With the best compliments

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Evolutionary Trends of Upper Cretaceous Inocerames

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The family of Inoceramidae (Bivalvia) is distributed from the Permian to the Upper Cretaceous age and has a great importance for the biostratigraphy of the Jurassic and Cretaceous, especially Upper Cretaceous system. The family of Inoceramidae (Giebel,1852) is defined in the Treatise on Invertebrate Paleontology (Part N, Vol.3,p.N 314,315) in the following manner :

"Variously shaped, concentrically lamellose or plicated Pteriacea with multiple ligamental pits; subequivalve to highly inequivalve with left valve more convex than right valve; radial ribbing present only rarely; commisure plane except where effected by radial ribbing; no anterior gape; posterior wing usually absent or small; ligamental area with usually numerous regularly arranged ligamental pits which commonly have curved sides and do not indent margins of area ; hinge teeth absent except in some Parainoceramus; inner ostracum nacreous (but not preserved in many specimens); outer ostracum formed of prismatic calcite."

The changes of shape and the changes of the shell sculpture during the Upper Cretaceous show phylogenetic trends, which may be discussed. There are changes in the shape of the ligamental area and the number and shape of the ligamental pits, too. However, in most cases the ligamental area is not preserved or preserved in a poor condition. Also the muscle scars and the prismatic layers of the shell are only little known. This is one of the reasons, which render more difficult to establish phylogenetic ranks or a model of the phylogenetic evolution of the Upper Cretaceous inocerames.

The trends of evolution of the Upper Cretaceous inocerames were observed in the European faunal province (Fig.1). According to the composition of Cretaceous bivalve faunes E.G.Kauffman (1973) recognizes 7 biogeographic provinces and subprovinces. If we limit our observation on the Upper Cretaceous inocerame faunes, as it was done by J.Sornay (1966), it is possible to distinguish 5 faunal provinces (European-westasiatic-northafrican province, Northamerican province, Pazific province, Madagascar province and New Zealand-Australian province). The distribution of the Inoceramus-labiatus-group (Fig. 1) shows the European-westasiatic-northafrican province according to J. Sornay (1966). The great distribution of the Inoceramus-labiatus-group is mainly influenced by the transgression during Cenomanian and Turonian age.

At first it is necessary to note the change of the number of the Upper Cretaceous inocerame species and subspecies in the European-westasiatic-northafrican province (Fig.2). With short interruptions during the plenus zone and the basal,part of the Middle Turonian the number of the species and subspecies increased till to the Middle Coniacian from 1 (base of the Cenomanian) to 34. During the Upper Coniacian the number of the species and subspecies is reduced to 10. During the Santonian we can notice a second maximum with 35 species and subspecies. After that the number of the species and subspecies is continually reduced.

The first scheme of the phylogenetic evolution of the Upper Cretaceous inocerames was established by H.Woods (1912). From the Albian species Inoceramus anglicus Woods developed two branches; one branch with Inoceramus crippsi Mantell, Inoceramus labiatus (Schlotheim), Inoceramus incostans Woods, Inoceramus balticus Böhm and Inoceramus undulatoplicatus F.Roemer. To the second branch belong Inoceramus pictus Sowerby, Inoceramus lamarcki Parkinson, Inoceramus involutus Sowerby and Inoceramus cordiformis Sowerby. Another scheme, by A. Tsagareli (1942), is very similar. It differs from the first scheme mainly in the position of Inoceramus involutus Sowerby near to the Inoceramus-inconstans-group and the near relationship of Inoceramus bohemicus Leonhard (=Inoceramus pictus bohemicus Leonhard) to Inoceramus labiatus (Schlotheim). The importance of the shell sculpture for phylogenetic and biostratigraphic purposes illustrated R.Heinz (1928). Further remarks about phylogenetic trends can be found especially in the studies by G.E.Kauffman (1970), J.Sornay (1966), O.

Seitz (1956,1961,1962,1965,1967 and 1970) and other.

One of the prerequisites for phylogenetic examinations is the knowledge of the vertical distribution of the species and subspecies. Figures 3 and 4 show the vertical distribution of the most important inocerames of Upper Cretaceous age (Cenomanian-Lower Campanian), as it is known at present according to the studies of O.Seitz (1956, 1961,1962,1965,1967 and 1970), K.A.Tröger (1966,1967), K.A.Tröger and W.Haller (1966), St.Cieslinsky (1963), M.M.Moskvin(1959), S.J. Pasternak,W.I.Gawriliachin, W.A.Ginda,S.P.Kozjubinskii and Ju.M.Senkowskii(1968), R.A.Chalafowa(1969) and others. Where it was possible, the phylogenetic evolution is shown by direct connections. In other cases the arrangement of the species on the pictures indicates possible relations.

Moreover, Fig.2 indicates wherever there are regularities in the vertical distribution of the shape and the shell sculpture and typical shell sculptures and shapes are bound to fixed time units. I distinguish 21 different shape types and some types of shell sculpture as radial elements (Rippen-radial ribs, Rippeln, Krenulationen, radiale Depressionen-radial depressions according to R.Heinz 1928 and O.Seitz,1970) and the pentagonal course of the undulations.

To the shape type one belong circular (1a), subcircular (1d) and ovate forms (1b,c,e). Especially the types 1a and 1d are distributed in the whole Upper Cretaceous (for example Inoceramus crippsi crippsi Mantell - Cenomanian, Inoceramus costellatus costellatus Woods-Upper Turonian, Inoceramus cycloides cycloides Wegner -Santonian, Inoceramus parvus Kozjub.-Maastrichtian). We know furthermore transitions between the types 1a-b-c, e.g. in the phylogenetic rank Inoceramus crippsi crippsi Mantell - Inoceramus crippsi hoppenstedtensis Tröger (Fig.3,numbers 1,2).

To the type two (2a,b-ovate and inaequivalve) belong especially Inoceramus pictus pictus Sowerby and Inoceramus lamarcki lamarcki Parkinson. Transitions are to be seen to the 2c-Inoceramus ernsti Heinz and may exist to the type 2d-Inoceramus schloenbachi Böhm too. The distribution of these types extends mainly from the Upper Cenomanian to the Lower Coniacian (Fig.3,numbers 11-19). It may be that there are connections to the Inoceramus-inconstans-group, too.

Explanation of the Figures

Fig. 1 : Biogeographic units of Cretaceous age according to G.E. Kauffman (1970) and distribution of the Inoceramus-labiatus-group (Lower Turonian).
I - North European Province, I/1 - Boreal Subprovince, I/2 - Gulf and Atlantic Coast Subprovince, I/3 - Western Interior Subprovince, II/1 - Japanese--East Asian Subprovince, II/2- Northeast Pacific Subprovince, III - W and E Mediterranean Subprovinces, III/1 - North African Subprovince,III/2 - Carribean Province, III/3 - Middle Asian Subprovince, III/4 - North Indian Ocean Subprovince, IV- Austral Province, Australian and New Zeeland Subprovinces, V - East African (Madagascar) Province, VI - South Atlantic Subprovince, VII- Andean Subprovince

Fig. 2 : The time distribution of the main types of the Upper Cretaceous Inoceramus species and subspecies in the European-Westasiatic-Northafrican province in the timespan between Cenomanian and Maastricht.

Fig. 3 : Vertical distribution of the Cenomanian, Turonian and Coniacian inocerames of the genus Inoceramus (most important species and subspecies).
1. I.crippsi crippsi Mantell, 2. I.crippsi hoppenstedtensis Tröger, 3. I.- virgatus Schlüter, 4. I.tenuis Mantell, 5.I. pictus pictus, Sowerby, 6. I.pictus bohemicus Leonhard, 7. I.labiatus mytilooides Mantell, 8.I.labiatus labiatus(Schlotheim), 9. I.labiatus opalensis Böse, 10.I.labiatus hercynicus Petrascheck, 11. I.apicalis Woods, 12. I.inaequivalvis inaequivalvis Schlüter, 13. I. striatoconcentricus striatoconcentricus Gümbel,14.-15.- I.lamarcki lamarcki Parkinson, 16.I. lamarcki stümckei Heinz, 17. I.lusatiae Andert, 18. I.ernsti Heinz, 19. I. schloenbachi Böhm, 20. I.costellatus pietzschi Tröger, 21. I.costellatus costellatus Woods, 22. I.fiegei mytiloidiformis Tröger, 23.I.mantelli mantelli (Mercey) Barrois, 24. I.kleini G.Müller, 25. I. percostatus G.Müller, 26. I.koeneni G.Müller, 27. I.involutus Sowerby, 28. I.fasciculatus Heine, 29. I.subquadratus subquadratus Schlüter, 30. I. subquadratus crenelatus Seitz, 31. I. subquadratus complicatus Heine.

Fig. 4 : Vertical distrobution of the Santonian and Lower Campanian inocerames of the genus Inoceramus (most important species and ~~subspecies~~).
32. I.pachti pachti Arch., 33. I.Cardissoides cardissoides Goldfuss, 34. I. pinniformis Willett, 35. I.patootensiformis Seitz, 36. I. angustus Beydenburg, 37.I. undulatoplicatus undulatoplicatus F.Roemer, 38.I. cycloides cycloides Wegner, 39. I.rhomboides rhomboides Seitz, 40. I. cordiformis cordiformis Sowerby, 41. I. haenleini G.Müller, 42. I. mülleri mülleri Petrascheck

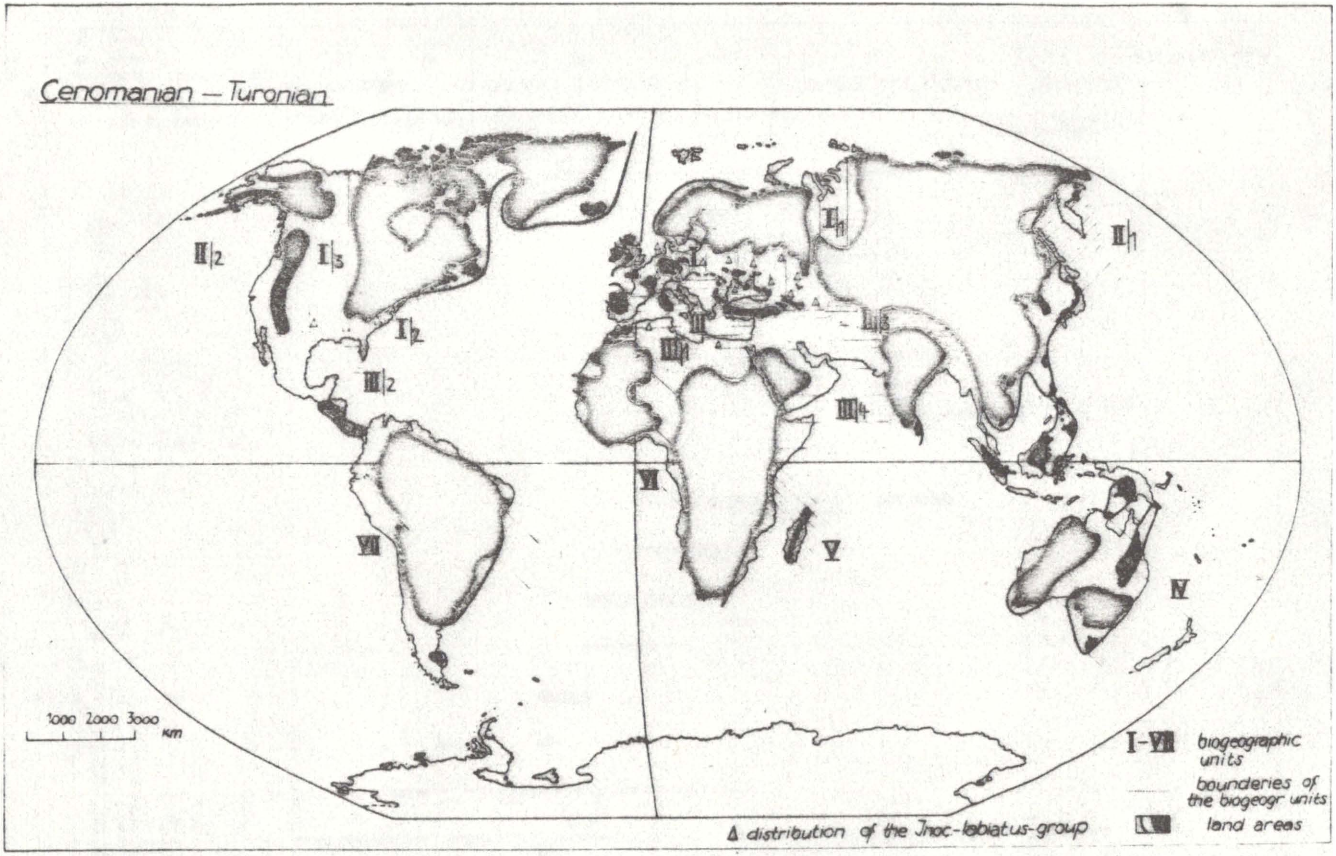

Fig. 1 K.A.Tröger

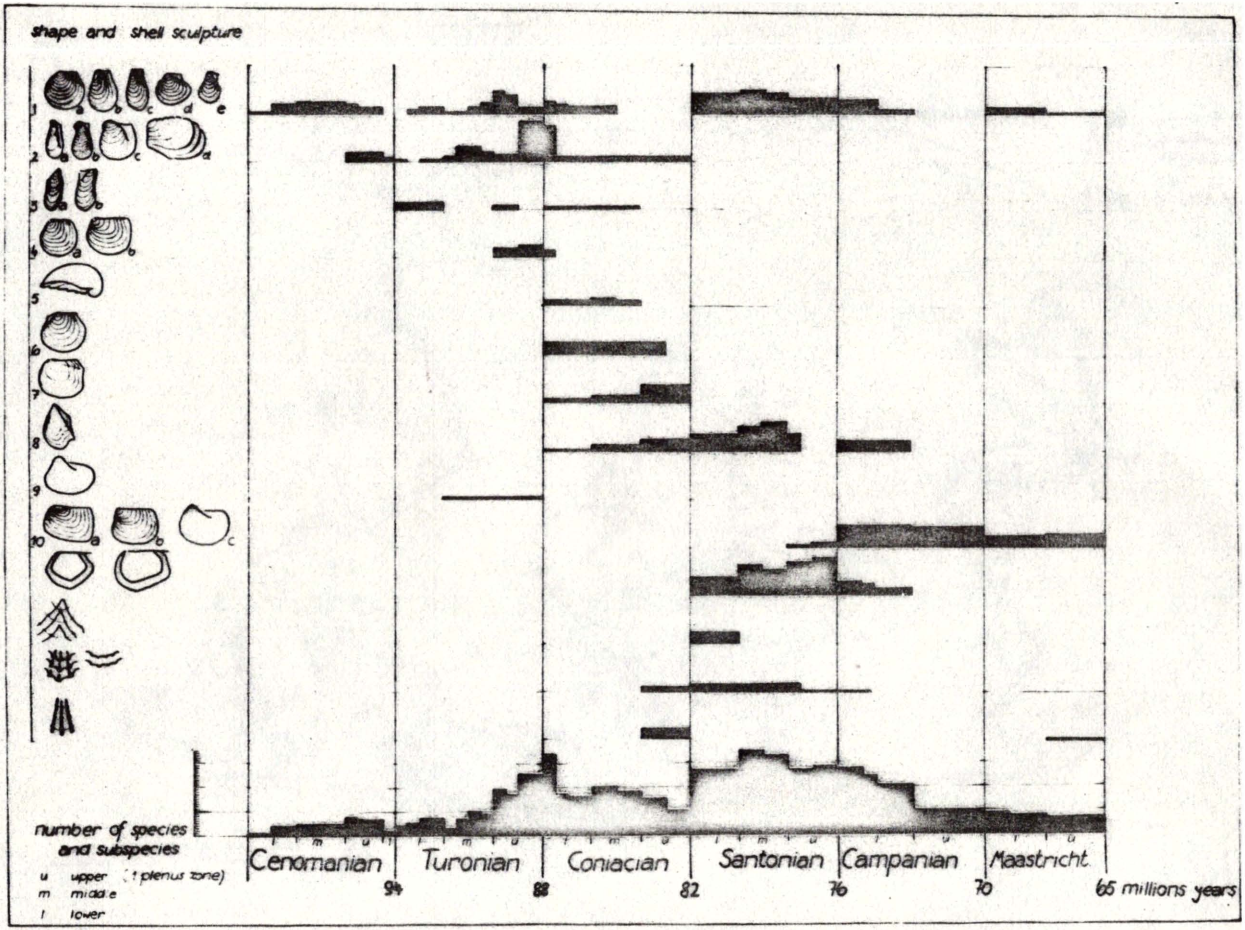

Fig. 2 K.A.Tröger

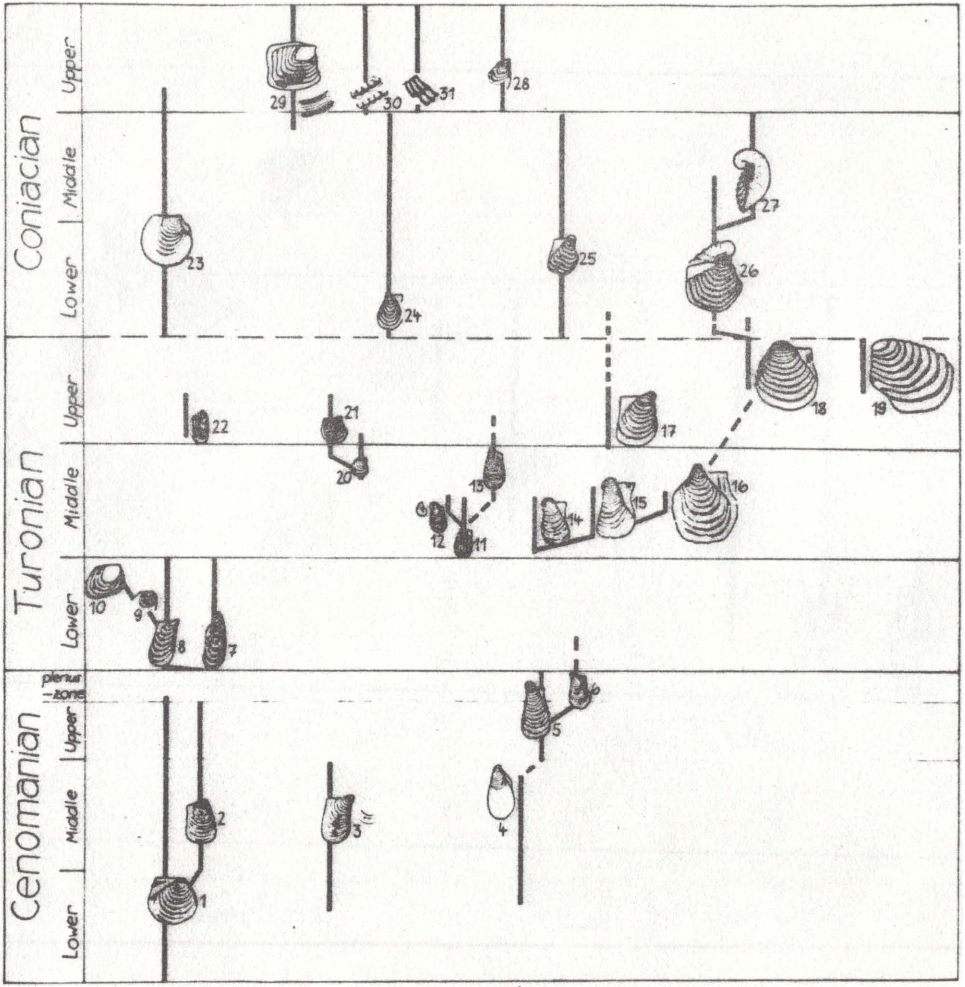

Fig. 3

K.A.Tröger

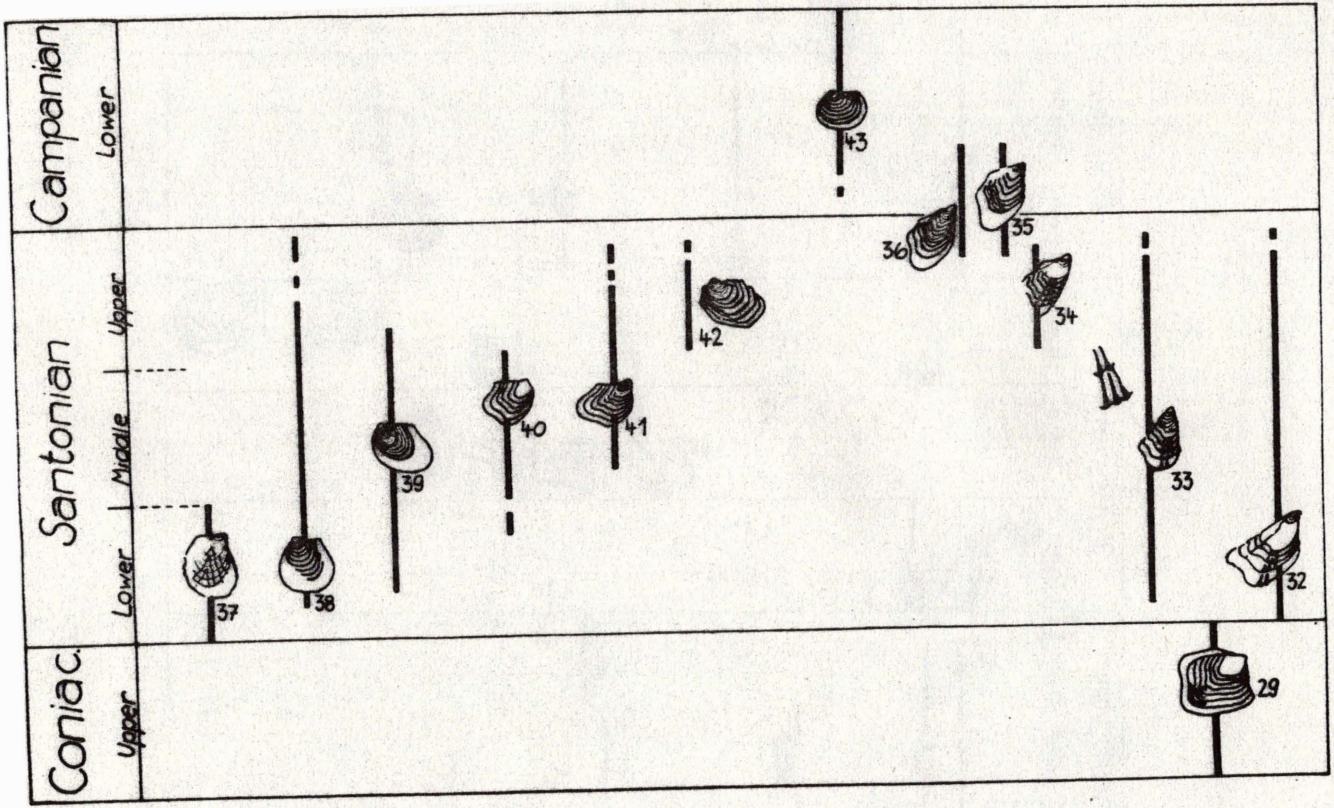

Fig. 4 K.A.Tröger

The <u>type 3</u> (obliquely ovate and elongate) is represented by Inoceramus labiatus (Schlotheim) and Inoceramus mytiloides Mantell from the Lower Turonian. According to H.Woods (1912) these forms arose from Inoceramus crippsi Mantell. According to A.Tsagareli (1942) they arose from Inoceramus bohemicus Leonhard (=Inoceramus pictus bohemicus Leonhard). From Inoceramus labiatus mytiloides Mantell we may observe a phylogenetic rank to Inoceramus labiatus hercynicus Petrascheck (Fig.3,numbers 7-10). Further representants of this shape type are distributed only in the Upper Turonian and the Coniacian. The forms of the Upper Turonian (Inoceramus fiegei mytiloidiformis Tröger Fig.3,number 22) are related to the Inoceramus-inconstans-group.

The <u>type 4</u> (subquadrate to suborbicular, subequivalve or inequivalve) is distributed especially in the Upper Turonian and Coniacian. Representants of this type are members of the Inoceramus-inconstans-group s.l. It may be, that there are transitions to the type 3 d. Sometimes it is difficult to put the boundaries between the Inoceramus-lamarcki-group and the Inoceramus-inconstans-group.

The shape <u>type 5</u> (highly inaequivalve, left valve coiled in spiral) can be observed especially in the Lower and Middle Coniacian. These are the so-called involute inocerames for example Inoceramus koeneni G.Müller and Inoceramus involutus Sowerby. Further investigations of the ligamental area must prove, if they arose from the Inoceramus-lamarcki-group (H.Woods,1912; K.A.Tröger,1969 - Fig. 3, numbers 26,27) or from the Inoceramus-inconstans-group (A.Tsagareli,1942). In every case they represent a final stage of evolution.

The <u>type 6</u> (subcircular to ovate forms with anterior area) is known especially from the Coniacian (Inoceramus-mantelli-group) but also rarely from the Santonian (Inoceramus cordiinitialis ickernensis Seitz - Lower Santonian, O.Seitz,1961).

The <u>type 7</u> (subquadrate to subcircular, equivalve with small radial depressions) can be observed in the upper part of Coniacian (Inoceramus subquadratus subquadratus Schlüter,Fig.3,number 29). According to O.Seitz (1970) the Sphenocerames (type 8) arose from Inoceramus-subquadratus-group.

The <u>type 8</u> (trigonal,equivalve with radial depressions) is distributed with some stratigraphic important species as Inoceramus pachti pachti Arch., Inoceramus cardissoides cardissoides Goldfuss, Inoceramus pinniformis Wilett, Inoceramus angustus Beyenburg and Inoceramus patootensiformis Seitz in the Santonian and Campanian age (Fig.4, numbers 32-36). Together with this type we find the maximum of the radial sculpture elements.

The type 9 was observed in the Turonian age.

The type 10,a,b (subquadrate with elongated hinge line) is represented by Inoceramus balticus Böhm, Inoceramus typicus Whitf., Inoceramus barabini Morton. The representants of this type are common in the Campanian and Maastrichtian sediments.

In the same manner as we can observe a change of the shape of the inocerame shell during the Upper Cretaceous, there can be seen a change of the shell sculpture, too, which was for the first time described by R.Heinz (1928). The first radial sculpture elements can be found at inocerames of Coniacian age. The maximum of the radial sculpture elements belongs to the Santonian age. A pentagonal course of the concentric undulations we can note especially during the Santonian age.

All these phylogenetic trends can be used for biostratigraphic purposes and can be observed in similar manner in other biogeographic provinces and subprovinces.

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