

I M M I G R A T I O N   O F   C E P H A L O P O D S   I N T O   T H E  
G E R M A N I C   M U S C H E L K A L K   B A S I N   A N D   I T S  
I N F L U E N C E   O N   T H E I R   S U T U R E   L I N E

M. Urlichs & R. Mundlos  
Stuttgart, Bad Friedrichshall

Abstract: Only few, probably more tolerant, genera of the stenohaline group of cephalopods have managed to get established in the Germanic Basin. These include *Germanonautilus*, *Serpianites* and *Paraceratites* as well as *Ceratites* which evolved from the latter in this new province. In *Serpianites* (Lower Muschelkalk/Upper Anisian) and the early ceratites (Upper Muschelkalk/Upper Anisian) we observe an iterative reduction of sutural complexity. Radiation of ceratites from the ancestral *Paraceratites* (*Progonoceratites*) *atavus* *atavus* took place during the *atavus* and *pulcher/robustus* Zones of the Upper Anisian.

#### INTRODUCTION

During the last decade major revisions of the Germanic Muschelkalk (AIGNER, 1982; DURINGER, 1982; HAGDORN, 1978; KOZUR, 1974; SCHULZ, 1972; SCHWARZ, 1975 etc.) have provided faciological and stratigraphic background on which the history of the cephalopods appears in a new light. This review builds also on previous taxonomic revision of part of the Muschelkalk cephalopods (URLICH & MUNDLOS, 1980, MUNDLOS & URLICH, 1984). We follow the stratigraphic schemes of GEYER & GWINNER (1964) for Southwest Germany and of KOZUR (1974) for the rest of the basin.

#### LOWER MUSCHELKALK

##### A. Geographic distributions

In Lower Muschelkalk times (Upper Anisian) the Germanic Basin had its connections with the Tethys in the east (Silesian-Moravian and East Carpathian Gates; see HAGDORN, this volume). The cephalopods reflect this immigration route, but their distributional patterns differ significantly from those of epibenthic immigrants. Thus

Reprinted from:

Lecture Notes in Earth Sciences, Vol. 1, Heidelberg 1985

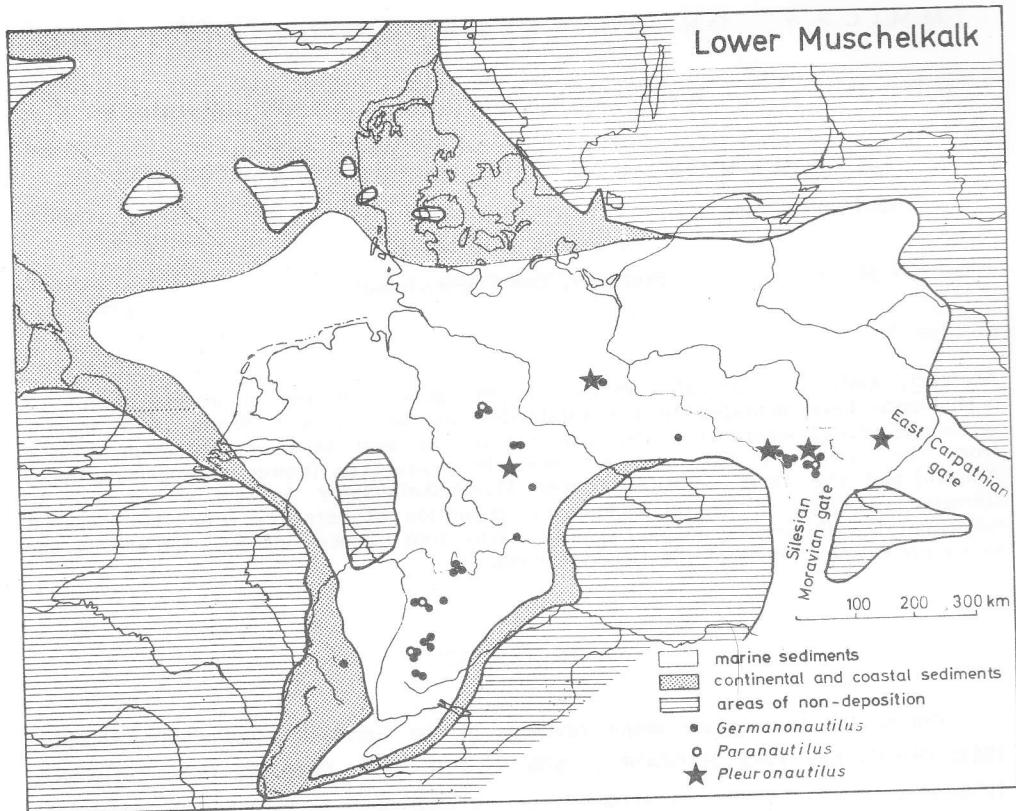


Fig. 1: Range of nautiloids in the Lower Muschelkalk (Upper Anisian) of the Germanic Basin. Paleogeography after ZIEGLER (1982), FISHER (1984) and SCHWARZ (1975). Fauna compiled after ALBERTI (1864), ASSMANN (1937), ECK (1872), FRANZ (1903), FRITSCH (1906), LAUGHIER (1963), MUNDLOS & URLICH (1984), RASSMUSS (1915), TRAMMER (1972), VOSSMERBÄUMER (1970, 1972), WALTHER (1927).

the nautiloids show high concentrations in the southwest (Fig. 1), which may be due to post-mortem drift in southerly currents of the otherwise poor swimmers (LEHMANN; 1976: 110). It should also be noted that the data base is different for the genera *Paranautilus* and *Pleuronautilus*, which are known only from a few localities, and for *Germanonautilus*, which is common throughout the basin.

The distribution of the ammonoids is similar: occurrences of *Serpianites antecedens* are sparse, but distributed all over the euhaline parts of the Germanic Basin. *Noetlingites strombecki* (see map by KELBER, 1977; Fig. 1) and *Beneckea buchi* have similar distributions and are therefore not contained in our paleogeographic map (Fig. 2). This map shows, however, the distribution of rarer ammonoids, of which *Acrochordiceras* is known only from Lower Silesia (NOETLING, 1880) and *Beyrichites* only from the Holy Cross Mountains (TRAMMER, 1972), i.e. from areas close to the

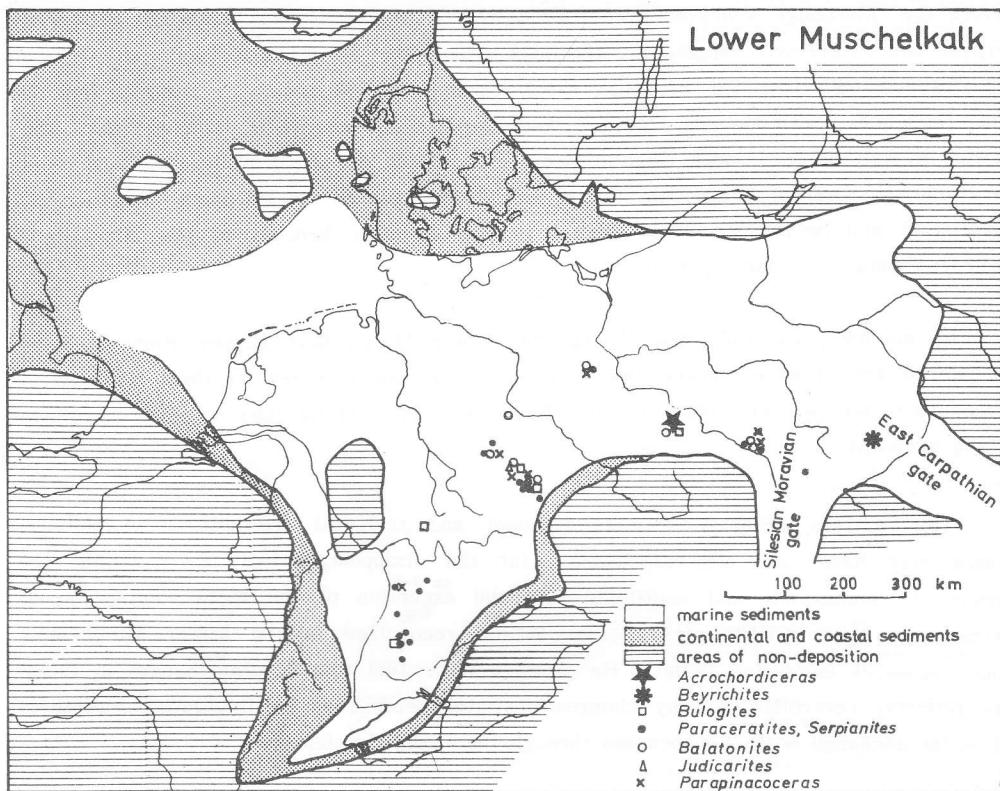


Fig. 2: Range of Ceratitaceae (except *Beneckeia* and *Noetlingites*) and *Parapinacoceras* in the Lower Muschelkalk (Upper Anisian) of the Germanic Basin. Paleogeography after ZIEGLER (1982), FISHER (1984) and SCHULZ (1975). Fauna compiled after ASSMANN (1937), BEYRICH (1854, 1858), CLAUS (1921), ECK (1865, 1891), FRITSCH (1906), GIEBEL (1853), MAYER (1971), NOETLING (1880), PICARD (1889, 1899), RASSMUSS (1915), ROTHE (1951, 1959), SCHMIDT (1907, 1935), TRAMMER (1972), VOSSMERBÄUMER (1970, 1972), WAGNER (1888, 1923), WALTHER (1927), WURM (1914).

gates. Immigration from this direction is also expressed by the higher species diversities in Silesia and Thuringia as compared to Hessen, Franconia and Swabia, where salinities temporarily were unfavourable for stenohaline genera.

#### B. Stratigraphic ranges

Species of *Balatonites* and *Bologites* are restricted to the lower and middle parts of the Lower Muschelkalk (Upper Anisian; KOZUR, 1974: 9, 12), while *Judicarites* is found only in its upper part. For some species, stratigraphic ranges differ in different areas. *Beneckeia buchi*, for instance, occurs in Thuringia from the "Myophorien-Schichten" (mu 1 $\alpha$ ) to the "Schaumkalk" (mu 2 $\alpha$ ), while in southwest Germany it appears not

before the "Mergelige-Schichten" and reaches to the "Spiriferinabank" (mu 2). Similarly, *Serpianites antecedens* ranges in Thuringia from the "Oolithbank" (mu 1B 00) to the "Schaumkalk" (mu 2x) and the Black Forest only in the *buchi* Horizon (mu 2) and the beds with *Homomya albertii*. *Noetlingites strombecki* is known from the Lower as well as the Upper Gogolin Beds (ECK, 1865: 59, 107), while it is restricted to a narrow interval below the "Oolithbank" (mu 1B 00) in Thuringia (VOLLRATH, 1924: 134) and occurs somewhat earlier in two dolimitic benches of the "Mergelige-Schichten" (mu 1; SCHMIDT, 1907: 28).

In summary we find that during the Lower Muschelkalk (Upper Anisian) many cephalopod genera have entered the Germanic Basin, but that few of them managed to spread into the western parts of the basin and only during part of their presence in the dispersal center.

This pattern probably reflects regional and temporal fluctuations in salinity, which may have been also responsible for the disappearance of newly immigrated species of ammonoids and nautiloids with the exception of the more tolerant genus *Germanonautilus*. SCHULZ (1972, Fig. 2) has recognized in the Lower Muschelkalk four cycles of increasing salinity. He also noted (p. 166) that "cyclic changes in facies are probably controlled less by changes in water depth than by fluctuating intensities of water exchange with the open sea through the Upper Silesian Gate".

#### MIDDLE MUSCHELKALK

After closure of the East Carpathian and shallowing of the Silesian-Moravian Gates by the end of the Lower Muschelkalk (SENKOWICZOWA & SZYPERKO-SLIWCZYSKA, 1975), a new connection was established in the Southwest of the basin (RI-YNASKA, 1975; Fig. 4), as evidenced by the appearance of the first ceratites in the upper part of the Middle Muschelkalk in Lorraine (LAUGHIER, 1963: 51).

#### UPPER MUSCHELKALK

##### A. Geographic distributions

By the beginning of the Upper Muschelkalk (Upper Anisian), the Silesian-Moravian Gate was closed and the East Carpathian Gate reopened to a limited extent (SENKOWICZOWA & SZYPERKO-SLIWCZYSKA, 1975). As a result, faunal immigrations were now limited to the Burgundy Gate.

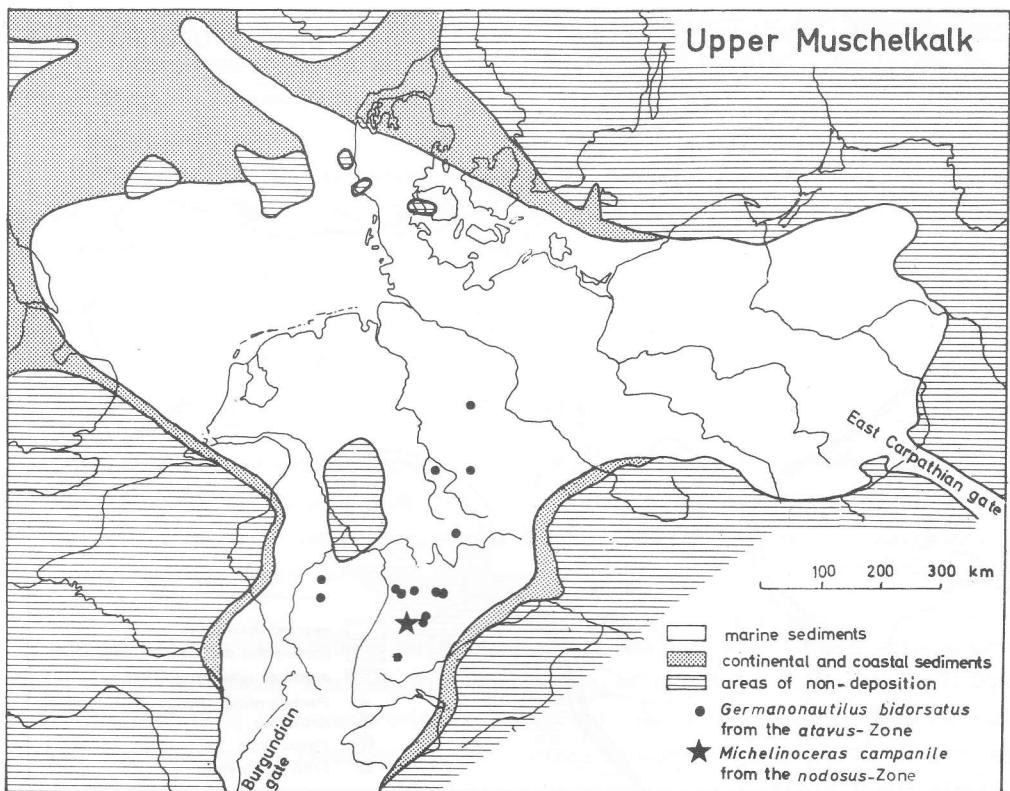


Fig. 3: Range of nautiloids in the *atavus* Zone (Upper Muschelkalk, Upper Anisian) of the Geramnic Basin. Paleogeography after ZIEGLER (1982) and SENKOWICZOWA & SZYPERKO-SLIWCZYN SKA (1975). Fauna compiled after ALBERTI (1964), BUSSE (1954), KELBER (1974), KÖNIG (1920), MUNDLOS & URLICHES (1984), STROMBECK (1849), URLICHES & SCHRÖDER (1980).

The first recorded occurrence of ceratites *Paraceratites* (*Progonoceratites*) *atavus* and *Ceratites* (*Doloceratites*) *primitivus* is below the "Hauptencrinitenbank" of Würzburg (GEISLER, 1939); but since two such beds are developed in this area (HOFFMANN, 1967: 22, 24) that GEISLER failed to identify, the exact level of these occurrences is Upper "Hauptencrinitenbank". The oldest well correlated occurrence *Paraceratites* (*Progonoceratites*) *flexuosus flexuosus* is in the "Trochitenbank 2" of Northern Baden (KÖNIG, 1920: 27; URLICHES & MUNDLOS, 1980: 3), which HAGDORN & MUNDLOS (1982: 347) identify with the lower "Hauptencrinitenbank" of Lower Franconia.

Somewhat higher in the section ("Haßmersheimer Mergel 2") two specimens of *P. (Pr.)atavus atavus* have been described (KÖNIG, 1920: 31), which are somewhat older than the fauna of the same species and its relatives recently discovered in the "Haßmersheimer Mergel 3" of Swabia immediately below "Trochitenbank 4" (UR -

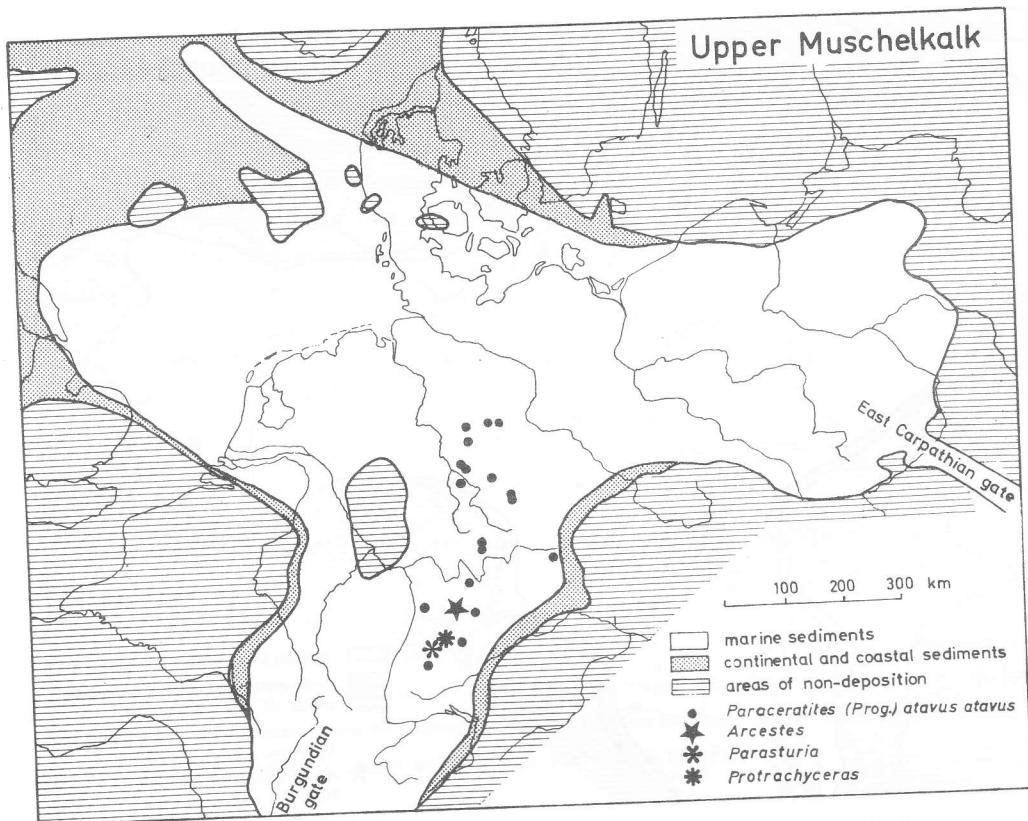


Fig. 4: Range of ceratitids in the *atavus* Zone (Upper Muschelkalk, Upper Anisian) of the Germanic Basin. Paleogeography after ZIEGLER (1982) and SENKOWICZOWA & SZYPERKO-SLIWCZYNSKA (1975). Fauna compiled after PENNDORF (1951), PHILIPPI (1901), RIEDEL (1918), ROTHE (1955), SPATH (1934), URLICH (1978), URLICH & MUNDLOS (1980).

LICH & MUNDLOS, 1980). Other occurrences of *P. (Pr.) atavus atavus* are known from Upper Franconia, Hessen, Thuringia and from the margin of the Harz Mountains (MAUBEUGE, 1947; exact locality unknown). Above (Fig. 3) as well as in Lorraine (MAUBEUGE, 1947; exact locality unknown). Above the "Trochitenbank" only *P. (Pr.) flexuosus flexuosus* and *C. (Do.) primitivus* seem to survive.

The fast dispersal of the ceratites from the western gate over the entire western part of the Germanic Basin during the *atavus* Zone was probably facilitated by the establishment of euhaline conditions. During the following *pulcher/robustus* Zone the ceratites reached also the eastern parts of the basin, for which the East Carpathian Gate did not provide a direct immigration route.

The spread of *Germanonautilus* follows a similar pattern. It first appears in south-west Germany in the "Zwergfauna-Schichten" immediately above the base of the

Upper Muschelkalk, i.e. earlier than the first ceratites (MUNDLOS & URLICHES, 1984; Fig. 6), whose range it shares in the *atavus* Zone (Fig. 3) as well as during the geographic expansion in subsequent stages.

Other cephalopods (*Michelinoceras*, Fig. 3; *Arcestes*, *Parasturia* and *Protrachyceras*, Fig. 4) are only known in Swabia, i.e. near the Burgundy Gate, through which they came either as unsuccessful immigrants or as drifted shells.

#### MODIFICATION OF SUTURE LINES

##### A. Lower Muschelkalk (Upper Anisian)

The transition from an ammonitic to a ceratitic configuration in the suture line in the earliest ceratites has been described earlier (URLICHES & MUNDLOS, 1980), so that a short review plus the comparison with a similar reduction in ceratite immigrants of the Lower Muschelkalk will suffice in this context.

In the Lower Muschelkalk *Serpianites antecedens* has the largest stratigraphic range. Upon reexamining material from the margin of the Black Forest (M. SCHMIDT 1935; MAYER, 1971) it became evident that it only partly matches the holotype (MB C 436) with respect to cross section, rib pattern and umbilical width. Associated are specimens that are more densely ribbed and have a wider umbilicus, and should properly be assigned to different species (see KOZUR, 1974: 11).

The close relationship of these forms to Alpine species has long been known. "Of all known ceratites, none is closer to *Ceratites antecedens* from the German Lower Muschelkalk than *Ceratites binodosus*. The only profound difference is in the suture line with shallow lobes that are uniformly incised only at the base and with broad, non-incised saddles" (MOJSISOVICS, 1882: 20). In perfectly preserved specimens, however - the one studied by us was affected by neither pressure solution nor deformation - one may see that the incisions climb the sides of the lobe and that the saddles are slightly undulose (Fig. 5b). Except for the undulose saddles, this configuration is so similar (deep, narrow lobes and narrow saddles) to that in *Paraceratites binodosus* (Fig. 5a) that "*Ceratites*" *antecedens* might be attributed to the same genus. Since juvenile stages, however, have a weak keel as characteristic for *Serpianites*, we tentatively assign "*Ceratites*" *antecedens* to this genus. In other specimen from the same horizon the lobes are not as deep and incised only at the base (Fig. 5c) suggesting that the suture line was quite variable in these populations. The specimens from the stratigraphically younger "Schaumkalk" (mu x) of Thuringia have "a broad and shallow first auxiliary lobe" (SCHMIDT, 1935: 205), which indicates that there has been a progressive "ceratitization" of the suture line also in this lineage.

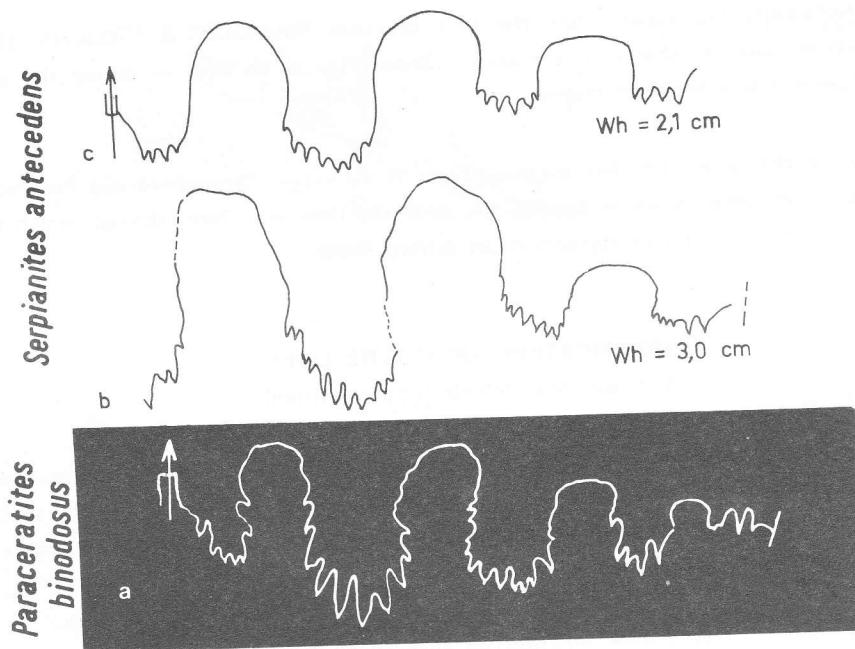


Fig. 5: External sutures of *Paraceratites* and *Serpianites* (drawn reversed)

a) *Paraceratites binodosus* (HAUER). Upper Anisian; Diliskelessi/ Turkey. Orig. ARTHABER 1915, pl. 12, fig. 1; SMNS 12505.-- x 3.

b) *Serpianites antecedens* (BEYRICH). Lower Muschelkalk; beds with *Homomya albertii*; Freudenstadt/Northern Württemberg. Orig. M. SCHMIDT 1935, pl. 13, fig. 6; SMNS 12420.-- x 2,2.

c) *Serpianites antecedens* (BEYRICH). Lower Muschelkalk; beds with *Homomya albertii*, Bösingen near Freudenstadt/Northern Württemberg. Orig. M. SCHMIDT 1907, pl. 2, fig. 6; SMNS 15105.-- x 3,0.

A ceratitic suture line is also observed in the Lower Muschelkalk species *Noetlingites strombecki*. But since its close relationship to *Grambergia* (KOZUR, 1974:11) has been challenged by PARNES (1975: 19), it can not be quoted as another case of secondary ceratitization.

A similar statement could be made for *Beneckeia*. In specimens from the Lower Muschelkalk of Thuringia (FRITSCH, 1906: 264; KOZUR, 1974: 10) the lobes are incised at the base. But neither relationships to *Intornites* (KOZUR, 1974) nor to *Beneckeia buchi* (with smooth lobes) have been settled.

#### B. Upper Muschelkalk (Upper Anisian)

The ceratites are one of the best known and representative examples of evolutionary radiation in marginal epicontinental seas. Having the highest similarity with paracera-

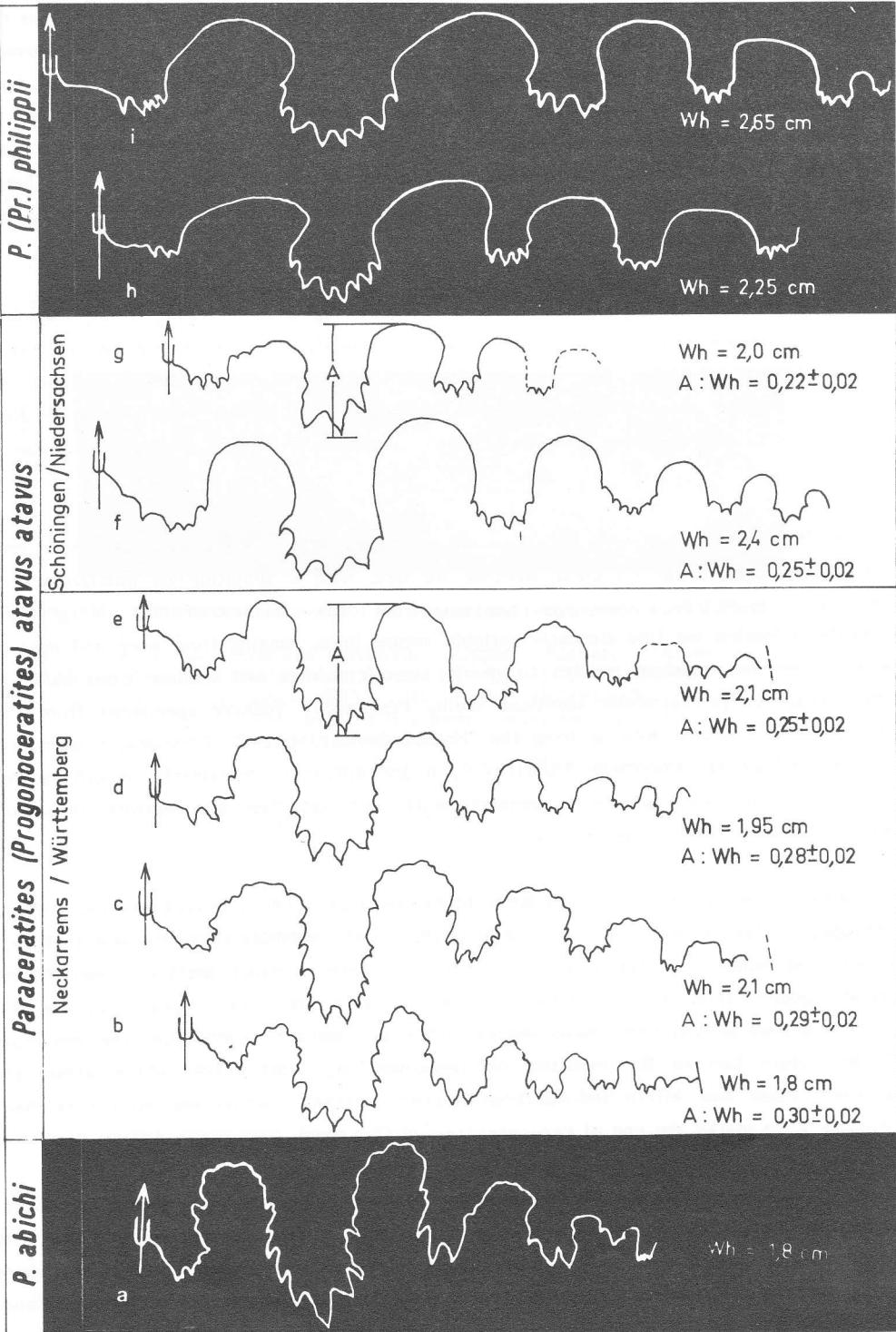
tites of the Tethys, *Paraceratites (Progonoceratites) atavus atavus* is regarded as the founder species. Its representatives from the Haßmersheim Marls 3 of Neckarrems (near Stuttgart) show a highly variable suture line. Some specimens (Fig. 6b-c) have highly undulose saddles and strong lobe incisions ascending at the flanks, similar to the sutures of Alpine species of *Paraceratites* (Fig. 6a). Other specimens from the same bed, however, have nearly smooth saddles. Ratios of sutural amplitude to whorl height (A/Wh) are 0,28 - 0,30 in specimens with strongly undulose saddles and 0,25 in individuals in which this undulosity is reduced.

Re-examination of specimens from a probably higher level (Elm, Lower Saxony), in contrast, showed that saddles were invariably smooth, and the incision of the lobes weaker and not ascending (Fig. 6 f-g). The A/Wh ratios of the shallow sutures are 0,22 - 0,25. This means that these forms already had a typical ceratitic suture line, although their shell geometry does not allow taxonomic separation from *P. (Pr.) atavus atavus*.

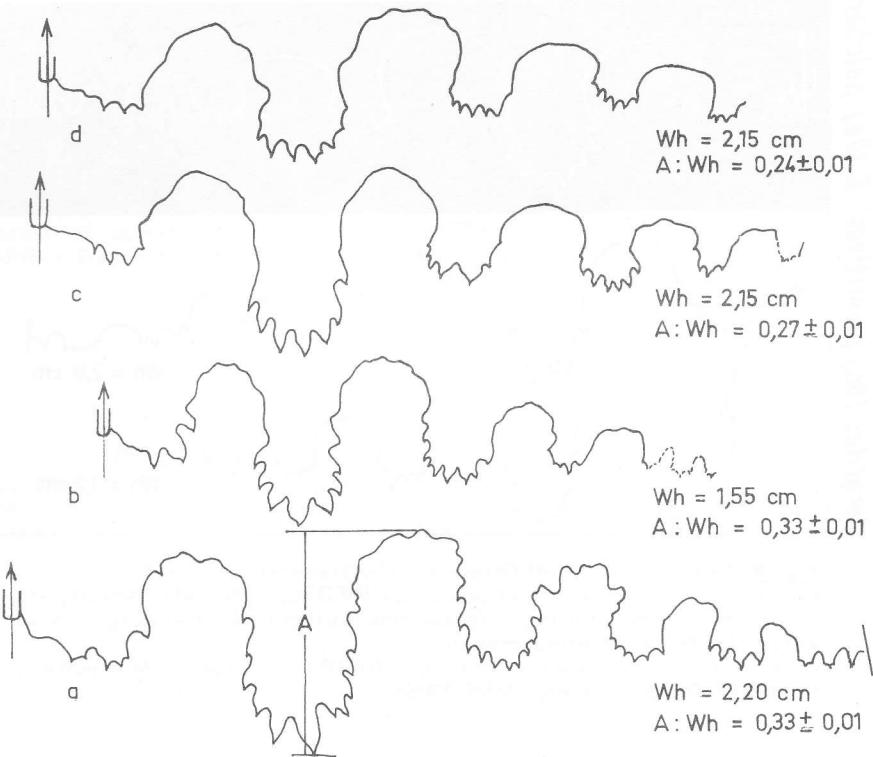
Since *P. (Pr.) flexuosus flexuosus* is associated with the previous species in very early assemblages, it is not clear whether we deal with a simultaneous immigrant or a descendant. In *P. (Pr.) flexuosus flexuosus* from the "Haßmersheimer Mergel 3" in northern Swabia we find similarly variable suture lines, ranging from deep and heavily incised lobes and undulose saddles to nearly smooth saddles and shallow lobes (A/Wh = 0,26 - 0,33) in geometrically identical shells. Presumably younger specimens from the Elm, Lower Saxonia, as well as from the "Haßmersheimer Mergel" of Swabia, in contrast, have reduced sutural amplitudes (A/WH = 0,23) and almost to completely smooth saddles (Fig. 7d). Again, shell geometry remains unaffected and does not warrant taxonomic separation even at the subspecies level.

Among the immediate descendants of *Paraceratites (Pr.) atavus atavus*, *P. (Pr.) philippii neolaevis* and *P. (Pr.) philippii philippii* resemble their ancestor in whorl section and number of marginal nodes, but they have a wider umbilicus and smooth sutural saddles (Fig. 6 h-i). Other subspecies, such as *P. (Pr.) atavus discus* and *P. (Pr.) atavus sequens* also have shallow lobes and smooth saddles i.e. the reduction of the suture line to the ceratitic configuration has clearly taken place within the Germanic Basin and within the subgenus *Progonoceratites*, whose end in the *pulcher/robustus* Zone marks the end of *Paraceratites* in this basin.

*P. (Pr.) atavus atavus*, however, seems to have given rise to a second and more successful lineage. It is heralded by specimens with a less arched venter, and with dichotomous sculpture and shallow lobes in the phragmocone. These features they share with *Ceratites (Doloceratites) primitivus*, in which the dichotomous sculpture extends



*Paraceratites (Progonoceratites) flexuosus flexuosus*



Wh = whorl height. A = amplitude, depth of the lateral lobe.

Fig. 7: Variations of the external sutures of *Paraceratites (Progonoceratites) flexuosus flexuosus* (PHILIPPI).-- x 3.

a-c) Upper Muschelkalk, *atavus* Zone, Haßmersheimer Mergel 3, Upper Anisian; Neckarrems/Northern Württemberg. SMNS 24570, 24601, 24603.  
 d) Upper Muschelkalk, *atavus* Zone, Upper Anisian. Schöningen/Niedersachsen. SMNS 23066.

Wh = whorl height, A = amplitude, depth of the lateral lobe.

Fig. 6: Phylogeny of the external sutures of *Paraceratites (Progonoceratites)*.-- x 3.

- Paraceratites abichi* (MOJSISOVICS); Upper Anisian, Schreyer-alm/Austria; SMNS 10987-1.
- Paraceratites (Progonoceratites) atavus atavus* (PHILIPPI); Upper Muschelkalk, *atavus* Zone/Upper Anisian, Neckarrems/Northern Württemberg; SMNS 24506, 24507, 24520, 24528.
- Paraceratites (Progonoceratites) atavus atavus* (PHILIPPI), Upper Muschelkalk, *atavus* Zone/Upper Anisian, Schöningen/Niedersachsen; SMNS 24562, 24563.
- Paraceratites (Progonoceratites) philippi neolaevius* (PENN-DORF); Upper Muschelkalk, *pulcher/robustus* Zone, Schöningen/Niedersachsen; SMNS 14691.
- Paraceratites (Progonoceratites) philippi philippi* (RIEDEL); Upper Muschelkalk, Schöningen/Niedersachsen, SMNS 24685.

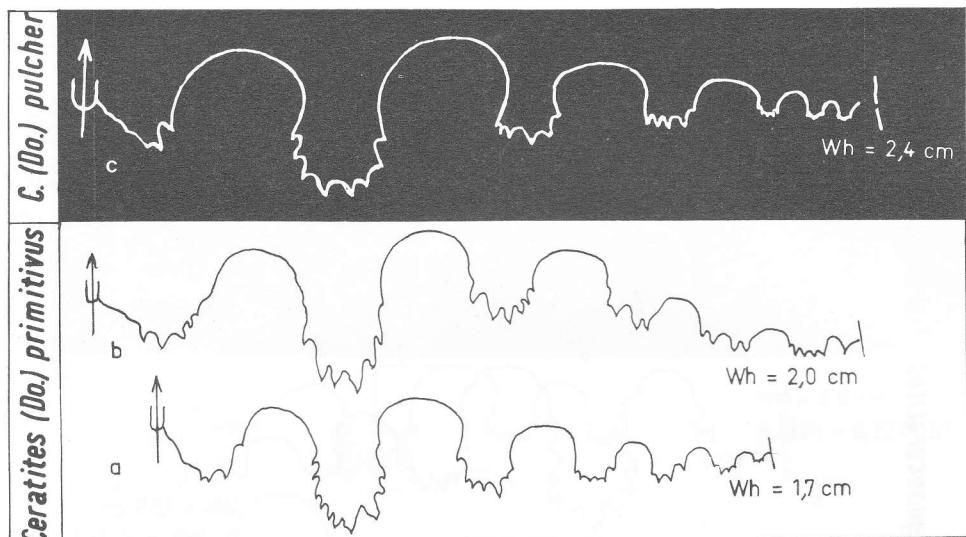


Fig. 8: External sutures of *Ceratites (Doloceratites)*.-- x 3.  
 a-b) *Ceratites (Doloceratites) primitivus* RIEDEL; Upper Muschelkalk, *ata-*  
*vus* Zone, Upper Anisian; Neckarrems/Northern Würtemberg; SMNS  
 24724, 24709; (b: reversed drawn).  
 c) *Ceratites (Doloceratites) pulcher* RIEDEL; Upper Muschelkalk,  
 Schöningen/Niedersachsen; SMNS 23068.

to the body chamber even in adult specimens, while the venter is flat or slightly arched and the suture ceratitic with ascending incisions (Fig. 8 a-b). *C. (Do.) primitivus*, in turn gave rise to *C. (Do.) pulcher* with a completely ceratitic suture line (Fig. 8c) and thereon to the radiation of the other ceratitids as outlined by WENGER (1957; Fig. 44).

Although taxonomic procedure requires clear distinction of features at the generic level, some tolerance must be allowed for in the transition fields. Therefore we assign the Germanic species of *Progonoceratites* to the morphologically similar *Paraceratites* of the Alpine province, even though their suture may be ceratitic. Only species in which this suture is combined with truly ceratitic shell geometries and sculptures should be assigned to the descendant genus *Ceratites*.

Since the suture line is variable in the earliest Germanic ceratites, separation of the subfamilies *Paraceratitinae* SILBERLING and *Ceratitinae* MOJSISOVICS is not justified. As neither SILBERLING (1962) nor TOZER (1981) provide a diagnosis for the subfamily *Paraceratitinae*, it is implied that its distinction should be mainly based on the suture.

Outside the Germanic Basin, ceratitic suture lines are known from *Gewanites* and *Israelites* from the Sephardic Province. This emphasizes that we deal with a general trend related to the immigration into marginal epicontinental basins. The multiple occurrence of such evolutions accounts for the renaissance of the ceratitic suture

line in the Middle Triassic in a fashion that had been dominant already in the Lower Triassic.

Acknowledgements: We thank A. Seilacher (Tübingen) for encouraging us to write this paper and for translating it. K. Bandel (Erlangen), A. Bartholomä (Neuenstein), H. Hagdorn (Künzelsau), H. Jaeger (Berlin) and H.U. Schwarz (Bochum) made valuable suggestions.

Location of specimens: MB = Paläontol. Museum of the Humboldt University, Berlin; SMNS = Staatliches Museum für Naturkunde, Stuttgart.

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