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Larval head structures of *Licinus silphoides* Rossi and their phylogenetic implications (Coleoptera: Carabidae)

by **R. G. Beutel**

Abstract: The head of the larva of *Licinus silphoides* (L 3) is described in detail. Structures of the head of larvae of Licinini and Panagaeini are interpreted phylogenetically. The following synapomorphic character states suggest a sistergroup relationship between Licinini and Panagaeini: small relative size of the head, nearly parallel sided frontal sutures and strongly elongated frontoclypeolabral apotome, posterior tentorial grooves distinctly diverging anteriorly, elongation of antennae, serrate mandibular blade, short maxillae, weakly sclerotized submentum, stout labial palps, elongated prepharynx, short and wide pharynx, caudal position of cerebrum within head capsule. The supertribe Callistitae (incl. Chlaeniini, Oodini, and Licinini) erected by KRYZHANOVSKY (1976) is probably paraphyletic. The presence of a membranous, densely pubescent labral margin is a highly significant apomorphic character state, and a possible synapomorphy of Licinini (in part?). The broad, distinctly bordered gula with widely separated posterior tentorial grooves is a synapomorphy of *Badister* and *Licinus*. The presence of a strong spur at the base of each labial palp is a possible synapomorphy of *Licinus*. The following character states are considered as synapomorphies of Caraboidea Limbata: postocular and cervical ridges present (groundplan), intercrossing antennal muscles, epipharyngeal transverse bulge and rim form a closing mechanism of the preoral cavity together with corresponding structures of the completely levelled hypopharynx.

I. Introduction

1. Preliminary notes

Older and more recent classifications of Carabidae are exclusively or largely based on characters of adults, and no agreement upon the phylogeny of higher taxa has been achieved yet (BALL, 1979). The available information on carabid larvae is far more restricted than that on adults, and only very few taxa have been studied for internal structures. It is almost self-evident that study of larval structures is needed for a broader understanding of the complex process of (ge-)adephagan evolution. A more comprehensive knowledge of structures and functions of different life stages will almost inevitably yield a basis for a solid classification which truly reflects phylogeny.

The present analysis of structures of the larval head aims at a clarification of the phylogeny and systematic position of Licinini.

2. Materials and methods

Specimens of *Licinus silphoides* were collected under stones in the arid Crau area, 8 km e. of St. Martin de Crau, Southern France. They were fixed in FAE, and stored in ethanol. Specimens were imbedded in Histoplast S for microtome sections (5 µm). The sections were stained with haemalaun and eosin. Drawings were carried out using an ocular grid (stereo microscope). Scanning electron microscopy was accomplished after specimens were cleaned with ultra sound, dried ('critical point' method), and coated with gold-palladium (Cambridge Stereoscan 250 Mk 2).

The following taxa were examined for outgroup comparison: *Trachypachus holmbergi* Mannerheim (L 3), *Metrius contractus* Eschscholtz (L 1), *Omophron variegatum* Olivier (L 3), *O. limbatum* F. (L 1-3), *Opisthius richardsoni* Kirby (L 3), *Carabus coriaceus* L. (L 3), *Blethisa multipunctata* L. (L 3), *Scarites* F. sp. (L 3), *Broscus cephalotes* L. (L 3), *Oodes* Bonelli sp. (L 3), *Chlaenius* Bonelli ssp. (L 3), *Dicaelus* Bonelli sp, *Panagaeus bipustulatus* Fabricius (L 3), *Brachinus explodens* Duftschmid (L 1). A panagaeine larva from Mexico (Durango, Rte 45, 12,2 mi s. El Banco, 5200') could not be assigned to a genus with certainty. It keys to *Panagaeus* in V. EMDEN (1942). Muscles are named and numbered in accord with v. KÉLER (1966).

II. Morphological results

1. Head capsule

1.1. General appearance, external structures (Figs 1-3, 7-8).

Head of larvae of *L. silphoides* very small in proportion to the size of thorax and abdomen. Connected with the prothorax by an extremely broad membranous collar, conspicuously directed upwards. Cuticle of the head capsule thin and unpigmented in most parts. Darker coloration restricted to the dorsolateral area of the head capsule, especially around the stemmata. Head nearly parallel-sided, only slightly narrowed posteriorly.

Frontoclypeolabral apotome broadly reaches the hind margin of the head capsule. Frontal sutures almost straight, only very slightly converging posteriorly. Adnasalia moderately developed and rounded. Me-

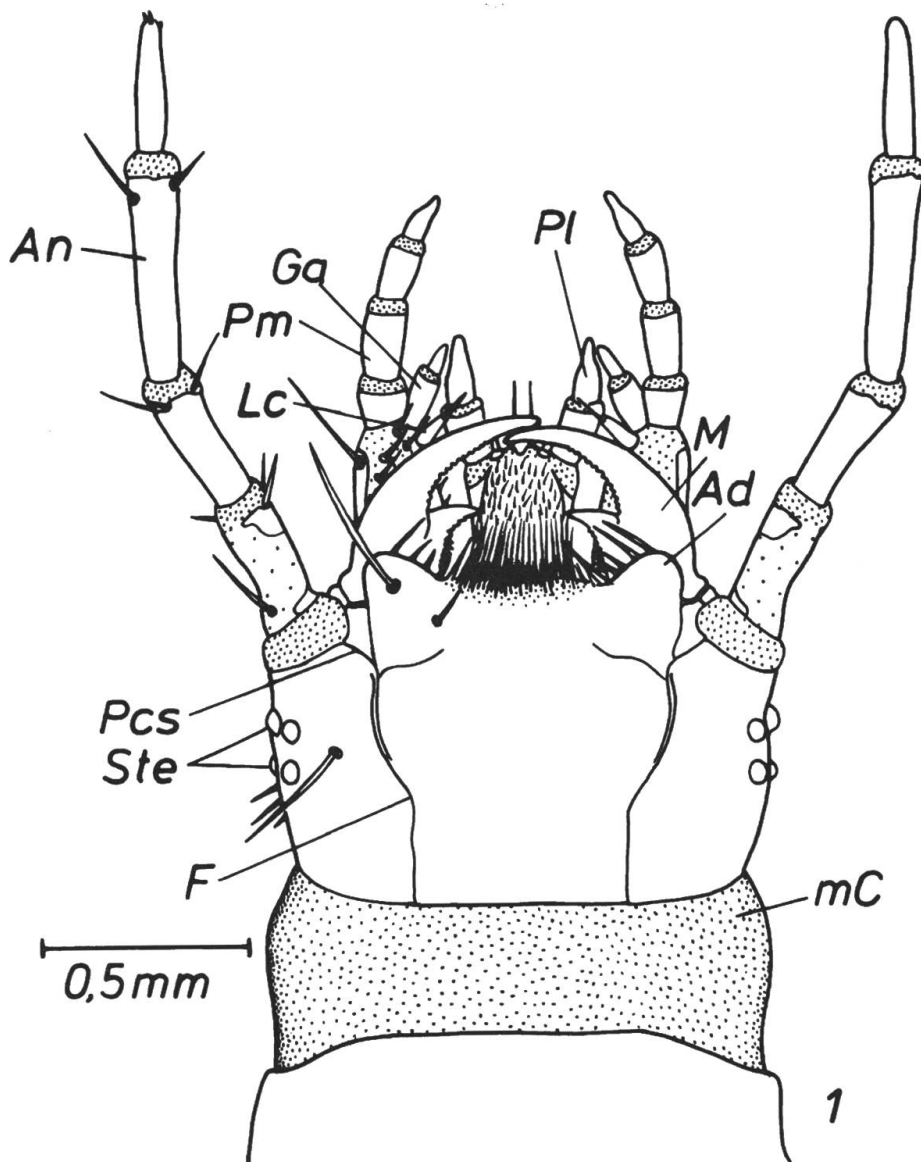


Fig. 1: *Licinus silphoides*, head: dorsal view: a, muscle attachment; Ad, adnasale; ahyb, anterior hypopharyngeal bar; An, antenna; aTa, anterior tentorial arm; C, cardo; dsts, dorsal stipital sclerite; dTa, dorsal tentorial arm; eb, epipharyngeal bulge; F, frontal suture; Ga, galea; Gf, ganglion frontale; Gu, gula; Hy, hypopharynx; hyf, hypopharyngeal fringe of hairs; Lc, lacinia; M, mandible; mC, membranous collar; Mt, mentum; Pcs, paraclypeal suture; phyb, posterior hypopharyngeal bar; Pl, palpus labialis; Pm, palpus maxillaris; Pmt, prementum; Po, postocciput; psp, palpal spine; pTa, posterior tentorial arms; pTg, posterior tentorial grooves; Sm, submentum; St, stipes; Ste, stemmata; tm, transverse muscle; v. KÉLER's numbers are used for muscles.

sal edge set with a row of medially directed, strong setae. Anterior margin of clypeolabral region concave, completely devoid of prominent nasal structures, membranous, with a dense brush of forward projecting hairs. Paraclypeal suture present (Fig. 1). Six stemmata arranged in two vertical rows. Postorbital and cervical ridges absent. Postocciput narrow, absent from the dorsal part of the hind margin of the head capsule as a result of the posterior expansion of the frontoclypeolabral apotome. Postoccipital apodeme poorly developed.

Posterior tentorial grooves widely separated. Gular area broad, bordered by distinct sutures externally. Gular sutures correspond with distinct internal ridges which strongly converge posteriorly, and meet shortly before they reach the hind margin of the head capsule, thus forming a high, median apodeme (mid-gular apodeme).

Broad submental area semimembranous, laterally bordered by distinct sutures and corresponding internal ridges.

1.2. Tentorium (Figs 4-6).

Posterior tentorial arms widely separated, flat and unusually thin. Originate from the submento-gular ridges in the central area of the ventral wall of the head capsule. Dorsal tentorial arms slender, attached to the dorsal wall of the head capsule laterally to the frontal suture. Anterior arms oval in cross section, distinctly stronger than posterior and dorsal arms. Anterior tentorial grooves not elongated. Cranial part of the anterior arms not fused to the dorsal wall of the head capsule. Tentorial bridge absent.

2. Appendages of the head and their musculature

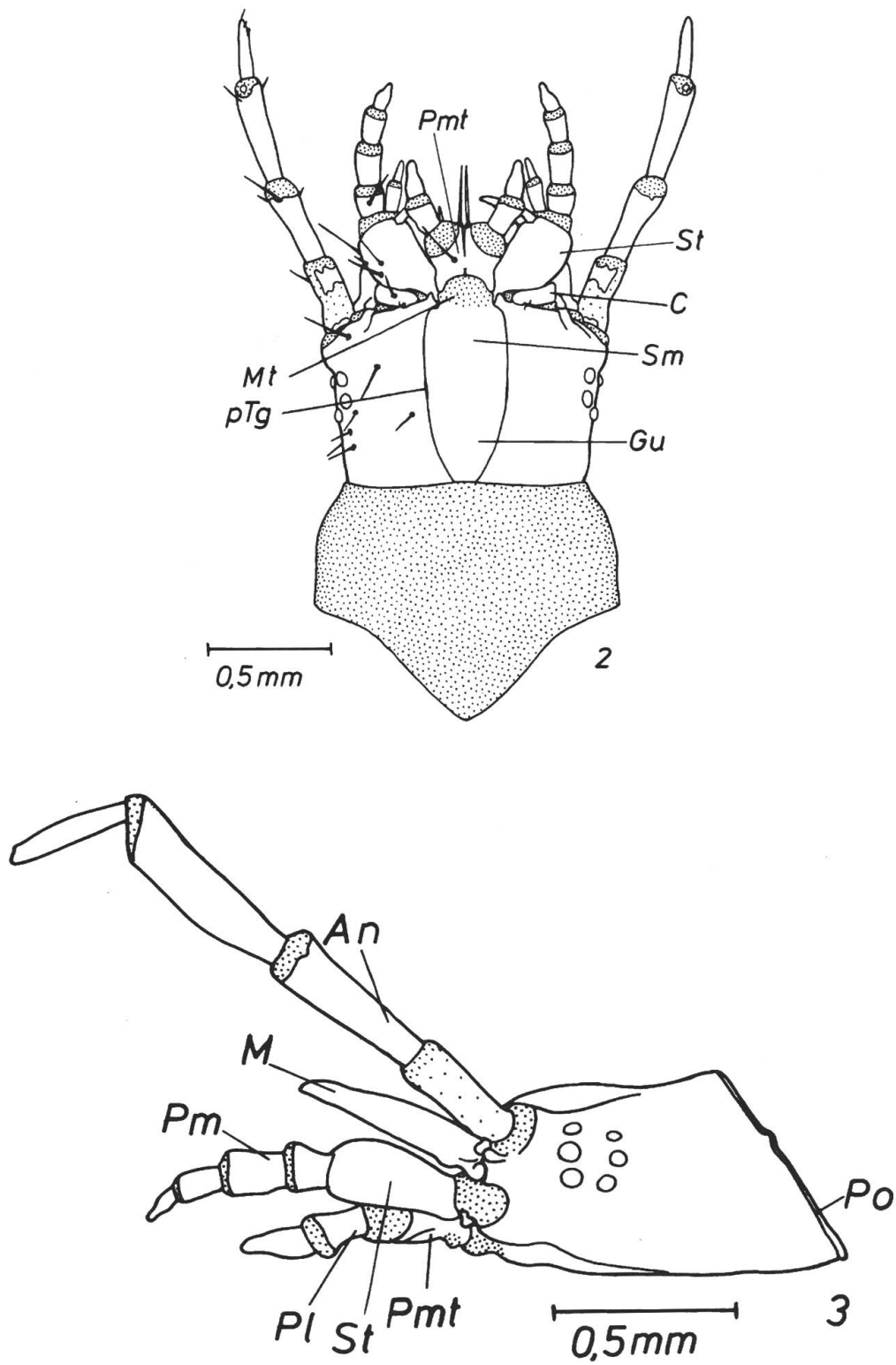
2.1. Labrum (Figs 1, 7).

Labrum fully intergrated into frontoclypeolabral apotome. Ventral labral peg not present.

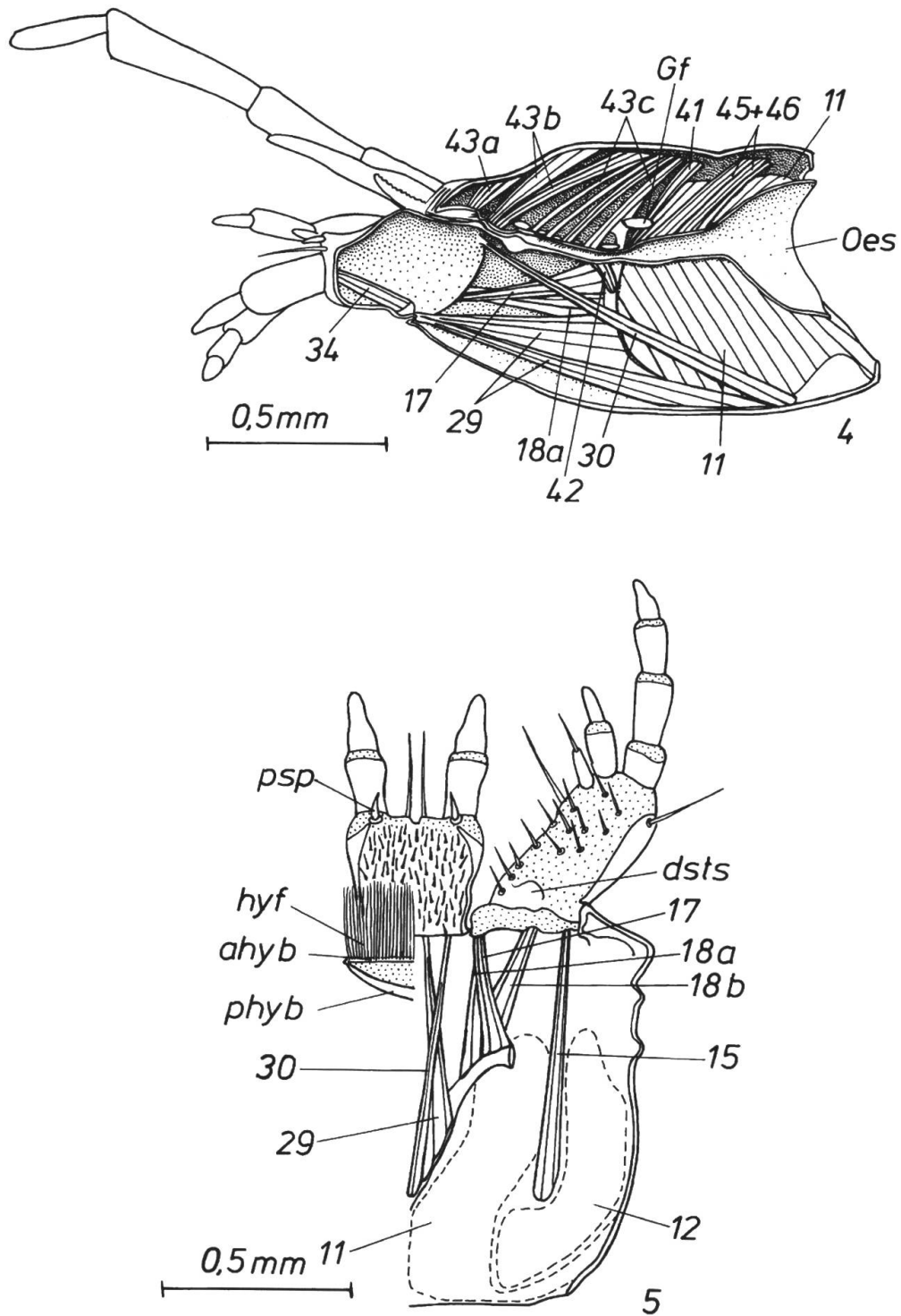
No labral muscles are present.

2.2. Antenna (Figs 1, 2).

Extremely elongated, more than twice as long as the mandible. Large intermediate section of antennomere I unpigmented and scarcely sclerotized. Length ratio of segments: 1 : 1.2 : 1.55 : 0.8. Antennomere III very slightly dilated distally. Small sensory appendage present.



Figs. 2-3: *Licinus silphoides*, head: 2, ventral view: 3, lateral view.



Figs. 4-5: *Licinus silphoides*: 4, sagittal section, ventral part. 5, horizontal section, ventral part.

Musculature (Fig. 6):**M. 1: *M. tentorioscapalis anterior***

Originates from the proximal parts of the dorsal and anterior tentorial arms; attached posteriorly to the base of the scapus.

F: extensor of the antenna

M. 2: *M. tentorioscapalis posterior*

Originates from the posterior side of the dorsal tentorial arm; attached dorsally to the base of the scapus.

F: levator of the antenna

M. 4. *M. tentorioscapalis medialis*

Originates from the anterior side of the dorsal tentorial arm, dorsally to M. 1; attached anteriorly to the base of the scapus.

F: Protractor of the antenna

2.3. Mandible

(Figs 1, 7).

Fairly short and falciform. Blade slender and rather blunt at the apex. Stout, curved retinaculum finely denticulate along mesal edge. Single mesal edge of the blade serrate except for the apicalmost section. Penicillum present but minute.

Musculature (Figs. 4-6):**M. 11: *M. craniomandibularis internus***

Originates from the mid-gular apodeme and from extensive parts of the ventral and dorsolateral areas of the head capsule including adjacent parts of the postoccipital apodeme; attached to adductor apodeme.

F: adductor

M. 12: *M. craniomandibularis externus*

Originates from the ventrolateral area of the head capsule; attached to the abductor apodeme.

F: abductor

2.4. Maxilla

(Figs 2, 5, 8).

Fairly short and broad. Ventral sclerite of the cardo articulates with anterior margin of the head capsule by means of a well developed condylus. Mesal cardo sclerite absent. Ventral side of stipes sclerotized, dorsal surface largely membranous. Only a narrow lateral section and the mediobasal region are sclerotized. Stiff setae present along mesal edge and on the dorsal surface of the stipes. Lacinia moderately long, with a stiff, apical seta. Galea 2-segmented. Basal segment about 1.5 times as long as the lacinia, distal segment about as long as the lacinia

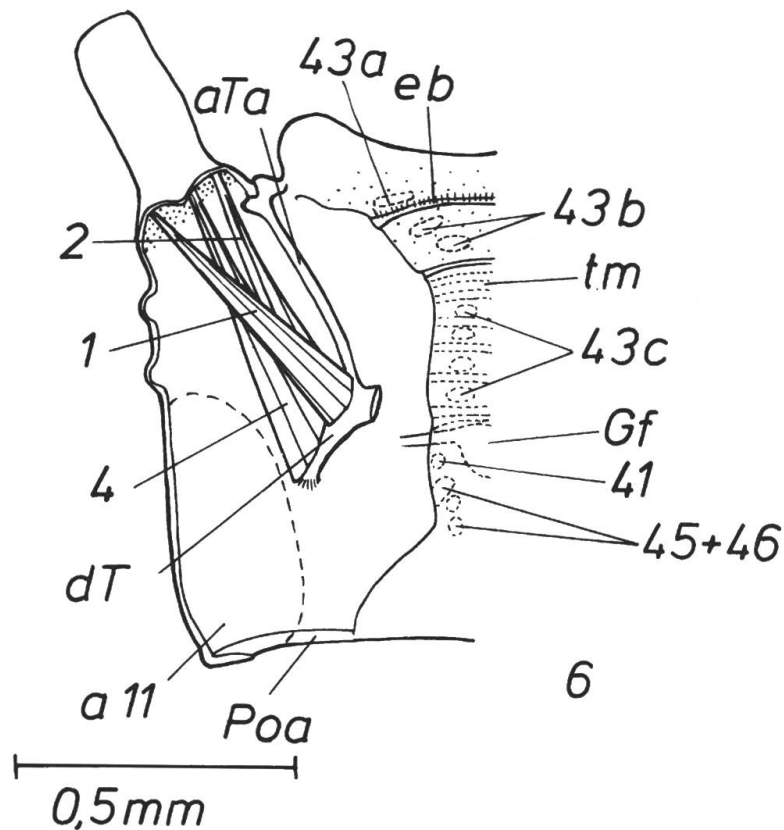


Fig 6: *Licinus silphoides*, horizontal section, dorsal part.

and slender. Maxillary palp slightly more than twice as long as the galea. Length ratio of palpomeres: 1 : 1.45 : 1.1: 0.9.

Musculature

(Fig. 5).

M. 15. M. craniocardinalis externus

Originates from the posterior region of the ventral wall of the head capsule between the areas of origin of M. 11 and M. 12. Attached to the lateral edge of the ventral sclerite of the cardo.

F: extensor of the maxilla

M. 17. M. tentoriocardinalis

Originates from the lateral side of the posterior tentorial arm; attached to the mesal edge of the ventral sclerite of the cardo.

F: flexor of the maxilla

M. 18. M. tentoriostipitalis

M. 18a originates from the lateral side of the posterior tentorial arm ventral to M. 17; attached to the mediobasal edge of the stipes.

F: flexor of the maxilla, together with M 17

M. 18 b originates from the ventral wall of the head capsule laterally to the base of the posterior tentorial arm; attached to the lateral edge of the dorsal sclerotization of the stipital base.

F: levator and retractor of the maxilla

M. 23. *M. stipitopalpalis*.

Originates from the ventral wall of the stipes; mesally attached to the base of palpomere I.

F: flexor of the maxillary palp

2.5. Labium (Figs 2, 4, 5, 8).

Submentum semimembranous, laterally bordered by distinct, nearly parallel submental sutures which correspond with internal ridges. The posterior margin defined by the position of the posterior tentorial grooves. Mentum membranous. Ventral and lateral parts of prementum sclerotized, dorsal surface membranous, densely covered with forward projecting hairs. Strong spur present at the base of each palp. Ligula concave. Ligular setae long. Ligular concavity continuous with a narrow cleft on the ventral side of the prementum. Palpomeres stout, about equal in length. Internal median apodeme at the base of the prementum serves as muscle attachment area.

Musculature (Figs 4, 5):

M. 29. *M. tentoriopraementalis inferior*

Originates from the mesal side of the gular ridge and from the proximal part of the posterior tentorial arm. Mesally attached to the posterior edge of the prementum.

F: retractor of the prementum

M. 30. *M. tentoriopraementalis superior*

Originates from the posteriormost section of the gular ridge, anterior to the mid-gular apodeme; dorsolaterally attached to the hind margin of the prementum.

F: retractor of the prementum

M. 34. *M. praementopalpalis internus*

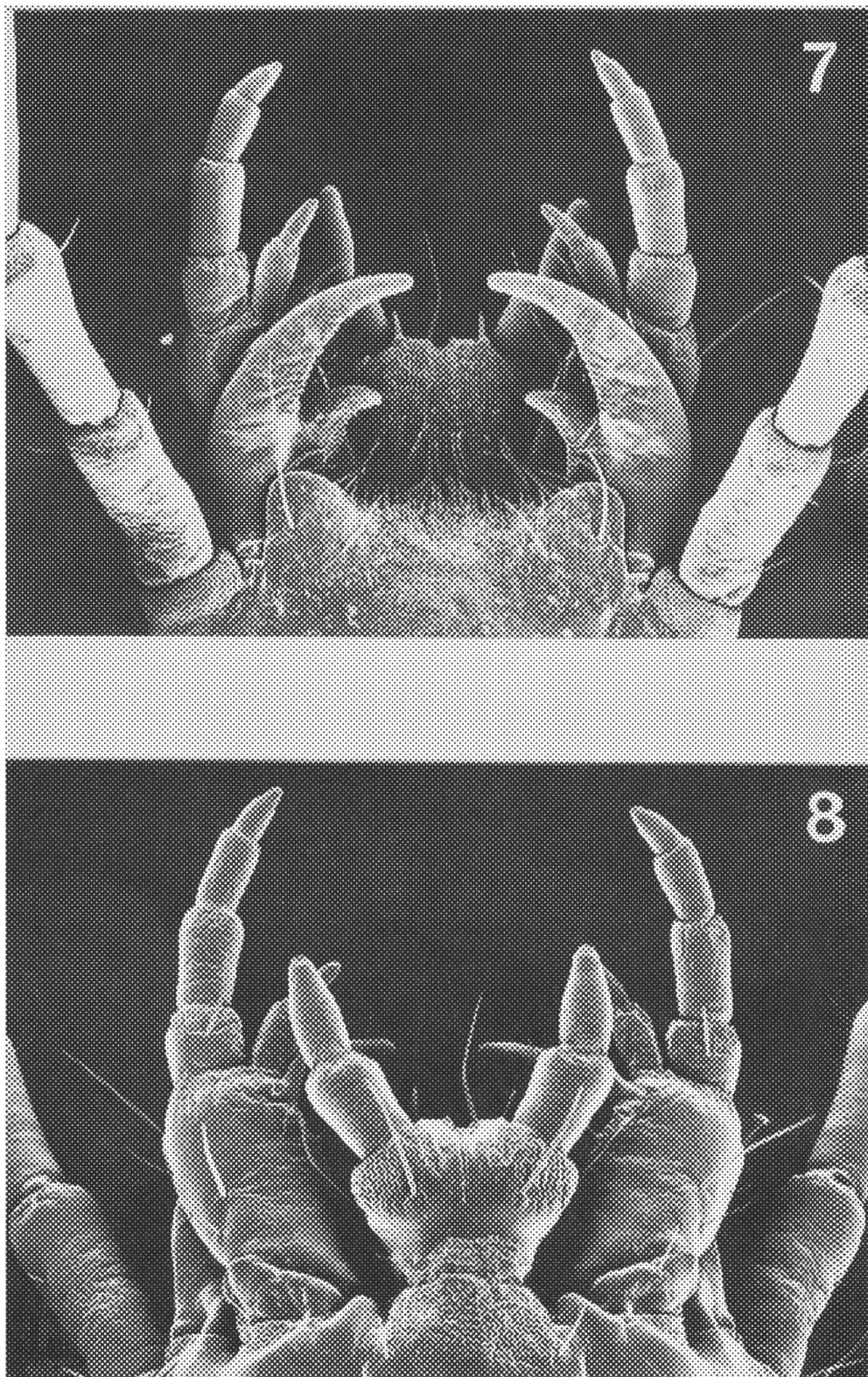
Originates from the median apodeme of the prementum; laterally attached to the base of palpomere I.

F: extensor of the labial palp

3. Preoral cavity

3.1. Epipharynx (Figs 4, 6).

Anterior part of the preepipharynx (not fused with the hypopharynx)



Figs 7-8: *Licinus silphoides*, head: 7, mouthparts, dorsal view. 8, mouthparts, ventral view.

laterally) membranous and set with irregularly distributed short hairs. Anterior section of the preepipharynx separated from posterior part by a nearly semicircular, transverse bulge. Bulge set with a regular row of short, forward projecting hairs. Transverse sulcus separates the preepipharynx from the postepipharynx. Postepipharynx distinctly elongated, fused with the posterior part of the hypopharynx laterally, thus forming a closed tube (prepharynx).

Musculature (Figs 4, 6):

M. 43. *M. clypeopalatalis*

Complex muscle, composed by many components which may be assigned to three major sub-units.

M. 43 a: composed by four bundles, which originate from the anterolateral region of the frontoclypeolabral apotome; attached to the semicircular transverse bulge of the preepipharynx.

F: dilator of the cibarium

M. 43 b: Composed by 2 bundles. The anterior bundle originates posterior to M. 43 a and is inserted posterior to the semicircular bulge of the preepipharynx. The posterior bundle originates anteromesally to the attachment area of M. 43 c, and is attached to the preepipharynx posteromesally to the anterior bundle of M. 43 b.

F: opener of the functional mouth, dilator of the prepharynx

M. 43 c: composed by 4 bundles which arise from a common area of origin, mesally to the attachment of the dorsal tentorial arm; successively attached to the postepipharynx.

F: dilator of the posterior part of the prepharynx

Strong transverse epipharyngeal muscle bands separate M. 43 c from M. 43 b and M. 41. Less strongly developed transverse muscles separate the bundles of M. 43 c.

F: the transverse muscle bands function as compressors of the prepharynx.

3.2. Hypopharynx

(Figs 4, 5).

Separated from the dorsal wall of the prementum by a transverse chitinous bar, which is set with a dense, regular row of long, forward projecting hairs. Strongly sclerotized, semicircular chitinous bar separates the anterior part of the hypopharynx from the posterior part which is fused with the postepipharynx. The area enclosed by these structures fits closely together with the area of the preepipharynx which is bordered by the anterior bulge and the posterior sulcus, thus

providing an efficient closing mechanism of the preoral cavity. Posterior part of hypopharynx lightly sclerotized.

Musculature (Figs 4, 5).

M. 41. M. frontohypopharyngalis

A thin muscle which originates posteriorly to the attachment area of M. 43 c; attached to the posterolateral margin of the hypopharynx.

F: retractor and levator of the mouth angle

M. 42. M. tentoriohypopharyngalis

Composed by few thin fibres which arise from the mesal side of the posterior tentorial arm; ventrolaterally attached to the hypopharynx, slightly anterior to the attachment of M. 41.

4. Pharynx

Short, wide, and round in cross section. Continuous with the extremely wide oesophagus.

Musculature (Fig 4, 6).

M. 45, 46: M. frontobuccalis anterior and posterior

M. 45 and 46 are represented by 3 bundles, which originate from the posteriormost region of the frontoclypeolabral apotome. They are successively attached to the dorsal pharyngeal wall.

F: dilators of the pharynx

M. 51: M. verticopharyngalis is absent

M. 52: M. tentoriopharyngalis is absent

5. Cerebrum

Cerebrum and suboesophageal ganglion shifted posteriorly to the cervical region.

III. Discussion of selected characters (Table I)

The determination of the polarity of character states is based on the outgroup comparison method (WATROUS & WHEELER, 1981). Taxa which can be assigned to a basal stock of Geadephaga based on the iso-

chaetous or nearly isochaetous condition of the protibia such as Trachypachini, Metriinae, Opisthiini, Cicindelinae, and Carabini are used as outgroup.

1. Head capsule

1.1. Relative size

The unusually small relative size of the head of larvae of Licinini and Panagaeini (GARDNER, 1938; JEANNEL, 1941-42; MOORE, 1965; LUFF, 1980; pers. obs., Figs 1, 9, 11) is derived and a possible synapomorphy of both tribes (char. state 1).

The decrease in size in larvae of Licinini and Panagaeini may have evolved as a result of snail-feeding habits (ARNETT, 1960-63; LUFF 1980).

1.2. Frontoclypeolabral apotome nearly parallel-sided, expanded posteriorly

A strongly expanded, nearly parallel-sided frontoclypeolabral apotome as found in larvae of Licinini and Panagaeini (GARDNER, 1938; V. EMDEN, 1942; MOORE, 1965; LUFF, 1980; ARNDT, 1991; pers. obs., Figs 1, 9, 11) is derived, and a possible synapomorphy of both tribes (char. state 1).

Enlargement of this sclerite is also found in other geadephagan larvae such as *Gehringia* (LINDROTH, 1960), Cychrini, Chlaeniini (Fig. 13), Helluonini, and Brachinini (THOMPSON, 1979), and has certainly taken place several times. However, the frontoclypeolabral apotome is not parallel-sided in these taxa.

The coronal suture is completely absent from larvae of *Licinus*, *Badister* (LUFF, 1980), and *Dicrochile brevicollis* Chaudoir (MOORE, 1965). The frontoclypeolabral apotome broadly reaches the hind margin of the head capsule in these taxa. This highly derived condition may be a result of parallel evolution in larvae of *Licinus* and *Badister* on one hand, and in larvae of *Dicrochile brevicollis* on the other (char. states 2, 2*).

1.3. Gula and posterior tentorial grooves

The posterior tentorial grooves are distinctly diverging anteriorly in larvae of *Dicaelus* (Fig. 10), and probably in larvae of *Lestignathus cursor* Erichson and *Dicrochile brevicollis* (ventral suture forked ante-

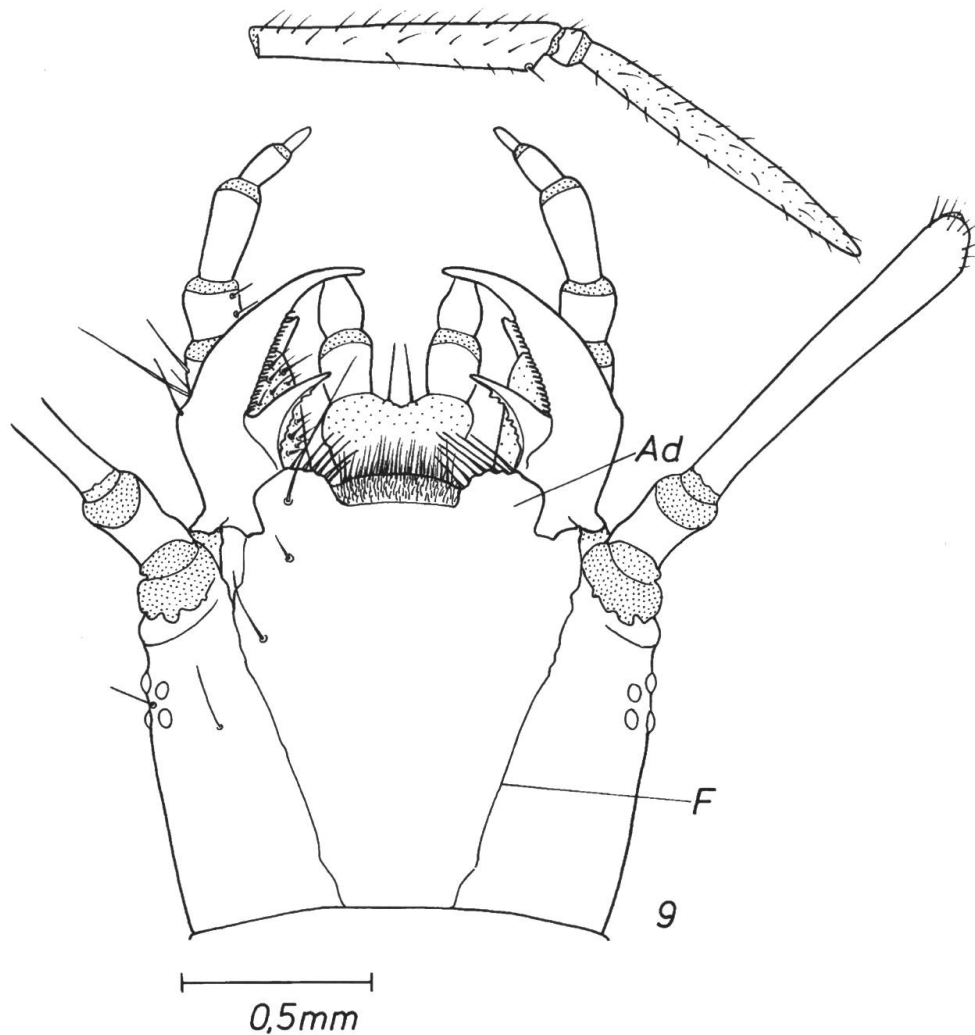


Fig 9: *Dicaelus* sp., head, dorsal view.

riorly; MOORE, 1965). The same condition is found in larvae of *Panagaeus*. This condition may be interpreted as a derived groundplan feature and possible synapomorphy of Licinini and Panagaeini (char. state 1).

The presence of a broad, distinctly bordered gular area and widely separated posterior tentorial arms as found in larvae of *Licinus* and *Badister* (JEANNEL, 1941-42) is considered a synapomorphy of both genera (char. state 2).

The widely separated posterior tentorial arms of larvae of Loriccerini are obviously the result of convergency.

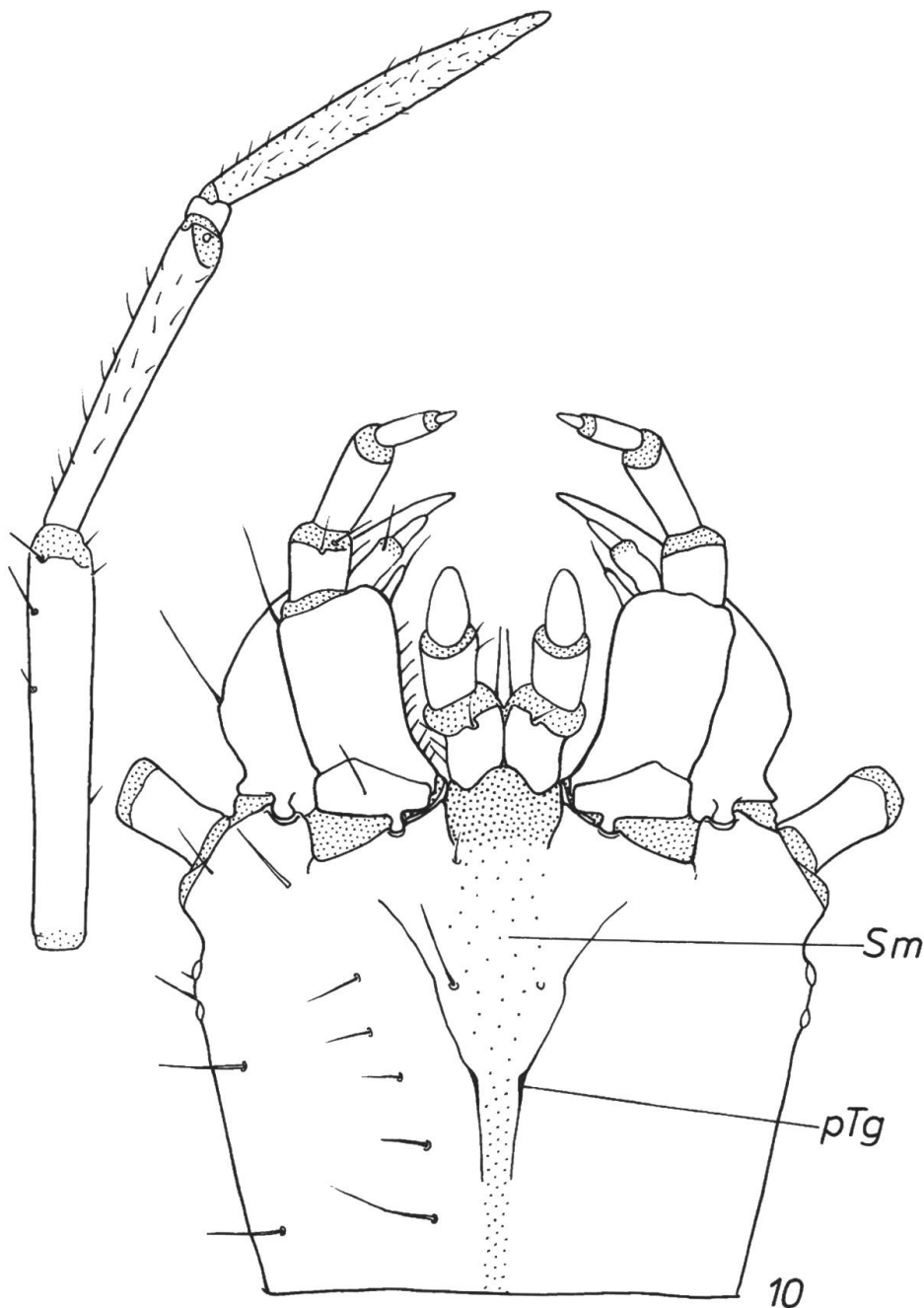


Fig 10: *Dicaelus* sp., head, ventral view.

1.4. Epicranial and postocular ridges

Cervical ridges are present in larvae of *Lestignathus cursor* (MOORE, 1965), but absent from other larvae of Licinini (GARDNER, 1938; MOORE, 1965; THOMPSON, 1979; LUFF, 1980; ARNDT, 1991). The absence is probably a secondary feature. Loss of the cervical and postocular ridges is a fairly common feature within Geadephaga (THOMPSON, 1979), and of little significance for phylogenetic analysis.

The presence of both ridges is considered a derived groundplan feature and possible synapomorphy of Caraboidea Limbata (JEANNEL, 1941-42).

Both ridges are primarily absent from larvae of Hydradephaga, Trachypachini, Gehringiini, Opisthiini (LINDROTH, 1960), Cicindelinae, Paussinae, Metriinae, Omophroninae, Cychrini, Carabini, Nebriini, Notiophilini, Elaphrini, and Loriccerini (THOMPSON, 1979).

1.5. Tentorial bridge absent

The absence of the tentorial bridge from larvae of *L. silphoides* is an apomorphic character state, and probably correlated with the wide separation of the posterior tentorial arms (char. state 1). A tentorial bridge is present in larvae of *Dicaelus* sp. and *Panagaeus bipustulatus* (char. state 0).

The absence from larvae of *Omophron variegatum* and *O. limbatum* (BEUTEL, 1991) is the result of convergency. The tentorial bridge is interrupted in larvae of *Nebria* (SPENCE & SUTCLIFFE, 1982).

2. Clypeolabral margin

2.1. Nasale

A concave, membranous, densely pubescent nasale which is devoid of prominent nasal structures, is present in *Licinus* and *Dicaelus* (Fig. 9), and is also described for larvae of *Badister* (LUFF, 1980) and *Diplocheila* (V. EMDEN, 1942; Fig. 15) (char. state 1). This highly unusual feature, which is not found in any other geadephagan larvae, has been proposed as a general feature of larvae of Licinini by ARNDT (1991). The interpretation as a synapomorphy of the tribe would imply that the presence of a triangular nasal projection in larvae of *Dicrochile brevicollis* (MOORE, 1965) is a secondary feature.

Prominent nasal structures are also absent from larvae of Panagaeini excl. *Tefflus* (V. EMDEN, 1942), however, the anterior margin is sclerotized and not pubescent (char. state 0,5).

Distinct nasal teeth of different shape and arrangement are found in the majority of carabid larvae incl. Chlaeniini (Fig. 13; THOMPSON, 1979).

2.2. Adnasal setae

The presence of a row of strong, mesally directed adnasal setae in

larvae of *L. silphoides* (6), *Dicaelus* sp. (6, Fig. 10), *Badister* (2 long setae, 2 short setae; LUFF, 1980), and *Diplocheila* (2; V. EMDEN, 1942, Fig. 15) is considered apomorphic. 4 setae seem to be present in larvae of *Dicrochile brevicollis*, and 7 or more in *Lestignathus cursor* (MOORE, 1965, Figs 3, 6). The adnasalia of larvae of *Dilonchus* are strongly reduced (GARDNER, 1938). The presence or absence of a row of setae is not mentioned in the description. Only 3 inconspicuous setae are present in larvae of *Zargus crotchianus* (ARNDT, 1991).

It is unclear at present whether this apomorphic character state is a groundplan feature of Licinini or a result of parallel evolution in several genera.

3. Antenna

3.1. Length

Antennae which are at least 1.5 times as long (char. state 1), but in most cases more than twice as long as the mandibles (char. state 2), are found in larvae of Licinini and Panagaeini (V. EMDEN 1942; pers. obs., Figs 1, 10-13). This is a derived condition and a possible synapomorphy of Panagaeini and Licinini (char. states 1, 2).

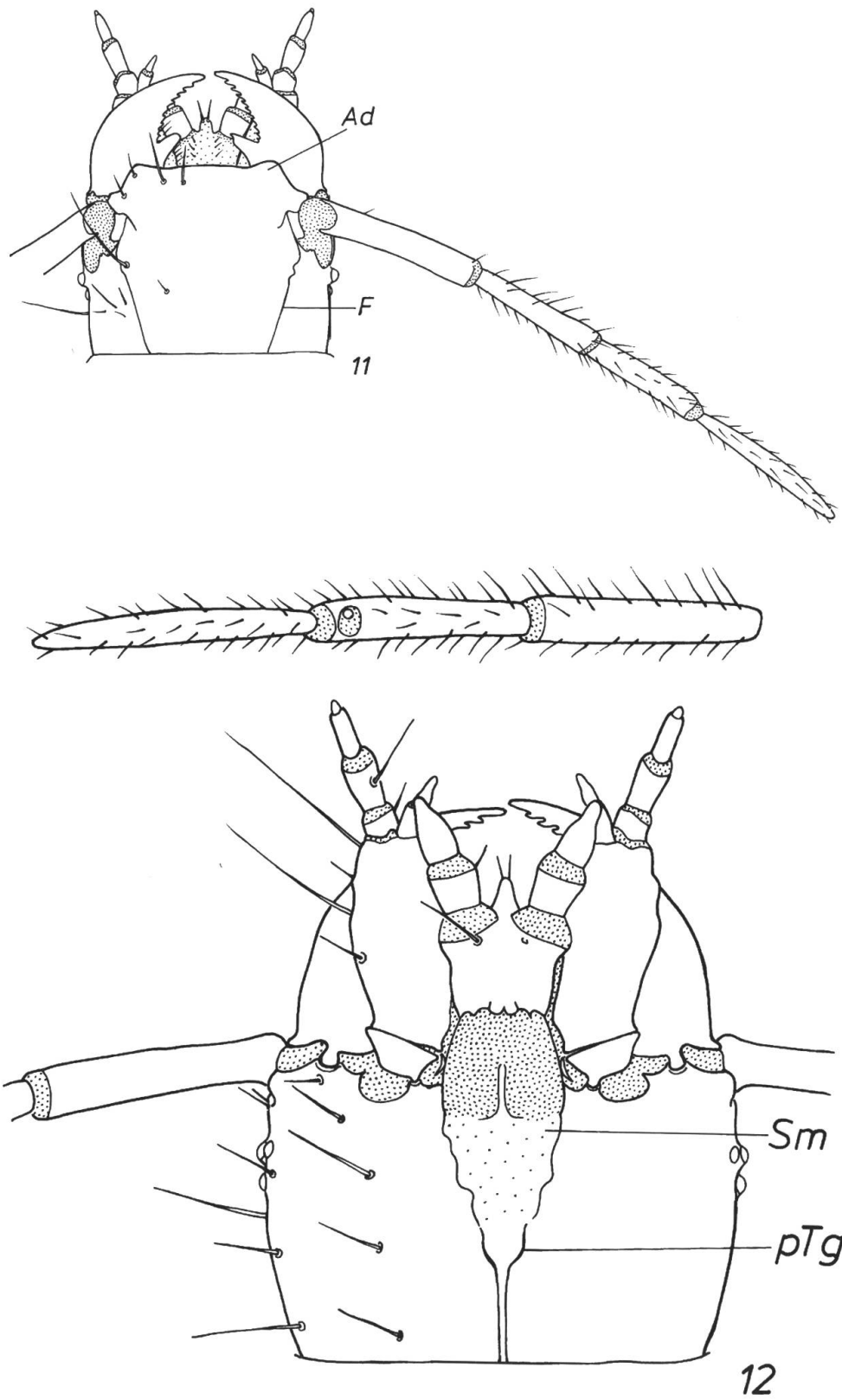
3.2. Semimembranous antennomeres

Semimembranous zones of antennomeres are present in larvae of *L. silphoides* and *Dicaelus* sp. (Figs 9, 10), and are also described for larvae of *Badister* (ARNDT, 1991) and *Dilonchus* (GARDNER, 1938; Fig. 21). This is considered a derived feature and a possible synapomorphy of Licinini (char. state 1). A similar condition is not described for other larvae of Geadephaga so far.

3.3. Pubescence

Antennal pubescence is absent from larvae of *Licinus*, *Badister* (LUFF, 1980), *Diplocheila* (V. EMDEN, 1942), *Zargus crotchianus*, *Dicrochile* (MOORE, 1965), and *Dilonchus* (GARDNER, 1938). It is present in larvae of *Dicaelus* (Figs 9, 10), *Lestignathus* (MOORE, 1965), and Panagaeini (V. EMDEN, 1942; pers. obs., Figs 11, 12). The presence is an apomorphic character state (char. state 1).

Whether antennal pubescence is a derived groundplan feature of Licinini and Panagaeini and secondarily absent from several larvae of Licinini, or a result of parallel evolution in both tribes remains open to question.



Figs 11-12: *Panagaeine Larva*, head: 11, dorsal view. 12, ventral view.

3.4. Antennal muscles

Intercrossing antennal muscles as found in larvae of *L. silphoides*, *Panagaeus bipustulatus*, *Scarites* sp., *Broscus cephalotes*, and *Pterostichus nigritya* (Paykull) (TRÖSTER, 1987) are certainly apomorphic.

The groundplan condition (anterior attachment of M. 1, posterior attachment of M. 2, dorsal attachment of M. 4) is found in larvae of *Trachypachus holmbergi*, *Amphizoa lecontei*, *Metrius contractus*, *Omophron variegatum* (BEUTEL, 1991), *Carabus coriaceus*, and in *Cicindela campestris* L. (BREYER, 1989).

The derived arrangement of antennal muscles is considered a possible synapomorphy of Caraboidea Limbata (JEANNEL, 1941-42).

4. Mandibles

4.1. Blade

A serrate cutting edge of the mandible is found in larvae of Licinini excl. *Diplocheila* (V. EMDEN, 1942; GARDNER, 1938; MOORE, 1965; LUFF, 1980; ARNDT, 1991), and in Panagaeini excl. *Tefflus* (Figs. 11, 12; V. EMDEN, 1942). This feature is almost certainly derived as serrate cutting edges are absent from the vast majority of geadephagan larvae. The presence could be interpreted as a groundplan feature of Licinini and Panagaeini, and as a possible synapomorphy of both tribes (char. state 1). However, this interpretation is rather uncertain. It implies secondary absence from larvae of *Diplocheila* and *Tefflus* (0R?).

Serration of the mandibular blade may be correlated to snail feeding habits.

A characteristic row of denticles on the ventral side of the mandibular blade has been observed by ARNDT (1991) in several larvae of Licinini. This highly interesting feature may turn out as an important synapomorphy of the tribe.

4.2. Retinaculum

A spiniferous serration on the edge of the retinaculum is found in larvae of *Licinus*, *Badister* (LUFF, 1980), and *Dicrochile* (MOORE, 1965) (char. state 1). The retinacular serration is obsolete in larvae of *Dicaelus* and *Dilonchus* (GARDNER, 1938) (char. state 0,5R), and absent from larvae of *Zargus crotchianus* (ARNDT, 1991), *Lestignathus* (MOORE, 1965), and *Diplocheila* (V. EMDEN, 1942) (char. state 0R?). Retinacular serration may have developed independently in larvae of *Licinus* and

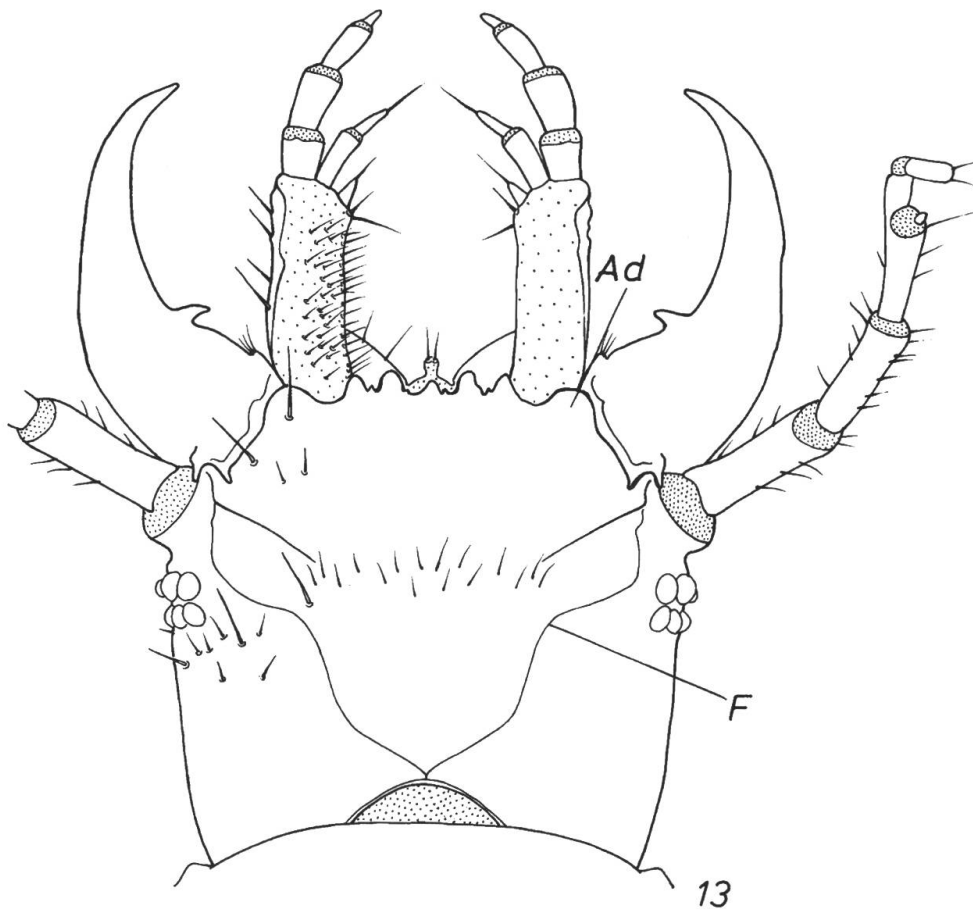


Fig. 13: *Chlaenius* sp., head. dorsal view.

Badister on one hand, and *Dicrochile* on the other. The interpretation of this character remains rather uncertain.

A strongly denticulate retinaculum is also found in larvae of Cychrini (V. EMDEN, 1942). A correlation of retinacular serration to snail-feeding habits is quite likely.

5. Maxilla

5.1. Shape of the stipes

The stipes of larvae of Licinini and Panagaeini is rather short and broad (GARDNER, 1938; JEANNEL, 1941-42; V. EMDEN, 1942; MOORE,

1965; pers. obs., Figs 10, 12). This is considered a derived feature and as a possible synapomorphy of both tribes (char. state 1).

The stipes of most carabid larvae (incl. Chlaeniini, Fig. 14) is elongate and slender (THOMPSON, 1979).

6. Labium

6.1. Submentum

The submentum is weakly sclerotized, broad, and distinctly bordered laterally in larvae of *L. silphoides*, *Dicaelus* sp. (Fig. 10), *Badister* (JEANNEL, 1941-42), and the larvae of Panagaeini examined (Fig. 12). This is considered a possible synapomorphy of Licinini and Panagaeini (char. state 1).

The submentum is characterized by a narrow, median membranous zone, and is not distinctly bordered laterally in larvae of *T. holmbergi*, *M. contractus*, *C. coriaceus*, *Oodes* sp., *Chlaenius* ssp. (Fig. 14), and other larvae examined. A similar condition as described above is only found in larvae of *Loricera*. This is almost certainly due to convergency.

6.2. Ligula

A concave ligula as found in larvae of *Licinus* (LUFF, 1980) and *Dicaelus* sp. is apomorphic (char. state 1, 1*?). This derived character state has probably evolved independently in both genera. A convex ligula is present in larvae of *Badister* (LUFF, 1980) which is probably more closely related to *Licinus* than *Dicaelus* (see char. 1.3). The plesiomorphic character state (char. state 0) is also found in larvae of *Diplocheila* (V. EMDEN, 1942), *Lestignathus*, *Dicrochile* (MOORE, 1965), *Dilonchus* (GARDNER, 1938), *Zargus* (ARNDT, 1991), and in larvae of the vast majority of geadephagan tribes including Panagaeini (THOMPSON, 1979).

6.3. Premental spine

A strong spine is present near the base of the palps in larvae of *L. silphoides* and other species of the genus (LUFF, 1980). This is considered an apomorphic character state and a possible synapomorphy of *Licinus* (char. state 1).

Spines of similar position and shape are not described for other members of Geadephaga so far (V. EMDEN, 1942; THOMPSON, 1979; MOORE, 1965; LUFF, 1980).

6.4. Labial palps

Stout labial palps as found in larvae of Licinini (GARDNER, 1938; V.

EMDEN, 1942; MOORE, 1965; LUFF, 1980; ARNDT, 1991) and Panagaeini (V. EMDEN, 1942) are considered derived and as a possible synapomorphy of Licinini and Panagaeini (char. state 1).

More or less elongate and slender palpomeres are found in the vast majority of carabid larvae including Chlaeniini (THOMPSON, 1979; pers. obs., Fig. 14).

6.5. Extrinsic muscles of the prementum

The origin of the extrinsic premental muscles from the gular ridges in larvae of *L. silphoides* is considered apomorphic (char. state 1).

The shifting of the origins of Mm. tentoriopraementales superior and inferior is correlated to the separation of the posterior tentorial grooves and the presence of secondarily developed gular ridges.

The extrinsic premental muscles originate from the mesal side of the posterior tentorial arms in larvae of *Dicaelus* sp., *Panagaeus bipustulatus*, and in other geadephagan larvae examined so far (char. state 0).

7. Preoral cavity

7.1. Hypopharynx

The hypopharyngeal platform is continuous with the dorsal wall of the prementum on one level in larvae of *L. silphoides* and *Dicaelus* sp. The same condition is found in larvae of *Amara* (DORSEY, 1943), *P. nigrita* (TRÖSTER, 1987), *Scarites* sp., *B. cephalotes*, *Panagaeus bipustulatus*, and *Brachinus explodens*. This character state is considered a possible synapomorphy of Caraboidea Limbata (JEANNEL, 1941-42).

A well defined hypopharynx, which is clearly separated from the dorsal wall of the prementum by a deep fold, is present in larvae of *T. holmbergi*, *Omophron* (BEUTEL, 1991), *C. coriaceus* (BEUTEL, in press), *Nebria* (SPENCE & SUTCLIFFE, 1982), and *C. campestris* (BREYER, 1989). This is almost certainly the groundplan character state of Adephaga.

7.2. Preoral closing mechanism

An anterior preepipharyngeal bulge, a posterior preepipharyngeal sulcus, and corresponding structures of the surface of the levelled hypopharynx provide an efficient closing mechanism of the preoral cavity in larvae of *L. silphoides* and *Dicaelus* sp. The same condition is found in larvae of *Scarites* sp., *B. cephalotes*, and *P. nigrita* (TRÖSTER, 1987). This is certainly a derived feature and a possible synapomorphy of Caraboidea Limbata (JEANNEL, 1941-42).

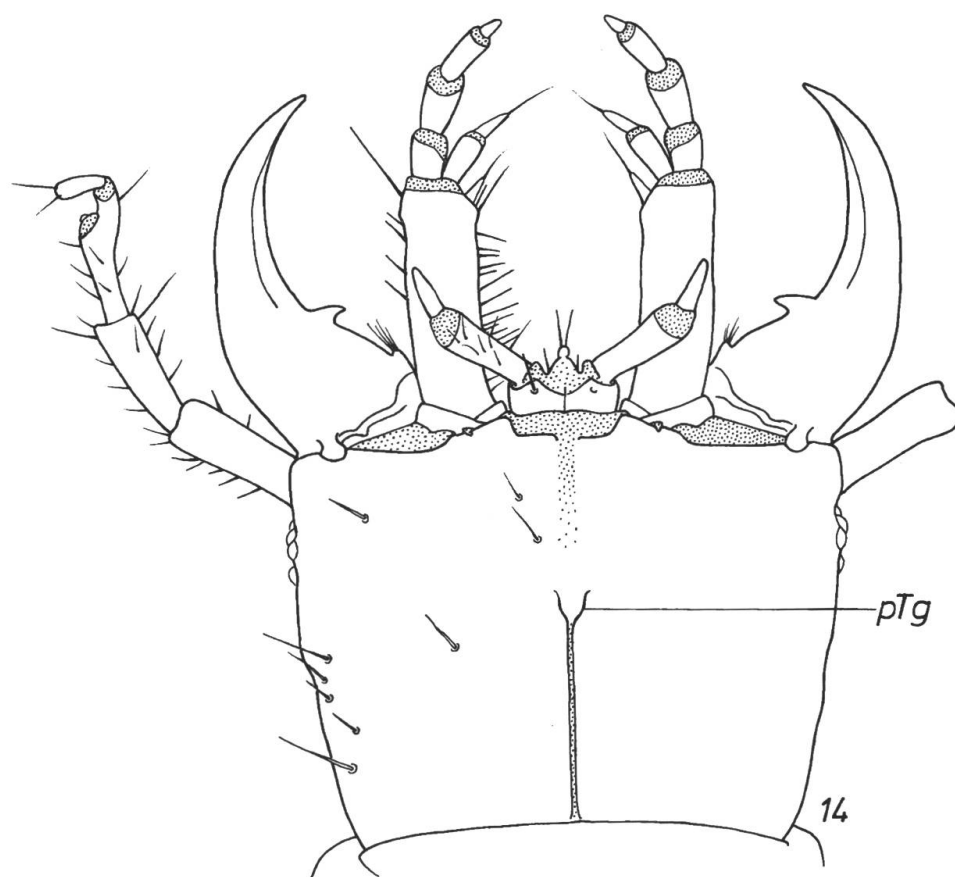


Fig. 14: *Chlaenius* sp., head, ventral view.

The preoral cavity is closed by contact of the epipharyngeal surface with the strongly bulging hypopharynx in larvae of *T. holmbergi*, *C. coriaceus*, and *Nebria* sp. (SPENCE & SUTCLIFFE, 1982). This is considered as the adepagan groundplan character state.

7.3. Extension of the prepharynx

The prepharynx and the attachment area of the three subunits of *M. frontobuccalis* anterior is considerably extended in larvae of *L. silphoides*, *Dicaelus* sp., and *Panagaeus bipustulatus*. This condition is certainly apomorphic (char. state 1). Elongation of the prepharynx is obviously correlated to the strong expansion of the frontoclypeolabral apotome in larvae of Licinini and Panagaeini, and may be a synapomorphy of both tribes.

8. Pharynx

8.1. Shape and extension

The pharynx of *L. silphoides*, *Dicaelus* sp., and *Panagaeus bipustula-*

tus is short, relatively wide, and posteriorly adjacent to an exceptionally wide oesophagus. This is considered an apomorphic character state and a possible synapomorphy of Licinini and Panagaeini (char. state 1).

8.2. *M. verticopharyngalis*

The absence of *M. verticopharyngalis* from larvae of *L. silphoides*, *Panagaeus bipustulatus*, and other geadephagan larvae (e.g. *Nebria*, SPENCE & SUTCLIFFE, 1982; *P. nigrita*, TRÖSTER, 1987) is apomorphic. The character is of little value for phylogenetic analysis.

8.3. *M. tentoriopharyngalis*

The absence of *M. tentoriopharyngalis* from larvae of *L. silphoides* is apomorphic. The muscle is also absent from larvae of *Omophron* (BEUTEL, 1991) and *C. campestris* (BREYER, 1989).

The muscle is present but thin in larvae of *Panagaeus bipustulatus*. It is quite likely that this muscle has been reduced several times independently. The absence of *M. tentoriopharyngalis* is probably correlated to the loss of the tentorial bridge in larvae of *L. silphoides* and *Omophron*.

9. Cerebrum

9.1. Position

Cerebrum and suboesophageal ganglion are located in the broad cervical region in larvae of *L. silphoides*. This is a highly derived character state which has not been described for other adephagan larvae so far (char. state 2). This uncommon position is certainly a result of the elongation of the prepharynx, the extension of the attachment area of prepharyngeal and pharyngeal dilators, of the posterior extension of the frontoclypeolabral apotome, and finally of the small relative size of the head capsule. The brain is distinctly shifted posteriorly in larvae of *Dicaelus* sp. and *Panagaeus bipustulatus*, but still within the head capsule. This condition is considered a derived groundplan feature and a possible synapomorphy of Licinini and Panagaeini (char. state 1).

IV. Concluding remarks

The results of this study strongly suggest that Licinini and Panaga-

eini together form a monophyletic unit. Most of the common derived features such as small relative size of the head, elongation of antennae, broad and short maxillae, stout labial palps are probably correlated to snail feeding-habits, which may be an apomorphic character state of the last common ancestor of both tribes. The hypothesis of a common ancestry of Licinini and Panagaeini is much more parsimonious than to assume parallelism or convergency in a considerable number of common derived character states shared by both groups.

None of the presumptive synapomorphies of Licinini and Panagaeini is found in members of Chlaenini and Oodini, which are combined with Licinini in the supertribe Callistidae by KRYZHANOVSKIY (1976). This implies that Callistidae KRYZHANOVSKIY are paraphyletic.

The monophyly of the genera of Licinini and the monophyly of Panagaeini cannot be taken as granted so far. More material needs to be examined.

A close relationship between *Licinus* and *Badister* is supported by the widely separated posterior tentorial arms, and the broad, distinctly bordered gula.

Licinini and Panagaeini are members of Caraboidea Limbata (JEANNEL, 1941-42), which are characterized by 3 synapomorphic character states.

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