Varunidae H. Milne-Edwards, 1853, and Ocypodidae Rafinesque, 1815

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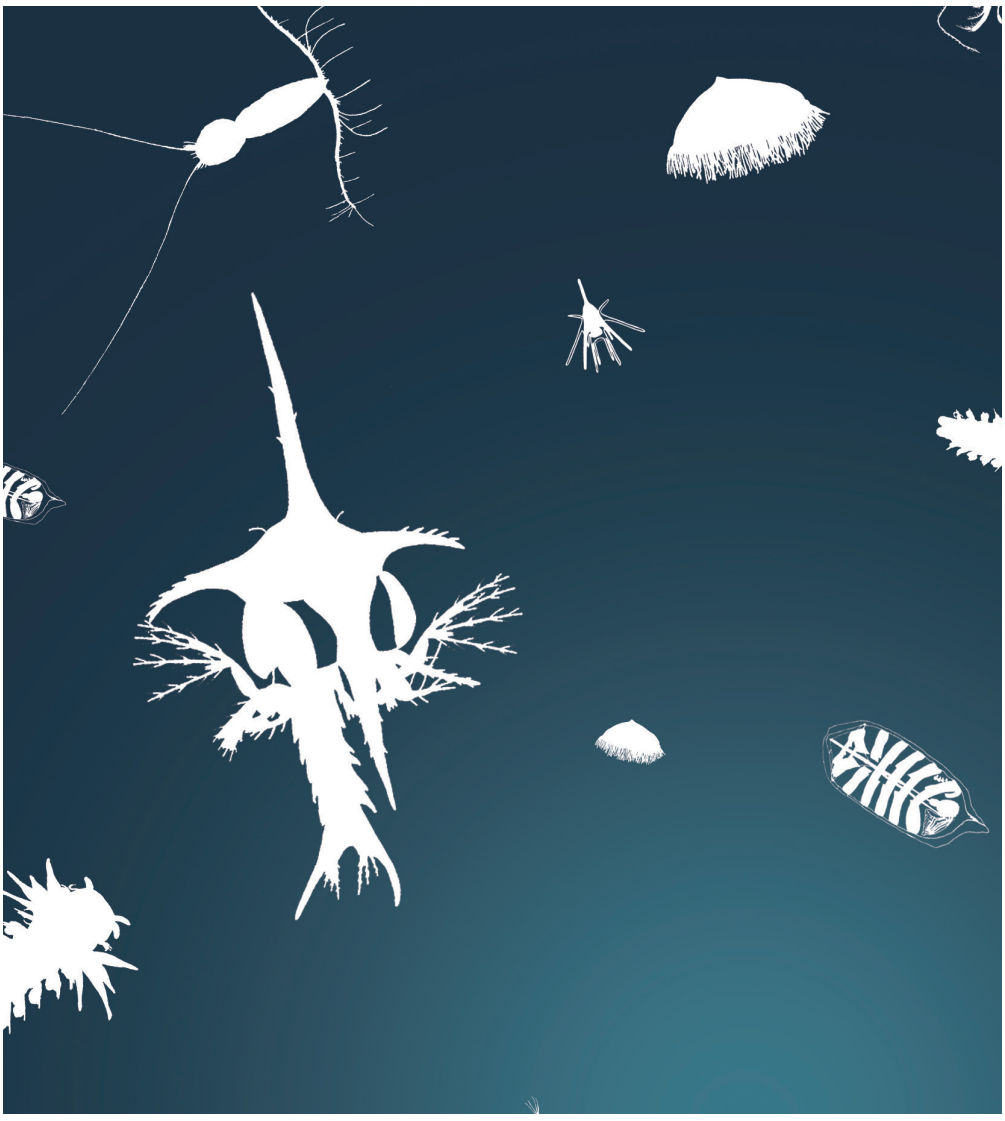

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Contents

Decapoda

Infraorder: **Brachyura**

Section: **Eubrachyura**

Subsection: **Thoracotremata**

Families: **Varunidae H. Milne-Edwards, 1853, and Ocypodidae Rafinesque, 1815**

Author: Jose A. Cuesta and Juan Ignacio González-Gordillo

1 Summary

Varunids and ocypodids are Thoracotremata crabs inhabiting tropical and temperate seas worldwide. The adult forms are mainly semi-terrestrial (e.g. *Ocypode*, *Leptuca*, *Minuca*) and intertidal (e.g. *Hemigrapsus*, *Cyclograpsus*, *Gaetice*), although there are also some catadromous species (e.g. *Eriocheir*). Larval development is always linked to the sea. Varunidae comprises 160 species, and larval stages are known for 38 of them. For Ocypodidae, data exists on larval stages for 27 out of the 138 described species. In both groups, a combination of larval features exists that allows distinction at a familial level. This leaflet presents the known larval stages of the 11 species, 6 varunids and 5 ocypodids, distributed in ICES area: *Asthenognathus atlanticus*, *Brachynotus atlanticus*, *B. sexdentatus*, *Eriocheir sinensis*, *Hemigrapsus sanguineus*, *H. takanoi*, *Leptuca pugilator*, *Minuca minax*, *M. pugnax*, *Afruca tangeri*, and *Ocypode quadrata*. The leaflet includes a key to identify zoea and megalopa stages of these species, with some exceptions where no accurate morphological characters are present which would allow clear distinction.

2 Introduction

Families Varunidae and Ocypodidae belong to the brachyuran subsection Thoracotremata Guinot, 1977. Varunidae was considered a subfamily, Varuninae, of the former family Grapsidae MacLeay, 1838. However, after the works of Schubart *et al.* (2000, 2002), it was elevated to family level based on larval morphology and molecular data. Later, Ng *et al*. (2008) placed Asthenognathinae in Varunidae after it was removed from Pinnotheridae De Haan, 1833, based on larval morphology, molecular data, and re-examination of adult morphology.

Regarding Ocypodidae, Shih *et al*. (2016) recently made a systematic review of the family based on molecular data, and considered three subfamilies: Gelasiminae, Ocypodinae, and Ucidinae. Moreover, they proposed a new arrangement of genera, recognizing *Afruca* as a valid genus.

Listed below are the species belonging to the families Varunidae and Ocypodidae, which are currently recorded in ICES area. The taxonomic status is according to WoRMS (2019):

Order Decapoda

Family Varunidae H. Milne Edwards, 1853

Subfamily Asthenognathinae Stimpson, 1858

Asthenognathus atlanticus Monod, 1933

Subfamily Varuninae H. Milne Edwards, 1853

Brachynotus atlanticus Forest, 1957

Brachynotus sexdentatus (Risso, 1827)

Eriocheir sinensis H. Milne Edwards, 1853

Hemigrapsus sanguineus (De Haan, 1835)

Hemigrapsus takanoi Asakura and Watanabe, 2005

Family Ocypodidae Rafinesque, 1815

Subfamily Gelasiminae Miers, 1886

Leptuca pugilator (Bosc, 1802)

Minuca minax (LeConté, 1855)

Minuca pugnax (Smith, 1870)

Subfamily Ocypodinae Rafinesque, 1815

Afruca tangeri (Eydoux, 1835)

Ocypode quadrata (Fabricius, 1787)

Please note that the previous European records of the invasive crab *Hemigrapsus penicillatus* (see Noël *et al.* 1997; Gollasch 1999; and others) have been reassigned to the sibling species *H. takanoi*, according to Geburzi *et al*. (2015).

3 Distribution

Asthenognathus atlanticus

Adult habitat: muddy fine sand to mud; on echinoids and commensal with polychaetes (Manning and Holthuis, 1981); from the intertidal zone down to 210 m depth (Glémarec and Hily, 1979; d'Udekem d'Acoz, 1999).

ICES area distribution: English Channel, Bay of Biscay and Galicia (d'Udekem d'Acoz, 1999; Jourde *et al*., 2012).

Worldwide distribution: Northeast Atlantic to Angola (Manning and Holthuis, 1981); Mediterranean – Alboran Sea, Banyuls-sur-Mer (d'Udekem d'Acoz, 1999), and Algeria (Glémarec and Hily, 1979; Grimes *et al*., 2016).

Brachynotus atlanticus

Adult habitat: sandy substrata with pebbles; intertidal rocky shores.

ICES area distribution: Gulf of Cadiz (González-Gordillo *et al*., 1990).

Worldwide distribution: Northeast Atlantic to Morocco, Sahrawi Republic,

and Mauritania (Forest, 1957; d'Udekem d'Acoz, 1999); Mediterranean – Alboran Sea (García-Raso, 1984).

Brachynotus sexdentatus

Adult habitat: muddy and sandy bottoms with pebbles; from intertidal zone to 10 m (Ateş, 1999).

ICES area distribution: Bay of Biscay (Nöel *et al*., 1997), Gulf of Cadiz (González-Gordillo *et al*., 1990), and Swansea (UK; Naylor, 1957), but extinct in the UK, according to Clark (1986).

Worldwide distribution: Northeast Atlantic; Mediterranean – Alboran Sea and spanish mediterranean coast (Marco-Herrero *et al*., 2015), Adriatic, Ionian and Aegean Seas, and the coast of Israel and Egypt; Black Sea (d'Udekem d'Acoz, 1999).

Eriocheir sinensis

Adult habitat: catadromous species – juvenile and adult stages live in estuaries and upstream of rivers. Females migrate to brackish waters for reproduction, and larval development takes place in the sea. Megalopae return to estuaries.

ICES area distribution: species has been introduced to ICES area. It can be found along the coasts of the English Channel, North Sea, and Baltic Sea (d'Udekem d'Acoz, 1999), Seine and the Gironde estuaries in France (Vincent, 1996; Herborg *et al*., 2003), Tagus river in Portugal (Cabral and Costa, 1999), and Miño and Guadalquivir rivers in Spain (Ferdinand-Martinez and Carrera, 2003; Cuesta *et al*., 2006).

Worldwide distribution: native to the east coast of China, from Hong Kong to North Korea (Hymanson *et al*., 1999). Invasive species in North America, in St Lawrence River and Ontario, Canada (Poore, 2004; de Lafontaine, 2005), San Francisco Bay (Rudnick *et al*., 2003, 2005), Chesapeake Bay (Ruiz *et al*., 2006), Lake Erie (Nepszy and Leach, 1973), and Hudson River (Schmidt *et al*., 2009). In Asia it has been found in the Tazeh Bekandeh River in northern Iran (Robbins *et al*., 2006), Lake Ladoga in Russia (Panov, 2006), and Shatt Al-Basrah Canal in Iraq (Clark *et al*., 2006).

Hemigrapsus sanguineus

Adult habitat: intertidal coastal and estuarine habitats, exposed rocky shores, sand and gravel substrata, commonly occupying habitats with high hydrodynamics (Dauvin *et al*., 2009).

ICES area distribution: species has been introduced to ICES area. It can be found along the coastline from the English Channel to the North Sea (Epifanio, 2013). Other intermediate locations are listed in Dauvin *et al*. (2009).

Worldwide distribution: native to Japan, Korean Peninsula, Taiwan, and China. Invasive species from Maine to North Carolina (NW Atlantic), English Channel to the North Sea (NE Atlantic; Epifanio, 2013); and Croatia (Mediterranean; Schubart, 2003).

Hemigrapsus takanoi

Adult habitat: intertidal and subtidal substrata of gravel, sand, oyster beds, and under boulders and rocks; commonly occupying habitats with low hydrodynamics (Dauvin *et al*., 2009; Miyajima and Wada, 2017).

ICES area distribution: species has been introduced to ICES area; from

Laredo (Spain; Noël, 1997) to the western Baltic Sea (Geburzi *et al*., 2015), including the south coast of England (Ashelby *et al*., 2017). Invasive species in France, The Netherlands, Belgium, and the UK (Wood *et al*., 2015).

Worldwide distribution: native to inner bays and estuaries of East Asia from the coast of the Russian Far East (Marin, 2013) to the Korean Peninsula (Lee *et al*., 2013) and Japan (Asakura and Watanabe, 2005).

Leptuca pugilator

Adult habitat: sandy and muddy beaches bordering marshes, along banks of tidal creeks, and in marshes with *Salicornia* (Williams, 1984).

ICES area distribution: USA – Cape Cod to North Carolina (Williams, 1984).

Worldwide distribution: western Atlantic, from Cape Cod to Pensacola (Florida), in The Bahamas, and in Santo Domingo (Crane, 1975; Williams, 1984).

Minuca minax

Adult habitat: muddy substrata of marshes, and sandy mud with phanerogams and high organic content (Gray, 1942; Kerwin, 1971).

ICES area distribution: USA – Cape Cod to North Carolina (Williams 1984).

Worldwide distribution: western Atlantic, to Matagorda (Texas; Williams, 1984).

Minuca pugnax

Adult habitat: muddy marsh environments.

ICES area distribution: USA, Provincetown (Massachusetts) to Hampton (New Hampshire; Johnson, 2014).

Worldwide distribution: Northwest Atlantic, to Florida (Johnson, 2014).

Afruca tangeri

Adult habitat: intertidal to 5 m; soft habitats with muddy or sandy-muddy substrata and high organic content, sometimes partially covered by the cordgrass *Spartina maritima* or *Salicornia*.

ICES area distribution: restricted to Gulf of Cadiz (Zariquiey Álvarez, 1968; González-Gordillo *et al*., 1990) and Mira estuary (southwestern Portugal; Lourenço *et al*., 2000).

Worldwide distribution: eastern Atlantic, to southern Angola (Manning and Holthuis, 1981), the archipelagoes of São Tomé and Príncipe (Forest and Guinot, 1966), and Cape Verde (Monod, 1956).

Ocypode quadrata

Adult habitat: supralittoral, along the ocean and harbour sandy beaches.

ICES area distribution: USA, from Rhode Island to North Carolina (Williams, 1984).

Worldwide distribution: western Atlantic coast, Massachusetts to Rio Grande do Sul (Brazil), including the Bermudas, Jamaica and Fernando de Noronha archipelago (Brazil; Williams, 1984).

4 Number and general morphology of larval stages

The larval development of crabs of the Varunidae and Ocypodidae families comprises two consecutive phases: zoea and megalopa (decapodid), like that of almost all Brachyura. Zoeal stages are characterized by a globose carapace with conspicuous dorsal and rostral spines, maxillipeds with long distal setae that are used for swimming, and a pleon with 5–6 segments that ends in a fork-shaped telson. Both Varunidae and Ocypodidae comprise 5 zoeal stages (ZI–ZV) in their life cycle. The first three stages lack pleopods and carry 4, 6, and 8 distal natatory setae on the exopod of the first and second maxillipeds, respectively. The fourth stage shows uniramous (buds) pleopods and 10 natatory setae on the exopod of the first and second maxillipeds (although some ocypodids can show only 8–9 setae). The last zoeal stage (ZV) shows well developed biramous pleopod buds and 10–13 natatory setae (generally 12 setae) on the first and second maxillipeds. Megalopae of both families have a morphology similar to juvenile crabs, with a depressed carapace, 5 well developed pereiopod pairs (first chelate) and the pleon provided with pleopods that allow them to move in the water column. Species of both families only present one stage of megalopa before the metamorphosis to juvenile.

Larval diagnostic features for Varunidae

Characteristics of the zoeal stages:

i) Presence of dorsal, rostral, and lateral spines on the carapace.

ii) Antennal exopod well developed with medial setae, generally similar in size or longer than protopod.

iii) Maxillule with setation pattern 1, 5 on the endopod.

iv) Maxilla with setation pattern 2 + 2 on the endopod, and zoea I with 4 + 1 marginal setae on the exopod (scaphognatite).

v) Maxilliped I basis with 2 + 2 + 3 + 3 setae, zoea I with 2, 2, 1, 2, 5 setae on the endopod.

vi) Maxilliped II basis with 1 + 1 + 1 + 1 setae, and 0, 1, 6 setae on the endopod.

vii) Pleon without lateral expansions or distolateral processes on pleonite 5.

viii) Telson furcated with median notch, and furcal rami unarmed.

ix) Dorsolateral knobs on pleonites 2, 2, and 3 or 2–4.

Characteristics of the megalopa stage:

i) Antennular endopod present.

ii) Antenna with 10 segments.

iii) Mandibular palp setation: 0, 5–13.

iv) Scaphognatite with 39–90 marginal setae.

v) Epipod present in the second maxilliped.

vi) Pleopods with 3 cincinnuli.

vii) Uropod setation: 1, 8–13.

Larval diagnostic features for Ocypodidae

Characteristics of the zoeal stages:

i) Presence of dorsal and rostral spines on the carapace. Lateral spines can be absent or present. Dorsal spine smaller than the height of the carapace (although not conspicuous in *Afruca tangeri*, according to Rodríguez and Jones, 1993) and distinctly curved backwards.

ii) Antennal exopod well developed with terminal setae, not reaching the end of protopod.

iii) Maxillule with setation pattern 0, 4 on the endopod.

iv) Maxilla with setation pattern 1 + 2 on the endopod, and zoea I with 4 + 1 marginal setae on the exopod (scaphognatite).

v) Maxilliped I basis with 2 + 2 + 3 + 2–3 setae, zoea I with 2, 2, 1, 2, 5 setae on the endopod.

vi) Maxilliped II basis with 1 + 1 + 1 + 1 setae and 0, 0, 5 setae on the endopod.

vii) Pleon with or without lateral expansions and distolateral processes on pleonite 5.

viii) Dorsolateral knobs on pleonites 2 and 3.

ix) Telson furcated with median notch. Furcal rami with or without dorsal and lateral spines.

Characteristics of the megalopa stage:

i) Antennular endopod present.

ii) Antenna with 10 segments.

iii) Mandibular palp setation: 0, 0, 7 (*A. tangeri*) or 2, 18 (*O. quadrata*).

iv) Scaphognatite with 60–70 marginal setae.

v) Epipod present in the second maxilliped.

vi) Uropod setation: 1, 12 (*A. tangeri*) or 6, 26 (*O. quadrata*).

Selected references

- ***Asthenognathus atlanticus***: under previous scientific name *Tritodynamia atlantica*; Bocquet (1965), partial description of larval stages (ZI–ZV + M) reared in the laboratory.
- ***Brachynotus atlanticus***: Rodríguez *et al*. (1992), complete description of larval stages (ZI–ZV + M) reared in the laboratory.
- ***Brachynotus sexdentatus***: Cuesta *et al*. (2000), complete description of larval stages (ZI–ZV + M) reared in the laboratory.
- ***Eriocheir sinensis***: Kim and Hwang (1995), complete description of larval stages (ZI–ZV + M) reared in the laboratory; Kamanli *et al*. (2018), complete description of larval stages (ZI–ZV + M) reared in the laboratory.
- ***Hemigrapsus sanguineus***: Hwang *et al*. (1993), complete description of larval stages (ZI–ZV + M) reared in the laboratory.

- ***Hemigrapsus takanoi***: Landeira *et at*. (2019), complete description of larval stages (ZI–ZV + M) reared in the laboratory.
- ***Afruca tangeri***: under previous scientific name *Uca tangeri*; Rodríguez and Jones (1993), complete description of larval stages (ZI–ZV + M) reared in the laboratory; Spivak and Cuesta (2009), larval description of the extra-stage ZVI, reared in the laboratory.
- ***Leptuca pugilator***: under previous scientific name *Gelasimus pugilator*; Hyman (1920), description of larval stages (ZI–ZII) reared in the laboratory; ZIII–ZV and megalopa described from planktonic specimens.
- ***Minuca minax***: under previous scientific name *Gelasimus minax*; Hyman (1920), description of larval stages (ZI–ZII) reared in the laboratory; ZIII–ZV and megalopa described from planktonic specimens.
- ***Minuca pugnax***: under previous scientific name *Gelasimus pugnax*; Hyman (1920), description of larval stages (ZI–ZII) reared in the laboratory; ZIII–ZV and megalopa described from planktonic specimens.
- ***Ocypode quadrata***: Díaz and Costlow (1972), complete description of larval stages (ZI–ZV + M) reared in the laboratory.

5 Taxonomic key

Zoeal stages

1. Antennal exopod short, smaller than half of the protopod, with terminal setae (Figure 2d)…… **2**
Antennal exopod well developed, longer than half of the protopod, with medial setae (Figure 5b)……. **4**

2. Carapace lateral spines absent (Figure 7a)…… ***Leptuca pugilator, Minuca pugnax, Minuca minax****
Carapace lateral spines present (Figure 2a, 6b)…….. **3**

3. Pleonite 4 laterally expanded, telson furcae not longer than telson plate (Figure 2c)……. ***Ocypode quadrata***
Pleonite 4 not expanded laterally, telson furcae longer than telson plate (Figure 6c)……..... ***Afruca tangeri***

4. Dorsolateral knobs present on pleonite 2 (Figure 3a)…… ***Brachynotus atlanticus***
Dorsolateral knobs present on other pleonites…….. **5**

5. Dorsolateral knobs present on other pleonites 2-4 (Figure 8)…….. ***Eriocheir sinensis***
Dorsolateral knobs present on pleonites 2-3 (Figure 1a, 5a)……..... **6**

6. Carapace dorsal spine longer than rostral spine and recurved (Figure 1a)……...
…….. ***Asthenognathus atlanticus***
Carapace dorsal spine not longer than rostral spine, straight or slightly recurved…… **7**

7. Carapace dorsal spine straight and twice longer than carapace height
……..……. ***Brachynotus sexdentantus***

Carapace dorsal spine slightly curved and slightly longer than carapace height…… ***Hemigrapsus sanguineus, H. takanoi*****

Megalopa stage

1. Uropod basal segment without setae (Figure 9b)…….. ***Asthenognathus atlanticus***
Uropod basal segment with setae (Figure 10c, 11a, 14b)...…… **2**

2. Uropod basal segment with 2 or more setae……... **3**
Uropod basal segment with 1 seta (Figure 11a)…….. **4**

3. Uropod basal segment with 2 setae (Figure 14b)……. ***Eriocheir sinensis***
Uropod basal segment with 6 setae (Figure 10c)……. ***Ocypode quadrata***

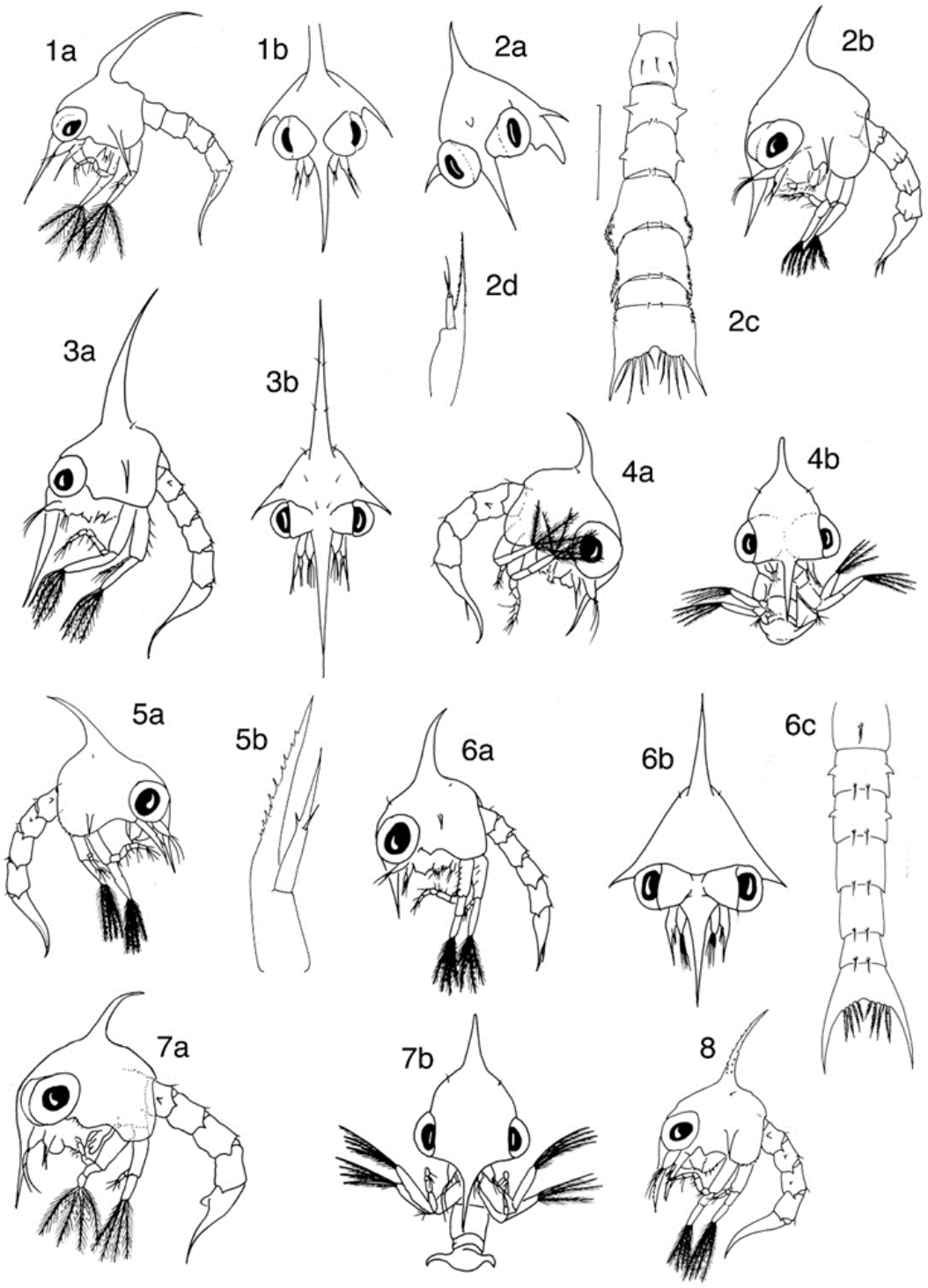
4. Setae of antennal flagellum segment 5 long and overlapping setae of terminal segment (Figure 12b)……... **5**
Setae of antennal flagellum segment 5 long but no overlapping setae of terminal segment…… ***Afruca tangeri***

5. Uropod distal segment with 9 setae (Figure 12c)…… **6**
Uropod distal segment with 10-12 setae (Figure 13b)…… **7**

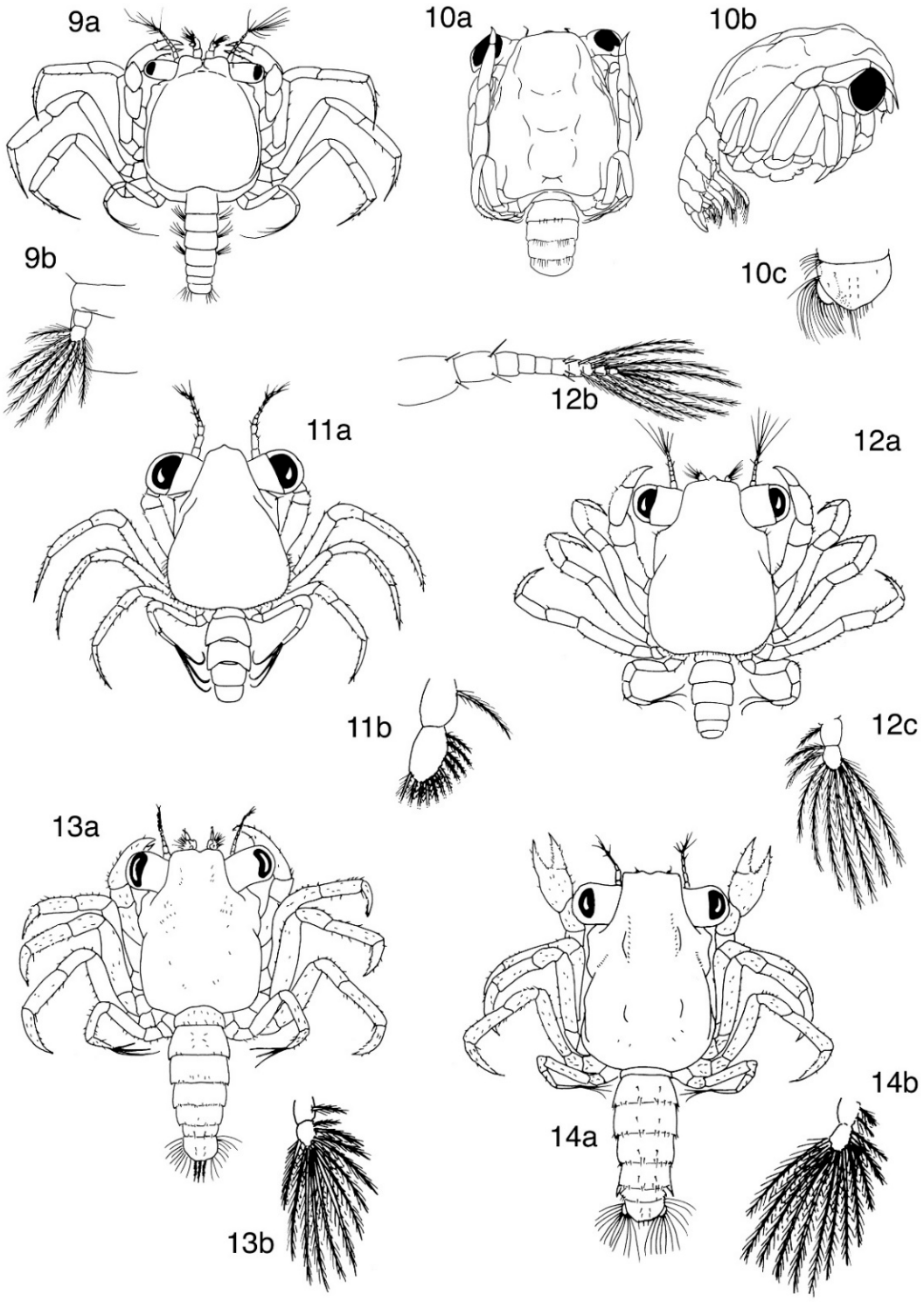
6. Mandibular palp setation: 0, 0, 8……..... ***Brachynotus atlanticus***
Mandibular palp setation: 0, 0, 9……. ***Brachynotus sexdentatus***

7. Uropod distal segment with 10 setae……..... ***Hemigrapsus takanoi***
Uropod distal segment with 11-12 setae (Figure 13b)…….. ***Hemigrapsus sanguineus****

6 Figures



Figures 1–8. General morphology of Varunidae and Ocypodidae zoeal larval stages 1. ***Asthenognathus atlanticus,*** **1a. lateral view (ZI), 1b. frontal view (ZI); 2.** ***Ocypode quadrata,*** **2a. frontal view (ZI), 2b. lateral view (ZI), 2c. pleon (ZIII), 2d. antenna (ZI); 3.** ***Brachynotus atlanticus,*** **3a. lateral view (ZI), 3b. frontal view (ZIII); 4.** ***Minuca minax,*** **4a. lateral view (ZI), 4b. frontal view (ZI); 5.** ***Hemigrapsus sanguineus,*** **5a. lateral view (ZI), 5b. antenna (ZI); 6.** ***Afruca tangeri,*** **6a. lateral view (ZI), 6b. frontal view (ZII), 6c. pleon (ZIII); 7.** ***Leptuca pugilator,*** **7a. lateral view (ZI), 7b. frontal view (ZI); 8.** ***Eriocheir sinensis,*** **lateral view (ZI). All figures redrawn from: 1. Bocquet (1965) as** ***Tritodynamia atlantica*****; 2. Díaz and Costlow (1972); 3. Rodríguez** ***et al.*** **(1992); 4. Hyman (1920) as** ***Gelasimus minax*****; 5. Hwang** ***et al.*** **(1993); 6. Rodríguez and Jones (1993) as** ***Uca tangeri*****; 7. Hyman (1920) as** ***Gelasimus pugilator*****; 8. Kim and Hwang (1995). Drawings not to scale.**



Figures 9–14. General morphology of Varunidae and Ocypodidae megalopa larval stage: 9. *Asthenognathus atlanticus*, 9a. dorsal view, 9b. right uropod; 10. *Ocypode quadrata*, 10a. dorsal view, 10b. lateral view, 10c. left uropod and telson; 11. *Afruca tangeri*, 11a. dorsal view, 11b. uropod; 12. *Brachynotus atlanticus*, 12a. dorsal view, 12b. antenna, 12c. uropod; 13. *Hemigrapsus sanguineus*, 13a. dorsal view, 13b. uropod; 14. *Eriocheir sinensis*, 14a. dorsal view, 14b. uropod. All figures redrawn from: 9. Bocquet (1965) as *Tritodynamia atlantica*; 10. Díaz and Costlow (1972); 11. Rodríguez and Jones (1993) as *Uca tangeri*; 12. Rodríguez *et al*. (1992); 13. Hwang *et al*. (1993); 14. Kim and Hwang (1995). Drawings not to scale.

7 Links to further information

WoRMS

Asthenognathus atlanticus	http://www.marinespecies.org/aphia.php?p=taxdetails&id=107468
Brachynotus atlanticus	http://www.marinespecies.org/aphia.php?p=taxdetails&id=107447
Brachynotus sexdentatus	http://www.marinespecies.org/aphia.php?p=taxdetails&id=107450
Eriocheir sinensis	http://www.marinespecies.org/aphia.php?p=taxdetails&id=107451
Hemigrapsus sanguineus	http://www.marinespecies.org/aphia.php?p=taxdetails&id=158417
Hemigrapsus takanoi	http://www.marinespecies.org/aphia.php?p=taxdetails&id=389288
Afruca tangeri	http://www.marinespecies.org/aphia.php?p=taxdetails&id=955160
Leptuca pugilator	http://www.marinespecies.org/aphia.php?p=taxdetails&id=955239
Minuca minax	http://www.marinespecies.org/aphia.php?p=taxdetails&id=955266
Minuca pugnax	http://www.marinespecies.org/aphia.php?p=taxdetails&id=955270
Ocypode quadrata	http://www.marinespecies.org/aphia.php?p=taxdetails&id=158432

Molecular information

Selected 16S and COI DNA barcode sequences of the species from the families Varunidae and Ocypodidae present in ICES area. In the cases where several sequences existed for the same species, links are presented for all sequences, and for selected 16S and COI DNA barcode sequences. The selection was performed based on the following criteria when several sequences existed for the same species: (i) most recent and/or longest sequence, (ii) the sequence included in previous phylogenetic studies, and (iii) testing by BLAST. All 16S and COI DNA barcode sequences are adopted from Genbank and were tested by BLAST.

Asthenognathus atlanticus	https://www.ncbi.nlm.nih.gov/nuccore/241993774
Brachynotus atlanticus	https://www.ncbi.nlm.nih.gov/nuccore/27524884
Brachynotus sexdentatus	https://www.ncbi.nlm.nih.gov/nuccore/?term=txid135464[Organism:noexp]
16S sequence	https://www.ncbi.nlm.nih.gov/nuccore/AJ278832
Eriocheir sinensis	https://www.ncbi.nlm.nih.gov/nuccore/?term=txid95602[Organism:noexp]

16S sequence	https://www.ncbi.nlm.nih.gov/nuccore/AF105243
COI sequence	https://www.ncbi.nlm.nih.gov/nuccore/MG935182
Hemigrapsus sanguineus	https://www.ncbi.nlm.nih.gov/nuccore/?term=txid40176[Organism:noexp]
16S sequence	https://www.ncbi.nlm.nih.gov/nuccore/GU731425
COI sequences	https://www.ncbi.nlm.nih.gov/nuccore/KX579065 https://www.ncbi.nlm.nih.gov/nuccore/KX579066
Hemigrapsus takanoi	https://www.ncbi.nlm.nih.gov/nuccore/?term=txid764359[Organism:noexp]
16S sequence	https://www.ncbi.nlm.nih.gov/nuccore/AJ278835
COI sequence	https://www.ncbi.nlm.nih.gov/nuccore/KT209537
Afruca tangeri	https://www.ncbi.nlm.nih.gov/nuccore/?term=txid53281[Organism:noexp]
16S sequence	https://www.ncbi.nlm.nih.gov/nuccore/AB813666
COI sequence	https://www.ncbi.nlm.nih.gov/nuccore/LC150399
Leptuca pugilator	https://www.ncbi.nlm.nih.gov/nuccore/?term=txid6772[Organism:noexp]
16S sequences	https://www.ncbi.nlm.nih.gov/nuccore/Z79659 https://www.ncbi.nlm.nih.gov/nuccore/Z79660 https://www.ncbi.nlm.nih.gov/nuccore/Z79661 https://www.ncbi.nlm.nih.gov/nuccore/Z79662
COI sequence	https://www.ncbi.nlm.nih.gov/nuccore/MK308325
Minuca minax	https://www.ncbi.nlm.nih.gov/nuccore/?term=txid504420[Organism:noexp]
16S sequence	https://www.ncbi.nlm.nih.gov/nuccore/LC150350
COI sequences	FJ693516-693560 (sequence code range)
Minuca pugnax	https://www.ncbi.nlm.nih.gov/nuccore/?term=txid53306[Organism:noexp]
16S sequences	https://www.ncbi.nlm.nih.gov/nuccore/LC087924

	https://www.ncbi.nlm.nih.gov/nuccore/LC087925
COI sequences	https://www.ncbi.nlm.nih.gov/nuccore/LC087954
	https://www.ncbi.nlm.nih.gov/nuccore/LC087955
Ocypode quadrata	https://www.ncbi.nlm.nih.gov/nuccore/?term=txid53310[Organism:noexp]
16S sequences	MG805665-805798 (sequence code range)
COI sequences	KY568729-568760 (sequence code range)

8 Terminology

The explanation of the terminology has been taken, with modifications, from Ingle (1992), Martin *et al*. (2014), and Clark and Cuesta (2015). Terminology descriptions are modified according to brachyuran larval morphology.

Antenna Second pair of cephalic appendages, involved in sensory perception. Antennae can be absent. When present, it can be formed by a protopod, endopod, and exopod (not always) with different degree of development (according to larval stage and taxonomical position).

Antennule First pair of cephalic appendages, involved in chemosensory perception. In zoeal stages, it is a uniramous biflagellated appendage that presents a primary flagellum (bearing aesthetascs and setae) and an accessory flagellum (can be absent in the first stages and appears as a bud in subsequent stages). In the megalopa larval stage, it includes a basal segmented peduncle. The primary flagellum is annulated and the accessory flagellum (when present) bears setae.

Basis Second segment of the larval appendages. Endites are present in the maxillar basis.

Carapace Layer covering cephalon and thorax of zoea and megalopa larvae. Rostral, dorsal, and lateral spines can be present in zoea.

Coxa First segment of the larval appendages. Endites are present in the maxillar coxa.

Endite Lobes in the basis and coxa of the maxilla, bearing setae and/or spines.

Mandible Third pair of cephalic appendages, involved in the mastication of food. Mandibles are present from the first zoeal stage with two main functions: incisor and molar. An endopod palp bud appears in the last zoeal stages. In the megalopa stage, the endopod palp is segmented with setation, and the incisor and molar portions of the mandible can no longer be distinguished.

Maxilla Fifth pair of cephalic appendages, belonging to the mouthparts, and involved in feeding. It consists of a protopod (with coxal and basial endites), an endopod (unsegmented, but it can be bilobed), and an exopod (scaphognathite).

Maxilliped Three pairs of thoracic appendages. In the zoeal phase, the first two pairs are used for swimming, while the third pair is only present as a bud in the last stages. In the megalopa stage, all three pairs are mouthparts.

Maxillule The fourth pair of cephalic appendages, belonging to the mouthparts involved in feeding. It consists of a protopod (with coxal and basial endites), an endopod (segmented), and an exopod (absent in first zoea, present as a plumose seta in subsequent stages, and well developed and segmented in the megalopa).

Megalopa Last larval stage, characterized by the utilization of the pleopods for motility (swimming activity). It is a transitional stage between the planktonic zoeal phase and the benthonic juvenile stages. The pereiopods are developed and functional, and are primarily used to catch or capture prey items, instead of motility.

Pereiopod Thoracic appendages. In the first zoeal stages pereiopods are absent. In the last stages they are present as non-functional buds with the first pair bilobed (= chelipeds). Pereiopods are well developed and functional in the megalopa stage, although not involved in motility.

Pleon Third body tagma composed of 5/6 segments, called pleonites, and a terminal portion called telson.

Pleonite Segment of the pleon. The first zoea stages posses 5 pleonites. The sixth pleonite can be present in the last larval stages, and is generally well developed in the megalopa phase, although in some species it is always absent. Pleonites II–V bear pleopod buds (non-functional) throughout the zoea phase, and are also present in the pleonite VI (functional) in the megalopa.

Pleopod Pleonal natatory appendages. Present as non-functional buds on pleonites II–V or VI during the zoea phase, and functional on pleonites II–VI in the megalopa phase. Pleopods of pleonites II–V are biramous, formed by a protopod (without setation), an exopod with a variable number of long natatory setae, and a small endopod with a variable number of cincinnuli (hocked setae). Cincinnuli are used to link the pair of pleopods of the same pleonite, allowing synchronical swimming. The fifth pair of pleopods on the sixth pleonite, called uropods, are uniramous (endopod absent), and setation can be present in the protopod and exopod (natatory setae).

Telson Terminal portion of the pleon. Different morphologies can be observed in the zoea phase depending on the taxonomical position. In the megalopa phase, the morphology is similar in all species, a plate-like quadrate with the posterior margin rounded (with a concave or convex shape).

Zoea First larval phase, with a variable number of stages (1–8). It is characterized by motility (swimming activity), using mouthpart appendages (maxillipeds). In the last stages, pereiopods and pleopods appear as non-functional buds with different degree of development.

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