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RAPID COMMUNICATION

The significance of the graptoloid *Amphigraptus divergens* from the (mid-Rawtheyan) type section of the Ashgill Series, Ordovician

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Abstract. *Amphigraptus divergens* Lapworth is known to be restricted, in Britain, to the *linearis* Biozone, and its occurrence in the type Ashgill Series reinforces Rickards' prior independent attribution of that part of the type Ashgill to the *linearis* Biozone. The thecal structure revealed in this paper allies *A. divergens* to the dicellograptids rather than the leptograptids, hence it is placed in the family Dicranograptidae. The evolutionary origin of *Amphigraptus* is almost certainly rooted in *Dicellograptus*.

Keywords: Ashgill Series, Ordovician, graptolites.

1. Introduction

The partly-enrolled mature specimen of *Amphigraptus divergens* (Hall, 1859a) was discovered in 2003 by the author from the type Ashgill Series exposed in Watley Gill, Westerdale, Howgill Fells, Cumbria. The locality (Fig. 1) is that central to his (2002) argument that the middle part of the Rawtheyan Stage should be referred to the *linearis* Biozone in the graptolite sequence. The identification of *A. divergens* from this locality reinforces that claim because in Britain the species is restricted to the *linearis* Biozone (Taylor *et al*. in press). Indeed the genus itself has been recorded no higher than the *linearis* Biozone. The subspecies *A. divergens radiatus* Lapworth (1876) occurs in both the *clingani* and *linearis* biozones, whilst *A. distans* Elles and Wood (1903) occurs in the *linearis* Biozone. In North America (see Ruedemann, 1947, p. 373) *A. divergens* occurs in the *gracilis* Biozone as does a very similar species, *A. multifasciatus* (Hall, 1859a). The genus *Amphigraptus*, therefore, when considered globally, only occurs in the *linearis* Biozone or earlier. The problem remains that the *complanatus, anceps* and *extraordinarius* biozones have not been identified in the type Ashgill Series, and the only 'space' available for them is Ingham's (1966) trilobite zones 7 and 8 (that is, the uppermost few metres of the Cautley Mudstone Formation and the Ashgill (Shales) Formation). This problem would be partially solved if Elles' (1925) suggestion, that the *complanatus* Zone was merely a modified *linearis* Zone, proved correct.

2. Evolution of *Amphigraptus*

The thecal form (Fig. 2c) of introverted thecal apertures, presence of a geniculum, thickened rim of the infragenicular wall, and gently convex supragenicular wall with a central spine in the case of proximal thecae, clearly allies *Amphigraptus* with *Dicellograptus*. Williams (1982, p. 239) suggested that "this 'genus' may represent a recurring *Leptograptus* mutation"; he had doubts about the generic validity. However, it is likely that *Amphigraptus* is unrelated to *Leptograptus*, which has very simple thecae. It is possible that *Amphigraptus divergens* derived directly from a species of *Dicellograptus* simply by growth of thecal cladia, either singly or in pairs, and by subsequent occasional branching of those cladia. No change in thecal style would have been needed, no change in dimensions and, as far as one can ascertain, no change in development. The precise origin of the thecal cladia has not been observed in detail, but given the lateral apertural incisions consequent upon the introversion of the ventral apertural wall, it seems more likely that cladia could develop laterally than from a simple aperture, such as those in *Leptograptus*. The latter is possible, as in *Pleurograptus*, but is less likely.

Since *Amphigraptus* occurs earlier in North America (see below) it is possible that the genus migrated to Britain where it began later and survived later. Or it is possible, given the rarity of both the genus and the species, that it is simply rare and long-ranging, and that its known record has an element of chance in it. A third possibility, inferred by Williams (1982), is that the (earlier) North American forms are quite different, possibly related to *Leptograptus*; the local details are as yet unclear, but should they prove to be leptograptids then a new generic name will be needed for British *Amphigraptus* species.

3. Systematics

Class GRAPTOLITHINA Bronn, 1849
Order GRAPTOLOIDEA Lapworth, 1875
Family DICRANOGRAPTIDAE Lapworth, 1873

Emended diagnosis. Uniserial or uni–biserial, horizontal or reclined or initially scandent, branches in one genus; thecae with conspicuous sigmoid curvature, some species elaborated; development, where known, of diplograptid type.

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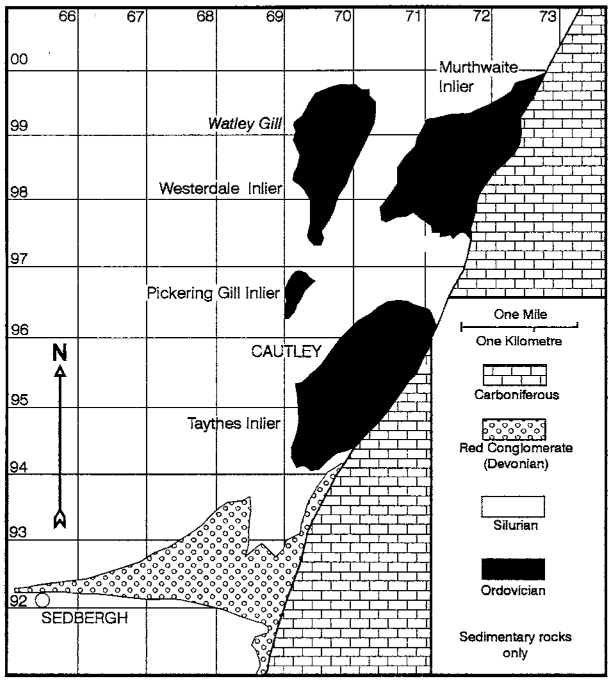

Figure 1. General geological setting of the Ashgill Series (black) in the Howgill Fells, Yorkshire, UK and the position of the type sections (Westerdale) including Watley Gill which yielded the specimen of *Amphigraptus divergens* Hall. UK National Grid shown, sheets NY and SD.

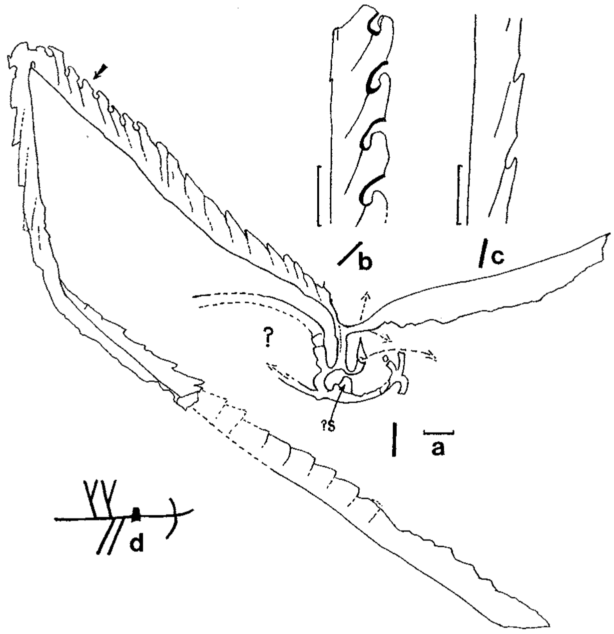

Figure 2. *Amphigraptus divergens* (Hall, 1859a). Sedgwick Museum X.41388a from locality 1 of Rickards (2002), mid-Rawtheyan Stage, Ashgill Series, on Watley Gill, Westerdale. (a) Specimen showing complex proximal region preservationally enrolled with numerous stipes. (b) Enlargement of part of left-hand (arrowed) bent stipe showing true nature of thecae. (c) Enlargement of part of left-hand bent stipe (arrowed) showing loss of thecal details on tectonic compression parallel to stipe length. (d) Diagrammatic unrolling of stipe arrangement. Heavy bars indicate tectonic stretching direction; s and arrow indicates possible sicular region; dashed arrows indicate possible additional stipe growth with stipe parts going into rock; interrogative indicates preservationally doubtful area; scale bars 1 mm.

Remarks. The genus *Amphigraptus* was placed in the family Nemagraptidae by Bulman (1970; and see Williams, 1982) but the thecal structure revealed in this paper (Fig. 2b) indicates closer affinity with such genera as *Dicellograptus* rather than with *Leptograptus*, necessitating the emendation of the family diagnosis above.

Genus *Amphigraptus* Lapworth, 1873

Type species. *Graptolithus divergens* Hall (1859a) subsequently designated Miller (1889).

Emended diagnosis. Rhabdosome probably horizontal with two main stipes, almost straight, with rigid lateral branches produced singly or in pairs, some secondary branches; thecae with dicellograptid introversion and sigmoidal curvature.

Remarks. Bulman (1970) refers in his diagnosis to 'compound' stipes, as does Ruedemann (1947) and Williams (1982). However, there seems to be no basis for this: whilst the stipes are often 'thickened' (as Ruedemann (1947) points out) they each seem to have only a single thecal series. In fact, the use of the term 'compound' seems to have changed and is today used to describe stipes with several thecal series developed, rather than cladia which have secondary branches.

Amphigraptus divergens (Hall, 1859a)

Figure 2a–d

1859a *Graptolithus divergens* sp. nov.; Hall, p. 509, text-fig. 9.
1859b *Graptolithus divergens* Hall; Hall, p. 57, text-fig. 9.
1865 *Graptolithus divergens* Hall; Hall, pp. 12–13, text-fig. 11.
1868 *Graptolithus (Coenograptus) divergens* Hall; Hall, p. 179, text-fig. 12.
1876 *Amphigraptus divergens* (Hall); Lapworth, pl. 3, fig. 70.
1903 *Amphigraptus divergens* (Hall); Elles & Wood, pp. 122–3, pl. 18, fig. 1, text-fig. 73.
1908 *Amphigraptus divergens* (Hall); Ruedemann, pp. 271–2, pl. 15, figs 2, 3, text-figs 187–190.
1947 *Amphigraptus divergens* (Hall); Ruedemann, pp. 372–3, pl. 59, text-figs 27–32.
1977 *Amphigraptus divergens* (Hall); Walters, p. 950, pl. 1, fig. A.
1982 *Amphigraptus divergens divergens* (Hall, 1859a); Williams, pp. 237–8, figs 5d,e, 6a–c.

Type specimens. Hall's (1859a) specimens from the *gracilis* Zone of the Normanskill Shale of New York State and refigured by Ruedemann (1908, 1947). According to Williams (1982) there is some doubt about the actual type specimen.

Material. A single specimen, Sedgwick Museum X.41388a,b (part and counterpart) from locality 1 of Rickards (2002, pp. 3, 15) in the Rawtheyan Stage, Ashgill Series, Ordovician of Watley Gill, Westerdale, Howgill Fells. Preservation is in part pyritized, in part flattened, the latter especially towards the distal parts of each stipe. Some tectonic deformation is present (see Fig. 2a–c) with cleavage planes almost normal to bedding. The periderm in places is clearly quite thick, especially at the proximal end, which would undoubtedly have strengthened the colony.

Diagnosis. Two main stipes, horizontal or slightly reclined, possibly gently curved; lateral branches either singly or in pairs; thecae long, with geniculum and apertural introversion.

Description. At least 10 stipes can be identified within a 2 mm radius of the proximal end. Two of these will be the primary stipes, giving eight branches. Of the branches two groups originate as pairs from primary stipes, and the remaining four are individual branches. The actual specimen is shown in Figure 2a and a diagrammatic representation of the stipes and branches in Figure 2d. The stipes have a dorsoventral width of 1.10 mm distally, or a little bit more or less depending on the direction of tectonic deformation (stretching direction indicated by heavy bars on figures). The proximal dorsoventral width cannot be seen because true profiles have not been identified; it is clear, however, that considerable peridermal thickening occurs proximally.

The position of the sicula is unclear. One portion of the proximal region (**s**, arrowed) may represent downgrowing thecal tubes on a sicula, but all this region is secondarily thickened with cortical tissue so development cannot be seen.

The proximal thecae are very thickened with cortical deposits. However, distal thecae are well seen in full profile, either flattened or in low relief. Where best preserved they show long thecal tubes with thickened infragenicular selvages, a geniculum, a supragenicular wall which leans outwards gently, and is slightly convex, and introverted apertures (Fig. 2b). Only where tectonic stretching is considerable or the thecae badly flattened, do they appear to be simple, long tubes (Fig. 2c). Thecal overlap is about one half, and inclination of the thecal tubes about 20°. Thecal spacing is about 8–10 in 10 mm, perhaps a little higher proximally; and the proximal thecae appear to have short spines on the midpoint of the free ventral wall.

Remarks. I have examined the North American type and other collections, and the Scottish material, and in my view the thecae, whether flattened or nearly so, are not well preserved and thecal details are obscured. The thecae undoubtedly ally this species with dicellograptids rather than with the nemagraptid/leptograptid groups, which have simpler thecae; hence I prefer to place *Amphigraptus divergens* in the family Dicranograptidae. In all previous descriptions the thecae have not been clearly seen and have been assumed to be simple tubes because on non-profile flattening and especially with some tectonic deformation, they may appear so (Fig. 2c). As pointed out by Williams (1982) *A. divergens divergens* occurs only in the *linearis* Biozone in Britain, which is exactly the horizon deduced on independent grounds for locality 1 on Watley Gill by Rickards (2002). *A. d. divergens* differs from *A. d. radiatus* Lapworth (1876), which occurs in the *clingani* and *linearis* biozones (Elles & Wood, 1903), in that the branching in the latter is reduced in number and closer to the proximal end. Further work is needed to determine whether this is a real difference. *A. distans* Elles & Wood (1903) has more widely-spaced branching than *A. divergens*, narrower stipes, more widely-spaced thecae, and the thecae themselves may be of simpler nature; whether this species should be referred to a revised *Amphigraptus* is doubtful. *A. distans* occurs in the *linearis* Biozone.

North American representatives of the genus occur as early as the *gracilis* Biozone (see Ruedemann, 1947, p. 375); as Williams (1982) points out, they seem identical to the later forms from Britain. Either *A. divergens* is a quite long-ranging though uncommon species, or there are detailed (?thecal) differences not yet apparent from the preservational types available to us. *A. multifasciatus* (Hall, 1859a) is known from only two specimens (Ruedemann, 1947, p. 373) and is not dissimilar to *A. d. radiatus* in that the stipes radiate from close to the proximal end. It differs from the latter in that a great deal of secondary branching also occurs, although the extent to which this might develop in old age, together with the excess cortical tissue development, is unknown at present.

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