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A revision of some British Lower Bajocian stephanoceratid ammonites

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ABSTRACT

Members of the ammonite family Stephanoceratidae from the Middle Jurassic, Lower Bajocian, Laeviuscula to Humphriesianum zones of South West England are revised. These comprise faunas resulting from periodic migrations and possibly hybridization. The taxonomic positions of *Teloceras* Mascke, 1907, *Kumatostephanus* Buckman, 1922, *Gibbistephanus* Buckman, 1928 and *Pseudoteloceras* Pavia and Fernández-López, 2016 are considered in the light of new research. A new subfamily Kumatostephaninae is erected and hypotheses are presented regarding the evolution of some Early Bajocian stephanoceratids. *Pseudoteloceras digbyi* sp. nov. represents the earliest '*Teloceras*-like' morphology from the late Sauzei Zone. Refinement is made of the scheme of faunal horizons for the Lower Bajocian.

1. Introduction

Studies of the evolution and taxonomy of some stephanoceratid ammonites (Middle Jurassic, Aalenian to Lower Bajocian) have generated a number of different phylogenetic models (e.g. Weisert, 1932; Westermann and Riccardi, 1985; Fernández-López and Pavia, 2015; Westermann, 1995; Pavia and Fernández-López, 2016; Howarth, 2017). According to Fernández-López and Pavia (2015) the family Stephanoceratidae Neumayr, 1875, comprises five subfamilies: Stephanoceratinae Neumayr, 1875; Garantianinae Wetzel, 1937; Cadomitinae Westermann, 1956; Mollistephaninae Fernández-López and Pavia, 2015, and Freboldtitinae Fernández-López and Pavia, 2015.

This investigation concerns the origin of the well-known genus *Teloceras* that is very characteristic of the Upper Humphriesianum Zone in Western Tethys. *Teloceras*-like ammonites appear suddenly and commonly in the rocks of early Humphriesianum Zone age and have been described by Pavia and Fernández-López (2016), who provided reasons for the separation of these early forms as a new genus, *Pseudoteloceras* Pavia and Fernández-López, 2016, from the Romani Subzone of the Humphriesianum Zone. It is, however, unclear whether this early group evolves directly into *Teloceras* sensu stricto or whether *Teloceras* arises, with homologous morphology, anew in the Upper Humphriesianum Zone, as there is an apparent time-rock gap, free of *Teloceras*-like ammonites, in the middle of the Humphriesianum Zone of Western Europe. For this reason, and for the present, the taxon *Pseudoteloceras* is used here for these *Teloceras*-like ammonites up to and including the *labrum* horizon of the Humphriesianum Zone (Fig. 1).

In the Aalenian and Bajocian of Dorset and Somerset, the ammonite record is particularly rich and *Teloceras*-like ammonites are well represented in the late Early Bajocian and early Late Bajocian part of the succession. They are particularly common around Oborne, but strata of suitable age crop out infrequently elsewhere, e.g. Dundry in Somerset. The strata are present as thin limestone beds, separated by erosion surfaces, with common, well-preserved ammonites and typically show consistency of faunal composition regionally. In many cases beds may represent more or less simultaneous events with minimal mixing of specimens of different ages and there are distinct horizons in which it is possible to discriminate a range of intraspecifically variable shells that are almost certainly a single palaeobiospecies (Callomon, 1985; Chandler and Callomon, 2009). The record is, however, discontinuous and the cryptic appearance of species is commonplace. In some cases this may be due to migratory events. The establishment of a bi-directional migration route into British waters from the Eastern Pacific, is now widely accepted (e.g. Sadki and Mouterde, 1994; Sandoval et al., 2012; Fernández-López and Pavia, 2015; Sandoval and Chandler, 2015). We conclude that some stephanoceratid species found in Dorset and Somerset are immigrants that have evolved elsewhere.

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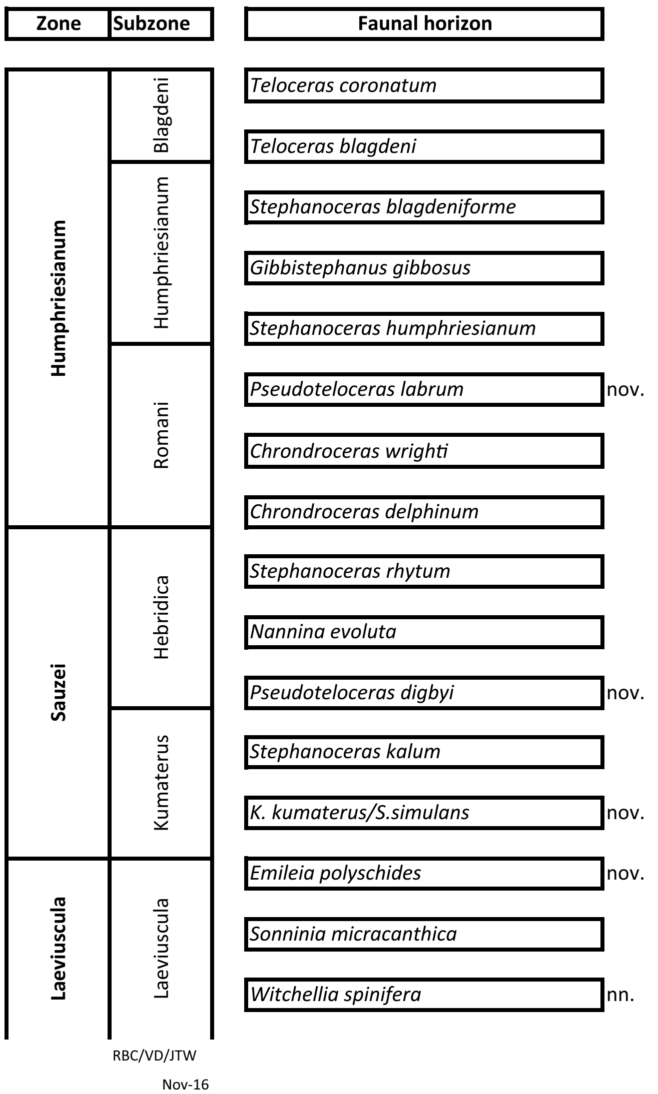

Fig. 1. The ammonite faunal horizons of the Inferior Oolite (part — Bajocian Stage only) of Dorset and Somerset, UK. Horizons are labelled by a characteristic guide fossil. The scheme is based on Callomon and Chandler (1990) amended Chandler et al. (2006). New horizons introduced here are labelled nov and those resurrected from previous use a nn. Zones and subzones shown on the left.

New research on the Inferior Oolite of Dorset enables us to suggest probable evolutionary routes for the stephanoceratids *Kumatostephanus*, *Pseudoteloceras*, *Gibbistephanus* and *Teloceras*. New collections from the late Sauzei Zone of Dorset connect the taxa under investigation from the Laeviuscula and Humphriesianum zones. The subfamily Kumatostephaninae nov. is erected to include ammonites of the genus *Kumatostephanus* and allied genera.

The scheme of faunal horizons introduced by Callomon and Chandler (1990) emended by Callomon and Cope (1995) and then by Chandler et al. (2006) has been subject to a number of changes necessitating subdivision of its alphanumeric codes. In this form, further change to the scheme is likely to cause confusion. We are therefore abandoning the alphanumeric codes and employing species names that typify the horizon as guide fossils. In most cases, these are the same names used in previous schemes but without their attendant codes. The faunal horizon table (Fig. 1) therefore reflects this change. The zonal scheme is that of Chandler et al. (2006) with additions and modifications. For brevity, the term faunal horizon is shortened to horizon throughout and full generic and species names of faunal horizons are given in Fig. 1, but shortened to specific names only in the text.

Acronyms, repositories, terminology and locality codes. WCC — Wessex Cephalopod Club Collection; BGS — British Geological Survey, Keyworth, Nottingham, UK; NHMUK — Natural History Museum, London, UK; CAMSM — Sedgwick Museum, Cambridge, UK. Website articles by C. F. Parsons and a symposium book by Chandler and Whicher, 2015 are cited as pers. com. Synonymy lists follow Matthews (1973).

Abbreviations. [M] and [m]; macroconch and microconch respectively; HT; LT; holotype and lectotype; * type species. Locality codes and map references. A map of the area is given as Fig. 2.

1 — Sh-SL, Sherborne, Sandford Lane (ST628 178); 2 — Ob-FQ, Oborne, Frogden Quarry (ST 649 183); 3 — Ob-OW, Oborne, Oborne Wood (ST648 188), 4 — Ob-MCF, Oborne, Mill Close Farm (ST655 183), 5 — MH-MW, Miller's Hill, Milborne Wick (ST662 205); 6 — Be-HP, Beaminster, Horn Park (ST458 022), 7 — D-SMR, Dundry, Somerset, South Main Road Quarry (ST 567655). Stratigraphical sections for main locations described in the text are given as Figs. 3–5.

2. Systematic description and taxonomical issues arising

Subclass AMMONOIDEA von Zittel, 1884, Order AMMONITIDA Fischer, 1882, Suborder AMMONITINA Fischer, 1882, Superfamily STEPHANOCERATOIDEA Neumayr, 1875, Family STEPHANOCERATIDAE Neumayr, 1875

Remarks: The Family Stephanoceratidae is reported worldwide and includes numerous genera and species, many of these introduced by Quenstedt (1883–1885), Mascke (1907) and Buckman (1909–1930) along with numerous additions (e.g. Weisert, 1932; Schmidtill and Krumbeck, 1938; Pavia, 1983). As is generally the case in palaeontology most of the genera and species are based on the morphology of a few specimens and are necessarily subjective. In addition, many species are based on specimens that are the nuclei of larger forms. Inevitably the decision of where to draw the line between taxonomic entities on the time scale of progressive horizons is arbitrary. The presence of gaps in the stratigraphical record makes such divisions apparently easier but is frequently confounded by the finding of a more complete record elsewhere. Further complications arise due to the common homeomorphy between ammonites of different taxa. Accurate stratigraphical control is therefore essential and sadly is almost invariably absent from the historical museum material on which most of the taxonomy is based.

In Britain stephanoceratid ammonites of the subfamily Stephanoceratinae first appear as extreme rarities in rocks of Aalenian age, the earliest records so far being from Horn Park Quarry near Beaminster in Dorset (Senior et al., 1970; Callomon and Chandler, 1990) from the late Bradfordensis and Concavum zones. Howarth (2017, p. 7, fig. 4, 1c-d) figured the stratigraphically oldest example of a *Riccardiceras* found by J.H. Callomon in the 1960s. We reject the systematic opinions of e.g. Sandoval et al. (2012); Fernández-López (2014) and Fernández-López and Pavia (2015), who included *Riccardiceras* in the Otoitidae Mascke, 1907. In contrast to Dorset, *Riccardiceras* is relatively common in the Late Aalenian of northern Italy (Vacek, 1886) and Portugal (Rocha et al., 1990; Callomon and Chandler, 1994).

The general morphology of the early species is evolute and serpenticonic with or without spines or tubercles, but generally quite finely ribbed, probably evolving from *Erycites gonionotum* (Benecke, 1865) (Callomon and Chandler, 1994; Westermann, 1995). Such forms have been given various morpho-generic names, for example *Riccardiceras* Westermann, 1995 and *Westermannites*

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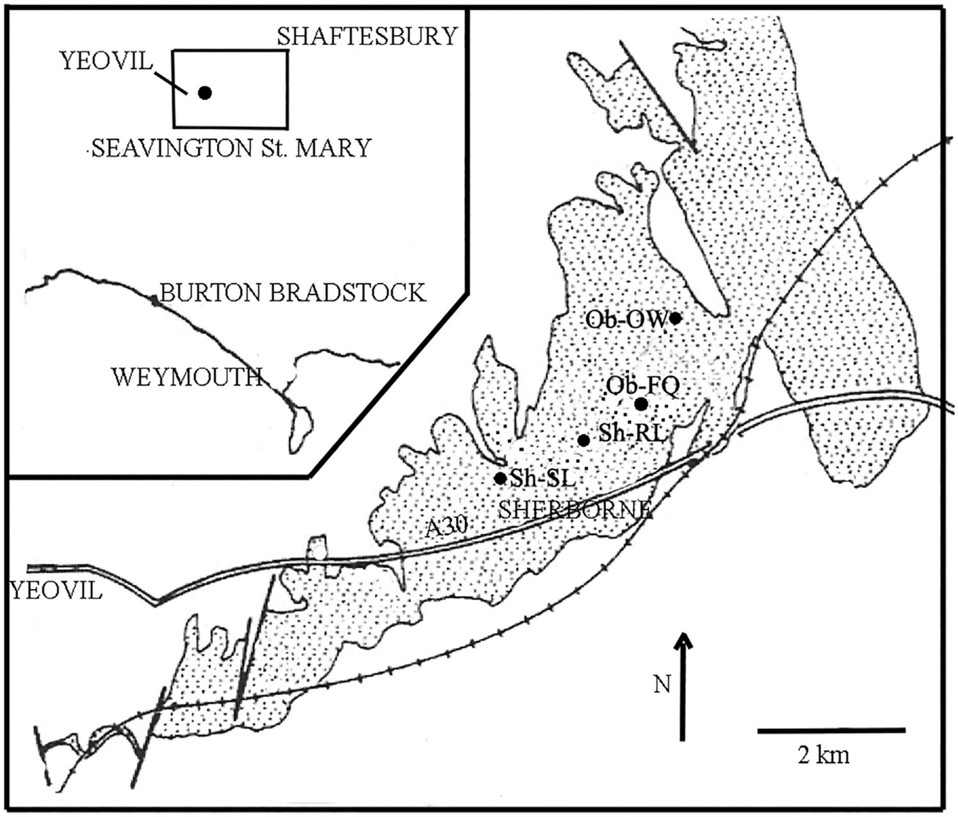

Fig. 2. Outcrop of the Inferior Oolite (dotted) in the Sherborne region of southwest England. Localities are marked by a dot and code: Sh-SL — Sherborne, Sandford Lane; Sh-RL — Sherborne, Redhole Lane; Ob-FQ — Oborne, Frogden Quarry; Ob-OW — Oborne, Oborne Wood.

Dietze et al., 2001. These are the oldest members of a small number of chronoclines, reaching from the Concavum Zone of the late Aalenian to at least the Blagdeni Subzone of the late Early Bajocian, Humphriesianum Zone. They occur intermittently until the late Laeviuscula Zone after which they increase in abundance and diversity in the Sauzei Zone and in later strata. Extreme serpenticonic ammonites with spines on the body-chamber, generally termed *Skirroceras* Mascke, 1907 are generally believed to be in decline by the late Sauzei or early Humphriesianum zones having been superseded by *Stephanoceras* sensu stricto. In the *gibbosus* horizon of the Humphriesianum Zone, at one discrete level accompanied by the main occurrence of *Gibbistephanus gibbosus* Buckman, 1928, relatively common serpenticones occur that are similar to *Stephanoceras* (*Skirroceras*) *nelchinanum* Imlay, 1964. The Dorset specimens are larger but seldom larger than 30 cm and lack tubercles. They are also very like *Stephanoceras* (*Skirroceras*) *juhlei* Imlay, 1964, apart from the presence of tubercles on that species. We surmise, that at that time the *Skirroceras* lineage persisted in the Eastern Pacific, returning to Britain along with the genus *Gibbistephanus*.

The first appearance of broad, coarsely ribbed stephanoceratids in Southern England is cryptogenic in the *micracanthica* horizon of the Laeviuscula Subzone as *Kumatostephanus*. Chandler et al. (2013) pointed to the evolute, platyconic *S.* (*Riccardiceras*) *richardsoni* (Dietze et al., 2001) as possibly giving rise to *Kumatostephanus turgidulus* (Quenstedt, 1886) as an ancestral link but evolving elsewhere.

Apart from the relatively evolute, moderately strongly ribbed stephanoceratids such as *Kumatostephanus kumaterus* Buckman, 1922 and stout forms with strong spines termed *Kumatostephanus perjucundus* Buckman, 1927, the genus *Stemmatoceras* Mascke, 1907 [**Ammonites humphriesianus coronatus* Quenstedt, 1886 (=*Stephanoceras frechi* Renz, 1913)], has historically become the recipient for any stephanoceratid bearing a broad whorl section and coarse ribbing and has been assumed by many authors to be the origin of *Teloceras*. Here the use of the genus *Stemmatoceras* is discontinued for now, because (1) the type-specimen of the type-species is the nucleus of a larger specimen and therefore difficult to evaluate and (2) because its precise stratigraphical level is unknown (Ohmert, 1990). The type-specimen comes from the Giganteus-Ton of Eningen, unter Achalm, (Middle Swabian Alb, Germany), which ranges from the lowermost Pinugis-Subzone sensu German workers (=uppermost Sauzei Zone of English workers) up to the lowermost Blagdeni Subzone of the Humphriesianum Zone (Ohmert, 1988, 1990; Ohmert et al., 1995). The view of Ohmert (1990, 1994), that the type-specimen originates from the *frechi* horizon of the Pinguis Subzone is supported by collections from the Upper Rhine area (Ohmert, 1994), however, coronate ammonites also occur in the upper part of the Giganteus-Ton of the area and *Teloceras*-like ammonites already occur in the lower part of the Giganteus-Ton (Ohmert, 1990).

The late Sauzei to early Humphriesianum zones appears to be an episode, where influxes of new ammonite species arrive in Dorset. Between the *rhytum* and *wrighti* horizons very stout *Stephanoceras* occur. They are in every respect, apart from the broadness of the venter, similar to *Stephanoceras mutabile* (Quenstedt, 1886) and appear to form part of the variability of that species. In terms of broadness, these specimens could also be termed *Stephanoceras* cf. *umbilicum* (Quenstedt, 1886). These ammonites are relatively common in Frogden Quarry bed 4b (lower) but stand apart from *Pseudoteloceras*. Some later, rotund specimens may also represent this group of *Stephanoceras* from the *humphriesianum* and *blagdeni* horizons.

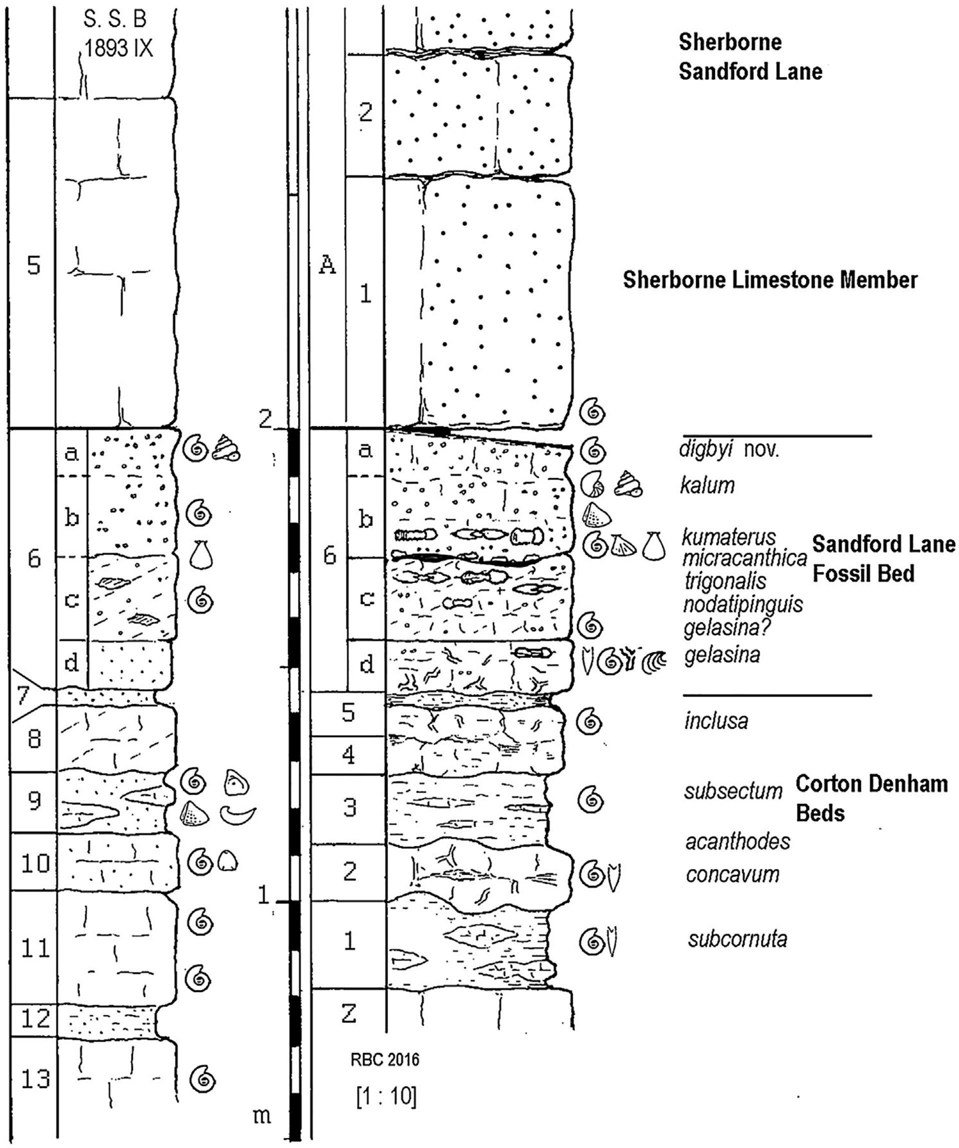

Fig. 3. Diagrammatic representation through the Inferior Oolite at Sandford Lane (Sh-SL) after Callomon and Chandler (1990). Horizons in italics and given by species name. New horizons introduced here are labelled nov and those resurrected from previous use a nn.

Studies made of stratigraphically controlled collections from the Laeviuscula to Humphriesianum zones of Dorset and Somerset enable us to demonstrate the relationship between *Kumatostephanus*, *Pseudoteloceras Gibbistephanus* and *Teloceras*.

Subfamily KUMATOSTEPHANINAE nov.

It has long been recognised that the ammonites known as *Kumatostephanus* (Buckman, 1922 in Type Ammonites 1909–1930) stand apart from other stephanoceratids collectively included in the Stephanoceratidae (Arkell and Playford, 1954). With so many morphological features in common with other morphospecies in the family, it was not clear where to draw consistent dividing lines. As a result of research conducted in the Sherborne area the horizontal variability of the stephanoceratid fauna has now been characterized horizon by horizon, and it is clear that *Kumatostephanus*, *Pseudoteloceras*, *Gibbistephanus*, and *Teloceras* are linked by morphological similarities and form an evolutionary sequence stretching from the Laeviuscula Zone to the Niortense Zone. For these taxa we erect a new subfamily, the Kumatostephaninae.

Description. In most members of the subfamily the style of the ribbing and venter is diagnostic. The primary ribs are straight or very slightly concave towards the aperture. The secondary ribs are strongly developed, prorsiradiate, bifurcating or trifurcating with rounded crests and sinuous inter-rib troughs. In some specimens, these arise from ventro-laterally located spine bases, sometimes of extraordinary length and shape. The ribs cross the venter flexing back slightly, in some species, to form a sub-chevron with their counterpart, and are often out of symmetry with the opposite flank. The strength of the ribbing weakens slightly on the ventral crest, sometimes producing a narrow central band. Ribbing and ornament continues to the termination. Whorl sections are usually depressed and often broad apart from early forms of *Kumatostephanus* that retain an evolute planulate style of morphology. Mouth-borders are plain, terminating in a simple sinuous aperture, in *Pseudoteloceras*, *Teloceras* and *Gibbistephanus* but form a prominent collar in many *Kumatostephanus* spp., where the profile of the termination curves-back in a ventro-dorsal direction more acutely than in *Stephanoceras*. Adult shells are smaller in size than average contemporary *Stephanoceras*.

Early members of the subfamily have relatively simple sutures compared to other contemporary stephanoceratids (Fig. 6). The

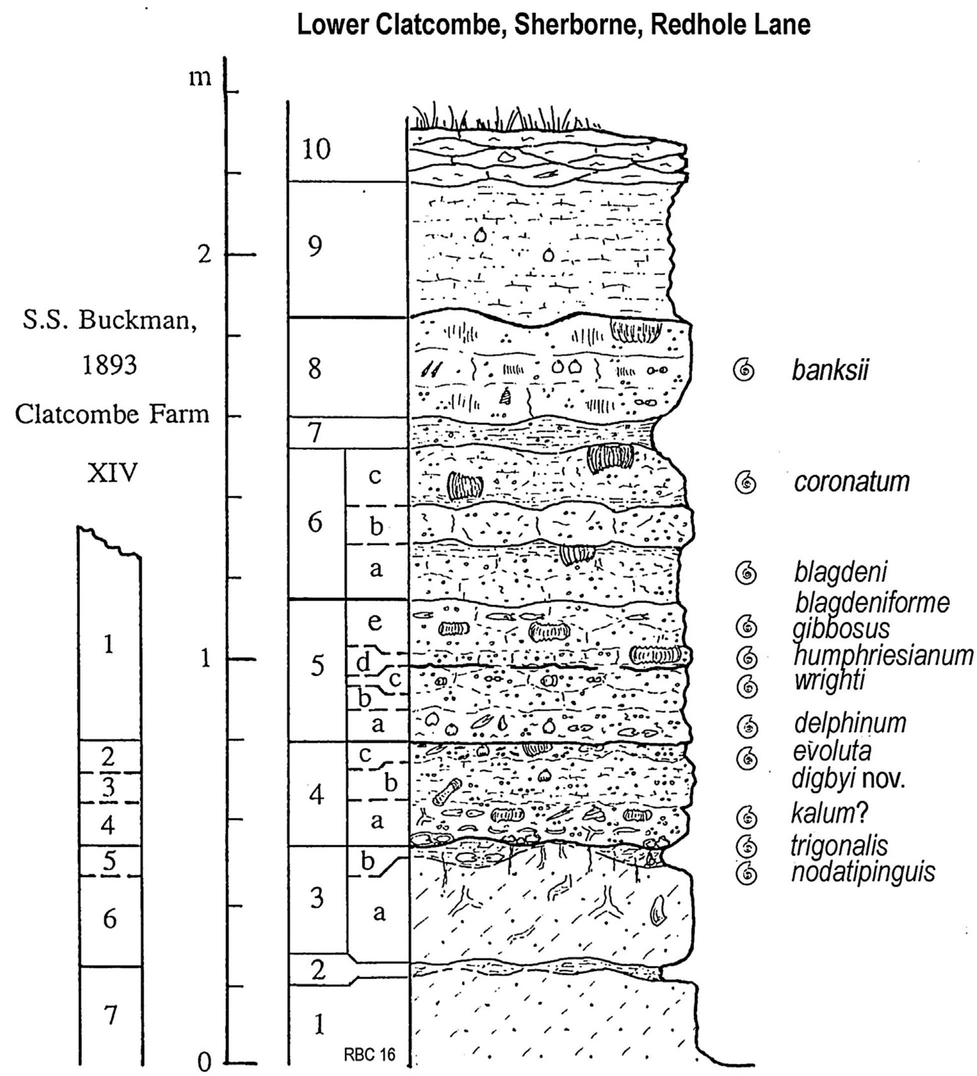

Fig. 4. Diagrammatic representation through the Inferior Oolite at Lower Clatcombe, Redhole Lane. (Sh-RL). Horizons in italics and given by species name. Buckman's (1893) section is shown on the left. New horizons introduced here are labelled nov and those resurrected from previous use a nn.

broader species generally show increased complexity, but the suture line is variable, dependent on shell morphology. The venter is so wide in some later specimens that the 1st lateral lobe is sometimes situated on it. This arises due to the exceptional shape of the whorl-section, where the venter has broadened as far as the spines. This implies that the position of the lateral lobe has not resulted from the relocation of the spines or tubercles (Galácz pers. com.).

The microconchs (Fig. 14) of the Kumatostephaninae intergrade in morphology with those of contemporary stephanoceratids and are conservative in morphology over extended time durations. For this reason, it is not clear which microconchs relate to the fauna of macroconchs in each horizon. Adult microconchs (Fig. 14) have well-developed lappets originating from the medio-lateral aspect of the apertures. They include *Gerzenites* Westermann, 1954; *Itinsaites* McLearn, 1927; *Normannites* Munier-Chalmas, 1892, and *Epalxites* Mascke, 1907. The dimorphic size-ratio is, between 3:1 and 5:1 depending on the horizons from which the sample is taken.

Each horizon in which assemblages of *Kumatostephanus*, *Pseudoteloceras*, *Gibbistephanus* and *Teloceras* are recorded in Dorset and Somerset represent, with little doubt, in each case variants of single palaeobiospecies.

Remarks. The evolution, of the new subfamily is mapped vertically over a succession of at least nine faunal horizons, nowhere more clearly than in Southern England and is based on numerous adult specimens from each horizon. In the course of evolution members of the subfamily changed in sculpture and intraspecific variability. The oldest British record of the lineage is probably that of *K. turgidulus* in the *micracanthica* horizon of the Laeviuscula Zone, with the terminal members of the group being species of *Teloceras* in the Niortense Zone.

The most plausible ancestors of the Kumatostephaninae occur in strata deposited in the Pacific, predating the arrival of *Kumatostephanus* sensu stricto in the British Laeviuscula Zone. In order to explain the succession of Kumatostephaninae in Western Europe it is necessary to postulate periodic migrations to and from the Eastern Pacific in the Early Middle Jurassic (Sadki and Mouterde, 1994; Sandoval et al., 2012). Local extinctions may have resulted in short absences from some strata and it is also possible that reintegration of separated faunas resulted in hybridization as is commonly seen with modern molluscs (Kronenberg, 2008).

Riccardiceras richardsoni from the Laeviuscula Zone, Sayni Subzone of Bruton, Somerset, UK and *K.* cf. *turgidulus* have similarities in common which lead us to propose that *R. richardsoni*

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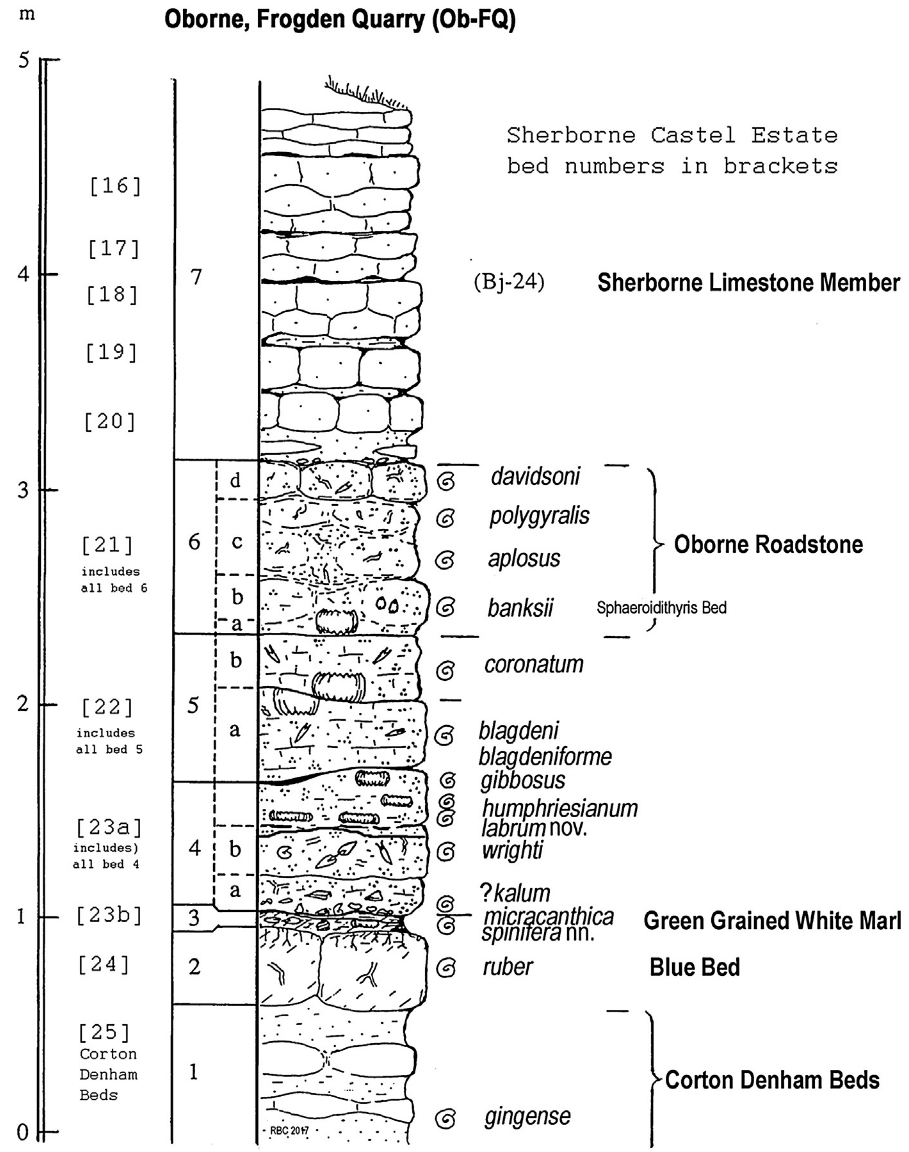

Fig. 5. Diagrammatic representation through the Inferior Oolite at Frogden Quarry (Ob-FQ) after Chandler et al (2014). Horizons in italics and given by species name. New horizons introduced here are labelled nov and those resurrected from previous use a nn. Sherborne Castle Estate quarry numbers on left.

or a similar species may be ancestral to species included here in the newly erected subfamily Kumatostephaninae. *R. richardsoni* and the earliest *Kumatostephanus* are of relatively small size (around 17 cm) for adult macroconchs and have slightly depressed whorl sections. *K.* cf. *turgidulus* has stronger, more distant ribbing that persists to the termination, stronger primary ribs and pronounced tubercles at mid-whorl position. A number of specimens from the Eastern Pacific have strong similarities to Kumatostephaninae, but the exact equivalent of their age in Europe remains unknown. *Stemmatoceras* cf. *triptolemus* (Bean in Morris and Lycett, 1851) and *Stemmatoceras* cf. *S. palliseri* (McLearn) in Imlay (1964, pl. 21, figs. 1, 3 and 2, 4 respectively), are similar to *Kumatostephanus. Stemmatoceras* n. sp. indet. Imlay (1964: pl. 20, figs. 1–4) is very close to some specimens of *Pseudoteloceras* from the *wrighti* to *labrum* horizons of Dorset. It is also probable that migrations of species such as *Stemmatoceras ursinum* Imlay (1964: pl. 22, figs. 1–3) and of forms similar to some *Pseudotoites* with broadening and depression of the whorl, and development of stronger tubercles or spines gave rise to such forms as *G. gibbosus* Buckman, 1928 of the Humphriesianum Zone. The latter has strong morphological affinities to *Kumatostephanus*, particularly *K. perjucundus*, thus *Gibbistephanus* is likely to a represent a surviving branch derived from similar ancestral species. *Kumatostephanus paucicostae* (Fernández-López, 1985: pl. 21, fig. 1) from the Laeviuscula Zone of Spain has a morphology similar to early *Kumatostephanus* and may represent one of the first arrivals into European seas.

Arkell and Playford (1954) described ammonites from the Newmarracarra Limestone of Western Australia which they placed in the equivalent of Oppel's (1862, p. 128) Sowerbyi Zone. In modern terms, this is equivalent to approximately the Concavum to Laeviuscula zones of Western Europe. The ammonites they depicted could therefore be a little older than the migration of the first *Kumatostephanus* into Western Europe. Of particular interest is a fragment (pl. 39, figs. 1a-b.) identified as *Stephanoceras* (*Stemmatoceras*) aff. *triptolemus* (Morris and Lycett, 1851) which is clearly a *Kumatostephanus*. Another specimen figured by Arkell and Playford (1954, pl. 34, fig. 1) is *Pseudotoites robiginosus* Crick, 1894, HT. This specimen has a whorl morphology very close to some specimens from Dorset that match exactly with *G. gibbosus*.

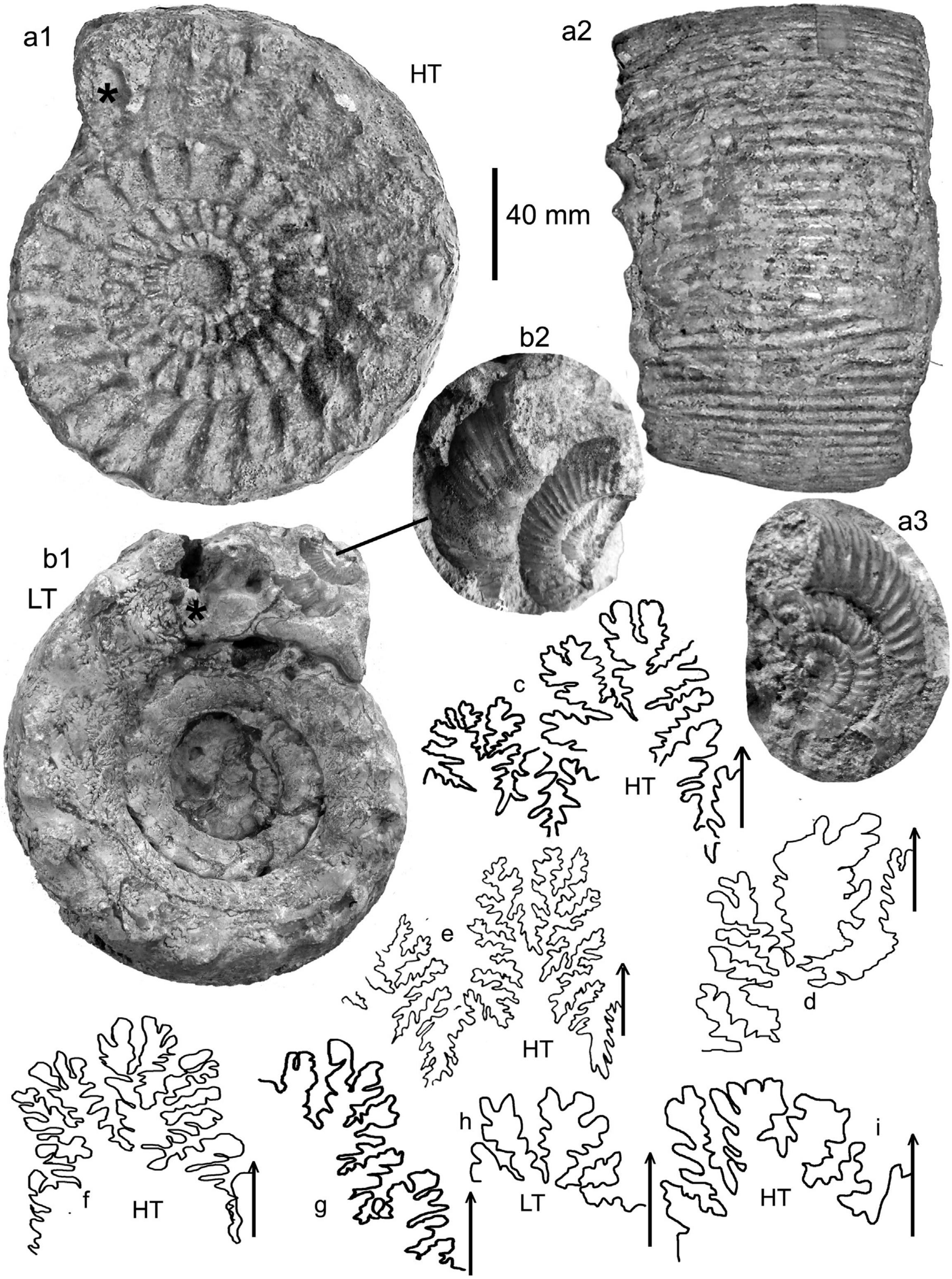

Fig. 6. (a1–3) *Teloceras *blagdeni* (Sowerby, 1818), HT, NHMUK C38265. Insert a3 shows a partial specimen of *Leptosphinctes* on reverse side of specimen. Sherborne area (Oborne), probably Frogden Quarry bed 5 top or 6 Blagdeni or Banksii subzones. (b1–2) *Teloceras calix* (Smith, 1817), LT, NHMUK C671. Insert b2 showing a *Leptosphinctes* preserved in the body-chamber, Sherborne, probably Frogden Quarry, bed 5 top or 6, Blagdeni or Banksii subzone. (c–i) Suture line drawings (not to scale) at approximately the same dimensions on each specimen. Arrows indicate direction of the aperture. (c) *Pseudoteloceras digbyi* sp. nov. HT, WC0632; (d) *Pseudoteloceras boursicoti*, WC0611; (e) *Teloceras blagdeni*, HT, NHM C 38265; (f) *Pseudoteloceras labrum*, HT, GSM 17450; (g) *Teloceras banksii*, NHM C78542; (h) *Teloceras calix*, LT, NHM C671; (i) *Gibbistephanus gibbosus*, HT, GSM 49350. A black star indicates the last preserved suture. Specimens not coated with ammonium chloride prior to photography. Scale bar 40 mm.

Pseudotoites carlottensis (Whiteaves, 1876), in Arkell (1954, fig. 11, p. 588 and fig. 12, p. 589) also shows strong similarities with some Dorset specimens.

Five faunas of the Kumatostephaninae can be discriminated in southwest England between the Laeviuscula and Humphriesianum zones (pars) separated by non-sequences.

- *K. kumaterus* and *perjucundus* in *micracanthica* horizon of the Laeviuscula Zone to the *kumaterus* horizon, Sauzei Zone (Chandler et al., 2013).
- *Pseudoteloceras digbyi* sp. nov. in *digbyi* horizon, upper Sauzei Zone (Figs. 7 and 14 b, d, h, i).
- *Pseudoteloceras boursicoti* Pavia and Fernández-López, 2016, in *wrighti* horizon, Humphriesianum Zone, Romani Subzone (Figs. 11, 12 b and c).
- *Pseudoteloceras labrum* (Buckman, 1922), *labrum* horizon. Humphriesianum Zone, Romani Subzone, bed 4biii of Oborne (Figs. 12 a, 13).

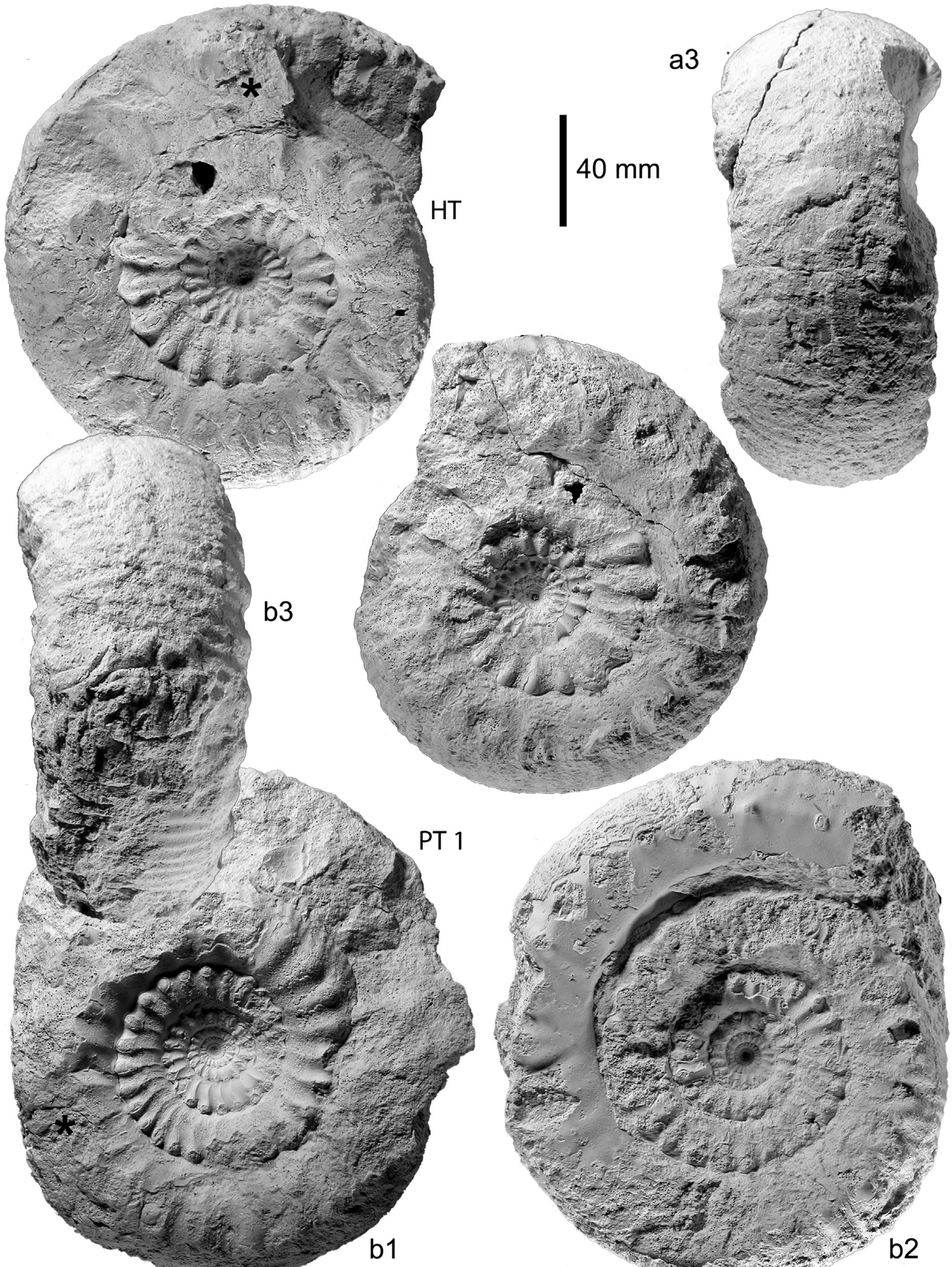

Fig. 7. (a and b) *Pseudoteloceras digbyi* [M]; (a1–3) WC0632, HT. (b1–3) NHMUK PICA5585, PT1. Bed 4b, Sauzei Zone, Hebridica Subzone, *digbyi* horizon, Redhole Lane, Clatcombe, Dorset. A black star indicates the last preserved suture. Specimens coated with ammonium chloride prior to photography. Scale bar: 40 mm.

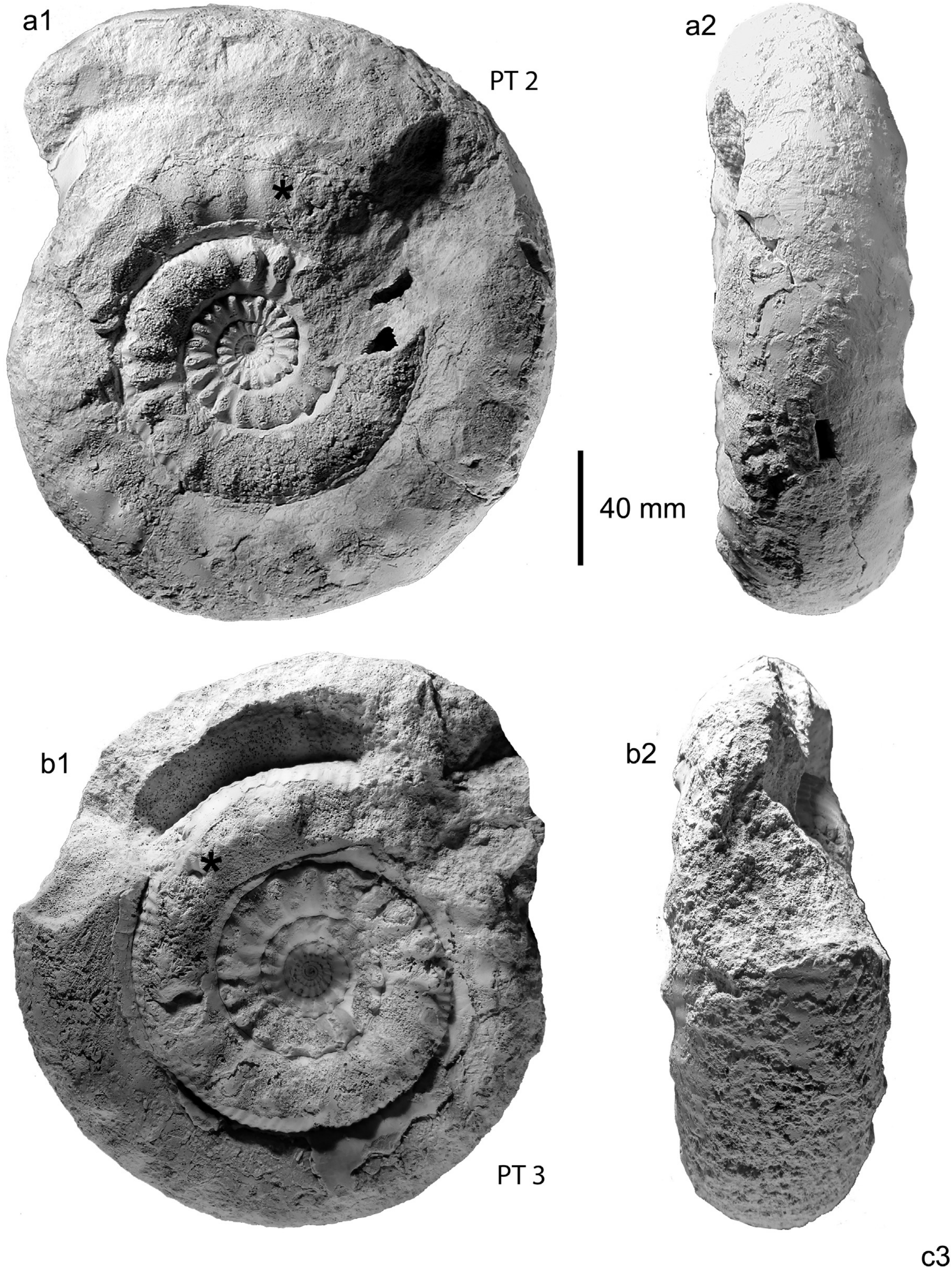

Fig. 8. (a and b) *Pseudoteloceras digbyi* [M]; (a1–3) WC0738, PT2. Specimen closest to *Kumatostephanus perjucundus*, bed 4b, lower part, Redhole Lane, Clatcombe, Dorset. (b1–2) WC0502, PT3. Specimen retaining features of *Kumatostephanus*, Bed 4b, Sauzei Zone, Hebridica Subzone, *digbyi* horizon, Redhole Lane, Clatcombe, Dorset. A black star indicates the last preserved suture. Specimens coated with ammonium chloride prior to photography. Scale bar: 40 mm.

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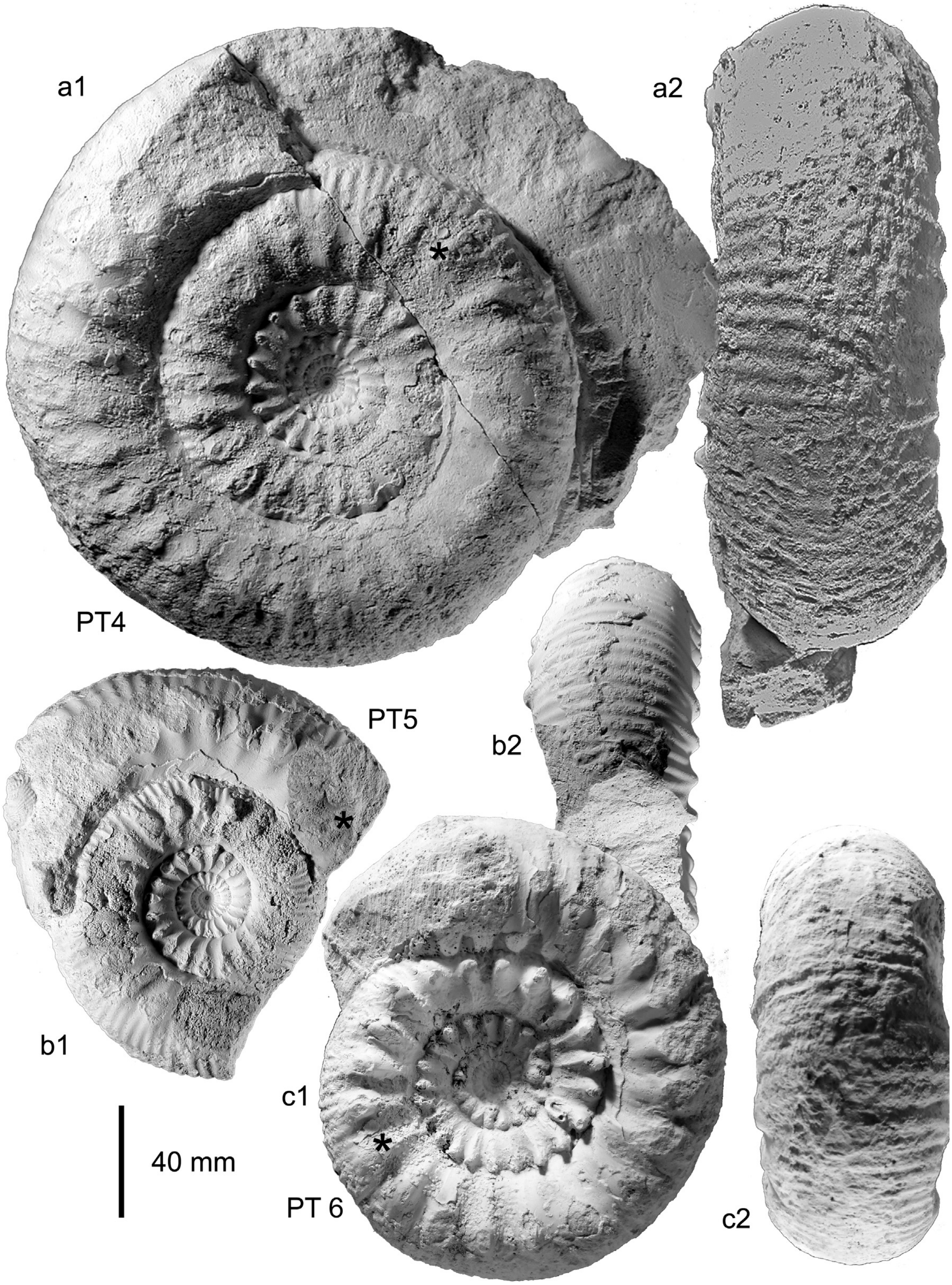

Fig. 9. (a and c) *Pseudoteloceras digbyi* [M]; (a1–2) WC0737, PT4. (b1–2) WC0740, PT5.?small adult [M]. (c1–2) WC0643, PT6, small adult [M]. Bed 4b, Sauzei Zone, Hebridica Subzone, *digbyi* horizon, Redhole Lane, Clatcombe, Dorset. A black star indicates the last preserved suture. Specimens coated with ammonium chloride prior to photography. Scale bar: 40 mm.

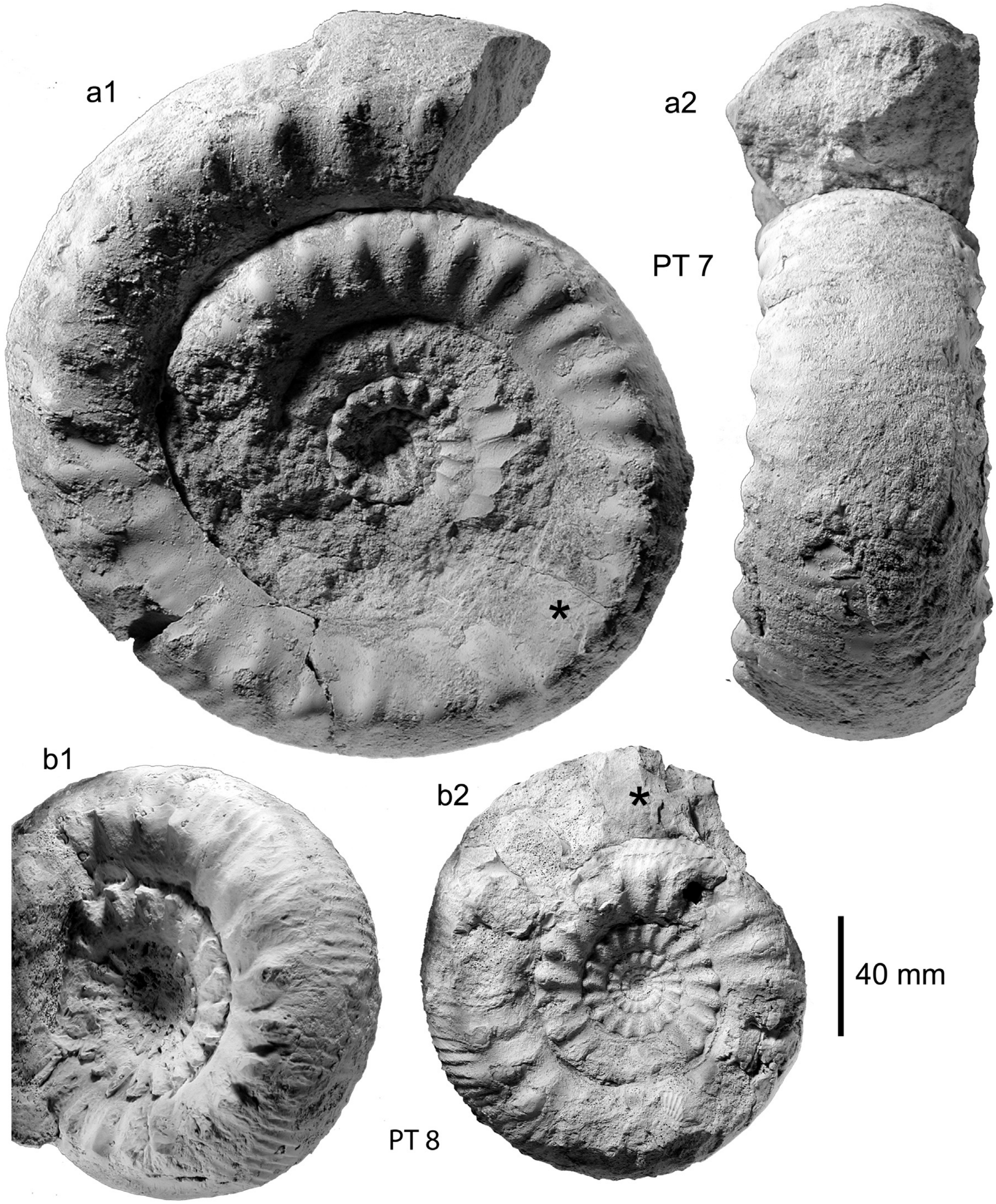

Fig. 10. (a and b) *Pseudoteloceras digbyi* [M]; (a1–2) WC0740, PT7. (b1–2) WC0644, PT8. Views of different sides of the same specimen. Bed 6a, Sauzei Zone, Hebridica Subzone, *digbyi* horizon, Sandford Lane, Dorset. A black star indicates the last preserved suture. Specimens coated with ammonium chloride prior to photography. Scale bar: 40 mm.

- *G. gibbosus* in *gibbosus* horizon, Humphriesianum Zone (Fig. 15) marking the survival the genus beyond traditional interpretation.

The abundant *Teloceras* in superjacent strata are not discussed here. Suture lines are of limited use at this high level of biostratigraphical resolution and any study of a large number of specimens soon reveals that they are as variable as the morphology of the shells themselves. A range of sutures for the new subfamily are given as Fig. 6.

Genus ***Pseudoteloceras*** Pavia and Fernández-López, 2016.

Type species: *Pseudoteloceras croisillense* Pavia and Fernández-López, 2016, fig. 3.

Pseudoteloceras digbyi sp. nov. [M & m]

Fig. 7, a1-3 HT; b1-3 PT1. Fig. 8, a1-2 PT2; b1-2 PT3. Fig. 9, a1-2 PT4; b1-2 PT5; c1-2 PT6. Fig. 10, a1-2 PT 7; b1-2 PT8. Fig. 14, e1-2 PT9; f1-2 PT10.

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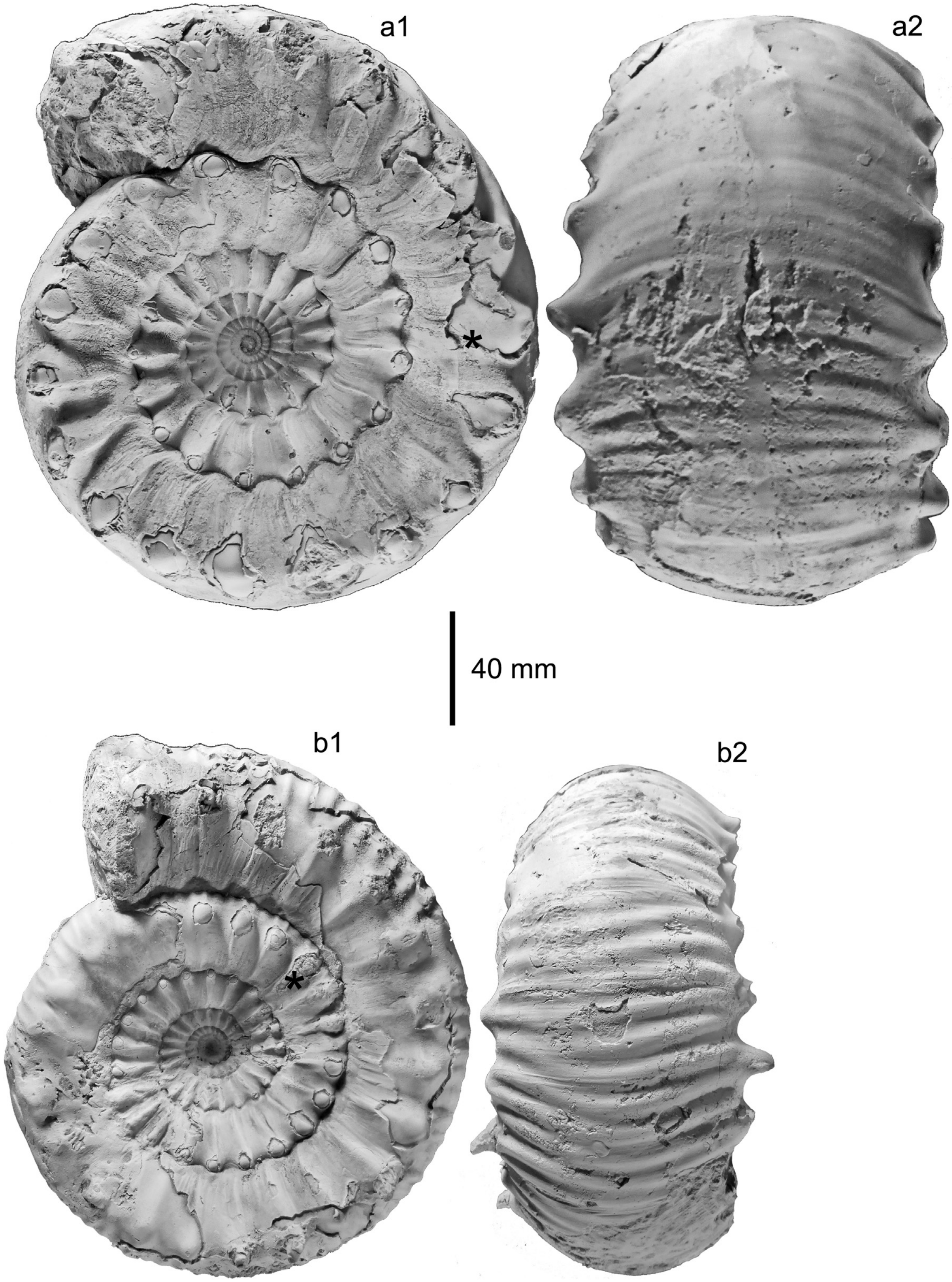

Fig. 11. (a and b) *Pseudoteloceras boursicoti* [M]; (a1–2) WC0611, Broad specimen figured as *Teloceras labrum* by Callomon and Chandler, 1990. (b1–2) WC0612, slender specimen. Bed 4b middle part, Humphriesianum Zone, Romani Subzone, *wrighti* horizon, Frogden Quarry, Oborne, Dorset. A black star indicates the last preserved suture. Specimens coated with ammonium chloride prior to photography. Scale bar: 40 mm.

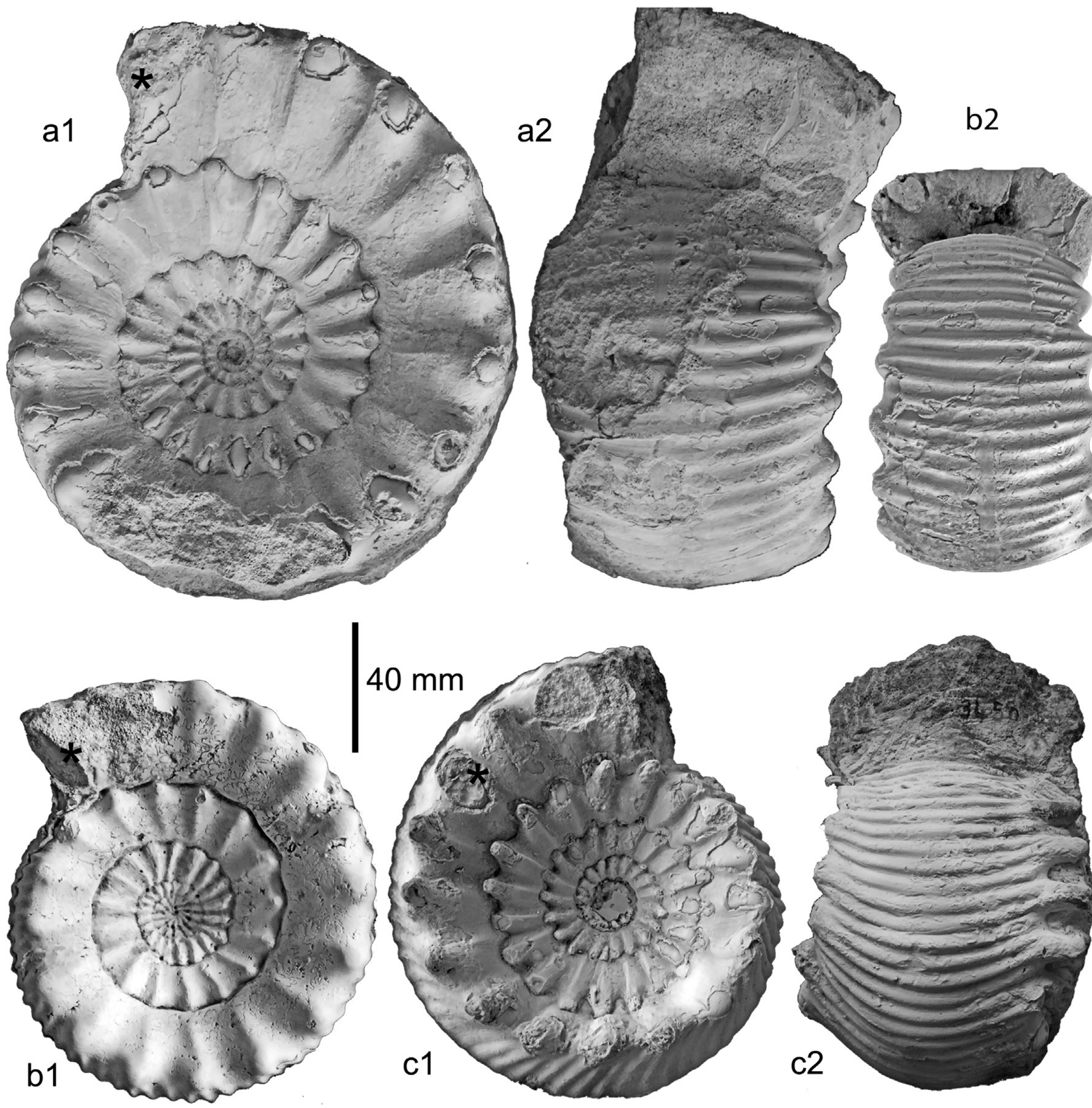

Fig. 12. (a1–2) *Pseudoteloceras labrum* [M], WC5276, Bed 4b top, Humphriesianum Zone, Romani Subzone, *labrum* horizon, Frogden Quarry, Oborne, Dorset. (b1–2) *Pseudoteloceras boursicoti* [M], WC2205; (c1–2) *Pseudoteloceras boursicoti* [M], WC5275, Bed 4b middle part, Humphriesianum Zone, Romani Subzone, *wrighti* horizon, Frogden Quarry, Obo rne, Dorset. A black star indicates the last preserved suture. Specimens coated with ammonium chloride prior to photography. Scale bar: 40 mm.

No published accounts exist that allow us to produce a reliable synonymy. The macroconchs appear to have evaded prior description.

Diagnosis: Medium sized, macroconchs and microconchs, [M], 10–25 cm diameter, [m] around 5 cm diameter. The inner whorls are cadiconic and *Teloceras*-like, followed by rapid uncoiling of the umbilical seam to a sub-planulate morphology. The inner whorl cross-section is trapezoid to sub-quadrate with a broad whorl breadth and with flattening of the venter. This produces a sharp angle between the umbilical wall and venter at which primary ribs develop into long, coarse spines. The primary ribbing is strong dividing into three moderately strong secondaries. Ribbing on the venter is often out of phase on either half of venter, weakened at the mid-line, sometimes producing a smooth band. Rib density at small diameters declines with growth, then increases. Ribbing and spines persists to the aperture that is plain and sinuous lacking a developed collar in most specimens. Complete shells are morphologically intermediate between *Kumatostephanus* and *Pseudoteloceras*.

The suture line (Fig. 6) is relatively simple in planulate forms and complex in broad forms, with 1st lateral saddle E/L being asymmetric and higher than the second lateral saddle. Microconchs (Fig. 14e and f) retain a conservative style of morphology and the suture is less complex.

Type specimens Holotype. Fig. 7, a1-3 HT, WC0632 from Redhole Lane (Sherborne, S England).

Figured paratypes. NHMUK PICA5585, WC0738, WC0502, WC0737, WC0740, WC0643 from Redhole Lane. WC0740, WC0644, WC0725, WC0720 from Sandford Lane, Sherborne, Dorset. Five specimens not figured.

Derivation of name: In honour of the Wingfield Digby family of Sherborne Castle Estates, who for over a century, have granted consent to carry out geological research on Estate land on which many classic localities lie, including sites where numerous types designated by past workers have been obtained.

Type locality and stratigraphical horizon: Holotype: Redhole Lane, bed 4b. Paratypes: Redhole Lane, bed 4b and Sandford Lane,

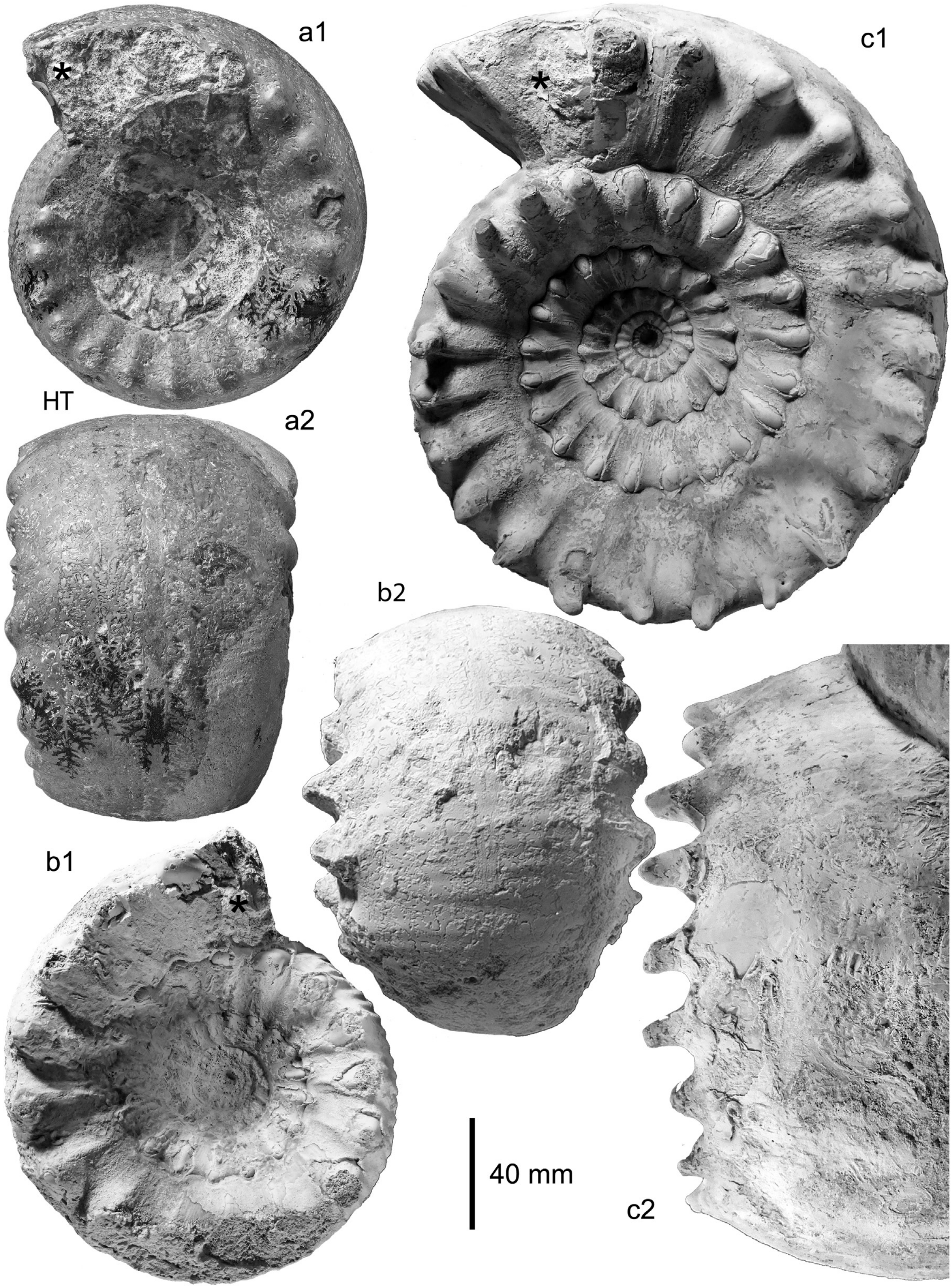

Fig. 13. (a1–2) *Pseudoteloceras labrum*[M], HT, GSM 47150, '*Epalxites* hemera' = bed 4b top part, Frogden Quarry, Oborne, Dorset. (b1–2) CP4800, Parsons Collection, bed 4b, top, Humphriesianum Zone, Romani Subzone, *labrum* horizon, Oborne Wood, Oborne, Dorset. (c1–2) WC0712; (c1–2). Largest specimen recorded to date, bed 4b top, Humphriesianum Zone, Romani Subzone, *labrum* horizon, Frogden Quarry, Oborne, Dorset. A black star indicates the last preserved suture. Specimens coated with ammonium chloride prior to photography apart from a1–2. Scale bar: 40 mm.

bed 6a. Both sites near Sherborne, Dorset, UK, Inferior Oolite Formation, Middle Jurassic, Bajocian, Sauzei Zone, *digbyi* horizon.

Remarks: *P. digbyi* links stephanoceratid-like *Kumatostephanus* with *Teloceras*-like specimens of later strata. In the *digbyi* horizon the range of variability includes specimens that could still be included in *Kumatostephanus*. A number of species figured in the literature may well be similar in age to *P. digbyi* sp. nov. [M] but have not been recorded with adequate stratigraphical precision to make firm judgement. To avoid future confusion we have not listed these. The specimens depicted here have all been collected in situ and represent the variability of the population at one stratigraphical level, the *digbyi* horizon of the Sauzei Zone. It is now proven that the top of the Fossil Bed of Sandford Lane (bed 6a) and of Redhole Lane (bed 4b) are very close in age (*digbyi* horizon). One specimen (WC0200, Fig. 16b1-2) collected from the top of bed 3 of Miller's Hill, Milborne Wick may represent a further horizon of the Sauzei Zone containing a fauna of *Pseudoteloceras* not described here. This single specimen has differences from specimens from other horizons, however, a detailed study of the stratigraphy of the locality has not been possible.

Kumatostephanus rugosus (Westermann, 1954) [m] and allied species are microconchs associated with *Kumatostephanus* from which *P. digbyi* evolves. Presumably the microconchs of *P. digbyi* sp. nov, are not markedly different. *Epalxites lepsiusi* Westermann, 1954 *non* Gillet, 1937 and *Epalxites* cf. *anceps* (Quenstedt, 1886) represent the best candidates for the microconch partners of *P. digbyi* (Fig. 14e1-2; f1-2). It is our view that, like the macroconchs, the microconchs display a range of morphology and that *Pseudoteloceras* arises from the coarse end member of the population.

Pseudoteloceras croisillense Pavia and Fernández-López, 2016 [M & m]

Holotype. *Pseudoteloceras *croisillense* Pavia and Fernández-López, 2016, text fig. 3 [=*Ammonites blagdeni*, Sowerby *in* d'Orbigny, 1842–1851, pl. 132].

Fig. 11, a1-2; b1-2. Fig. 12, b1-2; c1-2 [M]. Fig. 14, b1-2; d1-2; h1-2; i1-2 [m].

(?)1951 *Teloceras lotharingicum* Maubeuge, p. 79, pl. 6, fig. 4, [M].

1951 *Teloceras geometricum* Maubeuge, p. 76, pl. 4, fig. 4, [M].

(?)1983 *Kumatostephanus* (*Stemmatoceras)* sp. (="*Stemmatoceras ellipticum* Mascke" nomen nudum. Pavia, p. 110, fig. 28, [M].

v1990 *Teloceras labrum* Buckman. Callomon and Chandler, p. 110, pl. 4, figs. a-b; [M].

2016 *Pseudoteloceras croisillense* gen. et sp. nov. Pavia and Fernández-López, p. 200 text fig. 3, [M].

The genus *Pseudoteloceras* was erected with four species: *P. croisillense*, *Pseudoteloceras maerteni* and *P. boursicoti* along with *Pseudoteloceras geometricum* (Maubeuge, 1951), considered by these authors to be the root of the genus. The genus was erected to separate '*Teloceras*'-like specimens from the Early Humphriesianum Zone from the *Teloceras* sensu stricto of the Late Humphriesianum Zone to Niortense Zone, on the grounds of an apparent absence of such forms over the middle part of the Humphriesianum Zone throughout Western Europe. The authors erected as type for *P. croisillense* a specimen figured by Orbigny (1847, p. 396, pl. 132) and as a photograph by Pavia (1983, fig. 29) and repeated in Pavia and Fernández-López (2016). This specimen has an unknown stratigraphical provenance: "d'Orbigny (1847 in 1842-1851, p. 396) did not give any indication of the type-locality of the holotype, except a general reference to the area of Les-Moutiers-en-Cinglais in Calvados". Pavia and Fernández-López (2016, p. 6) have collected in that region and, based on morphological comparison with new specimens and matrix similarity, concluded that the specimen probably came from bed 6 of "Les Fours à Chaux" in the area of Croisilles. Extreme caution should be exercised over this view since the specimen used principally to make this comparison is in a poor state of preservation, see Pavia and Fernández-López (2016, fig. 5). In addition, this specimen is different from others of their type series. All but one of the macroconchs are small pre-adults. The suture depicted (p. 5, fig. 4) is that of a microconch rather than that of the macroconch type specimen, which is available in d'Orbigny's figure (1847, pl. 132). Since homeomorphy is common among ammonites of this family, it would have been better to designate a specimen as type whose exact locality and horizon is certain.

Pavia and Fernández-López (2016) include in *Pseudoteloceras* on purely morphological grounds the species: *P. croisillense*, *P. maerteni* and *P. boursicoti* without any separation by stratigraphical horizon which presumably represent the range of variability of specimens in the early Humphriesianum Zone. The specimens of *P. boursicoti* (Pavia and Fernández-López, 2016, fig. 9) are smaller but identical to members of the fauna from the middle part of bed 4b at Frogden Quarry (Oborne, Dorset) and within the variability range of that species. We are therefore able to accept the taxon erected by Pavia and Fernández-López (2016), based on the type series but retaining doubt about the holotype. We found in Dorset *P. boursicoti* in the *wrighti* horizon of the Romani Subzone, Humphriesianum Zone. The best match for the microconchs included here as *P. boursicoti* is *Epalxites anceps* (Westermann, 1954, fig. 14, b, d, h and i)

Specimens from Dorset (Figs. 11 ; 12 b and c) show the full range of variability in well-preserved examples and include the specimen figured by Callomon and Chandler (1990, p. 111, pl. 4.) as *T. labrum* Buckman, included in synonymy with *P. croisillense* by Pavia and Fernández-López (2016).

Pseudoteloceras labrum (Buckman, 1922) [M & m].

Holotype: *Teloceras labrum* Buckman, 1922, pl. 350a-b.

Fig. 12, a1-2. Fig. 13, a1-2 HT refigured; b1-2; c1-2 [M]. Fig. 14, a1-2; c1-2 [m]

At Oborne Wood (Parsons, 1976) and at the present Frogden Quarry, there is an upward extension of bed 4b with an additional horizon beyond that previously reported (*labrum* horizon nov.), with large specimens of *Pseudoteloceras*. Notably, *Dorsetensia* spp. typical of the middle part of bed 4b, is absent and *Chrondroceras* spp. are less common. The *Teloceras* in this level are generally much larger than in the subjacent horizon with phragmocone diameters as large as 25 cm. They have very broad whorl sections and intermediate morphology between *P. boursicoti* and *Teloceras blagdeni.* They are very close by morphology to the holotype of *Teloceras labrum* Buckman, 1922, refigured here (Fig. 13, a1-2) and included in *Pseudoteloceras*. We regard these specimens to be *P. labrum* Buckman and the upper part of bed 4bi to be the type horizon. In Type Ammonites, Buckman (1925 in 1909–30, V, p. 74), states that *T. labrum* comes from the *Epalxites* hemera. This, according to Buckman's chart (p. 74) lies below the *pygmaeus* (blagdeni) hemera, equating at Frogden Quarry (Oborne area) to part of bed 4. The matrix of the type specimen matches the upper part of bed 4b and is therefore earlier than the time gap identified in strata of Western Europe over which *Teloceras* is reported to be absent. We surmise that the difference in age between the *wrighti* horizon and the top of bed 4b at Oborne may be very small and that *P. croisillense* is an earlier transient of *P. labrum*. Microconchs are morphologically similar to those from the *wrighti* horizon, but often larger. They are included here as *Pseudoteloceras labrum* [m] (Fig. 14, a and c) and match morphotypes of *E. anceps* and *Itinsaites mackenzii* (McLearn, 1929). At Burton Bradstock, beds of the late Humphriesianum Zone are missing or have not yielded diagnostic ammonites. One specimen of *Pseudoteloceras* sp. [m] (NMW G264 13.152) (Fig. 14, g1-2) probably comes from the late Sauzei Zone of that locality.

Genus ***Teloceras*** Mascke, 1907

Type species. *Ammonites *blagdeni* (J. Sowerby, 1818).

Until there is better understanding regarding the position of *Pseudoteloceras* and its relationship to *Teloceras* sensu stricto we

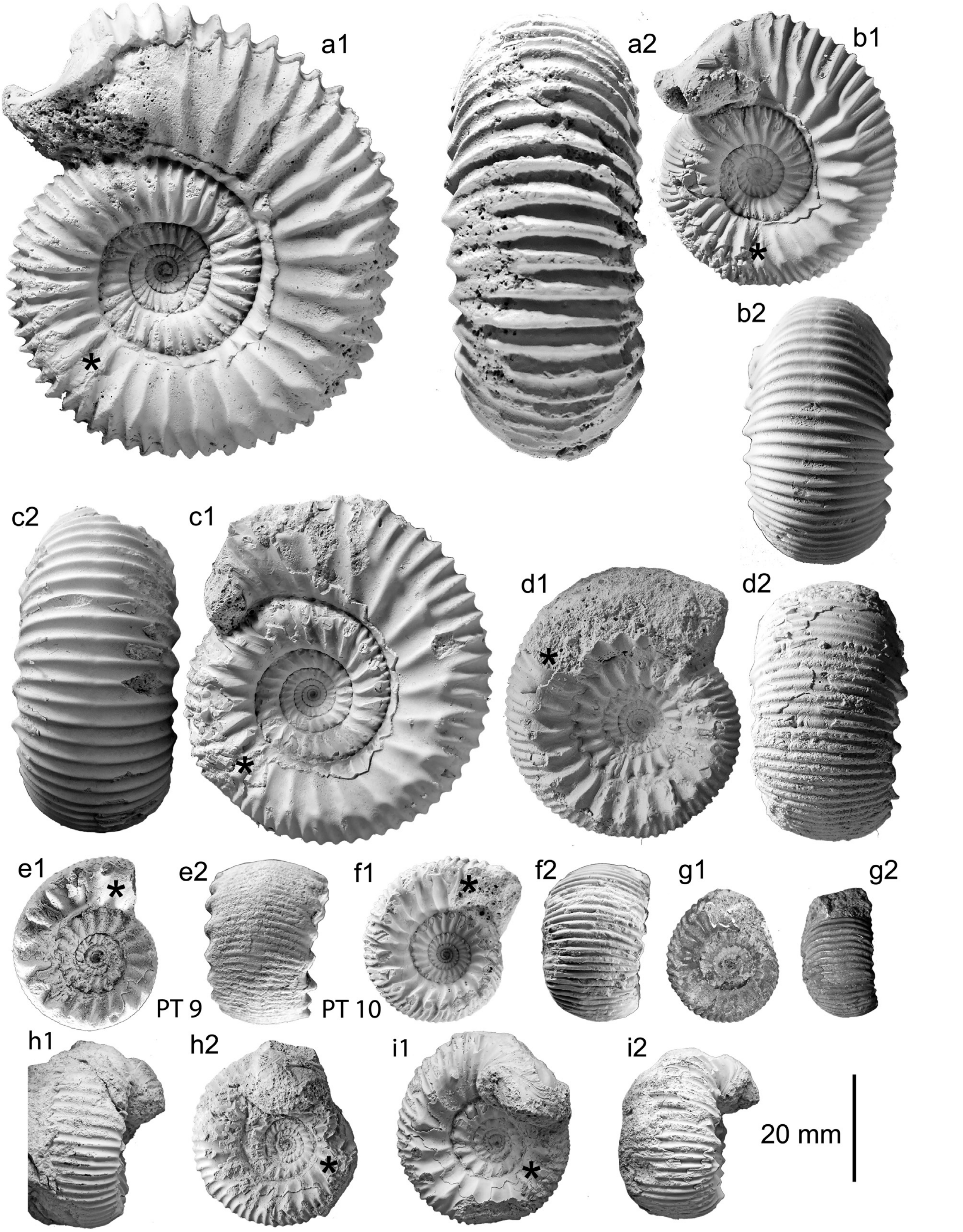

Fig. 14. (a–i) *Pseudoteloceras* [m]. (a1–2); (c1–2), *P. labrum* WC0729 and WC0727, Bed 4b top, Humphriesianum Zone, Romani Subzone, *labrum* horizon, Frogden Quarry, Oborne, Dorset. (b1–2); (d1–2); (h1–2); (i1–2), *P. boursicoti*, Bed 4b middle, Humphriesianum Zone, Romani Subzone, *wrighti* horizon, Frogden Quarry, Oborne, Dorset. (e1–2), (f1–2), *P. digbyi*, bed 6a, Late Sauzei Zone, *digbyi* horizon, Sandford Lane, Dorset. A black star indicates the last preserved suture. Specimens coated with ammonium chloride prior to photography. Scale bar: 20 mm.

have retained the name *Teloceras* only for specimens occurring above the *humphriesianum* horizon (Fig. 1). The type species of *Teloceras* is *T. blagdeni*; it is the subzonal index of the Blagdeni Subzone of the Humphriesianum Zone of the Lower Bajocian. The label on this specimen states the locality as Sherborne; it in all likelihood was obtained from Frogden Quarry or thereabouts. The type was figured as a colour print by Sowerby, (1818, pl. 201) and by S.S. Buckman (1908, pls. 2 and 3, Fig. 1) as a high quality drawing. An examination of the type specimen (NHMUK 43908c) of *T. blagdeni* (Fig. 6, a1-2) proves it to have come from strata at the

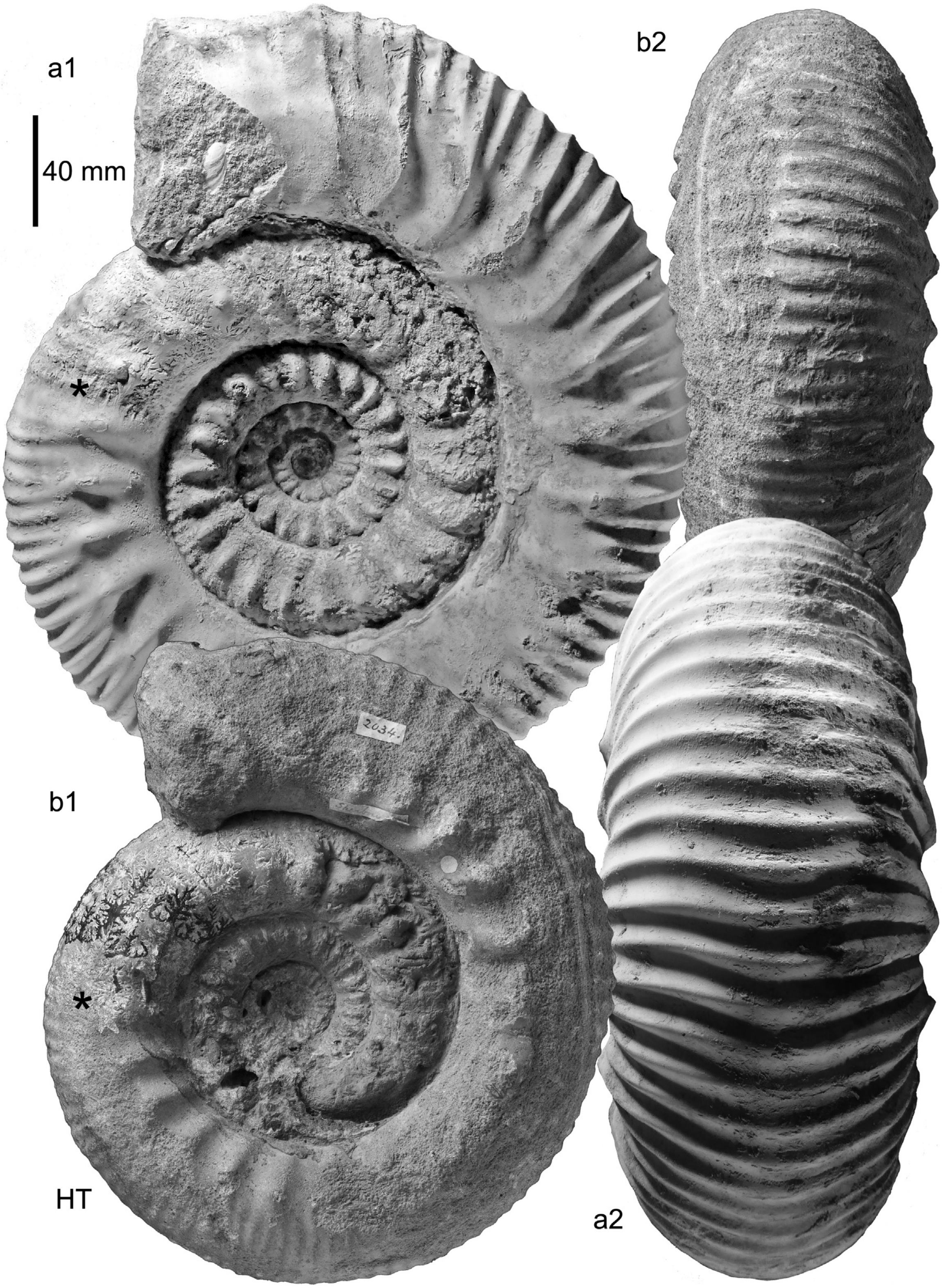

Fig. 15. (a and b) *Gibbistephanus gibbosus* [M]. (a1–2), WC0615, junction of bed 4 and 5, Humphriesianum Zone, Humphriesianum Subzone, *gibbosus* horizon, Frogden Quarry, Oborne, Dorset. (b1–2) GSM 49350, HT, Humphriesianum Zone, Humphriesianum Subzone, *gibbosus* horizon, Frogden Quarry, Oborne, Dorset. A black star indicates the last preserved suture. Specimen (a1–2) coated with ammonium chloride prior to photography; specimen (b1–2) not coated. Scale bar: 40 mm.

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junction of bed 5 and 6 based on new research in the type area. One side of the type specimen, assumed to be the upper eroded surface, has embedded in it, three partial, but well preserved examples of *Leptosphinctes* sp. (Fig. 6, a3). At Oborne, this genus has its first occurrence in bed 5b of the Niortense Zone, however, *Leptosphinctes* spp. has been recorded from earlier strata (e.g. Galácz, 2012; Pavia and Zunino, 2012). Thus, the type of *T. blagdeni* and specimens from bed 4b (*labrum* horizon nov.) are separated by a considerable stratigraphical gap.

A further observation concerns the lectotype of *Ammonites calix* (Smith, 1817) NHMUK C671 (Fig. 6, b1). This taxon was brought to our attention by A. Galácz (pers. com.) and appears to have been neglected by previous workers. The original type specimen is unavailable and Cox, 1930, designated a lectotype with a

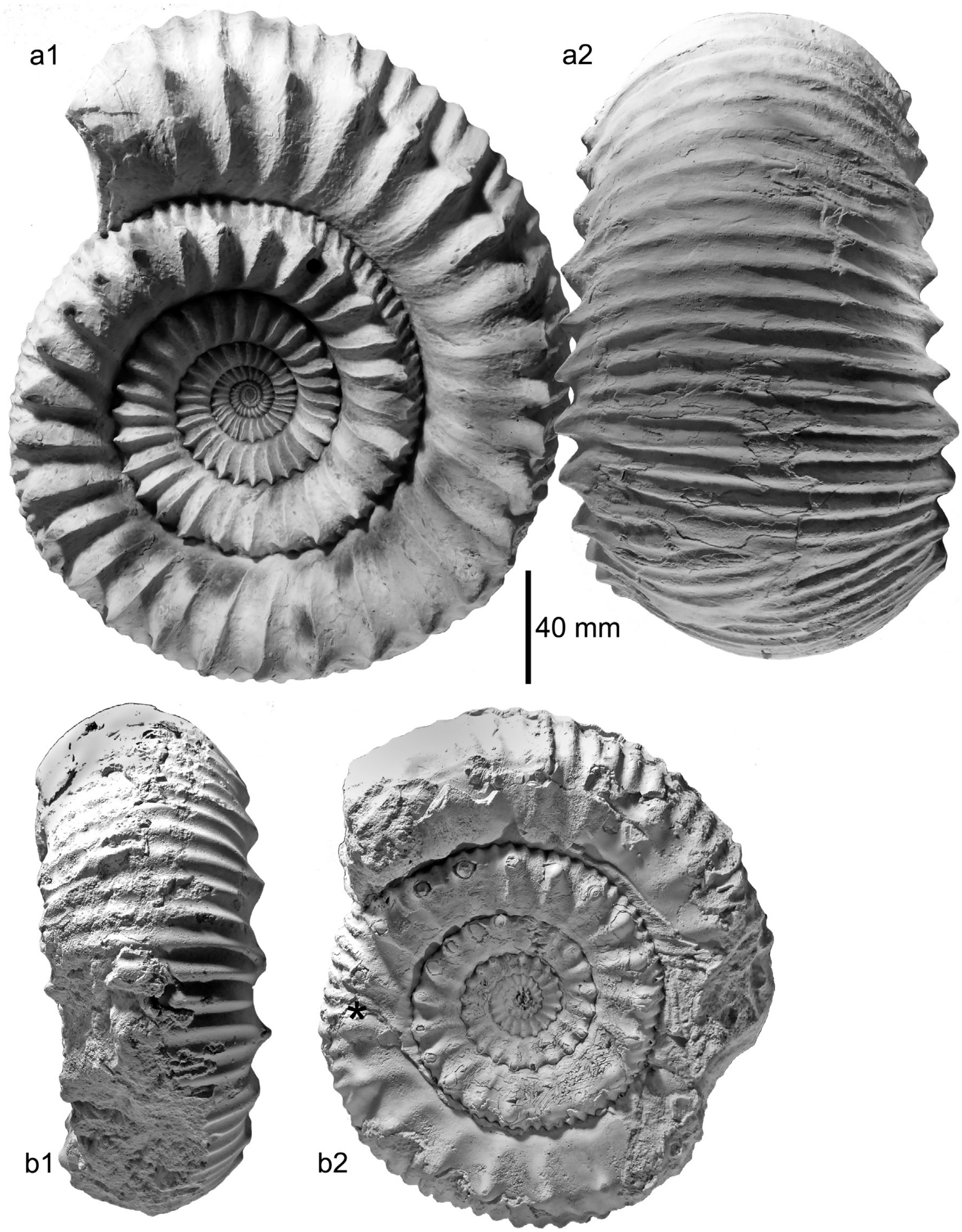

Fig. 16. (a1–2) ?*Gibbistephanus* or *Teloceras* sp., ES0001, E. Scherer collection, Humphriesianum Zone, Mössingen-Öschingen, Germany. (b1–2), *Pseudoteloceras* sp. WC0200, bed 4, Sauzei Zone, Millers Hill, Milborne Wick, Somerset. A black star indicates the last preserved suture on specimen (b1–2). The last suture is obscured by shell on specimen (a1–2). Specimens coated with ammonium chloride prior to photography. Scale bar: 40 mm.

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description and figure, therefore this taxon is not a nomen oblitum and we highlight its existence here to revitalize its use. The specimen figured by Cox (1930, fig. 12) is a form with features resembling *Gibbistephanus* and Cox himself suggested its synonymy with *Stephanoceras brodiaei* (Sowerby, 1822), however, this taxon is older and not conspecific in our view. *A. calix* precedes by date the publication of *T. blagdeni*, NHMUK C43908 and we provisionally place it in *Teloceras* pending further study. This specimen, subsequent to Cox's description, has been sectioned (Fig. 6, b1), it has a relatively narrow whorl breadth and is moderately evolute compared to contemporary *Teloceras*. It has identical features of preservation to the type of *T. blagdeni*

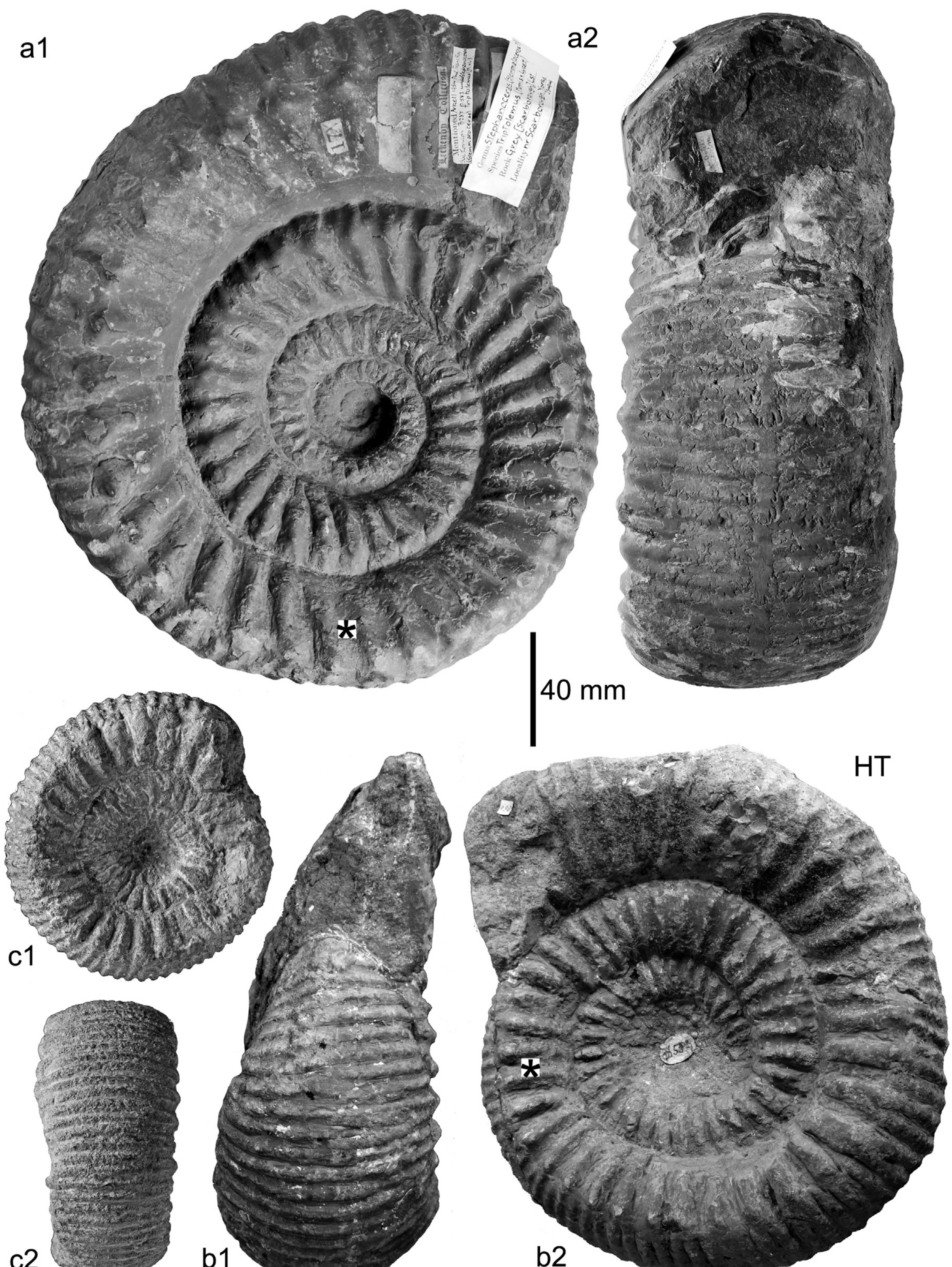

Fig. 17. (a–c) *Ammonites triptolemus*, [M]. (a1–2), CAMSMJ.34949. (b1–2) NHMUK 46553, HT. (c1–2), GSM 25254. Scarborough Limestone, Yorkshire. A black star on a white background indicates the last preserved suture. Specimens not coated with ammonium chloride prior to photography. Scale bar: 40 mm.

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(Sowerby, 1818) and has similar well preserved partial *Leptosphinctes* embedded in one surface. It likely comes from the same horizon in which it and *T. blagdeni* are variants of the variable *Teloceras* morphology at that level.

The specimens of bed 5b in the Oborne area comprise a variety of *Teloceras*-like ammonites, which share features with *T. labrum* and *T. blagdeni*. The holotype of *T. blagdeni* is atypical and morphologically closer to *T. labrum* than to the majority of specimens of *Teloceras* from bed 5a and b, the strata traditionally accepted as representing the Blagdeni Subzone. In bed 5a there exist many finely nodose forms matching *Teloceras multinodosum* (Quenstedt, 1886). Many have features in common with *G. gibbosus* Buckman (see below) and we postulate that they may represent hybrids between *Teloceras* and *Gibbistephanus*, or the extreme coarse variant of *Gibbistephanus* returning to Dorset as a migrants from the Eastern Pacific.

In Britain, the middle part of the Humphriesianum Zone is typified by common *Stephanoceras humphriesianum* (Sowerby, 1825), but *Teloceras*-like ammonites are notably absent. However, one of us (V.D.) reports the presence of *Teloceras*-like specimens in collections made from the Humphriesianum Zone, Humphriesianum Subzone of the Swabian Alb (Fig. 16).

We are thus faced with the question of whether there really is a gap in the *Teloceras* succession in Western Europe or that this is an artefact of collection failure. Does *Teloceras* sensu stricto have a continuous ancestry deriving from *Kumatostephanus* in the late Sauzei Zone with *Pseudoteloceras* as part of a chronocline ending in the Banksii Subzone or has this characteristic morphology arisen more than once either by migration of iterative evolution? This is discussed further below.

The known distribution of *Pseudoteloceras* and *Teloceras* is mainly documented in the North West European Province: France (d'Orbigny, 1847 in 1842-1851dOrbigny, 1842d'Orbigny, 1847 in 1842-1851dOrbigny, 1842d'Orbigny, 1847 in 1842-1851; Haug, 1907; Pavia and Martire, 2010; Pavia et al., 2013, Belgium (Maubeuge, 1951), Germany (Ohmert, 1988), Italy (Della Bruna and Martire, 1985), and particularly Dorset, from where most examples have come (Morris and Lycett, 1851; Buckman, 1922; Arkell, 1933; Parsons, 1976; Callomon and Chandler, 1990; Chandler et al., 2013).

Genus ***Gibbistephanus*** Buckman, 1928

Holotype: *Gibbistephanus *gibbosus* Buckman, pl. 780, figs. a-b, HT.

Fig. 15, a1-2; b1-2 HT refigured.

v1928 *Gibbistephanus *gibbosus*, nov. Buckman, pl. 780, figs. a-b.

(?)1964 *Stemmatoceras* cf. *S. triptolemus* (Morris and Lycett). Imlay, p. B49, pl. 21, figs. 1 & 3.

(?)1964 *Stemmatoceras* cf. *S. palliseri* (Mc Learn). Imlay, p. B48, pl. 21, figs. 2 & 4.

(?) 1964 *Stemmatoceras ursinum* Imlay. Imlay, p, B49, pl. 22, figs. 1-3.

(?)1964 *Teloceras itinsae* Mc Learn. Imlay, p. B50, pl. 23, figs. 9-10.

(?)1980 *Zemistephanus alaskensis* n. sp. ♀. Hall and Westermann, p. 32, pl. 5, figs. 1a-b.

(?)1983 *Kumatostephanus* (*Stemmatoceras*) sp. Pavia, pl. 17, figs. 1-3.

1983 *Kumatostephanus* (s.s.) *acuticostatum* Weisert. Pavia, p. 108, pl. 18.

1983 *Teloceras* (subgen?) *dubium* (Schmidtill and Krumbeck). Pavia, p. 112, pl. 20, fig. 1.

(?)1983 *Teloceras* (subgen?) *subcoronatum* (Oppel). Pavia, p. 116, pl. 21, fig. 3.

(?)1995 *Stemmatoceras frechi* (Renz). Ohmert et al., p. 81, pl. 6, fig. 1.

1995 *Stemmatoceras rauricum* n. sp. Ohmert et al., p. 86, pl. 7, figs. a-b.

v2013 *Kumatostephanus triplicatus* (Renz). Chandler et al., p. 293, fig. 8, A1-2 and B1-2.

2015 *Teloceras* (*Paviceras*) n.sp. [aff. *arietis* (Maubeuge)]. Dietze et al., p. 39, pl. 12.

(?)2015 *Stephanoceras* cf. *zieteni* (Quenstedt). Dietze et al., p. 37, pl. 7, figs 1-2.

(?)2015 *Teloceras latiumbilicatum* Schmidtill and Krumbeck. Dietze et al., p. 39, figs. 23-24.

Diagnosis: Macroconchs up to 40 cm diameter. Specimens are evolute, with broad, depressed whorl sections. The primary ribs are short and concave towards the aperture and developed along their length into stout tubercles or spines, from which two or three secondary ribs develop. The ribbing has broad, rounded crests and is strongly developed to the aperture. The venter is sub-ovoid in most specimens at the midpoint of which the ribbing fades slightly and flexes back. The mouth-border lacks the strongly developed collar seen in contemporary *Stephanoceras* and the body chamber length is shorter being between three quarters and one whorl in length.

Type locality and stratigraphical horizon: The type specimen comes from Frogden Quarry, Oborne. Research here proves its stratigraphical position to be at the junction of bed 4c and bed 5 at Frogden Quarry and Oborne generally. Infrequent specimens also occur in the upper ironshot part of bed 4c and stand apart from the *Stephanoceras* fauna of that horizon (*humphriesianum* horizon).

Discussion: Buckman named these forms *G. gibbosus*, Buckman, 1928; pl. 780, figs. a-b, HT, and in all respects; apart from their larger size, they share many morphological features with *Kumatostephanus*, but are separated from western European Sauzei Zone species by a time gap or reduction in numbers. Specimens figured by Ohmert et al. (1995, pl. 6, fig. 1 and pl. 7, figs. a-b) included in *Stemmatoceras* sensu Ohmert, bridge this gap and may represent the continuation of the chronocline into the Humphriesianum Zone. Specimens very close to those figured by Ohmert et al., 1995 occur at the top of bed 9c (*rhytum* horizon) of Burton Bradstock (South Dorset) and may represent the progress of the *Kumatostephanus* lineage of Kumatostephaninae into the latest Sauzei Zone, but are already distinct from *Pseudoteloceras*. We suppose that *Kumatostephanus* became locally extinct or reduced in Western Europe, but returned sporadically as *Gibbistephanus* larger and more coarsely ribbed, but in all other respects, differing little from coarsely ribbed *Kumatostephanus.* Specimens resembling *Gibbistephanus,* such as *Teloceras itinsae* (McLearn, 1929) and *S.* cf. *S. palliseri* (McLearn) both sensu Imlay (1964, pl. 23, figs. 9-10 and pl. 21, figs. 2 and 4 respectively) and specimens figured by Hall and Westermann (1980, pl. 5, figs. 1a-b) as *Zemistephanus alaskensis* are probable candidates for forms present in the Pacific during the absence of *Kumatostephanus* from Western Europe. Hall and Westermann (1980) indicate an age for *Z. alaskensis* (1980, p. 19, table 4) to be Humphriesianum Zone, Romani Subzone, making such forms good candidates for a return to Western Europe slightly later. A bi-directional exchange of species is likely since many of the variants in both Europe and the Eastern Pacific display common features. Specimens with very prominent, deep ribbing, such as that depicted by Sadki, (1996, pl. 9 and 10) as *Zemistephanus* are also likely to have strong affinities to *Gibbistephanus*. The microconchs of the British specimens and those of *Zemistephanus* depicted in Hall and Westermann (1980, pl. 2 and 5) have features in common that support their affiliation to Kumatostephaninae.

3. Discussion

The central question is whether *Teloceras* sensu stricto evolves from *Kumatostephanus* in the Sauzei Zone via *P. digbyi*, *P. boursicoti* and *P. labrum* or whether homeomorphic morphology arises again in the upper Humphriesianum Zone.

Pavia (1983) and recently Pavia and Fernández-López (2016) suggested that the genus *Teloceras* sensu stricto of the Blagdeni Subzone stands apart from earlier forms of *Teloceras*-like ammonites recently named by them as *Pseudoteloceras* and that *Teloceras*-like ammonites evolved twice separated by a short stratigraphical break over Western Europe. They concluded that *Teloceras* has evolved from *Stemmatoceras* via an intermediate form such as the genus *Paviceras* Gauthier et al., 1996 in the late Humphriesianum Subzone, and did not evolve from *Pseudoteloceras* of the earlier Romani Subzone. The type species of the genus *Paviceras* is *Stemmatoceras hoffmanni* Schmidtill and Krumbeck (1938, pl. 13 fig. 6) that is considered here as a broad member of the genus *Stephanoceras*.

The Sauzei and Humphriesianum zones of the Inferior Oolite Formation of southwest England contain evidence of a number of ammonite migratory events some of which occur closely in time, but where significant evolution has occurred elsewhere, leading to the establishment, temporary and permanent, of major new taxa in the area. For example, in the late Bradfordensis to early Concavum zones (Aa-12 to 13) the arrival in Dorset of the first stephanoceratids occurs (Callomon and Chandler, 1990), with forms closely related to *Coeloceras* sensu Vacek (1886) and sensu Hantken in Prinz (1904) and placed in *Riccardiceras* by Westermann (1995). These ammonites are of an evolute, serpenticone, *Skirroceras*-style of morphology that persists into the late Lower Bajocian and constitute the subfamily Stephanoceratinae. *Kumatostephanus* first appears suddenly in the Laeviuscula Zone representing the root of the subfamily Kumatostephaninae in Western Europe. Specimens included in *Zemistephanus* by Sadki (1996) from the Laeviuscula Zone of Morocco may represent extreme coarse variants of the *Kumatostephanus* morphology probably evolving to *Gibbistephanus*.

There is persistent similarity between faunas of stephanoceratids from Western Europe and those of the Pacific. It is possible that geographical isolation was inadequate to ensure the establishment of non-interbreeding populations and migration and hybridization may have occurred (Kronenberg, 2008). Homeomorphy due to parallel morphological evolution observed in the ammonites from different provinces of similar age is noted by Arkell and Playford (1954, p. 597): "It appears that at any given time and place an ammonite stock may by evolutionary radiation, or deployment, give rise to various 'genera', more or less parallel to those produced by other stocks in other parts of the world at the same or at a different time".

The absence of both *Kumatostephanus* and *Teloceras* in the middle part of the Humphriesianum Zone in Western Europe and their reappearance later may result from migration and retreat or local extinction. It is difficult to envisage homeomorphs with features fitting perfectly the probable evolutionary trend of *Teloceras* from the Romani Subzone, arising from a different lineage less than a subzone after the earlier form has disappeared. This gap may be smaller than previously reported as we have now established that *P. labrum* occurs in the top of bed 4b (*labrum* horizon) at the top of the Romani Subzone. In time terms the 'gap' between this level and the arrival of abundant *Teloceras* spp. is very short.

If, however, we are to postulate a de novo arrival for *Teloceras* sensu stricto in the late Humphriesianum Zone, then rather than arising from *Paviceras*, there is a basis for considering that the *Teloceras* morphology arises as the extreme coarse broad variant of *Gibbistephanus*. A number of specimens in German private collections show all intermediate characters clearly (Fig. 16, a1-2), however, hybridization between *Teloceras* and *Gibbistephanus* following a brief separation is also plausible.

A brief comment is needed on *Ammonites triptolemus* Bean in Morris and Lycett, 1851, [M] that we tentatively include in the subfamily Kumatostephaninae. The original figure of this species, a drawing, is misleading and there are erroneous interpretations. Arkell and Playford (1954, p. 583) report that the holotype of Morris and Lycett's species could not be located, they cite Sedgwick Museum specimen CAMSMJ.34949 and Geological Survey Museum specimen GSM 25254 to be synonymous and from the type area, the Scarborough Limestone of Yorkshire. The type specimen does, however, exist and is in the collection of the Natural History Museum, London (NHMUK 46553), and was figured by Pavia (1983, pl. 20, fig. 2). The three cited specimens are figured here (Fig. 17a–c). In Dorset, specimens close to the type occur in a horizon above *S. humphriesianum* and below that of *G. gibbosus*, and the morph has an infrequent occurrence below. The three cited specimens do have some features in common with *Gibbistephanus*, but their exact affinity remains uncertain. The majority of specimens possess a broad quadrate venter rather than the ovoid profile typical of *Gibbistephanus* and exact matches for the Yorkshire specimens appear absent from South West England.

4. Conclusion

The new subfamily Kumatostephaninae is erected to include the genera *Kumatostephanus*, *Pseudoteloceras*, *Teloceras* and *Gibbistephanus*. The subfamily ranges from the late Laeviuscula Zone of the Lower Bajocian to the Niortense Zone of the Upper Bajocian. Different evolutionary routes are discussed. (a) *Kumatostephanus* gives rise to *Pseudoteloceras* through to *Teloceras* sensu stricto of the early Late Bajocian. (b) *Kumatostephanus* persists beyond the Sauzei Zone giving rise to *Gibbistephanus* in the Humphriesianum Zone. Extreme coarse variants of *Gibbistephanus* are homeomorphs of *Teloceras* and may account for conclusions stating that *Teloceras* arises from *Stemmatoceras* sensu Pavia (1983), Ohmert (1990), Ohmert in Ohmert et al., 1995 etc. in the late Humphriesianum Zone. (c). Geographical separation may have been inadequate to prevent hybridization of some populations of Kumatostephaninae resulting in frequent hybrids resembling *Teloceras*.

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