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## Tithonian Chitinoïdellids of the South-Tethyan Margin of the Maghreb: New data from northern Tunisia

*Les chitinoïdelles tithoniennes de la Marge sud-téthysienne du Maghreb : nouvelles données du Nord tunisien*Houaïda Sallouhi<sup>a</sup>, Mabrouk Boughdiri<sup>a,\*</sup>, Fabrice Cordey<sup>b</sup><sup>a</sup> Département des sciences de la Terre, faculté des Sciences de Bizerte, 7021 Jarzouna, Tunisia<sup>b</sup> Département des sciences de la Terre, CNRS UMR 5125 « Paléoenvironnements et paléobiosphère », université Claude-Bernard Lyon 1, 69622 Villeurbanne, France

## ARTICLE INFO

## Article history:

Received 7 April 2010

Accepted after revision 16 August 2011

Available online 21 October 2011

Presented by Philippe Taquet

## Keywords:

Chitinoïdellids

Taxinomy

Biozonation

Phylogeny

Tithonian

Northern Tunisia

## Mots clés :

Chitinoïdelles

Taxinomie

Biozonation

Phylogénie

Tithonien

Tunisie septentrionale

## ABSTRACT

Recent investigations based on bed-by-bed sampling of the Béni Kleb Formation (Fm) of Northern Tunisia (Kimmeridgian-Middle Berriasian) provide new data on Tithonian chitinoïdellid associations. Fourteen species from seven genera (*Daciella* Pop, *Borziella* Pop, *Longicollaria* Pop, *Dobeniella* Pop, *Cubanella* Pop, *Popiella* Reháková and *Chitinoïdella* Doben) are first documented in Tunisia. Their stratigraphic range fits the standards proposed for other Tethyan regions. In addition, three new species are described: *Chitinoïdella carthagensis* sp. nov., *Ch. hegarati* sp. nov. and *Ch. popi* sp. nov. They are compared to the recently revised taxa from the southern Carpathian ranges where the chitinoïdellid populations were observed at various levels and revealed to be well diversified. The established biozonation is discussed and a phyletic pattern is proposed.

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## R É S U M É

Sur la base d'un échantillonnage banc par banc, de récents travaux entrepris sur la formation (Fm) Béni Kleb du Nord tunisien (Kimméridgien-Berriasien moyen) ont fourni de nouvelles données sur les chitinoïdelles tithoniennes. Quatorze espèces appartenant à sept genres (*Daciella* Pop, *Borziella* Pop, *Longicollaria* Pop, *Dobeniella* Pop, *Cubanella* Pop, *Popiella* Reháková and *Chitinoïdella* Doben) sont pour la première fois documentées de Tunisie. En outre, trois espèces nouvelles sont décrites : *Chitinoïdella carthagensis* sp. nov., *Ch. hegarati* sp. nov. et *Ch. popi* sp. nov. Elles sont comparées aux taxons récemment révisés dans les Carpathes méridionales où les chitinoïdelles ont été observées à différents niveaux et se sont avérées des plus diversifiées. Les biozonations établies sont discutées et un modèle phylétique est proposé.

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## 1. Introduction

The Tethyan pelagic sediments of the Upper Jurassic–Lower Cretaceous transition are mainly characterized by a small microfossil group of axially symmetrical planktonic protozoans included in three families based on the morphology of their lorica. These can be microgranular (Chitinoideiellidae Trejo, 1975), combined microgranular and hyaline (Semichitinoideiellidae Nowak, 1978) or only hyaline (Calpionellidae Bonet, 1956; Duben, 1963). Although the biological affinities of this widely distributed Tethyan group are still uncertain and a matter of debate, its high stratigraphic potential for the biozonation of Upper Jurassic–Lower Cretaceous series has been applied since the sixties of the last century. The biozonations currently in use for the Upper Tithonian–Lower Valanginian (e.g. Andreini et al., 2007; Grün and Blau, 1996; Michalík et al., 2009 and references therein; Oloríz et al., 1995; Reháková and Michalík, 1997; Remane et al., 1986 and references therein) consider that the lowermost Chitinoideiella zone spans the Lower–Upper Tithonian transition levels. It was first defined in the West Carpathians by Borza (1969) and correlated to the ammonite zones by Enay and Geysant (1975) and Cecca et al. (1989) after biostratigraphic analyses of successions from the Sub-betic range of SE Spain and Ardèche in SE France. Biostratigraphic investigations of Ammonitico Rosso successions from the Italian Venetia area allowed Grandesso (1977) to bring more precisions to the zonal content: small forms of the *Ch. dobeni* group occur in the lower part and specimens of *Ch. boneti* in the upper one. The formal subdivision of the Chitinoideiella zone into the Dobeni and the Boneti Subzones was provided by Borza (1984) and Borza and Michalík (1986). Within these Subzones, all Chitinoideiellid species had been assigned to the single genus *Chitinoideiella* Doben, 1963 until Pop (1997, 1998a) revised its taxonomy on the basis of an abundant material from the south Carpathian range; five new genera (*Dobeniella*, *Cubanella*, *Longicollaria*, *Borziella* and *Cylindrella*) were then introduced by this author. In the central and West Carpathian Pieniny klippen Belt areas, Reháková (2002) recognized all the genera described by Pop (1997, 1998a) and proposed another new genus (*Popiella*) limited to the single species *P. oblongata*.

From the South–Tethyan margin of the Maghreb, chitinoideiellid faunas described from the Moroccan Prérif (e.g. Bachnou, 1992; Benzaggagh, 2000; Benzaggagh and Atrops, 1995) were all assigned to the genus *Chitinoideiella* and were used mainly for biostratigraphic purposes. The Dobeni and Boneti Subzones of the Chitinoideiella zone were recognised and correlated to the ammonite zones.

In Northern Tunisia, *Chitinoideiella boneti* had been mentioned in the “Tunisian Dorsale” (“TD”) to identify its corresponding zone (Boughdiri et al., 2005; Combémoré et al., 1981); however, its first illustration was provided by Boughdiri et al. (2006) in the “Tunisian Trough” (“TT”). Recent investigations of Tithonian successions from these areas led to the identification of rich chitinoideiellid assemblages described here and first documented in Tunisia. New species are introduced and their stratigraphic distribution is detailed. A phyletic approach is proposed taking into

account revised complementary data from the Moroccan Prérif and the Carpathian Ranges.

## 2. Studied sections: location and stratigraphic context

Among six sections bearing chitinoideiellids and calpionellids, only three were chosen (Fig. 1): the Jebel (J.) Oust section of the “TD” (Bir M’Cherga area, NE Tunisia) and the J. Jédidi and J. Chaabane sections of the “TT” (Mejez el Beba area, NW Tunisia). Their location and detailed palaeogeographic setting are described in previous papers (e.g. Boughdiri et al., 2007, 2009; Cordey et al., 2005; Soussi, 2002, 2003).

In these areas, these sections are part of the Béni Kleb Fm (Peybernès, 1992 *emend.* Boughdiri et al., 2006) composed by marls and pseudonodular limestones with *Saccocoma* and calpionellids, including four successive units: limestone beds with intercalated thin marly layers (unit A), marl/limestone alternations with relatively thicker marly levels (unit B). Follows another carbonate unit (C) and again a marl/limestone alternation (D) with chert nodules and rare turbidites. Chitinoideiellid faunas studied in this paper are observed within the uppermost beds of Unit C and the lowermost part of unit D.

## 3. Biostratigraphy

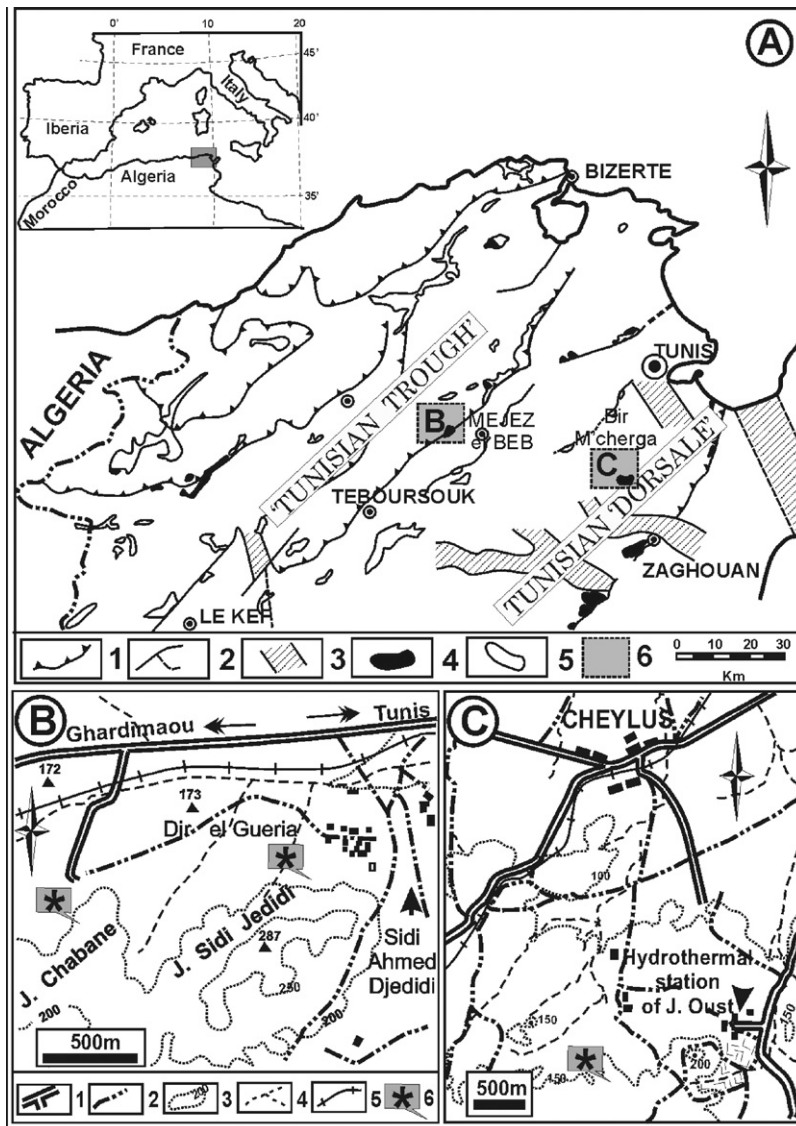
### 3.1. Reference stratigraphic scale

The standard referred to in this work is that of Remane et al. (1986). Complementary updated data of Pop (1994, 1996), Boughdiri et al. (2006, 2009) and Michalík et al. (2009) were also considered. For the correlation of ammonite and praecalpionellid scales we used the standard proposed by the “Groupe français d’études du Jurassique” G.F.E.J (1997).

### 3.2. Faunal distribution and biozonation

Within bed “JD 60” of the Jédidi section, a rich assemblage of small chitinoideiellids comprises: *Longicollaria dobeni* (Borza), *Dobeniella colomi* (Borza), *D. cubensis* (Furrazola–Bermúdez), *D. bermudezi* (Furrazola–Bermúdez), *D. tithonica* (Borza), *Borziella slovenica* (Borza) and *Daciella svinitensis* Pop.

A comparable assemblage was encountered within bed “CH 21” of the Chaabane section where, in addition, the genus *Daciella* Pop is represented by two species: *D. aff. banatica* Pop and *D. gr. svinitensis* Pop. The bed “OU 81.A” of the J. Oust section carries also very similar associations among which we also identified *Popiella oblongata* Reháková and *Cubanella cristobalensis* (Furrazola–Bermúdez). All these associations and co-occurrent taxa of the Dobeni Subzone were also identified in the Carpathian Range (e.g.: Pop, 1997, 1998a, 1998b; Reháková, 2002). This allows us to correlate the beds “JD. 60” (J. Jédidi), “CH 21” (J. Chaabane) and “OU 81.A” (J. Oust) as co-eval (Fig. 2). They are dated here to the upper Dobeni Subzone (Chitinoideiella Zone) because the oldest association of the bed “OU 78.A” (J. Oust) includes only *L. dobeni*



**Fig. 1.** Location of the studied sections. A: Northern Tunisia. 1: Thrust fault; 2: Main fault; 3: Trough; 4: Jurassic outcrops; 5: Triassic exposure; 6: Study area. B, C: Location of sections (B: Jebels Jédidi and Chaabane; C: J. Oust). 1: Highway; 2: Gravel road; 3: Elevation; 4: Creek; 5: Railway tracks; 6: Position of successions.

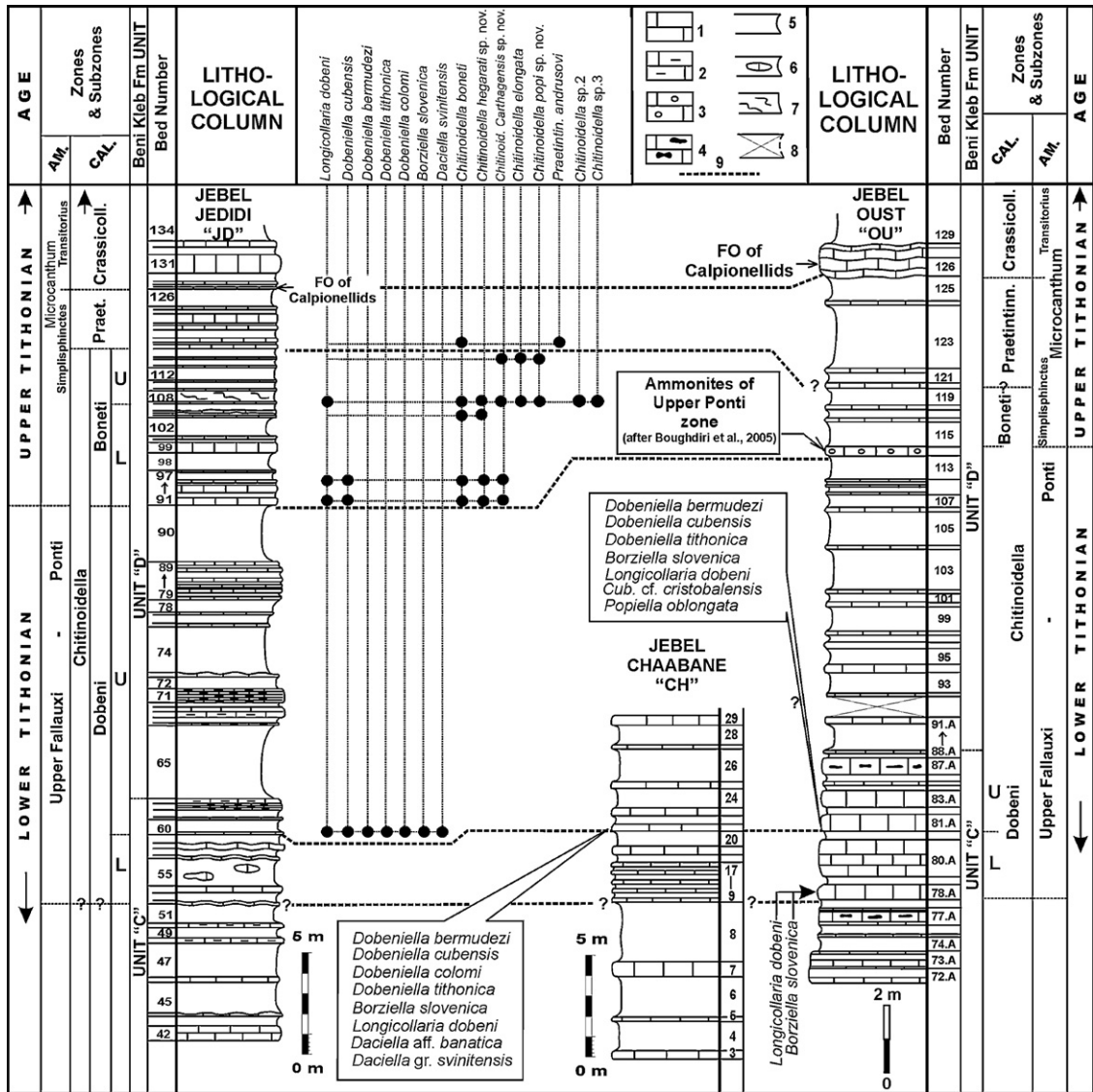
**Fig. 1.** Localisation des coupes étudiées. A : Tunisie du Nord. 1 : Chevauchement ; 2 : Faille majeure ; 3 : Fossé ; 4 : Affleurement jurassique ; 5 : Affleurement triasique ; 6 : Zone d'étude. B, C : Localisation des coupes (B : Jebels Jédidi et Chaabane, C : J. Oust). 1 : Route principale ; 2 : Piste ; 3 : Courbe de niveau ; 4 : Ravin, oued ; 5 : Chemin de fer ; 6 : Position des coupes.

and *Borziella slovenica* in its lower part. Thus, the lower limit of the Dobeni Subzone can be traced below the bed “OU 78.A” of Jebel Oust which is older than the above-mentioned coeval beds “JD 60”, “CH 21” and “OU 81.A”.

Higher in the Jédidi section, the bed “JD 91” shows the first occurrence of *Chitinoidea carthagensis* sp. nov. and *Ch. hegarati* sp. nov. together with *Dobeniella cubensis* (Furrázola-Bermúdez) and *L. dobeni*. The bed “JD 95” has the same association to which corresponds also the first occurrence (F.O.) of *Ch. boneti* Doben and *Ch. carthagensis* sp. nov. and below which we place the boundary between the Dobeni and Boneti Subzones. In J. Oust, this limit can be traced on top of bed “OU 114” where Boughdiri et al. (2005)

gathered an ammonite association of the uppermost Ponti Zone.

The bed “JD 107” (J. Jédidi) is mainly characterized by the FO of *Ch. cf. elongata* Pop, *Ch. popi* sp. nov. The same occurrence of *Ch. elongata* in the upper part of the Boneti Subzone was also documented within the Carpathian range by Pop (1997, 1998a, 1998b) and Reháková (2002). In J. Jédidi, the upper limit of the Boneti Subzone (= upper limit of the Chitinoidea Zone) is placed below the bed “JD 117” where *Praetintinnopsella andrusovi* (Borza) co-occurs with *Ch. boneti* for the first time. The first hyaline calpionellids appear within the bed “JD 127” (Boughdiri et al., 2006), which base indicates the boundary between the



**Fig. 2.** Lithological succession, chitinoideid distribution and biostratigraphy of the studied sections. 1: limestone; 2: marly limestone; 3: nodular limestone; 4: limestone with silex; 5: marls; 6: olistolithes; 7: slumps; 8: covered level; 9: correlation line.

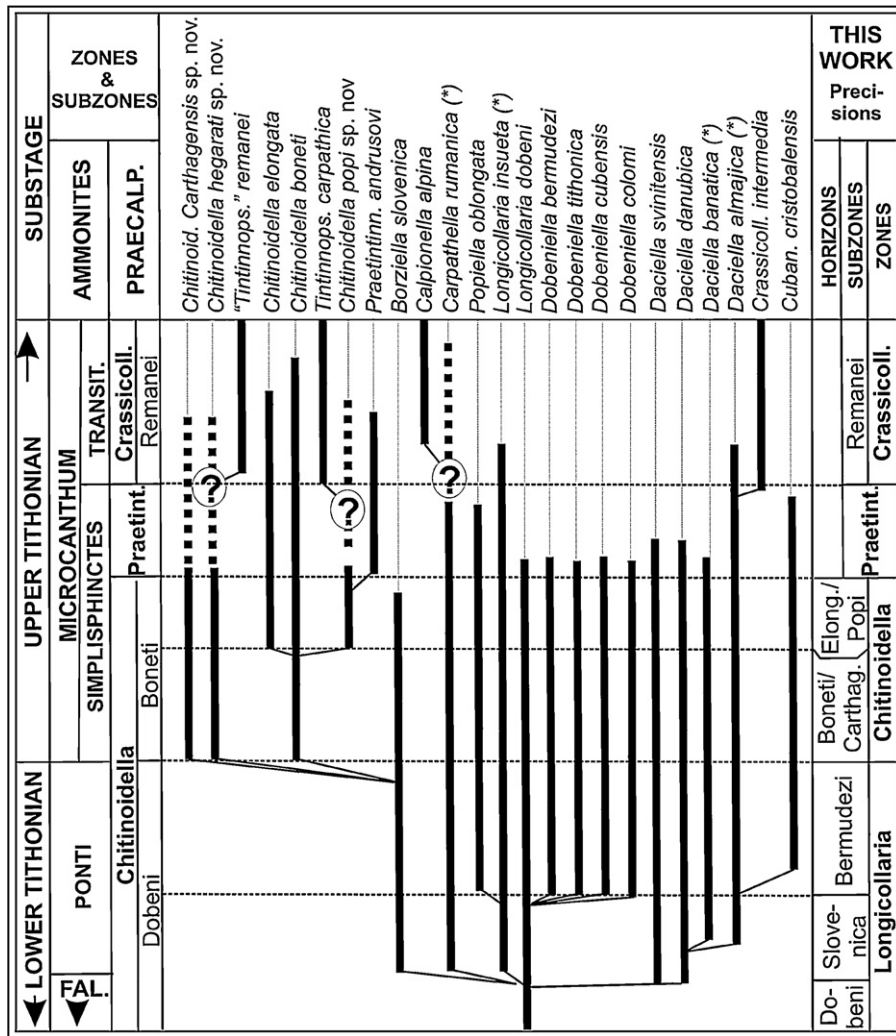
**Fig. 2.** Succession lithologique, répartition des chitinoïdellidés et stratigraphie des coupes étudiées. 1 : calcaire ; 2 : calcaire marneux ; 3 : calcaire noduleux ; 4 : calcaire à silex ; 5 : marnes ; 6 : olistolithes ; 7 : niveaux glissés ; 8 : niveau tendre couvert ; 9 : trait de corrélation.

Praetintinnopsella and Crassicolonia zones and which is correlated with the bed “OU 126” of J. Oust where the same datum was detected by Boughdiri et al. (2005).

In conclusion, the Chitinoideid distribution within the studied sections agrees with those obtained in the Carpathian Range where the succession is more complete and the assemblages are the most diversified. The biozonation established here easily fits their proposals for northern Tethys Margin regions. Nevertheless, some biozonation data are worth commenting. From top to base, as shown on Fig. 3, the index genus *Chitinoideidella* does not span the whole Chitinoideidella zone but only its upper part (=Boneti Subzone). Thus, an updated Chitinoideidella zone should be restricted to the upper part of the classic Chitinoideidella zone (=Boneti Subzone). Furthermore, within this

updated Chitinoideidella zone, *Ch. elongata* and *Ch. popi* characterize its upper part; their FO can be considered to trace the base of a new Elongata/Popi Subzone (=the top of the classic Boneti Subzone or a Boneti/Carthagensis Subzone).

Lower, under the updated chitinoideidella zone (Fig. 3), only the index species *L. dobeni* marks the lowermost part of the ex. Dobeni Subzone. Higher, *Borziella svinitensis* and many species of the genus *Daciella* appear and, in the upper part, all *Dobeniella* species appear among which *D. bermudezi* is the most diversified. Consequently, considering these bioevents, another updated biozonation is proposed here: a Longicollaria zone can be considered as a new equivalent of the ex. Dobeni zone. It includes henceforth a lower Dobeni Subzone, a medium Slovenica Subzone and an upper Bermudezi subzone (Fig. 3).



**Fig. 3.** Synthetic phyletic approach: Chitinoideidellid evolution during Lower-to-Upper Tithonian transition. (\*): Species known in the Carpathian Ranges and their stratigraphic range (after Pop (1998)); mentioned here for their close affinities with Tunisian taxa expressing potential phyletic relationships.  
**Fig. 3.** Approche phylétique synthétique : évolution des chitinoïdeidés au cours de la transition Tithonien inférieur–Tithonien supérieur. (\*): Espèces connues dans les Carpathes méridionales avec leur répartition stratigraphique (d’après Pop, 1998) ; elles sont mentionnées ici pour leurs affinités étroites avec des taxons tunisiens exprimant des liens phylétiques potentiels.

**4. Systematics**

**4.1. New chitinoideidellid species from Northern Tunisia**

Thin sections bearing the new species described below will be housed in the Geology museum of the Tunisia Geological Survey (Office National des Mines [ONM]).

**Family:** *Chitinoideidellidae* Trejo, 1975  
**Genus:** *Chitinoideella* Doben, 1963  
*Chitinoideella popi* sp. nov.

(Plate 1, Figs. 32 and 33)

**Holotype**  
 Specimen on Plate 1, Fig. 32 (ONM/HS 0409/JD 107.1).

**Paratype**  
 Specimen on Plate 1, Fig. 33 (ONM/HS 0409/JD 107.3).

**Material and Depository reference**

Five specimens from the Jéjidi section: ONM/HS 0409/JD 107.1–4, ONM/HS 0409/JD 115.1.

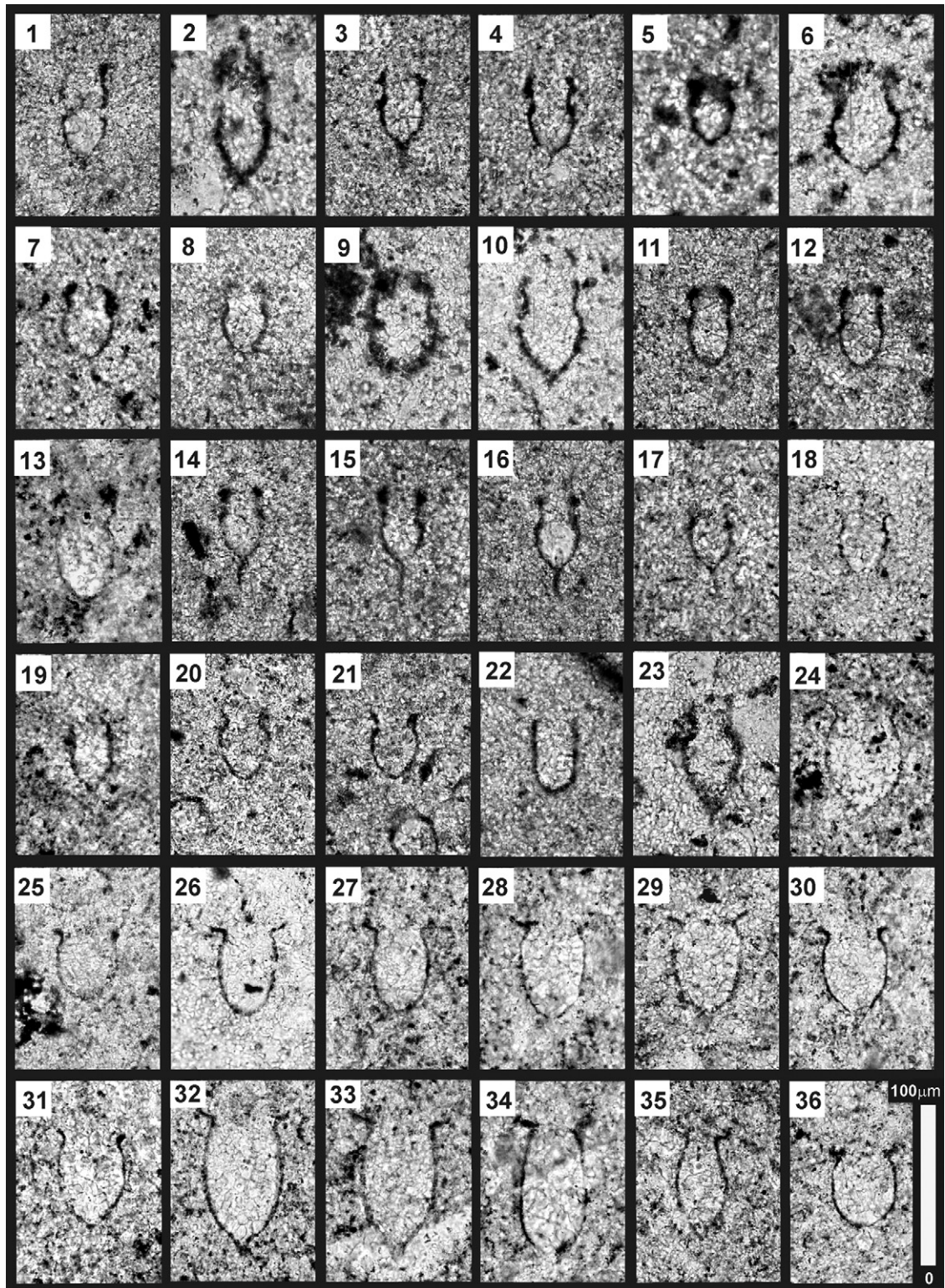
**Etymology**

The specific name is chosen in memory of Grigore Pop, a former geologist from the Geological Institute of Romania (Bucharest) specialist of calpionellid palaeontology and biostratigraphy. He revised the genus *Chitinoideella* and described the majority of the chitinoideidellid taxa currently in use.

**Diagnosis**

Elongated bell-shaped lorica with a conical aboral pole terminating in a well-marked caudal appendage. Large oral opening surrounded by a concave outwardly deflected collar, which is lense-like in section. The lorica is 70–85 µm long and 40–50 µm wide; the length/width (L/l) ratio is 1,7–1,8. Measurements of the holotype: L = 85 µm, l = 48 µm; L/l = 1,77.

**Type locality**



**Plate 1.** Chitinoideidls from Lower-to-Upper Tithonian transition beds of northern Tunisia: taxon, layer, age (Calpionellid zone and/or Subzone; substage). Scale bar in fig. 36 (100  $\mu\text{m}$ ). 1–2. *Longicollaria dobeni* (Borza), 1: JD60. 2: OU81.A, Chitinoideella zone, upper Dobeni Subzone; Lower Tithonian. 3–6. *Dobeniella tithonica* (Borza), 3–4: JD60. 5: OU81.A (small form). 6: OU81.A (big form), Chitinoideella zone, upper Dobeni Subzone; Lower Tithonian. 7–10. *Dobeniella cubensis* (Furrazola-Bermúdez), 7: CH21. 8: JD60 (small form). 9–10: OU81.A (big form), Chitinoideella zone, upper Dobeni Subzone; Lower Tithonian. 11–13. *Dobeniella bermudezi* (Furrazola-Bermúdez), 11–12: JD60 (small form), Chitinoideella zone, upper Dobeni Subzone; Lower Tithonian.

The Jédidi section (Mejez el Beba area, NW Tunisia)

#### Type beds

Beds JD 107 and JD 115 of the Jédidi section, upper Boneti Subzone

#### Remarks

*Chitinoidella popi* sp. nov. can be distinguished from *Ch. elongata* Pop by its concave collar, small preoral constriction, larger preoral opening and maximum width located at the middle part of the bowl. It is different from *Ch. boneti* in its elongated shape, the preoral constriction and the concave lense-like aspect of the collar. *Ch. popi* is a perfect homeomorph of the calpionellid *Tintinnospella carpathica* (Murgeanu and Filipescu). It also displays the same bowl shape of *Remaniella* gr. *catalanocolomi* Pop.

#### Age

Upper Tithonian, upper Boneti Subzone (Chitinoidella zone).

#### *Chitinoidella carthagensis* sp. nov.

(Plate 1, Figs. 26–29)

#### Holotype

Specimen on Plate 1, Fig. 28 (ONM/HS 0409/JD 107.7).

#### Paratype

Specimen on Plate 1, figs. 26, 27 and 29 (ONM/HS0409/JD115.02, (ONM/HS0409/JD107.18 ONM/HS 0409/JD 95.1)

#### Material and Depository reference

14 specimens from the Jédidi section; references: ONM/HS 0409/JD 95.1.

ONM/HS 0409/JD 107.5–10, ONM/HS0409/JD107.17–19, ONM/HS0409/JD91.03, ONM/HS0409/JD95.04–05, ONM/HS0409/JD103.03, and ONM/HS0409/JD115.02.

#### Etymology

The species name refers to the city of Carthage (814–146 B. C.), the capital of the Carthaginian Empire which included Tunisia. The Jédidi section is located 85 km to the southeast of former Carthage.

#### Diagnosis

Elongated bell-shaped lorica with a polygonal bowl. This latter is rather ellipsoid with a rounded aboral pole in oblique sections. Just below the large preoral opening, the bowl flanks converge towards the lower part where they are abruptly attached to a conical aboral pole at the end of which a small and smoothed caudal appendage is observed. A short angular “shoulder”-like feature characterizes the upper part of the bowl where the maximum width can be measured. The collar is outwardly deflected forming an angle of nearly 90° with the external edge of the oral opening. The lorica length is 55–65 µm and its width is 32–45 µm with a L/l = 1.4–1.6. Measurements of the holotype (L = 61 µm, l = 39 µm; L/l = 1.56).

#### Type locality

The Jédidi section (Mejez el Beba area, NW Tunisia).

#### Type level

Beds JD 91, JD 95, JD 103, JD 107 and JD 115 of the Jédidi section, lower Boneti Subzone (Chitinoidella Zone).

#### Remarks

*Chitinoidella carthagensis* can be easily differentiated from the co-occurrent species *Ch. boneti*, *Ch. elongata* and *Ch. popi* by its polygonal shape and maximal width that

13: JD103 (big form), Chitinoidella zone, lower Boneti Subzone; Upper Tithonian. 14–16. *Dobeniella colomi* (Borza), JD60, Chitinoidella Zone, upper Dobeni Subzone; Lower Tithonian. 17. *Daciella danubica* Pop, JD60, Chitinoidella Zone, upper Dobeni Subzone; Lower Tithonian. 18, 20, 21. *Borziella slovenica* (Borza), 18: CH21, 20, 21: JD60, Chitinoidella Zone, upper Dobeni Subzone; Lower Tithonian. 19. *Daciella svinitensis* Pop, CH21, Chitinoidella zone, upper Dobeni Subzone; Lower Tithonian. 22. *Popiella oblongata* Reháková, JD60, Chitinoidella Zone, upper Dobeni Subzone; Lower Tithonian. 23. *Cubanella cristobalensis* (Furrazola-Bermúdez), OU81.A, Chitinoidella Zone, upper Dobeni Subzone; Lower Tithonian. 24. *Chitinoidella boneti* Doben, JD103, Chitinoidella zone, lower Boneti Subzone; Upper Tithonian. 25, 30, 31. *Chitinoidella hegarati* sp. nov., 25: oblique section (ONM/HS 0409/JD 107.12), 30: holotype (ONM/HS 0409/JD 91.01), 31: paratype (ONM/HS 0409/JD 103.02), Chitinoidella Zone, upper Boneti Subzone; Upper Tithonian. 26–29. *Chitinoidella carthagensis* sp. nov., 28: holotype (ONM/HS 0409/JD 107.7), 26, 27 and 29: paratypes (ONM/HS0409/JD115.02, ONM/HS0409/JD107.18 ONM/HS 0409/JD 95.1), Chitinoidella zone, Boneti Subzone; Upper Tithonian. 32–33. *Chitinoidella popi* sp. nov., 32: holotype (ONM/HS 0409/JD 107.1), 33: paratype (ONM/HS 0409/JD 107.3), Chitinoidella Zone, upper Boneti Subzone; Upper Tithonian. 34. *Chitinoidella* cf. *elongata* Pop, JD107, Chitinoidella zone, upper Boneti Subzone; Upper Tithonian. 35. *Chitinoidella* sp. 1, JD107, Chitinoidella Zone, upper Boneti Subzone; Upper Tithonian. 36. *Chitinoidella* sp. 2, JD107, Chitinoidella Zone, upper Boneti Subzone; Upper Tithonian.

**Planche 1.** Planche 1. Chitinoidelles du passage Tithonien inférieur/Tithonien supérieur de la Tunisie septentrionale. Mentions : taxon, couche, âge (zone et/ou sous-zone ; sous-étage). Barre d'échelle = 100 µm (cf. fig. 36). 1–2. *Longicollaria dobeni* (Borza), 1 : JD60. 2 : OU81.A, zone à Chitinoidella, sous-zone à Dobeni (partie supérieure) ; Tithonien inférieur. 3–6. *Dobeniella tithonica* (Borza), 3–4 : JD60. 5 : OU81.A (forme de petite taille), 6 : OU81.A (forme de grande taille), zone à Chitinoidella, sous-zone à Dobeni (partie supérieure) ; Tithonien inférieur. 7–10. *Dobeniella cubensis* (Furrazola-Bermúdez), 7 : CH21. 8 : JD60 (forme de petite taille). 9–10 : OU81.A (forme de grande taille), zone à Chitinoidella, sous-zone à Dobeni (partie supérieure) ; Tithonien inférieur. 11–13. *Dobeniella bermudezi* (Furrazola-Bermúdez), 11–12 : JD60 (forme de petite taille), zone à Chitinoidella, sous-zone à Dobeni (partie supérieure) ; Tithonien inférieur. 13 : JD103 (forme de grande taille), zone à Chitinoidella, sous-zone à Boneti (partie inférieure) ; Tithonien supérieur. 14–16. *Dobeniella colomi* (Borza), JD60, zone à Chitinoidella, sous-zone à Dobeni (partie supérieure) ; Tithonien inférieur. 17. *Daciella danubica* Pop, JD60, zone à Chitinoidella, sous-zone à Dobeni (partie supérieure) ; Tithonien inférieur. 18, 20, 21. *Borziella slovenica* (Borza), 18 : CH21, 20–21 : JD60, zone à Chitinoidella, sous-zone à Dobeni (partie supérieure) ; Tithonien inférieur. 19. *Daciella svinitensis* Pop, CH21, zone à Chitinoidella, sous-zone à Dobeni (partie supérieure) ; Tithonien inférieur. 22. *Popiella oblongata* Reháková, JD60, zone à Chitinoidella, sous-zone à Dobeni (partie supérieure) ; Tithonien inférieur. 23. *Cubanella cristobalensis* (Furrazola-Bermúdez), OU81.A, zone à Chitinoidella, sous-zone à Dobeni (partie supérieure) ; Tithonien inférieur. 24. *Chitinoidella boneti* Doben, JD103, zone à Chitinoidella, sous-zone à Boneti (partie inférieure) ; Tithonien supérieur. 25, 30, 31. *Chitinoidella hegarati* sp. nov., 25 : section oblique (ONM/HS 0409/JD 107.12), 30 : holotype (ONM/HS 0409/JD 91.01), 31 : paratype (ONM/HS 0409/JD 103.02), zone à Chitinoidella, sous-zone à Boneti (partie supérieure) ; Tithonien supérieur. 26–29. *Chitinoidella carthagensis* sp. nov., 28 : holotype (ONM/HS 0409/JD 107.7), zone à Chitinoidella, sous-zone à Boneti (partie supérieure) ; Tithonien supérieur. 26, 27 and 29 : paratypes (ONM/HS0409/JD115.02, (ONM/HS0409/JD107.18 ONM/HS 0409/JD 95.1), zone à Chitinoidella, sous-zone à Boneti ; Tithonien supérieur. 30–31. *Chitinoidella hegarati* sp. nov., 30 : holotype (ONM/HS 0409/JD 91.01), 31 : (ONM/HS 0409/JD 103.02), zone à Chitinoidella, sous-zone à Boneti (partie supérieure) ; Tithonien supérieur. 32–33. *Chitinoidella popi* sp. nov., 32 : holotype (ONM/HS 0409/JD 107.1) ; 33 : paratype (ONM/HS 0409/JD 107.3), zone à Chitinoidella, sous-zone à Boneti (partie supérieure) ; Tithonien supérieur. 34. *Chitinoidella* cf. *elongata* Pop, JD107, zone à Chitinoidella, sous-zone à Boneti (partie supérieure) ; Tithonien supérieur. 35. *Chitinoidella* sp. 1, JD107, zone à Chitinoidella, sous-zone à Boneti (partie supérieure) ; Tithonien supérieur. 36. *Chitinoidella* sp. 2, JD107, zone à Chitinoidella, sous-zone à Boneti (partie supérieure) ; Tithonien supérieur.

can be taken just below the collar. The oblique sections of *Ch. carthagensis* differ from the *Daciella* species in the following traits: a larger size, a smaller and smoothed caudal appendage and the absence of a thickened wall on the “shoulder”-like feature below the preoral opening. They can be easily distinguished from axial and oblique sections of *Ch. hegarati* by their elongated ellipsoid shape.

#### Age

Lowermost Upper Tithonian, lower Boneti Subzone of the Chitinoïdella Zone.

#### *Chitinoïdella hegarati* sp. nov.

(Plate 1, Figs. 25, 30–31)

1995 *Chitinoïdella bermudezi*- Benzaggagh et Atrops, fig. 4:7

1997? *Chitinoïdella* sp1- Grün and Blau, pl. 1, fig. 7

2000 *Chitinoïdella bermudezi*- Benzaggagh, pl. 5, fig. 7

2007 *Chitinoïdella boneti* - Andreini et al., pl. I, fig. 1, 3 and 4).

#### Holotype

Specimen on Pl. 1, Fig. 30 (ONM/HS 0409/JD 91.01).

#### Paratypes

Specimen on Pl. 1, Fig. 25, 31 (ONM/HS 0409/JD 107.12, ONM/HS 0409/JD 103.02).

#### Material and Depository reference

12 specimens from the Jédidi section; thin sections and references: ONM/HS0409/JD91.01–02, ONM/HS0409/JD 95.02–03, ONM/HS0409/JD103.01–02 and ONM/HS0409/JD107.11–16.

#### Etymology

The species name is chosen in memory of Gérard Le Hégarat, a former palaeontologist and stratigrapher from the Claude Bernard University of Lyon (France), specialist of ammonites and calpionellids of the Jurassic–Cretaceous boundary and particularly Berriasian markers.

#### Diagnosis

Fairly isometric bell shaped to polygonal lorica with parallel lateral edges. The oblique section of *Ch. hegarati* is spheroid to slightly elongated ( $L = 40\text{--}60\ \mu\text{m}$ ,  $l = 30\text{--}40\ \mu\text{m}$ ;  $L/l = 1.3\text{--}1.5$ ). Conical aboral pole terminating in a caudal appendage (rounded in oblique sections). Large oral opening surrounded by a collar outwardly deflected in its distal extremity, its lower part being small and cylindroid with a small preoral constriction. Parallel to fairly rounded lateral flanks converge to the oral part through a “shoulder”-like structure. For axial sections,  $L = 50\text{--}65\ \mu\text{m}$ ,  $l = 38\text{--}43\ \mu\text{m}$ ;  $L/l = 1.2\text{--}1.5$  and the maximum width can be measured by the middle of the lorica. Measurements of the holotype:  $L = 57\ \mu\text{m}$ ,  $l = 39\ \mu\text{m}$ ;  $L/l = 1.46$ .

#### Type locality

The Jédidi section (Mejez el Bebb area, NW Tunisia).

#### Type level

Beds JD 91, JD95, JD 103 and JD 107 of the Jédidi section, lower Boneti Subzone (Chitinoïdella Zone).

#### Differentiation

*Ch. hegarati* is different from *Ch. carthagensis* in the following traits: isometric bowl, subparallel lorica flanks and characteristic preoral constriction. The maximum width of *Ch. hegarati* can be measured at the middle of the bowl,

whereas that of *Ch. carthagensis* can be taken just below the collar. Compared to *Ch. hegarati*, *Ch. boneti* has rather rounded bowl flanks devoid of the preoral constriction. *Daciella banatica* has a smaller size and a narrower aboral pole terminating in a longer caudal appendage.

Specimens of *Ch. hegarati* sp. nov. are morphologically close to some published forms referred to as *Ch. boneti* (see synonymy list). We consider that *Chitinoïdella boneti* includes specimens with rounded edges of the bowl and a conical aboral pole and a suddenly outward deflected collar without a constriction (see Plate 1, Fig. 34 of this work). These new forms are perfect homeomorphs of a microgranular nature for “*Tintinopsella*” *remanei* Borza which appears just above, in the lower part of the calpionellid Crassicollaria zone.

#### Age

Upper Tithonian, lower Boneti Subzone (Chitinoïdella zone).

#### 4.2. Species first documented in Tunisia

The species first documented in Tunisia are briefly described below with a particular focus on their synthetic range considering other published data from the Carpathians.

#### Genus *Chitinoïdella* Doben, 1963

#### *Chitinoïdella* cf. *elongata* Pop, 1997

(Plate 1, Fig. 34)

1969 *Chitinoïdella boneti* Doben–Borza, pl. LXVIII, fig. 8

1997 *Chitinoïdella elongata*–Pop, fig. 1: 2, 2 Photos 3–4.

2002 *Chitinoïdella elongata*–Reháková, p. 2, fig. 5–8

#### Description

Cylindroid lorica showing a conical aboral pole marked by a caudal appendage. Large oral pole bounded by an outwardly deflected collar directly attached to the preoral opening. Measured at the lower third of the lorica, the maximum width is  $l = 39\ \mu\text{m}$  with a length of  $L = 82\ \mu\text{m}$ ;  $L/l = 2.1$ .

#### Age

Upper Tithonian, upper Boneti Subzone (Chitinoïdella Zone) to lower Remanei Subzone (Crassicollaria Zone of calpionellids).

#### *Chitinoïdella boneti* Doben Trejo, 1963

(Plate 1, Fig. 24)

This species was already mentioned from Tunisia, its first figuration is due to Boughdiri et al. (2006). Its synonymy listed below includes only important references where one can find more exhaustive data.

1963 *Chitinoïdella boneti* n.sp.- Doben, p. 42, pl. 6, figs. 1–5

1965 *Tintinnopsella carpathica* (Murgeanu et Filipescu) - Furrázola-Bermúdez, pl. 4, fig. 2

1969 *Chitinoïdella boneti* Doben - Borza, p. 78, pl. 67, figs. 3–16; pl. 68, figs. 1–13

1975 *Tintinnopsella carpathica* (Murgeanu et Filipescu) - Trejo, pl. XII, fig. 34



- 1985 *Chitinoidea boneti* Doben - Remane, p. 564, fig. 13.  
 1989 *Chitinoidea boneti* Doben - Cecca et al., p. 114, pl. 6, fig. 1, 2, 4, 6, 7  
 1993 *Chitinoidea boneti* Doben - Lakova, pl. I, figs. 7–8  
 1995 *Chitinoidea boneti* Doben - Reháková, pl. I, figs. 6–7  
 1995 *Chitinoidea boneti* Doben - Oloriz et al., pl. I, fig. 3  
 1997 *Chitinoidea boneti* Doben - Grün et Blau, p. 208, pl. I, fig. 7  
 1998 *Chitinoidea boneti* Doben - Pop, pl. I, fig. 3  
 2002 *Chitinoidea boneti* Doben - Reháková, p. 370, fig. 2. 1–4  
 2006 *Chitinoidea boneti* Doben - Boughdiri et al. fig. 4. 1–2  
 2007 *Chitinoidea boneti* Doben - Gloria et al., pl. I, figs. 3–5.

#### Diagnosis

*Chitinoidea boneti* shows a bell-shaped test, with a large oral opening crowned by a deflected collar and a pointed aboral pole. The rounded lorica converges on the oral opening via a well-marked preoral constriction. Commonly, dimensions are 55–83 µm in length and 40–50 µm in width with a L/l ratio smaller than 1,5.

#### Age

Upper Tithonian, Boneti Subzone (Chitinoidea Zone).

#### Occurrence

The Jedidi and Chaabane sections (Mejez el Beb area, NW Tunisia).

#### *Chitinoidea* sp. 1

(Plate 1, Fig. 35)

Cylindroid to spindle-shaped lorica with a conical aboral extremity ending with a sharp caudal appendage. Preoral opening narrow to moderately large surrounded by an outwardly deflected arched collar. The bowl of this species is morphologically close to that of the Berriasian calpionellid genera *Calpionellopsis* and some specimens of *Tintinnopsella oblonga*. Measurements of the figured specimen: L= 68 µm, l= 38 µm; L/l= 1,79.

#### Age

Upper Tithonian, Upper Boneti Subzone (Chitinoidea Zone).

#### *Chitinoidea* sp. 2

(Plate 1, Fig. 36)

#### Description

Spheroidal to slightly elongated lorica with a rounded aboral pole. Medium-sized oral opening with an arched and outwardly deflected collar. This is directly attached to the lorica without any intermediate cylindrical lower part. Measurements of the figured specimen: L= 50 µm, l= 40 µm; L/l= 1,25.

#### Differentiation

This form can be distinguished from *Ch. elongata* by its narrower oral opening its arched collar and the maximum of its width that can be measured in the middle part of the bowl.

#### Age

Upper Tithonian, Upper Boneti Subzone (Chitinoidea Zone).

#### Genus *Borziella* Pop, 1997

#### *Borziella slovenica* (Borza, 1969)

(Plate 1, Figs. 20 and 21)

- 1969 *Chitinoidea slovenica*–Borza, pl. LXVI, fig. 8–9  
 1993 *Chitinoidea slovenica* Borza–Lakova, pl. I, fig. 2  
 1995 *Chitinoidea slovenica* Borza–Reháková, pl. I, fig. 3  
 1995 *Chitinoidea slovenica*–Benzaggagh and Atrops, pl. 4, fig. 4  
 1997 *Borziella slovenica* (Borza)–Pop, fig. 2, Photos 14 and 15  
 1998 *Borziella slovenica* (Borza)–Pop, pl. I, fig. 16 and 17  
 2000 *Chitinoidea slovenica* (Borza)–Benzaggagh, pl. 5, fig. 3.  
 2002 *Borziella slovenica* (Borza)–Reháková, fig. 2: 9–12  
 2007 *Borziella slovenica* (Borza)–Andreini et al., pl. I, fig. 1

#### Description

Spheroidal to ovoidal lorica with a rounded aboral pole. The preoral part is bounded by an outwardly deflected collar close to a slight constriction L= 43 µm, l= 28 µm; L/l= 1,5.

#### Age

Lower-to-Upper Tithonian transition, Chitinoidea Zone.

#### Genus *Popiella* Reháková, 2002

#### *Popiella oblongata* Reháková

(Plate 1, Fig. 22)

- 1998 *Daciella svinitensis*–Pop, fig. 2, Photo 19  
 2002 *Popiella oblongata*–Reháková, p. 372, fig. 4: 10–12

#### Description

Two specimens of elongated cylindrical lorica with a rounded aboral pole. The oral part, as wide as the lorica bowl (l= 36 µm), does not display a collar. The total height is L= 64 µm with a L/l ratio = 1,8.

#### Age

Lower-to-Upper Tithonian transition, upper Dobeni Subzone (Chitinoidea Zone)–Praetintinnopsella Zone.

#### Genus *Dobeniella* Pop, 1997

#### *Dobeniella cubensis* (Furrazola-Bermúdez, 1965)

(Plate 1, Figs. 7–10)

- 1965 *Tintinnopsella cubensis*–Furrazola-Bermúdez, pl. 1, fig. 1a–c; pl. 2, figs. 1–5; pl. 5, fig. 1  
 1966 *Chitinoidea cubensis* (Furrazola-Bermúdez)–Borza, pl. X, fig. 10  
 1969 *Chitinoidea cubensis* (Furrazola-Bermúdez)–Borza, pl. XIX, fig. 4  
 1995 *Chitinoidea cubensis* (Furrazola-Bermúdez)–Reháková, pl. I, fig. 10

1995 *Chitinoidea cubensis* (Furrazola-Bermúdez)–Benzaggagh et Atrops, fig. 4. 8

1997 *Dobeniella cubensis* (Furrazola-Bermúdez)–Pop, fig. 2, Photos 5–6.

1998b *Dobeniella cubensis* (Furrazola-Bermúdez)–Pop, pl. I, fig. 27–29.

2002 *Dobeniella cubensis* (Furrazola-Bermúdez)–Reháková, p. 372, fig. 3: 4–6

2007 *Dobeniella cubensis* (Furrazola-Bermúdez)–Andreini et al., pl. I, fig. 8.

#### Remark

Two specimen groups of different sizes are observed within *Dobeniella* species described below. Smaller representatives are interpreted here as juvenile forms.

#### Description

Ovoid to elongated lorica with a conical aboral extremity terminating in a long caudal appendage in axial sections. Large preoral opening surrounded by a composite collar formed by an inner annular part (circular in section) and a straight and outwardly deflected one.

Measurements: small specimens: L = 42 µm, l = 29 µm; L/l = 1,45; big specimens: L = 57 µm, l = 39 µm; L/l = 1,47.

#### Age

Lower-to-Upper Tithonian transition, upper Dobeni Subzone (Chitinoidea Zone)-lower Praetintinnopsella Zone.

#### *Dobeniella bermudezi* (Furrazola-Bermúdez, 1965) (Plate 1, Figs. 11–13)

1965 *Tintinnopsella bermudezi*–Furrazola-Bermúdez, pl. 1, fig. 2a–c; pl. 2, fig. 6, 8; pl. 3, fig. 1; pl. 5, fig. 2

1966 *Chitinoidea bermudezi* (Furrazola-Bermúdez)–Borza, pl. X, fig. 11

1969 *Chitinoidea bermudezi* (Furrazola-Bermúdez)–Borza, pl. XIX, fig. 1–2

1995 *Chitinoidea bermudezi* (Furrazola-Bermúdez)–Reháková, pl. I, fig. 10

non 1995 *Chitinoidea bermudezi* (Furrazola-Bermúdez)–Benzaggagh and Atrops, fig. 4:7 (= *Ch. hegarati* nov. sp.)

1998 *Dobeniella bermudezi* (Furrazola-Bermúdez)–Pop, pl. I, fig. 22–24

non 2000 *Dobeniella bermudezi* (Furrazola-Bermúdez)–Benzaggagh, pl. 5, fig. 7 (= *Ch. hegarati* nov. sp.)

2002 *Dobeniella bermudezi* (Furrazola-Bermúdez)–Reháková, fig. 3: 7–9

2007 *Dobeniella bermudezi* (Furrazola-Bermúdez)–Andreini et al., pl. I, fig. 6–7

#### Description

Bell-shaped to elongated lorica with a conical aboral pole terminating in a short caudal appendage. The large preoral part is followed by an elongated composite collar. The external part is short and cylindrical at the base and outwardly deflected near the oral aperture. The annular internal piece is lenticular and sharp.

Measurements: small specimens: L = 42 µm, l = 29 µm; L/l = 1,45; big specimens: L = 57 µm, l = 39 µm; L/l = 1,47.

#### Age

Lower-to-Upper Tithonian transition, upper Dobeni Subzone (Chitinoidea Zone)-lower Praetintinnopsella Zone.

#### *Dobeniella tithonica* (Borza, 1966) (Plate 1, Figs. 3–6)

1966 *Chitinoidea tithonica*–Borza, pl. LXVII, figs. 1–2

1977 *Chitinoidea* cf. *tithonica* Borza–Grandesso pl. II, fig. 7

1990 *Chitinoidea tithonica* Borza–Michalík et al., pl. 3, fig. 1

1993 *Chitinoidea tithonica* Borza–Lakova, pl. I, fig. 3

1995 *Chitinoidea tithonica* Borza–Reháková, pl. I, fig. 5 non 1995 *Chitinoidea tithonica* Borza–Benzaggagh et Atrops, fig. 4–5 (= *Borziella* aff. *Slovenica*)

1997 *Dobeniella tithonica* (Borza)–Pop, fig. 2: 9

1998b *Chitinoidea tithonica* (Borza)–Pop, pl. I, fig. 25–26

2000 *Chitinoidea tithonica* (Borza)–Benzaggagh, pl. 5, fig. 4

2002 *Chitinoidea tithonica* (Borza)–Reháková, fig. 3: 10–12

#### Description

Bell shaped lorica with a conical aboral pole terminating in a long caudal appendage (new character). The walls of the bowl are subparallel with fairly straight edges that converge on the preoral part through a “shoulder”-like feature. The preoral opening is attached to a cylindrical lower part of the collar of which the upper part is composite and made of two pieces: an inner annular one lodging on the end of the cylindrical structure and an external piece outwardly deflected, arched and lens-like in section. Measurements: small specimens: L = 37 µm, l = 29 µm; L/l = 1,28; big specimens: L = 57 µm, l = 43 µm; L/l = 1,32.

#### Age

Lower-to-Upper Tithonian transition, upper Dobeni Subzone (Chitinoidea Zone)-lower Praetintinnopsella Zone.

#### *Dobeniella colomi* (Borza, 1966) (Plate 1, Figs. 14–16)

1966 *Chitinoidea colomi*–Borza, pl. X, fig. 4–7

1995 *Chitinoidea colomi* Borza–Reháková, pl. I, fig. 4

1995 *Chitinoidea colomi* Borza–Benzaggagh et Atrops, fig. 4: 3

1997 *Dobeniella tithonica* (Borza)–Pop, fig. 2: 9

2000 *Chitinoidea colomi* (Borza)–Benzaggagh, pl. 5, fig. 2

2002 *Dobeniella colomi* (Borza)–Reháková, fig. 4: 1–3

#### Description

Bell-shaped lorica with a conical aboral pole terminating in a long caudal appendage (new character). Large preoral part followed part by a subcylindrical collar, the

wall of which is notably thickened at the distal extremity marking an annular piece (circular in section) surrounding the wide oral aperture. Measurements:  $L=45\ \mu\text{m}$ ,  $l=29\ \mu\text{m}$ ;  $L/l=1.7$ .

#### Age

Lower-to-Upper Tithonian transition, upper Dobeni Subzone (Chitinoidea Zone)–lower Praetintinnopsella Zone.

#### Genus *Longicollaria* Pop, 1997

##### *Longicollaria dobeni* (Borza, 1966)

(Plate 1, Figs. 1–2)

1966 *Chitinoidea dobeni*–Borza, pl. IX, fig. 1–2

1993 *Chitinoidea dobeni* Borza–Lakova, pl. I, fig. 5–6

1995 *Chitinoidea dobeni* Borza–Reháková, pl. I, fig. 2

1997 *Chitinoidea dobeni* (Borza)–Pop, fig. 2: 12–13

1998 *Longicollaria dobeni* (Borza)–Pop, pl. I, fig. 1–4

2002 *Longicollaria dobeni* (Borza)–Reháková, fig. 4: 1–3

2007 *Longicollaria dobeni* (Borza)–Andreini et al., pl. I, fig. 2

#### Description

Elongated ovoid lorica with a conical aboral pole terminating in a sharp and comparatively long caudal appendage in axial sections. A slight constriction in the preoral segment is followed by a subcylindrical collar thickened at the distal end. The length of the collar and that of the bowl are comparable.

Measurements: small specimens:  $L=37\ \mu\text{m}$ ,  
 $l=29\ \mu\text{m}$ ;  $L/l=1.28$ ; big specimens:  $L=57\ \mu\text{m}$ ,  
 $l=43\ \mu\text{m}$ ;  $L/l=1.32$ .

#### Age

Lower-to-Upper Tithonian transition, Chitinoidea Zone–lowermost Praetintinnopsella Zone.

#### Genus: *Daciella* Pop, 1998

##### *Daciella svinitensis* Pop, 1998

(Plate 1, Fig. 19)

1998 *Daciella svinitensis*–Pop, fig. 2: 19–20

2002 *Daciella svinitensis* Pop–Reháková, fig. 3: 1–3.

#### Description

Cylindrical elongated lorica of a single specimen with a conical aboral pole terminating in a caudal appendage. Large oral pole surrounded by a cylindrical short collar at the distal part of which a thickening of the wall is characteristic. Measurements:  $L=43\ \mu\text{m}$ ,  $l=22\ \mu\text{m}$ ;  $L/l=1.9$ .

#### Age

Upper-to-Lower Tithonian transition, Chitinoidea Zone–lowermost Praetintinnopsella Zone

#### *Daciella danubica* Pop, 1998

(Plate 1, Fig. 17)

1969 *Chitinoidea* sp.–Borza, pl. LXIX, fig. 4

1998 *Daciella danubica*–Pop, fig. 2, fig. 14–18

2002 *Daciella danubica* Pop–Reháková, fig. 2: 17–20.

#### Description

Conical to ovoid lorica with an aboral pole ended with a caudal appendage. Large preoral opening characterized by a wall thickening and a shoulder-like feature where a cylindrical collar is attached. Measurements:  $L=39\ \mu\text{m}$ ,  $l=27\ \mu\text{m}$ ;  $L/l=1.44$

#### Age

Upper-to-Lower Tithonian transition, Chitinoidea Zone–lowermost Praetintinnopsella Zone.

#### Genus: *Cubanella* Pop, 1998

##### *Cubanella cristobalensis* (Furrazola-Bermúdez), 1965

(Plate 1, Fig. 23)

1965 *Calpionella cristobalensis*–Furrazola-Bermúdez, Pl. 1, fig. 3a–c; pl. 3, fig. 5–8; pl. 5, fig. 3

1966 *Chitinoidea cristobalensis* (Furrazola-Bermúdez)–Borza, pl. X, fig. 12

1977 *Chitinoidea cristobalensis* (Furrazola-Bermúdez)–Grandesso, pl. II, fig. 6

non 1995 *Chitinoidea* aff. *cristobalensis* (Furrazola-Bermúdez)–Benzaggagh and Atrops, fig. 4: 9 (= *Ch. gr. boneti*)

1997 *Cubanella cristobalensis* (Furrazola-Bermúdez)–Pop, fig. 1: 6; fig. 2: 10–11.

#### Description

Elongated lorica with an ovoid to conical bowl. This is made of an ovoid upper part and a conical aboral extremity terminating in a long caudal appendage. Moderate to large preoral opening surrounded by a subcylindrical simple collar.

Measurements:  $L=79\ \mu\text{m}$ ,  $l=36\ \mu\text{m}$ ;  $L/l=2.19$

#### Age

Upper-to-Lower Tithonian transition, upper Dobeni Subzone (Chitinoidea Zone)–lowermost Praetintinnopsella Zone.

## 5. Phyletic approach and discussions

Pop (1998a) discussed the details of the chitinoideid evolution during the Lower-Upper Tithonian transition and proposed several phyletic lineages relating chitinoideids and calpionellids. Reháková (2002, fig. 5) presented the stratigraphic distribution and possible lineages in the evolution of chitinoideids where evolutionary trends were discussed at the species level. In continuation of these works, published biostratigraphic and palaeontological data from the Carpathians complemented by those presented here allow us to rethink the potential phyletic relationships among these microbiomarkers (Fig. 3).

The phylogenetic history of chitinoideids starts from their high diversity as old as the uppermost lower Tithonian (upper Fallauxi Zone of ammonites); their ancestors are still uncertain.

Within this interval, two main groups characterize the lower part of the Dobeni Subzone: the genus *Daciella* and the assemblage composed of *Carpathella rumanica*, *Borziella slovenica* and *Longicollaria insueta* (= group II). Both groups display common characters with *L. dobeni*, the oldest species of the Chitinoidea Zone. These characters

consist of the conical aboral pole for *Daciella* and the simple collar surrounding the lorica bowl for group II. This leads us to consider, as already stated by Reháková (2002), *L. dobeni* as a possible common ancestor. In addition, this same pioneer species could have given rise to *Daciella svinitensis* and *D. danubica*, a first phyletic datum marking the lowermost part of the Dobeni Subzone.

Higher within this subzone, *Daciella banatica* and *D. almajica* Pop could have derived from *D. danubica*, which shows the same general morphology but differs in size as well as the outwardly deflected distal part of the collar. *D. danubica* could have given rise to *Cubanella cristobalensis*, which displays the same cylindrical collar and conical aboral pole terminating in a comparatively long caudal appendage. In contrast to the hypothesis of Reháková (2002), all the *Dobeniella* species, which appear at the same stratigraphic level (upper part of the Dobeni Subzone), could have been derived from *L. dobeni*, which is characterized by the thickened distal end of the collar also observed among the *Dobeniella colomi* representatives. This thickening characteristic feature can be considered a primitive character that would have been detached to evolve into the inner annular part of the composite collar of *Dobeniella bermudezi*, *D. cubensis* and *D. tithonica*. These lineages do not fit the phyletic scheme proposed by Benzaggagh and Atrops (1995, fig. 1–3), who admitted that “*Chitinoidea slovenica*” is a common ancestor for “*Ch.*” *dobeni*, “*Ch.*” *colomi* and “*Ch.*” *tithonioca* and also stated that “*Ch.*” *slovenica* gave rise to “*Ch.*” *bermudezi*, “*Ch.*” *boneti*, “*Ch.*” *cubensis* and “*Ch.*” *cristobalensis*. In fact, our different interpretation is supported by the different Chitinoideid range charts. For example, as observed in the Carpathians and confirmed in Northern Tunisia, the FO of *Dobeniella bermudezi*, *D. cubensis* and *Cubanella cristobalensis* marks the upper part of the Dobeni Subzone and not the Boneti Subzone as obtained by Benzaggagh and Atrops (1995) in the Moroccan Prerif.

We also agree with Reháková (2002) that *Longicollaria insueta* of our group II exhibits many common characters with *Popiella oblongata*, which is interpreted as its direct descendant.

At the base of the Boneti Subzone, a phyletic lineage could have linked *Borziella slovenica* to the *Chitinoidea boneti* group as well as the new species *Chitinoidea hegarati* and *Chitinoidea carthagensis*. In fact, these forms share many characters such as the isometric to slightly elongated bowl, some dimensional characters and the outwardly deflected collar with a more or less marked swelling at its base.

In the upper part of the Boneti Zone, *Ch. boneti* representatives display tight affinities with *Ch. elongata* and *Ch. popi* sp. nov. which differ in their elongated bowl and the aspect of the collar deflection. These species would have been derived from *Ch. boneti* by a cladogenetic process.

As far as the relationships between Chitinoideids and Calpionellids are concerned, we retain the same idea formulated by Reháková and Michalik (1997), Pop (1998a) and Reháková (2002), who stated that many chitinoideid species are perfect homeomorphs of calpionellid ones

and differ only in the features of the lorica. Across the Lower-Upper Tithonian boundary, the same evolutionary pattern may have concerned *Ch. popi* sp. nov. as a direct ancestor of *Preatintinnopsella andusovi* and *Tintinnopsella carpathica*. In fact, apart from their lorica, the degree of similarity between these species is particularly high. Similarly, only the lorica distinguishes oblique sections of *Chitinoidea hegarati* sp. nov (see Plate 1, fig. 25) from “*Tintinnopsella remanei*”, the index species of the lowermost calpionellid Subzone. Furthermore, the tight affinities between the same *Ch. popi* and *Ch. carthagensis*, on one hand, and *Remaniella* species of the Lower Berriasian, on the other, is also worth underlining.

## 6. Conclusion

Previous studies of Chitinoideid faunas from the South-Tethyan regions of Maghreb dealt only with scarce and unrevised taxa from the Prerif (Morocco) or sporadic representatives from disparate sections of Tunisia. The Chitinoideid faunas studied here include the most diversified assemblages of Maghreb, including a great majority of taxa described in the North-Tethyan areas. In view of the important number of new species recently introduced from the Carpathians, we present here three new *Chitinoidea* species and fifteen other morphotypes included in five genera. Their range is very comparable to that obtained in the Carpathian Range and the established biozonation fits the standards currently in use for the whole Tethyan Realm. Although the proposed phyletic approach needs to be completed, it nevertheless offers potential lineages at the species level where evolutionary data are well placed within the *Chitinoidea* Zone and can serve as biostratigraphic markers. Future works may be focused on the taxonomy of the *Preatintinnopsella* group so far restricted to the unique *P. andrusovi* species. Its stratigraphic range is around the LO of Chitinoideids and the FO of Calpionellids, which leads us to consider the detailed analysis of its phyletic relationships with these groups of great relevance. In fact, the evolution of chitinoideids, semichitinoideids and calpionellids across the Jurassic-Cretaceous boundary shows phylogenetic characteristics which are of great interest for solid long distance correlations.

## Acknowledgments

We sincerely thank an anonymous reviewer, Prof. Daniela Reháková from the University of Bratislava (Slovakia) and the editorial board of the C. R. Palevol, who greatly improved a first draft of this paper. Particular thanks can be addressed to M. Benzaggagh of the University of Meknès, the third referee with whom we did not share his opinion, but respect special aspects of calpionellid palaeontology and stratigraphy.

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