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The morphology of the labrum (epipharynx, ikrioma and aboral surface) of adult Aphodiini (Coleoptera: Scarabaeidae: Aphodiinae), and its implications for systematics

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Abstract. The morphology of the labrum (epipharynx, ikrioma and aboral surface) of adult Aphodiini is figured and discussed. An updated glossary of the constitutive parts is presented.

Keywords. Aphodiinae, glossary of terms, labrum morphology, taxonomic characters

Introduction

There are few studies that describe and illustrate the epipharynx of adult Aphodiinae (Dellacasa 1978, 1983; Nel and de Villiers 1988; Bordat 1992; Stebnicka and Howden 1995; Deloya and Guerrero 1998; Godwin 2002; Gordon and Skelley 2007). Unfortunately, terminology has not been standardized and not all structures have been named. Although Godwin (2002) produced the most thorough work to date, it remains unpublished. Therefore we present an updated and illustrated terminology for labral characters of adult Aphodiinae (= Aphodiidae *sensu* Dellacasa and Dellacasa et al. 2005), with an emphasis on members of the tribe Aphodiini. This terminology should apply equally well to all members of the subfamily.

Most published accounts on the epipharynx (*sensu lato*) deal with diagnoses and systematics of Coleoptera larvae. Within the Scarabaeoidea, the larval epipharynx was first figured by Schiödte (1874) for *Geotrupes stercorarius* (Linnaeus) (Geotrupidae). Böving (1921) illustrated the larval epipharynx of *Popillia japonica* Newman (Scarabaeidae: Rutelinae) and first coined the term 'epipharynx' as used in larval scarabaeoid taxonomy. However, it was Rittershaus (1927) who first named parts of this structure when she described and figured the larval epipharynges of *Phyllopertha horticola* (Linnaeus) and *Anomala dubia* (Scopoli) [as *Anomala aenea* Degeer] (Scarabaeidae: Rutelinae). Hayes (1928, 1930) dealt with the morphology, taxonomy and biology of scarabaeoid larvae and was the first to use characters of the epipharynx to diagnose subfamilies and genera. Hayes (1930) was also the first author to use descriptive terms to define epipharyngeal characters.

Böving (1936) deemed Hayes' terminology insufficient, and so proposed a new set of terms, with a peculiar terminology derived from Latinized old Greek words. Böving (1936) recognized two types of epipharynx among the scarabaeoid larvae, one "generalized and fundamental" found in the Trogidae, Aphodiinae and Lucanidae. The other, "highly specialized and complicated" found in the larvae of most other family groups. Böving (1936) stated that, because the epipharynges of the larvae he dealt with possess the

second, highly specialized type, the terminology he defined could only be referred and applied to these groups.

Although the morphology of the epipharynx (*sensu lato*), has been figured and generally diagnosed since Sturm (1805), it has only recently been used in the characterization of adult Aphodiinae. Schmidt (1922), in his monograph on world Aphodiinae, presented a few schematic figures of the mouth parts, including the epipharynx, and this was probably the first use of the epipharynx as a discriminating character at the genus-group level within the Aphodiinae. With a comparative study of epipharynx, aedeagus and habitus, Paulian (1942) re-evaluated most of the *Aphodius* subgenera from the Afrotropical region, raising many to generic rank. In more recent years the realization that structures of the labrum represent one of the most important character sets available to analyse and ascertain the taxonomic affinities within Aphodiinae at the genus-group level, has resulted in it being routinely used (e.g. Dellacasa 1983; Bordat 1992; Gordon and Skelley 2007; Stebnicka 2007). Dellacasa et al. (2001) extensively used the characters of the epipharynx to help define all type species for genera of the Aphodiini (Aphodiinae *sensu* Dellacasa et al. 2001).

Although Böving (1936) stated that the terms he created for the larval epipharynx of certain scarabaeid subfamilies cannot be applied to the same structures found in larvae of other family groups, Dellacasa (1978) adopted Böving's terminology for the epipharynx of adult Aphodiinae. This arbitrary application of identical terminology for different and often non homologous epipharyngeal structures has been criticized by Godwin (2002). For example, Godwin remarks that Böving's "proplegmatium" refers to lateral parial plicate regions of the epipharynx, conversely Dellacasa's "proplegmatium" is a single plicate process positioned transversally at about the basal third of the same structure.

When producing phylogenies based on the characters of epipharyngeal structures, one must be aware that because the epipharynx is a mouth part, it is subject to adaptive pressures hence prone to exhibit convergent characters. For example, since most adult Aphodiinae feed on dung, the differences in the morphology of their epipharynx compared to those of saprophagous taxa are particularly evident. However, if the structural homologies are believed indispensable in a phylogenetic analysis, the first step towards their use is to standardize terminology for each homologous structure [Homology is here intended as "a correspondence in type of structure between parts or organs of different organisms, due to evolutionary differentiation from the same or a corresponding part or organ of same remote ancestor" and, more specifically, serial homology as "a correspondence of an organ of one segment with that of another of a different segment if the two are derived from corresponding parts" (Torre-Bueno 1937)]. However, it is very difficult to ascertain homologies within the various epipharyngeal structures of the adults and those of larvae, even if taxa pertaining to the same family-group are only taken into consideration. The level of difficulty increases when trying to associate homologous epipharyngeal structures of adults and those of the larvae from different family-group taxa.

The priority principle is not required for morphological terminology, but its application does seem appropriate in this case. Essentially, to modify the nomenclature of epipharyngeal structures again, even if arbitrarily adopted will increase the confusion over the terminology. Nevertheless the new terms proposed by Godwin (2002) are used here.

Methods

Methods used for the removal and mounting of the labrum will vary according to personal preferences, the method described below is partly based on that published by Bordat (1992) and is suitable for all Scarabaeidae.

Preparation. Freshly killed material can be dissected immediately. Dried material will require softening, which is best achieved in water (distilled or deionized) with a few drops of surfactant (e.g. domestic detergent) over a 12 to 24 hour period at ambient temperature. This time period depends on size and initial preservation treatment of specimens. The softening process can be accelerated by placing the specimen in boiling water, however, this process may result a drastic solution that should be avoided. Note that this treatment may have a deleterious effect on the future availability of genetic material from specimens.

Dissection. The entire dissection process should be conducted under a dissecting microscope and in an excavated glass block (or other suitable dish) in water (preferably distilled or deionised) to reduce the risk of accidental loss of parts.

Equipment:

- 2 pairs of very fine pointed stainless steel antimagnetic watchmaker's forceps (No. 5A or 5);
- 1 brush with fine point (size 000 or 00);
- 1 stainless steel headless micropin attached to a match-stick or similar;
- 1 toothpick with one end modified to a flat point.

For mounting the labrum it is useful to prepare a microslide in the following manner: with a glasscutter, cut a square cover glass (for example size 18 x 18 mm) as in Fig. 58 in order to obtain 3 pieces of 6 x 12 mm and 3 pieces of 6 x 6 mm; glue the shorter side of a 6 x 12 mm piece to a card with a vinylic adhesive (e.g. PVA); the labrum will be mounted on the "slide" in a thin film of dimethyl hydantoin formaldehyde (D.M.H.F.) (Steedman 1958) and then covered with a 6 x 6 mm piece of cover glass (Fig. 59:a-d).

The D.M.H.F. is crystal clear and permits observations of minute details whilst setting hard and thus affording maximum protection, moreover being water soluble, it permits removal of the labrum for re-orientation should the need arise. Alternative mounting media can be used such as Canada balsam or euparal. However, these require a more detailed and time-consuming treatment of the material to be embedded (see Schauff 1986; Brown 1997; and references therein for methodology).

The dissection can proceed as follow:

a – after softening (as above), with forceps remove the head capsule at the level of the occipital foramen;
b – hold the head with the ventral side up by inserting the toothpick into the occipital foramen; the same can be done with the forceps but great care is needed to avoid damaging the head capsule;
c – with the point of the forceps carefully remove the mentum by separating its base from the head capsule (Fig. 54), then remove the maxillae at their basal articulation (Fig. 55) and finally the mandibles (Fig. 56). In the oral cavity, connected to the ventral surface of the head near its anterior margin, is the labrum (Fig. 57);
d – remove the labrum by carefully inserting a micropin between the ventral surface of the head and the labrum. The same can be done in larger specimens by using the fine point of the forceps;
e – the dissected parts (mentum, maxillae and mandibles) can be removed from the water with a fine brush and mounted as discussed below;
f – mount the labrum on the prepared microslide (see above) in a film of D.M.H.F. (or other suitable mounting media, see above) and cover it with a cover slip;
g – glue the head capsule back on the dissected specimen using a water-soluble glue.

It is always good practice to retain dissected parts (mentum, maxillae and mandibles), data and other labels with the specimen to which they belong, since disassociation of specimen, parts and data can be disastrous. The use of the microslide prepared as described instead of the standard microscope slides, allows the labrum to be kept with the rest of the specimen on the same pin as shown in Fig. 60.

MORPHOLOGY OF LABRUM

The **labrum** is a well differentiate head appendage characteristic for each taxon, or at least for each group of taxa. Its oral surface is the most complex, with numerous sclerites, and groups of setae and chaetae that probably have tractile, tactile and gustatory functions (Miller 1961).

The imprecise application of the term "epipharynx" is one of the principal causes of the nomenclatural confusion in the morphological diagnosis of the labrum parts. Though the term epipharynx should exclusively be applied to the oral surface of the labrum, it is currently used to describe the entire structure, and traditionally the epipharynx and labrum have been treated synonymously (e.g. Böving 1936; Dellacasa 1978). However, in adult Aphodiinae the labrum is divisible into three parts: **1) epipharynx; 2) ikrioma; 3) aboral surface.**

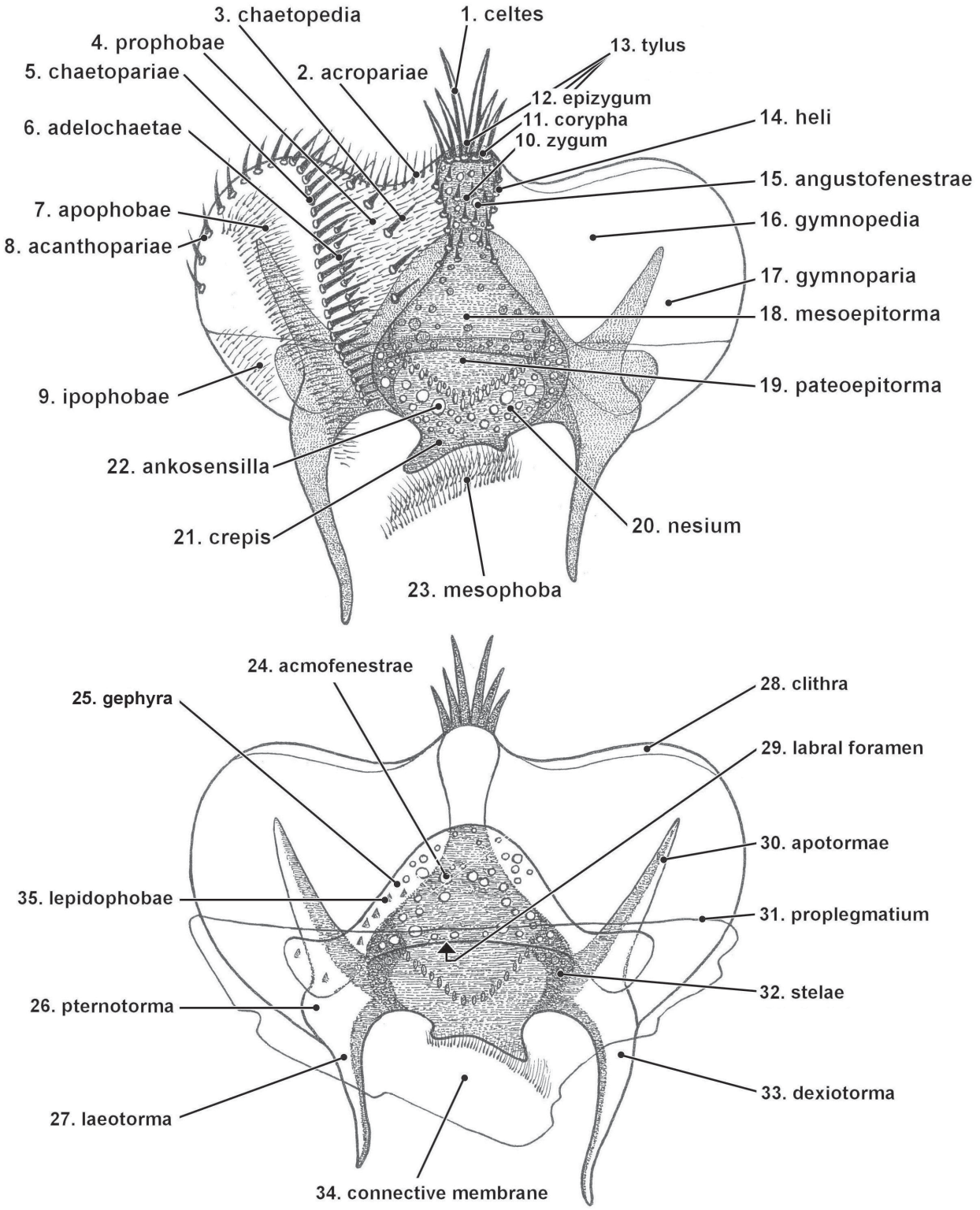

Figure 1-2. Labrum general terminology. **1)** Epipharynx. **2)** Labral aboral surface and inner scleromes.

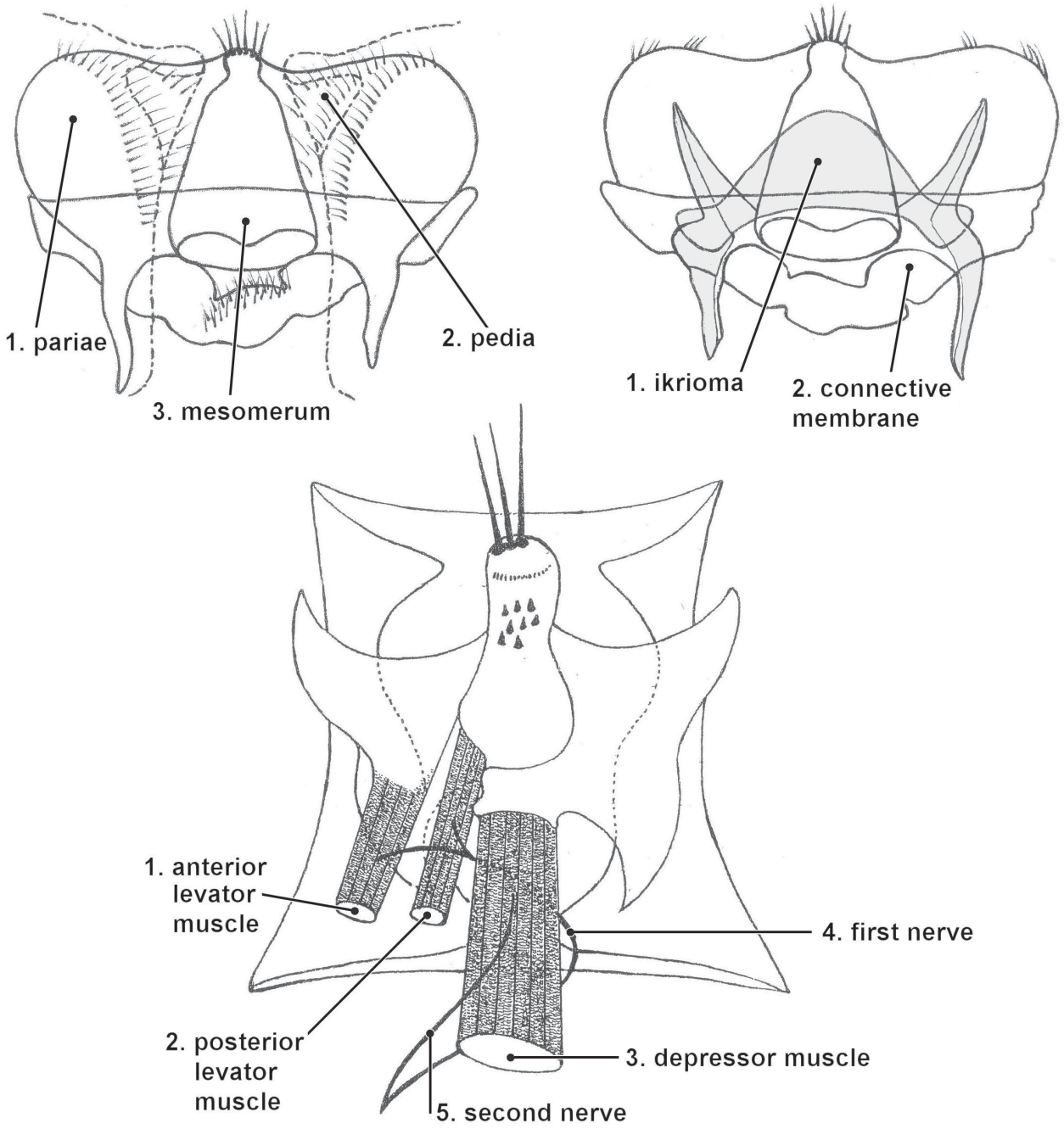

Figure 3-5. Labrum general terminology. **3)** Epipharyngeal regions. **4)** Aboral frames. **5)** Epipharyngeal muscles and nerves.

In addition, the following muscles and nerves (after Zombori and Steinmann 1999) are found in the labral frame: epipharyngeal anterior levator muscle (Fig. 5:1); epipharyngeal posterior levator muscle (Fig. 5:2); epipharyngeal depressor muscle (Fig. 5:3); first epipharyngeal nerve (Fig. 5:4); second epipharyngeal nerve (Fig. 5:5).

1. EPIPHARYNX

The epipharynx (Fig. 1-3) is the oral surface of a movable blade, the labrum, connected to the inferior surface of epicranium (endocranium) within the epistomal area. In groups of closely related species, it usually lacks significant morphological differences, thus enabling the definition of homogeneous groupings at supraspecific level.

Two main forms of epipharynx are distinguishable in adult Aphodiinae (e.g. Stebnicka and Howden 1995): a) those adapted mainly for coprophagy; and b) those adapted mainly for saprophagy.

a) Epipharynx adapted mainly for coprophagy (Fig. 6) are those in which the acropariae are dense, brush-like; chaetopariae are relatively slender, more elongate and densely arranged; prophobae and apophobae are usually dense and more or less widely diffused; corypha is often distinctly protruding anteriorly and generally with several relatively elongate celtes; the tylus is thickly sclerotized and possesses numerous heli and fenestrae; nesium is well defined and evident.

b) Epipharynx adapted mainly for saprophagy (Fig. 7) are those in which the acropariae are reduced to a few sparse heavy setae positioned towards the tylus; chaetopariae are relatively stout, but are short and sparse; prophobae and apophobae are absent; corypha generally not produced beyond anterior margin, and with a few short apical celtes; epitorma and nesium are either faint or completely lacking.

For diagnosing the epipharyngeal scleromes plural terminology is used to define parial processes and singular terminology for hidden processes.

The epipharynx is divisible in to three regions (Fig. 3), commencing medially and proceeding toward the lateral margins, are the: **A) mesomerum** [Godwin (2002) remarks that Dellacasa's *haptolachus* and *haptomerum* become needless synonyms of *mesomerum* when it is ascertained that the *proplegmatium* is only the transverse line marking the insertion of the membrane connecting the aboral surface of labrum with the *endocranium*.]; **B) pedia; C) pariae.**

These three structures affect the shape of the **anterior epipharyngeal margin**. The varying development of these structures results in variation of the margin, and the various combinations of their parts give shape to the anterior margin of the epipharynx: the lateroapical angles may be distinct and prominent (Fig. 8) or rounded and not prominent (Fig. 9a); the anterior margin of the pedia may be either simply convex (Fig. 10) or concavely arcuate (Fig. 11a), either crenulate by a series of pubescent lobes (Fig. 12) or, though rarely, almost straight (Fig. 13a).

When the epitorma (the medial structure of mesomerum) does not reach the anterior epipharyngeal margin its centre, the **saeptum**, may be convex (Fig. 14) or concave (Fig. 15).

A. Mesomerum

Mesomerum (Fig. 3:3) is the central region of the epipharynx usually predominantly occupied by the epitorma. Basally it joins the pharyngeal limit with an asymmetrical process (**crepis,** Fig. 1:21). Descending from the crepis there is a group of more or less dense and elongate setae (**mesophoba,** Fig. 1:23) that are obliquely and asymmetrically positioned on the sclerotized pre-oral membrane.

The **epitorma** is the medial, symmetrical and palatiform structure, often entirely sclerotized that usually extends from near the base to the apex of the epipharynx. This plate is fused to the internal tormae (laeotorma, Fig. 2:27, and dexiotorma, Fig. 2:33, of the ikrioma) at the base, so that the epipharynx appears to be furnished with skeletal structures. Laterally, it is bordered at the anterolateral margin by the pedia, which is usually densely setose. The epitorma often bears areas of round, thin and light fenestrae that seem to mark the location of several sensillae. The shape of the lateral margins of epitorma when considered in total or in part, is an important taxonomic character. These margins can be entirely convexly curved, straight (triangular epitorma) or, more or less deeply, concavely sinuate medially. In the most frequent shape, the epitorma has a broad base and a narrow apex. In a few taxa it is reduced to the basal part (Fig. 17) or more rarely, almost obsolete (Fig. 16). The epitorma consists of the: 1) pateoepitorma; 2) mesoepitorma; 3) tylus.

1) Pateoepitorma (Fig. 1:19) is the basal third of the epitorma. The most evident feature of the pateoepitorma is a "V" (Fig. 18); or "U" (Fig. 19) shaped line of round or elliptical sensillae (**ankosensilla,** Fig. 1:22) placed in a thin fenestra. Toward the base, below the line of ankosensillae, there are two triangular areas adjoined medially (**nesium,** Fig. 1:20), furnished with large, round, thin fenestrae

which may bear sensilla. The curvature of the lateral margins of pateoepitorma may be concave (Fig. 20a) or convex (Fig. 21).

2) Mesoepitorma (Fig. 1:18) is the central third of the epitorma. The curvature of the lateral margins of mesoepitorma, like those of the pateoepitorma may be straight (Fig. 22), concave (Fig. 20b) or convex (Fig. 23). In some instances, the mesoepitorma margins are so deeply inwardly sinuate, that the mesoepitorma becomes isthmus-like.

3) Tylus (Fig. 1:13) is the bulbous apical third of the epitorma, that may or may not reach the anterior margin of epipharynx. The tylus is formed by three parts: zygum; corypha; epizygum.

The **zygum** (Fig. 1:10) is the proximal part of the tylus extending to just below the sockets of the coryphal celtes. Its surface often bears several fenestrae for sensilla (**angustofenestrae,** Fig. 1:15), similar to those on the nesium. Several short, broad based chaetae (**heli,** Fig. 1:14) line its apico-lateral margin, sometimes similar setae are scattered medially (Fig. 24).

The **corypha** (Fig. 1:11) is the crown of heavy chaetae (**celtes,** Fig. 1:1) placed on the apical margin of the zygum. This consists rarely of four and usually of two or six celtes, which can be arranged regularly on a transverse line (a **broad corypha,** Fig. 13b) or irregularly and densely arranged in a medial tuft (a **narrow corypha,** Fig. 26). The celtes can be equal or unequal in length. In addition, there are some taxa in which the corypha consists of just two equal, large tusk-like celtes (Fig. 27a).

The corypha, relative to the apical margin of epipharynx can be:

- Produced foreword on a rostrum, where the tylus is projected beyond the epipharyngeal margin (a **produced corypha,** Fig. 28);

- Subapical, where the celtesal sockets lie below the epipharyngeal margin (a **recessed corypha,** Fig. 29);

- Placed on a sclerotized ramp where the celtes are variously produced on a perpendicular, superplanar process in an oral direction, away from the epipharyngeal plain (**ramped corypha**). Most often, the celtes are paired on the steps of the ramp (Fig. 30a);

- Rarely there are just two short stout celtes, placed at the apex of the super-planar process (Fig. 31) or seldom, only one apical celte (Fig. 35); infrequently the super-planar process is widened and transversely flattened toward the apex and, in this case, the celtes are usually missing (Fig. 33a); very rarely the corypha posses a single large central celte (Fig. 34).

In a few instances the corypha has peculiar characteristics restricted to a single taxon, thus rendering a generalized diagnosis of supra-specific groups impossible (Fig. 36-38).

The **epizygum** (Fig. 1:12) generally is a small, less sclerotized area beyond the corypha and the apical epipharyngeal margin.

B. Pedia

The **pedia** (Fig. 3:2) are two parial triangular regions anterolaterally and contiguous to the epitorma, bordered toward the lateral epipharyngeal margin by a distinct row of large, socketed chaetae (**chaetoparia**, Fig. 1:5) on the outside region of the pariae.

The major taxonomic characters of the pedia relate to their chaetotaxy. Generally, the pedia are clothed by a dense, uniform field of fine setae (**prophobae,** Fig. 1:4) that often widen proximally to the clypeo-labral commissure (Fig. 39a). In a few taxa the setae are limited to the distal half or only to a small area near the apex of the epitorma (Fig. 40). The setae in some taxa may be so dense, that they are in contact with all adjacent setae, and single seta are often indistinguishable (Fig. 32). In such cases, the setae are often mixed and overlapped by the chaetopariae. Conversely, if setae are scant, there are noticeable open areas and often asetose gaps appear toward the chaetopariae (Fig. 7).

Adjacent to the apical margin of the pedia there is usually a transverse row of slightly robust setae (**acropariae,** Fig. 1:2), that sometimes extend to the narrow parial small areas (**clithra,** Fig. 2:28) on the aboral surface of labrum. Acropariae may have a similar density to the setae of prophobae, or be denser and brush-shaped, or sparse and reduced in number. They rarely fail to reach the epipharyngeal margin (**deep acropariae**).

Large, socketed chaetae are usually scattered among the setae of the prophobae (**chaetopedia,** Fig. 1:3). The variation in shape and arrangement of these chaetopedia are taxonomically important, and should be investigated thoroughly.

All forms of chaetae are wider medially than at their base. Therefore, some form of basal constriction occurs at the insertion to the socket. This basal constriction is asymmetrical and limited to the side adjacent to the apical margin of epipharynx. The side adjacent to the base of epipharynx is usually straight. The constriction may be basally abrupt and narrow or gradual occupying the basal quarter of the chaeta. The various forms of chaetae arise from the pattern of this basal constriction. **Pugiform chaetae** (Fig. 11b) have a gradual basal constriction and appear sharply triangular; **acinaciform chaetae** (Fig. 47) differ from pugiform by having an abrupt basal constriction, sometimes this is so small that the chaetae appear to join the basal articulation directly, without a basal constriction. The shape of the chaetae can also vary between straight or regularly curved (**monocurved chaetae,** Fig. 42) to distinctly bisinuate (**policurved chaetae,** Fig. 33b).

Based on length, the chaetae may be **heteromorphic** (Fig. 30b) when some apical chaetae are two or more times longer than some basal chaetae; or **homomorphic** (Fig. 51a) when chaetae are all approximately of the same length.

Chaetae of the pedia may be:

– Irregularly scattered, and more or less equally abundant apically and basally (Fig. 6);
– Irregularly scattered apically and absent basally (Fig. 43);
– Arranged sublinearly near the anterior epipharyngeal margin and irregularly scattered basally (Fig. 45);
– Arranged sublinearly near anterior epipharyngeal margin and basally absent (Fig. 44);
– Arranged sublinearly near anterior epipharyngeal margin and in oblique linear rows parallel to chaetopariae (Fig. 46);
– Arranged sublinearly in oblique linear rows parallel to chaetopariae (Fig. 39b);
– Absent, with only prophobae (**pubipedia,** Fig. 41);
– A short oblique row of stout chaetae overlapped by chaetopariae (**adelochaetae,** Fig. 9b).
– Entirely glabrous pedia are named **gymnopedia** (Fig. 1:16, 33c).

C. Pariae

The **pariae** (Fig. 3:1) are the lateral regions of the epipharynx, and are usually well defined and broadly triangular. They are bordered medially by the densely chaeto-setose pedia, laterally and apically by the epipharyngeal margins. As with the pedia, the main characters of the pariae relate to their chaetotaxy. Commencing from the mesal margin of the epitorma and proceeding towards the lateral epipharyngeal margins four groups of setae and/or chaetae may be distinguished: 1) chaetopariae; 2) acanthopariae; 3) apophobae; 4) ipophobae.

1) Chaetopariae (Fig. 1:5) are two conspicuous rows of large, socketed, apicomesally pointing chaetae which arise from the basal narrow margin of the pedia running to the anterior margin of epipharynx, adjoining the proximal part of the acanthopariae that align the lateral margin. The chaetopariae are considered **elongate** when longer than five times the width of the basal socket (Fig. 11c), and **short** when equal to or less than five times the width of the basal socket (Fig. 48). In addition, they may be homogeneous or heterogeneous in length. In taxa with **homogeneous chaetae** all chaetae are nearly equal in length (Fig. 52a). In taxa with **heterogeneous chaetae** the apical chaetae are usually longer, almost twice the length of the basal chaetae (Fig. 49a). Rarely, are the apical chaetae shorter than the basal chaetae.

2) Acanthopariae (Fig. 1:8) are rows of robust chaetae occurring along the lateral epipharyngeal margin, which gradually diminish in size from apex to base.

3) Apophobae (Fig. 1:7) are thin setae, often occurring in a dense patch situated immediately laterodistally to the heavy chaetopariae and often separated from the chaetopariae by a narrow, longitudinal oblique asetose gap. When the apophobae are more extensive, they occur from the thin laterobasal membrane on the mesophoba to the base of the acanthopariae or they extend from the clypeo-labral commissure to the apex or just short of the apex of the chaetopariae. Rarely are the apophobae absent.

4) Ipophobae (Fig. 1:9) are composed of thin setae, generally more slender and delicate than those of the apophobae, located in a dense patch postero-laterally to the pariae and usually separated from the apophobae by a relatively large glabrous area (**gymnopariae**, Fig. 1:17). Rarely do the ipophobae join the apophobae or are completely absent, although they are sometimes reduced to a few sparse setae.

2. IKRIOMA

The **ikrioma** (Fig. 4:1) is an aboral rigid sclerotized frame of the labrum generally forming an "H" shaped sclerite.

The two tormae (**laeotorma** and **dexiotorma**, Fig. 2:27; 2:33) of the ikrioma project basally into the endocranium and usually are more or less asymmetrical. A process extending laterally from the base of laeotorma is named the **pternotorma** (fig. 2:26). The tormae frequently have an apical extension reaching beneath the pariae and latero-basally beneath the gephyra (**apotormae**, Fig. 2:30). The posterior tormae is usually bent mesally (Fig. 27) or laterally (Fig. 50). The tormae are structures that join apically to the labrum, project posteriorly into the endocranium, and serve as muscle attachment points. In some taxa the tormae are angulate so that their posterior half point mesally.

Dexiotorma and laeotorma are connected apically by a bridge-like structure: the **gephyra** (Fig. 2:25) which is convexly arched in the aboral direction to form the **labral foramen** (Fig. 2:29). The width of the foramen may be narrower (Fig. 49b) or wider (Fig. 51b) than the base of the epitorma. The sclerotized gephyra generally extends apically from the foramen to the middle of the labrum, and is often campanulate in form (**roof of foramen**).

The gephyra bears several large round spots (**acmofenestrae**, Fig. 2:24) variously arranged. These structures, appearing to be thin fenestrae, possibly function similarly to those found on the rest of epipharynx, i.e., they are probable sites of a sensilla function. They may be arranged in a short line of four or fewer fenestrae (Fig. 53) or in a longer line of ten or more fenestrae (Fig. 25) just distal to the insertion of the clypeo-labral membrane, or the fenestrae may be scattered over the campaniform area that extends up to half the distance from the clypeo-labral membrane mesally to the apex of the labrum, while being progressively closer to clypeo-labral membrane laterally (Fig. 28b). Sometimes the proximal margin of gephyra may appear to be irregularly crenulate; this is caused by the proximity of the fenestrae.

The junction of the tormae with the pateoepitorma and with the basal angles of the gephyra is the most heavily sclerotized part, consequently the least transparent, since it comprises the junction of two different planes. At each side, it forms a columnar structure, the **stela** (Fig. 2:32). The stelae form the lateral wall of the labral foramen and are immediately adjacent to the lateral fenestrae of nesium. They are composed of elements of the tormae (dexiotorma, laeotorma, apotormae, epitormae) and the gephyra.

3. ABORAL SURFACE

The **aboral surface** (Fig. 2) of labrum is relatively smooth, since most of the structural characters are internal or on the oral (epipharyngeal) surface.

The single most prominent structure on the aboral surface is a transverse line (**proplegmatium**, Fig. 2:31), which marks the insertion of the membrane that connects the aboral surface of the labrum to the endocranium. There appears to be no variation in the form of the clypeo-labral commissure, and it is an invaluable landmark character in describing the labral shapes.

A second feature is the thin, transparent, scale-like spines (**lepidophobae**, Fig. 2:35). The lepidophobae can be either absent, dense, sparse or overlapping. In dense lepidophobae, the scales are separated longitudinally by a distance less than the length of the scale; in sparse lepidophobae the scales are separated by a distance greater than their length. In an overlapping lepidophobae (Fig. 52b), many scales overlap and touch adjacent scales. The lepidophobae can be short, long or wide. Short scales (Fig. 11d) are roughly equilateral in shape; long scales are three times longer than the scale base width; wide scales are three times wider at the scale base than in length. Sometimes the lepidophobae are also scattered on the lateral areas of aboral surface.

GLOSSARY

aboral labral surface (Fig. 2): smooth outer labral surface, on which the only relevant structures are the proplegmatium and lepidophobae.

acanthopariae (Fig. 1:8): row(s) of robust chaetae along the lateral epipharyngeal margin, gradually diminishing in size from apex towards the base.

acmofenestrae (Fig. 2:24): large round fenestrae variously scattered on the gephyra.

acropariae (Fig. 1:2): transverse rows of setae slightly more robust than those of prophobae placed near the apical epipharyngeal margins and sometimes extended to the clithra.
adelochaetae (Fig. 1:6): short oblique rows of stout chaetae overlapped by chaetopariae.
angustofenestrae (Fig. 1:15): small fenestrae or sensilla.
ankosensilla (Fig. 1:22): series of round or elliptical sensilla on the nesium.
apophobae (Fig. 1:7): fine setae often occurring in a dense patch located immediately laterodistally to the heavy chaetopariae.
apotormae (Fig. 2:30): apical extensions of the tormae reaching beneath the pariae and laterobasally to the gephyra.
celtes (Fig. 1:1): heavy chaetae forming the apical crown or the central tuft of corypha.
chaetopariae (Fig. 1:5): conspicuous rows of large socketed chaetae arising from the basal narrow margin of the pedia and pointing apicomesally to the anterior margin of epipharynx, reaching the proximal part of the acanthopariae.
chaetopedia (Fig. 1:3): type of pedia on which large socketed chaetae are variously scattered among the setae of the prophobae.
clithra (Fig. 2:28): narrowly extended aboral anterolateral area onto which sometimes the acropariae are extended.
connective membrane (Fig. 2:34, 4:2): the membrane connecting the aboral surface of labrum to the endocranium.
corypha (Fig. 1:11): the crown or the central tuft of heavy chaetae (celtes) inserted on the apical margin of zygum.
crepis (Fig. 1:21): asymmetrical process joining basally the mesomerum to the pharyngeal apical limit.
dexiotorma (Fig. 2:33): the right hand side (oral dorsad) elongate process of ikrioma, relatively strongly sclerotized and projecting basally into the endocranium.
epipharynx (Fig. 1): the adoral surface of the labrum.
epitorma: the median symmetrical and palatiform structure, usually entirely sclerotized, normally extending from almost the base to the apex of epipharynx, in which the pateoepitorma, mesoepitorma and zygum are found.
epizygum (Fig. 1:12): a small sclerotized area (usually lacking), beyond the corypha and the apical margin of epipharynx.
fenestra: a transparent glassy spot or window in a membrane.
gephyra (Fig. 2:25): apical bridge-like connection between dexiotorma and laeotorma, convexly arched in the aboral direction to limit the labial foramen.
gymnopariae (Fig. 1:17): glabrous, more or less wide, lateral area of the pariae.
gymnopedia (Fig. 1:16): glabrous pedia.
haptolachus: synonym for part of mesomerum.
haptomerum: synonym for part of mesomerum.
heli (Fig. 1:14): short, stout and broad based chaetae.
ikrioma (Fig. 4:1): rigid sclerotized inner frame, generally "H" shaped in form, made by the tormae, stelae and gephyra.
ipophobae (Fig. 1:9): slender setae, often located in a more or less dense patch posterolaterally on the pariae.
labral foramen (Fig. 2:29): opening in ikrioma and limited distally by gephyra.
labrum: the upper lip, head appendage characteristic for each taxon, at least at genus-group level, in which three parts are distinguishable: epipharynx, ikrioma and aboral surface.
laeotorma (Fig. 2:27): the left hand side (oral dorsad) elongate process of ikrioma, more or less strongly sclerotized and projecting basally into the endocranium.
lepidophobae (Fig. 2:35): thin transparent scale-like chaetae, often scattered on the gephyra.
mesoepitorma (Fig. 1:18): the central third of the epitorma.
mesomerum (Fig. 3:3): central region of the epipharynx.
mesophoba (Fig. 1:23): area of more or less dense and elongate setae positioned asymmetrically below crepis.
nesium (Fig. 1:20): small triangular area below the series of ankosensillae toward the base of epitorma.

pariae (Fig. 3:1): broadly triangular lateral regions of epipharynx, usually well defined.
pateoepitorma (Fig. 1:19): the basal third of the epitorma.
pedia (Fig. 3:2): parial triangular regions of the epipharynx, anterolaterally contiguous to the epitorma and bordered toward the lateral epipharyngeal margin by chaetopariae.
prophobae (Fig. 1:4): usually a dense and uniform field of fine setae, widened proximally to the clypeolabral commissure.
proplegmatium (Fig. 2:31): transverse line marking the insertion of the membrane connecting the dorsal surface of labrum to the endocranium.
pternotorma (Fig. 2:26): process extending laterally from the base of the tormae.
pubipedia: an entirely pubescent pedia, lacking intermixed chaetae.
saeptum: center of the anterior epipharyngeal margin.
sensilla: sensory organs.
stelae (Fig. 2:32): heavily sclerotized columnar structures connecting the tormae with the base of the pateoepitorma and with the basal angles of the gephyra.
tylus (Fig. 1:13): the narrow and bulbous apical third of the epitorma.
zygum (Fig. 1:10)**:** the proximal part of tylus immediately below the sockets of coryphal celtes.

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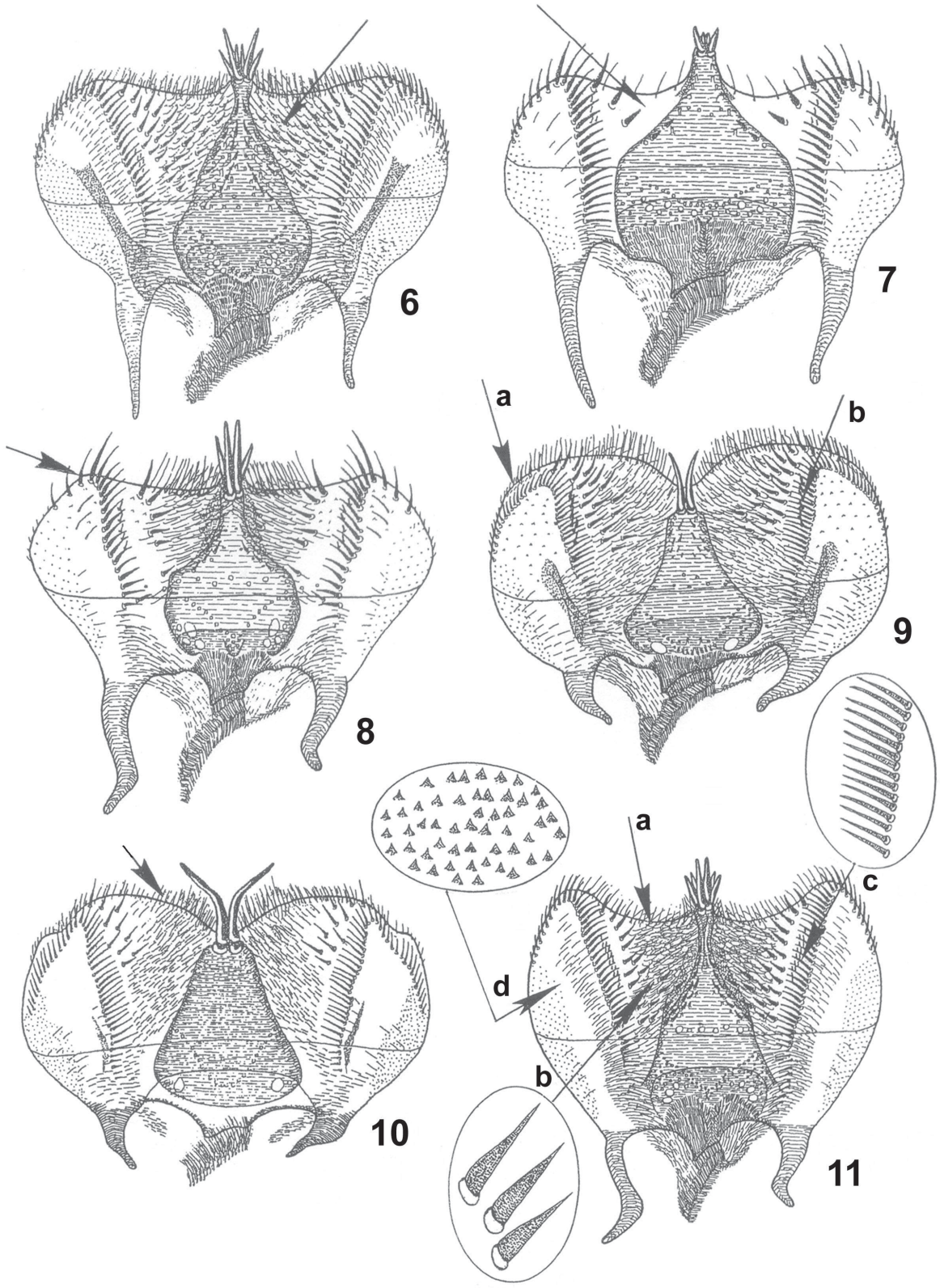

Figure 6-11. Epipharyngeal features. **6)** *Aphodius fimetarius* (Linné, 1758). **7)** *Xeropsamobeus desertus* VanDyke, 1918. **8)** *Luxolinus luxatus* (Horn, 1887). **9)** *Gonaphodiellus hoffmanni* (Islas, 1945). **10)** *Gonaphodiellus opisthius* (Bates, 1887). **11)** *Dellacasiellus kirni* (Cartwright, 1944).

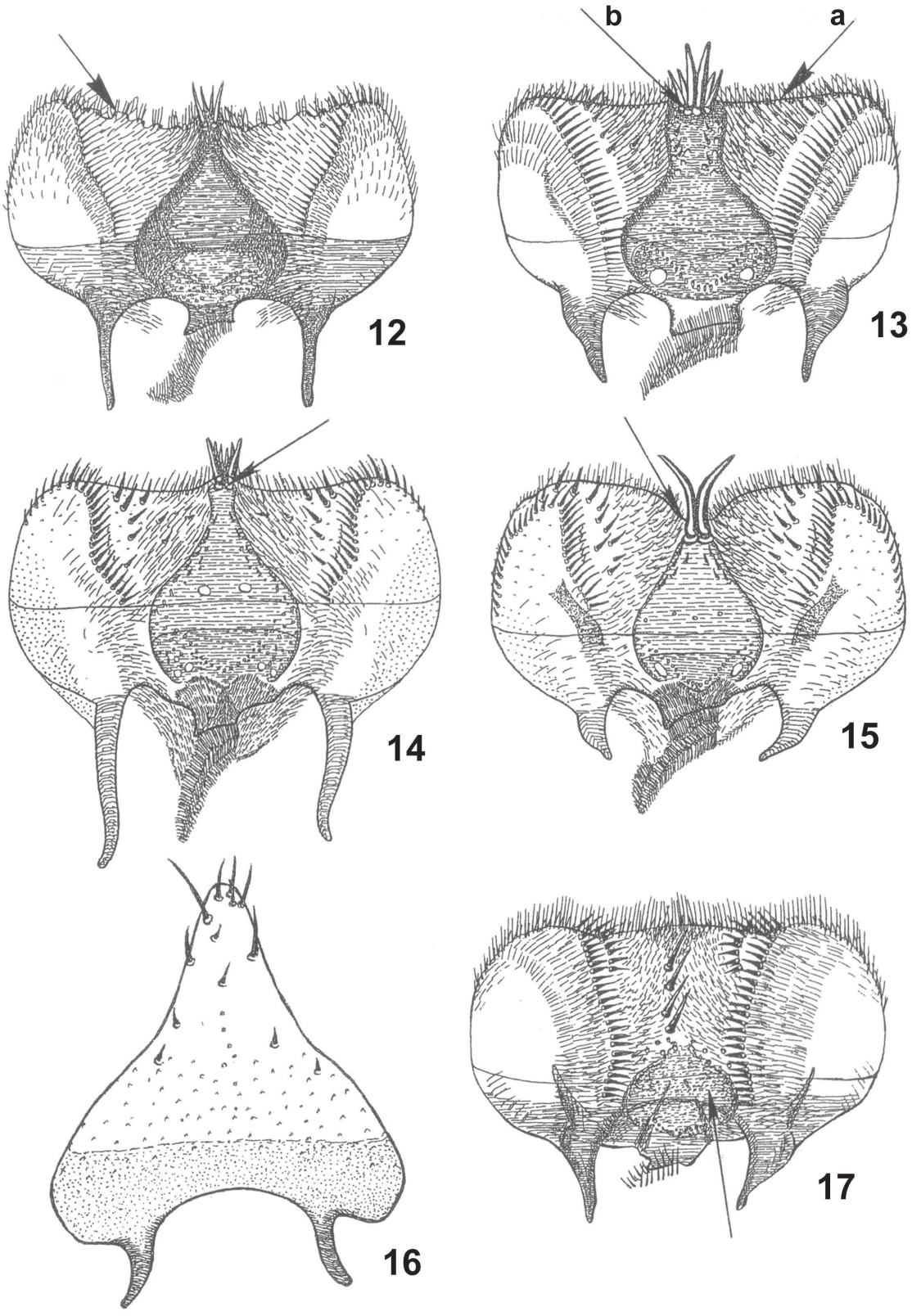

Figure 12-17. Epipharyngeal features. **12)** *Diapterna hamata* (Say, 1824). **13)** *Labarrus lividus* (Olivier, 1789). **14)** *Neotrichonotulus inurbanus* (Gordon and Howden, 1973). **15)** *Blackburneus aegrotus* (Horn, 1870). **16)** *Oxycorythus morawitzi* Solsky, 1876. **17)** *Acrossus luridus* (Fabricius, 1775).

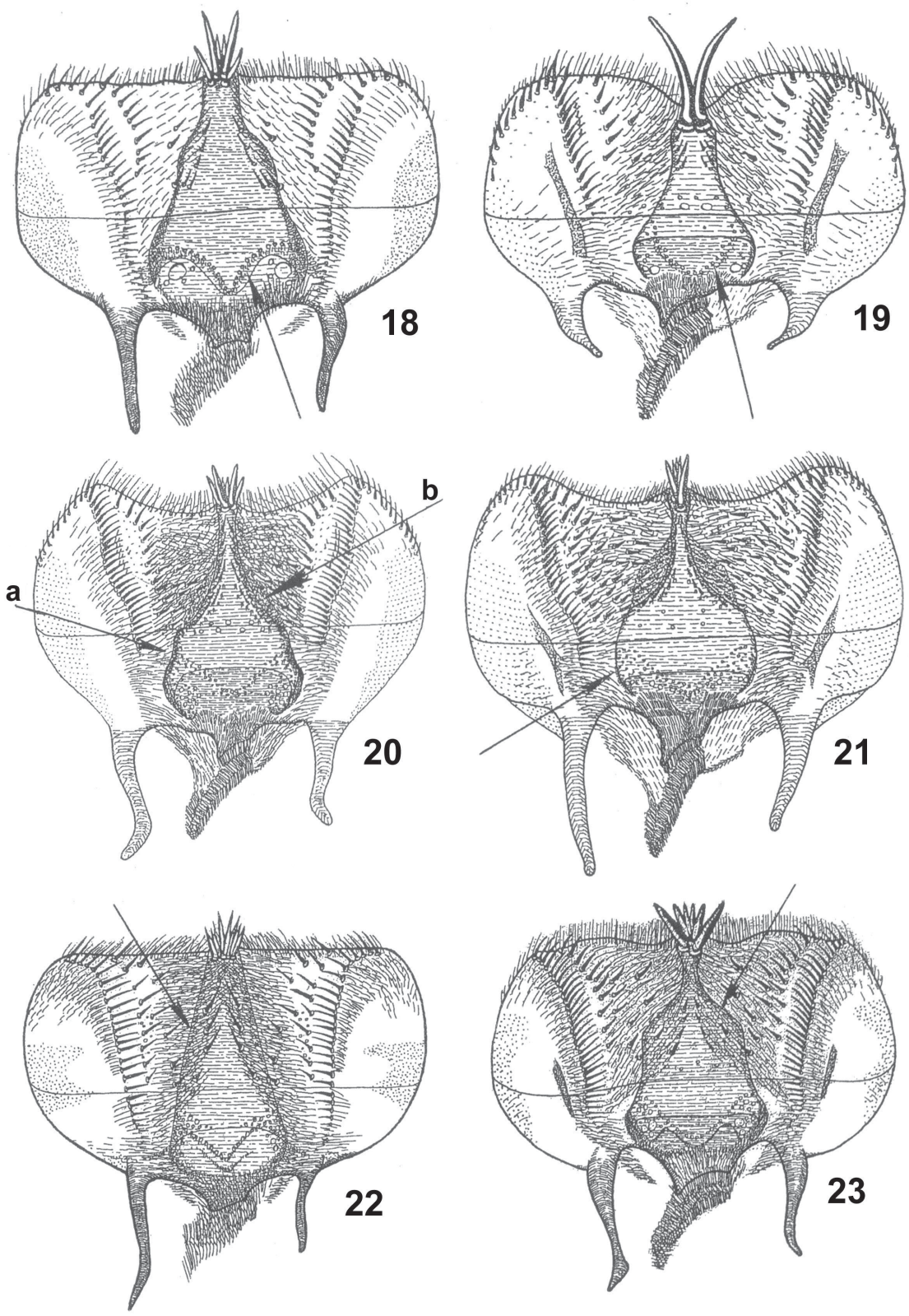

Figure 18-23. Epipharyngeal features. **18)** *Cephalocyclus pullatus* (Schmidt, 1913). **19)** *Blackburneus tenuistriatus* (Horn, 1887). **20)** *Dellacasiellus concavus* (Say, 1823). **21)** *Cryptoscatomaseter magnificens* (Robinson, 1940). **22)** *Cephalocyclus luridiventris* (Harold, 1862). **23)** *Cephalocyclus luteolus* (Horn, 1887).

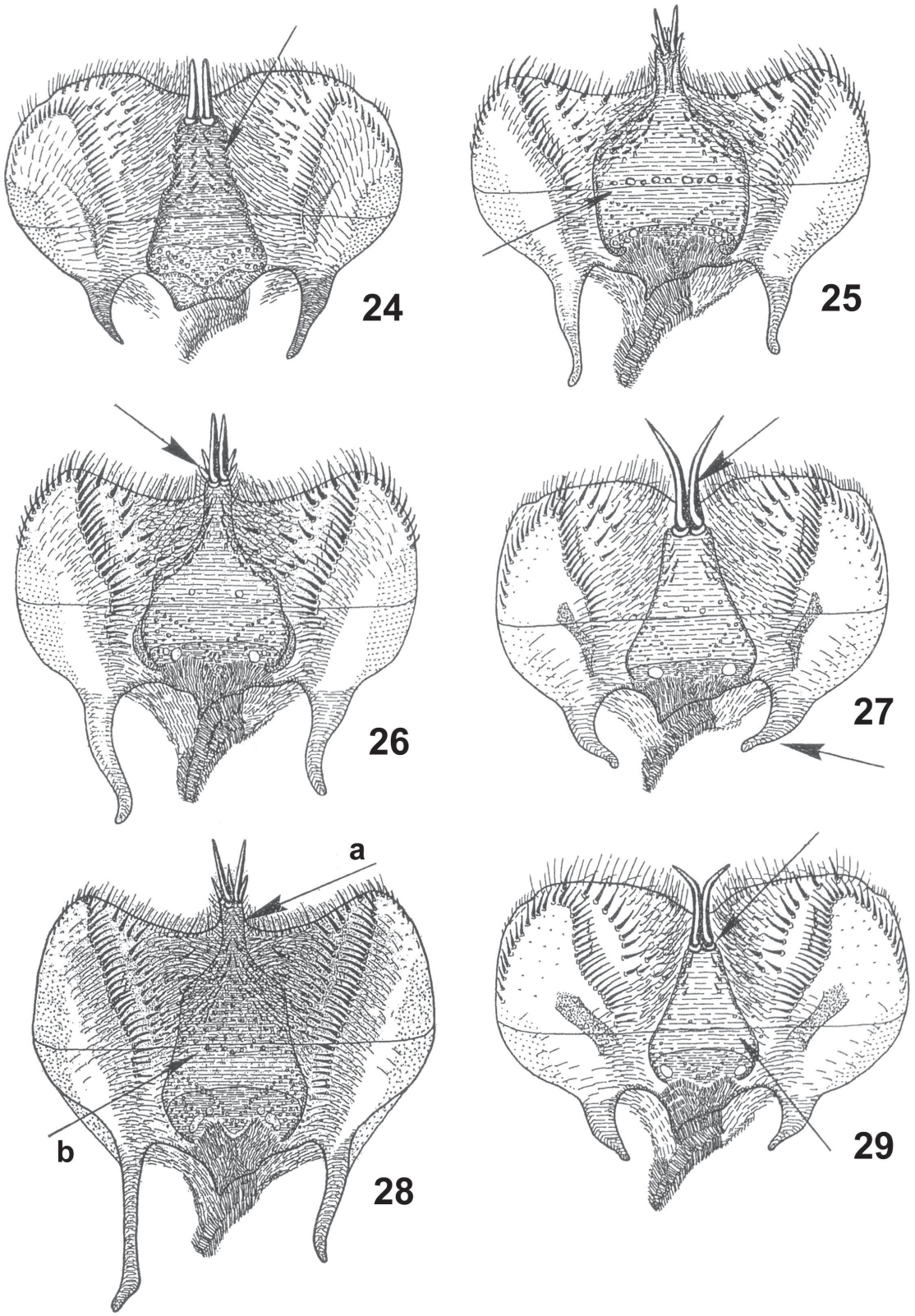

Figure 24-29. Epipharyngeal features. **24)** *Cesamexico constricticollis* (Bates, 1889). **25)** *Haroldiellus lansbergei* (Harold, 1874). **26)** *Pseudagolius coloradensis* (Horn, 1870). **27)** *Blackburneus saylorea* (Robinson, 1940). **28)** *Coelotrachelus kuntzeni* (Schmidt, 1913). **29)** *Blackburneus troglodytes* (Hubbard, 1894).

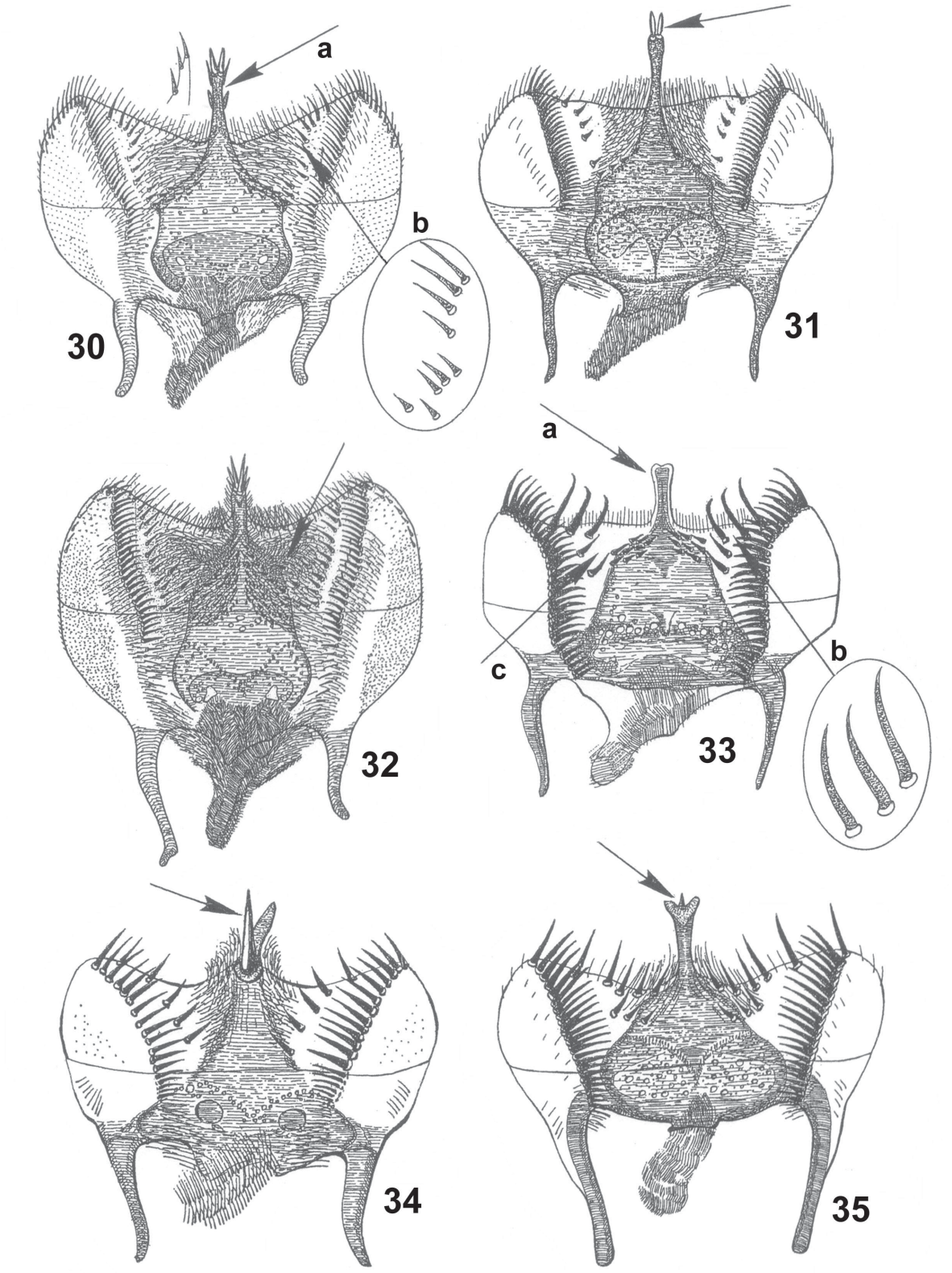

Figure 30-35. Epipharyngeal features. **30)** *Tetraclipeoides giulianii* (Gordon, 1977). **31)** *Tetraclipeoides denticulatus* (Haldeman, 1848). **32)** *Coelotrachelus symbius* (Gordon and Howden, 1973). **33)** *Ammoecius elevatus* (Olivier, 1789). **34)** *Plagiogonus arenarius* (Olivier, 1789). **35)** *Loraspis frater* (Mulsant and Rey, 1870).

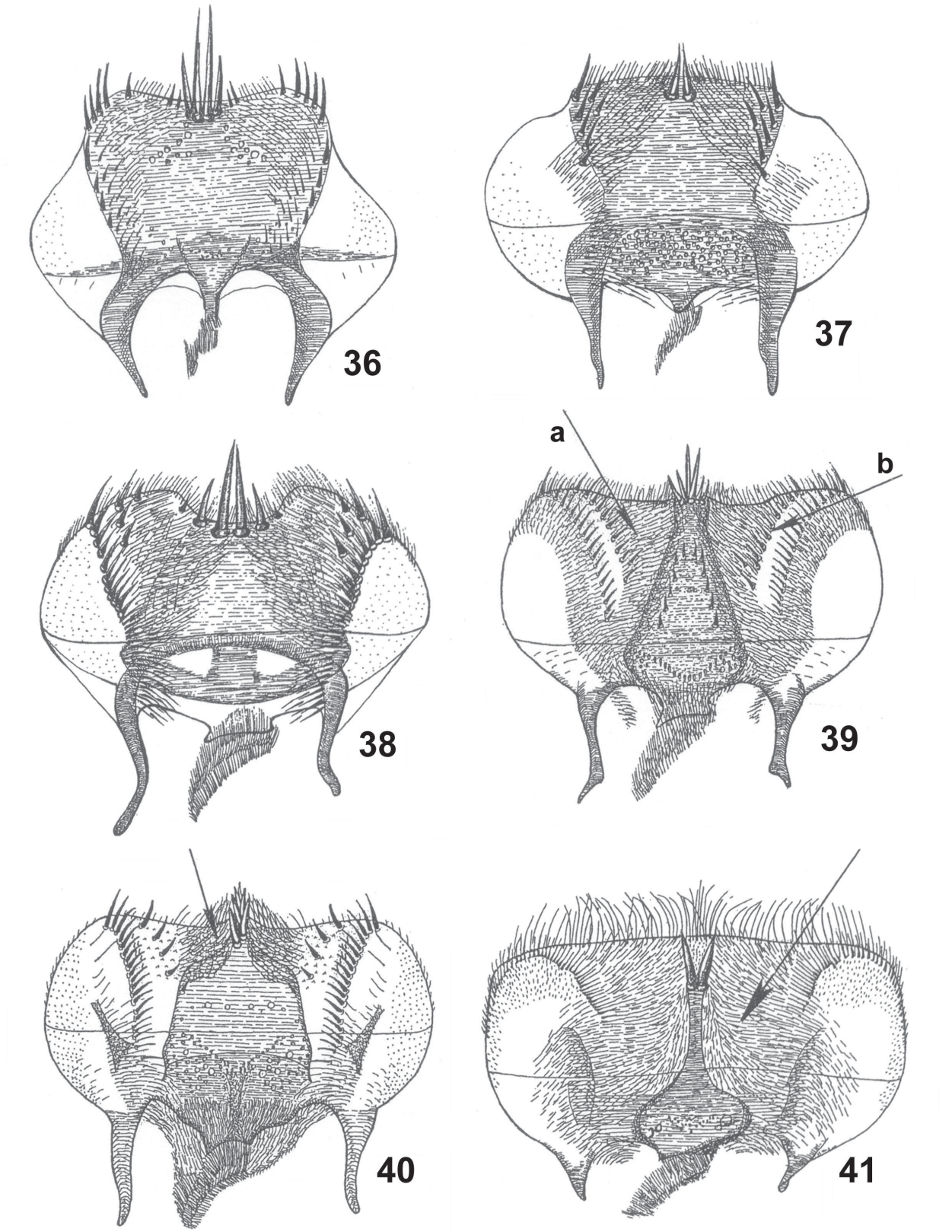

Figure 36-41. Epipharyngeal features. **36)** *Neagolius liguricus* (Daniel, 1902). **37)** *Neagolius penninus* (Daniel, 1902). **38)** *Neagolius praecox* (Erichson, 1848). **39)** *Cephalocyclus durangoensis* (Bates, 1887). **40)** *Cinacanthus militaris* (LeConte, 1858). **41)** *Emadiellus rufopustulatus* (Wiedeman, 1823).

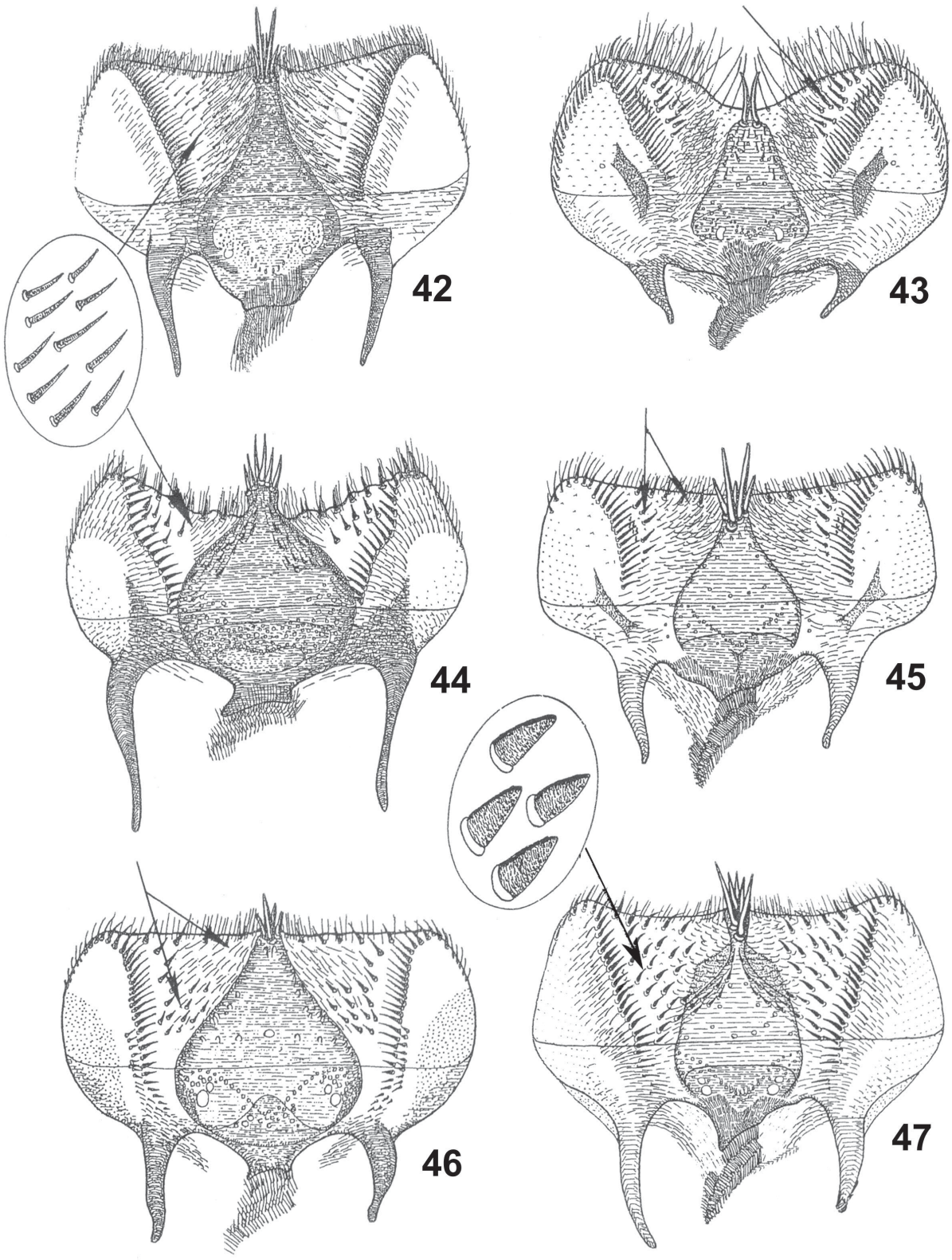

Figure 42-47. Epipharyngeal features. **42)** *Melinopterus prodromus* (Brahm, 1790). **43)** *Gonaphodiellus caracanus* (Balthasar, 1970). **44)** *Diapterna omissa* (LeConte, 1850). **45)** *Oxyomus setosopunctatus* (Schmidt, 1911). **46)** *Ferrerianus biimpressus* (Schmidt, 1909). **47)** *Cryptoscatomaseter ochreipennis* (Horn, 1871).

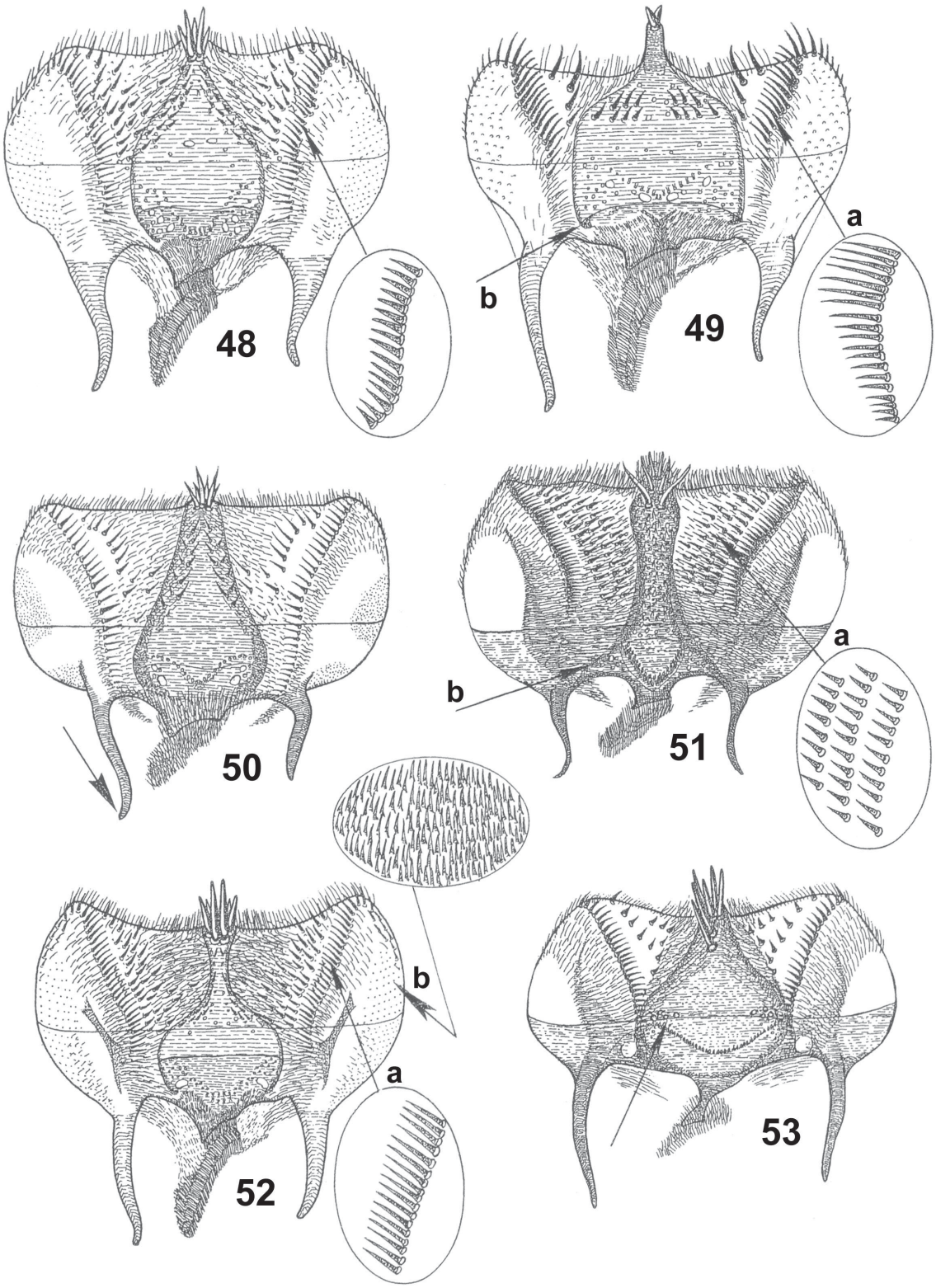

Figure 48-53. Epipharyngeal features. **48)** *Cryptoscatomaseter explanatus* (LeConte, 1878). **49)** *Oscarinus spiniclypeus* (Hinton, 1934). **50)** *Cephalocyclus fuliginosus* (Harold, 1863). **51)** *Drepanocanthoides walshii* (Horn, 1870). **52)** *Cryptoscatomaseter oklahomensis* (Brown, 1928). **53)** *Stenotothorax badipes* (Melsheimer, 1844).

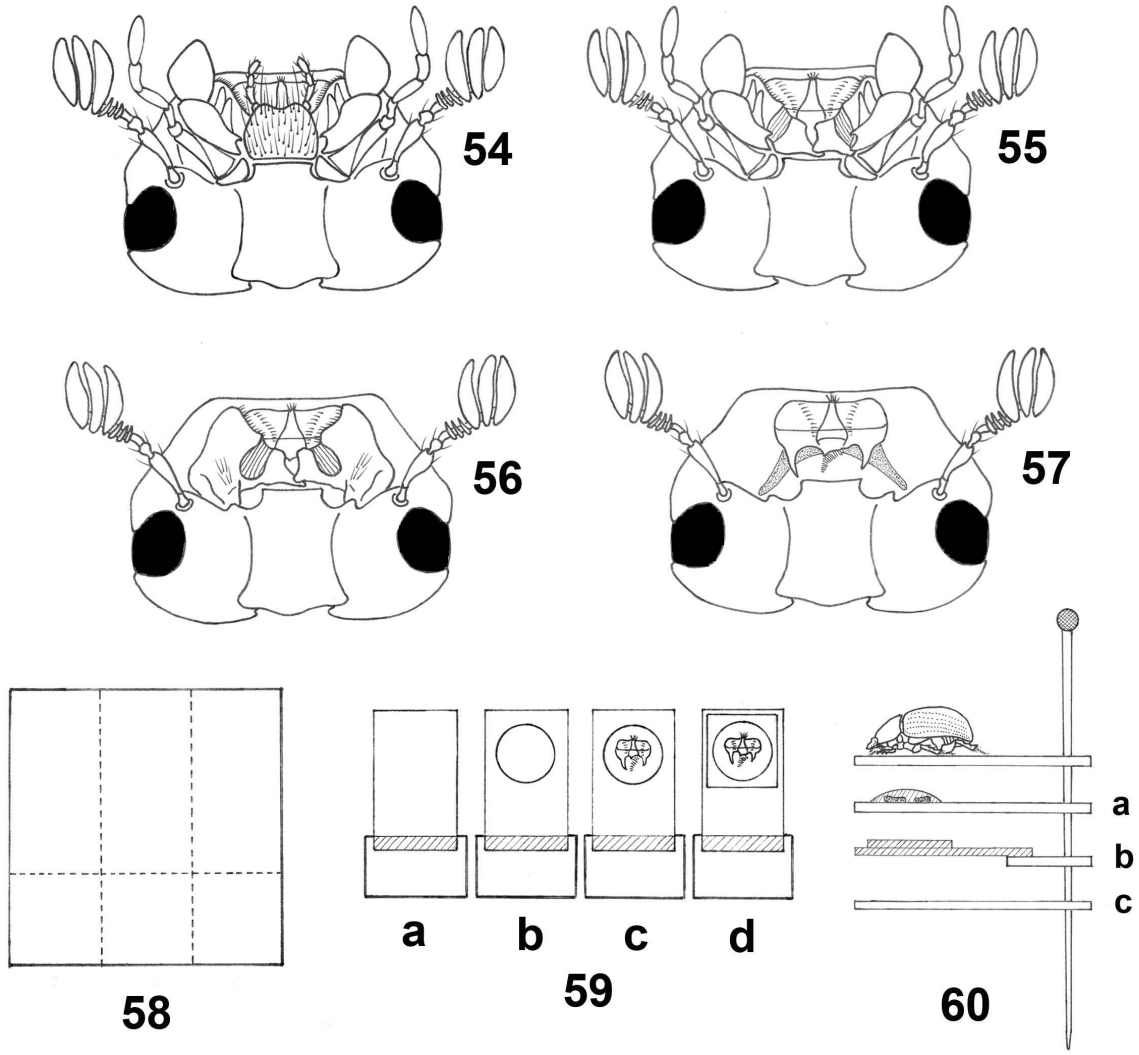

Figure 54-60. Dissection and mounting of parts. **54-57)** Sequential steps for removing the labrum from the head of an Aphodiinae. **58)** Preparation of the slide (dashed lines represent the line of cutting). **59a-d)** Sequential steps for mounting the labrum. **60)** Suggested order of the cards pinned under a specimen (a: card with D.M.H.F. mounted dissected parts; b: slide with labrum; c: label with collecting and other data).