# PROXIMAL STRUCTURE AND DEVELOPMENT IN THE ORDOVICIAN GRAPTOLITE *PARISOGRAPTUS* CHEN AND ZHANG, 1996

*by* JÖRG MALETZ *and* YUANDONG ZHANG

ABSTRACT. The proximal development of *Parisograptus* Chen and Zhang is described from three-dimensionally preserved specimens. The unique development features an origin of proximal thecae like a string of pearls vertically upon each other on the reverse side of the rhabdosome with the dorsal sides of the initial stipes placed side by side. The development differs strongly from that found in the superficially similar *Arienigraptus* in which the first thecal pairs grow downwards side by side, even though the rhabdosome shapes are quite similar. It represents a first step towards the development of a completely biserial rhabdosome and eventually leads to the biserial, monopleural glossograptids.

KEY WORDS: Ordovician, graptolites, taxonomy.

PROXIMAL end developments are nowadays regarded as the most reliable characters for phylogenetic interpretations of graptolite evolution (Fortey and Cooper 1986; Mitchell 1987; Maletz and Mitchell 1996; Melchin 1998). However, it is often difficult or even impossible to obtain reliable data on the proximal development of graptolites because of the inadequate preservation as flattened films of periderm material. Therefore, the proximal development of many graptolites is unknown and awaits the rare surfacing of better-preserved specimens.

The best material to investigate the proximal development of graptolites is pyritized internal moulds and series of three-dimensionally preserved growth stages chemically isolated from the rock matrix. This well-preserved material sometimes gives astonishing insights and exciting new information even in supposedly simple forms, as is documented here for the two-stiped, reclined glossograptids of the genus *Parisograptus* Chen and Zhang, 1996.

Isolated specimens and relief material of isograptids are known mainly from the *Isograptus victoriae* group and supposedly confirm the simple isograptid development with two reclined stipes of all species. In his investigation of isograptids, Cooper (1973), however, differentiated the *Isograptus caduceus* and the *Isograptus victoriae* groups, based on the number of pendent thecae and other characters of the rhabdosome shape. Isolated material of isograptids was not known at the time.

Only in the advanced glossograptids is the proximal development known to be more complex (Maletz and Mitchell 1996). *Arienigraptus* and *Pseudisograptus* exhibit a prominent manubrium. The genera *Cryptograptus*, *Glossograptus* and *Kalpinograptus* possess a monopleural-biserial rhabdosome. More recently the new genus *Parisograptus* Chen and Zhang, 1996 was described for isograptids with a proximal development resembling that of *Arienigraptus*. The proximal development type was interpreted (Chen and Zhang 1996, fig. 11.4B) as possessing initial thecae having a downward-outward growth path nearly identical to that in *Arienigraptus*, but showing an increased overlap of the downward-growing parts in reverse view. Our reinvestigation, however, has shown that the proximal development in *Parisograptus* is unique, and quite different from this earlier interpretation. It turns out that the resemblance to the structure in *Arienigraptus* is only superficial.

### THE PROXIMAL DEVELOPMENT

A number of isograptid specimens referred to *Parisograptus curvithecatus* (Hsü) by Chen and Zhang (1996) are preserved in full relief and show the proximal development in some detail, but do not reveal growth lines (Pl. 1). The earliest development is not visible, as later parts of the initial thecae cover this. Therefore, the exact origin and development of $th1^2$ and $th2^1$ are still uncertain. The later development and growth of thecae is well displayed by the available specimens, and this is the material from which the interpretation is derived.
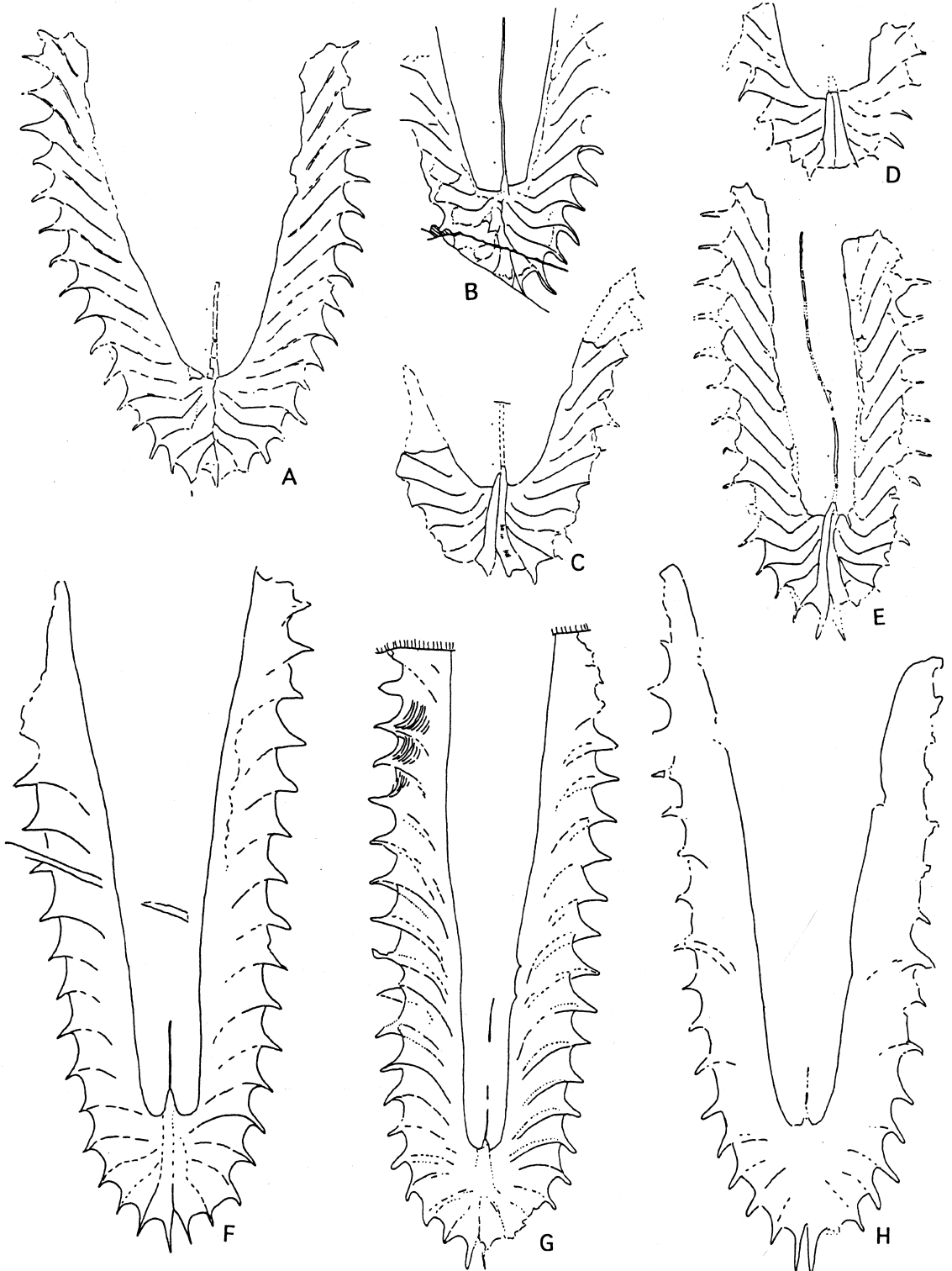
*Obverse view*

Three specimens are available to demonstrate the proximal development in obverse view (Pl. 1, figs 1, 5, 7; Text-fig. 1c–e). In this view the early growth of the initial thecae is covered. The sicula and $th1^1$ are symmetrically arranged with the plane of symmetry between them. They grow parallel to each other, except for the apertural part in which they bend outwards away from each other. Their apertures leave a deep and slender indentation between their ventral sides. This development represents the typical glossograptid condition: the isograptid symmetry of the first thecal pair. The rutelli on the sicula and on $th1^1$ are strongly developed. The relief specimens do not show the exact origin of $th1^1$, which is expected to be in the prosicula, as it is only about 0·2 mm below the sicular apex. The origins of the second ($th1^2$, $th2^1$) and third ($th2^2$, $th3^1$) thecal pairs are hidden behind the sicula and $th1^1$, but later thecal origins are visible. Thecal pairs 3–5 show a strong curvature in their growth. The growth is obliquely downwards initially, but aperturally changes to a horizontal to slightly upward direction. The origins of thecal pairs 3 and 4 are visible above each other close to the dorsal sides of the sicula and $th1^1$, respectively (Text-fig. 1c, e). The origin of thecal pair 5 appears at the point where the dorsal side of the stipes reaches the sicula and $th1^1$. Later thecae show the typical dichograptid thecal origin and development with a dorsal origin of all thecae and the strong development of rutelli typical of most glossograptids.
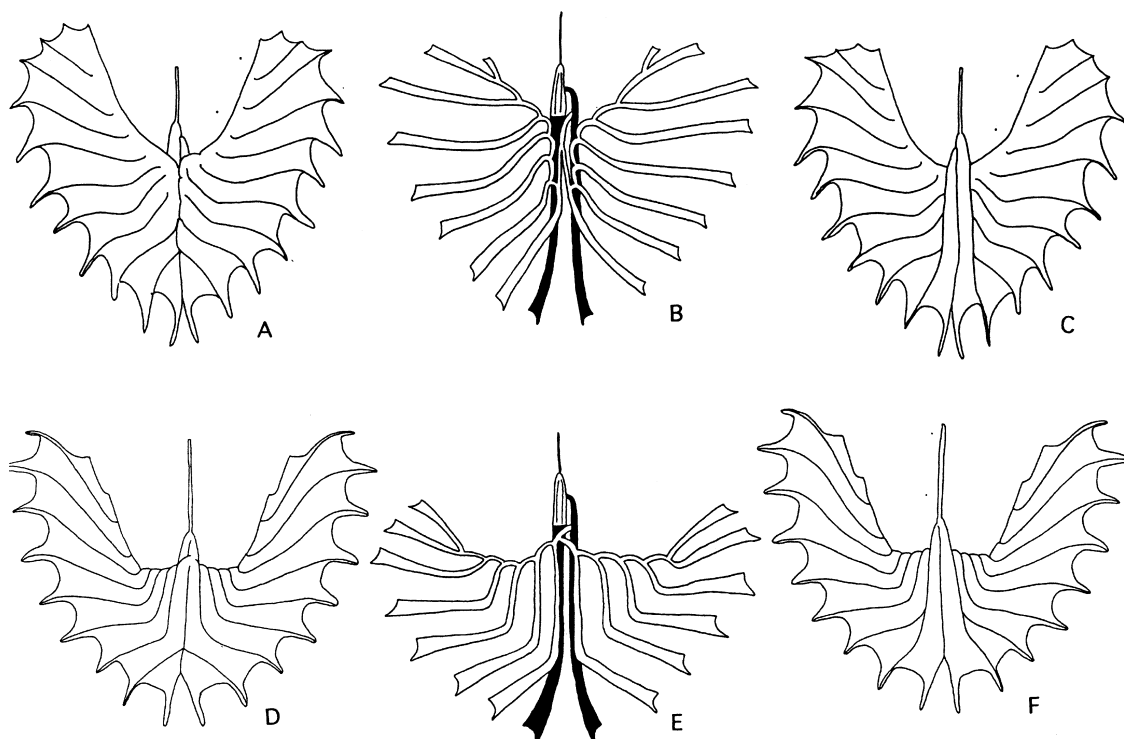
*Reverse view*

The reverse view of *Parisograptus* is known from two specimens. In reverse view most parts of the sicula and $th1^1$ are covered by later thecal growth (Pl. 1, figs 2–4, 6). Only the supradorsal part and a short subapertural part of these thecae are visible. As juveniles are not available for study, the exact origin of $th1^2$ and $th2^1$, the proximal structure and development, are unknown. The thecal origins are only exposed from thecal pair 3 onwards and the crossing canals of $th1^2$ and $th2^1$ are covered by later thecae. The proximal development is inferred to be of the isograptid type with $th1^2$ as the dicalycal theca, but is not visible in the specimens. A clear median suture completely separates both stipes. The origins of thecal pairs 3–5 are placed upon each other with the initial thecal growth apparently being upwards (Text-figs 1a–b, 2a–b). Unfortunately no growth lines are visible in the specimens to confirm this observation. The thecal growth direction of the proximal thecae is more clearly visible in reverse view. The growth is obliquely downwards initially and horizontal to somewhat upwards aperturally.

   The proximal development differs considerably from the interpretation given by Chen and Zhang (1996, fig. 11-4b), in which the initial thecae were indicated to originate in a horizontal line similar to that in *Arienigraptus zhejiangensis*. On the contrary, the material shows that the thecal origins are placed each upon the other in a vertical sequence. The median suture between the stipes is not constructed by the lateral walls of $th1^2$ and $th2^1$ as in *Arienigraptus*, but by the dorsal sides of the two stipes (Text-fig. 2a, c). The

TEXT-FIG. 1. *Parisograptus caduceus* (Salter, 1853). A, NIGP 126523, AEP40, Hengtang section, Jianshan, Zhejiang, China; ×6·5. B, NIGP 126524, Hengtang section; ×6·5. C, NIGP 126527a, AEP40, Hengtang section; ×6·5. D, NIGP 126529, AEP42, Hengtang section; ×6·5. E, NIGP 126522, AEP41 Hengtang section; ×6·5. F, PMO 113·795, Bogo Shale, horizon 1, coll. O. Schmidt-Gündel; ×6·5. G, YPM 20328, Marathon region, Texas (Berry 1960, pl. 12, fig. 1: *Isograptus forcipiformis* var. *latus* Ruedemann); ×6·5. H, GSC 102632, Lévis, Québec, Canada; ×6·5.

TEXT-FIG. 2. Thecal diagrams and reconstructions of *Parisograptus caduceus* (Salter) and *Arienigraptus zhejiangensis* Yu and Fang. A, C, reconstructions of *Parisograptus caduceus* (Salter) in reverse (A) and obverse (C) views. D, F, reconstructions of *Arienigraptus zhejiangensis* Yu and Fang in reverse (D) and obverse views (F). B, *Parisograptus caduceus* (Salter), thecal diagram. E, *Arienigraptus zhejiangsis* Yu and Fang, thecal diagram.

thecal diagram (Text-fig. 2B) shows the inferred development also of the first two thecal pairs. The initial development is supposedly isograptid dextral with th1$^2$ as the dicalycal theca, as is known from relief material and isolated specimens of the *Isograptus victoriae* group (Bulman 1932; Williams and Stevens 1988) and also in the monopleural glossograptids (Maletz and Mitchell 1996). The proximal development is shown in Text-figure 2B, but is actually covered by the initial growth of the later thecae (see Text-fig. 2A). The available relief material (Text-fig. 2A, C) confirms the initial and distal growth of the later thecal pairs.

## COMPARISON OF PROXIMAL DEVELOPMENT

Isograptus

The relatively simple isograptid development in the *Isograptus victoriae* group is well known and has even been illustrated correctly by Moberg (1892) for material referred to *Isograptus gibberulus* Nicholson from Scania, southern Sweden. Bulman (1932) illustrated material of the same form again in detail. The material shows a relatively high number of pendent thecae and a compact large rhabdosome.

In reverse view the proximal development of the *Isograptus victoriae* group shows the descending crossing canals of th1$^2$ and th2$^1$ with all later thecae originating more distally on the stipes (Text-fig. 3). Even in the biserial *Cardiograptus* the crossing canals of th1$^2$ and th2$^1$ are exposed and the thecal origins of all later thecae are visible in reverse view (Text-fig. 3). In *Parisograptus* the thecal origins in the proximal end are above each other in a vertical succession. Owing to the growth of the initial thecae the crossing canals of th1$^2$ and th2$^1$ are not exposed on the reverse side.

Arienigraptus

The proximal end structure of *Parisograptus* (Text-fig. 2A, C) closely resembles that of *Arienigraptus* (Text-fig. 2D, F) at first sight, especially in obverse view. However, the thecae grew obliquely downwards instead in *Parisograptus*, rather than downwards parallel to each other as in *Arienigraptus*. In addition, in *Parisograptus* the point of origin of the second to fourth or fifth thecal pairs is hidden in obverse view behind the sicula and th1[1], whereas in *Arienigraptus* the thecal origins are visible as a string of pearls at the dorsal side of the stipes (Text-fig. 2D–F). In reverse view, the differences are even more pronounced. The origin of the thecae on the vertically oriented dorsal side of the stipes in *Parisograptus* (Text-fig. 2A) is obvious and conspicuously different from the horizontal alignment of the thecal origins in *Arienigraptus zhejiangensis* (Text-fig. 2D). This is a fundamental difference in development and clearly precludes the close phylogenetic relationship of *Parisograptus* to *Arienigraptus*. The difference is even more pronounced in the thecal diagrams (Text-fig. 2B, E).

## EVOLUTION

The evolution of the Glossograptidae was described by Maletz and Mitchell (1996) in some detail and is not repeated here. A slightly more generalised diagram (Text-fig. 3) is shown to indicate the phylogenetic relationship of *Parisograptus*, leaving out details that are not relevant to the discussion. The defining synapomorphy of the whole group is the isograptid symmetry (character 1). The two-stiped reclined rhabdosome is a symplesiomorphic character retained from ?*Isograptus dilemma* and the ancestral stock of the reclined tetragraptids (Maletz and Mitchell 1996). The isograptid proximal development (symplesiomorphic character b) is shared with all dichograptids and anisograptids (Maletz 1992c).

The genus *Isograptus* was interpreted by the Maletz and Mitchell (1996) to lead independently to biserial rhabdosome shapes at least three times, showing a high level of parallelism in the Glossograptidae. One lineage can be followed through *Pseudisograptus* and *Exigraptus* to the true Diplograptina (characters 2–4). The *Isograptus victoriae* lineage clearly developed into *Cardiograptus* without change in the proximal development. The development of the biserial, dipleural rhabdosome was the only change (character 4) necessary. Clearly a parallel evolution is evident in developing a biserial, dipleural rhabdosome.

Maletz and Mitchell (1996) interpreted *Isograptus caduceus* as an intermediate form leading through *Skiagraptus* and *Bergstroemograptus* to the monopleural glossograptids. The data, however, for this third lineage were scanty and details difficult to explain. The proximal development of the *Isograptus caduceus* group (now *Parisograptus*) was unknown and there was a considerable structural gap in the interpretation of the evolution between the supposedly simple isograptid development of *Parisograptus* and the incipient biserial, monopleural development in *Bergstroemograptus*. The development in *Parisograptus* now gives better evidence about the changes involved and supports this earlier interpretation. *Parisograptus* clearly displays an incipient biserial rhabdosome, a structural character not visible, however, in flattened specimens. This new synapomorphy, the initially biserial, dipleural rhabdosome (character 5) defines *Parisograptus*, but is not retained in its descendants. The covering of the crossing canals on the reverse side of the colony (character 6), however, is the defining synapomorphic character for the whole lineage. This character is not found in the *Isograptus victoriae* lineage, but is shared with *Bergstroemograptus crawfordi* (Whittington and Rickards 1969: *Skiagraptus* sp., Finney and Chen 1984) and all monopleural glossograptids. In *Bergstroemograptus* it is associated already with a true biserial rhabdosome (character 4) showing a partially monopleural arrangement of the stipes (character 7). Little information is available as to how the transition was actually created. The genus *Bergstroemograptus* is known only from the lower Llanvirn (higher part of *Holmograptus lentus* Biozone and *Nicholsonograptus fasciculatus* Biozone: Darriwilian 2, 3; VandenBerg and Cooper 1992). This interval is considerably above the first occurrence of true monopleural species (character 8) of the genera *Glossograptus* and *Cryptograptus* in the upper Arenig *Undulograptus austrodentatus* Biozone. Thus, it might not be a true intermediate, but represent a sideline of this evolution. However, the genus is the only one showing an intermediate structure to that of the completely monopleural
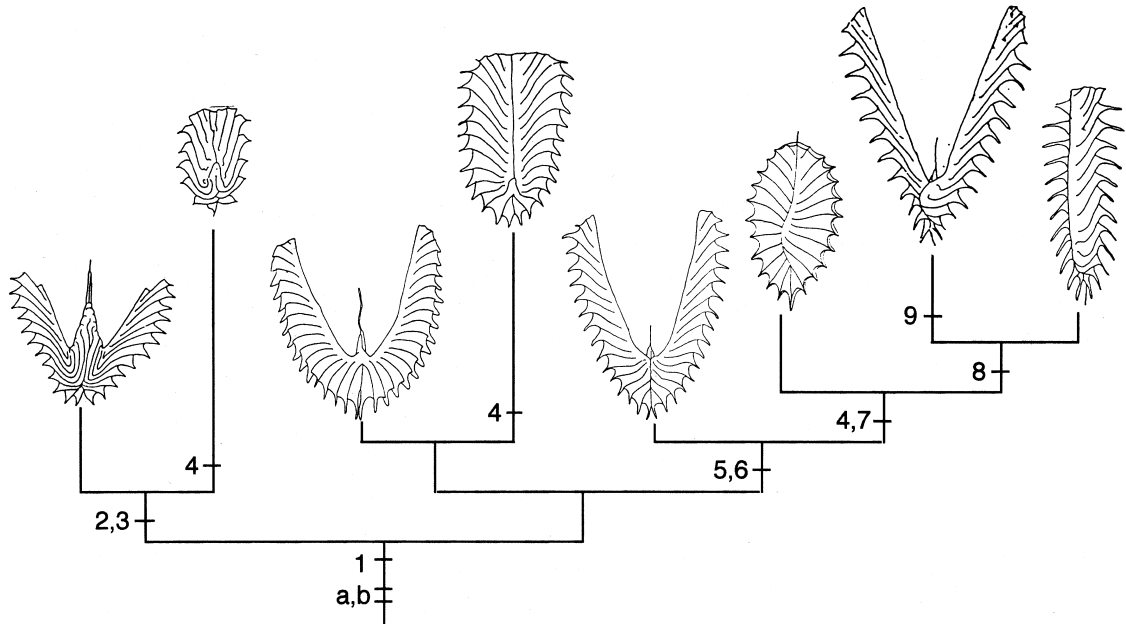
TEXT-FIG. 3. Cladistic interpretation of the Glossograptidae (based on Maletz and Mitchell 1996), indicating the position of *Parisograptus*. Symplesiomorphic characters are: a, reclined rhabdosome; b, two-stiped rhabdosome. Synapomorphic characters are: 1, isograptid symmetry; 2, left-handed origin of th1$^2$; 3, manubrium; 4, biserial, dipleural rhabdosome; 5, initially biserial, dipleural rhabdosome; 6, crossing canals covered; 7, initially monopleural rhabdosome; 8, fully monopleural rhabdosome; 9, secondarily two-stiped rhabdosome. Figured specimens from left to right: *Pseudisograptus manubriatus janus*, *Exigraptus uniformis*, *Isograptus victoriae maximodivergens*, *Cardiograptus uniformis*, *Parisograptus caduceus*, *Bergstroemograptus crawfordi*, *Kalpinograptus* sp., *Glossograptus holmi*. The reconstruction of all species is based on individual specimens preserved in reverse view. Magnification varies slightly from specimen to specimen.

glossograptids as other species from the biostratigraphic interval under consideration are not known in detail.

It is interesting to note that a similar crowding of proximal thecae in the reclined two-stiped genera *Arienigraptus* and *Parisograptus*, as well as in *Kalpinograptus* (Quiao 1977; Maletz and Mitchell 1996, text-fig. 2, figs 1–2) is developed probably independently more than once in the reclined two-stiped Glossograptidae. As *Kalpinograptus* is a secondarily reclined, two-stiped genus, here the thecal crowding is not developed independently, but retained from the monopleural glossograptid ancestor (Maletz and Mitchell 1996). One of the reasons for this development of thecal crowding may be a need for strengthening of the weakest part of the rhabdosome, but details remain unexplained. A comparison of structural details in the Glossograptidae indicates a lot of homoplasy and parallelism in the evolution of this group. The two-stiped, reclined rhabdosome in *Kalpinograptus* has to be interpreted as a convergence and reflects the origin of the monopleural glossograptids from an isograptid ancestor.

## SYSTEMATIC PALAEONTOLOGY

*Repositories.* The material investigated is housed in the type collection at the Nanjing Institute of Geology and Palaeontology (NIGP); the Geological Survey of Canada, Ottawa (GSC); the Palaeontological Museum, Oslo, Norway (PMO); and the Yale Peabody Museum, New Haven, Connecticut, USA (YPM).

Order GRAPTOLOIDEA Lapworth, 1875
Suborder DIDYMOGRAPTINA Lapworth, 1880
Family GLOSSOGRAPTIDAE Lapworth, 1873 (emend. Maletz and Mitchell, 1996)

Genus PARISOGRAPTUS Chen and Zhang, 1996

*Type species. Isograptus curvithecatus* Hsü, 1959 (syn. of *Isograptus forcipiformis* Ruedemann, 1904).

*Included species. Isograptus caduceus* Salter, 1853; *Isograptus caduceus australis* Cooper, 1973; *Isograptus caduceus* var. *horrida* Harris, 1933; *Isograptus caduceus* var. *imitata* Harris, 1933; *Isograptus caduceus latus* Ruedemann, 1904 [= *Parisograptus caduceus* (Salter)]; *Isograptus chinghaiensis* Hsü, 1959 [?= *Parisograptus forcipiformis* (Ruedemann)]; *Isograptus curvithecatus* Hsü, 1959 [= *Parisograptus forcipiformis* (Ruedemann)]; *Isograptus elegans* Tzai, 1968 [= *Parisograptus horridus* (Harris)]; *Isograptus forcipiformis* Ruedemann, 1904; *Isograptus pertensus* Harris, 1933 [= *Parisograptus horridus* (Harris)]; *Isograptus subtilis* Williams and Stevens, 1988.

*Diagnosis.* Reclined two-stiped glossograptid with initially biserial, dipleural rhabdosome in which the proximal thecal pairs originate upon each other in a vertical succession. Crossing canals of th1$^1$ and th1$^2$ are covered by later thecae.

*Remarks.* The details of the proximal development are not known for most species included here in *Parisograptus*. A good indication for inclusion in this genus is the relatively short supradorsal part of the sicula and of th1$^1$ in most species, and the slender stipes that do not widen distally. The species were formerly included in the *Isograptus caduceus* group by Cooper (1973). The development has not been described in any of these species.

Three-dimensionally preserved material of *Parisograptus forcipiformis* (Ruedemann) was first figured by Keller (1956, pl. 1, fig. 7) as *Isograptus* sp. The specimen is preserved in obverse view. It shows the parallel growth and symmetry of the sicula and th1$^1$, as well as the hidden origins of the next few thecal pairs and their oblique downward growth paths. All details are comparable with the development seen in *Parisograptus caduceus*.

*Parisograptus imitatus* (Harris, 1933) might not show the development clearly as can be inferred from relief specimens from Spitsbergen (Cooper and Fortey 1982, fig. 54). The median furrow of one specimen could indicate the dorsal sides of the stipes, but the details are uncertain. The species also bears a relatively high supradorsal part of the sicula and th1$^1$. Therefore, this species is interpreted here as an intermediate to the *Isograptus victoriae* group. Cooper (1973), however, described and figured flattened material of *Parisograptus imitatus* (Harris), including the type material, that might more clearly indicate parisograptid development through the shape of the interthecal septa in the proximal ends.

The description of *Isograptus pertensus* Harris (1933) was based on a strongly tectonized specimen of *Parisograptus horridus* (Harris), a common but rarely described species from the upper Castlemainian to lower Darriwilian. Maletz (1992*a*, fig. 4c) illustrated the type specimen of *Parisograptus horridus*. The species was also found to be common in the *Undulograptus austrodentatus* Zone fauna of the Bogo Shale, Norway (Schmidt-Gündel 1994), where it is associated with well-preserved specimens of *Parisograptus caduceus* (Text-fig. 1F). It is present in the Cow Head Group of western Newfoundland (Williams and Stevens 1988, text-fig. 63s: *Isograptus caduceus australis*).

The proximal development of *Parisograptus caduceus* has not been described so far from relief specimens, but a well-preserved flattened specimen from the Bogo Shale of Norway was figured by Maletz (1992*a*, fig. 4a). The specimen clearly shows the interthecal septa and, thus, gives an idea of parts of the development. The origins of thecal pairs 3–5 appear to be hidden behind the sicula and th1$^1$. The supradorsal parts of the sicula and th1$^1$ are fairly short relative to the total sicula length.

*Parisograptus caduceus* (Salter, 1853)

Plate 1, figures 1–7; Text-figures 1A–H, 2A–C

1853    *Didymograptus caduceus* Salter, p. 87, fig. 1.
1947    *Isograptus forcipiformis* var. *latus* Ruedemann, p. 353, pl. 57, figs 41–42.

*non* 1959   *Isograptus curvithecatus* Hsü, p. 168, text-fig. 2, pl. 2, figs 12–13 [= *Parisograptus forcipiformis*].

     1960   *Isograptus forcipiformis latus* Ruedemann; Berry, p. 67, pl. 212, fig. 1.

     1970   *Isograptus forcipiformis latus* Ruedemann; Cooper, p. 980, text-fig. 1.

*pars* 1971   *Isograptus caduceus* (Salter); Cooper, pp. 902–909, text-fig. 2a [*non* text-fig. 2b–h = *Arienigraptus angulatus*].

     1992   *Isograptus caduceus caduceus* (Salter); Maletz, p. 60, fig. 4a–b.

     1996   *Parisograptus curvithecatus* (Hsü); Chen and Zhang, p. 88, pl. 11.1, figs 3, 5–6, 8–9; pl. 11.2, figs 2–4; fig. 11.2A; fig. 11.3A, D–E.

     1996   '*Isograptus*' *caduceus australis* Cooper; Chen and Zhang, p. 86, pl. 11.1, figs 1–2, 4, 7; pl. 11.2, fig 1; fig. 11.3B–C.

     1997*a*   *Isograptus caduceus* (Salter); Maletz, p. 745, fig. 7m.

     2001   *Parisograptus curvithecatus* (Hsü); Chen, Zhang and Mitchell, fig. 7A.

     2001   '*Isograptus*' *caduceus australis* Cooper; Chen, Zhang and Mitchell, fig. 7F.

     2001   '*Isograptus*' *caduceus latus* Ruedemann; Chen, Zhang and Mitchell, fig. 8H.

*Type material*. GSC 26571a,b is the neotype as defined and described by Cooper (1971). The topotypes figured by Cooper (1971, text-fig. 2b–f) belong to *Arienigraptus angulatus* (Mu, Geh and Yin, *in* Mu *et al.* 1962), a species commonly associated with *Parisograptus caduceus* at Lévis.

*Type locality*. Salter (1853) indicated the type locality to be the Lauzon precipice. This is most probably in the Côte Fréchette area, as only there is *Parisograptus caduceus* found to be common in certain layers, in the 'western section' of Maletz (1997). The neotype material collected by F. F. Osborne and described by Cooper (1971) also came from this section. The material is, therefore, from the 'Upper *Shumardia* Limestone', biostratigraphically placed in the *Undulograptus dentatus* – *Holmograptus lentus* biozones (Maletz 1997).

*Description*. Isograptid with strongly reclined to distally parallel-sided stipes; often V-shaped rhabdosome. The length of the sicula is *c.* 2·7–3·0 mm without the rutellum. The length of the nema is highly variable and can be longer than the stipes. A slender, but deep, indentation is visible between sicula and th $1^1$. The supradorsal length of the sicula measures 0·3–0·6 mm. The stipes are 1·4–1·8 mm wide, measured without the rutelli, and 1·9–2·2 mm with the rutelli when mature. The measurements were constantly taken at th6 for comparison. The stipes can be more than 20 mm long in mature specimens, but most specimens are smaller, with a stipe length of 12–15 mm. The 2TRD values vary considerably between specimens. The ranges are *c.* 1·4–1·9 mm at th2, *c.* 1·7–2·0 at th5 and 2·0–2·3 at th10. The values tend to be lower in specimens with a more rounded rhabdosome shape.

*Remarks*. Originally the specimens of *Parisograptus caduceus* described here were identified as *Parisograptus curvithecatus* (Hsü, 1959). Hsü (1959) described *Parisograptus curvithecatus* from a *c.* 100-m-thick black shale interval at Tsaidam, Chinghai Province, China (now spelt Chiadam, Qinghai Province). The faunal list includes 18 species, few of which are useful to infer a more precise age. Unfortunately the shale was not sampled bed by bed and faunal associations were not recorded. The most time-indicative species is *Holmograptus spinosus* (Ruedemann) (recorded as *Didymograptus nodosus* Harris), a species restricted to the upper part of the *Holmograptus lentus* Biozone of early Llanvirn age (Maletz 2001). The holotype and only specimen of *Isograptus curvithecatus* as well as its faunal association indicate the identity of the material with *Parisograptus forcipiformis*, even though the specimen is poorly preserved. Also, the second isograptid species, *Isograptus chinghaiensis* Hsü,

---

EXPLANATION OF PLATE 1

Figs 1–7. *Parisograptus caduceus* (Salter, 1853). 1, NIGP 126522, obverse view of a mature specimen with parallel sided stipes; ×4·5. 2–3, NIGP 126524. 2, reverse view, enlargement of 3 with different light direction; ×20. 3, reverse view, showing the superimposed origins of proximal thecae; ×15. 4, 6, NIGP 126523. 4, reverse view, somewhat distorted large specimen with open rhabdosome; ×10. 6, enlargement of specimen; ×18. 5, NIGP 126527a, well preserved obverse view showing isograptid symmetry of sicula and th$1^1$; ×10. 7, NIGP 126529, obverse view, thecal apertures partially lacking; ×18.

PLATE 1



MALETZ and ZHANG, *Parisograptus*
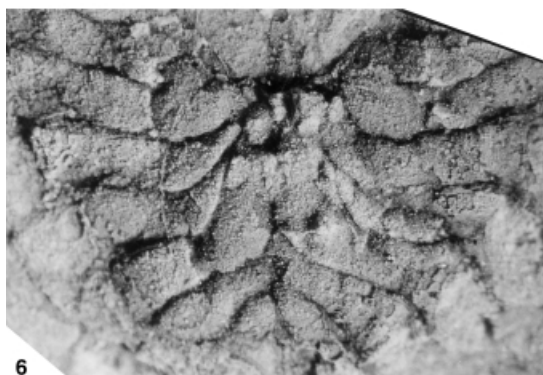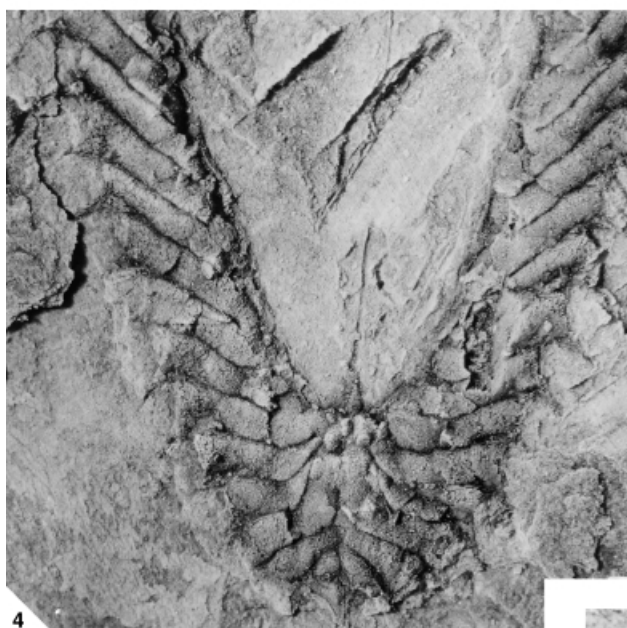
might belong to *Parisograptus forcipiformis* instead. Both species bear longer downward-growing proximal thecae and, thus, the proximal end has a deeper appearance than *Parisograptus caduceus*.

The sections collected by Hsü (1959) are now known to be the Shihuigou and Oulongbuluke sections. Graptolites from the sections were described by Mu *et al*. (1962) and more recently by Chen *et al*. (2001). None of the publications, however, includes specimens of *Parisograptus forcipiformis*. Chen *et al*. (2001) described only the *Undulograptus austrodentatus* Biozone fauna, which is represented in the lower part of the succession. The faunas of the higher parts of the succession have not been redescribed so far.

The material described by Chen and Zhang (1996) as *Parisograptus curvithecatus* (Hsü) differs considerably from Hsü's (1959) material and is referred to *Isograptus caduceus* here. The specimens are identical in dimensions and shape to that of the Québec type material. Differences can only be seen in the more open U-shaped rhabdosome of some of the specimens, a shape not found in this species in the Québec material. A single specimen in the Chinese collection matches the typical shape of the Québec material (Pl. 1, fig. 1). The possibility exists that both forms are separate species, but this needs to be supported by statistical investigation and additional material.

*Biostratigraphical range and distribution*. The three-dimensionally preserved material from the Hengtang section, Jianshan, Zhejiang, China originates from the *Undulograptus sinicus* Sub-biozone of the *Undulograptus austro-dentatus* Biozone. In Québec the species is present in the *Undulograptus austrodentatus* – *Holmograptus lentus* biozones (Maletz 1997, fig. 5). The species is associated with *Sinograptus rastritoides* Mu in Arctic Canada (GSC 49469 of Lenz 1977). In the uppermost part of the *Holmograptus lentus* Zone it is replaced by *Parisograptus forcipiformis*. This species is associated with *Holmograptus spinosus* and *Bergstroemograptus crawfordi* in Québec and western Newfoundland, as well as in Australasia (Maletz 2001). Both species range into the *Nicholsonograptus fasciculatus* Zone in the Table Head Group of western Newfoundland (Maletz 1998). *Parisograptus forcipiformis* is the youngest isograptid known (Maletz 1992*b*). The oldest *Parisograptus caduceus* specimens might come from the Yapeenian, but data are scarce and need to be reconfirmed. The species is preceded by a number of *Parisograptus* species in the late Castlemainian [Cooper 1973: *Parisograptus caduceus imitatus* (Harris), *Parisograptus caduceus australis* (Cooper)].

REFERENCES

BERRY, W. B. N. 1960. Graptolite faunas of the Marathon Basin, west Texas. *University of Texas Publication*, **605**, 179 pp.

BULMAN, O. M. B. 1932. On the graptolites prepared by Holm 2–5. *Arkiv för Zoologi*, **24A** (9), 1–29.

CHEN XU and ZHANG YUANDONG 1996. Isograptids of China. 82–89. *In* WANG HONGZHEN and WANG XUNLIAN (eds). *Centennial memorial volume of Prof. Sun Yunzhu (Y. C. Sun): palaeontology and stratigraphy*. China University of Geosciences Press, Beijing.

—— —— and MITCHELL, C. E. 2001. Early Darriwilian graptolites from central and western China. *Alcheringa*, **25**, 191–210.

COOPER, R. A. 1970. Tectonic distortion of a syntype of *Isograptus forcipiformis latus* Ruedemann. *Journal of Paleontology*, **44**, 980–983.

—— 1971. The identity of *Isograptus caduceus* (Salter) *sensu stricto*. *Journal of Paleontology*, **45**, 902–909.

—— 1973. Taxonomy and evolution of *Isograptus* Moberg in Australasia. *Palaeontology*, **16**, 45–115.

—— and FORTEY, R. A. 1982. The Ordovician graptolites of Spitsbergen. *Bulletin of the British Museum* (*Natural History*)*, Geology*, **36**, 157–302, 6 pls.

FINNEY, S. C. and CHEN, X. 1984. *Bergstroemograptus* n. gen. *crawfordi* (Harris) from the Ordovician of western Newfoundland. *Canadian Journal of Earth Sciences*, **21**, 1194–1199.

FORTEY, R. A. and COOPER, R. A. 1986. A phylogenetic classification of the graptoloids. *Palaeontology*, **29**, 631–654.

HARRIS, W. J. 1933. *Isograptus caduceus* and its allies in Victoria. *Proceedings of the Royal Society of Victoria, New Series*, **46**, 79–114.

HSÜ, S. C. 1959. A new graptolite fauna from the Lower Ordovician shale of Tsaidam, Chinghai province. *Acta Palaeontologica Sinica*, **7**, 161–192.

JENKINS, C. J. 1982. *Isograptus gibberulus* (Nicholson) and the isograptids of the Arenig Series (Ordovician) of England and Wales. *Proceedings of the Yorkshire Geological Society*, **44**, 219–248.

KELLER, B. M. 1956. Ordovician graptolites of the Chu-Iliyskiye Mountains. *Transactions of the Geological Institute*, Moscow, **1**, 50–102, 4 pls. [In Russian: translated version, 1962, *International Geological Review*, **4** (12), 1366–1404, 4 pls].

LAPWORTH, C. 1873. On an improved classification of the Rhabdophora. *Geological Magazine*, **10**, 500–504, 555–560.

—— 1875. *In* HOPKINSON, J. and LAPWORTH, C. 1875. Descriptions of the graptolites of the Arenig and Llandeilo rocks of St. David's. *Quarterly Journal of the Geological Society of London*, **31**, 631–672, pls 33–37.

—— 1880. On new British graptolites. *Annals and Magazine of Natural History*, Series 5, **5**, 149–177.

LENZ, A. C. 1977. Some Pacific Province graptolites from the Ordovician of northern Yukon, Canada. *Canadian Journal of Earth Sciences*, **14**, 1946–1952.

MALETZ, J. 1992a. The Arenig/Llanvirn boundary in the Quebec Appalachians. *Newsletters on Stratigraphy*, **26**, 49–64.

—— 1992b. Biostratigraphie und Paläogeographie von Unterordovizischen Graptolithenfaunen des östlichen Kanadas und Skandinaviens. Dissertation, Technische Universität Berlin, 246 pp., 113 figs, 10 pls.

—— 1992c. The proximal development in Anisograptids (Graptoloidea, Anisograptidae). *Paläontologische Zeitschrift*, **66**, 297–309.

—— 1997. Arenig biostratigraphy of the Pointe-de-Lévy slice, Québec Appalachians, Canada. *Canadian Journal of Earth Sciences*, **34**, 733–752.

—— 1998. Das Ordovizium von Rügen und seine paläogeographische Stellung aufgrund der Graptolithenfaunen. Habilitationsschrift, Ernst-Moritz-Arndt Universität Greifswald, 185 pp., 53 figs.

—— 2001. A condensed Lower to Middle Ordovician graptolite succession at Matane (Québec, Canada). *Canadian Journal of Earth Sciences*, **38**, 1531–1539.

—— and MITCHELL, C. E. 1996. Evolution and phylogenetic classification of the Glossograptidae and Arienigraptidae (Graptoloidea): new data and remaining questions. *Journal of Paleontology*, **70**, 641–655.

MELCHIN, M. J. 1998. Morphology and phylogeny of some early Silurian 'diplograptid' genera from Cornwallis Island, Arctic Canada. *Palaeontology*, **41**, 263–315.

MITCHELL, C. E. 1987. Evolution and phylogenetic classification of the Diplograptacea. *Palaeontology*, **30**, 353–405.

MOBERG, J. C. 1892. Om nagra nya graptoliter fran Skanes Undre graptolitskiffer. *Geologiska Föreningen i Stockholm Förhandlingar*, **14**, 339–350.

MU, A. T., LEE, C. H., GEH, M. Y. and YIN, J. X. (MU, E. Z., LI, J. J., GE, M. Y. and YIN, J. X.) 1962. *Graptolites from Chilianshan*. Geology of Chilianshan, Volume 4 (Palaeontology), no. 2. Science Press, Beijing, 127 pp.

QUIAO, X. D. 1977. *Kalpinograptus*, a new graptolite from the Saergan Formation in Kalpin of Xinjiang. *Acta Palaeontologica Sinica*, **16**, 287–293.

RUEDEMANN, R. 1904. Graptolites of New York, Part 1. *New York State Museum, Memoir*, **7**, 1–807.

—— 1947. Graptolites of North America. *Geological Society of America, Memoir*, **19**, 1–652.

SALTER, J. W. 1853. *In* BIGSBY, J. J. 1853. On the geology of Quebec and its environs. *Quarterly Journal of the Geological Society of London*, **9**, 87.

SCHMIDT-GÜNDEL, O. 1994. Die unterordovizischen Graptolithenfaunen des Bogo- und Lo-Schiefers (Sør-Trøndelag, West-Norwegen). Dissertation, Technische Universität Berlin, 286 pp.

TZAI, D. T. 1968. New species of early Ordovician graptolites from central Kazakhstan. *Paleontological Journal*, **4**, 493–497.

VANDENBERG, A. H. M. and COOPER, R. A. 1992. The Ordovician graptolite sequence of Australasia. *Alcheringa*, **16**, 33–85.

WILLIAMS, S. H. and STEVENS, R. K. 1988. Early Ordovician (Arenig) graptolites of the Cow Head Group, western Newfoundland, Canada. *Palaeontographica Canadiana*, **5**, 167 pp., 34 pls.

JÖRG MALETZ

Department of Geology
State University of New York at Buffalo
772 Natural Sciences and Mathematics Complex
Buffalo, New York 14260–3050, USA
e-mail jorgm@acsu.buffalo.edu

ZHANG YUANDONG

Nanjing Institute of Geology and Palaeontology
East Beijing Road 39
Nanjing 210008, China
e-mail ydzhang@jlonline.com