NEW CLADID AND FLEXIBLE CRINOIDS FROM THE MISSISSIPPIAN (TOURNAISIAN, IVORIAN) OF ENGLAND AND WALES

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Abstract: The modern study of fossil crinoids began with J. S. Miller who, in 1821, described specimens from southern England, nearby Wales and other regions, and named several common Early Carboniferous genera. Later, in 1950–60, James Wright monographed all known Early Carboniferous crinoids from the British Isles. In spite of such previous scrutiny, we recognize here two new genera among species already described: *Glamorganocrinus* gen. nov. (type species: *Ophiurocrinus gowerensis* Wright, 1960) from South Wales and *Mendipocrinus* gen. nov. (type species: *Poteriocrinus latifrons* Austin and Austin, 1847) from southern England. These new genera increase the number of advanced cladid genera in the Ivorian Substage of the Tournaisian in western Europe to 18, and the total number of crinoid genera to 36. A review of species assigned to *Mespilocrinus* has led to the recognition of *M. granulifer* De Koninck and LeHon, 1854 as a *nomen dubium*. A new species of *Mespilocrinus*, *M. wrighti*

sp. nov., is described from the Ivorian of South Wales; this is the most highly derived species of the genus, as based on a phylogenetic analysis including ten species and 13 characters, with *Pycnosaccus* as the outgroup. A single, well-ordered tree resulted from this analysis. Interpretation of this tree suggests that the centre of evolution for *Mespilocrinus* was North America, where three species appeared during the Kinderhookian (early Tournaisian), rapidly achieving morphological disparity within the genus. This radiation event was part of the overall explosive radiation of crinoids following the Late Devonian mass extinction event when crinoid diversity was at a global minimum during the Frasnian. Recovery began during the Famennian, followed by an explosive radiation in the Tournaisian.

Key words: Crinoids, new taxa, Mississippian, Tournaisian, England, Wales.

THE first modern work on crinoids was ‘A natural history of the Crinoidea or lily shaped animals’ by J. S. Miller (1821). In this work, the author defined the Crinoidea as they are presently understood, i.e. a group of echinoderms separate from starfish and including both stalked and unstalked forms. The primary focus of Miller’s treatise was on Early Carboniferous and Jurassic crinoids from England, particularly from the Somerset/Avon region, but it also included material from Lancashire/Yorkshire, South Wales (Caldy Island) and southern Ireland. Miller (1821) defined Early Carboniferous crinoid genera that are among the most characteristic and cosmopolitan crinoids worldwide in that time interval: *Actinocrinites*, *Cyathocrinites*, *Poteriocrinites*, *Platycrinites* and *Rhodocrinites*.

More recently, James Wright published numerous contributions between 1911 and 1960, with his comprehensive monograph on Carboniferous crinoids (Wright 1950–60) being the most significant. Wright redescribed

and summarized all Carboniferous crinoids known from England, Scotland, Wales and Ireland. This monograph showcased Wright’s keen skill as a collector, and it reflected the understanding of crinoids and the application of specific and generic concepts during the middle part of the twentieth century. Since Wright completed his work, relatively few studies have dealt directly with Early Carboniferous crinoids from England and Wales. Among those that have are Westhead (1979), Donovan and Sevastopulo (1985, 1988), Donovan (1986, 1992), Donovan and Westhead (1987), Donovan and Veltkamp (1990), Donovan *et al.* (2005) and Ausich and Sevastopulo (2001), who revised the crinoid fauna at Hook Head, County Wexford, Ireland, including equivalent faunas in South Wales and the Avon/Somerset region.

The present contribution is part of a larger study on the global evolutionary palaeoecology of Early Carboniferous, or Mississippian (Heckel and Clayton 2005), crinoids. Prerequisite to this macroevolutionary analysis is

establishment of accurate generic concepts, facies distributions and temporal ranges of genera. These data will be used to test the relationships between generic longevity, eurytopy (environmental breadth) and geographical range within and between the various crinoid clades in order to assess the patterns of evolutionary success and failure among Late Palaeozoic crinoids. As part of this study, all known species and genera of Mississippian crinoids from western Europe have been reviewed, and type specimens have been observed directly in museum collections where possible, in order to assess correct generic assignment.

Herein, we report on two new genera recognized from among previously described species: *Glamorganocrinus* gen. nov. and *Mendipocrinus* gen. nov., and describe a new species, *Mespilocrinus wrighti* sp. nov. All three new taxa are from the Ivorian Substage of the Tournaisian Stage, being close in age to the Hook Head crinoid fauna (Ausich and Sevestopulo 2001), but possibly slightly younger (Mitchell *et al.* 1986). These new genera bring the total crinoid generic richness of the Ivorian of Western Europe to 36, 18 of which are advanced cladids (Ausich and Kammer 2006).

SYSTEMATIC PALAEOLOGY

Terminology follows Ubaghs (1978), and higher-order taxonomy follows Moore and Teichert (1978), with modifications by Simms and Sevestopulo (1993) and Ausich (1998). Specimen numbers bear the following institutional prefixes: GSM, the Geological Survey Museum, British Geological Survey, Keyworth; NMW, the National Museum of Wales, Cardiff; BMNH, the Natural History Museum, London; NMS, National Museums of Scotland, Edinburgh.

Class CRINOIDEA Miller, 1821

Subclass CLADIDA Moore and Laudon, 1943

Order DENDROCRINIDA Bather, 1899

Remarks. We follow McIntosh (2001) in placing pinnulate cladid crinoids in the order Dendrocrinida, which contains both pinnulate and non-pinnulate taxa. The Poteriocrinida as defined by Moore *et al.* (1978) is probably a polyphyletic grouping composed of several pinnulate taxa derived from the Dendrocrinida *sensu* Moore *et al.* (1978).

Family SCYTALOCRINIDAE Moore and Laudon, 1943

Genus GLAMORGANOCRINUS gen. nov.

Derivation of name. After the Vale of Glamorgan, Wales.

Type species. *Ophiurocrinus gowerensis* Wright (1960).

Diagnosis. Crown slender, five arms total; cup low-bowl shape with medium-thick plates, wider than high; infrabasals very small, nearly covered by column; basals slightly wider than high; radials wider than high with plenary facets; anal sac long and slender, composed of smooth, hexagonal plates; arms composed of short, wide brachials that resemble columnals in aboral view.

Glamorganocrinus gowerensis (Wright, 1960)

Text-figure 1F–G; Table 1

1960 *Ophiurocrinus gowerensis* Wright, p. 329, appendix, pl. A, figs 7–8.

Types. Holotype, GSM 85252, a complete crown preserving the anal sac. Paratype, GSM 85251A, a partial crown.

Description. Crown slender. Aboral cup low bowl-shaped with a convex base, height to width ratio approximately 0.4; plates smooth, lacking ornamentation, slightly tumid with distinct sutures; infrabasals very small, slightly visible in side view; basals hexagonal, slightly wider than high, height to width ratio approximately 0.8; radials pentagonal, wider than high, height to width ratio approximately 0.6, with plenary facets. Three anal plates in cup; radianal largest; anals arranged in typical advanced cladid arrangement with anal X to the left of and above the radianal, and a space for the right tube plate, which is missing but the outline is clear, above the radianal. Anal sac elongate, originally about twice as long because the distal portion is folded behind the proximal portion; composed of smooth, hexagonal plates, no evidence of pores along sutures. Arms five, atomous in all rays; brachials wider than long, rectangular, resemble columnals in aboral view; pinnules present, one per brachial, robust. Column circular, heteromorphic with distinct nodals and internodals.

Remarks. Wright's (1960, appendix pl. A, fig. 7) illustration of the holotype has inked-in plate boundaries for both the aboral cup and the anal sac. The plate boundaries on the lower half of the anal sac and the anal plates above the anal X must have been inferred by Wright as these plates are not preserved (Text-fig. 1F). The radianal, anal X and right tube plates are the primanal, secundanal and tertanal, respectively, of Webster and Maples (2006).

Comparisons. *Glamorganocrinus* gen. nov. has five atomous arms with rectangular brachials similar to those of *Ophiurocrinus* Jaekel, 1918. Although the arms are similar to those of *Ophiurocrinus*, the aboral cup is distinctly bowl-shaped rather than conical. The cone-shaped cup of *Ophiurocrinus* has high infrabasals clearly visible in side

TEXT-FIG. 1. A–D, *Mespilocrinus wrighti* sp. nov., NMW 81.8G.6825, holotype, Blucks Pool Limestone, Bosherton area, near Linney Head, Pembrokeshire. A, B ray view. B, C ray view. C, C–D interray view. D, aboral view with C–D interray at top. E, *Mendipocrinus* (gen. nov.) *latifrons* (Austin and Austin, 1847), GSM 7603, holotype, Black Rock Limestone, Mendip Hills, Somerset, B ray view. F–G, *Glamorganocrinus* (gen. nov.) *gowerensis* (Wright, 1960), Penmaen Burrows Limestone Group, Three Cliffs Bay, Gower, West Glamorgan. F, GSM 85252, holotype, posterior view; the two long arms are the B and E rays. G, GSM 85251A, paratype, anterior view. All $\times 3$.

TABLE 1. Measurements (in mm) of *Glamorganocrinus* (gen. nov.) *gowerensis* (Wright, 1960).

Ray	Crown H	Cup H, W	Infrabasal H, W C	Basal H, W BC	Radial H, W C	Arms L
GSM 85252, holotype	19.3	2.4, 5.5	0.5, 1.2	1.7, 2.1	1.3, 2.0	15.6
GSM 85251 A, paratype	21.7	2.7, 6.4	–, –	1.7, 2.0	1.6, 2.5	21

view (Moore *et al.* 1978), unlike the almost hidden infrabasals of *Glamorganocrinus*.

Glamorganocrinus is placed in the Scytalocrinidae because this family includes other five-armed genera with plenary radial facets such as *Ophiurocrinus*, *Gilmocrinus* Laudon, 1933 and *Anemetocrinus* Wright, 1938, all of which have a cone-shaped cup. Most genera in the Scytalocrinidae have cone-shaped cups, although the type genus, *Scytalocrinus* Wachsmuth and Springer, 1880, has a bowl-shaped cup like *Glamorganocrinus* (Moore *et al.*

1978). *Gilmocrinus* not only has a bowl-shaped cup, but also elongate, subcuneate brachials (Kammer *et al.* 2007). *Anemetocrinus* has biserial arms (Moore *et al.* 1978).

Occurrence. Penmaen Burrows Limestone Group, Three Cliffs Bay, Gower, West Glamorgan (British Grid ref. SS 535 881). Wright (1960, p. 329) recorded the horizon as Z zone of Vaughan's (1905) coral zonation, which is of Ivorian or late Courceyan age (Leeder 1992). Upper Courceyan rocks of the Penmaen Burrows Limestone Group include the Shipway Limestone and Tears Point Limestone, both of which were deposited in a middle to outer ramp succession (Adams *et al.* 2004). Presumably, *Glamorganocrinus gowerensis* was collected from one of these two limestones. Burchette *et al.* (1990) reported crinoid-rich packstones from the Shipway Limestone. V. P. Wright (pers. comm. 2003) confirmed that the best crinoid material at Three Cliffs Bay is Ivorian in age.

Family PACHYLOCRINIDAE Kirk, 1942

Genus MENDIPOCRINUS gen. nov.

Derivation of name. After the Mendip Hills, Somerset, England.

Type species. *Poteriocrinus latifrons* Austin and Austin, 1847.

Diagnosis. Crown cylindrical, slender; cup low-bowl shape with relatively thin plates, wider than high; infrabasals very small, nearly covered by stem; basals slightly wider than high; radials twice as wide as high with plenary facets; arm branching isotomous, very regular, arms closely abutted; arms branch on primibrachial 1 and a second time on secundibrachial 8; primibrachial 1 very elongate, proximal secundibrachials elongate, distal ones quadrangular, tertibrachials elongate, rectangular.

Mendipocrinus latifrons (Austin and Austin, 1847)

Text-figure 1E; Table 2

- 1847 *Poteriocrinus latifrons* Austin and Austin, p. 82, pl. 10, fig. 4.
 1878 *Scaphiocrinus latifrons* (Austin); Sladen, p. 248.
 1880 *Pachylocrinus latifrons* (Austin); Wachsmuth and Springer, p. 116.

TABLE 2. Measurements (in mm) of *Mendipocrinus* (gen. nov.) *latifrons* (Austin and Austin, 1847); GSM 7603, holotype.

Crown	Cup	Infrabasal	Basal	Radial	Arms
H	H, W	H, W	H, W	H, W	L
Ray		C	BC	B	
24.1	3.3, 5.0	0.9, 0.5	1.2, 1.7	1.1, 2.1	21.3

- 1886 *Woodocrinus latifrons* (Austin); Wachsmuth and Springer, p. 242.

- 1943 *Pachylocrinus latifrons* (Austin and Austin); Bassler and Moodey, p. 581.

- 1951b *Pachylocrinus? latifrons* (Austin and Austin); Wright, p. 65, pl. 31, fig. 5.

Type. Holotype, and sole specimen known, is a relatively complete crown (GSM 7603).

Description. Crown cylindrical, slender. Aboral cup low bowl-shaped with a convex base, height to width ratio approximately 0.67; plates thin, smooth, lacking ornamentation; infrabasals very small, slightly visible in side view; basals hexagonal, wider than high, height to width ratio approximately 0.7; radials pentagonal, wider than high, height to width ratio approximately 0.5, with plenary facets. Apparently three anals as a partial radianal and right tube plate are preserved along with a space for the anal X, which is missing. Anal sac unknown. Arm branching isotomous, very regular, first branching on primibrachial 1, second branching on secundibrachial 8; arms closely abutted. Brachials all rectangular, ranging from elongate to quadrangular; primibrachial 1 elongate, about twice as high as wide; proximal secundibrachials less elongate, distal secundibrachials quadrate; tertibrachials elongate. Pinnules not observed, but arms are tightly closed. Column circular, homeomorphic.

Comparisons. *Mendipocrinus* differs from true *Pachylocrinus* Kirk, 1942 (Kammer and Ausich 1993) by having primibrachial 1 axillary, rather than primibrachial 2; primibrachial 1 is unusually elongate; the brachials are rectangular, rather than subcuneate or cuneate; the arms closely abut; the isotomous arm branching is very regular rather than uneven; and the basals are not bulbous and larger than the radials. *Mendipocrinus* is more similar to *Dinotocrinus* Kirk, 1941 and *Borocrinus* Ausich and Sevastopulo, 2001 (like *Dinotocrinus*, except first branching is higher on the A ray), but both of these genera have subcuneate brachials and narrow arms that do not closely abut. *Aphelecrinus* Kirk, 1944 differs in having a cone-shaped cup, clearly visible infrabasals and subcuneate arms that do not closely abut.

Mendipocrinus is placed in the Pachylocrinidae because it has a low, bowl-shaped cup, infrabasals that are not readily visible in side view, plenary facets, three anals in the cup, and isotomous branching two or more times (Moore *et al.* 1978; Kammer and Ausich 1993).

Occurrence. Tournaisian (Ivorian), Black Rock Limestone, Mendip Hills, Somerset. The precise locality was not recorded by Austin and Austin (1847), who noted that in their experience this taxon is restricted to the Mendips. The Black Rock Limestone is still a valid stratigraphical term in the Mendip Hills (Adams *et al.* 2004).

Subclass FLEXIBILIA von Zittel, 1895
 Order SAGENOOCRINIDA Springer, 1913
 Superfamily LECANOOCRINACEA Springer, 1913
 Family MESPIOCRINIDAE Jaekel, 1918

Genus MESPIOCRINUS De Koninck and Le Hon, 1854

Type species. *Mespilocrinus forbesianus* De Koninck and Le Hon, 1854, by the subsequent designation of Miller (1889).

Diagnosis. Small, subglobose crown with short arms that may be slightly twisted clockwise or anticlockwise from aboral view; primibrachial 2 axillary, secundibrachial 2 or 3 axillary; no radianal, CD basal enlarged with large anal X sitting above, outside the cup.

Remarks. All five nominal species, including the new species, of western European *Mespilocrinus* are reviewed. Additionally, six species from North America (Webster 2003) are included in a phylogenetic analysis of *Mespilocrinus*. These are: *M. konincki* (Hall, 1859) from the Kinderhookian Chouteau Limestone and Osagean Burlington Limestone; *M. blairi* (Miller and Gurley, 1895) from the Chouteau Limestone; *M. chapmani* Springer, 1920, from the Kinderhookian Maynes Creek Formation (F. Gahn, pers. comm. 2006) and the Osagean Burlington Limestone; *M. thiemi* Springer, 1920, from the Burlington Limestone; *M. romingeri* Springer, 1920, from the Osagean New Providence Shale and Fort Payne Formation; and *M. myllos* Ausich, Goldstein and Yates, 2000, from the Osagean Muldraugh Formation.

Mespilocrinus forbesianus De Koninck and Le Hon, 1854

- 1854 *Mespilocrinus forbesianus* De Koninck and Le Hon, p. 112, pl. 2, fig. 1a–e.
 1920 *Mespilocrinus forbesianus* De Koninck and Le Hon; Springer, p. 193, pl. 5, figs 1–3.
 1943 *Mespilocrinus forbesianus* De Koninck and Le Hon; Ubaghs, p. 1, text-figs 1–10.
 1954 *Mespilocrinus forbesianus* De Koninck and Le Hon; Wright, p. 177, pl. 47, fig. 11.

Specimens examined. NMS 1958.1.1619, hypotype, Coplow Knoll (Wright 1954, pl. 47, fig. 11). BMNH E 21586, paratype, Tournaisian, Yorkshire [sic] (Clitheroe or Bowland in Lancashire rather than Yorkshire). BMNH E 71026, non-type, Coplow Knoll, Westhead Collection.

Diagnosis. A species of *Mespilocrinus* with the top of the CD basal even with the tops of adjacent radials; infrabasals convex, exposed; no cup or arm torsion; primibrachial 1 smaller than underlying radial; maximum calyx width

at the radials; two bifurcations per ray; columnals homeomorphic.

Remarks. Columnals normal, not spindle-shaped. The paratype is a small crown that resembles fig. 522.2 in Moore and Teichert (1978), as well as plates 2 and 6 in De Koninck and LeHon (1854). The specimen from Coplow Knoll in the Westhead Collection is a good-sized cup and column that is indeed an *M. forbesianus*. BMNH E 21586 was collected in the nineteenth century when Clitheroe and the Forest of Bowland were part of Yorkshire before they were included in Lancashire. In his 'Geology of Yorkshire', Phillips (1836) included many specimens collected from the Clitheroe and Forest of Bowland (or Bolland) regions (Ausich and Kammer 2006).

Occurrence. Tournaisian, lower Chadian. Coplow Knoll, Clitheroe, Lancashire (British Grid ref. SD 750 431) and, questionably, the Forest of Bowland, Lancashire.

Mespilocrinus granifer De Koninck and LeHon, 1854
 (*nomen dubium*)

- 1854 *Mespilocrinus granifer* De Koninck and Le Hon, pl. 2, fig. 6a–c.

Remarks. Of this species only a single cup is known; it has five equal basals with no enlarged CD basal and a single anal plate in the cup. The specimen illustrated in De Koninck and LeHon (1854) is too poor to identify the genus and, consequently, this taxon is here considered a *nomen dubium*.

Mespilocrinus depressus Wright, 1936

- 1936 *Mespilocrinus depressus* Wright, p. 409, pl. 10, figs 2, 6; text-figs 36–37.
 1939 *Mespilocrinus depressus* Wright; Wright, p. 62, pl. 5, figs 13, 15; text-figs 81–82.
 1954 *Mespilocrinus depressus* Wright; Wright, p. 180, pl. 47, figs 8, 10, 13, 17–18, 25.

Specimens examined. NMS 1958.1.1651, holotype, no. 1 Bed, Seafeld Tower Limestone, west of Kirkcaldy, Fife, Scotland (Wright 1954, pl. 47, figs 8, 17, 25; text-figs 100–101). NMS 1958.1.1652–1657, same bed and locality.

Diagnosis. A species of *Mespilocrinus* with the top of the CD basal even with the tops of adjacent radials; infrabasals concave, exposed; no cup or arm torsion; primibrachial 1 smaller than underlying radial; maximum calyx width at the radials; one bifurcation per ray; columnals unknown.

Remarks. *Mespilocrinus depressus* has infrabasals that are depressed, not visible in side view. In contrast, *M. pringlei*, also from the Lower Limestone Group, is larger and the infrabasals are not depressed.

Occurrence. Brigantian. Seafield Tower Limestone, Lower Limestone Formation, west of Kirkcaldy, Fife (British Grid ref. NT 279 896); Hurler Limestone [= St Monance White Limestone (MacGregor 1996)], Lower Limestone Formation, St Monance, Fife (NO 524 014).

Mespilocrinus pringlei Wright, 1954

1954 *Mespilocrinus pringlei* Wright, p. 178, pl. 47, figs 7, 9, 14–16, 19–24.

Specimens examined. NMS 1958.1.1633, holotype, no. 1 Bed, Invertiel, Fife (Wright 1954, pl. 47, figs 15, 20, 24, text-figs 102–103). NMS 1958.1.1634–1640, same bed and locality. BMNH E 70985, non-type, Lower Limestone Group, Macbie Hill, Peebles-shire. BMNH E 15184–6, non-types, three cups, Lower Limestone Group, St Monance, Fife. BMNH E 2158–9, non-types, three cups, no. 1 Bed, Invertiel, Fife. All localities in Scotland.

Diagnosis. A species of *Mespilocrinus* with the top of the CD basal even with the tops of adjacent radials; infrabasals convex, exposed; no cup or arm torsion; primibrachial 1 smaller than underlying radial; maximum calyx width at the radials; one bifurcation per ray; columnals homeomorphic.

Remarks. This is a small species, the infrabasals are not depressed and are visible in side view, and the columnals have a distinct spindle shape.

Occurrence. Brigantian. no. 1 Bed, Lower Limestone Formation, Invertiel, Fife (British Grid ref. NT 265 900); Lower Limestone Formation, Macbie Hill, Scottish Borders (NT 185 515); Hurler Limestone of Lower Limestone Formation, St Monance, Fife (NO 524 014); Lower Limestone Formation, Kirkcaldy, Fife (NT 279 896); Lower Limestone Formation, Carlops, Scottish Borders (NT 160 559); Lower Limestone Formation, Broadstone near Beith, North Ayrshire (NS 363 532).

Mespilocrinus wrighti sp. nov.

Text-figure 1A–D; Table 3

Derivation of name. In honour of V. Paul Wright (Cardiff University), who kindly led us to Mississippian localities in South Wales in 2003.

Holotype. NMW 81.8G.6825.

Diagnosis. Crown small, subglobose; maximum width at first axillary, primibrachial 2; infrabasals completely cov-

TABLE 3. Measurements (in mm) of *Mespilocrinus wrighti* sp. nov., NMW 81.8G.6825, holotype.

Crown H, W Ray	Cup H, W	Basal H, W BC	Radial H, W B
> 11.2, 11.4*	2.9, 8.9	2.0, 3.0	2.2, 4.4

*Crown widest at primibrachial 2.

ered; CD basal tapers upwards to support narrow anal X plate; radials and proximal primibrachials have a sinistral torsion in aboral view; radial facets plenary; primibrachial 1 larger than underlying radial; arms closely abutting; only one bifurcation per ray preserved, total number unknown; columnals unknown.

Description. Crown small, subglobose, maximum width at first axillary, primibrachial 2; aboral cup bowl shaped; infrabasals completely covered by stem attachment; basals mostly exposed, CD basal larger than others and tapers upwards where it supports a narrow anal X plate that is poorly preserved; radials twice as wide as high, radial facet plenary, nearly straight; no interradial/interbrachial plates; radials and proximal arms display a subtle sinistral torsion as viewed aborally with each adjacent plate sitting higher from A to C rays (D–E rays mostly covered); arms closely abutting; primibrachial 1 fixed in aboral cup; primibrachial 2 axillary, at least two secundibrachials, further bifurcations unknown. Columnals, a weathered proxistele only, too poorly preserved to determine if homeomorphic or spindle shaped.

Remarks. Most other species of *Mespilocrinus* have the infrabasals partly exposed, rather than completely covered as in *M. wrighti* sp. nov. and *M. myllos*. Moving from A to C rays, each radial sits higher than the previous one producing a subtle sinistral spiral in the cup plates, which contrasts with the dextral spiral in cup plates of *M. konincki*. The type species, *M. forbesianus*, has no spiral in the cup plates.

The only other Tournaisian *Mespilocrinus* from Europe is *M. forbesianus*; similar-aged species in North America include *M. chapmani* (late Kinderhookian–late Osagean), *M. konincki* (late Kinderhookian–early Osagean) and *M. thiemi* (early Osagean). All four have the infrabasals exposed around the stem attachment scar, unlike *M. wrighti*. In *M. forbesianus*, the radials are not spirally offset from one another, and the CD basal has parallel sides with the top horizontal and even with adjacent radials. *Mespilocrinus konincki* (see Springer 1920, pl. 5, figs 4–15) has an elongate and irregular-shaped anal X (pl. 5, figs 9a, 13b) similar to *M. wrighti*, but it differs in having the infrabasals clearly visible and the spiral offset pattern of the cup plates is reversed (pl. 5, figs 12, 13a–b). Both *M. thiemi* and *M. chapmani* have angustary facets and widely separated arms, unlike *M. wrighti*.

Occurrence. Tournaisian (Ivorian). Blucks Pool Limestone, Bosherton area, near Linney Head on the Pembrokeshire coast (British Grid ref. SR 966 947). Adams *et al.* (2004) indicated that Ivorian rocks in South Pembrokeshire are the Blucks Pool Limestone, which supercedes the Black Rock Limestone in this region.

PHYLOGENETIC ANALYSIS OF MESPILOCRINUS

Mespilocrinus is currently known only from the Mississippian of Europe and North America with ten valid species (Table 4; *M. granifer* is here considered a *nomen dubium*). It is the oldest genus of the Mespilocrinidae, with all other genera restricted to the Pennsylvanian or Permian (Moore 1978). Choice of outgroup to determine character order for a phylogenetic analysis is, thus, from a different family. Springer (1920, p. 191) suggested that *M. thiemi* Springer, 1920, with its angustary facets, was derived from *Pycnosaccus* Angelin, 1878 by loss of the radianal. Therefore, *Pycnosaccus*, which ranges from the Upper Silurian to Upper Devonian (Moore 1978), was chosen as the outgroup, which here consists of the combined characters for *P. scrobiculatus* (Hisinger, 1840), *P. nodulosus* Angelin, 1878 and *P. tenuibrachiatus* Springer, 1920 from Moore (1978) (Table 4).

Characters

The following is a detailed discussion of characters and character coding used in the species-level phylogenetic analysis of *Mespilocrinus*. The data for this analysis

include 13 binary and multistate characters that are equally weighted and unordered (Table 4).

1. Radianal. All species of *Mespilocrinus* lack a radianal, contrary to *Pycnosaccus*. The absence of the radianal is judged to be the derived character state [0, present; 1, absent].
2. CD basal. The CD basal is the largest basal in *Mespilocrinus*. In *Pycnosaccus*, the top of the CD basal is below the top of the radials because the anal X plate is within the aboral cup. In some species of *Mespilocrinus* the CD basal has pushed the anal X plate out of the cup, and the top of the CD basal is even with or above the top of the radials. Thus, this appears to be the derived character state [0, below top of radials; 1, even with or above top of radials].
3. Cup torsion. *Mespilocrinus* is unusual in that some species display cup torsion that is either dextral (clockwise) or sinistral (anticlockwise), when viewed aborally. *Pycnosaccus* lacks torsion, so torsion must be derived in *Mespilocrinus* because only some species possess this character [0, none; 1, dextral; 2, sinistral].
4. Infrabasal circlet. Nearly all species of *Mespilocrinus* have a convex infrabasal circlet, except for *M. depressus* where it is concave [0, convex; 1, concave].
5. Infrabasals visible. Most species of *Mespilocrinus* have some portion of the infrabasals visible, except for *M. myllos* and *M. wrighti* in which the infrabasals are completely covered by the stem attachment area [0, visible; 1, covered].
6. Radial facets. The radial facets of *Pycnosaccus* are both curved and angustary. In *Mespilocrinus* the radial facets may range from clearly angustary and curved, e.g. *M. thiemi*, to curved, e.g. *M. chapmani*, to straight and plenary, e.g. *M. forbesianus* [0, curved or angustary; 1, straight, plenary].
7. Primibrachial 1 size. In all species of *Mespilocrinus* except *M. wrighti*, primibrachial 1 is smaller than the subjacent radial [0, smaller than radial; 1, larger than radial].
8. Primibrachial axillary. In *Pycnosaccus*, primibrachial 1 is axillary, whereas in *Mespilocrinus* primibrachial 2 is axillary [0, one; 1, two].
9. Maximum crown width. In *Pycnosaccus* and all species of *Mespilocrinus* except *M. wrighti* maximum crown width is at the top of the radials. In *M. wrighti* maximum width is at primibrachial 1 [0, at radials; 1, at primibrachial 1].
10. Arm spacing. In *Pycnosaccus*, the arms are clearly separated with open spaces between them when closed, which is also true for some species of *Mespilocrinus*, e.g. *M. thiemi*. Most species of *Mespilocrinus* have closely abutted arms when closed, e.g. *M. forbesianus* [0, separated; 1, closely abutted].
11. Bifurcations in line per ray. Bifurcations in line per ray are the maximum number of axillary plates in line on any given ray. *Pycnosaccus* has three bifurcations in line per ray, whereas species of *Mespilocrinus* have either two or one [0, three; 1, two; 2, one].
12. Arm torsion. In addition to cup torsion, some species of *Mespilocrinus* exhibit arm torsion, which is not directly linked to cup torsion. Two species exhibit dextral cup torsion, whereas six exhibit dextral arm torsion when viewed aborally. Sinistral arm torsion was not observed (*M. wrighti* with sinistral cup torsion does not preserve enough arm brachials to determine if torsion is present) [0, none; 1, dextral].

TABLE 4. Character matrix used in the phylogenetic analysis of *Mespilocrinus* with *Pycnosaccus* as the outgroup. See text for discussion of the 13 characters and their character states. Polymorphic character states listed in parentheses. Age ranges shown in Text-figure 2.

Taxon	Characters
<i>Pycnosaccus</i> Angelin, 1878	00000 00000 000
<i>M. blairi</i> (Miller and Gurley, 1895)	10000 10101 21?
<i>M. chapmani</i> Springer, 1920	10000 00100 001
<i>M. depressus</i> Wright, 1936	11010 10101 21?
<i>M. forbesianus</i> De Koninck and LeHon, 1854	11000 10101 110
<i>M. konincki</i> Hall, 1859	10(01)00 10101 111
<i>M. myllos</i> Ausich, Goldstein and Yates, 2000	1?001 00101 1?0
<i>M. pringlei</i> Wright, 1954	11000 10101 211
<i>M. romingeri</i> Springer, 1920	10100 00101 21?
<i>M. thiemi</i> Springer, 1920	10000 00100 201
<i>M. wrighti</i> sp. nov.	10201 11111 ???

13. Columnals. *Mespilocrinus* is unique among flexible crinoids in having elongate, spindle-shaped columnals below the typical disc-shaped columnals of the proxistele (Springer 1920, pl. 5) in four of its species: *M. chapmani*, *M. konincki*, *M. pringlei* and *M. thiemi*. *Pycnosaccus* columnals are disc shaped [0, disc shaped only; 1, spindle shaped below proxistele].

Methodology and results

Parsimony-based character analysis was performed using PAUP* 4.0b10 (Swofford 2001) on 13 characters for ten species of *Mespilocrinus* and the outgroup *Pycnosaccus*. All characters are equally weighted and unordered. Polymorphism is coded as a multistate character (only one instance in character 3). An exhaustive search using the branch and bound option found a single tree with the shortest length of 19 steps (CI, 0.84; HI, 0.21; RI, 0.81; RC, 0.68) (Text-fig. 2).

The generation of a single tree by PAUP indicates that the character data (Table 4) are well ordered with a minimal amount of homoplasy, as indicated by the low value of HI. Interpreting the cladogram as a phylogeny suggests that *Mespilocrinus* was derived from *Pycnosaccus* by the loss of the radial (character 1), the raising of the first axillary from primibrachial 1 to 2 (ch. 8), and the addi-

tion of spindle-shaped columnals (ch. 13) (node A in Text-fig. 2). The more primitive character states for *Mespilocrinus* include angustary or curved radial facets (ch. 6) and widely separated arms (ch. 10), as exhibited by *M. chapmani* and *M. thiemi*. Additionally, *M. chapmani* has at least three arm bifurcations per ray, similar to *Pycnosaccus*, whereas all other species have fewer arm bifurcations per ray with two bifurcations per ray in *M. thiemi*, *M. romingeri*, *M. blairi*, *M. depressus* and *M. pringlei* (node B in Text-fig. 2). The remaining taxa, *M. konincki*, *M. forbesianus*, *M. myllos* and *M. wrighti*, form a clade with only one bifurcation per ray (node E in Text-fig. 2).

The next synapomorphies to consider, as shown by the clade rooted by *M. romingeri*, include closely abutting arms (ch. 10) and dextral arm torsion (ch. 12) (node C in Text-fig. 2). This large clade of eight species, from *M. romingeri* to *M. wrighti*, consists entirely of species with the arms folded in tightly to form subglobose crowns, along with the loss of some characters and the addition of new characters in various combinations. Newly derived characters within this clade include dextral cup torsion (ch. 3) in *M. romingeri*; straight, plenary facets (ch. 6) in all but *M. myllos* (node D in Text-fig. 2); CD basal extends to the top or above adjacent radials (ch. 2) as in *M. depressus*, *M. pringlei* and *M. forbesianus*; loss

TEXT-FIG. 2. Cladogram of the single most parsimonious tree of *Mespilocrinus* based on data in Table 4. Length, 19; CI, 0.84; HI, 0.21; RI, 0.81; RC, 0.68. Time units defined in Table 5. Important synapomorphies at nodes as follows: A, radial lost, primibrachial 2 becomes axillary, spindle-shaped columnals; B, arm branching reduced from three to two bifurcations per ray; C, arms become closely abutting with dextral arm torsion; D, radial facets become straight, plenary, rather than curved and angustary; E, arm branching reduced to one bifurcation per ray; F, loss of spindle-shaped columnals; G, infrabasals covered by stem attachment.

of spindle-shaped columnals (node F in Text-fig. 2); infrabasals concave (ch. 4) as in *M. depressus*; infrabasals covered (ch. 5) as in *M. myllos* and *M. wrighti* (node G in Text-fig. 2); sinistral cup torsion (ch. 3), primibrachial 1 larger than the subjacent radial (ch. 7) and maximum crown width at primibrachial 1 (ch. 9) as in *M. wrighti*. Overall, *M. wrighti* is the most highly derived species of *Mespilocrinus* with the greatest number of character state changes (eight out of ten preserved) from the outgroup. It differs from all other species of the genus in having (1) sinistral cup torsion, (2) primibrachial 1 larger than the radials and (3) maximum crown width at primibrachial 1. Although it is highly derived relative to other species of *Mespilocrinus*, we judge that these differences are not sufficient to place it in a new genus.

The time ranges (Table 5) for the ten species of *Mespilocrinus* are plotted on the cladogram (Text-fig. 2). Although this single tree appears to be well ordered relative to character-state evolution, it is not well ordered stratigraphically. Basically, the time ranges for the different species appear to be randomly distributed, except that the two Time 9 species, *M. pringlei* and *M. depressus*, are grouped together. However, upon closer inspection there are discernible patterns that we interpret as follows.

1. The centre of evolution for *Mespilocrinus* was North America where three species appeared simultaneously in Time 1: *M. chapmani*, *M. blairi* and *M. konincki*. There are no species of *Mespilocrinus* from Time 1 in Western Europe, which may reflect the almost complete lack of preserved crinoids in this interval, the only species being *Taxocrinus macrodactylus* (Phillips, 1841) (Lane *et al.* 2001).

TABLE 5. Chronostratigraphic definition of time units for Mississippian crinoid occurrences in Europe and North America (Text-fig. 2), based on Leeder (1992), Jones (1996), Hance *et al.* (2002), Lane and Brenckle (2005) and Heckel and Clayton (2005).

Time unit	Chronostratigraphy	
	Europe	North America
10	Serpukhovian, Pendleian	Chesterian, late
9	Visean, Brigantian	Chesterian, early
8	Visean, Asbian	Meramecian, late
7	Visean, Holkerian	Meramecian, early
6	Visean, Arundian	Osagean, latest (upper Keokuk–lower Warsaw)
5	Visean, late Chadian	Osagean, late (lower Keokuk)
4	Tournaisian, early Chadian	Osagean, middle
3	Tournaisian, Ivorian	Osagean, early
2	Tournaisian, late Hastarian	Kinderhookian, latest
1	Tournaisian, early Hastarian	Kinderhookian, late

2. Morphological disparity was achieved rapidly during Time 1, as shown by the widely spaced distribution of *M. chapmani*, *M. blairi* and *M. konincki* on the tree. This radiation event was part of the overall explosive radiation of crinoids following the Late Devonian mass extinction event when crinoids fell to their global minimum during the Frasnian (Baumiller 1994) and began recovering during the Famennian (Waters *et al.* 2003), followed by explosive radiation in the Tournaisian (Kammer and Ausich 2006).

3. The European and North American occurrences are chronostratigraphically mixed, indicating migration between these two areas, certainly from North America to Europe, but the reverse route cannot be ruled out (Kammer *et al.* 2007).

4. The European occurrences in Times 3, 4 and 9 correspond to the three highest times of crinoid generic richness in Western Europe during the Mississippian (Ausich and Kammer 2006). Thus, the limited occurrences in these time intervals are probably the taphonomic artefact of a fragmentary fossil record, thus adding to the stratigraphical incongruity of the tree.

5. Assuming there was a radiation during Time 1, the relatively late appearances of *M. thiemi* and *M. romingeri*, between *M. chapmani* and *M. blairi*, may simply reflect non-preservation of an earlier origin for their lineages in North America. The same can be said for *M. pringlei* and *M. depressus* in Europe. The clade rooted by *M. konincki* shows only a modest stratigraphical incongruity with the slightly younger *M. forbesianus*, appearing before the older *M. wrighti* in Europe. *Mespilocrinus* is a small crinoid and was susceptible to disarticulation like many crinoids (Ausich and Sevastopulo 1994). Thus, it is reasonable to assume that the face-value record of *Mespilocrinus* may be biased by poor preservation.

Thus, the PAUP character analysis with one well-resolved tree for *Mespilocrinus* (Text-fig. 2) does appear to record a clear pattern of character evolution with reasonable stratigraphical congruity if a radiation is assumed during Time 1. The lack of stratigraphical order for some species is probably a taphonomic artefact of low taxonomic richness during Times 1, 2, 6 and 7 in western Europe (Ausich and Kammer 2006) or, in the case of North America, non-preservation of the origin of lineages.

CONCLUSIONS

Two new genera of advanced cladid crinoids are recognized among previously described species from Wales and England: *Glamorganocrinus* and *Mendipocrinus*. These new genera bring the total crinoid generic richness of the Ivorian of Western Europe to 36, 18 of which are advanced cladids.

The new flexible crinoid species *Mespilocrinus wrighti* is described from the Ivorian of Wales. A phylogenetic analysis of ten species of *Mespilocrinus*, with *Pycnosaccus* as the outgroup, yielded a single tree. *Mespilocrinus wrighti* is the most highly derived species of the genus because of the greatest number of character state changes from the outgroup. Species time ranges and geographical occurrences, plotted on the tree, suggest that the centre of evolution for *Mespilocrinus* was in North America because three North American species widely spaced on the tree appeared simultaneously in the Kinderhookian (Time 1). This large morphological disparity achieved during Time 1 was part of the overall radiation of crinoids following the Late Devonian mass extinction event when crinoids fell to their global minimum during the Frasnian and began recovering during the Famennian, followed by explosive radiation in the Tournaisian. Species of *Mespilocrinus* were apparently able to migrate between North America and Europe, and possibly in the reverse direction. The lack of stratigraphical order for some species on the tree is probably a taphonomic artefact of low taxonomic richness during Times 1, 2, 6 and 7 in western Europe, or in the case of North America, non-preservation of the origin of lineages.

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