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New records of the lower Oxfordian ammonite *Protophites insociale* (Bukowski, 1887) from southern Poland

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ABSTRACT

Three adult specimens of the rare lower Oxfordian ammonite species *Protophites insociale* (Bukowski) are described from two sections of southern Poland, Ogrodzieniec and Zalas. Based on their globular phragmocone, geniculate body chamber, suture line, looped ribs, and age, they have been included in the Pachyceratidae. In the present study *Protophites* (microconch) and *Tornquistes* (macroconch) are considered as a sexual dimorphic pair.

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Sexual dimorphism; Protophites; Tornquistes; Oxfordian; Poland

Introduction

The records of lower Oxfordian ammonites from Poland are mostly of perisphinctids (e.g. Matyja and Giżejewska 1979; Głowniak 2002, 2012; Matyja and Głowniak 2003). Różycki (1953) studied several localities in southern Poland and cited the presence of several Callovian-Oxfordian ammonites. His specimens were lost during the World War II; the remaining ones (123 specimens) are kept in the Polish Geological Institute (Warsaw) and of them 75% are perisphinctids.

Matyja and Giżejewska (1979) noted that in Poland, the upper Callovian–lower Oxfordian ammonites show interesting trends: in southern and central Poland they mostly have affinities with the fauna of the Submediterranean Province, while in northern Poland they were considerably influenced by the Subboreal fauna.

The purpose of this paper is to describe three adult specimens of the rare lower Oxfordian ammonite *Protophites insociale* (Bukowski 1887) collected from, lower Oxfordian sections at Ogrodzieniec and Zalas, southern Poland (Figure 1). The study of these specimens

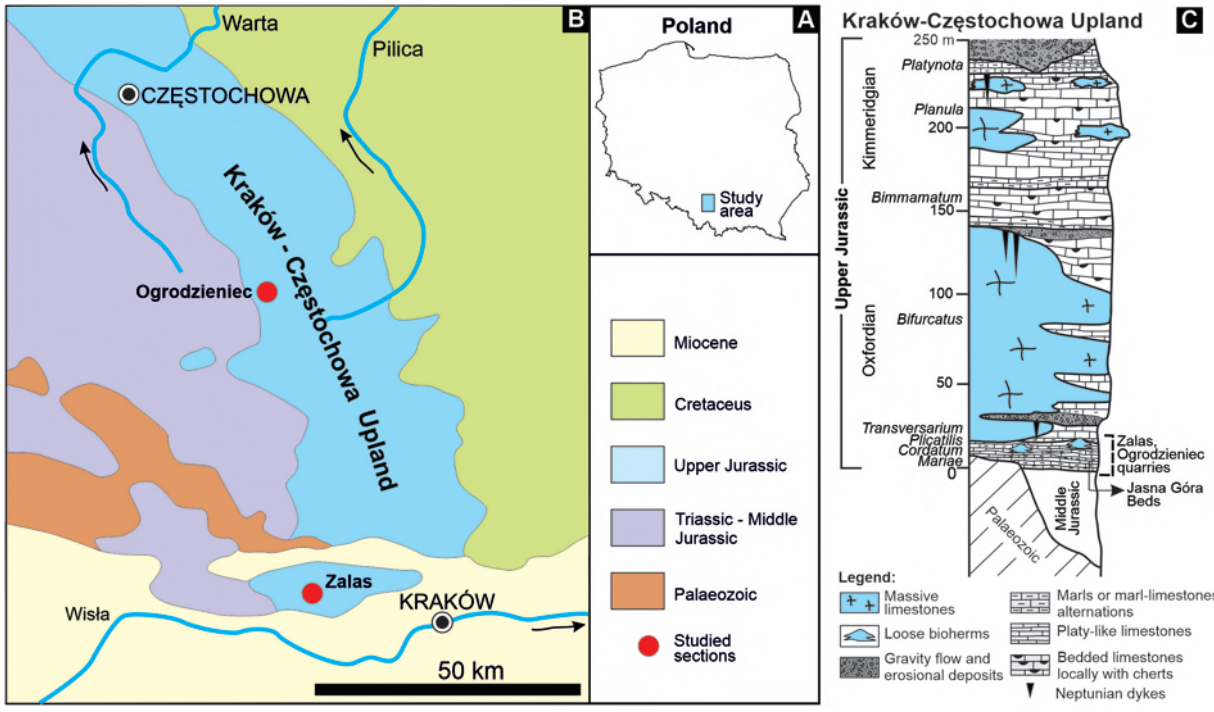

Figure 1. Geological map and general stratigraphy. (A–B) geological map of southern Poland showing the two studied localities of Zalas and Ogrodzieniec. (C) General stratigraphy of the Kraków-Częstochowa area and the position of the two studied sections, Zalas and Ogrodzieniec (after Matyszkiewicz et al. 2015).

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also allow us to revise several groups of ammonites from France, Poland and Switzerland that have been assigned to different genera under confusing systematic classifications.

Abbreviation: GIUS: Museum of the Faculty of Natural Sciences of the University of Silesia in Katowice, Poland.

Biostratigraphy of the studied sections

Two sections, Zalas (50°04'56.5"N; 19°38'35.5"E) and Ogrodzieniec (50°27'44.6"N; 19°31'23.6"E) were studied (Figure 2). Two *Protophites* specimens (GIUS 8–3756/Tq2–3) were recorded from Zalas (Figure 1) associated with typical lower Oxfordian Bukowski Subzone (Cordatum Zone) forms of *Taramelliceras bukowskii* (Siemiradzki) (Figure 2A), *Cardioceras* (*Cardioceras*) *cordatum* (Sowerby) (Figure 2B), *Bukowskites minax* (Bukowski) (Figure 3A) and *Perisphinctes bernensis* de Loriol (Figure 4A).

The biostratigraphy of the lower part of the Ogrodzieniec section (upper Callovian – lower Oxfordian) has recently been updated based on the collection of ammonites (Jain and Mazur 2021; Jain and Salamon 2022; Jain et al. 2022a, 2022b; Jain et al. 2023a, 2023b). One specimen (GIUS 8–3756/Tq1) was recorded from the dark green argillaceous glauconitic marls with phosphatic nodules (= bed α of Głowniak 2012). This bed is equivalent to bed 16 of Dembicz et al. (2006, p. 146) who noticed the presence of *Quenstedtoceras lamberti* (typical of the upper Callovian Lamberti Zone) and *Quenstedtoceras mariae* (typical of the lower Oxfordian Mariae Zone). Later, Głowniak (2012, p. 123) also reported that the bed yielded reworked ammonites of both zones.

Recently, Jain and Mazur (2021) recorded *Peltoceratoides* (*Parawedekindia*) *gerberi* Prieser and *Euaspidoceras* sp. from the overlying bed 'b' (= bed 1a Głowniak 2012). *Peltoceratoides* (*P.*) *gerberi* is a characteristic early Oxfordian Bukowskii Subzone, Cordatum Zone form (see Prieser 1937; Bourseau 1977; Tchoumatchenco and Khrischev 1992). This early Oxfordian Bukowskii Subzone assignment to bed 'b' also matches with the age inferred by other works (see Różycki 1953; Głowniak 2002; Matyja and Głowniak 2003; Barski et al. 2004; Dembicz et al. 2006). *Euaspidoceras*, the co-occurring species, is long ranging, spanning from the late Callovian Athleta Zone to the late Oxfordian Bimammatum Zone (see Énay and Howarth 2019). Jain and Mazur (2021), from the underlying bed 'a' (lower part; limestones; = bed β of Głowniak 2012) recorded *Kosmoceras rotundum* and assigned it to the upper Callovian Lamberti Zone. The recorded *Protophites* (this study) comes from the upper part of bed 'b' of Jain and Mazur (2021) (= bed α of Głowniak 2012). Hence, for now, following Głowniak (2012) and based on the occurrences of the aforementioned species, the occurrence of *Protophites* is assigned to the lower Oxfordian Mariae Zone. Genus *Protophites* Ebray, as such, ranges from early to mid-Oxfordian (see Bert 2003).

Thus, the studied specimens of *Protophites insociale* (Bukowski) are assigned to the lower Oxfordian (Bukowski Subzone at Zalas and Mariae Zone at Ogrodzieniec sections).

Systematic palaeontology

Adult or mature modifications of the ammonoid shell are a prerequisite to determine sexual dimorphism (see review in Klug et al. 2015). Changes in the coiling of the last whorl or uncoiling (Klug 2001; Korn and Klug 2003; Parent 2021) are the only definite mature modifications indicating terminal growth.

Order Ammonitida Haeckel, 1866
Suborder Ammonitina Fischer, 1882
Superfamily Perisphinctoidea Steinmann, 1890
Family Pachyceratidae Buckman, 1918

Genus *Protophites* Ebray, 1858

Type species: *Protophites oxfordianus* Ebray, 1858; original designation.

Remarks

The genus includes the microconchs of the species of the macroconchiate genus *Tornquistes* Lemoine (1910) (Bourseau 1977; Schweigert 2018). If *Protophites* and *Tornquistes* would be synonymised, *Tornquistes* would become a junior synonym. The macroconchs (*Tornquistes*) are relatively large ammonites with two morphologic groups, one with strongly uncoiled (geniculate) adult body chamber, while the other with more involute and weakly uncoiled adult body chamber; mostly known from the Cordatum (lower Oxfordian) and Plicatilis (middle Oxfordian) zones (e.g. de Loriol 1896; Charpy 1976; Bourseau 1977; Thierry and Charpy 1982; Benetti and Pezzoni 1983; Bert 2009). The sexual dimorphism based on adult size differences between forms of *Tornquistes* (Thierry and Charpy 1982), has recently been cast in doubt (see Bert 2003, 2009, Enay & Howarth 2109) and here disregarded.

Protophites insociale (Bukowski, 1887)

Figures 3-4; Table 1

*1887 *Sphaeroceras insociale* n. sp. – Bukowski: 125, pl. 26: 14 (holotype).
1887 *Macrocephalites* f. indet. – Bukowski: 127, pl. 26: 16.
1900 *Sphaeroceras chapuisi* Oppel (1857) – de Loriol: pl. 4: 19–20.
1900 *Macrocephalites greppini* de Loriol, 1898 – de Loriol: 57, pl. 4: 17–18.
1951 *Christolia christoli* Beaudoin 1851 – Jeannet: 106, pl. 31: 10
1951 *Christolia nux* d'Orbigny (1850) – Jeannet: 107, pl. 31: 11
1953 *Pachyceras insociale* Bukowski (1887) – Różycki: 51, 56; lost material.
1953 *Pachyceras bukowskii* n. sp. – Różycki: 51.
1966 *Goliath*. (*Pachyc.*) sp. – Enay: 162.
1976 *Pachyceras greppini* – Charpy: 136, pl. 3: 5.
2002 *Tornquistes chapuisi* (Oppel) – Marchand et al.: 472, pl. 1: 11–12.
2002 *Tornquistes* sp. – Marchand et al.: 473, pl. 1: 10.
2009 *Tornquistes* sp. – Quereilhac et al.: 7, pl. 7: 1–3, 5.
2018 *Protophites christoli* (Beaudoin) – Schweigert: pl. 26: 6 (right).

Material

Three adult, almost complete specimens, deposited in the collection of the Faculty of Natural Sciences of the University of

Table 1. Dimensions and shape indexes of *Protophites insociale* (Bukowski 1887). D: diameter in mm, D_{ls}: diameter at last septum, U/D: relative umbilical width, T/D: relative whorl width, H/D: relative whorl height. [M]: macroconch (female), [m]: male.

Protophites insociale (Bukowski 1887)	D	U/D	T/D	H/D	T/H	D_{ls}	
GIUS 8–3756/Tq1 (Ogrodzieniec) [m]	21.1	0.32	0.41	0.35	1.17	16.0	Fig. 3.1A–1D
GIUS 8–3756/Tq2 (Zalas) [m]	19.8	0.34	0.40	0.29	1.36	16.3	Fig. 3.2A–2D
GIUS 8–3756/Tq3 (Zalas) [m]	22.5	0.33	0.40	0.35	1.14	18.4	Fig. 3.3A–3D
Holotype [m]	17.5	0.29	0.43	0.38	1.13	–	Figure 4A
(Bukowski 1887: pl. 26: 16) [M]	14.0	0.21	0.93	0.50	1.86	–	Figure 4B

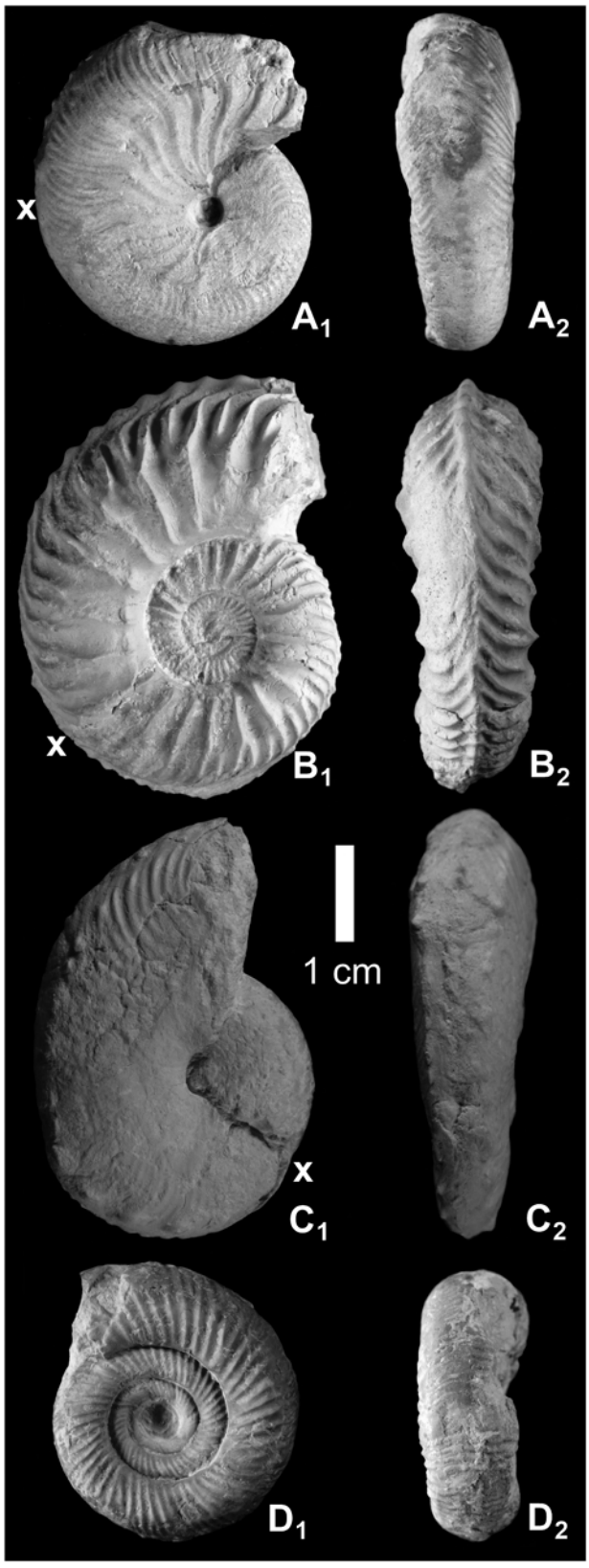

Figure 2. Ammonite assemblage recorded from Zalas assigned to lower Oxfordian, Cordatum Zone, Cordatum Subzone. A: *Taramelliceras bukowskii* (Siemiradzki), GIUS 8–3756/Tb. B: *Cardioceras* (*Cardioceras*) *cordatum* (Sowerby), GIUS 8–3756/Cc. C: *bukowskites minax* (Bukowski), GIUS 8–3756/Bm. D: *Perisphinctes bernensis* de Loriol, GIUS 8–3756/Pb. Bar is 1 cm.

Silesia in Katowice, Poland. One specimen is from Ogrodzieniec (GIUS 8–3756/Tq1) and two from Zalas (GIUS 8–3756/Tq2 and GIUS 8–3756/Tq3).

Description

Phragmocone (observed from about $D = 7–10$ mm): spherocone with suboval, wider than high whorl section, and relatively narrow umbilicus. Ribbing composed of primary ribs originating on the umbilical wall, crossing the flank slightly prosocline, and most bifurcate in the upper half of the flank in narrowly splayed secondaries. In the half-whorl behind the last septal suture two or three pairs of secondary ribs, separated by a constriction, are looped. Septal suture line not frilled, typically perisphinctoid, with the sequence E–L–U_2–U_3 developed through the ventral area and the flank (up to the umbilical shoulder).

Body chamber: it begins at $D = 16–18$ mm; contracted and geniculate – uncoiling to form a straight segment (shaft) and then bending adorally up to the peristome. The ribbing remains as in the phragmocone but with no constrictions. The peristome is not completely preserved in any of our specimens that seem nearly complete.

Discussion

The three specimens described are adults, as indicated by their strong geniculate uncoiling (Figs. 3–4). They are considered microconch males due to their small adult size, and the fact that ribbing remains isocostate up to end of the body chamber. The 'perisphinctid' ribbing with ventrolaterally looped ribs and the structure of the suture line place them into the Perisphinctoidea, either in the family Tulitidae or the Pachyceratidae because of the globular phragmocone with geniculate body chamber. However, considering the early Oxfordian age of the present specimens we assign them to the Pachyceratidae.

The present specimens are very similar to some male (microconch) specimens of *Kheraiceras* Spath (1924) from upper Bathonian to lower Callovian rocks (e.g. Enay et al. 1994: pl. 56: 2; Dietl et al. 2021: fig. 12.3; Parent et al. 2023: fig. 6C). However, the latest known *Kheraiceras* (Bullatimorphitinae, Tulitidae) are late early Callovian (Callomon et al. 1992), leaving a long time-gap for relating our early Oxfordian specimens with the Bullatimorphitinae. The inclusion of the Pachyceratidae among the Macrocephalitinae Buckman, 1922 by Arkell (1957) suggests that he assumed, under his classification, a derivation of the Pachyceratidae from the Tulitidae (that is *Kheraiceras*). Mangold (1988: fig. 9) elaborated a phylogenetic model that assumes the origin of the Pachyceratidae from *Kheraiceras*. If this would be the case, then the resemblance of the microconchs could have a genetic basis. Alternatively, Callomon (in Donovan et al. 1981) suggested that the Pachyceratidae would be derived from *Subgrossouvria* Spath (1924).

The adult size and shell-shape of our specimens are practically identical to the holotype by monotypy of *Sphaeroceras insociale* Bukowski (1887: pl. 26: 14) whose corresponding macroconch could be the small phragmocone figured by Bukowski (1887: pl. 26: 16) as *Macrocephalites* f. indet. Indeed, this specimen is more inflated in the outermost whorl and does not show signs of uncoiling at comparable size, suggesting it is either incomplete or juvenile. These specimens were assigned to *Pachyceras* Bayle (1878) by Różycki (1953, p. 51, 56) but, according to their shell-shape, sculpture,

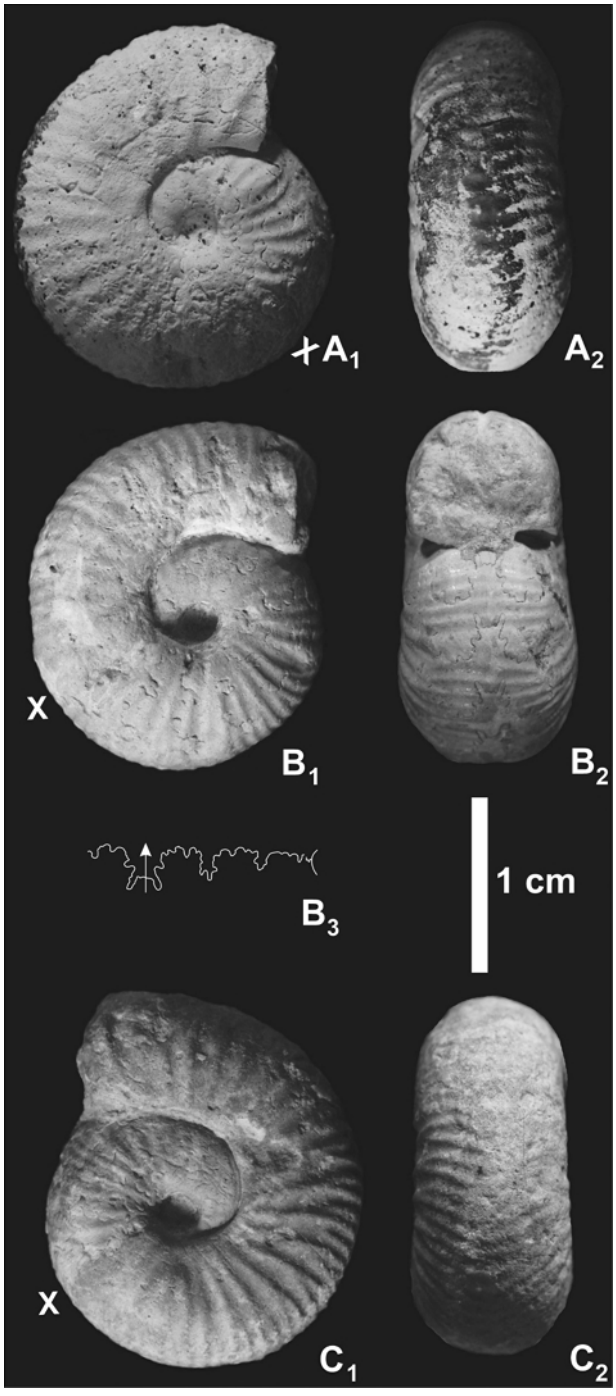

Figure 3. *Protophites insociale* (Bukowski 1887). A: Ogrodzieniec, specimen no. GIUS 8–3756/Tq1. B: Zalas. E–H: Specimen no. GIUS 8–3756/Tq2. C: Specimen no. GIUS 8–3756/Tq3. Bar is 1 cm.

and stratigraphic position, they belong to *Protophites* (as microconchs of *Tornquistes*). Unfortunately the holotype of *S. insociale* comes from an indeterminate position within the lower Oxfordian section of Częstochowa, Poland (Bukowski 1887, p. 125), possibly upper Mariae or lower Cordatum zones (see Figure 1B). The holotype (by monotypy) and the possible female macroconch are refigured herein in Figure 4A-B. Our specimens matches almost perfectly with the holotype of *P. insociale*, the only difference is that in the holotype of this latter, the ribs of the adult body chamber are somewhat thickened in the upper flank. Since our specimens are most likely older they could belong to an earlier transient; but intraspecific variation or different preservation (taphonomic differentiation; see Jurkowska and Kołodziej 2013) could be alternative explanations.

The specimen figured by Jeannet (1951: pl. 31: 11) as *Protophites nux* (Cordatum Zone of Herznach, Switzerland) is essentially identical to our specimens, differing only by its wider whorl section and its peristome with the typical expansion preserved. However, *Protophites nux* (d'Orbigny 1850) is different: smaller, more narrowly umbilicate and, especially, the ribbing consists of straight primary ribs that gradually thicken through the upper flank (Cottreau 1927: pl. 44: 10–11). According to Cottreau (1927, p. 40) there were originally two specimens under the name *Ammonites nux* in the collection of d'Orbigny, thus we take the opportunity to designate as lectotype of *Ammonites nux* d'Orbigny (1850) the specimen figured by Cottreau (1927, pl. 44, figs. 10–11).

A group of specimens that match our specimens as well as those of Bukowski (1887) discussed above are those figured as *Sphaeroceras chapuisi* (Oppel, 1857) by de Loriol (1900: pl. pl. 4: 19–20; herein refigured in Figure 4C-D). The specimen figured as *Macrocephalites greppini* de Loriol (1898) by de Loriol (de Loriol 1900: pl. 4: 18) could be the inner whorls of an evolute macroconch (refigured here in Figure 4E). The last whorl of this latter specimen is more widely umbilicate, thus would correspond to a growth stage of the female which is not developed by the male. Indeed, most Jurassic male ammonites matured earlier than the females, then halting its development at a smaller size (e.g. Guex 1970; Klug et al. 2015; Parent and Zatoń 2016; Jain and Mazur 2021). All these specimens have been included in *Tornquistes* by Enay (1966; 1997), and also by Marchand et al. (2002) under confusing nomenclature. Marchand et al. (2002: pl. 1: 10–12) and Quereilhac et al. (2009: pl. 7: 1–3, 5) have described other sets of specimens from the French Jura and Niort (France) that perfectly match the specimens of de Loriol (1900).

Other ammonites that show resemblance with our specimens are those of the genus *Neomorphoceras* Arkell (1953) (Plicatilis – Transversarium zones), type species: *Neomorphoceras chapuisi* (Oppel 1857). But there are significant differences: (1) the phragmocone of *N. chapuisi* is not spheroconic, but more compressed and more evolute, (2) its ribbing shows the primary ribs stronger than the secondaries, (3) it bears abundant and well-marked constrictions, and (4) in many specimens there is a ventral groove shortly developed in the inner or middle whorls. Additionally, the present specimens assigned to *P. insociale* have pairs of secondary ribs looped, a feature unknown in *Neomorphoceras*. It is interesting to mention the microconchiate male specimen of *Neomorphoceras collinii* (Oppel, 1863) with lappets, from the Luciaeformis Subzone (Transversarium Zone) of Poitou (France), figured by Quereilhac (2000: 61: 1).

Age

The age of our specimens is early Oxfordian. The specimens from Zalas belong to the Bukowski Subzone (Cordatum Zone) and the one from Ogrodzieniec is assigned to the Mariae. The specimens figured by de Loriol (1900) also belongs to the Mariae Zone. The specimens of Bukowski (1877) would be Mariae to early Cordatum zones in age, as discussed above.

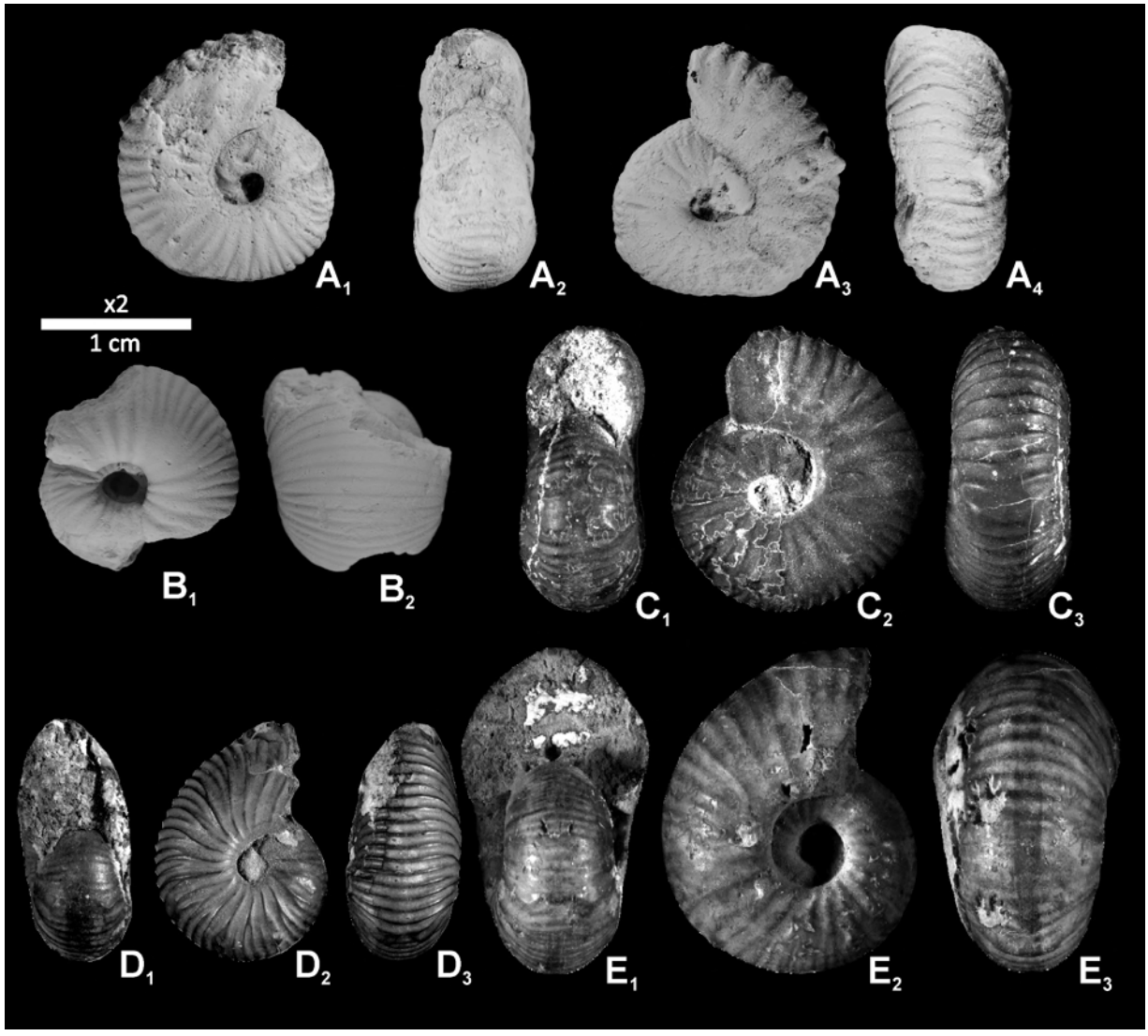

Figure 4. *Protophites insociale* (Bukowski 1887). (A): Holotype of *Sphaeroceras insociale* (in Bukowski 1887: pl. 26: 14), IPUW-1887-1-16. (B): Specimen figured as *Macrocephalites* f. indet by Bukowski (1887: pl. 26: 16), IPUW-1887-1-19. (C–D): Specimens figured as *Sphaeroceras chapuisi* (Oppel 1857) by de Loriol (1900: pl. 4: 19–20),MNHN.F.A26197 and MNHN.F.A26198. (E): Specimen figured as Macrocephalites greppini de Loriol, 1898 by de Loriol (1900: pl. 4: 17), MNHN.F.A26218. –all double size (x2). (A–B) photographs by Martin Maslo (IPUW: institut für Paläontologie, Universität Wien). (C–E): Photographs by Jocelyn Falconnet, 2007-RECOLNAT ANR-11-INBS-0004 (MNHN: Muséum national d'Histoire naturelle, Paris, France).

Conclusion

Three adult ammonite specimens assigned to *Protophites insociale* (Bukowski) are described from the lower Oxfordian of two localities, Ogrodzieniec and Zalas (southern Poland). Based on their stratigraphic position (lower Oxfordian) and morphological characteristics such as 'perisphinctid' ribbing and structure of the suture line, they are assigned to Pachyceratidae. In the present study and following other authors, *Protophites* (microconch) and *Tornquistes* (macroconch) are considered as a dimorphic pair. The macroconchs are much larger with two morphologic groups, one with strongly uncoiled (geniculate) adult body chamber, while the other with more involute and weakly uncoiled adult body chamber; mostly known from the Cordatum and Plicatilis zones (lower and middle Oxfordian, respectively).

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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