The Mandible of Silverfish (Insecta: Zygentoma) and Mayflies (Ephemeroptera): Its Morphology and Phylogenetic Significance[1]

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Abstract. The mandibles of several mayfly larvae have been investigated in order to reconstruct the groundplan of the mandibular muscles and of the mandibular articulation of Ephemeroptera. The results indicate the presence of three points of mandibular attachment to the cranium in the groundplan of Ephemeroptera. The posterior point of articulation in mayflies corresponds to the posterior (primary) mandibular joint of other Dicondylia. The remaining two points of attachment together form an anterior articulation complex made up of an anterolateral and a postero-medial part. These attachment points of the mayfly mandible are compared with the condition in silverfish. It is shown that in Zygentoma there is a similar anterior articulation complex present. This is interpreted as a groundplan character of Dicondylia. The posteromedial part of this complex in both Zygentoma and Ephemeroptera probably is the homologue of the anterior (secondary) mandibular joint of the remaining Dicondylia. The anterolateral part is secondarily modified in mayflies, where it forms a device to withstand the chewing pressure during adduction of the mandible. The primary mandibular articulation in both mayflies and silverfish is elongated and located dorsally to the secondary one, which results in an oblique axis of mandibular movement. In contrast to this plesiomorphic arrangement, the remaining Dicondylia have developed an almost horizontal axis of mandibular movement as well as a tight ball-and-socket type of mandibular articulation. As a consequence of the tightened mandibular articulation, the anterior articulation complex has been simplified in these groups, and a subgenal ridge is developed. The mandibular musculature of Ephemeroptera and Zygentoma is plesiomorphic in retaining several mandibulo-tentorial muscles as well as two cranial abductor muscles. In all other pterygote lineages the dorsal tentorial muscles are lost, and only a single cranial abductor muscle is present. The mandibular muscles of the silverfish *Tricholepidion gertschi* show additional plesiomorphies, namely the lack of a mandibulo-hypopharyngeal muscle and the retention of a ligamentous transverse tendon. The groundplan of the dicondyle insect mandible is reconstructed, and the phylogenetic significance of this character complex is discussed. The mandibles of both Zygentoma and Ephemeroptera do not show any traces of segmentation, thus the assumption of a telognathic insect mandible thereby cannot be supported. The distribution of all investigated mandibular characters support a sistergroup relationship between Ephemeroptera and the remaining pterygote orders, the Metapterygota.

Key words. Dicondylia, phylogeny, phylogenetic systematics.

1. INTRODUCTION

The subimagines and imagines of mayflies do not continue feeding, and their mandibles as well as their other mouthparts are highly atrophied in these life stages. However, the aquatic larvae still bear well-developed mandibles. Several authors have investigated the head morphology of mayfly larvae, but came to quite differ-

[1] This paper is dedicated to Professor Dr. Karl-Ernst Lauterbach (Bielefeld, Germany).

ent results and conclusions regarding the mandibular articulation.

SNODGRASS (1950, 1951) recognized just one mandibular joint in the mayfly mandible, whereas other workers notified two mandibular articulations (BÖRNER 1909; KUKALOVÁ-PECK 1985, 1991; SCHÖNMANN 1981) in different species. Some authors even stated three separate articulations (ARENS 1989; BROWN 1961; STRENGER 1953, 1970, 1975, 1977, 1979).

Similarly, descriptions of silverfish mandibles vary considerably. While all authors agree on the presence of

an anterior articulation, SNODGRASS (1950, 1952, 1960) repeatedly referred to the anterior condyle as being located at the gena, whereas CHAUDONNERET (1950) observed an anterior condyle on the laterodorsal angle of the clypeus.

In recent publications some authors also claim the presence of a (at least vestigial) segmentation of the mandible in both Zygentoma (KRAUS 1998; KUKALOVÁ-PECK 1998) and Ephemeroptera (KUKALOVÁ-PECK 1998). Interpreting the mandible as composed of the entire telopodite, they revived the dispute between MANTON's (1964) idea of a 'whole-limb jaw' in the groundplan of Tracheata and the concept of a gnathobasic mandible in these groups (LAUTERBACH 1972a).

These obvious inconsistencies in both description and interpretation of the mandible in mayflies and silverfish led to the present study. It is aimed to reconstruct the condition of the mandible in the respective groundplans, and to present new arguments for the still controversially discussed early phylogenetic branching events of the Dicondylia.

2. MATERIALS AND METHODS

2.1. Specimens examined

Zygentoma

• *Tricholepidion gertschi* Wygodzinsky, 1961 (Lepidothrichidae)

This North American relic silverfish is known to possess some unique plesiomorphic traits not only within Zygentoma (WYGODZINSKY 1961), but also regarding the groundplan of Dicondylia (KRISTENSEN 1998). For instance it is the sole known recent species of all dicondyle insects that has retained the mandibular transverse ligament, otherwise well known from Archaeognaths and entognath insect orders (BOUDRE-AUX 1979a). However, its entire mandibular musculature as well as its mandibular articulations have not previously been subject to a close examination.

Ephemeroptera

• *Oniscigaster wakefieldi* McLachlan, 1873 (Oniscigastridae)

This species represents one of the two New Zealand representatives of a mayfly family with amphinotic distribution. Its imago is considered to resemble the mayfly groundplan in many aspects (MCLACHLAN 1873; PENNIKET 1962; KLUGE et al. 1995), so it seemed worthwhile to have also a closer look at its larva. The larva feeds mainly on detritus (MCLEAN 1970).

• *Nesameletus* sp. (Nesameletidae)

Nesameletidae is another mayfly taxon with amphinotic distribution. Its phylogenetic relationship within Ephemeroptera is up to now not satisfactory resolved (KLUGE et al. 1995).

The larvae of the New Zealand genus *Nesameletus* mainly feed on diatoms (own observation).

• *Ameletopsis perscitus* Eaton, 1899 (Ameletopsidae)

The New Zealand species of the amphinotic distributed Ameletopsidae belongs to one of the very few mayfly families with larvae with exclusively carnivorous habits. Ameletopsids are known to engulf other water insects (CAMPBELL 1985). The gut contents of the larger specimens used for this study consisted mainly larvae of *Nesameletus* and caddisfly larvae.

A. perscitus was chosen for this study to observe the impact of a totally different nutrition on the anatomy of the mandible.

2.2. Additionally used material for comparisons

Zygentoma:

Nicoletiidae:	*Cubacubana* spec.
Lepismatidae:	*Lepisma saccharina Linné,* 1758
	Ctenolepisma spec.

Ephemeroptera:

Ameletidae:	*Ameletus inopinatus* Eaton, 1887
	Metrehtus balcanicus (Ulmer, 1920)
Ametropodidae:	*Ametropus fragilis* Albarda, 1878
Baetidae:	*Baetis rhodani* (Pictet, 1843)
	Baetis vernus Curtis, 1834
	Centroptilum luteolum (Müller, 1776)
Coloburiscidae:	*Coloburiscus humeralis* (Walker, 1853)
Ephemerellidae:	*Serratella ignita* (Poda, 1761)
	Torleya major (Klapalek, 1905)
Heptageniidae:	*Ecdyonurus venosus* (Fabricius, 1775)
Leptophlebiidae:	*Habroleptoides confusa* Sartori & Jacob, 1986
Metretopodidae:	*Metretopus borealis* (Eaton, 1901)
Oligoneuriidae:	*Oligoneuriella rhenana* (Imhoff, 1852)
Oniscigastridae:	*Oniscigaster distans* Eaton, 1886
Polymitarcyidae:	*Ephoron virgo* (Olivier, 1791)
Potamanthidae:	*Potamanthus luteus* (Linne, 1767)
Rallidentidae:	*Rallidens mcfarlanei* Penniket, 1966
Siphlaenigmatidae:	*Siphlaenigma janae* Penniket, 1962
Siphlonuridae:	*Siphlonurus croaticus* Ulmer, 1920
	Siphlonurus lacustris (Eaton, 1870)

Odonata:

Aeshnidae:	*Aeshna cyanea* Müller, 1764
Calopterygidae:	*Calopteryx virgo* Linne, 1758

Plecoptera:

Taeniopterygidae:	*Taeniopteryx* spec.

Ensifera:

Gryllidae:	*Acheta domesticus* Linné, 1767

2.3. Methods

Fixation. The material used was preferably fixed by a mixture of 95% ethanol, 35% formaldehyde, and acetic acid (66:33:10). After 24 hours or longer it was transferred to 80% ethanol. Some species *(Ametropus, Metretopus)* were fixed in ethanol only.

Manual dissection. Larvae were dissected under 80% ethanol on a layer of paraffin in a Petri dish. To observe muscles, they were stained with basic fuchsin. To observe cuticular structures, specimens were kept in 10% potassium hydroxide under room temperature for several days, until the soft tissues dissolved. Then the cuticle was stained with Chlorazol Black. To duplicate the mandible movements, the mandible as well as its muscles were manipulated by a Dumont forceps.

Light microscopy. Specimens used for microscopic sectioning were dehydrated in ethanol and then stored three times at 50°C in propan-2-ol for 24 hours each time. Then the material was gradually transferred to paraffin at 50 °C and finally transferred to Paraplast Plus™ at 60 °C. There the specimens were kept under vacuum conditions for 24 hours to optimize their penetration. Finally the material was embedded in Paraplast Plus™. Sections of 5-7 µm thickness were obtained with a rotation microtome. Sections were stained with Delafield's hematoxylin, counter-stained with erythrosin, and observed with a Zeiss-Axioplan microscope. Photographs were taken with a Zeiss-MC 100 camera.

Scanning electron microscopy (SEM). Specimens were dehydrated through a stepwise immersion in ethanol and acetone, and then dried by critical point drying. The mounted material was coated with a 20 nm Au/Pd layer and examined with a Cambridge Stereoscan 250 MK 2 scanning electron microscope at 10 kV.

2.4. Abbreviations

Ml	cranial adductor muscle of mandible (M. cranio-mandibularis internus)
M2	anterior cranial abductor muscle of mandible (M. cranio-mandibularis externus anterior)
M3	posterior cranial abductor muscle of mandible (M. cranio-mandibularis externus posterior)
M4	dorsolateral tentorial muscle (M. tentorio-mandibularis externus dorsalis)
M5	ventrolateral tentorial muscle (M. tentorio-mandibularis externus ventralis)
M6	dorsomedial tentorial muscle (M. tentorio-mandibularis internus dorsalis)
M7	ventromedial tentorial muscle (M. tentorio-mandibularis internus ventralis)
M8	hypopharyngeal protractor muscle (M. mandibulo-hypopharyngealis)
M9	adductor muscle of labrum (M. frontolabralis)
M10	abductor muscle of labrum (M. frontoepipharyngealis)
Ml 1	dilatator muscle of cibarium (M. clypeopalatalis)
M12	mouth retractor muscle (Retractor angulorum oris)
M13	dorsal dilatator muscles of pharynx (Dilatator pharyngis)
M14	circular pharynx muscle (M. anularis stomodaei)
M15	longitudinal pharynx muscles (M. longitudinalis stomodaei)
M16	dorsal suspensor muscle of stomodaeum (M. verticopharyngealis)
M17	lateral dilatator muscle of pharynx (Dilatator pharyngis lateralis primus)
M18	suspensor muscle of tentorium
M19	antennal muscles (Mm. antennarum)
M20	tentorial adductor muscle of cardo (M. tentoriocardinalis)
M21	tentorial adductor muscle of stipes (M. tentoriostipitalis)
M22	cranial adductor muscle of galeolacinia (M. craniolacinialis)
M23	tentorial connective muscle
aac	anterior articulation complex
ab	antennal base
ac	anterior condylus
aclp	anteclypeus
ant	antenna
alp	anterolateral part of anterior articulation complex
ao	aorta
ap	apodeme
ata	anterior tentorial arm
atp	anterior tentorial pit
br	supraoesophageal ganglion
cc	corpora cardiaca
clp	clypeus
conn	circumoesophaeal connective
ct	cuticula
cte	corpotentorium
dta	dorsal tentorial arm
epd	epidermis
eph	epipharynx
fb	fat body
fr	frons
ge	gena
ge$_i$	inflected part of gena
hyp	hypopharynx
inc	incisivi
lb	labium
lbr	labrum
le	lateral compound eye
If	lateral fold
lig	transverse ligament
lo	lobus opticus
md	mandible
mg	mandibular groove
mil	mandibular lateral ledge
mmo	morphological mouth opening
mn	mandibular notch
mo	mola
mx	maxilla
Nant	antennal nerve
Nlbr	labral nerve
oc	occiput
ol	lateral ocellus
om	median ocellus
pa	posterior articulation
pc	posterior condylus
pclp	postclypeus
pg	postgena

plb	palpus labialis	ptp	posterior tentorial pit
pmx	palpus maxillaris	sc	scapus
poc	postocciput	scr	sclerotised cranial ridge of alp
pocph	postoccipital phragma	sg	subgena
pocrd	postoccipital ridge	sgrd	subgenal ridge
pp	processus paratentorialis of anterior articulation com-plex	smr	sclerotised mandibular ridge of pmp
		stom	stomodaeum
pmp	posteromedial part of anterior articulation complex	tp	tentorial plate
pro	prostheca	tr	trachea
pta	posterior tentorial arm	vx	vertex
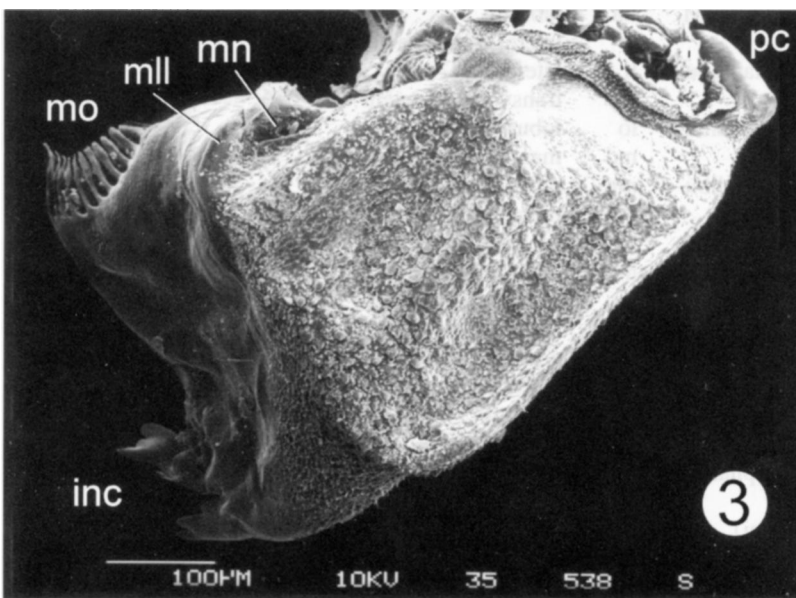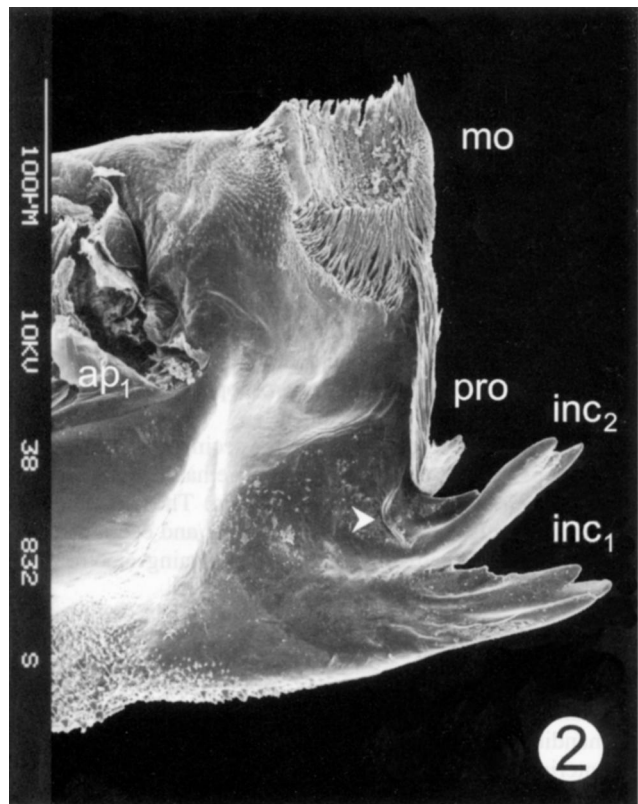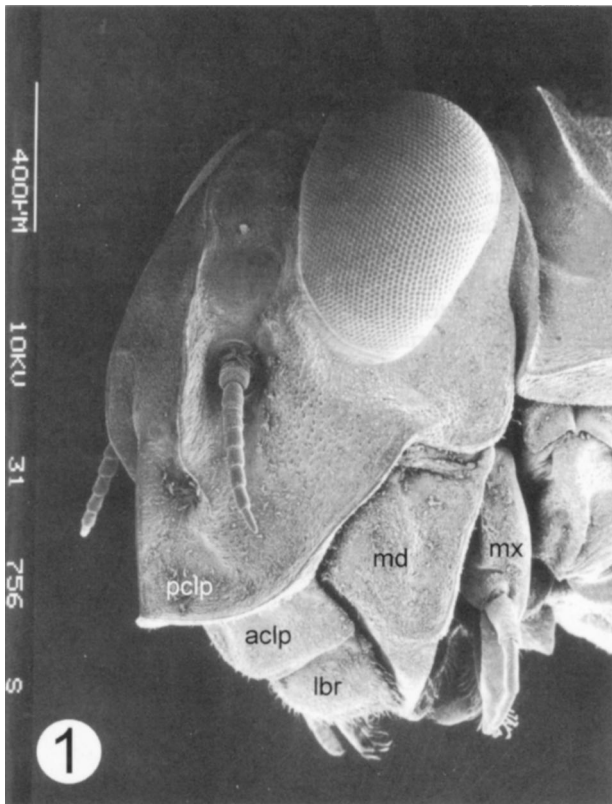
Fig. 1. *O. wakefieldi,* head of larva, lateral view, SEM.

Fig. 2. *O.wakefieldi,* left mandible, posterior view, SEM. Arrows indicate desclerotised area.

Fig. 3. *O. wakefieldi,* left mandible, lateral view, SEM.

3. RESULTS

3.1. *Oniscigaster wakefieldi* McLachlan, 1873

Mandible

The larva of *O. wakefieldi* bears orthognathous mouth-parts (Fig. 1). (The term 'orthognathous' rather than 'hypognathous' is used herein, because the term 'hypognathous' is also used as a synonym for the term 'opisthognathous' by various authors (see VON KÉLER 1963 but NICHOLS et al. 1989)). The mandible is well developed and heavily sclerotized. It resembles the mandible of an orthopteroid insect, but the mandible's outer basal edge declines from its caudal to its frontal end. Each mandible bears two well-developed incisivi, a prostheca and a molar region (Fig. 2). The mandibles are sharply bent inwards frontally, so that their anterior surfaces lie behind the epipharynx in the transverse plane. Externally only the posterior mandibular articulation is partly visible (Fig. 1). It is located at the hind angle of the mandible (Figs. 1, 3, 5). The postero-lateral part of the mandible is basally elevated forming a laterally compressed and elongated roller-like condyle (Figs. 3-5). The roller has an oblique position with an axis that lies at an angle of about 55° to the transverse plane. The medial end of the roller is located anterior and also slightly dorsal to its lateral end. The central part of the roller runs inside a socket that is formed by the postgena. The socket is shaped as a hollow groove that is bordered medially as well as laterally by two regions that are heavily sclerotized (Fig. 5).

At the basal frontolateral edge of each mandible an anterior articulation complex (aac) is located: its antero-lateral part (alp) is represented by an elongated mandibular notch into which the inner margin of the inflected cranium projects (Figs. 4, 6). This mandibular notch (mn) is formed as an oblique, elongated impression of the mandibular body, that is situated distally to the basal mandibular edge, and thus well separated from the latter (Figs. 3, 7). Hereby the anterolateral border of the notch (mll), which is heavily sclerotized, partly overlaps the notch itself, thus creating a hollow groove (Figs. 3, 7). The sclerotized cranial ridge (scr, Fig. 5) at the margin of the inflected gena (Figs. 32c, d) perfectly fits into this groove, together forming a loose hinge joint (Fig 6). This is the structure that has been described in different mayfly larvae as anterior articulation, slider, or guiding structure by previous authors (STRENGER 1953-1979; BROWN 1961; KUKALOVÁ-PECK 1985, 1991; ARENS 1989).

Immediately behind and dorsally to this joint the posteromedial part (pmp) of the anterior articulation complex is located. The basal outer rim of the mandible is heavily sclerotized and slightly indented in this region,
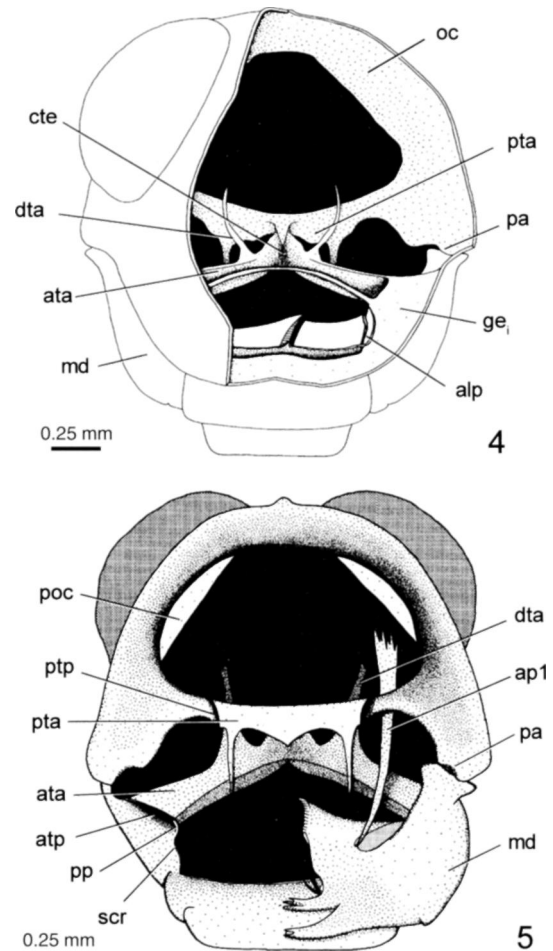

Fig. 4. *O. wakefieldi*, mazerated head from anterior. The head capsule has been partly removed to enable a view onto tentorium, inflected gena, and anterolateral part of the anterior articulation complex.
Fig. 5. *O. wakefieldi*, mazerated head from posterior, view onto tentorium and right mandible. Other mouthparts have been removed to enable a look onto the cranial part of the anterior mandibular articulation and the anterior tentorial pit.
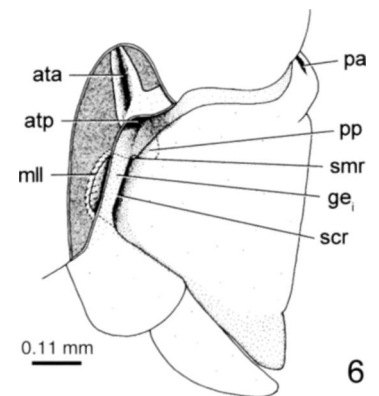

Fig. 6. *O. wakefieldi*, left mandible in lateral view. The lateral head capsule has been partly removed to enable a look onto the anterior articulation complex.

forming a small, saddle-like socket (Fig. 7, smr). Dorsally, the cranial processus paratentorialis (pp, see also below) is attached to this part of the mandibular rim. forming another point of articulation. In this way the mandibular rim forms an acute angle with the roller-like processus paratentorialis (Fig. 6).

The axis of mandibular movement runs between the posterior articulation and the posteromedial part of the anterior articulation complex. The posterior articulation lies dorsally and laterally of the posteromedial part of the anterior articulation complex, thus creating an oblique axis of mandibular movement.

Tentorium

The anterior tentorial pits are located at the inner edge of the inflected ventral parts of the genae, and thus not visible externally. Only after removing all the mouthparts a view from posterior reveals the position of the anterior tentorial pits (Figs. 5, 8, atp). Their position is confluent with the ventrolateral border of the sclerotized cranium. The anterior tentorial pits mark the point of invagination of the anterior tentorial arms (ata) that are well developed (Figs. 4. 5). Close to the anterior edge of the anterior tentorial pit an elongated, heavily
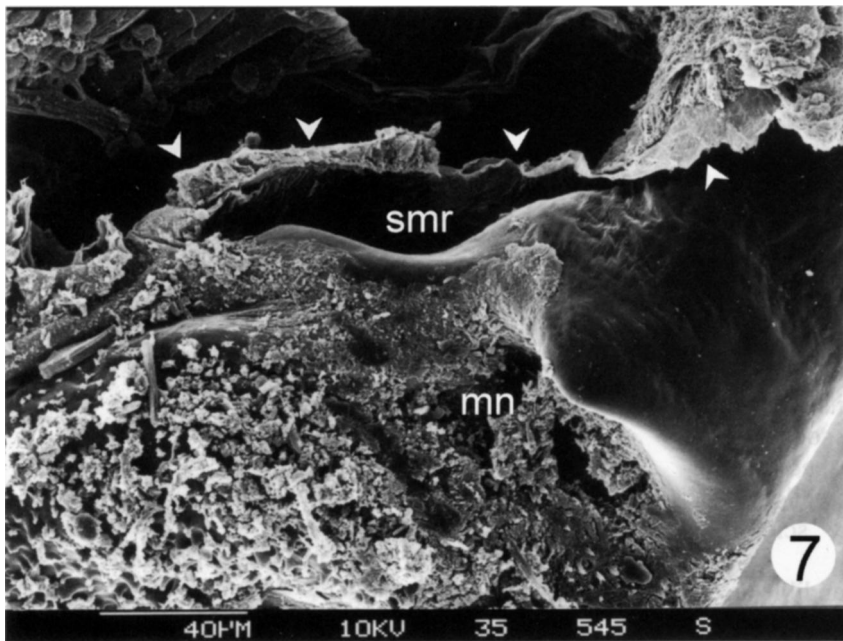

Fig. 7. *O. wakefieldi*, right mandible, anterior articulation complex, laterodorsal view, SEM. Arrows indicate the membraneous connection of the mandible with the basal cranial border. The progression of the membrane thus marks the border between external and internal environment.
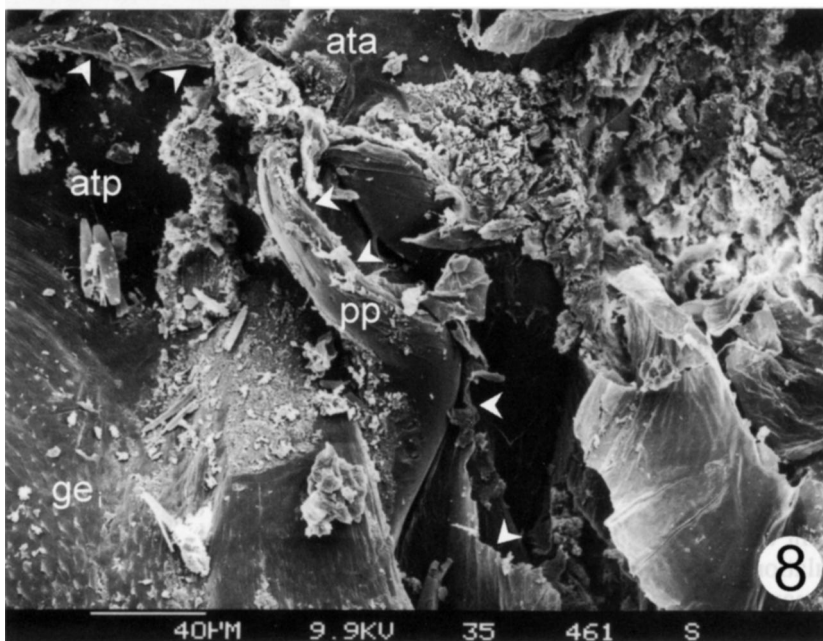
Fig. 8. *O. wakefieldi*, cranial part of left anterior articulation complex, anterior tentorial pit, and processus paratentorialis in posterior view, SEM. Arrows indicate the membraneous connection of the cranium with the basal mandibular rim. The progression of the membrane thus marks the border between external and internal environment.

sclerotized processus is present (Figs. 5, 6, 8, 32f). This structure is termed herein as *processus paratentorialis* (pp), as it is not formed by the invaginated anterior tentorial arm itself, but it is clearly an external structure formed by the cranium and positioned laterally of the craniomandibular basal connective membrane (Fig. 8). This processus paratentorialis is part of the anterior articulation complex, and articulates with the basal outer rim of the mandible. Its position near the **anterior** edge of the anterior tentorial pit is defined herein as *anterocondylate*.

The anterior tentorial arms arise well separated from the clypeus in a somewhat posterior position and taper as they converge and become united with the posterior tentorial arms (Fig. 4). The anterior tentorial arm is *u*-shaped in cross section (Figs. 29b, 32f-g). The anterior tentorial arm is also slightly twisted as it converges medially, where it splits off the dorsal arm (dta, Figs. 4, 5, 32a-f), that is formed as a broad plate-like extension. Immediately medial to the antenna the dorsal tentorial arm is attached to the epidermis by tonofibrillae. Besides the extrinsic muscles of the antenna, some ventral mandibular muscles are also attached to it.

Mandibular muscles

The mandibular muscles basically consist of two groups. The dorsal muscles take their origin on the cranium and insert by apodemes at the basal mandibular edge. The ventral muscles originate on the the tentorium or hypopharynx and insert at the mandibular edge or at the body of the mandible.

For details on the homology of muscles see discussion.

a) Dorsal muscles

(Ml) M. cranio-mandibularis internus (cranial adductor muscle of mandible):

(crml) muscle cranio-mandibulaire 1 BITSCH 1963
(adcm) muscle adducteur cranien médial + (abcmd) muscle abducteur cranien medial CHAUDONNERET 1950
(a.m.p.) Adductor mandibulae posticus BÖRNER 1909
(6) Dorsal adductor muscles BROWN 1961
(MA) dorsaler Mandibeladduktor, cranialer Mandibeladduktor STRENGER 1953, 1970, 1975, 1977
(MAa-MAd) dorsaler Mandibeladduktor SCHÖNMANN 1981

The cranial adductor muscle is the most powerful mandibular muscle. It consists of several bundles of muscle fibres. Its apodeme rises as a strong tendon at the inner side of the basal mandibular rim, just between the molar region and the posterior articulation (Figs. 5, 11). This tendon soon splits off a second branch, that is somewhat thinner than the main tendon. Each branch is apically broadened forming a plate-like attachment for

different portions of M1. Both sides of the major plate are points of attachment for those three portions, that extend to the vertex (Fig. 32a). Other portions that insert at both sides of the minor tendinous plate, extend to the postoccipital ridge as well as to the occiput and postocciput itself (Figs. 9-10). All portions of this muscle serve as adductor of the mandible.

(M2) M. cranio-mandibularis externus anterior (anterior cranial abductor):

(crm2) muscle cranio-mandibulaire 2 BITSCH 1963
(adcl) muscle adducteur cranien lateral CHAUDONNERET 1950
(r.m.a.) Remotor mandibulae anticus BÖRNER 1909
(3a) cranial abductor muscle BROWN 1961
(25a) cranialer Mandibelabduktor SCHÖNMANN 1981

This relatively small and short abductor muscle inserts at a short and tenuous apodeme immediately posterior to the posteromedial part of the anterior articulation complex. It extends in an oblique direction dorsally and posterior to its lateral origin at the gena just below the compound eye (Figs. 9, 32g). This muscle serves together with the following one as an abductor of the mandible. Additionally, its action probably tightens the attachment between the processus paratentorialis and its corresponding mandibular socket by compressing the two components of the joint.
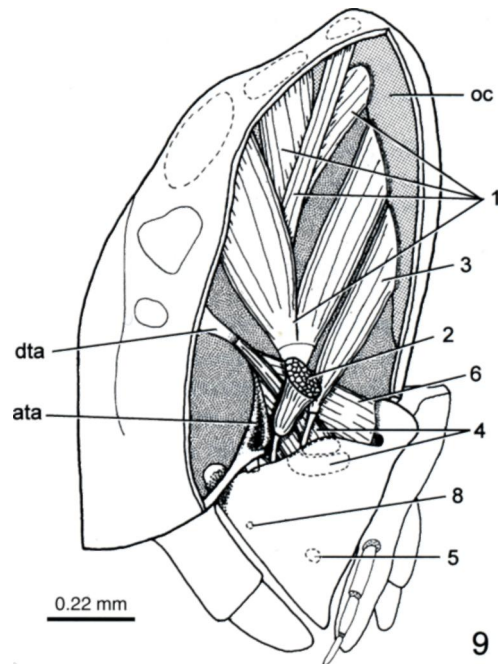

Fig. 9. *O. wakefieldi,* lateral view of the larval head. The lateral cranium has been partly removed to show the mandibular articulation and the lateral mandibular muscles.
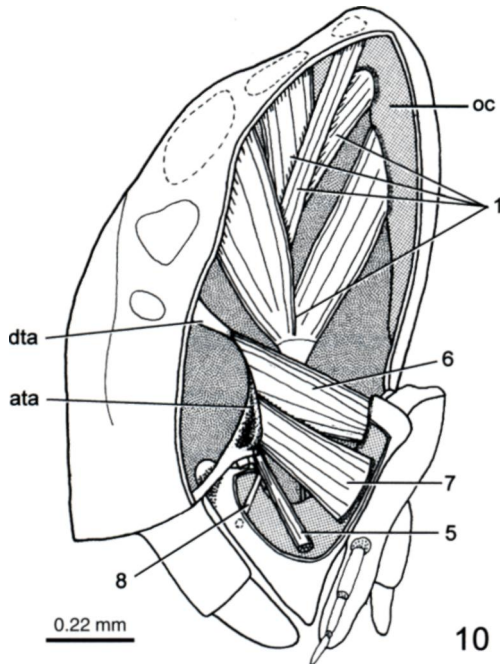
Fig. 10. *O. wakefieldi,* lateral view of the larval head. The lateral cranium, parts of the lateral mandibular wall, and the muscles M2-M4 have been removed to enable a look onto the mandibular muscles M5-M8.

(M3) M. cranio-mandibularis externus posterior (posterior cranial abductor):

(crm3) muscle cranio-mandibulaire 3 BITSCH 1963
(abca) muscle abducteur cranien anterieur CHAUDONNERET 1950
(r.m.p.) Remotor mandibulae posticus BÖRNER 1909
(3b) cranial abductor muscle BROWN 1961
(25) cranialer Mandibelabduktor STRENGER 1953, 1970, 1975, 1977
(25b) cranialer Mandibelabduktor SCHÖNMANN 1981

It inserts at the basal outer mandibular rim on a moderately sized, plate-like apodeme that is located approximately in the middle between the posteromedial part of the anterior articulation complex and the posterior articulation. It extends medially of the M. craniomandibularis externus anterior in an oblique direction to its broad origin at the lateral part of the postoccipital ridge (Fig. 9) This muscle serves as an abductor of the mandible.

b) Ventral muscles:

(M4) M. tentorio-mandibularis externus dorsalis (dorsolateral tentorial muscle)

(ttm2) BITSCH 1963
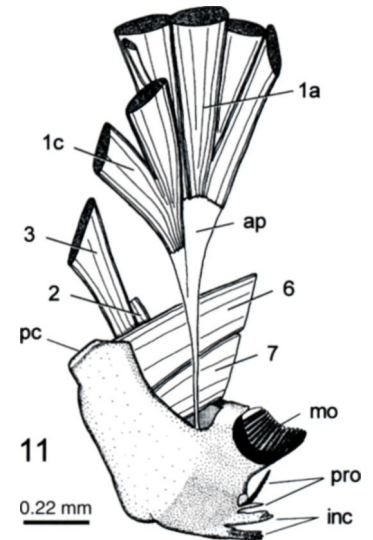(abtl) muscle abducteur tentorial latéral CHAUDONNERET 1950

Fig. 11. *O. wakefieldi,* left mandible with musculature in posterior view. M5 is not visible, M8 has not been drawn.

(4) tentorial abductor muscles BROWN 1961 [in partim]
(25') tentorialer Mandibelabduktor, Abductor tentoricus STRENGER 1953, 1970, 1975, 1977
(25') tentorialer Mandibelabduktor SCHÖNMANN 1981

This muscle consists of two adjacent portions. Both insert on the mandibular body just below the tendon of (3), approximately half way between processus paratentorialis and posterior articulation (Fig. 9). Its upper portion originates on the dorsal tentorial arm, its lower portion on the anterior tentorial arm. This muscle probably serves as an abductor of the mandible.

(M5) M. tentorio-mandibularis externus ventralis (ventrolateral tentorial muscle):

(adml) BITSCH 1963
(adt) muscle adducteur tentorial principal CHAUDONNERET 1950
(a.m.t.) Adductor mandibulae tentoricus BÖRNER 1909
(5) tentorial adductor muscles BROWN 1961 [in partim]
(26b) tentorialer Mandibeladduktor, Adductor tentoricus STRENGER 1970
(26) tentorialer Mandibeladduktor, Adductor tentoricus STRENGER 1977
(26a) tentorialer Mandibeladduktor SCHÖNMANN 1981

This rather small muscle takes its origin at the anterior tentorial arm close to the processus paratentorialis (Figs. 9, 10). It extends in an oblique direction ventrocaudad to its insertion on the distal area of the mandibular body. It assists in adducting the mandible.

(M6) M. tentorio-mandibularis internus dorsalis (dorsomedial tentorial muscle):

(ttm3) BITSCH 1963
(abtp) muscle abducteur tentorial postérieur CHAUDONNERET 1950
(4) tentorial abductor muscles BROWN 1961 [in partim]
(26') Adductor tentoricus STRENGER 1970. 1977
(26c) tentorialer Mandibeladduktor SCHÖNMANN 1981

This muscle originates at the dorsal as well as the anterior tentorial arm below the areas of origin of (4) and (7). It extends backwards to the upper inner end of the mandible, inserting at its inner rim just below the posterior mandibular condyle (Figs. 9, 10). It probably serves as an adductor as well as a rotator of the mandible.

(M7) M. tentorio-mandibularis internus ventralis (ventromedial tentorial muscle):

(ttml) muscle tentorio-mandibulaire 1 BITSCH 1963
(adt') muscle adducteur tentorial accessoire CHAUDONNERET 1950
(a.m.t.) Adductor mandibulae tentoricus BÖRNER 1909 [in partim]
(5) tentorial adductor muscles BROWN 1961 [in partim]
(26) tentorialer Mandibeladduktor. Adductor tentoricus STRENGER 1970
(26a) tentorialer Mandibeladduktor. Adductor tentoricus STRENGER 1977
(26b) tentorialer Mandibeladduktor SCHÖNMANN 1981

This rather big muscle originates below (4) on the anterior tentorial arm (Fig. 10). It runs caudad and inserts on the medial wall of the mandibular cavity, just between the insertions of (1) and (6). It acts as an adductor of the mandible.

(M8) M. mandibulo-hypopharyngealis (protractor muscle of hypopharynx):

(adm2) BITSCH 1963 ?
(adh) muscle adducteur hypopharyngien CHAUDONNERET 1950
(zgm.) Zungenmuskel BÖRNER 1909
(7) hypopharyngeal-mandibular muscle BROWN 1961
(29) STRENGER 1953. 1970. 1975
(29) SCHÖNMANN 1981

The smallest muscle of the mandible takes its origin below the anterior articulation on the mandibular body (Figs. 9-10, 32g). It extends mediad and caudad and inserts with a long thin tendon on the basal lateral edge of the hypopharynx. Though often described as an adductor of the mandible, it could as well serve as protractor of the hypopharynx.

3.2. *Nesameletus* sp.

The mouthpart are slightly opisthognathous (Fig. 12). The pars incisiva is modified: instead of two incisivi there is a large gouge developed. Basally of the gouge the bipartite prostheca is present, but its lower part is strongly reduced to a single bristle (Fig. 14). The pars molaris is very similar to the condition in *O. wakefieldi* bearing several cuticular rows on its surface. Externally only the posterior mandibular articulation is partly visible, whose mandibular part is formed as a roller-like condyle. The cranial socket is accordingly shaped as a hollow groove that is bordered medially as well as laterally by two regions that are heavily sclerotized.
At the basal frontolateral edge of each mandible the anterior articulation complex is located, that is represented by an anterior and posterior part. Both parts are not exposed, but are easily visible from outside, as due to their heavy degree of sclerotization the dark colouring shines through the overlying lateral body wall. Its anterior part also features an elongated mandibular depression (Fig. 14) into which the inner margin of the inflected cranium fits. This hinge joint is somewhat shorter than the one in *O.wakefieldi*, but otherwise there are no differences to observe.
In contrast to this, the posterior part of the anterior articulation complex in *Nesameletus* sp. is somewhat different in both shape and position. It is very well separated from the anterior part and located approximately halfway between the latter and the posterior (primary) mandibular articulation (Figs. 13. 14) at the **posterior** edge of the anterior tentorial pit. This condition is herein referred to as *posterocondylate*.
The basal outer rim of the mandible in this region is heavily sclerotized and elevated, forming an elongated pedestal with a plane dorsal surface (Fig. 14). Dorsally the likewise plate-like processus paratentorialis makes contact with the elevated mandibular rim, forming a broad and plane area of contact that is heavily sclerotized. The anterior tentorial arms are very similar to the ones in *O.wakefieldi*. They also exhibit an *u*-shaped cross-section. The position of the anterior tentorial pits is also confluent with the ventrolateral border of the sclerotized cranium.

Mandibular muscles (Figs. 12-13)

a) Dorsal muscles

(M1) M. cranio-mandibularis internus:

The cranial adductor muscle is also the biggest mandibular muscle. Its apodeme is elongated to serve as attachment for several muscle bundles that are all placed in line and run parallel to each other from their origins
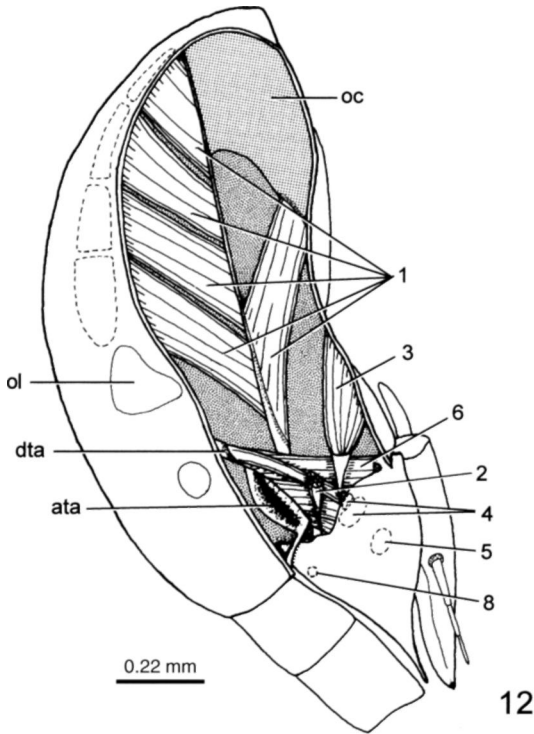
Fig. 12. *Nesameletus* sp., lateral view of the larval head. The lateral cranium has been partly removed to show the mandibular articulation and the lateral mandibular muscles.
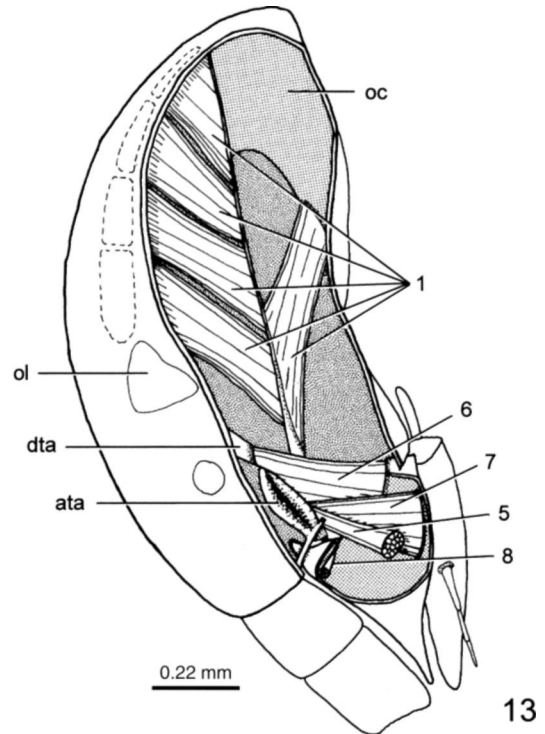
Fig. 13. *Nesameletus* sp., lateral view of the larval head. The lateral cranium, parts of the lateral mandibular wall, and the muscles M2-M4 have been removed to enable a look onto the mandibular muscles M5-M8.

at the vertex. A smaller portion takes its origin at the lateral postoccipital ridge.

(M2) M. cranio-mandibularis externus anterior:

The anterior cranial abductor muscle is very small, but otherwise shows no difference from the respective muscle in *O. wakefieldi*.

(M3) M. cranio-mandibularis externus posterior:

The posterior abductor muscle is somewhat shorter compared with the respective one in *O. wakefieldi*, but has basically the same attachment points and orientation.

b) Ventral muscles

(M4) M. tentorio-mandibularis externus dorsalis:

This muscle is very similar in both shape and orientation to the condition in *O. wakefieldi* and there are two different layers present.

(M5) M. tentorio-mandibularis externus ventralis:

(M5) is somewhat bigger than the corresponding muscle in *Oniscigaster*. In addition its insertion is somewhat dorsal compared with the latter. Otherwise there are no big differences to observe.

(M6)-(M8) are identical in shape and orientation to the respective ones in *O. wakefieldi*.

3.3.   *Ameletopsis perscitus* (Eaton, 1899)

The head capsule of the carnivorous A. perscitus is much broader than its thorax (Fig. 15). The entire head is dorsoventrally flattened and is capable of spacious movements in dorsoventral direction.

Mandible

Basally, the mandible of A. perscitus is almost circular in cross section. It is slightly curved inwards at its anterior third (Fig. 16). The mola is absent, the lateral inci-
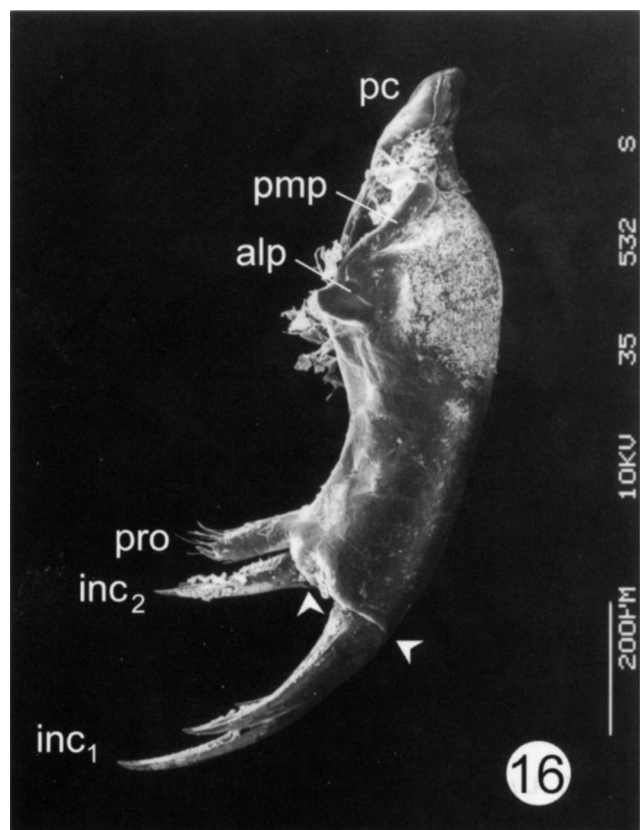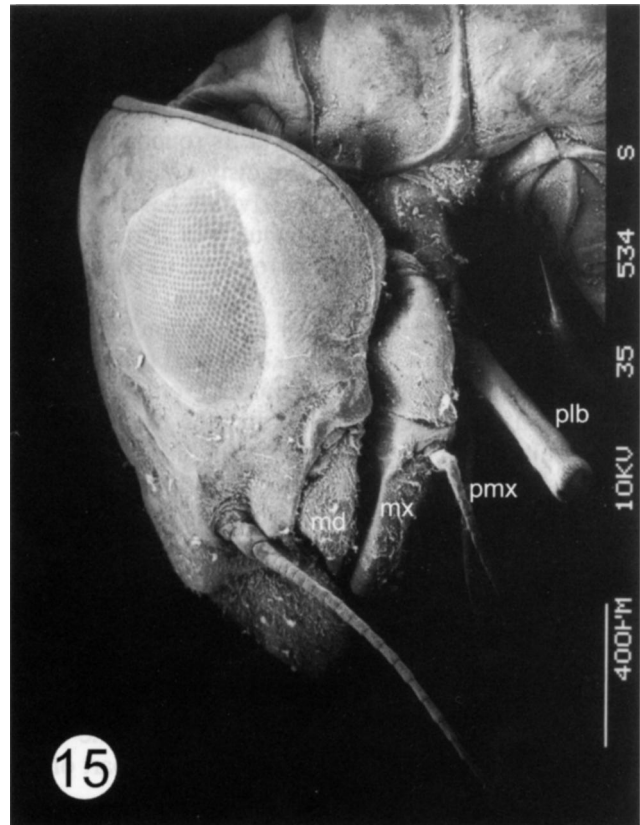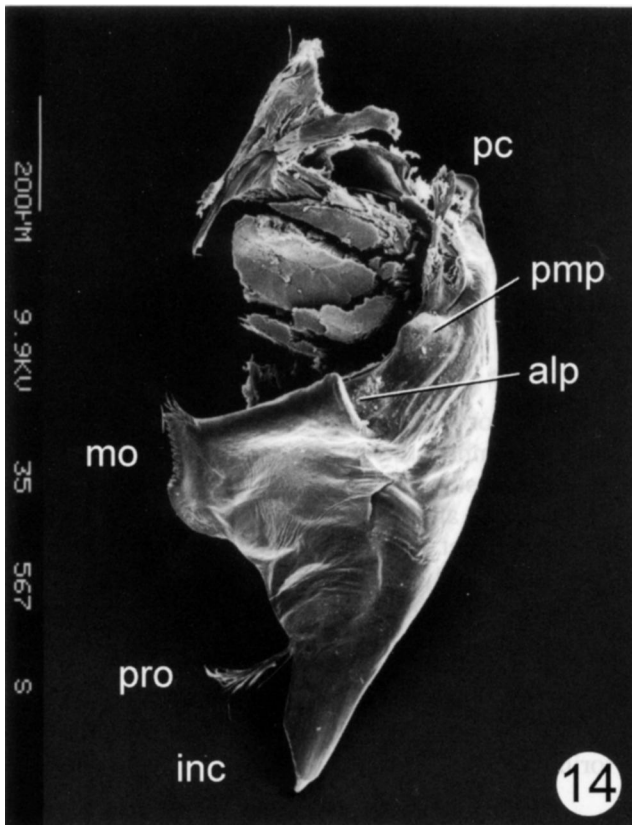
Fig. 14. *Nesameletus* sp., left mandible in anterior view, SEM.

Fig. 15. *A. perscitus,* larval head in lateral view, SEM.

Fig. 16. *A. perscitus.* left mandible. The arrows indicate desclerotised strips at the base of incisivi, SEM.

sivus (inc₁) is extended to a dagger-like cusp with three prongs at its tip. The medial incisivus (inc₂) is somewhat shorter and lies well separated from the former parallel to a thickened and massive prostheca, that has just few stout bristles scattered at its rounded tip. The prostheca as well as the medial incisivus point medially to the mouth opening. Both incisivi are basally desclerotised (Fig. 16, arrows) and thus to a certain extent flexible. It takes no great effort to move the incisivi inwards by manipulation.

The anterior part of the anterior articulation complex is flattened and barely visible as a flattened triangle. The mandibular hollow groove is missing, only a shallow impression of the cuticula indicates the remnants of a mandibular notch (Fig. 16).

The posterior part of the anterior articulation is widely separated from its anterior part and thus shows the *posterocondylate* condition. It probably serves as the functional anterior articulation. The basal mandibular rim is strongly thickened and forms an extended sclerotised strip. With the mandible completely adduced, the processus paratentorialis clings to the strip's caudal end from medially.

The lateral cranial border does not overlap the basal mandibular rim at this area, so the posterior part of the anterior articulation complex is easily seen externally, whereas the posterior mandibular articulation is covered by a duplicature of the ventrocaudal corner of the lateral cranium (Fig. 17).

At its posterior tip the mandible tapers into a tongue-like condyle that is slightly curved. The condyle extends almost in a parasagittal direction. Medially and laterally, it is embedded in a cranial socket shaped as a furrow. The medial border of the cranial socket is formed by the postocciput.

Tentorium

The anterior tentorial arm is very thin and clasp-like, but it resembles the characteristic *u*-shaped cross cut. The processus paratentorialis is formed as a small knob, that is attached medially to the respective mandibular socket. Medially the anterior tentorial arm broadens widely to form a large and flat dorsal tentorial arm (Fig. 18). Dorsocaudal to the antennae the dorsal tentorial arm is attached to the cranium. A corporotentorium is not present: both anterior tentorial arms extend separated from each other as two almost invisible tiny chitinuous lamellae to the posterior tentorium.
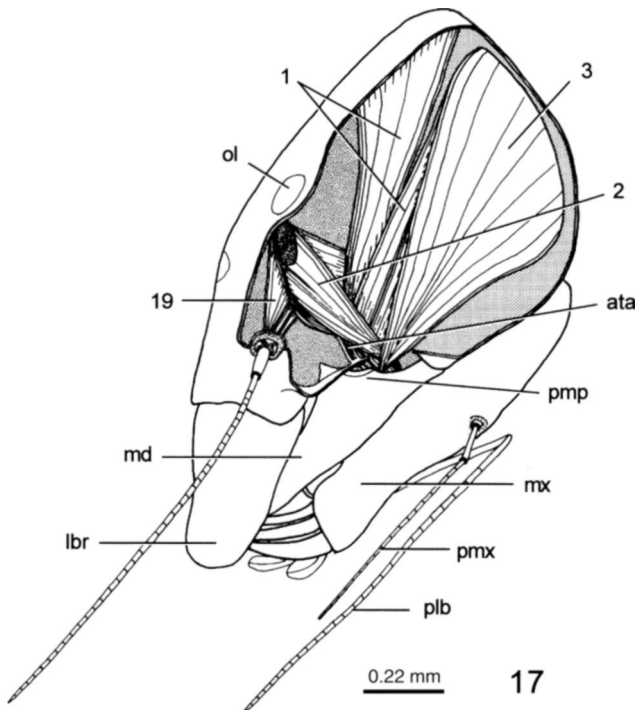

Fig. 17. *A. perscitus,* lateral view of the larval head. The lateral cranium has been partly removed to show the mandibular articulation and the lateral mandibular muscles.
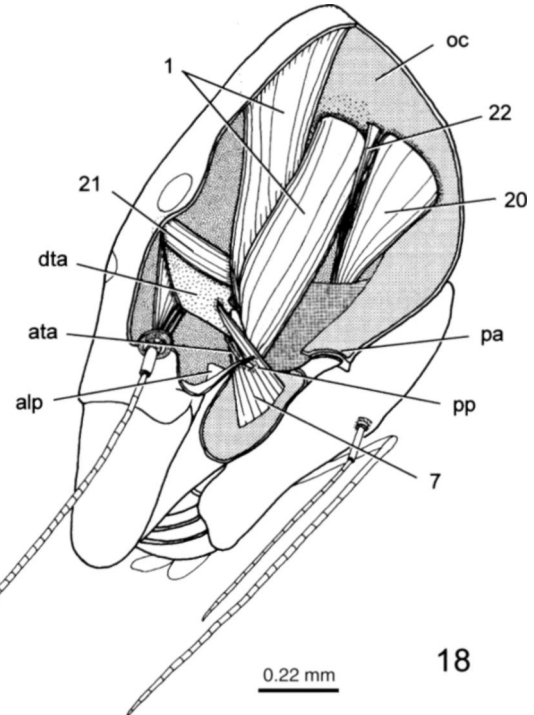

Fig. 18. *A. perscitus,* lateral view of the larval head. The lateral cranium, parts of the lateral mandibular wall, and the muscles M2-M3 have been removed to enable a look onto the medial mandibular muscle M7.

Mandibular muscles (Figs. 17-19)

(Ml) M. cranio-mandibularis internus:

The massive cranial adductor muscle inserts at a very short apodeme, that invaginates at the frontomedial basal rim of the mandible. It consists of just two large parts that originate at the ipsilateral vertex and at the postoccipital rim.

(M2) M. cranio-mandibularis externus anterior:

The anterior cranial abductor muscle is greatly enlarged compared to the respective muscles of the other investigated species. Also its origin as well as its insertion is somewhat different:
The anteroventral part of the muscle originates laterally of M19 at the upper side of the broadened dorsal tentorial arm. In some of the investigated specimens this part of the muscle even overlaps the lateral border of the dorsal tentorial arm and extends to its lower side.
The posterodorsal part of the muscle originates at the frons, closely behind the dorsal tentorial arm and frontolaterally to the lateral ocellus.
Both parts of the muscle extend laterocaudally. Shortly in front of their common insertion, both parts of M2 cross M3 medially. In contrast to all other examined species, the point of insertion lies well separated from the posterior part of the anterior articulation process in the posterior third of the mandible, approximately in between the processus paratentorialis and the posterior articulation. An apodeme is not present.

(M3) M. cranio-mandibularis externus posterior:

The posterior cranial abductor muscle is a very big, flat muscle, whose origin extends parallel to the occipital

ridge across the entire occiput. It extends ventrocraniad and crosses in its distal third M2 laterally. It inserts without apodeme anterior to the insertion of M2 and immediately behind the posterior part of the anterior articulation complex at the lateral basal rim of the mandible.

(M4), (M5), (M6), (M8) are absent.

(M7) M. tentorio-mandibularis internus ventralis:

The only ventral muscle of the mandible surrounds the anterior tentorial arm from ventrally. Its origin lies on both sides of the dorsal tentorial arm.The muscle extends from its origin in an oblique direction laterocaudal and inserts at the hind third of the mandibular body's medial side.

3.4.   *Tricholepidion gertschi*

Mandible

The mandible of *T. gertschi* is elongated (Fig. 20). It bears a well developed pars incisiva and pars molaris (Fig. 27). The mandibular body has an approximately circular cross-section, and the opening of the mandibular cavity is directed dorsomedially. From its posterior to its anterior end the basal mandibular rim slopes inwards and slightly downwards. The posterior (primary) articulation is located at the caudal basal end of the mandibular rim (Fig. 26). Its condyle is formed as an elongated and heavily sclerotized ledge. It fits into the slightly curved lower hind angle of the head, thus creating a ginglymus. At the basal frontolateral edge of the mandible an anterior articulation complex is located (Figs. 21, 24-25):
Its lateral part comprises an elongated cuticular ledge of the mandible (mll) that fits into a kink of the ventrolateral margin of the clypeus. This mandibular lateral ledge is well separated from the basal mandibular edge. Medial to this sclerotised ledge the clypeal margin rests on the horizontally flattened mandibular body, that is slightly impressed in that region to form a shallow groove (mg), but without particularly strong slerotizations (Fig. 25).
The lateral basal mandibular margin is again more conspicuous as a sclerotised mandibular ridge (smr. Fig. 25). It forms together with a large processus paratentorialis the medial part of this anterior articulation complex. The processus paratentorialis clings to the medial side of the mandibular ridge (Fig. 33d). In this way the lateral clypeal border together with the processus paratentorialis form a yoke-like cuticular framework of the cranium that encloses the lateral mandibular rim. The processus paratentorialis does not extend across the lat-
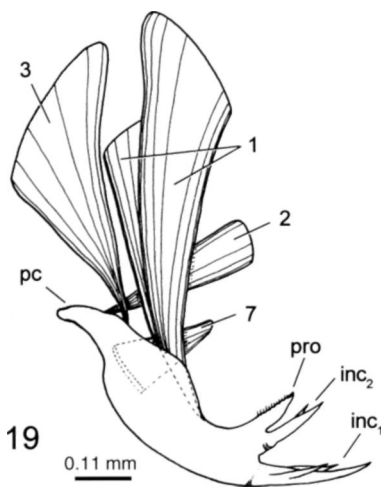

Fig. 19. *A. perscitus,* left mandible with entire musculature from posteroventral.

erobasal rim of the mandible, but clearly is positioned medially to it.

Apart from the lateral mandibular ledge, almost the entire anterior articulation complex is not visible from outside, as it is overlapped by the protruding antennal base and the antenna itself. Only when the antennal base is removed, a view of the entire articulation complex and the anterior tentorial pit is revealed. However, the processus paratentorialis is still an external struc-

ture, as the connecting membrane between basal mandible and cranium is located medially of the processus paratentorialis.

Tentorium

The anterior tentorial pit is overlapped by the antennal ridge and thus not visible externally. It is located below the antenna at the ventral border of the anterolateral
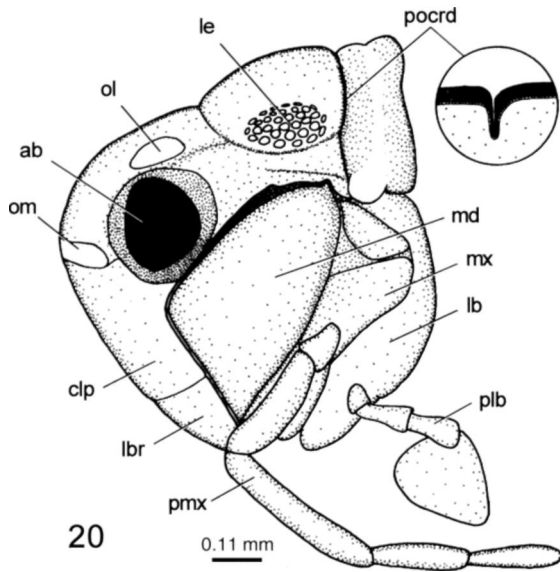

Fig. 20. *T. gertschi,* head in lateral view, antenna removed. Circle shows a magnified schematic histological cut through postoccipital ridge.
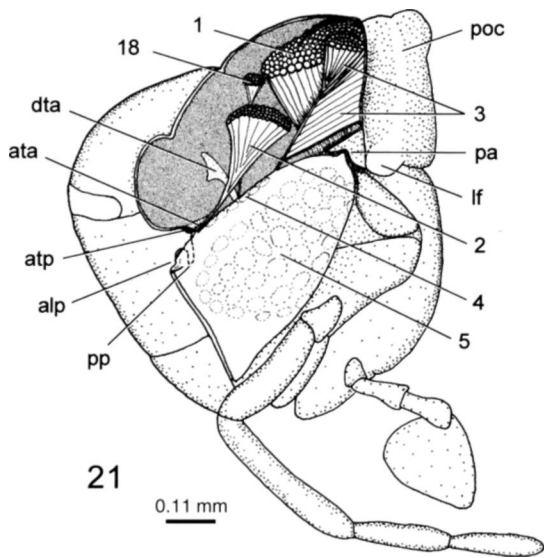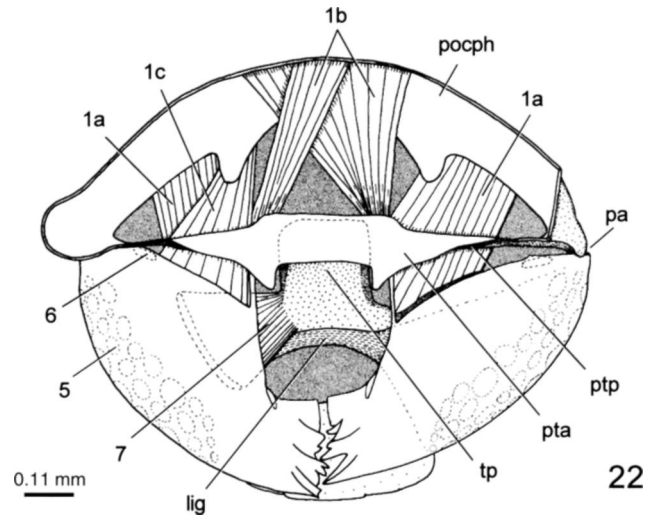

Fig. 22. *T. gertschi,* head in posterior view, postocciput and all mouthparts except of mandibles removed. M7 and M1c are also removed to show the transverse ligament and the remaining portions of M1.

Fig. 21. *T. gertschi,* head in lateral view, antenna and parts of the lateral cranium removed to show the mandibular muscles.
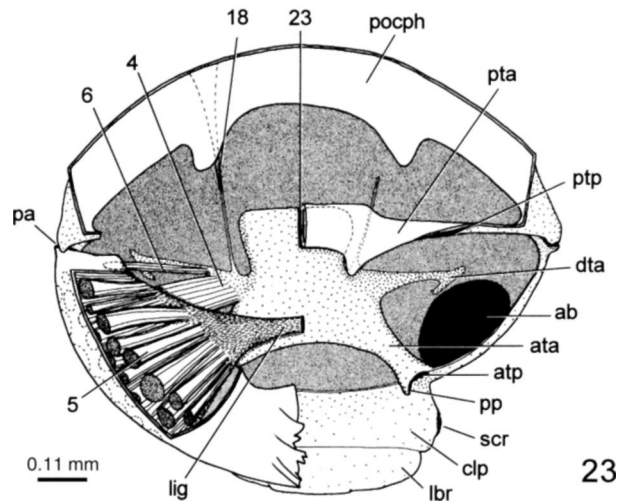

Fig. 23. *T. gertschi,* head in posterior view. Postocciput. left posterior tentorial arm, M18 of right side, and all mouthparts except of left mandible removed to show the anterior tentorial arm and the cranial part of the anterior articulation complex. The left mandible is partly opened to show M5.

cranium. The anterior tentorial arms medially split off a dorsal tentorial arm that is attached to the cranium by tonofibrillae. Additionally, a tiny apodeme extends dorsad from the basis of the dorsal tentorial arm. The suspensor muscle of the tentorium (M18, Figs. 23, 30, 33f) is attached to this apodeme. The anterior tentorial arms converge posteriorly and turn into the tentorial plate, which overlaps the posterior tentorial arms from anterior. The posterior tentorial arms however are well separated from the tentorial plate and only connected medially by a short muscular layer, the tentorial con-

nective muscle (M23, Figs. 23, 30). The posterior tentorial pit is not visible externally. Directly behind of the mandibles, a conspicuous transverse fold crosses the head, that internally is represented by a massive cuticular phragma (Figs. 20, 22-23). This transverse fold is regarded as homologue of the postoccipital suture herein (see discussion). When the specimen is dissected from behind and the posterior head region behind the phragma is removed, the posterior tentorial pit becomes apparent as inconspicuous elongated slit (Figs. 22-23).
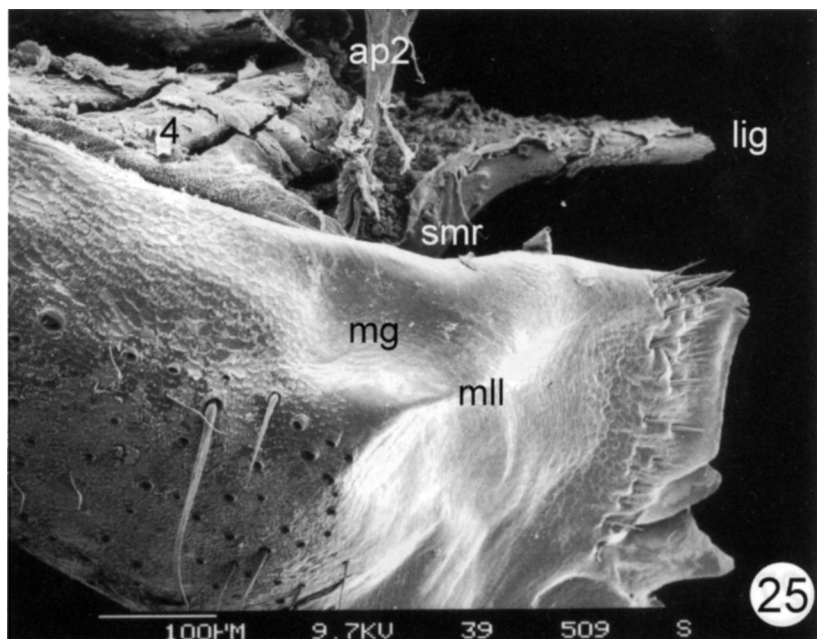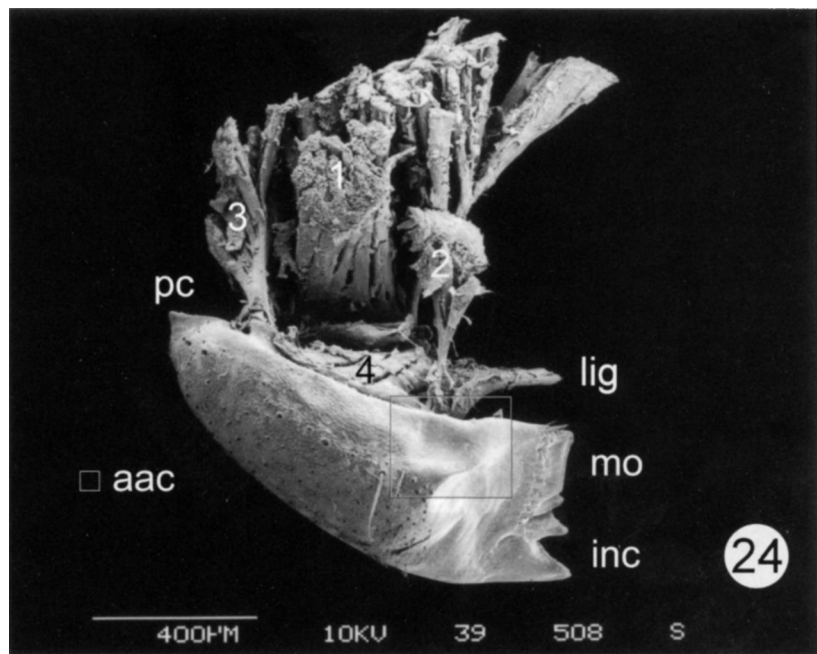

Fig. 24. *T. gertschi,* right mandible with attached musculature in anterior view, SEM.

Fig. 25. *T. gertschi,* right mandible, anterior articulation complex, SEM.

Mandibular muscles (Figs. 21-23, 28, 33)

a) Dorsal muscles

(M1) M. cranio-mandibularis internus:

The cranial adductor muscle is the most voluminous mandibular muscle. The medial side of the mandibular body is extended and forms a blunt-edged triangle that turns into the mandibular apodeme. Its tendon along with the entire inner basal border of the mandible forms an attachment for those portions of the M. cranio-mandibularis internus (1a, 1c) that originate from the ipsilateral vertex. A separate, smaller portion (1b) originates from the head region posterior of the chitinuous
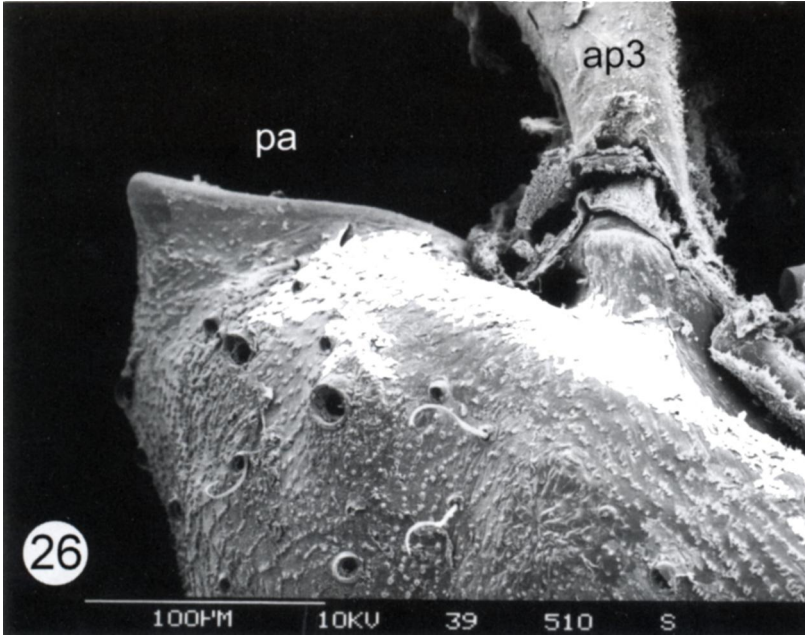

Fig. 26. *T. gertschi.* right mandible, posterior articulation, SEM.

Fig. 27. *T. gertschi,* mola and incisivi of right mandible from posterior, SEM.

phragma and extends to the medial side of the mandibular apodeme.

(M2) M. cranio-mandibularis externus anterior:

This relatively small and short abductor muscle has its origin immediately anterodorsal of the compound eye on the lateral cranial wall. It extends anteroventrally and inserts on a long and tenuous apodeme immediately posterior to the posteromedial part of the anterior articulation complex.
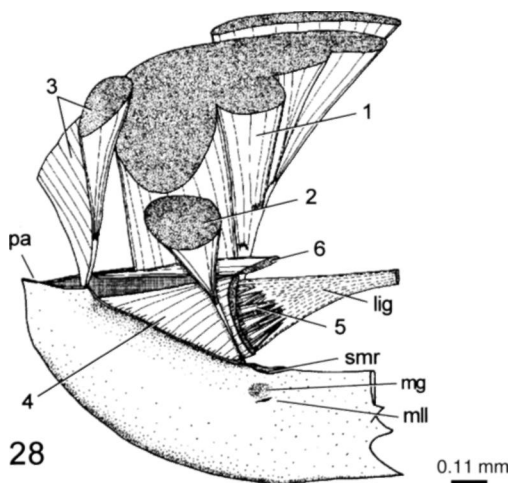

Fig. 28. *T. gertschi,* right mandible with musculature from anterior. M7 is not visible.
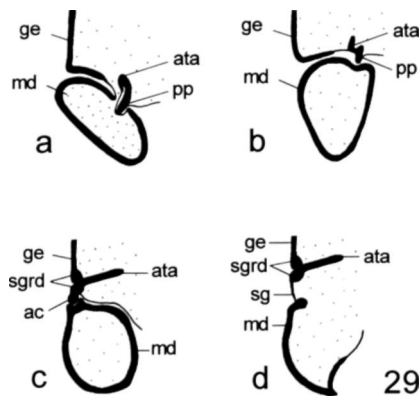

Fig. 29. The development of the anterior condyle and the subgenal ridge in Dicondylia: Schematised cross-sections through the right mandible and cranium at the level of the proc. paratentorialis in a.) Zygentoma *(Tricholepidion gertschi)* b.) Ephemeroptera *(Siphlonurus croaticus)* c.) Metapterygota *(Acheta domesticus).* d.) Cross-section between anterior and posterior mandibular articulation to show the subgena in Metaptergota *(Acheta domesticus).* For further explanation see also text.

(M3) M. cranio-mandibularis externus posterior:

This muscle consists of two portions that both insert with a common tendon on the basal outer mandibular rim just below the compound eye. The anterior portion has its origin on the lateral cranium directly above the compound eye. The posterior portion originates on the lateral part of the chitinuous phragma.

b) Ventral muscles

(M4) M. tentorio-mandibularis externus dorsalis:

This flat muscle originates at the lateral brink of the pretentorium and inserts at the basal lateral border of the mandible between the anterior and posterior articulation.

(M5) M. tentorio-mandibularis externus ventralis:

Almost the entire mandibular cavity is filled by this massive muscle, that extends medially. It originates with several portions from a broad ligamentous connection that links the respective muscles of both sides of the head. The transverse ligament closely approaches the tentorium posteroventrally, and the cross-section reveals even some attachments between the two structures.

(M6) M. tentorio-mandibularis internus dorsalis:

This small and inconspicuous muscle extends from the lower third of the dorsal tentorial arm to its insertion at the dorsal posterolateral angle of the mandible.

(M7) M. tentorio-mandibularis internus ventralis:

M7 is a flat muscle that originates from the ventral side of the tentorium where the anterior tentorial arm takes its rise from the corporotentorium. It inserts just ventrally of the insertion of (M1) at the upper inner side of the mandibular cavity. It extends thus behind all other ventral muscles.

(M8) M. mandibulo-hypopharyngealis:

The presence of a mandibular-hypopharyngeal muscle could neither be confirmed in a dissected specimen nor in a histological cross-cut section series.

3.5.   *Lepisma saccharina*

The mandible in *L. saccharina* is very reminiscent of the condition in *T. gertschi,* but it differs in the reduced pars molaris, the presence of M8, the disappearance of the transventral ligament and consequent shift of M5 to the anterior tentorial arm (see also FÜRST V. LIEVEN 2000).

4. DISCUSSION

4.1. Functional aspects of the mandibular movement

4.1.1. Zygentoma

The anatomy of the posterior articulation allows mainly two possible modes of mandibular movements:

First there is a gliding movement along the longitudinal axis of the posterior condyle, that would result in an oblique gliding of the entire mandible in anteromedial or posterolateral direction. This movement would mainly be caused by the action of the ventral muscles. Recent observation on living specimens of *Lepisma saccharina* by FÜRST V. LIEVEN (2000) establishes that this indeed is the prevailing mode of mandibular movement during feeding. In this case the anterior articulation complex solely serves as a guiding structure for the mandible. Especially the processus paratentorialis does not serve as a condyle, but only as a medial guiding brace, that prevents the mandible from tilting inwards.

Second a limited rotation around the longitudinal axis of the posterior articulation would result in a slight abductional and adductional movement. In this case the mandible would rotate around an axis between the anterior and posterior condyle. M3 would act abductor and M1 would act as adductor of the mandible.

As the anterior articulation complex is just a loose connection, it needs additional tightening. This may the explain the insertion of M2 close to the posteromedial part of the articulation complex.

Regarding the loose anterior articulation complex as well as the possibility to perform also pro- and retractorial movements, it may be justified to term this kind of mandibular arrangement as *facultative dicondyly*.

4.1.2. Ephemeroptera

- *Oniscigaster wakefieldi*

The main difference compared to the mandibular articulation of silverfish concerns the modified anterior articulation complex. Especially its posteromedial part plays a different role in the movement of the mandible. The processus paratentorialis rests medially of the mandibular rim, but it also extends on top of it, thus serving as a true secondary condyle. It is still not a tight ball-and-socket joint, but just a loose attachment that can easily be disconnected when the mandible is lowered. In this case also the anterolateral part of the anterior articulation complex gets disconnected, and its anterior border forms an acute angle with the inflected gena. The posterior articulation accordingly rotates around its longitudinal axis. This position could be ob-

served in living as well as in fixated specimens, especially when the entire cibarium was filled with collected detritus.

The mandibular notch of the anterior articulation complex is not able to perform an extensive pro- and retractional gliding along the genal margin, because it is inhibited posteriorly by the processus paratentorialis and anteriorly by the transverse margin of the clypeus (Fig. 5). Thus it seems not appropriate to term this structure as "slider" or "sliding articulation" as proposed by several authors before (ARENS 1989; KUKALOVÁ-PECK 1991). SCHÖNMANN (1979, 1981) and STRENGER (1953, 1970, 1973, 1975, 1977, 1979) interpreted this conspicuous mandibular hollow groove and its cranial counterpart as a device that has to withstand and absorb the forces (i.e. the pressure of the mola) of the respective adducting contralateral mandible, and I completely agree with this interpretation.

From its lowered position the mandible can be protracted until the anterior articulation complex gets in contact. This movement is obviously caused by the action of M2. Only when the anterior articulation complex is tightly connected, the change to an abductional/adductional movement can take place. Then the mandibular notch of the anterolateral part rotates around the sclerotised genal margin, and the mandibular rim of posterolateral part rotates around the processus paratentorialis. The axis of rotation runs between the posteromedial part of the anterior articulation and the posterior articulation.

During the more or less transversly orientated ab- and adduction the condyle of the posterior joint describes a complicated path. When the abduction takes place, the roller first glides along its longitudinal axis posterolaterad. At the same time it rotates clockwise (at least the left mandible, the right mandible accordingly counterclockwise) around its socket, until the longitudinal axis of the roller lies in the frontal plane. Additionally the roller gets lifted laterally and lowered medially, until its longitudinal axis has reached the horizontal plane. Adducting the mandible, the posterior condyle describes the same movements in opposite sequence.

This trace I have observed by manipulating the mandible in fixed specimens, and my own observation on feeding *Baetis* and *Siphlonurus* (unpublished data) coincide, where I have found this movement to happen repeatedly with a high frequency. In addition. BROWN (1961) observed in Baetidae (Ephemeroptera) also this rhythmic slide of the posterior articulation along its longitudinal axis.

The observed movements of the posterior articulation should also imply some rotation of the entire mandible around the processus paratentorialis. Such a movement is most likely caused by the action of M7.

• *Nesameletus sp.*

The entire anatomy and function of the mandibular articulation is basically the same as in *O. wakefieldi*. The main difference concerns the shape and position of the posterolateral part of the anterior articulation complex. In *Nesameletus* both parts of the anterior articulation complex are widely separated, because its posteromedial part is located at the **posterior** end of the anterior tentorial arm. This results in a position that lies more dorsal and thus also affects the rotational axis of the mandibular swing. Another interesting feature is the structure of its posteromedial part. The mandibular rim is elevated and forms a broad and flat plateau on which the likewise flattened processus paratentorialis rests. Possibly the rotation of the entire mandible around the posterolateral part of the anterior articulation complex is increased in *Nesameletus sp.*

• *Ameletopsis perscitus*

The anatomy of the mandible is strongly modified. The loss of the mola. the reduction of the ventral mandibular muscles, and the missing mandibular notch of the anterior articulation complex are linked with the carnivorous life habits.

The partes molares of *O.wakefieldi* are placed ventrally of the morphological mouth opening. Here they compress the detritus that has been accumulated by maxillae and mandibular tips of incisivi. *A. perscitus* however engulfs entire insect larvae. Voluminous molae would only be obstructive to the prey's quick passage through the cibarium.

In addition it is necessary to reach a great width of abduction for those mouthparts that seize the prey, cling to it, and engulf it into the pharynx. This requirement can only be fulfilled by a reduction of the tentorio-mandibular muscles that limit the range of abduction. This may explain the loss of M4-M6 in *A. perscitus.*

In *O. wakefieldi* the mandibular notch stabilises the mandible during feeding and enables the transfer of the chewing pressure to the cranial side wall and the tentorium. In *A. perscitus* no chewing pressure of the molae is effective, so the loss of the mandibular notch becomes understandable. The missing chewing pressure also led to the reduction of the anterior tentorial arms that serve as place of origin for the M7 and the processus paratentorialis. This reduction - like the loss of a common corporotentorium - might also be correlated with additional space required for the extremely expansible pharynx.

The apodemes of all three cranio-mandibular muscles are very much shortened or even lost. Thus the muscles grow in length compared to the condition in *O.wakefieldi* or *Nesameletus sp.* As a result the muscles are able to perform a much faster ad- or abduction of the mandible, which is without any doubt a huge selective advantage for a carnivorous insect.

Most intriguing are the very different points of attachment of the anterior cranial abductor muscle, M2. The anterior shift of its origin as well as the posterior shift of its insertion brings along a different direction of M2. that increases its protractional component.

Accordingly the insertion of the posterior cranial abductor M3 is now located anterior of the insertion of M2, which increases the refractional component of the former. The reinforced ability to perform re- and protractional movements of the entire mandible goes ahead with the shape of the posterior condyle, whose longitudinal axis lies in the parasagittal plane. When the mandible is entirely adducted, the processus paratentorialis is located at the posterior end of its mandibular socket. In abducted position the processus paratentorialis is located at the anterior end of the mandibular socket.

It may be not the mandible that is initially used for seizing the victim, but the enormously enlarged maxilla, whose galeolacinia is modified to a huge claw. The mandible may be used to cling to the prey and to engulf it into the pharynx during adduction. When it becomes abducted, the incisivi must be retracted without pulling the victim out of the mouth again. In this context the desclerotised strips at the basis of the incisivi could be of importance. They allow a passive jackknifing of the incisivi, so they can easily be retracted and pass the prey laterally without difficulty. This passive jackknifing has not been observed in living specimens yet, but the ability to do so can easily be proven by manipulating the incisivi.

4.2. The anterior mandibular articulation of Zygentoma and Ephemeroptera: a brief history of misunderstandings

HENNIG (1953) was not the first one who realised the presence of a dicondylous mandible in Zygentoma, but he was the first to point out its phylogenetic significance by establishing the monophyletic taxon Dicondylia. It has been BÖRNER (1909), who early recognized the similarities between the "thysanuroid" mandible of Zygentoma and Ephemeroptera on the one hand and the "orthopteroid" mandible of the remaining pterygote insects on the other hand, which he called Metapterygota. However, a detailed comparison of the mandibular articulations as well as their muscles has never been undertaken or failed, because species were not chosen which were still close to the respective groundplans.

Additionally, the authors who described the mandible of silverfish came to different conclusions. While all authors agreed on the presence of an anterior articula-

tion, in detail their observation of this character differed considerably. SNODGRASS (1950, 1952, 1960) repeatedly located in *Lepisma* and *Ctenolepisma* the anterior condyle "on the ventrally inflected angle of the gena, ...a short distance behind the clypeus", CHAUDONNERET (1950) instead observed in *Thermobia* an anterior condyle on the laterodorsal angle of the clypeus. In fact both of them have been right and wrong. CHAUDON-NERET observed only the anterolateral part of the anterior articulation complex, while SNODGRASS took the processus paratentorialis of the posteromedial part for the anterior condyle. Later it was SMITH (1988) who briefly mentioned a "semipermanent" anterior mandible articulation in Zygentoma, and KUKALOVÁ-PECK (1991), who for the first time referred to the anterior articulation of silverfish as "two sockets which fit into a clypeotentorial yoke". KUKALOVÁ-PECK (1985, 1991) however did not recognize the presence of the posteromedial part of the anterior articulation in mayfly larvae. SNODGRASS (1950) recognized only the primary mandibular joint in the Ephemeroptera and thus assumed a convergent development of the secondary joint in both Zygentoma and Metapterygota. STRENGER (1953, 1970, 1975, 1977, 1979) and BROWN (1961) always observed an anterior, middle, and posterior mandibular attachment to the cranium in various mayfly species throughout different families, but did not try to homologise these attachment points with the anterior (secondary) and posterior (primary) joints of other Dicondylia. However, SCHÖNMANN investigated *Siphlonurus aestivalis* (Siphlonuridae), a mayfly that is thought to resemble the mayfly groundplan in many aspects (SCHÖNMANN 1981), but he could not confirm the presence of the middle attachment in this species. He thought of the middle attachment of the ephemeropteran mandible as homologue of the secondary mandibular joint of other Dicondylia, and assumed its reduction in *Siphlonurus*.

This study clearly confirms the results of STRENGER and BROWN. The anterior attachment corresponds to the anterolateral part of the anterior articulation complex, and the middle attachment to its posteromedial part. Most interesting however is the fact that all species investigated by STRENGER and BROWN exhibit the posterocondylate condition. Here the processus paratentorialis is located well separated from the anterolateral part of the anterior articulation complex and thus very easy to distinguish as separate articulation. A closer look at *Siphlonurus aestivalis*, the species investigated by SCHÖNMANN, indeed revealed that this species shows the anterocondylate condition just as *O. wakefieldi* does. SCHÖNMANN overlooked the posteromedial part of the anterior articulation, simply because it was absent from that location where it has been previously found in other species. My subsequent investigation of various mayfly nymphs throughout the order leads to the as-

sumption that, in addition to the posterior mandibular articulation, an anterior articulation complex with two attachment points between cranium and mandible can indeed be attributed to the groundplan of larval Ephemeroptera. Moreover, a comparison of the two different character states of its posteromedial part to the condition in silverfish clearly points to an anterocondylate condition in the groundplan of Ephemeroptera. Besides *O. wakefieldi* I have found the plesiomorphic anterocondylate character state of the mandible in Ametropodidae, Siphlonuridae, Ameletidae, Coloburiscidae, and Siphlaenigmatidae, whereas in all other investigated families the posterocondylate condition was found (Nesameletidae, Baetidae, Heptageniidae, Oligoneuriidae, Leptophlebiidae, all investigated Ephemeroidea and Pannota). In any case the shift from anterocondylate to posterocondylate mandible must have happened several times in the evolution of mayflies, as there are several distinct monophyla (for instance Baetoidea, see STANICZEK 1996, or Setisura, see MCCAFFERTY 1991), that still have a basal anterocondylate taxon (Siphlaenigmatidae, Coloburiscidae), whereas other taxa inside this monophylum have aquired the posterocondylate condition (Baetidae, Heptageniidae + Oligoneuriidae).

4.3. The homology of the mandibular joints throughout the Dicondylia

There is a remarkable correspondence between the mandibular articulation in silverfish and mayflies. Both exhibit an anterior articulation complex, whose posterior part is formed by a processus paratentorialis that is located immediately ventral to the anterior tentorial pit. These processus represent homologous structures, and thus should be attributed to the groundplan of Dicondylia. An independent development of such a peculiar arrangement in Zygentoma and Ephemeroptera appears unlikely. The anterolateral part of the anterior articulation complex is however somewhat different in mayflies and silverfish: In Zygentoma, including *T. gertschi*, it is the lateral clypeal border that forms a cuticular stiffening which makes contact with the mandibular groove. In mayfly larvae the mandibular groove is deeply excavated and encloses the inflected gena. However, it seems likely to interpret the altered anterior articulation complex of mayfly larvae as a modified anterior part of the dicondylian articulation complex that fits the specialized demands for the intake and compressing of aquatic detritus. The alteration of the mandibular groove to a mandibular notch in mayfly larvae and the shift of its cranial counterpart to the gena thus represent autapomorphies of Ephemeroptera. A common origin of the anterolateral part of the anterior artic-

ulation and its subsequent change in mayflies appears more likely than its independent acquirement in both Zygentoma and Ephemeroptera.

The homology of the posterior (primary) articulation throughout the insects is obvious. It is more difficult to determine the precursor structure of the secondary articulation, that is formed as ball-and-socket joint in the remaining pterygote insect orders. Generally, the condyle of the anterior articulation is located at the basal lateral margin of the clypeus in Odonata (ASAHINA 1954; HAKIM 1964) as well as in the orthopteroid (SNODGRASS 1935; STRENGER 1942; WALKER 1931, 1933) and other lower pterygoid orders (CRAMPTON 1932; MOULINS 1968). In Zygentoma it is also the clypeal border that contributes to the anterolateral part of the anterior articulation complex. It might be tempting to homologise the anterolateral part with the secondary condyle of the remaining pterygotes (see FÜRST VON LIEVEN 2000). However, this would not only demand a secondary shift of the cranial part of the anterolateral joint to the gena in mayflies, but also an independent development of the functional anterior articulation in mayflies and Metapterygota. There are more facts that do not concur with that hypothesis: first of all the mandibular groove of the anterior articulation in Metapterygota is generally located at the basal rim of the mandible, but in both Zygentoma and Ephemeroptera it is well separated hereof. It is in fact the processus paratentorialis that articulates with the basal mandibular rim. Second, it is the processus paratentorialis that works as the functional anterior articulation in mayfly larvae. It seems likely that a similar structure already served in the groundplan of Pterygota as functional condyle, from which the conditions in Ephemeroptera and Metapterygota derive. Otherwise an independent development of different structures as anterior joint in Ephemeroptera and Metapterygota had to be assumed. Last but not least the anterior condyle in Metapterygota is always associated with the position of the tentorial arm (SNODGRASS 1935), which would again point to the posteromedial part of the anterior articulation complex as homologue to the anterior mandibular articulation of Metapterygota. Accordingly, the anterolateral part of the anterior articulation must have been lost in Odonata and Neoptera.

4.4. The homology of the postoccipital ridge throughout Dicondylia

In Archaeognatha there is a prominent suture that extends across the head from one posterior mandible condyle to the other. The lateral ends of the suture are located slightly anterior to the primary mandibular condyle. This is also the case in Pterygota, when there is an occipital ridge present. Thus BITSCH (1963) named it *occipital suture*. Internally this suture is partly extended into two large laterodorsal cranial apodemes, that have been accordingly termed occipital phragmata. In *Machilis* the cranial remotor muscle of the mandible is attached to the medial part of this ridge, just medial of the two laterodorsal phragmata. The phragmata are points of insertion for the dorsal longitudinal muscles of the prothorax. Medially of the phragmata the dorsal mandibular remotors of the mandible (crm1 BITSCH 1963) are attached to the ridge. LAUTERBACH (1972b) realised that in Pterygota the prothoracic and neck muscles are usually attached to the postoccipital ridge, and thus homologized the archaeognathan suture in question with the *postoccipital ridge* of pterygote insects. Moreover, he also realised the plesiomorphic presence of small pleural folds in *T. gertschi*, that have been conserved from the groundplan of Ectognatha (LAUTERBACH 1972b).

The present study indeed confirms these homologisations, and specifies the account on *T. gertschi* in LAUTERBACH's (1972b) scenario on the evolution of the postoccipital ridge in Ectognatha:

In *T. gertschi* there is a cranial transverse fold present (Fig. 20, circle) that is internally extended into a prominent large and flattened ridge. It is not only present at the laterodorsal part of the head, but it stretches as a continuous apodeme across the entire laterodorsal cranium (Fig. 23). This extended ridge serves also as an attachment area for the prothoracic muscles. Moreover, a minor part of the cranial adductor muscle (M1) is attached to the posterior side of the phragma. In Ephemeroptera and other Pterygota also a minor part of M1 originates from the postoccipital ridge. The overall similarity of the apodeme in Archaeognatha and *T. gertschi* on the one hand and the matching muscular attachments of the postoccipital ridge of the remaining Zygentoma and Pterygota on the other hand clearly indicate their homology. The structure in question is indeed homologous to the postoccipital ridge of other Dicondylia.

In the past there has been some confusion on the head sutures of *T. gertschi*: WYGODZINSKY (1961, fig. 6) marked the transverse fold erroneously as membraneous area, and SHAROV (1966, fig. 47B) followed him in this regard. A part of the postocciput itself is inhomogenously pigmented and heavily folded crosswise, so WYGODZINSKY (1961) took one of these folds posterior to the postoccipital ridge for the latter. LAUTERBACH (1972b, fig. 7), obviously relying on these data, erroneously homologised one of the posterior folds with the postoccipital ridge. BOUDREAUX (1979b, fig. 52) took the postoccipital ridge for the occipital ridge, and the fold on the postocciput itself for the postoccipital ridge. Nevertheless it has been LAUTERBACH (1972b), who

Tab. 1. Synonyms of the mandibular muscles in Ectognatha.

This publication	BITSCH(1963) Archaeognatha	CHAUDONNERET (1950) Zygentoma: *Thermobia domestica*	BÖRNER(1909) Zygentoma Ephemeroptera	BROWN (1961) Ephemeroptera	STRENGER (1953-1977) Ephemeroptera	SCHÖNMANN (1981) Ephemeroptera
M. cranio-mandibularis internus Ml	muscle cranio-mandibulaire 1 (crml)	adducteur cranien médial abducteur cranien médial (adcm, abcmd)	Adductor mandibulae posticus (a.m.p.)	dorsal adductor muscles (6)	dorsaler (cranialer) Mandibeladduktor (MA)	dorsaler Mandibeladduktor (MAa-d)
M cranio-mandibularis externus anterior M2	muscle cranio-mandibulaire 2 (crm2)	adducteur cranien latéral (adcl)	Remotor mandibulae anticus (r.m.a.)	cranial abductor muscle (3a)	–	cranialer Mandibelabduktor (25a)
M. cranio-mandibularis externus posterior M3	muscle cranio-mandibulaire 3 (crm3)	abducteur cranien antérieur (abca)	Remotor mandibulae posticus (r.m.p.)	cranial abductor muscle (3b)	cranialer Mandibelabduktor (25)	cranialer Mandibelabduktor (25b)
M. tentorio-mandibularis externus dorsalis M4	muscle tentorio-mandibulaire 2 (ttm2)	abducteur tentorial latéral (abtl)	–	tentorial abductor muscles (4) (in partim)	tentorialer Mandibelabduktor (25')	tentorialer Mandibelabduktor (25')
M. tentorio-mandibularis externus ventralis M5	adducteur mandibulaire 1 (adml)	adducteur tentorial principal (adt)	Adductor mandibulae tentoricus (a.m.t.) (in partim)	tentorial adductor muscles (5) (in partim)	Adductor tentoricus (26b, 26)	tentorialer Mandibeladduktor (26a)
M. tentorio-mandibularis internus dorsalis M6	muscle tentorio-mandibulaire 3 (ttm 3)	abducteur tentorial postérieur (abtp)		tentorial abductor muscles (4) (in partim)	Adductor tentoricus (26')	tentorialer Mandibeladduktor (26c)
M. tentorio-mandibularis internus ventralis M7	muscle tentorio-mandibulaire 1 (ttm 1)	adducteur tentorial accessoire (adt')	Adductor mandibulae tentoricus (a.m.t.) (in partim)	tentorial adductor muscles (5) (in partim)	Adductor tentorialer (26, 26a)	tentoricus Mandibeladduktor (26b)
M. mandibulo-hypopharyngealis M8	adducteur mandibulaire 2 (adm 2) ?	adducteur hypopharyngien (adh)	Zungenmuskel (zgm.)	hypopharyngeal-mandibular muscle (7)	(29)	(29)

pointed out for the first time the distinct reduction of the postocciput along with the cranial pleural folds in the remaining Dicondylia. Taking this into account, the reduced size of the postocciput as well as the loss of pleural folds may indeed be putative synapomorphics of (Lepismatidae + Nicoletiidae) and Pterygota.

4.5. The anterior tentorial arms throughout Dicondylia

Compared to other Dicondylia, SNODGRASS (1951, 1952) noticed a different position of the anterior tentorial pits of both Zygentoma and Ephemeroptera in regard to the lateral cranial wall. As shown in this study, the anterior tentorial pit in both groups is not visible externally, because it is located at the basal sclerotized margin of the inflected lateral cranium. But, contrary to SNODGRASS (1951), this does not imply a location "...*mesad* of the mandibles". In fact, the anterior tentorial pit along with the processus paratentorialis is located immediately dorsal to the laterobasal rim of the mandible, as the laterobasal part of the mandible in both Ephemeroptera and Zygentoma is likewise curved inwards.

In the basal orthopteroid lineages the anterior tentorial pits are generally present as elongated slits in both the epistomal and subgenal sutures, the anterior condyle being located at the very corner where the lateral elypeal margin bends over to the pleurostoma. In Odonata the anterior tentorial pits are also located in the subgenal ridge (SNODGRASS 1928).

These differences in the location of the anterior tentorial pit along with its associated condyle led TUXEN (1970, *fide* KRISTENSEN 1975) to believe in an independent development of the anterior mandibular articulation. In fact it is more plausible and parsimonious to assume a simple lateral shift of the anterior tentorial arm in Metapterygota. This went along with a strengthening of the lateral wall that resulted in the development of the subgenal ridge. LAUTERBACH (1972b) assumes the development of a subgenal ridge already in the groundplan of Dicondylia. However, in all investigated Zygentoma as well as in all investigated Ephemeroptera I have not found a prominent internal ridge like the one that is developed in the orthopteroid insects for instance (*contra* CHAUDONNERET 1950 and STRENGER 1952). Apparently it is the lateral shift of the anterior tentorial arm, that goes along with the development of a true subgenal ridge (Fig. 29). Additionally, a broadening of the lateral part of the anterior tentorial arms took part to counterpart the enhanced forces during feeding. However, this character complex is not properly investigated throughout Odonata. but it might well be possible, that the development of a subgenal ridge can be attributed

as an apomorphic character state to the groundplan of Metapterygota.

Furthermore, the anterior tentorial arm in Ephemeroptera has also a significantly posterior position compared to the anterior tentorial arms of Zygentoma, Odonata, and also of the orthopteroid insect orders (HUDSON 1945, 1946). Anterior to the anterior tentorial pit the mandibular notch of the anterior articulation complex is located, so the development of the massive notch is probably responsible for the back shift of the anterior tentorial arm. This posterior position of the anterior tentorial arm is considered as an autapomorphy of Ephemeroptera (STANICZEK 1996). as in Odonata there seems to be the same condition as in orthopteroid orders (SNODGRASS 1928, 1955; SHORT 1955).

4.6. The homology of the mandibular musculature throughout Dicondylia

It is surprisingly easy to compare the mandibular musculature of Archaeognatha (as documented by Bitsch 1963), Zygentoma, and Ephemeroptera and to trace its fate up to the Metapterygota. Fig. 30 summarizes the homologies of the mandibular muscles as seen in this contribution, and Tab.1 lists the terminology of previous authors. SNODGRASS (1935, 1950) differentiated just one pair of dorsal and two pairs of ventral muscles in ectognath insects. According to him, the anterior pair of the ventral muscles would be the homologue to the mandibulo-hypopharyngeal muscles of higher pterygote insects. However, the actual situation is more complex:

In Archaeognatha there is one big remotor muscle (crm1, BITSCH 1963), that extends with a long apodem from the occiput to the posterior mandibular rim. This muscle can be homologized with M1, the cranial adductor of the mandible. There are also two cranial promotors in Archaeognatha (crm1, crm2, BITSCH 1963), both inserting at the anterior basal rim of the mandible. They clearly correspond to M2 and M3, the anterior and posterior cranial abductors. Both muscles are present in all investigated Zygentoma and some of the investigated Ephemeroptera, and thus can be attributed to the groundplan of Ectognatha. M2 is certainly present in the groundplan of Ephemeroptera, but obviously has been lost in many mayfly families. The loss of M2 in Ephemeridae, Palingeniidae, Euthyplociidae, and Heptageniidae (STRENGER 1953-1977) is probably correlated with a tightening of the anterolateral part of the anterior articulation complex and a further immobilizing of the mandible (ARENS 1989). In all other pterygote lineages, there is only one cranial abductor present, that usually originates from the postoccipital ridge. Hence it is homologized with M3. M2 obviously
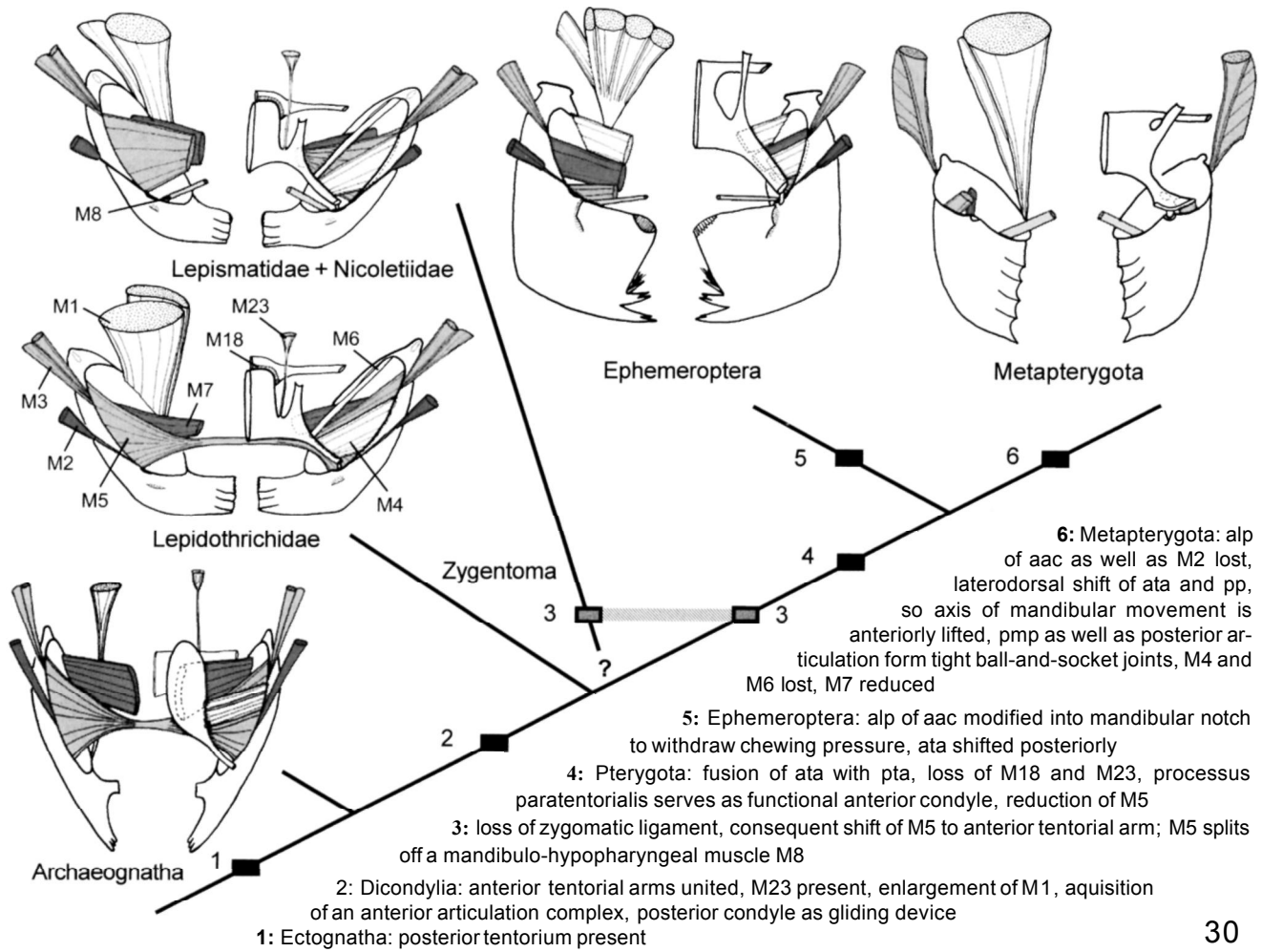
6: Metapterygota: alp
of aac as well as M2 lost,
laterodorsal shift of ata and pp,
so axis of mandibular movement is
anteriorly lifted, pmp as well as posterior ar-
ticulation form tight ball-and-socket joints, M4 and
M6 lost, M7 reduced

5: Ephemeroptera: alp of aac modified into mandibular notch
to withdraw chewing pressure, ata shifted posteriorly

4: Pterygota: fusion of ata with pta, loss of M18 and M23, processus
paratentorialis serves as functional anterior condyle, reduction of M5

3: loss of zygomatic ligament, consequent shift of M5 to anterior tentorial arm; M5 splits
off a mandibulo-hypopharyngeal muscle M8

2: Dicondylia: anterior tentorial arms united, M23 present, enlargement of M1, aquisition
of an anterior articulation complex, posterior condyle as gliding device

1: Ectognatha: posterior tentorium present

30

Fig. 30. Phylogenetic argumentation scheme of Ectognatha, only characters regarding mandible and tentorium are listed. For further explanation see also text.

is lost in both Odonata and Neoptera, which is probably correlated with the fixed anterior articulation, too. BÖRNER (1909) assumed the cranial abductor muscle of *Locusta (*Caelifera) to be homologue of both M2 and M3 of the mayfly larva, because it has two portions, one of which originates at the gena, the other at the postoccipital ridge. However, in the groundplan of Dicondylia M2 also has two portions, and this condition is also still preserved in Zygentoma. Therefore it seems more likely that the bipartite cranial abductor of Caelifera is rather the homologue of M2 only.

In Archaeognatha there is a big ventral adductor muscle extending from the mandible to the transverse medial ligament (adm1-adm5) (BITSCH 1963). Though described as several separate muscles by BITSCH, I have not been able to verify these separated portions in either histological cross-sections or dissected specimens of *Petrobius brevistylis*. The transverse ligament and the

associated muscle (M5) is still unaltered in *T. gertschi*, and the respective muscle in Archaeognatha (adm) is without any doubt homologous to the latter. In (Lepismatidae + Nicoletiidae) on the one hand and Pterygota on the other hand the transverse ligament is lost and the origin of M5 has shifted to the anterior tentorial arm. Additionally, a small mandibulo-hypopharyngeal muscle (M8) is present in both taxa. Previous authors (e.g. SNODGRASS 1935) homologized M8 of Pterygota with the ventral adductor muscle adm of Archaeognatha, but the comparison of *T. gertschi* with other Zygentoma rather points to an origin of M8 as split off from M5. In my view it is most likely that the mandibulo-hypopharyngeal muscle M8 is primarily missing in the groundplan of both Ectognatha and Dicondylia, and the character distribution obviously points to the aquisition of a mandibulo-hypopharyngeal muscle as an apomorphic character state of (Lepismatidae + Nicoletiidae) +

Pterygota. Additionally, the tendency to reduce M5 and M8 is often regarded as a possible autapomorphy of Metapterygota (Kristensen 1998), although in dragonflies (in larvae and adults) both muscles are still rather well developed (Snodgrass 1955; Short 1955).

In Archaeognatha there are three tentorial muscles, that extend from the anterior (ttm2, ttm3) and posterior (ttml) mandibular rim to the anterior tentorial arm (Bitsch 1963). The latter muscle is easy to homologise with M7 in T. gertschi, but due to the enormous enlargement of the insertion of M5 at the medial side of the mandibular rim, the insertion of M7 is shifted ventrally to the mandibular body in the groundplan of Dicondylia.

The derivation of M6 is not obvious. It is present at the medial mandibular rim of all investigated Zygentoma and Ephemeroptera. It may represent a split off from ttml, but more parsimonious is the assumption of a homology with ttm3 of Archaeognatha. However, this implies the shift of its insertion to the medial side of the mandibular rim in the groundplan of Dicondylia. This leaves ttm2 as possible homologous muscle to M4, that is present as distinct layer with identical course in all investigated Zygentoma and Ephemeroptera.

Apart from all these minor uncertainties it becomes obvious, that in the groundplan of Dicondylia there is a distinct superficial layer of muscles present, that extends from the anterior tentorial arm to the basal mandibular rim. This distinctive muscle layer is entirely lost in Odonata and Neoptera, which may count for another putative autapomorphy of Metapterygota.

4.7. Do the Zygentoma including *Tricholepidion gertschi* represent a monophylum?

WYGODZINSKY (1961) described the western Nearctic relic species *T. gertschi*, and assigned it to the taxon Zygentoma. However, *T. gertschi* lacks many of the characters that are generally referred to as autapomorphies of Zygentoma or even Dicondylia (*see* KRISTENSEN 1991). This would leave *T. gertschi* the sistergroup of the remaining Dicondylia. The results of the present investigation indeed confirm the studies of BOUDREAUX (1979a) and KRISTENSEN (1998) regarding the presence of a ligamentous connection between the ventral mandibular adductor muscles M5, which consequently has to be assumed in the groundplan of Dicondylia. In contrast to all other Zygentoma as well as Pterygota, the mandibulo-hypopharyngeal muscle is missing in *T. gertschi*. This muscle is also absent in the myriapod and entognath lineages, and to my knowledge absent in Archaeognatha as well (contra BITSCH 1963). So the splitting off from the mandibulo-hypopharyngeal muscle M8 of M5 as well as the latter's separation and shift to
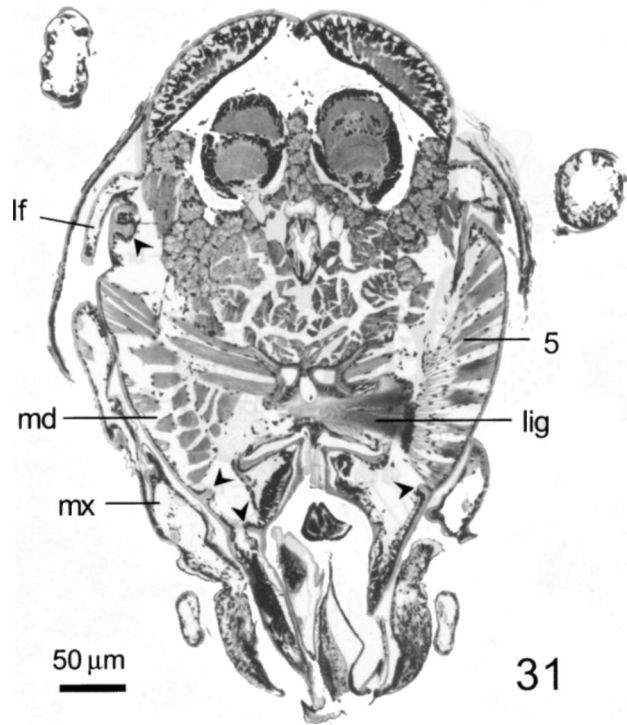

Fig. 31. *P. brevistylis,* histological cross-section through the head at the level of the partes molares. Four black arrows indicate the inner sclerotised ridges of the mandible.

the respective anterior tentorial arm could indeed be taken as arguments for a sistergroup relationship of (Lepismatidae+Nicoletiidae) with Pterygota rather than Lepidothrichidae. The reduction of the postocciput as well as of the pleural folds in these taxa might also be added to the above mentioned characters as putative synapomorphies.

On the other hand KRISTENSEN (1998) discusses, besides the reduction of superlinguae, another two characters as possible autapomorphies of Zygentoma, namely sperm conjugation and shape of the apical segment of the labial palp. However, a broadened distal labial palp segment occurs in a variety of mayfly larvae, and is also commonly seen throughout different insect orders, so I do not consider this as strong evidence for the monophyly of Zygentoma. Previously not discussed phylogenetically is another peculiar feature of the Zygentoman labial palp: it bears four segments (CHAUDONNERET 1950; PACLT 1963, 1967). Apart from the distal one all segments are also equipped with intrinsic muscles (CHAUDONNERET 1950). In the groundplan of Pterygota the labial palp is made up of three segments only. In both Archaeognatha and the entognath orders the labial palps never exceed three segments as well. So one might a priori think of the four-segmented labial
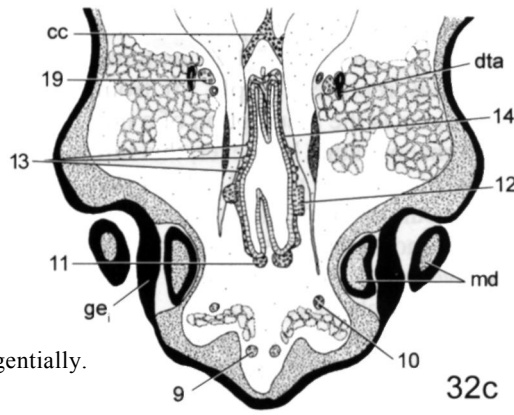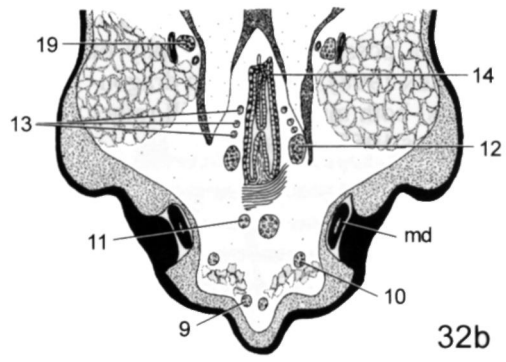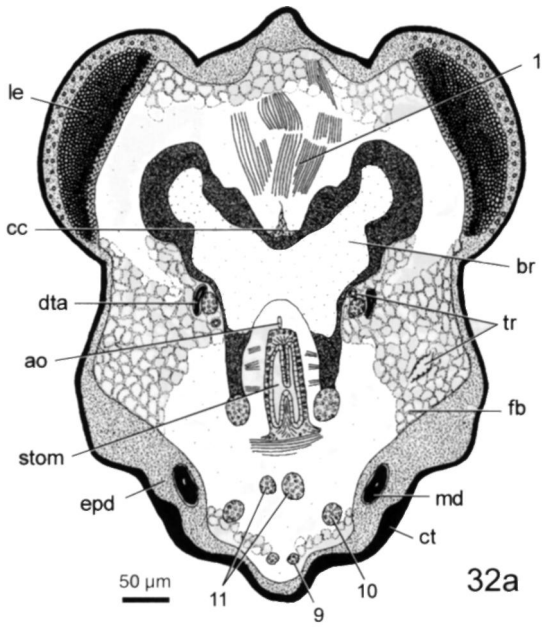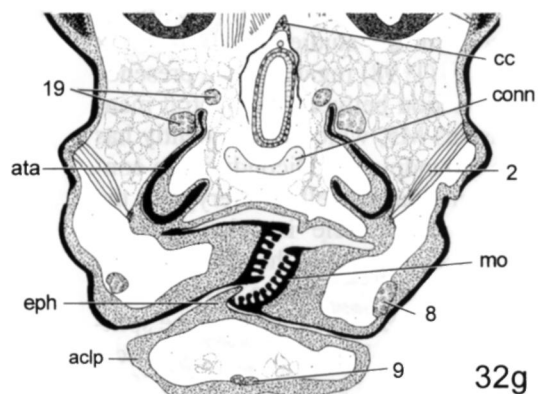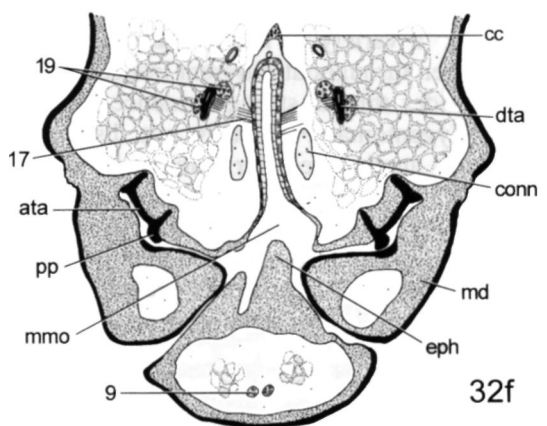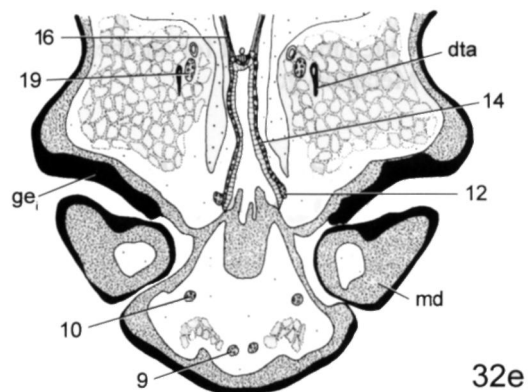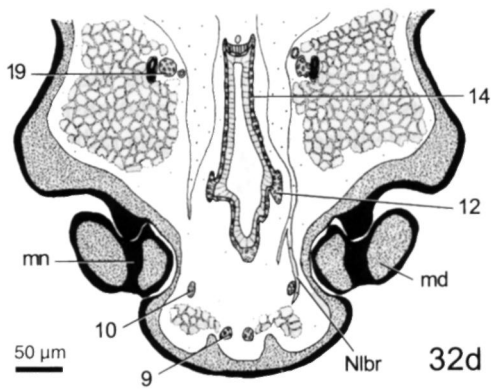
Fig 32a-g. *O. wakefieldi*, histological cross-sections through the larval head from anterior to posterior at different levels of the mandible. The mandible has been cut tangentially.
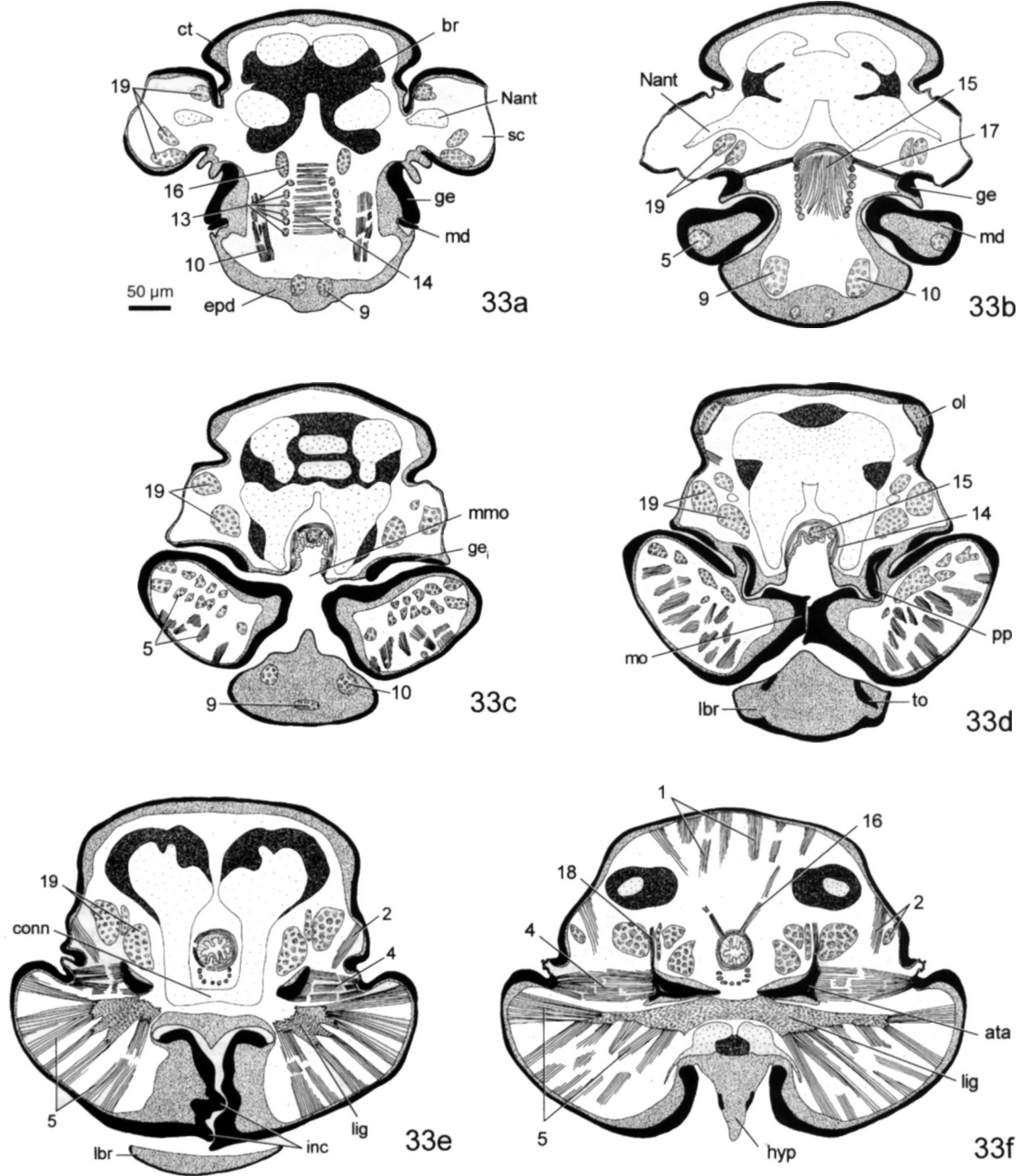
Fig 33a-f. *T. gertschi*, histological cross-sections through the head from anterior to posterior at different levels of the mandible. The mandible has been cut tangentially.

palp of Zygentoma as an autapomorphic character state. On the other hand in Chilopoda a four-segmented palpus on the second maxilla is exhibited. It seems that the condition in Zygentoma could as well be interpreted as the preserved tracheate groundplan in this respect.

STURM (1997) investigated the mating behaviour of *T. gertschi*, whose males -as well as the males of other silverfish (STURM 1987a)- deposit the spermatophore on a self-spun web rather than on a peduncle like the Entognatha and Archaeognatha (STURM 1987b). At first this behaviour could be evaluated as an autapomorphic character of the Zygentoma. However it might as well be attributed to the Dicondylian groundplan. Similarly the presence of the tentorial connective muscle M23

could be interpreted either as autapomorphy of Zygentoma, as well as a character aquired in the stemline of Dicondylia, that has been reduced in Pterygota due to the fusion of anterior and posterior tentorial arms.

At present the most parsimonious assumption would be the monophyly of Zygentoma. but it would only need few opposite characters or a different character weighting to assume a sistergroup relationship between *T. gertschi* and all other Dicondylia. Obviously the present data are contradictory and still too scarce to decide with a considerable amount of certainty if the Zygentoma represent a monophylum or not.

4.8. The transformation from monocondylous to dicondylous mandible, and the early branchings of Dicondylia

Fig. 30 summarizes the gradual changes in tentorium, mandibular musculature and modes of articulation in ectognath insects, and the probable phylogenetic branchings as implied by the distribution of these characters:

1) The monocondylous mandible of Archaeognatha is able to swing in multiple planes. It bears several groups of muscles: two cranial promotor muscles (M2, M3). one cranial remotor muscle (M1). two tentorial adductor muscles (M4, M6), and one transversely connected adductor muscle (M5) which move the mandible. With respect to the character distribution in entognathous insects (TUXEN 1959), this condition is proposed for the groundplan of Ectognatha as well.

2) In the groundplan of Dicondylia, as preserved in *T. gertschi*, the mandible still retains the transverse ligament that links the ventral tentorial adductor mucles M5. All other muscles are retained, too. The lack of the mandibulo-hypopharyngeal muscle is also a plesiomorphic trait shared with Archaeognatha. In contrast to the latter, the mandible in the groundplan of Dicondylia has aquired an additional articulation complex anterior of the primary joint that restricts the movements of the entire mandible and serves as a guiding mechanism for the movements of the mandible. The anterior promotor M2 now acts as a stabilizer of the anterior articulation complex. The cranial adductor muscle Ml gets significantly enlarged due to the different mode of movement. The entire mandible is able to perform anteromediad respectively posterolaterad orientated pro- and retractional movements as well as an ab- and adductional movement. This is possible by the means of an elongated posterior condyle and the anterior articulation complex. Due to the increased transverse forces that occur during chewing, the anterior tentorial arms become united.

3) Lepismatidae+Nicoletiidae (and Pterygota) aquired a hypopharyngeo-mandibular muscle M8. that proba-

bly acts as protractor of the hypopharynx. The postocciput is significantly reduced. The mandibular transverse ligament is lost, and the ventral adductor muscle M5 becomes attached to the anterior tentorial arm. This enables the mandibles to move separately from each other. Otherwise the pattern of movement as well as the anatomy of the mandibular articulation in the groundplan of (Lepismatidae + Nicoletiidae) remains unaltered.

4) In the groundplan of Pterygota the processus paratentorialis extends onto the mandibular rim and starts to serve as true mandibular condyle. The anterolateral part of the anterior articulation complex is still preserved. There is still a pro- and retractional gliding of the entire mandible possible, but the ab- and adductional component of the mandibular movement increases. This is reflected in the beginning reduction of M5 and further enlargement of M1. The increasing transverse forces lead to another reinforcement of the inner skeletal frame, as both anterior and posterior tentorial arms fuse to form the characteristic pterygote tentorium. Consequently the suspensor muscles of the anterior tentorial arms (M18) and possibly also M23 are lost.

5) In the groundplan of Ephemeroptera the pro-and retractional movement is diminished by the alteration of the anterolateral part of the anterior articulation complex to form a deep mandibular notch, into which the genal margin fits. The anterior tentorial arms have shifted posteriorly to make room for the enlarged posteromedial part of the anterior articulation complex, that is still close together in an anterocondylate condition. The anterior cranial abductor muscle is retained.

6) In the groundplan of Metapterygota both articulations become fixed into tight ball-and-socket-types of articulations. The axis of mandibular swing is about horizontal. The anterior cranial abductor muscle M2 and the tentorial abductor muscles M4, M6 and M7 are lost. The anterior tentorial arms along with the anterior condyle shift laterally. A subgenal ridge is developed to sustain the enhanced chewing pressure. The change to an obligatory dicondyle movement has taken place.

All of the investigated mandibular characters underscore the plesiomorphic character state of the mandible of Zygentoma and Ephemeroptera in many respects, and on the other hand point to a sistergroup relationship between Odonata and Neoptera with possible several synapomorphic character states:

- acquisition of a tight ball-and-socket-type of articulation, connected with the loss of the ability to protract and retract the entire mandible, broadening of the anterior tentorial arm
- dorsal shift of the anterior articulation which is correlated with the anterior lifting of the mandibular axis of rotation

- acquisition of a subgenal suture and subsequent lateral shift of the anterior tentorial arm along with the processus paratentorialis
- loss of the anterolateral part of the anterior articulation complex
- loss of the anterior mandibular abductor muscle, M2
- loss of the dorsal tentorial abductor muscles, M4 and M6
- loss of tentorial adductor M7

This entire character complex thus can be added to the previously suggested autapomorphies of Metapterygota as repeatedly summarized by KRISTENSEN (1975, 1981, 1991, 1998), such as the supression of imaginal moults, the presence of occlusor muscles in abdominal stigmata, the reduction of the terminal filament, and the tracheation pattern of wings and legs. Molecular data also support a sistergroup relationship between Ephemeroptera and Metapterygota (WHEELER 1989).
On the other hand KUKALOVÁ-PECK (1985, 1991) assumed a sistergroup relationship between Ephemeroptera and Odonata. mainly by means of fossil wing characters. Wing characters may be difficult to polarize, because the outgroups have no wings at all. The fusion of galea and lacinia is also often cited as a putative synapomorphic character of Palaeoptera, but STANICZEK (2000) discusses the possibility that the fused parts of the maxilla in Odonata may not represent galea and lacinia at all, but lacinia and palpus maxillaris instead. However, the assumption of a sistergroup relationship between Ephemeroptera and Odonata implies an independent development of a ball-and-socket type of mandible along with the associated changes in musculature and tentorium in both Odonata and Neoptera. I do not consider this to be likely.

4.9. Gnathobasic versus telognathic insect mandible

The transformation of the first postantennal appendage into mandibles in crustaceans, myriapods and insects has always been a major argument for a common origin of these groups, which consequently led to their becoming the monophyletic taxon Mandibulata (SNODGRASS 1938; LAUTERBACH 1980). However, MANTON (1964) postulated an independent development of the mandible in Crustacea and Tracheata. In contrast to the obviously gnathobasic mandible of crustaceans, MANTON claimed a so-called "whole-limb jaw" in the groundplan of the Tracheata that is assumed to be made up of the entire telopodite.

While there are also other arguments besides the mandible for upholding the Mandibulata concept (for a comprehensive review of this topic see WÄGELE 1993),

there are still different views about the composition of the mandible in the groundplan of the Mandibulata and the groundplans of its subordinate groups:
Some authors assume a tripartite mandible in the groundplan of the Tracheata, which is interpreted either as an entire telopodite (KRAUS & KRAUS 1994, 1996) or as a coxopodite composed of three podites (KRAUS 1998; KUKALOVÁ-PECK 1998). These authors refer also to the mandibles of Archaeognatha. Zygentoma, or even larval Ephemeroptera (KUKALOVÁ-PECK 1998) as segmented or at least showing traces of segmentation. However, the data obtained from this study do not support this point of view. The existence of alleged "sutures and sulci" that, according to KUKALOVÁ-PECK (1998), occur in the mandible of mayflies, could not be confirmed. It seems that KUKALOVÁ-PECK overinterpreted the anterolateral and ventrolateral edges and angles of the mayfly mandible or even the externally visible borders of respective muscle attachments as remnants of segment borders. In my opinion the conditions that are actually present do not justify these conclusions.
Similarly, throughout all investigated species of Zygentoma. including *T. gertschi*, no traces or remnants of a segmentation of the mandible could be demonstrated. These findings remain in conflict with the postulated traces of segmentation in the mandible of Zygentoma by KRAUS & KRAUS (1994) and KRAUS (1998), that however have not been documented. CHAUDONNERET (1950) in his detailed study on the firebrat *Thermobia domestica* did not observe an external segmentation in its mandible either, but nevertheless suggested a composite mandible made up of three segments, his only evidence being the splitting of the mandibular nerve into three main motoric branches. Whether this actually reflects a postulated former partition remains doubtful, as usually all main nerves tend to split when they have to supply different muscles.

KRAUS & KRAUS (1994, 1996) observed in the machilid *Trigoniophthalmus alternatus* Silvestri, 1904 "vestiges of original articulations between composing segments". Also KUKALOVÁ-PECK (1998) interpreted externally visible sutures in the mandibles of Archaeognatha as remnants of podite borders. In fact, a look onto a histological cross-section of the mandible of *Petrobius brevistylis* reveals that these sutures refer to heavily sclerotised sulci. The same condition as shown in Fig. 31 has been verified earlier also in *Petrobius maritimus* by MANTON (1964) and in several other machilids by BITSCH (1963). These sulci mark the proximal and distal borders of the ventral muscle attachments. Obviously these inner ridges serve as devices that were secondarily developed in order to strengthen the entire mandible against forces that are effective during feeding, rather than indicating vestigial borders of leg podomeres. Finally an alleged tripartite mandible in

Diplura (MARCUS 1951) has never been confirmed by other workers on that group.

All in all, the assumption of a telognathic mandible in the groundplan of insects currently is not substantiated by morphological data. In addition to that, molecular data, especially the mode of expression of the homeobox gene *distalless (dll)*, point to a gnathobasic mandible in the groundplan of insects (POPADIC et al. 1996), and due to recent studies by SCHOLTZ et al. (1998) even in the groundplans of all mandibulate lineages.

KUKALOVÁ-PECK's (1998) hypothesis of a tripartite mandible in the groundplan of Crustacea is not substantiated by the evidence obtained from both recent and fossil material: based on the comparison of recent species, LAUTERBACH (1972a) convincingly derived the origin of the crustacean mandible not from the entire protopodite, but only from its basal part, namely the coxopodite along with its endite, as still can be observed in the larval development of many basal crustaceans today. The gnathal lobe is always formed by the endite of the enlarged coxopodite (SNODGRASS 1952).

In addition to that, WALOSSEK & MÜLLER (1990, 1998) discuss the appendages of several Cambrian fossils from the Orsten fauna which were assigned to the stem lineage of Crustacea. In these fossils, WALOSSEK & MÜLLER draw the attention to a separate endite proximal to the undivided limb base, the latter carrying both exopodite and endopodite. Thus, according to its position the authors convincingly homologize this proximal podite in the first postantennal segment with the coxopodite, hence the mandible. But WALOSSEK & MÜLLER evaluate the evolutionary aquisition of the coxopodite as an autapomorphic trait of Crustacea only, and omit to discuss the consequences of their findings in regard to the Mandibulata concept. If we accept the homology of the crustacean and the insect mandible, and this seems to be straightforward due to their identical body position as well as their structural similarities as modified appendages of the first postantennal segment, then these Cambrian fossils indeed could be as well taken as representatives of the stem lineage of Mandibulata. In fact, this has already been suspected by LAUTERBACH (1988).

Taking all known facts into account, then there is currently little doubt that the mandible in the groundplan of Mandibulata is a gnathobasic one, that is basically formed by a single podite, namely the enlarged coxopodite along with its endite. In the groundplan of Tracheata the telopodite becomes lost. This view however implies a secondary subdivision of the mandible in the myriapod lineages.

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