

# Remarks on relative phenotype stability in two Tithonian ammonite species first described from the Tunisian Dorsale – a preliminary approach to interpreting metapopulation dynamics in ammonites

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With 4 figures

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**Abstract:** Two rare ammonite species are recorded and illustrated for the first time from the Tithonian of Tunisia: *Simocosmoceras* cf. *adversum* (OPPEL) and *Micracanthoceras* (*Corongoceras*) *symbolum carthaginoustensis* n. subsp. These records are interpreted in the ecological context of metapopulation dynamics.

**Zusammenfassung:** Zwei seltene Ammonitenarten werden erstmals aus dem Tithonium von Tunesien beschrieben und abgebildet: *Simocosmoceras* cf. *adversum* (OPPEL) and *Micracanthoceras* (*Corongoceras*) *symbolum carthaginoustensis* n. subsp. Das Vorkommen dieser Taxa wird im ökologischen Zusammenhang mit der Dynamik von Metapopulationen zu erklären versucht.

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## 1. Introduction

Pioneer approaches to Upper Jurassic stratigraphy in the Tunisian Dorsale and nearby areas were made during the later 19<sup>th</sup> century and the first two decades of the 20<sup>th</sup> century, even with mentioning of ammonite species (e.g., KOBELT 1885; BLANCKENHORN 1888; ROLLAND 1888; AUBERT 1892; BALTZER 1893; CANAVARAI 1893; PERVINQUIÈRE 1903, 1907; DE STEFANI 1907; GENTIL 1924). The first Upper Jurassic ammonite biozonation for the Tunisian Dorsale was presented by SOLIGNAC (1927) who identified ammo-

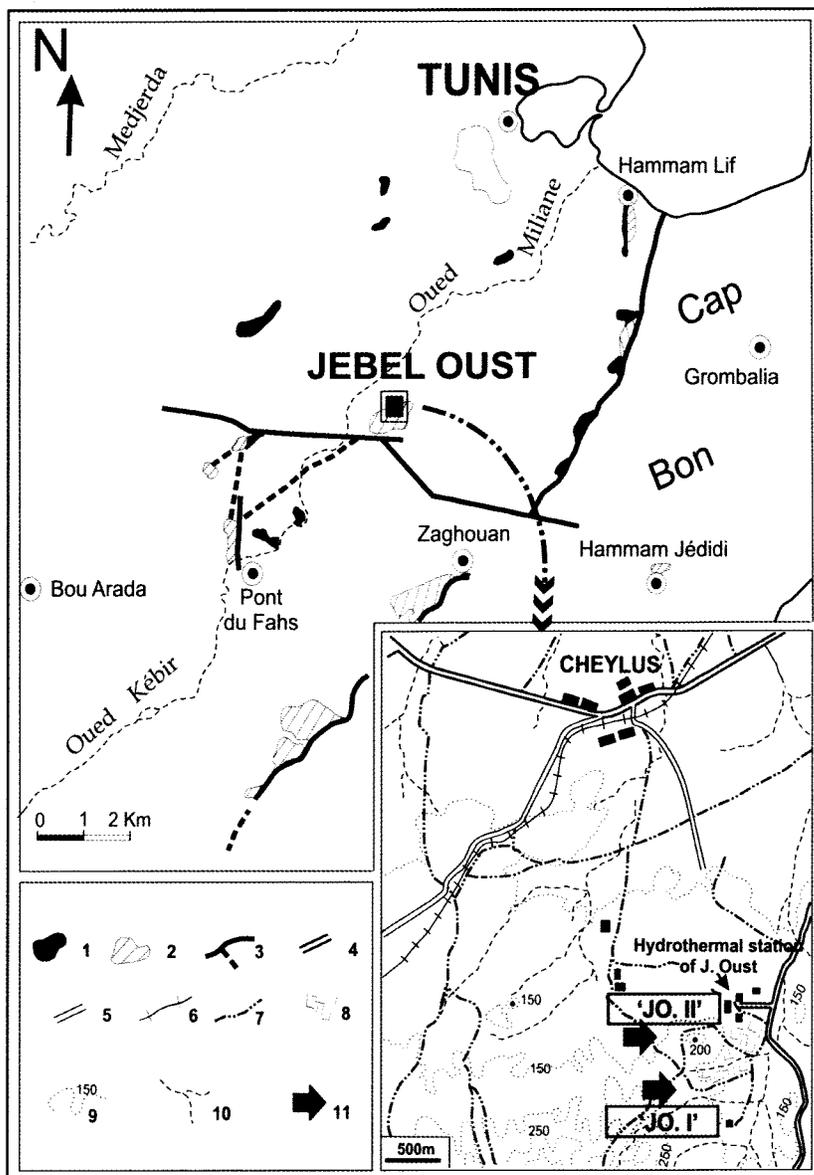
nites presently interpreted as informative for characterizing Oxfordian – Berriasian deposits. Biostratigraphical units at the ammonite biozonal level were formally proposed in the middle of the past century (e.g., CASTANY 1951, 1955), and the second half of the 20<sup>th</sup> century was the time for the improvement of micro- and macrofossil biostratigraphy (e.g., COLOM et al. 1953; BISMUT et al. 1967; MEMMI 1967; BONNEFOUS 1972; BUSNARDO & MEMMI 1972; MEMMI & MAAMOURI 1974; THIBIEROZ, 1974; DONZE et al. 1975; MEMMI & SALAJ 1975; COMBÉMOREL et al. 1985; BALUSSEAU & CARIOU 1982; BOUGHDIRI 1994; ENAY et al. 1999; BOUGHDIRI et al. 1999; SOUSSI et al. 1999).

Most recently, two papers contributed to updated biostratigraphy in the Tunisian Dorsale and nearby areas. ENAY et al. (2005) focused on ammonite assemblages of the Kimmeridgian/Tithonian boundary and their precise comparison with Algerian and Sicilian records. BOUGHDIRI et al. (2005) reported fossil assemblages collected from the Jebel Oust area for updating Upper Jurassic – lowermost Cretaceous ammonite and calpionellid biostratigraphy in the Tunisian Dorsale (NE Tunisia), and provided the first biozonal stratigraphy in upper Kimmeridgian and Tithonian limestone/marl sections, proving fossil assemblages to be typically Tethyan.

## **2. Remarks on the Jurassic of the Djebel Oust and stratigraphic location of the ammonites described**

The Djebel Oust is a ca. 400 m high mountain located south-westwards from the town of Tunis (Fig. 1). Close to the hydrothermal station of the Djebel Oust and related to a significant E-W fault-trend, Jurassic deposits crop out. Lower Jurassic limestones show unconformable contact with Middle Jurassic limestones and marls, which in turn underlie Kimmeridgian and Tithonian deposits. The latter crop out and have been investigated in the northern slope of the Djebel Oust where they dip 30–40°N. The studied sections JO.I and JO.II are located in the northeastern flank of the range [Section JO.I from A 36°31.77'N, 010°03.76'E to B 36°31.88'N, 010°03.83'E; and Section JO.II: from A' 36°32.02'N, 010°03.64'E to B' 36°32.04'N, 010°03.60'E].

Upper Jurassic lithological succession and fossiliferous horizons in section 'JO.I' are shown in Fig. 2. They are mainly made of light-brown to grey limestone with centimetre- to, exceptionally, metre-thick marly intercalations. A single, 60–65 cm thick bed underlies well-bedded limestone packages, which show bed-thickness frequency succession as follow: 10–15 cm and less than 10 cm (29 and 20 beds, respectively), 20 cm (16 beds), 22–25 cm and 40 cm (8 beds), and 30–35 cm (6 beds). Ferruginization and irregular to undulated top-surface of beds are common, and cases of pinching-out limestone horizons within marly intervals exist. Reddish coloration



**Fig. 1.** Location of the Djebel Oust and the sections studied in the Tunisian Dorsale. Triassic (1), Jurassic outcrops (2), fault (3), managed road (4), track (5), railway (6), foot-path (7), roman ruins (8), topographic contour lines (9), river, ravine (10), and section setting (11).

occurs in marly intercalations, and it is typical upwards in the section in nodular-like, fossiliferous marly limestones and ammonitico rosso-like facies. Inner-mould and incomplete preservation made rather difficult ammonite identification at the species level, but allowed valuable information for biostratigraphy. Aptychi, mainly *Lamellaptychus*, are occasionally frequent, and other macrofossil remains belong to scarce bivalves and belemnites. Ammonite assemblages F1 to F17 identified by BOUGHDIRI et al. (2005) indicated Lower Kimmeridgian to Lower Tithonian deposits for JO.I section. In faunal assemblage F13, BOUGHDIRI et al. (2005) mentioned the occurrence of *Simocosmoceras* sp. (see below), which was the first report of this genus in northern Africa.

Section 'JO. II' is disturbed by intense faulting that induced bedding discontinuity and hence the need for identification of four subsections, although no significant change in bed-dipping was observed: (subsection A) Grey limestones and yellowish marls (10 m); (Subsection B) light-grey, yellow and reddish slightly nodular limestones with alternation of white-to-cream marly horizons (8 m); (Subsection C) thin, grey, nodular, limestones (debris flows) showing bioturbation, white-marly intercalations and occasional well-bedded, centimetre-thick, limestones (6,2 m); and (Subsection D, Fig. 2) white to light-grey marly horizons with intercalated thin limestone beds below, and slightly thicker marly horizons showing intercalation of grey nodular limestones with irregular top-surfaces (debris flows) above. Throughout subsection D, the thickness of particular limestone beds and marly horizons varies between some centimetres and 170 cm. Recent improving of sample preparation in faunal assemblage F38 of BOUGHDIRI et al. (2005) revealed the occurrence of a single specimen of *Micracanthoceras* (*Corongoceras*) *symbolum* (OPPEL) *carthaginoustensis* n.subsp. (see below).

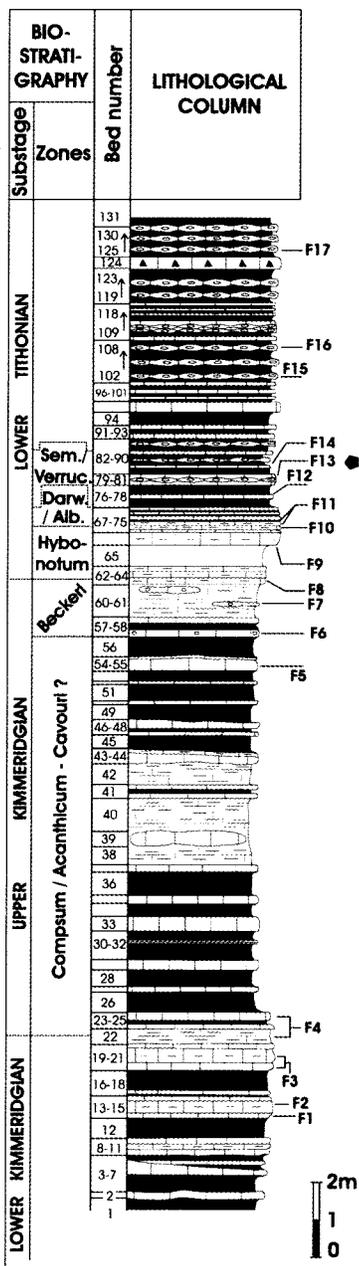
### 3. Systematic description

Superfamily	Perisphinctoidea STEINMANN in STEINMANN & DÖDERLEIN, 1890
Family	Aspidoceratidae ZITTEL, 1895
Subfamily	Aspidoceratinae ZITTEL, 1895

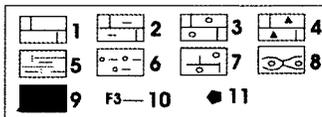
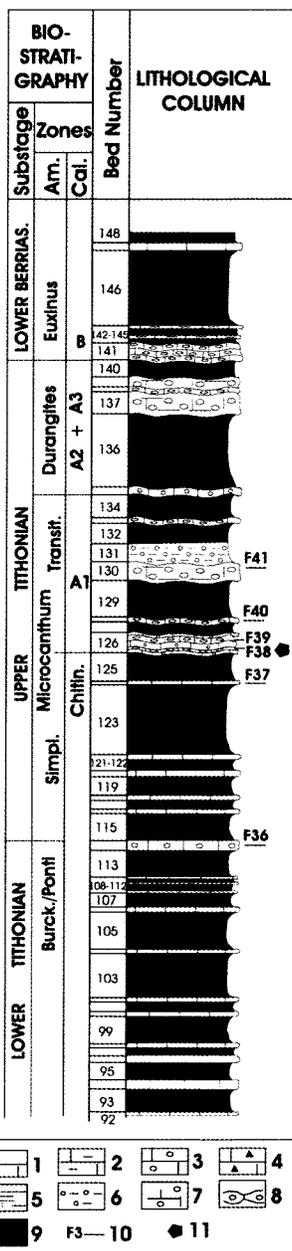


**Fig. 2.** Lithology, biostratigraphic interpretation and location of faunal assemblages in the sections where the ammonites described were collected. Limestone (1), marly limestone (2), nodular limestone (3), cherty limestone (4), calcareous marls (5), nodular bed with marly matrix and irregular bedding surfaces (6), nodular bed with calcareous matrix and irregular bedding surfaces (7), breccia (8), marly level (9), faunal assemblages (10), stratigraphic horizon for the specimens described (11).

JO. I. Section



JO. II. Section - Subsection D



Remarks: Following the most recent revision of supra-genus level interpretation of *Simocoscoceras* SPATH (VILLASEÑOR et al. 2003), the placement of this cryptic genus at the family level is an open question due to the rarity of records. However, these authors recognized that *Simocoscoceras* morphologically resembles aspidoceratid ammonites. SCHWEIGERT (1997) interpreted *Simocoscoceras* as dimorphic couple (microconch) of the aspidoceratid genus *Pseudhimalayites*, the latter ranging from the early Oxfordian to the late early Tithonian. Two basic questions arise from SCHWEIGERT's hypothesis: (i) an extremely long biostratigraphic range at the genus level, which is rarely known among Late Jurassic Ammonitina; and (ii) the interpretation of extreme phenotype expression in dimorphic couples of Aspidoceratidae, which is contradicted by data in CHECA (1985). Further research is needed for a conclusive interpretation of this cryptic genus *Simocoscoceras*.

Genus *Simocoscoceras* SPATH, 1925

*Simocoscoceras* cf. *adversum* (OPPEL)

Fig. 3

cf. 1870 *Coscoceras adversum* OPPEL in ZITTEL, p. 99, pl. 8, figs. 9-10.

Material: One fragment belonging to an inner mould.



**Fig. 3.** *Simocoscoceras* cf. *adversum* (OPPEL); body-chamber fragment of a microconchiate adult specimen (Oust-200013-1); Djebel Oust, Section JO.I, Lower Tithonian, Semiforme/Verruciferum Zone. –  $\times 3$ .

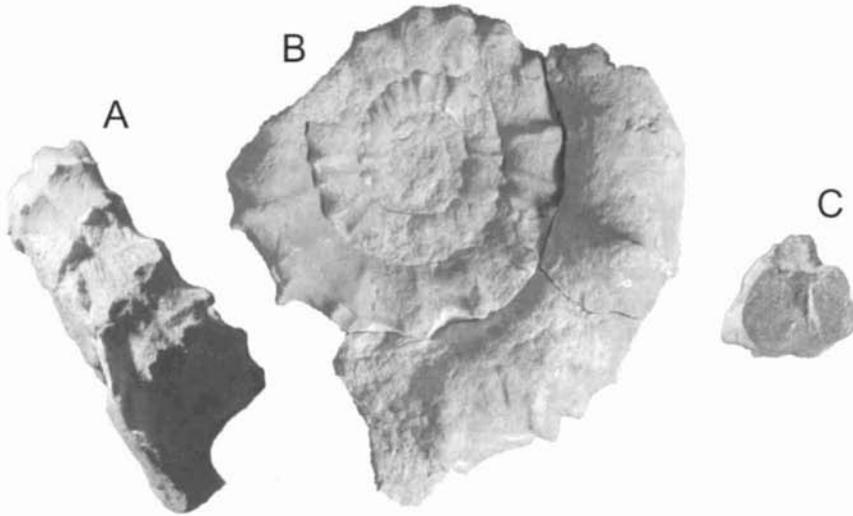
Description: The identified fragment shows the external part of the right flank of a probably mature specimen according to its shell size clearly above of 10 mm and most probably below 20 mm. Eight to nine peripheral tubercles and three mid-flank tubercles are clearly preserved, together with the typical “zigzag” ribbing in this species – i.e., two-by-two, outer ribs coalesce with a single tubercle of the row located at the mid-flank, as well as they coalesce with separate tubercles on the periphery. No rib-gemination has been observed, and no data are available about coiling degree and venter sculpture.

Comparative analysis and biochronostratigraphy: Even being a fragment, the ammonite remain described is easily interpretable at both the genus and species level. Given its particular ribbing, the unambiguous sculpture differences between *Simocoscoceras* species, the geographic area in

which was collected, and the palaeobiogeographic range admitted for *Simocoscoceras adversum* (OPPEL), the fragment described belongs unequivocally to *Simocoscoceras* and cannot be interpreted as any of densely ribbed *Simocoscoceras* species. However, incomplete preservation impedes a more conclusive interpretation within the known intra-species diversity in *Simocoscoceras adversum* (OPPEL).

Belonging to faunal assemblage F13 identified by BOUGHDIRI et al. (2005), which also contains *Pseudolissoceras* sp., *Semiformiceras* sp., and diverse phylloceratids, the age corresponds to the Early Tithonian Semi-forme/Verruciferum Chron. Extended biostratigraphical comments for the complete section are compiled in BOUGHDIRI et al. (2005).

Family Himalayitidae SPATH, 1925  
Subfamily Himalayitinae SPATH, 1931  
Genus *Micracanthoceras* SPATH, 1925  
Subgenus *Corongoceras* SPATH 1925 emend. TAVERA 1984



**Fig. 4.** A-C: *Micracanthoceras* (*Corongoceras*) *symbolum carthaginoustensis* n. subsp. **A:** ventral region slightly displaced from its location in the phragmocone. **B:** left-side view of incomplete adult showing the rear part of the body-chamber, **C:** whorl section placed at correspondence with its location in the body-chamber. All views belong to the same specimen (Oust-200035b); Djebel Oust, Section JO.II, subsection D, Upper Tithonian, *Micracanthum* Zone. – Natural size.

*Miracanthoceras (Corongoceras) symbolum carthaginoustens* nov.  
subsp. Fig. 4 A-C

Holotype: Specimen illustrated on Fig. 4A-C, no. Oust-200035b, at present housed in the palaeontological collection of the University of Granada.

Etymology: In allusion to both the old Mediterranean people that colonized North Africa in the Tunisian region, and the geographical site where the holotype was collected.

Type locality: After the Djebel Oust, southwest from Tunis.

Type horizon: Bed of the Upper Tithonian (Microcanthum Zone).

Material: One incomplete specimen preserved as an inner mould.

Measurements. In millimetres for shell diameter of reference (D); the size of the umbilicus (U); inter-tubercle whorl-width (Wd), and inter-tubercle whorl-height (Wh); number of umbilical or primary ribs per quarter-whorl (UR4); number of external or ventral ribs per quarter-whorl (ER4); number of constrictions per quarter-whorl (C); number of peripheral tubercles per quarter-whorl (T4). All these values referred to a given diameter. (\*) for approximate values.

D	U	Ww	Wh	U/D	Ww/D	Wh/D	Ww/Wh	UR4	ER4	C4	T4
80*	49	24,5	22,5	0,61*	0,31	0,28	1,1	3	4	1	3
68,2	38	22	17,5	0,56	0,32	0,25	1,25	–	–	–	–
53,5	29,9	16	14	0,56	0,30	0,26	1,14	5	9	0	5
44,5	25	15*	11,2	0,56	0,34*	0,25	1,34*	4	9	1	4
40,5	22	11*	10	0,54	0,27*	0,25	1,1*	5-6	9-10	0	5-6
27	14,3	–	7	0,53	–	0,26	–	8*	–	1	5-6
22,5*	13	–	5,6*	0,57*	–	0,25*	–	9-10	–	1-2	2-3

Description: The analyzed specimen shows slight oblique compression and better preservation of its left-side, on which detailed observations were available. The total size is slightly larger than 80 mm, and the phragmocone reaches ca. 78 mm. The specimen preserves the outer half-whorl as belonging to the rear part of the body chamber. On the assumption of body-chamber length close to 270° for the OPPEL species (TAVERA 1984), and despite final looser coiling, it seems that this specimen did not reached the final growth regardless the potential preservation of adapertural sculpture (i.e., irregular ribbing). The remaining inner mould belongs to the phragmocone, which is relatively well preserved, although the nucleus is plugged by sediment. The umbilicus is shallow (i.e., no distinct umbilical wall) and large (i.e., coiling mean-value of 0,56-57) and the whorls tangent throughout the ontogeny. Looser coiling affecting the body-chamber does not indicate, necessarily, the complete growth of the individual. The whorl-section clearly varies if considered between tubercles or in coincidence with them. Whatever the case considered, the flanks gradually diverges from the

umbilical seam to shell periphery. Inter-tubercle whorl sections are subquadrate, slightly wider than high ( $Ww/Wh \geq 1$ ). In coincidence with tubercles, whorl sections are typically trapezoidal showing maximal width in correspondence to the venter and a more accentuated divergence of flanks towards shell periphery. A distinct feature is the narrow furrow excavated in the mid-line of the venter, at least throughout the outer whorl of the phragmocone and presumably also in inner whorls. The sculpture is relatively coarse, strong throughout the ontogeny, made of ribs that bi- or trifurcate on the venter near the flank/venter boundary and, therefore, no rib-subdivision can be identified within the umbilicus. No true intercalatory ribs have been observed but rather incomplete secondary ribs that more or less gradually smoothed on the ventral region. Progressively, the points of rib-subdivision are inflated, and tuberculation increases, firstly as rounded and then spatula-like tubercles. Presumably, preserved tubercles correspond to the base of prominent spines that would be slightly separated from the flanks, since traces of them have not been identified on the inner mould. Rib crowding decreases with shell growth, especially from 25 mm onwards, when phenotype expression is distinctive, typical for this species. This sculptural trend is accentuated in the outermost phragmocone and the body-chamber, giving a particular ornamental appearance to this specimen, which represents an extreme phenotype that could be interpreted as species variety or subspecies. The ventral sculpture consists of two or three secondary ribs, the aboral one supporting lamellar-like tubercles on both sides of the ventral furrow. No ventral ribs cross the ventral furrow, and smoothing of adoral secondary elements is common in each rib-subdivision. There are one-to-three constrictions per whorl, all of which being parallel to ribbing and showing a prominent adoral edge. No data exist about peristomal structures.

**Comparative analysis and biochronostratigraphy:** According to TAVERA (1984), the OPPEL species *symbolum* has large phenotype variability in shell sculpture, lesser in coiling and whorl-shape, and shows middle and outer whorls with low-crowded ribs. At present, there is inconclusive interpretation of its relationships with morphologically close "species" proposed by TAVERA (1984) from the Betic Cordillera (Southern Spain), such as *leanzai* and *ornatum*, which show coarse and widely separate ribs. In fact, when dealing with the envisaged as high-variable species *symbolum*, this author only identified gradual or secondary differences among these ammonites. In addition, the interpretation of some of the smaller "species" he described, such as *minor*, might be revisited. Such an uncertainty inserts in the unfavourable, and difficult to improve, context of never-complete sampling of "contemporaneous" ammonites (i.e., age-equivalent specimens according to biostratigraphical resolution) showing phenotype discontinuity; and difficulty increases especially when sculpture was coarse. All of this

points to an old problem: how much “species” per biohorizon? In fact, we agree with the valuable, lumping approach made by TAVERA (1984; i.e., lumping of nomenclatural, existing species), but his interpretation of Upper Tithonian himalayitids must be considered preliminary, at least in the cases mentioned (see also below).

CECCA (1985) studied a single specimen from Monte Lacerone (Central Apennines), the preservation of which largely impeded its precise description. This Author interpreted the specimen as *Corongoceras symbolum* (OPPEL). As far as a comparative analysis is possible, this Apulian specimen looks clearly different from the Tunisian specimen described, but its inclusion within the morphological plexus of *symbolum* OPPEL – *ornatum* TAVERA – *leanzai* TAVERA can be accepted (see above).

The specimen morphologically closest to the Tunisian one described was depicted by ZITTEL (1870, pl. 16, fig. 7a), but his illustration only shows a very incomplete fragment of the phragmocone. Concerning the hypothetical occurrence of morphologically similar specimens with very distant, spaced ribs in Stramberk (ZITTEL 1870) and Tunisia (this paper), there are two potential interpretations – i.e., they could be local phenotypes or not. In the first case, they would be geographic variants or subspecies, true subspecies restricted to still poorly delimited areas in the western-central Tethys but unknown from other inhabited areas eastwards (e.g. Madagascar). In the second case, they would show a particular morphology within the biogeographical range of the species – i.e., particular phenotypes without geographical restriction. On the basis of both the wide range envisaged for *Micracanthoceras* (*Corongoceras*) *symbolum* (OPPEL) by TAVERA (1984) and the information available, the two hypotheses are feasible. In order to reinforce the recognition and significance of distinct phenotypes, and to adapt the interpretation to ICZN guidelines, we favour the interpretation at the subspecies level assuming the known, larger biogeographical range for the whole species.

Belonging to faunal assemblage F38 identified by BOUGHDIRI et al. (2005), which also contains *Micracanthoceras microcanthum* (OPPEL) cf. morphotype C of TAVERA, *Aulacosphinctes* sp. gr. *sulcatus* TAVERA, *Aulacosphinctes* sp., diverse phylloceratids and loose himalayitids, together with the first occurrence of true hyaline tintinnoids (i.e., calpionellids), the age corresponds to the Late Tithonian, Microcanthum Chron. Extended biostratigraphical comments for the complete section, and subsection, are compiled in BOUGHDIRI et al. (2005).

#### 4. Final remarks

The two specimens described have differential significance on the palaeobiological ground even belonging to two taxa with wide biogeographical

ranges. The occurrence of *Simocosmoceras* cf. *adversum* (OPPEL) in north-Africa is first reported and hence Lower Tithonian ammonite biostratigraphy is improved for the Tunisian Dorsale. Moreover, from a palaeobiogeographical point of view (see the most updated map in VILLASEÑOR et al. 2003), this record cannot surprise as far as reported from the southern margin of the Mediterranean Tethys, at an intermediate region between two relatively close areas, such as southeastern Iberia and Apulia, in which the occurrence of *Simocosmoceras* is well known (OLÓRIZ 1978; CRESTA & PALLINI 1984). Even taking into account limitations linked to the incomplete preservation of the fragment described, its phenotype deviation respect to individuals from populations in southern Europe seems to be minimal, if any. In contrast, individuals from separate populations in the Pacific (Argentina; cf. LEANZA & OLÓRIZ 1987), as well as in the Caribbean area (Cuba and Mexico; cf. MYCZYNSKI 1990; VILLASEÑOR et al. 2003), show clear phenotype deviation. Given that published specimens are interpreted to be co-specific (Argentinean) and/or belonging to close-related species (Cuban and Mexican specimens), it derives that separate populations adapted to local environmental conditions, irrespectively from their distance with respect to “core” populations-and-areas. In addition, these separate populations experienced distinct ecological stress and, most probably, trade-offs within the local communities in which they were involved (“captured”). A comparatively strong genetic control on phenotype expression could explain the relative stability in shell morphology and, especially, sculpture (stabilized reaction norm), which were only disturbed by clearly different environmental, and hence ecological, conditions – i.e., neritic seas connected to the proto-Pacific ocean in Argentina. When the occupation of new shelves accentuated the environmental stress (indirectly evidenced by lithofacies in Cuba and Mexico), fragmentation, patch dynamics and conditions for the origination of new, related species occurred, showing greater change in shell morphology and, especially, ornamentation.

In contrast to the comparatively rare, phenotypically stable *Simocosmoceras*, genus *Micracanthoceras* was frequent during the late Tithonian elsewhere in the Tethyan Ocean and adjacent shelves (see the most updated palaeobiogeographic map in CECCA 1999). Within *Corongoceras*, rightly reinterpreted at the subgenus level by TAVERA (1984), the species *Micracanthoceras* (*Corongoceras*) *symbolum* (OPPEL) inhabited a large biogeographic range that included north-Africa (e.g., ROMAN 1936; BACHNOU & ATROPS 1996; BENZAGGAGH & ATROPS 1997). A typical feature of the OPPEL species, as reinterpreted by TAVERA (1984), is its relatively high phenotype instability, plasticity (i.e., resulting from high-active reaction norm), especially in that concerning inter-ribbing space in mature adults and/or body-chambers. In addition, it is foreseeable that different morphotypes could be restricted to particular areas within the wide biogeographical

range of the species, which inhabited mainly epiocceanic areas, but also shelves, from Madagascar to north-Africa, Iberia and Apulia (to compare specimens depicted in ZITTEL 1868; ROMAN 1936; COLLIGNON 1960; LINARES & VERA 1966; TAVERA 1984). Even recognizing that himalayitids are incompletely known and that future research is needed for updated interpretation of species-level structure, sytematics and taxonomy, on the basis of more adequate samplings, several hypotheses could explain phenotype plasticity according to current information. Diversified genomes with low genetic control on phenotype expression usually result in within-species phenotype discontinuity which, in turn, poses the problem of interpreting the role of morphology for identification in sexual mating. However, when particular phenotypes seems to be restricted geographically, the interpretation at the subspecies level better adapt our understanding of biodiversity, or phenotype diversity, even more when fossil species are considered (e.g. VILLASEÑOR et al. 2003, for the genus *Simocosmoceras* above mentioned). In such a context, metapopulation theory (GILPIN & HANSKI 1991) should be taken into account more frequently. In accordance, a significant research-program would be to investigate degrees in phenotype instability (i.e., reaction norms) from core areas to peripheral ones in reinterpreted, updated, himalayitid species. Hence, we will improve the understanding of ecological trade-offs and stress dynamics (e.g. KNEITEL & CHASE 2004) in order to interpret metapopulation dynamics (e.g., interpatch movement) in ammonoids, and the corresponding biospecies structure within meta-community models (e.g. WILSON 1992).

In the conceptual context alluded above, the case-study of *Simocosmoceras* cf. *adversum* (OPPEL) and *Micracanthoceras* (*Corongoceras*) *symbolum* *carthaginoustensis* n. subsp., first reported from Tunisia, shows the possibility for interpreting how different were reaction norms in these two species with wide biogeographical ranges. As it is well-known from present cephalopods (e.g., coleoidea), it is assumed that widespread ammonite species occupied their biogeographic ranges most probably according to metapopulation models, and metacommunities. Hence, the influence of environmental gradients and/or differences was phenotypically expressed through differential sensibility of developmental thresholds in these organisms. The example selected shows species with a larger biogeographical range and comparatively stabilized phenotype (i.e. *Simocosmoceras* cf. *adversum*) in contrast to other showing smaller biogeographic ranges but more instable phenotypes (*Micracanthoceras* (*Corongoceras*) *symbolum* *carthaginoustensis*). The proposed interpretation envisaged the case-study as the probable result of differential control of genotypes on phenotype expression, combined with the possibility for local, ecological forcing (biogeographical imprint) – i.e., lower genetic control and higher local,

geographical, imprint for *Micracanthoceras (Corongoceras) symbolum carthaginoustensis*.

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