A REVISION OF THE STRATIGRAPHIC HISTORY OF THE GENUS \textit{STEPHANOLITHION} \\
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INTRODUCTION
The genus \textit{Stephanolithion} is elliptical in shape with a modified protolith rim possessing lateral spines or protuberances. The central area has two to eight arms arranged, typically, symmetrically around a small central vertical spine. The genus was first designated by Deflandre in 1939 and is one of the oldest establish nannofossils genera. Because of their morphology species are easily identified and have an uncluttered taxonomy and synonymy. This has also led them being widely used as biostratigraphic marker species. One or more species of this genus have appeared in all the published zonation schemes for the Jurassic. In the most recent scheme (Bown, Cooper and Lord 1988) a total of six species of this genus were used in defining zones or subzones.

As a result of new species being defined and the adjustment of ranges of established species, it has become necessary to revise the stratigraphic history and evolutionary lineage of the genus \textit{Stephanolithion}.

This paper is a result of research carried out to establish an early to mid Mesozoic biozonation (Bown et al. 1988) and also as part of the author's Ph.D studies.

HISTORY OF STUDY
The first detailed study of the genus \textit{Stephanolithion} was undertaken by Rood and Barnard (1972). Even though they examined most of the Jurassic their study was selective and incomplete with some ammonite zones remaining unexamined. In that paper, the subspecies \textit{S. speciosum octum} and the species \textit{S. hexum} were described. The study explained the evolution of \textit{S. speciosum} into \textit{S. speciosum octum} and \textit{S. hexum} but did not suggest any evolutionary link to \textit{S. bigotii}. Additionally, although showing \textit{Stephanolithion} as continuing into the Early Cretaceous with the species \textit{S. laffittei}, the authors questioned the validity of the generic assignment of this species.

The next publication involving this genus was Medd (1979) on the Haddenham and Gamlingay boreholes in Cambridgeshire. Medd mainly covered the Late Jurassic and recognised one new species and two new subspecies; \textit{Stephanolithion carinatum}, \textit{S. speciosum elongatum} and \textit{S. bigotii maximum}. No discussion of the evolutionary history of the genus was attempted although the range of \textit{S. bigotii} was extended upward into the Kimmeridgian.

Perch-Nielsen (1985), updated the evolutionary history of \textit{Stephanolithion} to include the new data from Medd (1979). Furthermore, she suggested that the ancestor of \textit{Stephanolithion} was \textit{Stradnerlithus comptus}, which may have given rise to \textit{S.speciosum} in the Early Bajocian. She also considered that \textit{S.speciosum} was the ancestor of \textit{S. speciosum octum} and possibly \textit{S. hexum}, as well as Medd's \textit{S. speciosum elongatum} and \textit{S. carinatum}. She placed the Cretaceous species \textit{S. laffittei} into a separate genus \textit{Rotelapillus}, thus restricting the genus \textit{Stephanolithion} to the Jurassic.

Cooper (1987) studied material from the type Volgian and from these samples one new species of \textit{Stephanolithion} was described, \textit{S. atmetros}, and a new combination was proposed; \textit{S. helotatus} (basionym \textit{Corollithion helotatus} Wise & Wind 1977). Additionally, the last occurrence of \textit{S. bigotii} was extended from the Kimmeridgian up to the Middle Volgian.

EVOLUTIONARY LINEAGE
The first occurrence of the oldest species in this genus, \textit{S. speciosum}, is considered to be at the top of the Early Bajocian (see Fig.) The most likely ancestor for this species is \textit{Stradnerlithus asymmetricus} (Rood et al. 1971), Medd (1979). This species occurs in the same samples as \textit{S. speciosum} and is morphologically similar, having eight bars in the central area but lacking the lateral spines of \textit{S. speciosum}. In the Late Bajocian, \textit{S. speciosum} gave rise to \textit{S. speciosum octum} by an increase in the length of the lateral spines. The next evolutionary change occurred in the Bathonian with the first occurrence of \textit{S. hexum}; this species has only six bars in the central area and long lateral spines. The probable ancestor for this species is \textit{S. speciosum}.
octum which, although it has eight bars, does possess long lateral spines.

*S. speciosum speciosum* also gave rise to a number of other forms during the later part of the Middle Jurassic. At the top of the Bathonian, *S. elongatum* first appeared. This species is similar to *S. speciosum speciosum* in that it has short lateral spines and eight arms in the central area. However, its shape is considerably more elliptical than *S. speciosum speciosum*. Also first recorded at this level is a large form of *S. speciosum speciosum* very similar in size to the forms of *S. bigotii* seen in the Early Oxfordian that have been assigned to the subspecies *S. bigotii maximum*. Due to a lack of adequate photographs this form has not yet been formally described. Another species with *S. speciosum speciosum* as its possible ancestor is *S. carinatum* which appeared first in the Oxfordian. This latter species has short lateral spines and seven or eight arms randomly arranged in the central area, in contrast to *S. speciosum speciosum* which has symmetrically arranged arms.

The next significant event in the evolutionary history of the genus *Stephanolithion* was the first occurrence of *S. bigotii bigotii* in the lower part of the Callovian. This species appears to have evolved from *S. hexum* by the loss of a pair of central area arms. Subsequent subspeciation appears to be evidenced by the occurrence of the short-ranging *S. bigotii maximum* (topmost Callovian to early Oxfordian). This subspecies is very similar in form to *S. bigotii bigotii* but is much larger (*S. bigotii bigotii* has an average size with spines of 4.3 X 3.5 m whereas *S. bigotii maximum* is defined as being over 6.0 X 3.0 m). Also probably related to *S. bigotii bigotii* is *S. helotatus*. It has four arms in the central area but its lateral spines are very short, and can be absent on etched specimens. *S. helotatus* first appears in the Kimmeridgian and ranges up into the Middle Volgian. In the Middle Volgian, the last true species of *Stephanolithion*, *S. atmetros* appears. It has an elliptical shape, small or no lateral spines and a single pair of arms in the central area forming a crossbar parallel to the small axis of the ellipse. It is likely that *S. atmetros* evolved from *S. helotatus* by the loss of, or merging of, a pair of arms. The highest occurrence of this species in the Jurassic is basal Portlandian and no true species of *Stephanolithion* are known from the Cretaceous.

The Cretaceous species *S. laffittei*, is now regarded as belonging to the genus *Rotelapillus*, not *Stephanolithion*, and this species can be shown to have evolved from *R. radians* during the terminal Jurassic stage. The species *R. radians*, the ancestral form of the *Rotelapillus*, probably evolved from the species *Stradnerlithus fragilis* an eight armed form of this genus. Both of these species have been recorded from the Middle Volgian and, even though *S. fragilis* is elliptical rather than round like *R. radians*, in these Middle Volgian samples, many of the specimens of *S. fragilis* have very low ellipticity.

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SPECIES CITED

*Rotelapillus laffittei* (Noel, 1957) Noel 1973
*Rotelapillus radians* Noel 1973
*Stephanolithion atmetros* Cooper 1987
*Stephanolithion bigotii* Deflandre 1939
*Stephanolithion bigotii maximum* Medd 1979
*Stephanolithion carinatum* Medd 1979
*Stephanolithion helotatus* (Wind & Wise, 1977) Cooper 1987
*Stephanolithion hexum* Rood & Barnard 1972
*Stephanolithion speciosum* Deflandre 1954
*Stephanolithion speciosum elongatum* Medd 1979
*Stephanolithion speciosum octum* Rood & Barnard 1972
*Stradnerlithus asymmetricus* (Rood et al. 1971) Medd 1979
*Stradnerlithus fragilis* (Rood & Barnard 1972) Perch-Nielsen 1984
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Development of the *Stephanololithion* lineage during the Jurassic