A biostratigraphic method based on a quantification of fossil tracheophyte characters — its application to the Lower Devonian Posongchong flora (Yunnan Province, China)

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The biostratigraphic method used here is based on a quantification of individual plant characters and not on determination of whole fossils. The method is as follows: (i) each biocharacter found at a given locality receives a score according to whether it is primitive or derived, so that the biocharacter score increases with increasing derivation; (ii) the biostratigraphic coefficients of well-dated localities are calculated, the biostratigraphic coefficient of a given plant locality being the mean of all the biocharacter scores; and (iii) the scores of these well-dated localities are used to build a reference scale to which localities under investigation will be compared. A detailed example is developed for Early Devonian times and the updated quantification table of Targrove (Wales) is presented. An application of the method to the Posongchong flora (Yunnan Province, China), including its quantification table, is also demonstrated. It suggests that the mean age of this flora might late Pragian (Lower Devonian). This is the first direct biostratigraphical dating of the Posongchong flora.

Key-words—Biostratigraphic method, Quantification, Plant characters, Lower Devonian, Posongchong flora (China).

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साराँश

अश्मित ट्रेकियोफाइटी लक्षणों के परिमाण पर आधारित एक जैवस्तरिक विधी–अधरि डिवोनियन पोसाँगचाँग वनस्पति जात (यूनान प्रांत, चीन) में इसकी उपयोगिता

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इस शोध-पत्र में एक जैवस्तरिक विश्लेषण विधि एक पौधे के लक्षणों पर आधारित है, न कि सभी पादपाश्मों पर। इस विधी में प्रत्येक जैवलक्षण को यह देखा जाता है कि यह आद्य है अथवा व्युत्पादित। फिर आयु निर्धारित स्थानों के जैवस्तरिक गुणाँकों की गणना की जाती है। अब इन्हीं स्थानों का उपयोग सन्दर्भों को बनाने में किया जाता है। इसी विधि से पौसाँगचाँग वनस्पतिजात की आयु निर्धारण का यह पहला प्रयास है।

IN 1994, Gerrienne and Streel proposed a biostratigraphic method based on the quantification of morphological and anatomical features of Devonian tracheophyte (sensu Kenrick & Crane, 1991) remains. Whereas current biostratigraphic methods require specific or generic determinations, Gerrienne and Streel's method has been developed to avoid obligatory determination of the fossil plants and has thus the advantage of using almost every fossilized plant remain at a locality, well-preserved or not. In this method, plants are considered to be sets of morphological and anatomical features and not systematic entities. In this paper, I present the general principles of the method, illustrate several quantification tables and apply the quantification method to the recently described Chinese Posongchong flora, which has not been so far satisfactorily dated.

METHOD OF STUDY

The principles of this method are as under:

1. For a given period, a quantification table has to be built, in which each biocharacter found during that period receives a score according to whether the character is primitive or derived. The character score increases with increasing derivation.
2. Using this quantification table, the biostratigraphic coefficient of any locality of that period can easily be calculated. This coefficient is the

percentage of the points scored by all the observed characters at this locality over the maximum possible for these characters. The biostratigraphic coefficient is an indication of the relative age of the locality.

3. A reference scale may then be elaborated for that period, based on several well-dated localities, to which the other fossiliferous outcrops under study can be compared.

THE QUANTIFICATION METHOD IN THE LOWER DEVONIAN

Gerrienne and Streel (1994) have illustrated a detailed example from the Lower Devonian, using seven well dated localites ranging from the base to the top of the Lower Devonian. They have selected 11 different biocharacters: those of the axes (main axis mean diameter, branching type, emergences, photosynthetic surfaces), anatomical structure (stelar type, xylem maturation, tracheid ornamentation), sporangia (shape, aggregation type, presence or absence of a dehiscence line) and spore production. Each state of these biocharacters was attributed a score (Table 1).

Table 1—Quantification of selected characters of Early Devonian plants. =D8 =3D mean diameter

Characters	Character state	Score
Axis diameter	ø ≤ 1.0 mm	0
	1.0 mm < ø ≤ 2.0 mm	1
	2.0 mm < ø ≤ 3.5 mm	2
	3.5 mm < ø ≤ 6.0 mm	3
	6.0 mm < ø ≤ 12.0 mm	4
	12.0 mm < ø	5
Axis branching	None	0
	Isotomous and/or K- or H-branching	1
	Anisotomous (lateral axis ø ≥ main axis ø/2)	2
	Main axis ø/2 > lateral axis ø ≥ main axis ø/4	3
	Main axis ø/4 > lateral axis ø	4
Axial emergences	None	0
	Unvascularized, irregularly arranged	1
	Unvascularized, regularly arranged	2
	Regularly arranged with trace to base	3
	Vascularized, regularly arranged, simple shape	4
	Vascularized, complex shape	5
Photosynthetic surfaces	None	0
	Elaborated terete dichotomous axes	1
	Planated dichotomous axes	2
	Laminar surfaces	3
Stelar type	Massive protostele	0
	Actinostele	1
	Polystele	2
Xylem maturation	Indefinite	0
	Exarch	1
	Centrarch	1
	Mesarch	2
Tracheid ornamentation	Annular	0
	Spiral	1
	Reticulate with scalariform pits	2
	Reticulate with circular bordered pits	3
Sporangial shape	Axis enlargment	0
	Individualized, reniform or oval	1
	Fusiform with stalk	1
Sporangial aggregation	Terminal, solitary	0
	Terminal, aggregated	1
	Lateral, solitary	1
	In compact spikes	2
	In lateral clusters	2
	On a specialized organ	2
Sporangial dehiscence	No dehiscence line	0
	Dehiscence line with no specialized cells	1
	Specialized structure for dehiscence	2
Spore production	Biometric homospory	0
	Biometric heterospory	1
	Biometric and morphological heterospory	2

The seven selected localities are:

1. *Targrove, Wales*—In 1994, nine different morphological types were quantified by Gerrienne and Streel (1994). Since then, other plants have been described and/or discovered in this locality (see for example Edwards *et al.*, 1995). These newly described plants have been taken into account here and a new quantification table (with 15 different morphological types) has been built. The biostratigraphic coefficient obtained this time is very similar to the previous one (10 instead of 9 in 1994). The age of the locality, which belongs to the spore assemblage zone MN (Fanning *et al.*, 1988), is Early Gedinnian (=3D? Lochkovian). The new quantification table is presented in Table 2.

A = *Cooksonia cambrensis* Edwards
in Edwards & Fanning 1985; Fanning *et al.* 1992
B = *Cooksonia hemisphaerica* Lang
in Lang 1937; Edwards & Fanning 1985; Fanning *et al.* 1992
C = *Cooksonia pertoni* Lang
in Edwards & Fanning 1985; Fanning *et al.* 1992
D = *Renalia* n. sp. 1
in Edwards & Fanning 1985
E = *Renalia* n. sp. 2 (= fertile specimen with trifurcation)
in Edwards & Fanning 1985

Table 2—Biostratigraphic coefficients of the plant macrofossils of Targrove (Early Lochkovian), Wales

Targrove	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	TOTAL
Axis diameter (/5)	0	0	0	0	0	0	0	0	0	-	0	0	1	1	1	3 (/70)
Axis branching (/4)	0	1	1	2	2	1	1	1	1	1	1?	1	0	1	0	14 (/60)
Axial emergences (/5)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1 (/75)
Photosynthetic surfaces (/3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0 (/45)
Stelar type (/2)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0 (/0)
Xylem maturation (/2)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0 (/0)
Tracheid ornamentation (/3)	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	0 (/3)
Sporangial shape (/1)	0	0	1	1	0	1	0	0	1	0	1	1	-	-	-	6 (/12)
Sporangial aggregation (/2)	0	0	0	2	1	0	0	0	0	0	0	0	-	-	-	3 (/24)
Sporangial dehiscence (/2)	0	0	0	0	0	2	0	1	1?	-	-	1	-	-	-	5 (/20)
Spore production (/2)	0?	0	0	-	-	0	0	0	-	0	0?	-	-	-	-	0 (/16)
TOTAL: 32 (/325)																
BIOSTRATIGRAPHIC COEFFICIENT: 10																

F = *Risilitheca salopensis* Edwards *et al.*
in Edwards *et al.* 1995 (= cf. *Cooksonia caledonica* in Fanning *et al.* 1992, and, may be, cf. *Cooksonia caledonica* in Edwards & Fanning 1985)
G = *Salopella marcensis* Fanning *et al.*
in Fanning *et al.* 1992 (= *Salopella* sp. in Edwards & Fanning 1985)
H = *Tarrantia salopensis* Fanning *et al.*
in Fanning *et al.* 1992
I = *Uskiella reticulata* Fanning *et al.*
in Fanning *et al.* 1992 (= "ellipsoidal sporangia" or "incomplete oval sporangium"
in Edwards & Fanning 1985
J = cf. *Uskiella reticulata* Fanning *et al.*
in Fanning *et al.* 1992
K = Bifurcating sporangia
in Edwards & Fanning 1985; Fanning *et al.* 1992
L = Indeterminate sporangia
in Fanning *et al.* 1992 (= cf. *Yarravia* sp. in Edwards & Fanning 1985)
M = axis with anatomy
in Lang 1937; Edwards *et al.* 1979
N = divided sterile axes
in Edwards & Fanning 1985; Fanning *et al.* 1992
O = Spiny sterile axis
in Edwards & Fanning 1985

2. *Nonceveux, Belgium (Leclercq, 1942; Gerrienne, 1990, 1993)*—Six morphological types have been considered. The age of Nonceveux, based on spores, is Late Lochkovian (spore assemblage zone MN in Steemans, 1989). The biostratigraphic coefficient of this locality is 18 (Table 3).
3. *La Gileppe, Belgium (Steemans & Gerrienne, 1984; Gerrienne, 1990, 1992a, 1993)*—Five different morphological types have been scored. The age based on spores is Late Lochkovian or Early Pragian (spore assemblage zone BZ in Steemans & Gerrienne, 1984; Steemans, 1989). The biostratigraphic coefficient of this locality is 27 (Table 3).
4. *Brecon Beacons, Wales*—Eleven different morphological types have been scored. The age of this quarry (Early Siegenian) is given by Richardson *et al.* (1982) and the floristic assemblage has been described by, among others, Croft and Lang (1942), Edwards (1968, 1969a, 1969b, 1970, 1980, 1981), Edwards and Kenrick (1986), Shute and Edwards (1989) and Edwards *et al.* (1989). The quantification table is presented in Gerrienne and Streel (1994, Table 3). The biostratigraphic coefficient of this locality is 35 (Table 3).
5. *Fooz-Wepion, Belgium (Stockmans, 1940; Fairon-Demaret, 1977; Gerrienne, 1991b, 1992b, 1992c, 1993)*—Ten morphological types have been quantified. The age of Fooz-Wepion is Early Emsian (spore assemblage zone AB in Steemans, 1989). The biostratigraphic coefficient of this locality is 45 (Table 3).
6. *Marchin, Belgium*—Thirteen different morphological types have been scored. The age of this locality is Early Emsian (spore assemblage zone AB in Steemans, 1989). This locality has yielded numerous plant macrofossils (Gerrienne, 1983, 1988, 1990, 1991a). The quantification of the characters shown by these macrofossils and the subsequent biostratigraphic coefficient for Marchin (45) are presented in Gerrienne and Streel (1994; Table 2).
7. *Locality B, Canada (Gensel & Andrews, 1984; data found in Andrews et al., 1975; Gensel,*

Table 3—Reference scale for the Lower Devonian. Biostratigraphic coefficients of the selected localities. For spore zones, see Streel et al. (1987) and Steemans (1989)

	STAGES	SPORE ZONES	COEFFICIENTS	REFERENCE LOCALITIES
LOWER DEVONIAN	EMSIAN	AP		
			55	LOCALITY B (CANADA)
		FD		
		AB	45	FOOZ-WEPION (BELGIUM) MARCHIN (BELGIUM)
	?			
	PRAGIAN	PoW	35	BRECON BEACONS (WALES)
		BZ	27	LA GILEPPE (BELGIUM)
	LOCH-KOVIAN	MN	18	NONCEVEUX (BELGIUM)
			10	TARGROVE (WALES)

1979; Hueber, 1992)—Four different types have been considered. The age of the locality is Late Emsian (spore assemblage zones FD-AP boundary). This age can be deduced from Gensel (1982), Richardson and McGregor (1986) and Streel *et al.* (1987). The biostratigraphic coefficient of this locality is 55 (Table 3).

The biostratigraphic coefficients of the seven localities have been calculated and the reference scale has been built (Table 3). This example shows that biostratigraphic results obtained by using the quantification method are comparable in precision with dating based on palynological assemblage zones.

This method has been based mainly on European and North American floras. Assuming that the plant evolution rate in China during Lower Devonian was not significantly different, the reference scale will here be used to test the Posongchong flora of the Yunnan Province (China).

QUANTIFICATION METHOD APPLIED TO THE POSONGCHONG FLORA

Age of the Posongchong flora

According to Hao (1989a), the age of the Posongchong flora may be assumed to be Late Siegenian (we would now say Pragian). Table 4 in this paper has been constructed according to the data given by Hao (1989a). It shows that the Posongchong Formation in the Wenshan District, which yielded an extensive flora, has only been dated in a very indirect way. The Posongchong Formation in the Wenshan District is overlaid by the Pojiao Formation, where no biostratigraphic data has been presented. The Pojiao Formation is also found in the adjacent Guangnan and Funing districts. In these areas, the Pojiao Formation has been shown by conodonts to be Early Emsian in age. This Formation in the Guangnan and Funing districts from the Yunnan Province has béen correlated by marine invertebrates with the Lower Yujiang Formation from the Guangxi Province, which has been demonstrated to be also Early Emsian. This latter Formation overlies the Nagaoling Formation, which has been shown using conodonts to be Late Siegenian (Pragian) in age. So, it is assumed that the Posongchong Formation is a lateral equivalent to the Nagaoling Formation and that it is Late Pragian in age too. Several comments to this should be made.

1. The Pojiao Formation in the Guangnan and Funing districts has been shown to be Early Emsian. The diachronism of the lithological units is a well-known phenomenon. For example, Steemans (1989) has clearly demonstrated that several lithological units from the Lower Devonian of Belgium are diachronous (Steemans, 1989, p. 339). This diachronism can be demonstrated even over very short distances (less than 10 km). A spectacular example of such a diachronism in Belgium is the Bois d'Ausse Formation which ranges from Late Lochkovian at Pépinster to Late Pragian at Dave (less than 60 km) (Hance *et al.,* 1992, fig. 7). So, the Early Emsian age of the whole Pojiao Formation in the Guangnan and Funing districts has still to be demonstrated.
2. Should the whole Pojiao Formation in these two districts be of Early Emsian age, this should not imply that the Pojiao Formation in the Wenshan District, which has so far not been dated, is Early Emsian too. Anyway, even if this formation was demontrated to be Early Emsian in age, it would not imply that the underlying Posongchong Formation is Late Pragian.

Table 4—About the age of the Posongchong flora (from Hao 1989a). See text for further explanation.

YUNNAN PROVINCE				GUANGXI PROVINCE
Wenshan District		Guangnan and Funing District		
Pojiao Formation *No biostratigraphic data*	Lithologic correlation	Pojiao Formation *Early Emsian (based on conodont)*	Biostratigraphic correlation	Lower Yujiang Formation *Early Emsian (based on conodont)*
Posongchong Formation *No biostratigraphic data*		Posongchong Formation *No biostratigraphic data*		Nagaoling Formation *Late Siegenian (based on conodont)*

3. The correlation of the Posongchong Formation in the Wenshan District (Yunnan Province) with the Late Siegenian (Pragian) Nagaoling Formation (Guangxi Province, at least 100 km from the Wenshan District) is very indirect and based on lithological evidence only. As shown by Steemans (1989) again, long distance correlation should not be used for stratigraphic purposes.
4. The plants collected from the Posongchong Formation are collectively grouped under the name "Posongchong flora". However, these plants come from several localities scattered in the Posongchong Formation. According to the fact that the lithological units might be strongly diachronous (see above), these various localities might well be of different ages.

The biostratigraphical potential of the presently described plants from the Posongchong Formation is poor using standard methods based on taxonomy. Indeed, apart from the subcosmopolitan genera *Zosterophyllum* and *Psilophyton*, which indicate a Pragian - Early(?) Emsian age, the other taxa are endemic and thus do not help at all in the dating of this flora.

Description of plants from Posongchong flora

Adoketophyton subverticillatum (Li & Cai) Li & Edwards 1992

This plant consists of dichotomously branching axes, with terminal compact strobili in which lateral units are inserted oppositely and decussately, so that they form four vertical rows. Each unit comprises a stalked, fan-shaped, bract-like appendage bearing an adaxial sporangium. This plant was originally named *Zosterophyllum subverticillatum* by Li & Cai 1977.

***Discalis longistipa* Hao 1989a**

This zosterophyll has creeping axes showing common H- and K- branching. Its disc-like sporangia are borne laterally each at the top of a long stalk. They form loose spikes. Axes, stalks, and sporangia bear spines with expanded oblate apices. The plant is homosporous.

***Eophyllophyton bellum* Hao 1988**

This mainly isotomously branched plant bears lateral divided laminate structures interpreted as leaves. Vegetative and fertile leaves are similar. Fertile units consist of two sporophylls. The circular to reniform sporangia-like bodies are borne laterally in single rows on facing sides of rachides of the two opposite sporophylls. Leaves are characterized by a system of veins that parallels the morphology of the leaf. Leaves are interpreted as megaphylls. The protostele is columnar and centrarch.

***Gumuia zizzata* Hao 1989b**

This homosporous plant has creeping and erect axes and dichotomous branching. Axes bear both lateral and terminal, round or transversely elliptical sporangia. Sporangia are sessile or borne on a very short stalk; they are usually alternate on the zigzag-shaped fertile axes.

***Huia recurvata* Geng 1985**

This plant possesses isotomously and anisotomously branched axes, with terminal spikes. The spirally arranged sporangia are ovate, adaxially and downwardly recurved. The plant is homosporous and its protostele is centrarch.

***Psilophyton primitium* Hao 1995**

The plant is made of isotomously and, in distal regions, pseudomonopodially branched axes. The fertile branches dichotomize up to 2-4 times and are terminated by paired sporangia. The sporangia are usually erect and elongate-elliptical. Fertile branches end in a sparse cluster of sporangia, each cluster includes 4-16 pairs of sporangia.

***Stachiophyton yunnanense* Geng 1983**

The plant consists of pseudomonopodially (isotomous in distal parts) branched axes. The lateral branches are planated. Each fertile branch terminates in a strobilus. The axis of the strobilus is covered with helically arranged sporophylls, which bifurcate at their tip. Each sporophyll bears one sporangium on its adaxial surface. The plant is probably homosporous.

***Yunia dichotoma* Hao & Beck 1991**

The spiny axes of this taxon are characterized by cruciate dichotomy. Associated, but not in organic connection with the vegetative axes, are numerous elongate-elliptical or ovoid, homosporous sporangia.

Table 5—Biostratigraphic coefficients of the plant macrofossils of the Posongchong flora (Yunnan Province, China)

Posongchong Formation	A	B	C	D	E	F	G	H	I	TOTAL
Axis diameter (/5)	2	3	1	4	4	2	2	2.5	1.5	22 (/45)
Axis branching (/4)	1	1	1	2	2.5	2	3	1	2	15.5 (/36)
Axial emergences (/5)	0	1	0	0	0	0	1	1	0?	3 (/45)
Photosynthetic surfaces (/3)	0	0	3	0	2	0	2	0	0?	7 (/27)
Stelar type (/2)	-	-	-	0	-	-	0	0	-	0 (/6)
Xylem maturation (/2)	-	-	-	1	-	-	1	1	-	3 (/6)
Tracheid ornamentation (/3)	0?	1	-	2	-	-	2	2	-	7 (/15)
Sporangial shape (/1)	1	1	1	1	1	0	1?	1	1	8 (/ 9)
Sporangial aggregation (/2)	2	1	2	2	2	1	2	2?	2	16 (/18)
Sporangial dehiscence (/2)	2	2	2	-	1?	2	-	2	-	11 (/12)
Spore production (/2)	0	0	-	0	0	0	-	0	-	0 (/12)
TOTAL: 92.5 (/231)										
BIOSTRATIGRAPHIC COEFFICIENT: 40										

The circular to elliptical protostele is interpreted to be centrarch.

Zosterophyllum australianum Lang & Cookson (Hao 1992)

The spikes of this homosporous plant bear short-stalked, rather large, transversely elliptical sporangia, each with a wide, thickened, distal border. Sporangia are borne close together, helically inserted, and usually in four or five longitudinal rows.

QUANTIFICATION OF POSONGCHONG FLORA

The quantification of all these plants is presented in Table 5.

A = *Zosterophyllum australianum* Lang & Cookson
in Hao 1995 (data taken from Hao 1992)

B = *Discalis longistipa* Hao
in Hao 1989a

C = *Adoketophyton subverticillatum* (Li & Cai) Li & Edwards
in Li & Edwards 1992

D = *Huia recurvata* Geng
in Geng 1985

E = *Stachiophyton yunnanense* Geng
in Geng 1983

F = *Gumuia zizzata* Hao
in Hao 1989b

G = *Eophyllophyton bellum* Hao
in Hao 1988; Hao & Beck 1993

H = *Yunia dichotoma* Hao & Beck
in Hao & Beck 1991

I = *Psilophyton primitium* Hao
in Hao 1995

The biostratigraphic coefficient of the Posongchong flora is 40. According to the reference scale for the Lower Devonian (Table 3), this indicates that the age of this flora could be Late Pragian, as its score is bigger than that of the Brecon Beacons locality (Early Pragian-score 35) and smaller than the scores of the Fooz-Wépion and Marchin localities (Early Emsian-scores 45). Nevertheless, it must be emphasized that the Posongchong flora does not come from a single locality, but from several fossiliferous outcrops scattered in the Posongchong Formation. As already pointed out (see above), the age of a lithological unit may vary considerably from one place to another. So, the age given by the quantification method should be considered as the mean age of the flora, as this flora possibly integrates components of slightly different ages. Anyway, the result obtained here reinforces the Late Pragian datation proposed by Hao (1989a).

CONCLUSION

The biostratigraphic method of Gerrienne and Streel (1994), based on a quantification of the plant characters, applied to the Posongchong flora (Yunnan Province, China) as a whole, indicates that this flora might be of Late Pragian age. This is the first direct biostratigraphical dating of this flora.

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