the two piercing stylets. When a blood vessel is tapped, blood is drawn into the food-canal by the activity of the suction pump, which consists of two hollow cavities in the head. The first chamber is probably the mouth opening; the second is formed by the pharynx. The walls of both cavities consist of an arrangement of ring-like muscles that compress the pump. Dilator muscles which extend into the head capsule expand the suction pump. The interaction of these antagonistic muscle groups contract and expand the pump and promote the transport of blood into the foregut. Particular muscles of the proboscis sheath and the retractor muscles which are attached to the head remove the

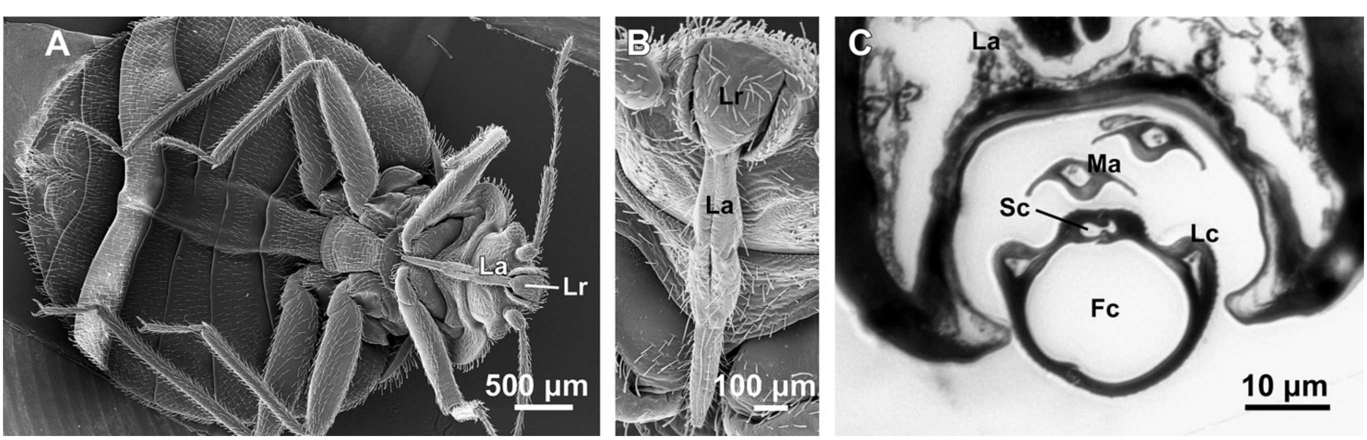

Fig. 2. The head and mouthparts of the bed bug *Cimex lectularius* (Cimicidae, Heteroptera). A. The piercing-proboscis folded under the body. B. The labium (La) forms a sheath covering to the piercing structures; labrum (Lr). C. Cross-section of proboscis. The piercing structures are formed by mandibles (Ma) and interconnected laciniae (Lc); the laciniae surround the food-canal (Fc) and salivary canal (Sc).

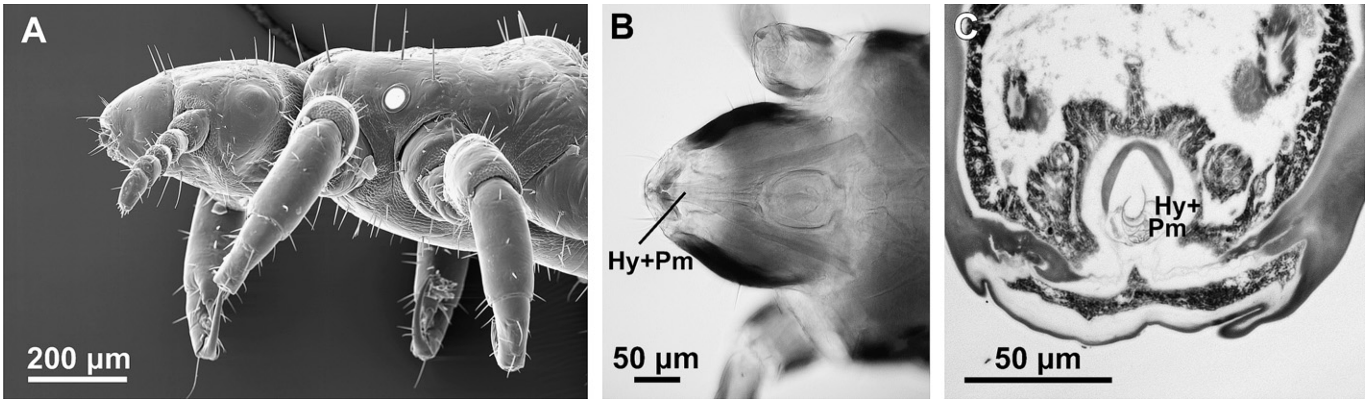

Fig. 3. A. Anterior body of a head louse *Pediculus humanus capitis* (Anoplura). Piercing structures are retracted into the head and not visible. B. Transparent preparation showing the piercing structures inside the head. C. Cross-section of the frontal head; piercing structures (hypopharynx Hy, prementum Pm) in a cavity, formed partly by rudimentary maxillae and mandibles.

piercing apparatus. A hydrostatical mechanism is involved to compensate the volume of the stylets in the head capsule and allows complete withdrawal and protraction (Tröster, 1990). Up to one third of the insect's body mass can be ingested in a single sucking cycle, and the insect can imbibe several meals of blood each day (Lehane, 2005).

3.1.3. *Diptera (flies and midges)*

We listed eight groups of Diptera that are known to be at least occasionally parasitic on humans and that may transfer a great variety of pathogens (Table 1). Generally, they visit their host organisms for brief periods of time to extract blood. All imagines of Diptera have more or less elongated sucking mouthparts and a suction pump in the head. The most prominent part of the proboscis is formed by the labium which ensheathes the other components (i.e., labrum, mandibles, laciniae and hypopharynx) and leads to the sponge-like labellum (homologs to the labial palps) at the apex. The food-canal is formed at least partly by the labrum while the elongated hypopharynx builds the salivary canal.

3.1.3.1. Culicidae (mosquitoes). Mosquitoes are commonly not specialized to particular host organisms. The bulk of the worldwide 3500 species is potentially of great importance for humans (Lehane, 2005) since they may transmit various pathogens (Table 1). The piercing-proboscis is several millimeters long and usually slightly shorter than the body. Generally, only the females are blood-feeders. In addition to a blood diet, female Culicidae feed on plant fluids (e.g., floral nectar), which are the only sources of food for the males. Accordingly, the piercing structures of the male proboscis are reduced (Wahid et al., 2003). The female proboscis in typical hematophagous mosquitoes, such as from the genera *Aedes*, *Anopheles* and *Culex*, consists of long, thin stylets formed by the labrum, mandibles, laciniae and hypopharynx, which lie in a groove of the labium (Fig. 4A and C). When the insect is at rest, all piercing structures are enveloped by the labium and the proboscis is folded under the body.

The labrum forms a thin and almost entirely enclosed tube with an angular apex, and together with the hypopharynx it forms the food-canal of proboscis (Fig. 4B). The paired mandibles are modified to thin acutely pointed structures. The paired laciniae of the maxillae are long, extremely thin and finely serrate at the tip (Fig. 4D); they build the main organ for piercing (Snodgrass, 1959). Inside the head capsule are protractor and retractor muscles which are attached to the base of the laciniae and cause its forward and backward movements. Elastic structures store energy for a rapid protraction when the respective muscle is released (Wenk, 1980). The multi-segmented and often elongate maxillary palp emerges from the base of the maxillae (Fig. 4A). The hypopharynx is likewise greatly elongated and forms a singular stylet which contains the very thin salivary canal (Fig. 4B). The labella form the apex of the labium and bear sensory organs (Fig. 4C), which presumably serve to locate a suitable area of the skin to penetrate.

To begin feeding, the labella of the proboscis are brought into contact with the host. The labium remains on the outside the host's body and bends backward when the stylets penetrate the skin. The laciniae cut deeper into the skin by sliding longitudinally against each other, while the fine teeth at the apex provide temporary anchorage. The other piercing organs are probably pulled along with the laciniae since appropriate muscles are not found in all investigated species (Smith, 1985). Blood is withdrawn from small blood vessels. The average amount of blood taken by *Aedes aegypti* is 4.2 μl; the rate of uptake is about 0.0016 μl/s (Kingsolver and Daniel, 1995). As in other Diptera, a series of two suction pumps ensure a continuous stream of blood. The anterior pump is a formation of the preoral cavity, it has a solid floor and a flexible roof, which is stretched and compressed by muscle activity. The posterior suction pump is located in the pharynx; that can be extended by muscles and is probably the more powerful of the two suction pumps (Kingsolver and Daniel, 1995).

The withdrawal of stylets is probably achieved by the alternating forward and backward motion of the laciniae. At the same time, the mosquitoes pull the piercing organs out of the host's skin by extending their legs and by contraction of head muscles.

3.1.3.2. Simuliidae (black flies). Many species of these hematophagous insects are host-specific, whereby only a small fraction of the 1500 species are relevant to humans (Lehane, 2005). The female Simuliidae are small but very unpleasant blood-feeders. Their mouthparts are relatively short and form a hardly recognizable piercing-proboscis (Fig. 5A). Their stab causes a pool of blood to form under the skin from which they are able to suck using their short proboscis. The labrum, mandibles, laciniae and hypopharynx compose the actual piercing organ, which lies in a groove formed by the labium which apically bears the labella (Fig. 5A) (Wenk, 1962; Chaudonneret, 1990).

The labrum is a triangular, elongated plate, which together with the anteriorly positioned mandibles form the food-canal (Fig. 5B). To begin feeding, the labrum and hypopharynx are extended and press against the host's skin so that the terminally positioned teeth bend forward or backward. The serrate mandibles lie adjacent to each other and overlap. The contraction of the adductor muscles results in a scissors-like movement of the

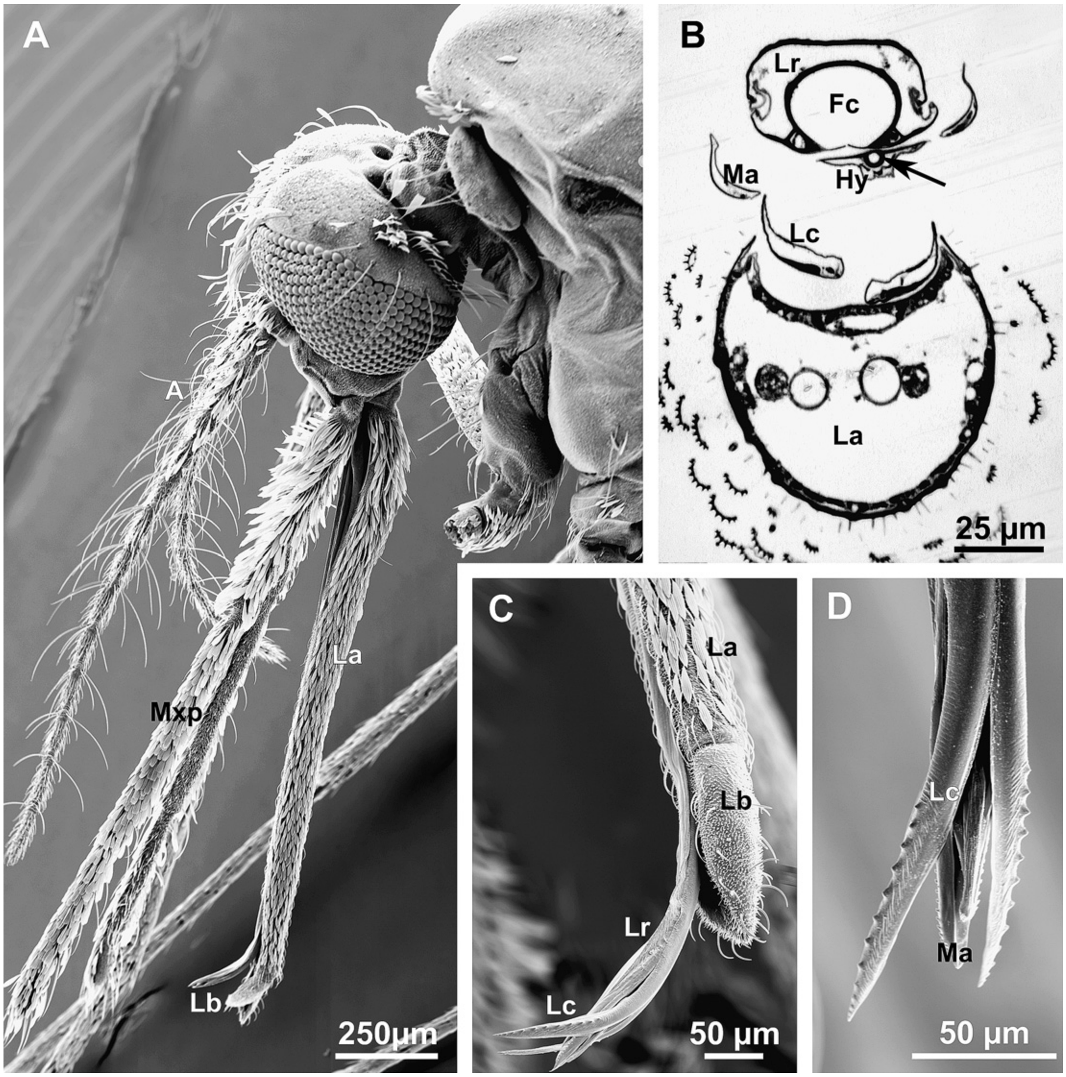

Fig. 4. Head and proboscis of a female mosquito *Anopheles stephensi* (Culicidae, Diptera). A. Piercing structures lie in the scaled sheath, which is formed by the labium (La); apex formed by the labella (Lb); large maxillary palps (Mxp); antenna (A). B. Cross-section of proboscis; the labrum (Lr) forms the food-canal (Fc), which is covered by hypopharynx (Hy); arrow points to the salivary canal; due to preparation, the stylets (mandibles Ma; laciniae Lc) are displaced outside the groove of labium (La). C. The piercing structures, labrum (Lr) and laciniae (Lc) protrude beyond the labella (Lb). D. The tips of the lacinia (Lc) and the mandibles (Ma) are finely serrate.

mandibles leading to an incision in the skin (Wenk, 1962; Chaudonneret, 1990). During abduction, a torsion of the mandible stores energy that is released during the cutting motion (Wenk, 1980). The curving of the labrum exposes the wound, and the laciniae are plunged into the lateral sides of the opening. The teeth at the apex of the laciniae serve to anchor the proboscis. Retractor muscles of the laciniae force the head and hypopharynx deeper into the wound. The hypopharynx is lancet-shaped and bears rows of teeth on the apex. During protraction the teeth are erected backward and lead to the flexion of the labrum during the piercing process (Wenk, 1962). The sequence of piercing movements is continued as the mandibles perform further cutting movements including a slight protraction (Wenk, 1962; Sutcliffe and McIver, 1984). Blood is sucked from the wound under the epidermis where it has accumulated around the piercing organ. The labella are spread apart and form a tube between the laciniae and labrum allowing blood to be taken up (Wenk, 1962). The salivary groove of the hypopharynx is covered by the mandibles and directs saliva to the tip of the proboscis (Fig. 5B). A component in the saliva of Simuliidae effectively prevents clotting and may lead to allergic reactions in many host organisms.

3.1.3.3. Psychodidae: Phlebotominae (sandflies). The females of the genus *Phlebotomus* and related genera are tiny blood-feeders that can transfer pathogens. They are distributed mainly in the tropics and subtropics, especially in the Mediterranean region and increasingly in Central Europe (Table 1). These insects are only a few millimeters large. The proboscis is usually less than 1 mm long and thin (Fig. 6A); it consists of the labrum, the paired mandibles and laciniae. The labrum is groove-like and apically dentate; it covers the piercing organs (Fig. 6B). It also forms the food-canal, which is enclosed by one of the mandibles and partly by the laciniae as well as the hypopharynx. The slender laciniae are concave and bear razor sharp tips. The elongated and acute hypopharynx contains the salivary canal, which runs in a groove-like ridge that is anteriorly closed by the second mandible. The maxillae bear multi-segmented and relatively long palps that are outfitted with numerous sensory organs (Fig. 6A). The labium forms the sheath surrounding the stylets (Fig. 6C) and carries the sponge-like labella at the tips which form a guiding channel for the stylets (Fig. 6B and D).

The sclerotized slender mandibles have a fine dentate apex, and they normally overlap each other when at rest. The strong

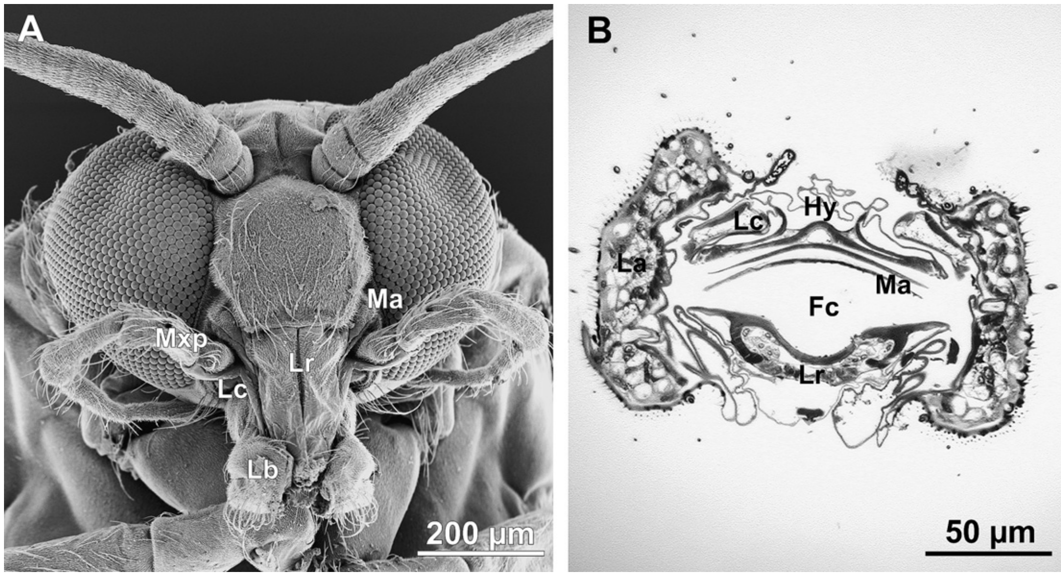

Fig. 5. A. Head of the black fly *Simulium* sp. (Simuliidae, Diptera), in frontal view. The piercing structures (mandible Ma, lacinia Lc) of the short proboscis are hidden by the labrum (Lr), labella (Lb) form sponge-like organs with numerous sensory setae. The maxillary palps (Mxp) arise from the maxillary base under the compound eyes. B. Cross-section of the piercing-proboscis at about mid-length. The food-canal (Fc) is formed by labrum (Lr) and one mandible (Ma); the second mandible covers the groove of hypopharynx (Hy) through which saliva flows. The labium (La) encloses the piercing structures laterally.

adductor muscles move the dentate mandibular tips outward which cut laterally into the host tissue. The teeth of the laciniae probably help to anchor the piercing-proboscis in the tissue (Brinson et al., 1993). The puncture creates a small amount of bleeding under the skin, from which the small and unspectacular insects suck blood with their short piercing-proboscis (Smith, 1985).

3.1.3.4. Ceratopogonidae (biting midges). The biting midges, with a length less than 2 mm, belong to the smallest blood-feeding insects. The most important group is the genus *Culicoides* with approximately 1400 species worldwide (Lehane, 2005).

The length of the piercing-proboscis is only 0.1–0.2 mm (McKeever et al., 1988). The mouthparts consist of the sclerotized labrum, which is acutely pointed at the tip, the toothed mandibles and the thin laciniae. The maxillary base bears a 5-segmented maxillary palp. The hypopharynx is also dentate and is as long as the other components. The labium envelopes the stylets and apically bears the short two-segmented labial palp. The labrum covers the mouthparts frontally and forms the anterior side of the food-canal, which is covered by one mandible posteriorly. The second mandible lies behind the first and together with the hypopharynx forms the salivary canal (McKeever et al., 1988; Chaudonneret, 1990).

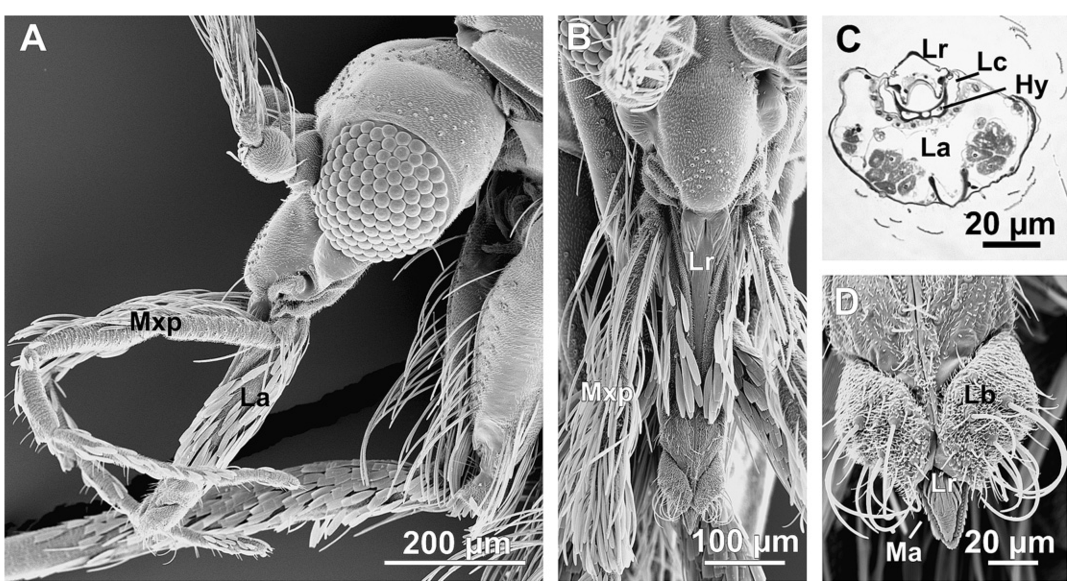

Fig. 6. A. Head and mouthparts of the sandfly *Phlebotomus duboscqi* (Phlebotominae, Diptera). The multi-segmented maxillary palps (Mxp) serve as sensory organs next to the proboscis; the piercing structures are covered by the labium (La). B. Frontal view of proboscis. C. Cross-section of proboscis; food-canal lies between labrum (Lr) and hypopharynx (Hy); laciniae (Lc). D. Apex of the piercing-proboscis consists of the labella (Lb) with many sensory setae; the piercing structures, i.e., labrum (Lr) and mandibles (Ma) project beyond the proboscis apex.

At the start of feeding, the host's skin is stretched by the apical teeth of the labrum. The mandibles are saw-like blades that slightly cross over each other. They are connected to each other by a prominent edge on one mandible which fits into a groove-like depression on the other mandible. The mandibles along with the underlying hypopharynx form a functional unit. Muscle contractions force the tips of the mandibles to pull apart and together. The resulting movements are saw-like and the outer side of the serrate mandible laterally cuts the tissue of the host. The contraction of the adductor muscle pushes the mandible forward and over each other. The laciniae are U-shaped in cross-section and the apex is finely serrated. The backward-directed teeth probably serve as an anchorage for the proboscis in the wound (McKeever et al., 1988; Chaudonneret, 1990).

3.1.3.5. Rhagionidae (snipe flies). Some females of snipe flies are blood-feeders that occasionally attack people with a very painful bite (Nagatomi and Soroida, 1985; Lehane, 2005). The short mouthparts of the blood-feeding representatives of the genera *Spaniopsis* and *Symphoromyia* are strongly sclerotized and cut into the host's skin probably using the sword-like mandibles and the stylet-shaped laciniae (Nagatomi and Soroida, 1985). The blood which accumulates on the surface of the wound is sucked up. At present, few detailed descriptions of the mouthparts and the biology of blood-feeding Rhagionidae are available (Nagatomi and Soroida, 1985; Kerr, 2010).

3.1.3.6. Tabanidae (horse flies, deer flies). In many species of the Tabanidae the females are blood-feeding insects. They are mainly parasitic on various mammals while some species are specialized to feed on blood from reptiles and amphibians (Lehane, 2005). The body size of horse flies reaches up to 25 mm; nevertheless, most species have a relatively short piercing-proboscis (Fig. 7A).

The proboscis consists of the same components as those in Culicidae, except that they are much shorter, wider and more robust. The labrum forms a deep gutter which serves as the food-canal; it is wide and covers the piercing structures frontally. Its lateral margins do not entirely enclose the food-canal and it bears sensory organs at the apex (Fig. 7B). The mandibles are blade-like and dentate at the tip (Fig. 7C). The paired mandibles overlap each other and cover the posterior surface of the food-canal. The hypopharynx lies between the mandibles and laciniae; it is flattened and contains the opening of the salivary duct. The paired laciniae lie posteriorly; they form slender stylets which bear fine teeth at the apex. The two-segmented maxillary palp is located adjacent to the other components of the mouthparts (Fig. 7A). The basal section of the labium forms a short sheath which covers the piercing structures posteriorly. The labellar lobes are large and well-separated; they overlap each other posteriorly and surround the distal section of the piercing structures from posterior (Fig. 7A and D). The medial surface of the labella exhibits sclerotized channels (Fig. 7D) which branch out laterally and serve to distribute the saliva (Chaudonneret, 1990; Seifert, 1994).

When feeding, the serrate tips of the blade-like mandibles and laciniae press against the host's skin. The piercing organ functions like a pair of scissors that upon closure cuts into the host since the inner margins are dentate (Wenk, 1980). Due to the lack of muscles, neither the mandibles nor the labrum can be actively extended. However, the laciniae can protrude for the entire length of the labrum. Therefore, it is assumed that the extendable laciniae, on the one hand, serve as an anchorage for the proboscis due to their

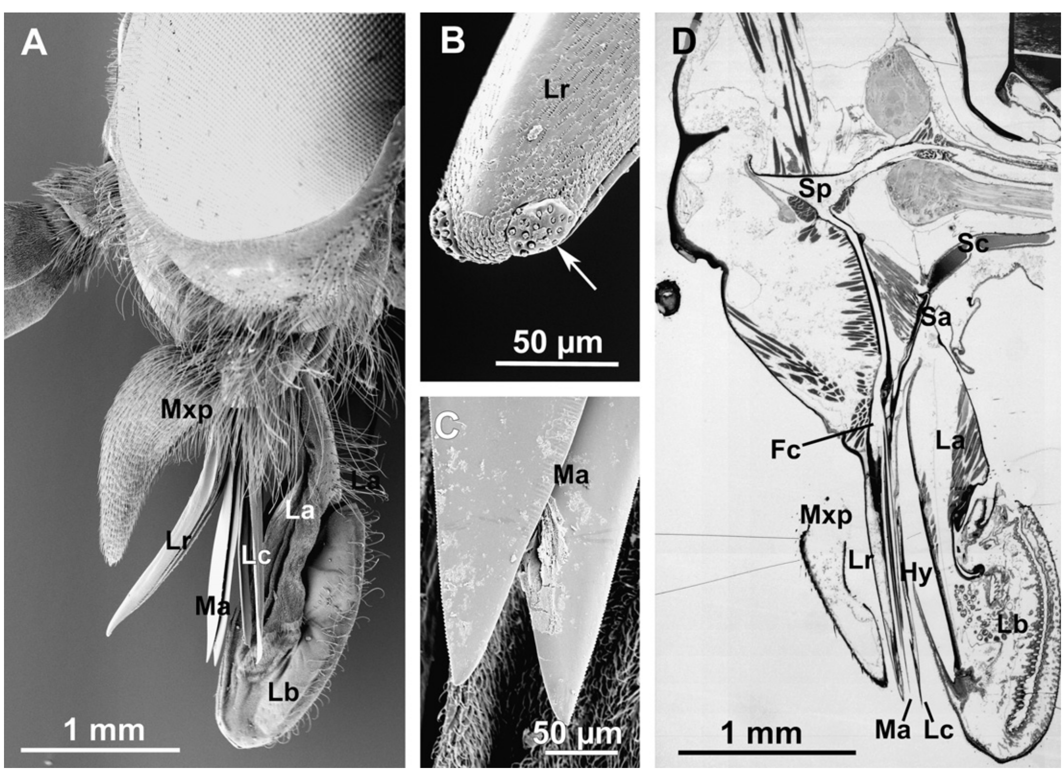

Fig. 7. The mouthparts of the horse fly *Tabanus bromius* (Tabanidae, Diptera). A. Lateral view of head and mouthparts. The piercing structures consist of labrum (Lr), mandibles (Ma) and laciniae (Lc); at rest they lie in a groove of the labium (La). Note that the position of the piercing structures is artificial due to the preparation; maxillary palps (Mxp); labella (Lb). B. Apex of labrum (Lr) with sensory organs (arrow). C. Mandibles (Ma) crossed showing fine serrate edges. D. Longitudinal section of head. Food-canal (Fc) is formed by labrum (Lr) and leads to a suction pump (Sp) in the head. The salivary canal (Sc) opens into a salivarium (Sa), which forms the pump at the base of the hypopharynx (Hy). The labium (La) bears the large labella (Lb). The piercing structures consist of mandibles (Ma) and laciniae (Lc).

backward-directed teeth at the tips and, on the other hand, by contraction of the retractor muscles, the laciniae force the proboscis deeper into the skin, enabling the mandibles to continue cutting (Smith, 1985; Chaudonneret, 1990). Blood is taken into the food-canal which lies between the groove-like labrum and the mandibles and which is directly connected to the suction pump in the head (Fig. 7D). A salivary pump forces saliva, which contains anti-coagulating substances, through the salivary channel to the tip of the hypopharynx (Fig. 7D), where it enters the host's tissue.

Noteworthy are the species of several genera, e.g., *Pangonia, Philoliche* and *Corizoneura* that have a proboscis longer than their body. The proboscis points forward, and both males and females use it to extract nectar from flowers. The extended labium forms a trough which encases the much shorter piercing structures that are used by the females to feed on blood (Morita, 2008). While hovering, the blood-feeding females probe the host's skin with their long proboscis; then the long labium is moved aside to expose the short piercing-proboscis. The fly lands on the host, plunges the stylets into the skin and sucks blood (Dierl, 1968). The mouthpart specializations for nectar feeding in some species of *Philoliche* are accompanied by the reduction of the mandibles. However, these species are still capable of extracting blood even from large mammals such as a rhinoceros (Morita, 2008).

3.1.3.7. Glossinidae (tsetse flies). This group of flies contains 23 species distributed throughout Africa with an additional species confined to a small region of the Arabian Peninsula. The Glossinidae are between 6 and 14 mm long. They are viviparous, i.e., the females give birth to pre-pupal larvae, which take no food and undergo metamorphosis within a few hours (Krinsky, 2002a,b).

The piercing-proboscis of the tsetse fly is 3–4 mm long, and at rest it is normally held in a position pointing straight forward (Fig. 8A). The actual piercing apparatus consists of the elongated labrum, the hypopharynx and labium. These components are enclosed laterally by the slightly longer maxillary palps, which form a paired sheath for the proboscis (Fig. 8A–C). The piercing apparatus is very thin with a diameter of about 0.1 mm; it is flexible and bent slightly downward. The food-canal consists of the groove-like and acute labrum, which is enclosed ventrally by the labium (Fig. 8C). The hypopharynx is a slender tube, which lies in a transverse fold of the labial groove and extends to the middle of the labella. The labium is thickened proximally; apically it bears the very short labella, which serve as piercing structures. To feed, the proboscis unfolds downward, while the maxillary palps are still directed forward (Fig. 8B). The tip of the proboscis is pressed against the host's skin, and the labella, which are apically equipped with backward-directed teeth, are everted. The inner margins of the labella are also serrate and outfitted with teeth-like cuticular ridges (Fig. 8D). During feeding, the inner teeth are turned outward and drill through the skin with a rasping motion. Protractor and retractor muscules at the proboscis base bend elastic sclerits of the proboscis that indirectly lead to rasping motions of the serrated cuticula ridges of the labellum (Wenk and Renz, 2003). The mouthparts of the *Glossina* flies pierce the skin by repeated withdrawal and penetration of the proboscis, each time in a slightly shifted direction. The flies feed on the pool of blood which accumulates under the skin. In this manner, the insects can very rapidly consume a meal of blood. The mechanism of labellar movements is not fully understood and probably results from a change in hemolymph pressure inside the labium (Smith, 1985; Wirtz, 1989).

3.1.3.8. Muscidae: Stomoxinae (stable flies). The proboscis of blood-feeding flies of the genus *Stomoxys* and other hematophagous species of Muscidae folds together into a z-shaped structure. The

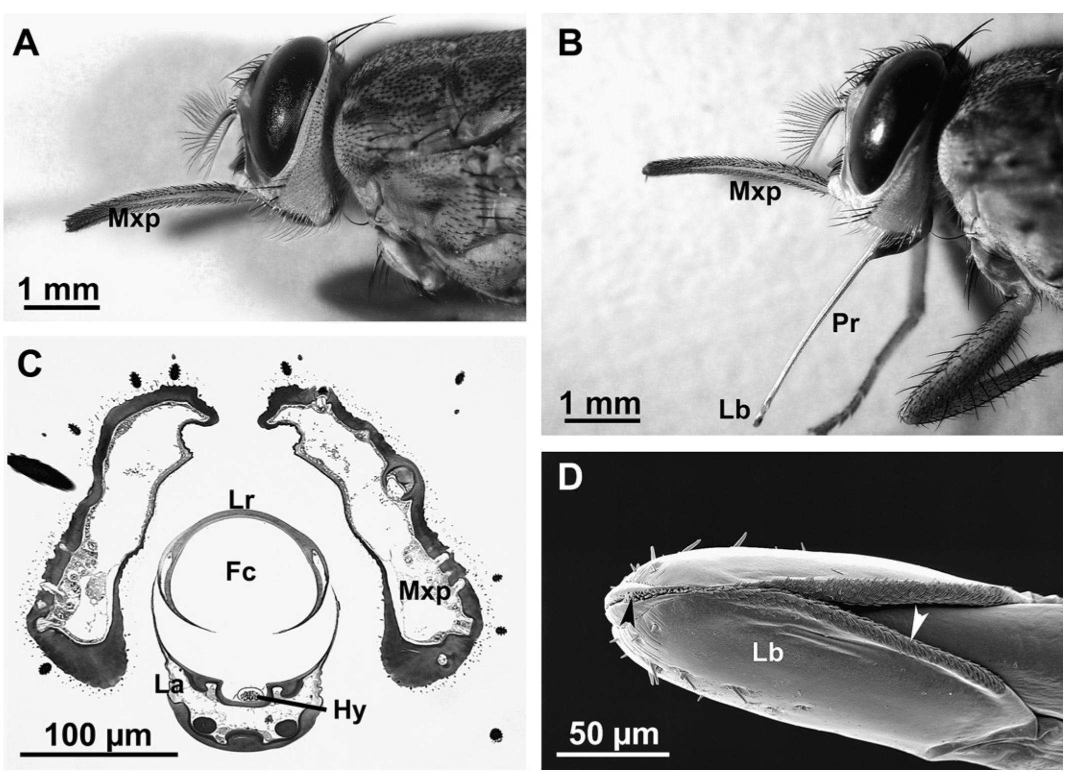

Fig. 8. The head and mouthparts of the Tsetse Fly (*Glossina* sp., Glossinidae, Diptera). A. Position of proboscis when not in use; maxillary palps (Mxp) cover proboscis laterally. B. Position of proboscis (Pr) when prepared to feeding; proboscis withdrawn from the enveloping sheath; apex formed by labella (Lb). C. Cross-section of proboscis. Maxillary palps (Mxp) cover the piercing structures, which are formed by labrum (Lr) with a food-canal (Fc) and labium (La); the thin hypopharynx (Hy) lies in a groove of the labium. D. Labella (Lb) with serrate edges (arrows); their movements puncture the skin.

piercing-proboscis of *Stomoxys* is generally about 5–8 mm long. When at rest, the proboscis is directed straightly forward (Fig. 9A). The proboscis consists of the tubular labrum, which forms the food-canal and which is laterally tightly enclosed by the almost tubular labium (Fig. 9A and B). The maxillary palps are short; no sheath covers the proboscis, and no piercing stylets are present. The thin hypopharynx, through which the salivary canal runs, lies between the labrum and labium. The short labellum at the apex of the labium forms the actual piercing structure, which is functionally connected to the labium by a movable joint. Its medial surface is provided with 5 pairs of large, serrate ridges (referred to as the prestomal-teeth) around the entrance to the food-canal, in addition to several sharp lateral ridges (Iwasa, 1983; Chaudonneret, 1990). To feed, the proboscis first unfolds downward (Fig. 9A), and the labellar apex (Fig. 9B) presses against the host's skin. The short labella spread apart, permitting the prestomal-teeth and the sharp ridges of the labellar underside to cut into the skin (Chaudonneret, 1990) (Fig. 9C). The prestomal-teeth are rotated slightly to drill into the tissue. The penetration is similar to that in the tsetse fly and functions like a drill head. Additionally, it is known that the teeth in *Stomoxys* rotate on the length axis of the penetrated proboscis, a process which is particularly painful to the host probably because the tissue is torn open and causes bleeding under the skin on which the fly then feeds (Lehane, 2005).

3.1.4. Siphonaptera (fleas)

Adult fleas are few millimeters long, laterally compressed; they are wingless and excellent jumpers. The imagines feed exclusively on blood. Over 90% of the approximately 2500 species are parasitic blood-feeders (Lehane, 2005); about 20 species are relevant to humans and may transfer pathogens (Table 1).

The short piercing-proboscis of fleas is about as long as the head (Fig. 10A). It consists of two main components, i.e., the unpaired and acutely pointed labrum (also termed as the epipharynx) and the paired laciniae, which are enclosed by the labial palps posterio-laterally (Wenk, 1953; Michelsen, 1996/97) (Fig. 10B). A groove on the median surface of the labrum serves as an extension of the food-canal and passes directly into the large suction pump of the pharynx. The laciniae enclose the labrum laterally and the food-canal posteriorly (Fig. 10D); they are distally serrate and bear backward-directed teeth (Fig. 10C). The laciniae originate from a lever-like structure at the maxillary base to which muscles attach. The leverage allows the laciniae to be pulled back and stretched against an elastic cuticle. Upon release of a click-mechanism the stored energy of a compressed resilin pad rapidly thrust the laciniae downward (Wenk, 1953; Chaudonneret, 1990; Wenk and Renz, 2003). The rapid sequence of this hammering forces the laciniae deeper into the skin and probably pulls the labrum, as well. The long, multi-segmented maxillary palp originates from the maxillary base. Its first segment (termed by many authors as the maxillary palpifer) is enlarged and leaf-like (Fig. 10B) and serves as a muscle attachment site for the piercing mechanism (Michelsen, 1996/97). Both laciniae possess a length-wise canal for the flow of saliva from the hypopharynx to the tip of the stylets (Wenk, 1953). The posterior base of the piercing structures is enclosed by the labium, which distally bears a three-segmented labial palp (Fig. 10B). The labium does not penetrate into the host, but serves as a guiding channel for the stylets. When a blood vessel is tapped and blood is sucked, only the labrum (epipharynx) remains in the skin (Lehane, 2005).

3.1.5. Lepidoptera: Noctuidae (owlet moths)

The males of a few moth species of the genus *Calyptra* occasionally suck blood from humans (Bänziger, 1971, 1980; Zaspel et al., 2007, 2011). Their mouthparts are constructed like those of other Noctuidae, except that they possess special features, which also occur in fruit-piercing noctuids (Büttiker et al., 1996; Zaspel et al., 2011). The proboscis consists of the paired galeae of the maxillae which are spirally coiled in resting position. The galeae are firmly connected to each other to form a sucking tube, which acts as both the food and salivary canal. The labrum is very small, the mandibles are reduced, and the labium is a small plate-like sclerite on the ventral side of the head that bears the three-segmented labial palps (Krenn, 2010). The tip of the proboscis bears long and robust thorn-like structures, which are possibly derived from sensory organs (Büttiker et al., 1996) and which can be erected by change in the hemolymph pressure within the galeae (Bänziger, 1970; Zaspel et al., 2011).

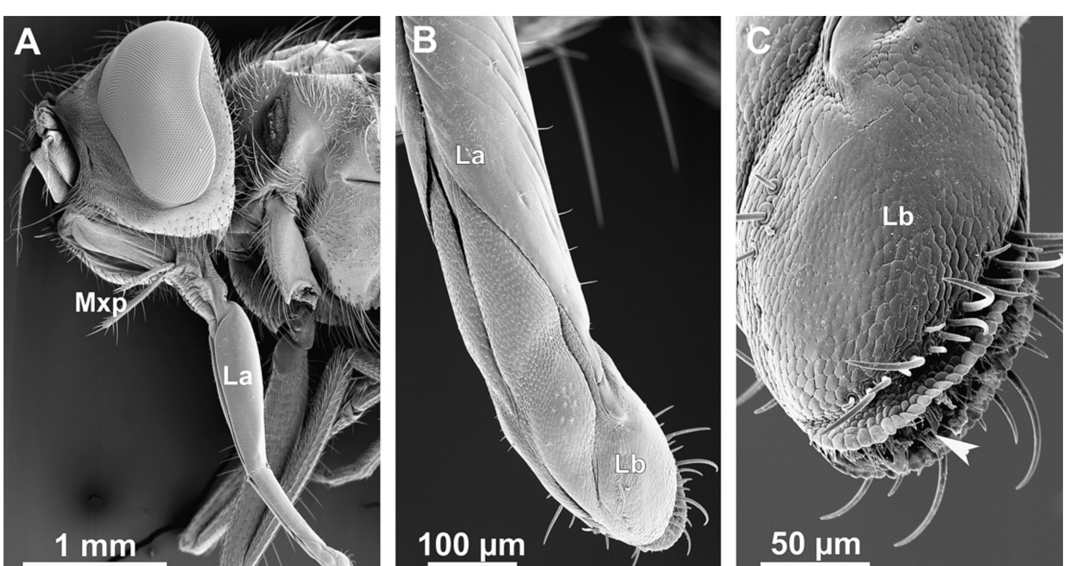

Fig. 9. A. Head with extended piercing-proboscis of stable fly *Stomoxys* sp. (Muscidae, Diptera); proboscis formed by labrum and labium (La); maxillary palps (Mxp) serve as short sensory organs under the head. B. The short labella (Lb) articulate on the labium (La) and constitute the apex of the piercing-proboscis. C. Labella (Lb) with serrate inner surface (arrow) that rotate outward to drill into the host's skin.

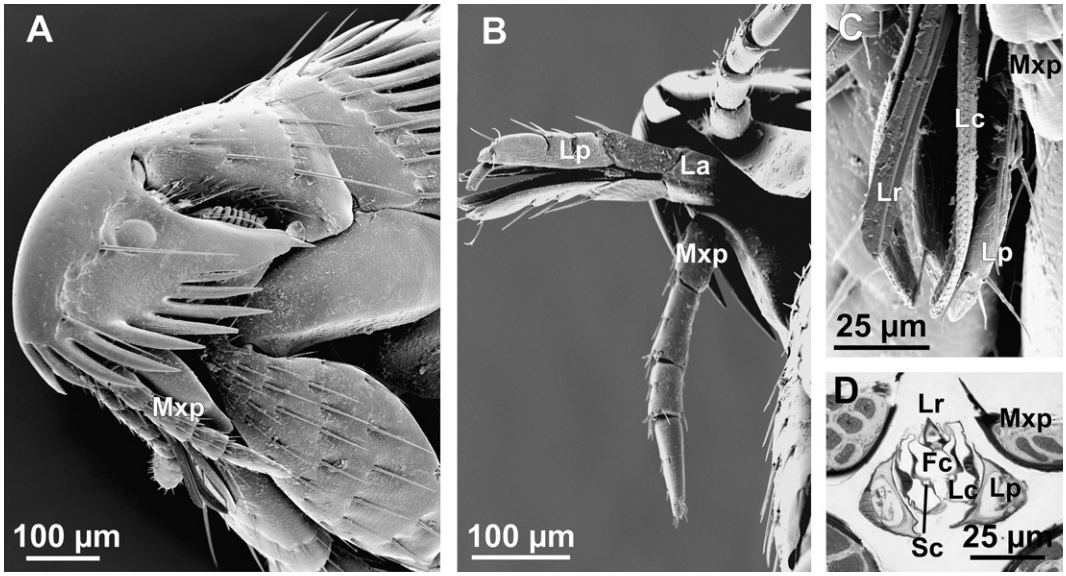

Fig. 10. Mouthparts of the flea *Ctenocephalides* sp. (Siphonaptera). A. Head bears robust backward-pointing prongs, which cover the base of the proboscis and the maxillary palps (Mxp). B. Ventral view of piercing-proboscis; piercing structures (laciniae Lc, labrum Lr) are covered posteriorly by labial palps (Lp) and labium (La). C. Piercing organs consist of a labrum (Lr) and paired laciniae (Lc). D. Cross-section of proboscis. Food-canal (Fc) formed by labrum (Lr); salivary canal (Sc) runs through each lacinia (Lc).

The uncoiling of the proboscis is caused by an increase of internal hemolymph pressure (Bänziger, 1971; Krenn, 2010). To feed, the apex of the proboscis is pressed against the host's skin and the galeae move forward against each other in the longitudinal direction. This leads to lateral bending of the proboscis until the apical teeth of one galea cut into the skin, while the other galea serves as a stabilizing anchor. The alternating progression of a galea cutting, while the other serves as anchorage, drives the proboscis deep into the host's skin, resulting in antiparallel spindle movements (Zaspel et al., 2011). This occurs with a frequency of about 15 advancing movements per second. The withdrawal of the proboscis follows the same principle, except that the pressure in the proboscis is lessened and the thorn-like projections are are folded back (Bänziger, 1975, 1980).

3.2. *Organs of food consumption in blood-feeding Acari (ticks and mites)*

3.2.1. *Ixodidae (ticks)*

The piercing organs of Ixodidae consist of the ventral extension of the capitulum (termed hypostome), the paired chelicerae and pedipalps (Fig. 11A, B and D). The hypostome is a flattened part ventral to the mouth. Its underside bears many backward-directed teeth which serve to firmly attach the tick to the host's skin (Gruner et al., 1993). In species that only briefly suck blood (e.g., *Argas* spp.), the teeth are rudimentary; in females of species that suck for a long period of time (e.g., *Ixodes* spp.), the teeth are strongly developed (Babos, 1964). The chelicerae form the actual organ of piercing. Each chelicera consists of a thickened base (which contains muscles) and a long shaft (which contains the tendons and nerves) connected to the pair of movable cutting plates (Sonenshine, 1991). The knife-like terminal segments of the chelicera (Fig. 11D) can be extended and turned laterally to cut into the skin of the host organism (Sonenshine, 1991). The shafts of the chelicerae form a canal together with the upper side of the hypostome (Fig. 11E). The canal is used for the ingestion of blood and for the flow of saliva into the wound, as well (Sonenshine, 1991). In the preoral cavity the suction canal is divided into two courses: one serves as the salivary canal and leads to the opening of the salivary duct and the other forms the food-canal which leads to the suction pump in the foregut (Gruner et al., 1993). The four-segmented pedipalps are flattened and lie in the direction of the body dorsal to the hypostome and cover the piercing organs dorsally (Fig. 11C). In the Ixodidae the first segment is shortened and not movable, the second and third segments are large and flattened, and the fourth segment is modified into a short sensory organ at the tip of the pedipalps (Fig. 11B). The pedipalps bear many small sensory organs and play an important role in the location of the host and feeding (Sonenshine, 1991).

To feed, *I. ricinus* lowers the anterior body section while the posterior section is raised. The chelicerae are forced out of their sheath by contractions of the trunk musculature. They are pressed against the skin and are pushed into the host's skin. They cut the skin by moving laterally the serrate terminal segment of each chelicera. The tip of the hypostome is shoved into the wound and becomes firmly anchored by hooks. Within 12–15 min, the hypostome is driven completely into the skin. The pedipalps do not penetrate the skin. The paired salivary glands open at the medial side of the coxa of the pedipalps (Wenk and Renz, 2003). Saliva introduced into the wound numbs the injection site, inhibits blood clotting and increases bleeding (Gruner et al., 1993). Mature females of *I. ricinus* can imbibe blood for 7–8 days, filling their midgut diverticula with blood more than 200 times their body weight. The weight gain in *Boophilus annulatus* from a fresh larva to a fully engorged female can exceed 10,000 times the body weight (Gruner et al., 1993).

3.2.2. *Larvae of Trombiculidae (chiggers)*

The larvae of Trombiculidae are temporary parasites of vertebrates, while the nymphs and adult mites are predatory on small arthropods. The mite, *Trombicula autumnalis*, is only about 0.25 mm long; its feeding on human skin creates an unpleasant and persistent itching (Gruner et al., 1993). *Trombicula* has a pair of strong chelicerae, the distal ends of which are each equipped with a laterally movable sickle-like terminal segment. To feed, the skin of the host organism is pierced by these organs, a process which is reinforced by the claws of the pedipalps (Kampen, 2002). The larvae inject a salivary fluid into the wound that contains

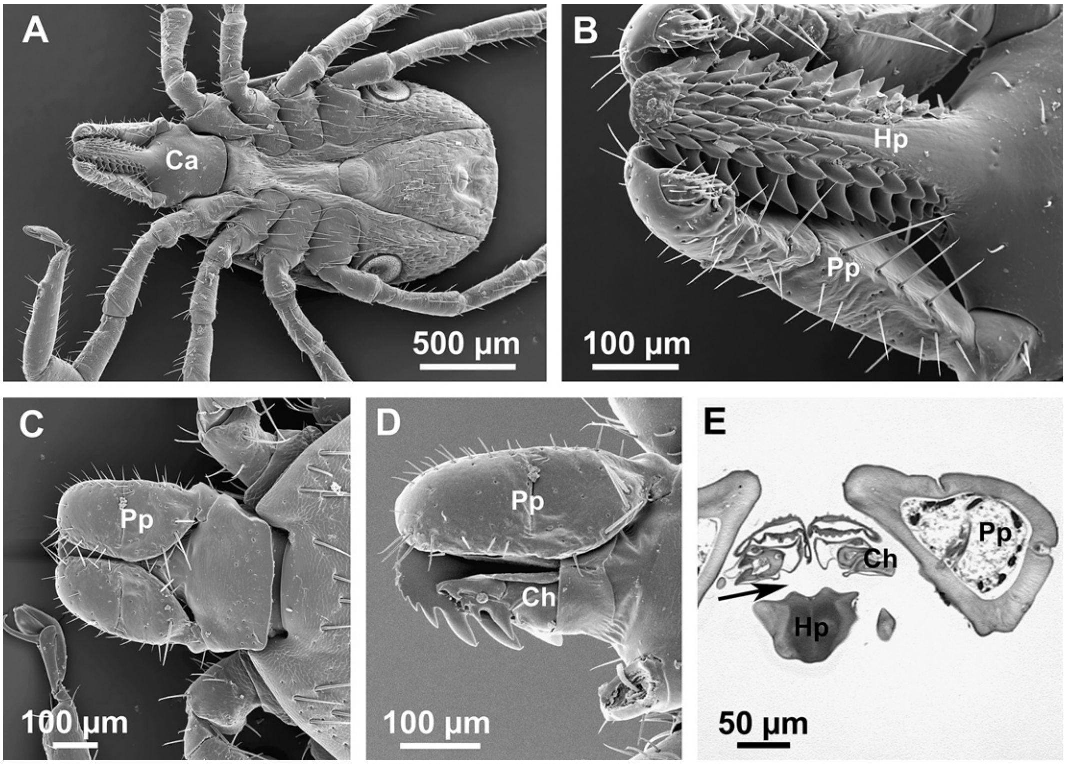

Fig. 11. A. Ventral view of the tick *Ixodes ricinus* (Ixodidae, Acari); the capitulum (Ca) on the anterior body constitutes the piercing organ. B. The capitulum is ventrally extended forming the toothed hypostome (Hp), which anchor the tick in the host's skin; in ventral view pedipalps (Pp) in lateral position. C. Dorsal view of the proboscis covered by the broad pedipalps (Pp). D. View of chelicera (Ch) after removal of left pedipalp. E. Cross-section of the piercing-proboscis. The food-canal (arrow) lies between the chelicerae (Ch) and hypostome (Hp).

anesthetizing, anti-coagulating and histolytic substances to help dissolve the tissue. A small canal is formed in the skin, its linings are hardened by other components of saliva to form a boundary to the healthy tissue. After several hours the saliva dissolves deeper layers and a short tube, the so-called stylostome, is formed. Since feeding entails alternate stages of imbibing and salivary discharge, the stylostome develops successively (Kampen, 2002). In this manner, the mouthparts which are only a few hundredths of a millimeter long are able to feed from the damaged upper layers of the skin to depths that are several tenths of a millimeter long (Gruner et al., 1993). The larvae feed for several hours at the same site before leaving the human host (Kampen, 2002).

4. Discussion

4.1. The functional principles of piercing blood-sucking mouthparts

Arthropods are commonly viewed as annoying or potentially dangerous animals. Comparison of the number of blood-feeding species – about 12,000 (Lehane, 2005) – with the rough estimate of at least 1.1 million described species of Insecta and about 48, 000 species of Acari (Burda et al., 2008) shows that only a tiny fraction are hematophagous. Probably less than one tenth of blood-feeding Arthropoda attack humans. In sum, there are probably less than a thousand blood-feeding arthropod species which are medically relevant to humans but many more are of economical interest when domestic animals are considered. Despite their relatively small number they are of great importance since most blood-feeding insects transmit human pathogens in all parts of the world (Table 1).

In hematophagous Arthropoda, feeding encompasses the search for a host organism, localization for a suitable place to extract blood, the actual puncturing of the host's skin, the ingestion of blood and its digestion (Lehane, 2005). Convergent evolution in the various taxa of blood-feeding insects has led to various piercing blood-sucking mouthparts. Likewise, the blood-feeding ticks have also developed a functionally similar piercing-proboscis, whereas chiggers do not possess a proboscis, but suck enzymatically liquefied tissue of the host. All piercing blood-sucking organisms have a food-canal, a separate salivary duct, and mouthparts with structures to puncture, anchor and pierce which are usually enveloped by soft sheath-like parts (Table 2). The construction of a piercing-proboscis reflects the functional requirements of sucking blood from the skin of a vertebrate. Based on the comparison of the mouthparts, it can be concluded that structures are required to puncture after first contact, likewise structures which anchor the normally very thin piercing structures in the host's tissue are indispensable for the piercing process. These functional components are found in all groups of insects and ticks; however, the structures evolved from different morphological components of the basic set of the mouthparts (Table 2).

The typical piercing-proboscis of a blood-feeder is usually relatively short compared with the proboscis of a nectar-feeding insect. In contrast to nectar-feeding proboscides (see summaries by Krenn et al., 2005; Borrell and Krenn, 2006) most piercing-proboscides have a long and thin piercing stylet-shaped structures that are strongly sclerotized and often apically finely serrate. When at rest, the stylets are normally enclosed in a sheath or withdrawn or folded under the body. The sheaths are never inserted into the body of the host organism, and in almost all insects they are formed by the labium. The first step in feeding is to firmly anchor the piercing-proboscis, so that the piercing forces can be transmitted to the skin efficiently. Puncturing and penetration proceed by mechanisms that allow the often very thin and fragile structures to pierce through tough body parts of the host. Three basic principles of piercing mechanisms can be distinguished: (1) the jigsaw-principle whereby the piercing structures, which are outfitted with sharp teeth at the tips, thrust into the host's skin by alternate movements of protraction and retraction; (2) the scissors-principle whereby movements of the cutting organ in mediad direction carve into the skin; and, (3) the drilling-principle whereby a rasping structure perform rotating and torsions movements to open the skin. The mechanical forces used for rapid protraction of the piercing organs are enhanced by bending or torsion of elastic sclerites and/or by click- release of compressed resilin pads (Wenk, 1980).

Piercing-sucking mouthparts are present also in other insects, such as aphids and Heteroptera, which puncture plant tissue to suck on the sap (Weber, 1933) or hard-shelled plant seeds (Wenk et al., 2010). In many instances, a protective tissue must be broken, before the fluid can be ingested. As with the proboscis of blood-feeders, the piercing-sucking mouthparts are equipped with structures that function like a jigsaw and the salivary ducts are similarly constructed as well (Wenk et al., 2010).

Separate tubes, one for imbibing blood and another one for the transport of saliva, are almost always present in blood-sucking proboscides. As in all insects with an elongated proboscis the blood-feeding insects possess a large suction pump in the head, which is directly connected to the food-canal and which transports blood into the foregut. The functional mechanism is presumably similar in all groups, although it has been examined in detail for only a few species (Kingsolver and Daniel, 1995; Wenk et al., 2010). As with nectar-sucking insects, the suction pump is a hollow cavity of the preoral or/and pharyngial alimentary tracts that can be expanded and constricted by muscular action, and is associated with a valve structure to ensure the direction of flow (Eberhard and Krenn, 2005). On the one hand, the piercing organs are very thin, so that they can puncture the skin, on the other hand, the size of the food-canal is a crucial parameter for suction and is also dependent on the physical properties of the blood (Kingsolver and Daniel, 1995). The diameter of a food-canal is often only slightly larger than the diameter of an individual blood cell (Lehane, 2005).

Many of the small blood-feeders possess very short proboscides which are only able to superficially pierce skin. They discharge substances through the salivary canal into the wound to promote bleeding under the skin. The resulting pool of blood is sucked up. "Pool-feeders" include representatives of Simuliidae, Psychodidae, Tabanidae, Glossinidae and Stomoxinae, as well as Ixodidae (Lehane, 2005). Many long-tongued blood-feeders can also suck directly from the punctured blood vessels and capillaries. Their bite neither produces a clear hemorrhage nor secondary bleeding, e.g., Anoplura, Reduviidae, Cimicidae, Siphonaptera and Culicidae and Ceratopogonidae. Representatives of Siphonaptera, Culicidae and Glossinidae may utilize both strategies of feeding (Lehane, 2005).

Unlike the saliva of many flower-visiting insects, which serves to dilute the nectar, the saliva produced by blood-feeders contains various bioactive substances including anticoagulants, vasodilators, antihistamines, immunosuppressors and inhibitors of platlet aggregation that prevent blood clotting and that reduce the sensation of pain in the host organism (Wenk et al., 2010). An overview of the components and their effects is given in Lehane (2005). Normally only minute quantities of anticoagulate substances are sufficient to sustain the flow of blood for the duration of feeding. Relatively little is known about substances which reduce pain or cause other effects, such as blood vessel constriction (Lehane, 2005). The salivary canals always consist of sclerotized parts, which are usually as long as the piercing organs and which also penetrate the skin. Unlike flower-visiting insects, saliva must be applied into the wounded tissue, a superficial application would be insufficient. Another functional condition and characteristic of blood-feeding arthropods is a powerful salivary pump that functions like a pressure-pump to force saliva through the usually very narrow canal into the wound (Wenk et al., 2010). The salivary glands are often the organs where the pathogens are harbored and from there they gain access to the wounds.

Some pathogens lead to life-threatening diseases in many parts of the world. In addition, the discharge of saliva in some species may lead to allergic reactions of the hosts.

Table 1 gives an overview of the diversity of human-related pathogens, infections and diseases that can be transmitted by hematophagous Arthropoda. For most pathogens, the blood-feeding insects, mites or ticks are true hosts, i.e., the pathogen is transmitted after multiplication in the arthropod. Most of these pathogens are injected with the saliva, i.e., all arboviruses (transmitted by ticks, mosquitoes, sandflies, etc.), several species of *Borrelia* and of *Rickettsia* (mainly transmitted by ticks), *Plasmodium* spp. (transmitted by anopheline mosquitoes), *Trypanosoma brucei gambiense* and *T. B. rhodesiense* (transmitted by *Glossina* spp.). However, several pathogens are vomited from the alimentary tract into the stab wound, i.e., *Yersinia pestis* (transmitted by fleas), *Leishmania* spp. (transmitted by sandflies). Another strategy is the migration of the pathogen through the labium into the stab wound, like in Filariae (transmitted by mosquitoes, horse flies and black flies, respectively). Several insects do not transmit pathogens via the mouthparts, but with the feces; sometimes after the arthropod has been injured. The microorganisms are actively smeared into the stab wound or into small lesions of the skin by skin scratching of the human hosts, i.e., *Rickettsia* spp. (transmitted by lice), *Trypanosoma cruzi* (transmitted by assassin bugs). Although rarely, also mechanical transmission without previous multiplication of the pathogen in the blood-feeding arthropod may occur. Important examples are *Bacillus anthracis*, *Francisella tularensis*, and other bacteria transmitted by Tabanidae (horse flies) and other arthropods. The possible mechanical transmission of certain viruses by arthropods is not yet fully understood.

4.2. Evolution of hematophagous Arthropoda

The ability to extract blood from vertebrates evolved many times independently within the Insecta and at least twice within the Acari. The starting points for the evolution of blood-feeding must have been (1) ectoparasites with chewing mouthparts, (2) predatory nutrition, (3) unspecialized uptake of fluids from the surface of plants and animals, (4) floral nectar consumption, and (5) the uptake of liquids from thick-skinned fruits or hard-shelled plant seeds.

All representatives of the Phthiraptera live on vertebrates. The Anoplura (sucking lice) have common ancestors with ectoparasitic Amblycera (bird lice) and Ischnocera (animal lice), which feed on feathers or hairs, both using biting-chewing mouthparts (Dathe, 2003). The representatives of Anoplura, however, represent the only group of blood-feeders that permanently and in all stages of their development live on their host. This group includes the only species which are specialized for blood-feeding on humans, i.e., *Phthirus pubis*, *Pediculus capitis* and *Pediculus humanus*. Their closest relatives are found on monkeys and apes (Maier and Habedank, 2002; Aspöck and Walochnik, 2007). The very unusual piercing-proboscis of the Anoplura is clearly a modification of the basic biting-chewing mouthparts of other taxa of Phthiraptera (Tröster, 1990).

Siphonaptera are currently regarded to have a close phylogenetic relationship with Mecoptera (for discussions, see Grimaldi and Engel, 2005; Krenn, 2007). The latter exhibit chewing mouthparts and which could possibly have served as the starting point for the evolution of blood-feeding fleas. This is indicated by the fact that the larvae of fleas inhabit nests of animals where they use their biting-chewing mouthparts to feed on detritus and bloody feces of the adult fleas. If indeed it turns out to be true that the closest relative of fleas are the wingless Boreidae, which are moss eaters, it can be hypothesized that the ancestors of fleas could have been transported along with the collected nest material into the nests of mammals and birds, and that this may constitute the evolutionary starting point for blood-feeding habits of Siphonaptera (Kristensen, 1999).

Acari of the family Trombiculidae are a special case since they lack an elongated piercing organ, instead they carve into the skin of the host with their short chelicerae, hold themselves firmly to the host and drink up the enzymatically liquefied tissue (Kampen, 2002). It can be supposed that biting and rasping the host's skin represents the evolutionary starting point for their development.

A second starting point for the evolution of hematophagy in arthropods is predatory feeding, for example, the Reduviidae and perhaps also the Ixodidae. In these groups it can be assumed that a piercing organ already existed and that these animals completed the transition from predatory nutrition to ectoparasitism. The proboscis of all bugs, regardless of food preference, is functionally constructed to pierce animal tissues or various plant, for example, to bore into hard-shelled plant seeds. Saliva is applied to lubricate the piercing structures (Wenk et al., 2010) and enzymatically dissolve the plant tissue permitting it to be sucked up.

All Diptera exhibit mouthparts which can only take up liquid food (Krenn et al., 2005). Mapping the occurrences of blood-feeding species in a taxon onto a family tree of the Diptera shows that hematophagy arose in the order at least 12 times (Wiegmann et al., 2011). However, not all blood-feeding taxa include representatives which are relevant to humans. The piercing-proboscis of Diptera is derived from a functionally dapping or lapping proboscis which is found in various groups. Many of these insects show no special feeding preferences and suck liquid from various open food sources, such as floral nectar, vegetable saps, droppings of aphids, lachrymal fluids, wounds and sweat from the skin of mammals, fresh excrement and liquids on rotting substances. Blood-feeding Diptera require organs to puncture the host's skin. Their piercing organs are either formed by the mandibles, maxillae or the serrate labella. All blood-feeding non-calyptate Diptera use the mandibles for piercing (Nagatomi and Soroida, 1985). However, since the mandible was lost in the evolution of the stem group of the Cyclorrhapha (Matsuda, 1965), the labella became the secondary piercing organ which penetrates the skin in the Glossinidae and blood-feeding Muscidae (Schremmer, 1961).

The females of many hematophagous Diptera possess a piercing-proboscis with which they are additionally able to feed on floral nectar. Since the proboscis of the males is used exclusively for nectar feeding, it lacks mandible and maxillary stylets. Piercing structures are absent in both sexes in the tropical Culicidae of the genus *Toxorhynchites* since, both sexes feed exclusively on plant fluids and nectar, in particular (Snodgrass, 1959). In some Calyptrata evolution has taken a reverse course since nectar-feeding flies gave rise to blood-feeders. In the Stomoxydinae and the Glossinidae, both sexes are blood-feeders, and the two groups are independently derived from flower-visiting ancestors (Schremmer, 1961). The same hypothesis is discussed for Tabanidae which include several long-tongued flower-visiting taxa (Morita, 2008).

The blood-feeding moths constitute a special case. Only the males of certain representatives of the Noctuidae facultativly take up blood of mammals and, occasionally, humans, in addition to juices from thick-skinned fruits (Bänziger, 1970; Zaspel et al., 2007, 2011). The females of these species and both sexes of other closely related species have been observed to puncture and feed on fruits (Bänziger, 1970, 1975). The morphology of the proboscis and the mechanism of piercing are nearly identical for both kinds of food intake (Bänziger, 1970; Büttiker et al., 1996; Zaspel et al., 2011). It is clear that feeding on fruits by puncturing their skin gave rise to blood-feeding. While the females of most blood-feeding insects utilize the proteins in the blood meal for the production of their eggs, in blood-feeding Noctuidae only the males have been observed to take blood. This suggests that minerals in the blood are the essential resources which the moths are seeking, since male Lepidoptera in the tropics frequently take up mineral rich fluid (Downes, 1973; Beck et al., 1999). The search for minerals may also be the reason why some Lepidoptera take in lachrymal fluids. In most cases, the morphology of the proboscis differs fundamentally from that of piercing blood-feeding species (Büttiker et al., 1996; Zaspel et al., 2011). So far, a piercing-proboscis has been found in only one species of a facultatively tear-sucking noctuid (Hilgartner et al., 2007).

Anoplura are the only blood-feeding ectoparasites which permanently and in all developmental stages live on the host organism. All other blood-feeding arthropods are temporary parasites and after the blood meal has been taken they depart quickly from the host. This is especially true for Diptera which are strong fliers capable of considerable speed. These insects are able to consume large quantities of blood in a very short period of time. Prerequisites are a powerful suction organ and internal sensory equipment to supply information about the degree of fullness in the gut (Lehane, 2005). Furthermore, a powerfull flight apparatus is mandatory since weight increase of huge meals of blood (e.g., twice the body weight in many Culicidae) can be problematic for flight. Moreover, a physiological problem arises since water is quickly separated from the blood which then runs the risk of thickening (Lehane, 2005). Ticks visit their host organisms during a relatively short phase of their lives, often consuming large amounts of food and therefore sucking relatively long. Their strategy is to be inconspicuous and to take blood from inaccessible parts of the host.

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