Hydrodynamically controlled anagenetic evolution of Famennian goniatites from Poland

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This paper reports on the evolution of ammonoids belonging to the family Tornoceratidae from the Devonian of Janczyce in the Holy Cross Mountains, Poland. Steady and gradual changes in conch morphology of the goniatite lineage *Phoenixites frechi–Tornoceras subacutum–T. sublentiforme* occurred in concert with water shallowing during the deposition of the Lower Famennian cephalopod limestone. Biometric analysis of ammonoid conch and facies analysis of the cephalopod limestones have been applied to assess the possible relationship between shell geometry and environmental changes. Results show that ratios of whorl width / diameter as well as whorl width / whorl height decreased, while distance from the venter to the greatest whorl width / diameter increased with time, thereby reducing hydrodynamic drag of the shells, probably in response to increasing water turbulence. The interpretation presented here is in agreement with similar cases from the literature. However, this kind of environmentally controlled evolution has hitherto been recognized only in Jurassic and Cretaceous ammonoids. Conch morphology may be considered as an indicator of palaeobathymetry.

Key words: Ammonoidea, hydrodynamics, evolution, environmental changes, Devonian, Poland.

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Introdution

Ammonoids are one of the most prodigious groups of fossil animals; they have long attracted students of evolution due to their outstanding fossil record, extraordinary diversification, wide distribution and rapid extinction. While their fossil record is well documented, patterns of ammonoid evolution have yet to be fully explored. The most commonly postulated factor controlling ammonoid evolution is sea level-fluctuation (e.g., Bayer and McGhee 1984; House 1993; Korn 1995; Klug 2002; Wani 2003), which may lead to paedomorphosis, as documented by Korn (1995) for the Late Devonian ammonoids, as well as to other evolutionary changes in ammonoid shell morphology. Commonly, such patterns of ammonoid shell modification are observed in successions recording the regressive phases of transgressive-regressive cycles. Falls in relative sea-level and increases in water turbulence can trigger evolutionary changes manifested in gradual modifiactions in ammonoid shell geometry. This phenomenon has been well documented among Mesozoic ammonoids (e.g., Bayer and McGhee 1984; Jacobs et al. 1994). However, it is poorly known in their Palaeozoic counterparts. This paucity of data on evolutionary patterns among goniatitids is apparently caused by the scarcity of appropriate sections for population studies of this group.

The extraordinarily rich material from the lower Famennian cephalopod limestone from Janczyce (Holy Cross Mountains, Poland) offers new insights into patterns and factors controlling ammonoid evolution in the Palaeozoic. The assemblage from Janczyce is strongly dominated by tornoceratid goniatitids, a group with worldwide distribution. Its representatives are common in the Middle and Upper Devonian rocks of Europe (Holy Cross Mountains, Rhenish Slate Mountains, Harz, Montagne Noire, Pyrenees, Cantabrian Mountains), North Africa (Morocco, Algeria), Asia (Ural, Timan), Australia (Canning Basin), and North America (e.g., House and Price 1985; Becker 1993; Becker et al. 2000).

Institutional abbreviation.—MWG, Museum of the Faculty of Geology, Warsaw University, Warsaw, Poland.

Geological setting

The goniatitid assemblage described herein was collected from the Janczyce section (GPS position data: 50°46'1.20" N, 21°13'58.80" E), in the eastern Holy Cross Mountains, Poland (Fig. 1). The outcrop is situated in the eastern part of the Łagów Syncline in the Kielce Region. The goniatitids were

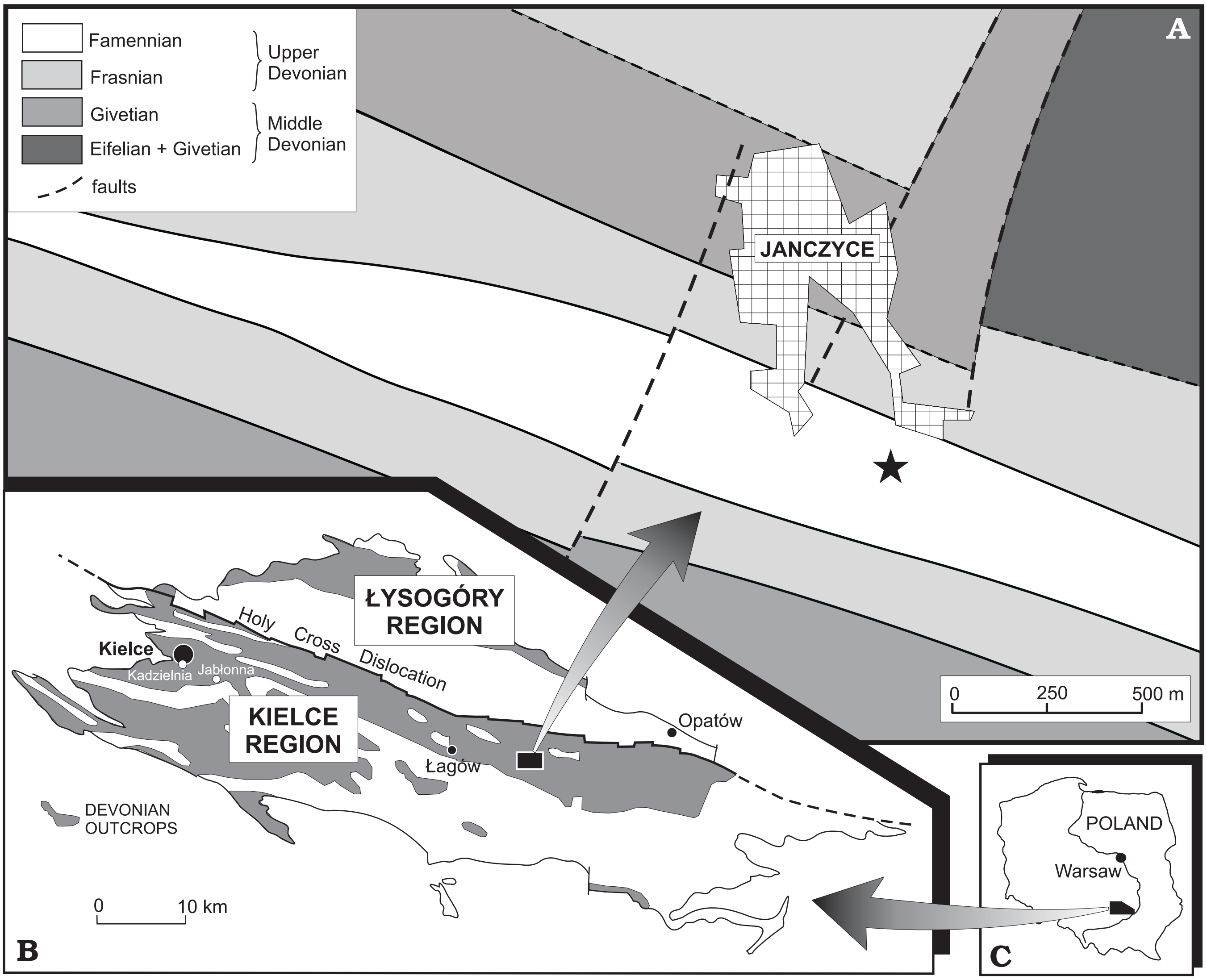


Fig. 1. Location of the Janczyce area (**A**) within the Holy Cross Mountains (**B**) and its position within Poland (**C**). The Janczyce outcrop is marked with an asterisk. Map of the Holy Cross Mountains modified after Mizerski (1995). Janczyce geological map after Narkiewicz and Olkowicz-Paprocka (1983).

collected from a 1.2 metre thick cephalopod limestone, part of the over 200 metres thick Łagów Beds (Makowski 1991; Matyja and Narkiewicz 1995; see Fig. 2). This unit is a series of generally poorly fossiliferous (except for small brachiopods, tentaculitids, and rare goniatitids), regulary bedded, dark-grey laminated marly limestones (Narkiewicz and Olkowicz-Paprocka 1983).

The Janczyce cephalopod limestone contains a rich cephalopod fauna (goniatitids, cyrto- and orthoconic nautiloids) together with rare brachiopods, gastropods, and bivalves. These rocks are very similar in lithology and age to other cephalopod limestone intercalations known from Europe and other parts of the world. They occur in the Upper Devonian of the Rhenish Slate Mountains and the Harz Mountains (Germany), the Montagne Noire (France), the Moravian Karst (Czech Republic), the Carnic Alps (Austria, Italy), the Cantabrian Mountains (Spain), and in the Anti-Atlas chains of southern Morocco (Wendt and Aigner 1985).

The cephalopod limestone of the Janczyce section was found in 1918 by Jan Samsonowicz, who mapped this area geologically (Makowski 1991). On the basis of goniatitid material from this section, Makowski (1962, 1991) described sexual dimorphism.

According to Makowski (1991), the Janczyce cephalopod limestone is lenticular. It splits into a number of layers which differ in colour and faunal composition. Makowski (1991) recognized five beds within this limestone (Fig. 2). He also noted the presence of two sedimentary discontinuity surfaces stained with oxidized iron minerals. These mark the boundaries between Beds 1–2 and 3–4.

The age of the cephalopod limestone has been determined using conodonts. Wolska (1967) identified the Fammenian *Palmatolepis crepida* Zone. More detailed studies have further constrained the age to Middle (Szulczewski 1992; Matyja and Narkiewicz 1995) or Upper *Palmatolepis crepida* Zone (according to Woroncowa-Marcinowska 2002).

Material and methods

The material used in this study was collected from a temporary outcrop—a trench dug in a field of a local farmer. After the fieldwork was finished, the exposure was covered. It is believed that the Janczyce site may be completely worked-out.

During the fieldwork in 2001 and 2002 a few hundred tornoceratid goniatites were collected. The first rich ammonoid material coming from this locality was collected by Henryk Makowski in the middle of the twentieth century. Makowski was interested in the problem of sexual dimorphism in ammonites, so that he collected and described only adult specimens. Moreover, he gave only the diameters of his specimens and did not measure other parameters of the shell (see Makowski 1991). We also noticed the presence of juvenile and adolescent specimens. Therefore, both collections were compared, but only the present authors' collection was used in this study. The measurements were taken from all ontogenetic stages of the ammonoids found. Accordingly, the original variability spectrum of the "palaeopopulations" for each part of the log was reproduced as accurately as possible.

Ammonoid specimens, especially large ones, are usually incompletely preserved. The body chamber is usually damaged, and fragments of the aperture are preserved only in a few specimens. However, most of the goniatitids extracted from the rocks are three-dimensionally preserved, which allowed us to use them in this study. The body chambers are usually filled with silty sediment while the phragmocones consist of clear calcite or are filled with silty sediment, which caused damage of the septa. Therefore in most specimens the early whorls cannot be observed. Ammonoids with incomplete conchs, usually caused by body chamber damage, specimen corrosion or erosion, were not used in this work. Many specimens have the wrinkle-layer structure preserved (see Niechwedowicz 2003) which is interpreted as "fingerprint"-like impression of the soft body (e.g., Senior 1971; Doguzhaeva and Mutvei 1996).

Description of goniatitid morphotypes

Most of the goniatitids examined belong to the family Tornoceratidae. The remainder represent the family Cheiloceratidae, including *Cheiloceras subpartitum* (Münster, 1839) which is the index fossil of the *Cheiloceras II* α Zone (zonation of Wedekind 1913).

Makowski (1991) was the first to observe the evolutionary lineage within Tornoceratidae from the Janczyce section. This evolutionary lineage is composed of three major species: *Phoenixites frechi* (Wedekind, 1918), *Tornoceras subacutum* Makowski, 1991 and *Tornoceras sublentiforme* Sobolew, 1914 (see Fig. 3). *T. sublentiforme* was regarded as a junior synonym of *T. typum* by Korn and Klug (2002). However, differences in conch morphology and suture line between these forms allow us to regard *Tornoceras sublentiforme* as a valid taxon.

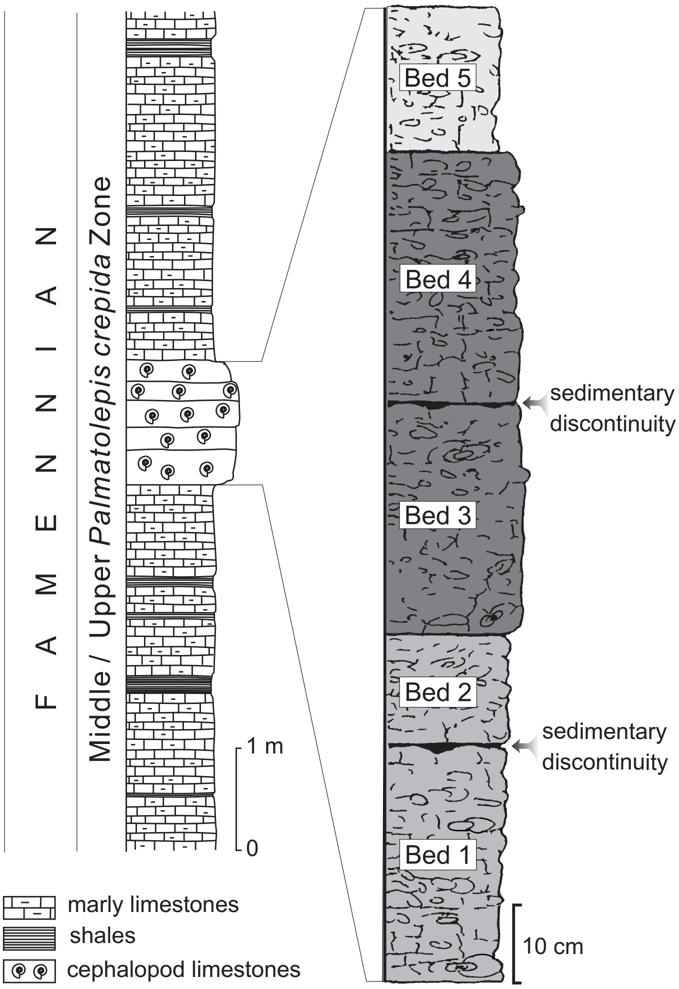


Fig. 2. Position of the studied Janczyce cephalopod limestones within the complex of laminated marly limestones (Łagów Beds). Cephalopod limestone log after Makowski (1991).

Becker (1993) suggested possible relationships between some representatives of the studied Tornoceratidae lineage and other Late Devonian species. According to him, *T. subacutum* and *T. sublentiforme* are closely related to the oxyconic *Oxytornoceras acutum*. However, there are some differences between these forms, especially in the suture line and shell ornamentation (presence of furrows in *O. acutum*; see Becker 1993: 363). Moreover, *O. acutum* is considerably smaller and stratigraphically younger. Thus, *T. subacutum* and *T. sublentiforme* seem to represent endemic forms that evolved in isolation, probably only in the Holy Cross Mountains Basin. Representatives of this lineage are also known from other localities in the Holy Cross Mountains: Kadzielnia (Makowski 1991) and Jabłonna (Jerzy Dzik, personal communication 2003); see Fig. 1. These taxa probably evolved from *Phoenixites frechi*, which is a long-ranging and

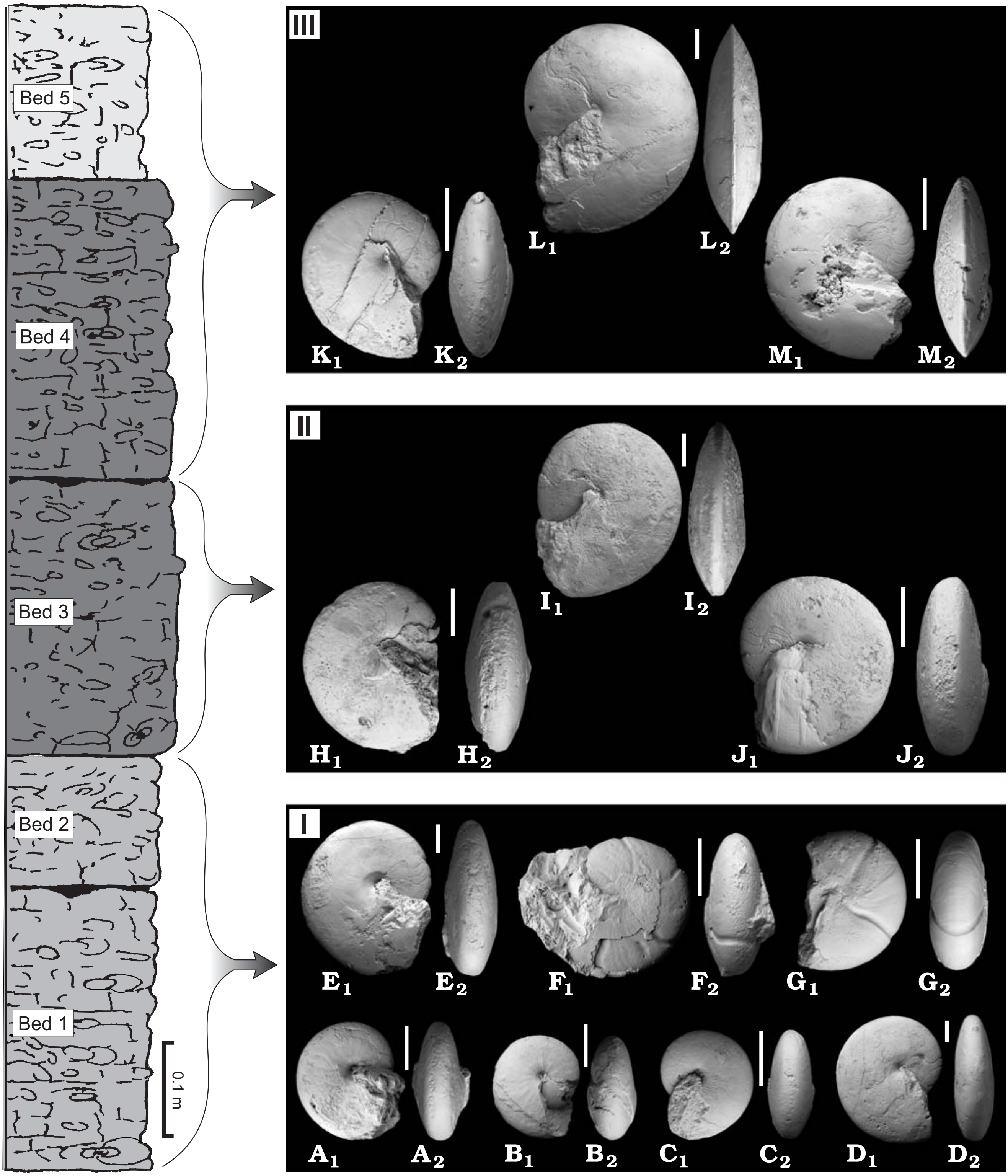


Fig. 3. Typical representatives of morphotype populations occurring in the cephalopod limestone sequence in Janczyce, Holy Cross Mountains, Poland. The log has been split into three parts, each of them containing different ammonoid assemblages. I (Beds 1, 2) contain *Phoenixites frechi* (Wedekind, 1918) specimens: MWG ZI/08/006/25 (**A**), MWG ZI/36/015 (**B**), MWG ZI/08/067 (**C**), and MWG ZI/08/024 (**D**); note also the presence of other goniatitids: *Falcitornoceras* aff. *korni* (Becker, 1984), MWG ZI/08/283 (**E**), *Simicheiloceras* cf. *schrickeli* Becker, 1993, MWG ZI/36/294 (**F**), and *Cheiloceras* (*Cheiloceras*) *subpartitum* (Münster, 1839), MWG ZI/36/293 (**G**). II (Bed 3) contains *Tornoceras subacutum* Makowski, 1991 specimens: MWG ZI/36/152 (**H**), MWG ZI/08/040 (**I**), and MWG ZI/08/042 (**J**), some of ammonoids belonging to this group (those with rounded venter) display intermediate characters between *Phoenixites frechi*–*Tornoceras subacutum*. III (Beds 4, 5) contain *Tornoceras sublentiforme* Sobolew, 1914 specimens: MWG ZI/08/008/54 (**K**), MWG ZI/08/055 (**L**), and MWG ZI/08/009/17 (**M**). A_1–K_1, lateral view; A_2–K_2, ventral view. Note the trend in morphological shell modifications observed on ascending the log. Scale bars 10 mm.

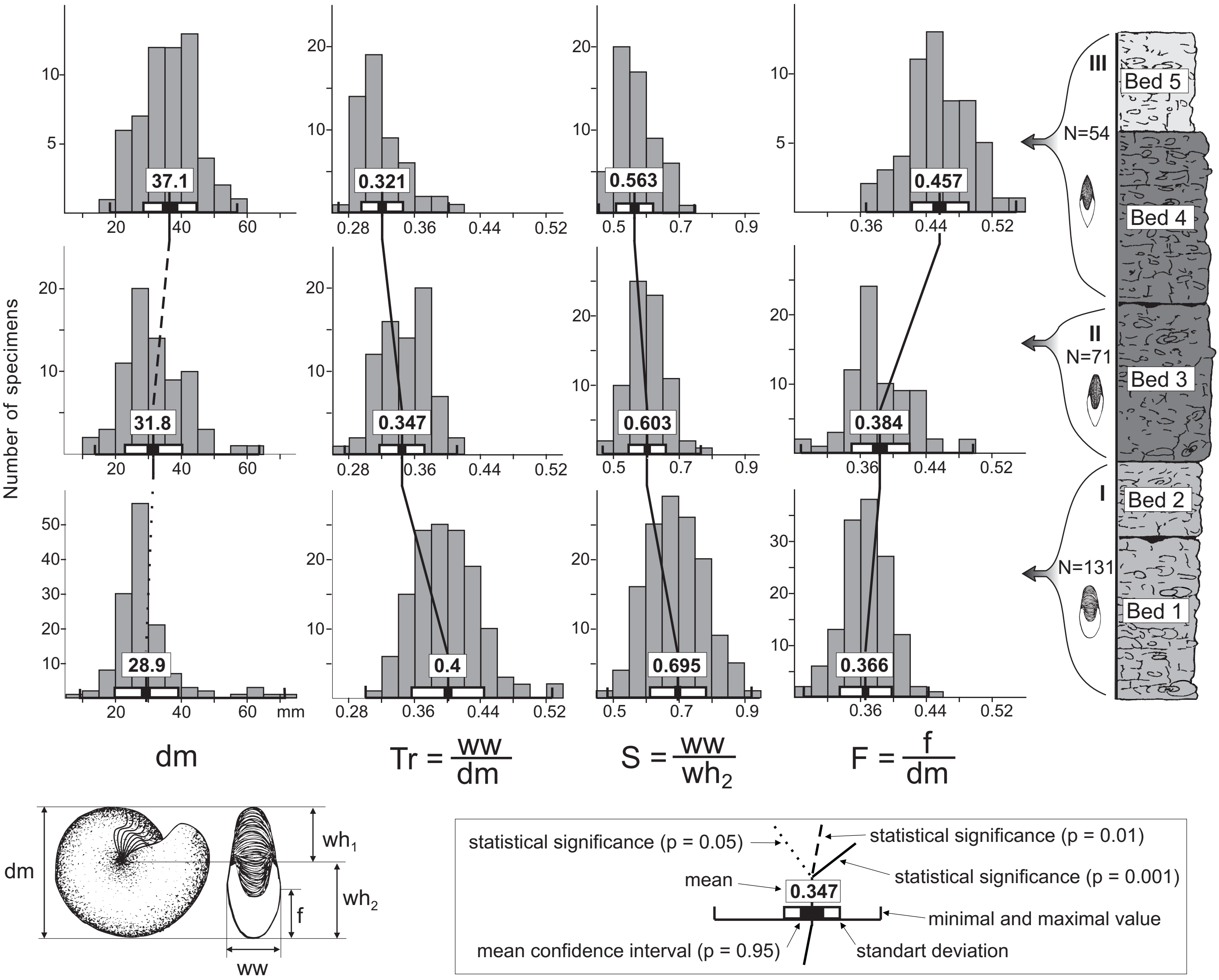


Fig. 4. Results of the biometrical analyses. Trends in shell shape modifications can be clearly seen in succeeding beds of the analysed section. The values of the morphological parameters *Tr* and *S* decrease with time while the values of the parameter *F* tend to increase upwards through the succession. This is expressed in the disc-shaped and more compressed conchs of the ammonoids from Beds 4 and 5. Mean values of the diameter also increase upwards. Note that differences between the means of the morphological parameters (*dm, Tr*, *S*, and *F*) are statistically significant (p = 0.05–0.001). See the text for the details. I–III, morphotype populations.

geographically widespread Devonian form (Becker 1993; Becker et al. 2000).

Each species belonging to the studied lineage occurs in a different part of the succession (see Fig. 3) and exhibits high intraspecific variation (see histograms in Fig. 4). Some of the specimens are intermediate forms between named taxa and cannot be easily assigned to any of them. This confirms that the succession of goniatitids found in the Janczyce section is a good example of an anagenetic evolutionary lineage.

Another example shows a different possible interpretation of taxonomy within ammonoids. An ammonoid assemblage from the Triassic of Siberia, with similar variability in shell morphology to those from Janczyce, was studied by Dagys and Weitschat (1993). Although adult conch morphology of those ammonoids differs considerably, their early ontogenetic stages are nearly identical. Hence all specimens were assigned to one species. By analogy, it cannot be excluded that all ammonoids from Janczyce cephalopod limestone might also belong to a single species. We had difficulties in identifying some specimens, especially from the group II in Fig. 3, as some of them (e.g., Fig. 3J) show intermediate characters between *Phoenixites frechi–Tornoceras subacutum*. It clearly indicates that the systematics of the Famenian goniatites requires thorough revision. This is, however, beyond the scope of our paper.

Because of the various ways in which the fauna studied may be interpreted taxonomically, the goniatitids were investigated not as species but rather as populations of morphotypes from successive Beds. They were separated into the following three morphotype populations (Fig. 3):

(I) Morphotypes with involute, slightly depressed discoconic shells, with a rounded venter; found in Beds 1 and 2; see Fig. 3 (I). Type-representative taxon of this group is *Phoenixites frechi*. This sample consists of 131 specimens.

(II) Morphotypes with a more compressed, involute conch and a rounded to subtrapezoidal shaped venter, found in Bed 3. 71 specimens were used in the study, with *Tornoceras subacutum* as a typical representative; see Fig. 3 (II).

(III) The most slender morphotypes among those investigated; have involute, oxyconic shells, with a sharp-edged venter, some forms having a slightly rounded venter and in some a slight keel appears but only on the body chamber; found in Beds 4 and 5; see Fig. 3 (III). *Tornoceras sublentiforme* is typical of this group. The sample consists of 54 specimens.

All studied Tornoceratidae have involute conchs. The body chamber extends more than 270°. Suture lines are very similar in all populations (see Niechwedowicz 2003). The slenderness of the shell in almost all specimens studied can be categorized as either less compressed ($Tr = 0.3–0.5$; *sensu* Jacobs 1992) or compressed with Tr mean values less than 0.3 (for definition of morphological parameters see Fig. 4).

Besides the goniatite species mentioned above, the Janczyce cephalopod limestone also contains other tornoceratids: *Falcitornoceras* aff. *korni* (Becker, 1984), *Simicheiloceras* cf. *schrickeli* Becker, 1993 (see Fig. 3), and *Exotornoceras superstes* (Wedekind, 1908).

Biometric analysis

Measurements of the ammonoid conch were taken from the body chamber (as shown in Fig. 4) using calipers and rounded to 0.1 mm. Altogether, 256 specimens have been measured: 131 from the first morphotype population (Beds 1–2), 71 from the second (Bed 3) and 54 specimens from the third (Beds 4–5). As mentioned above, the measurements were all taken from ammonoid growth stages present within the Janczyce cephalopod limestone. Sexual dimorphism, although suggested by Makowski (1962, 1991), appears to be doubtful within the studied assemblage and was not taken into account in this investigation. Results of measurements are shown in Fig. 4.

The simplest way to document evolutionary trends is to plot morphological parameters through time. Raupian coiling parameters (see Raup 1967) are useful for describing ammonoid spiral shell geometries, under the assumption of isometric growth, and have been used by numerous ammonite workers (e.g., Ward 1980; Bayer and McGhee 1984; Jacobs 1992; Korn 2000; Klug 2001; Korn and Klug 2001, 2003). These parameters as well as the F coiling parameter, proposed by Chamberlain (1976), were also used in this study. The morphological variables applied in this paper are (see Fig. 4): Tr, thickness ratio—whorl width (ww)/diameter (dm), S, shape of aperture (= relative whorl thickness)—whorl width (ww)/ whorl height (wh_2), and F, flank position—distance from the venter to the greatest whorl width (f)/diameter (dm).

Two of the Raupian coiling parameters (D, distance from the coiling axis and W, whorl expansion rate; see Raup 1967) were not used because all of the ammonoids investigated have involute conchs (with nearly the same D values) and have the same whorl expansion rate (W). Moreover, thickness ratio (Tr) and whorl shape (S) influence drag to a greater extent than the coiling parameters D and W and thus are of greater relevance in ammonoid hydrodynamics (Jacobs 1992).

Results

Thickness ratio (Tr) and shape of aperture (S).—These parameters describe the slenderness of the conch (Tr) and the whorl (S). Their values tend to decrease with time. In the upper Beds (4 and 5) the most slender ammonoids occur. The greatest mean value changes in Tr and S occur between the populations from Beds 1–2 and Bed 3 (Tr mean value changes from 0.400 to 0.347, and S mean value from 0.695 to 0.603; see Fig. 4). All observed differences between mean values are statistically significant ($p = 0.001$).

Flank position (F).—This parameter describes the position of the widest cross-section of the whorl. Its values increases upwards through the succession. The greatest values of whorl width for ammonoids from the lower beds occur close to the venter, while in ammonoids from the upper beds they lie close to umbilicus. The greatest modifications of F mean values are—in contrast to Tr and S parameters—between Bed 3 and Beds 4–5 (F mean values change from 0.384 to 0.457; see Fig. 4). This is expressed in the disc-shaped conch of the ammonoids from Beds 4 and 5. Differences between mean values of this parameter are statistically significant ($p = 0.001$).

Diameter (dm).—Mean values of diameter also increase with time and differences between means are significant (Fig. 4).

This biometrical analysis clearly shows how representatives of the investigated ammonoid population became more compressed and disc-shaped with time. Particularly notable is that the evolution of this lineage progressed in easily identifiable stages. The greatest changes in conch slenderness (as expressed in Tr and S values) are observed between Beds 1–2 and Bed 3 (see Fig. 4). This may be considered as the first stage of shell shape modification (“thickness stage”). In contrast, the coiling parameter F shows the greatest modification in mean value between Bed 3 and Beds 4–5, while Tr and S both tend to change more slowly. Moreover, during this stage the ventral part of goniatitid shells tends to become sharper. This is the second stage of morphological shell modification.

Hydromechanical design of the goniatitid shells from Janczyce

It is generally accepted that most ammonoids were poor swimmers (e.g., Kennedy and Cobban 1976; Lewy 2002). They were not well designed for continuous rapid swimming and acceleration (Jacobs and Chamberlain 1996). Some ammonoid workers (e.g., Chamberlain 1976; Bayer and McGhee 1984; Jacobs 1992; Jacobs et al. 1994) have suggested that there is a close relationship between mode of life and shell morphology in ammonoids. According to these authors, the ammonoid shell produced hydrodynamic drag during swimming. Shell shape, as mathematically defined, allows hydrodynamic efficiency and ammonoid swimming ability to be calculated. The great disparity in ammonoid conch morphologies suggests that some ammonoids swam slowly, others more rapidly.

Experiments show that water movement near the shell surface during ammonoid swimming was not the same on each part of conch. The greatest water turbulence was created in the umbilicus and behind the shell (Chamberlain 1976). Moreover, the greater the area of ammonoid cross-section the greater the drag that is produced. On the other hand, slender shells cannot accommodate as much muscular tissue for swimming as depressed shells. Therefore, compressed ammonoids might have achieved lower hydrodynamic efficiency (Kazushige Tanabe, personal communication 2006). Muscle scars are not preserved in the investigated material and therefore hydrodynamic efficiency cannot be calculated in this way.

Ammonoids would have been most hydrodynamically efficient in fast swimming when their shells were as slender as possible, with little or no umbilicus and with a sharp-edged venter. In biometric terms this kind of shell will have low Tr and S but high F values. Oxyconic shell shapes match this description very well.

This is not, however, the ideal type of ammonoid conch. If it had been, all ammonoids should have been oxyconic. Experiments show that compressed ammonoids were most hydrodynamically efficient only in high-energy environments (e.g., Jacobs et al. 1994). This means that oxycones could not swim fast but rather were able to cope with high-energy water flow. In deeper, usually low-energy environments, this shell morphology was not preferred as the energy consumption of oxyconic ammonoids was apparently much greater than depressed ammonoids (Jacobs 1992).

There is one additional force (other than drag) which operates in water environments. This is hydrostatic pressure, the value of which increases with depth. Compilation of ammonoid sutural complexity and shape of whorl cross-section allows calculation of shell strength and resistance against the force of hydrostatic pressure. Implosion depth of the shell and likely habitat depth limit can be calculated (Hewitt 1996). Hewitt (1996) observed that habitat depth limit of depressed ammonoids was much deeper, even by comparison with more compressed varieties of the same taxon (see also Jacobs et al. 1994). This could be a result of reduced mechanical strength of oxyconic whorls.

Accordingly, habitat depth limitation can be calculated on the basis of theoretical modelling of hydrodynamic drag and of implosion depth of ammonoid shells. *Tornoceras uniangulare*, which is very similar in shell morphology and sutural complexity to *Phoenixites frechi* from Beds 1 and 2 of the Janczyce section, yielded a depth estimate of 160 metres (Hewitt 1996). The oxyconic ammonoid *Beloceras*, similar in shell geometry to *Tornoceras sublentiforme* (occurring in Beds 4–5), has a much shallower habitat depth limit, calculated at 53 metres (Hewitt 1996).

Thus, shells of more depressed ammonoids were presumably poorer in swimming under high-energy water flow conditions but were resistant to hydrostatic pressure. Their power consumption level was optimal at greater depths, while compressed oxyconic ammonoids supposedly preferred much shallower environments because of lower tolerance of hydrostatic pressure and higher hydrodynamic efficiency. Depressed forms were possibly well adapted to slow, continuous swimming but moderately or poorly adapted to fast continuous swimming and acceleration. This is the opposite to compressed, oxyconic forms which seem to have been good at fast continuous swimming and acceleration, but rather moderate or even poor at slow, continuous swimming (Jacobs and Chamberlain 1996).

Moreover, the size of ammonoid shells influences drag and power consumption during swimming (Jacobs and Chamberlain 1996). With increasing size, drag increases as a function of area whereas power availability increases as a function of volume (Jacobs 1992). Additionally, larger forms travelling at higher velocities are more efficient if they are more compressed (lower value of Tr). This can be concluded from the distribution of conch forms in the Janczyce succession (see Fig. 4).

Increases in the prominence of shell ornamentation would also increase hydrodynamic drag. In the Janczyce material this factor is insignificant because all ammonoids have smooth conchs.

Facies analysis of the cephalopod limestones

Facies analysis has been applied in examining the depositional environment of the Janczyce cephalopod limestones and their possible correlations with trends in ammonoid shell shape. The following facies characteristics were observed:

Beds 1–2.—(1) Dark grey in colour; (2) containing more depressed goniatitids with a rounded venter: *Phoenixites frechi*, *Cheiloceras* (*Cheiloceras*) *subpartitum*, *Simicheiloceras* cf. *schrickeli, Falcitornoceras* aff. *korni*, and *Exotornoceras superstes*, Fig. 3 (I); (3) cyrto- and orthoconic nautiloids cha-

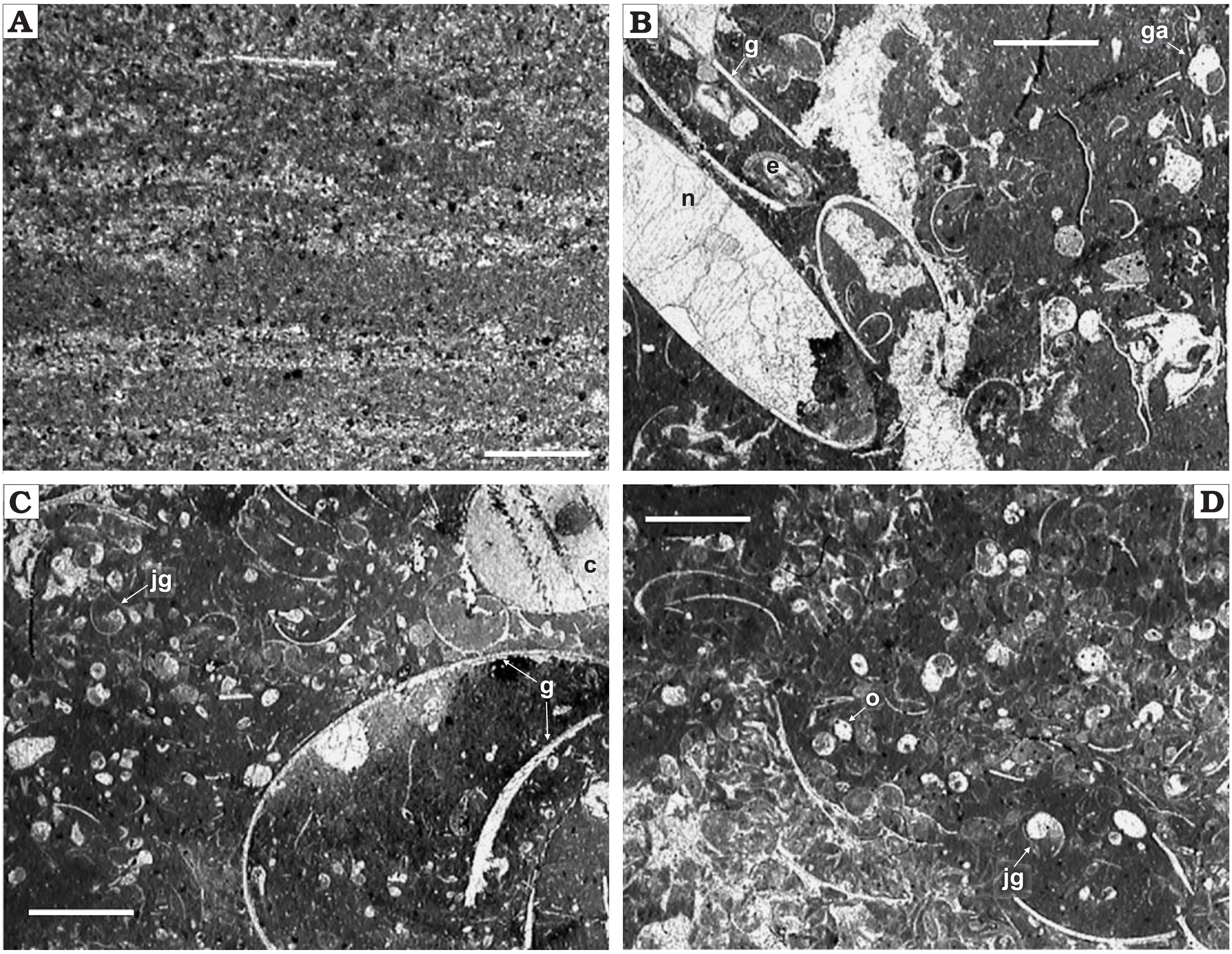


Fig. 5. Thin sections from the Janczyce section. **A**. Laminated marly limestone (MWG ZI//36/296); sampled below the cephalopod limestone log. **B**. Cephalopod wackestone (MWG ZI//36/301); Bed 1. Note the presence of goniatitids (g), orthoconic nautiloids (n), gastropods (ga), entomozoacean ostracodes (e) and poor sorting of bioclasts. **C**. Cephalopod wackestone (MWG ZI//36/303); Bed 3. Note the presence of goniatitids (g), juvenile goniatitids (jg), crinoids (c) and molluscan shell debris. **D**. Cephalopod packstone (MWG ZI//36/305); Bed 5. Note the presence of juvenile goniatitids (jg), benthic ostracode (o). Note also the best sorting of bioclasts in this bed. Scale bars 2 mm.

otically dispersed; (4) placoderm remains; (5) pelagic ostracods (family Entomozoidae, Fig. 5B); (6) maximum abundance of crinoids and gastropods; (7) unsorted, small to large bioclasts.

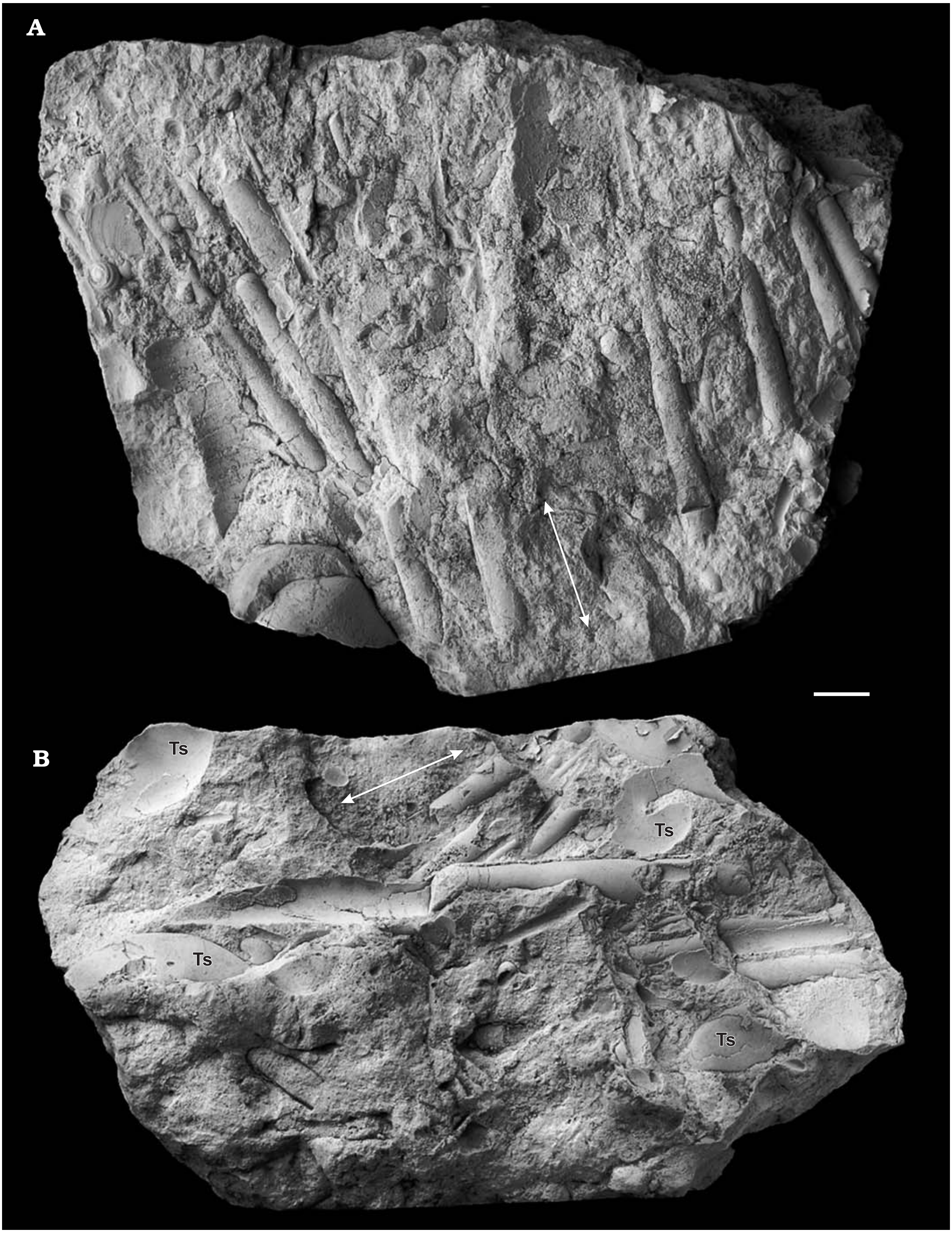
Bed 3.—(1) Black in colour; (2) containing more compressed goniatitids with a subtrapezoidal venter (*Tornoceras subacutum*), some forms with a slightly rounded venter (transitional forms: *Phoenixites frechi–Tornoceras subacutum*, Fig. 3 (II); (3) very few cyrtoconic nautiloids; (4) moderate abundance of crinoids and gastropods.

Beds 4–5.—(1) Black (Bed 4) or grey (Bed 5) in colour; (2) only compressed, oxyconic forms occur (*Tornoceras sublentiforme*, Fig. 3 (III)); (3) absence of cyrtoconic nautiloids; only orthoconic forms occur, usually oriented (Fig. 6); (4) benthic ostracodes (Fig. 5D); (5) crinoids and gastropods rare or absent; (6) well-sorted bioclasts, usually smaller in comparison with those from Beds 1–3; much less matrix.

Depositional environment

A number of workers (e.g., Tucker 1973; Wendt et al. 1984; Wendt and Aigner 1985; Santantonio 1994; Szulczewski et

Fig. 6. **A**. Current- or wave-oriented orthoconic nautiloids (MWG ZI/08/285); Bed 5 of the Janczyce cephalopod limestone. **B**. Current- or wave-oriented orthoconic nautiloids (MWG ZI/08/284) occurring together with *Tornoceras sublentiforme* (Ts); Bed 5 of the Janczyce cephalopod limestone. Arrows indicate current or wave direction. Scale bar 10 mm. →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al. 1996) have expressed the opinion that cephalopod limestones were often deposited on pelagic carbonate platforms and platform slopes. These platforms were usually tectonic or volcanic in origin. Because of strong stratigraphic condensation and sedimentary discontinuity surfaces, sedimentary rate must have been very low (1 to 5 m per million years; Wendt and Aigner 1985). The depositional depth of cephalopod limestones has been calculated at several tens to several hundreds of metres (Wendt and Aigner 1985).

The depositional environment of the Janczyce cephalopod limestone seems to have been very similar to other examples of this type of rock. During the Middle and Late Devonian the palaeogeography of the Holy Cross Mountains was dominated by a shallow-marine carbonate platform (Szulczewski 1995). Its growth caused the separation of northern and southern intra-shelf basins. During the late Frasnian and the early Famennian the platform was drowned and transformed into a pelagic carbonate platform. The northern margin of the shallow-marine carbonate platform, where Janczyce area was situated, drowned in the Late Frasnian, marking the beginning of monotonous, laminated marl basin sedimentation in this area. The pelagic carbonate platform was characterised by differential bottom morphology, probably caused by Late Devonian extensional tectonics as suggested, among others, by Racki and Narkiewicz (2000). This resulted in the formation of isolated carbonate platforms succeeding the condensed cephalopod limestones (Szulczewski 1995; Szulczewski et al. 1996). The origin of pelagic carbonate platforms is connected to early-orogenic block faulting and differential subsidence (similar trends were reported from Morocco by Wendt et al. 1984).

Little is known about the palaeogeography of the eastern part of the Holy Cross Mountains because there are very few outcrops. However, some sedimentary structures have been described from this area. Slump structures indicating northwards transportation of sediment were noted from Łagów (Radwański and Roniewicz 1962) (see Fig. 1), similar in age to the Janczyce cephalopod limestone, may be evidence of the existence of a tectonically active isolated pelagic carbonate platform in the Janczyce area. The cephalopod limestone must have been deposited on the top of this pelagic platform. Sedimentary discontinuities described by Makowski (1991) as well as the great abundance of conodonts (Tatiana Woroncowa-Marcinowska, personal communication 2002) suggest condensation. This is in agreement with the cephalopod limestone depositional model.

Trends in faunal and facies changes discovered in the Janczyce sequence may be summarised as follows:

(1) The earliest tornoceratid morphotypes in the succession were depressed forms with a rounded venter (Beds 1–2). These were followed by more compressed forms with a subtrapezoidal venter (Bed 3) and finally, the most compressed, oxyconic forms with a sharp-edged venter (Beds 4 and 5).

(2) Other goniatitid genera occur only in the lower part of the sequence: specimens of *Cheiloceras*, *Simicheiloceras*, *Falcitornoceras*, and *Exotornoceras* were found in Beds 1–2. All these goniatitids have a more depressed conch with a rounded venter, like *Phoenixites frechi* which occurs in the same beds.

(3) Upwards decrease in the abundance of cyrtoconic nautiloids, with no specimens found in Beds 4 and 5.

(4) Chaotic orientation of orthoconic nautiloids in the lower layers of the sequence as compared with current- or wave-orientation in Beds 4–5; this suggests shallower, even subtidal, high-energy environments (e.g., Wendt and Aigner 1985; Wendt 1995).

(5) Changes in the ostracod fauna, with deep-water entomozoids (see Olempska 1992) being found only in the lower part of sequence, while benthic ostracodes occurred in the upper Beds.

(6) Placoderm remains have been noted only from the lower part of the Janczyce section.

(7) Upward decrease in crinoids and gastropods.

(8) Upward decrease in biodiversity. In the upper layers, only one species of goniatitid (*Tornoceras sublentiforme*) occurs and the benthic fauna is clearly impoverished.

(9) Upward decrease in abundance of large bioclasts and matrix, and increase in fine shell debris, suggesting a high-energy environment for Beds 4–5 (microfacies changing from wackestones in Beds 1–2 to packstones in the upper beds).

The microfacies in the lower part of the cephalopod limestone shows some differences in comparison with Beds 4 and 5. However, these probably are not significant (Stanisław Skompski, personal communication 2002). Tucker (1973) suggested that diagenetic processes could have obliterated the original texture of the Devonian cephalopod limestones. Thus, other facies features seem to be more useful as palaeoenvironmental indicators.

Macrofacies analysis clearly shows that the upper beds of the Janczyce cephalopod limestone were deposited in a higher energy regime than the lower layers. This high-energy environment was probably a result of bottom current or wave activity, as indicated by parallel alignment of orthoconic nautiloids. The Janczyce cephalopod limestone sequence seems to represent a shallowing-upward cycle.

Another possibility—*post mortem* shell accumulation—that could account for the origin of these ammonoid-bearing sediments can be excluded. Most of the goniatitids from the Janczyce cephalopod limestone are preserved with the body chamber intact. This suggests that the ammonoid shells were not transported very far to their site of deposition (e.g., Korn 1995). The presence of juvenile goniatitid shells (Fig. 5) that do not show extensive breakage also suggests that the goniatitids were deposited within the habitat realm of the population (see Tanabe et al. 1993). Such a great number of ammonoid specimens in the Janczyce cephalopod limestone seems to be the result of condensation, which has often been noted for cephalopod limestones. The presence of sedimentary discontinuity surfaces noted by Makowski (1991) supports this interpretation. The large number of conodont specimens also favours stratigraphic condensation.

Discussion

Ammonoid abundance relates closely to sea-level fluctuations, being generally greater when sea-level is high and less when it is low (e.g., House 1993). This is the result of reduction in habitat area during regression which may lead to extinction, known as the species-area effect (Wani 2003). The opposite can happen as well, as documented by Monnet et al. (2003).

To survive environmental changes, ammonoids had to adapt (Bayer and McGhee 1984; Jacobs et al. 1994; Korn 1995; Seki et al. 2000; Kawabe 2003). According to these authors, sea-level change is a very important factor promoting ammonoid evolution; they suggest that ammonoids were restricted to some extent to environments hydrodynamically appropriate to their shell morphologies. Compressed, oxyconic ammonoids were better adapted for living in high-energy, usually shallow-water environments, while depressed forms probably had optimal power consumption in low-energy, generally deeper environments.

The likelihood of relative sea-level changes in the Holy Cross Mountains during the Middle/Late *Palmatolepis crepida* Zone time has been suggested by other authors. Neptunean dykes noted from the Kadzielnia Quarry in Kielce are the result of an extensional tectonic regime (Racki and Narkiewicz 2000). This kind of regime leads to block-faulting and thus to varying bottom palaeomorphology. Tectonic block uplifts might have led to local shallowing or even emergence of the block, as has been described for Gałęzice (Szulczewski et al. 1996).

Eustatic sea-level changes might also have occurred. Narkiewicz (1987) postulated a local regression during the Middle *Palmatolepis crepida* Zone. This may be correlated with a small regressive pulse just before the eustatic transgression described by Johnson et al. (1985). However, the occurrence of this event in the Holy Cross Mountains is doubted by some authors (Szulczewski 1990). Also during the Late *Palmatolepis crepida* Zone, a global regressive pulse has been suggested by some authors (Dopieralska 2003; Schülke and Popp 2005). Dopieralska (2003) used neodymium (Nd) isotopic composition of conodonts as a tool to investigate Late Devonian sea-level fluctuations. She concluded that the Nd isotopic composition of conodonts reflects sea-level fluctuations, with values decreasing during the regressive phases. According to Dopieralska, the regressive event during the Late *Palmatolepis crepida* Zone was one of five prominent eustatic events during the late Frasnian and early Famennian (see also Buggisch 1991). Apart from this event, the two Kellwasser events, also recorded as condensed cephalopod facies, were deposited during regressive pulses (Dopieralska 2003). These results, however, contrast with the opinion of some other workers (e.g., Szulczewski 1995; Racki and Narkiewicz 2000) who have suggested that cephalopod limestone deposition is associated with periods of deepening.

The conclusion here is that the two factors of block-tectonics and eustatic sea-level fluctuations must have influenced facies distribution in the Holy Cross Mountains during the Late Devonian (e.g., Szulczewski 1989). A relative sea-level fall during the Middle/Late *Palmatolepis crepida* Zone may have also happened in the Janczyce area. This is consistent with our proposed cephalopod limestone facies interpretation.

Hydromechanical analyses of the ammonoids studied together with the facies analysis allow calculation of approximate depositional depths. Depositional depth of the lower layers of Janczyce cephalopod limestone can be estimated at about 160 metres using the formula of Hewitt (1996). Similar neritic depth values were suggested for the deposition of laminated marly limestones (Flügel 1982) like those associated with the Janczyce cephalopod limestone. In contrast, the upper beds of the cephalopod limestone sequence may have been deposited at only a few metres depth.

A cephalopod limestone intercalation of similar age in the Kadzielnia Quarry is also thought to have been deposited during the same regressive phase (Narkiewicz 1987). Although this outcrop is located a few tens of kilometres west of Janczyce (see Fig. 1) and is situated on the southern margin of the Holy Cross Mountains Famennian pelagic carbonate platform, there are similarities between the localities. Makowski (1991) noted the presence of a very similar tornoceratid lineage within the Kadzielnia cephalopod limestone. Cephalopod limestones from these localities differ in colour, microfacies, and associated facies. In addition, the Kadzielnia cephalopod limestone contains very few fossils. However, the presence of a very similar ammonoid succession suggests similar depositional environments.

Conclusions

This paper reports on the morphological evolution of Famennian Tornoceratidae from the Holy Cross Mountains (Poland). Biometrical analysis of goniatitids, together with facies analysis of the cephalopod limestone, leads to the following conclusions:

(1) Biometrical analysis shows various trends in shell shape changes in this ammonoid lineage. These are decreases in the values of thickness ratio (*Tr*) and shape of the aperture (*S*), and increase in the values of flank position (*F*) coiling parameters;

(2) The parameters *Tr*, *S*, and *F* appear to have the greatest relevance to ammonoid hydrodynamics. As with analogous examples from the literature, these trends in the values of coiling parameters are interpreted as adaptations in shell shape among ammonoids living in high-energy environments. This interpretation is supported by the trend in morphology of the venter geometry: from round through trapezoidal to sharp-edged. Oxyconic ammonoids, representing the final stage in shell shape, occur in the upper part of the Janczyce sequence. This kind of conch morphology is thought to have the lowest

power consumption during swimming in high-energy environments;

(3) Facies analysis of the cephalopod limestone suggests a shallowing-upwards cycle. The presence of pelagic ostracodes (family Entomozoidae) in the lower part of the succession, benthic shallow-water ostracodes and current- or wave-oriented orthoconic nautiloids in the upper part and general upward biodiversity decrease confirms this inference;

(4) Relative sea-level fall, proposed in this case, may have been caused by tectonic uplift and/or eustatic regression. Both factors may have been involved, since extensional tectonic movements and eustatic regressive pulses both occurred in the Middle/Late *Palmatolepis crepida* Zone when the Janczyce cephalopod limestone was deposited;

(5) Morphological evolution of the studied tornoceratid lineage appears to be associated with a relative sea-level fall. This provides one more example of this kind of environmentally controlled evolution, but is probably the first documented in Palaeozoic ammonoids. This can be considered as a subsidiary tool for interpreting the relative depth of sediment deposition. However, much more data from other lineages and ages is needed to support a relationship between sea-level change and evolutionary trends in ammonoid shell.

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