



## Calcareous nannofossils of the uppermost Bedoulian and lower Gargasian of La Tuilière - St-Saturnin-lès-Apt (area of the Aptian stratotype, Vaucluse, SE France)

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**Abstract:** An 148 m composite section located in the Gargas area stratotype in southeastern France has been studied for its calcareous nannofossil content. The four sections span the upper Bedoulian to lower Gargasian with the stadial boundary located within the basal section south of the village of Clavaillan. A total of 75 samples was processed to inventory taxonomy and stratigraphic distributions.

*Eprolithus floralis* is present at the base of the stratigraphic succession. The lowest occurrence of this species, which marks the base of Subzone NC7A, has been documented in the uppermost lower Aptian (Bedoulian) in other sections in southeastern France. The highest occurrence of the genus *Micrantholithus* has been utilized to delineate the base of Subzone NC7B. This subzonal boundary was placed at 48 m in the Les Gays I section (113.5 m in the composite) below the lowest occurrence of the foraminififer *Globigerinelloides ferreolensis* in the suprajacent sample (50 m). The lowest occurrence of *Braarudosphaera africana* is identified as a regional biohorizon in lower Subzone NC7A and a local proxy for the Bedoulian/Gargasian boundary. This event was placed at 15.5 m in the Clavaillan section at the base of the *Dufrenoyia furcata* Zone and within the "Niveau Blanc inférieur" marker bed (NB1).

The genus *Nannoconus* is abundant to very abundant in all samples examined. Taxonomic rigor has resulted in the recognition of five main morphologic groups (A-E), including all but one of the 15 species discriminated over this relatively short stratigraphic interval. Four main *Nannoconus* assemblage bio-zones - with one subdivision - have been distinguished through semi-quantitative analyses and organized relative to these taxonomic groupings. Assemblage Biozone B is restricted to the Bedoulian and has been correlated to the lower portion of Subzone NC7A (i.e., NC7A1). Assemblage biozones GI and GII (A-B) have been correlated to the upper portion of Subzone NC7A (i.e., NC7A2) and Biozone GIII to Subzone NC7B within the Gargasian.

*Assipetra* is another solution-resistant genus included in semi-quantitative analyses, where its species were separated into small and large forms based on a size of 10 µm. The highest percentages of large morphotypes are within the Bedoulian in the lower 10.5 m of the Clavaillan section, roughly coeval to an acme of large *Assipetra* observed in the basal portion of the Serre Chaitieu section in the nearby Vocontian Basin.

### Key-words:

- Aptian stratotype;
- Gargasian;
- Bedoulian/Gargasian boundary;
- calcareous nannofossils;
- *Nannoconus*;
- taxonomy;
- biostratigraphy

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**Résumé :** *Nanno fossiles calcaires du Bédoulien sommital et du Gargasien inférieur de La Tuilière - St-Saturnin-lès-Apt (région du stratotype de l'Aptien, Vaucluse, Sud-Est de la France).*- Une coupe composite de 148 m localisée dans la région stratotypique de Gargas (Sud-Est de la France) a été étudiée pour son contenu en nannofossiles calcaires. Les quatre coupes couvrent le Bédoulien supérieur et le Gargasien inférieur. La limite entre Aptien inférieur (Bédoulien) et Aptien supérieur (Gargasien) a été reconnue à la partie inférieure de la coupe basale au sud du village de Clavaillan. Un total de 75 échantillons ont été préparés pour l'analyse taxinomique et stratigraphique.

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*Eprolithus floralis* est présent dans les premiers échantillons de la succession stratigraphique. La première apparition de cette espèce qui marque la base de la sous-zone NC7A a été documentée dans la partie sommitale de l'Aptien inférieur (Bédoulien) dans d'autres coupes du Sud-Est de la France. La dernière apparition du genre *Micrantholithus* a été utilisée pour identifier la base de la sous-zone NC7B. Cette limite de sous-zone a été placée à 48 m dans la coupe Les Gays I (113,5 m dans la coupe composite) en dessous de la première apparition du foraminifère planctonique *Globigerinelloides ferreolensis* dans l'échantillon du dessus (50 m). La première apparition de *Braarudosphaera africana* est identifiée comme un horizon régional à l'intérieur de la partie inférieure de la sous-zone NC7A et un repère local pour la limite Bédoulien/Gargasien. Cet événement a été placé à 15,5 m dans la coupe de Clavaillan à la base de la Zone à *Dufrenoyia furcata* (ammonite) et dans le "Niveau Blanc inférieur" (marqueur NB1).

Une attention particulière a été portée aux Nannoconidés toujours abondants à très abondants dans tous les échantillons. Sur cet intervalle stratigraphique relativement court, cinq groupes morphologiques principaux (A-E) avec une quinzaine d'espèces ont été identifiés. Quatre biozones à *Nannoconus*, dont une subdivisée en deux sous-zones, ont été distinguées. La biozone B est limitée au Bédoulien et a été corrélée à la partie inférieure de la sous-zone NC7A (i.e., NC7A1). Les biozones GI et GII (A-B) ont été corrélées à la partie supérieure de la sous-zone NC7A (i.e., NC7A2) et la biozone GIII à la sous-zone NC7B dans le Gargasien.

*Assipetra*, un autre genre résistant à la dissolution, a également été pris en considération dans les analyses semi-quantitatives. Ses représentants ont été séparés en petites et grandes formes sur la base d'un seuil de taille de 10 µm. Les taux les plus élevés de grands morphotypes sont reconnus dans les 10,5 m inférieurs de la coupe de Clavaillan (Bédoulien). Cet épisode est à peu près équivalent de l'acmé à grande *Assipetra* observée dans la partie basale de la coupe de Serre Chaitieu dans le bassin Vocontien voisin.

#### Mots-clefs :

- Aptien stratotype ;
- Gargasien ;
- limite Gargasien/Bédoulien ;
- nannofossiles calcaires ;
- Nannoconus ;
- taxinomie ;
- biostratigraphie

## 1. Introduction

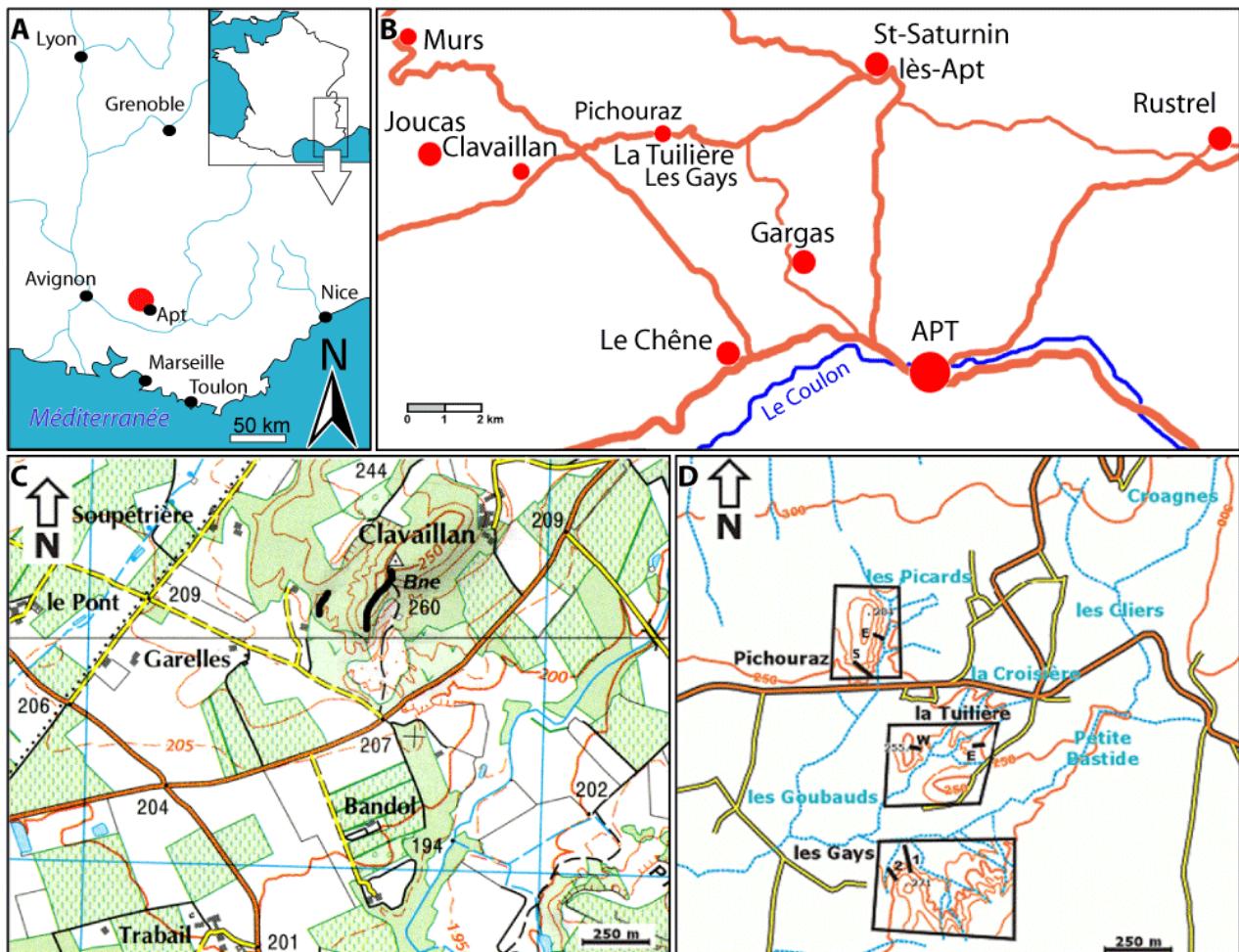
The Aptian calcareous nannofossils of south-eastern France have been previously studied by several researchers. DEFLANDRE and DEFLANDRE-RIGAUD (1962, 1967) published their pioneering taxonomic work on *Nannoconus* from Carniol ("Haute-Provence"). The first attempts at Lower Cretaceous biostratigraphy by means of calcareous nannofossils, with reference to the stratotype areas, were by MANIVIT (1971) and THIERSTEIN (1971, 1973). The latter established the first Lower Cretaceous nannofossil biozonation. The detailed taxonomical study of the calcareous nannofossils of two Aptian substages type sections (Cassis-La Bédoule, Lower Aptian and Gargas, Upper Aptian) was carried out by BARRIER (1977a, 1977b). More recently, in a collective volume dedicated to the Lower Aptian stratotype, BERGEN (1998) published a thorough inventory of the Bédoulian calcareous nannofossils, as well as data on stratigraphic ranges and semi-quantitative distributions. The Aptian-Albian calcareous nannofossil biostratigraphy of the neighbouring Vocontian area was reviewed by HERRLE and MUTTERLOSE (2003) and most recently for the lower to upper Aptian by GIRAUD *et al.* (2018).

## 2. The studied area

The four studied sections are located near the hamlet of La Tuilière, included in the village of Saint-Saturnin-lès-Apt (Fig. 1). These sections are the Clavaillan Hill, south Pichouraz Hill and the Les Gays Farm area (two sections). For further information about their geographic location, relationships and geological setting, see DUTOUR (2005), and MOULLADE *et al.* (2006, 2008, 2017).

By compositing these four sections, we estimate the total thickness of Aptian sediments measured in this area at around 148 m (with a gap between the top of Clavaillan and the base of Pichouraz East sections, see MOULLADE *et al.*, 2017):

- the Clavaillan section comprises the uppermost Bedoulian (*sensu* ATROPS & DUTOUR, 2005: *Deshayesites grandis* Zone) and the lowermost Gargasian (*Dufrenoyia furcata* Zone), 17 samples;
- the south Pichouraz section comprises the lower part of the Gargasian substages (*Dufrenoyia furcata* Zone), 16 samples;
- the Les Gays sections 1 and 2 slightly overlap the top of the south Pichouraz section and include the lower Gargasian (mainly *Dufrenoyia furcata* Zone and *Cheloniceras martini* Zone for the top of the sections), 42 samples (34 for Les Gays 1+ 8 for Les Gays 2).



**Figure 1:** Geographic location of the area studied. **A)** Apt area in SE France; **B)** studied sections; **C)** Clavaillan area; **D)** Pichouraz East and South; La Tuilière W; Les Gays 1 and 2.

The average spacing between samples is about 2 m.

MOULLADE *et al.* (2006, 2017) divided the relatively homogeneous lithostratigraphy in this area into five main units from the base to top:

1. 22 m of marly grey limestones (terminal Bedoulian, *Deshayesites grandis* Zone);
2. 32 m of blue-grey marls (12 m gap between top Clavaillan section and base south Pichouraz section) framed by two "niveaux blanc" levels (NB1 and NB2);
3. 21 m of bluish grey marls changing into yellowish blue marls in the upper half;
4. 11 m of yellowish marls with centimeter intercalations of marly limestones, limonitic beds, and pyritized-limonitic nodules; and
5. 62 m of soft laminated bluish grey marls.

Details of the composite section and sample levels, in addition to the ammonite and foraminiferal stratigraphies, are summarized in MOULLADE *et al.* (2017).

### 3. Materials and methods

Nannofossil preservation is heterogeneous in the material studied. For *Nannoconus*, there is no special problem due to the relatively great size and robustness of the specimens, especially in the lower part of the studied sections (Clavaillan). As for the other nannofossils, preservation appears related to the calcium carbonate content. In the Clavaillan section, the sediments are composed of shaly limestones, where the high content in CaCO<sub>3</sub> seems to be directly related to the abundance of *Nannoconus* tests and the poor preservation of the other nannofossils components (especially small specimens). In the other sections (*i.e.*, South Pichouraz and Les Gays), marls and calcareous shales are the dominant lithologies and the nannofossils preservation is very good. This basic contrast in nannofossils preservation introduces bias in calcareous nannofossil distributions.

All analyses undertaken on our material are based on optical observations only (no SEM analyses were performed). Two smear slides were



prepared for each sample: One slide with a higher concentration of sediment to investigate all nannofossil components and one slide with a relatively dilute amount of sediment for semiquantitative analyses. No special cleaning methods were used in sample preparations.

The "semi-quantitative" approach employed is unconventional (see LAMBERT & LAPORTE-GALAA, 2005, for further details). This approach did not account for the actual nannofossil abundance, but instead are counts of an individual taxon or a group of taxa to the total nannofossil population. For this exercise, two types of estimates were made:

- for each sample, a minimum of thirty to forty specimens of *Nannoconus* were both photographed and drawn. This was considered an adequate representation of relative abundance within the genus (see LAMBERT & LAPORTE-GALAA, 2005);
- five hundred specimens of *Nannoconus* were counted to estimate the ratio of *Assipetra infracretacea* to *A. terebrodentarius*.

TREMOLADA and ERBA (2002) have illustrated the importance of the size variation of both *A. infracretacea* and *A. terebrodentarius* during Aptian time. These authors noted that large specimens are more frequent in the lower Aptian. We have carried out a semi-quantitative distribution of these two species. Threshold given by these authors is 7.5 µm. However, for operational reasons (technical limitations related to the microscope) we have applied a 10 µm threshold.

We have introduced a new index, the ratio between *A.i + A.t* and *Nannoconus*. The estimated frequency have been obtained after counting 500 specimens of *Nannoconus*. This index allows us to provide a relative frequency of these two nannofossils. The *A.i + A.t* (big / small with a threshold at 10 µm) ratio have been obtained if the number of specimens is equal to or greater than 50 specimens of *Assipetra* (in one smear slide). Four intervals can be distinguished:

1. Clavaillan, samples 2385 to 2390, *A.i + A.t / N* = 12 to 15%, *A.i + A.t* large forms / *A.i + A.t* small forms = 40 to 70%.
2. Clavaillan, samples 2391 to 2410, Pichouraz sud samples 2270 to 2286, *A.i + A.t / N* = lower than 5%, *A.i + A.t* large forms / *A.i + A.t* small forms = not applicable (not enough specimens observed).
3. Les Gays 1, samples 2309 to 2321, *A.i + A.t / N* = 8 to 10%, *A.i + A.t* large forms / *A.i + A.t* small forms = 10 to 30%.
4. Les Gays 1, samples 2322 to 2341, *A.i + A.t / N* = lower than 1%, *A.i + A.t* large forms / *A.i + A.t* small forms = Not applicable (not enough specimens observed).

#### 4. Biostratigraphy

**Nannoconid assemblage biozones.** Four local *Nannoconus* assemblage zones - including one divided into two subzones - have been recognized in the materials studied (Figs. 2, 4) and integrated with the event stratigraphy (see § "Nannofossil biozonation" below):

**1. Biozone B (Bedoulian):** Clavaillan 2385 to 2393 samples

- Group E, *N. wassallii* (abundant);
- Group D, *N. bucheri* (abundant);
- Group C, *N. quadriangulus* (rare);
- Group B, *N. circularis* (abundant);
- others: *N. elongatus* (rare), *N. steinmannii* (very rare).

**2. Biozone GI (Gargasian):** Clavaillan samples 2394 to 2410 samples, south Pichouraz samples 2270 and 2272. The complete *Nannoconus* association is as follows:

- Group E, *N. aff. grandis* (rare), *N. kamptneri* (rare), *N. bonetii* (present), *N. wassallii* (abundant), *N. clavaillanensis* (present);
- Group D, *N. bucheri* (abundant), *N. vocontiensis* (rare);
- Group C, *N. quadriangulus* (rare), *N. inconspicuus* (rare);
- Group B, *N. circularis* (abundant);
- Group A, *N. boletus* (rare).

**3a. Biozone GII (Subzone GIIA):** south Pichouraz samples 2274 to 2292

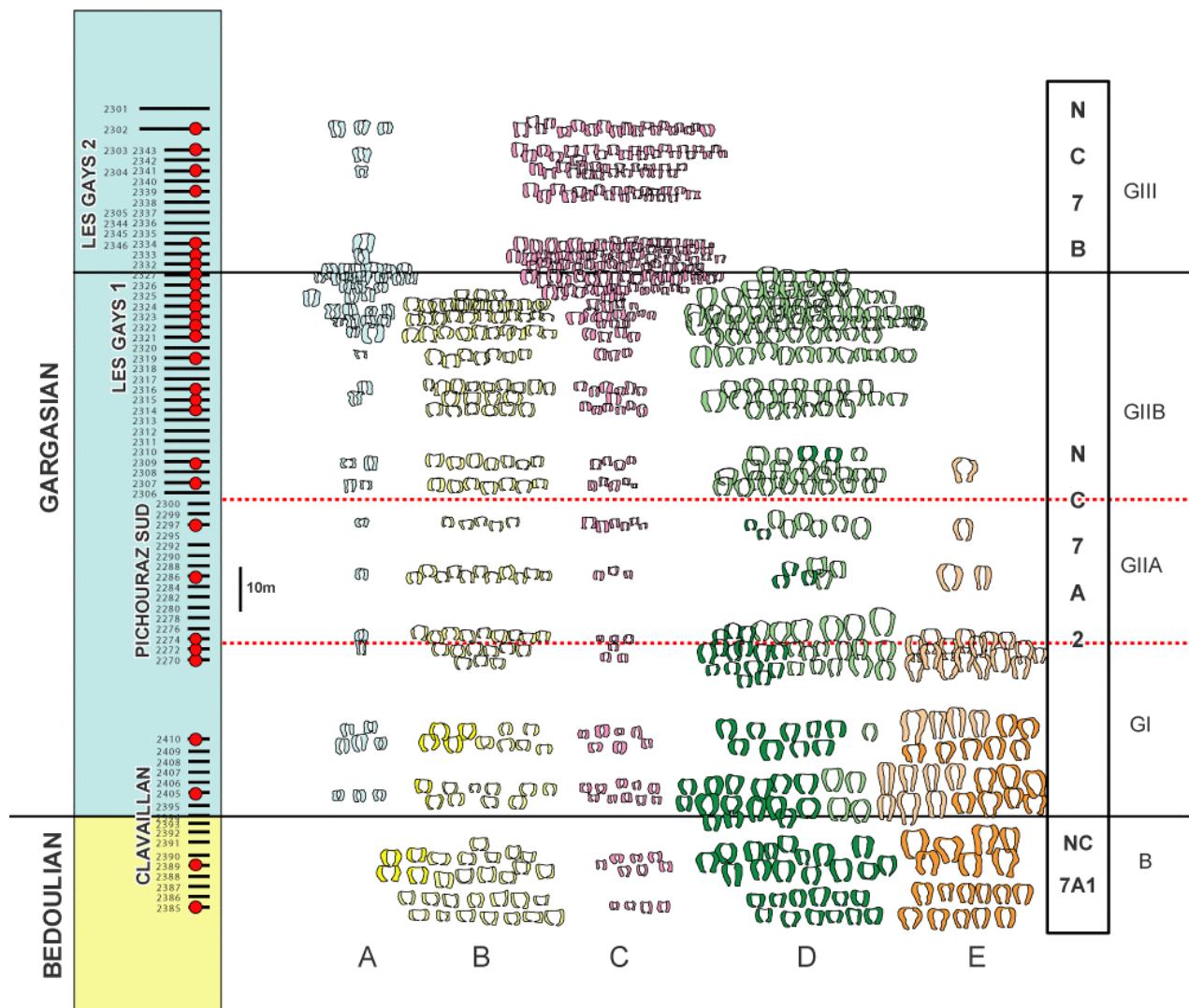
- Group D, *N. bucheri* (rare), *N. vocontiensis* (abundant);
- Group C, *N. quadriangulus* (rare);
- Group B, *N. globulus* (present), *N. circularis* (abundant);
- Group A, *N. boletus* (rare);
- drastic reduction of Group E at the base of the unit.

**3b. Biozone GII (Subzone GIIB):** south Pichouraz samples 2295 to 2300, Les Gays 1 Samples 2306 to 2327

- Group D, *N. bucheri* (rare), *N. vocontiensis* (abundant);
- Group C, *N. quadriangulus* (rare);
- Group B, *N. globulus* (present), *N. circularis* (abundant);
- Group A, *N. boletus* (rare), *N. carniolensis* (rare).

**4. Biozone GIII,** samples Les Gays 1 samples 2332 to 2343, Les Gays 2 samples 2346 to 2301

- Group C, *N. quadriangulus* (very abundant);
- Group A, *N. boletus* (present);
- extinctions of Groups B and D at the base of the unit.



**Figure 2:** Semi-quantitative *Nannoconus* distributions.

A = *N. boletus* / *N. carniolensis*

B = *N. aff. globulus* (dark yellow), *N. circularis* (light yellow)

C = *N. truitii*, *N. inconspicuus*, *N. quadriangulus*

D = *N. bucheri* (dark green), *N. vocontiensis* (light green)

E = *N. wassallii* (dark brown); *N. aff. borealis* / *N. bonetii* / *N. kampfneri* (yellow brown)

**Nannofossil biozonation:** The standard NC zonation of ROTH (1978), as emended by BRA- LOWER *et al.* (1993), is employed herein for consistency with previous regional studies in south- eastern France. The following stratigraphic sub- divisions are proposed for this study (Fig. 3):

- Lower Subzone NC7A1: Clavaillan samples 2385 to 2393

The interval from the first occurrence of *Epro- lithus floralis* (present at the base of the composite section) to the first occurrence of *Braarudo- sphaera africana*. The lowest occurrence of *Br. africana* is in Sample 2394 (15.5 m) in the Clavaillan section. This interval contains *Nannoconus* assemblage Biozone B. The highest abundances of *Assipetra* and highest percentages of large morphotypes (> 10 µm) relative to small are re- stricted to the lower 10.5 m (sample 2390 and below) of the Clavaillan section. Sporadic occur-

rences of *Nannoconus steinmannii* and *Conusphaera rothii* were observed throughout. *Nannoconus elongatus* is restricted to the lower part of this interval.

- Upper Subzone NC7A2: Clavaillan samples 2394 to 2410, south Pichouraz samples 2270 to 2300, Les Gays 1 samples 2306 to 2327

The interval from the first occurrence of *Braarudo- sphaera africana* to the last occurrence of *Micrantholithus* spp. This interval includes *Nannoconus* assemblage biozones GI and GII. The lowest occurrences of *N. boletus* and *N. voconti- ensis* were observed at the base of this interval. The highest occurrences of *Diazomatolithus leh- manii* and "wide" *Nannoconus* (*N. circularis*, *N. vocontiensis*, *N. bucheri*) were observed at the top of this interval. The ratio of large to small *As- sipetra* is higher in the upper portion of this inter- val (*Nannoconus* assemblage Biozone GIIB).



- Subzone NC7B: Les Gays 1 samples 2332 to 2343, Les Gays 2 samples 2346 to 2301

The interval between the last occurrence of *Micrantholithus* spp. and the first occurrence of *Prediscosphaera columnata* (not present at the top of the composite section). This interval contains *Nannoconus* assemblage Biozone GIII. Short *Nannoconus* with wide axial canals (*N. truittii* and *N. quadriangulus*) are very abundant throughout this subzone, but rare below. A significant change in the nannoconid populations at the base of this subzone between samples 2327 and 2332 in the Les Gays I section is further reinforced by highest common occurrences and tops of both *N. circulans* and *N. vocontiensis*, in addition to the top of *N. bucheri*. The lowest occurrences of *Stoverius achylosus* and *Orastrum perspicuum* were also observed at the base of this subzone.

**Regional nannofossil studies:** The first comprehensive Lower Cretaceous nannofossil biostratigraphic scheme by THIERSTEIN (1971) was founded on a composite of fourteen sections located in southeastern France. THIERSTEIN (1973) later published range charts of this research and the five outcrops encompassing the Aptian included the Bedoulian and Gargasian historical stratotypes. These data and interpretations provided the foundation for the Aptian zonal stratigraphy both regionally and globally for the bases of NC6 to NC8. More recent Aptian nannofossil biostratigraphic and paleoecologic studies in southeastern France are summarized in Figure 4, along with the integrated ammonite and foraminiferal biozonations.

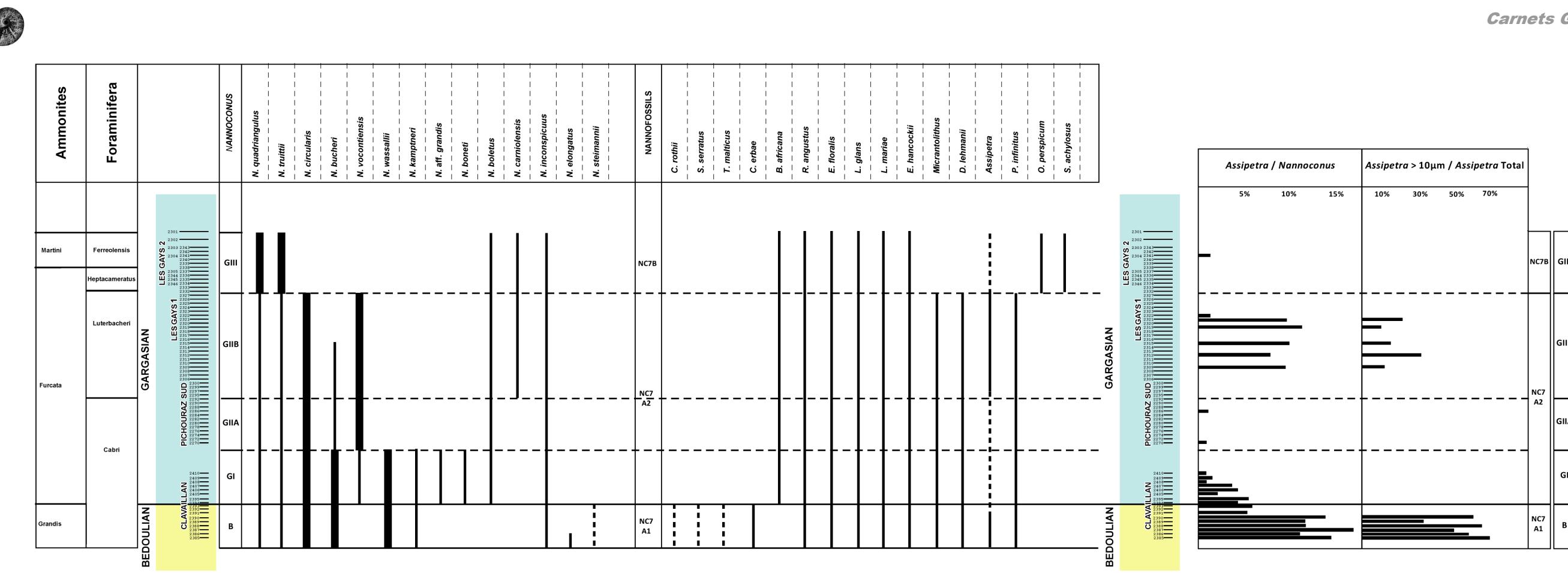
Multidisciplinary stratigraphic research on the lower Aptian historical stratotype in the Cassis-La Bédoule area (South Provencal Basin) is summarized by MOULLADE *et al.* (1998). BERGEN (1998) published the calcareous nannofossil biostratigraphy and abundance trends of some key genera in the same volume and bracketed the section from the upper portion of Subzone NC5C to the lower 6 m of Subzone NC7A (*M. hoschulzii* ranges to the top of the section, Bed 175B). The lowest occurrence of *Eprolithus floralis* (Bed 169A) marked the base of Subzone NC7A, followed upwards by the bases of *Braarudosphaera africana* (Bed 172B), *Radiolithus planus* (Bed 173), and *Chiastozygus platyrhethum* (Bed 174B).

Two biostratigraphic-paleoecologic studies (HERRLE & MUTTERLOSE, 2003; GIRAUD *et al.*, 2018) in the nearby Vocontian Basin overlap stratigraphically in lower Subzone NC7A (Fig. 4). The multidisciplinary study on the Notre-Dame-de-Rosans section by GIRAUD *et al.* (2018) assessed early Aptian paleoecologic trends across the OAE1a event within their detailed chronologic framework. The majority of the 45.5 m measured section was placed in Subzone NC6B based on the presence of *Rhagodiscus angustus* at its base and the absence of *Conusphaera rothii* throughout. The base of Subzone NC7A was placed 4 m above the black shales of the "Niveau GOGUEL" (~9.5 m below the

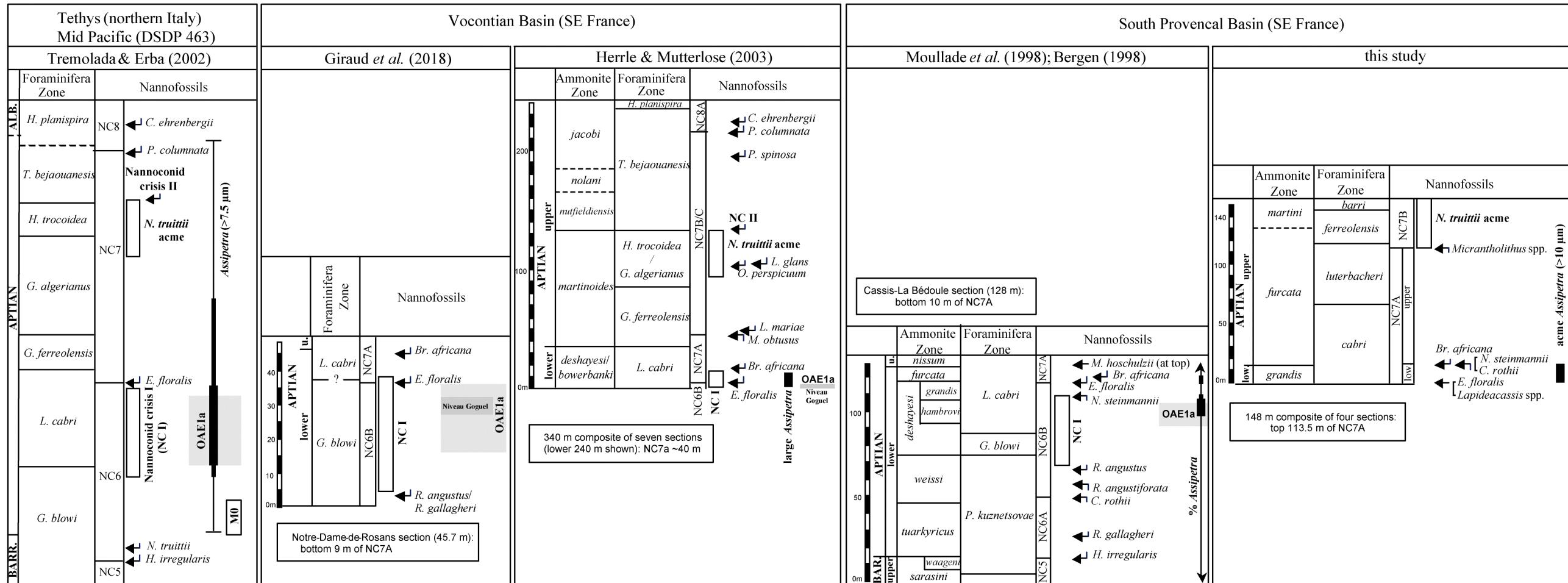
top of the section) on the lowest occurrence of *Eprolithus floralis* and roughly equivalent to the lowest occurrence of the foraminifer *Leupoldina cabri*. They also reported the following sequence of lowest occurrences within Subzone NC7A relative to the top of the "Niveau GOGUEL": *Radiolithus planus* (8 m), *Eprolithus apertior* (12.5 m), and *Braarudosphaera africana* (13 m). *Micrantholithus hoschulzii*, the extinction of which marks the top of Subzone NC7A, ranges to the top of this section.

HERRLE and MUTTERLOSE (2003) investigated the nannofossil biostratigraphy and assemblages from a 340 m composite of seven sections spanning the upper lower Aptian (Zone NC6) to lowermost Albian (Subzone NC8B). They documented a sequence of 23 nannofossil appearance/extinction events, in addition to abundance trends of the genera *Nannoconus*, *Assipetra*, and *Repagulum*. These results were integrated to the lithostratigraphy (esp. black shales and other key beds), ammonite and foraminiferal biozonations, and interpreted eustatic cycles. The lowest occurrence of *Eprolithus floralis* (base Subzone NC7A) was placed 1 m above the "Niveau GOGUEL" black shales near the base of the composite section. The highest occurrence of *Micrantholithus obtusus* was used to mark the top Subzone NC7A, as opposed to the original marker species (*M. hoschulzii*) proposed by BRALOWER *et al.* (1993). This event was placed 7.7 m below the Niveau Noire Calcaire 2 in the same section. Within the lower half of the approximately 40 m of Subzone NC7A in this Serre Chaitieu section, the following nannofossil radiation was documented from bottom to top: *Radiolithus planus*, *Eprolithus apertior*, *Braarudosphaera africana*, *Br. hockwoldensis*, and *Eprolithus varolii*/*Corollithion acutum*. In addition, a 13 m interval from the Niveau GOGUEL (OAE1a) to the Niveau Blanc straddling the NC6/NC7A boundary was observed to be nearly devoid of *Nannoconus*, but containing elevated percentages of large *Assipetra infracretacea* (> 6 µm) and *A. terebrodentarius* (> 10 µm). HERRLE and MUTTERLOSE (2003) equated this interval to the nannoconid crisis of ERBA (1994) and formerly designated it as nannoconid crisis I (NCI).

HERRLE and MUTTERLOSE (2003) could not differentiate Subzone NC7C because the lowest occurrence of *Rhagodiscus achlyostaurion* was not observed in the Serre Chaitieu section. Their combined Subzone NC7B/C, approximately 170 m thick and spanning three sections, was delineated at its top by the lowest occurrence of *Prediscosphaera columnata*. Within this combined subzone, a sequence of five lowest occurrences are distributed into three discrete intervals from bottom to top: (1) *Lapideacassis mariae* followed above by *Prediscosphaera* sp. near the base; (2) *Orastrum perspicuum* followed immediately above by *Lapideacassis glans* in the middle; and (3) *Prediscosphaera spinosa* near the top of Subzone NC7B/C.



**Figure 3:** Nannoplankton stratigraphic distributions.



**Figure 4:** Comparisons to relevant nannofossil research.





MUTTERLOSE (1989, 1991) described a late Aptian acme in *Nannoconus truittii*, noting its occurrence in both Boreal and Tethys sections. HERRLE and MUTTERLOSE (2003) documented a nannoconid acme in the lower upper Aptian of their composite in southeastern France, ranging from the middle *Globigerinelloides algerianus* to the base of the *Ticinella bejaouaensis* foraminiferal zones. HERRLE and MUTTERLOSE (2003) defined the rapid decrease in *Nannoconus* spp. at the top of this acme as nannoconid crisis II (NCII).

TREMOLADA and ERBA (2002) studied the Aptian biostratigraphy, paleoecology, and morphometrics of *Assipetra infracretacea* and *Assipetra terebrodentarius* from individual cores in northern Italy (Cismon) and the mid Pacific (DSDP Site 453), providing insight and calibration for the current work (Fig. 4). They found that the highest percentages of large specimens ( $> 7.5 \mu\text{m}$ ) relative to normal-sized specimens for both species occurred within the upper lower Aptian "SELLI" event (OAE1a). This acme of large *Assipetra* occurred in the upper portion of Zone NC6 is also associated with the first nannoconid crisis (NCI). TREMOLADA and ERBA (2002) summarized the abundance and stratigraphy of *Assipetra* from the uppermost Barremian (NC5) to lower Albian (lower NC8) relative to the magnetostratigraphy and foraminiferal zones. Their definitions of zones NC6 to NC8 (Fig. 4) are congruent with the aforementioned research in southeastern France (BERGEN, 1998; MOULLADE *et al.*, 1998; HERRLE & MUTTERLOSE, 2003; GIRAUD *et al.*, 2018), as well as the calibration of the late Aptian *Nannoconus truittii* acme (NCII) with HERRLE and MUTTERLOSE (2003).

## 5. Discussion

The composite of four sections in the South Provencal Basin spans the upper portion of Subzone NC7A to the lower portion of Subzone NC7B (see § "Nannofossil biozonation" above). The lowest occurrence of *Braarudosphaera africana* can be used as an event to further subdivide Subzone NC7A in southeastern France, whereas Subzone NC7C (base on the first occurrence of *Rhagodiscus achlyostaurion*) was not delineated in these same regional studies (Fig. 4).

*Lapideacassis* and *Eprolithus floralis* were observed throughout the entire composite of four sections studied (Fig. 3). The presence of both *L. mariae* and *L. glans* at the base of the composite in Subzone NC7A are both lower (in NC7B/C) than reported by HERRLE and MUTTERLOSE (2003) in the nearby Vocontian Basin. Conversely, the lowest occurrence of *Stoverius achylosus* was determined to be higher in this study (base Subzone NC7B) relative to original zonal framework (NC6A, BRALOWER *et al.*, 1993) and the historical Bedoulian stratotype (NC6B, BERGEN, 1998).

Two stratigraphic anomalies in the lower half of the Clavaillan section are: (1) the occurrences of *Conusphaera rothii* and *Nannoconus steinmannii* with *Eprolithus floralis*; and (2) increased percentages of large *Assipetra*. BRALOWER *et al.* (1993) defined the top of Subzone NC6A on the highest occurrence of *Conusphaera rothii* and placed the top of *Nannoconus steinmannii* immediately above in the basal portion of Subzone NC6B; they defined the base of Subzone NC7A on the lowest occurrence of *Eprolithus floralis*. BERGEN (1998) confirmed this subzonal stratigraphy in the historical Bedoulian stratotype, but placed the top of *Nannoconus steinmannii* much higher - immediately below the base of Subzone NC7A. Both *N. steinmannii* and *Conusphaera rothii* are extremely rare in Clavaillan samples. When contrasted to the continuous presence of *Eprolithus floralis*, redeposition is a likely explanation for these extremely rare occurrences. TREMOLADA and ERBA (2002) documented the highest percentage of large versus normal-sized *Assipetra* in the upper part of Zone NC6 below the lowest occurrence of *Eprolithus floralis*. They associated the "acmes" of these large forms with maximum TOC values during OAE1a in cores in northern Italy and the mid Pacific. Disparate taxonomy (*i.e.*, size) and counting methodologies could explain the apparent age discrepancies in the "acmes" of these large morphotypes. However, the possibility of diachroneity - or a second, late early Aptian acme in large *Assipetra* - must be considered. HERRLE and MUTTERLOSE (2003) also observed an acme in large *Assipetra* in lowermost Subzone NC7A in the Vocontian Basin (Fig. 4).

The lowest occurrence of *Braarudosphaera africana* at 15.5 m above the base of the Clavaillan section correlates to the base of *Dufrenoyia furcata* Zone and falls within the "Niveau Blanc inférieur" (NB1) marker (see MOULLADE *et al.*, 2017). Elsewhere in the South Provencal Basin at the Cassis-La Bédoule section, this event was placed 2.5 m above the base of the *Dufrenoyia furcata* Zone and 3 m above the base of NC7A (MOULLADE *et al.*, 1998; BERGEN, 1998). Ten other nannofossil events associated with the *Braarudosphaera africana* horizon at Clavaillan (Fig. 3) indicate a disconformity and would explain this slight discrepancy in correlation to the ammonite zonal stratigraphy in the basin. In the Vocontian Basin, the lowest occurrence of *Br. africana* was placed 9 m above the base of NC7A in the Notre-Dame-de-Rosans section by GIRAUD *et al.* (2018) and approximately 17 m above the base of NC7A in the Serre Chaitieu section by HERRLE and MUTTERLOSE (2003).

The highest occurrence of the genus *Micrantholithus* in sample 2327 (48 m) in the Les Gays I section is used herein to mark the base of Sub-



zone NC7B; the lowest occurrence of the foraminifer *Globigerinelloides ferreolensis* is immediately above in sample 2332 (50 m; MOULLADE *et al.*, 2017). Seven other nannofossil bioevents (lowest and highest occurrences) have been associated with the boundary between subzones NC7A and NC7B in this study; abundance changes of five *Nannoconus* species were also observed at this stratigraphic level (Fig. 3). All these data indicate a significant change between samples 2327 and 2332 in the Les Gays I section. In the Vocontian Basin, HERRLE and MUTTERLOSE (2003) used the highest occurrence of *Micrantholithus obtusus* to mark the base of Subzone NC7B, as opposed to the highest occurrence of the genus. The strong abundance increase in short nannoconids with wide axial canals at the base of Subzone NC7B could be related to the base of the *Nannoconus truitii* acme correlated to the middle of the *Globigerinelloides algerianus* foraminiferal Zone (TREMOLADA & ERBA, 2002; HERRLE & MUTTERLOSE, 2003). However, it is associated with the base of the underlying *Globigerinelloides ferreolensis* foraminiferal Zone herein.

## 6. Systematic paleontology

The Mesozoic classification of BOWN and YOUNG (1997) is mainly followed, with some modification to the ordinal classification proposed by WATKINS and RAFFI (2020). PERCH-NIELSEN (1985) and YOUNG *et al.* (1997, 2022) were also used for classification.

### Order EIFELLITHALES RODD *et al.*, 1971

Imbricate muroliths.

#### Family CHIASTOZYGACEAE (ROOD *et al.*, 1973) VAROL & GIRGIS, 1994

##### Genus *Staurolithites* CARATINI, 1963

Imbricate muroliths with a central axial cross. *Vagalapilla* BUKRY, 1969, *Vekshinella* LOEBLICH & TAPPAN, 1963, and *Staurorhabdus* NOËL, 1972, are considered junior synonyms.

##### *Staurolithites handleyi* LEES, 2007

Pl. 3, fig. 13

Small coccolith (< 4 µm) with a delicate cross.

Distribution: Sporadic in the Gargasian marls.

##### *Staurolithites mutterlosei* CRUX, 1989

Pl. 3, fig. 14

This relatively large coccolith has a spiraled extinction pattern. The bright cross is slightly off-axis, but the arms are at right angles. It occurs sporadically throughout the Gargasian.

##### *Staurolithites rectus* BLACK, 1971a

Pl. 3, figs. 15-16

This relatively large coccolith (< 6 µm) has a wide central area spanned by a prominent axial cross. Optically, the relatively broad, parallel-sided arms are divided by longitudinal sutures.

Distribution: Sporadic in all the samples.

#### Genus *Bukrylithus* BLACK, 1971a *Bukrylithus ambiguus* BLACK, 1971a

Pl. 3, fig. 17

The well-developed axial cross broadens towards the center; its base arched on the proximal surface.

Distribution: Sporadic in the Gargasian marls.

#### Genus *Rhabdophidites* (MANIVIT, 1971) LAMBERT, 1987

The murolith base is minute relative to the elongate, bladed stem. For further discussion about this genus, see COVINGTON and WISE (1987, p. 632).

##### *Rhabdophidites moeslensis*

MANIVIT, 1971

Pl. 3, figs. 20-21

Stem is greater than 10 times the coccolith length (< 1 µm). The stem tapers in both directions as in *Lithraphidites*, but that genus has no basal coccolith.

Distribution: Sporadic in the samples studied. MANIVIT (1971) has reported this nannofossil from the Albian.

##### *Rhabdophidites parallelus* (WIND & ČEPEK, 1979) LAMBERT, 1987

Pl. 3, figs. 18-19, 22

The basal coccolith is 1-2 µm and the distal shield composed of around 20 elements (LAMBERT, 1987). Stem length is about 3-4 times the coccolith length.

Distribution: Sporadic in all the samples.

#### Genus *Chiastozygus* GARTNER, 1968

The central area is occupied by a diagonal cross; the angle between the arms is variable.

##### *Chiastozygus platyrhetum* HILL, 1976

Pl. 4, figs. 4-5

Description: "Central area spanned by a central cross, the arms of which are oriented symmetrically about the principal axes of the ellipses. The crossbars and the rim are approximately equal in width" (HILL, 1976, p. 129). The crossbar is located slightly above the rim and each arm appears bisected longitudinally in cross-polarized light.

Distribution: Sporadic in the Gargasian marls. BERGEN (1998) placed the lowest occurrence of this species in the upper Bedoulian within the lower portion of Zone NC7.

##### *Chiastozygus aff. tenuis* BLACK, 1971a

Pl. 4, figs. 1-3, ? 9

This taxon mostly closely resembles *Chiastozygus tenuis*, from which it differs by having a stem and a cross that slightly deviates from the main ellipse axes. The cross arms are orthogonal. Specimens observed appear conspecific to the specimen of "*Zyglolithus*" *litterarius* (GÓRKA) in



THEIRSTEIN (1971, Pl. 1, figs. 3-4), but *Chiastozygus litterarius* (GÓRKA, 1957) MANIVIT, 1971, is a Maastrichtian species with a bright, spiraled rim extinction pattern (see REINHARDT & GÓRKA, 1967; BERGEN, 1998).

Distribution: Sporadic in all the samples.

#### Genus *Tegumentum*

***Tegumentum stradneri***

***Tegumentum stradneri***

Pl. 4, figs. 6-7

The arms form an acute angle to the minor ellipse axis. Specimens were observed with crosses that were asymmetric (Pl. 4, fig. 6) to symmetric (Pl. 4, fig. 7) to the ellipse axes.

Distribution: Sporadic throughout the samples.

#### Genus *Percivalia* BUKRY, 1969

*Percivalia* is characterized by an inner rim area composed of several narrow tiers of elements (BUKRY, 1969). The lath-shaped elements of these tiered cycles are upright and exhibit a first order white birefringence. The central area may be occupied by a variety of central structures.

##### *Percivalia fenestratus*

(WORSLEY, 1971) WISE, 1983

Pl. 7, fig. 3

This species has an imperforate central area; in cross-polarized light, two nodes may be noticed in the minor axis of the central area.

Distribution: Sporadic in all the samples.

##### *Percivalia hauxtonensis* BLACK, 1973

Pl. 7, figs. 1-2

*Percivalia hauxtonensis* is a medium to large species with two longitudinal central perforations and a distal boss. BLACK (1973) illustrated five electron photomicrographs (proximal and distal views) and provided measurements of nine specimens (7.2-9.0 µm in length). The longitudinal central openings of the lower Cenomanian holotype are rimmed by a cycle of elements, akin to the two specimens illustrated herein. The light photomicrographs of an upper Albian specimen illustrated by BRALOWER and BERGEN (1998) is smaller (5.7 µm) and lacks a distal boss. The upper Albian specimen illustrated by BURNETT in GALE et al. (1996) and again in BURNETT (1998) does not exhibit the rim birefringence pattern of *Percivalia*.

Distribution: This species was recorded within *Percivalia fenestratus* during sample analyses.

#### Genus *Zeugrhabdotus* REINHARDT, 1965

Murolith with a bridge along the short axis (distal view). Without any electron photographs it has been impossible to take into consideration the proximal ultrastructure (grid or other element) to differentiate the genera *Zygodiscus* and *Zeugrhabdotus* (*sensu* LAMBERT, 1987).

#### *Zeugrhabdotus bicrescenticus*

(STOVER, 1966)

BURNETT in GALE et al., 1996

Pl. 4, fig. 19

Massive bridge composed of two distinct calcitic series. Some specimens belonging to this species have been previously put in the species *Z. diplogrammus* (for instance, see MANIVIT, 1971, Pl. 13, figs. 5-6). But this author places into the same species name (*Z. diplogrammus*) some coccoliths clearly different (e.g., *Tranolithus manifestus* STOVER, 1966, see MANIVIT, 1971, Pl. 13, figs. 2, 4, 12-13). See discussion about *Zeugrhabdotus diplogrammus* here below.

Distribution: Sporadic in all the samples.

#### *Zeugrhabdotus choffatii*

ROOD et al., 1973

Pl. 4, fig. 15

A very small to small coccolith characterized by a simple bridge with a central opening corresponding to a hollow stem base. The Bathonian holotype is very small (2.4 µm). MUTTERLOSE and WISE (1990) provided an excellent electron photomicrograph of a Valanginian specimen recovered from the east Antarctic margin (3.5 µm); the Aptian specimen illustrated herein is 3.2 µ in length.

Distribution: Sporadic in the Gargasian marls.

#### *Zeugrhabdotus cf. diplogrammus*

(DEFLANDRE in DEFLANDRE & FERT, 1954)

BURNETT in GALE et al., 1996

Pl. 4, figs. 10-11, 18

Much confusion exists about the species *Zygodiscus diplogrammus* described by DEFLANDRE in 1954 based on poorly illustrated North Africa Miocene specimens. The initial description indicated "elliptique à marge étroite, à bord lisse; aire centrale occupée selon son petit axe par deux barres parallèles". We put in cf. *diplogrammus sensu* HILL, 1976, coccoliths close to those illustrated by HILL.

Distribution: Sporadic in the Gargasian shales.

#### *Zeugrhabdotus howei*

BOWN in KENNEDY et al., 2000

Pl. 4, fig. 17

BOWN (in KENNEDY et al., 2000) described this species to account for specimens identified as "*Zygodiscus elegans*" (GARTNER, 1968) BUKRY, 1969. BERGEN (1998) illustrated a Bedoulian specimen as *Lordia* sp.

Distribution: The species is sporadic in the Aptian samples examined.

#### *Zeugrhabdotus moulladei* BERGEN, 1998

Pl. 4, fig. 14

Small murolith with a transverse bar composed by two opposing bright plates separated by a dark central stem.

Distribution: Sporadic in the Gargasian marls.

***Zeugrhabdotus noeliae* ROOD et al., 1971**

Pl. 4, figs. 16, 23-25

The Oxfordian holotype of *Zeugrhabdotus noeliae* is an electron photomicrograph (distal view) of a very small specimen (2.9 µm). Light microscope identification of this species by various Mesozoic researchers has been highly variable (see YOUNG et al., 2022). Very small muroliths (2-3 µm) with a transverse central bar have been assigned to this species herein. This group constitutes one of the main components of the recovered nannoflora (up to 25-35% of the assemblage).

***Zeugrhabdotus xenotus***

(STOVER, 1966)

**BURNETT in GALE et al., 1996**

Pl. 3, fig. 26

The specimen illustrated is oriented parallel to the polarizing direction.

Distribution: Sporadic in the Gargasian marls.

***Zeugrhabdotus* sp. 1**

Pl. 4, figs. 21-22

Murolith with a narrow, bicyclic rim and a large central area. The outer rim cycle is broader and less birefringent than the bright inner rim cycle. The inner rim cycle broadens around the contacts with a narrow central transverse bar. The bar appears constructed of two elements and supports a solid distal stem which has an oblong base in plan view. *Zeugrhabdotus clarus* BOWN, 2005, is an Albian-Cenomanian species described from the northwest Pacific Ocean. This species has a broader rim and corresponding smaller central area; its more prominent bright inner rim cycle has strongly spiraled extinction. The bar elements of *Z. trivectis* BERGEN, 1994, are optically grouped into a bundle of three elements slightly offset from each other, as opposed to the two-element bundle of *Zeugrhabdotus* sp. 1.

Distribution: Sporadic in all the samples.

**Genus *Parhabdolithus* DEFLANDRE, 1952**

Murolith with a massive wall, which differentiates it from *Zeugrhabdotus*, and a bridge supporting a generally well developed central process, which differentiates it from *Rhagodiscus*.

***Parhabdolithus embergeri*  
(NOËL, 1958) STRADNER, 1963**

Pl. 4, figs. 12-13

A size variation was observed between smaller (Pl. 4, fig. 13) and larger specimens (Pl. 4, fig. 12).

Distribution: Sporadic to frequent in all the samples.

***Parhabdolithus imperfossus*****(BLACK, 1972) LAMBERT, 1987**

Pl. 5, figs. 13-15

Very tiny nannofossils (2-4 µm) with very long and thin stem are observed in our samples (Pl. 5, fig. 14, distal view, and Pl. 5, fig. 15, profile view). LAMBERT (1987) discussed the possible link between *Parhabdolithus imperfossus* initially described in SEM and *Rhagodiscus achlyostaurion* described in photonic microscopy. From a structural point of view with the absence of hole in the proximal rim, the species could be considered as a *Rhagodiscus* (see BERGEN, 1998, p. 246). However, LAMBERT (1987) described several morphotypes based on the size of the coccolith and the form of the coccospHERE.

Distribution: Sporadic in all the Gargasian samples.

***Parabdolithus infinitus***

(WORSLEY, 1971)

**THIERSTEIN in ROTH & THIERSTEIN, 1972**

Pl. 9, figs. 2-3, 7-8

This species exhibits a low birefringence (first order grey) and has two elliptical central openings aligned with the major ellipse axis. This nannofossil is frequently overgrown and can be difficult to discern from *Calccalathina erbae* when the two openings are obliterated (see also BERGEN, 1998). The size criterion could be used to discriminate both species: *Parabdolithus infinitus* (Pl. 9, figs. 2-3, 7-8) is smaller than *Calccalathina erbae* (Pl. 9, figs. 4-5, 10).

Distribution: Frequent in the Bedoulian, sporadic in the Gargasian.

**Genus *Rhagodiscus* REINHARDT, 1967**

This diverse genus is reserved for loxoliths with low distal rim and a central area filled by a granular plate. The central plate may be perforate and a distal stem may or may not be present. Specimens referred to this genus typically represent between 5-10% of assemblages recovered during this study.

***Rhagodiscus angustus*  
(STRADNER, 1963) REINHARDT, 1971**

Pl. 5, figs. 6, 9; Pl. 9, figs. 24-25

This species has a subrectangular outline and a wide hollow stem. The central area is reduced to where the stem periphery may touch the inner distal rim margin.

Distribution: BERGEN (1998) placed the lowest occurrence of *R. angustus* in the middle Bedoulian within Subzone NC6B of BRALOWER et al. (1993, 1995) based on its evolution from *R. gallagheri*.



**Rhagodiscus asper**  
**(STRADNER, 1963) REINHARDT, 1967**

Pl. 5, figs. 1-2, 4-5, 8

Coccolith size is variable from small (3-5 µm) to large specimens up to 10 µm. The distal rim is broad; a hollow, circular stem is present.

Distribution: Frequent in all studied samples.

**Rhagodiscus gallagheri**  
**RUTLEDGE & BOWN, 1996**

Pl. 5, figs. 10-11

This small species (3.5-5 µm) has a narrowly elliptical outline.

Distribution: Present in all samples.

**Rhagodiscus splendens**  
**(DEFLANDRE, 1953) VERBEEK, 1977**

Pl. 5, figs. 3, 7

This species has a long hollow, tapered distal stem. The birefringent stem base has a serrate periphery.

Distribution: Sporadic in the samples examined.

**Genus Tranolithus**  
**(STOVER, 1966) LAMBERT, 1987**  
**Tranolithus gabalus STOVER, 1966**

Pl. 4, fig. 20

Small to medium-sized coccolith characterized by the presence of two central "block" oriented along the minor ellipse axis.

Distribution: Sporadic in the rich Gargasian marls.

**Genus Eiffellithus REINHARDT, 1965**  
**Eiffellithus hancockii BURNETT, 1997**

Pl. 9, fig. 15

This small nannofossil has a broad, bicyclic rim; the bright inner rim cycle nearly closes the central area. It has a simple axial cross atypical for the genus *Eiffellithus*.

Distribution: This species occurs sporadically throughout all the samples, including the Uppermost Bedoulian. BERGEN (1998) placed its lowest occurrence in the middle Bedoulian (lower NC6B Subzone).

**Genus Calcicalathina THIERSTEIN, 1971**

Large loxoliths with a relatively narrow, imbricated distal shield and a large central area filled by a mass of granular elements that rise above the distal rim.

**Calcicalathina erbae BERGEN, 1998**

Pl. 9, figs. 4-5, 9-10

The diagnosis by BERGEN (1998) is "a species of *Calcicalathina* with a low central area showing sharp distinction between rim (1<sup>st</sup> order yellow birefringence) and coarsely-granular central area".

Distribution: *C. erbae* occurs continuously in the Bedoulian (Clavaillan section, *Deshayesites grandis* Zone) and is rare in the Gargasian marls.

**Order STEPHANOLITHIALES**

**BOWN & YOUNG, 1997**

**Family STEPHANOLITHICEAE**

**LACK, 1968**

**Genus Rotelapillus NOËL, 1972**

*Rotelapillus crenulatus*

**(STOVER, 1966) PERCH-NIELSEN, 1984**

Pl. 8, fig. 2

This distinct species has a circular to subcircular outline, eight radial central bars, and lateral nodes extending from the rim periphery.

Distribution: This species occurs sporadically in samples examined.

**Genus Stoverius PERCH-NIELSEN, 1986**

The diagnosis of the genus is "round to broadly elliptical coccoliths with a wall of more or less vertical elements, a cycle of proximal elements and a central cross." The cross and inner rim cycle exhibit a first order white birefringence, whereas the outer rim cycle exhibits a very faint birefringence. PERCH-NIELSEN (1986) differentiated *Corollithion* STRADNER, 1961, by its hexagonal outline and *Rotelapillus* NOËL, 1972, by its eight central bars. There is a clear phylogenetic relationship between the genera *Stoverius* (with *St. achylosus*) and *Corollithion* (with *C. protosignum* and *C. signum*), see LAMBERT, 1993.

**Stoverius achylosus**

**(STOVER, 1966) PERCH-NIELSEN, 1986**

Pl. 7, figs. 16-19

The species was described for circular to broadly elliptical coccoliths; the holotype has an orthogonal cross aligned with the ellipse axes.

Distribution: The lowest occurrence of this species was observed in sample 2327 (Les Gays 1 section) at the base of the nannofossil Subzone NC7B. BERGEN (1998) placed the lowest occurrence within the middle Bedoulian in Subzone NC6B, immediately below the lowest occurrence of *Rhagodiscus angustus*. BRALOWER *et al.* (1993) placed its base further down in the lower Aptian, immediately below the top of Subzone NC6A.

**Genus Corollithion STRADNER, 1961**

*Corollithion ? madagaskarensis*

**PERCH-NIELSEN, 1973**

Pl. 4, fig. 8

Distribution: Rare in the Gargasian marls.

**Genus Stradnerlithus BLACK, 1971a**

*Stradnerlithus ellipticus*

**(BUKRY, 1969) PERCH-NIELSEN, 1984**

Pl. 7, fig. 15; Pl. 8, fig. 9

Distribution: This species occurs sporadically in the Gargasian marls.



**Order PODORHABDALES**  
**(Rood et al., 1971) BOWN, 1987**  
**Family CRETARHABDACEAE**  
**THIERSTEIN, 1973**  
**Genus *Cretarhabdus***  
**BRAMLETTE & MARTINI, 1964**

The central area is occupied by an axial cross and net.

***Cretarhabdus conicus***  
**BRAMLETTE & MARTINI, 1964**

Pl. 5, figs. 12, 18-20

There is variability in coccolith size and central area construction. Large specimens with distinct axial crosses and vaulted central areas (Pl. 5, fig. 12) are more typical of the Maastrichtian holotype.

Distribution: This species occurs sporadically in samples examined.

**Genus *Microstaurus* BLACK, 1971a**

The thick proximal shield is noticeably smaller than the distal shield; the central opening contains an axial cross-structure.

***Microstaurus chiastius***  
**(WORSLEY, 1971) BRALOWER et al., 1989**

Pl. 5, fig. 16

BRALOWER et al. (1989) emended the species to include specimens with small central areas less than one-half the coccolith length.

Distribution: The species occurs sporadically in the Gargasian.

***Microstaurus quadratus* BLACK, 1971a**  
Pl. 5, fig. 21

Specimens with central areas greater than one-half the coccolith length are referred to this species, following BRALOWER et al. (1989).

Distribution: *M. quadratus* occurs sporadically in the samples examined.

**Genus *Retecapsa* BLACK, 1971a**

The genus is distinguished by having an axial cross with lateral bars.

***Retecapsa schizobrachiata***  
**(GARTNER, 1968)**  
**GRÜN in GRÜN & ALLEMANN, 1975**

Pl. 5, fig. 17

The bar is the major axis trifurcates at the rim margin and the one in the minor axis bifurcates. Coccolith size is variable.

Distribution: The species is sporadic in Gargasian samples.

**Genus *Grantarhabdus* BLACK, 1971a**

The genus is distinguished by its diagonal central cross.

***Grantarhabdus meddii* BLACK, 1971a**

Pl. 5, fig. 22

The diagonal cross is symmetric to the ellipse axes and the bars form an acute angle to the minor ellipse axis. The holotype of *Grantarhabdus unicornis* (STOVER, 1966) BLACK, 1972, has a diagonal cross asymmetric to the ellipse axes.

Distribution: This species occurs sporadically in the samples examined.

**Order PODORHABDALES**  
**(ROOD et al., 1971) BOWN, 1987**  
**Family AXOPODORHABDACEAE**  
**BOWN & YOUNG, 1997**  
**Genus *Axopodorhabdus***  
**WIND & WISE in WISE & WIND, 1977**  
***Axopodorhabdus dietzmannii***  
**(REINHARDT, 1965) WIND & WISE, 1983**

Pl. 6, figs. 4, ? 8

This medium to large species of *Axopodorhabdus* is distinguished by its narrowly elliptical outline and broad transverse bars.

Distribution: It occurs sporadically in the Gargasian.

**Genus *Tetrapodorhabdus* BLACK, 1971a**  
***Tetrapodorhabdus coptensis***

BLACK, 1971a

Pl. 6, figs. 2-3, ? 5, 6

Small to medium-sized species with bars that form an acute angle with the minor ellipse axis.

Distribution: It occurs sporadically in the samples examined.

***Tetrapodorhabdus decorus***  
**(DEFLANDRE in DEFLANDRE & FERT, 1954)**  
**WIND & WISE in WISE & WIND, 1977**

Pl. 6, figs. ? 1, 7

The holotype is a light photomicrograph in profile. In plan view, it has been associated with a symmetric diagonal cross where the orthogonal bars flare near the rim margin and form circular openings.

Distribution: Sporadic in the samples.

**Genus *Acaenolithus* BLACK, 1973**

This genus (first described by BLACK for Albian specimens) is related to the Family Arkhangelskiellacea well represented in Upper Cretaceous series.

***Acaenolithus* ? sp.**

Pl. 3, fig. 23

We ascribed to this genus very small coccoliths with alternate extinction of the cross arms. In the absence of observations in SEM, it seems very difficult to precisely determine the ultra structure.

Distribution: Sporadic in the richest Gargasian samples.



**aff. *Misceomarginatus***  
**WIND & WISE in WISE & WIND, 1977**  
Pl. 3, figs. 24-25

The general aspect including rims and central cross is close to *Misceomarginatus* (and also to the close genus *Diloma* WIND & CEPEK, 1979). The quadrants seem free or spanned by a diagonal bar.

Distribution: Sporadic in the samples.

**Family COCCOLITHACEAE NOËL, 1965**

Circular or elliptical coccoliths composed by two superimposed rim composed by radial calcitic elements with a strong angle between them in the external part (junction of the two rims). This particularity allows a very good cohesion between the coccoliths on the coccospHERE. The two rims are linked in their internal sides by a calcitic tube. The central area is occupied (or not) by variable filling taking place indistinctly on the proximal or distal rims.

**Genus *Flabellites* THIERSTEIN, 1973**

Original diagnosis: "Presence of an inner cycle of the distal shield composed of elongated calcitic elements, one or two clusters of these elements often extend beyond the elliptical periphery of the coccolith" (THIERSTEIN, 1973, p. 41).

***Flabellites biforaminis* THIERSTEIN, 1973**

Pl. 6, figs. 9-11

Morphologic variation observed includes coccolith size and outline, as well as the size and shape of the central openings.

Distribution: This species is present in all our samples.

**Family BISCUTACEAE BLACK, 1971a**

**Genus *Biscutum***  
**BLACK in BLACK & BARNEs, 1959**

*Biscutum* is retained for non-imbricating, elliptical placoliths constructed of two broad shields and an inner distal tube cycle. In cross-polarized light, the shields are faint and the narrow tube cycle is bright. *Palaeopontosphaera* NOËL, 1965, is considered a junior synonym herein; the two species included within *Biscutum* are taxonomically problematic due to uncertainties regarding their holotypes. Discussion of these genera and their included species is a topic beyond the current study (see LAMBERT, 1993, p. 206).

***Biscutum constans***  
**(GÓRKA, 1957) BLACK, 1968**

Pl. 6, fig. 17

GÓRKA (1957) described this species from the upper Maastrichtian and indicated a length of 5-9 µm. It is founded on a rudimentary drawing of a normally elliptical specimen (1.38 aspect ratio) shown to have a single cycle of fifteen radial elements (19-20 described) and an open center (de-

scribed as smooth) approximately 0.44 of the coccolith width. Current usage has evolved into a small to medium (3-8 µm), normally elliptical species with a narrow central area, bright tube cycle and dark central plate (see YOUNG et al., 2022). That concept is followed herein.

Distribution: *Biscutum constans* and *B. dubium* have been counted as a single taxon and are frequent in samples (5-15% of assemblages).

***Biscutum dubium***  
**(NOËL, 1965) GRÜN in GRÜN et al., 1974**

Pl. 6, fig. 22

Small elliptical coccoliths with a central area nearly filled by a distal boss are identified as this species (see GRÜN & ZWEILI, 1980; KAENEL & BERGEN, 1993). *Biscutum ellipticum* (GÓRKA, 1957) is not appropriate because the original description indicates a very large size (length 18 µm) and the accompanying sketch of an Upper Maastrichtian specimen shows ten rim elements with curved sutures and an open center. The presence of a central boss distinguishes *B. dubium* from *B. constans*.

**Genus *Discorhabdus* NOËL, 1965**

***Discorhabdus ignotus***  
**(GÓRKA, 1957) PERCH-NIELSEN, 1968**

Pl. 6, fig. 16

Very small circular placoliths with faint birefringence and a closed center were identified as this constant background species (2.5-5% of assemblages).

***Discorhabdus serratus* WORSLEY, 1971**

Pl. 9, figs. 1, 6

Shields composed by 8 to 12 elements with blunt terminations. The central area is occupied by a stem (distal view) and not by a central open area as mentioned by WORSLEY (1971).

Distribution: This form was found only in the lower part of the Clavaillan section (*Deshayesites grandis* Zone).

**Genus *Haqius* ROTH, 1978**

Large circular coccolith with a reduced central area.

***Haqius circumradiatus***  
**(STOVER, 1966) ROTH, 1978**

Pl. 6, figs. 18, 23

This large circular coccolith is easily recognizable. The rim is composed of 30-35 elements and exhibits a faint first order white birefringence.

Distribution: This species occurs sporadically in samples.

**Genus *Watznaueria* REINHARDT, 1964**

Three species were assigned to this elliptical genus, which comprises 20-35% of the nannoplankton population in samples examined.

***Watznaueria barnesae*****(BLACK, 1959) PERCH-NIELSEN, 1968**

Distribution: This species is common to abundant in samples.

***Watznaueria britannicus*****(STRADNER, 1963) REINHARDT, 1964**

Pl. 6, figs. 20-21

Specimens with disjunct bridges were assigned to this species, which is much less frequent than *Watznaueria barnesae*.

Distribution: Present in all samples.

***Watznaueria ovata* BUKRY, 1969**

Pl. 7, fig. 11

Specimens observed with large central openings were typically smaller than the medium-sized specimens originally illustrated by BUKRY (1969).

Distribution: The species occurs sporadically in the Gargasian.

**Genus *Pickelhaube*****APPLEGATE *et al.* in COVINGTON & WISE, 1987*****Pickelhaube furtiva*****(ROTH, 1983) APPLEGATE *et al.*  
in COVINGTON & WISE, 1987**

Pl. 7, fig. 4

This large, delicate nannofossil was often observed broken in Gargasian sediments, where it is very rare.

**Genus *Crucibiscutum* JAKUBOWSKI, 1986**

This genus is reserved for elliptical Biscutaceae with a central tube and axial central structure.

***Crucibiscutum salebrosum*****(BLACK, 1971a) JAKUBOWSKI, 1986**

Pl. 7, figs. 5-9

The broad species concept maintained herein includes variations in coccolith size, the ratio of the central area size to rim width, and the construction of the axial cross. *Crucibiscutum salebrosum* has priority over other Cretaceous species that may be distinguished on these characteristics.

Distribution: Present throughout the Gargasian.

**Genus *Manivitella* THIERSTEIN, 1971*****Manivitella pemmatoidea*****(DEFLANDRE *in MANIVIT*, 1965)****THIERSTEIN, 1971**

Pl. 7, fig. 14

The similar large species *Tubodiscus jurapelicus* (WORSLEY, 1971) ROTH, 1973, was not differentiated during sample analyses.

Distribution: This taxon occurs sporadically in the samples examined.

**Genus *Tubodiscus* THIERSTEIN, 1973*****Tubodiscus burnettiae*****BOWN *in KENNEDY *et al.**, 2000**

Pl. 7, figs. 12-13

This medium-sized species of *Tubodiscus* has a relatively broad inner rim cycle.

**Genus *Diazomatolithus* NOËL, 1965**

Description: Circular to subcircular coccolith with a central area always empty.

***Diazomatolithus lehmanii* NOËL, 1965**

Pl. 6, figs. 12-15

Outside of size, variants with narrow (Pl. 6, figs. 12-13) and broad (Pl. 6, figs. 14-15) rims were observed. Those with narrow rims and large centers may represent *Diazomatolithus galicianus* KAENEL & BERGEN, 1996, but were not differentiated during sample analyses.

Distribution: Although *Diazomatolithus* does not reach the NC7B subzone in our samples, this Late Jurassic genus is recorded above the Aptian.

**Order BRAARUDOSPHAERALES****(AUBRY, 2013) LEES & BOWN, 2016**

LEES and BOWN (2016) included Braarudosphaeraceae DEFLANDRE, 1947, and Nannococcaceae DEFLANDRE, 1959, within their emended definition of this order. YOUNG *et al.* (2022) tentatively placed the Polycyclolithaceae FORCHHEIMER, 1972, within this order.

**Family BRAARUDOSPHAERACEAE  
DEFLANDRE, 1947**

Pentagonal coccoliths constructed of superimposed plates. Genera are distinguished by the intersection of the sutures and periphery. The present-day species *Braarudosphaera bigelowii* is composed of a single layer of pentagonal elements (12 per coccospHERE), whereas fossil species can be more complex with individual coccoliths composed of numerous layers (see LAMBERT, 1986).

**Genus *Braarudosphaera*****DEFLANDRE, 1947*****Braarudosphaera africana*****STRADNER, 1961**

Pl. 7, fig. 22

Distribution: This species was not observed in the lower part of the Clavaillan section (Bedoulian) and is sporadic in the Gargasian. BERGEN (1998) placed the base of *Br. africana* in lowermost Subzone NC7A, immediately above the base of *Eprolithus floralis*.

***Braarudosphaera bigelowii*****(GRAN & BRAARUD, 1935)****DEFLANDRE, 1947**

Pl. 7, figs. 20-21

Distribution: The species occurs sporadically in the samples examined.

**Genus *Micrantholithus*****DEFLANDRE in DEFLANDRE & FERT, 1954**

The highest occurrences of both species of *Micrantholithus* coincide with the "Nannoconus crisis level" in the materials studied. BRALOWER *et al.* (1993) defined the top of Subzone NC7A on the highest occurrence of *Micrantholithus hoschulzii*, whereas HERRLE and MUTTERLOSE (2003) modified the definition of the genus.

***Micrantholithus hoschulzii*****(REINHARDT, 1966) THIERSTEIN, 1971**

Each element has a triangular shape.

***Micrantholithus obtusus* STRADNER, 1963**

Pl. 8, fig. 10; Pl. 9, fig. 14

The elements have a typical V-shaped outline due to their indented peripheries.

**Family CALCIOSELENIACEAE****KAMPTER, 1937****Genus *Calciosolonia* GRAN, 1912*****Calciosolenia fossilis*****(DEFLANDRE in DEFLANDRE & FERT, 1954)****BOWN in KENNEDY *et al.*, 2000**

Pl. 8, figs. 21-23

Relative to modern coccolithophores, individual coccolith morphology could vary from large rhombohedra in the middle part of the cell (Pl. 8, fig. 23) to elongated rhomboedra in the distal part of the cell (Pl. 8, figs. 21-22).

Distribution: Sporadic throughout the samples studied.

**Family CALYPTROSPHAERACEAE****BOUDREAUX & HAY, 1969****Genus *Orastrum*****WIND & WISE in WISE & WIND, 1977*****Orastrum perspicuum*****VAROL in AL-RIFAIY *et al.*, 1990**

Pl. 7, figs. 23-24

Coccolith composed of a single plate surrounded by a narrow rim. The central plate is less birefringent than the rim.

Distribution: This lowest occurrence of this species is in Subzone NN7B in the material studied. HERRLE and MUTTERLOSE (2003) placed this event below the *N. truitti* acme in Subzone NN7B/C.

**Genus *Isocrystallithus* VERBEEK, 1977*****Isocrystallithus partitum*****(VAROL in AL-RIFAIY *et al.*, 1990)****BERGEN, 1998**

Pl. 8, figs. 17-18

This holococcolith has two central plates separated by a transverse bridge composed of four calcite elements. The original description of this species suggested that these four elements could be the remnants of a short distal process. BERGEN (1998) first associated these basal plates with complete specimens having short, tapered distal

processes and transferred the species into *Isocrystallithus*. The genus *Orastrum* does not have a distal process or central bridge.

Distribution: This species is sporadic in the Gargasian marls.

**Genus *Calculites*****PRINS & SISSINGH in SISSINGH, 1977*****Calculites dispar*****VAROL in AL-RIFAIY *et al.*, 1990**

Pl. 8, figs. 15-16; Pl. 9, fig. 18

These small elliptical holococcolith are composed by four unequal plates surrounded by a narrow rim. A longitudinal suture separates the two smaller central plates symmetric across the minor ellipse axis. Obtuse angled sutures extend from the poles of the longitudinal suture to delineate two larger plates symmetric across the major ellipse axis.

Distribution: This species is sporadic in the upper Bedoulian and Gargasian marls.

**Genus *Zebrashapka*****COVINGTON & WISE, 1987**

The original description and electron photomicrographs of this monopsefic genus by COVINGTON and WISE (1987) indicate that this is a holococcolith.

***Zebrashapka vanhintei*****COVINGTON & WISE, 1987**

Pl. 8, figs. 3-5

This holococcolith is easily recognizable.

Distribution: Sporadic in rich Gargasian samples.

**Family POLYCYCLOLITHACEAE****(FORCHHEIMER, 1972) VAROL, 1992**

PERCH-NIELSEN (1985) assigned *Assipetra* ROTH, 1973, and *Hayesites* MANIVIT, 1971, to this family, but they do not conform to the emended definition of Polycyclolithaceae by VAROL (1992) due to their lack of a two-tiered construction. BOWN and YOUNG (1997) referred to *Assipetra* and *Hayesites* as "uncertain polycycloliths." They are tentatively placed in this family herein because of their radial symmetry and petaloid elements.

**Genus *Eprolithus* STOVER, 1966**

*Eprolithus* has a wall constructed of two tiers of vertical to sub-vertical, petaloid elements (5-9) connected by a medial diaphragm.

***Eprolithus floralis*****(STRADNER, 1962) STOVER, 1966**

Pl. 8, figs. 6-8; Pl. 9, figs. 21-23

*Radiolithus planus* STOVER, 1966 (Pl. 9, figs. 21-22) was included within *Eprolithus floralis* during sample analyses.

Distribution: The lowest occurrence of *Eprolithus floralis* marks the base of Subzone NC7A, which occurs below the lowest sample examined for this study (see BERGEN, 1998; HERRLE & MUTTERLOSE, 2003; GIRAUD *et al.*, 2018).

**Family LAPIDEACASSACEAE****BOWN & YOUNG, 1997****Genus *Lapideacassis* BLACK, 1971b*****Lapideacassis glans* BLACK, 1971b**

Pl. 8, figs. 11-12; Pl. 9, figs. 12-13, 17

This species was distinguished by its low, broad profile and irregular outline.

***Lapideacassis mariae* BLACK, 1971b**

Pl. 8, fig. 13

This species was distinguished by its high, relatively narrow profile and irregular outline. No intermediate forms have been observed between this species and *L. glans*.

Distribution: *Lapideacassis mariae* and *Lapideacassis glans* are sporadic in the studied samples, including the lower Aptian (Bedoulian). BERGEN (1998) did not report the genus from the lower Aptian historical stratotype. HERRLE and MUTTERLOSE (2003) placed the lowest occurrences of both species in the Gargasian (Subzone NC7B/C).

***Lapideacassis* sp.**

Pl. 9, figs. 11, 16

Rare specimens with relatively high, narrow profiles and smooth outlines were observed, but more information is needed to interpret their relationship to the other two species of *Lapideacassis*.

Distribution: This nannofossil was observed only in the lower part of the Clavaillan section (Bedoulian).

**Family MICRORHABDULACEAE****DEFLANDRE, 1963****Genus *Lithraphidites* DEFLANDRE, 1963*****Lithraphidites carniolensis*****DEFLANDRE, 1963**

Pl. 8, fig. 14

Distribution: This species is sporadic in all the samples examined.

**Genus *Hayesites* MANIVIT, 1971*****Hayesites irregularis*****(THIERSTEIN in ROTH & THIERSTEIN, 1972)****APPLEGATE et al. in COVINGTON & WISE, 1987**

Pl. 8, figs. 19-20

Distribution: This Aptian-Albian species occurs sporadically in the samples examined.

**Genus *Assipetra* ROTH, 1973*****Assipetra infracretacea*****(THIERSTEIN, 1973) ROTH, 1973**

Pl. 3, fig. 6; Pl. 10, fig. 22

THIERSTEIN (1973) described this species as "having two sets of flat crystal plates, one set piercing the other at an obtuse angle" and remarked that light microscope specimens having subrectangular to suboval shapes with 4-6 radial sutures. All four specimens illustrated by THEIRSTEIN (1973) - transferred between the SEM and

LM - appear subrectangular and suboval outlines (*op. cit.*, Pl. 1, figs. 6, 19) could be a consequence of specimen orientation. Aspect ratios of these four original specimens vary between 1.1-1.3 and a maximum diameter of 5-10 µm was given for the species. The diagnosis of *A. infracretacea larsonii* by TREMOLADA and ERBA (2002) restricted this subspecies to specimens greater than 7.5 µm, but Bown (2005) considered a number of these specimens to be side views of *Assipetra terebrodentarius*. A size of 10 µm is used herein to separate two morphotypes of *A. infracretacea*.

***Assipetra terebrodentarius*****(APPLEGATE al. in COVINGTON & WISE, 1987)****RUTLEDGE & BERGEN in BERGEN, 1994**

Pl. 3, fig. 12; Pl. 10, figs. 21, 23-24

APPLEGATE et al. (in COVINGTON & WISE, 1987) stated that *Assipetra terebrodentarius* "is more globular, has more numerous and angular projecting elements, and often displays a regular, spiral construction not observed in *A. infracretacea*". The diagnosis of *A. terebrodentarius youngii* by TREMOLADA and ERBA (2002) restricted this subspecies to specimens greater than 7.5 µm. Bown (2005) emended this subspecies for specimens greater than 8.0 µm because the species holotype is 7.7 µm. A size of 10 µm is used herein to separate two morphotypes of *A. terebrodentarius* (see §3. Materials and methods).

Distribution (including *A. infracretacea*, Fig. 3): The semi-quantitative analysis of the distribution of these two species that we carried out (see §3. Materials and methods) shows that the record of these nannofossils is not continuous with two intervals where they are relatively frequent:

1. lower Aptian, *Deshayesites grandis* Zone and
2. a part of the upper Gargasian, middle part of the *Dufrenoyia furcata* Zone.

For these two intervals the *A.i* + *A.t* large forms / *A.i* + *A.t* small forms observed confirm the 2002 TREMOLADA and ERBA's work. The large specimens are clearly more frequent in the lower Aptian (*Deshayesites grandis* Zone) of the the studied section (i.e., the lower portion the Clavailian section) compared to the upper Aptian (*Dufrenoyia furcata* Zone).

**Genus *Tetralithus* GARDET, 1955**

The genus *Tetralithus* has been created in 1955 for Miocene nannofossils probably reworked from Cretaceous sediments. For a discussion of differences between *Tetralithus* and *Quadrum* the readers are referred to PRINS and PERCH-NIELSEN (in MANIVIT et al., 1977).

***Tetralithus ? maticus* WORSLEY, 1971**

Pl. 9, fig. 20

This small, square nannolith is composed of four elements separated by orthogonal sutures that intersect the midpoints of the peripheries. Individual elements are wedge-shaped, being



thicker along the axes offset 45 degrees to the sutures. This form resembles *Quadrum*, but four species of that genus are restricted to the Upper Cretaceous.

Distribution: This taxon was observed only in the basal portion of the Clavaillan section (Bedoulian).

#### Genus *Conusphaera* TREJO, 1969

##### *Conusphaera rothii*

(THIERSTEIN, 1971) JAKUBOWSKI, 1986

Pl. 9, fig. 19

Distribution: This species was observed sporadically in the Clavaillan section (Bedoulian) along with *Eprolithus floralis*. It is possible that these rare, sporadic specimens are redeposited. BRA-LOWER et al. (1993) defined the base of Subzone NC6B on the highest occurrence of *Conusphaera rothii* and the top of this subzone on the lowest occurrence of *Eprolithus floralis*. The stratigraphic ranges of these two marker species are separated by approximately 63 m (22 samples) in the historical Bedoulian stratotype (BERGEN, 1998).

#### Family NANNOCONACEAE

DEFLANDRE, 1959

#### Genus *Nannoconus* KAMPTNER, 1931

*Nannoconus* specimens are illustrated both in the photographic plates and as drawn profiles of actual specimens (Fig. 2). These profiles were drawn from photographs of the first thirty specimens encountered in each of 29 samples (red dots in Fig. 2). This process has been used to illustrate the significant morphological variations. These variations make it often difficult the direct reference to the original diagnosis (holotype). Many *Nannoconus* specimens do not fit with the corresponding diagnosis or/and present a lot of intermediate forms between two type species (see for instance on Fig. 2 the group B with *N. globulus* / *N. circularis*).

The taxonomic concepts of DERES and ACHÉRITÉ-GUY (1980) are followed. Please refer to this publication for more taxonomic information. Fifteen species - including three subspecies - have been organized into five groups based on strong morphological affinities. All have central cavities. They are presented herein relative to these groupings:

- Group A: constricted outline with *N. boletus*, *N. carniolensis*
- Group B: rounded outline with *N. circularis*, *N. aff. globulus*
- Group C: cylindrical outline with *N. elongatus*, *N. inconspicuus*, *N. quadriangulus*, *N. truittii*
- Group D: short, conical outline with *N. bucheri*, *N. vocontiensis*
- Group E: elongate, conical outline with? *N. aff. borealis*, *N. bonetii*, *N. aff. grandis*, *N. kamptneri*, *N. wassallii*

*Nannoconus steinmannii* has a conical outline and is the only species with a central canal.

#### Group A: constricted outline

##### *Nannoconus boletus*

DEFLANDRE & DEFLANDRE-RIGAUD, 1962

Pl. 1, figs. 12, ? 13; Pl. 2, figs. 6, 31, ? 32;  
Pl. 3, figs. ? 1, 2, ? 3, 4-5

##### *Nannoconus carniolensis*

DEFLANDRE & DEFLANDRE-RIGAUD, 1962

Pl. 3, figs. ? 7, 8-11

Both species included in this group were first illustrated in 1962 and formally described five years later. The group includes nannoconids with a distinct external restriction at the middle to upper portion of the test, resulting in a more or less mushroom-shaped outline in longitudinal view ("boletus edulis" is a well-known and appreciated mushroom). The distinction between the two species is often subtle. *N. carniolensis* is shaped more like a pot, whereas *N. boletus* is more fungiform. Both species are small to medium-sized (< 10 µm), in congruence with specimens first illustrated by DEFLANDRE in 1962. The oldest specimens recovered from the upper part of the Clavaillan section are more rectangular in longitudinal outline with a low relief constrictions and roughly equivalent wall to and central cavity thicknesses.

Distribution: *N. boletus* occurs sporadically throughout the Gargasian, but is more frequent around the NC7A/NC7B boundary. The smallest forms of *N. carniolensis*, which are uncommon overall, seem restricted to *Nannoconus* assemblage zone GIIB.

#### Group B: rounded outline

##### *Nannoconus circularis*

DERES & ACHÉRITÉ-GUY, 1980

Pl. 1, figs. 10-11, 31; Pl. 2, figs. 25-26, 28;  
Pl. 10, fig. 15

##### *Nannoconus aff. globulus*

BRÖNNIMANN, 1955

Pl. 1, figs. 8-9, 30; Pl. 2, figs. 23-24, ? 27

This group includes more or less circular to rectangular forms with a large internal cavity and a thin wall (wall thickness << internal cavity). From a semi-quantitative point of view it seems to be very difficult to distinguish the two species which appears in the Aptian sediments and probably represent two poles of a same population. Depending to the preservation (calcite overgrow) is it possible to transform a thin walled with large central cavity *N. circularis* in a more robust and thick walled with a more narrow central cavity. *N. circularis* has frequently a quadrangular shape compared to *N. aff. globulus* with is globular shape.

Distribution: This group is abundant throughout Subzone NC7A, but absent from Subzone NC7B.

**Group C: cylindrical outline*****Nannoconus elongatus*  
BRÖNNIMANN, 1955**

Pl. 10, figs. 6-7, ? 8

This relatively large cylindrical *Nannoconus* (> 10 µm) has a thick wall and open central cavity approximately equal in width.

Distribution: This rare species was observed only in the lower part of the Clavaillan section.

***Nannoconus inconspicuus*  
DEFLANDRE & DEFLANDRE-RIGAUD, 1962**

Pl. 10, fig. 16

***Nannoconus quadriangulus*  
DEFLANDRE & DEFLANDRE-RIGAUD, 1962**Pl. 1, figs. 14-15, 17-18, 32;  
Pl. 2, figs. 1-2, 7-16, 29, 31***Nannoconus truittii* BRÖNNIMANN, 1955**

Pl. 1, figs. 16, 33; Pl. 2, figs. 3-5

Two subspecies of *Nannoconus quadriangulus* (i.e., *N. quadriangulus quadriangulus* and *N. quadriangulus apertus*) were first illustrated in 1962, but formally described in 1967 by DEFLANDRE and DEFLANDRE-RIGAUD. Both subspecies are not considered herein. They correspond to small to medium-sized (up to 9 µm) quadrangular forms with a relatively thick wall and a rectangular central cavity (ratio wall thickness / central cavity close to 1). These authors described also a very small species *Nannoconus inconspicuus* (length around 2 µm). This group includes all the rectangular to subrectangular forms (including the smallest ones) varying from 2/3 to 8/9 µm. *N. truitti*, another small quadrangular form with a thicker wall, which was first described by BRÖNNIMANN in 1955, is also ascribed to this group.

**Group D: short, conical outline (horseshoe-shaped)*****Nannoconus bucheri* BRÖNNIMANN, 1955**

Pl. 1, figs. 2, 5, 28-29; Pl. 10, figs. 12-14

***Nannoconus vocontiensis*  
DERES & ACHÉRITÉGUY, 1980**Pl. 1, figs. 1, 3-4, 6-7, 30; Pl. 2, figs. 17-22;  
Pl. 10, fig. 25

Apparently these two species seem to represent a continuous lineage between thicker (wall) forms (*N. bucheri*) and thinner (wall) forms (*N. vocontiensis*) both species with a horseshoe type. The largest forms (10-15 µm, *N. bucheri*) are found mainly in the upper Bedoulian and lower Gargasian and the smaller ones (around 10 µm, *N. vocontiensis*) in the lower Gargasian.

Distribution: This group is common throughout and restricted to Subzone NC7A.

**Group E: elongate, conical outline*****Nannoconus bonetii* TREJO, 1959**

Pl. 10, figs. 11, 20

***Nannoconus aff. borealis*  
PERCH-NIELSEN, 1979**

Pl. 10, fig. 10

***Nannoconus aff. grandis*  
DERES & ACHÉRITÉGUY, 1980**

Pl. 1, fig. 19; Pl. 10, figs. 18-19

***Nannoconus kamptneri*  
BRÖNNIMANN, 1955**

Pl. 1, fig. 20; Pl. 10, fig. 17

***Nannoconus wassallii* BRÖNNIMANN, 1955**

Pl. 1, figs. 21-27; Pl. 10, fig. 9

In this group we have associated the very large / large forms (up to 25 µm) found in the Clavaillan section Gargasian and in the basal part of the south Pichouraz section. All these species include elongated conical (i.e., *Nannoconus aff. grandis* and *N. kamptneri*) to pear-shaped tests with a typical "pear" aspect. We can see a clear relationship between the more elongated species:

- narrowest forms with a ratio central width cavity / wall thickness < 1 (*N. bonetii*: Pl. 10, fig. 20; *N. aff. borealis*);
- narrowest forms with a ratio central width cavity / wall thickness = 1, *N. aff. grandis*: Pl. 1, fig. 19; Pl. 10, fig. 18; *N. kamptneri*: Pl. 1, fig. 19; Pl. 10, fig. 17);
- wider forms (with a ratio width cavity / wall thickness = 2), *N. wassallii*: Pl. 1, figs. 25-27.

Distribution: This group has been mainly observed in the Clavaillan upper part (Gargasian) and in the south Pichouraz two basal samples (i.e., 2270, 2272). However some *N. wassallii* occur sporadically in the Bedoulian and in the GII *Nannoconus* Zone.

**Other species:*****Nannoconus steinmannii* KAMPTNER, 1931**

Pl. 10, figs. 1-3

***Nannoconus cf. steinmannii*  
KAMPTNER, 1931**

Pl. 10, figs. 4-5

These conical to sub-conical *Nannoconus* (i.e., tapers apically) have a very narrow central canal.

Distribution: Very rare specimens were observed in the uppermost Bedoulian of the Clavaillan section (Subzone NC7A) whereas BRALOWER et al. (1993) and BERGEN (1998) placed its highest occurrence in Subzone NC6B.



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**Plates**



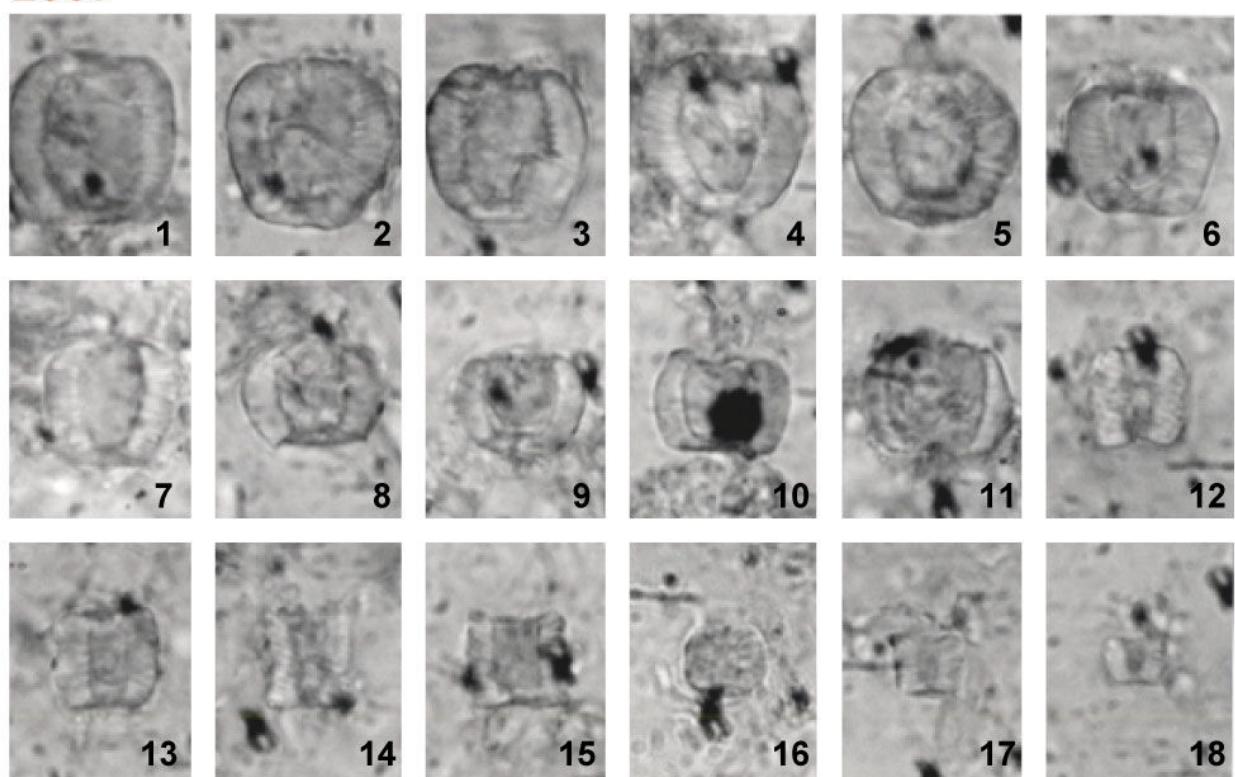
**Plate 1:** Association GIIA (sample 2307): fig. 1: *Nannoconus vocontiensis* DERES & ACHÉRITÉGUY, 1980; fig. 2: *Nannoconus bucheri* BRÖNNIMANN, 1955; figs. 3-4: *Nannoconus vocontiensis* DERES & ACHÉRITÉGUY, 1980; fig. 5: *Nannoconus bucheri* BRÖNNIMANN, 1955; figs. 6-7: *Nannoconus* aff. *N. vocontiensis* DERES & ACHÉRITÉGUY, 1980; figs. 8-9: *Nannoconus* aff. *globulus* BRÖNNIMANN, 1955; figs. 10-11: *Nannoconus circularis* DERES & ACHÉRITÉGUY, 1980; fig. 12: *Nannoconus boletus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962; fig. 13: ? *Nannoconus boletus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962; figs. 14-15: *Nannoconus quadriangulus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962; fig. 16: *Nannoconus truitii* BRÖNNIMANN, 1955; figs. 17-18: *Nannoconus quadriangulus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962.

Association GI (sample 2270): fig. 19: *Nannoconus* sp. aff. *grandis* DERES & ACHÉRITÉGUY, 1980; fig. 20: *Nannoconus kampfneri* BRÖNNIMANN, 1955; figs. 21-24: *Nannoconus boneti* TREJO, 1959; figs. 25-27: *Nannoconus wassallii* BRÖNNIMANN, 1955; figs. 28-29: *Nannoconus bucheri* BRÖNNIMANN, 1955; fig. 30: *Nannoconus* aff. *globulus* BRÖNNIMANN, 1955 (L), and *Nannoconus vocontiensis* DERES & ACHÉRITÉGUY, 1980 (R); fig. 31: *Nannoconus circularis* DERES & ACHÉRITÉGUY, 1980; fig. 32: *Nannoconus quadriangulus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962; fig. 33: *Nannoconus truitii* BRÖNNIMANN, 1955 (bottom).

For each *Nannoconus* species we illustrated several specimens in order to show the natural variation in size and shape. See Figure 2 for further explanations.

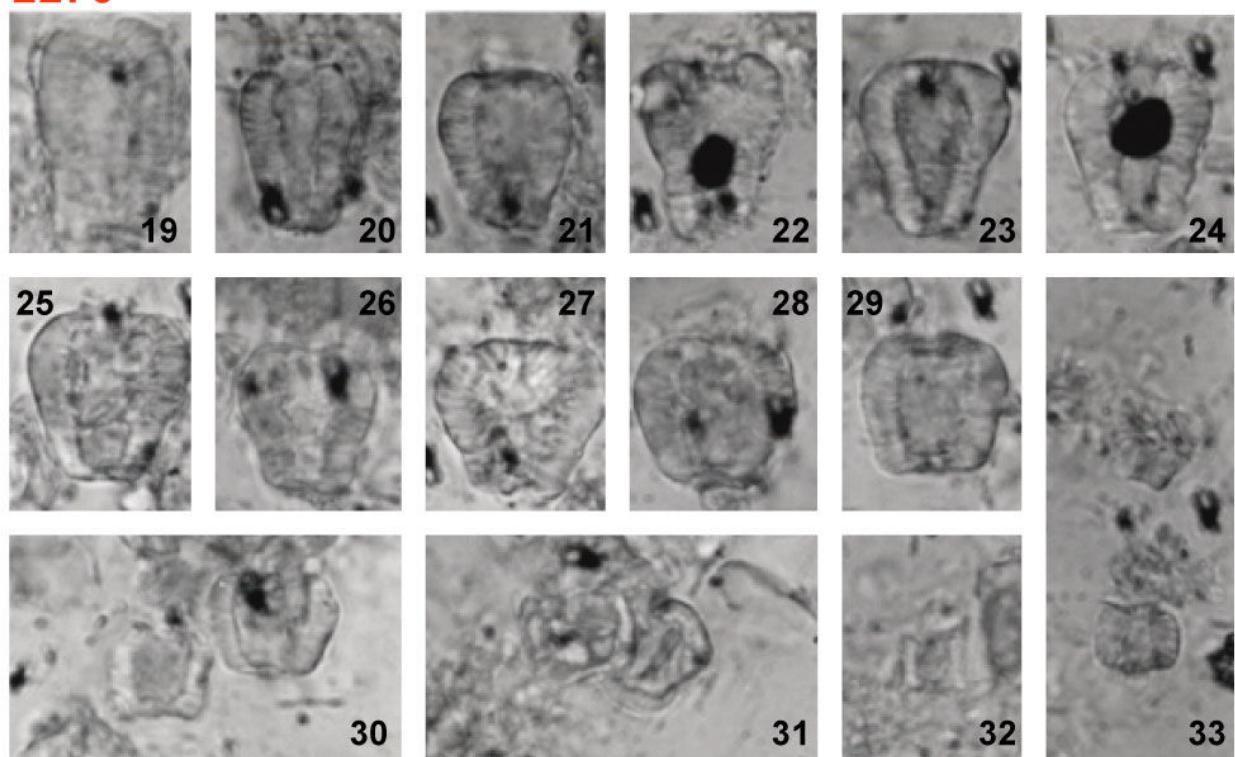


2307



10µm

2270



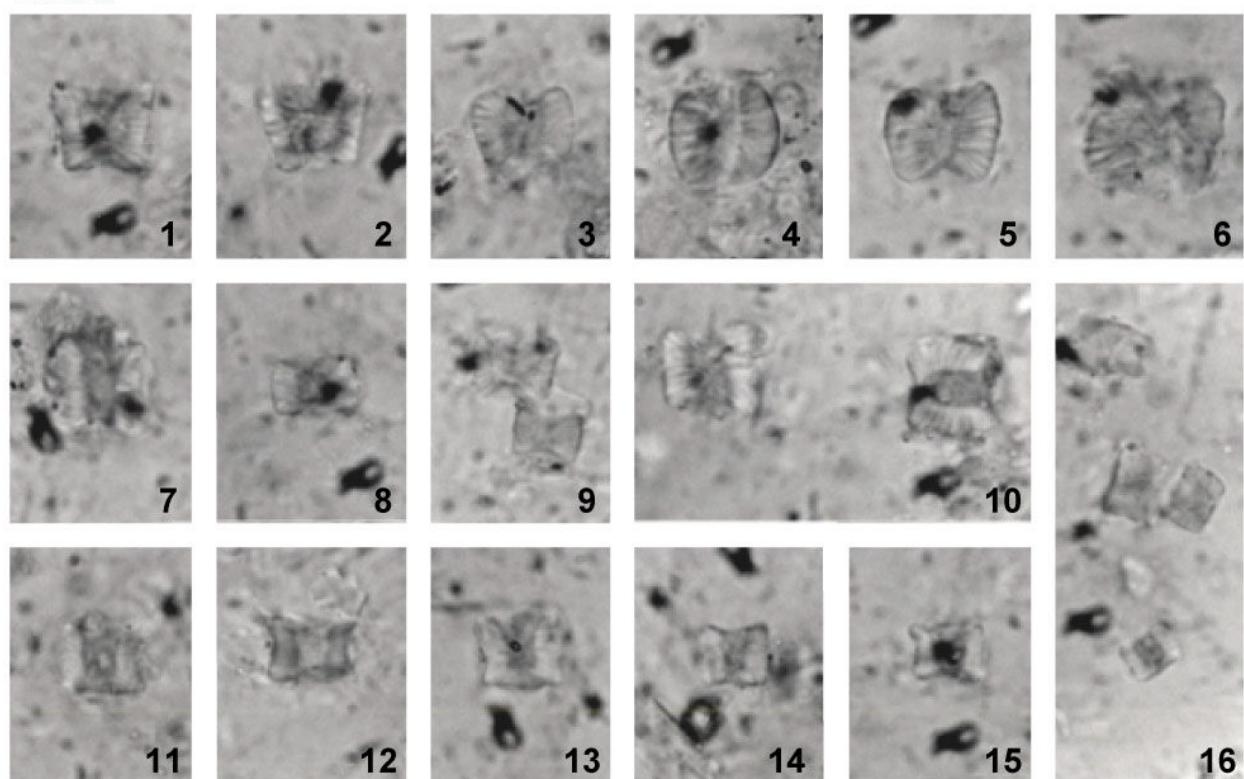


**Plate 2:** Association GIII (sample 2303): figs. 1-2, 7-16: *Nannoconus quadriangulus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962; figs. 3-5: *Nannoconus truittii* BRÖNNIMANN, 1955; fig. 6: *Nannoconus boletus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962.

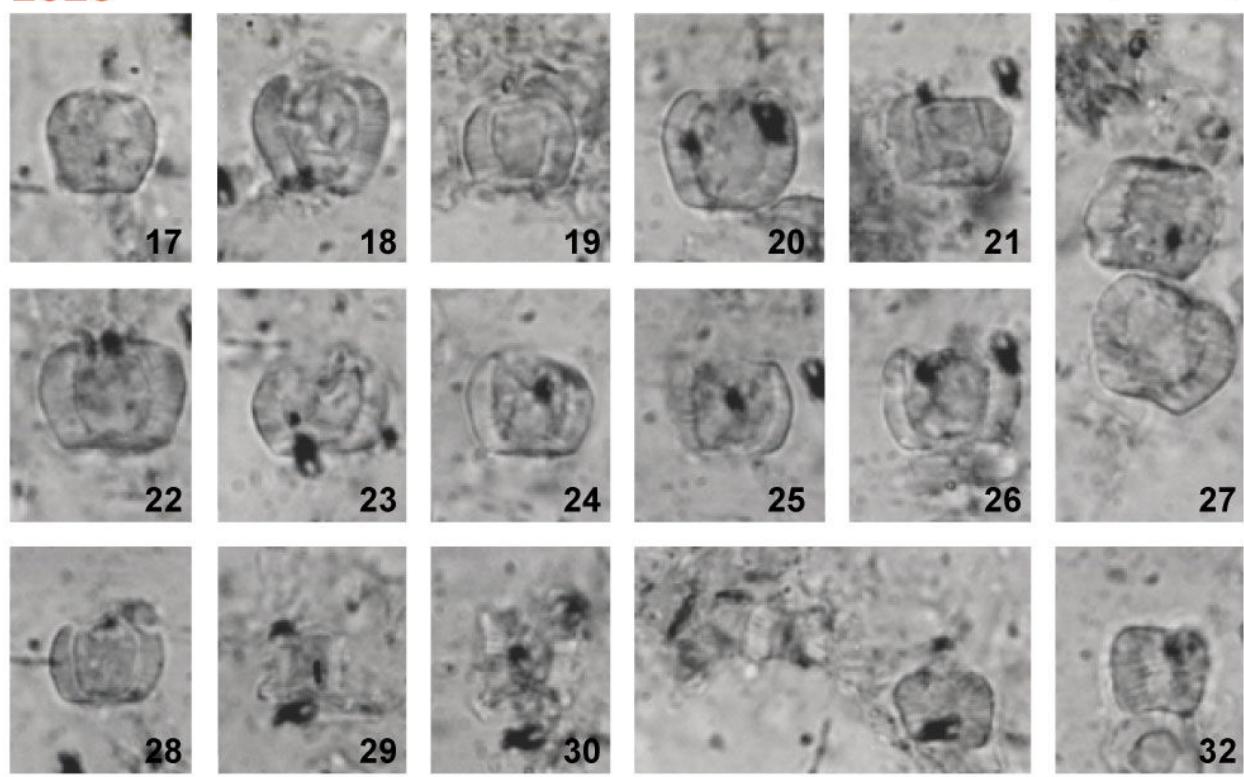
Association GIIB (sample 2323): figs. 17-22: *Nannoconus vocontiensis* DERES & ACHÉRITÉGUY, 1980; figs. 23-24: *Nannoconus* aff. *globulus* BRÖNNIMANN, 1955; fig. 25: *Nannoconus circularis* DERES & ACHÉRITÉGUY, 1980; figs. 26, 28: *Nannoconus globulus* BRÖNNIMANN, 1955; fig. 27: ? *Nannoconus* aff. *globulus* BRÖNNIMANN, 1955; figs. 29-30: *Nannoconus quadriangulus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962; fig. 31: *Nannoconus quadriangulus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962 (L), and *N. boletus* (R) DEFLANDRE & DEFLANDRE-RIGAUD, 1962; fig. 32: ? *N. boletus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962.



2303

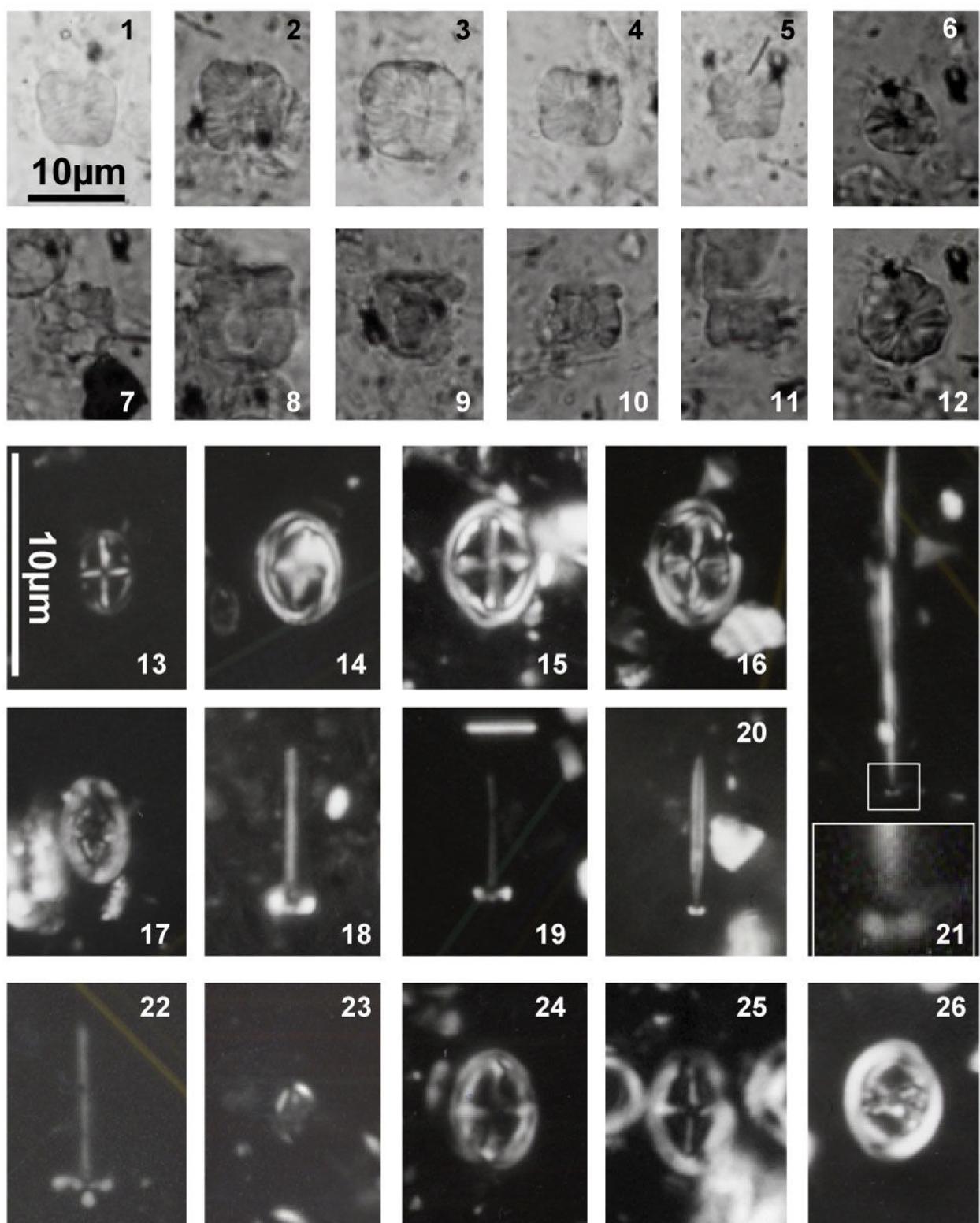


2323



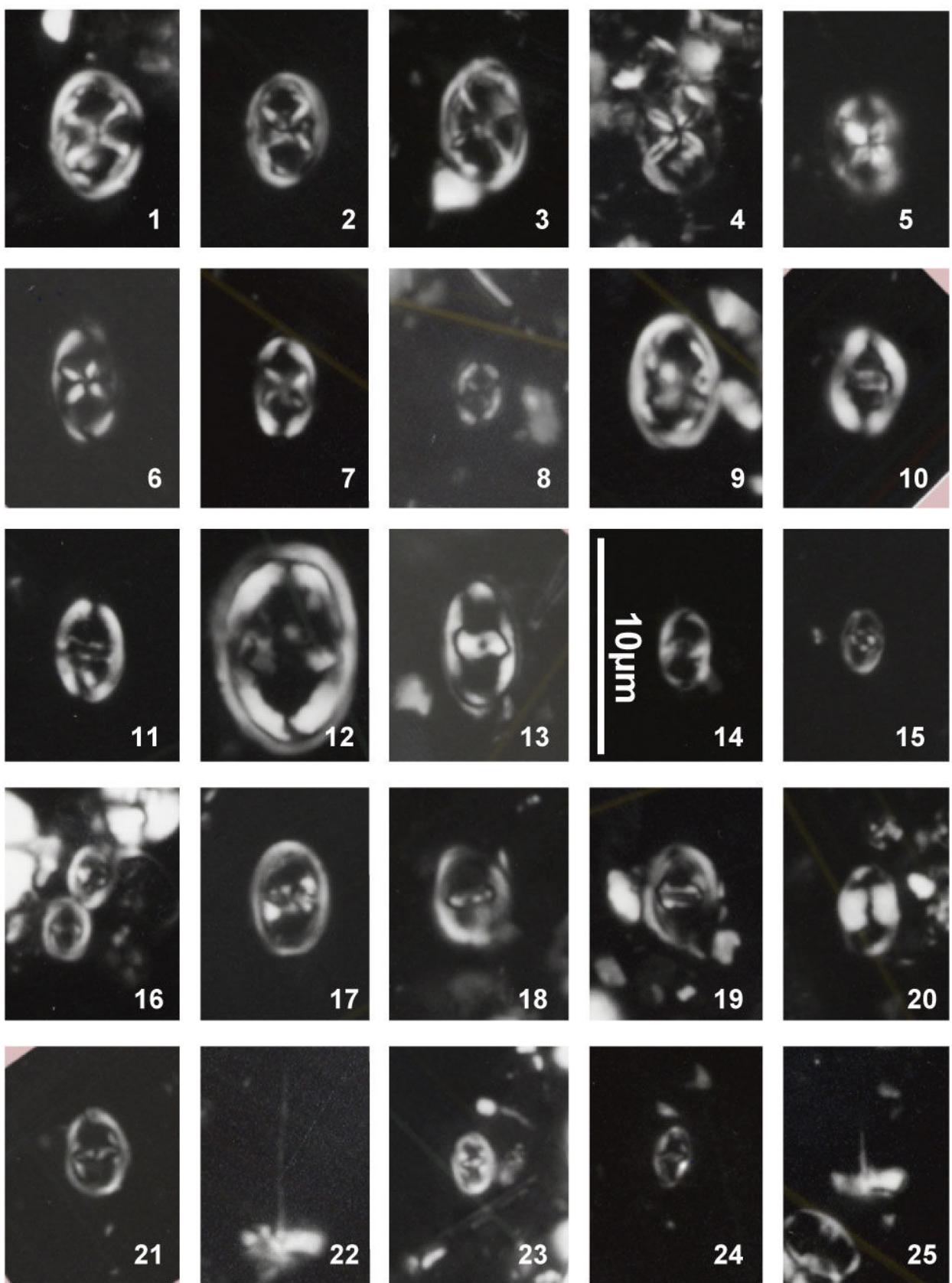


**Plate 3:** figs. 1, 3: ? *Nannoconus boletus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962 (sample 2312); figs. 2, 4-5: *Nannoconus boletus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962 (sample 2312); fig. 6: *Assipetra infracretacea* (THIERSTEIN, 1973) ROTH, 1973 (sample 2304); fig. 7: ? *Nannoconus carniolensis* DEFLANDRE & DEFLANDRE-RIGAUD, 1962 (sample 2304); figs. 8-11: *Nannoconus carniolensis* DEFLANDRE & DEFLANDRE-RIGAUD, 1962 (sample 2304); fig. 12: *Assipetra terebro-dentarius* (APPLEGATE al. in COVINGTON & WISE, 1987) RUTLEDGE & BERGEN in BERGEN, 1994 (sample 2324); fig. 13: *Staurolithites handleyi* LEES, 2007 (sample 2327); fig. 14: *Staurolithites mutterlosei* CRUX, 1989 (sample 2327); figs. 15-16: *Staurolithites rectus* BLACK, 1971a (fig. 15, sample 2332; fig. 16, sample 2310); fig. 17: *Bukrylithus ambiguus* BLACK, 1971a (sample 2302); figs. 18-19, 22: *Rhabdophidites parallelus* (WIND & CEPEK, 1979) LAMBERT, 1987 (fig. 18, sample 2332; fig. 19, sample 2292; fig. 22, sample 2310); figs. 20-21: *Rhabdophidites moesensis* MANIVIT, 1971 (fig. 20, sample 2317; fig. 21, sample 2310); fig. 23: *Acaenolithus* ? sp. (sample 2316); figs. 24-25: aff. *Misceomarginatus* WIND & WISE in WISE & WIND, 1977 (fig. 24, sample 2327; fig. 25, sample 2332); fig. 26: *Zeugrhabdotus xenotus* (STOVER, 1966) BURNETT in GALE et al., 1996 (sample 2339).



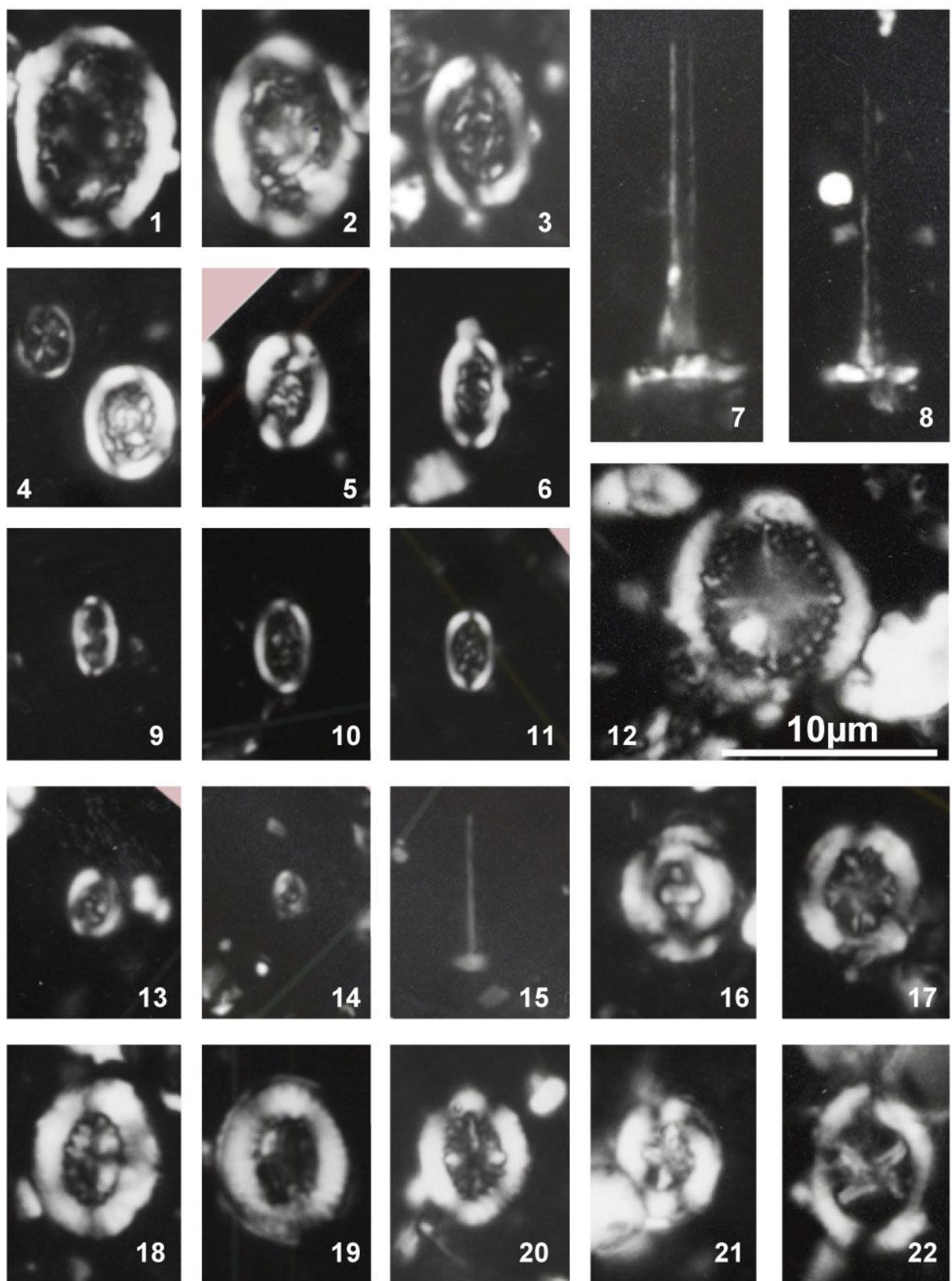


**Plate 4:** figs. 1-3, ? 9: *Chiastozygus* aff. *tenuis* BLACK, 1971a (figs. 1, 9, sample 2339; figs. 2-3, sample 2310); figs. 4-5: *Chiastozygus platyrhethum* HILL, 1976 (fig. 4, sample 2284; fig. 5, sample 2299); figs. 6-7: *Tegumentum stradneri* THIERSTEIN in ROTH & THIERSTEIN, 1972 (fig. 6, sample 2322; fig. 7, sample 2284); fig. 8: *Corollithion* ? *madasgaskarensis* PERCH-NIELSEN, 1973 (sample 2284); figs. 10-11, 18: *Zeugrhabdotus* cf. *diplogrammus* (DEFLANDRE in DEFANDRE & FERT, 1954) BURNETT in GALE et al., 1996 (fig. 10, sample 2327; fig. 11, sample 2284; fig. 18, sample 2327); figs. 12-13: *Zeugrhabdotus embergeri* (NOËL, 1958) PERCH-NIELSEN, 1985 (sample 2310); fig. 14: *Zeugrhabdotus moulladei* BERGEN, 1998 (sample 2322); fig. 15: *Zeugrhabdotus choffatii* RODD et al., 1973 (sample 2327); figs. 16, 23-25: *Zeugrhabdotus noeliae* RODD et al., 1971 (fig. 16, sample 2339; fig. 23, sample 2327; fig. 24, sample 2310; fig. 25, sample 2304); fig. 17: *Zeugrhabdotus howei* BOWN in KENNEDY et al., 2000 (sample 2302); fig. 19: *Zeugrhabdotus bicrescenticus* (STOVER, 1966) BURNETT in GALE et al., 1996 (sample 2322); fig. 20: *Tranolithus gabialis* STOVER, 1966 (sample 2284); figs. 21-22: *Zeugrhabdotus* sp. 1 (fig. 21, sample 2310; fig. 22, sample 2304).



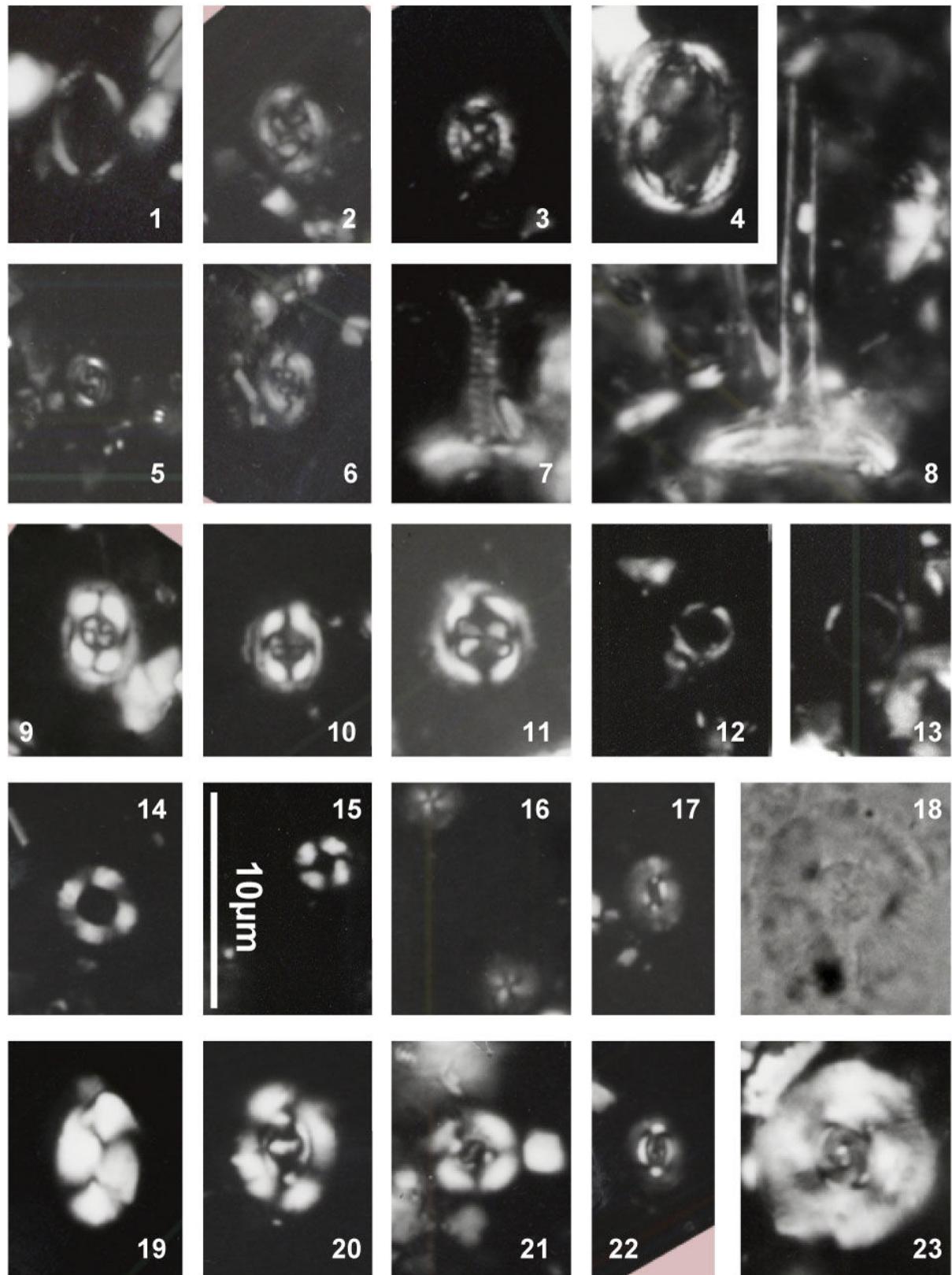


**Plate 5:** figs. 1-2: *Rhagodiscus asper* (DEFLANDRE, 1953) VERBEEK, 1977 (fig. 1, sample 2284; fig. 2, sample 2284); fig. 3: *Rhagodiscus splendens* (DEFLANDRE, 1953) VERBEEK, 1977 (sample 2332); figs. 4-5: *Rhagodiscus asper* (STRADNER, 1963) REINHARDT, 1967 (fig. 4, sample 2324; fig. 5, sample 2299); figs. 6, 9: *Rhagodiscus angustus* (STRADNER, 1963) RHEINARDT, 1971 - (fig. 6, sample 2295; fig. 9, sample 2295); fig. 7: *Rhagodiscus splendens* (DEFLANDRE, 1953) VERBEEK, 1977 (sample 2304); fig. 8: *Rhagodiscus asper* (STRADNER, 1963) REINHARDT, 1967 (sample 2304); figs. 10-11: *Rhagodiscus gallagheri* RUTLEDGE & BOWN, 1996 (fig. 10, sample 2299; fig. 11, sample 2299); fig. 12: *Cretarhabdus conicus* BRAMLETTE & MARTINI, 1964, large form (sample 2304); figs. 13-15: *Parhabdolithus imperfossus* (BLACK, 1972) LAMBERT, 1987 (fig. 13, sample 2299; fig. 14, sample 2310; fig. 15, sample 2295); fig. 16: *Microstaurus chiastius* (WORSLEY, 1971) BRALOWER *et al.*, 1989 (sample 2339); fig. 17: *Retecapsa schizobrachiata* (GARTNER, 1968) GRÜN in GRÜN & ALLEMANN, 1975 (sample 2327); figs. 18-20: *Cretarhabdus conicus* BRAMLETTE & MARTINI, 1964 (fig. 18, sample 2295; fig. 19, sample 2310; fig. 20, sample 2302); fig. 21: *Microstaurus quadratus* BLACK, 1971a (sample 2303); fig. 22: *Grantarhabdus meddii* BLACK, 1971a (sample 2342).



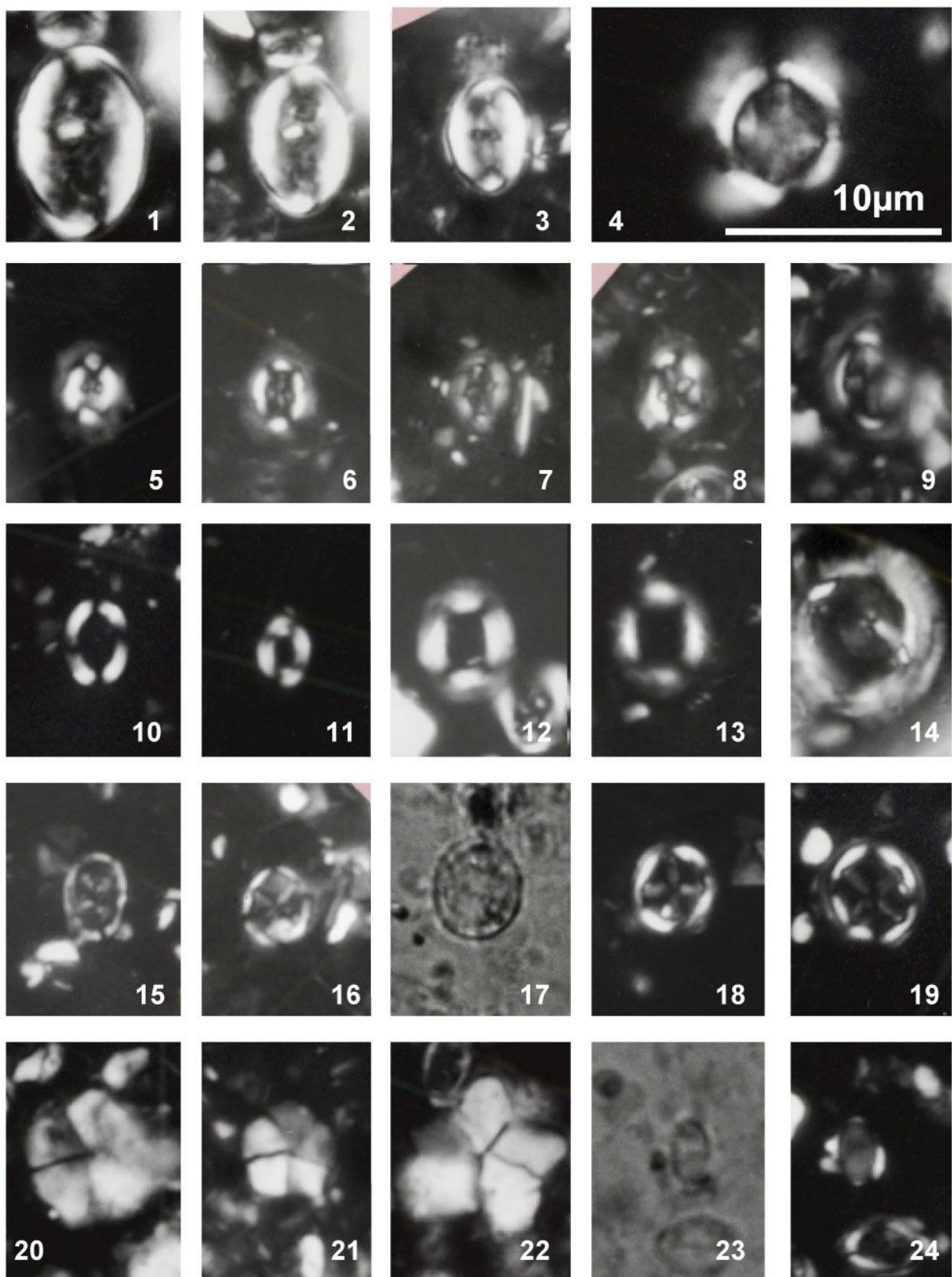


**Plate 6:** fig. 1: ? *Tetrapodorhabdus decorus* (DEFLANDRE in DEFLANDRE & FERT, 1954) WIND & WISE in WISE & WIND, 1977 (sample 2310); figs. 2-3, 6: *Tetrapodorhabdus coptensis* BLACK, 1971a (sample 2304); fig. 4: *Axopodorhabdus dietzmannii* (REINHARDT, 1965) WIND & WISE, 1983 (sample 2302); fig. 5: ? *Tetrapodorhabdus coptensis* BLACK, 1971a (sample 2304); fig. 7: *Tetrapodorhabdus decorus* (DEFLANDRE in DEFLANDRE & FERT, 1954) WIND & WISE in WISE & WIND, 1977 (sample 2346); fig. 8: ? *Axopodorhabdus dietzmannii* (REINHARDT, 1965) WIND & WISE, 1983 (sample 2305); figs. 9-11: *Flabellites biforaminis* THIERSTEIN, 1973 (fig. 10, sample 2327; figs. 9, 11, sample 2335); figs. 12-13: *Diazomalithus galicianus* KAENEL & BERGEN, 1996 (fig. 12, sample 2284; fig. 13, sample 2305); figs. 14-15: *Diazomatolithus lehmanii* NOËL, 1965 (fig. 14, sample 2295; fig. 15, sample 2284); fig. 16: *Discorhabdus ignotus* (GÓRKA, 1957) PERCH-NIELSEN, 1968 (sample 2339); fig. 17: *Biscutum constans* (GÓRKA, 1957) BLACK, 1968 (sample 2327); figs. 18, 23: *Haqius circumradiatus* (STOVER, 1966) ROTH, 1978 (sample 2324); fig. 19: Indeterminate, monstruous coccolith without central area? (sample 2284); figs. 20-21: *Watznaueria britannicus* (STRADNER, 1963) REINHARDT, 1964 (fig. 20, sample 2302; fig. 21, sample 2335); fig. 22: *Biscutum dubium* (NOËL, 1965) GRÜN in GRÜN et al., 1974 (sample 2327).



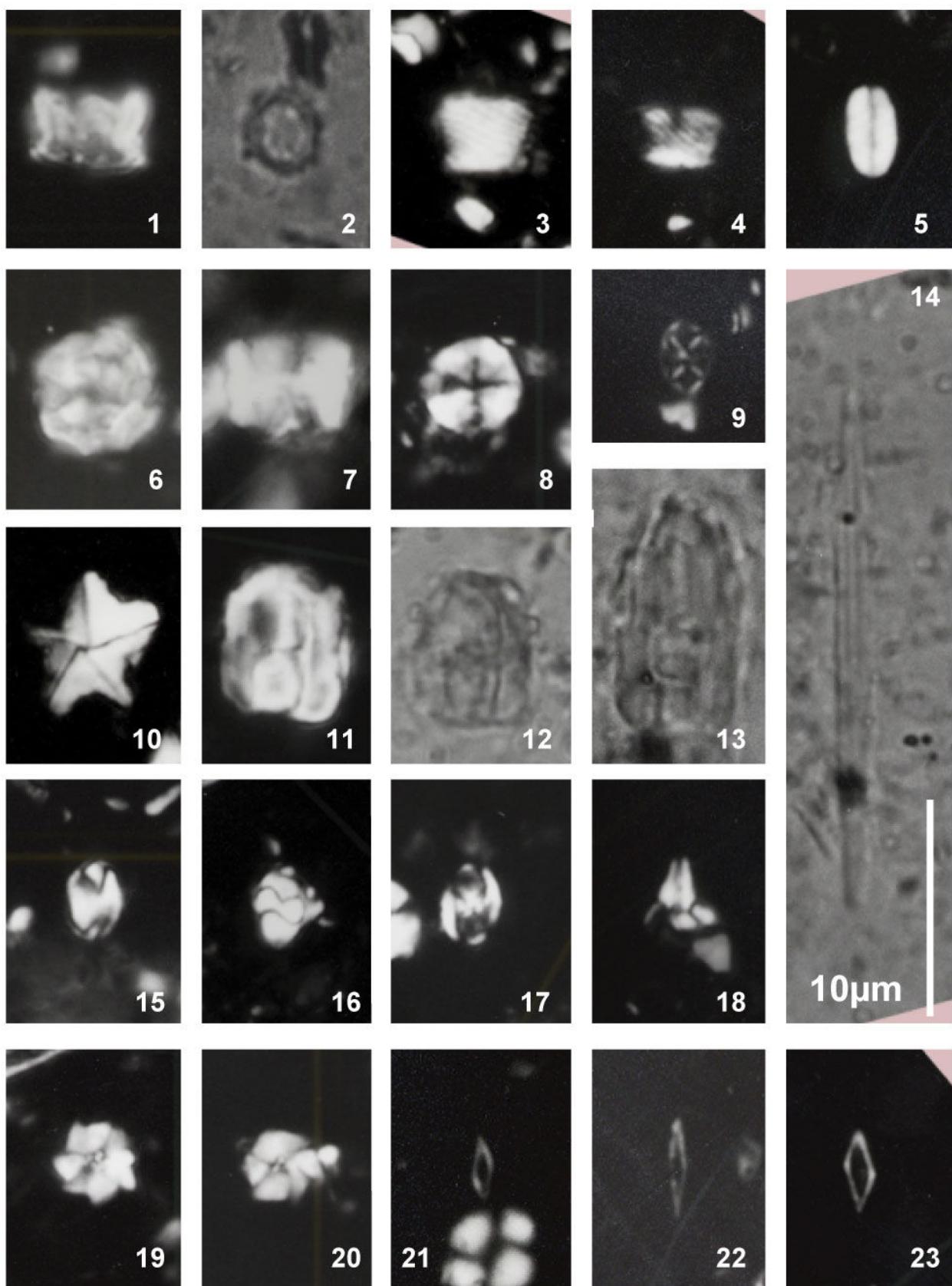


**Plate 7:** figs. 1-2: *Percivalia hauxtonensis* BLACK, 1973 (sample 2325); fig. 3: *Percivalia fenestratus* (WORSLEY, 1971) WISE, 1983 (sample 2339); fig. 4: *Pickelhaube furtiva* (ROTH, 1983) APPLEGATE *et al.* in COVINGTON & WISE, 1987 (sample 2304); figs. 5-9: *Crucibiscutum salebrosum* (BLACK, 1971a) JAKUBOWSKI, 1986 (fig. 5, sample 2332; figs. 6, 9, sample 2335; fig. 7, sample 2317; fig. 8, sample 2322); fig. 10: Indeterminate, missing central area? (sample 2284); fig. 11: *Watznaueria ovata* BUKRY, 1969 (sample 2310); figs. 12-13: *Tubodiscus burnettiae* BOWN *in* KENNEDY *et al.*, 2000 (fig. 12, sample 2317; fig. 13, sample 2327); fig. 14: *Manivitella pemmatoidea* (DEFLANDRE *in* MANIVIT, 1965) THIERSTEIN, 1971 (sample 2317); fig. 15: *Stradnerlithus ellipticus* (BUKRY, 1969) PERCH-NIELSEN, 1984 (sample 2335); figs. 16-19: *Stoverius achylosus* (STOVER, 1966) PERCH-NIELSEN, 1986 (fig. 16, sample 2335; figs. 17-18, sample 2302; fig. 19, sample 2304); figs. 20-21: *Braarudosphaera bigelowii* (GRAN & BRAARUD, 1935) DEFLANDRE, 1947 (fig. 20, sample 2284; fig. 21, sample 2305); fig. 22: *Braarudosphaera africana* STRADNER, 1961 (sample 2305); figs. 23-24: *Orastrum perspicuum* VAROL *in* AL-RIFAIY *et al.*, 1990 (sample 2346).



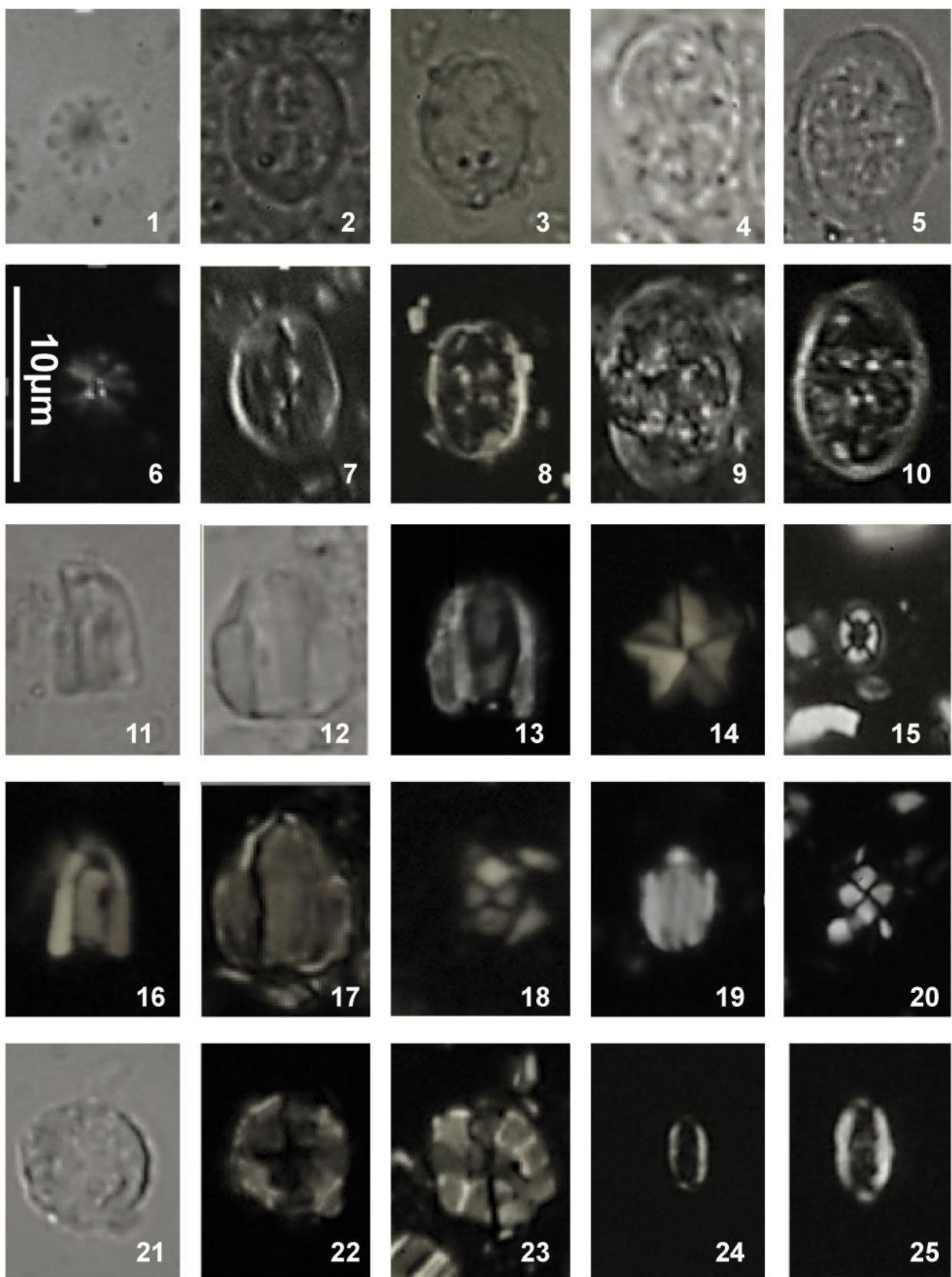


**Plate 8:** fig. 1 *Rotelapillus* sp., large profile shape (sample 2327); fig. 2: *Rotelapillus crenulatus* (NOËL, 1956) PERCH-NIELSEN, 1984, normal size natural light sample (sample 2299); figs. 3-5: *Zebrashapka vanhintei* COVINGTON & WISE, 1987 (fig. 3, sample 2339, fig. 4, sample 2304; fig. 5, sample 2304); figs. 6-8: *Eprolithus floralis* (STRADNER, 1962) STOVER, 1966 (figs. 6-7, sample 2335; fig. 8, sample 2284); fig. 9: *Stradnerlithus ellipticus* (BUKRY, 1969) PERCH-NIELSEN, 1984 (sample 2304); fig. 10: *Micrantholithus obtusus* STRADNER, 1963 (sample 2324); figs. 11-12: *Lapideacassis glans* BLACK, 1971b (sample 2284); fig. 13: *Lapideacassis mariae* BLACK, 1971b (sample 2335); fig. 14: *Lithraphidites carniolensis* DEFLANDRE, 1963 (sample 2304); figs. 15-16: *Calculites dispar* VAROL in AL-RIFAIY et al., 1990 (fig. 15, sample 2302; fig. 16, sample 2295); figs. 17-18: *Orastrum partitum* (VAROL in AL-RIFAIY et al., 1990) BERGEN, 1998 (fig. 17, sample 2292; fig. 18, sample 2310); figs. 19-20: *Hayesites irregularis* (THIERSTEIN in ROTH & THIERSTEIN, 1972) APPLEGATE al. in COVINGTON & WISE, 1987 (fig. 19, sample 2332; fig. 20, sample 2302); figs. 21-23: *Calciosolenia* (DEFLANDRE in DEFLANDRE & FERT, 1954) BOWN in KENNEDY et al., 2000 (fig. 21, sample 2345; fig. 22, sample 2304; fig. 23, sample 2322).



**Plate 9:** Clavaillan section

Deshayesites grandis Zone (Nannofossils association): figs. 1, 6: *Discorhabdus serratus* WORSLEY, 1971 (sample 2387); figs. 2-3, 7-8: *Parab dolithus infinitus* (WORSLEY, 1971) (figs. 2, 7, sample 2385; figs. 3, 8, sample 2393); fig. 4-5, 9-10: *Calicalathina erbae* BERGEN, 1998 (sample 2385); figs. 11 (LN), 16 (LP): *Lapideacassis* sp. (sample 2395); figs. 12 (LN), 17 (LP): *Lapideacassis glans* BLACK, 1971b (sample 2385); fig. 13: *Lapideacassis glans* BLACK, 1971b (sample 2387); fig. 14: *Micrantholithus obtusus* STRADNER, 1963 (sample 2385); fig. 15: *Eiffellithus hancockii* BURNETT, 1997 (sample 2389); fig. 18, *Calculites dispar* VAROL in AL-RIFAIY et al., 1990 (sample 2389); fig. 19: *Conosphaera rothii* (THIERSTEIN, 1971) JAKUBOWSKI, 1986 (sample 2387); fig. 20: *Tetralithus ? maticus* WORSLEY, 1971 (sample 2387); figs. 21-22: *Radiolithus planus* STOVER, 1966 (sample 2386); fig. 23: *Eprolithus floralis* (STRADNER, 1962) STOVER, 1966 (sample 2387); fig. 24: *Rhagodiscus angustus* (STRADNER, 1963) REINHARDT, 1971 (tiny specimen, sample 2387); fig. 25: *Rhagodiscus angustus* (STRADNER, 1963) REINHARDT, 1971 (sample 2395).



**Plate 10:** Clavaillan section

Deshayesites *grandis* Zone (*Nannoconus* association B): figs. 1-3: *N. steinmanii* KAMPTNER, 1931 (fig. 1, sample 2393; fig. 2, sample 2385; fig. 3, sample 2386); figs. 4-5: *N. cf. steinmanii* KAMPTNER, 1931 (sample 2387); figs. 6-7: *N. elongatus* BRÖNNIMANN, 1955 (fig. 6, sample 2385; fig. 7, sample 2386); fig. 8: ? *N. elongatus* BRÖNNIMANN, 1955 (sample 2386); fig. 9: *N. wassalli* BRÖNNIMANN, 1955 (sample 2385); fig. 10: *Nannoconus* aff. *borealis* PERCH-NIELSEN, 1979 (sample 2393); fig. 11: *N. boneti* TREJO, 1959 (sample 2393); fig. 12: *N. bucheri* BRÖNNIMANN, 1955 (large cavity, sample 2388); fig. 13: *N. bucheri* BRÖNNIMANN, 1955 (thin wall specimen, sample 2388); fig. 14: *N. bucheri* BRÖNNIMANN, 1955 (short specimen, sample 2388); fig. 15: *N. circularis* DERES & ACHÉRITÉGUY, 1980 (sample 2387).

Dufrenoya *furcata* Zone (*Nannoconus* association GI): fig. 16: *N. inconspicuus* DEFLANDRE & DEFLANDRE-RIGAUD, 1962 (sample 2407); fig. 17: *N. kampfneri* BRÖNNIMANN, 1955 (sample 2407); figs. 18-19: *N. aff. grandis* DERES & ACHÉRITÉGUY, 1980 (fig. 18, sample 2407; fig. 19, sample 2406); fig. 20: *N. boneti* TREJO, 1959 (sample 2407); figs. 21-24: *Assipetra*. 21-22: large forms (above 10µm), 23-24: small forms (below 10µm); figs. 21, 23-24: *Assipetra terebrodentarius* (APPLEGATE al. in COVINGTON & WISE, 1987) RUTLEDGE & BERGEN in Bergen, 1994 (sample 2386); fig. 22: *Assipetra infracretacea* (THIERSTEIN, 1973) ROTH, 1973 (sample 2386); fig. 25: *N. vocontiensis* DERES & ACHÉRITÉGUY, 1980 (sample 2407).

