TREATISE ONLINE

Number 108

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2018

KU PALEONTOLOGICAL INSTITUTE
The University of Kansas

Lawrence, Kansas, USA
ISSN 2153-4012
paleo.ku.edu/treatiseonline

PART V, SECOND REVISION, CHAPTER 20: SUBORDER DICHOGRAPTINA: INTRODUCTION, MORPHOLOGY, AND SYSTEMATIC DESCRIPTIONS

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Suborder DICHOGRAPTINA Lapworth, 1873

[Dichograptina LAPWORTH, 1873, table 1, facing p. 555; *nom. transl.* OBUT, 1957, p. 19; *ex* Dichograptidae LAPWORTH, 1873] [=suborder Didymograptina LAPWORTH, 1880, p. 192 *nom. correct.* JAANUSSON, 1960, p. 309; *ex* section Didymograpta LAPWORTH, 1880]

Multiramous to two-stiped graptoloids with biradiate isograptid proximal development and maeandrograptid proximal symmetry; colony shape scandent to reclined, horizontal, and pendent; prosicula small, with widening and much larger metasicula; thecae simple, widening tubes with or without rutellum; a sicular bitheca may be present in early taxa; branching dichotomous or cladial. *Lower Ordovician (upper Tremadocian,* Hunnegraptus copiosus *Biozone)–Middle Ordovician (upper Darriwilian*, Pterograptus elegans *Biozone):* worldwide.

INTRODUCTION

The Dichograptina is one of the two major groups of graptoloids originating from the earliest planktic graptolites of the family Anisograptidae (Fig. 1). According to MALETZ, CARLUCCI, and MITCHELL (2009), the Dichograptina and the Sinograpta (Sinograptina herein) can be regarded as sister groups. However, FORTEY and COOPER (1986) and LINDHOLM (1991) suggested a polyphyletic origin of derived graptoloids (non-bithecate graptoloids) from the Anisograptidae. Thus, the sister group relationship between the Anisograptidae and the supercohort Eugraptoloida (the Graptoloidea of BULMAN, 1970) as shown by MALETZ, CARLUCCI, and MITCHELL (2009) is unlikely to be correct and more research on the transition is needed.

LAPWORTH (1873) understood the Dichograptidae as the group of genera that includes two-stiped to multiramous taxa with simple thecae and dichotomous bifurcation or lateral branching. He listed the genera *Didymograptus*, *Tetragraptus*, *Dichograptus*, *Loganograptus*, and *Clonograptus*. OBUT (1957) erected the suborder Dichograptina for the families Dichograptidae, Tetragraptidae, Bryograptidae, and Didymograptidae, essentially confirming the classification of LAPWORTH (1873) for multiramous to pauciramous Lower to Middle Ordovician graptoloids. However, the name Dichograptina must be credited to LAPWORTH under the provisions of ICZN, 1999, Article 36. BULMAN (1970) used the term Didymograptina LAPWORTH, 1880 but included the Nemagraptidae, Dicranograptidae, and Phyllograptidae, taxa that are not closely related. The Didymograptina of BULMAN (1970) thus is a polyphyletic taxon and should not be used.

FORTEY and COOPER (1986) used the Dichograptina LAPWORTH, 1873 for the

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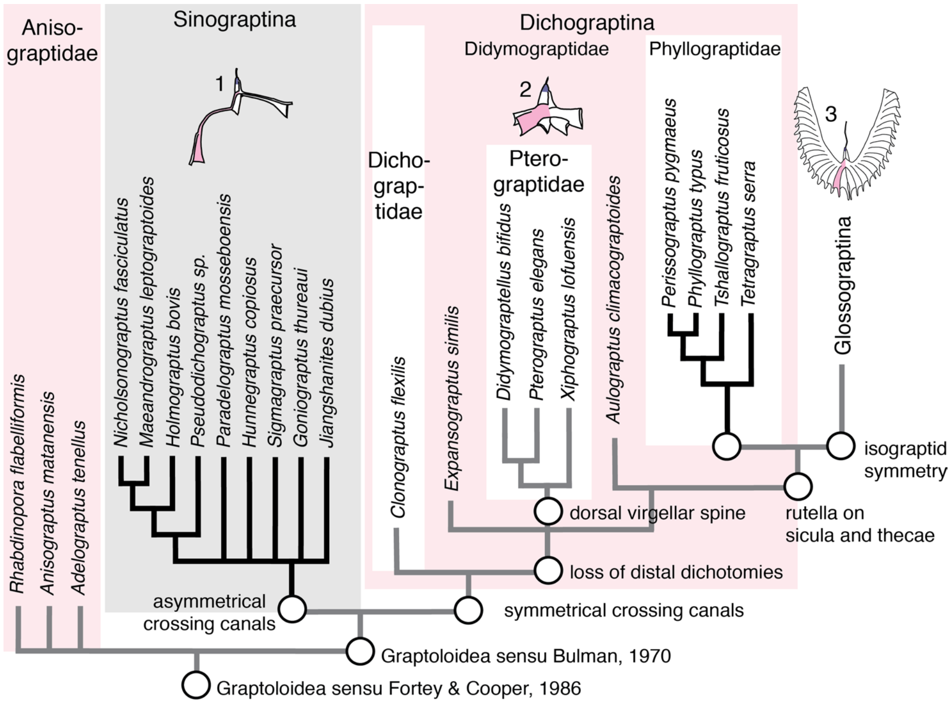


FIG. 1. Cladistic interpretation of the Dichograptina. The diagram also shows the different symmetries of the stipes in the Sinograptina (*1*), Dichograptina (*2*), and the glossograptid *Isograptus* (*3*) (adapted from Maletz, 2014).

non-virgellate graptoloids and introduced the new term Virgellina for all virgellate graptoloids. They defined the Dichograptina as "graptoloids lacking bithecae and virgella" (FORTEY & COOPER, 1986, p. 640) and referred the two superfamilies Dichograptacea and Glossograptacea to the taxon. MALETZ, CARLUCCI, and MITCHELL (2009) introduced the supercohort Eugraptoloida as a monophyletic taxon defining all nonbithecate graptoloids. Of these, the stem reclinatids and the Pan-Tetragrapta would be included in the Dichograptina. MALETZ (2014) referred four families to the Dichograptina: the Dichograptidae, Didymograptidae, Tetragraptidae, and the virgella-bearing Pterograptidae. He discussed the taxon as a paraphyletic unit with poor internal resolution.

MORPHOLOGY

The dichograptid sicula is known from few isolated specimens, and details of its development are unknown for most species, but a number of general features can be recognized (Fig. 2). It is easily differentiated from the sicula in the Sinograptina through the distinctly widening metasicula. The prosicula usually has less than one-quarter of the length of the sicula and widens gradually towards its aperture, as does the metasicula (Fig. 2.5–2.6).

The Dichograptina possess a distinct nema, which is formed as a slender rod at the tip of the prosicula. The nema is of variable length and may be quite long in some taxa, but is rarely modified. It may be thickened considerably as in *Tshallograptus fruticosus,* but true nematularia, common in the Glossograptina and derived taxa, have not been described for the Dichograptina. The differentiation of the conus and cauda (Fig. 2) has rarely been discerned in the prosicula of isolated material of the Dichograptina and may not be present in many taxa. WILLIAMS and CLARKE (1999) illustrated dichograptid siculae from

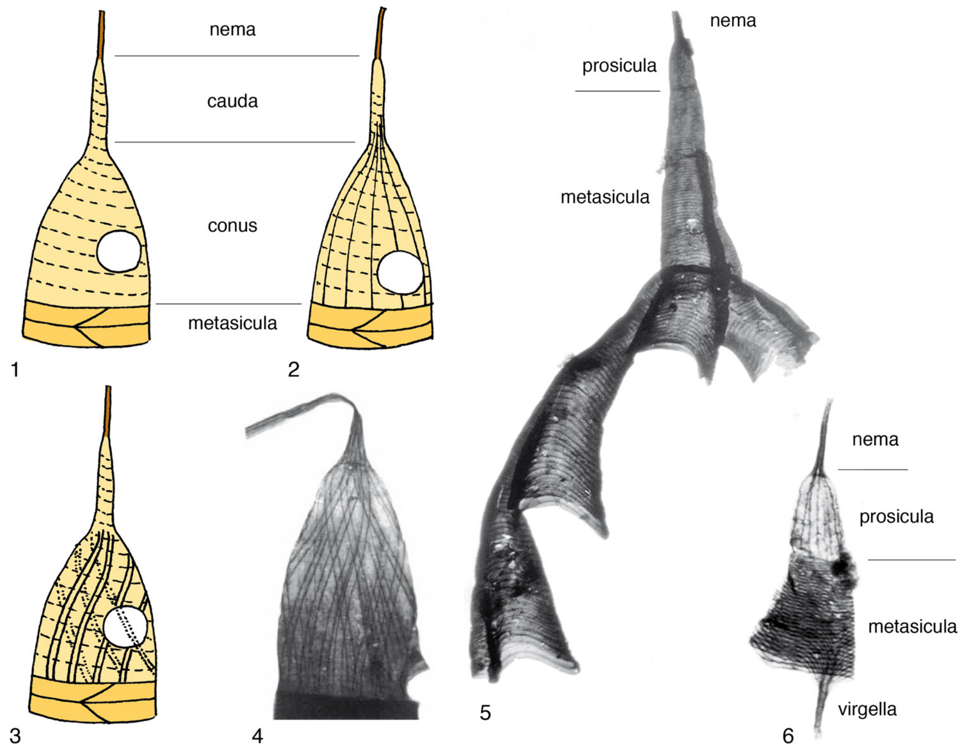


FIG. 2. Development of the sicula in Ordovician graptoloids. *1,* Anisograptidae; *2, Isograptus lunatus* HARRIS 1933; *3, Paratetragraptus approxima*tus (NICHOLSON, 1873); *4, Paratetragraptus approximatus* (NICHOLSON,1873), transmitted light photo; *5, Tshallograptus fruticosus* (HALL, 1858), GSC 125727, isolated proximal end showing fuselli, western Newfoundland; *6, Phyllograptus typus* HALL, 1865, GSC 125754, sicula with virgellar spine and simple longitudinal rods on prosicula, western Newfoundland (*1–4,* adapted from Williams & Clarke, 1999; *5–6,* Maletz, 2004).

a variety of taxa and discussed the reduction of the cauda (not the conus—WILLIAMS and CLARKE, 1999, confused the terms conus and cauda) in early Floian taxa. These authors recognized a number of features modifying the sicula of early dichograptids, such as the differentiation of the pro- and metasicula, the diaphragm, and the development of longitudinal strengthening rods in the prosicula. The prosicula (conus) widens slowly from the apex, usually with a ratio of ~1:2, and often forms a long cone. In some derived taxa, however, the prosicula may be wider than long and form a wide, nearly triangular structure (e.g., *Expansograptus abditus* WILLIAMS & STEVENS, 1988). The spiral line is prominent in many specimens, and the spiral may be most dense towards the apex of the prosicula (the cauda).

Typically, the prosicula has a number of longitudinal rods secreted on the outside of the cone. In tubaria from the late Tremadocian to early Floian, the longitudinal rods are paired (Fig. 2.3–2.4) and often run somewhat obliquely down the prosicula. This is seen in a number of phyllograptids and expansograptids illustrated by WILLIAMS and CLARKE (1999). Individual longitudinal rods can be seen in isograptids and may be characteristic for axonophorans, e.g., *Rectograpus gracilis* (ROEMER, 1861); see KRAFT (1926).

The metasicula is a simple, gradually widening cone formed from numerous fuselli (Fig. 2.5–2.6). It may be straight or moderately to strongly bent or curved. When present, curvature of the sicula is usually most pronounced close to the aperture and may be enhanced by the development of a rutellum.

The sicula is located in the center of the tubarium, and the plane of symmetry (bilateral plane in COOPER & FORTEY, 1982, fig. 8) cuts through it—termed maeandrograptid symmetry. A distinct ventral rutellum may be developed in derived dichograptids, but other apertural modifications of the sicula are rare.

The dorsal virgellar spine developed independently from a simple rutellum in *Phyllograptus* (Fig. 2.6) and in the Pterograptidae. Maletz (2010) discussed in detail the origin and evolution of the dorsal virgellar spine in the genus *Xiphograptus* and related taxa. The early xiphograptid *Didymograptellus* is the only member of this group that shows an origin of $th1^1$ in the middle part of the prosicula combined with an unusually large, parallel-sided prosicula. Both are characters found in the early planktic graptoloids of the family Anisograptidae but have not been recognized in any other Dichograptina. Thus, it may be possible that the pterograptids have an independent origin within the Anisograptidae and are not closely related to the rest of the Dichograptina.

MALETZ, CARLUCCI, and MITCHELL (2009) regarded the symmetrical branching (bifurcation) of the two first-order stipes as the defining character of the cohort Pan-Reclinata, a character that separates its members easily from the often highly asymmetrical development in the Sinograptina (Fig. 1). Both crossing canals grow symmetrically and at the same level across the reverse side of the sicula before forming the first stipes. The proximal end symmetry is maeandrograptid, a plesiomorphic character retained from the Anisograptidae, with the plane of symmetry passing through the sicula. $Th1^1$ and $th1^2$ are symmetrically placed flanking the sicula (Fig. 3.1–3.2).

The origin of $th1^1$ is generally in the lower portion of the prosicula, but in a few taxa it may be in the middle portion (e.g., *Didymograptellus*). A metasicular origin of $th1^1$ has been demonstrated for a few taxa of *Tetragraptus* (see SKEVINGTON, 1965) and from a population of *Tshallograptus fruticosus* (Fig. 2.5) from the *Didymograptellus bifidus* Biozone of western Newfoundland (MALETZ, 2004) but has not been confirmed from other species. It is common in taxa of the Didymograptidae (Figs. 3.3–3.6).

The dichograptinid tubarium is generally based on a biradiate proximal end with $th1^2$ as the first dicalycal theca. However, in a number of taxa, the development may be replaced by an independently derived condition in which the dicalycal theca is $th1^1$ (artus-type development). The change in proximal development type from isograptid (Fig. 3.3–3.4) to artus (Fig. 3.5–3.6) is best known in the genus *Baltograptus*. In the early species *Baltograptus geometricus* (TÖRNQUIST, 1901) and *Baltograptus vacillans* (TULLBERG, 1880), the proximal development is isograptid (MALETZ, 1994a; TORO & MALETZ, 2008), but in some later taxa it is artus type (MALETZ & AHLBERG, 2011; MALETZ & SLOVACEK, 2013). An isograptid proximal development is found in most expansograptids, while *Cymatograptus bidextro* TORO & MALETZ, 2008 has an artus-type development.

The first distal dicalycal thecae in the Dichograptina are $th3^1$ and $th3^2$, forming the tetragraptid proximal end with its biradiate development (MALETZ, 1992). Later dicalycal thecae are often placed irregularly along the stipes to form multiramous colonies and are increasingly delayed distally (LINDHOLM & MALETZ, 1989). Thus, the branching intervals become progressively longer.

The multiramous dichograptids of the family Dichograptidae are the most distinctive graptolites of the Dichograptina. They reached colony diameters of more than 80 cm in *Holograptus deani* ELLES & WOOD, 1902 specimens, similar to the earlier anisograptid *Paratemnograptus magnificus* (PRITCHARD, 1891). Colony development started from the sicula with two, first-order stipes (biradiate condition). Consecutive dichotomous branching led to a multiramous colony with numerous terminal branches (Fig. 4.1). During the evolution of the Dichograptina, the number of branches became reduced and

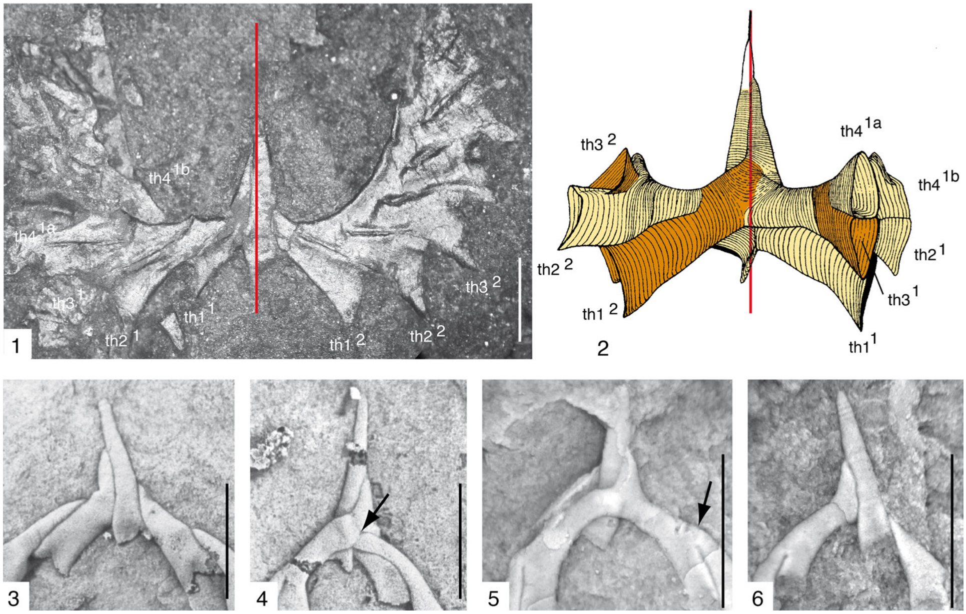


FIG. 3. Proximal development of the Dichograptina. *1, Tetragraptus reclinatus* ELLES & WOOD, 1902, LO 10598t, obverse view, *red vertical line* shows line of symmetry, Lerhamn drillcore, Sweden (new); *2, Tetragraptus* sp., reconstruction of proximal end in reverse view, *red vertical line* shows line of symmetry, dicalycal thecae (th1^{2}, th3^{1}, th3^{2}) in *darker color* (adapted from Bulman, 1970, fig. 53); *3–4, Baltograptus vacillans* (TULLBERG, 1880), PMU 23157, isograptid development in obverse (*3*) and reverse (*4*) views; *5–6, Baltograptus minutus* (TÖRNQUIST 1879), artus-type development in reverse (*5*) and obverse (*6*) views, PMU 23165, Nipan, Jemtland, Sweden, *arrows* in *4–5* indicate origin of th2^{1}; all scale bars, 1 mm (*3–6,* adapted from Maletz, 1994a).

two-stiped Didymograptidae appeared early in the Floian.

Dichograptina encompasses the full range of colony shapes, ranging from scandent (*Phyllograptus*) through reclined (*Tetragraptus*), horizontal, declined, and deflexed to pendent forms (*Didymograptus*). Pendent and deflexed forms are most common in pauciramous taxa. *Tshallograptus fruticosus* is a typical example of a deflexed two- to four-stiped species. Branching in the Dichograptina in general is dichotomous, through a bifurcation, with the stipe divisions typically Y-shaped. With rare exceptions, it only occurs at the growing tips of stipes. Lateral branching is present in some multiramous taxa, e.g. *Schizograptus*, but the precise method of branching in these has not been determined as no relief material or isolated specimens are available. The number of terminal stipes has been regarded as important and was used to differentiate genera and species in the past. It is now generally accepted, however, that the number might be variable and a species of *Dichograptus* does not invariably bear eight stipes. A certain intraspecific variation is to be expected, but additional complications may have been introduced by accidental loss of stipes and damage to the colonies during their lifetime.

Lateral branching is typical in *Pterograptus* species, but here the branching occurs in the form of cladial branching (SKWARKO, 1974; MALETZ, 1994b). The origin of the new stipe is from the aperture of the parent theca. Branching in this case is not at the growing tip of the stipe, but can occur at later stages in the growth of the colony.

The thecae of the Dichograptina are simple, aperturally widening tubes (Fig. 4.2–4.3). They range from straight to strongly

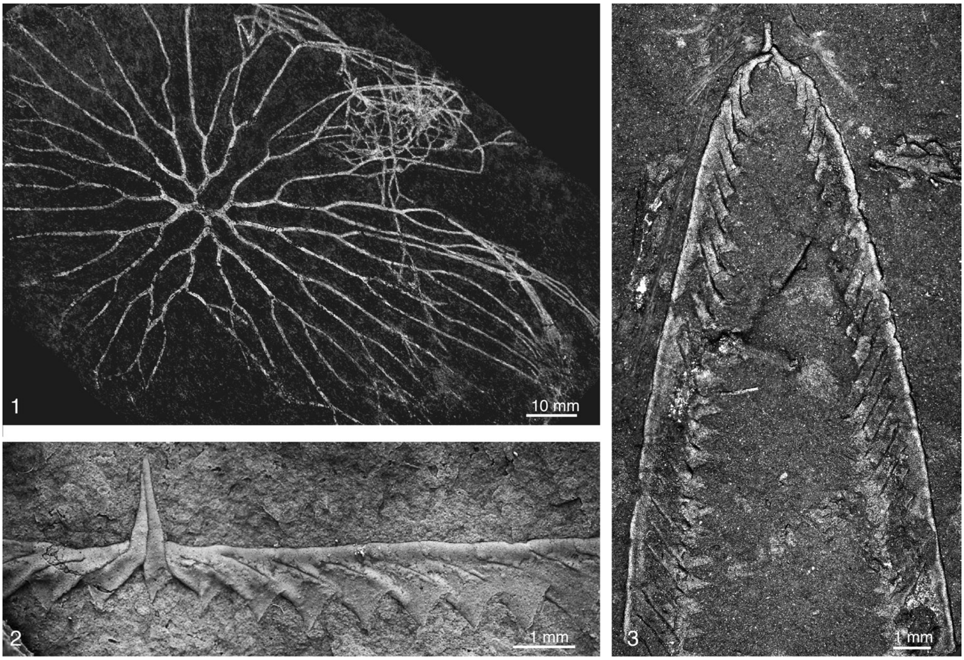


FIG. 4. Main tubarium features of the Dichograptina. *1. Clonograptus flexilis* (HALL, 1865). NMVP 309374, large multiramous colony showing dichotomous branching, Lancefield Quarry, Victoria, Australia, specimen originally illustrated in Morris (1988, Ph.D. thesis) (new); *2, Expansograptus holmi* (TÖRNQUIST, 1904), PMU 23166, latex, obverse view, Diabasbrottet, Västergötland, Sweden (new); *3, Didymograptus artus* (ELLES & WOOD, 1902), PMU 31742, reverse view, showing increase of thecal overlap and curvature, Fågelsångsdalen drill core, 22.9 m, Scania, Sweden, (new).

ventrally curved. Apertural modifications are rare and include extended rutella in some taxa. A few taxa (e.g., *Aulograptus*) develop more complex thecal apertures with genicular flanges and thickened apertural rims. Prothecal folding is present in some taxa. The most pronounced prothecal folding is seen in the genus *Cymatograptus*, but the details of this thecal development are unknown.

In many species with low thecal inclination, the stipes are largely parallel sided and the thecal overlap is low. In other taxa, thecae are larger distally, and the initial parts of the stipes show considerable widening (Fig. 4.3). In some, this widening decreases markedly after the first few thecae, when the zooids apparently reached their maximum size. In others, thecal size increases distally, both in length and apertural width and inclination. This may be due to continued thecal growth after the growing stipe tip has passed them. Thus, thecae may have reached extreme lengths, as in robust specimens of the *Didymograptus murchisoni* (BECK in MURCHISON, 1839) type (e.g., *Didymograptus clavulus* PERNER, 1895; see BOUČEK, 1973; *Didymograptus obesus* WANG, 1974) or in *Didymograptellus bifidus* (HALL, 1865) and related taxa (WILLIAMS & STEVENS, 1988; MALETZ, 1994a).

Family DICHOGRAPTIDAE Lapworth, 1873

[Dichograptidae LAPWORTH, 1873, table 1, facing p. 555] [incl. Schizograptinae GE in MU & others, 2002, p. 201; Mimograptinae GE in MU & others, 2002, p. 316]

Biramous to multiramous graptoloids with biradiate isograptid proximal development, symmetrically placed crossing canals and maeandrograptid proximal symmetry; prosicula small, with widening and much larger conical metasicula; sicular bitheca may be present in early taxa; thecae simple, widening tubes with or without rutellum; branching dichotomous to lateral. *Lower Ordovician* (*upper Tremadocian,* Hunnegraptus copiosus *Biozone)–Middle Ordovician (Dapingian*, Expansograptus hirundo *Biozone*).

Characters found in all Dichograptidae are a biradiate proximal end, a multiramous or pauciramous colony, simple thecae, and the absence of bithecae. Important details of the proximal development of many genera of the Dichograptidae are not clear. Thus, the family and the included taxa are largely based on inference and indirect evidence.

The Dichograptidae must be regarded as a paraphyletic taxon as the relationships to the Didymograptidae and Pterograptidae remain unclear. The roots of the Didymograptidae have not been explored due to the lack of sufficient material. The development of the prosicula and proximal development in the early Pterograptidae (e.g., *Didymograptellus*) similarly suggests that this family may have its roots independently in the Anisograptidae.

Dichograptus SALTER, 1863, p. 136, original spelling as *Dichograpsus* changed in ICZN, Opinion 650, 1963 [**Dichograpsus sedgwicki;* SD GURLEY, 1896, p. 64]. Large multiramous horizontal to subhorizontal tubarium with two to three consecutive bifurcations starting from a tetragraptid proximal end and without distal dichotomies; central disc in some species but not in others; thecae simple with moderate overlap. *Lower Ordovician (Floian,* Tshallograptus fruticosus *Biozone)–Middle Ordovician (Dapingian,* Isograptus maximodivergens *Biozone):* worldwide.——FIG. 5,*1a*. **D. sedgwicki,* lectotype (selected by ELLES & WOOD, 1902, explanation on pl. 10), BGS GSM 7650, Middle Skiddaw Slates, Braithwaite, Cumbria, UK, *arrow* indicates position of sicula (Elles & Wood, 1902, pl. 10,*3a*).——FIG. 5,*1b*. *D. octobrachiatus* (HALL, 1858), lectotype (selected by WILLIAMS & STEVENS, 1988, p. 24), GSC 931i, Lévis, Quebec, Canada (Hall, 1865, pl. 7,*1*).

Clonograptus HALL & NICHOLSON in NICHOLSON, 1873, p. 138, original spelling as *Clonograpsus* changed in ICZN, Opinion 650, 1963 [**Graptolithus rigidus* HALL, 1858, p. 121, SD MILLER, 1889, p. 179] [=*Temnograptus* NICHOLSON, 1876, p. 248 (type, *Dichograpsus multiplex* NICHOLSON, 1868, p. 129, OD), see LINDHOLM & MALETZ, 1989, p. 718; =*Anthograptus* TÖRNQUIST, 1904, p. 22 (type, *A. nidus*, M), see LINDHOLM & MALETZ, 1989, p. 718]. Multiramous, horizontal to subhorizontal dichograptid with increasing distances of numerous distal, more irregularly placed dichotomies; thecae simple widening tubes with moderate overlap and without extended rutella; proximal development isograptid, dextral or sinistral. *Lower Ordovician (upper Tremadocian*, Hunnegraptus copiosus *Biozone–Floian,* Tshallograptus fruticosus *Biozone):* worldwide.——FIG. 5,*3a*. **C. rigidus* (HALL), lectotype, GSC 935b, *arrow* indicates position of sicula (Lindholm & Maletz, 1989, p. 719, fig. 2D).——FIG. 5,*3b*. *C. flexilis* (HALL, 1858), lectotype, GSC 965c, *arrow* indicates position of sicula (Lindholm & Maletz, 1989, p. 724, fig. 3A).——FIG. *5,3c–e*. *C. multiplex* (NICHOLSON, 1868); *3c,* lectotype, NHMUK PM Q31, *arrow* indicates position of sicula (Lindholm & Maletz, 1989, fig. 7); *3d,* LO 1748T, holotype of *Anthograptus nidus* TÖRNQUIST, 1901(Lindholm & Maletz, 1989, fig. 11c); *3e,* reconstruction from latex cast of juvenile, dicalycal theca striped (Maletz, 1992, fig. 1e).

Loganograptus Hall, 1868, p. 237 [**Graptolithus logani* HALL, 1858, p. 115; OD]. Large multiramous horizontal to subhorizontal tubarium with two to three consecutive distal bifurcations starting from a tetragraptid proximal end and without distal dichotomies; central disc present; thecae simple with moderate inclination and overlap. *Lower Ordovician (Floian,* Baltograptus vacillans *Biozone)–Middle Ordovician (Dapingian,* Expansograptus hirundo *Biozone):* worldwide.——FIG. 5,*2*. **L. logani* (HALL), GSC 932a, Lévis, Quebec, Canada (Hall, 1865, pl. 9,*2*).

Orthodichograptus THOMAS, 1972, p. 529, [**O. robbinsi;* OD]. Large multiramous horizontal to subhorizontal tubarium with two to three consecutive distal bifurcations starting from a tetragraptid proximal end followed by one or more orders of delayed dichotomy; central disc present; thecae simple with moderate overlap. *Lower Ordovician (Floian,* Tshallograptus fruticosus *Biozone):* Australia.——FIG. 6. **O. robbinsi,* holotype, NMVP 73827 (upper specimen) and paratype, NMVP 83089 (lower specimen), Victoria, Australia (new).

Herrmannograptus MONSEN, 1937, p. 186 [**Graptolithus milesi* HALL in HAGER, 1861, p. 372; OD]. Multiramous dichograptid with a funicle formed by two first-order stipes comprised of two thecae each; up to seven or more orders of dichotomy with second and later dichotomies delayed; proximal end with sicular bitheca; bithecae lacking along stipes; thecae simple with slight rutellum. *Lower Ordovician (Floian,* ?Paratetragraptus approximatus *Biozone):* USA.——FIG. 7,*1a–e*. **H. milesi* (HALL in HAGER); *1a,* lectotype, AMNH 433/1; *1b–1e,* juvenile specimens from type slab, showing astogeny, sicular bitheca visible in *1e,* float, Monkton, Vermont, USA (Lindholm & Maletz, 1989, fig. 4).

Hunnegraptus LINDHOLM, 1991, p. 298 [**H. copiosus;* OD]. Multiramous dichograptids with long first-order stipes of uneven length; thecae slender, dichograptid with moderate overlap; proximal end isograptid, dextral or sinistral with sicular bitheca; sicula parallel sided, obliquely placed between the stipes; thecae along stipes with dorsal origins, lacking bithecae. *Lower Ordovician (upper*

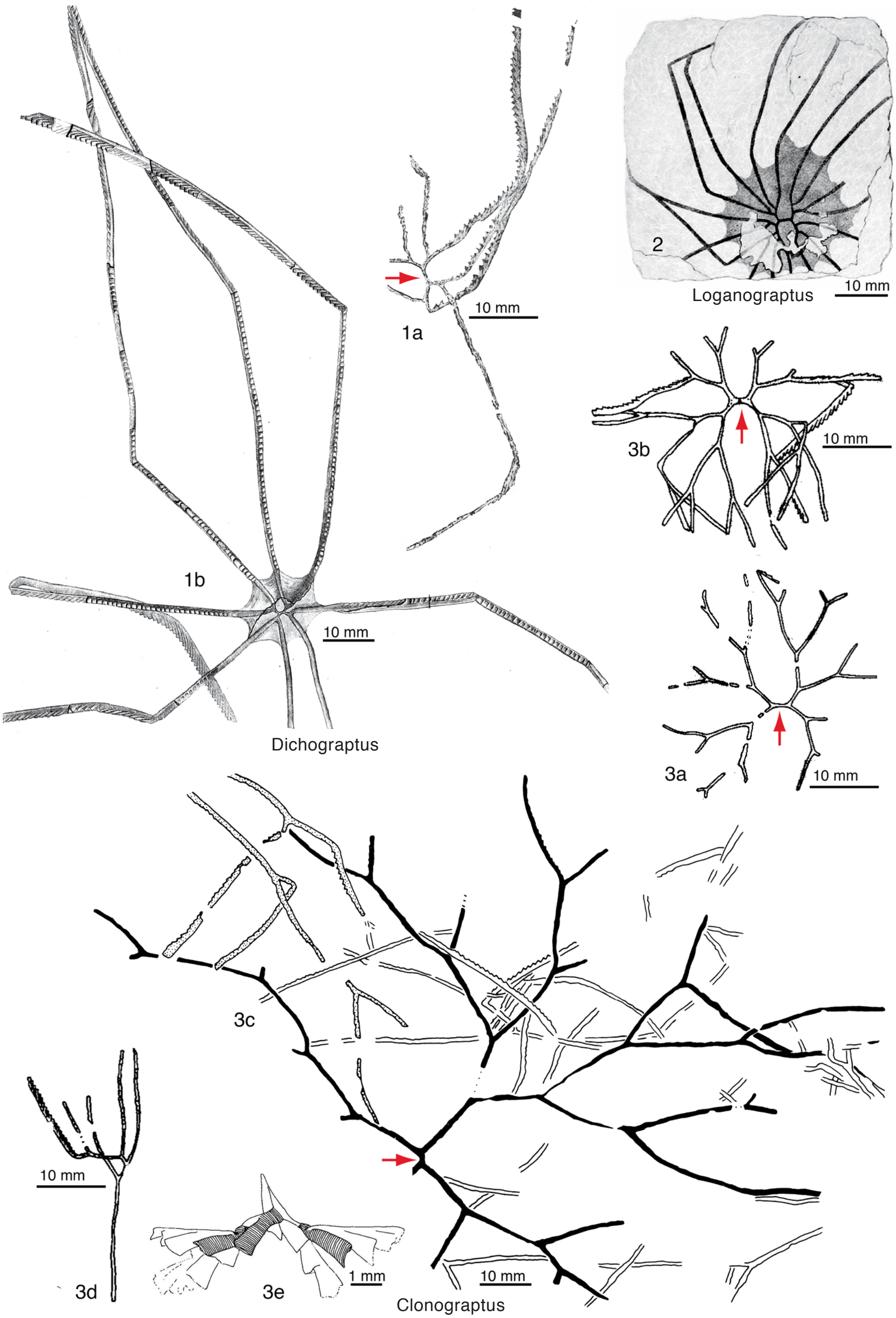
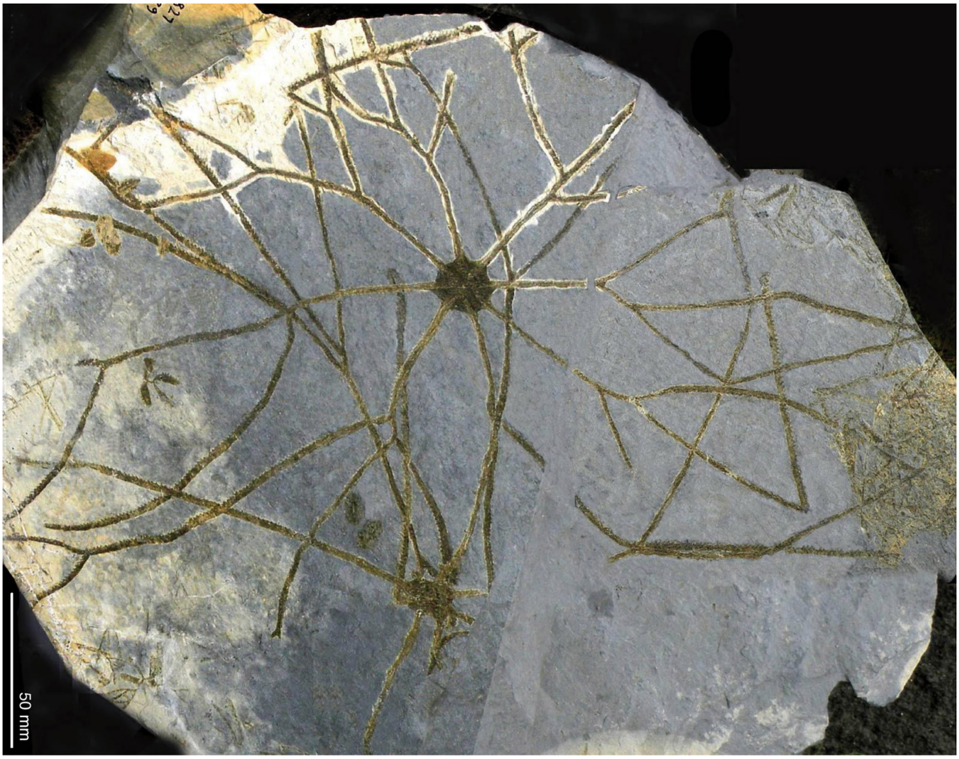


FIG. 5. Dichograptidae (p. 7).



Orthodichograptus

FIG. 6. Dichograptidae (p. 7).

Tremadocian, Hunnegraptus copiosus *Biozone):* Australia, ?China, Bulgaria, Norway, Sweden, Canada, USA, Argentina, Bolivia.——FIG. 7,*2a–d.* **H. copiosus; 2a,* holotype, PMO 58969, Galgeberg, Oslo, Norway; *2b,* LO 5978t, Slemmestad, Norway; *2c–2d,* LO 5976 and counterpart, Storeklev, Hunneberg, Sweden (Lindholm, 1991, fig. 8).

Holograptus HOLM, 1881a, p. 45 [**H. expansus;* M] [=*Rouvilligraptus* BARROIS, 1893, p. 109 (type, *Graptolithus richardsoni* HALL, 1865, p. 107, OD), see BULMAN, 1970, p. 114]. Multiramous colony based on tetragraptid proximal end; lateral stipes of third and later orders originate at irregular intervals on either side of parent stipes, which follow the growth direction of second-order stipes; lateral stipes can themselves produce further lateral stipes; central web may be present; often long second-order stipes before insertion of first lateral stipes. *Lower Ordovician (Floian,* Paratetragraptus approximatus/Tetragraptus phyllograptoides *Biozone):* Sweden, UK, France, Canada, Bolivia.——FIG. *8,1a.* **H. expansus,* holotype, NRM-PZ Cn 1500, *Tetragraptus phyllograptoides* Biozone, Diabasbrottet, Hunneberg, Sweden, *arrow* indicates position of sicula (Holm, 1881a, pl. 13,*1*).——FIG. *8,1b. H. deani* ELLES & WOOD, 1902, holotype, BU 1374, *arrow* indicates position of sicula, Skiddaw Slates, Buttermere, Newlands Valley, Cumbria, UK (Elles & Wood, 1902, pl. 8,*2a*).——FIG. *8.1c. H. richardsoni* (HALL, 1865), syntype, GSC 937a, Lévis, Quebec, Canada (Hall, 1865, pl. 12,*1*).

Schizograptus NICHOLSON, 1876, p. 248 [**Dichograpsus reticulatus* NICHOLSON, 1868, p. 143; OD] [=*Kellamograptus* RICKARDS & CHAPMAN, 1991, p. 45, (type, *Trochograptus australis* HARRIS & THOMAS, 1938a, OD), herein; =*Trochograptus* HOLM, 1881a, p. 48 (type, *T. diffusus,* M), herein; =*Ctenograptus* NICHOLSON, 1876, p. 248 (type, *Dichograpsus* (?) *annulatus* NICHOLSON, 1869, p. 233, OD), herein]. Multiramous tubarium with two dichotomous bifurcations producing a tetragraptid proximal end, followed by three or more orders of lateral branching produced on one side of parent stipe, which follows the growth direction of second-order stipes; thecal style poorly known. *Lower Ordovician (Floian* Paratetragraptus approximatus *Biozone)–Middle Ordovician (Dapingian,* Expansograptus hirundo *Biozone):* worldwide.——FIG. 8,*2a.* **S. reticulatus* (NICHOLSON), lectotype (selected by NICHOLSON, 1876, p. 248), NHMUK PM Q29, *arrow* indicates position of sicula, Skiddaw Slates, Scale Hill, Loweswater Cottages, Cumbria, UK (Elles & Wood, 1902, pl. 7)——FIG. 8,*2b. S. australis* (HARRIS & THOMAS, 1938a), holotype,

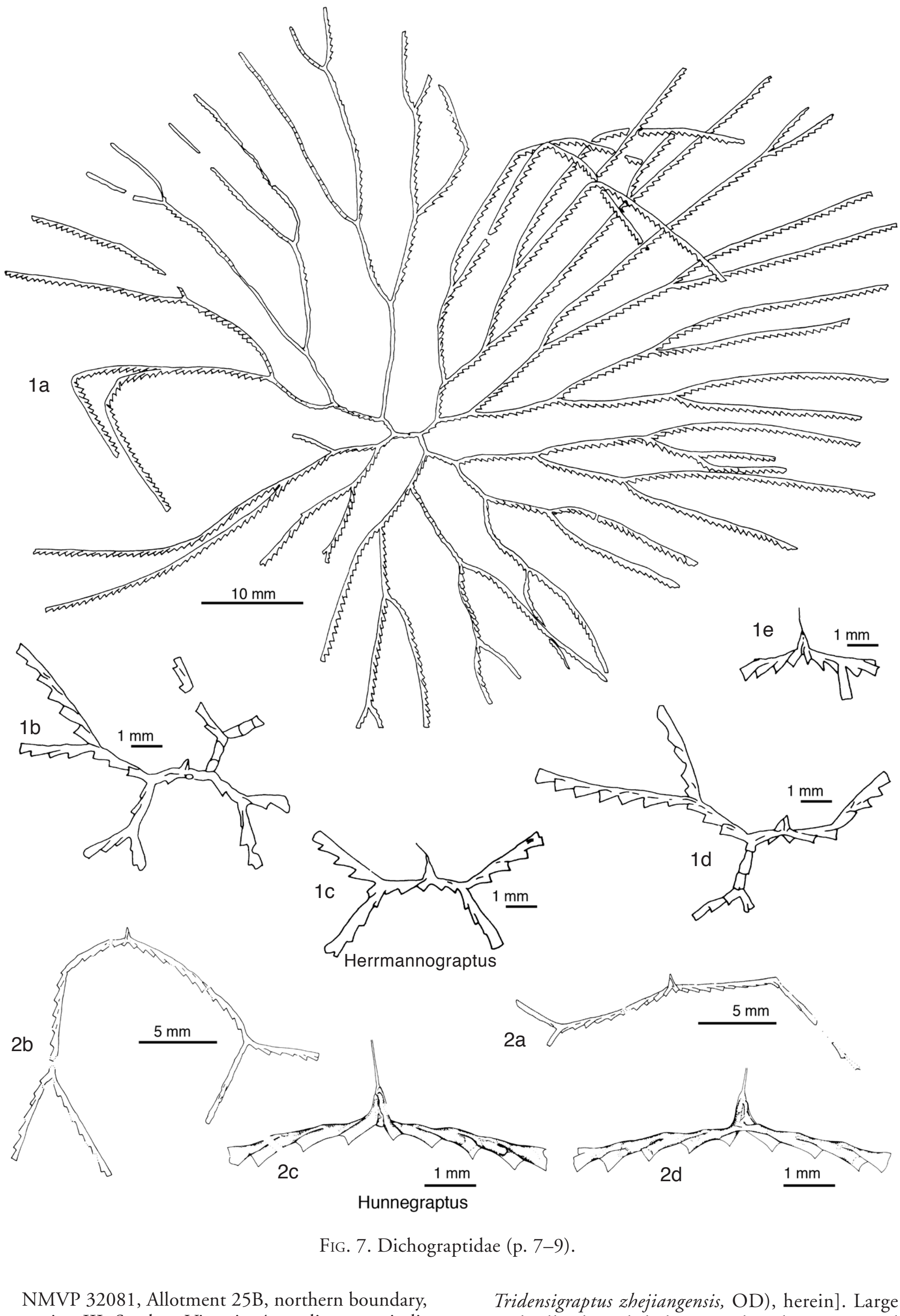


FIG. 7. Dichograptidae (p. 7–9).

NMVP 32081, Allotment 25B, northern boundary, section III, Sandon, Victoria, Australia, *arrow* indicates position of sicula (Rickards & Chapman, 1991, fig. 82).

Triaenograptus T. S. HALL, 1914, p. 115 [**T. neglectus;* M] [?=*Tridensigraptus* ZHAO, 1964, p. 638 (type, *Tridensigraptus zhejiangensis,* OD), herein]. Large umbrella-shaped dichograptid with tetragraptid proximal end; paired lateral branches (tridents) of third and later orders anastomose with adjacent branches in larger specimens; details of proximal end not known. *Lower Ordovician (upper Floian,*

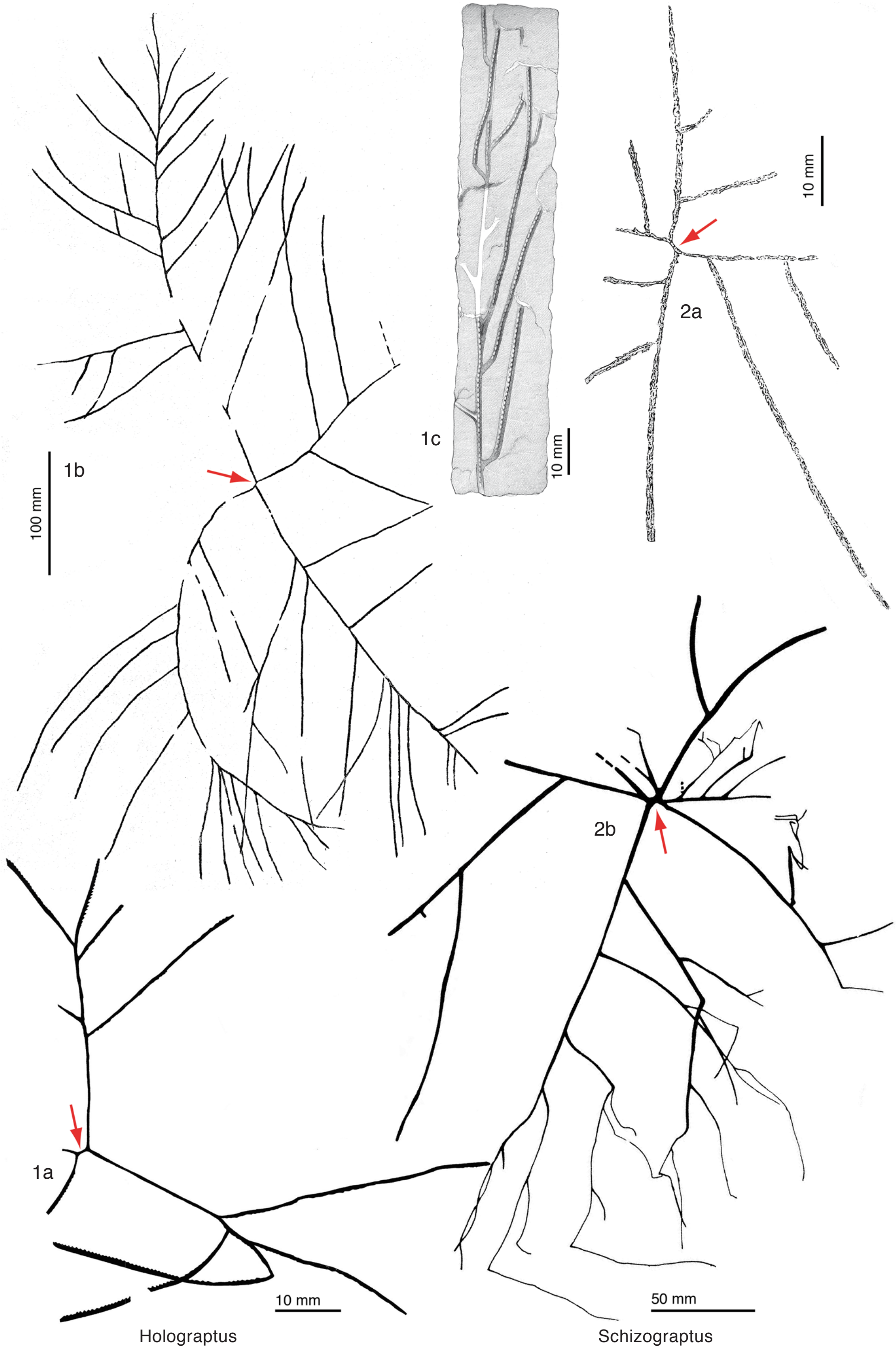


FIG. 8. Dichograptidae (p. 9–10).

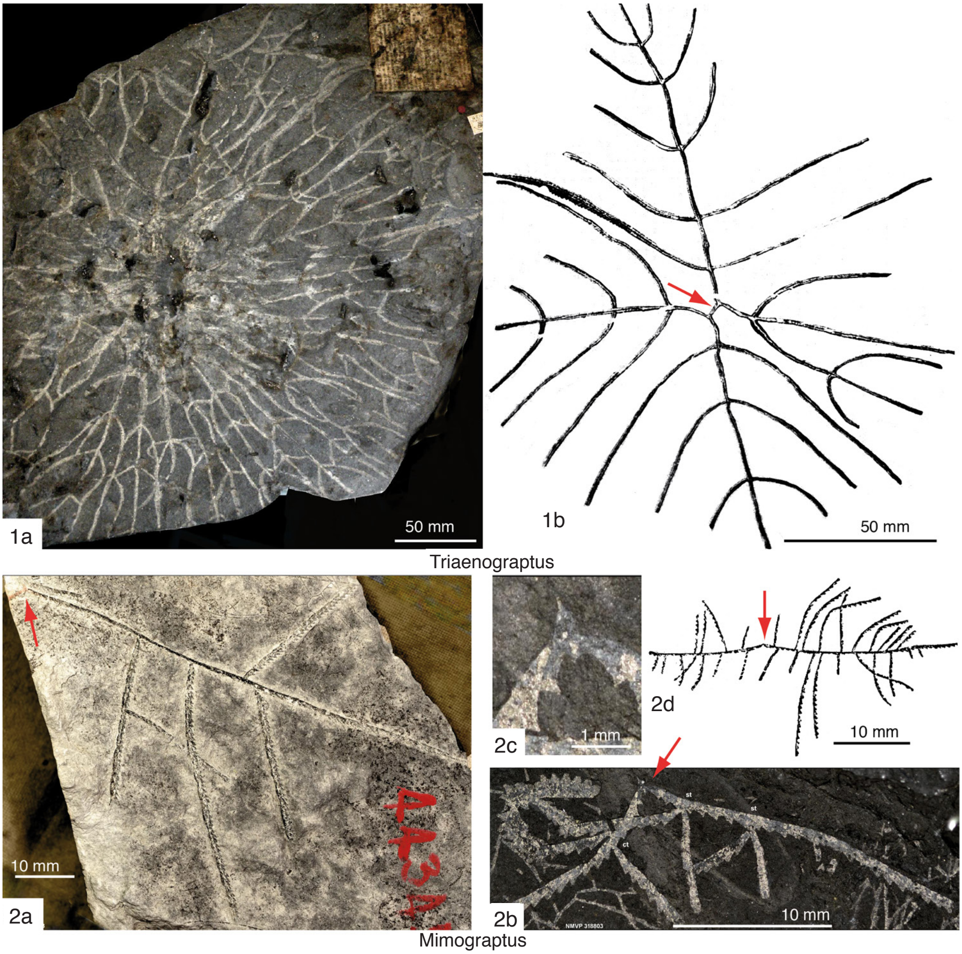


FIG. 9. Dichograptidae (p. 10–12).

Isograptus lunatus *Biozone)–Middle Ordovician (Dapingian*, Expansograptus hirundo *Biozone):* Australia, China.——FIG. 9,*1a*. **T. neglectus,* holotype, NMVP 132125, Barkers Creek Slate Quarry, north of Castlemaine, Victoria, Australia (new).——FIG. 9.*1b*. *T. zhejiangensis* (ZHAO, 1964), holotype, GMCH 1836, Duze, western Zhejiang, China; *arrow* indicates position of sicula (Zhao, 1964, pl. 3,*1*).

Mimograptus HARRIS & THOMAS, 1940, p. 197 [**M. mutabilis;* M] [=*Kstaugraptus* TZAJ, 1973, p. 5 (type, *K. obuti,* OD), herein]. Dichograptid based on two subhorizontal to declined main stipes and irregularly placed lateral stipes on both sides of main stipes; proximal end details unknown. *Lower Ordovician (upper Floian,* Didymograptellus bifidus *Biozone)–?Middle Ordovician (Darriwilian,* ?Levisograptus austrodentatus *Biozone):* China, Kazakhstan, Australia.——FIG. 9,*2a–2c*. **M. mutabilis; 2a,* NMVP 34927B, holotype, Allotment 41B, Parish of Campbelltown, Victoria, Australia, *arrows* indicates position of sicula (new); *2b–c,* NMVP 318805, specimen showing sicula, Victoria, Australia, *arrow* (*2b*) indicates position of sicula (new).——FIG. 9,*2d, M. obuti* (TZAJ, 1973), holotype, GM 1226/360, *arrow* indicates position of sicula, Chu-Iliy Mountains, southern Kazakhstan, interval is of Darriwilian age as it includes biserials (Tzaj, 1973, fig. a).

Suborder UNCERTAIN

Calamograptus CLARK, 1924, p. 61 [**C. porrectus;* OD]. Multiramous dichograptid with tetragraptid proximal end and long second-order stipes; distal stipe division intervals decreasing in length; thecal style and proximal development unknown. *Lower Ordovician (upper Tremadocian*, Clonograptus *Biozone):* Canada. [The taxon is based on two very poor specimens, possibly a senior synonym

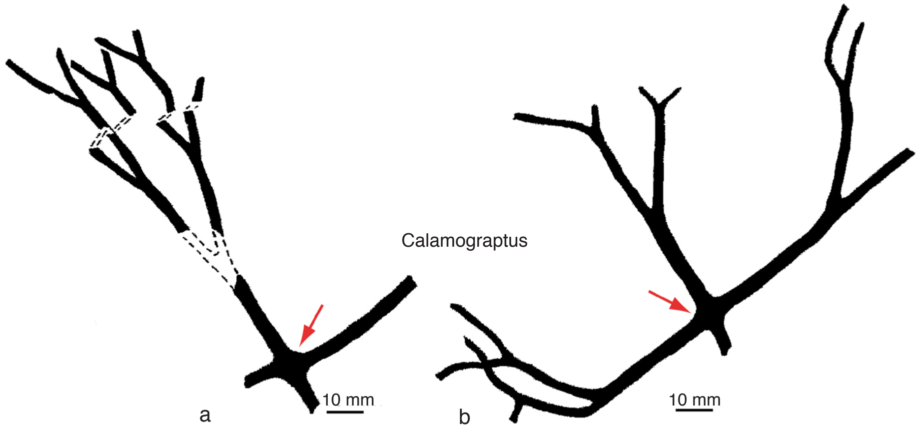


FIG. 10. Suborder Uncertain (p. 12–13).

of *Paratemnograptus.*]——FIG. 10,*a–b*. *C. porrectus* CLARK, 1924; *a,* holotype, MCZ IP 101402; *b,* paratype, MCZ IP 10140; North Ridge, Lévis, Quebec, Canada (Clark, 1924, pl. 5,*2* and 5,*1,* respectively).

Family PHYLLOGRAPTIDAE Lapworth, 1873

[Phyllograptidae LAPWORTH, 1873, table 1, facing p. 555] [=Tetragraptidae FRECH, 1897, p. 593 (*ex* subfamily Tetragraptini FRECH, 1897, p. 593; = Tetragraptidae MU, 1950, p. 180; =Tetragrapta in MALETZ, CARLUCCI, & MITCHELL, 2009, p. 12)]

Four- to two-stiped, pendent to horizontal, reclined, reflexed, and scandent, biradiate graptoloids produced by one proximal dichotomy and with th3^1 and th3^2 as only distal dicalycal theca; sicula conical, widening distinctly towards the aperture, with rutellum and small prosicula; thecae simple, widening tubes often with distinct rutellum; proximal end development isograptid, dextral. *Lower Ordovician (Floian*, Paratetragraptus approximatus *Biozone)–Middle Ordovician (Darriwilian,* Pterograptus elegans *Biozone):* worldwide.

The Phyllograptidae LAPWORTH, 1873 originally included only the scandent quadriserial dichograptids. It is here used for the paraphyletic clade identified as the family Tetragraptidae FRECH, 1897 by MALETZ (2014). MALETZ, CARLUCCI, and MITCHELL (2009, p. 12) defined their crown-clade Tetragrapta as "the common ancestor of *Tetragraptus serra* (BRONGNIART, 1828) and the first taxon to have distal dicalycal thecae limited to th3^1 and th3^2, forming a quadriramous rhabdosome." They referred to it as the superorder Pan-Tetragrapta but essentially accepted the clade as a monophyletic grouping. COOPER and FORTEY (1982) emended Phyllograptidae LAPWORTH, 1873 to include the genera *Phyllograptus* and *Xiphograptus,* based on the interpretation of the virgellar spine as a synapomorphy of the group. However, MALETZ (2010) considered the origin of the dorsal virgellar spine to be independent in *Phyllograptus* and *Xiphograptus*, based on chemically isolated material.

The members of the Phyllograptidae can be characterized through the presence of only two distal dichotomies, those at th3^1 and th3^2 (see MALETZ, 1992, fig. 1e). Stipe reduction by suppression of distal dichotomies is seen in some species, such as the two- to four-stiped members of *Tshallograptus fruticosus* (see HARRIS & THOMAS, 1938b; THOMAS, 1960). Stipe attitude is quite variable, while the proximal development with its compact crossing canals appears to be largely constant. COOPER and FORTEY (1982) showed some details of the proximal development of *Phyllograptus* and *Pseudophyllograptus* from isolated material and serial sectioning and compared it with the development in *Tetragraptus*. The

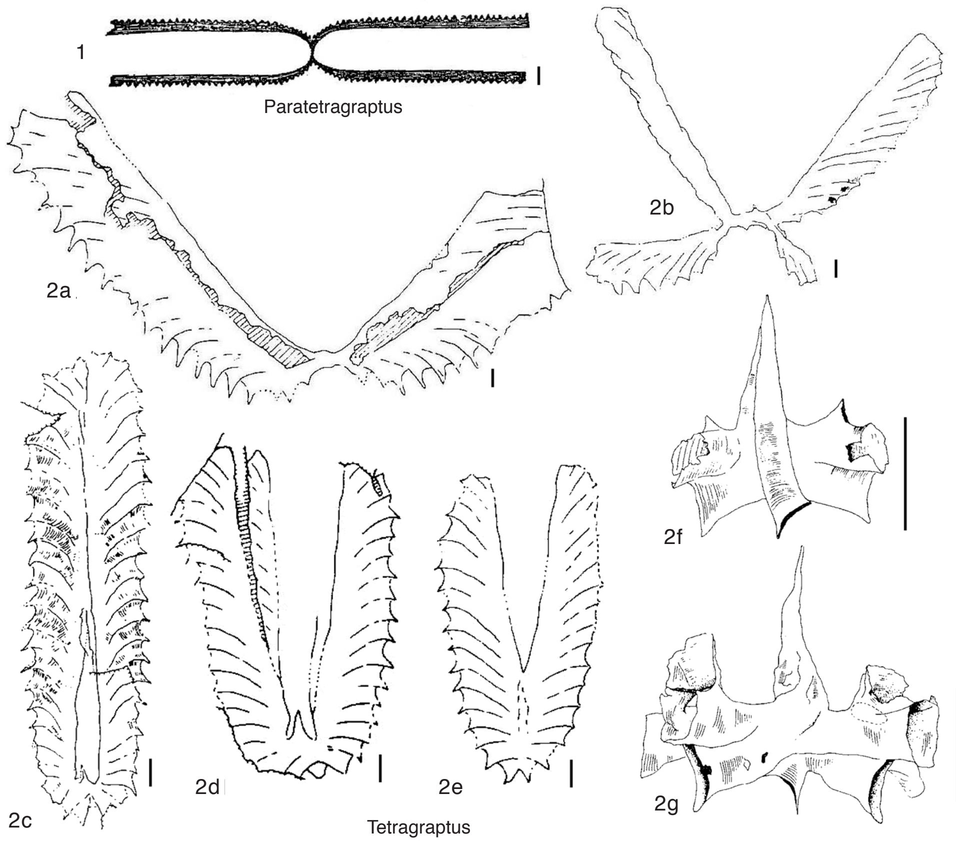


FIG. 11. Phyllograptidae (p. 14–15).

proximal development of *Pseudotrigonograptus* is known from the investigation of FORTEY (1971), showing that the construction of its tubarium is identical to that of other phyllograptids. The sicula develops a dorsal virgellar spine in the genus *Phyllograptus* (see COOPER & FORTEY, 1982; MALETZ, 2010), but the precise evolutionary origin of this feature has not been traced.

The evolutionary relationships of the genera *Tetragraptus* and the scandent phyllograptids were evaluated by STRANDMARK (1902) and COOPER and LINDHOLM (1985), among others, and it is clear that taxa such as *Tetragraptus phyllograptoides* STRANDMARK, 1902 and *Tetragraptus cor* (STRANDMARK, 1902) can be regarded as good indicators of this transition, even though the precise evolutionary relationships are not known. The appearance of partly scandent *Tetragraptus* species at several levels in the Lower to Middle Ordovician may indicate a complex repetitive evolution of phyllograptid-like species. COOPER and LINDHOLM (1985) suggested the existence of at least three independent lineages leading to phyllograptoid colonies, interpreted as an example of convergent evolution in graptolites.

Tetragraptus SALTER, 1863, p. 140, original spelling as *Tetragrapsus* changed in ICZN, Opinion 650, 1963 [**Graptolithus bryonoides* HALL, 1858, p. 126; OD (=*Tetragraptus serra* BRONGNIART, 1828, p. 71, see ELLES & WOOD, 1902, p. 66)] [*non Tetragrapsus* RATHBUN, 1918, p. 273, Decapoda]. Phyllograptid with four horizontal to reclined, reflexed and scandent stipes; proximal end isograptid, dextral, with wide crossing canals and tetragraptid proximal end; thecae with considerable overlap and moderate development of rutellum. *Lower Ordovician (Floian,* Paratetragraptus approximatus *Biozone)–Middle Ordovician (Darriwilian,* Pterograptus elegans *Biozone):* worldwide.——FIG. 11,*2a*. **T. serra,* lectotype, NHMUK PM 26995, Lévis, Quebec, Canada, scale bar, 1 mm (Cooper & Fortey, 1982, fig. 14).——FIG. *2b*. *T. bryonoides* (HALL), lectotype, GSC 978, scale bar, 1 mm (Cooper & Fortey, 1982, fig. 16).——FIG. 11,*2c*. *T. cor* (STRANDMARK, 1902), SGU 3844, 1-2 preservation, scale bar, 1 mm (Cooper & Lindholm, 1985, fig. 3g).——FIG. 11,*2d–e*. *T. phyllograptoides* STRANDMARK, 1902; *2d,* LO 5377t, specimen in 1-2 preservation; *2e,* LO 5372t, specimen in a-b preservation; scale bars, 1 mm (Cooper & Lindholm, 1985, fig. 1m and 1c).——FIG. 11,*2f–g*. *T. phyllograptoides triumphans* COOPER & FORTEY, 1982; *2f,* PMO NF3303, juvenile in obverse view; *2g,* PMO NF 3181, proximal end in reverse view showing massive crossing canals; scale bars, 1 mm (Cooper & Fortey, 1982, fig. 22c and 22g, respectively).

Paratetragraptus OBUT, 1957, p. 38 [**Tetragraptus approximatus* NICHOLSON, 1873, p. 136; OD]. Phyllograptid with nearly horizontal tubarium; proximal end with slightly deflexed funicle; paired, parallel-oriented second-order stipes; proximal development isograptid, dextral, with robust and wide crossing canals. *Lower Ordovician (Floian,* Paratetragraptus approximatus–Tshallograptus fruticosus *biozones):* worldwide.——FIG. 11,*1*. **P. approximatus* (NICHOLSON), lectotype, NHMUK PM 1996, Lévis, Quebec, Canada (G-locality, see Maletz, 1997), scale bar, 1 mm (Nicholson, 1873, fig. 2a).

Corymbograptus OBUT & SOBOLEVSKAYA, 1964, p. 27 [**Didymograpsus v-fractus* SALTER, 1863, p. 138; OD]. Deflexed, two-stiped phyllograptid with distally distinctly widening stipes; proximal development isograptid, dextral; low prosicular origin of th1[1]; crossing canals low on sicula; sicula long and slender as in *Tshallograptus* with mitre-shaped prosicula. *Lower Ordovician (Floian,* Cymatograptus protobalticus *Biozone)–Middle Ordovician (Darriwilian,* Corymbograptus retroflexus *Biozone):* China, UK, Czech Republic, Norway, Sweden, Canada, USA, Argentina, ?Bolivia.——FIG. 12,*3a–b*. **C. v-fractus* (SALTER); *3a,* neotype, BU 1005a, *Baltograptus jacksoni* Biozone, Buttermere, Skiddaw Slates, Cumbria, UK (Rushton, 2011, fig. 1A); *3b,* BU 1005b, proximal end of larger specimen, scale bars, 1 mm (Rushton, 2011, fig. 1D).——FIG. 12,*3c–d*. *C. v-fractus tullbergi* (MONSEN, 1937); drawings from latex cast, counterpart of holotype, PMO K0484, reverse view (*c*) and PMO 59957 obverse view (*d*); Oslo Region, Norway, scale bars 1 mm (new).——FIG. 12,*3e*. *C. retroflexus* (PERNER, 1895), MR 54919, proximal end in reverse view, Drahouš, Czech Republic, scale bar, 1 mm (new).

Pendeograptus BOUČEK & PŘÍBYL, 1952, p. 12 [**Tetragraptus pendens* ELLES, 1898, p. 491; OD]. Pendent phyllograptid with four stipes; proximal development isograptid, dextral; low prosicular origin of th1[1]; sicula long and slender. *Lower Ordovician (Floian,* Paratetragraptus approximatus *Biozone):* worldwide.——FIG. 12,*1*. **P. pendens* (ELLES), lectotype (selected by WILLIAMS & STEVENS, 1988, p. 38), NHMUK PM Q37, Barf, Loweswater Formation, Skiddaw Slates, Cumbria, UK, scale bar, 1 mm (adapted from Elles, 1898, fig. 13).

Tshallograptus VANDENBERG, 2017, p. 54 [**Graptolithus fruticosus* HALL, 1858, p. 128; OD]. Pendent to deflexed phyllograptid; proximal development isograptid, dextral; low prosicular origin of th1[1]; crossing canals low on sicula; sicula long and slender, with mitre-shaped prosicula. *Lower Ordovician (Floian,* Paratetragraptus approximatus–Didymograptellus kremastus *Biozones):* worldwide.——FIG. 12,*2a–c*. **T. fruticosus* (HALL); *2a,* GSC 79584, large, three-stiped specimen, Cow Head Group, western Newfoundland (Williams & Stevens, 1988, fig. 27s); *2b,* paratype, GSC 925, showing deflexed stipe ends, sicula merges into thickened nema (Hall, 1865, pl. 6,*1*); *2c,* lectotype, GSC 926, Isle d'Orleans, Quebec, Canada (misquoted as "Orleans Island, three miles above the River St. Anne" by Williams & Stevens, 1988); scale bar, 1 mm (Williams & Stevens, 1988, fig. 27G).

Phyllograptus HALL, 1858, p. 137 [**P. typus;* OD] [=*Phyllograpsus* HALL in NICHOLSON, 1872a, 1872b; non *Phyllograpsus* ANGELIN in SALTER, 1858 (=*Rhabdinopora* EICHWALD, 1855)]. Phyllograptid with four stipes united along dorsal margins, producing cruciform cross section; median septa reduced to framework of fornices and central columella with open foramen between thecae of adjacent series; sicula with dorsal virgellar spine, often strongly elongated and thickened, proximal development isograptid, dextral; thecae continuing to grow and elongate as tubarium itself continues to grow. *Lower Ordovician (Floian,* Tshallograptus fruticosus *Biozone)–Middle Ordovician (Dapingian,* Isograptus victoriae *Biozone):* Canada, USA, Australia, New Zealand, Argentina, China.——FIG. 13,*1a–e*. **P. typus; 1a,* lectotype, GSC 942b, ?G-locality, Lévis, Quebec, Canada; *1b–c,* PMO NF 3312, PMO NF 3314, isolated material in obverse (*b*) and reverse (*c*) views; *1d,* PMO NF3314, distal view of isolated fragment showing interthecal foramina; *1e,* reconstruction to show central columella; *1b–d,* Spitsbergen, Norway; scale bars, 1 mm (Cooper & Fortey, 1982, fig. 67a–b, 71, 71k, and 74, respectively).

Pseudophyllograptus COOPER & FORTEY, 1982, p. 241 [**Phyllograptus angustifolius angustifolius* HALL, 1858; OD]. Phyllograptid with four stipes united along dorsal margins, producing cruciform cross section; median septa cruciform, imperforate; proximal development isograptid, dextral. *Lower Ordovician (Floian,* Tetragraptus akzharensis *Biozone)–Middle Ordovician (Darriwilian,* Pterograptus elegans *Biozone):* worldwide.——FIG. 13,*2a–c*. **P. angustifolius* (HALL)*; 2a,* lectotype, GSC 939b; *2b,* paratype, GSC 939; *2c,* reconstruction to show median septum; *Levisograptus dentatus* Biozone Lévis, Quebec, Canada; *2a–b,* scale bars, 1 mm (Cooper & Fortey, 1982, fig. 48f, 48e, and 51, respectively).

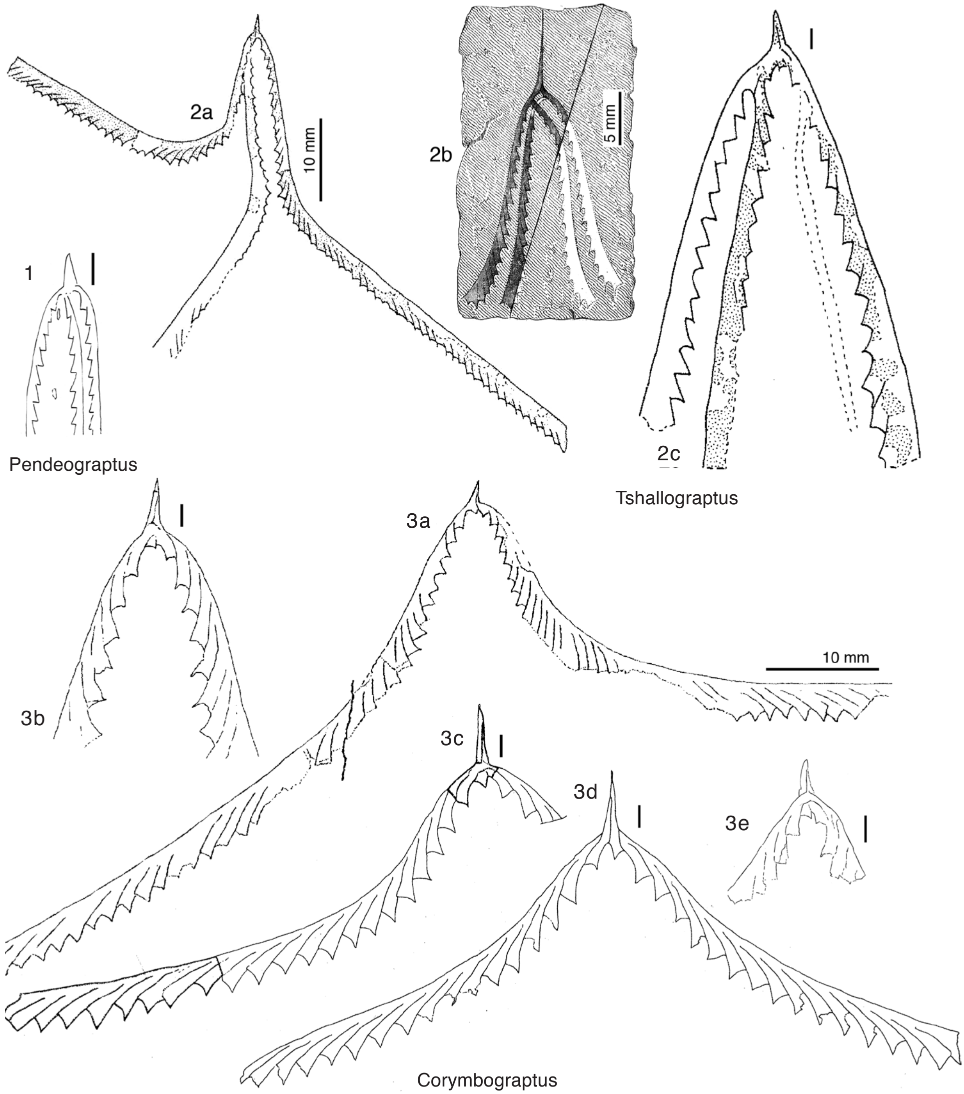


FIG. 12. Phyllograptidae (p. 15).

Pseudotrigonograptus MU & LEE, 1958, p. 397 (p. 416, English text) [**P. uniformis;* OD] [=*Tristichograptus* JACKSON & BULMAN, 1970, p. 108 (type, *Graptolithus ensiformis* HALL, 1858, p. 133, OD): FORTEY, 1971, p. 192]. Quadriserial or rarely triserial, scandent phyllograptid with stipes not only united along their dorsal margins, but also in lateral contact, elliptical in cross section; median septa cruciform, imperforate; proximal development isograptid, dextral; thecae may show continued growth. *Middle Ordovician (Dapingian,* Isograptus lunatus *Biozone–Darriwilian,* Holmograptus spinosus *or* Nicholsonograptus fasciculatus *Biozone):* worldwide.——FIG.14,*1a–b*. *P. ensiformis* (HALL, 1858); *1a,* lectotype (selected by RICKARDS, 1973, p. 598), GSC 949g, Cote Frechette section, Lévis, Quebec, Canada, scale bar, 1 mm (Hall, 1865, pl. 14,*4*); *1b,* cross section diagram Cooper & Fortey, 1982, fig. 53).——FIG.14,*1c–d, P. minor* MU & LEE, 1958, three-stiped taxon in different views (not preserved, see SMA70588 for a similar specimen), Spitsbergen, Norway; scale bars, 1 mm (Fortey, 1971, fig. 3).——FIG.14,*1e–f* (on one slab); **P. uniformis; 1e,* holotype,

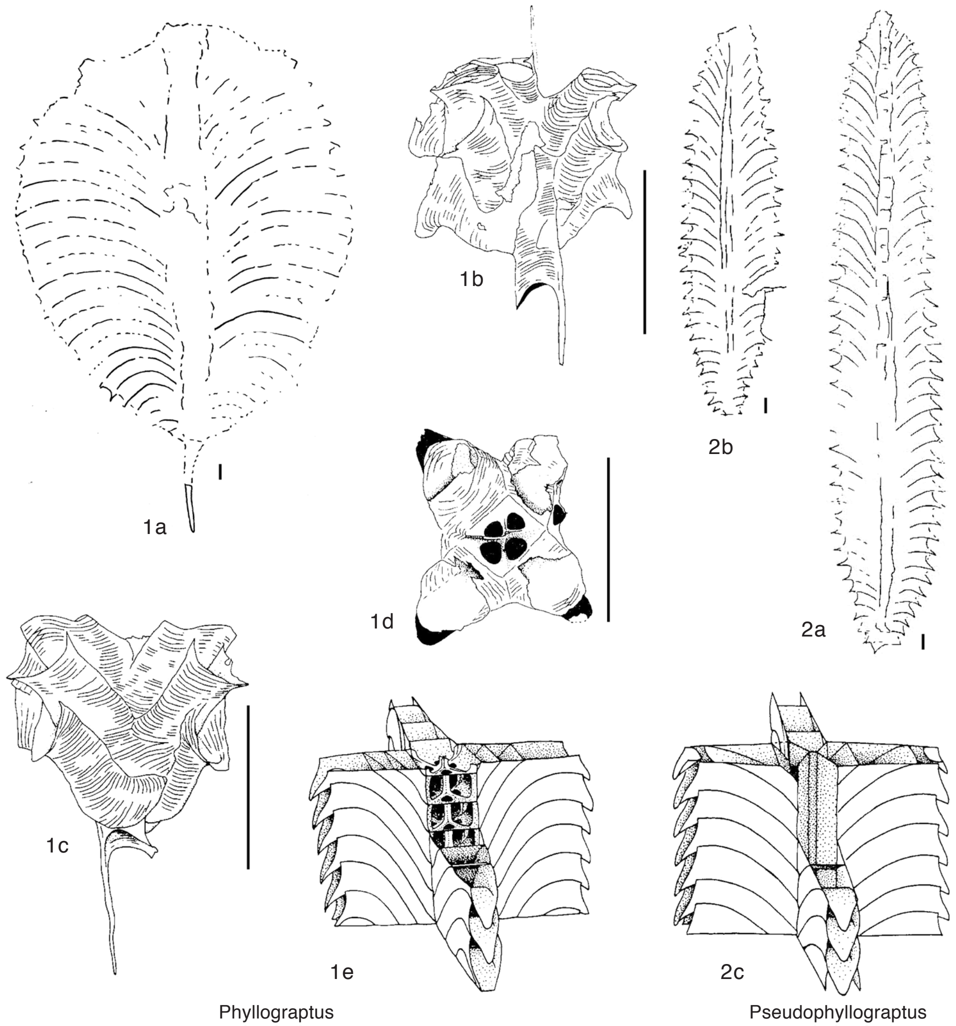


FIG. 13. Phyllograptidae (p. 15).

NIGP 9719, *Exigraptus clavus* Biozone, Ningkuo Shale, Huangnikang, Kiangshan, China, (new); *1f*, paratype, NIGP 9718; scale bars, 1 mm (new).

Family DIDYMOGRAPTIDAE Mu, 1950

[Didymograptidae MU, 1950, p. 180 (*emend.* MU & others, 2002, p. 228)] [incl. Aulograptinae HSÜ & CHAO, 1976, p. 137]

Two-stiped, pendent to horizontal, reclined, reflexed, and deflexed graptoloids; sicula conical, widening distinctly towards aperture, with small prosicula; thecae simple widening tubes; rutellum present in derived taxa; thecae rarely complex or with prothecal folding; proximal development isograptid, dextral or derived artus type. *Lower Ordovician (Floian,* Paratetragraptus approximatus *Biozone)–Middle Ordovician (Darriwilian,* Pterograptus elegans *Biozone):* worldwide.

The Didymograptidae is a poorly defined group of two-stiped taxa with a highly variable tubarium shape, ranging from pendent to reclined. The taxa are united by a conical sicula with a relatively small prosicula. The proximal development is of the isograptid dextral type or the derived artus type with the crossing canals symmetrically placed, but

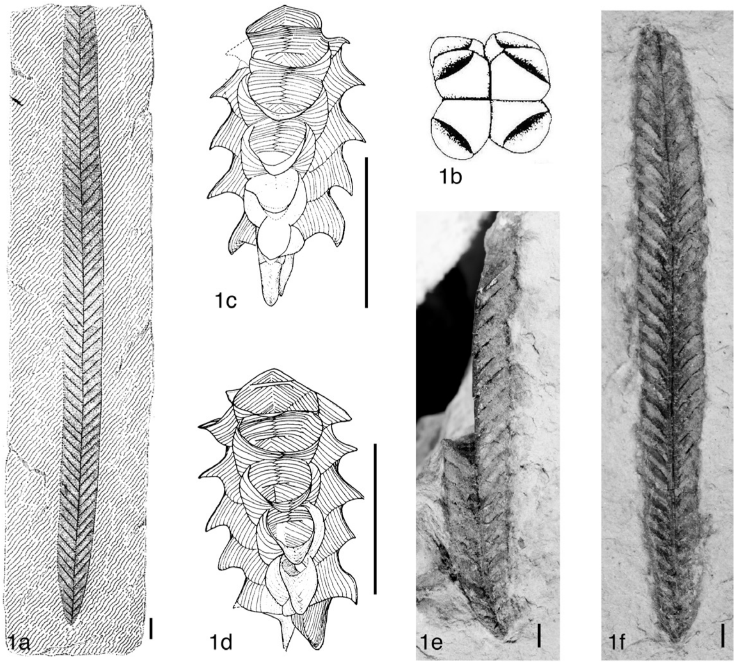


FIG. 14. Phyllograptidae (p. 16–17).

often showing distinct differences in width. The position of the foramen for th1[1] is in the lower part of the prosicula in early taxa (Fig. 15.1) but may be in the middle part of the metasicula (Fig. 15.2) and even in its lower part in derived forms. GUTIÉRREZ-MARCO (1986) considered the separation of genera or subgenera based on the presence of an isograptid- or artus-type proximal development in the genus *Didymograptus.* He differentiated the subgenus *Jenkinsograptus* with an isograptid-type development from *Didymograptus* with an artus-type development. MALETZ (1994a) and MALETZ and SLOVACEK (2013), however, preferred to keep species with isograptid- and artus-type developments in the genus *Baltograptus*, indicating that the position of the dicalycal theca might be of lesser importance for taxonomic interpretations.

The distinction of *Norvegiograptus* LI & others, 2014 based on the proximal development appears unclear. The authors state an artus-type development with a dicalycal th1[2] in the English translation of the text and show an isograptid, sinistral development (LI & others, 2014, fig. 2B). Further specimens identified as *Norvegiograptus liber* (MONSEN, 1937) show an artus-type development (LI & others, 2014, fig. 4) in dextral and sinistral specimens.

Numerous taxa have been referred to the genus *Didymograptus* in the past (MU & others, 2002) and many have been reassigned to other genera in recent decades due to the recognition of constructional differences in the proximal development and thecal style. The sigmagraptine genus *Acrograptus* TZAJ, 1969 largely includes species with a sigmagraptine parallel-sided sicula and slender, asymmetrically placed stipes. Species with a dorsal virgellar spine are now included in *Didymograptellus*, *Yutagraptus*, and *Xiphograptus*, as revised by MALETZ (2010) and are referred to the Pterograptidae. Most horizontal and some reclined and declined forms are now referred to *Expansograptus*.

Didymograptus M'COY, 1851 in SEDGWICK & M'COY, 1851–1854, p. 9, original spelling as *Didymograpsus*

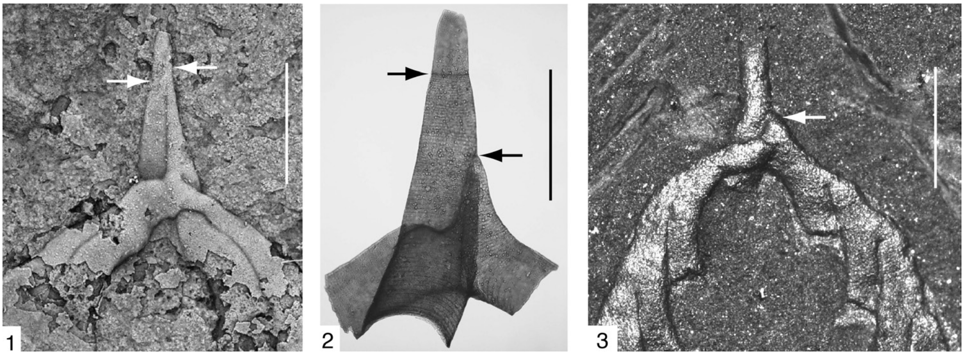


FIG. 15. The proximal development of the Didymograptidae. *1, Expansograptus* sp., PMU 23168, latex cast, low prosicular origin of th1^1, Hunneberg, Västergötland, Sweden (new); *2, Baltograptus kurcki* (TÖRNQUIST, 1901), SGU 9615, isolated specimen showing fuselli, metasicular origin of th1^1, artus-type development, Talubäcken, Dalarna, Sweden (new); *3, Didymograptus artus* (ELLES & WOOD, 1901), PMU 31742, reverse view, Fågelsångsdalen drill core, 22.9m, Scania, Sweden, all scale bars, 1 mm (new).

changed in ICZN, Opinion 650, 1963 [**Graptolithus murchisoni* BECK in MURCHISON, 1839, p. 694; SD MILLER, 1889, p. 185] [=*Cladograpsus* GEINITZ, 1852, p. 29 (type, *Graptolithus murchisoni* BECK in MURCHISON, 1839, p. 694, SD BULMAN, 1929, p. 169); =*Parazygograptus* KOZŁOWSKI, 1954, p. 439 (type, *P. erraticus,* OD), see MALETZ, 1994a, p. 30; =*Trigonograpsus* NICHOLSON, 1869, p. 231 (type, *T. lanceolatus*, M), see JACKSON & BULMAN, 1970, p. 108]. Pendent didymograptid with low metasicular origin of th1^1 and artus-type proximal development; stipes slender or distinctly widening distally; proximal end often covered by cortical overgrowth in gerontic specimens. *Middle Ordovician (Darriwilian,* Didymograptus artus–Pseudamplexograptus distichus *Biozones):* Belgium, UK, Czech Republic, France, Germany, Norway, Spain, Sweden, China, North Africa, Saudi Arabia, western Australia, Bolivia, Colombia, Peru.——FIG. 16,*1a. D. murchisoni* (BECK in MURCHISON), lectotype (selected by ELLES & WOOD, 1901, p. 40), BGS GSM 6820b, Gelli, near Llandrindod, Wales, UK, scale bar, 1 mm (Strachan & Kashogji, 1984, fig. 7).——FIG.16,*1b–d. D. artus* (ELLES & WOOD, 1901); *1b,* CPC 7010, isolated proximal fragment showing artus-type development, Williston Basin, Willara 1 drill core, Australia (Skwarko, 1968, fig. 2); *1c–d, Parazygograptus erraticus*, holotype, ZPAL G./III, complete specimen (*d*) and proximal end (c) showing fuselli, Poland, scale bar 1 mm unless otherwise stated (Kozłowski, 1954, fig. 9).——FIG. 16,*1e. Didymograptus* sp., NHMUK PM Q49, holotype of *Trigonograpsus lanceolatus*, scale bar, 1 mm (Jackson & Bulman, 1970, fig. 1).

Jenkinsograptus GUTIÉRREZ-MARCO, 1986, p. 199 [**Didymograptus spinulosus* PERNER, 1895, p. 22; OD]. Pendent didymograptid with low metasicular origin of th1^1 and isograptid-type proximal development; stipes slender or distinctly widening distally. *Middle Ordovician (Darriwilian,* Didymograptus artus–Nicholsonograptus fasciculatus *Biozones*): Belgium, UK, Czech Republic, France, Germany, Norway, Spain, Sweden, China, Saudi Arabia.——FIG. 16,*2a–b. J. spinulosus* (PERNER); *2a,* holotype, NM-L7564, *Corymbograptus retroflexus* Biozone, Šarka Formation, Osek near Rokycany, scale bar, 1 mm (adapted from Bouček, 1973, fig. 27a); *2b,* NHMUK PM Q5161, proximal end in reverse view, Llanfallteg Formation, South Wales, UK; scale bar, 1 mm (Fortey & Owens, 1987, fig. 112a).

Aulograptus SKEVINGTON, 1965, p. 25 [**Didymograptus cucullus* BULMAN, 1932, p. 15; OD (=*Didymograptus climacograptoides* BULMAN, 1931, p. 41, see MALETZ, 1997, p. 29)]. Pendent didymograptid with metasicular origin of th1^1; stipes subparallel, slowly widening distally; proximal development of isograptid type; thecae with strongly modified, geniculate thecal apertures. *Middle Ordovician (Lower Darriwilian,* Undulograptus austrodentatus–Nicholsonograptus fasciculatus *Biozones):* Belgium, UK, Czech Republic, Norway, Spain, Sweden, Canada, Argentina, Bolivia, Peru, China.——FIG. 16,*3a–c. A. climacograptoides* (BULMAN, 1931); *3a–3b,* originally described as the holotype of *A. cucullus,* NRM-PZ Cn 1261, obverse (*a*) and reverse (*b*) views, Hälludden, Öland, Sweden, scale bars, 1 mm (Bulman, 1932, pl. 1,*3–4*); *3c,* fragment showing thecal apertures, reconstruction (Bulman, 1932, pl. 1,*5*).

Baltograptus MALETZ, 1994a, p. 36 [**Didymograptus vacillans* TULLBERG, 1880, p. 42; OD] [=*Norvegiograptus* LI & others, 2014, p. 173 (type, *Didymograptus liber* MONSEN, 1937, p. 122, OD, =*D. kurcki* TÖRNQUIST, 1901), herein]. Horizontal to deflexed, declined and pendent didymograptids; sicula slender, with long supradorsal portion; proximal development of isograptid or artus type with moderately low origin of th1^1 from metasicula

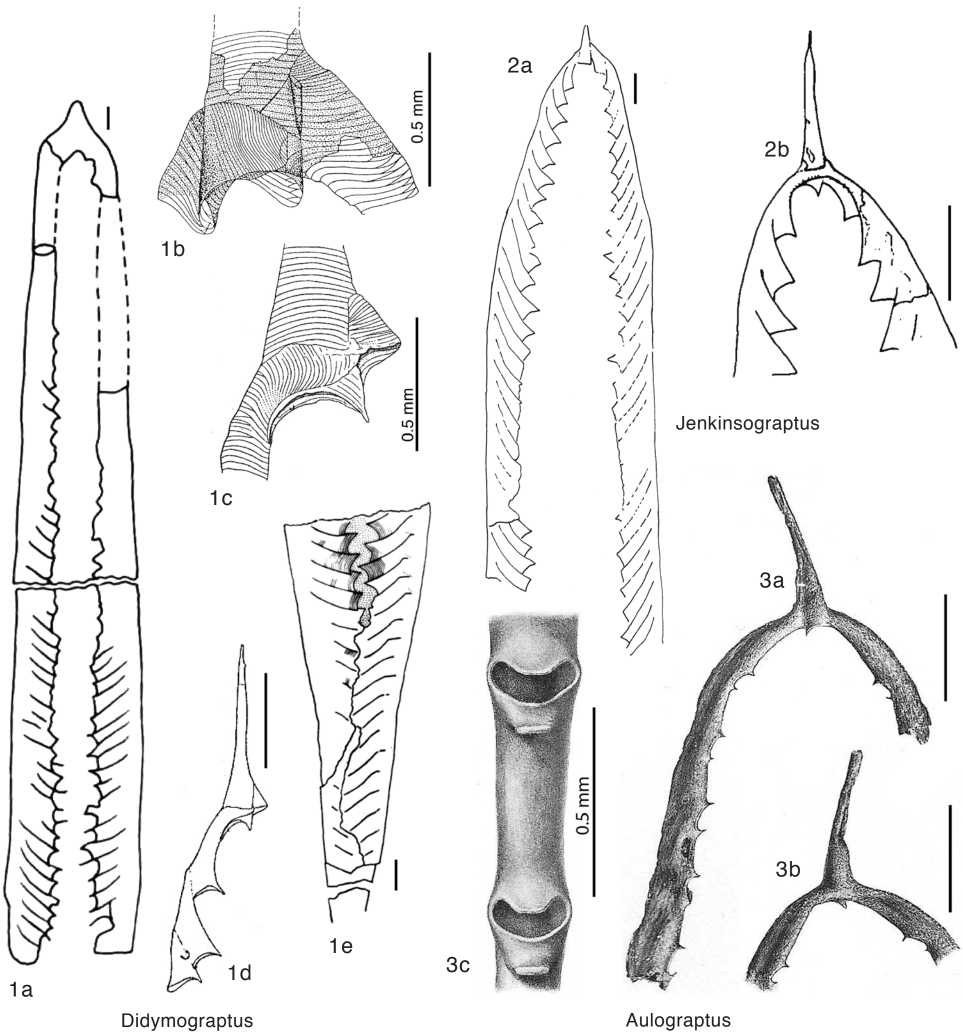


FIG. 16. Didymograptidae (p. 18–19).

and comparably long ventral free apertural length of sicula; isograptid suture very short or missing. *Lower Ordovician (Floian,* Cymatograptus protobalticus *Biozone*–Baltograptus minutus *Biozone):* UK, Czech Republic, France, Norway, Sweden, Turkey, Argentina, Bolivia, China.——FIG. 17,*2a–c*. **B. vacillans* (TULLBERG); *2a,* lectotype, LO 345t, Kiviks Esperöd, Scania, Sweden (new); *2b–c,* PMU 23157, reverse (*b*), and obverse view (*c*) drawing of latex cast, Diabasbrottet, Hunneberg, Sweden (new). All scale bars, 1 mm.——FIG. 17,*2d–e*. *B. kurcki* (TÖRNQUIST, 1901), *2d*, LO 1633t, proximal end, obverse view; *2e,* lectotype, LO 1632T, reverse view of molds; Tøyen Shale Formation, Jerrestad, Scania, Sweden, scale bars, 1 mm (Rushton, 2008, Folio. 2.51).

Cymatograptus JAANUSSON, 1965, p. 424 [**Didymograptus undulatus* TÖRNQUIST, 1901, p. 10; OD]. Slender, horizontal to subhorizontal or declined tubarium; thecae simple with moderate inclination and some species with prothecal folds; sicula relatively long and slender, with small (less than ¼ of sicular length) prosicula; supradorsal portion of sicula prominent and with long free ventral side of the aperture; proximal development type isograptid, dextral to artus type, dextral or sinistral; low prosicular origin of th1^1. *Lower Ordovician (Floian,* Paratetragraptus approximatus–Baltograptus jacksoni *biozones):* Norway, Sweden, Argentina, Australia (New South Wales), Bolivia, China, Canada.——FIG. 17,*1*. **C. undulatus* (TÖRNQUIST), lectotype, LO 1574T,

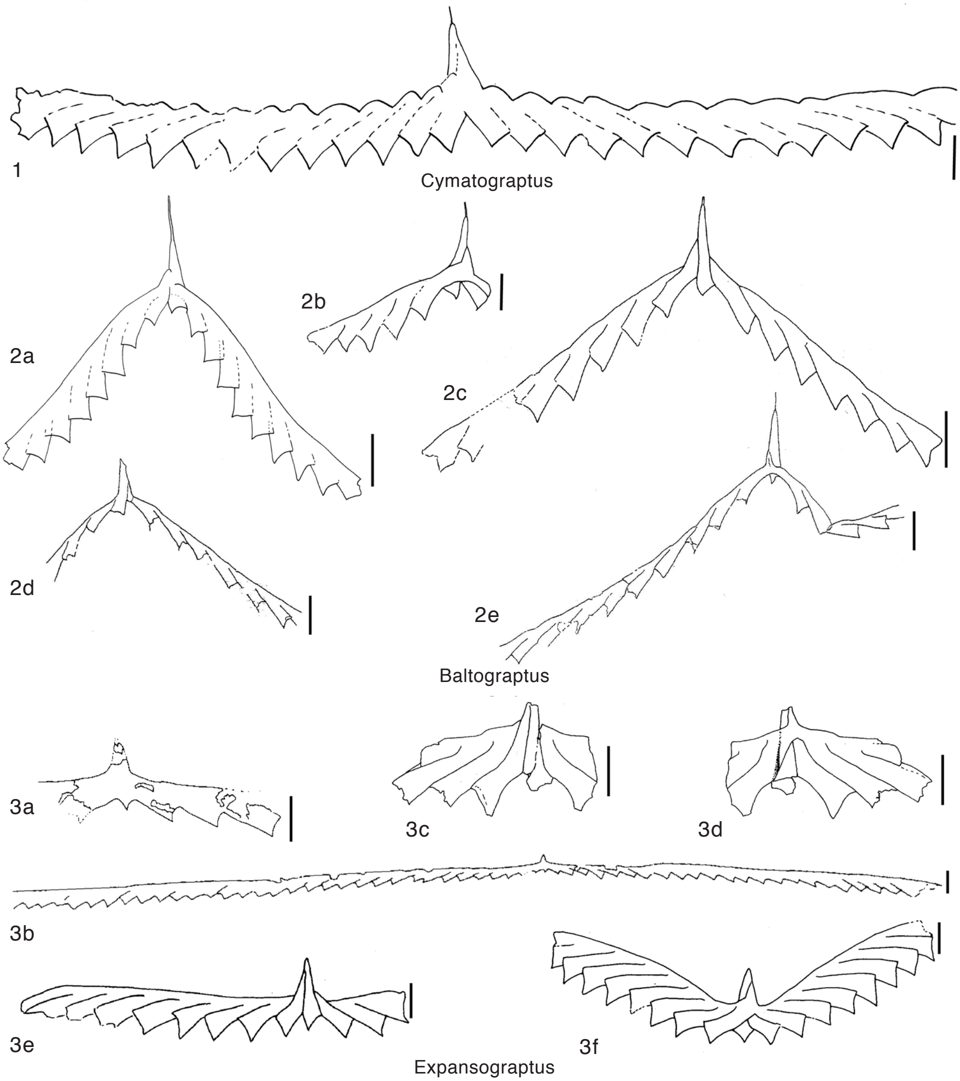


FIG. 17. Didymograptidae (p. 19–22).

Tetragraptus phyllograptoides Biozone, Diabasbrottet, Hunneberg, scale bar, 1 mm (new).

Expansograptus BOUČEK & PŘÍBYL, 1952, p. 13 [**Graptolithus extensus* HALL, 1858, p. 132; OD] [=*Extensograptus* BOUČEK & PŘÍBYL, 1952 (English abstract), p. 1, misspelling of *Expansograptus*]. More or less horizontal didymograptids with isograptid, dextral proximal development; proximal portion of sicula perpendicular to stipes; sicular and thecal apertures straight, without elaborations; origin of th1[1] low on prosicula; stipe width variable; crossing canals more or less symmetrically placed on sicula; crossing canal one is initially much wider than crossing canal two; length of isograptid suture variable. *Lower Ordovician (Floian,* Paratetragraptus approximatus *Biozone)–Middle Ordovician (Darriwilian,* Undulograptus austrodentatus *Biozone):* worldwide.——FIG. 17,*3a–b*. **E. extensus* (HALL), lectotype, GSC 976, proximal end (*a*) and complete specimen (*b*), scale bars, 1 mm (Cooper & Fortey 1982, fig. 40d–e).——FIG. 17,*3c–d*. *E. hirundo* (SALTER, 1863), obverse (*c*) and reverse (*d*) view, Tøyen Shale, Slemmestad, Oslo, Norway, scale bars, 1 mm (new).——FIG. 17,*3e*. *E. suecicus* (TULLBERG, 1880), T226, Tøyen section, Oslo, Norway, scale bar, 1 mm (new).——FIG. 17,*3f*. *E. urbanus* (MONSEN, 1937), PMU 23152B, drawing of latex cast in

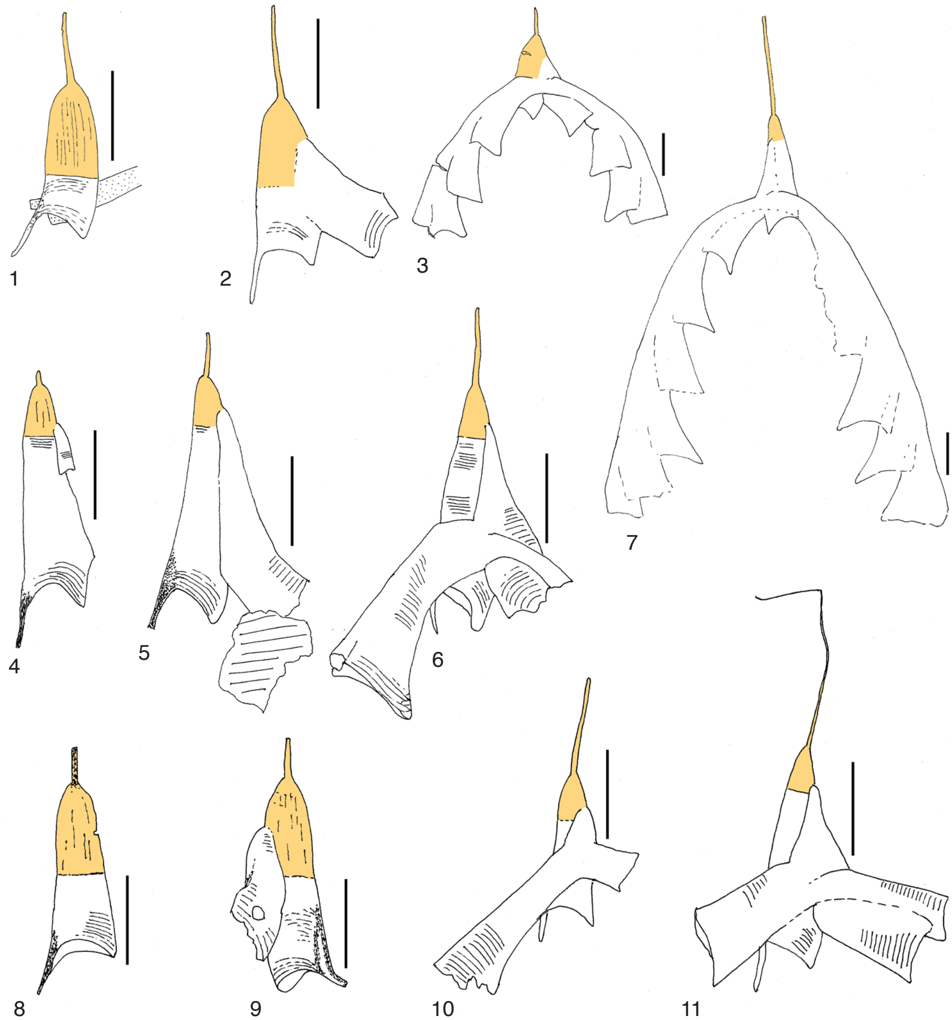


FIG. 18. Proximal ends of isolated pterograptids. *1–3, Didymograptellus bifidus* (HALL, 1865). *1,* Growing sicula, metasicula incomplete; *2,* complete sicula with th1[1]; *3,* proximal end of larger specimen; *4–7, Yutagraptus mantuanus* RIVA, 1994; *4,* sicula with initial part of th1[1]; *5,* sicula with incomplete th1[1]; *6,* proximal end in reverse view, showing virgellar spine; *7,* complete proximal end; *8–9, D. primus* MALETZ, 2010; *8,* incomplete sicula with prominent virgellar spine; *9,* juvenile with incomplete th1[1]; *10, Xiphograptus artus* MALETZ, 2010, proximal end showing artus-type development; *11, X. lofuensis* (LEE, 1961), proximal end with isograptid development; prosicula in *gray;* all scale bars, 0.5 mm (specimens adapted from Maletz, 2010).

reverse view, Diabasbrottet, Hunneberg, Sweden, scale bar, 1 mm (new).

Family PTEROGRAPTIDAE Mu, 1950

[Pterograptidae MU, 1950, p. 180] [*nom. emend.* MU, 1974, p. 231, *ex* Pterograptinae MU, 1950, p. 180]

Two-stiped, pendent to deflexed, and horizontal graptoloids; cladial branching in some taxa form secondarily multiramous tubaria; sicula conical, widening distinctly towards aperture and with small prosicula, or parallel-sided with wide prosicula; sicula with distinct dorsal virgellar spine and antivirgellar origin of th1[1]; thecae simple, widening tubes with moderate development of rutella; proximal development isograptid or artus type, dextral.

Lower Ordovician (Floian, Paratetragraptus akzharensis *Biozone)–Middle Ordovician (upper Darriwilian*, Pterograptus elegans *Biozone):* worldwide.

All taxa of the Pterograptidae possess a dorsal virgellar spine on the sicula. This spine can be seen as the defining synapomorphy. The family may be monophyletic, but no cladistic analysis of the group has yet been carried out. MALETZ, CARLUCCI, and MITCHELL (2009) showed a group of virgellate taxa among the stem reclinatids. The Pterograptidae incorporates the virgellate dichograptids, except for the four-stiped, scandent members of the genus *Phyllograptus* (see family Phyllograptidae p. 13–17) in which the virgellar spine evolved independently (MALETZ, 2010). The proximal part is quite variable with the dimension of the prosicula changing considerably from a comparably large prosicula in the early taxa (Figs. 18.1,3) to a small one in later taxa (Figs. 18.4,7,10–11). The proximal development is of the isograptid type, but derived species show an artus-type development (Fig. 18.10). All taxa show two main stipes with an orientation ranging from pendent to deflexed and horizontal, and, in a few cases, slightly reflexed proximally. The genera *Pterograptus* and *Pseudobryograptus* have a multiramous, pendent colony shape through the addition of thecal cladia.

The Pterograptidae originate in the Floian with the genus *Didymograptellus* bearing primitive, symplesiomorphic characters such as the origin of $th1^1$ in the middle part of the prosicula and simple thecae (Fig. 18.1–3). The earliest known species *Didymograptellus primus* MALETZ, 2010 from the *Tetragraptus akzharensis* to *Tshallograptus fruticosus* biozones already has a fully developed dorsal virgellar spine. The evolutionary origin of the dorsal virgellar spine is unknown as no morphologically intermediate taxa are available showing its formation. The development of the sicula with the large, parallel-sided prosicula, however, may indicate a close connection to the Anisograptidae, as in this group, the pro- and metasicula often appear to be parallel sided and do not show a widening from the aperture of the prosicula onwards.

Pterograptus HOLM, 1881b, p. 74 [**P. elegans;* M]. Pterograptid with long slender sicula, prosicula expanded, origin of $th1^1$ on metasicula, $th1^1$ dicalycal (artus-type development); alternating cladial branches on each theca of the two main stipes; main stipes declined to deflexed. *Middle Ordovician (upper Darriwilian,* Pterograptus elegans *Biozone):* UK, France, Germany, Portugal, Sweden, Norway, Canada, USA, Argentina, China, Australia, New Zealand.——FIG. 19,*1a–d.* **P. elegans; 1a–1b,* holotype, PMO 2697, Oslo Region, Norway (Holm, 1881b, fig. 2–3); *1c,* GSC 102784, flattened and bleached proximal end showing artus-type development (Maletz, 1994b, fig. 1).——FIG. 19,*1d. P. lyricus* KEBLE & HARRIS, 1934, paratype, NMVP 13755, showing zigzag pattern of main stipe, Victoria, Australia (new).——FIG. 19,*1e. P. scanicus* HOLM, 1881b, reconstruction (Bulman, 1970, fig. 77).

Didymograptellus COOPER & FORTEY, 1982, p. 220 [**Graptolithus bifidus* HALL, 1865, p. 73; OD]. Simple, parallel-sided sicula with a nearly straight aperture and prominent dorsal virgellar spine; prosicula large, at least ⅓ to ½ of sicular length; proximal development isograptid type, dextral, with high origin of $th1^1$ in prosicula; crossing canals low on sicula; thecae simple dichograptid with straight apertures; tubarium form pendent. *Lower Ordovician (Floian,* Tshallograptus fruticosus *Biozone)–Middle Ordovician (Dapingian,* Arienigraptus gracilis *Biozone):* Canada, USA, Argentina, Bolivia, China, Australia, New Zealand.——FIG. 19,*3.* **D. bifidus* (HALL), lectotype, GSC 910a, Lévis, Quebec (possibly Begin's Hill section), scale bar, 1 mm (Berry, 1962, fig. 2a).

Pseudobryograptus MU, 1957, p. 385 (p. 421, English translation) [**P. parallelus;* OD]. Small, pendent tubarium with 5–8 stipes; thecae simple with low inclination and overlap; branching after the initial dichotomy possibly by cladia generation; proximal development likely artus type. *Middle Ordovician (Darriwilian,* ?Holmograptus lentus *Biozone):* China, Argentina, Australia, ?Canada.——FIG. 19,*5a–b.* **P. parallelus; 5a,* holotype, NIGP 8863; *5b,* paratype, NIGP 8864; possibly *Holmograptus lentus* Biozone (originally cited as *Didymograptus hirundo* Biozone); Changshan, western Chekiang, China, scale bars, 1 mm (new).

Xiphograptus COOPER & FORTEY, 1982, p. 289 [**Didymograptus formosus* BULMAN, 1936, p. 24; OD]. Simple conical, considerably widening sicula with straight aperture and prominent dorsal virgellar spine (antivirgellar origin of $th1^1$); prosicula small, less than ¼ of sicular length; proximal development isograptid or artus type, $th1^1$ dextral and originating low in prosicula; crossing canals low on sicula, isograptid suture absent on reverse side; thecae simple dichograptid with straight apertures; tubarium form horizontal, declined, or

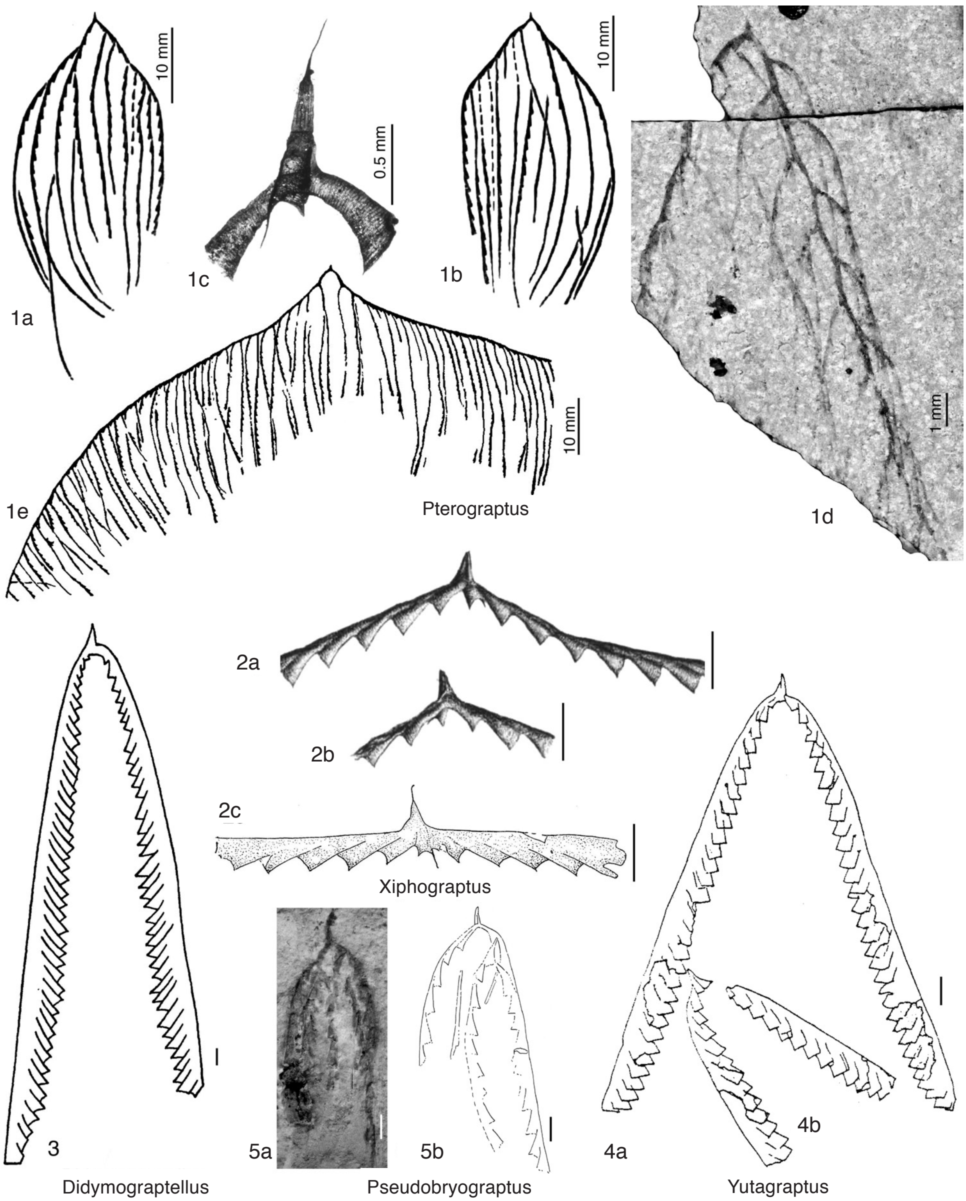


FIG. 19. Pterograptidae (p. 23–25).

less commonly, deflexed, with no or little distal widening of the stipes. *Lower Ordovician (Floian,* Tshallograptus fruticosus *Biozone)–Middle Ordovician (Darriwilian,* Pterograptus elegans *Biozone* and possibly to Dicellograptus vagus *Biozone):* worldwide.——FIG. 19,*2a–b.* **X. formosus* (BULMAN), lectotype, NRM-PZ Cn1264, obverse (*a*) and reverse (*b*) views, Hälludden, Öland, Sweden, scale bars, 1 mm (Bulman, 1936, pl. 1,*5–6*).——FIG. 19,*2c. X. lofuensis* (Lee, 1961), holotype, NIGP 10541, Dawan Formation, Majiang, Guizhou Province China, scale bar, 1 mm (Ni, 1988, fig. 1a).

Yutagraptus RIVA, 1994, p. 4 [**Y. mantuanus;* OD]. Simple conical, considerably widening sicula with straight aperture and prominent dorsal virgellar spine; prosicula small, less than ¼ of sicular length; proximal development isograptid type, dextral, with low origin of th1^1 in prosicula; crossing canals low on sicula, isograptid suture lacking on reverse side; thecae simple dichograptid with straight apertures;

tubarium form pendent with no or little distal widening of the stipes. *Middle Ordovician (Dapingian,* Didymograptellus bifidus *Biozone–Darriwilian*, Levisograptus austrodentatus or Levisograptus primus *Biozone):* Australia, Canada, USA, ?Iran.——FIG. 19,*4a–b*. **Y. mantuanus*, RPM 13677, holotype (*a*) and paratype (*b*) as associated on slab, Mantua, Utah, scale bar, 1 mm (Riva, 1994, fig. 3M–N).

ABBREVIATIONS FOR MUSEUM REPOSITORIES

AMNH: American Museum of Natural History, New York City, New York, USA
BGS GSM: British Geological Survey, Geological Survey Museum, Keyworth, Nottingham, UK
BU: Lapworth Museum, Birmingham University, Birmingham, UK
CPC: Commonwealth Palaeontological Collections, Geoscience Australia, Canberra, Australia (previously Bureau of Mineral Resources, BMR)
GM: Geological Museum, K. I. Satpayev Institute of Geological Sciences, Almaty, Kazakhstan
GSC: Geological Survey of Canada, Ottawa, Canada
GMCH: Geological Museum of China, Beijing, China
LO: Lunds Originale, Department of Geology, Lund University, Sweden
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
NHMUK: The Natural History Museum, London, UK (previously BMNH)
NIGP: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
NM: National Museum, Department of Paleontology, Prague, Czech Republic
NMVP: Museums Victoria, Melbourne, Australia
NRM-PZ Cn: Naturhistoriska Riksmuseet Stockholm, Sweden
OMR: B. Horák Museum, Rokychany, Czech Republic
PMO: Natural History Museum, Paleontological Type collections, University of Oslo, Norway
PMU: Palaeontological Collections, Museum of Evolution, Uppsala University, Sweden
RPM: Redpath Museum, McGill University, Montreal, Québec, Canada
SGU: Sveriges Geologiska Undersökning, Uppsala, Sweden
SM: Sedgwick Museum of Earth Sciences, Cambridge, UK
T: West Bohemian Museum, Pilsen, Czech Republic
ZPAL G: Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland

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