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An Upper Cretaceous arthropod assemblage from Villaggio del Pescatore (Campanian, Italy) and its implications for peri-Tethyan palaeobiogeography and palaeoecology

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Abstract: The Villaggio del Pescatore (VdP) fossil Lagerstätte represents the most significant Upper Cretaceous (lower–middle Campanian) palaeontological locality in Italy and the Mediterranean region. We present the first systematic revision of the VdP fossil assemblage with a focus on its previously undescribed arthropod fauna, providing new insights into its taxonomic diversity and palaeoenvironmental and palaeobiogeographical significance. Among the identified arthropods, a caridean assigned to the family Palaemonidae Rafinesque, a single cirolanid isopod, and an undetermined insect mark their first recorded occurrences in the latest Cretaceous of the peri-Mediterranean region. Their stratigraphic and biogeographic distribution suggest the presence of new taxa, although the available material precludes formal taxonomic designation. The co-occurrence of palaemonids and cirolanids, both associated with estuarine and lagoonal habitats, supports the interpretation of VdP as a marginal environment characterized by brackish to freshwater conditions. The abundance of small decapod exuviae suggests a nursery habitat, potentially reflecting reproductive dynamics akin to extant euryhaline or amphidromous palaemonids, and the taphonomy of larger arthropod carcasses suggests that microbial mat growth played a role in fossil preservation. Closely related arthropod taxa from the Early–Late Cretaceous with a widespread peri-Tethyan distribution (i.e. shared between the biotas of Las Hoyas in Spain and Jehol in China) suggest close biogeographical connections between Eurasian landmasses, consilient with the known vertebrate communities described from VdP. This study provides a foundational understanding of this community and offers novel perspectives on the ecosystem dynamics and faunal composition of this exceptional locality.

Key words: Arthropoda, Campanian, Decapoda, Insecta, Italy, Cretaceous.

THE Villaggio del Pescatore (VdP) fossil Lagerstätte stands as the most informative Upper Cretaceous (lower Campanian) palaeontological locality in Italy and the Mediterranean region. The site was discovered in 1984, and became the target of scientific excavations in the 1990s due to its fossil productivity, unusual taphonomy (Tarlao *et al.* 1993; Brazzatti & Calligaris 1995; Palci 2003), and the discovery of a complete and articulated hadrosauroid dinosaur skeleton (holotype of *Tethyshadros insularis* Dalla Vecchia 2009). More than 400 other fossils were collected during the quarrying process for the extraction of this specimen, hinting at the existence of a diverse and exquisitely preserved palaeobiota. At the time of writing, reported tetrapods include articulated specimens and isolated elements of multiple individuals assigned to *T. insularis* (Dalla Vecchia 2009, 2020; Chiarenza *et al.* 2021), isolated pterosaur and theropod elements (Dalla Vecchia 2018; Chiarenza *et al.* 2021), articulated individuals of the hylaeochampsid *Acynodon adriaticus* Delfino *et al.* 2008a, and other crocodylomorph material (Delfino *et al.* 2008b; Muscioni *et al.* 2023, 2024). Most of the items collected from the VdP are large

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and unprepared limestone slabs mainly preserving small teleosts, arthropods, plant material, faecal pellets and vertebrate coprolites.

Data presented here follow an ongoing systematic revision of all VdP material housed at the Museo Civico di Storia Naturale in Trieste (MCSNT), aiming to provide the first detailed quantification and revised taxonomic composition of the VdP fossil assemblage. This study focuses on the previously undescribed arthropod fauna of the VdP, including taxonomic identification, with palaeoenvironmental and palaeobiogeographical implications for a rich assemblage (Table S1).

MATERIAL & METHOD

Specimens

Specimens were collected during multiple quarrying campaigns between 1998 and 2000 at the VdP and are currently housed at the MCSNT. Specimens are preserved in centimetre-thick limestone slabs which commonly include multiple fossils. A total of 87 limestone slabs and more than 380 specimens have been examined and are discussed herein (Fig. 1A
). According to Dalla Vecchia (1999) and F. Bacchia (pers. comm. 2024), slabs were secured following field inspection of the carbonatic rubble produced by heavy machinery and fragmentation of matrix blocks. None of the described material has been manually prepared except for specimen MCSNT 57057, which underwent reconstructive restoration for display purposes. A complete list of discussed specimens is provided in Table S1.

Stratigraphic occurrence

The stratigraphic and palaeoenvironmental context of the VdP site has been largely discussed in the literature (Tarlao *et al.* 1993; Attura 1999; Palci 2003; Arbulla *et al.* 2006; Dalla Vecchia 2009; Cucchi & Piano 2013; Chiarenza *et al.* 2021; Consorti *et al.* 2021; Muscioni *et al.* 2023, 2024). The site includes carbonate rhythmites that have been informally divided into two alternating facies based on the colour (light-brown and a dark-black; Chiarenza *et al.* 2021, suppl. info.). Geochemistry analysis suggests that they represent different environmental conditions in the Cretaceous depositional basin: dark and lighter laminites would have recorded marine-influenced intervals and terrigenous/freshwater phases, respectively (Baldassarri 2024). Large decapod remains are found in similar abundances in both light- and dark-coloured laminae, whereas the small exuviae and other arthropods are mainly found in the lighter ones (Fig. 1B–C). This uneven distribution probably represents a taphonomic and observational bias, given that even the remains of relatively large decapods are barely visible on the dark-black slabs, and smaller specimens such as the faint exuviae impressions would have easily gone unnoticed during field collection without high-quality magnification, better lighting or contrast enhancement.

Original field reports (Dalla Vecchia 1999) combined with accurate analyses of photographic and archive data, constrain the stratigraphic occurrence of fossil slabs to an interval of *c.* 60 cm (Fig. 2) at 7 m above the basal contact of the laminites (i.e. lithological contact between Aurisina and Liburnian facies; Consorti *et al.* 2021). Overall, the VdP succession and its fossil-bearing beds have been dated to the early to middle Campanian (Chiarenza *et al.* 2021).

Imaging

Photographs of the specimens were taken with a SONY DSC-RX100M3 camera and a pocket USB microcamera. UV fluorescence was tested on a large sample of specimens without relevant results. Detailed micro-orthophotos with greater magnification were taken at the Entomology Laboratory of the MCSNT with a Leica MZ16 stereomicroscope, Leica Flexacam C1 camera, Leica objective lens Planaop ×1.0 and Leica LAS X software. To enhance the contrast and better assess anatomical features, some specimens were soaked in either tap water or an ethanol 50% solution prior to taking pictures.

SYSTEMATIC PALAEONTOLOGY

Phylum ARTHROPODA Gravenhorst 1843
Class MALACOSTRACA Latreille 1802
Order DECAPODA Latreille 1802
CARIDEA Dana 1852

PALAEMONIDAE Rafinesque 1815
Figures 1B, 3–8

Referred specimens. MCSNT 57038, 57039, 57040, 57041, 57043, 57047, 57057, 57072, 57081, 57094, 57095, 57102, 57126, 57131, 57132, 57160, 57189, 57226, 57227, 57228, 47/96, 92/122, 105/112, X/82.

Description. All specimens are incomplete individuals and are herein interpreted as mostly exuviae: carbonaceous traces visible in the thoracic areas of a few individuals suggest the occurrence of complete carcasses at the site. The most abundant elements are pereiopods, either isolated or associated to flagella, scaphocerites and rostra. None of the specimens preserves a full

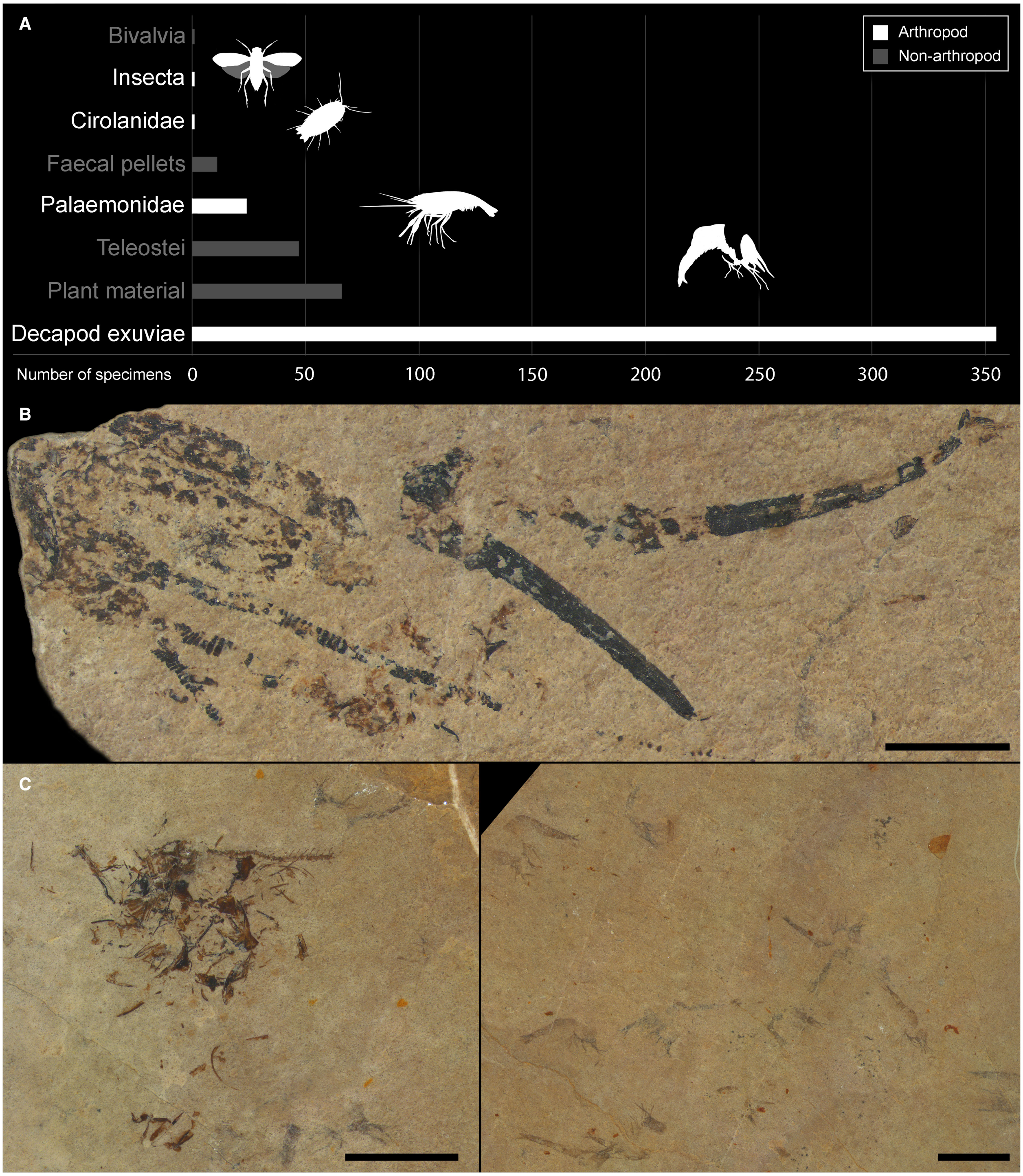

FIG. 1. The arthropod assemblage from Villaggio del Pescatore. A, relative abundance of individual fossil specimens identified in every arthropod-bearing slab; non-arthropod fossils are shown in a darker tone; notice the disproportionate amount of small decapod exuviae. B, specimen MCSNT 15/112 as an example of the average larger decapod (Palaemonidae indet.), preserving cephalic appendages and a partial chela in relatively poor condition. C, two details of slab MCSNT 10/51 showing a disarticulated teleost surrounded by small exuviae and orange plant material (left), and multiple small decapod exuviae with interspersed orange plant material (right). Scale bars represent 10 mm.

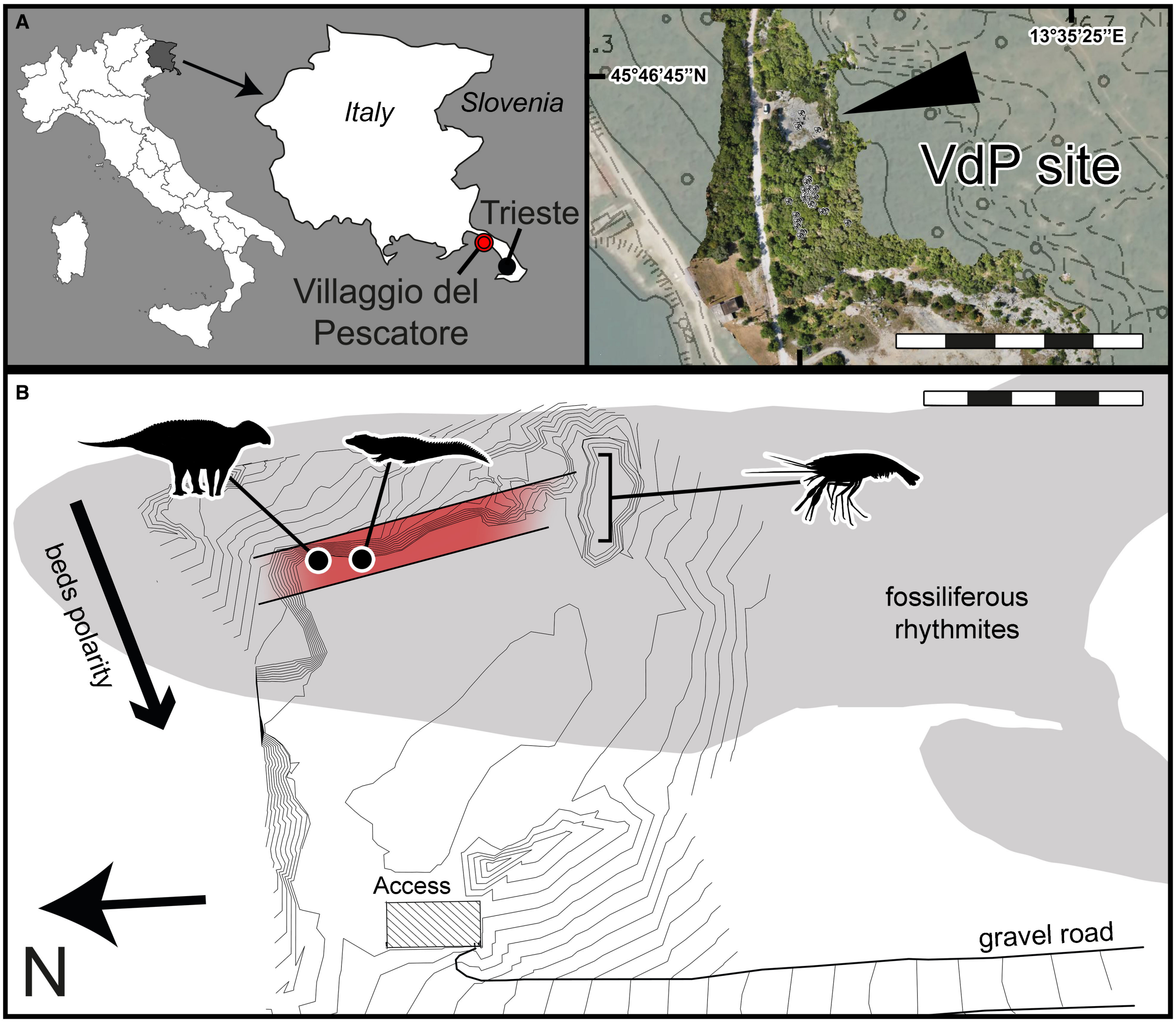

FIG. 2. Geographic setting and simplified locality map. A, geographic location of Villaggio del Pescatore (VdP; left) and detailed location of the fossil site (right). B, quarry map; most of the arthropod specimens with known stratigraphy came from a *c.* 1 m interval of productive slumped rhythmites (here highlighted in red); from these same layers, the holotypes of *Tethyshadros insularis* (MCSNT 57021; left silhouette) and *Acynodon adriaticus* (MCSNT 57248; right silhouette) were also recovered. Scale bars represent: 100 m (A); 15 m (B).

cephalothorax and/or pleon. As diagnostic anatomical traits are consistent throughout the sample, specimens assigned to Palaemonidae indet. are considered as different ontogenetic stages. The most complete specimen is 57057 (Fig. 3) but, given that it has undergone reconstructive restoration, it is not suitable for precise anatomical observations. A second, nicely preserved specimen is 57227 (Fig. 4A), which shows the caudal portion of the pleon and articulated uropodal exopod and endopod in addition to the cephalic region, providing a solid comparative reference to investigate the whole-body proportions of this taxon. Assuming that no significant disarticulation occurred along the missing pleonal region, 57227 measures *c.* 50 mm from the rostrum to the uropods or telson. Applying the same proportions to other less complete individuals such as 57040 and 57041 (Fig. 5), 57228 and X/82 (Fig. 6), the smaller individuals would have been *c.* 40–45 mm in length, whereas the larger ones would have measured *c.* 100–120 mm in length (Fig. 7A).

Carapace: The most complete carapace is preserved in specimen 57057 (Fig. 3). It is laterodorsally exposed and has an overall short and sub-rectangular shape, slightly narrowing anteriorly. Only the upper portion of the posterior margin is preserved, and a thickening/marginal carina is visible. The dorsal margin on the fossil appears slightly convex, possibly due to taphonomic compression and partial rotation. The unusual concavity just above the ocular incision is probably a taphonomic or preparation artefact. Specimen 57057 also bears the only articulated rostrum, which is long, straight and anteroventrally developed. It seems to have traces of multiple dorsal spines but

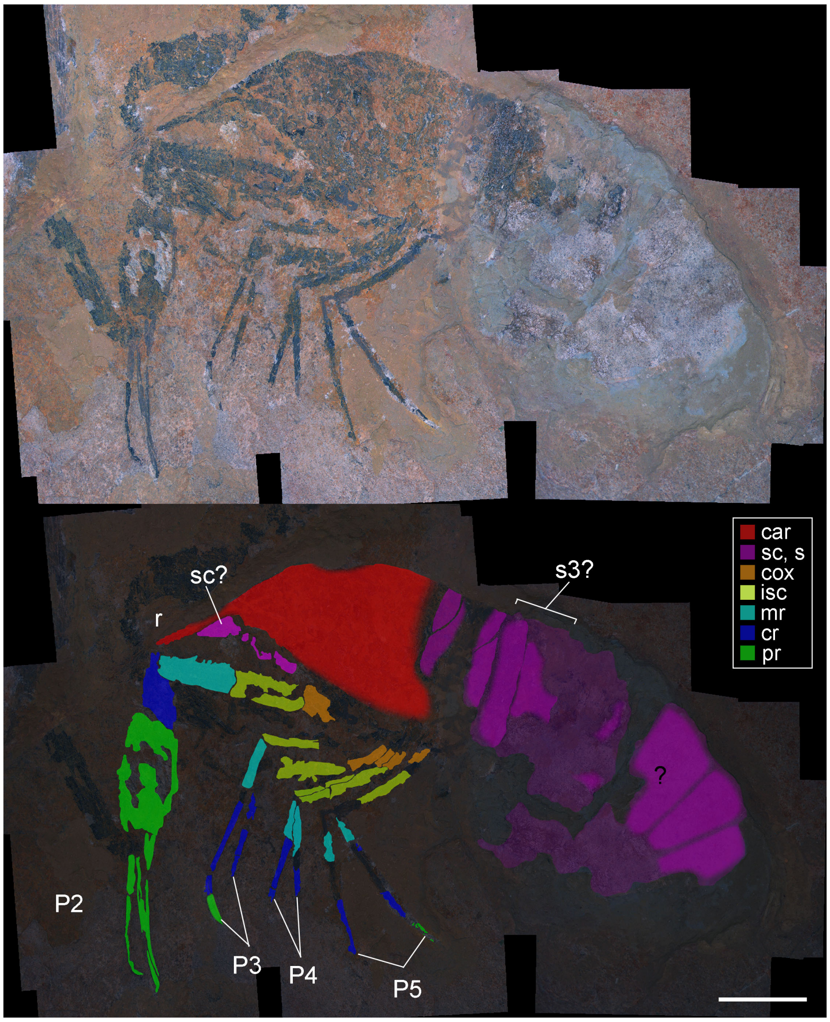

FIG. 3. Micro-orthophoto of Palaemonidae indet. MCSNT 57057 (above) and superimposed interpretative illustration (below). *Abbreviations*: car, carapace; cox, basis and/or coxa; cr, carpus; isc, ischium; mr, merus; P, pereiopod; pr, propodus; r, rostrum; s, pleonal somite; sc, scaphocerite. Scale bar represents 10 mm.

the poor preservation along its margins and possible preparation artefacts make any morphological interpretation problematic. Better preserved rostra are present in specimens 57189, 57227, 57040, 57041, 57228 and X/82 (Figs 4–6). Such individuals have a slightly S-shaped curve, at least four or five forward-directed dorsal spines and at least three ventral spines, with a pointed distal elongate tip and a medial carina along its entire longitudinal length (Fig. 7B). Several specimens preserve the distal portion of the rostrum with a distinct anteroventral orientation. A shallow and narrow ocular incision morphology might be inferred in specimens 57057 and 57227.

Pleon: Pleonal somites are preserved only in specimens 57057, 57227 and 57228. Somites 1–3 are partly recognizable only in specimen 57057 and preserved as a segmented, greyish mass (Fig. 3).

Pleura are too incomplete to enable reliable inference of the original margins, although the anterior overlap of s3 by s2 is recognizable. Specimen 57227 has six, rounded elements on the posteroventral half of the pleonal region, representing both sides of the fragmentary pleura (Fig. 4A). Their orientation hints at a moderate posteroventral curvature of the pleon. A single, elongate and subtriangular telson is preserved in specimen 57227, in slight overlap with the left uropodal endopod. A fairly complete uropodal exopod and endopod are preserved in 57227 and, more fragmentarily, in 57228 (Figs 4A, 6A). Uropodal endopods are narrower and distally pointier than the uropodal exopods. They lack significant ornamentation, except for a possible medial thickening or carina seen on the right uropodal endopod of 57227. Uropodal exopods are mediolaterally wider, with a broad distal end and a rounded diaeresis. Laterally, the margin of the carina terminates distally with a posterolaterally oriented spine just anteriorly of the diaeresis (Figs 4A, 6A). A polygonal right protopodite is preserved in 57227.

Cephalic appendages: Antennules, antennae and scaphocerites are preserved in a consistent manner in the VdP carcinofauna

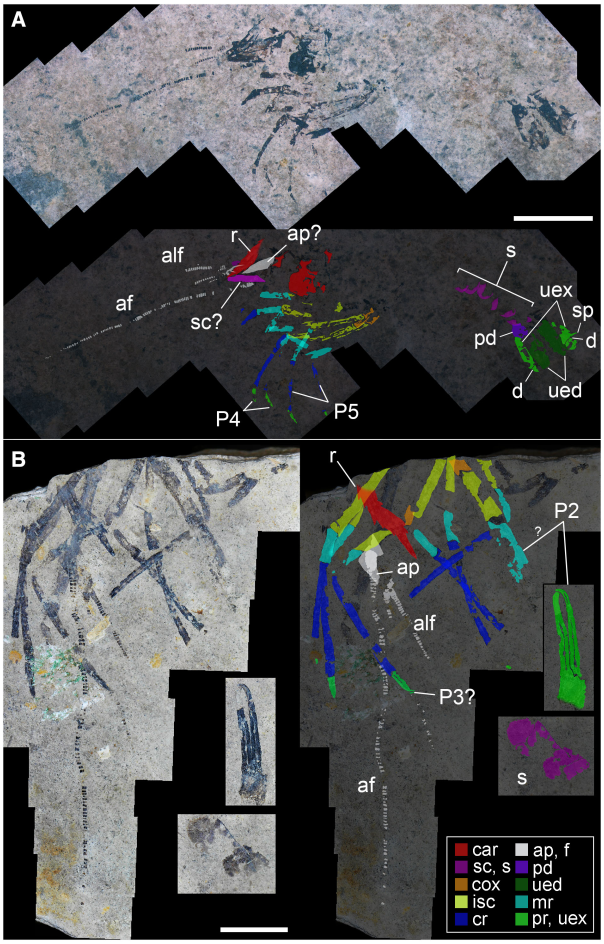

FIG. 4. Palaemonidae indet. MCSNT 57227 and MCSNT 57189. A, micro-orthophoto of specimen MCSNT 57227 (above) and superimposed interpretative illustration (below). B, micro-orthophoto of specimen MCSNT 57189 (left) and superimposed interpretative illustration (right). *Abbreviations*: af, antennal flagella; alf, antennule flagella; ap, antennular peduncle; car, carapace and/or cephalothorax fragments; cox, basis and/or coxa; cr, carpus; d, diaeresis; f, flagella; isc, ischium; mr, merus; P, pereiopod; pd, protopodite; pr, propodus; r, rostrum; s, pleonal somites; sc, scaphocerite; sp, spine; ued, uropodal endopod; uex, uropodal exopod. Scale bars represent: 10 mm (A); 5 mm (B).

(Figs 4–6). Where present, antennules are badly preserved, limited to a large proximal segment and/or with undistinguishable individual articula. At least two multiarticulate flagella are present on each antennule. The longer and thicker multiarticulate flagella are those of the antennae, which also preserve a large oval-shaped basal segment. The scaphocerite is preserved at least in specimens 57227, 57040, 57041, 57228, 105–112 and X/82. Where better preserved it extends past or at the same level as the antennules and shows a laminar morphology with a distolateral spine.

Thoracic appendages: Pereiopod 1 (P1) is partially preserved only in specimen 57228, where a reduced chelate propodus is visible anteriorly to P2 (Fig. 6A). The P1 chela has a similar morphology to P2 and is less than half the size of P2. P2 is the longest and bears a large, elongate chela, short and robust carpus, elongate and slightly thickened merus and ischium. Left and right P2 seem equal to subequal and proportionally consistent among the VdP specimens (although the chelae of 57040 seems somewhat proportionally smaller). The bulbous proximal portion of the propodus ends with a very elongate and almost straight dactylus and index. These have smooth margins devoid of distinct serrations and bearing a longitudinal groove, both terminating with hook-shaped distal parts (Fig. 8). The dactylus seems to be slightly longer than the index, and the general shape and proportion of the chela fit those of the extant *Macrobrachium* Bate 1868 and *Typhlocaris* Calman 1909, or fossil *Dusa* Münster 1839 and *Palaemon* Weber 1795; in particular, they are morphologically identical to those of *Palaemon antonellae* Garassino & Bravi 2003. In specimen 92/122 a particularly well-preserved surface on the proximal portion of the propodus is ornamented with small, rounded pits that are orange or yellowish in colour (Fig. 8B). The dorsal margin of the carpus and ischium in specimens 57057 and 57189 seems regularly dotted with linearly arranged tubercles: if not a taphonomic artefact, they may represent remnants of the original ornamentation (spine bases or tubercles). P3 and P4 are thin and distally elongate, with a well-developed, grooved and hook-shaped dactylus, which is larger in P3 at least in specimens 57057 and 57228 (Figs 3, 6A). A distal spine may be preserved at the carpo-propodial articulation.

Remarks. Although several specimens are extremely fragmentary, the character set shared by multiple individuals permits assignment to at least the family level. P1 and P2 chelae, coupled with their absence on the third, indicates an assignment to the Caridea Dana 1852 (Schweitzer *et al.* 2023). Among the European and western Laurasian record, Mesozoic carideans are known to date only from the Triassic of northern Italy (Pinna 1974; Garassino & Teruzzi 1993; Garassino *et al.* 1996), Jurassic of Germany (Schweigert & Garassino 2004; Winkler 2018, 2021; Winkler *et al.* 2024) and Cretaceous of Lebanon, Italy and Spain (Garassino & Ferrari 1992; Garassino 1994, 1997; Garassino & Teruzzi 1995; Bravi & Garassino 1998; Bravi *et al.* 1999; Garassino & Bravi 2003; Charbonnier *et al.* 2017). Based upon Schweitzer *et al.* (2023), the absence of a multiarticulate carpus of P2 and the larger size of P2 compared with P1 in the VdP specimens exclude the superfamilies Alpheoidea Rafinesque 1815, Crangonoidea Haworth 1825, Bresilioidea Calman 1896 and Pandaloidea Haworth 1825. The relatively developed rostrum with dorsal and ventral spines, chelate P1, P2 with dactylus and index meeting when flexed, and the absence of long distal setae, support the attribution to the superfamily Palaemonoidea Rafinesque 1815 (Schweitzer *et al.* 2023). Within the Palaemonoidea, the absence of cuspidate setae on the uropodal exopod diaeresis, the comparable development of P1 and P2, and the lack of a longitudinal carapace suture fit the Palaemonidae Rafinesque 1815, and rule out the holocenic Euryrhynchidae Holthuis 1950, the Desmocarididae Borradaile 1915, and the derived troglobiont Thyplocarididae Annandale & Kemp 1913. Other relevant family-level clades, Gnathophyllidae

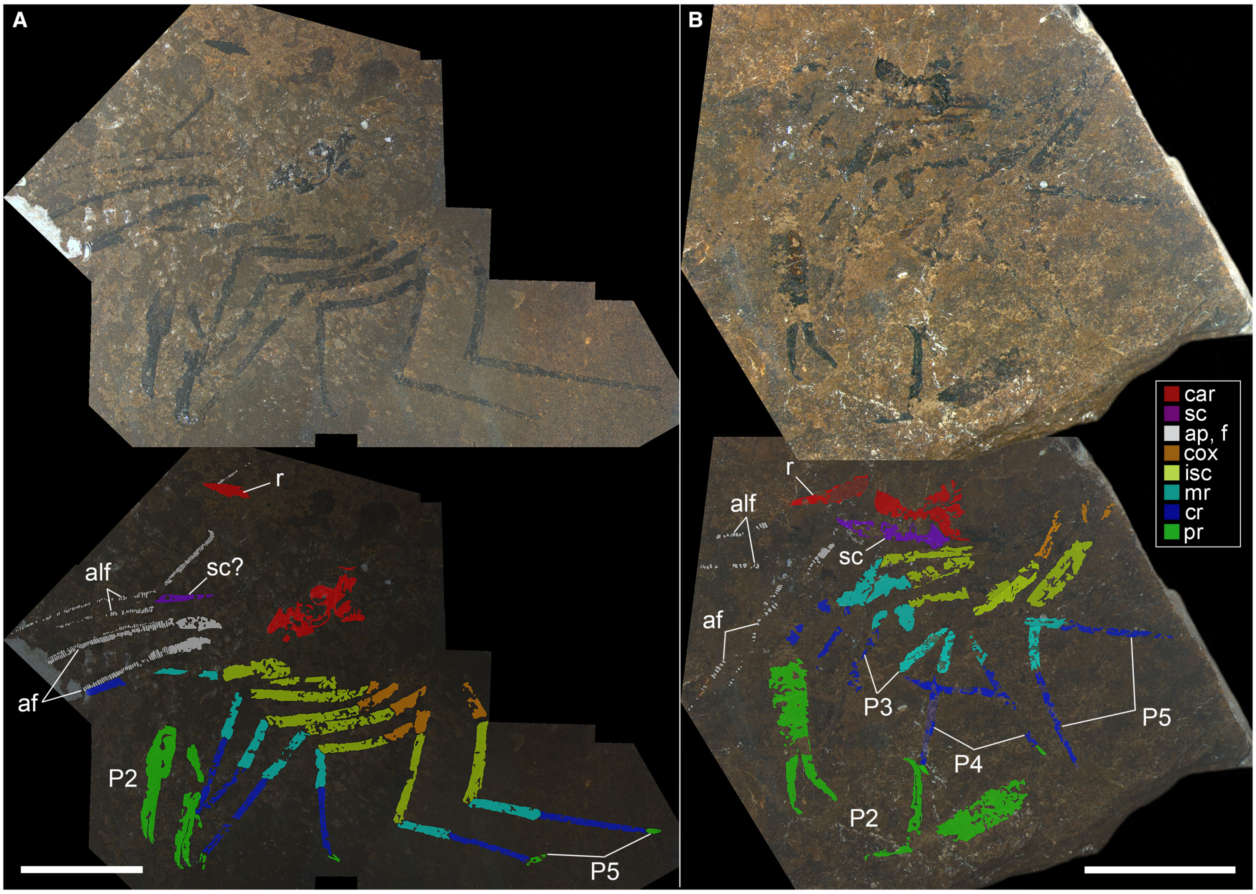

FIG. 5. Palaemonidae indet. MCSNT 57040 and MCSNT 57041. A, micro-orthophoto of specimen MCSNT 57040 (above) and superimposed interpretative illustration (below). B, micro-orthophoto of specimen MCSNT 57041 (above) and superimposed interpretative illustration (below). *Abbreviations*: af, antennal flagella; alf, antennule flagella; ap, antennular peduncle; car, carapace and/or cephalothorax fragments; cox, basis and/or coxa; cr, carpus; f, flagella; isc, ischium; mr, merus; P, pereiopod; pr, propodus; r, rostrum; sc, scaphocerite. Scale bars represent: 20 mm (A); 10 mm (B).

Dana 1852, Hymenoceridae Ortmann 1890, Kakaducarididae Bruce 1993 and Anchistioididae Borradaile 1915, are now subsumed within Palaemonidae (Mitsuhashi *et al.* 2007; Page *et al.* 2008; Kou *et al.* 2013; Chow *et al.* 2020) and require no separate consideration. Rostral proportions and chela form point further to the Palaemoninae, and among palaemonine genera the observable traits most closely match those of *Palaemon* Weber 1795. The only two other Cretaceous occurrences of this genus come from Italy: the Aptian–Albian *Palaemon antonellae* Garassino & Bravi 2003 and the Campanian–Maastrichtian *Palaemon vesolensis* Bravi *et al.* 1999. The palaemonid taxon from the VdP represents an almost coeval occurrence with *P. vesolensis* but is morphologically remarkably similar to the Aptian *P. antonellae*, from which it is virtually undistinguishable.

We prefer, however, to leave the specimens in open nomenclature due to their fragmentary condition, lacking sufficient morphological characters for an assignment to genus and species. In conclusion, we refer the specimens to the Palaemonidae with *Palaemon* sp. as a likely candidate.

EXUVIAE

?CARIDEA Dana 1852

Figures 1C, 9

Referred specimens. MCSNT 57046, 57069, 57077, 57079, 57084, 57089, 57092, 57122, 57134, 57135, 57155, 57158, 57160, 57167, 57186, 57189, 57198, 57217, 57222, 57223, 57224, 57225, 57231, 10/25, 10/43, 10/51, 15/17, 15/21, 15/30, 15/32, 15/34, 15/39, 15/86, 23, 23/12, 23/16, 23/24, 23/31, 23/56, 23/57, 23/58, 23/77, 36/48, 45/129, 47/101, 72/88, 92/114, 105/111, X/10, X/52, X/53, X/55, X/67, X/68, X/69, X/77, X/74, X/75, X/81, X/82, X/125, X/133, X/134, X/135, X/136.

Description. Counting more than 350 individuals, the exuviae are the most abundant fossils in the currently available VdP specimen collection. Except for a few specimens, they are mostly preserved in poor condition (Fig. 9A–K). Their size range is from less than 5 mm to 20–30 mm and all show clear

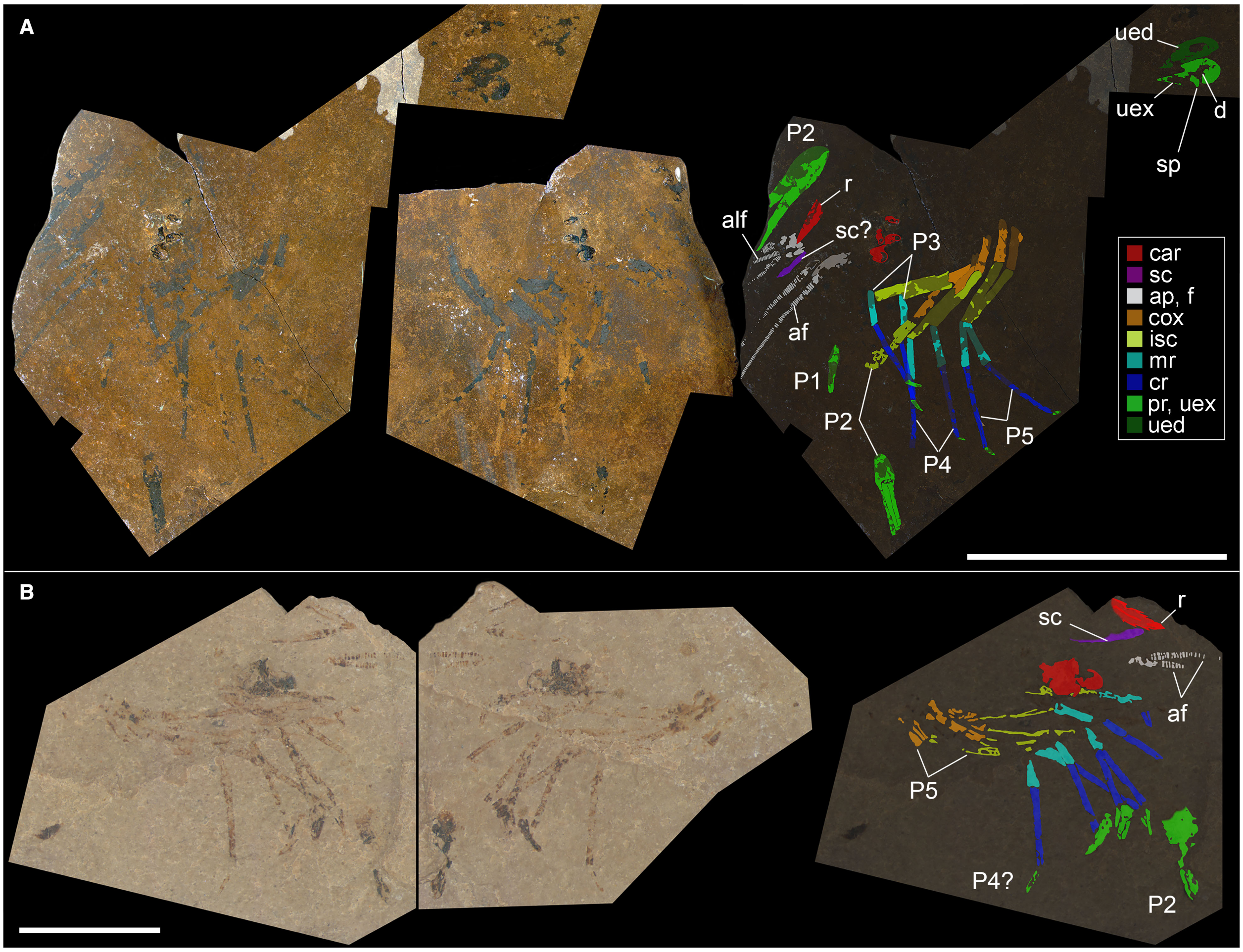

FIG. 6. Palaemonidae indet. MCSNT 57228 and MCSNT X/82. A, micro-orthophoto of specimen MCSNT 57228 (left) and superimposed interpretative illustration (right). B, micro-orthophoto of specimen MCSNT X/82 (left) and superimposed interpretative illustration (right). *Abbreviations*: af, antennal flagella; alf, antennule flagella; ap, antennular peduncle; car, carapace and/or cephalothorax fragments; cox, basis and/or coxa; cr, carpus; d, diaeresis; f, flagella; isc, ischium; mr, merus; P, pereiopod; pr, propodus; r, rostrum; sc, scaphocerite; sp, spine; ued, uropodal endopod; uex, uropodal exopod. Scale bars represent: 50 mm (A); 10 mm (B).

indications of their exuvial nature: they are preserved as faint, light grey traces, always with a defined dorsal separation and sharp disarticulation angle between cephalothorax and pleon. In fresh exuviae from extant taxa the same disarticulation is commonly observed (Fig. 9L), often accompanied by complex overlapping between parts and volumetric collapse of the pleon, due to the enhanced mobility of the empty exoskeleton. In general, they have an elongate cephalothorax with a rectangular outline and a slightly convex dorsal profile, deep subcircular ocular incision and very elongate S-curved rostrum. In a few specimens the rostrum seems to bear an undeterminable number of both dorsal and ventral spines, but it is unclear whether they represent genuine features or taphonomic alterations. The elongate pereiopods are not well preserved for assessment of the presence and number of chelae, which, if present, must have been small. A sharp, almost 90° pleonal bending is visible between s3 and s4. In the best-preserved specimens, s2 seems to bear a subrounded pleuron, partly overlapping s1–s3 pleura. The caudal region in every specimen clearly bears an elongate triangular telson and flaring uropodal exopod and endopod.

Remarks. Given that fine morphological details are poorly preserved, a family-level identification is not possible. All exuviae share the same overall morphology, suggesting that they belong to a single taxon. The few characters that can be identified are compatible with the infraorder Caridea, although preservation is too limited to confirm this assignment; we therefore conservatively refer the material only to Decapoda Latreille 1802. The exuviae could represent either a second, small-bodied decapod species or early ontogenetic stages of the same taxon as the larger Palaemonidae remains. Post-larval macrurans often resemble adults in gross form lacking secondary characters, and are difficult to diagnose even in extant species (Felder *et al.* 1985), hence the hypothesis that the VdP exuviae are juvenile individuals of the same taxon is plausible but cannot be confirmed.

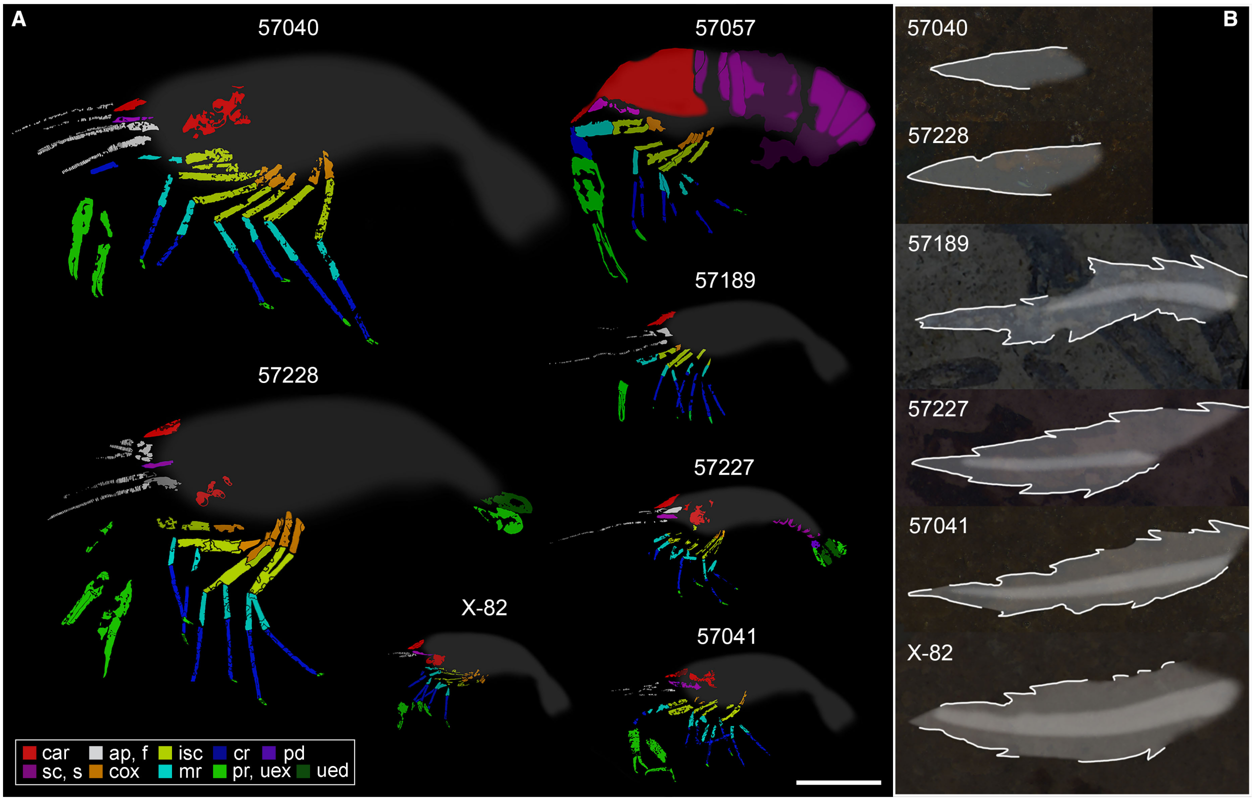

FIG. 7. Scale comparison of the most complete Palaemonidae indet. specimens and detail of the rostra. A, interpretative diagrams of the seven better preserved *Palaemon* sp. specimens at the same scale. B, the six better preserved rostra with interpretative drawings highlighting their margins and medial carinae. *Abbreviations*: ap, antennular peduncle; car, carapace and/or cephalothorax fragments; cox, basis and/or coxa; cr, carpus; f, flagella; isc, ischium; mr, merus; pd, protopodite; pr, propodus; s, pleonal somites; sc, scaphocerite; ued, uropodal endopod; uex, uropodal exopod. Scale bars represent 20 mm (drawings in part B not to scale).

Order ISOPODA Latreille 1816

CIROLANIDAE Dana 1852

Figure 10

Referred specimen. MCSNT 57229.

Description. The single dorsally exposed specimen (*c.* 10 mm long, 4.3 mm wide; Fig. 10) is not an exuvia but a whole articulated carcass, given that isopods characteristically undergo biphasic moulting which usually leaves exuviae split into two separate parts (i.e. Hyžný *et al.* 2013). Cephalothorax, seven pereonites, five unfused pleonites, pleotelson, and three uropodal rami are preserved. A couple of vaguely subcircular structures on the opposite lateral extremities of the cephalothorax might represent badly preserved eyes. Dark elongated structures anterior to the cephalothorax are likely to represent fragments of antennal peduncles or, possibly, extended limbs. No diagnostic cephalic appendages are discernible. The body is about twice as long as wide, broadest at the fourth or fifth pereonite; the pereon is *c.* 3.2-fold the pleon's length. At least the sixth and seventh pereonites bear coxae with the shape of a prominent caudally directed spine, similarly to species in the genera *Cirolana* Leach 1818 or *Sphaeromides* Dollfus 1897. Pleonites 2–3 bear caudolateral acute processes, and pleonite 5 is laterally enclosed by pleonite 4. The pleotelson is roughly triangular with convex margins, marginal thickening, and a median carina (as in some *Rocinela* Leach 1818), its length about half its anterior width. Uropods are ventrolaterally articulated; the subtriangular exopod is broader and longer than the endopod, and both extend beyond the pleotelson.

Remarks. Fossil isopods are often difficult to classify beyond family rank because the characters that diagnose living species, especially details of mouthparts and thoracic appendages, are seldom preserved (Hyžný *et al.* 2013; Bruce & Rodcharoen 2023). Specimen 57229 shows the hallmarks of the superfamily Cymothooidea Leach 1814: five unfused pleonites, laterally inserted biramous uropods, and an overall cymothoid body outline. Its small size and flattened, subtriangular uropods rule out Cymothoidae Leach 1814, and the uropod shape is incompatible with Aegidae White 1850. The remaining alternative, Cirolanidae Dana 1852, fits all observable characters: ovoid body, possible lateral eyes, prominent coxae on pereonites, five unfused pleonites, and dorsoventrally flattened uropods that form a caudal fan with the pleotelson (Hyžný *et al.* 2013). Within Cirolanidae the key of Hyžný *et al.* (2013) points tentatively to *Cirolana*

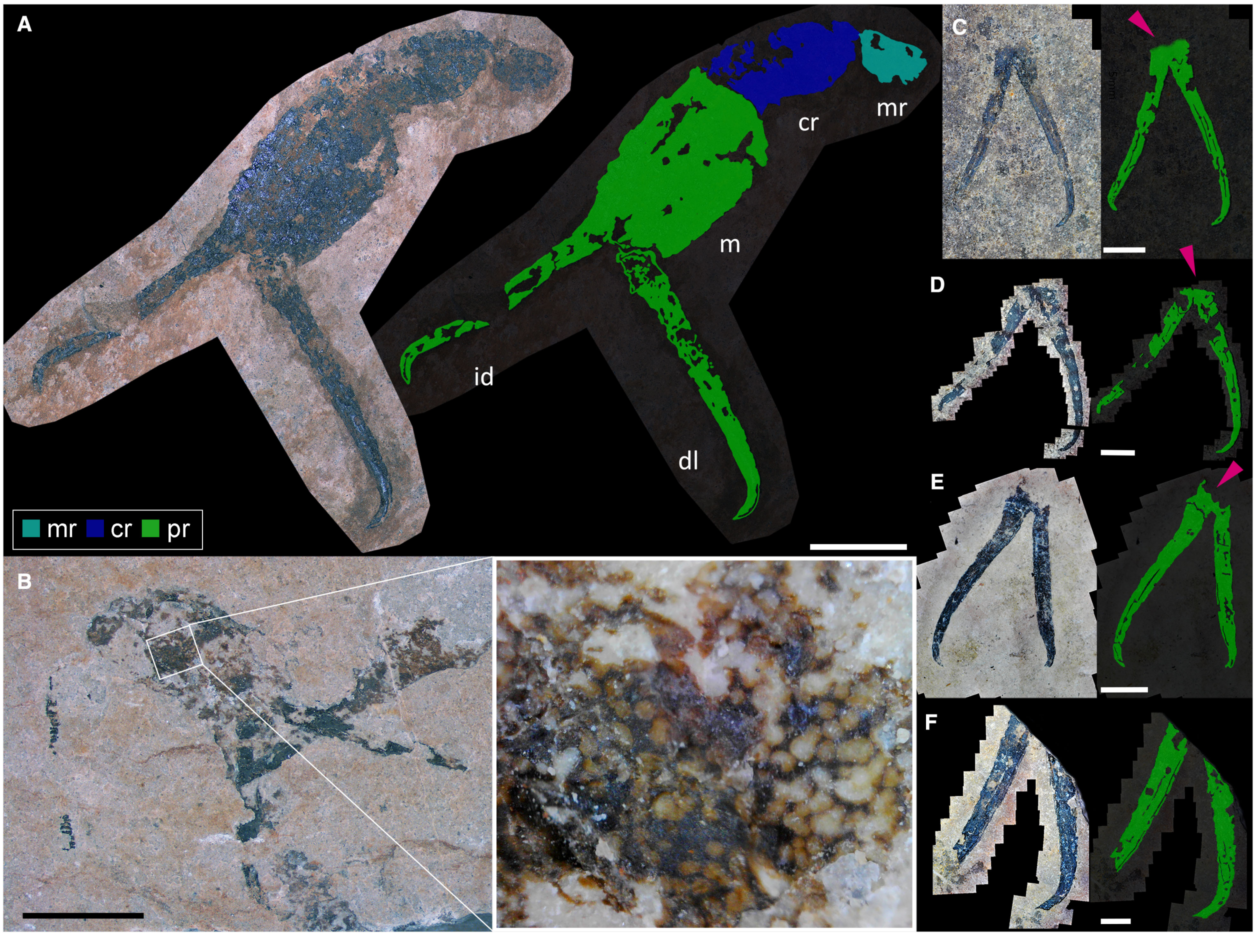

FIG. 8. Palaemonidae indet., isolated chelae. A, micro-orthophoto of specimen MCSNT 57133 (left) and superimposed interpretative illustration (right). B, micro-orthophoto of specimen MCSNT 92/122 (left) and detail of preserved ornamentation (right). C–F, micro-orthophoto of isolated chelae (left) and superimposed interpretative illustrations (right) of: C, MCSNT 57095; D, MCSNT 57132; E, MCSNT 57039; F, MCSNT 57031. Purple triangles indicate unusually fragmented chelae just proximal to the dactylus articulation. *Abbreviations*: cr, carpus; dl, dactylus; id, index; m, manus; mr, merus; pr, propodus. Scale bars represent: 5 mm (A, B); 2 mm (C–F).

Leach 1818, and the apparent enclosure of pleonite 5 would exclude genera such as *Metacirolana* Kussakin 1979, *Excirolana* Richardson 1912 or *Eurydice* Leach 1816. However, the absence of diagnostically important thoracic limbs precludes a secure genus-level assignment. We therefore refer specimen 57229 to Cirolanidae indet.

Class INSECTA Linnaeus 1758
cf. HETEROPTERA Latreille 1810
Figures 11, 12

Referred specimen. MCSNT 72/88.

Description. The specimen consists of two pairs of incomplete membranous wings, the distal portion of an abdomen and possibly very damaged and fragmentary filiform structures that may represent thread-shaped antennae or badly preserved limbs (Fig. 11A). These elements appear articulated in an unusual configuration around an empty space left by the missing body.

The four membranous wings are 4–5 mm long, preserved in slight overlap, with the putative forewings overlapping the hindwings. Both pairs are missing their proximal portions. The forewings are better preserved, with relatively well-defined margins. All four wings have a similar shape, with an elongated outline and well-defined apex. The original pigmentation of the forewings is preserved as a darker symmetric pattern. Individual veins are not clearly recognizable; however, the morphology of at least some wing cells on both forewings and hindwings can be inferred by the configuration of the pigmentation pattern. Namely, the wingtip on the forewings bears a roughly subtriangular shape separated from the rest of the wing by a dark transverse band; this has a very defined and arched distal margin, which may suggest the presence of a thicker, more sclerified subtriangular structure corresponding to the more intense

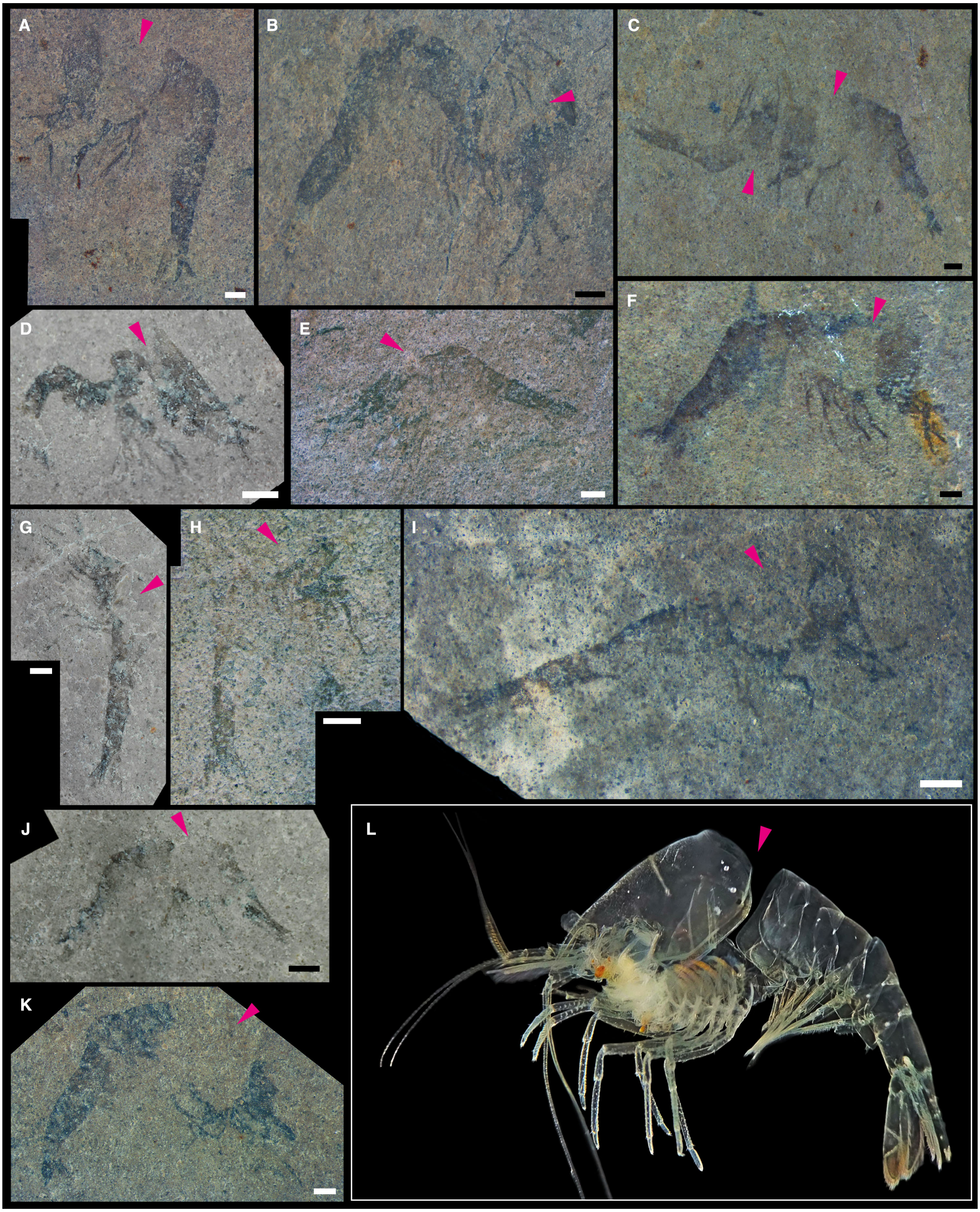

FIG. 9. Microscopic photos of selected exuviae (? Caridea) from slabs MCSNT 10/51 (A–C), 23/68 (D), 15/39 (E), 15/21 (F), 23/58 (G, J), 15/34 (H), 57 075 (I), X/82 (K). L, fresh exuvia of *Neocaridina davidi* Bouvier 1904, of similar size to the fossil ones for comparative purposes. Purple triangles indicate the dorsal separation from cephalothorax and pleon left by the moulting process. Scale bars represent 1 mm.

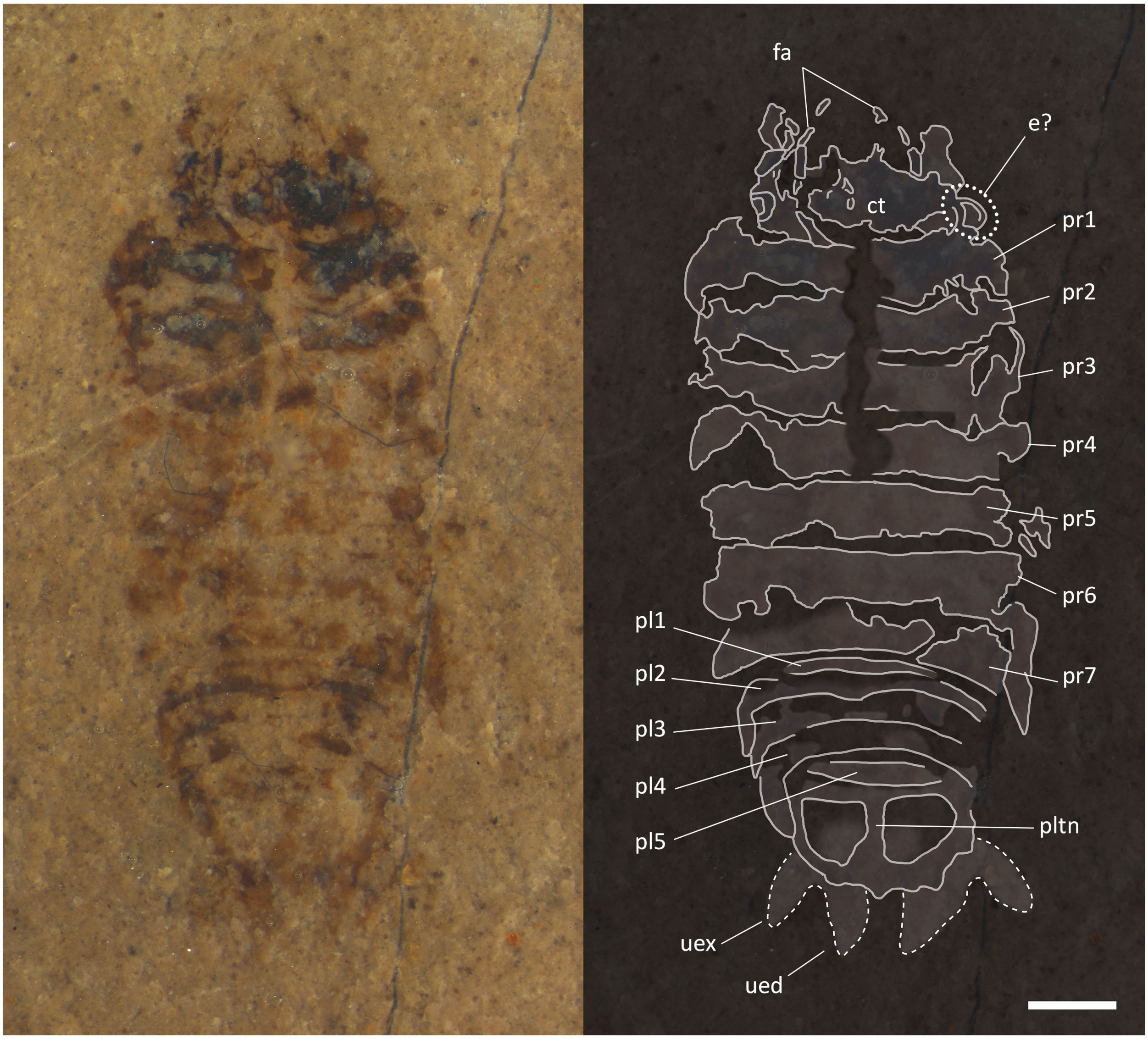

FIG. 10. Cirolanidae indet. MCSNT 57229. Micro-orthophoto of the specimen (left) and superimposed interpretative illustration (right). Dotted lines indicate elements of uncertain outline. *Abbreviations*: ct, cephalothorax; e, eye; fa, fragmentary appendages; pl, pleonite; pltn, pleotelson; pr, pereonite; ued, uropodal endopod; uex, uropodal exopod. Scale bar represents 1 mm.

pigmentation. Another dark band follows the forewing's posterior margin, proximally increasing in width and pigmentation intensity from the angle formed with the transverse one. The darker longitudinal bands thus envelop almost the entire wing margin, except for the triangular apical section, with less concentrated pigmentation. The left hindwing has a fading outline with fibrous texture along its posterior margin, suggesting the possible presence of setae. More complex patterns of additional pigmentation seem present at the middle portions of the wings, but taphonomic damage renders any further consideration impossible.

The distal portion of the abdomen measures *c.* 3 mm and only the putatively terminal urites are visible, with two short but well-defined and mediolaterally spread cerci. These are narrow and subtriangular in shape, with concave lateral margins and posteriorly directed acute tips. Medially to the cerci, a slightly prominent structure might represent the genitalia (gonapophysis). The posterior lateral margins of the last urite seems unusually prominent; this condition may be a taphonomic artefact, possibly due to dorsoventral compression. The putatively last urite is *c.* 1 mm in anteroposterior length, and its proximal end may be represented by a slight mediolateral constriction. The remaining proximal abdominal portion represents either one larger or two equally developed urites. The lateral margins of the preserved abdomen seem to show alternating bands of darker pigmentation, which may suggest a vertically striped pattern.

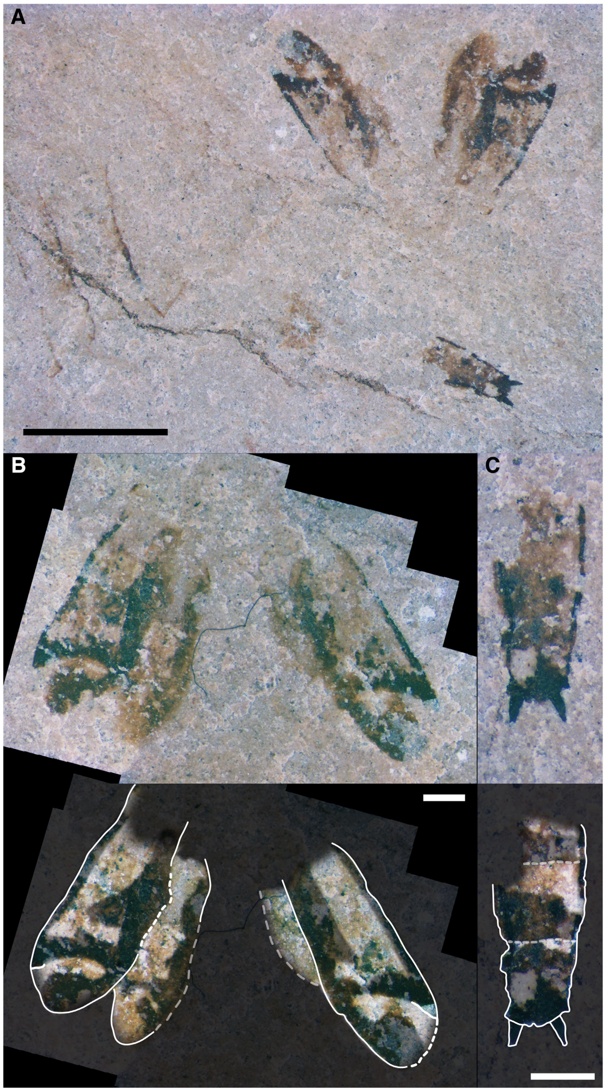

FIG. 11. Cf. Heteroptera MCSNT 72/88. A, micro-orthophoto of the specimen. B, detail of the wings (above) and superimposed interpretative drawing (below); dotted lines indicate uncertain margins possibly bearing setae. C, detail of the abdomen (above) and superimposed interpretative drawing (below); dotted lines indicate possible urite margins. Scale bars represent: 5 mm (A); 1 mm (B, C).

Remarks. The wing-tip pigmentation mirrors that of some living Mecoptera Packard 1886, such as *Neopanorpa pulchra* Carpenter 1945 (Hua *et al.* 2018), however, similar patterns evolved independently in neuropterans, trichopterans and orthopterans, therefore colour alone is not diagnostic. In addition, the wing transverse bands are straight and continuous, whereas in the aforementioned orders they follow the veins in broken segments. Although the elongate outline also recalls mecopteran wings, that interpretation would require most of the proximal blade to have been lost. A better match is the heteropteran hemelytron: the darker longitudinal band along the posterior margin reads as the clavus, and the distal transverse band marks the cuneus (Fig. 12A–D). The preserved abdominal tip (with laterally divergent, sub-triangular cerci) could recall either a bittacid scorpionfly or a heteropteran that retains cerci externally, such as Gerridae Leach 1815 (Fig. 12E–G). Because venation and other decisive characters are missing, specimen MCSNT 72/88 can be assigned only tentatively, most likely to Heteroptera indet., with Mecoptera as a less probable alternative.

DISCUSSION

Taphonomy

The arthropods from VdP occur in two distinct taphonomic states: (1) complete individuals, represented by exuviae and the articulated isopod carcass; and (2) clusters of largely articulated appendages that lack the volumetrically greater thorax and abdomen, as seen in the large palaemonids and the putative heteropteran insect. In normal decay sequences these delicate, lightly sclerotized appendages should disarticulate first, therefore their selective preservation requires explanation.

One possibility is preferential removal of nutrient-rich tissue by predators or scavengers. Several isolated chelae (e.g. MCSNT 57039, 57095 and 57132) still retain an articulated dactylus and index, whereas the manus is missing (Fig. 8C–E). Because the bulbous proximal propodus houses the powerful muscles that drive the dactylus, it would have been highly attractive to predators. Numerous extant vertebrates are carcinophagous, and the contemporaneous hylaeochampsid *Acynodon adriaticus* from the same beds shows durophagous adaptations and thus may have included crustaceans in its diet (Muscioni *et al.* 2024). However, predation alone cannot explain the consistent absence of cephalothorax and pleon in many specimens: most appendage clusters occur in life position, indicating that intact carcasses settled on the substrate before these body regions were lost.

A more plausible mechanism combines early microbial burial with subsequent biological or physical removal of exposed parts. In specimen MCSNT 72/88, two pairs of wings, the distal abdomen and possible antennal traces form a 'halo' around a void that once held the thorax and proximal limbs. A similar pattern appears in the palaemonids, where intact cephalic appendages, pereiopods and uropods are preserved, but the cephalothorax and pleon are missing. Such preservation suggests rapid entombment of thinner structures by cohesive sediment, most likely microbial mats, progressing upward from the substrate while leaving the bulkier portions exposed long enough for destruction by scavengers or decay.

This model matches earlier work on microbial influence in Konservat-Lagerstätten. Peñalver *et al.* (2002) first invoked microbial mats to explain unusual arthropod

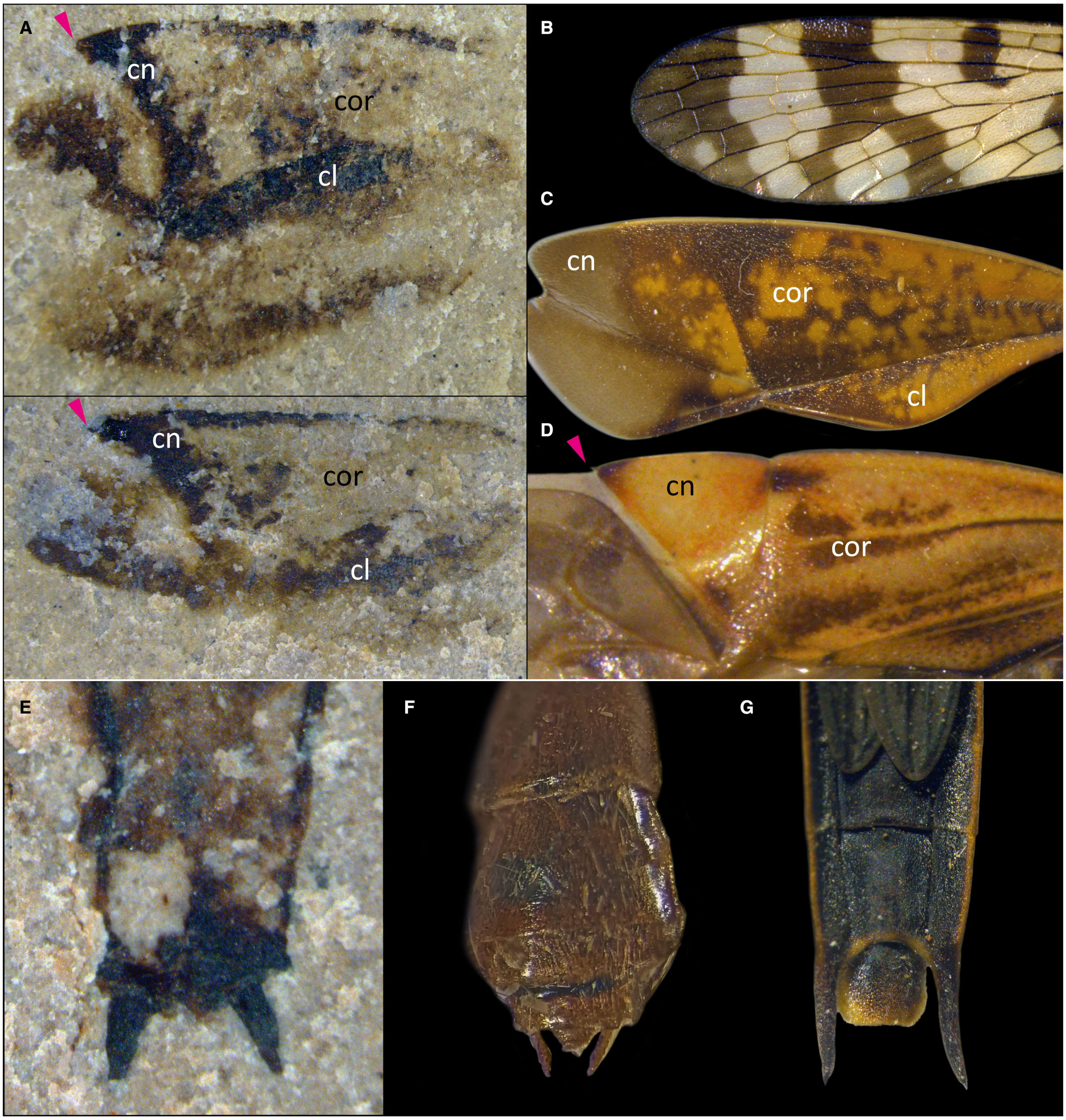

FIG. 12. Comparison of cf. Heteroptera MCSNT 72/88 with detail of living taxa. A, wings of MCSNT 72/88 (right wing mirrored for easier comparison). B, left forewing of an extant Panorpidae Linnaeus 1758; note the similarity in the pigmentation pattern, but also the evident differences with the fossil specimen. C, hemelytron of an extant Notonectidae Latreille 1802. D, detail of the hemelytron of the mirid *Closterotomus norwegicus* Gmelin 1790. E, detail of MCSNT 72/88 distal abdomen and cerci. F, detail of the distal abdomen and cerci of the extant bittacid *Bittacus hageni* Brauer 1860. G, detail of the distal abdomen and cerci of an extant Gerridae Leach 1815. Purple triangles indicate the more sclerified distal tip of the cuneus on the hemelytra. *Abbreviations*: cl, clavus; cn, cuneus; cor, corium. Images not to scale.

disarticulation, and later studies documented their key role in preserving arthropods, soft tissues and fragile trace fossils in laminated limestones worldwide (Martínez-Delclòs *et al.* 2004; Buscalioni & Fregenal-Martínez 2010; Carvalho *et al.* 2017; Iniesto *et al.* 2021; Dias & Carvalho 2022; Marugán-Lobón *et al.* 2023; Buscalioni *et al.* 2025). Interwoven cyanobacterial filaments and mucilage-rich biofilms stabilize sediment, trap fine particles and create rhythmites with high fossil-preservation potential, but they rarely leave direct microbially derived structures (Noffke *et al.* 2001; Peñalver *et al.* 2002; Fernández & Pazos 2013). Laboratory experiments confirm that burial in microbial mats slows decay, maintains articulation for years and promotes early mineralization (Iniesto *et al.* 2021).

Independent lines of evidence indicate a comparable setting at VdP. Stromatolitic clasts were reported by Tarlao *et al.* (1993); while Baldassarri (2024) proposed a microbial origin for the rhythmically laminated limestones, substantiating the claim with scanning electron microscopy–energy-dispersive x-ray images of possible fossil bacteria. Iniesto *et al.* (2021) showed that complete mat coverage of insect larvae can occur after *c.* 30 days. Under VdP conditions, small, nutrient-poor exuviae would have been rapidly engulfed by growing mats (and largely ignored by scavengers) whereas the thick cephalothoraxes of large palaemonids remained exposed for longer intervals, explaining their frequent loss (Fig. 13).

Palaeobiogeographic & palaeoenvironmental significance

Palaemonids. According to molecular, palaeontological and biogeographical evidence, the Palaemonidae probably originated in the Tethyan biogeographic realm during the Mesozoic (Anger 2013). They then passed through intense diversification from the Cretaceous to shortly after the Cretaceous–Palaeogene (K–Pg) extinction, resulting in their modern cosmopolitan distribution and high species richness (Anger 2013; Frolovà *et al.* 2022).

The Tethyan fossil record of *Palaemon* is so far restricted to Italy, and all known Cretaceous localities share similar environmental settings. The older Aptian species, *P. antonellae*, comes from the finely laminated Profeti Plattenkalk (Caserta, southern Apennines), a marginal sector of the Latium–Abruzzi Carbonate Platform. Sedimentological evidence indicates a low-energy, shallow, protected depression on a tidal flat, with episodic anoxia. Thin storm layers, stromatolitic growth, disarticulated fish remains, coprolites, and a diverse macroflora of gymnosperms and angiosperms occur in the same succession (Garassino & Bravi 2003; Bartiromo *et al.* 2009).

The Campanian–Maastrichtian *P. vesolensis* is recorded from the Monte Vesole Plattenkalk, close to the *P. antonellae* type locality. Dark bituminous laminae that yield decapods also preserve gastropods, plant macrofossils, charophyte gyrogonites, occasional stromatolitic lamination and storm deposits. These point to a stagnant, low-energy, lagoonal setting subject to recurring anoxia, tidal influence and intermittent freshwater input (Bravi *et al.* 1999).

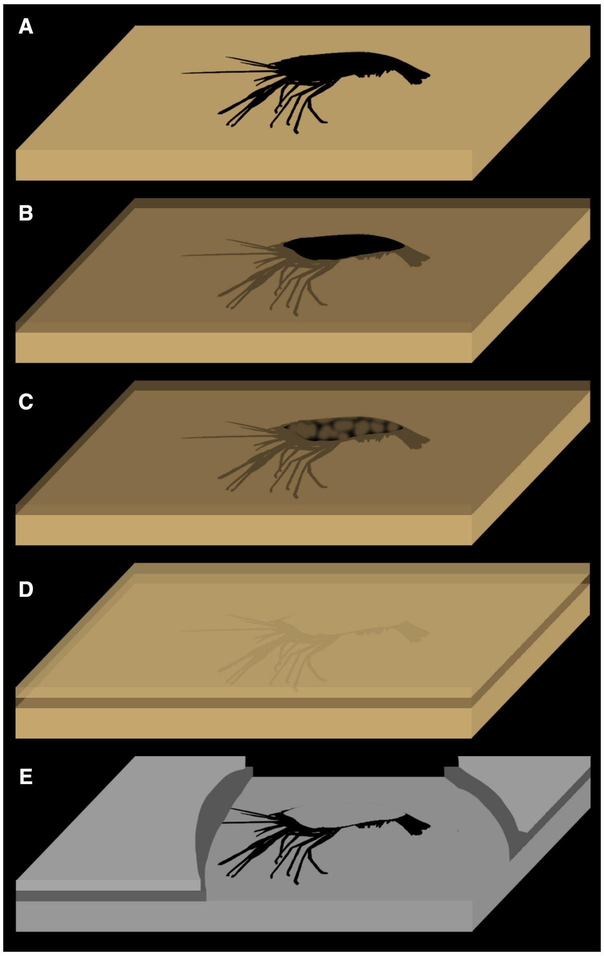

FIG. 13. The possible biostratinomic sequence based on Peñalver *et al.* (2002). A, arthropod carcass sinks onto the substrate. B, microbial community rapidly grows over thin structures and/or stabilizes new sediment, leaving thicker portions of the carcass exposed; to avoid the burial of the cephalothorax and pleon, a bottom-up sediment stabilization is required. C, the exposed pleon and cephalothorax are consumed by scavengers and/or destroyed by decomposition before complete burial. D, new deposition of sediment and/or further vertical growth of the microbial community covers the now incomplete carcass. E, the recovered specimen is preserved as an articulated set of appendages devoid of pleon and cephalothorax.

Stratigraphic, micropalaeontological and geochemical work on the fossil-bearing laminae at VdP shows alternating freshwater and marine influxes in a protected, low-energy microhabitat on the Adriatic–Dinaric Carbonate Platform margin (Chiarenza *et al.* 2021; Baldassarri 2024). A stromatolitic–microbialitic origin has been proposed for part of the lamination (Tarlao *et al.* 1993; Baldassarri 2024), and the occurrence of charophyte gyrogonites plus macrofloral remains indicates phases of predominantly freshwater or brackish conditions (Palci 2003; Chiarenza *et al.* 2021; Baldassarri 2024).

Middle-sized *Palaemon*-like shrimp are a recurrent element of Cretaceous Tethyan carbonate-platform faunas, although it is unclear whether they represent endemic platform taxa or a habitat-specific clade dispersed throughout the archipelago. This uncertainty is compounded by the 'waste-basket' use of *Palaemon* for many Cretaceous fossils. Given the repeated freshwater incursions, the preserved palaemonids were probably tolerant of brackish to freshwater estuarine conditions.

Although Palaemonidae are likely to have originated in marine settings, extant representatives occupy every stage of the marine-to-freshwater gradient, and a few species are truly euryhaline (Bauer 2023). Among extant taxa, there have been at least 10 independent freshwater invasions in *Palaemon* and nine in *Macrobrachium* (Murphy & Austin 2005; Wowor *et al.* 2009; Ashelby *et al.* 2012), demonstrating a high evolutionary potential for freshwater tolerance.

Late Cretaceous eustatic oscillations created widespread marginal, humid habitats across the European Archipelago. Combined with other biotic and abiotic drivers, this produced a peak in speciation of, for example, freshwater gastropods (Neubauer *et al.* 2021; Neubauer & Harzhauser 2022). Repeated sealevel changes could likewise have enabled coastal palaemonids to penetrate lowland brackish and freshwater networks, triggering habitat invasion: an explanation also invoked for the continental spread of tropical *Macrobrachium* (Anger 2013). If the abundant small exuviae and the rarer larger specimens are different growth stages of a single palaemonid species, their frequency suggests that the VdP water body was critical to key life stages. Individual exuviae occur in every visible stratigraphic layer, and many beds contain tens of similarly sized exuviae clustered with plant debris and teleost bones (Figs 1C, 14). The uniform size and random orientations imply dense resident populations of juveniles sharing one habitat.

Extant euryhaline and estuarine palaemonids use nutrient-rich, protected coastal settings (swamps, estuaries, mangroves, lagoons) as nurseries. Hyperosmoconforming adults (and sometimes post-larval juveniles) tolerate freshwater and disperse inland, while larvae and early juveniles still require brackish water (Moreira 1994; Duke *et al.* 2007; Meynecke *et al.* 2007; Vargas & Wehrtmann 2009). In undisturbed tropical lagoons, post-larval *Macrobrachium* can even form near-monospecific assemblages (Albertoni *et al.* 1999). Density and habitat-use studies show a strong positive relationship between palaemonid abundance and submerged vegetation or detritus that offers shelter and foraging surfaces (Fransozo *et al.* 2009; Moritzen *et al.* 2018).

The VdP exuviae therefore offer valuable palaeoenvironmental clues. Isotopic data (Palci 2003; Arbulla *et al.* 2006), unpublished geochemistry (Baldassarri 2024), charophytes, vascular-plant remains, and a possible hydrobiid gastropod all point to persistent freshwater input. Taken together with the exuvial evidence, the VdP setting must have provided a protected, highly productive habitat with fluctuating salinity, ideal for juvenile palaemonids. The clustered exuviae may also reflect gregarious behaviour. Unlike in true mass-mortality layers, whole carcasses are rare, suggesting that many individuals moulted in close spatial and temporal proximity under calm conditions. Concentration by bottom currents seems unlikely, given that other light components (plant fragments, faecal pellets, tiny fish skeletons, palynomorphs) show no comparable clustering. The VdP palaemonid shows no obvious specializations and resembles extant generalist species. Living freshwater or brackish water palaemonids are opportunistic omnivores, consuming prey, carrion, macrophytes, algae and detritus (Persson *et al.* 2008; Thorp & Rogers 2011; Carnevali *et al.* 2012; Kipyegon *et al.* 2023). The VdP species probably occupied a similar niche, grazing on microbes, algae and plant debris, preying on invertebrates, and scavenging vertebrate remains.

Small teleost bones at VdP are typically disarticulated and radially scattered in tight clusters (Fig. 1C). This pattern has been attributed to weak bottom currents but, given the low-energy setting and the lack of preferred orientation, scavenging by benthic fauna offers a simpler explanation. Generalist palaemonids (and other arthropods) would readily exploit teleost carcasses settling on the substrate, leaving the mechanical traces observed. The preserved decapod fauna therefore provides a plausible agent for the distinctive taphonomy of the VdP ichthyofauna.

Isopods. These organisms are among the most diverse peracaridans, with >10 600 extant species (Schram & Koenemann 2022; Hartebrodt *et al.* 2023; Boyko *et al.* 2024). Their fossil record remains patchy because lightly sclerotized cuticles decay rapidly and many taxa inhabited low-preservation settings (Maguire *et al.* 2018). From the Italian Mesozoic only three Triassic taxa are known: the sphaeromatid *Triassphaeroma magnificum* Basso & Tintori 1995, the serolid *Elioserolis alpina* Basso & Tintori 1995, and the asellotan *Fornicaris calligarisi* Selden *et al.* 2016. Cretaceous cirolanids are comparatively rare and mostly marine, with documented occurrences spanning the Berriasian–Maastrichtian of North America, Europe, Asia and Australia (e.g. Wieder & Feldmann 1992; Karasawa *et al.* 2008; Wilson *et al.* 2011; Bruce & Rodcharoen 2023). Extant Cirolanidae are cosmopolitan and predominantly shallow-marine, but many tolerate brackish or fresh water and numerous stygobiont lineages inhabit subterranean aquifers (Bruce 1986; Brusca *et al.* 1995; Baratti *et al.* 2010). Due to their distribution patterns and

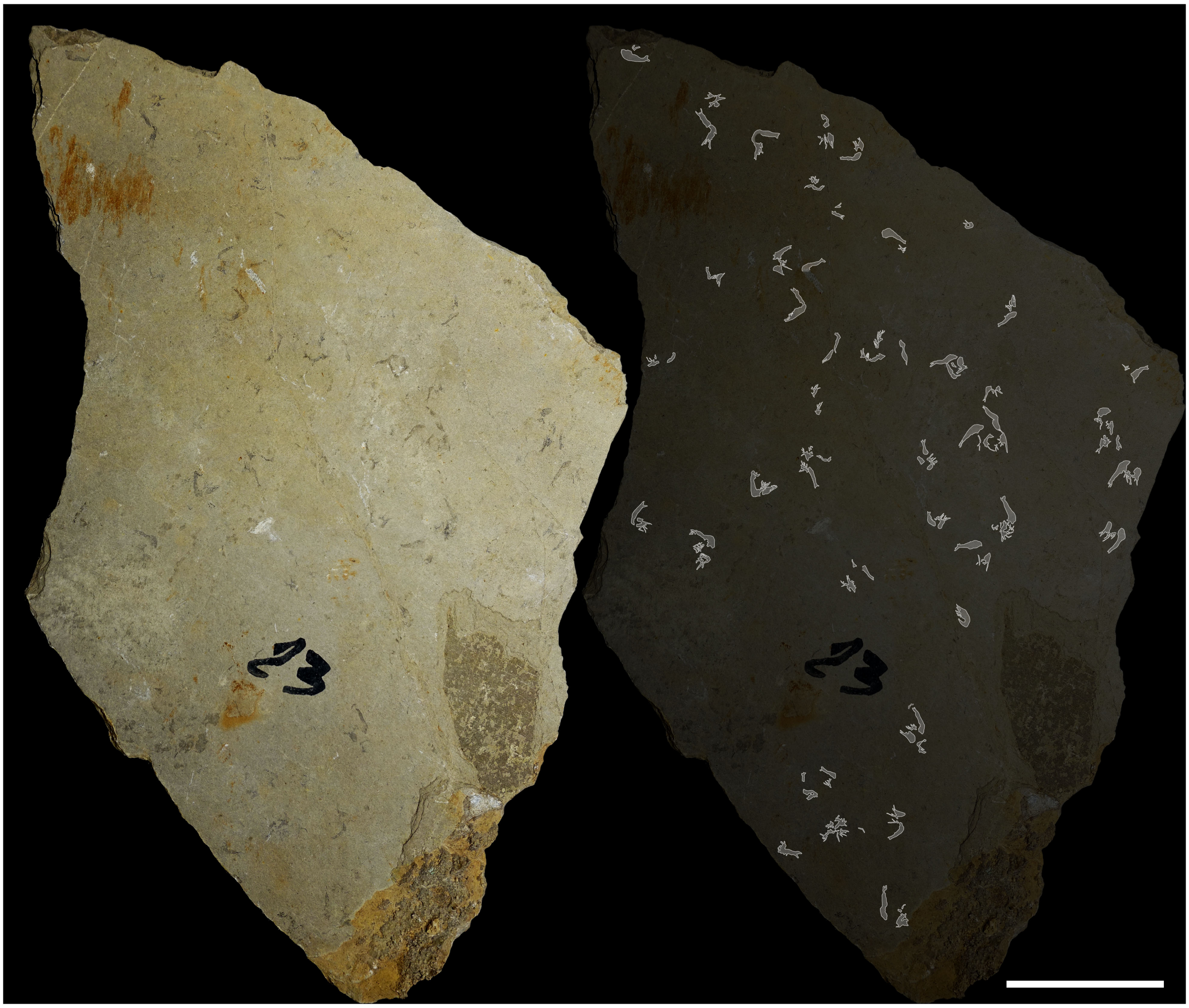

FIG. 14. Photo (left) of slab MCSNT 23 and superimposed highlight of individual unambiguous exuviae (right). The slab includes other fragmentary exuvial remains (scattered faint grey traces) and undeterminable plant material (orange fragments and traces). Scale bar represents 50 mm.

phylogenetic relationships, Euro-American stygobitic isopods and other arthropods are often considered Tethyan relicts (i.e. Coineau & Albuquerque 2001; Iliffe & Botosaneanu 2006; Hou *et al.* 2013). The modern diversity and distribution of Mediterranean and central American freshwater cirolanids probably originated from a combination of vicariance and dispersal events since the Mesozoic, descending from '*Cirolana*-like' ancestors that inhabited brackish or estuarine habitats on the margins of the Tethys during the Late Jurassic and Early Cretaceous (Baratti *et al.* 2010). Cretaceous freshwater or brackish forms are restricted to *Cymothoidana websteri* Jarzembowski *et al.* 2014 from the Barremian–Hauterivian Wealden Supergroup and *Dysopodus gezei* Schädel *et al.* 2025 from the Barremian of Lebanon.

The indeterminate cirolanid from VdP, being from the lower–middle Campanian and preserved in a facies interpreted as freshwater influenced, constitutes the second European record of a non-marine Cretaceous cirolanid and the youngest such occurrence known, and may be representative of the original stock ancestral to extant stygobitic taxa. Extant free-living members of Cirolanidae are either active predators or carnivorous scavengers (Bruce 1986; Brusca *et al.* 1995, 2007). Their conservative morphology, together with exceptional fossil examples, supports a similar scavenging–generalist ecology for extinct members (Wilson *et al.* 2011). As mentioned with the Palaemonidae, the VdP cirolanid may thus have been part of the resident crustacean community and could explain some of the local ichthyofaunal disarticulation patterns.

Insect. According to current evidence, the taxonomic placement of specimen MCSN 72/88 remains uncertain. The two most plausible provisional identifications, heteropteran versus mecopteran, would imply quite different palaeobiological interpretations. Heteroptera, a suborder of Hemiptera, ranks among the most diverse clades of hemimetabolous insects, with >42 000 extant species in almost 90 recognized families (Weirauch & Schuh 2011). The oldest unequivocal heteropteran fossil is the Middle Triassic *Arlecoris louisi* (Shcherbakov 2011), although molecular data push the group's origin and early diversification back into the Permian (Wang *et al.* 2015; Johnson *et al.* 2018). During the Mesozoic, heteropteran diversity rose to levels comparable with those of today, and many Cretaceous fossil Lagerstätten yielded abundant material, for example Las Hoyas (Martínez-Delclòs *et al.* 1995), New Jersey amber (Golub & Popov 2003), the Crato Formation (Martill *et al.* 2007), the Yixian Formation (Zhang *et al.* 2013), Canadian amber (McKellar & Engel 2012, 2013), Khasurty (Kopylov *et al.* 2020), and Myanmar amber (Ross 2024). Consequently, finding heteropterans in the Late Cretaceous Tethyan realm would not be surprising, although the Campanian material from Alberta (McKellar & Engel 2012, 2013) constitutes the only other latest Mesozoic record before the group reappears in post-K–Pg deposits. Mecoptera form an early diverging clade of holometabolans with a comparatively rich fossil record (*c.* 400 described species), although some 'mecopteroid' fossils may lie outside the crown group (Martill *et al.* 2007; Byers 2009). They are among the more common insects reported from the Mesozoic (Soszyńska-Maj *et al.* 2016, 2017; Lin *et al.* 2019; Montagna *et al.* 2024). From the Early Cretaceous onward the order shows a steady decline, reaching a modern-like diversity after the K–Pg event (Bashkuev 2010; Wang *et al.* 2014). Cretaceous mecopterans occur in most of the same Lagerstätten that yield heteropterans across Eurasia, Australia and South America, from the Berriasian–Barremian to the Cenomanian (Martill *et al.* 2007; Buscalioni & Fregenal-Martínez 2010; Krzemiński *et al.* 2014; Jarzembowski & Soszyńska-Maj 2016; Lin *et al.* 2019; Kopylov *et al.* 2020; Ross 2024). After the Cenomanian they vanish until the Eocene Baltic amber, leaving a conspicuous gap in the record (Rasnitsyn *et al.* 2016). A pronounced bias toward the Early Cretaceous characterizes not only Heteroptera and Mecoptera but Late Cretaceous insect fossils in general. An almost continuous +20 Myr gap (from the early Campanian to the Eocene) obscures global insect evolution, with only a few windows such as Canadian and Tilin Campanian ambers (Zheng *et al.* 2018). The early–middle Campanian biota of VdP thus partly bridges this gap. If MCSN 72/88 truly represents a heteropteran or mecopteran, it would mark the first direct evidence for either clade in Western Eurasia between the Early Cretaceous and the Eocene. Closely related Early Cretaceous taxa shared across the peri-Tethyan realm, including both Las Hoyas (Spain) and Jehol (China), suggest west-to-east dispersal (Buscalioni & Poyato-Ariza 2016). Such biogeographic links probably persisted into the Late Cretaceous, as also indicated by other faunal elements (Chiarenza *et al.* 2021; Muscioni *et al.* 2023; Díez Díaz *et al.* 2025). Ecologically, extant heteropterans occupy an extraordinary range of habitats and feeding modes, from terrestrial phytophages and mycetophages to aquatic predators and even oceanic skaters, including active predators, scavengers and vertebrate blood-feeders (Schaefer 2013; Weirauch *et al.* 2018; Cheng & Mishra 2022; Zhang *et al.* 2023). Because microhabitat preferences differ greatly even within lineages, and because MCSN 72/88 may represent an extinct clade, palaeoenvironmental inferences are risky. Although aquatic families such as Notonectidae or Gerridae could theoretically have frequented the brackish or freshwater phases of the VdP basin, the specimen lacks the diagnostic characters needed for such a conclusion. Fossil mecopterans are more informative ecologically: most extant and extinct members favour cool, shady, humid, forested settings with dense understory vegetation, usually near streams or other mesic ecotones, from temperate to tropical zones (Byers & Thornhill 1983; Byers 2009; Su *et al.* 2023). Palaeoclimate reconstructions for the Late Cretaceous Adriatic Carbonate Platforms range between a tropical, equatorial hot-arid belt and a warm, humid mid-latitude regime, probably with strong seasonality (Hay & Floegel 2012). Such conditions are compatible with locally dense tropical vegetation and could have sustained mecopteran populations if present at VdP.

CONCLUSION

This study represents the first description of the arthropod assemblage preserved in the early–middle Campanian deposits of the Villaggio del Pescatore Lagerstätte. One taxon represents a relatively large palaemonid caridean, probably *Palaemon* sp.; remarkably, a single individual of a cirolanid isopod and an undetermined insect are the first records from the latest Cretaceous of the peri-Mediterranean region. In light of their stratigraphic and biogeographic occurrence, these taxa are most likely to represent new species, although the available preserved elements prevent formal taxonomic designation. Furthermore, these fossil arthropods offer crucial proxies for understanding the taphonomic and palaeoenvironmental aspects of the VdP locality. The co-occurrence of palaemonids and cirolanids, both known to inhabit estuarine and lagoonal habitats, supports the interpretation of VdP as a coastal, marginal area characterized by brackish to freshwater conditions. The abundance of small decapod exuviae suggests that the area was inhabited by high densities of probable post-larval stages, possibly representing a nursery habitat. The co-occurrence of small exuviae and larger palaemonid specimens at various ontogenetic stages raises the question of whether all of the preserved decapods represent a single taxon, possibly mimicking the reproductive dynamics of extant euryhaline or amphidromous palaemonids. The occurrence of Cirolanidae in brackish and freshwater palaeoenvironments of the Cretaceous European–Mediterranean region provides valuable insights into the original pool of Tethyan species ancestral to extant stygobitic taxa. In this context, the VdP cirolanid taxon plays a pivotal role, having inhabited the same complex of carbonate platforms that would later be colonized by the stygobiont *Sphaeromides*. The unusual differential preservation of fine elements in larger arthropods and the only recovered insect suggests taphonomic processes compatible with microbial mat growth and interspecies interactions. The presence of cirolanid isopods and medium-to-large palaemonids aligns with scavenging activity on fish carcasses, which may have contributed to the recurrent disarticulation pattern observed in teleost remains.

Finally, all three identified taxa still have living relatives in the northern Adriatic region. In addition to both heteropterans and mecopterans, the euryhaline palaemonid *Palaemon antennarius* H. Milne Edwards 1837, and the stygobiont cirolanid *Sphaeromides virei* Brian 1923, remain locally well-known and culturally important species in traditional fisheries, naturalistic studies and regional identity, representing a unique opportunity for science communication and public engagement focused on this local palaeontological heritage. The presence of closely related arthropod taxa throughout the Early–Late Cretaceous distributed widely around the peri-Tethys and shared, for example, by the Las Hoyas biota in Spain and the Jehol biota in China, points to strong east–west biogeographic links across Eurasia. These longitudinal connections between the European Archipelago and the Asian mainland inferred from invertebrates are consistent with the vertebrate assemblages documented at VdP.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1002/spp2.70048):

Table S1. List of slabs of the VdP collection bearing arthropod remains. The inventory code, brief description of the arthropod material and mention of other fossils sharing the same slab are reported for each specimen. Approximate (~) or minimum numbers (>) indicate unprecise quantification of the referred fossil.

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