# THE DISTRIBUTION OF THE AMMONITE *GRAVESIA* (SALFELD, 1913) IN THE KIMMERIDGE CLAY FORMATION (LATE JURASSIC) IN BRITAIN

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Species of the ammonite *Gravesia* (Salfeld, 1913) have a widespread distribution in Europe over a relatively narrow stratigraphical range in the late Kimmeridgian and early Tithonian stages. The genus is a warm-water form that reaches its maximum stratigraphical range in the Submediterranean faunal province in central France and south Germany where six species have been recognised. Four of these, *G. gigas* (Zieten, 1830), *G. gravesiana* (d'Orbigny, 1850), *G. irius* (d'Orbigny, 1850) and *G. lafauriana* Hantzpergue, 1987 have been recorded in the Kimmeridge Clay Formation. A few examples have been found in cored boreholes, but most have come from the cliff and foreshore outcrops at Brandy Bay and Kimmeridge Bay in Dorset. The distribution of *Gravesia* in Britain is mostly restricted to the more calcareous parts of the succession where they represent migrations of a warmer water fauna into a region in which the ammonite assemblages were dominated by Subboreal forms of *Aulacostephanus* and *Pectinatites*. The palaeogeography of the late Jurassic in central and North West Europe comprised relatively small land areas separated by seaways that became progressively more restricted with time. In late Kimmeridgian and early Tithonian/Volgian times, migrations of warmer- and cooler-water ammonites through these seaways gave rise to mixed assemblages that enable correlations to be made between the local zonal schemes in the Submediterranean and Subboreal faunal provinces. *Gravesia* is one of the few ammonites that has a stratigraphical range that crosses the Kimmeridgian-Tithonian and Kimmeridgian-Volgian boundaries, and which has a large geographical distribution which includes much of North West and Central Europe and as far east as the Subarctic Urals. The known distribution of the genus in Britain is summarised herein, along with the first detailed account of its occurrence in the Kimmeridge Clay Formation in the Dorset type section.

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## INTRODUCTION

Species of the ammonite *Gravesia* were first recorded in Britain by Salfeld (1913) who collected *G. gravesiana* (d'Orbigny, 1850) and *G. irius* (d'Orbigny, 1850) from the Kimmeridge Clay Formation at and adjacent to Kimmeridge Bay, Dorset. He used these species to define two zones, *G. gravesiana* below and *G. irius* above, which he correlated with the *G. gravesiana* Zone and an overlying *G. gigas-G. irius* Zone in the Gigas Schichten in NW Germany (Salfeld, 1914), but did not define the limits of either zone in Dorset. Arkell (1933), notwithstanding Salfeld's (1913) statement that he had found "numerous examples", stated that *Gravesia* was rare over much of its stratigraphical range in Dorset and that *G. gravesiana* and *G. irius* were not represented in any British museum collection. Subsequently, Arkell (1947) combined Salfeld's (1913) zones into a single *Gravesia* Zone with a lower boundary which was stratigraphically significantly higher in the succession than Salfeld's original boundary. Cope (1967) described the genus as too rare in the Kimmeridge area sections for its stratigraphical range to be determined, and included Arkell's (1947) *Gravesia* Zone in a newly proposed *Pectinatites (Virgatosphinctoides) elegans*[1] Zone.

In a review of the published records of *Gravesia* in Britain Cox and Gallois (1981) concluded, on the basis of the limited evidence available, that the three species that had been recorded at that time, *G. gigas* (Zieten, 1830), *G. gravesiana* and *G. irius*, should be assumed to be contemporaneous. They confirmed Salfeld's (1913) observation that the genus ranged from the Maple Ledge Stone Band to the Yellow Ledge Stone Band, and noted that a few specimens had subsequently been recorded outside this range. This equates with a range from the middle part of the *Aulacostephanus (Aulacostephanoceras) autissiodorensis* Zone to a level high in the *Pectinatites (Virgatosphinctoides) scitulus* Zone. More recent collecting from the Kimmeridge Clay Formation at and adjacent to Kimmeridge Bay has shown *Gravesia* to be relatively common at some levels in the middle part of the formation. It is one of the few ammonite genera which has a widespread distribution in Europe over a relatively narrow stratigraphical range that crosses the Kimmeridgian-Tithonian and Kimmeridgian-Volgian boundaries. Its presence in England, northern France, Poland and the Urals in association with Subboreal species of

[1]Many of the ammonite-based zones in the Jurassic have been stated to be chronostratigraphical and referred to in publications by their species name alone (e.g. Planorbis Zone, Simms *et al.*, 2004). Those in the Kimmeridgian and Tithonian/Volgian in the UK are range biozones. The first reference here gives the full name (e.g. *Pectinatites (Virgatosphinctoides) elegans* Zone): for convenience, subsequent references are abbreviated (e.g. *elegans* Zone).

*Aulacostephanus* and *Pectinatites*, and its occurrence in central France and Germany in association with Submediterranean forms including *Aspidoceras, Glochiceras* and *Taramelliceras* make it especially useful for correlation between the local zonal schemes in the Tethyan and Boreal faunal realms. In this paper the known distribution of the genus in Britain is summarised, and the first detailed account of its occurrence in the Kimmeridge Clay Formation in the Dorset type section is provided.

## Distribution of *Gravesia* in the Kimmeridge Clay Formation

The Kimmeridge Clay Formation crops out almost continuously from the Dorset coast to the Yorkshire coast, and the formation has an extensive subcrop beneath younger rocks in eastern England and the southern North Sea (Figure 1). At outcrop, the mudstones weather rapidly to clay with the result that natural inland exposures are rare, and at any one time there are few man-made sections. The full thickness of the formation is exposed in the cliffs at and adjacent to Kimmeridge Bay and Ringstead Bay in Dorset (Figure 2), and these form the type sections for the Kimmeridge Clay Formation and the Kimmeridgian Stage (Arkell, 1947). The most extensive outcrops in the middle and upper parts of the formation are those in the actively eroding cliffs and intertidal areas between Brandy Bay [SY 889 795] and Chapman's Pool [SY 955 771] (Figure 2). These expose a total of *c.* 400 m of strata in the middle and upper parts of the formation out of a total of 550 m that has been proved in boreholes in that area (Gallois, 2000).

*Gravesia* is confined to a relatively narrow stratigraphical range in the middle part of the Kimmeridge Clay Formation (Figure 3), to beds between a little below the Maple Ledge Stone Band and the Cattle Ledge Stone Band that crop out in the cliffs and intertidal areas in Brandy Bay, Kimmeridge Bay

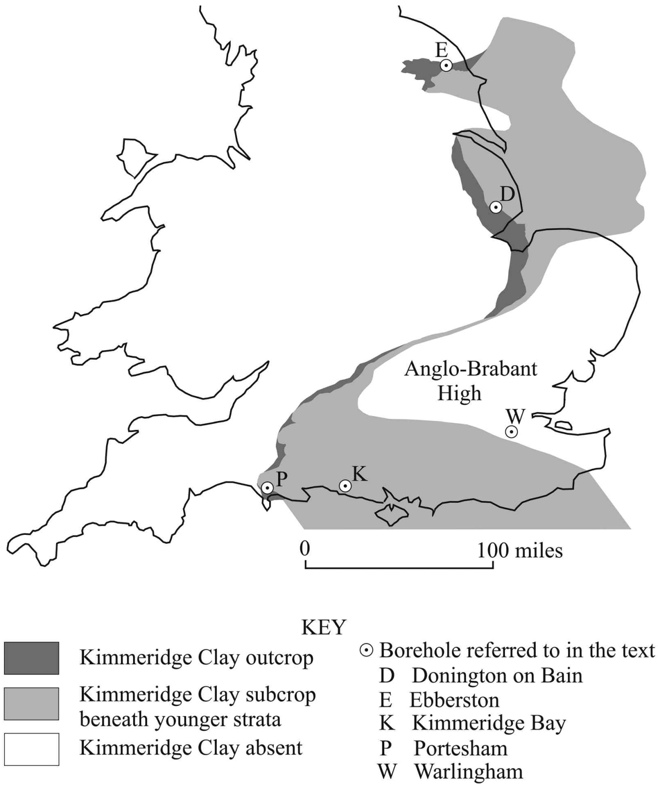


***Figure 1.*** *Geological sketch map of the English outcrop and subcrop of the Kimmeridge Clay Formation.*

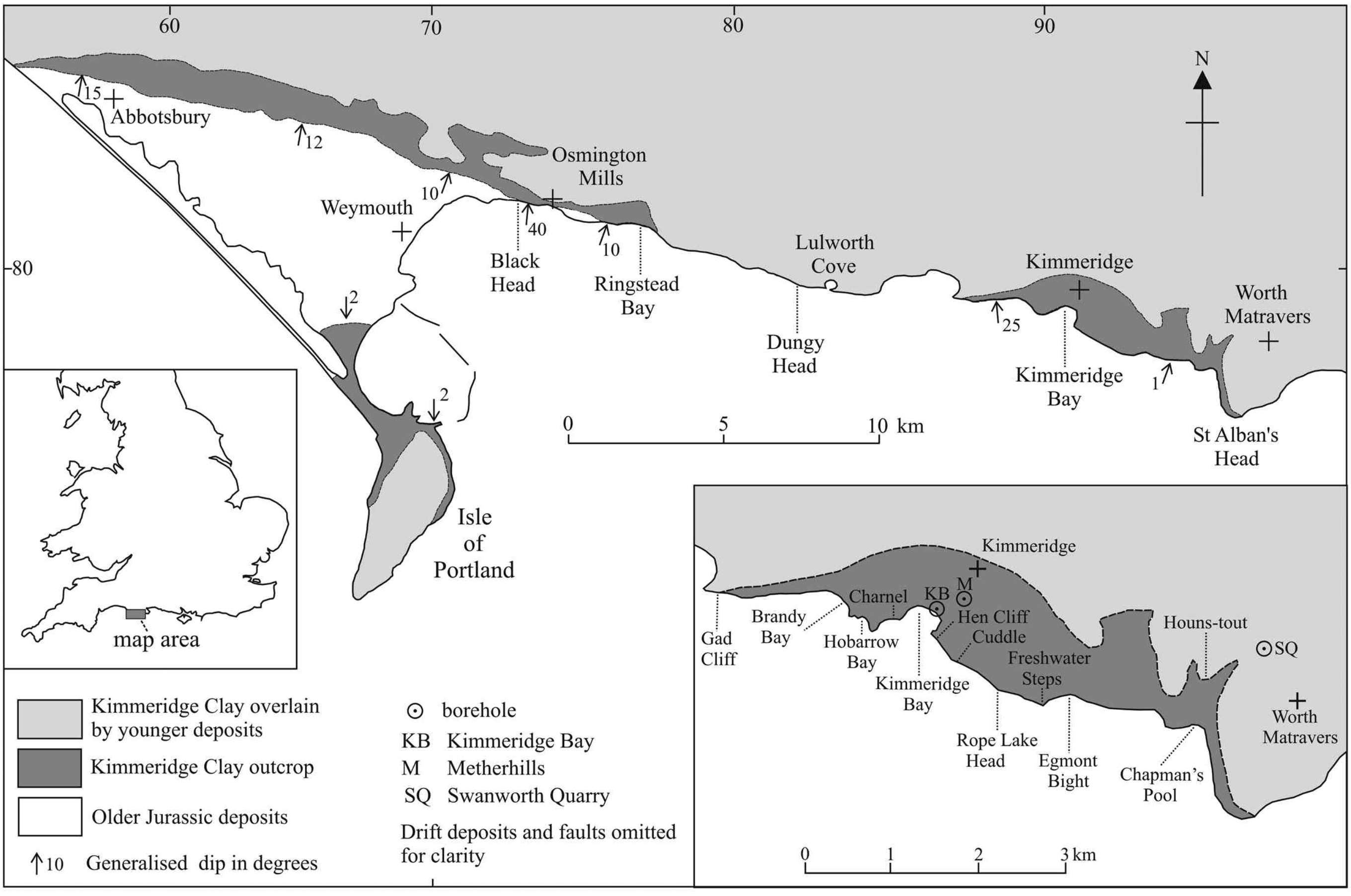


***Figure 2.*** *Geological sketch maps of the Kimmeridge Clay outcrop in the Dorset type area and the Kimmeridge Bay area showing localities referred to in the text.*

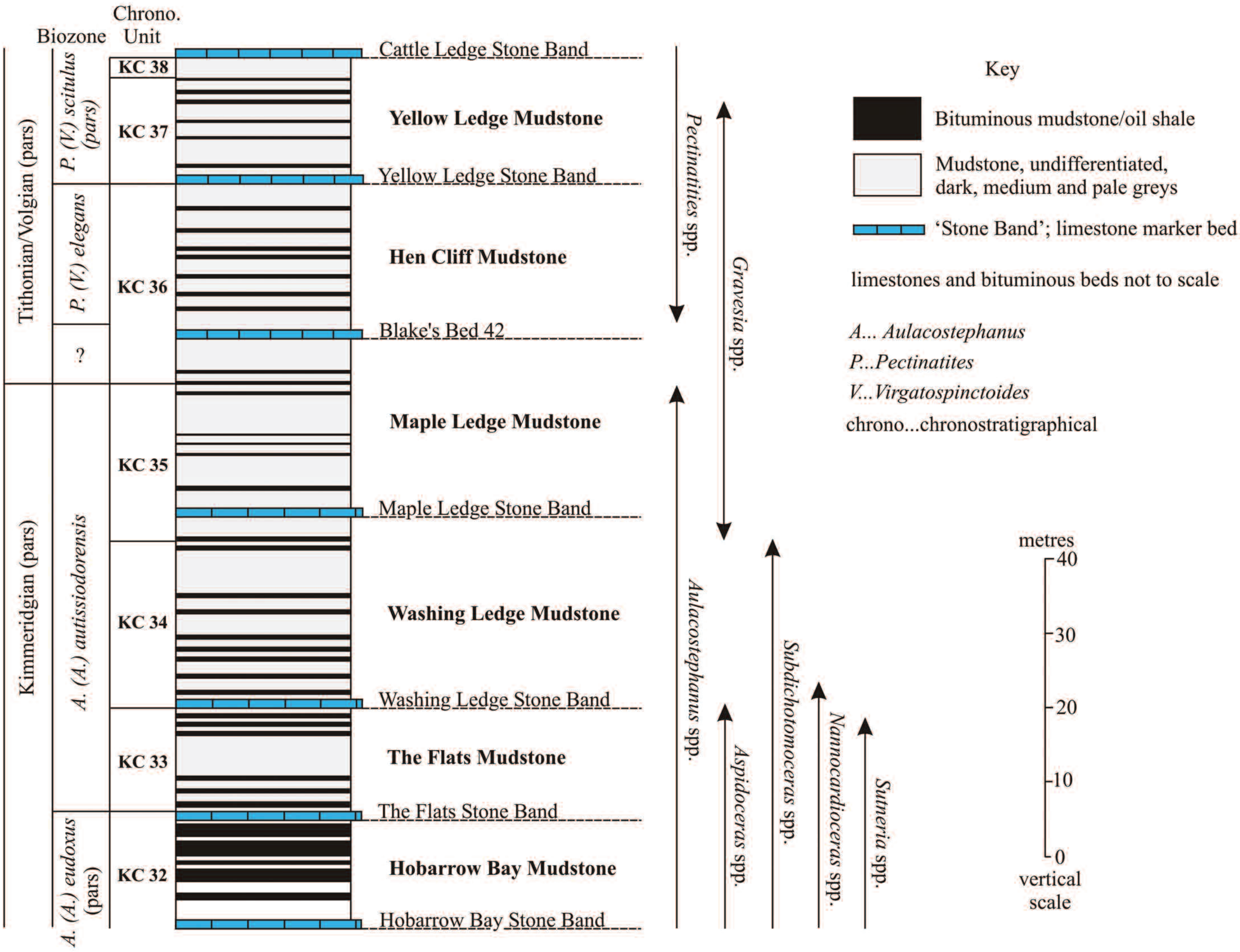


***Figure 3.*** *Simplified vertical section for the Kimmeridge Clay succession exposed in the cliff and foreshore sections between Hobarrow Bay and Cuddle showing the principal lithologies and ammonite ranges (after Cope, 1967, Cox and Gallois, 1981 and Van der Vyver MS, 1986), and the revised nomenclature (in bold) for the mudstones (Gallois, in press).*

and between Hen Cliff and Cuddle. The same succession is exposed in the Weymouth area at Black Head and Ringstead Bay, but the sections there are deeply weathered and tectonically disturbed. *Gravesia* has not been reported there.

The only permanent natural outcrops of the Kimmeridge Clay Formation outside Dorset are at Reighton [TA 126 779] on the Yorkshire coast, and on the Sutherland coast on extensive wave-cut platforms at and southwards from Helmsdale [ND 027 152]. At Reighton, the outcrops are disturbed by faulting and largely obscured by glacial deposits. Callomon and Cope (1971) recorded ammonites indicative of the *autissiodorensis* and *elegans* zones, and in Sutherland Kitchin (in Macgregor *et al.*, 1930) recorded "specimens of a *Perisphinctes*, comparable with forms characteristic of the *Gravesia* Zone". *Gravesia* has not been recorded at either locality. There are two published records of *Gravesia* collected from temporary inland exposures. Arkell (1933) referred to a specimen in the Hudleston Collection (BGS Y815) from the Upper Kimmeridge Clay at Swindon, Wiltshire, but this is a pectinatitid. Oates (1983) figured *G. gigas* from the *autissiodorensis* and *elegans* Zones, and *G. irius* from the elegans Zone in excavations at Aylesbury, Buckinghamshire. This last is the only published record of *G. irius* in the *elegans* zone in Britain. However, the succession at Aylesbury is highly condensed with major sedimentary breaks marked by erosion surfaces overlain by phosphatic pebble beds. For example, Oates (1983) recorded *Sutneria* 1 m below the *elegans* Zone at Aylesbury, but the same stratigraphical interval is represented by over 75 m of mudstones at Kimmeridge Bay. Furthermore, the precise positions from which the ammonites were obtained at Aylesbury is not well documented.

Elsewhere in England, *Gravesia* has been reported from a small number of cored research boreholes. Callomon and Cope (1971) recorded two specifically indeterminate juvenile *Gravesia* in the Upper Kimmeridge Clay (*elegans* Zone) in the Warlingham Borehole, Surrey [TQ 3476 5719], and single specimens were recorded in boreholes at Donington on Bain, Lincolnshire [TF 2399 8188], and at Portesham, Dorset [SY 6214 8554] and Kimmeridge Bay [SY 9097 7899] in Dorset (Gallois, 1979). These last three occurred at a similar stratigraphical level to one another in association with *Aulacostephanus* spp. indicative of the middle part of the *autissiodorensis* Zone. The full thickness of the middle part of the formation was continuously cored in research boreholes at Reighton and in the adjacent Vale of Pickering (Gallois, 1979; Herbin *et al.*, 1995). Geyssant (1990) recorded poorly preserved *Gravesia* sp. indet. in the *elegans* Zone in one of these boreholes at Ebberston [SE 893 816]. This is the most northerly recorded occurrence of the genus in Britain.

The Kimmeridge Clay Formation of most of the English onshore outcrop is made up of mudstone-dominated, small-scale (mostly 0.5 to 1.5 m thick) rhythms that fall into one of four types, many of which can be correlated over distances of tens of kilometres. Those in the middle part of the Kimmeridge

Clay comprise alternations of organic-rich and calcium-carbonate-rich mudstones (Figure 4) which have been interpreted as indicative of changes in water depth (Gallois, 2000) in response to global climate changes associated with orbital cycles (Weedon *et al.*, 2004). This type of rhythm is well displayed at and adjacent to Kimmeridge Bay where the organic-rich mudstones weather out as prominent ribs in the cliffs and form ledges in the intertidal area. The rhythms have been used to divide the succession into numbered beds that can be recognised in the cliff and foreshore exposures (Gallois, in press). The ammonites in the Kimmeridge Clay Formation are almost all fragile and crushed, and are difficult to study in the cliff sections where they are mostly damaged by weathering. Crushed, but otherwise relatively unweathered specimens are common at some stratigraphical levels on the wave-cut platforms with the result that most museum and figured specimens come from this source.

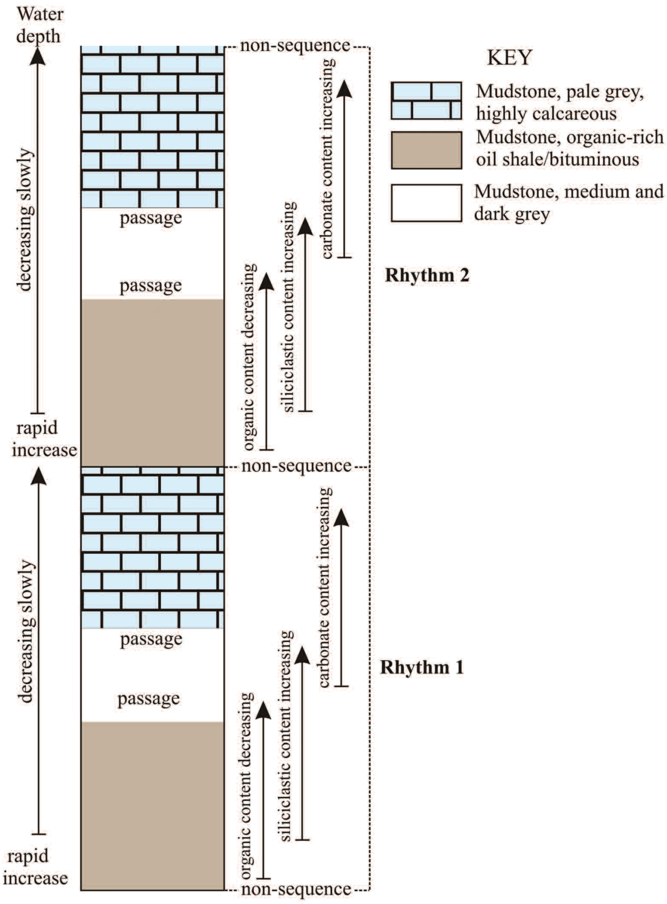


***Figure 4.*** *Generalised small-scale (fourth order) Kimmeridge Clay Type B (organic-rich) rhythm (after Cox and Gallois, 1981).*

## *Distribution of Gravesia in the Kimmeridge area*

The stratigraphical distribution of *Gravesia* in the exposures in Brandy Bay, Kimmeridge Bay and between there and Cuddle is summarised in Figures 3, 5 and 6. All of the published records refer to specimens which have come from strata that range in age from the middle part of the *autissiodorensis* Zone to low in the *scitulus* Zone (beds W20 to Y3 in Figures 5 and 6). Additional specimens were found at stratigraphically lower (W13) and higher (Y10) levels in the same zones in the present study. The genus is not as rare as that implied by some published accounts, but the inflated, weakly ribbed nature of the shell make it markedly more susceptible to damage and subsequent erosion when crushed than the shells of

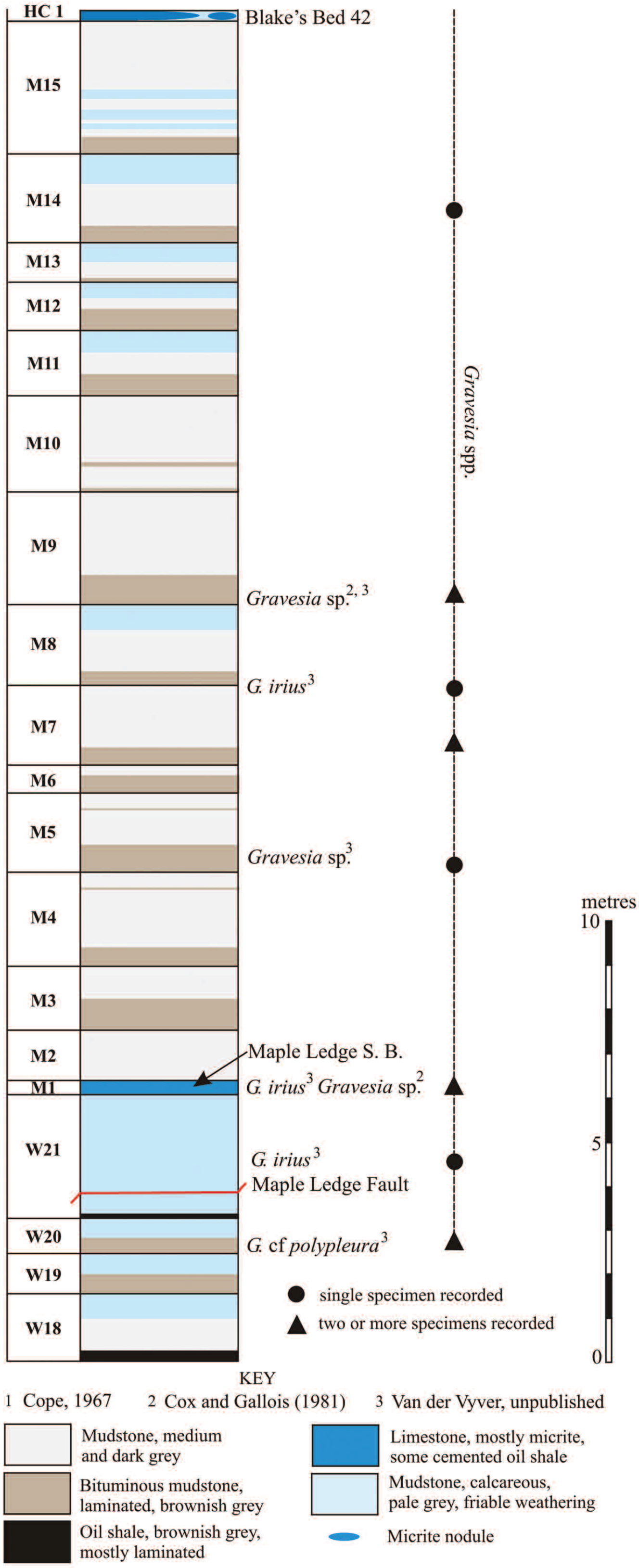


***Figure 5.*** *Distribution of* Gravesia *in the upper part of the Washing Ledge Mudstone (W18 to W21) and in the Maple Ledge Mudstone (M1 to M15). Kimmeridge Bay section showing the stratigraphical positions of specimens there and in the correlative beds in Brandy Bay.*

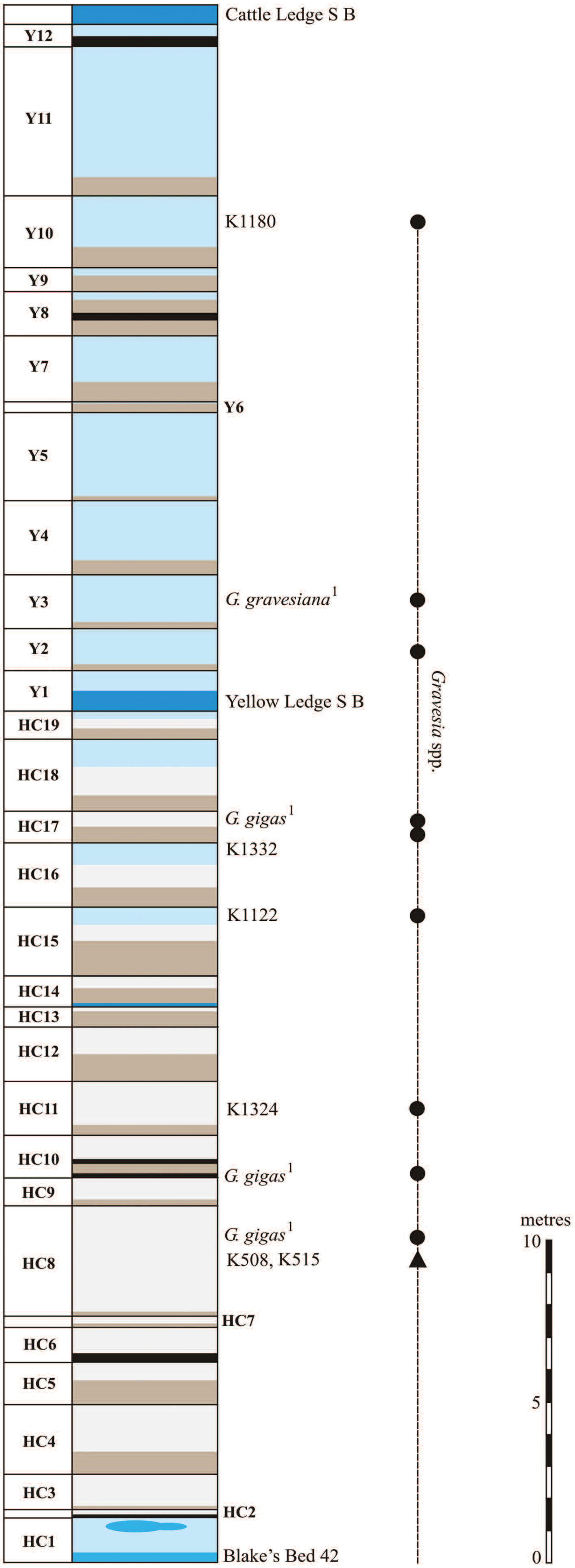


***Figure 6.*** *Distribution of* Gravesia *in the Hen Cliff Mudstone (HC1 to HC15) and the Yellow Ledge Mudstone (Y1 to Y12). Hen Cliff to Cuddle section showing the stratigraphical positions of specimens there and in the correlative beds in Brandy Bay.*

the contemporaneous aulacostephanids and pectinatitids. Specifically indeterminate specimens of *Gravesia* are relatively common at some levels in the wave-cut-platform outcrops of the middle part of the *autissiodorensis* Zone (beds W20 to basal M9) in Brandy Bay and Kimmeridge Bay, and in the *elegans* and *scitulus* zones between Hen Cliff and Cuddle (beds HC1 to Y8). Fewer specimens have been recorded in the highest part of the *autissiodorensis* Zone (the beds above Bed M9), but this partly reflects the relatively small extent of the foreshore exposures at this stratigraphical level (see Gallois, in press for details).

The preservation varies from water-worn impressions (Figure 7a) that have retained just enough of their ribbing to enable them to be distinguished from contemporaneous large *Aulacostephanus* and *Pectinatites*, to crushed shells in which the ornament, including in some cases colour, is preserved (Figure 7c). Most of the well-preserved specimens are coated with a thin (<1 mm thick) layer of secondary calcite that is difficult to remove without damaging the shell (Figures 7 d, e, f; Figure 8). Over 100 examples of *Gravesia* were noted in the present study. Most of these were too poorly preserved to collect or identify: only their stratigraphical positions were recorded. Almost all the better preserved specimens collected by one of the authors (SME) for the present study have a maximum diameter in the range 100 to 150 mm or 250 to 300 mm. Examples up to 400 mm diameter are present in the foreshore outcrops, but these commonly have a smooth body chamber, are more damaged when crushed, and are consequently more prone to erosion. Mature macroconchs described in the literature are mostly 150 to 400 mm in diameter with exceptional examples up to 500 mm.

A few specimens from the Dorset coast have been referred to as specifically determinable in published accounts, notably those by Arkell (1933, 1947), Cox and Gallois (1981), Cope (1967) and Salfeld (1913). Additional specimens were recorded by Van der Vyver (MS, 1986). The stratigraphical positions of these examples together with more recent records made by the present authors are included in Figures 5 and 6. The stratigraphical levels from which the specimens referred to by Arkell (1933) and Salfeld (1913) were obtained are insufficiently well known for them to be plotted. The positions of those recorded by Cope (1967), who described their stratigraphical levels as distances above or below the nearest stone band, are approximate. Van der Vyver's (MS, 1986) records are based on lithological logs that can be closely matched with those used in the present account.

The attribution of crushed specimens of *Gravesia* such as those in the Kimmeridge Clay Formation to species is difficult for a number of reasons. Hahn (1963) recognised five species based on a study of specimens housed in museums in France, Germany and Switzerland that had been collected over a period of more than 100 years. Almost all are in 3-D limestone preservation which enabled him to study their shapes, growth patterns, ornamentation and sutures. He used combinations of these characters to refine the descriptions of *G. gigas, G. gravesiana* and *G. irius*, and to define two new species, *G. hypselostoma* and *G. polypleura*. He identified two size ranges in *G. gravesiana* which he interpreted as normal mature and macrogerontic mature specimens, but did not describe any morphological difference between the two groups. Hantzpergue (1989) attributed similar size groupings in this and other species of *Gravesia* to sexual dimorphism.

Hantzpergue (1987, 1989) redescribed Hahn's (1963) species, and added a new species, *G. lafauriana* and several sub-species. He drew attention to the need to recognise the morphological differences between sexually dimorphic pairs and between immature and mature specimens within the same species or subspecies. He noted, for example, that microconchs of *G. gigas intermedia* Hantzpergue, 1989 and *G. gravesiana* were difficult to distinguish because the shape and ornamentation of the former was similar to that of the young stages of the latter. Scherzinger *et al.* (2006) agreed with this interpretation and concluded that specimens identified as *G. g. intermedia* by several authors (e.g. Zeiss *et al.*, 1996) fell

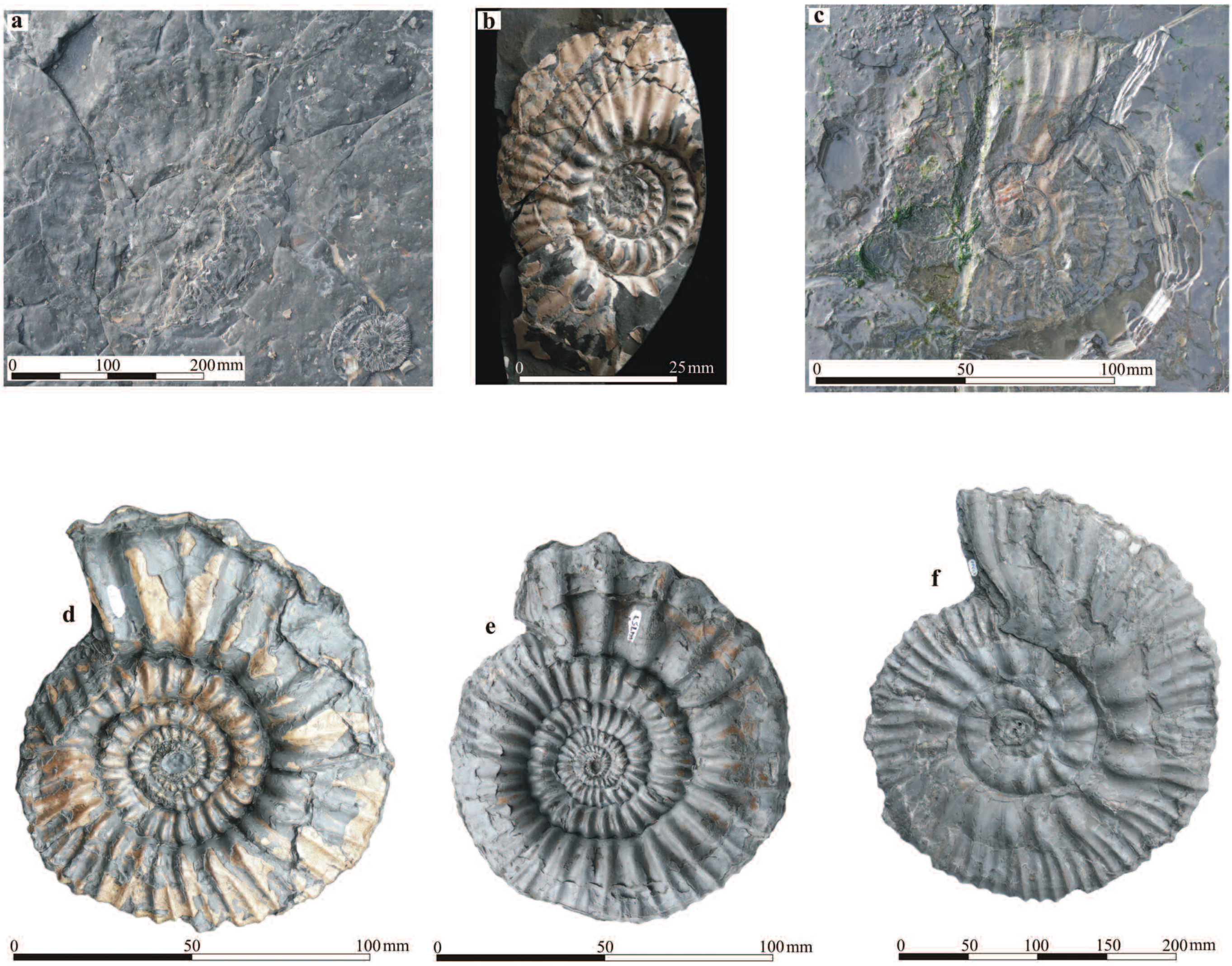


***Figure 7.*** *Examples of* Gravesia *preservation, and well-preserved examples from the autissiodorensis Zone in the Kimmeridge area. (**a**) Solution worn and eroded macroconch cf.* G. gigas *or* G. gravesiana*, Bed M 14, foreshore below Hen Cliff. (**b**) Inner whorls "close to* G. polypleura*" (Hantzpergue and Lafaurie, 1986), Kimmeridge Bay Borehole at 23.30 m depth; BGS- GSM 118161, Bed W 20, autissiodorensis Zone. (**c**) Crushed and fractured G. cf gravesiana, Bed Y2, scitulus Zone, foreshore below Cuddle. (**d**) Possible microconch of an early, undescribed form of* Gravesia*; K1581, Bed W13, autissiodorensis Zone, foreshore in Brandy Bay; more evolute than macrochonchiate forms of* Gravesia*. (**e**) Microconch of possible early form of* Gravesia *with well developed lappet, K1757, Bed W20, foreshore in Kimmeridge Bay, autissiodorensis Zone at a similar stratigraphical level to (**b**). (**f**)* G. *cf.* gravesiana *(M), K1078, Bed M10, autissiodorensis Zone, foreshore in Brandy Bay.*

within the variability of *G. gravesiana*. They also concluded from a study of the final diameters, ontogenetic stages, whorl heights and widths, and umbilical widths that macroconchs of *Gravesia* are highly variable. They suggested that all the specimens figured by Hantzpergue (1989) as microconchs are likely to represent small macroconchs. As an example of what they interpreted as the first unequivocal example of a *Gravesia* microconch, Scherzinger *et al*. (2006, figure 3) figured a specimen *G. gravesiana* in which the ventral part of the aperture has a lip-like extension. They interpreted this as the beginning of a ventral horn.

It follows from the above that even the best preserved of the crushed specimens collected from the Kimmeridge Clay Formation cannot be specifically identified with confidence using the criteria that were used to define the type material. None have retained their original shape, or anything even approximating to the whorl shapes described by Hantzpergue (1989) as characteristic of particular species (Figure 9). No suture has been recorded from any of the Kimmeridge Clay Formation material. However, many of the Kimmeridge Clay specimens comprise original shells that preserve details of the ornamentation that is absent from or poorly preserved in 3-D limestone casts. In addition, in contrast to many of the specimens housed in museum collections, the stratigraphical succession of the Kimmeridge Clay Formation specimens is known in detail.

One of the oldest recorded *Gravesia* in the Kimmeridge area is a specimen (BGS GSM 118161) from 2.97 m below the Maple Ledge Stone Band in the Kimmeridge Bay Borehole (Figure 7b). This was referred by Cox and Gallois (1981) to *G.* cf. *gigas* and subsequently described by Hantzpergue and Lafaurie (1983) as "close to *G.* cf. *polypleura*" (Hahn, 1963 amended to *G. lafauriana*, Hantzpergue, 1987). A similar specimen, from 3 m below the same stone band in Kimmeridge Bay, was found by Van der Vyver (MS, 1986) and identified by him as *G.* cf. *polypleura*. Cox and Gallois (1981) suggested that the borehole specimen and those from the Donington on Bain and Portesham boreholes referred to above came from stratigraphically similar levels. It is tempting to think that they might form a widespread faunal marker bed that is the correlative of the [*Gravesia*] Lafauriana Horizon of Acquitaine (Hantzpergue, 1989). However, more detailed measurements at Kimmeridge Bay confirm that although all three specimens and the Van der Vyver specimen are from Chronostratigraphical Bed

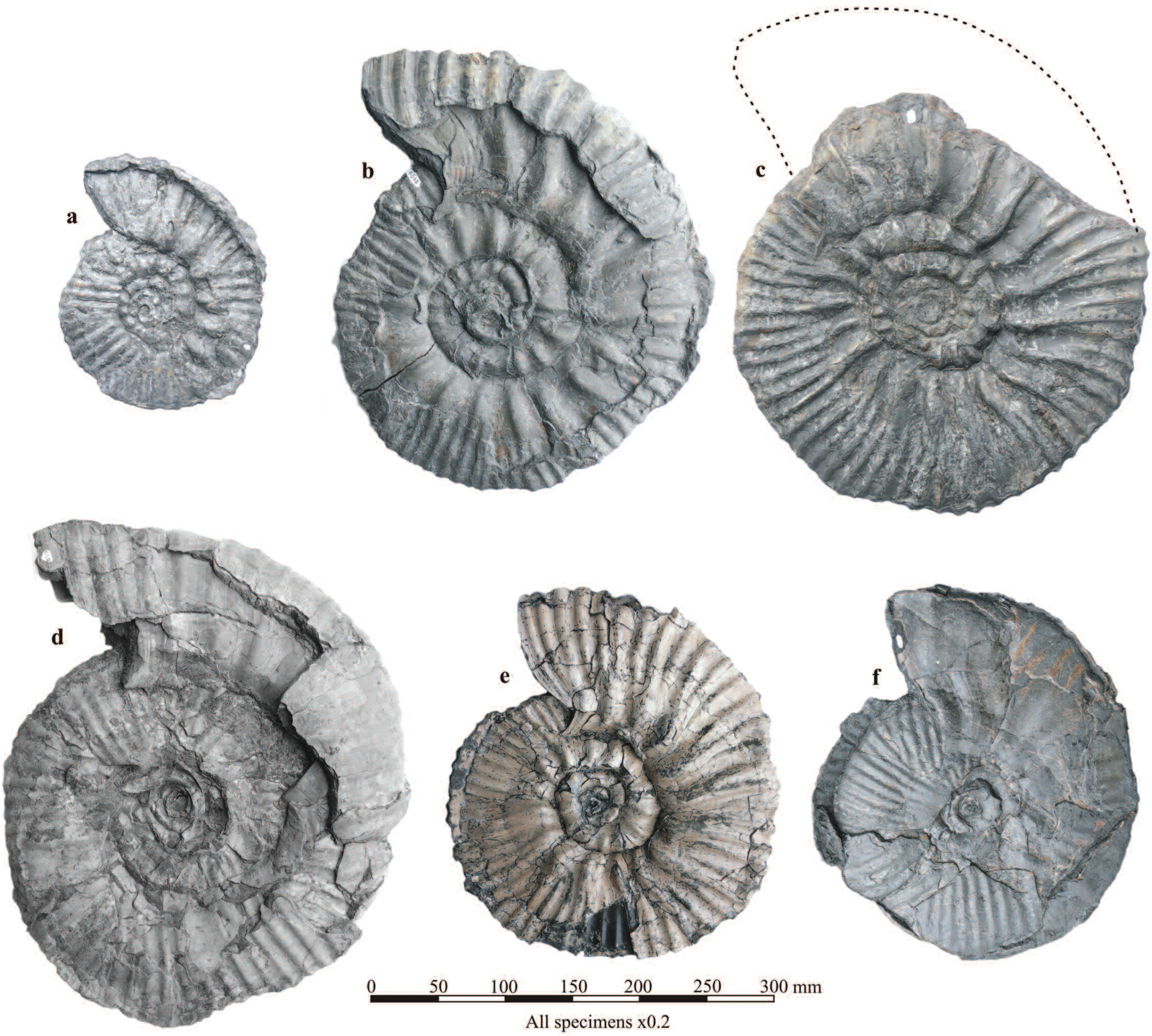


***Figure 8.*** *Examples of* Gravesia *from the elegans and scitulus zones in the Kimmeridge area.* ***(a)*** *Microconch or juvenile of* Gravesia *cf.* gigas, *K1324, Bed HC11, elegans Zone, foreshore below Hen Cliff.* ***(b)*** G. *cf.* gigas *(M), K508, Bed HC8, elegans Zone, foreshore below Hen Cliff; nodes weaker than those of* G. gigas *and more pronounced than the* bullae *of* G. gravesiana. ***(c)*** G. *cf.* gravesiana *(M), K1122, Bed HC15, elegans Zone, foreshore below Hen Cliff. (d)* Gravesia *sp.(M), K1332, Bed HC17, foreshore below Hen Cliff; fine ribbing and absence of bullae or nodes on the phragmocone distinguishes this example from the type specimens of* G. gigas *and* G. gravesiana. ***(e)*** G. *cf.* gravesiana *(M), K1647 Bed HC17, foreshore in Brandy Bay, bullae and ribbing similar to* G. gravesiana, *but shell details better preserved than in the type material.* ***(f)*** Gravesia *sp. (M) K1180, Bed Y10, scitulus Zone, foreshore below Cuddle, possible new species or subspecies as* ***(d)****; youngest* Gravesia *recorded to date in Britain.*

KC 35, the Kimmeridge Bay specimens are probably older than the other two (Figure 10).

Cox and Gallois (1981) and Van der Vyver (MS, 1986) recorded several specimens that they attributed to *G. irius* in the upper part of the *autissiodorensis* Zone in the beds between the Maple Ledge Stone Band and the top of Stink Corner Rib (beds W21 to basal M9) in Brandy Bay and Kimmeridge Bay. Salfeld's (1913) specimens from the *autissiodorensis* Zone presumably came from the same beds. There is no published record of *Gravesia* higher in the *autissiodorensis* Zone, almost certainly due to collection failure. Bed M9 above Stink Corner Rib to Bed M15 crop out in a poorly exposed weathered cliff in Kimmeridge Bay. The same beds are poorly exposed in Brandy Bay where they are disturbed by faulting, and the foreshore outcrops are largely sand covered (Gallois, in press). The upper part of Bed M9 and beds M10 to M15 are partially exposed in the wave-cut platform below Hen Cliff. Poorly preserved impressions of indeterminate *Gravesia* were recorded there in the present study (e.g. Figure 7a). Specimens of *Gravesia* that range from water-worn impressions to crushed shells are relatively common at several levels in the *elegans* and *scitulus* zones on the wave-cut platform between Hen Cliff and Cuddle. The correlative beds are poorly exposed in Brandy Bay where, to date, few *Gravesia* have been recorded at this stratigraphical level.

A selection of specimens that cover the full stratigraphical range of *Gravesia* recorded in the Kimmeridge area sections is shown in Figures 7 and 8. With the exception of one example from the British Geological Survey (BGS) collection, all the specimens are temporarily housed in the Etches Collection at Kimmeridge prior to their transfer to the new Museum of Jurassic Marine Life at Kimmeridge. The two oldest examples

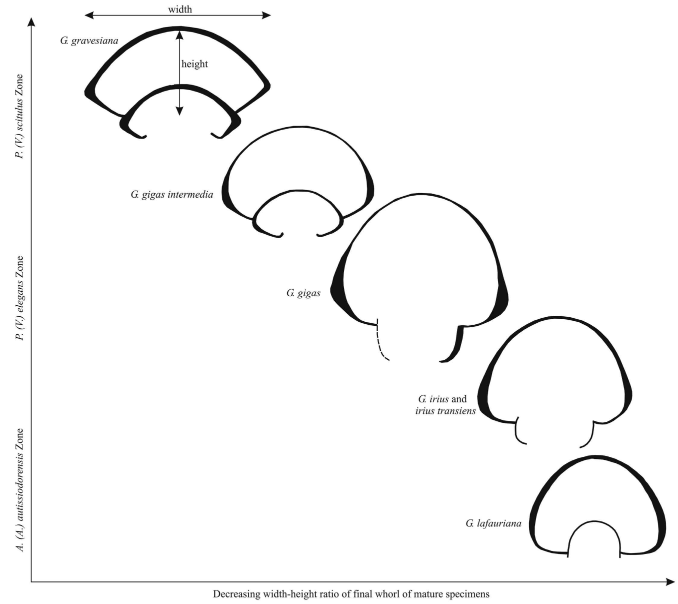


***Figure 9.*** *Changes in the cross section shape of the final whorl of species of mature* Gravesia *showing an increase in the width-height ratio with time (after Hantzpergue, 1989, figure 57).*

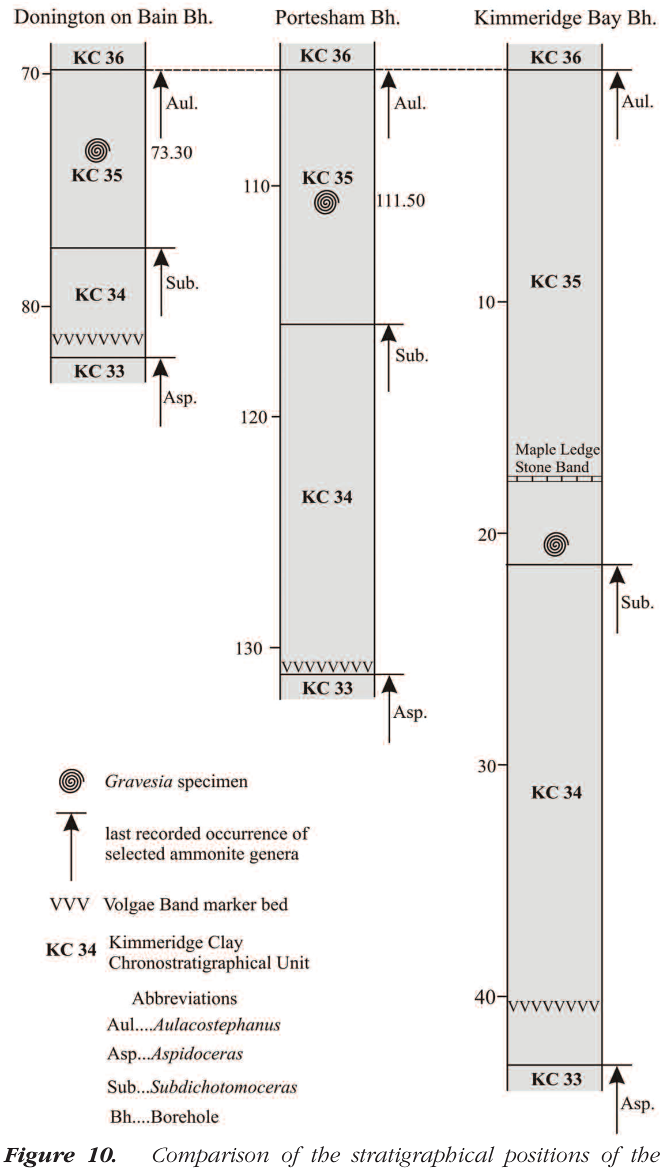


***Figure 10.*** *Comparison of the stratigraphical positions of the* Gravesia *recorded in the Donington on Bain (Lincolnshire), Portesham (Dorset) and Kimmeridge Bay (Dorset) boreholes.*

(K1581 and K1757), from 10 m and 3 m below the Maple Ledge Stone Band respectively, are interpreted here as early forms of *Gravesia*. Both are readily distinguishable from the *Aulacostephanus* with which they occur and from *Subdichotomoceras* in the lower part of the *autissiodorensis* Zone. They differ in whorl shape and ribbing style from figured examples of contemporaneous and near-contemporaneous *Tolvericeras (T.) murogense* (Hantzpergue), the suggested precursor of the gravesiids (Hantzpergue, 1989). They are morphologically similar to some examples of *Crussoliceras* from the early *Aulacostephanus (Aulacostephanoceras) eudoxus* Zone, and they have a similar whorl shape but a different ribbing style from *Tolvericeras (Pseudogravesia)* from the early Tithonian. If they are gravesiids, K1757 is the first published example of a microconch with a fully formed lappet, and K1581 is the first record of a *Gravesia* from the *autissiodorensis* Subzone in Britain.

Most of the specimens figured from the *elegans* and *scitulus* Zones fall within the ribbing styles of macroconchs of species and subspecies in the *G. gigas-G. gravesiana* group. In several examples (K508, K1078, K1180, K1647) the ribs adjacent to the peristome bend forward to form a lip at the aperture, a feature indicative of maturity in some macroconchs. Two specimens, K1332 and K1180, have a distinctly different ribbing style from *G. gigas* and *G. gravesiana* and may be examples of a new species or subspecies.

## Comparison with other European successions based on *Gravesia*

*Gravesia* has a widespread distribution in western Europe and eastwards as far as the Subarctic Urals, a region in which the interdigitation of the Subboreal and Submediterranean faunal provinces varied with time (Enay, 1972). The genus reached its acme, in terms of variety of species, in the Franco-German Biome, an area that stretched from the Atlantic coast of France eastwards via the Jura Mountains to south central Germany and Switzerland (Hantzpergue, 1989). The detailed stratigraphy of the *Gravesia*-bearing beds is of particular interest with respect to correlation of the beds adjacent to the Kimmeridgian-Tethyan and Kimmeridgian-Volgian stage boundaries. The Kimmeridge Clay succession exposed on the Dorset coast is the only one recorded to date in Europe that comprises an unbroken marine succession across these stage boundaries. In Britain, the Last Appearance Datum (LAD) of *Aulacostephanus* spp. is one of the most sudden and widespread biological events in the Mesozoic, and has been used as a chronostratigraphical marker to define the top of the Kimmeridgian Stage (Cox and Gallois, 1981). Prior to this, the same event had been used by Arkell (1933) to divide the Kimmeridgian Stage (*sensu anglico*) into a lower and upper substage, and the Kimmeridge Clay Formation into lower and upper parts. At present, the base of the Tithonian Stage is taken at the First Apperance Datum (FAD) of the ammonite *Hybonoticeras hybonotum* (Neumayr). However, in the absence of an agreed Global Boundary Stratotype Section and Point (GSSP), correlations within the Tethyan province and with sections in the Boreal Province remain uncertain. In the meantime, the LAD of *Aulacostephanus* spp. is the most useful marker at or close to the Kimmeridgian-Tithonian and Kimmeridgian-Volgian boundaries in central and northern Europe.

### France

In northern France, the sections geographically closest to the Dorset exposures, marine Kimmeridgian and Tithonian sediments are well exposed in cliffs and foreshores over a distance of 20 km on the Boulonnais coast between Cap Gris Nez and Equihen (Pruvost and Pringle, 1924). The succession comprises alternations of open-marine mudstones that are lithologically similar to parts of the early Kimmeridge Clay in Dorset, and shallow-water sandstones that are absent from the Dorset succession (Ager and Wallace, 1966). Salfeld (1914) recorded *Gravesia portlandica* (Loriol), which Hahn (1963) identified as a junior synonym of *G. gigas* (Zieten), in the Argiles de Châtillon Supérieures and the overlying Grès de la Crèche, and Geyssant (in Herbin *et al.*, 1995) recorded the same species in the same beds together with pectinatitid ammonites indicative of the *elegans* Zone. She also recorded *G. lafauriana* in the Argiles de Châtillon Inférieures with *Aulacostephanus* indicative of the *autissiodorensis* Zone. These assemblages are separated by an unconformity in the middle part of the formation that probably includes all or most of the Maple Ledge Mudstone of the present account. In SW France (Aquitaine) Hantzpergue (1983) also recorded a hiatus between beds with *Aulacostephanus* gr. *autissiodorensis, G. irius* and *G. polypleura* (syn. *G. lafauriana*) and beds with *G. gigas* and *G. gravesiana*. One of the suggested candidates for the Global Boundary Stratotype Section and Point (GSSP) for the base of the Tithonian Stage is a section at Mount Crussol in the Ardèche Department based on the FAD of *Gravesia* spp. (Gradstein *et al.*, 2004).

## Germany

In a systematic study of *Gravesia* based on museum specimens from southern Germany, eastern France and Switzerland, Hahn (1963) recorded the genus in the upper part of Weissjura $\zeta$1 to the middle part of Weissjura $\zeta$1 in association with Submediterranean ammonite assemblages. In a study of a wide range of fossil groups in the Jurassic in the Lower Saxony Basin in north Germany, Gramann *et al.* (1997) noted that few ammonites had been recorded from the latest Kimmeridgian. They described *G. gigas* in the 'Gigas Schichten' as "highly variable", and stated that the deposit was Tithonian in age. However, Schweigert (1999) noted that elsewhere in the same region beds described as 'Gigas Schichten' contain *G. irius* and are late Kimmeridgian (*autissiodorensis* Zone) in age.

## Russia

In the type area of the Volgian Substage, sections along the River Volga near the villages of Gorodishche and Dubky (central Russia), Hantzpergue *et al.* (1998) used the LAD of *Aulacostephanus* spp. to define the base of the Volgian. Above this, they recorded *G.* cf. *gigas* together with species of *Glochiceras, Illowaiskya* and *Neochetoceras*, genera that have not been recorded in the Kimmeridge Clay Formation. However, Scherzinger and Mitta (2006) thought that the *Gravesia* had been misidentified and was possibly an *Eosphinctoceras*. They too concluded that the only practical way to define the base of the Volgian Secondary Stage on the Russian Platform was the LAD of *Aulacostephanus*, but noted that it was not yet clear whether or not the assumption that this boundary was synchronous in Northwest Europe, Poland and Russia was correct. The succession exposed in the Kimmeridgian-Volgian boundary beds exposed on the east slope of the Subpolar Urals has recently been reviewed by Rogov and Price (2010) who noted the presence of *G. gravesiana* in the earliest Volgian together with *Pectinatites* indicative of the *elegans* Zone.

## Poland

Kutek (1986) described the occurrence of *Gravesia* in the Tithonian in the Polish Carpathians in association with Submediterranean genera: a similar association of *Gravesia* with Tethyan genera has been reported (Grigore and Marcu, 2009) from the western Carpathians in Romania. Malinowska (1989) noted that *Gravesia* had not been recorded from the late Jurassic of lowland (extra-Carpathian) Poland where the earliest Tithonian deposits are also characterised by Submediterranean ammonite forms. In central Poland, where they defined the base of the Volgian as the FAD of *Ilowaiskya klimovi* (Ilovaisky) a little above the LAD of *Aulacostephanus*, Kutek and Zeiss (1997) recorded mixtures of Subboreal and Submediterranean forms which did not include *Gravesia*.

## Summary and conclusions

Species of the ammonite *Gravesia* have a widespread distribution over a relatively narrow stratigraphical range in the latest Kimmeridgian and earliest Tithonian and Volgian in north-west, central and eastern Europe. The sections in the marine Kimmeridge Clay mudstones exposed on the Dorset coast at and adjacent to Kimmeridge Bay are stratigraphically more complete than any described in Europe. The use of *Gravesia* for correlation in Britain has been limited in the past by the scarcity of published records and an incomplete knowledge of the ranges of the individual species. Detailed collecting at Kimmeridge has shown that *Gravesia* is relatively common at some levels in the late Kimmeridgian *autissiodorensis* Zone and in the Tithonian/Volgian *elegans* and *scitulus* zones. Over 100 specimens were observed during the present survey, although most of them were badly crushed, poorly preserved shells. The better preserved examples show details of the shell structure and ornament that are either not present or are poorly preserved in the type and figured specimens of *Gravesia*, all of which are as 3-D limestone casts. However, it is difficult to assign many of the Kimmeridge Clay specimens to species because many of the morphological differences used to define the type specimens are not preserved in crushed examples. The relatively small number of museum specimens of *Gravesia* available for study has also created a problem. The ranges of sizes and ornamentation in what are presumed to be mature, immature and sexually-dimorphic populations is poorly known. Although several authors (Hantzpergue, 1989; Scherzinger *et al.*, 2006) have figured what they described as macroconchiate and microconchiate forms, none of these has a ventral lappet or horn that would unequivocally indicate it to be a microconch. One of the specimens figured in the present account (Figure 7e) has a well-developed lappet and is interpreted here as the microconch of a possible early form of *Gravesia*.

In Dorset, *G.* cf. *polypleura* and *G.* cf. *irius* have been recorded by earlier authors (Cox and Gallois, 1981; Hantzpergue and Lafaurie, 1983; Van der Vyver MS, 1986) from the *autissiodorensis* Zone, and *G. gigas* and *G. gravesiana* from the *elegans* and *scitulus* zones (Arkell, 1933; Cope, 1967). This distribution is similar to that of the *Gravesia* successions recorded in the latest Kimmeridgian and early Tithonian elsewhere in Europe.

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