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## Description of the postmarsupial manca stages of *Armadillidium granulatum* (Crustacea, Isopoda, Oniscidea)

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### ABSTRACT

The development of the postmarsupial manca stages of *Armadillidium granulatum* Brandt, 1833 was studied in detail by morphological analysis. Ovigerous females were reared separately under controlled conditions, allowing us to follow the stages of development from release from the marsupium until the appearance of the first juvenile stage, identified by the full development of the seventh pair of pereopods. Each newborn was followed to record the subsequent moults that identify the three postmarsupial manca stages. Manca stage M I had a mean duration of 6 h, manca stage M II 15 days, and manca stage M III 32 days. The cephalothorax width was measured to provide a growth measure for each stage. The mean values of the cephalothorax width were: 0.512 mm ( $\pm 0.083$  SD) for M I, 0.677 mm ( $\pm 0.058$  SD) for M II and 1.194 mm ( $\pm 0.079$  SD) for M III. The morphological modifications in the three postmarsupial manca stages were described, the body parts illustrated, and SEM images taken. The distinguishing characteristics among mancas were discussed, and comparisons made with manca stages of other terrestrial isopod species.

### ARTICLE HISTORY

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### KEYWORDS

Crustaceans; terrestrial isopods; Armadillidiidae; development; reproductive biology

### Introduction

*Armadillidium granulatum* Brandt, 1833 is a species of terrestrial isopod (Crustacea, Isopoda, Oniscidea) belonging to the family Armadillidiidae. Among the species of the genus *Armadillidium*, the species is characterized by strong granulation on the dorsal surface and a mesospheric conglobation (Vandel 1962). It is distributed along the Atlantic coasts of Bretagne (France) and Portugal, Mediterranean coasts east to Libya and western Turkey, and the southern coast of the Black Sea (Schmalfluss 2003). This species usually occurs in littoral environments, but it can not be categorized as a halophile (Soyer 1947). It can be also found in localities far from the coastline (Dolfuss 1899; Azam 1901) especially under stones, beneath vegetation, near ruins or old walls (Vandel 1955, 1962). *Armadillidium granulatum* is iteroparous and its reproductive period varies in different geographic areas: in Sardinia from May to June (Arcangeli 1925), and in France from August to September (Vandel 1962). The highest reproductive activity is in autumn, while a lower activity is in spring, with no activity in summer (Messina et al. 2011, 2012). *Armadillidium granulatum* usually lives on several kinds of substrata, such as rocky, silty-clayey, and pebbly substrata in environments populated by different plant communities (Messina et al. 2014).

Although this species has been collected many times, and from different sites within of its distributional range, the postmarsupial manca stages have been never described before, as in most terrestrial isopods. The aims of this study are to describe the manca stages of *Armadillidium granulatum* with a detailed morphological analysis, and to evaluate the differences in the various manca stages. Some comparisons with the manca stages of other oniscidean species are also presented.

### Materials and methods

Numerous specimens of *Armadillidium granulatum* were collected by Dr. Stefano Taiti (Researcher in Florence, Italy), in Cala Spalmatoio, Island of Giannutri, Tuscan Archipelago (DMS: 37°31'39" N, 15°04'20" E), at 10 m a.s.l., and then bred in Pisa (western Tuscany), in a climate room at 20°C, with a natural photoperiod. Ovigerous females were separated from the main livestock and bred separately. Each ovigerous female was kept in a Petri dish (Falcon® 351029, 100 × 15 mm<sup>2</sup>, with plaster of Paris substratum), periodically moistened and fed with slices of potato and plane-tree leaves (as in Montesanto and Cividini 2017).

After the release of the mancas from the marsupium, the mancas were counted, separated from the female and

raised in individual Petri dishes. For the purpose of recording the time of manca release, the ovigerous females were monitored daily. In the same way the postmarsupial mancas were observed every day, so that the moulting process and the time of each manca stage could be recorded.

Throughout postmarsupial development, 20 individuals of each postmarsupial manca stage were fixed in 70% ethanol for analysis. The manca stages were described in accordance with previous procedures (Araujo et al. 2004; Brum and Araujo 2007; Sokolowicz and Araujo 2008; Montesanto et al. 2012; Montesanto *Forthcoming*), including a morphological study of the appendages. Body parts were mounted on slides, and pencil drawings were made using a Carl Zeiss Standard 14 microscope equipped with a *camera lucida*. Final illustrations were prepared using the software GIMP ver. 2.8.14 as in Montesanto (2015, 2016). Samples for SEM (scanning electron microscopy) were dried out over a weekend at room temperature and then sputter coated with gold (Edwards Sputter Coater S150B). They were observed using a JEOL JSM-5410 at 15 kV; digital images were taken with the JEOL SemAfore system.

## Results

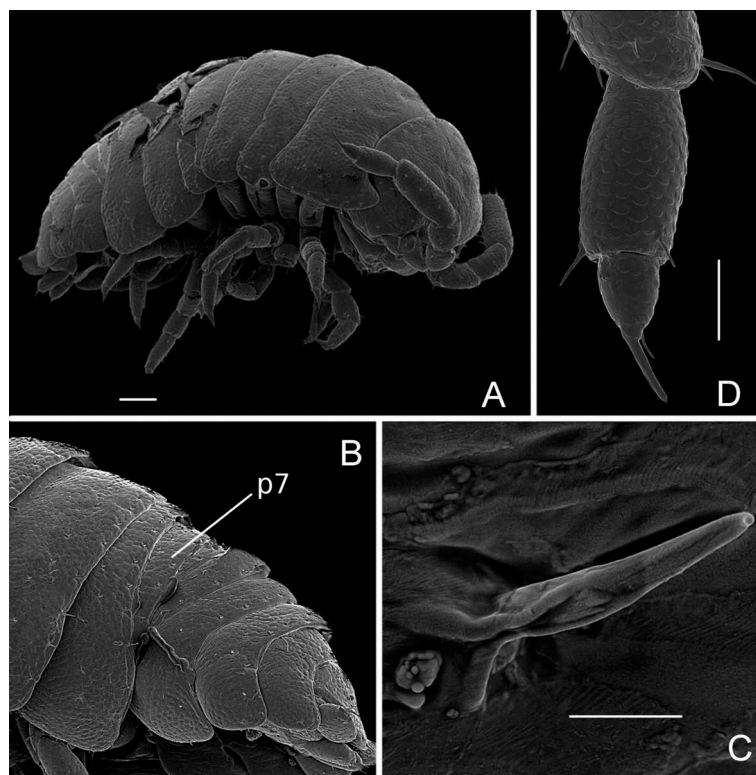
*Armadillidium granulatum* had three postmarsupial manca stages (called M I, M II, and M III), separated by ecdysis and

generally characterized by the absence of the first pleopods and non-functional seventh pereopods. The main characteristics that can be used to distinguish each stage are the length of the antennal flagellum articles, the number of ommatidia, the developmental level of pereopod 7, and the presence of the epimera of pereonite 7.

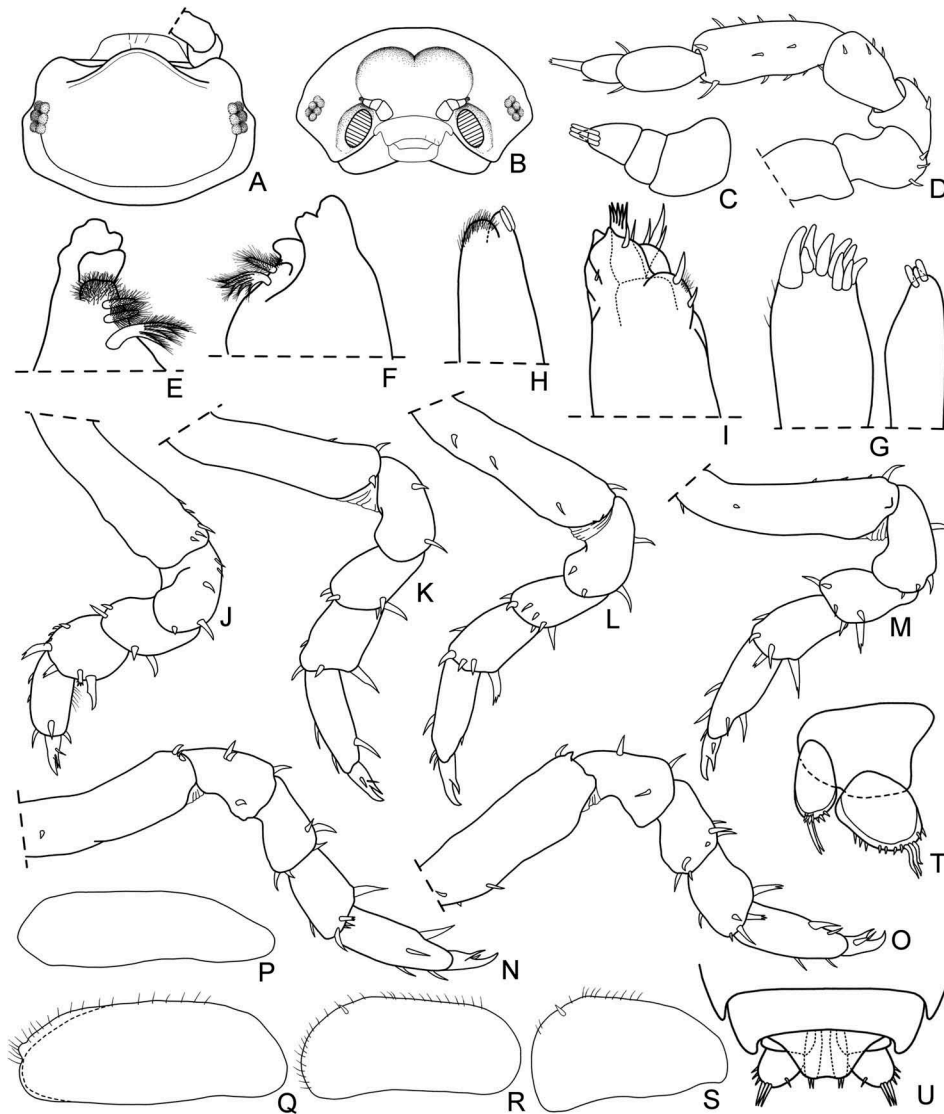
### *Manca stage M I*

The duration of this stage varied from a minimum of 5.1 h to a maximum of 6.3 h, with a mean value of 5.7 h ( $\pm 0.55$  SD). The mean cephalothorax width was 0.512 mm ( $\pm 0.083$  SD), with a minimum of 0.497 mm and a maximum of 0.528 mm. These mancae showed no pigmentation, except for the ommatidia and little spots on the pereonite margins. Calcification of the cuticle seemed incomplete as the body surface was not very tough. The mancas leave the mother's body and go exploring almost immediately around the Petri dish, but they did not eat. After posterior and anterior ecdysis, they ate the exuviae. Because of the transparency of the body it was possible to observe the exuviae inside the gut.

The dorsal surface has a few sparse scale-setae (Figure 1(A–C)) and the eyes 5–6 ommatidia (Figure 2(A–B)). Pereonite 7 is reduced, not fully developed, and has



**Figure 1.** *Armadillidium granulatum* Brandt, 1833. Manca stage M I. (A) Habitus, lateral view (scale 100  $\mu$ m). (B) Pleon, lateral view; p7, pereonite 7. (C) Seta (scale 10  $\mu$ m). (D) Antennal flagellum (scale bar = 100  $\mu$ m).



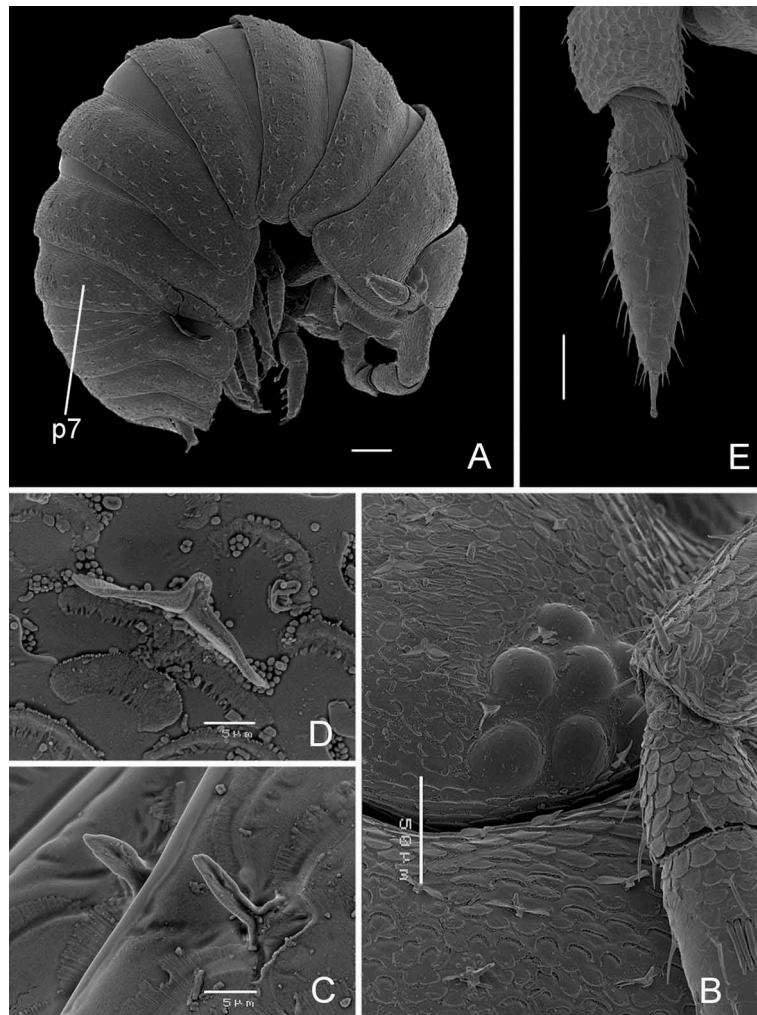
**Figure 2.** *Armadillidium granulatum* Brandt, 1833. Manca stage M I. (A) Cephalon, dorsal view. (B) Cephalon, frontal view. (C) Antennula. (D) Antenna. (E) Left mandible. (F) Right mandible. (G) Maxillula. (H) Maxilla. (I) Maxillipede. (J) Pereopod 1. (K) Pereopod 2. (L) Pereopod 3. (M) Pereopod 4. (N) Pereopod 5. (O) Pereopod 6. (P) Pleopod 2 exopod. (Q) Pleopod 3 exopod. (R) Pleopod 4 exopod. (S) Pleopod 5 exopod. (T) Right uropod. (U) Telson.

no epimera (Figure 1(A–B)). The cephalon (Figure 1(A–B)) has no frontal scutellum although there is a slightly pronounced concavity in frontal view. The antennula (Figure 2(C)) has three articles and three apical aesthetascs. The antennal flagellum (Figures 1(D) and 2(D)) is as long as the fifth article of the peduncle, is bi-articulated with the proximal article longer than the apical. There are no aesthetascs on the flagellum. The mandibles (Figure 2(E–F)) have a semidichotomized molar penicil, 1 + 1 free penicils on the left and 1 on the right mandible. The maxillula (Figure 2(G)) has 4 + 5 teeth, the endite with two short penicils and no hairs. The maxilla (Figure 2(H)) has few setae on the apical part of the lateral and medial lobes. The maxilliped (Figure 3(I)) palp has an apical setal tuft, and two setae in the basal article; the endite has two

teeth and one apical seta. Pereopods 1–6 (Figure 2(J–O)) have few setae; pereopods 7 and pleopods 1 are absent. Pleopod 2–5 exopods (Figure 2(P–S)) have one seta on the apical margin of pleopod 4 and 5 exopod, longer hairs on the apical margin of pleopod 3, 4, and 5 exopod, and no tracheal fields. Uropod (Figure 2(T)) has a subcircular exopod, as large as long, and an endopod as long as the exopod. The telson (Figure 2(U)) is trapezoidal, larger than long, with a slightly concave posterior margin.

### **Manca stage M II**

The duration of this stage varied from a minimum of 12 to a maximum of 16 days, with a mean value of 14.69 days ( $\pm 2.59$  SD). The mean cephalothorax width was 0.677 mm

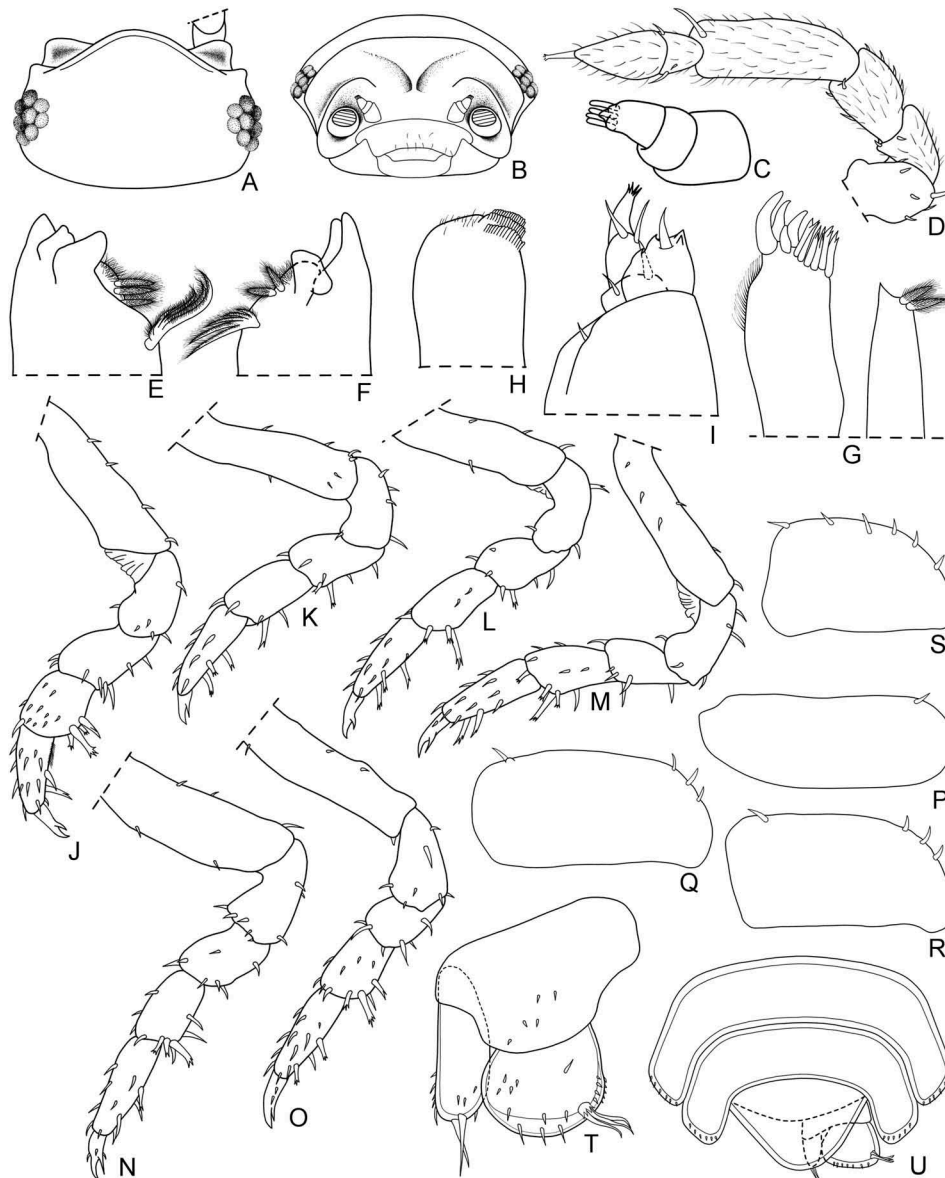


**Figure 3.** *Armadillidium granulatum* Brandt, 1833. Manca stage M II. (A) Habitus, lateral view; p7, pereonite 7 (scale bar = 100  $\mu\text{m}$ ). (B) Eye (scale bar = 50  $\mu\text{m}$ ). (C) Setae (scale bar = 5  $\mu\text{m}$ ). (D) Tricorn scale-seta (scale bar = 5  $\mu\text{m}$ ). (E) Antennal flagellum (scale bar = 50  $\mu\text{m}$ ).

( $\pm 0.058$  SD), with a minimum of 0.658 mm and a maximum of 0.685 mm. These mancas showed pigmentation on the cephalon and on the lateral and posterior margins of pereonites and pleonites. The calcification of the cuticle seems to be complete after the previous ecdysis. Even if the body is not completely transparent, it is possible to observe the presence of food in the gut as a dark area. At this stage, the mancas leave the mother in search of food.

Spiny and tricorn dorsal scale-setae are present on the body surface (Figure 3(A–D)). The eyes (Figures 3(A–B) and 4(A–B)) have 7–8 ommatidia. Pereonite 7 (Figure 3(A)) is still incomplete and with no epimera. The cephalon (Figure 4(A–B)) has a complete frontal line and hint of a triangular frontal scutellum. The antennula (Figure 4(C)) has three articles and four apical aesthetascs. The antennal flagellum (Figures 3(E) and 4(D)) is slightly shorter than the fifth article of the peduncle, and is bi-articulated with the proximal article shorter than the apical. There are

three aesthetascs on the second article (Figure 3(B)). The mandibles (Figure 4(E–F)) have a semidichotomized molar penicil, 2 + 2 free penicils on the left and 1 + 1 on the right mandible. The maxillula (Figure 4(G)) has 4 + 6 teeth (5 cleft), and an endite with two apical penicils. The maxilla (Figure 4(H)) has few setae on the apical part of the lateral and medial lobes. The maxilliped (Figure 4(I)) palp has an apical setal tuft, and two setae in the basal article; the endite had three teeth and one apical seta. The pereopods 1–6 (Figure 4(J–O)) have no particular modification but have more setae in comparison with the previous stage; pereopods 7 are present but not fully developed. Pleopods 1 are absent. Pleopod 2–5 exopods (Figure 4(Q–S)) have few setae on their margins and no tracheal fields. The uropod (Figure 4(t)) has a subcircular exopod, slightly longer than wide, and the endopod is slightly longer than the exopod. The telson (Figure 4(U)) is subtriangular, slightly wider than long with a rounded apex.



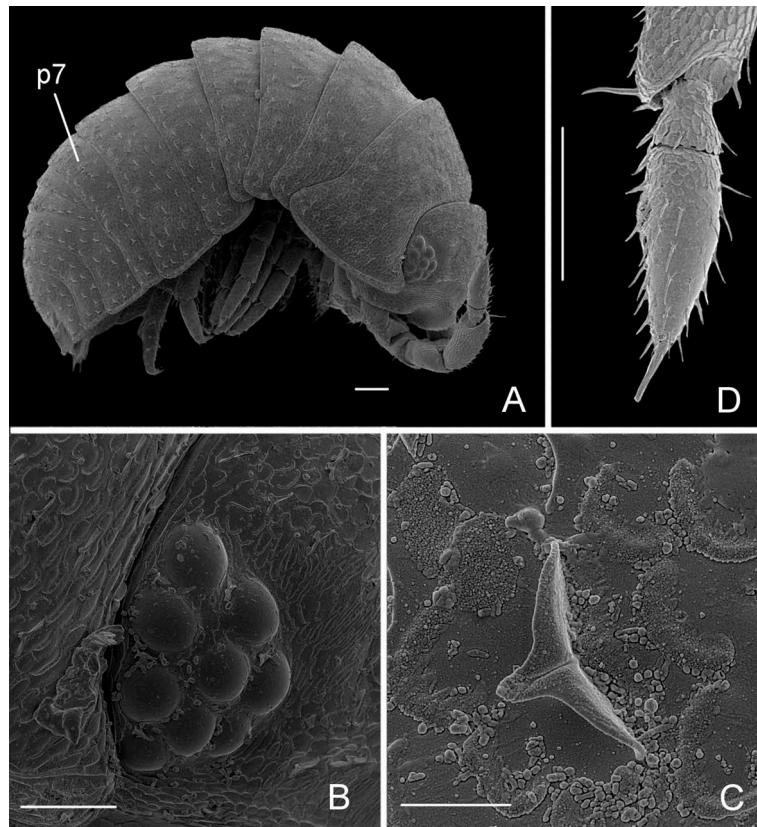
**Figure 4.** *Armadillidium granulatum* Brandt, 1833. Manca stage M II. (A) Cephalon, dorsal view. (B) Cephalon, frontal view. (C) Antennula. (D) Antenna. (E) Left mandible. (F) Right mandible. (G) Maxillula. (H) Maxilla. (I) Maxillipede. (J) Pereopod 1. (K) Pereopod 2. (L) Pereopod 3. (M) Pereopod 4. (N) Pereopod 5. (O) Pereopod 6. (P) Pleopod 2 exopod. (Q) Pleopod 3 exopod. (R) Pleopod 4 exopod. (S) Pleopod 5 exopod. (T) Right uropod. (U) Telson.

### Manca stage M III

The duration of this stage varied from a minimum of 29 to a maximum of 34 days, with a mean value of 32.51 days ( $\pm 2.54$  SD). The mean cephalothorax width was 1.194 mm ( $\pm 0.079$  SD), with a minimum of 1.096 mm and a maximum of 1.212 mm. This stage had more pigmentation than the previous stage, on the cephalon, pereonites and pleonites. Calcification of the cuticle was complete after the previous ecdysis.

The body surface has more dorsal tricorn scale-setae (Figure 5(A, C)). The eyes have external typical structures of nine ommatidia (Figures 5(A–B) and 6(A–B)).

Pereonite 7 (Figure 5(A)) is completely developed and has epimera. The cephalon (Figure 6(A–B)) has a more developed triangular frontal scutellum. The antennula (Figure 6(C)) has three articles and five apical aesthetascs. The antennal flagellum (Figures 5(D) and 6(D)) is slightly shorter than the fifth article of the peduncle, and is bi-articulated and with the proximal article much shorter than the apical. There are three aesthetascs on the second article. The mandibles (Figure 6(E, F)) have semidichotomized molar penicils, 2 + 2 free penicils on the left and 1 + 2 on the right mandible. The maxillula (Figure 6(G)) has 4 + 6 teeth (5 cleft), and an endite with two penicils. The maxilla (Figure 6(H)) has few setae on



**Figure 5.** *Armadillidium granulatum* Brandt, 1833. Manca stage M III. (A) Habitus, lateral view; p7, pereonite 7 (scale bar = 100  $\mu$ m). (B) Eye (scale bar = 50  $\mu$ m). (C) Tricorn scale-seta (scale bar = 5  $\mu$ m). (D) Antennal flagellum (scale bar = 100  $\mu$ m).

the apical part of lateral and medial lobes. The maxilliped (Figure 6(j)) palp has an apical setal tuft, and two setae in the basal article. The endite has three teeth and one apical seta. Pereopods 1–6 (Figure 6(J–O)) have no particular modification but have more setae, in comparison with the previous stage. Pereopods 7 are completely developed, with articles, but they are not functional and are folded on the pereonal sternites. Pleopods 1 are not fully developed. Pleopod 2–5 exopods (Figure 6(P–S)) have more setae on the margins, and no tracheal fields. The uropod (Figure 6(T)) has a subquadrangular exopod, slightly wider than long, and the endopod is longer than the exopod. The telson (Figure 6(U)) is triangular, slightly wider than long.

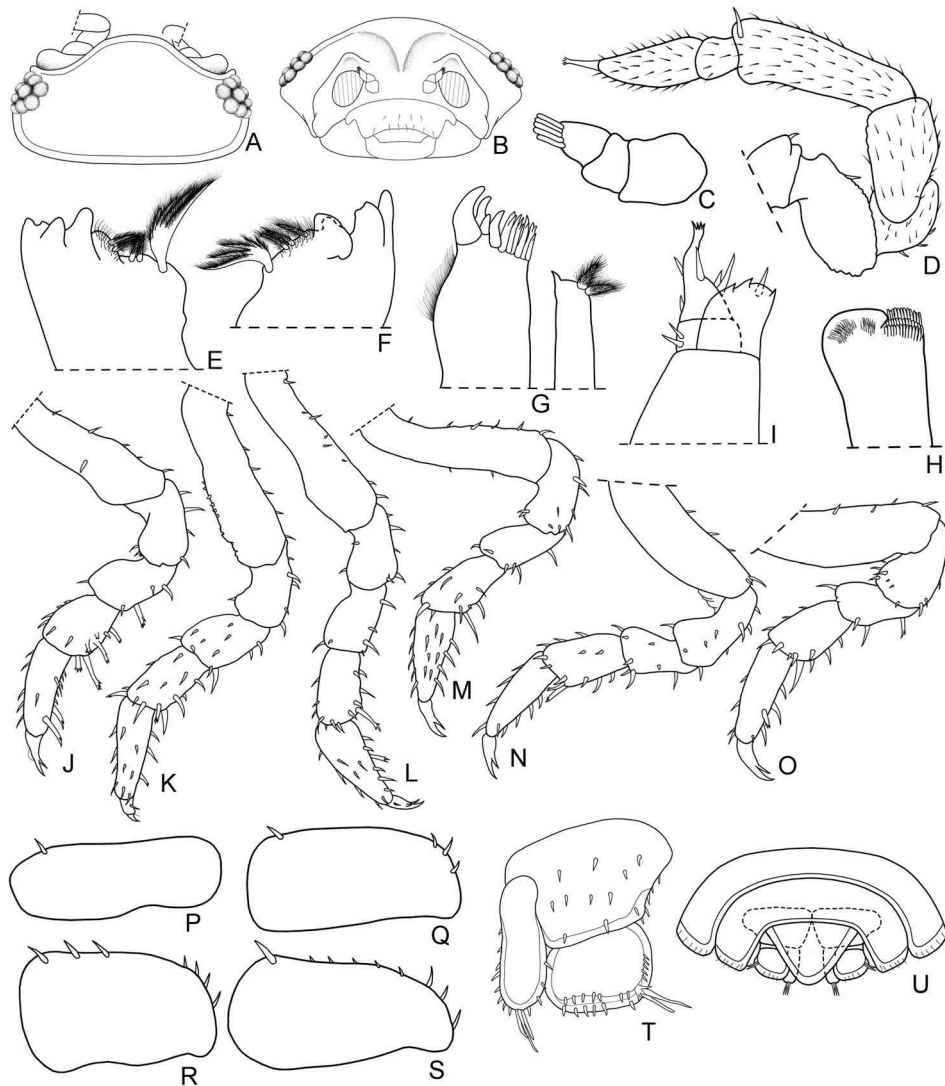
## Discussion

Although more than 3,700 species of terrestrial isopod have been described (Schmalfuss 2003; Sfenthourakis and Taiti 2015), manca stages are known for very few species. Studies on crustacean manca biology are limited due to many difficulties and technical problems, but these studies have greatly improved our knowledge of the life-history of different taxa (ontogeny of species-

specific traits), and may contribute to the reconstruction of the phylogeny of higher taxa ('Evo-Devo' perspective) (Anger 2006). One character that needs to be studied further is the duration of the three postmarsupial manca stages of terrestrial isopods. This feature is highly variable among species, especially the first manca stage, and this should be considered a priority for future studies. More data are needed, especially in different families besides the common families Porcellionidae and Armadillidiidae. Furthermore, the recent study of Montesanto (Forthcoming) has shown the presence of a stridulatory apparatus on the pereopods of the three manca stages of *Armadillo officinalis* (family Armadillidae) so far known only for the adult stages for its implications on the biotremology studies of this species (Montesanto and Cividini 2018; Cividini and Montesanto 2018a, 2018b, Forthcoming).

The postmarsupial mancas of *A. granulatum* show some significant differences when compared to manca stages of other terrestrial isopods. As reported for *Atlantoscia floridana* (Van Name, 1940) (Araujo et al. 2004), *Benthana cairensis* Sokolowicz, Araujo and Boelter, 2008 (Sokolowicz and Araujo 2008), *Porcellio siculoccidentalis* Vigliani, Lombardo and Caruso 1992



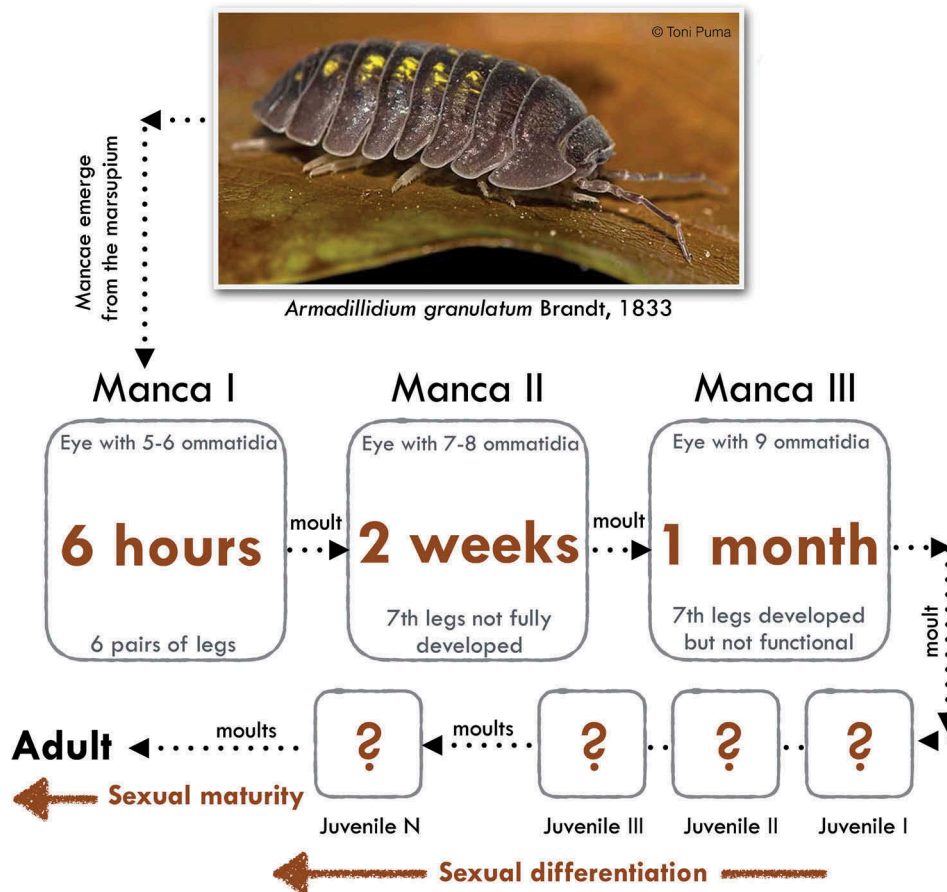


**Figure 6.** *Armadillidium granulatum* Brandt, 1833. Manca stage M III. (A) Cephalon, dorsal view. (B) Cephalon, frontal view. (C) Antennula. (D) Antenna. (E) Left mandible. (F) Right mandible. (G) Maxillula. (H) Maxilla. (I) Maxillipede. (J) Pereopod 1. (K) Pereopod 2. (L) Pereopod 3. (M) Pereopod 4. (N) Pereopod 5. (O) Pereopod 6. (P) Pleopod 2 exopod. (Q) Pleopod 3 exopod. (R) Pleopod 4 exopod. (S) Pleopod 5 exopod. (T) Right uropod. (U), telson.

(Montesanto et al. 2012), and *Armadillo officinalis* Duméril, 1816 (Montesanto [Forthcoming](#)) manca stage M I represents the last marsupial stage, when the mancae do not eat or moult. In *A. granulatum*, the first manca stage begins its moulting process outside the marsupium, and the duration of the first postmarsupial manca stage is about 6 h. The duration of the same manca stage is considerably different in other species of terrestrial isopods: in *Hemilepistus reaumurii* (Milne Edwards, 1840) it is 48 h (Kacem-Lachkar 1997), in *Porcellio dilatatus* Brandt, 1831 19 h (Brum and Araujo 2007), and in *A. floridana* 12 h (Araujo et al. 2004). In *P. siculoccidentalis* it is just one hour (Montesanto et al. 2012), and in *A. officinalis* this duration is even shorter (just half of an hour) because the moulting process

between M I and M II begins inside the marsupium. Therefore, in *A. officinalis* the duration of this stage outside the marsupium is the shortest among the postmarsupial mancae previously described (Montesanto [Forthcoming](#)). Although individuals of manca stage M I do not feed, they leave the mother's body and explore their surroundings. This behaviour was not always observed in other species of terrestrial isopods, but rather they usually remain under the mother's body for a kind of extended parental care (as reported e.g. in *Porcellio siculoccidentalis*: Montesanto et al. 2012; in *Armadillo officinalis*: Montesanto [Forthcoming](#)).

The description of the three postmarsupial mancae of *A. granulatum* has revealed some morphological differences. On the body surface, no granulations have



**Figure 7.** Schematic diagram with the main stages of postmarsupial development of *Armadillidium granulatum* Brandt, 1833.

been observed but the number of dorsal scale-setae increases from manca stage M I to M III. In the last stage only tricorn setae are present on the tergites of the pereon and pleon. The cephalon develops a frontal scutellum in manca stage M II and M III; in manca stage M I a large concavity is present. In the antennula, the number of apical aesthetascs varies from three in manca stage I to five in manca stages M III. The proportion of the two articles of the antennal flagellum changes from manca stages M I to manca stage M II; three aesthetascs appear on the flagellum of manca stage M II and are the same in manca stage M III. The main structure of the buccal appendages do not change in the three manca stages; the number of penicilis in the mandibles increases during development. The number of setae on the pereopods increases from manca stage M I to M III. Pereopod 1 does not have a well-defined hairy area on the carpus. Pereopods 7 are absent in the first manca stage, there are hints in the second stage, and they are fully developed but ventrally folded in the third manca stage. Pleopods 1 are absent in manca stages M I and M II, but appear in manca stage M III, although they are not well

developed. The setae on pleopod 2–5 exopods appear in manca stage M I and do not increase in number in the next stage; the presence of these kind of hairs in manca stage M I is remarkable, since they are not present in all the known manca stages of terrestrial isopods. The uropod and telson change substantially in shape and proportion in the three manca stages. [Figure 7](#) shows a pictorial summary of the main stages in postmarsupial development.

The development of the body of *A. granulatum* is similar to that described for other oniscidean manca stages. This involves a change in proportion of the articles of the antennal flagellum, development of the seventh pereonite and its epimera, and appearance of pereopod 7 and pleopod 1. Other minor differences are in the number of ommatidia, and in the number of setae in the margin of pereopods and pleopods (Araujo et al. 2004; Brum and Araujo 2007; Milatovic et al. 2010; Montesanto et al. 2012; Montesanto [Forthcoming](#)). The number of ommatidia can be different in the manca stages of other species of oniscidean isopods and this is related to the number of ommatidia of the adults. So, each species develops its

eye in a different way, with a different number of ommatidia in the three manca stages. Another remarkable characteristic is the presence of long hairs on the distal margin of pleopodal exopods in manca stage M I. This was also described by Brum and Araujo (2007) for *Porcellio dilatatus* (Family Porcellionidae) and the authors indicated this character as an adaptation to aquatic life inside the marsupium. In our opinion, this feature might be considered in further phylogenetic studies on the taxon Oniscidea especially within the Crinocheta (Schmalfuss 1989; Erhard 1998), as also reported in the study of Brum and Araujo (2007).

The results of the present study might also contribute to knowledge on the biology of this taxon and might have future implications on our understanding of the evolutionary biology of the family Armadillidiidae and of the suborder Oniscidea. Therefore, data are now needed to try to better understand why and how some morphological features of the postmarsupial manca stages are so variable while others are similar or sometimes identical to the adults. Such studies are currently underway in a number of other species, also for implementation in future ecotoxicological research (e.g. Agodi et al. 2015).

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## Disclosure statement

No potential conflict of interest was reported by the authors.

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## References

Agodi A, Oliveri Conti G, Barchitta M, Quattrocchi A, Lombardo BM, Montesanto G, Messina G, Fiore M, Ferrante M. 2015. Validation of *Armadillo officinalis*

- Duméril, 1816 (Crustacea, Isopoda, Oniscidea) as a bioindicator: in vivo study of air benzene exposure. *Ecotoxicol Environ Saf.* 114:171–178.
- Anger K. 2006. Contribution of larval biology to crustacean research: a review. *Invertebr Repr Dev.* 49:175–205.
- Araujo PB, Augusto MM, Bond-Buckup G. 2004. Postmarsupial development of *Atlantoscia floridana* (van Name, 1940) (Crustacea, Isopoda, Oniscidea): the manca stages. *J Nat Hist.* 38:951–965.
- Arcangeli A. 1925. Gli Isopodi terrestri della Sardegna. *Bollettino dei Musei di Zoologia e Anatomia Comparata della Regia Università di Torino.* 39:13–75.
- Azam J. 1901. Liste de Cloportides (Crustacés Isopodes terrestres) du Département du Var. *Bulletin de la Société d'études scientifiques et archéologiques de Draguignan.* 14:3–6.
- Brum PED, Araujo PB. 2007. The manca stages of *Porcellio dilatatus* Brandt (Crustacea, Isopoda, Oniscidea). *Revista Brasileira de Zoologia.* 24:493–502.
- Cividini S, Montesanto G. 2018a. Changes in turn alternation pattern in response to substrate-borne vibrations in terrestrial isopods. *Behav Processes.* 146:27–33.
- Cividini S, Montesanto G. 2018b. Differences in the pattern of turn alternation between juveniles and adults of *Armadillo officinalis* Duméril, 1816 (Isopoda, Oniscidea) in response to substrate-borne vibrations. *Acta Ethologica.* 21:59–68.
- Cividini S, Montesanto G. *Forthcoming*. Aggregative behavior and intraspecific communication mediated by substrate-borne vibrations in terrestrial arthropods: an exploratory study in two species of woodlice. *Behav Processes.*
- Dolfuss A. 1899. Catalogue des Isopodes terrestres (Cloportides) de France. *Feuille des Jeunes Naturalistes.* 29:186–190, 207–208.
- Erhard F. 1998. Phylogenetic relationships within the Oniscidea (Crustacea, Isopoda). *Israel J Zoology.* 44:303–310.
- Kacem-Lachkar H. 1997. Étude du développement post-embryonnaire d'*Hemilepistus reaumurii* (Audouin, 1826) (Isopoda, Oniscidea). *Crustaceana.* 70:513–526.
- Messina G, Montesanto G, Pezzino E, Caruso D, Lombardo BM. 2011. Diversity of terrestrial isopods in a protected area characterized by salty coastal ponds (Vendicari, Sicily). *J Nat Hist.* 45:2145–2158.
- Messina G, Montesanto G, Pezzino E, Sciandrello S, Caruso D, Lombardo BM. 2014. Plant communities preferences of terrestrial crustaceans (Isopoda: oniscidea) in a protected coastal area of southeastern Sicily (Italy). *Biologia.* 69:354–362.
- Messina G, Pezzino E, Montesanto G, Caruso D, Lombardo BM. 2012. The diversity of terrestrial isopods in the natural reserve “Saline di Trapani e Paceco” (Crustacea, Isopoda, Oniscidea) in northwestern Sicily. *Zookeys.* 176:215–230.
- Milatovic M, Kostanjsek R, Štrus J. 2010. Ontogenetic development of *Porcellio scaber*: staging based on microscopic anatomy. *J Crustac Biol.* 30:225–235.
- Montesanto G. 2015. A fast GNU method to draw accurate scientific illustrations for taxonomy. *ZooKeys.* 515:191–206.
- Montesanto G. 2016. Drawing setae: a GNU way for digital scientific illustrations. *Nauplius.* 24:e2016017.
- Montesanto G. *Forthcoming*. Presence of a stridulatory apparatus in the manca stages of isopods (Crustacea, Isopoda, Oniscidea). *Zookeys.*
- Montesanto G, Cividini S. 2017. A crossover design to assess feeding preferences in terrestrial isopods: a case study in a Mediterranean species. *Biologia.* 72:194–203.

- Montesanto G, Cividini S. 2018. The moult cycle of the terrestrial isopod *Armadillo officinalis* Duméril, 1816 (Crustacea: isopoda: oniscidea). *Acta Zoologica*. 99:263–273.
- Montesanto G, Musarra Pizzo G, Caruso D, Lombardo BM. 2012. The postmarsupial development of *Porcellio siculocidentalis*, with some data on reproductive biology (Crustacea, Isopoda, Oniscidea). *ZooKeys*. 176:87–101.
- Schmalfuss H. 1989. Phylogenetics in Oniscidea. *Monitore zoologico italiano, Nuova Serie, Monografia*. 4:3–27.
- Schmalfuss H. 2003. World catalog of terrestrial isopods (Isopoda: oniscidea). *Stuttgarter Beiträge zur Naturkunde, Serie A*. 654:1–341. [http://www.oniscidea-catalog.naturkundemuseum-bw.de/Cat\\_terr\\_isop.pdf](http://www.oniscidea-catalog.naturkundemuseum-bw.de/Cat_terr_isop.pdf).
- Sfenthourakis S, Taiti S. 2015. Patterns of taxonomic diversity among terrestrial isopods. *ZooKeys*. 515:13–25.
- Sokolowicz CC, Araujo PB. 2008. Postmarsupial manca of *Benthana cairensis* Sokolowicz, Araujo and Boelter (Isopoda, Philosciidae). In: Zimmer M, Charfi-Cheikhrouha F, Taiti S, editors. *Proceedings of the International symposium of Terrestrial Isopod Biology ISTIB-07; March 2007; Tunis (Tunisia)*. Aachen: Shaker Verlag. p. 91–99.
- Soyer B. 1947. Étude statistique des groupements d'animaux dans les associations végétales des environs de Marseille. *Bulletin du Museum d'Histoire Naturelle de Marseille*. 7:165–169.
- Vandel A. 1955. La faune isopodique cavernicole de l'Afrique du nord (Berbérie). *Notes biospéologiques*. 10:63–80.
- Vandel A. 1962. 66. Isopodes terrestres (deuxième partie). *Faune de France*. Paris (France): Le Chevalier; p. 511.