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EXTRAORDINARY DIMORPHISM IN THE PHYLLOGRAPTID *HARRISGRAPTUS* N. GEN. FROM THE EARLY BENDIGONIAN (EARLY FLOIAN, EARLY ORDOVICIAN) OF VICTORIA, AUSTRALIA

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ABSTRACT: Two graptolites from the early Bendigonian (Early Floian, Early Ordovician) formerly placed in *Didymograptus*, *D. eocaduceus* Harris, 1933 and *D. hemicyclus* Harris, 1933, are shown to be members of a single population that shows extraordinary dimorphism. This is mainly expressed in the tubarium habit which ranges from strongly reclined to horizontal, and in stipe width which changes systematically with tubarium shape. The population is placed in the new genus *Harrisgraptus* and placed in the family Phyllograptidae, characterised by well-developed sicular and thecal rutella.

Keywords: *Harrisgraptus* n. gen., Graptoloidea, Phyllograptidae, dimorphism, Floian, Bendigonian, Ordovician

Identification of graptolites involves the determination of a range of characters that includes the growth pattern (astogeny), particularly of the first few thecae, the number of stipes and their disposition (pendent, horizontal, reclined, scandent), the shape of the sicula and the shape and inclination of thecae, and stipe width. In many species, these exhibit relatively narrow biometric ranges so their measurement can be a useful tool for separating species of similar appearance (e.g. see VandenBerg 2017a).

Harrisgraptus n. gen. *eocaduceus* (Harris, 1933) does not fit this general pattern — so much so, that its first description was under two different names, *Didymograptus eocaduceus* and *D. hemicyclus*. In *D. eocaduceus*, Harris included specimens whose stipes are tightly dorsally curved in the proximal two or three pairs of thecae and then straight, whereas the dorsal curvature of stipes of *D. hemicyclus* is more open and persistent.

At the time of Harris' work, the number of stipes of a tubarium was still the primary criterion for classifying most graptolites. Thus, with *Isograptus* as a rare exception, two-stiped species were then all placed in *Didymograptus* M'Coy, 1851. Harris' 1933 paper was almost entirely devoted to isograptids, but included his two new species *D. eocaduceus* and *D. hemicyclus* because of their superficial resemblance to *Isograptus*. In 1952, Bouček & Příbyl redefined *Didymograptus* to only include pendent forms. This had the effect of excluding the two Harris species, but subsequent workers ignored this fact. Berry (1966) redescribed *Didymograptus hemicyclus* and designated a lectotype without discussing its generic assignment or similarity with other species. Beavis and Beavis (1974) described both *D. eocaduceus* and *D. hemicyclus* but, apart from designating a lectotype for the former, did not discuss either their generic assignment or the evident similarity of their proximal appearance — their description makes no reference to the rutella attached to the sicula and proximal thecae. The approach by Rickards and Chapman (1991) is more puzzling, placing two-stiped forms in an informal subdivision ('Section') they termed Didymograpti, in which they included horizontal, deflexed and pendent (but not reclined) forms, listing the (sub)genera *Didymograptus*, *Expansograptus*, *Corymbograptus* and *Didymograptellus* (and also including the sigmagraptid *Acrograptus gracilis*). They described both *D. hemicyclus* and *D. eocaduceus* and were the first to indicate the presence of the sicular rutellum ('mucronate apertural process') in both and included the presence of 'strongly denticulate, highly angled thecae' in the diagnosis of *D. hemicyclus*. They were also the first to remark on the close similarity between the two.

With its predominantly reclined habit, *Harrisgraptus* is difficult to accommodate in existing didymograptid genera whose habits range from horizontal to pendent. In addition, the presence of sicular and thecal rutella are characters that typify phyllograptids (Maletz et al. 2018) which indicates it should be placed in the Phyllograptidae.

Harrisgraptus eocaduceus (whose name appears first in Harris' paper) seems to be confined to Victoria where it is found only in the lower *Tshallograptus fruticosus* Biozone (Be1). Records from elsewhere, e.g. New Zealand (Cooper 1973, 1979), Canada (Lenz & Jackson 1986) and China (Mu et al. 2002) are based on specimens that lack the diagnostic sicular and thecal rutella so appear not to belong to *Harrisgraptus*. The New Zealand and Chinese specimens also come from much younger strata (mid-Darriwilian *Oncograptus upsilon* Biozone and younger).

SYSTEMATIC PALAEONTOLOGY

Suborder Dichograptina Lapworth, 1873
Family Phyllograptidae Lapworth, 1873

***Harrisgraptus* gen. nov.**

Etymology. Named for Dr William John Harris, one of Victoria's foremost graptolite researchers.

Type species. *Didymograptus eocaduceus* Harris, 1933

Diagnosis. Two-stiped phyllograptid with habit ranging from strongly reclined to horizontal; sicula and proximal thecae adorned with prominent rutella; thecae have curved ventral walls.

***Harrisgraptus eocaduceus* (Harris, 1933)**

1933 *Didymograptus eocaduceus*, sp. nov.; Harris, p. 109, pl. 6, fig. 8, text-figs 64–67
1933 *Didymograptus hemicyclus*, sp. nov.; Harris, p. 109–110, pl. 6, fig. 4, text-fig. 68
1935 *Didymograptus eocaduceus* Harris 1933; Benson & Keble, p. 282, pl. 30, fig. 20
1938 *Didymograptus hemicyclus* Harris; Harris & Thomas, p. 76, pl. 2, figs 21a–c
1962 *Didymograptus* cf. *hemicyclus* Harris; Mu & Chen, pl. 8, figs 19a, b
1966 *Didymograptus hemicyclus* Harris 1933; Berry, pp. 427–428, pl. 49, figs 5 & 6
1973 *Didymograptus hemicyclus* Harris; Cooper, text-fig. 6e
non 1973 *Didymograptus* cf. *eocaduceus* Harris; Cooper, text-fig. 6d

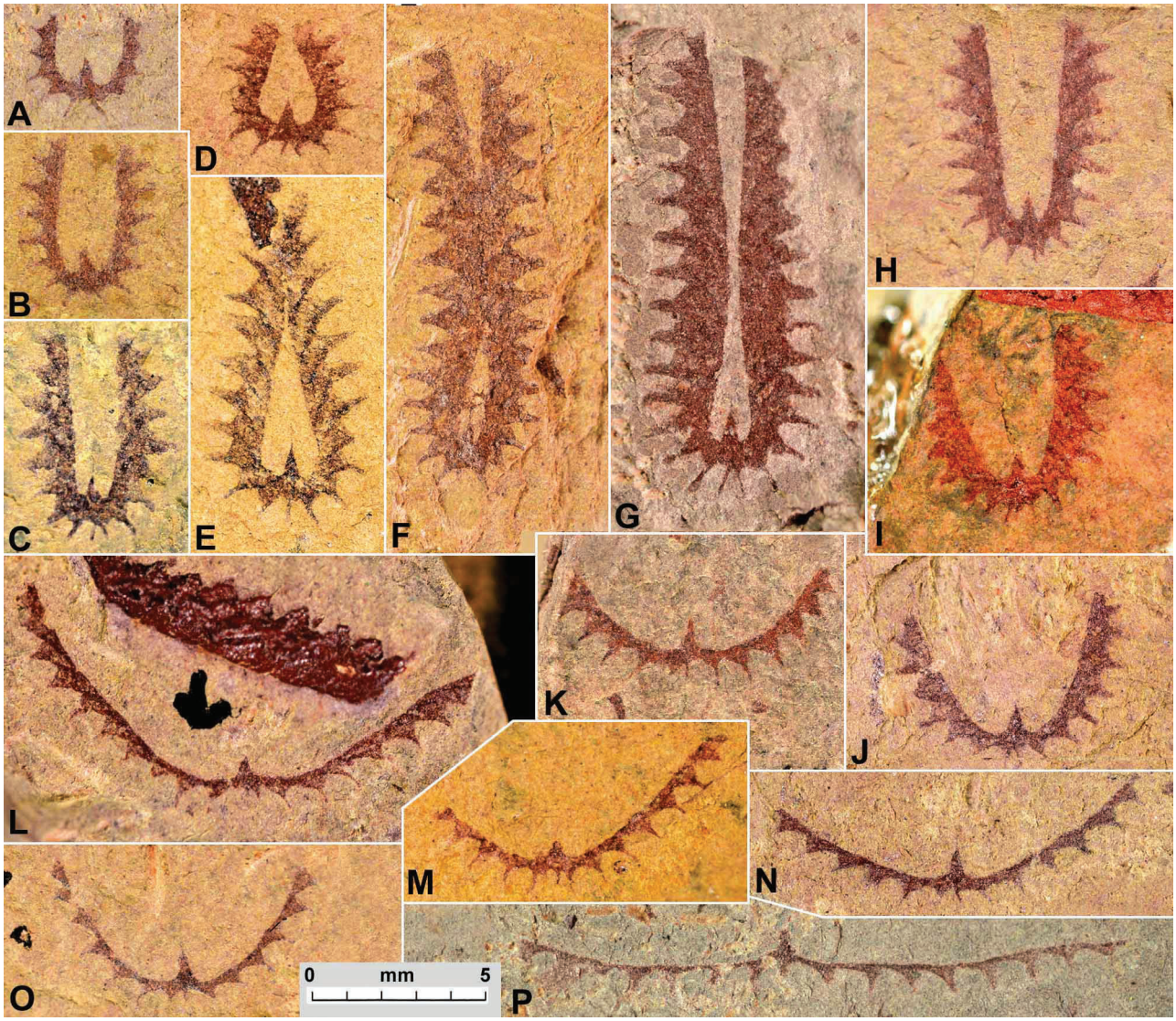

Figure 1: Photographs of tubaria of *Harrisgraptus eocaduceus* showing the extraordinary variation in habit and morphology. Alphabetical ordering follows steps in the transition from slender-stiped U-shaped (**A**) to wide-stiped U-shaped (**G**), after which stipes gradually become more divergent and slender (H–P), until they are fully extensiform (**P**). The gallery includes the lectotypes of *Didymograptus eocaduceus* (**H**) and *Didymograptus hemicyclus* (**K**). **A**: NMV P331436; **B**: NMV P331499; **C**: NMV P331389; **D**: NMV P318188; **E**: NMV P319254; **F**: NMV P42445; **G**: NMV P323912; **H**: NMV P13800; **I**: NMV P331506; **J**: NMV; **K**: NMV P13797; **L**: NMV P323974; **M**: NMV P331720; **N**: NMV P319252; **O**: NMV P331968; **P**: NMV P311706. All are from PL 2017, also known as the 'Good bed', parish of Campbelltown, from the lower *Tshallograptus* Biozone (Be1, VandenBerg 2017b).

1974 *Didymograptus eocaduceus* Harris 1933; Beavis & Beavis, p. 191, figs 4a, b
1974 *Didymograptus hemicyclus* Harris 1933; Beavis & Beavis, p. 191–193, figs 4c, d
1974 *Isograptus hemicyclus* (Harris, 1933); Tsay, pp. 92–93, text-fig. 27, pl. 9, figs 5, 6
non 1979 *Didymograptus* sp. cf. *D. hemicyclus* Harris, 1933; Cooper, p. 71, figs 43a–c
non 1986 *Didymograptus* cf. *D. hemicyclus*; Lenz & Jackson, fig. 6L
1991 *Didymograptus hemicyclus* Harris; Rickards & Chapman, pp. 73–74; text-figs 132, 152, pl. 23, figs c, d
1991 *Didymograptus eocaduceus* Harris; Rickards & Chapman, pp. 74; pl. 23, figs a, b
non 2002 *Didymograptus eocaduceus* Harris; Mu et al., pp. 308–309, pl. 91, figs 23, 24
non 2002 *Didymograptus* cf. *hemicyclus*; Mu et al., 309, pl. 90, figs 7, 8, pl. 91, fig. 18

Diagnosis. *Harrisgraptus* with tubarium having stipes ranging from strongly reclined, parallel to slightly convergent, to horizontal; sicula 1.2–1.7 mm long provided with short, very slender nema; sicula and proximal thecae adorned with prominent rutella; thecae have curved ventral walls.

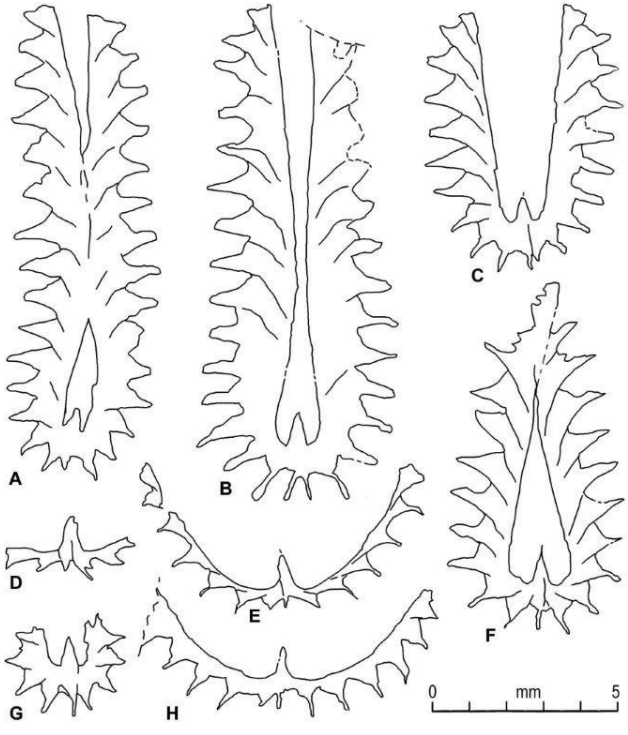

Figure 2: Drawings of the best-preserved tubaria of *Harrisgraptus eocaduceus.* The gallery includes the lectotype (**C**) and two paralectotypes of *Didymograptus eocaduceus* (**A, G**) (Harris 1933, pl. 6, figs 8a, 8b and text-figs 64 and 66), and the lectotype of *Didymograptus hemicyclus* (**H)** (Harris 1933, text-fig. 68 and pl. 6 fig. 4). Stipes in **A** and **F** are not fused but overlap slightly. **A**: NMV P42445; **B**: NMV P323912; **C**: NMV P13800; **D**: NMV P324161; **E**: NMV P 331968; **F**: NMV P319254; **G**: NMV P 332228; **H**: NMV P13797.

Lectotype. NMV P13800, from PL 2017, the 'Good bed', parish of Campbelltown, designated Beavis & Beavis (1974, p. 191) (Figures 1H and 2C).

Referred material. Paralectotypes P42718 (Figures 4C), P42445 (Figure 1F) (Harris 1933, text-figs 64, 66 and 67 respectively) and P323908. One additional paralectotype figured by Harris (text-fig. 65) has not been found. All material studied is lodged in the National Museum of Victoria (NMV).

Material and distribution. Thirty-eight measured specimens, of which one is from loc. A89, parish of Eppalock, three are from loc. S16A ('Molloy's'), allotment II, parish of Sandon, and the remainder from PL2017, the "Good bed", parish of Campbelltown. None show evidence of tectonic deformation (Figures 1–4). The species also occurs at S13 ('Oliver's common'), S19 NW, S22B, S26 and S36, all in the parish of Campbelltown and mostly collected by Thomas Smith. Specimens from S19 NW, S22B and S36 show significant tectonic deformation. All are from Be1, the lower *Tshallograptus fruticosus* Biozone (early Floian) (VandenBerg 2017b). The species is only known from Victoria.

Almost all specimens are preserved as brown or orange ferric oxide stains on pale brown bedding planes. The positions of interthecal septa can be seen in a few specimens by the density of the staining, but the proximal regions in virtually all specimens are too heavily stained to show such details.

Description. The length of the sicula is unusually variable, ranging from 1.2–1.8 mm. This is slightly shape-dependent: in U-shaped tubaria the length ranges from 1.00–1.85 mm, whereas in more open tubaria it ranges from 0.85–1.35 mm. The sicula is 0.4–0.6 mm wide at the aperture. It is straight to slightly curved and its longitudinal axis is distinctly asymmetrical with respect to the tubarium,

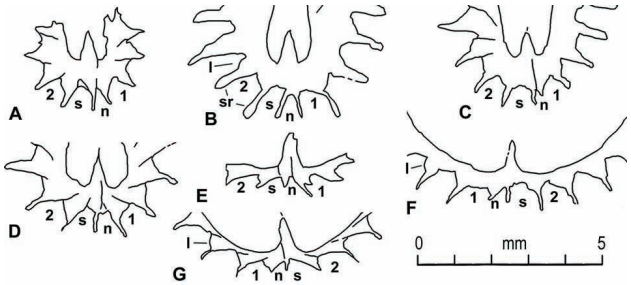

Figure 3: Proximal portions of selected tubaria showing various features. Apertures of the proximal thecal pair are th1[1] (1) and th2[1] (2), and s is the aperture of the sicula. Note the variable appearance of the notch (n) between the distal portions of the sicula and th1[1], and of thecal apertures, some of which have thecal lappets (l). Spatulate rutella are labelled sr. **A**: NMV P 332228; **B**: NMV P323912; **C**: NMV P13800; **D**: NMV P319254; **E**: NMV P324161; **F**: NMV P13797; **G**: NMV P 331968.

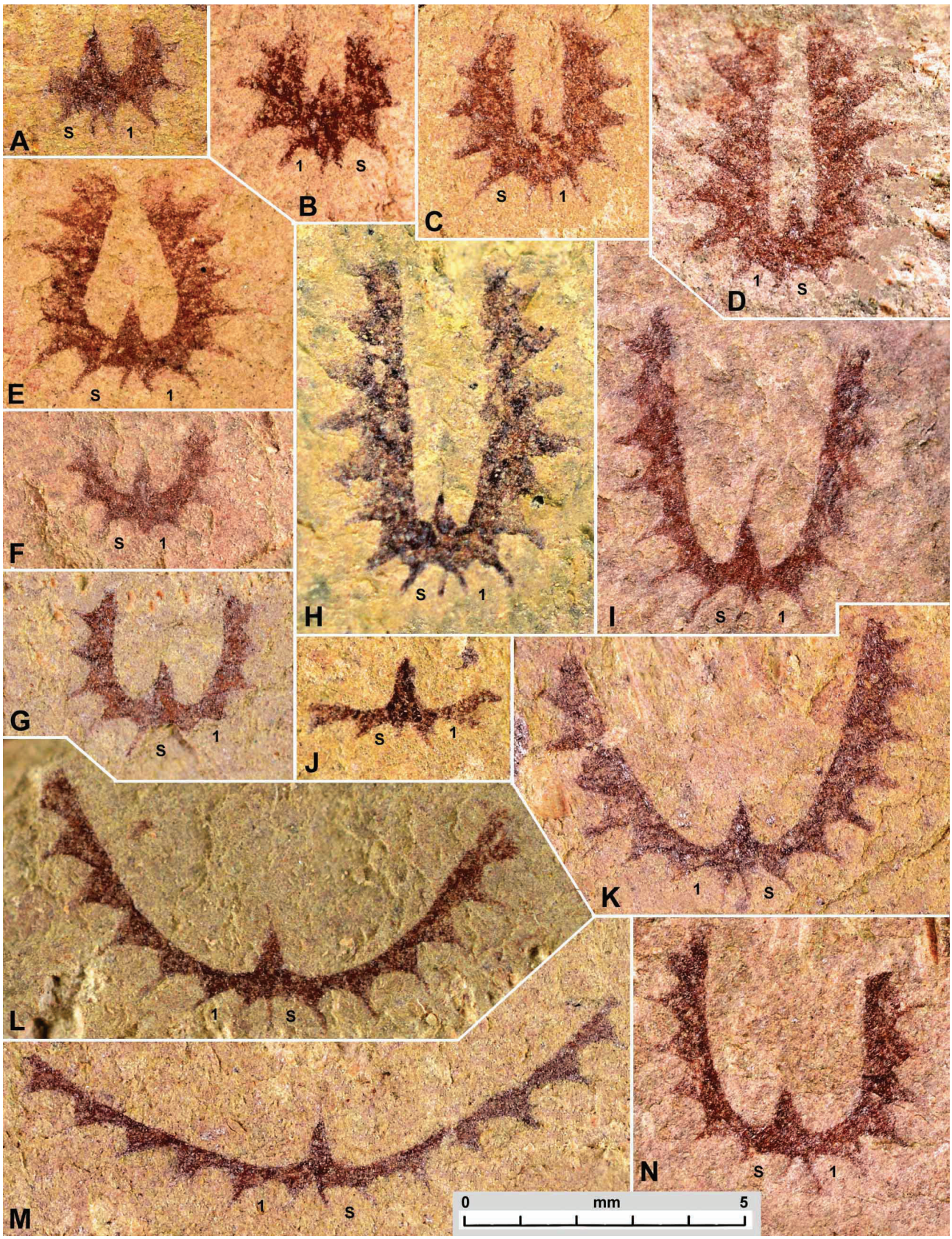

Figure 4: Early and intermediate growth stages of *Harrisgraptus eocaduceus* arranged to show the morphological range from narrowly U-shaped, wide-stiped morphs (A–D) and more slender stipes (E–H) to broadly reclined morphs with slender stipes (L, M) and an extensiform morph (J) at the other extremity of the shape spectrum. S and 1 are placed near the apertures of the sicula and th1[1] respectively. **A**: NMV P319253; **B**: NMV P328388; **C**: NMV P42718 (a paralectotype, pl. 6, fig. 8b in Harris 1933); **D**: NMV P324066; **E**: NMV P318188; **F**: NMV P319260; **G**: NMV P331436; **H**: NMV P331389; **I**: NMV P323914; **J**: NMV P324161; **K**: NMV P319251; **L**: NMV P323973; **M**: NMV P319252; **N**: NMV P323915. All are from PL 2017, also known as the 'Good bed', parish of Campbelltown, from the basal Bendigonian *Paratetragraptus approximatus* + *Tshallograptus* Biozone (VandenBerg 2017b).

'leaning' towards stipe 2 at an angle of up to 10°. The ventral side of the sicular aperture is furnished with a slender but prominent rutellum up to 0.9 mm long (Figure 3). Th1[1] originates high on the sicula and grows beyond the sicular aperture for a variable distance ranging from 0.25 mm to 0.6 mm. The sicula and th1[1] together form a nearly symmetrical structure that protrudes above the dorsal stipe margins for a distance of 0.7–0.9 mm (Figure 3). A V-shaped notch similar to that in *Isograptus* (e.g. Cooper 1973, fig. 5) occurs where the sicula and th1[1] separate, but unlike in *Isograptus*, its position is rarely along the plane of symmetry of the tubarium.

Thecae are ventrally curved, with the curvature increasing towards the aperture. Thecal walls are inclined at angles that vary both from individual to individual and within individual tubaria. Within this variability, a trend can be seen: in U-shaped tubaria the ventral walls are at considerably higher angles to the dorsal stipe margin than in broadly arcuate specimens, but this is probably more a function of stipe width, which decreases with increasing 'reclinedness' of the tubarium (Figure 5). In some tightly U-shaped tubaria, the most proximal thecae have 'negative' inclination — i.e. they are declined, with the remainder of thecae inclined upwards at angles of 90–60° (Figure 5). With increasing 'reclinedness', thecal walls become less inclined and in broadly reclined tubaria such as NMV P 331968 (Figure 3E), walls are inclined at 24–45° from the dorsal margin. In NMV P331706, which is essentially horizontal, the inclination is as low as 15–25° — it also has very slender stipes, 0.6–0.8 mm wide (Figures 1P, 5). Stipe width decreases with increasing 'reclinedness' (Figure 5, Table 1): in NMV P 13797, the lectotype of *Didymograptus hemicyclus* (Figure 1K) they are 0.5–1.10 mm wide, while in NMV P13800, lectotype of *Didymograptus eocaduceus* (Figure 1H) they are 1.4–1.9 mm wide. Correspondence between stipe width and tubarium shape is not uniform, however. In U-shaped tubaria, maximum stipe width can range from as low as 1.1 mm (NMV P331436, Figures 1A, 3G) to as high as 2.3 mm (NMV P323912, Figure 1B), i.e. differing by a factor of 2.

Rates of stipe widening similarly show much variation. Stipes with maximum width in excess of 2 mm can reach

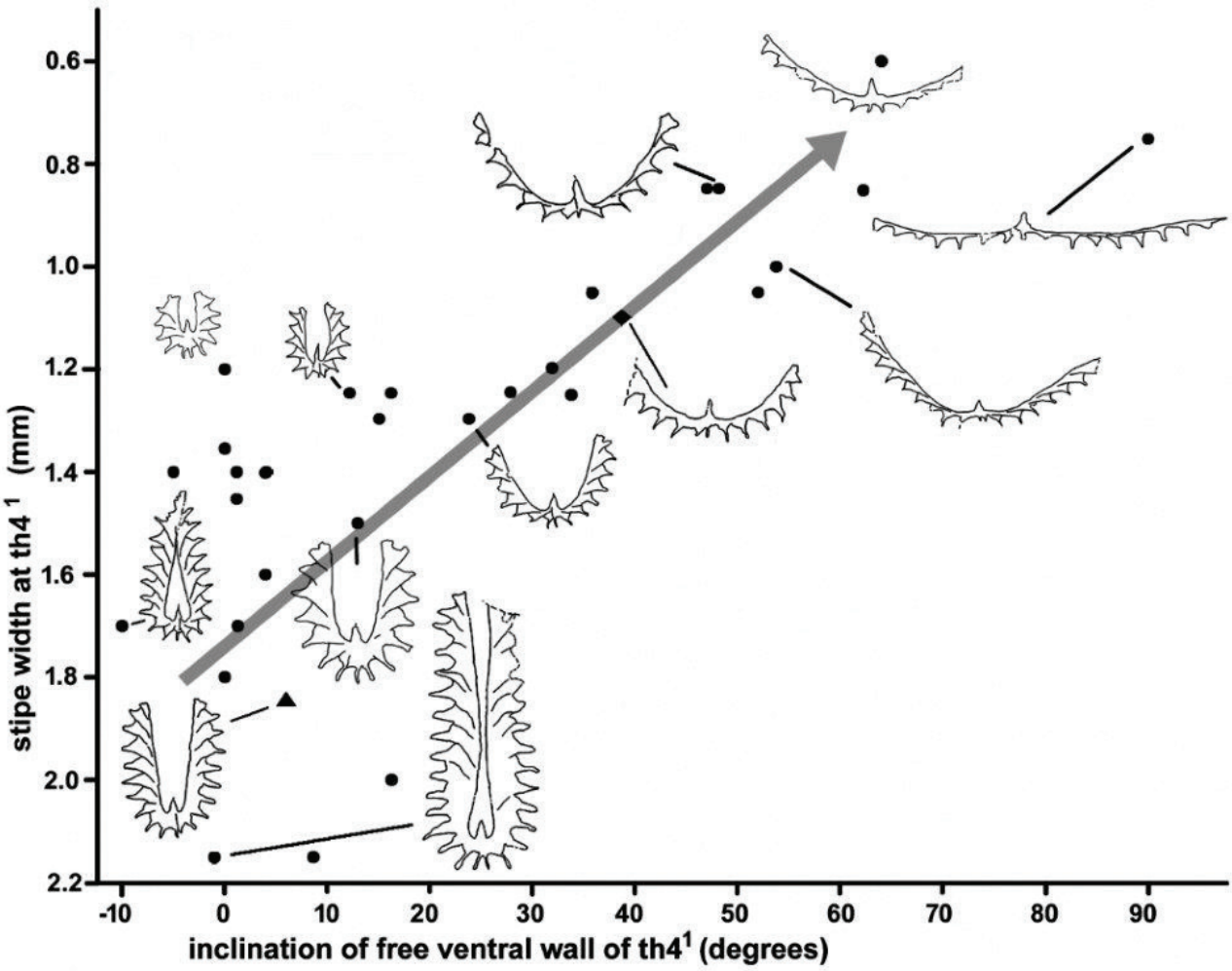

Figure 5: Scatter diagram showing the correlation of the tubarium shape of *Harrisgraptus eocaduceus* with the inclination of the thecal free ventral walls and stipe width. Negative angles are of downward-growing thecae. Note that stipe width on the vertical axis increases downwards. The arrow follows the increasing 'reclinedness'. The diagram includes the lectotypes of *Didymograptus eocaduceus* (triangle) and *D. hemicyclus* (diamond).

that width at th3, th4 or th5. Width is, however, shape-dependent: of tubaria with stipes with widths of 1.5 mm or more, 6 (of 9) have shape 1 (see Table 1 for shape classes), 6 (of 7) have shape 2, 1 (of 5) has shape 3, and none have shapes 4 and 5.

Rutella similar to the sicular rutellum project from the ventral margins of proximal thecae and are of similar length (0.35–0.75 mm, exceptionally 0.9 mm). In the proximal two or three pairs of thecae, the rutella are distinct from the apertures, projecting at a high angle from the apertural margin, but this distinction disappears rapidly (e.g. Figures 2B, F, 4G–I, L), or in some specimens more gradually, and ultimately the rutellum itself disappears (Figures 2B, C, F). In a few specimens, the most proximal rutella have broad, blunt terminations and appear to be spatulate (Figures 1B, 2B, 3B, G). Lateral apertural margins appear either straight of slightly concave but in some, the curvature is convex (outward) suggesting the presence of apertural lappets (e.g. Figures 2B, G, and particularly 2H, the lectotype of *D. hemicyclus*). Thecal spacing (2TRD) measured at th5 ranges from 1.4 mm to 2.1 mm and is not dependent on shape.

Table 1: Maximum stipe width of selected measured specimens of *Harrisgraptus eocaduceus.*

	Reg No	**Stipe widths @**						
	(NMV P)	**th1**	**th2**	**th3**	**th4**	**th5**	**th7**	**th10**
1	42445	1.55	1.35	1.40	1.70	1.85	1.85	1.85
2	318188		1.15	1.40		1.30	1.20	
3	319254	1.10	1.40	1.70	1.70	1.85	?	
4	323912	1.70	1.75	2.20	2.15	2.25	2.30	2.30
5	331394	1.05	1.35	1.20	1.15	1.40		
6	331501	0.90	1.20	1.30	1.40	1.40	1.35	
7	331502	1.50	1.60	1.70	1.60	1.60		
8	331544	1.40	1.75	1.30	1.40	1.45	1.35	
9	331645	1.20	1.45	1.60	1.40	1.70	1.70	
10	42718	1.35	1.35	1.20	1.20	0.95		
11	324066	1.25	1.20	1.40	1.80	1.75		
12	328129	1.70	1.75	1.70	2.00	1.95	2.00	
13	331972	1.30	1.40	1.35	1.35	1.30		
14	13800	1.40	1.35	1.60	1.85	1.90	1.70	
15	331389	1.35	1.30	1.60	1.70	1.70	1.55	
16	331436	1.10	0.95	1.00	0.80	0.80		
17	319251	0.90	0.80	1.20	1.30	1.40		
18	323908		1.35	1.30	1.25	1.40	1.25	0.75
19	323914	1.25	1.20	1.15	1.30	1.20		
20	331940	1.80	1.85	2.00	2.10	2.20	2.00	
21	13797	1.00	1.05	1.10	1.10			
22	319252	0.65	0.85	0.85	0.85	0.8		
23	323938	0.70	0.90	1.00	1.05	1.00		
24	323941	0.70	0.60	0.85	0.85	0.85	1.00	
25	323974	0.65	0.85	1.00	1.00		1.20	
26	331391	0.85	1.00	0.95	1.05	1.10		
27	331498	0.75	1.20	1.20	1.20	0.95		
28	331717	0.90	0.75	0.65	0.60		0.75	
29	331720	1.10	1.00	1.10	1.05	0.95	0.75	
30	331968	0.65	0.90	0.85	0.85	0.90		
31	331706	0.60	0.80	0.70	0.75	0.80	0.35	

Specimens are arranged by shape; 1–9 are horse-shoe shaped, 10–16 are U-shaped, 17–21 are V-shaped (with rounded proximal region), 22–30 are broadly reclined, 31 is horizontal.

Discussion. In the original descriptions of *Didymograptus eocaduceus* and *D. hemicyclus*, Harris (1933) was less influenced by the superficial resemblance of the former with *Isograptus caduceus* than its structure, although he stressed that the proximal structure was much simpler in *D. eocaduceus* and that it did not belong to *Isograptus*. Surprisingly, perhaps, he made only passing reference to its similarity with *D. hemicyclus*, stating that this form 'cannot be mistaken for any other, except possibly, when more than usually robust, for a *D. eocaduceus* narrower than usual'. He described the thecal apertures as having 'denticles' (rutella) in both species, but made no mention of the siculae having one.

Berry (1966) redescribed '*Didymograptus hemicyclus*' and confined his description to six specimens, one of which, NMV P13797, was designated the lectotype. Berry referred to the spine on the sicula as the virgella. Unfortunately his two illustrations are of little help in interpreting the proximal area and nature of the rutella and, contrary to the information supplied, are not both of the lectotype but of different specimens — pl. 49 fig. 6 is possibly of P43708 but the illustration is too poor to be certain. Berry made no reference to a possible similarity with '*Didymograptus eocaduceus*'.

Beavis and Beavis (1974) redescribed both '*Didymograptus eocaduceus*' and '*D. hemicyclus*', mentioning the rutella ('denticle') in *eocaduceus* as being 'less prominent than in *Isograptus*'. It is uncertain how much attention they paid to details of the thecal apertures: in their illustration of the holotype of *H. eocaduceus* (P13800, fig. 4a) they illustrate hair-like structures at the ventral apertural lips in three thecae ($th3^1$, $th5^1$ and $th6^1$), whereas these structures are the tapering extensions of the free ventral walls, which are present on the first five thecae on both stipes (see Figure 2C). The lectotype of '*D. hemicyclus*' (P13797, Figures 1K, 2H, 3F), which has more pronounced rutella (Figure 2H) was drawn without any such structures (their fig. 4c) and their description makes no mention of them.

Several authors have illustrated and described graptolites ascribed to either *Didymograptus eocaduceus* (or *D.* cf. *eocaduceus*), or to *Didymograptus* (cf.) *hemicyclus.* These include Cooper (1973, *D.* cf. *eocaduceus*, text-figs 6d); Tsay (1974, *Isograptus hemicyclus* , pl. 9 figs 5, 6, text-fig. 27); Lenz & Jackson (1986, *Didymograptus* cf. *hemicyclus*, fig. 6L); and Mu et al. 2002 (both *hemicyclus* and *eocaduceus*; pl. 90, figs 7, 8, pl. 91, figs 18, 23, 24. All are superficially similar to the Victorian species but none can be assigned to *Harrisgraptus* with any confidence–all lack the elongated proximal rutella typical of the genus. Most are from much younger strata. It therefore seems that *Harrisgraptus* is endemic to Victoria.

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Conflict of interest

The author declares no conflicts of interest.

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