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Mud lobster *Thalassina* Latreille, 1806 (Decapoda: Gebiidea: Thalassinidae), its Cenozoic occurrences in Italy and palaeobiogeography

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ABSTRACT

Two specimens of *Thalassina* sp. are reported from the lower Oligocene sediments cropping out at Salcedo, Italy. Although the material is not sufficiently preserved to be identified below the genus level, it represents an important addition to the known fossil record of the genus. *Thalassina* sp. from Salcedo is considered the oldest and the only fossil occurrence of the genus from Europe; indeed, the previous reports on *Thalassina grandidactylus* Robineau Desvoidy, 1849 from the Cretaceous of France and *Thalassina* sp. from the Pliocene of Italy are disputed herein. *Thalassina* is today known only from the Indo-West Pacific region; however, unequivocal evidence of *Thalassina* in the Oligocene strata of Europe suggests the origin of the genus in the west Tethyan (modern circum-Mediterranean area). Alternatively, the geographic distribution of the genus might be wider in the Oligocene than it is today. The Italian material presented herein comes from marine settings with strong fluvial influence, suggesting that the environmental preferences of *Thalassina* have not changed since the Oligocene.

KEY WORDS
Decapoda,
Malacostraca,
fossil,
Oligocene,
Pliocene,
Italy.

RÉSUMÉ

Le homard de boue Thalassina *Latreille, 1806 (Decapoda: Gebiidea: Thalassinidae), ses occurrences cénozoïques en Italie et sa paléobiogéographie.*
Nous signalons deux spécimens de *Thalassina* sp. provenant des sédiments de l'Oligocène inférieur de Salcedo, Italie. Bien que le matériel ne soit pas assez bien préservé pour être identifié au-dessous du niveau genre, il représente un apport important à la connaissance du registre fossile de ce genre. *Thalassina* sp. de Salcedo est considérée comme l'occurrence fossile la plus ancienne du genre en Europe. En effet, les signalisations de *Thalassina grandidactylus* Robineau Desvoidy, 1849 du Crétacé de France et d'une *Thalassina* sp. du Pliocène de Spicchio, Italie, sont contestées. De nos jours, Les *Thalassina* actuelles ne sont présentes que dans la région Indo-Ouest Pacifique ; cependant, la présence non-équivoque de *Thalassina* dans les couches oligocènes d'Europe suggère une origine téthysienne (région circum-Méditerranéenne actuelle). Une autre possibilité est que la distribution paléobiogéographique du genre eût été plus grande à l'Oligocène que de nos jours. Le matériel d'Italie étudié ici provient d'un environnement marin avec de fortes influences fluviales, ce qui suggère que les préférences environnementales de *Thalassina* n'ont pas changé depuis l'Oligocène.

MOTS CLÉS
Decapoda,
Malacostraca,
fossile,
Oligocène,
Pliocène,
Italie.

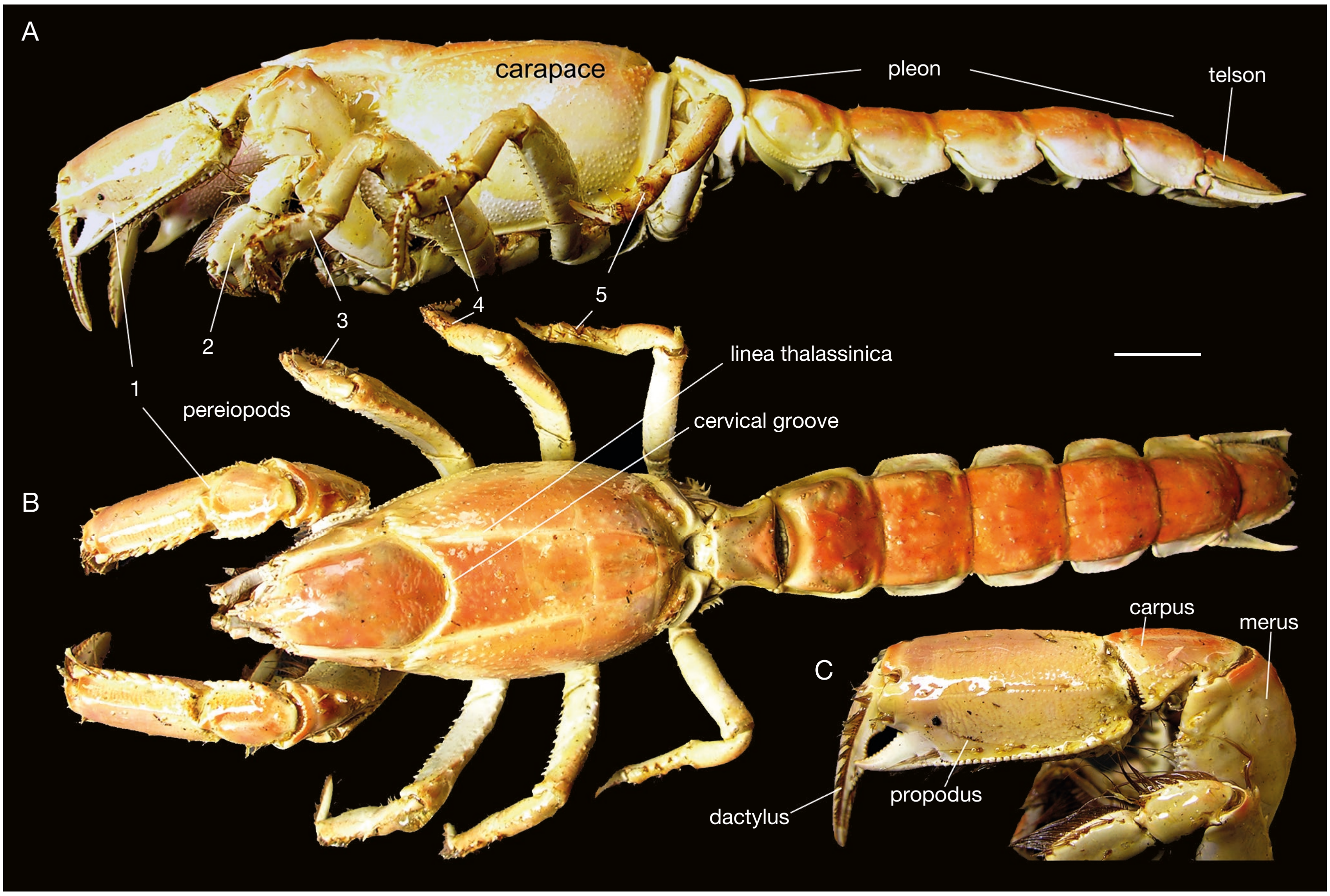

Fig. 1. — Body plan of *Thalassina* as exemplified on extant *T. anomala* (Herbst, 1804): **A**, lateral view; **B**, dorsal view; **C**, closer view on pereiopod 1. Photo: A. De Angeli). Scale bar: 10 mm.

INTRODUCTION

The mud lobster *Thalassina* Latreille, 1806 (Fig. 1) is a relatively well-studied genus, with several major contributions on its systematics and taxonomy published lately (e.g., Ngoc-Ho & de Saint Laurent 2009; Sakai & Türkay 2012). Individuals of some species can be fairly large, with the total length of 30 or even 35 cm (Holthuis 1991; Dworschak 2015), and together with strong calcification of their exoskeleton and chelipeds in particular, these animals have higher fossilisation potential than most fossorial shrimps of the groups Gebiidea and Axiidea (cf. Hyžný & Klompmaker 2015). Despite the fairly large size of *Thalassina*, the fossil record of the genus is rather poor (Table 1). Interestingly, all the occurrences spanning from the Miocene to the Holocene, overlap with the distribution of representatives of extant taxa (Ngoc-Ho & de Saint Laurent 2009; Sakai & Türkay 2012), i.e. the Indo-West Pacific area, including Australia (Bell 1844; Van Straelen 1928; Campbell & Woods 1970; Förster & Barthel 1978), Borneo (Collins *et al.* 2003) and Japan (Imaizumi 1953, 1969; Karasawa 1990, 1993; Karasawa & Nishikawa 1991; Karasawa & Inoue 1992; Karasawa & Nakagawa 1992; Ando *et al.* 2016).

An unequivocal evidence of *Thalassina* in the Oligocene strata of Europe presented herein sheds a new light on the origin of the genus and its palaeobiogeography. *Thalassina* has been resolved as basal in respect to other gebiideans excluding Upogebiidae (e.g., Tsang *et al.* 2008; Robles *et al.* 2009), thus, it is not surprising to find the genus in Oligocene strata. Its presence in Europe, outside the Recent distribution, seems to further support the origin of at least some modern Indo-West Pacific elements in the circum-Mediterranean region (Harzhauser *et al.* 2007; Renema *et al.* 2008; Hyžný 2011; Hyžný & Müller 2012). Alternatively, it may suggest that the geographic distribution of *Thalassina* was once wider than it is today. More fossil occurrences of the genus are needed for further implications to be made.

GEOLOGICAL SETTING

The material forming a basis for this study comes from lower Oligocene strata cropping out at Salcedo, Italy (Fig. 2). Lower Oligocene strata are exposed in the hilly area of the central part of Marostica and the eastern part of the Bassano hills. In the Valle del Ponte, the Oligocene strata consist of lignitic marls with volcanoclastic intercalations. The fossil content includes plant remains (leaves and seeds), gastropods, ostracods, malacostracans, small fish and frogs (Fabiani 1915; Piccoli 1967; Quaggiotto & De Angeli 2016). Lower Oligocene rocks at the localities Sostizzo and Salcedo repre-

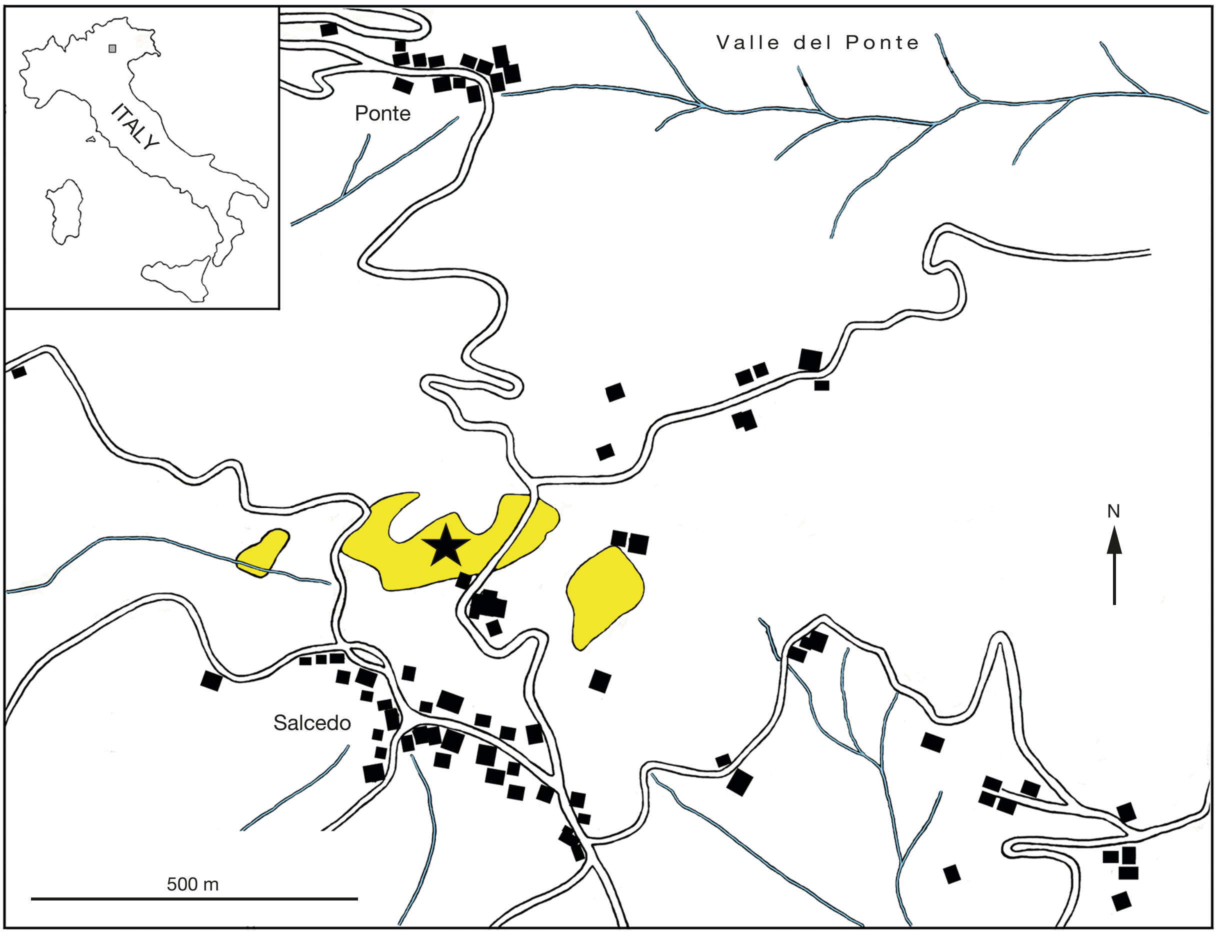

FIG. 2. — The study area of Salcedo, Italy. Exposed lower Oligocene strata are shown in yellow. The locality with *Thalassina* sp. is indicated with an asterisk (*).

sent well-bedded calcareous limestones containing abundant plant remains and fish (Piccoli 1967). The strata exposed in the Valle del Ponte were deposited in brackish or freshwater environment, whereas those from Sostizzo and Salcedo suggest the presence of marine environment with a strong fluvial influence. Numerous works examined the fossil content of these strata, including those on plants (e.g., Massalongo 1859; De Visiani 1862; Principi 1926), amber (Ragazzi & Roghi 2003), vertebrates (Bergnounioux 1953a, b, 1954; Bassani 1892; D'Erasmo 1922; Roccaforte *et al.* 1994; Mietto 1997), and decapod crustaceans (Milne-Edwards 1860; Michelotti 1861; Ristori 1892; Beschin & Garassino 1999; Table 2).

MATERIAL AND METHODS

The present study is based on two specimens referred to *Thalassina* sp. originating from the laminated limestones of Salcedo. One of them (MCZ.4516-I.G.367044) is an almost complete individual (Fig. 3), whereas the other specimen (MSNM i13569) represents an isolated pereiopod 1 (Fig. 4). Both specimens are flattened, especially the latter sample, obscuring some morphological details but still allowing taxonomic evaluation on the genus level. The material was documented photographically under normal light conditions. The studied specimens are housed in the Museo Civico di Storia Naturale di Milano (MSNM) and the Museo Civico "G. Zannato" di Montecchio Maggiore, Vicenza (MCZ).

SYSTEMATIC PALAEONTOLOGY

Order DECAPODA Latreille, 1802
Suborder GEBIIDEA de Saint Laurent, 1979
Family THALASSINIDAE Latreille, 1831

Genus *Thalassina* Latreille, 1806

TYPE SPECIES. — *Thalassina scorpionides* Latreille, 1806, a junior synonym of *Cancer* (*Astacus*) *anomalus* Herbst, 1804, by monotypy.

INCLUDED SPECIES. — See Table 1.

DIAGNOSIS. — Carapace laterally compressed with ocular and antennal spines on anterior margin. Rostrum moderately large; cervical groove distinct. Linea thalassinica extending whole length of carapace, convergent posteriorly, two horizontal and oblique suture posterior to cervical groove. Posterior margin of carapace with median concavity and dorsomedian process. Pleon longer than carapace, cylindrical, slender, pleonal pleura bordered with

TABLE 1. — Currently recognised *Thalassina* Latreille, 1806 species. Abbreviation: **IWP**, Indo-West Pacific (for extant species).

Taxon	Stratigraphic span	Distribution
T. australiensis Sakai & Türkay, 2012	Holocene	IWP
T. gracilis Dana, 1852	Holocene	IWP
T. kelanang Moh & Chong, 2009	Holocene	IWP
T. krempfi Ngoc-Ho & de Saint Laurent, 2009	Holocene	IWP
T. pratas Lin, Komai & Chan, 2016	Holocene	IWP
T. saetichelis Sakai & Türkay, 2012	Holocene	IWP
T. spinirostris Ngoc-Ho & de Saint Laurent, 2009	Holocene	IWP
T. spinosa Ngoc-Ho & de Saint Laurent, 2009	Holocene	IWP
T. squamifera de Man, 1915	Pleistocene–Holocene	IWP/Australia
T. emerii Bell, 1844	Pleistocene	IWP/Australia
T. anomala Herbst, 1804	Miocene-Holocene	IWP/Australia, Borneo, Japan
Thalassina sp. 1 *sensu* Ando *et al.* 2019	middle Miocene	Japan
Thalassina sp. 2 *sensu* Ando *et al.* 2019	middle Miocene	Japan
T. yamato Ando & Kishimoto *in* Ando, Kishimoto & Kawano, 2016	middle Miocene	Japan
T. tsuyamensis Ando & Kishimoto *in* Ando, Kishimoto & Kawano, 2016	early-middle Miocene	Japan
Thalassina sp.	early Oligocene	Italy

TABLE 2. — Decapod crustaceans reported from the lower Oligocene of Salcedo. Note that occurrences of portunoid crabs have not been revised until now.

Taxon	Reference
Dendrobranchiata/Penaeidae	
Penaeus sorbinii Beschin & Garassino, 1999	Beschin & Garassino (1999)
Caridea/Palaemonidae	
?*Palaemon* sp.	Ristori (1892)
Palaemon fabricii Michelotti, 1861	Michelotti (1861)
Gebiidea/Thalassinidae	
Thalassina sp.	Herein
Brachyura/Portunoidea	
Achelous obtusus A. Milne-Edwards, 1860	Milne-Edwards (1860)
Portunus arcuatus (A. Milne-Edwards, 1860)	Milne-Edwards (1860)
Portunus incertus (A. Milne-Edwards, 1860)	Milne-Edwards (1860)
Portunus cf. *P. convexus* (Ristori, 1889)	Ristori (1892)
Portunus aff. *P. radobojanus* (Bittner, 1884)	Ristori (1892)
Portunus aff. *P. stenaspis* (Bittner, 1884)	Ristori (1892)
Charybdis antiqua (A. Milne-Edwards, 1860)	Milne-Edwards (1860)
?*Scylla* sp.	Ristori (1892)
?*Psammocarcinus* sp.	Ristori (1892)

tubercles or denticles; pleonal sternites 2-5 with tubercles on transverse ridge between pleopods; telson longer than wide, unarmed. Pereiopods 1 and 2 subchelate, pereiopod 1 propodus with mesial and lateral tuberculate or spinuous carinae; pereiopod 2 ovate; pereiopods 3-5 simple (emended from Ngoc-Ho & de Saint Laurent 2009: 122).

COMMENTS

It has long been believed that the genus includes two species, *T. anomala* (Herbst, 1804) and *T. squamifera* De Man, 1915, with several other nominal taxa considered as junior synonyms of *T. anomala* (Holthuis 1991: 229). More recent revisions based on morphological characters (Ngoc-Ho & de Saint Laurent 2009; Sakai & Türkay 2012) have shown an unexpected diversity of the genus. The genus currently consists of thirteen valid species (Table 1).

Thalassina is characterised by subchelate pereiopods 1 and 2, with the pereiopod 1 propodus having tuberculate or spinous longitudinal carinae (ridges *sensu* Moh & Chong 2009) extending across it (Ngoc-Ho & de Saint Laurent 2009; Sakai & Türkay 2012). These carinae have a fairly good potential to be preserved in the fossil record and can be compared directly with the extant material as demonstrated recently by Ando *et al.* (2016).

The diagnosis of *Thalassina* presented above highlights the characters with good fossilization potential. In this respect, pereiopods 1 are of particular interest. They are often unequal in males, sometimes in females, and have similar morphology in both except for a stouter propodus and a larger proximal lower tooth on the dactylus of the major cheliped (Ngoc-Ho & de Saint Laurent 2009). The dactylus with longitudinal rows of tubercles is rather stout and is always at least twice longer than the fixed finger (Ngoc-Ho & de Saint Laurent 2009); such a condition is present only rarely in decapod crustaceans and together with the outline of distal elements of pereiopod 1 can be considered as a reliable character for attributing fossil material to the genus.

Importantly for palaeontological practice, the characters on pereiopods 1 (elements with the highest fossilization potential) have been recognised as taxonomically important on the species level (Ngoc-Ho & de Saint Laurent 2009; Sakai & Türkay 2012; Lin *et al.* 2016). For distinguishing species, a combination of characters on pereiopods 1 (e.g., the development of carinae) is always needed (Ngoc-Ho & de Saint Laurent 2009: table 2; Ando *et al.* 2016: table 2; Ando *et al.* 2019: table 1). The outline of the propodus appears not to be sufficient for attribution on the species level due to intraspecific variation (Ngoc-Ho & de Saint Laurent 2009). In general, two basic morphotypes can be recognized, the robust one and the slender one; in the slender morphotype the palm is three or more times longer than high (e.g., in *Thalassina pratas* Lin, Komai & Chan, 2016; *T. tsuyamensis* Ando & Kishimoto *in* Ando, Kishimoto & Kawano, 2016; or *T. emerii* Bell, 1844). It must be noted, however, that these forms represent two extremes of a continuous range of variability rather than a stable pattern. Consequently, the propodus outline cannot be considered as taxonomically

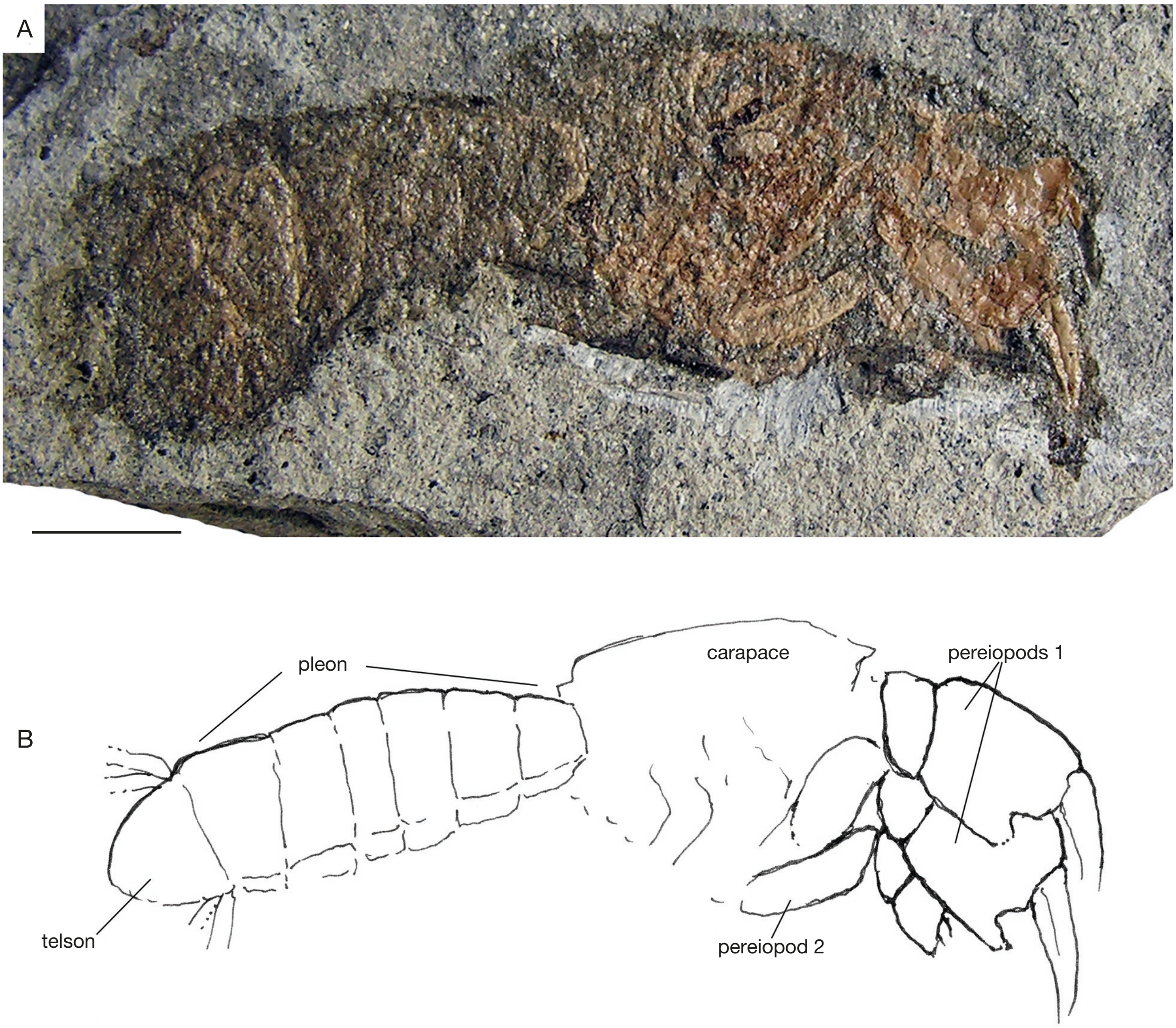

FIG. 3. — *Thalassina* sp. from the lower Oligocene of Salcedo, Italy, MCZ.4516-I.G.367044: **A**, flattened, almost complete specimen in natural light; **B**, interpretative drawing. Scale bar: 5 mm.

important if evaluated on a handful of specimens because both, sexual dimorphism and intraspecific variation, may have an impact on the morphology of pereiopods 1 (Ngoc-Ho & de Saint Laurent 2009; Sakai & Türkay 2012).

Thalassina sp.
(Figs 3; 4)

Material. — Flattened near-complete individual (MCZ.4516-I.G.367044; Fig. 3); articulated pereiopod 1 consisting of merus, carpus, propodus, and dactylus (MSNM i13569; donated by Claudio Beschin in 1994; Fig. 4).

Measurements. — MSNM i13569: propodus max length: 15.0 mm; propodus max height: 12.7 mm; carpus length: 7.8 mm; carpus height: 6.3 mm; merus length 13.5 mm; merus height 6.1 mm. MCZ.4516-I.G.367044: total length (preserved parts): 34.2 mm.

Locality and age. — Lower Oligocene (Rupelian) of Salcedo (Vicenza), NE Italy.

Description

Pereiopod 1 robust, similar, slightly unequal. Major cheliped merus ovoid in outline, approximately 2.5 times longer than high. Carpus short, triangular in outline. Manus slightly longer than high, distinctly higher than carpus; upper and lower margins parallel to each other; distal margin with a blunt tooth at articulation with dactylus; lateral surface poorly preserved, with faint carina running across the palm longitudinally in the upper half and two rows of indistinct tubercles on the lower half. Fixed finger short, triangular in outline, occlusal margin with small denticles. Dactylus much longer than fixed finger, elongated, slightly bent, ridged along lateral sides; occlusal margin with large blunt tooth positioned proximally. Minor chela slightly smaller than major chela. P2 merus elongated, carpus short and cup-shaped, propodus incomplete. Cuticular surfaces of all remains poorly preserved.

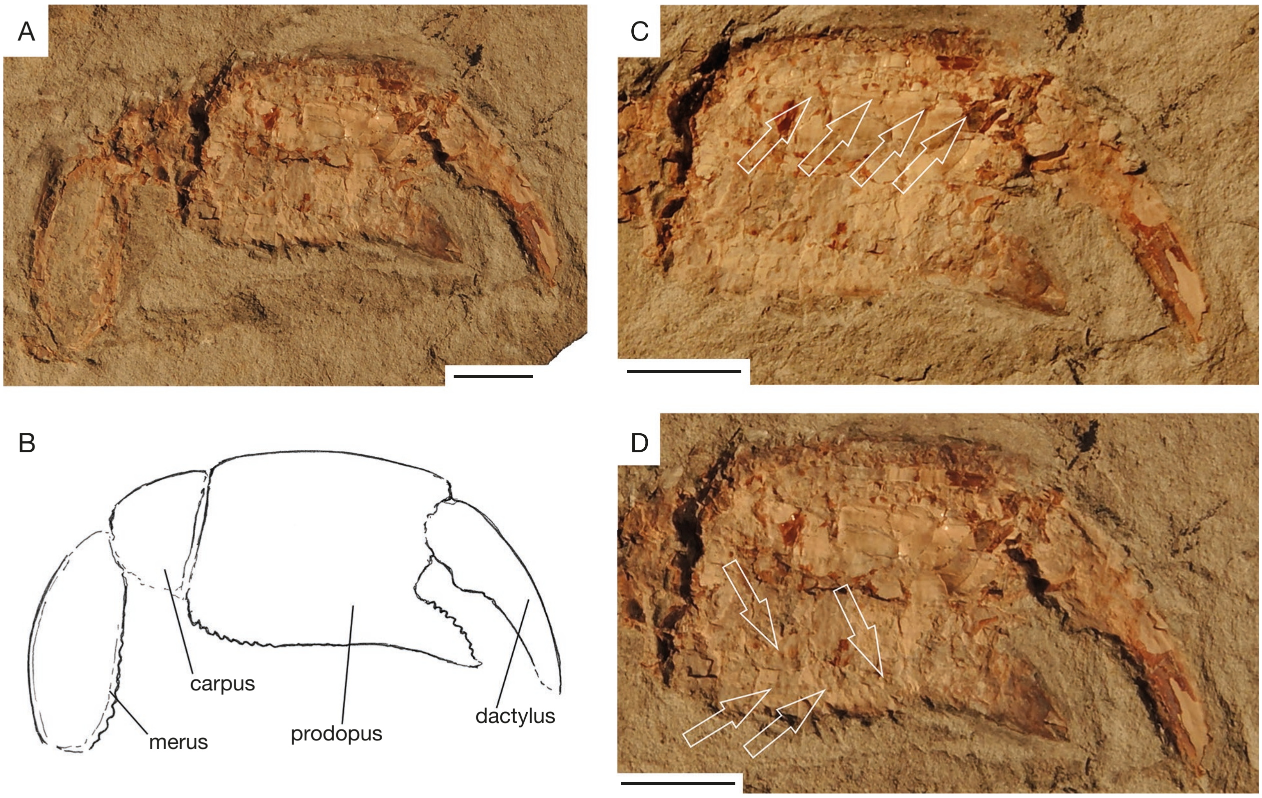

Fig. 4. — *Thalassina* sp. from the lower Oligocene of Salcedo, Italy, MSNM i13569: **A**, articulated cheliped consisting of merus, carpus, propodus and dactylus; **B**, interpretive drawing of the cheliped; **C**, detailed view on the chela showing a faint carina (indicated with arrows); **D**, detailed view on the chela showing two rows of tubercles (indicated with arrows). Scale bars: 5 mm.

Comments

The studied specimens are assigned to *Thalassina* based on the general morphology of pereiopod 1: a massive merus with an ovoid outline, a relatively small triangular carpus that is not as high as the propodus, and a subchela consisting of a propodus with a short fixed finger and a much longer and robust dactylus with a knobby tooth on its occlusal margin positioned proximally. Identification to the species is, unfortunately, not possible due to the insufficient preservation. Although one of the specimens (MCZ.4516-I.G.367044) shows virtually an entire animal, the individual is flattened and details are obliterated (Fig. 3). General outline of chelipeds is visible, but their armament and ornamentation are not discernible. Another specimen (MSNM i13569) represents a major pereiopod 1 consisting of the last four elements, i.e., merus, carpus, propodus and dactylus (Fig. 4). The cuticular surfaces are only partly preserved and carinae, important taxonomic characters (see above), are not recognizable. There are two faint rows of tubercles close to the lower margin and a faint carina extending across the palm in its upper half. The position of these characters suggests that the cheliped is slightly deformed, so the upper margin and characters positioned close to it are not discernible. Both studied specimens most probably represent the same species, although it cannot be stated for sure; the characters important for species identification (see above) are not preserved in a sufficient detail.

DISCUSSION

Palaeoenvironment

Thalassina is known from a range of habitats under marine influence, including estuaries, mangrove forests, and fully marine subtidal seagrass beds (Ng & Kang 1988; Ngoc-Ho & de Saint Laurent 2009; Lin *et al.* 2016). Known fossil occurrences are consistent with these environmental preferences. Some of the Miocene *Thalassina* from Japan have been reported from sediments deposited in a shallow marine coastal environment with preserved pollen from mangrove plants (Ando *et al.* 2016). The Italian material presented herein is reported from a marine setting with a strong fluvial influence (Mietto 1997). This means that the environmental preferences of *Thalassina* have not changed substantially since the Oligocene times. It is also possible that the range of environmental preference may have increased in the course of time; the sparse fossil record from the pre-Miocene strata is not sufficient for drawing further conclusions.

Palaeobiogeography

Thalassina anomala was recognised as the sister-taxon of a group uniting the other three sympatric species inhabiting Malaysia and Australia studied by Moh *et al.* (2013). The fossil record of *T. anomala* extends back to the Miocene as reported by various authors (Van Straelen 1928; Karasawa 1990; Karasawa & Nishikawa 1991; Karasawa & Inoue 1992;

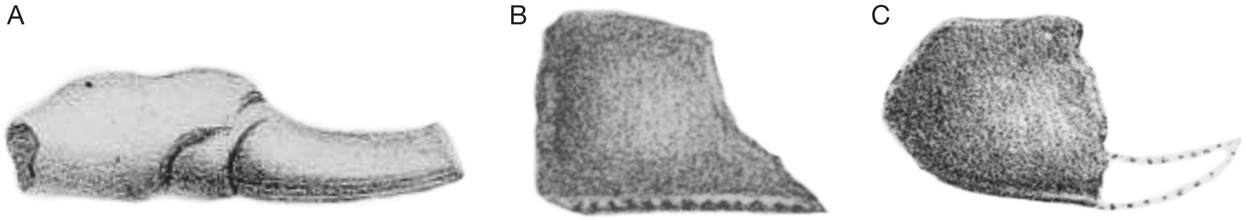

Fig. 5. — Disputed fossil occurrences of *Thalassina* Latreille, 1806 (see the text for more details): **A**, *Thalassina grandidactylus* Robineau-Desvoidy, 1849 from the 'Neocomian' of France (refigured from Robineau-Desvoidy 1849: pl. 5, fig. 16); **B**, *Thalassina* sp. from the Pliocene of Italy (refigured from Ristori 1891: pl. 1, fig. 16); **C**, *Thalassina* sp. from the Pliocene of Italy (refigured from Ristori 1891: pl. 1, fig. 17).

Collins *et al.* 2003), although Ngoc-Ho & de Saint Laurent 2009) noted that some of these occurrences may refer to another species. Indeed, *Thalassina anomala* reported from the Miocene of Japan (Karasawa & Inoue 1992; Karasawa 1993, 1997) was recently recognised to be a separate species, formally described as *Thalassina yamato* Ando & Kishimoto *in* Ando, Kishimoto & Kawano*,* 2016. The oldest fossil record of *Thalassina* in the Indo-Pacific region is *Thalassina tsuyamensis* Ando & Kishimoto *in* Ando, Kishimoto & Kawano*,* 2016 from the lower to middle Miocene of Japan. The oldest occurrence of *Thalassina* worldwide is *Thalassina* sp. from the lower Oligocene of Salcedo reported herein. This record suggests a Tethyan ancestry of the genus and further supports the idea that roots of the current Indo-Pacific decapod fauna lay in the circum-Mediterranean area (Schweitzer 2001; Hyžný 2011; Hyžný & Müller 2012; Hyžný *et al.* 2013) and not *vice versa* (cf. Müller 1984, 1979). Alternatively, *Thalassina* might have wider distribution in Oligocene times or before. In any case, a further occurrence of *Thalassina grandidactylus* Robineau-Desvoidy, 1849 from the 'Neocomian' of France was already disputed by A. Milne-Edwards (1860) who suggested an attribution to an astacidean lobster ("un Astacien"). This opinion was recently followed by Ando *et al.* (2016). Indeed, the specimen (refigured herein as Fig. 5A) consisting of a fragmentary propodus (without the fixed finger) with articulated dactylus (with only proximal part preserved) cannot be classified within any genus or species with certainty. *Thalassina grandidactylus* is considered a *nomen nudum* herein.

It is unknown for how long the genus persisted in the area of its presumed origin. Ristori (1891: 14, pl. 1, figs 16-17) reported and figured two isolated propodi of presumed *Thalassina* sp. from the Pliocene of Spicchio (Empoli, Italy); unfortunately, the material is lost (De Angeli & Garassino 2006). Based on the figures, this occurrence is disputed herein. As far as can be judged from figures alone, one specimen (Ristori 1891: pl. 1, fig. 16; refigured herein as Fig. 5B) is similar to *Calliaxina* Ngoc-Ho, 2003, a ghost shrimp known from the circum-Mediterranean area at least since the Miocene until today (Ngoc-Ho 2003; Hyžný 2012; Garassino *et al.* 2012). The second specimen may belong equally to some callianassoid ghost shrimp or a paguroid hermit crab (Ristori 1891: pl. 1, fig. 17; refigured herein as Fig. 5C). However, reliable identification of both specimens cannot be done based on figures alone.

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