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The Cretaceous coleoid *Dorateuthis syriaca* WOODWARD: morphology, feeding habits and phylogenetic implications

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(With 2 text-figures and 2 plates)

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Abstract

An exceptionally preserved coleoid from the Upper Cretaceous (Upper Santonian) of Lebanon is described. The specimen represents the rare species *Dorateuthis syriaca* WOODWARD 1883 of the family Plesiotheuthididae and is characterized by indications of soft tissue such as the buccal mass, mandibles, oesophagus, arms and the gladius. These details allow a refined description of the species, which WOODWARD (1883) based on a poorly preserved holotype and presented as a strongly idealized drawing. Furthermore, the specimen displays the stomach content, comprising exclusively fish remnants. The amount of ingested food reveals *Dorateuthis syriaca* as a voracious feeder whose diet suggests similar predatory habits as documented from modern squids.

The octobranchian nature of the specimen supports the still controversial systematic position of the Plesiotheuthididae within the Octobranchiomorpha. The oegopsid affinities of the gladius therefore point to parallel evolution.

Key words: Coleoidea, Plesiotheuthididae, Soft-part preservation, Stomach content, Upper Cretaceous

Kurzfassung

Ein außergewöhnlich erhaltener Coleoidee aus der oberen Kreide des Libanon wird beschrieben. Das Exemplar gehört der seltenen Art *Dorateuthis syriaca* WOODWARD 1883 aus der Familie der Plesiotheuthididae an. Es zeichnet sich durch Hinweise auf Weichteile aus und zeigt Buccalmasse, Mandibel, Oesophagus, Arme, und den Gladius. Diese Details erlauben eine Erweiterung der Artbeschreibung durch WOODWARD (1883), die auf einem schlecht erhaltenen Holotypus und einer stark idealisierten Zeichnung basiert. Darüber hinaus weist das Exemplar einen aus Fischresten bestehenden Mageninhalt auf. Die große Nahrungsmenge kennzeichnet *Dorateuthis syriaca* als gefräßigen Räuber, dessen Ernährungsweise denen moderner Kalmare vergleichbar war.

Die gut belegbare Achtarmigkeit dieses Coleoideen könnte für die kontroverisierte Einordnung der Plesiotheuthididae innerhalb der Octopodiformes sprechen. Die offensichtlichen Ähnlichkeiten mit den Gladii der modernen Oegopsiden dürfte demnach Ergebnis von Parallelevolution sein.

Schlüsselwörter: Coleoidea, Plesiotheuthididae, Weichteilerhaltung, Mageninhalt, Ober-Kreide

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Fig. 1: Locality map of Lebanon with indicated position of the Upper Cretaceous (Upper Santonian) Sahil Alma section. The outcrop at Sahil Alma is located on the west coast of Lebanon, about 25 km north-east of Beirut.

Introduction

The main problem in interpreting fossil coleoids and their relation to extant taxa is the extremely rare preservation of soft tissues. With few exceptions, the dataset on soft part morphology – e.g. the digestive systems – of the manifold fossil coleoid groups is still too poor to integrate such information in a consistent phylogenetic tree. One of the most promising localities to solve questions concerning the soft tissue morphology of fossil coleoids is located in Lebanon. There, the Upper Cretaceous "fish-shale" ("Fischschiefer") yields a large number of coleoid cephalopods along with crustaceans and fishes, being known to science since the late 1870s (LARTRET 1877, LEWIS 1878, FRAAS 1878, WOODWARD 1883, 1896, ROGER 1946). These fossil coleoids from Lebanon have been variously referred to in most synthetic studies such as NAEF (1921, 1922) or JELETZKY (1966). More recently, ENGESER and REITNER (1986) described a small fauna of Lebanese coleoids, including fragments of the genus *Dorateuthis*. As noted by ENGESER and REITNER (1986), however, the sampled specimens derive from different localities (Hadjoula, Hakel, Maifouk, Sahil Alma) that are of different stratigraphic age. *Dorateuthis syriaca*, redescribed in this study, was missing in this latest synthesis and is known only from the outcrops at Sahil Alma.

Material and geographical setting

A single specimen of the coleoid *Dorateuthis syriaca* WOODWARD 1883 is housed in the collection of the Natural History Museum Vienna (Inv. NHMW1998z0105/0000). It

was bought by the Museum in 1998 and derives from the Sahil Alma section in Lebanon. Only one slab is available, containing the dorsal part of the squid in ventral view. The counterpart of the slab is missing. This individual is conspecific with other specimens of *Dorateuthis syriaca* WOODWARD 1883 collected at the same locality. A comparison with photographs of the holotype housed in the Natural History Museum London, kindly provided by Dirk Fuchs (Berlin), confirmed the identification but showed that the original definition by WOODWARD (1883) was highly idealized and lacked important information. The specimen is exceptionally preserved and includes soft tissue, which is indicated as a brownish cover on the pale calcareous marl slab. Although the specimen is slightly distorted and compressed, it is sufficiently complete to allow biometric measurements of shape and size.

Sahil Alma is located about 25 km north-east of Beirut (text-fig. 1). For a more detailed description of the setting see WOODWARD (1883). The first dating of the section as "Senonian" by FRAAS (1878) was refined by EJEL & DUBERTRET (1966) as Upper Santonian based on planktonic foraminifera.

Systematic palaeontology

Phylum Mollusca CUVIER, 1795

Class Cephalopoda CUVIER, 1795

Subclass Coleoida BATHER, 1888

Superorder Octobrachiomorpha BANDEL and LEICH, 1986

(= Octopodiformes BERTHOLD & ENGESER, 1987)

Order "Trachyteuthimorpha" HAAS 2002 (paraphylum)

Suborder Prototeuthina NAEF, 1921

Family Plesiotеuthididae NAEF, 1921

Genus *Dorateuthis* WOODWARD, 1883

Type species: *Dorateuthis syriaca* WOODWARD 1883. Upper Santonian, Sahil Alma, Lebanon.

***Dorateuthis syriaca* WOODWARD, 1883**

(Fig. 2, Pl. 1, Figs 1-3; Pl. 2, Figs. 1-4)

1883 *Dorateuthis syriaca* WOODWARD: 4; pl. 1, figs. 1-2.

H o l o t y p e: British Museum of Natural History C5017.

Description of the new specimen (NHMW1998z0105/0000):

[descriptive terms follow CHENG & DUNNING (1998), MANGOLD & YOUNG (1998) and TOLL (1998)].

G l a d i u s

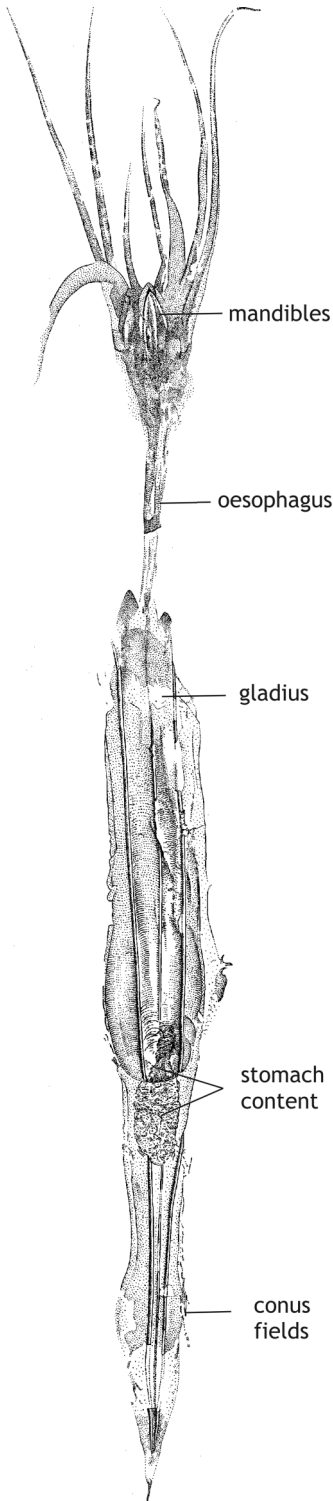
A slender, elongated gladius of 97 mm length and an anterior maximum width of 7 mm (the ventral side is visible). The apical angle can only be estimated to have ranged around 4-6° due to slight diagenetic deformation. The rachis is bordered by two main longitudinal axes (ridges) and bears a third, weaker median axis. The laterally widened outline of the fossil in the middle area of the gladius might point to the presence of narrow vanes, which are separated from the moderate-sized conus fields by a long, medial constriction. The somewhat arrow-like conus fields display a pattern of striae oriented in anterior direction (text-fig. 2).

S o f t t i s s u e a n d d i g e s t i v e o r g a n s

The buccal mass is preserved as an undifferentiated dark brown cover of 9 mm width. It bears mandibles of 6 mm length and 3 mm width, but the strict ventral-dorsal orientation of the beak obscures any other descriptive features. The circumoral appendages display 3 types of arms. The shortest pair is situated close to the beak, representing thin (0.7 mm) buccal tentacles of 23 mm length. It is followed by a pair of broad (at base 2 mm) tentacles, of which one tentacle is reflected in posterior direction. The maximum length of these tentacles is unknown because the termination seems to be missing in both. Finally, 2 pairs of equal length (42 mm) and 1.1 mm thickness are present. All 3 types of appendages display faint traces of sucker-like structures. There is no indication of a fifth pair of arms (text-fig. 2). The fifth arm pair with hooked clubs indicated by WOODWARD (1883) is pure fantasy and highly misleading. Even the dark elongated area to the left of the body in WOODWARD's (1833) drawing of the holotype turned out to be carving from preparation.

A gap between the head and the gladius is occupied by the oesophagus. The head, normally directly attached to the mantle, was dislocated approx. 80 mm to the anterior end of the body after the death of the animal and the following atony of its muscles. Starting from the buccal mass, the oesophagus can be traced as a distinct cord. Its preservation is probably due to the epithelium, which was lined with a chitinous cuticle as described from living coleoids (MANGOLD & YOUNG 1998). Laterally to the oesophagus, traces of the surrounding soft tissues are preserved as a light brown cover. This cover fades in the mantle cavity, where it is obscured by a vaguely circular dark-brown structure. The position of that structure would match an interpretation as the posterior salivary gland. The state of preservation, however, does not allow a definitive decision. The anterior part of the mantle is indicated by two distinct lappet-like structures of unknown affinity. The following part of the body down to the stomach shows various imprints of surface-near vessels along the dorsal part. These might have been part of the dorsal mantle musculature. The entire ventral part of the body is missing.

Parts of the digestive system are indicated by an elongated area containing strongly fragmented fish remains. This area is clearly separated into a "coarse" anterior part comprising entire vertebrae and large rib segments and a "fine" posterior part which displays highly digested fragments. Both areas are distinctly demarcated and the "coarse" part seems to overlap the "fine" one dorsally. The anterior/dorsal part is interpreted to represent the stomach, whereas the amorphous part in the posterior/ventral section might indicate chyme in the caecum or caecal sac.

***Dorateuthis* as a voracious feeder**

Modern coleoids are marine predators with high metabolic and conversion rates (AMARATUNGA 1983) and are also important prey for a great number of fishes, sea-birds, and marine mammals (e.g. HESS & TOLL 1981, PHILLIPS et al. 1999, GONZALEZ et al. 1994, PIERCE et al. 1994, JACKSON et al. 2000). This has prompted research into the role of squids in the trophic structure during the last few years (e.g. COELHO et al. 1997, PHILLIPS et al. 2001). A similar impact on trophic webs can be suggested for the ecosystem of the Late Cretaceous Tethys Ocean. Of course, instead of mammals and birds, marine reptiles along with fishes were probably the most important predators on coleoid cephalopods. Such an interrelation is well documented for the Triassic and Jurassic based on stomach contents (e.g. POLLARD 1968, MARTILL 1992).

In contrast, the feeding habits of the Mesozoic coleoids are insufficiently known. Thus, the ingested food of the Cretaceous *Dorateuthis syriaca* allows a peek into the feeding habits of a plesioeuthidid coleoid. The diet of modern squids is a broad spectrum of morphologically diverse prey comprising polychaetes, nemerteans, siphonophores, molluscs (including their own kind), crustaceans, echinoderms and fishes along with other organisms (BOLETZKY & HANLON 1983, BREIBY & JOBLING 1984, GUERRA & ROCHA 1994, NIXON 1987, 1988, SÁNCHEZ et al. 1998, PHILLIPS et al. 2001). Correspondingly, at least this specimen of *Dorateuthis syriaca* preyed on fish. No other fragments, for example those of crustaceans, are recognizable. Based on the size of the largest fish-vertebra, the victim was definitely not swallowed whole but rather bitten and torn into small pieces like Recent coleoids do. The preserved parts of the stomach content and the large amount of amorphous chyme in the caecum or caecal sac indicate that the specimen's digestive tract was full. As discussed by WESTERMANN et al. (2002), the duration of the digestion cycle seems to be faster in actively swimming cephalopods such as *Loligo vulgaris* and to be longer in benthic taxa such as *Nautilus pompilius* and *Octopus vulgaris*. A range from 4–6 h (*Loligo vulgaris*) to 12 h (*Nautilus pompilius*, *Octopus vulgaris*) and 15 h (*Sepia officinalis*) or even more (*Eledone cirrhosa*) as reaction to decreasing water temperature was reported by WESTERMANN et al. (2002). Taking into account the tropical water

Fig. 2: Drawing of *Dorateuthis syriaca* (NHMW1998z0105/0000).

of the Late Cretaceous Sea and the active predatory mode of life, the digestion duration of *Dorateuthis syriaca* can be hypothesized to have been rather short, ranging e.g. between 5-10 h. Hence, the food was consumed by the specimen no more than a few hours before its death. Lingering illness, hindering active preying, can be excluded as the cause of death.

Phylogenetic implications – still a Gordian knot?

The assignment of *Dorateuthis* to the Plesioeteuthididae is based on the rather small conus fields and the small gladius apical angle (ENGESER 1990). Whilst this assignment is undoubted by all recent coleoid workers (e.g. ENGESER & REITNER 1986, RIEGRAF 1995 and RIEGRAF et al. 1998), the systematic position of the Plesioeteuthididae with the type species *Plesioeteuthis prisca* (RÜPPEL 1829) is still controversial. DOYLE et al. (1994) and DONOVAN & TOLL (1988) consider the taxon as a member of the Decabrachia and discuss a close relation to the Oegopsida based on a proposed homology of the gladii of oegopsids and that of *Plesioeteuthis*. According to DONOVAN & TOLL (1988), *Plesioeteuthis* gladii are reminiscent of modern Ommastrephidae. For *Dorateuthis*, too, superficially similar gladii are found within extant Oegopsida, namely in *Gonatus* (Gonatidae) and *Onychoteuthis* (Onychoteuthidae) (see TOLL 1998 for comparison). Similarly, REITNER & ENGESER (1982) discuss a phylogenetic relation of their plesioeteuthid genus *Maioteuthis* with modern oegopsids.

These suggestions are opposed by BANDEL & LEICH (1986), ENGESER & BANDEL (1988) and ENGESER (1990), who discuss an affinity of the Plesioeteuthididae with the vampyromorphs based on the stellate arms of *Plesioeteuthis*; such arms point to the presence of a web, which was also proposed by JELETZKY (1966). Further, the octobranchian nature of *Plesioeteuthis*, *Leptoteuthis*, and *Trachyteuthis* was stressed by BANDEL & LEICH (1986) to support the vampyromorph affinity.

HAAS (2002) also demonstrated an affinity of the gladius of *Plesioeteuthis* with those of the Vampyromorpha and depicted a rather primitive gill system in *Plesioeteuthis*, which might reveal it as a stem-line representative of the octobranchiomorphs.

More or less stellate arms can be stated for *Dorateuthis syriaca* (especially for the holotype), and the octobranchian stage is evident as well. In contrast to the equal-sized arms of the Jurassic genera *Plesioeteuthis* and *Trachyteuthis*, the Cretaceous *Dorateuthis* displays differentiated arms.

MANGOLD & YOUNG (1998) emphasised the value of digestive systems for extant coleoid systematics. The proportions and position of the digestive system of *Dorateuthis* as interpreted above resemble those of the idealised scheme of *Abralia* (Oegopsida) described by MANGOLD & YOUNG (1998). Analogous are especially the long (but probably postmortally stretched) oesophagus and its ratio to the buccal mass. Unfortunately, these similarities also hold true for the digestive system of *Vampyroteuthis*. A decision on whether a crop was present – which, if present, would contradict an oegopsid affiliation and would support the position within the vampyromorph-lineage – is impossible due to the poor preservation.

Thus, the position of *Dorateuthis* and the plesioeteuthidids within the coleoids' phylogenetic tree remains unsolved. Herein, we tentatively prefer the grouping within the su-

perorder Octobrachiomorpha (sensu ENGESER 1990) based on the strict octobranchian stage. Despite the considerable weakness of that argumentation, in our opinion the alleged homology of the oegopsid gladius with that of the Plesiotheuthididae as stressed by DONOVAN & TOLL (1988) is based on even weaker ground. The fact that the gladii of the discussed genera of the Plesiotheuthididae resemble those of various oegopsid families (Gonatidae, Ommastrephidae, Onychoteuthidae) might equally well indicate analogous morphologies due to parallel evolution. The increase in arm morphology complexity from Jurassic to Cretaceous representatives could indicate an adaptation to new life habits and would further hint at a morphologic parallel evolution with the modern oegopsids.

Conclusions

Dorateuthis syriaca was an active predator feeding at least partly on fish. Remnants of its digestive system suggest the presence of a chyme-filled caecum or caecal sac next to stomach. Based on the mass and preservation of the ingested food, the specimen is interpreted to have preyed on fish only a few hours before its death. This species was an octobranchian, coleoid with 3 types of arms. Like several other Plesiotheuthididae, it shows a tendency to a stalked preservation of the circumoral appendages. Both features could be argued to indicate a close relation with the Octobrachiomorpha. In contrast, the gladius of *Dorateuthis syriaca* is reminiscent of that of a decabranchian oegopsid. It cannot be excluded, however, that the similarities with oegopsids (overall body-outline and gladius-shape) represent analogous developments due to adaptation to similar habits. Information on whether the Plesiotheuthididae had a crop could support a decision on a potential affiliation with the vampyromorphs. This calls for putting more emphasis on soft part morphologies of exceptionally preserved specimens in future studies. More detailed analysis of the so-called stomach contents might reveal differentiations of crop, stomach and caecum areas, which could then be applied to phylogenetic schemes if consistent patterns turn up.

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Plate 1

Dorateuthis syriaca WOODWARD, 1883

Fig. 1: Total view of the new specimen (NHMW1998z0105/0000).

Fig. 2: Enlarged buccal mass and basal arm crown area of Fig. 1.

Fig. 3: Holotype of *Dorateuthis syriaca* WOODWARD, 1883 (p. 4; pl. 1, figs. 1-2).

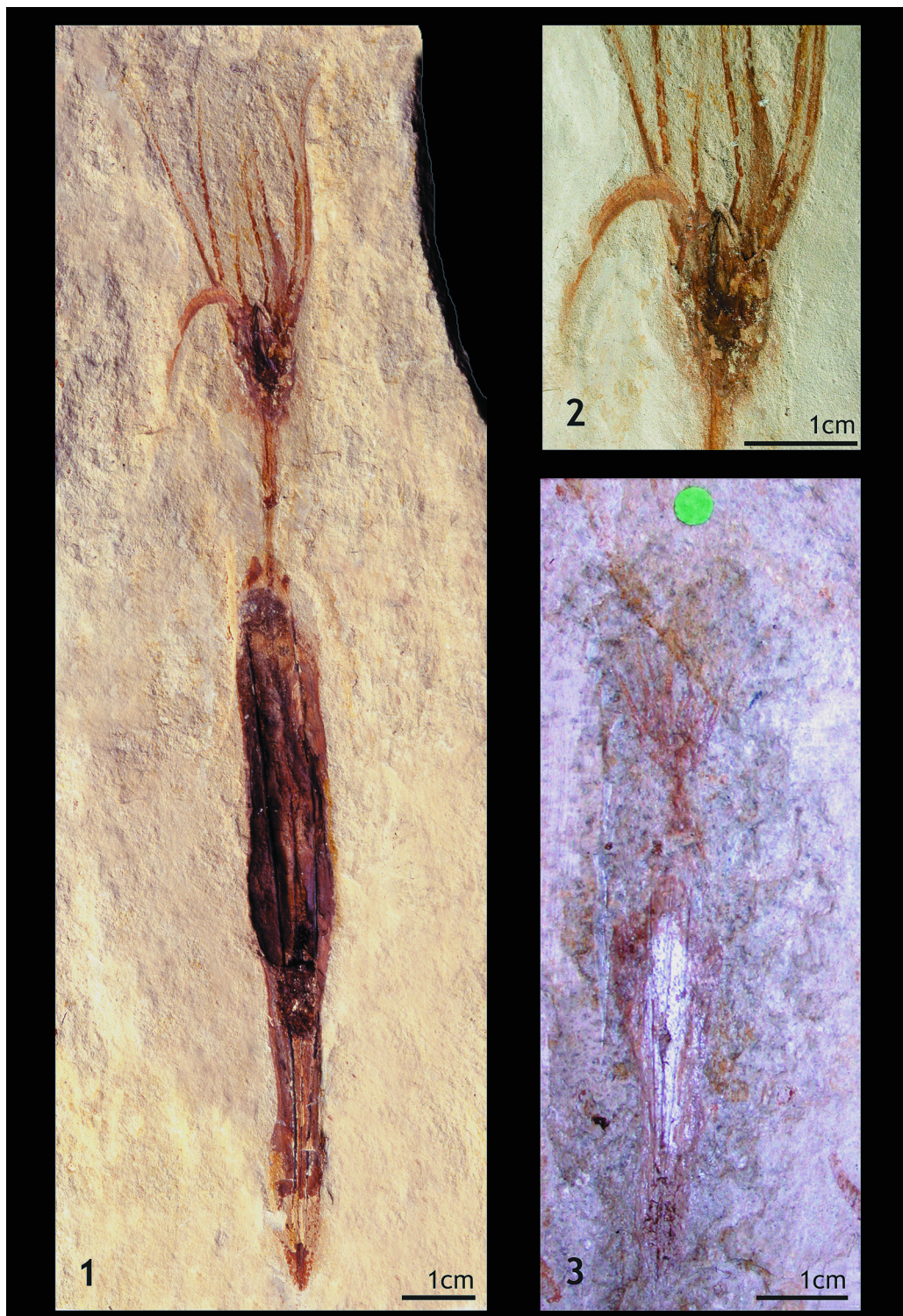


Plate 2

***Dorateuthis syriaca* WOODWARD, 1883**

Fig. 1: Detail of the buccal mass showing mandibles of specimen NHMW1998z0105/0000.

Fig. 2: Oesophagus and anterior part of the body.

Fig. 3: Enlarged digestive system with fish remnants.

Fig. 4: Details of the gladius and the conus fields.



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