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THE LATE LATE ALBIAN (*MORTONICERAS FALLAX* ZONE) CEPHALOPOD FAUNA FROM THE BRACQUEGNIES FORMATION AT STRÉPY-THIEU (HAINAUT, SOUTHERN BELGIUM)

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(2 figures, 10 plates)

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ABSTRACT. Excavations in 1989-1990 for the construction of a boat lift near the villages of Strépy and Thieu, east of Mons (province of Hainaut, southern Belgium), exposed a 40-metre section of the Bracquegnies Formation (Haine Green Sandstone Group; the 'Meule de Bracquegnies' of previous authors). Several hundred well-preserved, silicified cephalopods were collected from between 15 and 35 metres above the base of the sequence temporarily exposed there. The fauna is: *Eutrephoceras clementianum* (d'Orbigny, 1840), *Puzosia* (*Puzosia*) *mayoriana* (d'Orbigny, 1841), *Callihoplites tetragonus* (Seeley, 1865), *Discohoplites valbonnensis valbonnensis* (Hébert & Munier-Chalmas, 1875), *Cantabrigites cantabrigense* Spath, 1933, *Mortoniceras* (*Mortoniceras*) *fallax* (Breistroffer, 1940), *M.* (*M.*) *nanum* Spath, 1933, *Neophlycticeras* (*Neophlycticeras*) *blancheti* (Pictet & Campiche, 1859), *Stoliczkaia* (*Stoliczkaia*) *notha* (Seeley, 1865), *Anisoceras armatum* (J. Sowerby, 1817), *Hamites subvirgulatus* Spath, 1941, *Lechites* (*Lechites*) *gaudini* (Pictet & Campiche, 1861) and *Scaphites* (*Scaphites*) sp. juv. This assemblage is the first extensive fauna from the *Mortoniceras* (*Mortoniceras*) *fallax* Zone of the upper Upper Albian to be described from an expanded section. The assemblage is dominated by specimens referred to a highly variable, dimorphic *Callihoplites tetragonus* (> 250 specimens studied), of which many of the forms of *Callihoplites* described by Spath (1928) from the remanié Late Albian fauna at the base of the Lower Cenomanian Cambridge Greensand in eastern England are shown to be no more than intraspecific variants.

KEYWORDS: Ammonites, nautiloids, Cretaceous, Albian, taxonomy.

1. Introduction

The Bracquegnies Formation (Haine Green Sandstone Group; *sensu* Robaszynski et al., 2002; the 'Meule de Bracquegnies' of previous authors) is a series (some 40 metres thick at Harchies near Mons) of sandy, glauconitic marls, conglomerates, sandstones and sands, occasionally with common sponge remains, of Late Albian age, previously known from those parts of the Mons Basin (province of Hainaut, southern Belgium; see Fig. 1) where the Cretaceous sequence is at its greatest development. Amédro (1992, 2002) reviewed the previous literature on this unit, and provided an account of new exposures and faunas recovered in 1989-1990 during excavations for a boat lift in the communes of Strépy and Thieu. In excess of 70 metres of Cretaceous sediments were then exposed; some 12 metres of Wealden facies sands (i.e., the present-day Hainaut Group; see Robaszynski et al., 2002) were found to be unconformably overlain by 36.5 metres of Bracquegnies Formation, the base of this unit being formed by a 0.5 metre thick conglomerate (Fig. 2). Above, the interval between 15 and 35 metres yielded highly diverse, silicified molluscan assemblages, with predominant trigoniid and cardiid bivalves and turritellid gastropods (compare Briart & Cornet, 1868; Marlière, 1939), plus common ammonites. The latter are treated below as a single assemblage; reference is made to Amédro (2002: 62, fig. 17) for such limited information as was available on the occurrence of material within this interval. The Bracquegnies Formation is overlain unconformably by 3.5 metres of glauconitic sands with phosphatic nodules, representing the so-called 'Tourtia', of Turonian age, equivalent to the 'Mons Conglomerate Bed' (base of Thivencelles Formation; see Robaszynski et al., 2002).

2. The cephalopod assemblage

Several hundred well-preserved, silicified cephalopods were collected by various people (see Acknowledgements) from between 15 and 35 metres above the base of Bracquegnies Formation in the excavation pit. Based on several collections, the fauna is here shown to comprise:

Figure 1. Map of Belgium, showing the location of the excavation pit for the boat lift at Strépy-Thieu, province of Hainaut.

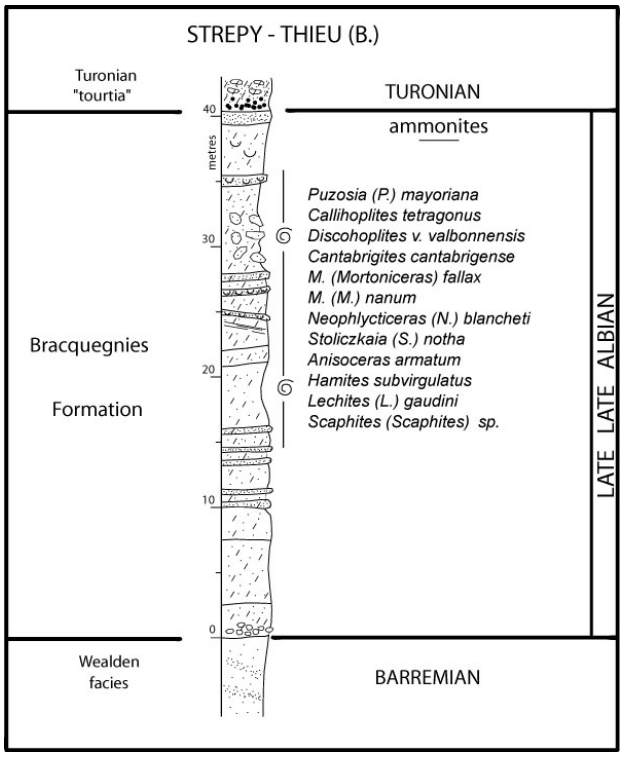

Figure 2. Log of the section, temporarily (1989-1990) exposed in the boat lift construction pit at Strépy-Thieu, with indication of provenance of ammonite taxa recorded herein (modified after Amédro, 2002).

Eutrephoceras clementianum, *Puzosia* (*Puzosia*) *mayoriana*, *Callihoplites tetragonus*, *Discohoplites valbonnensis valbonnensis*, *Cantabrigites cantabrigense*, *Mortoniceras* (*Mortoniceras*) *fallax*, *M.* (*M.*) *nanum*, *Neophlycticeras* (*Neophlycticeras*) *blancheti*, *Stoliczkaia* (*Stoliczkaia*) *notha*, *Anisoceras armatum*, *Hamites subvirgulatus*, *Lechites* (*Lechites*) *gaudini* and *Scaphites* (*Scaphites*) sp. juv. Assemblages are dominated by specimens referred to a highly variable, dimorphic *Callihoplites tetragonus* (well over 250 specimens studied), of which many of the forms of *Callihoplites* described by Spath (1928) are shown to be no more than intraspecific variants.

The age of the Strépy-Thieu assemblage is indicated by the presence of *Mortoniceras* (*M.*) *fallax*, a species originally described from the remanié phosphatised Late Albian fauna at the base of the Lower Cenomanian Cambridge Greensand of Cambridgeshire (eastern England). It was taken as the index of the lowest zone of the upper Upper Albian by Amédro (1981, 1992), and is equivalent to the lowest part of the classic, but now redundant, *Stoliczkaia dispar* Zone of authors. Amédro (2002: 23) defined the *fallax* Zone as the interval between the appearance of *M.* (*M.*) *fallax* and that of *M.* (*Subschloenbachia*) *perinflatum* (Spath, 1922). He rejected *Mortoniceras* (*Subschloenbachia*) *rostratum* (J. Sowerby, 1817) as a zonal fossil because it came from a condensed deposit. But, as Hancock (2003) has already noted, this is not the case. The holotype of *M.* (*S.*) *rostratum* comes from the expanded Upper Greensand of Oxfordshire. Current revision of the faunas from Montlaux, Alpes de Haute-Provence (France), originally described by Latil (1995), observations in Texas (Kennedy et al., 1998), and research in progress on the expanded Col de Palluel section in Hautes Alpes (France), indicate that the interval characterised by *M.* (*M.*) *fallax* is separated from that typified by *M.* (*S.*) *perinflatum* by an interval characterised by *M.* (*S.*) *rostratum*. Accordingly, the following zonal sequence can be recognised in the upper Upper Albian; it corresponds to the classic *Stoliczkaia dispar* Zone of authors, and to the 'Vraconnien' of Amédro (2002):

(youngest)
Arrhaphoceras (*Praeschloenbachia*) *briacensis* Zone
Mortoniceras (*Subschloenbachia*) *perinflatum* Zone
Mortoniceras (*Subschloenbachia*) *rostratum* Zone
Mortoniceras (*Mortonicras*) *fallax* Zone
(oldest)

3. Systematic palaeontology

The following conventions are used to indicate the repositories of specimens mentioned in the text: BMNH – The Natural History Museum, London (formerly British Museum of Natural History); HJJ – H. Jan Janssens Collection (Gulpen); NHMM – Natuurhistorisch Museum Maastricht, Maastricht; OUM – Oxford University Museum of Natural History; SMC – The Sedgwick Museum, Cambridge; STR – Lionel Gaudier (3 avenue du Stade, B-7070 Houdeng-Goegnies, Belgium) and Didier Lelubre (Strépy-Bracquegnies) collections. Dimensions of specimens are given in millimetres; D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus. Figures in parentheses are dimensions as a percentage of diameter, while * in the synonymy list indicates the first description of the species.

Order Nautilida Agassiz, 1847
Superfamily Nautiloidea de Blainville, 1825
Family Nautilidae de Blainville, 1825
Genus *Eutrephoceras* Hyatt, 1894

Type species. *Nautilus Dekayi* Morton, 1834: 33, pl. 8, fig. 4; pl. 13, fig. 4, by original designation (Hyatt, 1894: 555).

Eutrephoceras clementianum *(d'Orbigny, 1840)*
Pl. 8, Figs 8, 9

*1840 *Nautilus Clementianus* d'Orbigny: 77, Pl. 13bis, Figs 1-6.
1960 *Eutrephoceras clementianum* (d'Orbigny) 1840; Wiedmann: 168, Pl. 18, Fig. J (with synonymy).

Types. In his account of the species, d'Orbigny (1840) mentioned numerous specimens from diverse localities in France, and illustrated two, without giving their locality and horizon. All rank as syntypes. The catalogue of the d'Orbigny Collection identifies three specimens from 'Gates, Aube', with the letter 'T', indicating them to be the types. They are presumably the specimens 'Conduit par M. Clément Mulet, sur les tuileries de Gatis, commune de Giraudaux, Aube' mentioned by d'Orbigny (1840: 78). The 'tuilerie de Gaty', situated in the community of Géraudot, southeast of Troyes, nowadays is flooded, being part of the Seine water reservoir there. The quarry which was exploited in the nineteenth century exposed clays with *Lyelliceras lyelli* (Leymerie, 1841), documenting the base of the Middle Albian. Tintant & Gauthier (in Gauthier et al., 2006: 20, Pl. 2, Fig. 5) designated a lectotype for *E. clementianum*, and refigured this specimen.

Material. Five specimens: NHMM JJ 5596; STR 5, 27, 51 and 68.

Description. All specimens are phragmocones of juveniles, 19-39 mm in diameter. Coiling is involute, with a tiny, near-occluded umbilicus, and a depressed, reniform whorl section; the whorl breadth to height ratio is 1.4. Internal moulds are smooth, but where silicified shell is preserved, there is a reticulate ornament of delicate growth lines, longitudinal ridges and striae. The striae are concave and prorsiradiate on the flanks, sweep back and are concave across the ventrolateral shoulders, and form a broad concavity over the venter.

Discussion. Depressed whorl section and reticulate ornament of the juvenile characterise this species. Reference is made to Wiedmann (1960) for a full account of this species, and differences from others referred to the genus.

Occurrence. Middle and Upper Albian, western Europe and southern India.

Order Ammonoidea von Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Desmoceratoidea von Zittel, 1895
Family Desmoceratidae von Zittel, 1895
Subfamily Puzosiinae Spath, 1922a
Genus and subgenus *Puzosia* Bayle, 1878

Type species. *Ammonites planulatus* J. de C. Sowerby, 1827: Pl. 570, Fig. 5 (*non* von Schlotheim, 1820: 59 = *Ammonites mayorianus* d'Orbigny, 1841: 267, Pl. 79, Figs 1-3), by subsequent designation of H. Douvillé (1879: 91).

Puzosia *(Puzosia)* mayoriana *(d'Orbigny, 1841)*
Pl. 8, Figs 15, 16

1827 *Ammonites planulatus* J. de C. Sowerby: Pl. 570, Fig. 5 (*non* von Schlotheim, 1820: 59).
*1841 *Ammonites Mayorianus* d'Orbigny: 267, Pl. 79, Figs 1-3.
1984 *Puzosia (Puzosia) mayoriana* (d'Orbigny, 1841); Wright & Kennedy: 55, Pl. 3, Figs 1, 2, 4, 6, 9-12; Pl. 4, Figs 1, 2, 5-7; Text-Figs 1a, b, 2c, h, m; 3n-r; 4a-e (with synonymy).
1996 *Puzosia (Puzosia) mayoriana* (d'Orbigny, 1841); Kennedy (in Gale et al.): 552, Figs 10f; 11k, l; 14h-n.
2004 *Puzosia (Puzosia) mayoriana* (d'Orbigny, 1841); Kennedy & Jolkičev: 372, Pl. 1, Figs 4-6 (with additional synonymy).
2005 *Puzosia (P.) mayoriana* (Sowerby) [*sic*]; Reboulet et al.: 125, Fig. 3A.
2006 *Puzosia mayoriana* (d'Orbigny, 1841); Kennedy & Juignet (in Gauthier et al.): 96, Pl. 49, Fig. 4a-d.

Type. The lectotype, by subsequent designation of Wright & Wright (1951: 35), is BMNH C9381, the original of J. de C. Sowerby (1827: Pl. 570, Fig. 5), from the Cenomanian Lower Chalk of Hamsey, near Lewes, Sussex. Reference is made to Wright & Kennedy (1984: 56) for a discussion of the complexity of this matter.

Description. A single specimen, STR 16, comprises a 120o fragment of a phragmocone whorl with a maximum preserved whorl height of 12.6 mm. Coiling is evolute, the whorl section depressed, with broadly rounded flanks, ventrolateral shoulders and venter. Two well-developed, narrow constrictions are preserved on the fragment; they are prorsiradiate and feebly convex on the inner flank, concave on the outer flank, project forwards on the ventrolateral shoulders, and cross the venter in a slightly acute, subangular peak. The constrictions are flanked by an adapical collar rib, feeble on the flanks, but strengthened on ventrolateral shoulders and venter. The surface of the shell between constrictions and collar ribs is ornamented by numerous sinuous prorsiradiate striae on the flanks, which strengthen into narrow, crowded ribs on the ventrolateral shoulders, where they are projected forwards and cross the venter in a broad convexity.

Discussion. Wright & Kennedy (1984: 57) provided a comprehensive discussion of this species, to which reference is made.

Occurrence. Upper Albian to Upper Cenomanian; widespread throughout Europe, Africa, southern India and Japan.

Superfamily Hoplitoidea H. Douvillé, 1890
Family Hoplitidae H. Douvillé, 1890
Subfamily Hoplitinae H. Douvillé, 1890
Genus *Callihoplites* Spath, 1925a

Type species. *Ammonites catillus* J. de C. Sowerby, 1827: 123, Pl. 564, by original designation (Spath, 1925a: 81).

Callihoplites tetragonus *(Seeley, 1865)*
Pl. 1, Figs 1-18; Pl. 2, Figs 1-26; Pl. 3, Figs 1-24; Pl. 4, Figs 1-5; Pl. 5, Figs 1-6, 10-17

*1865 *Ammonites raulinianus* var. *tetragonus* Seeley: 243.
1865 *Ammonites acanthonotus* Seeley: 234, Pl. 11, Fig.5.
1928 *Callihoplites tetragonus* (Seeley); Spath: 210 (*pars*), Pl. 22, Figs 1, 2; Pl. 23, Fig.11; Text-Fig. 66a-c; *non* Pl. 22, Figs 9, 10 (var. *dorsetensis*).
1928 *Callihoplites gymnus* (Seeley MS) Spath: 213, Pl. 22, Figs 3, 4.
1928 *Callihoplites advena* var. *plana* Spath: 215.
1928 *Callihoplites acanthonotus* Spath: 216, Pl. 24, Fig. 14; Text-Figs 68a-c, 69b, c.
1928 *Callihoplites atavus* Spath: 219, Pl. 24, Fig. 22.
1928 *Callihoplites paradoxus* Spath: 219, Pl. 23, Fig. 8.
1928 *Callihoplites pulcher* Spath: 227, Pl. 24, Figs 11, 15; Text-Fig. 74a-d.
1928 *Callihoplites fuscus* Spath: 228, Pl. 24, Fig. 8.
1928 *Callihoplites senilis* Spath: 229 (*pars*), Pl. 23, Fig. 7; *non* Pl. 24, Fig.2 (var. *serrigata*); *non* Pl. 24, Fig. 4 (var. *laevigata*).
1968 *Callihoplites* aff. *gymnus* (Seeley); Renz: 39, Pl. 5, Fig. 7; Text-Fig.14i.
1968 *Callihoplites pulcher pulcher* Spath; Renz: 42, Pl. 4, Figs 16-18 (with additional synonymy).
1968 *Callihoplites pulcher lophotus* Spath; Renz: 43, Pl. 5, Fig.1; Text-Fig.14d (with additional synonymy).
1968 *Callihoplites acanthonotus* (Seeley); Renz: 43, Pl. 5, Fig. 2; Text-Fig.14m (with additional synonymy).
2002 *Callihoplites tetragonus* (Seeley); Amédro: 62, Pl. 6, Figs 1, 3.
2002 *Callihoplites seeleyi* (Spath); Amédro: 62, Pl. 6, Fig. 4.
2002 *Callihoplites pulcher* Spath; Amédro: 62, Pl. 6, Fig. 6.
2002 *Callihoplites* aff. *senilis* Spath; Amédro: 62, Pl. 6, Fig. 8.

Type. The holotype is SMC B1581, the original of Seeley (1865: 243), from the remanié phosphatised Late Albian fauna at the base of the Cenomanian Cambridge Greensand of Cambridgeshire (see Pl. 5, Figs 13-15 here).

Material. More than 250 specimens, including NHMM JJ 5732, 5734, 5736-5737, 5739-5740, 5743, 5746, 5752, 5764-5770, 5772, 5777-5778, 5782-5784, 5788, 5792, 5804, 12625-12626; STR a-c, 2, 7-9, 11-15, 18-19, 21-24, 26, 28, 41, 45, 48-49, 55, 82, 171, 218, 236, 240 and 263, plus unregistered specimens in the Gaudier and Janssens (HJJ) collections.

Description. All *Callihoplites* from Strépy-Thieu are here assigned to a single variable species that ranges from robust, coarsely ornamented individuals to more compressed, gracile ones with weak ornament. The inner whorls of a typical robust variant are shown by STR 218 (Pl. 1, Figs 1-5). At a diameter of 14 mm, coiling is moderately involute, with a depressed, reniform whorl section. Ornament comprises twelve broad, low ribs on the umbilical wall that bear coarse, conical umbilical tubercles. The outer flanks, ventrolateral shoulders and venter are smooth. As size increases, ribs appear at diameters of around 5-6 mm, strengthening progressively. The bullae give rise to pairs of prorsiradiate concave ribs, with additional ribs intercalated; with increasing diameter these develop into ventrolateral bullae aligned in an oblique, prorsiradiate position on the venter, where they are alternate rather than opposite, and linked by low, broad ribs in a distinctive zigzag fashion. The largest robust phragmocone seen is STR 8a, which is 45 mm in diameter (Pl. 4, Fig. 1). It and comparable specimens have an umbilicus that comprises around 30 % of the diameter, and is of moderate depth. The umbilical seam is notched to accommodate the bullae of the previous whorl, the umbilical wall concave and inclined outwards. The intercostal section is depressed trapezoidal, with the greatest breadth outside the umbilical shoulder. The costal whorl section is depressed hexagonal, the faces of the hexagon concave. Low broad ribs arise at the umbilical seam, strengthen across umbilical wall and shoulder, and develop into massive conical umbilical bullae, 10-11 per whorl. These give rise to pairs of ribs that link to coarse ventral bullae in zigzag fashion. The ventral clavi are elongated obliquely and give rise to low, broad and coarse ribs that decline progressively in elevation towards the mid-venter, such that the rib profile is concave. The clavi alternate in position on the two sides of the venter: the ribs, in consequence, follow a distinctive zigzag course. STR 8a (Pl. 4, Fig. 1), a macroconch, preserves a 240o sector of body chamber at the umbilical seam, and approximately 120º at the ventrolateral shoulder. The whorl section becomes compressed. The umbilicolateral tubercles are conical at the adapertural end of the body chamber, but weaken and transform into bullae, linked to the umbilical shoulder by a narrow, prorsiradiate rib. These tubercles give rise to groups of up to four low, delicate ribs that link in loop and zigzag pattern to the progressively weakening ventral clavi. The coarse ventral ribs of the phragmocone decline, and are replaced by low, broad, fold-like ribs, elevated at the mid-venter, which thus has a very obtusely fastigiate section. Phragmocones such as STR 240 (Pl. 2, Figs 17, 18), a microconch, have

a much less robust ornament, and the very simple pattern of juvenile ribbing described above is succeeded by a phase with bullae giving rise to three weak ribs that loop and zigzag between umbilicolateral and ventral tubercles. There are many variants of this type, with progressively weaker umbilicolateral tuberculation and increasing strength and number of flank ribs, leading to individuals such as STR 15 (Pl. 3, Figs 1, 2). In this specimen, over 40 ribs per whorl on the flanks correspond to around ten delicate, conical umbilicolateral tubercles that change into bullae towards the end of the adult phragmocone. With increasing compression, there are involute individuals such as STR 23 (Pl. 3, Figs 22, 23), where relatively coarsely tuberculate inner whorls are succeeded by late phragmocone whorls that are very feebly bullate, the bullae giving rise to bunches of strong flexuous ribs that link in groups at the ventral tubercles, or zigzag between. The narrow venter of these specimens is sinuous in profile, as a result of the alternate positions of the ventral clavi, feebly convex, and lack ribs. The extreme of variation is shown by STR 236 (Pl. 3, Fig. 24), where the dense, crowded, falcoid ribs and striae nearly efface on the outer flank, and some interspaces are deepened, and constriction-like.

Maturity in all these variants is characterised by progressive weakening of the umbilicolateral bullae in robust variants, and their total disappearance in gracile ones. The whorls become relatively higher, the ventral ribbing effaces, the venter becoming rounded and very obtusely fastigiate. Because most specimens retain silicified shell, sutures are rarely exposed, and it is not possible to detect either septal crowding or the position of the final septum. None of the specimens preserves the adult aperture, but body chambers may have occupied as much as 240o of the outer whorl. The largest adults seen are up to 55 mm in diameter, and although incomplete, are interpreted as macroconchs. Small adults, up to 45 mm diameter, are interpreted as microconchs.

Discussion. This large assemblage demonstrates wide intraspecific variation in a species of *Callihoplites* which reaches maturity at a small adult size. This small adult size alone distinguishes the present assemblage from large *Callihoplites* of the group of *auritus* (J. Sowerby, 1816), namely *C. catillus* (J. de C. Sowerby, 1827), *C. patella* Spath, 1927, *C. strigosus* Spath, 1927, *C. formosus* Spath, 1927 and *C. horridus* Spath, 1927, all of which may be no more than intraspecific variants of a single, dimorphic species. Instead, the material falls into the same size range as many of the adult *Callihoplites* from the younger, remanié Albian material incorporated into the Lower Cenomanian Cambridge Greensand of eastern England (Seeley, 1865), and also present at La Vraconne in Switzerland (Renz, 1968) and at Salazac (Gard, France; see Breistroffer, 1940; Latil, 1995; Amédro, 2002).

The earliest available name for material of the type found at Strépy-Thieu is *Ammonites raulinianus* var. *tetragona* of Seeley (1865), the flank ornament of which can be matched in many of our specimens. But the macroconch holotype of *tetragona* (see Spath, 1928: 210, Text-Fig. 66; and Pl. 5, Figs 13-15 here) has a more depressed whorl section than any of our material and a correspondingly broader venter. As Spath (1928: 211) noted, 'this species is one of the commonest in the "Cambridge Greensand", but like other highly ornamented ammonites, it is very variable. Seeley's type is an extreme, unusually geometrical and inelegant; and if a narrow interpretation of the present species were attempted, it would be difficult to match it among the hundreds of specimens available. Yet they obviously all belong to the same species, although this is connected by transitions with the various allied forms here separated for systematic convenience.'

Spath (1923-1943) described sixteen species of *Callihoplites* from the Cambridge Greensand, and there are many transitional forms between them, as he freely admitted. Because Spath did not recognise dimorphism, and compared macroconch phragmocones with adult microconchs with body chamber preserved, many of his Cambridge Greensand species can be synonymised on this basis alone. But the phosphatised Albian fossils found reworked into the Cambridge Greensand may represent a significant time interval rather than a single horizon. There is a marked unconformity between Albian Gault Clay and Cenomanian Cambridge Greensand, with all of the *Stoliczkaia dispar* Zone and part of the Lower Cenomanian absent according to Hart (1973). The reworked Albian phosphates at the base of the Cambridge Greensand may have been derived from a single phosphate nodule bed in the now eroded Gault Clay, or from several such nodule beds. As a result, it is not possible to distinguish between what may be variation in a contemporaneous population from variation through time in an evolutionary morphocline. The Strépy-Thieu assemblage, coming from an expanded succession, allows, for the first time, the recognition of the range of intraspecific variation in *Callihoplites* of this age. It reveals that a number of Cambridge Greensand species and varieties of Spath and later authors are intraspecific variants of *C. tetragonus,* whereas others are not present in the Strépy-Thieu material. They may represent one or more other species, of slightly different age.

Our collection has been carefully compared with the type material and other Cambridge Greensand specimens in the collections of the Sedgwick Museum, Cambridge (SMC) and of the Natural History Museum, London (BMNH). Key type and other specimens are shown here in Pl. 5, Figs 4-22. This study is the basis for the synonymy above, as discussed below.

The following are regarded as synonyms of a variable *Callihoplites tetragonus* on the basis of the Strépy-Thieu assemblages:

Callihoplites tetragonus (Seeley, 1865) var. *vulgaris* Spath, 1928: the holotype is BMNH C30373, the original of Spath (1928: Pl. 22, Fig. 1), a macroconch measuring 51 mm in diameter. It is a relatively stout individual, with strong lautiform ribbing, as seen in STR 7 (Pl. 3, Fig. 12) and STR 22 (Pl. 2, Figs 24, 25).

Callihoplites tetragonus (Seeley, 1865) var. *compressa* Spath, 1928: the holotype is BMNH C25182, the original of Spath (1928: Pl. 22, Fig. 2), a macroconch measuring 53 mm in diameter; corresponding nuclei are STR 18 (Pl. 3, Figs 14, 15). The most robust Strépy-Thieu individuals, STR 49 (Pl. 2, Figs 7, 8) and STR 28 (Pl. 2, Figs 9-11) resemble what Spath (1928: 221) referred to as transitions between *C. robustus* Spath, 1928 (220, Pl. 23, Fig.12; Text-Fig.70a, b) and *C. tetragonus* var. *vulgaris* (e.g., BMNH C39658), but these specimens are merely stout *C. tetragonus* var. *vulgaris* in morphological terms, lacking the crowded ribs of *robustus,* an ornament type not represented in the Strépy-Thieu material.

Callihoplites fuscus Spath, 1928 (228, Pl. 24, Fig. 8) is based on a macroconch (the holotype is BMNH C32214), of 70 mm in diameter. Comparable examples in the Strépy-Thieu assemblage include STR 23 (Pl. 3, Figs 22, 23).

Callihoplites senilis Spath, 1928 (229, Pl. 23, Fig. 7; Pl. 24, Figs 2, 4, 13) is based on an adult macroconch (the holotype is BMNH C32211; see Spath, 1928: Pl. 23, Fig. 7), 42 mm in diameter, with fine lautiform ribbing on the phragmocone which persists in subdued form on the body chamber. The corresponding microconch is *C. fuscus. Callihoplites senilis laevigata* Spath, 1928 (230, Pl. 24, Fig. 4) and *C. senilis serrigera* Spath, 1928 (230, Pl. 24, Fig. 2), both based on adult microconchs, do not find a match in the Strépy-Thieu assemblage.

Callihoplites acanthonotus (Seeley, 1865) is based on a pathological specimen, SMC B1484 (the holotype; compare Spath, 1928: Text-Fig. 68; and see Pl. 5, Figs 4-6 here) that has suffered non-lethal damage to the shell, resulting in a rounded venter on the phragmocone, with a thickened ventral rib that strengthens progressively on the body chamber, producing a siphonal bulla, and distinctive crenulated profile to the internal mould. The specimen may be an incomplete microconch. Pathology apart, the lautiform flank ribbing is matched in many of the Strépy-Thieu specimens, e.g. STR 2 (Pl. 3, Fig. 13 = Amédro, 2002: Pl. 6, Fig. 1), STR 14 (Pl. 3, Figs 3-5) and STR 13 (Pl. 3, Fig. 6).

Callihoplites atavus Spath, 1928 (219, Pl. 24, Fig. 22) is based on a microconch (the holotype is BMNH C39640); it finds a match in specimens such as STR 19 (Pl. 3, Figs 17-19), with a moderately strongly ornamented phragmocone and a feebly ornamented body chamber.

Callihoplites advena var. *plana* Spath, 1928 (215): the holotype is BMNH C31337, a Cambridge Greensand example that resembles specimens such as STR 236 (Pl. 3, Fig. 24) and STR 8a (Pl. 4, Fig. 1). The holotype of *C. advena* itself is BMNH C32222, a specimen from an unknown locality in the expanded Upper Albian Upper Greensand of southern England, possibly Oxfordshire according to Spath. It is a larger and probably earlier species than the present material, and does not find a match in the Strépy-Thieu assemblage.

Callihoplites paradoxus Spath, 1928 (219, Pl. 23, Fig. 8): the holotype is BMNH C32212, a compressed microconch that corresponds to STR 15 (Pl. 3, Figs 1, 2).

Callihoplites pulcher Spath, 1928 (227, Pl. 24, Figs 11, 15a, b; Text-Fig. 74a-d): the holotype is BMNH C32220, a microconch (Spath, 1928: Text-Fig. 74b). This finds a match in an unregistered specimen from Strépy-Thieu in the Janssens Collection (Pl. 5, Figs 1-3).

Callihoplites gymnus Spath, 1928 (213, Pl. 22, Figs 3, 4): the holotype is SMC B1644. This previously unfigured specimen is shown here in Pl. 5, Figs 10-12. It is an adult microconch, 45 mm in diameter, of a depressed, coarsely ornamented form. This specimen is very worn; the phragmocone whorls resemble certain of the Strépy-Thieu specimens (e.g., Pl. 2, Figs 7-11).

Other species, and their relationships with *C. tetragonus*, are as follows:

Callihoplites seeleyi (Spath, 1925): the holotype is BMNH C30368 (Spath, 1928: Pl. 21, Fig. 5), an adult microconch with strong lautiform ribbing on the phragmocone that is lost on the body chamber, which bears strong ventral clavi. This is a morphology not matched in the Strépy-Thieu material, although the phragmocone corresponds to that of STR 45 (Pl. 2, Figs 4-6). *Callihoplites seeleyi* var. *crenata* Spath, 1928 is based on BMNH C25168, the original of Spath (1928: Pl. 21, Fig. 9). It cannot be matched in the Strépy-Thieu material.

Callihoplites cratus (Seeley, 1865) (240, Pl. 21, Fig. 2): the lectotype is SMC B1517 (see Pl. 5, Figs 18, 19 here), a phragmocone 60 mm in diameter, presumably of a macroconch. It is a much larger than the Strépy-Thieu material, with a wide, crater-like umbilicus and strong, narrow ribs that loop to numerous blunt ventral clavi.

Callihoplites robustus Spath, 1928 (220, Pl. 23, Fig. 12; Text-Fig. 70a, b): the holotype is BMNH C876. This specimen (Spath, 1928: Text-Fig. 70) is a large phragmocone, again presumably of a macroconch, 60 mm in diameter, with a wide umbilicus, strong umbilical bullae and narrow, sharp, lautiform ribbing, the ribs linking to blunt ventrolateral clavi. It is no more than a robustly ornamented *C. cratus*.

Callihoplites leptus (Seeley, 1865) (240, Pl. 10, Fig. 5): the holotype is SMC B1537 (see Pl. 5, Figs 20-22 here). It has suffered considerable *post-mortem* crushing, producing a very compressed whorl section, and retains phosphatised shell. There are indications of a further 180o of whorl, now lost; the position of the final septum cannot therefore be determined. It is no more than a finely ribbed variant of *C. cratus*.

Callihoplites leptus var. *laevis* Spath, 1928 (226, Pl. 23, Fig. 6) is based on BMNH C4820, an adult body chamber with progressively weakening and effaced ornament, and rounding of the venter, these supposedly distinctive features (compare Spath) being merely adult modifications of a probable microconch.

Callihoplites glossonotus (Seeley, 1865) (235, Pl. 10, Fig. 4): the holotype is SMC B1485 (see Pl. 5, Figs 7-9 here). This is a pathological individual that has suffered sublethal damage in life, producing a rounded venter with a strong ventral rib. It is a possible synonym of *C. cratus*, as is BMNH C31128, the larger, non-pathological specimen figured by Spath (1928: Pl. 23, Fig. 2). The aspect of *C. cratus* and its synonyms, discussed above, in terms of both size and ornament, sets them apart from the other Cambridge Greensand species, and links them to the older species of the *Callihoplites auritus* group, as Spath acknowledged (1928: 221).

The holotype of *Callihoplites vraconensis vraconensis* (Pictet & Campiche, 1860) (231, Pl. 31, Fig.1a-c), refigured by Renz (1968: Pl. 5, Fig. 3), is no. L39878 in the collections of the Musée Géologique de Lausanne. It is a phosphatic internal mould of a phragmocone 35 mm in diameter, with a whorl breadth to height ratio of 0.91 according to the figures in Renz, eight prominent umbilical bullae that give rise to groups of three ribs that link to 24 ventral clavi, the mid-venter smooth, and raised into a low, blunt, rounded ridge. It cannot be matched in the Strépy-Thieu material, and represents a younger species, transitional in some respects to the genus *Arrhaphocera*s Whitehouse, 1927.

Occurrence. *Mortoniceras* (*M.*) *fallax* Zone, eastern England, southern Belgium and southeast France.

Genus *Discohoplites* Spath, 1925a

Type species. *Ammonites coelonotus* Seeley, 1865 (237, Pl. 10, Fig. 2 only), by original designation (Spath, 1925a: 83).

Discohoplites valbonnensis valbonnensis
(Hébert & Munier-Chalmas, 1875)
Pl. 4, Figs 6-23

*1875 *Ammonites valbonnensis* Hébert & Munier-Chalmas: 114, Pl. 4, Fig. 3.
1968 *Discohoplites valbonnensis valbonnensis* (Hebert [*sic*] et Munier-Chalmas); Renz: 23, Pl. 2, Fig. 6 (with synonymy).
1996 *Discohoplites valbonnensis valbonnensis* (Hébert & Munier-Chalmas, 1875); Kennedy (in Gale et al.): 553, Fig. 15b.
2002 *Hyphoplites (Discohoplites) valbonnensis* (Hébert & Munier-Chalmas); Amédro: 32, 62; Pl. 2, Fig. 8; Pl. 6, Figs 2, 5.

Type. Holotype, by monotypy, is the original of Hébert & Munier-Chalmas (1875: 114, Pl. 4, Fig. 3), from the Upper Albian of Salazac (Gard, France).

Material. Twenty specimens: NHMM JJ 5795; STR d, 29, 67, 91-92, 96, 114, 119, 128, 233, 253 and 267, plus seven in HJJ (unregistered).

Description. Specimens range from 12.3 to 38.2 mm in diameter. Coiling is moderately involute, the umbilicus comprising 24-26% of the diameter, shallow, with a low, flattened, outward-inclined wall, and narrowly rounded umbilical shoulder. The whorl section is compressed, with rounded inner flanks, flattened, convergent outer flanks, rounded ventrolateral shoulders, and a flattened venter with a narrow, deep, mid-ventral groove. Small umbilical bullae, 13-20 per half whorl, perch on the umbilical shoulder. They give rise to pairs of ribs that are blunt, straight and prorsiradiate on the inner flank, flexed back and convex at mid-flank, where they give rise to one or two concave ribs that form 'blades' to the corresponding straight 'handles' of the sickle-shaped ribs. Additional 'blades' intercalate, to give as many as 46 ribs per whorl at the ventrolateral shoulder. The ribs flatten markedly on the outer flank, sweep forwards across the ventrolateral shoulder, weakening progressively and forming an acute ventral chevron, interrupted by the mid-ventral groove.

Discussion. This homogeneous group of specimens show *D. v. valbonnensis* to be a well-defined species. There are no individuals that correspond to the range of species referred, with *D. valbonnensis*, to a broadly conceived *D. coelonotus*, as proposed by Scholz (1979: 72). *Discohoplites c. dorsetensis* Wright & Wright, 1949 (480, Pl. 28, Fig. 4) is a younger subspecies, with finer, more angular ribbing, and prominent umbilical tubercles on the inner whorls.

Occurrence. *Mortoniceras* (*M.*) *fallax* to *Arraphoceras* (*P.*) *briacensis* zones, southern and eastern England, southern Belgium, southeast France, Switzerland and Hungary.

Superfamily Acanthoceratoidea de Grossouvre, 1894
Family Brancoceratidae Spath, 1934
Subfamily Brancoceratinae Spath, 1934
Genus *Cantabrigites* Spath, 1933

Type species. *Mortoniceras* (*Cantabrigites*) *cantabrigense* Spath, 1933: 438, Pl. 41, Figs 3, 4; Pl. 45, Fig. 4, by original designation (Spath, 1933: 436).

Cantabrigites cantabrigense *Spath, 1933*
Pl. 8, Figs 1-3, 5, 10-12; Pl. 10, Fig. 3

*1933 *Mortoniceras* (*Cantabrigites*) *cantabrigense* Spath: 438, Pl. 41, Figs 3, 4; Pl. 45, Fig. 4.

1933 *Mortoniceras* (*Cantabrigites*) *subsimplex* Spath: 439, Pl. 39, Fig. 3; Pl. 42, Figs 3, 4; Pl. 44, Fig. 7.
1968 *Mortoniceras* (*Cantabrigites*) *cantabrigense cantabrigense* Spath; Renz: 58, Pl. 10, Figs 10a, b, 24; Text-Figs 20h, 21a, h (with synonymy).
1968 *Hysteroceras carinatum* Spath; Renz: 62, Pl. 11, Fig. 3a, b.
1979 *Hysteroceras* (*Cantabrigites*) *cantabrigense* (Spath, 1932); Scholz: 115, Pl. 29, Figs 11-13; Pl. 30, Figs 1-33; Text-Figs 40, 41.
1996 *Cantabrigites cantabrigense* Spath, 1933; Kennedy (in Gale et al.): 555, Figs 16i-k, 17f, h-j.
2002 *Cantabrigites subsimplex* (Spath); Amédro: 62, Pl. 9, Fig. 2.

Type. Holotype, by original designation of Spath (1933: 438), is SMC 81, the original of Spath (1933: Pl. 41, Fig. 2), from the remanié phosphatic Late Albian fauna at the base of the Lower Cenomanian Cambridge Greensand of Cambridgeshire.

Material. Six specimens: STR 64, 64a, 122, 123, 126 and 171.

Description. Specimens range from 10.6 to 12.6 mm in diameter. Coiling is very evolute; the umbilicus comprises 36-39% of the diameter and is shallow, with a low, feebly convex wall and more narrowly rounded umbilical shoulder. The whorl section is compressed (whorl breadth to height ratio 0.8 in STR 64a), with feebly convex, subparallel flanks, narrowly rounded ventrolateral shoulders, a narrow, very obtusely fastigiate venter, and a sharp, prominent, siphonal keel. The shell is near-smooth to a diameter of around 5 mm. Ornament first appears on the ventrolateral shoulders, in the form of coarse, prorsiradiate ribs, wider than the interspaces, and projected strongly forwards on the venter, where they rapidly decline, not extending to the mid-ventral keel. With increasing size, ornament comes to extend across the whole of the flanks. In the largest specimens, ornament comprises prominent bullae, perched on the umbilical shoulder, and separated by narrower interspaces, producing a distinctive notched appearance to the umbilical margin. These bullae give rise to pairs of low, broad, recti- to feebly rursiradiate ribs that efface on the mid-flank region, and connect to the coarse ventrolateral ribs, which are twice as numerous as the umbilical bullae.

indentA further specimen (STR 9; see Amédro, 2002: Pl. 9, Fig. 2a, b), now lost, is shown in Pl. 10, Fig. 3. The umbilicus comprises 30% of the diameter at an estimated diameter of 31 mm, with twelve weak umbilical bullae on the outer half whorl. These give rise to one or two primary ribs, with occasional additional intercalated ribs, to give a total of eighteen ribs per half whorl at the ventrolateral shoulder, where the ribs are strengthened into a feeble ventrolateral tubercle.

Discussion. These specimens are referred to *C. cantabrigense* on the basis of their ribbing style and feeble tuberculation; *C. subsimplex* comprises merely the more coarsely ornamented variants of the species.

Occurrence. *Mortoniceras* (*M.*) *fallax* to *M.* (*S.*) *perinflatum* zones, eastern England, southern Belgium, southeast France, Switzerland and Hungary.

Subfamily Mortoniceratinae H. Douvillé, 1912
Genus and subgenus *Mortoniceras* Meek, 1876

Type species. *Ammonites vespertinus* Morton, 1834: 40, Pl. 17, Fig. 1, by original designation (Meek, 1876: 448).

Mortoniceras *(Mortoniceras)* fallax
(Breistroffer, 1940)
Pl. 6, Figs 1-3; Pl. 7, Figs 1, 2; Pl. 10, Figs 8-11, 16

1932 *Mortoniceras* (*Pervinquieria*) *rostratum* (J. Sowerby); Spath: 400 (*pars*), Pl. 40, Fig. 1 only.
1932 *Mortoniceras* (*Pervinquieria*) *kiliani* (Lasswitz); Spath: 408, Pl. 38, Fig. 1.
*1940 *Pervinquieria fallax* Breistroffer: 137.
1940 *Pervinquieria kiliani* Lasswitz, var. *alstonensis* Breistroffer: 139.
1979 *Pervinquieria* (*Pervinquieria*) *fallax* Breistroffer, 1940; Scholz: 109, Pl. 29, Figs 3-5, 7, 8, 10.
1995 *Mortoniceras fallax* (Breistroffer, 1940); Latil: 71, Pl. 3, Figs 1-3; Pl. 4.
2002 *Mortoniceras* (*Mortoniceras*) *fallax* (Breistroffer); Amédro: 32, 62, Pl. 2, Figs 2, 3; Pl. 7.
2002 *Mortoniceras* (*Mortoniceras*) aff. *fallax* (Breistroffer); Amédro: 62, Pl. 8.
2002 *Mortoniceras* (*Mortoniceras*) *pachys* (Seeley); Amédro: 62, Pl. 9, Fig. 1.
2002 *Mortoniceras* (*Mortoniceras*) sp. [voisin de *M.* (*M.*) *fallax*]; Amédro: 62, Pl. 9, Fig. 3.

Type. The holotype, by original designation, is SMC B56 (see Pl. 10, Figs 9-11 herein), the original of Spath (1932: Pl. 40, Fig. 1 only), from the remanié phosphatised Late Albian fauna at the base of the Lower Cenomanian Cambridge Greensand of Cambridgeshire.

Material. Two specimens: STR 1 and 1a.

Description. The earliest growth stages seen in the material from Strépy-Thieu were represented by two additional specimens (STR 6, STR 7), both now lost. The smallest of these was a juvenile (Pl. 10, Fig. 8) retaining silicified shell, the inner whorls an estimated 48 mm in diameter, with part of a further whorl preserved to a whorl height of an estimated 25 mm. There are 24 umbilical bullae of variable strength on the penultimate whorl. These give rise to one or two ribs, with occasional intercalated ribs, the ribs becoming predominantly primaries as size increases. There is a very feeble lateral tubercle that migrates progressively outwards and strengthens as size increases, and a much stronger ventrolateral clavus.

The second specimen (Pl. 10, Fig. 16) was a crushed individual, measuring 115 mm in diameter, again retaining silicified shell. There are 11-12 coarse umbilical bullae of variable strength on the outer half whorl. The bullae give rise to one or two coarse, prorsiradiate ribs, with occasional ribs intercalated between, to give a total of 18-20 ribs on the outer half whorl. All ribs bear a lateral tubercle that strengthens and migrates progressively outwards as size increases, together with a well-developed ventrolateral clavus.

STR 1a (Pl. 6) is a well-preserved phragmocone, 160 mm in diameter. Coiling is very evolute, with only 25% approximately of the previous whorl covered. The wide umbilicus comprises 40% of the diameter and is of moderate depth, the convex wall merging with a broadly rounded umbilical shoulder. The whorl section is rounded-trapezoidal in intercostal section, with a broad fastigiate-carinate venter and a trapezoidal-polygonal costal section. There are fourteen primary ribs on the outer whorl; these are low, broad and coarse on the umbilical wall and shoulder, where most give rise to single coarse, broad, straight, prorsiradiate ribs, with an occasional adapical rib feebly connected to a bulla, and single intercalated ribs between primaries. The primary ribs bear a strong conical to feebly bullate lateral tubercle; the intercalated ribs either lack such a tubercle or have a weaker lateral tubercle than the primaries. All ribs bear a coarse, conical ventrolateral tubercle that gives rise to a coarse, prorsiradiate rib that sweeps forwards across ventrolateral shoulders and venter, declines markedly and forms a feebly obtuse ventral chevron with the mid-ventral keel at the apex.

STR 1 (Pl. 7) is an adult, with ventral regions of the last half whorl broken away, so that the original diameter can only be estimated as approximately 200 mm. Coarse bullae, perched on the umbilical shoulder, give rise to pairs of ribs, while single ribs intercalate between primaries, to give a total of 25 ribs per whorl. Primary ribs and some intercalated ribs bear a weak lateral tubercle. All ribs bear a strong, conical-clavate, inner ventrolateral tubercle. These gives rise to a prorsiradiate rib that declines progressively across the venter. On the body chamber, the primary and intercalated ribs alternate regularly at the adapical end, giving rise to exclusively primary ribs towards the aperture. These are coarse, straight and prorsiradiate, with well-developed umbilical and outer lateral bullae and strong conical ventrolateral tubercles. Towards the adult aperture, the ribs become markedly prorsiradiate and the lateral tubercles efface. Coarse strigations are preserved on the adapical part of the body chamber.

Discussion. *Mortoniceras* (*M.*) *fallax* co-occurs with *M.* (*M.*) *pachys* (Seeley, 1865) (227, Pl. 9, Fig. 4; see also Spath, 1932: 405, Text-Figs 130d, 138, 139) in the reworked Late Albian phosphates at the base of the Cenomanian Cambridge Greensand in eastern England. The holotype of *M.* (*M.*) *pachys* is SMC B54, a phosphatic internal mould, 50.4 mm in diameter, with patches of phosphatised shell preserved on the side figured by Seeley and Spath, the umbilicus blocked by phosphatised sediment. Coiling appears to have been moderately evolute, the umbilicus shallow, comprising an estimated 40% of the diameter. The umbilical wall is flattened and inclined outwards. The umbilical shoulder is broadly rounded. The whorl section is slightly depressed, with flattened, subparallel flanks, and a whorl breadth to height ratio of 1.1. The ventrolateral shoulders are quite narrowly rounded, the venter broad, and feebly convex to very obtusely fastigiate. There are 12-13 delicate primary ribs on the outer half whorl. They arise at the umbilical seam, and strengthen into delicate umbilical bullae. These give rise to pairs of delicate primary ribs, and there are also long intercalated ribs, to give a total of 24-25 ribs on the outer half whorl of the specimen at the ventrolateral shoulder. The ribs are delicate, crowded, straight and prorsiradiate on the inner flank, flexing back and convex at mid-flank, broadening, strengthening and flexing forwards across the ventrolateral shoulder. They project strongly forwards across the venter, where they are concave and form an obtuse chevron. They decline progressively across the venter and are separated from the siphonal keel by a narrow, smooth groove. There is a shallow, spiral depression on the inner flank, a very feeble mid- outer lateral bulla, and weak ventrolateral tubercle. The thickened ribs on the ventrolateral shoulder bear delicate spiral ridges and grooves. It differs from the holotype of *M.* (*M.*) *fallax* in having much finer, crowded ribbing, the ribs markedly flexuous, and incipiently falcoid. Also distinctive are the pronounced spiral lateral depression, and the broad, very obtusely fastigiate venter. Many of these characters are shared by the large Madagascan example figured by Spath (1932: Text-Fig. 139), and the large example from Armenia figured by Atabekian (1992: Pl. 125, Fig. 1; Pl. 127, Fig. 5). Spath had already noted in 1932 (406) the presence, in the Cambridge Greensand, of passage forms to what he termed *Mortoniceras kiliani*, that is to say *Mortoniceras fallax* of subsequent authors, and Amédro (1992: 212) suggested that *pachys* was the compressed and *fallax* the stout form of the species. The present material is too limited to clarify the matter, and all specimens referred to *M. fallax* here are coarsely ornamented, and very distinct from those referred to *M. pachys* by authors.

Mortoniceras (*M.*) *fallax* is closely related to *M.* (*M.*) *inflatum* (J. Sowerby, 1818). This species was comprehensively revised by Amédro et al. (2004). The species differ most obviously in that the lateral tubercle persists and strengthens through ontogeny in *M. fallax*, whereas it weakens progressively in *M. inflatum*. The whorl section of adult *M. fallax* is also distinctive, with the well-developed ventrolateral tubercles directed upwards and outwards from the venter.

Occurrence. *Mortoniceras* (*M.*) *fallax* Zone, southern and eastern England, southern Belgium, southeast France, Hungary, Armenia and Madagascar.

Mortoniceras *(Mortoniceras)* nanum *Spath, 1933*

Pl. 8, Figs 4, 6, 7, 13, 14; Pl. 9, Figs 1-8

*1933 *Mortoniceras* (*Pervinqueria*?) *nanum* Spath: 411, Pl. 43, Fig. 6; Pl. 46, Figs 4, 5; Text-Fig. 141.

1979 *Hysteroceras* (*Cantabrigites*) *cantabrigense subquadratum* (Spath, 1933); Scholz: 116 (*pars*), Pl. 30, Figs 15, 19, 21, 22 only.

2002 *Mortoniceras* (*Mortoniceras*) *nanum* Spath; Amédro: 62, Pl. 2, Fig. 12.

Type. The holotype, by original designation, is BMNH C35845, the original of Spath (1933: Text-Fig. 141), from the remanié Late Albian fauna at the base of the Lower Cenomanian Cambridge Greensand of Cambridgeshire.

Material. Fourteen specimens: NHMM JJ 5730-5731; STR 63, 110, 115, 117, 124-125, 127, plus five (HJJ, unregistered).

Description. Juveniles range from 12-22 mm in diameter, and include both robust and gracile individuals. The smallest robust individual is STR 110 (Pl. 8, Fig. 4), 12 mm in diameter. Coiling is very evolute, the umbilicus comprising 37% of the diameter, of moderate depth, with a flattened, outward-inclined wall and narrowly rounded shoulder. The intercostal whorl section is trapezoidal, the costal whorl section depressed polygonal. Sixteen coarse bullae perch on the umbilical shoulder and give rise to one or two ribs, with occasional long intercalated ribs, to give a total of 22 ribs per whorl at the ventrolateral shoulder. The ribs are coarse, straight to feebly convex, and recti- to feebly prorsiradiate. All ribs bear a conical inner ventrolateral tubercle and an outer ventrolateral clavus, borne on a strong, prorsiradiate rib. STR 127 (Pl. 8, Figs 6, 7) is interpreted as a gracile juvenile, with a less-depressed whorl section, and feeble ornament, the inner and outer ventrolateral tubercles borne on a strengthened rib.

An unregistered specimen in the Janssens Collection (Pl. 9, Figs 4-6) is 22 mm in diameter. Coiling is very evolute, the umbilicus comprising 41% of the diameter, of moderate depth, with a flattened, outward-inclined umbilical wall and narrowly rounded umbilical shoulder. The whorl section is trapezoidal in intercostal section and polygonal in costal section, with the greatest breadth at the umbilical bullae. Eighteen primary ribs per whorl arise at the umbilical seam and strengthen across the umbilical wall and shoulder into coarse umbilical bullae. These in turn give rise to one, or a pair of ribs, the second sometimes tenuously linked, and transitional to occasional intercalated ribs, to give a total of 23-24 ribs per whorl at the ventrolateral shoulder. The ribs are coarse and blunt; each bears a conical to feebly clavate inner ventrolateral tubercle, linked by a broad coarse transverse rib to a stronger outer ventrolateral clavus. This is linked by a weakening rib to a coarse blunt keel, flanked by broad grooves.

Discussion. These tiny specimens, with well-differentiated inner and outer ventrolateral tubercles, all appear to be juveniles of *Mortoniceras* (*M.*) *nanum*. Small adult size, and the combination of umbilical, inner and outer ventrolateral tubercles, distinguish this species from others. Scholz (1979: 116, Pl. 30, Figs 19, 21, 22) treated *M. nanum* as a 'morphotype' of *M.* (*Subschloenbachia*) *subquadratum* Spath, 1933 (435, Pl. 37, Fig. 6; Pl. 42, Figs 5, 9; Pl. 43, Fig. 7; Pl. 44, Fig. 6), and placed it and a whole range of diminutive Late Albian mortoniceratids into *Hysteroceras* (*Cantabrigites*). This conclusion is not valid in our view. The approach links micromorphs and microconchs together solely on the basis of size, and irrespective of relative age.

The subgeneric assignation of this species is unclear. The presence of inner and outer ventrolateral tubercles recalls *M.* (*Subschloenbachia*) rather than *M.* (*Mortoniceras*), where there is a single row, but typical *Subschloenbachia* are quadrituberculate, with an additional lateral row of tubercles present.

Occurrence. *Mortoniceras* (*M.*) *fallax* Zone, eastern England, southern Belgium, southeast France and Hungary.

Family Lyelliceratidae Spath, 1921

Subfamily Stoliczkaiinae Breistroffer, 1953

Remark. The classification of the Stoliczkaiinae used here is that of Wright & Kennedy (1994).

Genus and subgenus *Neophlycticeras* Spath, 1922b

Type species. *Ammonites brottianus* d'Orbigny, 1841 (29, Pl. 85, Figs 8-10) by original designation (Spath, 1922b: 107).

Neophlycticeras *(Neophlycticeras)* blancheti *(Pictet & Campiche, 1859)*

Pl. 4, Fig. 24; Pl. 10, Figs 1, 2

*1859 *Ammonites blancheti* Pictet & Campiche: 188, Pl. 23, Figs 2-6.

1994 *Neophlycticeras (Neophlycticeras) blancheti* (Pictet & Campiche, 1859); Wright & Kennedy: 563, Figs. 2a-m, 6d-f, 7a-h (with synonymy).

2002 *Neophlycticeras* (*Neophlycticeras*) *blancheti* (Pictet & Campiche); Amédro: 62, Pl. 9, Figs 4, 5.

Type. The lectotype, designated by Spath (1931: 323), is the original of Pictet & Campiche, 1859 (Pl. 23, Fig. 2) from the Upper Albian of La Vraconne, Sainte Croix, Switzerland (see discussion in Wright & Kennedy, 1994: 563).

Material. A single specimen, STR 4.

Description. STR 4 is crushed, and retains silicified shell. The original estimated diameter is 43 mm. The specimen appears to be an adult, with the last suture at a diameter of 36 mm. Coiling is very involute, the umbilicus comprising 14% approximately of the diameter, shallow, with a flattened wall and rounded shoulder. The whorl section is high, compressed, with feebly convex inner to middle flanks, convergent outer flanks, and a fastigiate venter. There are eleven primary ribs on the outer half whorl. These arise at the umbilical seam, strengthen across the umbilical wall and shoulder, and develop into feeble elongate bullae, or not. The ribs are low, broad, and coarse, straight to feebly flexuous, prorsiradiate on the flanks, and separated by single long or short intercalated ribs that strengthen progressively across the flank to match the primaries at the ventrolateral shoulder, where all ribs bear prominent ventrolateral clavi, connected to well-developed siphonal clavi by a low, broad, transverse rib. There are 17 ribs per half whorl at the ventrolateral shoulder.

A fragmentary juvenile (STR 8b), now lost, is shown in Pl. 10, Figs 1, 2. It had a maximum preserved whorl height of 12.5 mm. Bullate primary ribs are separated by up to four intercalated ribs, and all ribs bear feeble ventrolateral bullae and well-developed siphonal clavi.

Discussion. For a comprehensive revision of this species, reference is made to Wright & Kennedy (1994), who also noted its synonyms and presented a discussion of differences from other species referred to the subgenus.

Occurrence. *Mortoniceras* (*M.*) *fallax* Zone, southern England, southern Belgium, southeast France, Switzerland, Romania and Armenia.

Genus and subgenus *Stoliczkaia* Neumayr, 1875

Type species. *Ammonites dispar* d'Orbigny, 1841: 142, Pl. 45, Figs 1, 2, by subsequent designation (Diener, 1925: 179).

Stoliczkaia *(Stoliczkaia)* notha *(Seeley, 1865)*
Pl. 9, Figs 9-12

*1865 *Ammonites navicularis* Mantell var. *nothus* Seeley: 232.
1994 *Stoliczkaia* (*Stoliczkaia*) *notha* (Seeley, 1865); Wright & Kennedy: 569, Figs 5a-d, e; 8a-r; 9a-k; 10a-j (with full synonymy).

Material. A single unregistered specimen in the Janssens Collection (HJJ).

Dimensions.

D	Wb	Wh	Wb/Wh	U
24.8 (100)	10.2 (41.1)	13.2 (53.2)	0.77	3.4 (13.7

Description. The specimen is a wholly septate juvenile with traces of silicified shell preserved. Coiling is very involute, with a small, deep umbilicus comprising 13.7% of the diameter. The umbilical wall is flattened and subvertical, the umbilical shoulder narrowly rounded. The whorl section is compressed, with a whorl breadth to height ratio of 0.77, the greatest breadth below mid-flank, the inner flank feebly inflated, the outer flanks flattened and convergent, the ventrolateral shoulders narrowly rounded to subangular. The venter is fastigiate at the smallest diameters seen, but becomes rounded thereafter. There are eighteen primary ribs at the umbilical shoulder, which may be feebly bullate or not. Ribs are straight and prorsiradiate, and increase by branching and intercalation, most conspicuously on the outer flank. There are small but clearly differentiated ventrolateral clavi at the smallest diameter seen, but these efface progressively into mere angulations on the ventrolateral shoulder at the largest diameter seen. At the smallest diameter visible, a coarse, blunt rib crosses the venter in an obtuse chevron, with a feeble siphonal clavus at the apex of the chevron. This is rapidly lost, and for most of the outer whorl, the ventral rib is feebly convex, thickening over the mid-ventral region, and without a siphonal tubercle.

Discussion. Wright & Kennedy (1994: 569) provided a detailed revision of this species and discussed differences from other members of the subgenus.

Occurrence. *Mortoniceras* (*M.*) *fallax* Zone, eastern England, southern Belgium, southeast France, Switzerland, Sardinia, Angola, Ukraine (Crimea), Kopet Dag, Turkmenistan, Romania, and possibly Madagascar.

Suborder Ancyloceratina Wiedmann, 1966
Superfamily Turrilitoidea Gill, 1871
Family Anisoceratidae Hyatt, 1900
Genus *Anisoceras* Pictet, 1854

Type species. *Hamites saussureanus* Pictet (in Pictet & Roux), 1847 (118, Pl. 13, Figs 1-4) by original designation (Pictet, 1854: 705).

Anisoceras armatum *(J. Sowerby, 1817)*
Pl. 8, Figs 23-29; Pl. 9, Figs 18-21, 31, 32;
Pl. 10, Figs 14, 15

*1817 *Hamites armatus* J. Sowerby: 153, Pl. 168.
1979 *Anisoceras* (*Anisoceras*) *armatum* (J. Sowerby, 1817); Cooper & Kennedy: 200, Figs 13a, b; 14d-e; 16z, c, e, i; 17-19 (with full synonymy).
1979 *Anisoceras* (*Anisoceras*) *armatum* (J. Sowerby); Scholz: 25 (*pars*), Pl. 2, Figs 1, 5, 7 only.
1996 *Anisoceras armatum* (J. Sowerby, 1817); Kennedy (in Gale et al.): 573, Fig. 24d-f, h (with additional synonymy).
1998 *Anisoceras armatum* (J. Sowerby, 1817); Kennedy et al.: 35, Figs 30, 31, 32a-c, 33d-f, 36f.
2005 *Anisoceras armatum* (Sowerby); Reboulet et al.: 125, Fig. 3K.
2006 *Anisoceras armatum* (J. Sowerby, 1817); Kennedy & Juignet (in Gauthier et al.): 161, Pl. 47, Fig. 6a, b.

Type. The holotype, by monotypy, is the original of J. Sowerby (1817: Pl. 168), no. OUM K675a, b, from the Upper Albian Upper Greensand of Roke, 1.5 km (1 mile) NNE of Benson, Oxfordshire, England. It has recently been refigured by Kennedy et al. (1998: Fig. 30).

Material. Seven specimens: NHMM JJ 5763, JJ 12623, JJ 12624; STR 54 and 133-135.

Description. Short, curved, sometimes feebly helicoids fragments have whorl heights of up to an estimated 19 mm. The intercostal whorl section varies from slightly compressed to slightly depressed, subcircular. The rib index is 8-11 on the flanks. The dorsum bears numerous crowded, even, transverse, feebly convex, wiry ribs that link in pairs at strong flat-topped dorsolateral tubecles that are clearly the bases of septate spines. A pair of coarse, straight, prorsiradiate ribs link to larger ventrolateral tubercles, again the bases of septate spines. These are linked across the venter by a pair of broad ribs, borne on a low swelling. The pairs of tuberculate ribs are separated by one or more intercalated ribs.

A much larger specimen (STR 16), now lost, is shown in Pl. 10, Figs 14, 15. It comprises a straight shaft 150 mm long, with a maximum preserved whorl height of 42 mm. The rib index is 13-14. Pairs of ribs link at rounded tubercles low on the flank, and loop from them to long ventral clavi, with one or two simple ribs between the tuberculate groups. One of these latter ribs occasionally links to a ventral clavus.

Discussion. Reference is made to Kennedy et al. (1998) for a recent review of this species, and discussion of differences from other allied forms. The largest fragment compares well with the penultimate shaft of the holotype (Kennedy et al., 1998: Fig. 30).

Occurrence. *Mortoniceras* (*M.*) *inflatum* to *A*. (*P.*) *briacensis* zones. The geographic range extends from southern England to France, southern Belgium, Germany, Switzerland, Hungary, Spain, Zululand (South Africa), Mozambique, southern India and Texas.

Family Hamitidae Gill, 1871
Genus *Hamites* Parkinson, 1811

Type species. *Hamites attenuatus* J. Sowerby, 1814: 137, Pl. 61, Figs 4, 5, by subsequent designation (Diener, 1925: 65).

Hamites subvirgulatus *Spath, 1941*
Pl. 9, Figs 13, 14, 22-25; Pl. 10, Figs 4-7, 12, 13

*1941 *Hamites* (*Stomohamites*) *subvirgulatus* Spath: 645, Text-Fig. 234a-h.
1968 *Hamites* (*Stomohamites*) *subvirgulatus* Spath; Renz: 66, Pl. 11, Figs 13, 14; Text-Figs 23e, 24a (with synonymy).
1996 *Hamites subvirgulatus* Spath, 1941; Kennedy (in Gale et al.): 567, Text-Figs 20d, e, j; 25g, h, j; 26 j, k (with additional synonymy).

Types. The holotype is BMNH C39920, the original of Spath (1941: Text-Fig. 234a, b), from the Upper Albian *Mortoniceras* (*Subschloenbachia*) *perinflatum* Zone fauna of the Upper Greensand of Holworth House, Dorset. Paratype BMNH C39921 is the original of Spath (1941: Text-Fig. 234c, d), from the same horizon and locality.

Material. Eight specimens: NHMM JJ 5760-5762; STR 25, 106, 134, 136-137.

Description. All specimens are short, curved fragments, the largest 35 mm long, with a maximum preserved whorl height of 7.4 mm, and a whorl breadth to height ratio of 0.88. The whorl section is oval; the rib index is 5. The ribs are effaced on the dorsum in most specimens, strengthening across the dorsolateral margin, coarse, crowded, rounded and feebly prorsiradiate on the flanks, and transverse on the venter, where they are narrower than the interspaces. STR 25 (Pl. 10, Figs 12, 13) has flank and ventral ornament as in the other specimens, but the dorsum shows a persistence of the ribs, which split into a coarser adapical and weaker adapertural riblet.

Discussion. This hardly varying suite of specimens are referred to *H. subvirgulatus* on the basis of the compressed oval whorl section, combined with close, even ribbing. *Hamites virgulatus virgulatus* Brongniart, 1822 (see revision in Renz, 1968: 65, Pl. 11, Figs 9-11; Text-Fig. 23b-d) is more distantly ribbed; reference is made to Renz (1968) for a discussion of differences from other species.

Occurrence. *Mortoniceras* (*M.*) *fallax* to *M*. (*S.*) *perinflatum* zones of southern England, southern Belgium, southeast France, Sardinia, Switzerland, Poland and Madagascar.

Family Baculitidae Gill, 1871
Genus and subgenus *Lechites* Nowak, 1908

Type species. *Baculites gaudini* Pictet & Campiche, 1861: 112, Pl. 55, Figs 5-9, by original designation (Nowak, 1908: 350).

Lechites *(Lechites)* gaudini *(Pictet & Campiche, 1861)*
Pl. 8, Figs 20-22; Pl. 9, Figs 15-17, 26-30

*1861 *Baculites gaudini* Pictet & Campiche: 112, Pl. 55, Figs 5-9.
1977 *Lechites gaudini* (Pictet & Campiche); Cooper & Kennedy: 644, Figs 1, 1-38; 2, 1-30; 3; 4, 1-18; 5, 1-15; 6-8, 16-26 (with synonymy).
1979 *Lechites gaudini gaudini* (Pictet & Campiche, 1861); Scholz: 12, Pl. 1, Figs 1-9; Text-Fig. 5a, b.
1996 *Lechites* (*Lechites*) *gaudini* (Pictet & Campiche,

1861); Kennedy (in Gale et al.): 577, Figs 22a, c, d; 27e-i, l-o.

1997 *Lechites gaudini* (Pictet & Campiche, 1861); Klinger & Kennedy: 7, Figs 2a-c, m, 3 (with synonymy).

2001 *Lechites gaudini* (Pictet & Campiche, 1861); Klinger & Kennedy: 243, Figs 171, 172.

2002 *Lechites gaudini* (Pictet & Campiche); Amédro: 32, 62, Pl. 2, Fig. 7; Pl. 6, Fig. 9.

2005 *Lechites (L.) gaudini* Pictet and Campiche [*sic*]; Reboulet et al.: 125, Fig. 3L.

Material. Four specimens: NHMM JJ 5755-5757 and STR 15.

Description. STR 15 is typical of the four fragments; it is a body chamber 45.5 mm long, retaining silicified shell. The maximum preserved whorl height is 13.4 mm, the whorl breadth to height ratio is 0.93, the whorl section subcircular. The rib index is 3. Ornament is near-effaced on the dorsum, being reduced to low concave folds and striae, and growth lines. The ribs strengthen progressively from the dorsolateral margins to the venter, and are low, broad, and coarse, but narrower than the interspaces, straight and prorsiradiate, and crossing the venter in a very shallow convexity.

Discussion. Reference is made to Cooper & Kennedy (1977) for a comprehensive review of this species, its synonymy and a discussion of differences from other species referred to the genus.

Occurrence. *Mortoniceras* (*M.*) *fallax* to *A.* (*P.*) *briacensis* zones. The geographic range extends from southern England, northern and southern France, southern Belgium, Switzerland, Hungary, Romania, Sardinia, North Africa, Madagascar, Zululand, southern India, Japan to Mexico.

Superfamily Scaphitoidea Gill, 1871
Family Scaphitidae Gill, 1871
Subfamily Scaphitinae Gill, 1871
Genus and subgenus *Scaphites* Parkinson, 1811

Type species. *Scaphites equalis* J. Sowerby, 1813: 53, Pl. 18, Figs 1-3, by subsequent designation (Meek, 1876: 413).

Scaphites *(Scaphites) sp. juv.*
Pl. 8, Figs 17-19

Material. Four specimens: STR 111a, b, and two in HJJ (unregistered).

Description. STR 111b (Pl. 8, Fig. 19) is a nucleus, 8 mm in diameter. Coiling is relatively evolute, with a wide umbilicus and depressed whorl section. At the smallest diameters seen, ornament is of straight, narrow, wiry, prorsiradiate ribs that are well-developed on the flanks, but efface on the ventrolateral shoulders and venter. The ribbing pattern changes on the adapical 120o sector of the shell. The primary ribs become increasingly prorsiradiate and feebly convex, and bifurcate on the ventrolateral shoulders, where additional ribs intercalate. Secondary and intercalated ribs are fine, narrow, even, and near-transverse over the venter. The HJJ specimens are partially preserved phragmocones of about 9 mm in diameter, with depressed, reniform whorl section and minute conical umbilicus. Eighteen sharp, narrow, straight, prorsiradiate ribs arise on the umbilical wall, and strengthen across the flanks. All bear a small ventrolateral tubercle, incipient at the smallest diameter seen, but clearly differentiated from the rib at the greatest diameter preserved. These tubercles give rise to pairs of secondary ribs, which, together with occasional long and short intercalated ribs, strengthen across the venter, where they are near-transverse to feebly concave. STR 111a (Pl. 8, Figs 17, 18) is an essentially similar phragmocone fragment, 10.5 mm in diameter.

Discussion. These fragments are specifically indeterminate, but indicate the presence of a *Scaphites* of the group of *simplex* Jukes-Browne, 1875 (287, Pl. 14, Fig. 3) in the fauna.

Occurrence. *Mortoniceras* (*M.*) *fallax* Zone, Bracquegnies Formation, Strépy-Thieu (Hainaut, southern Belgium).

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Plate 1

Figures 1-18. *Callihoplites tetragonus* (Seeley, 1865); 1-5: STR 218; 6-8: STR a; 9-11: STR b; 12, 13: STR 82; 14, 15: STR c; 16: STR 24; 17, 18: STR 171. All specimens are from the upper Upper Albian, Bracquegnies Formation, Strépy-Thieu (Hainaut, southern Belgium). Figures 1, 2 are x 1; Figures 3-5, 12, 13, 16 are x 2, while Figures 6-11, 13-15, 17 and 18 are x 4.

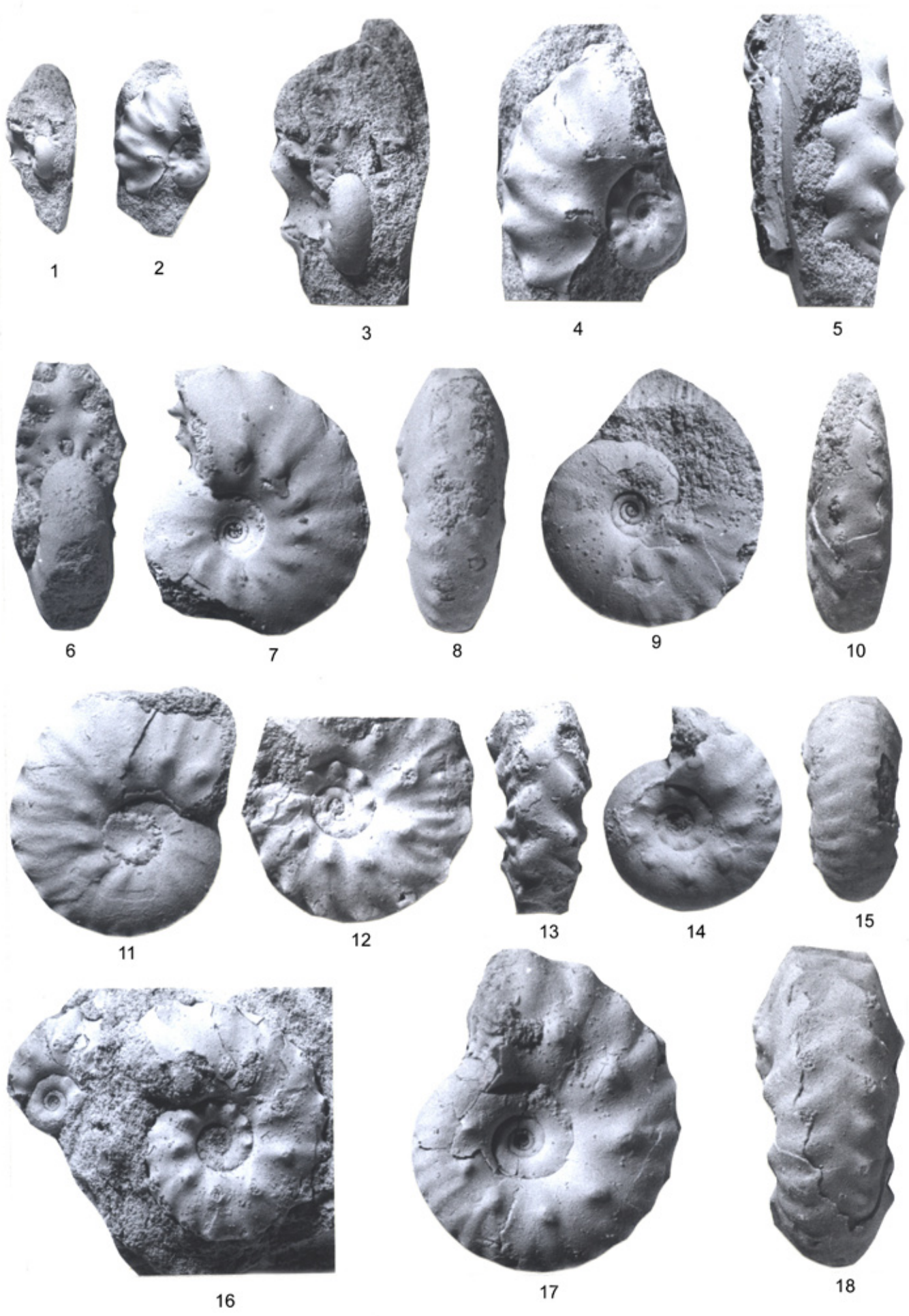
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Plate 2

Figures 1-26. *Callihoplites tetragonus* (Seeley, 1865); 1-3: STR 41; 4-6: STR 45; 7, 8: STR 49; 9-11: STR 28; 12-14: STR 9; 15, 16: STR 28; 17, 18: STR 240; 19-21: STR 11; 22, 23: STR 263; 24, 25: STR 22; 26: STR 48. All specimens are from the upper Upper Albian, Bracquegnies Formation, Strépy-Thieu (Hainaut, southern Belgium). Figures 1-6 are x 2, while Figures 7-26 are x 1.

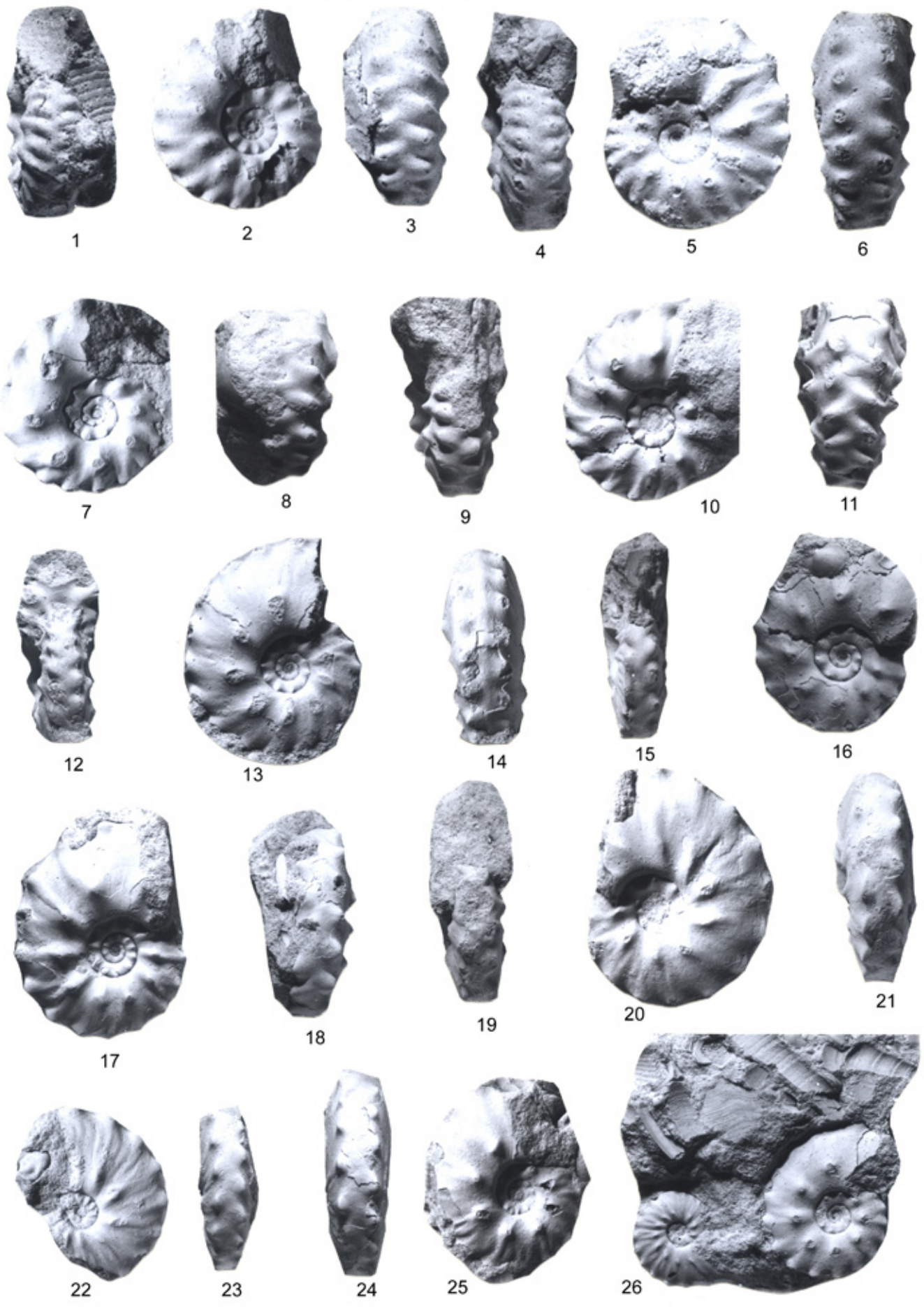
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Plate 3

Figures 1-24. *Callihoplites tetragonus* (Seeley, 1865); 1, 2: STR 15; 3-5: STR 14; 6: STR 13; 7, 8: STR 12; 9-11: STR 55; 12: STR 7 (see also Amédro, 2002: Pl. 6, Fig. 3); 13: STR 2 (see also Amédro, 2002: Pl. 6, Fig. 1); 14, 15: STR 18; 16, 21: STR 21; 17-19: STR 19; 20: STR 12; 22, 23: STR 23; 24: STR 236. All specimens are from the upper Upper Albian, Bracquegnies Formation, Strépy-Thieu (Hainaut, southern Belgium). All figures are x 1.

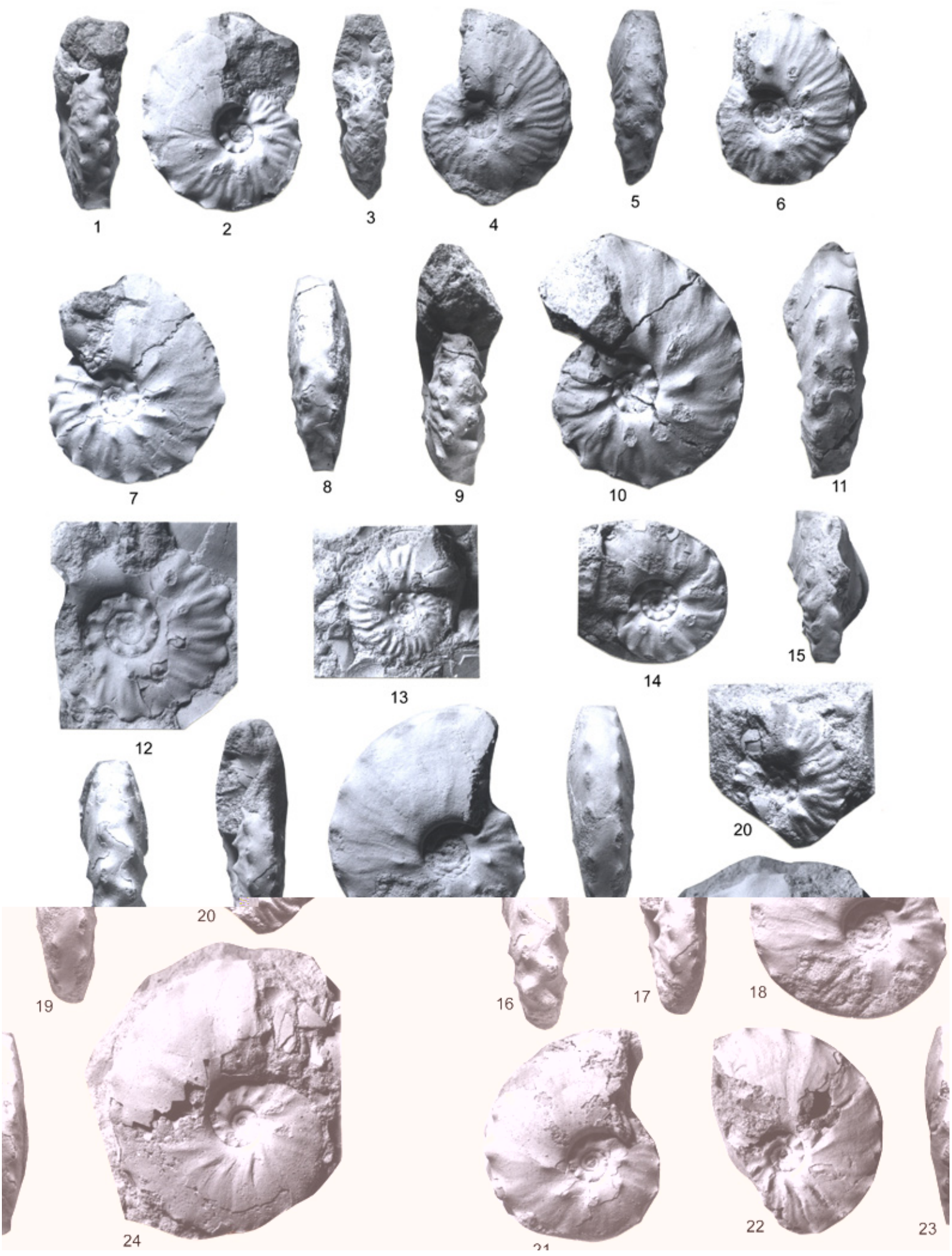
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Plate 9

Figures 1-8. *Mortoniceras* (*Mortoniceras*) *nanum* Spath, 1933; 1-3: NHMM JJ 5730; 4-6: Janssens Collection, unregistered; 7, 8: NHMM JJ 5731.

Figures 9-12. *Stoliczkaia* (*Stoliczkaia*) *notha* (Seeley, 1865); Janssens Collection, unregistered.

Figures 13, 14, 22-25. *Hamites subvirgulatus* Spath, 1941; 13, 14: NHMM JJ 5760; 22, 23: NHMM JJ 5761; 24, 25: NHMM JJ 5762.

Figures 15-17, 26-30. *Lechites* (*Lechites*) *gaudini* (Pictet & Campiche, 1861); 15-17: NHMM JJ 5756; 26, 27: NHMM JJ 5755; 28-30: NHMM JJ 5757.

Figures 18-21, 31, 32. *Anisoceras armatum* (J. Sowerby, 1817); 18, 19: NHMM JJ 12623; 20, 21: NHMM JJ 5763; 31, 32: NHMM JJ 12624.
All specimens are from the upper Upper Albian, Bracquegnies Formation, Strépy-Thieu (Hainaut, southern Belgium). All figures are x 2.

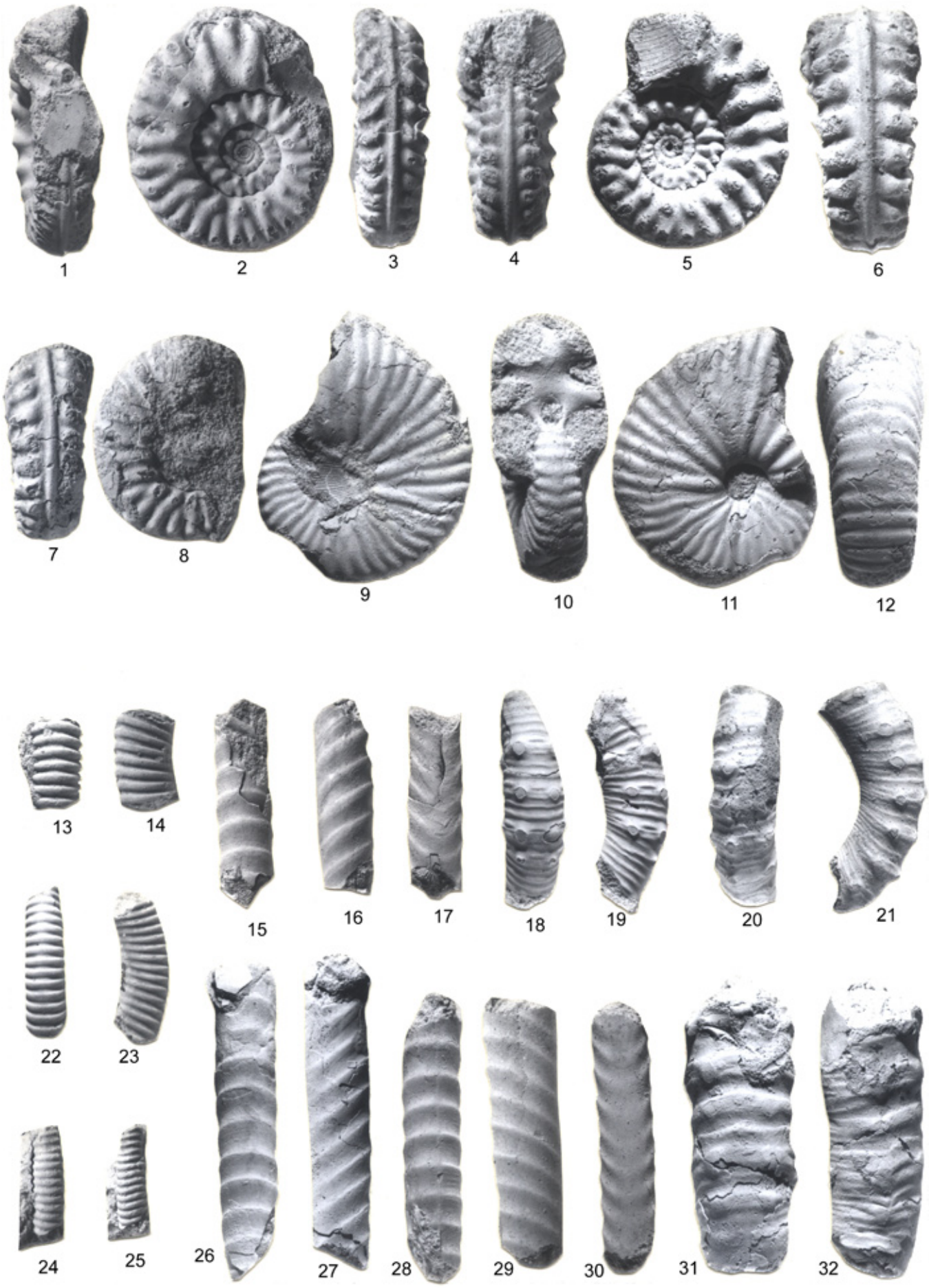
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Plate 10

Figures 1, 2. *Neophlycticeras* (*Neophlycticeras*) *blancheti* (Pictet & Campiche, 1859); STR 8b (see also Amédro, 2002: Pl. 9, Fig. 5).

Figure 3. *Cantabrigites cantabrigense* Spath, 1933; STR 9 (see also Amédro, 2002: Pl. 9, Fig. 2).

Figures 4-7, 12, 13. *Hamites subvirgulatus* Spath, 1941; 4: STR 106; 5: STR 136; 6, 7: STR 137; 12, 13: STR 25.

Figures 8-11, 16. *Mortoniceras* (*Mortoniceras*) *fallax* Breistroffer, 1940; 8: STR 6, now lost (see also Amédro, 2002: Pl. 9, Fig. 3); 9-11: holotype, SMC B56, from the remanié phosphatised Late Albian fauna at the base of the Lower Cenomanian Cambridge Greensand of Cambridgeshire; 16: STR 7, now lost (see also Amédro, 2002: Pl. 9, Fig. 1).

Figures 14, 15. *Anisoceras armatum* (J. Sowerby, 1817); STR 16, now lost (see also Amédro, 2002: Pl. 6, Fig. 7).
All specimens, apart from the original of Figs 9-11, are from are from the upper Upper Albian, Bracquegnies Formation, Strépy-Thieu (Hainaut, southern Belgium). Figures 1-3, 8-11, 14-17 are x 1, while Figures 4-7, 12, 13 are x 2.

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