Evolutionary Scenario of Rostrum Formation in the Rhynchota[1]

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Abstract—The biting mouthparts of the paraneopteran ancestor with elongated laciniae were transformed into the biting-sucking ones of primitive Psocoptera by modification of the laciniae into stylets, capable of protraction/retraction and of conducting liquid food into the cibarium. These insects fed on the contents of gymnosperm ovules. The recent Psocoptera represent a branch of Paraneoptera in which the primary (piercing-sucking) function of the laciniae has changed to chiseling and crushing of solid substrate. The psocopteran ancestors of Rhynchota switched from biting to piercing external plant tissues; the hind wall of the hypopharynx (in the hypognathous head) was transformed into the groove of the salivary pump as the insects switched to feeding on the contents of the plant conducting system. Swinging motion of the piercing mandibles with flexible stylet-like apices expanded the rotation of their bases, because of which the insertion of the hind branch of the genal abductors shifted to the subgena, the rudiment of the future lora. After that, the anterior mandibular articulation was lost and the mandibles were transformed into elaborate stylets. At the same time, retraction of the stylets into the head capsule caused a reversal of the subgenal abductor muscle, which became a protractor. Thysanoptera, specialized to feeding on the contents of plant cells, deviated at this particular stage of the mouthparts evolution. The formation of a completely closed (tubular) hypopharyngeal salivary pump and positioning of its apex between the maxillary stylets permitted elongation of the stylets and transformation of the mouthcone into a rostrum with suspended labium, while the glossa and paraglossa merged to form its apical segment. A transverse shift of the maxillary stylets relative to each other (the right one forward, and the left one backward) duplicated the canal between the stylets. The apex of hypopharyngeal salivary pump remained in the hind canal, which became only a salivary duct; the front canal became exclusively a food duct. The basic construction of the rostrum was thus complete. Suction of phloem-vessel contents with excessive water and sugar lead to the formation of the intestinal filter-chamber system. The filter-chamber was simplified or lost in the insects which secondarily switched to feeding on the cell contents with balanced food composition, as well as in predators, etc. Elongation of the stylets in the early Sternorrhyncha resulted in the formation of the crumena—an inner pouch near the rostrum base, which contained the loops of the stylets. Owing to sclerotization of its walls, the crumena was transformed into the basal apodeme of the labium (rostrum), improving its operation. In bugs with active raptorial habits, the rostrum shifted apically and the head became prognathous, elongate, and movable. The rostrum obtained a firm secondary articulation to the head capsule due to formation of a supplementary intercalary segment and the gular plate, which protected the space between the rostrum and cervix. The original type of substrate piercing is characterized by insertion of first the mandibular stylets and then the maxillary ones. A secondary type was formed in Auchenorrhyncha: after initial shallow insertion of mandibular stylets, further piercing is performed by maxillary stylets. This second type was preserved in true bugs (Heteroptera), but some of their advanced phylogenetic branches have reverted to the first type.

The rostrum of Rhynchota is a simple and efficient construction that has resulted from a profound transformation of the initial chewing mouthparts, namely the disappearance of the maxillae and mandibles, a strong modification of the labium and hypopharynx, and the development of the lora.

There are only two recent groups—psocids and thrips—representing intermediate stages of transformation of the typical chewing mouthparts of the re mote ancestors into the advanced rostrum of Rhyn chota. Psocids have already acquired free rod-lik laciniae, whereas the single remaining mandible i thrips is already modified into a stylet. The homolog between the laciniae of psocids and the maxillar stylets of thrips and Rhynchota was revealed b Börner (1904, 1929), who thus started the studies c the evolutionary development of mouthparts in thes groups. The early history of the study of mouthparts i Rhynchota has been covered by Puchkova (1980).

The origin and evolution of cephalic structures, an in particular the rostrum, have been covered in ex

tensive literature, reviewed by Matsuda (1965). A number of interesting works on this problem were published after this review (Denis and Bitsch, 1973; Parsons, 1974; Cobben, 1978; Hamilton, 1981; Backus, 1988, etc.).

In the evolution of Paraneoptera, the first essential modification of typical chewing mouthparts accompanied the origin of psocids, in which the laciniae became rod-like and lost their articulation with the stipes. The laciniae are not connected rigidly with other cephalic parts; their protraction and retraction are performed by antagonist muscles: the stipito-lacinial protractors and the tergo-lacinial retractors. There is no doubt about the homology of these muscles and those of the primitive chewing mouthparts (Matsuda, 1965). When articulation with the stipes was lost, the long tergo-lacinial flexor muscle drew the base of the lacinia deep into the head capsule, so that the stipito-lacinial adductor muscle turned by 180° at its lacinial end and became a protractor, antagonistic to the tergo-lacinial retractor. This event probably played the key role, determining all subsequent transformations of the mouthparts in Rhynchota.

Rhynchota originate not from the recent Psocida but from the extinct suborder Permopsocina, stemming, in its turn, from the extinct order Hypoperlida (Rasnitsyn, 1980a, 1980b, 1980c). According to the data of A.P. Rasnitsyn, both Permopsocina and Hypoperlida possessed sharp elongate mandibles and elongate laciniae. This author believed that Hypoperlida and Permopsocina fed on the contents of gymnosperm sporangia.

In the more advanced hypoperlid suborder, Strephocladina, the median margin of laciniae was dentate (Rasnitsyn, 1980c). This feature quite reliably indicates that the laciniae worked in the same way as the mandibles (i.e., were abducted and adducted), while preserving their articulation with the stipes. Therefore, in the less advanced suborder Hypoperlina, which gave rise to Strephocladina, the laciniae also had retained their initial articulation with the stipes; free inarticulate rod-like laciniae of the Rhynchota lineage must have appeared in psocids of the suborder Permopsocina.

A.P. Rasnitsyn noted that laciniae became stylet-shaped in Permopsocina (family Dichentomidae). One may assume that these insects destroyed the sheaths of sporangia with their mandibles, and then the laciniae extended to the liquid contents of immature ovules and formed a canal through which food could be imbibed. In this case, the need for extended axial protrusion of the lacinia is evident. Later, as the insects switched from feeding on the ovules to vegetative tissues, the function of mandibles may have changed from gnawing to piercing the substrate with their sharp tips, while the laciniae retained their sucking function. Deep penetration into plant tissues would be best justified if the stylets entered the deep conductive system, providing ample food. Within the framework of this hypothesis, the blunt-tipped separated laciniae of recent psocids should be regarded as a secondary modification, which occurred when the free laciniae acquired a different function (possibly chiseling or crushing) and became separated.

Strümpel (1983) distinguished between feeding on the liquid contents of the plant's conductive system (systembibition, including phloem- or xylembibition, respectively), and feeding on the contents of cells (localbibition). Insects feeding by systembibition, in particular all branches of Sternorrhyncha, primitively possess the filter chamber, developing at the contact of the anterior and posterior parts of their midgut and serving for quick excretion of excess water and sugars. Systembibition and the filter chamber together constitute a morphofunctional complex, whose presence is a primitive condition for Rhynchota (Emeljanov, 1987). Switching from system- to localbibition is usually accompanied by reduction or disappearance of the filter chamber.

In the reconstruction of consecutive stages of rostrum formation, the transformation of mandibles into stylets is most difficult to interpret. There exist four interrelated problems: (1) transformation of mandibles into stylets, (2) change from swinging motion of the mandibles to reciprocal motion of the stylets, (3) the origin and transformation of the muscles which finally became the stylet protractors, and (4) the homology of the protractor insertion areas, termed the lora or mandibular plates.

The greatest difficulties in reconstructing the evolutionary transformations are presented when profound (and therefore multi-stage) changes leave no evidence in the form of intermediate stages revealed by living organisms. The evolution of the rostrum in Rhynchota is definitely one of such cases. Thus, one must imagine the sequence of changes which would reflect the logical development of a construction while constantly preserving its adaptive significance, which allows the
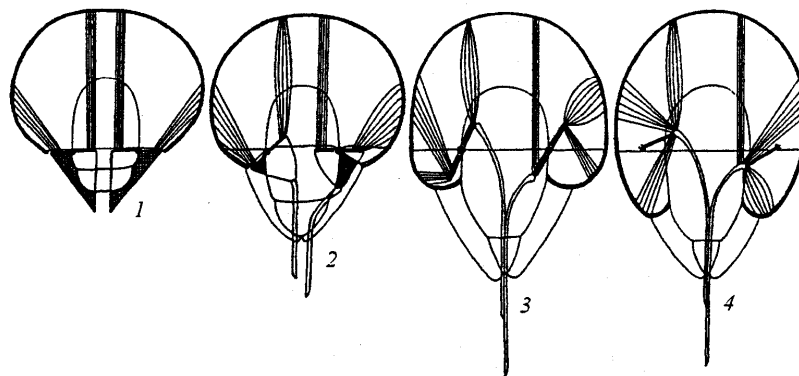
Figs. 1–4. Hypothetical scheme of transformation of chewing mandibles into stylets. A conventional frontal view through the "transparent" anterior wall of the head capsule. Chewing mandibles and major muscles of an ancestral psocid (*1*); stage of a primitive stylet articulated with a broad base of mandible (*2*); the mandible base is transformed into a rocker, while the genal abductor muscle splits in two branches as the range of mandible base rotation increases (*3*); anterior articulation of the mandible is disrupted and the rocker is transformed into a lever, while the epistomal branch of the genal abductor becomes a protractor (*4*). The left side of all diagrams except (*1*) shows the extreme abduction, and the right side, the extreme adduction. The part of the head capsule wall corresponding to the lora is shaded.

organism to exist in specific and successive environment.

The first two problems have not been directly addressed in the literature, but regarded as mere premises for solving the third and fourth problems. The problem of the lora homology and the origin of the mandibular stylet protractor, inserted on the lorum, gave rise to three groups of hypotheses, briefly reviewed and criticized by Denis and Bitsch (1973). According to these hypotheses, the lora were regarded as: (1) lateral parts of the postclypeus (Muir and Kershaw, 1911, 1912; Spooner, 1938; Evans, 1938; Ferris, 1943); (2) parts of the hypopharynx that have protruded outwards (Snodgrass, 1938; Du Porte, 1962; Parsons, 1964); (3) separated lateral parts of the genae, subgenae, or pleurostoma (Weber, 1928; Pesson, 1944; Qadri and Aziz, 1950; Akbar, 1957; Denis and Bitsch, 1973). Hypotheses of the first group fail to explain the origin of the clypeo-mandibular protractor muscle. In hypotheses of the second group, the stylet protractor is considered homologous with the tentorio-mandibular muscle, which on one end attaches basally to the hypopharynx, and on the other end enters the mandible and attaches to its lateral wall (Snodgrass, 1938); such a muscle is present in roaches and some other orthopteroid insects, and also in psocids (Prawdin, 1932). The weak point of this hypothesis is that one could hardly imagine viable insects with mouthparts corresponding to the intermediate stages of transformation of the mandible into the stylet and the muscle into the protractor.

The geno-subgenal hypothesis of lorum homology, considering the protractor of mandibular stylet as the former genal abductor of mandible, appears to be the only one that explains the whole sequence of transformations without presuming some clearly nonadaptive intermediate stages (Figs. 1–8).

With chewing mandibles preserved, deep penetration into the substrate can be achieved only by elongation of the preoral portion of the cranium, as observed in the scorpionfly, weevils, elephant louse, etc. The advanced forms of Hypoperlida–Strephocladina, which later gave rise to Dictyoneurida (Palaeodictyoptera) and some related extinct orders, evolved in this particular direction.

The ancestors of Rhynchota followed a different evolutionary path. Their mandibles switched from gnawing to piercing; initially, chiseling and piercing of the substrate might be accomplished by active adduction and abduction of the mandibles combined with lowering the entire head to press the mandibles into the substrate (the force line: head–neck–fore legs). This very motion is represented by the "nodding" movements in thrips. There are other insects with sharp mandibles in which the active functional phase falls on abduction (larva of the sawfly *Phyllotoma aceris*, cited after: Schwanwitsch, 1949).

In the piercing mouthparts, the active phase has shifted from adduction to abduction. As the stylet-like apical parts of mandibles elongated, they became
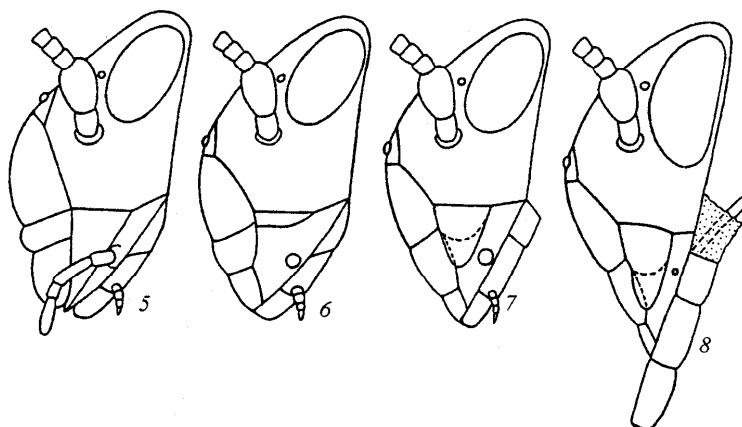
Figs. 5–8. Hypothetical scheme of head transformations from the psocopteran ancestor to Rhynchota: lateral view. Head of a psocid (*5*); two stages of lorum formation (*6, 7*); head of the common ancestor of Rhynchota with suspended rostrum (labium) (*8*). Fig. 6 corresponds to the stage shown in Fig. 2, and Figs. 7 and 8 correspond to the stage shown in Fig. 3.

flexible. The mandibles were initially fixed together (and with the maxillary stylets) by the labrum and partly the anteclypeus, which formed a groove and later a tube. The groove of the labrum was closed posteriorly with the labium. Owing to the flexibility of the mandibular apices (the primitive stylets), kept together by the labrum and labium, the swinging motion of mandibular bases was transformed into the reciprocal motion of mandibular apices. At this or an earlier stage, simultaneous movements of the mandibles could be combined with alternate ones, when at a given moment one mandible was driven into the substrate (abducted), and the other pulled out (adducted), etc.

The increasing range of protraction, and, correspondingly, retraction of mandibular stylets required a greater turning angle of their basal parts. From the mechanical standpoint, the best way to meet this requirement would be to divide the mandible into two segments: a broad base and a narrow stylet (Fig. 2). Such a construction allowed extreme adduction of mandibular bases, because the apices (stylets) no longer rested against one another. At this particular phase, the mandibular abductor, attached to the gena, widened at the base and finally split in two branches (Figs. 2, 3), because the beginning of abduction=protraction was performed by the lower part of this muscle, adjacent to the epigenal suture, whereas the final action depended on the upper part. The insertion site of the subgenal branch shifted forward (downward, in case of a hypognathous head) from the mandibular fulcrum and onto the opposite side of the subgenal suture, i.e., onto

the rudimentary lora. In this interpretation, the lora are separated from the genae by the subgenal suture, thus being homologous to the subgenae.

Matsuda (1965) reported two observations which he considered at variance with the presumed homology between the mandibular stylet protractor and the former mandibular abductor. First, according to Pesson (1944), the loral protractor of the mandibular stylet (in scale insects) is innervated by the epipharyngeal (preoral) nerve and therefore cannot have originated from a mandibular (postoral) muscle. However, Benwitz (1956) showed that the nerve in question (in *Corixa*) is not epipharyngeal but belongs to the subpharyngeal ganglion, even though it deviates from the common neuronal mass within the suprapharyngeal area. Second, Newcomer (1948) reported that the mandibular stylet protractor in the bug *Oncopeltus* developed as a fronto-mandibular rudiment and only later became associated with the lorum. However, considering the major transformations of the head along the evolutionary lineage of bugs in general and Lygaeidae (*Oncopeltus*) in particular, and the vague delimitation of frons, clypeus, genae, etc. in these insects, the initial position of the rudimentary muscle cannot be a conclusive evidence. Either the rudiment could have secondarily shifted, or the part of the cranium regarded as frontal by Newcomer is actually genal.

The separation of the mandibular stylet from the main body of the mandible may be considered an evolutionary novelty. Alternatively, one may suppose that

the stylet corresponds to the movable subapical part of a chewing mandible (the so-called lacinia mobilis), which is known in some crustaceans, ephemeropteran nymphs, and some other insects (Snodgrass, 1950).

Immediately after the subdivision of the mandible, its base was reduced to a rocker controlling the stylet (Fig. 3), while the stylet base shifted toward the median arm, close to the retractor insertion. The movement range of both the base and the stylet increased. The decisive, and basically the conclusive stage of mandibular stylet development occurred when the mandible base lost its anterior articulation and was transformed into the stylet lever (Fig. 4); this resulted in a simpler mechanism of stylet movement. These three events (subdivision of the mandible in two parts, transformation of the base into a rocker, and disruption of the anterior articulation) must have followed in rapid sequence. The mandibular lever is inserted on the head capsule between the lorum and the mandibular plate base, far from the base of anterior tentorial rami, indicating that it is the anterior articulation that was lost. As the anterior mandibular articulation broke, the two branches of the former geno-mandibular abductor muscle became antagonists (Fig. 4): the loral muscle became the protractor, and the upper muscle became the genal retractor. The latter works synergistically with the main mandibular muscle (initially the main adductor), which is attached to the vertical part of the head capsule.

As the massive mandible narrowed and moved into the preoral cavity, a gap appeared between the clypeus and the maxillary plate; this gap was then closed by the growing lora and the anterior margin of the maxillary plates (Figs. 5–8).

The separation of thrips from the lineage of Rhynchota occurred after the formation of the mandibular stylets and lora.

Thrips deviated from this lineage at an intermediate stage of rostrum formation. They switched to feeding on the contents of plant cells, which was accompanied by diminutiveness and did not require the sophisticated procedures of deep penetration into the substrate. In thrips, the mandibular muscles have completely lost their initial function, and piercing the substrate with mandibular stylets is accomplished entirely by the "nodding" movements of the head. The mandibular protractors disappeared, because the only remaining function was that of fixing the mandibles prior to penetration. Furthermore, one of the mandi-

bles disappeared because a single passive stylet was easier to drive into the substrate. The limited protraction of the mandible in thrips may employ a hydraulic mechanism, i.e., it may be accomplished by a local increase in the hemolymph pressure.

The asymmetrical mouthparts of thrips (Fig. 10) may be quite easily "traced back" to their initial symmetrical state. To do so, one has to mentally restore the right mandible (stylet) and the muscles associated with mandibular stylets, or, in other words, to "undo" the major autapomorphies of Thysanoptera (Fig. 9).

The symmetrical mouthparts of the direct common ancestors of Thysanoptera and Rhynchota are characterized by a mouthcone, in whose apical portion the bundle of mandibular and maxillary stylets is enclosed by a tube formed by the labrum. The food duct is formed by the maxillae, the mandibles envelope the maxillae laterally, and the maxillary plates with remaining palps are positioned still farther laterad. The hypopharynx is positioned behind the maxillary stylets and has a grooved hind wall that fits closely to the anterior wall of labium. The lateral parts of labium are folded anteriad and form the rudimentary labial sheath, which encloses the labrum near the apex. The labrum comprises three parts: postmentum, prementum, and partly merged glossae and paraglossae; the prementum bears palps.

The grooved hind wall of hypopharynx, pressed against the anterior wall of labium, forms a two-component salivary duct, which functions as a salivary pump and is controlled by the muscles of the hypopharynx. These muscles pull at the groove wall and draw the saliva from the salivary duct that opens basally at the hypopharynx; as the muscles relax, the elastic wall returns to its initial position and pushes the saliva out. The two-component salivary duct did not allow the mouthcone to elongate, or at least did not facilitate this process.

Further transformations of the mouthparts in the ancestral Rhynchota took place after the separation of the thysanopteran lineage.

First, the salivary pump was improved. The groove of the hypopharynx was transformed into a tube and separated from the labrum. The part of the hypopharynx wall directly adjacent to the primary opening of the salivary duct became the pump piston. The secondary opening of the salivary duct was located on the narrow apex of the hypopharynx. The morphological composition of the salivary pump was revealed by
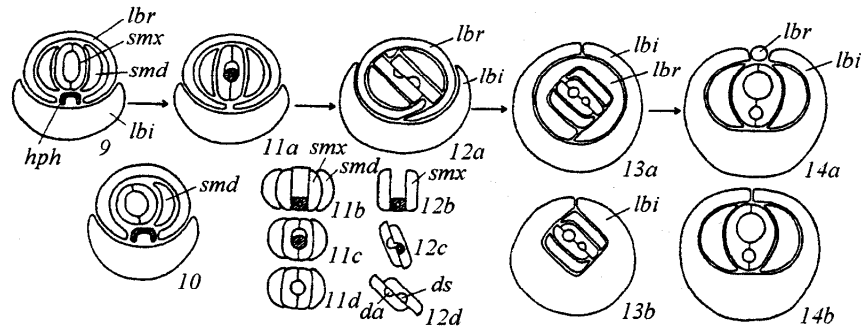
Figs. 9–14. Transformation of the mouthcone of the common ancestor of Rhynchota and Thysanoptera into the rostrum. Schematic transversal sections through the mouthcone (*9–11*) and rostrum (*12–14*), viewed from the apex. Common ancestor of Rhynchota and Thysanoptera (*9*); mouthcone of Thysanoptera (*10*); direct ancestor of Rhynchota after the formation of the hypopharyngeal syringe, with its apex aligned with the maxillary canal (*11a*), and three consecutive sections of these stylets from base to apex of the mouthcone (*11b–11d*); first representative of Rhynchota, characterized by the formation of two canals between the maxillary stylets (section at the labrum level) (*12a*), and three consecutive sections of maxillary stylets from base to apex (*12a–12d*); the stage of Sternorrhyncha, sections at the labrum level (*13a*) and distal to the labrum (*13b*); the stage of Auchenorrhyncha, sections at the labrum level (*14a*) and distal to the labrum (*14b*); *da*, food duct; *ds*, salivary duct; *hph*, hypopharynx (shaded); *lbi*, labium; *lbr*, labrum; *smd*, mandibular stylet; *smx*, maxillary stylet.

P. Pesson, based on the study of scale insect females (Pesson, 1944; see also Puchkova, 1980). At that stage, the separate hypopharyngeal syringe could be united with the maxillary food duct (Fig. 11); this modification was simple, because the maxillae were separated at the rostrum base and the hypopharynx formed the ventral wall of the preoral cavity. This allowed the saliva to be pumped into the substrate regardless of the rostrum length. This advantage probably outweighed the shortcomings of using the same canal alternately for excretion of saliva and intake of food. However, in Rhynchota the food and salivary ducts are separated, even though both run between the maxillary stylets. This state could be accomplished by a shift of the stylets relative to one another in the sagittal plane, made easier by a slight twist: the left stylet shifted backward, and the right one forward (Fig. 12). Thus a single canal was divided in two; the posterior canal (in a hypognathous head) became the salivary duct because it contained the apex of hypopharynx, whereas the anterior duct started to serve only for taking in food. Therefore, the saliva and food flows were again separated in the elongated rostrum. This allowed the insect to feed on the contents of the conductive system (systembibition). These processes (development of the salivary syringe, introduction of the hypopharynx apex into the duct, and separation of the ducts) appear to have occurred in rapid sequence. Traces of the sagittal shift of the stylets, exactly as described above, are quite evident in

the morphology of rostrum of Sternorrhyncha (especially Psyllina); the shift can also be reconstructed from the axial twist of the stylets and the overlapping margins of the labrum (Fig. 13).

As the rostrum elongated, the unmodified labrum remained in the basal position and later lost the function of fixing (enclosing) the stylets (Fig. 14). The elongating labium preserved the apical sensory complex, initially located on the glossae and paraglossae. Comparison of the labium of Thysanoptera with the rostrum of Rhynchota shows, as stated above, that the three initial segments of the rostrum correspond to the postmentum, prementum, and the merged glossae and paraglossae. In the rostrum of bugs, the so-called apical lobes are present (anteriorly) dorsally at the boundary of the penultimate and ultimate (3rd and 4th) segments. Some authors regard these lobes as rudiments of labial palps, and Puchkova (1980, and references therein) even calls them the labiopalpal lobes. This hypothesis is contradicted by the fact that such lobes are absent in Sternorrhyncha and Auchenorrhyncha, occupying more basal positions in the Rhynchota lineage. At the same time, representatives of subfamily Membracoidea (Cicadelloidea) within Auchenorrhyncha have a pair of triangular accessory sclerites, located posteriorly (ventrally) on the ultimate segment at its boundary with the penultimate one (Kramer, 1950; Emeljanov, 1987). These specific features of the above groups most probably represent evolutionary novelties, or autapomorphies.

As the labium was transformed into the rostrum, its sclerotized base detached from the head capsule wall, so that the rostrum remained suspended on the conical or cylindrical membrane (Fig. 8). This allowed the entire rostrum to be protracted or retracted by stretching or folding the membrane. At the mouthcone stage, the apices of all mouthparts were positioned at the same level, and the prementum lay under (behind) the labrum. Contrariwise, in the rostrum, only the first, basal segment, corresponding to the postmentum, lay at the level of the labrum and maxillary plate apices, whereas the second and third segments were located more distally. This free rostrum was fixed in the gap between the opisthognathous head and the sternal part of prothorax. In addition, it was kept in place by the stylets themselves, and laterally, by the fore coxae.

For feeding, the rostrum was protruded (practically back- and downward, its base getting close to the labrum) and then bent for- and downward to an approximately vertical position. Elongation of the stylets, necessary for systembibition, quickly resulted in an improved mechanism of stylet protrusion. The strongly elongated stylets were folded into a loop, and the so-called crumena was formed. The crumena is a closed inner canal or pouch, positioned at the rostrum base and directed up- and backward into the cervical area and the prothorax; it accommodates the looped stylets in a protracted state. The second segment of rostrum in many Sternorrhyncha (psyllids, scales) has a special "clutch" that allows the stylets to be packed into the crumena without releasing them from the rostrum (Weber, 1929b).

It may be assumed that the same clutching mechanism was involved also in the protrusion and abduction of rostrum prior to the stylet insertion. Later, the crumena became sclerotized, and some of the muscles attached to the rostrum base shifted on it. Thus the crumena was transformed into the basal apodeme of the rostrum, after which its primary function, namely that of a container for stylets, was lost. The development of this apodeme provided much better control of the rostrum. Among Sternorrhyncha, the apodeme is typically present in whiteflies, even though it is still tubular and retains a lumen (Weber, 1930, 1935).

The crumena is present in adult psyllids and scale insects (Weber, 1929a, 1929b) and absent in psyllid nymphs and all stages of aphids. The rostrum of aphids is permanently positioned more or less verti-

cally, which appears to be a secondary condition. The coccid-like nymphs of chermes and phylloxeras do not seem to have been studied in this respect. The position of rostrum in adult psyllids may be regarded as a case of retardation, or preservation of a larval state. If we assume that transformation of the crumena into the sclerotized apodeme initially occurred only in adult forms of ancient rhynchotes, then the presence and absence of the crumena in different groups of Sternorrhyncha can be easily explained.

The development of active predatory habits in Heteroptera was accompanied by increased movability of the head and the active functional role of the rostrum (= labium), which were needed for attacking the prey. The rostrum shifted apically and acquired a supplementary intercalary segment, providing articulation with the head, and the gular plate, strengthening the head capsule ventrally. In bugs, the basal apodeme of the rostrum rests on the second segment (initially the first one) and passes through the newly formed first segment (Matsuda, 1965).

Once evolved, this basic scheme of stylet morphology did not change. Despite high diversity of functional details, the structure itself was almost never subject to reduction; exceptions from this rule may be found in some bugs (Hydrometra; see below).

Peloridiidae and true bugs are characterized by spline (groove-and-fin) coupling between the maxillary and mandibular stylets. The successive stages of transformation of the chewing orthopteroid mouthparts into the rostrum are shown in the phylogenetic diagram (Fig. 15).

There are two main types of stylet insertion, referred to as "mandibles ahead" and "maxillae ahead" (Backus, 1988). In the first case, the mandibular stylets perform complete penetration before the maxillae; in the second case, the mandibular stylets are inserted not very deep (anchored) and further penetration is performed by the maxillae only. The "mandibles ahead" type is obviously the primitive one, at least because if it were not so, the mandibles would not be modified into the stylets at all. In addition, the outer mandibular stylets have "inherited" the active function from the mandibles. Indeed, this particular type of insertion is observed in Sternorrhyncha. The "maxillae ahead" type is present in Auchenorrhyncha, whereas Heteroptera display both types, "maxillae ahead" being undoubtedly the initial one.
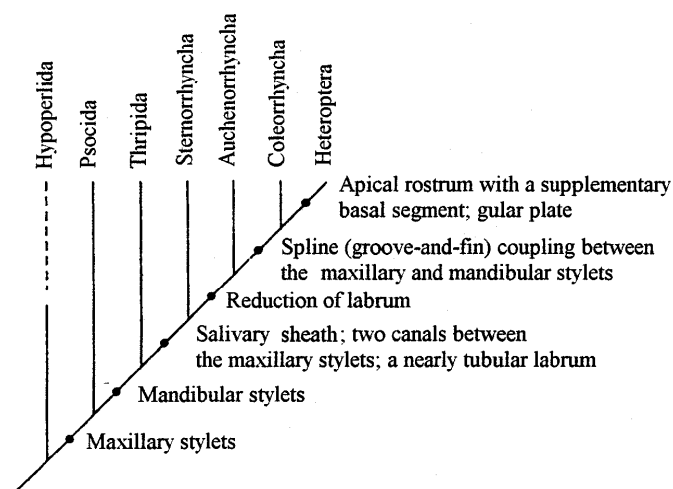
Fig. 15. Main stages of rostrum formation in Paraneoptera in relation to their phylogeny.

Cobben (1978) considered the rostrum of Gerromorpha as an initial state for his scheme of evolution of rostra and the insertion types. Moreover, he illustrated this scheme with an evidently secondary rostrum of *Hydrometra*, lacking a salivary duct (the disappearance of this duct can be easily traced within Gerromorpha, where such forms as *Hebrus* and *Velia* have almost normal rostra). It is hardly possible to assume that a salivary duct first appeared in Gerromorpha and that this group gave rise to all other members of Rhynchota. However, this hypothesis was accepted by Cobben (1978), though his views were in many respects vague and inconsistent when analyzed as a whole, rather than from a single quotation.[2] Additional apomorphic features of the rostrum in Gerromorpha are rather slender mandibular stylets, which are narrower than the maxillary stylets and do not envelope them.

E.A. Backus accepted and reproduced Cobben's scheme together with its inconsistency as regards the

evolution of rostrum in Sternorrhyncha and Auchenorrhyncha; she also regarded the "maxillae ahead" insertion type, typical of Gerromorpha, as primitive. However, Gerromorpha cannot be considered not only the most primitive Rhynchota, but even the most primitive bugs. A sufficiently well-founded variant of the phylogeny of Heteroptera is shown in Fig. 16.

Contrary to the views of E.A. Backus, the evolution of insertion systems, combined with a phylogenetic cladogram (Figs. 15, 16), looks as follows. (1) Sternorrhyncha: mandibular stylets ahead, salivary sheath, systembibition, secondary localbibition. (2) Auchenorrhyncha: maxillary stylets ahead, salivary sheath, systembibition, secondary localbibition. (3.1) Heteroptera: primitively maxillary stylets ahead, no salivary sheath, predation; secondary saprophagy and similar modes of feeding. (3.2) Secondarily: mandibular stylets ahead, no salivary sheath, localbibition—Cimicomorpha (partly). (3.3) Mandibular stylets ahead, salivary sheath, systembibition—Pentatomomorpha. In this scheme, the development of predatory habits is accompanied by reduction of the salivary sheath; reversal to systembibition leads to secondary development of the salivary sheath (Pentatomomorpha); development of localbibition does not lead to restoration of the salivary sheath; both cases of reversal to phytophagy in bugs are correlated with secondary development of the "mandibles ahead" mode; the maxillary stylets lose their innervation also in two cases (Sternorrhyncha and Pentatomomorpha).

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[2] In one part of his work, Cobben considers the absence of a salivary duct in the stylets of Gerromorpha (*Hydrometra, Gerris*) as a secondary phenomenon, whereas in another part, he states that it is in Gerromorpha that the second (salivary) duct first developed. Incidentally, Cobben's assumption that first Homoptera were predaceous is based solely on the presence of inner denticles on the maxillary stylets of *Tettigometra*; according to Cobben, denticles could develop only in predators. However, Sternorrhyncha and Auchenorryncha include no predaceous forms; these insects are phytophagous or (some cicadas) mycophagous.

The evolution of the outline of the stylet bundle can be traced. The bundle cross-section is isodiametric in the "mandibles ahead" system and considerably flattened in the dorsoventral direction in the "maxillae ahead" system. A flattened shape is observed in Auchenorrhyncha (except Fulgoroidea), Coleorrhyncha, and also in the bugs Enicocephalomorpha. In predaceous forms, which are phylogenetically more advanced than Enicocephalomorpha, the bundle loses its flattened outline and becomes thinner, while the mandibular stylets are not inserted deep into the prey. As Auchenorrhyncha switched to the "maxillae ahead" system, their maxillary stylets changed from rectangular, elongated to dorsoventrally rounded isodiametric outline, evidently to reduce the substrate resistance. The rounded cross-section led to twisting of the stylets, though the adaptive significance of this remains unknown. Fulgoroidea reveal no twisting of stylets; the cross-section of their maxillary stylets is ovoid, slightly compressed laterally. In Coleorrhyncha and Heteroptera the maxillary stylets are not twisted, either because of the spline coupling with the mandibular stylets, or because of the more complicated area of their contact. One may assume that the spline (groove-and-fin) coupling between the maxillae and mandibles first appeared in Peloridiidae and was preserved up to the derived Cimicomorpha and Pentatomomorpha; however, in a number of groups, it was reduced and even completely disappeared.

The narrowing of mandibular stylets is generally accompanied by their ventral shift, so that the maxillary stylets become pyriform in cross-section. Switching to phytophagy in the higher Heteroptera is accompanied by strengthening of the maxillo-mandibular spline coupling in the same area as in Coleorrhyncha. The cross-section of the maxillary stylets again becomes rectangular and elongated dorso-ventrally (more distinctly in Pentatomomorpha). The lateral compression of maxillary stylets may increase their flexibility in a specific plane, which may be related to their folding in loops or coils. The crumena is often present in Sternorrhyncha and Pentatomomorpha, whereas neither the crumena nor looping of the stylet bundle is known in Auchenorrhyncha. Thus, it may be assumed that the "mandibles ahead" system typically occurs in groups with longer stylets. Narrow mandibular stylets, not enclosing the maxillary stylets, are probably correlated only with the "maxillae ahead" system.
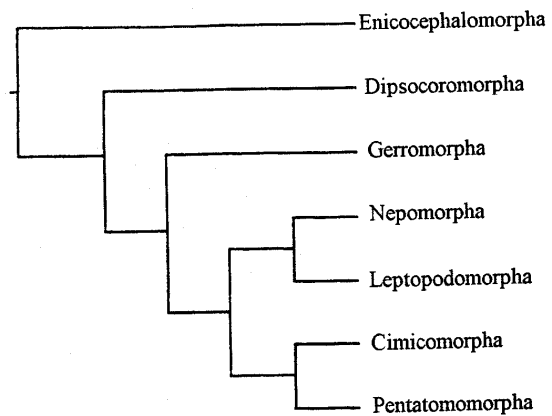
Fig. 16. A phylogenetic cladogram of Heteroptera (after Schuh, 1979).

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