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The Baltic nautiloids *Cyrtoceras ellipticum* LOSSEN 1860, *C. priscum* EICHWALD 1861, and *Orthoceras damesi* KRAUSE 1877

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With 5 figures

Kurzfassung: Die Typen von *Cyrtoceras ellipticum* LOSSEN 1860 und unserer Ansicht nach konspezifisches Material aus baltischen erratischen Blöcken des späten Llanvirn (Lasnamägium) ähneln sehr stark *Phthanoncoceras oelandense* EVANS & KING 1990 aus dem spätesten Arenig (frühes Kundium) von Schweden. *Cyrtoceras priscum* EICHWALD 1861, das zusammen mit *C. ellipticum* auftritt, gehört aufgrund seiner kurzen Wohnkammer und seines viel fortschrittlicheren Siphonalapparates zu einer anderen Gattung; wahrscheinlich ist es ein Vertreter der *Oonoceras*-Entwicklungslinie. Der Typus von *Orthoceras damesi* KRAUSE 1877 aus baltischen erratischen Blöcken des Beyrichienkalkes ist abgesehen von sehr feinen Anwachslinien glattschalig. Er stellt anscheinend ein späteres ontogenetisches Stadium in der Entwicklung eines Kionoceratiden mit prominenten feinen Längsrippen und Ringelung in frühen Stadien dar. Wahrscheinlich handelt es sich um eine abgeleitete Form der longikonen Hauptentwicklungslinie von *Spyroceras*, bei der die deutliche Schalenskulptur bei adulten Exemplaren verschwand.

Abstract: The type specimens of *Cyrtoceras ellipticum* LOSSEN 1860 and proposedly conspecific material from Baltic erratic boulders of late Llanvirn (Lasnamägian) age are closely similar to *Phthanoncoceras oelandense* EVANS & KING 1990 from the latest Arenig (early Kundan) of Sweden. *Cyrtoceras priscum* EICHWALD 1861, co-occurring with *C. ellipticum*, is generically distinct in its short living chamber and much more advanced siphuncular structure; it probably represents *Oonoceras* lineage. The type of *Orthoceras damesi* KRAUSE 1877 from the Baltic Beyrichienkalk erratic boulders, which is smooth, except for faint growth lines, appears to represent a later ontogenetic stage in development of a kionoceratid with prominent longitudinal riblets and annulations at early stages. It is probably a derivative of the main longiconic lineage of *Spyroceras*, in which prominent conch ornamentation disappeared in adult specimens.

Introduction

Straight to loosely coiled fossil conchs of Palaeozoic nautiloids are almost invariably found fragmented. Unlike tightly coiled later nautilids or ammonoids, they rarely provide a complete record of ontogeny in a single specimen. In effect, the most important diagnostic characters remain unknown in most named species of Palaeozoic nautiloids. Similar phragmocones may bear basically different embryonic and larval parts (RISTEDT 1968) and related species may differ only in the morphology of their adult living chamber. This makes such characters the most important taxonomically, especially at the species level.

A recognition of the course of conch ontogeny is thus crucial to nautiloid taxonomy. Although a great number of names has been introduced for ortho- and cyrtoconic Palaeozoic nautiloids by early workers, quite rarely their descriptions and illustrations provide enough information to enable taxonomic discrimination. Consequently, they can hardly be used to

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identify specimens other that of the types. This introduces a lot of inconvenience to taxonomy of the Palaeozoic nautiloids, and commonly results in unnecessary proliferation of names. The only way to avoid this is to revise old museum collections and to collect fossils in classic type localities to make early names fully available.

In the present paper three species of early Palaeozoic nautiloids, originally described or best known from Baltic erratic boulders, are discussed from this point of view. In case of the Ordovician *Cyrtoceras ellipticum* Lossen 1860 and *Cyrtoceras priscum* Eichwald 1861, lectotypes are proposed and described (see also Kiselev 1991) and their possible relationships to stratigraphically and regionally associated specimens are discussed. The third species is characteristic of the Baltic Beyrichienkalk, of Pridoli age. Beyrichienkalk boulders commonly contain nautiloids but, as the boulders are usually small, only fragments of longiconic conchs are available for study. The most numerous kinds of nautiloid conchs in these boulders are those with weakly annulated, almost smooth surfaces and long living chambers. Such conchs have been provisionally classified as *Eridites* (?) sp. (Dzik 1984). In 1988, while examining the original specimen of *Orthoceras damesi* Krause 1878 the senior author found that it is conspecific with them. Another, morphologically quite distinct kind of Beyrichienkalk orthoconic nautiloid phragmocone shows annulation and bears prominent longitudinal riblets. Such a morphology, with gradual ontogenetic disappearance of annulation, characterizes *Kionoceras.* A fortuitous find of a boulder of the Beyrichienkalk with a part of a nautiloid conch in situ that represents exactly the transition between these two apparently incompatible morphologies (Fig. 4e) shows that the latter are juvenile stages of *O. damesi.* Even more complete specimens of the species have subsequently been traced in a museum collection long ago investigated by Otto Schindewolf. The data on the complex ontogeny of the conch ornamentation in this species, as well as its internal morphology, are assembled below.

The type specimens of two species are in the collection of the Museum für Naturkunde of Humboldt Universität Berlin (abbreviated MB), that of the third one in the Geological-stratigraphical Museum of Sankt Petersburg State University (SPbGU). They are matched with proposedly conspecific specimens in collections by other authors housed in MB and in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (ZPAL). A part of this material was partially reviewed earlier (Dzik 1984) with application of open nomenclature.

Taxonomic Descriptions

Order Oncoceratida Flower in Flower Kummel 1950
Family Phthanoncoceratidae Evans & King 1990
Genus *Phthanoncoceras* Evans & King 1990

Type species: *Phthanoncoceras oelandense* Evans & King 1990; early Kundan of Öland, Sweden.

Phthanoncoceras ellipticum (Lossen 1860)

Figs. 1 a–e, 3 a–b

1860 *Cyrtoceras ellipticum* – Lossen: 27, pl. 1, fig. 3 a, b.

Lectotype: MB C.873 (designated here); Fig. 1 a, b.

Type horizon and locality: Erratic boulder of a grey, slightly marly cephalopod limestone found in Żary (Lower Silesia). The boulder contains also a fragmentary phragmocone of *Cochlioceras* sp., a pygidium of *Asaphus* sp. and a symmetrical spine of a trilobite (perhaps *Lonchodomas*). Judging from the lithology and associated fossils this is probably the Folkeslunda Limestone of Lasnamägian (late Llanvirn) age.

Diagnosis: Long living chamber, only a little less than half of the whole conch length. Conch gently curved, compression index at adult stages is about 0.7.

Description: The lectotype has a well preserved embryonic conch which is approxi-

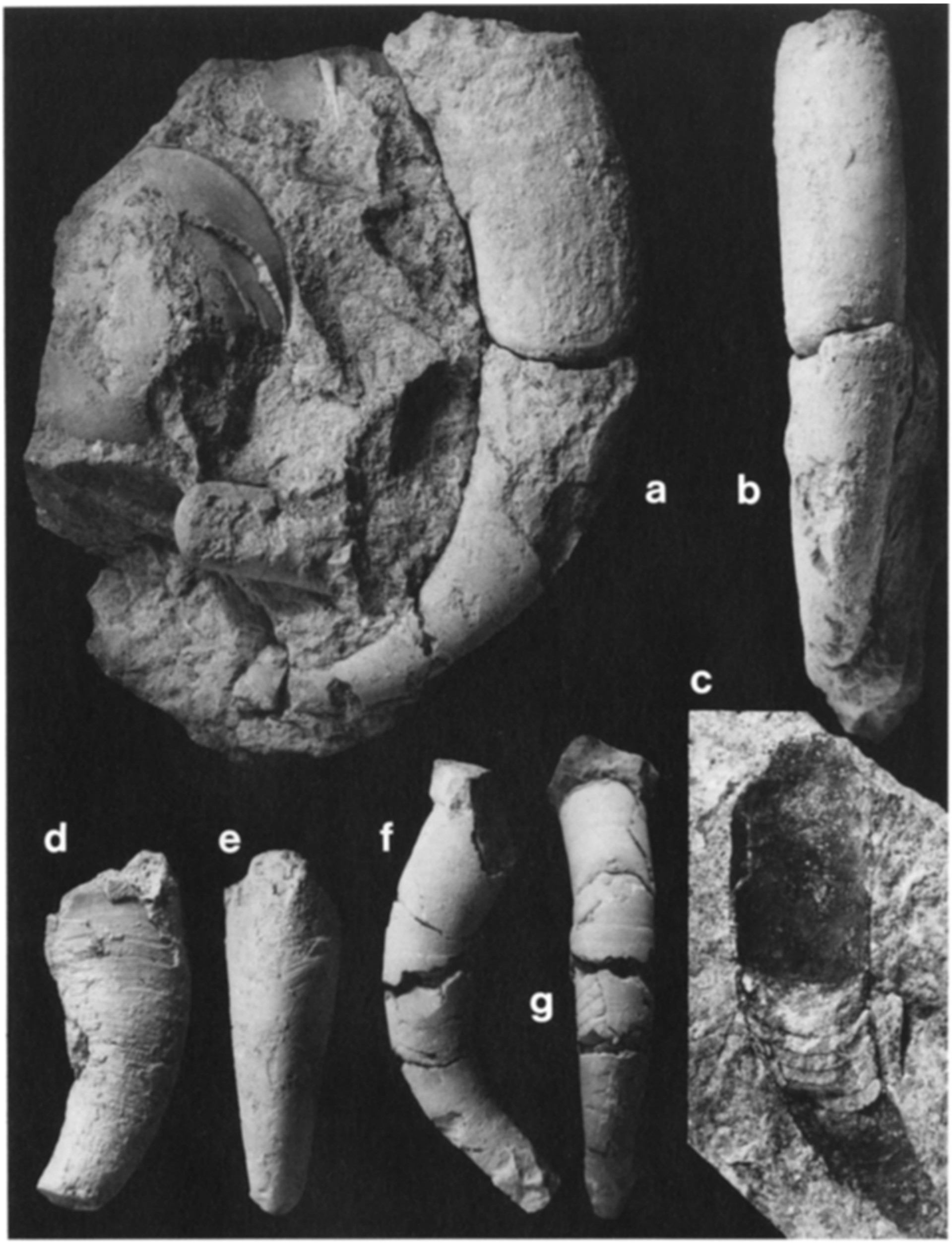

Fig. 1. a–e. ***Phthanoncoceras ellipticum*** (LOSSEN 1860), Lasnamägian (Late Llanvirn), glacial erratic boulders of Baltic origin. a–b: Lectotype MB C.873 in lateral and ventral views; Żary (Lower Silesia). c: Longitudinally split specimen MB C.869, Platte Nr. 3 of H. PATRUNKY, Bydgoszcz. d–e: Juvenile specimen MB C.872 in lateral and ventral views, same boulder.
f–g. *Oonoceras priscum* (EICHWALD 1861), specimen MB C.874 in lateral and ventral views, same boulders as c–e. All natural size.

mately 2.5 mm in diameter (Fig. 1a). Its apex is hemispherical and smooth. Growth lines are difficult to trace in this part of the specimen so it is not possible to reconstruct the course of early development from their appearance. The dorsal length of the phragmocone is 53.0 mm. First 25 mm of the phragmocone shows distinctly lower rate of expansion, which is a typical feature of the geometry of nautiloid conchs (see DZIK 1984: 73 for discussion). In the lectotype only the position of the siphuncle can be traced but a longitudinal section of its middle part is available in specimen MB C.869 (Fig. 1g) from a boulder (Platte Nr. 3), collected by H. PATRUNKY from the bank of the Vistula river in Bydgoszcz. Here the phragmocone is split medially. The siphuncle diameter is about 1.2 mm at the stage when dorsoventral phragmocone diameter is about 16.0 mm; it is a little less than 1 mm from the conch wall. Connecting rings are virtually cylindrical; they are sparitic and details of internal structure are not preserved.

The adult living chamber of the lectotype is 42.5 mm in length, its dorso-ventral diameter is 21.0 mm, lateral 15.0 mm. Surface ornamentation is well preserved in specimen MB C.872 from the Platte Nr. 3 of H. PATRUNKY. Growth lines are rather irregularly distributed, with numerous marks of apertural breakage and regeneration. They show a relatively deep V-shaped ventral sinus which gently extends to lateral sides. Its rather acute ventral course seems to be related to the weakly lachrymose section of the living chamber. Only above the midheight of the aperture is it strictly transverse to the longitudinal axis of the conch. At earlier ontogenetic stages the conch cross-section was more rounded.

Range of the species: All the four known Lasnamägian specimens of *Phthanonceras ellipticum* are very similar to each other. This suggests rather low population variability.

The lectotype and the only specimen of *Phthanoncoceras oelandense* from the early Kundan of Öland is virtually indistinguishable from *Ph. ellipticum.* Perhaps the living chamber is relatively shorter in the early Kundan specimen but its aperture is not completely preserved. It is clear from specimen MB C.869 that the connecting rings were thick and the siphuncle more or less cylindrical also in *Ph. ellipticum.* It remains unknown whether in the Lasnamägian type population of *Ph. ellipticum* diaphragms also occurred. EVANS & KING (1990) identified diaphragms in their specimen of *Phthanoncoceras* from the Kundan and attributed much taxonomic weight to this. Diaphragms were inherited also by primitive representatives of other nautiloid groups (endoceratids, discosorids) from their ellesmeroceratid ancestors. This is a primitive (plesiomorphic) character of little use in defining taxa of early nautiloids.

Apart from the diaphragms the only substantial specific difference between *Ph. oelandense* and *Ph. ellipticum* is the difference in age; EVANS & KING'S (1990) specimen being of latest Arenig and LOSSEN'S and PATRUNKY'S, of late Llanvirn age. In any case, it seems certain that they represent the same lineage.

Evolutionary relationships: A few primitive oncoceratids distinct from typical *Ph. ellipticum* occur with it in the Baltic Lasnamägian. ANSORGE (1990) illustrated an almost complete specimen of this species, identified as *Richardsonoceras* ? sp., from an erratic boulder. Conodont elements of *Eoplacognathus reclinatus* FÅHRÆUS 1966 extracted from the specimen rock matrix prove its Lasnamägian age. Although the aperture is not preserved, it is clear that the length of the chamber exceeds significantly its dorso-ventral diameter which suggests an affinity rather to *Phthanoncoceras* than *Richardsonoceras.*

Several similarly coiled undescribed specimens from the early Kundan of Hälludden, Öland, are housed in the collection of the Naturhistoriska Riksmuseet, Stockholm. In respect to ANSORGE'S (1990) specimen they seem to have shorter living chambers. This may parallel the differences between the early Kundan and Lasnamägian specimens of typical *P. ellipticum.*

Siphuncular structures similar to *Phthanoncoceras* are known among oncoceratids from significantly younger (Caradoc) Chinese strata of the Pagoda Limestone. *Richardsonoceras huanghuachangense* CHEN & ZOU 1985 has orthochoanitic septal necks and connecting rings concave in profile (CHEN & ZOU 1985: text-fig. 7). Whether this is an evidence of a direct relationship of the Chinese species to ***Phthanoncoceras ellipticum*** is unclear, as there are no data on the length of the adult living chamber.

Also *R. beianense* YING 1989 from the Early Ordovician Zetan Formation of Anhui should be considered among possible relatives of *Ph. ellipticum*, but the original description is based on a specifically undeterminable specimen (see YING 1989).

Although South China is now very distant geographically from the Baltic region, in the Ordovician it belonged to the same biogeographical realm of temperate climate (i.e. DZIK 1990). This is relevant to the nautiloid faunas of both regions which are undoubtedly closely related even if different names continue to be applied.

Distribution: The Platte Nr. 3 collected by H. PATRUNKY in Bydgoszcz shows the same kind of rock matrix as that in LOSSEN's original specimen. The nautiloid assemblage from this erratic boulder contains also a longiconic species of *Clinoceras* and the ellesmeroceratid *Cochlioceras*, both common in the Lasnamägian. Along with the erratic boulder material, some specimens of the species are known which were collected from in situ outcrops of the Folkeslunda Limestone of southern Sweden (they are in the collection of the Naturhistoriska Riksmuseet, Stockholm). The species seems thus to range from the early Kundan to late Lasnamägian of at least the western Baltic area.

Family Oonoceratidae HYATT 1900

Genus *Oonoceras* HYATT 1884

Type species: *Cyrtoceras acinaces* BARRANDE 1866; ?Kopanina Formation (Ludlow) of Bohemia.

Fig. 2. *Oonoceras priscum* (EICHWALD 1861), lectotype SPbGU I/III3 in lateral (a) and ventral (b) views, Lasnamägian of Hiumaa, Estonia; × 2.

Oonoceras priscum (Eichwald 1861)

Figs. 2a–b, 3c–d

1861 *Cyrtoceras priscum* sp.n. – Eichwald: 372, pl. 1, fig. 5.
1984 *Oonoceras* sp. – Dzik: text-fig. 15a, b, pl. 9, fig. 1a, b.

Lectotype: SPbGU I/III3 (designated herein); Fig. 2.
Type horizon and locality: *Orthoceras* limestone (Lasnamägian) of Hiiumaa island, Estonia.

Diagnosis: Conchs uniformly curved, of small adult size, 12–14 mm in dorsoventral diameter of aperture, only slightly compressed laterally and with incipient ventral sinus of the aperture.

Description: The lectotype is a rather poorly preserved internal mould of the last 31 mm of the phragmocone and the basal part of living chamber. Its maximum dorsoventral diameter is about 13 mm. The siphuncle is partially exposed by weathering, approximately 1.5 mm in diameter, with slightly swollen connecting rings. There are no signs of maturity in the distribution of septa.

The specimen of similar size found in an erratic boulder of Lasnamägian age (*Eoplacognathus foliaceus* Subzone) from Międzyzdroje, Pomerania (*Oonoceras* sp. of Dzik 1984: text-fig. 15) may be adult; this is suggested by condensed growth lines close to its aperture, although the

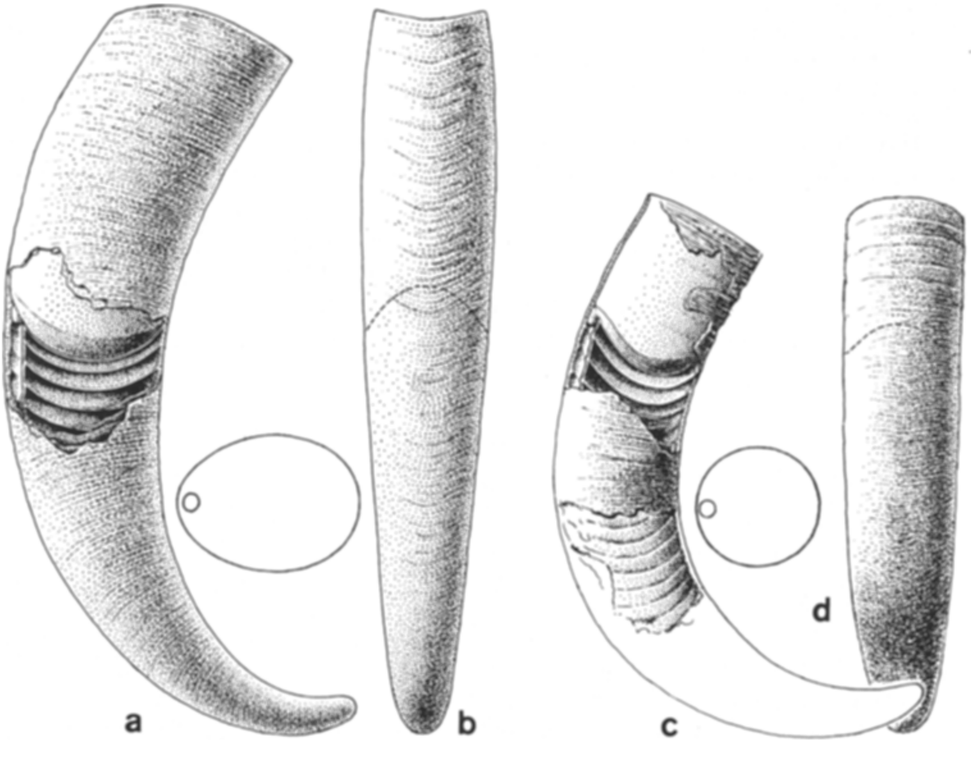

Fig. 3. Reconstructions of adult conchs of Lasnamägian Baltic oncoceratids. a–b: *Phthanoncoceras ellipticum* (Lossen 1860). c–d: *Oonoceras priscum* (Eichwald 1861) (modified after Dzik 1984: text-fig. 15a).

septa are uniformly distributed. Another probably adult specimen with complete aperture co-occurs with *Ph. ellipticum* in the Platte Nr. 3 of H. PATRUNKY. All these specimens of *C. priscum* are closely similar to each other not only in size but also in conch curvature, its cross section, and density of septa.

The conch surface ornamentation of *C. priscum* differs from that of the associated *Phthanoncoceras*. The growth lines are regularly distributed and almost strictly transverse to the conch long axis. The ventral sinus is quite incipient and widely rounded. As far as can be deduced from the recrystallized siphuncular wall in the only sectioned specimen of *C. priscum* (DZIK 1984: text-fig. 15b), it is closely similar to that of the Silurian *Oonoceras* (DZIK 1984: text-fig. 15c), but not to the Kundan *Phthanoncoceras* (EVANS & KING 1990: text-fig. 2).

Evolutionary relationships: The type species of *Oonoceras*, *Cyrtoceras acinaces* BARRANDE 1866, is late Silurian in age but, despite the great time distance, Silurian *Oonoceras* species are like their Ordovician relatives in having primitive thick connecting rings of the siphuncle. Also the very short living chamber of *C. priscum* make it very different from *Phthanoncoceras* but closely similar to *Oonoceras*. It seems thus reasonable to continue such a generic affiliation of this species.

There are some Ordovician species that may represent connecting links between early Ordovician *Oonoceras priscum* and late Silurian *O. acinaces*. *Richardsonoceras asiaticum* (YABE 1920) from the Chinese Pagoda Formation of Caradoc age (CHEN & ZOU 1985) may be congeneric as suggested by its siphuncle organization. It seems closer to *O. priscum* than to the type species of *Richardsonoceras*, *Cyrtoceras simplex* BILLINGS 1857, from the early Caradoc Leray beds of Canada. Both genera share short living chambers, and their conchs are much more elongated and curved than in associated oncoceratids, but in *Richardsonoceras* the adult living chamber narrows towards an aperture that has a distinct ventral sinus (see WILSON 1961).

Distribution: All known specimens of *Oonoceras priscum* are Lasnamägian (late Llanvirn). They are known from Estonia, Sweden, and glacial erratic boulders from Pomerania.

Order Orthoceratida KUHN 1940
Family Kionoceratidae HYATT 1900
Genus *Spyroceras* HYATT 1884

Type species: *Orthoceras crotalum* HALL 1861; Hamilton Group (Givetian) of New York.

Spyroceras damesi (KRAUSE 1877)

Fig. 4a–e, 5a–c

1877 *Orthoceras damesii* m. – KRAUSE: 25, pl. 1, fig. 11a,b.
1984 *Eridites* (?) sp. – DZIK: text-fig. 45a–c, pl. 32, fig. 4, 5, 9.
1984 *Kionoceras* cf. *doricum* (BARRANDE, 1868) – DZIK: text-fig. 48c, pl. 36, fig. 5.

Lectotype: MB C.862 (designated herein); Fig. 4b.

Type horizon and locality: Baltic Beyrichienkalk erratic boulder collected from shore of Vistula river in Bydgoszcz, Poland, Pridoli.

Emended diagnosis: Conchs at early stages weakly annulated and ornamented with sparse longitudinal riblets, later smooth. Cameral deposits with equally developed mural and episeptal parts; siphuncular deposits tend to unify in continuous ventral lining.

Diagnostic differences: *S. damesi* is distinct from all known species of *Spyroceras* in that the longitudinal ribs do not continue to the adult stages but gradually disappear. At least in better known Ordovician species of *Gorbyoceras* and *Spyroceras* cameral deposits developed only murally. It has to be kept in mind that both siphuncular and cameral deposits in

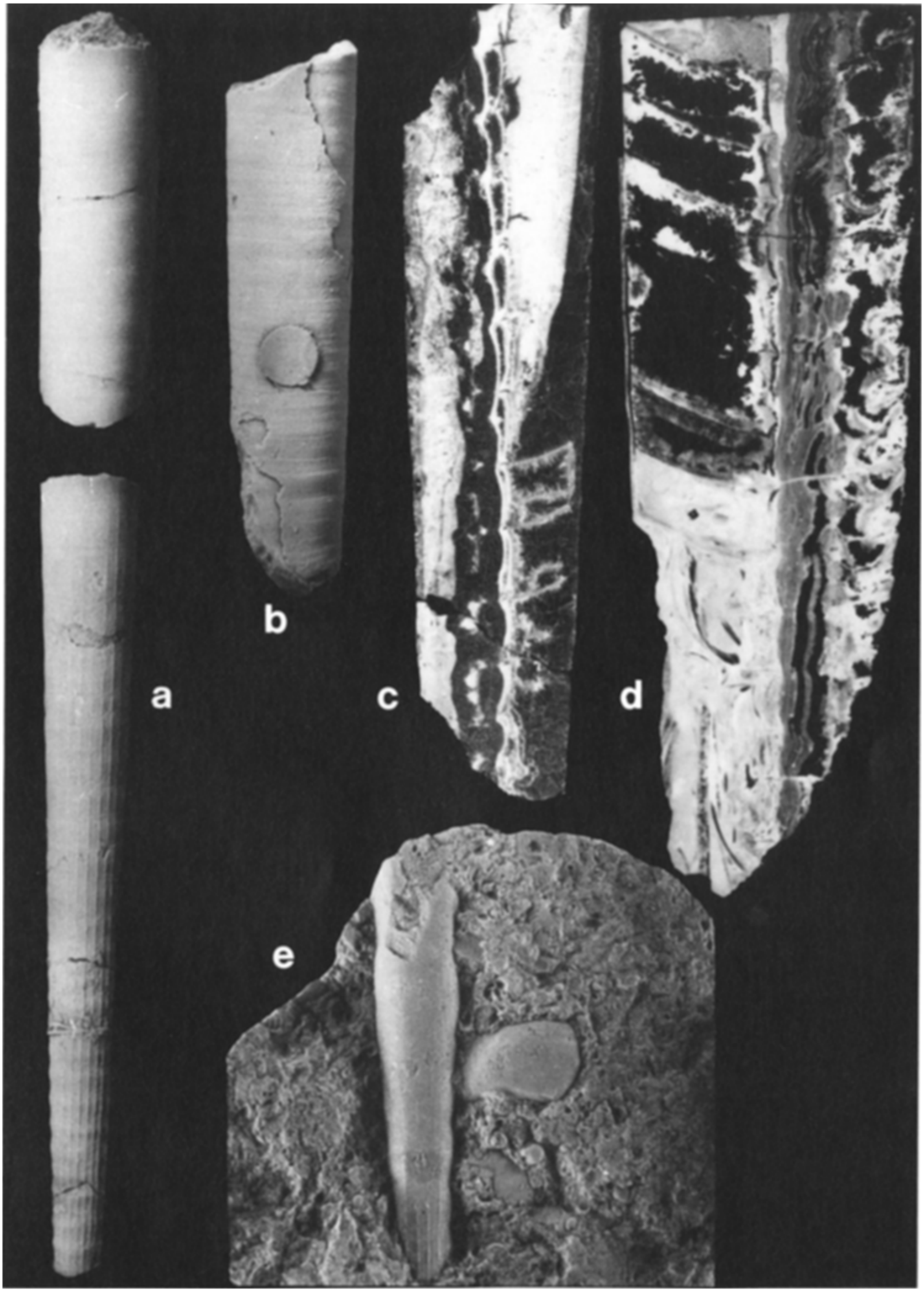

Fig. 4. *Spyroceras damesi* (Krause 1877), Pridoli, Beyrichienkalk glacial erratic boulders. a: Almost complete specimen MB C.865.3, Voigtsdorf. b: Lectotype MB C.862, Bydgoszcz. c: Thin section of phragmocone MB C.865.2, Voigtsdorf. d: MB C.864.1 Oderberg. e: Fragmentary specimen ZPAL N/873 in the Beyrichienkalk rock matrix, Międzyzdroje. a–b, e: × 1.5; c: × 3; d: × 4.

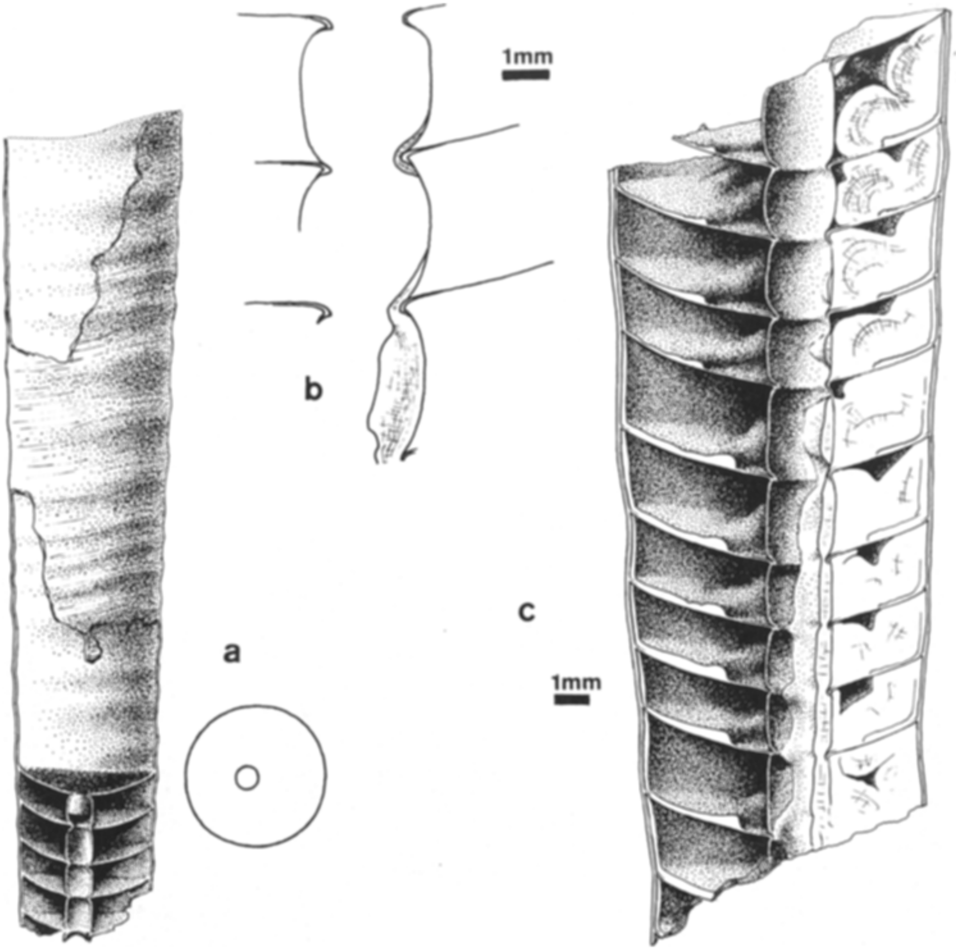

Fig. 5. *Spyroceras damesi* (Krause 1877), Pridoli, Beyrichienkalk, Orłowo (copied from Dzik 1984: text-fig. 45 a–c). a: Reconstruction of living chamber based on specimen ZPAL N/751; approximately natural size. b: Longitudinal section through siphuncle, ZPAL N/753. c: Reconstruction of a phragmocone section based on ZPAL N/742.

orthoconic nautiloids show extremely wide ranges of intrapopulation variability (Mutvei 1964; Dzik 1984), though they are generally believed to be diagnostic at generic or even family level. Kionoceratid genera other than *Spyroceras*, such as *Gorbyoceras* Shimizu & Obata 1936 and *Kionoceras* Hyatt 1884, differ in the much greater rate of conch diameter expansion.

Description: Orthoconic phragmocone of *S. damesi* increases in diameter about 5 mm in 100 mm, giving an angle of about 3°. The apex remains unknown; one may expect that it was typically pseudorthoceratid, that is with a blunt apex, as in related genera. The smallest specimen examined is about 2 mm in diameter. At early growth stages the conch is gently annulated (there is no correspondence between distribution of septa and annuli) and ornamented with longitudinal riblets, 14–22 in number. In the most complete specimen MB C.865.3, the annulation disappears at a diameter of about 7 mm. Riblets continue to occur until the diameter reaches about 9 mm, but in the specimen ZPAL N/873 the conch is smooth already at a diameter of 6 mm. Some specimens of uncertain age, possibly from strata older than Beyrichienkalk, preserve prominent ornamentation for much longer; for instance the phragmocone MB C.866 has well developed, though less numerous, longitudinal riblets at a diameter of 12 mm. Whether this is an effect of very wide intraspecific variability or rather that the continuously ornamented specimens represent older populations transitional between *S. damesi* and more typical species of *Spyroceras*, remains to be clarified.

The conch aperture shows an inconspicuous, wide and shallow ventral sinus; the dorsal side of the aperture forming a little more prominent lobe (Fig. 5 a).

The lectotype of *S. damesi* reaches 12 mm in diameter, while still being incomplete. The adult size of the species remains unknown, although some isolated living chambers from the Beyrichienkalk (for instance that attributed to *Sactoceras* sp.; Dzik 1984: pl. 36, fig. 8) may belong to this species. A poorly preserved and crushed specimen MB C.859 from the brickpit Mothlitz in Saxony was of an original diameter of about 21 mm and of a length of perhaps up to 100 mm. The course of growth lines is relatively variable, signs of repair to apertural damage are frequent.

Cameral deposits in the phragmocone started their development as thin mural covers, extending episeptal to more than half the distance from the conch wall to the siphuncle, but only ventrally continued their growth further until transforming themselves into a block filling the chamber completely, a narrow furrow in contact with the following septum being the last free space (Fig. 5 c). It is not clear whether any deposits developed hyposeptally.

The siphuncle of *S. damesi* is located slightly ventrally of the phragmocone center, its diameter is a little more than 20 % of the phragmocone diameter. Siphuncular deposits started their growth from septal necks, tending to spread over the adjacent surface of the connecting rings (Fig. 5 b), and later in ontogeny developed a laminar continuous cover along the ventral side of the siphuncle. The dorsal side remains free of deposits almost until the whole siphuncle is filled with deposits.

The distribution of both siphuncular and cameral deposits is suggestive of horizontal position of the conch during life.

Distribution: The species is known only from the Beyrichienkalk erratic boulders, widely occurring in north-eastern Germany and Poland.

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