Llandovery sporomorphs and graptolites from the Manbo Formation, the Mojiang County, Yunnan, China

Yi Wang* and Yuandong Zhang

LPS, Nanjing Institute of Geology and Palaeontology, CAS, Nanjing 210008, People's Republic of China

Llandovery sporomorphs and graptolites have been recovered from the Manbo Formation, Mojiang area, western Yunnan, China, which belonged to the Indo-China Palaeoplate in the Palaeozoic. The graptolite fauna, including 8 genera and 12 species, is considered Mid Telychian, Llandovery in geological age, confirming the existence of Llandovery rocks in this region. The Silurian stratigraphical sequence of this area is reconsidered as in the ascending order: Manbo Formation (Llandovery–early Wenlock), Shuiqing Formation (late Wenlock–Ludlow) and unnamed formation (Pridoli?). The sporomorph assemblage from the Manbo Formation includes seven species in five genera. The dominant members of this assemblage are *Tetrahedraletes medinensis* and *Laevolancis chibrikovae*. Based on the low diversity and low abundance, the geological age of this assemblage is considered to be approximately the Telychian, Llandovery. The parent plants of sporomorphs probably inhabited the landmass near Mojiang area, these sporomorph-producing plants probably included bryophyte-like land plants and primitive vascular land plants. The sporomorph evidence shows that the South China and Indo-China palaeoplates may have been in close proximity (maybe with some continental bridges linking them) to each other at least in the Llandovery. They were also closely related with Gondwanaland in the Llandovery.

Keywords: sporomorphs; graptolites; Manbo Formation; Llandovery; Indo-China, China

1. INTRODUCTION

The Silurian rocks of Mojiang, Yunnan have been studied since the 1960s. The [Regional Geological Survey of Yunnan \(1965\)](#) established the Mojiang Group as encompassing the whole of the Silurian. The next [Regional Geological Survey of Yunnan \(1973\)](#) reported graptolites from this group, and divided this group into three parts that were considered as the Lower, Middle and Upper Silurian. [Zhang *et al.* \(1996\)](#) named the strata of the Lower Silurian as the Shuiqing Formation and the Middle Silurian as the Manbo Formation. Zhang (see Zhang & Lenz 1997, 1999) restudied the Shuiqingliangzi section in the Mojiang area, where Llandovery graptolites were previously reported. The collected abundant and diverse graptolites turned out to be Homerian–Ludlow age, based on which they redefined the Silurian sequences in the Mojiang area as including the Manbo and Shuiqing formations (Wenlock–Ludlow) in ascending order. They also presumed that the Llandovery might be absent in this area, whereas the Pridoli was probably present. The [Regional Geological Survey of Yunnan \(1973\)](#) reported Llandovery graptolites from shales of the Mojiang Group, including *Monograptus priodon*, *Monograptus cf. sedgwickii*, *Pristiograptus hisingeri*. However, no Llandovery graptolites were confirmed in the studied section during ZYD's fieldwork in 1996 (see Zhang & Lenz 1999). As a result, the existence of Llandovery strata actually requires further fossil evidence.

Furthermore, the Mojiang area belongs to the Indo-China Palaeoplate ([figure 1](#)). More palaeontological evidences are necessary to study the geological evolution of this palaeoplate.

2. LOCALITY, MATERIALS AND GEOLOGICAL SETTING

The fossils were collected from a short section along the meandering footpath from Keman village to Dazhong village. This locality is situated approximately 20 km north of Jiulian town, Mojiang County, Yunnan Province ([figure 2](#)). The GPS locality is 23°31.997' N and 101°40.464' E.

The studied materials include the sporomorphs and graptolites ([figure 3](#)). Fourteen microfossil samples were collected from the black shales, sandy mudstones or muddy siltstones of the Manbo Formation. One productive microfossil sample is from the black shale, associated with the abundant graptolites. The graptolites were recovered from two beds of black shale and sandy mudstones. Based on the lithological characteristics, the sampled rocks belong to the lower part of the Manbo Formation ([figure 3](#)).

The type section of the Manbo Formation is located 12 km south of Mojiang, and comprise greyish green shales, muddy siltstones and interbedded limestones that are over 1500 m thick. Some graptolites had previously been reported from the shales, including *Monoclimacis cf. vomerina gracilis*, *Monograptus flemingii primus*, *Monograptus sp.*, *Pristiograptus sp.* ([Regional Geological Survey of Yunnan 1973; Zhang & Lenz 1999](#)). Among the reported species, *M. f. primus* occurs commonly in

* Author for correspondence (ywangngs@hotmail.com).

One contribution to a Special Issue 'Recent advances in Chinese palaeontology'.

Figure 1. The palaeoplates within southwest China in the Silurian (from the Chen & Rong 1993; Rong & Chen 2003). (Thin-dashed lines, international boundary; thin line, coast-line; thick- and thick dashed lines, boundary of palaeoplates or blocks; star, studied area.)

Figure 2. The locality of the studied area, Mojiang, Yunnan, China. (Dashed lines, international boundary; dotted lines, regional boundary; thick lines, motorway; thin lines, rural road; filled circles, village/town/city; square, studied area/locality.)

the early Wenlock strata in the British Isles (Rickards 1976), and therefore the Manbo Formation was partly regarded as of early Wenlock age. Based on the regional geological map, the rocks of our locality were always considered as Triassic (without any fossil evidence). Zhang & Lenz (1999) reported a few poorly preserved graptolites, identified as *Monograptus* sp., near our locality from isolated outcrops underlying Early Devonian strata, and considered the rocks as possibly of Late Silurian age. However, they also noted the need for further fossil evidence to establish the exact geological age. Based on our new collections (2007, 2008), abundant and well-preserved graptolites from a nearby outcrop indicate a Llandovery age (see below). Thus, the Silurian system of Mojiang area includes the Manbo Formation (Llandovery and early Wenlock), Shuiqing Formation (late Wenlock and Ludlow) and unnamed formation (Pridoli?).

Figure 3. Stratigraphical section of the Manbo Formation, Keman village, Mojiang, Yunnan, China. Location of sporomorph samples and graptolites.

3. GRAPTOLITE FAUNA AND AGE

There are two samples in the Keman section of Mojiang yielding graptolites: MJ101 and MJ102. The graptolites were preserved extensively only on several specific and thin bedding planes. The rock was originally black shale or siliceous shale, and secondarily weathered into a purple-red or pale purple colour as now seen. Most of the graptolites are fairly well preserved with complete specimens and clear morphologies, and not significantly distorted despite the severe tectonic activity that has occurred in the region. Some of the specimens are preserved in pyrite and are three-dimensional, while the rest are flattened. In those pyritic specimens, pyrite of strawberry-form with diameters of *ca* 50–80 μ m are observed densely assembled within the rhabdosomes (figure 4).

Samples MJ101 and MJ102 contain a fairly rich but less diverse fauna of graptolites, which includes abundant *Torquigraptus* cf. *pragensis* (Pribyl), *Torquigraptus* cf. *proteus* (Barrande), *Retiolites geinitzianus* (Hall), in association with *Monoclimacis crenulata* (*sensu* Elles and Wood), *Monoclimacis* sp., *Monograptus marri* (Perner), *Oktavites* cf. *spiralis* (Geinitz), *Paradiversograptus capillaris* (Carruthers), *Pseudoplegmograptus* sp. and *Pristiograptus* sp. The fauna indicates an age of Mid Telychian (Late Llandovery).

Among the common and stratigraphically significant species, *T.* cf. *pragensis* resembles *T. pragensis* (Pribyl), which was originally named in the Prague Basin (Pribyl 1943) and recently found also in the Hlinsko Zone of the northeastern Bohemian Massif (Storch & Kraft 2008), Wales (Zalasiewicz 1994) and Latvia (Loydell *et al.* 2006,

Figure 4. Telychian graptolites from the Keman section, Mojiang, Yunnan. (a,f) *Monoclimacis crenulata* (*sensu* Elles and Wood), (a) middle and distal parts, MJ101-68. (f) juvenile form with sicula, MJ101-68. (b,g) *Paradiversograptus capillaris* (Carruthers), (b) distal part showing the slender stipe and thecal morphology, MJ101-66a. (g) proximal part with sicular cladium, MJ101-81a. (c,d) *Torquigraptus* cf. *pragensis* (Pribyl), mature form and growth stage with proximal end, respectively, MJ101-9b, MJ101-56b. *Retiolites geinitzianus* (Hall), mature specimens from samples (e) MJ101-33, (j) MJ101-9a and (k) MJ101-57, respectively. *Monograptus marri* (Perner), proximal and distal parts, respectively, (h) MJ101-12, (i) MJ101-93. The scale bar is 1 mm for all figures.

sensu lato). *Torquigraptus pragensis* (Pribyl) indicates an age of *Monoclimacis griestoniensis* Biozone (Mid Telychian) in the Prague Basin. The present specimens identified as *T. cf. proteus* resembles *T. proteus* in many respects, but with developed thecal apertural spines. *Torquigraptus proteus* ranges commonly from the *Spirograptus turriculatus* Biozone to the *Monograptus crispus* Biozone, and also possibly the *M. griestoniensis* Biozone as occurs in Bohemia (Pribyl 1944; Storch & Kraft 2008) and Sardinia, Italy (Storch 1993), although it was also reported in Aeronian rocks of Britain (Elles & Wood 1913). *Retiolites geinitzianus* is fairly abundant in the present collection, and this species ranges from the *M. griestoniensis* Biozone to the earliest Wenlock (Rickards *et al.* 1977). *Pseudoplegmograptus* is also a common species in Telychian rocks.

Among the less abundant species in the present collection, *M. crenulata* is the index fossil for the eponymous biozone in Britain and a common species in the *Oktavites spiralis*–*Stomatograptus grandis* Biozone of China (Rickards & Chen 2002) or the *Monograptus tullbergi* Biozone of Ziyang, South China (Fu *et al.* 2006), and the upper *M. griestoniensis* Biozone to *M. tullbergi* Biozone in Bohemia (Storch 1994). The total stratigraphical range of *M. marri* is not yet precisely known. It occurs commonly in late Telychian rocks and extends up to the *Monoclimacis griestoniensis* Biozone (Loydell 1993). The species *P. capillaris* is poorly known, with occurrences both in the latest Aeronian (*Stimulograptus halli* Biozone) in Wales (Loydell 1993) and in the Mid-Late Telychian in Bohemia (distinguished as

Figure 5. LM images of the sporomorphs from the Manbo Formation, Mojiang, Yunnan, China. (a–c) *Tetrahedraletes medinensis* (Strother & Traverse 1979) emended (Wellman & Richardson 1993). (d,e) *Velatitetras* (*Nodospora*) *rugosa* (Strother & Traverse 1979; Steemans *et al.* 1996). (f) *Laevolancis chibrikovae* (Steemans *et al.* 2000). (g,h) *Laevolancis divellomedium* (Chibrikova 1959) Burgess & Richardson 1991. (i,j) *Imperfectotriletes patinatus* (Steemans *et al.* 2000). (k,l) *Imperfectotriletes vavrdovae* (Richardson 1988; Steemans *et al.* 2000). (m–o) *Morphon Ambitisporites avitus–dilatatus* sensu (Steemans *et al.* 1996). The scale bar is 10 µm for all figures.

Paradiversograptus capillaris pergracilis, Boucek & Přibyl 1953) and South China (Fu *et al.* 2006).

4. SPOROMORPH ASSEMBLAGE

(a) *Systematics*

Sample is the black shales. Sporomorphs were twice extracted from 25 g of rock using HCl–HF–HCl acid maceration techniques. The organic residue was sieved through a 10-µm mesh, without any oxidation. The sieved organic residues were mounted on glass cover-slips and attached to glass slides using the plastic mounting medium ‘Elvacite’. Slides were studied in normal transmitted light using a Zeiss photomicroscope III. All slides and specimens are stored in the Nanjing Institute of Geology and Palaeontology, CAS.

(i) *Cryptospores*

Genus *Tetrahedraletes* (Strother & Traverse 1979) emended (Wellman & Richardson 1993)

Type species: *Tetrahedraletes medinensis* (Strother & Traverse 1979)

Tetrahedraletes medinensis (Strother and Traverse) emended (Wellman & Richardson 1993; figure 5a–c)

Dimensions: 35(42)53 µm (22 specimens measured)

Genus *Velatitetras* (Burgess 1991)

Type species: *Velatitetras laevigata* (Burgess 1991)

Velatitetras (*Nodospora*) *rugosa* (Strother & Traverse 1979; Steemans *et al.* 1996; figure 5d,e)

Dimensions: 42 (45)50 µm (5 specimens measured)

Genus *Laevolancis* (Burgess & Richardson 1991)

Type species: *Laevolancis divellomedium* (Chibrikova) Burgess & Richardson 1991

Laevolancis chibrikovae Steemans *et al.* 2000 (figure 5f)

Dimensions: 36(40)48 µm (10 specimens measured)

Laevolancis divellomedium (Chibrikova) Burgess & Richardson 1991 (figure 5g,h)

Dimensions: 33(45)51 µm (6 specimens measured)

Genus *Imperfectotriletes* (Steemans *et al.* 2000)

Type species: *Imperfectotriletes patinatus* (Steemans *et al.* 2000)

Imperfectotriletes patinatus (Steemans *et al.* 2000; figure 5i,j)

Dimension: 40–44 µm (3 specimens measured)

Imperfectotriletes vavrdovae (Richardson) Steemans *et al.* 2000 (figure 5k,l)

Dimension: 39(41)46 µm (4 specimens measured)

(ii) *Trilete spores*

Genus *Ambitisporites* (Hoffmeister 1959)

Type species: *Ambitisporites avitus* (Hoffmeister 1959)

Morphon *A. avitus–dilutus sensu* Steemans *et al.* 1996 (figure 5m–o)

Dimension: 38(41)49 µm (4 specimens measured)

(b) Composition of the assemblage

The sporomorph assemblage consists of cryptospores and trilete spores, including seven species in five genera. Counts of all specimens present on 10 slides (54 identified specimens) indicate that cryptospores comprise 92 per cent and trilete spores 8 per cent of the total sporomorph content.

Cryptospores consist of tetrads and monads. The tetrads are one of the dominant types in this assemblage, includes two genera (*Tetrahedraletes* and *Velatitetras*), and are 50 per cent of the total sporomorph content. Most specimens of *T. medinensis* are well preserved, and ca 41 per cent of the total sporomorphs. Monads make up 42 per cent of the total sporomorph content, and include two genera: *Laevolancis* and *Imperfectotriletes*. *Laevolancis* make up 30 per cent of the total sporomorphs, and includes two species: *L. chibrikovae* and *L. divellomedium*. The dominant monad is *L. chibrikovae* comprising 18 per cent of the total sporomorph content. *Imperfectotriletes* consist of two species: *I. patinatus* and *I. vavrdovae*.

Trilete spores include the only crassitate spores, with one morphon: *A. avitus–dilutus*. Only 8 per cent of the total sporomorph content consists of trilete spores that are rare in this assemblage.

This assemblage is low abundance and low diversity, and probably belongs to the *avitus–dilutus* spore assemblage zone (SAZ; Richardson & McGregor 1986; Richardson & Edwards 1989; Steemans *et al.* 2000). The dominant members include *T. medinensis* and *L. chibrikovae*. This assemblage differs from many other assemblages of this age in the absence of permanent dyads and the persistence of envelope-enclosed tetrads.

(c) Age of the assemblage

The Mojiang assemblage is largely dominated by cryptospores (tetrads and monads), but contains true trilete spores. The dominant members are *T. medinensis* and *L. chibrikovae*. During the Katin to the Llandovery, assemblages are dominated by cryptospores, and are very similar with only minor differences reported (Gray 1985; Burgess & Richardson 1991; Richardson 1996; Wellman 1996; Steemans 1999a,b; Steemans *et al.* 2000; Wellman & Gray 2000; Beck & Strother 2001; Steemans & Pereira 2002). In the Late Ordovician and Early Silurian, assemblages of early Rhuddanian are very similar to those from the Ordovician. Many cryptospore

species disappear from the Rhuddanian to Sheinwoodian, no or very few new cryptospore species appear from the Aeronian to Sheinwoodian, and trilete spore are confined to one genus: *Ambitisporites*. The sporomorphs of the Mojiang assemblage are very similar to those from the Late Ordovician to Llandovery.

In the Mojiang assemblage, sporomorphs are of low diversity and low abundance. Previous studies of sporomorphs show that two major events occurred during the Upper Ordovician to Llandovery (Steemans 2000). The first is at the Hirnantian owing to the influence of glaciation on the high biodiversity of cryptospores and low biodiversity of trilete spores. The second is within the Telychian–Sheinwoodian, Silurian, where there is a minimum value of the sporomorph biodiversity. The low biodiversity of sporomorphs is from the Aeronian to the Sheinwoodian (Steemans 2000; Beck & Strother 2001; Rubinstein & Toro 2006; Richardson & Ausich 2007). Comparison with the biodiversity curves of Steemans (2000) indicates that the biodiversity of the Mojiang assemblage is very similar to that around the Telychian, Llandovery. The sporomorph evidence favours to a Mid Telychian, Llandovery, also indicated by graptolites.

5. PALAEOBOTANICAL SIGNIFICANCE

Most cryptospores are derived from the early land plants that are considered to have been bryophyte-like based on several lines of fossil evidence, including cryptospore size, dispersal patterns, and numbers (Gray 1985; Steemans 2000; Wellman & Gray 2000; Wellman *et al.* 2003; Steemans & Wellman 2004; Richardson & Ausich 2007). The Early Palaeozoic cryptospore assemblages were cosmopolitan (Gray 1985; Wellman & Gray 2000; Steemans & Wellman 2004). In the Llandovery, some cosmopolitan cryptospores are also reported, such as *T. medinensis* and *Dyadospora murusdensa* (Steemans 2000).

The composition of the Mojiang cryptospore assemblage shows low diversity and low abundance, and is dominated by *T. medinensis* and *L. chibrikovae*. No specimens of dyads are recovered from the Mojiang Llandovery rocks. Although the samples were not derived from terrestrial deposits, the report of these cryptospores indicates that there was a substantial terrigenous input in the Llandovery into the Mojiang area. The dominant terrestrial plants probably belonged to the cryptospore producing plants. An important difference might be the absence of permanent dyads and the persistence of envelope-enclosed tetrad-producing plants in the Mojiang area. Llandovery spore assemblages are very similar worldwide, suggesting that the parent floras were cosmopolitan, although the absence of dyad producers at Mojiang suggests that there may have been some minor regional variations. Early trilete spores are believed to have been produced by early vascular plants (Steemans & Wellman 2004). The trilete mark is a very important feature, and a functional structure, allowing spore germination. Up to now, the oldest true trilete spores are reported from the late Katin, Southeastern Turkey (Steemans *et al.* 1996).

In the Mojiang assemblage, *Imperfectotriletes*, including *I. vavrdovae* and *I. patinatus*, with a pseudo-trilete mark, are not considered as true trilete spores but as cryptospores (Steemans 2000; Steemans *et al.* 2000).

Figure 6. The Llandovery sporomorph localities on the palaeogeographical map of the Silurian (minor revision from [Chen *et al.* 2001](#)). 1, Pennsylvania, USA ([Strother & Traverse 1979](#); [Johnson 1985](#)); 2, New York, USA ([Miller & Eames 1982](#)); 3, Virginia, USA ([Pratt *et al.* 1978](#)); 4, Ontario, Canada ([Eley & Legault 1988](#)); 5, Anticosti Island, Quebec, Canada ([Duffield 1985](#); [Richardson & Ausich 2007](#)); 6, Nova Scotia, Canada ([Beck & Strother 2001](#)); 7, Wales, UK ([Burgess 1991](#)); 8, Ringerike, Norway ([Smelror 1987](#)); 9, Belgium (see [Steenmans *et al.* 2000](#)); 10, northeast Libya ([Richardson 1988](#)); 11, Saudi Arabia ([Steenmans *et al.* 2000](#); [Wellman *et al.* 2000](#)); 12, Brazil (see [Steenmans *et al.* 2000](#)); 13, Paraguay ([Gray *et al.* 1992](#); [Steenmans & Pereira 2002](#)); 14, northwest Argentina ([Rubinstein & Toro 2006](#)); 15, South Africa ([Gray *et al.* 1986](#)); 16, Canning Basin, Australia ([Foster & Williams 1991](#)); 17, Guizhou, China ([Wang *et al.* 1996](#)); 18, Mojiang, China (the present study).

Imperfectotrilites does not belong to true trilete spores, and was derived from cryptospore producing plants. True trilete spores are represented by morphons *A. avitus-dilutus*. Although true trilete spores are of low abundance (only 8% of the total sporomorph content) and low diversity (one genus and species), it indicates that the landmass near Mojiang area might have contained very small numbers of vascular plants.

6. PALAEOENVIRONMENT SIGNIFICANCE

The rocks of the Manbo Formation are clearly marine based due to the presence of graptolites, and are considered to have been deposited in an open-shelf environment. There is a terrestrial component—the sporomorph assemblage including cryptospores and trilete spores. The cryptospores and trilete spores were derived from an adjacent landmass. Cryptospores could be dispersed by wind, river and sea currents. Wind can blow most of cryptospores over 25 µm over short distances (a few meters to a few kilometres; [Gray 1985](#); [Steenmans & Pereira 2002](#); [Steenmans *et al.* 2007](#)). Rivers may transport the cryptospores to lakes or the sea where they are deposited a short distance from the shoreline. Sea currents may further transport some cryptospores a larger distance from the coasts, but usually not a great distance. In the Mojiang assemblage, some specimens were distorted, and some specimens well preserved. It is possible that these sporomorphs were transported from the coast to the open-shelf, preserved with the graptolites, however, it is not a very long distance.

[Steenmans *et al.* \(2000\)](#) considered that the parent plants of the sporomorphs were cosmopolitan and survived

under varied climatic conditions during the Ordovician to Llandovery. After marking all known Llandovery localities on a palaeoclimatological map ([figure 6](#)), it is very clear that most localities are distributed in the arid zone with a few localities in warm and cool temperate zones. There are no reports in the tropical and subtropical zone, although [Wang *et al.* \(1997\)](#) reported the cryptospores of late Katian age from the palaeoequator. However, during the Llandovery, the palaeoequator probably lacked the distribution of sporomorphs. The Mojiang sporomorph assemblage belongs to the arid zone, and is located near the tropical and subtropical zone. The early land plants were of small size, and probably lived in wet habitats, nearshore or inland.

7. PALAEOGEOGRAPHICAL SIGNIFICANCE

Two localities ([figure 6](#); 17, 18) are reported with Late Llandovery sporomorphs in China, the Guizhou and Mojiang areas. However, these localities belong to differ palaeoplates. Guizhou is located on the South China Palaeoplate and Mojiang on the Indo-China Palaeoplate. The present study and [Wang *et al.* \(1996\)](#) show that the sporomorphs from the two localities are very similar to each other. Based on the sporomorph evidence, it is probable that the South China and Indo-China palaeoplates could have been in close proximity (maybe with some continental bridges linking them) at least at the Llandovery.

Before the Silurian, the South China and Indo-China palaeoplates were connected with the Gondwana Palaeoplate based on similar cool water faunas. [Metcalf \(1992\)](#) considered that the South China and Indo-China

palaeoplates broke away from Gondwana probably during the Silurian. Foster & Williams (1991) reported earliest Silurian *T. medinensis* from the Canning Basin, Australia. The same cryptospore is also found from the Mojiang locality. *T. medinensis* is known from the Mid Ordovician–Early Devonian and found everywhere, although the transport of this cryptospore was not very long distance. The sporomorph evidence shows that the Indo-China and South China palaeoplates were possibly close to Gondwana in the Llandovery.

Llandovery sporomorph assemblages are found in at least 18 localities (listed on the explanation of figure 6) where cryptospores/trilete spores were described. After marking these localities at the Palaeogeographical map of the Silurian (Chen *et al.* 2001), it is found that all localities occur in the Southern Hemisphere. Currently there are no reports from the Northern Hemisphere. The continents that are most northerly (Kazakhstan, Siberia, etc.), have not been sampled for Silurian sporomorphs, so sampling bias is possible. However, the Mojiang and Guizhou localities in China are more northerly.

Hitherto described Llandovery sporomorph assemblages are all very similar, and the parent plants of these sporomorphs were cosmopolitan. Even by sea current, these sporomorphs probably could not have been transported over long distances (Steemans & Pereira 2002). The cryptospores and trilete spores are of continental origin; the large oceans are impassable geographic barriers for dissemination of these sporomorphs. Steemans & Pereira (2002) considered that the palaeocontinents at the Ordovician–Silurian boundary were close to each other. The Palaeogeographical distribution of vertebrates also suggest similar conclusions (Bleick *et al.* 2001). Steemans & Pereira (2002) concluded that the palaeogeographical reconstructions with narrow oceans separating the continents better explain the uniformity of the plants in Upper Ordovician and Llandovery. The sporomorph evidence favours palaeogeographical models with Gondwana and Laurentia close to each other.

8. CONCLUSIONS

Llandovery sporomorphs and graptolites have been recovered from the Manbo Formation, Mojiang area, western Yunnan, China. The graptolites include eight genera and ten species, and suggest a Mid Telychian, Llandovery age. This result indicates the existence of Llandovery rocks. The Silurian stratigraphical sequence is reconsidered to represent in the ascending order: Manbo Formation (Llandovery–early Wenlock), Shuiqing Formation (Late Wenlock–Ludlow) and unnamed formation (Pridoli?).

The sporomorph assemblage from the Manbo Formation include four genera, six species of cryptospores and one genus, one species of trilete spores. This assemblage is dominated by the cryptospores, probably belongs to the *avitus–dilutus* SAZ, and differs from many other assemblages of this age in the absence of permanent dyads and the persistence of envelope-enclosed tetrads. The dominated members are *T. medinensis* and *L. chibrikovae*. Based on the low diversity and low abundance, the geological age of this assemblage is approximately the Telychian, Llandovery. The parent plants of the sporomorphs inhabited the landmass near the Mojiang area, and these

sporomorph-producing plants include the bryophyte-like land plants and land plants.

The Mojiang area belongs to the Indo-China Palaeoplate. The sporomorph evidence shows that the South China and Indo-China palaeoplates could have been in close proximity at least in the Llandovery; the Indo-China and South China palaeoplates were close to Gondwanaland in the Llandovery. Based on the Llandovery sporomorph data worldwide, the favoured palaeogeographical model is with Gondwana and Laurentia close to each other.

We thank C. H. Wellman of Sheffield and Chen Xu of Nanjing, for the valuable suggestions. This research was supported by the CAS projects (KZCX2-YW-Q05-01; KZCX3-SW-122), NFSC grant and China MOST 973 programmes.

REFERENCES

- Beck, J. H. & Strother, P. K. 2001 Silurian spores and cryptospores from the Arisaig Group, Nova Scotia, Canada. *Palynology* **25**, 127–177. (doi:10.2113/0250127)
- Bleick, A., Turner, S. & Young, G. C. 2001 Cambrian–Ordovician vertebrate biogeography. In *Early palaeogeographies and biographies of western Europe and North Africa*. Université des Sciences et Technologies de Lille, Villeneuve d'Ascq, September 24–26, 2001.
- Bouček, B. & Přibyl, A. 1953 *On the genus Diversograptus Manck from the Silurian of Bohemia*, Svazek XX. Prague, Czech Republic: Sborník Ustředního Ústavu Geologického.
- Burgess, N. D. 1991 Silurian cryptospores and miospores from the type Llandovery area, south-west Wales. *Palaeontology* **34**, 575–599.
- Burgess, N. D. & Richardson, J. B. 1991 Silurian ceyptospores and miospores from the type Wenlock area, Shropshire, England. *Palaeontology* **34**, 601–628.
- Chen, X. & Rong, J. 1993 Ordovician plate tectonics of China and its neighbouring regions. In *Global perspectives on Ordovician geology* (eds B. D. Webby & J. R. Laurie), pp. 277–292. Rotterdam, The Netherlands: A. A. Balkkema.
- Chen, X., Ruan, Y. & Boucot, A. J. 2001 *Paleozoic climatological evolution of China*, pp. 1–325. Beijing, China: Science Press. [In Chinese.]
- Duffield, S. L. 1985 Land-derived microfossils from the Jupiter Formation (Upper Llandoveryan), Anticosti Island, Quebec. *J. Paleontol.* **59**, 1005–1010.
- Eley, B. E. & Legault, J. A. 1988 Palynomorphs from the Manitoulin Formation (Early Llandovery) of southern Ontario. *Palynology* **12**, 49–63.
- Elles, G. L. & Wood, E. M. R. 1913 *A monograph of British graptolites-IX*, pp. 415–486. London, UK: Palaeontographical Society.
- Foster, C. B. & Williams, G. E. 1991 Late Ordovician–Early Silurian age of the Mallowa Salt of the Carribuddy Group, Canning Basin, Australia, based on occurrences of *Tetrahedraletes medinensis* Strother & Traverse 1979. *Aust. J. Earth Sci.* **38**, 223–228. (doi:10.1080/08120099108727966)
- Fu, L., Zhang, Z. & Geng, L. 2006 *Silurian high-resolution graptolite biostratigraphy and biotic recovery in Ziyang, China*, pp. 1–151. Beijing, China: Geological Publishing House.
- Gray, J. 1985 The microfossil record of early land plants: advances in understanding of early terrestrialization, 1970–1984. In *Evolution and environment in the Late Silurian and Early Devonian* (eds W. G. Chaloner & J. D. Lawson). *Phil. Trans. R. Soc. Lond. B* **309**, 167–195.

- Gray, J., Theron, J. N. & Boucot, A. J. 1986 Age of the Cedarberg Formation, South Africa and early land plant evolution. *Geol. Mag.* **123**, 445–454. (doi:10.1017/S0016756800033537)
- Gray, J., Boucot, A. J., Grahn, Y. & Himes, G. 1992 A new record of early Silurian land plant spores from the Parana Basin, Paraguay (Malvinokaffric Realm). *Geol. Mag.* **129**, 741–752. (doi:10.1017/S0016756800008463)
- Hoffmeister, W. S. 1959 Lower Silurian plant spores from Libya. *Micropaleontology* **5**, 331–334. (doi:10.2307/1484424)
- Johnson, N. G. 1985 Early Silurian palynomorphs from the Tuscarora Formation in central Pennsylvania and their paleobotanical and geological significance. *Rev. Palaeobot. Palynol.* **45**, 307–360. (doi:10.1016/0034-6667(85)90006-5)
- Loydell, D. K. 1993 Upper Aeronian and Lower Telychian (Llandovery) graptolites from western Mid-Wales (part 2). *Monogr. Palaeontogr. Soc.* **147**, 56–180.
- Loydell, D. K., Mannik, P. & Nestor, V. 2006 Integrated biostratigraphy of the Lower Silurian of the Aizpute-41 core, Latvia. *Geol. Mag.* **140**, 205–229. (doi:10.1017/S0016756802007264)
- Metcalf, I. 1992 Ordovician to Permian evolution of Southeast Asian terranes: NW Australian Gondwana connections. In *Global perspectives on Ordovician geology* (eds L. Webby & J. R. Laurie), pp. 293–305. Rotterdam, The Netherlands: A. A. Balkema.
- Miller, M. A. & Eames, L. E. 1982 Palynomorphs from the Silurian Medina Group (Lower Llandovery) of the Niagara Gorge, Lewiston, New York, U.S.A. *Palynology* **6**, 221–254.
- Pratt, L. M., Phillips, T. L. & Dennison, J. M. 1978 Evidence of non-vascular land plants from the Early Silurian (Llandoveryan) of Virginia, U.S.A. *Rev. Palaeobot. Palynol.* **25**, 121–149. (doi:10.1016/0034-6667(78)90034-9)
- Pribyl, A. 1943 *Einige neue Graptolithen aus dem bohemischen und deutschen Silur*. Vestník Kralovské Ceske společnosti nauk, Trida matematicko-prirodovedna, pp. 1–26.
- Pribyl, A. 1944 The middle-European monograptids of the genus *Spirograptus* Gurich. Rozpravy Ceske akademie ved a umeni, Trida 2, **54**, 1–46.
- Regional Geological Survey of Yunnan 1965 *Geological reports of Po'er region (1:1000000)*, pp. 1–139. Kunming, China: Regional Geological Survey of Yunnan. [In Chinese.]
- Regional Geological Survey of Yunnan 1973 *Geological reports of Mojiang region (1:200000), Silurian System*, pp. 7–13. Xiaguan, China: Regional Geological Survey of Yunnan. [In Chinese.]
- Richardson, J. B. 1988 Late Ordovician and Early Silurian cryptospores and miospores from northeast Libya. In *Subsurface palynostratigraphy of northeast Libya* (eds A. El-Arnauti, B. Owens & B. Thusu), pp. 89–109. Benghazi, Libya: Garyounis University Publications.
- Richardson, J. B. 1996 Lower and Middle Palaeozoic records of terrestrial palynomorphs. In *Palynology: principles and applications*, vol. 2 (eds J. Jansonius & D. C. McGregor), ch. 18A, pp. 555–574. Dallas, TX: American Association of Stratigraphic Palynologists Foundation.
- Richardson, J. B. & Edwards, D. 1989 Sporomorphs and plant megafossils. In *A global standard for the Silurian system* (eds C. H. Holland & M. G. Bassett). Geological Series, no. 9, pp. 216–226. Cardiff, UK: National Museum of Wales.
- Richardson, J. B. & McGregor, D. C. 1986 Silurian and Devonian spore zones of the Old Red Sandstone continent and adjacent regions. *Geol. Surv. Can. Bull.* **364**, 1–79.
- Richardson, J. G. & Ausich, W. I. 2007 Late Ordovician–Early Silurian cryptospore occurrences on Anticosti Island (Ile d'Anticosti), Quebec. *Can. J. Earth Sci.* **44**, 1–7. (doi:10.1139/E06-100)
- Rickards, R. B. 1976 The sequence of Silurian graptolite zones in the British Isles. *Geol. J.* **11**, 153–184.
- Rickards, R. B. & Chen, X. 2002 Palaeontological data. 5. Graptolites. In *Telychian Rocks of the British Isles and China (Silurian, Llandovery Series)—an experience to test precision in stratigraphy* (eds C. H. Holland & M. G. Bassett), pp. 73–83. Cardiff, UK: National Museum of Wales.
- Rickards, R. B., Hutt, J. E. & Berry, W. B. N. 1977 Evolution of the Silurian and Devonian graptoloids. *Bull. Br. Mus. (Nat. Hist.) Geol.* **28**, 1–120.
- Rong, J. & Chen, X. 2003 Silurian biostratigraphy of China. In *Biostratigraphy of China* (eds W. Zhang, P. Chen & A. R. Palmer), pp. 173–236. Beijing, China: Science Press.
- Rubinstein, C. V. & Toro, B. A. 2006 Aeronian (Llandovery, Lower Silurian) palynomorphs and graptolites from the Lipeon Formation, Eastern Cordillera, north-west Argentina. *Geobios* **39**, 103–111. (doi:10.1016/j.geobios.2004.08.002)
- Smelror, M. 1987 Llandovery and Wenlock miospores and spore-like microfossils from the Ringerike district, Norway. *Norsk Geologisk Tidsskrift* **67**, 143–150.
- Steenmans, P. 1999a Cryptospores and spores from the Ordovician to the Llandovery; a review. *Acta Universitatis Carolinae, Geologica* **43**, 271–273.
- Steenmans, P. 1999b Paleodiversification des spores et des cryptospores de l'Ordovicien au Devonien inferieur. *Geobios* **32**, 341–352. (doi:10.1016/S0016-6995(99)80048-5)
- Steenmans, P. 2000 Miospore evolution from the Ordovician to Silurian. *Rev. Palaeobot. Palynol.* **113**, 189–196. (doi:10.1016/S0034-6667(00)00059-2)
- Steenmans, P. & Pereira, E. 2002 Llandovery miospore biostratigraphy and stratigraphic evolution of the Parana Basin, Paraguay—palaeogeographical implications. *Bulletin de la Société Géologique de France* **173**, 407–414. (doi:10.2113/173.5.407)
- Steenmans, P. & Wellman, C. 2004 Miospores and the emergence of land plants. In *The Great Ordovician biodiversity event* (eds B. D. Webby, M. L. Droser & I. G. Percival), pp. 361–368. New York, NY: Columbia University Press.
- Steenmans, P., Le Hérisse, A. & Bozdogan, N. 1996 Ordovician and Silurian cryptospores and miospores from southeastern Turkey. *Rev. Palaeobot. Palynol.* **93**, 35–76. (doi:10.1016/0034-6667(95)00119-0)
- Steenmans, P., Higgs K. T. & Wellman, C. H. 2000 Cryptospores and trilete spores from the Llandovery, Nuayyim-2 borehole, Saudi Arabia. In *Stratigraphic palynology of the Palaeozoic of Saudi Arabia* (eds S. Al-Hajri & B. Owens), pp. 92–115. *GeoArabia* Special Publication 1. Manama, Bahrain: Gulf PetroLink.
- Steenmans, P., Wellman, C. H. & Filatoff, J. 2007 Palaeophytogeographical and palaeoecological implications of a miospore assemblage of Earliest Devonian (Lochkovian) age from Saudi Arabia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **25**, 237–254. (doi:10.1016/j.palaeo.2007.03.009)
- Storch, P. 1993 Lower Silurian graptolites from southwestern Sardinia. *Boll. Soc. Paleontol. Ital.* **32**, 3–57.
- Storch, P. 1994 Graptolite biostratigraphy of the Lower Silurian (Llandovery and Wenlock) of Bohemia. *Geol. J.* **29**, 137–165.
- Storch, P. & Kraft, P. 2008 Graptolite assemblages and stratigraphy of the Lower Silurian Mrakotin Formation, Hlinsko Zone, NE interior of the Bohemian Massif (Czech Republic). *Bull. Geosci.* **83**, 1–188. (doi:10.3140/bull.geosci.2008.01.001)
- Strother, P. K. & Traverse, A. 1979 Plant microfossils from the Llandoveryan and Wenlockian rocks of Pennsylvania. *Palynology* **3**, 1–21.

- Wang, Y., Ouyang, S. & Cai, C. 1996 Early Silurian microfossil plants from the Xiushan Formation in Guizhou Province, China and their paleobotanical significance. *Palaeobotanist* **45**, 181–237.
- Wang, Y., Li, J. & Wang, R. 1997 Latest Ordovician cryptospores from southern Xinjiang, China. *Rev. Palaeobot. Palynol.* **99**, 61–74. (doi:10.1016/S0034-6667(97)00033-X)
- Wellman, C. H. 1996 Sporomorph assemblages from the 'Lower Old Red Sandstone' of Lorne, Scotland. In *Studies on early land plant spores from Britain* (ed. C. J. Cleal). Special Papers in Palaeontology, no. 55, pp. 41–101.
- Wellman, C. H. & Gray, J. 2000 The microfossil record of early land plants. *Phil. Trans. R. Soc. Lond. B* **355**, 717–732. (doi:10.1098/rstb.2000.0612)
- Wellman, C. H. & Richardson, J. B. 1993 Terrestrial plant microfossils from Silurian inliers of the Midland Valley of Scotland. *Palaeontology* **36**, 155–193.
- Wellman, C. H., Higgs, K. T. & Steemans, P. 2000 Spore assemblages from a Silurian sequence in Borehole Hawiyan-151 from Saudi Arabia. In *Stratigraphic palynology of the Palaeozoic of Saudi Arabia* (eds S. Al-Hajri & B. Owens). *GeoArabia* Special Publication, no. 1, pp. 116–133. Manama, Bahrain: Gulf PetroLink.
- Wellman, C. H., Osterloff, P. L. & Mohiuddin, U. 2003 Fragments of the earliest land plants. *Nature* **425**, 282–285. (doi:10.1038/nature01884)
- Zalasiewicz, J. 1994 Middle to Late Telychian (Silurian: Llandovery) graptolite assemblages of central Wales. *Palaeontology* **37**, 375–396.
- Zhang, Y. & Lenz, A. C. 1997 Uppermost Wenlock and Ludlow graptolites from southern Yunnan, China. *Can. J. Earth Sci.* **34**, 1220–1238. (doi:10.1139/e17-098)
- Zhang, Y. & Lenz, A. C. 1999 Silurian biostratigraphy of Mojiang area, southern Yunnan, China. *J. Stratigr.* **23**, 161–169. [In Chinese with English abstract.]
- Zhang, Y., Zhang, D. & Liu, S. 1996 *The stratigraphy of Yunnan Province, China*, pp. 1–366. Wuhan, China: The China Geosciences University Press. [In Chinese.]