Clausocalanus Giesbrecht, 1888

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Copepoda

Order: Calanoida
Family: Clausocalanidae Giesbrecht, 1893
Genus: *Clausocalanus* Giesbrecht, 1888

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1 Abstract

*Clausocalanus* is one of the most widespread and abundant genus of planktonic calanoid copepods in the world oceans. It is distributed in both coastal and offshore waters, and over a broad latitudinal range in both hemispheres. The core of each species and population is generally located in the epipelagic zone, but the vertical distribution of most species can extend down to meso- and bathypelagic zones. *Clausocalanus* species are smaller or only slightly larger than 1 mm in total length. The genus was thoroughly revised by Frost and Fleminger (1968). A previous ICES Identification leaflet for Plankton (No. 38; G. P. Farran, revised by W. Vervoort, 1951) covered three of the 13 described species of *Clausocalanus*. This new leaflet updates the previous two works, and presents taxonomic and ecological characteristics, along with results from molecular studies, on all 13 *Clausocalanus* species revised by Frost and Fleminger (1968).

2 Introduction

*Clausocalanus* is one of the most widespread genus of calanoid copepods worldwide, and is often a very abundant component of marine zooplankton communities. It is distributed in both coastal and offshore waters, and over a broad latitudinal range - from temperate, tropical and equatorial regions, to Subantarctic and Antarctic waters. It is most common in the epipelagic zone, where population cores generally occur. However, the vertical range of some species can extend down to meso- and bathypelagic layers. Most species are small, smaller or only slightly larger than 1 mm in total length. Males are generally smaller and much less abundant than females.

The biological traits of *Clausocalanus* have only been investigated for a few species. Data exists on respiration (Razouls, 1974; Paffenhöfer, 2006), feeding (Mazzocchi and Paffenhöfer, 1999; Isari and Saiz, 2011; Isari et al., 2014; Christou et al., 2017), reproduction (Mazzocchi and Paffenhöfer, 1998; Calbet et al., 2002; Cornils et al., 2007; Peralba et al., 2017), development (Bi and Benfield, 2006), and stage-specific mortality rates (Bi et al., 2011). Two spawning modes are present in the genus, with some species releasing the eggs into the water (*C. lividus*, *C. mastigophorus*, and *C. ingens*), and other species carrying the eggs in a sac or egg mass (*C. pergens*, *C. furcatus*, *C. arcuicornis*, and *C. jobei*; Saiz and Calbet, 1999; Peralba et al., 2017). This double mode of egg laying is a unique characteristic of *Clausocalanus* among Calanoida, with only two other possible exceptions reported for *Euaugaptilus* and *Chiridius* (Mauchline, 1998). *Clausocalanus* species are characterized by a particular swimming motion that is very fast and
convoluted, and is unique among small planktonic calanoids. This behaviour has been extensively analysed in *C. furcatus* individuals, but it also seems to be common among congeners (Mazzocchi and Paffenhöfer, 1998; Uttieri et al., 2008; Bianco et al., 2013). *Clausocalanus* species do not create typical feeding currents, but directly capture food particles that fall into a small frontal region of the copepod (Uttieri et al., 2008).

Developmental stages have been described so far only for *C. furcatus* (nauplii, Björnberg, 1972), *C. laticeps* and *C. brevipes* (copepodites I-V, Heron and Bowman, 1971).

The genus *Clausocalanus* was thoroughly and comprehensively revised by Frost and Fleminger (1968), who described five new species. The diagnosis and keys reported here are from that review, which remains the most complete text on *Clausocalanus* taxonomy. This leaflet presents the taxonomic and ecological characteristics of all 13 *Clausocalanus* species revised by Frost and Fleminger (1968). It should be noted that the following species have not been reported for the North Atlantic and the Mediterranean Sea: *C. brevipes*, *C. farrani*, *C. ingens*, *C. laticeps*, and *C. minor* (Wootten and Castellani, 2017).

The ICES Identification Leaflet for Plankton No. 38 on the copepod family *Pseudocalanidae* (= *Clausocalanidae*), authored by G. P. Farran and revised by W. Vervoort (1951), provided details on three *Clausocalanus* species (*C. arcuicornis*, *C. pergens* and *C. paululus*), together with the other three genera of the family (*Drepanopus*, *Drepanopsis* - now synonym of *Farrania*-, and *Ctenocalanus*).

The revision of the *Clausocalanus* genus by Frost and Fleminger (1968) was supported by Bucklin et al. (2003) and Bucklin and Frost (2009) based on mtCOI sequence variation between the 13 species of *Clausocalanus*. In addition, Blanco-Bercial and Alvarez-Marqués (2007) genetically differentiated *C. pergens*, *C. arcuicornis*, *C. jobei* and *C. lividus* in the Bay of Biscay (Cantabrian Sea) by developing a restriction fragment length polymorphism technique.

Molecular population genetic, phylogeographic and phylogenetic approaches have demonstrated genetic cohesion among populations of the cosmopolitan *C. arcuicornis*, while the Atlantic and Pacific Ocean populations of the biantitropical *C. lividus* are clearly differentiated (Blanco-Bercial et al., 2011).

In a study on DNA barcoding of marine copepods, Blanco-Bercial et al. (2014) reported “...all 13 described species of *Clausocalanus*, including multiple individuals from different ocean basins. All species clustered together in all analyses... . Interestingly, two individuals collected from Sagami Bay (Japan) and identified as *C. arcuicornis* Dana 1849 ... showed morphological oddities and were discriminated as a distinct clade with 12% or higher divergence from any of *C. arcuicornis* (or any other *Clausocalanus*) individuals. Since no intact individuals remained from the sample, a detailed morphological analysis cannot be done and we can only speculate that these individuals may represent either of two *Clausocalanus* that are incertae sedis (*C. latipes* T. Scott 1894 and *C. dubius* Brodsky 1950), or very divergent individuals of *C. arcuicornis*.”

**Diagnostic features of the genus *Clausocalanus* Giesbrecht, 1888**

*Clausocalanus* differs from other genera of the Clausocalanidae family by having the distal margin of basis of P3 ornamented with elaborate spinous processes (Boxshall and Halsey, 2004). Additional distinctive characteristics are:

i) Cephalosome and pedigerous segment 1 fused, pedigerous segments 4 and 5 fused
ii) Medial caudal seta short, located on dorsal surface of caudal ramus; lateral-most caudal seta reduced to a short, lateral spine; two apical and two subapical caudal setae long

iii) A1 segment 25 fused to distal posterior corner of segment 24

iv) Exopod of A2 1.5 or more times as long as endopod

v) Exopod of P1–P4 trimerous; endopod of P1 unimerous, of P2 bimerous, of P3 and P4 trimerous

vi) B2 of P2 and P3 broadening distally to about 1.5 or more times their width in region of attachment to B1; distal posterior margin with 3 or more spiniform processes.

**Female characteristics:**

i) Urosome of 4 somites

ii) Rostrum of 2 short, rigid spiniform processes

iii) A1 23-segmented with segments 8–9 and 24–25 fused

iv) Right and left P5 present, uniramous, trimerous, essentially symmetrical, distal segment produced distally into a short, pointed, bifid process.

**Male characteristics:**

i) Urosome of 5 somites

ii) Anal somite very short

iii) Rostrum single, median, knoblike, and protruding ventrally in all species except C. furcatus, which does not have a well-developed rostrum

iv) A1 with segments 1–2, 8–9, 13–14, 15–16, 20–21, and 24–25 completely fused, and with incomplete fusion of segments 4 to 8–9, 8–9 to 13–14, and 13–14 to 15–16.

v) Right and left P5 present, uniramous, rami of very unequal length, longer ramus somewhat styliform, pentamerous, 5th segment short and attached subapically to 4th segment; in all species except C. furcatus, longer ramus of P5 and genital pore always on left side (in C. furcatus usually on right side).

### 3 Distribution

The distribution of *Clausocalanus* species in the northern sector of the Atlantic Ocean was described by Williams and Wallace (1975), and was updated at the genus level by the Continuous Plankton Recorder Survey Team (2004, Figure 150), and by Wootton and Castellani (2017, map on page 308). *Clausocalanus* has been described in the eastern subtropical/tropical regions (Schnack-Schiel *et al.*, 2010) and along the Atlantic Meridional Transect, where the ecological niches and reproductive traits of eleven species were analysed (Peralba *et al.*, 2017). In the Mediterranean Sea, the vertical distribution of *Clausocalanus* species has been examined in epipelagic (Fragopoulu *et al.*, 2001; Peralba and Mazzocchi, 2004) and deep waters (Scotto di Carlo *et al.*, 1984), while their spatial distribution has been surveyed in the Ligurian Sea (Licandro and Icardi, 2009) and over the entire Mediterranean basin (Mazzocchi *et al.*, 2014). The seasonal cycle, and the species succession of the most abundant congeners, was investigated in a long-term time series in a coastal area of the western Mediterranean Sea (Mazzocchi and Ribera d’Alcalà, 1995; Mazzocchi *et al.*, 2012).
The following species distribution information was obtained from Frost and Fleminger (1968), Deevey and Brooks (1977), Scotto di Carlo et al. (1984), and Razouls et al. (2005-2019):

*C. arculicornis* (F: 1.1–1.6 mm; M: 0.9–1.3 mm); epipelagic (down to 500 m); tropical-subtropical, temperate; circumglobal; present in all oceans and in the Mediterranean Sea; not reported in Arctic, Subantarctic and Antarctic zones.

*C. brevipes* (F: 1.2–1.8 mm; M: 1.1–1.6 mm); epipelagic (down to 600 m); antarctic-subantarctic; circumglobal.

*C. farrani* (F: 0.9–1.2 mm; M: 0.7–1.0 mm); epipelagic (down to 1500 m); tropical-subtropical; present in the Atlantic, Pacific, and Indian oceans, and in the eastern Mediterranean Sea, Red Sea, and Arabian Sea.

*C. furcatus* (F: 0.8–1.8 mm; M: 0.7–1.1 mm); epipelagic (down to 500 m); tropical-subtropical; circumglobal, cosmopolite.

*C. ingens* (F: 1.4–1.9 mm; M: 1.0–1.1 mm); epipelagic; warm-temperate species of the southern hemisphere (recent reports of the species in the northwest Pacific Ocean and in the eastern Mediterranean Sea need confirmation).

*C. jobei* (F: 1.0–1.6 mm; M: 0.9–1.1 mm); epipelagic; tropical or tropical-subtropical; circumglobal.

*C. laticeps* (F: 1.1–1.7 mm; M: 1.0–1.3 mm); epipelagic (down to 500–700 m); Antarctic-Subantarctic species (the species presence in the East and South China seas needs confirmation).

*C. lividus* (F: 1.2–2.0 mm; M: 1.1–1.5 mm); epipelagic (down to 3000 m); subtropical and temperate; present in the Atlantic Ocean and in the Mediterranean Sea.

*C. mastigophorus* (F: 1.2–1.9 mm; M: 1.1–1.5 mm); epipelagic (down to 2000 m); tropical-subtropical; circumglobal; present in all oceans, in the Mediterranean Sea, East and South China seas, and Sea of Japan.

*C. minor* (F: 0.9–1.3 mm; M: 0.8–1.0 mm); epipelagic (down to 600 m); tropical; present in the Indian and Pacific oceans, Red Sea, and Arabian Sea, and recorded recently in the eastern Mediterranean Sea.

*C. parapergens* (F: 1.0–1.7 mm; M: 1.0–1.2 mm); epipelagic (down to 2000 m); tropical-subtropical; circumglobal, cosmopolite.

*C. paululus* (F: 0.7–0.9 mm; M: 0.5–0.6 mm); epipelagic (down to 800 m); subtropical; circumglobal; present in all oceans (biantitropical in the Pacific Ocean), in the Mediterranean Sea, Arabian Sea, and East and South China seas.

*C. pergens* (F: 0.7–1.1 mm; M: 0.5–0.7 mm); epipelagic-bathypelagic; warm temperate; circumglobal; present in all oceans, in the Mediterranean Sea, East and South China seas, and Sea of Japan.
4 Taxonomic key

For the present key, basic morphological characters that are useful for the identification of Clausocalanus species on a routine basis have been selected from the complete taxonomic key of Frost and Fleminger (1968). Most of these characters do not require dissections. The first most practical character for the diagnosis of Clausocalanus adult females is the shape of the seminal receptacle (ventral and dorsal lobes) in the genital segment, together with body length. In some cases, the lateral profile of forehead, the rostrum, and the shape of the genital segment are also useful diagnostic characters. The identification of males is more laborious. The most practical character is the position of seminal vesicle and spermatophore, coupled with body length and size of urosome segments.

Taxonomic key for the identification of adult females

1. Genital segment length equal to or shorter than UIII length (Figure 3).................................................................  C. furcatus (Brady, 1883)
Genital segment more than 1.5 times longer than UIII.......................... 2

2. In lateral view, ventral profile of genital segment conspicuously protuberant anterior to genital pores.................................................................................................................................................................................................................................................. 3
   In lateral view, ventral profile of genital segment not conspicuously protuberant anterior to genital pores.................................................................................................................................................................................................................................................. 4

3. In lateral view, rostrum short, thick, and straight (Figure 2).................................................................  C. farrani Sewell, 1929
   In lateral view, rostrum long, slender, and curved (Figure 2)..................................................................................................................................................................................................................................................  C. jobei Frost & Fleminger, 1968

4. 3P5 less than 2.0 times as long as 1P5 ...................................................................................................................... 5
   3P5 more than 2.0 times as long as 1P5 ...................................................................................................................... 8

5. Forehead usually strongly vaulted (Figure 1)......................  C. laticeps Farran, 1929
   Forehead not vaulted ............................................................................................................................................... 6

6. In lateral view, rostrum slender and curved, and forehead broadly rounded, protuberant above rostrum (Figure 1)....................  C. ingens Frost & Fleminger, 1968
   In lateral view, rostrum thick, straight or curved, and forehead broadly rounded but not markedly protuberant above rostrum......................................................... 7

7. Rostrum usually straight, tapered uniformly in either lateral or anterior view (Figure 1).................................................................  C. lividus Frost & Fleminger, 1968
   Rostrum usually curved ventroposteriad, not tapered uniformly in either lateral or anterior view (Figure 1).................................................................  C. mastigophorus (Claus, 1863)

8. Distance (L) between P3 basipodal spiniform processes 2 and 3 more than 2.0 times proximal width (D) of process 3 (Figure 2)........................  C. paululus Farran, 1926
   L less than 1.5 times D of process 3 ...................................................................................................................... 9

9. In lateral view, ventral profile of genital segment with a prominent step posterior to genital pores (Figure 2).................................  C. minor Sewell, 1929
In lateral view, ventral profile of genital segment without a prominent step posterior to genital pores................................................................. 10

10. In lateral view, s.r. dorsal lobe arising from anterior edge of ventral lobe; s.r. dorsal lobe not bulb-shaped (Figure 2) ..................  C. arcuicornis (Dana, 1849)  
In lateral view, portion of s.r. ventral lobe visible anterior to dorsal lobe; s.r. dorsal lobe usually bulb-shaped.................................................. 11

11. In lateral view, s.r. dorsal lobe digitiform or slightly constricted in region of attachment to s.r. ventral lobe; in lateral view, posterior margin of TIV-V rounded (Figure 3) .................................  C. pergens Farran, 1926  
In lateral view, s.r. dorsal lobe bulb-shaped, constricted in region of attachment to s.r. ventral lobe; in lateral view, posterior margin of TIV-V somewhat angular................................................................. 12

12. Caudal ramus more than 1.5 times as long as it is wide; A1 segment 2 more than 1.4 times as long as segment 24 (Figure 3)........  C. brevipes Frost & Fleminger, 1968  
Caudal ramus less than 1.5 times as long as it is wide; A1 segment 2 less than 1.4 times as long as segment 24 (Figure 3)......  C. parapergens Frost & Fleminger, 1968

**Taxonomic key for the identification of adult males**

1. In lateral view, seminal vesicle extending within prosome anterior to level of P1 articulation with C-TI; spermatophore extending by at least 1/4 of its length anterior to articulation of C-TI with TII.......................... 2  
In lateral view, seminal vesicle not extending within prosome anterior to level of P1 articulation with C-TI; spermatophore not extending or extending by less than 1/8 of its length anterior to the C-TI articulation with TII............................... 6

2. TL less than 0.70 mm (Figure 5)...........................................  C. paululus Farran, 1926  
TL greater than 0.70 mm.......................................................... 3

3. Prosome less than 5.7 times as long as UII (Figure 5)......  C. arcuicornis (Dana, 1849)  
Prosome more than 5.7 times as long as UII................................. 4

4. Left 5P5 armature includes two thick, curved, spiniform setae; 2P5 length more than 1.45 times greater than UII width (Figure 5) .................................................................  C. jobei Frost & Fleminger, 1968  
Left 5P5 armature consists of slender, usually straight setae; 2P5 length less than 1.45 times greater than UII width.................................................. 5

5. Right P5 bi- or trimerous, distal segment large (Figure 5) ......  C. minor Sewell, 1929  
Right P5 always bimerous, distal segment reduced (Figure 5) ..............................................................................  C. farrani Sewell, 1929

6. Longer ramus of P5 much shorter than urosome (Figure 6) ..................................................  C. brevipes Frost & Fleminger, 1968  
Longer ramus of P5 longer than urosome........................................ 7

7. Rostrum in lateral view not knoblike and not protruding ventrally; longer ramus of P5 usually on right side (Figure 6) ...............  C. furcatus (Brady, 1883)
Rostrum in lateral view knoblike and protruding ventrally; longer ramus of P5 on left side ................................................................. 8

8. TL less than 0.80 mm (Figure 6) .................................................. C. pergens Farran, 1926
   TL greater than 0.80 mm .......................................................... 9

9. Caudal ramus more than 1.6 times as long as it is wide (Figure 4) .................. C. laticeps Farran, 1929
   Caudal ramus less than 1.6 times as long as it is wide ........................ 10

10. 2P5 less than 4.4 times as long as it is wide (Figure 4) .......................... C. ingens Frost & Fleminger, 1968
    2P5 more than 4.4 times as long as it is wide .............................. 11

11. U1I more than 1.35 times longer than 2P5 (Figure 4) .............................. C. lividus Frost & Fleminger, 1968
    U1I less than 1.35 times longer than 2P5 .................................... 12

12. Prosome more than 6.45 times longer than U1I; two distal segments of right P5 usually well developed (Figure 4) ............... C. mastigophorus (Claus, 1863)
    Prosome less than 6.45 times longer than U1I; two distal segments of right P5 usually reduced (Figure 6) ...................... C. parapergens Frost & Fleminger, 1968

**Clausocalanus groups I, II and III**

The 13 Clausocalanus species were clustered by Frost and Fleminger (1968) in three groups based on morphological and morphometrical characters:

**Group I**  
Species: C. mastigophorus, C. lividus, C. ingens, and C. laticeps  
Size: > 1.2 mm  
Female: In lateral view, the dorsal lobe of the seminal receptacle is usually larger than the ventral lobe and is directed dorsal or dorso-anteriorly.  
Male: In lateral view, the seminal vesicle does not extend within prosome anterior to level of P1 articulation with C-TI, and the spermatophore does not extend or extends by less than 1/8 of its length anterior to the C-TI articulation with TII. Males of this group are easily distinguished from males of Group II, but are more difficult to separate from some males of Group III.

**Group II**  
Species: C. arcuicornis, C. farrani, C. jobei, C. minor, and C. paululus  
Female: In lateral view, the dorsal lobe of the seminal receptacle is usually smaller than the ventral lobe and is directed dorso-posteriorly.  
Male: easily distinguished by the anterior extension within the prosome of the seminal vesicle and the spermatophore sac.

**Group III**  
Species: C. pergens, C. brevipes, C. parapergens, and C. furcatus  
Female: In lateral view, the dorsal lobe of the seminal receptacle originates from the central or posterior part of the ventral lobe, is usually constricted
in the region of attachment to the ventral lobe, and is usually directed dorsally.

Male: In lateral view, the spermatophore sac extends within the prosome by no more than 1/8 of its length anterior to C-TI articulation with TII; the seminal vesicle usually does not extend anterior to the articulation of P1 with C-TI.

To determine whether the three groups are monophyletic evolutionary lineages, Bucklin and Frost (2009) examined phylogenetic relationships among all Clausocalanus species based on the combination of morphological, morphometrical, and molecular characters. The resulting phylogenetic tree resolved all four species of Group I, and four out of the five species of Group II. However, Group III was not well resolved. Based on DNA sequence data, C. furcatus and C. paululus did not cluster within any of the three groups, and may represent basal lineages that are distinct from all members of any group. Moreover, all molecular and combined analyses consistently paired C. arcuicornis (Group II) with C. parapergens (Group III).

**Practical tips for taxonomic identification**

- The *C. furcatus* adult female is the only female with a genital segment length equal to or smaller than UIII length. This character is immediately visible.

- Adult females of *C. pergens* and *C. paululus* can be distinguished in lateral view by (i) the dorsal profile of the prosome, which appears slightly curved in the latter species, and (ii) by the ventral profile of the genital segment, which appears uneven in *C. paululus*, with the seminal receptacle often inconspicuous.

- Adult females of *C. paululus* can be distinguished from those of *C. minor* by their body size.

- Adult females of *C. brevipes* (subantarctic) and *C. parapergens* (tropical and subtropical) are very similar. They can be distinguished by the length-width ratio of the caudal rami and the length of A1 segment 2 to segment 24.

- Males of *C. brevipes* are easily distinguished from all other species of *Clausocalanus* due to the fact that the longer ramus of P5 is shorter than the urosome.

- *C. lividus* adult females can be distinguished from the very similar *C. ingens* by the shape and curvature of the forehead and rostrum in lateral view.

- *C. farrani* and *C. jobei* adult females are very similar but can be distinguished by the shape of the rostrum in lateral view.
Figure 1. Females of *Clausocalanus* species Group I (not to scale). All drawings from Frost and Fleminger (1968).
Figure 2. Females of *Clausocalanus* species Group II (not to scale). All drawings from Frost and Fleminger (1968).
Figure 3. Females of *Clausocalanus* species Group III (not to scale). All drawings from Frost and Fleminger (1968).
Figure 4. Males of *Clausocalanus* species Group I (not to scale). All drawings from Frost and Fleminger (1968).
Figure 5. Males of *Clausocalanus* species Group II (not to scale). All drawings from Frost and Fleminger (1968).
Figure 6. Males of *Clausocalanus* species Group III (not to scale). All drawings from Frost and Fleminger (1968).
6  Links

WoRMS


Molecular information


Other useful links

https://www.st.nmfs.noaa.gov/nauplius/media/copepedia/taxa/T4000087/

7  Terminology

A1 antennule (first antenna)
A2 antenna (second antenna)
B1-B2 first, second basipodal segment of swimming leg
C-TI anterior portion of body including the cephalosome (C) and fused thoracic segment (TI) bearing P1
F female
M male
P1-P5 swimming legs 1-5
s.r. seminal receptacle
TII second thoracic segment (free)
TIV-TV fused fourth and fifth pedigerous segments
TL total length
UI-UII-UIII first (genital segment), second and third urosomal segments
8 Acknowledgements

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9 References


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