

Jurassic Vampyromorpha (dibranchiate cephalopods)

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With 21 figures in the text

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Abstract: The Late Jurassic squids *Plesiotenthis*, *Leptotenthis* and *Trachytenthis* 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 *Plesiotenthis* and *Leptotenthis* and of organic and aragonitic construction in *Trachytenthis*, 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 *Plesiotenthis*, *Leptotenthis* und *Trachytenthis* besaßen acht Arme, die an ihrer Basis durch eine Haut miteinander in Verbindung standen und zudem neben Zirren eine kurze Reihe von fleischigen Saugnapfen aufwiesen. Das Innenskelett ist bei *Plesiotenthis* und *Leptotenthis* vornehmlich organischer Zusammensetzung. Bei *Trachytenthis* 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 *Plesiotenthis prisca* (RÜPPELL 1829) *Leptotenthis gigas* v. MEYER 1834 and *Trachytenthis 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 *Plesiotenthis* as a member of the genus *Loligo* because of its similarity to this Recent squid. On the basis of similar arguments he placed *Trachytenthis* in the genus *Sepia*, the Recent cuttlefish. Almost 150 years later DONOVAN (1977) considered *Trachytenthis* a very close re-

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 *Plesiotenthis* and *Leptotenthis* as ancestors of the Recent Teuthida. *Trachytenthis*' similarities to *Sepia* were put down to convergence.

JELETZKY (1966) accepted NAEF's observations, i. e. that the shell of *Plesiotenthis* and *Leptotenthis* still retained a small guard and thus reflected their derivation from belemnite-like, phragmocone-bearing ancestors. A sizeable rudiment of the guard was considered characteristic of the suborder Prototeuthina. JELETZKY (1966) considered *Trachytenthis* 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 (*Plesiotenthis*, *Leptotenthis*) and Mesoteuthina (*Trachytenthis*) and the Recent suborder Mesoteuthina with the subgroups Oegopsida and the Myopsida (*Loligo*). Other orders besides Teuthida according to NAEF (1922) are the Belemnitida (*Acanthotenthis*) 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, embryos 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 Octopoda (= Octopoda) but eradicating the order Decapoda, which he split into five orders.

Arms of fossil cephalopods are rarely preserved so that a direct differentiation between Octopoda and Decapoda is rarely possible. We know from the study of FISCHER & RIOU (1982b) that octopods have roamed the sea from Jurassic times onwards. NAEF (1922) tells us that decapods also lived in that sea. Not all fossil decapods of NAEF's scheme had ten arms, but they were shown to exist in the Upper Jurassic in some cases, as in that of *Acanthoteuthis*. This cannot be doubted since ANGERMANN'S (1902) study and JOHNSON & RICHARDSON'S (1968) demonstration of ten arms in the Carboniferous *Jeletzkyia*. Thus octopods and decapods must have been around in Jurassic times with the characteristic morphological types of squid and cuttlefish on the one side and octopods on the other. Whereas squid rely on jet propulsion and fin movement for locomotion, many octopods also use their mobile arms when moving around on the bottom. The separate evolution of octopod and decapod cephalopods may have started very early, perhaps at the very origin of coleoid design, along with the evolution of the internal shell in the Upper Silurian (BANDEL et al. 1983). But even before that, some cephalopods with an external shell could have had eight arms, some could have had ten, and others even more. If observations carried out by KOLB (1961) can be verified, then ammonites had eight arms. This evidence comes from drag marks produced by a soft body hanging from a drifting ammonite shell before the dead animal came to rest on the muddy bottom of the Jurassic lagoon near Solnhofen (KOLB 1961: fig. 1-3). KOLB (1961, 1967) also interpreted roll marks of ammonites to show imprints of parts of the soft body, but these can be reconstructed with only the shell leaving impressions on the mud (SEILACHER 1963). If ammonites did have eight arms, then octopod and decapod organization could be seen as a totally independent trend in cephalopod evolution, decoupled from the character of the shell.

A closer look at Recent dibranchiate cephalopods shows that not only the number of arms, but also the construction of the suckers is different in the two groups (NAEF 1922: fig. 5). Octopod suckers are broadly attached to the arms or stalked, but all have a muscular wall. Decapod suckers, in contrast, extend from the arms, have cutinized rings and hardly any wall musculature. The presence of solid chitinous sucker rings is considered an improvement, since they allow the suckers to function without muscle action and suck even when the animal is dead. NAEF thought that the octopod suckers are more primitive and simple and may have been present in this form in the ancestors of all dibranchiate cephalopods. Considering the presence of chitinous rings in each sucker of the arms that surround the mouth, decapod arms differ from those of octopods not only in number, construction and efficiency, but also by their fossilization potential.

While arm hooks occur commonly in Jurassic rocks, no sucker rings have so far been found. Although the fossilization potentials of hooks and rings are about equal, not even sediments very rich in hooks (such as the Middle Jurassic concretions of Lukow; KULICKI & SZANIAWSKI 1972) contain any rings. While we

know that belemnites and phragmoteuthids had hooks, all Recent squid of the teuthid-decapod guild have sucker rings. *Acanthoteuthis* from the Solnhofen Lithographic Limestone, however, was equipped with hooks; even very minute and juvenile individuals had them (ENGESER & REITNER 1981 and own observations). If chitinized sucker rings had existed, they would be visible in this preservation.

Recent decapods produce chitinous sucker rings with a sharply dented upper edge (see for example CHUN 1914, 1975; DILLY & NIXON 1976; DILLY et al. 1977). CHUN (1914) demonstrated that in several species whose adult individuals do have hooks, juveniles are equipped only with sucker rings, which developmentally grow into hooks. From these observations and from his own studies NAEF (1921, 1922) concluded that the original structure of a decapod sucker is a ring from which the hook is derived in modern decapods by unilateral growth of the ring dentition. This difference between Recent and fossil decapods as regards the armament of the arms enables us to trace the development of Recent decapods (Metateuthina and Sepiida).

Vampyroteuthis

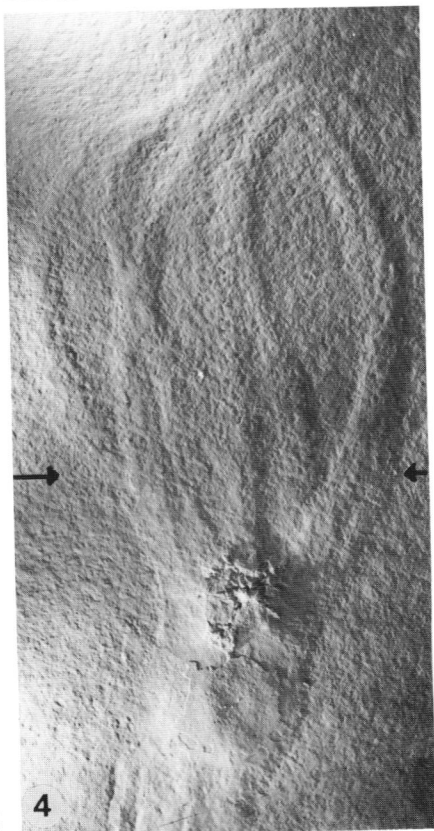
The deep sea octopod *Vampyroteuthis* is the only species of a family Vampyroteuthidae THIELE (1915), the suborder Vampyromorphina ROBSON (1929) and the order Vampyromorphida PICKFORD (1936). Vampyromorpha, modern Octopoda (= Octopida in JELETZKY 1966) and Teuthida are, therefore, of equal rank. The only other cephalopod representing a monogeneric whole order is the "living fossil" *Nautilus*.

THIELE (1915, in CHUN 1914, 1975) and NAEF (1921, 1922) considered that *Vampyroteuthis* belonged to the cirrate octopods (Cirrata) because of the morphology of their arms. JELETZKY (1966), on the other hand, regarded the presence of an internal shell in *Vampyroteuthis* to be a most important characteristic and placed less weight on the octopod organization of the arms. Consequently he considered the Vampyromorpha as a suborder of the order Teuthida.

Figs. 1—4

1—3: Imprints of the arms of *Plesiotheuthis prisca* produced when the animal touched vertically down onto the sediment with the parts of the arms extending beyond the arm-web. Afterwards the animal fell on its back and became preserved at the side of the imprints. Arrows point to the ventral arm pair, and H indicates the position of the head in Fig. 1. All individuals come from Blumenberg near Eichstätt, are about outgrown (21—22 cm long gladius) and are deposited in the Jura Museum at Eichstätt.

4: *Plesiotheuthis prisca* left scratch marks of the arms while touching down on the bottom in an inclined belly-up position. Actual arms are preserved below the arrows. Coll. SCHÖPFEL, Obereichstätt, 1:3.



Some of the facts that have helped to adequately place this small deep sea creature among normal dibranchiate organisms are (1) the presence of eight arms with an interbranchial web, two rows of cirri and a central row of suckers as in the Cirrata, and, (2) the presence of a gladius of basically teuthid character. PORTMANN (1958) stated that as far as its function was concerned, *Vampyroteuthis* could be regarded neither as an octopus nor as a squid. In his opinion *Vampyroteuthis* was a living fossil transitional between dibranchiate cephalopods with an inner skeleton and a form with basically no skeleton. There is as yet no geological record to document the origin of this genus and transition from squid to octopus. If *Vampyroteuthis* is the sole survivor of a once thriving group of dibranchiate cephalopods, then where are its fossil counterparts? Instead of the usual search for a modern counterpart of a fossil group our task is now to find a fossil fauna that is related to a "living fossil".

Observations

Plesiotenthis prisca

NAEF's (1922) studies have shown us that *Plesiotenthis prisca* was a Jurassic squid similar in external appearance to the Recent *Loligo*. Unlike in *Loligo*, however, the arms of *Plesiotenthis* are connected by an interbranchial web. KLINGHARDT (1943: fig. 9) discovered, that when descending to the sea-bottom, some of the dead squid landed on their arms in an upside down position. The web held the arms together in a funnel-like shape. The preserved landing mark consists of eight imprints. So does the mark figured by BARTHEL (1964: pl. 9, fig. 2; 1978: pl. 14, fig. 2) JELETZKY (1966: pl. 17, fig. 1), in which the body came to rest at the side of the landing mark left by the arms.

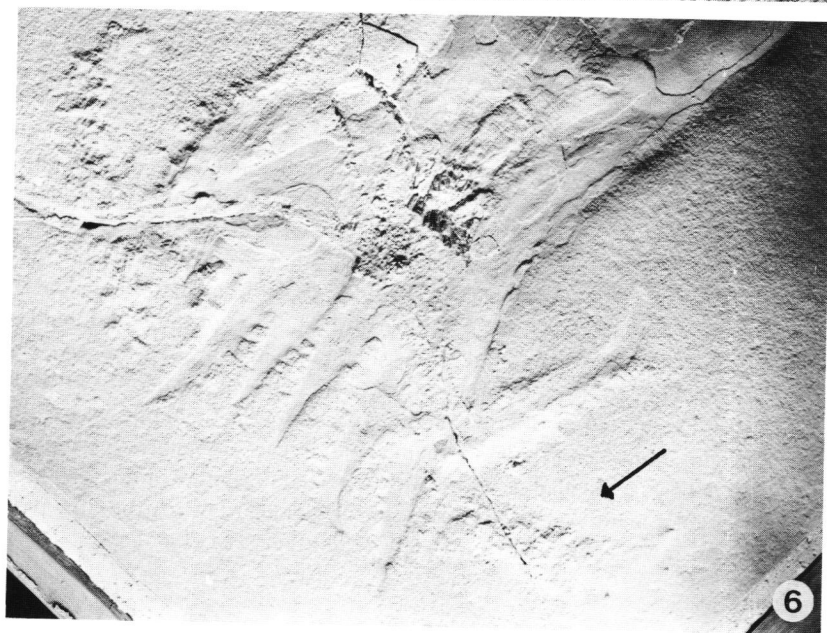
Four additional landing marks from the collection of the Jura Museum at Eichstätt (Fig. 1—3) show that when the animal's head touched the bottom the arms were not hanging down, but were rolled up and extended sideways in all directions being held in place by the web. In all three cases the dead squid fell to the side and landed on its back after its head had touched the sediment first. Arm pairs could thus be identified by their position and correlated to their imprints on the sediment. The length of the arm web between the arms of the ventral and the ventrolateral pair is the same; it is also similar between the dorsolateral and dorsal pair. The web angle is larger, however, between the lateral pairs and between the arms of the dorsal pair (Figs. 1—6).

In addition to the landing mark imprints of four pairs of arms can be seen beside the squid. NAEF (1922) thought that these eight arms were covered with cirri. He mentioned the presence of a fifth pair, but could not decide whether they were tentacles or not. BARTHEL (1978) reconstructed *Plesiotenthis* with 8 arms and two long tentacles as in Recent squid. Evidence for the presence of 10 arms in *Plesiotenthis* is based on a specimen (ZITTEL 1915: fig. 1276) that was re-

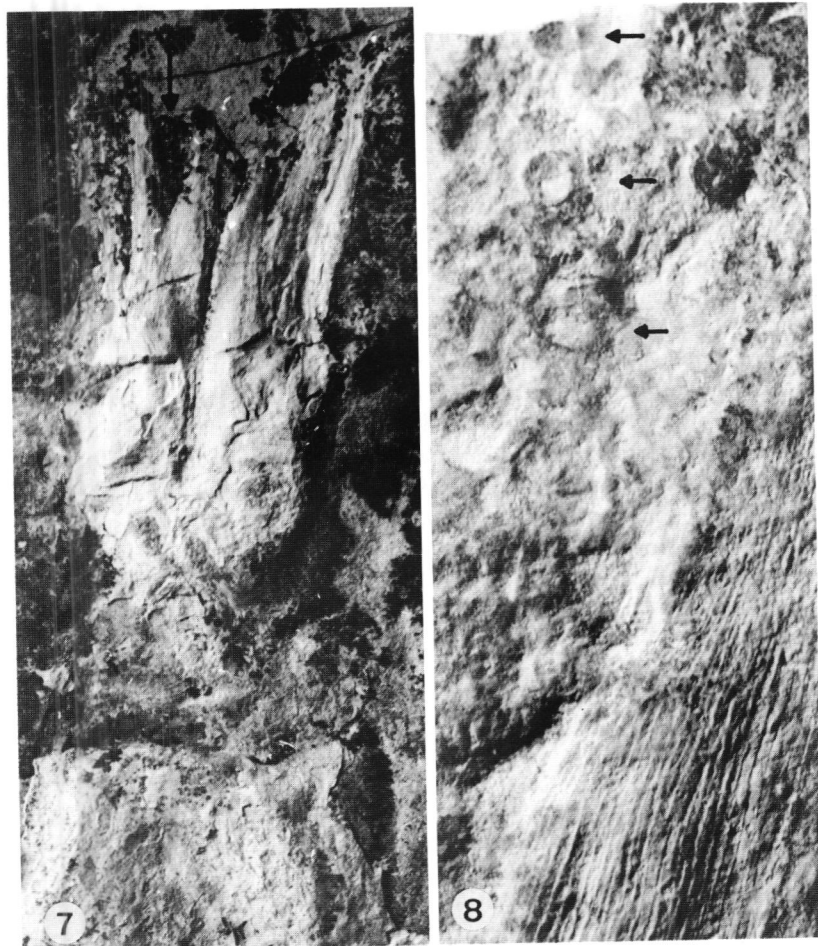
drawn by NAEF (1922: fig. 42a). Since this fossil managed to survive the otherwise destroyed collection of the Museum of the 'Institut für Paläontologie' in München, it could be restudied (Fig. 5 and 6). The animal is lying on its back and has been flattened into a thin sheet. Its gladius is 26 cm long and apical fins are well preserved, so are all arms, whose tissue is conserved within the imprints left in the sediment. After the animal had touched the bottom only the outermost ventrolateral pair of arms moved by folding backwards at the place where it was joined to the intrabranchial web. These two arms, therefore, left two impressions on the sediment, with tissue being preserved only in the ultimate impression (Figs. 5–6). Impressions of cirri are preserved on all eight arms, whereas the suckers left no clear imprints. The ventral pair of arms is the shortest (about 3 cm in length) all the others are approximately 5 cm long. The arm length of the landing marks, described above is also irregular (Fig. 1–3). The interbranchial web extends for somewhat more than one third of arm length and appears to be a little shorter between the two ventral arms.

An animal from the Obereichstätt collection dragged with its arms over the sediment before it settled on the sediment in a belly-up position (Fig. 4). In this case all eight arms left a trail before settling in their final position and being preserved as thin sheets at the end of their trail. This fossil can easily give the impression of having had a much larger arm circle than it really did.

Many features such as fins, muscular mantle, retractor muscles, ink sac and tube, stomach and liver (caecum), funnel, head and beak have been described and summarized by NAEF (1922) and KLINGHARDT (1943), but traces of the gills were never observed. In two individuals (Obereichstätt collection: fig. 17, and LEICH: fig. 12) the gills are preserved. In the first individual traces of both gills, those on the left and on the right side of the visceral mass, were imprinted on the thin sheet representing the compacted and altered viscera and their connective tissue. The second individual is equipped with a gladius 23 cm in length and a gill of 5.4 cm (Fig. 12). This shows that *Plesioteuthis* was a dibranchiate cephalopod. It also demonstrates that carcasses sinking to the bottom of the Solnhofen lagoons were well preserved and did not decay there. They must have been dead when they touched the bottom because they swam belly-up and because none of the many individuals studied shows any signs of active arm, fin or muscular mantle movement. Not one of the more than 50 individuals of *Plesioteuthis*, though having a well preserved gladius within, or connected to, a more or less well preserved muscular mantle, show even a rudiment of a guard or rostrum, the presence of which was assumed by NAEF (1922) and JELETZKY (1966).



Figs. 5–6. Arm-crown of *Plesioteuthis prisca* in the specimen from the Munich collection that served as original to ZITTEL, 1915 and NAEF, 1922. The ventrolateral pair of arms produced two marks: one when it touched down (arrows), the second when it folded back the free arm tips beyond the arm web. Fig. 6 is about natural size; Fig. 5 shows arms and marks with imprints of cirri (A) and suckers (B) in the enlargement(2:1).



Figs. 7–8. Head of a 92 cm long *Leptoteuthis gigas* from Langenthalheim (Fig. 7) with the arrow indicating position of the enlarged (2:1) Fig. 8 with fossilized arm (lower right) and imprints of suckers in its landing mark (3 arrows). The sucker imprints are 2.5 mm wide. Coll. LEICH.

Leptoteuthis gigas

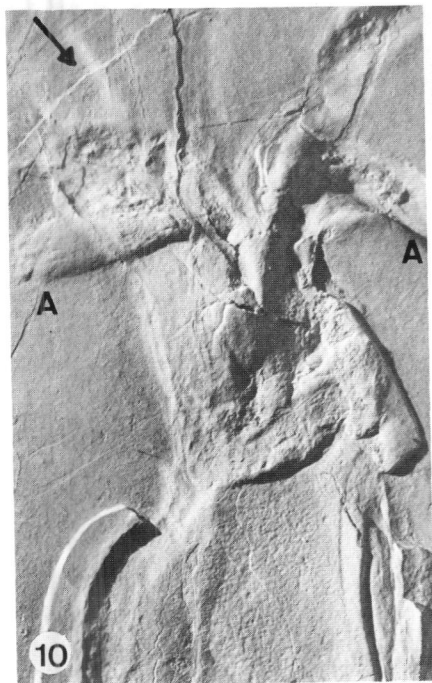
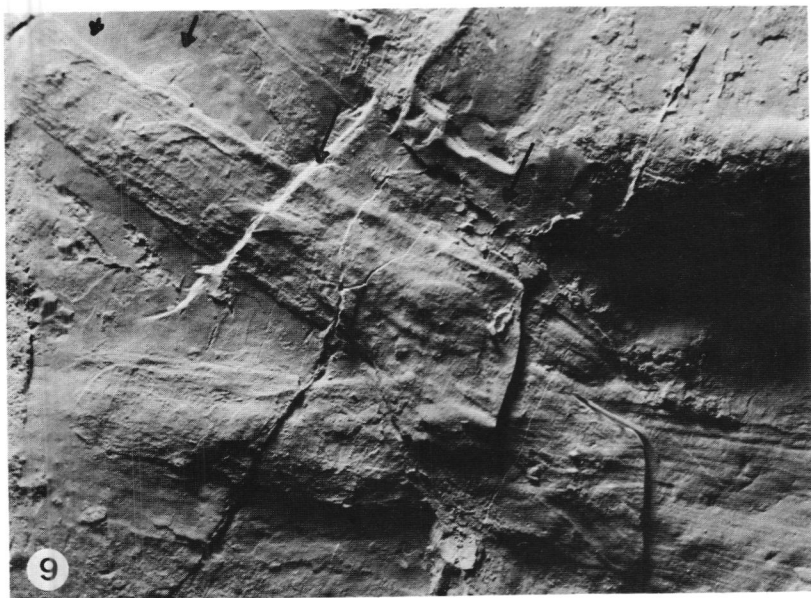
The museum of the 'Solenhofer Actienverein' houses an almost 1 m long specimen of *L. gigas* equipped with a gladius 71 cm long and up to 24 cm wide. The arms show a similar arrangement as *Plesiotentis* (Fig. 6). The animal landed on the sediment complete with eight arms which are preserved close to their impact-marks (Fig. 11). The dorsal arm pair is folded back at the place where it is joined to the interbranchial web. Arm prints lie about 30 cm in front of the beak that marks the position of the mouth while the arms themselves extend only about 17 cm from the mouth. For about one third of their length the arms are connected by a web. There are many *Leptoteuthis gigas* in the collections of Solnhofen fossils, but usually the head is poorly preserved so that the only visible details are eight short arms.

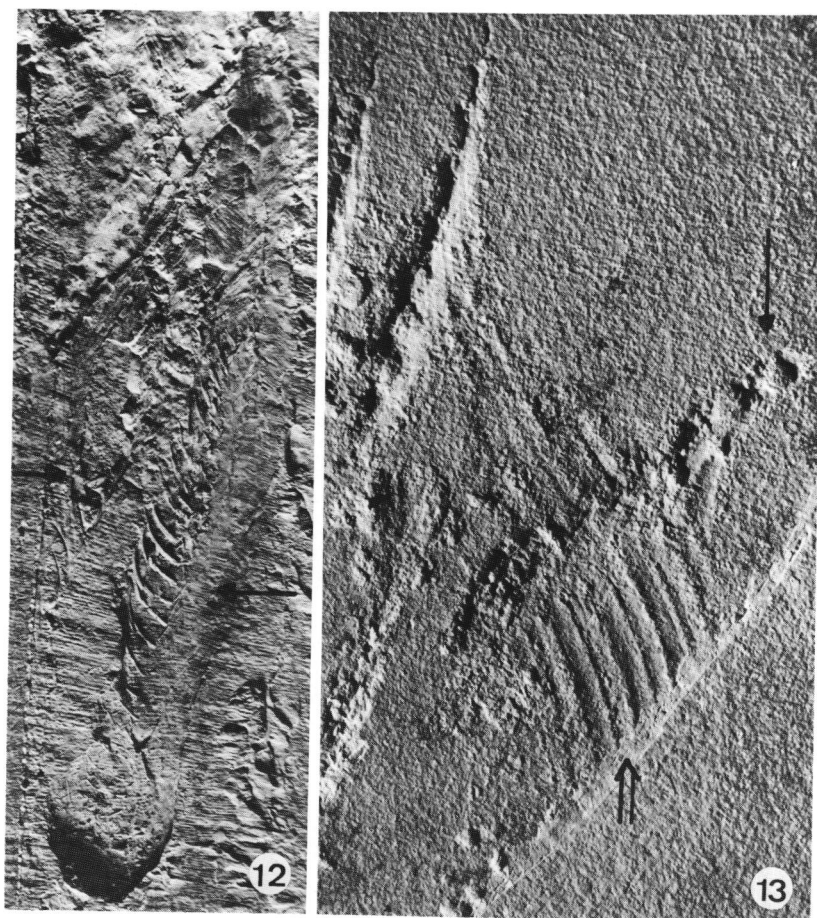
The morphology of the arms can be well reconstructed, however, from impressions on the sediment in three specimens from the Leich collection (Figs. 7–10, 13). Impressions of triangular cirri about 5 mm in length are to be seen in one arm of an individual 110 cm long (Fig. 9). They formed when the arm fell into its final position beside its own imprint on the muddy bottom. Scratch marks most probably produced by cirri, or perhaps by suckers, pulled over the sediment surface are found in another arm crown that has a width of about 40 cm (Fig. 13). Here suckers were imprinted on the sediment during the deposition of the third individual 92 cm in length (Figs. 7–8). Here the arms are well preserved and only the lateral pair with its folded-back portions has been lost. The three preserved pairs are straight. Between the ventral arms, which are slightly shorter than the others, the intrabranchial web is also a bit lower. When the arms touched the sediment surface, the median row of suckers was impressed on the mud (Fig. 8), before the arms finally settled beside their marks. These suckers were small and measured only about 2.5 mm in diameter.

Figs. 9–11

9–10: Head of a 110 cm long *Leptoteuthis gigas* from Solnhofen with distinct marks of arm-touchdown (Fig. 10 A) and indistinctly visible fossils of the arms (arrow which are enlarged in Fig. 9 to about natural size, showing cirri (arrows). Coll. LEICH.

11: Head of a large *Leptoteuthis gigas* (Museum of the Actienverein, Solnhofen) bearing a 71 cm long gladius. Landing marks lie in front of the arms (simple arrows) and the dorsal pair of arms has been twisted backwards beyond the edge of the arm-web before burial (double arrow).





Figs. 12–13

12: Gill-lamellae of *Plesiotheuthis priscas* imprinted on the ink sac. Arrows indicate the two gills. Loc. Daiting, Coll. LEICH (1:1).

13: Landing and scratch marks of suckers (arrow) and suckers and cirri (double arrow) in the arms of *Leptoteuthis gigas*; Coll. LEICH (2:1).

Trachyteuthis hastiformis

NAEF (1922: fig. 52) redrew CRICK's photograph (1896: pl. 14) of a well preserved *Trachyteuthis*. In doing so, however, he added, on each side of the arm circle, a tentacle that is not present in the very clear illustration of CRICK. The fins in NAEF's reconstruction are broad and follow the sides of the muscular mantle

up to its frontal end, which is legitimized by a 53 cm long individual from the Museum Berger in Eichstätt Harthof (Fig. 15). Here, fins were torn from the muscular mantle in the anterior portion of the body during compaction of the sediment; but the original place of attachment (33 cm in length) to the muscular mantle and the gladius below is still visible on the fossil. Fins are attached in a lateral position at the posterior portion of the muscular mantle and somewhat dorsoventrally further towards the anterior end. The head of this individual is 5.5 cm long and still has four arms attached (Fig. 16), while the others have not been preserved. These arms are 14 cm long and connected by a web attached in the lower third of the arm. They had been twisted backwards above the web prior to final deposition on the mud. In this case the animal touched the sediment with its posterior dorsal end first and then sank to the surface.

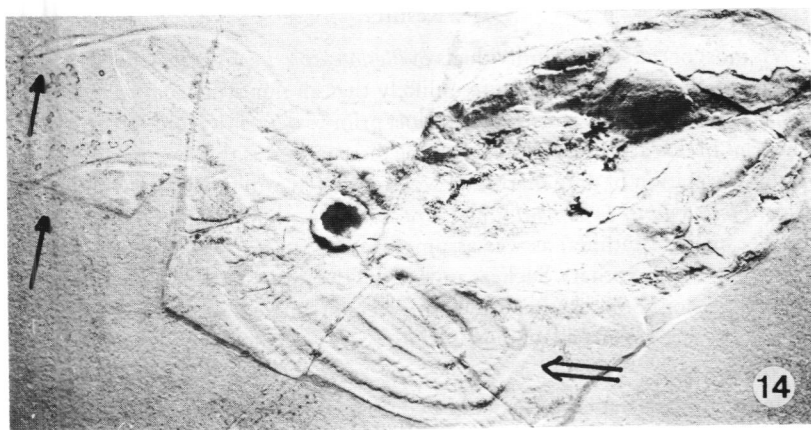


Fig. 14. Before landing on the ground a *Trachyteuthis hastiformis* with a 41 cm long gladius dragged four arms behind (simple arrow) scratching the mud before finally resting on the bottom (double arrow). The last tracks left clear marks of cirri. Coll. SCHÖPFEL, Gundolding (1:6).

An individual from the Gundolding collection has a 41 cm long gladius (Fig. 14). It has arrived at the sea floor drifting in an upright position, as it would have done when swimming, but with the arms hanging down. Two pairs of these arms left marks while being dragged along on the sediment surface. Close to the final burial place the drag marks of each pair cross, indicating that the corpse's orientation changed somewhat before it settled on its back with its posterior end first. Now all arms touched the bottom, but they became slightly pushed forwards and sideways when the inclined body finally came to rest in a horizontal position on the sediment. During this process, all eight arms scratched across the mud leaving their own marks and those of their two rows of cirri. These marks lead to

the place where the arms finally came to rest (Fig. 14). The web that connects all the arms around the mouth is 4 cm high. Arm pairs are of different length, the larger two measuring about 18 cm, the shorter ones 12–13 cm.

The fact that an animal with eight arms left trails of only four is explained by the way it sank to the bottom: in a slightly inclined position and with its dorsal side facing downwards. An individual of *Leptoteuthis sagittata* NAEF 1921 descended to the substrate in a similar manner (illustrated by CRICK 1915) with its dorsal surface down and only one pair of arms dragging behind on the sediment surface, thus creating the impression of two long tentacles. CRICK's figure was redrawn by NAEF (1922: fig. 43), who reconstructed these marks as tentacles. Since "tentacle" are now recognized as scratch marks, the creature described by CRICK had eight arms only.

Results

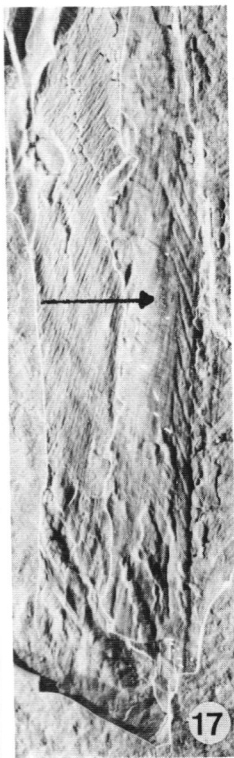
As most of the studied individuals of *Plesiotheuthis*, *Leptoteuthis* and *Trachyteuthis* are well preserved, it is quite unlikely that an important part of the body, such as the fifth pair of arms, had been lost prior to deposition on the sea bottom. Theories of ten-armed individuals can be disregarded as they were based on the misinterpretation of drag marks; all well preserved arm circles show only eight arms. *Plesiotheuthis*, *Leptoteuthis* and *Trachyteuthis*, therefore, are octopods and not decapods (Teuthida) as was assumed by NAEF (1922) and accepted by JELETZKY (1966) and others. Suckers and cirri of the three species had neither chitinated rings nor hooks. Rather, their arms were organized like those of the cirrate octopods (Cirrata) and of *Vampyroteuthis* (CHUN 1914, 1975, pl. 90; PICKFORD 1949) (Fig. 18).

In the Jurassic material, it could be confirmed that *Plesiotheuthis* had two gills. A locking apparatus connecting mantle and funnel was not observed, in contrast to JELETZKY's opinion. Neither could we find any trace of the postulated heavy calcification of the gladius in *Plesiotheuthis* and *Leptoteuthis*. If this calcification had been aragonitic and thin, it could perhaps have disappeared during diagenesis. There is no sizeable rudiment of a guard attached to the posterior end of the

Figs. 15–17

15–16: *Trachyteuthis hastiformis* with a 33 cm long gladius landed on the mud with its posterior end first leaving two marks (Fig. 15 arrow). The fins are well preserved but have been torn from the anterior margin of the muscular mantle. The detail of the head (Fig. 16) shows that arms have been twisted backwards from where the arm-web was attached to them (arrows). Museum Berger, Eichstätt.

17: Gills (arrow) of *Plesiotheuthis prisca* imprinted on the tissue of the visceral mass. Coll. SCHÖPFEL, Obereichstätt (1:1).



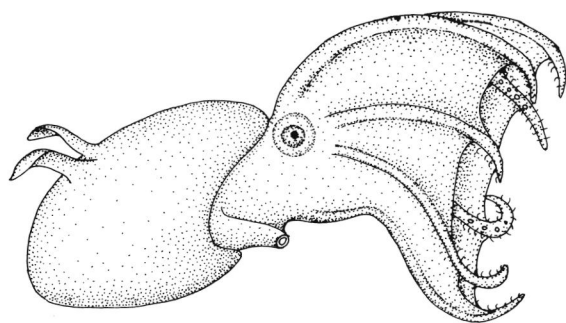


Fig. 18. *Vampyroteuthis infernalis* from the deep Atlantic Ocean. Redrawn from CHUN 1914: pl. 60, fig. 1.

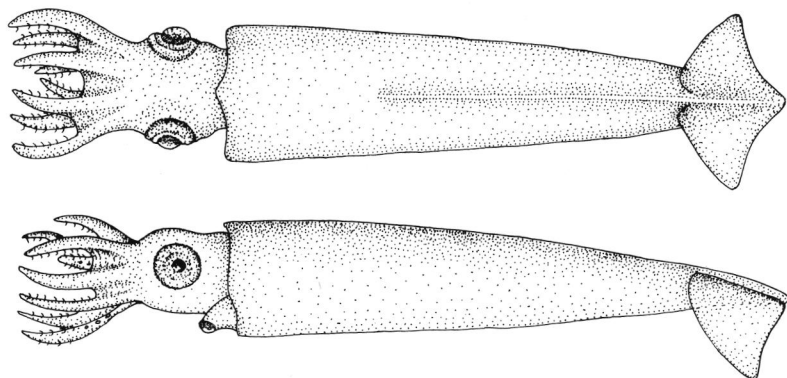


Fig. 19. Reconstructed *Plesiotenthis prisca* seen from the side and from above.

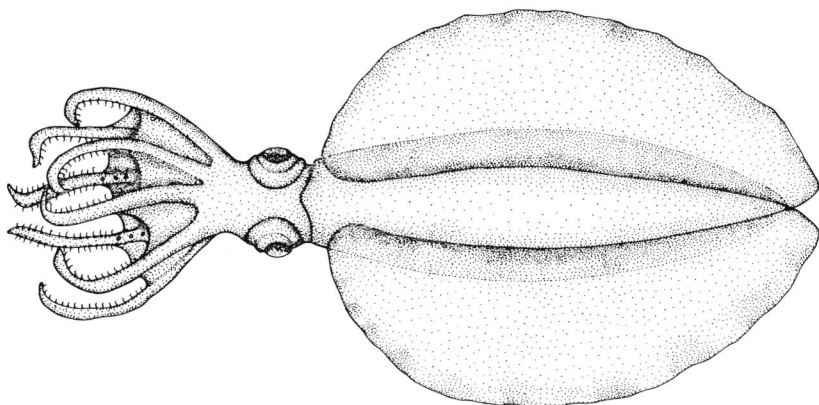


Fig. 20. Reconstructed *Trachyteuthis hastiforis* seen from above.

gladius in the two Jurassic squids, as was postulated by NAEF (1922) and JELETZKY (1966) and included in their diagnosis of the family and suborder. The gladius of *Trachyteuthis*, on the other hand, shows a strong dorsal calcification, with the calcitic or phosphatic pseudomorphs of the originally spherulitic aragonitic structure being still quite visible, but there is not either a trace of a rostrum.

FISCHER & RIOU (1982a) have recently described a new Middle Jurassic fauna of squids including three new genera. They claim, without conclusive evidence, that all their new species have ten arms. Their *Gramadella pivetaui* (1982a: pl. 6, figs 3 and 4) resembles very well the illustration of *Coccoteuthis* (= *Trachyteuthis*) *bastiformis* (Crick 1896), and its shell is as yet unknown. When reconstructed (Figs. 4 and 5) it is very similar to the reconstruction of *Trachyteuthis* (NAEF 1922: fig. 52). *Rhomboteuthis lehmani* (FISCHER & RIOU 1982a) has arms with traces of suckers or cirri, a poorly preserved gladius similar to that of *Plesiotenthis*, an interbranchial arm web, and an unknown number of arms. It cannot be regarded as sound evidence to reconstruct a model teuthid squid with ten arms, two of which are tentacles, as is suggested by FISCHER & RIOU. These authors consider *Gramadella* to be a Jurassic member of the myopsid squids (Metateuthoidea Myopsida), however, it could just as well be a close relative of the Upper Jurassic *Plesiotenthis* and *Trachyteuthis*. Also, these Middle Jurassic squids definitely had no chitinized sucker rings or hooks (FISCHER & RIOU 1982a: pl. 5, figs. 1,2; pl. 6, fig. 2) which should be regarded as stronger evidence compared to the uncertain number of arms and the unknown shell structure.

Conclusions

The arm morphology is a link between the three genera *Plesiotenthis*, *Leptotenthis* and *Trachyteuthis* (Figs. 19, 20). In all three genera the basal parts of the arms are joined by a strong web, and bear cirri and suckers of octopod construction. All eight arms are similar in size and morphology and tentacles are not developed. The contrast to Jurassic decapods such as *Acanthoteuthis* is very pronounced. These creatures do have ten arms of about the same length and each of them holds a double row of hooks. Also the arms are free up to the mouth (buccal mass).

Therefore, *Plesiotenthis*, *Leptotenthis* and *Trachyteuthis* are not decapods and can be connected neither to oegopsid or myopsid squids nor to sepiids. All these Recent dibranchiates have chitinized sucker rings and ring-derived hooks and ten arms, two of which are longer and serve as food-catching devices (tentacles). This modern branch of the decapods is however not directly related to Jurassic decapods such as *Acanthoteuthis*. Its ancestors are still unknown.

Instead of being placed into separate suborders (Prototeuthina, NAEF 1921, and Mesoteuthina, NAEF 1921) the three genera *Plesiotenthis*, *Leptotenthis* and *Trachyteuthis* should be placed in the same suborder. NAEF's diagnosis of the ge-

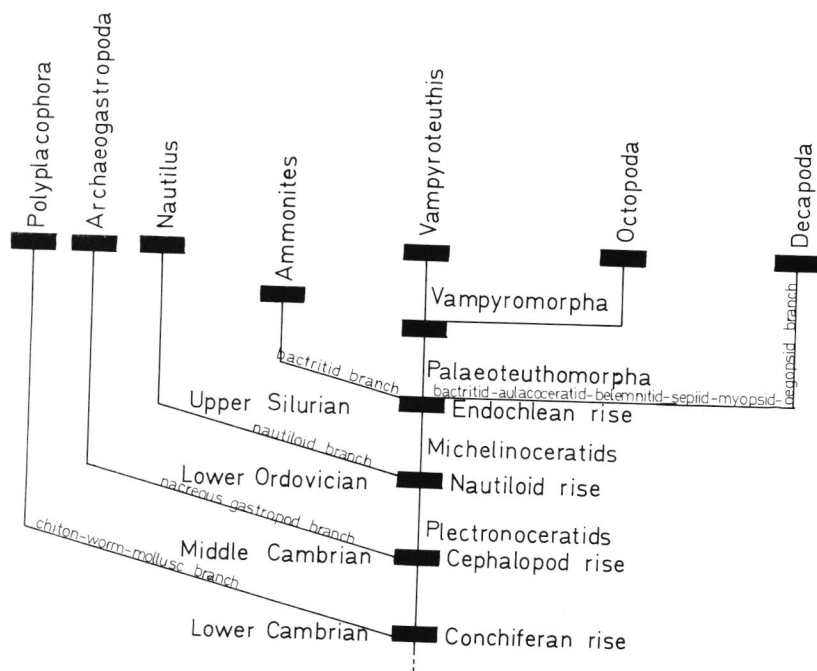


Fig. 21. Sketch demonstrating the possible relationship of the Vampyromorpha with the only surviving species *Vampyroteuthis infernalis* to other cephalopods and conchiferan molluscs in general. Only such groups are included that can be regarded as ancestors in direct lineage to the Vampyromorpha.

nus *Plesiotenthis* — apart from the morphology of the fins — only refers to shell features. The rudiment of the guard cannot be considered a shell characteristic as no such rudiment exists in this animal. The “strongly calcified gladius” of the Prototeuthina does not differ from that of the Oegopseina as assumed by JELETZKY (1966), but is extremely similar. Instead the three species, discussed here in detail, should be regarded as relatives of the “living fossil” *Vampyroteuthis* and members of the Vampyromorpha, which is either a separate suborder of the order Octopoda (Octopoda), or an order by itself.

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