

Dawsonia Nicholson: linguliform brachiopods, crustacean tail-pieces and a problematicum rather than graptolite ovarian vesicles

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ABSTRACT: Though little is known of the graptoloid reproductive mechanism, graptolites with putatively sac-like appendages, supposedly ovarian vesicles, have been known from the Moffat Shales Group, Southern Uplands, Scotland, for over 150 years. Locally, these co-occur with isolated, two-dimensional, discoidal or ovato-triangular fossils. In the 1870s, Nicholson interpreted these isolated fossils as being graptoloid ‘egg-sacs’ detached from their parent and existing as free-swimming bodies. He assigned them to his genus *Dawsonia*, though the name was pre-occupied by a trilobite, and named four species: *D. campanulata*, *D. acuminata*, *D. rotunda* and *D. tenuistriata*. A reassessment of Nicholson’s type material from the Silurian of Moffatdale, Scotland, and from the Ordovician Lévis Formation of Quebec, Canada, shows that *Dawsonia* Nicholson comprises the inarticulate brachiopods *Acrosaccus? rotundus*, *Paterula? tenuistriata* and *Discotreta* cf. *levisensis*, the tail-piece of the crustacean *Caryocaris acuminata* and the problematic fossil *D. campanulata*. Though *D. campanulata* resembles sac-like graptolite appendages, morphometric analysis reveals the similarity to be superficial and the systematic position of this taxon remains uncertain. There is no definite evidence of either *D. campanulata* or sac-like graptoloid appendages having had a reproductive function.

KEY WORDS: Arenig, Llandovery, Canada, graptolites, Henry Nicholson, reproduction, Scotland, Silurian, taxonomy

Our knowledge of reproductive structures and strategies in the animal fossil record is sparse. Though reproductive organs are occasionally found, they usually require exceptional preservation for their true nature to be discerned (e.g. Siveter *et al.* 2003; Dunlop *et al.* 2004). Whilst a certain amount is known of the reproductive strategies and mechanisms of the pterobranch hemichordates (Gilchrist 1915; Stebbing 1970; Dilly 1973; Hutt 1991), the extant sister group of the graptolites (Kozłowski 1947, 1948; Towe & Urbanek 1972; Crowther 1978; Cameron 2005), little is known about reproduction in the graptolites themselves (e.g. Urbanek & Jaanusson 1974). Likewise, as little is known of the buoyancy mechanism employed by the graptoloids (Bates 1987), any putatively vesicular graptoloid tissues (e.g. Fig. 1d, f) tend to attract interest and debate (e.g. Underwood 1993; Rickards *et al.* 1994).

There are many gaps in our knowledge of the earliest developmental stages of the graptolites, especially surrounding the events prior to the dispersal of their prosiculae (cone-shaped larvae). Working on well-preserved material from the Tremadoc of Poland, Kozłowski (1948) showed clutches of eggs and embryos in the autothecae of benthic graptolites; similar structures have also been found in *Reticulograptus tuberosus*, a bushy tuboid graptolite from Gotland, Sweden



(Bulman & Rickards 1966). Unlike the graptoloids, benthic graptolites have two types of thecae. These differentiated thecae have been interpreted as sexual dimorphs, with the smaller bithecae housing the male zooid and the larger autothecae housing the female (Kozłowski 1948), though this has yet to be confirmed. Nevertheless, the loss of bithecae in the graptoloids may indicate that their reproductive strategy altered as they colonised the plankton (Hutt 1991), and neither eggs nor embryos have been found in graptoloid thecae. Some workers have suggested that the graptolite synrhabdosome may represent short-lived congregations of several colonies in sexual congress (e.g. Zalasiewicz 1984) or asexually developing supercolonies (Ruedemann 1947; Bulman 1970). However, the nature of synrhabdosomes remains enigmatic (cf. Rigby 1993; Underwood 1993; Gutiérrez-Marco & Lenz 1998).

In order to assess whether putatively vesicular graptoloid tissues played a role in reproduction, a thorough re-evaluation of sac-like graptolite appendages has been undertaken (Fig. 1d, f) and also a re-evaluation of *Dawsonia* Nicholson 1873 (Figs 1, 2 & 3), which was originally interpreted as being an ovarian vesicle of a graptoloid detached from its parent colony. Though this genus has a long history of research, it has ‘caused confusion ever since it was first described’ (Williams

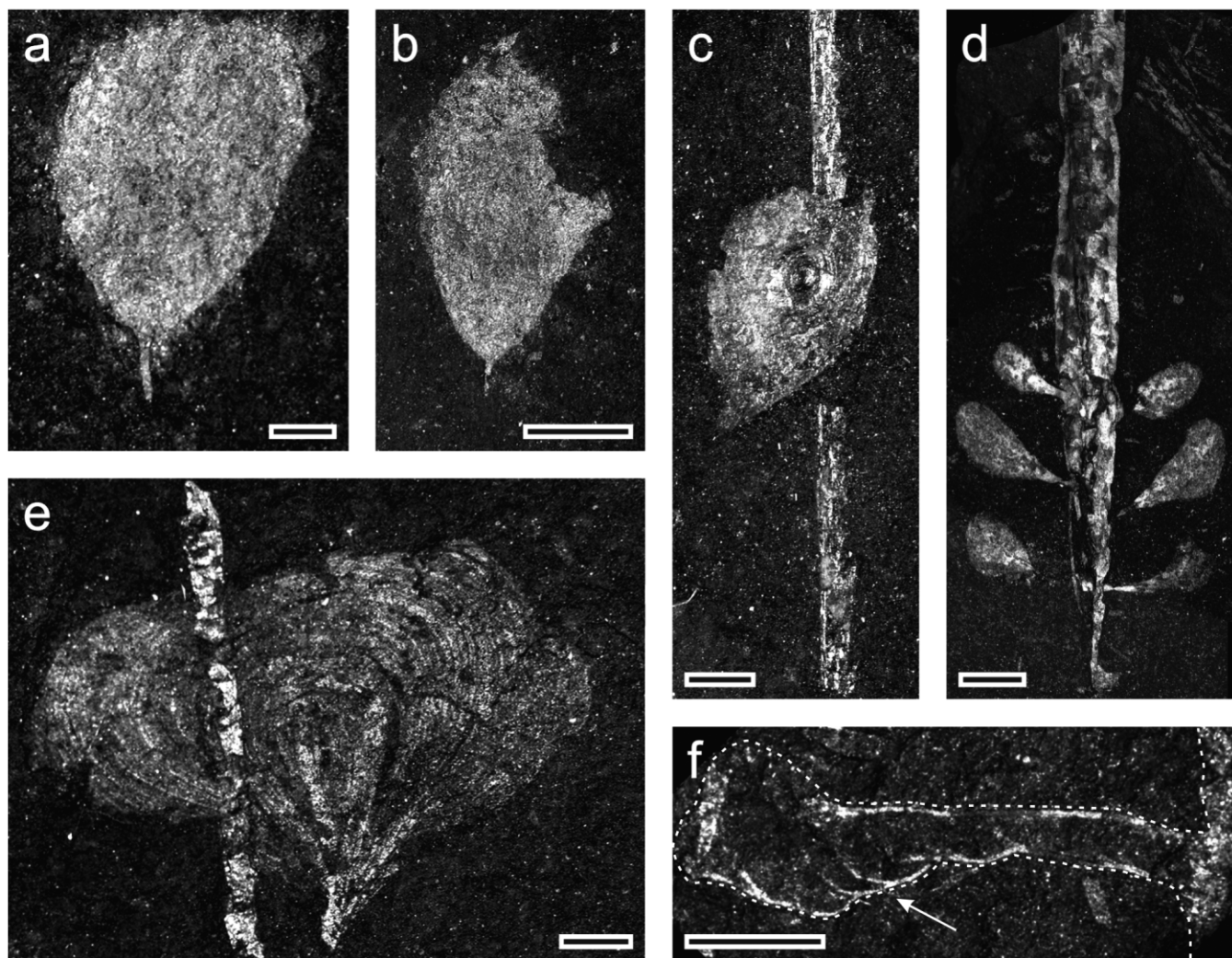


Figure 1 (a–c) *Dawsonia campanulata* Nicholson 1873 and (d–f) graptolites with appendages from Dob’s Linn, Birkhill Shale Formation: *D. campanulata* (a) lectotype, NHM QQ 253; (b) syntype, NHM QQ 254; (c) exhibiting a prominent ‘nipple’ and juxtaposed to an indet. monograptid, though preserved on a different sedimentary lamina, NHM QQ 255; (d) *Dittograptus?* sp. (Elles 1940) with well-preserved scopulae (‘graptogonophores’), SM A13731; (e) nemal vane of *?Pribylograptus incommodus* (Törnquist 1899) cf. Crowther (1978) overlain by indet. graptolite, see also Fig. 2h, NHM QQ 251; (f) detail of poorly-preserved scopula (‘graptogonophore’) of *Hallograptus bimucronatus* (Nicholson 1869): the paddle-shaped scopula (highlighted by dashed line), showing well-delineated proximal and distal margins with ‘branching’ structures (e.g. at arrow) representing concentric ?growth increments, scopula protrudes from the graptolite’s stipe at the right hand side of the image, BU 1420. All specimens photographed under reflected light. Nicholson’s specimens (a–c, e). Scale bar=1 mm (a–c, e–f); 500 μ m (d).

1981). This paper initially establish the context in which the fossils were originally interpreted and how they have been subsequently reinterpreted, prior to re-evaluating them based on original material and new specimens.

1. History of research

Prior to Kozłowski’s seminal monograph of 1948, the zoological affinities of the graptolites attracted much debate. They were initially thought to be a moss (von Bromell 1727), to be artefacts (Linnaeus 1768), or even, as Nimmo (1847) suggested, the tail spines of the Indian Ocean ray *Raja pastinaca*, though Nimmo had probably never seen a graptolite (Elles & Wood 1901–1918, p. xiii). Eventually, graptolites were recognised as colonies consisting of a series of cup-shaped orifices (thecae) and they were variously assigned to the Cnidaria and Bryozoa (see summaries in Elles & Wood 1901–1918; Kozłowski 1948; Crowther 1978). As the reproductive strategies employed in these groups differ considerably, no small

part of the discussion of their systematic position focused on the interpretation of rare, attached, putatively sac-like appendages (e.g. Nicholson 1872; Ulrich & Ruedemann 1931).

1.1. 1850–1870: sac-like appendages and ‘graptogonophores’

Graptolites bearing sac-like appendages have been known since the 1850s, but due to ‘various [unspecified] accidental difficulties’ (Logan *in* Hall 1865 and references therein) illustrations were not published until the next decade. These sac-like appendages were called ‘graptogonophores’ by Nicholson (1866) whilst Elles (1940) referred to ‘scopulae’ as a specific type of graptogonophore. Subsequently Bulman (1970, V11) stated that scopulae were composed of ramifying fibres rather than being sac-like, a definition echoed in Palmer & Rickards (1991). However, this term has also been recently used to refer to seemingly sac-like appendages (e.g. Bates & Kirk 1991). Detailed examination of *Hallograptus* spp. (including many specimens from the above works) shows that these

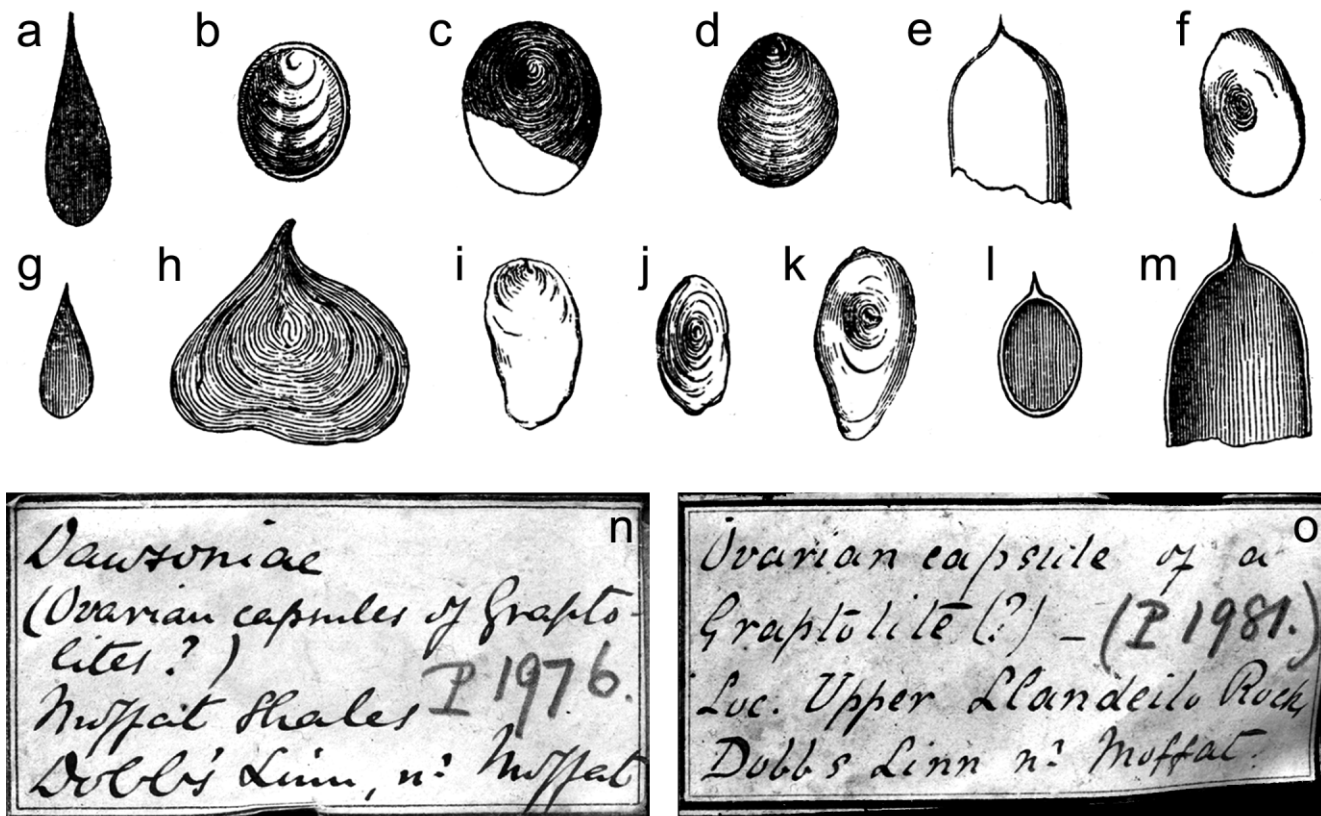


Figure 2 Nicholson's illustrations of supposed graptolite ovarian capsules, including (a–f) his *Dawsonia* type specimens (Nicholson 1873): (a) *D. acuminata*; (b) *D. rotunda*; (c–d) *D. tenuistriata*; (e–f); *D. campanulata*; (g–m) from Nicholson (1872; Fig. 41); (n–o) Nicholson's handwritten specimen labels, NHM.

appendages were originally composed of thin periderm and may have a sac-like appearance, although poorly preserved specimens may give the impression of being composed of ramifying fibres (AAP unpublished observations). The terms scopulae and graptogonophores are therefore used as synonyms, referring to the stalked sac-like appendages that are discussed in this paper (e.g. Fig. 1d, f).

Hall (1865) proposed that these sac-like appendages were reproductive bodies similar to hydrozoan gonothecae, and suggested that graptolites were closely related to the sertularians. It seems Hall's work captured the imagination of the young H. Alleyne Nicholson: Hall's monograph was likely used by Nicholson to aid the identification of the graptolites he collected in the Southern Uplands. Indeed, Nicholson (1866, 1872, 1873) regularly referred to Hall's work on graptolite reproduction.

Whilst collecting the Silurian strata of the Southern Uplands in the summer of 1866, Nicholson discovered a variety of discoidal and ovato-triangular fossils associated with graptolites (Fig. 2). Though not found attached to graptolites themselves, these fossils resemble the supposed reproductive organs described by Hall (1865), and Nicholson (1866) argued that they represented graptolite ovarian vesicles which had detached from their parent colony, and called them 'graptogonophores'. He supported Hall's argument for a hydroid affinity for the graptolites, suggesting that the concentrically 'ribbed' discoidal specimens represented vertical compressions of a sertularian-like graptogonophore, and that the ovato-triangular specimens were preserved in profile. Nicholson supported his interpretation by illustrating several examples where the discoidal and ovato-triangular specimens were closely associated with graptoloids (e.g. Fig. 1c).

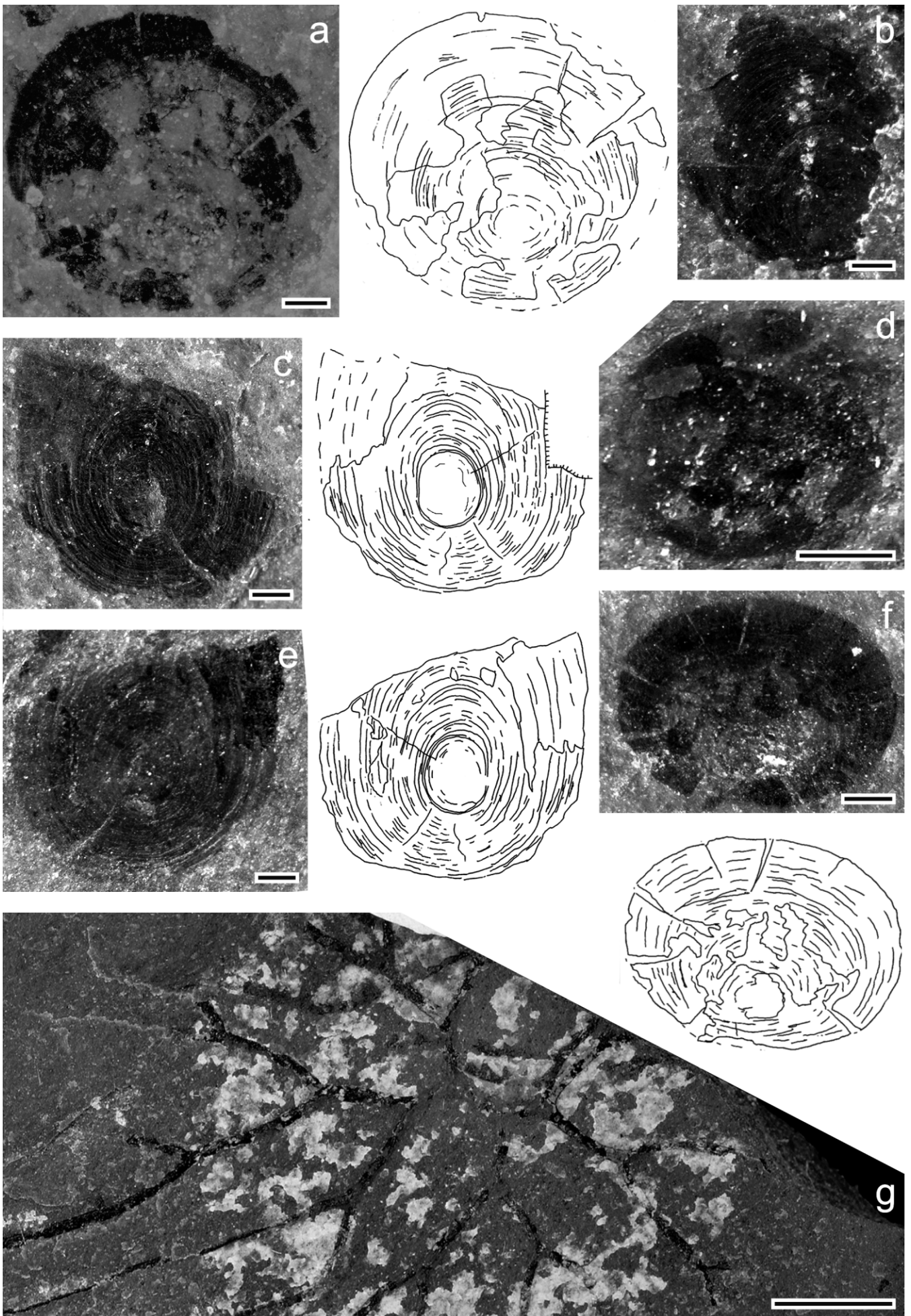
However, this work was controversial, drawing a vociferous reply from William Carruthers who argued that the associ-

ations of the supposed graptogonophores with graptolites were no more than fortuitous juxtapositions, and that the discoidal specimens most likely represented the brachiopod *Siphonotreta micula* (Carruthers 1867a). This precipitated a lengthy correspondence, with Nicholson (1867a, b, c, 1868b) arguing that graptolites were hydrozoans largely on the basis of their reproductive strategy, whilst the more vehement Carruthers (1867b, c, 1868a, b) stated that considerations of zoological position should be based on 'normal' characters such as colony construction rather than on rare and ambiguous evidence. The latter felt that whilst graptolites were closely allied to the Hydrozoa, they also shared characters with the Polyzoa. As much by perseverance as by any tendency to provide new information, Nicholson's view that graptolites were extinct hydrozoans became more widely accepted. Nicholson's work subsequently focused more on corals than graptolites (see Benton 1979); and, at this time, graptolite research itself also moved away from theoretical discussions of their affinity, with workers such as Lapworth focusing on the more practical concerns of taxonomy and biostratigraphy (e.g. Elles & Wood 1901–1918; Oldroyd 1990; Rushton 2001).

1.2. 1870–1900: Graptolite reproduction and *Dawsonia* Nicholson

Nicholson's theory of graptolite reproduction supposed that once sufficiently mature, the 'graptogonophore' detached itself from its connection with the parent colony and became a free-swimming zooid (Nicholson 1868a). This assertion was supported in part by evidence of the co-occurrence of 'graptogonophores' and graptolites with ramifying fibres (e.g. Fig. 1f) in the same strata (Nicholson 1872).

Nicholson (1873) noted that there were several distinct types of graptogonophore in the Ordovician Lévis Fm. at Point Lévis, Quebec. As it would be almost impossible to relate these



back to the individual graptolite species they came from, he referred them to the form genus *Dawsonia*, much in the manner that one names ichnotaxa independently of the animal that constructed them. Nicholson (1873) named four species: *D. acuminata*, *D. rotunda*, *D. tenuistriata*, and *D. campanulata*. Gurley (1896), also working in Point Lévis, added two further species: *D. monodon* and *D. tridens*.

These species have disparate temporal and geographical ranges. *D. campanulata* is only known from Early Silurian strata of the British Isles (Nicholson 1873; Lapworth 1876, 1876–77; Marr & Nicholson 1888; Peach & Horne 1899; Williams 1981, 1996), though it occurs in both Laurentia (in Moffatdale, Scotland, and Coalpit Bay, Donaghadee, Northern Ireland) and Avalonia (the English Lake District), which were on either sides of the Early Palaeozoic Iapetus Ocean at this time. *D. rotunda* and *D. tenuistriata* are only found in the Ordovician Quebec Group at Point Lévis, Canada (Nicholson 1873), and Gurley's species have only been recorded in the Ordovician of North America at Point Lévis, Quebec, and the Deep Kill, near Melrose, New York (Ruedemann 1904, 1934; Vannier *et al.* 2003). However, *D. acuminata* appears to be more cosmopolitan, with Nicholson (1873) stating that it occurs at both Point Lévis, Canada, and in northern England. Nicholson (1873) noted that his concept of *D. acuminata* was similar to *D. campanulata* in both stratigraphic range and form, though he acknowledged that its outline was notably more triangular and its mucro (proximal termination) less sharply delineated.

Nicholson (1873) believed that his localities in the UK and Canada were contemporaneous and of similar age to graptolites bearing sac-like appendages (Hall 1865; Nicholson 1872). Graptolite biostratigraphy now reveals this to be untrue (cf. section 4): *D. campanulata* is from Llandovery strata whilst the Point Lévis species co-occur with the Early Ordovician graptolite *Clonograptus* sp. (Fig. 3g). However, in the 1870s the age of the strata in the Southern Uplands sections was somewhat of an enigma (Oldroyd 1990; Rushton 2001), making correlation with North American sections problematic.

1.3. Twentieth century work on graptolite reproduction

The 20th century saw graptolite reproduction become a less prevalent area of research, and since a pterobranch affinity for graptolites has been clearly demonstrated (Kozłowski 1947, 1948; Towe & Urbanek 1972; Crowther 1978), Nicholson's work has become largely overlooked. However, biserial graptoloids with sac-like appendages unquestionably attached to their rhabdosome continued to be described as reproductive structures in the early twentieth century (e.g. Elles 1940). Likewise, Ulrich and Ruedemann (1931) reported dendroid graptolites with swollen, oval appendages purportedly homologous with bryozoan oecia. However, these correspond to bithecae in terms of position and arrangement, and the specimens are too poorly preserved to discern their precise nature (Kozłowski 1948).

The discovery of eggs and embryos inside the autothecae of benthic graptolites (Kozłowski 1948; Bulman & Rickards 1966) led to a reinterpretation of sac-like appendages in graptolites. Kozłowski (1948) considered Hall's supposed 'egg sacs' to be chitinous envelopes associated with the zooids,

though he did not speculate on their function, whilst Bulman (1964) figured several similar specimens in an early discussion of graptolite hydrodynamics. Similarly, more recent discussions of graptolite reproduction have not addressed these and other supposed reproductive organs (e.g. Crowther 1978; Hutt 1991; Underwood 1993). For example, the branching appendages described in Ruedemann (1936) were thought to represent epibionts (Kozłowski 1948). The swollen, oval appendages documented by Ulrich & Ruedemann (1931) might also be epibionts: Kozłowski (1965) showed that *Cephalocystis graptolithifilius*, a similar structure found on other graptolites, is in fact a cephalopod egg capsule comparable to those of the recent *Sepia officinalis* which encrusts the sea grass *Zostera*. Similarly, Underwood (1993) suggested that putative cases of connection between graptogonophores and graptolites as illustrated by Nicholson (1866), could plausibly represent parasitic outgrowths or epizoans colonising a graptolite 'benthic island' *sensu* Kauffmann (1978).

However, these and other examples of sac-like graptoloid appendages (Fig. 1d, f) are certainly distinct from the unambiguous parasites figured by Bates & Loydell (2000), but superficially similar in form and preservation to *D. campanulata* and *D. acuminata*. As such they require re-examination. Since Kozłowski's influential work, 'graptogonophores' have generally been described as sac-like or vane-like appendages with little comment as to their function (e.g. Bulman 1964; Koren & Rickards 1997).

1.4. A pterobranch-like model for graptolite reproduction?

Since scanning electron microscopy has been employed for studies of graptolite ultrastructure (e.g. Towe & Urbanek 1972; Crowther 1978, 1981), an affinity for graptolites with the pterobranch hemichordates has become widely accepted (e.g. Dilly 1993; Cameron 2005; Maletz *et al.* 2005). As such, recent discussions of reproduction in graptolites (e.g. Hutt 1991) have been premised on the belief that graptolites adopt pterobranch-like reproductive mechanisms (cf. Gilchrist 1915; Stebbing 1970).

The pterobranchs *Rhabdopleura* and *Cephalodiscus* reproduce both sexually and asexually (Hutt 1991). Though most zooids in *R. compacta* are neuter or sexually immature, certain zooids may metamorphose and develop either an ovum or testis (Stebbing 1970). Whilst the sexes are separate in *Rhabdopleura*, some species of *Cephalodiscus* colonies may be hermaphroditic, with certain zooids bearing both male and female reproductive organs (Horst 1939; Bulman 1970). Though its colonies are sessile and its zooids have limited movement, *Rhabdopleura* undergoes internal fertilisation, with its oviduct serving only as a conduit for sperm to reach the ova (Stebbing 1970). In both *Rhabdopleura* and *Cephalodiscus*, clutches of embryos remain in the creeping tube until they mature as ciliated, lecithotrophic larvae (Dilly 1973; Lester 1988a). The larva leaves the creeping tube as a free-swimming individual which secretes a collagenous, dome-shaped prosiculum (Dilly 1973; Dilly & Ryland 1985). Later, the larva metamorphoses under the prosiculum and emerges as a juvenile (Dilly & Ryland 1985; Lester 1988b) that settles on the substrate and later asexually buds to form a colony (Stebbing

Figure 3 (a–f) Linguliform brachiopods with camera lucida interpretations and (g) graptolite, from the Lévis Shale, Point Lévis, Quebec, Canada. (a–b, d) *Acrosaccus? rotundus* (Nicholson 1873): (a) pedicle valve, NHM BC 58609; (b) dorsal valve, NHM BC 58606; (d) lectotype, NHM BC 58598. (c, e) *Paterula? tenuistriata* (Nicholson 1873): (c) lectotype, NHM BC 58594; (e) counterpart NHM BC 58592. (f) *Discotreta cf. levisensis* (Walcott 1908), NHM BC 58614. (g) *Clonograptus* sp., NHM QQ 252. All specimens photographed under reflected light and are from Nicholson's material. All scale bars = 500 µm.

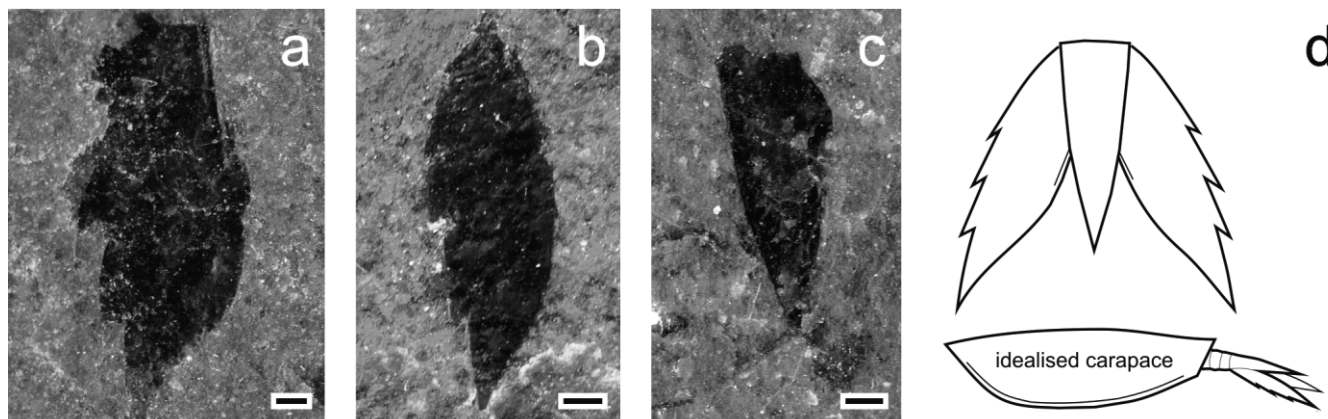


Figure 4 *Caryocaris acuminata* (Nicholson 1873) from the Lévis Shale, Point Lévis, Quebec, Canada. (a) Furcal ramus, lectotype NHM IC 495; (b) furcal ramus, NHM IC 457; (c) telson, NHM IC 474; (d) a reconstruction of the tail-piece and the whole animal (note schematic carapace). All specimens photographed under reflected light. Scale bars=500 µm.

1970; Dilly 1973). A recent study of *R. compacta* has shown that the taxon adopts a seasonal breeding strategy with peak reproduction occurring in the summer (Sato 2008).

Though there is little direct evidence of reproduction in the graptolite fossil record (cf. Hutt 1991), eggs and embryos have been reported in certain specimens (Kozłowski 1948; Bulman & Rickards 1966). This would be consistent with graptolites producing a free-swimming lecithotrophic larva, that later secretes a prosicula (equivalent to the pterobranch prosiculum) in the plankton before maturing (cf. Williams & Clarke 1999) and budding to form a colony.

1.5. Historical interpretations of *Dawsonia* Nicholson

1.5.1. *D. monodon*, *D. tridens*, *D. acuminata*, and *D. campanulata*: crustaceans, molluscs or algae? These mucronate species have received more attention than the other species, which are dealt with below. *D. monodon* and *D. tridens* were originally described by Gurley (1896), but have long been considered to be tail-pieces of the crustacean *Caryocaris* (Ruedemann 1934; Rolfe in Theokritoff 1964). Rolfe (1969, p. 316) stated that *Dawsonia* Nicholson is a junior synonym of *Caryocaris* Salter (1863), but did not re-examine Nicholson's material (Ian Rolfe, pers. comm. 2005). Though *D. acuminata* (Fig. 4) has all but vanished from the literature, *D. campanulata* is often used (see section 4).

In the catalogue of fossils from western Scotland, Lapworth (1876) considered *D. campanulata* to be a crustacean, perhaps due to its similarity and common co-occurrence with the putative crustaceans *Aptychopsis* Barrande (1872), *Peltocaris* Salter (1863), and *Discinocaris* Woodward (1866) (Lapworth 1876, 1876–77; Marr & Nicholson 1888; Peach & Horne 1899). These putative crustaceans look similar to certain species of *Dawsonia*: disarticulated valves of *Peltocaris* and *Aptychopsis* are similar to *D. campanulata* in outline, and *Discinocaris* has an ornament similar to that of *D. rotunda* and *D. tenuistriata*. However, none of the material examined in this study bears the characteristic dovetail symmetry that characterises complete specimens of these other taxa. Gürich (1928) also compared *D. campanulata* to *Peltocaris*, which he considered to be the covers of a hyolithid or chiton-like organism. However, this work offered no firm conclusions as to the affinities of *Dawsonia* Nicholson and the present authors have found no evidence of either hyolithids or chitons co-occurring in the same strata as it.

The affinities of *Aptychopsis*, *Peltocaris*, and *Discinocaris* remain uncertain. Rolfe (1969, p. 328) noted that 'they have been compared and confused with graptolite "swim bladders'

and "gonangia", eurypterid metastomata, hyolith opercula, polyplacophoran plates, bivalves, arthodire dermal plates, and brachiopod carapaces', and he noted there was no evidence to support an affinity for either *Aptychopsis*, *Peltocaris*, or *Discinocaris* with the phyllocarids. Rolfe (1969, pp. 328–329) suggested that these taxa may perhaps represent the aptychi of soft-bodied cephalopods rather than being crustacean carapaces. However, he did not go as far as synonymising *Aptychopsis*, *Peltocaris*, and *Discinocaris* with the aptychus morpho-genus *Sidetes* Giebel *sensu* Moore & Sylvester-Bradley (1957).

There is no good reason to group *D. campanulata* with these supposed aptychi. Indeed, neither Gürich's (1928) work nor a crustacean affinity gained serious consideration in the most recent re-examination of *D. campanulata*, which tentatively reinterpreted it as an alga (Williams 1981).

1.5.2. *D. rotunda* and *D. tenuistriata*: possible brachiopods?

Neither *D. rotunda* nor *D. tenuistriata* are mucronate; together they form a group of small, subcircular shelly fossils. Though Nicholson (1873) stated that *D. rotunda* and *D. tenuistriata* appeared too variable in form and appearance to be inarticulate brachiopods, this assertion was questioned from the outset (Carruthers 1867a; Ruedemann 1904, 1934). More recently, Benton (1979) noted that some of Nicholson's type material may be small brachiopods.

1.5.3. Misidentifications. Several incompatible forms have been erroneously assigned to *Dawsonia* Nicholson, principally because little or no reference was made to the type specimens. As Benton (1979) noted, the trace fossil *Lockeia* U. P. James (1879) was misdiagnosed as *Dawsonia* by U. P. James's son, J. F. James (1885, 1892). As *Dawsonia* is a body fossil, this name clearly cannot be applied to a trace fossil (Häntzschel 1965, 1975; Osgood 1970). However, the name '*Dawsonia cycla*' is still used for another fossil from the Cincinnati area which consists of small, black, shiny discs that are found encrusting the surfaces of nautiloid conchs. Though Frey (1989) thought that these discs may represent the attachment sites of the dendroid graptolite *Mastigograptus*, they are now thought to represent the epibiont *Sphenothallus* (Neal & Hannibal 2000).

1.6. The current status of *Dawsonia* Nicholson

The name '*Dawsonia*' is still widely used by graptolite workers (e.g. Williams 1996), though now it is almost exclusively used as shorthand for *D. campanulata*, which is its type species (Miller 1889). No consensus as to its taxonomic status or systematic position has yet emerged. Though the genus

Dawsonia was conceived to describe the egg sacs of a sertularian-like hydroid, this name has been applied to unrelated fossils from all of the major divisions of the bilateria. Its type species, *D. campanulata* was most recently interpreted as an alga (Williams 1981). *Dawsonia* Nicholson (1873) is a junior homonym of the trilobite *Dawsonia* Hartt in Dawson (1868) and a thorough treatment of this trilobite can be found in Axheimer (2006). Though the name *Dawsonia* Nicholson is therefore invalid, for the sake of simplicity we use the name *Dawsonia* to refer to Nicholson's genus rather than to the trilobite throughout this paper. Thus, it seems clear that *Dawsonia* Nicholson is in need of taxonomic revision.

2. Material and methods used in this study

2.1. Nicholson's types and comparative material

Much of Nicholson's type and figured material is housed in the Natural History Museum [NHM], London, which purchased a collection of 1400 graptolites from Nicholson in 1883 (Benton 1979). Much of the remaining portion of Nicholson's collection is held in the Aberdeen University Geology Department (Benton & Trewin 1978; Benton 1979). Nicholson's material from the Lake District lies in the Harkness and Marr collections of the Sedgwick Museum, Cambridge [SM].

The type material of *Dawsonia* Nicholson, as recognised by Benton (1979), is in the G. J. Hinde collection of the NHM, although some topotype and comparative material remains in the Aberdeen University Geology Department [AUGD]. All this material has been re-examined and the NHM material has been re-accessioned as part of this study. Nicholson did not identify any specimens from UK strata in this collection as *D. acuminata*, despite mentioning its occurrence in northern England (Nicholson 1873). Given that Nicholson's illustrations are often idealised woodcuts taking features from several specimens (Benton & Trewin 1978), it has been impossible to precisely determine his type specimens. However, as Nicholson's diagnoses can be recognised from his distinctive handwriting on the manuscript specimen labels (Fig. 2n, o), we have assigned lectotypes for each of his four species. *D. campanulata* remains the type species of the genus (subsequent diagnosis, Miller 1889 *contra* Ruedemann 1904, 1934). Other comparative material is housed in the British Geological Survey [BGS] collections at Keyworth, near Nottingham, the Ulster Museum, Belfast [BEL] and in the Lapworth Museum, University of Birmingham [BU].

In order to compare *Dawsonia* with the sac-like appendages of graptolites, an extensive search of museum holdings and appropriate literature was undertaken. *D. campanulata*-bearing localities in Moffatdale, southern Scotland and the Lake District of England were also re-collected to provide an unbiased sample of this species. It was not possible to collect field specimens of graptolites bearing sac-like appendages, perhaps due to their relative rarity, and museum collections are therefore relied upon entirely for such graptolites.

In addition to the occurrences of *Dawsonia* Nicholson noted in section 1.2 and above, Ruedemann (1904, p. 739) commented that '[*D. campanulata*] is very common in the Trenton (Normanskill) graptolite shales of New York and Canada.' However, this fossil could not be identified amongst Ruedemann's original collections, although there are plenty of graptolites bearing 'graptogonophores' in his material. In addition, Ruedemann (1908) reported that in 1889, H.M. Ami named three new species of *Dawsonia* from graptolitic strata in the St Lawrence region of Canada. However, no trace has been found of Ami's *Dawsonia* species in either the literature or in museum collections. Likewise, the present authors have been

unable to find Gurley's type specimens of *D. monodon* and *D. tridens*. Though they were once held in the collections of the New York State Museum, Albany, NY [NYSM] (Ruedemann 1934 & references therein), they are no longer in its possession. When Ruedemann (1904) illustrated *D. monodon* and *D. tridens* specimens from NYSM collections, he chose examples from the Quarry at the Deep Kill, near Melrose, New York, only copying Gurley's drawings of the Point Lévis material. This suggests that they were not in the NYSM at that time either. It may be that the specimens went missing at the very end of the 1800s when a long-term budget deficit led James Hall to sell many specimens to keep the Geological Survey and State Museum afloat (Ed Landing, pers. comm. 2004).

Though Ruedemann's (1904, 1934) material has been re-examined for comparative purposes, neither those specimens nor Nicholson's Point Lévis specimens clearly preserve the carapace. Given that *Caryocaris* taxonomy is primarily based on carapace morphology, it is not possible to determine whether Ruedemann's specimens are truly synonymous with Gurley's species. As such, this paper focuses on clarifying Nicholson's concept of the *Dawsonia* species rather than on entering the more nebulous realm of phyllocarid systematics.

2.2. Methods used and terminology employed

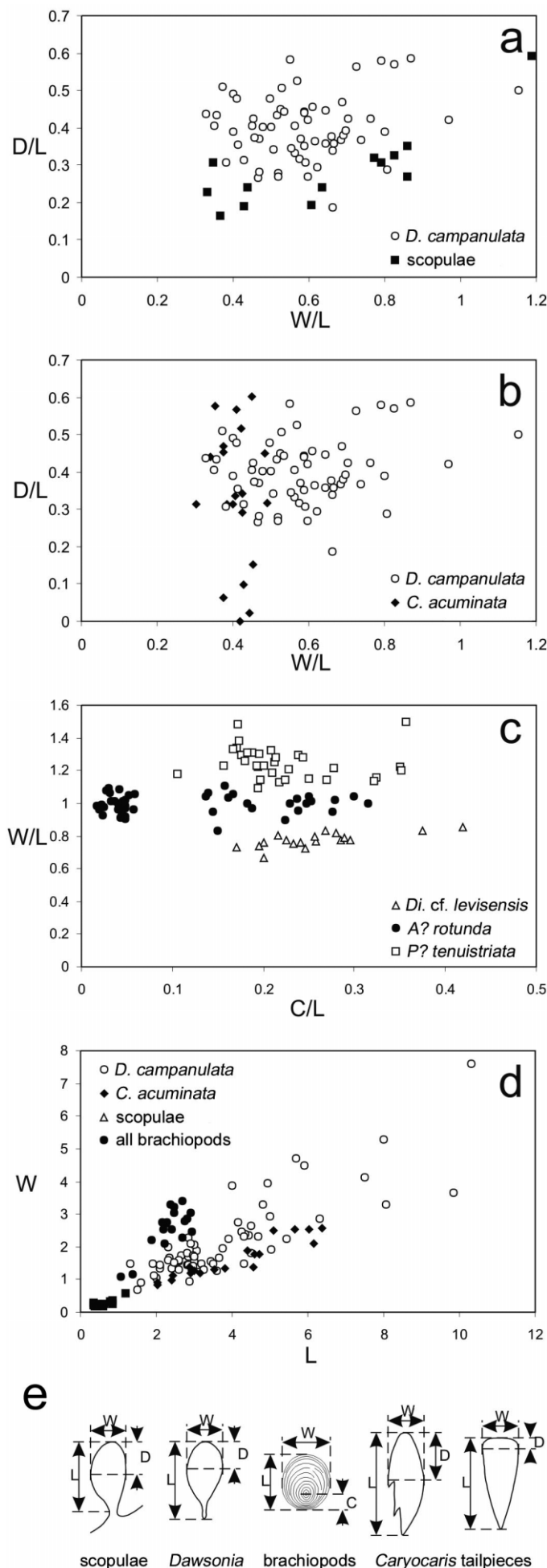
All fossils have been studied under reflected light microscopy. Additionally, uncoated specimens were examined at 15KV in backscatter mode in Hitachi S-3600N and LEO 435VP SEMs, with phases identified using energy dispersive X-ray analyses (EDS) using Oxford Instruments INCA and ISIS software, respectively. The electron microscope techniques used closely follow those described in Martill *et al.* (1992) and Orr *et al.* (2002). Illustrated images have been digitally enhanced to increase the contrast between fossil and matrix.

Details of repositories and specimen numbers are listed with the appropriate figures and in the systematic section; details of the criteria used in the morphometric analysis are given in Figure 5. As the brachiopod taxa were often incomplete, morphological measurements were taken on well-preserved growth-lines as well as on outlines, though in each case these are clearly distinguished in the appropriate figure caption. All measurements were made on camera lucida drawings of $\times 40$ or $\times 50$ optical magnification, and recorded to an accuracy of greater than one percent.

Morphological terms used in systematic descriptions are as employed in Holmer & Popov (2000) for the brachiopod species, in Rachebouef *et al.* (2000) and references therein for the *Caryocaris* tail-pieces, and defined in Figure 5 for *D. campanulata*. Because Nicholson's Point Lévis material consists entirely of disarticulated specimens, an assessment has been made as to which forms could plausibly conjoin, based on the present understanding of inarticulate brachiopods and of *Caryocaris*, in order to avoid unnecessary taxonomic inflation. Abbreviations used in the synonymy lists are those of Matthews (1973) and the qualifiers used in open nomenclature may be found in Bengtson (1988).

3. The nature of *Dawsonia* Nicholson

It is clear that *Dawsonia* Nicholson is polyphyletic. The lectotype of *D. acuminata* is a furcal ramus from the tail-piece of the crustacean *Caryocaris acuminata* (Fig. 4). Other fossils within the fauna include telsons and carapace fragments which are considered conspecific given the present understanding of *Caryocaris* morphology (Fig. 4d). The lectotypes of *D. rotunda* and *D. tenuistriata* are linguliform brachiopods (Fig. 3c, d) and have been tentatively re-assigned to the genera *Acrosaccus* and



Paterula respectively, and Nicholson's type collection also contains a form provisionally identified as *Discotreta* cf. *levisensis* (Fig. 3f). As no articulated specimens are present it cannot be unambiguously determine which shells articulated in life. However, two of the four discrete shell morphotypes shown in Figure 5c have indistinguishable outlines (with $W/L \sim 1$) and probably represent an unequivalved species. The other two shell morphotypes could not plausibly conjoin (cf. Fig. 5c), consistent with there being three species present in the collection. The systematic palaeontology of these taxa is dealt with in section 6.

The style of preservation of the above-listed *Dawsonia* species is different from that of the graptolite *Clonograptus* sp. which co-occurs in the Point Lévis fauna (Fig. 3g). This suggests that they were originally composed of non-graptolitic material. The graptolites are preserved as dull, black compressions, whereas the *Dawsonia* specimens are generally in relief, having a horny texture and some having a bronze, pyritous sheen. EDS analyses of the Point Lévis *Dawsonia* specimens reveals that they are preserved as phosphate with some associated pyrite (Fig. 6f, g). This composition is consistent with these taxa being linguliform brachiopods and caryocarid arthropods rather than graptolites, which are carbonaceous. Therefore, these species of *Dawsonia* are reassigned to their appropriate clades and can be discounted from any consideration of graptolite reproduction.

Though Nicholson (1873) mentioned the occurrence of *D. acuminata* in English strata, the present authors have been unable to identify it in UK collections. Morphometric analysis reveals that there is some overlap between *D. campanulata* and *C. acuminata* (Fig. 5b, d). However, even the most slender *D. campanulata* can be clearly distinguished from *C. acuminata* by the presence of a delineated mucro, its rounded latero-distal margin (Figs 1a–c, 4), and its composition (Fig. 6a–d). It therefore seems most likely that Nicholson was either referring to slender *D. campanulata* morphotypes as *D. acuminata*, or he was perhaps confusing the tail-pieces of *Caryocaris wrightii* which occur in strata of the British Isles (Rushton & Williams 1996; Vannier et al. 2003) with *C. acuminata*. To avoid unnecessary confusion, Nicholson's so-called *D. acuminata* from the British Isles has been included within the amended definition of *D. campanulata*, with *C. acuminata* only referring to his Canadian material.

There is little similarity between *D. campanulata* and *Caryocaris* tail-pieces (cf. Figs 1 & 4), or indeed with the *Dawsonia* species from Point Lévis, the most notable differences being in its composition and outline. It is preserved as an organic compression (Fig. 6a–d), unlike *Caryocaris*, which is preserved in phosphate (Fig. 6g). It is more symmetrical than either the carapace or furcal ramus of a *Caryocaris*, and notably more ovate than the *Caryocaris* telson. Its mucro is too centrally

Figure 5 Morphometric analyses. *Dawsonia campanulata* compared with (a) graptolite scopulae, and (b) the furcal rami and telsons (combined) of *Caryocaris acuminata*. (c) Morphometrics of brachiopod outlines and growth lines (combined) showing distinct populations corresponding to *Discotreta* cf. *levisensis*, *Acrosaccus? rotunda* (separate clusters reflect differences in beak position on dorsal and ventral valves) and *Paterula? tenuistriata*. (d) Absolute sizes (mm) of all of the above specimens. (e) Morphometric criteria: L = anterior-posterior length; W = lateral width; D = distance from blunt margin to centroid; C = distance from anterior margin to growth centre of brachiopod. *D. campanulata* specimens are those listed under additional material in Section 4; brachiopod and *Caryocaris* specimens are Nicholson's specimens from the Lévis Shale Fm., Point Lévis, Quebec, with specimen numbers listed in Section 4. Graptolite scopulae measurements based on those specimens illustrated in Ruedemann (1908), Elles (1940), Bates & Kirk (1991), Štorch (1994) and Koren' & Rickards (1997).

positioned to represent either an anterior horn or a postero-dorsal spine of the *Caryocaris* carapace, and it differs from the marginal spinules of the *Caryocaris* ramus in terms of size and position. Unlike a furcal ramus, the 'body' of *D. campanulata* is ovato-triangular rather than ovato-parallelogrammic, and it lacks a serrated lateral margin. Though lacking a mucro, the grossly teardrop form of the *Caryocaris* telson is similar in shape to *D. campanulata*. However, morphometric analysis (Fig. 5) reveals no overlap between *Caryocaris* telsons (where $D/L < 0.2$) and *D. campanulata* (where $0.2 < D/L < 0.6$).

Though *D. campanulata* shares a similar preservation style to the sac-like appendages seen in graptolites (Fig. 6a–e), there is no evidence to support a homology. Whilst both are found as silvery organic films in the black shales of the Southern Uplands, *Dawsonia* Nicholson cannot be recognised as a graptolite (Bulman 1970). Morphometric analysis reveals that the similarity between the two is superficial, with the graptolite appendages having a consistently more distal centroid (Fig. 5a). They are also more asymmetrical and more variable in their form than *D. campanulata*, and there is no discrete transition between their connecting rods and their lobate distal part, which is quite unlike the transition between the mucro and the lobate 'body' of *D. campanulata*. Though *D. campanulata* may be found in close association with graptolites, it is not attached to them; instead, they may be merely juxtaposed (e.g. Fig. 1c). Neither is there any good evidence to suggest that *D. campanulata* is a sac-like appendage broken from a graptolite. For one thing, its mucro tapers to a narrow point, rather than having a blunt or irregular end. Indeed, the connecting rod and margins of the sac-like graptolite appendage seem unlikely to break readily. They are well-defined in most specimens, having a similar mode of preservation to the nema. This suggests they are recalcitrant tissues and may have possessed a noticeable elasticity: Crowther (1978) noted that the nema displays a certain 'springiness' in acid-isolated specimens. In summary, there is no evidence for *D. campanulata* being a graptolite egg-sac, or for it being related to graptolites at all.

A concentric, raised, nipple-like structure occurs in several specimens of *D. campanulata* (e.g. Fig. 2f) and has previously been interpreted as evidence for it having originally had a hollow body (Williams 1981). Nicholson (1872, 1873) believed that this 'nipple' represented compression of a hollow three-dimensional egg-sac onto its more rigid mucro. However this does not appear to be the case, as many specimens reveal both a mucro and a 'nipple' (e.g. Fig. 1c), and some specimens show that *D. campanulata* may only partially overlap a 'nipple' (Fig. 6c). Instead, SEM investigation reveals the nipples to be composed of diagenetic pyrite adopting a rounded and concentric habit (cf. Allison 1988; Underwood & Bottrell 1994). As such, the 'nipple' is best considered to be a product of compression of *D. campanulata* onto pyrite formed in early (?pre-compaction) diagenesis rather than an intrinsic part of the fossil.

Poorly-preserved sac-like appendages in *Hallograptus bimucronatus* show that these stalked, lobate appendages are defined by two well-delineated, ramifying margins (Fig. 1f), one more proximal and the other more distal. Better preserved specimens show continuous periderm between these margins (AAP unpublished observations). The well-delineated, ramifying margins show fibres diverging from the margin towards the centre of the appendage (particularly clear on the more proximal margin in Fig. 1f); it appears that these may have joined together as concentric lines that seemingly 'cross-braced' between either margin. This would be consistent with these lines representing the remnants of fusellar structures like those seen in the *Orthoretiolites hami* scopula (Bates & Kirk 1991). Such a mode of fabrication would deny the possibility that

these structures formed a housing from which an 'egg-sac' could easily detach as Nicholson (1868a, 1872) suggested. Nicholson believed that *D. campanulata* represented a graptolite egg-sac that became a free-swimming entity, supposing that it was hollow and filled with eggs whilst housed in a cup of ramifying fibres connected to the graptolite. He proposed that this 'ovarian vesicle' slid out once it was able to swim freely. However, if *Hallograptus* constructed its appendages in a manner comparable to the scopula of *O. hami*, it would represent a plate-like, rather than cup-like, structure (cf. Bates & Kirk 1991).

It is extremely doubtful if sac-like graptolite appendages represent egg-sacs. The preponderance of these features in scalariform preservation suggests that they originated from the interthecal wall rather than connecting the thecae per se, so there is no direct evidence for their intimate connection with the zooid itself. Moreover, their regularity of form is inconsistent with what one would expect of an unambiguously vesicular structure such as the *Climacograptus wilsoni* vesicle (Williams 1994). Given that these structures are only known in the biserial graptolites, it seems unlikely that they are related to graptolite reproduction. Indeed, when such seemingly vesicular structures are found in graptolites they are often attributed to being flotation devices (e.g. Bulman 1964, 1970; Rickards 1975; Finney & Jacobson 1985). In fact, the supposed float structure on the nema of the Ordovician graptolite *Archiclimacograptus angulatus* (Bulman 1953) bears a remarkable similarity in shape to *D. campanulata* (cf. Finney & Jacobson 1985; Figs 3–4) although the latter occurs long after this graptolite had gone extinct. However, this similarity is almost certainly superficial. The 'float' has a distinctive ornament that runs parallel to its outline which is not seen in *D. campanulata*; and it is hard to imagine how such a float would break off a nema to form the neatly tapering mucro seen in *D. campanulata* or why these floats would cluster together in the manner so typical of *D. campanulata* assemblages.

4. Systematic palaeontology

Phylum *Arthropoda*, von Siebold & Stannius, 1845

Superclass *Crustacea* Pennant, 1777

Class *Malacostraca* Latreille, 1806

Subclass *Phyllocarida* Packard, 1879

Order *Archaeostraca* Claus, 1888

Family *Caryocarididae* Racheboeuf, Vannier & Ortega, 2000

Genus *Caryocaris* Salter, 1863

*1863 *Caryocaris* n. gen. Salter, p. 139.

non 1868 *Dawsonia* Hartt in Dawson, p. 655.

p. 1873 *Dawsonia* Nicholson, pp. 139–140 *pars*.

1896 *Dawsonia* Nicholson; Gurley, p. 88.

1904 *Caryocaris* Salter; Ruedemann, pp. 738–742.

1969 *Caryocaris* Salter; Rolfe in Moore, p. 316.

2000 *Caryocaris* Salter; Racheboeuf *et al.*, pp. 322–323.

Remarks. The synonymy above is in addition to the detailed list in Racheboeuf *et al.* (2000). In the absence of a carapace, a tail-piece consisting of elongate, leaf-shaped furcal rami and a shorter, narrow triangular telson is sufficient to diagnose the genus (Racheboeuf *et al.* 2000, p. 328).

Caryocaris acuminata (Nicholson 1873)

(Figs 4 & 6g)

vp. 1873 *Dawsonia acuminata* n. gen. et n. sp. Nicholson, pp. 140–141, figs 3a–a' *pars*.

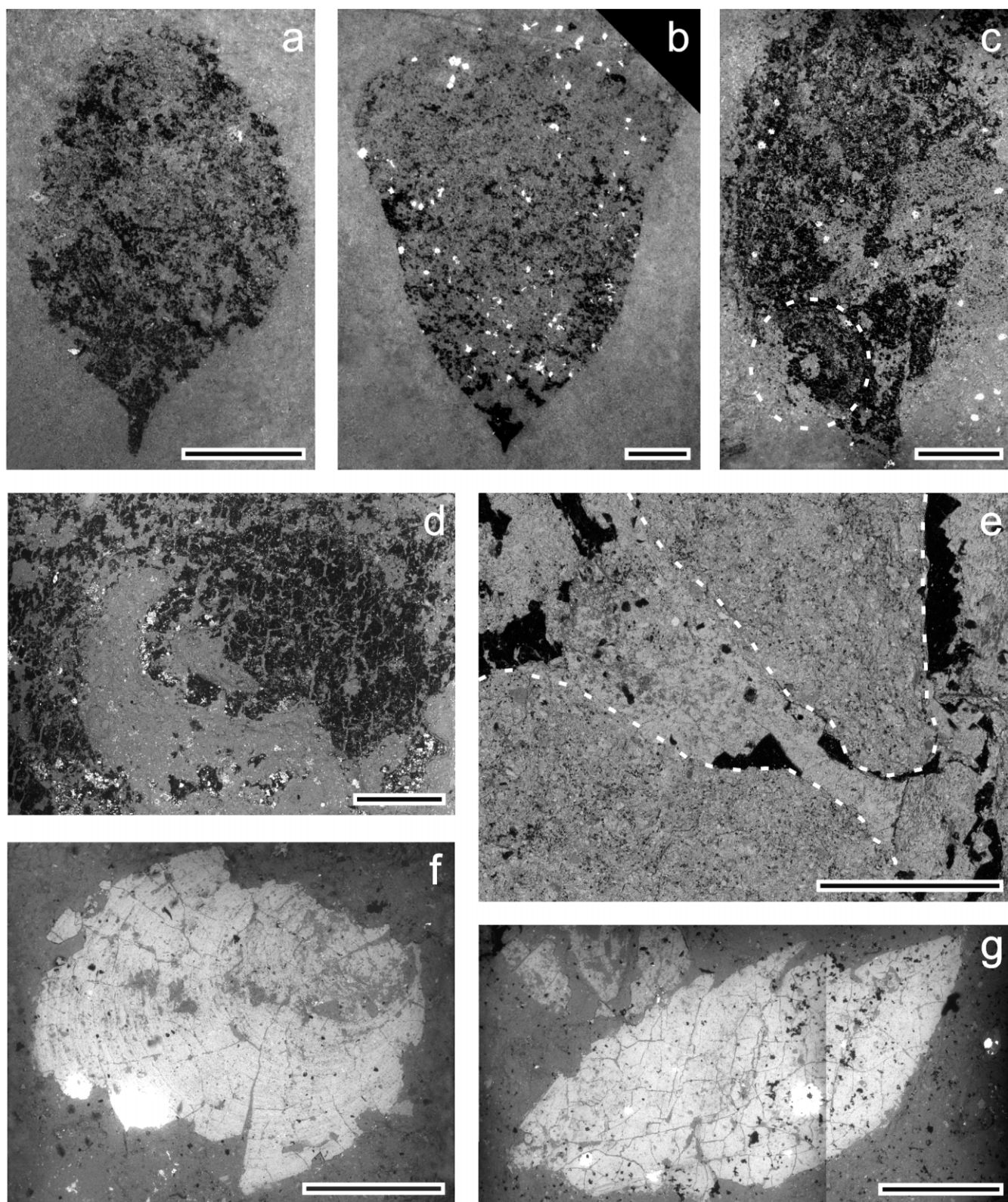


Figure 6 High contrast BS SEM images illustrating the preservation and morphology of (a–d) *Dawsonia campanulata*, (e) part of a graptolite scopula, (f) brachiopod, and (g) *Caryocaris*. The low brightness of *D. campanulata* and the scopula indicate preservation as organic compressions; the high brightness of the brachiopod and *Caryocaris* reflect their primary phosphatic compositions; white areas are accessory diagenetic minerals and weathering products. *D. campanulata*: (a) petal-shaped morph, BGS GSM 105817; (b) bell-shaped morph, BGS GSM 105816; (c) partially overlying and imprinting a diagenetic pyrite to produce a well-developed 'nipple' (outlined), SM A20905a; (d) close-up of a 'nipple' showing its concentric structure defined by diagenetic pyrite, SM A 20905a. (e) Holdfast and proximal body of scopula (outlined) attached to graptolite illustrated in Figure 1d (being the second scopula on the left hand side of this illustration), SM A13731. (f) *Acrosaccus rotundus*, syntype NHM BC 58607. (g) Furcal ramus of *Caryocaris acuminata*, NHM IC 483. Specimens from the Birkhill Shale Fm. of Duffkinnel Burn (a–b), Coalpit Bay (c, d) and Dob's Linn (e); and, Lévis Shale Fm., Point Lévis (f–g). Scale bar = 1mm (a–c, f–g); 500 μ m (d–e).

- v. 1873 *Caryocaris* sp. Nicholson, p. 143.
 . 1896 *Caryocaris oblongus* n. sp. Gurley, p. 87, pl. 4, fig. 2.
 p. 1896 *Caryocarus* [sic] *curvilatus* n. sp. Gurley, pp. 87–88
pars, ?pl. 4, fig. 3, ?pl. 5, fig. 3.
 . 1896 *Dawsonia monodon* n. sp. Gurley, p. 88, pl. 5, fig. 4.
 . 1896 *Dawsonia tridens* n. sp. Gurley, p. 88, pl. 5, fig. 5.
 non 1904 *Caryocaris* cf. *curvilineatus* [sic] Gurley; Ruedemann,
 p. 738, pl. 17, fig. 17.
 non 1904 *Caryocaris* cf. *oblongus* Gurley; Ruedemann, p. 738,
 pl. 17, figs 14–16.
 p. 1904 *Dawsonia tridens* Gurley; Ruedemann, p. 741 *pars*,
 ?pl. 17, fig. 18, non pl. 17, figs 19–20 [= *C. monodon*].
 p. 1904 *Dawsonia monodon* Gurley; Ruedemann, pp. 741–742
pars, fig. 105, ?pl. 17, figs 21–23, non pl. 17, figs 24–26
 [= *C. monodon*].
 non 1934 *Caryocaris curvilata* Gurley; Ruedemann, p. 92,
 pl. 22, figs 1–9.
 p. 1934 *Caryocaris monodon* (Gurley); Ruedemann, p. 93–95
pars, non pl. 22, figs 10–14.

Type material. Lectotype designated here, NHM IC 495 (furcal ramus), being the best preserved specimen of those identified by Nicholson as *Dawsonia acuminata*.

Additional material. Syntypes NHM IC 457–494, 496–498; AUGD 2754: No complete carapaces; 13 carapace fragments; 19 well-preserved furcal rami; seven telsons; 25 poorly-preserved or fragmentary furcal rami, telsons and indeterminate fragments. No articulated tail-pieces or complete carapaces were found in this material.

Type locality. Lévis Shale, Point Lévis, Quebec, Canada. Lévis Formation, Ordovician (Arenig).

Description. Carapace outline indeterminate; linear corrugated ornament on fragments. Tail-piece with narrow triangulate telson lacking ridge or carina; furcal rami elongate, leaf-shaped, ca. 1.5 times longer than telson on average, with acuminate distal margin, bearing large, triangular, posteriorly-directed spines along their outer margin; distinctive narrow ridge and furrow adjacent to its proximal inner margin along its proximal third. Telson ranges 1.8–2.9 mm in length and 0.9–1.5 mm in width. Furcal ramus ranges 2.7–6.1 mm in length and 1.3–2.5 mm in width; smaller specimens may only have two marginal spines (e.g. Fig. 4b), larger specimens are stouter and more asymmetrical, with slightly sigmoidal inner margin, and have three marginal spines (e.g. Figs 4a, 6g).

Remarks. Until the morphology of its carapace is better known, *C. acuminata* should remain a species separate from *C. monodon* and other caryocaridids. Thus *C. acuminata* refers exclusively to caryocaridids from Point Lévis and *C. monodon* refers to caryocaridids from the exposure at the Deep Kill at Melrose, as laid out in the synonymy above. Though the outline of the tail piece is similar in both localities, the morphology of the tail-piece alone is not well enough placed in the hierarchy of characters to determine synonymy at a species level (Racheboeuf *et al.*, 2000, p. 328). The variation in number of marginal spines may represent allometric growth (cf. Rushton & Williams 1996); however, small spines may not necessarily be apparent on poorly preserved specimens (see Fig. 4b).

Though the type specimens of *C. oblongus* Gurley, *D. monodon* Gurley and *D. tridens* Gurley are presumed lost, the original descriptions and illustrations are sufficiently good for his material from Point Lévis to be synonymised with *C. acuminata*. If it is ever found, Gurley's material is thus best considered to be topotypes of *C. acuminata*. *D. tridens* corresponds exactly with the present authors' observations on the furcal ramus of *C. acuminata*, whilst *D. monodon* most likely represents an articulated *Caryocaris* tail-piece preserved in

lateral view. *C. oblongus* presumably represents the fragments of a carapace. Nicholson (1873) also noted *Caryocaris* carapace fragments in the Point Lévis fauna. Similarly, *Caryocarus* [sic] *curvilatus*, described as an aberrant graptolite in Gurley (1896), is most likely an articulated abdomen and tail-piece. Likewise, we concur with Ruedemann (1934, p. 94) that *D. monodon* and *D. tridens* represent parts of a crustacean rather than being unusual graptolites.

Though no articulated specimens are present in Nicholson's collection, it seems more parsimonious to describe the disarticulated parts as one species rather than several. Nicholson described *D. acuminata* prior to mentioning the specimens which he referred to *Caryocaris* sp. As such, there seems little controversy in retaining the specific name *acuminata*, which refers to the pointed end of the furcal ramus.

Phylum Brachiopoda Duméril, 1806
 Subphylum Linguliformea Williams *et al.*, 1996
 Class Lingulata Gorjansky & Popov, 1985

Remarks. The three species of brachiopods from Nicholson's Point Lévis material are placed within the Lingulata on the basis of their organophosphatic composition, rudimentary articulation and larval shells. As noted above, many authors have considered them to be brachiopods, though they have not been formally assigned to the phylum until now.

Order Lingulida Waagen, 1885
 Superfamily Linguloidea Menke, 1828
 Family Paterulidae Cooper, 1956
 Genus *Paterula* Barrande, 1879

- non 1868 *Dawsonia* Hartt in Dawson, p. 655.
 p. 1873 *Dawsonia* Nicholson, pp. 139–140 *pars*.
 1879 *Paterula* n. gen. Barrande, pl. 110.
 2000 *Paterula* Barrande; Holmer & Popov, 2000, p. 75.

Paterula? *tenuistriata* (Nicholson 1873)
 (Fig. 3c, e)

- vp. 1873 *Dawsonia tenuistriata* Nicholson, pp. 141–142 *pars*,
 fig. 3c–d'.

Type material. Lectotype designated here, NHM BC 58594 (part), 58592 (counterpart), being the best preserved specimens of those identified by Nicholson as *Dawsonia tenuistriata*.

Additional material. NHM BC 58591, 58592, 58595–58597.

Type locality. Lévis Shale, Point Lévis, Quebec, Canada. Lévis Formation, Ordovician (Arenig).

Description. Shell with elongate oval outline, convex. Apex and limbus submarginal to subcentral. Anterior-posterior valve length 1.4–>3.4 mm, valve breadth 1.2–3.7 mm, typical specimen breadth >2 mm; length-width ratio 1.2–1.5, typically 1.35; maximum breadth at anterior-posterior midpoint. Growth lines continuous and fine, equally prominent, regular 0.04–0.1 mm spacing throughout the valve.

Remarks. Though this genus is typically unequivalved, only a single valve is present in Nicholson's collections. As *Dawsonia* Nicholson is an invalid taxon, there is no conflict of names. While there is some similarity between this form and the younger taxon *P. cf. portlocki* Geinitz (1852) as illustrated by Henningsmoen in Waern *et al.* (1948), the material described herein is too poorly preserved to properly compare the taxa. As such, Nicholson's collections need to be supplemented with additional material exhibiting the shell's internal

view before this taxon can be precisely placed. Therefore, the taxon has been kept in open nomenclature.

Superfamily Discinoidea Gray, 1840
Family Discinidae Gray, 1840
Genus *Acrosaccus*? Willard, 1928

non 1868 *Dawsonia* Hartt in Dawson, p. 655.
p. 1873 *Dawsonia* Nicholson, pp. 139–140 *pars*.
*1928 *Acrosaccus* n. gen. Willard, p. 258.
2000 *Acrosaccus* Willard; Holmer & Popov, 2000, p. 86.

Acrosaccus? *rotundus* (Nicholson 1873)
(Figs 3a–b, d, 6f)

v. 1873 *Dawsonia rotunda* Nicholson, pp. 141–142, fig. 3c–d'.

Type material. Lectotype designated here, NHM BC 58598, being the only specimen clearly identified by Nicholson as *Dawsonia rotunda*, though we recognise other better preserved material in his collection as listed below.

Additional material. NHM BC 58599–58612 (2 dorsal valves, 5 pedicle valves, 6 indet.)

Type locality. Lévis Shale, Point Lévis, Quebec, Canada. Lévis Formation, Ordovician (Arenig).

Description. Shell unequivaled with subcircular outline, equally biconvex. Beak slightly submarginal on one valve and submarginal to subcentral on the other. Anterior-posterior valve length 2.1–2.9 mm, valve breadth 2.1–3.0 mm; length-breadth ratio 0.95–1.1, typically slightly elongate. Growth lines continuous, some more prominent, regular 0.05–0.1 mm spacing, growth lines more clearly defined towards the anterior margin, particularly in valve with submarginal to subcentral beak.

Remarks. Though no articulated specimen is known, the two valves can be inferred as belonging to a single species as their outlines are indistinguishable, suggesting they once did meet. By comparison with the type species, *A. schuleri* Willard (1928), the valve with the more marginal beak is assumed to be the dorsal valve, the valve with the more central beak being the pedicle valve.

As *Dawsonia* Nicholson is an invalid taxon there is no conflict of names. However, Nicholson's collections need to be supplemented with additional material displaying conjoined valves and internal views for the generic assignment to be confirmed. Until then the taxon should remain in open nomenclature.

Superfamily ?*Acrotheloidea* Walcott & Schuchert in Walcott, 1908
Family ?*Acrothelidae* Walcott & Schuchert in Walcott, 1908
Subfamily ?*Conodiscinae* Rowell, 1965
Genus *Discotreta* Ulrich & Cooper, 1936

non 1868 *Dawsonia* Hartt in Dawson, p. 655.
p. 1873 *Dawsonia* Nicholson, p. 139–140 *pars*.
*1936 *Discotreta* n. gen. Ulrich & Cooper, 1936, p. 619.
2000 ?*Discotreta* Ulrich & Cooper, 1936; Holmer & Popov, 2000, p. 94–95.

Remarks. There appears to be some doubt as to the affinity of the genus, with Rowell (1965) considering it *Incertae Familiae* and Holmer & Popov (2000) expressing a degree of uncertainty in its systematic position. These specimens do not preserve sufficient characters to contribute to the debate. There is no doubt, however, in the status of the generic name,

as the invalidity of the name *Dawsonia* Nicholson avoids conflict.

Discotreta cf. *levisensis* (Walcott, 1908)
(Fig. 3f)

p. 1873 *Dawsonia tenuistriata* Nicholson; pp. 141–142 *pars*, non fig. 3c–d'.

*1908 *Acrothete levisensis* Walcott, 1908, p. 85, pl. 8, fig. 13.
1936 *Discotreta levisensis* (Walcott, 1908); Ulrich & Cooper, p. 619.
1938 *Discotreta levisensis* (Walcott, 1908); Ulrich & Cooper, pl. 6a.
1965 *Discotreta levisensis* (Walcott, 1908); Rowell, p. 282, fig. 176.
2000 *Discotreta levisensis* (Walcott, 1908); Holmer & Popov, figs 47, 2a–d.

Type material. Lectotype GSC 8230, paratypes GSC 8230a, b; housed in the Geological Survey of Canada collections.

Material. NHM BC 58613–58621.

Type locality. Lévis Shale, Ordovician (Arenig); Point Lévis, Quebec, Canada.

Diagnosis. As Ulrich & Cooper (1936).

Description. Shell unequivaled with transversely suboval outline, equally biconvex. Apex submarginal to subcentral and posteriorly positioned, seemingly more submarginal in one valve than the other. Anterior-posterior length 1.0–2.6 mm, valve breadths 1.2–3.4 mm, typical breadth around 3 mm; length-breadth ratio 0.65–0.9, typically 0.8; maximum breadth at anterior posterior midpoint. Growth lines continuous, more clearly defined away from the apex, regular 0.06–0.11 mm spacing throughout the valve.

Remarks. The quality of preservation, especially the lack of internal features, precludes precise assignment. The valve with the most submarginal apex is most likely the ventral valve by comparison with the specimens of *Di. levisensis* illustrated in Holmer & Popov (2000, Figs 47, 2a–d).

This species was originally accommodated in Nicholson's (1873) concept of *D. tenuistriata* which allowed for considerable variation in the position of the apex by comparison with the variably positioned 'nipples' (actually diagenetic pyrite) in *D. campanulata*. However, as Nicholson's description is of an elongate oval fossil, it seems best to remove this form from *D. tenuistriata* and compare it with *Di. levisensis*. As it is unknown whether Nicholson's Point Lévis material was collected from the precise locality and horizon of Walcott (1908), this material should not be assigned to type status.

Phylum, Class, Order & Family uncertain
Genus *Dawsonia* Nicholson

non 1868 *Dawsonia* Hartt in Dawson, p. 655.
p. 1873 *Dawsonia* Nicholson, pp. 139–140, *pars*.
p. 1889 *Dawsonia* Nicholson; Miller, p. 184.
non 1904 *Caryocaris* Salter; Ruedemann pp. 738–742.
non 1969 *Caryocaris* Salter; Rolfe in Moore, p. 316.
non 1970 *Lockeia* James; Osgood, pp. 308–312.
p. 1981 *Dawsonia* Nicholson; Williams, p. 55.
non 1989 *Dawsonia*; Frey, fig. 7.

Type species. *Dawsonia campanulata* Nicholson (1873); subsequent diagnosis, Miller (1889).

Diagnosis. Ovato-triangular carbonaceous fossil consisting of a flat, tapering lobate body and a sharply-delineated, narrow triangular mucro.

Dawsonia campanulata Nicholson
(Figs 1a–c, 6a–c)

- non 1837 *Prionotus pristis* Hisinger, p. 114, pl. 35, fig. 5.
 non 1843 *Graptolithus (Prionotus) Sedgewickii* [sic] Portlock,
 p. 318, pl. 19, fig. 1.
 p. 1866 *Graptolites sedgewickii* (Portlock) pl. 17, fig. 3 pars.
 v. 1867 *Diplograpsus pristis* (Hisinger); Nicholson, pp. 111–
 113, pl. 7, fig. 21–21b.
 v. *1873 *Dawsonia campanulata* Nicholson, pp. 142–143,
 fig. 3e–f.
 p. 1873 *Dawsonia acuminata* Nicholson, pp. 142–143, pars.
 v. 1877 *Dawsonia* sp.; Lapworth, p. 7, pl. 7, fig. 23a–d.
 . 1981 *Dawsonia campanulata* Nicholson; Williams p. 55, pl. 6,
 figs 1–15, pl. 7, fig. 6.
 . 1996 *Dawsonia* sp.; Williams, p. 196, pl. 36, fig. 16.

Type material. Lectotype NHM QQ 253.

Additional material. Syntypes in Nicholson's collection: NHM QQ 254–256 and AUGD 2158, 2168, 2636, 2748, 2751, 2830. Nicholson's material from other localities: NHM 257–260, and AUGD 2752, 2753. Material measured in Figure 5: BGS GSM 105814–9, GSE 10800–1, 3366, PHW 501–553, 18E 73, 81, 90, 94–5, 99, 102–4, 112–3, 117 and SM A38754. Other material: SM A20905a–c, A20906, BEL K681.

Type locality. Dob's Linn, near Moffat, Scotland. Birkhill Shale Formation, Silurian: Llandovery.

Range & horizons. Rhuddanian to Aeronian (Llandovery, Silurian) of the British Isles. Birkhill Shale Formation (Moffat Shale Group) in Dob's Linn, Garpol Linn, Plewlands Burn and Duffkinnel Burn, Southern Uplands, Scotland, and in Coalpit Bay, Donaghadee, Northern Ireland; Skelgill Formation (Stockdale Group) in Spengill, near Sedbergh, Howgill Fells, and Hol Beck, Skelgill, English Lake District.

Diagnosis. As genus.

Description. Specimens range in size from 3–12 mm length and 1–4 mm width, with the mucro itself being typically less than 0.5 mm in length, and seemingly isometric growth (Fig. 5).

Remarks. *D. campanulata* cannot be easily accommodated in any higher taxonomic group. It is clearly unrelated to graptolite scopulae, and bears little similarity to either phyllo-carids or algae. Although recent works have tried to accommodate it in these groups (cf. Rolfe 1969 and Williams 1981, respectively), neither assignment is entirely convincing. Meanwhile, Underwood (1993, fig. 4e) illustrated a carbonaceous fossil that looks conspicuously like *D. campanulata* as a faecal pellet. In the most detailed recent study of this species, Williams (1981) argued that it represented a spore-carrying alga. He stated that *D. campanulata* had an open, flared 'posterior margin, giving the [hollow] body a "crocus flower" type of appearance'. However, it is an order of magnitude larger than such spore-carrying alga in the modern oceans (Tappan 1980) and there is no evidence to suggest it had significant three-dimensionality in life. The 'nipples' seen associated with *D. campanulata* superficially suggest a three dimensionality, but, as noted in section 3, they actually represent compression of the fossil on to diagenetic pyrite in the sediment. This pyrite notably differs in fabric from the pyrite infill of hollow cavities (cf. Allison 1988; Underwood & Bottrell 1994). Moreover, *D. campanulata* lacks the morphological variation seen when unambiguously hollow tissues such as the *Climacograptus wilsoni* vesicle are found flattened in these shales (cf. Williams 1994). And, although the distal margin of *D. campanulata*'s lobate body may be fragmented (Fig. 1b), and, at times, less-well delineated than the proximal end and mucro (Fig. 6b), there are many examples showing a

well-defined, rounded distal margin (Figs 1a, c & 6a, c), suggesting that this represents variability in preservation rather than a crocus-flower-like morphology. With this in mind, *D. campanulata* is best considered to be a flat problematicum rather than a hollow alga.

5. Discussion

Nicholson remains one of the great early graptolite workers despite being wrong in his views of graptolite reproduction (Nicholson *passim*). It was not until Chlupáč (1970) discovered well-preserved caryocaridids in limestone nodules from the Ordovician of Bohemia that the morphology of their tail-piece was fully understood; hence it is understandable that Nicholson (1873) did not recognise *D. acuminata* as such, despite recognising *Caryocaris* carapaces in the Point Lévis fauna. Nicholson's assertion that *D. rotunda* and *D. tenuistriata* were not brachiopods appears at odds with his (1867a) claim that 'it is impossible that any palaeontologist, possessed of ordinary powers of observation, should fall into an error so gross [as to fail to recognise an inarticulate brachiopod]'.

Noting the variability of form within *D. tenuistriata*, for example, Nicholson (1873, p. 142) argued that describing the species as egg-sacs allowed for greater morphological plasticity, otherwise 'we should have to believe there were four or five distinct species of brachiopods in these beds which is very unlikely' (the information in Benton (1979) confirms that Nicholson was not accustomed to such faunal diversity in UK sections). It appears that he conflated the beak of the brachiopods with the variably positioned 'nipple' of *D. campanulata* (e.g. Fig. 2), a false homology that underpinned his *Dawsonia* concept. So, in an age before taphonomy and palaeoenvironment were generally considered, when many species were only known from disarticulated fragments, Nicholson explained the vagaries of variable preservation and differing morphology in a strikingly diverse fauna by appealing to his theory of graptolite reproduction.

6. Conclusions

There is no evidence to support the notion that *Dawsonia* Nicholson is in any way related to graptolite reproduction. Likewise, there is no strong case for sac-like appendages on graptolites having a reproductive function given the discovery of eggs and embryos in the thecae of benthic graptolites and our knowledge of reproduction in the pterobranchs (Kozłowski 1948; Bulman & Rickards 1966; Stebbing 1970; Dilly 1973; Hutt 1991). As such, the function of these sac-like appendages remains enigmatic, and these, along with the function of synrhabdosomes, should be re-examined in order to assess what, if any, role either plays with regard to graptolite reproduction.

All known species of *Dawsonia* Nicholson have been reassigned to valid genera except *D. campanulata*, which is best considered a problematicum. *D. acuminata* Nicholson, *D. tridens* Gurley and *D. monodon* Gurley represent the tail-pieces of *Caryocaris acuminata* (Nicholson 1873). It is suggested that *C. monodon* should not be used with reference to material from Point Lévis (*contra* Ruedemann, 1934). *D. rotunda* Nicholson is tentatively reassigned to the brachiopod genus *Acrosaccus*, and *D. tenuistriata* Nicholson is accommodated by the brachiopods *Paterula tenuistriata* and *Discotreta* cf. *levisensis* (Walcott 1908). The trace fossil diagnosed as *Dawsonia* Nicholson by J. F. James (1885, 1892) has long been known to represent the trace fossil *Lockeia* U. P. James (1879) (see

Benton 1979), whilst '*Dawsonia cycla*' most likely represents the epibiont *Sphenothallus* (Frey 1989; Neal & Hannibal 2000).

D. campanulata is a problematicum, currently being investigated by the authors. Though *Dawsonia* Nicholson is an invalid generic name, it would be premature to formally re-describe it until further information pertaining to the affinity of *D. campanulata* is available. That nobody has provided a more definite idea of what *D. campanulata* may represent in the hundred years since Nicholson's early death can be taken as a minor tribute to the man who clearly recognised its uniqueness.

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