The complete larval development of the spider crab, *Macropodia parva* (Crustacea, Decapoda, Majidae) from laboratory culture

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Summary

Two zoeae and the megalopa of the majid crab *Macropodia parva* were obtained from laboratory material. At 25±1°C and 35‰ salinity, the first crab appeared 12 days after hatching; survival to the first crab instar was 27%. The larval stages are described in detail and compared with those of the previously described species of the genus *Macropodia*. Zoeal characteristics of *M. parva* that differentiate it from other known *Macropodia* larvae are the naked telson furcae and the absence, in zoea II, of the exopodal setae on the basis of the maxillule.

Key words: Crustacea, Decapoda, Brachyura, Majidae, larval development, laboratory rearing, *Macropodia parva*

Introduction

The spider crab *Macropodia parva* Van Noort and Adema, 1985, is a small majid that is found in northeast Atlantic waters from the southern parts of the Scandinavian Peninsula to the Gulf of Cádiz (Iberian Peninsula) (Van Noort and Adema, 1985; Nöel, 1992). Within the Gulf of Cádiz, this species occurs in intertidal rock pools and bottoms with *Caulerpa prolifera* to a subtidal depth of 6 m.

Macropodia is represented in northeast Atlantic and Mediterranean waters by nine species (d'Udekem d'Acoz, 1999): *M. rostrata* (Linnaeus, 1761), *M. longirostris* (Fabricius, 1775), *M. tenuirostris* (Leach, 1814), *M. czernjanskii* (Brandt, 1880), *M. longipes* (Milne-Edwards and Bouvier, 1899), *M. intermedia* Bouvier, 1940, *M. linaresi* (Forest and Zariquey,

1964,) *M. deflexa* (Forest, 1978), and *M. parva* (Van Noort and Adema, 1985). Until *M. parva* was described as a new species, it was probably mistaken for the sympatric species *M. rostrata* or *M. linaresi*.

The larval morphology of *Macropodia* species has been superficially described for *M. rostrata* by Thompson (1836) [as ? *M. phalangium*], Stuxberg (1874) [as ? *Stenorhynchus rostratus*], Cano (1893) [as ? *Stenorhynchus phalangium*], Williamson (1915) [as *Inachus rostratus*], Lebour (1928) [as *M. rostratus*]; for *M. tenuirostris* by Lebour (1927 and 1928) [as *M. longirostris*]; for *M. deflexa* by Lebour (1928) [as *M. egyptia*]; and for *M. linaresi* by Guerao et al. (1998).

The complete larval development for *Macropodia* species is known for only three laboratory-cultured species: *M. tenuirostris* (Salman, 1981; Ingle, 1982;

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Ingle 1991), *M. rostrata* (Ingle, 1982; Ingle, 1991), and *M. longipes* (Guerao and Abelló, 1997). However, our knowledge on larval morphology for this genus is still not substantial.

The present study describes the zoeal stages and megalopa of *M. parva* under laboratory conditions, and the larvae are compared with those of other species of the genus.

Material and Methods

Two ovigerous crabs were caught in July 2000 within intertidal rock pools off El Chato beach (Cádiz – SW Spain) (36°28'30" N, 06°15'40" W). The adults were maintained in a 3-L glass beaker with well aerated, filtered, natural seawater and not fed.

After hatching, actively swimming larvae were transferred to a 2-L glass bucket, and 100 larvae were reared individually in 40 ml glass compartments. Water temperature was maintained at 25±1°C, and salinity was 35‰. Seawater was changed daily, and larvae were checked for evidence of molting. Larvae were fed daily with fresh *Artemia* nauplii. Rearing was terminated when all megalopa moulted to the first crab instar.

Exuviae and specimens were fixed in 4% neutral formalin and preserved in 70% ethanol. Descriptions of different instars were based on at least 10 specimens of each larval stage. Appendages were dissected in water and mounted in lactophenol. Line illustrations were made under a compound microscope (Zeiss Axioskop) equipped with Nomarski differential interference contrast optics and a camera lucida. The sequence of the zoeal description progresses from anterior to posterior and the setal armature on appendages is described from proximal to distal segments, following Clark et al. (1998). Setal groups on successive segments are separated by a comma and groups of setae on the same segment, or on different lobes of the same endite, are separated by a plus sign (+).

The following measurements were taken in lateral view with a calibrated ocular micrometer: distance from base to tip of the dorsal spine (DS); carapace length, from between eyes to the posterolateral margin (CL); and length of antenna, from base of eye to tip of the spinous process (AL). For the megalopa, carapace width (CW) was measured as the greatest distance across the carapace, and carapace length (CL) from the frontal to the posterior margin of the carapace. The sizes given are the arithmetic mean ±95% confidence intervals.

The spent females and complete larval series have been deposited in the Instituto de Ciencias Marinas de

Andalucía (CSIC) in Cádiz (Spain) under accession number MJ/2000-3.

Results

Development and duration of the larvae

The larval development of *M. parva* consist of two zoeal stages and a megalopa. At 25±1°C and 35‰ salinity, the first crab appeared 12 days after hatching; survival to the first crab instar was 27%. The duration and survival of each larval stage are shown in Fig. 1 and Table 1.

The description of morphological major features of each larval stage follow. The first zoea is described in detail, and the main differences of the second zoea are noted.

Larval description — *Macropodia parva* Van Noort and Adema, 1985

First Zoea (Figs. 2a,d; 3a,d; 4a,d; 5a,d; 6a; 7a)

Size: DS = 0.602 ± 0.009 mm; CL = 0.630 ± 0.006 mm; AL = 0.608 ± 0.008 mm. N = 21.

Chromatophore pattern: Reddish chromatophores on posterior base of dorsal carapace spine, antennal protopod, labrum, basis-exopod junction of second maxilliped, and posterolaterally parts on first

Fig. 1. Rearing records of *M. parva* reared at 25°C and 35‰ salinity. ZI, zoea I; ZII, zoea II; M, megalopa; CI, first crab.

Table 1. Duration and percentage survival of each larval stage of *M. parva* at 25°C and 35‰ salinity

Larval stages	Duration (days)		Survivors at end of stage (%)
	Mean	Range	
Zoea I	3.4	3–5	75.0
Zoea II	5.3	2–6	47.7
Megalopa	6.6	6–8	27.0

Fig. 2. *Macropodia parva*. A: zoea I, lateral view; B: zoea II, frontal view; C: zoea II, lateral view; D: zoea I, posterolateral margin of carapace; E: megalopa, dorsal view; F: megalopa, sternum; G: megalopa, lateral view (setae omitted). Scale bars: A–C, E–G = 500 µm; D = 100 µm.

abdominal somite; pinkish gray chromatophores on halfway of dorsal carapace spine, mandible, basis-coxa junction of second maxilliped, third maxilliped, ventrally parts on second and fourth abdominal somites, and posterolateral parts of fifth abdominal somite; black yellowy chromatophores on ventral parts of third and fifth abdominal somites and posterolateral parts of third and fourth abdominal somites; black chromatophores on posterolateral margins of carapace and gastric apparatus.

Carapace (Fig. 2A, D): Globose and smooth, with rostral and lateral spines absent; dorsal spine elongate, slightly curved backward; anteromedial process present; pair of anterodorsal and posterodorsal simple setae; plumose seta positioned on the surface of the margin; posterolateral margin with minute denticles and two sparsely plumose setae; eyes sessile.

Antennule (Fig. 3A): Uniramous, unsegmented and conical; endopod absent; exopod with short terminal

Fig. 3. *Macropodia parva*. Antennule, A: zoea I; B: zoea II; C: megalopa. Antenna, D: zoea I; E: zoea II; F: megalopa. Mandible, G: megalopa. Scale bars: 100 µm.

simple seta and four terminal aesthetascs of unequal size.

Antenna (Fig. 3D): Elongated protopod rounded terminally, without spinules; unsegmented and short endopod as acute bud; elongated exopod pointed terminally slightly shorter than protopod without distal spinules but with two medial simple setae.

Mandible: Incisor and molar process developed, irregularly dentated; palp absent.

Maxillule (Fig. 4A): Coxal endite with seven plumodenticulate setae; basal endite with four terminal plumodenticulate setae, two subterminal plumodenticulate setae, and proximal plumose seta; endopod 2-segmented with 0, 3 (1 subterminal + 2 terminal) sparsely plumose setae, respectively; epipodal and exopodal seta absent.

Maxilla (Fig. 4D): Coxal endite bilobed with 4 + 3 plumodenticulate setae; basal endite bilobed with 5 + 4 plumodenticulate setae; unsegmented endopod not bilobed, with 2 + 2 sparsely plumose setae; exopod (scaphognathite) with 10 plumose marginal setae plus one stout plumose process.

Fig. 4. *Macropodia parva*. Maxillule, A: zoea I; B: zoea II; C: megalopa. Maxilla, D: zoea I; E: zoea II; F: megalopa. Scale bars: 100 μ m.

First maxilliped (Fig. 5A): Coxa without setae; basis with nine medial sparsely plumodenticulate setae arranged as 2+2+2+3; endopod 5-segmented, longer than exopod, with 3, 2, 1, 2, 5 (1 subterminal + 4 terminal) sparsely plumodenticulate setae; exopod 2-segmented with four plumose natatory setae.

Second maxilliped (Fig. 5D): Coxa without setae; basis with sparsely plumodenticulate seta; endopod 3-segmented, smaller than exopod, with 0, 0, 1 plumodenticulate seta plus three sparsely plumodenticulate setae; exopod 2-segmented with four plumose natatory setae.

Third maxilliped (Fig. 6A): Biramous, endopod longer than exopod.

Pereiopods (Fig. 6A): Represented as incipient buds; chela bilobated.

Abdomen (Fig. 7A): Five somites; somite I naked; somites II–V with pair of minute simple setae on posterodorsal margin, second somite with pair of forwardly directed dorsolateral processes, somites III–V with long and terminally acute posterolateral processes.

Fig. 5. *Macropodia parva*. First maxilliped, A: zoea I; B: zoea II; C: megalopa; second maxilliped, D: zoea I; E: zoea II; F: megalopa. Scale bars: 100 μ m.

Pleopods: Incipient pleopods buds on somites II–V.

Telson (Fig. 7A): Bifid, with a deep median cleft; three pairs of plumodenticulate setae on posterior margin, second pair longest; telson forks with lateral spine on outer margin, but not distally spinulated.

Second zoea (Figs. 2b,c; 3b,e; 4b,e; 5b,e; 6b; 7b)

Size: DS = 0.916 ± 0.041 mm; CL = 0.853 ± 0.048 mm; AL = 0.809 ± 0.139 mm. $N = 17$.

Carapace (Fig. 2B, C): Anteromedial process more pronounced than in previous stage; three pairs of minute simple setae in frontal region; well developed supraocular eaves; ventral margin with two plumose + two sparsely plumose setae; eyes stalked and movable.

Antennule (Fig. 3B): Exopod terminally with one short terminal simple seta and six terminal aesthetascs.

Antenna (Fig. 3E): Exopod shorter than protopod; endopod more elongated.

Mandible: Palp present.

Maxillule (Fig. 4B): Basal endite with five terminal plumodenticulate setae, two subterminal plumodenticulate setae, and proximal plumose seta; exopodal seta absent.

Maxilla (Fig. 4E): Basal endite with 5 + 5 sparsely plumodenticulate setae; exopod with 17 plumose marginal setae, stout process now reduced to same size as rest.

Fig. 6. *Macropodia parva*. Third maxilliped, A: zoea I; B: zoea II; C: megalopa. Cheliped, D: megalopa. Scale bars: A, B, 50 µm; C, 100 µm; D, 250 µm.

First maxilliped (Fig. 5B): Exopod with six natatory setae.

Second maxilliped (Fig. 5E): Exopod with six natatory setae.

Pereiopods (Fig. 6B): Rudimentary; first pereiopod bilobed distally.

Abdomen (Fig. 2C, 7B): Posterolateral spines more elongate, somite 6 not differentiated.

Pleopods (Fig. 7B): Biramous buds more elongated.

Megalopa (Figs. 2e–g; 3c,f,g; 4c,f; 5c,f; 6c,d; 7 c–f)

Size: CL = 0.991 ± 0.103 mm; CW = 0.772 ± 0.085 mm. $N = 13$.

Carapace (Fig. 2e,g): Longer than broad, with small rostrum, directed ventrally; each protogastric region with dorsally directed blunt process with pair of plumose setae; tubercle on mesogastric region; prominent long spine present on cardiac region, posteriorly directed; five pairs of simple setae on anterodorsal region as drawn and pair of simple setae on posterodorsal region.

Antennule (Fig. 3C): Peduncle 3-segmented, without setae; unsegmented endopod, lobe naked; exopod 2-segmented, with two and four aesthetascs.

Antenna (Fig. 3F): Peduncle 4-segmented with 0, 1, 0, 1 setae; proximal segment of protopod with stout ventrally directed process; flagellum 4-segmented, with 0, 4, 0, 3 simple setae.

Mandible (Fig. 3G): Palp unsegmented, with terminal seta.

Maxillule (Fig. 4C): Coxal endite with seven sparsely plumose setae; basal endite with seven terminal plumodenticulate setae, five subterminal

Fig. 7. *Macropodia parva*. Abdomen, A: zoea I; B: zoea II; C: megalopa, dorsal view; D: megalopa, lateral view. Pleopods of megalopa, E: fourth pleopod; F: first pleopod. Scale bars: E, F, 100 µm; A–D, 500 µm.

sparsely plumodenticulate setae, and two proximal plumose setae; endopod reduced, unsegmented and naked.

Maxilla (Fig. 4F): Coxal endite unilobate, with five terminal plumose setae; basal endite with 3+6 sparsely plumodenticulate setae; endopod unsegmented, with long sparsely plumose seta; exopod with 20 marginal plumose setae plus two small simple setae on each lateral surface.

First maxilliped (Fig. 5C): Coxal endite with two plumose and two sparsely plumose setae; basal endite with 3+3+3 sparsely plumodenticulate setae; endopod reduced, unsegmented and naked; exopod 2-segmented, with four plumose setae on distal segment; epipod naked.

Second maxilliped (Fig. 5F): Endopod 4-segmented with 0, 1, 3, 4 plumodenticulate setae, respectively; exopod 2-segmented, with four terminal plumose setae; epipod naked.

Third maxilliped (Fig. 6C): Coxa with three simple setae; endopod 5-segmented, with 9+1, 3+2, 3, 7, 4 setae, respectively; exopod 2-segmented with four plumose setae on distal segment; epipod with 2+2 long plumodenticulate setae.

Pereiopods (Figs. 2E, 6D): First pereiopod 5-segmented, sparsely setose as shown, with small proximal tubercle on merus; pereiopods II–V slender and setose, with dactyl terminally acute; ischium of pereiopod II and III with a prominent curved hook-shaped process.

Sternum (Fig. 2F): Cheliped sternite with three pairs of small setae.

Abdomen (Fig. 7C, D): Abdomen with five somites plus telson; somite I with pair of posterodorsal simple setae; somites II–IV with two pairs of posterodorsal simple setae; somite V with three pairs of posterodorsal simple setae.

Pleopods (Fig. 7E, F): Present on somites II–V; endopods with two cincinuli; exopods of pleopods I, II, and IV with eight long plumose natatory setae, exopod of pleopod III with nine such setae. Uropods absent.

Telson: Longer than wide and bearing pair of dorsal setae.

Discussion

In the northeastern Atlantic and Mediterranean waters the family Majidae is represented by 19 genera and 51 species (d'Udekem d'Acoz, 1999). Although majid larvae consist of a wide variety of zoeal forms (see Ingle, 1979), all spider crabs are easily distinguishable from other Brachyura zoeae. Rice (1980) characterized larvae majids by the presence of only two zoeal stages, prominent plumose seta on the anteroventral margin of carapace, maxillule lacking exopod seta in first stage, at least nine marginal plumose setae on the scaphognathite, presence of an antennal endopod bud in the first stage and well developed pleopods in the second stage.

Zoeae of the genus *Macropodia* are also quite distinct from those of any other majid genus. Paula (1996) reported the following combination of features only shown by *Macropodia* zoeae: lack of rostral and lateral carapace spines and a small spine present on the telson furca (no longer than spines of inner margin of telson). Moreover, *Macropodia* shows three setae on the distal endopod segment of the maxillule. Differences between *Macropodia* zoeae are more difficult to establish. Comparative morphological and meristic data of larvae of five species of *Macropodia* are summarized in Table 2. Data are not shown for *M. deflexa* and *M. tenuirostris* noted by Lebour (1927, 1928), designated as *M. egyptia* and *M. longirostris*, respectively in those publications, because the larval descriptions are brief and not likely accurate. The presence of distal spinules on the spinous process and

exopod of the zoea I antenna can be used to separate *M. longipes*, *M. linaresi* and *M. tenuirostris* from *M. rostrata* and *M. parva*, which are lacking in the latter two species. In the first group, zoeae of *M. linaresi* can be differentiated by a straight dorsal carapace spine and a dorsal spine/antennule length (DS/AL) ratio that ranges of between 1.81–1.95. In contrast, *M. longipes* and *M. tenuirostris* show a slightly curved dorsal spine and a DS/AL ratio of 1.08–1.17 and 1.14–1.26, respectively (see Salman, 1981; Guerao and Abelló, 1997; Guerao et al., 1998). Differences between larvae of *M. longipes* and *M. tenuirostris* are not as evident. Guerao and Abelló (1997) reported that both species are primarily distinguished by size and in the number of setae on the scaphognathite of the second zoea, although those features are perhaps insufficient. Also, Lebour (1928) and Salman (1981) noted a pair of dorsal setae on the first abdominal somite of the second larval stage of *M. tenuirostris*, which does not appear in *M. longipes*.

Zoeae of *M. rostrata* and *M. parva* can be distinguished by the slightly curved dorsal spine of the latter that is straight in *M. rostrata*. However, these species have other exclusive characters that are not shared by the rest of *Macropodia* zoeae. *M. rostrata* is the only species of the genus that shows four setae at the distal segment of the endopod of the second maxilliped in the first zoea and an antenna that is longer than carapace length in the second zoea. *M. parva* is characterized by a naked telson furca in either stage, and by the absence of exopodal setae on the basis of the maxillule in the second zoea. The presence or absence of the exopodal seta is considered a distinctive feature (Rice, 1980). Only Ingle (1982) noted presumed intraspecific variability for this character in *M. rostrata* between specimens taken from British and Tunisian waters. However, this was likely due to confusion with larvae of *M. parva*.

When Ingle (1982) described the larval development of *M. rostrata* based on specimens from Isle of Man (North Atlantic Ocean) and the Tunisian coast (Mediterranean Sea), the species *M. parva* was unknown. Therefore, adults from the Atlantic Ocean or Mediterranean Sea could be incorrectly identified as *M. rostrata*. Thus, larval descriptions by Ingle (1982) may have been made from two different species. The fact is that the larval development of *M. parva* reveals that the maxillule of the second larval stage lacks an exopodal setae. The larval description based on specimens from Isle of Man, with an exopodal seta, probably belongs to *M. rostrata*, whereas specimens from the Tunisian coast lack an exopodal seta,

Table 2. Comparison of morphological characters for larval stages of *Macropodia* species from northeastern Atlantic and Mediterranean waters. (s): setae; Mxpd: maxilliped; (*): from Ingle's account of ovigerous females from Isle of Man; (†): Does not include "majid seta"; (‡): Feature observed in specimens from Tunisian coast; (§): from Ingle (1992); (**): from Ingle (1982) and Clark (pers. com.)

Features	<i>M. tenuirostris</i>	<i>M. longipes</i>	<i>M. linaresi</i>	<i>M. rostrata</i>	<i>M. parva</i>
Sources	Salman, 1981	Guerao and Abelló, 1997	Guerao et al., 1997	Ingle, 1982	Present study
Locality ovigerous females	United Kingdom	NE, Spain	E, Spain	United Kingdom	SW, Spain
ZOEA I					
Carapace length (mm)	0.98 (0.9–1.0)*	0.75–0.77	0.6–0.63	0.7–0.8	0.63
Dorsal spine length (mm)	1.14 (1.0–1.1)*	0.90–0.94	1.20–1.25	1.3–1.4	0.60
Antennal length (mm)	0.9–1	0.80–0.83	0.64–0.66	1.2	0.61
Carapace, dorsal spine	Curved	Curved	Straight	Straight	Curved
Carapace, ventrolateral setae†	1	1	2	1–2	2
Antenna, spinous process	Spinulated	Spinulated	Spinulated	Not spinulated	Not spinulated
Antenna, exopod	Spinulated	Spinulated	Spinulated	Not spinulated	Not spinulated
Mxpd II, endopod (s)	0,0,1 + 3	0,0,1 + 3	0,0,1 + 3	0,0,1 + 4	0,0,1 + 3
Telson, furca	Spinulated	Spinulated	Spinulated	Spinulated	Not spinulated
ZOEA II					
Carapace length (mm)	1.19 (1.1–1.2)*	0.9	—	0.8–0.9	0.85
Dorsal spine length (mm)	0.89	0.80–0.82	—	1.1–1.2	0.92
Antennal length (mm)	1.05 (1.1–1.2)*	0.87–0.89	—	1.3–1.4	0.81
Antenna, spinous process	Spinulated	Spinulated	—	Not spinulated	Not spinulated
Antenna, exopod	Spinulated	Spinulated	—	Not spinulated	Not spinulated
Maxillule, exopodal seta	0	1	—	0 (1)‡	0
Maxillule, coxa (s)	7	7	—	7 (9)§	7
Maxilla, scaphognathite (s)	17–20	17	—	16	17
Mxpd II, basis (s)	0	0	—	0 (1)§	1
Abdomen, 1st somite (s)	2 (0)**	0	—	0	0
Telson, furca	Spinulated	Spinulated	—	?	Not spinulated
MEGALOPA					
Total length (mm)	2.5	2.16	—	—	—
Carapace length (mm)	1.14 (1.5)*	1.10–1.15	—	1.2–1.3	1.0
Carapace width (mm)	0.98	0.78–0.82	—	—	0.78
Antenna, 2nd seg. peduncle (s)	1	0	—	0	1
Maxilla, endopod (s)	0	1	—	1	1
Maxilla, scaphognathite (s)	23–26	23–24	—	18–19	19–20
Mxpd I, coxa (s)	5	5	—	4	4
Mxpd I, basis (s)	9	11	—	9–10	10
Cheliped, merus spine	Large	Large	—	Small	Small
Abdomen, 5th somite (s)	4	4	—	6	6

suggesting they are larvae of *M. parva* and not intraspecific variations of *M. rostrata*.

As in the zoeal stages, the megalopa stage of *M. parva* closely follows the morphological pattern that is typical of the genus. Thus, megalopae of *Macropodia* can be characterized by this combination of features: an obtuse rostrum, the absence of orbital spines, a pair of obtuse protogastric processes, an obtuse cardinal spine, pereopods without coxal spines,

an abdomen with five somites, four pairs of pleopods, and an antenna consisting of eight articles. Rice (1988) noted the importance of the antenna as a conservative structure for phylogenetic studies. This also applies to *Macropodia*, which is distinct in having a 4-segmented flagellum with four setae each on the middle and distal segment. Other majid species with a 4-segmented flagellum bear a naked second segment.

Guerao and Abelló (1997) noted that the megalopa

of *M. tenuirostris* shows many affinities to that of *M. longipes*. They are similar in size, present a small ischial spine on the chela and a long proximal meral spine. The scaphognathite bears 23–26 marginal setae, the coxa of the first maxilliped bears five setae, and the fifth abdominal somite bears four setae. However, the megalopa of *M. tenuirostris* can be distinguished from that of *M. longipes* in having only one seta on the basal segment of protopod of the antenna, nine setae on the basis of the second maxilliped, and by the absence of setae on the endopod of the maxilla. Until now this last feature was exclusive to the megalopa of *M. rostrata*. Similarly, we can note that megalopae of *M. rostrata* and *M. parva* closely resemble each other by having a seta on the endopod and 18–20 setae on the scaphognathite of the maxilla, four setae on the coxal endite of the first maxilliped, a small proximal meral spine, and the fifth abdominal somite bearing six setae. Distinguishing between the two species is complicated and may only be possible based on the presence of a seta on the second segment of the antennal peduncle in *M. parva*.

As in *M. longipes* and *M. tenuirostris*, similar morphological characteristics of adults and larval stages of *M. rostrata* and *M. parva* indicate that these species are very closely related phylogenetically. Furthermore, in the Gulf of Cádiz, these species coexist in the same habitat. These combined features suggest that they may be subspecies. Recent advances in molecular taxonomy based on DNA sequences applied to these species could help to shed light on this question.

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