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Octobrachia - a diphyletic taxon?

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Abstract: Until today, the phylogenetic origin of the Octopoda and the Cirroctopoda is poorly understood, since a gladius that unambiguously links the fin supports of the both groups is still unknown from the fossil record. The present article summarises previous ideas concerning the phylogenetic and morphogenetic origin of the Octobrachia. Besides a general introduction into the gladius morphology of some coleoid families, the author focuses on two families whose gladii are well known, but which have never been considered before as potential ancestors of the Octobrachia: the Muensterellidae and the Palaeololiginidae. The author finally proposes three different phylogenetic scenarios for the derivation of the Octopoda and Ciroctopoda: A) a monophyletic origin from muensterellids, B) a monophyletic origin from palaeololiginids and C) a diphyletic origin from muensterellids and palaeololiginids.

Zusammenfassung: Bis heute ist der phylogenetische Ursprung der Octopoda und Cirroctopoda ungeklärt, da der Fossilbericht noch keinen Gladiustypen hervorgebracht hat, der die Gladiusrudimente dieser beiden Gruppen eindeutig verbinden könnte. Der vorliegende Artikel fasst die früheren Vorstellungen über den phylogenetischen und morphogenetischen Ursprung der Octobrachia zusammen. Neben einer allgemeinen Vorstellung von Gladien verschiedener Coleoidenfamilien stellt der Autor zwei Familien genauer vor, deren Gladien zwar gut bekannt sind, aber noch nie als mögliche Vorläufer der Octobrachia in Betracht gezogen wurden: die Muensterellidae und die Palaeololiginidae. Abschliessend stellt der Autor drei verschiedene phylogenetische Szenarien für der Ableitungen der Octopoda und Cirroctopoda vor: A) einen monophyletischen Ursprung von Muensterelliden, B) einen monophyletischen Ursprung von Palaeololiginiden und C) einen diphyletischen Ursprung von Muensterelliden und Palaeololiginiden.

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Introduction

The finned Cirroctopoda (= Cirrata) and the finless Octopoda (= Incirrata) are commonly regarded as sister-taxa and are therefore grouped together as Octobrachia (= Octopodiformes). The sister-group of the Octobrachia represents the Vampyromorpha, named after its only living representative *Vampyroteuthis infernalis*. The monophyly of the Octobrachia is supported by numerous cladistic analyses including both morphologic and molecular data sets (e.g. Young & Vecchione 1996, Young et al. 1998, Vecchione et al. 2000, Lindgren et al. 2004, Strugnell et al. 2005). Until today, even palaeontological studies do not doubt the monophyletic origin of the Octobrachia (Engeser & Bandel 1988, Doyle et al. 1994, Haas 2002, Bizikov 2004, Fuchs 2006).

According to the current morphological knowledge, both the unpaired fin support found in cirroctopods and the paired rods of some octopod families are usually seen as strongly modified derivates of a gladius similar to *Vampyroteuthis*. This hypothesis is mainly based on Late Cretaceous *Palaeoctopus newboldi* whose well-developed fins attach to a medially isolated gladius vestige. This early octopod clearly shows 1) that Octopoda has been primarily equipped with fins and 2) that Cirroctopoda and Octopoda diverged prior to the Late Cretaceous. Hence, the search for the phylogenetic origin of the Octobrachia means to search for an early Cretaceous or Jurassic group of coleoids with a gladius that connects a “vampyromorph” gladius and the bipartite gladius vestige of *Palaeoctopus*. As this type of gladius seems to be unknown in the fossil record, only a few considerations about the precise phylogenetic origin of the Octopoda/Cirroctopoda clade have been published (Doyle et al. 1994, Haas 2002, Bizikov 2004). Discussions on the morphogenetic origin of their fin supports are therefore strongly limited.

Since recent records of additional Cretaceous octopuses have thrown new light on the evolution of the Octobrachia (Fuchs et al. 2009), it is the aim of this article to summarise the most important theories on that topic, to check the presumed monophyly of the octobrachia and to look for alternative approaches concerning the morphogenetic origin of fin supports.

Previous theories on the phylogenetic and morphogenetic origin of the Octobrachia

On the basis of modern octopuses, Naef (1921: p. 695) suggested that the fin support represents a remnant of a gladius, the stiff, but flexible chitinous pen within the dorsal mantle of living teuthids.

Since Roger (1944a & b), when he presented the first specimens of Santonian *Palaeoctopus newboldi* (at that time the only known fossil octopus) with preserved fin supports, we have a first fossil link between the U-shaped fin supports of cirroctopods and the paired stylets of octopods. Roger (1946: fig. 14) later favoured a derivation of the Octobrachia from early teuthids.

Jeletzky (1966: p. 50), too, assumed that the Octobrachia "...must have become separated from the general teuthid stem considerably before the sepiid and teuthid branches". He considered the fin support as a reminiscent of a teuthid conus.

Donovan (1977: p. 43) first noted that the Octobrachia diverged from Mesozoic vampyromorphs. He stated: "Such a hypothesis would be supported by the fact that the gladius of *Palaeoctopus* could be derived from the wings or lateral fields of the loligosepiine gladius,…, the median field having been lost."

Fischer & Riou (1982) regarded *Proteroctopus ribeti* from the Middle Jurassic of La Voulte to be the oldest known octopod. Their arguments are however doubtful and rest primarily on the absence of a gladius vestige. Indeed, none of the coleoids from La Voulte show evidence of a gladius. In most cases, they are covered with mantle musculature or dissoluted. It is more likely, that *Proteroctopus* possessed a well developed gladius.

Doyle et al. (1994: fig.1) indicated again that the Loligosepiina, a fossil group with a gladius similar to *Vampyroteuthis*, is the root-stock of the Vampyromorpha, Octopoda and Cirroctopoda.

After a cladistic analysis based on living *Vampyroteuthis*, octopods and cirroctopods, Voight (1997: p. 318) concluded that the cirroctopod fin support represents a modified gladius and that the stylets of octopods evolved "de novo", i.e. independently from a gladius.

Young et al. (1998: p. 398) tried to reconstruct a "pre-octobrachian" (their "pre-octopod") by comparison with living *Vampyroteuthis* and by means of behaviour, but refer neither to an explicit group of direct ancestors nor to an explanation for the morphogenetic origin of the fin support.

Kluessendorf & Doyle (2000) suggested that *Pohlsepia mazonensis* from the Carboniferous Mazon Creek Formation represents a very early cirroctopod. This interpretation turn previous ideas about the time of origin of the Octobrachia upside-down, but it is highly problematic for the single specimen shows only a vague body outline.

In contrast to Donovan (1977) and Doyle et al. (1994), Haas (2002: p. 345, text-fig. 11) considered a group of the Teudopseina, the Trachyteuthididae, to be the stem-group of the Vampyromorpha, Octopoda and Cirroctopoda. He had the idea that the fin support of *Palaeoctopus newboldi* is "…equivalent to the lateral strengthening of the gladii of some "Trachyteuthimorpha".

Similar to Haas (2003), Bizikov (2004: p. 79) concluded that cirroctopods and octopods must have been evolved from ancestors with a wide anterior median field due to widely separated stellar ganglia in all living vampyropods. He stated: "…forms like *Teudopsis* Muenster, 1842 (family Teudopsidae) from the early Jurassic (Toarcian), in my opinion, seems to be the most likely ancestors of recent Octopoda, as they had a wide thick gladius with partly reduced median plate."

Fuchs et al. (2007a) presented a saddle-shaped structure from the Campanian of Vancouver Island (Canada) and preliminarily interpreted this enigmatic fossil to be an unpaired fin support of a cirroctopod.

Recently, Fuchs et al. (2009) described additional fin supports from the Upper Cenomanian of Lebanon. Since the new taxa *Keuppia levante*, *Keuppia hyperbolaris* and *Styletoctopus annae* respectively show a pair of medially separated fin supports, they belong without doubts to the octopod lineage. Whereas the blade-like fin supports of *Keuppia* point to a divergence time of Octopoda and Cirroctopoda during early Cretaceous times, the strongly reduced stylet-like vestiges of *Styletoctopus* rather indicates a significantly earlier separation. As the bipartite fin support of *Keuppia levante* und *Keuppia hyperbolaris* taken as united structure resemble a loligosepiid gladius, Fuchs et al. (2009) re-considered the idea of Donovan (1977) and Doyle et al. (1994) whereupon octobrachians might have been originated from loligosepiids.

Despite these new finds, a morphological chain of fossils that unambiguously document the evolutionary pathway within the Octobrachia is still missing until today.

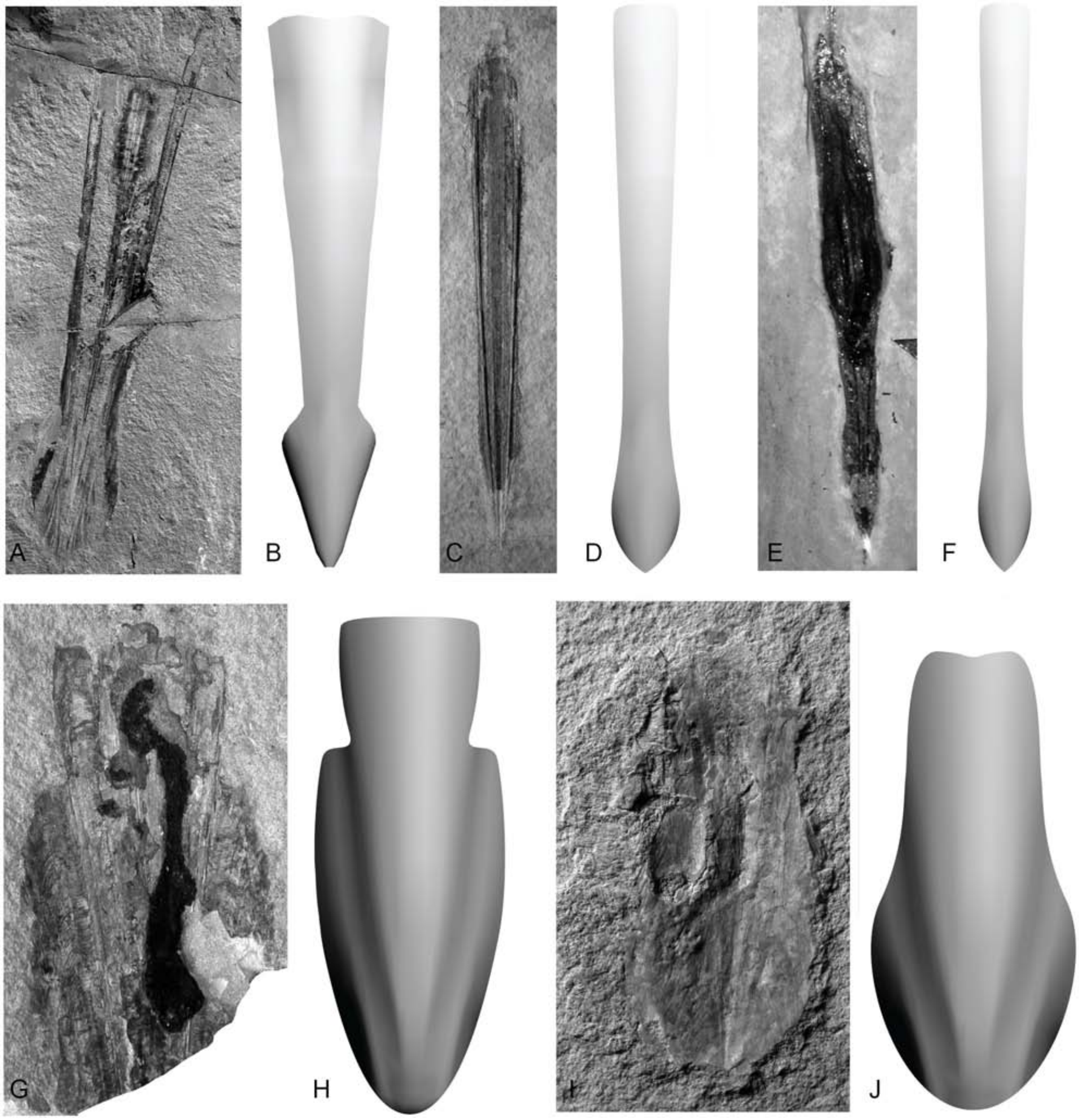
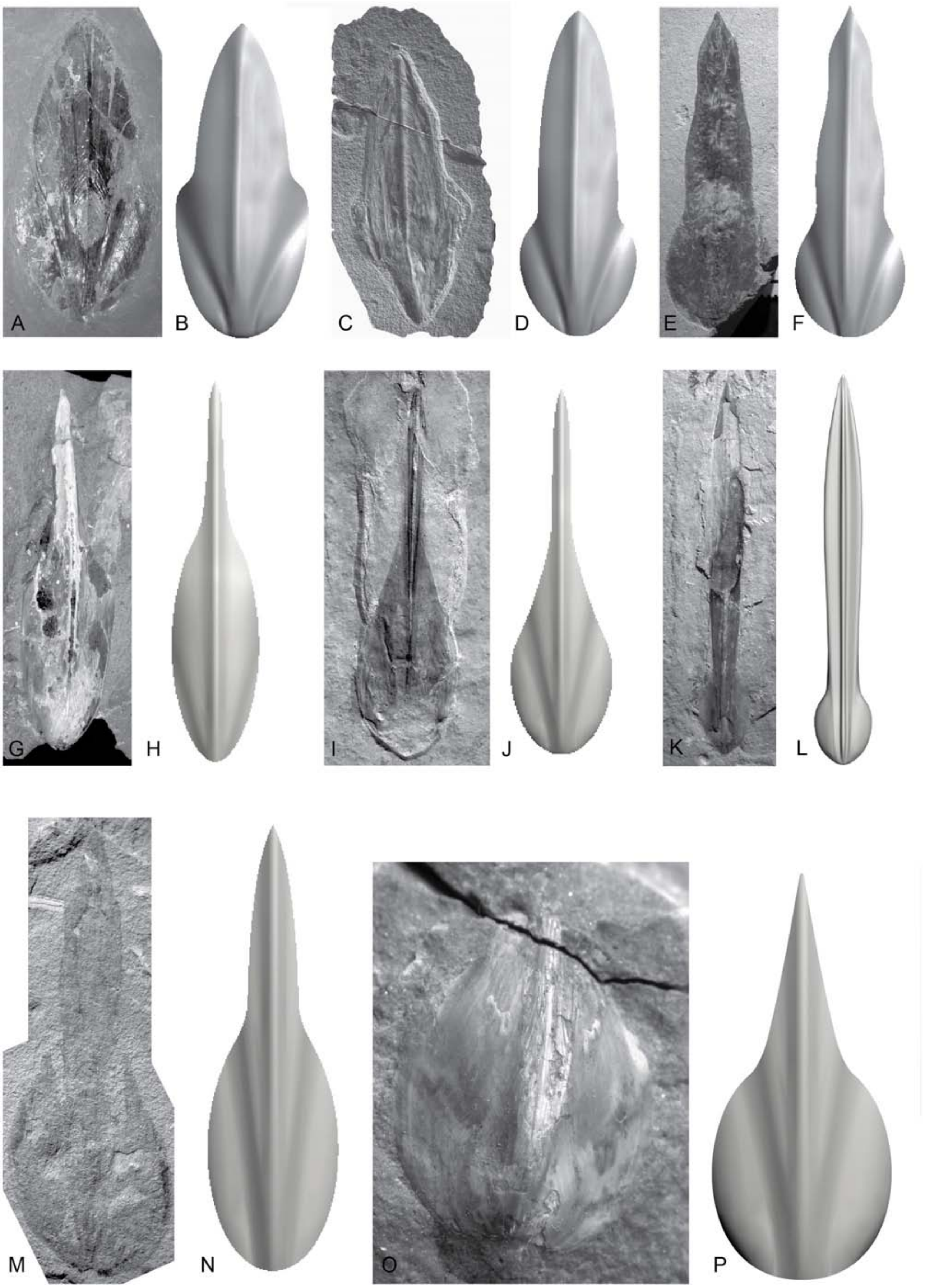


Fig. 1: A-F, Prototeuthidid gladii, G-H, loligosepiid gladii. A-B, *Paraplesioteuthis hastata* (Toarcian); C-D, *Dorateuthis tricarinata* (Tithonian); E-F, *Dorateuthis syriaca* (Cenomanian); G-H, *Parabelopeltis flexuosa* (Toarcian); I-J, *Doryanthes munsteri* (Tithonian).

Observations

Since the pioneers of coleoid research, the gladius is commonly considered to be the initial structure from which the fin supports of the octobrachia have derived. Indeed, apart from the gladius, there is no alternative shell component known from the fossil record that could have given rise to a fin support. In Mesozoic gladius-bearing coleoids as well as in modern *Vampyroteuthis*, the fins attach directly to the hyperbolar zones and partly to the lateral fields (Bizikov 2004). The medially isolated fin supports of *Keuppia* and *Palaeoctopus* show that the reduction must have affected the median field. Consequently, the search for the morphogenetic origin of the octobrachian fin support must be focussed on gladius types that signify evidence of a median field reduction.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← **Fig. 2:** Teudopseid gladii. A-F, trachyteuthidid gladii; G-P, palaeololiginid gladii. A-B, *Teudopsis subcostata* (Toarcian); C-D, *Trachyteuthis teudopsiformis* (Tithonian); E-F, *Glyphiteuthis libanotica* (Cenomanian); G-H, *Teudopsis bunelii* (Toarcian); I-J, *Palaeololigo oblonga* (Tithonian); K-L, *Rachiteuthis donovani* (Cenomanian); M-N, undescribed palaeololiginid (Cenomanian); O-P, *Styloteuthis convexa* (Turonian).

In contrast to the huge variety of modern teuthid gladii where morphological comparisons and thus classifications have proved to be highly problematic (Toll 1998), Mesozoic gladii can be easily classified into three different types (Fuchs 2006, Fuchs et al. 2007b, c, Fuchs & Weis 2008, in press): 1) the prototeuthidid-type, 2) the loligosepiid-type, and 3) the teudopseid-type.

In the evolutionary development of the prototeuthidid-clade, there is a distinct trend towards a rachis-like strongly elongated median field (Fuchs et al. 2007c). Hyperbolar zones and lateral fields, the fin attachment sites, are reduced and restricted to the most posterior part of the mantle (Fig. 1A-F). This pathway shows no evidence of a median field reduction and rather indicates a trend towards torpedo-shaped fast swimming forms with terminal fins that control the horizontal stability of the animal during a highly effective jet-propulsion.

The loligosepiid clade, which is repeatedly supposed to be the branch leading to living *Vampyroteuthis* (Fuchs & Weis 2008: fig. 8), is characterised by a wide anterior median field, but without any signs of a median field reduction (Fig. 1G-J).

Clear evidence of a median field reduction can be observed only in the Teudopseina (Fuchs et al. 2007b, Fuchs & Weis in press). With respect to this, Haas (2002) and Bizikov (2004) were right. However, the trachyteuthidid lineage (*Teudopsis subcostata – Trachyteuthis – Glyphiteuthis*), as suggested by Haas (2002), retains a well developed median field (Fig. 2A-F).

The other two lineages within the Teudopseina, the palaeololiginid and the muensterellid lineages, probably originated from forms similar to *Teudopsis bunelii* or *Teudopsis bollensis* (Fuchs & Weis in press). Both of them exhibit a narrow anterior median field when compared with *Teudopsis subcostata*. Particularly, *Teudopsis bunelii* with its rachis-like anterior median field might represent the root-stock of the Palaeololiginidae (Fig. 2G-L) and the Muensterellidae (Fig. 3A-D).

Within the palaeololiginid clade there is one lineage leading from Tithonian *Palaeololigo oblonga* to Cenomanian *Rachiteuthis donovani* (Fig. 2I-L). This branch seems to elongate the free rachis, i.e. this pathway is similar to prototeuthidids and therefore not characterised by a clearly reduced median field). However, the second lineage within the palaeololiginid clade is typified by a clear median field reduction. It is leading from *Palaeololigo* (or *Palaeololigo*-like forms) to a still undescribed Cenomanian form from Lebanon (Fuchs in revision) and probably to Turonian *Styloteuthis convexa* (Fig. 2M-P). The latter taxa exhibit a gladius with a median field that is considerably reduced in width and length.

The muensterellid clade, represented during the Tithonian by *Münsterella scutellaris* and *Celaenoteuthis incerta,* is exemplified by a gladius with an obviously short rachis and a cap-like posterior gladius end (Fuchs et al. 2003, Fuchs 2006). Their median field is virtually reduced to the rachis. Although late Cretaceous muensterellids, such as *Tusoteuthis*, *Enchoteuthis*, *Niobrarateuthis* and *Kansasteuthis*, developed a very long rachis, early Cretaceous (Albian) *Münsterella tonii* from Australia retains a short and remarkably narrow rachis (Wade 1993).

From all known types of Mesozoic gladii, the muensterellid gladius exhibits the smallest median field area (Fig. 3A-D). Additionally, muensterellids possess a second growth front, which allows the gladius to grow posteriorly.

In both groups, the palaeololiginids and the muensterellids, the rachis-like median field reaches the anterior end of the dorsal mantle. This means that a gladius restricted to the posterior part of the mantle is still unknown from the fossil record.

Phylogenetic and morphogenetic implications

The genera *Palaeoctopus*, *Keuppia* and particularly *Styletoctopus* unambiguously indicate that the phylogenetic origin of the Octobrachia occurred prior to the late Cretaceous (Fig. 4A-H).

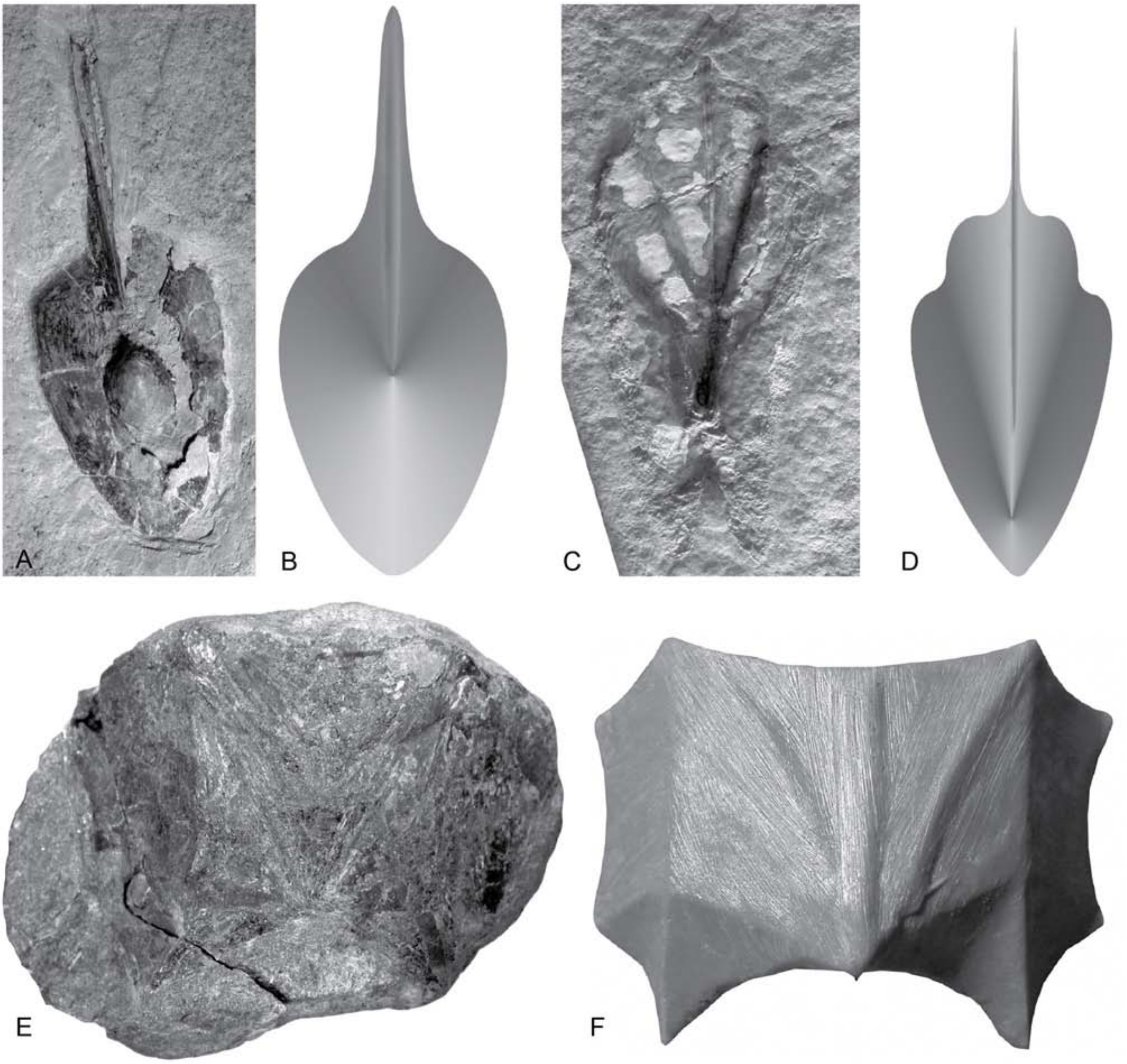

Fig. 3: Teudopseid gladii. A-D, muensterellid gladii; A-B, *Münsterella scutellaris* (Tithonian); C-D, *Celaeonoteuthis incerta* (Tithonian). E-F, presumed cirroctopod gladius vestige (Campanian).

Certainly, the Octobrachia might have originated from a group of ancestors, which is still unknown from the fossil record, but in the light of the current knowledge about fossil coleoids, the root-stock of the Cirroctopoda and Octopoda might have separated either from a muensterellid branch or from a palaeololiginid branch (Figs. 5-7).

At least three different branching patterns are conceivable:

Scenario A (Fig. 5): monophyletic origin from muensterellid ancestors

The octobrachian fin support (Fig. 3E-F) morphogenetically derived from a muensterellid gladius. This scenario is supported by the morphology on the saddle-shaped (or tent-like) fin support from the Campanian. Both structures, the presumed cirroctopod fin support and the muensterellid gladius, are unique in having two growth fronts, an anterior and a posterior. The entire reduction of the very short and narrow median field as present in *Münsterella* or *Celaenoteuthis* is only a little transformational step towards a U-shaped fin support.

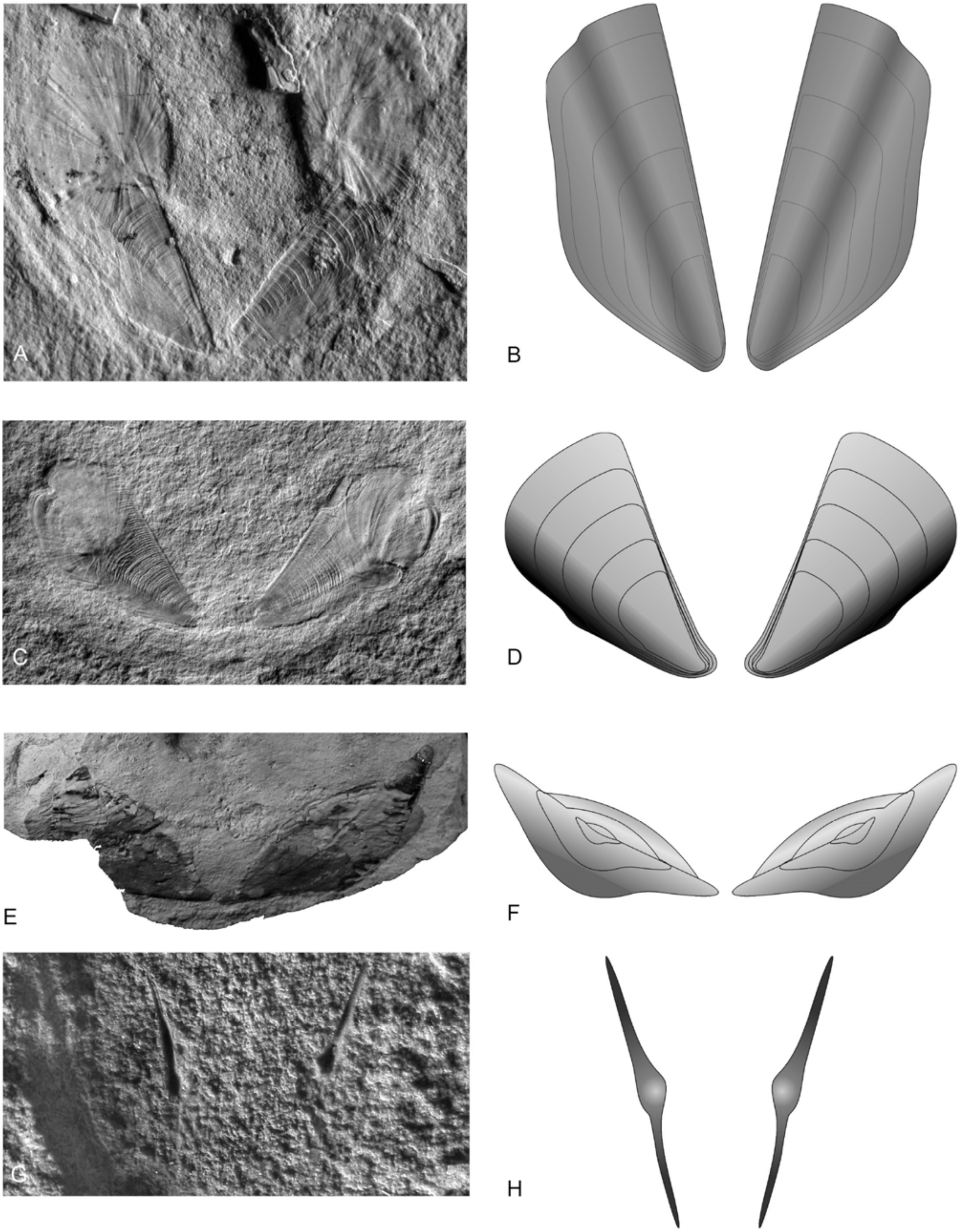

Fig. 4: A-F, palaeoctopodid gladius vestiges; A-B, *Keuppia hyperbolaris* (Cenomanian); C-D, *Keuppia levante* (Cenomanian); E-F, *Palaeoctopus newboldi* (Santonian); G-H, octopodid gladius vestige (*Styletoctopus annae*, Cenomanian).

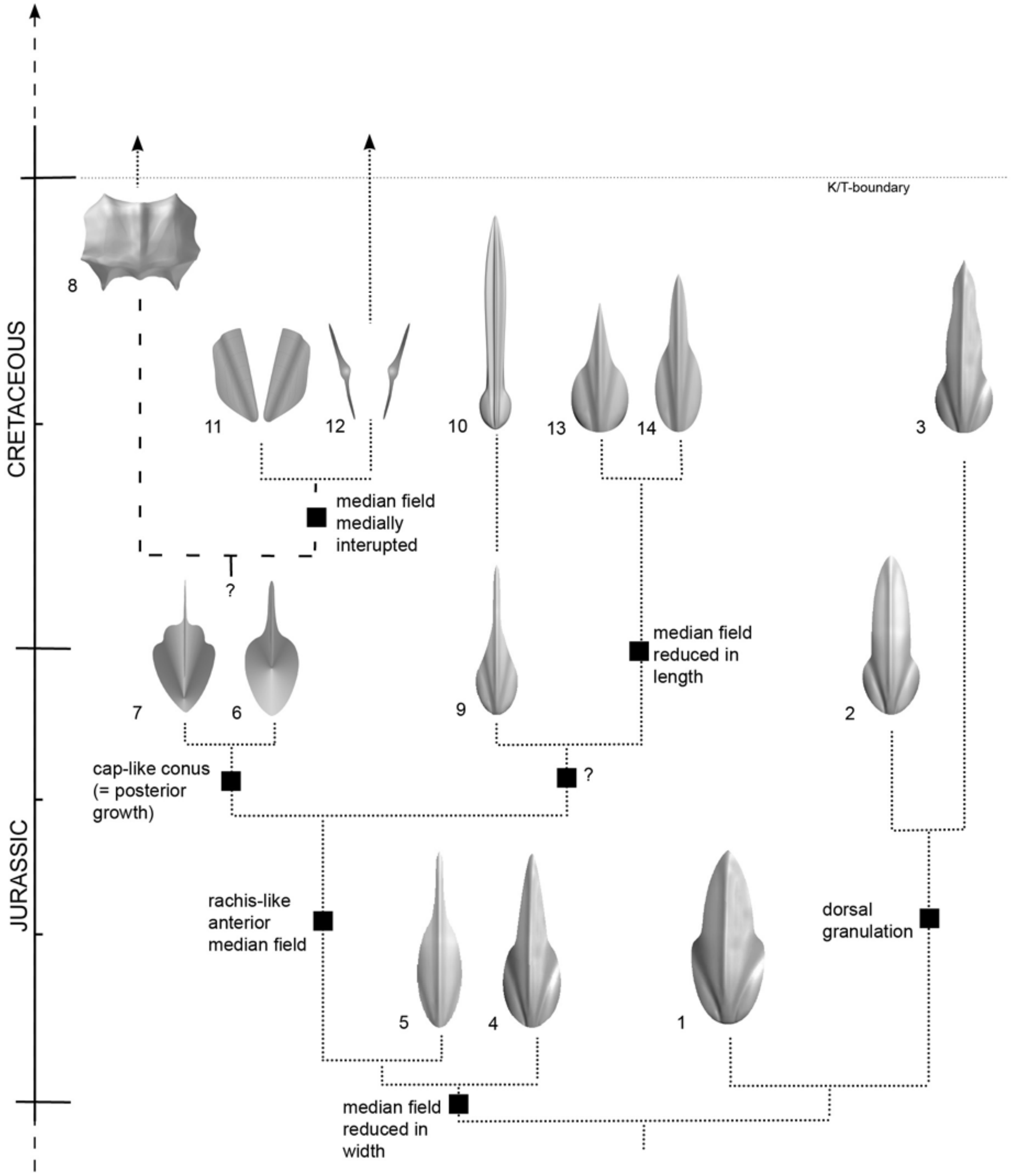

Fig. 5: Phylogenetic scenario (scenario A) indicating a monophyletic origin of the Octobrachia from the muensterellid lineage. **1.** *Teudopsis subcostata* **2.** *Trachyteuthis teudopsiformis* **3.** *Glyphiteuthis libanotica* **4.** *Teudopsis bollensis* **5.** *Teudopsis bunelii* **6.** *Münsterella scutellaris* **7.** *Celaeonoteuthis incerta* **8.** presumed cirroctopod **9.** *Palaeololigo oblonga* **10.** *Rachiteuthis donovani* **11.** *Keuppia hyperbolaris* **12.** *Styletoctopus annae* **13.** *Styloteuthis convexa* **14.** undescribed palaeololiginid.

Derivation of Cirroctopoda and Octopoda from muensterellids is furthermore supported by the bipartite vestiges of *Palaeoctopus* and *Styletoctopus*, which are also known to grow in two directions around a central nucleus (Fuchs et al. 2009). The absence of a posterior growth front in the genus *Keuppia* seems to contradict this scenario, but on the other hand, it must not necessarily challenge it, because *Keuppia* might already represent a strongly modified side-branch of the Palaeoctopodidae with a secondarily reduced posterior growth front.

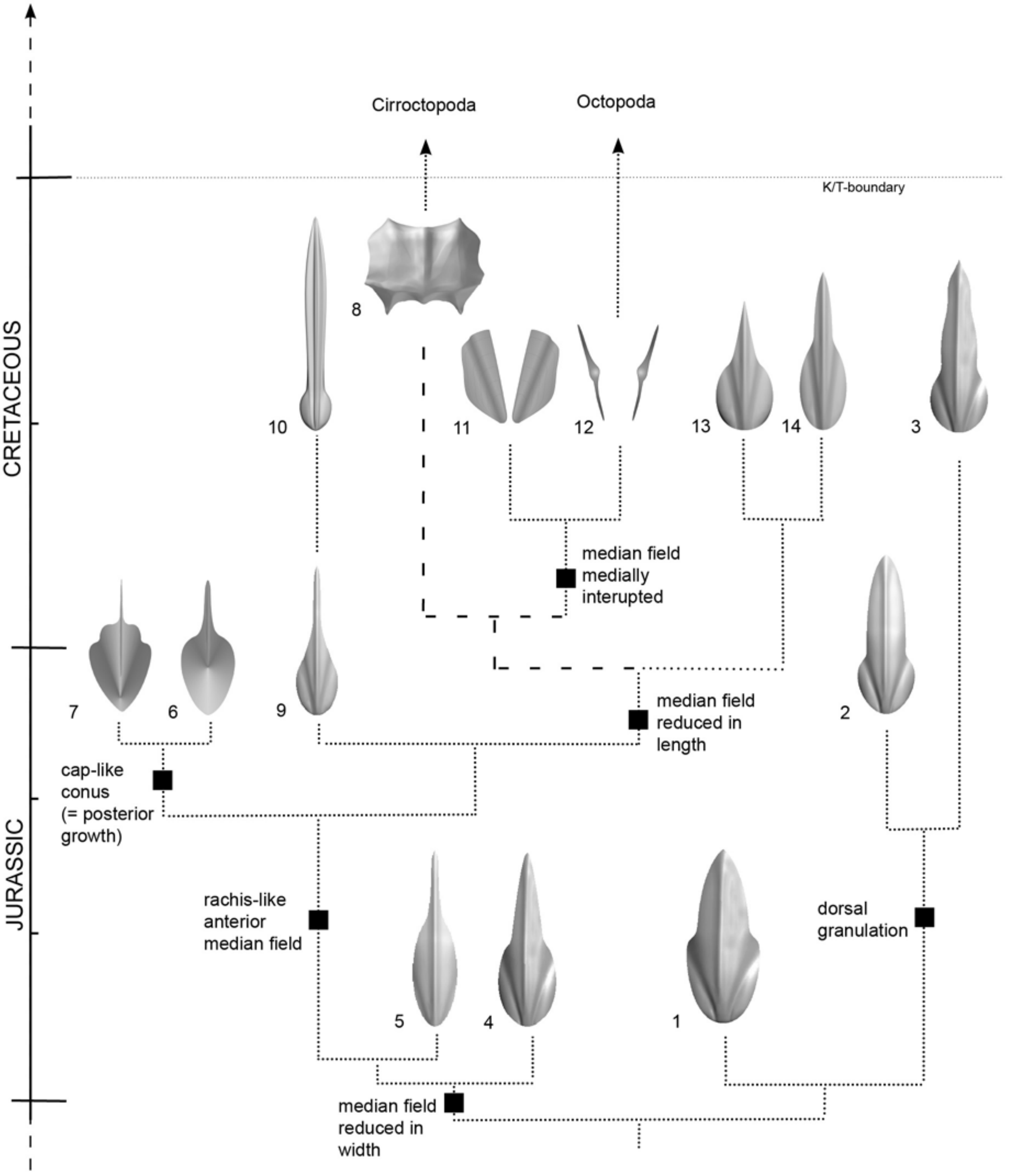

Fig. 6: Phylogenetic scenario (scenario B) indicating a monophyletic origin of the Octobrachia from the palaeololiginid lineage.

Scenario B (Fig. 6): monophyletic origin from palaeololiginid ancestors

The octobrachian fin support developed from a palaeololiginid gladius. This scenario is mainly based on an unusual type of late Cretaceous gladius, which is dominated by hyperbolar zones and lateral fields. This obviously indicates an evolutionary lineage within the Palaeololiginidae that is characterised through a strongly reduced median field. The octobrachian gladius vestige therefore possibly evolved from a side branch of the Palaeololiginidae. The (hypothetical) loss of a median field in this lineage would likewise produce a U-shaped gladius vestige; a subsequent median interruption a bipartite gladius vestige similar to *Keuppia*.

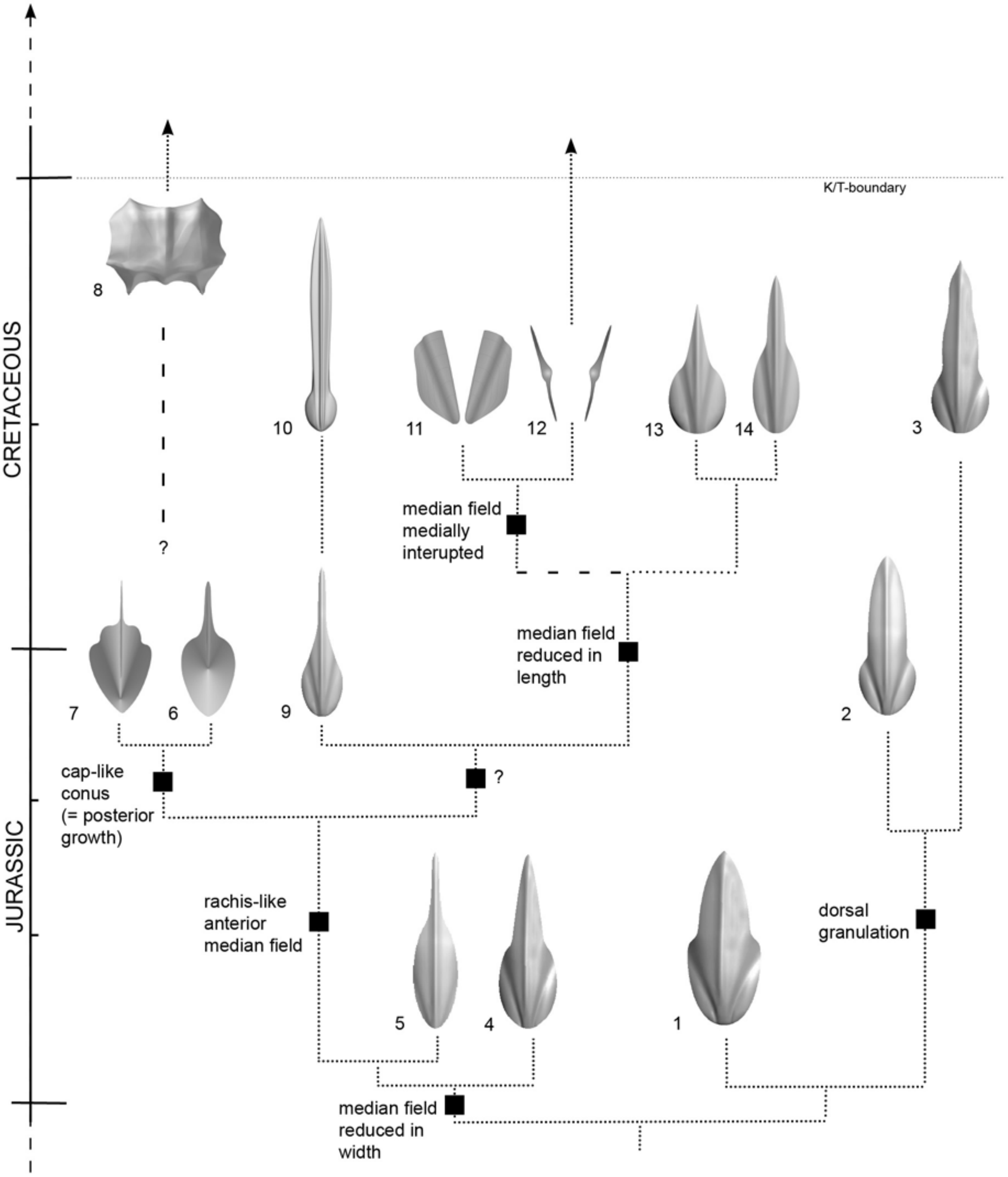

Fig. 7: Phylogenetic scenario (scenario C) indicating a diphyletic origin of the Octobrachia from the muensterellid lineage (Cirroctopoda) and the palaeololiginid lineage (Octopoda).

The existence of a posterior growth front in the Campanian cirroctopod is consequently a homoplasy. The posterior growth front in *Palaeoctopus* and *Styletoctopus* can be seen as the result of the progressive separation of the shell sacs, which are here situated in the lateral mantle.

Scenario C (Fig. 7): diphyletic origin from muensterellid and palaeololiginid ancestors

Octobrachia are not monophyletic because Cirroctopoda and Octopoda have different stem-groups. The existence of different lineages with a reduced median field opens the possibility of a polyphyletic origin of the Octobrachia.

In this scenario, the cirroctopod fin support evolved from a muensterellid gladius whereas the octopod gladius vestige can be interpreted as a derivation of a palaeololiginid gladius. The posterior growth front in the unpaired fin support is therefore a plesiomorphy adapted from a late Jurassic or early Cretaceous muensterellid. On the other hand, the gladius vestiges of *Keuppia*, *Palaeoctopus* and *Styletoctopus* developed by median interruption of the median field of a palaeololiginid gladius. The posterior growth front in *Palaeoctopus* and *Styletoctopus* is thereby the result of widely separated shell sacs.

Conclusions

Except the Muensterellidae and the Palaeololiginidae, none of the known gladius-bearing coleoids from the Mesozoic exhibit a gladius with a distinctly reduced median field. Taxa such as the Plesioteuthididae, Loligosepiidae or Trachyteuthididae retain a well-developed median field during their evolution. It is therefore likely that the gladius vestiges of cirroctopods and octopods originated from a palaeololigind or a muensterellid gladius. As a third possibility, cirroctopods have their roots in the muensterellid lineage, whereas the octopods originated independently from a palaeololiginid branch.

In each of the suggested scenarios, the Cirroctopoda and Octopoda evolved from an early teudopseid. Hence, the present reflections do not concur with the ideas of Haas (2002) and Bizikov (2004), who postulated an origin from forms with a comparatively wide anterior median field.

References

Bizikov, V.A. (2004): The shell in Vampyropoda (Cephalopoda): morphology, functional role and evolution.- Ruthenica supplement, **3:** 1-88.

Donovan, D.T. (1977): Evolution of the dibranchiate Cephalopoda.- Symposia of the Zoological Society of London, **38:** 15-48.

Doyle, P., Donovan, D.T. & Nixon, M. (1994): Phylogeny and systematics of the Coleoida.- Paleontological contributions, University of Kansas, **5:** 1-15.

Engeser, T. & Bandel, K. (1988): Phylogenetic classification of cephalopods.- In: Wiedmann, J. & Kullman, J. (eds.): Cephalopods - Present and Past: 105-115. Stuttgart, Schweizerbart´sche Verlagsbuchhandlung.

Fischer, J.-C. & Riou, B. (1982): Le pus ancien Octopode connu (Cephalopoda, Dibranchiata): *Proteroctopus ribeti* nov. gen., nov. sp., du Callovien de l'Ardeche (France).- Comptes Rendus de l'Academie des Sciences de Paris, Ser. B, **295:** 277-280.

Fuchs, D. (2006): Fossil erhaltungsfähige Merkmalskomplexe der Coleoidea (Cephalopoda) und ihre phylogenetische Bedeutung.- Berliner paläobiologische Abhandlungen, **8:** 1-115.

Fuchs, D. (in revision): A rare and unusual teudopseid coleoid from the Late Cretaceous of Lebanon.- In: Fuchs, D. (ed.): Proceedings of the 3rd International Symposium "Coleoid Cephalopods Through Time", Luxembourg.

Fuchs, D., Beard, G., Tanabe, K. & Ross, R. (2007a): Coleoid cephalopods from the Late Cretaceous North eastern Pacific.- In: Abstracts volume of the 7th International Symposium "Cephalopods - Present & Past", Sapporo.

Fuchs, D., Bracchi, G. & Weis, R. (2009): New records of octopods (Cephalopoda: Coleoidea) from the Late Cretaceous (Upper Cenomanian) of Hakel and Hadjoula (Lebanon).- Palaeontology, **52(1):** 56-81.

Fuchs, D., Engeser, T. & Keupp, H. (2007b): Gladius shape variation in the genus *Trachyteuthis* Meyer 1846 (Cephalopoda: Coleoidea) from the Late Jurassic Plattenkalks of Nusplingen (Kimmeridgian) and Solnhofen (Tithonian).- Acta Palaeontologica Polonica, **52(3):** 575-589.

Fuchs, D., Keupp, H. & Engeser, T. (2003): New records of soft parts of *Muensterella scutellaris* MUENSTER, 1842 (Coleoidea) from the Late Jurassic Plattenkalks of Eichstätt and their significance for octobrachian relationships.- Berliner paläobiologische Abhandlungen, **3:** 101-111.

Fuchs, D., Klinghammer, A. & Keupp, H. (2007c): Taxonomy, morphology and phylogeny of plesioteuthidid coleoids from the Upper Jurassic (Tithonian) Plattenkalks of Solnhofen.- Neues Jahrbuch für Geologie und Paläontologie, **245(2):** 239-252.

Fuchs, D. & Weis, R. (2008): Taxonomy, morphology and phylogeny of Lower Jurassic loligosepiid coleoids (Cephalopoda).- Neues Jahrbuch für Geologie und Paläontologie, **249(1):** 93-112.

Fuchs, D. & Weis, R. (in press): Taxonomy, morphology and phylogeny of Lower Jurassic teudopseid coleoids (Cephalopoda).- Neues Jahrbuch für Geologie und Paläontologie.

Haas, W. (2002): The evolutionary history of the eight-armed Coleoidea.- In: Summesberger, H. et al. (eds.): Cephalopods - Present & Past: 341-351 (Abhandlungen der Geologischen Bundesanstalt 57).

Jeletzky, J.A. (1966): Comparative morphology, phylogeny and classification of fossil Coleoidea.- Paleontological contributions, University of Kansas Mollusca, **7:** 1-166.

Kluessendorf, J. & Doyle, P. (2000): *Pohlsepia mazonensis*, an early "Octopus" from the Carboniferous of Illinois, USA.- Palaeontology, **43(5):** 919-926.

Lindgren, A.R., Giribet, G. & Nishigushi, M.K. (2004): A combined approach to the phylogeny of Cephalopoda (Mollusca).- Cladistics, **20:** 454-486.

Naef, A. (1921-23): Fauna e Flora del Golfo di Napoli. Cephalopoda.- Jerusalem, Friedlaender und Sohn. pp 917.

Roger, J. (1944a): Le plus ancien Cephalpode Octopode fossil connu: *Palaeoctopus newboldi* (Sowerby, 1846) Woodward.- Bulletin de la Societe Linneenne de Lyon, **13(9):** 114-118.

Roger, J. (1944b): Phylogenie des Cephalopodes Octopodes: *Palaeoctopus newboldi* (Sowerby, 1846) Woodward.- Bulletin de la Societe geologique de France, **14:** 83-99.

Roger, J. (1946): Les invertebres des couches a Poissons du Cretace superieur du Liban.- Memoires de la Societe Geologie de France, **51:** 1-92.

Strugnell, J., Jackson, J., Drummond, A.J. & Cooper, A.A. (2006): Divergence time estimates for major cephalopod groups: Evidence from multiple genes.- Cladistics, **22:** 89-96.

Toll, R.B. (1998): The gladius in teuthid systematics.- In: Voss, N.A. et al. (eds.): Systematics and Biogeography of Cephalopods. vol. **2:** 55-67, Washington (Smithonian Contributions to Zoology).

Vecchione, M., Young, R.E. & Carlini, D.B. (2000): Reconstruction of ancestral character states in neocoleoid cephalopods based on parsimony.- American Malacological Bulletin, **15(2):** 179-193.

Voight, J.R. (1997): Cladistic analysis of the octopods based on anatomical characters.- Journal of Molluscan Studies, **63:** 311-325.

Wade, M. (1993): New Kelaenida and Vampyromorpha: Cretaceous squid from Queensland.- Mem. Ass. Austras. Paleontols., **15:** 353-374.

Young, R.E. & Vecchione, M. (1996): Analysis of morphology to determine primary sister-taxon relationships within coleoid cephalopods.- American Malacological Bulletin, **12(1/2):** 91-112.

Young, R.E., Vecchione, M. & Donovan, D.T. (1998): The Evolution of Cephalopods and their present Biodiversity and Ecology.- South Africa Journal of Marine Science, **20:** 393-420.