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UPPER JURASSIC RUDISTAE OF THE MARGIN OF THE HOLY
CROSS MOUNTAINS, POLAND

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Abstract. — Twenty two species of Jurassic Rudistae (including 11 new ones) have been described from the margin of the Holy Cross Mountains (Góry Świętokrzyskie). A new genus *Macrodiceras* has also been erected. Conditions of asymmetry among the Rudistae have been discussed and their presumable causes analyzed. The influence exerted by ecological-facial factors on the development of the Rudistae has also been presented. Problems of the phylogeny of the Rudistae and their stratigraphic importance are discussed. The growth changes of shells in some species are described.

INTRODUCTION

The pelecypods described of the order Rudistae abound in the Upper Oxfordian (Astartian and Rauracian) deposits of the margin of the Holy Cross Mountains (Góry Świętokrzyskie). The materials, which were

placed at the writer's disposal, came from a rich collection of the Geological Institute in Warsaw and from his own collections. The most numerous and best preserved material comes from Dobrut near Radom, Błaziny near Iłża, Olechów near Ostrowiec Świętokrzyski, Sulejów on the Pilica, Kodrąb east of Radomsko and from the outcrops situated between Żerniki and Jaclów Karsznicki near Chęciny, as well as from a limestone quarry at Bukowa in the Małogoszcz Hills. Few and worse preserved specimens were found also in the Skórków anticline, at Grząby Bolmińskie and Zawichost on the Vistula. The material examined is assigned to the following five genera: *Diceras* Lamarck, 1805, *Macrodiceras* n.gen., *Eodiceras* Pčelincev, 1959, *Plesiodiceras* Munier-Chalmas, 1882 and *Epidiceras* Douvillé, 1935, represented by 22 species, including 11 new ones. The Jurassic rudistids have never before been described from Poland and hence the need of their detailed study and description.

Acknowledgements

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During his two visits in Leningrad, the present writer had the opportunity to study rich collections of the rudistids made available to him by Prof. V. F. Pčelincev (IGEGED of the Academy of Sciences, Leningrad) with whom he could discuss some problems concerning the taxonomy of this group. Mrs. Z. V. Krjachkova (IGEGED of the Academy of Sciences, Leningrad) rendered a collection of the Crimean rudistids accessible to the author, who extends his thanks to both these persons. Likewise, the author would like to thank Mr. E. Woźny (Geological Institute, Warsaw) for making available a collection of the Upper Jurassic rudistids from the environs of Radom, to Mrs. S. Pacuszka for a careful preparation of the fauna, as well as to Mrs. D. Oleksiak and Mrs. J. Modrzejewska (Geological Institute, Warsaw) for taking photographs.

The work has been prepared at the Department of Stratigraphy of

the Geological Institute. The collection of the Upper Jurassic rudistids here described is housed at the Museum of the Geological Institute where it has been given a catalogue number of I.G.1166.II (Archives of Geological Collections of the Geological Institute in Warsaw).

Abbreviations used:

l.l.v. — length of left valve,
l.r.v. — length of right valve,
l.s. — length of shell,

b.s. — breadth of shell,
l.v. — length of valve,
b.l.v. — breadth of left valve.

DESCRIPTION OF OUTCROPS

The rudistids most frequently occur in oolitic limestones of the Upper Oxfordian (Astartian)¹ in the eastern and western parts of the margin of the Holy Cross Mountains (Fig. 1; Table 1). The formations containing the fauna of the rudistids were described from this area by many authors (Pusch, 1837; Zejszner, 1868; Michalski, 1884; Siemiradzki, 1893; Lewiński, 1902, 1912; Samsonowicz, 1932, 1934, etc.).

Localities with the rudistids on the eastern margin of the Holy Cross Mountains

The first detailed descriptions of the Upper Jurassic limestones were presented in Lewiński's works (1902, 1907, 1912). Jurassic outcrops, including those of the Upper Oxfordian (Astartian) at Śniadków near Dobrut are described in detail by this author who also cites the fauna of dicerases and nerineas. The "Astartian" is assigned by Lewiński to the "*Oppelia tenuilobata*" zone. Samsonowicz (1932, 1934) gives detailed characteristics of the Astartian deposits and divides them into the Lower and Upper Astartian. The Lower Astartian are, according to him, white oolitic limestones, in some cases interbedded by intercalations of pelitic limestones with abundant fauna of dicerases, nerineas and corals. Many banded flints, forming a characteristic horizon, also occur in this part of limestones.

The Upper Astartian is represented by more thin-plated and less oolitic limestones, in some cases also by marly limestones with vast numbers of gastropods of the genus *Ptygmatis* Sharpe. The second horizon of flints known as "chocolate flints" is here recorded. Samsonowicz's division into the Lower and Upper Astartian was made on the

¹ According to the recent interpretation, settled during the Jurassic seminar which was held in Warsaw in 1964, the Astartian represents the highermost member of the Oxfordian. Since this problem continues to be still discussed, the present writer maintains the stratigraphic division of the Upper Jurassic in Poland which has been in force so far but, at the same time, he takes into account new recommendations in this matter.

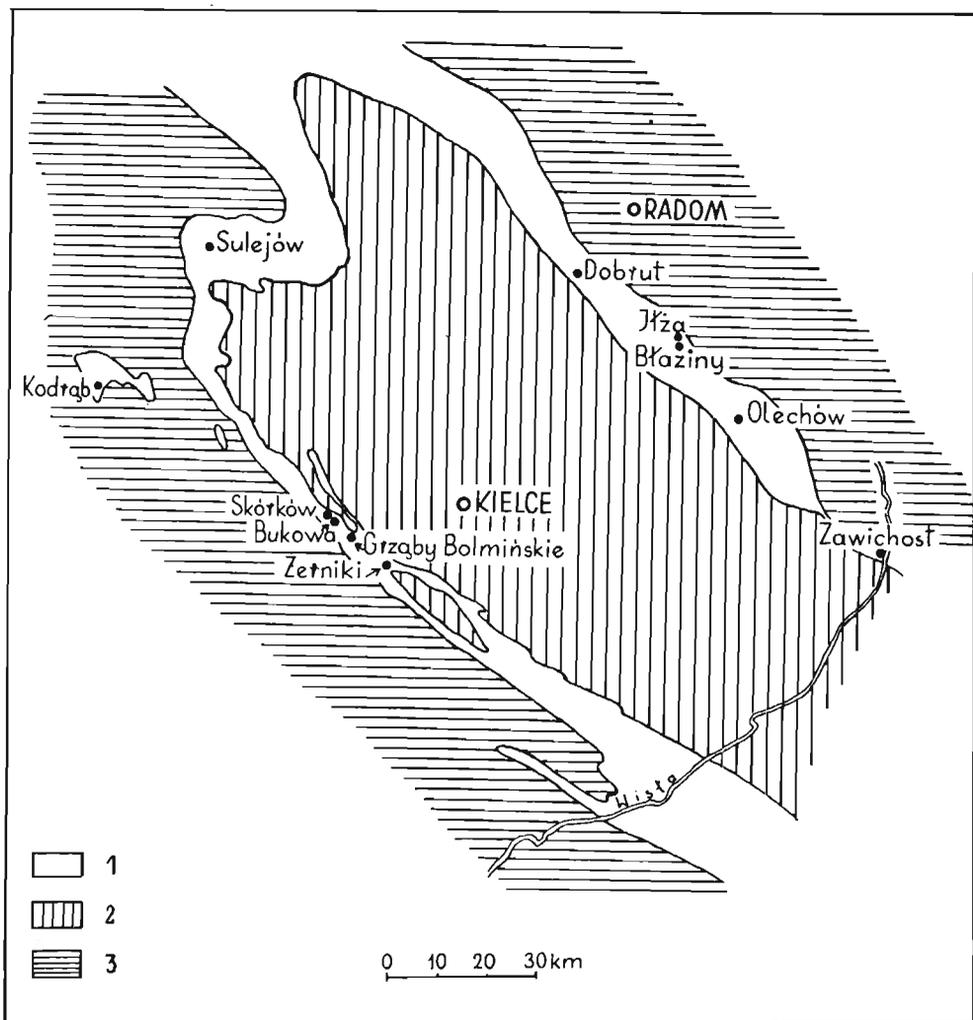


Fig. 1—Localities with rudistids in the Holy Cross Mountains: 1 Upper Jurassic, 2 Paleozoic, Triassic, Lower and Middle Jurassic, 3 Cretaceous.

basis of these two horizons. The rudistids were most frequently found in the Upper Oxfordian (Astartian) outcrops at Dobrut, Błaziny, Olechów and less frequently at Zawichost. The most abundant and best preserved species of the genera *Diceras* Lamarck, *Macrodiceras* n.gen. and *Plesiodiceras* Munier-Chalmas occur in the oolitic limestones of the Upper Oxfordian of Dobrut (Pl. I, Fig. 1), where also numerous gastropods of the superfamily Nerineacea are recorded. The most important of them are *Ptygmatis bruntrutana* (Thurm.), *P. carpathica* (Zejszner), *P. salomoniana* (Cott.), *Nerinea bernardiana* d'Orb., *N. sequana* Thirria, etc. The profile of limestones with dicerases and nerineas is represented by (from the bottom): white limestone, hard oolitic limestone cracked in

different directions and passing upwards into pelitic limestone with larger oolites. The thickness of these limestones does not exceed 4 m.

Table 1
Localities with rudistids

Species	Dobrut	Błaziny	Olechów	Zawichost	Żerniki	Grząby Bolmińskie	Fald Skórkowski	Sulejów	Bukowa	Końrąb
<i>Diceras arietinum</i> Lamarck . . .	+	+	+	+	+	+	+	+	+	
<i>D. brevicornum</i> n.sp.	+									
<i>D. impressum</i> n.sp.	+									
<i>D. originale</i> Bayle	+									
<i>Diceras</i> sp.	+				+			+		
<i>Macrodiceras balaklavense</i> (Pčelincev)	+							+		
<i>M. kozłowskii</i> n.sp.	+							+		
<i>M. longum</i> n.sp.	+							+		
<i>M. magnum</i> n.sp.	+									
<i>M. pčelincevi</i> n.sp.	+									
<i>M. polonicum</i> n.sp.	+									
<i>M. rotundatum</i> (Bayle)	+							+		
<i>M. spirale</i> n.sp.	+									
<i>Eodiceras eximium</i> (Bayle)		+			+			+		+
<i>E. planum</i> n.sp.								+		
<i>E. subeximium</i> n.sp.								+		+
<i>Eodiceras</i> sp.		+						+	+	+
<i>Plesiodiceras muensteri</i> (Goldfuss)	+									
<i>P. orthogonale</i> Pčelincev								+		+
<i>P. sulejoviense</i> n.sp.								+		
<i>P. yailense</i> Pčelincev	+	+						+		
<i>Epidiceras cotteau</i> (Bayle)								+		

Diceras also occur in higher layers in the Marylin quarry at Śniadków, but these are mostly only well-preserved steinkerns. The Upper Oxfordian (Astartian) deposits of the environs of Dobrut and Śniadków were divided into particular profiles and described in detail by Dembowska (1953). In this area, she adopted the division of the Astartian into the lower and upper ones.

At Błaziny near Iłża, the Upper Oxfordian (Astartian) outcrops in a few large quarries, in which 23 layers are distinguished. The rudistids occur in layers 16, 17 and 19 of the profile, described by Dembowska, but these data were first published in the present writer's work (Kar-

zewski, 1960). These layers are formed by oolitic limestones, sometimes light-cream in colour, containing a faunal detritus and a rich fauna of diceras and nerineas. The total thickness of these layers does not exceed 6 m. The entire profile of the Upper Oxfordian (Astartian) outcropped at Błaziny reaches more than 20 m in thickness. These are mostly oolitic or pelitic limestones with clearly visible banks of banded and "chocolate" flints, as well as — in the uppermost part — with a distinct layer with *Ptygmatis*.

The Upper Oxfordian (Astartian) deposits at Olechów near Ostrowiec Świętokrzyski are represented by (from the bottom): white limestones, compact limestones, pelitic or oolitic limestones, sometimes with detrital intercalations. White, pelitic limestones with many grains of oolites predominate, however, in this profile. *Diceras arietinum* Lam. and many nerineas also occur in it. White, oolitic limestones with flints and dolomitic, brittle limestones with rudistids and nerineas are in overlaying layers. Species of the genus *Ptygmatis* Sharpe occur in a special layer.

Samsonowicz (1923) mentions an abundant fauna which he found in the Upper Oxfordian (Astartian) of the area of Opatów. According to this author, diceras also occur in this area where they are recorded in the Magoń, Folwarczyska and Lemieszów troughs, in which they are, however, few and poorly preserved. Two horizons of flints (banded and "chocolate") are also distinguished in this area by Samsonowicz.

In the Upper Oxfordian deposits of Zawichost, the rudistids are few. This profile is represented by (from the bottom) coral and detrital limestones, intercalated by oolitic or coarse-oolitic limestones. They are overlain alternately by oolitic and pelitic limestones, the latter being compact, consisting of plates and passing upwards into soft, marly limestones or marls. A complete lithological profile and a list of fossils are given by Łuniewski (1923). In addition to species of the genus *Diceras* Lamarck, gastropods of the family Nerineidae, characteristic of this facies, also occur in this layer.

The Upper Oxfordian (Astartian) deposits of the entire north-eastern margin of the Holy Cross Mountains were synthetically discussed by Pożaryski (1948), who locally divided the Upper Oxfordian (Astartian) in the environs of Bałtów into three parts. This division was based on a certain lithological differentiation. The thickness of the Upper Oxfordian (Astartian) deposits was estimated by this author at about 160 m.

Localities with the rudistids on the western margin of the Holy Cross Mountains

A belt of the Upper Oxfordian (Astartian) outcrops, stretching for a few km between Żerniki and Jaclów Karsznicki (Pl. I, Fig. 2), has in its upper part a layer filled with diceras only. Gray, weathered limes-

tones with abundant oolites make up the deposits of this region. The thickness of the "dicerases layer" amounts to more than 0.5 m. Dicerases, embedded in a hard rock, are difficult to separate. Mostly, they are strongly damaged and this is the reason why only some of them are suitable for determination. Gastropods of the family Nerineidae are not numerous. *Ptygmatis bruntrutana* (Thurm.) is an only species cited by Świdziński (1931). More frequent are corals and pelecypods of the genera *Trichites* Plot and *Pachymytilus* Zittel.

In addition, the Rudistae occur in the Upper Oxfordian (Astartian) at Grząby Bolmińskie and Grzywy Korzeczkowskie in the environs of Kielce. This area was worked out by Pusch (1836, 1883), Michalski (1884), Siemiradzki (1893, 1922), Lewiński (1912) and Świdziński (1931, 1932). According to the last-named author, dicerases occur in the middle part of the Astartian which is developed in the form of a fairly thick series of oolitic and coral limestones with a bank of dicerases in its bottom. *Diceras* cf. *arietinum* Lam., *D.* cf. *suprajurensis* Thurm. and *Diceras* sp. are recorded in this series by Świdziński.

Upper Jurassic deposits with the fauna of the Rudistae occur in the entire range of Małogoszcz Hills. The Upper Oxfordian (Astartian) deposits are known from the Góra Brogowica in the environs of Małogoszcz where dicerases were found, in Skórków anticline, in the Bukowa quarry, and in a railroad excavation close to the Kielce-Częstochowa track, east of the village of Gruszczyn and south-west of the village of Stojewsko. The Rudistae are the most abundant in the Upper Oxfordian (Astartian) outcrops of Skórków anticline and at the Bukowa quarry.

The Upper Oxfordian (Astartian) of Skórków anticline is outcropped on two hills (Świdziński, 1932): Góra Skórkowska and Góra Frankowa. The profile has an identical appearance in all outcrops. These are reef, white and pelitic limestones with many dicerases and nerineas overlain by white plate and lithographic limestones. The latter are in turn overlain by white, hard, oolitic limestones, in some cases with flints. These layers contain many pelecypods of the genus *Trigonia* Bruguière and much less frequent brachiopods. In this profile, Świdziński (1932) distinguishes 13 layers, the last 6 of them being the Upper Oxfordian (Astartian). According to this author, dicerases are most abundant in layers 12 and 13.

The Upper Oxfordian (Astartian) deposits are also known from small excavations, which stretch northwards parallel to the Kimmeridgian formations which are outcropped on the opposite hill. No dicerases were found in these excavations.

The Upper Jurassic deposits of Kodrąb outcrop in a large quarry at Smotryszów and in the "Rogaszyń" quarry close to the Radomsko-Przedbórz highway. The Jurassic of Radomsko has first been mentioned

by Michalski (1884). Discussing Przedbórz Hills, Lewiński (1908) mentions the Jurassic deposits of Kodrąb and its environs. Siemiradzki (1922) describes profiles from Kodrąb, Smotryszów and Zapolice, citing an abundant fauna which includes dicerases from the Upper Oxfordian (Astartian) oolitic limestones. A detailed stratification and a list of the most important fossils are given by Łuniewski (1947), who discusses the deposits of the Upper Oxfordian (Rauracian and Astartian), Kimmeridgian and Cretaceous. The localization and description of the profiles, together with the description of fossils, including ammonites first described from this area, have been presented in one of the present writer's previous works (Karczewski, 1965). Large amounts of the rudistids, primarily of the genus *Eodiceras* Pčelincev, have been found by him in the Upper Oxfordian (Astartian).

At Smotryszów, the Upper Oxfordian (Astartian) deposits are developed in the form of white, hard, oolitic limestones, in some cases creamy in shade, with gastropods, pelecypods, brachiopods, corals and algae. These limestones, cracked in various directions, do not display bedding. Their thickness amounts to about 15 m. The rudistids relatively numerous.

In the "Rogaszyn" quarry, the Upper Oxfordian (Astartian) is represented by white, cracked, oolitic limestones in the form of huge, irregular blocks overthrust on each other, as a result of which it is impossible to distinguish any layers. This was also discussed by Łuniewski (1947). These limestones contain an abundant gastropods and thick-shelled pelecypods. Most gastropods belong to Nerineidae Zittel. They occur in banks together with corals. The thick-shelled pelecypods of the genera *Eodiceras* Pčelincev and *Trichites* Plot are relatively well-preserved.

In the area of Opoczno, the Upper Oxfordian (Astartian) deposits are the most fully and best developed at Sulejów on the Pillica. These formations were dealt with by Pusch (1833), Michalski (1884), Lewiński (1907), Premik (1926), Passendorfer (1924, 1934), Karczewski (1958) and Barczyk (1961). Pusch and Michalski gave an only general outline of the lithology and fauna of the oolitic limestones from Sulejów. Besides, they did not accurately settle the age of the Jurassic deposits. Lewiński (1907) was the first to divide them, on the basis of an abundant fauna, into particular layers. His profiles were supplemented by Passendorfer who assigned the "grab" layer, occurring in these deposits, yet to the Upper Oxfordian (Astartian). The fauna of ammonites from the Kimmeridgian deposits was first discussed by Barczyk (1961), who assigned the "grab" layer and underlying layers to the Lower Kimmeridgian. No ammonites are recorded in the Upper Oxfordian (Astartian), but dicerases and nerineas abound in it.

The Upper Oxfordian (Astartian) of Sulejów outcrops in a few larger

or smaller quarries on both banks of the Pilica river. On the left bank, large quarries are situated at Podkurnędz and on the right they are semicircularly scattered near the forest. Together, at Sulejów on both banks of the river there are 11 quarries, in which a more or less identical rocky series is outcropped. These are oolitic limestones or compact, pelitic limestones without oolites or with only few of them. A remarkable feature of these deposits is the fact that the strongly oolitic limestones contain very few pelecypods and gastropods, whereas in ooliteless or slightly-oolitic limestones they occur abundantly and are well-preserved, particularly so the thick-shelled pelecypods of the genus *Trichites* Plot and the rudistids.

In one of the quarries at Podkurnędz, the Upper Oxfordian (Astartian) deposits contain large banks and layers with trichites and diceras. In the upper part of the largest quarry, the diceras-nerinea layer is overlaid by a distinct trichites layer containing such species as *Trichites praealtus* Arkell, *Trichites* cf. *seebachi* Boehm, *Trichites* cf. *incrassatus* Boehm, *Trichites* sp. Many dicerases occur below this layer. The greatest number of dicerases (including young forms) and species of the genus *Plesiodiceras* Munier-Chalmas were collected in an outcrop near the forest which, according to Barczyk's (1961, pp.9,20) numeration, corresponds to outcrop 22. Specimens 0.5—15 cm long abundantly occur in oolitic-pisolitic limestones. The degree of their accumulation is so high that an average of 10 specimens may be found in 10 cu cm of the rock. Juvenile specimens of the rudistids, cemented together with the rock, are very similar to the species of the genus *Exogyra* Say. The fauna of dicerases is primarily accompanied by nerineas and many brachiopods and corals, the species of which are cited by Barczyk (1961).

In the environs of Pińczów, the Upper Oxfordian (Astartian) limestones occur at the foot of a hill called Góra Galicowa north of Sobków. In addition, they occur in the environs of Korytnica, Wierzbica and at Celiny. The geology of the vicinities of Pińczów has recently been worked out by Senkowicz (1959), who collected in this region an abundant fauna. Previously, this area was dealt with by Lewiński (1912), who described the Upper Jurassic profiles in the environs of Pińczów and, among the numerous fossils, also cited dicerases.

STATE OF PRESERVATION, METHODS OF STUDY AND TERMINOLOGY

Forms attaching to the substrate with their right or left valve have, on their larger valve, a more or less marked attachment area. In longitudinal sections through the beaks with attachment areas, different shapes of such surfaces are visible. Flat, concave, rough and funnel-like (Fig. 2) are the four, main types of attachment area which may be

distinguished. The presence of such a surface is a proof that the shell was at least for some time attached to the substratum in a stable position. In some cases (*Macrodiceras spirale* n.sp.; Pl. XIX, Figs. 1 a-b), owing



Fig. 2.—Forms of attachment area of rudistids: a flat, b concave, c irregular, d funnellike.

to a specific situation of the attachment area, which on the beak of valve includes considerable part of a whorl, the entire shell could keep a stable, vertical position. This enables the supposition that the attachment area thus situated was a direct cause of a very uniform twisting of the valve, which took the shape of an ascending spiral. After the separation, a valve with the attachment area, preserved in such a state, put up on a level plane, keeps its vertical position.

On some shells, the attachment area is very poorly visible, obliterated, abraded or lacking altogether. We may suppose that such an individual was torn off the substratum by, for instance, a stronger water current or by some other force in an early stage of its development. In some cases, in particular when the shell was attached in a suspended position or when it was inclined at a small angle, the weight of the shell itself could tear it off the substratum.

Among the specimens examined, some individuals are closely fused with others by the valves, with which the pelecypod was attached to the substratum. In such a case, the other individual, mostly of the same species, played the role of a substratum (Pl. XXVIII, Fig. 1 a-b). The individuals were attached to each other in different ways and we may suppose that sometimes the manner of attachment of one of them could be very inconvenient for another, which served as a substratum, as shown, for instance, in Pl. XXVIII, Fig. 4 a-b, in which the smaller individual was attached to the lateral area of the larger one, close to the latter's attachment area. With their growth, valves overlapped each other and consequently the shell of one of them could not open. Such "ingrowing" of one individual into another might even cause a premature death of the individual which played the role of a substratum.

The attachment area, which sometimes is very extensive and rough, enables the reconstruction of the substratum to which the individual was attached. According to Pčelincev (1959), underwater rocks, corals or other solid objects in the zones of not very deep waters, were used as a substratum. Of interest are the traces of attachment observed in species of the genus *Eodiceras* Pčelincev (Pl. XXVIII, Figs. 2, 3). They

are mostly elongate and have a rough surface. An oval attachment area is always concave and smooth. Sometimes, there are a few depressions. In the genus *Macrodiceras* n.gen., the attachment area frequently occurs in the form of an umbilical depression. In this case, the individual, attached to a conical substratum, simply grew around it (Pl. XXIX, Fig. 3). In the species of the genus *Plesiodiceras* Munier-Chalmas, the attachment area, although of a considerable size, is usually slightly marked. Within this genus, individuals were attached to the substratum at a small angle (20—30°), which is indicated by the inflection of the left valve reaching an almost horizontal position. A similar inflection of the larger valve is also observed in the genera *Diceras*, *Eodiceras* and *Epidiceras*.

An analogous inflection also occurs in *Tetracoralla*. Jakovlev (1964) concludes that a hornlike inflection in the conical coral was a result of a deviation of the aperture from the substratum, from which loam might reach the oral orifice, and imperil the life of the coral. In addition, Jakovlev believes that such forms lived in the zone of the surf and, consequently, attached to the substratum by a larger surface, growing with their convex side always facing the direction of the surf. The inflection of the Upper Jurassic rudistids seems to be caused by similar factors. The species of the genera referred to above might also occur in the zone of strong waving and turbulent sedimentation which is clearly indicated by the presence of oolitic limestones with pisolites containing the Jurassic rudistids. This is the most likely reason why they grew inflecting their larger valve in accordance with the direction of waving and, at the same time, protecting their aperture from impurities.

The material collected also contains the specimens in which the beak of valve, by means of which the representatives of particular species attached to the substratum, is broken-off. Although the larger valve might suffer such a damage when a specimen was separated from the rock during the preparation, it might well be, however, that it took place in living state (Pl. XV, Fig. 1). According to Pčelincev (1959), the broken-off beaks of larger valves testify to a premature detachment of a pelecypod from the substratum which caused its death.

Abraded parts of shells, in which, in some cases, the abrasion pierces clean through the valve (Pl. XXXI, Figs. 1, 4) occur on the surface of many, mostly larger, valves. Such valves were mostly abraded by boring pelecypods, whose elongate shells are sometimes visible embedded in rudistid valves (Pl. XXX, Fig. 3). We may guess that these animals bored the holes in already empty shells. It may also well be that the damage of outer surface was caused by some other animals yet in living state of the rudistid. This is confirmed by the fact that the holes and eroded places are visible only on the outer surface of valves and never

occur inside. In the majority of cases, they are observed on the larger valves which covered larger part of the pelecypod's body, i.e. in the place, in which the shell was, in living state, most exposed to all dangers.

During the study of the rudistids, the present writer's attention was particularly attracted to the spire line of the right valve. It turned out to be an important generic character, on the basis of which a new genus, *Macrodiceras* n.gen., could be separated. In the genera *Diceras* and *Macrodiceras* n.gen., the right valves increased and coiled up according to a certain definite line, for which a term *spire axis* is here suggested.

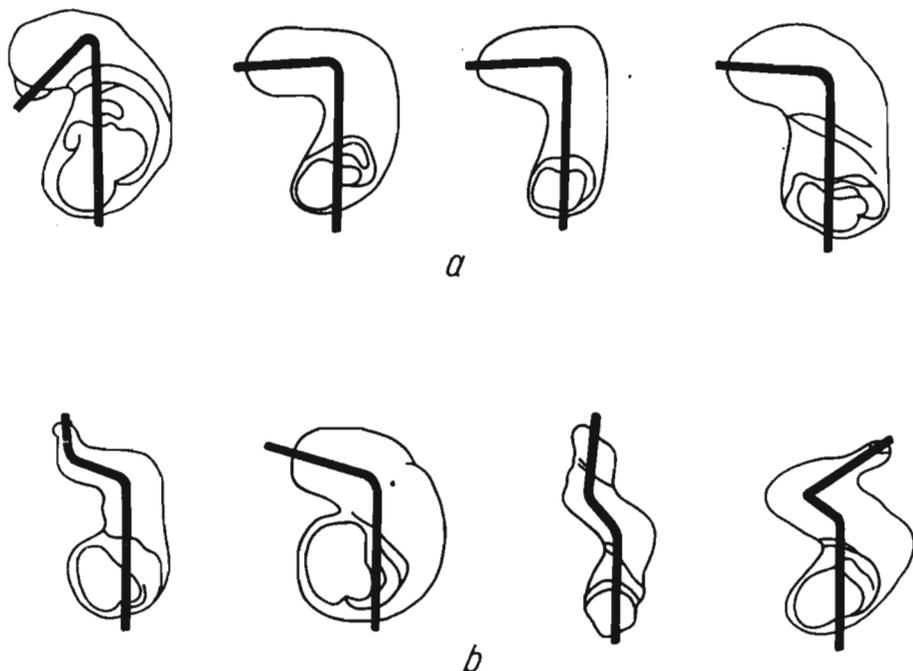


Fig. 3. — Spire axes of right valves: a *Diceras* Lamarck, b *Macrodiceras* n.gen.

If we orient the right valve so that its aperture is looking in our direction, we may observe that, in the species of the genus *Diceras*, the spire axis has a descending, and in the species of the genus *Macrodiceras* n.gen., ascending tendency (Fig. 3).

The terminology concerning teeth, dental sockets and muscle scars was settled by Douvillé (1886, 1935) and Bernard (1895). Literal symbols were used by Douvillé and numeral by Bernard. Numeral symbols are also used by Dechaseaux (1941b) and this seems to be more reasonable. Numeral symbols are clearer and, therefore, they have been used in the present work, the same as the system of designating muscle scars adopted after Dechaseaux (1941b): anterior muscle scars (ma) and posterior muscle scars (mp). This concerns the scars to which the ad-

ductor muscles were attached. The diductor muscle scars occur in the form of narrow, long grooves, hence they have been called ligament grooves.

PROBLEM OF PHYLOGENETIC RELATIONSHIPS

Hypotheses deriving the Rudistae from the Megalodontidae

Boehm (1882b) was the first to indicate a relationship between the genera *Megalodon* Sowerby and *Diceras* Lamarck. The fact that *Megalodus pumilis* Guembel has in fact a dicerasklike hinge, served him as a basis for his theory. He even separated this species as a genus *Protodiceras* which, according to his view, would be a direct ancestor of *Diceras*. This genetic relationship is understood by Boehm as likely although insufficiently demonstrated since, besides similarities, *Protodiceras* displays significant differences as compared with the rudistids (shells consisting of two identical valves, no traces of attachment). In addition, Boehm believes in the possibility of a relationship between some Megalodontidae and Cardiidae which together constitute a certain branch of the phylogenetic stem of the Rudistae, i.e. *Protodiceras* — *Pachymegalodon* — *Pterocardium*.

Dechaseaux (1939a, 1941b, 1943b), who decidedly rejects the theory deriving the first Rudistae from its contemporary *Pterocardium coralinum* (Leymerie), is a continuator of Boehm's conception. Her comparative studies on the hinges of *Megalodon* Sowerby, *Pachyerisma* Morris & Lycett, *Protodiceras* Boehm and *Diceras* Lamarck allowed her to find that some elements of their structure are common for all the genera mentioned above which would be indicative of their relationship. Such a conclusion is confirmed by the presence, in each of these genera, of the anterior muscle scar which is situated on a special support or myophore. The hinges of the genera *Megalodon* and *Protodiceras* display, however, a tendency to a gradual decrease in the size of posterior dental elements which, consequently, results in a hinge typical of *Diceras*, and vice-versa, *Pachyerisma* and *Pterocardium* display a tendency to a gradual increase in the size of the hinge plate and its elements which amounts to a hinge typical of Cardiidae. Hence, according to Dechaseaux (1939a, 1941b), the origin of the genus *Diceras* and other rudistids may be traced directly from the Megalodontidae Zittel. This author believes that *Pachyerisma* and *Pterocardium* constitute separate, parallel branch of the polyphyletic family Cardiidae Lam., which also derives from Megalodontidae Zittel.

Very interesting are also Dechaseaux's (1939a) observations on a gradual development of the posterior myophore in the Megalodontidae. The myophore of the genus *Megalodon* is very low and devoid of a sharp

inner margin which reaches below the hinge plate. This allows one to guess that juvenile forms were most likely devoid of myophore. Juvenile, about 1 cm long specimens of a *Diceras* have no posterior myophore. It is only in older specimens that at first a sharp crest appears which reaches below the hinge plate and a typical myophore is developed in fully mature forms. According to Dechaseaux, in the ontogenetic development of its myophore, the genus *Diceras* thus copies the characters of its direct ancestors, i.e. Megalodontidae.

Primitive representatives of *Diceras* were closely studied by Favre (1913). Such is *Diceras kobyi* Loriol from the Rauracian of Switzerland. Specimens of this species, attached to the substratum with their left valve, had a relatively thin valve and cardinal tooth less strongly developed than that of other species of the genus *Diceras*. In addition, posterior muscle scars were situated not on myophores, but directly on the inner wall of the valve. Inside, the muscle scars were bounded by a low ridge only. Since, in addition to the characters mentioned above, even the outline of the shell of this species resembles some shells of the Megalodontidae, Favre believes that it is a most primitive form of the Rudistae. These characters turned out to be common for the entire group of species having large shells attached to the substratum with their left valves. This group was distinguished by Douvillé (1935) as a separate genus *Epidiceras*.

Pčelincev (1959) maintains that among the Crimean specimens he met with the most primitive forms, similar in their outer look to the Megalodontidae and having beaks of valves bent anteriorly, as in typical megalodontis, and not twisted. According to Pčelincev, the relationship between the Rudistae and Megalodontidae was established on the basis of not only the structure of hinges and posterior muscle scars, but also the type of shell itself and the degree of its coiling. The studies on the Crimean rudistids allowed this author to introduce several changes to their taxonomy and, consequently, to form a new phylogenetic schema. Pčelincev and Douvillé are of the opinion that the family Megalodontidae or Cardiidae might be the ancestors of the Rudistae. Regardless of their acceptance of either the former or the latter as a starting family, these authors agree that the Rudistae have two fundamental phylogenetic branches. Within one of these stocks, there are forms attaching to the substratum with their left valve, and within the other those attaching with the right valve. If we take into account previous works by Boehm (1892), we may state that these stocks were related to one another by a direct, common ancestor of all Rudistae, that is, as was believed, the genus *Protodiceras*. Previously, some authors were of the opinion that these two great groups were related by the genus *Diceras*, the first ever known representative of the Rudistae. It was also believed that the

genus *Diceras* included forms which might attach to the substratum with both the left or the right valve. Pčelincev (1959) maintains that Douvillé (1935) was quite right to separate a group of species related to *Diceras sinistrum* and erect a new genus, *Epidiceras*, whose shells attached with their left valves, as opposed to the representatives of the genus *Diceras* sensu stricto attaching with their right valves. The representatives of the genus *Epidiceras* have very large shells and differ in several characters which make them considerably more similar to the Triassic megalodontids than are the representatives of the genus *Diceras* sensu stricto. *Epidiceras* makes up an independent side branch, consisting of forms also clearly different than the small shells of the *Diceras* type which attached with their left valves and which were given by Pčelincev (1959) a generic name of *Eodiceras*.

According to the last-named author, the genus *Diceras* constitutes a small branch of the phylogenetic schema, limited to the upper part of the Upper Jurassic only. He maintains that the differences between *Epidiceras* and *Eodiceras* are so great that these genera should be considered descendants of two different ancestors. The hypothesis that

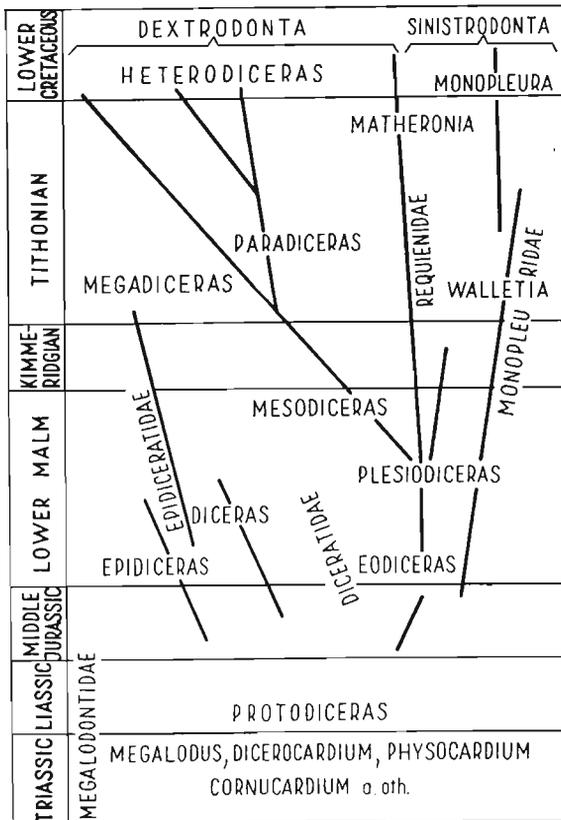


Fig. 4. — Phylogeny of rudistids, after Pčelincev (1959, p. 34, Fig. 5).

Valletia Munier-Chalmas, attaching itself by its left valve, may come from *Plesiodiceras* which attach with their right valve, is also rather unlikely. According to Pčelincev (1959), pelecypods attaching with the right valve, could never acquire the capability of attaching with the left valve, because the pelecypod's body, fulfilling its biological functions and adopted to resting on its left side, when changing position would be subject to a complex transformation process. Lodged in the hollow of the left valve, this body gradually took a normal position causing the deepening of the left valve with a simultaneous flattening of the right valve. The hinge would also change. According to Pčelincev, in view of these facts, the acceptance of a common ancestor for all families which make up the order Rudistae is wrong. A new phylogenetic schema is, therefore, suggested by Pčelincev (1959).

Hypotheses deriving the Rudistae from the Cardiidae

Quite different was Douvillé's (1935) approach to the origin of the Rudistae. He believes that *Diceras* originates from *Pterocardium*, this relationship being primarily based on changes involved in the change-over to the sessile mode of life. This was brought about as the beak of one of the valves attached to the substratum and the shell grew up in the form of a spiral. The presence of an immobile attachment area and the extension of the hinge, which takes place as the valves are twisted, lead to the simplification and transformation of the dentition characteristic of *Diceras*. According to Douvillé, *Diceras* is nothing else but a *Pterocardium* attached to the substratum. Douvillé also describes how young individuals attached to the substratum: young shells of *Pterocardium corallinum* (Leymerie), driven by a rapid water current, turned to one of the valves and, to arrest their movement, attached to a rough surface of the bottom. According to Douvillé, this might happen to all shells of this species which reached definite zones of turbulent water abounding in food and oxygen. They stayed in and adapted to such a new environment. This is the way in which the origin of the genus *Diceras* is presented by Douvillé. This hypothesis has so far been accepted, of course with certain modifications, by some palaeontologists. In his last work, Douvillé (1935) separates two large phylogenetic stocks which give rise to smaller groups. The first of them is the genus *Epidiceras*, whose shells attached to the substratum with the left valve. Later on, this group has been increased by the addition of several other genera such as, *Heterodiceras* Munier-Chalmas, *Requienia* Mathéron, *Toucasia* Munier-Chalmas, etc. The second group is represented by the genus *Diceras* (Fig. 5) whose shells attached with the right, larger valve. Here belong very many genera, the most important being *Valletia* Munier-

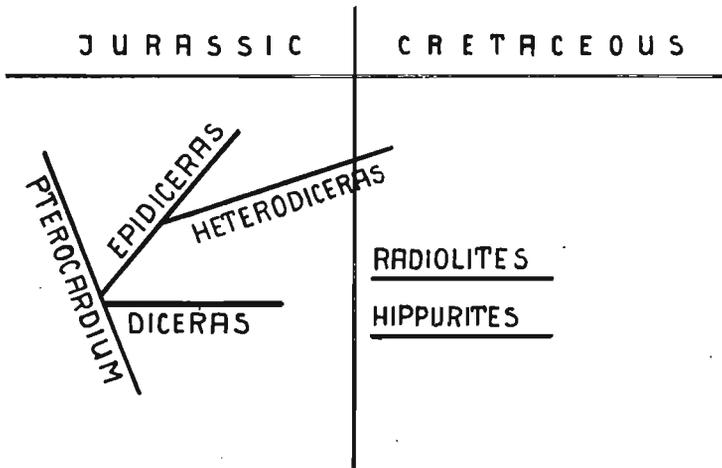


Fig. 5. — Phylogeny of rudistids, after Douvillé (1910, 1935).

-Chalmas, *Monopleura* Mathéron, *Hippurites* Lamarck, *Vaccinites* Fischer, *Radiolites* Lamarck, etc.

An attempt to evaluate the views on the origin of the Rudistae

Two opposite hypotheses concerning the origin of the Rudistae have, therefore, been brought forwards so far. Some authors are of the opinion that this is a group derived directly from the Triassic megalodonts (Boehm, 1882b — 1892; Dechaseaux, 1939a, 1941b, 1943b), whereas some others (Douvillé, 1935) derive it from the Jurassic thick-valved Cardiidae. The standpoint of the followers of both these hypotheses was, however, that the Rudistae came from one only ancestral group (in some cases, even one species). In this respect, new factors were introduced by the views of Pčelincev (1959), who also looks for the ancestors of the Rudistae among the Megalodontidae, but, at the same time, suggests that they originated from a few independent evolutionary lines (according to his terminology, "a polyphyletic descent"). The fact that the Jurassic rudistids display an already considerable differentiation which can be hardly explained as a result of a rapid evolution of one only lineage, is a starting point of Pčelincev's considerations. This justifies his erection of new families, genera and species. His view is also confirmed by the materials from the Holy Cross Mountains. Likewise, we should agree with Pčelincev in the matter of a radiative pattern of the differentiation of the Rudistae on particular areas, because this is an only explanation of such a great differentiation of them.

According to Boehm's and Dechaseaux's views, Pčelincev believes that the Megalodontidae are an initial group for all rudistids. It should be stated, however, that although they were benthonic forms, megalodontids

donts did not attach to the substratum as did the rudistids. Species of the genera *Protodicerias* and *Megalodon*, which occurred in the Triassic and Lower Jurassic, also did not attached themselves to the substratum. Accordingly, we may suppose that these genera, the same as *Cardiidae* (Boehm, 1882b, 1892; Dechaseaux, 1939a, 1941b, and others), could not be direct ancestors of the Upper Jurassic Rudistae. There was probably much reason in the views of Kutassy (1934), who maintained that the coincidence in the structure of hinges in megalodonts and the rudistids might result not so much from the relationship of these groups as from the convergent manner of their development. In addition to a certain similarity to megalodonts, all rudistids display fundamental differences — such as, for instance and primarily, a symmetry of valves (equivalve) in the *Megalodontidae* and asymmetry (inequivalve) in the rudistids, which was of course related with the latter's attachment to the substratum. These differences have been emphasized by Boehm as early as 1882 and 1892.

The *Chamidae* Gray which may be derived from the Rudistae is a group of Recent pelecypods most closely related to them. This fact is indicated by such important characters as the attachment to the substratum with either left or right valve, asymmetry of valves and a considerable similarity in the structure of hinges. The development of *Chamidae* dates back from the Upper Jurassic, that is, from the time of the extinction of the Rudistae. Such a great similarity to the Rudistae as that of *Chamidae* is displayed neither by megalodonts nor, and still much less, by *Cardiidae*. Consequently, placing as early as now these two last-named groups among the direct or indirect ancestors of the Rudistae does not seem to be justified. As yet, there are too many gaps and intervals in the suggested phylogenetic schema *Megalodon-Protodicerias-Dicerias*.

The radiation in the development of the Rudistae is observed, although on a smaller scale than in the Jurassic of the Crimea, in the Upper Jurassic of the Holy Cross Mountains. Two clearly differentiated groups of these pelecypods occur in this region, one of them consisting of the species which attached to the substratum with the left valve, and another within which there are the species which attached with the right valve. Mutual relationships within both these groups are shown in Fig. 6.

The rudistids which attached with the left valve were represented by the genera *Eodicerias* Pčelincev, *Epidicerias* Douvillé and *Plesiodicerias* Munier-Chalmas, whereas those attached with the right valve belonged to *Dicerias* Lamarck and *Macrodicerias* n.gen. In addition, species of the genus *Pterocardium* Bayan occur, together with the rudistids, in the Upper Jurassic of the Holy Cross Mountains. The relationship of the genera *Eodicerias* and *Plesiodicerias* cannot arouse any doubts. This fact

is confirmed by both the structure of hinges whose development could be traced on a series of the representatives of these genera and manner of attaching to the substratum with the left valve. One of the most important characters, that is, the development of the cardinal tooth was traced on growth series within the limits of both the genus *Eodicer*

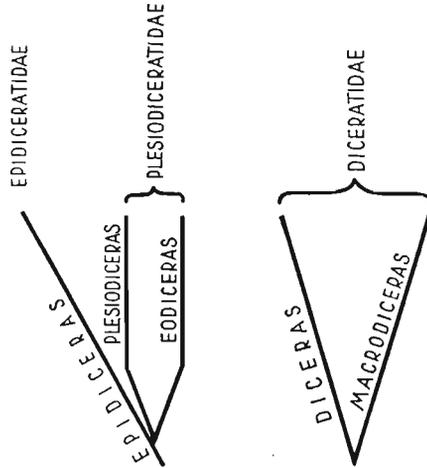


Fig. 6. — Phylogeny of Upper Jurassic rudistids in the Holy Cross Mountains.

and *Plesiodicer*. In the youngest growth stages, available to the present writer, cardinal teeth 3 are, in both genera, very similar to each other, except for a cusplike elevation occurring in *Plesiodicer* at the apex of the tooth in the central region, which enables the distinction between these two genera (Fig. 7). A clear differentiation of the cardinal tooth

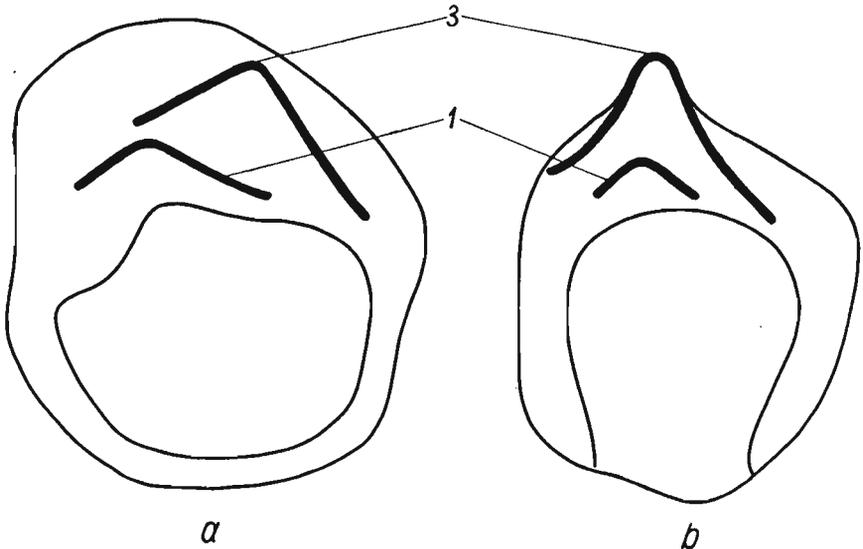


Fig. 7. — Schematic drawings of right valves of juvenile specimens: *a* *Eodicer* Pčelincev, *b* *Plesiodicer* Munier-Chalmas, 1, 3 outlines of teeth 1 and 3.

is visible only in older stages. The similarity of cardinal teeth of younger development stages in the species of the genera *Eodiceras* and *Plesiodiceras* seems to be one of the most certain proofs for their close relationship.

In the group under study, a somewhat secondary role is played by the genus *Epidiceras* Douvillé. Nevertheless, one can hardly agree with Pčelincev (1959) who maintains that this genus is quite different than *Eodiceras* and *Plesiodiceras*. After the comparison of the structure of hinges of the genera *Plesiodiceras* and *Epidiceras*, it appears that, for instance in the species *Plesiodiceras muensteri* (Goldfuss) and *Epidiceras cotteau* (Bayle), the cardinal tooth 3 in the hinge of the right valve is similarly developed as the anterior lateral tooth 1 (Fig. 8). In addition,

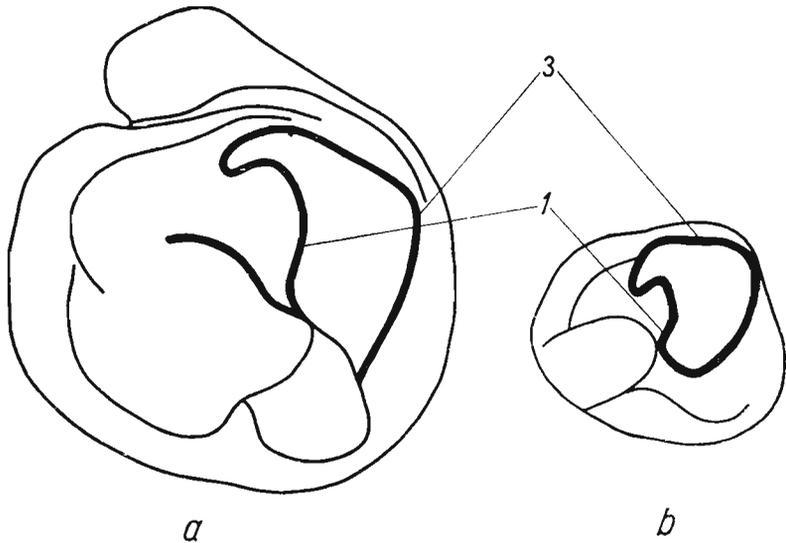


Fig. 8.—Schematic drawings of right valves: *a* *Epidiceras cotteau* (Bayle), *b* *Plesiodiceras muensteri* (Goldfuss), 1, 3 outlines of teeth 1 and 3.

the anterior and posterior muscle scars in both species are directly connected with the entire hinge plate. Such a great similarity in the structure of hinges in *Epidiceras* and *Plesiodiceras*, as well as — in the youngest stages — a similarity to the genus *Eodiceras*, undoubtedly places them in the same genetic group. According to the views of many authors (Douvillé, 1935; Dechaseaux, 1939*a,b*, 1941*a*; Pčelincev, 1959, etc.), the asymmetry in the Rudistae is a secondary character and consequently a conclusion may be drawn that within the *Epidiceras-Eodiceras-Plesiodiceras* generic group, the genus *Epidiceras*, with its almost symmetrical valves, is an initial form from which *Eodiceras* and *Plesiodiceras* were originated.

The genera *Diceras* and *Macrodiceras* n.gen. make up a group of pele-

cypods which attach to the substratum with the right valve. Their individuality is also emphasized by the structure of their hinges and development of muscle scars. On the basis of these characters it is, however, impossible to find which of them is an initial group. In the phylogenetic schema suggested (Fig. 6), only their descent from a common stock is, therefore, pointed out.

The division into the two groups mentioned above is in conformity with that used by Douvillé (1935) who assigns the species of the genera *Plesiodiceras*, *Epidiceras* and *Heterodiceras* to the forms which attach to the substratum with the left valve. The other group consists, according to him, of the species of the genus *Diceras* which attach with the right valve.

ASYMMETRY OF SHELLS

The attachment of the Rudistae to the substratum with either the right or left valve and, consequently, the development of the asymmetry of their shells, is undoubtedly one of the most interesting phenomena observed in the history of these pelecypods. It is no wonder, therefore, that so much space was given to this problem in various works. Munier-Chalmas (1882) was the first to discuss this phenomenon in the Rudistae and to draw from it far-reaching conclusions. Concerning the Rudistae, this author rejects such concepts as the right and the left valve. He compares the right valve of the forms attaching with the left valve, with the left valves of those attaching with the right valve, and ascertains that, since each of them has in its hinge one tooth and two dental sockets, these valves have very similar hinges. According to Munier-Chalmas, these valves are symmetrical and the hinge of one of them is simply a mirrorlike copy of that of the other. He designates the valves of the Rudistae by the first two letters of the Greek alphabet, alpha and beta, and calls the shells in which valve α is, at the same time, the right valve normal ones, and those in which valve α is the left valve — reversed ones. Munier-Chalmas' views aroused a heated discussion in the works of such authors as Douvillé (1935), Boehm (1882b, 1892), Dechaseaux (1939a, 1941b), etc. They were shared by Douvillé and, in part, by Bernard (1895) and critically received by Boehm, Dechaseaux and, recently, Pčelincev. Pčelincev (1959) assumes that fundamental differences, bearing the character of taxonomically important features, which make up a basis for his taxonomy applied to the Rudistae from the Upper Jurassic and the Cretaceous of the Crimea, occur between the two groups of the Rudistae which attach to the substratum with the left and the right valves. The division of the Rudistae into four main phylogenetic stocks, introduced by this author, has primarily been based

on the structure of the hinge. The development of the hinge in the course of the evolution of the Rudistae, depended — according to Pčelincev — on which of their valves were used by this group of pelecypods for the attachment to the substratum, and hence the division into the two suborders: the Dextrodonta and the Sinistrodonta. This is the way in which Pčelincev attempts to lead the entire, fairly complex taxonomy of the Rudistae from the dead end. The observations of the Polish material, including about 1,400 specimens (which belong to five genera, mostly *Diceras* Lamarck and *Macrodiceras* n.gen., and three families), seem to throw an interesting light on the pattern of the attachment of shells with either the left or right valve, and consequently to determine the type of the asymmetry of shells. In the material coming from the Holy Cross Mountains more than 50 per cent of all specimens belong to the species, which attach with the right valve. Analogous data for France, Switzerland, Czechoslovakia (Moravia), Germany and the U.S.S.R. (the Crimea) are as follows:

Table 2

Percentage of the species which attach with the right valve

France, Switzerland, Jurassic from Valfin, Bernois, S. Mihiel, Haute-Marne, Paris basin	Germany, Jurassic from Kelheim	Czechoslovakia, Moravia	Poland, Holy Cross Mts.	U.S.S.R., the Crimea
Thurman, 1852; Loriol, Royer & Tombeck, 1872; Bayle, 1873; Loriol & Bourgeat, 1886; Loriol & Lambert, 1893; Loriol & Koby, 1895; Munier-Chalmas, 1882; Douvillé, 1886—1935; Dechaseaux, 1941.	Boehm, 1882—1892; Schlosser, 1882.		Wójcik, 1914; Karczewski, 1968.	Pčelincev, 1959
2.5%	1%	less than 1%	more than 50%	6%

The data given above concern only the species which have been worked out and their descriptions published. It results from this table that in France, Switzerland, Germany, Czechoslovakia and the U.S.S.R. more than 90 per cent of the species of the rudistids were attached with the left valve, whereas in Poland such species make up only about 45 per cent. Such repartition of types of asymmetry, predominant among the Upper Jurassic rudistids of the Holy Cross Mountains, may be explained by two working hypotheses: on the one hand, by assuming that the asymmetry of the shell is not a character adaptively indifferent and, on the other, by considering the populations of the rudistids which, during that

period, settled the Holy Cross Mountains region, to be an isolated colony located on the border of the area of the rudistids. The "founder principle" (Mayr, 1963) might be applied to them.

As compared with the Upper Jurassic occurrence regions of the rudistids of France, Germany, Moravia, Switzerland and the Crimea, the Upper Jurassic of the Holy Cross Mountains is the northernmost area and, therefore, the conclusion may be drawn that thermal conditions of the environment were most likely to be decisive concerning the number of species attaching with the right or left valve. The species, which were attached with the left valve, could abound in the areas of warmer waters, whereas those which were attached with the right valve, developed in cooler waters, producing several new forms. The fact that the most exuberant development of the rudistids attached with the right valve took place in the Cretaceous and, besides, only in the south European areas (the Balkans, the Crimea), in what is known as the Alpine Cretaceous, may confirm the suggestions presented above. In Poland, the Cretaceous rudistids are very rare, known primarily from the Carpathian Cretaceous (Lefeld, 1968). It is, however, clear from few palaeoclimatic works (Bowen, 1961; Brooks, 1950; Loewenstam & Epstein, 1954; Ruchin, 1957 and — in Poland — Ciesliński & Witwicka, 1962) that the climate in the Cretaceous was colder than in the Jurassic. In one of his recent works Ruchin (1959) presents the supposition that during the Cretaceous period the equator ran through the English Channel, Brussels, Łódź and Kiev. This would imply that the mollusks of the moderate zone lived in the territories of Spitsbergen, Novaya Zemlya and Greenland and that the northern Scandinavia was situated nearer the equator than, for instance, the French Provence or the Balkan Peninsula, countries in which the Cretaceous rudistids developed exuberantly and reached large dimensions.

Apart from a rather complex problem of the migration of the earth poles and the equator, considering climate we should take into account definite temperature conditions, which were probably determined not so much by the distance from the presumable equator as, primarily, by water current conditions. In his well-known monograph, taking into consideration the distribution of the main continents and seas in the Upper Cretaceous, Brooks (1950) accepts, for instance, the presence of cold currents which caused that the dwarf forms of the rudistids developed in European areas contained between 50° and 55° north latitude. At the same time, this author emphasizes that, since the dwarf forms of the rudistids were recorded in the area between 5° and 20° north latitude, the equator was bound to be strongly shifted northwards. Brooks also explicitly expresses his opinion that the distribution of the rudistids might primarily depend on water temperature. The zone of normal rudistids with two peripheral zones of dwarf ones, which are connected with

the Thetis area, make up a convincing proof for the soundness of his reasoning. About sea streams influence on nerineids and rudistids distribution in Upper Jurassic of Europe writes also Ziegler (1965). In his work on Mesozoic climates, Schwarzbach (1961) also maintains that the Jurassic climate, although not stable, was on the whole warmer than at present and that it allows one to distinguish a distinct warm zone and a colder, "Boreal" zone. It is, therefore, not only the position of the equator, but also — and even more so — the regional current conditions which shape the marine temperature of a given area. The ratio of the species, which attach with the left valve, to those which attach with the right valve, changed together with changes of climate, and this in turn led to the formation of new groups of the rudistids. Consequently, we may assume that an abundant appearance of the rudistids, attaching with the right valve, in the Upper Jurassic testifies to a gradual cooling of the climate during that period. This phenomenon in the Upper Jurassic of Poland is also indicated by Pčelincev (1965). Discussing the spread of the Murchisoniata over the Upper Jurassic seas, this author expresses the following views (*l.c.*, p. 191): "It is clear from the character of the west-European Murchisoniata cited above that their distribution was most extensive in the Lusitanian. Together with corals, they reached England and even Poland where the influence of the Boreal province was already marked". Boreal influence decided the size and thickness of valves in both the rudistids and nerineaceans gastropods. The biggest and thickest shells of these mollusks, found in the Upper Jurassic deposits of Poland, rarely reached the dimensions of the shells of the same species from the Upper Jurassic of Germany, France or the Crimea which primarily was related with the temperature of water.

The above statements seem to justify the assumption on the influence, exerted by thermal factors on both the size and thickness of valves of the Upper Jurassic rudistids, and the ratio of the species, attaching with the right or left valve.

The influence exerted by temperature on the left or right-coiling of the Pleistocene foraminifers was studied by Ericson and Wollin (1964). In the boring cores, sampled from the Atlantic bottom and which were examined by these authors, the Pleistocene foraminifers *Globorotalia truncatulinoides* (d'Orbigny) and *G. menardi* (d'Orbigny) occurred in a somewhat peculiar sequence. In some samples almost all tests of *G. truncatulinoides* were coiled to the right, whereas in some others — to the left. After plotting the percentage of left- and right-coiled tests on the map of North Atlantic, it turned out that their distribution was consistently regular. This seems to indicate that some chemical or physical properties of the water disturbed the foraminifers' association. The temperature seems to be the most likely factor which is decisive in this case. In addition, these authors reflect on the question how, with

changes in temperature, the survival of a species may be directly affected by the manner of the coiling of tests. In their opinion, this influence depends indirectly on a genotype. Genes determining the direction of coiling a test are correlated with those determining the tolerance of a species to changes in temperature. Both groups of genes are transmitted hereditary as one whole (genetic or epigenetic correlation).

Another example is supplied by Vasiček's (1953) work. On the example of megalosphaerical and microsphaerical generations of foraminifers, this author gives interesting information on the left- and right-coiled individuals. Among the megalosphaerical individuals of some species, the right-coiled forms predominate, whereas in the microsphaerical individuals the ratio of the right- and left-coiled tests amounts to 1:1. The succession of generations is related, in these species, to the succession of the seasons of the year and, therefore, to temperature. Changes in the succession of generations may occur for a long time and, according to this author, may be used for stratigraphical purposes.

In the case of rudistids, the adaptation of species to definite environmental conditions, constitutes a somewhat different problem. It should be assumed that the pattern of the attachment of the shell and, consequently, the type of asymmetry (normal or inverted) was not an indifferent character, but had a definite adaptive significance. Most likely, it was related with a set of certain adaptive features which gave the inverted rudistids (with a free left valve) an adaptive advantage under the conditions of Boreal seas and the normal rudistids (with a free right valve) — under the conditions of warm seas. These observations are in conformity with the studies which revealed a varying adaptive significance of particular types of asymmetry in other mollusks. Very interesting data in this respect are given by Gauze and Šmaragdova (1939) in their work on the decrease in weight and mortality of the left- and right-coiled individuals of the gastropod *Fruticicola lantzi* Lndh. Both types of individuals were identically underfed in laboratory conditions, but it turned out that the left-coiled forms lost weight earlier and displayed a greater mortality than the right-coiled ones. According to these authors, this is an evidence of a different adaptive value to definite environmental conditions of the left- and right-coiled individuals. This might also result from the differences in metabolic activity, different degree of the utilization of energy in biological processes, etc. In the case of the rudistids, the factors of this type could, therefore, contribute, under definite thermal conditions, to a differential survival of the species, attaching with the left and right valve.

Almost equal number of species, attaching with either the left or right valve, which occur in the Upper Jurassic populations of the Holy

Cross Mountains region, may be also explained by acceptance of the "founder principle" suggested by Mayr (1963). The situation of the Holy Cross Mountains area, close to the northern boundary of the distribution of the Rudistae, may show that this area was settled as a result of a colonization by migrating populations ("isolates") from the main (Mediterranean) territory. Due to their limited population size "isolates" contained only part of a general genetic pool of parental populations. This factor may explain both different ratios of asymmetry (a great number of species attaching with the right valve) and a simultaneous occurrence of species, attaching with either the left or right valve. The last-named circumstance is more difficult to explain by the assumption of the adaptive predominance of one of the types of asymmetry. A presumable mechanism of the process of such a colonization consisted in a drift of few populations of planktonic larvae (e.g. in veliger stage) in sea currents, which transported them outside the boundaries of a normal distribution range. Subsequently, undergoing a metamorphosis, the larvae settled on sea bottom in a new area, forming isolated populations of their descendants whose pheno- and genotype variability, as a rule, deviated from those displayed in the main areas of occurrence. The reasoning presented above is supported by the results of Makridin's and Katz's (1966) studies on the geographical distribution of the Cretaceous brachiopods. A "bulge" in the distribution of some species (cf. Makridin & Katz, 1966, p. 100) has been found in the areas, mostly in straits, to which larvae were transported by warm sea currents. On the other hand, islands, archipelagoes or sea shallows were barriers for the penetration of larvae. Taking into account the similarity in the adaptive type of the rudistids and brachiopods (the sessile attachable benthos) and the spread of both groups by means of the planktonic larvae, we may say that the mechanism of forming colonies by the rudistids was similar to that in brachiopods.

PALAEOGEOGRAPHY, PALAEOECOLOGY
AND STRATIGRAPHIC SIGNIFICANCE

On the basis of our materials, we may state that the problems of palaeogeography, as well as migrations and distribution of the rudistids (extensively discussed in the Soviet literature), related to it, or what is known as the main centers, should be in a way supplemented. According to the data, found in literature, the main development center of the Jurassic rudistids was located in Paris Basin, from which these pelecypods gradually migrated eastwards by two routes: the northern one through the South Germany, Switzerland, the Carpathians and the Crimea, and the southern one through Italy, North Africa, Greece and Turkey. Se-

veral secondary development centers occur along both routes. In Poland, we are primarily interested in the northern route along which are Paris, Frankonian, Moravian, East Alpine, Balkan and Crimean centers. After the examination of the materials from the Holy Cross Mountains, it turned out that a development center of the Polish rudistids should also be included in the above list. An undoubtedly extensive and active development center, whose range covered a considerable area, was formed in the Upper Jurassic sea by abundant, well-preserved and differentiated rudistids of Poland which is indicated by the occurrence of them in boring cores of Olsztyn region. The northern distribution range of the Cretaceous rudistids in Europe, which reached as far as the southern coasts of the Scandinavian Peninsula, was yet more extensive as shown by specimens of these pelecypods found in Bastaden, Sweden (coll. of the Geol. Institute in Warsaw). Boreal rudistids of Sweden were mentioned by Lundegreen (1934) and Kühn (1949). According to Kühn, Boreal species of the Cretaceous rudistids occur in South England, Westphalia, Belgium, Northern France and South Sweden. In the Cretaceous these are small, dwarfish, sometimes thin-walled forms, which is ascribed by Kühn to climatic and facial conditions.

The Upper Jurassic rudistids from the Holy Cross Mts. occur in carbonate deposits, represented by oolitic, marly and detrital limestones and by marls. Oolitic limestones are frequently strongly differentiated. Very numerous rudistids from the environs of Sulejów were mostly found in oolitic limestones. This abundance of individuals within a few species was probably related with facial conditions, which in this area were particularly favourable to their development. Also noteworthy is the specific differentiation which might result from the formation of coral reef. A similar type of the facial differentiation with various assemblages of fauna is recorded near the villages of Dobrut and Śniadków near Radom. According to Dembowska (1953), in these localities the Upper Oxfordian (Astartian) limestones were deposited near a reef, which is indicated by their development marked by the presence of characteristic conglomerates of oolites and fragments of pelecypod-coral fauna, together with pelitic limestones, interbedded with marly intercalations. A very rich fauna of the Rudistae, represented primarily by the genera *Diceras* and *Macrodiceras* n.gen., occurs in these limestones. Species of these genera are found in variously developed carbonate deposits, *Diceras* being more frequent in oolitic limestones, and *Macrodiceras* n.gen. more or less uniformly distributed both in oolitic and pelitic limestones. Some of the species, such as *Macrodiceras longum* n.sp. and *M. pcelincevi* n.sp. have been found in marly and fine-oolitic limestones. Clearly, then, the changes occurring within a facies exerted a decisive influence on the distribution and development of the genera *Diceras* and

Macrodiceras n.gen. Any change in these conditions affected their composition, numbers and further development.

The Upper Oxfordian (Astartian) deposits from the environs of Radosko (Kodrań bolt), containing a rich fauna, are represented by oolitic and detrital limestones with many crushed organic remains. Despite the fact that many corals occur in this locality, Roniewicz (1960) suggests that there was no reef proper, but only certain accumulations of organisms as shown by the lack of coral fragments in the detrital material. No lithological differentiation is observed in the outcrops and exposures in which the rudistids occur. Loosely scattered individuals primarily of the species *Eodiceras eximium* (Bayle), including fairly numerous juvenile forms, are embedded in the sediment. In their shape and outer structure, as well as in the manner of attachment to the substratum they deceptively resemble some species of the ostreacean genus *Exogyra* (homeomorpha). This instance makes up one more proof of how great is the influence exerted by facial-ecological conditions on not only the separation and development of individual forms, but also on their similar shapes, despite the fact that they belong, in some cases, even to different orders.

The Upper Jurassic rudistids also abundantly occur in the Upper Oxfordian (Astartian) limestones of the entire range of Małogoszcz Hills, particularly great accumulations being recorded in the outcrops in Żerniki, Góra Bukowa, Skórków anticline and Grząby Bolmińskie. A layer in which representatives of *Diceras* and *Eodiceras* are densely embedded close to each other, stretches between Żerniki and Jaćłów (Pl. I, Fig. 2). Not even one species of the rudistids has ever been found below this layer. Very compact, strongly recrystallized limestones with few oolites make up the layer with the rudistids, which is differently developed than the underlying limestones and hence we may conclude on a certain facial differentiation in this area. This differentiation is also confirmed by the fauna of the rudistids accumulated in this layer. No lithological differentiation has been observed within the layer itself. Two genera, found in it, are represented by one species each, which in turn are represented by a great number of individuals. Such a great quantity of individuals might at first sight give an impression of uncommonly favourable living conditions which, in regard to these two species, might be even true. It seems, however, that we cannot assume any extraordinary development of the fauna of the rudistids in this area but only some kind of an isolation of few species, which here found an appropriate environment. On the other hand, as many as three genera of the Upper Jurassic rudistids with many species occur in the oolitic limestones of Dobrut and, therefore, in this particular case, we may certainly consider a mass development of these pelecypods.

Numerous accumulations of the rudistids in the Upper Jurassic

limestones are recorded also in the south-eastern margin of the Holy Cross Mountains in the environs of Błaziny, Olechów and Zawichost on the Vistula. In this area, the rudistids are the most abundant in the outcrops and quarries, in which the Upper Oxfordian (Astartian) deposits display a larger lithological differentiation. Here, the rudistids always occur in association with gastropods of the superfamily Nerineacea and with corals. In a large quarry at Błaziny near Ilża, the rudistids occur in the layers of differently developed limestones, but each of these layers also contains larger or smaller quantities of an organodetrital material. This facies of detrital-oolitic limestones with a rich fauna of the rudistids is also repeated in the environs of Olechów. The interdependence between the rudistids and their environment was marked in the Upper Oxfordian (Astartian) limestones in the entire area of the borders of the Holy Cross Mountains. The influence exerted by the rudistids on the environment might be expressed by the fact that individual species abundantly settled it, forming, in some cases, entire banks which might to a certain extent change the conditions predominating in such an environment. After the formation of a larger bank of shells of the rudistids, which were rigidly attached to the substratum, other organisms might appear in such an area of a relatively strong waving and in a way seek "shelter" in the banks of the rudistids. This is testified to by serpules and small accumulations of algae, bryozoans, etc. sometimes attached to the shells. Such an assemblage not only transformed the environment in the biological sense, but also could affect its chemism.

A wide distribution range and a great taxonomic differentiation of this group of pelecypods make them of course one of more important index fossils. This has already been emphasized in Poland by Wójcik (1914), in France by Douvillé (1910—1912) and Dechaseaux (1941b), in Germany by Boehm (1882, 1892) and in the U.S.S.R. by Pčelincev (1959). This problem was most extensively expanded by Dechaseaux. According to this author, who described species of the genera *Diceras* and *Heterodicerias*, they occur in the Rauracian, Sequanian, Kimmeridgian and Tithonian. The species of the genus *Diceras* Lamarck, which attached to the substratum with the right valve, occurred in the Rauracian and Sequanian deposits and for these stratigraphic units they are among the most important index fossils. The species of the genus *Plesiodiceras* occur only in the Sequanian and, therefore, they are also important index forms. The genus *Heterodicerias* occurs in the Kimmeridgian and Tithonian. Some species of the genus *Heterodicerias* sensu stricto are index forms for the Tithonian.

Since the fauna of Polish rudistids has never before been described, there was only little information on its suitability for the palaeogeographical, facial or stratigraphic purposes. After an accurate study of a wide variety of these problems, it turned out that at present the Jurassic

rudistids may for a certainty be used in the stratigraphic, palaeogeographical and facial considerations. This is caused to a considerable extent primarily by their mass occurrence with a relatively small vertical range, by their excellent state of preservation and wide geographical distribution.

SYSTEMATIC DESCRIPTIONS

Class **Lamellibranchiata** Blainville, 1816

Order **Rudistae** Lamarck, 1819

Family **Diceratidae** Dall, 1895

Diagnosis. — Shells large, inequivalved, the right one being always larger. An attachment area occurs on the beak of the right valve. The hinge of the right valve consists of a large cardinal tooth 3, first anterior lateral tooth 1 and, between them, dental socket 2'. The second anterior lateral tooth 2 and dental sockets 3' and 1' occur in the hinge of the left valve. Posterior muscle scar is mounted on high myophore. This family is represented by the genera *Diceras* Lamarck and *Macrodiceras* n.gen.

Genus *Diceras* Lamarck, 1805

Type species: *Diceras arietinum*, Lamarck, 1805.

Species assigned: *Diceras arietinum* Lamarck, *D. brevicornum* n.sp., *D. impressum* n.sp., *D. originale* Bayle and *Diceras* sp.

Stratigraphic and geographical range: Upper Oxfordian — Poland, France, Switzerland, U.S.S.R. Kimmeridgian — Germany, Czechoslovakia (Moravia).

Diagnosis. — Shells large, inequivalved, attaching to the substratum with the right valve. In some cases, attachment area is very small, situated on the beak of the right valve. Cardinal tooth 3 and a small first anterior lateral tooth 1 occur in the hinge of the right valve with dental socket 2', occurring between them. The hinge of the left valve consists of the second anterior lateral tooth 2 and dental socket 3' and 1'. Muscle scars strongly developed in both valves. Ligament grooves narrow, more or less deep, running over the outer surface of valves, from the beak to the end of the posterior hinge margin.

Remarks. — Erecting the genus *Diceras*, Lamarck (1805) combined under this name several forms from the Lower Valanginian of Salève, Switzerland, which were previously described by de Luca (1779). At present, the Swiss species are assigned to the genus *Heterodiceras* Munier-Chalmas, 1882.

Diceras arietinum Lamarck, 1805

(Pls. II-VII; Pl. X, Fig. 2; Pl. XXX, Fig. 3)

1805. *Diceras arietina* Lamarck; J. B. Lamarck, *Annales...*, p. 300, Pl. 55, Fig. 2a.
 1826. *Chama arietina* Goldfuss; A. Goldfuss, *Petrefacta...*, p. 206, Pl. 139, Fig. 2c.
 1941. *Diceras arietinum* Lamarck; C. Dechaseaux, *Rudistae...*, p. 12, Pl. 1, Figs. 1, 10-13; Pl. 2, Fig. 2.

Material. — Over 400 well-preserved specimens (right and left valves and complete shells).

Dimensions (in mm):

IG 1166.II	l. l. v.	IG 1166.II	l. r. v.	IG 1166.II	l. s.
162	48	156	35	167	65
164	70	158	49	169	105
173	75	172	66	171	108

Description. — Shells relatively large, inequivalved, with growth lines clearly visible on both valves. Attachment areas are frequently visible on the beak of the right, larger valve. The hinge of the right valve has a large cardinal tooth 3, first anterior lateral tooth 1 and a deep dental socket 2'. A distinct ligament groove is marked above the hinge margin. A relatively large anterior lateral tooth 2, dental socket 3', which surrounds it, and a smaller dental socket 1 occur in the hinge of the left valve. Ligament groove slightly shorter than in the right valve. Both valves with well marked muscle scars.

Growth stages of the right valve. A falciform cardinal tooth 3 is clearly visible in the smallest specimen (Pl. III, Fig. 1). Its upper part projects above the hinge margin and is slightly upturned towards the outer part of valve. A fairly large, semilunar dental socket 2' occurs anteriorly at the base of cardinal tooth. Tooth 1 is poorly visible, as a small convexity. Likewise, the posterior muscle scar is relatively low. On the other hand, ligament groove, running spirally from the base of the outer part of hinge margin up to the beak of valve, is clearly outlined. With the growth, particular hinge and muscle elements are subject to change. There appears an already normal first anterior lateral tooth 1 and ligament grooves begin to elongate. Muscle scars, in particular the posterior one, shift with the growth towards the middle and form a high myophore. A considerable thickening of the walls, in particular in the region of hinges, is observed in large-sized valves.

Growth stages of the left valve. The smallest valve (Pl. II, Fig. 1) has a well developed hinge plate with an equally well developed, projecting second anterior lateral tooth 2, which, in a narrow semicircle, is surrounded by dental socket 3'. Dental socket 1' forms a small depression. Posterior muscle scar is situated on a not very high myophore,

anterior — invisible. Beak fuses with the lateral surface of valve. No major differentiation is observed in larger valves in such hinge elements, as tooth 2 and dental sockets 3' and 1'. On the other hand, a gradual uncoiling of the beak is visible. If in the smallest valve, the beak contacts the surface of valve, in the largest one it is completely separated from the lateral surface and its spires form an uncoiling ascending spiral. A gradual deepening of ligament grooves is observed with the growth of the valve. Muscle scars (their myophores) are not subject to major changes.

Variability. — Many specimens of *D. arietinum* do not display a major variability. Some small differences are noted in the thickness of valves and length of the right valve. In addition, the attachment area of the right valve has sometimes a variable outline.

Remarks. — *D. arietinum* has some characters in common with the species of the genus *Macrodiceras* n.gen. These are, the attachment to the substratum with the right valve and a similarly developed hinge in both valves. On the other hand, it differs from them primarily in the length and spire of the right valve and in the size of shell. A tendency to the individualization of the beak was found in a series of specimens of the left valve of *D. arietinum* varying in age. The beak of the left valve in the species of *Macrodiceras* n.gen. is completely individualized and hence we may conclude that *D. arietinum* is a starting species of the genus *Macrodiceras* n.gen.

Occurrence. — Poland: Dobrut, Błaziny, Olechów, Zawichost, Żerniki, Grząby Bolmińskie, Skórków anticline, Sulejów on the Pilica, Bukowa; Upper Oxfordian (Astartian). France: Rauracian. Germany: Upper Oxfordian, Lower Kimmeridgian.

Diceras brevicornum n.sp.

(Pl. XII; Pl. XXVII, Fig. 1)

Holotype: Pl. XII, Fig. 3; IG 1166. II/2.

Type horizon: Upper Oxfordian (Astartian).

Type locality: Dobrut near Radom.

Derivation of the name: *brevicornum*, Lat. *brevis* = short, *cornus* = horn.

Material. — Thirty-one well-preserved specimens, including three shells.

Dimensions (in mm):

IG 1166.II/	l. r. v.	l. l. v.	IG 1163 II/	l. s.	b. s.
3—4	67	57	1	60	65
—	—	—	2	70	64
—	—	—	31	58	53

Diagnosis. — Shells strongly convex, with very short, anteriorly coiled beaks. The left valve has a distinct keel dividing its outer surface into two unequal parts, of which the posterior one is smaller.

Description. — Shells relatively small, strongly convex, inequivalved, the right valve being always larger and having a short, anteriorly coiled beak, on which an attachment area is rather poorly visible. A keel, dividing the outer surface of the right valve into two almost equal parts, runs along the entire right valve from its beak to the anterior margin. The left valve is less convex with a distinct, sharp keel which divides its outer surface into two unequal parts. Wide growth lines are clearly marked on both valves. Hinge plate not very large, but very well developed. A massive, excellently developed cardinal tooth 3, semicircularly running over the hinge plate, occurs in the hinge of the right valve. The first anterior lateral tooth 1 has the form of a small convexity pressed into dental socket 2', which separates these two teeth (3 and 1) forming a relatively deep, elongate depression. Muscle scars very strongly marked, the anterior one forming a characteristic concavity just below the anterior part of the hinge and posterior being mounted on a high myophore situated relatively high, i.e. halfway the height of the aperture of the right valve. The hinge of the left valve consists of a strong, conical second anterior lateral tooth 2 and dental sockets 3' and 1' entered by cardinal tooth 3 and the first anterior lateral tooth 1 of the right valve. The anterior muscle scar of the left valve occurs in the form of a slight elevation just below tooth 2. The posterior muscle scar, much the same as in the right valve, is mounted on a high myophore itself situated high, i.e. halfway the height of the aperture of the valve. Ligament grooves of both valves are only slightly marked.

Variability. — Particular specimens of this new species only slightly differ from each other in the coiling of the apical part and height of the posterior muscle scar. No major variability is displayed by the hinge.

Remarks. — In the size of its shells, *D. brevicornum* n.sp. is similar to *D. subarietinum* Pčelincev (1959) from which it differs, however, in a larger degree of asymmetry of valves and the presence of a distinct keel, dividing the outer surface of valves into two parts. The lack of a description of the structure of hinges in *D. subarietinum* does not unfortunately allow us for a comparison of this important element of valves with the hinge of *D. brevicornum* n.sp.

Occurrence. — Poland, Dobrut near Radom; Upper Oxfordian (Astartian).

Diceras impressum n.sp.

(Pls. VIII, IX, X, Fig. 1)

Holotype: Pl. VIII, Fig. 2; IG 1166.II/32.

Type horizon: Upper Oxfordian (Astartian).

Type locality: Dobrut near Radom.

Derivation of the name: Lat. *impressus* = compressed; after narrow, compressed valves of the shell.

Material.—About 30 well preserved specimens (mostly complete shells).

Dimensions (in mm):

IG 1166.II/	32	33	34	35	36
l. s.	74	72	98	68	95
b. s.	52	54	64	47	80

Diagnosis.—Shells large inequivalved, strongly narrowed. The right valve slightly shifted in relation to the left one and bent at an angle exceeding 90° . The left valve strongly projecting to the right.

Description.—Shells strongly narrowed, with valves obliquely shifted in relation to one another. In larger specimens, the right valve is twisted at an angle exceeding 90° . In smaller specimens, this angle is smaller than 90° . Both valves have a distinct keel, dividing the surface of a valve into two parts. Spirally outlined ligament grooves are clearly visible on both valves, the same as growth lines which are particularly distinct on smaller shells. Both the anterior and posterior muscle scars are strongly marked in the largest shell, whose inside is in part exposed (Pl. IX, Fig. 1b). Posterior muscle scar is mounted on high myophores which are identically situated in both valves. Anterior muscle scar forms a small depression above the hinge margin. On the hinge plate of both valves, teeth and dental sockets are developed similarly as those in *D. arietinum*, except for the hinge margin and cardinal tooth 3 of the right valve, which are strongly shifted posteriorly. Sometimes, a small attachment area is marked on the beak of the right valve in the form of a larger or smaller flattening or concavity of the oldest whorls of the right valve.

Variability.—Specimens of *D. impressum* n.sp. display a variable degree of the lateral flattening of their shell. Some differences are observed also in the degree of development of the attachment area which, in extreme cases, may include a considerable part of the oldest whorl.

Remarks.—*D. impressum* n.sp. is most similar to *D. arietinum* which is probably a result of their close relationship. This fact is indicated by the structure of hinges and morphology of muscle scars. In both species, cardinal tooth 3 of the right valve and second anterior lateral tooth 2 of the left valve are similarly developed, except for a difference in the position of cardinal tooth 3, which in *D. arietinum* is situated almost in the middle of the hinge plate, and in *D. impressum* n.sp.—on the periphery of the hinge margin (shifted far posteriorly). In addition, the

posterior muscle scar in *D. impressum* n.sp. is placed in a more central part of the valve than in *D. arietinum*.

Occurrence. — Poland: Dobrut near Radom: Upper Oxfordian (Astartian).

Diceras originale Bayle, 1873

(Pl. XI)

1873. *Diceras originale* Bayle; E. M. Bayle, Observation... p. 144, Pl. 17, Figs. 1—4.

1941. *Diceras originale* Bayle; C. Dechaseaux, Rudistae..., p. 17, Pl. 2, Fig. 14; Pl. 3, Figs. 2, 5—7.

Material. — About 120 well-preserved specimens (left and right valves).

Dimensions (in mm):

IG 1166.II/	61	62	63
l. r. v.	82	—	—
l. l. v.	—	65	90

Description. — The right valve elongated, mostly twisted at an angle of 90—120° to the left (as viewed from the aperture). A usually small attachment area frequently occurs on the beak. The outer surface is, in apical region, irregular, in some places depressed. Growth lines are visible over the entire length of the valves. Hinge margin slightly inclined posteriorly, with large cardinal tooth 3, which is deflected in a falciform manner parallel to the spire of the valve. Dental socket 2', similar in shape to that of other species of the genus *Diceras*, is situated anteriorly almost at the level of tooth 3. Tooth 1 is also similar to the teeth of this type in other species of *Diceras*. A distinct ligament groove runs above the hinge margin. The posterior muscle scar is mounted on a high myophore, which is slightly shifted to the middle of the valve, and the anterior one forms a fairly deep depression at the base of the anterior part of the hinge plate.

The left valve is smaller than the right, flatter, twisted in the form of an ascending spiral and with its beak projecting above the outer surface of valve. Outer surface, covered with distinct, wide growth lines, is divided into two parts by a sharp keel running from the edge of the valve up to the beak. Hinge plate very large and wide, which is the main character differing this species from others. Tooth 2 occurs in the lower and middle part of the hinge plate. It is shaped like a lingulate stripe, slightly turned outwards. Dental sockets 3' and 1' are small. Ligament

grooves in the form of deep furrows, semicircularly running around the upper part of the hinge margin, are very clearly outlined on a flat hinge plate. The posterior muscle scar, mounted on myophore, frequently reaches the posterior part of the hinge margin, the anterior forms an elongate depression surrounding the base and anterior part of tooth 2.

Variability. — Adult specimens do not display any major variability. Tooth 2 is sometimes variously developed on the hinge plate. In more flattened valves, it occurs in the form of a sizeable monticule and in more strongly uncoiled valves it is marked as a lingulate process turned outwards. In addition, in connection with a varying degree of coiling to the left, the right valves sometimes have their hinge margin situated at a varying angle to the lower edge of the valve. Muscle scars, in both right and left valves, are not differentiated, except for their situation at different levels, which is related to the degree of coiling of a given valve.

Remarks. — *D. originale* resembles, in its outer appearance, the species *D. arietinum* Lamarck and *D. strangulatum* Bayle, but fundamentally differs from them in the structure of the hinge plate, which in *D. originale* occupies nearly 3/4 of the space of the aperture of both the right and left valve, whereas in *D. arietinum* and *D. strangulatum* it occupies only 1/4 of the aperture of valves. In addition, it has somewhat differently shaped teeth of its hinge.

Occurrence. — Poland: Dobrut near Radom; Upper Oxfordian (Astartian). France: Rauracian.

Diceras sp.

(Pl. XXVI; Pl. XXVIII, Fig. 6; Pl. XXX, Fig. 2; Pl. XXXI, Figs. 1—3)

Material. — About 150 specimens.

Dimensions (in mm):

IG 1166.II/	561	562	563	564	565	566	567	568
l. v.	57	50	50	60	88	80	48	48

Description. — Right and left valves all damaged, relatively small. This is a fairly specific type of damage in the form of a groove, which comprises the aperture together with muscle scars and hinge plate. In the upper part of valves it is narrowed and, in some cases, reaches the beak of a valve. Of interest is the fact that this groove is in principle identically outlined on all valves. In addition, valves have a damaged outer surface, on which sometimes round eroded places are visible here

and there. Beaks of valves are more or less similarly coiled. In most cases, a distinct keel, dividing the surface of valve into two parts, is visible on the outer surface. The right valves are usually slightly larger.

Remarks. — Damaged hinge parts and other important elements of valves do not allow us for an accurate specific determination of the specimens. The conclusion may only be drawn on the basis of outer appearance that they might belong to *D. arietinum* Lamarck or some other species of the genus *Diceras* described in the present work. However, there is also a possibility of their being new forms.

Occurrence. — Poland: Dobrut, Żerniki, Sulejów on the Pilica; Upper Oxfordian (Rauracian, Astartian).

Genus *Macrodiceras* n.gen.

Type species: *Macrodiceras longum* n.sp.

Derivation of the name: Gr. *makros* = long; a diceratid with a strongly elongate shell.

Species assigned: *Macrodiceras balaklavense* (Pčel.), *M. kozlowskii* n.sp., *M. longum* n.sp., *M. magnum* n.sp., *M. pcelincevi* n.sp., *M. polonicum* n.sp., *M. rotundatum* (Bayle), *M. spiratum* n.sp.

Stratigraphic and geographical range: Poland: Upper Oxfordian, margin of the Holy Cross Mountains. France: Sequanian. U.S.S.R. (the Crimea): Rauracian.

Diagnosis. — Shells very large, inequivalved, always attaching to the substratum with the right, larger valve, which is mostly extended upwards and subsequently more or less coiled. Its apical part of the beak happens to be sometimes truncated by the attachment area, the latter being mostly large or very large. The left, smaller valve never makes up a flat lid. As the right one, it is massive, thick and frequently has a beak slightly coiled and projecting above the lateral surface. Both valves have very thick walls, massive, but relatively narrow hinge plate and a clearly marked muscle scars. The hinge of the right valve consists of a very large cardinal tooth 3, which in some species is shifted far posteriorly, first posterior lateral tooth 1 and dental socket 2'. The hinge of the left valve occupies a relatively large area, with the second anterior lateral tooth 2, strongly projecting above its surface. The last-named tooth is surrounded on the one posterior side by dental socket 3', and on the other (anterior) by the depression of the anterior muscle scar. Posterior muscle scar in both the right and left valves is mounted on high myophore. Anterior muscle scar forms depression in the lower anterior part of the hinge margin.

Remarks. — *Macrodiceras* n.gen. is to the greatest extent similar to the genus *Diceras* Lamarck. Fundamental differences between these two genera primarily consist in the structure of the right valve. *Diceras* has more convex and inequivalved shell, but its right valve is not much

larger than the left and in extreme cases this ratio amounts to 1:2 for the right one. The left valve has a beak, which frequently adheres to the lateral surface and in a way makes up a sort of lid of shell. On the other hand, *Macrodiceras* n.gen. has very large shell, sometimes three or four times as large as those of *Diceras*, which in addition are strongly elongate, particularly its right valve. This valve is usually strongly extended upwards, sometimes uncoiled (e.g. in *Macrodiceras longum* n.sp.) and, in all cases, terminating in a small apical whorl. Beak is frequently truncated by a large attachment area, never recorded in *Diceras*. Left valve of *Macrodiceras* n.gen. never forms a lid of shell and, as mentioned above, has strongly accentuated apical whorl, which frequently do not join the lateral surface of the valve, being elevated above it.

Discussing the family Diceratidae Dall, Pčelincev (1959) states that the existence within this family of only one genus *Diceras* Lamarck may be explained by a poor recognition of this group of the Rudistae. This statement seems to be by all means correct. All species, regardless of their attachment to the substratum with either the right or the left valve, have so far been assigned to only one genus, i.e. *Diceras* Lamarck. This led to an artificial extension of the concept of this genus, in which most species were included, belonging not only to other genera, but also even to other families.

Macrodiceras longum n.sp.
(Pls. XVI, XVII)

Holotype: Pl. XVII; IG 1166. II/710.

Type horizon: Upper Oxfordian (Astartian).

Type locality: Dobrut near Radom.

Derivation of the name: Lat. *longum* = long; after a very strongly elongate right valve.

Material. — About 60 well-preserved specimens, right valves only.

Dimensions (in mm):

IG 1166.II/	706	707	708	709	710
l. r. v.	53	80	104	110	175

Diagnosis. — Right valve strongly elongate and uncoiled, with a distinct keel running along the entire surface. Hinge plate small, with well-developed teeth and dental sockets. Anterior and posterior muscle scars well-developed. Posterior muscle scar mounted on a high myophore.

Table 3
Comparison of different species
of the genus *Macrodiceras* n.gen.

Species	Right valve	Left valve	Hinge	Muscles and hinge
<i>Macrodiceras longum</i> n. sp.	strongly elongate, narrow, with a single keel	—	small, slightly shifted posteriorly	well-developed
<i>M. balaklavense</i> Pčelincev	strongly elongate, thick	smaller, beak projecting above the lateral surface	large, regular	ligament groove poorly developed
<i>M. kozlowskii</i> n. sp.	strongly horizontally elongate, distinct growth lines, single keel	smaller; beak not contacting lateral surface; single keel	in normal position very large	very well-developed
<i>M. magnum</i> n. sp.	very large, massive; small attachment area; very wide growth lines, two keels	beak contacting lateral surface; two keels	—	—
<i>M. pcelincevi</i> n. sp.	elongate in the form of an inverted C, growth lines of uneven width; single, indistinct keel	—	not very large	poorly developed
<i>M. polonicum</i> n. sp.	very large; large aperture	—	very large, massive	very well-developed
<i>M. rotundatum</i> (Bayle)	elongate, spire axis elevated	helically coiled	not very large, shifted posteriorly	well-developed
<i>M. spirale</i> n. sp.	massive, strongly helically coiled; very large attachment area	—	narrow, strongly shifted posteriorly	well-developed

Growth stages of the right valve. The right valves are more or less elongate and, in some cases, flattened. A small hinge plate with the growth of valve slightly shifts anteriorly. Cardinal tooth 3 is strongly shortened and shifted to the posterior part of hinge plate. Dental socket 2' semicircular. Tooth 1 slightly marked and only on the largest valves. Posterior muscle scar is mounted on myophore, anterior one occurring in the form of a slight depression below the anterior part of hinge plate. Both valves display the tendency to uncoiling, which causes a change in the value of angle α between the first and second whorl (Fig. 9), which

in the smallest valve amounts to 90° and in successive, development stages considerably increases reaching 115° , 122° and 130° . A distinct keel runs through the middle of almost all valves from the aperture up to the beak. Two deep ligament grooves, which become shallower in the apical region of a valve, are visible below the keel.

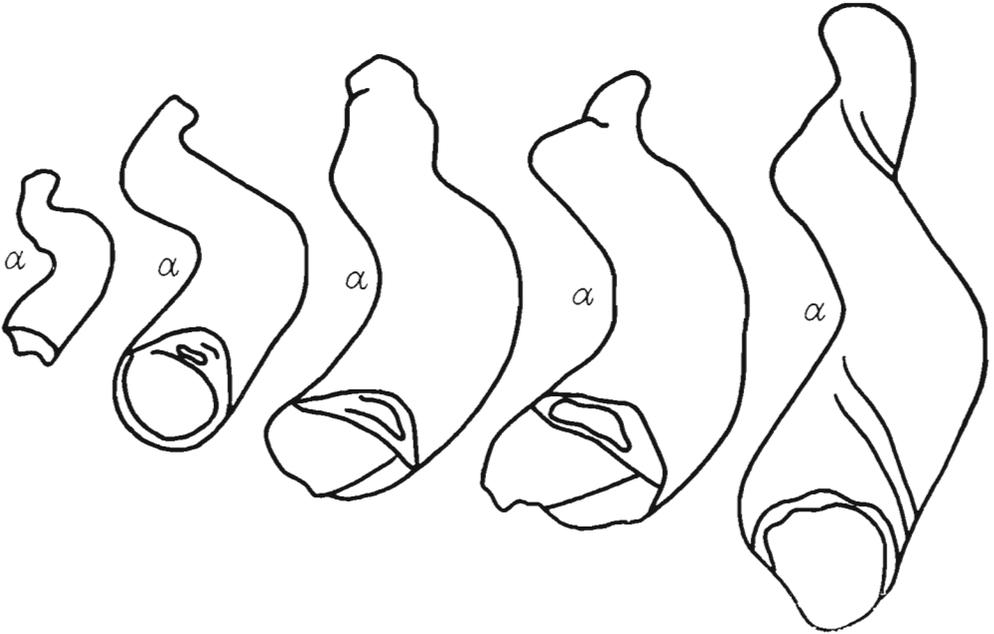


Fig. 9. — Series of *Macrodiceras longum* n.sp. — gradual increase of growth angle α is visible.

Variability. — Valves of *M. longum* n.sp. display a certain differentiation in the thickness of their walls, particularly so in the region of the hinge. The hinge plate, although relatively small in most cases, is also variously developed.

Remarks. — All specimens of this species so conspicuously differ in the shape of the right valve from other species of the genus *Macrodiceras* n.gen. that despite their hinge elements, which are damaged in some cases and the lack of the left valves — the separation of them and erection of a new species do not arouse any doubts.

Occurrence. — Poland: Dobrut near Radom, Sulejów on the Pilica: Upper Oxfordian (Astartian).

Macrodiceras balaklavense (Pčelincev, 1959)

(Pl. XIII, Fig. 2; Pl. XIV, Fig. 2)

Material. — Ten well-preserved specimens (right and left valves).
Dimensions (in mm):

IG 1166.II/	764	765
l. r. v.	114	110

Description. — Shell very large, inequivalved, with beak strongly coiled and deflected outwards. Right valve is larger, with attachment area sometimes well-preserved on its beak. Mildly marked keel divides the surface of the valve. The beak of the left valve slightly projects over its lateral surface. In the right valve, hinge consists of cardinal tooth 3, which is elongate parallel to the outer margin and dental socket 2', which in the central part is narrowed by a projecting lateral tooth 1. Anterior lateral tooth 2 is a main element of the hinge of the left valve. It is situated in an immediate neighbourhood of the anterior margin of the valve. A depression, which makes up dental socket 1', is visible in its lower part, and large dental socket 3', entered by the cardinal tooth of the right valve, is visible in its posterior part. A slightly marked, narrow ligament groove reaching, on the outer surface, almost as far as the beak, runs on both valves above the hinge margin.

Remarks. — This species, described by Pčelincev (1959) from the Rauracian of the Crimea, is — according to this author — very similar to *Paradiceras chantrei* (Munier-Chalmas) and to *P. bavaricum* (Zittel), from which it differs, however, in its attachment to the substratum with the right valve, whereas both mentioned species attached themselves with the left valve.

On the basis of the structure of the right valve, its spire axis and its dimensions, this species is here assigned to the genus *Macrodiceras* n.gen. The right valve of *M. balaklavense* (Pčelincev) is strongly extended upwards and afterwards, strongly coiled outwards and, therefore, the line of the spire (spire axis) of the right valve displays an ascending tendency typical of *Macrodiceras* n.gen. In addition, both the right and left valves are characterized by considerable dimensions, exceeding those of the species of the genus *Diceras* sensu stricto. These characters have been decisive concerning the assignment of this species to the genus *Macrodiceras* n.gen.

Occurrence. — Poland: Dobrut near Radom, Sulejów on the Pilica; Upper Oxfordian (Astartian). U.S.S.R. (the Crimea): Rauracian.

Macrodiceras kozlowskii n.sp.

(Pl. XV)

Holotype: Pl. XV, Fig. 1 a-b; IG 1166.II/774.

Type horizon: Oxfordian (Astartian).

Type locality: Dobrut near Radom.

Derivation of the name: in honour of Professor Roman Kozłowski, the most eminent Polish palaeontologist.

Material. — Two very well-preserved specimens, one of them a complete shell.

Dimensions (in mm):

IG 1166.II/774 — 1. s. 140

Diagnosis. — Shell very large, distinctly inequivalved, with strongly coiled beaks of both valves. The right, larger valve strongly extended horizontally, the left with a distinct keel. Hinge margin large, massive. Muscle scars and ligament grooves very well developed.

Description. — Shell very large, strongly inequivalved, with conspicuously coiled beaks of both valves. Distinct growth lines occur on the outer surface, in particular in the contact area of both valves. The right, larger valve is coiled and extended first to the left at an angle of 90°, then posteriorly and slightly upwards forming an apical whorl. The beak itself is slightly damaged. A distinct keel runs through the middle of the right valve dividing it into two parts. Ligament groove clearly outlined. The left valve also has distinct growth lines obliterated in the apical region. The beak of the left valve, not contacting the lateral surface, is uncoiled and elevated. A single, sometimes sharp keel obliterated, in all cases, in the apertural region, runs over the surface of the left valve. The left valve has distinct growth lines, is strongly uncoiled and does not contact the lateral surface. Hinge plate large, occupying nearly a half of shell aperture. Massive, large second anterior lateral tooth 2, in some cases slightly coiled, parallel to the coils of the entire valve, occurs in the middle, in the lower part of the hinge plate. Large, elongate dental socket 3' entered by a sizeable cardinal tooth 3 of the right valve, is situated in the posterior part of tooth 2. Dental socket 1 is also of considerable dimensions, which is indicative of the size of the first lateral tooth 1 of the right valve. Ligament groove starts from the hinge margin and runs through the bottom part of the spire towards the beak. Muscle scars very conspicuously marked, the posterior one mounted on a massive, slightly flattened myophore, the anterior forming a considerable depression in the lower anterior part of the hinge margin.

Remarks. — *M. kozlowskii* n.sp. is to the greatest extent similar to *M. rotundatum* (Bayle) and *M. magnum* n.sp. from which it fundamentally differs, however, being nearly three times as large as *M. rotundatum* (Bayle), having a differently developed keel, which divides the

outer surface of both valves, and having a hinge margin placed in a different position. In *M. rotundatum* (Bayle), the hinge margin of the right valve, with cardinal tooth 3, is shifted far posteriorly, whereas in *M. kozlowskii* n.sp. the hinge margin is in a normal position. *M. kozlowskii* n.sp. differs from *M. magnum* n.sp. primarily in the number of keels on both valves, dimensions and manner of coiling of the right and left valve. *M. magnum* n.sp. has on each valve two keels, which divide their surface into three parts, whereas *M. kozlowskii* n.sp. has on each valve a single keel which divides their outer surface into only two parts. As mentioned above, these two species also differ from each other in the manner of coiling of the right and left valve. In *M. magnum* n.sp. the beak of the left valve contacts the lateral surface of the valve, and in *M. kozlowskii* n.sp. the beak of the left valve becomes, with the spire, elevated above the lateral surface of the valve. The right valve of *M. magnum* n.sp. is slightly extended upwards and then descends to the lower part where at once it forms an apical whorl, whereas in *M. kozlowskii* n.sp. the right valve is only slightly elevated, but strongly coiled to the left at an angle of 90° and only from this place it coils forming an apical whorl.

Occurrence.—Poland: Dobrut near Radom; Upper Oxfordian (Astartian).

Macrodiceras magnum n.sp.

(Pl. XVIII)

Holotype: Pl. XVIII; IG 1166.II/776.

Type horizon: Upper Oxfordian (Astartian).

Type locality: Dobrut near Radom.

Derivation of the name: Lat. *magnum* = large; after large dimensions of the shell.

Material.—A single, very well-preserved shell.

Dimensions (in mm):

IG 1166.II/776—l. s. 125—b. s. 150

Diagnosis.—Shell very large, exceeding in size all species of the genus *Macrodiceras* n.gen. known so far. Wide growth bands are visible on the outer surface of both valves. A small, uneven attachment area occurs on the beak of the right valve. The left valve is also fairly large and, in addition to growth bands, two keels are visible on its surface dividing it into three parts.

Description.—Shell very large, massive, thick-valved, asymmetric, although its left valve is not transformed into a lid. The right valve is considerably extended upwards, then twisted forwards and the beak itself is slightly upturned posteriorly. The beak of the right valve is

truncated by a small and uneven attachment area. The outer surface of the right valve is covered with wide growth bands clearly marked from the center of the valve to the margin contacting the left valve. It is from this margin that two distinct keels run which divide the valve into three parts. Two relatively deep ligament grooves run from the hinge margin to the beak. The left valve is closely connected with the right one. Its strongly coiled beak contacts the lateral surface of the valve. Two sharp keels, dividing the surface of each valve into anterior, central and posterior parts, run from the beaks. This character was never recorded in other species of *Macrodiceras* n.gen. Both valves contact each other, in the anterior part of the shell, at an angle of 70° .

Remarks. — The holotype is a complete, well-preserved shell and, although it has been impossible to describe hinges and muscle scars, its external characters enabled its separation from all known species of *Macrodiceras* n.gen. These characters are primarily large dimensions of the shell and two distinct keels running over the surface of each valve. In these characters, this species fundamentally differs from *M. kozłowskii* n.sp., *M. balaklavense* (Pčelincev) and others.

Occurrence. — Poland: Dobrut near Radom; Upper Oxfordian (Astartian).

Macrodiceras pcelincevi n.sp.

(Pls. XX, XXI)

Holotype: Pl. XXI, Fig. 1 a-b; IG 1166.II/777.

Type horizon: Upper Oxfordian (Astartian).

Type locality: Dobrut near Radom.

Derivation of the name: *pcelincevi* — after the name of Prof. V. F. Pčelincev, a well-known Soviet specialist of Mesozoic pelecypods and gastropods.

Material. — Ten specimens (right valves).

Dimensions (in mm):

IG 1166.II/	777	778
l. r. v.	115	102

Diagnosis. — Valves large, massive, extended upwards and then coiled far to the left and posteriorly, forming an apical whorl. A concave attachment area is marked on this whorl. Hinge plate strongly developed, with large cardinal tooth 3. Posterior muscle scar mounted on high myophore, anterior in the form of depression.

Description. — Right valves large, with thick, massive walls and with

growth bands of variable width, clearly marked on the outer surface. The entire surface of the valve is very irregularly folded. The keel, dividing the surface of the valve into two parts, is very indistinct, oval and completely disappearing in the region of the aperture. Valves are strongly elongate, coiled far to the left and posteriorly, forming a small apical whorl which is truncated by a slightly convex attachment area. Hinge consists of cardinal tooth 3, situated in the posterior part of the hinge margin, very small tooth 1 and dental socket 2'. Muscle scars less strongly developed than those in other species of this genus, the posterior one being mounted on a relatively high myophore, running from the apertural margin below the hinge plate to the inside of the valve and anterior constituting an elongate depression, situated in the anterior region below the hinge margin. Two ligament grooves one deeper and the other less strongly outlined, are running spirally from the posterior part of the hinge margin up to the beak of the valve.

Remarks. — Despite the lack of the left valves, owing to a very characteristic development of the right valves shaped like an inverted C, a feature unknown in other species of the genera *Macrodiceras* n.gen. and *Diceras* Lamarck, a new species could be erected on the basis of the material described above. In addition, a varying width of growth bands and a very indistinct keel disappearing on the surface are also peculiar characters. *M. pcelincevi* n.sp. is most closely related to *M. magnum* n.sp. The right valve of both these species is strongly extended upwards and to the left. However, there is also a fundamental difference in the structure of their right valves. In *M. magnum* n.sp., an apical whorl is formed just above the elevation, whereas in *M. pcelincevi* n.sp. the valve is strongly coiled to the left and then posteriorly, forming, in the posterior part, an apical whorl. In addition, in *M. magnum* n.sp. two distinct keels occur on each valve dividing them into three parts, and in *M. pcelincevi* n.sp. there is only one (indistinct) keel dividing the right valve into two parts. Moreover the right valve of *M. magnum* n.sp. is almost twice as large as that of *M. pcelincevi*.

Occurrence. — Poland: Dobrut near Radom; Upper Oxfordian (Astartian).

Macrodiceras polonicum n.sp.

(Pl. XXII)

Holotype: Pl. XXII, Fig. 1a-b; IG 1166.II/787.

Type horizon: Upper Oxfordian (Astartian),

Type locality: Dobrut near Radom.

Derivation of the name: *polonicum* — so far recorded only in Poland.

Material. — Two fairly well-preserved specimens whose hinge plates and muscle scars are, however, damaged.

Dimensions (in mm):

IG 1166.II/787—1, r. v. 125

Diagnosis. — Valves very large, massive, the right ones strongly twisted to the left and somewhat upwards, with a small apical whorl. Outer surface even, covered with wide growth bands. The valve is divided into two parts by a single keel. Hinge plate and muscle scars strongly developed.

Description. — Right valve very large, with thick, massive walls and strongly extended aperture showing that the soft parts of the pelecypod were probably fairly large. Right from the aperture, the valve is strongly twisted to the left, then somewhat posteriorly and upwards, forming a small apical whorl. Outer surface covered with even, wide growth bands, obliterated in the apical region. A keel, dividing the valve into two parts, is oval and runs from the anterior part of apertural margin to the beak. Hinge of the right valve consists of a very strong, falciform cardinal tooth 3, which does not project above the hinge plate, a relatively large anterior lateral tooth 1 and a very large dental socket 2', which suggests that anterior lateral tooth 2 of the left valve was probably fairly large. Posterior muscle scar is very massive, mounted on a high and wide myophore running deep to the inside of the valve up to the apical region. Anterior muscle scar makes up a very long and relatively wide depression running far under the hinge plate. In the anterior part of the hinge plate, the depression of the anterior muscle scar forms a characteristic extension which, as the muscle scar extends to the inside of the valve, becomes progressively shallower and narrower. Ligament grooves are shallow, widely spaced, becoming shallower and then completely disappearing in the apical region of the valve.

The left valve is massive, with wide growth bands and beak slightly projecting above the lateral surface. A keel, dividing the valve into two parts, is very distinct over the entire length.

Remarks. — A characteristic structure of the right valve with its very massive hinge plate and excellently developed muscle scars, conspicuously differs this form from other, so far known, species of *Macrodiceras* n.gen. Some of its characters are in common with *M. magnum* n.sp. and *M. spirale* n.sp., from which *M. polonicum* n.sp. differs, however, in the manner of coiling of the valves, structure and position of hinges, dimensions of shells (or single valves) and development of attachment areas. Different also are the number and development of keels, which divide the valve into two or three parts.

Occurrence. — Poland: Dobrut near Radom. Upper Oxfordian (Astartian).

Macrodiceras rotundatum (Bayle, 1873)

(Pl. XIII, Fig. 1)

1941. *Diceras rotundatum* Bayle; C. Dechaseaux, Rudistae..., p. 14, Pl. 1, Figs. 3, 8, 9.*Material.* — Over 50 well-preserved right and left valves.*Dimensions* (in mm):

IG 1166.II/790 — 1. r. v. 80

Description. — Right valve elongate and, halfway its length, coiled at an angle of 90° or slightly more to the left and afterwards, with its beak only, posteriorly. Hinge consists of cardinal tooth 3, which is relatively small and slightly shifted posteriorly. Dental socket 2' strongly elongate anteriorly. First anterior lateral tooth 1 is slightly outlined in the lower part of dental socket 2'. Muscle scars slightly marked, posterior one on a not very high myophore, running to the margin of the lower part of aperture, anterior in the form of a longitudinal depression at the base of the anterior part of hinge. Growth bands clearly visible on the outer surface of the valve. A keel, diagonally running from the beak to the apertural margin, divides the valve into two parts.

Left valve almost helically coiled in the form of an ascending spiral. Lateral walls of whorls do not contact each other. Hinge consists of anterior lateral tooth 2 and dental socket 3' which was entered by cardinal tooth 3 of the right valve. Both tooth 2 and dental socket 3' are excellently preserved in most valves. Tooth 2 strongly inclined anteriorly, massive, strongly mounted. Dental socket 1' is outlined on its surface in the form of a slight depression. Dental socket 3' forms an arcuate, elongate depression which posteriorly surrounds tooth 2. A very distinct ligament groove runs semicircularly over the hinge margin. Muscle scars clearly marked, the posterior one on a high myophore reaching under the hinge plate, the anterior in the form of a small depression which joins the base of tooth 2. Outer surface of the valve covered with distinct growth bands running from the lower margin up to the beak. The valve is divided into two parts by a keel clearly marked in the apical region.

Variability. — *M. rotundatum* does not display any major variability, except for a small deviation in the development of muscle scars, particularly posterior ones.

Remarks. — *M. rotundatum* is to the greatest extent similar to *M. polonicum* n.sp. from which it differs, however, in dimensions and outline of the spire axis of the right valve. In *M. rotundatum* the spire axis is more elevated than in *M. polonicum* n.sp. The right and left valves have projecting beaks twisted laterally. The determination of *M. rotundatum* was based entirely on Dechaseaux's (1941) data. This author presented photographs of some specimens of Bayle, which were determined by him in the collection of École des Mines in Paris as *Diceras rotundatum*, but

which were never described or illustrated by him. On the basis of the spire axis and fairly large dimensions, this species has been assigned by the present author to the genus *Macrodiceras* n.gen. In addition, the ratio of the size of the right to that of the left valve was a decisive factor of such assignment.

Occurrence.—Poland: Dobrut near Radom, Sulejów on the Pilica; Upper Oxfordian (Astartian). France: Sequanian.

Macrodiceras spirale n.sp.
(Pl. XIX; Pl. XXIX, Fig. 4)

Holotype: Pl. XIX, Fig. 1 a-b; IG 1166.II/840.

Type horizon: Upper Oxfordian (Astartian).

Type locality: Dobrut near Radom.

Derivation of the name: *spirale*—after a strongly coiled right valve.

Material.—Four well-preserved specimens.

Dimensions (in mm):

IG 1166.II/840—l. r. v. 95

Diagnosis.—Right valves massive, strongly coiled spirally, with a very large attachment area on the beak. Hinge margin narrow, shifted posteriorly. Muscle scars and ligament grooves well-developed. Left valves flat, small.

Description.—Right valve large, massive, thick-walled, strongly coiled spirally. This coiling shortens the entire valve and gives it a circular shape (as viewed from the beak). Beak and part of whorl truncated by a large, concave attachment area, on which the first whorls are clearly marked. Valve covered with growth bands which are distinct over almost entire length. A keel running from the margin of the attachment area to the outer margin which contacts the left valve, divides the valve into two parts. Hinge plate very narrow, slightly shifted outwards and far to the posterior part. A middle-sized cardinal tooth 3, a well-developed first anterior lateral tooth 1 and a relatively strongly extended dental socket 2' are marked on the hinge plate. Two deep ligament grooves, running spirally up to the beak of valve, originate from the posterior and upper part of the hinge margin. Muscle scars well-developed. Posterior scar mounted on a high myophore, occurs on the wall of the valve nearer the hinge margin and runs far to the inside under the hinge plate up to the beak of the valve. Anterior scar slightly damaged, but it may be seen that it forms a slight depression in the lower anterior part of the hinge margin. Outer margin of the valve damaged. The left valve slightly flattened, smaller than the right, in its structure and shape only slightly differs from the left valves of other species of this genus. Hinge plate damaged. Posterior muscle scar strongly developed.

Remarks. — A specimen of the right valve has been chosen for a holotype. Its characteristic, spiral, almost circular coiling, so far unknown within the genus *Macrodiceras* n.gen., its unusually large attachment area and a narrow hinge margin, strongly shifted posteriorly, were decisive as to its specific separateness. The right valve of *M. spirale* n.sp. has a spire axis similar to those of the genus *Diceras* Lamarck. This is a single of this kind within the genus *Macrodiceras* n.gen.

Occurrence. — Poland: Dobrut near Radom; Upper Oxfordian (Astartian).

Family **Plesiodiceratidae** Pčelincev, 1959

Diagnosis. — Small, inequivalved and inequilateral shells attached to the substratum with the beak of the left, larger valve. The right valve gradually takes the form of a lid. Beaks moderately incurved. Cardinal tooth 3 predominates over other elements of the hinge in the right valve and corresponding dental socket 3' — in the left valve. Posterior muscle scars situated directly on the inner wall of valves. Anterior muscle scars mostly elevated up to the level of the hinge plate. Two genera of this family: *Eodiceras* Pčelincev and *Plesiodiceras* Munier-Chalmas occur in the Upper Jurassic of the Holy Cross Mountains.

Genus *Eodiceras* Pčelincev, 1959

Type species: *Diceras ursicinum* Thurmann, 1859.

Species assigned: *Eodiceras eximium* (Bayle), *E. planum* n.sp., *E. subeximium* n.sp., *Eodiceras* sp.

Stratigraphic and geographical range: Poland: Upper Oxfordian, Holy Cross Mountains. France: Rauracian, Sequanian, Kimmeridgian. U.S.S.R. (the Crimea): Sequanian.

Diagnosis. — Shells small, conspicuously inequivalved and inequilateral, with convex valves, the left valve being larger. Beaks of both valves moderately coiled. An attachment area varying in size occurs on the beak of the left valve. Hinge of the right valve consists of cardinal tooth 3 triangular in outline and a poorly developed first anterior lateral tooth 1. An arcuate dental socket for tooth 2 of the left valve is visible between these teeth. Anterior lateral tooth 2, large, elongate and triangular in outline, occurs in the hinge of the left valve. In its lower part, it has a small depression, which serves as a socket for tooth 1 of the right valve. Tooth 2, as usually, elevated parallel to the apertural plane of the valve. An arcuate, deep socket for the cardinal tooth is situated posteriorly and, partly, above tooth 2. Muscle scars are situated directly on the outer surface of valves. The posterior one, sometimes pressed into

the wall of valve, is elongate and internally separated by a roller which reaches under the hinge plate. The anterior, less depressed, is oval in outline.

Remarks. — The correctness of the separation of the genus *Eodicerias* by Pčelincev (1959) has also been confirmed by the studies on the Rudistae from the Holy Cross Jurassic. The observation of the development of hinge plate in a series of specimens, both the left and right valves, has indicated that particular elements of hinges in both valves were developed in a specific manner quite different from the development of hinges in the genus *Dicerias* Lamarck. In addition, *Eodicerias* differs from *Dicerias* as being attached with the left valve.

Eodicerias eximium (Bayle, 1873)
(Pl. XXIII, Figs. 1—13; Pl. XXVIII, Fig. 4 a-b)

1873. *Dicerias eximium* Bayle; Observation..., p. 154, Pl. 18, Figs. 4—6.
1893. *Dicerias eximium* Bayle; P. Loriol, Description..., p. 101, Pl. 7, Figs. 12—15.
1941. *Dicerias eximium* Bayle; C. Dechaseaux, Rudistae..., p. 23, Pl. 1, Figs. 5—6.
1959. *Eodicerias eximium* (Bayle); V. F. Pčelincev, Rudisty mezozoja..., p. 40, Pl. 1, Fig. 1 a, b; Text-fig. 7.

Material. — Over 250 well-preserved specimens, including 50 complete shells.

Dimensions (in mm):

IG 1166.II/	851	852	853	854	855	856	857	858	859	860	861	862	863
l. r. v.	8	13	18	21	22	33	45	—	—	—	—	—	—
l. l. v.	—	—	—	—	—	—	—	10	13	17	22	33	55

Description. — Shells small, convex, inequivalved. The left, larger valve sometimes has on its beak an attachment area. Growth bands, overlapping each other, occur on the lateral surface of valves of some shells.

Growth stages of the right valve. The hinge plate of the smallest valve still lacks many elements. Dental socket 2' and cardinal tooth 3 are only slightly outlined, first anterior lateral tooth 1, muscle scars and ligament grooves are still absent. Beak is completely fused with the lateral surface of valve. A well-developed cardinal tooth 3 appears with the growth in larger valves. At the same time, dental socket 2' becomes in these valves progressively deeper and both muscle scars appear. In some cases, the latter are shifted to the level of hinge plate. With growth, the valve becomes more convex and its beak gradually detaches from the

lateral surface strongly coiling towards the anterior part of the shell. Ligament grooves, which in adult individuals bifurcate in the region of hinges, become deeper and elongate.

Growth stages of the left valve. In the smallest individual, the hinge has an already clearly outlined dental socket 3' and anterior lateral tooth 2. Tooth 2 terminates anteriorly in a small swelling. Muscle scars lacking. An outline of the beak, slightly coiled anteriorly and still completely fused with valve surface, is visible on the outer part of the valve. Attachment area lacking. A distinct keel, dividing the valve into two unequal parts, runs from the beak to the lower margin of the valve. With the growth, first the anterior and then posterior muscle scars, which sometimes pass under the hinge plate, appear in larger valves. Hinge moves slightly to the posterior part of the valve and tooth 2 upturns outwards. The beak with the attachment area, most clearly visible on the largest valves, develop with the growth of the valve. The keel, dividing the valve into two parts, becomes, in the apertural region, more oval and an outline of narrow, growth bands appears on the surface of the valve. Ligament grooves appear in the form of narrow depressions in the region of hinge and, in adult individuals, reach almost as far as the beak.

Variability. — Both the left and the right valves are variably convex and display a varying degree of coiling (in particular the left ones). This is probably related with the manner of attaching to the substratum, which is also indicated by varying shapes and dimensions of attachment areas. In adult specimens, a differentiation is also displayed by ligament grooves and muscle scars, particularly the posterior ones.

Remarks. — *Eodiceras eximium* (Bayle), previously assigned to the genus *Diceras* Lamarck, is primarily characterized by cardinal tooth 3, elongated parallel to the hinge margin and by a strongly elongate anterior lateral tooth 2 of the left valve. These two main hinge elements and differently developed muscle scars make up fundamental differences between this species and all other species of the genus *Diceras*. These differences attracted attention of Bayle, who erected this species and called it "*eximium*", i.e. extraordinary.

Occurrence. — Poland: Kodrąb near Radomsko, Sulejów on the Pilica, Błaziny near Ilza, Żerniki and Jacłów Karsznicki near Chęciny; Upper Oxfordian (Astartian). France: Rauracian, Sequanian. Switzerland: Sequanian. U.S.S.R. (the Crimea): Sequanian.

Eodiceras planum n.sp.

(Pl. XXIII, Figs. 14—18a; Pl. XXVIII, Figs. 2—3)

Holotype: Pl. XXIII, Fig. 18 a-b; IG 1166.II/1105.

Type horizon: Upper Oxfordian (Astartian).

Type locality: Sulejów on the Pilica.

Derivation of the name: Lat. *planum* = flat; after a large, flat attachment area.

Material.—About 50 well-preserved specimens, including one shell.

Dimensions (in mm):

IG 1166.II/	1101	1102	1103	1104	1105
l. l. v.	10	18	23	26	39

Diagnosis.—Shells small, inequivalved. The left, larger valve has a very large attachment area, occupying 2/3 of the valve length. The attachment area makes up a level plane which truncates the apical part of the left valve almost to a half of its height. A large attachment area is observed even in the youngest individuals. Dental socket 3' and anterior lateral tooth 2 are clearly marked on hinge plate of the left valve and a well-developed cardinal tooth 3 and dental socket 2'—on hinge plate of the right valve. Muscle scars moderately developed on both valves.

Growth stages of the right valve. The smallest right valve is closely connected with the left one and hence there was no possibility to examine the structure of the hinges. This valve is slightly convex and considerably smaller than the left one. A very clear outline of the beak occurs on the outer surface, which otherwise is completely smooth. In a slightly larger valve, only the hinge margin is preserved. A large, strongly falciform cardinal tooth 3 and dental socket 2', which was entered by anterior lateral tooth 2 of the left valve, occur the hinge margin. Two ligament grooves run over cardinal tooth 3.

Growth stages of the left valve. The smallest valve is strongly connected with the right valve. Its beak is already truncated by a relatively large attachment area, which occupies 1/3 of the length of valve. Valve surface smooth, with two still short ligament grooves, which are visible in apical region, near the place of contact with the right valve. The attachment area considerably increases with the growth and, in the largest specimen, truncates the apical part of valve down to almost a half of its height. Ligament grooves considerably extend and deepen. The keel, dividing the surface into two parts and which in the smallest valve is yet indistinct, with the growth of valve becomes sharper and sharper. The attachment area extends and its main elements such as anterior lateral tooth 2 and dental socket 3', change their positions in relation to each other. Tooth 2, initially growing in the same plane as dental socket 3', with the growth of valve begins to project above dental socket 3', which—also with the growth of valve—deepens and shifts slightly posteriorly. The posterior muscle scar is marked, at first in the smallest

valve, in the form of a thin, roller-like swelling, which, with the growth, takes—in larger valves—a shape of a sharp keel running obliquely from the outer margin of the valve to its inside in the apical region. The anterior muscle scar, with the growth of the valve, shifts, in the form of an elongate depression, almost to the level of hinge plate.

Variability.—Adult individuals display a certain variability in the development of the beak of the left valve, which sometimes happens to be more or less uncoiled. The attachment area of the left valve is, in all cases, very large, but may take various shapes from elliptic to subround. In addition, it may be also concave.

Remarks.—*E. planum* n.sp. markedly differs from the remaining species of *Eodiceras* primarily in a large, flat attachment area, whose development was traced on the series of specimens described above. In addition, all species of the genus *Eodiceras* known so far have left valves relatively extended, whereas in *E. planum* n.sp. the left valve is strongly shortened as a result of it being truncated by the attachment area. Differences between species of the genus *Eodiceras* Pčelincev known so far and the species *E. planum* n.sp. are also recorded in the structure of hinges. An atrophy of anterior lateral tooth 1 is marked in the hinge of the right and left valves of the new species. Dimensions and structure of hinges, as well as the manner of attaching to the substratum with the left valve are characters which indicate the soundness of assigning the new species to *Eodiceras* Pčelincev.

Occurrence.—Poland: Sulejów on the Pilica; Upper Oxfordian (Astartian).

Eodiceras subeximium n.sp.

(Pl. XXIV, Fig. 4)

Holotype: Pl. XXIV, Fig. 4 a-b; IG 1166.II/1148.

Type horizon: Upper Oxfordian (Astartian).

Type locality: Kodrań near Radomsko.

Derivation of the name: Lat. *subeximium* = similar to *E. eximium*.

Material.—Ten specimens, including one complete shell.

Dimensions (in mm):

IG 1166.II/1148	l. s. 55	b. s. 67
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Diagnosis.—Shell middle-sized, bulgy, inequivalved. The left valve larger than the right. A distinct, large attachment area occurs on the beak of the left valve.

Description. — Shell middle-sized, strongly convex, inequivalved. The left valve larger than the right. The beak of the right valve coiled anteriorly and adhering to the lateral surface of the valve. The beak of the left valve coiled to the left, i.e. in the opposite direction than the beak of the right valve. The apex of the left valve is not uncoiled and the whorls adhere to each other. A relatively large, concave attachment area occupies the highermost parts of the left valve and a considerable part of the spire itself. Keels, dividing the outer surface of both valves into two, almost equal parts, run over the entire length of the valves from the beak to the anterior aperture. These keels are more sharply outlined in the apical region of both valves. Both valves are in principle smooth, except for narrow growth bands visible here and there in their surfaces. The hinge is in both valves identical with that of *E. eximium* (Bayle). Similar is also the development of muscle scars and ligament grooves.

Remarks. — The new species is to the greatest extent similar to *E. eximium*. Both have a similar structure of the hinge plate and muscle scars. The new species is, however, nearly twice as large as *E. eximium* and has a distinct connection of the beak of the left valve with its lateral surface, which was never recorded in *E. eximium*. In addition, a large, concave attachment area occurs on the beak of the left valve in *E. subeximium*, whereas no such area or, at most, very small one is recorded in *E. eximium*.

Occurrence. — Poland: Kodrąb near Radomsko; Upper Oxfordian (Astartian).

Eodiceras sp.

(Pl. XXIV, Figs. 1a-3)

Material. — About 90 specimens.

Dimensions (in mm):

IG1166.II/	1158	1159	1160
l. s.	30	33	38
b. s.	28	35	40

Description. — Shells small, inequivalved, partly damaged or occurring in the form of cores. Depressions, stretching almost over the entire length of whorls, are visible on the cores. These are traces of muscle scars. Shells are mostly deformed or with broken-off beaks of one of the valves. The external shape of both the shells and cores does

not, however, arouse any doubt as to their belonging to the genus *Eodicer* Pčelincev. This fact is indicated by the left valve which is larger than the right and by the manner of coiling of the beaks. A keel, which folds the valves at an angle of 90° and which is more clearly marked on the right valve, runs on the outer surface of the right and left valve.

Remarks. — Because of a poor state of preservation of the shells and for lack of single valves with hinges, this material could not be specifically determined.

Occurrence. — Poland: Błaziny, Iiża, Sulejów on the Pilica, Kodrąb near Radomsko, Bukowa; Upper Oxfordian (Astartian).

Genus *Plesiodiceras* Munier-Chalmas, 1882

Type species: *Diceras valfinense* Boehm, 1882.

Species assigned: *Plesiodiceras muensteri* (Goldfuss, 1882), *P. orthogonale* Pčelincev, 1959, *P. sulejoviense* n.sp., *P. yailense* Pčelincev, 1959.

Stratigraphic and geographical range: Upper Oxfordian: Poland, France, Switzerland, U.S.S.R. (the Crimea); Upper Oxfordian and Kimmeridgian: Germany.

Diagnosis. — Shells small, inequivalved and inequilateral, attached to the substratum with the left, larger valve. The right, smaller valve formed a lid of the shell. A spiral beak of the right valve closely adheres to its surface. Anterior lateral tooth 2 and, above it in the posterior part, a deep, triangularly outlined dental socket, reaching far below the hinge margin, occur in the left valve. Cardinal tooth 3 with its outline extended upwards and slightly wider at the base, is the most important element of the hinge of the right valve. A dental socket occurs below, in the anterior part of the cardinal tooth. Tooth 1 (the first anterior lateral tooth 1) is situated below dental socket 2. The anterior muscle scar is slightly concave in the middle and the posterior muscle scar is very large, massive and directly connected with the hinge plate, which — together with muscle scars — occupies, in the right valve, 2/3 of the inner surface. Ligament groove runs, in the form of a narrow furrow, obliquely from the beaks of valves to the hinge part.

Remarks. — Separating the group *Plesiodiceras* (which has now been raised to the rank of genus), Munier-Chalmas (1882) attracted attention to a main character which differed this group from the species of the genus *Diceras* sensu stricto, i.e. the posterior muscle scar directly connected with the hinge plate. Pčelincev (1959) believes that many other characters differ this genus from others.

According to him, these are a considerable difference in dimensions of both valves, a different degree of coiling of both valves and significant differences in the structure of hinges.

Plesiodiceras muensteri (Goldfuss, 1839-40)

(Pl. XXV, Fig. 11)

- 1839-40. *Chama Münsteri* Goldfuss; A. Goldfuss, *Petrefacta...*, p. 204, Pl. 138, Fig. 7 a, b.
1882. *Diceras Münsteri* Goldfuss; G. Boehm, *Die Fauna...*, p. 159, Pl. 25(9), Fig. 7 a, b.
1882. *Plesiodiceras valfinense* Munier-Chalmas; M. Munier-Chalmas, *Études critiques...*, p. 478.
1888. *Diceras (Plesiodiceras) Valfinense* Boehm; P. Loriol, *Études...*, p. 258, Pl. 28, Figs. 5—11.
1927. *Diceras (Plesiodiceras) valfinense* Boehm; V. F. Pčelincev, *Fauna jury...*, p. 82.
1941. *Heterodiceras (Plesiodiceras) münsteri* Goldfuss; C. Dechaseaux, *Rudistae...*, p. 35, Pl. 4, Figs. 1,1a, 2(?), 3—10, 13—14.
1959. *Plesiodiceras subvalfinense* Pčelincev; V. P. Pčelincev; *Rudisty mezozoja...*, p. 47, Pl. 1, non Figs. 3—8.

Material. — Three specimens (left valves).

Dimensions (in mm.):

IG 1166.II/1246	l. l. v. 28	b. l. v. 20
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Description. — Shells small, very inequivalved. The left valve larger than the right, massive, with smooth walls, strongly convex, with beak coiled anteriorly. Beak not connected with the lateral surface of valve. The right valve flat, with beak completely fused with the lateral surface. Hinge large, occupying the best part of the aperture of both valves. Cardinal tooth 3 of the right valve short, massive, wide at the base. The remaining hinge elements (dental sockets and secondary teeth) make up a very massive hinge plate. The aperture of the left valve is strongly decreased by its unusually thick walls, which is one of the most important characters of this species. The outer surface of the valve is covered with distinct, narrow growth bands. The beak of the valve is coiled anteriorly, but it is not ingrown in its lateral surface. A distinct and relatively sharp keel, dividing the surface of the valve into two parts, runs from the beak to the center of the valve, losing its clear-cut outline in the lower part of the valve, which becomes more oval at this point. A distinct attachment area probably occupied the part which surrounds a clearly visible, sharp keel.

A long and slightly incurved dental socket 3' is marked in the hinge of the left valve. Its curvature is in line with the direction of the spire of the valve. The remaining hinge elements are damaged. A distinct ligament groove runs above dental socket 3'. Muscle scars, in part damaged, occupied much space in the valve.

Remarks. — Despite the fact that the valves of *P. muensteri* from the Upper Jurassic of the Holy Cross Mountains were partly damaged,

it was not very difficult to determine them. Their external morphology, hinges and thickness of walls with a very small aperture, indicating a small capacity of the part of the valve, which contained the pelecypod's body, are characters decisive as to their specific assignment. This species was variously interpreted by several authors. Most forms, determined by Lorient (1888) as *Diceras (Plesiodiceras) valfinense*, are undoubtedly identical with *Chama muensteri* Goldfuss. In 1882, Boehm maintained that there were differences between *Diceras valfinense* and *D. muensteri*, but later, in the light of new studies, it turned out that these differences might be reduced to the intraspecific variability. The standpoint of Dechaseaux (1941), who places *D. valfinense* in the synonymy of *Plesiodiceras muensteri*, seems therefore to be correct. Upon this assumption, we may state that most forms of *P. subvalfinense* Pčelincev display differences which may be placed within limits of the intraspecific variability of *P. muensteri*.

Occurrence. — Poland: Dobrut near Radom; Upper Oxfordian (Astartian). Germany: Upper Jurassic. France: Sequanian. U.S.S.R. (the Crimea): Rauracian.

Plesiodiceras orthogonale Pčelincev, 1959

(Pl. XXV, Fig. 12)

1959. *Plesiodiceras orthogonale* Pčelincev; V. F. Pčelincev, Rudisty mezozoja..., p. 50, Pl. 2, Figs. 1 a, b, 2-3; Text-fig. 14.

Material. — Six specimens (shells).

Dimensions (in mm.):

IG 1166.II/1249	l. s. 32	b. s. 25
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Description. — Shells small, conspicuously inequivalved, convex on the side of the left valve. The left, larger valve in the form of a tapering horn. Its beak is coiled anteriorly and, subsequently, towards the inside of the shell. An attachment area occurs on the apical part. A distinct keel, sharp in the apical part and somewhat milder in the contact area of two valves, runs through the center of the left valve over its entire length, dividing it in halves. Not very distinct growth bands, more closely spaced in the apical region, occur on outer surface. The right valve flat, with its beak not projecting above its surface. Despite the damaged surface of this valve, a distinct, sharp keel completely shifted towards the posterior margin, may be distinguished on it. This keel folds the valve in this place at an angle of 90° and divides it into two, markedly unequal parts, which gives the impression of a certain convexity in the posterior part of

the valve. The right valve served as a lid, which covered the pelecypod's body.

Remarks. — Since all shells were shut tight and the valves could not be mechanically separated, it was impossible to describe the structure of hinges and muscle scars. A similar material was worked out by Pčelincev (1959) and this was the reason why no descriptions of the internal elements of shells were given by this author. Comparing this species with *P. subvalfinense* and *P. uzuntashi*, Pčelincev (1959) finds only slight morphological differences between them. Unfortunately, it is only on the basis of the external morphology that he establishes all new species within the genus *Plesiodiceras*, which is insufficient. In the case of *P. orthogonale* such observations were unfortunately impossible. In regard to the external morphology the specimens from the Holy Cross Mountains are in complete conformity with the holotype of Pčelincev.

Occurrence. — Poland: Sulejów on the Pilica, Kodrąb near Radomsko; Upper Oxfordian (Astartian). U.S.S.R. (the Crimea): Rauracian.

Plesiodiceras sulejoviense n.sp.

(Pl. XXV, Fig. 14)

Holotype: Pl. XXV, Fig. 14 a-c; IG 1166.II/1255.

Type horizon: Upper Oxfordian (Astartian).

Type locality: Sulejów on the Pilica.

Derivation of the name: *sulejoviense* — after the locality Sulejów.

Material. — Four well-preserved specimens (shells and valves).

Dimensions (in mm):

IG 1166.II/1255	l. s. 37	b. . 28
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Diagnosis. — Shells small, markedly inequivalved. The left, larger valve is more convex, with its beak coiled outwards. Attachment area indistinct. The right valve strongly flattened, round in outline, with its beak completely fused with the lateral surface. Large cardinal tooth 3 in the right valve and corresponding dental socket 3' in the left valve, together with secondary teeth and corresponding dental sockets of both valves, are the main elements of the hinge. Muscle scars and hinges occupy 4/5 of the interior surface of the right valve. In the left valve, muscle scars form depressions. Ligament grooves distinct.

Description. — Right valve smaller than the left, flatter, round, with a small beak completely fused with the lateral surface of the valve. A long, strong cardinal tooth 3, strongly projecting outside the hinge margin, occurs in the hinge of the right valve. Below it a distinct dental

socket 2', entered by conical tooth 2 of the left valve, occurs in the anterior part of the valve. Muscle scars strongly developed. The posterior muscle scar unites with the hinge plate and occupies nearly a half of the interior surface. It is elevated to the level of the posterior margin of the valve. The anterior, smaller muscle scar, slightly concave in the middle, unites with the base of the hinge plate. The concavity in which the upper part of the pelecypod's body was contained, is very small, elongate and sunken below the swelling of the posterior muscle scar.

The left valve is very convex, with its beak coiled anteriorly and, subsequently, towards the outer side of the valve. Surface covered with distinct growth bands. The hinge is slightly damaged, but an outline of the upper part of dental socket 3' and conical tooth 2 are clearly visible. The posterior muscle scar, slightly elevated, makes up a mild concavity separated by sharp roller from the depression of the valve, in which the pelecypod's body was contained. The anterior muscle scar has the form of a slight swelling of the wall just below tooth 2. Ligament grooves in both valves run in the form of narrow depressions from the hinge margin up to the beaks.

Remarks. — Muscle scars and some hinge elements of the right valve are the most characteristic features in which *P. sulejoviense* n.sp. differs from other species of the genus *Plesiodiceras*. Hinge plate and muscle scars occupy more than 4/5 of the interior of the right valve, which is a feature unknown in other species described so far. In addition, dental socket 2' in the right valve of the known species is more or less elongate, whereas in *P. sulejoviense* n.sp. it is round and depressed in the form of a cone. The shape of the left valve, its hinge elements and muscle scars are similar to those in other species of the genus *Plesiodiceras*, such as *P. muensteri* (Goldfuss) or *P. yailense* Pčelincev. Tooth 2 in the left valve of *P. sulejoviense* n.sp. is somewhat differently developed. It has the form of a cone, whereas in other species compared tooth 2 takes the shape of a sharp, elongate slat.

Occurrence. — Poland: Sulejów on the Pilica; Upper Oxfordian (Astartian).

Plesiodiceras yailense Pčelincev, 1959

(Pl. XXV, Figs. 1-10)

1959. *Plesiodiceras yailense* Pčelincev; V. F. Pčelincev, Rudisty mezozoja..., p. 52, Pl. 2, Figs. 4a, b.

Material. — Over 100 well-preserved specimens, including a series of the right and left valves, as well as complete shells.

Dimensions (in mm):

IG 1166.II/	1259	1260	1261	1262	1263	1264	1265	1266	1267	1268
l. r. v.	9	12	14	17	20	—	—	—	—	—
l. l. v.	—	—	—	—	—	12	15	16	18	30

Description. — Shells small, inequivalved. The right, smaller valve is flat, with its beak completely fused with the lateral surface of the valve. The left, larger valve is strongly convex, with a clearly visible keel running from the beak to the apertural margin. Growth bands are clearly marked on the outer surface of the valve.

Growth stages of the right valve. The anterior margin of the smallest specimen is slightly damaged. Hinge and the remaining parts of the valve are well-preserved. Triangular cardinal tooth 3 is marked in the hinge. Dental socket 2', still very indistinct, may be discerned at its base in the anterior part. Tooth 1 very indistinct, almost indiscernible. Ligament grooves invisible. Muscle scars already developed. The posterior muscle scar, considerably elevated, directly connected with hinge plate at an almost right angle. The anterior muscle scar in the form of a small swelling. With the growth, cardinal tooth 3 elongates, taking a slightly oblique position in relation to the plane of the hinge margin and, in the largest valve, it projects far outside the hinge margin. Tooth 1 and dental socket 2', the latter markedly separating teeth 3 and 1, are developed and shaped with the growth of the valve. Ligament grooves, at first still slight, become more and more distinct. As the right valve grows, muscle scars widen and rise to the level of the hinge plate. In the largest valve, they occupy a relatively extensive area and, consequently, the space, in which the pelecypod's body was contained, took a form of a narrow, elongate depression (Pl. XXV, Fig. 5 a). With the farther growth, the outer surface covers with concentric growth bands and the beak shifts considerably to the anterior part and closely adheres to the lateral surface of the valve.

Growth stages of the left valve. In the smallest specimen with a slightly damaged hinge, the dental socket 3' is marked irregularly. Tooth 2 very indistinct. Muscle scars poorly visible. Outer surface smooth with an already developed apical part. Since there are no traces of an attachment area on the beak, we may conclude that this valve was not yet attached to the substratum. Beak connected with outer surface. Dental socket 3' considerably deepens and dental socket 1' becomes fairly distinct with the growth of larger valves. Tooth 2 shifts far anteriorly, rising at the same time high above dental socket 3'. In the largest valve, hinge plate occupies nearly 1/3 of the interior surface. Muscle scars form slightly sunken swellings, the anterior one smaller and posterior larger, which, in the largest valve, make up a slight elevation connected in part

with the base of hinge plate. As the muscle scars rise to the level of hinge plate, the valve becomes deeper. Since the latter is much deeper than the right valve, a conclusion may be drawn that the main part of the pelecypod's body was contained in the left valve. Beak, with attachment area on it, also individualize with the growth of the valve. In the largest valve, beak is separated from the outer surface and coiled at an angle of about 70° towards the anterior margin. Keel, dividing the valve into two parts, also individualizes with the growth.

Variability. — Shells of *P. yailense* display a certain variability in the development of the left valve. A variable degree of its coiling and differences in size and shape of attachment area are observed. In addition, the right valve frequently displays differentiation in the thickness of walls, which is related with a variable degree of development of muscle scars, particularly posterior ones.

Remarks. — *P. yailense* from the Jurassic of the Crimea was described on the basis of complete, not separated shells. The data on the structure of hinges and muscle scars lacking, the description of the holotype is incomplete. Many, excellently preserved specimens of this species from the Jurassic of the Holy Cross Mountains will, therefore, supplement Pčelincev's material. During his stay in Leningrad, the present writer had an opportunity to compare the Polish specimens with the holotype of *P. yailense* and to find that they certainly belong to the same species. A similar opinion has also been expressed by V. F. Pčelincev, the author of the species (1966, oral communication).

Analyzing the development of hinge elements and muscle scars, it should be stated that an excessive growth of muscle scars in the right valve was one of the main reasons why the soft parts of the pelecypod's body were displaced from the right to the left valve. Pčelincev (1959) believes that this was primarily related with the attachment of a given valve to the substratum. With the interpretation of such type, a question arises why in other species within the genera *Diceras* Lamarck, *Macrodiceras* n.gen. and even *Heterodiceras* Munier-Chalmas the muscle scars are equal in size in both valves, despite the fact that the pelecypod was attached to the substratum with one of them only.

Not less interesting is also the development of hinges and apical parts with attachment areas. The sequence of appearance of particular hinge elements, such as cardinal tooth 3, then teeth 1, 2, etc., could be observed on a series of specimens of right and left valves. Such a sequence of appearance of particular hinge elements with the growth of an individual was certainly determined by the transition of the pelecypod from free to the sessile mode of life. An individual, having an only inceptive cardinal tooth in its hinge, was probably not yet attached to the substratum. It was only the development of other hinge elements, such as teeth 2

and 1 that considerably strengthened the entire shell; both valves, i.e. the right and the left, were immobilized and could not shift in relation to each other, which is essential for the pelecypods with the free benthonic mode of life. The first traces of attachment areas were found only in the specimens with all elements of their hinges, which should also testify to the correctness of the considerations presented above.

Occurrence. — Poland: Sulejów on the Pilica, Dobrut near Radom, Błaziny near Iłża; Upper Oxfordian (Astartian). U.S.S.R. (the Crimea): Rauracian.

Family **Epidiceratidae** Renngarten, 1950

Diagnosis. — Shells inequivalved. The left valve larger, with variously developed attachment area occurring on its beak. Hinges and muscle scars partly connected with each other. This family includes two genera: *Epidiceras* Douvillé, 1935 and *Megadiceras* Pčelincev, 1959. According to Pčelincev (1959), it represents a side branch in the development of the Rudistae (Fig. 4).

Genus *Epidiceras* Douvillé, 1935

Type species: *Diceras sinistrum* Deshayes, 1834.

Species assigned: *Epidiceras cotteaudi* (Bayle, 1873), *E. sinistrum* (Deshayes, 1834).

Stratigraphic and geographical range: Upper Oxfordian, Poland, France, U.S.S.R. (the Crimea).

Diagnosis. — Shells with valves almost equal in size. The left valve, with an attachment area on its beak, is slightly larger. Beaks of both valves are bent anteriorly and turned outside with a slight tendency to coil in the form of an ascending spiral. Hinges moderately developed. Tooth 2, elongate and parallel to the hinge margin, and irregular dental socket 1' occur in the left valve. In the right valve, cardinal tooth 3 is shaped like an oval cone. Muscle scars partly connected with the base of hinge margin. Posterior muscle scar entering under hinge plate.

Remarks. — Introducing the new generic name, Douvillé (1935) justified it by the fact that specimens of this genus attached to the substratum with the beak of the left valve, which fundamentally differs them from the genus *Diceras* sensu stricto. Pčelincev (1959) maintains that in the majority of cases only juvenile individuals attached to the substratum. He argues that the beak of the left valve has a very small attachment area and that both valves only slightly differ from each other in size. In addition, the details of the structure of hinges and muscle scars testify to his hypothesis.

Epidiceras cotteau (Bayle, 1873)

(Pl. XXV, Figs. 13, 15)

1873. *Diceras cotteau* Bayle; E. M. Bayle, Observation..., p. 153, Pl. 20, Figs. 5-6.
 1895. *Diceras cotteau* Bayle; P. Loriol, Études..., p. 35, Pl. 6, Fig. 3; Pls. 7-8, Fig. 1.
 1935. *Epidiceras Cotteau* Bayle; H. Douvillé, Les Rudistes..., p. 332.
 1941. *Diceras cotteau* Bayle; C. Dechaseaux, Rudistae..., p. 21, Pl. 2, Figs. 4, 10.
 1959. *Epidiceras cotteau* (Bayle); V. F. Pčelincev, Rudisty mezozoja..., p. 69, Pl. 4, Fig. 2.

Material. — Six juvenile individuals, including two complete shells.
Dimensions (in mm):

IG 1166.II/	1362	1261
l. r. v.	10	—
l. s.	—	25

Description. — Shell inequivalved. The left, larger valve has a strongly coiled beak, partly connected with the lateral surface of the valve. The beak itself and a small part of the left valve below the beak are strongly flattened. This is an area with which the shell was attached to the bottom. The left, semicircularly coiled valve (in the specimen described) is closely connected with the right, smaller valve. The right, relatively high valve has a distinct keel, which divides it into two almost equal parts. The beak of the right valve is strongly coiled and closely adheres to the lateral surface of the valve. No ornamentation is observed on either of the valves. The hinge plate, partly preserved on one only, juvenile, left valve, consists of anterior lateral tooth 2, which is slightly elongate and parallel to the hinge margin, as well as in the anterior part somewhat below tooth 2, of dental socket 1' which was entered by tooth 1 of the right valve. The remaining hinge elements are either destroyed or not yet developed, since, as mentioned above, this is the valve of a juvenile individual. Ligament grooves are also invisible. Muscle scars only slightly marked, the anterior one in the form of a small depression, the posterior — a roller-like swelling close to the margin of the shell.

Remarks. — According to Pčelincev (1959), the species described is somewhat similar to *E. sinistrum* (Deshayes) and *E. lorioli* Pčelincev from which it differs, however, in the structure of hinge plate, dimensions and a general outline. Specimens from the environs of Sulejów on the Pilica are to the greatest extent similar to the holotype, figured by Bayle (1873, Pl. 20, Figs. 5, 6) and to the specimens described by Loriol (1895, Pl. 6, Fig. 3; Pls. 7-8, Fig. 1) from the Jurassic of Bern.

Occurrence. — Poland: Sulejów on the Pilica; Upper Oxfordian (Astartian). France, Switzerland: Rauracian. U.S.S.R. (the Crimea): Rauracian.

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LEON KARCZEWSKI

RUDISTAE GÓRNEJ JURY OBRZEŻENIA GÓR ŚWIĘTOKRZYSKICH

Streszczenie

W pracy niniejszej opisano małże z rzędu Rudistae, występujące licznie w obrzeżeniu Gór Świętokrzyskich, w osadach górnego oksfordu (według dawnego ujęcia: rauraku i astartu). Materiał zebrano w odślonięciach i kamieniołomach okolic Dobrutu, Błazina, Olechowa, Sulejowa n. Pilicą, Kodrąbia, na obrzarze jury Radomska, Żernik i Bukowej, w pasmie małopolskim oraz w Zawichoście n. Wisłą (Fig. 1). W sumie zebrano około 1400 okazów, w większości doskonale zachowanych, należących do 5 rodzajów, w tym 1 nowy. W obrębie tych rodzajów wyróżniono 22 gatunki, z czego 11 nowych: *Diceras brevicornum* n.sp., *D. impressum* n.sp., *Macrodiceras kozłowski* n.sp., *M. longum* n.sp., *M. magnum* n.sp., *M. pcelincevi* n.sp., *M. polonicum* n.sp., *M. spirale* n.sp., *Eodiceras planum* n.sp., *E. subeximium* n.sp. i *Plesiodiceras sulejoviense* n.sp. W badaniach nad morfologią rudystów zwrócono uwagę na linię skreśtu prawej skorupy, stanowiącą ważną cechę diagnostyczną. Prawe skorupy niektórych gatunków narastały i skręcały się w stosunku do pewnej określonej linii, dla nazwania której zaproponowano termin „oś skreśtu”. Jeśli się ustawi pro-

stopadle prawą skorupę otworem do patrzącego, wtedy widać, że oś skrętu u gatunków rodzaju *Diceras* Lamarck ma wyraźną tendencję do opadania, gdy tymczasem u gatunków, nie należących do tego rodzaju, wykazuje ona tendencję do wznoszenia się. Cecha ta jest jedną z najważniejszych cech diagnostycznych, charakteryzujących nowy rodzaj *Macrodiceras* n.gen. Badania nad filogenezą rudystów potwierdziły opinię Kutassy (1934), że zbieżności w budowie zawiasów megalodontów i rudystów wynikają raczej z konwergentnego sposobu ich rozwoju, niż z pokrewieństwa tych grup. Autor podziela również zdanie Boehma (1882) i Dechaseaux (1939), że istnieją zbyt duże różnice między rudystami i małżami z grupy *Cardiidae*, aby można było mówić o możliwości pokrewieństwa między nimi.

W rozważaniach nad zjawiskiem radiacji adaptatywnej rudystów przedstawiono pogląd, że do grupy genetycznej *Eodiceras* Pöelincev i *Plesiodiceras* Munier-Chalmas, tj. rudystów przytwierdzających się do podłoża większą lewą skorupą, należy włączyć również rodzaj *Epidiceras* Douvillé. Przytwierdzanie się prawą lub lewą skorupą i rozwój związanej z tym asymetrii należy niewątpliwie do jednego z najciekawszych zjawisk w ich historii, co szczegółowo omawiał w swoim czasie Munier-Chalmas (1882). Jednakże asymetria rudystów wiąże się prawdopodobnie też z czynnikami ekologicznymi, które mogły określać sposób przytwierdzania się muszli prawą lub lewą skorupą. Badania materiałów z górnej jury obrzeżenia Gór Świętokrzyskich wykazały, że ponad 50% gatunków przytwierdzało się prawą skorupą. Opracowania rudystów z Krymu, Francji, Szwajcarii, Moraw i Niemiec wykazały, że na tych obszarach w górnej jurze ponad 90% gatunków przytwierdzało się lewą skorupą. Ponieważ górna jura obrzeżenia Gór Świętokrzyskich jest najdalej na północ wysuniętym obszarem, w porównaniu z górną jurą (zawierającą rudysty) wymienionych krajów, — wyrażono przypuszczenie, że o ilości gatunków przytwierdzających się prawą lub lewą skorupą decydować musiały termiczne warunki środowiska. Rudysty przytwierdzające się lewą skorupą pojawiać się mogły liczniej w obszarach wód cieplejszych, natomiast gatunki przytwierdzające się prawą skorupą intensywniej rozwijały się w strefach wód chłodniejszych, dając szereg nowych form. Masowe pojawianie się w górnej jurze rudystów, przytwierdzających się prawą skorupą, wskazuje prawdopodobnie na stopniowe ochładzanie się klimatu w tym czasie.

Omówiono także wpływ prądów morskich na wielkość muszli oraz ich rozprzestrzenienie geograficzne północne. Obecność chłodnych prądów powodowała, że karłowate formy rozwijały się na obszarach Europy między 50° i 55° szer. geogr. płn. Takie rozmieszczenie rudystów uzależnione być mogło przede wszystkim od temperatury wody; dowodzili tego tacy badacze, jak Brooks (1950) i Schwarzbach (1961). Przedstawiono również przykłady wpływu czynników termicznych na asymetrię u otwornic oraz przykład znaczenia przystosowawczego u niektórych lewo- i prawoskrętnych ślimaków. Omówiono również problem rozprzestrzenienia jurajskich rudystów, ich paleoekologię i znaczenie stratygraficzne. Na podstawie materiałów z górnej jury obrzeżenia Gór Świętokrzyskich można obecnie z całą pewnością wykorzy-

stać jurajskie rudysty w badaniach geologicznych, zarówno przy rozważaniach stratygraficznych, jak i paleogeograficznych czy facjalnych. Przyczynia się do tego w dużym stopniu masowe ich występowanie przy stosunkowo niewielkim zasięgu pionowym, bardzo dobry stan zachowania i szeroki zasięg geograficzny.

ЛЕОН КАРЧЕВСКИ

ВЕРХНЕЮРСКИЕ RUDISTAE ОБРАМЛЕНИЯ СВЕНТОКШИСКИХ ГОР,
ПОЛЬША

Резюме

В работе описаны пластинчатожаберные из отряда Rudistae, находимые в большом количестве в обрамлении Свентокшиских Гор в отложениях верхнего оксфорда. Материал происходит из естественных обнажений и каменноломен в окрестностях Добрута, Блазин, Олехова, Сулейова над Пилицей, Кодромбя, в юрской области Радомска, Жерник и Буковой, в полосе Малогоща, а также в Завихосте над Вислой (Фиг. 1). Собрано около 1400 образцов, в большинстве хорошей сохранности, принадлежащих 5 родам, в их числе одному новому. В составе этих родов выделено 22 вида, в том числе 11 новых: *Diceras brevicornum* n. sp., *D. impressum* n. sp., *Macrodiceras kozlowskii* n. sp., *M. longum* n. sp., *M. magnum* n. sp., *M. pcelincevi* n. sp., *M. polonicum* n. sp., *M. spirale* n. sp., *Eodiceras planum* n. sp., *E. subeximium* n. sp., и *Plesiodiceras sulejoviense* n. sp. При изучении морфологии было обращено внимание на линию завитка правой створки, являющуюся важным диагностическим признаком. Правые створки некоторых видов нарастали и завивались по соотношению к некоторой линии, для которой автором предложено название „ось завитка”. Если держать правую створку вертикально отверстием к наблюдателю, видно, что ось завитка у видов рода *Diceras* Lamarck имеет тенденцию к опусканию, в то время как у видов, не принадлежащих к этому роду, она имеет тенденцию к поднятию. Это один из основных признаков характеризующих новый род *Macrodiceras* n. gen. Исследования филогенеза рудистов подтвердили мнение Кутасси (Kutassy, 1934) о том, что черты сходства в строении замков мегалодонтов и рудистов скорее всего являются результатом конвергенции в их развитии, чем родства.

Автор поддерживает мнение Бэма (Boehm, 1882) и Дэшазо (Dechaseaux, 1939) о том, что между рудистами и пластинчатожаберными из группы *Cardiidae* существуют слишком большие различия, чтобы можно было предполагать их родственные связи.

В рассуждениях по вопросу адаптивной радиации рудистов представлено мнение о том, что к генетической группе *Eodiceras* Pčelincev и *Plesiodiceras* Munier-Chalmas — рудистов, прикрепляющихся к субстрату большей левой створкой, надо включить также род *Epidiceras* Douvillé. Прикрепление левой или правой створкой и развитие связанной с этим асимметрии принадлежит несомненно к одному из более интересных явлений в их истории. Это подробно обсуждал в свое время Мюние-Шальмас (Munier-Chalmas, 1882). Однако асимметрия рудистов вероятно связана также с экологическими факторами, которые могли определять способ прикрепления раковины правой или левой створкой. Исследования верхнеюрских материалов из обрамления Свентокржиских Гор показали, что более 50% видов прикрепляется правой створкой. Изучение рудистов Крыма, Франции, Швейцарии, Моравии и Германии доказало, что на этих территориях в верхней юре более 90% видов прикреплялось левой створкой. Так как верхняя юра Свентокржиских Гор является наиболее далеко выдвинутым к северу участком по сравнению с верхней юрой (с рудистами) в указанных местах, автор предполагает, что для прикрепления правой или левой створкой решающее значение имели термические условия среды. Рудисты прикреплявшиеся левой створкой могли появляться в большем количестве в бассейнах с более теплой водой, а виды, прикреплявшиеся правой створкой, обильнее заселяли зоны вод более холодных, образуя новые формы.

Появление в верхней юре в массовом количестве рудистов, прикреплявшихся правой створкой, вероятно указывает на то, что климат в это время постепенно охлаждался.

В работе рассмотрены также влияния морских течений на величину раковины и распространение рудистов в северном направлении. Наличие холодных морских течений было причиной того, что карликовые формы рудистов обитали в Европе между 50° и 55° северной широты. Такое размещение рудистов могло зависеть главным образом от температуры воды. Доказывали это такие исследователи как Брукс (Brooks, 1950) и Шварцбах (Schwarzbach, 1961). Автором приведены также примеры влияния термических факторов на асимметрию у фораминифер, а также пример адаптации у некоторых лево- и правозавитых брюхоногих.

Обсуждена проблема распространения юрских рудистов, их экология и стратиграфическое значение. Основываясь на верхнеюрских материалах из обрамления Свентокржиских Гор, автор уверен в том, что юрские рудисты безусловно могут быть использованы для стратиграфии, палеогеографии и установления фаций. Способствуют этому в значительной мере обильные находки рудистов, их сравнительно небольшое вертикальное распространение, очень хорошая сохранность и широкое географическое распространение.

PLATES

All figures of fossils in natural size

(except Pl. XXIV, Fig. 1c and Pl. XXV, Fig. 13)

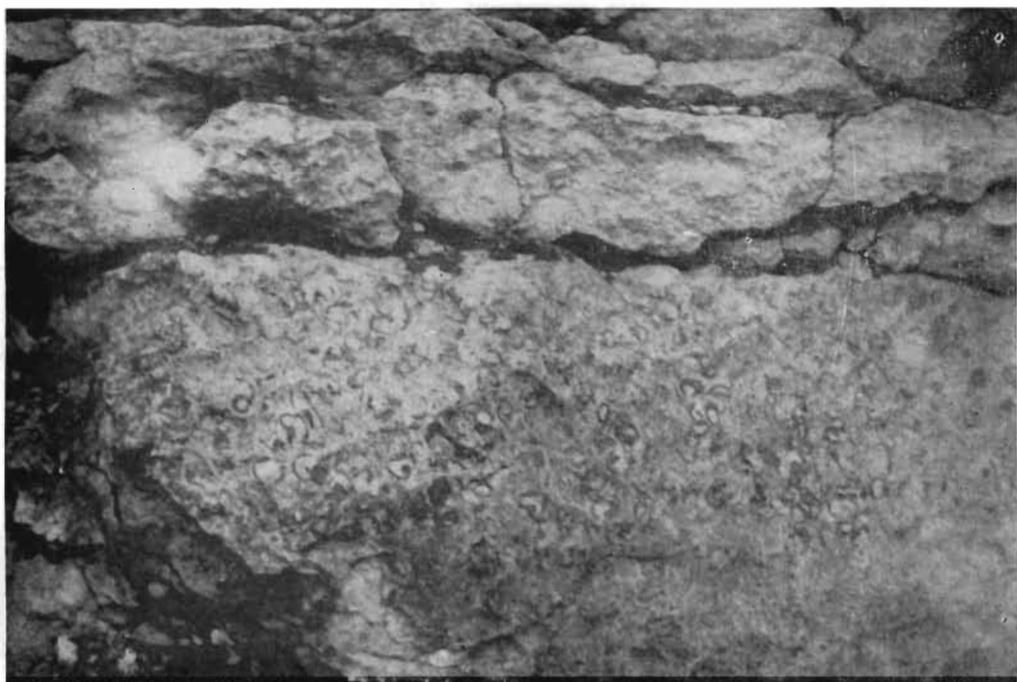
Plate I

Fig. 1. Outcrop of limestones with rudistids from Dobrut.

Fig. 2. Rudistid limestones from locality situated between Żerniki and Jaclów Karsznicki.



1



2



1



2



3



4



5



6

Plate II

Diceras arietinum Lamarck

Figs. 1-6. Growth series of the left valves (IG 1166.II/156—161); Dobrut, Upper Oxfordian.

Plate III

Diceras arietinum Lamarck

Figs. 1-5. Growth series of the right valves (IG 1166.II/162—166); Dobrut, Upper Oxfordian.



3



2



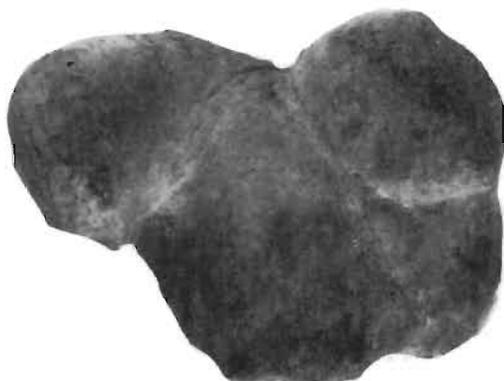
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4



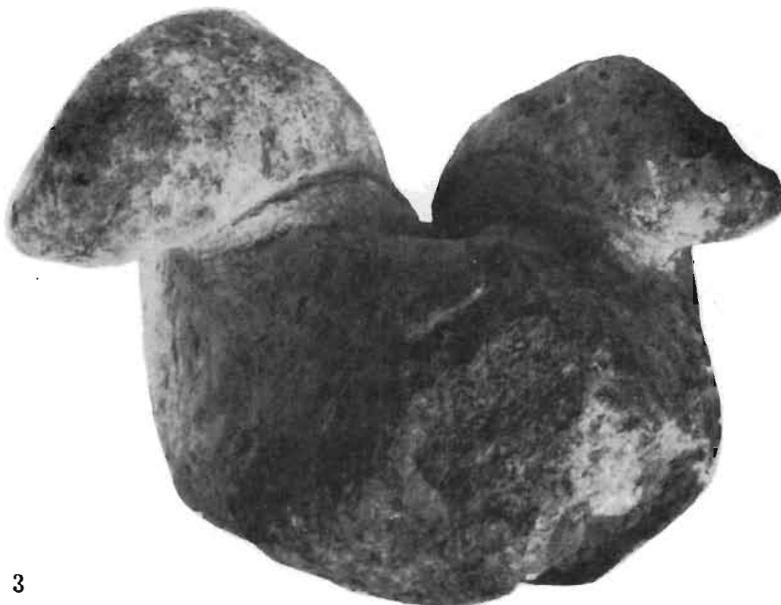
5



1



2



3

Plate IV

Diceras arietinum Lamarck

Figs. 1-3. Growth series of the shells (IG 1166.II/167—169); Dobrut, Upper Oxfordian.

Plate V

Diceras arietinum Lamarck

Fig. 1a. Interior of the shell, partly exposed.

Fig. 1b. Posterior view of the same (IG 1166.II/170).

Dobrut, Upper Oxfordian



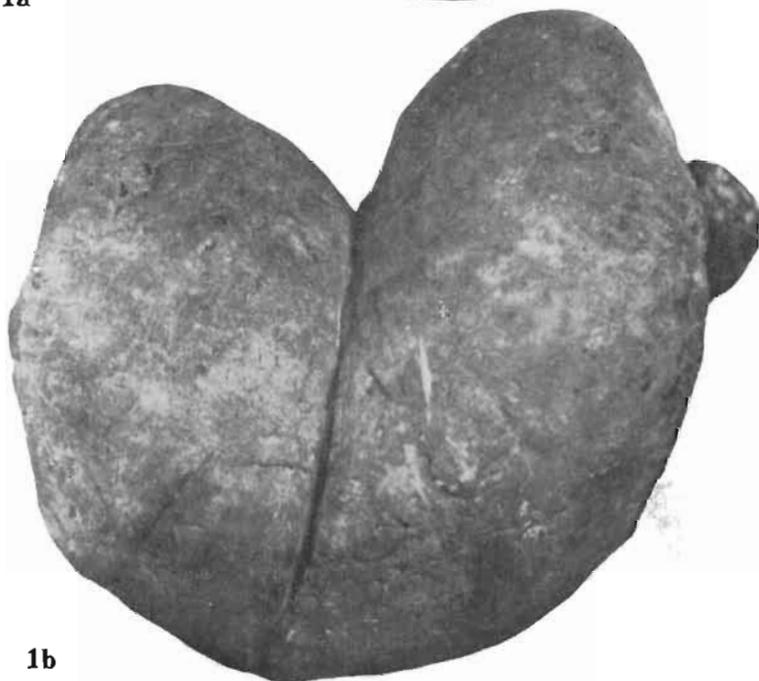
1a



1b



1a



1b

Plate VI

Diceras arietinum Lamarck

Fig. 1a. Posterior view.

Fig. 1b. Anterior view (IG 1166.II/171).

Skórków anticline, Upper Oxfordian

Plate VII

Diceras arietinum Lamarck

Fig. 1. Left valve: *a* hinge plate view, *b* external view, growth lines visible (IG 1166.II/172).

Fig. 2. Right valve: *a* hinge plate view, *b* external view (IG 1166.II/173).

Dobrut, Upper Oxfordian



1a



1b



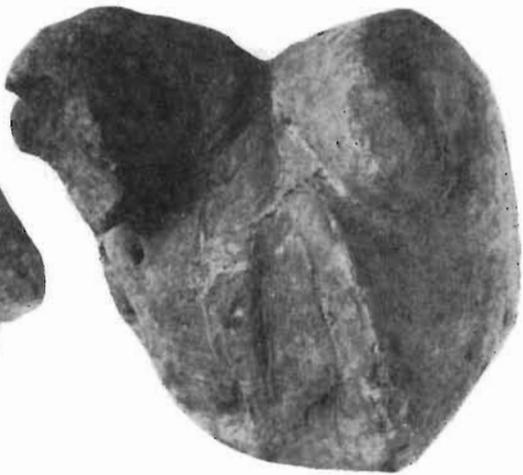
2a



2b



1



2



3

Plate VIII

Diceras impressum n. sp.

Figs. 1-3. Growth series of 3 shells, anterior view (IG 1166.II/35,32,34); Dobrut,
Upper Oxfordian.

Plate IX

Diceras impressum n. sp.

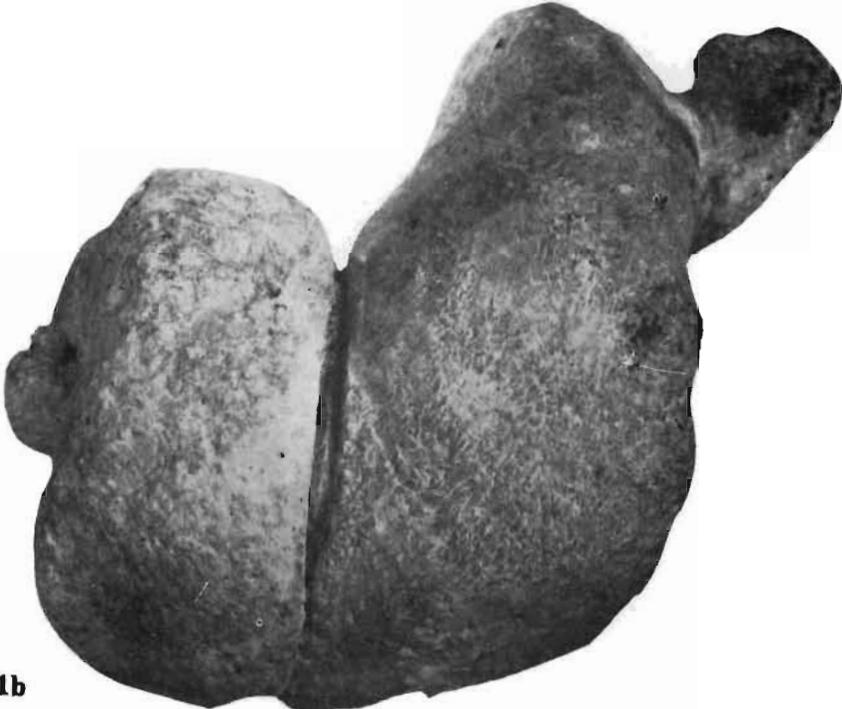
Fig. 1a. Interior of the shell partly exposed.

Fig. 1b. Posterior view (IG 1166.II/36).

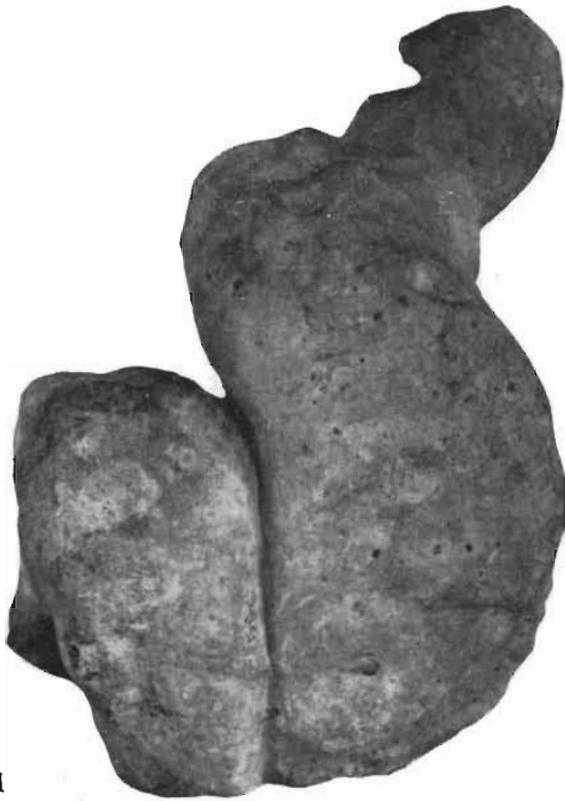
Dobrut, Upper Oxfordian



1a



1b



1



2

Plate X

Diceras impressum n. sp.

Fig. 1. Posterior view (IG 1166.II/34); Dobrut, Upper Oxfordian.

Diceras arietinum Lamarck

Fig. 2. Posterior view (IG 1166.II/169); Bukowa, Upper Oxfordian.

Plate XI

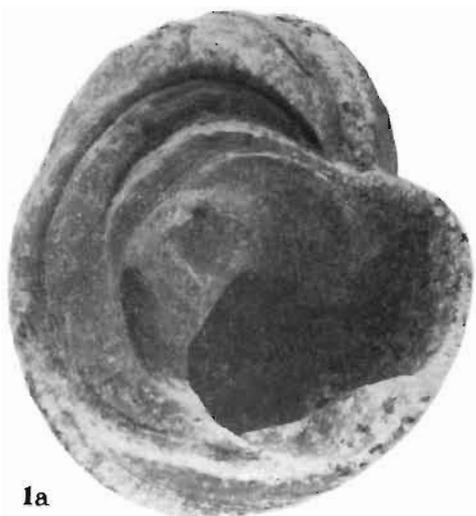
Diceras originale Bayle

Fig. 1. Left valve: *a* hinge plate view, *b* beak-side view (IG 1166.II/62).

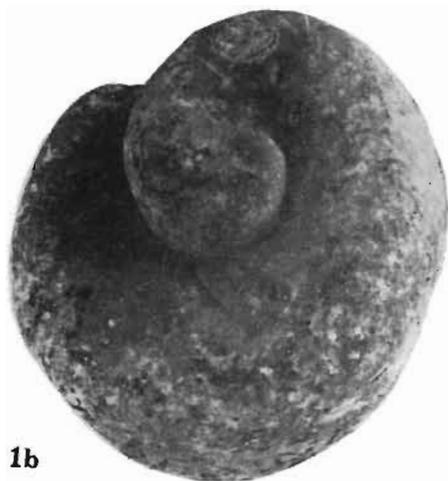
Fig. 2. Right valve (IG 1166.II/61).

Fig. 3. Left valve (IG 1166.II/63).

Dobrut, Upper Oxfordian



1a



1b



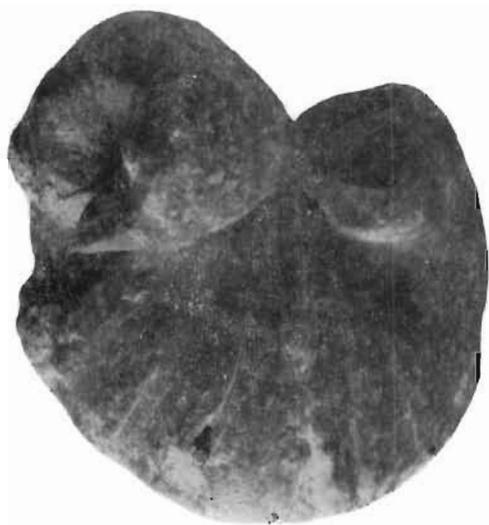
2



3



1



2



3

Plate XII

Diceras brevicornum n. sp.

Fig. 1. Right and left valves, hinge plate views (IG 1166.II/3—4).

Figs. 2, 3. Anterior views (IG 1166.II/1—2).

Dobrut, Upper Oxfordian

Plate XIII

Macrodiceras rotundatum (Bayle)

Fig. 1. Right valve (IG 1166.II/790).

Macrodiceras balaklavense (Pčelincev)

Fig. 2. Right valve, hinge plate view (IG 1166.II/764).

Dobrut, Upper Oxfordian



1



2



1



2

Plate XIV

Diceras impressum n. sp.

Fig. 1. Anterior view (IG 1166.II/33); Dobrut, Upper Oxfordian.

Macrodiceras balaklavense (Pčelincev)

Fig. 2. Right valve, external view (IG 1166.II/765); Sulejów; Upper Oxfordian.

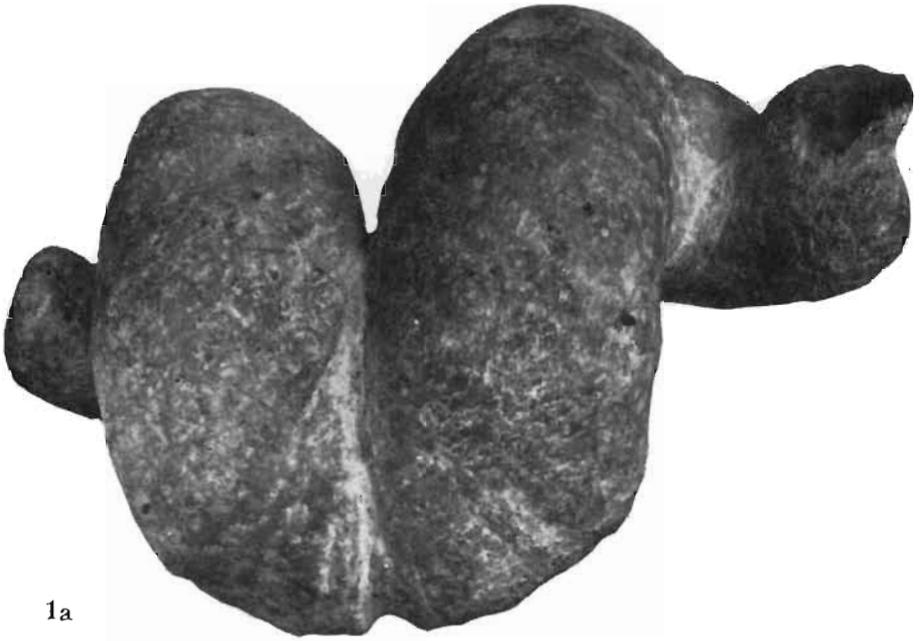
Plate XV

Macrodiceras kozlowskii n. sp.

Fig. 1a. Posterior view.

Fig. 1b. Anterior view (IG 1166.II/774).

Dobrut, Upper Oxfordian



1a



1b



1



2



3



4

Plate XVI

Macrodiceras longum n. sp.

Figs. 1-4. Growth series of the right valves (IG 1166.II/706—709); Dobrut, Upper Oxfordian.

Plate XVII

Macrodiceras longum n. sp.

Right valve (IG 1166.II/710); Dobřut, Upper Oxfordian.





Plate XVIII

Macrodiceras magnum n. sp.

Anterior view (IG 1166.II/776); Dobrut, Upper Oxfordian.

Plate XIX

Macrodiceras spirale n. sp.

Fig. 1a. Right valve, external view.

Fig. 1b. Right valve, beak-side view, with large attachment area (IG 1166.II/840);

Dobrut, Upper Oxfordian



1a



1b



1a



1b

Plate XX

Macrodiceras pcelincevi n. sp.

Fig. 1a. Right valve, hinge plate view.

Fig. 1b. Right valve, external view (IG 1166.II/778).

Dobrut, Upper Oxfordian

Plate XXI

Macrodiceras pcelincevi n. sp.

Fig. 1a. Right valve, hinge plate view.

Fig. 1b. Right valve, external view (IG 1166.II/777).

Dobrut, Upper Oxfordian



1a



1b



1a



1b

Plate XXII

Macrodiceras polonicum n. sp.

Fig. 1a. Right valve, hinge plate view.

Fig. 1b. Right valve, external view (IG 1166.II/787).

Dobrut, Upper Oxfordian

Plate XXIII

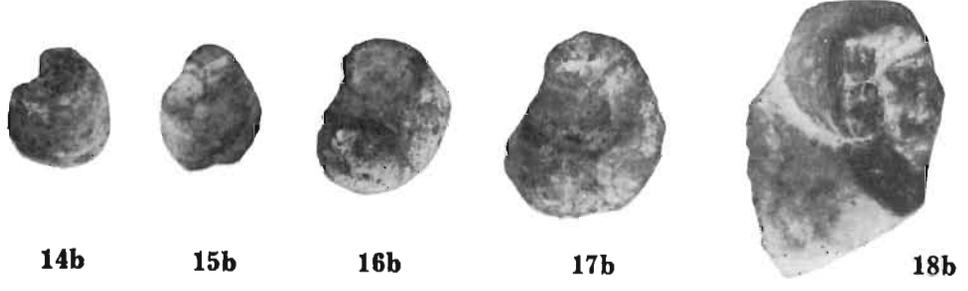
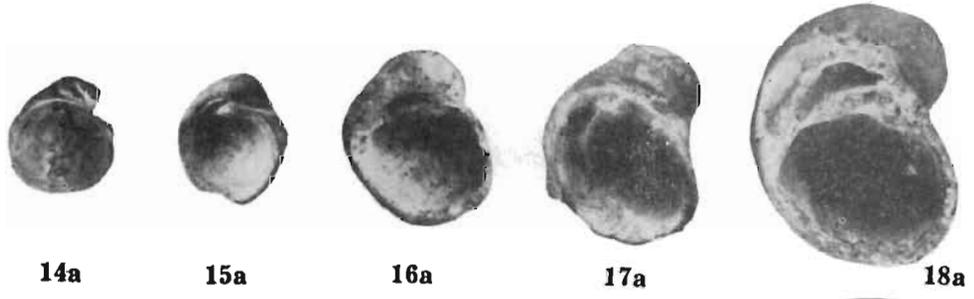
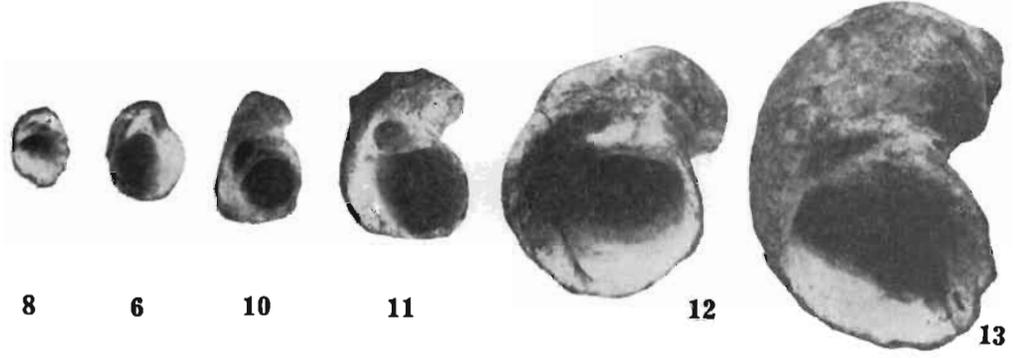
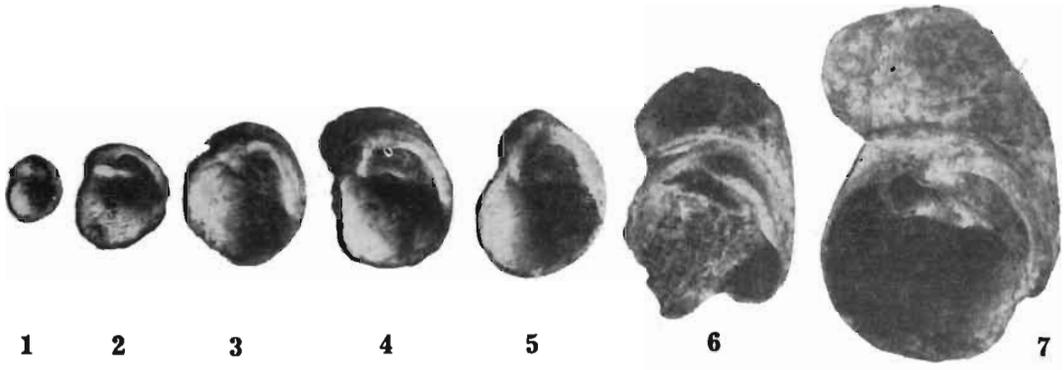
Eodiceras eximium (Bayle)

Figs. 1-7. Growth series of the right valves, hinge plate views (IG 1166.II/851—857);
Kodrań, Upper Oxfordian.

Figs. 8-13. Growth series of the left valves, hinge plate views (IG 1166.II/858—863);
Sulejów, Błaziny, Upper Oxfordian.

Eodiceras planum n. sp.

Figs. 14—18. Growth series of the left valves: *a* hinge plate views, *b* beak-side
views with large attachment area, the smallest specimen is the shell
(IG 1166.II/1101—1105); Sulejów, Upper Oxfordian.





1a



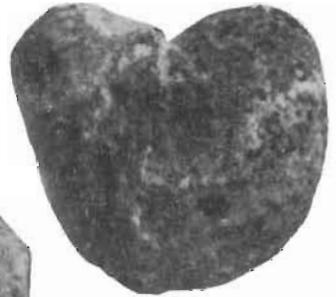
1b



2a



1c



2b



3



4a



4b

Plate XXIV

Eodiceras sp.

- Fig. 1. Steinkern: *a* posterior view, *b* anterior view, *c* anterior view $\times 2$ (IG 1166.II/1158); Błaziny, Upper Oxfordian.
- Fig. 2. Shell: *a* anterior view, *b* posterior view (IG 1166.II/1159); Kodrań, Upper Oxfordian.
- Fig. 3. Shell partly damaged, anterior view (IG 1166.II/1160); Sulejów, Upper Oxfordian.

Eodiceras subeximium n. sp.

- Fig. 4. Shell: *a* posterior view, *b* anterior view (IG 1166.II/1148); Kodrań, Upper Oxfordian.

Plate XXV

Plesiodiceras yailense Pčelincev

Figs. 1-5. Growth series of the right valves, hinge plate views. The greatest valve (Fig. 5b) seen also from external side (IG 1166.II/1259—1263); Dobrut, Upper Oxfordian.

Figs. 6-10. Growth series of the left valves, hinge plate views. The greatest valve (Fig. 10b) seen also from external side (IG 1166.II/1264—1268); Błaziny, Sulejów, Upper Oxfordian.

Plesiodiceras muensteri (Goldfuss)

Fig. 11. Left valve, hinge plate view (IG 1166.II/1246); Dobrut, Upper Oxfordian.

Plesiodiceras orthogonale Pčelincev

Fig. 12. Anterior view (IG 1166.II/1249); Sulejów, Upper Oxfordian.

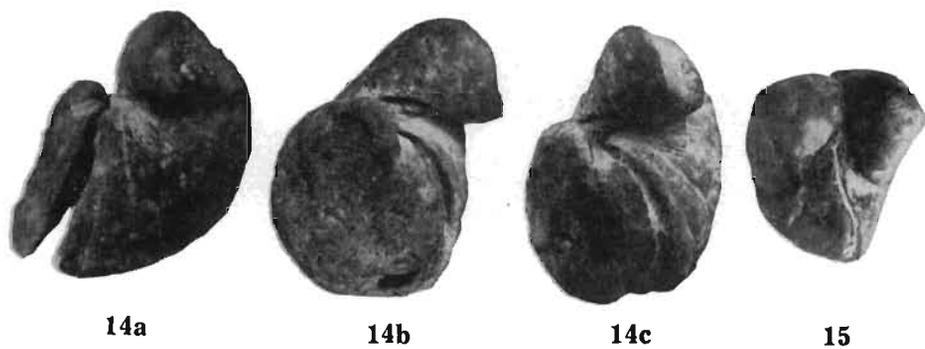
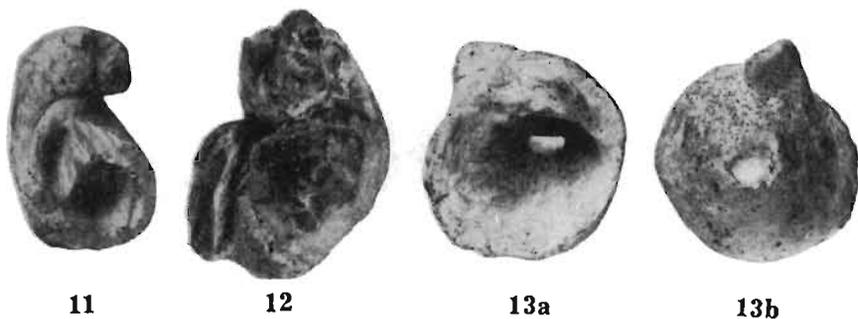
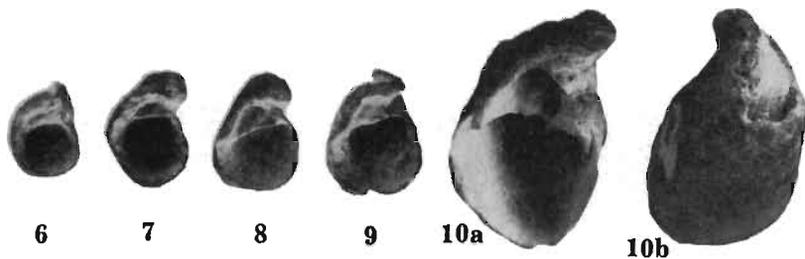
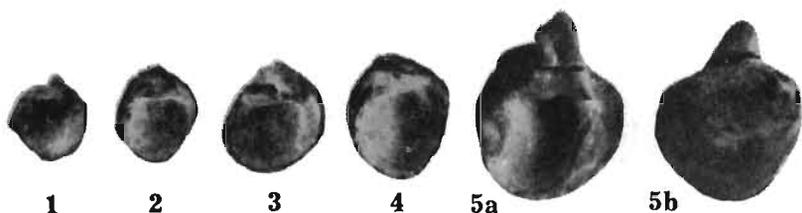
Epidiceras cotteawi (Bayle)

Fig. 13. Right valve: a hinge plate view, b external view $\times 3$ (IG 1166.II/1362).

Fig. 15. Anterior view (IG 1166.II/1361). Sulejów, Upper Oxfordian.

Plesiodiceras sulejoviense n. sp.

Fig. 14. a anterior view, b right valve, c partly side view (IG 1166.II/1255); Sulejów, Upper Oxfordian.





1



2



3a



3b

Plate XXVI

Diceras sp.

- Fig. 1. Valve, hinge plate view (IG 1166.II/561); Dobrut, Upper Oxfordian.
- Fig. 2. Valve, hinge plate view (IG 1166.II/563); Żerniki, Upper Oxfordian.
- Fig. 3. Valve: *a* external view, *b* hinge plate view (IG 1166.II/562); Sulejów, Upper Oxfordian.

Plate XXVII

Diceras brevicornum n. sp.

Fig. 1. Shell with internal surface partly exposed, small attachment area visible on the beak of the right valve (IG 1166.II/31).

Pterocardium corallinum (Leymerie)

Fig. 2. Left valve, hinge plate view (IG 1166.II/1367).

Fig. 3. Right valve: *a* external view, *b* hinge plate view (IG 1166.II/1368).

Dobrut, Upper Oxfordian



1



3a



2



3b



1a



1b



3



4a



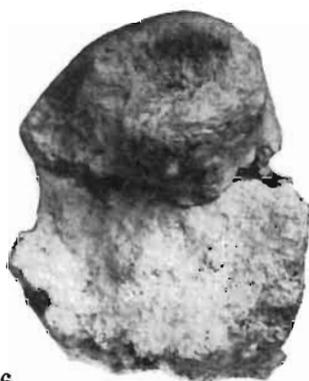
2



4b



5



6

Plate XXVIII

Plesiodiceras sp.

Fig. 1 a-b. Left valves of the young individuals attached on the larger valve as the substrate (IG 1166.II/1360); Błaziny, Upper Oxfordian.

Eodiceras planum n. sp.

Fig. 2. Left valve; on the beak a large, elongate, somewhat concave attachment area visible (IG 1166.II/1107).

Fig. 3. Left valve of the adult individual with a very large attachment area, medial part of this area strongly depressed (IG 1166.II/1106); Sulejów, Upper Oxfordian.

Eodiceras eximium (Bayle)

Fig. 4. Two left valves attaching each other, the larger valve being the substrate for the smaller one (IG 1166.II/864); Żerniki, Upper Oxfordian.

Macrodiceras sp.

Fig. 5. Elongate, somewhat concave attachment area visible on the beak of the valve (IG 1166.II/844); Dobrut, Upper Oxfordian.

Diceras sp.

Fig. 6. Very concave attachment area visible on the beak of the valve (IG 1166.II/568); Żerniki, Upper Oxfordian.

Plate XXIX

Macrodiceras sp.

- Fig. 1. Right valve of the young individual with a large, flat attachment area on the beak (IG 1166.II/848).
- Fig. 2. Right valve of the young individual with a funnellike attachment area beneath the beak (IG 1166.II/846).
- Fig. 3. Umbilical depression within the large attachment area visible on the beak (IG 1166.II/847).

Macrodiceras spirale n.sp.

- Fig. 4. Large, concave attachment area visible on the beak of right valve (IG 1166.II/841).

Dobrut, Upper Oxfordian



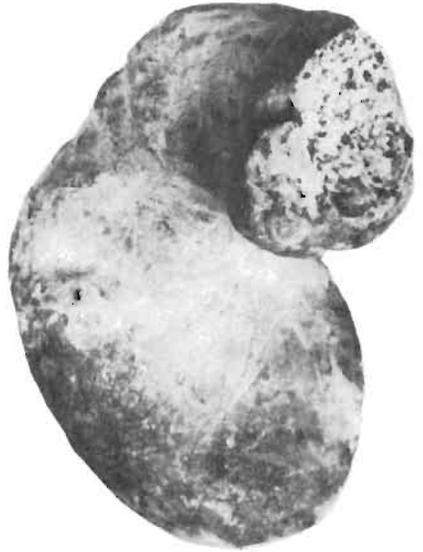
1



2



3



4



1



2a



2b



3

Plate XXX

Macrodiceras sp.

Fig. 1. Fragment of the apical part of the right valve with a very large attachment area (IG 1166.II/845); Dobrut, Upper Oxfordian.

Diceras sp.

Fig. 2 a-b. Right valve with a very concave attachment area on the beak (IG 1166.II/564); Sulejów, Upper Oxfordian.

Diceras arietinum Lamarck

Fig. 3. Shell with transversely cut right valve; inside the latter a small boring-lamellibranch visible (IG 1166.II/174); Dobrut, Upper Oxfordian.

Plate XXXI

Diceras sp.

Figs. 1-2. Right valves with numerous, large erosions on the surfaces (IG 1166.II/565, 566); Dobrut, Upper Oxfordian.

Fig. 3. Right valve with a strongly coiled beak, the latter being slightly cut off by the small attachment area (IG 1166.II/567); Sulejów, Upper Oxfordian.

Macrodiceras sp.

Fig. 4. Right valve with numerous erosions visible on the surface (IG 1166.II/849).

Fig. 5. Right valve of a young specimen with the large attachment area on the beak (IG 1166.II/850); Dobrut, Upper Oxfordian.



1



5



3



4



2