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Part V, Second Revision, Chapter 27: Superfamily Monograptoidea and Family Dimorphograptidae: Introduction, Morphology, and Systematic Descriptions

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PART V, SECOND REVISION, CHAPTER 27: SUPERFAMILY MONOGRAPTOIDEA AND FAMILY DIMORPHOGRAPTIDAE: INTRODUCTION, MORPHOLOGY, AND SYSTEMATIC DESCRIPTIONS

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Superfamily MONOGRAPTOIDEA Lapworth, 1873

[Monograptoidea Lapworth, 1873, table 1, facing p. 555] [*nom. correct.* Melchin & others, 2011, p. 294, *pro* Monograptidae Lapworth, 1873] [incl. suborder Monograptina Lapworth, 1880, p. 191, *nom. correct.* Obut, 1957, p. 18, *pro* Monograpta (Monoprionida) Lapworth, 1880, p. 191]

Biserial to uni-biserial and uniserial graptoloids with pattern J or derived pattern astogenies (patterns J, M, N); colony shape and thecal style highly varying; cladial branching and secondarily multiramous colonies common in taxa with pattern M astogeny. *Upper Ordovician (Hirnantian,* Metabolograptus persculptus *Biozone)–Lower Devonian (Pragian,* Uncinatograptus yukonensis *Biozone):* worldwide.

Melchin (1998, Table 1) referred the families Dimorphograptidae and Monograptidae to the Diplograptoidea and did not differentiate the Monograptoidea, following Mitchell (1987), who regarded the Monograptinae as a subfamily of the Monograptidae (see Neograptina in Melchin & others, 2011).

Fortey, Zhang, and Mellish (2005, p. 1255) introduced the name Monograptoidea but did not discuss the concept. Melchin and others (2011, p. 294) defined the Monograptoidea as “the most recent common ancestor of *Avitograptus avitus* and *Monograptus priodon* and all of its descendants,” and referred to node 1 in their figures 2 and 3 (2011, p. 284, 286), thus defining the taxon by the reference to a cladistic diagram (see Fig 1). The analysis of Melchin and others (2011, fig. 7) showed the Monograptoidea as a monophyletic clade with possible ancestral relationships to the genera *Normalograptus* Legrand, 1987 and *Avitograptus* Melchin & others, 2011, as an intermediate step to the akidograptids (*Akidograptus* Davies, 1929; *Parakidograptus* Li & Ge, 1981). The authors recognized the families Dimorphograptidae and Monograptidae as members of the Monograptoidea.

Family DIMORPHOGRAPTIDAE Elles & Wood, 1908

[Dimorphograptidae Elles & Wood, 1908, p. 347] [=Heteroprionidae Tullberg, 1883, p. 14; incl. Akidograptinae Li & Ge, 1981, p. 227]

Biserial and uni-biserial axonophoran graptoloids with a pattern J astogeny or a derived one; th1^2 absent in derived taxa with proximally uniserial tubarium; length of uniserial portion variable; colonies commonly septate with straight median septum, but median septum may be delayed; sicula may bear an ancora. *Upper Ordovician (Hirnantian,* Metabolograptus persculptus *Biozone)–Silurian (Llandovery, Rhuddanian,* Coronograptus cyphus *Biozone):* China, Russia, Australia (Victoria), Belgium, UK, Denmark, Sweden, Norway, Spain, Canada, USA, Argentina.

Elles and Wood (1908) originally defined the Dimorphograptidae as uni-biserial graptolites with a uniserial proximal portion and a biserial distal colony portion, following the original concept of Tullberg’s (1883)

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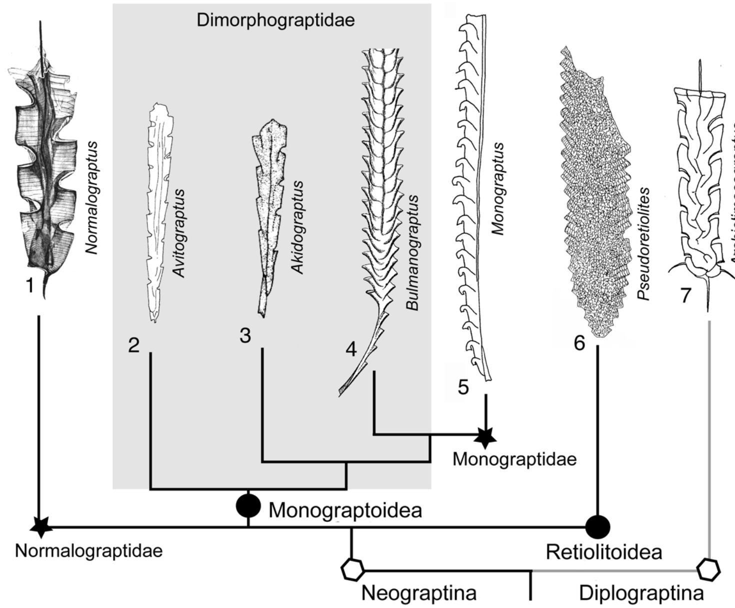

FIG. 1. Diagram showing the concept of the Dimorphograptidae (in gray box), following MELCHIN and others (2011). Specimen examples include: *1, Normalograptus brevis* (ELLES & WOOD, 1906); *2, Avitograptus avitus* (DAVIES, 1929); *3, Akidograptus ascensus* (DAVIES, 1929); *4, Bulmanograptus swanstoni* (LAPWORTH, 1876); *5, Monograptus priodon* (BRONN, 1835); *6, Pseudoretiolites perlatus* (NICHOLSON, 1868); *7, Archiclimacograptus* sp. (new, diagram adapted from data in Melchin & others 2011, fig. 2; graptolite specimens from various sources, not to scale).

Heteroprionidae. ELLES and WOOD (1908, p. 348) suggested the name change with the only argument being "to bring it into harmony with the names of the other families of the Graptoloidea." The change has been universally accepted, and the term Heteroprionidae is no longer used. LI (1987) discussed a possible independent origin of several lineages of dimorphograptids but did not include details of the proximal development. The idea was supported by the cladistic analysis of MELCHIN and others (2011), showing the presence of uni-biserial genera in more than one place in their cladistic interpretation. A uni-biserial development can be found independently in *Agetograptus* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968; *Dimorphograptoides* KOREN' & RICKARDS, 1996; and *Rhaphidograptus* BULMAN, 1936.

ŠTORCH and SERPAGLI (1993) emended the Akidograptinae, originally referred to the Orthograptidae (see LI & GE, 1981), and included the subfamilies Dimorphograptinae and Akidograptinae in the Dimorphograptidae. They changed the original concept of the Dimorphograptidae of TULLBERG (1883) considerably by including normal biserial taxa. KOREN' and RICKARDS (1996) elevated the Akidograptinae to family rank and kept the Dimorphograptidae and Akidograptidae as separate families. MELCHIN (1998, p. 301) provided a detailed diagnosis of the Dimorphograptidae. He indicated a pattern J astogeny with uni-biserial or fully biserial tubarium, a long, fully exposed sicula, variable thecal form, and a fully or partly septate tubarium. MELCHIN and others (2011, p. 295) defined the Dimorphograptidae as the "partial clade that includes the common ancestor of *Avitograptus avitus* and *Monograptus priodon* and all of its descendents, including *Dimorphograptus elongatus,* but excluding those taxa included in the family Monograptidae (i.e., excluding the uniserial monograptids)." The taxon is a paraphyletic clade at the base of the traditional

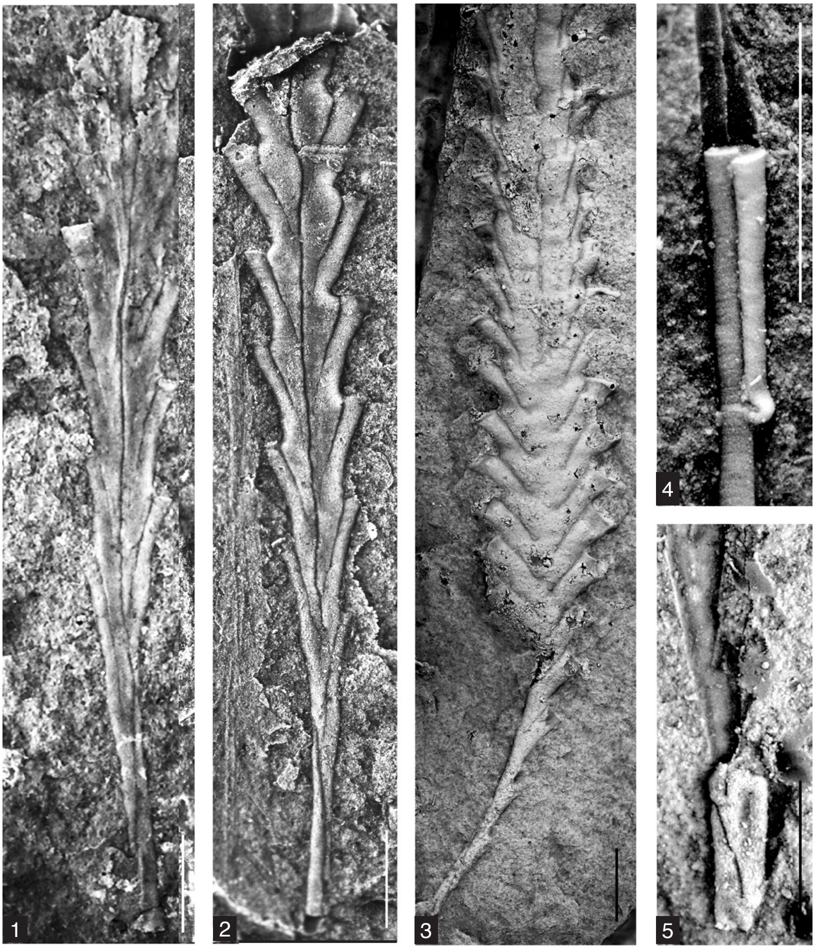

FIG. 2. *1–2, Parakidograptus acuminatus* (NICHOLSON, 1867); *1,* LO 1283t, obverse view, low relief, latex cast, Tomarp, Scania (new; drawing in Törnquist, 1897, pl. 2,*6*); *2,* LO 1284t, reverse view, low relief, latex cast, Tomarp, Scania (new; drawing in Törnquist, 1897, pl. 2,*7*); *3, Bulmanograptus swanstoni* (LAPWORTH, 1876), LO 476t, reverse view, latex cast, showing delay of median septum on reverse side, Bollerup, Scania (new; drawing in Kurck, 1882, fig. 5–6); *4, Huttagraptus acinaces* (TÖRNQUIST, 1899), LO 11856t, specimen showing origin and initial growth of th1, Röstånga drill core, Scania (Maletz & others, 2014, fig. 1*F*); *5, Dimorphograptus* sp., reverse view, Röstånga drill core, 33.55–33.62 m (new). Scale bars, 1 mm in all photos.

monograptids, the Monograptidae *s. str.* (see Fig. 1).

MORPHOLOGY

The Dimorphograptidae, as defined by MELCHIN and others (2011), include fully biserial to uni-biserial taxa with a variety of thecal shapes, thus differing considerably from the original concept of TULLBERG (1883), who included only taxa with a uniserial proximal end and a biserial distal end but did not consider the importance of details of the thecal construction. The phylogenetic relationships of many taxa are difficult to establish and the morphological variation of these is extreme.

The colonies of most Dimorphograptidae are slightly dorsally curved at the proximal end, at least in the uniserial part of derived taxa, but this tendency is also seen in *Akidograptus* and *Parakidograptus*. The two genera have colonies with strongly protracted proximal ends and long, slender thecae, either with a distinct geniculum and slightly outwards-inclined, supragenicular thecal walls or with outwards-inclined, ventral thecal walls and without a geniculum (Fig. 2.1–2.2). The thecal overlap is relatively high and the interthecal septa start slightly below the aperture of the previous theca. The straight median septum is complete on the obverse side but slightly delayed on the reverse side, indicating that th2^1 is the dicalycal theca.

PROXIMAL DEVELOPMENT

A pattern J or derived pattern J (J′) astogeny is generally assumed for the Dimorphograptidae (MELCHIN & MITCHELL, 1991; MELCHIN, 1998; MELCHIN & others, 2011), but these patterns are unknown from isolated material. Pattern J astogeny (Fig. 3.1) is supposed to show a very short downward-growing part of th1^1 and a normal biserial development with a distal origin of th1^2 on the upwards-growing part of th1^1 (see pattern H′ astogeny, MELCHIN, 1998, fig. *4B*). While a pattern H and H′ have two foramina at the base of the downward-growing part of th1^1, in pattern J, th1^1 grows directly upwards upon itself and the foramina are lacking (MELCHIN, 1998, fig. 2). In pattern J′ astogeny (Fig. 3.2), the proximal end is uniserial with a variable number of thecae in the uniserial part of the tubarium, and the growth direction of th1^2 is supposedly redirected above the first theca (see MELCHIN & others, 2011, p. 289).

The cladistic implications indicate that *Avitograptus* may be positioned at the base of the Dimorphograptidae and Monograptidae (MELCHIN & others, 2011, fig. 2). Thus, the interpretation of the proximal development of the genus *Avitograptus* is vital for the understanding of the origin of the group. This development is uncertain (MELCHIN & others, 2011, p. 295), as there are no isolated specimens available that show the presence of foramina at the termination of the downward growth of th1^1. A pattern H or I would therefore be an alternative interpretation for *Avitograptus*, not the pattern J astogeny as indicated by MELCHIN and others (2011).

Pattern J astogeny is observed in *Parakidograptus acuminatus* DAVIES, 1929, (Fig. 2.1–2.2) in partial relief and appears to be very similar to the development of early Monograptidae (see LUKASIK & MELCHIN, 1994, 1997; DAWSON & MELCHIN, 2007), in which the first theca does not grow downward but immediately outwards and upwards from its origin (Fig. 2.4). BULMAN (1932) interpreted the development of the closely related *Akidograptus acuminatus* quite differently. He indicated the presence of an initial downward growth of th1^1 and the presence of a reduced th1^2 in the proximal end. This construction has not been verified from further specimens.

A pattern J′ astogeny of *Dimorphograptus* (Fig. 3.2) with a distinct initial downward growth of the first theca and delay of the dicalycal theca (Fig. 3.3) was suggested in an illustration in KOREN’ and RICKARDS, 1996 (fig. 22*j*) but is not known from relief specimens.

DELAY AND DEVELOPMENT OF TH1^2

The earliest members of the Dimorphograptidae can be described as simple biserial axonophoran graptolites with an indeterminate proximal end. However, the name *Dimorphograptus* is generally related to taxa with a uniserial proximal end and a biserial distal end, in which the uniserial proximal end is formed through the redirection of th1^2 (pattern J′ astogeny). The length of the uniserial proximal end can range from one to numerous thecae and appears to be constant in length within each species. The delay of th1^2 development, the “dimorphograptid condition” of MELCHIN (1998, p. 278), may have developed at least four times in the evolution of Silurian axonophorans according to RICKARDS, HUTT, and BERRY (1977) and LI (1987), whereas MITCHELL (1987) thought this pattern arose only once. However, in the absence of isolated material for most taxa, this suggestion has not been verified.

Melchin and others (2011) recognized the origin of the aseptate genus *Agetograptus* with a delayed th1^2 as being independent from *Rivagraptus* and suggested these genera were derived from a *Glyptograptus*-type ancestor (Melchin & others, 2011, fig. 7). These authors did not include the genus *Dimorphograptoides* Koren’ and Rickards, 1996, in the analysis but thought that it might be closely related to *Pseudorthograptus obuti* (Rickards & Koren, 1974) which shows similar development, thereby suggesting another independent origin of an uni-biserial colony development. The proximal end illustrated by Bulman (1970, fig. 61), thought to show the development of *Dimorphograptus,* was re-identified as representing a specimen of *Agetograptus* (Melchin, 1998, p. 274).

MEDIAN SEPTUM

The genera *Akidograptus* and *Parakidograptus* show the indication of a complete median septum on the obverse side and a slight delay on the reverse side, indicating a dicalycal theca th2^1 (Fig. 3.1). The median septum is straight or nearly straight as is seen from its trace on the lateral tubarium wall. A relief specimen of *Bulmanograptus confertus* (Nicholson, 1868) from the Röstånga drill core has a complete median septum on the obverse side (Fig. 4.4). A single relief specimen of *Bulmanograptus swanstoni* (Lapworth, 1876) (Fig. 2.3) has four thecae in the uniserial proximal end, followed by eight pairs of alternating theca before the median septum starts on the reverse side. However, for most taxa referred to the Dimorphograptidae, the development of the median septum has not been described and considerable variation may be expected.

THECAL STYLE

The thecal style of the Dimorphograptidae varies between distinctly geniculate thecae with outwardly inclined, supragenicular, ventral thecal walls, to thecae with straight, outwardly inclined, ventral thecal walls. Details of the thecal development are not documented for most taxa. Genicular flanges appear to be absent or at least not visible in flattened specimens. The thecal apertures are straight and range from outwardly inclined to perpendicular to the length of the colony. In *Bulmanograptus confertus* (Nicholson, 1868) and related taxa, the thecal apertures appear slightly convex and bear a distinct apertural thickening. Fragments in ventral preservation show a distinct lateral widening of the thecal apertures associated with the thickened rims and the possible presence of paired apertural spines that are not visible in laterally preserved specimens (Fig. 4.2).

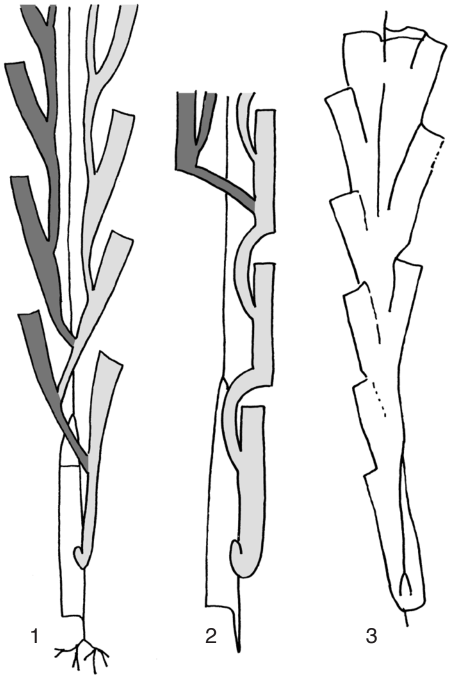

Fig. 3. Proximal development. *1*, *Parakidograptus*, pattern J astogeny (adapted from Štorch & Serpagli, 1993, fig. 4); *2*, *Dimorphograptus,* pattern J′ astogeny, (adapted from Melchin, 1998, fig. 8); *3*, *Dimorphograptus erectus*, showing initial downward growth of th1 in obverse view (adapted from Koren’ & Rickards, 1996, fig. 22*j*).

THE ANCORA

Specimens of *Akidograptus ascensus* and *Parakidograptus acuminatus* often show a distal branching of the virgella (Stein, 1965; Koren’ & Rickards, 1996; Štorch & Feist,

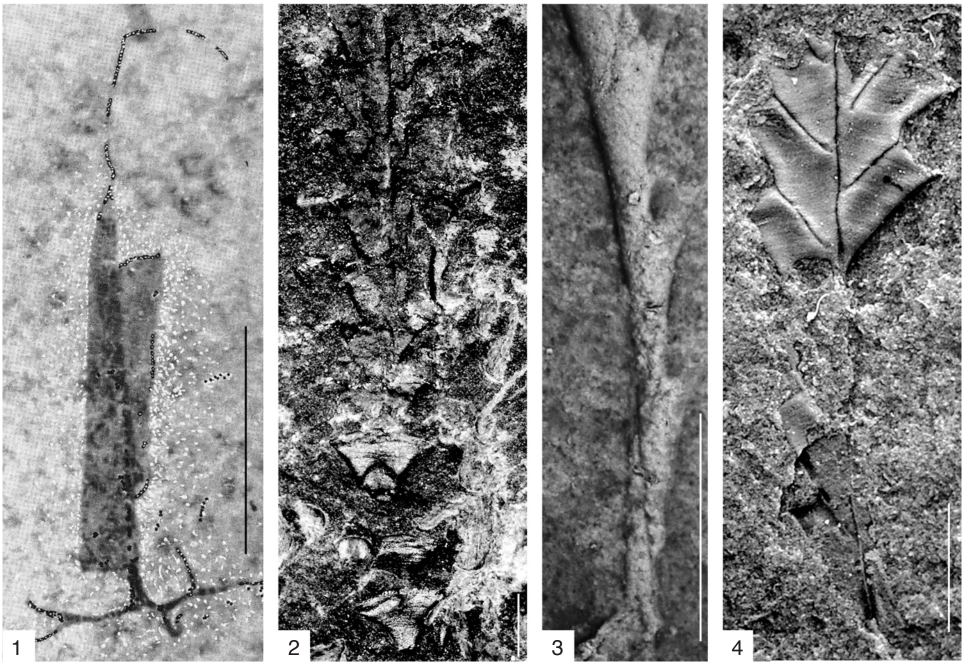

Fig. 4. *1, Akidograptus ascensus* (Davies, 1929), juvenile specimen showing ancora, Göttingen, 506-48 (Stein, 1965, pl. 15*B*); *2, Bulmanograptus* sp., fragment, ventral view, Röstånga drillcore, Scania, 36.40–36.30 m (new); *3, Bulmanograptus swanstoni* (Lapworth, 1876), LO 476t, counterpart, latex cast showing origin of th1 (new); *4, Bulmanograptus confertus* (Nicholson, 1868), Röstånga drillcore, Scania, 38.80–38.70 m, obverse view of distal end with complete median septum, proximal end preserved as a mold (new). Scale bars, 1 mm in all photos.

2008) reminiscent of the ancora umbrella of the Retiolitidae. This construction is best seen in juvenile specimens and is not preserved in most mature material. The construction, similar to that of the ancora of the Retiolitidae, is formed from a short virgellar spine that branches into two bars. At least two further dichotomous branching points may occur in the ancora of *Akidograptus ascensus* (Fig. 3.1; Fig. 4.1). A branched virgellar spine is also documented for a single specimen of *Avitograptus* sp. cf. *Avitograptus avitus* (Melchin & others, 2011, fig. 6*c*) and was shown by Stein (1965) in *Avitograptus avitus*.

Dimorphograptus Lapworth, 1876, p. 545 [**D. elongatus* Lapworth, 1876, p. 547; SD Bassler, 1915, p. 441] [=*Metadimorphograptus* Přibyl, 1948, p. 39 (Czech text), p. 47 (English text) (type, *D. extenuatus* Elles & Wood, 1908, p. 358, OD, herein)]. Straight to proximally curved dimorphograptid with long uniserial part; thecae with distinct geniculum and small, slit-like apertures; proximal development pattern probably of pattern J´ astogeny; biserial portion probably fully septate. *Silurian, (Llandovery, Rhuddanian,* upper Cystograptus vesiculosus *Biozone):* Morocco, China, New Zealand?, UK, France, Germany, Denmark, Sweden, Serbia, Canada (Arctic).——Fig. 6,*1a–b. D. extenuatus* Elles & Wood, 1908; scale bars, 1 mm; *1a,* lectotype (selected by Hutt, 1974, p. 55), UM K736, (Elles & Wood, 1908, pl. 35,*10a*); *1b,* SM A20814, proximal end showing sicula (Přibyl, 1948, fig. 4).——Fig. 6,*1c–e*. **D. elongatus;* scale bars, 1 mm; *1c,* BU 1423, curved specimen (Bulman, 1970, fig. 97,2*B*); *1d,* lectotype, BU 1423, straight specimen (Elles & Wood, 1908, pl. 35,*11a*); *1e,* curved specimen, Bornholm, Denmark, (Koren' & Bjerreskov, 1997, fig. 17*B*).

Akidograptus Davies, 1929, p. 9 [**A. ascensus;* OD]. Biserial monograptoid with protracted proximal end and early upward growth of first two thecae; proximal end probably with pattern J astogeny; thecae slender and elongated, strongly geniculate, with straight apertures lacking genicular flanges. *Silurian (Llandovery, Rhuddanian,* Akidograptus ascensus *Biozone*–Atavograptus atavus *Biozone):* China, UK, Germany, Denmark, Norway, Sweden, Canada (Arctic), USA.——Fig. 5,*2a–b*. **A. ascensus,*

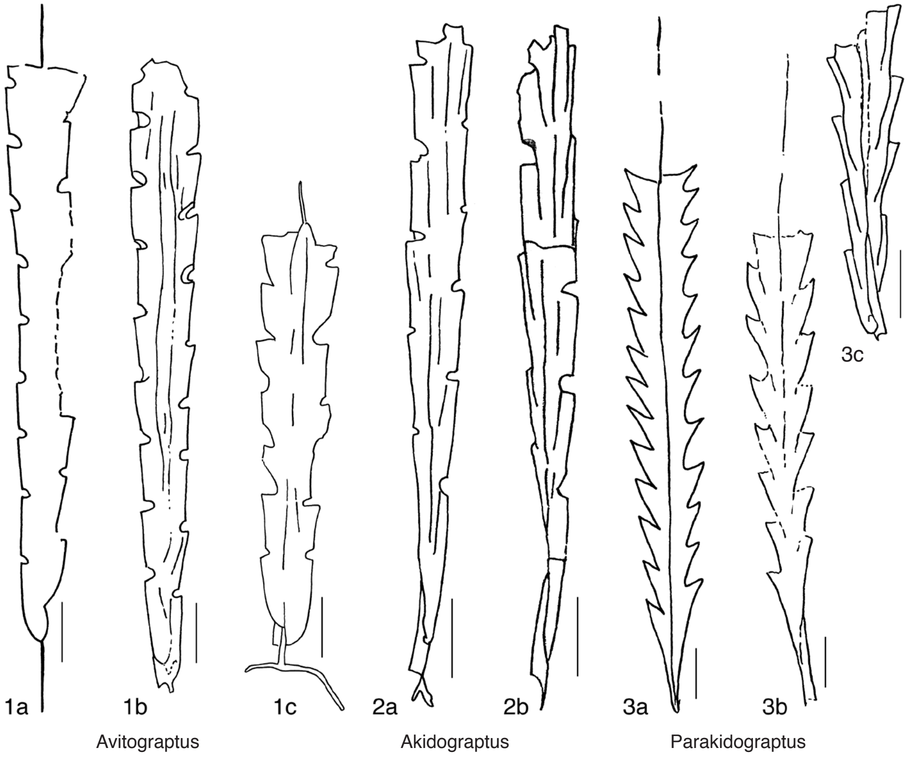

Fig. 5. Dimorphograptidae (p. 6–8)

scale bars, 1 mm; *2a,* holotype, SM A10021 (adapted from Melchin & others, 2011, fig. 6*G*); *2b,* holotype (adapted from Rigby, 2000).

Avitograptus Melchin & others, 2011, p. 295 [**Glyptograptus* (?) *avitus* Davies, 1929, p. 8, fig. 21; OD]. Biserial monograptoid with slender proximal end and possibly pattern J astogeny; th1^1 upturned at level of sicular aperture; th1^2 arises from point low within upward-grown portion of th1^1; thecae geniculate, slightly to moderately inclined; first thecal pair slightly elongated relative to subsequent thecae; complete median septum. *Upper Ordovician* (*Hirnantian*, Metabolograptus persculptus *Biozone*)*–Silurian (Llandovery, Rhuddanian*, Akidograptus ascensus *Biozone):* UK, Germany, Canada (Arctic).——Fig. 5,*1a–b.* **A. avitus* (Davies); scale bars, 1 mm; *1a,* holotype, SM A10019 (adapted from Davies, 1929, fig. 21); *1b,* topotype, GLAHM 131711 (adapted from Melchin & others, 2011, fig. 6*B*).——Fig. 5,*1c. Avitograptus* sp. aff. *A. avitus,* GLAHM 131712, showing branched virgella, scale bar, 1 mm (adapted from Melchin & others, 2011, fig. 6*C*).

Bulmanograptus Přibyl, 1948, p. 39 (Czech text), p. 47 (English text)[**Diplograpsus confertus* Nicholson, 1868, p. 526; OD] [=*Cardograptus* Hundt, 1965, p. 117, herein (type, *C. primus*, M; =*Cardograptus elongatus* Hundt, 1959, p. 19, *nom. nud.,* herein)]. Robust dimorphograptid with slender, often curved, uniserial proximal end of variable length; thecae proximally slender, with high inclination and straight ventral sides in biserial part; biserial part with or without median septum; thecae often with considerably thickened apertural rim. *Silurian (Llandovery, Rhuddanian,* Akidograptus ascensus–Atavograptus atavus *Biozones):* Morocco, China, Russia, UK, Czech Republic, Germany, Poland, Denmark, Sweden, Serbia, USA (Alaska), Canada (Arctic).——Fig. 6,*2a–b.* **B. confertus* (Nicholson); scale bars, 1 mm; *2a,* SM A20699, typical specimen, (Elles & Wood, 1908, pl. 35,*3a*); *2b,* BU 1368, proximal end (Elles & Wood, 1908, fig. 227*a*).——Fig. 6,*2c. B. primus* (Hundt, 1965), holotype, BAF 186/1715, scale bar, 1 mm (new).

Parakidograptus Li & Ge, 1981, p. 229 [**Diplograpsus acuminatus* Nicholson, 1867, p. 109; OD]. Biserial monograptoid with protracted proximal end and early upward growth of first two thecae; proximal end probably with pattern J astogeny; thecae slender and elongated, tubular, with straight, outwards-inclined apertures; median septum complete. *Upper Ordovician (Hirnantian,* Metabolograptus persculptus *Biozone)–Silurian (Llandovery, Rhuddanian,* Atavograptus atavus *Biozone):* China, Australia

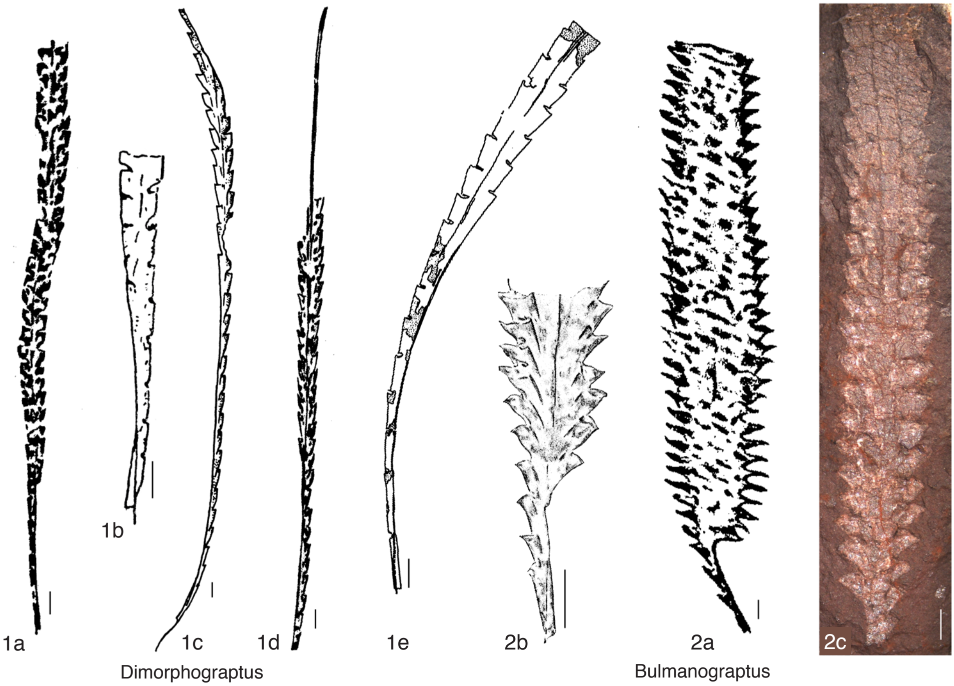

Fig. 6. Dimorphograptidae (p. 6–7)

(Victoria), UK, Czech Republic, Germany, Poland, Denmark, Sweden, Spain, Canada, USA.——Fig. 5,_3a–b._ *_P. acuminatus_ (Nicholson); scale bars, 1 mm; _3a,_ ?NHMUK PM 1310 (adapted from Nicholson, 1867, fig. 16_a_); _3b,_ SM A20672, small specimen (adapted from Elles & Wood, 1908, fig. 199). ——_5,3c. P. acuminatus praematurus_ (Davies, 1929), holotype, SM A10023, specimen showing obverse view and possible downward initial growth of th1, scale bar, 1 mm (adapted from Zalasiewicz, 2008).

ABBREVIATIONS FOR MUSEUM REPOSITORIES

BAF: TU Bergakademie Freiberg, Department of Geology, Germany.
BU: Lapworth Museum, Birmingham University, UK
GLAHM: Hunterian Museum, University of Glasgow, UK
NHMUK PM: The Natural History Museum, London, UK (formerly BMNH)
SM: Sedgwick Museum of Earth Sciences, Cambridge, UK

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