

# New data on the jaw apparatus of fossil cephalopods

YURI D. ZAKHAROV AND TAMAZ A. LOMINADZE

## LETHAIA



Zakharov, Yuri D. & Lominadze, Tamaz A. 1983 01 15: New data on the jaw apparatus of fossil cephalopods. *Lethaia*, Vol. 16, pp. 67-78. Oslo. ISSN 0024-1164.

A newly discovered fossil cephalopod jaw apparatus that may belong to Permian representatives of the Endocochlia is described. *Permorhynchus dentatus* n. gen. n. sp. is established on the basis of this apparatus. The asymmetry of jaws in the Ectocochlia may be connected with the double function of the ventral jaw apparatus, and the well-developed, relatively large frontal plate of the ventral jaw should be regarded as a feature common to all representatives of ectocochlian cephalopods evolved from early Palaeozoic stock. Distinct features seen in the jaw apparatus of Upper Permian endocochlians include the pronounced beak form of both jaws and the presence of oblong wings on the ventral mandible. □ *Cephalopoda*, jaw, operculum, aptychus, anaptychus, *Permorhynchus* n. gen., evolution, Permian.

Yuri D. Zakharov (Юрий Дмитриевич Захаров), Institute of Biology and Pedology, Far-Eastern Scientific Centre, USSR Academy of Science, Vladivostok 690022, USSR (Биолого-педагогический институт Дальневосточного научного центра Академии наук СССР, Владивосток 690022, СССР); Tamaz A. Lominadze (Тамаз Арцловиц Ломинадзе), Institute of Palaeobiology of Georgian SSR Academy of Science, Tbilisi 380004, USSR (Институт палеобиологии Академии наук Грузинской ССР, Тбилиси 380004, ССР; 19th August, 1980 (revised 1982 06 28)).

The jaw apparatus of Recent cephalopods is represented by two jaw elements (Fig. 1) and a radula which is situated between them. According to Akimushkin (1963), the jaw elements consist of three basic parts, the gullet plate, the frontal plate, and the wings (Fig. 2). (The wings may also be considered as a part of the frontal plate.) The more primitive Recent cephalopods (for example *Nautilus*) differ from all others in the large size of the jaws, the pronounced asymmetry, presence of calcareous elements in the jaws (the Sepioidea, Teuthoidea, and Octopoda, which belong to the endocochliate cephalopods, have mandibles made exclusively from chitinous materials), and many more longitudinal rows of radula teeth.

Information on the jaw apparatus in fossil cephalopods is rather fragmentary and contradictory. Recently in the living chambers of some orthoconic nautiloids a structure, termed aptychopsis, has been found (Turek 1978; Holland *et al.* 1978). This consists of three mutually compatible but isolated elements which we consider to have functioned as a primitive jaw apparatus. The two larger elements bear a distinct resemblance to some Mesozoic aptychi that, as we describe below, are most probably the ventral ammonoid jaw. The third element of this structure appears to be an underdeveloped dorsal jaw but one which has an obvious and well developed rostrum (see the slightly deformed structure in

Turek 1978, Fig. 7, but not the reconstruction in his Fig. 2). The mandibular nature of aptychopsis is supported by another feature, too: the aptychopsis elements do not completely close the nautiloid shell aperture as Turek (1978) suggested.

The most completely preserved living chamber with aptychopsisid remains is that figured by Turek (1978, Fig. 9), but unfortunately the subapertural end is flattened. The diameter of the aptychopsis of this specimen is 31 mm and the perimeter of the preserved end of the shell is 112 mm. Analysis of these dimensions suggests that the aptychopsisid area is no more than 77% of the area of the corresponding orthoceratid aperture; but these data do not seem to conform with the reconstructions of Turek (1978, Fig. 8) or Holland *et al.* (1978), who indicate that the aptychopsisid had an exclusively opercular function.

Other structures (rhyncholites) that are often found in association with Mesozoic nautiloids closely resemble the calcified portion of the dorsal mandibles of Recent *Nautilus* (Dieni 1975; Saunders *et al.* 1978; Shimansky 1949). Although rhyncholites are considered to be the remains of the dorsal mandibles of fossil nautiloids, there is no firm evidence that all structures that are known as rhyncholites belonged exclusively to this cephalopod group.

Structures known as conchorhynchids (Ruttenberg 1962) are considered to be the remains of ventral

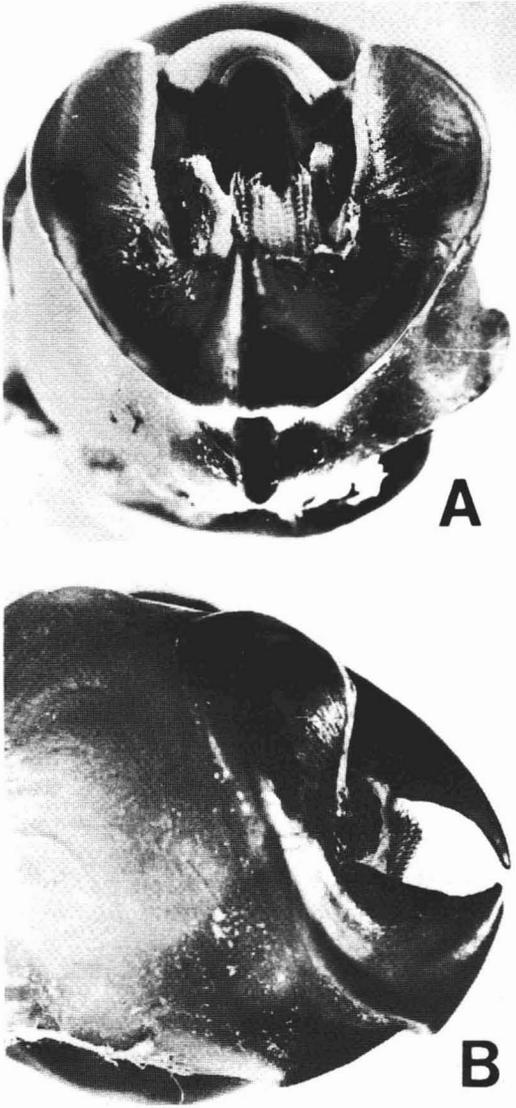


Fig. 1. Jaw apparatus of Recent squid (*Gonatus* sp.). □ A. Anterior view ( $\times 1.4$ ). □ B. Lateral view ( $\times 1.4$ ).

mandibles of fossil nautiloids. While this interpretation has been questioned (Schmidt-Effing 1972) the opinion that conchorhynchids are to be regarded as an exclusively nautiloid jaw element continues to be shared by many workers (Kanie *et al.* 1978; Saunders *et al.* 1978). However, according to Tanabe *et al.* (1980), late Palaeozoic and Mesozoic representatives of both rynchonellids and conchorhynchids may in part belong to the Ammonoidea. Records of paired jaw appara-

tuses in living chambers of fossil nautiloids are to our knowledge unknown.

Our knowledge on the belemnoid jaw apparatus is extremely scanty (Lehmann 1976).

Beak structures that somewhat resemble the dorsal mandibles of Recent cephalopods have been found within living chambers of some ammonoids (Meek & Hayden 1864; Lehmann 1972, 1976; Zakharov 1974) and similar structures were also found in isolation (Dagys & Dagys 1975). The mandibular nature of these structures, named counteraptychi – counteraptychi, counteranaptychi (Zakharov 1979a), has not been questioned, and it seems highly likely that they are the remains of the ammonoid dorsal jaw.

In the living chamber of ammonoids, some other structures known as aptychi – aptychi, anaptychi, have also been found. The function of these structures has been interpreted in two ways; some investigators considering them to function as ammonoid opercula (Trauth 1927–1938; Schindewolf 1958), others regarding them as the ventral ammonoid jaw (Meek & Hayden 1864). Recently Lehmann (1967, 1976) and Closs (1967) corroborated Meek & Hayden's hypothesis by the discovery of a radula positioned, in every example seen, between the beak-shaped structures and the aptychi (aptychi, anaptychi). The mandibular nature of these structures is also favoured by Dagys & Dagys (1975), who discovered on the inner surface of the anaptychus structures that seem to be homologous to the frontal and gullet plates of the ventral mandible of Recent endocochlian cephalopods. The anaptychi have a close morphological resemblance to the aptychi, especially with ones that have partly or completely accreted plates ('valves'). Thus it appears that there is no overriding reason for doubting the mandibular nature of the aptychi. In contrast to the anaptychus platform, the inner structure of the aptychus is believed to have consisted of thin chitinous material that has, so far, not been found fossilized.

Aptychus and anaptychus are considered by most writers to be the jaw apparatus of ammonoids, but Dagys & Dagys (1979) suggested that anaptychi (and the beak structures) are the remains of the jaw apparatus of non-skeletonized dibranchiate cephalopods. This conclusion, however, is at variance with other facts:

- (1) The correspondence between the aptychus outline and the outline of the corresponding ammonoid shell aperture is known from many ex-

amples (Schindewolf 1958, Pl. 8:2; Morton 1981, Figs. 1, 2); this feature was used by Schindewolf as the basis of his hypothesis regarding the opercular nature of aptychus and anaptychus.

(2) The analogy with the mandibles of Recent *Nautilus*, which also has an external skeleton, is strong, and Jurassic and Cretaceous anaptychi also have calcified elements (Strickland 1844; Nagao 1931; Holder 1958; Kanie *et al.* 1978; Zakharov 1979a; and Tanabe *et al.* 1980).

(3) The regular association of aptychi, anaptychi, and ammonoid shells; the aptychus and anaptychus evolution is seen to reflect the general outline of ammonoid evolution (Zakharov 1979a, Fig. 5).

Three generalizations can be made regarding the cephalopod jaw apparatus in relation to the shell:

- (1) Recent and fossil cephalopods with external shell have a most pronounced asymmetry of the jaws.
- (2) Only cephalopods with external skeletons have calcareous jaw elements.
- (3) The outline of the ectocochlian ventral jaw conforms in a very general way with that of the aperture (Zakharov 1979a).

It would appear that the correlation between the cephalopod jaw apparatus and shell appearance was the result of a change in the function of the ventral mandible of the ectocochlians, possibly reflecting a change in the main feeding habit. If the idea propounded by Lehmann (1976) is to be considered, then the aptychus and anaptychus had two functions: (1) that of a ventral jaw, and (2) protection.

However, it must be taken into account that at certain stages of development in some individual ammonoids (i.e. at the stage of terminal narrowing of the shell aperture) the apparatus structures examined could not possibly function as opercula (Meek & Hayden 1864; Zakharov 1979a), and the possibility that they served two functions can only be justified in the rare cases where the outline of the aptychi conforms to the shape of the living-chamber apertures.

Analysis of evolutionary trends in the Class Cephalopoda at least during the Mesozoic and Cainozoic leads us to conclude that there must be a functional reduction, in the sense of Schmal-

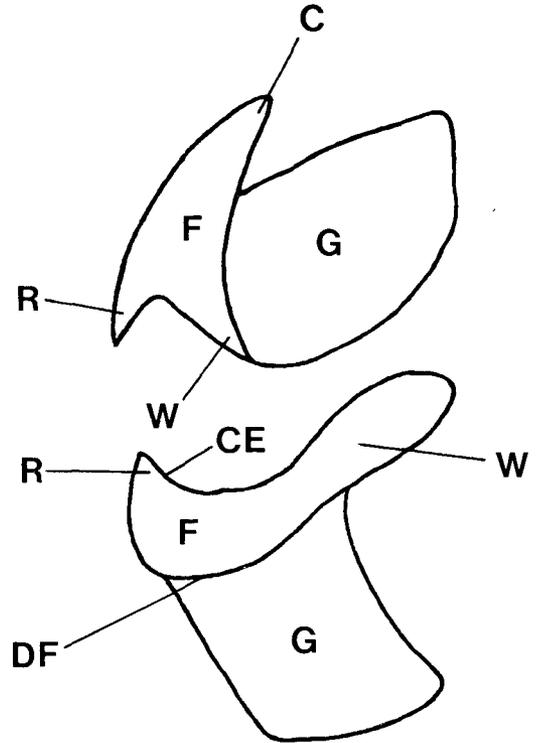


Fig. 2. Morphology of ventral (lower) and dorsal (upper) of Recent dibranchiate jaws. From Akimushkin (1963). F, frontal plate (the hood according to Clarke's terminology); DF, distal edge of the frontal plate; C, cornice; R, rostrum; CE, cutting edge; G, gullet plate (the lateral wall areas plus crest in Clarke's terminology).

hauzen (1969), in the use of the cephalopod jaw apparatus. We see the end result of this evolutionary trend in the Recent endocochlians, where this apparatus does not have a protective function.

Remains of cephalopod jaw apparatuses are more rarely preserved in the fossil record than their conch counterparts. Thus on the basis of available data it is difficult to judge the real distribution of the cephalopods themselves in time and space. Recent finds make up for some of the deficiencies in our knowledge, and although Mesozoic and Cainozoic rhyncholites were only found recently in the Mediterranean area of Europe (including the Crimea and Caucasus) and North Africa, Palaeozoic, Mesozoic and Tertiary rhyncholites are now known from all continental areas except Australia and Antarctica. They have been found in the circum-

Pacific belt, southern California (Teichert & Stanley 1975), Sakhalin Island (Zakharov 1979b), Cuba, Salvador (including sea floor sediments), the Mississippi region, and India (Teichert & Spinosa 1971). New data on the latest finds of Palaeozoic and Mesozoic anptychi (Dagys & Dagys 1975; Zakharov 1974, 1979b), aptychi (Farinacci *et al.* 1976), and remains of radulae (Lehmann 1976; Zakharov 1979b) have greatly added to our knowledge.

### A possible Permian endocochlian jaw apparatus from Primorye

During a study of the Capitan reef limestone section in a neglected corner of Nakhodka Bay in South Primorye in 1979, some interesting examples of jaw structures were found. These are described, with some reservation, as the remains of the jaw apparatus of large Endocochlia, as they most closely resemble the ventral jaw of the Recent endocochlian cephalopods, the Coleoidea. Comparisons with all known jaw apparati from fossil and Recent cephalopods indicate that the narrow oblong wings of the Primorye specimens resemble only those seen in the ventral jaws of the Sepioidea, Teuthoidea, and Octopoda. Therefore this new find *may be* the remains of the ventral jaws of an endocochliate cephalopod. The rostrum of these Permian cephalopod jaws is not preserved, but the outlines of some preserved parts of the frontal plate leave no doubt that these jaws, like their dibranchiate counterparts, have a beak form. One jaw fragment came from the uppermost beds of limestones at this section where nautiloids (*Lopingoceras* sp., *Cycloceras* sp., *Permonautilus* sp.) and the ammonoid *Xenodiscus* aff. *carbonarius* (Waagen) have been found; another better preserved specimen came from a loose boulder at the base of the section.

Finds of jaw apparatuses with fossil cephalopods having only endoskeletons are extremely rare; only the jaws of Mesozoic belemnoids have been illustrated in connection with impressions of the soft parts of the body (Crick 1897; Naef 1922). According to Lehmann (1976), there is a morphological similarity between these structures and the jaw apparatus of Recent dibranchiate cephalopods.

These new finds may shed light on the problem of the evolution of jaw apparatus in cephalopods that do not have an exoskeleton, and also pro-

vide a possible solution to the question of the functional significance of the aptychus. Recently, Farinacci *et al.* (1976) have carried out most interesting research on aptychus ultrastructures. They did not produce conclusive evidence in favour of the possible opercular function of the aptychus, although they are supporters of this school of thought. Here we demonstrate that the resemblance between the internal structures of obviously jaw-formed elements from the Permian of the Far East and those of Jurassic aptychi of Europe is a weighty argument in favour of the hypothesis that aptychi were mandibles.

The description of this new find from the Permian limestones of the Primorye region is given below.

### Genus *Permorrhynchus* Zakharov, n. gen.

*Derivation of name.* – After its occurrence in the Permian.

*Type and only species.* – *P. dentatus* Zakharov, n. gen. n. sp.

*Diagnosis.* – A wide-beaked structure with distinctly pronounced narrow wedge-shaped wings and strongly pronounced valliculum, restricted to inner surface of gullet plate; internal structure of the frontal and gullet plates cellular-prismatic.

*Discussion.* – There are no full data on the mandible morphology of fossil endocochlians in any publications, so it is extremely difficult to use available publications for comparison. The most distinctive features in *Permorrhynchus* are the excessive thickness of the frontal and gullet plates with the cellular-prismatic internal structure, and the presence of a wide transversal valliculum on the inner surface of the gullet plate; the latter being absent on the mandibles of Recent squids (Fig. 1). The internal structure of *Permorrhynchus* is very similar to that seen on the Jurassic genus *Punctaptychus* (Schindewolf 1958; Farinacci *et al.* 1976; Zakharov 1979a), but differs in that the cells in transverse section are less regular, their walls are more porous, and calcareous material is absent.

The unique morphological features of the described structures combined with the known signs of endocochlian and ectocochlian jaws leaves no doubt that they must be distinguished

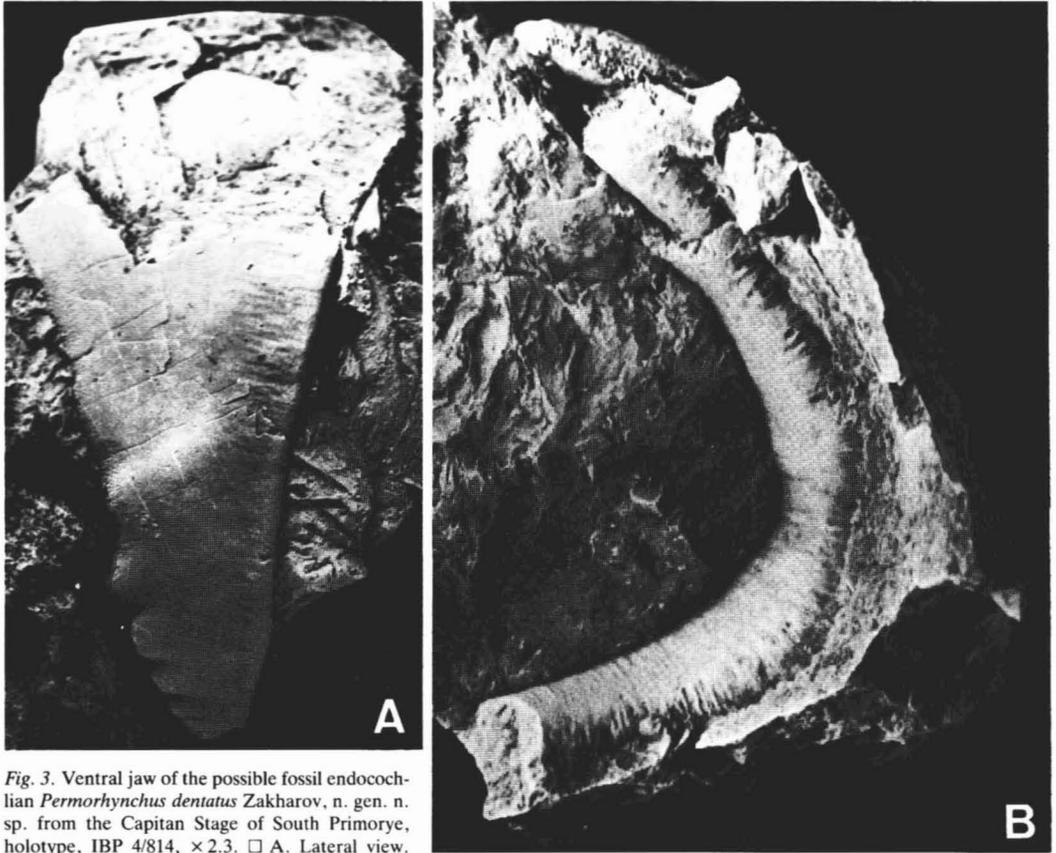


Fig. 3. Ventral jaw of the possible fossil endocochlian *Permorhynchus dentatus* Zakharov, n. gen. n. sp. from the Capitan Stage of South Primorye, holotype, IBP 4/814,  $\times 2.3$ . □ A. Lateral view. □ B. Dorsal view.

as a special taxon, a new genus in a parataxonomic classification.

*Distribution.* – Only one species of *Permorhynchus* from Chandalaz Suite of Lower Permian (Capitan Stage) of South Primorye has been found so far.

*Permorhynchus dentatus* Zakharov, n. sp.

Figs. 3–4

*Derivation of name.* – From Latin *dentatus*, referring to the presence of teeth at the distal part of the wings.

*Holotype.* – Institute of Biology and Pedology, Far-Eastern Scientific Centre, USSR Academy of Sciences (Vladivostok), No. IBP 4/814.

*Diagnosis.* – As for genus.

*Description.* – A chitinous, wide-beaked structure, with a strongly pronounced rostrum and narrow wedge-shaped wings that have six teeth at the distal end. The height of the holotype is 34 mm, the width 41 mm, and the length (taking into account dimensions of the fragment of the gullet plate) not less than 40 mm. The cutting edge of the frontal plate is subacute; at other places this plate has a maximum thickness of 3 mm; the largest parts being restricted to the rostral area. The gullet plate has a swelling that looks like a transverse valliculum (near the end of the frontal plate). The valliculum has a strongly pronounced sinus, orientated to the side of the rostrum (Fig. 5C). The valliculum width is 7.6 mm. The thickness of the gullet plate at the valliculum is 8.0 mm and 3.0 mm at the edge of the preserved fragment of the gullet plate. On

the surface of the cutting edge of the frontal plate, a fine cellular sculpture occurs. The external surface at the end of the frontal plate and the surface of the transverse valliculum are covered by sinuous folds orientated across the wings and valliculum. The frontal and gullet plates, including the transversal valliculum, have a triple-layered structure; a lower lamellar layer, median cellular layer and upper lamellar layer. These layers are believed to be chitinous in composition (they are black in transmitted light). The lower and upper layers of the described jaw are thin, the predominant part of the frontal and gullet plates being composed of the cellular layer with cellular-prismatic or cellular-tabular structures (cellular in transverse section). The cells are sub-polygonal or oval (Figs. 5–6), the walls of the cells often being chaotically curved. The diameter of the cell units is not constant, fluctuating from 0.07 to 0.8 mm, the thickness of the cell wall also varies from 0.02 to 0.14 mm (Figs. 5A, D; 6A, B). The walls of the prisms of the cellular layer have a porous structure (Figs. 5B; 6C, D), which consists of a thin chitinous lamella (Fig. 6D); these pores have diameters of 0.03–0.07 mm. The cavity of the prisms are filled by secondary calcareous material.

The second specimen was investigated only visually.

**Material.** – Fragments of two representatives of *Permorrhynchus dentatus* are known from Chandalaz Suite of Lower Permian (Capitan Stage, *Neogeoceras thaumastum* beds) of the Nakhodka Bay in South Primorye region.

**Discussion.** – The inner structure of the frontal and gullet plates of *Permorrhynchus dentatus* closely resembles that of Jurassic *Punctaptychus punctatus* (VOLTZ) from the Tithonian – Berriasian of Southwest Crimea (Zakharov 1979a, Pls. 17–18), but differs in that there is less regularity of the prisms in transverse section, and in the considerable porosity of the walls which is believed to be caused possibly by the absence of the primary calcareous elements in the Permian endocochlian mandible.

## Examples of fossil ectocochlian jaws

### *Collection of aptychi from the Upper Jurassic of Solnhofen*

In the Upper Jurassic (Lower Tithonian) sediments of Solnhofen in Bavaria (Malz 1977), fa-

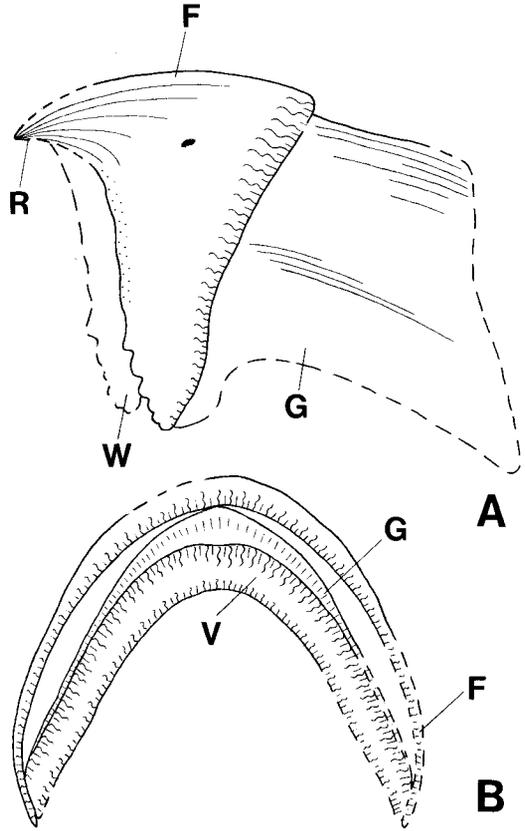


Fig. 4. *Permorrhynchus dentatus* Zakharov, n. gen. n. sp. Reconstruction of ventral jaw,  $\times 1.1$ . □ A. Lateral view. □ B. Dorsal view. R, rostrum; F, frontal plate; G, gullet plate; W, wing; V, transverse valliculum.

mous for the finds of the oldest birds, *Archeopteryx*, and some other organisms (echinoderms, insects, molluscs, crustaceans, fish, reptiles, plants), remains of ammonoid jaw apparatus are known.

We have seen unique material that essentially supplements the information on Solnhofen aptychi (this material was received from L. Sh. Davitashvili in 1974). The collection consists of five species (some aptychi were found *in situ* in the body chamber): *Lamellaptychus* cf. *lamellosus* (Parkinson) in the body chamber of *Glochiceras* (*Paralingulaticeras*) *lithographicum* (Oppel) (Fig. 7A), *Lamellaptychus* cf. *rectecostatus* (Peters) in the living chamber of *Sutneria* (?) sp. 2 (Fig. 8C), *Lamellaptychus* sp. found in the body chamber of *Sutneria* (?) sp. 1 (Fig. 7B), *Laevaptychus latus* (Parkinson) (Fig. 7C), and *Laevaptychus*

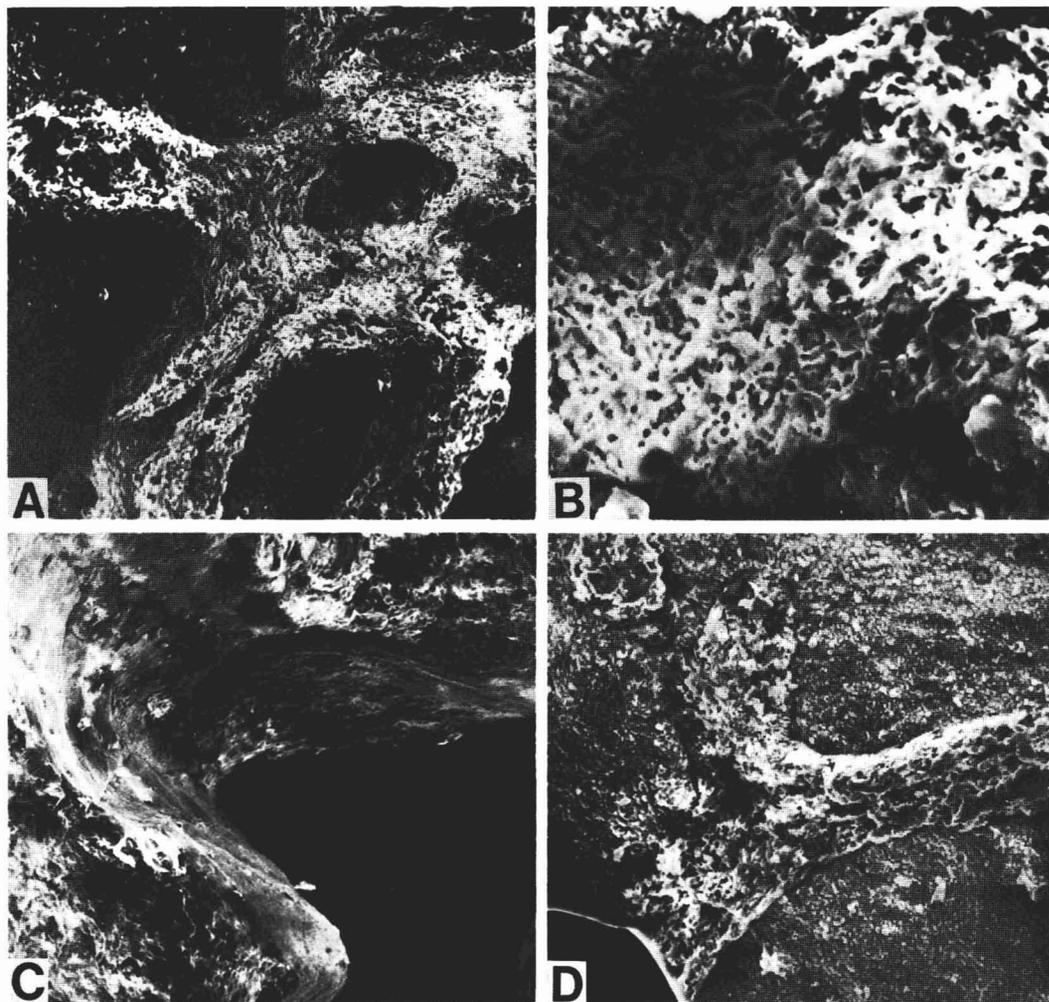


Fig. 5. *Permorhynchus dentatus* Zakharov, n. gen. n. sp. from the Capitan Stage of South Primorye, holotype, IBP 4/814. □ A. Cellular structure of transverse valliculum in cross-section,  $\times 280$ . □ B. Porous structure of the cell wall of the transverse valliculum in the same section,  $\times 470$ . □ C. The strongly pronounced cut (sinus) of transverse valliculum of gullet plate,  $\times 28$ . □ D. Cellular structure of transverse valliculum in cross-section,  $\times 140$ . All photographs were made using the SEM.

sp. (Fig. 9A–B). The length of the aptychi found in association with individual ammonites is only a little less than the apertural height of the accompanying body chamber. These data clearly support the idea that the aptychus is an ammonoid organ, i.e. the ventral mandible.

#### *A Late Cretaceous aptychus from Crimea*

Aptychi are widely distributed in Jurassic sediments, but are rare in the Upper Cretaceous. In this connection, the aptychus mould that has

been found by Naidin in Cenomanian sediments of the Crimea (Selbukhra Mountain) is of interest. This aptychus, determined as *Synaptychus* sp. indet. (Fig. 9C–D), consists of two partially accreted plates (valves) with thin concentric striations at the periphery (Fig. 9D). Its rostrum is feebly marked. The length of the aptychus is 21 mm, and the width is about 22 mm (the edge of left plate valve is not preserved). This is believed to be the first *Synaptychus* find in the Upper Cretaceous of the Crimea.

It is suggested that the morphological resem-

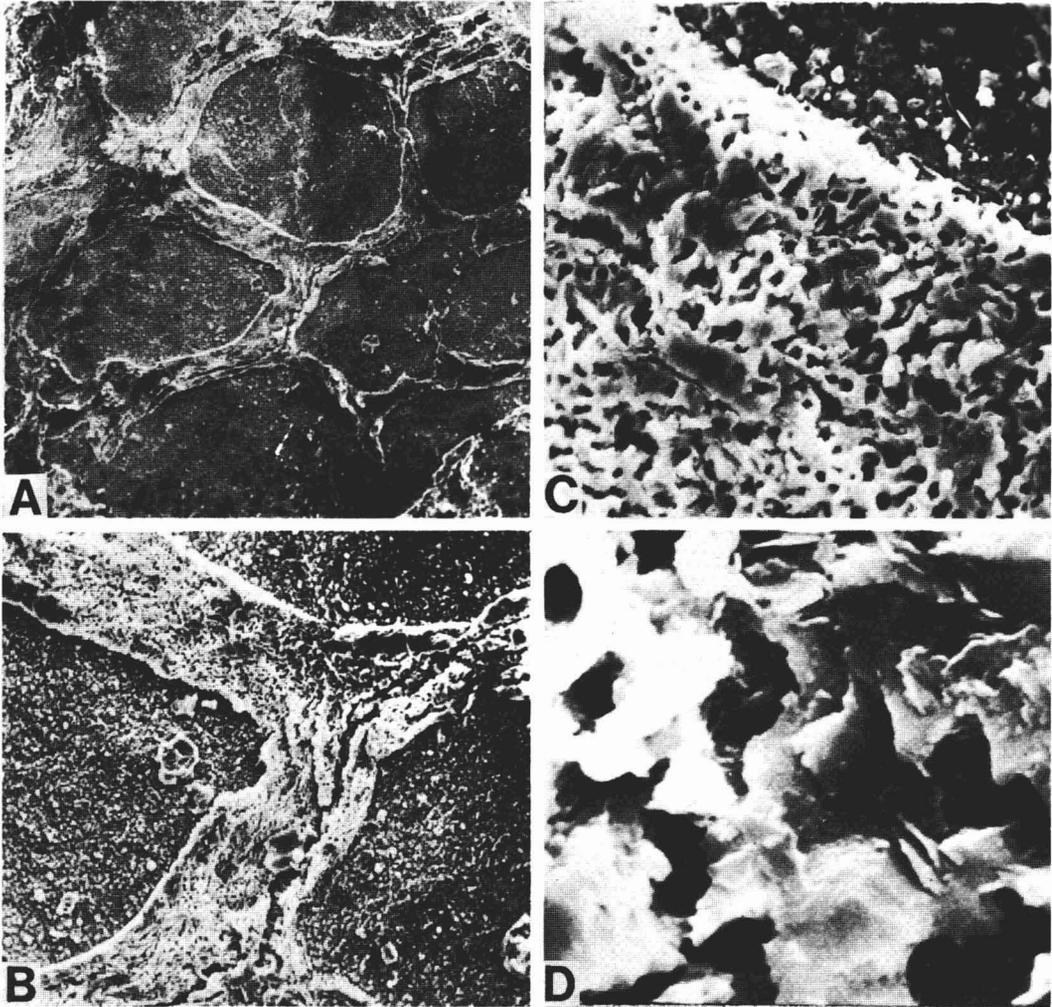


Fig. 6. *Permorhynchus dentatus* Zakharov, n. gen. n. sp. □ A. Cellular structure of gullet plate in cross-section,  $\times 47$ . □ B. Part of gullet plate with cellular structure in the same section,  $\times 140$ . □ C. Porous structure of the cell wall of gullet plate in the same section,  $\times 560$ . □ D. Chitinous lamella that composes the walls of the prisms of cellular layer in gullet plate (cross-section),  $\times 2800$ . All photographs were made using the SEM.

blance between the aptychi (with partially or completely accreted plates) and the anaptychi is conditioned by the similar functional morphology of these organs.

### Some problems of evolution of the cephalopod jaw apparatus

In trying to understand the evolution of the cephalopod jaw apparatus, the finds of a primitive

jaw type (genus *Aptychopsis* Barrande, previously considered to be elements of crustacean skeletons) in the living chamber of Silurian orthoconic cephalopod shells of Central Bohemia (Turek 1978) and southern Sweden (Holland, Stridsberg & Bergström 1978) seems to be very important. As these finds show, there is reason to suppose that the ventral jaws of the Silurian cephalopods (lateral valves of the operculum according to Turek) were considerably larger than the underdeveloped dorsal one (dorsal valve of the oper-

culum according to Turek). Taking into account the weak development of the dorsal jaw of the Silurian 'Orthoceras' cf. *omoenum* Barrande, it may be supposed that these structures originally had a protective role. We have no evidence about the development of the jaw apparatus in the later Orthoceratida.

The jaw apparatus of Recent and Mesozoic nautiloids (the jaws of the latter were reconstructed on the base of a study of fossil rhyncholites and conchorynchs) differs from that of their early relatives, the Orthoceratida, by a better developed dorsal jaw and an unbroken frontal plate of the ventral jaw.

There are no recent data comparing the evolutionary transformation of the aptychopsid type of jaw apparatus (peculiar to the Silurian cephalopods) to that of the aptychoid one (peculiar to the Devonian ammonoids) (Ruedemann 1916; Trauth 1927), because data on the bactritoid jaw apparatus are at present absent.

Within the ammonoids, the forms with anaptychoid type of jaw apparatus constitute the largest stock (Agoniatitida, excluding some Gephuroceratidae; Goniatitida; Ceratitida; and Lytoceratida, excluding the Ancyloceratina). This type of jaw apparatus may be considered as a conservative form, because there were no considerable alterations in the morphology of mandibular elements during the time of its existence (Devonian – Late Cretaceous). The ventral mandibles of ammonoids of this stock are uniplated (univalved) and have, as a rule, a chitinous composition. Only within some branches of Jurassic and Cretaceous Lytoceratida is there a jaw apparatus which contains calcareous elements, mainly in the apical position and between some chitinous layers (Strickland 1844; Nagao 1931; Holder 1958; Kanie 1958; Zakharov 1979a; Tanabe *et al.* 1980).

Ammonoids with aptychoid type of jaw apparatus form three branches of the stock mentioned above: the branch of Gephuroceratidae, which became extinct during the Carboniferous, and two Mesozoic branches – the Ammonitida and Ancyloceratina. It is suggested that the evolutionary transformation of the anaptychoid jaw apparatus to an aptychoid type was realized by paedogenesis (Zakharov 1979a). The most visible change in the morphology of the jaw apparatus (replacement of the anaptychoid type for an aptychoid form in some groups of ammonoids, i.e. Ammonitida at the Triassic–Jurassic boundary) is usually connected with considerable com-

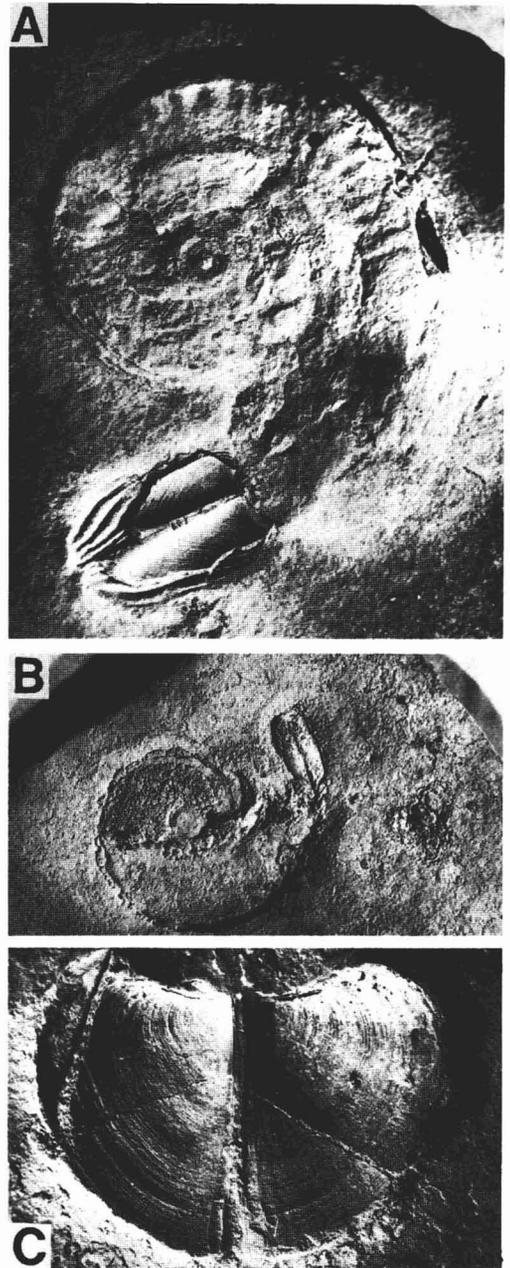


Fig. 7. Ventral jaws of fossil ectocochlians. Upper Jurassic (Lower Tithonian) of Solnhofen in Bavaria. The collection is kept in the Institute of Palaeobiology, Tbilisi. □ A. *Lamellaptychus* cf. *lamellosus* (Parkinson) in living chamber of *Glochyceras* (*Paralingulaticeras*) *lithographicum* (Oppel), IBP 4/815,  $\times 1$ . □ B. *Lamellaptychus* sp. in living chamber of *Sutneria* (?) sp. 1, IBP 2/815,  $\times 1$ . □ C. *Laevaptychus latus* (Parkinson), IBP 3/815,  $\times 1$ .

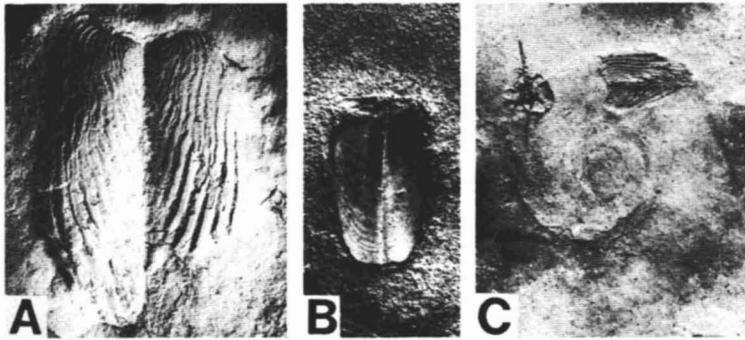


Fig. 8. Ventral jaws of fossil ectocochlians. Upper Jurassic of Solnhofen (Bavaria). The collection is kept in the Institute of Palaeobiology, Tbilisi. □ A. *Lamel-laptychus* cf. *rectecostatus* (Peters), IBP 4/815,  $\times 1$ . □ B. *Lamellaptychus* cf. *lamellosus* (Parkinson), the imprint of inner surface, IBP 5/815,  $\times 1$ . □ C. *Lamel-laptychus* cf. *rectecostatus* (Peters) in living chamber of *Sutneria* (?) sp. 2, IBP 6/815,  $\times 1$ .

plication of the ammonoid septa (sutures). This reconstruction of two most important organs may be hypothetically explained by the change in the mode of life and in particular by the trophic relations of many ammonoid groups in the early Jurassic.

Saunders *et al.* (1978) have investigated the morphology of fossil and recent nautiloids in detail and believe that the jaw apparatus of this cephalopod group has not changed much since Middle Triassic time.

Analysis of the development of the jaw apparatus in the ectocochlian cephalopods makes it possible to determine their general evolution from their early Palaeozoic ancestors with a well developed, relatively large frontal plate of ventral jaw usually sculptured by concentric ribs.

The material described here suggests that some features of the endocochlian jaw apparatus remained stable; for example, the presence of oblong wings in the ventral mandible and the distinctly pronounced beak form of both jaws. As far as this is a hypothesis, it may be said that

the evolution of the jaw apparatus of such large cephalopod groups as the endocochlian cephalopods, nautiloids, and to a lesser degree the ammonoids, apparently was mainly due to selection pressure under conditions of comparatively stable trophic interactions.

*Acknowledgements.* – Our thanks to all those involved in the collection of fossil invertebrates from the Permian limestones of South Primorye: Dr. Aleksandra V. Kiseleva, Dr. Antonina P. Nikitina (Geological Survey, Vladivostok), Dr. Galina V. Kotljars (All Union Geological Institute, Leningrad) and Dr. S. M. Tashchi (Pacific Institute of Geography, Vladivostok). A few years ago academician L. Sh. Davitashvili (Institute of Palaeobiology of Tbilisi, now the L. Sh. Davitashvili Institute), kindly passed the collection of fossil organisms from Solnhofen to one of the present authors. The aptychus from the Upper Cretaceous of Crimea was given to the authors by Prof. D. P. Naidin (Moscow University). The SEM micrographs were made by engineers – Mr. B. V. Dakus and Mr. A. V. Shaposhnikov (Laboratory of Electronic Microscopy of the Institute of Biology and Pedology, Vladivostok) and technical help was given by Mrs. O. G. Gein, Miss V. Iljina, and Mr. V. N. Chainikov (Laboratory of Palaeozoology of the Institute of

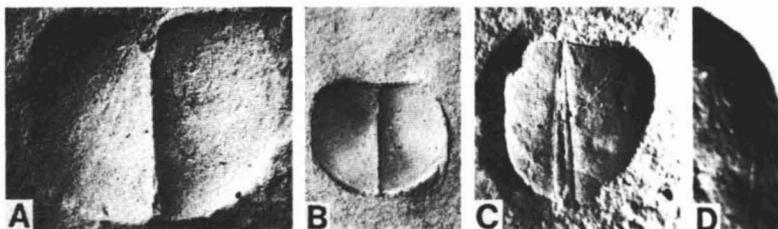


Fig. 9. Ventral jaws of fossil ectocochlians. □ A, B. *Laevaptychus* sp., IBP 7/815 and IBP 8/815,  $\times 1$ . Upper Jurassic of Solnhofen (Bavaria). The collection is kept in the Institute of Palaeobiology, Tbilisi. □ C, D. *Synaptychus* sp. indet., IBP 1/816. Upper Cretaceous, (Cenomanian) of Crimea (Selbukhra Mountain). Specimen is kept in the Institute of Biology and Pedology, Vladivostok. □ C. The imprint of external surface,  $\times 1$ . □ D. Concentric ribs of distal portion,  $\times 3$ .

Biology and Pedology, Vladivostok). Special thanks are due to Dr. John R. Senior (University of Durham) for assistance with the manuscript.



A contribution to Project No. 106 ('Permo-Triassic stage of geological evolution').

## References

- Akimushkin, I. I. (Акимущин, И. И.) 1963: *Головоногие моллюски морей СССР*. [The cephalopods of the USSR seas.] 235 pp. Издательство Академии наук СССР, Москва.
- Closs, D. 1967: Goniatites mit Radula und Kieferapparat in der Itarare – Formation von Uruquay. *Paläontol. Z.* 41, 19–37.
- Crick, G. G. 1897: On an exemplar of *Acanthoteuthis speciosa* Münster from the lithographic stone, Fichstätt, Bavaria. *Geol. Mag.* 4, 1–4.
- Dagys, A. S. & Dagys, A. A. (Дагис, А. С. и Дагис, А. А.) 1975: Морфология и функциональное значение апатихов. [Morphology and functional significance of anaptychus.] *Палеонтол. ж.* 1975: 2, 55–68.
- Dagys, A. S. & Dagys, A. A. (Дагис, А. С. и Дагис, А. А.) 1979: Анаптихи (морфология, функциональное значение, систематическая принадлежность и геологическая история). [Anaptychi (morphology, functional significance, systematic affinity and geological history).] *Тезисы докладов на Всесоюзном совещании 'Новые методы исследований и принципы систематики цефалопод (аммоноидей)'*. 21–23 мая 1979 г., 9–11. Москва.
- Dieni, I. 1975: Revisione di alcune specie giurassiche e Cretacea di rincheliti. *Palaeontographica Italica* 69 (39), 37–107.
- Farinacci, A., Mariotti, N., Matteucci, R., Nicosia, U. & Pallini, G. 1976: Structural features of some Jurassic and Early Cretaceous aptychi. *Boll. Soc. Paleontol. Ital.* 15:2, 111–143.
- Hölder, H. 1958: Ein neuer Anaptychus, vermutlich von *Psiloceras (Caloceras) torus* (d'Orb.). *Neues Jahrb. Geol. Paläontol. Monatsh.* 6, 280–282.
- Holland, B., Stridsberg, S. & Bergström, J. 1978: Confirmation of the reconstruction of *Aptychopsis*. *Lethaia* 11:2, 144.
- Kanie, Y., Tanabe, K., Fukuda, Y., Hirano, H. & Obata, I. 1978: Preliminary study of jaw apparatus in some late Cretaceous ammonites from Japan and Sakhalin. *J. Geol. Soc. Japan* 84: 10, 629–631.
- Lehmann, U. 1967: Ammoniten mit Kieferapparat und Radula aus Lias-Geschieben. *Paläontol. Z.* 41, 38–45.
- Lehmann, U. 1972: Aptychen als Kieferelemente der Ammoniten. *Paläontol. Z.* 46, 34–48.
- Lehmann, U. 1976: *Ammoniten. Ihr Leben und ihre Umwelt*. 171 pp. Stuttgart.
- Malz, H. 1977: *Solenhofener Plattenkalk: Eine Welt in Stein*. 109 pp. Museum beim Solenhofen Aktien-Verein. Maxber.
- Meek, F. B. & Hayden, F. V. 1864: Palaeontology of the Upper Missouri. *Smithson. Contrib. Knowledge*. 172, 1–135.
- Morton, N. 1981: Aptychi: the myth of the ammonite operculum. *Lethaia* 14:1, 57–61.
- Naef, A. 1922: *Die fossilen Tintenfische. Eine Paläozoologische Monographie*. 322 pp. Jena.
- Nagao, T. 1931. *Anaptychus* and *Aptychus* lately acquired from the Upper Cretaceous of Hokkaido. *Japan. J. Fac. Sci. Hokkaido Univ., Ser. 4, Geol., Mineral.* 1:2, 215–222.
- Ruedemann, R. 1916: Paleontologic contributions from the New York State Museum; *Spathiocaris* and *Diseinocarina*. *Bull. New York St. Mus.* 189, 98–102.
- Rutte, E. 1962: Der Kieferapparat triassischer Nautiliden. *Paläontol. Z.* 79–92.
- Saunders, W. B., Spinosa, C., Teichert, C. & Banks, R. C. 1978: The jaw apparatus of Recent *Nautilus* and its palaeontological implications. *Palaeontology* 21:1, 129–141.
- Schindewolf, O. H. 1958: Über Aptychen (Ammonoidea). *Palaeontographica. Abt. A, III*, 1–46.
- Schmalhauzen, I. I. (Шмальгаузен, И. И.) 1969: *Проблемы дарвинизма*. [The problems of Darwinism.] 493 pp. Наука, Ленинград.
- Schmidt-Effing, R. 1972: Ein Ceratid mit Kieferapparat aus dem Muschelkalk des Saarlandes. *Paläontol. Z.* 46, 49–55.
- Shimansky, V. N. (Шиманский, В. Н.) 1949: О систематическом положении ринхолитов. [On the systematic position of rhyncholites.] *Труды Палеонтологического института Академии наук СССР* 20, 199–208.
- Strickland, H. 1844: On certain calcareo-corneous bodies found in the outer chambers of ammonites. *Proc. Geol. Soc. London* 4 (11): 111, 449–452.
- Tanabe, K., Fucuda, Y., Kanie, Y. & Lehmann, U. 1980: Rhyncholites and conchorynchs as calcified jaw elements in some late Cretaceous ammonites. *Lethaia* 13:2, 157–168.
- Teichert, C. & Spinosa, C. 1971: Cretaceous and Tertiary rhyncholites from the western Atlantic ocean and from Mississippi. *University of Kansas. Paleontol. Contrib.* 58, 1–10.
- Teichert, C. & Stanley, G. D. 1975: Eocene rhyncholite from California. *Geology* 3, 178–180.
- Trauth, F. 1927: Aptychenstudien I. Über die Aptychen im Allgemeinen. *Annal. Naturhist. Mus. Wien* 41, 171–259.
- Trauth, F. 1928: Aptychenstudien II. Die Aptychen der Oberkreide. *Annal. Naturhist. Mus. Wien* 42, 121–193.
- Trauth, F. 1930: Aptychenstudien. III–V. Nachtrag zu dem 'Aptychen im Allgemeinen'. Nachtrag zu dem 'Aptychen der Oberkreide'. Die Aptychen des Dogger. *Annal. Naturhist. Mus. Wien* 44, 329–411.
- Trauth, F. 1931: Aptychenstudien. VI–VII. Zweiter Nachtrag zu dem 'Aptychen im Allgemeinen'. Die Aptychen des Malm und der Unterkreide. *Annal. Naturhist. Mus. Wien* 45, 17–136.
- Trauth, F. 1934: Die Anaptychen des Lias. *Neues Jahrb. Miner., Geol. Paläontol. Beilg.* 73, Abt. B, 70–99.
- Trauth, F. 1935a: Die Aptychen des Paläozoicum. *Jahrb. Preuss. Geol. Landesant.* 55, 44–83.
- Trauth, F. 1935b: Die Aptychen der Trias. *Sitzungsber. Akad. Wiss. Wien, math.-naturwiss. Kl., Abt. 1, 144: 9–10*, 455–482.
- Trauth, F. 1935c: Anaptychi und Anaptychus-ähnliche Aptychi der Kreide. *Neues Jahrb. Min., Geol. Paläontol., Abt. B*, 74, 448–468.
- Trauth, F. 1936: Aptychenstudien. VIII. Die Laevilamellaptychi des Oberjura und der Unterkreide. *Annal. Naturhist. Mus. Wien*. 47, 127–145.
- Trauth, F. 1937: Die Praestriaptychi und Granulaptychi des Oberjura und der Unterkreide. *Paläontol. Z.* 19, 134–162.
- Trauth, F. 1938. Die Lamellaptychi des Oberjura und der Unterkreide. *Palaeontographica* 88, Abt. A, 115–229.
- Turek, V. 1978: Biological and stratigraphical significance of the Silurian nautiloid *Aptychopsis*. *Lethaia* 11:2, 127–138.
- Zakharov, Yu. D. (Захаров, Ю. Д.) 1974: Новая находка

- челюстного аппарата аммоноидей. [A new find of ammonoid jaw apparatus.] *Палеонтол. ж.* 4, 127–129.
- Zakharov, Yu. D. (Захаров, Ю. Д.) 1979a: Морфология челюстного аппарата цефалопод и некоторые проблемы Эволюции. [Morphology of the jaw apparatus of cephalopods and some evolution problems.] In М. Н. Грамм (ред.): *Ископаемые беспозвоночные Дальнего Востока*, 60–79 Владивосток.
- Zakharov, Yu. D. (Захаров, Ю. Д.) 1979b: Новые находки ринхолитов, анаптихов, аптихов и остатков радулы цефалопод на территории СССР. [New finds of rhyncholites, anaptychi, aptychi, and remains of cephalopod radula at USSR territory.] In М. Н. Грамм (ред.): *Ископаемые беспозвоночные Дальнего Востока*, 80–91. Владивосток.