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Mouthpart Structure in Adult Scarab Beetles (Coleoptera: Scarabaeoidea)

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The structure of the epipharynx, mandibulae, maxillae and labium, with variations thereof is described. The most descriptive terms for named structures are stressed and new terms are proposed for unnamed structures. From a phylogenetic point of view the epipharynx, maxillae and labium appear to be important. Variations of the tentorium are discussed as supplementary characters to those of mouthparts.

Key words: Scarabaeoidea — scarab beetles — imaginal mouthpart structure — terminology — systematic relations.

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Die Strukturen von Epipharynx, Mandibulae, Maxillae und Labium werden mit den bei den verschiedenen Untergruppen vorliegenden Abwandlungen beschrieben. Für bisher unbenannte Strukturteile werden neue Termini vorgeschlagen. Von den bereits gebräuchlichen Begriffen werden diejenigen in die hier vorgeschlagene umfassende Terminologie aufgenommen, die beschreibend sind. Für die Analyse von Verwandschaftsbeziehungen innerhalb der Scarabaeoidea werden Struktur-Abwandlungen von Epipharynx, Maxillae und Labium als wichtig erachtet. Neben diesen Mundteilen erscheinen auch Merkmals-Ausprägungen des Tentorium phylogenetisch beachtenswert.

1 Introduction

During the course of a study to determine the phylogenetic significance of mouthpart structure in the Scarabaeoidea, inconsistencies were encountered in the general terminology used by students of this suprafamilia. Since several structures on the mouthparts are referred to by different names by various authors, and in other cases the same names are used widely for non-homologous structures, it was considered essential to establish a consistent set of terms for scarabaeoid mouthparts. A detailed comparison of taxa is beyond the scope of this paper, as it is only intended to show the different types of mouthparts in the Scarabaeoidea and as a guide for descriptive purposes.

It was necessary to coin new names for hitherto unnamed phylogenetically important structures, although the creation of yet more names in a system with numerous superfluous names is clearly undesirable. The terminology established here can hopefully be applied in works of a phylogenetic

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nature since the important homologies in the suprafamilia are identified. The terminology used by several authors [Böving 1936: imagines, Edmonds 1972: adults; MacGillivray 1923; Matsuda 1965; Snodgrass 1935], is combined to establish a consistent set of terms for the mouthparts of adult Scarabaeoidea. The classification system of Crowson [1981] is followed throughout in this study.

2 Materials and Methods

Mouthpart structure [MP-S][1] of male and female specimens in the following familiae were studied: Glaresidae (1 genus); Lucanidae (10 subfamiliae, 15 genera); Pleocomidae (1 genus); Trogidae (3 genera); Passalidae (2 subfamiliae, 2 genera); Ochodaeidae (8 genera); Geotrupidae (4 subfamiliae, 12 genera); Hybosoridae (4 genera); Ceratocanthidae (2 genera). The subfamiliae of the Scarabaeidae which were studied, include the Scarabaeinae (47 genera); Melolonthinae (36 genera); Hopliinae (8 genera); Aphodiinae (9 genera); Dynastinae (17 genera); Rutelinae (11 genera); Glaphyrinae (2 genera); Aulonocneminae (1 genus); Aclopinae (2 genera); Orphninae (1 genus); Aegialiinae (3 genera); Phaenomerinae (1 genus); Trichiinae (6 genera); Valginae (2 genera) and Cetoniinae (44 genera) were studied.
Dried specimens were softened for a few minutes in boiling water and then dissected. The mouthparts [MP] were placed in a 10 % KOH solution for 3—4 h to dissolve internal tissues. They were then placed in distilled water to which a few drops of acetic acid were added in order to neutralize the KOH. The MP were then dehydrated in 70 % ethanol for 1 h followed by 96 % ethanol for another hour, after which they were stained with acid fuchsin in 96 % ethanol. A final dehydration in 100 % ethanol for 30—60 min was followed by clearing the MP in xylol and mounting them in "Entellan" on microscope slides. Drawings were made with the aid of a Wild M3 microscope, and a drawing tube.

3 Results

In this study the epipharynx, mandibulae, maxillae and labium are considered to be the trophic apparatus of the Scarabaeoidea. Terms with abbreviations mentioned in the text are suggested for use in future descriptions of scarabaeoid MP. These and others are listed in the glossary of Tab 1.

Tab 1: Glossary of latin and english terminology of mouthparts in adult Scarab Beetles [Coleoptera: Scarabaeoidea].

Akronym	Term	Definition
Ap	apiculus	distal part of the mandibula
Br-a.r.t	bracchia anterior rudimentum tentorius	anterior tentorial arm rudiments, arising from the anterior secondary bridge, and extending antero-distally
Br-s.t	bracchia succedanea tentoria	tentorial arms arising from the posterior tentorial pits and extending meso-ventrally
Bru-g	bruscum galeare	dense brush of setae on the galea
Bru-lc	bruscum laciniosum	dense brush of setae on the lacinia
Bru-md	bruscum mandibulare	setal brush, proximal on the molar lobe of mandible

[1] Mouthpart structure, in further text: MP-S; Mouthparts, ift: MP

Tab 1 (continue)

Akronym	Term	Definition
Bs	basis	proximal part of the mandibula
Ca-g.d.a	callum galeare dorsale articulatum	dorsal articulatory sclerite of the galea, articulating with the parastipes
Ca-g.v.a	callum galeare ventrale articulatum	ventral articulatory sclerite or the galea, articulating with the parastipes
Ca-l	callum laterale	lateral sclerite on the apical part of the mandible
Ca-lb	calla labralia	lightly sclerotized labral sclerites, situated posterior of the lateral tormal processes
Ca-mb.mx	callum membrani maxillaris	maxacorial sclerite, meso-proximal of the stipes, attached to the rectacuta of the mandible
Ca-st.a.v.d	callum stipitale adjectivum ventrale distale	semicircular plate-like extension of the stipes ventralis
Ca-st.b.a	callum stipitale basale adjectivum	elongate plate-like extension of the stipes basalis
Ca-o	cavus ocularis	ocular cavity in head capsule
Cd	cardo	basal part of the maxillae, articulating with the hypostoma
Cj	coniuncta	soft flexible ventral sclerite, conjunctive between the mesal edge of Ap and Lo-ml
Cly	clypeus	lower part of the head to which the labrum is attached anteriorly
Con	condylus	condyle, ventral, posterior articulation of the mandible
Cor-ap.md	corniculum apicale mandibulare	apical mandible horn
Cor-bs.md	corniculum basilare mandibulare	basal mandible horn
Cr-ga	crista galearis	galeal ridge, sulcus between galea and stipes
Cr-st.cr	crista stipitalis cardinalis	cardostipital ridge, sulcus between cardo and stipes
D-di	dentes distales	maxadentes, distal teeth of the lacinia
D-pr	dentes proximales	proxadentes, proximal teeth of the lacinia
Fi-ap	fimbria apicales	setae on the apical margin of the distal part of the epipharynx
Fi-gl	fimbria gularis	suture between gula and submentum
Fr	frons	unpaired sclerite of caput
Ggl	ginglymus	anterior articulation of the mandible
Gl-ds	galea distales	distal part of the galea, disti-galea
Gl	galea	distal lobe of the lacinia
Gl-px	galea proximales	proximal part of the galea, sub-galea
Hyp	hypostoma	sclerite of the head capsule for the articulation of mandibles and maxillae

Tab 1 (continue)

Akronym	Term	Definition
Lc	lacinia	inner or mesal lobe of the maxilla
Li	ligula	fusion of the inner and outer ligular lobes
Lo-it	lobus intermandibularis	reduced epipharynx, intermandibular projection
Lo-li.i	lobi ligulares interiores	paraglossae or inner ligular lobes
Lo-li.e	lobi ligulares exteriores	glossae or outer ligular lobes
Lo-ml	lobi molares	proximal molar lobes of the basalis
Ma	mala	fusion of lacinia and galea
Me-ml	membranum molare	membrane on the dorsal surface of the mandible
Me-mx	membranum maxillare	membrane attaching the mandible to the maxilla maxacoria
Mo	mola	ridged grinding surface of the mandibles
Myc	mycangium	cavity on the molar lobe
Oc	occiput	posterior part of the epicranium
Pc-m.a	processus medianus anterior	median, anterior tormal process
Pc-m.p	processus medianus posterior	median, posterior tormal process
Pc-t.l	processus tormalis lateralis	tormal processes situated laterally on the epipharynx
Pe-cj	pecten coniunctives	mesal comb of the coniuncta
Pe-ds	pecten distalis	setal comb on the distal end of the apicales
Pe-if	pecten inferior	longitudinal row of fine setae on the dorsal surface of the apicalis, infrabrustia
Pe-ms	pecten medialis	setae on the mesal edge of the apicalis
Pe-mds	pecten medianus median brush	dense brush of setae, medio-anteriorly on the epipharynx
Per-sn	perixiguae sensillae	small sensory processes posterior to Pc-m.p, microsensillae
P-lt	pectines laterales	2 or more apically diverging, longitudinally rows of prostrate setae on the distal epipharynx
P-mx	palpi	maxillary or labial palps
Po-a.t	pons anterior tentorius	anterior tentorial bridge, formed by fusion of the anterior tentorial arm rudiments
Po-a.s	pons anterior succedaneus	anterior secondary bridge, formed by extensions of the posterior tentorial pits that unite anteriorly
Po-p.s	pons posterior succedaneus	posterior secondary bridge, formed by extensions of the posterior tentorial arms that unite mesally
Po-t.m	pons tentorius medianus	mesal tentorial bridge, formed by lateral extensions of the posterior tentorial pits that unite mesally

Tab 1 (continue)

Akronym	Term	Definition
Po	postocciput	posterior area of the cranium
Pe-sp.v	pecten superior ventralis	setal comb on the apical ventral comb
Pe-vt	pecten ventralis	longitudinal rows of fine setae of the ventral side of Ap
Prmt	praementum	most distal part of the labium
Pst	prostheca	mandibular set of hairs situated mesodistally of the molar lobe
Rct	receptaculum	cup-shaped sclerite on the Bs
Sbm	submentum	basal sclerite of the labium
S-cl	sutura-clypeolabralis	clypeo-labral suture, between labrum and clypeus
Sp-b	stipes basalis	median stipes, basic or median part of the stipes
Sp-c	stipes confinis	parastipes, part of the stipes, mesal of the Sp-b
Sp-l	stipes lateralis	latero-stipes lateral of the Sp-c, bearing the palpi
Sp-v	stipes ventralis	ventro-stipes
Ss	sensillum	sense organ
Ss-l	suspensorium labrale	inherent musculature of the epipharynx
St-md	setula medialis	tuft of setae on the mesal margin of the Ap
Tp	tapetum	membrane covering the molar surfaces, tapete

2.1 The labrum

The labrum is attached to the inner surface of the clypeus by the sutura-clypeolabralis [S-cl] (Fig 1, 2b,c). The position of the labrum in the mouth varies. In some primitive Scarabaeoidea such as the Geotrupidae, Trogidae and Lucanidae, the distal part of the labrum protrudes outside the preoral cavity and may be partly or totally fused to the clypeus, eg in Trogidae [*Omorgus radula* (Erichson 1843)], in which it is visible in dorsal view. The labrum may also be situated in the roof of the preoral cavity, eg Melolonthinae [*Macrodactilus* sp.], most Scarabaeinae, Ceratocanthidae, and others. The epipharynx is situated on the ventral aspect of the labrum.

2.2 The epipharynx (Fig 1—3)

The S-cl divides the epipharynx in a proximal and a distal part. In most groups the proximal part is thin and membranous, while the distal part is sclerotized (Fig 2a,b,c). In the Scarabaeinae, however, both parts are membranous (Fig 1). The apical margin of the distal part may vary from square (Fig 2a) to rounded but mesally slightly indented (Fig 2b), to the distal part being bilobed or partly bilobed (Fig 2c).

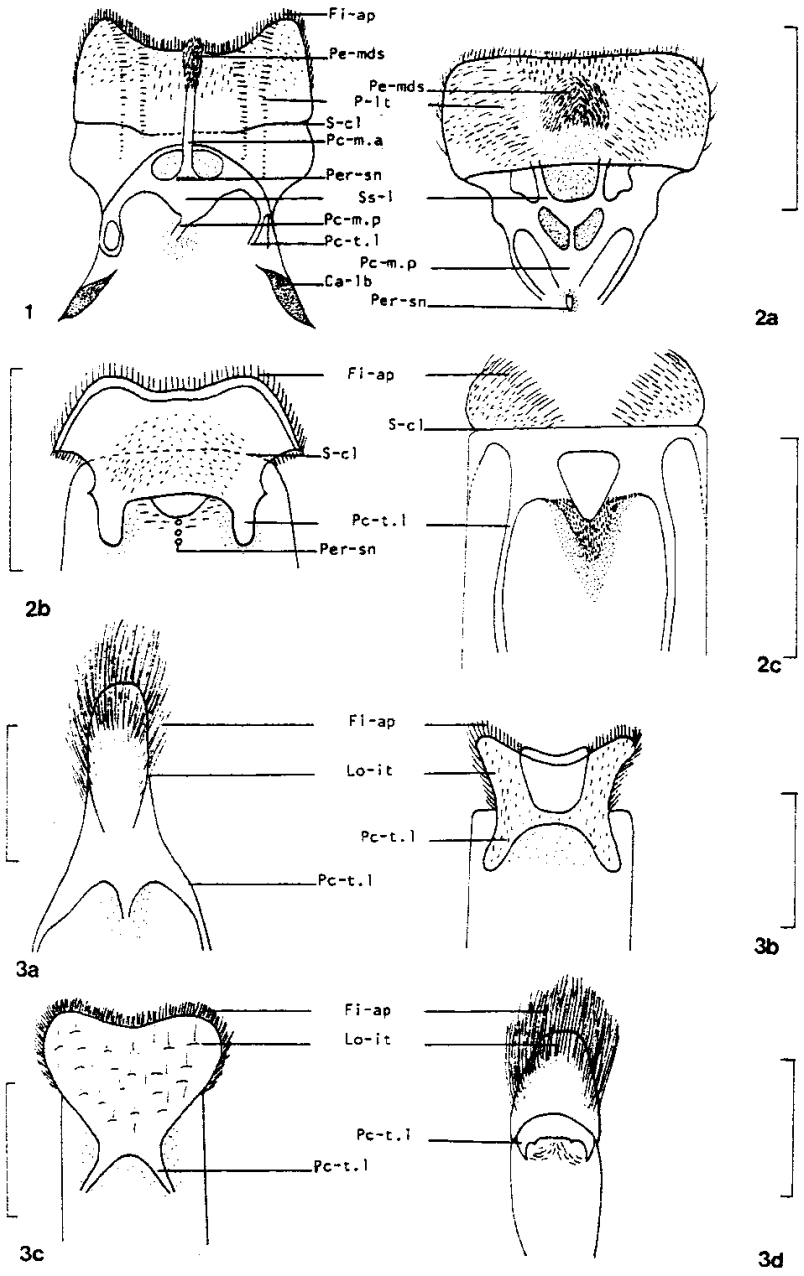

Fig 1—3: Structural variation of the epipharynx in Scarab Beetles [Coleoptera: Scarabaeoidea]. — 1 Hypothetical epipharynx [Eph] illustrating the fimbria apicales [Fi-ap], sutura-clypeolabralis [S-cl], calla labralia [Ca-lb], pectines laterales [Pe-l], suspensorium labrale [Ss-l], pecten medianus [Pe-mds], perexiguae sensillae [Per-sn], processus medianus anterior [Pc-m.a], processus medianus posterior [Pc-m.p], processus tormalis lateralis [Pc-t.l]. Not to scale. — **2a** Epipharynx of *Anoplotrupes* sp. (Geotrupidae), **b** Eph of *Omorgus radula* (Erichson 1843) (Trogidae), **c** Eph of *Trochalus* sp. (Melolonthinae). (Bar = 1 mm). — **3a** Lobus intermandibularis [Lo-it] of *Lamprima* sp. (Lucanidae), **b** *Nigidius bubalus* Sweder 1787, **c** *Aesalus* sp. (Lucanidae), **d** *Pleocoma octopagina* (Robertson 1970) (Pleocomidae) (Bar = 1 mm).

2.2.1 The distal epipharynx

The apical margin of the distal epipharynx is lined with setae, which are collectively referred to by Edmonds [1972] as the fimbria apicales [Fi-ap] (Fig 1, 2b, c, 3a, b, c, d). Medio-anteriorly the epipharynx is covered by a dense brush of setae, the pecten medianus [Pe-mds] (Fig 1, 2a). The Pe-mds may extend over the apical margin to form a pointed structure, corresponding in position to the corypha of Böving [1963] (Fig 1). The distal epipharynx is characterized by 2 or more apically diverging longitudinal rows of prostrate setae forming the pectines laterales [P-lt] corresponding in position to the chaetopariae of Böving [1936], and to the lateral files of Edmonds [1972] (Fig 1, 2a). The seta-less areas, to so-called zonae lateralis [Edmonds 1972] on the lateral sides of the distal epipharynx correspond to the gymnopariae of Böving [1936], with the acanthopariae forming the lateral margins of the epipharynx. The processus medianus anterior (Pc-m.a.] (Fig 1) is the central median area of the distal epipharynx and corresponds to the pedium [Böving 1936] and the zona centralis [Halffter 1961, cited by Edmonds 1972].

2.2.2 The proximal epipharynx

The proximal epipharynx is the membranous area posterior to the sutura-clypeolabralis. Posteriorly the suspensorium labrale [Ss-l] (Fig 1, 2a) [Edmonds 1972] bears the processus medianus posterior [Pc-m.p.] (Fig 1, 2a) or epitormae [Böving 1936], with 2 processus tormales laterales [Pc-t.l.] (Fig 1, 2a, b, c, 3a, b, c, d) [Edmonds 1972]. The processus medianus posterior is usually bent to the right in a dorsal view (Fig 1) and the processus tormales laterales [Böving 1936: pternotormae] may be single or double, or may end in a closed circle (Fig 1). The suspensorium labrale is usually lightly sclerotized or thick and membranous. Just posterior of the 2 processus tormales laterales, 2 distinct lightly sclerotized calla labralia [Ca-lb] (Fig 1) form part of the suspensorium labrale and articulate laterally with the ginglymus [Ggl] (Fig 4a, b, c, 5a, b, 6a, b, 7a, b) of a mandibula [Edmonds 1972]. The calla labralia are very distinct in the Scarabaeinae. Perixiguae sensillae [Per-sn] are present in some groups just posterior to the processus medianus posterior, or sometimes posterior to the processus medianus anterior (Fig 1, 2a, b).
In some familiae, eg the Lucanidae and Pleocomidae, the epipharynx is reduced to an elongate lobe, usually covered with very long setae, that extends between the basal piece of the mandibulae. This was referred to as an lobus intermandibularis [Lo-it] (Fig 3a, b, c, d) by Lacordaire [1856], cited by Holloway [1969]. No definite structures except 3 processes, possibly representing the processus tormales laterales and processus medianus posterior, can be recognized. According to Holloway [1969] the shape of the lobus intermandibularis or "reduced epipharynx", is closely associated with the shape of the mandibulae, and varies to a large extent between groups. Holloway [1969] mentioned that the lobus intermandibularis should not be used in phylogenetic studies, but as it is consistent in only Lucanidae and Pleocomidae, it probably is of phylogenetic importance.

2.3 The mandibulae (Fig 4—7)

Scarabaeoid mandibulae are usually complex as they serve dual functions, those of ingesting and masticating food particles. Additionally, the mandibulae may also be used for fighting between ♂♂, and may show a high degree of sexual dimorphism eg in the Lucanidae. 4 main types of mandibulae are illustrated to explain the basic structure of scarabaeoid mandibulae. As a result of variation in the mandibular structure, the terminology used in literature on mouthpart morphology is not consistent. For descriptive purposes it is convenient to divide the mandibula into 2 main parts, namely a proximal part or basis [Bs] and a distal part or apiculus [Ap].

2.3.1 The proximal part

The proximal part or basis [Bs] (Fig 4a, b, c, 5a, 6a, b, 7a, b) [Bishara 1958: manductorial part] of the mandibula is heavily sclerotized and bears 2 articulations latero-proximally, a dorsal ginglymus [Ggl] (Fig 4—7) and a ventral condylus [Con] [Edmonds 1972]. The ginglymus is also known as the acetabulum or the preartis [Matsuda 1965, MacGillivray 1923]. The ventral articulatory surface or condylus is also referred to as the postartis, condilo vero, ventral condyle or the hypocondyle [MacGillivray 1923] (Fig 4b, c, 5a, b, 6a, 7a, b). The abductor muscle is inserted on the latero-proximal edge of the basis and directly lateral to the condyle. The adductor muscle is inserted dorso-mesally on the proximal edge of the basis, adjacent to the lobi molares [Lo-ml]. A common feature of the basis in the Scarabaeinae is the presence of a receptaculum [Rct] [Edmonds 1972] (Fig 7a, b). This is a thin-walled, cup-shaped sclerite, attached rather loosely to the proximal surface of the basis between the articulations and the Lo-ml, and is thought to contain a mass of glandular tissue [Edmonds 1972]. Its position corresponds with what MacGillivray [1923] named the rectacuta, a very large and distinct sclerite forming the attachment of the mandibula to the caput capsula. It appears to be absent in all other groups.

2.3.2 The lobi molares (Lo-ml)

Mesally the basis bears the lobi molares. The latter (Fig 4a, b, c, 5b, 6a, b, 7a, b) are mesal extensions of the basis and are usually heavily sclerotized. The mola [Mo] vary in structure and shape: (a) In some primitive Scarabaeoidea, eg the Lucanidae, Passalidae and Glaresidae, each Mo bears several teeth and is then referred to as a toothed Lo-ml. (b) In type-2 of lobi molares, the Mo are characterized by parallel ridges (toothed or not) with troughs in between, eg most Geotrupidae, Hybosoridae, some Ochodaeidae, Cetoniinae, Rutelinae and Melolonthinae. (c) Type-3 which occurs in the Scarabaeinae is dorso-ventrally elongated with toothless or ridgeless surfaces. The Lo-ml are asymmetrical in that the left is concave and the right convex. They fit together like a mortar and pestle. Each surface consists of a series of so-called tritors [Hata & Edmonds 1983], that is, microscopic processes capable of trituration of food particles. The dorsal edge of the Lo-ml is finely serrated (Fig 7b). In ventral view a membranous flap-like structure extends over the dorsal part of the right Mo and over the ventral part in the left. It is known as the tapete or tapetum [Tp] [Hata & Edmonds 1983]. The Tp is soft and flexible, with transverse ridges (Fig 7a, b). In many cases, the membranum molare [Me-ml] (Fig 7a, b) is attached to the dorsal surface of the Lo-ml. This membrane is very distinct in the Scarabaeidae and is also present in some of the primitive Scarabaeoidea. The Me-ml probably corresponds to the mandacoria of MacGillivray [1923]. In some Hybosoridae [eg *Cryptogenius miersianus* Westwood 1846], some Ceratocanthidae [eg *Acanthocerodus singularis* Péringuey 1901] and some Rutelinae [eg *Anomala* sp. and *Anoplognathus* sp.], a very distinct cavity occurs in the lobus molaris, laterad of the mola. This is possibly a mycangium [Myc] [Crowson 1981] (Fig 6a). This structure has not been observed in any other scarabaeoid group besides those mentioned above. In certain Lucanidae [eg *Dorcus parallelopipedus* (Linnaeus 1758), *Colophon* sp., *Sinodendron cylindricum* (Linnaeus 1758), and *Nigidius bubalus* Sweder 1787], the basis is characterized by a dorsal tooth known as the corniculum basilare mandibulare [Cor-bs.md.) [Arrow 1951] (Fig 4a).

2.3.3 The apical part

The term apiculus [Ap] (Fig 4—7) is proposed for the distal part of the mandibula. It is also referred to as the incisor lobe and scissorial part [Bishara 1958], scraper [Edmonds 1972], and scissorial area [Prins 1965]. The term scraper can only be applied to the Scarabaeinae and perhaps the Ceratocanthidae in which the dorso-ventrally flattened lobe of the mandibula is thought to function as a food scraper [Edmonds 1972]. The term 'incisor lobe' can only be applied to cases in which the distal part of the mandibula bears several incisors or dentes as in the primitive Scarabaeoidea such as *Glaresis impressicollis* Petrovitz 1965 [Glaresidae], *Polynoncus bullatus* (Curtis 1845) [Trogidae], *Nigidius bubalus* and *Dorcus parallelopipedus* [Lucanidae] (Fig 4a, b, c, 5a) and not as in the Cetoniinae in which the Ap bears no teeth.

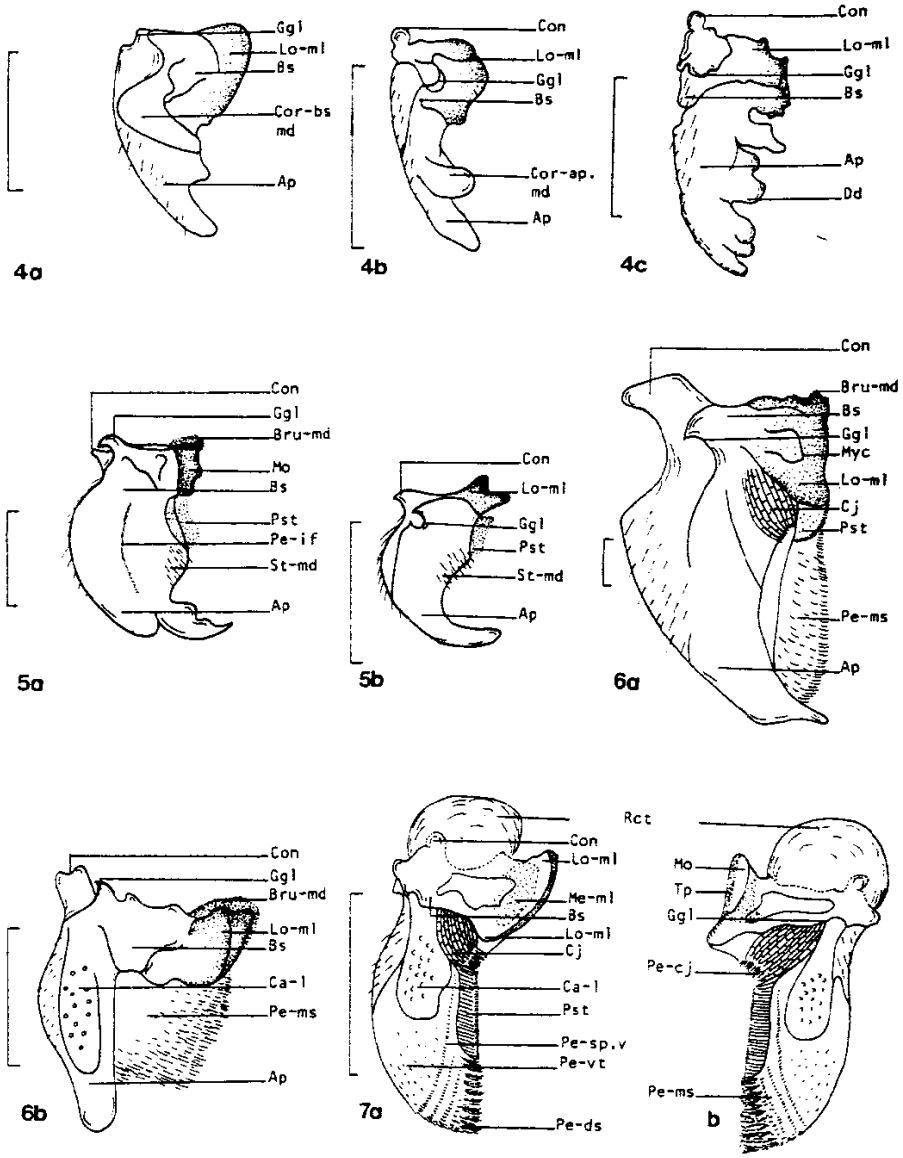

Fig 4—7: Structural variation of the mandibulae in Scarab Beetles [Coleoptera: Scarabaeoidea]. — **4** Right mandibula **a** *Nigidius bubalus* Sweder 1787 (Lucanidae) illustrating the apiculus [Ap], corniculum basilare mandibulare [Cor-bs.md], basis [Bs], ginglymus [Ggl], lobi molares [Lo-ml] (Bar = 1 mm), **b** *Dorcus parallelopipedus* (Linnaeus 1758) (Lucanidae) illustrating condyle [Con], corniculum apicale mandibulare [Cor-ap.md], **c** *Glaresis impressicollis* Pétrovitz 1965 (Glaresidae) illustrating dentes [Dd] (Bar = 1 mm). — **5** Right mandibulae **a** *Meridiobolbus* sp. (Geotrupidae) illustrating bruscum mandibulare [Bru-md], pecten inferior [Pe-if], prostheca [Pst], setula medialis [St-md] (Bar = 1 mm), **b** *Hybosorus illigeri* (Reiche 1853) (Hybosoridae) (Bar = 1 mm). — **6** Right mandibula **a** *Acanthocerodes* sp. illustrating the coniuncta [Cj], mycangium [Myc], pecten medialis [Pe-ms] (Bar = 0.07 mm), **b** *Pachnoda sinuata* (Fabricius 1758) (Cetoniinae) (Bar = 1 mm). — **7** Right and left mandibulae *Heteronites* sp. (Scarabaeinae) illustrating the callum laterale [Ca-l], membranum molare [Me-ml], pecten coniunctivus [Pe-cj], pecten distalis [Pe-ds], pecten medialis [Pe-ms], pecten superior ventralis [Pe-sp.v], pecten ventralis [Pe-vt], receptaculum [Rct], tapetum [Tp] (Bar = 1 mm).

The apical part of the mandibula varies to a large extent among the Scarabaeoidea. In some of the primitive familiae, eg the Lucanidae, Trogidae, Glaresidae, Ochodaeidae, Geotrupidae, and also in the highly derived Dynastinae, Melolonthinae and Rutelinae, the Ap is always strongly sclerotized, apically pointed and terminates in a single or double pointed tooth, with several sharp or blunt dentes occurring more proximally (Fig 4a, c). MacGillivray [1923]) distinguished between proxa- and distadentes, but mentioned that it is often impossible to distinguish between them. It is, therefore, suggested for systematic work that one should rather use the total number of dentes present.

Another type of apiculus occurring in the Scarabaeinae [eg *Heteronites* sp.] (Fig 7a, b) is a dorso-ventrally flattened, flexible blade which is thought to function as a food scraper [Edmonds 1972]. This blade is strengthened laterally by the callum laterale [Ca-l] extending from the basis longitudinally in the direction of the distal part of the blade (Fig 6b, 7a, b). Meso-proximally the Ap bears a soft flexible ventral sclerite between its mesal edge and the lobus molaris, known as the coniuncta [Cj] (Fig 6a, 7a, b) [Edmonds 1972]. The Cj is always present in the Scarabaeinae, all Ceratocanthidae (except *Ceratocanthus* sp.) some Hybosoridae [eg *Anaides fossulatus* Westwood 1841] and some Geotrupidae [eg Geotrupinae, *Frickius variolosus* Germain 1897]. It appears longitudinally ridged, each ridge consisting of a row of thick adhering setae. It was erroneously referred to as the prostheca by MacGillivray [1923]. The mesal edge varies considerably in this type of Ap. Most commonly it mesally bears a comb-like structure, the pecten medialis [Pe-ms], (Fig 7a, b) (probably the prostheca of some authors). Distally the mesal edge is narrowly incised and bears long setae which might be plumose. For the sake of convenience it will be referred to as the pecten distalis [Pe-ds] (Fig 6a, b; 7a, b). In a few genera of Scarabaeinae [eg *Heteronites* sp.] the mesal edge of the coniuncta also bears a comb which will be referred to as the pecten coniunctivus [Pe-cj] (Fig 7a, b).

A further variation on type-2 of Ap is the presence of one or more longitudinal rows of fine setae over most of the ventral aspect, the pecten ventralis [Pe-vt] (Fig 7a, b). Additionally one or more short rows may occur near the ventral apex of the Ap, which will be referred to as the pecten superior ventralis [Pe-sp. v.] (Fig 7a, b).

Type-3 of Ap is characterized by being heavily sclerotized and bearing a pointed apical tooth, but with a distinct membranous mesal edge. The mesal edge bears setae mesally which will be referred to as the pecten medialis [Pe-ms] (Fig 6a, b). The Pe-ms corresponds to the mesal sclerite of Sewak & Khan [1981], and it possibly represents the epipharyngeal bracon of Matsuda [1965], which is present in some Curculionidae. The Pe-ms is apparent in most Geotrupidae, all Hybosoridae and Ceratocanthidae, and some Rutelinae and Cetoniinae (Fig 6a, b).

Type-4 of Ap occurs in the Hybosoridae [*Hybosorous illigeri* Reiche 1853] and Geotrupidae [*Meridiobolbus* sp.] (Fig 5a, b). It is characteristically heavily sclerotized and is mesally curved with a tooth-like apical projection (Fig 5b). Proximally the mesal edge of the Ap bears a membranous lobe which might bear fine setae or spinulae. This lobe most probably corresponds to the prostheca of Matsuda [1965] and will be referred to as such. The prostheca [Pst] (Fig 5a, b, 6a) is situated between the Lo-ml and the Ap, and arises from the mesal margin of the Ap [Matsuda 1965]. The Pst is present, for example, in some Ochodaeidae, Geotrupidae, Hybosoridae, Ceratocanthidae and Melolonthinae (Fig 5a, b, 6a). The Pst has also been incorrectly homologized with the lacinia [Richards & Davies 1977, refer to MacGillivray 1923].

Immediately distad of the Pst a setal brush, the setula medialis [St-md] (Fig 5a, b) as well as a longitudinal row of fine setae similar to that of the pecten ventralis or pecten inferior [Pe-if] (Fig 5a) of MacGillivray [1923], may occur. A mandible horn may be present on the Ap, the so called corniculum apicale mandibulare [Cor-ap. md.] (Fig 4b) as in some Lucanidae [eg *Dorcus parallelopipedus*]. In the Pleocomidae the Ap is greatly reduced and apically pointed.

2.4 The maxillae (Fig 8—12)

The cardo [Cd] (Fig 8, 9, 10, 11, 12) forms the basal part of the maxillae and bears a forked articulatory process, the basal condylus [Snodgrass 1935], for articulation with the hypostoma [Hyp] (Fig 15, 17, 19). The proximal end of the cardo has 3 apodemes for the attachment of

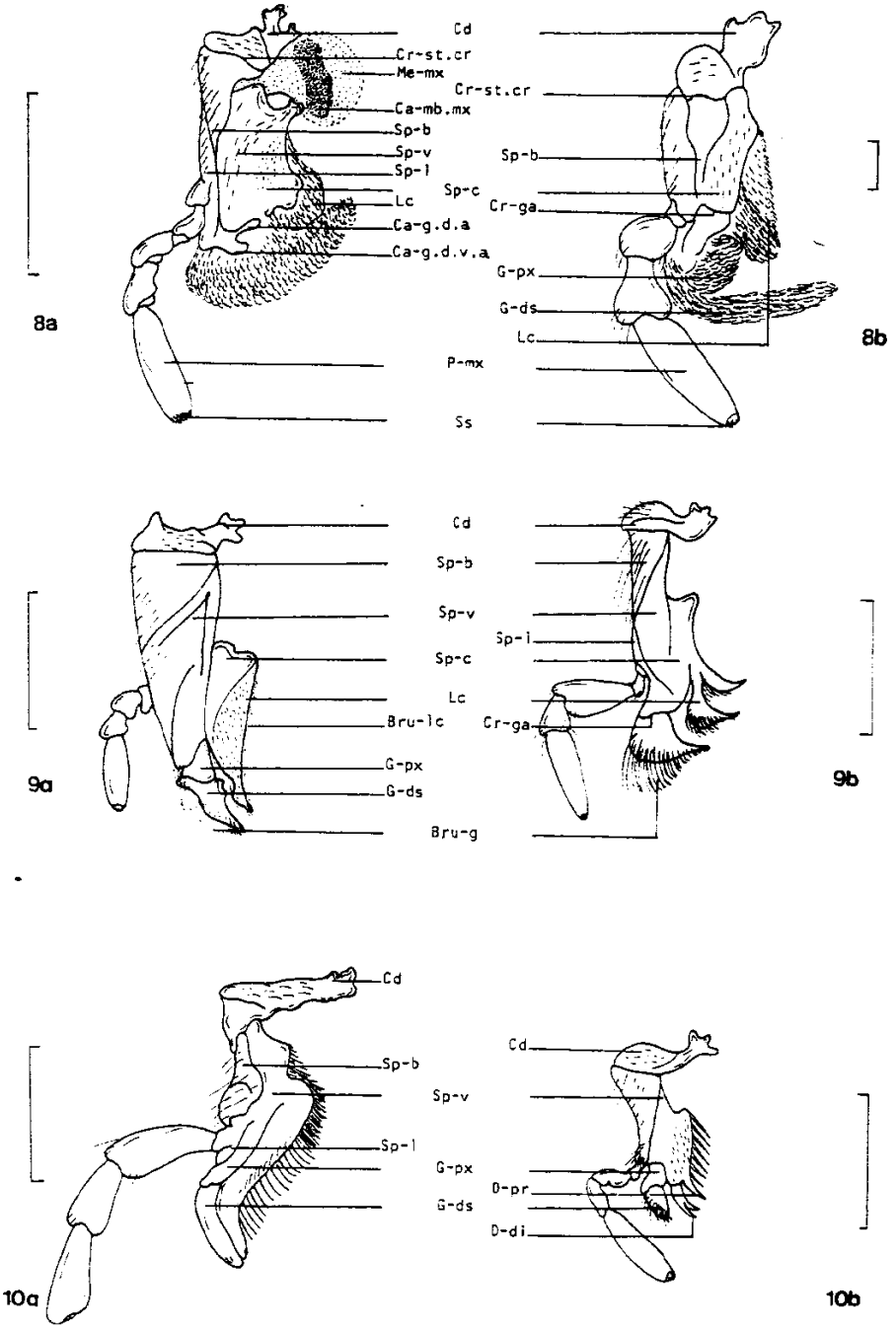

Fig 8—10: Structural variation of the maxillae in Scarab Beetles [Coleoptera: Scarabaeoidea]. — 8 Right maxilla, dorsal view a *Liatongus* sp. illustrating the cardo [Cd], crista stipidalis cardinalis [Cr-st.cr], callum galeare dorsale articulatum [Ca-g.d.a], callum galeare ventrale articulatum [Ca-g.v.a], callum membrani maxillaris [Ca-mb.dmx], galea [Gl], lacinia [Lc], membranum maxillare [Me-mx], palpi maxillares [P-max], sensillum [Ss], stipes basalis [Sp-b], stipes confinis [Sp-c], stipes lateralis [Sp-l], stipes ventralis [Sp-v] (Bar = 1 mm), b *Cloeotus* sp. illustrating crista galearis [Cr-ga], galea distalis [G-ds], galea proximalis [G-px] (Bar = 0.07 mm). — 9 Right maxilla, dorsal view: a *Pachnoda sinuata* (Fabricius 1758) (Cetoniinae) illustrating the bruscum galeare [Bru-g], bruscum laciniosum [Bru-lc] (Bar = 1 mm], b *Meridiobolbus* sp. (Geotrupidae) (Bar = 1 mm). — 10 Right maxilla, dorsal view: a *Prosopocoelus* sp. (Lucanidae) (Bar = 1 mm), b *Omorgus radula* (Erichson 1843) (Trogidae) illustrating dentes distales [D-di], dentes proximales [D-pr] (Bar = 1 mm).

the anterior dorsal muscle, and 2 groups of ventral adductors arising on the hypopharynx. The cardo is separated from the stipes by the crista stipitalis cardinalis [Cr-st.cr.] [Sewak & Khan 1981] (Fig 8a, b). Distally the cardo bears the stipes [Richard & Davies 1977], which is subdivided into the basistipes, ventrostipes and parastipes.

2.4.1 The stipes

(a) The stipes basalis [Sp-b] or proxistipes (Fig 8a, 9a, b, 10a, 11a, b, 12a, b) is also known as an 'enstipes' [MacGillivray 1923], 'eustipes' [Sewak & Khan 1981] or stipital sclerite one of Edmonds' [1972]. Laterally the Sp-b bears several long or short setae. It is often followed distally by a smaller sclerite, the stipes lateralis [Sp-l] (Fig 8a, 9b, 10a, 11b) which is also referred to as the distipes of palpifer by some authors.
(b) The stipes ventralis [Sp-v] (Fig 8a, 9a, b, 10a, b) is a ventro-median sclerite. It is suggested by Edmonds [1972] that scleritum stipitale-2 is the same as the subgalea or inner parastipes.
(c) A third sclerite, the stipes confinis [Sp-c] (Fig 8a, b, 9a, b, 12a, b) or subgalea as it is referred to by some authors, is situated more medially, bearing the galea and lacinia distally. Edmonds [1972] does not distinguish between the ventro- and parastipes, but only mentions scleritum stipitale-2. He also mentions a latero-distal sclerite or scleritum stipitale-3 of the ventral stipes. This scleritum is often hard to distinguish.
In the Lucaninae and Cladognathinae [Lucanidae], the Sp-b bears a partially divided elongate plate-like extension. Similarly, the Sp-v often bears a semicircular plate-like extension as in *Lucanus capriolus* (Linnaeus 1758). The terms callum stipitale basale adjectivum [Ca-st.b.a] and callum stipitale adjectivum ventrale distale [Ca-st.a.v.d] are suggested for these sclerites (Fig 11a]. The calla stipitales adjectiva do not occur in any other familiae of the Scarabaeoidea.
The membranum maxillare [Me-mx] (Fig 8a) is a name given by MacGillivray [1923] to the membrane located between the maxilla and the margin of the caput, attaching the mandibula to the maxilla. It is attached to the mesal margin of the maxilla near the proximal end of the stipes. This membrane bears a chitinized scleritum, which is attached to the rectacuta of the mandibula. No terminology could be traced for this sclerite, thus the term callum membrani maxillaris [Ca-mb.mx] (Fig 8a) is suggested therefore. The degree of development of this sclerite may vary among the Scarabaeoidea. The Ca-mb.mx is well developed in the Scarabaeinae and less developed in some Geotrupidae (Geotrupinae), and appears to be absent in all other scarabaeoid families.
The palpi maxillares [P-mx] are attached to the distal end of the latero-stipes and usually are 4-jointed but sometimes 5-jointed (Fig 8a, b). A sensillium [Ss] is usually present on the apex of the distal joint of the palpi maxillares (Fig 8a, b).

2.4.2 The endites

The endites of the maxilla or meso-distal lobes of the stipes are the galea and the lacinia. The galea is the more distal lobe on the stipes confinis, while the lacinia is the mesal endite of the stipes. As a result of the varied structure of the endites the following types could be distinguished:
(a) The most common form is present in the Scarabaeinae, Lucanidae, Ceratocanthidae, Geotrupinae and Passalidae. The lacinia [Lc] and galea [Gl] (Fig 8a, b, 9a, 12b) are distinct and are situated on the mesal and distal edge of the Sp-c. They consist of soft flexible densely setose lobes (Fig 8a, b). The Gl is separated from the stipes by a distinct crista galearis [Cr-ga] (Fig 8b, 9b). The Gl often consists of 2 distinct parts, the more proximal part, the galea proximalis [Gl-px] and the apical or distal part, the galea distalis [Gl-ds], bearing the galear-brush, eg in *Cloeotus* sp. (Ceratocanthidae) (Fig 8b, 9a, 10a, b). The Gl articulates with the Sp-c by means of 2 sclerotized structures, the callum galeare dorsale articulatum [Ca-g.d.a] and the callum galeare ventrale articulatum [Ca-g.v.a] [Edmonds 1972] (Fig 8a).
(b) The type-2 occurs in the Cetoniinae and most Geotrupidae. The Gl and Lc are distinctly separate structures. They are sclerotized and foot-shaped, with a dense brush of setae, the bruscum galeare [Bru-g]

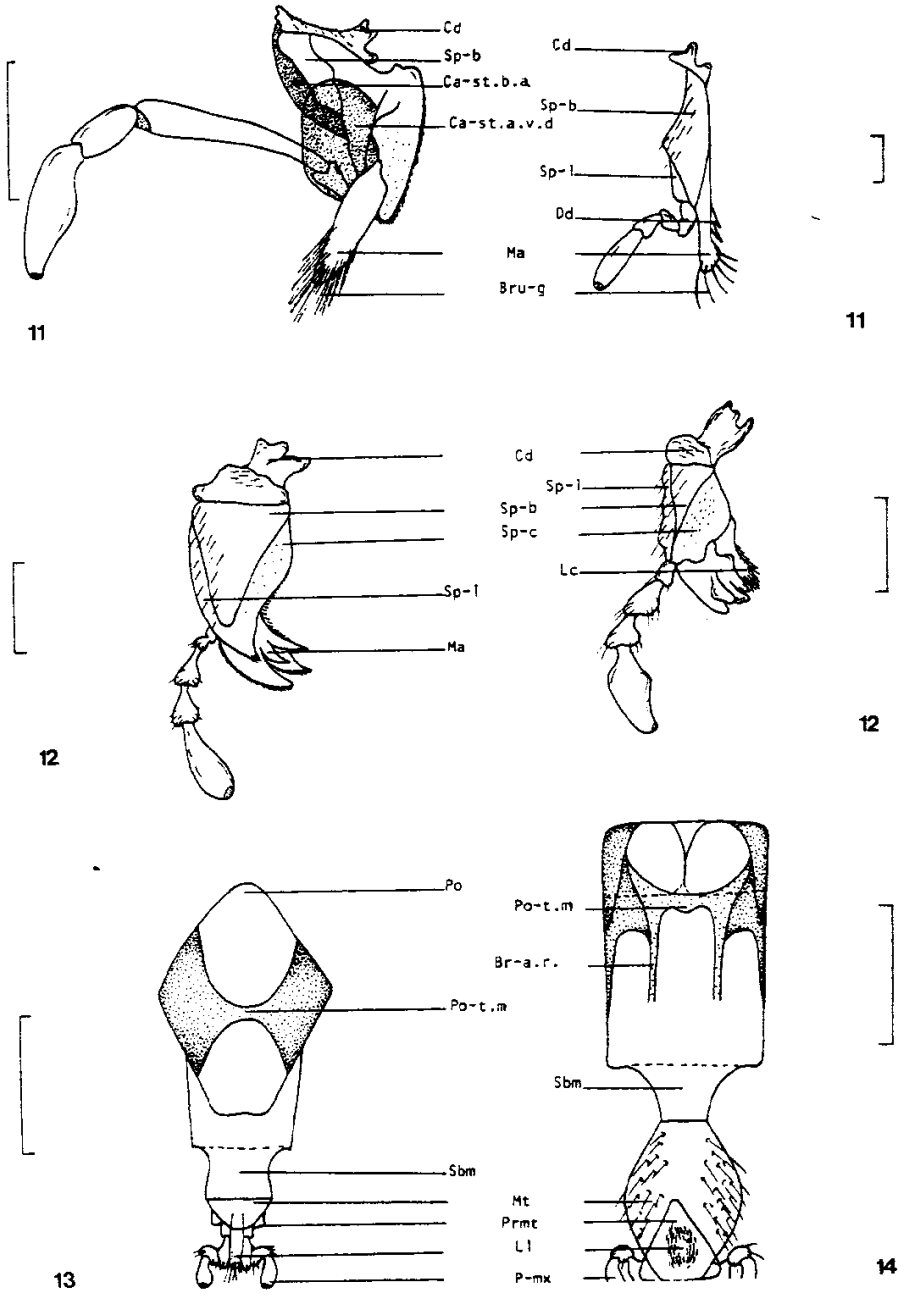

Fig 11, 12: Structural variation of the maxillae in Scarab Beetles [Coleoptera: Scarabaeoidea]. — **11** Right maxilla, dorsal view: **a** *Lucanus* sp. (Lucanidae) illustrating callum stipitale adjectivum ventrale distale [Ca-st.a.v.d], callum stipitale basale adjectivum [Ca-st.b.a], mala [Ma] (Bar = 1 mm), **b** *Glaresis impressicollis* (Glaresidae) (Bar = 1 mm). — **12** Right maxilla, dorsal view: **a** *Adoretus* (Rutelinae) (Bar = 1 mm), **b** *Melolontha* sp. (Melolonthinae) (Bar = 1 mm).

Fig 13, 14: Structural variation of the labium and tentorium in Scarab Beetles [Coleoptera: Scarabaeoidea]. — **13** Labium and tentorium, dorsal view; *Sinodendron cylindricum* (Linnaeus 1758) (Lucanidae) illustrating palpus labialis [P-mx], ligula [Ll], mentum [Mt], pons tentorius medianus [Po-t.m], postocciput [Po], praementum [Prmt], submentum [Sbm] (Bar = 1 mm). — **14** Labium and tentorium, dorsal view; *Macrodactilus* sp. (Melolonthinae) illustrating bracchia anterior rudimentum tentorius [Br-a.r.t] (Bar = 1 mm).

(Fig 9a, b, 11a, b) on the distal galeal edge. The Bru-g is also referred to as the galearastra or galeafimbrium by some authors. The Gl may be 2-jointed (Fig 9a, 10a) in Cetoniinae [eg *Pachnoda sinuata* (Fabricius 1758)]. The Gl may be fused apically and the Lc fused mesally to the Sp-c.
(c) Type-3 of maxilla is present in some of the primitive familiae of the Scarabaeoidea [eg Trogidae and some Lucanidae] (Fig 10a, b). The Gl usually consists of 2 parts, while the Lc which is also named the inner or inferior lobe, mesal lobe, lacinoidea or lacinella, is totally fused mesally to the Sp-c and bears a bruscum laciniosum [Bru-lc] mesally which consists of very stiff, lightly sclerotized setae. The Bru-lc is synonymous with the laciniarastra or laciniafimbrium of MacGillivray [1923]. The Lc may bear 3 teeth distally (Fig 10b), the dentes distales [D-di] [MacGillivray 1923] or a more proximal tooth the hamadens or dentes proximales [D-pr] (Fig 10b) may be present; the Lc is then referred to as armed.
(d) In some Scarabaeoidea, the galea and lacinia are fused to form a single lobe which is called the mala [Ma] [eg some Melolonthinae and Lucaninae] (Fig 11a, b). The Ma may bear 4—6 strong, distal teeth. A reduced Lc may be present in the form of a small, oval lobe with setae distally in Melolonthinae [eg *Melolontha* sp.], or a hooked tooth-like projection (Fig 11b). In some primitive Scarabaedea [eg Glaresidae and most Lucanidae], the maxillae are characterized by a Ma with a Bru-g consisting of long fine setae (Fig 11a) or long stiff bristles (Fig 11b).

2.5 The labium (Fig 13—20)

The labium is considered to comprise the structures distad of the gula, and consists of a submentum, mentum and praementum.

2.5.1 The submentum

The submentum [Sbm] is the relatively small, strongly sclerotized transverse proximal part of the postmentum which is situated immediately anterior of the gula. The submentum is either fused to the gula (Fig 14, 16, 17, 18) or separated from the gula by the fimbria gularis [Fi-gl] (Fig 15, 19). The hypostoma [Hyp] may be antero-laterally fused to the submentum (Fig 17) or may be separated from the submentum (Fig 15, 19). The submentum sometimes has anterior extensions that overhang the mentum ventrally (Fig 18).

2.5.2 The mentum

The mentum [Mt] forms the strongly sclerotized large distal part of the postmentum which is usually immovable (though in some Geotrupidae and Melolonthinae it is movable) and is always separated from the submentum by a sulcus (Fig 13—18). The apical margin of the Mt may vary considerably, eg: (a) It may be rounded anteriorly in Ochodaeidae [eg *Ochodaeus congoensis* Benderitter 1913] (Fig 18). (b) It may have a straight, transverse anterior edge in Lucanidae [eg in *Lucanus cervus* (Linnaeus 1758)] (Fig 15). (c) The anterior edge of the Mt may be mesally indented, appearing bilobed in Scarabaeinae [eg in *Sisyphus* sp.] (Fig 16, 17). This is the most common type in the Scarabaeoidea. The shape of the Mt has not been used in phylogenetic work but may be of importance at generic level. The Mt bears the praementum [Prmt] distally (Fig 13, 14, 15, 18, 19, 20).

2.5.3 The praementum

3 different types of praementum can be distinguished in the Scarabaeoidea: (a) The caraboid type: The Prmt is an externally visible structure. It shows remarkable similarities to that of the Carabidae, for example in the Lucanidae [eg ♀♀ of *Prosopocoelus* sp.] (Fig 19). (b) The Prmt is partly external with the anterior part folded backwards to form the anterior floor of the pre-oral cavity. In this case, it is usually evenly sclerotized, eg in some Melolonthinae (Fig 14). (c) The Prmt is situated completely within the anterior part of the pre-oral cavity. It is usually weakly sclerotized or membranous, covered with setae

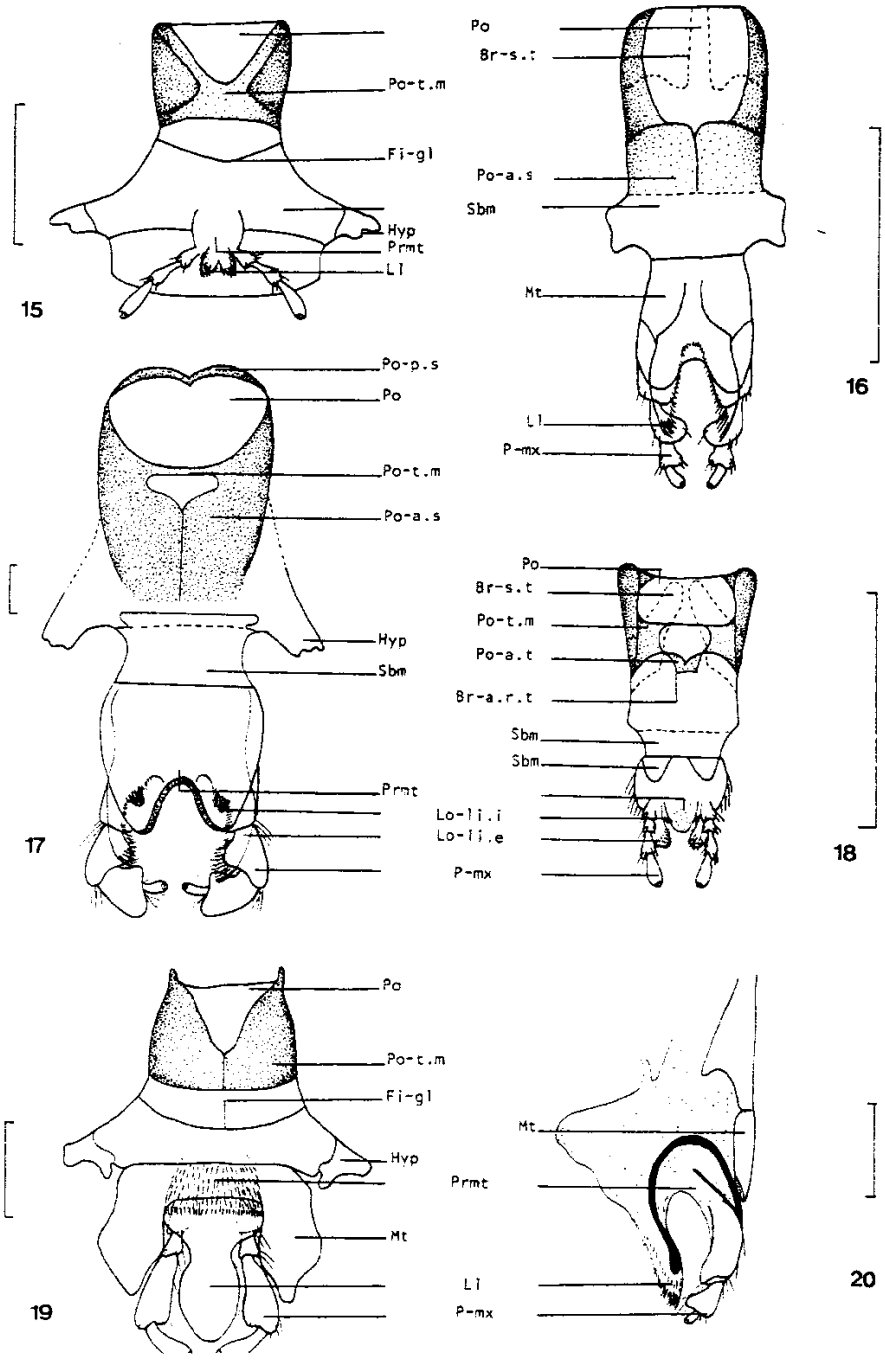

Fig 15—20: Structural variation of the labium and tentorium in Scarab Beetles [Coleoptera: Scarabaeoidea]. — **15** Labium and tentorium, dorsal view; *Lucanus cervus* (Linnaeus 1758) (Lucanidae) illustrating fimbria gularis [Fi-gl], hypostoma [Hyp] (Bar = 1 mm). — **16** Labium and tentorium, dorsal view; *Sisyphus* sp. (Scarabaeinae) illustrating bracchia succedanea tentoria [Br-s.t], pons anterior succedaneus [Po-a.s] (Bar = 1 mm). — **17** Labium and tentorium, dorsal view; *Pachylomerus* sp. (Scarabaeinae) illustrating lobi ligulares exteriores [Lo-li.e], lobi ligulares interiores [Lo-li.i], pons posterior succedaneus [Po-p.s.] (Bar = 1 mm). — **18** Labium and tentorium, dorsal view; *Ochodaeus congoensis* Benderitter 1913 (Ochodaeidae) illustrating (Bar = 1 mm). — **19** Labium and tentorium, dorsal view; *Prosopocoelus* sp. (♀) (Lucanidae) (Bar = 1 mm). — **20** Scarabaeinae labium, right lateral view (Not to scale).

and fused to the hypopharynx eg in Scarabaeinae and most Geotrupidae (Fig 17, 18, 20). In some Scarabaeinae it is sclerotized laterally but membranous mesally.

2.5.4 The appendages of the praementum

The Prmt always bears the palpi maxillares [P-mx] laterally, which are usually 3-jointed (Fig 14, 15, 20) and covered with setae. In some Scarabaeoidea, however, the P-mx consist of only 1 joint as in the Lucanidae [eg ♀♀ of *Odontolabis bellicosus* (Castelnau 1837)] or 2 joints as in the Passalidae [eg *Odontotaenius disjunctus* (Illiger 1800) and *Didimus sansibaricus* Harold 1880], or even 4 joints as in Scarabaeinae [eg *Sisyphus* sp. and *Pachylomerus* sp.] and in the Ochodaeidae [eg *Ochodaeus congoensis*] (Fig 13, 16, 18, 19). The shape of the individual joints vary from long and thin to thick, short and rounded.
In some genera, the Prmt bears hairy lobes distally. These consist of an outer pair, the paraglossae [MacGillivray 1923, Snodgrass 1935], and an inner pair, the glossae. In many cases, some of these lobes are absent, and consequently it becomes impossible to determine what the remaining lobes are. For that reason it is proposed that they should be called lobi ligulares [Lo-li]. The glossae and paraglossae would then respectively be known as the lobi ligulares interiores [Lo-li.i] and the lobi ligulares exteriores [Lo-li.e] (Fig 17, 18). Thus, the Lo-li may vary in number from 1—4 or they may be completely absent. The ligula may be single-lobed [eg *Prosopocoelus* sp.; MacGillivray 1923: alaglossa] (Fig 19), bilobed (1 pair of ligular lobes or duplaglossa) eg most Scarabaeinae (Fig 16, 20), or quadrilobed (or totaglossa — Lo-li.i and Lo-li.e present) eg most Geotrupidae and Ochodaeidae (Fig 17, 18), or completely absent eg in the Pleocomidae.

2.6 The gula

The postocciput [Po] or so-called 'gula' is a large ventral sclerite of the caput, situated between the lengthened posterior tentorial pits or 'gular sutures' on the ventral surface of the head capsule. The postocciput is fused anteriorly to the submentum of the labium at the fimbria gularis (Fig 15, 19). The shape of the gula is not consistant within familiae or suprafamiliae and thus is of no phylogenetic significance [Evans 1965].

2.7 The tentorium

The tentorium consists of a rather intricately shaped pons tentorius arising from the lengthened posterior tentorial pits and forming a "tent-like" structure on the floor of the head capsule. Unlike a similar condition found in termite soldiers, the bridge may be 'perforated' to varying degrees, resulting in the formation of 'secondary bridges'. 4 different types of tentoria are in existance.

2.7.1 An invaginated tentorium

In the Scarabaeoidea, the "primitive" type of tentorial bridge has invaginations in its anterior and posterior margins. A single invagination in the posterior margin occurs eg in the ♀♀ of *Prosopocoelus* sp. (Fig 19), whereas 2 invaginations occur in *Sinodendron cylindricum* and *Lucanus cervus* (Lucanidae) (Fig 13, 15).

2.7.2 A foraminated tentorium

In type (a) 2 foramina occur in the tentorial bridge, the posterior one being larger than the anterior one. In this way '3' secondary bridges are formed viz a pons posterior succedaneus [Po-p.s] (Fig 17, 21a, c),

pons tentorius medianus [Po-t.m] and a pons anterior succedaneus [Po-a.s] (the corporotentorium of Stickney (1923)) eg *Anachalcos convexus* Boheman 1857 (Fig 21a, b, c). — In type (b) only one foramen occurs, an anterior foramen. Consequently only a pons tentorius medianus [Po-t.m] and a pons anterior succedaneus [Po-a.s] (corporotentorium) occurs (Fig 18). Various modifications of tentoria are present, though it seems that the single-foramen-type (Fig 18) which is present in some Trogidae, Ochodaeidae, Hybosoridae, Geotrupidae, and Scarabaeidae, and with slight variation thereon in the Cetoniinae, some Melolonthinae, Rutelinae and Dynastinae, is the most common form.

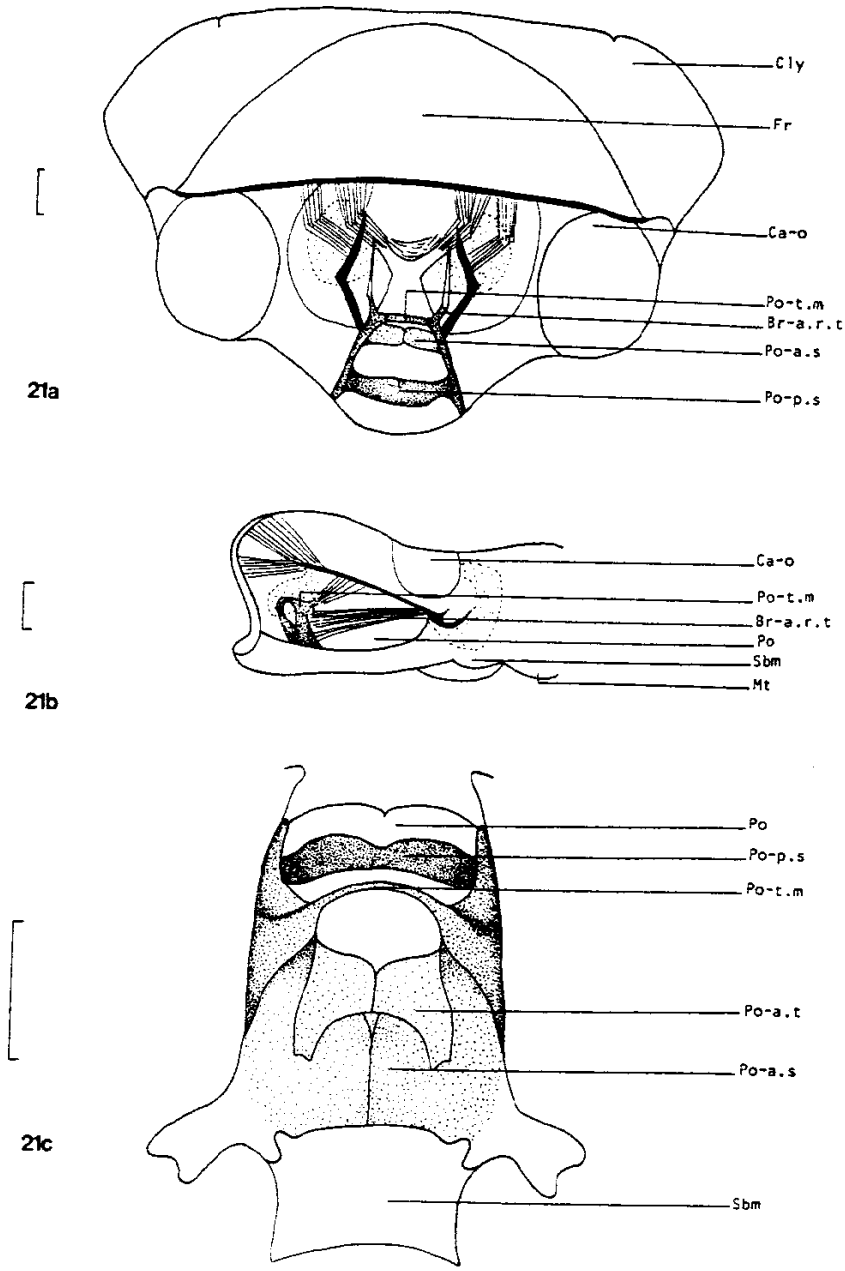

Fig 21: Structural variation of the tentorium in Scarab Beetles [Coleoptera: Scarabaeoidea]. — *Anachalcos convexus* Boheman 1857 (Scarabaeinae): **a** Posterior view of the tentorium in the headcapsule, with the vertex removed illustrating pons anterior succedaneus [Po-a.s], bracchia anterior rudimentum tentorius [Br-a.r.t], cavus ocularis [Ca-o], clypeus [Cly], frons [Fr], pons tentorius medianus [Po-t.m], pons posterior succedaneus [Po-p.s], postocciput [Po], **b** Lateral view of the tentorium in the headcapsule, **c** Dorsal view of the tentorium, when removed from the headcapsule (Bar = 1 mm).

2.7.3 Additional tentorial structures

(a) Bracchia succedanea tentoria [Br-s.t]

Some species, eg *Pleocoma octopagina* Robertson 1970 [Pleocomidae]; *Sarophorus* sp. [Scarabaeinae]; *Ochodaeus congoensis* [Ochodaeidae] and most Melolonthinae have bracchia succedanea tentoria (Fig 16, 18) arising from the posterior tentorial pits and extending meso-ventrally, almost meeting medially on the inner surface of the gula. Br-s.t are very distinct in *Ochodaeus congoensis* but reduced in most other Ochodaeidae. The morphological appearance of this character varies between familiae and may be phylogenetically significant.

(b) Bracchia anterior rudimentum tentorius [Br-a.r.t]

In this type the anterior secondary bridge bears 2 short arms antero-distally for a short distance and their bases may be fused (Fig 21a, b), eg in the Scarabaeinae. The pons posterior succedaneus usually lies at a lower level than the Po-t.m and pons anterior succedaneus. However, in some Melolonthinae [eg *Macrodactilus* sp.] (Fig 14) these Br-a.r.t arise from the Po-t.m, as the pons anterior tentorius and the pons posterior succedaneus are absent.

3 Discussion

Mouthparts may be subjected to various modifications or adaptations due to speciation and niche specialization during evolution. A common feature is the reduction or the elimination (for example in palp joints), and occasionally the reappearance of characters during evolution, eg an armed lacinia. To determine the adaptive significance of these characters, the possibility of convergence or parallelism should be taken into account. According to Blackwelder [1967], convergent resemblance is shared similarities in 2 phylogenetic lines, not due to common gene heritage, but to adaptation in one or both lines. The structure of the galea of the Lucanidae is similar to those of the Scarabaeinae and Ceratocanthidae. In the Lucanidae, a setose galea is not an adaptation for feeding, and its presence probably is the result of convergence. Thus, in the Lucanidae, a setose galea does not necessarily indicate close relationship with the Scarabaeidae and Ceratocanthidae.

Parallelism is the development of similar features based on common ancestry, which is not determined by the environment: Some mouthpart characters, eg the pecten medialis on the mandibula, are typical for and differently expressed in each group. The presence of a pecten medialis is an adaptation for juicy food substances and is present in the Cetoniinae, Ceratocanthidae, some Geotrupidae, some Hybosoridae and the Scarabaeinae. A character suitable for practical purposes is, and we quote from Blackwelder [1967]: "... any feature whose expression can be measured, counted or otherwise assessed ...". The modification of the pecten medialis between familiae (Fig 6a, b) is the result of environmental pressures, as it is an adaptation present in respectively dung-, fungus- and fruitfeeding beetles. Blackwelder [1967] mentioned that environmental resemblance may become fixed in genes by selection. The pecten medialis occurs constantly within the already named familiae, and it may therefore be concluded that these characters are examples of parallelism and are phylogenetically significant. MP-S of Scarabaeoidea are adapted for particular feeding habits such as wood, fungi, different types of dung, plantroots, leaves, fermenting plant matter and juicy substances of plants and fruits. Adult foliage-feeding and floricolous beetles are associated with mandibulae of which the basal molar part has coarsely ridged surfaces and a distal part which is often toothed, eg Melolonthinae and Rutelinae. The galea is usually also toothed or armed, while the lacinia usually is reduced to a small lobe.

Adults feeding on humus and organic matter have sharp apically pointed mandibulae with finely ridged mola, and the galea and lacinia are apically pointed, eg in some Geotrupidae.
The mandibulae of fungusfeeding adults, eg Ceratocanthidae and Orphninae, are apically pointed and bear a mesal brush, while the lobus molaris bears a characteristic mycangium, and the lacinia and galea consist of setose lobes.
The mandibulae of carrionfeeders are often sickle-shaped and acute, with ridged mola, while the lacinia bears several unci, eg in the Trogidae.
The mola of adult dungfeeding beetles usually consist of very fine tritors, while the apical part is membranous and the galea and lacinia consist of thick setose lobes eg in the Scarabaeinae and some Geotrupinae.
The mandibulae of some pollen- and fruitfeeders eg the Cetoniinae, are characterized by the presence of a well developed pecten medialis, a ridged mola and an armed lacinia. It is obvious that these structures are very adaptive and should be used with careful consideration. Crowson [1967] mentioned that structures with an unknown function such as the prostheca are of major importance in studies on relationship.
Characters on the epipharynx seem to be significant in taxonomic work. The distribution of setae, the number and development of the tormae and the shape of the anterior edge of the epipharynx are important characters at generic level, especially in the Geotrupidae, Ochodaeidae, Ceratocanthidae and Scarabaeidae. On subfamily level, fusion of the clypeus and the epipharynx (labrum) appears to be more important.
As might be expected, the mandibulae are the most adaptive MP-S. They are usually typical of a family eg in the Lucanidae, but some features may also be present in other familiae, that do not necessarily indicate relationship.
Maxillary structure varies to some extent between groups, but seems to be important on generic and family level eg in the Trogidae, Ochodaeidae, Dynastinae, Cetoniinae and Geotrupidae.
Labial characters are not generally used in taxonomic work. The development of the mentum and praementum in relation to ligular development is important on subfamily level, as well as the number of labial palp joints. Labial characters are significant in the Lucanidae, Geotrupidae, Ochodaeidae, Melolonthinae and Cetoniinae.
The tentorium of 'primitive' Scarabaeoidea shows much less variation within the different groups, in comparison with the higher scarabs (Scarabaeidae). Secondary structures of the tentorium are present in very few primitive Scarabaeoidea and seem to be significant, while they are probably not so important among the Scarabaeidae. The structures of the tentorium prove to be significant in the Lucanidae, Ochodaeidae, Geotrupidae and Ceratocanthidae.
The epipharynx, maxillae and labium seem to be the most reliable characters for phylogenetic studies. The labium and tentorium or "gular area" are constant and specific within most groups and appear to be potentially useful characters.

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