Dimorphism and evolution of the goniatite *Tornoceras* in the Famennian of the Holy Cross Mountains

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Makowski, H. 1991. Dimorphism and evolution of the goniatite *Tornoceras* in the Famennian of the Holy Cross Mountains. *Acta Palaeontologica Polonica* **36**, 3, 241-254.

A cephalopod limestone intercalation in the Early Famennian Łagów beds of Janczyce (eastern Holy Cross Mountains, Poland) contains, in each of its five layers, abundant fossil assemblages of goniatites. The lineage of *Tornoceras* is especially well represented there. It starts from typical *T. frechi* with rounded venter and ends in *T. sublentiforme* with sharp-edged venter. A bed-by-bed biometrical study has shown a bimodal size frequency distribution of conchs in each layer which is interpreted as sexual dimorphism. *T. frechi parvum* subsp. n. and *T. subacutum* sp. n., are proposed new, forms that represent successive connecting links within the lineage.

Key words: ammonites, Late Devonian, Poland, evolution, sexual dimorphism.

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Introduction

Tornoceras is a long-ranging and geographically widespread Late Devonian ammonoid. It ranges from the Middle Givetian to Early Famennian (House & Price 1985), being common in the whole continent of Laurentia (Bogoslovsky 1971, House 1963, 1978, Babin 1989), but known also from the South American (House 1978) and African (Bensaïd 1974, Göddertz 1987) parts of Gondwana. Although abundant in many localities it is still inadequately known, with its early ontogeny recognized in the Middle and Late Devonian (House 1965) and in the early Frasnian (Bogoslovsky 1971). Sexual dimorphism has been described in Early Famennian populations (Makowski 1962a, b).

In the present paper new rich material from the Famennian of the Holy Cross Mountains is described, which allows quantitative evidence for

sexual dimorphism in several populations of different geological age. It also shows gradual evolutionary transformation of the conch shape.

Geological setting

A relatively thick series of regularly bedded, dark-grey marly limestones crops out in the vicinity of the village Janczyce in the SE part of the Holy

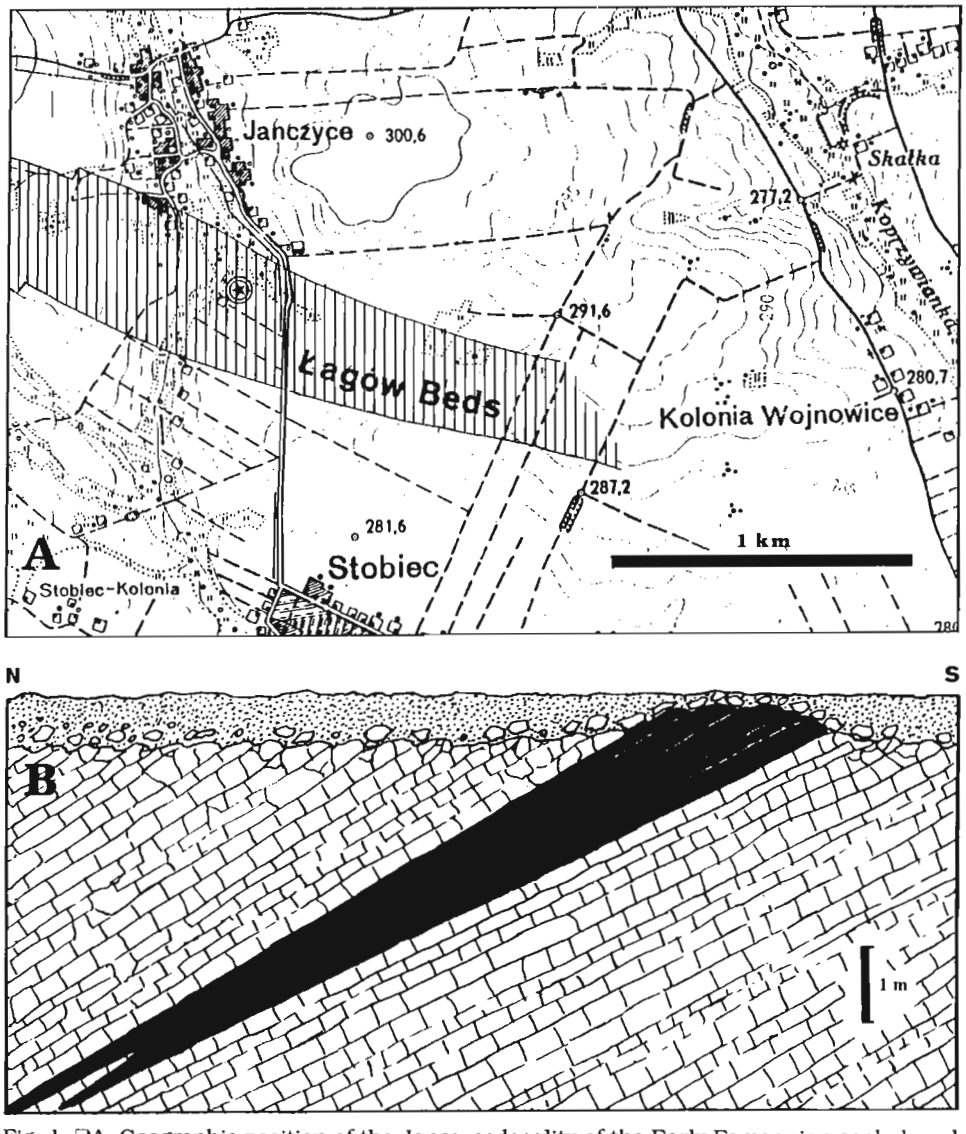


Fig. 1. ❑A. Geographic position of the Janczyce locality of the Early Famennian cephalopod limestones (marked with asterisk). ❑B. Schematic section of the trench in the field of Andrzej Grześkiewicz in Janczyce.

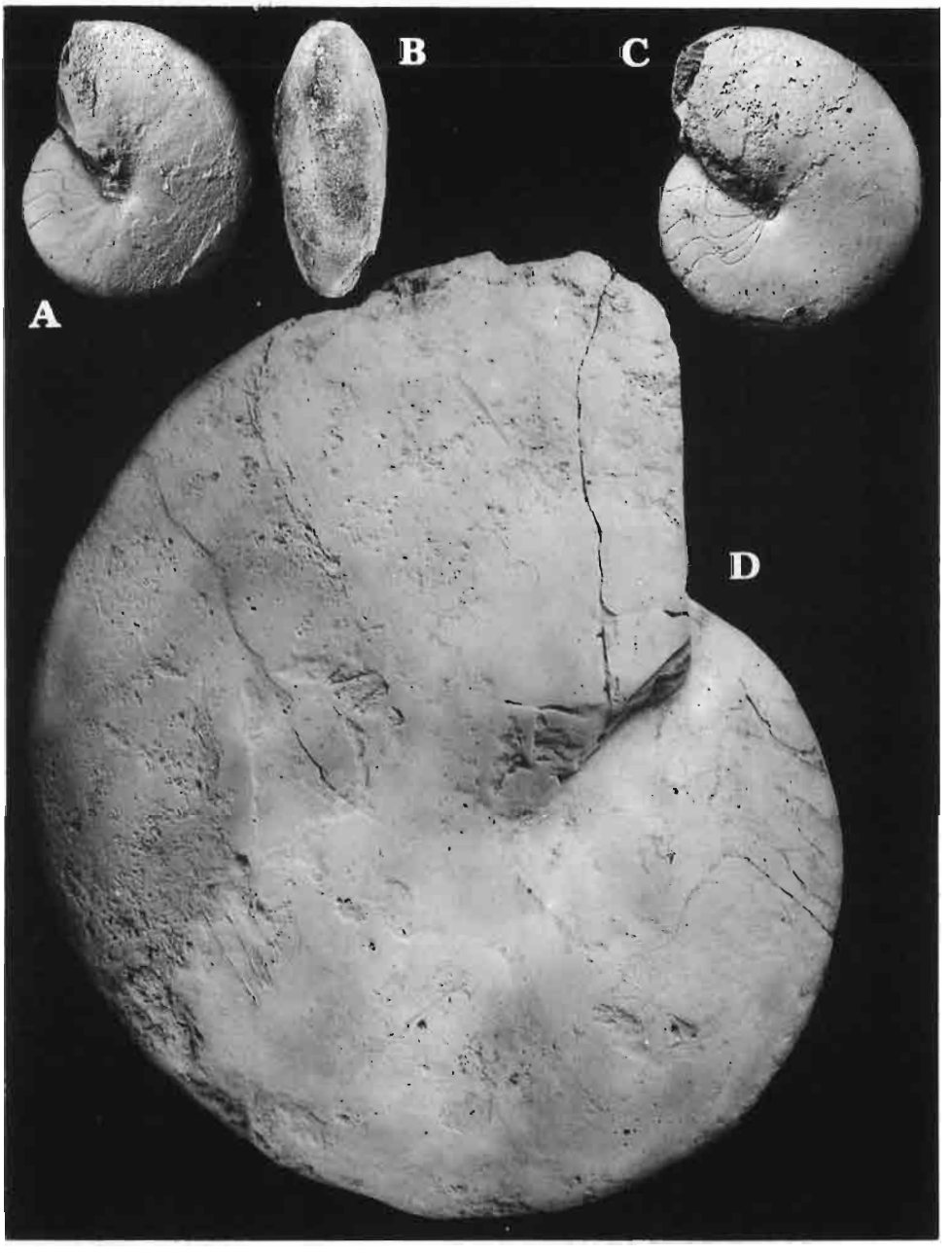


Fig. 2. *Tornoceras frechi* Wedekind 1918 from the bed 1 of the Janczyce lens of Early Famennian cephalopod limestone. ❑A, B. Microconch IGPUW Ja 116; × 2. ❑C. Microconch Ja 110; × 2. ❑D. Macroconch IGPUW Ja 101, diameter (D) - 130, height of the last whorl (H) - 78, width (W) - 45; × 1.

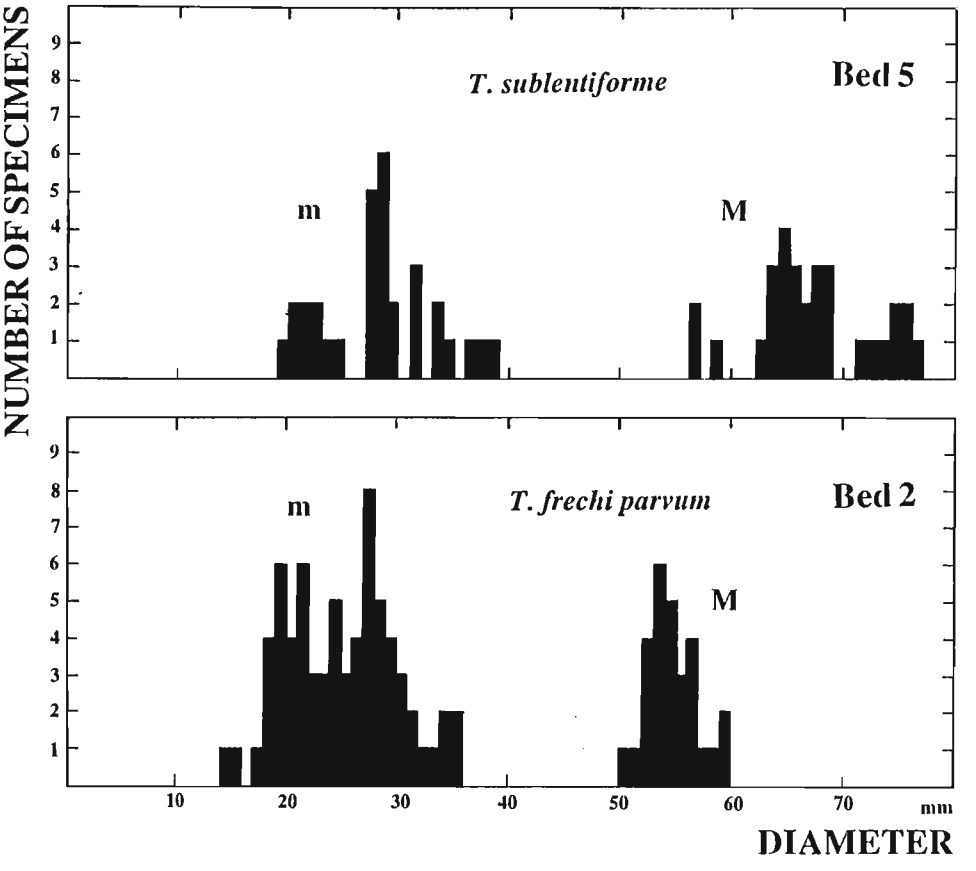


Fig. 3. Size frequency distribution of identifiable adult conchs of *Tornoceras* in beds 2 and 5 of the Janczyce lens of Early Famennian cephalopod limestone.

Cross Mountains (Narkiewicz & Olkowicz-Paprocka 1983). They are generally unfossiliferous except for rare brachiopods. Within these limestones an intercalation of a cephalopod limestone was found in 1918 by Jan Samsonowicz, who mapped the area geologically. The intercalation was exposed in a field owned by the local farmer Andrzej Grześkiewicz, on the right bank of a creek which is a tributary of the Koprzywianka river (Fig. 1A).

A trench was dug at the locality of the cephalopod limestone which appeared to form a lens of 120 cm thickness at the exposed eroded margin. The lens dipped towards the north at an angle of 30°. Seven meters further, when the excavation stopped, it was only 40 cm thick and had split into two separate parts with the same marly limestone in between as that above and below the lens (Fig. 1B). Particular beds within the lens differed markedly in coloration. The central part (beds 3-4) was a black limestone, the beds 1-2 were dark grey, darker than the topmost bed 5. Most remarkable were two bedding surfaces stained with oxidized iron minerals;

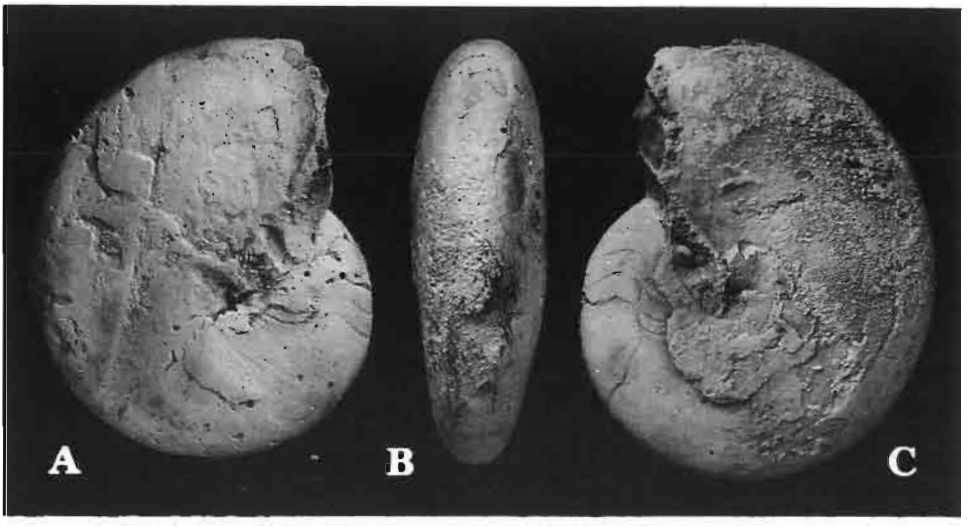


Fig. 4. *Tornoceras frechi parvum* subsp. n., from the bed 2. ❑A, B. Macroconch Ja 202, D - 56, H - 35, W - 18; ❑C. Holotype, macroconch IGPUW Ja 201, D - 56, H - 34; × 1.

they evidently represented sedimentary discontinuities that separated both sides of the central part of the lens (beds 2-3) enabling easy identification of the beds during the collection of fossils.

The cephalopod limestones at Janczyce are highly fossiliferous being almost a lumachelle. Most fossils are goniatites and straight nautiloids. Bryozoans and minute snails are common while brachiopods and bivalves occur only sporadically.

The age of the limestone can be determined because some of the cephalopod species are of correlative value. *Cheiloceras subpartitum* (Münster), which is common in Janczyce, was considered by Wedekind (1913, 1918, 1926) to be the index fossil of the *Cheiloceras* IIα Zone. In bed 1 two specimens of an interesting species have been found that was described by Lange (1929) as *Manticoceras nehdense* from Nehden in the Rhenish Slate Mountains. Putting aside the problem of its proper generic assignment it is of interest that it was also reported from the *Cheiloceras* IIα Zone.

Conodonts from the cephalopod limestones at Janczyce have been studied by Wolska (1967) who identified the *Palmatolepis crepida* Zone, which corresponds in age to *Cheiloceras* IIα. More detailed studies by Szulczewski (unpublished) show that the whole intercalation was deposited during the *P. crepida* Zone although conodont assemblages from beds separated by the discontinuity surfaces differ in composition.

Descriptions

Order Goniatitida Hyatt 1884
Family Tornoceratidae Arthaber 1911

Genus *Tornoceras* Hyatt 1884
Type species: *Goniatites uniangularis* Conrad 1842
Tornoceras frechi Wedekind 1918
Fig. 2.

Tornoceras frechi sp. n.; Wedekind 1918: p. 136, Text-fig. 41, Pl. 16: 9.
Tornoceras simplex (Buch); Makowski 1962a: p. 31, Pl. 11
Tornoceras simplex (Buch); Makowski 1962b: p. 38, 78, Text-fig. 11.

Material.– About 160 macroconchs, mostly fragmentary, and numerous well preserved microconchs from the bed 1.

Description.– Sexual dimorphism in the species was identified by Makowski (1962a, b). The body chamber of adult macroconchs cover about 7/8 of the last whorl. The reconstruction of the conch aperture presented in Makowski (1962a, b) was based on fragmentary specimens. Now a complete adult specimen, 95 mm in diameter, is available with a relatively well preserved aperture (Fig. 2D). Its contour is similar to that of *Manticoceras*, for instance *M. (Carinoceras) oxy* Clarke (see Miller 1938a, b). Macroconchs of this species from Janczyce reach diameters of 62 to 130 mm; a single incomplete specimen could be as large as 165 mm in diameter.

An interesting problem is the occurrence of unusually large macroconch specimens in the Early Famennian population of *T. frechi*. While the difference in the volume of the final body chamber between microconchs and macroconchs of usual size (60-70 mm) is approximately 1:10; in the case of these gigantic forms of more than 130 mm in diameter it may be up to 1:50. This must be of some biological importance regarding, for instance, sexual behaviour.

Gigantic macroconchs of *T. frechi* are known also from the locality of Kadzielnia at Kielce, Holy Cross Mountains, where in beds with *Cheiloceras (Staffites) curvispina* (Sandberger & Sandberger) Dr. K. Wuttke found in 1952 a specimen 210 mm in diameter. Similarly at Sobolew's (1911) locality on the left side of the Niwa Gorge in Łagów macroconch phragmocones occur up to 80 mm in diameter (thus complete conchs would be up to 130 mm in diameter). This is not only the case for Early Famennian populations since Petter (1959) reports fragmentary specimens of *T. 'simplex'* from the Frasnian of Algeria that were 130-220 mm in diameter.

According to my earlier interpretation (Makowski 1962a, b), macroconchs correspond to females and microconchs to males. Such a profound disparity in size of adult macroconchs is, in this context, of uncertain biological significance. Ivanov (1971, 1975) proposed that along with micro- and macroconchs a third form, named by him the megaconch, occurs in some ammonites. They are interpreted as adult specimens with an especially long life cycle.

Tornoceras frechi parvum subsp. n.
Figs 3, 4.
Holotype: IGPUW Ja 203 (Fig. 4).

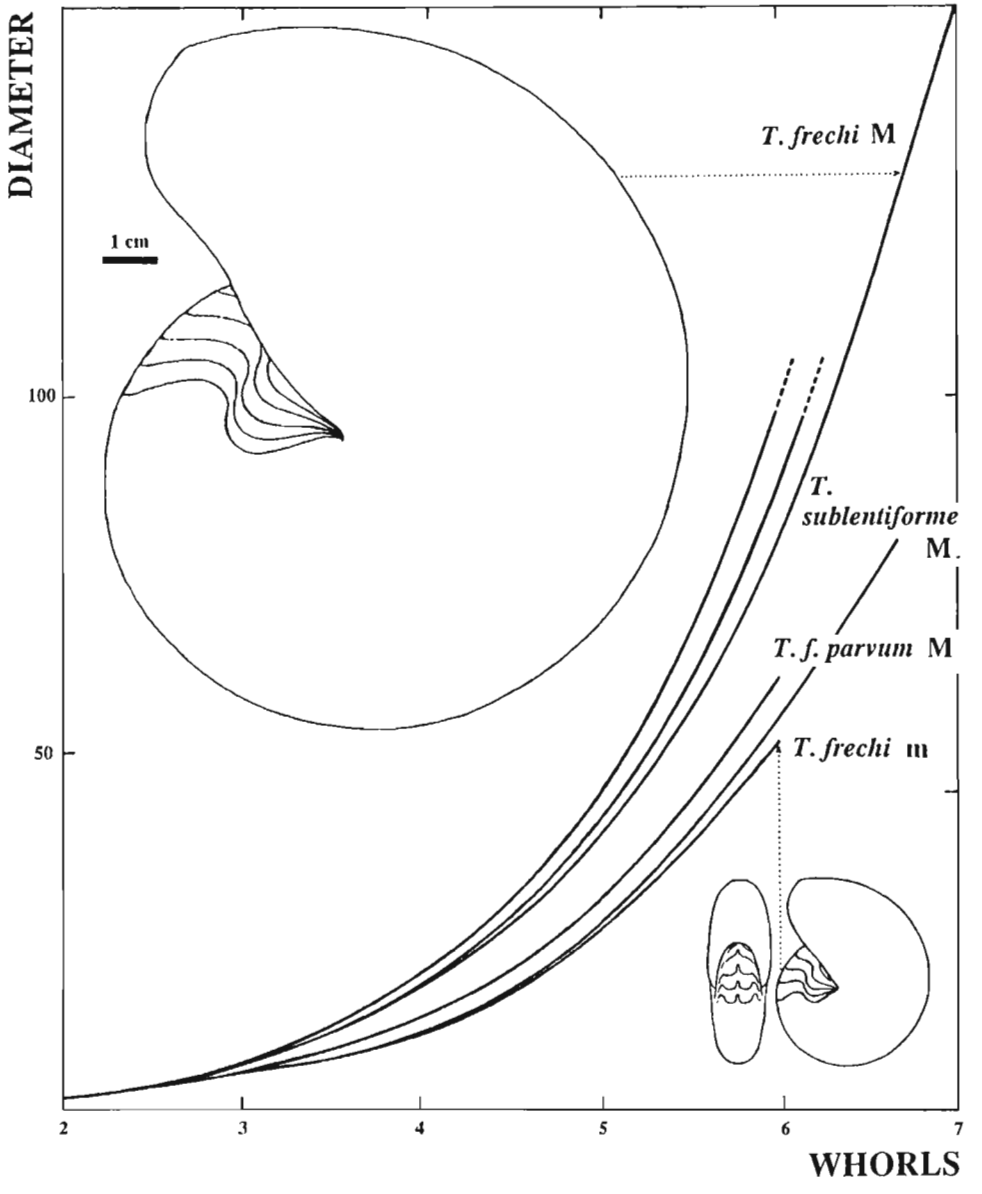


Fig. 5. Growth curves of *Tornoceras* conchs from Janczyce.

Type horizon and locality: Bed 2 of the cephalopod limestone of Janczyce, Holy Cross Mountains Poland; Famennian, *Cheiloceras* IIα Zone.

Derivation of the name: Referring to small size of adult specimens ('parvum' - small in Latin).

Diagnosis.– Macroconchs of small size (50-59 mm in diameter), the last whorl with slightly flattened venter.

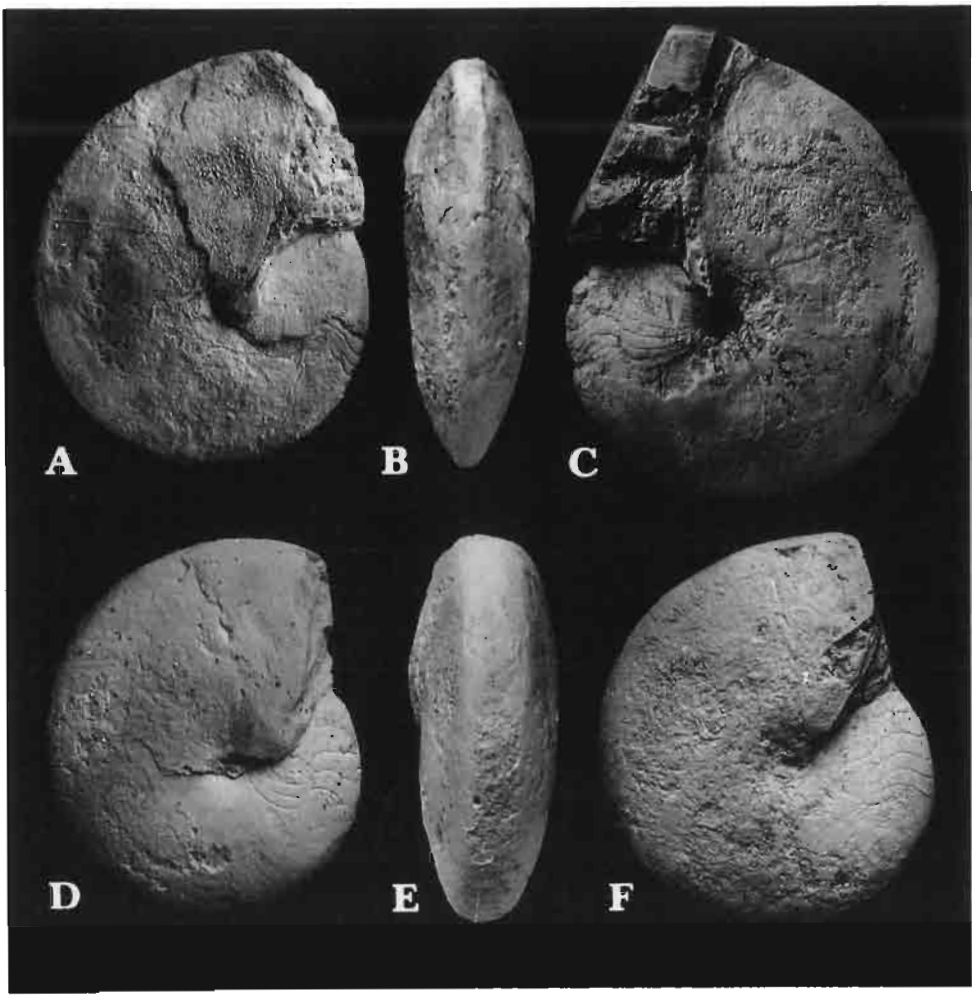
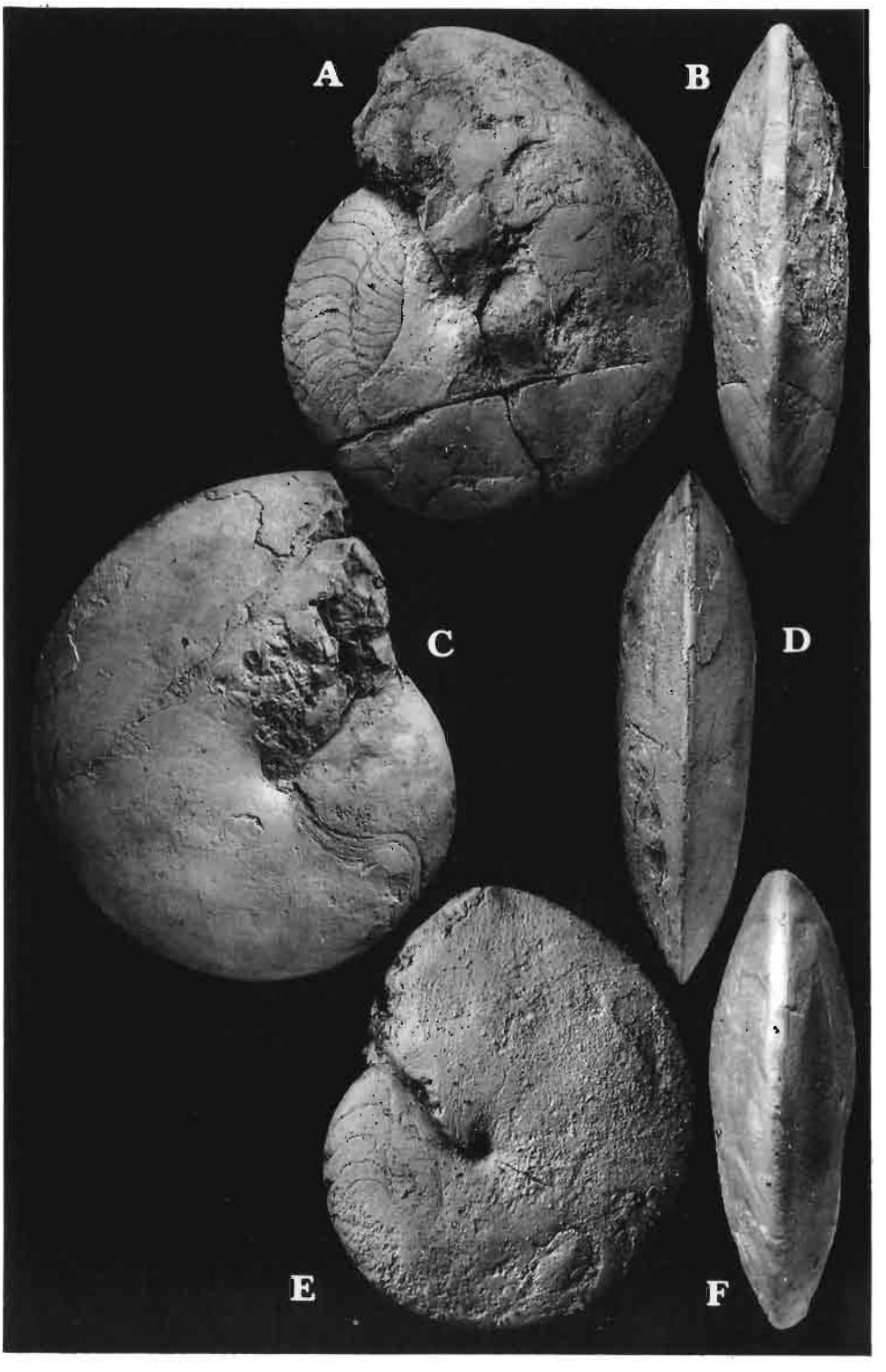


Fig. 6. *Tornoceras subacutum* sp. n. from the bed 3. ❑A, B. Holotype, macroconch IGPUW Ja 301, D - 55, H - 34, W - 17; × 1. ❑C. Macroconch IGPUW Ja 302, D - 58, H - 38, W - 19; × 1. ❑D, E. Microconch IGPUW Ja 303, D - 28, H - 17, W - 10; × 2. ❑F. Microconch IGPUW Ja 306; × 2.

Material.– 28 adult complete macroconchs and 67 microconchs from the bed 2.

Remarks.– In bed 2 of the Janczyce cephalopod limestone a population of *Tornoceras* occurs that differs from the preceding fauna (of the bed 1) in the much smaller adult size of macroconchs. Their conchs show a lower whorl expansion rate than in macroconchs of the older *T. frechi*. In effect

Fig. 7. *Tornoceras sublentiforme* Sobolew 1914. ❑A, B. Macroconch IGPUW Ja 405 from the bed 4 representing a morphotype transitional to *T. subacutum*, D - 59, H - 36, W - 16; × 1. ❑C, D. Macroconch IGPUW Ja 501 from the bed 5, D - 74, H - 41, W - 19; × 1. ❑E, F. Microconch IGPUW Ja 504 from the bed 5, D - 21, H - 13, W - 8; × 2.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B
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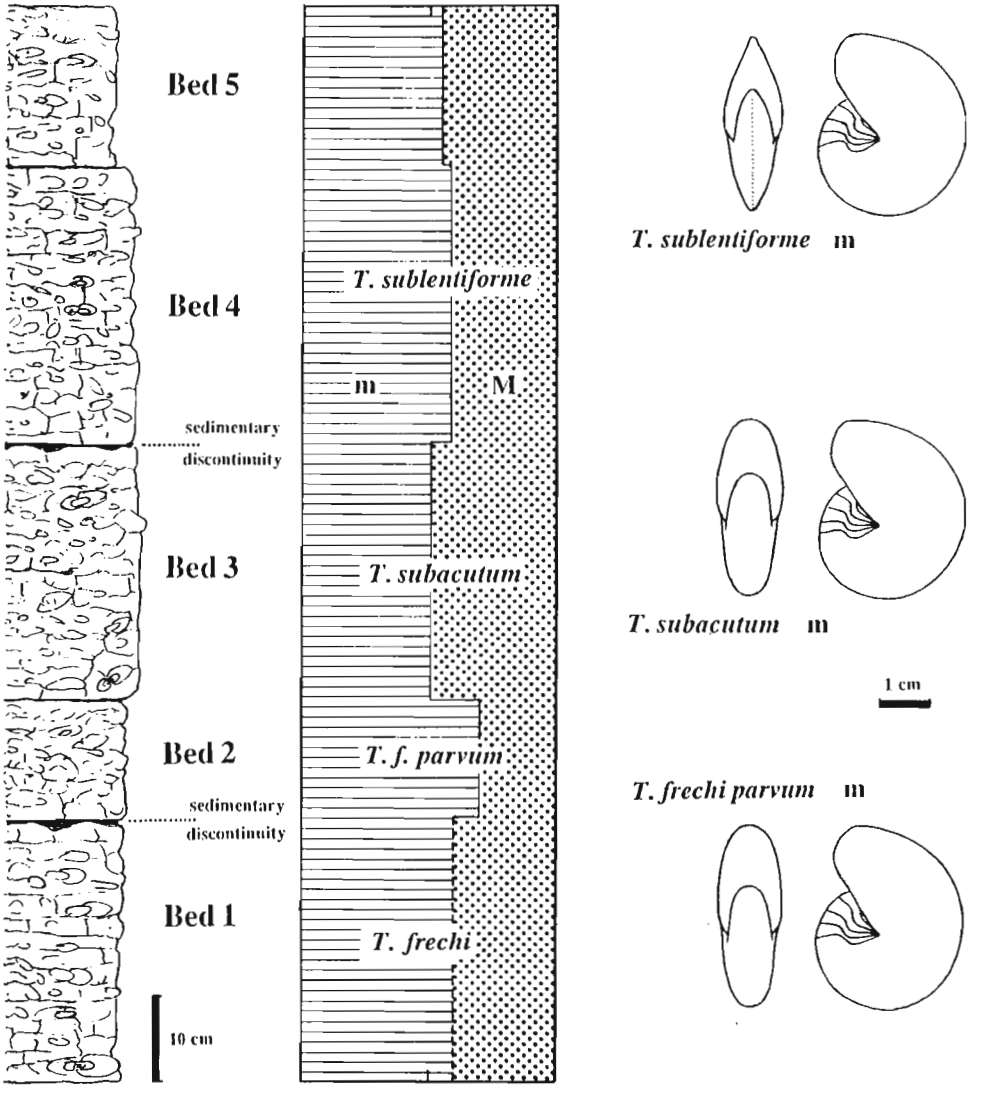

Fig. 8. Changes in ratios between macro- and microconchs of *Tornoceras* along the Janczyce section.

last whorls are somewhat lower and the final number of whorls is only 6 (Fig. 5). Also microconchs of *Tornoceras* from the bed 2, ranging from 14 to 36 mm in diameter (Fig. 3), are smaller than those from bed 1 (20-47 mm). This correlation, presumably biological in nature, provides additional support for the interpretation of different size groups of *Tornoceras* as sexual dimorphs.

Tornoceras subacutum sp. n.
Fig. 6.
Holotype: IGPUW Ja 301

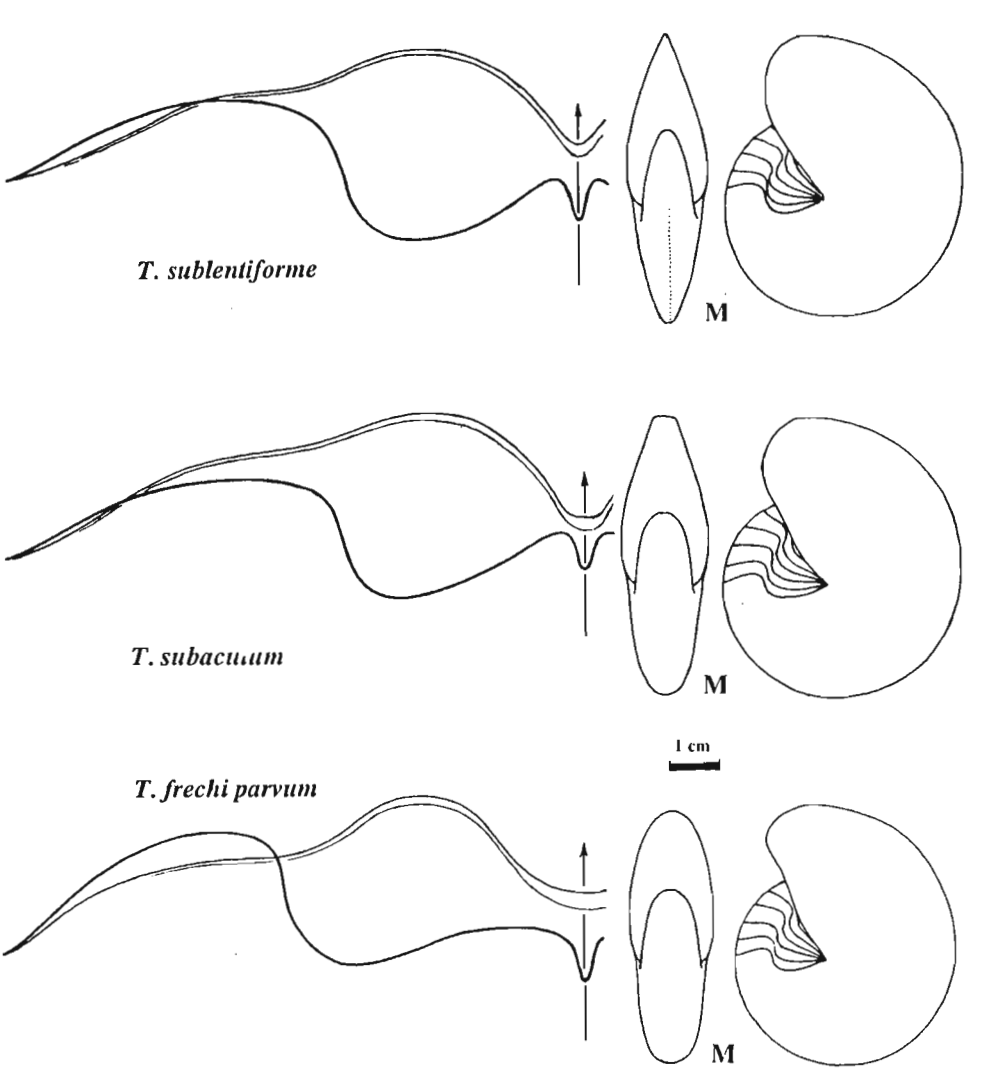

Fig. 9. Succession of conch form and growth and suture lines in the *Tornoceras frechi* - *T. sublentiforme* lineage in Janczyce.

Type horizon and locality: Bed 3 of the cephalopod limestone of Janczyce, Holy Cross Mountains, Poland; Famennian, *Cheiloceras* IIα Zone.

Diagnosis.– Macroconchs with narrowly trapezoidal cross-section of the venter; microconchs with rounded venter.

Material.– 31 adult complete macroconchs and 34 microconchs from the bed 3 of Janczyce, 2 macroconchs from *Cheiloceras* IIα beds of Kadzielnia.

Description.– Macroconch up to the stage of 4-5 whorls is openly umbilicate, later the umbilicus closes completely. The conch attains a discoidal shape with its greatest thickness close to the umbilicus. The venter is narrow but rounded. The final body chamber covers about 7/8 of the last whorl, in some specimens reaching only a little more than 3/4 of the whorl.

Close to the aperture of the adult conch a flattened (tabular) narrow venter developes which gives it a high trapezoidal cross-section.

Macroconchs have 6, or somewhat more, whorls. The whorl expansion rate is similar to that in *T. frechi parvum* subsp. n. (Fig. 5) the aperture is not preserved in adult specimens but most probably it was similar in shape to the preceding species.

The whorl expansion rate in microconchs is significantly lower. They contain 5-6 whorls. The adult aperture shows a deep ventral sinus and very shallow lateral sinuses (Fig. 9). In this respect the species does not differ from its successor, *T. sublentiforme*.

Tornoceras sublentiforme (Sobolew 1914)
Fig. 7.
Gomi-monomeroceras (Tornoceras) sublentiforme n. nom; Sobolew 1914: p. 56, Pl. 8: 14.
Tornoceras acutum Frech; Makowski 1962b: Text-fig. 2, 106

Material.– 53 complete adult macroconchs and 80 microconchs from bed 4 and 28 macroconchs and 34 microconchs from bed 5 of the Janczyce cephalopod limestone.

Description.– Like *T. subacutum* sp. n., in this species the conch remains umbilicate at 4-5 whorls and then the umbilicus closes completely. Beginning from 3-8 mm diameter the conch venter gradually sharpens and the cross section of the conch becames more and more lenticular. The adult body chamber covers 7/8 of the last whorl. The macroconch reaches 6 whorls, or somewhat more. The microconch differs in whorl expansion rate and has a slightly smaller number of whorls (5-6). Its shape is also lenticular. The suture line is quite variable in the species. This concerns especially the depth of the lateral lobe and its width which becames distinctly smaller with increasing size of the conch.

Remarks.– Sobolew (1914) established his species on the basis of a juvenile pyritized specimen that had been found reworked to Quaternary deposits at the Sieklucki brickpit in Kielce. Although it does not seem to differ from corresponding stages of the Janczyce specimens, the use of the name should be considered tentative. The holotype of possibly related *T. acutum* Frech 1902, which is the only adult specimen of the species illustrated (Frech 1902), represents probably a microconch. Clausen's (1968) specimen is a juvenile that is difficult to determine.

Tornoceras iowense Miller 1938 from the Early Frasnian of Iowa probably represents another, homeomorphic lineage of the tornoceratids.

Conclusions

In the Janczyce section a complete series of transitional populations of the *T. frechi* - *T. sublentiforme* lineage seems to be represented. In successive beds 3-5 the proportion of specimens with a narrow venter increases. The population in bed 4 is exactly transitional between those from beds below

and those above with extreme specimens fitting morphologically either typical *T. sublentiforme* from the bed 5 or typical *T. subacutum* sp. n. from the bed 3 (see Fig. 7A, B). A similar succession has also been identified in some other localities in the Holy Cross Mountains. In Kadzielnia, *T. subacutum* sp. n. and *T. sublentiforme* occur in the same order (Makowski *in* Szulczewski 1971) although beds with *T. frechi parvum* subsp. n. are apparently missing there.

Acknowledgements

Professor Michael House has kindly reviewed the manuscript and improved its language.

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Streszczenie

W miejscowości Janczyce występuje mała soczewka wapienna (skałka wapienna), która leży wśród wapieni ilastych famenu (poziom *Cheiloceras* IIα) i ma 120 cm grubości. W przekroju tej soczewki można wyróżnić 5 warstw na podstawie zabarwienia skał. Tu zebrano bogaty zbiór goniatytów z rodzaju *Tornoceras*.

Przedstawiony szereg ewolucyjny złożony z par dymorficznych, który pochodzi od *Tornoceras frechi* (Buch), a wyższe ogniwa tego szeregu to *Tornoceras frechi parvum* subsp. n., *Tornoceras subacutum* sp. n. i końcowe ogniwo *Tornoceras sublentiforme* (Sobolew).

Nowa gałąź ewolucyjna podrodzaju *Tornoceras* rozwija się na innej spirali skrętów niż *Tornoceras frechi*, ma ona krótszy promień wodzący i stąd powstają tutaj formy o mniejszej średnicy muszli.

Ewolucja tego szeregu goniatytów biegnie w kierunku zaostrzenia strony zewnętrznej muszli. U *T. frechi* i *T. frechi parvum* subsp. n. strona zewnętrzna jest zaokrąglona. Później widzimy, że u makrokonch *T. subacutum* sp. n. przekrój poprzeczny ostatecznej komory mieszkalnej ma zarys wysokiego trapezu, a mikrokoncha ma stronę zewnętrzną zaokrągloną. W końcu u *T. sublentiforme* przekrój poprzeczny muszli ma kształt soczewki i taki kształt mają również towarzyszące tutaj mikrokonchy.

W związku z opracowaniem tutaj goniatytów z rodzaju *Tornoceras* należy jeszcze zwrócić uwagę na zjawiska gigantyzmu u gatunku *Tornoceras frechi*. W Janczycach znane są okazy tego gatunku mające 130 mm średnicy, a jeden okaz miał zapewne 165 mm średnicy. W Górach Świętokrzyskich znane są dwa miejsca gdzie występują takie okazy, ale są to zjawiska rzadkie.