Establishment of a new shrimp family Chlorotocellidae for four genera previously assigned to Pandalidae (Decapoda, Caridea, Pandaloidea)

Tomoyuki Komai¹, Tin-Yam Chan², Sammy De Grave³

¹ Natural History Museum and Institute, Chiba, 955-2 Aoba-cho, Chuo-ku, Chiba 260-8682, Japan
² Institute of Marine Biology and Center of Excellence for the Oceans, National Taiwan Ocean University, 2 Pei-Ning Road, Keelung 20224, Taiwan
³ Oxford University Museum of Natural History, Parks Road, Oxford, UK

http://zoobank.org/86895CA3-596A-4015-8350-82EEF10F9885

Corresponding author: Tin-Yam Chan (tychan@mail.ntou.edu.tw)

Abstract

A new caridean shrimp family, Chlorotocellidae, is established to accommodate four genera previously assigned to Pandalidae, viz., Chlorotocella Balss, 1914 (type genus), Chlorocurtis Kemp, 1925, Anachlorocurtis Hayashi, 1975, and Miropandalus Bruce, 1983, which represents the sister clade to a clade consisting of all other pandalid genera (including the two genera previously assigned to Thalassocarididae) in a recent comprehensive phylogenetic analysis of Pandaloidea. Diagnoses are provided for the new family and its constituent genera, and a comparison with Pandalidae is provided, for which a new diagnosis is given.

Key Words

Anachlorocurtis, ASR analysis, Chlorotocella, Chlorocurtis, Miropandalus

Introduction

The caridean family Pandalidae Haworth, 1825 is predominantly composed of cold-water and deep-sea taxa, including several species of commercial importance (Holthuis 1980). An extensive multimarker molecular phylogenetic analyses of the family and the closely related Thalassocarididae by Liao et al. (2019) clarified that Thalassocarididae, represented by two genera, Thallassocaris Stimpson, 1860 and Chlorotocoides Kemp, 1925, are deeply nested within Pandalidae, and that four genera, Chlorotocella Balss, 1914, Chlorocurtis Kemp, 1925, Anachlorocurtis Hayashi, 1975, and Miropandalus Bruce, 1983, comprise the sister clade to the remaining clade consisting of all other pandalid genera. These four genera are represented by small-sized species inhabiting shallow subtidal waters in tropical to subtropical and often associated with cnidarians (Hayashi and Miyake 1968; Hayashi 1975; Bruce 1983; Okuno and Yokota 1995; Minemizu 2000, 2013; Kato and Okuno 2001; Kawamoto and Okuno 2003; Humann and DeLoach 2010; Horká et al. 2014; Anker and De Grave 2016) in sharp contrast to the ecologies of most Pandalidae. To incorporate the documented phylogenetic pattern into the formal classification of Caridea, together with considerations on the morphological distinctness and ecological traits of these taxa, we hereby propose a new family, Chlorotocellidae fam. nov. for these four genera and redefine the family Pandalidae.

Materials and methods

The morphological data assembled following an examination of the literature and direct examination of specimens of relevant taxa formed the basis of the phylogenetic analysis by Liao et al. (2019) and can be found in the online supplementary material for that study. Aside from the family diagnosis, diagnoses are provided for each genus in the new family; to shorten diagnoses, synapomorphies are in bold italics.
Illustrations showing diagnostic characters are given for Chlorotocella (*C. gracilis* Balss, 1914) and *Chlorocurtis* (*C. jactans* Nobili, 1904)), as no published modern illustrations are available in easily accessible literature for those taxa. The three species of *Anachlorocurtis* and the monotypic *Miropandalus* have been well illustrated in their respective type description, and thus, no additional figures are presented.

Details of specimens used for preparation of drawings are listed below. These specimens are deposited in the Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University, Hakodate, Japan (HUMZ), National Research Institute for Far Seas Fisheries, Shizuoka, Japan (NRIFSF), and the Natural History Museum and Institute, Chiba, Japan (CBM).

### Chlorotocellidae fam. nov.

*Chlorocurtis jactans* (Nobili, 1904): CBM-ZC 11596, 1 ovigerous female (cl 1.3 mm), Uehara, Iriomote Island, Yaeyama Islands, Ryukyu Islands, sea grass beds, 0.5–1 m at low tide, 18 July 2007, dip net, coll. T. Komai.

*Chlorotocella gracilis* Balss, 1914: CBM-ZC 12534, 1 male (cl 5.0 mm), TRV “Toyoshio-maru”, 2001-6 cruise, sn 4, W of Tanegashima Island, Osumi Islands, 30°33.30’N, 130°53.30’E, 47 m, 26 May 2001, dredge, coll. T. Komai; HUMZ-C 1556, 1 male (cl 4.1 mm), Tosa Bay, 40 m, 22 May 1960, coll. M. Toriyama.

Pandalidae Haworth, 1825

*Chlorotocus novaeezelandiae* (Borradaile, 1916): NRIFSF 578, 1 male (cl 17.0 mm), New Zealand, no other data.

*Heterocarpus ensifer* A. Milne-Edwards, 1881: HUMZ-C 255, 1 male (cl 33.0 mm), no data.

*Pandalus montagui* Leach, 1814: CBM-ZC 3422, 1 transitional male (cl 10.5 mm), Texel, The Netherlands, 8 April 1991.

### Systematics

Infraorder Caridea Dana, 1852
Superfamily Pandaloidea Haworth, 1825

Family Pandalidae Haworth, 1825

Type genus. *Pandalus* Leach, 1814, by original designation.


Diagnosis. Rostrum well developed, usually ventrally with teeth or rows of setae. Thoracic sternites 6–8 each with paired conspicuous prominences, teeth or protuberances (Fig. 3A). Pleomere 6 postero-lateral process usually terminating in small tooth. Telson with longitudinal row of spiniform setae located on dorsolateral ridges. Eyestalks subpyriform or kidney-shaped, cornea distinctly longer and wider than eyestalk. Antennular stylocerite with proximolateral projection, distally acuminate or rounded; article 2 usually with minute spiniform setae (Fig. 6A); outer flagellum with distal portion (distal to aesthetasc-bearing portion) usually well developed, consisting of numerous articles. Article 1 of mandibular palp with prominent expansion on inner distal margin (Fig. 6B). Maxilliped 2 with podobranch. Maxilliped 3 with or without exopod. Pereopod 1 fingers minute or completely reduced. Pereopod 2 subequal or unequal; basis with small process on lateral surface (Fig. 6C); carpal articulation greatly variable, but never tri-articulated. Arthrobranchs usually present on maxilliped 3 and pereopods.

Chlorotocellidae fam. nov.

http://zoobank.org/CBE45390-043A-46E8-9743-7F5B167255AD

Type genus. *Chlorotocella* Balss, 1914, by present designation.

Composition. *Chlorotocella* Balss, 1914 (two species), *Chlorocurtis* Kemp, 1925 (monotypic), *Anachlorocurtis* Hayashi, 1975 (three species) and *Miropandalus* Bruce, 1983 (monotypic).

Diagnosis. Rostrum, if present, without teeth or fringe of setae on ventral margin (Figs 1A, 4A). Thoracic sternites without conspicuous ornamentation, such as prominences, teeth or protuberances (Fig. 3B). Pleomere 6 postero-lateral process rounded or truncate (Figs 1C, 4B). Telson with dorsolateral spiniform setae located adjacent to lateral margins (Figs 1D, 4C). Eyestalks subcylindrical, cornea distinctly shorter than eyestalk (Figs 1E, 4D). Antennular stylocerite devoid of proximolateral projection, distally obliquely truncate, bi- or tridentate (Figs 1A, F, 4E); outer flagellum with distal portion (distal to aesthetasc-bearing portion) reduced, consisting only of few articles (Figs 1A, 4E). Maxilliped 2 without podobranch (Figs 1L). Maxilliped 3 with no exopod (Figs 2A, 5A). Pereopod 1 fingers absent (Figs 2B, 5B). Pereopod 2 always subequal; basis without small process on lateral surface of basis; carpus consistently divided into three articles (Figs 2C, 5D, 6D). Arthrobranchs always absent from maxilliped 3 and pereopods.

Remarks. Characters differentiating Chlorotocellidae fam. nov. and Pandalidae are summarized in Table 1, with the character states of Chlorotocellidae fam. nov. being synapomorphic against Pandalidae (see Liao et al. 2019).
Figure 1. *Chlorotocella gracilis* Balss, 1914, male (cl 5.0 mm), CBM-ZC 12534. **A.** Carapace, antennule and antenna, lateral view (left eye removed); **B.** Anterior part of carapace, lateral view; **C.** Pleon, lateral view; **D.** Telson, dorsal view; **E.** Left eye, dorsal view; **F.** Left antennular peduncle, dorsal view; **G.** Left antenna, ventral view; **H.** Left mandible, outer view; inset, palp, outer view; **I.** Left maxillule, outer view (coxal endite missing); **J.** Left maxilla, outer view; **K.** Left maxilliped 1, outer view; **L.** Left maxilliped 2, outer view; **M.** Endopod of left pleopod 1, ventral view.
Figure 2. *Chlorotocella gracilis* Balss, 1914, male (cl 5.0 mm), CBM-ZC 12534. Left thoracic appendages in lateral view. A. Maxilliped 3; B–F. Pereopods 1–5, respectively.
Supplementary figures of diagnostic characters can be found in Hayashi (1975: figs 1–3), Bruce (1983: figs 1–5), Hayashi (2007a: figs 538, 539, 542a–f), Hayashi (2007c: figs 557–559a–e), Horká et al. (2014: figs 1–8), and Ahyong (2015: figs 9, 10).

Amongst these characters, the division of the carpus of pereopod 2 and quite possibly the absence of ventral rostral teeth can readily be used to differentiate the two families, although determination of their polarity is not straightforward. In Chlorotocellidae the pereopod 2 car-
Figure 4. *Chlorocurtis jactans* (Nobili, 1904), ovigerous female (cl 1.3 mm), CBM-ZC 11596. A. Carapace, lateral view; B. Pleon, lateral view; C. Telson, dorsal view; D. Left eye, dorsal view; E. Left antennule, dorsal view (inner flagellum damaged); F. Right antennular peduncle, distal 2 articles, mesial view; G. Left antenna, ventral view (flagellum missing); H. Left mandible, outer view; I. Left maxillule, outer view; J. Left maxilla, outer view; K. Left maxilliped 1, outer view; L. Left maxilliped 2, outer view (epipod broken off).
pus is consistently divided into three articles, whereas in Pandalidae, the number of the carpal articles is quite variable according to taxa, but none are tri-articulate (cf. Komai 1994). The absence of ventral rostral teeth is also reported in three taxa of the pandalid genus *Plesionika* (Chace 1985) but with doubt (see Chace 1985; Komai et al. 2005; Hayashi 2009; Komai 2011; Li and Chan 2013). Such a similarity, if really present, can be resulted from homoplasy (Liao et al. 2019).

According to the Ancestral State Reconstruction (ASR) analysis by Liao et al. (2019), Pandalidae is characterized by the following synapomorphic features: (1) second article of the antennular peduncle with a few minute spiniform setae on the dorsodistal margin (Fig. 6A); (2) mandibular palp consisting of three articles (Fig. 6B); and (3) basis of pereopod 2 bearing a small process on the lateral surface (Fig. 6C). In these regards, Chlorotoconellidae shows the following plesiomorphic states: (1) mandibular palp tends to be reduced, being absent or consisting of two articles at most (Figs 1H, 4H); (2) second article of the antennular peduncle is unarmed on the dorsodistal margin (Figs 1A, F, 4E); and (3) basis of pereopod 2 being unarmed (Fig. 6D).

Nevertheless, an assessment of the polarity of the development of the mandibular palp is fraught with difficulty and heavily dependent on outgroup selection. In Caridea in general, however, a reduction of the mandibular palp is considered to be derived (e.g., Christoffersen 1987, 1989), as compared to the well-developed palp in Dendrobranchiata and most other Decapoda.

Furthermore, the other two characters are subject to reversal within Pandalidae (Komai 1994; Liao et al. 2019). In species of *Thalassocaris* and *Chlorotoxoides* (previously in their own family Thalassocarididae, but now considered part of Pandalidae), the second article of the antennular peduncle is devoid of spiniform setae and the basis of the second pereopods unarmed (Komai 1994).

In addition to the three aforementioned characters, the possession of a rounded laminar expansion at the inner distal angle of the first article of the mandibular palp

---

**Figure 5.** *Chlorocurtis jactans* (Nobili, 1904), ovigerous female (cl 1.3 mm), CBM-ZC 11596, left thoracic appendages in lateral view (except for C). A. Maxilliped 3; B. Pereopod 1; C. Same, propodus, mesial view; D–G. Pereopods 2–5, respectively.
(Fig. 6B, inset) might be synapomorphic to Pandalidae (Komai 1994; Liao et al. 2019), although a secondary loss of this structure is observed in Thalassocaris and Chlorocrotocoides (Komai 1994; Liao et al. 2019). It is impossible to evaluate the homology of this character for the taxa assigned to Chlorotocellidae, because in those taxa, the mandibular palp only comprises two articles (Chlorotocella) or is absent (Chlorocurtis, Anachlorocurtis and Miropandalus), and the homology of the articles has not been established in taxa with different numbers.

Genus Chlorotocella Balss, 1914


Type species. Chlorotocella gracilis Balss, 1914.

Diagnosis. Rostrum elongate, very slender, gently upturned, exceeding far beyond distal margin of antennal scaphocerite, dorsally armed with two teeth around rostral base (one postrostral); ventral margin unarmed (Fig. 1A). Carapace without projections on dorsal midline; supraorbital tooth present; suborbital lobe prominent, longer than antennal tooth, distally rounded, slightly constricted at base; pterygostomial tooth moderately small (Fig. 1A, B). Pleomeres 1–6 dorsally rounded; pleomeres 4 and 5 each with pair of posteralateral teeth; pleomere 5 with deep transverse groove near posterodorsal margin; pleuron with small posteroventral tooth (Fig. 1C). Pleomere 6 with minute postero- lateral tooth; posteroventral angle with minute tooth (Fig. 1C). Telson with additional anterior pair of spiniform setae located more mesial to other lateral series of spiniform setae; posterior margin narrow, slightly produced medially, with two pairs of unequal spiniform setae (Fig. 1D). Eye with ocellar spot (nebenauge) (Fig. 1E). Antennular peduncle article 1 armed with tooth on dorso- distal margin (Fig. 1A, F). Mandible with two-articulated palp (Fig. 1H). Maxillule palp without distal outer lobule (Fig. 1I). Maxilla with short, moderately slender endopod (Fig. 1J). Maxilliped 1 with coxal and basal endites well developed, both with row of setae on mesial margin; exopodal flagellum well developed (Fig. 1K). Maxilliped 2 endopod with dactylus located at distal portion of propodus; exopod well developed (Fig. 1L). Pereopod 1 fingers completely reduced (Fig. 2B). Pereopods 3–5 propodi each with closely spaced, short to long spiniform setae in distal 0.2; carpi each with few spiniform setae on lateral surface; meri usually with spiniform setae arranged in two rows; ischia each with spiniform seta on ventral surface in pereopods 3 and 4 (Fig. 2D–F). Male pleopod 1 endopod without appendix interna (Fig. 1M).

Composition. Chlorotocella gracilis; C. spinicaudus (H. Milne Edwards, 1837).

Distribution. Indo-West Pacific, South Australia; shallow subtidal to 60 m; free living in algal-rich habitats or facultatively associated with gorgonarians and hydroids.
Remarks. At present, two species are assigned to Chlorocurtis (De Grave and Fransen 2011), viz., C. graci-

lis (type species) and C. spinicaudus. Holthuis (1995) clarified that Hippolyte spinicaudus H. Milne Edwards, 1837 was a senior subjective synonym of Pandalus leptorhynchus Stimpson, 1860. In addition, a third taxon, which was placed in the synonymy of C. spinicaudus by De Grave and Fransen (2011), Pandalus (Parapandalus) leptorhynchus var. gibber Hale, 1924, was described from Gulf St Vincent, South Australia, characterized mainly by the prominently crested tergite of pleomere 3 (see Hale 1927). This taxon has been seldom mentioned in more recent literature. Ledoyer (1984) illustrated a specimen with a weakly crested tergite from Nouméa (New Caledonia), which he assigned to C. graci-

lis, but left it open as to whether this should be a distinct species or merely a “forme gibber” of C. graci-

lis. In contrast, Poore (2004) treated the taxon as a distinct species, C. gibber (Hale), noting it was restricted to the Gulf St Vincent (South Australia).

Because no modern descriptions are available for C. spinicaudus, the above generic diagnosis is largely based on C. graci-

lis and the summary information available on the other species. It seems possible that Hale’s (1924) tax-

on might be distinct from C. graci-

lis and C. spinicaudus as it is characteristic by having a highly crested tergite of the pleomere 3 (Hale 1924: pl. 4, fig. 6; 1927: fig. 35). Re-

assessment of the taxonomic status of C. spinicaudus and Pandalus (Parapandalus) leptorhynchus var. gibber will be necessary to fully clarify the taxonomy of the genus.

Genus Chlorocurtis Kemp, 1925


Type species. Chlorocurtis miser Kemp, 1925.

Diagnosis. Rostrum short but well developed, direct-

ed forward, reaching midlength of 1 antennu-

lar peduncle; dorsal margin crested, with five to seven teeth including two or three postrostral; ventral margin unarmed (Fig. 4A). Carapace with a highly conspicuous pro-

jections on dorsal midline; no supraorbital tooth; subor-

bital lobe absent; pterygostomial tooth moderately small (Fig. 4A). Pleomeres 1–5 dorsally rounded; pleomeres 1–3 with long, erect setae on dorsal surface; pleomeres 4 and 5 each without pair of postrostral teeth; pleomere 5 without deep transverse groove near posterodorsal margin, pleuron rounded posteriorly; pleomere 6 without postmedian tooth, posteroventral angle unarmed (Fig. 4B). Telson posterior margin rather broad, convex, with three pairs of unequal spiniform setae (Fig. 4C). Eye without ocellar spot (nebenauge) (Fig. 4D). Antennular peduncle article 1 unarmed on dorsodistal margin; stylo-

cerite obliquely truncate distally, distolateral angle termi-

nating in tooth, distomesial angle subacute to blunt; outer flagellum shorter than peduncle, distal portion reduced to single article (Fig. 4E). Short, club-like, modified setae present at ventrodorsal margin of article 2 of antennular peduncle (one seta) and distal margin of antennal scaphocerite (two setae) (Fig. 4F, G). Mandible without palp (Fig. 4H). Maxilliped 1 with coxal and basial endites well developed, both with row of setae on mesial margin; exopodal flagellum well developed (Fig. 4K). Maxilliped 2 endopod with dactylus located at distal portion of propodus; exopod well developed (Fig. 4L). Pereopods 3–5 propodi broadened distally, oblique flexor distal margins each with short rows of narrowly spaced long spiniform setae flanking field of short setae, forming prehensile structure together with dactylus folded back; carpi without spiniform setae on lateral surface; meri without spiniform setae; ischia without spiniform seta on ventral surface (Fig. 5E–G). Male pleopod 1 endopod without appendix interna.

Composition. Monotypic.

Distribution. Indo-West Pacific, intertidal to 10 m; seagrass beds.

Remarks. Chlorocurtis was originally established for Chlorocurtis miser by Kemp (1925).

Later, Holthuis (1947) synonymized Chlorocurtis miser with Virbius (?) jactans (Nobili, 1904) without any argumentation, although clearly correct. This synonymy has since been widely adopted (e.g., Holthuis 1955; Ledoyer 1968, 1984; Bruce 1976; Hayashi 2007b; Holthuis 1993; De Grave and Fransen 2011; Gan and Li 2018).

Genus Anachlorocurtis Hayashi, 1975


Type species. Anachlorocurtis commensalis Hayashi, 1975.

Diagnosis. Rostrum short, ascending in adults, reaching midlength of article 1 of antennular peduncle, terminating in acute tip or obliquely truncate distally with irregular dentition; dorsal and ventral margins usually unarmed. Carapace without supraorbital tooth; dorsal midline with two prominent processes, anterior one postrostral, irregu-

larly denticulate anteriorly, posterior one cardiac in posi-

tion, directed forward, acuminate; suborbital lobe absent; pterygostomial angle rounded, unarmed. Pleomeres 1–5 dorsally rounded; pleomeres 4 and 5 each without pair of postrostral teeth. Pleomere 5 without deep transverse groove near posterodorsal margin; pleuron rounded posteriorly. Pleomere 6 without postmedian tooth; posteroventral angle without tooth. Telson posterior margin truncate or rounded, with five pairs of unequal spiniform
setae. Eye without ocellar spot (nebenauge); **cornea with papilla-like tubercle.** Antennular peduncle article 1 unarmed on dorsodistal margin; stylocerite obliquely truncate distally, both distal angles dentate; outer flagellum shorter than peduncle, distal portion reduced to one or two articles. Mandible without palp. Maxillulæ palp with well-developed distal outer lobule bearing apical seta. Maxilliped 1 with coxal and basal endites poorly developed, narrow; exopodal flagellum absent. Maxilliped 2 endopod with dactylus located at mesial portion of propodus or fused to propodus; exopod absent. Articulation between carpal article 1 and 2 of pereopod 2 strongly oblique. Pereopods 3–5 propodi slightly narrowing distally, with few widely spaced minute spiniform setae on flexor margin; carpi without spiniform setae on lateral surface; meri of pereopods 3 and 4 each with one spiniform seta distolaterally and one minute spiniform seta at midlength of ventral surface. Male pleopod 1 endopod with small rounded lateral lobe far exceeded by well-developed appendix interna.

For illustrations see Hayashi (1975: figs 1–3), Hayashi (2007a: figs 538, 539, 542a–f); Horká et al. (2014: figs 1–8) and Ahyong (2015: figs 9, 10).


**Distribution.** Indo-West Pacific, shallow subtidal to 40 m; associated with antipatharian corals.

---

**Genus Miropandalus Bruce, 1983**


**Type species.** *Miropandalus hardingi* Bruce, 1983.

**Diagnosis.** *Rostrum absent. Carapace without supraorbital tooth; dorsal midline with two very prominent, erect processes, anterior one postrostral, tapering, posterior one cardiac in position, slightly curved, anterily, blunt; suborbital lobe absent; pterygostomial angle rounded or angular. Pleomere 1 with prominent protuberance; pleomere 3 with triangular crest on posterior half of dorsal midline; pleomeres 4 and 5 each without pair of postoralateral teeth; pleomere 5 without deep transverse groove near posteroethmoidal margin; pleuron rounded posteriorly. Pleomere 6 without posterovertical tooth; posterovertical angle unarmed. Telson posterior margin rounded, with several short spiniform setae. Eye without ocellar spot (nebenauge); cornea without papilla-like tubercle. Antennular peduncle article 1 unarmed on dorsodistal margin; stylocerite subtruncated distally, bi- or tridentate; outer flagellum shorter than peduncle, distal portion completely reduced. Mandible without palp. Maxillulæ palp with well-developed distal outer lobule, without apical seta. Maxilliped 1 with coxal and basal endites poorly developed, narrow; endopod stout; exopodal flagellum absent. Maxilliped 2 endopod with dactylus fused to propodus; exopod absent. Articulation between carpal article 1 and 2 of pereopod 2 strongly oblique. Pereopods 3–5 propodi narrowing distally, with few minute spiniform setae on flexor margin; carpi without spiniform setae on lateral surface; meri of pereopods 3 and 4 unarmed. Male pleopod 1 endopod with small rounded lateral lobe far exceeded by well-developed appendix interna.

For illustrations, see Bruce (1983: figs 1–5) and Hayashi (2007c: figs 557–559a–e).

**Composition.** Monotypic.

**Distribution.** West Pacific, subtidal to 58 m; associated with antipatharian corals.

---

**Acknowledgements**

This work was supported by grants from the Ministry of Science and Technology, Taiwan, R.O.C., and the Center of Excellence for the Oceans (National Taiwan Ocean University), which is financially supported by The Featured Areas Research Center Program within the framework of the Higher Education Sprout Project by the Ministry of Education in Taiwan, R.O.C.

---

**References**


