Review of the dinoflagellate cyst *Stephanelytron* Sarjeant 1961 emend

BERNARD COURTINAT

University Claude-Bernard Lyon 1; UFR Sciences de la Terre; 43 Boulevard du 11 novembre 1918, 69 622 Villeurbanne Cedex; France

ABSTRACT – The stratigraphic distribution of the Late Callovian to Early Oxfordian dinoflagellate cyst *Stephanelytron* Sarjeant 1961 emend provides new evidence pertaining to its evolution. Middle and Upper Callovian times favoured the development of speciations to a short-ranging *Stephanelytron* community with corona(s) in ventral–posterior position (*Stephanelytron* brontes, *S. callovianum*, *S. ceto* and *S. tabulophorum*) from eurytopic species with antapical coronas (*S. caytonense*, *S. membranoidium*, *S. redellifense* and *S. scarburghense*). The former group of species (except *S. tabulophorum*) may represent an example of peripatric speciation from an unfavourable mutation. The reduced stratigraphic range gives the appearance of an endemic population. The genus *Lagenadinium* Piel, 1985 is a junior synonym of *Stephanelytron* Sarjeant, 1961. A new emendation of *Stephanelytron*, two new combinations (*S. callovianum* and *S. membranoidium*) and two new species (*S. brontes* and *S. ceto*) are proposed. *J. Micropalaeontology*, 18(2): 169–182, December 1999.

INTRODUCTION

During an investigation of Jurassic dinoflagellate cyst assemblages in the Tethyan marine realm, the Middle and Upper Jurassic transition was studied in southeastern France (Fig. 1). The Callovian–Oxfordian boundary (*Athleta–Lambertia*/Minax ammonite zones; *Minax* Zone in the Sub-Mediterranean province = *Mariæ* Zone in the Boreal Realm following the Groupe Français d'étude du Jurassique, 1997) shows high dinoflagellate cyst diversities (Table 1) in association with abundant palynomaceral-1 (dark brown woody fragments of Whitaker et al., 1992) and palynomaceral-4 (black, charcoal or oxidized woody tissue), but a low input of terrestrial palynomacerals.

Previous studies of the Jurassic dinoflagellate cysts in southeastern France include Sarjeant (1968), Gitmez & Sarjeant (1972), Wolfard & Van Erve (1981), Taugourdeau-Lantz & Lachkar (1984, 1985), Smelror & Leereveld (1989) and Fauconnier et al. (1996).

The Callovian–Oxfordian boundary described by Smelror & Leereveld (1989) in a section located at the Montagne de Crussol (Rhône Valley) is characterized by the *Compositosphaeridium polonicum–Sentusidinium pilosum* (Cp–Sp) association. This association is defined by the common occurrence of *Endoscribula* galeritum (Deflandre, 1938) Vozzhennikova, 1967, *Escharisphaeridia pocockii* (Sarjeant, 1968) Erkmen & Sarjeant, 1980, *Gonyaulacysta jurassica* (Deflandre, 1938) Norris & Sarjeant, 1965, *Rhychosphaeridium cladophora* (Deflandre, 1938) Below, 1981, *Rigaudella aemula* (Deflandre, 1938) Below, 1982, *Barbatycysta pilosa* (Ehrenberg, 1854) Courtinat 1989, *Sentusidinium rioultii* (Sarjeant, 1968) Sarjeant & Stover, 1978, emend Courtinat 1989, *Sarculosopheraidium ?vestitum* (Deflandre 1938) Davey et al., 1966 and *Wanaea* spp. By contrast, *Mendicodinium groenlandicum* (Pocock & Sarjeant, 1972) Davey 1979 and *Trichodinium scarburghensis* (Sarjeant, 1964) Williams et al., 1993 are rare.

The dinoflagellate cyst assemblages described here belong to the *Compositosphaeridium polonicum–Sentusidinium pilosum* association of Smelror & Leereveld (1989). However, significant differences in relative abundances are observed. For example, in the shales and muddy limestones collected from the Chenier and Rondette localities (Fig. 1), dinoflagellate cyst assemblages are composed of relatively rare *E. galeritum*, *G. jurassica*, *R. cladophora*, *R. aemula*, *S. rioultii*, *S. vestitum* and *Wanaea* spp. *M. groenlandicum* is abundant. Comparison of dinoflagellate cyst assemblages in the Tethyan and Boreal Realms requires more data before the latitudinal/environmental control of species (Smelror & Leereveld, 1989) can be fully appreciated.

Despite differences between the dinoflagellate cyst assemblages of Crussol, Chenier and Rondette, one element is common in Europe. It concerns the association of holocavate species of *Chlamydophorella* Cookson & Eisenack, 1958, *Dinogodinium* Cookson & Eisenack, 1958 and *Stephanelytron* Sarjeant 1961 emend herein. Following Smelror & Leereveld (1989) such an association appears indicative of deep marine conditions. In the Chenier and Rondette sections, as well as Savournon (Fig. 1), this association of holocavate species constitutes a consistent and significant assemblage, in association with specimens of *Lagenadinium callovianum* Piel, 1985.

The objectives of the present study are to review the genus *Stephanelytron* and to discuss the evolutionary pathway proposed by Piel (1985) for this group of species with corona(s). The genus *Lagenadinium* Piel, 1985 is considered a junior synonym of *Stephanelytron* Sarjeant, 1961 emend.

SYSTEMATIC BACKGROUND

The genus *Lagenadinium* Piel, 1985 contains the type species *L. callovianum* Piel, 1985 and questionably *L. membranoidium* (Vozzhennikova, 1967) Lentin & Vozzhennikova, 1990. According to Piel (1985) the genus *Lagenadinium* has a subspherical to ovoidal holocavate cyst. An autophragm and an ectophragm are separated by hollow, non-tabular processes. The most typical element is the presence of one or two coronas at or near the antapex and the archeopyle is apical.

The type species *L. callovianum* Piel, 1985 is a proximochorate, holocavate cyst. The autophragm and ectophragm are clearly separated by smooth, non-tabular, tubiform, hollow processes. A short apical mamelon-like horn is present on both autophragm and ectophragm. The archeopyle is apical and the operculum, probably a compound one, remains attached. The cyst typically has two coronas that are located either on paraplates in the postcingular series, or perhaps on the posterior intercalary and adjacent postcingular paraplate. The average
size of the coronas is one-quarter of the width of the cyst (Piel, 1985: 112). When seen in optical cross-section, the elevation of coronas is low, about half the diameter. *L. membranoidium* (Vozzhennikova, 1967) Lentin & Vozzhennikova, 1990, possesses the main characters of the genus *Lagenadinium* (holocavate, numerous hollow processes, one corona which is approximately coincident with the 2" paraplate and an apical archeopyle). Lentin & Vozzhennikova (1990) questionably included this species in *Lagenadinium* because of its tendency to exhibit an intratabular process distribution.

At the time he erected the genus, Piel (1985) proposed the transfer of *S. scarburghense* Sarjeant 1961 to *Lagenadinium*. This transfer was not accepted by Riding (1987) because *S. scarburghense* has a single, prominent antapical corona and lacks an antapical horn, one of the principal generic criteria of *Lagenadinium*, despite the non-tabular arrangement of the processes in the ectocoel. Riding (1987) uses the criterion of an apical horn (*antapical horn* is probably a typographical error; p. 263) and one corona to refute the transfer because the original diagnosis or description did not mention formally
Review of the dinoflagellate cyst *Stephanelytron* Sarjeant 1961 emend

### Table 1. List of dinoflagellate cysts present in the described Callovian/Oxfordian assemblages of southeastern France.

| Species | Chenier | Rondette | Savouron |
|---------|---------|----------|----------|
| *Adriatophoebidium caeruleum* (Deflandre 1938b) Williams and Donnie 1966 emend. Staniford and Sarjeant 1990 | ● | ● | ● |
| *Aidolfia actinica* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Ampelophoebidium calvulaceum* Eiten 1976 | ● | ● | ● |
| *Ampelophoebidium cf. helveticum* (Davey 1982b) Davey 1982b | ● | ● | ● |
| *Arctophoebidium* (Sarjeant 1961a) emend. Below 1990 | ● | ● | ● |
| *Atopophoebidium parvum* Thomas and Cook 1968 | ● | ● | ● |
| *Atopophoebidium acutum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Barbatophoebidium crassotinctum* (Eiten and Sarjeant 1980) Courtaud 1989 | ● | ● | ● |
| *Barbatophoebidium falciferum* (Eiten 1982b) Courtaud 1989 | ● | ● | ● |
| *Barbatophoebidium rectum* (Sarjeant 1961a) emend. Below 1990 | ● | ● | ● |
| *Ceratothoa calvulaceum* (Sarjeant 1961a) emend. Below 1990 | ● | ● | ● |
| *Ceratothoa cf. robusta* (Sarjeant 1961a) emend. Below 1990 | ● | ● | ● |
| *Ceratothoa cf. helveticum* (Sarjeant 1961a) emend. Below 1990 | ● | ● | ● |
| *Ceratothoa cf. robusta* (Sarjeant 1961a) emend. Below 1990 | ● | ● | ● |
| *Ceratothoa helvetica* (Sarjeant 1961a) emend. Below 1990 | ● | ● | ● |
| *Chlorophoebidium delicatulum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium gramineum* (Sarjeant 1961a) emend. Below 1990 | ● | ● | ● |
| *Chlorophysothyrium oblongum* (Eiten and Sarjeant 1980) Courtaud 1989 | ● | ● | ● |
| *Chlorophysothyrium rectum* (Eiten and Sarjeant 1980) Courtaud 1989 | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
| *Chlorophysothyrium rectum* (Cookson and Eiten 1960b) Davey 1982b | ● | ● | ● |
an apical horn (Sarjeant, 1961: 111).

It is true that on S. scarburghense the processes are non-tabular and so the paratabulation is vaguely expressed. When all the other species of Stephanelytron (S. caytonense Sarjeant, 1961, S. creating Duxbury, 1983, S. redcliffense Sarjeant 1961, S. tabulophorum Stover et al., 1977) have processes frequently arranged in parasutural rows, both alternatives have merit (the transfert of S. scarburghense to Lagenadinium or retention in Stephanelytron; Wheeler & Sarjeant, 1990: 314).

These considerations show the difficulties in distinguishing these two genera. The difficulties are based on the distribution of autophragmal processes, the interpretation of the number of corona(s) (one or two) and the presence or absence of an apical horn. Large number of specimens with corona(s) in southeastern France confirm the absence of objective criteria that would clearly separate Stephanelytron and Lagenadinium. Consequently, the two genera are considered synonymous, i.e. Stephanelytron is a senior synonym of Lagenadinium.

**Explanation of Plate 1**

All photomicrographs ×728. All specimens photographed in plain transmitted light. Slides with figured specimens are presently housed in the Earth Sciences Collection of Claude-Bernard University, Villeurbanne, France. fig. 1. ? Stephanelytron brontes n. sp. Chenier locality. Sample CHE 08. Minax Zone (Early Oxfordian; Jurassic). Specimen ref. 63-23-CHE08-33.7/96.5. England Finder V34. Total length 64 μm. Specimen photographed in equatorial view; note the rather short horn, a tear under the horn mimetic of an intercalary archeopyle and the reduced corona in ventro-posterior position (presumed on the paraplate). fig. 2. ?Stephanelytron brontes n. sp. Sarjeant locality. Sample SAV 06. Lamberti Zone (Late Callovian; Jurassic). Specimen ref. 63-09-SAV06-52.6/108. England Finder J54/3. Total length 74 μm. Specimen photographed in equatorial view; note the long horn and the reduced corona in ventro-posterior position (presumed on 2nd paraplate). fig. 3. ?Stephanelytron brontes n. sp. Holotype. Savournon locality. Sample SAV 07. Lamberti Zone (Late Callovian; Jurassic). Specimen ref. 63-10-SAV07-48.9/106.1. England Finder L50/3. Total length 75 μm. Specimen photographed in equatorial view; note the rather long horn, a tear under the horn possibly suggesting an intercalary archeopyle and the reduced corona in ventro-posterior position (presumed on 2nd paraplate). fig. 4. ?Stephanelytron brontes n. sp. Chenier locality. Sample CHE 08. Lamberti Zone (Late Callovian; Jurassic). Specimen ref. 63-21-CHE08-45/99.1. England Finder S46/3. Total length 78 μm. Specimen photographed in lateral view; note the long horn with alignment of processes and a large tear under the horn which may be indicative of an apical archeopyle. fig. 5. Stephanelytron callovianum (Piel, 1985) comb. nov. Savournon locality. Sample SAV 15. Minax Zone (Early Oxfordian; Jurassic). Specimen ref. 63-06-SAV15-59/109.7. England Finder G60/4. Total length 30 μm. Specimen photographed in right lateral view, with the operculum still in place; note the two coronas in ventro-posterior position (presumed on the ps paraplate) and the nonparatabular processes and ill-defined rows of processes. fig. 6. Stephanelytron callovianum (Piel, 1985) comb. nov. Savournon locality. Sample SAV 10. Lamberti Zone (Late Callovian; Jurassic). Specimen ref. 63-13-SAV10-35.4/104.6. England Finder N36/1. Total length 42 μm. Specimen photographed in left lateral view, with the operculum still in place; note the two coronas in ventro-posterior position (presumed on the ps paraplate) and the fine nonparatabular processes. fig. 7. Stephanelytron callovianum (Piel, 1985) comb. nov. Savournon locality. Sample SAV 15. Minax Zone (Early Oxfordian; Jurassic). Specimen ref. 63-07-SAV15-52.8/108.4. England Finder J54/1. Total length 41 μm. Specimen photographed in left lateral view, with the operculum still in place; note the two coronas in antapical position and parasutural processes. fig. 8. Stephanelytron callovianum (Piel, 1985) comb. nov. Savournon locality. Sample SAV 01. Lamberti Zone (Late Callovian; Jurassic). Specimen ref. 63-03-SAV01-44.3/107.6. England Finder N45/1. Total length 44 μm. Specimen photographed in equatorial view, with the operculum still in place; note the coarse nonparatabular processes, one apical process and rest of ectophragm in apical area. fig. 9. Chlamydophorella ectostubulata Smelror 1989. Savournon locality. Sample SAV 11. Lamberti Zone (Late Callovian; Jurassic). Specimen ref. 63-16-SAV11-39.6/108. England Finder J67/1. Total length 45 μm. Specimen photographed in equatorial view; note the apical archeopyle and the delicate ectophragm supported by nonparatabular processes. fig. 10. Stephanelytron ceto n. sp. Savournon locality. Sample SAV 12. Lamberti Zone (Late Callovian; Jurassic). Specimen ref. 63-17-SAV12-63/104.4. England Finder N64/2. Total length 39 μm. Specimen photographed in left lateral view, with the reduced coronas in antapical and ventro-posterior positions (presumed on the ps paraplate) and a dense cover of intratabular and penitabular processes. fig. 11. Stephanelytron ceto n. sp. Holotype. Savournon locality. Sample SAV 17. Lamberti Zone (Late Callovian; Jurassic). Specimen ref. 63-18-SAV17-60.3/104. England Finder N61/4. Total length 34 μm. Specimen photographed in lateral view; note the apical archeopyle, the intratabular and penitabular processes, the well-defined paracingulum and the reduced corona in ventro-posterior position (presumed on the ps paraplate). fig. 12. Stephanelytron ceto n. sp. Savournon locality. Sample SAV 21. Minax Zone (Early Oxfordian; Jurassic). Specimen ref. 63-19-SAV21-33.7/102.4. England Finder P34. Total length 47 μm. Specimen photographed in equatorial view; note the apical archeopyle and the attached operculum, the reduced corona in ventro-posterior position (presumed on the ps paraplate). fig. 13. Chlamydophorella ovula Wheeler & Sarjeant 1980. Savournon locality. Sample SAV 11. Lamberti Zone (Late Callovian; Jurassic). Specimen ref. 63-15-SAV11-56.1/107. England Finder K57/4. Equatorial diameter 37 μm. Specimen photographed left lateral view; note the apical archeopyle, the delicate ectophragm supported by coarse nonparatabular processes. fig. 14. Stephanelytron membranoidium (Vozzhennikova, 1967) emend. Lentin & Vozzhennikova, 1990 comb. nov. Savournon locality. Sample SAV 02. Lamberti Zone (Late Callovian; Jurassic). Specimen ref. 63-04-SAV02-37.9/96.8. England Finder V38/2. Total length 40 μm. Specimen photographed in left lateral view; note the apical archeopyle, the well-developed corona in antapical position and the intratabular processes. fig. 15. Stephanelytron scarburghense Sarjeant, 1961 emend. Stover et al., 1977. Savournon locality. Sample SAV 15. Minax Zone (Early Oxfordian; Jurassic). Specimen ref. 63-07-SAV15-52.8/108.4. England Finder J54/1. Total length 36 μm. Specimen photographed in right lateral view; with the operculum still in place; note the two coronas in antapical and ventro-posterior positions and the nonparatabular processes. fig. 16. Stephanelytron scarburghense Sarjeant, 1961 emend. Stover et al., 1977. Savournon locality. Sample SAV 15. Minax Zone (Early Oxfordian; Jurassic). Specimen ref. 63-08-SAV15-62.8/104.2. England Finder O64/2. Total length 36 μm. Specimen photographed in left lateral view; note the operculum still in position, the two coronas in antapical and ventro-posterior positions and the nonparatabular processes. fig. 17. Chlamydophorella wallala Cookson & Eisenack 1960. Savournon locality. Sample SAV 10. Lamberti Zone (Late Callovian; Jurassic). Specimen ref. 63-14-SAV10-51.9/100.6. England Finder R53/1. Equatorial diameter 31 μm. Specimen photographed in plain transmitted light in apical view; note the form of processes similar to those of S. scarburghense figured on fig. 8. fig. 18. Stephanelytron redcliffense Sarjeant 1961 emend. Stover et al., 1977. Chenier locality. Sample CHE 05. Lamberti Zone (Late Callovian; Jurassic). Specimen ref. 63-24-CHE05-38.9/112.5. England Finder D40/3. Total length 47 μm. Specimen photographed in equatorial view; note the apical archeopyle, the corona in antapical position and parasutural processes. fig. 19. Stephanelytron scarburghense Sarjeant, 1961 emend. Stover et al., 1977. Savournon locality. Sample SAV 45. Minax Zone (Early Oxfordian; Jurassic). Specimen ref. 63-20-SAV45-40.2/100. England Finder R41/3. Coronas of a damaged specimen; note the processes connected by a membrane shaping a corona. fig. 20. Stephanelytron tabulophorum Stover et al., 1977. Savournon locality. Sample SAV 26. Minax Zone (Early Oxfordian; Jurassic). Specimen ref. 63-05-SAV26-54.8/112. England Finder E56. Total length 40 μm. Specimen photographed in equatorial view; note the apical archeopyle, the parasutural and penitabular processes and the over-reduced small corona in ventro-posterior position (presumed on 2" paraplate).
Review of the dinoflagellate cyst *Stephanelytron* Sarjeant 1961 emend
Table 2. Summary of selected morphological features of *Stephanelytron* species.

| species                                         | apical horn | corona | elements of paratabulation | arrangement of processes | type of processes | autophragm | archeopyle operculum |
|------------------------------------------------|-------------|--------|----------------------------|--------------------------|-------------------|------------|----------------------|
| *Stephanelytron redcliffense* Sarjeant 1961 emend. Stover et al., 1977 - types species | no          | one, smooth wall on 1"" paraplate; flaring; thick base with mass of setae or spinules | archeopyle and parasutural processes | few parasutural processes, transverse on paracingulum | cylindrical, tubiform to buccinate, non-perforate | smooth faintly granulate | probably apical free |
| *Stephanelytron brontes* new species            | yes long    | one, smooth wall on 2"" paraplate; low and straight; thick base; intra corona area smooth | archeopyle; only | dense cover of non paratabular processes | cylindrical, tubiform to buccinate, non-perforate | smooth faintly granulate | unknown |
| *Stephanelytron callovianum* (Piel 1985) comb. nov. | yes short   | one or two, smooth wall on ps paraplate; low and straight; thick base; intra corona area smooth | archeopyle; suggestion of paracingulum or parasulcus | dense cover of non paratabular processes | tubiform, non-perforate | smooth faintly granulate | apical (tA) free |
| *Stephanelytron caytonense* Sarjeant 1961 emend. Stover et al. 1977 | no          | one, smooth wall on 1"" paraplate; slightly flaring; thick base; intra corona area smooth | archeopyle; only | few non paratabular or a ill-defined row of processes | cylindrical, tubiform to buccinate, finely perforate | smooth | apical free |
| *Stephanelytron ceto* new species               | no          | one, smooth wall on ps paraplate; low and straight; thick base; intra corona area smooth | archeopyle, paracingulum, accessory archeopyle suture | dense cover of intratabular and pentatabular processes | cylindrical, tubiform to buccinate, non-perforate | smooth | apical free |
| *Stephanelytron cretaceum* Duxbury 1983         | no          | one, smooth wall on 1"" paraplate; slightly flaring; thick base; intra corona area densely granular | archeopyle, accessory archeopyle suture | few non paratabular processes | cylindrical, tubiform to buccinate, non-perforate | smooth faintly granulate | apical free |
| *Stephanelytron membranoidum* (Vozzhennikova 1967 emend. Lentin and Vozzhennikova 1990) comb. nov. | no          | one, smooth wall on 2"" paraplate; low and straight; thick base; intra corona area with processes | archeopyle, paracingulum, accessory archeopyle suture | dense cover of intratabular processes | probably cylindrical, tubiform to buccinate, non-perforate | smooth faintly granulate | apical (tA), free or remaining in place |
| *Stephanelytron scarburghense* Sarjeant 1961 emend. Stover et al. 1977 | no          | one or occasionally two, smooth wall on 1"" and 2"" (when two) paraplates; flaring; thick base and distal rim with mass of setae | archeopyle; only | few non paratabular processes | cylindrical, tubiform to buccinate, non-perforate | smooth | apical free |
| *Stephanelytron tabulophorum* Stover et al. 1977 | no          | one, smooth wall on 2"" paraplate; slightly flaring; thick base with processes intra area | archeopyle, paracingulum, accessory archeopyle suture | few parasutural and pentatabular processes | cylindrical, tubiform to buccinate, non-perforate | smooth faintly granulate | apical (tA), free |
Table 3. Proposed key for species of the genus *Stephanelytron* Sarjeant 1961 emend.

| Genus Stephanelytron Sarjeant 1961 emend. | one or two reduced coronas in ventral-posterior position | one or two elevated coronas in antapical position |
|------------------------------------------|--------------------------------------------------------|--------------------------------------------------|
| dense cover of non-tabular processes; paracingulum vaguely expressed | apical horn | length of apical horn >20% of the diameter of central body | one corona reduced; no intra corona processes | $R = 0.02-0.06$ |
| | | length of apical horn <20% of the diameter of central body | two or occasionally one coronas; no intra corona processes | $R = 0.06$ |
| processes in intratabular or parasutural and penitabular position; paracingulum well expressed | no apical horn | processes non-perforate | one corona reduced; no intra corona processes | $R = 0.03-0.06$ |
| | | | one corona; intra corona processes | $R = 0.04-0.08$ |
| | | apical length of apical horn <20% of the diameter of central body | one corona; intra corona area densely granular | $R = 0.14$ |
| | | | processes non-perforate | one or occasionally two coronas; intra corona area with mass of setae | $R = 0.12-0.20$ |
| | | | processes perforate | one or occasionally two coronas; intra corona area smooth | $R = 0.10-0.18$ |
| | | processes in parasutural position; paracingulum expressed by transverse processes | | |
| | | | processes non-perforate | one corona; intra corona area with setae or spinules | $R = 0.16-0.30$ |
| | | processes in intratabular position; paracingulum indicated by alignment of processes | | |
| | | | | one corona processes | $R = 0.10-0.30$ |

*S. callovianum*  
*S. ceto*  
*S. tabulophorum*  
*S. cretaceum*  
*S. scarburghense*  
*S. caytonense*  
*S. redcliffense*  
*S. membranoidium*
Table 4. Citations of species of *Stephanelytron* and selected species of *Chlamydophorella*, referred to ammonite zones.

| species                        | Citation of the first appearance | Other citations                                                                 | Citation of the last appearance |
|--------------------------------|----------------------------------|---------------------------------------------------------------------------------|---------------------------------|
| *Stephanelytron redcliffense*  | Feist-Burkardt and Wille 1992    | Sarjeant 1962 (*Cordatum* Zone; England)                                        | Feist-Burkardt and Wille 1992  |
|                               | (Koenei Zone; Germany)           | Sarjeant 1968 (*Cordatum*/*Cordatum* Zones; France)                             | (Mutabilis Zone; Germany)      |
|                               |                                  | Gitmez and Sarjeant 1972 (*Cymodoce*/*Baylei* Zones; France)                     |                                 |
|                               |                                  | Sarjeant 1979 (*Baylei* Zones; World excluding N. America)                       |                                 |
|                               |                                  | Erkmen and Sarjeant 1980 (*Lamberti* Zone; Scotland, England)                    |                                 |
|                               |                                  | Herngreen et al. 1984 (*Athleta*/*Lamberti* Zones; Netherlands)                  |                                 |
|                               |                                  | Aarhus et al. 1986 (*Cordatum*/*Cordatum* Zones; Norway)                        |                                 |
|                               |                                  | Berger 1986 (*Cordatum* Zone; Switzerland)                                       |                                 |
|                               |                                  | Dürrg 1988 (*Planula*/*Cymodoce* Zones; Germany)                                 |                                 |
|                               |                                  | Smelror 1988 (*Lamberti*/*Cordatum* Zones; Spitsberg)                            |                                 |
|                               |                                  | Thomas and Cox 1988 (*Serratum*/*Regulare* Zones; England)                       |                                 |
|                               |                                  | Prauss 1989 (*Athleta*/*Lamberti* Zones; Germany)                                |                                 |
|                               |                                  | Dimter and Smelror 1990 (*Jason* Zone; Germany)                                  |                                 |
|                               |                                  | Dodekova 1990 (Mid Callovian; Bulgaria)                                          |                                 |
|                               |                                  | Wierzbowski and Arhus 1990 (*Glosense* Zone; Barents Sea)                        |                                 |
| *Stephanelytron callovianum*   | Piel 1985 (Coronatum Zone; England) | Sarjeant 1968 (*Lamberti* Zone; France)                                           | Piel 1985 (*Lamberti* Zone; England) |
| (Piel 1985) comb. nov.         | (Lower Bathonian; Bulgaria)      | Couratinat 1980 (*Bimammatum* Zone; France)                                      | (Mid Kimmeridgian; Greenland)  |
|                               |                                  | Erkmen and Sarjeant 1980 (*Lamberti* Zone; England)                              |                                 |
|                               |                                  | Couratinat 1989 (*Minax*/*Acanthicum* Zones; France)                             |                                 |
| *Stephanelytron caytonense*    | Piel 1985 (Coronatum Zone; England) | Sarjeant 1968 (*Lamberti* Zone; England)                                           | Piel 1985 (Coronatum Zone; England) |
| Sarjeant 1961 emend.           | (Koenei Zone; Germany)           | Couratinat 1980 (*Bimammatum* Zone; France)                                      | (Mid Kimmeridgian; Greenland)  |
| Stover et al. 1977             |                                  | Erkmen and Sarjeant 1980 (*Lamberti* Zone; England)                              |                                 |
|                               |                                  | Couratinat 1989 (*Minax*/*Acanthicum* Zones; France)                             |                                 |
| *Stephanelytron ceto*         | Lamberti Zone this study         | Sarjeant 1968 (*Lamberti* Zone; France)                                           | Sarjeant 1968 (*Cordatum* Zone; England) |
| new species                   |                                  | Couratinat 1980 (*Bimammatum* Zone; France)                                      |                                  |
|                               |                                  | Erkmen and Sarjeant 1980 (*Lamberti* Zone; England)                              |                                  |
|                               |                                  | Couratinat 1989 (*Minax*/*Acanthicum* Zones; France)                             |                                  |
| *Stephanelytron cretaceum*     | Lamberti Zone this study         | Sarjeant 1968 (*Lamberti* Zone; France)                                           | Sarjeant 1968 (*Cordatum* Zone; England) |
| Duxbury 1983                  | (Lower Aptian; NW Europe)        | Couratinat 1980 (*Bimammatum* Zone; France)                                      |                                  |
|                               |                                  | Erkmen and Sarjeant 1980 (*Lamberti* Zone; England)                              |                                  |
|                               |                                  | Couratinat 1989 (*Minax*/*Acanthicum* Zones; France)                             |                                  |
| *Stephanelytron membranoidium* | Lamberti Zone this study         | Sarjeant 1968 (*Lamberti* Zone; France)                                           | Sarjeant 1968 (*Cordatum* Zone; England) |
| (Vozzhennikova 1967 emend.     | (Koenei Zone; Germany)           | Couratinat 1980 (*Bimammatum* Zone; France)                                      |                                  |
| Lentin and Vozzhennikova 1990 |                                  | Erkmen and Sarjeant 1980 (*Lamberti* Zone; England)                              |                                  |
| comb. nov.                    |                                  | Couratinat 1989 (*Minax*/*Acanthicum* Zones; France)                             |                                  |
| *Stephanelytron scarburghense* | (Planula/Galar Zones; Germany)   | Sarjeant 1968 (*Lamberti* Zone; France)                                           | Sarjeant 1968 (*Cordatum* Zone; England) |
| Sarjeant 1961 emend.           | (Harveyi Zone; Germany)          | Couratinat 1980 (*Bimammatum* Zone; France)                                      |                                  |
| Stover et al. 1977             |                                  | Erkmen and Sarjeant 1980 (*Lamberti* Zone; England)                              |                                  |
|                               |                                  | Couratinat 1989 (*Minax*/*Acanthicum* Zones; France)                             |                                  |
| *Stephanelytron tabulophorum*  | (Planula/Galar Zones; Germany)   | Sarjeant 1968 (*Lamberti* Zone; France)                                           | Sarjeant 1968 (*Cordatum* Zone; England) |
| Stover et al. 1977             | (Harveyi Zone; Germany)          | Couratinat 1980 (*Bimammatum* Zone; France)                                      |                                  |
|                               |                                  | Erkmen and Sarjeant 1980 (*Lamberti* Zone; England)                              |                                  |
|                               |                                  | Couratinat 1989 (*Minax*/*Acanthicum* Zones; France)                             |                                  |
| *Chlamydophorella raptibulata* | (Planula/Galar Zones; Germany)   | Sarjeant 1968 (*Lamberti* Zone; France)                                           | Sarjeant 1968 (*Cordatum* Zone; England) |
| Dodekova 1975                 | (Harveyi Zone; Germany)          | Couratinat 1980 (*Bimammatum* Zone; France)                                      |                                  |
|                               |                                  | Erkmen and Sarjeant 1980 (*Lamberti* Zone; England)                              |                                  |
|                               |                                  | Couratinat 1989 (*Minax*/*Acanthicum* Zones; France)                             |                                  |
| *Chlamydophorella ectotabulata*| (Planula/Galar Zones; Germany)   | Sarjeant 1968 (*Lamberti* Zone; France)                                           | Sarjeant 1968 (*Cordatum* Zone; England) |
| Smelror 1988                  | (Harveyi Zone; Germany)          | Couratinat 1980 (*Bimammatum* Zone; France)                                      |                                  |
|                               |                                  | Erkmen and Sarjeant 1980 (*Lamberti* Zone; England)                              |                                  |
|                               |                                  | Couratinat 1989 (*Minax*/*Acanthicum* Zones; France)                             |                                  |
| *Chlamydophorella wallai*     | (Planula/Galar Zones; Germany)   | Sarjeant 1968 (*Lamberti* Zone; France)                                           | Sarjeant 1968 (*Cordatum* Zone; England) |
| Cookson and Eisenack 1960      | (Harveyi Zone; Germany)          | Couratinat 1980 (*Bimammatum* Zone; France)                                      |                                  |
|                               |                                  | Erkmen and Sarjeant 1980 (*Lamberti* Zone; England)                              |                                  |
|                               |                                  | Couratinat 1989 (*Minax*/*Acanthicum* Zones; France)                             |                                  |

Citations of species of *Chlamydophorella* and selected species of *Chlamydophorella* referred to ammonite zones.
SYSTEMATIC MICROPALAEONTOLOGY
Division Pyrrophyta Pascher, 1914
Class Dinophyceae Fritsch, 1929
Order Peridiniales Haecckel, 1894
Genus Stephanelytron Sarjeant 1961 emend Stover, Sarjeant & Drugg, 1977, emend
1961 Stephanelytron Sarjeant: 109.
1977 Stephanelytron Sarjeant, emend Stover, Sarjeant & Drugg: 331.
1985 Lagenadinium Piel: 108

Original description
Sarjeant (1961: 109): “Organic shells of spherical to ovoidal shape, bearing on one face (at one end in ovoidal forms) one or more structures consisting of a circular membrane rising upwards from the shell surface and everted, surrounding a matte of short hairs or spines; this structure is henceforth termed a 'corona'. Elsewhere the shell bears tubular processes of varied character and arrangement.”

Stover et al. (1977: 331): “Cysts proximochorate with subspherical to ellipsoidal body composed of two wall layers. Inner wall, the autophagm, gives rise to usually short processes; outer wall, the ectophagm, thin and may be discontinuous. Processes frequently arranged in parasutural rows, less commonly non tubular; some forms have parasutural and scattered non tubular processes, pentabarbar processes being present one species. Processes cilindrical to tubiform, normally of uniform height or nearly so, but width may vary considerably. Paratabulation indicated by alignment of processes, on some species, formula: 1”, 5” X-6c, 5”", 0-1p, 1”", 2s. Archeopyle apical, operculum free, rarely attached; exact archeopyle shape and number of paraplates in operculum uncertain; antapical area typically with one or occasionally with two coronas.”

Emended description
Cysts subspherical to ellipsoidal, proximate to proximochorate, holocavate; autophagm psilate to scabrate with or without an apical horn; paratabulation generally indicated by archeopyle and on some cysts by the disposition of processes; processes are parasutural, penitabular or non-tabular; inferred paraplate formula: ?4", ? 5", X-26c, ?5”", 0-1p, 1”", 2s; archeopyle apical, operculum free; processes normally cylindrical, buccinate or tubiform; processes are entire or perforate; sometimes distal tips of processes are connected by trabeculae; on some specimens a laevigate thin ectophagm, entire or incomplete, frequently wrinkled, covers the processes; antapical pole with one or two coronas; coronas in antapical (1””) or ventral-posterior position (probably the 2””, 1p or ps paraplate); base of coronas relatively thick, laevigate or composed of dense mass of setae or spinules; distal diameter of corona may be greater or equivalent to proximal diameter; elevation of corona variable (10 to 100% of diameter).

Type species. S. recliifense Sarjeant 1961 emend Stover et al., 1977: 331–332, Plate 1, fig. 18

Holotype. Sarjeant, 1961: 109–110; pl. 15, fig. 11; text-fig. 10.
Dimensions. Length of central body, 36 μm; equatorial diameter of central body, 30 μm; length of processes, 5–9 μm R = 0.16–0.30 (R= length of processes/equatorial diameter of central body).
Age. Early Oxfordian (Cordatum Zone).
Geographical location. England (Yorkshire, Cayton Bay).
Diagnostic elements. See Tables 2 and 3.
Stratigraphic range. See Table 4.

Other species
?Stephanelytron bronte n. sp. (this study), Plate 1, figs 1–4

Holotype. This study, Plate 1, fig. 2
Dimensions. Length of central body (without horn), 50 μm; equatorial diameter of central body, 46 μm; length of processes, 2 μm; R = 0.04.
Age. Late Callovian (Lamberti Zone).
Geographical location. France (Ardèche, Savournon).
Diagnostic elements. See Tables 2 and 3.
Stratigraphic range. See Table 4.

Stephanelytron callovianum (Piel, 1985) comb. nov., Plate 1, figs 5–8

Holotype. Lagenadinium callovianum Piel, 1985: 108–110, pl. 1, fig. 1–6
Dimensions. Length of central body (without horn), 34 μm; equatorial diameter of central body, 29 μm; length of processes, 2 μm; R = 0.06.
Age. Early Callovian (Coronatum Zone).
Geographical location. England (Cambridgeshire, Warboys Borehole).
Diagnostic elements. See Tables 2 and 3.
Stratigraphic range. See Table 4.

Remarks. The age of the holotype of Stephanelytron callovianum indicated by Piel (1985: 112) is questionable because S. callovianum belongs to assemblages in which Wamaea thyssanota Woollam, 1982 is dominant. This species appears in the Athleta Zone according to Riding (1987) and Riding & Thomas (1992).

Stephanelytron caytonense Sarjeant 1961 emend Stover et al., 1977: 332.

Holotype. Sarjeant 1961: 109–110, pl. 15, fig. 16; text-fig. 10.
Dimensions. Length of central body, 65 μm; equatorial diameter of central body, 60 μm; length of processes, 6–11 μm; R = 0.10–0.18.
Age. Early Oxfordian (Cordatum Zone).
Geographical location. England (Yorkshire, Cayton Bay).
Diagnostic elements. See Tables 2 and 3.
Stratigraphic range. See Table 4.

Stephanelytron ceto n. sp. (this study), Plate 1, figs 10–12

Holotype. This study, Plate 1, fig. 11.
Dimensions. Length of central body, 34 μm; equatorial diameter of central body, 40 μm; length of processes, 1–2 μm; R = 0.03–0.06.
Age. Early Oxfordian (Minax zone).
**Geographical location.** France (Ardèche, Chenier).

**Diagnostic elements.** See Tables 2 and 3.

**Stratigraphic range.** See Table 4.

*Stephanelytron cretaceum* Duxbury, 1983

**Holotype.** Duxbury, 1983; p. 56, pl. 7, figs 5–6

**Dimensions.** Length of central body, 52 μm; equatorial diameter of central body, 49 μm; length of processes, about 7 μm (from original illustration); \( R = 0.11 – 0.13 \).

**Age.** Late Aptian.

**Geographical location.** England (Isle of Wight).

**Diagnostic elements.** See Tables 2 and 3.

**Stratigraphic range.** See Table 4.

*Stephanelytron membranoidium* (Vozzhennikova, 1967), comb. nov., Plate 1, fig. 14

**Holotype.** *Chlamydophorella membranoidea* Vozzhennikova, 1967: 114–115, pl. 48, figs 9a–b (holotype lost)

**Dimensions.** Length of central body, 46 μm; equatorial diameter of central body, 43 μm; length of processes, 5–6 μm; \( R = 0.11 – 0.13 \).

**Lectotype.** Lentin & Vozzhennikova, 1990: 103, pl. 10, figs 6–7.

**Dimensions.** Length of central body, 47 μm; equatorial diameter of central body, 51 μm; length of processes, 5–6 μm; \( R = 0.10 – 0.12 \).

**Age.** Late Jurassic.

**Geographical location.** Russia (Moscow region).

**Diagnostic elements.** See Tables 2 and 3.

**Stratigraphic range.** See Table 4.

*Stephanelytron scarburghense* Sarjeant, 1961 emend Stover et al., 1977: 333, Plate 1, figs 15, 16, 19

**Holotype.** Sarjeant, 1961: 111; pl. 15, figs 12–13.

**Dimensions.** Length of central body, 45 μm; equatorial diameter of central body, 40 μm; length of processes, 5–8 μm. \( R = 0.12 – 0.20 \).

**Age.** Early Oxfordian (*Cordatum* Zone).

**Geographical location.** England (Yorkshire, Scarborough Castle Cliff).

**Diagnostic elements.** See Table 2 and Table 3.

**Stratigraphic range.** See Table 4.

*Stephanelytron tabulophorum* Stover et al., 1977, Plate 1, fig. 20

**Holotype.** Stover et al., 1977: 333, pl. 1, figs 13a–c.

**Dimensions.** Length of central body, 67 μm; equatorial diameter of central body, 40 μm; length of processes, 1–4 μm; \( R = 0.04 – 0.08 \).

**Age.** Late Callovian (*Athleta* Zone).

**Geographical location.** Germany (Reutlingen).

**Diagnostic elements.** See Tables 2 and 3.

**Stratigraphic range.** See Table 4.

**New species**

?*Stephanelytron brontes* n. sp. Plate 1, figs 1–4; Fig. 2

**Derivation of name.** From the name of one of the three Cyclops, Brontes son of Ouranos and Gaea in classical Greek mythology.

**Diagnosis.** Cysts subspherical to ellipsoidal, proximate, holoca-vate; incomplete ectophragm supported by buccinate to tubiform and entire processes. An apical horn formed both by autophragm and ectophragm is typically present. Length of apical horn about one-quarter to one-half of the central body. Processes non-tabular, of short length. Paratabulation unknown, the single diagnostic feature being the vaguely expressed paracingulum and alignment of processes along the horn. Archeopyle type unknown. One corona in a ventral-posterior position is present probably on the 2° paraplate; base of coronas relatively thick, laevigate; elevation of corona low (10% of diameter).

**Holotype.** SAV 07; coordinate 48.9/106.1; England Finder L50/3; Pl. 1, Fig. 2; specimen housed in the University Claude-Bernard Lyon 1 Collection, France.

**Stratum typicum.** Late Callovian; top of the *Lamberti* Zone.

**Locus typicus.** Savournon locality, Ardèche Department, France.

**Dimensions.** Holotype—length of horn, 21 μm; length of central body, 54 μm; equatorial diameter of central body, 40 μm; length of processes, 1–2 μm; diameter of corona, 14 μm; \( R = 0.02 – 0.05 \).

**Variations.** Length of horn, 16–28 μm; length of central body, 42–66 μm; equatorial diameter of central body, 28–45 μm; length of processes, 1–3 μm; diameter of corona, 10–16 μm; \( R = 0.02 – 0.06 \); 21 measured specimens.

**Distribution and occurrence.** Chenier section (*Minax* Zone in the Sub-Mediterranean province = *Mariae* Zone in the Boreal Realm); Savournon section (*Lamberti* Zone; *Minax* Zone).

**Comparisons and remarks.** ?*S. brontes* has an elongate horn (one-quarter to one-third of the length of the central body); on *S. callovianum* the horn is short (not more than one-tenth the length of the central body). ?*S. brontes* is reported with doubt to the genus *Stephanelytron* because the archeopyle is unknown. The specimen figured in Plate 1, fig. 6 shows a tear that could be an apical archeopyle. On the holotype (Plate 1, fig. 3) and other specimens (e.g. Plate 1, fig. 4), a possible opening that may be an intercalary archeopyle is observable. If this proves to be the case, a new genus will be required.
Plate diameter). It is parasutural and penitabular on S. It is characterized by parasutural and penitabular processes. These two species have similar ranges (Fig. 4). Some workers have commented on the gradation between S. caytonense and S. redcliffense (Stover et al., 1977: 333; Fensome, 1979: 25), but they have not been synonymized and their ranges differ. The extinction of the two species may be contemporaneous."}

**Derivation of name.** From the name of the daughter of Pontos (The Sea) and Gaea (The Earth) in classical Greek mythology.

**Diagnosis.** Cysts subspherical to ellipsoidal, proximate, holocorate; incomplete ectophragm supported by a dense cover of small buccinate to tubiform and entire processes. Apical horn absent. Processes penitabular and intratabular, of small length. Paratabulation formula unknown; the paratabular features relatively thick, laevigate; elevation of corona low (10% of diameter).

**Holotype.** SAV 17; coordinate 60.3/104; England Finder N61/4; Plate 1, fig. 11; specimen housed in the University Claude-Bernard Lyon 1 Collection, France.

**Stratum typicum.** Early Oxfordian; base of the Minax Zone in the Sub-Mediterranean province = Mariæ Zone in the Boreal Realm.

**Locus typicus.** Savournon locality, Ardèche Department, France.

**Dimensions.** Holotype—length of central body, 34 μm; equatorial diameter of central body, 40 μm; length of processes, 1–2 μm; diameter of corona, 8 μm; R = 0.03–0.06.

**Variations.** Length of central body, 30–35 μm; equatorial diameter of central body, 36–44 μm; length of processes, 1–3 μm; diameter of corona, 8–10 μm; R = 0.03–0.07; 12 measured specimens.

**Distribution and occurrence.** Crussol section (base of Minax zone); Rondette section (base of Minax Zone); Savournon section (top of Lamberti Zone; Minax Zone)

**Comparisons and remarks.** S. ceto has probably one corona on the ps paraplate similar in position to *S. callovianum*, but the latter has two coronas. On *?S. brontes* and *S. tabulophorum* the corona is on the 2"" paraplate (Table 2). *S. ceto* has processes similar to those of *?S. brontes*, but has no horn. The arrangement of processes is intratabular and penitabular, while it is parasutural and penitabular on *S. tabulophorum*. Otherwise, *S. ceto* possesses a dense cover of processes, whereas *S. tabulophorum* has scattered processes.

**EVOLUTION AND SPECIATION EVENTS IN STEPHANEYTRON**

The stratigraphic ranges of the species in *Stephanelytron* (Table 4) provide new evidence about the evolution of this genus. These considerations are speculative as the exact function of the corona is unknown. Piel (1985: 117–118, fig. 4) hypothesized that *Chlamydophorella*-like forms are ancestors of *Stephanelytron*. Wheeler & Sarjeant (1990: 315–316), assumed that the hypothesis of Piel (1985) was correct i.e. that the coronas of the *Stephanelytraceae* evolved from a single process of *Chlamydophorella* (e.g., *C. ovula* Wheeler & Sarjeant 1990). Such a scenario is conceivable, but it can also be proposed that a corona resulted from the coalescence of processes or the coalescence of processes and part of the ectophragm (see Plate 1, fig. 19). The oldest species of *Stephanelytron* (*S. scarburghense*; Early Callovian) may have originated from the *Chlamydophorella* present at that time, i.e. *C. raritubular* Dodekova, 1975 or *C. ectotubulata* Smelror, 1989 (Plate 1, fig. 9) or from another *Chlamydophorella*-like form. *S. cretaceum*, one of the two representatives of the genus in the Cretaceous, may have developed from *S. membranoidium* (the option shown in Fig. 4) or from the *Chlamydophorella* lineage. The common ancestor from *Chlamydophorella*-like forms theory explains the fact that *S. cretaceum* has strongest affinities with the Jurassic species (*S. caytonense*, *S. redcliffense* and *S. scarburghense*) rather than *?Stephanelytron brontes*, *S. callovianum* and *S. ceto*. It is conceivable that similar speciation mechanisms gave rise to comparable forms (i.e. *S. cretaceum* and *S. scarburghense*).

Sarjeant (1962: 495) suggested that *S. scarburghense* gave rise to *S. caytonense*. These two species have similar ranges (Fig. 4). Some workers have commented on the gradation between *S. caytonense* and *S. redcliffense* (Stover et al., 1977: 333; Fensome, 1979: 25), but they have not been synonymized and their ranges differ. The extinction of the two species may be contemporaneous. *S. caytonense* first appears in the mid-Callovian, whereas *S. redcliffense* appears in the Lower Callovian (Table 4). Their close similarities and the time lag of their first occurrence argues for a relationship between *S. redcliffense* and *S. caytonense* in which *S. redcliffense* could be the ancestor of *S. caytonense*. They may represent two forms (?subspecies) of a polytypic species where forms (?)subspecies occupied distinctive geographical areas. This might explain why *S. redcliffense* and *S. caytonense* are apparently never found together, except in northwest Europe (England), where the two geographical regions are connected. *S. tabulophorum*, a short-ranging species, is characterized by parasutural and penitabular processes. These characters, only known on this species, may have evolved from a parasutural arrangement of processes like those of *S. redcliffense*.

The *?Stephanelytron brontes*, *S. ceto* and *S. callovianum* complex, with distinctive coronas, is assumed to be derived from *S. scarburghense* because of the non-paratabular arrangement of processes. However, a *Chlamydophorella* ancestor, possibly *C. ectoabulata*, cannot be excluded.

The type species of *S. membranoidium* shows a corona, but numerous specimens have been found without this character. It is conceivable that this long-ranging species has some of the features of both *Stephanelytron* and *Chlamydophorella*.

The probably eurytopic species (*S. caytonense*, *S. membranoidium*, *S. redcliffense* and *S. scarburghense*), characterized by elevated antapical coronas, favoured the reproductive isolation of the short-ranging *Stephanelytron* community characterized by reduced ventral–posterior corona ("S. brontes*, *S. callovianum*, *S.
ceto and S. tabulophorum). These speciations are concentrated during the mid-Late Callovian. The restricted geographical distribution of S. tabulophorum (France, Germany and the Netherlands) and S. callovianum (Bulgaria, England and France) argues for palaeoecological control. The two characteristic new species, ?S. brontes and S. ceto, appear to be endemic stenotopic species related to an allopatric speciation event. In the absence of geographical isolation and in the case of genetic change due to unfavourable mutation, the new population may have little chance of succeeding. That is the case of peripatric speciation inducing polytypic species (Mayr, 1954). ?S. brontes, S. callovianum and S. ceto may represent a case of peripatric speciation from an unfavourable mutation.
ACKNOWLEDGMENTS

This research was supported by the Arts & Sciences, Bron, France. Many thanks are due to F. Atrops (Univ. Claude-Bernard, Lyon 1) for guidance on the Callovian–Oxfordian ammonite zonation and to Jim Riding and Chris Denison for their constructive suggestions as to how to improve the manuscript.

Manuscript received 16 December 1998
Manuscript accepted 20 April 1999

REFERENCES

Arhus, N., Birkelund, T. & Smelror, M. 1986. Biostratigraphy of some Callovian and Oxfordian cores off Vega, Helgeland, Norway. Norsk Geologisk Tidsskrift, 69: 39–56.

Berger, J. P. 1986. Dinoflagellates of the Callovian-Oxfordian boundary of the ‘Liesberg-Dorf’ quarry (Berner Jura, Switzerland). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 172: 331–355.

Courtinat, B., in Courtinat, B. & Gaillard, C. 1980. Les dinoflagellés des Calcaires litsés de Trent (Oxfordien supérieur). Inventaire et répartition comparées de la microflora benthique. Document du Laboratoire de Géologie de Lyon, 78: 3–122.

Courtinat, B. 1989. Les organoclastes des formations lithologiques du Malm dans le Jura Méridional. Systématique, biostratigraphie et éléments d’interprétation paléoenvironnement. Document du Laboratoire de Géologie de Lyon, 105: 361 pp.

Davy, R. J. 1979. The stratigraphic distribution of dinocysts in the Portlandian (latest Jurassic) to Barremian (Early Cretaceous) of northwest Europe. American Association of Stratigraphic Palynologists, Contribution Series 5B, 49–81.

Davy, R. J. 1982. Dinoflagellate cyst stratigraphy of the Latest Jurassic to Early Cretaceous of the Haldager No.1 borehole, Denmark. Danmarks Geologiske Undersøgelser, Series B, 6: 1–77.

Davy, R. J. 1987. Palynological zonation of the Lower Cretaceous, Upper and lowermost Middle Jurassic in the Northwestern Papuan Basin of Papua New Guinea. Geological Survey of Papua New Guinea. Geologic Survey of Papua New Guinea, 13: 1–77.

Dimter, A. & Smelror, M. 1990. Callovian (Middle Jurassic) marine microplankton from southwestern Germany: biostratigraphy and palaeoenvironmental interpretations. Palaeogeography, Palaeoclimatology and Palaeoecology, 80: 173–195.

Dodekova, L. 1990. New Upper Bathonian dinoflagellate cysts from north-eastern Bulgaria. Bulgarian Academy of Sciences, Palaeontologiya, Stratigraphy and Lithology, 2: 17–34.

Dodekova, L. 1990. Dinoflagellate cysts from the Bathonian – Tithonian (Jurassic) of North Bulgaria. I. Taxonomy of Callovian dinoflagellate cysts. Geologia Balcanica, 20: 3–45.

Dodekova, L. 1992. Dinoflagellate cysts from the Bathonian – Tithonian (Jurassic) of North Bulgaria. II. Taxonomy of Oxfordian and Kimmeridgian dinoflagellate cysts. Geologia Balcanica, 22: 33–69.

Dürr, G. 1988. Palynostratigraphie des Kimmernium und Tithonium von Süddeutschland und Korrelation mit borealen Floren. Tübinger Mikro-palaeontologische Mitteilungen, 5: 1–159.

Duxbury, S. 1983. A study of dinoflagellate cysts and acritarchs from the Lower Greensand (Aptian to Lower Albian) of the Isle of Wight, Southern England. Palaeoentographica, 186: 18–80.

Erkmen, U. & Sarjeant, W. A. S. 1980. Dinoflagellate cysts, acritarchs and tasnaminids from the Uppermost Callovian of England and Scotland: with a reconsideration of the ‘Xanthidium pilosum’ problem. Geobios, 13: 45–99.

Fauconnier, D., Courtinat, B., Gardin, S., Lachkar, G. & Rauscher, R. 1996. Biostratigraphy of Jurassic and Triassic successions in the Balazuc-1 borehole (GF programme). Stratigraphic setting inferred from dinoflagellate cysts, pollen, foraminifera and calcareous nanofossils. Marine and Petroleum Geology, 13: 707–724.

Feist-Burkhardt, S. & Wille, W. 1992. Jurassic palynology in southwest Germany - state of the art. Cahiers de Micropaléontologie, N.S., 7: 141–156.

Fensome, R. A. 1979. Dinoflagellate cysts and acritarchs from the Middle and Upper Jurassic of Jameson Land, East Greenland. Grønlands Geologiske Undersøgelse, 132: 1–117.

Gimenez, G. U. 1970. Dinoflagellate cysts and acritarchs from the Basin of Kimeridgian (Upper Jurassic) of England, Scotland and France. Bulletin of the British Museum (Natural History), Geology, 18: 233–2331.

Gimenez, G. U. & Sarjeant, W. A. S. 1972. Dinoflagellate cysts and acritarchs from the Kimeridgian (Upper Jurassic) of England, Scotland and France. Bulletin of the British Museum (Natural History), Geology, 21: 173–257.

Groupe Francais d’étude du Jurassique 1997. Biostratigraphie du Jurassique ouest-européen et méditerranéen: zonations parallèles et distribution des inverts et microfossiles. In Cariou, E. & Hantzpergue, P. (Coordinators). Bulletin des Centres de Recherche Elf Exploration et Production, Memoire, 17: 440 pp.

Habib, D. & Drugg, W. S. 1983. Dinoflagellate age of Middle Jurassic – Early Cretaceous sediments in the Blake–Bahama Basin. Initial Reports of the DSDP, 26: 623–638.

Herzog, G. F. W., DE Boer, K. F., Romein, B. J., Lissenberg, T. H. & Wijkers, N. C. 1984. Middle Callovian beds in the Achterhoek Eastern Netherlands. Mededelingen Rijks Geologische Dienst, 37: 96–123.

Kunitz, J. K. & Voehennkova, T. F. 1990. Fossil dinoflagellate from the Jurassic, Cretaceous and Paleogene deposits of the USSR. A re-study. American Association of Stratigraphic Palynologists, Contributions Series No. 23: 1–220.

Lister, J. K. & Batten, D. J. 1988. Stratigraphic and palaeoenvironmental distribution of early Cretaceous dinoflagellate cysts in the Hurlfords Farm Borehole, west Sussex, England. Palaeontographica, 210: 9–89.

Mayr, E. 1954. Change of genetic environment and evolution. In Huxley, J. (Ed.), Evolution as a Process. Allen and Unwin, London: 157–180.

Odin, G. S. & Odin, C. 1990. Echelle numérique des temps géologiques. Géochronique, 35: 12–21.

Piel, K. M. 1985. Lagenastrum, a new dinoflagellate cyst from British Middle–Late Callovian rocks, a possible evolutionary intermediate between Stephaniastrum and Gardoniinum. Review of Palaeobotany and Palynology, 45: 107–119.

Prauss, M. 1989. Dinozostraten–Stratigraphie und Palynofazies in oberem Lias und Dogger von NW-Deutschland. Palaeoentographica, Abt. B, 214: 1–124.

Riding, J. B. 1987. Dinoflagellate cyst stratigraphy of the Nettleton Bottom Borehole (Jurassic: Hettangian to Kimeridgian), Lincolnshire, England. Proceedings of the Yorkshire Geological Society, 46: 91–169.

Riding, J. B. & Thomas, J. E. 1988. Dinoflagellate cyst stratigraphy of the Kimeridgian Clay (Upper Jurassic) from the Dorset coalfield, southern England. Palynology, 12: 65–88.

Riding, J. B. & Thomas, J. E. 1992. Dinoflagellate cysts of the Jurassic System. In Powell, A. J. (Ed.), A Stratigraphic Index of Dinoflagellate Cysts. British Micropalaeontological Society Special Publication. Chapman and Hall, London: 7–98.

Sarjeant, W. A. S. 1961. Microplankton from the Kellaways Rock and Oxford Clay of Yorkshire. Palaeontology, 4: 90–118.

Sarjeant, W. A. S. 1962. Microplankton from the Amphill clay of Melton, South Yorkshire. Palaeontology, 5: 478–497.

Sarjeant, W. A. S. 1968. Microplankton from the Upper Callovian and Lower Oxfordian of Normandy. Revue de Micropaléontologie, 10: 221–242.

Sarjeant, W. A. S. 1979. Middle and Upper Jurassic Dinoflagellate cysts: the world excluding North America. American Association of Stratigraphic Palynologists, Contributions Series 5B, 2: 133–157.

Smelror, M. 1988. Late Bathonian to Early Oxfordian dinoflagellate cyst stratigraphy of Jameson Land and Milne Land, East Greenland. Rapp. Grønlands Geol. Undersøgelser, 137: 137–159.

Smelror, M. 1989. Chlamydophorella ectotabulata sp. nov., a gonyaulacoid dinoflagellate cyst from the Late Bathonian to the Oxfordian of the Arctic. Review of Palaeobotany and Palynology, 61: 139–145.

Smelror, M. & Leereveld, H. 1989. Dinoflagellate and acritarch
assemblages from the Late Bathonian to Early Oxfordian of Montagne Crussol, Rhône Valley, Southern France. Palynology, 13: 121–141.

Stancliffe, R. P. W. 1991. Dinoflagellate cysts from the Oxfordian (Upper Jurassic) of Skye, Scotland and Southern Dorset, England. Journal of Micropalaeontology, 10: 185–202.

Stover, L. E., Sarjeant, W. A. S. & Drugg, W. S. 1977. The Jurassic dinoflagellate genus Stephanelytron: emendation and discussion. Micropaleontology, 23: 330–338.

Taugourdeau-Lantz, J. & Lachkar, G. 1984. Stratigraphie par les marqueurs palynologiques sur la bordure ardéchoise du Bassin du Sud-Est. Documents du Bureau de Recherches Géologique et Minière, 81-1: 59–71.

Taugourdeau-Lantz, J. & Lachkar, G. 1985. Stratigraphie par les marqueurs palynologiques sur la bordure ardéchoise du Bassin du Sud-Est. Documents du Bureau de Recherches Géologique et Minière, 95-11: 149–163.

Thomas, J. E. & Cox, B. M. 1988. The Oxfordian–Kimmeridgian stage boundary (Upper Jurassic): dinoflagellate cyst assemblages from the Harome Borehole, North Yorkshire, England. Review of Palaeobotany and Palynology, 56: 313–326.

Wheeler, J. W. & Sarjeant, W. A. S. 1990. Jurassic and Cretaceous palynomorphs from the Central Alborz Mountains, Iran: their significance in biostratigraphy and palaeogeography. Modern Geology, 14: 267–374.

Whitaker, M. F., Giles M. R. & Cannon, J. C. 1992. Palynological review of the Brent Group, UK sector, north sea. In Morton, A. C., Haszeldine, R. S., Giles, M. R. & Brown, S. (Eds), Geology of the Brent Group, Geological Society Special Publication, 61: 169–202.

Wiersbowski, A. & Arhus, N. 1990. Ammonite and dinoflagellate cyst succession of an Upper Oxfordian–Kimmeridgian black shale core from the Nordkapp Basin, southern Barents Sea. Newsletters on Stratigraphy, 22: 7–19.

Wolfard, A. & Van Erve, A. W. 1981. Crussolia deflandrei nov. gen. et nov. sp., a dinoflagellate cyst from the Jurassic (Callovian–Lower Oxfordian) of Montagne Crussol, Rhône Valley, France. Review of Palaeobotany and Palynology, 34: 321–329.

Zotto, M., Drugg, W. S. & Habib, D. 1987. Kimmeridgian dinoflagellate stratigraphy in the southwestern North Atlantic. Micropaleontology, 33: 193–213.