COMPARATIVE MORPHOLOGY OF THE MANDIBLES OF SEVEN GENERA OF EPHEMEROIDEA (EPHEMEROPTERA)

CHRISTIAN ELPERS
Ing.-Büro Dr. Ludwig, Herrenstr. 14, 76133 Karlsruhe

The structure of the larval mandibles of seven genera of the Ephemeroidea were examined in detail by scanning electron microscopy. The molar surface of all investigated ephemeroidean mayfly larvae is composed of a series of solid and brush-like ridges. The seven genera can be divided into two groups by the cuticular brush-like structure between the molar surface and the inner canine.

INTRODUCTION

When analysing the feeding behaviour and the microstructure of the mouthparts of *Palingenia longicauda*, the structure of the molar surface of the mandible reveals a structure very similar to that found on the molar surface of *Potamanthus luteus* (Potamanthidae; ELPERS & TOMKA, 1994a). *Palingenia longicauda* and *Potamanthus luteus* both belong to the Ephemeroidea within the order Ephemeroptera. In order to determine whether this structure is common within the Ephemeroidea, the mandibles of species of seven genera of Ephemeroidea were analysed. Knowledge of the structure of mouthparts is not only is necessary to understand the functioning of mouthpart movements and food processing of the larvae, but is also important in the search for apomorphic characters for phylogenetic systematics.

METHODS

The mandibles were dissected from the larvae, sonicated for 30 seconds, air dried and platinum coated. The prepared parts were examined with a Hitachi s-700 scanning electron microscope. Where possible, freshly molted and older larvae were examined.
Although MCCAFFERTY (1991) proposed a new phylogenetic systematic for the Ephemeroidea, the family grouping given by HUBBARD (1990) was followed in this study (see discussion for further explanation). The following ephemeroidean larvae were analysed: *Palingenia longicauda* (Palingeniidae), *Potamanthus luteus* (Potamanthidae), *Povilla corporeali* and *Ephoron virgo* (Polymitarcyidae), *Ephemera danica* (Ephemeridae), *Campylocia* sp. and *Euthyplocia* sp. (Euthyplociidae).

RESULTS

Morphology of mandibles

The mandibles of the Ephemeroidea show a more or less prominent mandibular tusk as is found for example in *Palingenia longicauda* (Fig. 1). Two areas found on the mandibles of

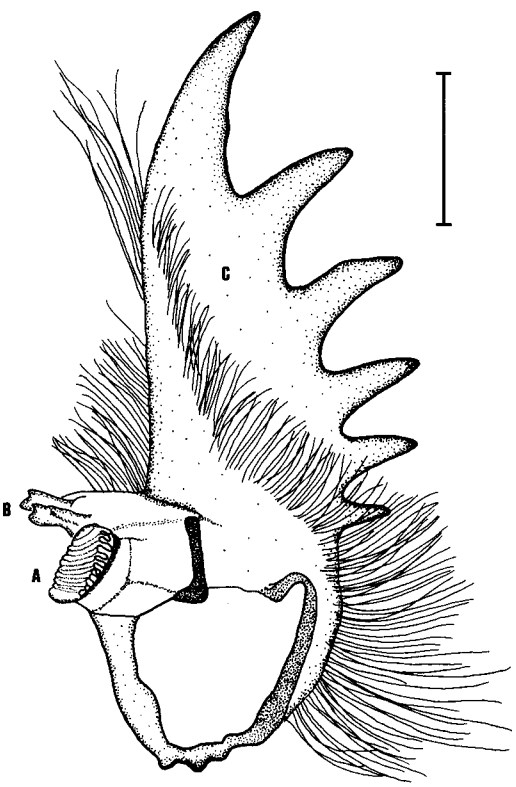

Fig. 1. Overview of the mandible of *Palingenia longicauda*. A: molar surface; B: canines; C: mandibular tusk (scale = 1 mm).

the Ephemeroidea where analysed in detail: first, the molar surface and second, the area between the molar surface and the inner canine of the mandible (Fig. 1).

Molar surface

The structure of the molar surface of the mandibles is found within all examined larvae: the molar surface is built of two repeating parts: a solid ridge and a brush-like ridge. The brush-like ridge consists of rows of microtrichae («setae» of cuticular origin) which are oriented right-angled to the solid ridge (*Palingenia longicauda*, Fig. 2; *Ephoron virgo*, Figs 4b, d-f; *Povilla adusta*, Fig. 5; *Potamanthus luteus*, Figs 6a, c+d; *Ephemera danica*, Figs 7a, b, d+f; *Campylocia* sp., Figs 8a, b+d; *Euthyplocia* sp., Figs 9a-d). This structure of the molar surface is bound on both the left and the right mandible.
Special care has to be taken when comparing the structures of the mandibles: one has to take into account, whether the mandibles are of freshly molted larvae or of larvae which had already been using their mandibles for a longer period of feeding action. Fig. 2 shows the mandible of a freshly molted larva of *P. longicauda*, the structure is in a more or less original condition. In contrast, Fig. 3 (c+d) shows the ridges of the molar surface of the mandible of *P. longicauda* in a worn condition. Nevertheless the original structure of the molar surface can be visualized even from the worn mandible shown in Fig. 3.
The ridges of the molar surface of the right mandible of *Campylocia* sp., shown in Fig. 8b, are worn irregularly. The part of the molar surface towards the canines is more worn than the part towards the edge of the mandible where the surface is in a somewhat original condition. The molar surface of the mandibles of *E. virgo* (Fig. 4d-f) are worn irregularly as well.

Ridge

On the right mandible of *P. longicauda* a ridge arises between the inner canine and the molar surface. The ridge is studded with microtrichae (Fig. 3a+b). A similar ridge is found on the right mandible of *P. adusta* (Fig. 5b) and *E. virgo* (Fig. 4a+c). The ridge on the mandible of *P. adusta* and *E. virgo* differs slightly to that of *P. longicauda* (Fig. 3a+b) in that these ridges

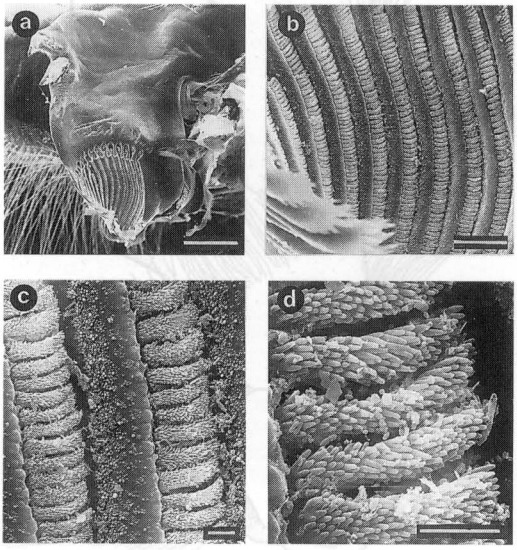

Fig. 2. *Palingenia longicauda,* freshly molted. a: overview of the left mandible; b: molar surface showing brush-like and solid ridges; c: brush-like and solid ridges on molar surface; d: brush-like ridges on molar surface (scale: a = 250 µm; b = 50 µm; c, d = 5 µm).

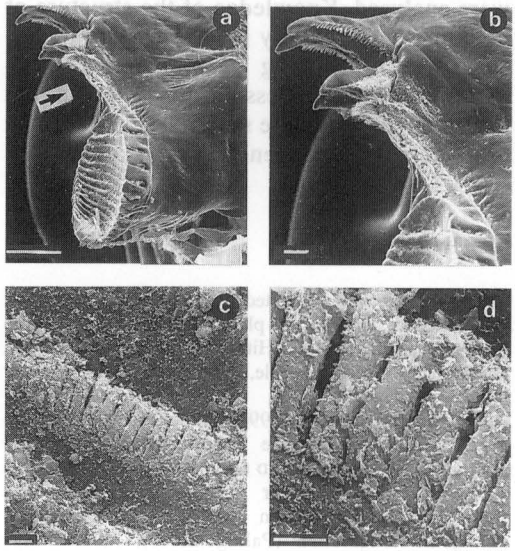

Fig. 3. *Palingenia longicauda*, worn mouthparts. a: overview on the right mandible (arrow); b: ridge between inner canine and molar surface; c: brush-like and solid ridges on molar surface, worn; d: brush-like ridge on molar surface, worn (scale: a = 250 µm; b = 50 µm; c, d = 5 µm).

are more or less composed of two ridges which are studded with microtrichae as well.

Cuticular brush

On the right mandibles of *P. luteus, E. danica, Campylocia* sp., and *Euthyplocia* sp. no ridge is developed between the inner canine and the molar surface as is described for *P. longicauda, E. danica*, and *P. adusta*. Instead, there is a more or less plane surface between inner canine and molar surface. On this plane surface, a cuticular brush arises on the right mandibles of *P. luteus* (Fig. 6a+b), *E. danica* (Fig. 7a+c), *Campylocia* sp. (Fig. 8a+c), and *Euthyplocia* sp. (Fig. 9a, c+e).

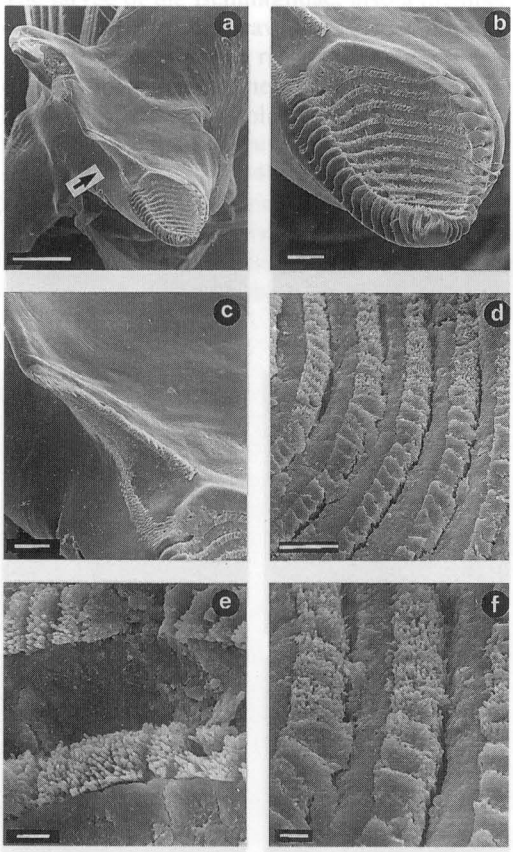

Fig. 4. *Ephoron virgo*. a: overview of the right mandible (arrow indicates position of ridge shown in c); b: ridges on molar surface; c: ridge between inner canine and molar surface; d: brush-like and solid ridges on molar surface, irregularly worn; e: brush-like and solid ridges on molar surface; f: brush-like and solid ridges on molar surface (enlargement of d) (scale: a = 250 µm; b, c = 50 µm; d = 25 µm; e, f = 5 µm).

DISCUSSION

Ecology

The mandibles of the Ephemeroidea function as tools for concentrating food particles and for diminishing the amount of water which is ingested because of the aquatic habitat of the larvae (BROWN, 1961). The mayfly larvae have evolved different molar surfaces to separate food and water (e.g. ARENS, 1989, 1990; BROWN, 1961; ELPERS & TOMKA, 1994a, 1992; WICHARD *et al.* 1995). Within the Ephemeroidea all larvae investigated have evolved a similar structure (Figs 2-9).

STRENGER (1970) found for the larvae of *Palingenia longicauda* that the solid ridges of the one mandible fit against the brush-like ridges of the other mandible. Whether this is true for all ephemeroidean larvae has yet to be determined. For *Palingenia longicauda* this would mean that when food particles are situated on the molar surface, and the mandibles close, a solid ridge presses food particles onto a brush-like ridge. The brushes are somewhat elastic. Water can be pressed out of the food particles, and they are concentrated and remain in their place. This principle of solid and elastic structures on the mandibles recalls the process of pressing and forming pills in chemistry or pharmacology. If on the other hand two solid

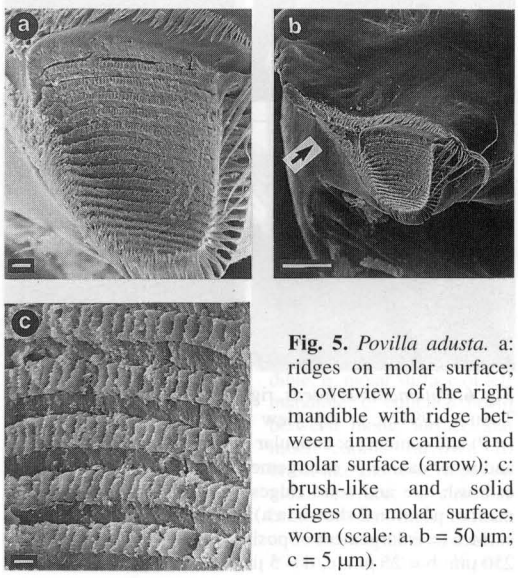

Fig. 5. *Povilla adusta*. a: ridges on molar surface; b: overview of the right mandible with ridge between inner canine and molar surface (arrow); c: brush-like and solid ridges on molar surface, worn (scale: a, b = 50 µm; c = 5 µm).

structures would be pressed onto each other, e.g. two glass plates, and there would be clay and water in between, clay and water would be squeezed out and the plates would slip along each other. That means no food particles would be formed, moreover no food particles would remain in between.

The food particles are compacted by the closing movement of the mandibles. The larvae of *Palingenia longicauda* form pellets out of the food particles situated on the molar surface of the mandibles (LANDOLT *et al.*, 1995). These pellets are then transported towards the pharynx. Although the gut contents of larvae of *Potamanthus luteus* and *Ephemera danica* were analysed, no such pellets were found. One possible explanation could be the consistency of the substrate that the larvae inhabit. Larvae of *Palingenia longicauda* feed on particles which derive from the clay substrate they live in. Larvae of *Ephemera danica* live in a more sandy substrate. Therefore, a portion of the food ingested by larvae of *Ephemera danica* is of sandy substrate and may inhibit the building of pellets as are found in the gut of *Palingenia longicauda*, because they do not stick together as particles of clay substrate would. As larvae of *Ephoron virgo* live in a substrate intermediate to that of *Palingenia* and *Ephemera*, they should be analysed in terms of gut contents.

Several larvae (Figs 4, 8) show irregular worn ridges of the molar surface of the mandible. Whether this is the normal situation within mayfly larvae or a form of wear and tear of a single individual still has to be determined.

The function of the brush-like structure on the right mandible between the molar surface and the inner canine of some ephemeroidean larvae (Figs 6-9) remains unknown. It probably does not substitute for the function of the prostheca because larvae of *Potamanthus luteus* still have the prostheca on the right mandible (Fig. 6a).

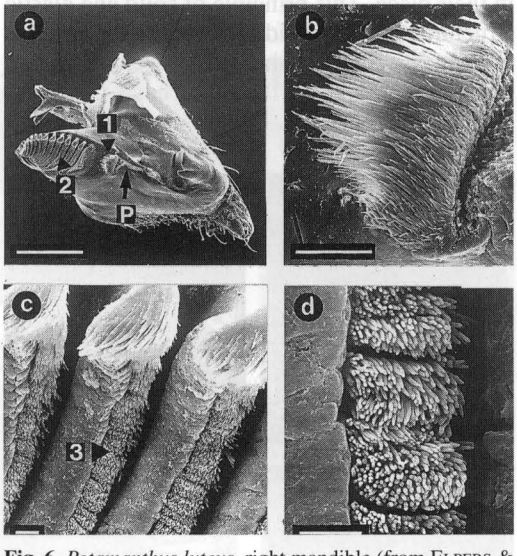

Fig. 6. *Potamanthus luteus*, right mandible (from ELPERS & TOMKA 1994b). a: top view of molar surface, prostheca (= P) and canines; b: cuticular brush between molar surface and inner canine (= enlargement of position 1 shown in a); c: brush-like and solid ridges on molar surface (enlargement of position 2 shown in a); d: brush-like ridge on molar surface (= enlargement of position 3 shown in c) (scale: a = 250 µm; b = 25 µm; c, d = 5 µm).

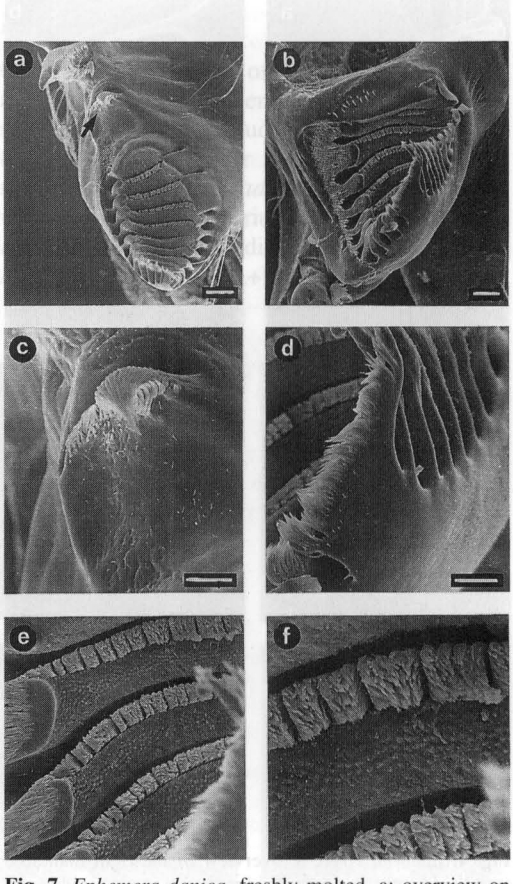

Fig. 7. *Ephemera danica*, freshly molted. a: overview on right mandible (arrow = cuticular brush); b: overview on left mandible; c: cuticular brush between inner canine and molar surface; d: structure of the left mandible; e: brush-like and solid ridges on molar surface; f: brush-like and solid ridges on molar surface (scale: a, b = 50 µm; c-e = 25 µm; f = 5 µm).

Phylogeny

The mandibular structures can also be viewed from a phylogenetic point. The structure of the molar surface of the mandibles with solid and brush-like ridges is similar within the Ephemeroidea but seems to be different from the molar surface of other mayflies, for example *Baetis* (BROWN, 1961, ARENS, 1989, 1990), *Rhithrogena* (ARENS, 1990), *Epeorus* (ARENS, 1990), *Ecdyonurus* (ARENS, 1989, 1990) or *Oligoneuriella* (ELPERS & TOMKA, 1992). Whether this microstructure of the molar surface is only to be found within the Ephemeroidea has to be determined on a greater variety of larvae.

The larvae of the Behningiidae, also a member of the Ephemeroidea, have not evolved a molar surface with alternating ridges. In contrast to all other analysed ephemeroidean larvae, they have reduced their molar surface to a sharp ridge due to their carnivorous feeding habits (ELPERS & TOMKA, 1994b).

Nevertheless, the species of the Ephemeroptera have evolved characteristic patterns among the nerves, muscles and structure of the mouthparts as a result of the habitat they are living in.

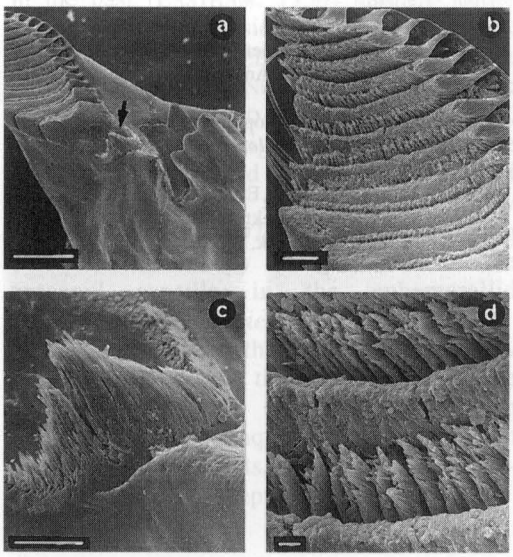

Fig. 8. *Campylocia* sp. a: overview of the right mandible with molar surface and canines (arrow = cuticular brush); b: ridges of molar surface; c: cuticular brush between inner canine and molar surface; d: brush-like and solid ridges on molar surface (scale: a = 250 µm; b, c = 50 µm; d = 5 µm).

These characteristic patterns can be used in searching for apomorphic characters to suggest the phylogenetic system. Although there is evidence for the above statements, these results can only be preliminary and need to be analysed on a larger number of individuals of different species and families.

The brush-like structure and the ridge between inner canines and molar surface was found only on the right mandible and may be a syn-apomorphic character for certain groups of mayflies within the Ephemeroidea (Table 1). Nevertheless, Table 1 does not give a sister relationship of certain families of the Ephemeroidea but shows only the distribution of the characters found on the mandibles of the analysed species.

The relevance for the phylogenetic relationship within the Ephemeroidea of these characteristic features has to be determined by a comparison with the other apomorphic characters already found. If the ridge between inner canine and molar surface or the cuticular brush between

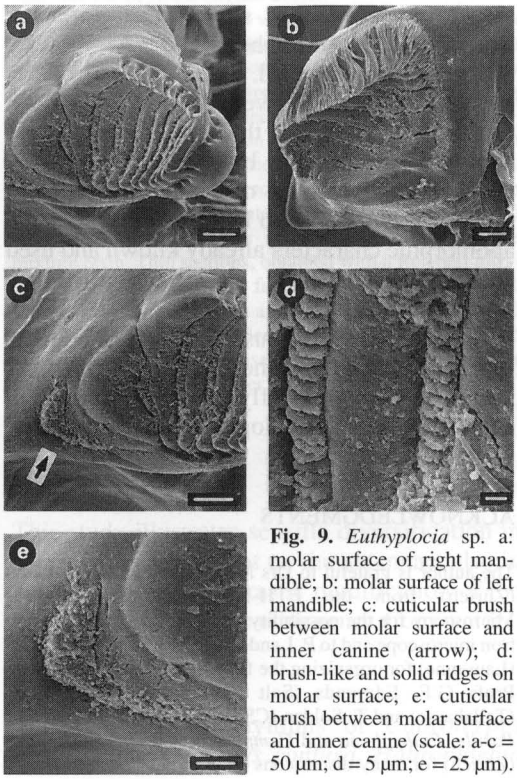

Fig. 9. *Euthyplocia* sp. a: molar surface of right mandible; b: molar surface of left mandible; c: cuticular brush between molar surface and inner canine (arrow); d: brush-like and solid ridges on molar surface; e: cuticular brush between molar surface and inner canine (scale: a-c = 50 µm; d = 5 µm; e = 25 µm).

Table 1. Distribution of characters found on the mandibles of some species of Ephemeroidea.

Species (Family)	Molar surface with solid and brush-like ridges	Ridge between inner canine and molar surface (right mandible)	Cuticular brush between inner canine and molar surface (right mandible)
Palingenia longicauda (Palingeniidae)	++	++	- -
Ephoron virgo (Polymitarcyidae)	++	++	- -
Povilla corporeali (Polymitarcyidae)	++	++	- -
Potamanthus luteus (Potamanthidae)	++	- -	++
Ephemera danica (Ephemeridae)	++	- -	++
Campylocia sp. (Euthyplociidae)	++	- -	++
Euthyplocia sp. (Euthyplociidae)	++	- -	++

inner canine and molar surface determines to be a synapomorphic character, then the family/ subfamily grouping given by MCCAFFERTY (1991) will not fit the grouping that might result on the base of this study. Therefore the classification of the Ephemeroidea McCafferty proposed was not used. The author works on the basis of families given by HUBBARD (1990) until the relevance of the found characters is analysed. It has to be outlined that the phylogenetic relevance of the characters found in this study still has to be checked against the apomorphic characters already known and used for the phylogenetic classification of the Ephemeroidea.

Nevertheless, the discussed structures on the mandibles, as well as the structure of the other mouthparts of the mayfly larvae, are important for ecological and phylogenetic investigations.

ACKNOWLEDGMENTS

The author is grateful to Drs M. Müller and R. Herrmann (Zürich) from the ETH-Laboratory for Electron Microscopy for the possibility of using the scanning electron microscope and to P. Landolt (Fribourg) and M. Sartori (Lausanne) for organizing the field trip to Hungary. I thank Profs G.F. Edmunds (Salt Lake City), W.L. Peters (Tallahasse) and T. Soldan (CSFR) for the gift of larvae of *Povilla, Euthyplocia* and *Campylocia* and Dr. Ivan Tomka (Zürich) for many discussions on mayflies.

REFERENCES

ARENS, W. 1989. Comparative functional morphology of the mouthparts of stream animals feeding on epilithic algae. Arch. Hydrobiol. Suppl. 83: 253-354.

ARENS, W. 1990. Wear and tear of mouthparts: a critical problem in stream animals feeding on epilithic algae. Can. J. Zool. 68: 1896-1914.

BROWN, D.S. 1961. The morphology and functioning of the mouthparts of *Cloeon dipterum* L. and *Baetis rhodani* PICTET (Insecta: Ephemeroptera). Proc. Zool. Soc. London. 136: 147-176.

ELPERS, C. & TOMKA, I. 1992. Struktur der Mundwerkzeuge und Nahrungsaufnahme bei den Larven von *Oligoneuriella rhenana* IMHOFF (Ephemeroptera: Oligoneuriidae). Mitt. Schweiz. Ent. Ges. 65: 119-139.

ELPERS, C. & TOMKA, I. 1994a. Structure of mouthparts and feeding habits of *Potamanthus luteus* (LINNÉ) (Ephemeroptera: Potamanthidae). Arch. Hydrobiol. Suppl. 99(1/2): 73-96.

ELPERS, C. & TOMKA, I. 1994b. Mouthparts of the predaceous larvae of the Behningiidae (Insecta: Ephemeroptera). Arch. Hydrobiol. Suppl. 99(4): 381-413.

HUBBARD, M.D. 1990. Mayflies of the world. A catalog of the family and genus group taxa (Insecta: Ephemeroptera). Flora & Fauna Handbook No. 8, Sandhill Crane Press, Inc., Gainesville, Florida.

LANDOLT P., SARTORI M., ELPERS C. & TOMKA I. 1995. Biological studies of *Palingenia longicauda* (OLIVIER) (Ephemeroptera: Palingeniidae) in one of its last European refuges - Feeding habits, ethological observations and egg structure. pp. 273-281 *In*: L.D. CORKUM & J.J.H. CIBOROWSKI (Eds) Current directions in research on Ephemeroptera, Canadian Scholar's Press Inc., Toronto.

MCCAFFERTY, W.P. 1991. Toward a phylogenetic classification of the Ephemeroptera (Insecta): a commentary on systematics. Ann. Entomol. Soc. Am. 84(4): 343-360.

STRENGER, A. 1970. Zur Kopfmorphologie der Ephemeridenlarve *Palingenia longicauda*. Zoologica 117: 1-26.

WICHARD W., ARENS W. & EISENBEIS G. 1995: Atlas zur Biologie der Wasserinsekten. Gustav Fischer Verlag, Stuttgart, Jena, New York, 338 p.