# Origin of the lower jaw in cephalopods: a biting issue

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with 4 figures

**Abstract:** A survey of serial, histological sections of cephalopod embryos at early and advanced morphogenetic stages provided evidence that always the cutting edge of the lower jaw is first connected, by a thin organic membrane, to the cutting edge of the upper jaw. The lower jaw rudiment does not exhibit any separation of the right from the left half. The evolutionary origin of the lower jaw, which has no obvious homologue in other molluscs, remains a matter of debate.

**Keywords:** Cephalopoda • jaws • development • evolution • origin

**Kurzfassung:** Die Untersuchung histologischer Schnittserien von Cephalopodenembryonen in frühen und fortgeschrittenen Morphogenesestadien ergab, dass die Beisskante des Unterkiefers immer zuerst mit der Beisskante des Oberkiefers durch eine dünne organische Membran verbunden ist. Der Unterkiefer zeigt keine sichtbare Trennung in eine rechte und eine linke Hälfte. Der evolutive Ursprung des Unterkiefers, für den bei anderen Mollusken kein Homologon vorzuliegen scheint, bleibt Gegenstand der Diskussion.

**Schlüsselwörter:** Cephalopoda • Kiefer • Entwicklung • Evolution • Ursprung

## Introduction

Cephalopods have a strong muscular buccal mass carrying powerful biting tools: the so-called jaws, which are also termed mandibles or beaks. The hard cutting edges at the anterior end of the upper and lower jaw together function like a pair of scissors or clippers when moved by the mandibular muscles (KEAR 1994; UYENO & KIER 2005, 2007). In most species the edge of the upper jaw forms a more or less prominent rostrum; for biting it moves downwards along the inner side of the cutting edge of the lower jaw, to cut off pieces from a large food item. The shape of the jaws varies greatly among cephalopods, particularly with regard to the lower jaw (NIXON 1988). In some ammonites the enlarged outer shield (hood) of the lower jaw apparently served an opercular function, probably along with acting as an antagonist for the upper jaw (LEHMANN 1990). However, the great morphological diversity of the jaws of Cretaceous Ammonoidea (TANABE & LANDMAN 2002) shows that an opercular function of the lower jaw cannot be generalized.

The upper jaw of cephalopods is very likely homologous to the jaws of other molluscs, namely Scaphopoda (SHIMEK & STEINER 1997), Monoplacophora (HASZPRUNAR & SCHAEFER 1997) and Gastropoda (e. g. LUCHTEL et al. 1997); in prosobranch and opisthobranch gastropods the jaws may be paired and/or further subdivided (VOLTZOW 1994; GOSLINER 1994).

The evolutionary morphology of the lower jaw of cephalopods is not yet elucidated. It seems at least conceivable, however, that the lower jaw of cephalopods comprises derivatives of the lateral parts of an ancestral jaw, the outer ends of which have become united ventrally in the sagittal plane of the buccal mass (BOLETZKY 1999). This idea raises the question whether the developmental origin of the lower jaw in living cephalopod embryos tells us something about the first appearance of a lower jaw in the common cephalopod ancestor. As the jaws of *Nautilus* show basically the same pattern as the coleoid jaws (NAEF 1923; TANABE & FUKUDA 1987), one may safely speculate about the common ancestor of the whole class Cephalopoda (ENGESER 1996).

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## Material and methods

Serial sagittal, frontal, and cross sections of various cephalopod embryos (collected in the bay of Banyuls or obtained in the aquarium, and fixed at different developmental stages) were used. Selected sections were drawn using a Leitz camera lucida (drawing arm). All histological sections were 7 μm in thickness. The material used for the preparation of these sections had been fixed in Halmy or Bouin's fluid, preserved in 70 % ethanol, and subsequently embedded in paraffin. After cutting, mounting, and dissolving the paraffin, sections were stained with either Azan or Masson's trichrome.

## The jaws of newly hatched cephalopods

The immediate "goal" of embryonic development in cephalopods is the achievement of a viable hatchling able to live as an active predator, capable of catching and ingesting live prey. The jaws of cephalopod hatchlings vary greatly in shape and size, partly in relation to the respective size of the newly hatched animal – that in turn depends on the size of the egg from which it developed (BOLETZKY 1974). The example shown here are the jaws of a loliginid squid hatchling (Fig. 1). Although they are very delicate, they already exhibit the most typical parts of coleoid jaws, such as the hood and rostrum in the upper jaw and the hood and wings in the lower jaw (CLARKE & MADDOCK 1988; external lamella in KLUG et al. 2005), but their actual shape resembles only remotely adult squid jaws (NAEF 1923: pl. 17 fig. 1). In contrast to the adult condition, the lower jaw has a den-

ticulated cutting edge, a character that seems to be limited to very small planktonic cephalopods (BOLETZKY 1974), and to the peculiar pygmy squids of the genus *Idiosepius* where it occurs also in the adult (ADAM 1986).

## Morphogenesis of the buccal mass and the formation of jaws

Based on semi-schematic drawings of medial sagittal sections of embryos cut at different developmental stages, NAEF (1928: 117, 126, 152, 198, 225, 240, 274, 287) illustrated the stomodaeal invagination and the subsequent folding processes that characterize the formation of the buccal mass. NAEF's text-fig. 100 is reproduced here as Fig. 2; it shows some of the changes occurring from stage XIV (a) to stage XVII (b), especially the elevation of the papilla containing the salivary gland duct (Gd) and the strong folding of the inner lip (Jl) and the outer lip (Al). What it does not show is the delicate line which in fact connects the tip of the upper jaw (Ok) to the tip of the lower jaw (Uk). Similar figures were produced by more recent authors (BOLETZKY 1967; MEISTER 1972; FUCHS 1973). None of these illustrations shows the early connection between upper and lower jaw. Representing a thin organic membrane, the connecting line is inconspicuous in sagittal sections, and depending on the staining technique, it can easily go unnoticed. Once recognized, usually in relatively large embryos at advanced stages (Fig. 3), it is always detected in smaller embryos (if staining is insufficient, phase contrast optics will provide the evidence). In any event,
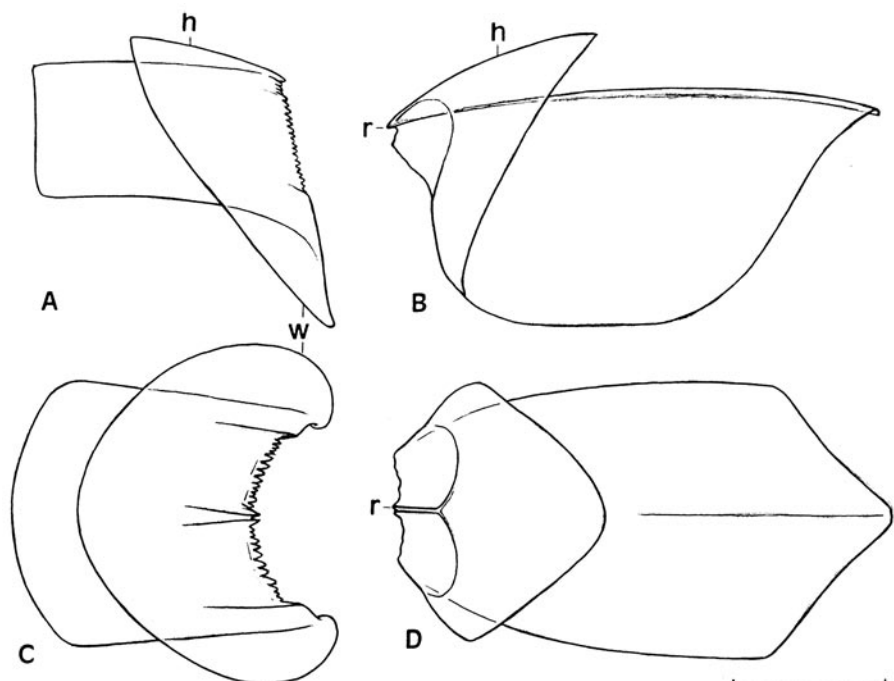


**Fig. 1.** The nearly transparent jaws of a newly hatched squid (*Loligo vulgaris*) obtained by maceration of a fresh-dead specimen. Lateral view of lower (A) and upper jaw (B). Ventral view of lower jaw (C) and dorsal view of upper jaw (D). Note the denticulation on the cutting edge of the lower jaw. – h, hood; r, rostrum; w, wing. – Scale bar = 0.1 mm.
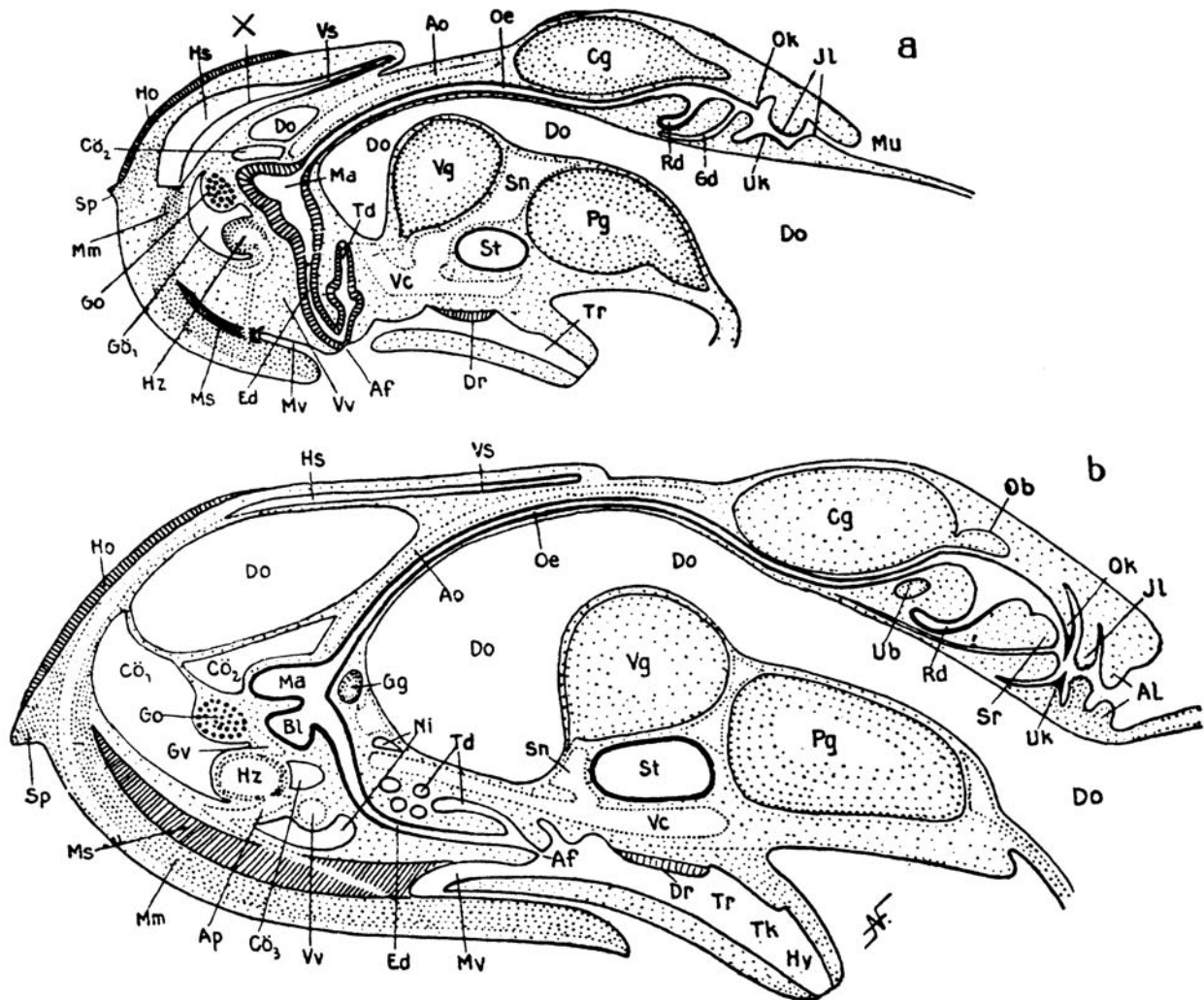
**Fig. 2.** A reproduction of NAEF's (1928) Text-fig. 100: Medial sections of two embryos of *Sepietta oweniana*, in semischematic representations; **a**: stage XIV, **b**: stage XVII (about x60 natural size). – Af, anus; Al, outer lip; Bl, caecum; Cg, cerebral ganglion; Cö, coelome, pericardium; Do, yolk organ; Dr, funnel organ; Ed, hindgut; Gd, salivary gland duct; Gg, Ganglion gastricum; Go, gonad; Ho, Hoyle's organ; Hs, shell membrane inside the shell sac; Hy, membrane closing the funnel tube; Hz, heart; Jl, inner lip; Ma, stomach; Mm, muscular mantle; Ms, mantle cavity septum; Mu, mouth opening; Ni, kidney; Ob, upper buccal ganglion; Oe, foregut; Ok, upper jaw; Pg, pedal ganglion; Rd, radula pouch; Sp, terminal spine; Sr, subradular organ; St, statocyst (tangentially cut); Td, ink duct and gland; Tk, rudiment of funnel valve; Tr, funnel tube; Ub, lower buccal ganglion; Uk, lower jaw; Vc, Vena cava; Vg, visceral ganglion.

the presence of a membrane can also be verified in cross sections or in frontal sections (Fig. 4) from stage XII onwards. In stages up to and including stage XI of NAEF (1928), no trace of the membrane or any jaw rudiments are yet present.

## Discussion

The cells that must have secreted the material composing the early organic membrane appear to detach from it during stages XII and XIII. Special fixation techniques (e. g. osmic acid shock fixation) will have to be used in future studies to minimize or avoid any fixation artifacts that may be responsible for a detachment of the mem-

brane. This membranous sheet, which stretches from the space between the inner and outer lip (Figs. 4A–C) to the oesophagus, and which is also connected with the membrane lining the radular sac and the buccal palps (BANDEL 1988), becomes integrated in the upper and lower jaw (Fig. 3). It remains to clarify how and when the portion of the membrane that connects the cutting edges of the jaws disappears. It may be torn when the muscles of the buccal mass become fully functional and start working. Whatever the mechanism responsible for its elimination, the connecting membrane disappears prior to the loss of the epithelial membrane derived from the outer lip that is responsible for mouth closure during late embryonic stages (BOLETZKY 2003: 163).
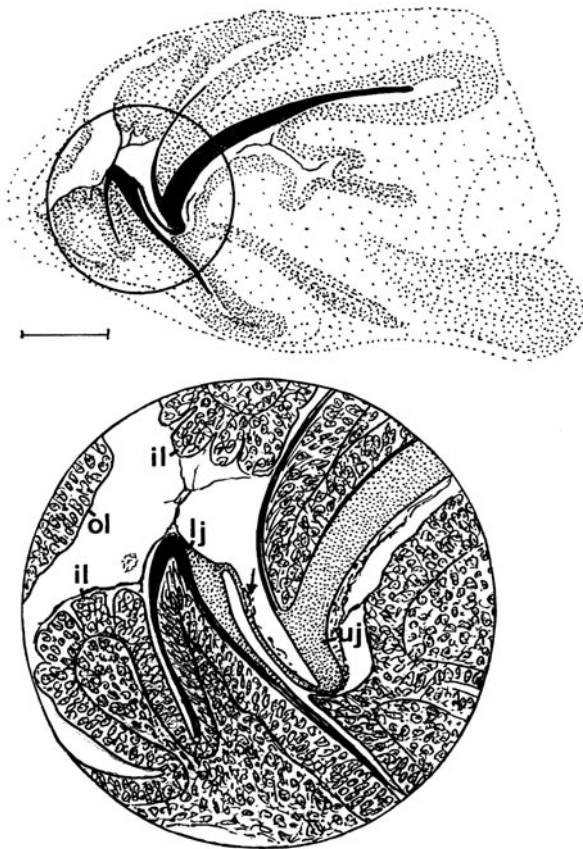
**Fig. 3.** Camera lucida tracing of a medial sagittal section of buccal mass in a *Sepia officinalis* embryo at stage XVII–XVIII of NAEF (1928). The main figure (scale bar = 0.1 mm) shows the upper and lower jaws and the connecting membrane in black, the circled part, at higher magnification (below), shows the details of the connecting membrane (arrow) between upper (uj) and lower jaw (lj) and differentiation of the inner surface of each cutting edge, the black layer probably corresponding to the tanned parts of the jaws. Note the splitting organic membranes in the pore of the rugged inner lip (il), whereas the outer lip (ol) is completely closed.

The presence of an early organic membrane raises several interesting questions, especially with regard to the fact that the upper and lower jaw are known to be formed from organic material secreted by highly specialized cells, the so-called beccublasts (DILLY & NIXON 1976). If the organic membrane and the jaws are both secreted by these beccublasts, the question arises: is there a replacement of secretory cells, or are the beccublasts differentiated long before the other cells of the buccal mass are ready to function? The fact that the organic membrane appears to close the inner lip pore (leading to the space lying behind the outer lip) is also noteworthy. It should be recalled here that the entire digestive tract develops as a closed system until the anal pore opens around stages XV–XVII of NAEF (1928). Once the anal pore is formed, peristaltic intestinal movements pumping perivitellin fluid into the gut appear to maintain a

certain pressure inside the digestive tract (unpubl. pers. obs.).

The question of the evolutionary origin of the lower jaw is not easily answered by simply observing the development of the jaws during organogenesis. The single membrane of organic material, which is subsequently moulded by the elevation of folds and ridges that fill most of the space of the buccal cavity, does not visibly "recapitulate" any paired structure in the lower jaw. However, what should be considered more closely in early organogenesis is the establishment of the ridges producing the beccublast populations responsible for the upper and lower jaw formation. Figs. 4D–F demonstrate the close topological link between these ridges in the lateral walls of the buccal cavity. Since the upper and lower jaw must ultimately be co(ad)apted in functional terms, the hypothesis (mentioned in the Introduction) suggesting a secondary splitting of an originally clasp-shaped anlage into two crescent-shaped rudiments – adjacent and complementary to one another – is certainly attractive when speculating about the outset of cephalopod jaw development.

## Acknowledgements

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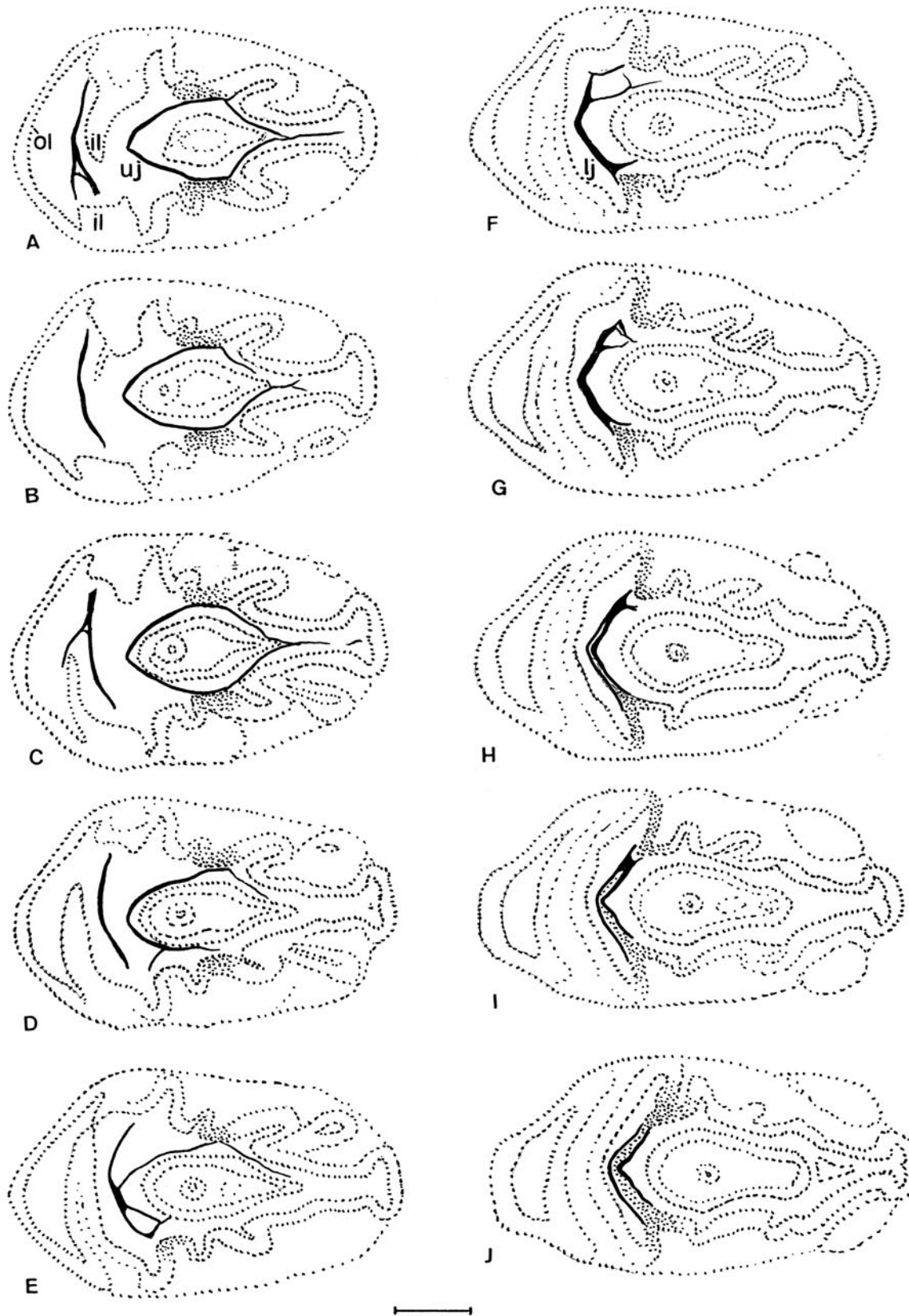
**Fig. 4.** Camera lucida tracings of serial frontal sections of buccal mass in a *Rossia macrosoma* embryo at stage XIV–XV of Nᴀᴇꜰ (1928). Starting from the most dorsal level (A), increasingly deeper (more ventral) levels are represented (NB: sections are 7 m in thickness). Behind the closed outer lip (ol), the pore of the inner lip (il) is still very large (A–D); it disappears in E, where the membranous connection is visible between the upper jaw (uj; note stippled ectodermic surfaces representing the attachment zones) and the lower jaw (lj). The lower jaw alone is visible from F to J, with its lateral attachment zones (stippling). Note that the cutting plane is slightly slanting (cf. stippling in E). – Scale bar = 0.1 mm.

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