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New Early Devonian Charophyta from Gondwana

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Abstract — Early Devonian charophytes are reported from Australia (Buchan, Victoria) and Europe (Landeyran, southern France): *Moellerina australica* n. sp. Feist and *Pinnoputamen occitanicum* n. sp. Feist. Sedimentological data and associated faunas from these localities accord with both species having inhabited lacustrine or estuarine environments. A critical review of Devonian biotopes confirms that, as with present day species, Mid Palaeozoic charophytes could not have lived in open marine habitats. Originating in Baltica during the Silurian, charophytes appeared in Gondwana in the earliest Devonian.

Charophyta / Early Devonian / Gondwana / new species / evolution / palaeobiogeography

Résumé — Nouvelles charophytes du Gondwana dans le Dévonien inférieur. Deux espèces de charophytes, provenant d'Australie (Buchan, Victoria) et d'Europe (Landeyran, sud de la France) sont décrites : *Moellerina australica* n. sp. Feist et *Pinnoputamen occitanicum* n. sp. Feist. Les données sédimentologiques sur ces gisements ainsi que les faunes associées aux charophytes suggèrent un habitat lacustre ou d'estuaire. Une analyse critique des biotopes à charophytes dans le Dévonien confirme qu'à l'instar des formes actuelles, les charophytes du Paléozoïque moyen n'auraient pu subsister dans des environnements marins. Originaires de Baltica au Silurien, les charophytes apparaissent au Gondwana dans le Dévonien inférieur.

Charophyta / Dévonien inférieur / Gondwana / nouvelles espèces / évolution / paléobiogéographie

INTRODUCTION

In charophyte evolutionary history, the Devonian was a period of highest structural diversification (Grambast, 1974) when all three orders composing the group, Moellerinales, Sycidiales and Charales became established (Feist & Grambast-Fessard, 2005). Charophytes appeared in the Late Silurian, but their origin remains cryptogenic. To date the oldest undoubted charophyte is the Late Silurian *Moellerina laufeldi* Conkin *et* Conkin from Ludlow deposits of Gotland (Conkin & Conkin, 1992). Other algal remains tentatively attributed to charo-

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phytes and assigned to *Sycidium* Sandberger are slightly older, having come from the Llandovery-Wenlock transition of Anticosti (Mamet *et al.*, 1992). Thus the origin of the Charophyta may well be sought in Baltica.

Intense specific diversification and geographic dispersal did not occur earlier than Mid to Late Devonian times, when many species, especially those of the genera *Moellerina* Ulrich and *Sycidium* Sandberger became cosmopolitan. Although all taxa of ordinal rank were represented, numerical abundance of species and localities remained very low during the Early Devonian. This scanty knowledge currently limits the full characterisation of the physiognomy of charophyte floras for this time period. All previously known Early Devonian sites, with the exception of the Mont Wagner locality, Spitsbergen, on Baltica (Feist & Grambast-Fessard, 1985) are all from the Gondwanan South China (Wang *et al.*, 1980; Li & Cai, 1982). We report here on the discovery of new species from Buchan (Victoria, southeastern Australia) and Landeyran (southern France) which significantly enhances the Early Devonian charophyte record. These areas, now far distant from each other, were both associated with the north Gondwana margin at that time.

GEOGRAPHIC AND BIOSTRATIGRAPHIC SETTINGS

Buchan, eastern Victoria, Australia (Fig. 1)

The locality occurs on the western flank of the Murrindal Synclinorium, near the township of Buchan. The locality is within the Fairy Formation, a unit of the Early Devonian Snowy River Volcanics Group of eastern Victoria. The latter is a complex sequence of mainly acid volcanics and subordinate non-volcanic and volcanic-derived sediments (Fletcher, 1963; Orth *et al.*, 1995). Unconformably overlying the Snowy River Volcanics is the highly fossiliferous Buchan Group, a late Pragian-Emsian sequence commencing with a basal dolomitic sequence with, locally, minor siliclastic sediments (Spring Creek Member of the Buchan Caves Limestone of Teichert & Talent, 1958).

The Fairy Formation consists predominantly of sandstones, reworked tuffs and siltstones, with minor volcanic black shales and conglomerates, with local areas of calcareous beds towards the top of the Formation (Fletcher, 1963; Orth *et al.*, 1995). The sample locality (Fig. 1) is within a 20 to 30 m lenticular interval of tuffaceous sandstones and siltstones, tuffs, clayed siltstones and shales with two horizons of limestone nodules. A rich fossil assemblage that includes charophytes, ostracods, fish remains and terrestrial plant fragments occurs in the nodules; the dark shales often contain abundant conchostracans (Warren & Talent, 1967; Orth *et al.*, 1995; Talent *et al.*, 2000; Johanson *et al.*, 2006, in press). The lenticular unit that produced the nodules was sampled by trenching; it occurs approximately 700 m southwest of the junction of Spring and Fairy creeks. In this area, the fairy Formation is underlain by the Carson Creek Ignimbrite and overlain by 200 to 250 m of acidic volcanics (MacRae and Jellung ignimbrites).

As the onset of Buchan Caves Limestone sedimentation is argued to be equivalent to the latest Pragian (*pirenae* Conodont Zone), it has been inferred that the stratigraphically appreciably lower Fairy Formation is approximately mid to possibly late Pragian in age (Mawson *et al.*, 1992; Talent *et al.,* 2000; Johanson *et al.,* 2006, in press). The associated fauna of conchostracans, non-marine ostracods and fish is consistent with a freshwater environment or possibly the

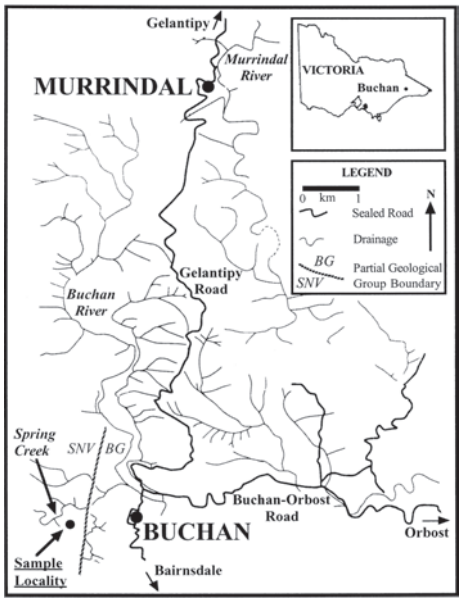


Fig. 1. Buchan Locality, southeastern Australia. Sampling locality for limestone nodules within the Fairy Formation. *SNV* = Snowy River Volcanics Group; *BG* = Buchan Group.

upper reaches of an estuary, or within a brackish coastal lake.

Landeyran Quarry, southern France
(Figs 2-5)

Charophytes were obtained by one of us (R.F.) from the lowermost beds of the basal Devonian sequence in the southeastern Montagne Noire, southern France (Figs 2-4). The sequence starts with a 12m lower member of the Rocs Nègres Formation and is of Lochkovian age (Feist & Schönlaub, 1974; Feist, 1985). It outcrops at the northern extremity of the abandoned Landeyran Quarry. This site is situated in the southwestern foothills of Mont Peyroux adjacent to departmental road D136 between Causses-et-Veyran and St. Nazaire-de-Ladarez villages, 1 km north of the southern Landeyran bridge (Fig. 5). At this locality the earliest Devonian detrital sequence unconformably overlaps Lower Ordovician slates. This earliest Devonian sequence consists of ferrugineous, graded microconglomerates, quartzitic arenites, calcareo-dolomitic variegated sandstones alternating with gritty dolomites displaying evidence of pedogenesis episodes. The depositional environment is one of a flat coastal milieu with marine incursions into a deeply weathered hinterland with lateritic soils and river deposits forming local coastal deltas. The sequence is characterised by a succession of "AB-AB-AB" sedimentary cycles where a transgressive gritty phase (A) is succeeded by a calcareo-dolomitic regressive phase (B) tending to emersion with evidence of microkarstification and reworking at the end of the cycle abruptly superseded by the A phase of the next cycle. Palaeosols with associated charophyte remains and pre-evaporitic deposits indicate a very shallow, supra to intertidal depositional setting.

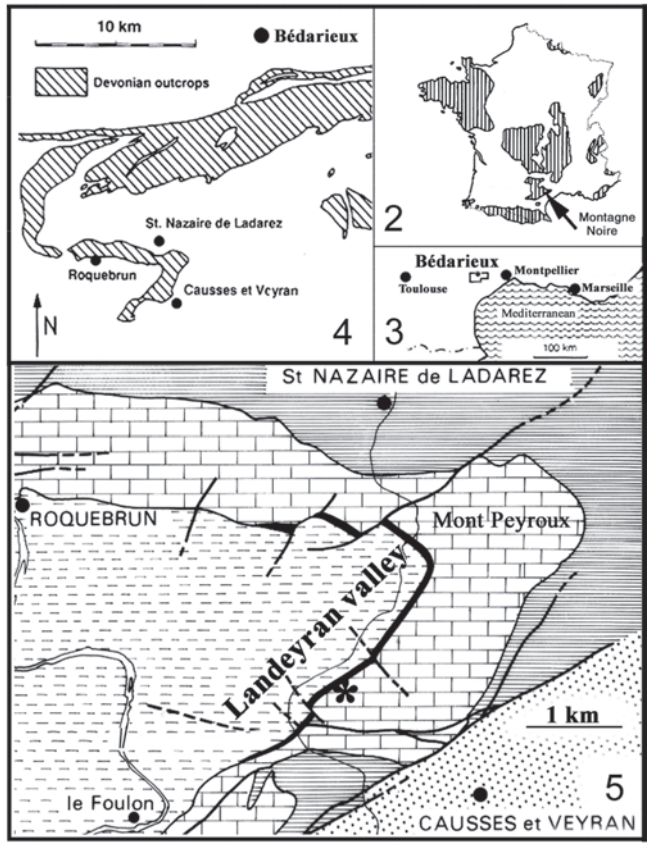
Charophytes are concentrated at the top of marly calcareo-dolomitic beds in the topmost two metres of the sequence where they occur coated with iron-oxid which enabled their extraction from the hard rock by acid etching.

DESCRIPTIONS OF NEW SPECIES (M. Feist)[1]

***Pinnoputamen occitanicum* M. Feist, sp. nov.** (Sycidiales, Pinnoputamenaceae). Figs 6-10

See also: Feist & Feist (1997: fig. 1, p. 401). *Pinnoputamen* sp. *sensu* Feist & Grambast-Fessard (2005: p. 99; fig. 48d-f).

1. The classification adopted in this paper follows Feist & Grambast-Fessard (2005).



Figs 2-5. **2.** Location of the Montagne Noire at the southern edge of the French Massif Central (shaded: Palaeozoic on outcrop). **3.** Location of the southeastern Montagne Noire south of Bédarieux. **4.** Distribution of stratigraphic units in the Montagne Noire south of Bédarieux with location of the studied area. **5.** Location of Landeyran Quarry, the Charophyte site. Key: brick signature: Devonian with basal transgressional sequence in black; horizontal lineation: Carboniferous; interrupted lines: Lower Ordovician; stippled: post-Palaeozoic.

Diagnosis. Utricles bilaterally symmetrical, each face bearing one group of long vertical stemlets and four branching short stemlets, three of which bear antheridial moulds. General shape subglobular; dimensions: LPA, 650 –1025 µm; LED, 700-1100 µm; ISI, 88 on average.

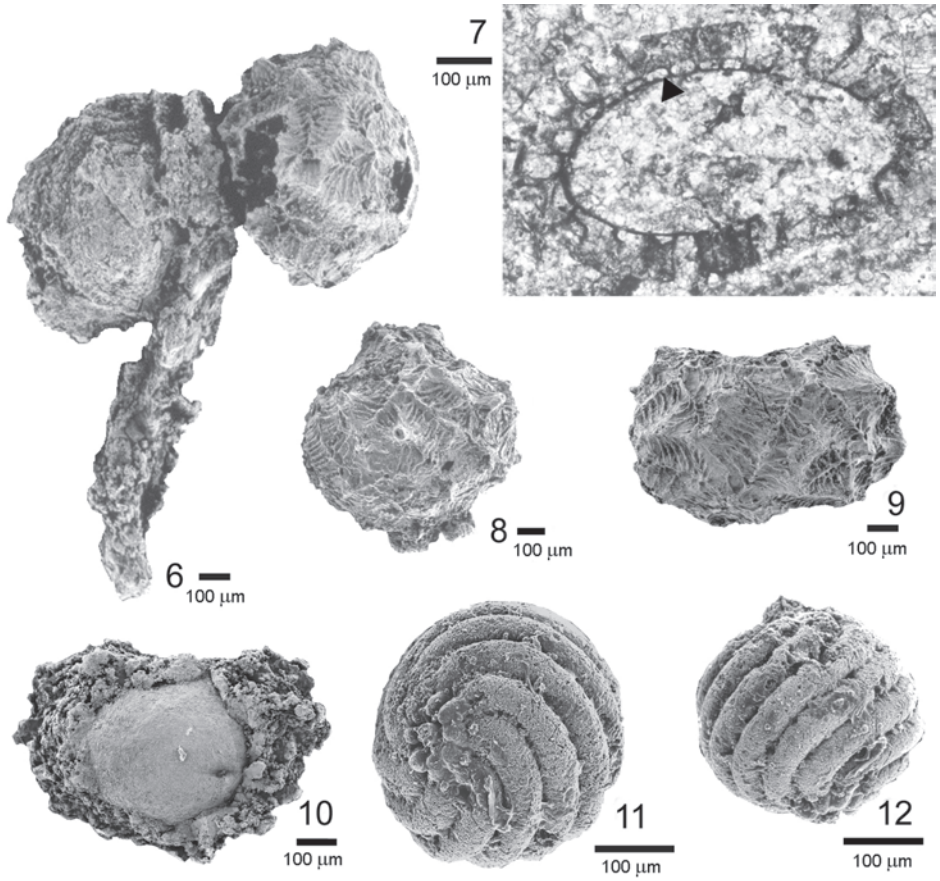
Holotype. CF.2976-1. University Montpellier-II, France.

Paratypes. CF-2976-2 to 5.

Type-locality. Landeyran Quarry, near Causses-et-Veyran, Hérault, France.

Type-level. Roc Nègres Formation, top of lower member, Lower Devonian: Lochkovian.

Description. During the fossilization, the originally calcified cell structures were diagenetically replaced by hematite, thus excellently preserved cell structures can be observed after acid etching, whereas remains of internal structures are only poorly preserved. The general structure of the utricle of the Landeyran species is shown schematically in Fig. 13 as if it were open, with the dorsal line facing and the ventral bract cells at each end. We recognize the dorsal-ventral line, with a ramified branch on each side. Each branch bears three antheridia which entirely cover the surface of the fructifications (Figs 6, 8, 9). Although the disposition of sexes is different in extant forms (antheridia and oogonia are never coalescent in extant species), these antheridia show the same



Figs 6-10. *Pinnoputamen occitanicum* Feist, n. sp. **6.** Two utricles attached to a fragment of thallus. **7.** Tangential section of a utricle showing gyrogonite cells (arrow) below the utricle wall. **8.** Holotype, lateral view showing casts of antheridial shields (Feist & Feist, 1997, fig. 1a). **9.** Paratype, lateral view, showing casts of antheridial shields and lateral branches (Feist, Liu & Tafforeau, 2005, fig. 20). **10.** Internal mould of a gyrogonite within its utricle.
Figs 11-12. *Moellerina australica* Feist, n. sp. **11.** Paratype, basal view, exhibiting the dextral spiralization. **12.** Holotype, lateral view.

and typical complex structure that characterizes the Charalean antheridia. Inside the utricle cover is a globular mould representing the gyrogonite (Fig. 10), as confirmed by its multicellular wall seen in a thin section of a utricle (Fig. 7). The orientation of these cells cannot be determined but their number must be quite high as we count 8-9 sectioned cells in a quarter of a gyrogonite (Feist, Liu & Tafforeau, 2005).

Affinities. The features exhibited by *P. occitanicum* recall the type-species of *Pinnoputamen* described by Wang & Lu (1980) from the Middle Devonian of southern China. The only but notable difference is that *P. yunnanensis* displays no antheridia. Even in case of an exceptional preservation, it seems there would be no space for antheridia in this small 500 µm utricle. *P. occitanicum* also shows similarities with *Costacidium* Langer, from the

Middle Devonian of Germany (Langer, 1991) whose utricles are bilateral and bear hollows that could represent badly preserved antheridia.

Remarks. The gyrogonite surrounded by antheridia is undoubted evidence of bisexuality. Being of earliest Devonian age, it is the oldest example of this feature, not only in the charophyte group but also in all the plant kingdom (Feist & Feist, 1997). With respect to Land Plants, the oldest record of male and female gametangia, but separated, is from the Rhynie Chert (Rice *et al.,* 1995), which is 5 million years younger than the material described here. Moreover, evidence of bisexuality in Land Plants was not definitively known earlier than in the Upper Devonian Lycophyta (Cleal, 1995).

***Moellerina australica* M. Feist, sp. nov.** (Moellerinales, Moellerinaceae).
Figs 11, 12

Diagnosis. Gyrogonites of *Moellerina* characterized by their cell number, 8, joined to their general shape, subglobular with acute poles, and to their dimensions of 220 to 310 µm in diameter. Basal plate undivided, protruding to the exterior.

Holotype. CF. 3016-1, University Montpellier-II, France.

Paratype. CF. 3016-2.

Type-locality. Buchan, East Victoria, Australia.

Type-level. Fairy Beds, Lower Devonian: Pragian.

Affinities. By its gyrogonite devoid of utricle, the dextral spiralization and relatively low number (8) of enveloping cells, *M. australica* is referred to *Moellerina*. The new species resembles most *M. convoluta* (Peck) Peck *et* Morales in general shape; it too is thinned at the apex and base, at least in some specimens of this extremely variable species (Peck & Morales, 1966). However, the two poles are more distinctly protruding in *M. australica*. *M. convoluta,* moreover, differs from the Australian species in its greater size (448 × 476 µm) and higher cell number (9-11). Thus description of *M. australica* as a new species seems justified.

Remark. *M. australica* is the oldest charophyte species from Australia.

DISCUSSION

Moellerina is poorly represented before the Middle Devonian. The fossil record consists of only one occurrence in the Late Silurian, *M. laufeldi* Conkin *et* Conkin from Gotland, Sweden (Conkin & Conkin, 1992), and two occurrences in the Early Devonian, *M.* cf. *convoluta* Peck *et* Morales from Spitsbergen (Feist & Grambast-Fessard, 1985) and *M. australica*. The appearance of *Moellerina* in East Gondwana, shortly after its first occurrence in Baltica, is not in accord with the

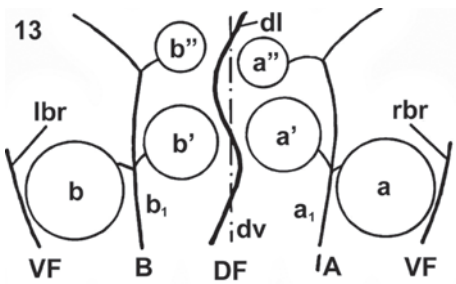


Fig. 13. *Pinnoputamen occitanicum* Feist n. sp. Schematic reconstruction of the utricle (A, basal cell of right branch; a1, right branch; a, a' a'', lower, middle and upper right antheridia; B, B1, b, b', b'', same, left branch; DF, dorsal face; dl, dorso-ventral line; dv, dorso-ventral plane of symmetry; lbr, left bractea; rbr, right bractea; VF, ventral face).

hypothesis of a wide oceanic separation between those crustal blocks in Early Devonian times.

Regarding *Pinnoputamen*, close affinities between *P. occitanicum* and *P. yunnanensis* suggest the latter was derived directly from the former. Migration from southern France to Yunnan, southern China, both parts of the Gondwanan Realm during the Early and Middle Devonian, may have occurred along the northern margin of Gondwana. For the Landeyran species, which lived in stressful conditions of an unstable near-shore environment, bisexuality, by immediate availability of both gametes, would have certainly been an advantageous adaptation. However, possibly because bisexuality may lead to sterility, the bisexual *Pinnoputamen* evolved structures with separate sexes in circumstances where freshwater lakes and ponds developed on land.

It has often been suggested that Palaeozoic charophytes were marine as they are sometimes associated with marine fossils such as conodonts and brachiopods, for example in the Cerro Gordo shale beds of the Lime Creek Formation of Rockford Quarry, Iowa (Peck & Morales, 1966) and the Szepai Formation of Dale, Xiangzhou County, China (Wang *et al.*, 1980). However, it is obvious from the biology of extant Characeae that charophytes are thalleous plants attached by thin rhizoids to soft substrates. They can live only in shallow (0-20 m depth), relatively quiet, and well oxygenated fresh or brackish waters. Remains of vegetative parts of a *Sycidium* from Marjino, Ukraine (Karpinsky, 1906, figs 46–53), as well as the thin rhizoids of *Palaeonitella cranii* (Kidston *et* Lang) Pia from the Rhynie Chert of Scotland, are nearly identical to extant species. Assignment of *P. cranii* to the Charophyta has recently been confirmed by discovery of gyrogonites and antheridia associated with thalli and rhizoids (Kelman *et al.*, 2004). We argue that with similar vegetative organs, extant and Paleozoic forms must have lived under similar environmental conditions. Among Devonian charophyte localities, most are characterized by near-shore or coastal environments, such as Landeyran, where charophytes occur at the top of regressive sequences where supratidal deposition prevailed. Charophytes may be transported from inland environments into nearshore marine environment to become allochtonous components among normal marine biotas. Some occurrences are doubtless intra-cratonic, such as the record of *Sycidium* in the Mid-Devonian of Congo (Choubert, 1931) and the Downtonian *Trochiliscus podolicus* Croft of the Old Red Sandstone (Croft, 1952). Devonian charophyte habitats that may be classed as "marine" by their associated faunas were obtained from shallow carbonate platforms (Racki, 1982; Day, 1995) characterized by relatively low salinity (Racki, 1982; Kaümierczack, 1975). Similar extant low salinity (brackish) "marine" habitats of the Characeae in the Baltic Sea still provide conditions favourable to charophyte growth and reproduction (Schubert *et al.*, 2003).

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