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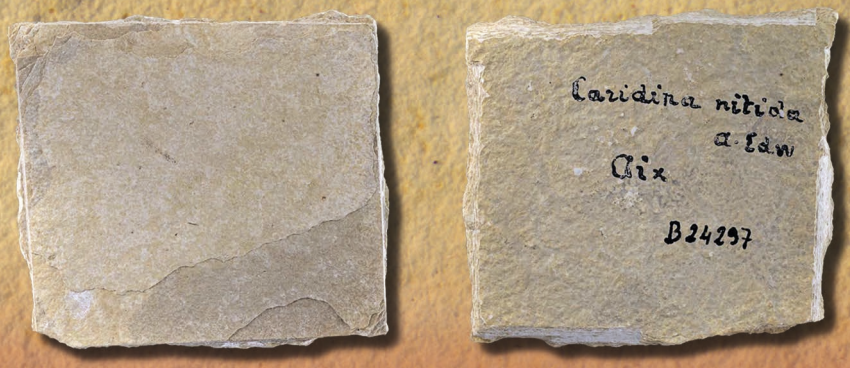
Valentin de MAZANCOURT & Denis AUDO



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Revision of *Dugastella nitida* n. comb. (Crustacea: Decapoda: Atyidae), a freshwater shrimp from the Oligocene of Aix-en-Provence

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ABSTRACT
The fossil shrimp species *Caridina nitida* A. Milne-Edwards, 1879 described from the Oligocene lacustrine deposits of Aix-en-Provence was considered to be a *nomen dubium*. Based on newly discovered specimens at the type locality, we provide an illustrated re-description of this species. The detailed morphological study leads us to place *C. nitida* within the extant genus *Dugastella* Bouvier, 1912. These new data support the hypothesis of a fresh to slightly brackish palaeoenvironment. A specimen possibly corresponding to A. Milne-Edward's holotype was found in the collections of the Muséum national d'Histoire naturelle but since the fossil shrimp is not visible anymore (destroyed), a neotype is designated among the new specimens.

KEY WORDS
Decapoda,
Caridea,
Atyidae,
lacustrine,
Lagerstätte,
palaeoenvironment,
neotypification,
new combination.

RÉSUMÉ
Révision de Dugastella nitida *n. comb. (Crustacea: Decapoda: Atyidae), une crevette d'eau douce de l'Oligocène d'Aix-en-Provence.*
L'espèce de crevette fossile *Caridina nitida* A. Milne-Edwards, 1879 provenant des sédiments lacustres d'Aix-en-Provence et datant de l'Oligocène était considérée comme *nomen dubium*. À partir de nouveaux spécimens découverts dans la localité type, nous proposons une re-description illustrée de cette espèce. L'étude morphologique nous conduit à la placer au sein du genre actuel *Dugastella* Bouvier, 1912. Ces nouvelles données renforcent l'hypothèse d'un paléoenvironnement dulcicole à légèrement saumâtre. L'holotype de A. Milne-Edwards a été retrouvé dans les collections du Muséum national d'Histoire naturelle mais la crevette fossile n'étant pas visible (détruite), un néotype est désigné parmi les nouveaux spécimens décrits.

MOTS CLÉS
Decapoda,
Caridea,
Atyidae,
lacustre,
Lagerstätte,
paléoenvironnement,
néotypification,
combinaison nouvelle.

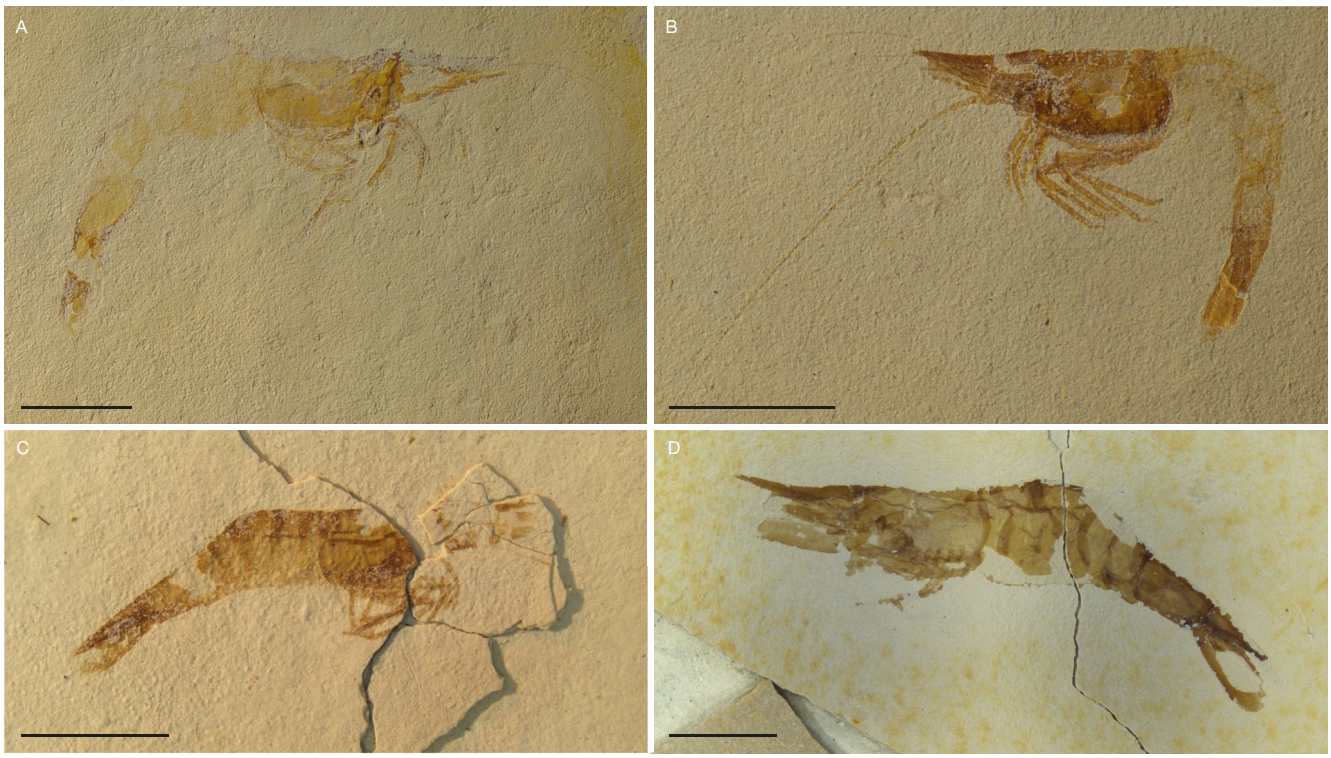

FIG. 1. — Specimens of *Dugastella nitida* (A. Milne-Edwards, 1879), n. comb.: **A**, MNHN.F.A59324a; **B**, neotype MNHN.F.A59323 (composite image of part and counter-part); **C**, MNHN.F.A90841; **D**, MNHN.F.A90842a. Scale bars: 5 mm.

INTRODUCTION

The freshwater shrimp family Atyidae De Haan, 1849 is one of the most diversified among the Caridea Dana, 1852 with 543 extant species distributed in 46 genera (DecaNet 2024), having colonised freshwater habitats on all continents except Antarctica (De Grave *et al.* 2008). For as long as they have been studied, the Atyidae were thought to have an ancient origin compared to other shrimp families (Ortmann 1894; Bouvier 1925; Bănărescu 1973), however very few fossils were discovered to confirm this hypothesis. The oldest fossils considered to belong to the Atyidae are the three species of *Delclosia* Rabadà, 1990 from the Lower Cretaceous of Spain (Rabadà 1990, 1993; Garassino 1997; López-Horgue & Bodego 2017), which are often used as a calibration point for molecular phylogenies (von Rintelen *et al.* 2012; de Mazancourt *et al.* 2019). A dubious species is the fossil *Caridina nitida* A. Milne-Edwards, 1879 from the lacustrine marl deposits of Aix-en-Provence (southern France). The description is rather succinct and the attribution to the extant genus *Caridina* H. Milne Edwards, 1837 is mostly based on its freshwater palaeoenvironment, which quickly led carcinologists to raise doubts regarding its generic affinities (Ortmann 1894). In the original publication, A. Milne-Edwards (1879) did not mention where the type material was deposited and how many specimens were part of the study. More recent collections made in the same deposits of Aix-en-Provence yielded shrimp fossils that were reported by Nury (1988), Nury & Thomassin (1994) and figured by Gaudant *et al.* (2018). These shrimps were identified as penaeids based on the supposedly brackish/estuarine habitat (Crosnier *in* Nury 1988), oblivious to the shrimp described by A. Milne-Edwards from the same location.

The aim of the present study is to revise the status of *Caridina nitida* based on these newly collected specimens, amend the original description and provide illustrations of the fossils.

MATERIAL AND METHODS

This study is based on a total of 11 specimens of *Dugastella nitida* (A. Milne-Edwards, 1879), n. comb., all kept in the palaeontological collection of the Muséum national d'Histoire naturelle (MNHN, Paris, France).

Specimens were documented with a digital single lens hybrid camera equipped with a macrolens (Canon MPE 65 mm) or a digital microscope, using image stacking and stitching to obtain images completely in focus and with a sufficient resolution. Extant specimens were photographed under 70% ethanol and slight traces of bubbles (streaks) were digitally removed without affecting the aspect of the specimen in the final image. Fluorescence imaging for fossil specimens was attempted, but they did not show any clear fluorescence under UV, green or blue light illumination.

High resolution images were used as basis for line drawings made with a vector-graphic software following the method of Coleman (2003, 2006).

GEOLOGICAL SETTING AND PALAEOENVIRONMENT

The fossils were found near the village of Les Figons, *c.* 8 km N-W of Aix-en-Provence, southern France, in the "insect bed"

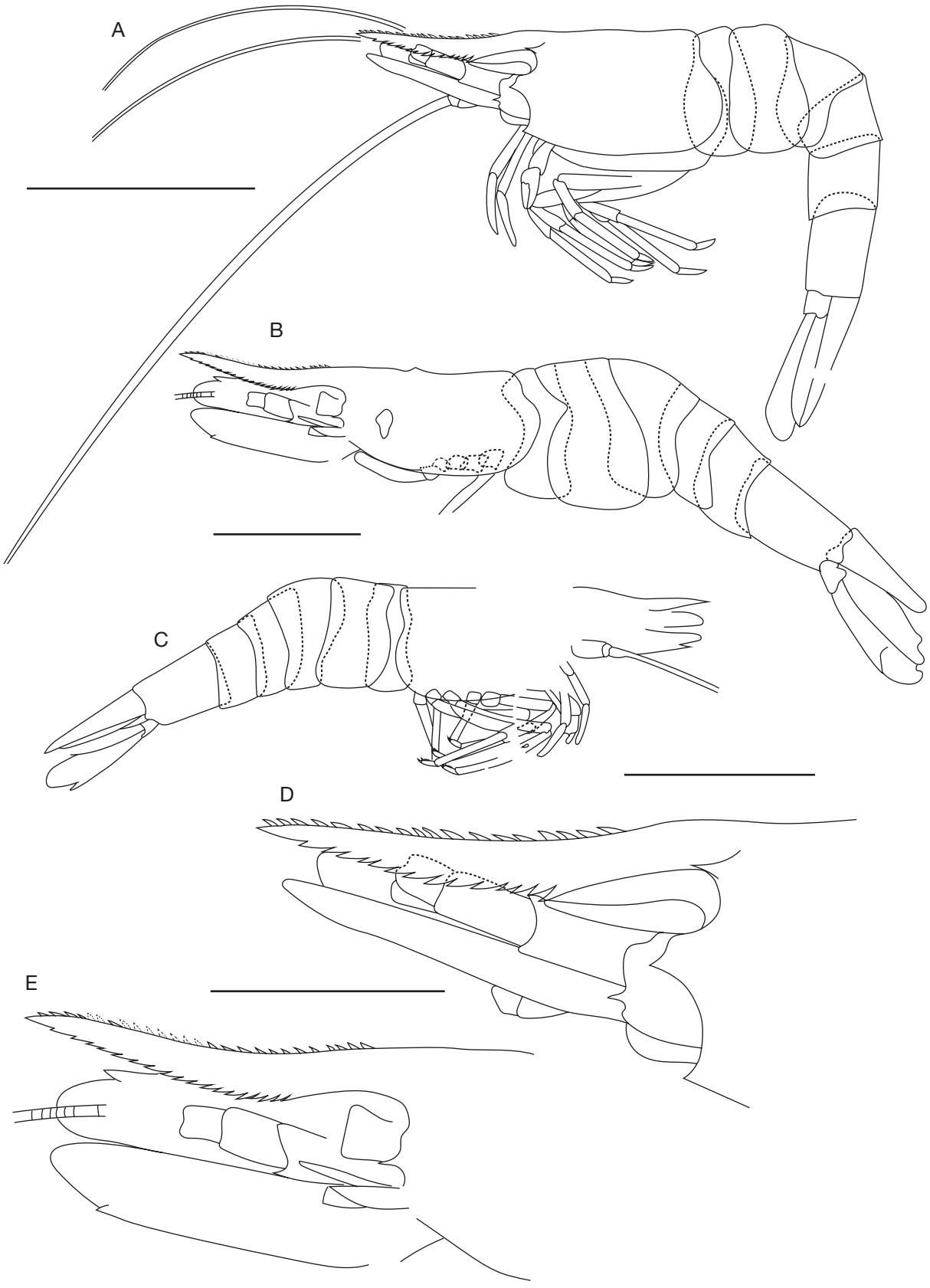

FIG. 2. — Interpretative drawings of *Dugastella nitida* (A. Milne-Edwards, 1879), n. comb.: **A**, **D**, MNHN.F.A59323; **B**, **E**, MNHN.F.A90842; **C**, MNHN.F.A90841. Scale bars: A-C, 5 mm; E, 2 mm.

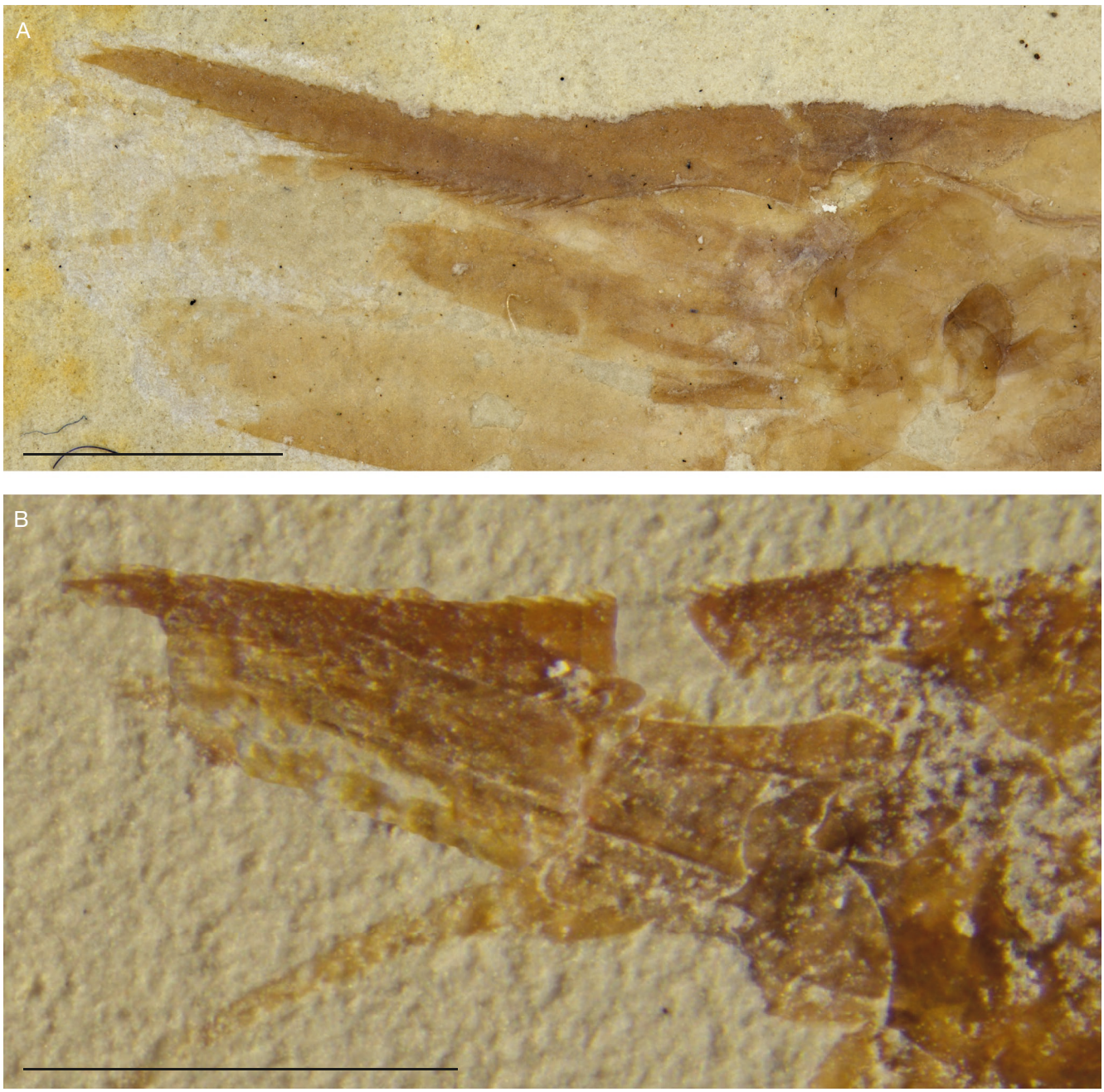

FIG. 3. — Detailed views of the rostrum of *Dugastella nitida* (A. Milne-Edwards, 1879), n. comb.: **A**, MNHN.F.A90842a; **B**, neotype MNHN.F.A59323 (composite image of plate and counter-plate). Scale bars: 2 mm.

composed of a very thinly laminated marl of creamy to blueish colouration, below a thick level of hard white limestone covered by a gypsum bed.

Refer to Gaudant *et al.* (2018) for an extensive account of the geology and palaeoenvironment of this deposit.

INSTITUTIONAL ABBREVIATIONS

MNHN	Muséum national d'Histoire naturelle, Paris, France;
MNHN.F	Muséum national d'Histoire naturelle, collection de Paléontologie, Paris, France;
MNHN-IU	Muséum national d'Histoire naturelle, collection d'invertébrés marins actuels, Paris, France.

SYSTEMATIC PALAEONTOLOGY

Super-order EUCARIDA Calman, 1904
Order DECAPODA Latreille, 1802
Infra-order CARIDEA Dana, 1852
Family ATYIDAE De Haan, 1849

Genus *Dugastella* Bouvier, 1912

TYPE SPECIES. — *Dugastella marocana* Bouvier, 1912 (Fig. 8) by monotypy.

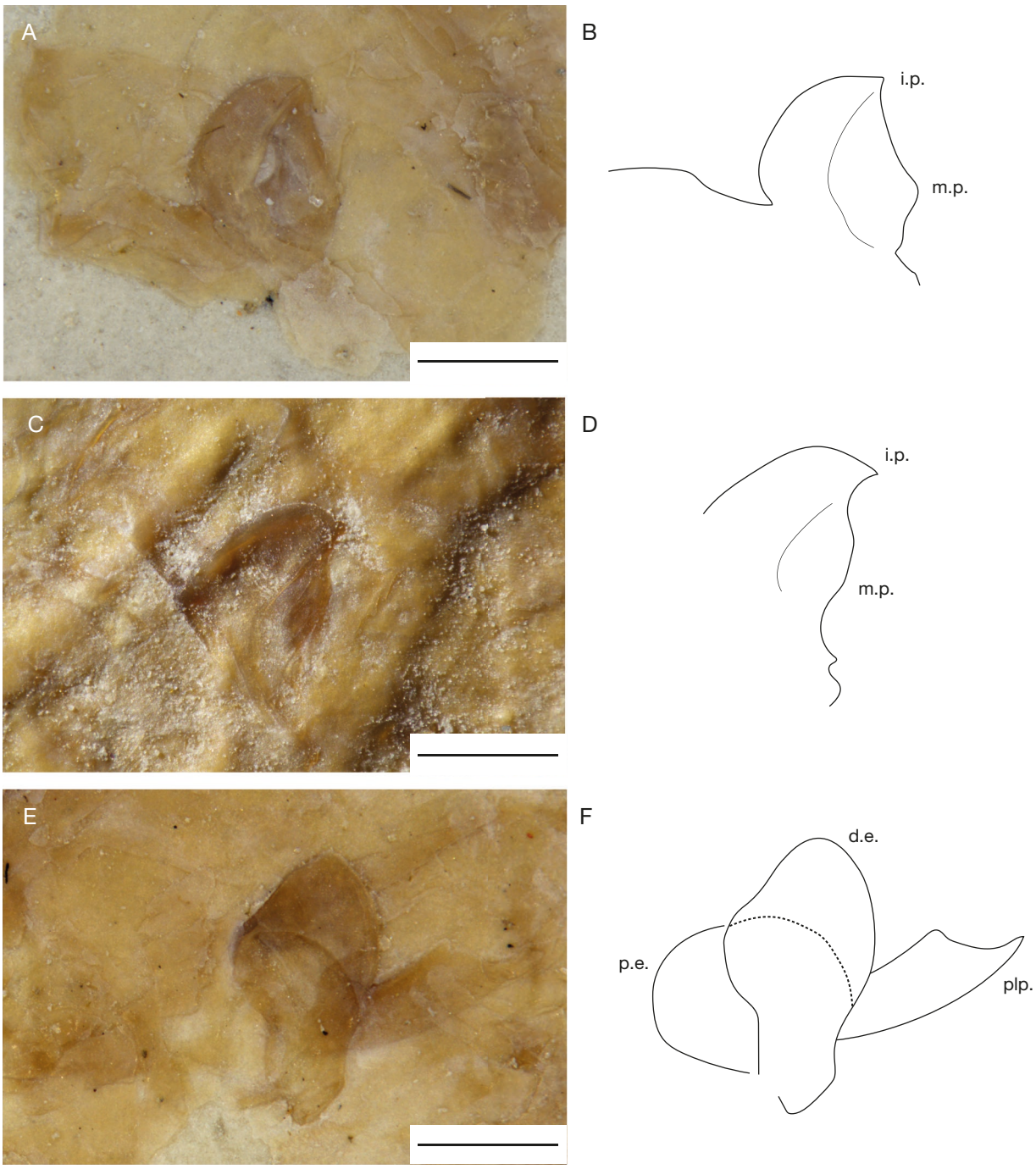

FIG. 4. — Detailed views and interpretative drawings of mouthparts of *Dugastella nitida* (A. Milne-Edwards, 1879), n. comb.: **A**, **B**, mandible of MNHN.F.A90842a; **C**, **D**, mandible of MNHN.F.A59324a; **E**, **F**, first maxilla of MNHN.F.A90842a. Abbreviations: **i.p.**, incisor process; **m.p.**, molar process; **p.e.**, proximal endite; **d.e.**, distal endite; **plp.**, palp. Scale bars: 0.5 mm.

INCLUDED SPECIES. — *Dugastella marocana*, *Dugastella valentina* (Ferrer Galdiano, 1924), *Dugastella nitida* (A. Milne-Edwards, 1879) †† n. comb.

DIAGNOSIS (FROM Sket & Zakšek 2009). — Paratyine genus with supraorbital and suborbital teeth, and with a pterygostomial carapace border jutting out (pterygostomial spine); dorsal rostral denticulation not continued posteriorly on carapace; maxilliped I exopodal lobe gradually narrowed distally, with terminal flagellum as long as width of lobe; pereiopods I-III or more with exopodites; mature male pereiopods III-IV not distally widened, dactylus not pectinate; pereiopod V dactylus comb-like; male pleopod I endopodite short, ribbon-shaped, with parallel side borders, part of distal border extended into comparatively wide appendix interna, which is approximately twice as long as it is wide; male pleopod II with sausage-shaped appendix masculina, which is set in the distal half with long straight spines (longer than appendix masculina diameter), moderately longer than appendix interna. All known species are epigean, with fully developed corneas.

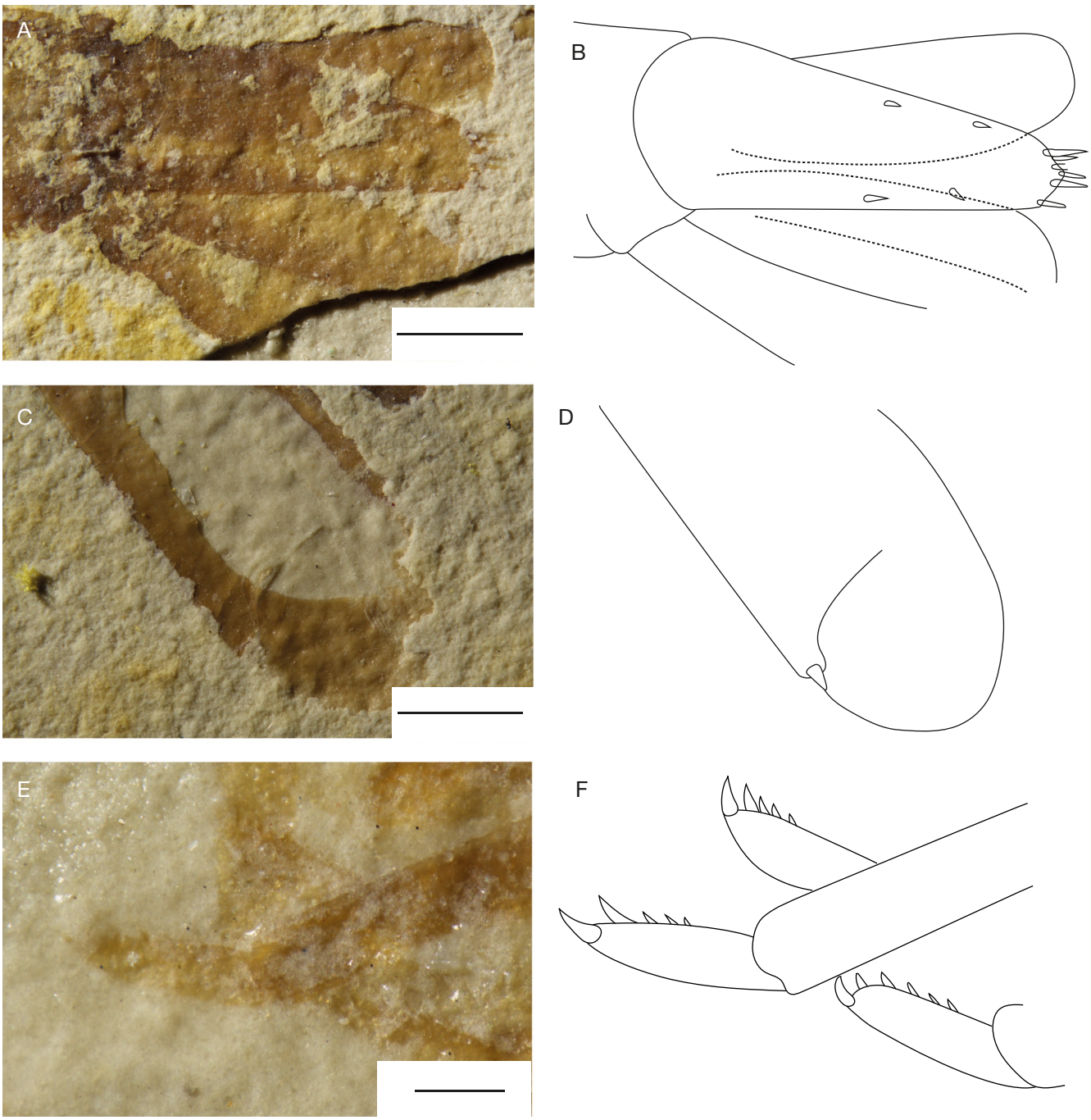

Fig. 5. — Detailed views and interpretative drawings of anatomical parts of *Dugastella nitida* (A. Milne-Edwards, 1879), n. comb.: **A**, **B**, telson of MNHN.F.A90843; **C**, **D**, uropod of MNHN.F.A90842a; E, F, distal end of pereiopods of MNHN.F.A90841. Scale bars: A, C, 1 mm; E, 0.2 mm.

Dugastella nitida (A. Milne-Edwards, 1879), n. comb. (Figs 1-7)

Caridina nitida A. Milne-Edwards, 1879: 77-78.

"penaeid shrimps" – Crosnier *in* Nury 1988: 305, pl. 6, figs 4, 7. — Nury & Thomassin 1994: 103; Gaudant *et al.* 2018: 464, 475, fig. 14C, D.

Type material. — **Neotype** (designated herein) • **France**. 1 specimen; near Aix-en-Provence, "Insect bed" of Les Figons; Late Oligocene, late Chattian; MNHN.F.A59323 (Figs 1A, B; 2A, D; 3B, also figured by Gaudant *et al.* 2018: fig. 14C).

Type locality. — Aix-en-Provence, France.

Type age. — Late Oligocene (late Chattian).

Additional material. — Same locality data as neotype; MNHN.F.A59324 (also figured by Gaudant *et al.* 2018: fig. 14D), series of eight specimens numbered from MNHN.F.A90841 to MNHN.F.A90848.

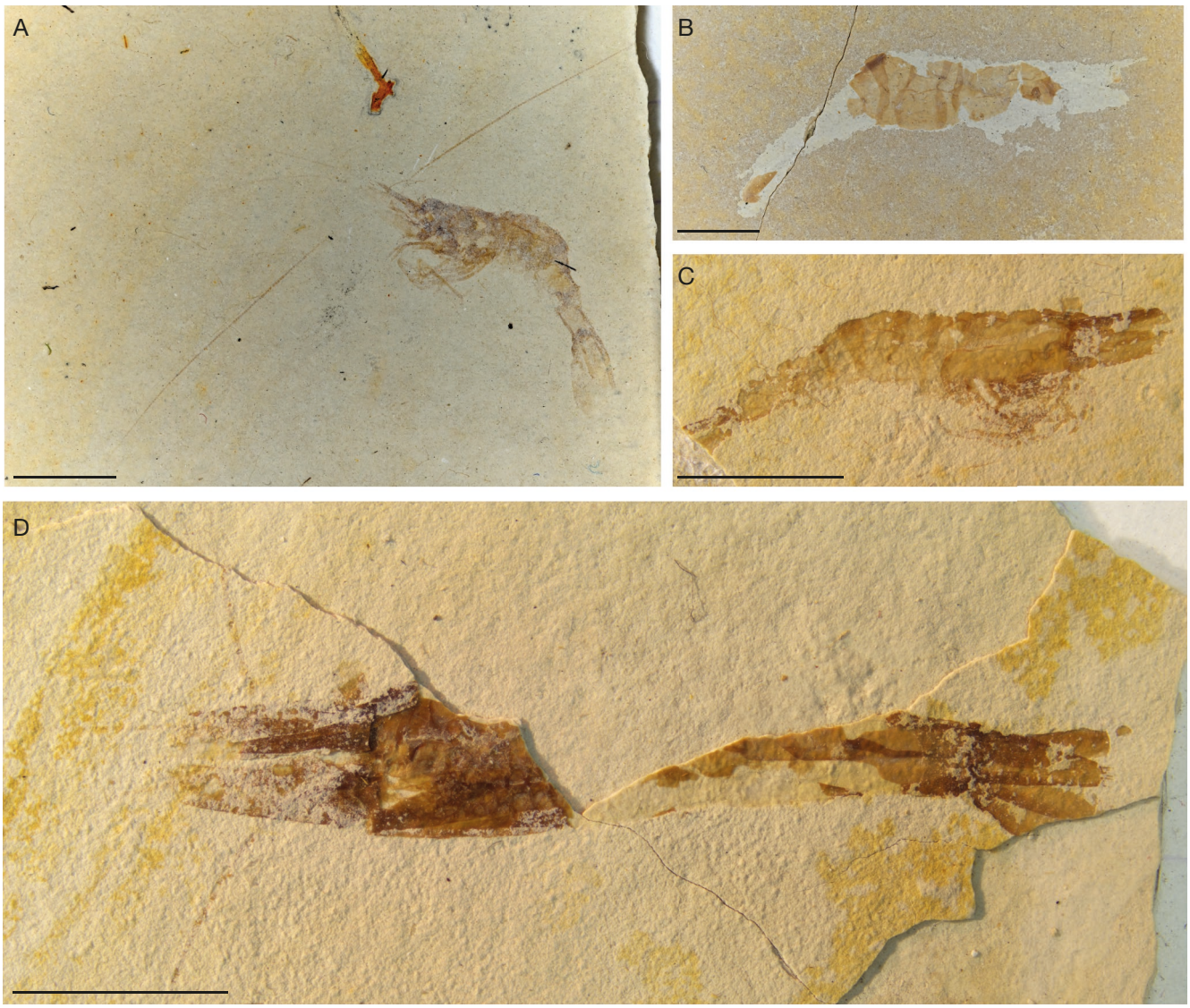

Fig. 6. — Specimens of *Dugastella nitida* (A. Milne-Edwards, 1879), n. comb.: **A**, MNHN.F.A90846; **B**, MNHN.F.A90842b; **C**, MNHN.F.A90844; **D**, MNHN.F.A90843. Scale bars: 5 mm.

Comparative material. — *Dugastella marocana* Bouvier, 1912: Settat spring, Chaouia, Morocco, 1913, P. Pallary coll., MNHN-IU-2016-11857 (ex MNHN-Na-11925).

Amended description

Small sized shrimp (total body length 17-27 mm). Rostrum compressed, acute, slightly curved upwards distally with a weakly convex part near its basis, bearing on its dorsal margin 18-26 moveable teeth arranged in a continuous series beginning anteriorly to the orbit and reaching the apex, leaving an unarmed proximal portion of the rostrum, and 14-18 serrations on its ventral margin (Fig. 2D, E). Rostrum overreaching scaphocerite and about as long as carapace (0.9-1.1 times carapace length). Carapace smooth, without grooves. In the best-preserved specimens, supra-orbital tooth visible on the carapace. Antennal tooth fused with lower orbital angle. Pterygostomial angle acute and slightly produced anteriorly. Eyes well developed with peduncle reaching half of basal segment of antennular peduncle. Cornea not preserved. Flagellum of the antenna at least as long as the body. Long scaphocerite (4.7 times as long as wide). Antennules rarely preserved but longer than carapace. Long stylocerite, almost reaching first segment of antennular peduncle. Basal segment about as long as second and third segments combined. Mouthparts visible in some specimens: mandibles robust, with the incisor process bearing at least one denticle, lacking a palp (Fig. 4A-D), and first maxilla composed of a distal endite narrower at its base and with a somewhat straight inner margin on its distal end, a broad round proximal endite and a palp (Fig. 4E, F). Third maxilliped long. First and second pereiopods with small chela, dactylus about as long as palma. Pereiopods 3 to 5 similar, propodus 2-4 times as long as dactylus, few spiniform setae on dactylus (Fig. 5E, F), the distal one being the largest. Pleopods not preserved in our additional specimens. Long pleon with typical caridean hump on the third segment. Sixth somite 0.6-0.7 times as long as carapace, 1.3-2 times as long as fifth somite, 0.8 times as long as telson. Telson 2.8 times as long as wide, with three pairs of dorsolateral

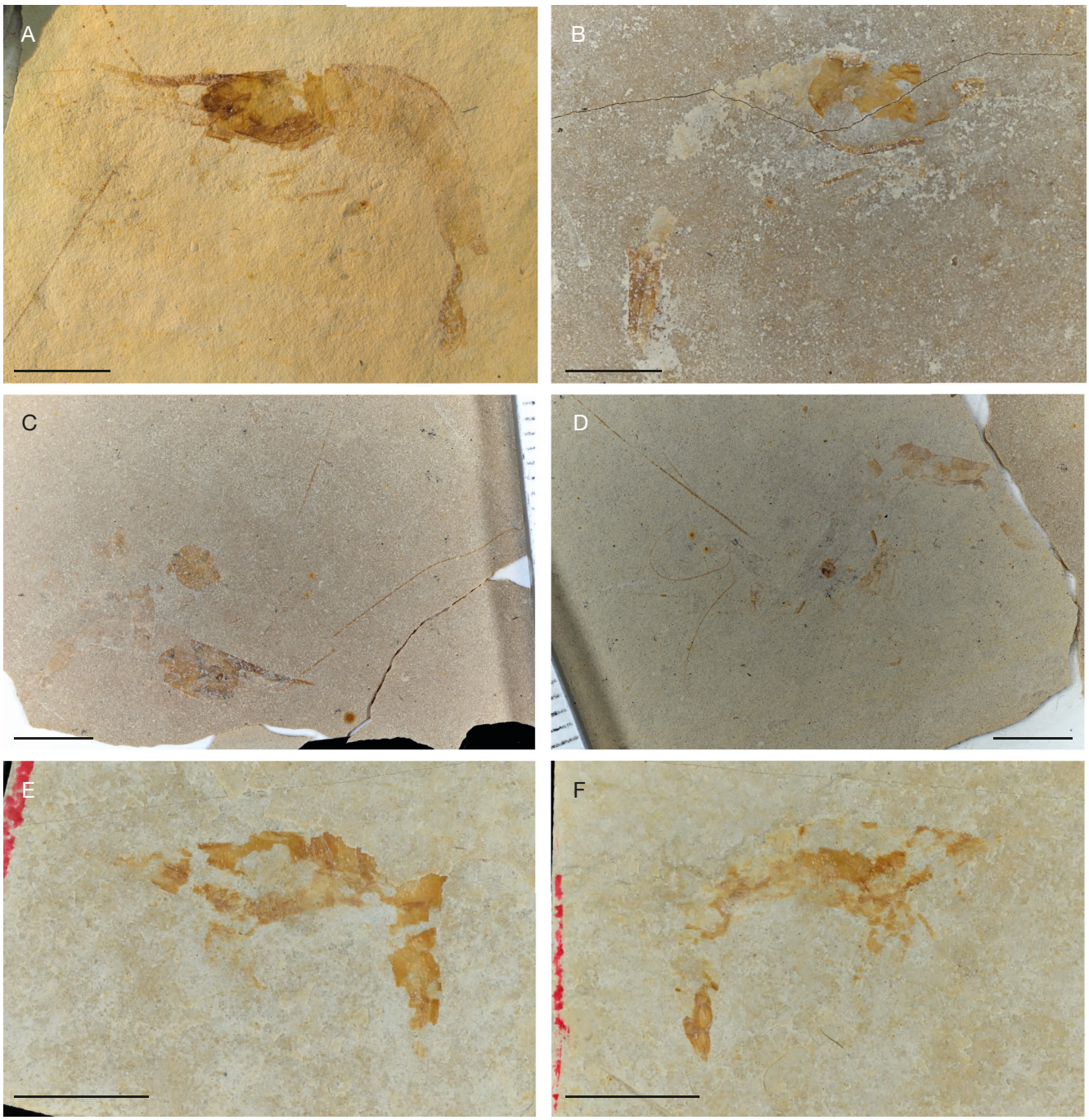

FIG. 7. — Specimens of *Dugastella nitida* (A. Milne-Edwards, 1879), n. comb.: **A**, MNHN.F.A90845a; **B**, MNHN.F.A90845b; **C**, MNHN.F.A90847a; **D**, MNHN.F.A90847b; **E**, MNHN.F.A90848a; **F**, MNHN.F.A90848b. Scale bars: 5 mm.

spiniform setae, with 6 distal setae and an acute projection on its posterior margin (Fig. 5A, B). Uropodal exopod with diaeresis bearing a single large spiniform seta (Fig. 5C, D). Endopod slightly shorter or as long as exopod (Fig. 5A, B).

DISCUSSION

As already stated, A. Milne-Edwards (1879) provided a very succinct description. The use of singular to refer to the fossil "notre fossile" (A. Milne-Edwards 1879: 78) strongly suggests that only one specimen was available, the holotype by monotypy. A stone slab labelled as "*Caridina nitida* A. Edw.; Aix" was found in the palaeontological collections of the MNHN (accession number MNHN.F.B24297) accompanied with the hand-written manuscript of the original publication, which led us to identify it as A. Milne-Edwards (1879)'s holotype, however the slab has no visible fossil on it (Fig. 9). It is probable that parts of the stone where the fossil was broke off and the specimen

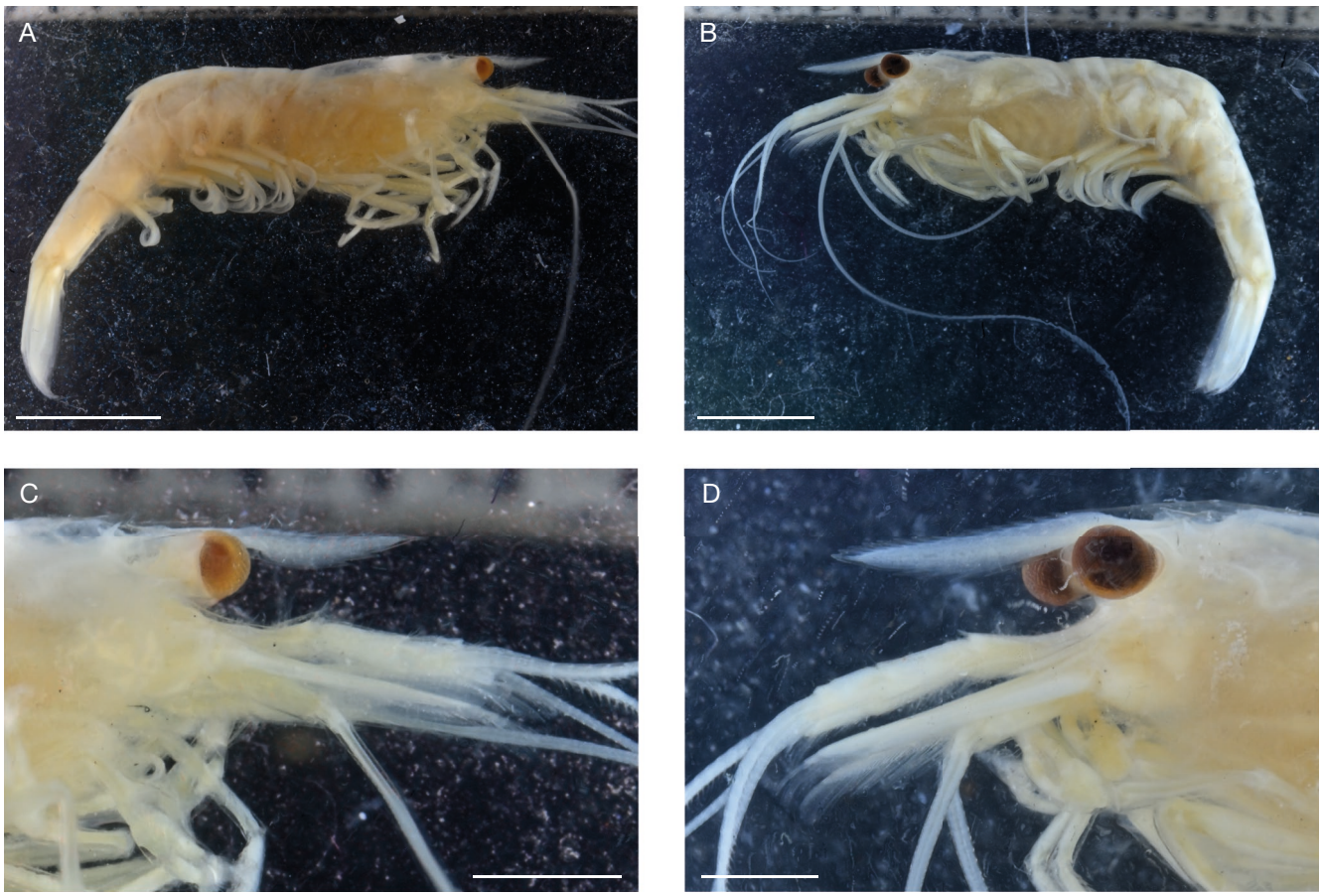

FIG. 8. — Specimens of *Dugastella marocana* Bouvier, 1912, MNHN-IU-2016-11857: **A**, **B**, whole body; **C**, **D**, detailed views of the rostrum; **C**, corresponds to specimen figured in A; **D**, corresponds to specimen figured in B. Scale bars: A, B, 3 mm; C, D, 1 mm.

got lost. Due to the poor state of the holotype, in order to clarify the taxonomic status of *Caridina nitida* A. Milne-Edwards, 1879 and in agreement to the article 75.3 of the International Code of Zoological Nomenclature, we hereby designate the specimen MNHN.F.A59323 as the neotype of the species. This specimen's morphology is consistent with the succinct original description of the former type and comes from the same locality and geological horizon (lacustrine marl of Aix-en-Provence).

Caridean shrimp species are particularly rare in the fossil record (Schweitzer *et al.* 2023; De Grave & Fransen 2011), and even more so for freshwater species. Their delicate cuticle requires perfect conditions that are only met in Konservat-Lagerstätten such as in Aix-en-Provence, which in turn allow for the preservation of minute details and sometimes internal organs (de Mazancourt *et al.* 2022).

The original placement of the species within the genus *Caridina* cannot be maintained due to morphological differences detailed further and the biogeographical inconsistency, provided that this genus currently only occurs in the Indo-Pacific area and Africa. There is however little doubt regarding the affinities of the species with extant representatives of *Dugastella* based on the following characters: a pair of supra-orbital teeth present; unarmed proximal portion of the dorsal margin of the rostrum; acute forward projection of the pterygostomial angle; and weak convexity at the proximal dorsal area of the rostrum (cf. Zariquiey-Alvarez 1968: 81; Sket & Zakšek 2009: 792). These characters also enabled to rule out the other extant genus of atyid shrimp living in European epigean waters, *Atyaephyra* de Brito Capello, 1867, which bears post-orbital teeth on the dorsal margin of the rostrum and no projection on the pterygostomian margin. *Dugastella nitida* (A. Milne-Edwards, 1879), n. comb. can easily be separated from its extant congeners based on the number of teeth on the rostrum: 10-15 dorsal teeth and 2-6 teeth on the ventral margin for *D. marocana* (from Bouvier 1925), 13-19/9-13 for *D. valentina* (from Zariquiey-Alvarez 1968) and 18-26/14-18 for *D. nitida* (A. Milne-Edwards, 1879), n. comb. (present study).

Some authors have erroneously cited the genus *Dugastella* as occurring in the fossil record (Rabadà 1993; Garassino 1997) because of an erroneous reading of Rabadà's work (1990) in which he only compared his fossil species of *Delclosia* to extant genera, including *Dugastella*. Our study is in fact the first report of a fossil species of *Dugastella*.

Species of *Dugastella* are considered to have "primitive" characters among the Atyidae, including the presence of exopodites on their pereiopods (like in *Xiphocaris* von Martens,

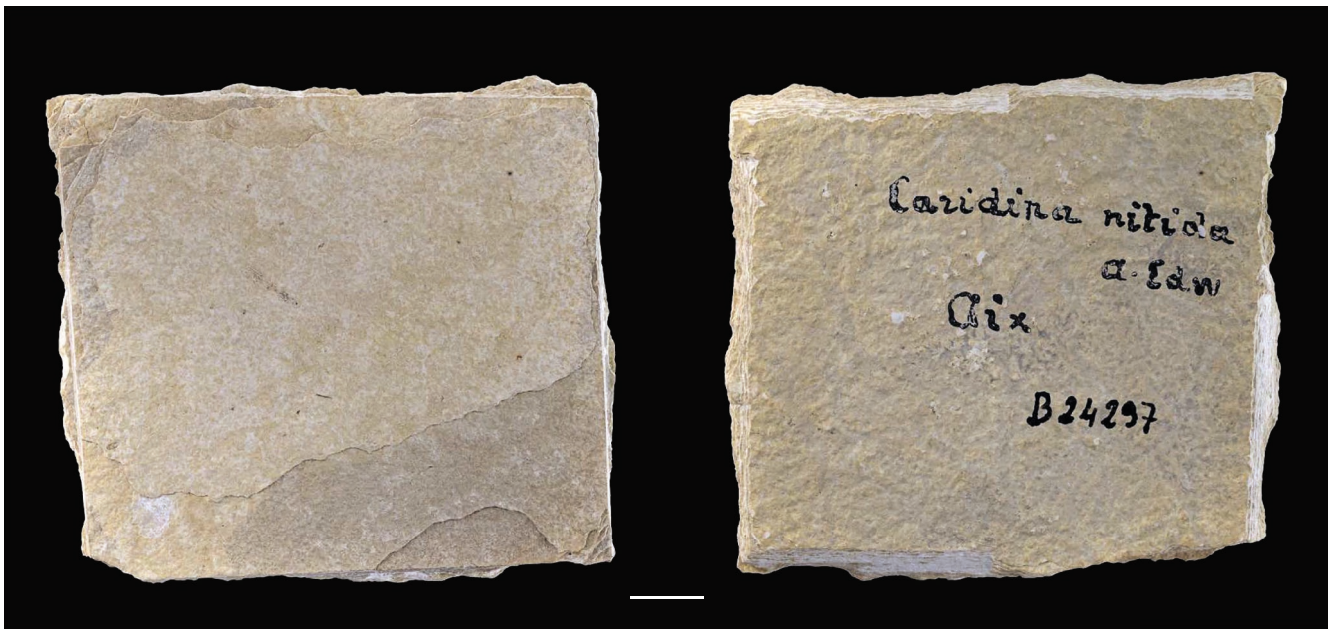

Fig. 9. — Supposed remains of the holotype of *Caridina nitida* A. Milne-Edwards, 1879, MNHN.F.B24297. **Left**, top view; **right**, bottom view. Scale bar: 10 mm.

1872, the sister-group of the Atyidae), supra-orbital spines (like in basal atyids such as *Paratya* Miers, 1882, *Atyaephyra*, *Syncaris* Holmes, 1900, etc.), a single spine on the uropodal diaeresis and eight pairs of pleurobranchs (Bouvier 1912; 1925). These conclusions have since been confirmed through molecular phylogenetic analyses that recovered *Dugastella* related to other taxa sharing these plesiomorphic traits such as *Atyaephyra*, *Palaemonias* Hay, 1901 or *Paratya* in a clade of ancient origin within the Atyidae (*Paratya* group, see von Rintelen *et al.* 2012). Based on the distribution of extant species of this genus (Spain and Morocco, cf. Christodoulou *et al.* 2016), previous authors hypothesized that it originated during the Cenozoic (Bouvier 1925; Balss 1925), which the present findings support. This new occurrence of *Dugastella* in the late Oligocene of southern France suggests that it used to have a wider distribution across the Mediterranean region and has regressed since then. The genus is now restricted to two refugia in Eastern Spain and Morocco, likely following the drying up of the Mediterranean Sea known as the Messinian Salinity Crisis and the subsequent climate changes (de Mazancourt *et al.* 2022). Interestingly, the oldest known fossils attributed to the family Atyidae, i.e. the three species of *Delclosia* were all found in Cretaceous fresh to brackish water deposits of the Mediterranean region (Spain) like the three known species of *Dugastella*. Fossils of *Delclosia* are not as well preserved as our specimens and diagnostic characters are not visible to allow for a more precise placement within the Atyidae. *Delclosia roselli* (Vía, 1971) seems to possess supra-orbital teeth (Rabadà 1990; 1993) which could suggest a close connection with the extant European atyids, including *Dugastella*, but which is above all a plesiomorphic trait within the Atyidae (species of *Syncaris* which is the most basal group of the family according to the latest phylogenies and are found in North America also possess supra-orbital teeth). Species of *Delclosia* however show marked differences in rostrum length and armature among each other and with *Dugastella*, which raises doubts regarding their congeneric status.

Extant species of *Dugastella* are known to be euryhaline as they are found living in brackish lagoons (Sanz & Gómez 1984), weakly saline springs (Bouvier 1912; 1925) but also in fully freshwater streams (Bataller & Porras 2007), thus tolerating salinities between 0.1 and 6.5 ‰ (Sanz & Gómez 1984). Our fossil species belonging to the same genus reinforces the conclusions by Gaudant *et al.* (2018) according to whom the palaeoenvironment of Aix-en-Provence during the Oligocene was a lagoon of varying salinity over time, very similar to the conditions prevailing today in the lagoons near Valencia (e.g. La Albufera) where *D. valentina* (Ferrer Galdiano, 1924) lives today (Ferrer Galdiano 1924; Zariquiey-Alvarez 1968). Furthermore, the extended parental care behaviour exhibited by the two extant species of the genus is a peculiar derived character among the Atyidae (Cuesta *et al.* 2006; Rodríguez & Cuesta 2011; Huguet *et al.* 2011) which one may hypothesize to be present in our fossil species.

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