

## Review of the dinoflagellate cyst *Stephanelytron* Sarjeant 1961 emend

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**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. calloviaum*, *S. ceto* and *S. tabulophorum*) from eurytopic species with antapical coronas (*S. caytonense*, *S. membranoidium*, *S. redcliffense* 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. calloviaum* and *S. membranoidium*) and two new species (?*S. brontes* and *S. ceto*) are proposed. *J. Micropalaeontol.* 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–Lamberti/Minax* ammonite zones; *Minax* Zone in the Sub-Mediterranean province = *Mariae* 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 palynomorphs.

Previous studies of the Jurassic dinoflagellate cysts in southeastern France include Sarjeant (1968), Gitmez (1970), 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 *Endoscrinium galeritum* (Deflandre, 1938) Vozzhennikova, 1967, *Escharisphaeridia pocockii* (Sarjeant, 1968) Erkmen & Sarjeant, 1980, *Gonyaulacysta jurassica* (Deflandre, 1938) Norris & Sarjeant, 1965, *Rhynchodiniopsis cladophora* (Deflandre, 1938) Below 1981, *Rigaudella aemula* (Deflandre, 1938) Below, 1982, *Barbatacysta pilosa* (Ehrenberg, 1854) Courtinat 1989, *Sentusidinium rioultii* (Sarjeant, 1968) Sarjeant & Stover, 1978 emend Courtinat 1989, *Surculosphaeridium 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 abundance 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 *Chlamydochorella* Cookson & Eisenack, 1958, *Dingodinium* 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 calloviaum* 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. calloviaum* Piel, 1985 and questionably ?*L. membranoidium* (Vozzhennikova, 1967) Lentini & 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. calloviaum* Piel, 1985 is a proximochoerate, 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

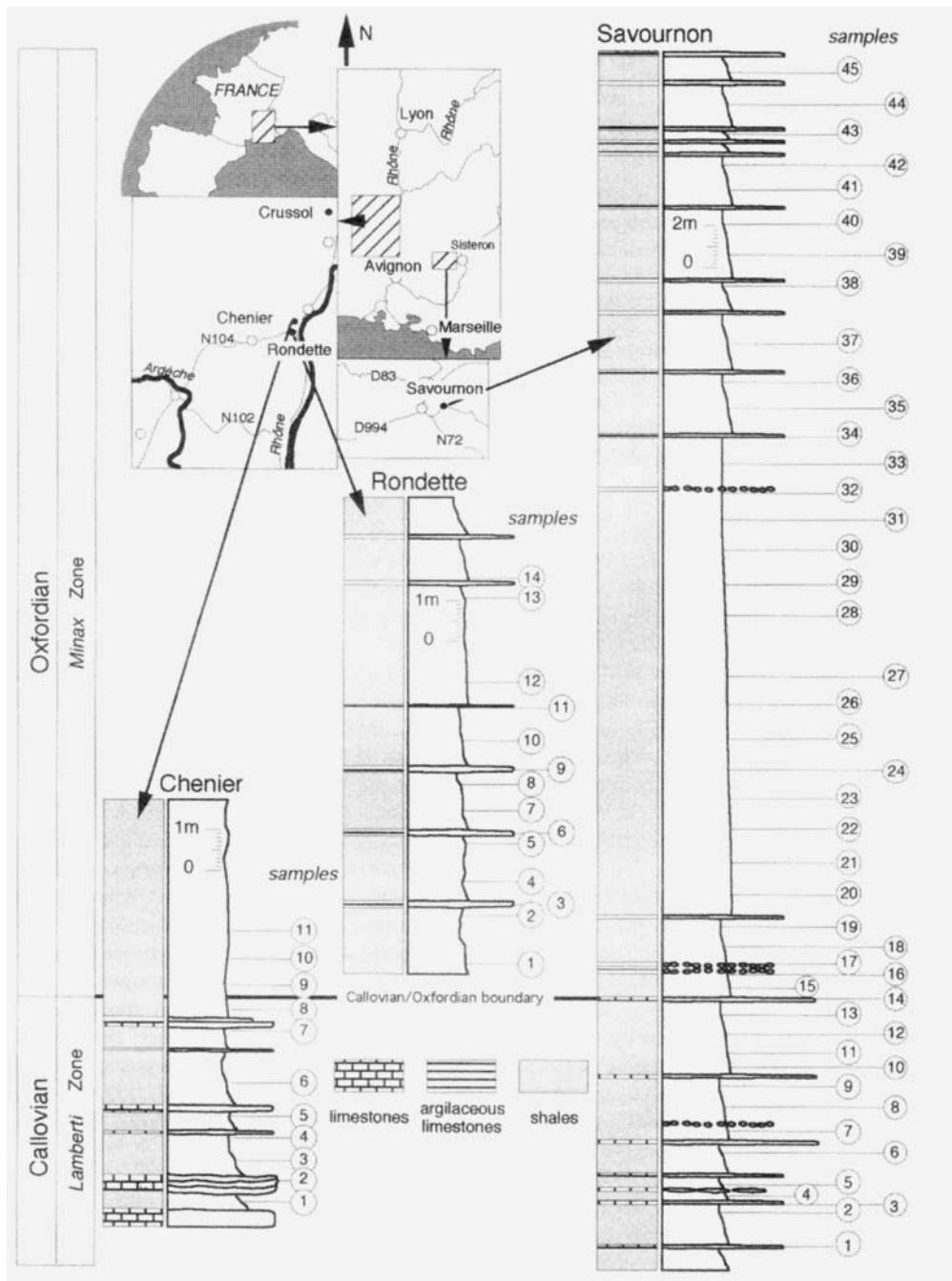


Fig. 1. Location map of the studied sections in southeastern France (Chenier, Rondette and Savournon).

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<sup>nd</sup> 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

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

species	Chenier	Rondette	Savourmon
<i>Achnatosphaeridium caulervii</i> (Deflandre 1938b) Williams and Downie 1966 emend, Stancliff and Sarjeant 1990	●	●	●
<i>Aldorfia dictyota</i> (Cookson and Eisenack 1960b) Davey 1982b	●	●	●
<i>Amboosphaera calloviana</i> Fensome 1979	●	●	●
<i>Amphorula cf. expiratum</i> (Davey 1982b) Courtinat 1989	●	●	●
<i>Arklelea teichophera</i> (Sarjeant 1961a) emend. Below 1990	●	●	●
<i>Atopodinium haromense</i> Thomas and Cox 1988	●	●	●
<i>Atopodinium prostaticum</i> Drugg 1978 emend. Masure 1991	●	●	●
<i>Barbatacysta creberbarbata</i> (Erkmen and Sarjeant 1980) Courtinat 1989	●	●	●
<i>Barbatacysta pilosa</i> (Ehrenberg 1854) Courtinat 1989	●	●	●
<i>Barbatacysta verrucosa</i> (Sarjeant 1968) Courtinat 1989	●	●	●
<i>Chlamydophorella ectotabulata</i> Smelror 1989	●	●	●
<i>Chlamydophorella ovula</i> Wheeler and Sarjeant 1990	●	●	●
<i>Chlamydophorella wallala</i> Cookson and Eisenack 1960b	●	●	●
<i>Chytroisphaeridia cerastes</i> Davey 1979d	●	●	●
<i>Chytroisphaeridia chytroides</i> (Sarjeant 1962) Downie and Sarjeant 1965 emend. Davey 1979d	●	●	●
<i>Chytroisphaeridia hvalina</i> (Baynaud 1978) Lentini and Williams 1981	●	●	●
<i>Ciathroctenocystis asapha</i> (Drugg 1978) Stover and Helby 1987b	●	●	●
<i>Cleistosphaeridium sarmentum</i> Stancliff 1991	●	●	●
<i>Compositosphaeridium polonicum</i> (Gorka 1965) Erkmen and Sarjeant 1980	●	●	●
<i>Ctenidodinium combazii</i> Dupin 1968	●	●	●
<i>Ctenidodinium continuum</i> Gocht 1970b	●	●	●
<i>Ctenidodinium ornatum</i> (Eisenack 1935) Deflandre 1938b	●	●	●
<i>Dichadoonvauxia sellwoodii</i> Sarjeant 1975	●	●	●
<i>Dinodinium hardsvaldtii</i> Herngreen et al. 1984	●	●	●
<i>Downiesphaeridium polyacanthum</i> (Gitmez 1970) Islam 1993	●	●	●
<i>Ellipsoidictyum cinctum</i> Klement 1960	●	●	●
<i>Endoscrinium galeritum</i> (Deflandre 1938b) Vozzhennikova 1967	●	●	●
<i>Endoscrinium luridum</i> (Deflandre 1938b) Gocht 1970b	●	●	●
<i>Epilopsphaera gochtii</i> (Fensome 1979) Brenner 1988	●	●	●
<i>Epilopsphaera reticulatum</i> (Valensi 1953) Courtinat 1989	●	●	●
<i>Escharisphaeridia rudis</i> Davies 1983	●	●	●
<i>Escharisphaeridia ruqosa</i> (Courtinat in Courtinat and Gaillard 1980) Courtinat 1989	●	●	●
<i>Evansia barentsensis</i> (Smelror 1988a) Below 1990	●	●	●
<i>Evansia deflandrei</i> (Wolfard and Van Erve 1981) Below 1990	●	●	●
<i>Evansia evitti</i> (Pocock 1972) Jansonius 1986	●	●	●
<i>Evansia cf. reticulospinosa</i> (Dodekova 1975) Jansonius 1986	●	●	●
<i>Fronia tornatilis</i> (Drugg 1978) Lentini and Williams 1981	●	●	●
<i>Gonvaucysta centricornata</i> Ridina 1983	●	●	●
<i>Gonvaucysta eisenackii eisenackii</i> (Deflandre 1938b) Gorka 1965 emend. Sarjeant 1982b	●	●	●
<i>Gonvaucysta jurassica adecta adecta</i> Sarjeant 1982b	●	●	●
<i>Gonvaucysta jurassica adecta longicornis</i> Sarjeant 1982b	●	●	●
<i>Gonvaucysta jurassica desmos</i> Poulsen 1991	●	●	●
<i>Gonvaucysta jurassica jurassica</i> Sarjeant 1982b emend. Poulsen 1991	●	●	●
<i>Hystriochidinium ? lanceolatum</i> Davies 1983	●	●	●
<i>Impletosphaeridium lumectum</i> (Sarjeant 1960) Islam 1993	●	●	●
<i>Impletosphaeridium polytricum</i> (Valensi 1947) Islam 1993	●	●	●
<i>Impletosphaeridium tribuliferum</i> (Sarjeant 1962) Islam 1993	●	●	●
<i>Kallosphaeridium hvornatum</i> Prauss 1989	●	●	●
<i>Korvstocysta pachyderma</i> (Deflandre 1938b) Woollam 1983	●	●	●
<i>Liesbergia liesbergensis</i> Berger 1986	●	●	●
<i>Limbodinium absidatum</i> (Drugg 1978) emend. Ridina 1987b	●	●	●
<i>Lithodinia callomonii</i> (Sarjeant 1972) Gocht 1976	●	●	●
<i>Lithodinia cavtonensis</i> (Sarjeant 1959) Gocht 1976	●	●	●
<i>Lithodinia jurassica</i> Eisenack 1935 emend Gocht 1975b	●	●	●
<i>Lithodinia cf. reticulata</i> (Dodekova 1975) Gocht 1976	●	●	●
<i>Mendicodinium oronlandicum</i> (Pocock and Sarjeant 1972) Davey 1979c	●	●	●
<i>Mosaicodinium mosaicum</i> (Dodekova 1975) Dodekova 1990	●	●	●
<i>Nannoceratopsis gracilis</i> Alberti 1961 emend. Evitt 1962	●	●	●
<i>Nannoceratopsis pellicuda</i> Deflandre 1938b emend. Evitt 1961b	●	●	●
<i>Nannoceratopsis tricerus</i> Drugg 1978	●	●	●
<i>Pareodinia ceratophora</i> Deflandre 1947c emend. Below 1990	●	●	●
<i>Pareodinia ceratophora scoenaeus</i> (Sarjeant 1972) Lentini and Williams 1973 emend. Below 1990	●	●	●
<i>Pareodinia prolouata</i> Sarjeant 1959	●	●	●
<i>Pilosidium asymmetrum</i> (Fenton et al. 1980) Courtinat 1998	●	●	●
<i>Pilosidium echinatum</i> (Gitmez and Sarjeant 1972) Courtinat 1989	●	●	●
<i>Pilosidium fensomei</i> Courtinat 1989	●	●	●
<i>Pilosidium myriatrichum</i> (Fensome 1979) Courtinat 1989	●	●	●
<i>Prolixosphaeridium arapulosum</i> (Deflandre 1937b) Davey et al. 1966	●	●	●
<i>Rhynchodiniopsis cladophora</i> (Deflandre 1938b) Below 1981a	●	●	●
<i>Ricauddella aemula</i> (Deflandre 1938b) Below 1982b	●	●	●
<i>Scrimodinium crystallinum</i> (Deflandre 1938b) Klement 1960	●	●	●
<i>Sentusidinium erythrocorum</i> Erkmen and Sarjeant 1980	●	●	●
<i>Sentusidinium rioutii</i> (Sarjeant 1968) Sarjeant and Stover 1978 emend. Courtinat 1989	●	●	●
<i>Sentusidinium sparsibarbatum</i> Erkmen and Sarjeant 1980	●	●	●
<i>Sentusidinium villersense</i> (Sarjeant 1968) Sarjeant and Stover 1978	●	●	●
<i>Sirmiodiniopsis orbis</i> Drugg 1978	●	●	●
<i>Sirmiodinium grossi</i> Alberti 1961	●	●	●
<i>Stephanelytron brontes</i> nov. sp., this study	●	●	●
<i>Stephanelytron callovianum</i> (Piel 1985) comb. nov. this study	●	●	●
<i>Stephanelytron cavtonense</i> Sarjeant 1961a emend. Stover et al. 1977	●	●	●
<i>Stephanelytron ceto</i> nov. sp. this study	●	●	●
<i>Stephanelytron membranoidium</i> (Vozzhennikova 1967) comb. nov., this study	●	●	●
<i>Stephanelytron redcliffense</i> Sarjeant 1961a emend. Stover et al. 1977	●	●	●
<i>Stephanelytron scarburghense</i> Sarjeant 1961a emend. Stover et al. 1977	●	●	●
<i>Stephanelytron tabulophorum</i> Stover et al. 1977	●	●	●
<i>Surculosphaeridium ? vestitum</i> (Deflandre 1938b) Davey et al. 1966	●	●	●
<i>Systematophora cf. valensi</i> (Sarjeant 1960) Sarjeant 1961	●	●	●
<i>Trichodinium erinaceoides</i> Davies 1983	●	●	●
<i>Trichodinium scarburghense</i> (Sarjeant 1964) Williams et al. 1993	●	●	●
<i>Tubotuberella apatela</i> (Cookson and Eisenack 1960) Ioannides et al. 1977 emend Sarjeant 1982	●	●	●
<i>Tubotuberella dancaardi dancaardi</i> (Sarjeant 1968) Stover and Evitt 1978	●	●	●
<i>Tubotuberella vozhennikovae</i> (Sarjeant 1982) Jan du Chêne et al. 1986	●	●	●
<i>Valensia ovulum</i> (Deflandre 1947) Eisenack 1963 emend Courtinat 1989	●	●	●
<i>Wanaea acollaris</i> Dodekova 1975	●	●	●
<i>Wanaea fimbriata</i> Sarjeant 1961	●	●	●
<i>Wanaea thysanota</i> Woollam 1982	●	●	●

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. cretaceum* 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  $\times 728$ . 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  $\mu\text{m}$ . 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 2<sup>nd</sup> paraplate). **fig. 2.** ? *Stephanelytron brontes* n. sp. Savournon locality. Sample SAV 06. *Lamberti* Zone (Late Callovian; Jurassic). Specimen ref. 63-09-SAV06-52.6/108. England Finder J54/3. Total length 74  $\mu\text{m}$ . Specimen photographed in equatorial view; note the long horn and the reduced corona in ventro-posterior position (presumed on 2<sup>nd</sup> 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  $\mu\text{m}$ . 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 2<sup>nd</sup> 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  $\mu\text{m}$ . 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  $\mu\text{m}$ . 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  $\mu\text{m}$ . 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-SAV15-52.8/1084. England Finder J54/1. Total length 41  $\mu\text{m}$ . 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 coarse nonparatabular processes. **fig. 8.** *Stephanelytron callovianum* (Piel, 1985) comb. nov. Savournon locality. Sample SAV 01. *Lamberti* Zone (Late Callovian; Jurassic). Specimen ref. 63-03-SAV01-44.3/104.6. England Finder N45/1. Total length 44  $\mu\text{m}$ . 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.** *Chlamydothorella ectotabulata* Smelror 1989. Savournon locality. Sample SAV 11. *Lamberti* Zone (Late Callovian; Jurassic). Specimen ref. 63-16-SAV11-59.6/108. England Finder J61. Total length 45  $\mu\text{m}$ . 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  $\mu\text{m}$ . Specimen photographed in equatorial view; note the apical operculum still in place, the reduced corona in ventro-posterior position (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  $\mu\text{m}$ . 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  $\mu\text{m}$ . 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.** *Chlamydothorella ovula* Wheeler & Sarjeant 1990. 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  $\mu\text{m}$ . 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  $\mu\text{m}$ . 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 35  $\mu\text{m}$ . 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 SAV15. *Minax* Zone (Early Oxfordian; Jurassic). Specimen ref. 63-08-SAV15-62.8/104.2. England Finder O64/2. Total length 36  $\mu\text{m}$ . 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.** *Chlamydothorella 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  $\mu\text{m}$ . 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  $\mu\text{m}$ . 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  $\mu\text{m}$ . 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<sup>nd</sup> paraplate).

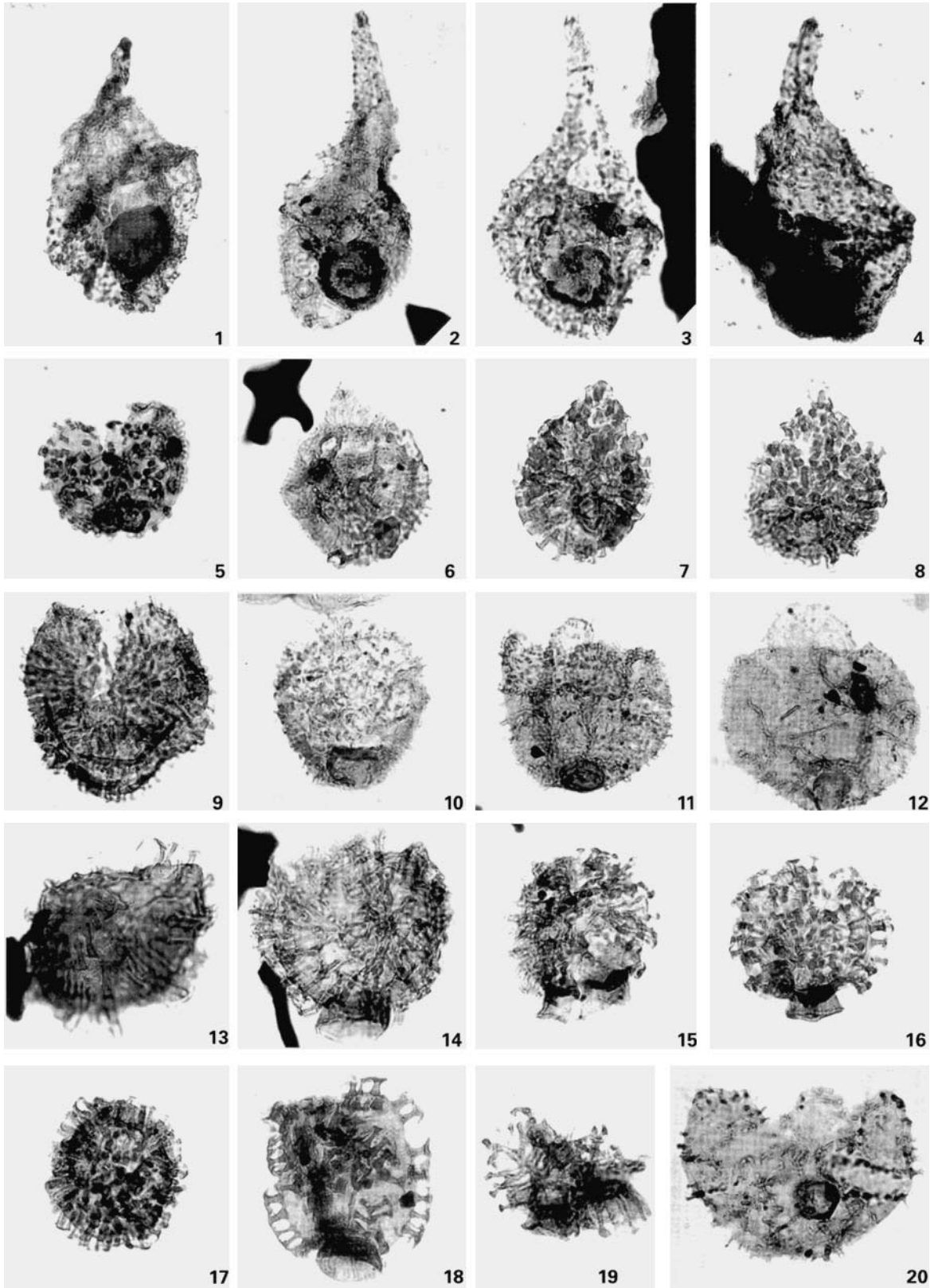


Table 2. Summary of selected morphological features of *Stephanelytron* species.

species	apical horn	corona	elements of paratabulation	arrangement of processes	type of processes	autophragm	archeopyle operculum
<i>Stephanelytron redcliffense</i> Sarjeant 1961 emend. Stover et al., 1977 - types species ? <i>Stephanelytron brontes</i> new species	no yes long	one, smooth wall on 1 <sup>st</sup> paraplate; flaring; thick base with mass of setae or spinules one, smooth wall on 2 <sup>nd</sup> paraplate; low and straight; thick base; intra corona area smooth	archeopyle and parasutural processes archeopyle; only	few parasutural processes, transverse on paracingulum dense cover of non paratabular processes	cylindrical, tubiform to buccinate, non-perforate cylindrical, tubiform to buccinate, non-perforate	smooth faintly granulate smooth faintly granulate	probably apical free unknown
<i>Stephanelytron callovianum</i> (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 para- cingulum or parasulcus	dense cover of non paratabular processes	tubiform, non-perforate	smooth faintly granulate	apical (tA) free
<i>Stephanelytron caytonense</i> Sarjeant 1961 emend. Stover et al. 1977	no	one, smooth wall on 1 <sup>st</sup> paraplate; slightly flaring; thick base; intra corona area smooth	archeopyle; only	few non paratabular or a ill-defined row of processes	tubiform to buccinate, finely perforate	smooth	apical free
<i>Stephanelytron ceto</i> 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 penitabular processes	cylindrical, tubiform to buccinate, non-perforate	smooth	apical free
<i>Stephanelytron cretaceum</i> Duxbury 1983	no	one, smooth wall on 1 <sup>st</sup> 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
<i>Stephanelytron membranoidium</i> (Vozzhennikova 1967 emend. Lentin and Vozzhennikova 1990) comb. nov.	no	one, smooth wall on 2 <sup>nd</sup> 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
<i>Stephanelytron scarburghense</i> Sarjeant 1961 emend. Stover et al. 1977	no	one or occasionally two, smooth wall on 1 <sup>st</sup> and 2 <sup>nd</sup> (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
<i>Stephanelytron tabulophorum</i> Stover et al. 1977	no	one, smooth wall on 2 <sup>nd</sup> paraplate; slightly flaring; thick base with processes intra area	archeopyle, paracingulum, accessory archeopyle suture	few parasutural and penitabular 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 <i>Stephanelytron</i> Sarjeant 1961 emend.						
one or two reduced coronas in ventral-posterior 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	? <i>S. brontes</i>
			length of apical horn <20% of the diameter of central body	two or occasionally one coronas; no intra corona processes	R = 0,06	<i>S. calloivianum</i>
one or two elevated coronas in antapical position	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	<i>S. ceto</i>
				intra corona processes	R = 0,04-0,08	<i>S. tabulophorum</i>
	processes non-tabular	apical horn	length of apical horn <20% of the diameter of central body	one corona ; intra corona area densely granular	R = 0,14	<i>S. cretaceum</i>
			processes non-perforate	one or occasionally two coronas; intra corona area with mass of setae	R = 0,12-0,20	<i>S. scarburghense</i>
		no apical horn	processes perforate	one or occasionally two coronas; intra corona area smooth	R = 0,10-0,18	<i>S. caytonense</i>
			processes non-perforate	one coronas; intra corona area with setae or spinules	R = 0,16-0,30	<i>S. redcliffense</i>
processes in parasutural position; paracingulum expressed by transverse processes	processes in intratabular position; paracingulum indicated by alignment of processes		one coronas; intra corona processes	R = 0,10-0,30	<i>S. membranoidium</i>	

Table 4. Citations of species of *Stephanelytron* and selected species of *Chlamydochorella*, referred to ammonite zones.

species	Citation of the first appearance	Other citations	Citation of the last appearance
<i>Stephanelytron reddiffense</i> Sarjeant 1961 emend. Stover et al. 1977  types species	Feist-Burkardt and Wille 1992 ( <i>Koeneigi</i> Zone; Germany)	Sarjeant 1962 ( <i>Cordatum</i> Zone; England) Sarjeant 1968 ( <i>Mariae/Cordatum</i> Zones; France) Gitmez and Sarjeant 1972 ( <i>Cymodoce/Baylei</i> Zones; France) Sarjeant 1979 ( <i>Mariae/Baylei</i> Zones; World excluding N. America) Erkmen and Sarjeant 1980 ( <i>Lamberti</i> Zone; Scotland, England) Herngreen et al. 1984 ( <i>Athleta/Lamberti</i> Zones; Netherlands) Arhus et al. 1986 ( <i>Mariae/Cordatum</i> Zones; Norway) Berger 1986 ( <i>Mariae</i> Zone; Switzerland) Dürr 1988 ( <i>Planula/Cymodoce</i> Zones; Germany) Smelror 1988 ( <i>Lamberti/Mariae</i> Zones; Spitsberg) Thomas and Cox 1988 ( <i>Serratum/Regulare</i> Zones; England) Prauss 1989 ( <i>Athleta/Lamberti</i> Zones; Germany) Dimter and Smelror 1990 ( <i>Jason</i> Zone; Germany) Dodekova 1990 (Mid Callovian; Bulgaria) Wierzbowski and Arhus 1990 ( <i>Glosense</i> Zone; Barents Sea)	Feist-Burkardt and Wille 1992 ( <i>Mutabilis</i> Zone; Germany)
? <i>Stephanelytron brontes</i> new species	<i>Lamberti</i> Zone this study		<i>Minax</i> Zone this study
<i>Stephanelytron callovianum</i> (Piel 1985) comb. nov.	Dodekova 1990 (Lower Bathonian; Bulgaria)	Piel 1985 ( <i>Coronatium</i> Zone; England)	Piel 1985 ( <i>Lamberti</i> Zone; England)
<i>Stephanelytron caytonense</i> Sarjeant 1961 emend. Stover et al. 1977	Prauss 1989 ( <i>Coronatium</i> Zone; Germany)	Sarjeant 1968 ( <i>Lamberti</i> Zone; France) Courtinat 1980 ( <i>Bimammatum</i> Zone; France) Erkmen and Sarjeant 1980 ( <i>Lamberti</i> Zone; England) Courtinat 1989 ( <i>Minax/Acanthicum</i> Zones; France)	Fensome 1979 (Mid Kimmeridgian; Greenland)
<i>Stephanelytron ceto</i> new species	<i>Lamberti</i> Zone this study		<i>Minax</i> Zone this study
<i>Stephanelytron cretaceum</i> Duxbury 1983	Davey 1979 ( <i>Runctoni</i> Zone; NW Europe)	Lister and Batten 1988 (Lower Aptian; England)	Duxbury 1983 (Early Aptian; England)
<i>Stephanelytron membranoidium</i> (Vozzhennikova 1967 emend. Lentin and Vozzhennikova 1990) comb. nov.	Habid and Drugg 1983 (Late Callovian; Blake Bahama basin)	Sarjeant 1979 ( <i>Weatleyensis</i> Zone; World excluding N. America) Davey 1982 (Early Portlandian/Hauterivian; Denmark) Zotto et al. 1987 ( <i>Baylei/Cymodoce</i> Zones; N. Atlantic)	Davey 1987 (Late Hauterivian; Papua New Guinea)
<i>Stephanelytron scarburghense</i> Sarjeant 1961 emend. Stover et al. 1977	Feist-Burkardt and Wille 1992 ( <i>Herveyi</i> Zone; Germany)	Sarjeant 1968 ( <i>Mariae/Cordatum</i> Zones; France) Erkmen and Sarjeant 1980 ( <i>Lamberti</i> Zone; Scotland, England) Berger 1986 ( <i>Coronatium</i> Zone; Switzerland) Dürr 1988 ( <i>Planula/Galar</i> Zones; Germany) Riding and Thomas 1988 ( <i>Baylei/Mutabilis</i> Zones; England) Prauss 1989 ( <i>Coronatium</i> Zone; Germany) Dodekova 1990 (Mid Callovian; Bulgaria) Stancliffe 1991 ( <i>Pseudochordata</i> Zone; England) Feist-Burkardt and Wille 1992 ( <i>Herveyi</i> Zone; Germany)	Zotto et al. 1987 ( <i>Autissiodorensis</i> Zone; N. Atlantic)
<i>Stephanelytron tabulophorum</i> Stover et al. 1977	Prauss 1989 ( <i>Jason</i> Zone; Germany)	Stover et al. 1977 ( <i>Athleta/Lamberti</i> Zones; Germany) Herngreen et al. 1984 ( <i>Athleta/Lamberti</i> Zones; Netherlands)	<i>Minax</i> Zone this study
<i>Chlamydochorella raritubulae</i> Dodekova 1975	Sarjeant 1979 ( <i>Morrisi</i> Zone; World)	Dodekova 1975 (Late Bathonian; Bulgaria)	Dodekova 1990 (Late Callovian; Bulgaria)
<i>Chlamydochorella ectotabulata</i> Smelror 1988	Smelror 1989 ( <i>Variabile</i> Zone; Greenland)	Smelror 1988 ( <i>Discus</i> Zone; Spitsberg) Dodekova 1990 (Late Bathonian; Bulgaria)	Smelror 1988 ( <i>Densiplicatum</i> Zone; Spitsberg)
<i>Chlamydochorella wallala</i> Cookson and Eisenack 1960	Habid and Drugg 1983 (Late Callovian; Blake Bahama basin)	Davey 1987 (Early Oxfordian/Early Kimmeridgian; Papua New Guinea) Dodekova 1992 (Late Oxfordian; Bulgaria)	Sarjeant 1979 ( <i>Giganteus</i> Zone; World)



## SYSTEMATIC MICROPALAEONTOLOGY

Division **Pyrrhophyta** Pascher, 1914

Class **Dinophyceae** Fritsch, 1929

Order **Peridiniales** Haeckel, 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 mat 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 autophragm, gives rise to usually short processes; outer wall, the ectophragm, thin and may be discontinuous. Processes frequently arranged in parasutural rows, less commonly non tabular; some forms have parasutural and scattered non tabular processes, penitabular processes being present one species. Processes cylindrical 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<sup>?</sup>, 5<sup>''</sup> X-6c, 5<sup>'''</sup>, 0-1p, 1<sup>''''</sup>, 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; autophragm 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-?6c, ?5''', 0-1p, 1<sup>''''</sup>, 2s; archeopyle apical probably type (tA), 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 ectophragm, entire or incomplete, frequently wrinkled, covers the processes; antapical pole with one or two coronas; coronas in antapical (1<sup>''''</sup>) or ventral-posterior position (probably the 2<sup>''''</sup>, 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. redcliffense* 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  $\mu\text{m}$ ; equatorial diameter

of central body, 30  $\mu\text{m}$ ; length of processes, 5-9  $\mu\text{m}$   $R=0.16-0.30$  ( $R$ =length of processes/equatorial diameter of central body).

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

**Geographical location.** England (Yorkshire, Cayton Bay).

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

**Stratigraphic range.** See Table 4.

### Other species

?*Stephanelytron brontes* n. sp. (this study), Plate 1, figs 1-4

**Holotype.** This study, Plate 1, fig. 2

**Dimensions.** Length of central body (without horn), 50  $\mu\text{m}$ ; equatorial diameter of central body, 46  $\mu\text{m}$ ; length of processes, 2  $\mu\text{m}$ ;  $R=0.04$ .

**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  $\mu\text{m}$ ; equatorial diameter of central body, 29  $\mu\text{m}$ ; length of processes, 2  $\mu\text{m}$ ;  $R=0.06$ .

**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 *Wanaea thysanota* 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  $\mu\text{m}$ ; equatorial diameter of central body, 60  $\mu\text{m}$ ; length of processes, 6-11  $\mu\text{m}$ ;  $R=0.10-0.18$ .

**Age.** Early Oxfordian (*Cordatium* 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  $\mu\text{m}$ ; equatorial diameter of central body, 40  $\mu\text{m}$ ; length of processes, 1-2  $\mu\text{m}$ ;  $R=0.03-0.06$

**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  $\mu\text{m}$ ; equatorial diameter of central body, 49  $\mu\text{m}$ ; length of processes, about 7  $\mu\text{m}$  (from original illustration);  $R$ =about 0.14.

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

**Dimensions.** Length of central body, 46  $\mu\text{m}$ ; equatorial diameter of central body, 43  $\mu\text{m}$ ; length of processes, 5–6  $\mu\text{m}$ ;  $R$ =0.11–0.13.

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

**Dimensions.** Length of central body, 47  $\mu\text{m}$ ; equatorial diameter of central body, 51  $\mu\text{m}$ ; length of processes, 5–6  $\mu\text{m}$ ;  $R$ =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  $\mu\text{m}$ ; equatorial diameter of central body, 40  $\mu\text{m}$ ; length of processes, 5–8  $\mu\text{m}$ .  $R$ =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  $\mu\text{m}$ ; equatorial diameter of central body, 40  $\mu\text{m}$ ; length of processes, 1–4  $\mu\text{m}$ ;  $R$ =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

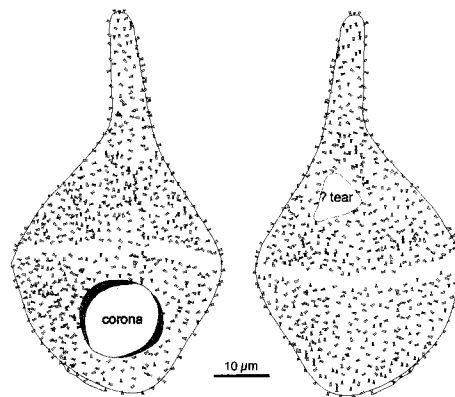


Fig. 2. Idealized specimen of ?*Stephanelytron brontes* (from holotype).

**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, holocavate; 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<sup>nd</sup> 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  $\mu\text{m}$ ; length of central body, 54  $\mu\text{m}$ ; equatorial diameter of central body, 40  $\mu\text{m}$ ; length of processes, 1–2  $\mu\text{m}$ ; diameter of corona, 14  $\mu\text{m}$ ;  $R$ =0.02–0.05.

**Variations.** Length of horn, 16–28  $\mu\text{m}$ ; length of central body, 42–66  $\mu\text{m}$ ; equatorial diameter of central body, 28–45  $\mu\text{m}$ ; length of processes, 1–3  $\mu\text{m}$ ; diameter of corona, 10–16  $\mu\text{m}$ ;  $R$ =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.

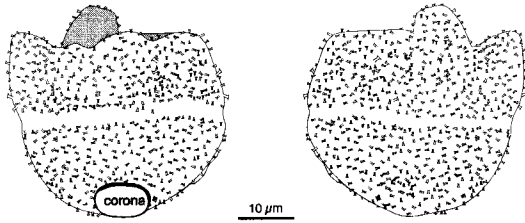


Fig. 3. Idealized specimen of *Stephanelytron ceto* (from holotype).

*Stephanelytron ceto* n. sp.  
Plate 1, figs 10–12; Fig. 3

**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, holocavate; 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 being five precingular paraplates, a paracingulum and an archeopyle. Archeopyle apical. One corona in ventral–posterior position is present probably on the ps paraplate; base of coronas 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 = *Mariae* 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<sup>nd</sup> 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 STEPHANELYTRON

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 *Chlamydothorella*-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 *Stephanelytracae* evolved from a single process of *Chlamydothorella* (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 *Chlamydothorella* present at that time, i.e. *C. raritubulae* Dodekova, 1975 or *C. ectotabulata* Smelror, 1989 (Plate 1, fig. 9) or from another *Chlamydothorella*-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 *Chlamydothorella* lineage. The common ancestor from *Chlamydothorella*-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 *Chlamydothorella* ancestor, possibly *C. ectotabulata*, 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 *Chlamydothorella*.

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.*

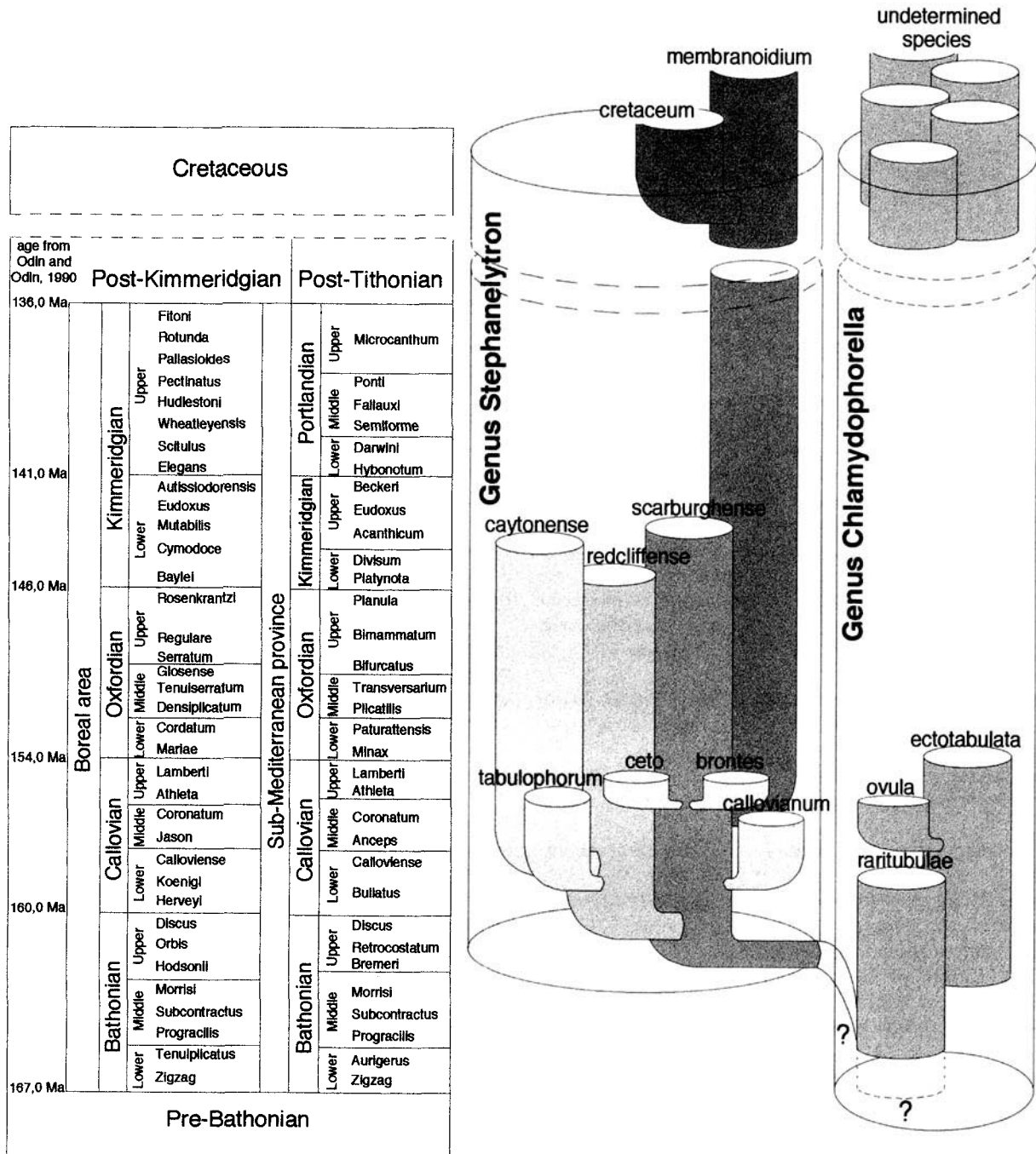


Fig. 4. Speculative scenario of evolutionary relationship between *Stephanelytron* and *Chlamydophorella* species (correlation of ammonite zones from Groupe Francais d'étude du Jurassique, 1997).

*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. callovanum* (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. callovanum* and *S. ceto* may represent a case of peripatric speciation from an unfavourable mutation.

## ACKNOWLEDGEMENTS

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

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