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Upper Tithonian Himalayitidae Spath, 1925 (Perisphinctoidea, Ammonitina) from Le Chouet (Drôme, France): implications for the systematics

CAMILLE FRAU[1], LUC G. BULOT[2] and WILLIAM A.P. WIMBLEDON[3]

[1]9bis Chemin des Poissonniers, 13600 La Ciotat, France; camille_frau@hotmail.fr
[2]Aix-Marseille Université, UMR-CNRS 7330 CEREGE, Centre Saint-Charles, case 67, place Victor Hugo 3, 13331 Marseille cedex 03, France; bulot@cerege.fr
[3]School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, United Kingdom; mishenka1@yahoo.co.uk

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Abstract: This contribution focuses on the late Tithonian ammonite faunas belonging to the Family Himalayitidae Spath in the key-section of Le Chouet (Drôme, France). The great majority of specimens from the Mediterranean Tethys, previously referred to *Durangites* Burckhardt, are now interpreted as juveniles and/or microconchs of the highly variable species *Protacanthodiscus andreaei* (Kilian). Moreover, comparison between specimens from France, Spain and Bulgaria formerly assigned to *Durangites astillerensis* Imlay and the type material of this species, supports the introduction of *Boughdiriella chouetensis* gen. nov. et sp. nov. Further, the revision of the type specimens of *D. astillerensis* and *Durangites* of the *D. vulgaris* group shows that the former species deserves a new generic status, for which *Parrasiella* gen. nov. is erected. *Toucasiella,* previously only known from Spain and Tunisia, is also reported for the first time from south east France. The revision of the "Mediterranean *Durangites*" supports the rejection of a *Durangites* spp. Zone as part of the standard zonation for the upper Tithonian, and its replacement by the *P. andreaei* Zone (= *D. vulgaris* Zone *sensu* Sarti, 1988).

Key words: Himalayitidae, late Tithonian, Mexico, ammonite faunas, taxonomy, Mediterranean Tethys.

Introduction

Within the activity of the Berriasian Working Group (International Subcommission on Cretaceous Stratigraphy — I.S.C.S.), macrofossil sampling in the upper Tithonian to lower Berriasian interval has promoted the collection of new ammonite faunas from southeast France. A first account of the most significant late Tithonian Perisphinctoidea (Ammonitina) from Le Chouet (Drôme, France) highlighted several taxonomic and biostratigraphic problems (Bulot et al. 2014). Regarding the family Himalayitidae Spath, 1925, the genus *Micracanthoceras* Spath, 1925 was discussed and the new genera *Ardesciella* and *Pratumidiscus* were introduced for Mediterranean himalayitids that had previously been attributed to *Corongoceras* Spath, 1925 or *Riasanites* Spath, 1923.

A new biostratigraphic scheme was proposed for the upper Tithonian of Le Chouet (Wimbledon et al. 2013; Bulot et al. 2014). A *Moravisphinctes fischeri* Subzone was introduced for the upper part of the *Micracanthoceras microcanthum* Zone that correlates with the uppermost part of the calpionellid *Tintinopsella remanei* and *Crassicolaria intermedia* Subzones (*Crassicollaria* Zone). In the uppermost upper Tithonian, a *Protacanthodiscus andreaei* Zone (= *D. vulgaris* Zone *sensu* Sarti, 1988) was defined on the first occurrence of the genus *Protacanthodiscus* Spath, 1923. This zone coincides in calpionellid terms with the uppermost part of the *C. intermedia* Subzone and lower part of the *C. colomi* Subzone.

However, both papers lack description of the fauna that supports rejection of the use of a *Durangites* spp. Zone in the standard zonation of the upper Tithonian (Geyssant 1997). Thus, in the present paper, special attention is given to "Mediterranean *Durangites*", that are either reinterpreted as juvenile and microconch forms of *Protacanthodiscus* and/or *Boughdiriella* gen. nov. Detailed examination of *Durangites* Burckhardt, 1912 supports the introduction of *Parrasiella* gen. nov. for the peculiar *Durangites* of the *D. astillerensis* group Imlay, 1939. Finally, the first report of *Toucasiella* Enay, Boughdiri & Le Hégarat, 1998a in southeastern France sheds light on the phylogeny of late Tithonian himalayitids.

Geological setting

The reader is referred to the work of Wimbledon et al. (2013) and Bulot et al. (2014) for further details about the lithology, biostratigraphy (ammonites, calpionellids and calcareous nannofossils) and magnetostratigraphy of the Le Chouet section. To avoid redundancy, we chose to synthesize the data discussed herein on Fig. 1. A map of the Mexican localities is presented on Fig. 2 and their geological descriptions are to be found in Burckhart (1912), Imlay (1939), Verma & Westermann (1973) and Olóriz et al. (1999).

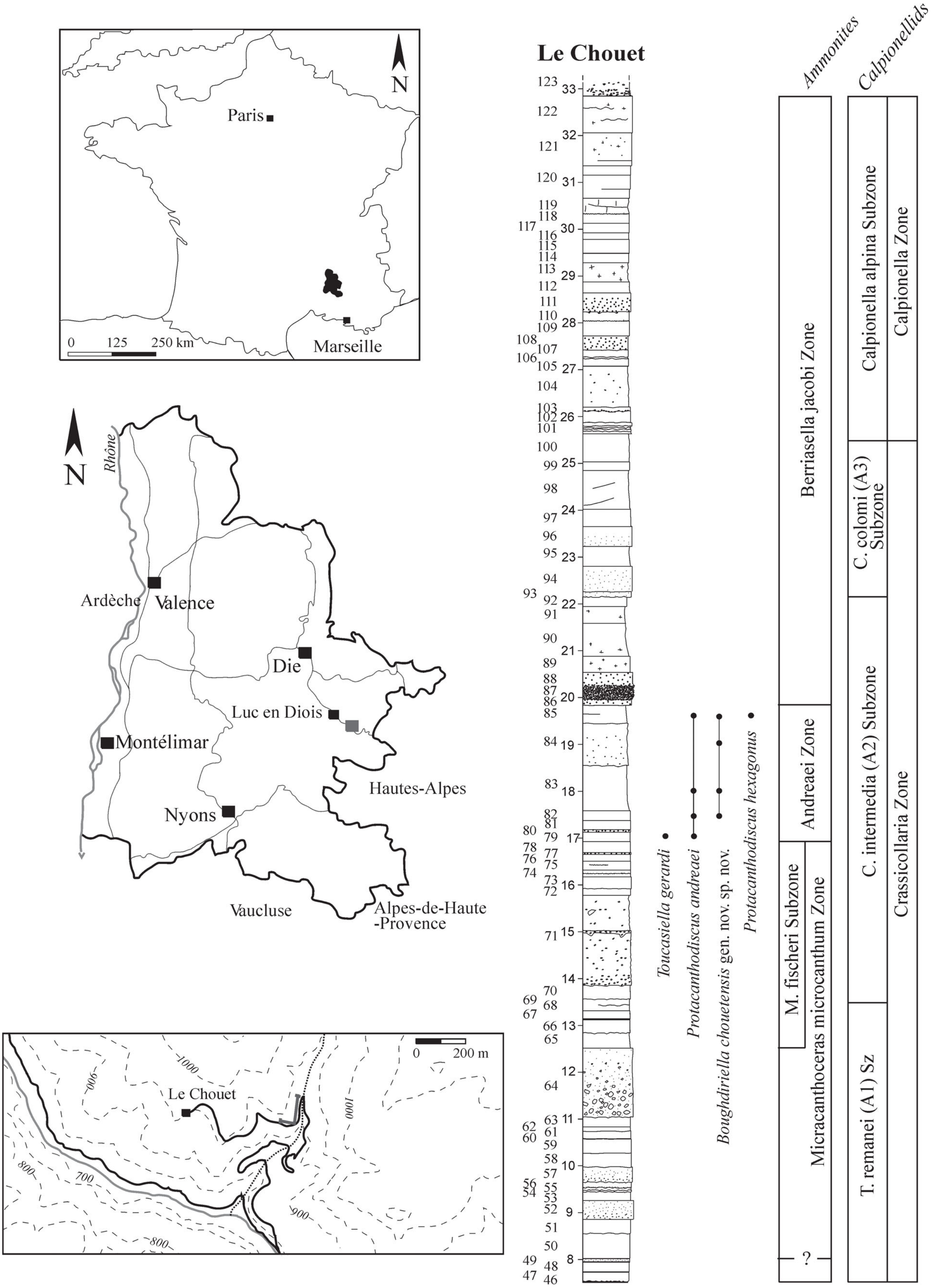

Fig. 1. Locality map of Le Chouet (Les Près, Drôme, SE France), integrated stratigraphy and distribution of the late Tithonian Himalayitidae studied in this paper (modified after Wimbledon et al. (2013)).

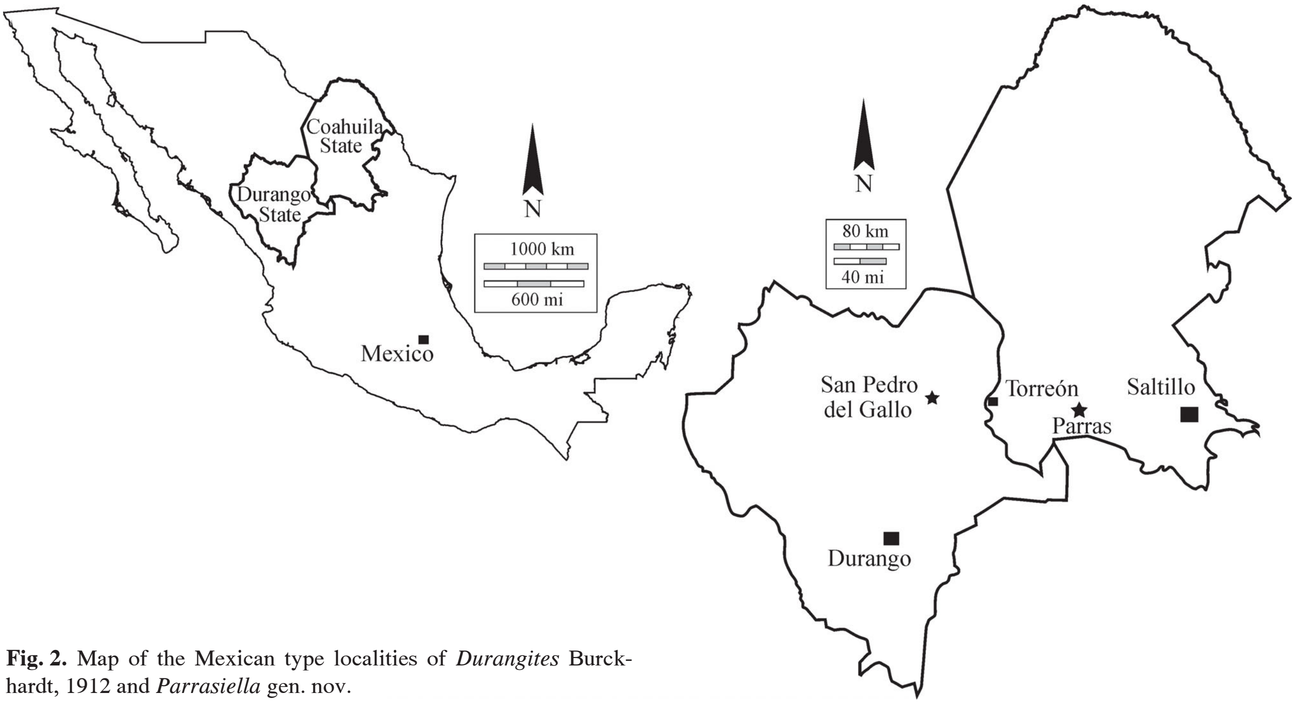

Fig. 2. Map of the Mexican type localities of *Durangites* Burckhardt, 1912 and *Parrasiella* gen. nov.

Systematic paleontology

All dimensions of specimens are given in millimetres: Dmax = larger measurable diameter, D = diameter, Wh = whorl height, U = umbilical diameter. Ratios such as Wh/D and U/D are dimensions as a percentage of the diameter at the point of measurement. The suture terminology is that of Korn et al. (2003). The bed numbers for the Le Chouet section follow that of Wimbledon et al. (2013) and Bulot et al. (2014) as shown on Fig. 1.

Acronyms. Unless otherwise mentioned, all specimens are deposited in the Frau/Bulot collection at the *Musée Paléontologique de Provence* (MPP) of Aix-Marseille University. Other specimens studied herein are deposited in the paleontological collections of the Universidad Nacional Autonoma de Mexico (UNAM), University of Michigan (U.M.) and University of Lyon-1 (FSL).

Order: **Ammonitida** Fisher, 1882
Suborder: **Ammonitina** Fisher, 1882
Superfamily: **Perisphinctoidea** Steinmann, 1890
Family: **Himalayitidae** Spath, 1925
Genus: *Durangites* Burckhardt, 1912

Type species: *Durangites vulgaris* Burckhardt, 1912, by subsequent designation of Cantú-Chapa (1968, p. 22).

When introducing his new genus, Burckhardt (1912) did not designate a type species. The subsequent designation as type species of *Durangites acanthicus* Burckhardt, 1912 by Roman (1938, p. 323) is invalid under article 67.5 of the I.C.Z.N. As already pointed out by Cantú-Chapa (1968, p. 22) and Verma & Westermann (1973, p. 253–254), *Durangites acanthicus* is a problematic species based on a single, incomplete and poorly preserved specimen that only shows two of the four ornamental stages that characterize the genus *Durangites* as it was originally defined by Burckhardt (1912, p. 144).

On the contrary, re-examination of the well-preserved type series of *Durangites vulgaris* shows that this species exhibits the four ornamental stages that were given in the original definition. As a consequence, the designation of *D. vulgaris* as type species of *Durangites* by Cantú-Chapa (1968, p. 22) should be considered as valid, albeit for the wrong reasons.

The lectotype (UNAM IGM 504) of *D. vulgaris* Burckhardt (1912, pl. 37, figs. 1, 2, 5, 18, refigured herein Fig. 3B) by subsequent designation of Tavera (1985, p. 158) is unfortunately lost (Moreno-Bedmar, personal communication, 2014). According to article 72.4 of the I.C.Z.N., the type series is composed by all the specimens figured by Burckhardt (1912) on pl. 37, figs. 1–35 and pl. 38, figs. 1–4, as well as any other specimen mentioned in the text. For the reasons given above, we designate as neotype the specimen UNAM IGM 504a of Burckhardt (1912, pl. 37, figs. 3, 4, 6, 9), re-illustrated herein (Fig. 3B). This designation is in agreement with article 75.3 of the I.C.Z.N.

Emended diagnosis: Small-sized planulate ammonites with a compressed shell and a deep evolute umbilicus ($0.34 < U/D < 0.45$). Rounded to sub-quadrate whorl section with well-defined umbilical wall. When preserved, body chamber generally occupies almost half of the last whorl. Ornamentation varies through ontogeny and three different stages can be recognized.

Primary stage ($D < 10$ mm) characterized by straight and fine ribs, simple or bifurcate on the upper third of the flank; feeble lateral and small ventro-lateral tubercles; deep smooth ventral sulcus (“*stade microcanthus*” and “*stade Köllikeri*” of Burckhardt).

Secondary stage marked by straight simple and intercalatory ribs mostly divided on upper part of the flank; dis-

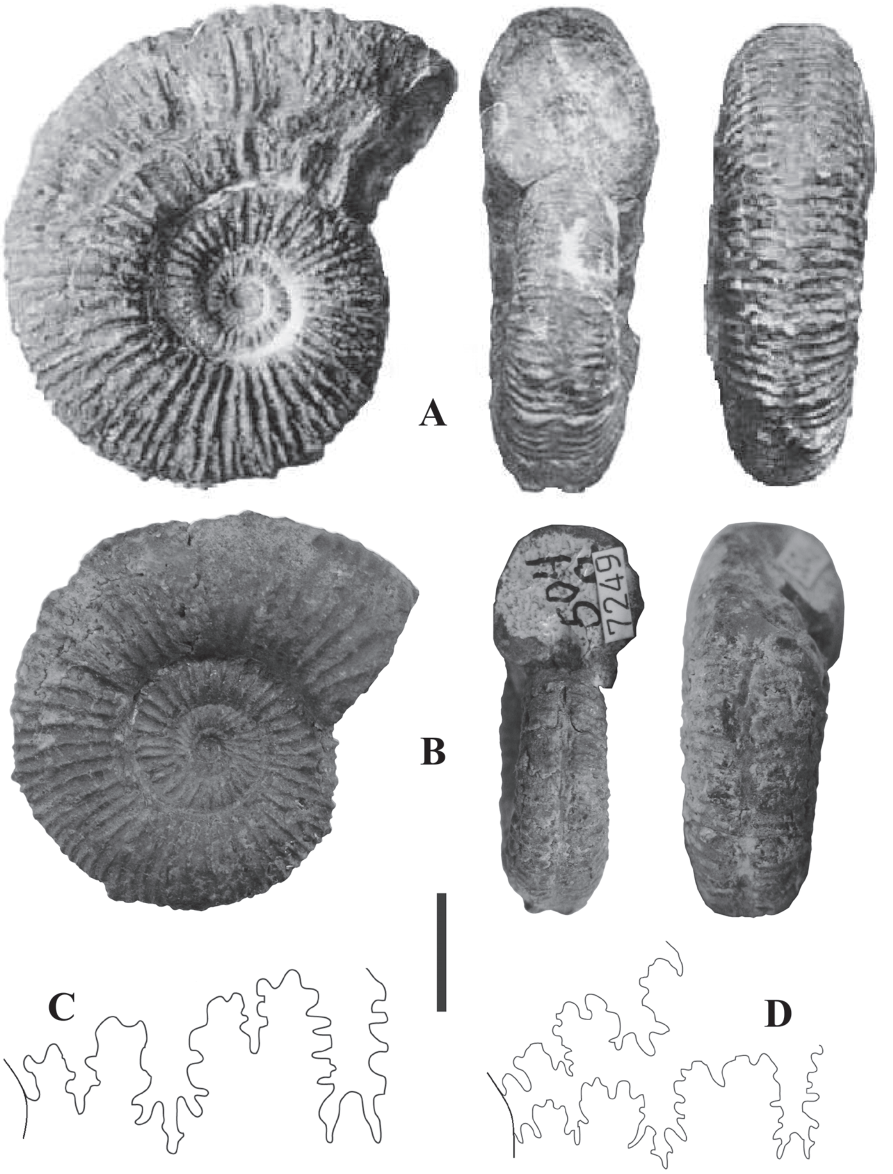

Fig. 3. *Durangites vulgaris* Burckhardt, 1912. **A** — The lost lectotype of *D. vulgaris* reproduced after Burckhardt (1912, pl. 37, figs. 1, 2, 5); **B** — The neotype IGM 504a, MPIG; **C** — Suture line (×2) of the lost lectotype reproduced after Burckhardt (1912, pl. 37, fig. 18); **D** — Suture line (×2) of the neotype reproduced after Burckhardt (1912, pl. 37, fig. 6). Bar scale is 10 mm.

appearance of lateral tubercles; development of prominent radially elongated ventro-lateral tubercles; smooth ventral furrow ("*stade typique*" of Burckhardt).

Final stage characterized by mostly divided radiate to rursiradiate ribs; progressive disappearance of the ventro-lateral tubercles and replacement of smooth ventral furrow by a flattened ventral band with weakened ribs that may curve adorally ("*stade adulte*" of Burckhardt).

Suture line simple with bifid external lobe and trifid adventive lobe; large asymmetrical external saddle with higher external branch (Fig. 3C and D).

Dimorphism: The existence of dimorphic pairs in Mexican *Durangites* was suggested by Verma & Westermann (1973, p. 254). A re-examination of the material illustrated by Burckhardt (1912) allows us to distinguish two morphotypes.

A first group of small-sized forms (Dmax < 40 mm) match perfectly the diagnosis of the genus given above. This group includes: *D. vulgaris* pro parte, *D. acanthicus*, *D. latesellatus* Burckhardt, 1912, *D. incertus* Burckhardt, 1912 and *D. nodulatus* Burckhardt, 1912.

The other morphotype encompasses larger forms (Dmax > 40 mm); it is characterized by distinctive secondary and final growth stages marked by higher rib(s) densities, attenuated tubercles, an individualized ventral band throughout ontogeny, and by the scaphitoid shape to the outer whorls due to the fast growth rate of the last whorl. This group includes: *D. vulgaris* pro parte, *D. humboldti* Burckhardt, 1912, *D. densestriatus* Burckardt, 1912 and *D. fusicostatus* Burckhardt, 1912. Additionally, *D. coghlani* (Aguilera in Castillo & Aguilera, 1895) and *D. alencasteri* Verma & Westermann, 1973 also belongs to this group. *D. heilprini* (Aguilera in Castillo & Aguilera, 1895) merely corresponds to a juvenile of this group.

Even if the features that suggest the distinction of the two morphological variants strongly suggest intrageneric sexual dimorphism, the preservation of Mexican specimens allows no sign of a differentiated peristome that could support such an interpretation. Moreover, even though the great majority of the specimens were collected at Cerro de Las Liebres, Burckhardt (1912, p. 220–221) clearly stated that the thickness of the "*couches à Durangites*" of the San Pedro del Gallo area (Durango State) exceeds 100 metres. It is therefore not possible to assume that the taxa are synchronous, even though Imlay (1939, p. 15 and 18) suggested that the specimens collected by Burckhardt originated from a limited number of phosphatic limestone concretions. If so, the Mexican taxa listed above may only represent typological morphotypes of a single paleobiological species.

It should be noted that Enay et al. (1998b) proposed sexual dimorphism between the genera *Durangites* and *Protacanthodiscus*. This view is not retained herein and will be discussed below.

Specific content: In our opinion, *Durangites* should be strictly restricted in its scope to the species listed above, as illustrated by Aguilera in Castillo & Aguilera (1895), Burckhardt (1912), Verma & Westermann (1973) and Olóriz et al. (1999).

Durangites zigzagcostatus Cantú-Chapa, 2006 is based on juvenile specimens with dense ribbing that forms a chevron across the venter. These specimens most likely belong to the group of "*Kossmatia*" *victoris* (Burckhardt, 1906).

Durangites astillerensis Imlay, 1939, and the species *D. juanensis*, *D. latiumbilicatum* and *D. galeanense* described by Cantú-Chapa (1968) should be excluded from *Durangites* because they do not show the succession of ontogenetic stages which we describe above and which will be further discussed in the description of *Parrasiella* gen. nov. section of this paper. *D. vulgaris* and *D.* cf. *D. acanthicus* from Cuba illustrated by Imlay (1942, pl. 3, figs. 1, 5–7) belong to the same group. Moreover, they belong to a very specific assemblage dominated by *Salinites* Cantú-Chapa, 1968, a genus that never occurs in the classical "*Kossmatia*"–*Durangites*–"*Corongoceras*" assemblage of San Pedro del Gallo and Sierra de Catorce. *Durangites rarifurcatus* Imlay, 1939 also seems to be related to *Parrasiella* gen. nov.

Other records from Cuba (Myczynski, 1989) and California (Anderson, 1945) are based on material too poorly preserved for identification.

Outside the New World, *Durangites* has been reported from the Mediterranean (Enay et al. 1971; Enay & Geyssant 1975; Cecca et al. 1983; Tavera 1985), Bulgaria (Ivanov et al. 2010), India (Shome & Bardhan 2009), and the Russian Pacific coast (Sey & Kalacheva 1983). In our opinion none of these records truly belong to *Durangites*. The Mediterranean occurrences will be addressed in detail in the *Protacanthodiscus* and *Boughdiriella* gen. nov. sections of this paper. *Durangites* cf. *heilprini*, *Durangites*. sp. A and *Durangites* sp. from Kutch (India, Shome & Bardham 2009) falls into the range of variation of *Micracanthoceras brightoni* Spath, 1931. Finally, preservation of the *Durangites* sp. ind. from Primorye (Sey & Kalacheva 1983, pl. 2, fig. 5) does not allow identification at the genus level.

Occurrence: Since the work of Enay et al. (1971) and Enay & Geyssant (1975), *Durangites* has been considered as a widespread key genus defining the top of the Tithonian Stage. This view needs to be completely reconsidered in the light of the taxonomic opinions presented herein.

As herein understood, *Durangites* is a strictly Mexican genus and is a major element of the "*Kossmatia*"–*Durangites*–"*Corongoceras*" assemblage of Verma & Westermann (1973): an assemblage that was originally considered to be a late Tithonian fauna, based on the study of the Caja Formation (Sierra de Catorce). According to the preliminary revision of Olóriz et al. (1999), *Durangites* is restricted and dominant in the upper part of the Caja Formation where it co-occurs with less frequent *Substeueroceras* and rare "*Kossmatia*". Calibration with calpionellids at this locality indicates a late early to middle Berriasian age for this fauna (Olóriz et al. 1999). A *Substeueroceras-Durangites* assemblage was also reported by Adatte et al. (1994a,b, 1996) just below the *Crassicollaria*/*Calpionella* zones boundary *sensu* Remane et al. (1986). Therefore, the first occurrence of *Durangites* in the late late Tithonian cannot be ruled out. Nevertheless, it should be noted that the base of the *Calpionella* Zone is ill defined in the sections studied (Adatte et al., 1996, p. 679) and that with the exception of a single doubtful specimen (*Durangites* sp. in Adatte et al. 1994b, pl. 2, fig. 5) the fauna is still to be formally documented.

Genus **Parrasiella** gen. nov.

Type species: *Durangites astillerensis* Imlay, 1939.

Derivation of name: From Sierra de Parras, a north-central region of Mexico.

Diagnosis: Small-sized discoidal ammonite with a shallow and wide open umbilicus ($0.40<U/D<0.47$). Sub-rounded to ovate whorl section, with convex flank. Body chamber generally occupies almost half of the last whorl. Highly distinctive ornamentation of bifurcated and parabolic ribs at the end of the phragmocone. Posterior branches of bifurcate ribs marked by radially elongated ventro-lateral tubercles that delimit a shallow ventral band. Body chamber ornamentation composed of bifurcate and simple rursiradiate ribs that cross the venter with a slightly weakening.

Specific content: Beside the type species, *Parrasiella* gen. nov. comprises *Durangites rarifurcatus* Imlay, 1939; *Durangites galeanense* Cantú-Chapa, 1968; *Durangites latiumbilicatum* Cantú-Chapa, 1968 and *Durangites juanensis* Cantú-Chapa, 1968.

Remarks: The type species of *Parrasiella* gen. nov. has previously been included in the genus *Durangites* following the work of Imlay (1939, 1942) and Cantú-Chapa (1968). As herein understood, the genus *Parrasiella* differs by its evolute coiling, shallow umbilicus, rounded whorl section throughout ontogeny and the regular disposition of ventro-lateral tubercles on the phragmocone. In the literature, the type species of *Parrasiella* gen. nov. has been reported from the western Tethys (Boughdiri 1994; Enay et al. 1998b;

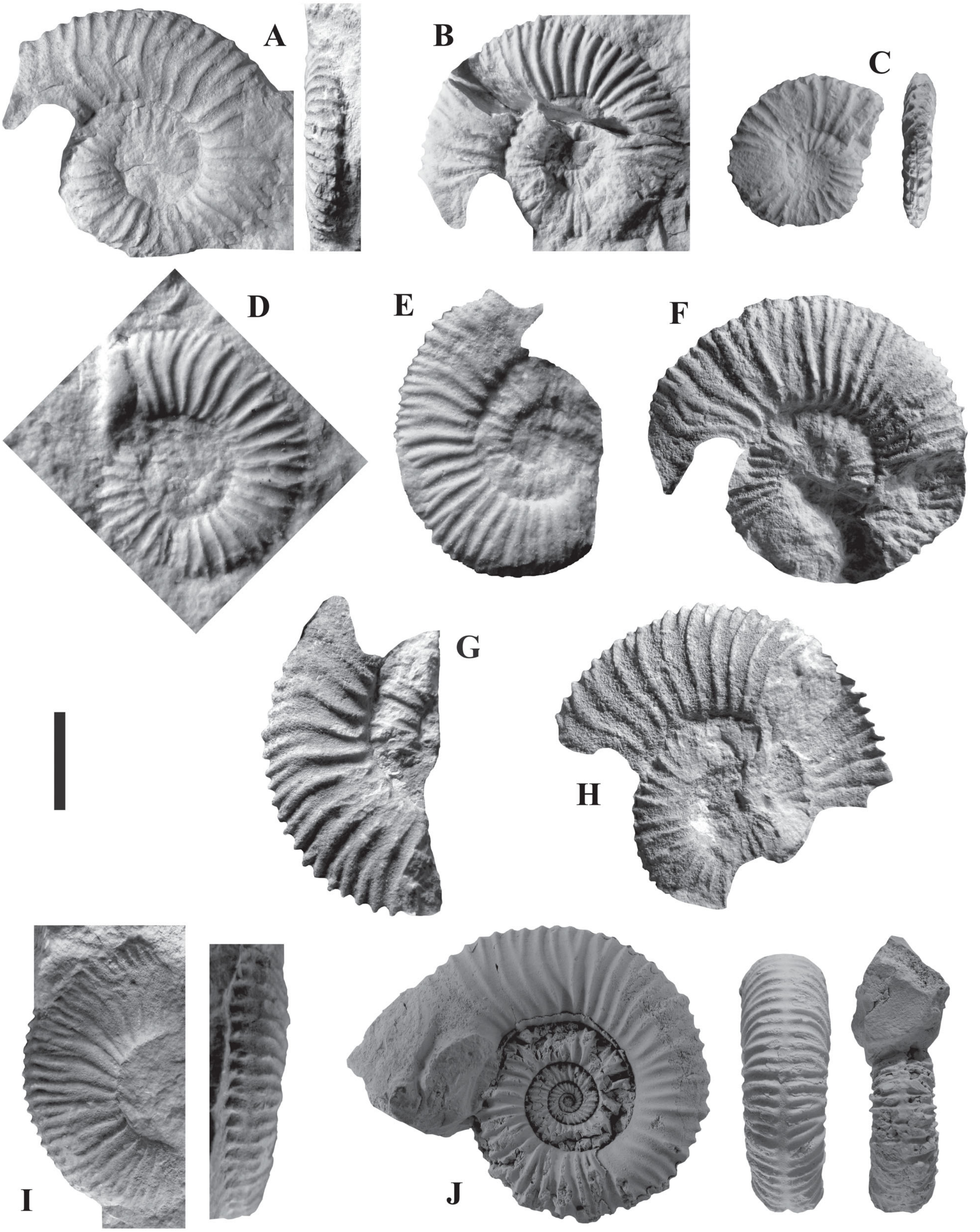

Fig. 4. *Boughdiriella chouetensis* gen. and sp. nov. from the late Tithonian (*P. andreaei* Zone) of Le Chouet. **A** — Holotype MPP-CHT.19/26 [m] (bed 83); **B** — MPP-CHT.18/12 [m] (bed 82); **C** — MPP-CHT.21/94 [m] (bed 85); **D** — MPP-CHT.21/93 [m] (bed 85); E — MPP-CHT.21/33 [m] (bed 85); **F** — MPP-CHT.19/29 [m] (bed 83); **G** — MPP-CHT.21/64 [m] (bed 85); **H** — MPP-CHT.21/23 [m] (bed 85); **I** — MPP-CHT.19/16 [?m] (bed 83); **J** — Lateral and ventral views of the holotype (U.M. 17707) of *Parrasiella astillerensis* (Imlay 1939, pl. 10, figs. 10–12) from Mexico (Sierra de Parras, Coahuila). Bar scale is 10 mm.

Ivanov et al. 2010). In our view, none of the specimens illustrated are actually of the Mexican species: these will be discussed in the *Boughdiriella* gen. nov. section of this paper.

Occurrence: According to Imlay (1939, p. 5), *Parrasiella astillerensis* co-occurs with *Salinites grossicostatum* (Imlay, 1939), *Salinites ecarinatum* (Imlay, 1939), and misidentified *Durangites* cf. *acanthicus*. At locality K2, Imlay (1939) reported *Durangites rarifurcatus* in association with *Salinites*. In Mexico, *D. galeanense*, *D. latiumbilicatum* and *D. juanensis* were also described in association with *S. grossicostatum* by Cantú-Chapa (1968).

The age of the *Salinites* Cantú-Chapa, 1968 and *Parrasiella* gen. nov. assemblage is unclear and the two genera are not members of the classical "*Kossmatia*"–*Durangites*–"*Corongoceras*" assemblage of San Pedro del Gallo and Sierra de Catorce (Mexico).

In Cuba, Myczynski (1999) reports *Salinites* at the base of the upper part of the La Zarza member above the "*Vinalesites*–*Protancyloceras*" assemblage, and from the El Americano member. According to Myczynski & Pszczółkowski (1994) and Myczynski (1999), both units are of late Tithonian age based on the presence of tintinnoids. However, this age has been much debated (see Cobiella-Reguera & Olóriz 2009, with references). According to the last-cited authors, the upper part of the El Americano member belongs to the upper *Crassicollaria* and/or *Calpionella* zones, and that indicates a late late Tithonian to early middle Berriasian age.

Parrasiella astillerensis (Imlay, 1939)
Fig. 4J

1939 *Durangites astillerensis* n. sp. — Imlay, p. 46, pl. 10, figs. 10–12

Types: by original designation, According to Imlay (1939, p. 46), the holotype is the specimen U.M. 17707. It is herein re-illustrated (Fig. 4J). Imlay (1939) designated as paratype another specimen (U.M. 20008).

Type locality: Both specimens originate from locality 34 of Imlay (1939) in the Sierra de Parras (Coahuila, north-central Mexico) from the La Casita formation.

Remarks: The type specimen of *Parrasiella astillerensis* bears long lateral necked lappets. It should be noted that the other species are only known from a few specimens with no aperture visible. In our view, *P. latiumbilicatum* and *P. juanensis* described by Cantú-Chapa (1968) are closely related to, if not synonyms of, *Parrasiella astillerensis.* It should be noted that the ornamentation of the early whorls of *P. astillerensis* matches well that seen in *P. rarifurcatus* and *P. galeanense.* Both taxa are characterized by a larger adult size, but their apertures are unknown. Pending new studies on the Mexican faunas, these species could represent the macroconch of *P. astillerensis*.

Occurrence: *Parrasiella astillerensis* occurs in north-central Mexico and western Cuba. As discussed above the precise age of *P. astillerensis* is disputed.

Genus *Boughdiriella* gen. nov.

Type species: *Boughdiriella chouetensis* gen. et sp. nov.

Derivation of name: Dedicated to Mabrouk Boughdiri, Head of the Geological Sciences Department of Bizerte University (Tunisia), for his contribution to the systematics of late Tithonian ammonites.

Diagnosis: Small-sized dimorphic ammonites with a discoidal and evolute shell. Sub-circular whorl section in inner whorls; compressed sub-oval whorl section in adult. Shallow and moderately open umbilicus. Umbilical wall slightly convex. Ornamentation of inner whorls (up to D ~ 10 mm) composed by rigid, straight, simple ribs. From D ~ 15 mm to the end of the body chamber, ribs flexuous, prominent and bifurcated on the upper third of the flanks. Scarce trifurcate, and intercalated ribs. Venter marked by a shallow furrow. The suture line is unknown.

Remarks: Understanding of the "Mediterranean *Durangites*" has been based on a limited number of specimens illustrated by Cecca et al. (1983), Tavera (1985), Boughdiri (1994), Enay et al. (1998b), and Ivanov et al. (2010), specimens that were referred to *D. vulgaris* and/or *Parrasiella astillerensis*. Detailed examination of the important material collected at Le Chouet shows that the similarities to *Durangites* and *Parrasiella* gen. nov. are only superficial. Both genera differ in their marked tuberculated stage on the ventral area, distinctive whorl sections and steep umbilical margin.

Occurrence: *P. andreaei* Zone (base of the calpionellid *C. colomi* Subzone), late Tithonian. *Boughdiriella* gen. nov. is known from Spain (Tavera, 1985), South East France (Boughdiri 1994; Enay et al. 1998b — this paper) and Bulgaria (Ivanov et al. 2010). Potential occurrence in Tunisia (Boughdiri et al. 1999), Turkey (Enay et al. 1971), Italy (Sarti, 1995) and Morocco (Benzaggagh & Atrops 1997, p. 158) needs to be illustrated.

Boughdiriella chouetensis nov. sp.
Fig. 4A–I

1985 *Durangites acanthicus* Burckhardt — Tavera, p. 156, pl. 18, fig. 11
1994 *Durangites* (*Durangites*) n. sp. 5 — Boughdiri, p. 123–128, pl. 1, figs. 24, 28–32
1994 *Durangites* (*Durangites*) *astillerensis* Imlay — Boughdiri, pl. 1, figs. 20–23
1998b *Durangites* (*Durangites*) gr. *astillerensis* Imlay — Enay et al., fig. 2, n° 17
1998b *Durangites* (*Durangites*) *astillerensis* Imlay — Enay et al., fig. 2, n° 12
1998b *Durangites* (*Durangites*) aff. *astillerensis* Imlay — Enay et al., fig. 2, n° 1–3
1998b *Durangites* (*Durangites*) *vulgaris* Burckhardt — Enay et al., fig. 2, n° 4
1998 *Durangites* (*Durangites*) sp. — Enay et al., fig. 2, n° 5
2010 *Durangites* (*Durangites*) aff. *astillerensis* Imlay — Ivanov et al., pl. 3, fig. 5

Type: The holotype is the specimen MPP-CHT.21/65 herein illustrated on Fig. 2A.

Paratypes: MPP-CHT.18/12, MPP-CHT.21/17, MPP-CHT.21/18, MPP-CHT.21/23, MPP-CHT.19/29, MPP-CHT.21/28, MPP-CHT.21/29, MPP-CHT.21/33.

Derivation of name: After Le Chouet.

Type locality: Le Chouet, near Les Près (Drôme, France).

Diagnosis: Small-sized dimorphic ammonites with a discoidal and evolute shell. Sub-circular whorl section in inner whorls; compressed sub-oval whorl section in adult. Shallow and moderately open umbilicus. Umbilical wall slightly convex. Ornamentation of inner whorls (up to D ~10 mm) composed by rigid, straight, simple ribs. From D ~15 mm to the end of the body chamber, ribs flexuous, prominent and bifurcated on the upper third of the flanks. Scarce trifurcate, and intercalated ribs. Venter marked by a shallow furrow. The suture line is unknown.

Measurements: See Table 1.

Remarks: Although there is no significant ornamental and/or size difference between micro- and macroconchs, sexual dimorphism is recognizable. Microconchs are characterized by short lateral lappets (Fig. 4A,B,D and E) while macroconchs show a collared aperture (Fig. 4F,G and H).

Compared to *Durangites vulgaris*, *Boughdiriella chouetensis* gen. et sp. nov. is easily distinguished by its compressed sub-rectangular whorl section and the absence of a short stage with tubercles on the venter.

Specimens of *B. chouetensis* illustrated in the literature have generally been assigned to *Parrasiella astillerensis*. That species differs in its open umbilicus, sub-oval whorl section, and a phragmocone end that has a prominent and long tuberculated section on its venter. The phragmocone — body chamber transition is marked by 'pinched' ventro-lateral tubercles.

Hegaratia busnardoi Patrulius & Avram, 1976 shows some superficial similarities to *B. chouetensis*, but it can be easily distinguished by its higher U/D ratio, coarse bifurcate ribs and lateral constrictions.

Berriasella (*Picteticeras*) *jauberti* (Mazenot, 1939) shows morphological similarities with *B. chouetensis,* but differs in its larger adult size (60 to 85 mm), evolute coiling, sub-rectangular whorl section throughout ontogeny and higher rib density.

Occurrence: As for the genus. At Le Chouet, *B. chouetensis* occurs at the top (e.g. beds 82 to 85) of the *P. andreaei* Zone (base of the calpionellid *C. colomi* Subzone), late Tithonian.

Genus *Protacanthodiscus* Spath, 1923

Type species: *Hoplites andreaei* Kilian, 1889; by original designation.

Emended diagnosis: Middle to large-sized (Dmax < 165 mm) dimorphic ammonites with an open ($0.40 < U/D < 0.50$) and relatively deep umbilicus in the adult stage. Subcircular whorl section, with convex flanks on juveniles, which become progressively sub-rectangular to sub-hexagonal on adults. Ornamentation mainly composed of bifurcate, and trifurcate ribs with a tubercle at the furcation point. Some ribs can be looped. On the body chamber, bifurcate ribs are ended on the ventral shoulder by a latero-ventral tubercle on the first, or occasionally the second, branch. Ventral area marked by a more or less flattened ventral band, depending on the shape of the whorl section. Suture line is simple with large trifid lateral lobe, which is as deep as the external lobe.

Dimorphism: Roman (1936, p. 22) gave the first diagnosis of *Protacanthodiscus*, subsequently emended by Tavera (1985, p. 197). In the opinion of the latter author, *Protacanthodiscus* is a dimorphic genus. In his unpublished thesis, Boughdiri (1994) reconsidered the systematic content of *Protacanthodiscus* and included it as a subgenus of *Durangites* accommodating macroconch forms. Subsequently, Boughdiri (personal communication, 2011) suggested that the "Mediterranean *Durangites*" figured by Tavera (1985) could be: "*inner whorls and/or juveniles of other species that would belong to other closely allied genera*" (english translation). The present study supports this opinion (see synonymy list of *Protacanthodiscus andreaei*). Moreover, the comparatively expanded succession at Le Chouet shows that the first occurrence of *Protacanthodiscus* occurs at a lower level than that of *Boughdiriella* gen. nov., that was until now regarded as a "Mediterranean *Durangites*".

Table 1: Measurements of *Boughdiriella chouetensis* gen. and sp. nov. U/D and Wh/D ratios are dimensions as a percentage of the diameter at the point of measurement.

Specimen	D	Wh	U	U/D	Wh/D
CHT 19–26	28	9	11	0.39	0.32
CHT 19–16	29	11	12	0.41	0.38
CHT 19–19	/	12	18	/	/
CHT 19–26	28	9	11	0.39	0.32
CHT 19–29	36	11	15	0.42	0.31
CHT 18–12	26	8.5	9.5	0.37	0.33
CHT 21–22	30	10	13	0.43	0.33
CHT 21–23	/	12	18	/	/
CHT 21–24	38	12	17	0.45	0.32
CHT 21–64	/	11	/	/	/
CHT 21–83	20	7	8	0.40	0.35
CHT 21–93	29	11	13	0.45	0.38
CHT 21–94	18.5	6	8	0.43	0.32

The hypothesis of sexual dimorphism between true *Durangites* and *Protacanthodiscus* is also to be ruled out in Mexico, where no *Protacanthodiscus stricto sensu* have been collected in association with *Durangites* (see Verma & Westermann 1973). Contrary to the opinion of Boughdiri (1994) and Enay et al. (1998b), we consider that *Acanthodiscus euthymiformis* Burckhardt, 1912 and *Acanthodiscus transatlanticus* Burckhardt, 1912 cannot be included in *Protacanthodiscus.*

Remarks: Spath (1923, p. 305) introduced the genus *Protacanthodiscus* (based on *Hoplites andreaei* Kilian, 1889) without diagnosis and specific content. When creating the family Himalayitidae (Spath, 1925, p. 144), Spath included *Hoplites incompositus* Retowski, 1893 in *Protacanthodiscus.* This species has since been transferred to the Neocomitidae (Bogdanova et al. 1984; Khimchiashvili 1989); and the description and the original figure leave no doubt that the *H. incompositus* is a neocomitid species.

Tavera (1985), considered that *Hoplites heterocosmus* Canavari, 1899 and *Hoplites bonarellii* Canavari, 1899 belong to *Protacanthodiscus*, and he described four news species from the Betic Cordilleras: *Protacanthodiscus coronatus* Tavera, 1985; *P. darwini* Tavera, 1985; *P. nodosus* Tavera, 1985; and *P. berriasensis* Tavera, 1985.

The expanded conception of *Protacanthodiscus* of Boughdiri (1994) was only partly accepted by Enay et al. (1998a,b) and Boughdiri et al. (1999). Despite the introduction of *Kilianites* by Enay et al. (1998c) (type species: *P. canavarii* Enay, Boughdiri & Le Hégarat, 1998c) and *Hegaratites* Boughdiri, Enay & Le Hégarat, 1999 (type species: *Hegara-*

tites rheouisensis Boughdiri, Enay & Le Hégarat, 1999); the exact content of *Protacanthodiscus* remained unclear for those authors.

Based on the material at our disposal, we consider that *P. andreaei* shows a large morphological intraspecific variability that encompass the typological species *P. coronatus*, *P. darwini* and *P. nodosus*. Further, examination of *Neoperisphinctes falloti* Tavera (non Kilian, 1889); *Durangites singularis* Tavera, 1985; *Durangites sutneroides* Tavera, 1985; *D. gigantis* Tavera, 1985 and *Durangites apertus* Tavera, 1985, suggest that these species also fall in the range of variation of *Protacanthodiscus andreaei*.

Contrary to the opinions of Boughdiri (1994) and Enay et al. (1998b), we consider that *Hoplites macphersoni* Kilian, 1889 and *H. malladae* Kilian, 1889 are in need of a proper revision and cannot be included in *Protacanthodiscus*. This is also the case for *Hoplites heterocosmus* and *H. bonarellii,* originally described by Canavari (1899).

Occurrence of *Protacanthodiscus* in the New World is based on material described by Steuer (1897), Anderson (1945), Leanza (1945, 1968), Rivera (1951), Cantú-Chapa (1967) and Imlay & Jones (1970). As already suggested by Klein (2005), the taxonomy of those forms is doubtful. Examination of the type material of *Hoplites quadripartitus* Steuer, 1897, *Protacanthodiscus pacificum* Rivera, 1951 and *P. puenteingaensis* Rivera, 1951 has convinced us that these species are homeomorphic with true *Protacanthodiscus* and that they deserve a generic status in their own right. This systematic problem will be addressed elsewhere, as part of the revision of the fauna from the Puente Inga formation (Lima Coast, Peru).

Specific content: *Protacanthodiscus andreaei* (and its synonyms: *Hoplites* (*Acanthodiscus*) *andreaei* Kilian *var. punica* Pervinquière, 1907; *Protacanthodiscus coronatus*, *P. darwini*, *P. nodosus*, *Durangites singularis*, *D. sutneroides*, *D. gigantis*, and *D. apertus*), *P. savornini* (Roman, 1936), *Protacanthodiscus berriasensis* and "*Corongoceras*" *hexagonus* Tavera, 1985.

Occurrence: At Le Chouet, *Protacanthodiscus* is restricted to the uppermost Tithonian (top of the calpionellid *C. intermedia* Subzone and lower part of the *C. colomi* Subzone). In Spain, occurrence of *P. berriasensis* in the *E. cularensis* horizon (base of the *B. jacobi* Zone) suggests that the genus occurs as a rarity in the middle part of the *C. colomi* Subzone. To our knowledge, the genus is reported from SE France, Italy, Spain, Bulgaria, Morocco, Tunisia and Algeria.

Protacanthodiscus andreaei (Kilian, 1889)
Figs. 5A–L, 6A–E and 7A–C

1889 *Hoplites Andreaei* — Kilian, p. 670, pl. 32, fig. la,b
1889 *Hoplites* (*Acanthodiscus*) *Andreaei* Kilian var. *Punica* — Pervinquière, p. 38, pl. 2, fig. l2a,b
pars 1939 *Berriasella Andreaei* (Kilian) — Mazenot, p. 96, pl. 12, fig. la,b, non fig. 4a,b
non 1960 *Berriasella* (*Protacanthodiscus*) aff. *andreaei* (Kilian) — Collignon, pl. CLXV, fig. 665
non 1960 *Berriasella* (*Protacanthodiscus*) aff. *andreaei* var. *variabilis* Collignon, pl. CLXV, figs. 666, 667
?1960 *Protacanthodiscus andreaei* (Kilian) — Christ, p. 125, pl. 9, fig. 5
1979 *Protacanthodiscus andreaei* (Kilian) — Sapunov, p. 1985, pl. LVII, fig. 6
1983 *Durangites acanthicus* Burckhardt — Cecca et al., p. 128, pl. 5, fig. 1a,b
1985 *Protacanthodiscus andreaei* (Kilian) — Tavera, p. 198, pl. 26, figs. 5a,b, 6, text-fig. 15H
1985 *Protacanthodiscus* sp. 1 gr. *andreaei* (Kilian) — Tavera, p. 199, pl. 26, figs. 1a,b, 2, text-fig. 15E,I, text-fig. 12H
1985 *Protacanthodiscus berriasensis* n. sp. — Tavera, p. 206, pl. 26, fig. 1a,b, pl. 28, fig. 1a,b, text-fig. 15D
1985 *Protacanthodiscus coronatus* n. sp. — Tavera, p. 200, pl. 27, fig. 1a,b, text-fig. 15A
1985 *Protacanthodiscus darwini* n. sp. — Tavera, p. 203, pl. 26, figs. 3, 4, text-fig. 15B
1985 *Protacanthodiscus nodusus* n. sp. — Tavera, p. 202, pl. 27, fig. 2, text-fig. 15C
1985 *Durangites singularis* n. sp. — Tavera, p. 168, pl. 17, figs. 6–9, text-fig. 12E
pars 1985 *Durangites sutneroides* n. sp. —Tavera, p. 168, pl. 18, figs. 1, 2, 3, 5, non fig. 4a,b
1985 *Durangites heilprini* (Aguilera) — Tavera, p. 164, pl. 18, figs. 6, 7, text-fig. 12G
1985 *Durangites gigantis* n. sp. — Tavera, p. 162, pl. 18, figs. 8, 9, text-fig. 12A,B
1985 *Durangites acanthicus* Burckhardt — Tavera, p. 156, pl. 18, figs. 10a,b, 11, text-fig. 12C
1985 *Durangites vulgaris* Burckhardt — Tavera, p. 157, pl. 18, figs. 12, 13a,b, text-fig. 12I
1985 *Durangites apertus* n. sp. — Tavera, p. 161, pl. 18, figs. 14, 15a,b, text-fig. 12F
1985 *Durangites* cf. *astillerensis* Imlay — Tavera, p. 166, pl. 18, fig. 16, text-fig. 12D
1985 *Neoperisphinctes falloti* (Kilian) — Tavera, p. 132, pl. 16, fig. 10a,b
1994 *Protacanthodiscus* (*Protacanthodiscus*) *andreaei* (Kilian) — Boughdiri, p. 147, pl. 3, figs. 1a,c, 3a,b, pl. 4, fig. 2
1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. A — Boughdiri, p. 208, pl. 3, fig. 5
1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 3 — Boughdiri, p. 168, pl. 3, fig. 7
1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 4 — Boughdiri, p. 170, pl. 2, fig. 17
1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 7 — Boughdiri, p. 176, pl. 3, fig. 2
1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 11 — Boughdiri, p. 186, pl. 3, fig. 6
1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 12 — Boughdiri, p. 188, pl. 4, fig. 1
1994 *Protacanthodiscus* (*Protacanthodiscus*) *coronatus* (Tavera) — Boughdiri, p. 151, pl. 4, figs. 6, 7
1994 *Durangites* (*Durangites*) *humboldti* (Burckhardt) — Boughdiri, p. 99, pl. 1, figs. 33a,b, 34
1994 *Durangites* (*Durangites*) *juanense* (Cantú-Chapa) — Boughdiri, p. 106, pl. 1, fig. 34
1998b *Durangites* (*Protacanthodiscus*) *andreaei* (Kilian) — Enay et al., figs. 2, n° 16a,b (=Kilian, 1889, pl. 32, fig. la,b)
1998b *Durangites* (*Durangites*) *juanensis* Cantú-Chapa — Enay et al., figs. 2, n° 6, 7 (=Boughdiri, 1994, pl. 1, fig. 35)
1998b *Durangites* (*Durangites*) *humboldti* Burckhardt — Enay et al., figs. 2, n° 8–10a,b
1998b *Durangites* (*Protacanthodiscus*) sp. — Enay et al., figs. 2, n° 11
1998b *Durangites* (*Protacanthodiscus*) *apertus* (Tavera) — Enay et al., figs. 2, n° 13–14
2010 *Protacanthodiscus* cf. *andreaei* (Kilian) — Ivanov et al., pl. 3, fig. 3
2010 *Durangites* aff. *fusicostatus* Burckhardt — Ivanov et al., pl. 3, fig. 1a,b
2010 *Durangites* cf. *vulgaris* Burckhardt — Ivanov et al., pl. 3, fig. 2a,b
2010 *Durangites singularis* Tavera — Ivanov et al., pl. 3, fig. 4
2010 *Protacanthodiscus apertus* (Tavera) — Benzaggagh et al., fig. 5i
2010 *Durangites humboldti* Burckhardt — Benzaggagh et al., fig. 5n
non 2013 *Protacanthodiscus coronatus* (Tavera) — Szives & Főzy, p. 301, pl. 1, figs. 2, 4 (=Himalayitidae gen. nov. et sp. nov.)
non 2013 *Protacanthodiscus andreaei* (Kilian) — Szives & Főzy, p. 300, pl. 5, fig. 4a,b, pl. 6, fig. 5a,b, pl. 8, fig. 10a,b (=Himalayitidae gen. nov. et sp. nov.)
non 2013 *Protacanthodiscus andreaei* (Kilian) — Főzy & Scherzinger, p. 257 (=Himalayitidae gen. nov. et sp. nov.)

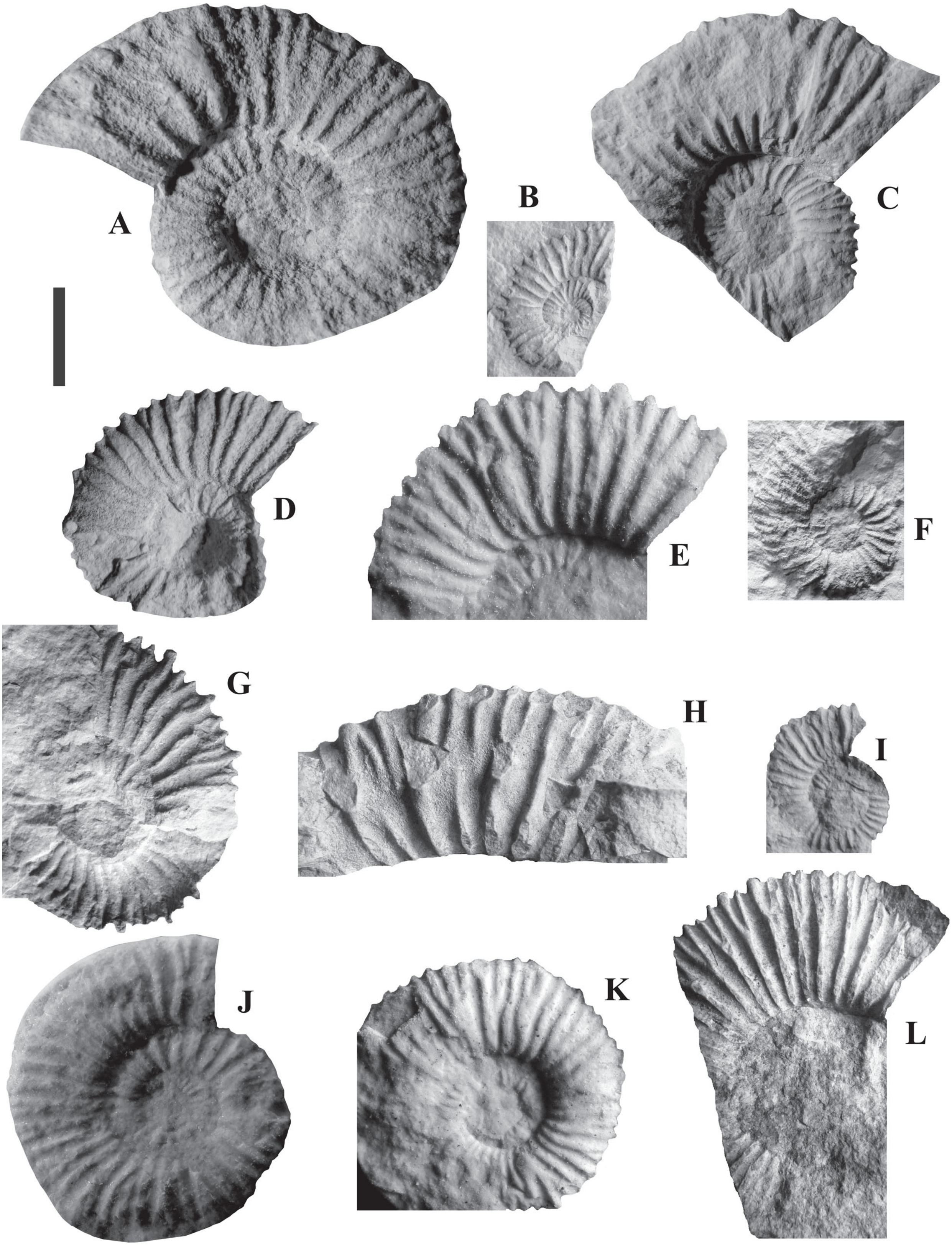

Fig. 5. Adult/subadult microconchs of *Protacanthodiscus andreaei* (Kilian) from the late Tithonian (*P. andreaei* Zone) of Le Chouet. **A** — MPP-CHT.21/57 (bed 85), **B** — MPP-CHT.21/87 (bed 85), **C** — MPP-CHT.19/13 (bed 83), **D** — MPP-CHT.21/25 (bed 85), **E** — MPP-CHT.18/20 (bed 82), **F** — MPP-CHT.21/31 (bed 85), **G** — MPP-CHT.19/24 (bed 83), **H** — MPP-CHT.15/06 (bed 79), **I** — MPP-CHT.21/19 (bed 85), **J** — MPP-CHT.21/96 (bed 85), **K** — MPP-CHT.19/34 (bed 83), **L** — MPP-CHT.15/21 (bed 79). Bar scale is 10 mm.

Holotype: The specimen illustrated by Kilian (1889, p. 670, pl. 32, fig. la,b) from the De Verneuil collection (FSL.13056). It was re-illustrated by Enay et al. (1998b, figs. 2–16a,b).

Material: MPP-CHT.15/4, MPP-CHT.15/6, MPP-CHT.15/21, MPP-CHT.18/1, MPP-CHT.18/20, MPP-CHT.19/7, MPP-CHT.19/12, MPP-CHT.19/13, MPP-CHT.19/14, MPP-CHT.19/15, MPP-CHT.19/24, MPP-CHT.19/25, MPP-CHT.19/31, MPP-CHT.19/34, MPP-CHT.19/35, MPP-CHT.21/5, MPP-CHT.21/7, MPP-CHT.21/16, MPP-CHT.21/19, MPP-CHT.21/20, MPP-CHT.21/25, MPP-CHT.21/26, MPP-CHT.21/27, MPP-CHT.21/32, MPP-CHT.21/35, MPP-CHT.21/37, MPP-CHT.21/38, MPP-CHT.21/39, MPP-CHT.21/40, MPP-CHT.21/41, MPP-CHT.21/57, MPP-CHT.21/62.

Measurements: See Table 2.

Description: A detailed examination of the material at our disposal reveals marked sexual dimorphism. Microconchs (Dmax < 50 mm) exhibit three ontogenetic stages:

- On inner whorls (D<15 mm), the ornamentation is composed of straight, rigid, prosiradiate ribs marked by small punctiform shoulders at the furcation point;
- To D ~ 30 mm, ornamentation is irregular, composed of rigid bifurcate ribs. The furcation point is higher on the flank. The umbilical wall and margin are more abrupt. The whorls section is sub-circular;
- On the adult stage (D > 30 mm), ornamentation is characterized by marked irregular ribbing. Most of the ribs bifurcate on the mid flank with more or less strong lateral tubercles at the furcation point. Generally, on bifurcate ribs, the adoral branch is ended by a pinched ventro-lateral tubercle on the axis of the coiling. At that stage, ribs can also be simple, trifurcate, intercalated or looped. Several specimens possess regular prosiradiate and flexuous bifurcate ribs on the body chamber. At the mouth of the shell, the whorl section is more or less sub-oval to sub-rectangular.

Macroconchs (Dmax up to 165 mm) also show three ontogenetic stages:

- The juvenile stage is similar to that of the microconchs;
- The intermediate stage can reach D ~ 50 mm. Compared to the microconchs, this stage is marked by dense and flexuous ribs. The furcation point is lower on the flank;
- At the adult stage, two marked morphotypes can be distinguished. (1) A slender group characterized by a dense ribbing and a sub-rectangular whorl section, higher than wide. The ribs are mainly bifurcated and the tubercles are feeble or absent. The ventral band is attenuated and the ribs can cross the venter with a shallow weakening. (2) A robust group characterized by larger size, an irregular and coarse ribbing pattern and a marked sub-hexagonal whorl section with a flattened ventral area. Trifurcate ribs are common, with massive tubercles at the furcation point.

Table 2: Measurements of *Protacanthodiscus andreaei* (Kilian). U = umbilical diameter, Wh = whorl height, D = diameter. U/D and Wh/D ratios are dimensions as a percentage of the diameter at the point of measurement.

Specimen	D	Wh	U	U/D	Wh/D
CHT 15–04	/	17.5	/	/	/
CHT 15–06	40	17	15	0.38	0.43
CHT 15–21	40	15	16	0.40	0.38
CHT 18–01	/	/	/	/	/
CHT 18–20	/	15	/	/	/
CHT 19–07	17	6	8.5	/	0.35
CHT 19–12	19	6	7	0.37	0.32
CHT 19–13	36	14.5	15	0.42	0.40
CHT 19–14	31	12	/	/	0.39
CHT 19–15	37	13	18	0.49	0.35
CHT 19–24	38	12.5	13	0.34	0.33
CHT 19–25	55	21	24	0.44	0.38
CHT 19–31	22	7	10	0.45	0.32
CHT 19–34	28.5	10.5	10	0.35	0.37
CHT 19–35	62	22	26	0.42	0.35
CHT 21–05	/	20	/	/	/
CHT 21–07	32	11	12	0.38	0.34
CHT 21–16	/	/	/	/	/
CHT 21–19	16	6	7	0.44	0.38
CHT 21–20	22	8.5	8	0.36	0.39
CHT 21–25	24	8	8.5	0.35	0.33
CHT 21–26	21	8	8	0.38	0.38
CHT 21–27	36	12	15	0.42	0.33
CHT 21–32	/	14	15.5	/	/
CHT 21–35	29.5	10.5	10	0.34	0.36
CHT 21–37	/	/	/	/	/
CHT 21–38	37	23	22	0.59	0.62
CHT 21–39	/	/	/	/	/
CHT 21–40	/	/	/	/	/
CHT 21–41	70	28	28	0.40	0.40
CHT 21–57	34	13	12.5	0.37	0.38
CHT 21–62	41	14	17	0.41	0.34

Occurrence: Beds 79 to 85, *P. andreaei* Zone (top of calpionellid *C. intermedia* Subzone and lower part of the *C. colomi* Subzone), upper Tithonian. As outlined by Tavera (1985), the appearance and increase in abundance of the species is gradual. *P. andreaei* is reported from South East Spain and France, Italy, Bulgaria, Tunisia and Morocco. Since *D. vulgaris* Tavera *non* Burckhardt is herein considered as a microconch of *P. andreaei*, the *D. vulgaris* Zone of Sarti (1988) is a junior subjective synonym of the *P. andreaei* Zone introduced by Wimbledon et al. (2013).

Protacanthodiscus hexagonus (Tavera, 1985)
Fig. 7D

1985 "*Corongoceras*" *hexagonus* Tavera, p. 195, pl. 28, figs. 3a,b, 4a,b, text-fig. 17H

2010 *Protacanthodiscus hexagonus* Tavera — Benzaggagh et al., p. 309, figs. 5, l-m

Type: The holotype is specimen T.Co.3.1. from the Tavera collection, deposited in the collections of the University of Granada.

Material: MPP-CHT.21/7.

Description: The single specimen shows the first ontogenetic stage of the type-species of *Protacanthodiscus*. By comparison to *P. andreaei*, the intermediate stage is very reduced and the morphology that characterizes the adult stage of the robust macroconch occurs at a diameter similar to that seen in small adult microconchs. Trifurcations and lateral and ventral tubercles are prominent. The whorl section is almost sub-hexagonal.

Remarks: Tavera (1985) separated a group of "*Corongoceras*", based on "*C.*" *hexagonus*, seen as the phyletic link between *Corongoceras sensu lato* (=*Ardesciella* Bulot et al. 2014) and *Protacanthodiscus*. This view is not supported by

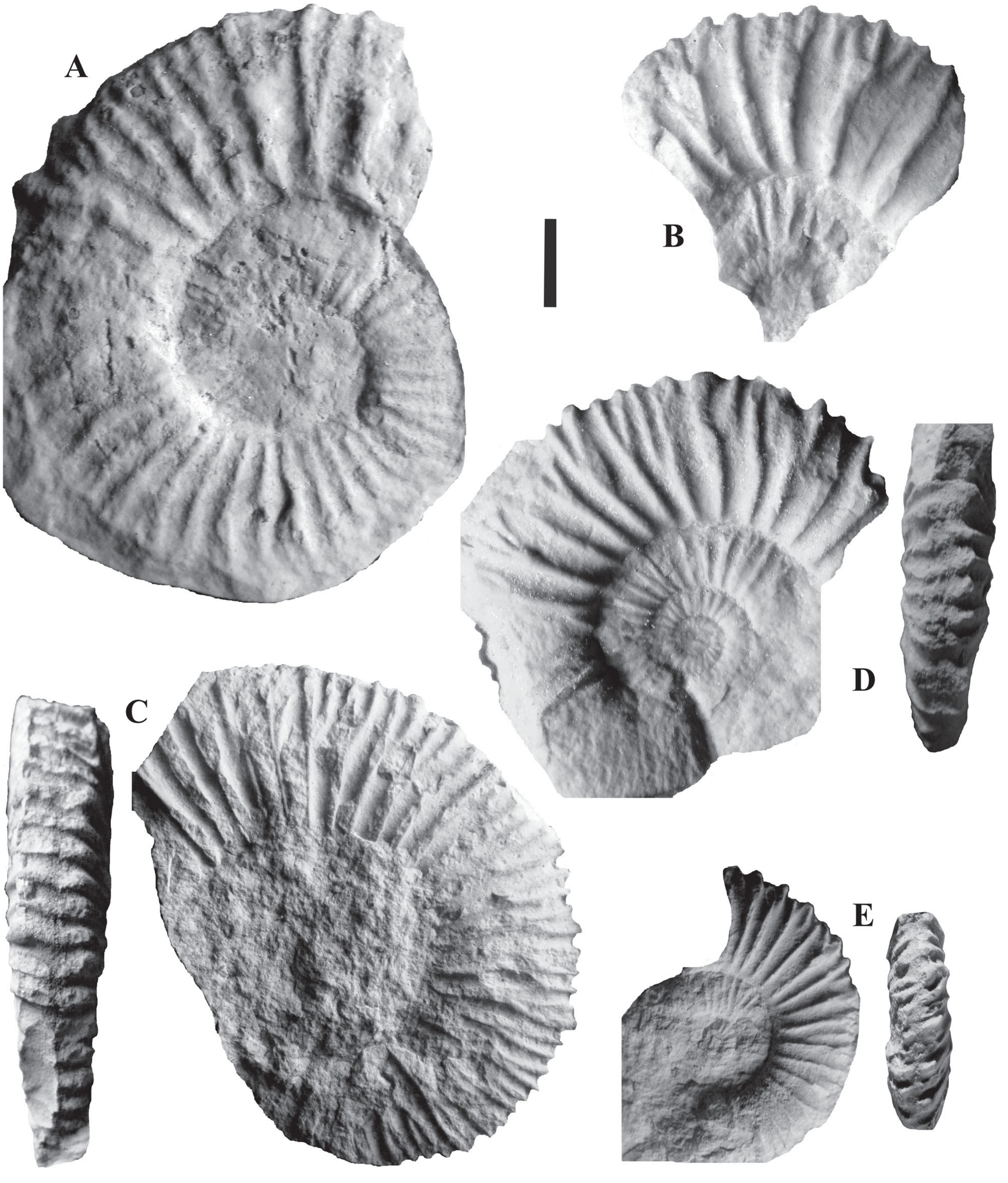

Fig. 6. Adult macroconchs of *Protacanthodiscus andreaei* (Kilian) from the late Tithonian (*P. andreaei* Zone) of Le Chouet. **A** — MPP-CHT.21/41 (bed 85), **B** — MPP-CHT.21/5 (bed 85), **C** — MPP-CHT.21/54 (bed 85), **D** — MPP-CHT.21/5 (bed 85), **E** — MPP-CHT.21/27 (bed 85). Bar scale is 10 mm.

the observed stratigraphical fossil distribution at Le Chouet, where *P. hexagonus* co-occurs with the last *P. andreaei* at the top of the upper Tithonian. In our opinion, *P. hexagonus* present a peramorphic change combined with miniaturization. Such forms have already been documented in several perisphinctid lineages and have been called miniconchs (see discussion in Davis et al. 1996).

Occurrence: Bed 85, top of *P. andreaei* Zone (middle part of the calpionellid *C. colomi* Subzone), upper Tithonian. *P. hexagonus* is only known in southeast France, Spain and Morocco.

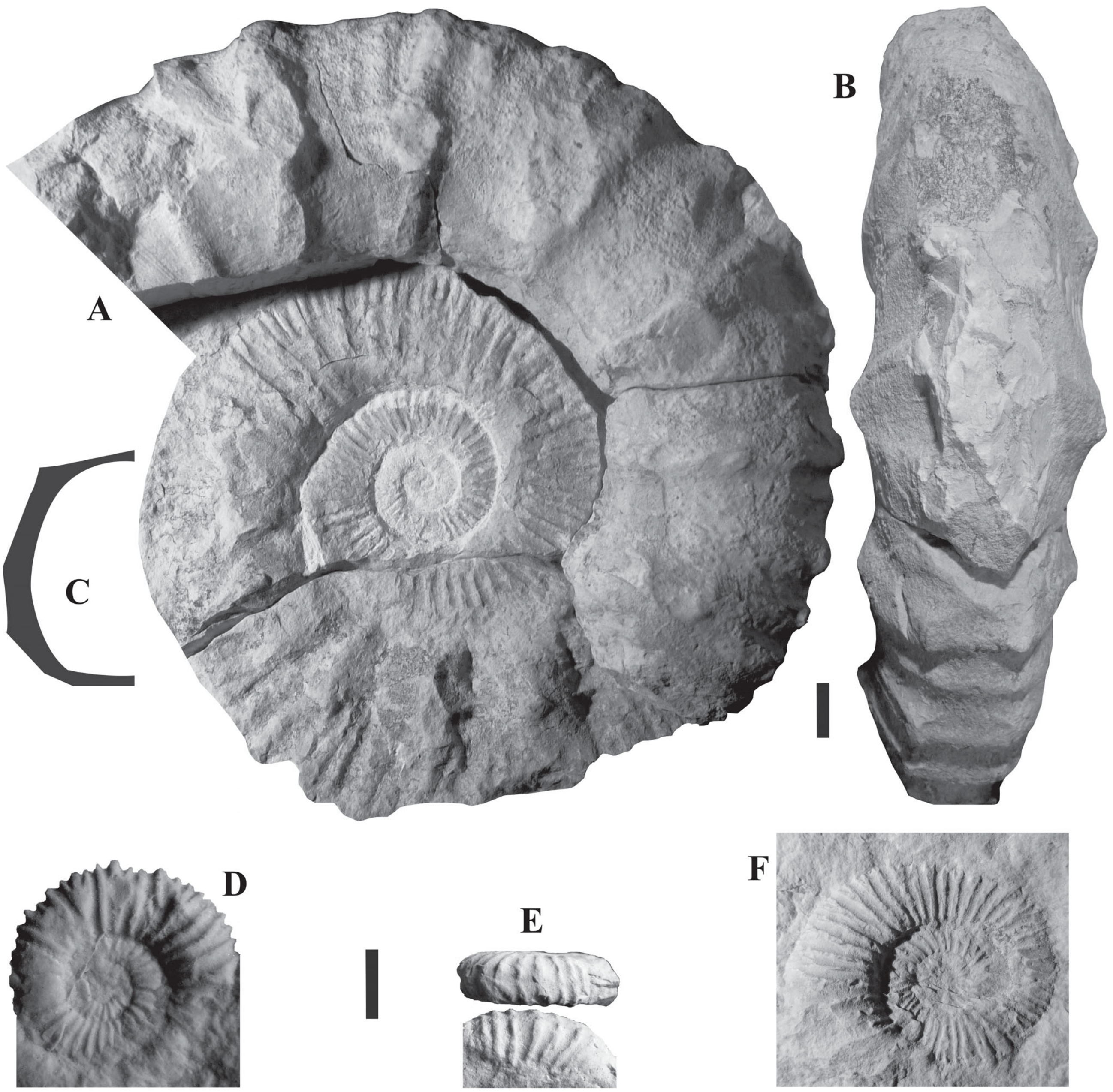

Fig. 7. Lateral (**A**), ventral (**B**) views, and whorl section at about D = 131 mm (**C**) of complete macroconch of *Protacanthodiscus andreaei* (Kilian) from the late Tithonian (*P. andreaei* Zone) of Le Chouet: MPP-CHT.21/95 (bed 85). **D** — *Protacanthodiscus hexagonus* (Tavera) from the *P. andreaei* Zone (bed 85) of Le Chouet: MPP-CHT.21/7. *Toucasiella gerardi* Enay et al., from the *P. andreaei* Zone of Le Chouet: **E** — MPP-CHT.15/9 [m] (bed 79), **F** — MPP-CHT.15t/14 [m] (bed 79). Bar scale is 10 mm.

Genus *Toucasiella* Enay, Boughdiri & Le Hégarat, 1998a

Type species: *Toucasiella gerardi* Enay, Boughdiri, Le Hégarat, 1998b; by original designation.

Toucasiella gerardi Enay, Boughdiri & Le Hégarat, 1998a
Fig. 7E–F

1994 *Durangites* (*Durangites*) *mazenoti* (Mazenot, 1939) non (Breistroffer, 1937) — Boughdiri, pl. 1, figs. 7, 8a,b, 11, 12

1998a *Toucasiella gerardi* n. sp. Enay et al., p. 471, figs. 1–21

Holotype: the unnumbered specimen illustrated by Enay et al. (1998a, fig. 4) from Cabra (Spain).

Material: MPP-CHT.15t/14 and MPP-CHT.15/9.

Description: The specimen MPP-CHT.15/9 is an incomplete body-chamber of a typical microconch form. It shows the extreme adult ornamental pattern of *T. gerardi*, with strong and spaced simple ribs, ended by externo-lateral and ventro-lateral tubercles (compare with fig. 18a–b in Enay et al. 1998a). At the end of the body chamber, the whorl section is sub-rectangular, the ventral furrow is weak and it is crossed by the ribs.

The specimen MPP-CHT.15t/14 perfectly matches the morphological and ornamental pattern of the adult macroconch of *T. gerardi*, in its middling size, compressed section, single and bifurcate ribs with lateral tubercles at the furcation points (compare with fig. 8 in Enay et al. 1998a).

Remarks: According to Enay et al. (1998a), *Toucasiella gerardi* is based on small-sized himalayitids from the *M. microcanthum* Zone (*Chitinoidella* Zone) of south east Spain and central Tunisia. Our specimens originate from a higher level at the base of the *P. andreaei* Zone (*Crassicollaria* Zone, top of the *C. intermedia* Subzone).

However, it should be noted that Boughdiri et al. (1999, p. 107) reported *Toucasiella gerardi* from bed RHS-4 in the Sidi Khalif Formation (Tunisia). Due to the dolomitization of the lower part of that formation, there is no consensus on the calpionellid biostratigraphic scheme at the base of the upper Tithonian (see Boughdiri et al. 1999, fig. 2). Thus, there is no counter-argument to consider an expansion of the *C. intermedia* Subzone in the Sidi Khalif Formation. This hypothesis is more consistent with the calpionellids data at Le Chouet (Wimbledon et al. 2013; Bulot et al. 2014).

Occurrence: Bed 79, *P. andreaei* Zone (top of the *C. intermedia* Subzone), upper Tithonian. Beside the well-documented occurrences in SE Spain and Tunisia, this is the first report of the species in SE France.

Conclusion

Due to morphological convergence and misdated stratigraphic occurrences, the taxonomy of himalayitid genera is still at a very preliminary stage. The overlooked late Tithonian endemism of the family at the genus level is much higher than was previously assumed in the literature. This is reflected by our introduction of *Parrasiella* gen. nov. for Mexican and Cuban species hitherto considered to be true *Durangites*. Evidence suggests that the latter genus only occurs in the lower to lower middle Berriasian of Mexico. As a consequence, the use of *Durangites* as a marker for the late Tithonian should be abandoned.

Also, none of the records of the genus in the Mediterranean Tethys belong to *Durangites*: the great majority of these reports refer to inner whorls and/or juveniles of *Protacanthodiscus* or to *Boughdiriella chouetensis* gen. et sp. nov. The record of the himalayitids is very homogenous across the regions of the Mediterranean and it is dominated by the highly variable species *Protacanthodiscus andreaei*. As a result, the geographical and stratigraphical pattern of the species is very useful in defining a zone at the top of the upper Tithonian.

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