Heterochrony in the evolution of Late Devonian Ammonoids

DIETER KORN

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In the goniatite family Prionoceratidae, the transition from *Mimimitoceras* to *Balvia* provides an example of rapid size decrease resulting from progenesis. In the *Prionoceras-Mimimitoceras* stock the adult conch continued to be of rather uniform shape and size (about 60 mm) and species diversification was expressed mostly in changing juvenile morphology. In the *Balvia* branch, which had developed in the *Wocklumeria* Stufe, the adult size diminished strongly (not more than 16 mm). Progenetic *Balvia* displays conch morphology of ancestral *Mimimitoceras* juveniles, with distinct ornamentation types that were added terminally.

Key words: ammonoids, Late Devonian, Germany, evolution, heterochrony.

Dieter Korn, Institut und Museum für Geologie und Paläontologie, Eberhard-Karls-Universität, Sigwartstraße 10, 7400 Tübingen, Germany.

Introduction

Among invertebrates, ammonoids best exemplify evolutionary patterns such as heterochrony - the change in timing or rate of developmental events (McKinney & McNamara 1991) - that may be expressed as neoteny and progenesis. While studies on these subjects are numerous for Mesozoic ammonites (e.g. Kennedy 1977; Marchand & Dommergues 1988; Landman 1989), reports on Paleozoic equivalents are rare and limited to Carboniferous and Permian faunas (Swan 1988; Frest *et al.* 1981; Glenister & Furnish 1988).

Prionoceratids are Late Devonian to Permian goniatites, usually with subglobose or discoidal, involute conchs that invariably display five sutural elements (E, A, L, U, I in the symbolic representation of Wedekind). Their discontinuous evolution is characterized by several extinction events followed rapidly by extensive radiations, that alternate with long geological periods of slow evolution and character stasis. In addition, several evolutionary patterns such as paedomorphosis (neoteny, progenesis), bradytelic and tachytelic evolution are recognizable.

Extensive collections (about 1500 specimens) of Late Famennian prionoceratid ammonoids from the Rhenish Massif demostrate the relationship between 'normal' ancestral forms and descendant 'dwarfs' of the same ammonoid family. This dwarfism is a result of progenesis - the early offset of developmental events (McKinney & McNamara 1991) - resulting in paedomorphic goniatites displaying the preadult morphology of their non-progenetic ancestors. These new collections provide the basis for a comprehensive view of all known Late Devonian prionoceratid species. The ten newly erected species, briefly characterized in this report, will be fully described in a subsequent paper (Korn in press b) revising the Devonian and earliest Carboniferous prionoceratid ammonoids.

Material

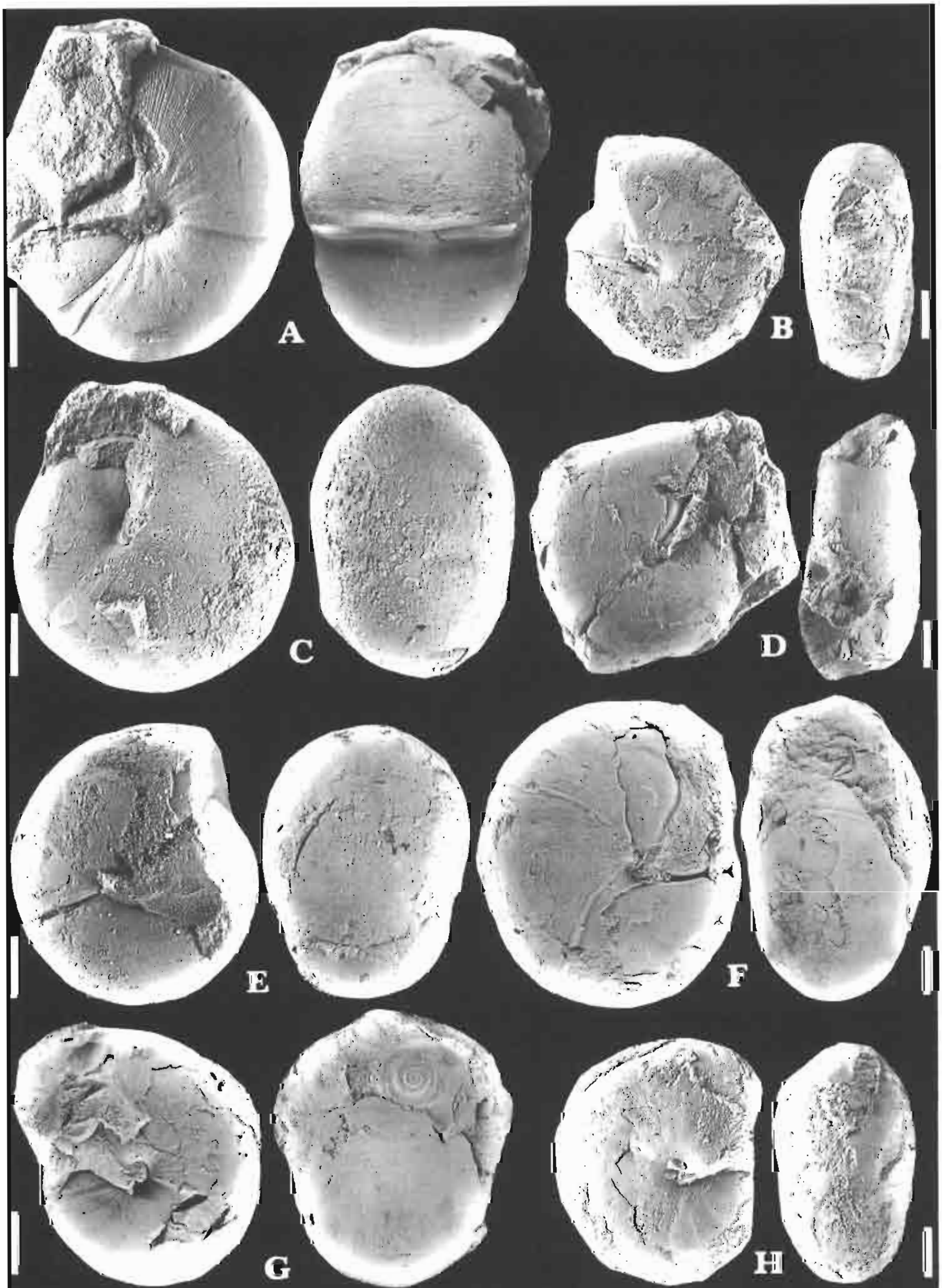
All study material was collected from cephalopod limestones outcropping in the Northern Rhenish Massif (coll. F. Ademmer, W. Bottke, D. Korn, F.A. Roters) and Lower Silesia (coll. D. Korn), silicified carbonates of the Launceston Area in Cornwall (coll. G. Trost) as well as from shales of the Maider Basin of Morocco (coll. J. Wendt). Rhenish and Silesian material is preserved with test ornament (Figs 1, 2), but specimens from the other localities are silicified or hematitized internal moulds.

The late Late Devonian Wocklumeria Stufe can be divided into five ammonoid zones (from beginning to end, Early *Kalloclymenia subarmata* Zone, Late *K. subarmata* Zone, Early *Parawocklumeria paradoxa* Zone, Late *P. paradoxa* Zone, *Acutimitoceras prorsum* Zone), of which some can be even finer subdivided (Korn in press c). At least, nine separate ammonoid assemblages within the *Wocklumeria* Stufe, five within the *Clymenia* Stufe, and four within the *Prolobites* Stufe can be distinguished (Fig. 3).

All specimens from the Rhenish Massif and from Lower Silesia (Dzikowiec) were precisely collected bed-by-bed (sometimes more than 100 specimens from a single horizon), allowing exact stratigraphical correlation to the standard ammonoid zonation. Thus, correct faunal assemblages can be reconstructed that allow determination of different species co-occurence. Very rich faunas from Ober-Rödinghausen, Dasberg and Müssenberg allow the identification of ancestor-descendant relationships within the family Prionoceratidae (Fig. 5).

Reversal in abundance of specimens during the *Wocklumeria* Stufe (Fig. 4: decreasing in *Mimimitoceras*, increasing in *Balvia*) preclude the

Fig. 1. Prionoceratid ammonoids from the Late Devonian *Wocklumeria* Stufe of the Rhenish Massif. Scale bar - 5mm. ❑A. *Mimimitoceras trizonatum* Korn 1988, holotype SMF 51250 from Reigern. ❑B. *Mimimitoceras lentum* sp. nov., holotype SMF 60160 from Ober-Rödinghausen. ❑C. *Mimimitoceras alternum* sp. nov., holotype SMF 60161 from Dasberg. ❑D. *Mimimitoceras geminum* sp. nov., holotype SMF 60162 from Ober-Rödinghausen. ❑E. *Mimimitoceras rotersi*



sp. nov., holotype SMF 60163 from Ober-Rödinghausen. ❑F. *Mimimitoceras liratum* (Schmidt 1924), Städtisches Museum Menden, unnumbered specimen, from Dasberg. ❑G. *Mimimitoceras fuerstenbergi* sp. nov., holotype SMF 60164 from Müssenberg. ❑H. *Mimimitoceras nageli* sp. nov., holotype SMF 60165 from Dasberg.

possibility that sexual dimorphism explains the dimensional differences outlined below.

Evolution of the family Prionoceratidae

The origin of the prionoceratid ammonoids is still unclear. A hypothetical ancestor of this group could be an Early Famennian member of the family Cheiloceratidae with involute conch form on all growth stages.

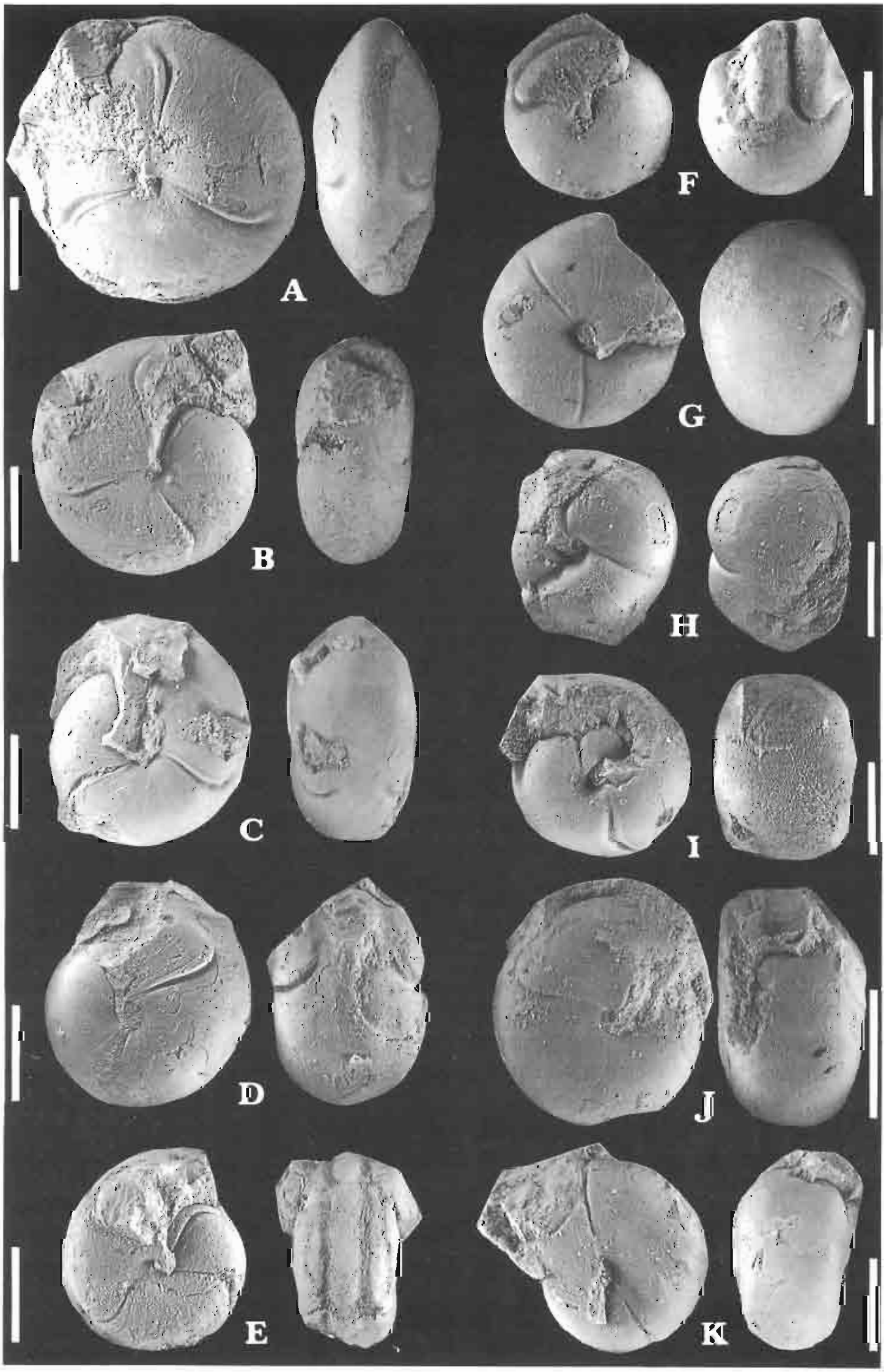
In the Late Famennian, the evolution of the prionoceratids parallels that of the clymeniids, which show a much broader radiation. Up to the Hangenberg Event (near the end of the Late Devonian), the prionoceratids are much less diverse (about 20 different species in three genera) compared with the co-occuring clymeniids (more than 40 genera with more than 300 species). However, the prionoceratids were the only ammonoid group that survived the Devonian-Carboniferous boundary, forming the origin of all later ammonoids.

Like most of the clymeniids, morphologically advanced Late Devonian prionoceratids did not survive the Hangenberg Event. Presumably starting from one single surviving species, a rapid adaptive radiation of the prionoceratids took place during the latest Devonian *Acutimitoceras prorsum* Zone and the earliest Carboniferous *A. acutum* Zone (Figs 3, 5). This remarkable diversification developed in the absence of any competition from other ammonoids (Korn in press a). As suggested by some similarities to the clymeniids in conch shapes, the prionoceratids exploited a range of niches that was occupied by the clymeniids in the Late Famennian. All these species became extinct without any descendants at the end of the Tournaisian stage.

Occurrence of prionoceratids in post-Devonian rocks is sporadic, comprising mainly large conchs that appear to be conservative elements in the ammonoid faunas. Except for a few modifications, their general morphology did not change during a timespan of about 50 million years.

Descendants of the prionoceratids (families Maximitidae and Pseudohaloritidae) are known from Late Carboniferous and especially Permian rocks (Frest *et al.* 1981). In analogy to the Late Devonian genus *Balvia*, these are very small ammonoids of usually 1 to 2 cm in diameter. They bear many peculiar types of ornamentation, such as ribs, nodes, constric- →

Fig. 2. Prionoceratid ammonoids from the Late Devonian *Wocklumeria* Stufe of the Rhenish Massif. Scale bar - 5mm. ❑A. *Balvia lens* sp. nov., holotype SMF 60166 from Effenberg. ❑B. *Balvia falx* sp. nov., holotype SMF 60167 from Ober-Rödinghausen. ❑C. *Balvia minutula* sp. nov., holotype SMF 60168 from Dasberg. ❑D. *Balvia globularis* (Schmidt 1924), SMF 60169 from Müssenberg. ❑E. *Balvia nucleus* (Schmidt 1924), SMF 60170 from Ober-Rödinghausen. ❑F. *Balvia biforme* (Schindewolf 1937), SMF 60171 from Effenberg. ❑G. *Mimimitoceras fuerstenbergi* sp. nov., paratype SMF 60172 from Dasberg. ❑H. *Mimimitoceras trizonatum* Korn 1988, SMF 60173 from Dasberg. ❑I. *Mimimitoceras liratum* (Schmidt 1924), SMF 60174 from Effenberg. ❑J. *Mimimitoceras geminum* sp. nov., paratype SMF 60175 from Ober-Rödinghausen. ❑K. *Mimimitoceras lentum* sp. nov., paratype SMF 60176 from Ober-Rödinghausen.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tions, spiral riblets and parabolic lappets that are not known from other Paleozoic ammonoids. In addition, they modify their suture lines within the basic set of five elements (E, A, L, U, I) from simple, rounded lobes to ceratitic and even ammonitic sutures. All prionoceratids became extinct during the Late Permian.

Prionoceras and *Mimimitoceras*

Morphological range of the non-progenetic Late Devonian prionoceratid genera *Prionoceras* and *Mimimitoceras* is very restricted: almost all the species are discoidal or globose, with a closed umbilicus and weak ornamentation. Both genera contain conservative forms with convex or slightly biconvex growth-lines and constrictions. In *Mimimitoceras*, the shell constrictions are accompanied by an apertural shell thickening.

During the Late Famennian, three radiations of the *Prionoceras-Mimimitoceras*-lineage are recognizable in the middle European faunas. The most important of these adaptive radiations was that of the *Wocklumeria* Stufe, with at least eight species. Within these species, major morphological specific differences occur in juvenile individuals between 8 and 20 mm in diameter, whereas adults of more than 25 mm in diameter appear rather uniform in different species. By contrast, juveniles and adults in *Prionoceras* do not differ significantly in their morphology.

The juvenile stages of species of *Mimimitoceras* show variations concerning both conch form and ornamentation. Some (*M. liratum, M. trizonatum*) have a slightly open umbilicus, whereas others are completely involute. Notably the course of the growth-lines and constrictions differs significantly: in some species (*M. liratum, M. trizonatum, M. fuerstenbergi*) they are biconvex with a tendency to form a ventrolateral salient, in others (*M. lentum, M. geminum*) they extend across the flanks and venter in an almost linear direction. The strongest constrictions can be seen in *M. trizonatum*, where they induce a triangular coiling of the whorls, whereas other species bear weaker shell constrictions that are always accompanied by the characteristic shell thickening. Maximal conch diameter of the *Mimimitoceras* species is about 60 mm.

Balvia

The short-ranging genus *Balvia* also shows a radiation within the *Wocklumeria* Stufe, where it is represented by at least six distinctive species. All share derived characters which support the view that they belong to a monophyletic taxon.

Species of *Balvia* differ significantly from the ancestral genus *Mimimitoceras*. The most important distinguishing feature is adult conch dimension: 'normal' *Mimimitoceras* adults reach up to 60 mm in diameter, whereas the diminutive *Balvia* range only up to 16 mm. Additionally, the biconvex course of growth lines in all species of *Balvia* shows a pronounced ventrolateral salient that is enhanced to form parabolic lappets

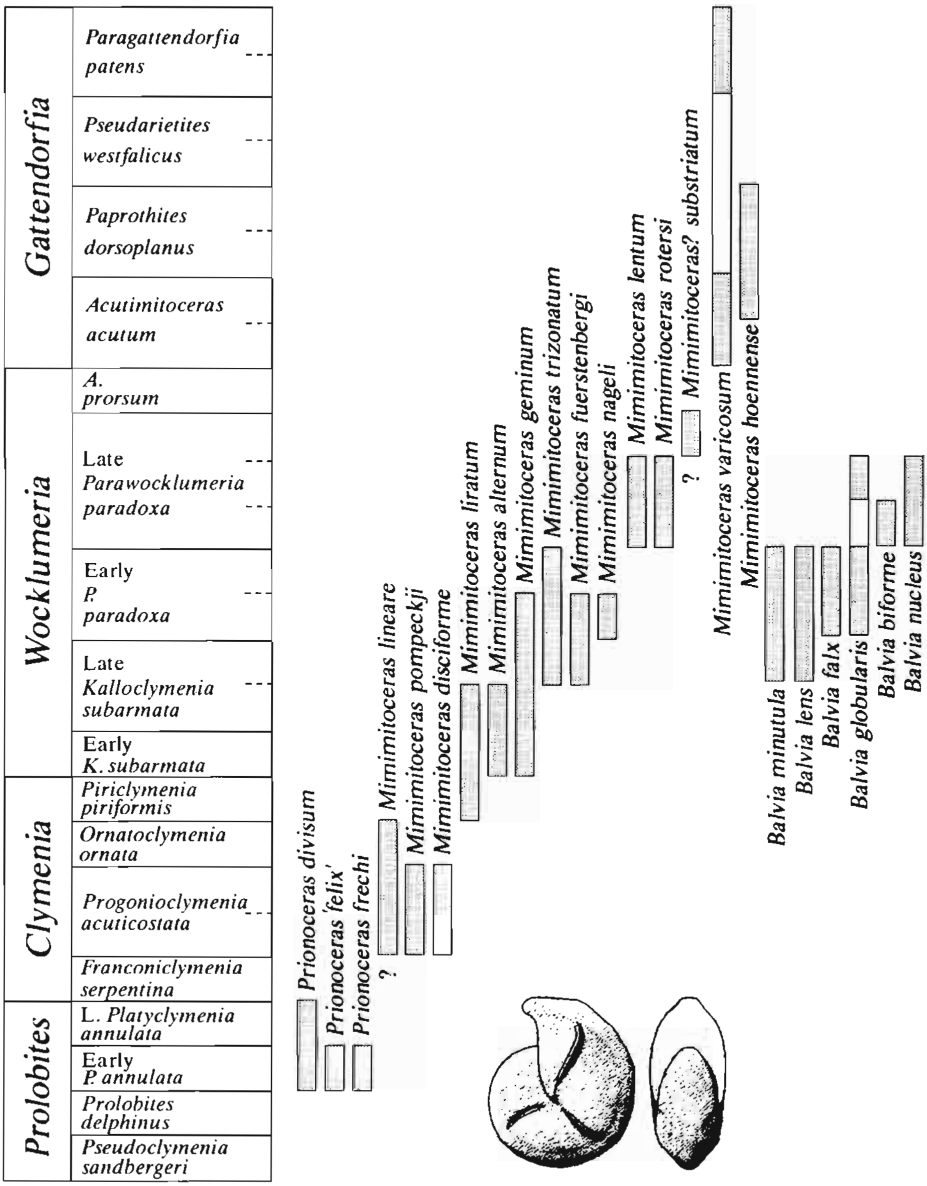

Fig. 3. Stratigraphical occurence of Late Devonian and earliest Carboniferous prionoceratid species. Based on data from the Rhenish Massif.

during phylogeny. The progressive specific diversification in the stratigraphically younger species of *Balvia* can also be observed in the form of characteristic longitudinal ventrolateral grooves, a feature not known from other Late Devonian prionoceratids.

Morphological homologies are the involute conch in adult forms and particularly the shell constrictions that are accompanied by an apertural

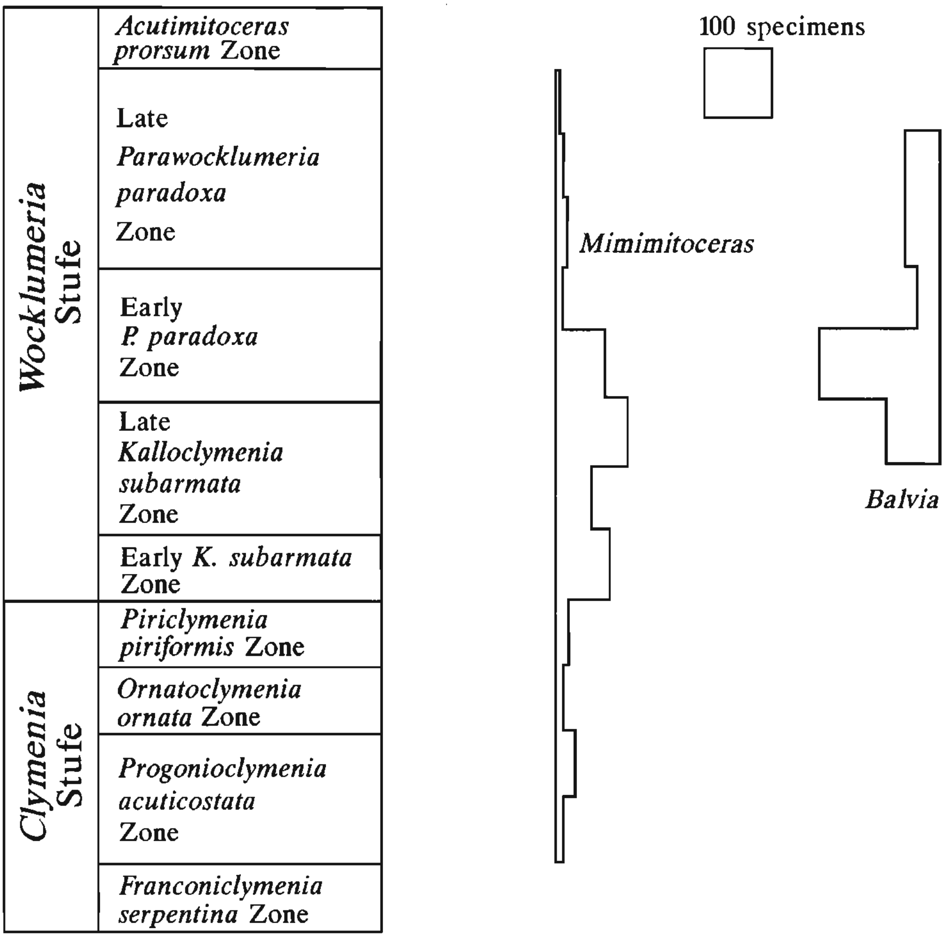

Fig. 4. Number of prionoceratid specimens. collected in particular horizon of the Late Devonian beds of the Rhenish Massif.

thickening. Furthermore, *Balvia* shows a slightly open umbilicus in very young stages, a feature common to some species of *Mimimitoceras*.

Evolutionary transition from *Mimimitoceras* to *Balvia*

Although a phyletic lineage on the species level cannot be presented. it seems to be clear which species comes closest to the proposed lineage.

Mimimitoceras liratum shares most features with *Balvia*. and it is also an attractive candidate to be the ancestor because of its stratigraphic proximity. At 10 mm diameter, the narrowly umbilicate pachyconic conch displays strong shell constrictions running in a slightly biconvex course over the flanks to form a low ventrolateral salient. Ventrally, constrictions

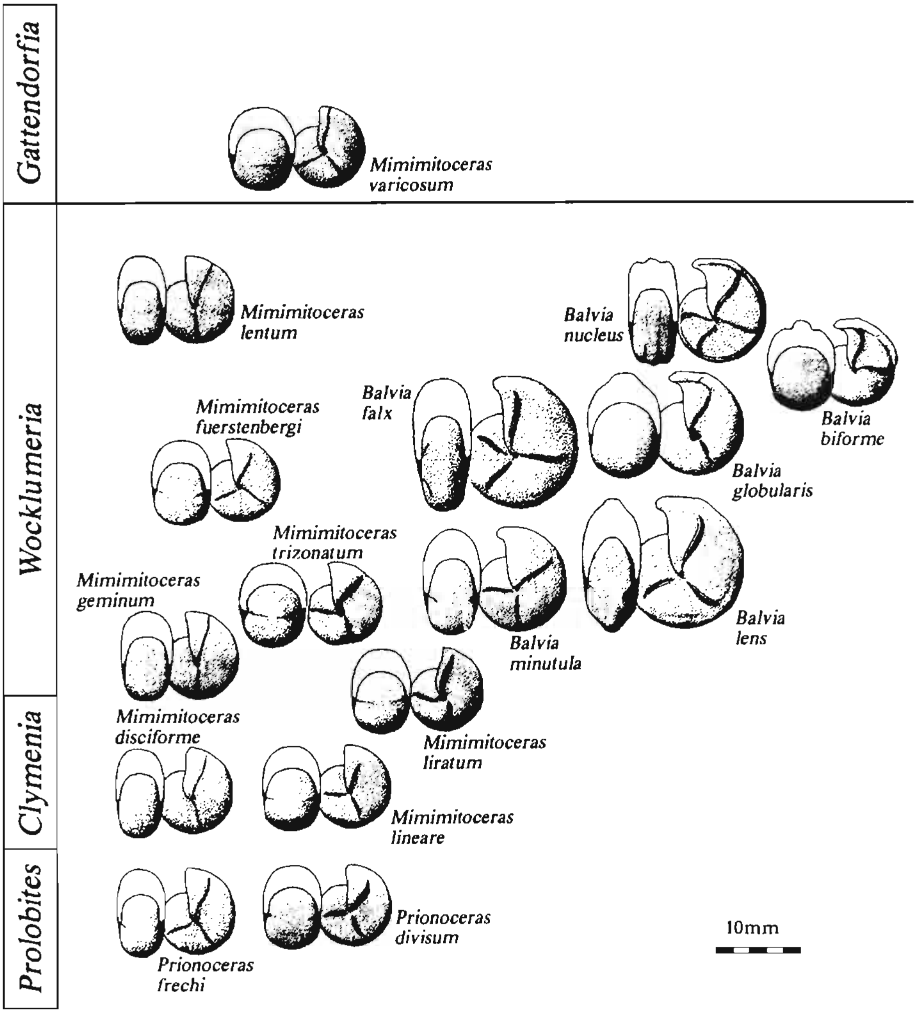

Fig. 5. Chronomorphoclines of Late Devonian prionoceratid species. All drawings in equal magnification, presented are juveniles of *Prionoceras* and *Mimimitoceras* and adults of *Balvia*.

become much weaker and are not visible on the mid-ventral area. This ornamentation closely resembles that of the proposed earliest *Balvia* species, *Balvia minutula*. Up to 8 mm diameter, individuals are similar to *M. liratum*, but a terminal stage with a much more distinct ventrolateral salient of the growth-lines and shell constrictions is then added.

The evolution from *Mimimitoceras* to *Balvia* and within the genus *Balvia* shows different evolutionary patterns. According to the terminology of Gould (1977), Alberch *et al.* (1979) and McNamara (1990) the abrupt dimensional decrease from *Mimimitoceras* to the diminutive *Balvia* is to be termed progenesis (local progenesis in terms of McKinney & McNamara 1991). Stratigraphically older species of *Balvia* bear the juvenile mor-

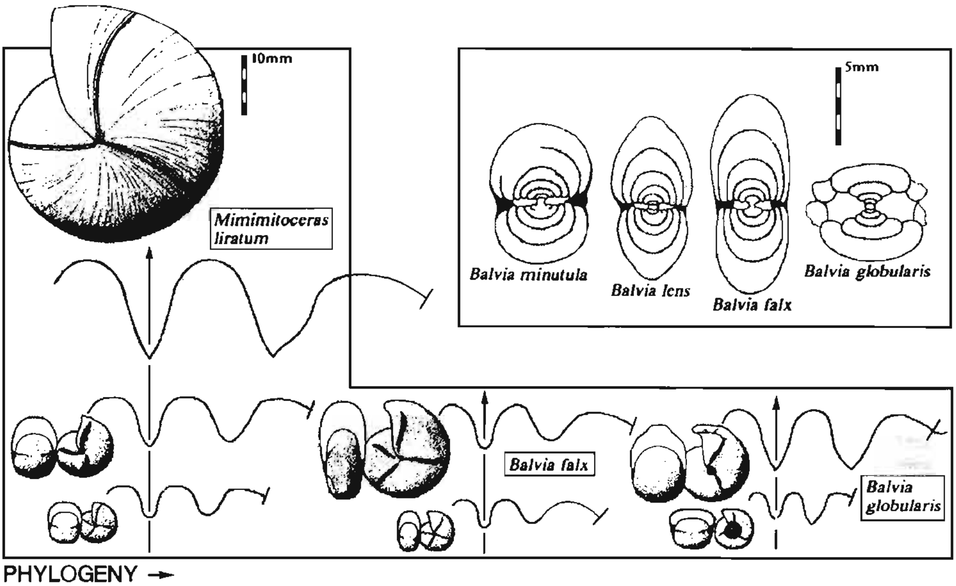

Fig. 6. Progenetic evolution from *Mimimitoceras* to *Balvia*.

phology of ancestral, non-progenetic *Mimimitoceras*. This can be best exemplified by the comparison of the suture line: Adult *Balvia falx* maintains the rounded lobes displayed by similar-sized specimens of the proposed ancestor species, *Mimimitoceras liratum* (note, however that in *M. liratum* the lobes become pointed later in ontogeny - Fig. 6).

Evolution within the genus *Balvia* is typical of acceleration (McNamara 1990). Later and more derived species of *Balvia* are characterized by the terminal addition of pronounced apertural projections and distinctive ventrolateral grooves. Furthermore, there is a trend toward greater umbilical diameter in the early stages and to pointed sutural lobes. *Balvia globularis*, for example, has a barrel-shaped conch that has pointed lobes even at a diameter of 4 mm (Fig. 6), a much smaller diameter than in compable species of *Mimimitoceras*.

Discussion

Progenesis is understood as a major process that increases evolutionary potential by allowing more adaptive flexibility (Gould 1977; Levinton 1988). In the case of the Late Devonian prionoceratids, it can be regarded as an important adaptive innovation, being followed by a rapid proliferation of the genus that enabled the diminutive *Balvia* to exploit a wider range of niches.

Adaptive radiation of the prionoceratids started already in the lower *Wocklumeria* Stufe (Fig. 2), where for the first time the preadult and the

Tab. 1. Matrix of the diagnostic characters of the *Prionoceras* species mentioned in the text.

	whorl width/diameter ratio	umbilicus	growth lines	shell constrictions
Prionoceras divisum (Münster 1832)	at 30mm Dm: 0.60 at 15mm Dm: 0.70	closed	fine; rectiradiate; slightly biconvex	usually three; moderately strong on flanks
Prionoceras frechi (Wedekind 1913)	at 30mm Dm: 0.45 at 15mm Dm: 0.50	closed	fine; rectiradiate; biconvex	three to four; moderately strong; on flanks
Prionoceras felix sp. nov.	at 30mm Dm: 0.70 at 15mm Dm: 0.80	closed	lamellose; rursiradiate slightly biconvex	none

adult morphology differed significantly. Thus an ecological separation of juveniles and adults can be postulated to have led to adaptations to local conditions that provided opportunity for precocious maturation.

Landman (1989) suggested that the adult progenetic *Pteroscaphites* lived in a part of the water column different from that of the adult non-progenetic *Scaphites*, and that the tiny mature *Pteroscaphites* commonly co-occurred with juvenile *Scaphites*. In analogy, mature *Balvia* individuals have been collected frequently from rocks containing abundant juveniles of *Mimimitoceras* and other ammonoids (especially clymeniids), as well as adults of other 'dwarfs', that also are probably progenetic ammonoids (e.g. *Glatziella, Linguaclymenia, Parawocklumeria*). In horizons containing large individuals, *Balvia* specimens are usually rare.

An ecological causation of heterochronic processes, as postulated by McKinney (1986), may be the reason for the high evolutionary rate of latest Devonian ammonoids. The evolution of the Late Famennian prionoceratids presumably reflects sea level fluctuations, especially a regressive trend that can be postulated for the middle part of the *Wocklumeria* Stufe (contrary to Johnson *et al.* 1985, who favored a transgressive trend). This shallowing evoked a diversification of the pelagic habitat, resulting in allopatric speciations that led to the adaptive radiation observed in both goniatites and clymeniids. Unstable conditions may have been the direct cause of rapid maturation (Gould 1977).

Diagnoses of new species

Mimimitoceras alternatum sp. nov.
Fig. 1C.

Holotype: SMF 60161 (coll. Korn 1989).

Type horizon and locality: Dasberg; early *K. subarmata* Zone of *Wocklumeria* Stufe.

Diagnosis.– Species of *Mimimitoceras* with the following characters: conch pachycone (ww/dm: 0.70) at 25 mm diameter, pachycone (ww/dm: 0.80) at 15 mm diameter and globose (ww/dm: 0.90) at 5 mm diameter.

Tab. 2. Matrix of the diagnostic characters of the *Balvia* species mentioned in the text.

	whorl width/diameter ratio	umbilicus	growth lines	shell constrictions and spiral grooves
Balvia minutula sp. nov.	at 12mm Dm: 0.65 at 6mm Dm: 0.75	after 4mm Dm closed	fine; biconvex; moderately high ventrolat. salient	three to four; moderately strong no spiral groove
Balvia lens sp. nov.	at 12mm Dm: 0.45 at 6mm Dm: 0.60	after 4mm Dm closed	fine; biconvex; high ventrolat. salient	three or four; moderately strong weak spiral groove
Balvia falx sp. nov.	at 12mm Dm: 0.50 at 6mm Dm: 0.55	after 6mm Dm closed	fine; biconvex; moderately high ventrolat. salient	three or four; moderately strong; no spiral groove
Balvia globularis (Schmidt 1924)	at 12mm Dm: 0.85 at 6mm Dm: 1.00	after 9mm Dm closed	fine; biconvex; very high ventrolat. salient	varying number; strong; in adult strong spiral groove
Balvia biforme (Schindewolf 1937)	at 10mm Dm: 0.80 at 6mm Dm: 0.90	after 7mm Dm closed	fine; biconvex; very high ventrolat. salient	varying number; strong; in adult very strong spiral groove
Balvia nucleus (Schmidt 1924)	at 12mm Dm: 0.60 at 6mm Dm: 0.60	after 4mm Dm closed	fine; biconvex; high ventrolat. salient	usually four; strong; in adult and praeadult strong spiral groove

Umblicus narrow in early stages, closed after 10 mm diameter. Growth lines fine, rursiradiate and convex. Radial shell constrictions only in early stages, in adults as internal shell wall thickenings.

Mimimitoceras fuerstenbergi sp. nov.
Fig. 1G.

Holotype: SMF 60164 (coll. Korn 1987).

Type horizon and locality: Müssenberg; early *P. paradoxa* Zone of *Wocklumeria* Stufe.

Diagnosis.– Species of *Mimimitoceras* with the following characters: conch pachycone (ww/dm: 0.75) at 25 mm diameter, pachycone (ww/dm: 0.80) at 15 mm diameter and globose (ww/dm: 0.90) at 5 mm diameter. Umbilicus narrow in early stages, closed after 8 mm diameter. Growth lines fine, rursiradiate and convex. Radial shell constrictions weak.

Mimimitoceras nageli sp. nov.
Fig. 1H.

Holotype: SMF 60161 (coll. Korn 1989).

Type horizon and locality: Dasberg; early *P. paradoxa* Zone of *Wocklumeria* Stufe.

Tab. 3. Matrix of the diagnostic characters of the *Mimimitoceras* species mentioned in this report.

	whorl width/diameter ratio	**umbilicus**	**growth lines**	**shell constrictions and apertural thickenings**
Mimimitoceras lineare (Münster 1839)	at 35 mm Dm: 0.65 at 20 mm Dm: 0.75 at 8 mm Dm: 0.75	closed	very fine rectiradiate slightly convex	at 35 mm Dm: none at 15 mm Dm: weak; very weak thickening
Mimimitoceras pompeckji (Schindewolf 1923)	at 25 mm Dm: 0.55	closed	very fine rursiradiate very convex	at 25 mm Dm: very weak; very weak thickening
Mimimitoceras disciforme (Schindewolf 1926)	at 25 mm Dm: 0.40 at 12 mm Dm: 0.55	closed	coarse rursiradiate very convex	at 25 mm Dm: very weak; very weak thickening
Mimimitoceras liratum (Schmidt 1924)	at 35 mm Dm: 0.70 at 20 mm Dm: 0.70 at 10 mm Dm: 0.80	after 5 mm Dm closed	fine rectiradiate slightly convex	coarse with coarse thickening; in youth rursiradiate
Mimimitoceras trizonatum Korn 1988	at 25 mm Dm: 0.70 at 15 mm Dm: 0.80 at 5 mm Dm: 1.00	after 10 mm Dm closed	fine rectiradiate slightly biconvex	coarse with coarse thickening; in youth very strong
Mimimitoceras alternatum sp. nov.	at 25 mm Dm: 0.70 at 15 mm Dm: 0.80 at 5 mm Dm: 0.90	after 10 mm Dm closed	fine rectiradiate convex	at 20 mm Dm: none at 10 mm Dm: weak; very weak thickening
Mimimitoceras fuerstenbergi sp. nov.	at 25 mm Dm: 0.75 at 15 mm Dm: 0.80 at 5 mm Dm: 0.90	after 8 mm Dm closed	fine rursiradiate convex	very weak, only on flanks visible; very weak thickening
Mimimitoceras nageli sp. nov.	at 25 mm Dm: 0.50 at 10 mm Dm: 0.70	closed	fine rursiradiate convex	at 20 mm Dm: very weak, only on flanks; very weak thickening
Mimimitoceras geminum sp. nov.	at 25 mm Dm: 0.50 at 10 mm Dm: 0.70	closed	fine rursiradiate biconvex	weak, convex, only on flanks visible; weak thickening
Mimimitoceras lentum sp. nov.	at 25 mm Dm: 0.50 at 10 mm Dm: 0.60	closed	fine rectiradiate biconvex	weak, linear, very weak thickening on flanks
Mimimitoceras rotersi sp. nov.	at 20 mm Dm: 0.75	closed	extremely fine rectiradiate convex	weak, linear, very weak thickening on flanks
Mimimitoceras varicosum (Schindewolf 1923)	at 25 mm Dm: 0.55 at 15 mm Dm: 0.65 at 5 mm Dm: 0.80	after 5 mm Dm closed	fine rectiradiate biconvex	coarse on flanks and venter with weak thickening
Mimimitoceras hoennense Korn in press a	at 25 mm Dm: 0.55 at 15 mm Dm: 0.65 at 5 mm Dm: 0.80	closed	fine rectiradiate convex	weak on flanks and venter with very weak thickening
Mimimitoceras? substriatum (Münster 1839)	at 25 mm Dm: 0.70	closed	very coarse rectiradiate convex	weak on flanks and venter with weak thickening

Diagnosis.– Species of *Mimimitoceras* with the following characters: conch thickly discoidal (ww/dm: 0.50) at 25 mm diameter, pachycone (ww/dm: 0.70) at 10 mm diameter. Umbilicus very narrow or closed in all stages. Growth lines fine, rursiradiate and convex. Radial shell constrictions very weak.

Mimimitoceras geminum sp. nov.

Fig. 1G.

Holotype: SMF 60162 (coll. Korn 1978).

Type horizon and locality: Ober-Rödinghausen; early *P. paradoxa* Zone of *Wocklumeria* Stufe.

Diagnosis.– Species of *Mimimitoceras* with the following characters: conch thickly discoidal (ww/dm: 0.50) at 25 mm diameter, pachycone (ww/dm: 0.70) at 10 mm diameter. Umbilicus very narrow or closed in all stages. Growth lines fine, rursiradiate and biconvex. Radial shell constrictions only visible on flanks. Growth lines and shell constrictions differ in their course.

Mimimitoceras lentum sp. nov.

Fig. 2K.

Holotype: SMF 60160 (coll. Korn 1978).

Type horizon and locality: Ober-Rödinghausen: late *P. paradoxa* Zone of *Wocklumeria* Stufe.

Diagnosis.– Species of *Mimimitoceras* with the following characters: conch thickly discoidal (ww/dm: 0.50) at 25 mm diameter, pachycone (ww/dm: 0.60) at 10 mm diameter. Umbilicus very narrow or closed in all stages. Growth lines fine, rectiradiate and biconvex. Radial shell constrictions only visible on flanks. Growth lines and shell constrictions run parallel.

Mimimitoceras rotersi sp. nov.

Fig. 1E.

Holotype: SMF 60163 (coll. Korn 1978).

Type horizon and locality: Ober-Rödinghausen: late *P. paradoxa* Zone of *Wocklumeria* Stufe.

Diagnosis.– Species of *Mimimitoceras* with the following characters: conch pachycone (ww/dm: 0.75) at 20 mm diameter, umbilicus closed. Growth lines extremely fine, rectiradiate and linear. Radial shell constrictions weak.

Balvia minutula sp. nov.

Fig. 2C.

Holotype: SMF 60168 (coll. Korn 1989).

Type horizon and locality: Dasberg; late *K. subarmata* Zone of *Wocklumeria* Stufe.

Diagnosis.– Species of *Balvia* with the following characters: conch pachycone (ww/dm: 0.65) at 12 mm diameter, pachycone (ww/dm: 0.75) at 6 mm diameter. Umbilicus very narrow or closed in all stages. Growth lines fine, biconvex. Three or four radial shell constrictions, no spiral groove.

Balvia lens sp. nov.
Fig. 2A.
Holotype: SMF 60166 (coll. Korn 1975).
Type horizon and locality: Effenberg; late *K. subarmata* Zone of *Wocklumeria* Stufe.

Diagnosis.– Species of *Balvia* with the following characters: conch thickly discoidal (ww/dm: 0.45) at 12 mm diameter, pachycone (ww/dm: 0.60) at 6 mm diameter. Umbilicus very narrow or closed in all stages. Growth lines fine, biconvex. Three or four radial shell constrictions, weak spiral groove.

Balvia falx sp. nov.
Fig. 2B.
Holotype: SMF 60167 (coll. Korn 1978).
Type horizon and locality: Ober-Rödinghausen; early *P. paradoxa* Zone of *Wocklumeria* Stufe.

Diagnosis.– Species of *Balvia* with the following characters: conch thickly discoidal (ww/dm: 0.50) at 12 mm diameter, thickly discoidal (ww/dm: 0.55) at 6 mm diameter. Umbilicus very narrow or closed in all stages. Growth lines fine, biconvex. Three or four radial shell constrictions, no spiral groove.

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Streszczenie

Ewolucja goniatytów Prionoceratidae w późnym famenie, w szczególności przejście od *Mimimitoceras* do *Balvia*, jest przykładem szybkiego ewolucyjnego zmniejszania rozmiarów dorosłych osobników w wyniku progenezy. W obrębie gałęzi *Prionoceras-Mimimitoceras* muszle dojrzałych osobników osiągały około 60 mm średnicy, nie zmieniając istotnie kształtów w trakcie wzrostu. Różnice między gatunkami objawiają się więc głównie w morfologii młodocianych muszli. W gałęzi *Balvia* która wyodrębniła się w piętrze woklumeriowym, rozmiary dorosłych osobników nie przekraczają 16 mm. Progenetyczna *Balvia* wykazuje więc cechy morfologiczne młodocianych osobników wyjściowego *Mimimitoceras*, ale z odmienną ornamentacją na końcowych stadiach ontogenezy.