

On some Upper Cretaceous ammonites from western Uzbekistan

DAVID J. WARD^{1, 2}, CHRIS KING[†], NOEL J. MORRIS^{1, 3} and WILLIAM JAMES KENNEDY^{4*}

¹ Science Group, Natural History Museum, Cromwell Road, London, SW7 5BD, UK

² Crofton Court, 81 Crofton Lane, Orpington, Kent BR5 1HB, UK; e-mail: david@fossil.ws

³ e-mail: niccamore@gmail.com

⁴ Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, UK, and Department of Earth Sciences, South Parks Road, Oxford OX1 3AN, UK; e-mail jim.kennedy@oum.ox.ac.uk

[†] Deceased

* Corresponding author

ABSTRACT:

Ward, D.J., King, C., Morris, N.J. and Kennedy, W.J. 2023. On some Upper Cretaceous ammonites from western Uzbekistan. *Acta Geologica Polonica*, **73** (4), xxx–xxx. Warszawa.

Upper Cretaceous ammonites are described from six horizons in the mammal-bearing terrigenous-clastic sequences of western Uzbekistan, as follows: Upper Cenomanian, with *Placenticer* sp. juv. cf. *cumminsi* Cragin, 1893 and *Metoicoceras geslinianum* (d'Orbigny, 1850); Lower Turonian with *Tragodesmoceras* cf. *mauryae* Kennedy and Wright, 1981, *Placenticer* *kharsmense* (Lahusen, 1884), *Watinoceras coloradoense* (Henderson, 1908), *Watinoceras amudariense* (Arkhangelsky, 1916b), *Metasigaloceras rusticum* (J. Sowerby, 1823), *Morrowites wingi* (Morrow, 1935), *Sciponoceras* cf. *bohemicum bohemicum* (Fritsch, 1872), and *Yezoites amudariensis* (Arkhangelsky, 1916b); Middle Turonian with *Collignonoceras woollgari woollgari* (Mantell, 1822); Upper Turonian with *Lewesiceras mantelli* (Wright and Wright, 1951) and *Placenticer* *crassum* Ilyin, 2020; a single *Placenticer* *semiornatum* (d'Orbigny, 1850) from around the Coniacian/Santonian boundary, and Santonian *Placenticer* *polyopsis* (Dujardin, 1837).

Key words: Ammonites; Upper Cretaceous; western Uzbekistan.

INTRODUCTION

In this contribution we describe Upper Cretaceous ammonites from western Uzbekistan (Text-fig. 1), collected by DJW, CK and NM between 1997 and 2002, in order to clarify the age of the diverse vertebrate faunas (fish, amphibians, reptiles, birds and mammals) of the predominantly non-marine terrigenous-clastic sequences developed in the area. These were first discovered in the 1970's by Professor Lev Nessonov of the then Leningrad State University and Zoological Institute, Russian Academy of Sciences, Leningrad (now Sankt Petersburg). There is an extensive literature on the vertebrate faunas (e.g., Nessonov 1985, 1990, 1995; Nessonov *et al.* 1994, 1998, etc.),

together with numerous papers by Professor David Archibald of San Diego State University and his colleagues (for example Archibald and Averianov 2005; Archibald *et al.* 1998, 2001; Averianov and Archibald 2016, 2017 and references therein). Ammonites from the marine intervals were first documented by Lahusen (1884) who described and figured two species of *Placenticer* Meek, 1876. A more complete account, that also dealt with the bivalves, is that of Arkhangelsky (1916b), whose work is illustrated by beautiful photographs. Subsequent publications dealing with ammonites from the present area and more widely in central Asia include those of Luppov (1963), Ilyin (1957, 1958, 1959, 1975, 2000), and Kim *et al.* (2007).

STRATIGRAPHY AND LOCALITY DETAILS

The stratigraphy of the Cretaceous rocks that yielded the present faunas was described by Arkhangel'sky (1916a, b, 1931), who provided detailed sections of key localities. The formal lithostratigraphic framework for the Cretaceous of western Uzbekistan is complex (Nessov 1985; Abdiazimova 1988; see also discussion in Feldmann *et al.* 2007; Averianov and Sues 2017; Kim *et al.* 2007; McCann 2017). The succession accumulated on the northern margin of the Amu Darya Basin, the environments, interpreted by McCann (2017, p. 439) as follows: "Broadly, the region comprised a coastal-marine transition zone, with the coastline advancing and retreating over time, these changes being related to major marine incursions from the east." The scattered outcrops (Text-fig. 1) span various intervals, and the extent of the marine units that yielded the ammonites below varies through time.

Key units mentioned in the text are as follows:

(youngest)

- Laulau Formation
- Aitym Formation
- Bissekty Formation
- Kendytube Formation
- Beshtyube Formation
- Uchkuduk Formation

(oldest)

Their geographic distribution, relationships to other units, and to regional biostratigraphic units is set out in Kim *et al.* (2007, text-fig. 10).

There is no continuous sequence of ammonite faunas. The single Upper Cenomanian, and the Turonian faunas are discussed in terms of the zonal sequence developed in Europe, as set out below:

(youngest)

UPPER TURONIAN

- *Forresteria* (*Harleites*) *petrocoriensis* Zone (part)
- *Prionocyclus germari* Zone
- *Subprionocyclus neptuni* Zone

MIDDLE TURONIAN

- *Collignoniceras woollgari* Zone

LOWER TURONIAN

- *Mammites nodosoides* Zone
- *Fagesia catinus* Zone
- *Watinoceras devonense* Zone

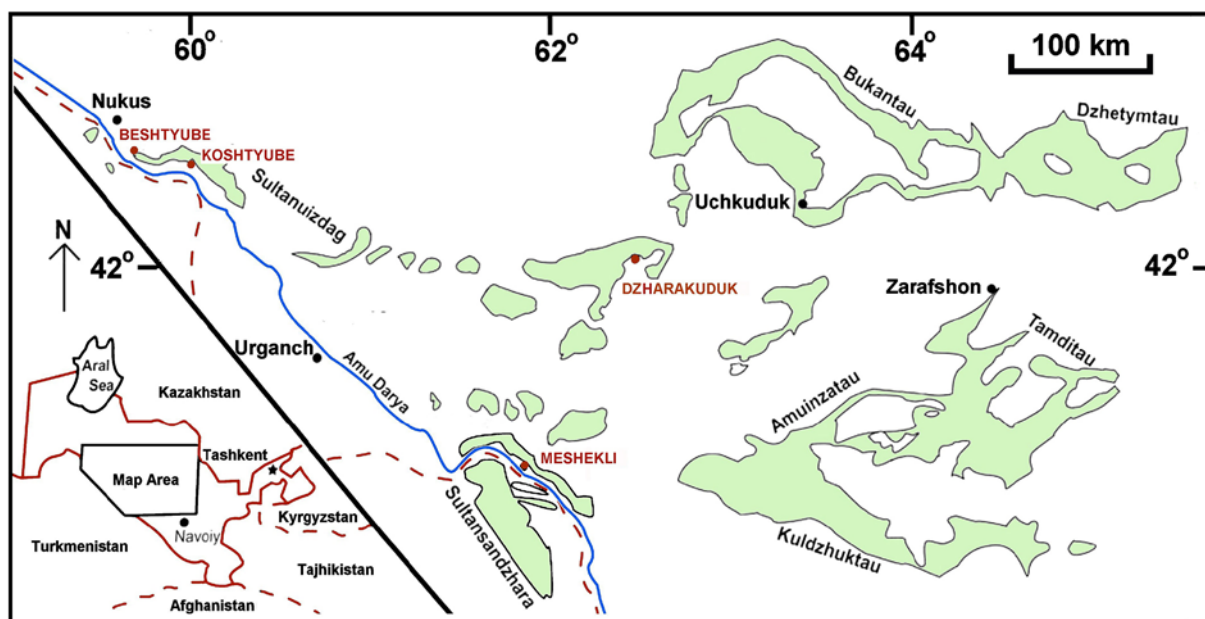
UPPER CENOMANIAN

- *Neocardioceras juddii* Zone
 - *Metoicoceras geslinianum* Zone
 - *Calycoceras guerangeri* Zone
- (oldest)

Details and ammonite faunas of relevant localities (Text-fig. 1) are set out below.

Dzharakuduk

The section in the Dzharakuduk escarpment (N 42°06'30" E 62°37'00") was first described by Arkhangel'sky (1916a, section X, pp. 14–16, text-fig. 6). A horizon 3.4 m above the base of the Uchkuduk Formation yielded *Placentoceras* sp.



Text-fig. 1. Localities cited in the text, and Cretaceous outcrops (shaded) in western Uzbekistan (modified after Feldman *et al.* 2007, text-fig. 1).

juv., cf. *cumminsi* Cragin, 1893 and fragments of *Metoicoceras geslinianum* (d'Orbigny, 1850), indicating the Upper Cenomanian *geslinianum* Zone. Fragments of *Placentoceras* also occur up to 80 cm below.

The Laulau Formation around coordinates N 42°07' E 61°38' has yielded the Santonian marker *Placentoceras polyopsis* (Dujardin, 1837), and was the source (Dzirakuduk, Kyzylkum) of Arkhangelsky's *Placentoceras kysylcumense* (1916b, p. 45, pl. 7, figs 4–7), a subjective junior synonym of Dujardin's (1837) species.

Beshtyube

This locality (N 42°21'18" E 59°47'17") is a series of extensive outcrops on the escarpment overlooking the Amu Darya River (the Oxus of antiquity) south of the town of Nukus. Two sections here were described by Arkhangelsky (1916a, his sections I and II, text-figs 1 and 2 on pp. 5 and 6). It exposes an incomplete 49 m section in the Beshtyube Formation. Concretions 19.5 m above the base of the section (within bed 5 of Arkhangelsky's section I) yield large *Placentoceras kharesmense* (Lahusen, 1884); those around 22.5 m above the base are the source of *P. kharesmense*, *Watinoceras coloradoense* (Henderson, 1908), and *Morrowites wingi* (Morrow, 1935). The last two species are precisely dated in the Global Stratotype Section for the base of the Turonian stage at Pueblo, Colorado (Kennedy *et al.* 2000, 2005), where *W. coloradoense* first occur above the last *Watinoceras devonense* Wright and Kennedy, 1981 *sensu stricto* and below the first *Mammites nodosoides* (Schlüter, 1871) in an interval that yields rare *Fagesia catinus* (Mantell, 1822), whilst *M. wingi* first occurs below the first occurrence of *Mammites nodosoides* and ranges into the lowest part of the range of *Collignonicerias woollgari*. The present association is correlated with the *catinus* Zone of the European sequence.

A layer of large subspherical concretions approximately 37.3 m above the base of the section (within bed 4 in Arkhangelsky's 1916a section II) yielded Middle Turonian *Collignonicerias woollgari woollgari*.

Koshtyube

This section (N 42°21'55" E 59°58'39") lies in the escarpment cut by the Nukus-Turtkul road 17.5 km east of Beshtyube. It probably corresponds to the 'Kochtyube' site of Arkhangelsky (1916a, part of

his section IV described on pp. 8 and 9). The upper part of the Khodzshakul Formation (4 m+) is overlain by 36.5 m+ of the lower part of the Beshtyube Formation. Concretions 19–21 m above the base of the latter yielded the Lower Turonian *Watinoceras coloradoense* fauna, with *Tragodesmoceras* cf. *mauryae* Kennedy and Wright, 1981, *Placentoceras kharesmense*, *W. coloradoense*, *Metasigaloceras rusticum* (J. Sowerby, 1823), *W. amudariense* (Arkhangelsky, 1916b), *Morrowites wingi*, *Sciponocera* cf. *bohemicum bohemicum* (Fritsch, 1872), and *Yezoites amudariensis* (Arkhangelsky, 1916b).

Meshekli

Cretaceous sediments are exposed almost continuously for a distance of over 10 km in river cliffs and riverside escarpments on the NE side of the Amu Darya river, near the village of Meshekli (N 42°13'35" E 61°44'22"). The area was studied by Arkhangelsky (1916a, his section XV, p. 20, text-fig. 9, near Zengelkuigan; XVI, p. 21, text-fig. 10, p. 22, and XVII, p. 22, near Meshekli itself). The section extends from the Kendyktyube Formation to the Karakata and Bukhara Formations.

The upper part of the Kendyktyube Formation that outcrops on the foreshore north of Meshekli extends to the top of the escarpment at Zengelkuigan. It has yielded the Upper Turonian *Lewesiceras mantelli* (Wright and Wright, 1951), and numerous *Placentoceras crassum* Ilyin, 2000.

Above, the lower part of the 5–6 m thick Laulau Formation yielded a single specimen of *Placentoceras semiornatum* (d'Orbigny, 1850), a poorly dated species indicating a horizon around the Coniacian–Santonian boundary. Santonian *Placentoceras polyopsis* occur in a shell bed 3 m above the base.

CONCLUSIONS

To summarise the above, the faunas recognised, and their ages are as follows:

- Uchkuduk Formation: Upper Cenomanian *Metoicoceras geslinianum* fauna;
- Beshtyube Formation: Lower Turonian *Watinoceras coloradoense* fauna and Middle Turonian *Collignonicerias woollgari woollgari* fauna;
- Kendyktyube Formation: Upper Turonian *Lewesiceras mantelli* fauna;
- Laulau Formation: Santonian *Placentoceras polyopsis* fauna.

SYSTEMATIC PALAEONTOLOGY (W.J. Kennedy)

Repositories of specimens

The following abbreviations are used to indicate the repositories of specimens cited in the text:

BMNH: The Natural History Museum, London, UK.

MNH: Muséum National d'Histoire Naturelle, Paris, France.

OUMNH PAL: Oxford University Museum of Natural History, Oxford, UK.

Conventions

Dimensions are given in millimetres: D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; c = costal dimension; ic = intercostal dimension. Figures in parentheses are dimensions as a percentage of the diameter.

Order Ammonoidea Zittel, 1884

Suborder Ammonitina Hyatt, 1889

Superfamily Desmoceratoidea Zittel, 1895

Family Pachydiscidae Spath, 1922

Genus *Lewesiceras* Spath, 1939

TYPE SPECIES: *Ammonites peramplus* Mantell, 1822 (p. 200), by the original designation of Spath (1939, p. 296).

Lewesiceras mantelli Wright and Wright, 1951
(Pl. 1, Figs 13–16)

1951. *Lewesiceras mantelli* Wright and Wright, p. 20.

2019. *Lewesiceras mantelli* Wright and Wright, 1951; Kennedy, p. 57, pl. 13, figs 8–15, 18–26; pl. 14, figs 1–13; pl. 15, figs 1–5; pl. 16, figs 1–5; pl. 26, figs 3–5; text-figs 29–33; 34d–f (with synonymy).

2019. *Lewesiceras mantelli* Wright and Wright, 1951; Kennedy and Kaplan, p. 39, pl. 6, figs 1–13; pl. 7, figs 1, 2, 4–7, 11, 16; pl. 16; text-fig. 17a–c.

TYPE: The holotype, by monotypy, is BMNH C88587, the original of Sharpe (1853, pl. 10, fig. 3), from “the Middle Chalk of Wiltshire”. It was refigured, most recently, by Kennedy (2019, pl. 13, figs 18–20).

MATERIAL: OUMNH PAL-KY.6169, from Meshekli; OUMNH PAL-KY.3870, from the foreshore of the Amu Darya, 20 m north of Meshekli, both from

the upper part of the Kendyktyube Formation, Upper Turonian.

DESCRIPTION: OUMNH PAL-KY.6169 (Pl. 1, Figs 13–16) is a nucleus 50 mm in diameter retaining recrystallized shell. Coiling is involute, the umbilicus comprising 26% approximately of the diameter, of moderate depth, with a flattened umbilical wall and broadly rounded umbilical shoulder. The whorl section is slightly compressed, with a whorl breadth to height ratio of 0.86, the flanks feebly convex, the ventrolateral shoulders broadly rounded, the venter feebly convex. On the penultimate whorl, an estimated 10 strong conical/bullate tubercles perch on the umbilical shoulder. On the outer whorl, the bullae weaken progressively with increasing diameter. They give rise to straight prorsiradiate ribs that sweep forwards over the outermost flanks and ventrolateral shoulders, where they are concave, weaken, and cross the venter in a very feeble convexity. Up to two ribs intercalate between successive primaries; they arise on the outer flank.

OUMNH PAL-KY.3870 (Pl. 1, Figs 15, 16) is a larger, crushed individual with a maximum preserved diameter of 70 mm. The pattern of ribbing is as in the previous specimen, with blunt umbilical bullae; there is a well-developed constriction at the mid-point of the adapertural half of the outer whorl.

DISCUSSION: See Kennedy (2019, p. 57) and Kennedy and Kaplan (2019, p. 39). Specimens assigned to *Lewesiceras asiaticum* Ilyin, 1959 (p. 248, pl. 7, figs 1, 2; pl. 8, figs 1, 2; text-fig. 10) have the same style of ribbing and tuberculation as specimens from the Upper Turonian *Subprionocyclus neptuni* Zone Chalk Rock of southern England described by Kennedy (2019), and is a clear synonym. It was dated as Coniacian by Ilyin.

OCCURRENCE: Upper Turonian, *Subprionocyclus neptuni* and *Prionocyclus germari* zones, Northern Ireland, southern and eastern England, France, Belgium, Germany, Poland, the Czech Republic, Ukraine (Crimea), Kazakhstan, Uzbekistan and, possibly, Austria.

Family Muniericeratidae Wright, 1952
Genus *Tragodesmoceras* Spath, 1922

TYPE SPECIES: *Desmoceras clypealoides* Leonhard, 1897 (p. 57, pl. 6, fig. 2), by the original designation of Spath (1922, p. 127).

Tragodesmoceras cf. *mauryae* Kennedy and Wright,
1981
(Pl. 1, Figs 10–12)

1981. *Tragodesmoceras mauryae* Kennedy and Wright, p. 502, text-fig. 3a–d.

TYPE: The holotype, by original designation, is MNHN d'Orbigny Collection 6787a, from the Middle Turonian *Collignoniceras woollgari* Zone fauna of the Tuffeau de Touraine of Bourré, Loir-et-Cher, France, the original of Kennedy and Wright (1981, p. 502, text-fig. 3).

MATERIAL: OUMNH PAL-KY.6119, collected *ex situ*, Beshtyube Formation, Lower Turonian, Kosh-tyube.

DESCRIPTION: OUMNH PAL-KY.6119 is a 90° whorl sector of an internal mould, in part body chamber, the maximum preserved whorl height 33 mm. Coiling is moderately involute, the umbilicus shallow, with a flattened wall and broadly rounded umbilical shoulder. The whorl section is compressed, with a whorl breadth to height ratio of 0.67, the cross-section ovoid, the greatest breadth low on the feebly convex flanks, the ventrolateral shoulders broadly rounded, the venter feebly convex. Primary ribs arise on the umbilical wall and strengthen across the umbilical shoulder without developing into bullae. They are low, feebly rursiradiate across the flanks, strengthening on the ventrolateral shoulders and venter, which they cross in a feeble convexity. Two ribs intercalate between successive primaries, arising around mid-flank and strengthening progressively to match the primaries on ventrolateral shoulders and venter.

DISCUSSION: The fragment compares well with the silicone cast taken from the dorsum of the outer whorl of the holotype, figured by Kennedy and Wright (1981, text-fig. 3a, b), who discuss differences from other species referred to the genus.

OCCURRENCE: As for material.

Superfamily Hoplitioidea H. Douvillé, 1890
Family Placenticeratidae Hyatt, 1900
Genus *Placenticer* Meek, 1876

TYPE SPECIES: *Ammonites placenta* DeKay, 1828, p. 278, by the original designation of Meek (1876, p. 462).

Placenticer *kharesmense* (Lahusen, 1884)
(Pl. 2; Pl. 3, Figs 4–8; Pls 4, 5; Text-fig. 2)

1884. *Ammonites Kharemsensis* Lahusen, p. 134, pl. 2; pl. 3, fig. 1.

1916b. *Placenticer* *kharesmense* Lahusen, 1884; Arkhangelsky, p. 40, pl. 6, fig. 5; pl. 7, fig. 1; text-figs 11–14.

1907. *Placenticer* *kharasmense* Romanofsky, 1884; Vredenberg, p. 115.

1925. *P. [lacenticer* *kharesmense* Lahusen in Romanofsky; Diener, p. 186.

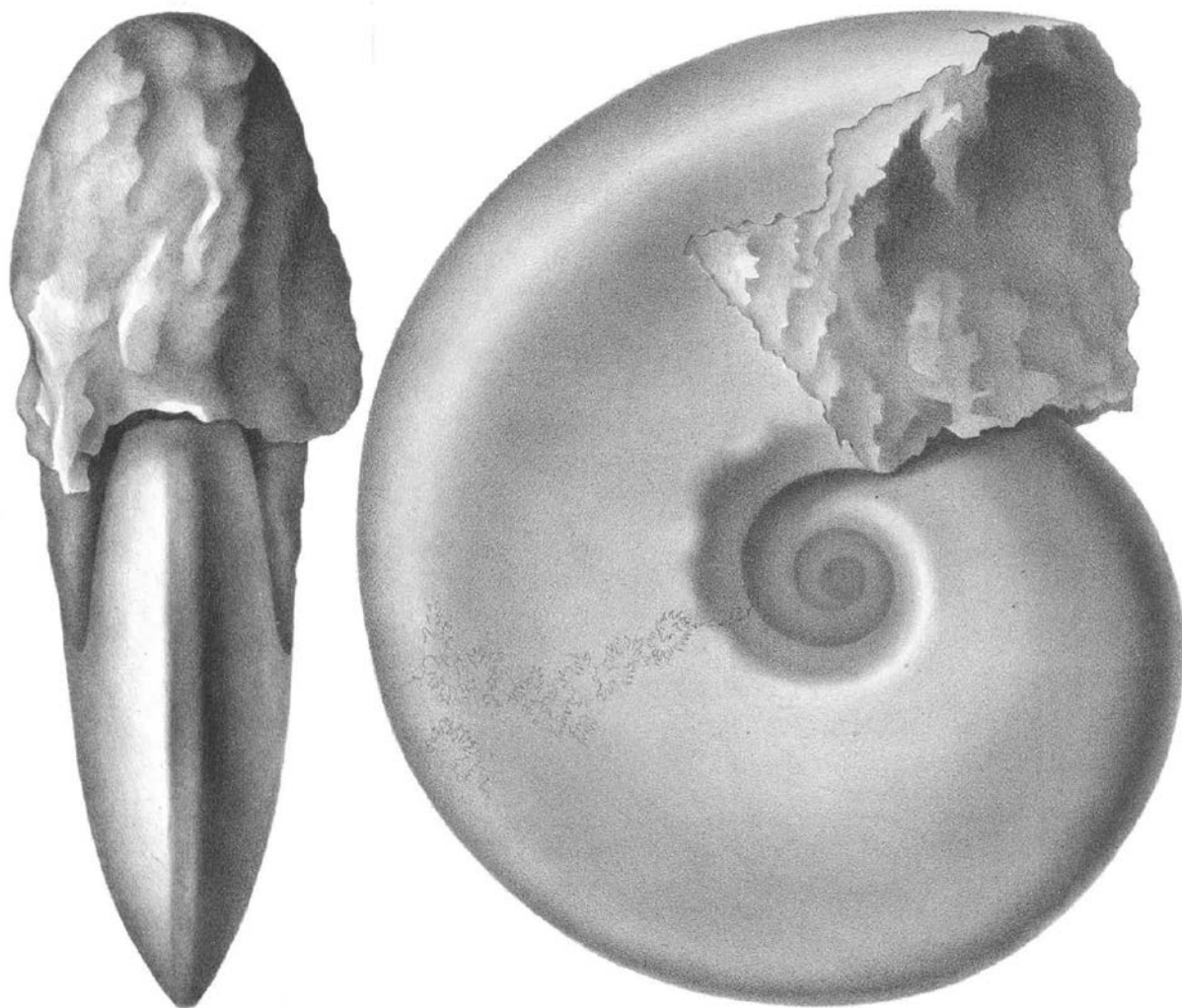
1989. *Placenticer* *kharesmense* (Lahusen, 1884); Klingler and Kennedy, p. 386.

2020. *Proplacenticer* *kharesmense* (Lahusen), 1884; Ilyin, p. 40, pl. 10, figs 1–3; text-fig. 18.

TYPE: The holotype, by monotypy, is the original of Lahusen (1884, p. 134, pl. 2; pl. 3, fig. 1; see Text-fig. 2 herein), from Beshtyube.

MATERIAL: OUMNH PAL-KY.6074–6086, from the Beshtyube Formation, Lower Turonian, Besh-tyube.

DESCRIPTION: Lahusen's original figures are reproduced here as Text-fig. 2. The holotype is a large individual; Lahusen gives the diameter as 420 mm. Parts of two, possibly three interfering sutures are shown, suggesting the specimen may be an adult. If these are indeed the final septa, at a diameter of 330 mm approximately, then the specimen retains approximately 180° of body chamber. Coiling is involute, the small, shallow umbilicus comprising 23% approximately of the diameter. The umbilical wall is flattened and outward-inclined. On the phragmocone, the whorl breadth to height ratio appears to be around 0.64, the greatest breadth at the umbilical shoulder, the flanks feebly convex, the middle and outer flanks converging to narrowly rounded ventrolateral shoulders, the venter apparently feebly concave at the beginning of the outer whorl, but flattening thereafter. The figure of the apertural view shows the whorl section at the largest preserved diameter to be compressed, with a whorl breadth to height ratio of an estimated 0.44, the umbilical shoulder broadly rounded, the flanks feebly convex, and converging to broadly rounded ventrolateral shoulders and a flattened venter. The phragmocone is smooth. The body chamber bears low bullae, perched on the umbilical shoulder, of which only the adapical 90° sector, with three, and possibly part of a fourth bulla preserved. The figure of the external suture (Lahusen 1884, pl. 2, fig. 1a) includes seven, possibly eight lobes.



Text-fig. 2. *Placenticerus kharesmense* (Lahusen, 1884). Copies of Lahusen's original figures (1884, pl. 2; pl. 3, fig. 1) of the holotype, from Beshtyube in western Uzbekistan. The original specimen was stated to be 420 mm in diameter.

What is interpreted as the smallest specimen attributable to the species in the present collection is OUMNH PAL-KY.6085 (Pl. 3, Figs 4, 5), a 120° whorl fragment with a maximum preserved whorl height of 37 mm. Coiling is very involute, the umbilicus very shallow, the umbilical wall flattened and outward-inclined, the umbilical shoulder broadly rounded. The whorl section is very compressed, the whorl breadth to height ratio 0.43, the greatest breadth just outside the umbilical shoulder. The inner flanks are feebly convex, the outer flanks flattened and convergent, the ventrolateral shoulders very narrowly rounded, the very narrow venter flattened. There are five low, relatively broad, widely separated concave ribs on the outer flank of the fragment.

The remaining specimens, with one exception, are wholly septate.

OUMNH PAL-KY.6074 (Pl. 2) has a maximum preserved diameter of 170 mm. The dimensions of the inner whorls are:

| | D | Wb | Wh | Wb:Wh | U |
|----------------------|----------------|----------|----------------|-------|----------------|
| OUMNH PAL-KY.6074 at | 138.0 (100) | — (—) | 73.1 (53.0) | — | 18.0 (13.0) |

There is no ornament, and the ventrolateral shoulders become progressively blunter as size increases.

OUMNH PAL-KY.6083 (Pl. 3, Figs 6, 7) is a 120° whorl fragment with a maximum preserved whorl height of 55 mm, the whorl breadth to height ratio 0.59. The flanks are smooth, apart from two small,

widely separated umbilical bullae. And, in contrast to the previous specimen, there are small, blunt ventral clavi that alternate in position on either side of the venter.

OUMNH PAL-KY.6086 (Pl.5) was over 300 mm in diameter when complete, and is septate to 200 mm diameter; there is a single well-preserved umbilical bulla on the outer whorl.

The largest phragmocone fragment, OUMNH PAL-KY.6076 (Pl. 4), is over 220 mm in diameter, with a maximum preserved whorl height of 108 mm and a whorl breadth to height ratio of 0.6 approximately. There is one well-preserved umbilical bulla towards the adapertural end of the fragment, and a possible second at the apertural end.

DISCUSSION: The present material is problematic. Where large populations of *Placenticer* are known, they show wide intraspecific variation. The best known are the Upper Cenomanian to Upper Turonian *Placenticer* *cumminsi* Cragin, 1893 (Kennedy 1988, p. 26, pl. 1, figs 29–36; pl. 3, figs 10–15; text-figs 9, 10a–c, g, 11c, 12–19), and the Coniacian *Placenticer* *kaffrarium* Etheridge, 1904 (Klinger and Kennedy 1989, p. 268, text-figs 9–14a, 19–20, 22–99), where individuals that lack ventral clavi occur with those in which they are developed at varying ontogenetic stages, as are inner ventrolateral and umbilical tubercles. It is on the basis of such intraspecific variation in *Placenticer* species that we regard co-occurring individuals both with (Arkhangelsky 1916b, pl. 6, fig. 5; pl. 7, fig. 1; see Pl. 3, Figs 6, 7 herein) and without umbilical bullae and ventral clavi (Pl. 2) as members of a variable *kharesmense*.

The relationship of *kharesmense* to *cumminsi* is unclear. Of the present specimens of *kharesmense*, similar variants occur in *cumminsi*. OUMNH PAL-KY.6085 (Pl. 3, Figs 4, 5) is comparable to the originals of Kennedy (1988, pl. 1, figs 33–36); OUMNH PAL-KY.6074 (Pl. 2) to the albeit smaller phragmocone shown in Kennedy (1988, text-fig. 15); OUMNH PAL-KY.6083 (Pl. 3, Figs 6, 7) to the original of Kennedy (1988, text-fig. 12e, f). The specimen figured by Arkhangelsky (1916b, pl. 6, fig. 5; pl. 7, fig. 1) is illustrated reduced by two-thirds, and has a diameter calculated as just over 200 mm. It has ventral clavi, and small, conical, widely separated umbilical tubercles, corresponding to the original of Kennedy (1988, text-fig. 12e, f), which is 120 mm in diameter. The two differ, however, in adult size: specimens of *cumminsi* interpreted as microconchs range from 120–165 mm in diameter, specimens interpreted as macroconchs range from 200–240 mm

in diameter, whereas the holotype of *kharesmense* is 420 mm in diameter: 75% larger. The two are kept separate here, with no great conviction.

OCCURRENCE: Lower Turonian of western Uzbekistan.

Placenticer *crassum* Ilyin, 2000

(Pl. 3, Figs 1–3; Pl. 6, Figs 1–13; Pl. 7, Figs 9–13)

2000. *Placenticer* *crassum* Ilyin, p. 51, pl. 18, fig. 1; pl. 19, figs 1–5; pl. 20, fig. 4; text-fig. 26.

TYPE: The holotype, by original designation is no. 110/178, the original of Ilyin (2000, pl. 19, fig. 3), from his *Lewesicer* *asiaticum* Zone, regarded as Coniacian by him, but Upper Turonian herein, of Koshabulak on the Amu Darya.

MATERIAL: OUMNH PAL-KY.3869, from the banks of the Amu Darya 20 m north of Meshekli; OUMNH PAL-KY.6131–6187, from an 8 m interval in the upper part of the Kendyktyube Formation, Upper Turonian, Meshekli.

DESCRIPTION: There are three successive ontogenetic stages represented by the present material. The first ontogenetic stage is illustrated by OUMNH PAL-KY.6135 and 6150. OUMNH PAL-KY.6135 (Pl. 6, Figs 3–5) is a phragmocone 58 mm in diameter, retaining well-preserved recrystallized shell. Coiling is involute, the umbilicus comprising 23% of the diameter, very shallow, with a low, flattened, outward-inclined wall. The umbilical shoulder is narrowly rounded, the whorl section very compressed, with feebly convex inner flanks and flattened, convergent outer flanks. The ventrolateral shoulders are sharp, the narrow venter concave between. Seven to eight low, broad, feeble prorsiradiate ribs per half whorl are present on the adapical half of the outer whorl, and link to much stronger concave ribs on the outer flank that weaken and efface before reaching the ventrolateral shoulder. OUMNH PAL-KY.6150 (Pl. 6, Figs 10, 11), 72.6 mm diameter, has only faint traces of concave ribs on the outer flank. Stronger ornament of umbilical bullae, ribs and ventral clavi characterise the second stage. Thus OUMNH PAL-KY.6149 (Pl. 6, Figs 1, 2) is a phragmocone fragment with the following dimensions:

| | D | Wb | Wh | Wb:Wh | U |
|-------------------|---------------|----------------|----------------|-------|----------------|
| OUMNH PAL-KY.6149 | 72.8 (100) | 20.0 (27.4) | 35.3 (48.5) | 0.57 | 14.0 (19.2) |

The narrow venter has sharp shoulders at the adapical end of the outer half whorl, the venter slightly concave between; at the adapertural end the shoulders are rounded, and the venter very feebly convex. There are numerous weak ventral clavi, and two very widely separated conical umbilical tubercles on the 180° whorl fragment. OUMNH PAL-KY.3869 (Pl. 7, Figs 9–11) is a phragmocone 73 mm in diameter. At the adapical end of the outer whorl, the narrow venter is sulcate, with narrowly rounded ventrolateral shoulders, bearing clearly differentiated clavi from 180° beyond the adapical end of the outer whorl onwards that extend to the greatest preserved diameter, where they are beginning to efface. There are well-developed widely separated umbilical bullae and low, broad, widely separated ribs on the outer flank, some developing into low, rounded outer lateral tubercles. OUMNH PAL-KY.6162 (Pl. 6, Figs 12, 13), a phragmocone, has four conical umbilical bullae on the adapertural half whorl that give rise to pairs of low, broad, near-obsolete ribs that strengthen into low conical swellings on the outer flank, with the feeblest of low, broad ribs extending onto the outermost flanks, and weak ventral clavi. The dimensions are as follows:

| | D | Wb | Wh | Wb:Wh | U |
|-------------------|---------------|----------|----------------|-------|----------------|
| OUMNH PAL-KY.6162 | 81.2 (100) | — (—) | 38.3 (47.2) | — | 13.5 (16.6) |

OUMNH PAL-KY.6158 (Pl. 6, Figs 8, 9), also a phragmocone, has the following dimensions:

| | D | Wb | Wh | Wb:Wh | U |
|-------------------|---------------|----------------|----------------|-------|----------------|
| OUMNH PAL-KY.6158 | 80.0 (100) | 26.1 (32.6) | 39.3 (49.1) | 0.66 | 14.0 (17.5) |

There are widely separated umbilical bullae, as in the previous specimen, that give rise to low, broad, very widely separated ribs, three or four per half whorl, on the outer flanks, and weak ventral clavi on the adapical end of the outer whorl.

The third growth stage is characterised by the broadening of the venter, rounding of the ventrolateral shoulders and an absence of ventral clavi. OUMNH PAL-KY.6183 (Pl. 3, Figs 2, 3) is a 120° sector of body chamber retaining recrystallized shell with a maximum preserved whorl height of 40.6 mm and a whorl breadth to height ratio of 0.8. The umbilical wall is flattened and outward-inclined, the umbilical shoulder broadly rounded, the inner flank region feebly convex, the outer flanks converging to a broad, rounded, arched venter. Two large, blunt umbilical bullae are present. OUMNH PAL-KY.6131 (Pl. 7, Figs 12, 13) is a body chamber 105 mm in diameter with small ventral clavi at the adapical end, thereafter

lost, the ventrolateral shoulders becoming rounded, the venter broadening and flattening. The largest fragment, OUMNH PAL-KY.6168 (Pl. 3, Fig. 1) is part of a phragmocone, with a maximum preserved whorl height of 64.8 mm, and a whorl breadth to height ratio of 0.66, the inner flanks feebly convex, the outer flattened and convergent, the ventrolateral shoulders broadly rounded, the venter relatively broad, and very feebly convex. There is no ornament.

The typically placenticeratid suture (Pl. 6, Fig. 8) follows a straight line across most of the flanks, projecting forwards on the outermost part.

DISCUSSION: The successive ontogenetic stages, notably the second stage with umbilical bullae, flank ribs and outer lateral tubercles, distinguishes *cras-sum* from other Turonian species such as *kharensense* and *cumminsi*, discussed above; *Placenticeras kutuzovae* (Ilyin, 1975) (p. 164, pl. 29, fig. 3; pl. 34, fig. 8; see also Ilyin 2000, p. 37, pl. 8, fig. 7; pl. 9, Figs 2–5; text-fig. 8) is known from small specimens only with umbilical bullae that give rise to pairs of falcoid ribs that terminate in well-developed ventral clavi; *Placenticeras arkhangelskii* (Ilyin, 1959) (p. 191; see Ilyin 2000, p. 41, pl. 10, fig. 4, pl. 11, fig. 3; text-fig. 19) is also known from small specimens only, is very compressed, lacks ventral clavi, and has weak falcoid ribbing.

It is tempting to regard small specimens with body chambers in the third ontogenetic stage (Pl. 3, Figs 2, 3; Pl. 7, Figs 12, 13) as possible microconchs, and phragmocones of comparable size and larger (Pl. 3, Fig. 1) as macroconchs, but it is unclear if the small individuals with stage three morphology are adult.

OCCURRENCE: Upper Turonian, Meshekli.

Placenticeras semiornatum (d'Orbigny, 1850)
(Pl. 7, Figs 1, 2)

1850. *Ammonites semiornatus* d'Orbigny, p. 212.

1955a. *Ammonites (Placenticeras) semiornatus* d'Orbigny; Sornay, Figs 1–3.

1984. *Placenticeras semiornatum* (d'Orbigny, 1850); Kennedy, p. 44, pl. 1, Figs 4–6; pl. 4, Figs 3–5, 7, 8; text-Figs 13b, 29d.

1989. *Placenticeras semiornatum* (d'Orbigny, 1850); Klinger and Kennedy, p. 388.

TYPES: Two specimens of *Ammonites semiornatus* are listed in the catalogue of the d'Orbigny Collection as no. 7179, the locality given as Tours. Sornay (1955a) designated the more complete individual lectotype;

they were refigured by Kennedy (1984), the lectotype as pl. 4, figs 7, 8; the paralectotype fragment as pl. 4, figs 3–5. The horizon of the types is uncertain, but probably Santonian.

MATERIAL: OUMNH PAL-KY.3867, from the Coniacian–Santonian boundary, lower part of the Laulau Formation, north of Meshekli.

DIMENSIONS:

| | D | Wb | Wh | Wb:Wh | U |
|-------------------|---------------|----------------|----------------|-------|----------------|
| OUMNH PAL-KY.3867 | 63.6 (100) | 21.9 (34.4) | 31.9 (50.2) | 0.69 | 10.8 (17.0) |

DESCRIPTION: The specimen is a wholly septate internal mould. Coiling is very involute, the shallow umbilicus comprising 17% of the diameter, the umbilical wall flattened and outward-inclined, the umbilical shoulder narrowly rounded and blunt. The whorl section is compressed, the whorl breadth to height ratio 0.69; the inner flanks are very feebly convex, the outer flanks flattened and convergent. The ventrolateral shoulders are sharp, the narrow venter concave between at the adapical end of the outer whorl; at the adapertural end the ventrolateral shoulders are narrowly rounded, the venter flattened. There are feeble concave ribs on the outer flank where the surface of the mould is well-preserved; they are linked to long, low clavi, perched on the ventrolateral shoulders.

DISCUSSION: The specimen differs in no significant respects from the phragmocone of the holotype at the same diameter. For discussion see Kennedy (1984, p. 44).

OCCURRENCE: As for types; the present specimen is from around the Coniacian–Santonian boundary, occurring 3 meters below the occurrence of undoubted Santonian *Placenticerias polyopsis*.

Placenticerias polyopsis (Dujardin, 1837) (Pl. 8, Figs 1–11; Text-fig. 3)

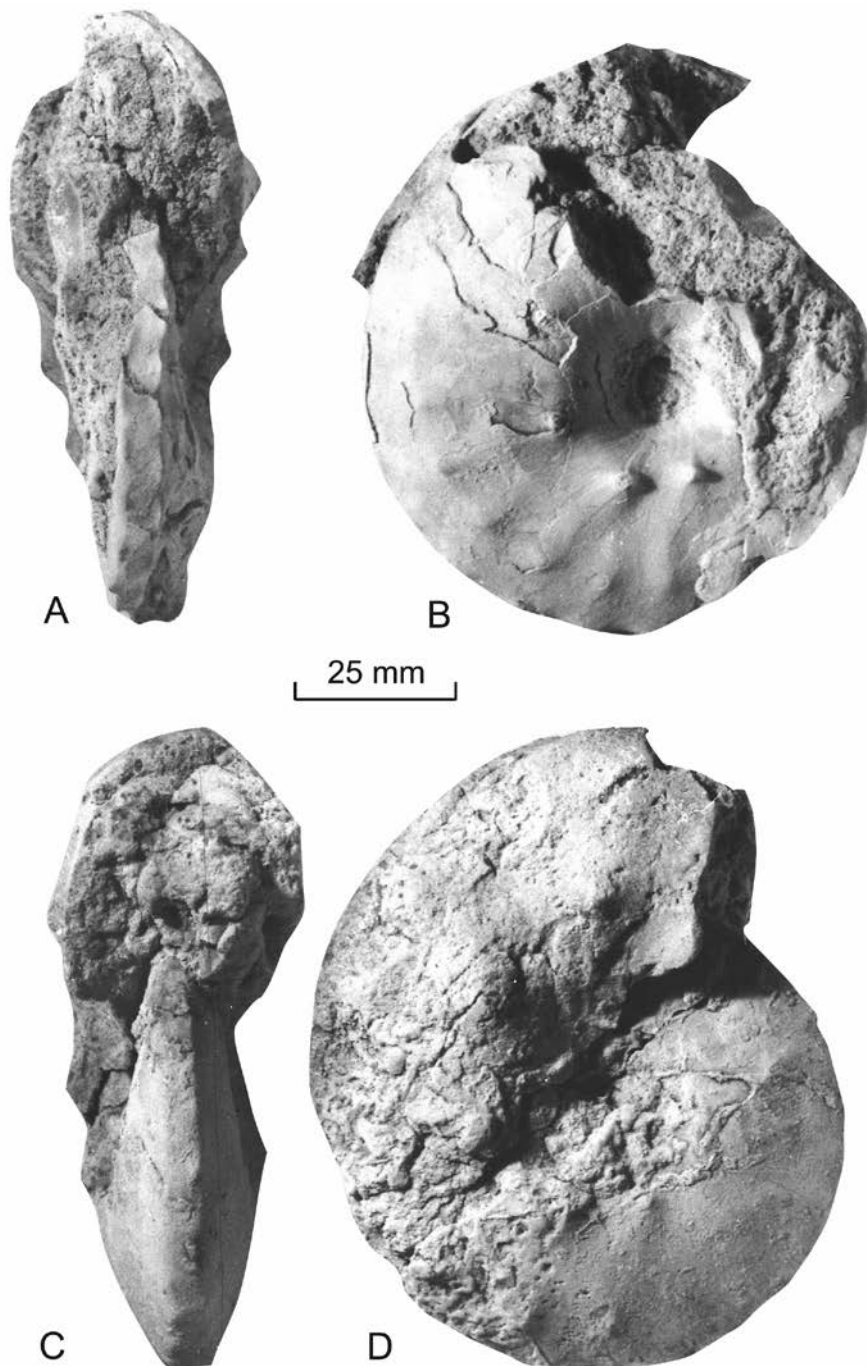
1837. *Ammonites polyopsis* Dujardin, p. 232, pl. 17, fig. 12.
1916b. *Placenticerias kysylcumense* Arkhangelsky, p. 45, pl. 7, figs 4–7; text-fig. 16.
1925. *Placenticerias kysylcumense* Archangelsskij; Diener, p. 186.
1975. *Stantonoceras polyopsis amudariense* Ilyin, p. 171, pl. 32, fig. 3; pl. 35, fig. 14.
1983. *Placenticerias polyopsis* (Dujardin, 1837); Kennedy and Wright, p. 856, pls 85–87; text-figs 1–4 (with synonymy).

1989. *Placenticerias kysylcumense* Archanguelski; Klinger and Kennedy, p. 386.
1989. *Placenticerias polyopsis amudariense* (Iljin, 1975); Klinger and Kennedy, p. 387.
1995. *Placenticerias polyopsis* (Dujardin, 1837); Kennedy in Kennedy *et al.*, p. 410, pl. 17, figs 2–7, 9, 10; pl. 18, figs 7–12; text-fig. 21 (with additional synonymy).
2000. *Stantonoceras kysylcumense* (Arkhangelsky, 1916); Ilyin, p. 55, pl. 21, fig. 2; pl. 22, figs 1, 2; text-fig. 30.
2000. *Stantonoceras polyopsis amudariense* Iljin, 1975; Ilyin, p. 56, pl. 34, figs 4, 5; text-fig. 31.
2007. *Stantonoceras kysylcumense* (Arkhangelsky, 1916); Kim *et al.*, p. 125, pl. 64, fig. 3.
2017. *Placenticerias polyopsis* (Dujardin, 1837); Summesberger and Kennedy in Summesberger *et al.*, p. 182, pl. 9, figs 3, 4, 6; pl. 10, figs 1, 6 [with additional synonymy].

TYPES: Dujardin (1837, pl. 17, fig. 12) illustrated two specimens; the original of his fig. 12a, a juvenile macroconch, was designated lectotype by Kennedy and Wright (1983, p. 856), who reproduced the original figures as their text-fig. 1. The specimens, from the ‘Craie Tufau’ of Touraine in France, have not been traced.

MATERIAL: OUMNH PAL-KY.3868, from the Laulau Formation, 3 m above the base, foreshore of the Amu Darya 20 m north of Meshekli. OUMNH PAL-KY.6188–6192, 6195–6198, from 8 m above the base of the Laulau Formation, Meshekli. OUMNH PAL-KY.6193, 6194, 6200, from the Laulau Formation, Dzharakuduk, the locality that yielded the type material of Arkhangelsky’s *Placenticerias kysylcumense* (1916b, p. 45, pl. 7, figs 4–7).

DESCRIPTION: Specimens range from 48–93 mm in diameter, and most retain recrystallized shell. The largest wholly septate specimen, OUMNH PAL-KY.6198 (Pl. 8, Figs 5–7), is an estimated 60 mm in diameter. Other specimens retain some body chamber. Coiling is very involute, the umbilicus comprising around 15% of the diameter, of moderate depth, with a flattened, outward-inclined wall and broadly rounded umbilical shoulder. There are both gracile and robust variants. OUMNH PAL-KY.6191 (Text-fig. 3C, D), 86 mm in diameter, is a gracile variant. It has an intercostal whorl breadth to height ratio of 0.49 at the beginning of the outer whorl, the whorl section broadening markedly as size increases. There are feeble umbilicolateral bullae that strengthen markedly as size increases, with low, broad, concave ribs on the outer flank that link to blunt ventral clavi,



Text-fig. 3. *Placenticerias polyopsis* (Dujardin, 1837). A, B – OUMNH PAL-KY.6192; C, D – OUMNH PAL-KY.6191; both specimens are from 8 m above the base of the Laulau Formation, Santonian, Meshekli.

with additional clavi intercalating between, the clavi alternating in position on either side of the venter. There are weak inner ventrolateral tubercles on some of the ribs. OUMNH PAL-KY.6190 (Pl. 8, Figs 2–4) is a juvenile robust variant with a maximum pre-

served diameter of 58 mm. The whorl section broadens progressively; there are massive conical umbilicolateral tubercles, four per half whorl; they give rise to pairs of low, broad, feeble ribs that link to strong, blunt rounded-clavate inner ventrolateral tubercles,

with weaker ventral clavi that alternate in position on either side of the venter. The distinctive pattern of whorls that become increasingly massive as whorl height increases is well shown by specimens such as OUMNH PAL-KY.3868 (Pl. 8, Figs 9–11), 92 mm in diameter. OUMNH PAL-KY.6192, 82 mm in diameter (Text-fig. 3A, B) has a lower rate of increase of whorl inflation and weaker but still progressively strengthening flank ornament.

The sutures are not seen.

DISCUSSION: The present material compares well with that from France and Austria documented by previous authors (Kennedy and Wright 1983; Kennedy in Kennedy *et al.* 1995; Summesberger and Kennedy in Summesberger *et al.* 2017). *Stantonoceras polyopsis amudariense* Ilyin, 1975 (p. 171, pl. 32, fig. 3; pl. 35, fig. 14) falls within the range of variation of the species as here interpreted.

OCCURRENCE: The species ranges throughout most, if not all of the Santonian. There are records from Touraine, Aquitaine, the Corbières, and the Beausset Basin (Var) in France, north-western Spain, northern Germany, the Gosau Group in the Northern Calcareous Alps, Austria, and western Uzbekistan.

Placenticerias sp. juv., cf. *cumminsi* Cragin, 1893
(Pl. 7, Figs 3–8)

compare:

1893. *Placenticerias syrtalis* Morton var. *cumminsi* Cragin, p. 237.

1988. *Placenticerias cumminsi* Cragin, 1893; Kennedy, p. 26, pl. 1, figs 29–36; pl. 3, figs 10–15; text-figs 9, 10a, c, g, 11c, 12–19 (with synonymy).

MATERIAL: OUMNH PAL-KY.6224, 6225, 6227, from 3–4 m above the base of the Uchkuduk Formation, Upper Cenomanian, Dzharakuduk.

DESCRIPTION: OUMNH PAL-KY.6225 (Pl. 7, Figs 3–5) is an almost wholly septate juvenile with the following dimensions:

| | D | Wb | Wh | Wb:Wh | U |
|-------------------|---------------|----------------|----------------|-------|---------------|
| OUMNH PAL-KY.6225 | 54.3 (100) | 14.6 (26.9) | 28.5 (52.5) | 0.51 | 9.1 (16.8) |

Coiling is very involute, the tiny, shallow umbilicus comprising 16.8% of the diameter, the umbilical wall flattened and outward-inclined with a quite broadly rounded umbilical shoulder. The whorl section is very compressed, with a whorl breadth to

height ratio of 0.51, the greatest breadth just outside the umbilical shoulder, the inner flanks very feebly convex, the outer flanks flattened and convergent, the ventrolateral shoulders very narrowly rounded, the venter sulcate between. Widely separated low, broad, concave ribs are present on the adapertural part of the outer whorl; the adapical part appears to have been smooth.

OUMNH PAL-KY.6224 (Pl. 7, Figs 6–8) has the following dimensions:

| | D | Wb | Wh | Wb:Wh | U |
|-------------------|---------------|----------------|----------------|-------|----------|
| OUMNH PAL-KY.6224 | 59.8 (100) | 16.8 (28.0) | 34.6 (57.9) | 0.49 | – (–) |

The relative proportions and whorl shape compare well with those of the previous specimen; it appears to lack ornament. OUMNH PAL-KY.6227 is a wholly septate fragmentary internal mould of the outermost flank and ventrolateral shoulder of one side and the venter of a much larger individual perhaps 100–110 mm in diameter when complete. The narrow venter is flattened with numerous well-developed ventral clavi.

DISCUSSION: These fragments are compared to *cumminsi* on the basis of their resemblance to contemporaneous individuals from the Britton Formation of north-central Texas; OUMNH PAL-KY.6225 finds a match with the original of Kennedy (1988, pl. 1, figs 35, 36); OUMNH PAL-KY.6227 with the original of Kennedy (1988, text-fig. 12e, f).

OCCURRENCE: As for material.

Superfamily Acanthoceratoidea de Grossouvre, 1894

Family Acanthoceratidae de Grossouvre, 1894

Subfamily Acanthoceratinae de Grossouvre, 1894

Genus *Watinoceras* Warren, 1930

(= *Arkhangelskiceras* Ilyin, 1958, p. 425)

TYPE SPECIES: *Watinoceras reesidei* Warren, 1930 (p. 67, pl. 3, fig. 2; pl. 4, figs 9–12), by the original designation of Warren (1930, p. 66); = *Acanthoceras amudariense* Arkhangelsky, 1916b (p. 48, pl. 7, figs 8–13; non var. *horridum* pl. 8, figs 8–10, 14, 15).

Watinoceras amudariense (Arkhangelsky, 1916b)
(Pl. 1, Figs 4–7)

1916b. *Acanthoceras amudariense* Arkhangelsky, p. 48 (pars), pl. 7, figs 8–13; non var. *horridum*, pl. 8, figs 8–10, 13, 14.

1981. *Watinoceras amudariense* (Arkhangelsky, 1916); Wright and Kennedy, p. 51, pl. 10, figs 6, 14; text-figs 19n, q (with synonymy).
1988. *Watinoceras reesidei* Warren; Cobban, p. 5, pl. 1, figs 1–26; text-fig. 3 (with synonymy).
2019. *Watinoceras reesidei* Warren, 1930; Kennedy and Kaplan, p. 47, pl. 1, fig. 7.
- ?2020. *Watinoceras* sp.; Wilmsen *et al.*, p. 9, text-fig. 5c.

TYPE: The lectotype, by the subsequent designation of Wright and Kennedy (1981, p. 51) is the original of Arkhangelsky (1916b, pl. 7, fig. 12; pl. 7, fig. 9 is the ventral view of the same specimen). Arkhangelsky's (1916b) pl. 7, figs 8 and 13 are views of the same paralectotype; pl. 7, figs 10 and 11 are two further specimens, and a further 55 specimens are mentioned in the original publication, all from Beshtyube.

MATERIAL: OUMNH PAL-KY.6115, 6116, 6117a–b; all are from the Beshtyube Formation, collected *ex situ*, Lower Turonian, Koshtyube.

DESCRIPTION: OUMNH PAL-KY.6117a–b are internal (Pl. 1, Figs 4, 5) and external mould of a 180° whorl sector with a maximum preserved diameter of 24.3 mm. Coiling is very evolute, the shallow umbilicus comprising 32% of the diameter, the umbilical wall low and flattened, the umbilical shoulder broadly rounded. The intercostal whorl section is compressed, with feebly convex subparallel flanks, broadly rounded ventrolateral shoulders and a feebly convex venter. The whorl breadth to height ratio is 0.8 approximately. There are 14 primary ribs on the fragment. They arise at the umbilical seam, and strengthen across the umbilical wall and shoulder without developing into a bulla. They are straight and feebly prorsiradiate on the inner and middle flanks, flexing forwards across the outermost flanks and ventrolateral shoulders, linking to feeble to obsolete ventral clavi, linked across the venter by a transverse rib. Additional ribs intercalate; some are long; others are very short, arising on the ventrolateral shoulder. All have a comparable ventral development as the primaries.

OUMNH PAL-KY.6115 (Pl. 1, Figs 6, 7) is a larger, 120° whorl sector, with a maximum preserved whorl height of 12.5 mm, and an estimated diameter of over 30 mm. The pattern of ribbing is much as in the previous specimen, but at the greatest preserved whorl height, there are suggestions of a feeble inner ventrolateral tubercle.

DISCUSSION: Wright and Kennedy (1981, p. 52) regarded *Watinoceras reesidei* Warren, 1930 (p. 67,

pl. 3, fig. 2; pl. 4, figs 9–12) as a synonym of *amudariense*. Cobban (1988, p. 6) kept the species separate, remarking that although the inner whorls of the two species were indistinguishable, the body chambers were different. He noted that “Arkhangelskii observed that the venter is narrow and flat on the early whorls but, as the shell enlarges, the venter becomes more rounded, and the ribs cross it in a forwardly directed chevron. Adult venters like that illustrated by Arkhangelskii (1916, pl. 7, fig. 9) have not been observed on any American species of *Watinoceras*. In addition, *W. amudariense* attains much larger sizes than *W. reesidei*. One of the type specimens of Arkhangelskii (1916, p. 49) is 53 mm in diameter, and Il'in (1957, fig. 1) illustrated a specimen that may be still larger.” However, the ventral view referred to by Cobban (Arkhangelsky 1916b, pl. 7, fig. 9) is problematic. The ribs pass straight across the venter on the adapicalmost few ribs visible, the succeeding ribs are interrupted by an irregularity, the ‘chevron’ initially asymmetric, and possibly absent on the adaperturalmost visible rib. Furthermore, Arkhangelsky's 53 mm diameter specimen has not been figured. The relationship between these species can only be resolved by a re-examination of Arkhangelsky's types.

Watinoceras sp. of Wilmsen *et al.* (2020, p. 9, text-fig. 5c) from the Debarsu Formation of Central Iran may belong here (Markus Wilmsen, personal communication, 2023).

OCCURRENCE: Lower Turonian of western Uzbekistan, southern England, and, possibly, Central Iran. Specimens assigned to *W. reesidei* by authors are known from Alberta, north-eastern British Columbia in Canada, Montana in the United States Western Interior, and the Münsterland Basin in northern Germany.

Watinoceras coloradoense (Henderson, 1908)
(Pl. 1, Figs 1–3)

1908. *Acanthoceras coloradoensis* Henderson, p. 259, pl. 13, figs 10, 11.
- 1916b. *Acanthoceras amudariense* var. *horridum* Arkhangelsky, p. 49, pl. 8, figs 8–10, 14, 15.
1981. *Watinoceras coloradoense praecursor* Wright and Kennedy, p. 53, pl. 10, figs 4, 8, 9, 11, 15, 17, 18; text-figs 19g, k.
1988. *Watinoceras coloradoense* (Henderson); Cobban, p. 7, pl. 2, figs 1–23; pl. 3, figs 4, 5; text-fig. 4 (with synonymy).
2007. *Watinoceras (Watinoceras) coloradoense* (Henderson, 1908); Kim *et al.*, pl. 60, figs 1–5.

2019. *Watinoceras coloradoense* (Henderson, 1908); Kennedy and Kaplan, p. 48, pl. 18, fig. 6; text-fig. 18c, d [with additional synonymy].

TYPE: The holotype, by original designation, is USNM 30877, the original of Henderson (1908, p. 259, pl. 13, figs 10, 11), from the Lower Turonian Greenhorn Limestone near Lyons, Boulder County, Colorado, in the United States Western Interior. It was refigured by Wright and Kennedy (1981, text-fig. 18e, f), and Kennedy and Kaplan (2019, text-fig. 18d).

MATERIAL: OUMNH PAL-KY.3872, from the Beshtyube Formation, Lower Turonian, Beshtyube. OUMNH PAL-KY.6166 comes from the same unit at Koshtyube.

DESCRIPTION: OUMNH PAL-KY.3872 (Pl. 1, Figs 1–3) is an internal mould of a 180° whorl sector with a maximum preserved diameter of 35 mm. The maximum preserved whorl height is 12.3 mm. The intercostal whorl section is rounded-rectangular, the costal section polygonal, with the greatest breadth at the inner ventrolateral tubercle. There are ten primary ribs on the fragment. Small bullae perch on the umbilical shoulder, and give rise to straight prorsiradiate ribs that strengthen across the flanks and link to strong inner ventrolateral bullae, linked by a strong, feebly prorsiradiate rib to a stronger outer ventrolateral clavus, the clavi linked across the venter by a strong, transverse rib. OUMNH PAL-KY.6166 is a small fragment that appears to belong to the present species, with well-developed inner and outer ventrolateral tubercles.

The outer whorl of the larger specimen figured by Arkhangelsky (1916b, pl. 8, figs 3, 9, 10) as his var. *horridum*, from Beshtyube, agrees well with the present specimen.

DISCUSSION: See Cobban (1988) for a comprehensive account of this species. Synonyms based on material from western Uzbekistan are *Acanthoceras amudariense* var. *horridum* Arkhangelsky, 1916b (p. 49, pl. 8, figs 8–10, 14, 15), and *Arkhangelskiceras costatum* Ilyin, 1959 (p. 212, pl. 4, fig. 2; pl. 5, fig. 1; text-fig. 6).

Watinoceras coloradoense praecursor Wright and Kennedy, 1981 (p. 53, pl. 10, figs 4, 8, 9, 11, 15, 17, 18; text-figs 19g, k) was distinguished from the nominate subspecies by its authors on the basis that “the fine-ribbed stage persists longer, the venter is broader, the inner two-thirds of the ribs is more recirradiate, the whorl section is higher and the coiling is more evolute.”

OCCURRENCE: Lower Turonian, Colorado, western Kansas, and north-eastern New Mexico in the United States Western Interior, western Alberta and north-eastern British Columbia in Canada, Nuevo Leon in north-eastern Mexico, the Münsterland Basin and Saxony in Germany, the Sergipe Basin in north-eastern Brazil, central Tunisia, western Uzbekistan and, possibly, Maine-et-Loire in north-western France. *Watinoceras coloradoense praecursor* is only known from the Lower Turonian of Devon in southwest England.

Subfamily Mammitinae Hyatt, 1900

Genus *Metoicoceras* Hyatt, 1903

TYPE SPECIES: *Ammonites swallowi* Shumard, 1860, p. 591, by the subsequent designation of Shimer and Shrock (1944, p. 591).

Metoicoceras geslinianum (d’Orbigny, 1850)

(Pl. 10, Figs 7–10)

1841. *Ammonites catillus* Sowerby; d’Orbigny, p. 325, pl. 97, figs 1, 2.

1851. *Ammonites Geslinianus* d’Orbigny, p. 146.

1981. *Metoicoceras geslinianum* (d’Orbigny, 1851); Wright and Kennedy, p. 62, pl. 17, fig. 2; pl. 18, figs 1, 2; pl. 19, figs 1, 2; pl. 20, figs 1–3; pl. 21, figs 1, 2; text-figs 19c–e, 20, 21a–d (with synonymy).

1998. *Metoicoceras geslinianum* (d’Orbigny, 1850); Kaplan *et al.*, p. 172, pl. 13, figs 19, 20 (with additional synonymy).

2006. *Metoicoceras geslinianum* (d’Orbigny, 1850); Kennedy and Juignet in Gauthier, p. 119, pl. 58, fig. 9; pl. 59, fig. 2.

2007. *Metoicoceras geslinianum* (d’Orbigny, 1850); Kim *et al.*, pl. 59, fig. 1.

2022. *Metoicoceras geslinianum* (d’Orbigny, 1850); Guendouz *et al.*, p. 12, text-fig. 5a (with additional synonymy).

LECTOTYPE: The lectotype, by the subsequent designation of Kennedy *et al.* (1981, p. 64), is MNHN R.4287, the original of *Ammonites catillus* d’Orbigny, 1841 (pl. 97, figs 1, 2). It has been refigured by Sornay (1955b, text-figs 3, 4), Kennedy *et al.* (1981, text-fig. 13), Wright and Kennedy (1981, text-fig. 21a, b), and Gauthier (2006, pl. 59, fig. 2). The provenance of the lectotype is discussed in detail by Kennedy *et al.* (1981, p. 70) and Kennedy and Juignet in Gauthier (2006, p. 119); preservation suggests it is from the Upper Cenomanian Couche d’Argile in the environs of Saumur in Maine-et-Loire, France.

MATERIAL: OUMNH PAL-KY.6221/2 and 6237, from the Uchkuduk Formation, Upper Cenomanian, Dzharakuduk.

DESCRIPTION: OUMNH PAL-KY.6221/2 (Pl. 10, Figs 7, 8) is a poorly preserved fragment of ?body chamber retaining recrystallized shell, 85 mm long, with a compressed whorl section. Ribs arise on the damaged umbilical wall, and strengthen into blunt umbilical bullae. These give rise to one or two broad, blunt, prorsiradiate ribs, while additional ribs intercalate. All of the ribs link to poorly differentiated inner ventrolateral tubercles and well-developed outer ventrolateral clavi. OUMNH PAL-KY.6237 (Pl. 10, Figs 9, 10) is a better-preserved fragment, with well-developed conical inner ventrolateral tubercles and outer ventrolateral clavi.

DISCUSSION: Although slight, the present material compares well with specimens from southern England; OUMNH PAL-KY.6221/2 with the original of Wright and Kennedy (1981, pl. 21, fig. 1), OUMNH PAL-KY.6237 with the original of their pl. 20, fig. 2.

OCCURRENCE: Index species of the late Cenomanian Old World *geslinianum* Zone. The geographic distribution extends from southern England to France, Spain, Portugal, the Czech Republic, Germany, Morocco, Algeria, Tunisia, Libya, Egypt, Israel, Jordan, Oman, western Uzbekistan, Nigeria, Angola, Columbia, Brazil, Texas, New Mexico, Colorado, Kansas, Utah and elsewhere in the United States Western Interior.

Subfamily Euomphaloceratinae Cooper, 1978
Genus *Morrowites* Cobban and Hook, 1983

TYPE SPECIES: *Mammites wingi* Morrow, 1935 (p. 467, pl. 51, fig. 2; pl. 52, fig. 2; text-fig. 2), from the Lower Turonian of Cloud County, Kansas, by the original designation of Cobban and Hook (1983, p. 9).

Morrowites wingi (Morrow, 1935)
(Pl. 1, Figs 8, 9; Pl. 9, Figs 1–9)

1935. *Mammites wingi* Morrow, p. 467, pl. 51, fig. 2; pl. 52, fig. 2; text-fig. 2.
1983. *Morrowites wingi* (Morrow); Cobban and Hook, p. 9, text-figs 3, 4 (with synonymy).
1984. *Mammites wingi wingi* Morrow, 1935; Kennedy *et al.*, p. 37, text-fig. 2m–o.

2009. *Morrowites wingi* (Morrow, 1935); Lehmann and Herbig, p. 65, pl. 2, figs o–p (with additional synonymy).
2014. *Morrowites wingi* (Morrow, 1935); Amédéo and Devalque in Robaszynski *et al.*, p. 137, pl. 5, fig. 3.
2016. *Morrowites wingi* (Morrow, 1935); Kennedy and Gale, p. 270, text-fig. 7.
2018. *Morrowites wingi* (Morrow, 1935); Amédéo and Matignon in Amédéo *et al.*, p. 192, fig. 130a, b.
2019. *Morrowites wingi* (Morrow, 1935); Kennedy and Kaplan, p. 54, pls 23, 24; text-fig. 21.

TYPE: The holotype is the original of Morrow (1935, p. 467, pl. 52, fig. 2b, c), refigured by Kennedy and Kaplan (2019, text-fig. 21), KUMIP 28269, housed in the collections of the University of Kansas Natural History Museum and Biodiversity Center, Lawrence, Kansas. It is from the Lower Turonian Jetmore Chalk Member of the Greenhorn Limestone of Cloud County, Kansas.

MATERIAL: OUMNH PAL-KY.6113–6118, 6127, collected *ex situ* from the Beshtyube Formation, Lower Turonian, Koshtyube; OUMNH PAL-KY.6087–6092/1–2, from the Beshtyube Formation, Lower Turonian, Beshtyube.

DESCRIPTION: OUMNH PAL-KY.6113 (Pl. 9, Figs 4–8) consists of an internal mould of a nucleus with a 180° sector of the succeeding whorl, all of which is body chamber, the maximum preserved diameter 41 mm. The nucleus, at a diameter of 20 mm has an estimated 10 low, broad, prorsiradiate primary ribs at the ventrolateral shoulder, all of which bear well-developed oblique ventrolateral clavi. One interspace is deepened into a ventrolateral and ventrolateral constriction. On the outer whorl, primary ribs arise at the umbilical seam, and strengthen across the umbilical wall and shoulder, without developing into clearly differentiated bullae. Primary ribs are strong, coarse, and feebly prorsiradiate across the flanks, some but not all developing an incipient inner ventrolateral bulla. There are strong outer ventrolateral clavi, linked across the venter by a broad, transverse rib. Additional ribs intercalate, and have a comparable ventrolateral and ventral development as the primaries.

OUMNH PAL-KY.6087 is a well-preserved external mould; a silicone cast taken from it is figured here (Pl. 1, Figs 8, 9). The maximum diameter is an estimated 80 mm approximately. The inner whorls have an estimated diameter of 40 mm. Coiling is involute, the small umbilicus deep, and comprising 24% of the diameter approximately, the umbilical

wall high, feebly convex and outward-inclined, the umbilical shoulder broadly rounded. Primary ribs arise at the umbilical seam and strengthen across the umbilical wall; some but not all develop into strong subspinose conical umbilical tubercles. The ribs are strong, straight and prorsiradiate, strengthening progressively across the flanks, and linking to strong conical to feebly clavate inner ventrolateral tubercles. A strong feebly prorsiradiate rib links to strong outer ventrolateral clavi, linked across the venter by a low, broad, transverse rib.

OUMNH PAL-KY.6092/1 (Pl. 9, Fig. 9) is a 90° sector of body chamber, with one flank worn away. The maximum preserved whorl height is 56 mm. There are four conical/bullate umbilical tubercles of variable strength on the fragment. They give rise to low, broad, straight ribs that link to strong conical inner ventrolateral tubercles; there is also a single intercalated rib that also bears a strong conical inner ventrolateral tubercle. The most completely preserved rib has a weaker, conical to feebly clavate outer ventrolateral tubercle. OUMNH PAL-KY.6092/2 is a fragment of the penultimate whorl of this specimen, with well-developed umbilical bullae, conical inner and clavate outer ventrolateral tubercles.

OUMNH PAL-KY.6127 (Pl. 9, Figs 1–3) is a 60° sector of phragmocone with a maximum preserved whorl height of 51 mm. The whorl section is slightly depressed, the flanks feebly convex, the ventrolateral shoulders broadly rounded, the broad venter feebly convex in intercostal section. There are two well-preserved ribs on the fragment, with well-developed umbilical bullae, conical inner and clavate outer ventrolateral tubercles. The imperfectly preserved suture has a broad, moderately incised bifid E/A.

DISCUSSION: *Morrowites depressus* (Powell, 1963) (p. 1228, pl. 168, figs 1–3; pl. 170, figs 4, 5; pl. 171, fig. 1; text-figs 5e, 6f–h; see revision in Cobban and Hook 1983, p. 11, pl. 6, figs 1, 2; text-fig. 5) has a massive shell with a very depressed whorl section and much stronger tuberculation than the present species. *Morrowites subdepressus* Cobban and Hook, 1983 (p. 11, pl. 1, figs 8–13; pl. 3, figs 19, 20; pl. 4, figs 1–3, 12–16; pl. 7; text-figs 6, 7) was distinguished from *M. wingi* by its authors on the basis of the more depressed whorl section. Lehmann and Herbig (2009, p. 67) provide additional discussion.

OCCURRENCE: Lower Turonian, Kansas, Colorado and New Mexico in the United States, southern England (as subspecies *revelerioides* Wright and Kennedy, 1981), northern Aquitaine and Provence

in France, the Münsterland Basin, Germany, Morocco, western Uzbekistan and Japan. As noted above, the species ranges into the Middle Turonian *Collignonicerias woollgari* Zone in southern Colorado (Kennedy *et al.* 2000, 2005).

Subfamily Mammitinae Hyatt, 1900

Genus *Metasigaloceras* Hyatt, 1903

TYPE SPECIES: *Ammonites rusticus* J. Sowerby, 1817 (p. 44, pl. 177), by the original designation of Hyatt (1903, p. 106).

Metasigaloceras rusticum (J. Sowerby, 1817)

(Pl. 10, Figs 13, 14)

1817. *Ammonites rusticus* J. Sowerby, p. 44, pl. 177.

1916b. *Mammites* (?) *rusticus* Sow. subsp. *amudariensis* Arkhangelsky, p. 54, pl. 6, figs 1, 2, 7; pl. 7, fig. 14; text-fig. 19.

1981. *Metasigaloceras rusticum* (J. Sowerby, 1817); Wright and Kennedy, p. 83, pl. 18, fig. 3; pl. 27; text-fig. 28 (with synonymy).

2019. *Metasigaloceras rusticum* (J. Sowerby, 1817); Kennedy and Kaplan, p. 51, pl. 22; text-fig. 19 (with additional synonymy).

TYPE: The holotype, by monotypy, is OUMNH PAL-K.2048, the original of J. Sowerby (1817, p. 44, pl. 177), from the Lower Turonian of Combe Pyne, near Lyme Regis in Devon, south-east England. It was refigured by Wright and Kennedy (1981, pl. 27) and Kennedy and Kaplan (2019, text-fig. 19).

MATERIAL: OUMNH PAL-KY 3874 and 6104, from the Beshtyube Formation, Koshtyube, Lower Turonian.

DESCRIPTION: OUMNH PAL-KY.3874 (Pl. 10, Figs 13, 14), has a maximum preserved diameter of 96 mm, retains extensive areas of recrystallized shell, and is in part body chamber. Coiling is involute, the umbilicus of moderate depth, and comprising 25% of the diameter, the umbilical wall convex, the umbilical shoulder broadly rounded. The intercostal whorl section is slightly depressed, with a whorl breadth to height ratio of 1.1, the flanks convex, the ventrolateral shoulders broadly rounded, the venter broad and feebly convex. The greatest breadth is around mid-flank. On the damaged adapical part of the outer whorl there are four very feeble low, broad primary ribs, and a single ventrolateral tubercle; the remainder of the venter is damaged. On the adapertural 90°

sector, three low, broad, feeble ribs arise on the umbilical wall, and are prorsiradiate across the flanks, linking to massive conical tubercles in an outer lateral/inner ventrolateral position. They give rise to pairs of low, broad ribs, the adapical one transverse, the adapertural one feebly prorsiradiate, both linking to a strong conical to feebly clavate outer ventrolateral tubercle, the tubercles linked across the venter by a broad, transverse rib. The ventral rib profile is concave between the outer ventrolateral tubercles. OUMNH PAL-KY.6104 is a much larger body chamber fragment of one flank with a maximum preserved whorl height of 73 mm.

DISCUSSION: See Wright and Kennedy (1981, p. 83) and Kennedy and Kaplan (2019, p. 51). *Mammites* (?) *rusticus* Sow. subsp. *amudariensis* Arkhangelsky, 1916b (p. 54, pl. 6, figs 1, 2, 7; pl. 7, fig. 14; text-fig. 19), from the right bank of the Amu Darya near Nazar-khan does not bear separation. The figures are of a 180° whorl sector with an estimated maximum preserved diameter of 128 mm. It is from Beshtyube.

OCCURRENCE: Lower Turonian of southern and eastern England, the Boulonnais, Haute Normandie, Gard, Alpes-Maritimes and Alpes de Haut-Provence in France, the Münsterland Basin in northern Germany, and western Uzbekistan.

Family Collignoniceratidae Wright and Wright, 1951
Subfamily Collignoniceratinae Wright and Wright, 1951

Genus *Collignoniceras* Breistroffer, 1947

TYPE SPECIES: *Ammonites woollgari* Mantell, 1822, p. 197, pl. 21, fig. 16; pl. 22, fig. 7, by the original designation of Meek (1876, p. 453) as type species of *Prionotropis* Meek, 1876 *non* Fieber (1853) for which Breistroffer (1947, unpagged) proposed *Collignoniceras* as *nomen novum*.

Collignoniceras woollgari woollgari (Mantell, 1822)
(Pl. 10, Figs 1–6, 11, 12)

1822. *Ammonites woollgari* Mantell, p. 197, pl. 21, fig. 16; pl. 22, fig. 7.
1916b. *Prionotropis Woolgari* Mantell, 1822; Arkhangelsky, p. 46, pl. 6, figs 3, 4.
2001. *Collignoniceras woollgari woollgari* (Mantell, 1822); Kennedy *et al.*, p. 42, text-figs 10–15 (with synonymy).
2019. *Collignoniceras woollgari woollgari* (Mantell, 1822);

Kennedy and Kaplan, p. 61, pl. 4, fig. 1; pl. 30, figs 1–4, 7–8; pl. 31, figs 1–10; pls 32, 33; text-fig. 24.

TYPES: The lectotype is BMNH C5682, the original of Mantell (1822, pl. 21, fig. 16), from the Middle Chalk near Lewes, Sussex, England, by the subsequent designation of Wright and Wright (1951, p. 35). Presumed paralectotypes are BMNH C5742a, b, from the same locality.

MATERIAL: OUMNH PAL-KY.3871, 6122–6125, 6126a–h, from Beshtyube, OUMNH PAL-KY.6128a–e from Koshytube, all Beshtyube Formation, Middle Turonian.

DESCRIPTION: The present material consists predominantly of whole and fragmentary nuclei (Pl. 10, Figs 1–6), the largest 30 mm in diameter. The best-preserved of these, OUMNH PAL-KY.6126a (Pl. 10, Figs 4, 5), is 23.2 mm in diameter. Crowded primary ribs are straight and prorsiradiate on the flanks, most arising from tiny umbilical bullae, and bearing feeble inner ventrolateral bullae, together with stronger outer ventrolateral and siphonal clavi. OUMNH PAL-KY.3871 (Pl. 10, Figs 11, 12) is a larger, 120° whorl fragment with a maximum preserved whorl height of 26 mm, retaining recrystallized shell. Five strong primary ribs arise at the umbilical seam, sweep forwards and strengthen across the umbilical wall, and develop into strong umbilical bullae. These give rise to single broad, coarse, prorsiradiate ribs that strengthen across the flanks, and link to strong inner and outer ventrolateral and siphonal clavi. There is a single intercalated rib bearing a siphonal clavus preceding the adaperturalmost primary rib.

DISCUSSION: *Collignoniceras woollgari woollgari* is the early form of the species. It differs from *C. woollgari regulare* (Haas, 1946) (see revision in Kennedy *et al.* 2001, p. 45, text-figs 17–23, 49L; Kennedy and Kaplan 2019, p. 63, pl. 34), in having more siphonal tubercles than ventrolateral ones on the middle and later phragmocone whorls, and looped ribs connecting opposite ventrolateral horns over the venter. These features generally separate body chambers, although they may occur on some body chambers of *C. woollgari regulare*.

The presence of a single intercalated rib and associate siphonal clavus towards the adapertural end of OUMNH PAL-KY.3871 (Pl. 10, Fig. 12) indicate the present material to belong to *woollgari woollgari*.

The juvenile figured by Arkhangelsky (1916b, p.

46, pl. 6, figs 3, 4) from Tshushka-kul in the Turgay region, cannot be assigned to either subspecies.

OCCURRENCE: Middle Turonian, *Collignonicer* *woollgari* Zone, *C. woollgari woollgari* Subzone and correlatives. There are records from southern England, France, the Münsterland and Saxonian basins in Germany, the Czech Republic, Spain, western Uzbekistan, the United States Gulf Coast and Western Interior, California and Oregon, Mexico, Japan, and Northern Australia.

Suborder Ancyloceratina Wiedmann, 1966
Superfamily Turrilitoidea Gill, 1871
Family Baculitidae Gill, 1871
Genus *Sciponoceras* Hyatt, 1894

TYPE SPECIES: *Hamites baculoides* Mantell, 1822 (p. 123, pl. 23, figs 6, 7), by the original designation of Hyatt (1894, p. 578).

Sciponoceras cf. *bohemicum bohemicum* (Fritsch, 1872)
(Pl. 11, Figs 1–6)

1872. *Baculites faujassi* Lamarck var. *bohémica* Fritsch, p. 49, pl. 13, figs 23–25, 29, 30.

2020. *Sciponoceras bohemicum bohemicum* (Fritsch, 1872); Kennedy, p. 169, pl. 51, figs 1–7, 9, 14–22; pl. 52, figs 1–13.

TYPES: The lectotype, by the subsequent designation of Wright (1979, p. 285), is the original of *Baculites faujassi* Lamarck var. *bohémica* of Fritsch (1872, p. 49, pl. 13, fig. 25). Fritsch figured four additional specimens which are paralectotypes. All are from the 'Priesener Schichten von Lenešic bei Lauen' in the Usti nad Labem region of the Czech Republic, and are housed in the collections of the Národní Museum, Prague.

MATERIAL: OUMNH PAL-KY.6093–6099, 6100 (collective of 7 specimens), 6101 (collective of 13 specimens), 6102 (collective of 19 specimens), collected *ex situ* from the Beshtyube Formation, Lower Turonian, Koshtyube.

DESCRIPTION: The material comprises internal moulds of fragments of phragmocones and body chambers with whorl heights of up to 13 mm. The whorl section is compressed oval, the whorl breadth to height ratio varying around 0.8. Ornament is of

strongly prorsiradiate coarse ribs that strengthen across the flanks; the rib index is four. The ribs strengthen further across the venter, where they are very feebly convex. In OUMNH PAL-KY.6100a (Pl. 11, Figs 1, 2), the interspace succeeding every fourth rib is strengthened into a constriction, best developed on ventrolateral shoulders and venter.

DISCUSSION: *Sciponoceras bohemicum anterius* Wright and Kennedy, 1981 (p. 115, pl. 31, figs 4–6, ??, 8, 10, 11; pl. 32, figs 9, 10, 12–15) of the Upper Cenomanian *Neocardioceras juddii* Zone differs from the nominate subspecies in having ribs and constrictions that cross the venter in a broad arch rather than near-transversely, the flanks flattened, with frequent constrictions every one and a half to two major diameters, extending across the flanks and present on the dorsum.

OCCURRENCE. As for material. *S. bohemicum anterius* is only known from the Upper Cenomanian *juddii* Zone of southern and central England. *Sciponoceras bohemicum bohemicum* is known from the Upper Turonian, *Subprionocyclus neptuni* Zone of southern and eastern England, northern France, northern Spain, Germany, the Czech Republic, Austria, and Poland.

Superfamily Scaphitoidea Gill, 1871
Family Scaphitidae Gill, 1871
Subfamily Otoscapitinae Wright, 1953
Genus *Yezoites* Yabe, 1910

TYPE SPECIES: *Scaphites perrini* Anderson, 1902 (p. 114, pl. 2, figs 71–73), by the subsequent designation of Diener (1925, p. 213).

Yezoites amudariensis (Arkhangelsky, 1916b)
(Pl. 11, Figs 7–18)

1916b. *Scaphites amudariensis* Arkhangelsky, p. 56, pl. 8, figs 11–13.

1925. *Scaphites amudariensis* Archangel'skij; Diener, p. 196.

1949. *Hoploscapites amudariensis* Arkhangelsky; Glazunova and Liverovskii in Luppov, p. 230, pl. 62, text-fig. 3.4–3.6 (copies of Arkhangelsky 1916b, pl. 8, figs 11–13).

2016. *Hoploscapites amudariensis* (Arkhangelsky, 1916); Klein, pp. 104, 106.

TYPES: The original of Arkhangelsky (1916b, pl.

8, fig. 13), from Beshtyube, is here designated lectotype; the originals of figs 11 and 12 are paralectotypes

MATERIAL: OUMNH PAL-KY.3873, 6105–6112, collected *ex situ*, from the Beshtyube Formation, Lower Turonian, Koshtyube.

DESCRIPTION: OUMNH PAL-KY.3873 (Pl. 11, Figs 15–18) and 6108 (Pl. 11, Figs 13, 14) are macroconchs. OUMNH PAL-KY.3873 is 24.2 mm long. The coiling of the phragmocone is involute, the deep umbilicus tiny, the whorl section depressed reniform, the whorl breadth to height ratio 1.5, the greatest breadth around mid-flank. Narrow primary ribs arise on the umbilical wall and strengthen across the umbilical shoulder. They are straight and prorsiradiate on the flanks, across which they strengthen, and link to small ventrolateral bullae. These give rise to pairs of ribs, which loop across the venter, where they are near-transverse and link to the tubercles on the opposite flank. Additional nontuberculate ribs intercalate on the ventrolateral shoulder, the ventrolateral shoulders and venter ornamented by crowded delicate ribs. The umbilical wall at the adapical end of the body chamber shaft has a distinctive bulge that partially conceals the umbilicus of the phragmocone. The umbilical wall of the shaft is convex, the whorl section depressed, with convex flanks, broadly rounded ventrolateral shoulders and a broad, feebly convex venter. Delicate strongly prorsiradiate ribs extend across the flanks, and link to small ventrolateral bullae that increase progressively in size along the shaft. They give rise to pairs of delicate ribs, while additional ribs intercalate to produce a dense ornament of delicate ribs on ventrolateral shoulders and venter. The flank ribbing effaces around the final recurved sector. The ventrolateral bullae strengthen, and give rise to pairs of progressively strengthening secondary ribs that pass straight across the venter. The adult aperture is preceded by a strong constriction. OUMNH PAL-KY.6108 is a somewhat worn macroconch 22.7 mm long.

OUMNH PAL-KY.6105 (Pl. 11, Figs 7–12) is a complete microconch, 15.6 mm long. The ornament is very delicate. That of the coiled sector is a weaker version of that of the macroconch. The umbilical seam of the shaft is straight, and does not partially conceal the umbilicus of the spire, as is the case in the macroconch. The umbilical wall of the shaft is very feebly convex, the whorl section very depressed, the ornament a subdued version of that of the macroconch. On the final recurved sector the ornament effaces, and

there is a strong constriction, succeeded by a strong rib. The actual aperture is slightly flared, with a broad, very obtuse ventral projection; a well-developed dorsolateral lappet is well-exposed on one flank.

DISCUSSION: The depressed, reniform whorl section of *amudariensis* is a feature that distinguishes it from European species such as the Upper Turonian *Yezoites bladenensis* (Schlüter, 1872) (see revision in Kennedy 2020, p. 199, pl. 62, figs 1–8, 11–36; text-fig. 67a), Coniacian *Yezoites arnaudi* (de Grossouvre, 1894) (see revision in Kennedy 1984, p. 150, pl. 31, figs 20–24, text-fig. 42a, b), Coniacian *Yezoites fritschi* (de Grossouvre, 1894), and Coniacian–Lower Santonian *Yezoites orbignyi* Kennedy, 1995 (in Kennedy *et al.* 1995, p. 433, pl. 30, figs 22, 32, 35, 36).

OCCURRENCE: Lower Turonian of western Uzbekistan.

Acknowledgements

CK, NJM and DJW wish to thank David Archibald (San Diego State University, California, USA) for introducing us to the Cretaceous of Uzbekistan, for providing all necessary logistical support for our excursions (1997–2006) across the desert, and for encouraging us with wisdom, humour and Baltika beer after arduous days in the field at 44°C. We were accompanied in the field by Hans-Dieter Sues and Cathy Škrabec (Royal Ontario Museum, Toronto, Canada); Cory Redman (San Diego State University, California, USA); Tatiana Malyskina (Institute of Geology and Geochemistry, Russian Academy of Sciences, Ekaterinburg, Russia); Alexander Averianov, Anton Rezvy, Pavel Skutschas and Igor Danilov (Institute of Zoology, St. Petersburg, Russia), Oleg Tsaruk (Tashkent) and Yuri Chikin (Institute of Zoology, Tashkent). We would particularly like to thank our driver Viktor (Navoiy, Uzbekistan) who drove us to places where no motorised vehicles had visited before and Boris Veretennikov (Tashkent) for sharing his unrivalled geological and geographical knowledge of the Kyzylkum Desert. There were many other colleagues who participated in the URBAC expeditions assisted in various ways as well as the hospitality of the villagers of Dzharakuduk, who erected two yurts and provided us with fresh bread and the occasional goat.

This project was supported by grants to David Archibald from the National Science Foundation (EAR 9804771 and 0207004) and the National Geographic Society (6281–98, 5087–93, 5901–07). We also acknowledge with gratitude the extensive help given by the Navoiy Mining and Metallurgy Combine, Vasily Vasilovich (Zarafshon), and the co-operation of Director Azimov, Institute of Zoology, Uzbek Academy of Sciences, Tashkent. WJK thanks Eliza Howlett and David

Sansom (Oxford) for technical input; Irek Walaszczyk (Warsaw) for linguistic and literature support, and inoceramid identification; Francis Améro (Calais) and Markus Wilmsen (Dresden), for their reviews of an earlier version of the manuscript, and Anna Żylińska for her meticulous editing.

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Manuscript submitted: 27th February 2023

Revised version accepted: 21st June 2023

PLATES 1–11

PLATE 1

1-3 – *Watinoceras coloradoense* (Henderson, 1908), OUMNH PAL-KY.3872, Beshtyube Formation, Lower Turonian, Beshtyube, associated with, in 1, *Inoceramus* ex gr. *lamarcki* Parkinson, 1819.

4-7 – *Watinoceras amudariense* (Arkhangelsky, 1916b). 4, 5 – OUMNH PAL-KY.6117; 6, 7, OUMNH PAL-KY.6115, both specimens *ex situ*, Beshtyube Formation, Lower Turonian, Koshtyube.

8, 9 – *Morrowites depressus* (Morrow, 1935), silicone cast from OUMNH PAL-KY.6087, Beshtyube Formation, Lower Turonian, Beshtyube.

10-12 – *Tragodesmoceras* cf. *mauryae* Kennedy and Wright, 1981, OUMNH PAL-KY.6119, *ex situ*, Beshtyube Formation, Lower Turonian, Koshtyube.

13-16 – *Lewesiceras mantelli* Wright and Wright, 1951. 13, 14 – OUMNH PAL-KY.6169, Aitym Formation, Upper Turonian, Meshekli; 15, 16 – OUMNH PAL-KY.3870, Aitym Formation, Upper Turonian, on the foreshore of the Amu Darya, 20 m north of Meshekli.

Figures 1–3, 8–16 are $\times 1$; figures 4–7 are $\times 2$.

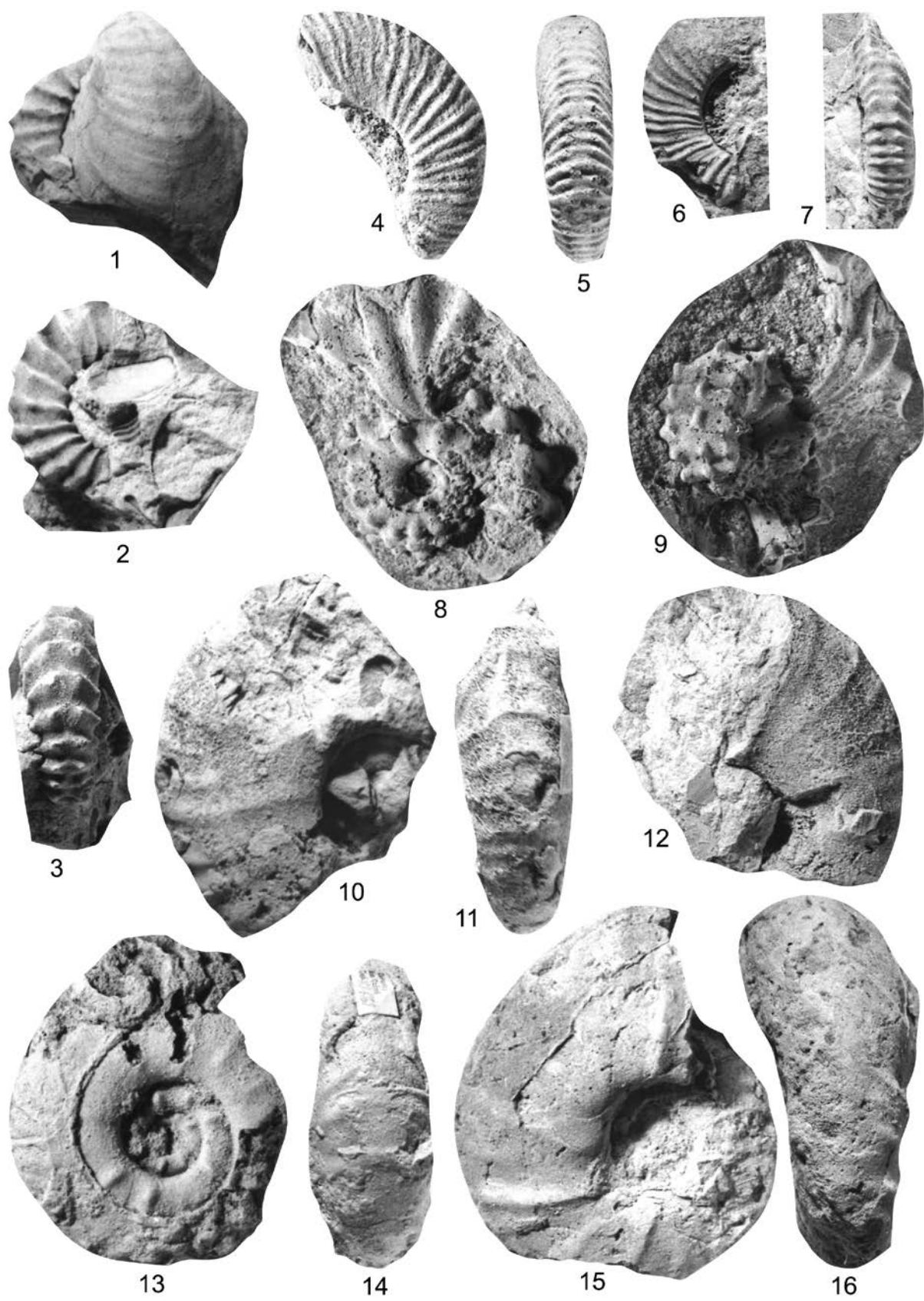


PLATE 2

Placenticeras kharesmense (Lahusen, 1884), OUMNH PAL-KY.6074, Beshtyube Formation,
Lower Turonian, Beshtyube.

All figures are $\times 1$.



PLATE 3

1-3 – *Placenticerias crassum* Ilyin, 2000. 1 – OUMNH PAL-KY.6168; 2, 3 – OUMNH PAL-KY.6183. Both from the Kendytube Formation, Upper Turonian, Meshekli.

4-8 – *Placenticerias kharesmense* (Lahusen, 1884). 4, 5 – OUMNH PAL-KY.6085; 6, 7 – OUMNH PAL-KY.6083; 8 – OUMNH PAL-KY.6089. All from the Beshtyube Formation, Lower Turonian, Beshtyube.

All figures are $\times 1$.

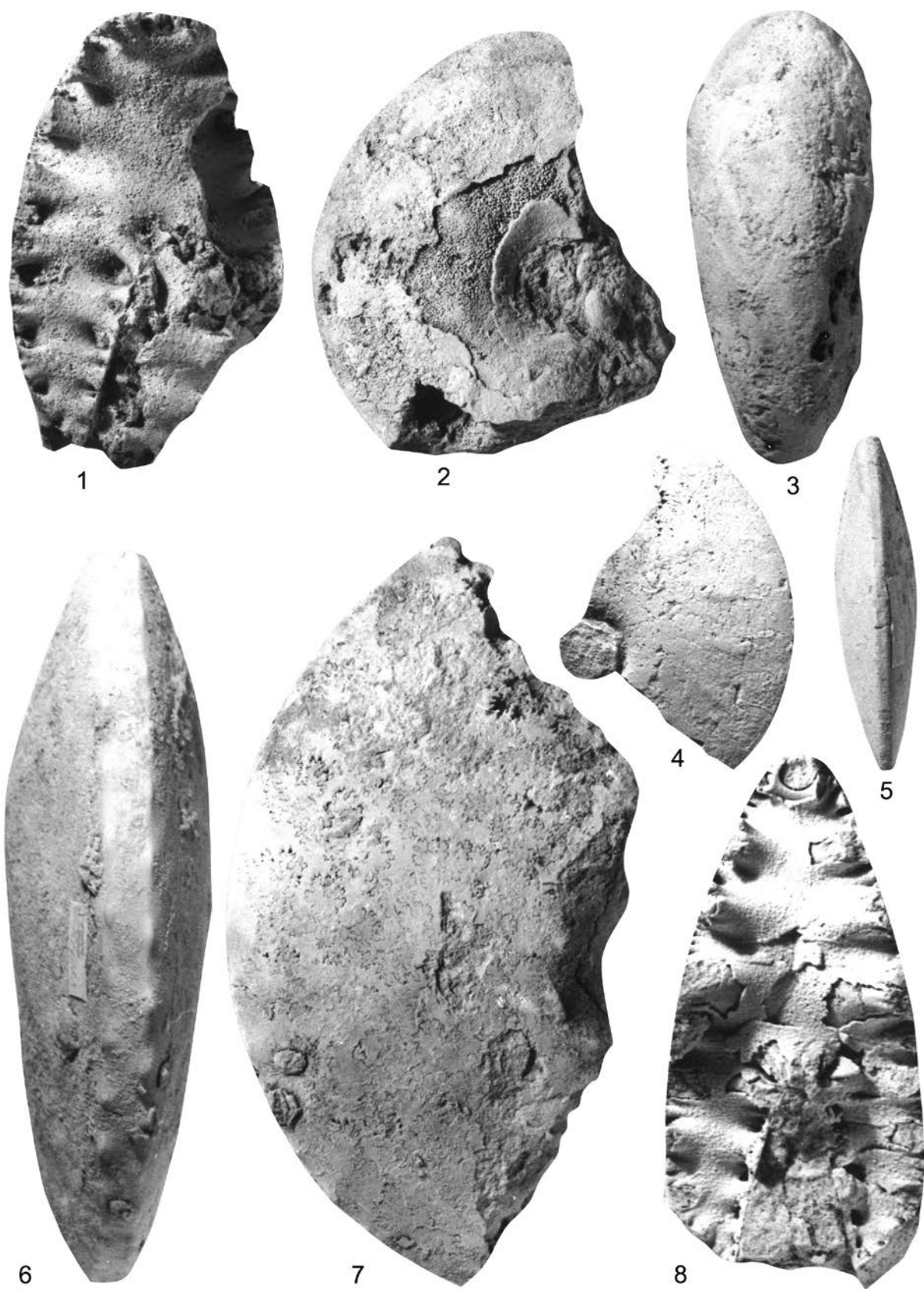


PLATE 4

Placenticeras kharesmense (Lahausen, 1884), OUMNH PAL-KY.6076, Beshtyube Formation,
Lower Turonian, Beshtyube.

Figure is $\times 1$.



PLATE 5

Placenticeras kharesmense (Lahausen, 1884), OUMNH PAL-KY.6086, Beshtyube Formation,
Lower Turonian, Beshtyube.

Figure is $\times 0.67$.



PLATE 6

Placenticerias crassum Ilyin, 2000. 1, 2 – OUMNH PAL-KY.6149; 3-5 – OUMNH PAL-KY.6135; 6, 7 – OUMNH PAL-KY.6168; 8, 9 – OUMNH PAL-KY.6158; 10, 11 – OUMNH PAL-KY.6150; 12, 13 – OUMNH PAL-KY.6162. All from the Kendytube Formation, Upper Turonian, Meshekli.

All figures are $\times 0.96$.

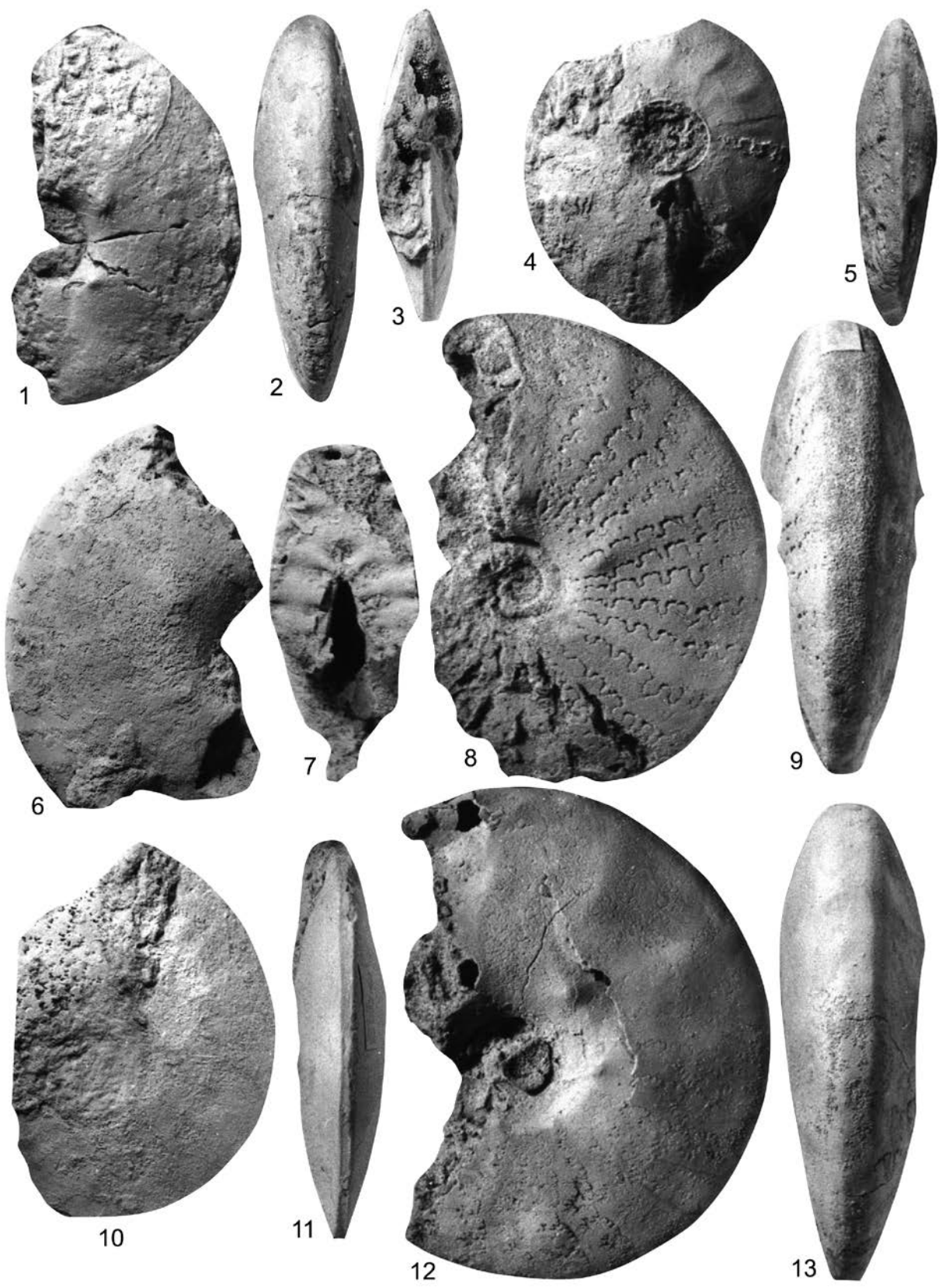


PLATE 7

1, 2 – *Placenticerias semiornatum* (d'Orbigny, 1850), OUMNH PAL-KY.3867, *ex situ*, lower part of the Laulau Formation, Coniacian/Santonian boundary interval, north of Meshekli.

3-8 – *Placenticerias* sp. juv., cf. *cumminsi* Cragin, 1893, 3-5 – OUMNH PAL-KY.6225; 6-8 – OUMNH PAL-KY.6224. Both from the Uchkuduk Formation, 3–4 m above the base, Upper Cenomanian, Dzharakuduk.

9-13 – *Placenticerias crassum* Ilyin, 2000, 9-11 – OUMNH PAL-KY.3869, Meshekli; 12, 13 – OUMNH PAL-KY.6131, 20 m north of Meshekli. Both from the Kendytube Formation, Upper Turonian.

All figures are $\times 1$.

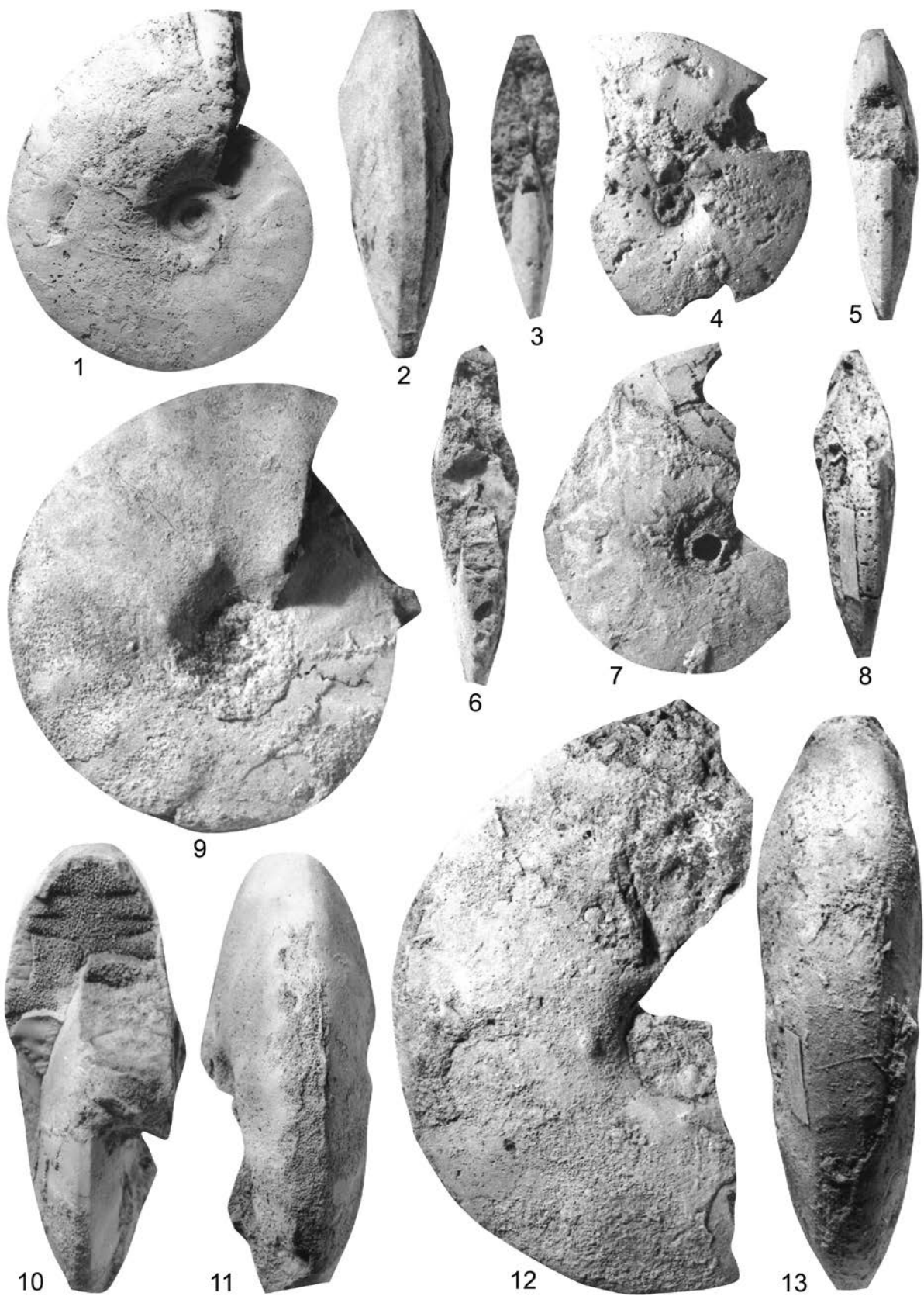


PLATE 8

Placenticerias polyopsis (Dujardin, 1837). 1, 8 – OUMNH PAL-KY.6197, Meshekli; 2-4 – OUMNH PAL-KY.6190, Meshekli; 5-7 – OUMNH PAL-KY.6198, Meshekli; 9-11 – OUMNH PAL-KY.3868, foreshore of the Amu Darya 20 m north of Meshekli. All specimens are from the Laulau Formation, Santonian.

All figures are $\times 1$.

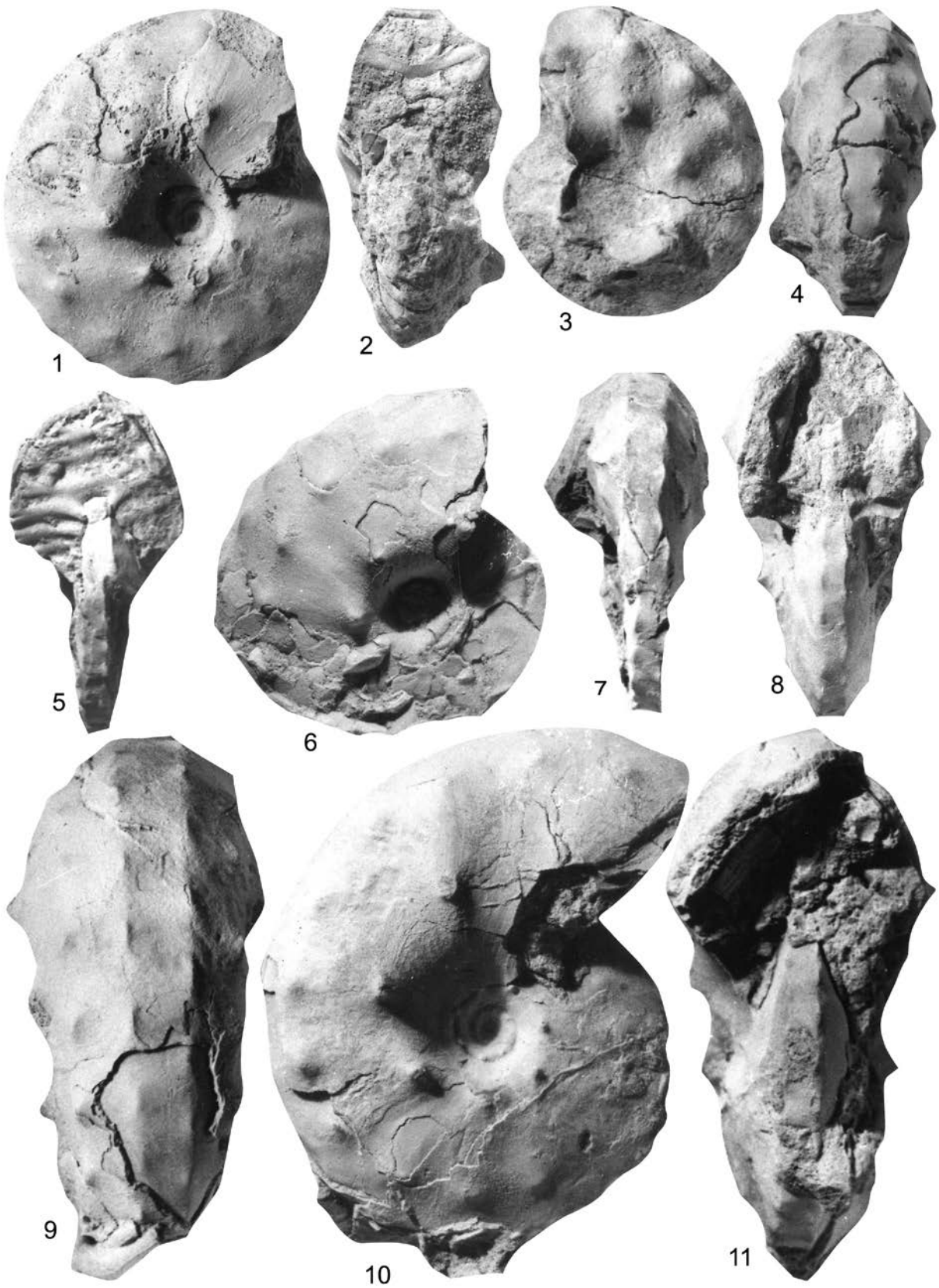


PLATE 9

Morrowites wingi (Morrow, 1935), 1-3 – OUMNH PAL-KY.6127, Koshtyube; 4-8 – OUMNH PAL-KY.6114, Koshtyube; 9 – OUMNH PAL-KY.6092/2, Beshytube. All specimens are from the Beshytube Formation, Lower Turonian.

Figures 1–6, 9 are $\times 1$; figures 7 and 8 are $\times 2.5$.



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PLATE 10

1-6, 11, 12 – *Collignonicerias woollgari woollgari* (Mantell, 1822). 1 – OUMNH PAL-KY.6128a, Koshtyube; 2 – OUMNH PAL-KY.6128c, Koshtyube; 3 – OUMNH PAL-KY.6128b, Koshtyube; 4, 5 – OUMNH PAL-KY.6126a, Beshtyube; 6 – OUMNH PAL-KY.6122, Beshtyube; 11, 12 – OUMNH PAL-KY.3874, Beshtyube. All specimens are from the Beshtyube Formation, Middle Turonian.

7-10 – *Metoicoceras geslinianum* (d'Orbigny, 1850). 7, 8 – OUMNH PAL-KY.6221; 9, 10 – OUMNH PAL-KY.6237. Both specimens are from the Uchkuduk Formation, Upper Cenomanian, Dzharakuduk.

13, 14 – *Metasigaloceras rusticum* (J. Sowerby, 1823). OUMNH PAL-KY.3874, Beshtyube Formation, Lower Turonian, Koshtyube.

Figures 1–6 are ×2; figures 7–14 are ×1.

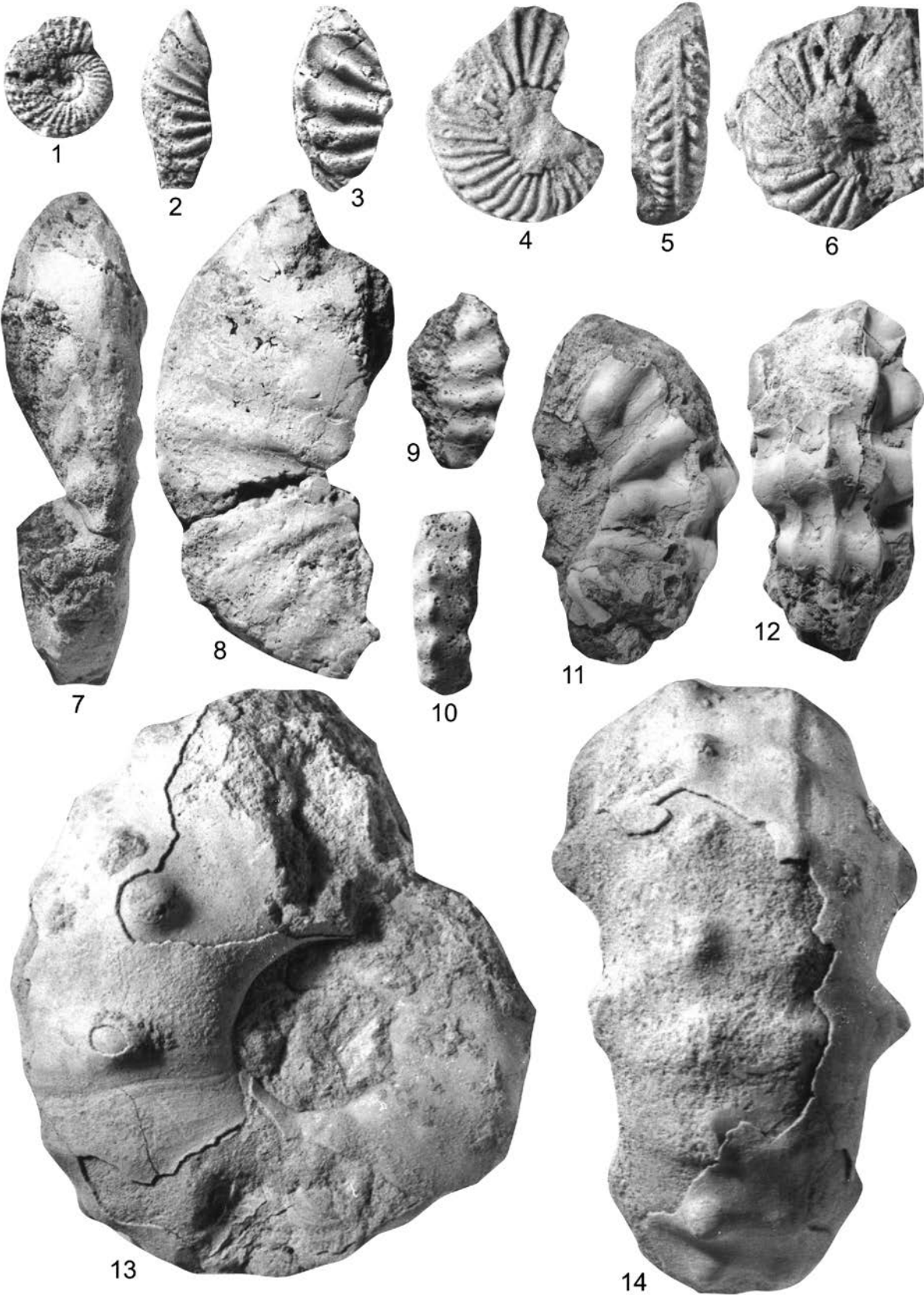


PLATE 11

1-6 – *Sciponoceras* cf. *bohemicum bohemicum* (Fritsch, 1872). 1, 2 – OUMNH PAL-KY.6100a; 3, 4 – OUMNH PAL-KY.6100c; 5, 6 – OUMNH PAL-KY.6100b. All specimens are *ex situ*, Beshtyube Formation, Lower Turonian, Beshtyube.

7-18 – *Yezoites amudariensis* (Arkhangelsky, 1916b). 1-12 – OUMNH PAL-KY.6105, a microconch; 13, 14 – OUMNH PAL-KY.6108, a macroconch; 15-18 – OUMNH PAL-KY.3873, a macroconch. All specimens are *ex situ*, Beshtyube Formation, Lower Turonian, Koshtyube.

All figures are $\times 2$.



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