Stratigraphical and geographical distribution of Mississippian (Lower Carboniferous) Crinoidea from Scotland

Thomas W. Kammer¹ and William I. Ausich²

² School of Earth Sciences, 155 South Oval Mall, The Ohio State University, Columbus, Ohio 43210, USA. E-mail: ausich@geology.ohio-state.edu

ABSTRACT: A total of 47 genera, in 80 species, of Mississippian, or Lower Carboniferous, crinoids are evaluated from 61 localities in Scotland based on a modern update of the literature, study of museum collections, and new field work. Among the 80 species, 76 are considered valid, with eight requiring new combinations of genus and species names. In addition, one species is considered a *nomen dubium*, and three can only be assigned at the generic level. Asbian faunas have a moderate generic richness of 13. Brigantian faunas have the highest generic richness at 40. Arnsbergian faunas have the lowest generic richness at three. There are no Mississippian crinoid faunas in Scotland older than Asbian. The dominant Brigantian crinoid faunas occur in limestones and shales in the shallow shelf marine intervals of Yoredale-style cyclothems. The Asbian faunas occur in shallower, nearshore mudstones and limestones of Yoredale-style cyclothems. The late Viséan (Brigantian) fauna is more similar in overall taxonomic composition to the global record for the Serpukhovian rather than the Viséan. This reflects the establishment of the Late Palaeozoic Crinoid Macroevolutionary Fauna, dominated by advanced cladid crinoids, by the end of the Viséan in Scotland.



KEY WORDS: Echinodermata, United Kingdom

James Wright (1878–1957), of Kirkcaldy and later Edinburgh, was the key figure in the study of Lower Carboniferous, or Mississippian (Heckel & Clayton 2005), crinoids in Scotland. His first contribution was in 1911 (Wright 1911–1912) and his endeavours ended with his great monograph on the British Carboniferous Crinoidea (Wright 1950–1960). In between these 'bookends' he published an additional 37 papers and monographs (Webster 2003), including 'The Scottish Carboniferous Crinoidea' (Wright 1939). The overwhelming majority of previous knowledge about Scottish Mississippian crinoids can be attributed to Wright. Some of the more common Scottish taxa were noted by Phillips (1836), Austin & Austin (1843–1847), and Bather (1920), although Wright (1939) pointed out that many of these were identified incorrectly.

The present paper summarises the current state of knowledge for Scottish Mississippian crinoids based on newer systematic work and revisions since Wright's work, although illustrations of all species discussed are in Wright (1950-1960). This present contribution is part of a larger study on the global evolutionary palaeoecology of Mississippian crinoids. Prerequisite to this analysis is the establishment of accurate generic concepts, facies distributions and temporal ranges of genera. With these data it is planned 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. These data for Scotland are presented in the present paper. Previously, these similar data have been presented for England and Wales (Ausich & Kammer 2006). A subsequent paper for Ireland is

planned, which will expand upon Sevastopulo (2002). In addition to genera, major Mississippian crinoid clades are discussed, because these clades have been shown to exhibit characteristic facies distributions (Kammer & Ausich 1987, Kammer *et al.* 1998). These include two orders of the subclass Camerata, the orders Diplobathrida and Monobathrida; the subclass Cladida; the subclass Flexibilia; and the subclass Disparida. Within the Cladida, primitive cladids have ramulate arm branching (widely spaced, non-branching side branches), whereas advanced cladids have pinnulate arm branching (closely spaced, non-branching side branches on every arm plate). Subdivision into these clades follows Simms & Sevastopulo (1993) and Ausich (1996, 1998), and further explanation and definition of these clades can be found in Moore & Teichert (1978) and Hess *et al.* (1999).

1. Mississippian crinoids from Scotland

Most Mississippian crinoids from Scotland have not received systematic treatment after Wright (1950–1960). Since that time, the *Treatise on Invertebrate Paleontology* (Moore & Teichert 1978) has been published, and age-equivalent Mississippian crinoids have been studied in detail in North America (e.g., Burdick & Strimple 1982; Chesnut & Ettensohn 1988). Such studies have contributed to a much more rigorous definition of genera. The goal of the present study is to apply modern generic concepts to all Mississippian crinoids from Scotland and to document the facies and temporal distribution of these crinoid genera. Accordingly, the generic assignments, many new, of crinoid species from Scotland are listed in Appendix A. Changes to the generic status of species are

¹ Department of Geology & Geography, West Virginia University, Morgantown, West Virginia 26506-6300, USA. E-mail: Thomas.Kammer@mail.wvu.edu



Figure 1 Generic richness of crinoid faunas from Scotland (Table 2) by time unit (Table 1). Compare with data for England and Wales (Ausich & Kammer 2006, fig. 1).

noted, together with a brief justification. No attempt is made here at species-level synonymy. The taxonomic revisions are based on both updating the literature for Scottish crinoids and study of type specimens from the following museums: National Museum of Scotland (Wright Collection); British Geological Survey, Keyworth; Natural History Museum, London; Sedgwick Museum, Cambridge. Authors of genera are listed in Webster (2003).

In summary, the following changes have been made; please see Appendix A for taxonomic notes. Generic assignments in Wright (1950–1960) are denoted by brackets. These changes include:

- *Cribanocrinus* [*Rhodocrinites*] *baccatus* (Wright, 1937), **new combination**
- *Litocrinus* [Kallimorphocrinus] scoticus contractus (Wright, 1933), new combination
- *Adinocrinus* [*Hydreionocrinus*] *artus* (Wright, 1945), **new combination**
- *Aphelecrinus* [*Abrotocrinus*] *angustatus* (Wright, 1934), **new combination**
- *Cosmetocrinus* [*Aphelecrinus*] *dunlopi* (Wright, 1936), **new combination**
- *Exaetocrinus* [*Erisocrinus*] *carlopsensis* (Wright, 1939), **new** combination
- *Lanecrinus* [*Decadocrinus*] *fifensis* (Wright, 1934), **new combination**
- *Pelecocrinus* [*Poteriocrinites?*] *magnus* (Wright, 1937), **new combination**

One species is recognised as a nomen dubium:

Apographiocrinus? scoticus (Wright, 1942), nomen dubium

2. Crinoid localities and faunal analysis

2.1. Introduction

Scottish Mississippian crinoids occur only in the Asbian and Brigantian substages of the Viséan and the Arnsbergian substage of the Serpukhovian (Fig. 1 and Table 1, Times 8, 9, and 11). Faunas from all Scottish localities are dominated by advanced cladid crinoids. Their North American equivalents include the late Meramecian and early and late Chesterian, respectively (Burdick & Strimple 1982; Webster & Groessen 1990; Jones 1996; Gradstein *et al.* 2004). Older crinoid faunas, Hastarian through Holkerian (Times 1–7, Table 1), occur in the Mississippian of England, Wales, and Ireland (Sevastopulo 2002; Ausich & Kammer 2006). Marine localities with crinoids



Figure 2 The ten localities with the highest crinoid generic richness in Scotland; 9IN=Invertiel; 9RS=Roscobie; 9CL=Carlops; 9ST= Seafield Tower; 9PL=Penton Linns; 9KK=Kirkaldy; 9CH=Chapel; 9DL=Duloch; 9MB=Macbiehill; 8AR= Ardross; (Appendices A and B).

are essentially confined to the Midland Valley and Southern Borders (Appendix B). These two areas are the Midland Valley Basin and Northumberland Basin, respectively, separated by the Southern Uplands (Read *et al.* 2002). Detailed information on specific localities and their stratigraphy is given in Forsyth & Chisholm (1977), MacGregor (1996), Purnell & Cossey (2004), and Whyte (2004).

The oldest Mississippian fossiliferous marine rocks in Scotland are of late Viséan (Asbian and Brigantian) age and occur in the Strathclyde Group, formerly the Calciferous Sandstone Measures (Wilson 1974, 1989; Browne *et al.* 1999). Thus, there are no crinoids older than Asbian (Time 8, Table 1) in Scotland. Older Carboniferous deposits in Scotland are represented by rocks of terrestrial and volcanic origin (Browne *et al.* 1999; Read *et al.* 2002).

2.2. Asbian, Time 8

In the Midland Valley of Scotland, the Asbian consists of all but the uppermost formation (Pathhead Formation) of the Strathclyde Group (Browne et al. 1999). Formations are composed of sedimentary and volcanic rocks, including coal and lacustrine or lagoonal oil shale. The Strathclyde Group is dominantly fluvial and lacustrine in origin, with sporadic marine beds that are better developed in the east (Read et al. 2002). Marine beds are referred to as marine bands of which there are several in the Strathclyde Group, particularly in the Pittenweem Formation, including: Macgregor Marine Bands (St Andrews Castle Marine Band, Pittenweem Marine Band, Witch Lake Marine Band, etc.), West Braes Marine Band, Balmore Marine Band, and Ardross Limestone (Wilson 1974, 1989; Browne et al. 1999). Most of these marine bands have a low generic richness of crinoids; Ardross (8AR) in Fife, with six genera, has the greatest richness (Fig. 2 and Appendix B).

Asbian rocks in central Scotland are predominantly nonmarine clastics ranging from mudstones to sandstones and include lacustrine or lagoonal oil shales, coals, seatearths, and ironstones (Wilson 1989) and represent fluvial, lacustrine, and deltaic deposits (Read *et al.* 2002). The marine rocks include limestones, mudstones, and silty mudstones. These rocks comprise Yoredale-type cyclothems in which marine rocks are succeeded by upward-coarsening fluvial-deltaic deposits capped by palaeosols and coals (Browne *et al.* 1999; Read *et al.* 2002; Kassi *et al.* 2004). These cyclothems resulted from glacioeustatic changes in sea level associated with





Figure 3 A. Pie chart showing proportions of macrofossil crinoid genera during the Brigantian (late Viséan, Time 9) in Scotland. Compare with both the Viséan and Serpukhovian of the world in B and C (Kammer & Ausich 2006).

Gondwanan glaciers (Smith & Read 2000; Wright & Vanstone 2001). We examined the MacGregor Marine Bands between Ansthruther and Pittenweem in Fife. The marine bands are dolomudstones containing bioclastic lag deposits, which appear to be storm deposits. They are interbedded with oil shales of probable lagoonal origin (Read *et al.* 2002, p. 264). This, together with tidal laminations within the immediately overlying siltstones, indicates close proximity of the marine bands to a low-energy shoreline.

At the St Andrews shore section, approximately 300 m of the Asbian Pittenweem Formation are exposed, including three marine bands that total approximately 9 m in thickness, or just 3% of the formation. Marine bands include: West Sands Marine Band (or Cuniger Rock Marine Band), Witch Lake Marine Band, and St Andrews Castle Marine Band (Forsyth & Chisholm 1977; Browne *et al.* 1999). The Witch Lake Marine Band consists of approximately 3.6 m of mudstone and includes the 15 cm crinoidal limestone Encrinite Bed near the centre (Forsyth & Chisholm 1977), which may record maximum water depth.

The Witch Lake Marine Band contains crinoids, brachiopods, molluscs, and bryozoans (Forsyth & Chisholm 1977). It most likely represents shallow marine deposition associated with a rapid glacioeustatic rise in sea level that transgressed fluvial-deltaic environments (Read *et al.* 2002; Kassi *et al.* 2004). The presence of both crinoids and bryozoans indicates fully marine, stenohaline conditions (Kammer & Lake 2001). Crinoid species richness from the Encrinite Bed is three: *Tubulusocrinus doliolus* (Wright 1936) (see Kammer & Ausich 2007), *Ureocrinus bockschii* (Geinitz) (Wright 1952a, p. 112), and *Mantikosocrinus wrighti* (Yakovlev & Ivanov) (as *Dicromyocrinus geminatus* (Trautschold) in Wright 1952a, p. 111). Asbian crinoid richness is relatively low, with only 13 genera (Fig. 1). These Asbian faunas are composed primarily of advanced cladids, with the diplobathrid camerate *Cribanocrinus* and two flexibles.

2.3. Brigantian, Time 9

In the Scottish Midland Valley, the Brigantian consists of the Pathhead Formation at the top of the Strathclyde Group and the overlying Lower Limestone Formation of the Clackmannan Group (Browne et al. 1999; Whyte 2004). Marine horizons are more common in the Pathhead Formation than in the underlying formations of the Strathclyde Group, with the Pathhead Formation resembling the overlying Lower Limestone Formation (Read et al. 2002, p. 266) Crinoids occur in the Lower Ardross Limestone, Upper Ardross Limestone, and St Monance White Limestone of the Pathhead Formation and the various limestone members of the Lower Limestone Formation including (in stratigraphical order) the Hurlet Limestone or St Monance Brecciated Limestone (3.5 m), the St Monance Little Limestone (0.6 m), the Charlestown Main Limestone (1.5 m), the Seafield Marine Band or Main Hosie Limestone, the Mid Kinniny Limestone or Mid Hosie Limestone (0.6 m), and the Upper Kinniny Limestone or Top Hosie Limestone (0.3 m) (Forsyth & Chisholm 1977; Browne et al. 1999). The Lower Limestone Formation is at least 225 m thick, yet the limestones total only 6.5 m, or about 3% of the formation. Like the Strathclyde Group, the Lower Limestone Formation is composed of Yoredale-type cyclothems in which marine rocks are succeeded by upward-coarsening fluvial-deltaic deposits capped by paleosols and coals (Browne et al. 1999; Read et al. 2002; Kassi et al. 2004). However, the greater amount of limestone, commonly packstones and grainstones, in the marine zones of

Time Unit	Western Europe	Chronostratigraphy	Coral/Brach Zone ¹	Starting Time m.y. ³	Duration m.y. ³	Duration m.y. ²
11	E2	Serpukhovian, Arnsbergian		323.4	>3.0	>3.0
10	E1	Serpukhovian, Pendleian		326.4	3.0	5.0
9	V3c	Viséan, Brigantian	D2	328.6	2.2	3.5
8	V3b	Viséan, Asbian	D1	332.5	3.9	2.0
7	V2b,V3a	Viséan, Holkerian	S2	339.2	6.7	4.5
6	V2a, V1b	Viséan, Arundian	S1	342.8	3.6	6.5
5	V1a	Viséan, upper Chadian	C2	345.3	2.5	1.5
4	Tn3c	Tournaisian, lower Chadian	C1	345.8	0.5	1.0
3	Tn3a,b,c	Tournaisian, Ivorian	Z	349.0	3.2	4.0
2	Tn2	Tournaisian, Hastarian	K2		Total H	lastarian
1	Tn1b	Tournaisian, Hastarian	K1	359.2	10.2	6.0
			Total Du	ration, m.y.	41 ± 2	>37.0

Table 1 Chronostratigraphical definition of time units for British crinoid occurrences; based on Vaughan's $(1905)^1$ coral/brachiopod zones, Leeder (1992), Jones $(1996)^2$, Hance *et al.* (2002), and Gradstein *et al.* (2004)³. Vaughan's (1905)coral/brachiopod zones are included because many of Wright's (1950–1960) localities were dated on this basis

the Lower Limestone, as compared to the more argillaceous marine zones of the Strathclyde Group, suggests a more open marine setting farther offshore due to more widespread marine transgressions at this time. Read *et al.* (2002, p. 275) reported that 'the Lower Limestone Formation is the interval with the strongest marine influences during the Scottish Carboniferous.' This more open marine setting is probably the reason for the greater number of genera in the Brigantian (40) versus the Asbian (13) (Fig. 1) and the fact that 89% of the crinoid localities are from the Brigantian (Appendix B). Kammer & Ausich (2006) argued that crinoids flourished in open marine settings away from salinity fluctuations. As during the Asbian, these cyclothems resulted from glacioeustatic changes in sea level associated with Gondwanan glaciers (Smith & Read 2000; Wright & Vanstone 2001).

Of the 61 localities in Scotland with identified crinoids, 54 are Brigantian (Time 9) in age. Nine of these localities have six or more genera (Fig. 2, Appendix B). Localities with 10 or more genera are all in the Lower Limestone Formation and include: Invertiel, Fife (30); Roscobie, Fife (22); Carlops, Scottish Borders (16); and Seafield Tower, Fife (14). Stratigraphical details for Invertiel, Roscobie, and Seafield Tower (part of the Kinghorn Coast) are described in Whyte (2004).

The Brigantian faunas of Scotland and adjacent England include the youngest occurrences of genera that are typical of the Tournaisian and Viséan of North America. Perhaps most notable is the genus *Cribanocrinus*. This is the youngest report of this genus, and the only younger reports of the order Diplobathrida are from the Serpukhovian of Russia and Algeria (Arendt 2002; Webster *et al.* 2004). In addition, the following genera have their youngest occurrences in these faunas: *Adinocrinus, Allocatillocrinus, Blothrocrinus, Mespilocrinus, Pelecocrinus* and *Wachsmuthicrinus.*

2.4. Pendleian and Arnsbergian, Times 10 and 11

The Pendleian (Time 10) in Scotland is composed of the Limestone Coal Formation and the lower part of the Upper Limestone Formation (Browne *et al.* 1999; Read *et al.* 2002). The majority of the Upper Limestone Formation is Arnsbergian. No crinoids have been reported from the Limestone Coal Formation. Crinoids have been reported from the marine horizons in the middle of the Upper Limestone Formation at only one locality, Garpel Water, Muirkirk, East Ayrshire (11GW, Appendix B) (Whyte 2004, p. 100–2). These include *Platycrinites muirkirkensis* (Wright, 1956, p. 291), *Allagecrinus garpelensis* (Wright, 1952a, p. 142), and

Ureocrinus bockschii (Wright, 1952a, p. 112), all presumably of Arnsbergian age. *Woodocrinus whytei* (Wright, 1951b) also occurs at Garpel Water (locality 9GW, Appendix B) in the Lower Limestone Formation.

3. Discussion and conclusions

With a richness of 40 genera, the crinoid fauna of the Brigantian (Time 9) dominates the Mississippian of Scotland. With just a few exceptions, the 13 genera of the Asbian (Time 8) are essentially a subset of the Brigantian (Table 2), although many of the species are different. The species listed in Appendix A are all valid species according to the rules of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). However, in reviewing all these species for their correct generic assignments, it was clear that many of these species are subjective synonyms, and if synonymised, would occur in both the Asbian and Brigantian. Revision of species-level taxonomy is beyond the scope of the present paper, but it does not appear that there was a significant evolutionary turnover between the Asbian and Brigantian.

Rather, it is hypothesised that the jump in generic richness from 13 to 40 between the Asbian and Brigantian (Fig. 1, Times 8 and 9) reflects the more widespread occurrence of preferred environments during the Brigantian. The drop to only three genera in the Arnsbergian (Time 11) appears to reflect the subsequent loss of these environments during deposition of the Upper Limestone Formation, which is limited in exposure and has reported crinoids only at Garpel Water (locality 11GW, Appendix B).

The Brigantian fauna with 40 genera includes seven species of microcrinoids (Table 2). This is a relatively large number of microcrinoids and reflects the deliberate search by Wright (1950–1960) for these small forms. In general, microcrinoids are reported in few studies because they involve the microscopic examination of sediment residues (Lane & Sevastopulo 1982). The remaining 33 genera are all macrocrinoids, which are the type of crinoids almost always reported in the literature. These genera are dominated by advanced cladids (67%), with subordinate numbers of flexibles (24%), and camerates (9%); there are no disparids or primitive cladids (Table 2). When compared with a global database for the Viséan and Serpukhovian (Fig. 3), it is readily apparent that the Brigantian fauna is more similar to the Serpukhovian than the Viséan, even though it is of late Viséan age. This is because

CRINOIDS FROM SCOTLAND

Table 2Seriated temporal distribution of western European crinoid genera. Occurrences in Scotland indicated by 1;additional occurrences in Western Europe by X. ? denotes questionable occurrences in Scotland. Microcrinoids areseparated, because of probable sampling biases

Genera		Time Units									
	1	2	3	4	5	6	7	8	9	10	11
Diplobathrid Camerates											
Cribanocrinus				Х	Х			1	1		
Gilbertsocrinus			Х	Х	Х						
Rhodocrinites			Х								
Monobathrid Camerates											
Camptocrinus									1		
Ectocrinus								Х	Х		
Acrocrinus							Х				
New Genus B				Х	Х						
Eumorphocrinus				Х	Х						
Pimlicocrinus				Х							
New Genus A				Х							
Brahmacrinus				Х							
Pleurocrinus			Х	Х	Х			Х	Х	Х	
Thinocrinus			Х	Х	Х						
Actinocrinites			Х	Х	Х						
Amphoracrinus			Х	Х	Х						
Iotacrinus			Х	Х							
Aryballocrinus			Х								
Physetocrinus			X								
Dialutocrinus			X								
Platycrinites			X	X	Х	Х		Х	1	X	1
Dichocrinus			Х	Х							
Disparids											
Halysiocrinus?					Х						
Synbathocrinus			Х	Х	Х			Х			
Primitive Cladids											
Barycrinus				Х	Х						
Edapocrinus				Х							
Cyathocrinites			Х	Х	Х						
Advanced Cladids											
Adinocrinus									1		
Ampelocrinus									1		
Cymbiocrinus?									Х		
Exaetocrinus									1		
Exochocrinus									Х		
Fifeocrinus									1		
Forthocrinus									1		
Hosieocrinus									1		
Intermediacrinus									Х		
Pedinocrinus									1		
Pelecocrinus									1		
Tyrieocrinus									1		
Rhabdocrinus									1	Х	
Woodocrinus									1		
Cosmetocrinus								Х	1		
Anemetocrinus								1	1	Х	
Balearocrinus (Spain)								Х			
Derbiocrinus								Х	Х		
Hydreionocrinus								Х	1	Х	
Idosocrinus								1			
Mantikosocrinus								1			
Mixocrinus								Х			
Tubulusocrinus								1			
Ophiurocrinus								1?		Х	

Table 2Continued.

Genera	Time Units										
	1	2	3	4	5	6	7	8	9	10	11
Parazeacrinites								x	1		
Scotiacrinus								1	1	х	
Ureocrinus								1	1	X	1
Phanocrinus						х	х	1	1		
Hvpselocrinus					Х	Х	Х	1			
Aphelecrinus				Х	Х		Х	1	1		
Springericrinus				Х							
Culmicrinus			Х					Х			
Gilmocrinus			Х		Х						
Borucrinus			Х	Х	Х		Х				
Abrotocrinus			Х								
Erincrinus			Х								
Fiannacrinus			Х								
Glamorganocrinus			Х								
Graphiocrinus			Х								
Holcocrinus			Х								
Maevecrinus			Х								
Mendipocrinus			Х								
Paracosmetocrinus			Х								
Scytalocrinus			Х						1		
Bollandocrinus			Х	Х				?	?		
Gaelicrinus			Х								
Sostronocrinus			Х								
Poteriocrinites			Х	Х	Х						
Blothrocrinus			Х	Х				1	1		
Lanecrinus					?				1		
Flexibles											
Ainacrinus									1		
Artichthyocrinus									1		
Caldenocrinus									1		
Wachsmuthicrinus									1		
Amphicrinus									1		
Aexitrophocrinus								1	1?		
Enascocrinus								1	1		
Onychocrinus						Х	Х	Х	1		
Dieuryocrinus				Х							
Euryocrinus				Х							
Forbesiocrinus			Х								
Mespilocrinus			Х	Х					1		
Taxocrinus	Х		Х	Х	Х						
Disparid Microcrinoids											
Allagecrinus									1		1
Allocatillocrinus									1		
Kallimorphocrinus									1		
Litocrinus								Х	1		
Thaminocrinus									1		
Cladid Microcripoids											
Abrachiocrimus								v			
Aulodesocrinus								А	1		
Carlonsocrinus									1		
Cydonocrimus									x		
Lageniocrinus								х	X		
Sycocrinites								X	18		
Generic Richness	0	0	0	0	0	0	0	13	40	0	3

there are a greater number of camerate genera in the early Viséan than the late Viséan, producing a higher average for the total Viséan as the Middle Palaeozoic Macroevolutionary Crinoid Fauna was waning (Ausich *et al.* 1994). By the Serpukhovian, advanced cladids formed the majority of crinoid taxa when the Late Palaeozoic Macroevolutionary Crinoid Fauna was established (Kammer & Ausich 2006). The Brigantian fauna is also notable for the large percentage of flexibles (23%), which is higher than the global record for the Viséan (11%) and the Serpukhovian (6%) (Fig. 3). The reason for the greater number of flexibles is unknown, but probably reflects the occurrence of the preferred environments for flexibles during the Brigantian in Scotland.

4. Acknowledgements

We thank Lyall Anderson (National Museum of Scotland), Mike Howe (British Geological Survey), Andrew Smith and David Lewis (Natural History Museum, London), and Dan Pemberton and Rod Long (Sedgwick Museum, Cambridge) for access to collections and assistance with locality information. In particular, Lyall Anderson was very helpful with requests for information. Ruth Robinson and Tony Prave (University of St Andrews) kindly showed us numerous outcrops in Fife. George Sevastopulo (Trinity College, Dublin) and Andrew Smith (Natural History Museum, London) made important improvements to the final manuscript. This research was supported by the US National Science Foundation (EAR-02059068 and EAR-0206307).

5. Appendix A

List of species assignments to genus without regard to species level synonymies; key references and page numbers are provided. Where a species has been reassigned, a brief explanation is given. Only those species of each genus reported from Scotland are included. See Webster (2003) for complete bibliographic citations. Species localities are keyed to Appendix B. Time ranges by genera are listed in Table 2.

DIPLOBATHRIDS

CRIBANOCRINUS

- *Cribanocrinus (né Rhodocrinites) baccatus* (Wright, 1937); Wright, 1958, p. 313, **n. comb.** Occurrence: 9BE, 9BT, 9CQ, 9EL, 9FH, 9HH, 9IN, 9MB, 9RS, 9SM, 9ST. The globose calyx shape and lack of plate sculpturing ally this species with *Cribanocrinus*.
- Cribanocrinus sp. 8AR, 9BR, 9BS, 9CL, 9CU, 9KK, 9PL.

MONOBATHRIDS

CAMPTOCRINUS

Camptocrinus compressus Wright, 1937; Wright, 1958, p. 307. Occurrence: 9IN.

PLATYCRINITES

- *Platycrinites conglobatus* (Wright, 1937); Wright, 1956, p. 277. Occurrence: 9IN.
- Platycrinites crassiconus (Wright, 1937); Wright, 1956, p. 278. Occurrence: 9CA, 9CL, 9DU, 9IN, 9RS, 9ST.
- *Platycrinites muirkirkensis* Wright, 1956, p. 291. Occurrence: 11GW.
- *Platycrinites invertielensis* (Wright, 1942); Wright, 1956, p. 293. Occurrence: 9IN.
- Platycrinites spiniger (Wright, 1937); Wright, 1956, p. 292. Occurrence: 9CL, 9DU, 9IN, 9KK, 9OM, 9RS, 11GW(?).

DISPARIDS ALLAGECRINUS

- Allagecrinus austinii Carpenter & Etheridge, 1881; Wright, 1952a, p. 139. Occurrence: 9CL, 9HO, 9IN.
- Allagecrinus garpelensis Wright, 1932; Wright, 1952a, p. 142. Occurrence: 11GW.

ALLOCATILLOCRINUS

Allocatillocrinus scoticus (Wright, 1933); Wright, 1952a, p. 147. Occurrence: 9IN.

KALLIMORPHOCRINUS

Kallimorphocrinus elongatus (Wright, 1932); Wright, 1952a, p. 146. Occurrence: 9AM, 9DA, 9DR, 9DU, 9HO, 9IN, 9LI, 9LM, 9MD, 9PW, 9SK.

LITOCRINUS

- Litocrinus extensus (Wright, 1952a, p. 146); Lane & Sevastopulo, 1982, p. 258. Occurrence: 9CL.
- *Litocrinus scoticus* (Wright, 1932); Wright, 1952a, p. 143; Lane & Sevastopulo, 1982, p. 258. Occurrence: 9CL, 9CO, 9DU, 9IN, 9LM, 9PW, 9RS.
- Litocrinus (né Kallimorphocrinus) scoticus contractus (Wright, 1933) **n. comb**. Occurrence: 9CL. Litocrinus scoticus contractus is a subspecies because it has a narrower aboral cup. The species was assigned to Litocrinus by Lane & Sevastopulo (1982).

THAMINOCRINUS

Thaminocrinus biplex (Wright, 1932); Wright, 1952a, p. 142; Strimple & Watkins, 1969, p. 217. Occurrence: 9CL, 9IN.

CLADIDS

- ADINOCRINUS
- Adinocrinus (né Hydreionocrinus) artus (Wright, 1945); Wright, 1951b, p. 88, **n. comb**. Occurrence: 9IN, 9RS, 9ST. These are all cups that have small, isolated basals with the radials in contact with the infrabasals. They are low, saucershaped, with a basal concavity. They are closely comparable to Adinocrinus nodosus (Wachsmuth & Springer 1886) from the early Viséan of North America (Kammer & Ausich 1994).

AMPELOCRINUS

Ampelocrinus plumosus Wright, 1951b, p. 93. Occurrence: 9PL.

ANEMETOCRINUS

- Anemetocrinus biserialis Wright, 1938; Wright, 1950, p. 24. Occurrence: 9CH, 9CL, 9CS, 9CT, 9DL, 9HM, 9IN, 9MB, 9PP, 9RS, 9ST.
- Anemetocrinus ardrossensis Wright, 1938; Wright, 1951a, p. 27. Occurrence: 8AR.
- Anemetocrinus wilsoni Wright, 1952b, 1960, p. 330. Occurrence: 8/9TH.
- Anemetocrinus covensis (Wright, 1934), 1951a, p. 28. Occurrence: 8CH.
- Anemetocrinus pentonensis (Wright, 1934), 1951a, p. 28. Occurrence: 9CS, 9PL.

Anemetocrinus sp. Occurrence: 9RS.

APHELECRINUS

- Aphelecrinus (né Abrotocrinus) angustatus (Wright, 1934); Wright, 1951b, p. 69, n. comb. Occurrence: 8AR, 8ES.
- This species has a conical cup. Thus, it cannot be an *Abrotocrinus*, which has a low bowl-shaped cup. It has the characters of *Aphelecrinus*: first primbrachial axillary on all rays, two isotomous bifurcations per ray, three anals, and

a pentagonal column. Kirk (1944, p. 198) reported that *A. mundus* has a pentagonal stem, although the Treatise stated that the column is typically round, but *A. mundus* and *A. oweni* are subpentagonal. It appears that *Aphelecrinus* has a round to pentagonal column. The holotype has a large anal sac with rectangular plates (Wright, 1951b, pl. 31, fig. 8 and text-fig. 36). *Aphelecrinus* has a large anal sac (Moore *et al.* 1978, fig. 428.2c).

- Aphelecrinus dilatatus Wright, 1945; Wright, 1951a, p. 45. Occurrence: 9IN, 9RS.
- Aphelecrinus roscobiensis Wright, 1945; Wright, 1951a, p. 46. Occurrence: 9RS.
- Aphelecrinus parvus Wright, 1945; Wright, 1951a, p. 46. Occurrence: 9IN
- Aphelecrinus sp. Wright, 1951a, p. 47. Occurrence: 9RS.

APOGRAPHIOCRINUS

Apographiocrinus? scoticus (Wright, 1942); Wright, 1952a, p. 119, **nomen dubium**. Occurrence: 9CL.

These are all tiny specimens only a few mm in size. Wright's (1952a, pl. 35, figs 7–10) photographs failed to state the magnification, which was about $\times 10$ or $\times 20$. The cups are poorly preserved, and the arms are missing. The cups have a very small single anal plate, the anal X, which is unlike the much larger single anal plate of *Apographiocrinus*. Although the arms are not preserved, Wright (1952a) stated that primibrachial 2 is axillary, which is unlike *Apographiocrinus* where primibrachial 1 is axillary. The cups are crushed but are apparently low. They do not fit either *Apographiocrinus* or *Cymbiocrinus*; no other genera come close. It seems best to consider this taxon as a **nomen dubium**.

AULODESOCRINUS

Aulodesocrinus parvus Wright, 1942; Wright, 1951b, p. 73. Occurrence: 9IN.

BLOTHROCRINUS

Blothrocrinus thorntonensis Wright, 1952b; Wright, 1960, p. 331. Occurrence: 8/9TH.

CARLOPSOCRINUS

Carlopsocrinus bullatus Wright, 1933; Wright, 1954a, p. 181. Occurrence: 9CL.

COSMETOCRINUS

Cosmetocrinus (né Aphelecrinus) dunlopi (Wright, 1936); Wright, 1951a, p. 43, n. comb. Occurrence: 9PL, 9RS.

The holotype has three bifurcations in line per ray on both the C ray and the apparent A ray (Wright, 1951a, pl. 11, fig. 1). *Aphelecrinus* has only two bifurcations in line per ray, whereas *Cosmetocrinus* has two or three.

EXAETOCRINUS

Exaetocrinus (né Erisocrinus) carlopsensis (Wright, 1939); Wright, 1951b, p. 101, **n. comb.** Occurrence: 9CL.

This is a juvenile; the photographs in Wright (1951b, pl. 30, figs 11, 12) are magnified \times 5. The only known arm plates are the first primibrachial on each arm, which are axillary and extremely long as is common among juveniles (Peters & Lane 1990). Wright placed this species in *Erisocrinus* because of the lack of anal plates, but that is a Pennsylvanian-age genus. Unlike *Erisocrinus*, this species has its infrabasals visible in side view. This species fits well in *Exaetocrinus* Strimple & Watkins, 1969 (Moore *et al.* 1978, p. T705), which was reported from the Viséan of Scotland and Morocco, as well as the Pennsylvanian of North America. It is unclear why Moore *et al.* (1978) reported this genus from

Scotland because neither Strimple & Watkins (1969, p. 181) nor Webster (2003) listed this genus from Scotland.

FIFEOCRINUS

Fifeocrinus tielensis (Wright, 1936); Wright, 1951a, p. 42. Occurrence: 9AK, 9BA, 9BH, 9CT, 9CW, 9IN, 9RS.

FORTHOCRINUS

Forthocrinus lepidus Wright, 1942; Wright, 1951b, p. 72. Occurrence: 9AK, 9CL, 9IN.

HOSIEOCRINUS

Hosieocrinus caledonicus (Wright, 1936); Wright, 1952a, p. 137. Occurrence: 9ST.

HYDREIONOCRINUS

- *Hydreionocrinus formosus* Wright, 1939; Wright, 1951b, p. 89. Occurrence: 9SM.
- *Hydreionocrinus amplus* Wright, 1951b, p. 84. Occurrence: 9IN, 9RS.

HYPSELOCRINUS

Hypselocrinus ardrossensis Wright, 1951a, p. 33. Occurrence: 8ES.

IDOSOCRINUS

Idosocrinus bispinosus Wright, 1954b; Wright, 1960, p. 332. Occurrence: 8/9TH.

Idosocrinus tumidus Wright, 1954b; Wright, 1960, p. 332. Occurrence: 8LB.

LANECRINUS

Lanecrinus (né Decadocrinus) fifensis (Wright, 1934); Wright, 1951b, p. 59, n. comb. Occurrence: 9CL, 9IN, 9RS.

This is a *Lanecrinus* as it has three anals, primibrachial one axillary, 10 arms, and zig-zag brachials, all characters of the genus (Kammer & Ausich 1993). It is very similar to *L. fountainensis* (Worthen 1882) from the Genevievian, lower Monteagle Limestone (Burdick & Strimple 1982, p. 117). These two species are both from the Brigantian and may even be conspecific. The small size of *L. fifensis* strongly suggests these are juveniles, so the elongated brachials may be a juvenile feature.

MANTIKOSOCRINUS

Mantikosocrinus wrighti (Yakovlev & Ivanov, 1956), Wright, 1952a, p. 111 as *Dicromyocrinus geminatus* (Trautschold, 1867). Occurrence: 8SA.

According to Moore *et al.* (1978), *Dicromyocrinus geminatus* (Trautschold) of Wright (1952a) equals *D. wrighti* of Yakovlev and Ivanov, which Strimple (1966) referred to *Mantikosocrinus*, a genus that also occurs in the Chesterian of the USA.

OPHIUROCRINUS

Ophiurocrinus? arbiglandensis (Wright, 1934); Wright, 1950, p. 22. Occurrence: 8AS.

This does have some of the characters of *Ophiurocrinus*, including five atomous arms, but the cup is low conical/high bowl-shaped rather than high conical as typical for the genus. The brachials are also cuneate rather than rectangular. Wright (1950) stated that the posterior is normal with three anal plates, but the holotype does not have the posterior exposed. Thus, this species is questionably assigned to *Ophiurocrinus*. It also resembles *Gilmocrinus* with the arms being similar to *G. dactyloides* in Ausich &

Sevastopulo (2001, pl. 10, figs 2, 7, 8), but the cup is not high conical as in *Gilmocrinus*.

PARAZEACRINITES

Parazeacrinites konincki (Bather, 1912); Wright, 1952a, p. 107.
Occurrence: 9AB, 9BE, 9BF, 9BG, 9BH, 9CH, 9CL, 9CS, 9CT, 9CU, 9CW, 9DA, 9DL, 9HO, 9IN, 9KK, 9MB, 9OB, 9OM, 9PP, 9RH, 9RS, 9RY, 9TS.

PEDINOCRINUS

Pedinocrinus clavatus (Wright, 1937); Wright, 1951b, p. 77. Occurrence: 9RS.

PELECOCRINUS

Pelecocrinus (né Poteriocrinites?) magnus (Wright, 1937); Wright, 1950, p. 9, n. comb. Occurrence: 9CH, 9HM, 9IN, 9RS, 9ST.

This species consists of large, thin, isolated cup plates of an advanced cladid as shown by the angustary radial facets with a distinct fulcral ridge. The thin plates are unlike *Poteriocrinites*. The thin plates and angustary facets are similar to *Parisocrinus* and *Pellecrinus*, but these genera lack a distinct fulcral ridge. Instead, the radial facets are very similar to *Pelecocrinus fiscellus* (Meek & Worthen 1870) from the Tournaisian Burlington Limestone of Iowa, and the cup plates are similar to *Pelecocrinus insignatus* Kirk, 1941 also from the Burlington Limestone. This is apparently the youngest occurrence of *Pelecocrinus*.

PHANOCRINUS

- Phanocrinus ardrossensis (Wright, 1934); Wright, 1951b, p. 97. Occurrence: 8AR, 8ES.
- *Phanocrinus calyx* (M'Coy, 1849); Wright, 1951b, p. 94. Occurrence: 9AK, 9BG, 9BH, 9CC, 9CH, 9CU, 9CW, 9DA, 9DL, 9IN, 9LM, 9PL, 9PP, 9RS, 9RY, 9ST, 9TS.
- *Phanocrinus scoticus* (de Koninck, 1858); Wright, 1951b, p. 96. Occurrence: 9LM.
- *Phanocrinus gordoni* Wright, 1939; Wright, 1951b, p. 99. Occurrence: 9CL, 9IN, 9OM, 9ST.
- *Phanocrinus stellaris* (Wright, 1934); Wright, 1951b, p. 98. Occurrence: 9CH, 9IN, 9RS, 9SM, 9ST.
- *Phanocrinus? altus* Wright, 1942; Wright, 1951b, p. 101. Occurrence: 9CL.

RHABDOCRINUS

- Rhabdocrinus pentonensis (Wright, 1937); Wright, 1950, p. 16. Occurrence: 9PL.
- Rhabdocrinus scotocarbonarius (Wright, 1937); Wright, 1950, p. 13. Occurrence: 9BA, 9BH, 9CH, 9CW, 9IN, 9KN, 9LM, 9RS, 9ST.

SCOTIACRINUS

- Scotiacrinus ardrossensis Wright, 1945; Wright, 1951b, p. 76. Occurrence: 8AR.
- Scotiacrinus tyriensis (Wright, 1937); Wright, 1951b, p. 75. Occurrence: 9IN, 9RS.

SCYTALOCRINUS

Scytalocrinus seafieldensis Wright, 1948; Wright, 1951a, p. 34. Occurrence: 9ST.

TUBULUSOCRINUS

Tubulusocrinus (né Ureocrinus) doliolus (Wright, 1936); Wright, 1952a, p. 116; Kammer & Ausich, 2007. Occurrence: 8SA. This species has five atomous arms and a tubular, uncalcified anal sac (Kammer & Ausich, 2007). It has previously

been assigned to *Hydriocrinus*, then *Ulocrinus*, and finally *Ureocrinus* (Wright, 1952a). *Hydriocrinus* has an essentially identical cup, but it has more than five arms with bifurcations at primibrachial one or higher and is only known from the upper Carboniferous (Middle Pennsylvanian) (Moore *et al.* 1978, p. T643). *Ulocrinus* has a thick-plated conical cup and 10 arms, and is also only known from the Middle and Upper Pennsylvanian (upper Carboniferous) (Moore *et al.* 1978, p. T701). *Tubulusocrinus doliolus* is similar to *Ureocrinus bockschii*, (also from the Encrinite Bed at St Andrews) in having five arms (Wright & Strimple 1945). However, it is distinct in having a conical cup composed of thin plates, whereas *Ureocrinus* has a high-bowl, globose cup with thick plates, and is constricted at the top of the cup, rather than at the proximal primibrachials (Moore *et al.* 1978, p. T701).

TYRIEOCRINUS

Tyrieocrinus laxus Wright, 1945; Wright, 1952a, p. 117. Occurrence: 9CL, 9CT, 9DL, 9IN, 9RH, 9RS, 9ST.

UREOCRINUS

Ureocrinus bockschii (Geinitz, 1846); Wright, 1952a, p. 112. Occurrence: 8/9TH, 9AB, 9BE, 9BH, 9BR, 9BS, 9CB, 9CC, 9CL, 9CM, 9CO, 9CP, 9CQ, 9CR, 9CT, 9CU, 9CW, 9DA, 9DL, 9DO, 9GI, 9IN, 9KK, 9MB, 9OM, 9PL, 9RS, 9SH, 9SM, 9ST, 9TB, 9TQ, 9TS, 11GW.

WOODOCRINUS

- Woodocrinus gravis Wright, 1936; Wright, 1951b, p. 53. Occurrence: 9IN, 9RS.
- *Woodocrinus liddesdalensis* Wright, 1936; Wright, 1951b, p. 52. Occurrence: 9PL.
- Woodocrinus pentonensis Wright, 1951b, p. 56. Occurrence: 9PL.
- Woodocrinus whytei Wright, 1936; Wright, 1951b, p. 57. Occurrence: 9GW.

FLEXIBLES

- AEXITROPHOCRINUS
- Aexitrophocrinus jaekeli (Moore & Plummer, 1940); Wright, 1954a, p. 153; Moore, 1978, p. T195, fig. 165.1. Occurrence: 8AR.
- Aexitrophocrinus? strimplei (Wright, 1946); Wright, 1954a, p. 156; Webster, 2003. Occurrence: 9IN, 9MB, 9ST.
- This was a new combination by Webster (2003). This species is known only from cups with up to two primibrachials, the second being axillary. The cup is most similar to *Aexitrophocrinus* (Miss.) and *Synerocrinus* (Penn.). The CD basal extends to the top of the radials and even beyond in one specimen (Wright 1954a, pl. 43, fig. 15). The stem attachment area does not cover most of the basals. Because the arms are lacking on known specimens, this species is questionably placed in *Aexitrophocrinus*.

AINACRINUS

Ainacrinus smithi (Wright, 1934); Wright, 1954a, p. 151. Occurrence: 9AK.

AMPHICRINUS

Amphicrinus scoticus Springer, 1920; Wright, 1954a, p. 149. Occurrence: 9AB, 9AK, 9BA, 9BG, 9CH, 9CL, 9CU, 9DL, 9HM, 9IN, 9LD, 9RS, 9ST, 9TS.

ARTICHTHYOCRINUS

Artichthyocrinus springeri Wright, 1923; Wright, 1954a, p. 160. Occurrence: 9HM, 9IN, 9KK, 9RS, 9TL.

CALDENOCRINUS

Caldenocrinus curtus Wright, 1946; Wright, 1954a, p. 158. Occurrence: 9IN, 9RS, 9ST.

ENASCOCRINUS

Enascocrinus redesdalensis (Wright, 1952b); Wright, 1954a, p. 154. Occurrence: 8/9RD, 8/9TH.

MESPILOCRINUS

Mespilocrinus depressus Wright, 1936; Wright, 1954a, p. 180. Occurrence: 9KK, 9SM.

6. Appendix B

Mespilocrinus pringlei Wright, 1954a, p. 178. Occurrence: 9BS, 9CL, 9IN, 9KK, 9MB, 9SM.

ONYCHOCRINUS

- *Onychocrinus liddelensis* Wright, 1954a, p. 171. Occurrence: 9PL.
- *Onychocrinus wrighti* Springer, 1920; Wright, 1954a, p. 170. Occurrence: 9IN, 9KK.

WACHSMUTHICRINUS

Wachsmuthicrinus ponderosus Springer, 1920; Wright, 1954a, p. 166. Occurrence: 9VT.

Localities (61) in Scotland with reported crinoid crown and calyx occurrences with current county and approximate British Grid Coordinates. The number in the code is the age (Table 1). Genus richness in parentheses at the end of each locality name. 9GW and 11GW are the same locality but indicate the Lower Limestone Formation and the Upper Limestone Formation, respectively.

Locality		Current	British
Code	Locality	County	Grid
8AS	Arbigland shore, Solway Firth (1)	Dumfries and Galloway	NX 994 573
8AR	Ardross (6)	Fife	NO 509 004
8CH	Cove Harbour, Cockburnspath (1)	Scottish Borders	NT 786 716
8LB	Lothian Burn (1)	Midlothian	NT 247 664
8ES	shore between Elie and St Monance (3)	Fife	NO 512 008
8SA	St Andrews (3)	Fife	NO 513 169
9AB	Aberlady (3)	East Lothian	NT 465 798
9AM	Auchenmade (1)	North Ayrshire	NS 341 483
9AK	Auchenskeith (5)	North Ayrshire	NS 312 466
9BA	Bankend (3)	South Lanarkshire	NS 64 36
9BE	Beith (3)	North Ayrshire	NS 346 537
9BH	Bishop Hill (5)	Perth and Kinross	NO 185 040
9BG	Bogie: possibly Wester Bogie near Chapel? (3)	Fife	NT 248 934
9BF	Bowfield near Paisley (1)	Renfrewshire	NS 391 585
9BS	Broadstone near Beith (3)	North Ayrshire	NS 363 532
9BR	Brockley, Lesmahagow (2)	South Lanarkshire	NS 81 39
9BT	Brunston, Penicuik (1)	Midlothian	NT 235 605
9CB	Campbeltown (1)	Argvll and Bute	NR 721 206
9CM	Campsie (1)	Stirling	NS 582 821
9CL	Carlops (16)	Scottish Borders	NT 160 559
9CC	Catcraig, near Dunbar (2)	East Lothian	NT 715 72
9CH	Chapel (6)	Fife	NT 251 939
9CP	Chapel Point (1)	East Lothian	NT 741 758
9CT	Charlestown (5)	Fife	NT 060 835
9CW	Clatteringwell Quarry (5)	Fife	NO 188 037
9CR	Corrie Burn (1)	Stirling	NS 472 959
9CO	Cowdens (2)	Fife	NO 301 040
9CO	Crichton Quarry, Pathhead (2)	Midlothian	NT 395 641
9CÙ	Cults, near Pitlessie (5)	Fife	NO 347 084
9DA	Dalry (4)	North Ayrshire	NS 295 495
9DO	Dockra, Beith (1)	Avrshire	NS 373 534
9DR	Draffen (1)	East Ayrshire	NS 424 454
9DL	Duloch (6)	Fife	NT 134 855
9DU	Dunbar (3)	East Lothian	NT 686 787
9EL	Elie (1)	Fife	NT 503 998
9GI	Gilmerton (1)	City of Edinburgh	NT 295 685
9GW	Garpel Water, Muirkirk (4)	East Ayrshire	NS 690 255
9HM	Hairmyres (4)	South Lanarkshire	NS 602 537
9HH	Harelaw Hill (1)	Dumfries and Galloway	NY 428 794
9НО	Howwood (3)	Renfrewshire	NS 395 601
9IN	Invertiel (30)	Fife	NT 265 900
9KN	Kinnesswood (1)	Perth and Kinross	NO 181 034
9KK	Kirkcaldy (7)	Fife	NT 279 896
9LD	Ladeddie (2)	Fife	NO 443 120
9LM	Lesmahagow (4)	South Lanarkshire	MS 815 395
9MB	Macbiehill (6)	Scottish Borders	NT 185 515
9MD	Midton (1)	South Avrshire	NS 412 300
90M	Oxwell Mains near Dunbar (4)	East Lothian	NT 705 764
9PL	Penton Linns, Liddesdale (9)	Dumfries and Galloway	NY 431 772–NY 437 774

Locality		Current	British
Code	Locality	County	Grid
9PW	Poniel Water (2)	South Lanarkshire	NS 833 341
9PP	Potmetal Plantation NW of Kirkcaldy (3)	Fife	NT 235 918
9RS	Roscobie (22)	Fife	NT 091 930
9ST	Seafield Tower or Seafield Shore (14)	Fife	NT 280 885
9SK	Skateraw (1)	East Lothian	NT 735 752
9SM	St Monance (5)	Fife	NO 524 014
9TS	Teasses, near Largo (4)	Fife	NO 405 077
9TL	Thornliebank (1)	East Renfrewshire	NS 549 592
9TB	Tiel Burn, west of Kirkcaldy (1)	Fife	NT 245 901
9TQ	Trearne Quarry (1)	North Ayrshire	NS 373 533
9VT	Vale of the Tweed, between Roxburgh and Kelso (1)	Scottish Borders	NT 685 325
8/9TH	Thornton Burn (5)	East Lothian	NT 739 740
11GW	Garpel Water, Muirkirk (4)	East Ayrshire	NS 690 255

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ty	Grid	
1 Lanarkshire	NS 833 341	
	NT 235 918	
	NT 091 930	
	NT 280 885	
Lothian	NT 735 752	
	NO 524 014	
	NO 405 077	
Renfrewshire	NS 549 592	
	NT 245 901	
n Ayrshire	NS 373 533	
al Dandam	NT 605 225	

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MS received 19 May 2006. Accepted for publication 14 May 2007.