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Jurassic Vampyromorpha (dibranchiate cephalopods)

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With 21 figures in the text

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Abstract: The Late Jurassic squids *Plesioteuthis*, *Leptoteuthis* and *Trachyteuthis* had eight arms which were joined by a basal arm web and bore cirri and a short median row of fleshy suckers. The internal shell is of mainly organic construction in *Plesioteuthis* and *Leptoteuthis* and of organic and aragonitic construction in *Trachyteuthis*, and shows no remnants of chambers or rostra. The squids from the Solnhofen Lithographic Limestone belong to the order Vampyromorpha of the dibranchiate cephalopods and represent the fossil counterparts of the living fossil *Vampyroteuthis infernalis*.

Key words: Molluscs, Cephalopods, evolution, soft-parts, diagenesis, Jurassic.

Zusammenfassung: Die oberjurassischen Tintenfische *Plesioteuthis*, *Leptoteuthis* und *Trachyteuthis* besaßen acht Arme, die an ihrer Basis durch eine Haut miteinander in Verbindung standen und zudem neben Zirren eine kurze Reihe von fleischigen Saugnäpfen aufwiesen. Das Innenskelett ist bei *Plesioteuthis* und *Leptoteuthis* vornehmlich organischer Zusammensetzung. Bei *Trachyteuthis* ist der organische Schulp von außen zudem aragonitisch mineralisiert. Die Schulpe zeigen keine Reste von Kammern oder Rostra. Die Tintenfische der Solnhofener Plattenkalke gehören in die Ordnung Vampyromorpha der dibranchiaten Cephalopoden. Sie stellen die fossilen Verwandten der rezenten Reliktart *Vampyroteuthis infernalis* dar.

Introduction

Squid-like cephalopods from the Upper Jurassic Lithographic Limestone of Solnhofen and Eichstätt (Southern Germany) are well known. Of these the three species *Plesioteuthis prisca* (RÜPPELL 1829) *Leptoteuthis gigas* v. MEYER 1834 and *Trachyteuthis hastiformis* (RÜPPELL 1829) have been preserved not only complete with shell but also with much of their soft body. They have, therefore, attracted much attention and been subject of a number of studies by different authors over the last 150 years.

RÜPPELL (1829) originally described *Plesioteuthis* as a member of the genus *Loligo* because of its similarity to this Recent squid. On the basis of similar arguments he placed *Trachyteuthis* in the genus *Sepia*, the Recent cuttlefish. Almost 150 years later DONOVAN (1977) considered *Trachyteuthis* a very close re-

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lative and ancestor of the Recent *Sepia* because of similarities in construction and in the dorsal surface mineralisation of the "cuttlebone" in both species. NAEF (1922) saw *Plesioteuthis* and *Leptoteuthis* as ancestors of the Recent Teuthida. *Trachyteuthis*' similarities to *Sepia* were put down to convergence.

JELETZKY (1966) accepted NAEF's observations, i. e. that the shell of *Plesioteuthis* and *Leptoteuthis* still retained a small guard and thus reflected their derival from belemnite-like, phragmocone-bearing ancestors. A sizeable rudiment of the guard was considered characteristic of the suborder Prototeuthina. JELETZKY (1966) considered *Trachyteuthis* an "aberrant form".

NAEF (1922) defined the Teuthida (= Teuthoida) as an order of the subclass Dibranchiata and the class Cephalopoda and divided it into the two fossil suborders Prototeuthina (*Plesioteuthis, Leptoteuthis*) and Mesoteuthina (*Trachyteuthis*) and the Recent suborder Mesoteuthina with the subgroups Oegopsida and the Myopsida (*Loligo*). Other orders besides Teuthida according to NAEF (1922) are the Belemnitida (*Acanthoteuthis*) and the Sepiida (*Sepia*). JELETZKY (1966) added the octopod suborder Vampyromorphina to NAEF's scheme of decapod Teuthida and created the new orders Aulacocerida and Phragmoteuthida by splitting the Belemnitida as defined by NAEF.

Tentacles and gills

The number of arms and gills is of major importance in the classification of living cephalopods. NAEF (1921) subdivided the subclass of the dibranchiate cephalopods (= Coleoidea) into the two orders Decapoda and Octopoda. The division of the coleoids into orders with ten arms and others with eight has proven to be sensible. During ontogeny, embryoes of all dibranchiate cephalopods form ten arm buds from their rudiment of the foot. In Decapoda, these grow into arms, whereas in the case of the Octopoda two are arrested in growth (NAEF 1928).

The Dibranchiata are, by definition, characterized by two gills; but since these are usually not preserved in fossils [the first case of undoubtedly fossilized gills is described further on in this paper (Fig. 12, 17)], paleontologists prefer the term coleoids or endocochlear cephalopods.

Apart from some Tertiary and subrecent *Argonauta* brood chambers (BANDEL & DULLO 1985) only two fossil octopods [*Palaeoctopus* from the Upper Cretaceous of Lebanon (WOODWARD 1896) and *Proteroctopus* from the Middle Jurassic of France (FISCHER & RIOU 1982b)] have so far been described. Phragmocone and gladius bearing coleoids have been described and found in much greater numbers. In his classification of the Coleoidea JELETZKY (1966) created a mixture of biological and paleontological nomenclature retaining the order Octopida (= Octopoda) but eradicating the order Decapoda, which he split into five orders.