

A revision of the Turrilitidae (Cretaceous Ammonoidea) from the Cambridge Greensand

M. R. Cooper, Durban

With 10 figures

COOPER, M. R. (1998): A revision of the Turrilitidae (Cretaceous Ammonoidea) from the Cambridge Greensand. – N. Jb. Geol. Paläont. Abh., 207: 145–170; Stuttgart.

Abstract: The Turrilitidae of the Cambridge Greensand are represented by 6 species assigned to 4 genera viz. *Turrilitoides hugardianus* (D'ORBIGNY), *Ostlingoceras puzosianum* (D'ORBIGNY), *Mariella bergeri* (BRONGNIART), *Paraturrilites escherianus* (PICTET), *P. circumtaeniatus* (KOSSMAT) and *P. hillyi* DUBOURDIEU. Sexual dimorphism is suspected in *Turrilitoides* and, perhaps also, *Ostlingoceras*. The genus *Paraturrilites* is resurrected.

Zusammenfassung: Die Turrilitidae sind im Cambridge-Greensand durch 6 Arten vertreten, die 4 Gattungen zugeordnet werden, nämlich *Turrilitoides hugardianus* (D'ORBIGNY), *Ostlingoceras puzosianum* (D'ORBIGNY), *Mariella bergeri* (BRONGNIART), *Paraturrilites escherianus* (PICTET), *P. circumtaeniatus* (KOSSMAT) und *P. hillyi* DUBOURDIEU. Sexualdimorphismus wird bei *Turrilitoides* (und auch bei *Ostlingoceras*) vermutet. Die Gattung *Paraturrilites* wird wieder aufgestellt.

The present study is a continuation of the revision of the Cambridge Greensand faunas based upon statistical analysis of material in the Sedgwick Museum (SM), Cambridge. Like earlier studies in this series (COOPER & KENNEDY 1978, 1987, COOPER 1990), it demonstrates that many co-existing generic nominal species are based upon intraspecific variants (morphotypes) of a single polytypic species.

As currently perceived, the turrilites comprise an allegedly polyphyletic group of helically-coiled Cretaceous ammonites which first appeared early in the Middle Albian and attained their acme in the Lower Cenomanian; the undoubtedly examples are known from the Upper Cenomanian (COBBAN & KENNEDY 1981). Although widely believed to have given rise to late Cretaceous Turoceratinae (MATSUMOTO 1967, KLINGER & KENNEDY 1978, WRIGHT 1981), the evidence is not overwhelming and the similarities could be the result of convergence.

Suborder Turrilitina BESNOSOV & MIKHAILOVA, 1983
 Superfamily Turrilitaceae MEEK, 1876
 Family Turrilitidae MEEK, 1876
 Subfamily Turrilitinae MEEK, 1876
 Genus *Turrilitoides* SPATH, 1923

Type species: *Turrilites hugardianus* D'ORBIGNY; by original designation.

Diagnosis: Generally small, non-tuberculate turrilites with well-developed, simple, oblique ribs and the siphuncle situated near the top of the exposed whorl face. In small forms (?microconchs), ornament becomes obsolete on the adult body chamber and there is a collared apertural constriction.

Remarks: The genus *Turrilitoides* was introduced (SPATH 1923, p. 525) for a group of turriliticone ammonites which first appeared in the upper Middle Albian, derived from early Middle Albian *Proturrilitoides*. Such a phylogeny is supported both morphologically and stratigraphically, and is widely accepted (SPATH 1937, KLINGER & KENNEDY 1978, CHIRIAC 1981, 1988); it involves reductions in the spiral angle and size of the umbilicus, i. e. tighter coiling, accompanied by a shift of the siphuncle to the upper margin of the flank and, in the (?microconch, loss of ornament on the adult body chamber.

As noted by SPATH (1937, p. 520), there are many embarrassing passage forms between *Turrilitoides* and *Paraturrilites*, e. g. SM B 98582 (Fig. 4.1), 98585 (Fig. 1.28) and 98592 (Fig. 1.19), an observation re-emphasized herein, under discussion of the latter taxon, and a phyletic relationship is indicated (SCHOLZ 1979).

- Turrilitoides hugardianus* (D'ORBIGNY, 1842) Figs. 1.1-32, 2, 6, 7A, 8B
 1842 *Turrilites hugardianus* D'ORBIGNY. – p. 588, pl. 147, figs. 9-11.
 1847 *Turrilites hugardianus* D'ORBIGNY. – PICTET in PICTET & ROUX, p. 155, pl. 15, fig. 12.
 1854 *Turrilites hugardianus* D'ORBIGNY. – PICTET, p. 712.
 1860 *Turrilites hugardianus* D'ORBIGNY. – OOSTER, p. 95.
 1861 *Turrilites intermedius* PICTET & CAMPICHE. – p. 127, pl. 57, fig. 14.
 1861 *Turrilites hugardianus* D'ORBIGNY. – PICTET & CAMPICHE, p. 128, pl. 57, figs. 1-7.
 1866 *Turrilites hugardianus* D'ORBIGNY. – PICTET & RENEVIER, p. 105.
 1875 *Turrilites toucasi* HÉBERT & MUNIER-CHALMAS. – p. 117, pl. 5, fig. 8.
 1923 *Turrilitoides hugardianus* (D'ORBIGNY). – SPATH, p. 75.

Fig. 1. *Turrilitoides hugardianus* (D'ORBIGNY). 1, SM B98741; 2, SM B98734; 3, SM B98583; 4, SM B98737; 5, SM B98750; 6, SM B98739; 7, SM B39379; 8-10, SM B98740; 11, SM B98733; 12, SM B98747; 13, SM B98738; 14, SM B98736; 15, SM B98752; 16, SM B98742; 17, SM B98735; 18, SM B98577; 19, SM B98592; 20, SM B98580; 21, SM-B98584; 22, SM B98576, 23, SM B98745; 24, SM B98743; 25, SM B39339; 26, SM B39356; 27, SM B39358; 28, SM B98585; 30, no number; 31, SM B39341; 32, SM B39347. *Ostlingoceras puzosianum* (D'ORBIGNY). 29, SM-B39377. All x 1.

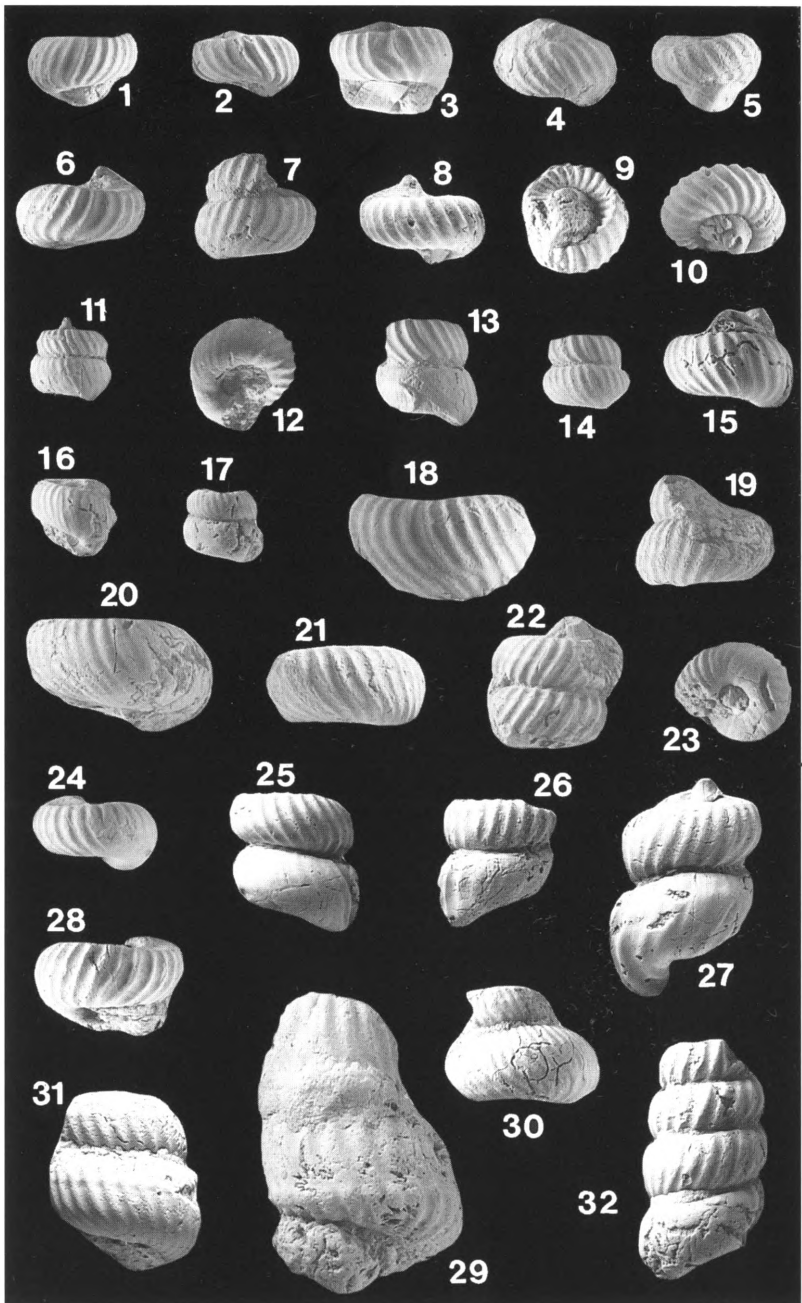


Fig. 1 (Legend see p. 146)

- 1875 *Turrilites hugardianus* D'ORBIGNY. – NEUMAYR, p. 32.
 1890 *Turrilites hugardianus* D'ORBIGNY. – RENEVIER, p. 339.
 1926a *Turrilitoides hugardianus* (D'ORBIGNY). – SPATH, p. 429.
 1931 *Turrilitoides* cf. *hugardianus* (D'ORBIGNY). – BREISTROFFER, p. 232.
 1936 *Turrilitoides hugardianus* (D'ORBIGNY). – BREISTROFFER, p. 67.
 1937 *Turrilitoides hugardianus* (D'ORBIGNY). – SPATH, p. 526, pl. 58, figs. 12-20, text-figs. 184a-i.
 1937 *Turrilitoides intermedius* (PICTET & CAMPICHE). – SPATH, p. 527.
 1937 *Turrilitoides hugardianus* var. *crassicosata* SPATH. – p. 527, pl. 58, fig. 20.
 1937 *Turrilitoides toucasi* (HÉBERT & MUNIER-CHALMAS). – SPATH, p. 528, text-figs. 185a-d.
 1940 *Turrilitoides hugardianus* (D'ORBIGNY). – BREISTROFFER, p. 80.
 1947 *Turrilitoides hugardianus* (D'ORBIGNY). – BREISTROFFER, p. 44.
 1947 *Turrilitoides hugardianus* var. *crassicosata* SPATH. – BREISTROFFER, p. 44.
 1947 *Turrilitoides toucasi* (HÉBERT & MUNIER-CHALMAS). – BREISTROFFER, p. 44.
 1947 *Turrilitoides intermedius* (PICTET & CAMPICHE). – BREISTROFFER, p. 44.
 1947 *Turrilitoides* sp. nov. – BREISTROFFER, p. 44.
 1962 *Turrilitoides intermedius* (PICTET & CAMPICHE). – WIEDMANN, p. 189, pl. 13, fig. 7.
 1968 *Turrilitoides (Turrilitoides) hugardianus hugardianus* (D'ORBIGNY). – RENZ, p. 84, pl. 17, figs. 18-21, text-fig. 30a-d.
 1968 *Turrilitoides (Turrilitoides) hugardianus crassicosatus* SPATH. – RENZ, p. 84, pl. 17, figs. 22-23.
 1968 *Turrilitoides (Turrilitoides) intermedius* (PICTET & CAMPICHE). – RENZ, p. 84, pl. 17, figs. 24-26, text-fig. 30f.
 1968 *Turrilitoides hugardianus* (D'ORBIGNY). – WIEDMANN & DIENI, p. 78, pl. 9, fig. 3, text-figs. 57-58.
 1971 *Turrilitoides (Turrilitoides) hugardianus* (D'ORBIGNY). – NAGY, p. 20, pl. 2, figs. 5-6.
 1971 *Turrilitoides (Turrilitoides) hugardianus* aff. *crassicosatus* SPATH. – NAGY, p. 21.
 1973 *Turrilitoides (Turrilitoides) hugardianus* (D'ORBIGNY). – NAGY, p. 94.
 1973 *Turrilitoides (Turrilitoides) hugardianus* aff. *crassicosatus* SPATH. – NAGY, p. 94.
 1978 *Turrilitoides hugardianus* D'ORBIGNY. – KLINGER & KENNEDY, pl. 9, fig. K.
 1979 *Turrilites (Turrilitoides) hugardianus hugardianus* D'ORBIGNY. – SCHOLZ, p. 34, pl. 7, figs. 1-14, text-figs 11A-D.
 ?1979 *Turrilites (Turrilitoides) hugardianus densicosatus* PASSENDORFER. – SCHOLZ, p. 35.
 1981 *Turrilitoides hugardianus* (D'ORBIGNY). – CHIRIAC, p. 45.
 1988 *Turrilitoides hugardianus* (D'ORBIGNY). – CHIRIAC, p. 53.
 1988 *Turrilitoides intermedius* (PICTET & CAMPICHE). – CHIRIAC, p. 52.
 1988 *Turrilitoides toucasi* (HÉBERT & MUNIER-CHALMAS). – CHIRIAC, p. 52.
- Holotype: SPATH (1937, p. 526) selected as lectotype the original of the smaller of the two individuals figured by D'ORBIGNY (1842, pl. 147, figs. 9-10) from Montagne des Fiz, Savoy, France; it is in the Muséum d'Histoire Naturelle de Paris, MHNP-R1059.
- Material: 63 specimens, SM-B39260, 39337, 39339-43, 39346-7, 39349, 39351, 39353-4, 39356, 39358, 39360, 39362-64, 39374, 39377, 39379, 41239-41, 98534, 98543, 98576-77, 98579-81, 98583-85, 98587-88, 98590-94, 98733-43, 98745-50, 98752-53, 98755, 99333 and one unnumbered SM specimen, all preserved as phosphatic internal moulds.

Diagnosis: A *Turrilitoides* displaying substantial variation in rib density, from 16-43 per whorl (usually 26-28). All ribs are single and oblique but, on the adult body chamber, they may weaken considerably, becoming flexuous and sometimes bifurcating (Fig. 1.18) or even trifurcating; in some (?microconchs) the last 3/4 of a whorl becomes smooth (Fig. 1.25-26, 32, 2.6, 12). The apical angle is moderately small (Fig. 1.32), generally between 10-20°, but sometimes (?macroconchs) as high as 43° (Fig. 2.21-23). Coiling is both sinistral and dextral.

Intraspecific variation: The most noteworthy variation in the material available relates to rib density, which varies between 16-43 ribs per whorl with a distinct peak at 26-28 (Fig. 6). This distribution is somewhat lower than the peak identified by SCHOLZ (1979), but is based on less material. Although, invariably, ribbing is single up to the final adult whorl, densely ribbed variants, e. g. SM-B99333, show bifurcating ribs on the adult body chamber, viz. the character used to separate *T. toucasi* (HÉBERT & MUNIER-CHALMAS). The apical angle is reasonably constant (Fig. 7A), with most individuals falling between 10-19°, but does range up to 43° in *intermedius* morphotypes, i. e. ?macroconchs. Coiling is both sinistral and dextral, with a slight preponderance of the former.

An intriguing feature of the material assigned here is that although many individuals are adult at relatively small size (Fig. 4B), and preserve a smooth or almost smooth adult body chamber (Fig. 1.25), *intermedius* morphotypes attain a much larger adult size and retain strong ribbing to the largest preserved diameter, without any sign of modification to the body-chamber ornament. This suggests either the species is dimorphic or that two different species are involved; here the former interpretation is preferred.

Remarks: Despite noting transitions, SPATH (1937) considered two species of *Turrilitoides* to be present in the Cambridge Greensand, viz. *T. hugardianus* (D'ORBIGNY) and *T. toucasi* (HÉBERT & MUNIER-CHALMAS), the latter distinguished by frequent bifurcation, and occasionally even trifurcation, of the ribs on the body chamber. Although such bifurcation is not common, it occurs on the adult body chamber of some small individuals which are interpreted as microconchs. As a result, the differences are not considered taxonomically significant and SCHOLZ (1979) is followed in regarding *Turrilitoides toucasi* a subjective junior synonym of *T. hugardianus*.

Turrilitoides hugardianus var. *crassicostata* SPATH (1937, p. 527, pl. 58, fig. 28) was based on a single distantly ribbed individual but, as there is every transition with typical *T. hugardianus*, this varietal name is not used here.

Turrilitoides intermedius (PICTET & CAMPICHE) (1861, p. 127, pl. 57, fig. 14) was separated from *T. hugardianus* by having '... straighter ribs, a less acute spiral angle, less elevated whorls, and much less conspicuous ornamentation of the lower surface of the whorls' (SPATH 1937, p. 527). As noted by SPATH (1937) and RENZ (1968) however, not only is *T. intermedius* a very

close ally of the present species but it is also strictly contemporaneous. A straightening of the ribs, and their reduction on the adoral face, can be seen in several Cambridge Greensand specimens, e. g. SM-B39351. The differences in spiral angle are accompanied by a much-larger adult size and, here, it is suspected that *T. intermedius* is based on macroconchs of *T. hugardianus*.

Turrilitoides vibrayeanus (D'ORBIGNY) (1842: 589, pl. 148, figs. 1-4; KLINGER & KENNEDY 1978, Fig. 9F-G, I-J, Q) is a poorly known Middle Albian species which differs from (?)macroconchs of the present species in being weaker and more-densely ribbed.

Turrilitoides densicostatus (PASSENDORFER) (1930, p. 673, pl. 4, fig. 70) is another Middle Albian species which is very close to the present material but, until Middle Albian populations are analysed, its exact status is uncertain. According to SCHOLZ (1979), topotype material (from the condensed Albian of the Polish Tatra) has 32-38 ribs per whorl and a spiral angle of 26-27°. Although this falls within the range of variation of the present material, it is at the upper end and a shift in population structure, viz. morphotype frequency, seems to have occurred. Interestingly, KLINGER & KENNEDY (1978, pl. 9, figs. M, O) figure what appear to be a microconch and macroconch of this species. Whereas the microconch shows the same rib density and loss of ornament to the adult body chamber as the present species, the macroconch is more-densely ribbed.

Occurrence: *Turrilitoides hugardianus* (D'ORBIGNY) is known from the uppermost Albian (upper Inflatum and lower Dispar Zones) of England, France, Switzerland, Hungary and Sardinia.

Genus *Paraturrilites* BREISTROFFER, 1947

Type species: *Turrilites gresslyi* PICTET & CAMPICHE, by original designation.

Diagnosis: An Upper Albian turrilite with relatively wide apical angle and oblique ribs with 3 rows of tubercles of varying strength. Ribs are continuous onto the adoral face and, in some, they are looped between tubercles, or intercalated on the adapical shoulder. A fourth row of tiny tubercles may develop at the umbilical edge.

Discussion: Current taxonomic opinion (cf. KENNEDY 1971, KENNEDY & JUIGNET 1983, KLINGER & KENNEDY 1978) suggests that *Paraturrilites* and *Mariella* are synonyms; unfortunately this opinion focuses on *Paraturrilites*

Fig. 2. *Turrilitoides hugardianus* (D'ORBIGNY). 1, SM B98749; 2, SM B98588; 3, SM B98593; 4, SM B98755; 5, SM B98587; 6, SM B98747; 7, SM B98594; 8, SM B98748; 9, SMB98590; 10, SMB98591; 11, SMB39337; 12, SMB98581; 13, SM B98746; 14, SM B98755; 15, SM B98745; 16, SM B98748; 17, SM B98753; 18-19, SM B41242; 20, SM B98752; 21, SM B41239; 22, SM B98534; 23, SM B98579; 24, SM B98581; 25, SM B41240. All x 1.

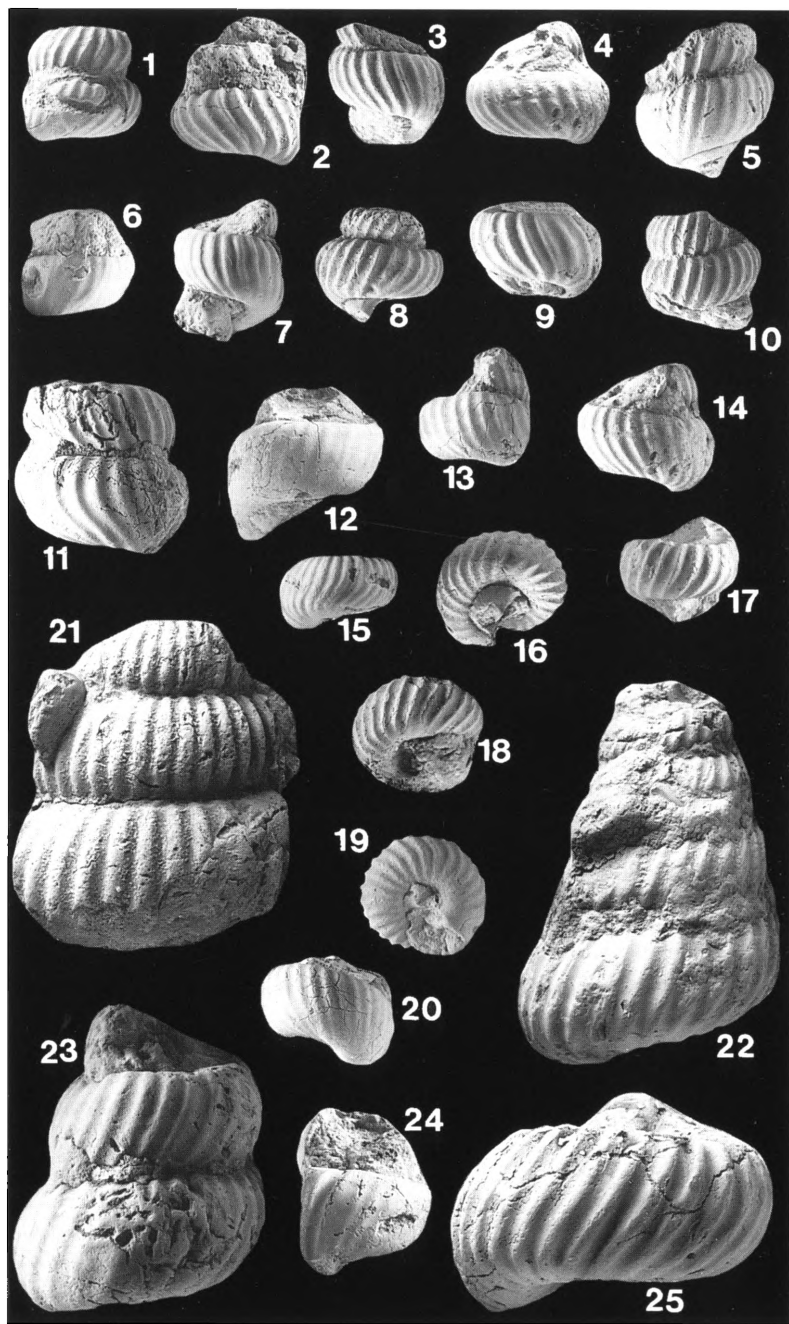


Fig. 2 (Legend see p. 150)

being a replacement name for allegedly unavailable *Mariella* when, in fact, it should focus on the characters of the type species. The side-by-side occurrence of trituberculate *Turrilites gresslyi* PICTET & CAMPICHE (type species of *Paraturrilites* BREISTROFFER, 1947) and quadrituberculate *Turrilites bergeri* BRONGNIART (type species of *Mariella* NOWAK, 1916), emphasizes a dichotomy in turrilite evolution (cf. SCHOLZ 1979) which, unfortunately, has been masked by taxonomic "lumping". Whereas workers familiar with the Upper Albian turrilites of Europe (SCHOLZ 1979, CHIRIAC 1981, 1988) have endorsed a phyletic relationship between *Turrilitoides* and *Paraturrilites* (which is supported here), KLINGER & KENNEDY (1978) questionably derive *Mariella bergeri* (BRONGNIART), type species of the genus, from the "anisoceratid" *Pseudhelicoceras*. Therefore, both morphological and current phylogenetic interpretations contradict the view that *Paraturrilites* and *Mariella* are synonyms.

In the writer's opinion, *Paraturrilites* is a valid taxon descended from *Turrilitoides* by acquisition of 3 rows of tubercles (cf. SCHOLZ 1979); weakly tuberculate *nobilis* morphotypes, and numerous embarrassing transitions (cf. SPATH 1937), provide the connection. The basis of the genus is the Upper Albian plexus of species, *P. escherianus* - *P. taeniatius* - *P. circumtaeniatius* - *P. hillyi*. *Paraturrilites* is easily distinguished from *Mariella* by having only 3 rows of tubercles, as opposed to 4, on the exposed whorl face; where a fourth tubercle develops it is positioned at the umbilical edge, not on the lower part of the exposed whorl as in *Mariella*, i. e. the 4th rows of tubercles are not homologous.

- Paraturrilites escherianus* (PICTET, 1847) Figs. 3-4, 5.10-16, 7B, 8A, 9-11
- 1847 *Turrilites escherianus* PICTET. - p. 410, pl. 15, fig. 11.
- 1861 *Turrilites gresslyi* PICTET & CAMPICHE. - p. 132, pl. 57, figs. 11-13.
- ? 1862 *Turrilites stachei* VON HAUER. - p. 641, pl. 1, figs. 3-8.
- ? 1865 *Turrilites bergeri* BRONGNIART. - STOLICZKA, p. 185, pl. 86, fig. 6 only.
- 1875 *Turrilites weistii* SHARPE. - JUKES-BROWNE, p. 289.
- 1875 *Turrilites gresslyi* PICTET & CAMPICHE. - NEUMAYR, p. 901.
- 1877 *Turrilites cantabrigiensis* JUKES-BROWNE. - p. 493.
- 1877 *Turrilites nobilis* JUKES-BROWNE. - p. 493, pl. 21, fig. 1.
- 1890 *Turrilites gresslyi* PICTET & CAMPICHE. - RENEVIER, p. 339.
- 1897 *Turrilites wiestii* var. *cantabrigiensis* JUKES-BROWNE. - COWPER-REED, p. 16.
- 1897 *Turrilites nobilis* JUKES-BROWNE. - COWPER-REED, p. 116.
- 1900 *Turrilites nobilis* JUKES-BROWNE. - JUKES-BROWNE, p. 460.
- non 1907 *Turrilites gresslyi* PICTET & CAMPICHE. - BOULE, LEMOINE & THÉVENIN, p. 57, pl. 13, fig. 2 (= *Mariella oehlerti*).
- 1910 *Turrilites gresslyi* PICTET & CAMPICHE. - PERVINQUIÈRE, p. 54.
- non 1923 *Turrilites* cf. *gresslyi* PICTET & CAMPICHE. - SPATH, p. 289 = *Mariella oehlerti*).
- 1925 *Turrilites gresslyi* PICTET & CAMPICHE. - DIENER, p. 83.
- 1926 *Turrilites cantabrigiensis* JUKES-BROWNE. - SPATH, p. 429.
- 1926 *Turrilites nobilis* JUKES-BROWNE. - SPATH, p. 429.

- non 1929 *Turrilites gresslyi* PICTET & CAMPICHE. – COLLIGNON, p. 65, pl. 6, fig. 15 (= *Mariella oehlerti*).
- 1937 *Mariella cantabrigiensis* (JUKES-BROWNE). – SPATH, p. 518, pl. 57, fig. 36, pl. 58, figs. 1-2, text-figs. 181 a-b, 182 d-e.
- 1937 *Mariella nobilis* (JUKES-BROWNE). – SPATH, p. 520, pl. 58, figs. 10-11, text-fig. 182 a-c.
- 1937 *Mariella escheriana* (PICTET). – SPATH, p. 521.
- 1940 *Turrilitoides* (?) sp. nov. – BREISTROFFER, p. 82.
- 1940 *Mariella nobilis* var. *cruciana* BREISTROFFER. – p. 78.
- 1947 *Paraturrilites nobilis* var. *brownei* BREISTROFFER. – p. 80.
- ?1963 *Paraturrilites gresslyi* (PICTET & CAMPICHE). – COLLIGNON, p. 47, pl. 258, fig. 1122.
- 1968 *Mariella* (*Mariella*) *gresslyi bifurcata* RENZ. – p. 89, pl. 17, fig. 42.
- 1978 *Mariella* (*Mariella*) *cantabrigiensis* (JUKES-BROWNE). – KLINGER & KENNEDY, p. 26.
- non 1978 *Mariella* (*Mariella*) cf. *gresslyi* (PICTET & CAMPICHE). – KLINGER & KENNEDY, p. 26, fig. 7E (= *P. circumtaeniatus*).
- 1979 *Turrilites* (*Paraturrilites*) *escherianus* (PICTET). – SCHOLZ, p.38, pl. 7, figs. 5, 17-32, pl. 8, figs. 1-11, text-fig. 11E-1.
- 1981 *Mariella* (*Mariella*) *gresslyi* PICTET & CAMPICHE. – CHIRIAC, p. 45.
- 1981 *Mariella* (*Mariella*) *cantabrigiensis* (JUKES-BROWNE). – CHIRIAC, p. 45.
- 1981 *Mariella* (*Mariella*) *nobilis* (JUKES-BROWNE). – CHIRIAC, p. 45.
- 1988 *Mariella* (*Mariella*) *nobilis* (JUKES-BROWNE). – CHIRIAC, p. 52.
- 1988 *Mariella* (*Mariella*) *gresslyi* (PICTET & CAMPICHE). – CHIRIAC, p. 52.
- 1988 *Mariella* (*Mariella*) *cantabrigiensis* (JUKES-BROWNE). – CHIRIAC, p. 52.

Material: 75 specimens, SMB38501, 38507-9, 38511-12, 41219-41226, 41230-31, 41233, 41236, 98515-25, 98527-33, 98535-38, 98540-42, 98544-54, 98556-57, 98559-61, 98563-75, and one without number.

Diagnosis: A late Albian (Dispar Zone, typically the lower part) species of *Paraturrilites* with a spiral angle of 18-38°, peaking at 20-30°. Ornament comprises simple oblique ribs, 18-36 per whorl but generally between 24-30, ornamented with 3 rows of tubercles; occasionally some specimens develop a tiny tubercle at the umbilical edge. Strength of both ribbing and tuberculation is highly variable, and tubercles vary from rounded to clavate. Coiling is both sinistral and dextral.

Intraspecific variation: The most noteworthy variation shown by the present material is in rib density and strength of ornament. As can be seen from Figure 9, there is marked covariance, with coarsely ribbed individuals also being more strongly tuberculate. Moreover, there is every transition from individuals in which ribbing predominates and tuberculation is very weak (Figs. 3.1, 4.1), i. e. *Turrilites nobilis* JUKES-BROWNE, to forms in which

Fig. 3. *Paraturrilites escherianus* (PICTET). 1, SM B41238; 2, SM B98546; 3, SM B98530; 4, SM B98523; 5, SM B98533; 6, SM B98571; 7, SM B98566; 8, SM B98523; 9, SM B98570; 10-11, SM B98563; 12, SM B38512; 13, SM B98527; 14, SM B38509; 15, SM B98521; 16, SM B41230. All x 1.

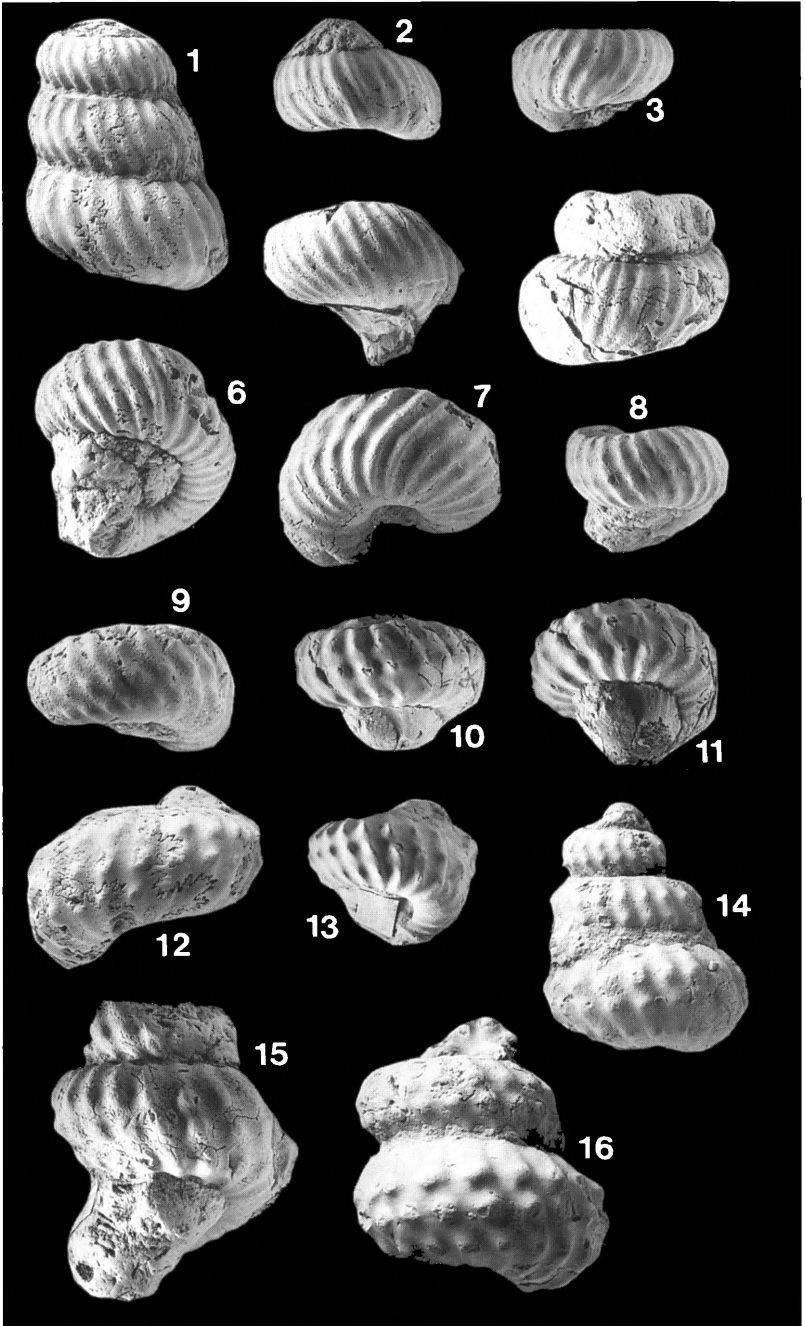


Fig. 3 (Legend see p. 153)

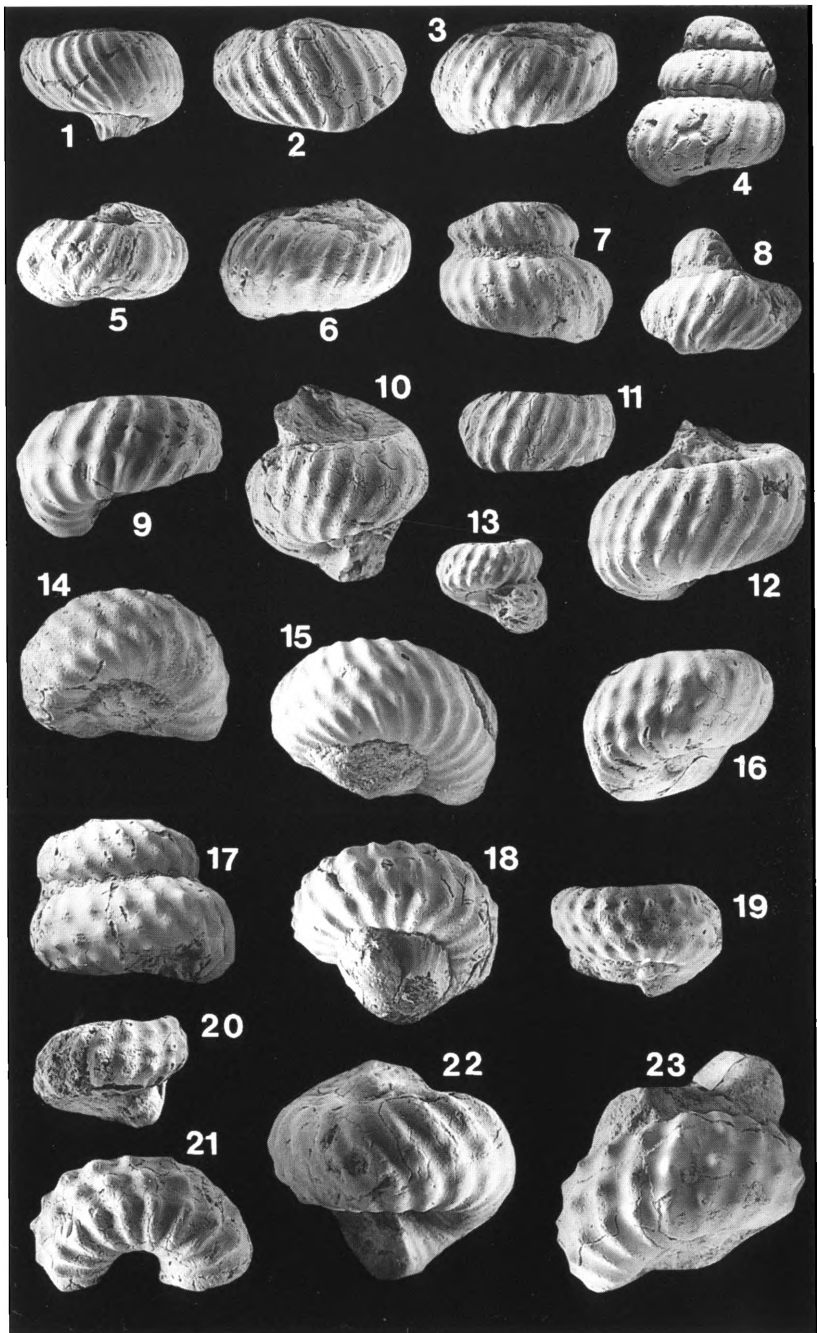


Fig. 4 (Legend see p. 156)

tuberculation dominates, i. e. *T. cantabrigiensis* JUKES-BROWNE (Figs. 3.16, 4.23). The latter species generally has been separated from *T. gresslyi* PICTET & CAMPICHE in possessing rounded and not spirally elongated tubercles. However, as noted by SPATH (1937) and SCHOLZ (1979), there is every gradation between these two morphotypes and formal taxonomic separation serves no useful purpose.

The apical angle of *M. escherianus* varies from 18-38°, with most individuals falling between 20-30°, but the available material is insufficient to gauge this variation fully. Coiling is both sinistral and dextral in about equal proportions. An interesting feature of the shell form of *T. escherianus* is that whorl height is almost exactly half the diameter (Fig. 10).

The Cambridge Greensand material shows a wide scatter in size (Fig. 8A), with most individuals attaining a whorl height of 10-15mm. However an absence of peristomal fragments, together with rare much larger individuals, e. g. SM-B98539 (Fig. 5.14, 16), suggests that this is an artefact of preservation. This is supported by closely allied *P. circumtaeniatus* which only develops an adult peristomal constriction at a whorl height of about 40 mm.

Other variation encountered in the material to hand includes the development of an incipient 4th tubercle on the umbilical shoulder, e. g. SM-B41227, the coalescing or bifurcating of ribs on the adoral surface or even at the adoral shoulder, e. g. SM-B38508, SM-B98530 (Fig. 3.3), and the intercalation of weak ribs on the adapical shoulder, e. g. SM-B98554, thereby anticipating the condition in younger *P. circumtaeniatus* (KOSSMAT). SM-B38501 (Fig. 5.10-11) shows somewhat flattened flanks and has the adoral two rows of tubercles closely spaced near the spiral suture and widely separated from the adapical row of tubercles. It is close to the lectotype of *P. gresslyi* (PICTET & CAMPICHE) (cf. RENZ 1968, pl. 17, fig. 30) and also, in its flattened flanks, approaches *P. taeniatus* (PICTET & CAMPICHE) (RENZ 1968, pl. 18, fig. 1).

Remarks: The range of variation in the present material supports the view (SCHOLZ 1979) that the following taxa have no biological standing and are best regarded as subjective junior synonyms of *P. escherianus* (PICTET): *Turrilites gresslyi* PICTET & CAMPICHE, *T. stachei* VON HAUER, *T. cantabrigiensis* JUKES-BROWNE, *T. nobilis* JUKES-BROWNE, *Mariella nobilis* var. *cruci-*

Fig. 4. *Paraturrilites escherianus* (PICTET). 1, SM B98582; 2, SM B98548; 3, SM B98551; 4, SM B24398; 5, SM B98575; 6, SM B98551; 7, SM B98531; 8, SM B98528; 9, SM B98540; 10, SM B98557; 11, SM B98524; 12, SM B98566; 13, SM B98732; 14, SM B98570; 15, SM B98515; 16, SM B98536; 17, SM B41221; 18, SM B98558; 19, SM B98535; 20, SM B98537; 21, SM B98549; 22, SM B98541; 23, SM B98542. All x 1.

ana BREISTROFFER, *Mariella nobilis* var. *brownei* BREISTROFFER and *Mariella gresslyi bifurcata* RENZ.

Although many individuals appear to be transitional between *Turrilitoides hugardianus* (D'ORBIGNY) and the strongly ribbed, weakly tuberculate "nobilis" morphotypes of *P. escherianus*, the two are maintained as distinct since acquisition of tubercles is a major event in turrilite evolution. Typically *T. hugardianus* is adult at smaller diameters, has a smaller apical angle, lacks tuberculation entirely, and often has a smooth adult body chamber.

In the absence of well-preserved material, *Paraturrilites? camachoensis* (BÖSE) (CLARK 1965: 43, pl. 13, fig. 8, pl. 18, fig. 8) from the Upper Albian of Mexico is difficult to assess; its appears to be more sparsely ribbed than *P. escherianus* (cf. CLARK 1965). *Paraturrilites stoliczkai* (COLLIGNON) (STOLICZKA 1865, p. 185, pl. 86, fig. 6) is based on a very large individual with 3 exposed rows of tubercles and a 4th at the umbilical edge; it could be simply an adult of *P. escherianus* but, without additional material, its precise affinities are difficult to determine.

Occurrence: *Paraturrilites escherianus* (PICTET) is characteristic of the uppermost Albian (lower part of the Dispar Zone). It is currently reported from England, France, Switzerland, Hungary, Iran, Morocco, Angola, Zululand, Madagascar and Texas.

- Paraturrilites circumtaeniatus* (KOSSMAT, 1895) Fig. 5.5
- 1865 *Turrilites gresslyi* PICTET & CHAMPICHE. – STOLICZKA, p. 186, pl. 87, figs. 1-5.
- 1895 *Turrilites circumtaeniatus* KOSSMAT. – p. 141, pl. 18, figs. 4-5.
- 1907 *Turrilites circumtaeniatus* KOSSMAT. – BOULE, LEMOINE & THÉVENIN, p. 57, pl. 13, fig. 4.
- non 1917 *Turrilites circumtaeniatus* KOSSMAT. – WOODS, p. 11, pl. 5, figs. 2-3 (= *M. thomsoni*).
- non 1926 *Turrilites circumtaeniatus* KOSSMAT. – SCOTT, p. 145, pl. 1, figs. 10-11 (= *M. worthensis*).
- 1937 *Turrilites circumtaeniatus* KOSSMAT. – SPATH, p. 518.
- 1947 *Turrilites circumtaeniatus* KOSSMAT. – BREISTROFFER, p. 80.
- 1963 *Paraturrilites* aff. *circumtaeniatus* (KOSSMAT). – COLLIGNON, p. 46, pl. 258, fig. 1120.
- 1973 *Turrilites (Turrilites) circumtaeniatus* KOSSMAT. – HENDERSON, p. 87.
- 1978 *Mariella (Mariella) circumtaeniata* (KOSSMAT). – KLINGER & KENNEDY, p. 6, pl. 5, figs. A-C, text-figs 3G, 6D.
- 1978 *Mariella (Mariella) cf. gresslyi* (PICTET & CAMPICHE). – KLINGER & KENNEDY, p. 26, pl. 7, fig. E.
- 1979 *Turrilites circumtaeniatus* KOSSMAT. – SCHOLZ, p. 39.
- 1979 *Mariella (Mariella) circumtaeniatus* (KOSSMAT). – COOPER & KENNEDY, p. 228, figs. 31E-F, 39H.

Material: A single specimen, SM-B41234, preserved as a phosphatic internal mould.

Diagnosis: A species of *Paraturrilites* with looped and intercalated ribs on the adapical face of the whorl flank, as a result greatly exceeding the number of tubercles in the adapical row. A fourth row of very small tubercles is sometimes developed at

the umbilical edge. Strength of ornament is variable and, usually, there are 20-30 rows of tubercles per whorl. Coiling is both sinistral and dextral.

Description: The single fragment represents half a whorl of a sinistrally-coiled individual showing 3 rows of tubercles situated on 14 oblique ribs. The adapical row of tubercles is positioned slightly above midflank, and the adoral row at the spiral suture. On the adapical face an extra rib is intercalated between adjacent main ribs and extends onto the flank as far as the adapical row of tubercles before becoming obsolete.

Remarks: This single fragment shows the characteristic feature of the species, viz. substantially more ribs to the adapical shoulder than there are tubercles in the adapical row.

Paraturrilites circumtaeniatus differs from *P. escherianus*, from which it is descended, by a marked increase in size, and the development of intercalated and looped ribs on the adapical face of the whorl flank in the middle to adult growth stages. Material collected by the writer from the upper *dispar* Zone (*perinflatum* Subzone) in Zululand suggests that the early whorls of *P. circumtaeniatus* are similar to *P. escherianus* and that easy discrimination is only possible at fairly large size. The Zululand specimen of *Mariella* cf. *gresslyi* (KLINGER & KENNEDY 1978, pl. 7, fig. E) has regularly intercalated ribs on the adapical shoulder and is best assigned to *P. circumtaeniatus*.

Paraturrilites taeniatus (PICTET & CAMPICHE) (RENZ 1968: 91, pl. 18, fig. 1, text-fig. 32g), of which *P. canaliculatus* (BREISTROFFER) (RENZ 1968: 91, pl. 18, fig. 2, text-figs. 31g, 32f) may be an extreme variant, is very similar to *P. circumtaeniatus* but has the adapical row of tubercles higher on the flank, so that midflank of the whorls is flattened to slightly concave, and it lacks intercalated and looped ribs on the adapical whorl face.

Occurrence: *Paraturrilites circumtaeniatus* (KOSSMAT) is typical of the uppermost Albian and is reported from India, Madagascar, Zululand, Angola and now southern England; although it replaces *P. escherianus* in the *perinflatum* Subzone, it may appear already in the *gardonica* Subzone.

Paraturrilites cf. *hillyi* (DUBOURDIEU, 1953)

Fig. 5.6-7

Compare:

1953 *Turrilites hillyi* DUBOURDIEU. – p. 46, pl. 4, figs. 1-3.

non 1963 *Mariella hillyi* DUBOURDIEU. – COLLIGNON, p. 46.

1965 *Mariella hillyi* DUBOURDIEU. – CLARK, p. 44.

1978 *Mariella (Mariella) hillyi* DUBOURDIEU. – KLINGER & KENNEDY, p. 26.

Fig. 5. *Mariella bergeri* (BRONGNIART). 1, SM B41218; 2-3, SM B41216; 4, SM B41217. *Paraturrilites circumtaeniatus* (KOSSMAT). 5, SM B41234. *Paraturrilites* cf. *hillyi* (DUBOURDIEU). 6-7, SM B98526. *Ostlingoceras puzosianum* (D'ORBIGNY). 8-9, SM B39376; 12, SM B39375. *Paraturrilites escherianus* (PICTET). 10, SM B38501; 11, SM B38501; 12, SM B39375; 13, SM B41221; 14, SM B98534; 15, SM B98532; 16, SM B98554. All x 1.

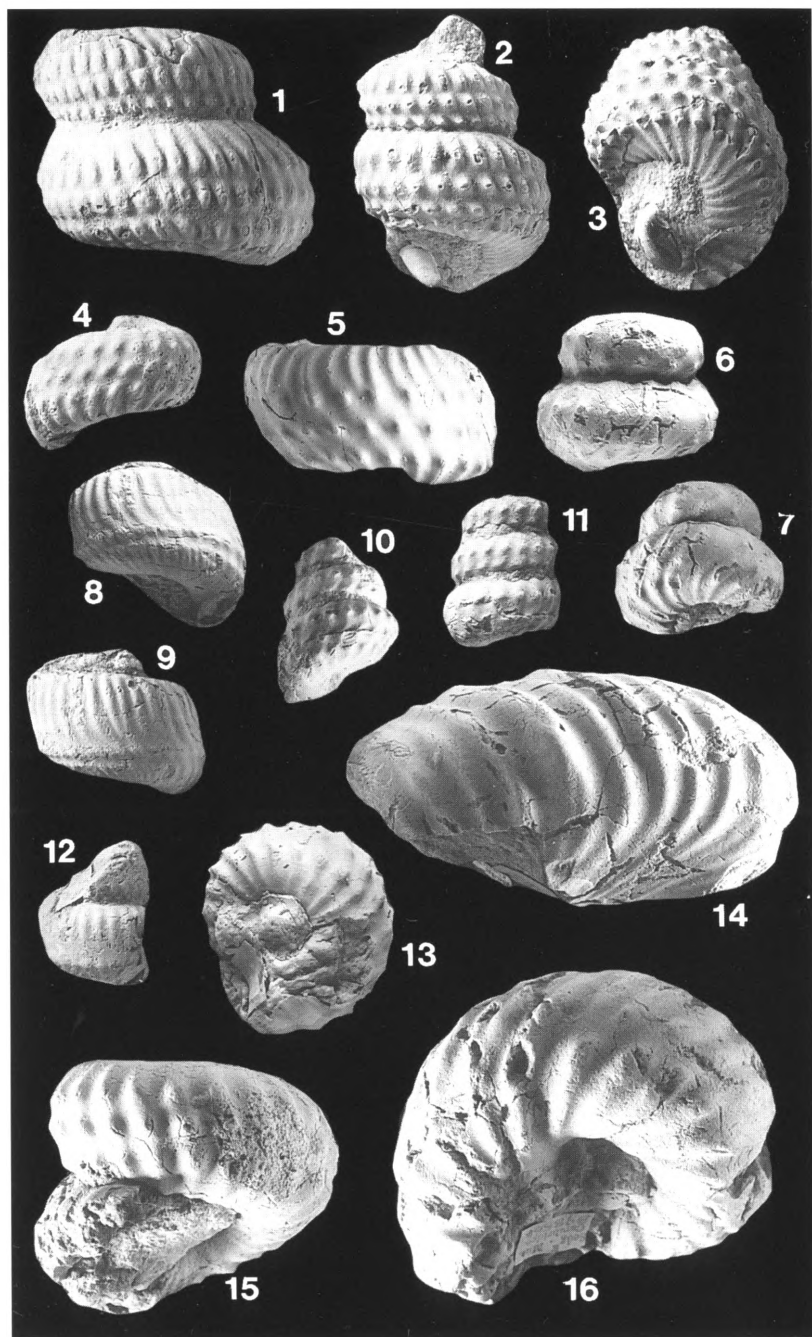


Fig. 5 (Legend see p. 158)

Material: A single specimen, SM-B98526, preserved as a phosphatic internal mould.

Diagnosis: A small (?immature) species of *Paraturrilites* with weak ornament and only two rows of tubercles exposed on the flanks, the third row hidden in the spiral suture. Ribs may be looped between the tubercles.

Description: A dextrally coiled turrilite with about 17 very weak oblique ribs per whorl, each ornamented with 3 rows of tubercles. The adapical row of tubercles is strongest, with well-developed rounded nodes on the penultimate whorl becoming more pointed and smaller on the final whorl. The central row comprises tiny pointed tubercles situated just above the spiral suture and the adoral row, comprising tubercles similar in strength to the central row, is hidden in the spiral suture. In one instance the normally simple ribs are looped between the central and adoral tubercles. Single ribs cross the adoral face of the whorls obliquely, with an adorally convex curvature.

Remarks: The strongly convex flanks of the present individual, with virtually obsolete ribbing and only 2 visible rows of tubercles, are distinctive. Because *Paraturrilites hillyi* is based on a unique specimen, intraspecific variation is unknown but, to judge from such closely allied species as *P. escherianus* (PICTET) and *P. circumtaeniatus* (KOSSMAT), is likely to be

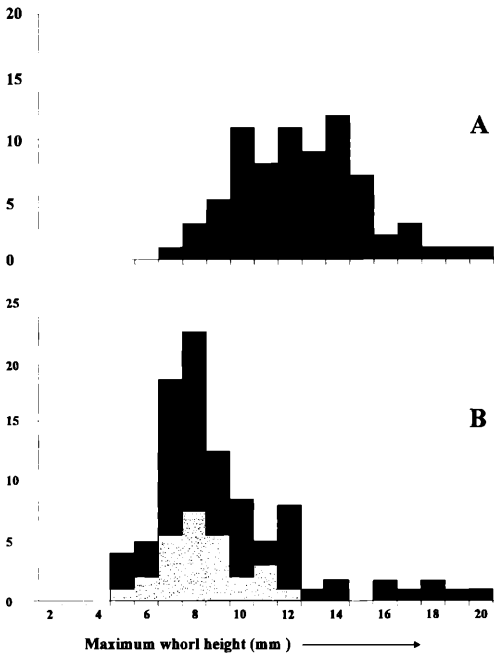


Fig. 6. A frequency histogram of rib density in *Turrilitoides hugardianus* (D'ORBIGNY); black = sinistral coiling, white = dextral coiling.

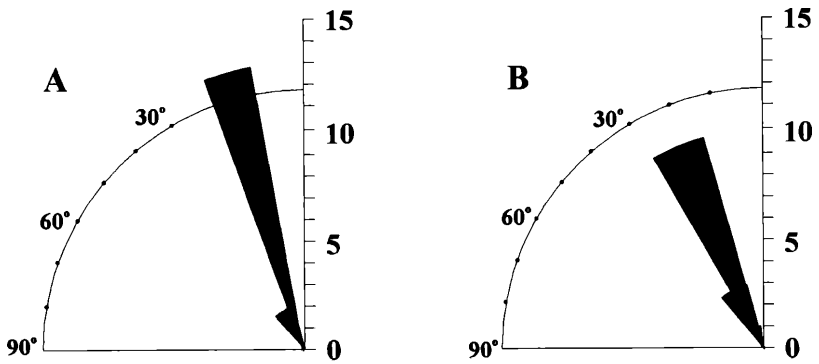


Fig. 7. Frequency and variation in the apical angles of (A) *Turrilitoides hugardianus* (D'ORBIGNY), (B) *Paraturrilites escherianus* (PICTET).

considerable. As a result, although the present specimen does not have the equidistant flank tubercles seen in the holotype, this may not be significant taxonomically. Superficially it resembles some individuals of *Mariella worthensis* (ADKINS & WINTON) (cf. CLARK 1965, pl. 16, fig. 5, pl. 13, figs. 5, 12), but the Texan species has 4 rows of tubercles.

Occurrence: *Paraturrilites hillyi* (DUBOURDIEU) is known with certainty only from the Upper Albian of Algeria. However, it may be present also in the Upper Albian (lower part of the Dispar Zone) of southern England.

Genus *Mariella* NOWAK, 1916

Type species: *Turrilites bergeri* BRONGNIART; by original designation.

Remarks: SPATH (1937) was followed by KLINGER & KENNEDY (1978) in favouring the phylogeny *Pseudhelicoceras* - *Mariella* - *Turrilites*; this suggests any resemblance between *Mariella* and the foregoing turrilites is the result of convergence. However, KLINGER & KENNEDY's (1978) concept of *Mariella* is polyphyletic and both SCHOLZ (1979) and CHIRIAC (1981, 1988) derive *Mariella* s. s. from *Paraturrilites*.

Mariella bergeri (BRONGNIART, 1822)

Fig. 5.1-4

1822 *Turrilites bergeri* BRONGNIART. - p. 395, pl. 7, fig. 3.

1836 *Turrilites bergeri* BRONGNIART. - BUCKLAND, p. 65, pl. 44, fig. 14.

1842 *Turrilites bergeri* BRONGNIART. - D'ORBIGNY, p. 590, pl. 143, fig. 5 only.

1848 *Turrilites bergeri* BRONGNIART. - QUENSTEDT, p. 300, pl. 21, fig. 26.

1848 *Turrilites bergeri* BRONGNIART. - BRONN, p. 1329.

1850 *Turrilites bergeri* BRONGNIART. - D'ORBIGNY, p. 127.

1854 *Turrilites bergeri* BRONGNIART. - PICTET, p. 712, pl. 56, fig. 7.

non 1857 *Turrilites bergeri* BRONGNIART. - SHARPE, p. 65, pl. 26, fig. 9 (= *M. essenensis*), 10 (= *M. lewesiensis*).

- 1859 *Turrilites bergeri* BRONGNIART. – CHENU, p. 96, text-fig. 420.
- 1860 *Turrilites bergeri* BRONGNIART. – OOSTER, p. 94.
- 1861 *Turrilites bergeri* BRONGNIART. – PICTET & CAMPICHE, p. 134, pl. 58, figs. 1-2.
- 1861 *Turrilites bergeri* var. *miliaris* PICTET & CAMPICHE. – p. 136, pl. 51, fig. 5.
- 1866 *Turrilites bergeri* BRONGNIART. – PICTET & RENEVIER, p. 106.
- 1875 *Turrilites bergeri* BRONGNIART. – JUKES-BROWNE, p. 289.
- 1875 *Turrilites bergeri* BRONGNIART. – NEUMAYR, p. 32.
- 1879 *Turrilites bergeri* BRONGNIART. – PRICE, p. 78.
- 1885 *Turrilites bergeri* BRONGNIART. – QUENSTEDT, p. 587, pl. 46, fig. 10.
- 1890 *Turrilites bergeri* BRONGNIART. – RENEVIER, p. 339.
- non 1903 *Turrilites bergeri* BRONGNIART. – CHOFFAT, p. 15, pl. 1, figs. 4-6 (= ? *M. oehlerti*).
- 1903 *Turrilites bergeri* var. *miliaris* PICTET & CAMPICHE. – CHOFFAT, p. 15.
- ? 1910 *Turrilites bergeri* var. *numida* PERVINQUIÈRE. – p. 53, pl. 5, figs. 12-13.
- ? 1910 *Turrilites bergeri* var. *quadrituberculatus* BAYLE. – PERVINQUIÈRE, p. 53.
- 1925 *Turrilites bergeri* BRONGNIART. – DIENER, p. 80.
- non 1926 *Turrilites bergeri* BRONGNIART. – SCOTT, p. 144, pl. 2, fig. 2 (= *M. worthensis*).
- 1929 *Turrilites bergeri* BRONGNIART. – COLLIGNON, p. 42, pl. 6, fig. 19.
- 1930 *Turrilites* cf. *bergeri* BRONGNIART. – PASSENDORFER, p. 673.
- 1931a *Turrilites bergeri* BRONGNIART. – BREISTROFFER, p. 1203.
- 1931b *Turrilites bergeri* BRONGNIART. – BREISTROFFER, p. 233.
- 1931 *Turrilites bergeri* var. *numida* BAYLE. – COLLIGNON, p. 50, pl. 5, fig. 17.
- 1933 *Turrilites bergeri* BRONGNIART. – COLLIGNON, p. 73.
- 1936a *Turrilites bergeri* BRONGNIART. – BREISTROFFER, p. 24.
- 1936b *Turrilites bergeri* BRONGNIART. – BREISTROFFER, p. 63.
- 1936b *Turrilites bergeri* var. *miliaris* PICTET & CAMPICHE. – BREISTROFFER, p. 66.
- 1937 *Mariella bergeri* (BRONGNIART). – SPATH, p. 510, pl. 57, fig. 28, text-fig. 178.
- 1937 *Mariella bergeri* var. *crassituberculatus* SPATH. – p. 513.
- 1937 *Mariella miliaris* (PICTET & CAMPICHE). – SPATH, p. 514, pl. 57, figs. 25-26, text-fig. 179.
- 1940 *Mariella bergeri* BRONGNIART. – BREISTROFFER, p. 37.
- 1940 *Mariella bergeri* var. *crassituberculata* SPATH. – BREISTROFFER, p. 37.
- non 1940 *Mariella bergeri* var. *conduciensis* BREISTROFFER. – p. 79 (= ? *M. oehlerti*).
- 1940 *Mariella miliaris* (PICTET & CAMPICHE). – BREISTROFFER, p. 37.
- 1940 *Mariella miliaris* var. *diegoensis* BREISTROFFER. – p. 37.
- 1947 *Paraturrilites bergeri* (BRONGNIART). – BREISTROFFER, p. 46.
- 1947 *Paraturrilites bergeri* var. *crassituberculata* SPATH. – BREISTROFFER, p. 46.
- 1947 *Paraturrilites miliaris* (PICTET & CAMPICHE). – BREISTROFFER, p. 46.
- 1947 *Paraturrilites miliaris* var. *diegoensis* (BREISTROFFER). – p. 46.
- 1958 *Turrilites bergeri* BRONGNIART. – ANDERSON, p. 193, pl. 11, fig. 2.
- 1960 *Mariella (Mariella) fricki* MURPHY & RODDA. – p. 848, pl. 103, fig. 7.
- 1960 *Mariella (Mariella,) bergeri* (BRONGNIART). – CHIRIAC, p. 454, pl. 5, figs. 10-11, text-fig. 5.
- 1960 *Mariella (Mariella) bergeri* var. *crassituberculata* SPATH. – CHIRIAC, p. 456, pl. 1, figs. 12-13.
- 1960 *Mariella (Mariella) miliaris* (PICTET & CAMPICHE). – CHIRIAC, p. 456, pl. 1, figs. 14-16, pl. 2, figs. 17-20.
- 1960 *Mariella bergeri* (BRONGNIART). – DRUSHTCHIC & KUDRJAVCEV, p. 266, pl. 12, figs. 2-3. -

- 1962 *Paraturrilites (Bergericeras) bergeri* (BRONGNIART). – WIEDMANN, p. 190.
- 1962 *Paraturrilites (Bergericeras) bergeri crassituberculatus* (SPATH). – WIEDMANN, p. 190, pl. 11, fig. 1.
- 1962 *Paraturrilites (Bergericeras) miliaris* (PICTET & CAMPICHE). – WIEDMANN, p. 190.
- 1968 *Paraturrilites (Bergericeras) bergeri bergeri* (BRONGNIART). – WIEDMANN & DIENI, p. 80, pl. 7, fig. 5, pl. 9, figs. 2, 5.
- 1968 *Paraturrilites (Bergericeras) miliaris* (PICTET & CAMPICHE). – WIEDMANN & DIENI, p. 81.
- 1978 *Mariella (Mariella) bergeri* (BRONGNIART). – KLINGER & KENNEDY, p. 28, text-fig. 6E only.
- 1978 *Mariella (Mariella) miliaris* (PICTET & CAMPICHE). – KLINGER & KENNEDY, p. 29, pl. 3, fig. J, text-fig. 8E.
- non 1978 *Mariella (Mariella) cf. bergeri* (BRONGNIART). – KLINGER & KENNEDY, p. 28, pl. 1, fig. H.
- 1979 *Turrilites (Bergericeras) bergeri bergeri* BRONGNIART. – SCHOLZ, p. 40, pl. 8, figs. 12, 14-15, 17, pl. 9, fig. 1, text-fig. 11J.
- ?1979 *Turrilites (Bergericeras) bergeri quadrituberculatus* BAYLE. – SCHOLZ, p. 40, pl. 8, fig. 13.
- 1981 *Mariella (Mariella) bergeri bergeri* (SPATH). – CHIRIAC, p. 45.
- 1981 *Mariella (Mariella) bergeri crassituberculata* (SPATH). – CHIRIAC, p. 45.
- 1988 *Mariella (Mariella) bergeri bergeri* (SPATH). – CHIRIAC, p. 52.
- 1988 *Mariella (Mariella) bergeri crassicostata* (SPATH). – CHIRIAC, p. 52.
- 1988 *Mariella (Mariella) miliaris* (PICTET & CAMPICHE). – CHIRIAC, p. 52.

Material: Three specimens, SM-B41216-18, all preserved as phosphatic internal moulds.

Diagnosis: Sinistrally and dextrally coiled turrilites with a spiral angle of between 27-38°. Ornament comprises simple oblique ribs, 25-50 per whorl, ornamented by 4 rows of more or less prominent, equidistant tubercles in which the second row is situated at midflank and the fourth row in the spiral suture.

Intraspecific variation: Although the available material is insufficient for useful discussion regarding intraspecific variation, it does display noteworthy variation in rib density (27-36 per whorl) and tubercle strength. As might be expected, tuberculation is strongest on coarsely ribbed variants, e. g. SM-B41216-17 (Figs. 5.2-3) and most subdued on the densely ribbed variant, SM-B41218 (Fig. 5.1).

Remarks: The present material is transitional in rib density between *M. bergeri* and *M. miliaris* and, in the case of SM-B41218 (Fig. 5.1), is probably better referred to the latter "species". However, intraspecific variation in *P. escherianus* and *T. hugardianus* suggests that density and strength of ribs/tubercles varies enormously within contemporaneous populations of turrilites, and is a poor character on which to base taxonomic separation. For this reason, the writer follows WIEDMANN & DIENI (1968) in regarding *M. miliaris* – *M. bergeri* – *M. crassituberculata* – *M. crassituberculata extrema* a transition series covering the intraspecific variation within a contempora-

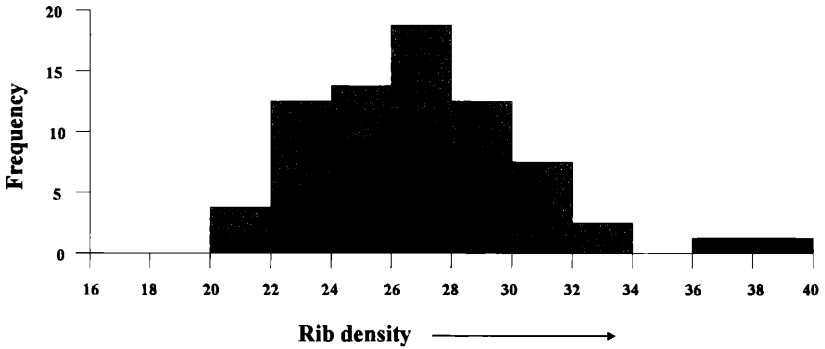


Fig. 8. Frequency histogram of maximum whorl height for (A) *Paraturrilites escherianus* (P ICTET), and (B) *Turrilitoides hugardianus* (D'ORBIGNY) where white = individuals preserving adult (smooth) body chamber.

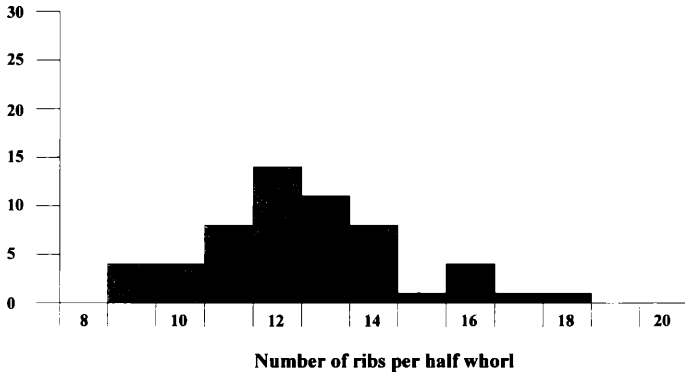


Fig. 9. Frequency histogram of rib density in *Paraturrilites escherianus* (P ICTET) where black = very weakly to weakly tuberculate individuals and white - moderately to strongly tuberculate individuals.

neous population of polytypic individuals. *Mariella fricki* MURPHY & RODDA falls well within the range of variation of this species and also is regarded as conspecific.

Occurrence: *Mariella bergeri* (BRONGNIART) is a characteristic species of the Upper Albian (typically upper Dispar Zone) where it is recorded from as far afield as England, France, Switzerland, Hungary, Iran, possibly North Africa, Sardinia, Mozambique, Zululand, Madagascar, India, California and South America. Two of the Cambridge Greensand specimens are preserved in a pale brown phosphate which contrasts strongly with the very dark chocolate-brown, almost black, phosphatic preservation of most of the Cambridge Greensand material; it suggests that material from different stratigraphic horizons may be represented.

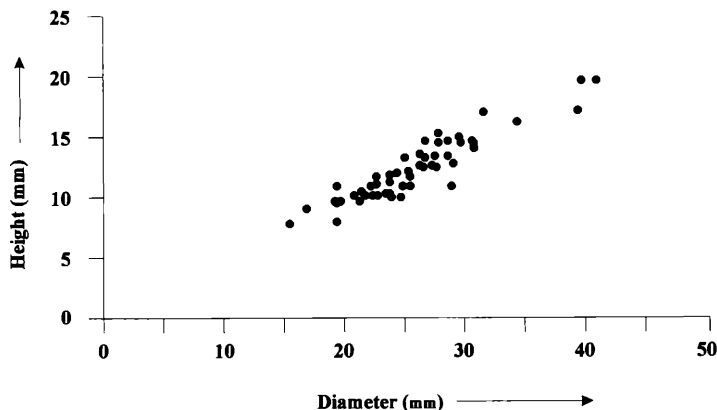
Genus *Ostlingoceras* HYATT, 1900Type species: *Turrilites puzosianus* D'ORBIGNY; by original designation.*Ostlingoceras puzosianum* (D'ORBIGNY, 1842) Fig. 1.29, 5.8-9, 121842 *Turrilites puzosianus* D'ORBIGNY. – p. 587, pl. 143, figs. 1-2.1847 *Turrilites puzosianus* D'ORBIGNY. – PICTET, p. 151, pl. 15, fig. 9.1848 *Turrilites puzosianus* D'ORBIGNY. – BRONN, p. 1329.1850 *Turrilites puzosianus* D'ORBIGNY. – D'ORBIGNY, p. 127.1854 *Turrilites puzosianus* D'ORBIGNY. – PICTET, p. 712.1862 *Turrilites puzosianus* D'ORBIGNY. – PICTET & CAMPICHE, p. 139, pl. 59, figs. 3, 5-6.1866 *Turrilites puzosianus* D'ORBIGNY. – PICTET & RENEVIER, p. 106.1875 *Turrilites puzosianus* D'ORBIGNY. – NEUMAYR, p. 33.1878 *Turrilites puzosi* D'ORBIGNY. – BAYLE, pl. 99, figs. 1-2.1890 *Turrilites puzosianus* D'ORBIGNY. – RENEVIER, p. 339.1897 *Turrilites puzosianus* D'ORBIGNY. – COWPER-REED, p. 116.1900 *Turrilites puzosianus* D'ORBIGNY. – JUKES-BROWNE, p. 460.1907 *Turrilites puzosianus* D'ORBIGNY. – PERVINQUIERE, p. 100.1936 *Turrilites puzosianus* D'ORBIGNY. – BREISTROFFER, p. 63.1937 *Ostlingoceras puzosianum* (D'ORBIGNY). – SPATH, p. 523, pl. 58, figs. 38-40.1960 *Ostlingoceras puzosianum* (D'ORBIGNY). – CHIRIAC, p. 463, pl. 4, figs. 36-40.1963 *Ostlingoceras puzosi* (D'ORBIGNY). – COLLIGNON, p. 44, pl. 257, fig. 1113.1968 *Ostlingoceras* (*Ostlingoceras*) *puzosianum* (D'ORBIGNY). – WIEDMANN & DIENI, p. 79, pl. 9, figs. 1, 4.1968 *Ostlingoceras* (*Ostlingoceras*) *sublaevigatum* WIEDMANN & DIENI. – p. 79, pl. 15, fig. 4.1968 *Ostlingoceras* (*Ostlingoceras*) *puzosianum* (D'ORBIGNY). – RENZ, p. 92, pl. 18, figs. 12-15.1968 *Ostlingoceras* (*Ostlingoceras*) *puzosiforme* SPATH. – RENZ, p. 93, pl. 18, fig. 18.1978 *Ostlingoceras* (*Ostlingoceras*) *puzosianum* (D'ORBIGNY). – KLINGER & KENNEDY, p. 14.

Fig. 10. Frequency histogram of whorl height (as a % of diameter) for *Paraturrilites escherianus* (PICTET).

1979 *Turrilites (Ostlingoceras) puzosianus* D'ORBIGNY. – SCHOLZ, p. 42, pl. 9, figs. 4-13, text-fig. 11K.

1988 *Ostlingoceras (Ostlingoceras) puzosianum* (D'ORBIGNY). – CHIRIAC, p. 52.

Material: 3 specimens, SM-B39377, 39375-76, all preserved as phosphatic internal moulds.

Description: Sinistrally coiled turrilites with a small apical angle of about 15° and broad flattened flanks. Ornament comprises 20-40 simple ribs (normally 20-30) which flex adorally and weaken near the spiral suture where two rows of closely spaced tubercles, separated by a narrow almost smooth band, are situated. The ribs continue onto the adoral face of the whorls.

Intraspecific variation: As in other turrilites, the 3 specimens available show significant variation in the density and strength of ribbing and tuberculation. On SM-B39375 (Fig. 5.12) ribs are virtually effaced from the adoral half of the flank, whereas on SM-B39376 (Fig. 5.8-9) ribs occasionally coalesce prior to joining the tubercles; SM-B39376 tubercles lacking a rib are commonly intercalated between adjacent ribs. SM-B39377 (Fig. 1.29) is a rather different larger individual with coarser stronger ribbing which does not weaken on the adoral surface. In addition, it does not have a spiral groove close to the adoral shoulder. The writer is tempted to interpret it as a macroconch, but the material is insufficient.

Occurrence: *Ostlingoceras puzosianum* (D'ORBIGNY) is recorded from the Upper Albian (Dispar Zone) of England, Spain, France, Switzerland, Hungary, and Madagascar.

Acknowledgements

I should like to thank Dr. B. RICKARDS (Cambridge) for the loan of material and Dr. M. K. HOWARTH and Mr. D. PHILLIPS, both of the British Museum (Natural History), for access to material in their care.

Literature

- ADKINS, W. S. 1920: The Weno and Pawpaw Formations of the Texas Comanchean. – Univ. Texas Bull., **1856**: 1-172; Austin.
- ANDERSON, F. M. (1958): Upper Cretaceous of the Pacific Coast. – Bull. geol. Soc. Amer., **71**: 1-378, 75 pls.; Richmond.
- BAYLE, E. (1878): Fossiles principaux des terrains. – Explic. Carte géol. France, **4**, (1) (Atlas): 158 pls.; Paris.
- BOULE, M., LEMOINE, P. & THEVÉNIN, A. (1906-07): Paléontologie de Madagascar. III. Cephalopodes crétacés des environs de Diego-Suarez. – Ann. Paléont., **1** (4): 173-192, 7 pls.; **2** (1): 21-76, pls. 8-15; Paris.
- BREISTROFFER, M. (1931): Sur l'étage Albien en Chartreuse (Isère et Savoie). – C. R. Acad. Sci., Paris, **193** (23): 1202-1204; Paris.
- (1933): Étude de l'étage Albien dans le Massif de la Chartreuse (Isère et Savoie). – Ann. Univ. Grenoble, **8** (2/3): 187-236; Grenoble.

- BREISTROFFER, M. (1936): Les subdivisions du Vraconien dans le Sud-Est de la France. – Bull. Soc. géol. France, (5) **6**: 63-68; Paris.
- (1940): Revision des ammonites du Vraconien de Salzac (Gard) et considérations générales sur ce sous-étage Albien. – Trav. Lab. Géol. Univ. Grenoble, **22**: 71-171; Grenoble.
- (1947): Sur les zones d'ammonites dans l'Albien de France et d'Angleterre. – Trav. Lab. Géol. Univ. Grenoble, **26**: 17-104; Grenoble.
- 1953. L'évolution des turrilitidés albiens et cénomaniens. – C .R. Acad. Sci., **237**: 1349-1351; Paris.
- BRONGNIART, A. (1822): Title?. In: CUVIER, G. & BRONGNIART, A.: Description géologiques des environs de Paris. New edition, viii + 428 pp., 16 pls., 2 maps; Paris.
- BRONN, H. G. (1848): Index palaeontologicus. A. Nomenclator palaeontologicus. Handbuch einer Geschichte der Natur, **3** (1): lxxxiv + 775 pp.; Stuttgart.
- BUCKLAND, W. (1836): Geology and mineralogy, considered with reference to natural theology. Bridgewater Treatise, vi, 2 vols., xvi + 599 pp., vii + 129 pp., 87 pls; London.
- CASEY, R. (1961): A monograph of the Ammonoidea of the Lower Greensand, Part II. – Palaeont. Soc. Monogr., 45-118, pls. 11-25, text-figs. 14-38; London.
- CHENU, J. G. (1859): Manuel de Conchyliologie et de Paléontologie conchyliologique. **1**: vii + 508 pp.; Paris.
- CHIRIAC, M. 1960: Reprezentati ai familie Turrilitidae MEEK, 1876 in cretacicul Dobrogei de sud. – Stud. Cercetari Geol., **5**: 449-474, 4pls.; Bucarest.
- 1981: Amoniti cretacic du Dobrogea de sud. Studia biostratigrafic. – Edit. Acad. R. S. R.: 1-145, 33pls.; Bucarest.
- 1988: Espèces et sous-espèces d'ammonites dans le Crétacé de la Dobrogea Meridionale. – Mem. Cent.-Dept Geol. Inst. Geol. Geophys., **33**: 45-90, 16 pls., 31 figs.; Bucarest.
- CHOFAT, P. (1903): Contributions à la connaissance géologique des colonies portugaises d'Afrique. I. Le Crétacique du Conducia. – Mem. Comm. geol. Port.,: 1-32, 9 pls.; Lisbon.
- CLARK, D. L. 1965: Heteromorph ammonoids from the Albian and Cenomanian of Texas and adjacent areas. – Mem. geol. Soc. Amer., **95**: 1-99, 24 pls., 22 figs.; New York.
- COBBAN, W. A. & HOOK, S. C. (1981): New turrilitid ammonite from mid-Cretaceous (Cenomanian) of south-west New Mexico. – Circ. New Mex. Bur. Min. Miner. Res., **130**: 22-29; Socorro.
- COLLIGNON, M. (1929): Les céphalopodes du Cénomaniens pyriteux de Diego-Suarez. – Ann. Paléont., **18**: 1-56, 2 pls.; Paris.
- (1932): Les Ammonites pyriteuses de l'Albien supérieur du Mont Raynaud, Madagascar. – Ann. géol. Serv. Mines Madagascar, **2**: 5-36, 4 pls; Tananarive.
- (1963): Atlas des fossils caractéristiques de Madagascar (ammonites Albien), **10**: 1-184, pls. 242-317; Serv. géol.; Tananarive.
- COOPER, M. R. (1990): A revision of the Scaphitidae (Cretaceous Ammonoidea) from the Cambridge Greensand. – Neues Jb. Geol. Paläont., Abh., **178**: 285-308, 11 figs.; Stuttgart.
- COOPER, M. R. & KENNEDY, W. J. (1978): A revision of the Baculitidae of the Cambridge Greensand. – Neues Jb. Geol. Paläont., Mh., **1977**: 641-658; Stuttgart.

- Cooper, M. R. (1987): A revision of the Puzosiinae (Cretaceous ammonites) of the Cambridge Greensand. – Neues Jb. Geol. Paläont., Abh., **174**: 105-121; Stuttgart.
- (1979): Uppermost Albian (*Stoliczkaia dispar* Zone) ammonites from the Angolan littoral. – Ann. S. Afr. Mus., **77** (10): 175-308, 82 figs.; Cape Town.
- COWPER-REED, F. R. (1897): A handbook of the geology of Cambridgeshire (Cambridge). xi + 276 pp., figs.; Cambridge.
- DIENER, C. (1925): Fossilium Catalogus, I. Animalia 29, Ammonoidea Neocretacea (1) **9**: 1-244. Junk; Berlin.
- DRUSHTCHIC, V. V. & KUDRYAVTSEV, M. P. (1960): Ammonites. In: Atlas of the Lower Cretaceous fauna of northern Caucasus and Crimea. Trudy vses. Nauchno-issled. Inst. Priir. Gazov. **1960**: 249-355 (in Russian). NB: KUDRAJCEV in the text is a mistake (I think) in transliteration.
- DUBOURDIEU, G. (1953): Ammonites nouvelles des Monts du Mellègue. – Bull. Serv. Carte géol. Algérie, (1, Paléont.), **16**: 1-76; Tunis.
- HERBERT, E. & MUNIER-CHALMAS, A. (1875): Appendice paléontologique. Description du terrain crétacé supérieur du Bassin d'Uchaux. – Ann. Sci. géol., **6**: 113-132, pls. 4-6; Paris.
- HENDERSON, R. A. (1973): Clarence and Raukumara Series (Albian - ?Santonian) Ammonoidea from New Zealand. – J. roy. Soc. N. Zealand, **3** (1):-123, 20 figs.; Wellington.
- IMMEL, H. 1987. Die Kreideammoniten der nördlichen Kalkalpen. – Zitteliana, **15**: 3-163, 14 pls., 5 figs., 19 tables; München.
- JAYET, A. (1926): Sur les mélanges de faunes de l'Albien du Genevois (Haute-Savoie). – C. R. Soc. phys. Geneve, **43** (3): 155-158; Geneve.
- JUKES-BROWNE, A. J. (1875): On the relations of the Cambridge Gault and Greensand. – Quart. J. geol. Soc. Lond., **31**: 256-314, pls. 14-15; London.
- (1877): Supplementary notes on the fauna of the Cambridge Greensand. – Quart. J. geol. Soc. Lond., **33**: 485-504, pl. 21; London.
- (1900): The Gault and Upper Greensand of England. Cretaceous rocks of Britain. – Mem. geol. Surv. Gt Britain, **14**, 1-499, 2 pls.; London.
- KENNEDY, W. J. (1971): Cenomanian ammonites from southern England. – Spec. Pap. Palaeont., **8**: 1-133, 64 pls.; London.
- KENNEDY, W. J. & JUIGNET, P. (1983): A revision of the ammonite faunas of the type Cenomanian. I. Introduction, Ancyloceratina. – Cret. Res., **4**: 3-83, 40 figs.; XXX.
- KLINGER, H. C. & KENNEDY, W. J. (1978): Turrilitidae (Cretaceous Ammonoidea) from South Africa, with a discussion of the evolution and limits of the family. – J. Moll. Stud., **44**: 1-48, 9 pls., 11 figs;
- KOSSMAT, F. (1895): Untersuchungen über die Südindische Kreideformation. – Beitr. Paläont. Geol. Öst.-Ung., **9**: 97-203 (1-107), pls 15-25 (1-11); Vienna.
- MARCINOWSKI, R. (1980): Cenomanian ammonites from German Democratic Republic, Poland, and the Soviet Union. – Acta geol. Polonica, **30** (3): 215-325, 19 pls., 14 figs.; Warszawa.
- MARCINOWSKI, R. & NAIDIN, D. P. (1976): An Upper Albian ammonite fauna from Crimea. – Acta Geol. Polon., **26** (1): 83-119; Warszawa.
- MATEI, V. (1970): Fauna vraconiana de pe valea Macla. – Daride seama ale sedintelor paleont., **55**: 81-84; Bukarest.

- MATSUMOTO, T. (1967): Evolution of the Nostoceratidae (Cretaceous heteromorph ammonoids). – Mem. Fac. Sci. Kyushu Univ., (D, Geology), **18** (2): 331-347, pls. 18-19, 1 text-fig.; Fukuoka.
- MURPHY, M. A. & RODDA, P. U. (1960): Molluscs of the Cretaceous Bald Hills Formation of California. – J. Paleont., **34** (5): 835-858, pl. 7, fig. 2; Tulsa.
- NAGY, I. Z. (1971): A vracónni alemelet es kutatásanak története Magyarországon. – Fragm. Min. Pal., **4**: 81 - 107; Budapest.
- (1973): Lower Cretaceous cephalopods from the Mts. Bakony, Hungary. – Ann. Hist.-nat. Mus. Nat. Hung. (Min. Palaeont.), **63**: 13 - 35; Budapest.
- NEUMAYR, M. (1875): Die Ammoniten der Kreide und die Systematik der Ammonitiden. – Z. dt. geol. Ges., **27**: 854-924; Berlin.
- NOWAK, J. (1916): Über die bifiden Loben der oberkretazischen Ammoniten und ihre Bedeutung für die Systematik. – Bull. Acad. Sci. Cracovie, (B), 1916: 1-10, **67**; Kraków.
- ORBIGNY, A. D. (1840-42): Paléontologie française. Terrains Crétacé. I: Céphalopodes. 662 pp., 148 pls.; Paris: Masson.
- (1850): Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés. **2**: 1-428; Paris: Masson.
- OOSTER, W. A. (1857-63): Pétrifications remarquables des Alpes suisses. Catalogue des céphalopodes fossiles des Alpes suisses, Parts 1-5 (1857-60), Suppl. (1863): xxx + 376 pp., 61 pls.; Geneve.
- PARKINSON, J. (1811): On the organic remains of a former world. 3: xvi + 479 pp., 22 pls; London.
- PASSENDORFER, E. (1930): Étude stratigraphique et paléontologique du Crétacé de la Serie Hautatrique dans les Tatras. – Trav. Serv. geol. Pologne, **2** (4): 509-676, 6 pls.; Warszawa.
- PERVINQUIERE, L. (1907): Études de paléontologie tunisienne. 1, Céphalopodes des terrains secondaires du système crétacique. – Mem. Carte géol. Tunisie, 428 pp., 27 pls.; Paris.
- (1910): Sur quelques ammonites du Crétacé algérien. – Mem. Soc. géol. France, (Paleont.), **42**: 1-86, pls. 10-16; Paris.
- PICTET, F. J. (1847): In: PICTET, F. J. & ROUX, W. (1847-54): Description des mollusques fossiles qui se trouvent dans les Grès Verts des environs de Genève. – Mem. Soc. Phys. Hist. natur. Genève, **11** (1847): 257-412, 51 pls.; Genève.
- (1854): Traite de Paléontologie. 2nd ed., ii, Cephalopodes: 583-716; Paris.
- PICTET, F. J. & CAMPICHE, G. (1861-64): Description des fossiles du terrain crétacé des environs de Ste-Croix. – Materiaux Paléont. Suisse, **2**: 1-752, pls. 44-98; Genève.
- PICTET, F. J. & RENEVIER, E. (1866): Notices géologiques et paléontologiques sur les Alpes vaudoises et les régions environnantes. IV: Céphalopodes de Cheville. – Bull. Soc. Vaud. Sci. natur., **9**: 117-138, pls. 3-5; Lausanne.
- PRICE, F. G. H. (1879): The Gault. viii + 81pp.; London.
- QUENSTEDT, F. A. (1845-49): Cephalopoden. – In: Petrefaktenkunde Deutschlands. 1. Abth., **1** (1845): 1-104; **2** (1846): 105-184; **3** (1847): 185-264; **4-5** (1848): 265-472; **6** (1849): 473-580, 36 pls.; Tübingen.
- RENEVIER, E. (1890): Monographie géologique des Hautes-Alpes Vaudoises. – Mat. Carte géol. Suisse, **16**: 1-563, 7 pls., 128 figs.; Genève.
- RENZ, O. (1968): Die Ammonoidea im Stratotyp des Vraconnien bei Sante-Croix (Kanton Waadt). – Mem. suisse Pal., **87**: 1-97, 18 pls., 33 figs.; Basel.

- SCHOLZ, G. (1973): Sur l'âge de la faune d'Ammonites au Château près de St-Martin-en-Vercors (Drôme) et quelques considérations sur l'évolution des Turrilités et des Hoplitidés vracono-cénomaniens. – *Géologie Alpine*, **49**: 119-129; Grenoble.
- (1978): Beiträge zur Kenntnis des ostalpinen Alb. I. Oberalb-Ammoniten aus dem Kampenwandvorland (Chiemgauer Alpen). – *Mitt. Bayer. Staatsgl. Paläont. hist. Geol.*, **18**: 39-44, 3 pls., 2 figs; München.
- (1979): Die Ammoniten des Vracon (Oberalb, dispar-Zone) des Bakony-Gebirges (Westungarn) und eine Revision der wichtigsten Vracon-Arten der West-Mediterranen Faunenprovinz. – *Palaeontographica*, A, **165**, 1-80, 13 pls., 21 figs.; Stuttgart.
- SCOTT, G. (1926): Études stratigraphiques et paléontologiques sur les terrains crétacés du Texas. – Thèses, Fac. Sci., Grenoble University, 218 pp., 3 pls.; Grenoble.
- SEELEY, H. G. (1865): On ammonites of the Cambridge Greensand in the Woodwardian Museum, Cambridge. – *Ann. Mag. Natur. Hist.*, **16**: 225-247, pls. 10-11; London.
- SHARPE, D. (1853-57): Description of the fossil remains of Mollusca found in the Chalk of England. i: Cephalopoda – *Palaeont. Soc. Monogr.*, 1-68, 26 pls.; London.
- SPATH, L. F. (1923): Excursion to Folkestone, with notes on the zones of the Gault. – *Proc. Geol. Assoc.*, **34**: 7-76; London.
- (1931-47): A monograph of the Ammonoidea of the Gault. – *Palaeontogr. Soc. [Monogr.]*, **2** (1931-1943): 312-787, pls. 31-72; London.
- STOLICZKA, F. (1865): The fossil Cephalopoda of the Cretaceous rocks of southern India. – *Mem. geol. Surv. India, palaeont. indica*, (3), Parts 2-13: xii+41-216, pls. 26-94; Calcutta.
- VON HAUER, E. F. (1862): Ueber die Petrefakten der Kreideformation des Bakonyer Waldes. – *Sitzungsber. Akad. Wiss. Wien, math.-nat. Klasse*, **94**: 631-659, 3 pls.; Wien.
- WIEDMANN, J. (1962): Ammoniten aus der Vascogotischen Kreide (Nordspanien). I. Phylloceratina, Lytoceratina. – *Palaeontographica*, A, **118**: 119-237, pls. 8-14, 58 figs.; Stuttgart.
- (1962b): Unterkreide-Ammoniten von Mallorca. I. Lief.: Lytoceratina, Aptychi. – *Abh. Akad. Wiss. Lit. Mainz, Math.-naturw. Kl.*, **1962** (1): 1-148, 10 pls., 36 figs.; Wiesbaden.
- WIEDMANN, J. & DIENI, I. (1968): Die Kreide Sardiniens und ihre Cephalopoden. – *Palaeontogr. ital.*, **64**: 1-171, 101 figs., 18 pls.; Pisa.
- WOODS, H. (1891): Catalogue of the type fossils in the Woodwardian Museum (Cambridge). 120 pp.; Cambridge.
- (1917): The Cretaceous faunas of the northeastern part of the South Island of New Zealand. – *Palaeont. Bull., N. Zealand geol. Surv.*, **4**: 1-41, 20 pls.; Wellington.
- WRIGHT, C. W. (1957): In: MOORE, R. C. (Ed.): *Treatise on invertebrate paleontology*, Part L, Mollusca 4, Cephalopoda, Ammonoidea, 490 pp.; Geol. Soc. Amer., Boulder; Univ. Kansas Press, Lawrence.
- (1981): Cretaceous Ammonoidea. – In: HOUSE, M. R. & SENIOR, J. R. (Eds.): *The Ammonoidea*, pp. 157-174. Academic Press; London.

Bei der Tübinger Schriftleitung eingegangen am 6. November 1996.

Revidiertes Manuskript zum Druck angenommen am 2. Juni 1997.

Anschrift des Verfassers:

Dr. M. R. COOPER, University of Durban-Westville, Dept. Geology, Private Bag X54001, 4000 Durban, Südafrika.