

Revision of *Hamites wernickei* Wolleemann, 1902 (Cephalopoda, Ancyloceratina) from the classic Lüneburg section (Upper Cretaceous, northern Germany)

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ABSTRACT:

Niebuhr, B. and Jagt, J.W.M. 2016. Revision of *Hamites wernickei* Wolleemann, 1902 (Cephalopoda, Ancyloceratina) from the classic Lüneburg section (Upper Cretaceous, northern Germany). *Acta Geologica Polonica*, **66** (4), 627–644. Warszawa.

A re-examination of heteromorph ammonites of late Campanian age from the Zeltberg section at Lüneburg has demonstrated that the type series of *Hamites wernickei* in fact comprises two different species that are here assigned to the nostoceratid *Nostoceras* Hyatt, 1894 and the polyptychoceratid *Oxybeloceras* Hyatt, 1900. *Nostoceras (Didymoceras) wernickei* (Wolleemann, 1902) comb. nov., to which three of the four specimens that were described and illustrated by Wolleemann (1902) belong, has irregularities of ribbing and tuberculation and changes its direction of growth at the transition from the helicoidal whorls to the hook, which is a typical feature of members of the subfamily Nostoceratinae. Torsion of body chambers is not developed in hairpin-shaped ammonite species, which means that the species name *wernickei* is no longer available for such polyptychoceratine diplomoceratids. Consequently, the fourth specimen figured and assigned to *Hamites wernickei* by Wolleemann (1902) is here transferred to *Oxybeloceras* and considered conspecific to material from the Hannover area (Lehrte West Syncline) as *O. aff. crassum* (Whitfield, 1877). In addition to the “*Heteroceras*-Schicht des Mucronaten-Senons” of Lüneburg (*bipunctatum/roemeri* Zone, upper upper Campanian), the geographic range of *N. (D.) wernickei* probably includes Upper Austria, Tunisia and the Donbass region, while *O. aff. crassum* is known from the Hannover area (northern Germany), southern France, northern Spain and Upper Austria.

Key words: Campanian; Ammonites; *Nostoceras*; *Oxybeloceras*; Taxonomy; Europe.

INTRODUCTION

Wolleemann (1902) described and illustrated a suite of ammonite species that he had collected at the Zeltberg Quarry of Lüneburg (Niedersachsen, c. 30 km south-south-east of Hamburg, northern Germany) at the end of the nineteenth century. Notable are bituberculate heteromorphs which he assigned to a new species, *Hamites wernickei* (see Wolleemann 1902, p. 95). Wolleemann noted

that, “The sculpture is so simple and characteristic that, on the basis of this, the species is easily recognised and differentiated from *Hamites* species already known” [“Die Sculptur ist so einfach und charakteristisch, dass die Art leicht an dieser erkannt und von den bereits bekannten *Hamites*-Arten unterschieden werden kann”]. The type series of Wolleemann’s new species falls into two size categories: I. three large-sized specimens represent well-separated, U-shaped curved portions of bituberculate hetero-

morphs (i.e., Wolleermann 1902, pl. 4, fig. 4; pl. 5, figs 1, 2), and II. a single small, hairpin-like specimen develops approximated parallel shafts, originally interpreted as the inner portions of a polyptychoceratid [“innere Windung” *sensu* Wolleermann 1902, p. 95, pl. 4, fig. 5].

Subsequent records of heteromorph ammonites under the name of *wernickei* were either not figured (e.g., Diener 1925; Pożaryski 1948; Wiedmann 1964; Klinger 1982; Kaplan *et al.* 2005), showed unequivocally different species of the subfamily Polyptychoceratinae [e.g., Mikhailov 1951; Wiedmann 1962; Klinger 1976; Tzankov 1982; Kennedy and Summesberger 1984 (in part); Lommerzheim 1995; Kaplan *et al.* 1996; Küchler 2000] or were species of indeterminate familial assignment [Pervinquierè 1907; Naidin in Krymgolts 1974; Kennedy and Summesberger 1984 (in part)]. In most cases, what authors understood to represent the species named *wernickei* were the three large U-shaped curved individuals from the type series (Wolleermann 1902, pl. 4, fig. 4; pl. 5, figs 1, 2) (see e.g., Pervinquierè 1907; Mikhailov 1951; Wiedmann 1962; Naidin in Krymgolts 1974; Klinger 1976; Tzankov 1982). Küchler (2000) even included the small hairpin-like specimen (Wolleermann 1902, pl. 4, fig. 5) in it. Kennedy and Summesberger (1984, p. 167) adopted the species name *wernickei* for both size categories, I (i.e., larger specimens of Kennedy and Summesberger 1984, pl. 10, figs 1, 9) and II (i.e., small specimens of Kennedy and Summesberger 1984, pl. 9, figs 6, 7), listing it as *Pseudoxybeloceras* (*Parasolenoceras*) *wernickei* (Wolleermann, 1902). However, they did not include the small specimen figured by Wolleermann (1902, pl. 4, fig. 5) in their size category II, yet discussed the possibility that it, “may be better referred to ‘*Hamites*’ *interruptus* Schlüter, 1872”. In our opinion, the four specimens illustrated under the name *wernickei* by Wolleermann (1902) in fact belong to two different families, genera and species, as follows.

Species I. Of the three large heteromorphs illustrated in his pl. 4, fig. 4 and pl. 5, figs 1 and 2, Wolleermann (1902) noted that, “A few compressed and twisted whorls of the tuberculate *Heteroceras polyplocum* are at times quite similar to our hamitid” [“Einzelne zusammengedrückte und verdrehte Windungen der mit Knoten versehenen Form des *Heteroceras polyplocum* sind unserem Hamiten bisweilen sehr ähnlich”]. All three distinctly U-shaped specimens of Wolleermann (1902) develop a change in direction of growth [“deutliche Torsion der Wohnkammer”, *sensu* Wiedmann 1962, p. 209] and irregularities of ribbing and tuberculation which are missing in polyptychoceratines, yet are characteristic of the Nostoceratinae. Although Wolleermann (1902, p. 96) noted that the large-sized heteromorphs, named *wernickei*, ap-

peared to be relatively common together with his *Heteroceras polyplocum* [“zh. = ziemlich häufig, MH. = *Heteroceras*-Schicht des Mucronaten-Senons”], additional, similarly shaped “*Hamites*” specimens have never been recovered subsequently, not in large suites of Polyptychoceratinae from the Lehrte West Syncline near Hannover (Niebuhr *et al.* 1997; Niebuhr 2004; Jagt 2013), nor in the “Haldemer Schichten” at the Stemweder Berg (Kennedy and Kaplan 1997), the Münsterland Cretaceous Basin (Lommerzheim 1995; Kaplan *et al.* 2005), Tercis les Bains, southwest France (Odin *et al.* 2001) and the Vistula River Valley, Poland (Błaszkiwicz 1980). Kaplan *et al.* (2005, pp. 30, 43) recorded *Pseudoxybeloceras* (*Parasolenoceras*) *wernickei* from older strata in the southeastern part of the Münsterland Cretaceous Basin (i.e., Beckum Member, Coesfeld Formation; lowermost upper Campanian), but failed to illustrate the single specimen available to them. Pożaryski (1948) had earlier noted “*Hamites wernickei* Woll.” from the Polish *Didymoceras donezianum* Zone (equivalent to the north German *bipuctatum/roemeri* Zone; upper upper Campanian), but did not provide an illustration either. However, these records were not confirmed by Błaszkiwicz (1980).

Wiedmann (1962, p. 209) designated as lectotype of *wernickei* the original of Wolleermann (1902, pl. 5, fig. 1). Later, Kennedy and Summesberger (1984, p. 166), apparently unaware of Wiedmann’s prior designation, selected the original of Wolleermann’s pl. 4, fig. 1 as lectotype (actually a gastropod; it should have stated pl. 4, fig. 4); this is an error. It seems clear that all three authors understood the species name *wernickei* to be applicable to large-sized, U-shaped heteromorphs (Wolleermann 1902, pl. 4, fig. 4; pl. 5, figs 1, 2). Unfortunately, the Wolleermann Collection which was housed at the museum and the “Altes Kaufhaus” of Lüneburg was destroyed in a fire in December 1959 (i.e., predating Wiedmann’s lectotype designation). In other words, Wiedmann’s lectotype is lost. However, in the collection of the Bundesanstalt für Geowissenschaften und Rohstoffe (BGR), Hannover, two U-shaped body chambers and *c.* 20 fragments of the coiled portion of *wernickei* from the Zeltberg Quarry in Lüneburg are kept, collected in 1956 and 1980 by Friedrich Schmid. Furthermore, in the BGR Berlin-Spandau collection, the collection of the Senckenberg Naturhistorische Sammlungen Dresden and in the collection of D. Schumacher (Lüneburg), are six, one and seven fragments of the coiled portion with up to four whorls in contact, respectively. These specimens are here described and illustrated for the first time.

Species II. The original of the small, hairpin-like specimen of Wolleermann (1902, pl. 4, fig. 5) is housed in the

BGR Berlin-Spandau collection. It clearly is a member of the subfamily Polyptychoceratinae. Conspecific material is known from the upper Campanian of the Hannover area (northern Germany), as described and illustrated by Jagt and Neumann (2006), in open nomenclature [*Oxybeloceras* aff. *crassum* (Whitfield, 1877); see also Jagt 2013]. The size of the teardrop-shaped opening is similar to that in material from the upper Campanian of Montana, Wyoming and Colorado, and rib density overlaps. Jagt and Neumann (2006) remarked that the limited material from the Lehrte West Syncline near Hannover (MAB 3290a–b; C. Holschemacher Collection, Berlin) appeared to have less closely spaced ribbing on the smaller limb and a less regular occurrence of ventrolateral tubercles. For now, we prefer to keep this form in open nomenclature until better-preserved material becomes available.

ASSOCIATED AMMONITE FAUNA AND BIOSTRATIGRAPHY

In addition to *N. (D.) wernickei* and *O. aff. crassum*, as here interpreted, Wolleermann (1902) mentioned from the “*Heteroceras*-Schicht des Mucronaten-Senons” (as recently identified by one of us, BN): *Menuites wittekindi* (Schlüter, 1872), *Menuites portlocki portlocki* (Sharpe, 1855), *Hoploscaphites greenlandicus* (Donovan, 1953) and *Gaudryceras mite* (von Hauer, 1866). “*Heteroceras polyplacum* A. Roemer sp.” of Wolleermann (1902) does not belong to *Nostoceras* (*Bostrychoceras*) *polyplacum* (Roemer, 1841), but rather refers to the helicoidal portions of *N. (D.) wernickei* (see below). Furthermore, *Pseudoxybeloceras* (*Parasolenoceras*) *interruptum* (Schlüter, 1872), *Lewyites elegans* (Moberg, 1885) and *Hoploscaphites compressus* (Roemer, 1841) have recently been identified from upper Campanian strata exposed at the Zeltberg Quarry (Niebuhr, in prep.).

Large-sized species of *Nostoceras* (*Didymoceras*), in association with *M. wittekindi*, *M. p. portlocki*, *Ps. (Pa.) interruptum*, *H. greenlandicus* and *H. compressus*, are typical of the *bipunctatum/roemeri* Zone (upper upper Campanian) of the Lehrte West Syncline near Hannover (Niedersachsen, northern Germany, c. 100 km south of Lüneburg). *Lewyites elegans* first appears in the lower upper Campanian and ranges into the *bipunctatum/roemeri* Zone (Niebuhr 1996, 2004; Niebuhr *et al.* 1997, p. 223; Küchler and Schneider 2013). *Gaudryceras mite* is a long-ranging taxon, with records from Turonian to Maastrichtian strata (Kennedy and Summesberger 1979; Summesberger and Kennedy 1996). Only the upper upper Campanian is indicated in

the collections from the “*Heteroceras*-Schicht des Mucronaten-Senons” at Lüneburg.

REPOSITORIES OF MATERIAL

BGR MA: Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover, Germany.

BGR X: Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin-Spandau, Germany.

MAB: Oertijdmuseum De Groene Poort, Boxtel, the Netherlands.

MMG: Senckenberg Naturhistorische Sammlungen Dresden, Museum für Mineralogie und Geologie, Sektion Paläozoologie, Dresden, Germany.

MN: Museum für Naturkunde, Berlin, Germany.

NHMM: Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands.

SH: Detlef Schumacher Collection, Lüneburg, Germany.

SYSTEMATIC PALAEOLOGY

Abbreviations used are as follows: D – diameter; vL – ventral length of nostoceratids, measured between lower and upper rows of tuberculation; Ah – apertural height; Wh – whorl height; Wb – whorl breadth; Ri – rib index, number of ribs in a distance equal to the whorl height; Rr – rib ratio, ventral length divided by rib number.

- Order Ammonoidea von Zittel, 1884
- Suborder Ancyloceratina Wiedmann, 1966
- Superfamily Turrilitoidea Gill, 1871
- Family Nostoceratidae Hyatt, 1894
- Subfamily Nostoceratinae Hyatt, 1894
- Genus *Nostoceras* Hyatt, 1894

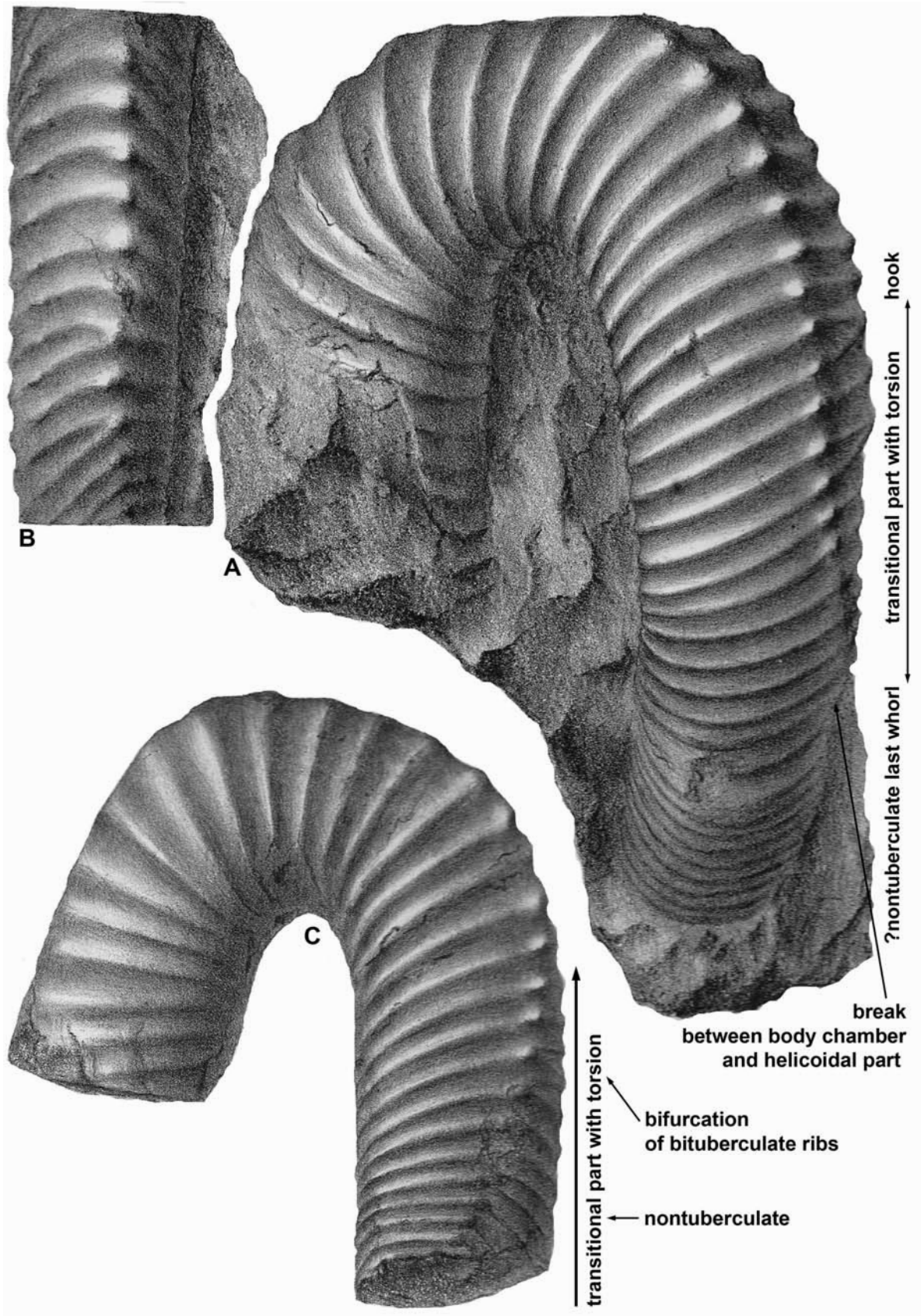
TYPE SPECIES: *Nostoceras stantoni* Hyatt, 1894 = *Ancyloceras? approximans* Conrad, 1855, by original designation of Hyatt (1894, p. 569).

REMARKS: The classification of Wright *et al.* (1996, p. L245) is followed here.

Subgenus *Didymoceras* Hyatt, 1894

TYPE SPECIES: *Ancyloceras? nebrascensis* Meek and Hayden, 1856, by original designation of Hyatt (1894, p. 574).

DIAGNOSIS: Early growth stage of either loose and ir-



regular helical coils or straight limbs connected by elbows, even hamitoid; followed by a middle growth stage of helical whorls just touching or not so; body chamber in a retroversal whorl, U- or C-shaped.

Nostoceras (Didymoceras) wernickei (Wollemann, 1902) comb. nov.
(Text-figs 1–3, 5–7)

pars * 1902. *Hamites Wernickei* Wollemann, p. 95, pl. 4, fig. 4; pl. 5, figs 1–2 [non pl. 4, fig. 5 = *Oxybeloceras* aff. *crassum* (Whitfield, 1877)].

? 1907. *Hamites (Anisoceras?) Wernickei* Wollemann; Pervinquier, p. 86, pl. 3, fig. 33.

non 1951. *Anisoceras wernickei* Wollemann; Mikhailov, p. 40, text-fig. 9, pl. 1, fig. 1 (= Polyptychoceratinae sp. indet.).

non 1962. *Neancyloceras wernickei* (Wollemann); Wied-

mann, p. 209, pl. 12, fig. 5 (= Polyptychoceratinae sp. indet.).

? 1974. *Neancyloceras wernickei* (Wollemann, 1902); Naidin in Krymgolts, p. 169, pl. 57, fig. 4.

non 1976. *Neancyloceras* sp. cf. *Neancyloceras wernickei* (Wollemann), 1902; Klinger, p. 73, pl. 33, fig. 4; text-figs 8i, 10f (= Polyptychoceratinae sp. indet.).

? 1984. *Pseudoxybeloceras (Parasolenoceras) wernickei* (Wollemann, 1902); Kennedy and Summesberger, p. 166, pl. 10, fig. 1 only.

non 1984. *Pseudoxybeloceras (Parasolenoceras) wernickei* (Wollemann, 1902); Kennedy and Summesberger, p. 166, pl. 6, fig. 3 [= *Lewyites elegans* (Moberg, 1885)]; pl. 9, figs 6–7 [= *Oxybeloceras* aff. *crassum* (Whitfield, 1877)]; pl. 10, figs 8–9 (= Polyptychoceratinae sp. indet.).

non 1995. *Pseudoxybeloceras (Parasolenoceras) (?) cf. wernickei* (Wollemann, 1902); Lommerzheim,



Text-fig. 2. *Nostoceras (Didymoceras) wernickei* (Wollemann, 1902); reillustration of *Hamites wernickei* of Wollemann (1902, pl. 5, fig. 1); U-shaped body chamber with adult aperture, transitional part with torsion and bifurcation of ribs. Natural size

Text-fig. 1. *Nostoceras (Didymoceras) wernickei* (Wollemann, 1902). **A–B** – Reillustration of *Hamites wernickei* of Wollemann (1902, pl. 5, fig. 2); adult bituberculate specimen with complete U-shaped body chamber and younger portions of the last whorl; note torsion of transitional part and break between body chamber and helicoidal part, and ventral view of the same, respectively, showing details of the transitional part with rib bifurcation. **C** – Reillustration of *Hamites wernickei* of Wollemann (1902, pl. 4, fig. 4); U-shaped body chamber and transitional part with torsion and bifurcation of ribs. All specimens are natural size

p. 68, pl. 7, figs 5–6a-c (= Polyptychoceratinae sp. indet.).
 non 1996. *Pseudoxybeloceras* (*Parasolenoceras*) *wernickei* (Wollemann, 1902); Kaplan *et al.*, p. 41, pl. 35, figs 6–7 (= Polyptychoceratinae sp. indet.).
 non 2000. *Pseudoxybeloceras* (*Parasolenoceras*) ?*wernickei* (Wollemann); Kűchler, pl. 12, figs 1–3 [= *Oxybeloceras* aff. *Crassum* (Whitfield, 1877)].

TYPES: Lectotype, designated by Wiedmann (1962, p. 209), was the original of Wollemann (1902, pl. 5, fig. 1; reillustrated here as Text-fig. 2) which had been lost in December 1959. To replace this we here designate a neotype, BGR MA 14514. Locus typicus is the Zeltberg Quarry at Lűneburg, Niedersachsen, northern Germany. Stratum typicum is the “*Heteroceras*-Schicht des Mucronaten-Senons” of Wollemann (1902), which is the equivalent of the *bipunctatum/roemeri* Zone (upper upper Campanian), c.1.5 myr below the Campanian

DIMENSIONS:

Collection number	Growth stage	Tubercles, swellings, constrictions	vL of body chamber	Wh of body chamber	Wh of helicoidal whorl	Wb/Wh	Rr (vL/ribs)	Ri (ribs equal Wh)
pl. 4, fig. 4	late	bituberculate	> 215 mm	36 mm			7.7	5–7
pl. 5, fig. 1	late	bituberculate	> 280 mm	43–45 mm			8.5	7–9
pl. 5, fig. 2	late, middle	bituberculate ?nontuberculate	285 mm	38–44 mm	34 mm		8.3 3.0	7.5 11
BGR MA 14514	late	bituberculate	> 270 mm	32–38 mm			9.3	5.5
BGR MA 14515	late	bituberculate	> 280 mm	32–41 mm			9.5	5.5
BGR MA 14520	mid., W1	nontuberculate			54 mm		2.8	19
BGR MA 14518	mid., W1	nontuberculate			53 mm	0.9	4.5	15
BGR MA 14516	mid., W1	nontuberculate			50 mm		4	13
BGR MA 14517	mid., W1	nontuberculate			49 mm		3.3	14
BGR MA 14519	mid., W1	nontuberculate			48 mm	0.6	3.4	
SH 42	middle, W1–W4	W4: nontub. W3: ?lower row W2: nontub. W1: nontub.			W4: 31 mm W3: 38 mm W2: 46 mm W1: 46 mm	0.5 0.5 0.5 0.6	2.6 3.1 4.0	12 12.5 11.5
BGR X 13000	middle, W1–W3	nontuberculate, 5 constrictions			W3: 24 mm W2: 33 mm W1: 42 mm		2.5 2.8 3.8	13 14 13
BGR X 13001	middle, W1–W2	nontuberculate			W2: 37 mm W1: 41 mm		3.4 3.4	11 12
MMG NsK 3	early, W4 middle, W1–W3	W4: ? W1–W3: bituberculate, W3: constriction			W4: >14 mm W3: 22 mm W2: 33 mm W1: 40 mm		2.6 2.5 3.3	9 11 12
SH 49	middle	few swellings			26–40 mm		2.3–3.3	12
SH 48	mid., W1	older: nontub., younger: bitub.			33–39 mm	0.9–1	3.0	12.5
BGR X 13002	mid., W3	nontuberculate			22–28 mm	0.7–0.6	2.2	11
BGR MA 14523	early	bituberculate			18–22 mm	0.7–0.8	1.8	13
BGR MA 14521	early	bituberculate			16 mm	0.8	1.4	13
SH 41	early	nontuberculate			15 mm	1.1	3.5	7
SH 31	early	bituberculate			9–10 mm	0.8–1	1.2–1.8	9–10

Table 1. Dimensions of *Nostoceras* (*Didymoceras*) *wernickei* (Wollemann, 1902). Grey: Wollemann’s (1902) specimens; bold: BGR MA 14514, designated neotype

ian/Maastrichtian boundary (compare Niebuhr *et al.* 2011).

MATERIAL: In addition to the neotype (BGR MA 14514, see above), one U-shaped body chamber (BGR MA 14515) and approximately 25 fragments of helicoidal whorls (e.g., BGR MA 14516–14523; BGR X 13000–13006; MMG NsK 3; and SH 31, SH 41–42, SH 48–49).

DESCRIPTION: *Nostoceras (D.) wernickei* is both sinistrally (Text-figs 1A–B, 2, 3B–C) and dextrally coiled (Text-fig. 1C). Phragmocone and body chamber whorls have Wb/Wh ratios of 0.5–1. Adult body chambers are distinctly U-shaped, enlarged towards the aperture and may become pipe-like; weak collared constrictions can appear. Rib indices of body chambers are 5–9, while in helicoidal whorls they may reach 11–19 (with a mean value of 13). Rib ratios show the same differentiation: phragmocones of the middle growth stage are more finely ribbed with ratios smaller than 4.5, while more coarsely ribbed body chambers have ratios of 7.5–9.5 (Table 1). The change in ribbing density appears abruptly (see Text-fig. 1A).

The three body chambers illustrated by Wolleemann (1902, reillustrated here in Text-figs 1–2) and the two completely preserved body chambers housed in the BGR Hannover collection (Text-fig. 3) are quite similar with two *c.* 60 mm-long, near-parallel shafts separated by a 20–30 mm wide opening between them. The curved sector connecting the shafts is subcircular. This habitus of body chambers has led previous authors to refer this species to the Polyptychoceratinae. The three specimens of Wolleemann (1902) (see Text-figs 1–2) and one of the BGR Hannover individuals (Text-fig. 3B) show the torsion of the transitional part. The body chambers and transitional parts bear coarse, distant, sharp bituberculate ribs that are mostly annular or bifurcate, and may zigzag a few times between separated tubercles. Wolleemann (1902, p. 95) also observed this in his *Hamites wernickei* when he wrote, “Die meisten Rippen verlaufen von dem Knoten der Externkante ungetheilt über die Externseite zum Knoten der anderen Externseite; in einzelnen Fällen findet eine Gabelung in der Weise statt, dass ein Knoten der einen Externkante je eine Rippe zu zwei neben einander stehenden Knoten der anderen Externkante entsendet”. Tuberculation is regular, coarsens towards the curved sector of the body chamber and, in most cases, effaces during the transition to the coiled middle growth stage (Text-fig. 1A, C).

Apart from one of Wolleemann’s specimens (1902, pl. 5, fig. 2a; reillustrated here as Text-fig. 1A) there are no specimens which show the transition from the

helically coiled middle growth stage to the merely loosely connected body chamber. At this particular point, most fragments are broken as a result of differential preservation (see Text-figs 1, 3), also observed by Wolleemann (1902, figure caption of pl. 5, fig. 2a). All fragments of W1–W4 (i.e., the last four whorls) with Wh 22–54 mm have simple, mostly nontuberculate primaries (Table 1). Specimen BGR X 13000 bears 1–2 collared constrictions per whorl between Wh 33–42 mm. Whorls of the early growth stage are helicoidal up to a minimum Wh 16 mm, are mostly bituberculate, but, in a few cases, can also be nontuberculate (Text-figs 5D, 6B). Low Wb/Wh ratios of the middle growth stage, developed in specimen SH 42 (Text-fig. 7), seem to be of primary nature and not the result of compaction.

DISCUSSION: *Nostoceras (Didymoceras) wernickei* ranks among the larger European nostoceratid ammonites with U-shaped body chambers attaining up to 285 mm, and is comparable in this respect to *Nostoceras (Didymoceras) postremum* (Błaszkievicz, 1980) from the Lehrte West Syncline, *c.* 100 km south of Lüneburg, which has a loosely connected C-shaped body chamber up to 300 mm (Niebuhr 2004; see Text-fig. 4A–B here). Both *N. (D.) wernickei* from Lüneburg and *N. (D.) postremum* from the Lehrte West Syncline are defined by their distinct body chambers. In *N. (D.) wernickei* coiling in the middle growth stage is helicoidal with whorls not touching or barely so, and the early growth stage is regular openly coiled. However, helicoidal whorls of the middle growth stage between Wh 22–54 mm are not diagnostic and show considerable similarities, both in dimensions and ornament, to mostly nontuberculate *Nostoceras (Bostrychoceras) polyplacum* (Roemer, 1841) (see in particular Kennedy and Kaplan 1997, p. 52, pl. 39, fig. 4; pl. 41, figs 1, 9; pl. 43, figs 1, 4–5; pls 44, 46). The last three whorls (W1–W3) of MMG NsK 3 (Text-fig. 6D) are comparable with the bituberculate last whorl of the adult macroconch of *N. (B.) polyplacum* of Kennedy and Kaplan (1997, pl. 48); however, W3 displays a collared constriction in the present individual. Similarly, bituberculate whorls of the early growth stage of *N. (D.) wernickei* of a Wh smaller than 22 mm (e.g., BGR MA 14523; see Text-fig. 5D) are quite similar to *N. (B.) polyplacum* of Kennedy and Kaplan (1997, pl. 40, figs 1–4, 6–7; pl. 42, figs 1, 3–5, 7; pl. 43, figs 2, 3), which was subsequently referred to as *Nostoceras (Didymoceras) sp. 1* by Kuchler and Odin (2001).

It is not possible to assign isolated fragments of helicoidal whorls of the middle and early growth stages between Wh 9–54 mm to one of these nostoceratid taxa.



	<i>Nostoceras (Bostrychoceras) polyplacum</i> Stemwede ¹ and Hannover ² , Germany	<i>Nostoceras (Didymoceras) postremum</i> , holotype Vistula River Valley, Poland ³	<i>Nostoceras (Didymoceras) postremum</i> Hannover, Germany ²	<i>Nostoceras (Didymoceras) wernickei</i> Lüneburg, Germany ⁴
body chamber				
maximum vL	150 mm	140 mm	300 mm	285 mm
Wh	38–65 mm	42–64 mm	40–70 mm	32–45 mm
Rr	6.3	4.5	4.5–11.5	7.7–9.5
Ri	7–8	10	6–11	5–9
shape	irregular, short hook	medium C-shaped	medium to large C-shaped	large U-shaped
tuberculation	2 ventral rows, irregular	2 ventral rows, irregular	2 ventral rows, irregular	2 ventral rows, regular
constrictions	apertural	apertural	apertural	none
ribs	dense simple primaries, identical to helicoidal part	simple primaries, similar to helicoidal part	macroconchs: distant coarse primaries, few bifurcations microconchs: simple primaries, similar to helicoidal part	distant coarse primaries, few bifurcations
helicoidal part				
Wh	W5–W1 = 10–56 mm	W1 = 42–50 mm	W4–W1 = 27–50 mm	W6–W1 = 9–54 mm
Wb/Wh	0.54–1	0.8–0.9	0.5–0.72	0.5–1
Rr	2.7–3.3	2.0–3.1	4.8	1.2–4.5
Ri	11–13	10–13	6–11	11–19
coiling	early: loosely, mid: close	loosely	loosely	loosely
tuberculation	early: bituberculate, mid: mostly nontuberculate	mid: uni- to bituberculate, very weak	early: bituberculate, mid: nontuberculate	early: bituberculate, mid: nontuberculate
constrictions	few	none	none	none, or 1–3 per whorl
ribs	dense simple primaries, few bifurcations	dense simple primaries, few bifurcations	dense simple primaries	dense simple primaries

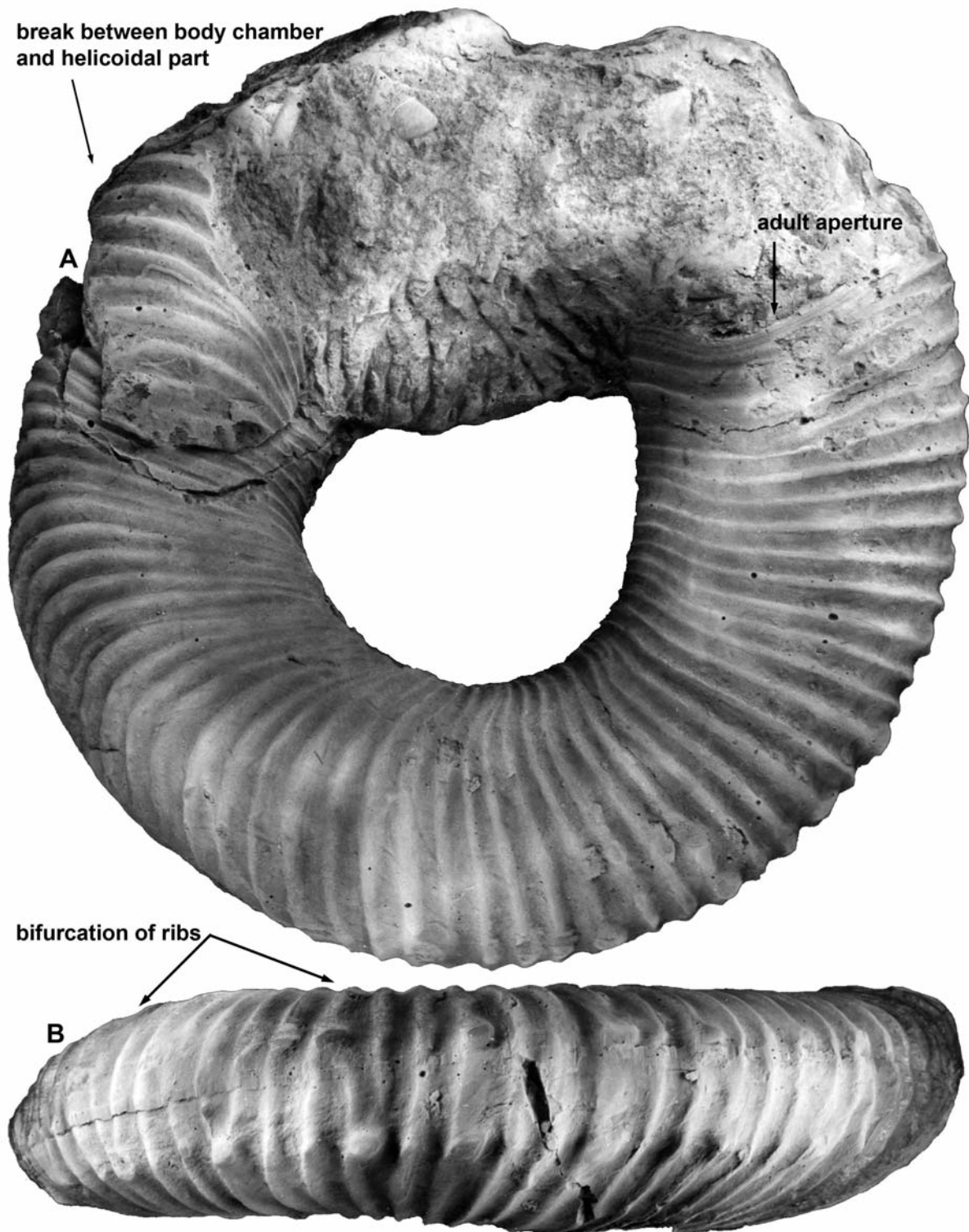
Table 2. Comparison of *Nostoceras (Bostrychoceras) polyplacum*, *N. (Didymoceras) postremum* and *N. (Didymoceras) wernickei* from Germany and Poland; according to ¹ Kennedy and Kaplan (1997), ² Niebuhr (2004), ³ Błaszkiwicz (1980), ⁴ the present paper

At Lüneburg, helicoidal parts of up to four whorls are associated exclusively with distinct, only loosely connected U-shaped body chambers of *N. (D.) wernickei*. The very short body chamber of *N. (B.) polyplacum* is closely associated with the last phragmocone whorl and therefore often preserved attached in large suites from the “Haldemer Schichten” at Stemweder Berg (Kennedy and Kaplan 1997), the Lehrte West Syncline near Hannover (Küchler and Schneider 2013) and Tercis les Bains, southwest France (Küchler and Odin 2001). However, *polyplacum*-like body chambers are unknown from Lüneburg, and therefore, it is assumed that contemporary nostoceratid helicoid whorls are conspecific with *N. (D.) wernickei*.

Nostoceratid heteromorphs develop a change of approximately 90 degrees in their direction of growth in transition from the septate helicoidal whorls to the

hook. As defined for *Nostoceras (Didymoceras)* (see Wright *et al.* 1996, p. L247) the middle and final portions of body chambers have their characteristic two rows of tubercles in a ventral position. In the older portion of body chambers (transitional part; see Text-figs 1–4), venter and tuberculation shift to the external side of the whorl. In the Lüneburg material, this phenomenon was referred to as “twisted whorls” [“verdrehte Windungen”] by Wollema (1902, p. 95) and “torsion of the body chamber” [“Torsion der Wohnkammer”] by Wiedmann (1962, p. 209). Associated are irregularities in ribbing and tuberculation, i.e., bifurcation of ribs [“Gabelung” of Wollema 1902, p. 95]. These features are lacking in the “species” *wernickei* of the genera *Hamites*, *Anisoceras*, *Neancyloceras* and *Pseudoxybeloceras* to which the authors listed above referred the material. The transitional part with torsion clearly

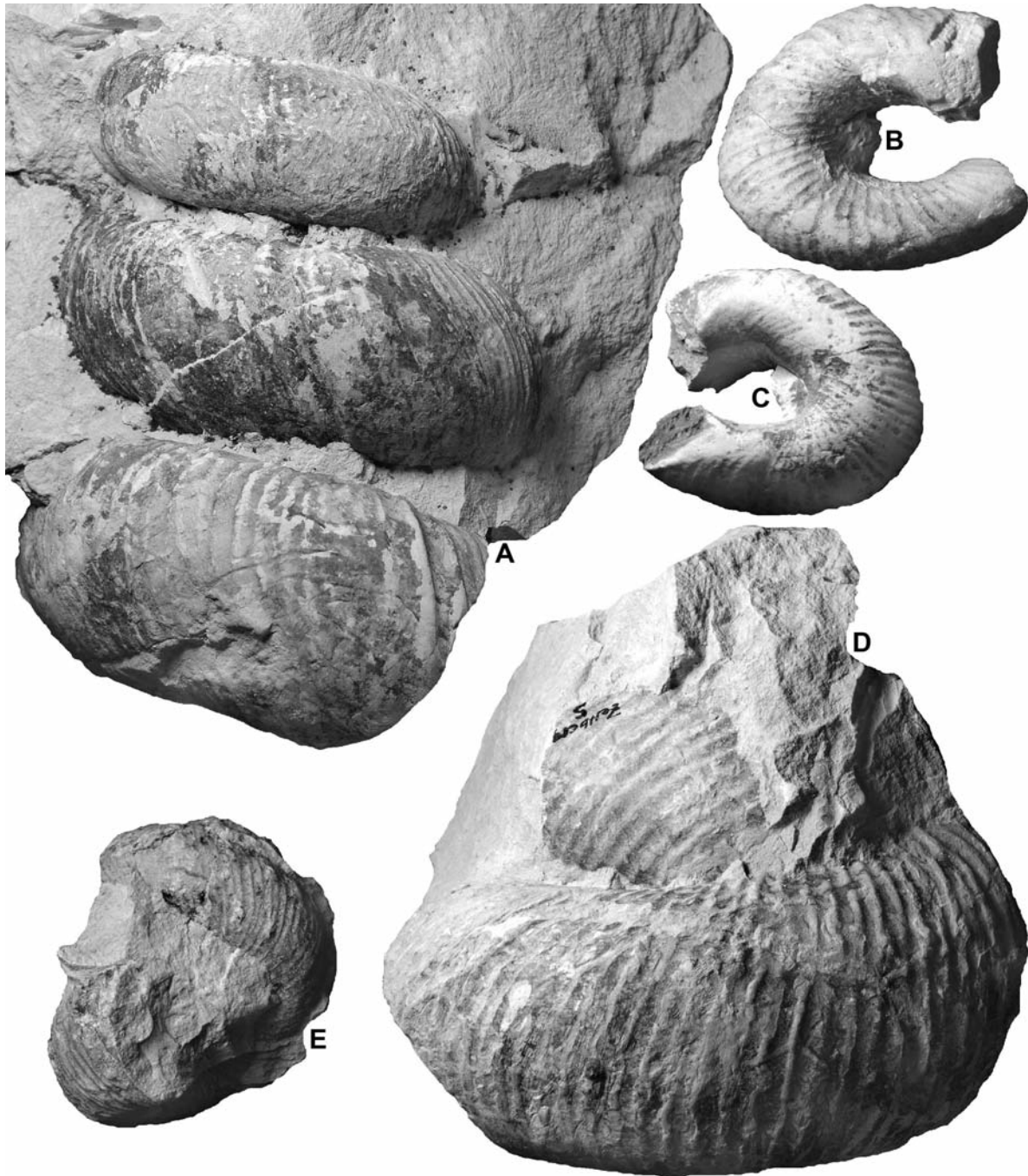
Text-fig. 3. *Nostoceras (Didymoceras) wernickei* (Wollema, 1902) from the Zeltberg Quarry at Lüneburg, northern Germany. **A** – BGR MA 14515; U-shaped body chamber with transitional part, bituberculate and with delicate, regular ribbing. **B–C** – BGR MA 14514, neotype; U-shaped body chamber with adult aperture and beginning of transitional part, bituberculate and of delicate, regular ribbing, and ventral view of the curved portion of the body chamber, respectively. All specimens are natural size



Text-fig. 4. Reillustration of *Nostoceras (Didymoceras) postremum* (Błaszkiwicz, 1980) from the Lehrte West Syncline near Hannover (Niebuhr 2004, pl. 1). BGR MA 13592; **A** – lateral view; **B** – ventral view of a complete, C-shaped body chamber with adult aperture, transitional part with bifurcation of ribs as well as younger portions of the last whorl; largest known specimen ($D = 200$ mm), bituberculate and with delicate, regular ribbing; note break between body chamber and helicoidal part. Both views are $\times 0.75$

demonstrates that *wernickei* belongs to the Nostoceratidae. However, large bituberculate, U-shaped body chamber fragments without torsion, as illustrated by Pervinquière (1907, pl. 3, fig. 33), Naidin in Krymgolts (1974, pl. 57, fig. 3) and Kennedy and Summesberger (1984, pl. 10, fig. 1 only) look quite similar and are

barely distinguishable from the middle and final portions of nostoceratid body chambers. The localities from which the authors listed above recorded their material also yielded other nostoceratid taxa [in part associated with typical *N. (B.) polyplacum*; see, in particular, Kennedy and Summesberger 1984, pl. 9, figs 4,



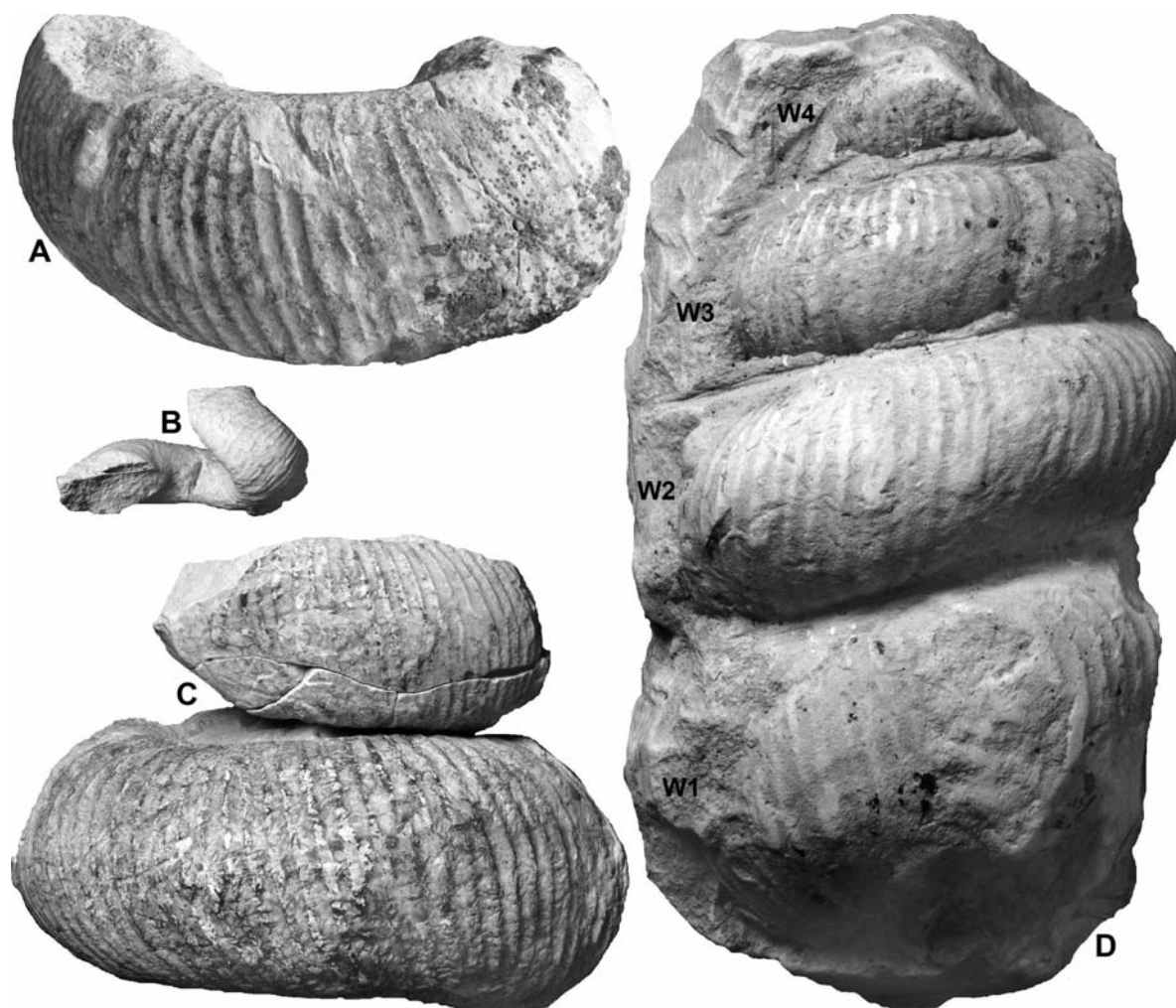
Text-fig. 5. *Nostoceras (Didymoceras) wernickei* (Wollemann, 1902) from the Zeltberg Quarry at Lüneburg, northern Germany; helicoidal parts. **A** – BGR X 13000; three nontuberculate whorls (W1–W3) of the loosely coiled middle growth stage, five collared constrictions visible. **B–C** – BGR X 13002; nontuberculate whorl of the middle growth stage, in lateral and top views, respectively. **D** – BGR MA 14517; nontuberculate last whorl (W1) and fragment of W2 of the middle growth stage. **E** – BGR MA 14523; bituberculate whorl of the loosely coiled early growth stage; septum visible. All specimens are natural size

8, 13–14] and several other index ammonites of late Campanian age. Therefore, it is most likely that *N. (D.) wernickei* also appears in Upper Austria, Tunisia and the Donbass region. Furthermore, Mikhailov (1951, pl. 1, fig. 1 = ?), Wiedmann (1962, pl. 12, fig. 5 = ?), Klinger (1976, pl. 33, fig. 4 = ?), Kennedy and Summesberger [1984, pl. 6, fig. 3 = *Lewyites elegans* (Moberg, 1885); pl. 9, figs 6–7 = *Oxybeloceras* aff. *crassum* (Whitfield, 1877); pl. 10, figs 8–9 = ?] and Kaplan *et al.* (1996, pl. 35, figs 6–7 = ?) figured at least five different polyptychoceratines under the species name *wernickei*.

Although Wolleemann (1902) assigned his material to the genus *Hamites*, he discussed at length similarities to *Heteroceras polyplacum*, as follows, “Einzelne zusammengedrückte und verdrehte Windungen der mit

Knoten versehenen Form des *Heteroceras polyplacum* sind unserem *Hamites* bisweilen sehr ähnlich” and “Einige Bruchstücke ... [of his *Heteroceras polyplacum*] ... haben durch Verdrückung und Verdrehung eine *Hamites*-artige Gestalt angenommen und wurden deshalb im Lüneburger Museum unter der Bezeichnung *Hamites* und *Helicoceras* aufbewahrt” (Wolleemann 1902, pp. 95, 97). However, all subsequent authors adopted Wolleemann’s (1902) first familial assignment. Consequently, the specific name *wernickei* is no longer available for Polyptychoceratinae.

The present U-shaped body chambers of *N. (D.) wernickei* are similar to hooks of *Didymoceras cheyennense* (Meek and Hayden, 1856) from the Western Interior of the United States (see Kennedy *et al.* 2000). However, in that species shafts are shorter, the youngest



Text-fig. 6. *Nostoceras (Didymoceras) wernickei* (Wolleemann, 1902) from the Zeltberg Quarry at Lüneburg, northern Germany; helicoidal parts. **A** – SM 48; half a whorl of the middle growth stage, older portion nontuberculate and younger portion bituberculate. **B** – SM 31; weakly bituberculate whorl of the loosely coiled early growth stage. **C** – SM 49; two nontuberculate whorls (W2–W3) of the middle growth stage, more tightly coiled, septa visible; note that both sides of W3 are broken. **D** – MMG NsK 3; four whorls (W1–W4) of the middle growth stage, more tightly coiled, W1 and W2 bituberculate, W3 and W4 nontuberculate but with collared constrictions. All specimens are natural size

parts with adult aperture are approximated so that the opening between shafts is oval rather than U-shaped. Furthermore, the early and middle growth stages are utterly different, both in coiling and ornament. We also note that

the helicoidal parts of *N. (D.) wernickei* differ from those of most species of *Didymoceras* in comprising more whorls in the middle growth stage (W1–W4), and in the successive part of the early growth stage (W5–W6)



Text-fig. 7. *Nostoceras (Didymoceras) wernickei* (Wollemann, 1902) from the Zeltberg Quarry at Lüneburg, northern Germany. SM 42; recently in the exhibition of the Museum Lüneburg; largest helicoidal portion known, consisting of four mostly nontuberculate whorls (W1–W4) of the loosely coiled middle growth stage, W3 having a few weak tubercles of the lower row. Natural size

whorls are regularly openly coiled. For that reason, we consider *N. (D.) wernickei* to be a discrete species.

STRATIGRAPHY AND DISTRIBUTION: In addition to the occurrence at Lüneburg (*bipunctatum/roemeri* Zone; upper upper Campanian), *N. (D.) wernickei* probably appears in the upper Campanian of the Gschliefgraben (Upper Austria), Tunisia and the Donbass region.

Family Diplomoceratidae Spath, 1926
Subfamily Polyptychoceratinae Matsumoto, 1938
Genus *Oxybeloceras* Hyatt, 1900

TYPE SPECIES: *Ptychoceras crassus* Whitfield, 1877, by original designation.

DIAGNOSIS: Two straight shafts in hairpin-like, tight contact except for tear-shaped, narrow opening at the elbow linking shafts; narrow, sharp ribs bear two rows of small ventral tubercles; constrictions lacking.

REMARKS: Wright *et al.* (1996, p. L255) regarded *Oxybeloceras* as a synonym of *Solenoceras* Conrad, 1860; however, this view is not adopted here.

Oxybeloceras aff. *crassum* (Whitfield, 1877)
(Text-fig. 8)

pars * 1902. *Hamites Wernickei* Wolleemann, p. 95, pl. 4, fig. 5 only [non pl. 4, fig. 4; pl. 5, figs 1, 2 = *Nostoceras (Didymoceras) wernickei* (Wolleemann, 1902)].

1976. *Solenoceras wernickei* (Wolleemann, 1902); Klinger, p. 73.

non 1976. *Neancyloceras* sp. cf. *Neancyloceras wernickei* (Wolleemann), 1902; Klinger, p. 73, pl. 33, fig. 4; text-figs 8i, 10f (= Polyptychoceratinae sp. indet.).

pars 1984. *Pseudoxybeloceras (Parasolenoceras) wernickei* (Wolleemann, 1902); Kennedy and Summesberger, p. 166, pl. 9, figs 6, 7 only [non pl. 6, fig. 3 = *Lewyites elegans* (Moberg, 1885); pl. 10, fig. 1 = ?*Nostoceras (Didymoceras) wernickei* (Wolleemann, 1902); pl. 10, figs 8, 9 = Polyptychoceratinae sp. indet.].

1984. *Pseudoxybeloceras (Parasolenoceras) interruptum* (Schlüter, 1872); Kennedy and Summesberger, p. 167, pl. 6, figs 5, 10, 11.

2000. *Pseudoxybeloceras (Parasolenoceras) ?wernickei* (Wolleemann); Kuchler, pl. 12, figs 1–3.

pars 2000. *Pseudoxybeloceras (Parasolenoceras)* cf. in-

terruptum (Schlüter); Kuchler, pl. 12, figs 9, 10 only [non pl. 12, figs 4–8 = Polyptychoceratinae sp. indet.].

2001. *Oxybeloceras* sp.; Kennedy and Odin, p. 481, pl. 2, fig. 17.

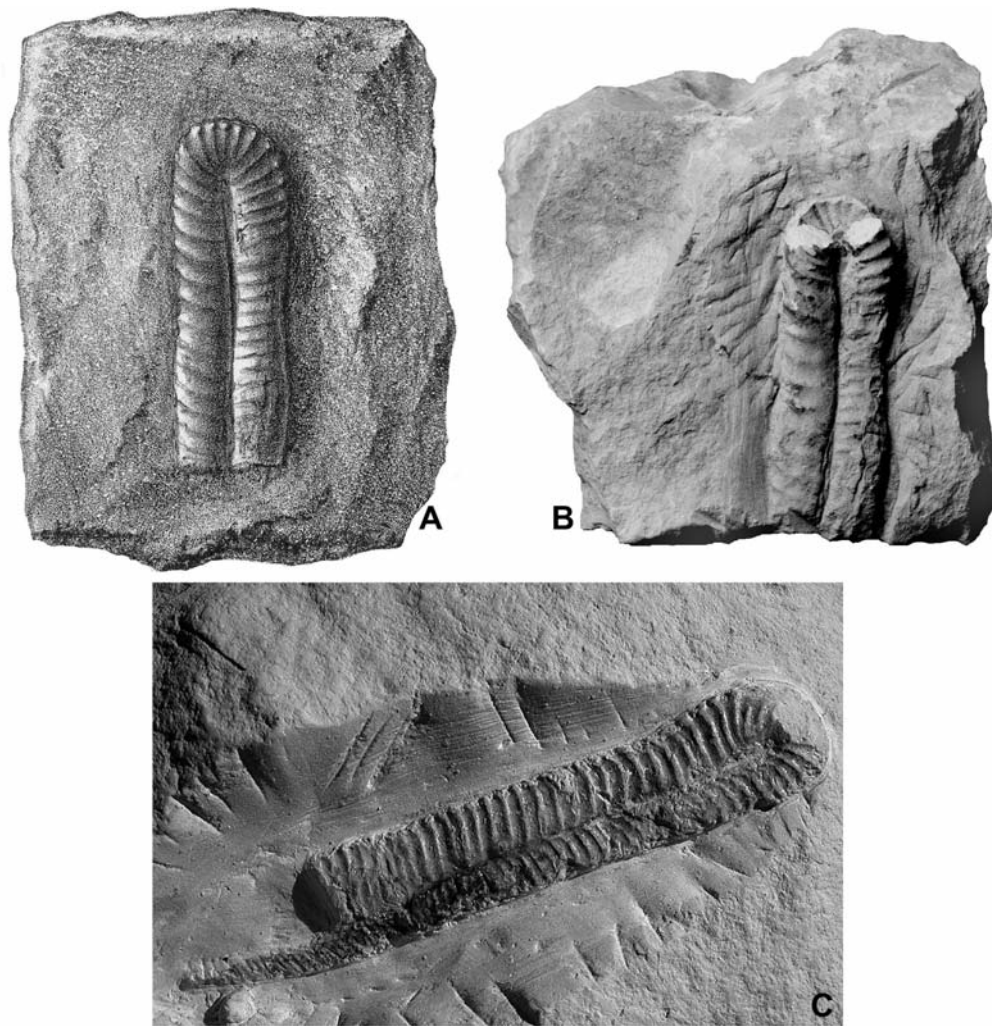
2006. *Oxybeloceras* aff. *crassum* (Whitfield, 1877); Jagt and Neumann, p. 567, fig. 1A–C.

2013. *Oxybeloceras* aff. *crassum* (Whitfield, 1877); Jagt, p. 138, fig. 1.

MATERIAL: The original of Wolleemann (1902, pl. 4, fig. 5), in the BGR Berlin-Spandau collection (BGR X 5873), of which MMG NsK 4 and NHMM 2015 019 are plaster casts. The specimen comes from the Zeltberg Quarry at Lüneburg, Niedersachsen, northern Germany, from the “blauer Mergel” (as noted on the associated label) of the “*Heteroceras*-Schicht des Mucronaten-Senons”, i.e., upper upper Campanian (*bipunctatum/roemeri* Zone).

DESCRIPTION: The single specimen from Lüneburg (Text-fig. 8A–B), preserved as a composite mould, attains an overall length of 45 mm and consists of two straight, parallel limbs in close approximation, both limbs preserved for equal lengths and Wh *c.* 7 mm. The curved sector, with an elbow diameter of 14.2 mm, is associated with a small, elongate, teardrop-shaped opening; early whorls and aperture are missing. The ornament consists of strong, straight ribs, $Ri = 3.5–4$; ?each rib (probably due to poor preservation; compare Wolleemann 1902, p. 95) has a weak, inconspicuous bullate ventrolateral tubercle. Ribs are straight and prorsiradiate on the smaller limb, rectiradiate on the curved sector and rursiradiate and more widely spaced on the larger limb, weakening on the venter. No constrictions or sutures seen.

DISCUSSION: Two straight, hairpin-like, closely adpressed shafts and a tear-shaped opening associated with the curved sector are characteristic of the genus *Oxybeloceras* and differentiate it from *Pseudoxybeloceras (Parasolenoceras)*. In addition, species of *Solenoceras* are similar, albeit often bear constrictions. *Oxybeloceras* aff. *crassum* is not common in northern Germany. To date merely a handful of specimens are known (Wolleemann 1902; Jagt and Neumann 2006; Jagt 2013). The three specimens from the Lehrte West Syncline near Hannover (one of which is refigured here in Text-fig. 8C), are closely comparable in size and general habitus to Wolleemann’s individual, with overall lengths of 38.5 mm, 85.5 mm and 56 mm, elbow diameters of 15.5 mm, 18 mm and 10 mm and $Ri = c. 4$). Jagt and Neumann (2006) and Jagt (2013) discussed at



Text-fig. 8. *Oxybeloceras* aff. *crassum* (Whitfield, 1877). **A** – Reillustration of *Hamites wernickei* of Wollemani (1902, pl. 4, fig. 5) from the Zeltberg Quarry at Lüneburg, northern Germany; natural size. **B** – BGR X 5873, holotype, the original of Wollemani (1902, pl. 4, fig. 5); two parallel shafts of equal length and whorl height and the connecting curved sector (note subsequent damage to the latter); natural size. **C** – Reillustration of *Oxybeloceras* aff. *crassum* (Whitfield, 1877) of Jagt (2013, fig. 1) from the Lehrte West Syncline near Hannover, *minor/polyplocum* Zone (C. Holschemacher Collection, Berlin); two parallel shafts of unequal length and whorl height and the connecting curved sector; $\times 1.5$

length the affinities to the North American species *Oxybeloceras crassum* (Whitfield, 1877) and *Spiroxybeloceras kimbriense* Kennedy and Cobban, 1999, which both are close in style of ribbing, rib index and general habitus. Jagt and Neumann (2006) remarked that the limited material from the Lehrte West Syncline near Hannover (MAB 3290a–b; C. Holschemacher Collection, Berlin) appeared to have less closely spaced ribbing on the smaller limb and a less regular occurrence of ventrolateral tubercles. Material from other European countries (see below) also is rare and of mediocre preservation, but it would appear that the size of the teardrop-shaped opening is similar to that in specimens

of *O. crassum* from the upper Campanian of Montana, Wyoming and Colorado, and rib density overlaps. For now, we prefer to keep this form in open nomenclature until better-preserved material becomes available.

STRATIGRAPHY AND DISTRIBUTION: Apart from the Lüneburg specimen from the *bipunctatum/roemeri* Zone (upper upper Campanian), *O. aff. crassum* is known from the uppermost lower to lowermost lower upper Campanian (upper *vulgaris/stolleyi* to *minor/polyplocum* zones) of the Lehrte West Syncline near Hannover, northern Germany; the lower upper Campanian (*Pseudoxybeloceras* Zone) of Tercis les Bains, southwest

France; the upper upper Campanian (*polyplacum* to *pulcherrimus* zones) of Navarra, northern Spain, and the upper Campanian of the Gschlieflgraben, Upper Austria.

CONCLUSIONS

In view of the fact that the species name *wernickei* (of Wollema 1902) is here restricted to three (out of four) of the originally illustrated late late Campanian (*bipunctatum/roemeri* Zone) heteromorphs from the Zeltberg Quarry (Lüneburg, northern Germany) that have irregularities of ribbing and tuberculation and a change in direction of growth at the transition from the helicoidal whorls to the hook, the single hairpin-shaped diplomoceratid (polyptychoceratine) specimen is in need of a new name. The former are assigned to the subfamily Nostoceratinae as *Nostoceras* (*Didymoceras*) *wernickei* (Wollema, 1902) comb. nov., while the latter is referred to as *Oxybeloceras* aff. *crassum* (Whitfield, 1877). Comparison with previous records of heteromorph taxa under the name of *wernickei* demonstrates that the geographic range of *N. (D.) wernickei* probably also included Upper Austria (Gschlieflgraben), Tunisia and the Donbass region; *O.* aff. *crassum* is known from the Hannover area (northern Germany), southeast France, northern Spain and Upper Austria (Gschlieflgraben).

Acknowledgements

We wish to thank to J. Erbacher (BRG, Hannover) and A. Ehling (BGR, Berlin-Spandau) for access to material in their care, to D. Schumacher (Lüneburg) for donating his specimens from the Zeltberg Quarry at Lüneburg and for assisting with field work, images and measurements, to C. Holschemacher (Berlin) for making material from the Hannover area available for study, and to M. Röthel and R. Winkler (SNSD) for preparatory and photographic assistance. W.J. Kennedy (Oxford, U.K.) and H.C. Klinger (Cape Town, South Africa) are thanked for constructive comments on an earlier typescript.

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Manuscript submitted: 20th December 2015

Revised version accepted: 30th April 2016