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Structural features of some Jurassic and Early Cretaceous Aptychi

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ABSTRACT — We have examined the structures and microstructures of six Aptychi « genera » (i.s. TRAUTH) *ranging from Toarcian to Neocomian* (Cornaptychus, Laevicornaptychus, Lamellaptychus, Punctaptychus, Laevilamellaptychus, Laevaptychus). *Most of the specimens originate from various sites of Central Italy and Germany.*

The microstructural unity and a structural differentiation have been recognized in the constructive patterns of all types of Aptychi.

It is possible to recognize a unique evolutive trend caused by the gradual development and arrangement of their medial tubular layer.

The study of structure, through the identification of the various characters (gradual development of the above mentioned character, persistence of primitive characters in the " embryo ") determined the identification of a phyletic line from the Toarcian to the Neocomian (Cornaptychus-Lamellaptychus). *We also hypothesized another phyletic line* (Laevicornaptychus-Laevaptychus).

RIASSUNTO — [Caratteri strutturali di alcuni Aptici del Giurassico e del Cretacico inferiore]. *E' stata effettuata una analisi approfondita sulla struttura di 6 generi (i.s.* TRAUTH) *di Aptici* (Cornaptychus, Laevicornaptychus, Lamellaptychus, Punctaptychus, Laevilamellaptychus, Laevaptychus) *provenienti da varie località dell'Italia, della Germania, della Svizzera e dell'Etiopia. L'eterogeneità della provenienza ci ha assicurato la validità e persistenza dei caratteri osservati a prescindere da fattori geografici e ambientali. Lo studio microstrutturale ha rivelato la unitarietà del gruppo nell'identico modello di accrescimento. Tutti i tipi esaminati infatti risultano accresciuti per sovrapposizione di lamelle giustapposte, inclinate verso l'apice, perforate o imperforate a seconda dei generi.*

Dall'esame di tutto il gruppo è emerso inoltre un carattere evolutivo comune a tutte le forme che consiste nell'originarsi e nell'estendersi dello strato tubulare mediano. A questo carattere comune si contrappongono almeno due tipi di architettura: uno caratterizzato dall'esistenza di un distinto strato lamellare superiore (Lamellaptychus) *e un altro in cui lo strato lamellare superiore non è altro che la continuazione degli elementi strutturali dello strato mediano tubulare* (Laevaptychus). *Tra questi due tipi esiste una forma di transizione che presenta entrambi i modelli di organizzazione: il primo nella sua fase giovanile e il secondo nello stadio maturo* (Laevilamellaptychus). *E' stata anche riconosciuta la presenza di uno stadio iniziale nei Lamellaptici e Laevilamellaptici che per forma e microstruttura è assolutamente identico ai Cornaptici. La presenza di questa struttura e il riconoscimento delle modalità con cui essa si trasforma parzialmente in strato tubulare, ha portato al riconoscimento di una linea filetica che da forme toarciane primitive, attraverso forme di transizione del Dogger, si afferma con caratteri evoluti nel Malm e soprattutto nel Neocomiano. Un'altra linea filetica si rivela ipotizzabile in base alle analogie di strutture tra generi isocroni toarciani* (Cornaptychus-Laevicornaptychus) *e alto giurassici* (Lamellaptychus-Laevaptychus).

INTRODUCTION

Many of the authors concerned with the study of Aptychi have done research on their structure, looking for a contribution to solving the problem of their systematic and functional interpretation.

In this study we intend to give additional contribution to the knowledge of the architectural and microstructural characteristics of the Jurassic and early Cretaceous Aptychi, some of which have never been investigated for this purpose.

This study is based on many strictly oriented thin sections and, for the first time, on scanning electron

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microscope observations. It was possible to verify the structural features of the various types of Aptychi, belonging, according to Trauth classification, to the following « genera »: *Cornaptychus, Lamellaptychus, Laevicornaptychus, Laevaptychus, Laevilamellaptychus, Punctaptychus.*

It was attempted to clarify the systematic and evolutive relationships of such Aptychi. Finally their various functional interpretations are discussed.

The material under study extends from Toarcian to Neocomian. Most of it originates from the quarry of Serra San Quirico, 20 km West of Jesi (Central-eastern Apennines). In this quarry, opened in the « Scisti ad Aptici » formation of the lower Tithonian, a very abundant association was collected, with numerous specimens rather well preserved. Other material was collected in various sites of the Apennines, the Alps, Southern Germany and Ethiopia. Some specimens were kindly furnished by museums and collectors.

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PREVIOUS STRUCTURAL STUDIES

Previous works on the Aptychi concerned mainly their systematic position and their taxonomy, or attempts to determine their function.

Even studies devoted mainly to their structure have often been subordinated to these purposes, especially by past authors.

We are going to give here only brief accounts on the most representative of these studies, and defer to the historic synthesis of Trauth (1927) and Scatizzi (1934) for a more complete picture.

The investigation on the structural features of the Mesozoic Aptychi was started in the first half of the last century. As observed by Meneghini and Bornemann (1876), various authors (Bourdet, Meyer, Voltz, Glocker, Coquand, Quenstedt, Pictet) in describing the structure of the various aptychi « *laeves* » or « *cellulosi* » (*Laevaptychus* of Trauth) and « *imbricati* » or « *lamellosi* » or « *sulcati* » and « *punctati* » (*Lamellaptychus* and *Punctaptychus* of Trauth), debate extensively on the structure of the medial layer (tubular or cellular) and on its connection with the upper layer, not taking into account the different orientation of their thin section.

During this period some authors disagree with the general interpretation of Aptychi as Ammonite *opercula*. For instance, Meyer (1831) compared *Aptychus laevis* to the « cuttle fish bone » and Coquand (1841) placed the Aptychus structure between those of *Teudopsis* and *Sepia.*

In the second half of the last century, Zittel (1868) stated that Aptychi are divided generally in three layers, the medial layer being tubular. Meneghini and Bornemann (1876) furnish the first detailed interpretation of the Aptychus structure, drawing carefully some subradial section of *Lamellaptychus* (*Aptychus profundus*), *Punctaptychus* (*Aptychus punctatus*) and *Laevaptychus* (*Aptychus meneghinii*). This last section belongs to the best known Aptychus, already described and illustrated even in its structure by De Zigno (1870). In this study, the main structural elements of Aptychi are rather correctly related and it is pointed out, as well, that it is necessary to take into consideration the orientation of the sections, recognizing that the radial section are the most useful.

Schwartz (1894) analyzed the structure to find, through it, a valid attribution of Aptychi and perhaps the function of them. Therefore the structural analysis appears overshadowed by the interest for the anatomo-functional question. Thanks to sections partially better oriented than those used by some previous authors, he recognizes that the mesh pattern of the layer known as « cellular » did not reflect a real separation of the various « cells ». He believed these organs to be the poison bearers on the basis of the continuity of the various small cells and above all because they terminate on the outer surface of the Aptychus.

In 1927 Trauth, beginning his long series of fundamental monographies on Aptychi, referring largely to the work of Meneghini and Bornemann, defined the structural features of all the Aptychi genera which are analyzed one by one.

It should be pointed out that in this work the absence of the intermediate cellular layer is made evident in one part of *Cornaptychus*. He also suggested a ventral position in a fold of the mantle of Aptychus *in vivo,* and he reaffirmed the opercular function.

In 1934 Scatizzi, recalling an hypothesis of Scalia (1922), also previously made by Pictet (1854), compares the three layers of Aptychi to the three layers which form the « *basalia* » of Cirripeds. From this comparison he is convinced that they are Crustaceans, and attributes them to the Phyllocarids on the basis of morphological similarity.

Schindewolf (1958) has done a very accurate study of the Aptychus structure, particularly of *Laevaptychus.* He emphasizes the close genetic connection among the three layers forming the wall of the Aptychi. He recognizes the constructive pattern in the overlapping of cup-shaped thin layers. Chiefly he based his observations on eroded specimens and oriented thin sections of *Laevaptychus,* even if sometimes cuts do not seem exactly well oriented. Also, he extended the constructive pattern of *Laevaptychus* to *Lamellaptychus* and *Spinaptychus.* In addition Schindewolf used the results of his structural analysis for a functional interpretation. He compares Aptychi to structure similar to the hood of living *Nautilus* and regards them as *opercula,* outside the shell, secreted by tentacles created for this purpose, as in the female *Argonauta.*

AGE AND SOURCE OF MATERIAL

Aptychi considered here for our structural analysis, come from several Italian and European localities; some specimens come from Ethiopia. The various origins of specimens confirmed that the examined characters were independent by geographic and environmental factors.

Toarcian — The oldest specimens are Toarcian in age; they were collected in the following places of Central Apennines and in Germany: Pettino (Perugia), Polino (Terni), Battiferro (Terni), San Polo dei Cavalieri (Roma), Boschitello di Vizzini (Catania), Holzmaden (Germany).

Aalenian-Callovian — Other Aptychi were found in layers which range from Aalenian to Callovian. It is not possible to define a more detailed chronological subdivision because truly significant faunas are absent. Specimens of this age have been collected near San Polo dei Cavalieri (Roma) and Battiferro (Terni).

Oxfordian-Middle Tithonian — Many specimens come from Sant'Angelo Romano (Roma), Serra San Quirico (Ancona), Poggio San Vicino (Macerata), Campo Nocecchio (Ancona), Sette Comuni (Vicenza), Cerungoli (Siena), Châtel Saint Denis (Fribourg), Solnhofen (Bavaria). Some small Aptychi were been degaged together with Foraminifers and Ostracods, already published by Farinacci (1965) and Oertli (1967). The marly level, in which this assemblage was found, is situated near Acquasparta (Martani Mounts, Terni).

Upper Tithonian-Neocomian — Aptychi of these ages come from: Poggio San Romualdo (Ancona), Martani Mounts (Terni), Puez Alp (Dolomites, Bolzano), Canove (Vicenza), Barbate Val Trompia (Brescia), Harar (Ethiopia).

LIST OF EXAMINED FORMS

Aptychi under study were first subdivided into genera, species and subspecies, following closely Trauth classification (1927-1938).

This classification is not examined here critically at the species and subspecies level. Species characters in fact do not seem to correspond to structural modification. Genera, instead, correspond essentially to various types. In fact they were established on groups of forms already separated on the basis of structure (*cellulosi, lamellosi, embriciati,* etc.). Therefore, as a rule, we agree to Trauth taxonomy at genus level. A few observations and slight amendments will be made in the detailed discussion of each genus.

The species under study are listed in table 1.

METHODS

The major part of our observations was made on oriented thin sections in the polarized light (crossed nicols). Moreover various specimens which were etched by diluted hydrochloric acid or naturally eroded have been used.

Seriated dry-peels placed one-half millimeter from each other have been processed to study the inner arrangement of structural elements. The microstructure has been studied by means of scanning electron microscope on fracture surfaces and polished etched sections. The radial section turned out to be most useful in making the structure reconstruction; that is a thin section obtained cutting Aptychi across from apex to lateral margin perpendicularly to the growth lines. Such a section must also be perpendicular to inner and to outer surfaces of the « valve » (fig. 1). Considering that the structural elements are subconcentrically arranged in respect to the apex, the radial

Cornaptychus lythensis (QUENSTEDT?)	Holzmaden	Toarcian
Cornaptychus spp.	Leonessa, Polino, San Polo dei Cavalieri, Strettura, Battiferro.	Toarcian-Callovian
Laevicornaptychus sp.	Pettino, Polino.	Toarcian
Lamellaptychus beyrichi (OPPEL)	Serra San Quirico, Poggio San Vicino.	Malm
L. beyrichi (OPPEL) var. *fractocosta* TRAUTH	Serra San Quirico.	Lower Tithonian
L. beyrichi (OPPEL) var. *moravica* (BLASCHKE)	Serra San Quirico.	Lower Tithonian
L. beyrichi (OPPEL) var. *subalpina* (SCHAFHÄUTL)	Serra San Quirico, Poggio San Romualdo.	Tithonian
L. steraspis (OPPEL)	Serra San Quirico.	Lower Tithonian
L. murocosta TRAUTH	Serra San Quirico, Poggio San Vicino.	Malm
L. submortilleti TRAUTH	Serra San Quirico.	Lower Tithonian
L. lamellosus (PARKINSON)	Serra San Quirico, Poggio San Vicino.	Malm
L. lamellosus (PARKINSON) var. *euglypta* (OPPEL)	Poggio San Vicino.	Kimmeridgian
L. lamellosus (PARKINSON) var. *solenoides* (RÜPPEL)	Serra San Quirico.	Lower Tithonian
L. sparsilamellosus (GÜMBEL)	Campo Nocecchio, Poggio San Vicino, Châtel St. Denis, Sette Comuni.	Malm
L. inflexicosta TRAUTH	Serra San Quirico.	Lower Tithonian
L. lamellosus (PARKINSON) var. *cincta* TRAUTH	Serra San Quirico.	Lower Tithonian
L. angulocostatus (PETERS)	Martani Mounts, Puez.	Upper Tithonian-Neocomian
L. angulocostatus (PETERS) var. *atlantica* (HENNIG)	Barbate Val Trompia.	Upper Tithonian-Neocomian
L. hauffianus (OPPEL)	Solnhofen.	Tithonian
Punctaptychus punctatus (VOLTZ)	Serra San Quirico, Poggio San Vicino, Poggio San Romualdo.	Malm
P. rectecostatus CUZZI	Poggio San Vicino.	Kimmeridgian
Laevilamellaptychus crassissimus (HAUPT)	Serra San Quirico.	Lower Tithonian
Laevaptychus latus (PARKINSON)	Harar.	Malm
L. latus (PARKINSON) var. *uhlandi* TRAUTH	Poggio San Vicino.	Kimmeridgian
L. latus (PARKINSON) var. *taxopora* TRAUTH	Serra San Quirico, Martani Mounts, Poggio San Romualdo.	Malm
L. latus (PARKINSON) var. *rimosa* QUENSTEDT	Serra San Quirico.	Lower Tithonian
L. latissimus TRAUTH	Solnhofen.	Tithonian
L. latissimus var. *seriopora* TRAUTH	Serra San Quirico.	Lower Tithonian
L. latissimus var. *rimosa* TRAUTH	Serra San Quirico.	Lower Tithonian
L. lautlingensis TRAUTH	Poggio San Vicino.	Kimmeridgian
L. longus (MEYER) var. *seriopora* TRAUTH	Poggio San Vicino, Poggio San Romualdo, Châtel St. Denis.	Malm
L. tenuilongus TRAUTH	Solnhofen.	Tithonian
L. tenuilongus TRAUTH var. *heteropora* (THURMANN)	Serra San Quirico.	Lower Tithonian

Table 1 - List of examined forms.

section is the most clarifying to the reciprocal relationship among elements. So it is possible to reconstruct ontogenetic development from the initial to the mature stage.

TERMINOLOGY

Trauth was the first scientist, from 1927 to 1938, to standardize the morphological terminology using known terms and proposing new ones.

In 1957 Arkell summarized the terminology proposed by Trauth in his works and added new terms. During the drafting of our work, Arkell terminology was found to be wanting for extremely detailed purposes.

In text-fig. 1 few new terms are indicated in addition to the known ones, but in spite of that, we will introduce additional descriptive terms in the structural treatment. Their meaning will be explained as they are introduced for the first time. Since the function and physiological position of Aptychi are still being debated, we point out that their orientation and terminology are only conventional, as was indicated by Schindewolf (1958).

STRUCTURAL DESCRIPTIONS

Lamellaptychus and Punctaptychus question

In establishing the genus *Punctaptychus,* Trauth made evident the close relationship to the genus *Lamellaptychus,* from which it differs only because the ridges on the outer side entirely cover the interposed furrows communicating to the outside by rows of pores.

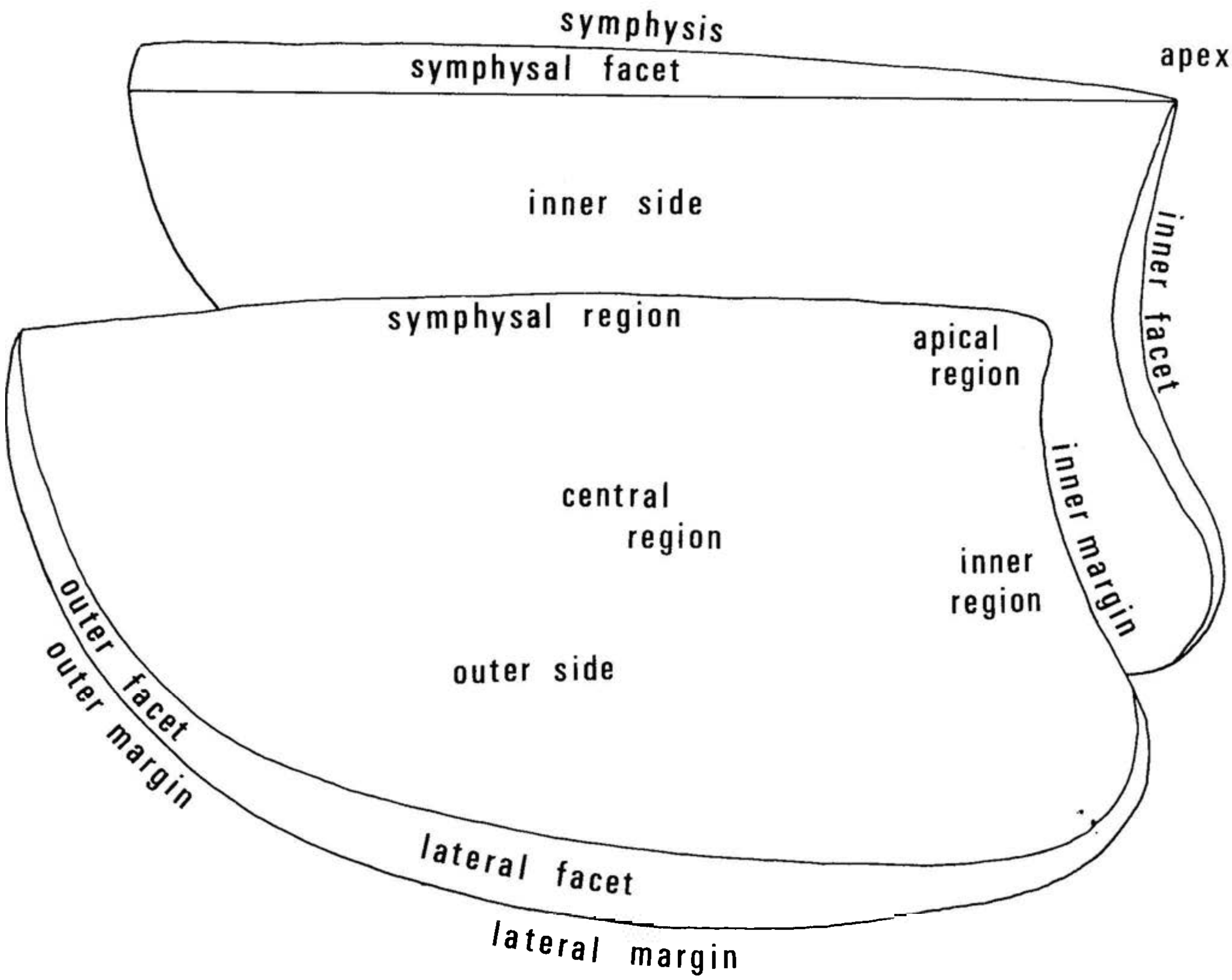


Fig. 1 - Morphological nomenclature of Aptychi (redrawn and partially modified from Arkell).

We must remember that Trauth (1935b) pointed out, repeating a similar observation by Zittel, that the Punctaptychi are more diffused in the paleogeographic province Alpino-mediterranean and extremely rare outside of that province. This is in agreement with the examination of our material of the Oxfordian-lower Neocomian, where the major part of the specimens is composed of Punctaptychi. As Trauth (1938) pointed out, the Punctaptychi and Lamellaptychi found on site are associated with the same type of Ammonites (*Haploceras, Oppelia*).

Subsequently Scatizzi (1934) again confirmed the close relation between the two genera of Trauth proposing therefore to classify them as two subgenera of a single genus *Lamellaptychus* (*Costaptychus*) and *Lamellaptychus* (*Punctaptychus*). In spite of that, Arkell (1957) considers the two taxa as being still separated into two genera. Scatizzi (1934) in addition pointed out the possibility that Punctaptychi, eroded on the outer side, might be macroscopically determined as Lamellaptychi (Pl. 6, fig. 1), due to the fact that the most marked distinction between the two genera consists in the complete overlapping of the furrows in Punctaptychi.

The examination of the abundant material showed that the possibility proposed by Scatizzi happens very frequently, and only through the examination of oriented thin sections it is possible to attribute many forms to *Punctaptychus* rather than to *Lamellaptychus*.

It should be pointed out that in the literature we find quite a large number of species and subspecies being referred to the genus *Lamellaptychus,* while only a few are referred to *Punctaptychus* and only one, *P. punctatus* (VOLTZ), is largely diffused. It should also be pointed out that the eroded Punctaptychi recognized as such in the examination of the oriented thin section, are easily classified as Lamellaptychi. This is due to the similarities in the pattern of the ribs of Lamellaptychi and of those of Punctaptychi when the latter ones are eroded. This was made evident by Cuzzi (1960), who, in spite of that, did not taxonomically relate the two forms.

It is clear that many Lamellaptychi in the literature are none other than eroded Punctaptychi, even if they are, without a doubt, real Lamellaptychi, as demonstrated by structural analysis of numerous specimens. That is, Aptychi with no ridges overlapping the furrows of the outer side.

In agreement with Scatizzi (1934) we accept the Lamellaptychi and Punctaptychi as two subgenera of a single genus entity, confirming that the attribution to one or the other type is certain in most cases only after the examination of a radial thin section.

It should be pointed out that the major part of the observations was done on specimens referred to *L.* (*Punctaptychus*).

LAMELLAPTYCHUS STRUCTURE
(Text-fig. 2; Pl. 2, fig. 4; Pl. 3, figs. 3-5; Pl. 6, figs. 1-3)

The Lamellaptychi we examined have the typical three layers structure known in the literature: basal or lower layer, medial tubular or cellular layer, upper lamellar layer.

Besides these three classic structural elements, we noted the presence of a fourth distinct element placed in the apex part of the « valve ». Due to its position inside the valve and because of the meaning of a differentiated initial stage of development we have given it the name of initial ontogenetic stage.

PLATE 1

Figs. 1, 2, 4, 5, 8 - *Cornaptychus.* 1) Toarcian, Polino, x 2; 2) Toarcian, San Polo dei Cavalieri, x 1.25; 4) Toarcian, Polino, x 1.5, associated with *Hildoceras bifrons* f. *graeca* RENZ; 5) Dogger, San Polo dei Cavalieri, x 1.5; 8) Toarcian, Holzmaden, x 1.4.

Fig. 3 - *Laevicornaptychus,* Toarcian, Pettino, x 3.

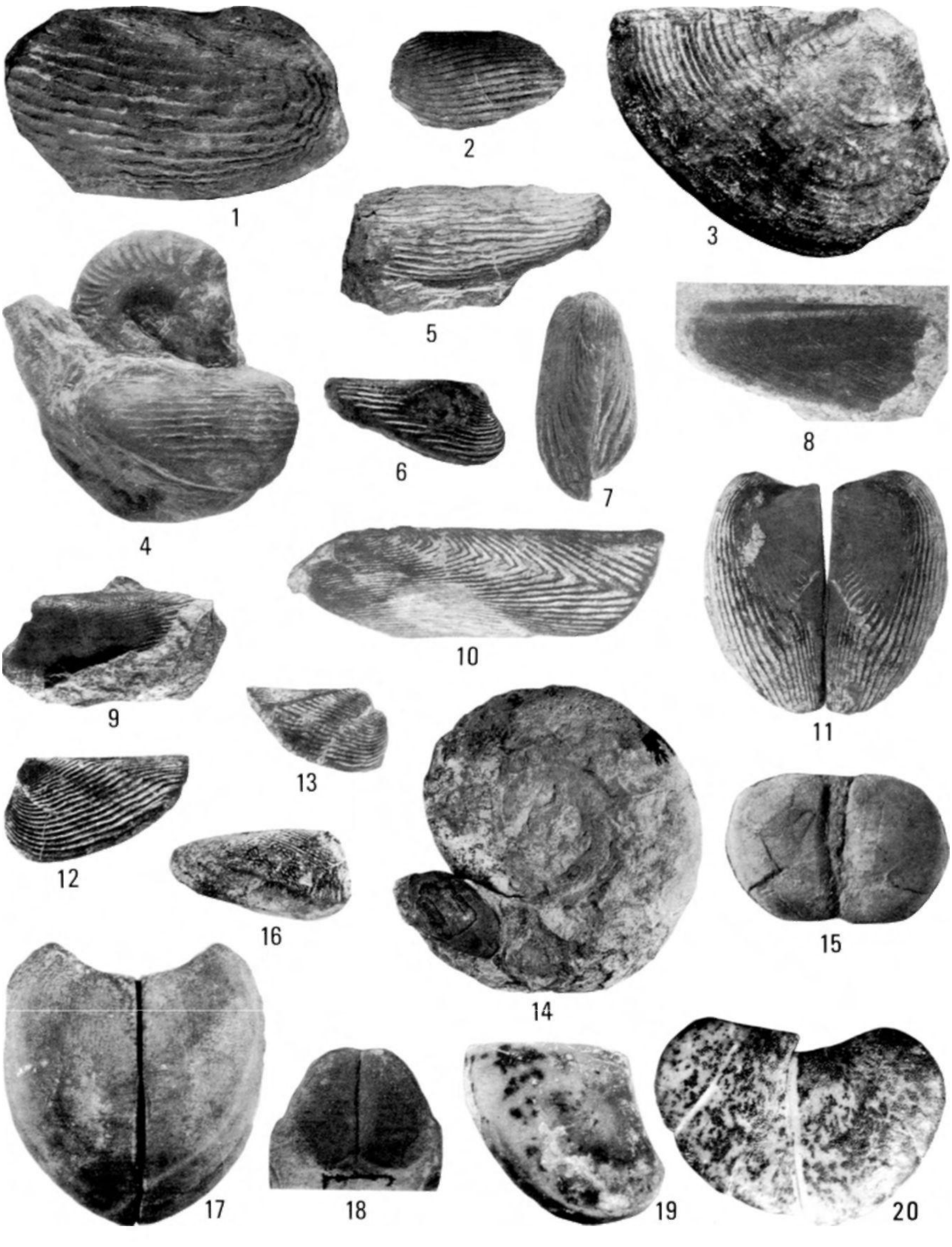
Figs. 6, 7, 10, 12, 13 - *Lamellaptychus.* 6) lower Tithonian, Serra San Quirico, x 1; 7) Kimmeridgian, Poggio San Vicino, x 1.3; 10) Neocomian, Puez, x 3; 12) lower Tithonian, Serra San Quirico, x 1; 13) lower Tithonian, Serra San Quirico, x 1.6.

Figs. 9, 11 - *Lamellaptychus (Punctaptychus).* 9) Kimmeridgian, Poggio San Vicino, x 0.6; 11) lower Tithonian, Serra San Quirico, x 1.

Fig. 14 - Aspidoceratid with a pair of Laevaptychi on the distal part of the body chamber. Upper Tithonian, Poggio San Romualdo, x 0.3.

Figs. 15, 17, 18, 19, 20 - *Laevaptychus.* 15) Kimmeridgian, Poggio San Vicino, x 0.9; 17) Kimmeridgian, Poggio San Vicino, x 1.2; 18) Tithonian, Solnhofen, x 1; 19) lower Tithonian, Serra San Quirico, x 1; 20) lower Tithonian, Serra San Quirico, x 0.5.

Fig. 16 - *Laevilamellaptychus,* lower Tithonian, Serra San Quirico, x 2.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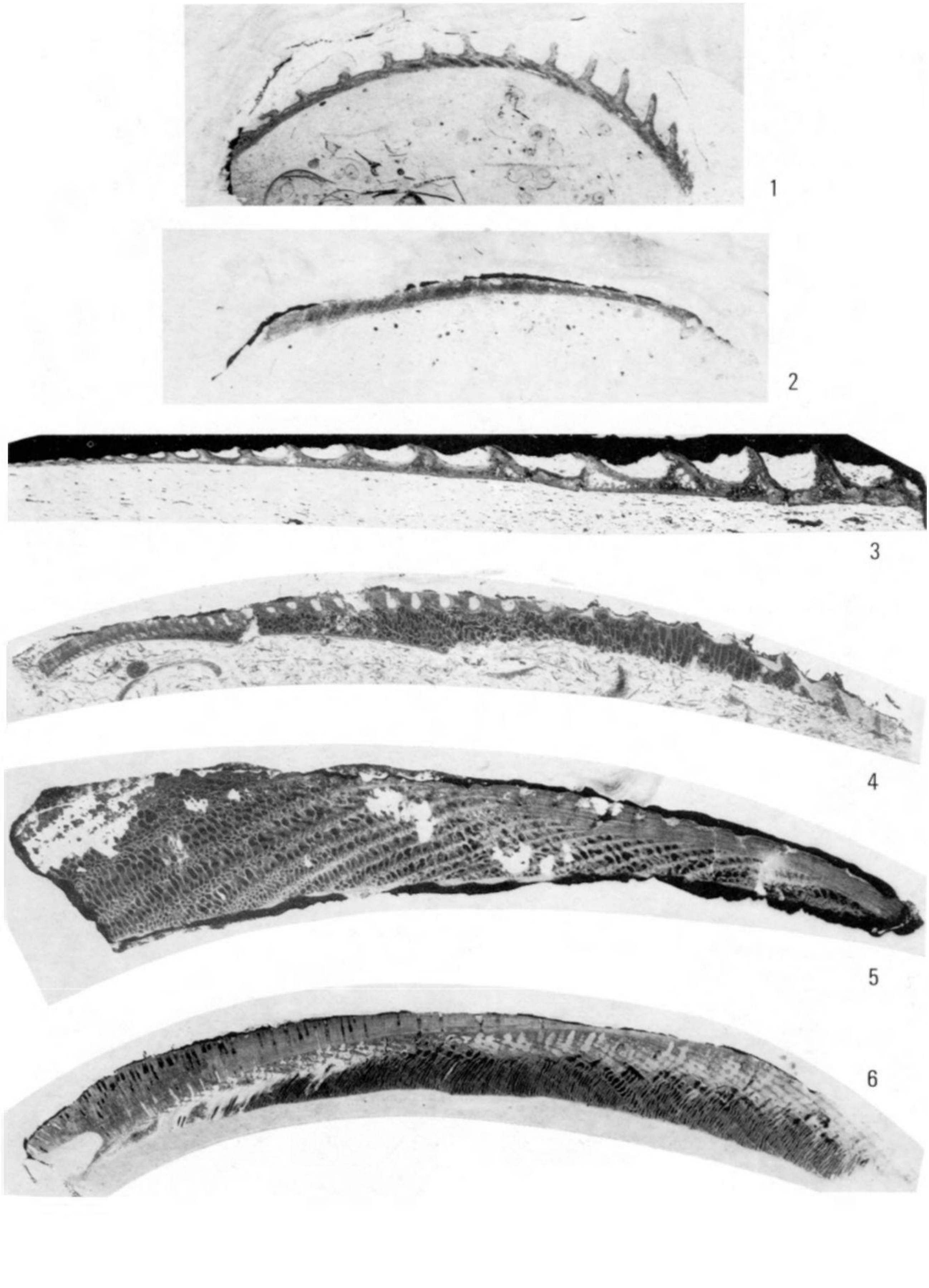
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Initial ontogenetic stage

This structural element placed in the apex region of each valve (Pl. 3) is recognized only in those sections passing through the apex; in fact it is reduced in dimensions and covered by the upper lamellar layer on the outer side and is not discernible from the lower lamellar layer on the inner side. It is also hardly visible in the radial sections because it is very often eroded or hidden by obliterating mineralizations (silicifying, pyritization processes).

In the radial section, the initial ontogenetic stage shows a similar morphology to that of adult *Lamellaptychus,* characterized by an alternated succession of protuberances more or less oblique and spiny, and by depressions (ridges and furrows respectively), which increase gradually and regularly from the apex. The dimensions of the initial ontogenetic stage (maximum length 4 mm, number of ribs 9-14), the morphology and the structure are in every way similar to those forms well known in literature as « small Aptychi ». These occur quite frequently,

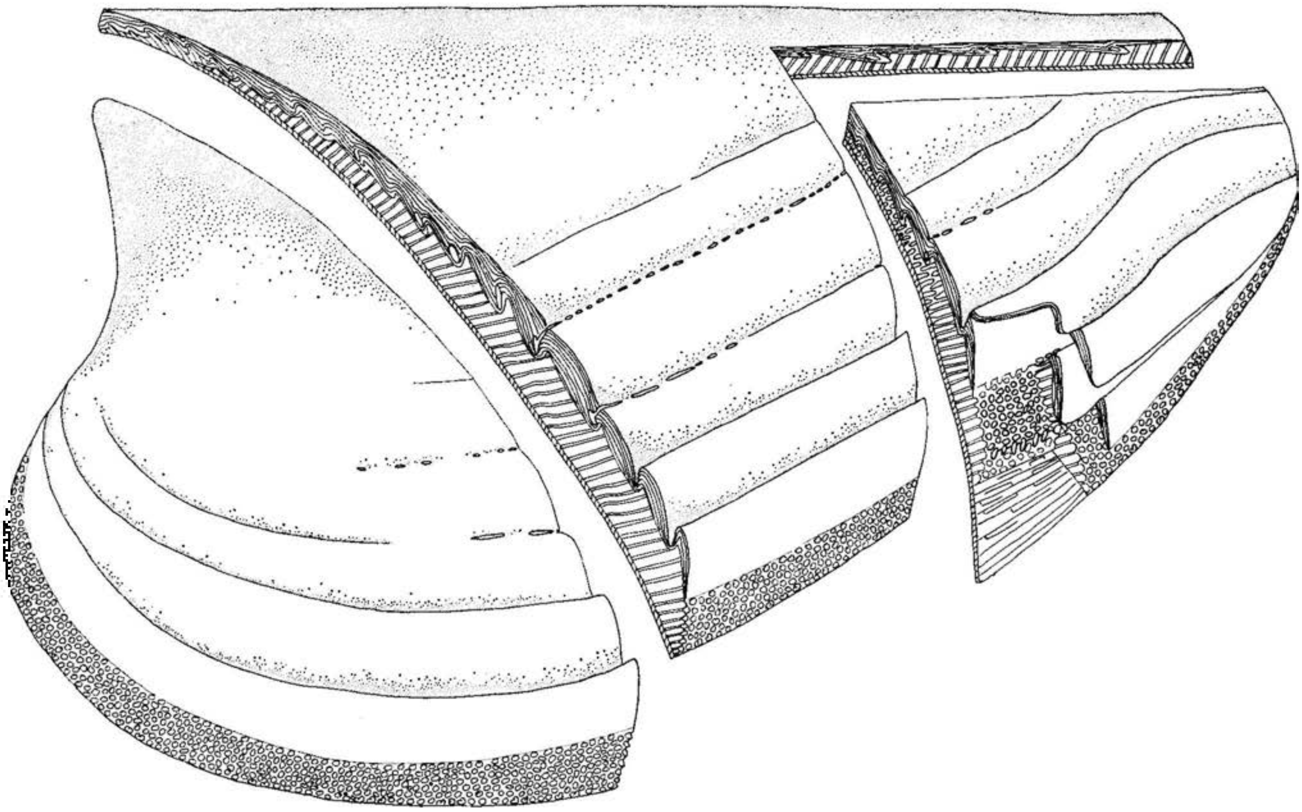

Fig. 2 - Schematic drawing of the structure of *Lamellaptychus (Punctaptychus).*

PLATE 2

All negative prints of radial sections.

Fig. 1 - *Cornaptychus,* Toarcian, Polino (Terni), x 7.5.
Fig. 2 - *Laevicornaptychus,* Toarcian, Pettino (Perugia), x 8.
Fig. 3 - *Cornaptychus,* Aalenian, San Polo dei Cavalieri (Roma), x 4.5.
Fig. 4 - *Lamellaptychus (Punctaptychus),* Lower Tithonian, Serra San Quirico (Ancona), x 4.5.
Fig. 5 - *Laevilamellaptychus,* Lower Tithonian, Serra San Quirico (Ancona), x 10.
Fig. 6 - *Laevaptychus,* Tithonian, Sette Comuni (Vicenza), x 3.5.

as the Ammonite « embryos » in the microfacies together with the Ammonite nepionic and neanic stages of Jurassic and lower Cretaceous limestones, and should really be considered as Aptychus initial stage of development (Pl. 4, fig. 1).

From the microstructural point of view, this stage is characterized by a succession of thin layers, 50-70 μ thick, more or less overlapping and slightly imbricate and rather regularly inclined (about 40°-50°) towards the apex.

The single thin layers in their lower portion tend to decrease the inclination and to be arranged subparallel to the outer surface of the valve. The thin layers on outer ridges show instead a tendency to cover, as a hood, the top of these ridges.

The laminae forming the initial ontogenetic stage are optically isooriented and therefore are clearly discernible, at crossed nicols, from the upper lamellar layer which covers them (Pl. 3, figs. 1, 2).

Basal lamellar layer

This is a layer of moderate thickness, about 0,9-0,19 mm, formed similarly to the initial ontogenetic stage, by thin layers 50-70 μ thick, overlapping, imbricated and inclined toward the apex region (Pl. 4, figs. 3, 4). These thin layers show a more marked tendency to lengthen and to be arranged subparallel to the outside concave surface. On this side, groups of thin layers appear as thin concentric striae, some more prominent than others, and interpreted by the authors as growth lines.

In the radial section breaks are sometime discernible between consecutive thin layers and appear with a certain regularity, connecting some small tube of the tubular intermedial layer to the outside (Pl. 4, fig. 2).

Medial tubular layer

In the radial section this layer appears to be formed by a continuous series of small tubes subperpendicular to the outer surface of the Aptychus. The tubular layer originates from the start of the initial ontogenetic stage and gradually increases in thickness until it makes up almost the entire thickness of the valve in proximity of the lateral facet. This constitutes the outer portion of the Aptychus which is recognized by the rapid increase in thickness in the tubular layer. Quite often, in the adult Aptychi, the last rib or two are more sharply defined than the others from the mass of the Aptychus. In this case the examination of the section at first shows a marked decrease and then the complete absence of the tubular layer on the entire outer zone. The last ribs directly overlie on the basal layer and they appear more prominent than the others, due to the reduction or the absence of the tubular layer. Generally the single small tubes tend to have a slight curving pattern towards the lateral facet and are continuous and undivided from their base to their upper margin.

The interruptions which are present at times, even in perfectly radial sections are exclusively due to the variable vertical and lateral inclination of the small tubes, that is, to their ondulated pattern. At times we notice regular interruptions inclined towards the apex,

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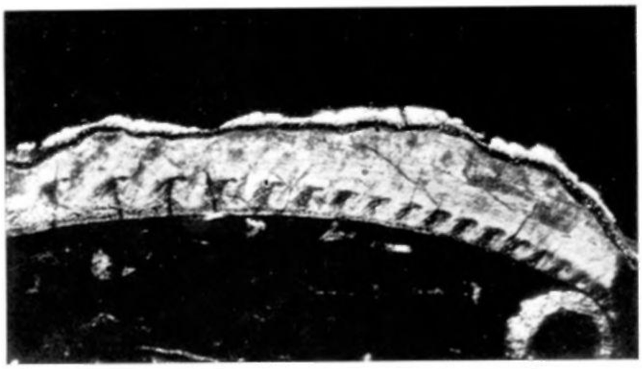
PLATE 3

Lamellaptychus

Figs. 1, 2 - 1) Radial section with well preserved initial ontogenetic stage (IOS), at the end of which, on the left, begins the medial tubular layer (MTL), covered by the upper lamellar layer (ULL). 2) Detail of fig. 1, showing the initial ontogenetic stage (IOS) covered by the upper lamellar layer (ULL).
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
Light microscope, 1) x 12.5; 2) x 50.

Figs. 3, 4, 7 - Radial section in proximity of the apex; 3) the upper lamellar layer entirely covers the initial ontogenetic stage, quickly smoothing it; 4) detail of fig. 3; we see a ridge of the initial ontogenetic stage formed by inclined laminae. The thin laminae of the upper lamellar layer tightly wrap around the ridge, forming a narrow fold in correspondence of the ridge top, where the laminae thin down. 7) Detail of fig. 3 showing a portion with ridges and furrows of the initial ontogenetic stage and the laminar layer, immediately above.
Age: Lower Tithonian. Locality: Serra San Quiririco (Ancona).
SEM, 3) x 120, 4) x 60, 7) x 300.

Figs. 5, 6 - Details of the initial ontogenetic stage; fig. 5 shows two ridges of the embryo terminal part and fig. 6 shows two ridges of the initial part. Note the increase in their dimensions.
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
Light microscope, x 150.



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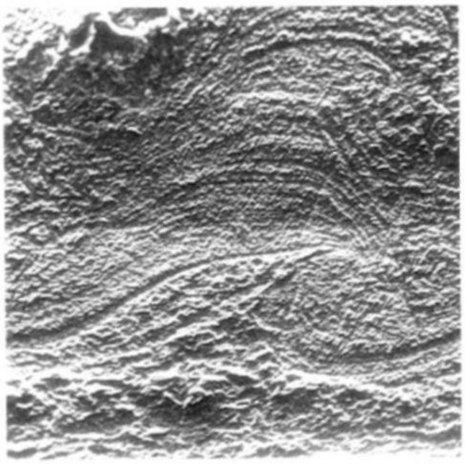

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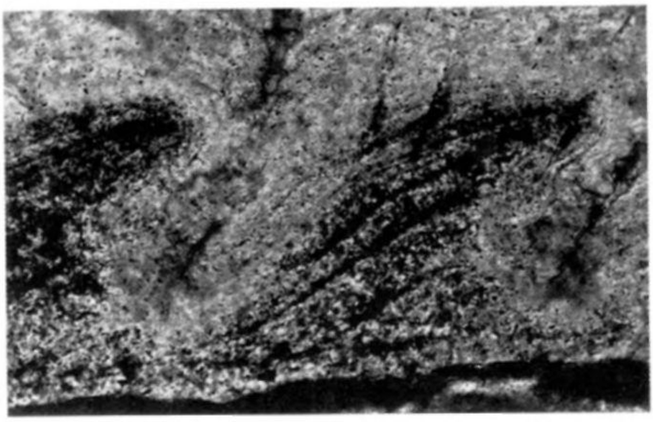

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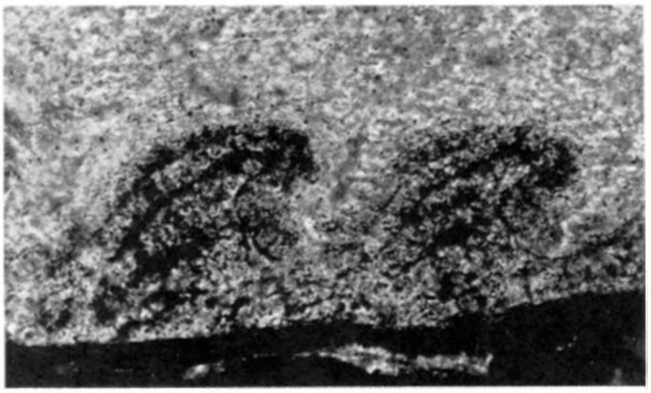

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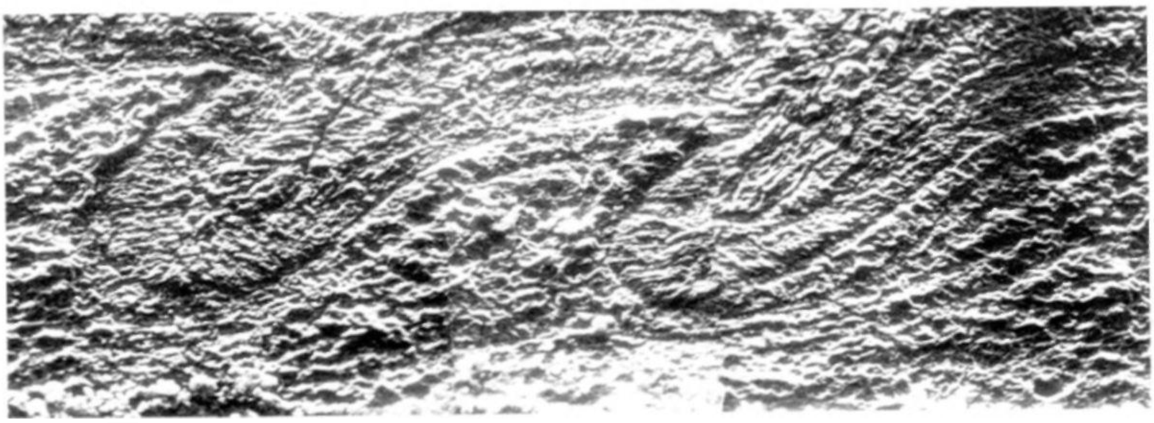

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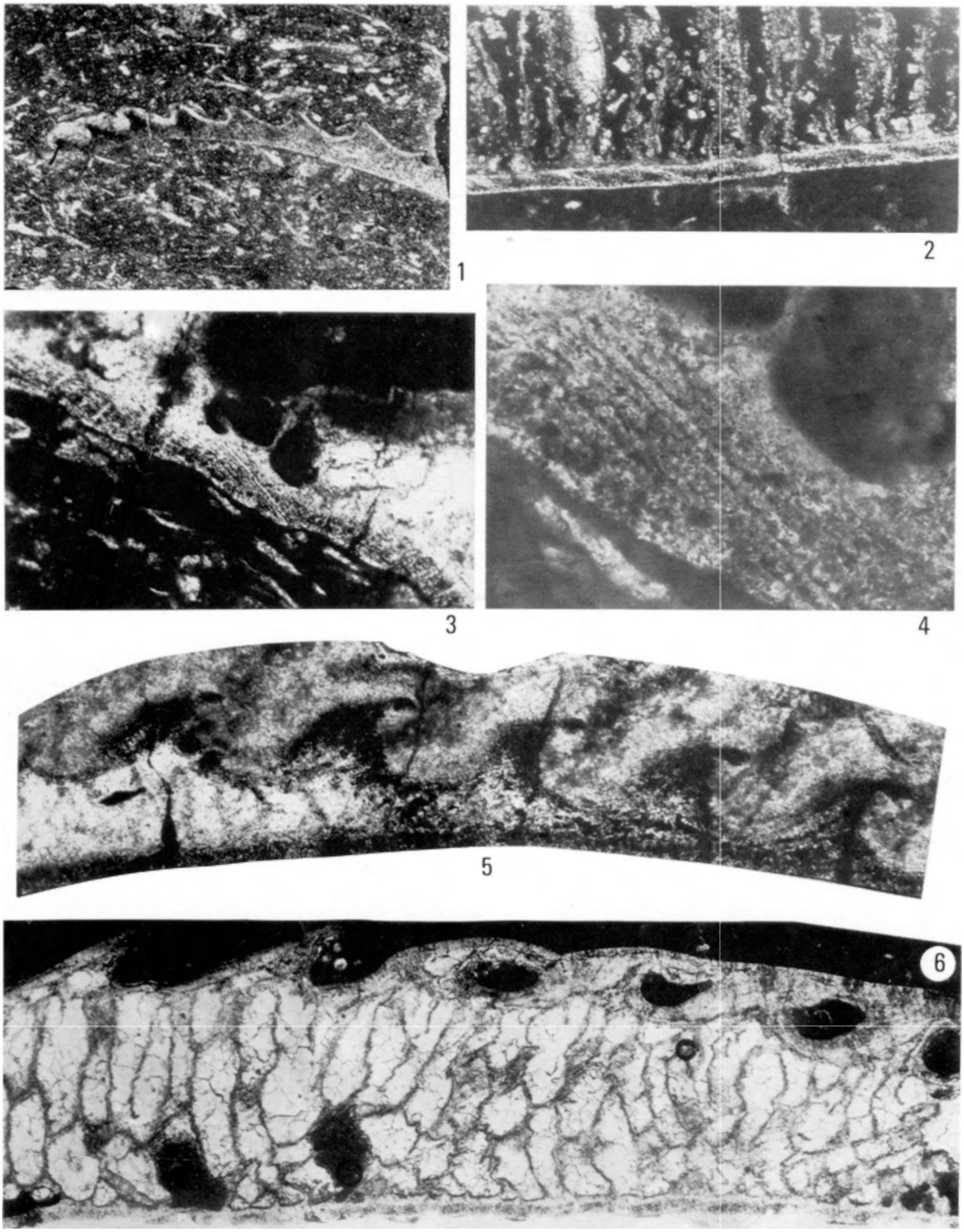
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that are clearly unlike those due to the irregularity of the pattern of the small tubes (Pl. 4, fig. 6). These interruptions show a subrectilinear pattern and are parallel to each other, to the thin layers of the initial ontogenetic stage, to the ridges thin layers and to the laminae of the basal layer.

The small tubes have a subpolygonal section (Pl. 5, figs. 1-5) with a diameter of 0.20-0.35 mm, which stays slightly constant for the entire extension, with the exception of the basal section, where it is nearly lower.

In the upper portion, the tubular layer ends with a ridged and furrowed surface. The small tubes appear open on the apex side and in the depressions, while on the back of the ridges they are covered by a continuous lamina. This lamina is formed by thin layers optically iso-oriented with the thin layers of the initial ontogenetic stage, especially in the section closer to it. The small tubes are arranged concentrically in respect to the apex, tightly overlying each other. Their overall look in transversal section is that of a bee-hive (Pl. 5, figs. 2, 5).

From the microstructural point of view the thin walls of the small tubes appear to be made of overlapping thin layers imbricate and inclined towards the apex, just as the other structural elements studied up to now (Pl. 5, fig. 6). Moreover, in the longitudinal and transversal section, the walls of each small tube appear to be doubled (Pl. 5, figs. 1-5), separated by a thin fissure. We presume from this characteristic that each small tube is separated by its own wall and that the double wall look is due to the bordering walls of contiguous small tubes. However we cannot presume the double wall look as being a definite characteristic of the small tubes because the individual wall for each tube is not consistent. It is also true that the absence of the double wall might mean the fusion of these same double walls.

The tubular layer starts at about 3-4 mm from the apex (Pl. 4, fig. 5), through a differentiation in the lamellar layer that, up to that point, constituted the initial ontogenetic stage. The thin layers of that stage, which were continuous up to this point, appear here to separate in two parts, an upper part including that portion of the thin layer which forms the ribs in the initial ontogenetic stage and a lower part formed by the rest of the thin layer oriented geometrically and optically as those of the embryo. The continuous lower part, at this point, forms the basal layer. The upper part remains discernible in the body of the ridges at crossed nicols examination.

Small oval gaps, arranged either parallel or irregularly to the laminae, appear between these two parts assuming the typical subcylindrical appearance of the small tubes of the median layer while gradually increasing in height.

Upper lamellar layer

This consists of thin laminae closely overlapped which form a blanket decreasing in thickness from apex to lateral facet, completely disappearing on this facet. That is, the open ends of the small tubes are visible on the lateral facet. This lateral facet appears smooth only on specimens considered aged due to the closeness of the growth lines, which appear on the outer part of the concave side.

PLATE 4

Lamellaptychus

Fig. 1 - Embryo showing the beginning of the covering process by the upper lamellar layer (lighter colored layer). Age: Lower Tithonian. Locality: Serra San Quirico (Ancona). Light microscope, x 40.

Figs. 2, 3, 4 - Radial sections showing in detail the basal lamellar layer. 2) Shows the presence of breaks appearing as thicker and lighter colored lamellae. 3) Succession of embricated laminae, inclined towards the apex (on the left). 4) Enlarged detail of fig. 3. Age: Lower Tithonian. Locality: Serra San Quirico (Ancona). Light microscope, 2) x 9, 3) x 25, 4) x 110.

Fig. 5 - Radial section showing the transition between initial ontogenetic stage and medial tubular layer, occurring gradually but rapidly. Age: Lower Tithonian. Locality: Serra San Quirico (Ancona). Light microscope, x 28.

Fig. 6 - Central portion of the radial section showing the three layers. The tube walls, particularly where the section cuts cortically, appear to be formed by superposed laminae, equally inclined towards the apex, same as the lamellae of the ridges and of the basal layer. Age: Lower Tithonian. Locality: Serra San Quirico (Ancona). Light microscope, x 20.

The laminae forming this layer tend to cover the previous morphology and therefore they assume a pattern that varies according to the geometry of the ridges and furrows on which it lies. The laminae are thicker on the surface of those ridges turning towards the lateral facet and are thinner inside the furrows (Pl. 5, fig. 1). This type of deposition extends up to where the lamina slightly bends and continues on to the next ridge, instead oof wedging within a furrow. Thus we obtain thusly a leveling of the various heights of ridges in respect to the furrows (Pl. 4, fig. 6), and these furrows are converted into tunnels lodged among successive ridges. These tunnels are connected to the outside by a series of thin small channels subperpendicular to the outer surface (Pl. 5, figs. 7, 8).

These thin channels appear as rows of pores, roughly parallel, in the convex part of a well preserved Aptychus.

In the radial section, these tunnels have an approximate pyriform outline and are elongated toward the apex (Pl. 4, fig. 6); the small communication canals open, as a rule, almost close to the dorsal part of the previous ridge. At times the tunnel end is not completely closed and in place of the series of small canals there is a continuous fissure.

In the older part of the Aptychus, towards the lateral facet, the lamellar layer thins down gradually until it almost disappears. At first it is unable to bridge the depressions between two consecutive ridges as the reciprocal distance is gradually increasing, and then it can barely cover them with a very thin layer.

The thin laminae which form the upper lamellar layer, appear by SEM to be made by thin tablets arranged in rows so as to form very thin sheets. These are grouped in larger units. These units strongly decrease to a few thin sheets at the major bending and thinning points as on the top of the ridges. The sheets are separated by very thin inner layers, that originally were probably filled by an organic matrix.

The specimens we attribute to *Lamellaptychus* have a thinner upper lamellar layer. Each lamina shows a uniform thickness over the ridges and furrows and the ridges never tend to turn backward.

In thin section at crossed nicols, the upper lamellar layer shows an irregular and slight fading, similar to a pleocroic phenomenon, as well as having a straw-yellow brown colouring.

Structural model

On the basis of the above mentioned structural characteristics and our interpretation, we reconstructed a model of *Lamellaptychus* and of its particular growth as outlined in text-fig. 2.

First we must point out the existence of a critical point in the ontogenetic development of each valve, corresponding to an « aperture zone ». It divides the initial ontogenetic stage, formed by a succession of overlapping laminae inclined towards the apex, from the adult stage, where the three classic structural stages of the Aptychi, basal, tubular and upper lamellar are differentiated.

It should also be pointed out that the basal and the tubular layers together with the thin layers of the initial ontogenetic stage, form an homogeneous body, as they all have the same particular growth, based on the overlapping of a succession of thin layers, parallel and inclined towards the apex.

The upper lamellar layer forms a second structural element not directly connected to the previous one.

The element which homogenizes the basal and tubular layers and the initial ontogenetic stage can be found in those single thin layers which form this last stage. In these thin layers a mutation occurs during a certain point of growth of the Aptychus, and it results in the separation of the unmineralized portion, in its central part. This mutation causes the diversification of the above mentioned layers. That is, the single thin layers are without holes in the initial ontogenetic stage, while in the aperture zone they differentiate in three portions: the basal and the upper layers are unperforated, the medial layer is perforated. The small tubes are formed by the alignment of holes of successive thin layers.

In the tubular layer the unperforated portions of each lamina are reduced to thin mineralized partitions. Their overlapping forms the walls of the small tubes (Pl. 5, fig. 6; Pl. 6, fig. 2).

The perforated portion of each thin layer increases rapidly in size; in this way the tubular layer becomes the most developed part in the thickness of the Aptychus. The basal portions of the thin layers forming the upper lamellar layer maintain the same size, while the upper portions at first cover the entire body back of the ridges and then gradually decrease to cover only the back of the more aged ridges. This is clear at crossed nicols observation of a radial section. The size of the portion of optically oriented ridges as the initial ontogenetic stage, decreases gradually as we get farther from the apex.

The upper lamellar layer is independent from the tubular and basal layer; in fact it always irregularly covers the oblique thin layers that form the tubular and basal layers and does not show any connection at any point. In addition, numerous embryos of Aptychi lodged in rocks which contain adult Lamellaptychi, show that the initial ontogenetic stages are exclusively made of a succession of oblique and overlapping thin layers. The upper lamellar layer is almost always absent, sometime being represented by only a few subhorizontal laminae, and only in the apex zone of the « embryo » (Pl. 4, fig. 1).

Cornaptychus structure

(Text-fig. 3; Pl. 2, figs. 1, 3; Pl. 6, figs. 4-11).

The genus *Cornaptychus* was formulated by Trauth for those Aptychi of the Upper Lias and of the Dogger which show an outer morphology of furrows and ridges as the Lamellaptychi, but differ from them due to a lower layer of organic nature (generally corneous-chitinous, according to the author) and also for the absence or weak development of the intermediate tubular layer. According to Trauth, the calcareous part of these Aptychi is formed by two or three layers: one layer of oblique overlapping lamellae and a thin compact upper layer (« gelbe Schicht » of Quenstedt). To these two layers an intermediate tubular layer is added, which develops from the lamellar layer, especially in the youngest forms (Dogger). In this case, the intermediate layer has a continuous thin density. Instead the tubular layer, in the Lamellaptychi, is the most developed element in the valve. The thickness of the entire shell is proportionate to that of the median layer, therefore the distinction between the three-layer Cornaptychi and those Lamellaptychi, represented by a few forms of the Dogger, is obtained by Trauth through the B/L dimensional ratio, as well as by the presence or absence of the basal corneous layer.

Cornaptychi of the Toarcian

These Aptychi resemble the Lamellaptychi on the outside, but have a very thin valve, a lateral facet slightly differentiated and the presence of a small triangular shaped area in the symphysal portion which is somewhat lower in respect to the rest of the Aptychus. The ribs on the outer surface are thin, sharply and irregularly inclined. The inner surface shows thin growth lines concentric to the apex.

In the specimens originating from Holzmaden, this surface has a thin black outer layer marked by fine growth lines. The radial section of the Holzmaden specimens shows very clearly the oblique structure of thin layers, which are overlapping, imbricated and disposed in groups slightly unfused. These thin layers are parallel to each other and have the same angulated bend in respect to the inner surface. They tend to decrease this bend in the basal portion of the Aptychus and in addition they form the body of the ridges. Over this layer we find another bright yellow layer which entirely covers the morphology of the valve and gives more relief to the ridges. This layer corresponds to the « gelbe Schicht » of Quenstedt and is described by Trauth as « porenloshomogenen, braunlichgranen bräunlichen oder gelben 'Oberschicht' » (1927, p. 215).

It shows delicate thin lines, unconformable to the lamellae of the inferior layer.

Pl. 6, fig. 6 also shows this layer covering the lateral facet as well. We have examined a few Aptychi of the umbro-marchigiano Toarcian. These Aptychi show no black interior layer, due to the fossilization

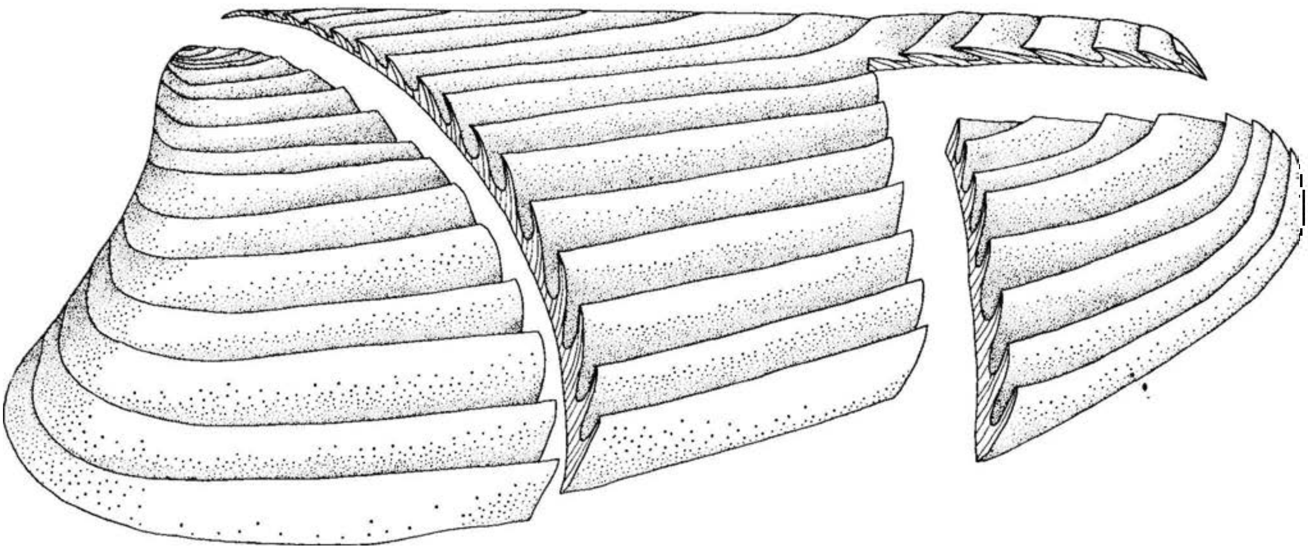


Fig. 3 - Schematic drawing of the structure of *Cornaptychus*.

state which did not permit the preservation of any organic element.

In the radial section they appear to be formed exclusively by the lamellar layer, similar to the layer of Holzmaden *Cornaptychus*.

In some specimens we notice the presence of a thin superior layer unconformed to the underlying lamellae. The outer morphology and structural arrangement of *Cornaptychus* show surprising similarity to the initial ontogenetic stage of the Lamellaptychi of the Malm.

Cornaptychi of the Dogger

A few specimens of the Aalenian-Callovian have been examined in the radial section (Pl. 2, fig. 3). These forms belong to the three-layers Cornatptychi of Trauth. They show distinctly an initial stage and an adult stage. The first stage is very developed at times and is formed by two layers: one of oblique lamellae and the other homogeneous unconformed over the previous one. The second stage shows the tubular intermediate layer with the form as already described for the Lamellaptychi. This layer maintains a continuous thin thickness and is better developed in that part lying under each ridge which turns towards the apex.

The thick median layer at times appears to have disarranged and ill-defined small tubes which are instead formed by irregular cavities of varying dimensions.

Evolutive trends in the Cornaptychus-Lamellaptychus group

The « *lamellati* » Aptychi we examined, originating from extended stratigraphic intervals (Toarcian-Neocomian), have structural characteristics which show a close evolutive interdependence between the oldest and the more advanced forms.

The most evident evolutive trend, already pointed out by Trauth, is the creation and the gradual development of the intermediate tubular layer. This layer is absent in the Toarcian forms, present, but with a thin thickness in the Aalenian-Callovian forms, and with prominent thickness in the Malm and Neocomian forms.

The creation and development of the medial tubular layer happened simultaneously with an increase in the total dimensions of the shell. This trend is in close relation to the increase in individual dimension, therefore causing the entire structure to become lighter in weight.

PLATE 5

Lamellaptychus

Figs. 1, 3 - Medial tubular layer and upper lamellar layer, no direct relationship appears between them. Section not perfectly radial.
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
SEM, 1) x 110, 3) x 60.

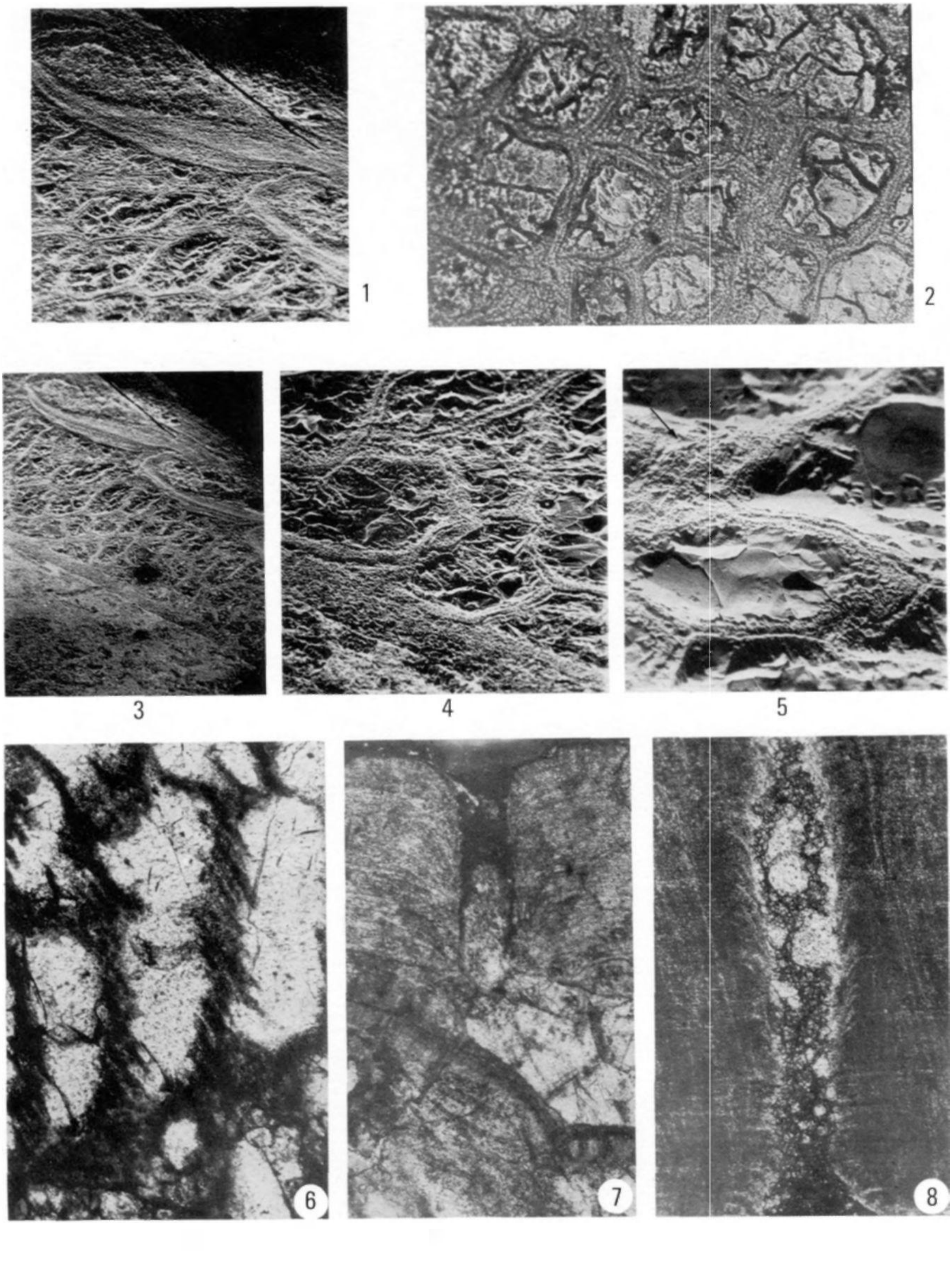
Fig. 2 - Dry peel, transversal section of tubes of medial tubular layer, where is clearly evident the subpoligonal outline. Each tube is formed by its own single wall. The tight contiguity of the tubes gives the walls the appearance of being double.
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
Light microscope, x 120.

Figs. 4, 5 - Medial tubular layer: the double wall of the tubes is clearly evident. 5) The section touches a point of a tube wall (arrow).
Note that the wall structure is formed by inclined and superposed lamellae.
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
SEM, 4) x 140, 5) x 340.

Fig. 6 - Detail of a radial section showing that the tube walls of the medial tubular layer are formed by inclined and superposed lamellae.
Age: Kimmeridgian. Locality: Poggio Son Vicino (Macerata).
Light microscope, x 50.

Lamellaptychus (Punctaptychus)

Figs. 7, 8 - Small canals of the upper lamellar layer. 7) The small canal opens in a tunnel in the lower side; a ridge is discernible on the lower left side; 8) detail showing how the lamellae of the upper lamellar layer stop in correspondence of the small canal with a slight inflection on the lower side.
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
Light microscope, 7) x 40, 8) x 90.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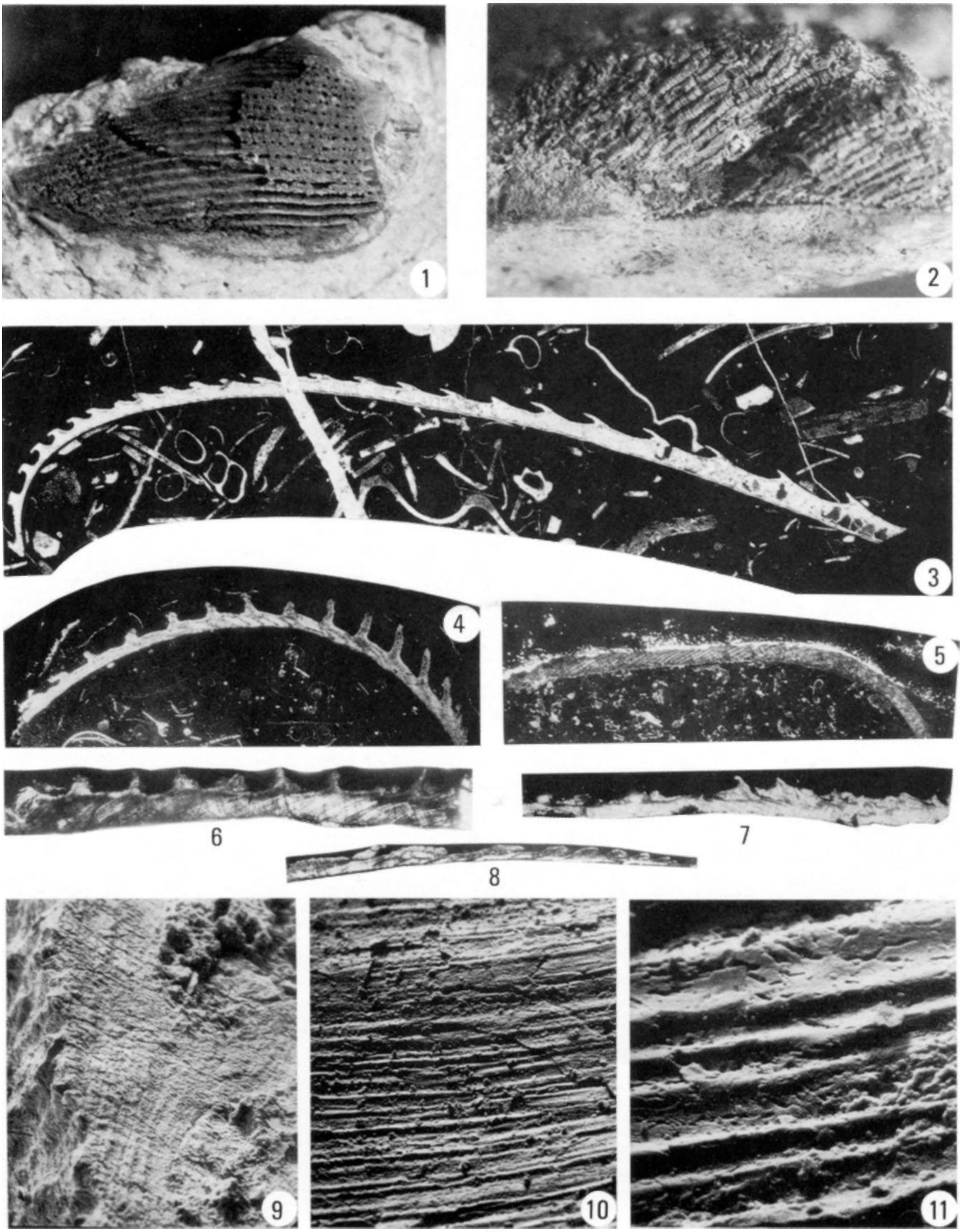
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At the same time, in connection with the development of the tubular layer, there appears a further evolutive trend consisting in the gradual reduction of the homogeneous lamellar layer. This layer which makes up the main body of the Toarcian forms, is still quite developed in the Aalenian-Callovian forms and is considerably reduced in the Tithonian-Neocomian forms where it is confined to the first apex portion. This lamellar layer is now exclusively an embryonic stage in these forms and seems to have disappeared completely in some Lamellaptychi of the Neocomian, as for example in *Lamellaptychus angulocostatus* PETERS.

The outside morphology of furrows and ridges of the Lamellaptychi originates in the Toarcian forms that have no intermediate tubular layer and is preserved also in the newer forms where the lamellar layer is considerably reduced or absent.

This fact is dependent on the continuity of a better functional adjustment. In fact those first Aptychi which opened some holes in their bodies did not deviate from their previous growth structure. They just layed perforate lamellae in their median part in place of unperforated lamellae. This phenomenon which causes a lighter weight structure, can be interpreted as confirming the progression of a characteristic which advanced the functional harmony of the structure.

LAEVILAMELLAPTYCHUS STRUCTURE
(Text-fig. 4; Pl. 2, fig. 5; Pl. 7, figs. 1-6; Pl. 8, figs. 1-6)

Laevilamellaptychus is not a very common form or, at least, it is not quoted in the literature as often as the other Aptychi. From the morphological and structural point of view, this form presents some characters of transition between *Lamellaptychus,* already described, and the more known *Laevaptychus* which will be described later on. Morphologically it is rather slender, but it always has a thicker shell in respect to the Lamellaptychi of the same lenght; it differs from the Laevaptychi due to the presence of frequent ornamentations on the outer surface. It is also characterized by an outer facet which is much larger than the facet of the

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PLATE 6

Fig. 1 - *Lamellaptychus (Punctaptychus),* through a partial erosion we notice a typical Lamellaptychi's ornamentation under a typical Punctaptychi's covering.
Age: Upper Tithonian. Locality: Poggio San Romualdo (Ancona).
Light microscope, x 2.5.

Fig. 2 - *Lamellaptychus,* inner mould of tubes, showing the tubes to be continuous and undivided. Notice as well some alignments perpendicular to the tubes axis and parallel to the lamellae of their walls.
Age: Upper Tithonian. Locality: Poggio San Romualdo (Ancona).
Light microscope, x 6.

Fig. 3 - *Lamellaptychus,* subradial section. The specimen is characterized by a considerable overall thinness and by the upper lamellar layer.
Age: Upper Tithonian-Neocomian. Locality: Poggio San Romualdo (Ancona).
Light microscope, x 9.

Fig. 4 - *Cornaptychus,* radial section revealing very prominent ribs and the absence of the tubular layer.
Age: Toarcian. Locality: Polino (Terni).
Light microscope, x 7.5.

Fig. 5 - *Cornaptychus,* detail of a radial section of a partially eroded specimen. The erosion smoothened the ornamentation but the lamellae forming the Aptychus body are clearly evident.
Age: Toarcian. Locality: Boschitello di Vizzini (Catania).
Light microscope, x 6.

Figs. 6-8 - *Cornaptychus,* radial sections. Figs. 6-7 show the lamellar layer covered by the upper layer. Fig. 8 shows a detail of the apex portion. Notice the strong similarity to the Lamellaptychi " embryos ".
Age: Toarcian. Locality: Holzmaden (Germany).
Light microscope, 6) x 12.5, 7) x 6, 8) x 14.

Fig. 9 - *Cornaptychus,* radial section showing inclined superposed laminae and their terminals on the inner side (on the left), which form the growth lines. Notice also that the laminae make up the body of the ridges (on the right).
Age: Toarcian. Locality: Holzmaden (Germany).
Light microscope, x 70.

Figs. 10, 11 - *Cornaptychus,* inner surface portion of the corneous layer. Clear parallel pattern of growth lines. Fig. 11 enlarged detail of Fig. 10.
Age: Toarcian. Locality: Holzmaden (Germany).
SEM, 10) x 120, 11) x 300.

other two genera, when compared to the surface.

On the inner side, the symphysal and inner facets are quite developed and clearly discernible.

In well preserved specimens the outer surface does not have ridges as in *Lamellaptychus,* but is not completely smooth as in *Laevaptychus.* It has a surface with a delicate waved or submeandrous pattern.

Because of this characteristics the outer surface of the valve is similar to that of *Lamellaptychus* (*Punctaptychus*).

From the structural point of view it shows an initial ontogenetic stage similar, for some of its cha-

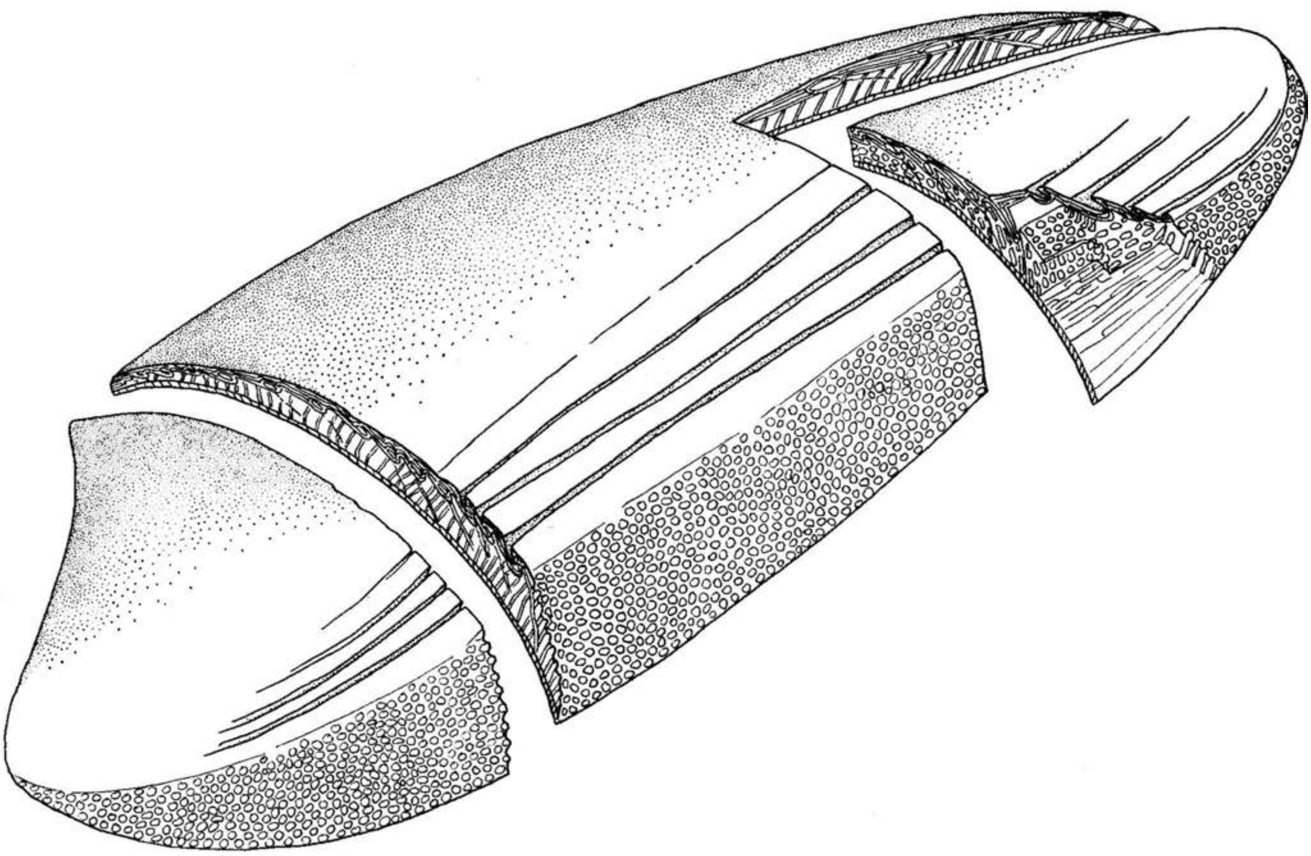


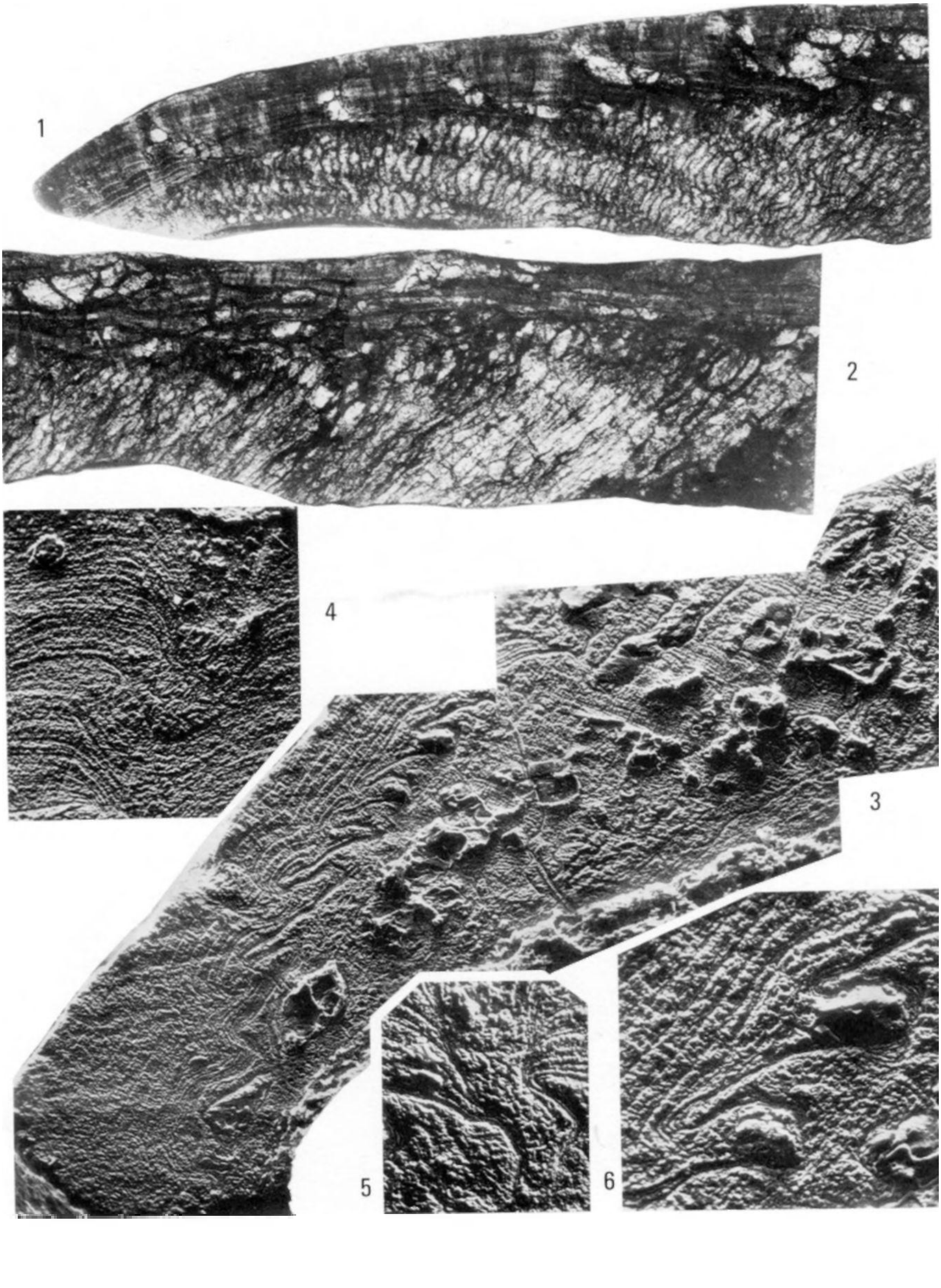
Fig. 4 - Schematic drawing of the structure of *Laevilamellaptychus.*

PLATE 7

Laevilamellaptychus

Figs. 1, 2 - Radial section. Fig. 2 is the continuation of fig. 1. The basal layer is very faint in the portion corresponding to the apex region; in the remaining portion it is absent due to erosion. The medial tubular layer is characterized by the presence of tabulae parallel to each other. Notice the pores crossing the upper lamellar layer and connecting the medial tubular layer with the outside.
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
Light microscope, x 25.

Figs. 3-6 - 3) Radial section of the valve initial portion. 4-6) Details of fig. 3. The lower left side of the apex region, in fig. 3, reveals the beginning of the medial tubular layer being arranged in an alignment pattern. 4-5) Details of the upper lamellar layer in correspondence of the pores. 4) On the upper right side we notice the small canal, very faint. 5) The laminae become thinner and cover the entire wall of the small canal which is filled with micrite. 6) Note the upper lamellar layer formed by sets of lamellae.
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
SEM, 3) x 120, 4-6) x 300.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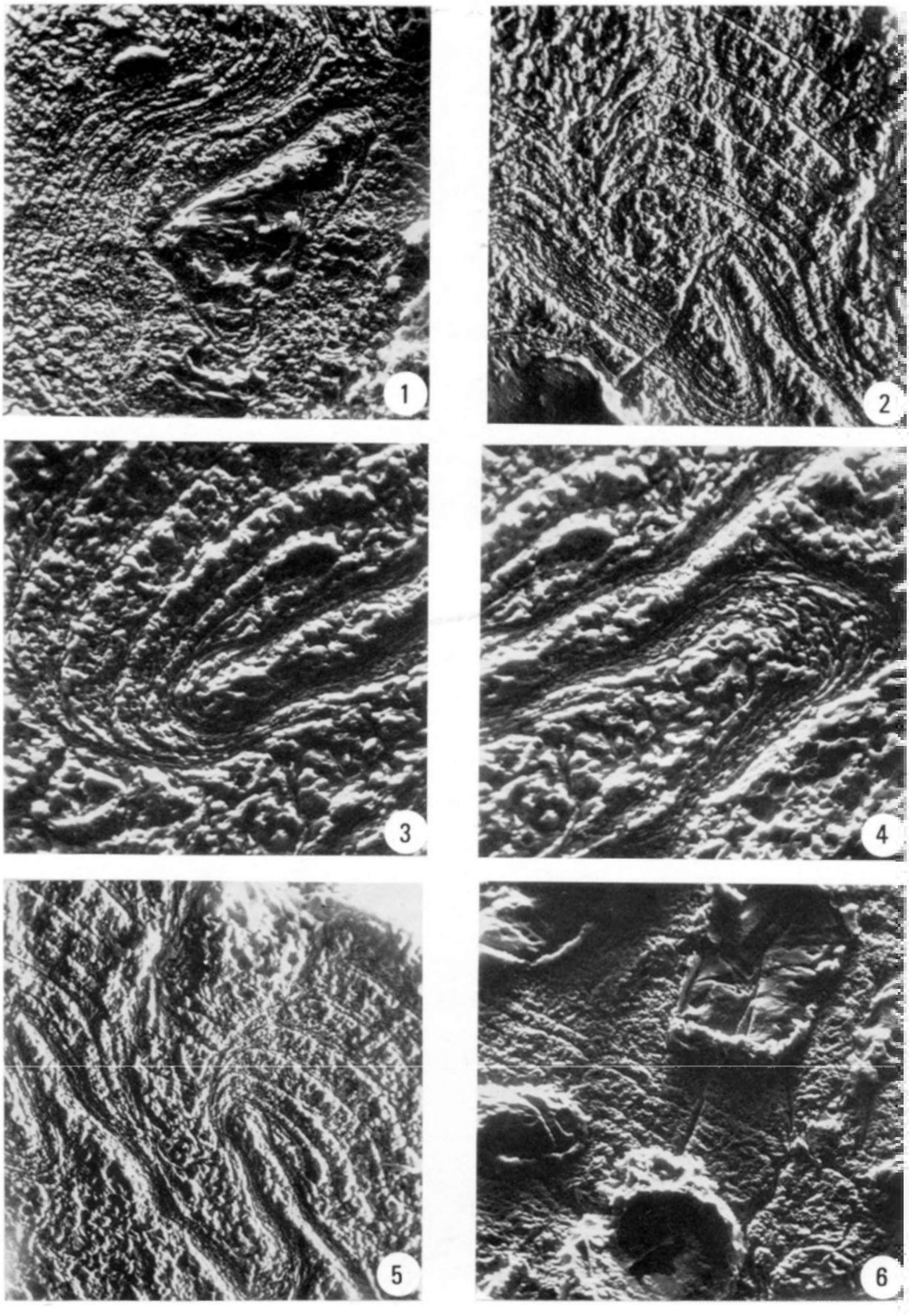
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racteristics, to *Lamellaptychus,* and an adult stage which seems to have some characteristics that will clearly appear later in *Laevaptychus,* that is, the subdivision in series of the small tubes and the continuity between the tubular and the upper lamellar layers.

Initial ontogenetic stage

This stage is present in the apex extremity of this genus as it is in *Lamellaptychus* but in much smaller dimensions and in a different position in the Aptychus in respect to the basal and upper layers (Pl. 7, figs. 1-3).

In radial section observation of a specimen of *Laevilamellaptychus,* a structure of ridges and furrows is discernible inside the Aptychus body in the position corresponding to the apex zone and to the zone adjacent, which resembles the initial ontogenetic stage of *Lamellaptychus.*

The ridges are subregular and inclined towards the apex as in *Lamellaptychus* (Pl. 7, fig. 6), but while in this last one the initial ontogenetic stage forms the inferior initial part of the valve, in *Laevilamellaptychus* the structure of ridges and furrows is between the upper lamellar layer and some openings which indicate the presence of the medial tubular layer.

Basal lamellar layer

The basal lamellar layer of these Aptychi is similar to that of *Lamellaptychus* already described.

Medial tubular layer

The medial tubular layer is formed by rows of small tubes not continuous as in *Lamellaptychus,* but separated in various sectors.

This separation happens in different ways: it could be due to the narrowing of the lumen of small tubes, to regular transversal inflections of the same tubes, or to the thickening of the lamellae along an alignment subparallel to the lateral facet. If it is due to the inflection of tubes, we will observe, in radial section, two successive orders of small tubes separated by an other series of tubes, sectioned in the minimum diameter.

Instead, if the separation is due to the thickening of thin layers, some real separations are formed between the successive tubes, which we shall call « tabulae » for reference purposes.

The various tabulae separate each successive sector until the last sector of small tubes emerges on the outer surface giving a perforated look to the lateral facet. In the radial section the beginning of the tubular layer in the apex region can be recognized by the presence of some cavities (Pl. 7, fig. 3; Pl. 8, fig. 1). They are found in the middle between the basal lamellar layer and the first ridges of the initial ontogenetic stage. These cavities have attained a size similar to that which they will have as tubes in the future, but at the moment they are not yet developed in height. For this reason they have a vacuolar look. As the Aptychus grows, these vacuoles are gradually substituted by a series of well arranged tubes (Pl. 7, figs. 1-3). These small tubes are formed, as in the

PLATE 8

Laevilamellaptychus

Fig. 1 - Detail of apex region with the presence of laminae of the upper lamellar layer and a cavity which indicates the proximity of the medial tubular layer.
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
SEM, x 300.

Fig. 2 - Detail of apex region showing the laminae of the upper lamellar layer and the first ridge. Notice how the successive laminae deviate gradually from the ridge morphology.
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
SEM, x 300.

Figs. 3, 4 - Detail of the second ridge and of the furrow under it. Notice the varying thickness of the laminae of the upper lamellar layer immediately above the ridge and inside the furrow (3) and the very thin density of the laminae covering the furrow (4).
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
SEM, x 600.

Fig. 5 - Detail showing the inflection of the lamellae of the lamellar layer in correspondence of a pore, notice also how the direction of the pore is related to that of the following ridge.
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
SEM, x 300.

Fig. 6, - Detail of the medial tubular layer revealing the cavities of two series of tubes and the set of parallel lamellae separating them.
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
SEM, x 300.

Lamellaptychi, because of the absence of mineralization of the intermediate portion of embricated lamellae.

Laevilamellaptychus shows some characteristics similar in part to Lamellaptychi and in part to Laevaptychi, at the border of the superior limit of this tubular layer and of the upper lamellar layer.

The lamellae, which make up the tabulae and walls of the small tubes, meet in the apex portion to form some ridges. These ridges are smaller and more irregular than those in *Lamellaptychus* and contribute in a minor way to the ornamentation of the outer surface.

Farther ahead, towards the lateral facet, the lamellae forming the tabulae inflect and cover the Aptychus outer surface as in *Laevaptychus,* instead of forming a ridge and then stopping, as in *Lamellaptychus.* Whereas, in *Laevilamellaptychus,* the small tubes stop at the base of the tabula portion, comparable to the ridges of *Lamellaptychus;* therefore some furrows appear where each tabula inflects and forms a pattern parallel to the inner surface. In seriate cortical section the furrows formed by the initial ontogenetic stage are arranged concentrically to the apex in the apex region. In the central region we notice the furrows with the same pattern due to the inflection of the laminae. In the symphysal and inner regions the furrows deviate from the subconcentric pattern and take on a subradial look, at times also with a lengthening perpendicular to their pattern in the central zone. These furrows are coated with the upper lamellar layer which partially smoothes the reliefs.

Upper lamellar layer

As we have mentioned, *Laevilamellaptychus* does not have a true differentiated upper lamellar layer. Instead, the outer surface is covered by the lamellae which have formed the tabulae of the tubular layer of the adult stage. When the lamellae meet an inflection made by a ridge or meet the channel at the end of an inclined tabula, in the central region, they coat them with a layer of various dimensions. This layer is thicker on the top of the ridges and thinner on the bottom. In correspondence to the furrows, the disproportion between the coating of the outer sides and the coating of the inner sides, forms some horizontally elongated tunnels. The base of the furrows remains farther away from the opening of the furrow on the outer side of the Aptychus, which builds up towards the apex.

Above this, the tunnel openings are at first covered and then irregularly skipped over by the successive laminae. Therefore we notice some weak inflections subparallel to the outer margin that give a faint alternating pattern of ridges and furrows with the tunnel openings on the surface.

These concentric tunnels are continuous at the tabulae inflection points where they are formed and then are quickly limited to a continuous succession of small oval openings, varying in length and concentrically arranged in the central region, but parallel to the symphysis and to the lateral facet in their respective zones.

The openings of contiguous rows are alternatively arranged and this causes the characteristic meandering pattern of the upper layer of these Aptychi.

Laevaptychus structure
(Text-fig. 5; Pl. 2, fig. 6; Pl. 9, fig. 3; Pl. 10, figs. 1-7)

The Laevaptychi differentiate sharply from the other Aptychi we studied, not only for the morphological point of view but also from the structural one. Morphologically they are thicker and broader and lack any ornamentations. As they lack a differentiated initial ontogenetic stage and their upper lamellar layer is directly connected to the tubular layer, their structure is simpler, as clearly demonstrated by Schindewolf (1958).

Initial ontogenetic layer

The Aptychus apex portion does not differ much from the rest of the valve, even in the radial section.

There is a gradual reduction of the tubular layer thickness, ending up as a thin crevice between the basal lamellar layer and the upper layer. Sometimes the tubular layer maintains a normal thickness up to the apex but appears to be formed by confusely arranged tubes, irregular and smaller than in the rest of the medial layer.

Basal lamellar layer

This portion of the valve is formed by a succession of thin laminae inclined and overlapping, as in the other Aptychi.

Medial tubular layer

It is much thicker in the entire valve than in the valve of *Lamellaptychus* and of other Aptychi. Also in *Laevaptychus* the small tubes and walls are formed by the superposition of unmineralized parts on mineralized parts of overlapping lamellae and, as in *Laevilamellaptychus,* the tabulae are rather frequent. Here too, they are formed either by a narrowing of the lumen of the tubes or by a zone of rapid lateral inflection of the same tubes. Here too the tabulae cut the tubes orthogonally to their length, dividing them into various sectors. They are continuous in respect to the inferior layer and also to the upper layer which is formed entirely by their flection towards the apex. Finally the tabulae may be faintly visible on the body of the medial layer until they fade away. But they are always evident near the upper layer where they penetrate with a wide inflection. Moreover, the tabulae are thicker in the portion near the lateral facet, which is the more adult one, therefore the parts of the tubes between two contiguous tabulae are shorter. At the boundary between the median and the upper layers, at the maximum curvature point of the tabulae, the small tubes are short and wide. Sometimes, especially in the newer forms, we notice a vacuolar zone which may reach a considerable thickness (Pl. 9, fig. 2). At the point of transition between the median and superior zones, the small tubes are often connected through the vacuolar zone to the pores that cross the upper lamellar layer. Pl. 9, figs. 1-5 clearly show the double walls of the tubes created by the adjacent walls of contiguous tubes.

Upper lamellar layer

As we mentioned earlier, the upper lamellar layer is formed by the continuation of the tabulae of the medial tubular layer. They tend to be arranged parallel to the outer surface, thickening and covering the preceding laminae up to the apex. For this reason

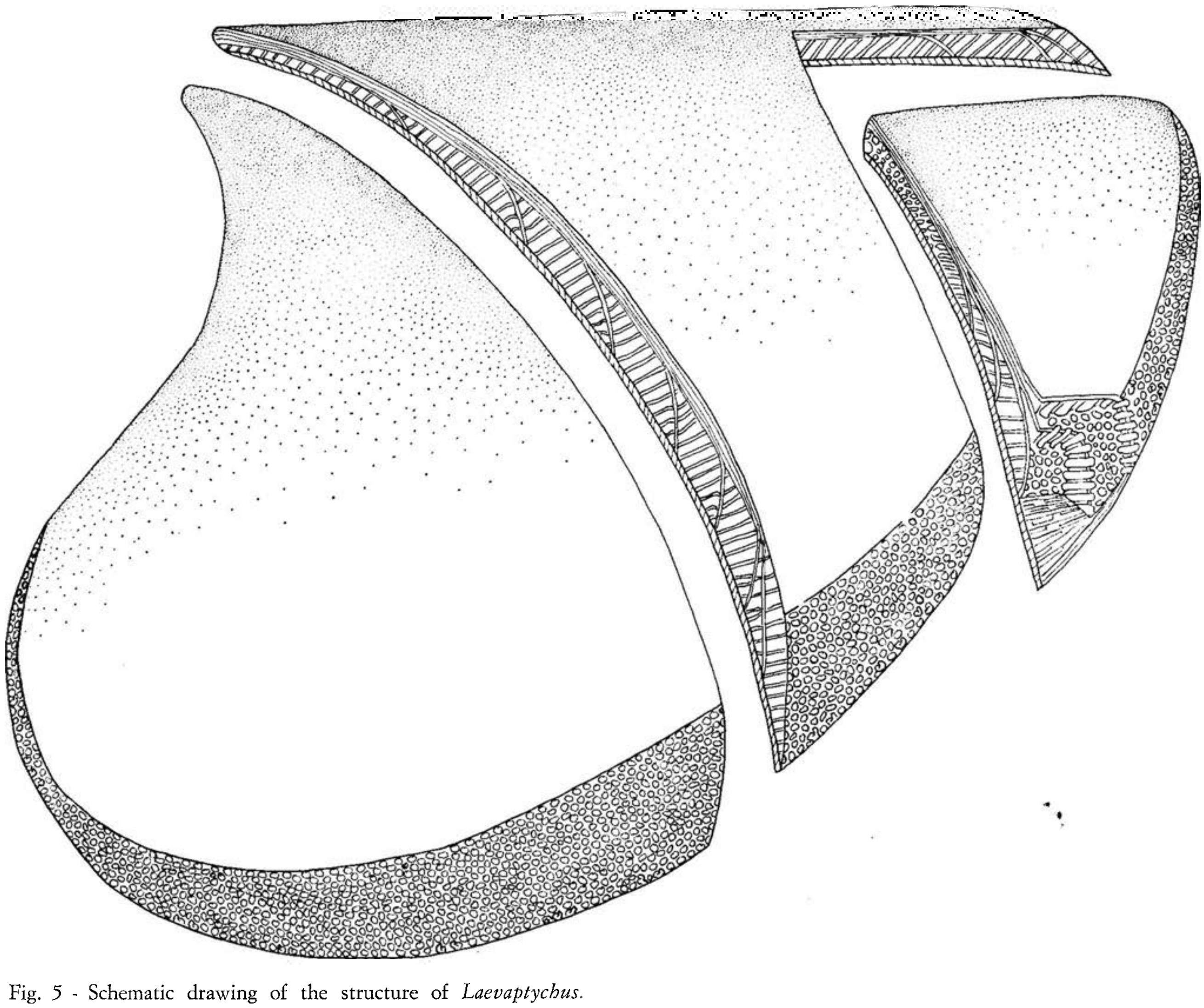


Fig. 5 - Schematic drawing of the structure of *Laevaptychus*.

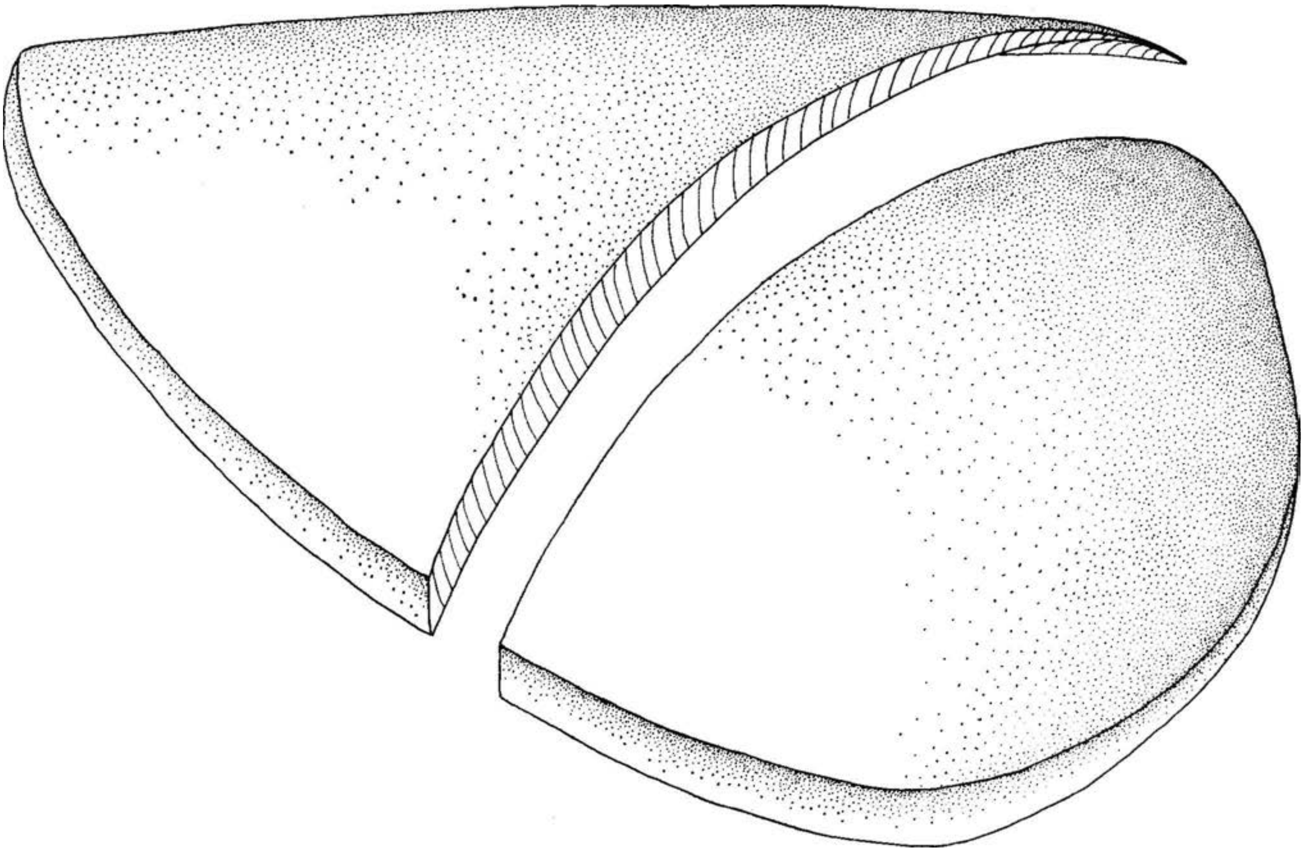


Fig. 6 - Schematic drawing of the structure of *Laevicornaptychus*.

PLATE 9

Laevaptychus

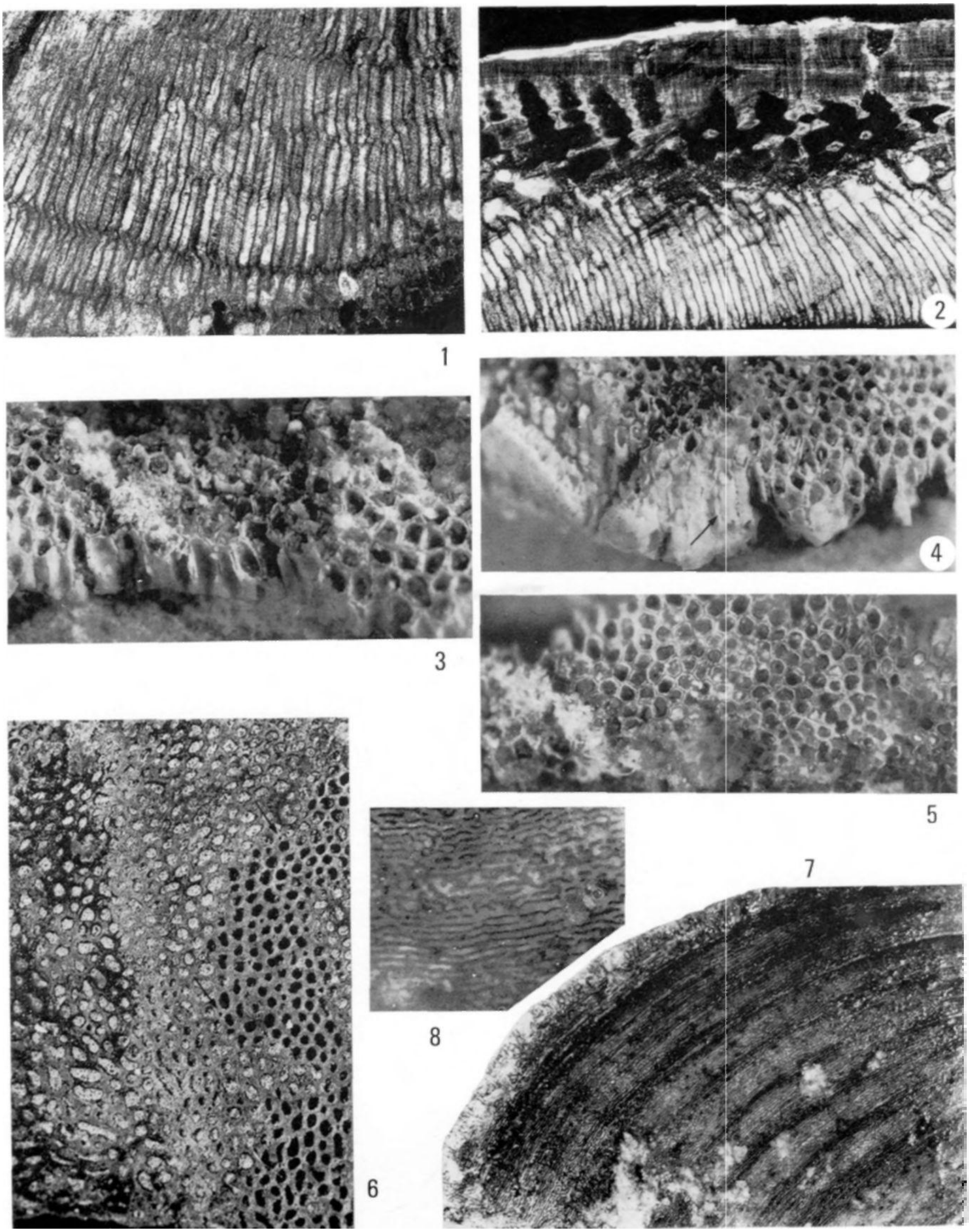
Fig. 1 - Section subparallel to the outer surface, showing various series of tubes of the medial tubular layer. The tabulae separating the series of tubes are due to the tubes inflections with slight thicknenings of their walls.
Age: Lower Tithonian. Locality: Serra San Quirico (Ancona).
Light microscope, x 15.

Fig. 2 - Radial section showing the upper lamellar layer and the medial tubular layer. Between the two layers we notice an example of a conspicuous vacuolar zone, which seems to be typical of the Neocomian specimens.
Age: Tithonian. Locality: Sette Comuni (Vicenza).
Light microscope, x 15.

Figs. 3-5 Various views of the inner side of a naturally eroded specimen, showing the tubes double walls. In fig. 4 notice the superposed lamellae (arrow).
Age: Tithonian. Locality: Sant'Angelo Romano (Roma).
3) x 30, 4) x 10, 5) x 10.

Fig. 6 - Detail of outer surface. The arrows show the second class pores.
Age: Malm. Locality: Harar (Ethiopia).
x 6.

Figs. 7, 8 - View of slightly etched inner side. On the entire surface we notice the typical submeandrous look concentrically arranged of the transition between the basal lamellar layer and the tubular layer. Fig. 8 shows an enlarged detail of the same.
Age: Upper Tithonian. Locality: Poggio San Romualdo (Ancona).
7) x 6, 8) x 25.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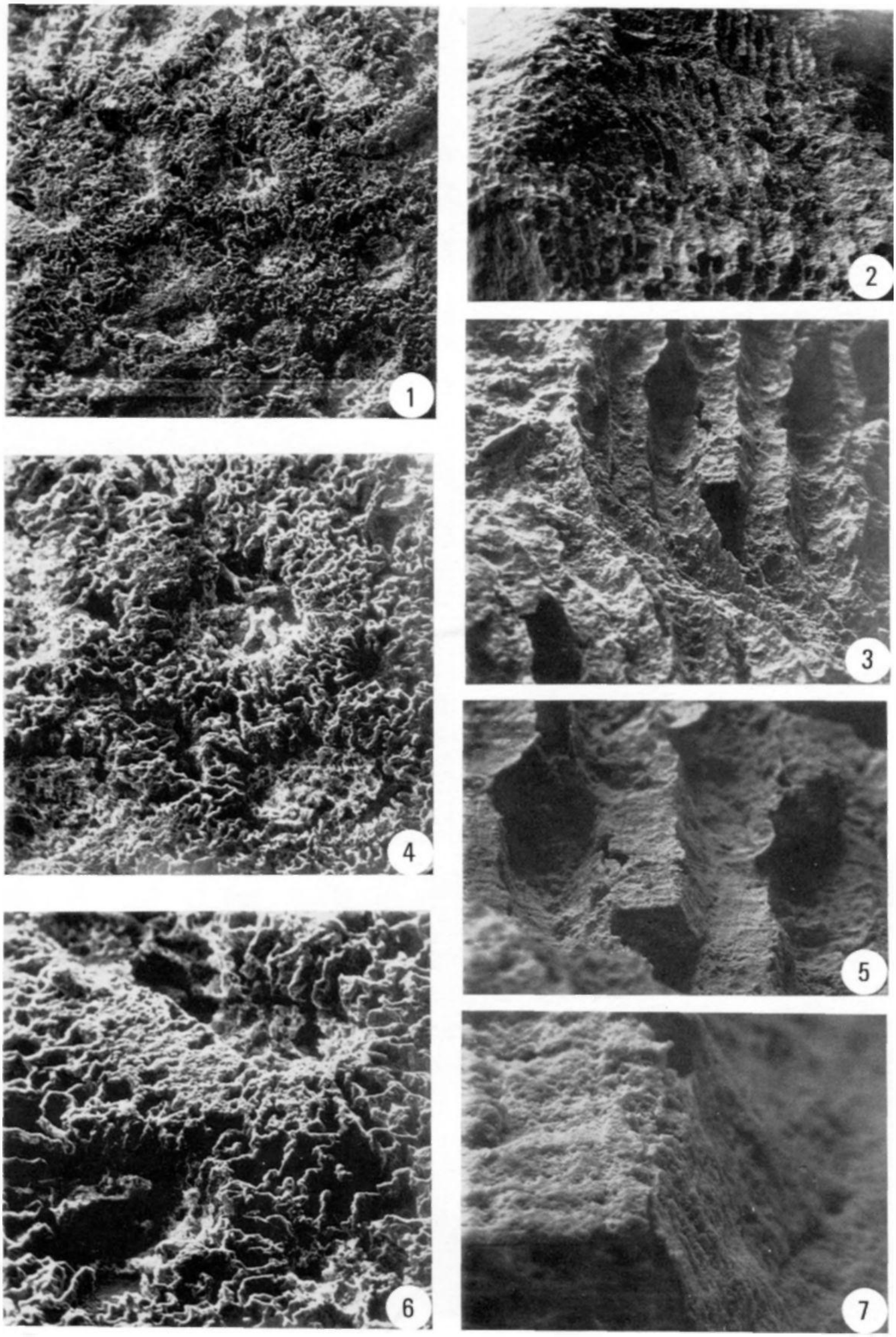
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the upper lamellar layer is thicker in the apex region and thinner in the outer region. This layer is perforated by numerous scattered pores which originate, as in *Laevilamellaptychus* at the point of inflection of the tabulae, that is where they deviate from the upper layer. Here too, as in *Lamellaptychus* (*Punctaptychus*) and in *Laevilamellaptychus*, the laminae bend near the pore covering it on the more external side. On the outer margin only a lamina covers the tubular layer and reaches the outer facet through an inflection. Whereas, at the apex and along the inner facet, the overlapping laminae of the upper lamellar layer extend gradually outwards, protruding over the outside, the apex and the inner facet therefore giving them a blade look.

Laevicornaptychus structure

Some Aptychi with a completely smooth upper surface were found in the fossil bearing beds of Pettino (Perugia) and Polino (Terni), Toarcian in age. They can be attributed to *Laevicornaptychus*. The outer morphology of these forms is similar to *Laevaptychus* and in radial section appears formed by the overlapping of unperforated lamellae which are inclined toward the apex and parallel as in the coevi Cornaptychi. No differentiated upper or basal layer can be noticed.

STRUCTURAL PATTERN AND EVOLUTIONARY IMPLICATIONS

The study concerning the structure of the Jurassic and Cretaceous Aptychi which we had at our disposal, allowed us to make the following considerations: the Aptychi are secreted by a reproductive epithelium adjacent to their outer side and to the lateral facet. This is clearly evident in *Laevaptychus*, as Schindewolf already pointed out, and in *Laevilamellaptychus*. We observe that the Aptychus growth takes place in their outer zone and on the entire convex surface, even in the oldest apex region, with the simultaneous deposition of a continuous lamina. This pattern uniformity can be recognized, according to Schindewolf, by a series of skull cap growths overlapping on the outer side and on the lateral facet. It is a characteristic of *Laevaptychus* and partly also of *Laevilamellaptychus* and not found in other examined Aptychi as the German Author believed. The research proved that the acquisition of such a growth process could be the result of a long evolutive process starting from a partially different structural pattern. In the oldest mineralized forms present in the Toarcian, the growth occurs through the frontal overlapping of inclined and parallel lamellae, not overlapping on the outer side.

In the well preserved specimens of Holzmaden the upper layer (« gelbe Schicht » of Quenstedt) can be clearly recognized as a poorly mineralized layer, probably of corneous nature, surrounding and covering the outer side as well as the lateral facet.

The growth occurs only frontally and there is no contemporaneous and simultaneous deposition of calcium carbonate on the dorsal side.

This is true for the Cornaptychi, marked by furrows and ridges, as well as for the Laevicornaptychi, with smooth surface.

In the Cornaptychi of the Dogger, with tubular medial layer, and in the Lamellaptychi (*Punctaptychus* and *Lamellaptychus* i.s. Trauth), we notice an upper lamellar layer of varying thickness, formed by thin calcitic lamellae parallel to each other and to the dorsal surface. This layer never shows a direct connection to the inclined laminae forming the embryonic stage and the tubular layer. There is no skull cap growth in these forms, as meant by Schindewolf. Therefore this lamellar layer must be interpreted as

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PLATE 10

Laevaptychus

Figs. 1, 4, 6 - Portion of outer surface lightly etched. Note that the pores have their own wall formed by radially arranged elements. Second class pores are visible in the coalescence zones. Fig. 4 is the enlargement of fig. 1.
Age: Malm. Locality: Harar (Ethiopia).
SEM, 1) x 35, 4) x 70, 6) x 130.

Figs. 2, 3, 5, 7 - Fracture surface in the tubular layer, subparallel to the tubes pattern. 3, 5, 7) Details, gradually enlarged, of fig. 2. In fig. 2 we notice the tubes with alternating parallel zones of rapid inflection. Fig. 3 shows a detail of an inflection zone (tabula). Figs. 4 and 7 show the subpoligonal section of tubes, which are formed by overlapping lamellae perpendicular to the tubes axis.
Age: Upper Tithonian. Locality: Poggio San Romualdo (Macerata).
SEM, 2) x 15, 3) x 70, 5) x 120, 7) x 620.

being a cover layer secreted by the superposed epithelium probably concurrently with the time of accretion on the lateral facet, and without a direct connection. The beginning of deposition of the upper lamellar layer is probably subsequent to that of the median layer as demonstrated by the many Aptychi embryos found in sediments which completely lacked it. The connection between the tubular and the upper lamellar layer seems to be present in *Laevilamellaptychus.*

In the adult portion of this form the structural pattern is similar to that of *Laevaptychus,* even though Trauth disagrees with this.

In the young portion where we find an initial stage of furrows and ridges, the upper lamellar layer is not directly connected to the tubular medial layer.

Only at a certain point of the ontogenetic development the laminae of the frontal structure extend and cover the entire outer surface.

According to our data we can distinguish two groups having different forms: one is composed of Aptychi formed almost completely by whole lamellae overlapping and imbricated. This group includes all the low Jurassic forms (*Cornaptychus* and *Laevicornaptychus*).

The second group is composed of Aptychi formed by imbricated lamellae with a perforated central portion. This group includes the middle-upper Jurassic and Cretaceous forms (*Lamellaptychus, Laevilamellaptychus* and *Laevaptychus*). This last group can be then subdivided into two types with different growth structure: one with an upper lamellar layer well distinct from the underlying portions, and another where the upper lamellar layer is the continuation of the medial tubular layer.

The Lamellaptychi should be included in the first group and the Laevaptychi in the second. The Laevilamellaptychi have an intermedian type of structural pattern. Whereas, from the microstructural point of view, all the Aptychi we studied show a substantial unity. Their microstructure consists in the overlapping of superposed calcareous lamellae, embricated, perforated or not, and inclined towards the apex.

We took note that the walls of the small tubes and the pores of the upper lamellar layer have double, not single walls.

Each tube and each pore has its own wall, therefore two adjacent tubes or pores are separated by two contiguous walls. The reproductive epithelium entered, at least, the distal portion of the pores and tubes therefore the mineralization occurred only in their peripheric zone. This is especially clear in Plate 10, figs. 1, 4, 6 which shows a portion of *Laevaptychus* outer surface, slightly etched, by SEM observation.

The wall surrounding each pore is of uniform thickness and formed by many radial elements alternated by small « cells ».

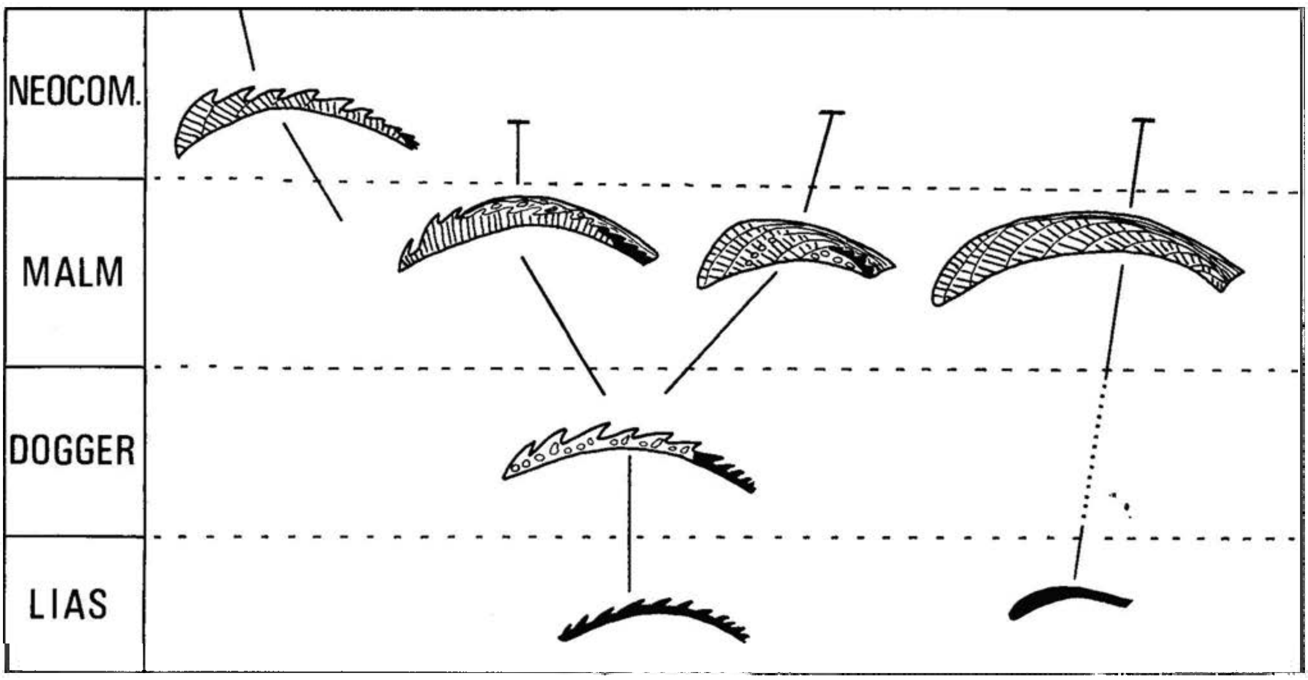

Fig. 7 - Hypothetical reconstruction of the phyletic relationship among the genera here examined.

When there is space between two walls, it is filled by caotic and meandrous radial elements. There are some small cavities in the most distal points, which appear as second class pores, arranged around the others.

In the Laevaptychi and in the Laevilamellaptychi and, at times, in the Lamellaptychi, the tubular medial layer is characterized by a recurring thickening of the tubes walls (tabulae).

In reality this thickening often only seems to be so due to a rapid and simultaneous lateral deviation of the coeval portion of tubes which form the tabula. These sudden lateral deviations often are the reason for the characteristic « elongate cells » look of the sections of these Aptychi. These cells are separated by thicker parts or by a much smaller « cell ». The deviations cause an apparent narrowing of the lumen of the tubes up to their terminal point or to the presence, in the section, of rows of adjacent tubes cut at the point of minimum diameter.

Pl. 10, figs. 2, 3 at SEM, show in detail a sudden lateral deviation of small tubes. The increase in thickness, in tens of microns, of the lamellae forming the basic element of the Aptychus structure, could be considered a daily accretion due to physiologic activity during a 24 hour period of time, just as we have seen for other molluscs (Rhoads and Pannella 1970, and other works mentioned here). In this case the tabulae, clearly evident in *Laevaptychus* and *Laevilamellaptychus,* could be due to slowing down periods or periodic stops of this daily secretory activity.

The tabulae occur more often in adult Aptychi, probably in the terminal phase of their growth.

The sudden changes in direction that we notice could be interpreted as being caused by the overlapping, after a brief stoppage, of the new structural elements. Therefore the tabulae have the same meaning of concentric growth lines on the inner side. Each stria is formed by numerous minor lines, corresponding to each single lamella. In this case it is difficult to understand the absence or the irregular presence of tabulae in the Lamellaptychi.

The acquisition and growing importance of the tubular medial layer is the basic evolutive element common to the whole group of Jurassic and Cretaceous Aptychi. This evolutive variation can be followed in the well known and documented phyletic line that, from the Cornaptychi of the Toarcian without tubular layer, goes through the Cornaptychi of the Dogger with a weak tubular layer and on to the Lamellaptychi with a very developed tubular layer.

This succession is confirmed by the presence of the differentiated initial ontogenetic stage in the Lamellaptychi morphologically and structurally quite similar to the oldest Cornaptychi. The relative dimensions of this stage increase gradually from the newer forms (some Neocomian Lamellaptychi can even be without it), to the oldest forms, up to the point where it makes up the whole valve of the Liassic Cornaptychi. We could also assume for the Laevilamellaptychi an evolutive acquisition of the tubular layer, because of the presence of an initial very reduced ontogenetic stage formed by inclined and unperforated laminae. Whereas in the Laevaptychi there is no differentiated initial ontogenetic stage and the tubular layer appears in the entire apex region. Still the probability exists of an evolutive connection between them and the Toarcian forms of *Laevicornaptychus.* We base this comparison on the strong morphological similarity, clearly evident in their general subtriangular look, in the distinct inner facets on the inner surface and in the absence of ridges and furrows. These forms show, in the radial section, a structure composed exclusively of overlapping whole lamellae.

If such evolutive connection could be confirmed by stratigraphically intermedian findings, we would have, in time, a process of gradual acquisition of the tubular layer and a contemporaneous decrease and eventual disappearance of the lamellar layer in the hypothetical line *Laevicornaptychus-Laevaptychus* as it is for the other forms we studied.

If this were the case, the evolutive lines or, at least, those of *Laevicornaptychus-Laevaptychus* and *Cornaptychus-Lamellaptychus,* would show the same evolutive trends and could be completely recognizable at their first appearance.

In the Malm, especially in the higher portion, when we observe in our region the explosive development of the three types of Aptychi (*Laevaptychus, Laevilamellaptychus* and *Lamellaptychus*) we see the contemporaneous presence of the three structural patterns. From a rational and architectural point of view, the most advanced among them is *Laevaptychus.*

The three forms of Malm represent a mosaic of characters; if we take into consideration the presence of tubes and the structure simplification (complete loss of differentiated ontogenetic stage, acquisition of an overlapping skull-cap structural pattern) as the group evolutive trend, the best evolutive aspect is attained in one of them, *Laevaptychus.*

The more evoluted *Laevaptychus* and *Laevilamellaptychus* rapidly disappear at the base of the Cretaceous while the Lamellaptychi group is the only one to go on till the end of the Neocomian, probably because it still had its evolutive potential. The Neocomian forms of Lamellaptychi have no embryo and frequently show tabulae (text-fig. 7).

FUNCTIONAL INTERPRETATION: AN UNSOLVED PROBLEM

The limitation and the purposes of our study are only marginally concerned with the interpretation of the Aptychus functional attribution, as this problem seemed satisfactorily solved by the work of Schinde wolf (1958). But some recent studies (Lehmann 1967-1975) have introduced a new interpretation which reopens the problem, as it is based on favorable findings. In this regard, we think it is useful to make a brief critical analysis on the question of functional interpretation.

At the present, the interpretation of the Aptychi as belonging to the Ammonites appears to be well documented; in fact the shell specimens of Ammonites containing Aptychi or those associated with them are very numerous in the classic beds of Solnhofen and of Holzmaden. To these we can add the numerous individual findings from various sources known in literature. In addition we have one illustrated in Pl. 1, fig. 14, of an Aspidoceratid containing a pair of Laevaptychi in the most outer part of its living chamber (Poggio S. Romualdo, Marche, Upper Tithonian in age).

One of the main arguments against this hypothesis (see Scatizzi 1934), is the strong occurrence of Aptychi not associated to Ammonites shells. This is easily explained especially on the basis of the greater preservation quality of the Aptychi, which are originally calcitic, in respect to the shells which are aragonitic. The Aptychus calcitic nature has been proved analytically many times (Schindewolf 1958, Barbera Lamagna 1970). It is confirmed here by diffractometric analysis on Lamellaptychi of the Tithonian of Serra S. Quirino (Ancona), and by the classic colorimetric method of Feigl (Müller 1967) on well preserved Toarcian specimens of Holzmaden.

Considerably more difficult is the interpretation of the position of the Aptychi during life and their function. A large number of Aptychi have been found in the living chamber of Ammonite shells. Since the outline of many Aptychi corresponds quite well to the form of the aperture of the Ammonite shells associated with them, this led to general interpretation of the Aptychi as opercular structures. This fact has been particularly discussed and emphasized by Trauth (1927-1938) and by Schindewolf (1958).

But these two Authors differ considerably in the interpretation of the Aptychi position in life, their growth pattern and the mechanism which permits their opercular function.

Trauth believed the Aptychi were contained in a fold of the reproductive mantle, in a ventral position, similar to the « normal Stellung » of many Aptychi found in the Ammonite living chambers.

Schindewolf (1958) opposed Trauth conception with many valid criticisms based mainly on two points: the Aptychus growth direction which is opposite to that resulting from the position proposed by Trauth, and the calcitic nature of its valve which suggests a generator different from the mantle which secretes the aragonitic shell. He proposes for the Aptychi a dorsal position outside the shell and an origin similar in every way to that of cephalic hood of living *Nautilus*.

A different functional interpretation and a different position in life was recently illustrated in a series of studies by Lehmann (1967-1975).

On the basis of some favorable findings, by the analysis of transversal seriate sections of Ammonite living chambers containing Aptychi, this author makes a critical comparison between them and the Cephalopods maxillary apparatus.

He proposes the function of lower jaws for the Aptychi and consequentely their position immediately behind the mouth. The upper jaws could appear to be unmineralized structures. This author admits that the opercular function, at least for the Laevaptychi, is correct. He hypothesizes a possible evolutive trend tending to give the lower jaws an opercular function.

This new hypothesis by Lehmann reopens a question which was thought to be closed. In fact Schindewolf hypothesis was a good answer to the structural and morphological characteristic of the Aptychi.

The evolution tendency to an increase of the tubular layer and the consequent lightening of the two valves fitted well with the hypothesis of the cephalic hood.

Finally we should remember that all known Cephalopods possess a cephalic cartilage.

Lehmann's findings are rather convincing, especially regarding the Toarcian forms. Still it is difficult to imagine through which process and through what mechanical means of the lower jaws, the Aptychi could acquire the opercular function during the evolution. In addition it is difficult to understand how the upper jaws did not undergo a mineralization process, while the lower jaws were mineralize and so increased in size to seem almost disproportionate in respect to their function.

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