

Palynology of the dinosaur-bearing Wealden facies in the natural pit of Bernissart (Belgium)

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Abstract

A palynological study of the dinosaur-bearing Wealden facies at a depth of 322 m in the "natural pit with Iguanodons" of Bernissart (Belgium) is presented. The palynomorphs of 16 clay and silt samples collected in 1878–1881 during the dinosaur excavations are of continental origin. The botanical affinities of the 85 palynological taxa are mainly ferns, gymnosperms and freshwater algae. Also encountered are pollen grains of angiospermous affinity (biorecord Superret-croton) whose germinal apparatus is questioned. The distinction between the biorecord Hauterivian-cactisule and *Cerebropollenites mesozoicus* is discussed. It is suggested that the vegetation was distributed around the unstable lacustrine environment of the Bernissart area, in relation to the formation of the natural pit and local dissolution of deep anhydrites. Ferns, Taxodiaceae, freshwater algae and angiosperms lived close to the lake though gymnosperms were thriving on neighbouring hills. The occurrence of early angiosperms at Bernissart documents their development in disturbed and unstable environments during the Barremian–Aptian.

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1. Introduction

The natural pit of Bernissart (Mons Basin, Belgium) is well-known because of its exceptional fossil content: at least 28 specimens of *Iguanodon bernissartensis* Bouleenger, 1881 (including the holotype), one specimen of *Iguanodon atherfieldensis* (Hooley, 1925) Norman, 1980, numerous fishes, turtles, crocodiles, amphibians, insects and fragments of plants were extracted between 1878 and

1881 from a coal mine at depths of 322 and 356 m (see Martin and Bultynck, 1990 for a complete reference list). The fossil content has been the subject of a considerable number of scientific investigations (see Norman, 1987) and continues to be a source of reference material for palaeontological studies (e.g. Taquet, 1975; Norman, 1986, 1996). During the past 30 years, the first descriptions of some taxa discovered in the natural pit have been revised (e.g. Buffetaut, 1975; Norman, 1980; Taverne, 1982; Bultynck, 1992; Taverne, 1999) and circumstances surrounding the discovery of the dinosaur discussed (Norman, 1987). However, a detailed palynological

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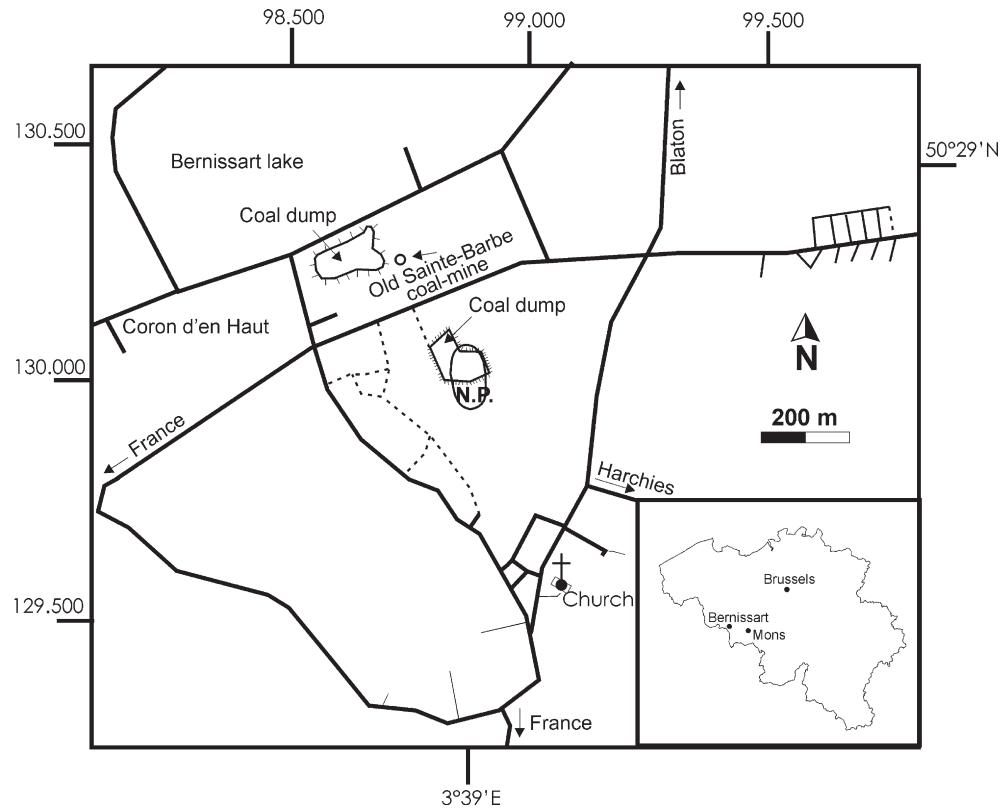


Fig. 1. Location of the N.P. = natural pit with Iguanodons of Bernissart (from Delmer and Van Wichelen, 1980, modified). At the top and the left sides of the map = Belgian Lambert coordinates (km); at the bottom and the right sides of the map = international coordinates (reference: Greenwich meridian).

analysis of the dinosaur-bearing Wealden facies of this exceptional site has not been carried out hitherto. The palynology of the Wealden facies of Belgium and northern France (other than at Bernissart) was covered in the pioneering work of Delcourt and Sprumont (1955, 1956,

1959a,b) and revised by Delcourt et al. (1963). However, according to Batten (1996), “little has been published on Belgian and French Purbeck–Wealden strata. Work by Delcourt and Sprumont (1955, 1959a,b) was pioneering but taxonomically inadequate”. We here propose the first

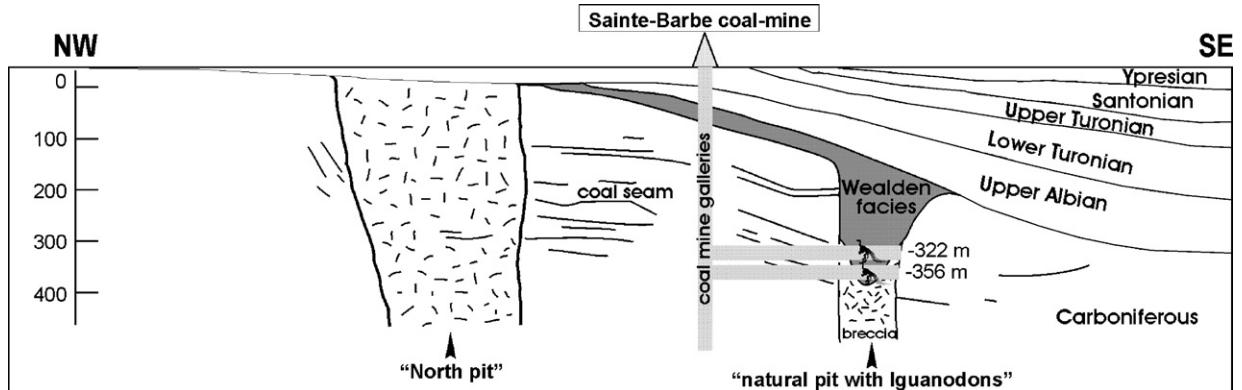


Fig. 2. Schematic NW–SE section of the northern border of the Mons Basin near the natural pit with Iguanodons of Bernissart (Delmer, 1989, modified). The natural pit, formed in the detritic carboniferous coal-bearing sediments, is filled with the Wealden facies sediments and overlain by Upper Albian to Ypresian deposits. The Iguanodons were found in the mine galleries at 322 and 356 m deep.

detailed palynological study of the Wealden facies from the level at a depth of 322 m in the natural pit of Bernissart, where the majority of the dinosaurs have been found.

2. Geological setting

The natural pit of Bernissart is located in the Mons Basin (Belgium, Fig. 1), which can be regarded as the northeastern part of the Paris Basin (Marlière, 1970). The sedimentary succession of the Mons Basin begins with the Wealden facies and extends up to Middle–Upper Albian, Upper Cretaceous and Cenozoic deposits (Marlière, 1970). The Wealden facies of the natural pit of Bernissart are attributed to the Sainte-Barbe Clays Formation (Robaszynski et al., 2001).

In 1878, at a depth of 322 m in one of the galleries of the Sainte-Barbe coal mine of Bernissart, miners suddenly found themselves digging through fossil bones instead of coal. Several complete specimens of dinosaurs were discovered in at least four separate levels of a natural pit (Fig. 2; Norman, 1987). Other complete skeletons of dinosaurs were later found at a depth of 356 m. The “Iguanodons of Bernissart” were among the first complete skeletons of dinosaurs to be found anywhere. Other bone fragments were recently discovered in the borehole drilled through the Wealden facies of the “natural pit” (Ricqlès de and Yans, 2003; Yans et al., 2005).

3. Methods

For the purpose of palynological analysis, we processed 16 samples of silts and clays collected from the same level as the dinosaur excavations during 1878–1881 at a depth of 322 m in the natural pit of Bernissart. According to observations made at the time (notes enclosed with the samples), the samples were collected “à gauche” and stored in the collections of the Royal Belgian Institute of Natural Sciences (Brussels). Preparations for palynological studies are carried out by mechanical and chemical methods. Each sediment sample is tested for the presence of carbonate by the addition of a few drops of dilute hydrochloric acid, 20 g is then crushed in a mortar. 70% hydrofluoric acid is added for 24 h. The insoluble fluorides are eliminated with boiling 10% hydrochloric acid, the residue is then washed three times with water. The organic residue is poured into a tube with 10% nitric acid for oxidation, heated in a double boiler for 1–2 min, then washed and centrifuged. The organic residue is filtered through a 100 µm mesh sieve in order to remove large debris. The filtrate is sieved through a 5 µm micro-mesh nylon sieve, then the 5–100 µm fraction is washed

with water, and concentrated by centrifuging. The final residue is strewn on a cover-slip by means of cellosolve (hydroxyethyl cellulose), dried and mounted upside down with Canada balsam on a microscope slide. The observations and determinations noted herein are based on light microscope examination, mainly using an interferential–differential contrast objective (after Nomarski). The position of each illustrated palynomorph (Figs. 3 and 4) on its slide is given after the “England Finder”.

To illustrate the morphology of some pollen grains, a drop of water containing palynomorphs is placed on a square cover-slip. After evaporation, the cover-slip is mounted on a standard stub, sputter coated with platinum and observed with a JEOL (type 840 A) scanning electron microscope (SEM) operating at an accelerating voltage of 15 kV.

The morphographic classification of Potonié and Kremp (1954, 1955), modified by Potonié (1956, 1958, 1960, 1966, 1970a,b, 1975), Dybová and Jachowicz (1957), Butterworth and Williams (1958) and Dettmann (1963), is used herein. Also used is the nomenclature *sensu* Hughes and collaborators (see complete reference list in Hughes, 1994) for two discussed taxa. The preparations are housed in the Royal Belgian Institute of Natural Sciences at Brussels (Belgium).

4. Palynological content

The following taxa have been recognized:

Microspores, megaspores and pollen grains

Anteturma Proximegerminantes Potonié, 1970

Turma Triletes-Azonales (Reinsch, 1881) Potonié and Kremp, 1954

Subturma Azonotriletes (Luber, 1935) Dettmann, 1963

Infraturma Laevigati, Quasilaevigati (Bennie and Kidston, 1886) Potonié, 1956

Auritulinasporites deltaformis Burger, 1966

Biretisporites potoniaei (Delcourt and Sprumont, 1955) Delcourt et al., 1963

Cardioangulina crassiparietalis Döring, 1965

Concavisporites jurienensis Balme, 1957

Cyathidites australis Couper, 1953

Cyathidites minor Couper, 1953

Dictyophyllidites harrisii Couper, 1958

Matonisporites equinoxinus Couper, 1958

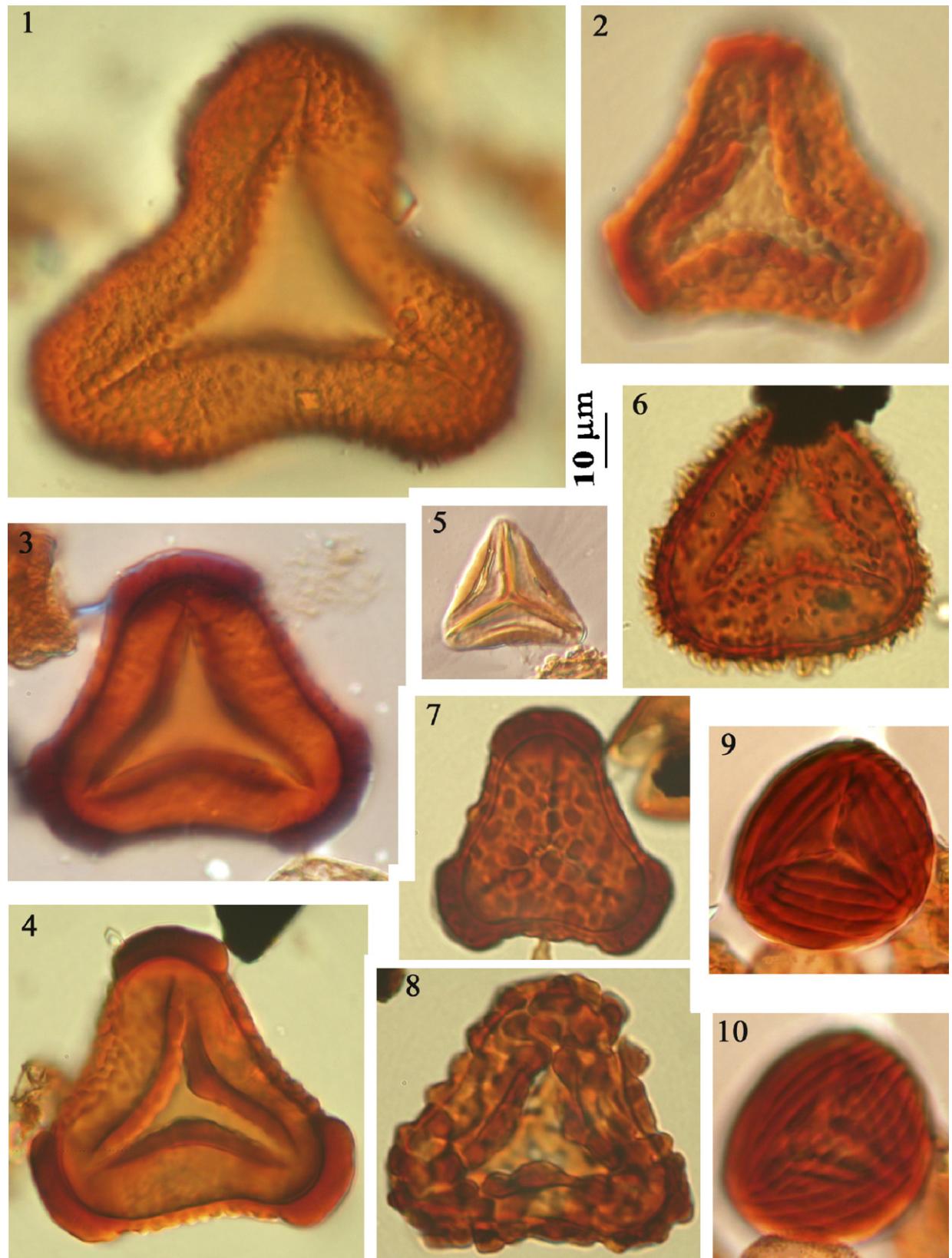
Punctatisporites major (Couper, 1958) Dörhöfer, 1977

Stereisporites antiquasporites (Wilson and Webster, 1946) Dettmann, 1963

Undulatisporites undulapolus Brenner, 1963

- Infraturma Apiculati (Bennie and Kidston, 1886)
Potonié, 1956
- Subinfraturma Baculati Dybová and Jachowicz, 1957
Baculatisporites comaumensis (Cookson, 1953)
Potonié, 1956
Echinatisporis varispinosus (Pocock, 1962) Srivastava, 1975
Neoraistrickia truncatus (Cookson, 1953) **Potonié, 1956**
Osmundacidites wellmanii Couper, 1953
Pilosporites ericus Delcourt and Sprumont, 1955
Pilosporites trichopapillosum (Thiergart, 1949)
Delcourt and Sprumont, 1955 (Fig. 3, 6)
Pilosporites verus Delcourt and Sprumont, 1955
 Subinfraturma Granulati, Scabri Dybová and Jachowicz, 1957
Concavissimisporites punctatus (Delcourt and Sprumont, 1955) Brenner, 1963
Concavissimisporites variverrucatus (Couper, 1958) Brenner, 1963
Concavissimisporites verrucosus (Delcourt and Sprumont, 1955) Delcourt et al., 1963 (Fig. 3, 1)
Impardecispora apiverrucata (Couper, 1958) Venkatachala, Kar and Raza, 1969
 Subinfraturma Verrucati Dybová and Jachowicz, 1957
Converrucosporites platyverrucosus Brenner, 1963
Gemmatriletes sp.
Rubinella sp. (Fig. 3, 8)
 Infraturma Murornati **Potonié and Kremp, 1954**
Cicaticosisporites brevilaesuratus (Couper, 1958) Kemp, 1970 (Fig. 3, 9 and 10)
Cicaticosisporites hallei Delcourt and Sprumont, 1955
Cicaticosisporites hughesi Dettmann, 1963
Cicaticosisporites mohrioides Delcourt and Sprumont, 1955
Costatoperforosporites foveolatus Deák, 1962
Foveotriletes subtriangularis (Brenner, 1963) Paden Philips and Felix, 1970
Klukisporites foveolatus Pocock, 1964
Stoverisporites lunaris (Cookson and Dettmann, 1958) Burger in Norwich and Burger, 1976
Retitriletes austroclavatidites (Cookson, 1953) Döring, Krutzsch, Mai and Schulz in Krutzsch, 1963
- Staplinisporites caminus* (Balme, 1957) Pocock, 1962
Tripartina sp.
 Subturma Lagenotriletes **Potonié and Kremp, 1954**
 Infraturma Trifoliati, Barbati Potonié, 1970
Dijkstraisporites helios (Dijkstra, 1951) **Potonié, 1956**
Membranisporites trifoliaceus Delcourt and Sprumont, 1955
 Turma Vestitriletes Potonié, 1970
 Suprasubturma Perinotrilites (Erdman, 1947) Dettmann, 1963
Densoisporites triradiata Delcourt and Sprumont, 1955
Densoisporites velatus (Weyland and Krieger, 1953) Krasnova, 1961
 Turma Triletes-Zonales (Bennie and Kidston, 1886)
Potonié, 1956
 Subturma Auritotriletes **Potonié and Kremp, 1954**
 Infraturma Auriculati (Schopf, 1938) Dettmann, 1963
Matonisporites crassiangulatus (Balme, 1957) Dettmann, 1963
Plicatella trichacantha macrorhyza Maljatkina, 1949
Plicatella parviangulata (Döring, 1966) Dörhöfer, 1977
Rouseisporites granospeciosus (Delcourt and Sprumont, 1955) Delcourt et al., 1963
Triporoletes reticulatus (Pocock, 1962) Playford, 1971
Trilobosporites bernissartensis (Delcourt and Sprumont, 1955) **Potonié, 1956**
Trilobosporites crassiangularis Döring, 1965
Trilobosporites sp. (Fig. 3, 2, 4, 7)
Trilobosporites hannonicus (Delcourt and Sprumont, 1955) **Potonié, 1956**
 Infraturma Appendiciferi **Potonié, 1956**
Appendicisporites potomacensis Brenner, 1963
 Infraturma Tricrassati Dettmann, 1963
Coronatispora valdensis (Couper, 1958) Dettmann, 1963
Sestrosporites pseudoalveolatus (Couper, 1958) Dettmann, 1963
 Subturma Zonotriletes Waltz, 1935
 Infraturma Cingulati (Potonié and Klaus, 1954) Dettmann, 1963

Fig. 3. (1) *Concavissimisporites verrucosus* (Delcourt and Sprumont, 1955) Delcourt et al., 1963; sample 7, slide 4 (L59₄). (2–4 and 7) *Trilobosporites* spp., illustrations showing the variability of the sculpture. (2) Sample 12, slide 2 (R37₂); (3) sample 12, slide 2 (T35/4); (4) sample 7, slide 5 (G60₁); (7) sample 7, slide 5 (K54). (5) *Gleicheniidites senonicus* (Ross, 1949) Dettmann, 1963; sample 12, slide 5 (U40₂). (6) *Pilosporites trichopapillosum* (Thiergart, 1949) Delcourt and Sprumont, 1955; sample 7, slide 5 (P51). (8) *Rubinella* sp.; sample 7, slide 5 (F51). (9, 10) *Cicaticosisporites brevilaesuratus* (Couper, 1958) Kemp, 1970; sample 7, slide 4 (O50₁).



- Subinfraturma Latingulati Potonié, 1970
Gleicheniidites feronensis Delcourt and Sprumont, 1959
Gleicheniidites senonicus (Ross, 1949) Dettmann, 1963 (Fig. 3, 5)
Infraturma Zonati Potonié and Kremp, 1954
Subinfraturma Euzonati, Coronati Potonié, 1970
Aequitriradites dubius Delcourt and Sprumont, 1955 (Fig. 4, 1 and 2)
Minerisporites marginatus (Dijkstra, 1951) Potonié, 1956
Turma Monoletes Ibrahim, 1933
Suprasubturma Acavatomonoletes Dettmann, 1963
Subturma Azonomonoletes Luber, 1935
Infraturma Laevigatomoleti Dybová and Jachowicz, 1957
Laevigatosporites ovatus Wilson and Webster, 1946
Infraturma Ornati Potonié, 1956
Punctatosporites scabratus (Couper, 1958) Singh, 1971
Anteturma Variegerminantes Potonié, 1970
Turma Saccites Erdtman, 1947
Subturma Monosaccites (Chitaley, 1951) Potonié and Kremp, 1954
Infraturma Saccizonati Bharadwaj, 1957
Applanopsis dampieri (Balme, 1957) Döring, 1961
Applanopsis trilobatus (Balme, 1957) Döring, 1961
Subturma Disaccites Cookson, 1947
Abietinaepollenites microalatus (Potonié, 1931) Potonié, 1951
Alisporites bilaterialis Rouse, 1959
Cedripites cretaceus Pocock, 1962
Parvisaccites radiatus Couper, 1958
Podocarpidites ellipticus Cookson, 1947
Vitreisporites pallidus (Reissinger, 1938) Nilsson, 1958 (Fig. 4, 8)
Turma Aletes et Kryptoperlates Potonié, 1966
Subturma Azonoletes (Luber, 1935) Potonié and Kremp, 1954
Infraturma Psilonapiti Erdtman, 1947
Taxodiaceaepollenites hiatus (Potonié, 1931) ex Potonié, 1958
Infraturma Granulonapiti Cookson, 1947
Araucariacites australis (Cookson, 1947) Couper, 1953
Spheripollenites sp.
Infraturma Circumpollini (Pflug, 1953) Klaus, 1960
Classopollis sp.
Turma Plicates (Naumova, 1939) Potonié, 1960
Subturma Costates Potonié, 1970
Infraturma Costati Potonié, 1970
Ephedripites montanaensis Brenner, 1968 (Fig. 4, 6)
Ephedripites zaklinskaiae Azéma and Boltenhagen, 1974
Subturma Monocolpates (Monosulcites) et Zonocolpates Potonié, 1970
Infraturma Quasilaevigati et Microsculptati Potonié, 1970
Cycadopites carpentieri (Delcourt and Sprumont, 1955) Singh, 1971
Cycadopites minimus (Cookson, 1947) Pocock, 1970
Cycadopites nitidus (Balme, 1957) De Jersey, 1964
Infraturma Sculptati Potonié, 1970
Hauterivian-cactisule (in Hughes and McDougall, 1987) (Fig. 4, 3, 4 and 5, and 5, 1 to 6)
Superret-croton (in Hughes et al., 1979) (Fig. 4, 9 and 10, and 5, 7 to 12)
Subturma Tricolpates, Triptyches Potonié, 1970
Infraturma Heterotricolpati, Praecolpati Potonié, 1970
Eucommiidites minor Groot and Penny, 1960
Eucommiidites troedssonii (Erdtman, 1948) Potonié, 1958 (Fig. 4, 7)
Eucommiidites sp.
Turma Poroses (Naumova, 1939) Potonié, 1960
Subturma Monoporines Naumova, 1939
Perinopollenites elatoides Couper, 1958
“Algae”
Botryococcus sp.
Ovoidites parvus (Cookson and Dettmann, 1959) Nakoman, 1966 (Fig. 4, 11)
Ovoidites spriggi (Cookson and Dettmann, 1959) Zippi, 1998 (Fig. 4, 13)
Schizosporis reticulatus (Cookson and Dettmann, 1959) Pierce, 1976 (Fig. 4, 12)

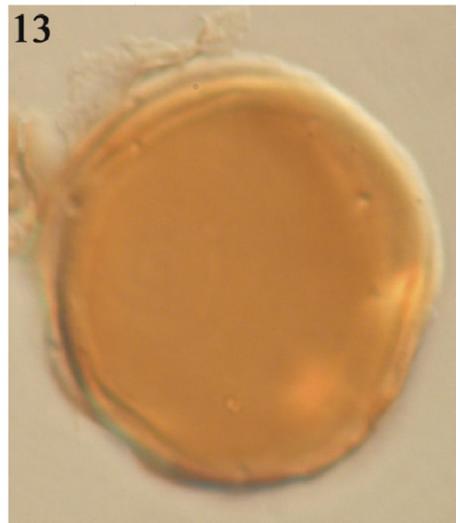
Fig. 4. (1) *Aequitriradites dubius* Delcourt and Sprumont, 1955. (1) Sample 12, slide 5 (L45₂); (2) sample 7, slide 4 (K53₄). (3–5) Biorecord Hauterivian-cactisule modified in Hughes, 1994. (3) Sample 9, slide 7, K57; (4) sample 7, slide 5, K58; (5) sample 7, slide 4 (P40₄). (6) *Ephedripites montanaensis* Brenner, 1968; sample 7, slide 5 (F50₁). (7) *Eucommiidites troedssonii* (Erdtman, 1948) Potonié, 1958; sample 9, slide 2 (D55₂). (8) *Vitreisporites pallidus* (Reissinger, 1938) Nilsson, 1958; sample 9, slide 6 (J52₃). (9, 10) Biorecord Superret-croton, modified in Hughes, 1994. (9) Sample 7, slide 3 (R47₃); (10) sample 7, slide 2 (Q49). (11) *Ovoidites parvus* (Cookson and Dettmann, 1959) Nakoman, 1966; sample 9, slide 7 (J49₄). (12) *Schizosporis reticulatus* (Cookson and Dettmann, 1959) Pierce, 1976; sample 9, slide 2 (E61₄). (13) *Ovoidites spriggi* (Cookson and Dettmann, 1959) Zippi, 1998; sample 9, slide 1 (H50₄). 15 µm scale bar is only for 8–10.



15 µm



13



5. Discussion

Several previous studies have dealt with the palynology of the Wealden facies from the northern part of Europe (Delcourt and Sprumont, 1955; Hughes, 1955; Couper, 1958; Lantz, 1958; Von der Brelie, 1964; Döring, 1964, 1965, 1966; Burger, 1966; Hughes and Moody-Stuart, 1967; Norris, 1969; Kemp, 1970; Herngreen, 1971; Batten, 1973; Amerom et al., 1976; Dörhöfer, 1977; Hughes and McDougall, 1990). The palynological association of Bernissart is typically “Wealden” in aspect, with many of the palynomorphs identified having been reported previously by Delcourt and Sprumont (1955), Delcourt et al. (1963) and others. We note that the specimen regarded as *incertae sedis* by Delcourt and Sprumont (1955, pl. IV, Fig. 9a) may be an angiosperm: these authors suggest that the figured palynomorph could be a dinocyst, but it rather looks like a columellate-tectate pollen grain. The two taxa Hauterivian-*cactisulc* and Superret-*croton* require further explanation.

5.1. Biorecord Hauterivian-*cactisulc*

The biorecord Hauterivian-*cactisulc* was defined by Hughes and McDougall, 1994 (Figs. 4, 3 to 5, and 5, 1 to 6). This taxon is very distinctive in the “stratotypic” Wealden facies and also in the Bernissart samples, particularly with regards to its small size and typical morphology (thick uneven warty tectum with micro-echinate sculpture). It may be related to a rather polymorphous whole, whose members distribute themselves among several palynological assemblages from Laurasia, which deserve further explanation. According to the more conventional morphological system, this whole matches with the genera *Cerebropollenites* Nilsson, 1958, and *Tsugaepollenites* (Potonié and Venitz, 1934) ex Potonié, 1958, whose botanical affinities resemble the recent *Tsuga* pollen according to Srivastava (1987, about *Cerebropollenites* sp. A and B), or the recent *Sciadopitys* pollen as established by Thiergart [1936, as *Pollenites serratus* (in Raatz, 1937), after *Sciadopitys-pollenites serratus* (Potonié and Venitz, 1934, sic) Raatz, 1937] and Rouse (1959, as Designate V6 cf. *Sciadopitys*). Hughes and McDougall

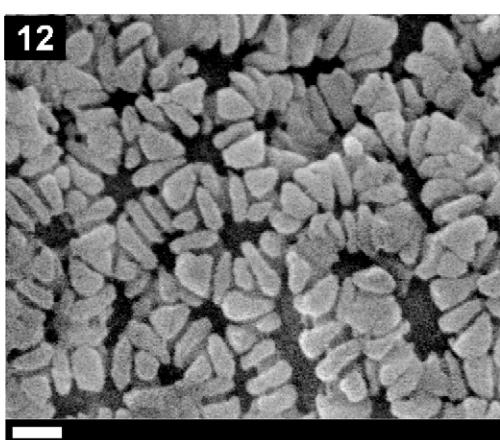
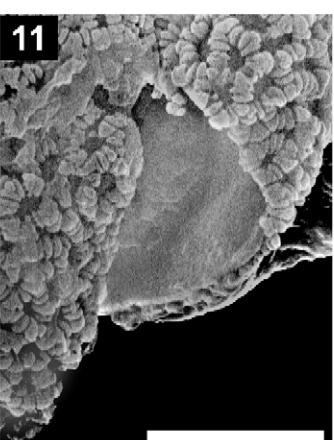
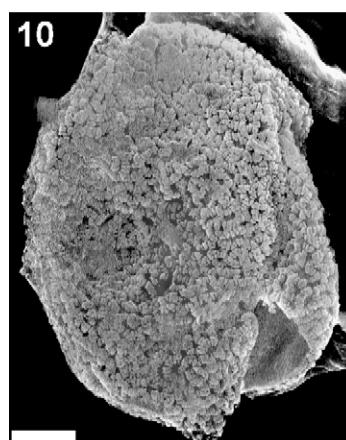
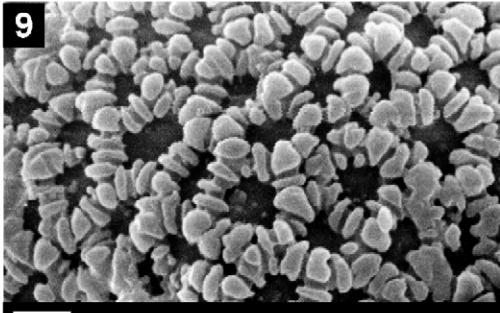
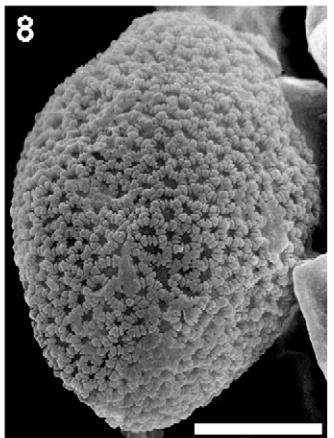
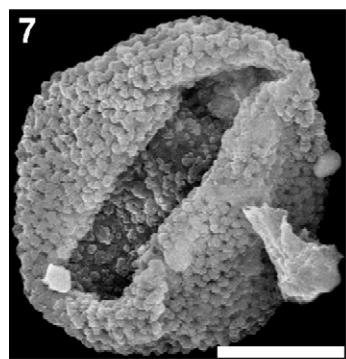
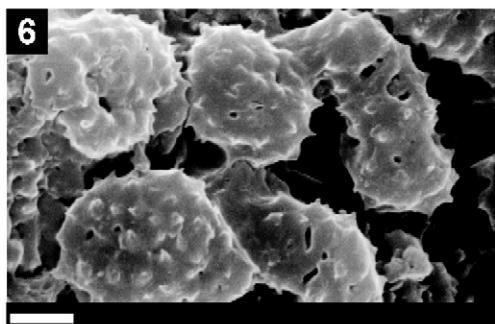
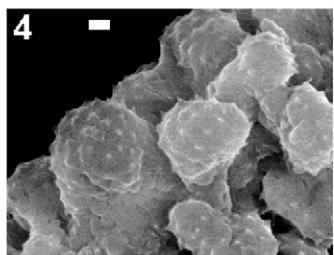
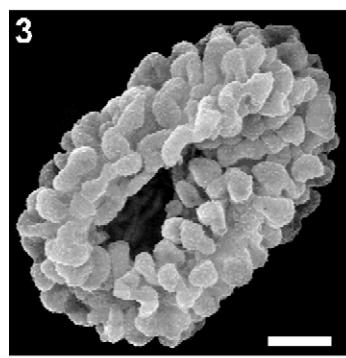
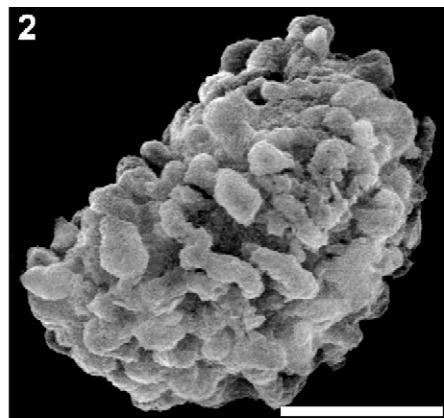
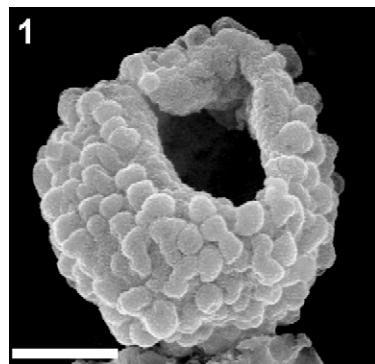
consider the botanical affinity of this biorecord to be enigmatic (1987, p. 271: “may represent irrelevant gymnosperms or something lower”), these authors suggest the possibility that it may be a forerunner of the Angiosperms (1994, p. 180: “possible antecedent of MCT pollen”), but highlight the analogy between its sculpture and that of the recent *Sciadopitys* pollen. Comparison with descriptions and figures by Erdtman (1964, Fig. 65), Callen (1976, p. 24), Van Campo-Duplan (1951, table III, Fig. 1, p. 9) and Van Campo (1978, pl. 29, Fig. 4-6) confirm the botanical affinity of the genus *Cerebropollenites* with recent *Sciadopitys* pollen.

5.2. Biorecord Superret-*croton*

The biorecord Superret-*croton* (Figs. 4, 9 and 10, and 5, 7 to 12) was defined by Hughes et al. (1979). This taxon clearly exhibits an angiospermous affinity. In the “stratotypic” Wealden facies of the Weald and Wessex Sub-basins, dated by the occurrence of interstratified levels of ammonites and dinoflagellate cysts (Harding, 1986, 1990), the stratigraphic distribution of the biorecord Superret-*croton* ranges from the middle Barremian to the earliest Aptian (Hughes, 1994). Later Yans et al. (2004) therefore suggested a middle Barremian to earliest Aptian age for the studied sediments. In the description of the species *Stellatopollis hughesii*, from the Upper Barremian (?) of Egypt, Penny (1986) regarded it to be equivalent to the biorecord Superret-*croton*. The crotonoid sculpture exhibited by this taxon resembles that seen in the Liliaceae, the Euphorbiaceae or the Buxaceae.

A particular point must be highlighted: despite the observation of numerous palynomorphs that have been attributed to the biorecord Superret-*croton*, a definite sulcus has not been identified; some longitudinal folding or splitting appearance may be present, but it is neither constant nor well defined. The published illustrations of both this biorecord and *Stellatopollis hughesii* do not clearly show such a germinal opening; however, it is mentioned in the definition of the biorecord and in the diagnosis of the species. Therefore, these equivalent taxa could be inaperturate; further research may resolve this question.

Fig. 5. Sample BER 7. (1–6) Biorecord Hauterivian-*cactisulc*. Note the variability of the germinal opening (from almost circular to elongated). (4) Detail of the sculpture of the pollen grain illustrated in 3. (6) Detail of the sculpture of the pollen grain illustrated in 5. (7–12) Biorecord Superret-*croton*. (7) This pollen grain shows a deformation which simulates a sulcus (longitudinal hollow in which sculptural elements are visible); (8) non-deformed pollen grain; (9) detail of the sculpture of the pollen grain illustrated in 8; (10) this pollen grain is teared; (11) same pollen grain as illustrated in 10, showing through the tear the smooth nexine inner face (endexine *sensu stricto*?); (12) detail of the sculpture of the pollen grain illustrated in 10. Scale bar=10 µm, except 4, 6, 9 and 12=1 µm. Location of the illustrated grains: grains of 5 and 8: slide no. 1; grains of 1, 2 and 7: slide no. 2; grains of 3 and 10: slide no. 3.



6. Environment of deposition and vegetation

The occurrence of dinoflagellate cysts, foraminifer linings and marine “algae” in the Wealden facies of the eastern part of the Mons Basin indicates that the succession was deposited under marine influence (Yans et al., 2002). However, the palynomorphs of the studied level of Bernissart (located in the western part of the Mons Basin) are of continental origin only.

Deep boreholes drilled in the Mons Basin demonstrated partial and local dissolution of deeply buried anhydrites immediately below the natural pits (Delmer et al., 1982; Delmer, 1989; Dupuis and Vandycke, 1989; Rouchy et al., 1993). As observed in other areas, the result of this partial dissolution of deeply buried anhydrites is local and repetitive collapses in the upper rocks create space resulting in the formation of geomorphological depressions at the surface (Stanton, 1966; Gutiérrez, 1996; Warren, 1999). One can assume that the fauna and flora of Bernissart were trapped in a lake and quickly covered by sediments with a relatively high rate of deposition. This assumption is supported by (1) the continental origin of the palynomorphs, (2) the freshwater lacustrine fauna trapped in the pit (crocodiles, salamander, freshwater fishes, turtles), (3) the very good preservational state of the fossils, (4) the laminated structure of the sediments at this level, typical of lacustrine environment of deposition (Spagna et al., 2004; Fig. 6), and (5) the dimension of the sedimentation area of the natural pit of Bernissart (110 m × 70 m, Delmer and Van Wichelen, 1980).

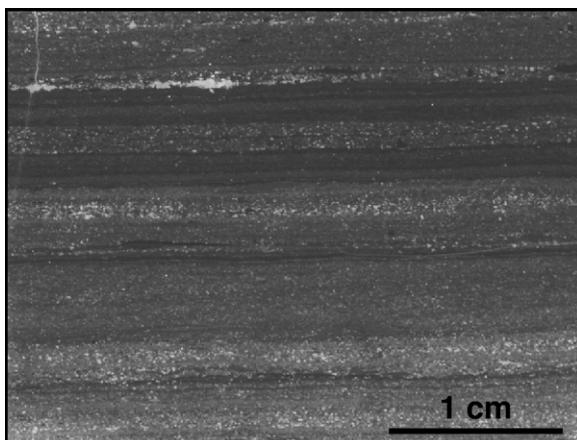


Fig. 6. Microphotograph exhibiting the laminated structure of the Wealden facies of Bernissart (322 m of depth) under light transmission.

The plants were growing in and around the episodic lake of Bernissart (Fig. 7). Some of the palynological taxa are probably the products of plant species previously described (Seward, 1900; Harris, 1953; Alvin, 1953, 1957, 1960, 1968, 1971), mainly related to “algae”, ferns and gymnosperms. The palynological assemblage is very well preserved, suggesting that the mother-plants grew close to the place where the palynomorphs were buried. Most of the taxa identified are the products of ferns (e.g. *Cicatricosporites*, *Concavissimisporites*, *Gleicheniidites*, *Pilosporites* and *Trilobosporites*). Some of the smooth-walled trilete spores are related to Cyatheaceae or Dicksoniaceae; *Dictyophyllidites harrisii* is similar to *in situ* spores of Matoniaceae (Harris, 1961). The palynomorphs related to ferns are frequently associated with woody fragments and cuticle scraps. The hygrophilous flora (Taxodiaceae, ferns and lycophytes) was probably deposited more or less *in situ*, in a local lake created by the natural pit collapses (Fig. 7). The “algal” assemblage is characterized by common to abundant *Schizosporites* and *Ovoidites* (zygospores of Zygnemataceae) and by the green colonial “alga” *Botryococcus*. The latter usually lives in freshwater (lakes, swamps and blackwater ponds) of temperate and tropical regions, and is known to tolerate seasonally cold climates (Batten and Grenfell, 1996).

Pollen grains of gymnosperms include *Applanopsis* (Podocarpaceae), *Ephedripites* (Ephedrales), *Eucommiidites*, Hauterivian-cactisulc (Sciadopityaceae) and *Taxodiaceae pollenites hiatus* [Cupressaceae (Taxodiaceae)]; *Classopollis* (Cheirolepidaceae) pollen grains are very scarce. Although the conifers do produce high numbers of pollen grains (10 million in each *Pinus* cone according to Gaussen, in Abbayes et al., 1963), a relatively poor proportion is observed in the studied level. This suggests that conifers thrived on distant neighbouring hills and that a small proportion of their pollen grains were transported into the sedimentation area by rivers and wind. Numerous abietaceous cones have been reported from the Wealden facies of Belgium (Alvin, 1953, 1957, 1960): the occurrence of *Pityostrobus bernissartensis* Alvin, 1957 (= *Pityostrobus bommeri* Alvin, 1953), and *P. corneti* (Coemans, 1866) Alvin, 1953, related to *Pinus* and *Keeteleria* respectively, emphasizes the presence of Abietaceae at Bernissart, with a wide range of cones belonging to extinct and recent genera. “Taxodiaceae” twigs are present in the Wealden facies of Belgium (Harris, 1953). *Vitreisporites* indicates the presence of Caytoniaceae (Pteridosperms).

The pollen grains of the biorecord Superret-croton (*nomenclature sensu* Hughes, 1994) are the products

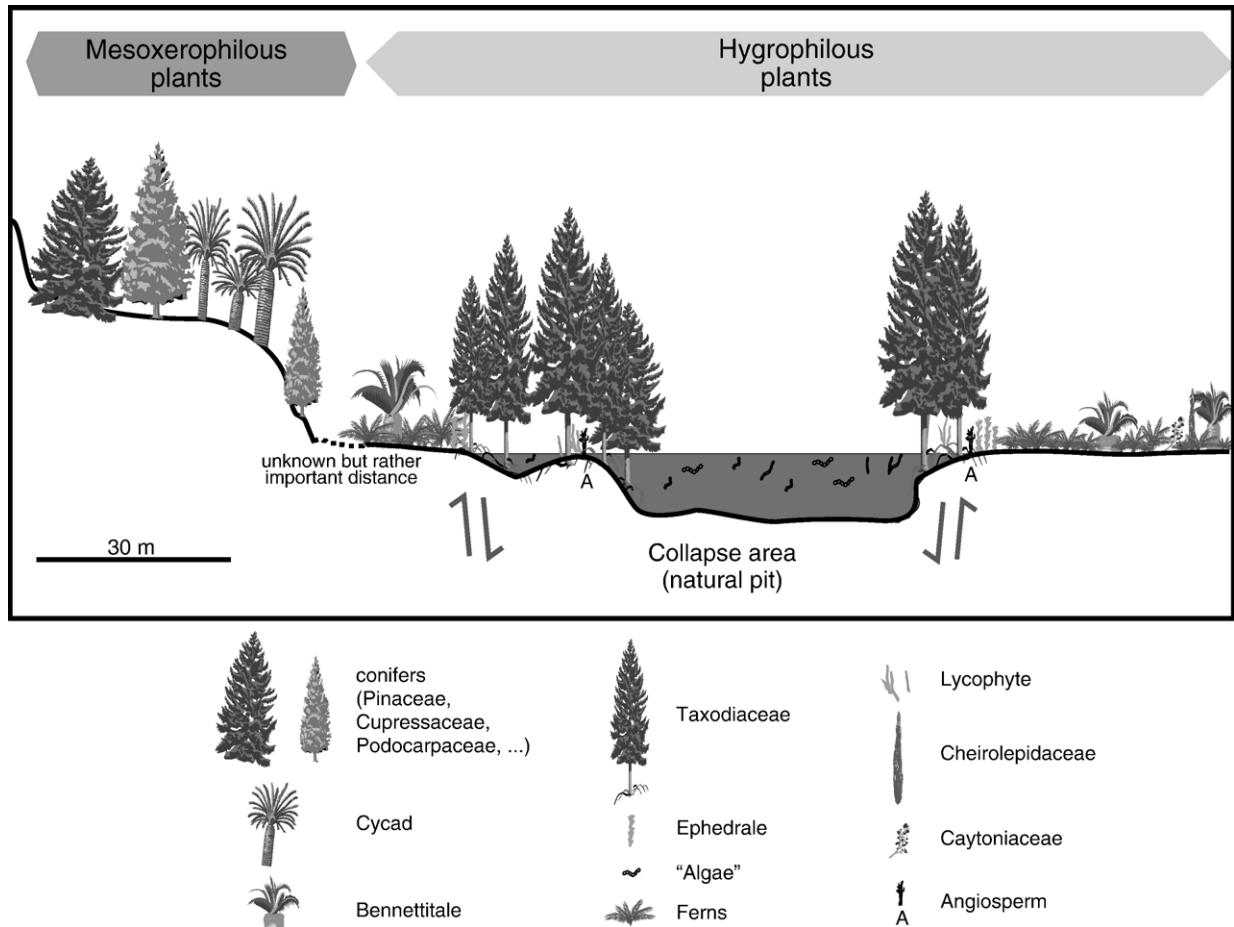


Fig. 7. Schematic representation of the flora near the natural pit of Bernissart, based on the palynological taxa discovered at 322 m of depth. Note that the lake and the distribution of the vegetation are associated with the space created by the formation of the natural pit due to deep, partial and local dissolution of anhydrites.

of angiosperms. The specimens of this taxon represent a very small proportion of the palynomorphs (less than 1%) in Bernissart. This proportion of angiosperms is consistent with those observed in other coeval palynological records in other sites (e.g. Portugal, Heimhofer et al., 2005). Wing and Boucher (1998) and Felid et al. (2004) demonstrate that the earliest angiosperms were of small stature, most probably herbaceous or woody plants, thriving predominantly in unstable or disturbed environments. The geomorphological depression (lake) at Bernissart was an unstable-disturbed sub-environment. Heimhofer et al. (2005) suggest that the ecological strategies of early angiosperms and their dominance in disturbed habitats might explain their rapid diversification in the late Barremian to Aptian. The presence of this flora at Bernissart in middle Barremian to earliest Aptian dated sediments, deposited in an original and very unstable sub-

environment, documents the ecology of early angiosperms.

7. Conclusions

The palynological content of the *Iguanodon*-bearing Wealden facies of Bernissart is reported for the first time here. The palynomorphs are of continental origin. This is consistent with the lacustrine environment suggested by (1) the fauna previously described in the natural pit, (2) the sedimentological data and (3) the dimensions of the depositional area. Ferns, freshwater algae and gymnosperms are the dominant floristic groups. The ferns and freshwater algae probably lived in and around the lake. Gymnosperms pollen grains were transported from neighbouring hills. The rare occurrence of pollen grains of the angiosperm biorecord Superret-croton sensu Hughes (1994) confirm the ecology of early angiosperms in

unstable or disturbed conditions, such as those of the lake of Bernissart; these pollen grains may be inaperturate.

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