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Age, distribution, and phylogeny of the peculiar Late Devonian ammonoid *Soliclymenia*

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ABSTRACT:

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New records of the triangularly coiled *Soliclymenia paradoxa* (MÜNSTER, 1839) from Dzikowiec (Sudetes, Poland) allow the study of intraspecific variability. It can be demonstrated that at least three species within the genus *Soliclymenia* can be separated. The genus has a limited stratigraphic distribution within the "*Wocklumeria* Stufe" of the Late Devonian, but a wide geographic range within the tropical seas.

Key words: Ammonoidea, *Soliclymenia*, Late Devonian, Poland, Triangular coiling.

INTRODUCTION

Soliclymenia is one of the most bizarre Palaeozoic ammonoids with its triangularly coiled conch. Based on the available geological records, it is one of the most rare Late Devonian ammonoid genera. Species of this genus have long been known; the circular coiled *S. solarioides* has been described by von BUCH (1839) from Silesia and the extraordinary triangularly coiled *S. paradoxa* by MÜNSTER (1839) from Franconia. More material, exclusively from Dzikowiec (formerly Ebersdorf) in Silesia, was only rarely referred to, i.e., by TIETZE (1871), FRECH (1897), and SCHINDEWOLF (1937). Rather frequently, the old material was re-figured. By 1937, when SCHINDEWOLF erected *Soliclymenia* and added a third species *S. semiparadoxa*, only eight specimens were known to represent the genus.

RUAN (1981) figured more material from Daihua (Guizhou, South China) and described the new species *S. recticostata*. Material published by BOGOSLOVSKY (1981) under the name *S. solarioides* was later (KORN in KORN & KLUG 2002) interpreted as non conspecific with von BUCH's specimen and was renamed *Borisiclymenia ishikayensis* KORN, 2002. It differs from *S. solarioides* in the morphology of the ribs.

Recent field-work in the classical outcrop of Dzikowiec provided more material of *Soliclymenia*. Some fragmentary specimens were collected by Robert NIEDŹWIEDZKI (RN) (*S. paradoxa*, coll. 2003), but the best specimens described herein were discovered by Jan Bartosz POSIECZEK (JBP) in 2001 near the northern end of the abandoned quarry. These new specimens allow a revision of the genus and the species *S. paradoxa* which is re-described and figured.

NEW MATERIAL OF *SOLICLYMENIA*

Fifteen specimens of *Soliclymenia* from Dzikowiec (Text-fig. 1) are available for study: There are four spec-

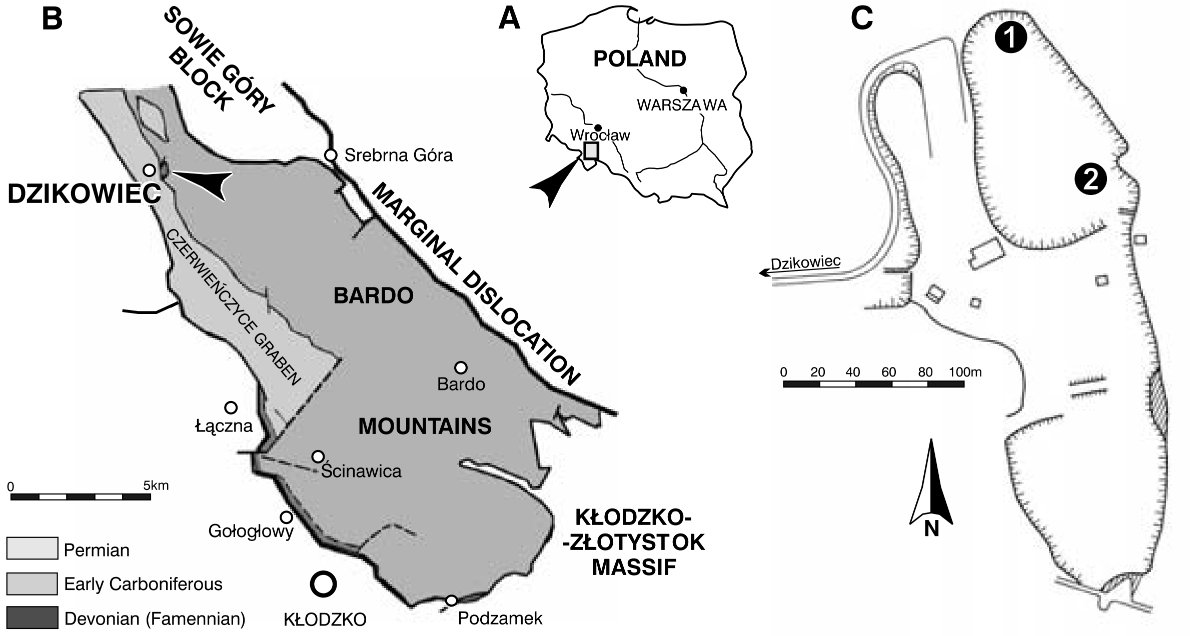

Fig. 1. The location of the Dzikowiec quarry in the Sudetes, Poland (after BERKOWSKI 2002); A – The Position of the Bardo Mountains in Poland; B – Geological outline of the Bardo Mountains with the Dzikowiec locality; C – Sketch of the Dzikowiec quarry with indication of the two sections, (1) and (2), illustrated in text-fig. 2

imens of *S. solarioides* (MGUWr 5306s, MGUWr 5311s, and MGUWr 5314s, coll. JBP; MGUWr 1760s coll. TIETZE), one specimen of *S. semiparadoxa* (Göttingen collection), and ten specimens of *S. paradoxa* (two specimens in the Göttingen collection; MGUWr 1760s, coll. TIETZE; MGUWr 5301s, MGUWr 5303s, MGUWr 5304s, MGUWr 5307s, MGUWr 5310s, and MGUWr 5313s, coll. JBP; MGUWr 5335s, coll. RN).

All specimens of *Soliclymenia* with the catalogue numbers abbreviated MGUWr, except for MGUWr 1760s which comes from an old TIETZE collection, were found *in situ* in several consecutive layers of grey (upper part) and red (lower part) organodetrital limestone (packstone, wackestone) about 0.4 metres thick. They form the middle part of a big block (5 m length, 2.5 m thick, see also MAZUR (1987, fig. 4) of clymeniid limestone which is disconformably overlain by a block of early Tournaisian *Gattendorfia* limestone (Text-fig. 2). The block of clymeniid limestone had probably been displaced on the fault (MAZUR 1987). In the layers with *Soliclymenia*, platform elements of conodonts including *Polygnathus communis communis, Palmatolepis gracilis sigmoidalis, Pseudopolygnathus marburgensis trigonicus*, and *Bisphathodus stabilis* were recovered. These conodont taxa have a wide stratigraphic range, from the Upper *expansa* Zone to the Middle *preculsata* Zone. Both blocks are separated with a thin layer of black claystone.

In the other sections of Dzikowiec, a similar claystone separates the clymeniid and *Gattendorfia* limestones (see DZIK 1997). The block of clymeniid limestone (2.0 – 3.0 metres thick) belongs entirely in the "*Wocklumeria* Stufe", and geopetal indicators show that the normal stratigraphical succession of the layers is preserved. Therefore one may state that *Soliclymenia* layers come from the upper part of the clymeniid limestone (approximately 0.8 – 0.4 m below the top of this unit). The age of the clymeniid limestone was determined on the basis of conodonts by FREYER (1968) from the Middle *expansa* Zone to the Lower *praesulcata* Zone (HAYDUKIEWICZ 1990). The upper part of the clymeniid limestone (approximately 1 m), from which specimens of *Soliclymenia* were recovered, contains conodonts of the Lower *praesulcata* Zone (RUDYK 2002).

In the clymeniid limestone, numerous fossils of nektonic organisms (e.g., cephalopods, conodonts) are present, and benthic fauna (e.g., trilobites) are much rarer. Analysis of our collection (383 specimens) and the collection of LEWOWICKI (1959, 328 specimens) demonstrates that nektonic genera make up 81 % of the faunal assemblage.

Famenian and Tournaisian limestones from Dzikowiec represent carbonate platform deposits (CHOROWSKA & WAJSPRYCH 1995). The domination of

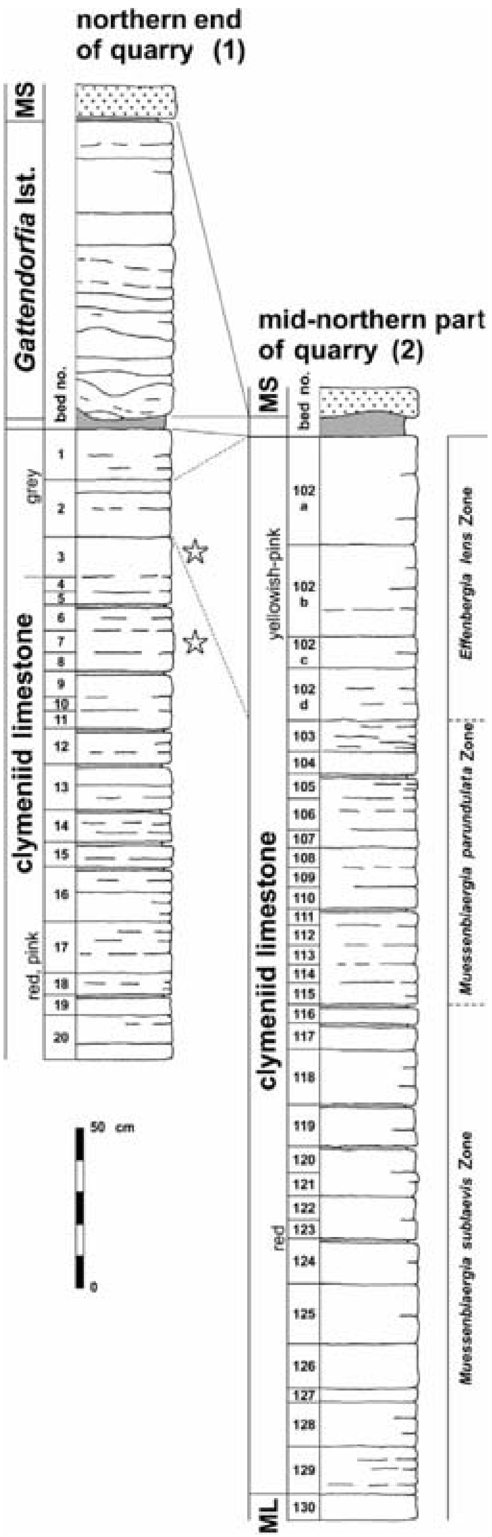

Fig. 2. Two columnar sections, measured at the northern end of the quarry (1) and the mid-northern part (2), showing their ammonoid stratigraphy and the horizons in which specimens of *Soliclymenia* were collected (indicated by asterisks). Bed numbers in the northern section refer to LEWOWICKI (1959). ML – Main Limestone, MS – micaceous sandstone

the nektonic fauna from the clymeniid limestone, the existence only of solitary non-dissepimented rugosan corals and heterocorals (BERKOWSKI 2002), as well as the presence of palmatolepid-bispathodid conodont biofacies (RUDYK 2002) proves that the limestone was deposited in pelagic and relatively deep-water conditions, away from the coast on the outer part of the carbonate platform.

In the grey Main Limestone (the "Hauptkalk" immediately below the clymeniid limestones), the predominant fossils are numerous colonial rugose and tabulate corals, algae, benthic foraminifera, cyanobacteria, and stromatoporoids, i.e., a typical Devonian community of the photic zone. All those mentioned organisms are missing in the clymeniid limestones, except for rare foraminifers, algae, and rugose corals (BERKOWSKI 2002). Therefore, it is likely that the clymeniid limestone unit was deposited near the boundary of the photic zone on the outer margin of the carbonate platform.

GEOLOGICAL AGE OF *SOLICLYMENIA*

Since the study of SCHINDEWOLF (1937), there has been no doubt that the occurrence of *Soliclymenia* from Dzikowiec belongs in the *Wocklumeria* Stufe of the Late Devonian ammonoid stratigraphy. The exact position within this stage, however, could only be estimated by SCHINDEWOLF. He proposed an age of the early *Wocklumeria* Stufe, immediately below the first occurrences of the genera *Kamptoclymenia* and *Parawocklumeria*.

The recent re-examination of the outcrop confirms SCHINDEWOLF's estimate. In the meantime, however, his "zone of *Kalloclymenia subarmata* and *K. brevispina*" was subdivided into three successive ammonoid zones (KORN 2000) including: the *Muessenbiaergia sublaevis* Zone, the *M. parundulata* Zone, and the *Effenbergia lens* Zone (Text-fig. 2). Perhaps the middle and, more probably, highest of these contains the *Soliclymenia* fauna. This age assignment is supported by several reasons. One is that the two parallel sections in the abandoned quarry near Dzikowiec show rock successions which differ only slightly in their composition. A section at the northern end of the quarry was measured by LEWOWICKI (1959); he listed two metres of clymeniid-bearing red limestones, of which the topmost bed (15 cm thick) yielded *Kamptoclymenia endogona* SCHINDEWOLF, 1937, and therefore it belongs in the *K. endogona* Zone (Text-fig. 2). From near this section, JBP collected the majority of the new material described herein; it comes from 0.4 – 0.8 metres below the top of the red limestones, i.e., from a horizon older than the *K. endogona* Zone.

Another section measured by DK at the eastern wall in the mid-northern part of the old quarry (Text-fig. 2) shows three metres of red, nodular limestones which follow the grey "Hauptkalk", and are themselves overlain by five centimetres thick dark shales. In the red limestones, no indication of the *Kamptoclymenia endogona* Zone or younger Late Devonian zone was found. In this section, ammonoid records show little vertical variation; the red limestones, approximately three metres thick, belongs entirely to the early "*Wocklumeria* Stufe". A rich sample from the top of the clymeniid limestone yielded more than 160 ammonoid specimens; most abundant are *Linguaclymenia similis* (MÜNSTER, 1839), *Cymaclymenia striata* (MÜNSTER, 1832), and various species of *Mimimitoceras*, *Glatziella*, and *Effenbergia*. The fauna is characteristic for the *Effenbergia lens* Zone of the late Famennian. Conodont investigations by RUDYK (2002) demonstrated that the highest part of the "*Wocklumeria* Stufe" is missing in this section. According to this investigation, the layer with *S. solarioides* represents a lower part of the Upper *expansa* Zone.

A fragmentary specimen from Dasberg, in the Rhenish Massif in Germany (coll. KORN 1989), comes from an assemblage with *Muessenbiaergia sublaevis* (MÜNSTER, 1832), *M. ademmeri* (KORN & PRICE, 1987), *Kalloclymenia* sp., *Mimimitoceras trizonatum* KORN, 1988, and *Effenbergia lens* (KORN, 1992), and is also assigned to the *Effenbergia lens* Zone.

PALAEOGEOGRAPHIC DISTRIBUTION OF *SOLICLYMENIA*

Soliclymenia is currently known from only four places: (1) Dzikowiec (formerly Ebersdorf), Silesia (von BUCH 1839; TIETZE 1871; SCHINDEWOLF 1937), represented by *S. solarioides* (von BUCH, 1839), *S. paradoxa* (MÜNSTER, 1839), and *S. semiparadoxa* SCHINDEWOLF, 1937 (Text-fig. 3); (2) Schübelhammer, Franconia (MÜNSTER 1839), represented by *S. paradoxa* (MÜNSTER, 1839) [additional material was there obviously never collected]; (3) Dasberg, Rhenish Massif, with a record of a small fragmentary specimen of *S. solarioides* by DK (unpublished); and (4) Daihua, Guizhou (RUAN 1981), represented by *S. paradoxa* (MÜNSTER, 1839) and *S. recticostata* RUAN, 1981.

It is noteworthy that *Soliclymenia* has a wide palaeogeographic distribution within the tropical Late Devonian seas. This phenomenon, however, is not surprising since there is hardly any provincialism detectable when occurrences of ammonoid genera are analysed (KORN 2001).

PHYLOGENY OF *SOLICLYMENIA*

The unusual morphology of *Soliclymenia* was, as in the nearly co-occurring wocklumeriid ammonoids, one reason for an alternative, non-Darwinian evolutionary theory. SCHINDEWOLF (1945, 1950) regarded them as degenerate and used them as evidence for typolysis, the pre-programmed extinction of groups, being the last phase of the three-phased Typostrophe Theory. KORN (2003) showed that this theory cannot be supported by the empirical data, which in fact supports the Darwinian view of evolution.

The phylogeny of *Soliclymenia* is problematic because there is no really similar latest Devonian ammonoids known. SCHINDEWOLF (1937) recognised this riddle; he proposed a common ancestor (which was not known and largely conjecture) for both *Soliclymenia* and the also triangularly coiled wocklumeriid ammonoids.

The species of *Soliclymenia* (of which the type species *S. solarioides* is not triangularly coiled) share the following morphological features (Text-fig. 3): the conchs are small and may reach only 20 mm in diameter, the umbilicus is extremely wide (approximately 0.70 of the conch diameter), the aperture is very low, with a whorl expansion rate of only 1.35, the whorl cross section is ventrally depressed and crescent-shaped, the wide venter shows often a keel which in adults is accompanied by longitudinal grooves on both sides, the conch is strongly ribbed; the ribs are usually concave on the flank and bent forward to a prominent ventrolateral projection, and the simple suture line shows only three rounded lobes, an internal, a lateral, and an external lobe. The septal shape is not known, and hence, it cannot be excluded that these lobes are only caused by the depressed geometry of the whorl cross section.

Such a combination of characters can only be seen in the contemporary genus *Glatziella* RENZ, 1914, which is also particularly known from Dzikowiec (Text-fig. 4B). The most similar species is *G. helenae* (RENZ, 1914); this also shows strong concave ribs, a wide umbilicus (0.55 of the conch diameter), and a ventral keel accompanied by grooves. It also has slightly depressed whorls, but in general, it is less serpenticonic than *Soliclymenia solarioides*. The juvenile suture line of *G. helenae* resembles that of *Soliclymenia* (Text-fig. 4A). Adult *G. helenae* show a wide ventral saddle (SCHINDEWOLF 1937).

Kamptoclymenia endogona has a similar conch with very wide umbilicus (uw/dm = 0.60), a depressed whorl cross section, and a rounded mid-ventral keel. Its inner whorls show a tendency toward triangular or tetrangular coiling (SCHINDEWOLF 1937). The suture line of *K.*

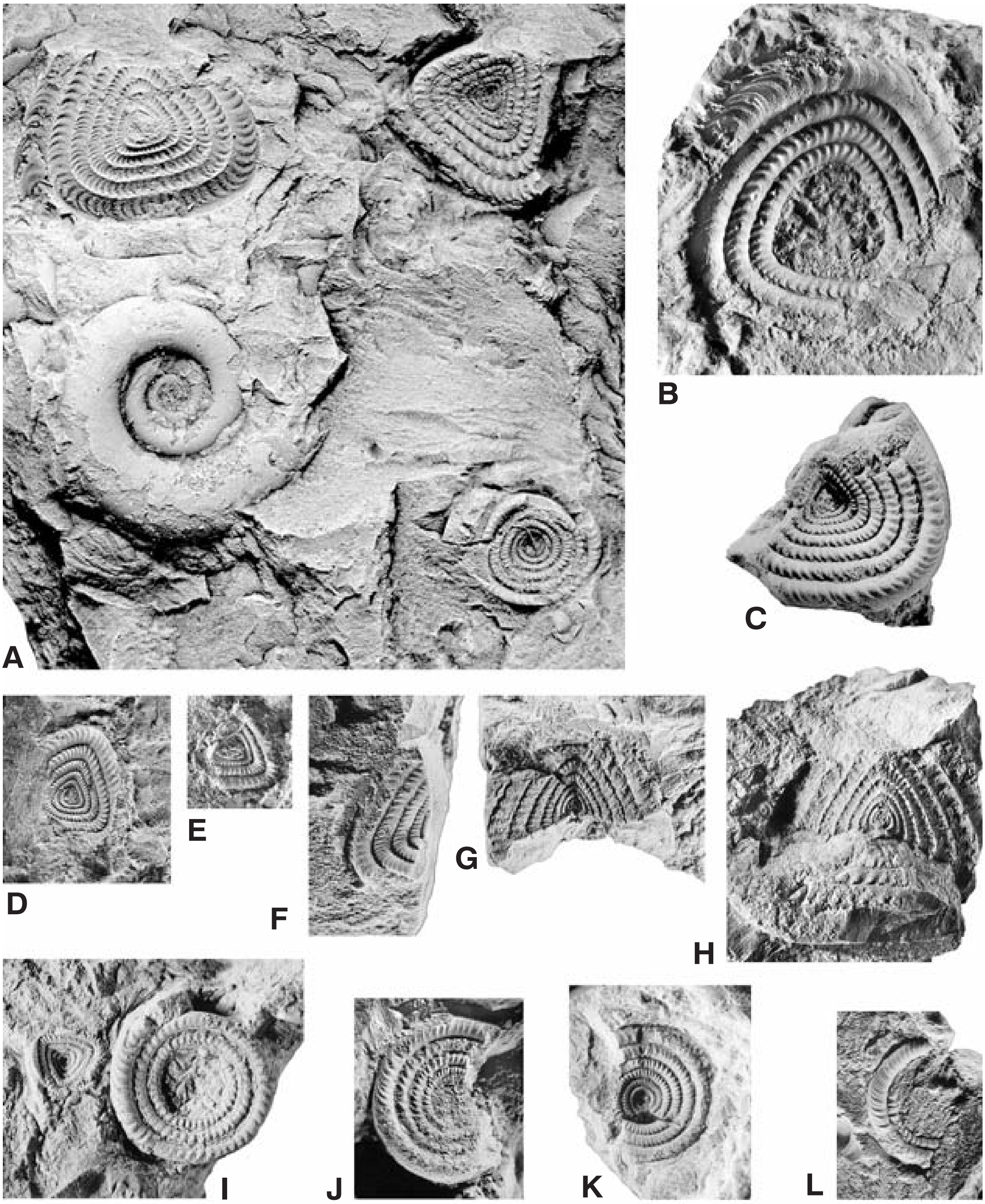

Fig. 3. Specimens of *Soliclymenia* from Dzikowiec, all × 2.5; A – *S. paradoxa* (MÜNSTER, 1839) (upper two specimens), *S. semiparadoxa* SCHINDEWOLF, 1937 (lower right specimen); Göttingen specimen. B – *S. paradoxa* (MÜNSTER, 1839), specimen MGUWr 5303s. C – *S. paradoxa* (MÜNSTER, 1839), specimen MGUWr 5313s; D – *S. paradoxa* (MÜNSTER, 1839), specimen MGUWr 5301s; E – *S. paradoxa* (MÜNSTER, 1839), specimen MGUWr 5304s; F – *S. paradoxa* (MÜNSTER, 1839), specimen MGUWr 5310s; G – *S. paradoxa* (MÜNSTER, 1839), specimen MGUWr 5307s; H – *S. paradoxa* (MÜNSTER, 1839), specimen MGUWr 5312s; I – *S. paradoxa* (MÜNSTER, 1839) (left specimen), *S. solarioides* (von BUCH, 1839) (right specimen), specimen MGUWr 1760; J – *S. solarioides* (von BUCH, 1839), specimen MGUWr 5306s; K – *S. solarioides* (von BUCH, 1839), specimen MGUWr 5314s; L – *S. solarioides* (von BUCH, 1839), specimen MGUWr 5311s

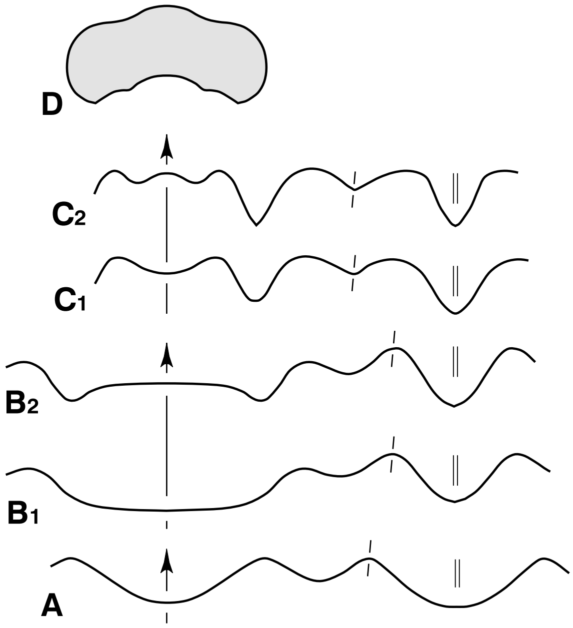

Fig. 4. Suture lines and whorl cross section of representatives of the family Glatziellidae [A-C after SCHINDEWOLF (1937); D after RUAN (1981)]; A – *Soliclymenia solarioides* (von BUCH, 1832); B – *Glatziella helenae* (RENZ, 1914), juvenile and adult suture line; C – *Postglatziella carinata* SCHINDEWOLF, 1937, juvenile and adult suture line; D – *Soliclymenia paradoxa* (MÜNSTER, 1839), × 5

endogona is simple and closely resembles *Glatziella helenae*. *Kamptoclymenia* does not show ribs and is, in this character, different from *Soliclymenia*.

Among stratigraphically older clymeniids, there are some platyclymeniids known which show some similarities to *Soliclymenia*. Species of *Pleuroclymenia* SCHINDEWOLF, 1934, *Progonioclymenia* SCHINDEWOLF, 1937, and *Borisiclymenia* KORN, 2002 are widely umbilicate (uw/dm = 0.50 – 0.60), ribbed, and show depressed whorl cross-sections. They also have simple suture lines like *Soliclymenia*, but they do not possess a keel. Their ribs extend almost straight across the flanks.

If all of the morphological characters are considered, the following conclusion can be made: *Soliclymenia* and *Glatziella* are sister groups. Both share some apomorphic characters such as the shape and course of the ribs, the wide umbilicus, the ventrolateral grooves with the keel, and the simple suture line. Additionally, the families Glatziellidae (genera *Glatziella* RENZ, 1914, *Liroclymenia* CZARNOCKI, 1989, *Postglatziella* SCHINDEWOLF, 1937, and *Soliclymenia* SCHINDEWOLF, 1937) and the family Parawocklumeriidae (genera *Kamptoclymenia* SCHINDEWOLF, 1937, *Parawocklumeria* SCHINDEWOLF, 1926, etc.) show sister group relations. The ancestral species of both families share the characters of an involute, serpenticonic conch and a very simple suture line. This ancestor has not yet been discovered.

HOW MANY SPECIES OF *SOLICLYMENIA*?

The rarity of *Soliclymenia* prevents a statistic analysis of the conch shape, and therefore it was questionable if the three Central European species can be strictly separated, or if they represent a continuous morphocline from the circular *S. solarioides*, and passing the semi-triangular *S. semiparadoxa* toward the triangular *S. paradoxa*. To solve this problem, the angularity of the whorl spirals was measured in all of the available specimens and also from illustrations in the literature (SCHINDEWOLF 1937, RUAN 1981). The degree of angularity was computed as follows. In the scanned images of the specimens, a circle that exactly matches the outline of the whorl, was drawn in the corner of the triangular volution (for the inner whorls, the outline of the umbilicus was used, allowing for some minor errors in the calculations). The ratio conch diameter/ corner circle diameter provides the degree of angularity as used in the following account. A circularly coiled form has thus the angularity index 1 (conch diameter and corner circle have almost the same value), and a perfect triangle would have an infinite high value.

The analysis leads to the following results. All the three species of *Soliclymenia* found near Dzikowiec are valid. Although there is some variation in the triangularity within *S. paradoxa*, there are no intermediates between *S. paradoxa* and *S. semiparadoxa*. *S. paradoxa* has the most triangular whorls between 2.5 and 4.0 millimetres conch diameter, and later whorls show a continuous decrease in triangularity.

In *S. semiparadoxa*, which is only known from the holotype, the mode of triangularity is different. The early whorls up to 3.0 millimetres in diameter are almost circular, and a rounded triangularity is introduced in later stages. In this respect, it is markedly different from the coiling shape of *S. paradoxa*. *S. semiparadoxa* cannot therefore be regarded as an intermediate between *S. paradoxa* and *S. solarioides*.

The Chinese specimens (RUAN 1981) belong to two different species. They are figured on RUAN's pl. 27, of which figures 1 to 3 show two specimens of *S. paradoxa*. Their general conch form and sculpture closely resemble the material from Dzikowiec, but the angularity index for the two specimens is relatively low. Nevertheless, based on the angularity index, they fall within the variability of *S. paradoxa* from Dzikowiec.

The second Chinese species *S. recticostata* RUAN, 1981 is more difficult to evaluate. In contrast to the other three species of *Soliclymenia*, the ribs of *S. recticostata* extend almost straight over the flanks. This feature, however, may be a juvenile character; both specimens figured by RUAN are very small (dm = 5.0 – 6.0 mm). In this developmental stage, the similar species *S. semiparadoxa* also has almost straight ribs. Without examination of the original material, the question of specific independence cannot be answered. Thus, the validity of *S. recticostata* is accepted with reservation at this time.

THE ECOLOGY OF *SOLICLYMENIA*

Some species of *Soliclymenia* possess one of the most spectacular conch morphologies of all known ammonoids. It is not only conspicuous because of the triangular coiling, but also because of the extremely serpenticonic conch and the crescent-shaped, keeled whorl cross sections.

According to the calculations by RAUP (1967), SAUNDERS & SHAPIRO (1986), as well as OKAMOTO (1996), the whorl expansion rate (WER) can be used as a measure for the body chamber length and orientation of the aperture of the living animal. *Soliclymenia* with its very low WER (1.35) has a long body chamber (more than one volution). Its aperture thus had a horizontal orientation during lifetime, i.e. facing directly upward. Such an aperture, in addition to the small conch, suggests a nekto-planktonic life-style. At least, a bottom-oriented life is not likely because this would require extremely long tentacles or prominent extensions of the body of the animal beyond the aperture of the conch..

The functional value of triangular coiling in *Soliclymenia* is problematic. SCHINDEWOLF (1937, 1938, 1945, 1950) saw a degeneration, an “ageing” of the lineage with its pre-programmed extinction. “Degeneration” is very unlikely because of the wide geographic distribution of the genus. A plausible explanation for the triangular coiling cannot be provided at present.

Among the other conch characters, the strong ventrolateral projection of the growth lines and the two ventral grooves with the mid-ventral keel are worth mentioning. Such a combination of characters is especially known from dwarfed ammonoids, such as the Late Devonian genera *Effenbergia*, *Balvia*, *Glatziella*, *Kamptoclymenia*, and *Linguaclymenia* (KORN 1995a, 1995b), as well as the Early Carboniferous *Nomismoceras* and *Entogonites* (NICOLAUS 1963).

TAXONOMIC DESCRIPTIONS

Abbreviations of cited repositories: MGUWr – Geological Museum of the Institute of Geological Sciences of Wrocław University. Abbreviations used in the text are dm – conch diameter, ww – whorl width, wh – whorl height, uw – umbilical width, ah – apertural height.

Family Glatziellidae SCHINDEWOLF, 1937
Genus *Soliclymenia* SCHINDEWOLF, 1937

GENUS DEFINITION: Glatziellidae with very wide umbilicus (uw/dm approximately 0.70). Whorl cross section ventrally depressed, crescent-shaped. Venter with a wide, rounded keel. Sculpture with sharp ribs on the flanks which form a concave arc. Growth line course concavo-convex with prominent ventrolateral projection and moderately deep ventral sinus. Suture line simple with shallow and wide lateral and external lobe. Sutural formula E L I.

Soliclymenia paradoxa (MÜNSTER, 1839)
(Text-fig. 3 A-I, 5 A-G, J-L)

1839. *Clymenia paradoxa* n. sp. MÜNSTER, p. 41, pl. 16, fig. 6a-d.
1843. *Clymenia paradoxa* MÜNSTER; MÜNSTER, p. 41, pl. 16, fig. 6a-d.
1871. *Clymenia paradoxa* MÜNSTER; TIETZE, p. 136, pl. 16, fig. 14.
1897. *Clymenia paradoxa* MÜNSTER; FOORD & CRICK, p. 32.
1897. *Clymenia paradoxa* MÜNSTER; FRECH, pl. 36, fig. 5a.
non 1902. *Phenacoceras ? paradoxum* MÜNSTER; FRECH, p. 63, pl. 3, fig. 5.
non 1904. *Aganides paradoxus* MÜNSTER; FRECH, p. 165.
1913. *Clymenia* (*Rectoclymenia*) *paradoxa* MÜNSTER; FRECH, p. 42.
1914. *Clymenia paradoxa* MÜNSTER; RENZ, p. 104.
1937. *Soliclymenia paradoxa* MÜNSTER; SCHINDEWOLF, p. 60, pl. 1, fig. 4b, 6-8.
1958. *Soliclymenia paradoxa* MÜNSTER; MILLER & FURNISH, p. 256, text-fig. 2B.
1981. *Soliclymenia paradoxa* MÜNSTER; RUAN, p. 108, pl. 27, fig. 1-3.
1982. *Progonioclymenia* (*Soliclymenia*) *paradoxa* MÜNSTER; PRICE, p. 131, fig. 5.1E.
1985. *Soliclymenia solarioides* von BUCH; HOUSE, 124, pl. 6.7.21.

DIAGNOSIS: *Soliclymenia* with strong triangular coiling throughout ontogeny.

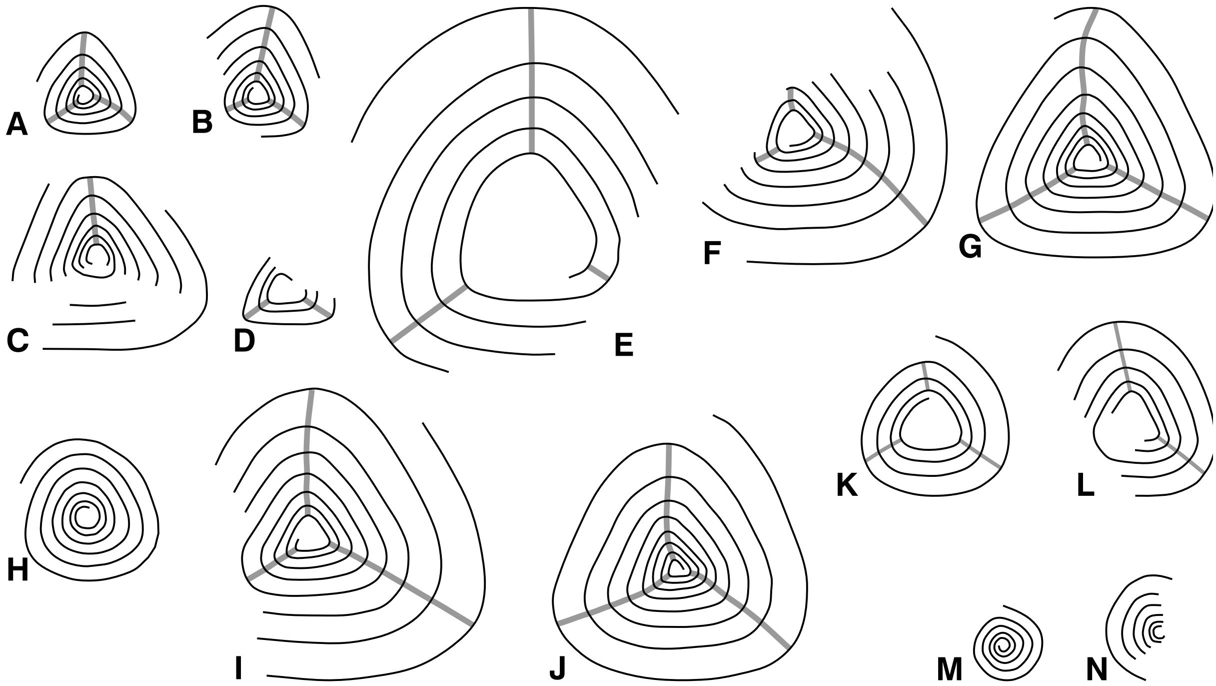

Fig. 5. Whorl outlines of specimens of *Soliclymenia*, all × 2.5, some specimens are reversed for comparison, grey line indicates the position of coiling corners; A – *S. paradoxa*, specimen MGUWr 1760s; B – *S. paradoxa*, specimen MGUWr 5304s; C – *S. paradoxa*, specimen MGUWr 5307s; D – *S. paradoxa*, specimen MGUWr 5301s; E – *S. paradoxa*, specimen MGUWr 5303s; F – *S. paradoxa*, specimen MGUWr 5313s; G – *S. paradoxa*, Göttingen specimen; H – *S. semiparadoxa*, Göttingen specimen; I – *S. paradoxa*, Göttingen specimen; J – *S. paradoxa*, London specimen 66 384 [after SCHINDEWOLF (1937)]; K – *S. paradoxa*, specimen 33533 [after RUAN (1981)]; L – *S. paradoxa*, specimen 33532 [after RUAN (1981)]; M – "*S. recticostata*", specimen 33535 [after RUAN (1981)]; N – "*S. recticostata*", specimen 33534 [after RUAN (1981)]

MATERIAL: 10 specimens are available for study. Many are fragmentary and contribute little to the knowledge of the species. The following descriptions are based on the two specimens in the Göttingen collection (SCHINDEWOLF 1937), one specimen from the old collection of Wrocław (SCHINDEWOLF 1937), and six new specimens (MGUWr 5301s, 5303s, 5304s, 5307s, 5312s, 5313s) collected recently by JBP that range in diameter from 4 to 20 millimetres.

DESCRIPTION: Except for a more elaborated view on the intraspecific variability, little can be added to the extensive description of the species by SCHINDEWOLF (1937). Therefore, the following account will especially focus on the results gained from the new material.

Coiling variability was noticed by SCHINDEWOLF (1937), who figured one specimen in which the distance of the coiling angles is slightly less than 120 degrees. The new material provides greater details of the coiling variability in *S. paradoxa*. Variability does not only involve the distance of the angles, but also the degree of curvature of the whorl segments and the angularity of the corners (Text-figs 5, 6). The new material shows such differences, and in addition some individuals display some variability in the morphology of the whorl segments. All of the investigated specimens show at least one common feature, that is, the degree of triangularity (measured by the angularity of the corners) decreases during ontogeny.

Specimen MGUWr 5307s most closely resembles the material described by SCHINDEWOLF (1937). It has strong triangular coiling, and all the corners show the same angularity. There is only a slight coiling reduction during ontogeny. The whorl segments between the corners are almost linear (Text-fig. 5C).

Specimen MGUWr 5313s shows a rather rapid decrease of triangular coiling during ontogeny. The corners have, in the inner whorls, distances of a little less than 120 degrees (Text-fig. 5F).

In specimen MGUWr 5304s, the coiling triangle is irregular. The specimen shows one narrow, one medium, and one wide corner, and the whorl segments between the corners vary from linear to moderately rounded (Text-fig. 5B).

MGUWr 5303s has the greatest diameter, and this specimen shows the four terminal whorls. This specimen also shows the least triangularity. The whorls have

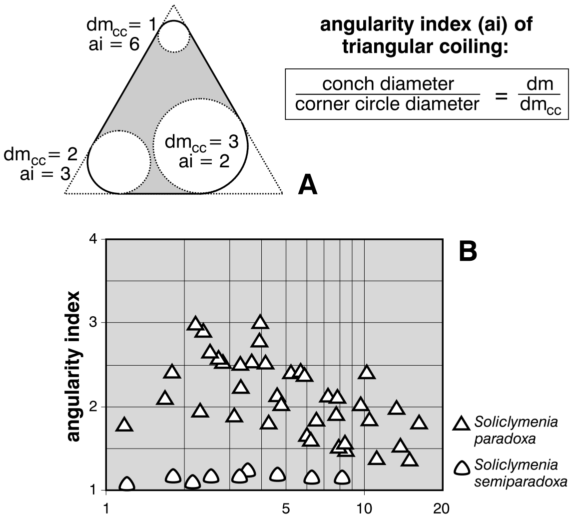

Fig. 6. The angularity index in species of *Soliclymenia*, A – explanation of the calculation of the angularity index in a triangle with three different corners (of which the lower left one represents the maximum angularity in *S. paradoxa*); B – bivariate plots of the angularity index in the two species *Soliclymenia paradoxa* and *S. semiparadoxa* (incl. "*S. recticostata*"). The plot displays the ontogenetic reduction of the angularity index in *S. paradoxa*, and the increase in *S. semiparadoxa*

a rounded triangular outline with a coiling triangle that has two flattened and one rather rounded side (Text-fig. 5E). The sculpture weakens continuously during the last four volutions; in the terminal whorl, ribs are only barely visible. In this stage, sharp riblets are present which are concave on the flank and project toward a very high ventrolateral salient.

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