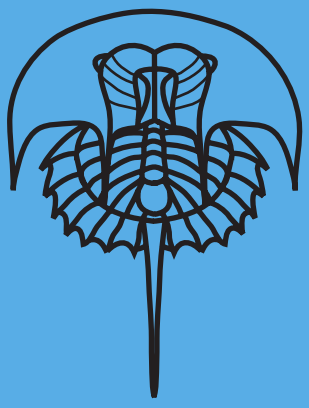

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Part V, Second Revision, Chapter 25: Superfamily Retiolitoidea and Family Neodiplograptidae: Introduction, Morphology, and Systematic Descriptions

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PART V, SECOND REVISION, CHAPTER 25: SUPERFAMILY RETIOLITOIDEA AND FAMILY NEODIPLOGRAPTIDAE: INTRODUCTION, MORPHOLOGY, AND SYSTEMATIC DESCRIPTIONS

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Superfamily RETIOLITOIDEA Lapworth, 1873

[Retiolitoidea Lapworth, 1873, table 1, facing p. 555, *nom. correct.* Kozłowska-Dawidziuk, Lenz, & Bates, 2003, p. 51, ex Retioloidea Lapworth, 1873, table 1, facing p. 555] [=*partim* order Retiolitina Mikhaylova, 1970, p. 103]

Neograptine axonophorans with scandent, biserial, dipleural, bistipular to unistipular tubarium; proximal development pattern supposedly of pattern H astogeny or a derived pattern, but development unknown in many taxa; thecae with straight to curved ventral walls; distinct geniculum present in some, with or without genicular additions; ancora, ancora umbrella, and ancora sleeve in derived Retiolitidae. *Upper Ordovician (Katian,* Paraorthograptus pacificus *Biozone)–Silurian, Ludlow (Ludfordian,* Saetograptus leintwardinensis *Biozone):* worldwide.

Kozłowska-Dawidziuk, Lenz, and Bates (2003) regarded the presence of the ancora umbrella as the defining character for the Retiolitoidea and included the ancorate petalolithines in the clade. Melchin and others (2011) extended the concept of the Retiolitoidea by including the Neodiplograptidae (Fig. 1), and stated that a number of synapomorphies lay at the base of the redefined clade. No morphological diagnosis was provided for the taxon, but it was defined as "the most recent common ancestor of *Metabolograptus ojsuensis* and *Retiolites geinitzianus* and all of its descendants (Melchin & others, 2011, node 3, fig. 2–3)." The authors expanded the concept of the Retiolitoidea considerably from what was generally understood to be a retiolitid by adding a number of taxa that bear no indications of a true ancora. Melchin and others (2011, p. 296, node 3 in fig. 3) considered the presence of inclined, distal apertural thecal walls and inclined, interthecal septa as important synapomorphies of the Retiolitoidea, although there are no interthecal septa present in the derived retiolitines. The base of node 3 is collapsed into a polytomy in their figure 3, indicating the low bootstrap support of the nodes in this region of their cladogram (Melchin & others, 2011, fig. 2).

EVOLUTION

The Retiolitoidea originated in the Upper Ordovician through a normalograptid ancestor, but the precise biostratigraphic timing of the origin of the clade is uncertain (see Melchin & others, 2011, fig. 7). The oldest members of the Retiolitoidea appear to be *Neodiplograptus charis* (Mu & Ni, 1983) and *Metabolograptus ojsuensis* (Koren' & Mikhaylova in Koren', Mikhaylova, & Tzai, 1980) from the late Katian (Melchin & others, 2011).

The Retiolitoidea includes a basal paraphyletic family Neodiplograptidae with a

Maletz, Jörg. 2019. Part V, Second Revision, Chapter 25: Superfamily Retiolitoidea and family Neodiplograptidae: Introduction, morphology, and systematic descriptions. Treatise Online 117:1–8, 4 fig.

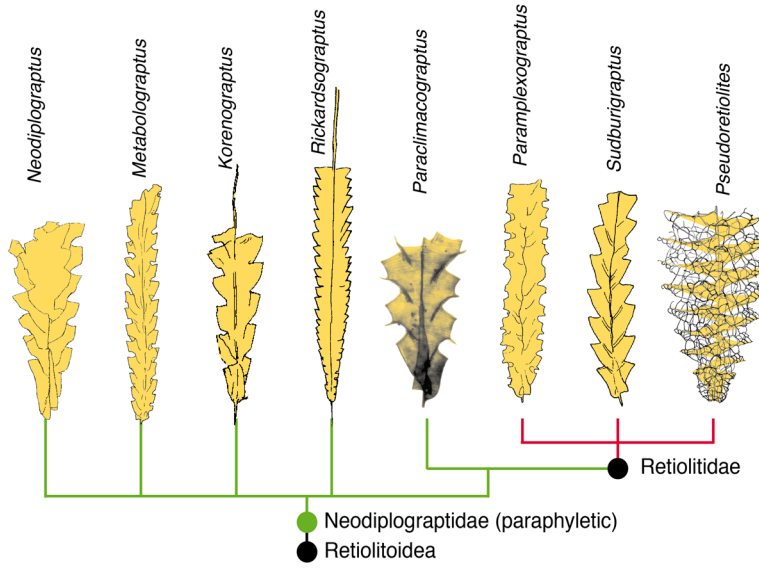

FIG. 1. Cladogram explaining the concept of the Retiolitoidea and the paraphyletic Neodiplograptidae; specimens from various sources, not to scale (new, based on data in MELCHIN & others, 2011).

number of very similar genera showing an initial low disparity and low diversity in the uppermost Ordovician to lowermost Silurian. In the Llandovery, however, the diversification increased considerably with the evolution of the ancora sleeve and the following radiation of the Retiolitidae (see Lenz & others, 2018).

Family NEODIPLOGRAPTIDAE Melchin & others, 2011

[Neodiplograptidae MELCHIN, MITCHELL, NACZK-CAMERON, FAN, & LOXTON, 2011, p. 296] [incl. Cameragraptidae HUNDT, 1953b, p. 3, *nom. dub.*]

Biserial, dipleural neograptines with pattern H proximal development type or derived one; first thecal pair with outward-inclined apertures forming lip in derived taxa; thecae often showing considerable biform development; ventral side of thecae rounded to geniculate, distally straight with outward-inclined straight apertures; medium septum complete, partial or lacking; interthecal septae outward inclined. *Upper Ordovician (upper Katian,* Paraorthograptus pacificus *Biozone)–Silurian, Llandovery (Telychian,* Monoclimacis griestoniensis *Biozone): worldwide.*

MELCHIN and others (2011, p. 296) analyzed the early Silurian biserial axonophorans and erected the family Neodiplograptidae as "the partial clade that includes the most recent common ancestor of *Metabolograptus ojsuensis* and *Retiolites geinitzianus,*" and referred quite a number of taxa to the Retiolitoidea. MALETZ (2014), however, identified only taxa with an ancora sleeve meshwork as the Retiolitoidea and preferred to include the non-ancorate Petalolithinae in the Neodiplograptidae.

The Neodiplograptidae, as defined by MELCHIN and others (2011), represents a poorly resolved clade with a basal polytomy (Fig. 1), indicating the difficulty of differentiating the individual taxa based on the largely flattened material available for investigation. As a paraphyletic taxon, the Neodiplograptidae led to the monophyletic Retiolitidae through a number of steps in the development of the ancora umbrella and ancora sleeve as an external, secondary development around the biserial tubarium. MELCHIN and others (2011) separated the retiolitid *Paramplexograptus* MELCHIN & others, 2011 from the neodiplograptid

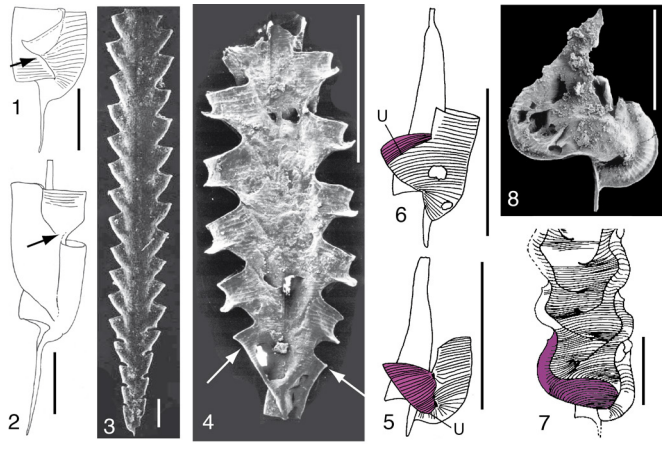

FIG. 2. Morphology and proximal development of the Neodiplograptidae. *1–3, Rickardsograptus tcherskyi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & NIKOLAEV, 1967); *1,* juvenile showing late origin of th1[2] from large flange (new); *2,* origin of th2[1] from distal part of th1[2] (new); *3,* SEM photo of large specimen in relief showing geniculate proximal thecae and non-geniculate distal thecae (Melchin & others, 2011, fig. 4G); *4, Paraclimacograptus innotatus* (NICHOLSON, 1869), showing outward-inclined apertures with lip (*arrows*) on proximal end and geniculate thecae with strong genicular flanges (Koren' & Rickards, 2004, fig. 29); *5,* pattern H astogeny in the normalograptid *Metaclimacograptus orientalis* (OBUT & SOBOLEVSKAYA, 1966) showing unconformity (*u*) at origin of th1[2] tube; *6,* pattern H′ astogeny in *Korenograptus nikolayevi* (OBUT, 1965) with delayed unconformity (*5-6,* adapted from Melchin, 1998, fig. 4a–b) *7, Cystograptus penna* (HOPKINSON, 1869), reverse view (adapted from Jones & Rickards, 1967, fig. 2D); *8, Cystograptus vesiculosus* (NICHOLSON, 1868), juvenile, obverse view (Koren' & Rickards, 2004, fig. 12). Scale bars, 1 mm.

Paraclimacograptus through the lack of a median septum in *Paramplexograptus*. Otherwise the two genera are basically inseparable (Fig. 1).

MORPHOLOGY

The proximal development (Fig. 2) of the Neodiplograptidae ranges from a pattern H astogeny to a pattern H′ astogeny. The details of the proximal development of many of the taxa included in the analysis of MELCHIN and others (2011, Appendix 1) were listed as based on unpublished information. Thus, the proximal development types have to be regarded as uncertain until further material is published. The proximal development of *Neodiplograptus* and *Metabolograptus* has not been demonstrated from chemically isolated material or relief specimens showing growth lines. The proximal development of *Rickardsograptus tcherskyi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & NIKOLAEV, 1967) is known from isolated material (MELCHIN 1998; MELCHIN & others, 2011). The species shows a distal origin of th1[2] from a wide flange of th1[1] (Fig. 2.1–2.2), indicating a pattern H′ astogeny. A pattern H′ astogeny (Fig. 2.6) can also be seen in *Korenograptus nikolayevi* (OBUT, 1965) as was demonstrated by MELCHIN (1998, pl. 1,*4–9*) and LOYDELL and MALETZ (2009). The genus *Cystograptus,* with its extremely elongated sicula and long undulating thecae, is included preliminarily in the Neodiplograptidae following ŠTORCH (1985) and MELCHIN and others (2011, p. 296), who suggested a derivation from a species of *Neodiplograptus* or *Metabolograptus*. JONES and RICKARDS (1967) illustrated a possible pattern H astogeny for *Cystograptus penna* (HOPKINSON, 1869), which can also be supported by a single specimen of *Cystograptus vesiculosus* (NICHOLSON, 1868) illustrated by KOREN' and RICKARDS (2004). In both taxa, the origin of th1[2] appears to be very low on the th1[1] at the point of change from downward to upward growth (Figs. 2.7–2.8) and not from an upward-growing flange on

th1[1]. Details of the number and position of proximal foramina are not available.

The thecal style of the Neodiplograptidae ranges from simple outward-inclined thecae with straight ventral wall and aperture to strongly geniculate thecae with ventral thecal walls parallel to the tubarium midline. Many taxa are biform with the thecal style changing considerably from the proximal to the distal end. A number of geniculate proximal thecae are found in *Metabolograptus*, while the colony quite abruptly changes to nongeniculate thecae distally (Fig. 2.3). In other genera, the change in thecal style is more gradual and imperceptible and is difficult to see in poorly preserved, flattened specimens. MELCHIN and others (2011, p. 296) indicated that the most characteristic synapomorphies of their Neodiplograptidae include the presence of inclined distal thecal subapertural walls and inclined interthecal septa. Genicular elaborations largely include flanges (Fig. 2.4), but these may appear similar to spines in the typical lateral preservation of the tubaria.

Neodiplograptus LEGRAND, 1987, p. 62 [**Diplograptus magnus* LAPWORTH, 1900, p. 132; OD]. Neodiplograptids with pattern H proximal development type with rapidly widening proximal end; thecae sharply geniculate proximally and with slightly rounded, non-geniculate ventral side in distal thecae; thecal inclination increasing significantly through the proximal to mesial regions; full median septum distally. *Upper Ordovician (upper Katian,* Paraorthograptus pacificus *Biozone)–Silurian, Llandovery, (Aeronian,* Neodiplograptus magnus *Biozone):* worldwide.——FIG. 3,*1a–b*. **N. magnus* (LAPWORTH), River Wye, Rhayader, Wales, UK; *1a*, lectotype, BU 1295, poor external mold; *1b*, topotype, BU 1296, obverse view, scale bar, 1 mm (Zalasiewicz, 2000).

Korenograptus MELCHIN & others, 2011, p. 297 [**Glyptograptus gnomus* CHURKIN & CARTER, 1970, p. 24; OD]. Neodiplograptids with a pattern H proximal development type or derived type; colony parallel sided or widening slowly from the proximal end; thecae with slightly rounded to straight, non-geniculate ventral side; full median septum distally. *Upper Ordovician (?upper Katian,* Paraorthograptus pacificus *Biozone)–Silurian, Llandovery, (Rhuddanian,* Neodiplograptus magnus *Biozone):* worldwide.——FIG. 3, *2a–b*. **K. gnomus (*CHURKIN & CARTER), Alaska, USA; *2a*, USNM 161727; *2b*, holotype, USNM 161644; scale bars, 1 mm (Churkin & Carter, 1970, fig. 11f and 11e, respectively).——FIG. 3,*2c*. *K. magnus* (CHURKIN & CARTER, 1970), GSC 135126, Cape Manning, Nunavut, Canada, scale bar, 1 mm (Melchin & others, 2011, fig. 5i).

Metabolograptus OBUT & SENNIKOV, 1985, p. 55 [**Diplograptus modestus siberica* OBUT, 1955, p. 138; OD] [=*Persculptograptus* KOREN' & RICKARDS, 1996, p. 32 (type, *Diplograpsus persculptus* SALTER, 1873, p. 28, OD); MELCHIN & others, 2011, p. 296]. Neodiplograptids with pattern H proximal development type; colony parallel sided or widening slowly from proximal end; thecae with sharp to bluntly rounded genicula; full median septum, gently sinuous proximally; sinuous interthecal septa; subapertural walls parallel to moderately inclined. *Upper Ordovician (?upper Katian,* Paraorthograptus pacificus *Biozone*)*–Silurian, Llandovery (Rhuddanian,* Huttagraptus acinaces *Biozone):* worldwide.——FIG. 3,*3a*. Possibly *Metabolograptus praecursor* (KOREN' & RICKARDS, 2004), GSC 135121, topotype (species unrecognizable, as based on distal fragments), scale bar, 1 mm (Melchin & others, 2011, fig. 5a).——FIG. 3,*3b*. **M. sibericus* (OBUT), holotype, CSGM211/6a, scale bar, 1 mm (Melchin & others, 2011, fig. 6a).——FIG. 3,*3c*. *M. persculptus* (ELLES & WOOD, 1907), lectotype, GSM 11782, scale bar, 1 mm (Williams, 1983, pl. 66,*3*).

Paraclimacograptus PŘIBYL, 1947, p. 4 [**Climacograpsus innotatus* NICHOLSON, 1869, p. 238; OD]. Neodiplograptids with a pattern H' proximal development type; colony parallel sided or widening slowly from the proximal end; thecae with sharp to bluntly rounded genicula; genicula with ventrally projecting hood; thecae with wide apertural excavations, everted apertures, and slightly to moderately inclined supragenicular walls; median septum partial in proximal end, complete distally. *Upper Ordovician (Hirnantian,* Metabolograptus persculptus *Biozone)–Silurian, Llandovery (Rhuddanian,* Coronograptus cyphus *Biozone):* worldwide.——FIG. 3,*4a–b*. **P. innotatus* (NICHOLSON); *4a*, holotype, possibly NHMUK PM P.1949 (see Benton, 1979; Strachan, 1997), Dob's Linn, Moffat, Scotland, UK (Nicholson, 1869, pl. 9,*16*); *4b*, GSC 104929, isolated specimen, Sakmara Formation, southern Urals, Russia (Russel, Melchin, & Koren' 2000, fig. 1,*9*). Scale bars, 1 mm.

Rickardsogratus MELCHIN & others, 2011, p. 297 [**Diplograptus* (?) *tcherskyi* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & NIKOLAEV, 1967, p. 59; OD]. Neodiplograptids with a pattern H′proximal development, or possibly pattern H astogeny in earlier taxa; thecae show pronounced widening mesially, which corresponds to change to more inclined and more gently sigmoidal to straight thecae. *Silurian, Llandovery (Rhuddanian,* Atavograptus atavus–Neodiplograptus magnus *Biozones):* worldwide.——FIG. 3,*5a–b*. **R. tcherskyi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA,

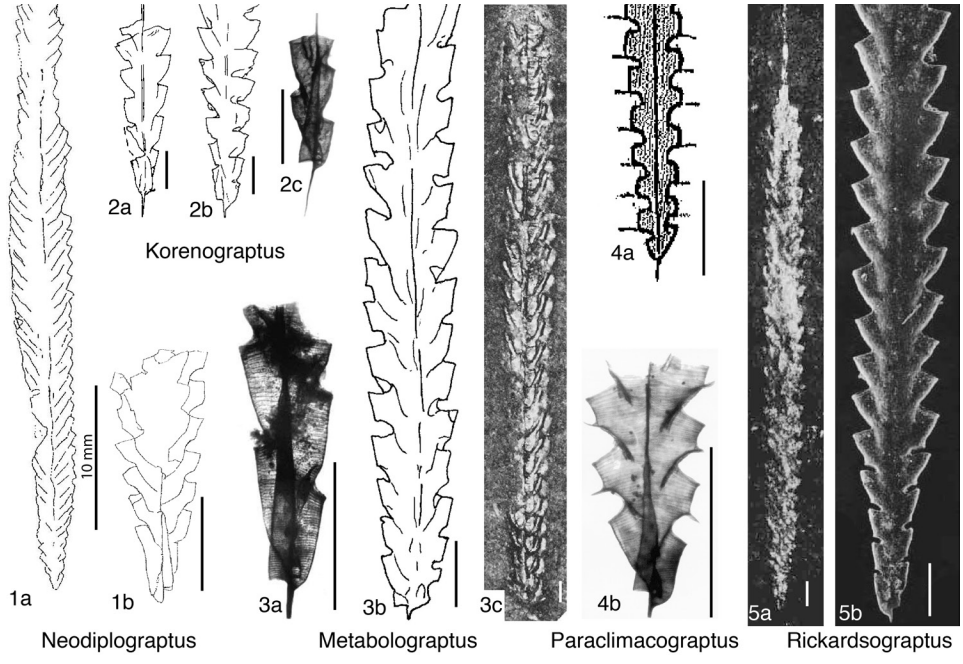

FIG. 3. Neodiplograptidae (p. 4–5).

& NIKOLAEV); *5a*, holotype, flattened specimen, (Obut & Sobolevskaya in Obut, Sobolevskaya, & Nikolaev, 1967, pl. 3,*1*); *5b*, isolated specimen in obverse view, GSC 135120, Arctic Canada (Melchin & others, 2011, fig. 4g). Scale bars, 1 mm.

UNCERTAIN STATUS

Genera listed here are either difficult to interpret and uncertain as to whether they belong to the family Neodiplograptidae, or poorly characterized and unrecognizable as valid. The genus *Cystograptus* has been considered to be related to *Neodiplograptus* (see ŠTORCH, 1985; MELCHIN & others, 2011), but since it shows features not known from any other genus of the Neodiplograptidae, it cannot be reliably included here. The genus shows an extremely elongated sicula unlike any other neodiplograptid. The U-shaped initial thecae of the colony and the long sigmoidally curved thecae are reminiscent of an *Undulograptus* BOUČEK, 1973 species from the Middle Ordovician. A closer relationship, however, is unlikely. The proximal development type of *Cystograptus* appears to be a pattern H astogeny with a delayed dicalycal theca, indicated by the distal origin of the median septum. *Cystograptus* bears a conspicuously extended three-vaned nematularium that is overgrown by the advancing stipes in mature specimens (URBANEK, KOREN', & MIERZEJEWSKI, 1982).

Cameragraptus HUNDT, 1953b has been erected validly but is based on unrecognizable scalariform biserials. HUNDT (1953b) included a number of species in this genus, all based on the form of the nematularium. SCHAUER (1971, p. 35) indicated that most specimens identified as *Cameragraptus* by HUNDT (1953b) may belong to *Neodiplograptus thuringiacus* (KIRSTE, 1919), but this cannot be verified.

Cystograptus HUNDT, 1942, p. 205 [**C. speciosus;* SD JONES & RICKARDS, 1967, p. 181–182; =*Diplograpsus vesiculosus* NICHOLSON, 1868, p. 61, see JONES & RICKARDS, 1967, p. 181]. Neodiplograptids with strongly elongated sicula and long, doubly sigmoid thecae; proximal development

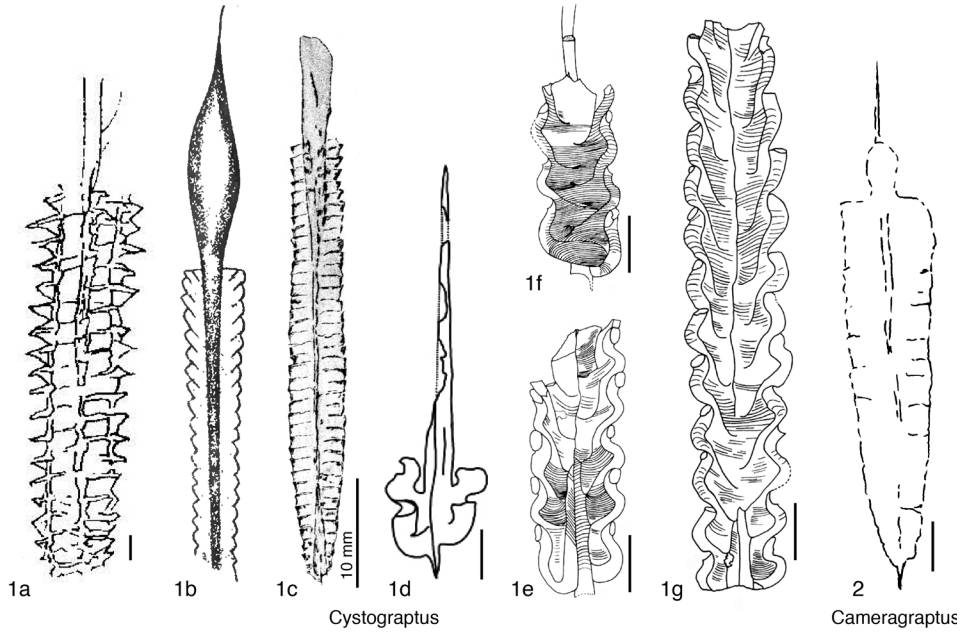

FIG. 4. Neodiplograptidae, uncertain status (p. 5–6).

of modified pattern H astogeny; median septum straight to slightly undulate, delayed; robust three-vaned nematularium proximally overgrown in mature colonies. *Silurian, Llandovery (Rhuddanian,* Parakidograptus acuminatus *Biozone–Aeronian,* Coronograptus cyphus *Biozones):* Britain, Czech Republic, Denmark, Germany, Sweden, Kazakhstan, Canada, USA.——FIG. 4,*1a–d*. **C. vesiculosus* (NICHOLSON)*; 1a,* holotype of *C. speciosus,* repository unknown (Münch, 1952, pl. 10,*8*); *1b*, holotype, original illustration, possibly NHMUK PM P.1880 (see BENTON, 1979; STRACHAN, 1997), magnification unknown (Nicholson, 1868, pl. 3,*11*); *1c*, BU 1231, typical specimen with nematularium, Dob's Linn, Scotland, UK (Elles & Wood, 1907, pl. 28,8c); *1d*, juvenile showing long sicula (Štorch, 2015, fig. 4g). Scale bars, 1 mm unless marked otherwise.——FIG. 4,*1e–g*. *C. penna* (HOPKINSON, 1869), *Lagarograptus acinaces* Biozone, Rheidol Gorge, UK; *1e*, SM A57550, proximal end, reverse view; *1f*, SM A23952, proximal end, obverse view; *1g*, SM A23607, long specimen showing distal insertion of median septum; scale bars, 1 mm (Jones & Rickards, 1967, fig. 1–2).

Cameragraptus HUNDT, 1953b, p. 3 (no pagination in paper) [**C. cuneatus*, HUNDT, 1953b, p. 4, fig. 7 (not fig. 4 as stated in the text); SD herein]. [Figure is a scalariform view of a biserial.] *Silurian, Llandovery (Rhuddanian–Aeronian):* Germany.——FIG. 4.*2*. *C. cuneatus*, holotype, BAF 186/4211, scale bar, 1 mm (Blumenstengel & others, 2006, pl. 1,*1B*).

ABBREVIATIONS FOR MUSEUM REPOSITORIES

BU: Lapworth Museum, Birmingham University, UK
CSGM: Central Siberian Geological Museum, Novosibirsk, Russia
GSC: Geological Survey of Canada, Ottawa, Canada
GSM: Geological Survey Museum, London, UK
LO: Lunds Originale, Department of Geology, Lund University, Sweden
NHMUK PM: The Natural History Museum, London, UK
NIGP: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
SM: Sedgwick Museum of Earth Sciences, Cambridge, UK

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