

## An unexpected Cenozoic record of palinurid lobsters (Achelata) from the lower Eocene of “Pesciara” (Bolca, Verona) and Monte Postale (Altissimo, Vicenza), northeastern Italy

GIOVANNI PASINI\* - ALESSANDRO GARASSINO\*\* - ROBERTO ZORZIN\*\*\* - LUCA GIUSBERTI\*\*\*\*

(\* Via Alessandro Volta, Appiano Gentile, Como, Italia)

(\*\* Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, California, USA)

(\*\*\* Museo Civico di Storia Naturale, Verona, Italia)

(\*\*\*\*Università degli Studi di Padova, Padova, Italia)

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### ABSTRACT

An in-depth study of the spiny lobsters (Palinuridae LATREILLE, 1802) from the lower Eocene (upper Ypresian) of “Pesciara” of Bolca (Verona) and Monte Postale (Altissimo, Vicenza) in Veneto (NE Italy) allowed a reappraisal of their systematic assignment. Indeed, the careful review of the type series of *Justitia desmaresti* (SECRÉTAN, 1975) plus some additional unreported specimens allowed to identify two genera within the Palinuridae, *Eolinurus* n. gen. with *E. desmaresti* (SECRÉTAN, 1975) n. comb. and *Justitia* HOLTHUIS, 1946 with *J. confusa* n. sp. A third genus, *Lessinoachela* n. gen. with *L. scaligera* n. gen., n. sp., for its peculiar morphological characters, is not assigned to any family within the Achelata. Moreover, one incomplete specimen compared with *Justitia* and one “puerulus” larval stage are reported, allowing a new look at the spiny lobster assemblage from the Monte Postale environment.

Finally, the “Pesciara” record represents the unique evidence from the Eocene of Europe due to the presence of three spiny lobster genera within the same palaeoenvironment, partially sharing morphological characters with the representatives of the Palinuridae.

**Key words:** Crustacea, Decapoda, Palinuridae, lower Eocene, “Pesciara”, Monte Postale, Veneto, NE Italy.

### RIASSUNTO

La revisione dei palinuridi (Palinuridae LATREILLE, 1802) dell'Eocene inferiore (Ypresiano superiore) della “Pesciara” di Bolca (Verona) e del Monte Postale (Altissimo, Vicenza) in Veneto (Italia nordorientale) ha permesso una rivalutazione della loro posizione sistematica. L'attento riesame del materiale tipo e di alcuni esemplari inediti attribuiti a *Justitia desmaresti* (SECRÉTAN, 1975) ha consentito infatti di riconoscere due generi assegnati alla famiglia Palinuridae: *Eolinurus* n. gen. con *E. desmaresti* (SECRÉTAN, 1975) n. comb. e *Justitia* HOLTHUIS, 1946 con *J. confusa* n. sp. Un terzo genere, *Lessinoachela* n. gen. con *L. scaligera* n. gen., n. sp., per alcuni caratteri peculiari, non è assegnato a nessuna famiglia nell'ambito degli Achelata. Un esemplare incompleto confrontato con *Justitia* e un “puerulus” (stadio giovanile) vengono inoltre segnalati per la prima volta, ampliando le nostre conoscenze sulla composizione e varietà di palinuridi presenti nel deposito eocenico del Monte Postale.

In conclusione, il sito della “Pesciara” rappresenta l'unica testimonianza dell'Eocene europeo avente tre generi nello stesso paleoambiente che condividono in parte caratteri morfologici con i rappresentanti della famiglia Palinuridae.

**Parole chiave:** Crustacea, Decapoda, Palinuridae, Eocene inferiore, “Pesciara”, Monte Postale, Veneto, Italia settentrionale.

### INTRODUCTION

The spiny lobsters from the lower Eocene Konservat-Lagerstätte of “Pesciara” of Bolca (Verona; Fig. 1) are known at least starting from the second decade of Eighteenth century (DESMAREST, 1817). However, the first detailed study was carried out by SECRÉTAN (1975) who described the spiny lobsters

under the name “*Palinurus desmaresti* DE ZIGNO, 1915”, though she suggested the potential presence of two different taxa in the assemblage. BESCHIN *et al.* (2001, p. 93) concurred with this hypothesis, pointing out the potential presence of *Justitia* among these specimens. In the same year, GARASSINO AND NOVATI

(2001) revised and re-described *Palimurus desmaresti*, proposing to transfer it to the extant *Justitia* HOLTHUIS, 1946 and attempting to solve the problem of the authorship of the species, subsequently disentangled by GIUSBERTI *et al.* (2015) who assigned it to SECRÉTAN (1975). Finally, PASINI *et al.* (2019, p. 247) confirmed *Justitia desmaresti* (SECRÉTAN, 1975) as a valid species within the genus. However, the extensive re-examination of all the available Bolca's specimens of spiny lobsters undertaken during the preparation of the work by PASINI *et al.* (2019) led us to reappraise their systematic assignment within the Palinuridae. Indeed, the main purpose of this paper is a critical review of the diagnostic characters of the lectotype, paralectotypes, and additional specimens of SECRÉTAN'S taxon in order to verify their right assignment to *J. desmaresti*.

#### GEOLOGY AND PALAEOENVIRONMENT OF "PESCIARA" AND MONTE POSTALE

The fossiliferous site of "Pesciara" of Bolca (eastern Monti Lessini, Verona province; Fig. 1B), also known as "Monte Bolca", is a large calcareous olistolith surrounded by volcanic and volcanoclastic deposits and extending a few hundred m<sup>2</sup>. Its stratigraphic thickness is around 19 m and it is made up of alternating fossiliferous laminites and coarse-grained biocalcarenes and biocalcirudites with molluscs and larger foraminifera (e.g., PAPAZZONI AND TREVISANI, 2006). The site is known since about five centuries and it is worldwide renowned for outstanding abundance, diversity, and exquisite preservation of its fossils, especially fishes, coming from the laminites (PAPAZZONI AND TREVISANI, 2006; FRIEDMAN AND CARNEVALE, 2018; MARRAMÀ *et al.*, 2016, 2021). Based on its alveolinid and calcareous nannofossil content, "Pesciara" was referred to zone SBZ 11 of SERRA-KIEL *et al.* (1998) and zone CNE 6 of AGNINI *et al.* (2014), corresponding to a latest Ypresian age, between 48.96 and 48.5 Myr. (PAPAZZONI AND TREVISANI, 2006; PAPAZZONI *et al.*, 2017; MARRAMÀ *et al.*, 2021). The stratigraphic succession of the nearby Monte Postale (Vicenza province; Fig. 1B), located a few hundred meters north of "Pesciara", represents the most complete Eocene succession in the area as it consists of 130 m of limestones recording complex lateral facies changes from fine-grained limestones (laminites included) to massive corallgal bioconstructed limestones forming a discontinuous coral belt along the north side of Monte Postale (VESCOGNI *et al.*, 2016; PAPAZZONI

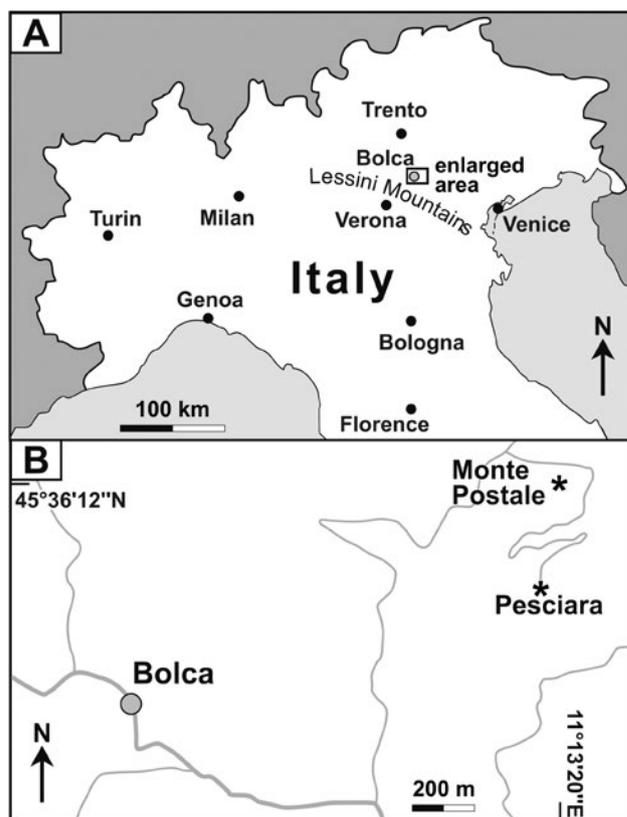


Fig. 1 – (A) and (B) Map of the fossiliferous localities of "Pesciara" and Monte Postale in the surroundings of the village of Bolca (Verona, northeastern Italy). From PASINI *et al.* (2019)

*et al.*, 2017). At least three intervals of fossiliferous laminites with fishes, plants, and invertebrates were recognized (PAPAZZONI *et al.*, 2017) at Monte Postale, whose succession spans the entire CNE 5 calcareous nannofossil zone and a large part of the SBZ 11 larger foraminiferal zone (latest Ypresian, between 50.5 and 48.96 Myr.; PAPAZZONI *et al.*, 2017).

According to recent studies, laminites of Monte Postale were originated in a "lagoon" with at least periodic anoxic conditions at the bottom and surrounded by corallgal buildups with peri-reefal areas densely vegetated by seagrass beds and mangroves, a palaeoenvironment different from that of "Pesciara", representing a low-energy intraplatform basin with permanent bottom dysoxia or anoxia in a peri-reefal system that was strongly influenced both by coastal and pelagic environments (MARRAMÀ *et al.*, 2016, 2021; VESCOGNI *et al.*, 2016). Based on chondrichthyan assemblages, MARRAMÀ *et al.* (2021) recently inferred that the palaeobiotopes of both sites were likely characterized by depths reaching

40-50 m, supporting previous assumptions of a shallow-water inner shelf scenario.

Crustaceans are a significant component of the so-called “minor fauna” (arthropods, jellyfishes, annelids, and molluscs) of laminites of both “Pesciara” and Monte Postale sites (see GIUSBERTI *et al.*, 2015; PASINI *et al.*, 2019).

#### A UNIQUE CENOZOIC RECORD OF SPINY LOBSTERS

Based upon SCHWEITZER *et al.* (2015), just three genera of the Palinuridae are known to date in the fossil record from the Cenozoic of Europe, as follows: *Archaeocarabus* M'COY, 1849 (fossil) from the Lutetian of UK; *Justitia* HOLTHUIS, 1946 (fossil-extant) from the Lutetian of Italy; *Linuparus* WHITE, 1847 (fossil-extant) from the Ypresian of UK, Priabonian/Rupelian of Germany, and Miocene of Japan. The fossil species of these genera were recorded as single representatives of the family in different European palaeoenvironments, fitting perfectly the main diagnostic characters of the belonging genus.

We point out that the “Pesciara” record represents the unique evidence from the Eocene of Europe including three spiny lobster genera within the same palaeoenvironment having peculiar morphological characters only partially shared with the representatives of the Palinuridae (see Systematic description).

#### PROBLEMS RELATED TO THE SYSTEMATICS OF SPINY LOBSTERS FROM “PESCIARA” AND MONTE POSTALE

Although NOVATI AND GARASSINO (2001) and GIUSBERTI *et al.* (2015) provided a short description of *Justitia desmaresti*, their attention was mainly focused on the nomenclatural aspects of this species, overlooking an in-depth review of the main morphological characters useful for the right systematic assignment of this species.

Indeed, the current careful review of the specimens listed by PASINI *et al.* (2019, p. 247) has raised some doubts about their assignment to *Justitia* (see Systematic description). Based upon HOLTHUIS (1991), the main problem that we met revising the spiny lobsters from “Pesciara” and Monte Postale was the inability to clearly distinguish some diagnostic characters, especially those of the frontal region, such as the supraorbital spines and the rostrum that are badly or insufficiently preserved, strongly crushed, dorso-ventrally compressed, and usually fragmentary.

As already pointed out by SECRÉTAN (1975, p. 339), the anterior cephalic region results deformed and/or compressed in almost all specimens by the thickness of the two paired rounded, globular, and hard calcified mandibular process that makes difficult to establish the right shape of the supraorbital spines and rostrum. Based upon the lateral position of eyes and cephalic appendages, very close to the eyes, we could suppose that the supraorbital spines were very short. However, our revision of the spiny lobsters of “Pesciara” and Monte Postale has pointed out that the presence of the supraorbital spines is still unclear (Fig. 2). Indeed, based upon the fossil record of some genera, such as *Archaeocarabus*, *Linuparus*, and *Palinurus*, in which the supraorbital spines are always clearly evident and strongly calcified, the direct observation of the studied specimens by natural and UV light did not highlight clearly strong calcified supraorbital spines in the frontal region. Moreover, we could suppose that the supraorbital spines were absent based upon the preservation of some soft and delicate anatomical parts, such as the eyes, muscles, and pleopods, usually very hard to preserve.

In conclusion, we prefer for the principle of parsimony to assign two genera herein described within the Palinuridae having some morphological characters, typical of the family (see discussion of *Eolinurus* n. gen. and *Justitia*), whereas the third described genus was not assigned to any family within the Achelata SCHOLTZ AND RICHTER, 1995 due to its very peculiar morphological characters (see discussion of *Lessinoachela* n. gen.).

Finally, based upon HOLTHUIS (1991), KARASAWA *et al.* (2013), and SCHWEITZER *et al.* (2015), we have focused our attention on some characters preserved in the studied specimens not checked previously, such as the original epicuticle of carapace and pleonal somites, combined, when preserved, with the ornamentation of telson, useful for the comparison with the genera of the Achelata.

#### MATERIAL AND NOMENCLATURE NOTES

PASINI *et al.* (2019, p. 247) listed 28 specimens as belonging to *Justitia desmaresti* (lectotype, paralectotypes, and additional specimens). A careful check of Bolca's collections in Verona and Padova museums allowed us to identify two specimens previously unreported by PASINI *et al.* (2019): MCSNV 05 figured by SECRÉTAN (1975: pl. 15, fig. 3) and MGP-PD 7445-7446 (part and counterpart), both supposed to be



Fig. 2 – Frontal region of *Eolinurus* n. gen. in dorsal view (A) and complete body in lateral view (B), and *Lessinoachela* n. gen. (C), showing some anatomical parts such as the distal spines of a2 segments and the pereiopods well preserved, whereas the supposed strongly calcified supraorbital spines are never evident in the genera from “Pesciara”. HOLTHUIS (1991) and SCHWEITZER *et al.* (2015) clearly highlighted that all genera of the Palinuridae always have well-developed strong calcified supraorbital spines (see for instance the extant specimen of *Justitia* in lateral view illustrated in Fig. 2D) (specimens not in scale)

collected from “Pesciara”. Moreover, the review of literature and material listed by PASINI *et al.* (2019) allowed us to rectify some previous mistakes:

- GIUSBERTI *et al.* (2015, p. 116), reassessing the nomenclature of *Justitia desmaresti*, designated the lectotype of the species among ten syntypes originally figured by SECRÉTAN (1975): the remaining specimens of the original type series became therefore paralectotypes [see the Article 74.1.3 of ICZN Code (1999)]. GIUSBERTI *et al.* (2015, p. 116) listed only three of the ten paralectotypes figured by SECRÉTAN (1975) stating that they were “*the best specimens in which the main morphological characters are preserved*”. The authors, however, did not make explicit that the type series of *Palinurus desmaresti* was made up of eighteen (at least) specimens, some of them only listed or cited in the text by SECRÉTAN (1975). The type series of the nominal species, therefore, was originally listed by SECRÉTAN (1975, pp. 338-341) as follows: specimens n. 02, 05, 17-17bis, 18-20, 23-23b, 24, 25-25bis, 92, 93-93bis, 94, 95, 96 (“Museo Civico di Storia Naturale di Verona”), specimen 6804 (Museo di Geologia e Paleontologia dell’Università di Padova) and one unnumbered specimen from the Naturhistorisches Museum of Vienna. To complicate matters, SECRÉTAN (1975) originally introduced some mistakes in transcribing the catalogue numbers of the spiny lobsters housed in the Verona’s museum, partly due to confused numbering of part and counterpart of the same specimen (see below). Possibly because of the unintentional omission by GIUSBERTI *et al.* (2015) and mistakes introduced by SECRÉTAN (1975), PASINI *et al.* (2019) erroneously included some paralectotypes of *J. desmaresti* in their “additional material”;
- the specimen MCSNV 90bis reported among the paralectotypes of *J. desmaresti* listed by GIUSBERTI *et al.* (2015) is instead the counterpart of the lectotype MCSNV 23 designated by GIUSBERTI *et al.* (2015);
- the specimen MCSNV 89 figured by SECRÉTAN (1975, pl. 13, fig. 2) and mentioned as paralectotype by GIUSBERTI *et al.* (2015) has instead the catalogue number MCSNV Cr 57 and represents the counterpart of the specimen MCSNV 92, listed among the additional specimens by PASINI *et al.* (2019);
- the specimen MSNM i22867 listed among the additional specimens of *J. desmaresti* by PASINI *et al.* (2019) is the counterpart of the paralectotype MCSNV 94.

The reappraisal of the specimens assigned to *J. desmaresti* by GIUSBERTI *et al.* (2015) and PASINI *et al.* (2019) allow us to identify three genera, as follows: *Eolinurus* n. gen. with *E. desmaresti* (SECRÉTAN, 1975) n. comb. (11 specimens) (Figs. 3A, B) and *Justitia* HOLTHUIS, 1946 with *J. confusa* n. sp. (9 specimens) (Figs. 4A, B) (Palinuridae LATREILLE, 1802); and *Lesinoachela* n. gen. with *L. scaligera* n. gen., n. sp. (1 specimen) (Figs. 3C, D) (Family indeterminate). Moreover, one incomplete specimen compared with *Justitia* (Figs. 4C, D) and one specimen representing the so-called “puerulus” larval stage (Fig. 17) are herein reported for the first time from Monte Postale (Altissimo, Vicenza).

Finally, the following specimens, MSNVE 4927, MCSNV M05, MCSNV 91-91bis (part and counterpart), MGP-PD 6804, MGP-PD 7443-7444 (part and counterpart), MGP-PD 7447-7450 (part and counterpart), and GBA 2010/275/0053 (former coll. no. 2319) [paralectotype of *Justitia desmaresti* (SECRÉTAN, 1975) not figured by SECRÉTAN (1975)] are removed from the studied sample listed by PASINI *et al.* (2019) due to the impossibility to check the main diagnostic characters of the above-mentioned genera (see Systematic description). Moreover, the specimen MCSNV 21-21bis (part and counterpart), not considered by PASINI *et al.* (2019), is discarded due to its poor preservation.

Abbreviations are as follows:

- Institutional:**
  - CMC – Cerato collection, Bolca (Verona);
  - MCSNV, MCSNV Cr, MCSNV B, MCSNV M – Museo di Storia Naturale di Verona;
  - MFB, MFB IG – Museo dei Fossili, Bolca (Verona);
  - MGP-PD – Museo di Geologia e Paleontologia dell’Università di Padova;
  - GBA – Geological Survey of Austria, Vienna (Austria);
  - MNHN – Muséum national d’Histoire naturelle, Paris (France);
  - MSNM – Museo di Storia Naturale di Milano;
  - MSNVE – Museo di Storia Naturale Giancarlo Ligabue, Venezia;
  - RP – Museo Diocesano di Scienze Naturali “A. De Nardi”, Vittorio Veneto (Treviso);
- Anatomical:**
  - lcp – carapace length;
  - lpl – pleon length;
  - lt – total length of body (excluding antennae)
  - P1-P5 – pereopods 1-5;
  - s1-s5 – pleonal somites 1-5;
  - wcp – carapace width.



Fig. 3 – Ornamentation of carapace and pleon. **A)** *Eolinurus desmaresti* (SECRÉTAN, 1975) n. comb., MCSNV 23, lectotype, carapace. **B)** *Eolinurus desmaresti* (SECRÉTAN, 1975) n. comb., CMC6, pleon. **C)** *Lessinoachela scaligera* n. gen., n. sp., MCSNV 95, holotype, carapace. **D)** *Lessinoachela scaligera* n. gen., n. sp., MCSNV 95, holotype, pleon. Scale bar equals 1 cm

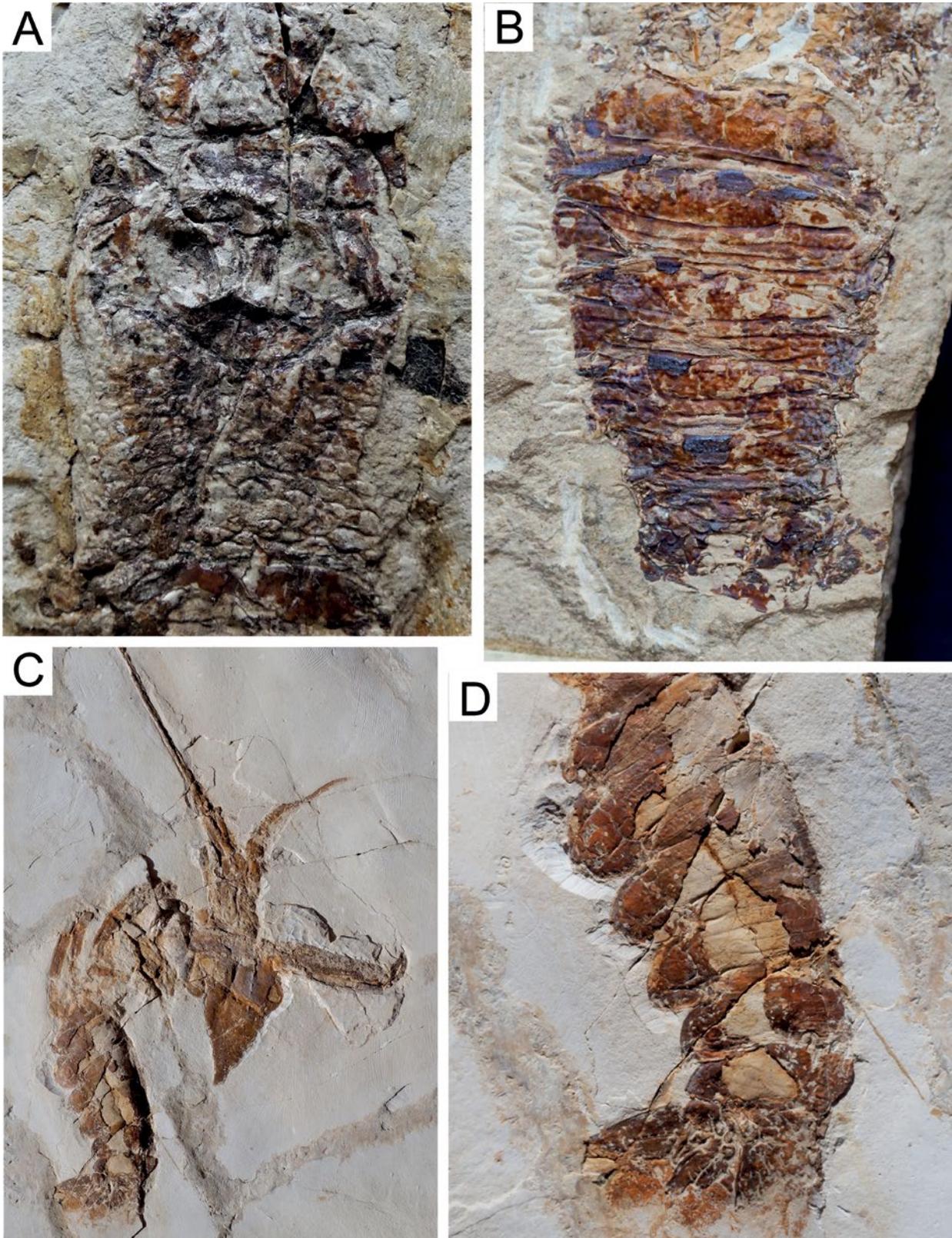


Fig. 4 – Ornamentation of carapace and pleon. **A)** *Justitia confusa* n. sp., MCSNV 17bis, paratype, carapace. **B)** *Justitia confusa* n. sp., MCSNV M02, paratype, pleon. **C)** *Justitia* sp., MFB IG 91130, general view. **D)** *Justitia* sp., MFB IG 91130, pleon. For the scale of the specimens see Figs. 11, 13 and 14

## SYSTEMATIC DESCRIPTION

**Infraorder Achelata SCHOLTZ AND RICHTER, 1995**  
**Family Palinuridae LATREILLE, 1802**  
**Genus *Eolinurus* nov.**

*Diagnosis*

Subcylindrical carapace uniformly granulated; cervical groove slightly convex medially and located in anterior third; uniformly granulated s1-s5 with subtriangular embossed pleura; s6 with squamiform tergum and subtriangular embossed pleuron; short a1 flagellum, shorter than last segment of a1 peduncle; short, stout, and granulated P1; thin, elongate, and granulated P2-P5; telson with three parallel longitudinal ridges.

*Etymology*

The name is derived from Eocene, second epoch of the Palaeogene period, and *Palinurus*; hence a *Palinurus*-like spiny lobster from the Eocene; gender masculine.

*Type species*

*Palinurus desmaresti* SECRÉTAN, 1975.

*Discussion*

The approach to the systematics appears sometimes different between fossil and extant genera of spiny lobsters. Indeed, different is the criterion used to select the main diagnostic characters important not only to identify a genus, but also to distinguish it from the other ones. Therefore, there are sometimes some inconsistencies among diagnoses provided for fossil and extant genera.

For instance, the diagnoses for the fossil genera of the Achelata SCHOLTZ AND RICHTER, 1995 provided by SCHWEITZER *et al.* (2015) result sometimes ambiguous and restrictive, due to the scarce number of characters preserved in the fossil spiny lobsters, whereas the diagnoses provided by HOLTHUIS (1991) list a wide range of characters not always observable in the fossil spiny lobsters because usually the harder main body structures are only preserved.

HOLTHUIS (1991) reported three families within the Achelata, as follows: Scyllaridae LATREILLE, 1825 (fossil-extant), Palinuridae LATREILLE, 1802 (fossil-extant), and Synaxidae BATE, 1881 (fossil-extant), whereas SCHWEITZER *et al.* (2015) reported three families, as follows: Cancrinidae BEURLIN, 1930 (fossil), Palinuridae, and Scyllaridae.

The general body shape and arrangement of the cephalic appendages clearly rule out the belonging of the studied specimens to the Cancrinidae and Scyllaridae.

The studied specimens from Bolca have a mix of characters shared with some genera within the Palinuridae and Synaxidae.

SCHWEITZER *et al.* (2015) listed 15 fossil-extant genera of the Palinuridae, nine exclusively from the Mesozoic and six reported from the Cenozoic, as follows: *Archaeocarabus* M'COY, 1849 (fossil), *Jasus* PARKER, 1883 (fossil-extant), *Justitia* HOLTHUIS, 1946 (fossil-extant), *Linuparus* WHITE, 1847 (fossil-extant), *Palinurus* WEBER, 1795 (fossil-extant), and *Panulirus* WHITE, 1847 (fossil-extant).

We exclude the belonging of the studied specimens to *Archaeocarabus* in having different carapace shape, grooves, and ornamentation.

As reported in the diagnosis of *Jasus* provided by SCHWEITZER *et al.* (2015), this genus would have subcylindrical carapace with well-marked cervical groove and subrectangular telson. These characters can't be, however, considered peculiar of the genus since they are shared among all representatives of the family. Moreover, two characters, such as the stout P1 and long slender P2-P5, are shared with *Archaeopalinurus*, *Palinurus*, *Palinurina*, *Panulirus*, *Projasus*, and *Puerulus* and so we cannot consider them as peculiar of *Jasus*.

The short a1 flagellum, shorter than last segment of a1 peduncle and the telson with tuberculate median longitudinal ridges are characters of the studied specimens shared with the species of *Jasus*, the sole genus within the Palinuridae to have these peculiar characters. However, the pleon of the studied specimens does not have the squamiform or scalloped sculpturation before transverse striae peculiar and unique of *Jasus*. Moreover, the shape of the cervical groove strongly projected backward to form two distinct elongate branches of the groove distinguish *Jasus* from the studied specimens. Finally, the spiny ornamentation of the carapace in *Jasus* rules out assignment of the studied specimens to this genus.

*Justitia*, known to date with four extant species and one fossil species (see discussion below) has the carapace with heavy squamiform sculpturing that rules out assignment of the studied specimens to this genus.

*Linuparus* has the subrectangular carapace with the median longitudinal ridge forming the typical Y shape that exclude the belonging of the studied specimens to this genus.

As reported in the diagnosis of *Palinurus* provided by SCHWEITZER *et al.* (2015), this genus would have subcylindrical carapace with well-marked cervical groove, P1 shorter than P2-P5, long slender P2-P5, and subrectangular telson. However, the subcylindrical carapace with well-marked cervical groove and

the subrectangular telson cannot be considered peculiar of the genus since they are shared among all representatives of the family. The P1 shorter than P2-P5 could allow to assign the studied specimens to this genus based on the diagnosis provided by SCHWEITZER *et al.* (2015, p. 6). This character should be considered as peculiar and unique of this genus, but it is not true. Indeed, based upon SCHWEITZER *et al.* (2015) and HOLTHUIS (1991) some fossil and extant genera of the family, such as *Archaeopalinurus*, *Jasus*, *Palinurina*, *Panulirus*, *Projasus*, and *Puerulus*, share the same character. The presence of P1 shorter than P2-P5 in some genera of the family raises a doubt about the assertion that “P1 almost always same length or only slightly longer than other pereopods” reported by SCHWEITZER *et al.* (2015, p. 1) in the diagnosis of the Palinuridae, pointing out a general lacking uniformity in the diagnostic evaluations. Finally, the granulated ornamentation of the carapace, and s6 with squamiform tergum and subtriangular embossed pleuron exclude the belonging of the studied specimens to this genus.

*Panulirus* has the carapace with spines arranged in parallel ridges or uniformly arranged, s1-s6 terga with grooves, and s1-s6 pleura with one or two hooked spines backward directed that exclude the assignment of the studied specimens to this genus. Moreover, the smooth pereopods, reported in the diagnosis provided by SCHWEITZER *et al.* (2015) rules out definitively the belonging of the studied specimens in having P1-P5 strongly granulated.

Besides the above-mentioned genera, HOLTHUIS (1991) listed three other genera within the Palinuridae exclusively extant, as follows: *Palinustus* A. MILNE-EDWARDS, 1880; *Projasus* GEORGE AND GRINDLEY, 1964; and *Puerulus* ORTMANN, 1897.

The carapace with spines arranged in parallel ridges or uniformly arranged, s1-s6 terga with grooves, and s1-s6 pleura with one or two hooked spines backward directed typical of *Palinustus*, *Projasus*, and *Puerulus* exclude the belonging of the studied specimens to these genera.

Based upon HOLTHUIS (1991) and FRAAIJE *et al.* (2020), three genera belong to the Synaxidae, as follows: *Palibythus* DAVIE, 1990 (extant); *Palinurellus* VON MARTENS (1878) (fossil-extant), and *Palaeopalinurellus* FRAAIJE, VAN BAKEL, JAGT AND BROCHET, 2020 (fossil).

Based upon HOLTHUIS (1991) the genera of the Synaxidae have the body covered only with granules (including pereopods), large flat rostrum, and lack of the supraorbital spines.

Two characters, such as s6 with squamiform tergum and subtriangular embossed pleuron and telson

with three parallel longitudinal granulated ridges exclude the belonging of the studied specimens to *Palibythus* and *Palinurellus*. Finally, we also exclude the assignment of the studied specimens to the fossil *Palaeopalinurellus* in having the posterior part of the carapace densely covered with scale-like tubercles.

Based upon the above-mentioned observations, we can exclude the belonging of the studied specimens to the Synaxidae. On the contrary, some characters, such as the strong multi-articulated a2 flagellum slightly longer than the body (short in the Synaxidae); the median and distal spiny a2 segments; and the shape of the cervical groove allow us to assign them to the Palinuridae.

In conclusion, we can assert that the combination of some morphological characters, such as the uniformly granulated carapace; s1-s5 uniformly granulated, with subtriangular embossed pleura; s6 with squamiform tergum and subtriangular embossed pleuron; and telson with three parallel longitudinal granulated ridges, does not fit any fossil or extant genus of the Palinuridae, justifying the description of the new genus *Eolinurus* within the family to accommodate the studied specimens.

#### *Included fossil species*

Type species only.

#### ***Eolinurus desmaresti* (SECRÉTAN, 1975) n. comb.**

Figures 2A-B, 3A-B, 5-9

#### *Selected synonyms*

1855 *Palinurus Desmarestii* DE ZIGNO *in litt.* – MASSALONGO, p. 32 [*nomen nudum*].

\*1975 *Palinurus desmaresti* DE ZIGNO. – SECRÉTAN, pp. 339, 340, pl. 12, fig. 1; pl. 13, figs. 2, 3, 5; pl. 15, fig. 1 (non pl. 13, figs. 1, 4; pl. 14, figs. 1–4; pl. 15, figs. 2–4; pl. 16, figs. 3, 4).

1985 *Palinurus* sp. – PINNA, p. 108, fig. 7.

2001 *Justitia desmaresti* (MASSALONGO, 1854). – GARASSINO AND NOVATI, p. 259, figs. 3, 4A, 5 (non figs. 1, 2, 6, 7).

2011 *Palinurus desmaresti* (De Zigno, 1915) – CERATO, p. 76 (text figure).

2014 *Justitia desmaresti* (MASSALONGO, 1854). – GIUSBERTI *et al.*, p. 82, fig. 5.

2014 *Justitia desmaresti* (MASSALONGO, 1854). – DE ANGELI AND GARASSINO, p. 11.

2015 *Justitia desmaresti* (SECRÉTAN, 1975). – GIUSBERTI *et al.*, pp. 116, 118, figs. 3 (non fig. 1).

2019 *Justitia desmaresti* (SECRÉTAN, 1975). – PASINI *et al.*, 247, 249, fig. 9A (non figs. 9B–D).

### Diagnosis

As for the genus plus median and distal a2 segments with a strong distal outer spine; a2 segments with strongly tuberculate inner margin having three small spines directed forward; P1 propodus with granulated median ridge; telson with squamiform ornamentation on the half proximal part.

### Lectotype

MCSNV 23-90bis (part and counterpart, dorsal view) [illustrated by SECRÉTAN (1975: pl. 12, fig. 1 and pl. 13, figs. 3, 5), GIUSBERTI *et al.* (2015: fig. 3) and PASINI *et al.* (2019: fig. 9A)]. Originally designated as lectotype by GIUSBERTI *et al.* (2015).

### Paralectotypes

MCSNV 24 (dorsal view) [illustrated by SECRÉTAN (1975: pl. 15, fig. 1)]; MCSNV 25-25bis (part and counterpart, dorsal view); MCSNV 93-93bis (part and counterpart, dorsal view) [illustrated by SECRÉTAN (1975: pl. 14, fig. 1)]; MCSNV Cr 57-92 (part and counterpart, dorsal view) [illustrated by SECRÉTAN (1975: pl. 13, fig. 2)]; MCSNV 94-MSNM i22867 (part and counterpart, ventral view). Herein are reported only the paralectotypes confidently ascribable to *E. desmaresti*.

### Additional material

CMC 6 (dorsal view); MCSNV 96 (dorsal view), MGP-PD 7448-7449 (part and counterpart, lateral view); RP-V85 (dorsal view) [unpublished specimen not previously reported by GIUSBERTI *et al.* (2015) and PASINI *et al.* (2019)]; MNHN F A51537 (Conte Gazola collection) (part and counterpart, dorsal view).

### Type locality

“Pesciara” of Bolca (Verona).

### Geological age

Late Ypresian (early Eocene).

### Description

Middle-sized spiny lobster (It between *c.* 17 cm to over 20 cm).

**Carapace.** Subcylindrical carapace slightly narrowing frontally; dorsal surface covered with closely spaced small granules uniformly arranged; deep cervical groove gently convex medially and located in anterior third; lateral margins slightly convex; posterior margin slightly concave; supraorbital spines and rostrum not observable.

**Pleon.** Subrectangular s1-s5 with granulated terga and subtriangular embossed pleura; s1-s5 slightly

decreasing in size posteriorly; subtrapezoidal s6 with squamiform tergum and subtriangular embossed pleuron; telson with three granulated longitudinal ridges, one median and two lateral ridges running along its upper half length; telson with squamiform ornamentation on the half proximal part.

**Cephalic appendages.** Lateral subovoidal short-stalked eyes; short a1 flagellum, shorter than last segment of a1 peduncle; median and distal a2 segments with a strong distal outer spine; a2 segments with strongly tuberculate inner margin having three small spines directed forward; median and distal a2 segments covered with closely spaced small granules uniformly arranged; median and distal a2 segments with a raised, strong median ridge; strong multi-articulated a2 flagellum as long as the body length.

**Thoracic appendages.** Stout short P1 propodus with raised median ridge; strong hook-shaped P1 dactylus slightly curved distally; P1 elements covered with closely spaced small-medium granules uniformly arranged; thin elongate P2-P5, with closely spaced small granules uniformly arranged.

**Pleonal appendages.** Petaloid pleopods. Uropodal exopod and endopod proximal half outer margin with an elongate triangular hardened scale, longitudinal radiate fringed striae on the half distal part; longitudinal radiate fringed striae of uropodal exopod covered with parallel rows of small spiny tubercles proximally.

### Taphonomy

The careful study of the specimens herein assigned to *Eolinurus desmaresti* n. comb. allows us to identify only one specimen (CMC 6, Fig. 9A) preserved with the original granulated ornamentation of the terga exocuticle, generally eroded or completely lacking in other specimens. Such unfavourable state of preservation exposed an underlying endocuticle that results smooth with transverse parallel striae (RP-V85, MCSNV 25-25bis, Fig. 9B), not reflecting the real granulated ornamentation of the terga typical of *Eolinurus* n. gen. (Fig. 3B). This previously undervalued taphonomic aspect created confusion for establishing the real characters of the terga ornamentation in *Eolinurus* n. gen. (uniformly granulated) and *Justitia* (transverse parallel striae).

In conclusion, this extensive review of the lectotype, paralectotypes, and additional material clearly pointed out that *Palinurus desmaresti* SECRÉTAN (1975) does not fit the diagnostic characters of *Justitia*, allowing herein its reassignment to *Eolinurus desmaresti* (SECRÉTAN, 1975) n. comb.

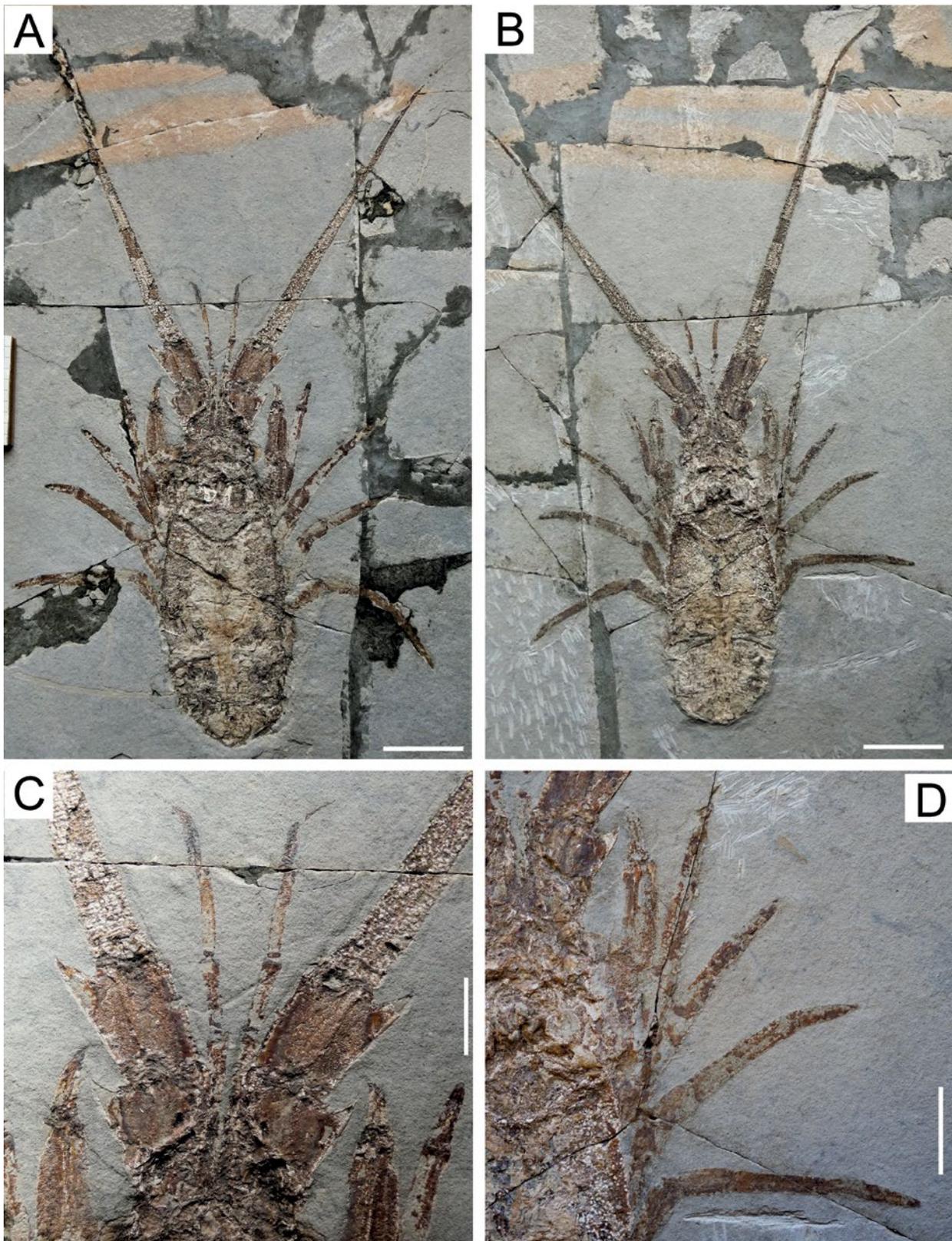


Fig. 5 – *Eolinurus desmaresti* (SECRÉTAN, 1975) n. comb. **A**) MCSNV 23, lectotype, dorsal view (part). **B**) MCSNV 90bis, lectotype, dorsal view (counterpart). **C**) MCSNV 90bis, lectotype, close-up of the cephalic appendages. **D**) MCSNV 90bis, lectotype, close-up of the thoracic appendages. Scale bars of A and B equal 2 cm, scale bars of C and D equal 1 cm

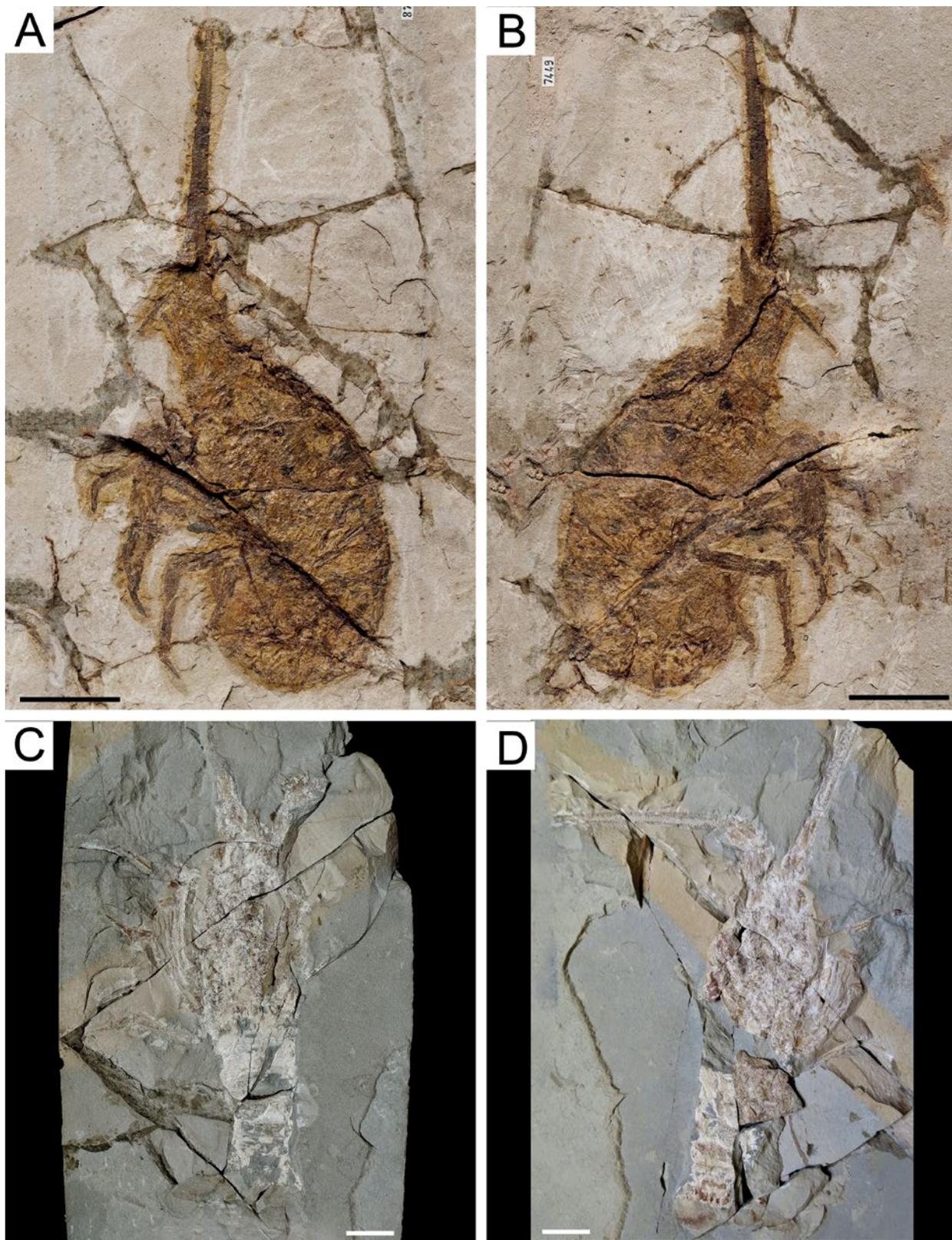


Fig. 6 – *Eolinurus desmaresti* (SECRÉTAN, 1975) n. comb. **A**) MGP-PD 7448, lateral view (part). **B**) MGP-PD 7449, lateral view (counterpart). **C**) RP-V85, dorsal view (part). **D**) RP-V85, dorsal view (counterpart). Scale bars of A and B equal 5 cm, scale bars of C and D equal 3 cm

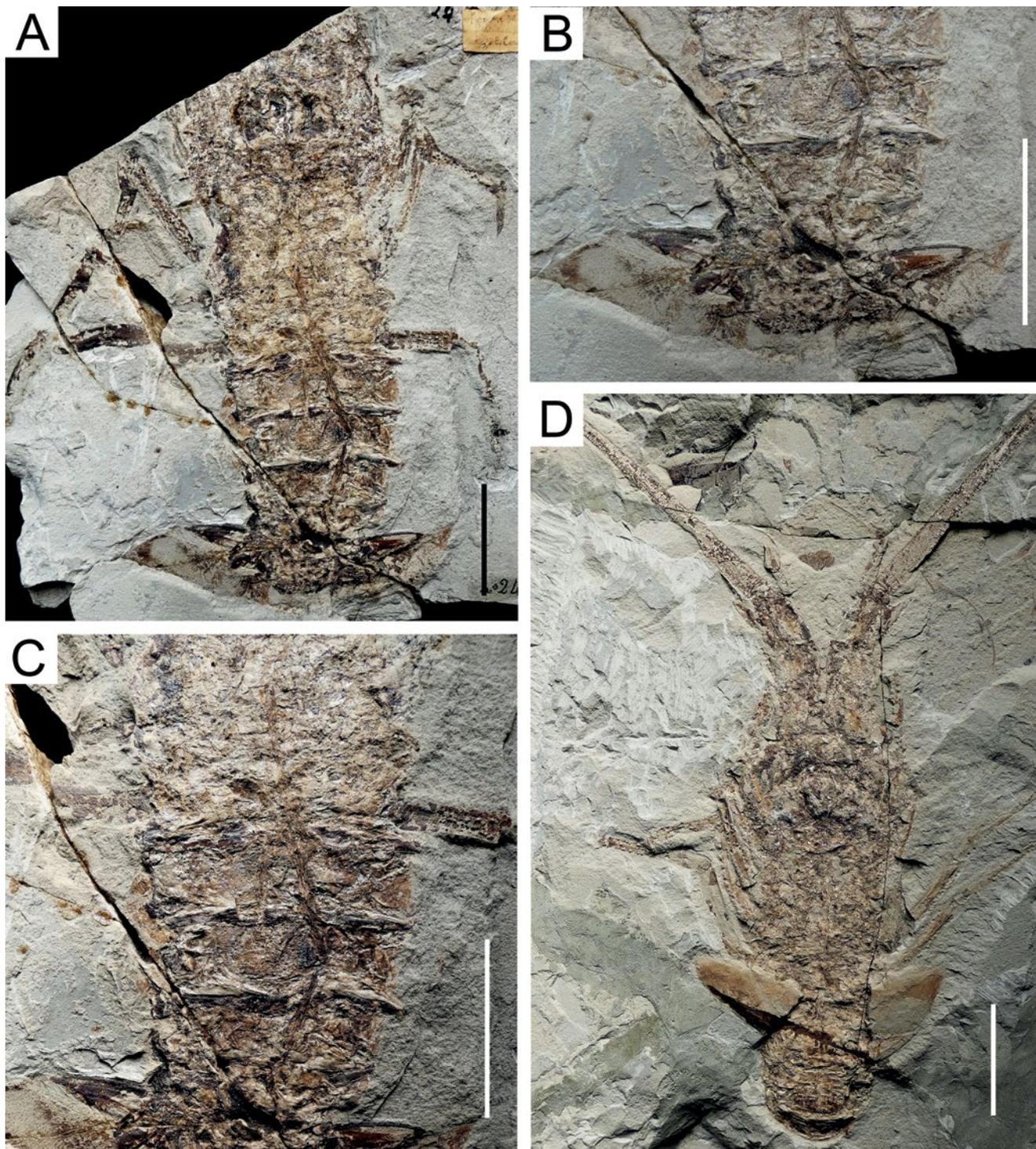


Fig. 7 – *Eolinurus desmaresti* (SECRÉTAN, 1975) n. comb. **A**) MCSNV 24, paralectotype, dorsal view. **B**) MCSNV 24, paralectotype, close-up of the tail fan. **C**) MCSNV 24, paralectotype, close-up of the pleon. **D**) MCSNV 94, paralectotype, ventral view. Scale bars equal 5 cm

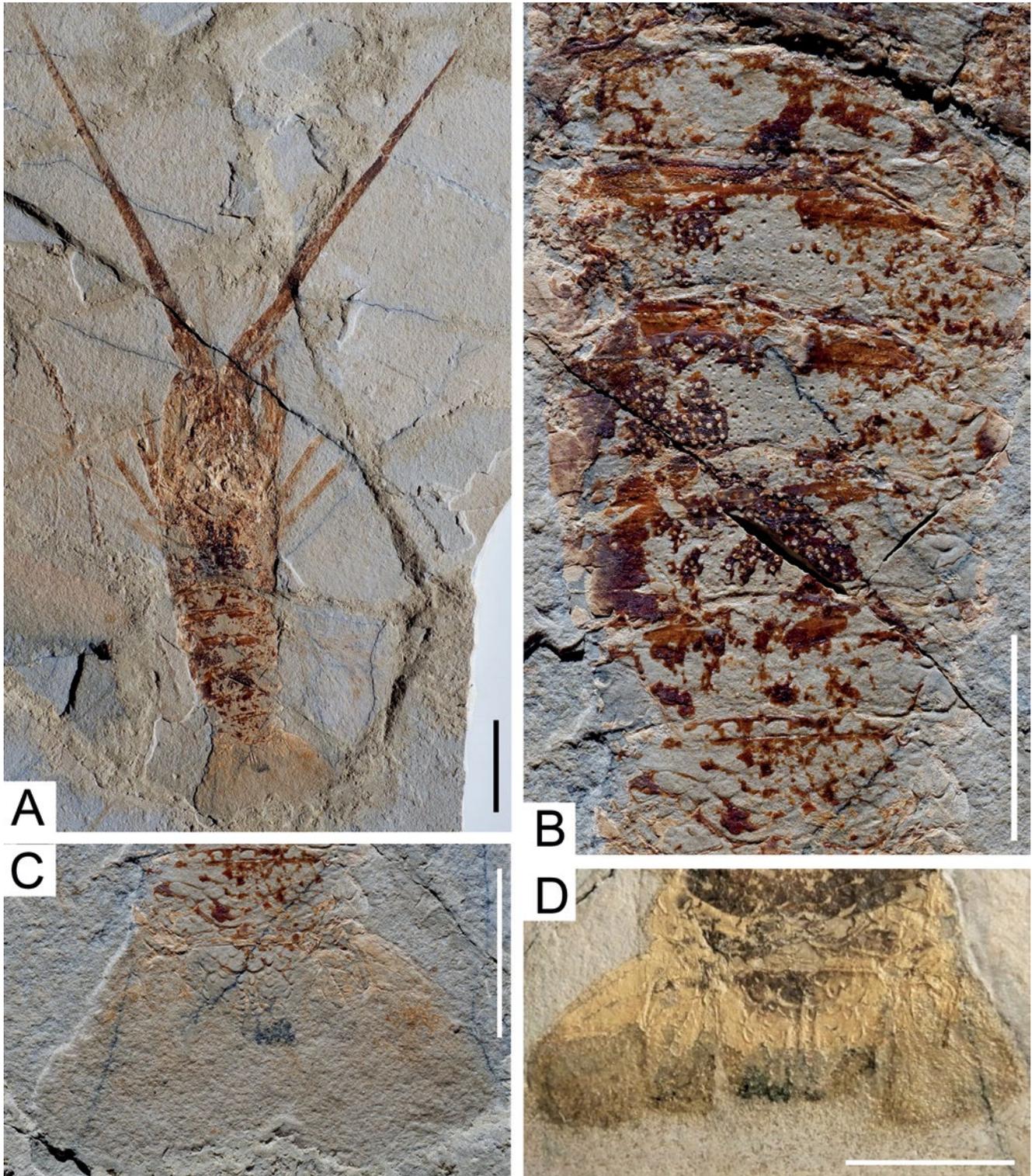


Fig. 8 – *Eolinurus desmaresti* (SECRÉTAN, 1975) n. comb. **A**) CMC 6, dorsal view. **B**) CMC 6, close-up of the pleon. **C**) CMC 6, close-up of s6 and tail fan. **D**) CMC 6, elaborate photographic reconstruction of the tail fan. Scale bar of A equals 2 cm, scale bars of B-D equal 1 cm

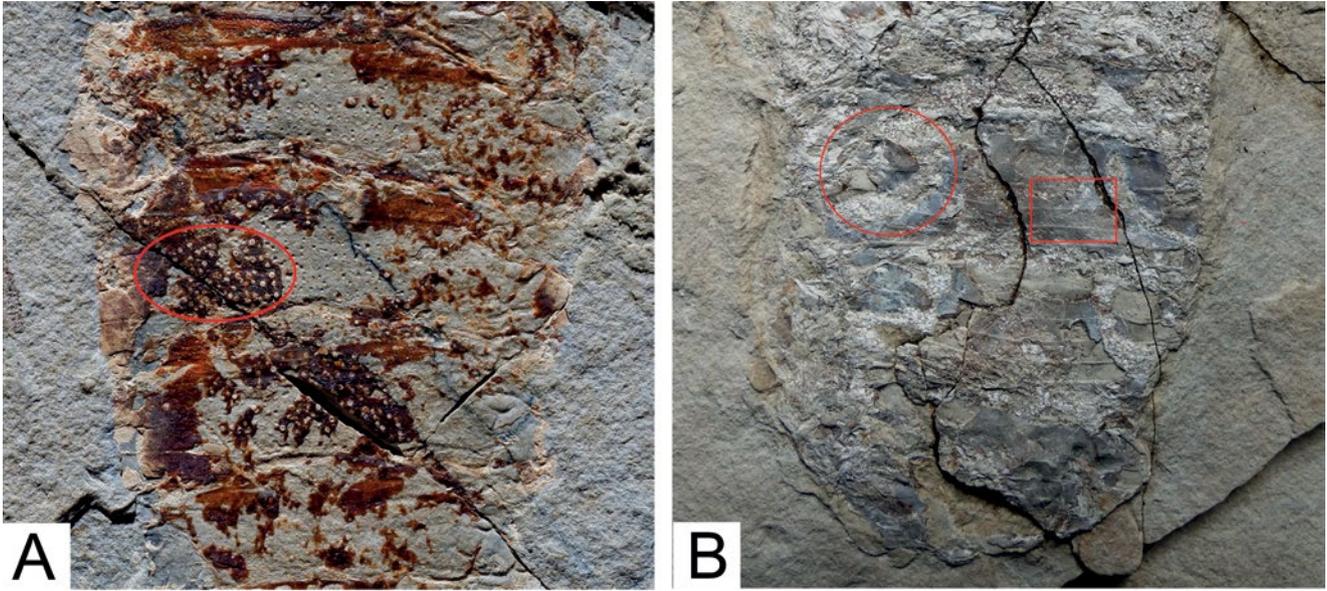


Fig. 9 – *Eolinurus desmaresti* (SECRÉTAN, 1975) n. comb. **A**) CMC 6, close-up of the pleon, showing the original granulated ornamentation of the terga exocuticle (red circle). **B**) MCSNV 25, paralectotype, close-up of the pleon, showing the original granulated ornamentation of the terga exocuticle partially preserved on both sides of each somite (red circle) and the endocuticle that results smooth with transverse parallel striae on the medial part of each somite (red rectangular)

### Genus *Justitia* HOLTHUIS 1946

#### Type species

*Palinurus longimanus* H. MILNE EDWARDS, 1837 by original designation.

#### Included fossil species

*Justitia vicetina* BESCHIN, DE ANGELI AND GARASSINO, 2001; *Justitia confusa* n. sp. (herein).

#### *Justitia confusa* n. sp.

Figures 4A-B, 10-13

2019 *Justitia desmaresti* (SECRÉTAN, 1975). – PASINI *et al.*, p. 247, fig. 9B (non *Palinurus desmaresti* SECRÉTAN, 1975).

#### Diagnosis

Subcylindrical granulated carapace with some scattered tubercles/spinules on the frontal and gastric regions and with imbricate scales on branchial and cardiac regions; granulated s1 tergum; granulated s2-s5 terga crossed by 2-3 complete parallel transverse striae; subtrapezoidal s6 with embossed tergum; P1 shorter and stronger than P2-P5.

#### Etymology

From the Latin language *confusus*, *a*, *um* (=confused), alluding to its previous systematic misinterpretation.

#### Holotype

MSNVE 6298 (dorsal view).

#### Paratypes

MCSNV M 02 (dorsal view - juvenile; paralectotype of *Palinurus desmaresti* SECRÉTAN, 1975); MCSNV M 18 (dorsal view - juvenile; paralectotype of *Palinurus desmaresti* SECRÉTAN, 1975); MCSNV Cr17 (lateral view - adult; paralectotype of *Palinurus desmaresti* SECRÉTAN, 1975); MCSNV B17-17bis (part and counterpart, dorsal view - juvenile; paralectotype of *Palinurus desmaresti* SECRÉTAN, 1975); MCSNV 20 (dorsal view - juvenile; paralectotype of *Palinurus desmaresti* SECRÉTAN, 1975); MCSNV 23B (dorsal view - adult; paralectotype of *Palinurus desmaresti* SECRÉTAN, 1975); MFB IG 132590-132605 (part and counterpart, dorsal view - juvenile); MGP-PD 7445-7446 (part and counterpart, dorsal view - adult).

#### Note 1

Three small-sized specimens (MCSNV M 02, MCSNV B17-17bis, MFB IG 132590-132605) are herein considered as intermediate juvenile stages based on morphometric evidence. In the extant spiny lobsters, for example, the carapace length of mature males and females of the Mediterranean and eastern Atlantic well-known *Palinurus elephas* (FABRICIUS, 1787) ranges from a minimum size respectively between 7 and 8.5 cm, reaching a total body length

of *c.* 40-60 cm in the male and *c.* 21-50 cm in the female (GIBSON-HALL *et al.*, 2018), whereas the first “puerulus” not benthonic stage reaches a total body length of *c.* 5 cm (for full discussion see GUERAO *et al.*, 2006). Therefore, these specimens having the carapace length under 7 cm could be considered as pertaining to juvenile (immature) specimens.

#### Note 2

MCSNV 19 (juvenile, lateral view; lcxp: *c.* 4 cm) is herein tentatively assigned to this species for the partially preserved imbricate scales on cardiac and branchial regions and tuberculate a2 segments with outer and inner smooth margins. However, since the pleon was restored and coloured simply to improve the specimen's appearance, it was hard to check the presence of transverse striae, diagnostic character of *Justitia*.

#### Type locality

“Pesciara” of Bolca (Verona).

#### Geological age

Late Ypresian (early Eocene).

#### Description

Small to middle-sized spiny lobster (lt between *c.* 6 cm to 13 cm).

**Carapace.** Subcylindrical granulated carapace with some scattered tubercles/spinules on the frontal and gastric regions and with imbricate scales on branchial and cardiac regions; deep cervical groove gently convex medially and located in anterior third laterally; posterior margin slightly concave; supra-orbital spines and rostrum not visible.

**Pleon.** Subrectangular s1-s5 equal in size with subrounded rough pleura; granulated s1 tergum; granulated s2-s5 terga crossed by 2-3 complete parallel transverse striae; subtrapeziodal s6 with embossed tergum (MCSNV M 02); telson not preserved.

**Cephalic appendages.** Thin elongate basal a1 segment; median and distal a2 segments covered with closely spaced small granules uniformly arranged; median a2 segment with smooth outer and inner margins; distal a2 segment with smooth inner margin and outer margin with one distal spine; strong multi-articulated a2 flagellum almost as long as the body length.

**Thoracic appendages.** Thin elongate P2-P5; P1 shorter and stronger than P2-P5; P2-P5 equal in

length; P1-P5 covered with closely spaced small granules uniformly arranged.

**Pleonal appendages.** Petaloid pleopods on s2-s4. Uropodal exopod and endopod not preserved.

#### Discussion

*Justitia* was established by HOLTHUIS (1946) to accommodate the formerly known extant *Palinurus longimanus* H. MILNE EDWARDS, 1837 and its variety *P. longimanus mauritianus* MIERS, 1882, although no definition of the new genus was included and its main characters were stated in his key to the determination of the genera of the Palinuridae only (HOLTHUIS, 1946, p. 113).

Based upon the diagnoses provided by POUPIN (1994, p. 39) and SCHWEITZER *et al.* (2015, p. 5), we can assign some specimens previously belonging to the type series of *desmaresti* to *Justitia* for the distinctive squamiform ornamentation of the cardiac and branchial regions of the carapace and the pleonal somites with complete parallel transverse striae, characters unique of this genus.

POUPIN (1994) listed the four extant species of *Justitia* that differ each other for the sculpturing of the carapace, shape of pereopods, and number of transverse striae on s1-s5 terga.

P1 shorter and stronger than P2-P5 and thin elongate P2-P5 are characters shared between the fossil specimens and the extant *J. chani* POUPIN, 1994, *J. japonica* (KUBO, 1955), and *J. vericeli* POUPIN, 1994, though the fossil specimens have a different sculpturing of the carapace regions.

BESCHIN *et al.* (2001, p. 92) reported the only fossil species known to date, *J. vicetina* BESCHIN, DE ANGELI AND GARASSINO, 2001, from the middle Eocene (middle Lutetian) of NE Italy. It clearly differs from the studied specimens for the gastric region covered with imbricate scales and branchial and cardiac regions covered with parallel transverse grooves (*vs.* frontal and gastric regions with some scattered tubercles/spinules and branchial and cardiac regions with imbricate scales on the studied specimens).

In conclusion, *J. confusa* n. sp. is herein proposed, representing the oldest fossil record for the genus, and supporting the close affinities already highlighted between several taxa of the lower Eocene marine fauna from the “Pesciara” and Monte Postale and the extant faunas of the Indo-Pacific tropical warm waters (see TYLER, 1975; MARRAMÀ *et al.*, 2019, 2021 among the others).

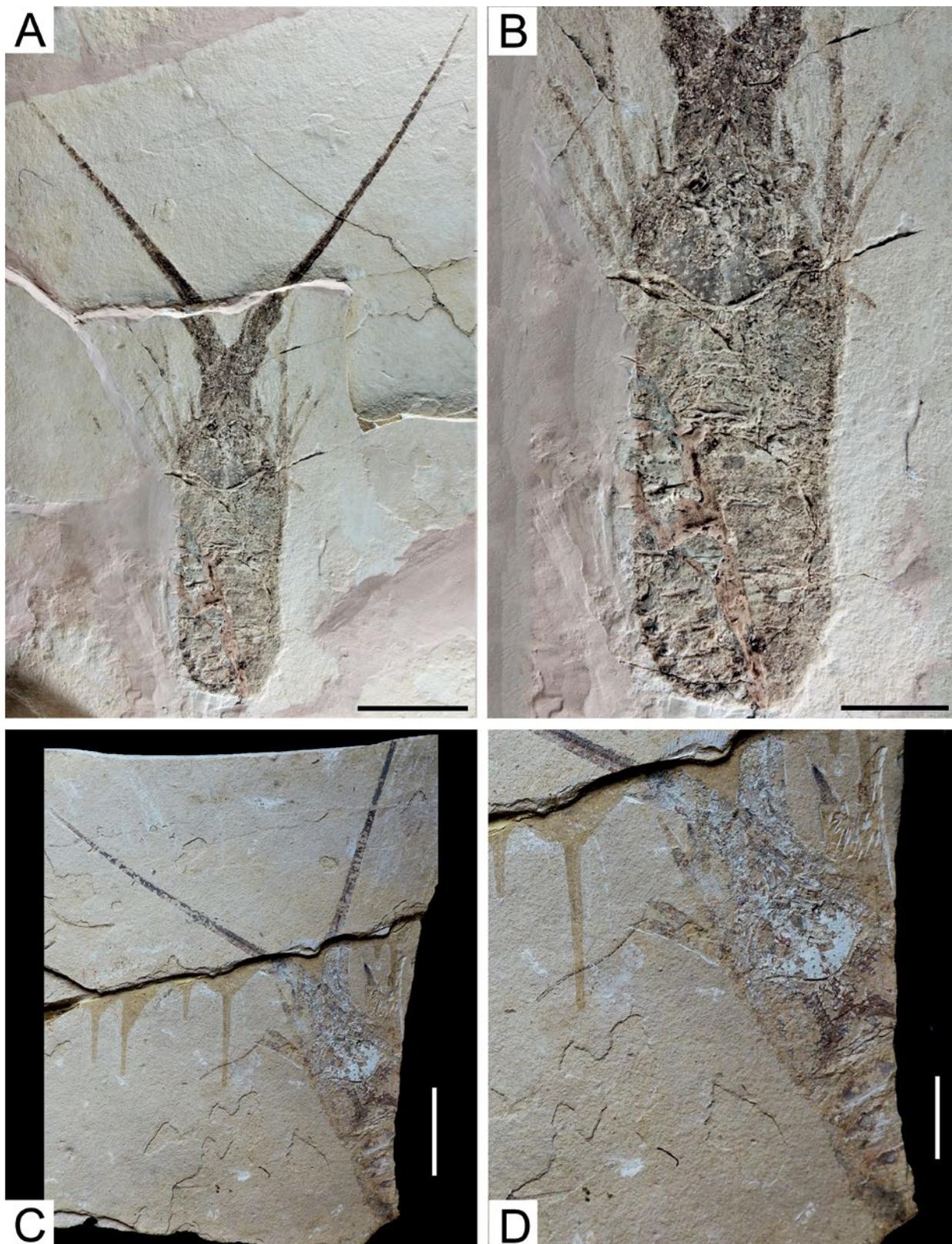


Fig. 10 – *Justitia confusa* n. sp. **A**) MSNVE 6298, holotype, dorsal view. **B**) MSNVE 6298, close-up of the carapace and pleon, dorsal view. **C**) MCSNV 23B, paratype, dorsal view. **D**) MCSNV 23B, paratype, close-up of carapace and pleon, dorsal view (UV light). Scale bars of A and C equal 2 cm, scale bars of B and D equal 1 cm

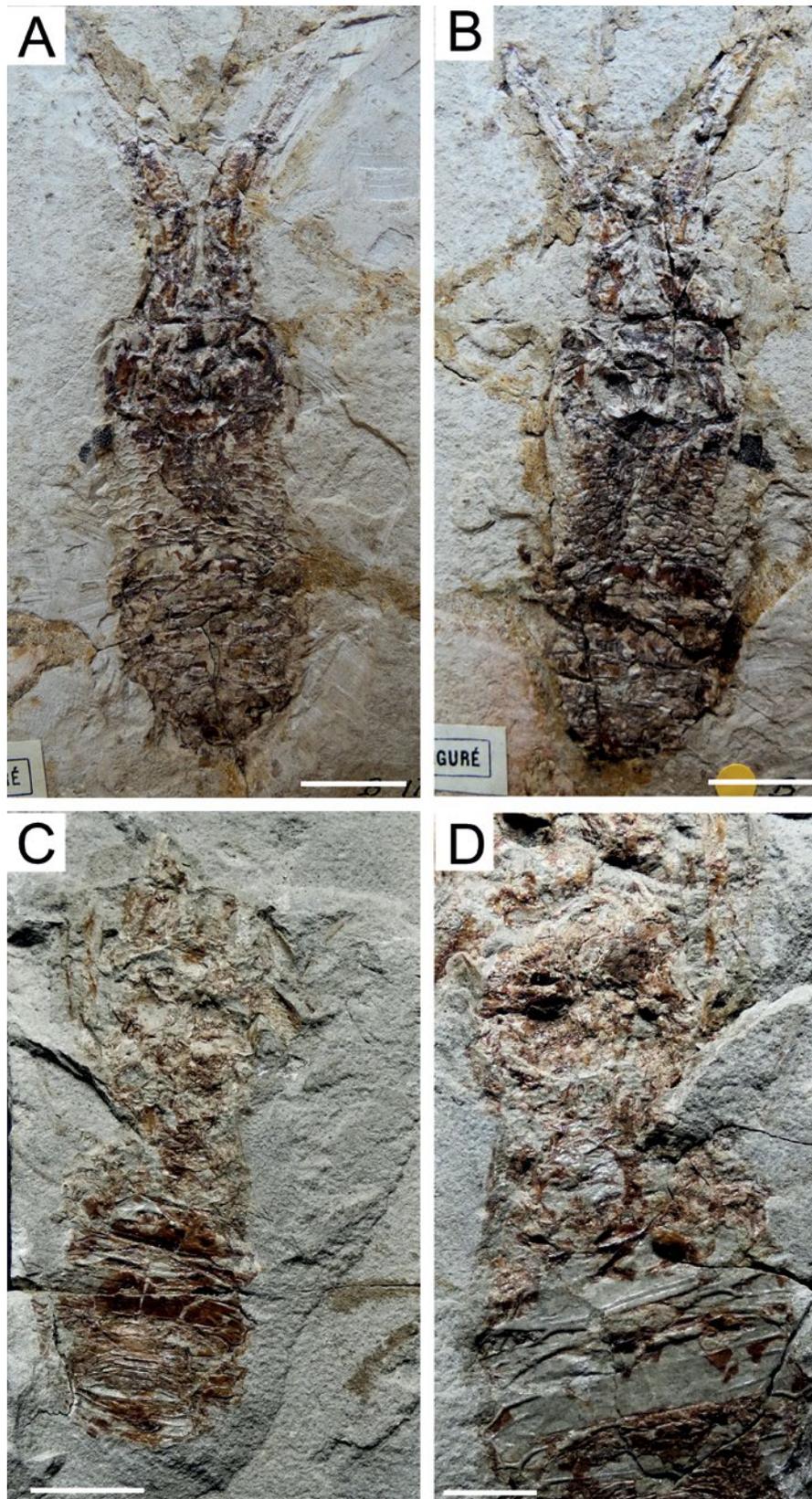


Fig. 11 – *Justitia confusa* n. sp. **A**) MCSNV B17, paratype, dorsal view (part). **B**) MCSNV B17bis, paratype, dorsal view (counterpart). **C**) MFB IG 132590, paratype, dorsal view (part). **D**) MFB IG 132605, paratype, close-up of the imbricate scales on branchial and cardiac regions and transverse striae on s2 terga, dorsal view (counterpart). Scale bars of A-C equals 4 cm, scale bar of D equals 2 cm

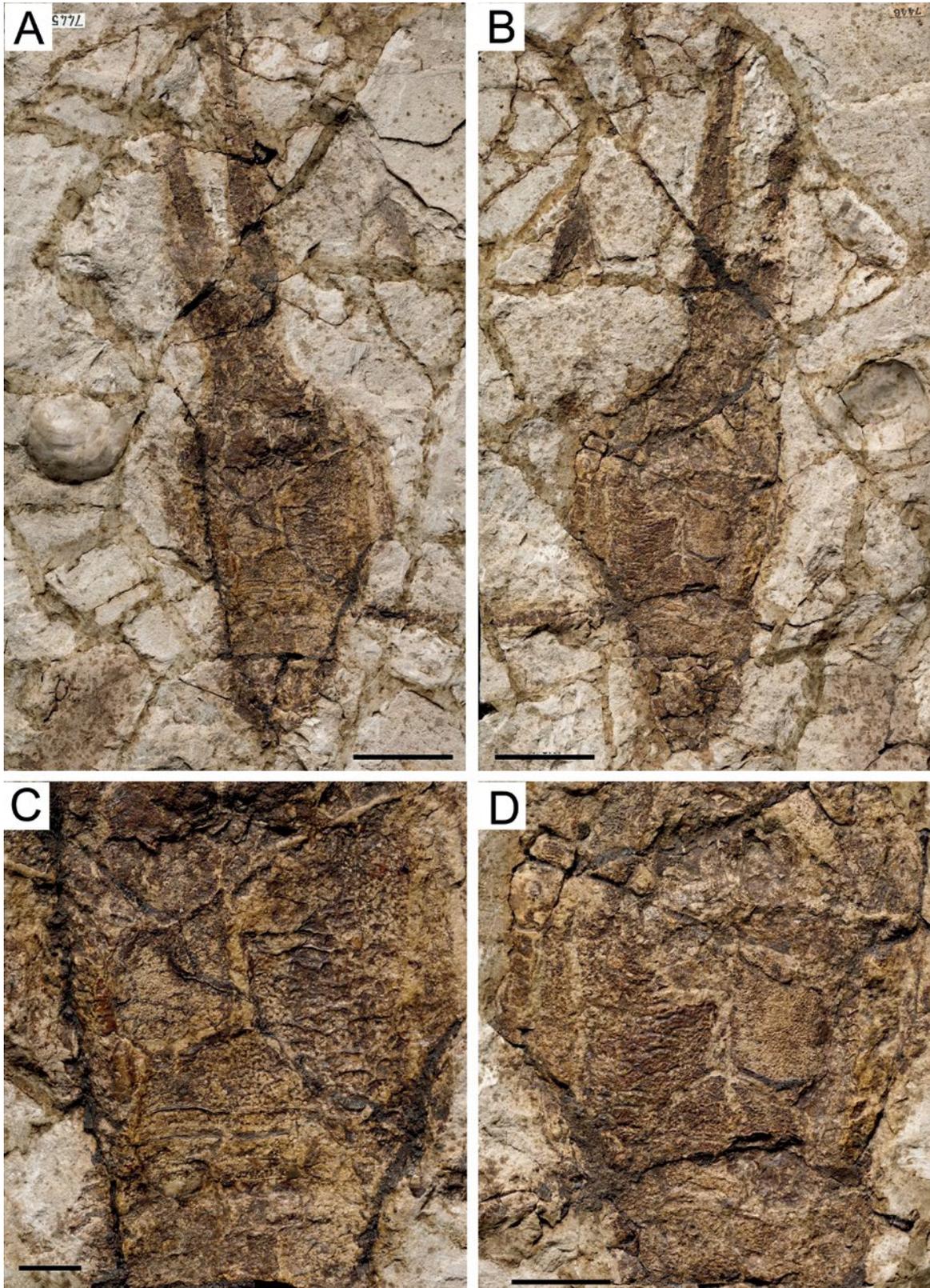


Fig. 12 – *Justitia confusa* n. sp. **A**) MGP-PD 7445, paratype, dorso-lateral view (part). **B**) MGP-PD 7446, paratype, dorso-lateral view (counterpart). **C**) MGP-PD 7445, paratype, close-up of the imbricate scales on branchial and cardiac regions. **D**) MGP-PD 7446, paratype, close-up of the imbricate scales on branchial and cardiac regions. Scale bars of A and B equal 4 cm, scale bars of C and D equal 1 cm

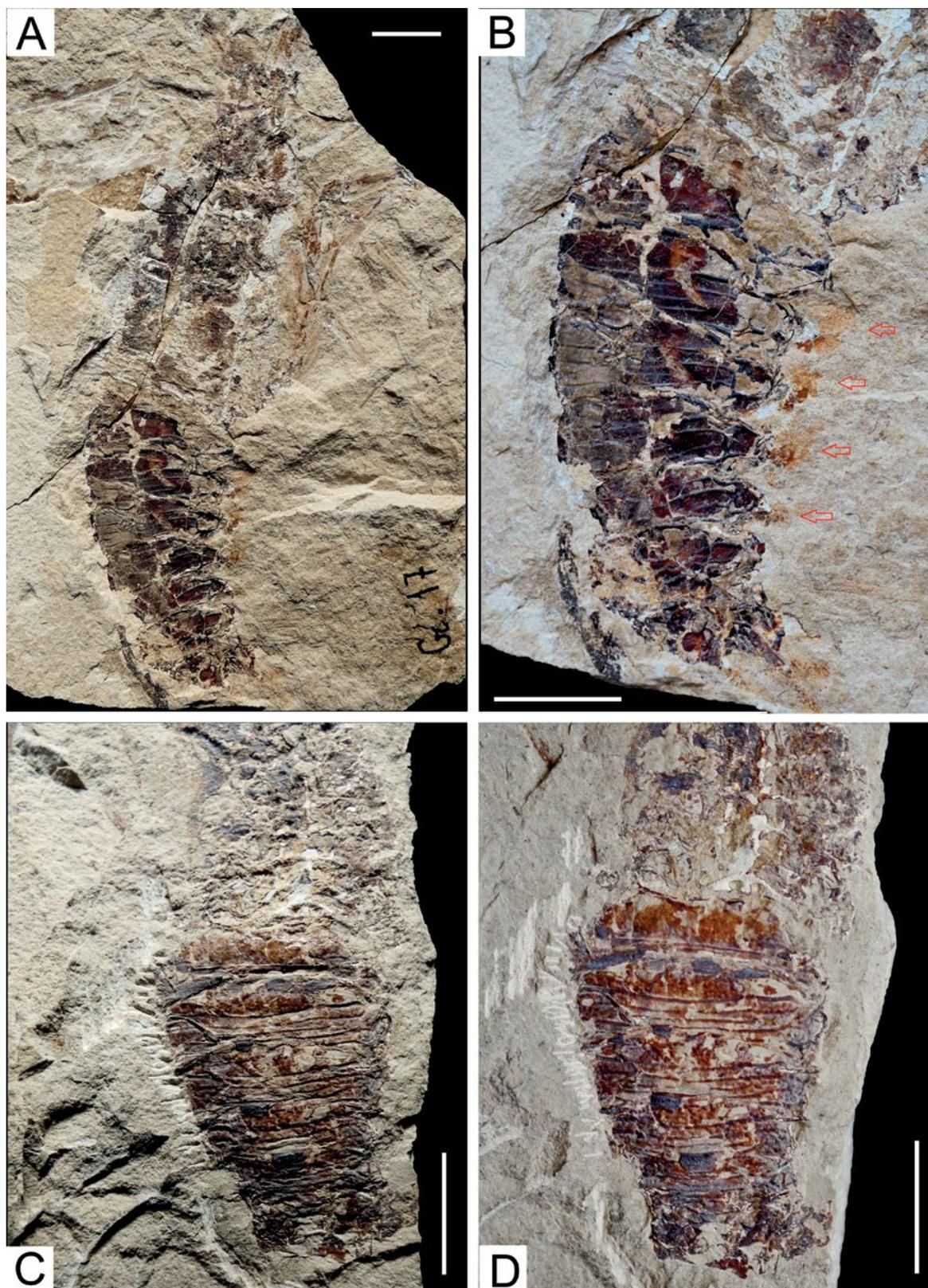


Fig. 13 – *Justitia confusa* n. sp. **A)** MCSNV Cr17, paratype, lateral view. **B)** MCSNV Cr17, paratype, close-up of the pleon with transverse striae on the terga and petaloid pleopods (red arrows) (UV light). **C)** MCSNV M 02, paratype, dorsal view. **D)** MCSNV M 02, paratype, close-up of the pleon with transverse striae on the terga (UV light). Scale bar of A equals 4 cm, scale bar of B equals 2 cm, scale bars of C and D equal 1 cm

***Justitia* sp.**

Figures 4C-D, 14

2019 *Justitia desmaresti* (SECRÉTAN, 1975). – PASINI *et al.*, p. 247, fig. 9D (non *Palinurus desmaresti* SECRÉTAN, 1975).

**Material**

MFB IG 91130, Monte Postale (Altissimo, Vicenza).

**Geological age**

Late Ypresian (early Eocene).

**Note**

PASINI *et al.* (2019, p. 247) listed this specimen among the additional specimens of *J. desmaresti*, misinterpreting its provenance. The specimen was not collected from “Pesciara”, but from Monte Postale as attested by the lithology of the matrix different between the localities: fine-grained greyish to yellow laminated micritic limestone at “Pesciara” *vs.* coarser whitish laminites with common test of *Alveolina* at Monte Postale.

**Description**

Medium/large-sized spiny lobster (lpl: c. 18 cm).

**Carapace.** Partially preserved; five aligned spiny tubercles forming a longitudinal ridge for which is impossible to check the precise position due to the partial and fragmentary carapace; dorsal surface finely granulated.

**Pleon.** Subrectangular s1-s5 slightly decreasing in size posteriorly; smooth s1 tergum; smooth s2-s3 terga with 3 complete parallel transverse striae; smooth s4-s5 terga with 4 complete parallel transverse striae; subrounded embossed s1-s5 pleura; subrectangular s6 shorter than the previous ones; subtriangular embossed s6 pleuron; telson partially preserved with embossed rigid proximal part.

**Cephalic appendages.** a1 not preserved; median and distal a2 segments with smooth inner and outer margins; strong multi-articulated a2 flagellum slightly longer than the body.

**Thoracic appendages.** Strong extremely elongate P1 (c. 20 cm); subrectangular elongate P1 carpus; subrectangular P1 propodus twice as long as the carpus; strong hook-shaped P1 dactylus slightly curved distally; outer surface of P1 carpus, propodus, and dactylus covered with closely spaced strong tubercles uniformly arranged; P2 not preserved; P3-P5 partially preserved; thin, relatively elongate, and smooth P3-P5 ischia; thin smooth P3-P5 meri, twice as long as ischia.

**Pleonal appendages.** Pleopods not preserved; uropodal exopod and endopod as long as the telson; proximal half outer margin of exopod and endopod with a triangular, hardened, and embossed scale, having a deep median transverse groove and thin tuberculate fringed striae on the half distal part.

**Discussion**

Based upon HOLTHUIS (1991) we can just compare the studied specimen with *Justitia* for two shared characters: strong extremely elongate P1 with hook-shaped dactylus and s2-s5 terga with complete parallel transverse striae. Indeed, among the genera of the Palinuridae, only *Justitia* has strong extremely elongate P1 with hook-shaped dactylus as in *J. longimanus* (H. MILNE EDWARDS, 1837) and *J. mauritiana* (MIERS, 1882) although the P1 is not subchelate in the studied specimen like that of the extant species. Moreover, among the genera of the Palinuridae, only *Justitia* has complete parallel transverse striae on pleonal terga.

However, we tentatively compare the studied specimen with *Justitia* due to the lack of the carapace having the most important diagnostic characters for its precise systematic assignment, and so we leave it in open nomenclature.

Finally, we point out that the specimens herein assigned to *J. confusa* (see above) were collected from “Pesciara” layers only, whereas the studied specimen is the sole adult specimen collected from Monte Postale, representing one of the biggest spiny lobsters discovered to date. Moreover, the coarser whitish laminites of Monte Postale are supposed to be originated in a “lagoon” with at least periodic anoxic conditions at the bottom and surrounded by coralgal buildups with peri-reefal areas densely vegetated by seagrass beds and mangroves; a palaeoenvironment different than “Pesciara” that instead illustrates a low-energy basin with permanent bottom dysoxia or anoxia in a peri-reefal system strongly influenced both by coastal and pelagic environments (MARRAMÀ *et al.*, 2016; PASINI *et al.*, 2019).

In conclusion, based on the large size of the studied specimen like that of the extant representatives of *Justitia* and the different palaeoenvironments of the fossiliferous localities, we can't exclude the hypothesis that the studied specimen could represent a new taxon within *Justitia* although its systematic assignment can be solved only through discovery by better-preserved specimens from the same locality.

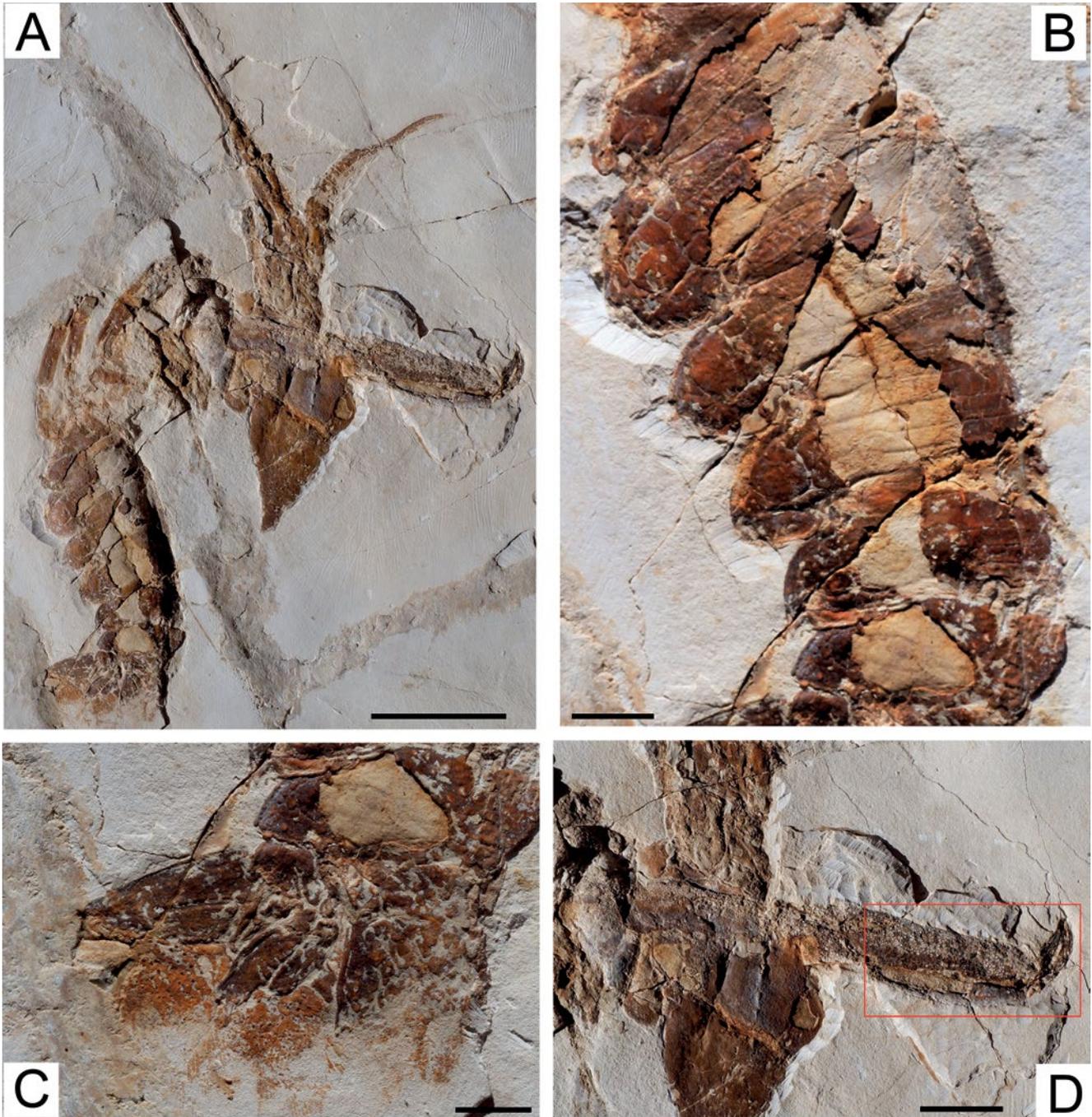


Fig. 14 – *Justitia* sp. **A)** MFB IG 91130, dorso-lateral view. **B)** MFB IG 91130, close-up of the pleon with transverse striae on the terga. **C)** MFB IG 91130, close-up of the tail fan. **D)** MFB IG 91130, close-up of the elongate superimposed P1 (red rectangular). Scale bar of A equals 10 cm, scale bars of B and C equal 2 cm, scale bar of D equals 4 cm

**Family indeterminate**  
**Genus *Lessinoachela* nov.**

*Diagnosis*

Subcylindrical carapace with slightly inflated, convex lateral margins; carapace strongly tuberculate with small-medium-sized tubercles arranged randomly (gastric and epibranchial regions) and uniformly (branchial regions); triangular-shaped rounded gastric region strongly projected forward; supraorbital spines absent; deep, convex, smooth cervical groove, deeply V-shaped medially; posterior margin strongly concave with a smooth deep groove; raised, postfrontal, transverse rim convex frontally made by aligned strong tubercles; transverse row joined laterally to the cervical groove, forming a raised cephalic shield; subrounded s1-s5 dorsally with granulated terga crossed by two marginal transverse, rounded grooves finely crenulate posteriorly; achelate P1-P5.

*Etymology*

From Lessinia, the geographical area near Verona where the fossiliferous sites of Bolca crop out, and the infraorder Achelata, hence “Achelata from the Lessinia”. Gender: feminine.

*Type species*

*Lessinoachela scaligera* n. gen., n. sp., by monotypy.

*Discussion*

SECRÉTAN (1975, p. 340) originally discussed this specimen and although she pointed out that the dorsal ornamentation of the carapace is “*grossièrement écaillée*” (grossly scaly) and “... *ce qui, sur la contreimpreinte, détermine une sorte de réseau d'épaississement en forme de mailles* (on the counterpart forms a kind of mail-shaped thickness), she assigned it to *Palinurus desmaresti*.

We do not concur with this interpretation. Indeed, the dorsal carapace ornamentation with well-separated strong tubercles arranged in transverse lines on branchial regions and similar in the gastric and cardiac regions, never squamiform does not fit the typical ornamentation of *Justitia* (see above). Moreover, the deep smooth cervical groove convex medially, deeply V-shaped and the peculiar ornamentation of the pleonal somites are additional characters that rule out the belonging of this specimen to *Justitia*.

Based upon HOLTHUIS (1991), the studied specimen has dorsal carapace ornamentation with

well-separated thick, large-sized tubercles arranged in transverse lines on branchial regions and similar in the gastric and cardiac regions shared with *Sagmariasus* HOLTHUIS, 1991. We exclude, however, the belonging of the studied specimen to *Sagmariasus* in having smooth s1-s6 terga (*vs.* s1-s5 terga crossed by two marginal transverse, rounded ridge finely crenulate posteriorly in the studied specimen).

Moreover, based upon HOLTHUIS (1991) and SCHWEITZER *et al.* (2015), the combination of some characters, such as the postfrontal region marked posteriorly by a transverse convex rim of closer tubercles convex frontally; the gastric and cardiac regions with granulated tubercles similar to those on the branchial region; the branchial region adorned dorsally by transverse, lined, and strong large-sized tubercles equally spaced each other, alternate with sparse small granules; and subrounded s1-s5 with smooth terga crossed by two marginal transverse, rounded ridge finely crenulate posteriorly, rule out the systematic assignment of the studied specimen to the known fossil and extant genera within the Palinuridae and Synaxidae.

In conclusion, the new genus *Lessinoachela* is herein erected to accommodate the studied specimen, leaving its assignment to the family level in open nomenclature within the Achelata.

*Included fossil species*

Type species only.

***Lessinoachela scaligera* n. gen., n. sp.**

Figures 2C, 3C-D, 15, 16

1975 *Palinurus desmaresti* DE ZIGNO. – SECRÉTAN, p. 340, pl. 14, figs. 2–4 (non *Palinurus desmaresti* SECRÉTAN, 1975).

*Diagnosis*

As for the genus.

*Etymology*

From Della Scala or Scaligeri, noted family that ruled Verona during the late 13<sup>th</sup> and the 14<sup>th</sup> centuries.

*Holotype*

MCSNV 95, paralectotype of *Palinurus desmaresti* Secrétan, 1975 [illustrated by Secrétan (1975: pl. 14, figs. 2–4)].

*Type locality*

“Pesciara” of Bolca (Verona).

*Geological age*

Late Ypresian (early Eocene).

*Material and measurements*

One large-sized specimen, slightly compressed dorso-ventrally, preserved as dorsal counterpart (MCSNV 95 – lcxp: c. 14.8 cm, from the a1 to the posterior margin; wcxp: c. 9.9 cm maximum width at level of cervical groove).

*Note*

Between the Eighteenth and Nineteenth centuries, it was customary to prepare and restore fragmentary specimens on the “Pesciara” slabs with the aim of not only reassembling the plates, but also inserting fragments to esthetically complete the fossil specimens. The inaccurate preparation techniques combined with the scarce anatomical knowledge resulted in purely subjective interpretations of the organisms’ anatomy. In this specific case, the UV light aided in discovering that the presumed left antenna that appears as bifid (overlapping of two antennal flagella) was deliberately inserted to complete the first pereiopod, in order to simulate an unlikely chelate cheliped. The left antenna portion doesn’t certainly belong to the studied specimen based on the actual on-site presence of the original flagellum of the right antenna, as highlighted in Fig. 15.

*Description*

*Carapace.* Subcylindrical carapace with slightly inflated, convex lateral margins; triangular-shaped rounded frontal region strongly projected forward; supraorbital spines absent; orbits not observable; deep, convex, smooth cervical groove, deeply V-shaped medially; posterior margin strongly concave with a smooth deep groove; raised, post-frontal, transverse rim convex frontally made by aligned strong tubercles; transverse row joined laterally to the cervical groove, forming a raised cephalic shield covered by medium-sized tubercles, larger posteriorly, arranged more or less uniformly; gastric region covered by small-medium sized tubercles arranged randomly; epibranchial regions covered by large-sized tubercles arranged randomly; branchial region covered by transverse, lined, and large-sized tubercles flattened dorsally and equally spaced each other, decreasing in size laterally and alternate with sparse smaller tubercles.

*Pleon.* Subrounded s1-s5 dorsally with granulated terga crossed by two marginal transverse, round-



Fig. 15 – *Lessinoachela scaligera* n. gen., n. sp., MCSNV 95, holotype. The black lines in the upper right corner show the piece of slab preserving the supposed bifid a2 segments and flagellum erroneously joined to the P1 distal part based upon the precise anatomical position of the right a2 flagellum. Scale bar equals 3 cm

ed grooves finely crenulate posteriorly; s1-s5 pleura poorly preserved; s6 and telson not preserved.

*Cephalic appendages.* Eyes not preserved; basal and median a1 segments preserved, the first one longer than the second one; right strong multi-articulated a2 flagellum, shorter than the body.

*Thoracic appendages.* Slender elongate P1 with short triangular dactylus; P2-P5 partially superimposed and preserved; strongly granulated achelate P2-P5 with submarginal ridge on propodus; P4 with setae along the margins of propodus.

*Pleonal appendages.* Not preserved.

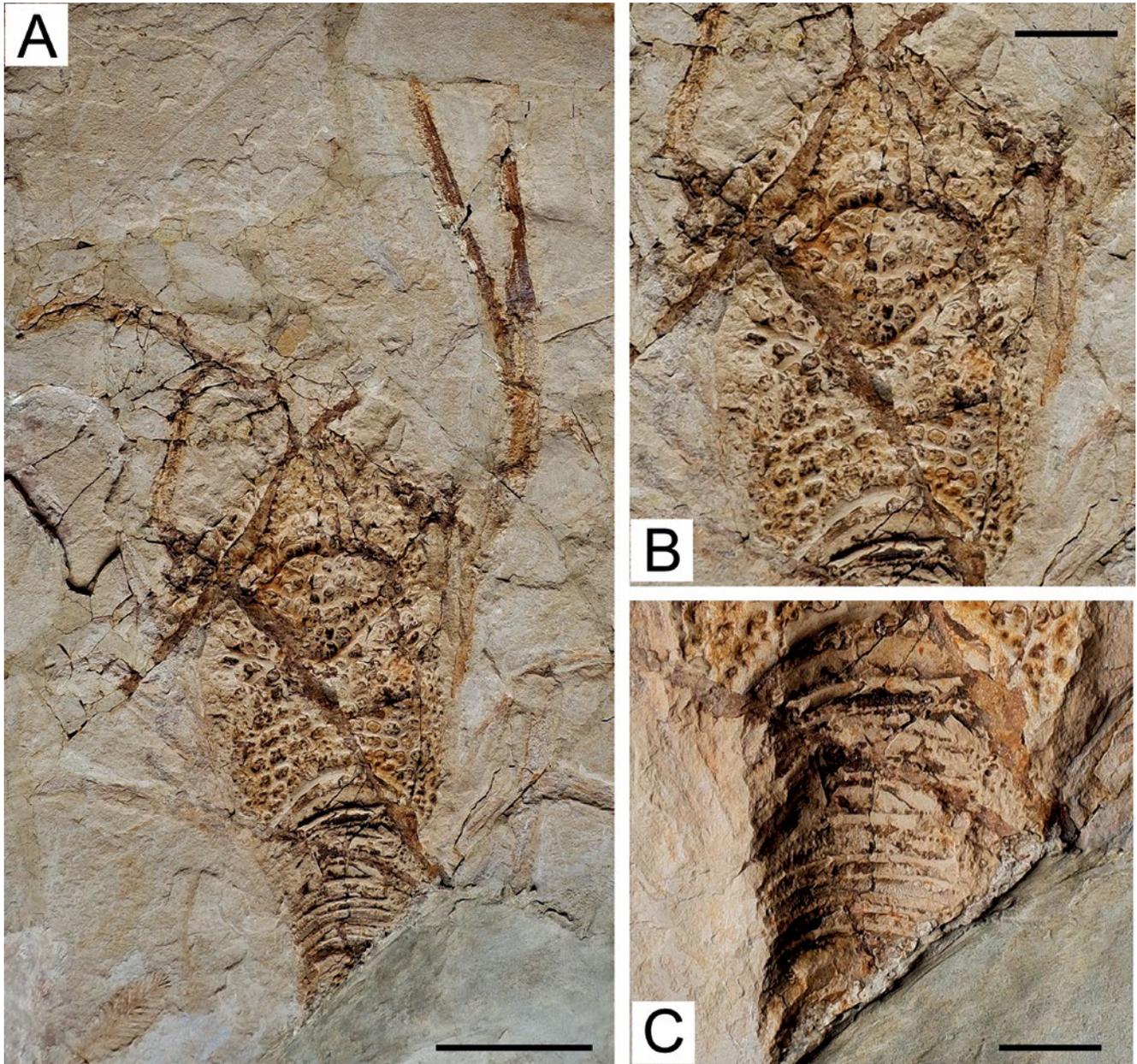


Fig. 16 – *Lessinoachela scaligera* n. gen., n. sp. **A**) MCSNV 95, holotype, dorsal view. **B**) MCSNV 95, holotype, close-up of the carapace. **C**) MCSNV 95, holotype, close-up of the pleon. Scale bar of A equals 6 cm, scale bars of B and C equal 2 cm

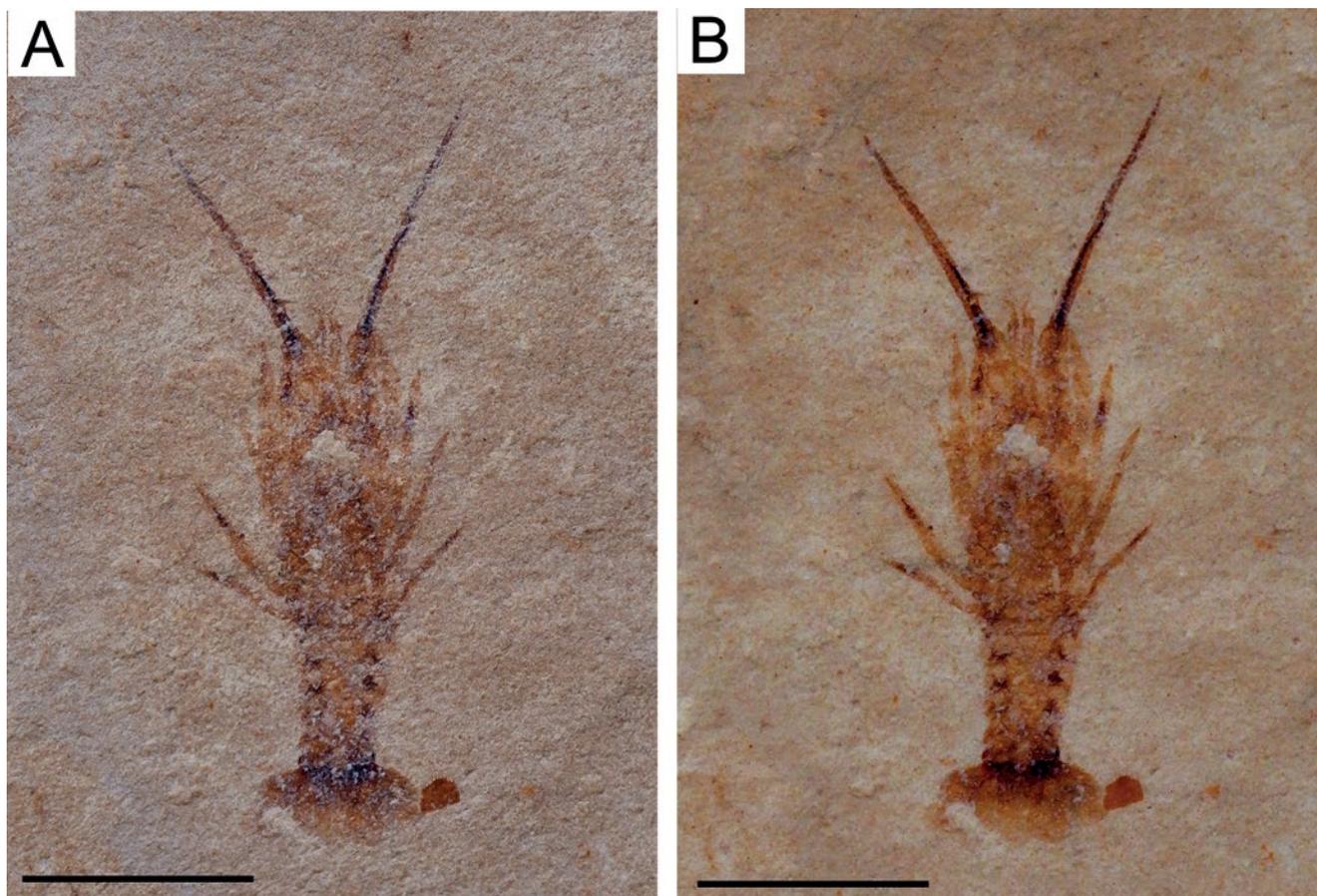


Fig. 17 – “puerulus” larval stage. **A**) MCSNV 43.2020, dorsal view (dry), UV light. **B**) MCSNV 43.2020, dorsal view (alcohol-impregnated). Scale bar equals 0.5 cm

### “puerulus” larval stage

Figure 17

#### Material and measurements

MCSNV 43.2020 (tl: c. 1.5 cm, excluding antennae).

#### Locality

Monte Postale (Altissimo, Vicenza).

#### Geological age

Late Ypresian (early Eocene).

#### Description

Small-sized specimen with cervical groove not distinct, tail fan in dorsal view, pleonal and thoracic appendages exposed on both sides of the body; flagellate antennae shorter than the body; P1 appears longer than P2-P5. Telson divides in a rigid proximal part and a flexible distal part; subrectangular proximal part with two small distal spines, three thin longitudinal ridges (one median and two

lateral), and inverted V-shaped inferior margin; subrounded flexible part with thin parallel longitudinal striae.

#### Discussion

The very small specimen from Monte Postale represents the “puerulus” larval stage (see note 1 in *J. confusa* n. sp.), largely resembling the adult features (see HAUG AND HAUG, 2013, 2016). Indeed, the carapace morphology and the dorsal ornamentation resemble those of the mature specimens of *Eolinurus desmaresti* (SECRÉTAN, 1975) n. comb.

The presence of larval, juvenile, and adult (mature) specimens of spiny lobsters in the “Pesciara” and Monte Postale palaeoenvironments allows us to attest that close to both “basin” conditions were favourable to the post benthic-stages life and development of several different spiny lobster taxa, showing at the same time some diversity in the composition of the spiny lobster communities in the two different depositional contexts.

## CONCLUSIONS

Despite the problematic runs in the systematic arrangement and its relative incompleteness due to the impossibility of recognize some main characters of the frontal shape in the studied specimens, this study allows us to point out several inconsistencies in the previous studies with a reappraisal of the spiny lobsters from the “Pesciara” and Monte Postale Konservat-Lagerstätten.

The review of the specimens previously assigned to *Justitia desmaresti* (SECRÉTAN, 1975) allowed to highlight the real status of this species and to identify two distinct, previously undetected taxa within this species, enlarging our knowledge on the spiny lobster assemblage of the lower Eocene “Pesciara” and Monte Postale palaeoenvironments.

The different depositional conditions and slightly different age between “Pesciara” and Monte Postale basins can partially explain the reasons of the presence of three taxa of spiny lobsters (*Eolinurus desmaresti*, *Justitia confusa* n. sp., and *Lessinoachela scaligera* n. gen., n. sp.) from “Pesciara” than in the Monte Postale basin where the crustacean record seems instead scarcer and less differentiate (see also discussion in PASINI *et al.*, 2019: 264 and list below). For instance, the extant *Justitia* species are widespread in several localities from Indo Pacific and in western Atlantic Oceans (for full data see POUPIN, 1994), mostly living on rocky or sandy coral limestone bottoms, usually reported from around 50 to 300 m depth, an environment more comparable with the “Pesciara” basin conditions as reconstructed by MARRAMÀ *et al.* (2016).

Indeed, the sole adult spiny lobster specimen reported from Monte Postale (*Justitia* sp.), though not assigned at specific level, clearly shows characters different from those observed in the species from “Pesciara”.

Moreover, a very small, complete “puerulus” larval stage was herein reported for the first time from Monte Postale.

Finally, a new updated complete list of the decapod species reported to date from the “Pesciara” and Monte Postale Konservat-Lagerstätten (Veneto, N Italy), is herein provided (Appendix 1).

## ACKNOWLEDGEMENTS

We wish to thank B. FAVARETTO (Museo di Storia Naturale Giancarlo Ligabue, Venezia) and I. TOMELLERI (Museo di Storia Naturale di Verona) for the photos of the specimens housed in the palaeontological collections under their care; M. CERATO (Bolca, Verona) who allowed us the study of two specimens housed in the collection of the Museo dei Fossili di Bolca; M. CAMERIN (Museo Diocesano di Scienze Naturali “A. De Nardi”, Vittorio Veneto, Treviso) who allowed us the study of the specimen of *Eolinurus desmaresti*, housed in the collections; S. CASTELLI (Dipartimento di Geoscienze dell’Università di Padova) for accurate photographic documentation and figures preparation; M. FORNASIERO (Museo di Geologia e Paleontologia dell’Università di Padova) for her precious help during “excavation” in the deposits of the Museo di Geologia e Paleontologia dell’Università di Padova; R. SIGISMONDO (Varese) for additional photos useful to complete the iconographic section. We are also very grateful to F. ROSSI (Director of the Museo di Storia Naturale di Verona) and to L. LATELLA (editor of “Studi e Ricerche sui Giacimenti Terziari di Bolca”) for hosting this article. Finally, we thank F.J. VEGA (Instituto de Geología, Universidad Nacional Autónoma de México, Coyoacán, Mexico) for careful review and criticism.

## APPENDIX 1

Complete updated list of the Decapoda genera and species and distribution in the laminites of “Pesciara” – Monte Postale Konservat-Lagerstätten, based upon present review (from PASINI *et al.*, 2019, modified).

	“Pesciara”	Monte Postale
Order Decapoda Latreille, 1803		
Genus <i>Bolcacalliax</i> HYŽNÝ in PASINI <i>et al.</i> , 2019 <b><i>Bolcacalliax eocenica</i></b> (SECRÉTAN, 1975)	X	
Genus <i>Penaeus</i> FABRICIUS, 1798 <b><i>Penaeus bolcensis</i></b> SECRÉTAN, 1975	X	
Genus <i>Eolinurus</i> n. gen. <b><i>Eolinurus desmaresti</i></b> (SECRÉTAN, 1975) n. comb.	X	
Genus <i>Justitia</i> HOLTHUIS, 1946 <b><i>Justitia confusa</i></b> n. sp.	X	
Genus <i>Justitia</i> HOLTHUIS, 1946 <b><i>Justitia</i></b> sp.		X
Genus <i>Lessinoachela</i> n. gen. <b><i>Lessinoachela scaligera</i></b> n. gen., n. sp.	X	
Genus <i>Scyllarides</i> GILL, 188 <b><i>Scyllarides bolcensis</i></b> DE ANGELI AND GARASSINO, 2008		X
Genus <i>Archaeocypoda</i> SECRÉTAN, 1975 <b><i>Archaeocypoda veronensis</i></b> SECRÉTAN, 1975	X	
Genus <i>Eotrachynotocarcinus</i> BESCHIN, BUSULINI, DE ANGELI AND TESSIER, 2007 <b><i>Eotrachynotocarcinus airagbii</i></b> BESCHIN, BUSULINI, DE ANGELI AND TESSIER, 2007	X	
Genus <i>Enoplonotus</i> A. MILNE-EDWARDS, 1860 <b><i>Enoplonotus armatus</i></b> A. MILNE-EDWARDS, 1860	X	
Genus <i>Lophopanopeus</i> RATHBUN, 1898 <b><i>Lophopanopeus bolcensis</i></b> (SECRÉTAN, 1975) n. comb.	X	
Genus <i>Lophoranina</i> FABIANI, 1910 <b><i>Lophoranina maxima</i></b> BESCHIN, BUSULINI, DE ANGELI AND TESSIER, 2004	X	X

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#### ADDRESSES OF THE AUTHORS

GIOVANNI PASINI

Via Alessandro Volta, 16  
22070 Appiano Gentile (Como) – Italia  
e-mail: giovannialdopasini@gmail.com

ALESSANDRO GARASSINO

Research Adjunct, Department of Earth and Biological Sciences, Loma Linda University  
Loma Linda, CA 92354 – Stati Uniti  
e-mail: alegarassino@gmail.com

ROBERTO ZORZIN

Museo Civico di Storia Naturale di Verona  
Lungadige Porta Vittoria, 9  
37129 Verona – Italia  
e-mail: roberto.zorzin@comune.verona.it

LUCA GIUSBERTI

Dipartimento di Geoscienze,  
Università degli Studi di Padova  
Via Gradenigo, 6  
35131 Padova – Italia  
e-mail: luca.giusberti@unipd.it