





https://doi.org/10.11646/zootaxa.5051.1.14 http://zoobank.org/urn:lsid:zoobank.org:pub:6B276081-8960-4AED-B0AE-B907F9109D54

# Two new marine cyclopinids (Crustacea: Copepoda: Cyclopoida) from interstitial habitats in Korea

# TOMISLAV KARANOVIC

Hanyang University, College of Natural Sciences, Department of Life Science, Seoul 04763, Republic of Korea. • tomislav.karanovic@gmail.com

# Abstract

Marine cyclopoids, and especially cyclopinids, are poorly studied because their diversity is highest in marginal habitats, such as intertidal interstitial and anchialine caves, or in highly inaccessible abyssal and hadal depths. Two new cyclopinids are described here, both from two different sandy beaches in Korea. Among four species currently recognized in the genus, *Heterocyclopina koreaensis* **sp. nov.** is most closely related to *H. vietnamensis* Pleşa, 1969 from similar habitats in Vietnam. *Koreacyclopina wellsi* **gen. et sp. nov.** shares its sexually dimorphic third exopodal segment of the second leg with the Antarctic genus *Pseudocyclopina* Lang, 1946, but differs from all six known species by numerous features, some of which are observed for the first time within cyclopinids. Both Korean species belong to the family Hemicyclopinidae, but the monophyly of this group has not yet been demonstrated.

Key words: cyclopoids, intertidal zone, new genus, new species, stygofauna, taxonomy

#### Introduction

Copepods are relatively well studied in Korea, both as free-living forms in marine (Soh et al. 2010; Lee et al. 2012) and freshwater environments (Chang 2009, 2010), as well as parasites of other organisms (Kim, 2008). However, utilization of novel taxonomic methods, such as the study of microstructures (Karanovic & Cho, 2012, 2016, 2017; Karanovic & Lee, 2012; Karanovic et al. 2013) and DNA (Karanovic & Kim, 2014a, 2014b; Karanovic et al. 2014, 2015; Kim et al. 2014), and survey of marginal and previously understudied habitats, such as marine interstitial (Karanovic 2014, 2017; Karanovic et al. 2012a, 2012b; Karanovic & Lee, 2016), resulted in numerous recent additions. Some three-quarters of the world's ice-free coastlines consist of sandy shores (Brown & McLachlan 2006) and Korea has 12,478 kilometers of coastline along three seas (Pruett & Cimino 2000). There are no published data on how much of the Korean coastline is sandy, but it is a significant ecosystem here. Like in most developed economies, this ecosystem is under constant anthropogenic pressure and, being a marginal habitat, is rarely included in protected natural reserves. However, marine interstitial harbours a disproportionate level of biodiversity (Gray 1997; Karanovic 2008; Thrush et al. 2006), which is yet to be fully appreciated and understood (Armonies & Reise 2000; Gray 2002; Zeppelli et al. 2015). While most interstitial copepods belong to harpacticoids (Giere 1993), a survey of interstitial habitats in Korea brought to light two interesting cyclopinid copepods, one belonging to the genus Heterocyclopina Plesa, 1969, while the other showed some similarities with the genus Pseudocyclopina Lang, 1946. Only two cyclopinids were known previously from Korea: the currently endemic Cyclopinoides orientalis Chang, 2011, and the relatively widely distributed East Asian Paracyclopina nana Smirnov, 1935 (see Chang 2009, 2011). The latter species was described by Smirnov (1935) from Vladivostok (Russia), later found also in China (Shen 1979) and Japan (Ueda et al. 2001), and has become in recent years a model organism for various genomic and physiological studies (Lee et al. 2015, 2017; Jeong et al. 2015).

The genus *Heterocyclopina* was described by Pleşa (1969) for a single interstitial species from Vietnam. He considered it most closely related to *Procyclopina* Herbst, 1955, at the time a monotypic genus described from sandy beaches of Brazil (Herbst 1955). Lotufo (1995) redescribed the type species of *Procyclopina* from a different locality and described three new species, all from Brazil. One of the new species described by Lotufo (1995) was

relatively similar to the type species of *Procyclopina*, but the other two were very different. In fact, the latter were more similar to *Heterocyclopina*, but Lotufo (1995) was probably unaware of Pleşa's (1969) paper. Martínez Arbizu (2001a) discovered specimens of *Heterocyclopina* in China, which he provisionally identified as belonging to the same species as that described by Pleşa (1969) from Vietnam, although he noticed some differences. Unfortunately, he provided no illustrations for those specimens in that or any other paper, so their specific status remains uncertain. Martínez Arbizu (2001a) also argued that *Heterocyclopina* should be considered a junior subjective synonym of *Procyclopina*, in the light of newly discovered intrageneric variability of the latter from Brazil by Lotufo (1995). Martínez Arbizu (2001a) misinterpreted armature formulae of some swimming legs in those two genera, which were corrected by Karanovic (2008: p. 172), who reinstated the genus *Heterocyclopina* described one new species from sandy beaches of Australia, and also transferred two Brazilian *Procyclopina* species described by Lotufo (1995) into this genus. Karanovic (2008) also argued that *Heterocyclopina* is not at all closely related to *Procyclopina*, but is instead more closely related to *Parapseudocyclopinodes* Lindberg, 1961. Today, *Heterocyclopina* contains the following four species (Walter & Boxshall 2019): *H. vietnamensis* Pleşa, 1969 (type species); *H. feiticeira* (Lotufo, 1995); *H. uguaipuku* (Lotufo, 1995); and *H. plesai* Karanovic, 2008.

The genus *Pseudocyclopina* contains six species (Walter & Boxshall 2019), all from Antarctica (Elwers *et al.* 2001). Four of them were described by Elwers *et al.* (2001), who also revised the generic diagnosis and redescribed the type species from the type material deposited by Giesbrecht (1902). The genus was established by Lang (1946), who noted the sexually dimorphic second leg exopod as a unique feature among cyclopinids. Lindberg (1952) provided a short diagnosis and tentatively included one more species from the Northern Atlantic, which is now considered a member of a different genus (Walter & Boxshall 2019). Finally, Pesce & Pandourski (2002) described the sixth species from Antarctica, albeit without males. Males are also unknown for three species described by Elwers *et al.* (2001).

Cyclopinid systematics is still in a state of flux (Boxshall & Jaume 2012 and references therein), which is perhaps best illustrated by the fact that Walter & Boxshall (2019) list Heterocyclopina in the family Cyclopinidae and the supposedly closely related genus Procyclopina in the family Hemicyclopinidae. Both genera were considered members of the allegedly monophyletic Hemicyclopinidae by Martínez Arbizu (2001a), in addition to the above mentioned Pseudocyclopina, Parapseudocyclopinodes, and four other genera. However, the genus Pseudocyclopina was considered a member of Cyclopinidae by Elwers et al. (2001), with one of the co-authors being Martínez Arbizu. As noted by Boxhall & Halsey (2004), the phylogenetic analysis presented by Martínez Arbizu (2001a) as a justification for the establishment of the Hemicyclopinidae was not parsimony based and hinged on a single character, which is also present in at least four unrelated genera. Some of the characters used by Martínez Arbizu (2000a, 2000b, 2001a, 2001b, 2006) to define supposedly monophyletic families of cyclopinids were shown by Karanovic (2008) to be part of intraspecific variability, and sometimes even mere asymmetries. A polyphyletic nature of cyclopinids was already suspected by Ho (1986), Ho & Thatcher (1989), and Huys & Boxshall (1991), based on the analysis of morphological characters. It was confirmed by Khodami et al. (2017), based on the analysis of four genes and 205 copepod species. However, the molecular phylogeny presented by Khodami et al. (2017) did not recover monophyly of previously proposed monophyletic families (where they had representatives of more than one genus). The same authors proposed another two new families, each containing a single cyclopinid genus, and one of them a single species. This certainly contributes very little to our understanding of the phylogenetic relationships between cyclopinid genera, but unfortunately, no comprehensive, parsimony based test of the validity of the new families has yet been carried out (Boxshall & Jaume 2012).

# Material and methods

All specimens were collected from the intertidal zone in four localities in Korea, using the Karaman-Chappuis method. This sampling technique involves digging a hole on the beach down to the water level and then decanting the inflowing interstitial water and filtering it through a plankton net (mesh size 30 µm). All samples were fixed in 99 % ethanol, sorted in the laboratory also in 99 % ethanol, using an Olympus SZX12 dissecting microscope with PLAPO objectives and magnification of up to 200x. Locality data and number of specimens are listed for each species separately and all material is deposited in the National Institute of Biological Resources (NIBR), Incheon, South Korea.

Some specimens were dissected and mounted on microscope slides in Faure's medium (see Stock & von Vaupel Klein 1996), and dissected appendages were then covered by a coverslip. For the urosome, two human hairs were mounted between the slide and coverslip during examination, to prevent squashing. All line drawings were prepared using a drawing tube attached to a Leica MB2500 phase-interference compound microscope, equipped with N-PLAN (5x, 10x, 20x, 40x and 63x dry) or PL FLUOTAR (100x oil) objectives. Specimens that were not drawn were examined in glycerol and, after examination, were stored in 99.9 % ethanol. Specimens for scanning electron microscopy (SEM) were transferred into pure isoamyl-acetate for two hours, critical-point dried, mounted on stubs, coated in gold, and observed under a Hitachi S-4700 scanning microscope on the in-lens detector, with an accelerating voltage of 10 kV and working distances between 12 and 13.5 mm; micrographs were taken with a digital camera.

The terminology for morphological characters follows Huys & Boxshall (1991), except for the numbering of setae on the caudal rami (not used) and small differences in the spelling of some appendages (antennula, mandibula, maxillula instead of antennule, mandible, maxillule); the latter as an attempt to standardise the terminology for homologous appendages in different crustacean groups.

#### Results

# Order Cyclopoida Burmeister, 1834

Family Cyclopinidae Sars, 1913

#### Genus Heterocyclopina Pleşa, 1969

*Heterocyclopina koreaensis* sp. nov.

(Figs. 1–7)

Type locality. Korea, South Coast, Bangjukpo, beach, intertidal sand, 34°37.826'N 127°47.574'E.

**Specimens examined.** Holotype female dissected on one slide, collected from the type locality, 19 August 2013, leg. T. Karanovic.

Paratypes: one male (allotype) and two females dissected on one slide each, two females in alcohol, and two females on one SEM stub (together with specimens of *Koreacyclopina wellsi*; row no. 2), all collected from Korea, West Coast, Jeonbuk-do, Gyeokpo-ri, Gyeokpo beach, intertidal sand, 35°37.953'N 126°28.118'E, 13 April 2013, leg. T. Karanovic.

Etymology. The species name refers to Korea. It is an adjective for place, made with the Latin suffix "-ensis"

**Description.** Female (based on holotype and six paratypes). Body length, excluding caudal setae, from 335 to 385 µm. Colour of preserved specimens yellowish and nauplius eye not visible. Integument on all somites smooth (Figs 1, 2), with light bacterial cover, spinules only on anal somite and caudal rami, cuticular pores on all somites, and sensilla on all but penultimate somite; hyaline fringes of prosomites smooth, of urosomites serrated. Habitus (Figs. 1A, 2A) slender in dorsal view and without pronounced distinction between prosome and urosome, distinction more pronounced in lateral view, prosome about 1.3 times as long as urosome, greatest width in dorsal view at posterior end of cephalothorax. Body about 4.8 times as long as wide in dorsal view and cephalothorax 1.5 times as wide as genital double-somite. First pedigerous somite not fused to cephalothorax, but its tergites partly covered with posterior extensions of cephalothoracic shield (Fig. 1C). Pedigerous somites without lateral expansions. Rostrum (Fig. 1B) well-developed, membranous, very broad. Cephalothorax (Figs. 1A, B, C, 2A) 1.6 times as long as wide, about 1.3 times as long as free prosomites combined, representing around one third of body length. Second to fourth free prosomites (Figs. 1D, E, F, 2B, C, D) progressively shorter and narrower towards posterior end and with fewer cuticular organs.

First urosomite (Fig. 2D) shortest, laterally expanded in posterior part.

Genital double-somite (Figs. 2E, 3H, 4A, B) about 1.3 times as long as wide in ventral view, widest anterior part nearly 1.3 times as wide as posterior margin; anterior part (second urosomite) with one pair of narrowly spaced dorsal sensilla (Fig. 3H), dorsal median pore, one pair of ventral pores next to copulatory pore (Fig. 4A), and one pair of lateral pores next to sixth legs (Fig. 3G); posterior part (third urosomite) with one pair of more widely spaced dorsal sensilla than in anterior part (Fig. 2E), dorsal median pore, one pair of ventral pores and sensilla each (Fig. 4A), two pairs of lateral sensilla, and one pair of lateral pores (Fig. 4B). Median copulatory pore (Fig. 4A) wide and short, situated in first quarter. Copulatory duct short, narrow, rigidly sclerotized, directed posteriorly. Seminal receptacles (Fig. 4A) small, ovoid, spaced very closely, even more rigidly sclerotized than copulatory duct, with internal folds, reaching more than half of anterior part of double-somite, together representing 37% of somite width. Oviducts not rigidly sclerotized and therefore not clearly visible. Genital apertures situated laterally, covered by reduced sixth legs. Fourth urosomite (Fig. 1G, 2F, 4A, B) with sensilla and pores as in third urosomite, except without median dorsal pore. Fifth urosomite (Fig. 4A, B) with single pair of widely spaced ventral pores. Sixth (anal) urosomite (Figs. 1H, 2G, 4A, B) with one pair of large dorsal sensilla, one pair of dorsal pores, diagonal rows of large spinules in shallow anal sinus, and posterior row of spinules; anal operculum very short, broad, covered by hyaline fringe of fifth urosomite.

Caudal rami (Figs. 2H, 3A, B, 4A, B) cylindrical, about five times as long as wide, narrowly spaced on anal somite, diverging posteriorly, with pair of dorsolateral pores in last third, minute spinules at base of lateral and outer apical setae, posterior ventral row of large spinules, and seven setae. All setae slender and bipinnate, and all except dorsal seta uniarticulated at base; dorsal seta about 1.2 times as long as ramus, inserted very close to median posterior corner, biarticulated at base; anterior lateral seta smallest, about 0.7 times as long as one ramus width, inserted at first third of ramus length; posterior lateral seta 1.4 times as long as ramus width, inserted slightly anterior than second third of ramus length; outermost and innermost apical setae slightly shorter and more slender than posterior lateral seta; principal apical setae with breaking planes, inner one nearly four times as long as caudal ramus and twice as long as outer one.

Antennula (Figs. 1A, B, 3C, 4C) reaching two thirds of cephalothoracic shield with its distal tip, stout, smooth, cylindrical but tapering towards distal end, 15-segmented but second segment with signs of incomplete segmentation along caudal margin, with most setae smooth and slender and all aesthetascs short and slender; armature formula (ae = aeshetasc) 3.14.2.2.2.1.1.1.1.0.2.2+ae.2.2+ae.6+ae; no setae with breaking planes, only three subapical setae on fifteenth segment biarticulated, one seta on fifth and one on sixth segment short and spiniform; second segment largest and longest, but incomplete segmentation suggesting fusion of at least four ancestral segments, about 1.3 times as long as wide; twelfth segment second longest, about 1.3 times as long as wide; about as long as thirteenth and fourteenth segments combined.

Antenna (Fig. 5A) slender, cylindrical, three-segmented but with some signs of ancestral five-segmented state; coxa minute, largely fused to allobasis, unornamented; allobasis with short surface suture along inner margin indicating ancestral segment boundary between basis first endopodal segment, twice as long as wide, unornamented, armed with one inner and one outer (exopodal) seta, both of similar length, about half as long as basis; first endopodal segment 0.8 times as long as basis, twice as long as wide, with spinules along outer convex margin, and with single inner seta; second endopodal segment slightly longer and more slender than first endopodal, with five inner setae (one lateral and four subapical; one subapical seta spiniform, other slender); third endopodal segment slightly shorter than first endopodal, 2.6 times as long as wide, with four strong prehensile apical setae, one slender apical seta, and two slender subapical setae.

Mandibula (Fig. 5B) with large coxa, smaller basis, two-segmented endopod, and four-segmented exopod, although first exopodal segment with small incomplete suture; coxal gnathobase with relatively wide cutting edge consisting of large teeth (ventralmost largest), several small spinules in between teeth, and two setae at dorsal corner; dorsalmost seta on cutting edge unipinnate, about 1.6 times as long as other, smooth seta; basis 2.3 times as long as wide, with single inner seta; endopod 0.7 times as long as basis, with two setae on first and five setae on second segment; exopod slightly shorter than basis but much more slender, with armature formula 1.1.1.2.

Maxillula (Fig. 5C) unornamented, composed of well-developed praecoxa and three-segmented palp; arthrite of praecoxa with six strong apical spines and three spiniform setae, proximalmost seta longest and strongest; palp slightly smaller than praecoxa, composed of large rectangular coxobasis, ovoid small endopod, and ovoid and even smaller exopod; coxobasis 2.3 times as long as wide, with single exopodal seta and four inner setae (two very strong and two slender); endopod as long as width of basis, about 1.4 times as long as wide, with two lateral and four apical slender setae; exopod 0.8 times as long as endopod, as long as wide, with four apical slender setae.

Maxilla (Fig. 5D) stout, 2.6 times as long as wide, tapering towards distal end, unornamented, composed of praecoxa, coxa, basis, and three-segmented endopod; praecoxa largest, quadrate, with four setae on proximal



**FIGURE 1.** *Heterocyclopina koreaensis* **sp. nov.**, paratype female 1, SEM photographs, all in lateral view: A, habitus; B, anterior part of cephalothorax with rostrum and proximal part of antennula; C, posterolateral corner of cephalothoracic shield, partly overlapping free first pedigerous somite; D, tergite of second pedigerous somite; E, tergite of third pedigerous somite; F, tergite of fourth pedigerous somite; G, fourth urosomite; H, sixth urosomite with anterior part of caudal rami.



**FIGURE 2.** *Heterocyclopina koreaensis* **sp. nov.**, paratype female 2, SEM photographs, all in dorsal view: A, habitus; B, second pereiopodal somite; C, third pedigerous somite; D, fourth pedigerous somite and first urosomite; E, genital double-somite (fused second and third urosomites); F, fourth urosomite; G, sixth urosomite; H, caudal rami.



**FIGURE 3.** *Heterocyclopina koreaensis* **sp. nov.** SEM photographs; A-G, paratype female 1, lateral view; H, paratype female 2, dorsal view: A, anterior part of caudal rami; B, posterior part of caudal rami; C, distal part of antennula; D, first swimming leg; E, second swimming leg; F, fifth leg; G, sixth leg; H, anterior part of genital double-somite with left sixth leg.



FIGURE 4. *Heterocyclopina koreaensis* sp. nov., holotype female, line drawings: A, urosome, ventral view; B, urosome, lateral view; C, antennula.

endite and one seta on distal endite; coxa 0.7 times as long as praecoxa, also quadrate, with three setae on both proximal and distal endites; basis half as long as coxa, with basally fused, smooth and robust claw and two articulated setae, proximal seta strong and bipinnate, 1.5 times as long as claw, distal seta smooth and minute; endopod 1.5 times as long as basis, first segment twice as long as second and armed with two strong setae, second segment twice as long as third and armed with one strong seta and one short and smooth seta, third segment minute, with one strong and two slender setae.



**FIGURE 5.** *Heterocyclopina koreaensis* **sp. nov.**, holotype female, line drawings: A, antenna; B, mandibula; C, maxillula; D, maxilla; E, maxilliped.



**FIGURE 6.** *Heterocyclopina koreaensis* **sp. nov.**, holotype female, line drawings: A, first swimming leg; B, second swimming leg; C, third swimming leg; D, fourth swimming leg; E, fifth leg.



**FIGURE 7.** *Heterocyclopina koreaensis* **sp. nov.**, allotype male, line drawings: A, urosome, ventral view; B, urosome, lateral view; C, antennula; D, fifth leg.

Maxilliped (Fig. 5E) prehensile, slender, almost four times as long as wide, tapering in proximal half but cylindrical in distal half, seven-segmented, composed of syncoxa, basis, and five-segmented endopod; syncoxa almost ovoid, 1.7 times as long as wide, unornamented, with four elements on proximal endite and two on distal endite; basis half as long as syncoxa, with row of slender spinules on inner margin and two setae on only endite; first endopodal segment triangular, small, with single sender seta; second endopodal segment longest, cylindrical, twice as long as wide, with single slender seta; third endopodal segment half as long as second endopodal, 1.25 times as long as wide, with two prehensile setae; fifth endopodal segment twice as long as fourth endopodal, as long as wide, with two prehensile and two slender setae.

Swimming legs (Figs. 3D, E, 6A, B, C, D) composed of short praecoxa, rectangular large coxa, triangular basis, three-segmented exopod, three-segmented endopod, and coxae of opposite appendages connected with intercoxal sclerite; coxae of all legs with pore on anterior surface, row of minute spinules on outer distal corner, and slender seta on inner distal corner; intercoxal sclerites with slightly concave distal margin, and all, except on first leg, with two parallel rows of spinules on posterior surface; basis with convex inner margin, slender outer seta, strong inner spine on first leg and short spiniform process instead on other legs, anterior pore (except on fourth leg), row of spinules at base of endopod, and spiniform process between exopod and endopod; all exopodal and endopodal segments with spinules along outer margin and also along distal margin on anterior surface, first exopodal segment also along inner margin; second endopodal and third exopodal segments with single cuticular pore each; first exopodal segment with single outer spine; second exopodal segment with outer spine and inner seta; first and second endopodal segment seta formula 5.5.5.5 and spine formula 3.4.4.3; third endopodal segment of fourth leg 1.6 times as long as wide.

Fifth leg (Fig. 3F, 6E) small, two-segmented, with short intercoxal sclerite; first segment 1.4 times as wide as long, with posterior row of minute spinules and single outer seta; distal segment slightly longer but much narrower than first, 1.4 times as long as wide, with spinules along both inner and outer margins, apical central seta and two subapical spines; inner spine about as long as apical seta, about 1.5 times as long as second segment or outer spine.

Sixth leg (Figs. 3G, H, 4B) simple triangular cuticular plate, 1.6 times as wide as long, unornamented, with inner strong spine, which about 1.5 times as long as outer slender seta.

Male (based on allotype). Urosome (Fig. 7A, B) slightly more slender than in female, and second and third urosomites fully articulated, but ornamentation as in female.

Caudal rami (Fig. 7A, B) slightly shorter than in female, but armature and ornamentation without significant differences.

Antennula (Fig. 7C) longer and more robust than in female in comparison to cephalothorax, strongly digeniculate, 15-segmented, with proximal geniculation between ninth and tenth segments, and distal geniculation between thirteenth and fourteenth segments; armature formula: 1.1.9.2.2.1+ae.2.1.2+ae.3+ae.1.2.2.1+ae.10+2ae; thirteenth and fourteenth segments with strong cuticular ridges along anterior (geniculating) surface; eleventh, twelfth, and thirteenth segments with short spiniform seta each, all other setae slender and most also smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, and all four swimming legs as in female.

Fifth leg (Fig. 7D) three-segmented; first segment similar to female; second segment with single inner seta; third segment similar to second in female, but shorter and with one additional inner seta.

Sixth leg (Fig. 7B) with inner spine and two slender setae; outer seta 1.4 times as long as central seta and 2.5 times as long as spine.

**Variability.** The holotype (and only) female from Bangjukpo was larger and longer than any paratype female (all from Gyeokpo) (410 μm vs. 335-385 μm), but no other differences were observed.

#### Koreacyclopina gen. nov.

**Diagnosis.** First pedigerous somite not fused to cephalothorax, but covered with cephalothoracic shield. Fifth pedigerous somite smooth. Genital double-somite with large depression around single median copulatory pore, with small ovoid receptacula seminis. Spermatophores glued together, forming large but compact triangular flap. Caudal rami long and slender, with minute proximal lateral setae. Antennula 13-segmented in female, 16-segmented in male. Antenna with two exopodal setae. Mandibula with two setae on first endopodal segment, and three setae on last

exopodal segment. Maxillula with four setae on basis, seven setae on endopod, and four setae on exopod. Maxilliped long and slender. All swimming legs with three-segmented exopods and endopods, without inner seta on first exopodal segment, and with two rows of spinules on intercoxal sclerite; second endopodal segment of first to third legs with single seta, that of fourth leg with two setae; third endopodal segment of first and fourth leg with five setae, that of second and third leg with six setae; third exopodal segment of first to fourth leg with spine formula 3.4.4.3 and seta formula 5.5.5.5. Fifth leg in both sexes two-segmented, with single outer seta on first segment; second segment in female with three spines and single apical seta; second segment in male with six elements (three spines, one apical seta, and two spiniform inner setae). Sixth leg with three elements in male and two in female. Third exopodal segment of male second leg with distal spine fused to somite, smooth, and shorter than other spines.

**Etymology.** The generic name is composed of the country name Korea and the existing generic name *Cyclopina* Claus, 1862, the latter being the type and most speciose genus of the Cyclopinidae.

Type and only species. Koreacyclopina wellsi sp. nov.

#### Koreacyclopina wellsi sp. nov.

Type locality. Korea, East Coast, Uljin, beach, intertidal sand, 36°18.309'N 129°22.648'E.

**Specimens examined.** Holotype female dissected on one slide, allotype male dissected on one slide, four paratypes (three females and one male) dissected on one slide each, two paratypes (one female and one male) in alcohol, and two paratype females on one SEM stub (together with other specimens of *Koreacyclopina wellsi* and with specimens of *Heterocyclopina koreaensis*; row no. 1), all collected from the type locality, 6 May 2016, leg. T. Karanovic.

Two paratypes (one female and one male) dissected on one slide each, five female paratypes on one SEM stub (together with other specimens of *Koreacyclopina wellsi* and with specimens of *Heterocyclopina koreaensis*; row no. 3), and 15 paratypes (nine females, three males, and three copepodids) in alcohol, all collected from Korea, West Coast, Wido Island, beach, intertidal sand, 35°35.089'N 126°15.196'E, 12 April 2013, leg. T. Karanovic.

**Etymology.** The species is named in honour of the late Prof. John Wells, in recognition of his contributions to the taxonomy of cyclopinid copepods (Wells 1965, 1967), which perhaps remained in the shadow of his colossal contributions to the taxonomy and systematics of harpacticoid copepods (Wells 2007).

**Description.** Female (based on holotype and 12 paratypes). Body length, from 525 to 540 µm. Colour of preserved specimens yellowish and nauplius eye not visible. Integument on all somites smooth (Figs 8, 9), with very little bacterial cover, minute spinules only on anal somite and caudal rami, cuticular pores on all somites, and sensilla on all but penultimate somite; hyaline fringes of prosomites smooth, of ursomites serrated. Habitus (Figs. 8A, 9A) relatively slender in dorsal view, but with pronounced distinction between prosome and urosome (especially in lateral view), prosome ovoid, about 1.3 times as long as urosome, greatest width in dorsal view at posterior end of cephalothorax. Body about 3.3 times as long as wide in dorsal view and cephalothorax twice as wide as genital double-somite. First pedigerous somite not fused to cephalothorax, but completely covered with posterior extension of cephalothoracic shield (see Fig. 8C). Pedigerous somites without lateral expansions. Rostrum (Fig. 8B) well-developed, membranous, very broad. Cephalothorax (Figs. 8A, B, C, 9A, B, C) 1.3 times as long as wide, about twice as long as free prosomites combined, representing around 38% of body length. Second to fourth prosomites (Figs. 8D, E, 9D, E) progressively shorter and narrower towards posterior end, and with fewer cuticular organs.

First urosomite (Figs. 9F) shortest, laterally expanded in posterior part.

Genital double-somite (Figs. 8F, 9G, 11A, B, C) about 1.15 times as long as wide in ventral view, widest anterior part 1.4 times as wide as posterior margin; anterior part (second urosomite) with one pair of narrowly spaced dorsal sensilla, dorsal median pore, and one pair of lateral pores next to sixth legs; posterior part (third urosomite) with one pair of narrowly spaced dorsal sensilla, one pair of lateral sensilla, and two pairs of widely spaced ventral pores. Median copulatory pore inside large depression, small, triangular, covered by large triangular flap formed by glued spermatophores. Copulatory duct short, narrow, rigidly sclerotized, directed anteriorly and extended anteriorly past seminal receptacles. Seminal receptacles very small, ovoid, spaced widely and forming cross-like structure with copulatory duct, slightly less rigidly sclerotized than copulatory duct, without internal folds. Oviducts not rigidly sclerotized and therefore not clearly visible. Genital aperture situated laterally, covered by reduced sixth legs. Fourth urosomite (Figs. 9G, 11A) with sensilla and pores as in third urosomite, except ventralmost pair of pores more narrowly spaced. Fifth urosomite (Fig. 8G, 9H, 11A) with one pair of widely spaced ventral pores and one pair of

lateral pores. Sixth urosomite (Figs. 8H, 9H, 11A) with one pair of large dorsal sensilla, one pair of lateral sensilla, one pair of dorsal pores, one pair of ventral pores, two diagonal rows of minute spinules in narrow and deep anal sinus; anal operculum very short, narrow, covered by posterior margin of fifth urosomite.

Caudal rami (Figs. 8A, 9A, H, 10A, 11A) cylindrical, about six times as long as wide, narrowest in central part, narrowly spaced on anal somite, slightly diverging posteriorly, with pair of ventrolateral pores around midlength, minute spinules at base of lateral and outer apical setae, posterior ventral row of large spinules, and seven setae. Almost all setae broken in all examined specimens, so their size could only be estimated from width of remaining basal part; all except dorsal seta uniarticulated at base; dorsal seta inserted close to median posterior corner, biarticulated at base; anterior lateral seta minute, hardly larger than some sensilla, inserted at about two fifths of ramus length; posterior lateral inserted dorsolaterally at about three quarters of ramus length; principal apical setae with breaking planes.

Antennula (Figs. 8A, 9A, 10D, 11D, E) reaching two thirds of cephalothoracic shield with its distal tip, stout, cylindrical but tapering towards distal end, 13-segmented but second segment with signs of incomplete segmentation along posterior margin, with most setae smooth and slender and both aesthetascs short and slender, row of small spinules only on first segment; armature formula 3.12.3.5.1.1.1.1.+ae.2.2.6+ae; one large seta on tenth and one on thirteenth segment with breaking planes, only two subapical setae on thirteenth segment biarticulated; second segment largest and longest, about 0.9 times as long as wide; tenth segment second longest, about 1.1 times as long as wide; thirteenth segment 1.7 times as long as wide, about as long as eleventh and twelfth segments combined.

Antenna (Figs. 10F, 11F) slender, cylindrical, five-segmented, composed of short coxa, long basis, and even longer three-segmented endopod; coxa half as long as wide, unarmed and unornamented; basis 2.6 times as long as wide, with longitudinal row of minute spinules along outer margin, several large spinules on inner margin, one inner and two outer (expodal) slender and smooth setae; first endopodal segment 0.7 times as long as basis, 2.2 times as long as wide, with spinules along outer convex margin, and with single inner seta; second endopodal segment slightly longer and more slender than first endopodal, with several longitudinal rows of small spinules along outer margin, and five setae on inner margin (one lateral and four subapical; one subapical seta spiniform, other slender); third endopodal segment slightly shorter than first endopodal, 3.2 times as long as wide, with tuft of spinules on outer distal corner, four strong prehensile apical setae, one slender apical seta, and two slender subapical setae.

Mandibula (Figs. 10B, F, 12A) as in previous species, except last exopodal segment with three setae, last endopodal segment longer, dorsalmost tooth on cutting edge shorter, most teeth on cutting edge multicuspidate, cutting edge with more spinules, and basis, endopod, and exopod with large spinules.

Maxillula (Figs. 10B, 12B, C) as in previous species, except with extra slender seta on endopod, and also distal part of endopod more elongated (and consequently lateral setae inserted more proximally).

Maxilla (Fig. 12D) more tapering distally than in previous species but also 2.6 times as long as wide, unornamented, segmentation as in previous species, armature as in previous species, except proximal coxal endite with only two setae, third endopodal segment with only two setae, and distal basal seta (spine?) not fused to basis.

Maxilliped (Figs. 10C, 12E) as in previous species, except syncoxa with spinules along outer margin, third endopodal segment more elongated (2.3 times as long as wide and 0.8 times as long as second endopodal), and third endopodal segment with single prehensile seta (in total only four prehensile setae on endopod).

Swimming legs (Figs. 10G, H, 13A, B, C, D, E, F) segmentation, ornamentation, and most armature as in previous species, except second endopodal segment of fourth leg with two inner setae; third endopodal segment of fourth leg nearly 1.9 times as long as wide.

Fifth leg (Figs. 8F, 10E, 13G) segmentation and most armature and ornamentation as in previous species, except each segment with anterior cuticular pores, and second segment with additional outer spine.

Sixth leg (Fig. 9G) as in previous species, except slender seta much shorter.

Male (based on allotype). Urosome (Fig. 14A) as in previous species slightly more slender than in female, and second and third urosomites fully articulated, but ornamentation as in female; genital somite slightly longer than in previous species.

Caudal rami (Fig. 14A) significantly shorter than in female (about 4.3 times as long as wide), but armature and ornamentation without significant differences.

Antennula (Fig. 14B) shape, segmentation, geniculation, ornamentation, and most armature as in previous species, except ultimate segment comparatively shorter, and armature formula 1.1.7.2.2.2+ae.3.1.3+ae.4+ae.1.2.2.1+a e.10+2ae.



**FIGURE 8.** *Koreacyclopina wellsi* **gen. et sp. nov.**, SEM photographs, all in lateral view; A & B, paratype female 1 from Wido; C-H, paratype female 2 from Uljin: A, habitus; B, anterior part of cephalothorax with rostrum and proximal part of antennula; C, posterior corner of cephalothoracic shield, partly overlapping free first pedigerous somite; D, tergite of second pedigerous somite; E, tergite of third pedigerous somite; F, first urosomite and genital double-somite (fused second and third urosomites), with fifth legs and attached spermatophores; G, fourth urosomite; H, sixth urosomite.



**FIGURE 9.** *Koreacyclopina wellsi* **gen. et sp. nov.,** SEM photographs, all in dorsal view; A & B, paratype female 3 from Wido; C-H, paratype female 4 from Uljin: A, habitus; B, posterior median part of cephalothorax; C, anterior tip of cephalothorax; D, second pedigerous somite; E, third and fourth pedigerous somites; F, first urosomite; G, genital double-somite (fused second and third urosomites) and fourth urosomite; H, fifth and sixth urosomites with anterior part of caudal rami.



**FIGURE 10.** *Koreacyclopina wellsi* **gen. et sp. nov.**, SEM photographs, A-C, paratype female 2 from Uljin; D & E, paratype female 1 from Wido; F, paratype female 5 from Wido; G & H, paratype female 6 from Wido: A, anterior part of caudal rami in lateral view; B, mandibular palp, maxillula, and maxilla; C, maxilliped; D, distal part of antennula; E, fifth legs; F, antenna and mandibular palp; G, endopod of first swimming leg; H, exopod of first swimming leg.



**FIGURE 11.** *Koreacyclopina wellsi* **gen. et sp. nov.**, holotype female, line drawings: A, urosome, ventral view; B, gonopore and seminal receptacles, without spermatophores; C, spermatophores, removed from urosome and flattened; D, left antennula; E, distal tip of right antennula; F, antenna.



**FIGURE 12.** *Koreacyclopina wellsi* **gen. et sp. nov.**, holotype female, line drawings: A, mandibula; B, maxillular gnathobase; C, maxillular palp; D, maxilla; E, maxilliped.



**FIGURE 13.** *Koreacyclopina wellsi* **gen. et sp. nov.**, holotype female, line drawings: A, first swimming leg; B, second swimming leg, without last two endopodal segments; C, endopod of second swimming leg; D, intercoxal sclerite of third swimming leg; E, third endopodal segment of third swimming leg; F, fourth swimming leg; G, fifth leg, slightly awkwardly mounted.



**FIGURE 14.** *Koreacyclopina wellsi* **gen. et sp. nov.**, allotype male, line drawings: A, urosome, ventral view; B, antennula; C, third exopodal segment of second swimming leg; D, second and third endopodal segments of second swimming leg; E, third exopodal segment of fourth leg; F, second and third endopodal segments of fourth swimming leg.

Antenna, mandibula, maxillula, maxilla, and maxilliped as in female.

Swimming legs (Fig. 14C, D, E, F) as in female, except third exopodal segment of second leg with distal spine fused with segment, short, and smooth.

Fifth leg (Fig. 14A) segmentation and most armature as in female, except second segment with two extra inner setae and apical seta much longer.

Sixth leg (Fig. 14A) as in previous species, but outer seta twice as long as central seta and inner spine.

**Variability.** One female from Wido with lateral pore on third pedigerous somite situated more anteriorly (almost in line with two central lateral sensilla). Flap formed by fused spermatophores remarkably uniform.

# Discussion

Heterocyclopina koreaensis sp. nov. is most similar to the type species of the genus, H. vietnamensis. They share the same armature formula of the mandibula, all swimming legs, and fifth legs in both sexes, as well as the shape and armature of the caudal rami, shape of the seminal receptacles, and articulation of the male antennula. Major differences in the female characters include the length of the distal lateral seta on the caudal rami (about twice as long as proximal lateral seta in *H. koreaensis* vs. as long as proximal lateral seta in *H. vietnamensis*), length of the dorsal seta on the caudal rami (1.1 times as long as caudal ramus in *H. koreaensis* vs. 0.8 times in *H. vietnamensis*), width of seminal receptacles (representing 37% of double-somite width in H. koreaensis, vs. less than 20% in H. vietnamensis), articulation of the antennula (ancestral segments 2-5 not fully articulated on anterior surface in H. koreaensis, vs. all 18 segments fully articulated in *H. vietnamensis*), articulation of the antenna (basis and first endopodal segment largely fused in H. koreaensis, vs. these segments fully articulated in H. vietnamensis), armature of the antenna (exopodal seta present in *H. koreaensis*, vs. absent in *H. vietnamensis*), and articulation of the mandibular exopod (one-segmented in H. koreaensis, vs. four-segmented in in H. vietnamensis; although note that in both species it carries five setae). Also, mouth appendages in *H. vietnamensis*, as illustrated by Pleşa (1969), mostly have fewer setae than in *H. koreaensis*, but these could easily be missed in these small cyclopoids, especially with inferior optics in older light microscopes. Scanning electron microscopes (SEMs) were not widely available in the late 1960s (Outley et al. 1965), so Plesa (1969) did not examine his animals with an SEM. Major differences in male characters include the length of the apical seta on the fifth leg (longer than apical spine in H. koreaensis vs. shorter than apical spine in *H. vietnamensis*) and length of central seta on the sixth leg (nearly twice as long as inner spine in H. koreaensis vs. about as long as inner spine in H. vietnamensis). Plesa (1969) did not illustrate the armature of the male antennula (except for the large aesthetasc on the last segment), so these characters cannot be compared, and neither can details of somite ornamentation. Martínez Arbizu (2001a) claimed to have studied specimens of H. vietnamensis from China with a four-segmented mandibular exopod (similar to that of H. koreaensis), but gave no illustrations or other descriptions. Given the nature and number of differences between the Vietnamese and Korean species, the specific status of the Chinese population would need to be re-examined, which would require a detailed description. It would not be surprising that we are dealing with a number of closely related congeners, as was recently confirmed with molecular data and geometric morphometrics for some other marine copepods from this region (Karanovic et al. 2018). The Australian H. plesai Karanovic, 2008 differs from H. koreaensis by longer caudal rami with a more robust proximal lateral seta, larger seminal receptacles, an additional exopodal seta on the antenna, absence of the outer seta on the third endopodal segment of the second leg, an additional seta on the second endopodal segment of third and fourth legs, and a clearly 19-segmented female antennula; unfortunately, males are still unknown for this species (Karanovic 2008). The Brazilian H. feiticeira (Lotufo, 1995) and H. uguaipuku (Lotufo, 1995) both differ from the new species by a two-segmented male fifth leg, although the armature is not different. The latter also has a different armature of the second to fourth swimming legs, as well as longer caudal rami. The former has an additional seta on the second endopodal segment of the fourth leg and a short dorsal seta on the caudal rami (see Lotufo 1995).

*Koreacyclopina wellsi* gen. et sp. nov. is remarkable among cyclopinids because all examined females had two spermatophores attached and glued together in a large triangular flap-like structure, which rested in a large ventral depression on the genital double-somite. A superficially similar condition was observed and illustrated so far only in *Cyclopinodes elegans* (T. Scott, 1894) by Giesbrecht (1900), but in this species there seems to be hardly any additional material added to the two upside-down spermatophores, and there is no ventral depression on the genital

double-somite. The exact nature of this complex structure in the new genus would have to be examined further histologically, as it is impossible to conclude whether it contains any female integument even by studying SEM photographs. It is easy to dissect, always stays together as a compact unit, is remarkably uniform in shape in all specimens, and no females were observed without it. Another remarkable character of the new genus is its sexually dimorphic third exopodal segment of the second leg, with the distal spine being fused to the somite, smooth, and shorter than the other spines. This character was so far observed only in the genus *Pseudocyclopina* Lang, 1946, and the details of its shape and size suggest a common ancestry rather than convergent evolution. The two genera share a number of other characters, including the armature of the caudal rami, segmentation and most armature of the female fifth leg, and most armature of the male fifth leg. However, they differ in numerous characters (see Elwers et al. 2001; Pesce & Pandourski 2002). Most of the differences are reductions in armature or segmentation of appendages (and therefore could probably be interpreted as apomorphies) in the new genus: female antennula 13-segmented (vs. 15- or 16-segmented in Pseudocyclopina), first endopodal segment of the mandibula with two setae (vs. three), second endopodal segment of the mandibula with five setae (vs. six), basis of the maxillula with four setae (vs. five), first exopodal segments of all swimming legs without inner seta (vs. with inner seta), second endopodal segments of first to third swimming legs with single inner seta (vs. two), third endopodal segment of the first swimming leg with five setae (vs. six), first segment of the female fifth leg without inner seta (vs. with), and the male fifth leg three-segmented (vs. two-segmented). However, three setae on the last exopodal segment of mandibula in the new genus (vs. two in *Pseudocyclopina*) and an elongated prehensile maxilliped (vs. short) suggest that the Korean representative is not an extremely reduced member of *Pseudocyclopina*, but they shared a common ancestor before any diversification in the latter genus. This scenario does not contradict available zoogeographical evidence, since all six *Pseudocyclopina* species are Antarctic endemics and can be distinguished from each other only by size, proportions of some segments and armature, and very rarely by armature formulae of any appendages (Elwers et al. 2001; Pesce & Pandourski 2002). All this points to an explosive radiation from a single common Antarctic ancestor, while its divergence from the Korean genus must have occurred much earlier.

In the key to genera of cyclopinids provided by Boxshall and Halsey (2004) *Koreacyclopina* would key out as *Glareolina* Huys & Boxshall, 1990. The latter genus was established by Huys & Boxshall (1990) for a single species, described only after females from France by Herbst (1953). It differs from the Korean genus by much larger and differently shaped seminal receptacles, shorter caudal rami without a proximal lateral seta, and a 20-segmented antennula. They share the armature of the antenna (probably a plesiomorphic character), swimming legs and most mouth appendages, but it is possible that some smaller setae on the maxilla and maxilliped were omitted by Herbst (1953). This, and the lack of male characters, precludes any further analysis of the affinity between these genera. Karanovic (2008) synonymised *Glareolina* with the genus *Hemicyclopina* Herbst, 1953, after describing one new species from Australia that showed intermediate characters between the two genera. *Hemicyclopina* now includes four valid species (Walter & Boxshall 2019) and is the type genus of the supposedly monophyletic family Hemicyclopinia are the genera Arbizu 2001a). Karanovic (2008) also argued that the closest relatives of *Hemicyclopina* are the genera Arbizu (2000a) to be members of another supposedly monophyletic family: Cyclopettidae. However, none of the three genera has a sexually dimorphic second leg exopod, and all are probably only remotely related to *Koreacyclopina*.

Unfortunately, incomplete descriptions of many species and a lack of molecular data for a great majority of them, are among the main reasons for the current state of flux in cyclopinid systematics. The most comprehensive molecular phylogeny of copepods so far (Khodami *et al.* 2017) included only 12 cyclopinids, some of them not even identified to the genus level. Unfortunately, no members of the Hemicyclopinidae were studied, and only one species from Cyclopettidae. The fact that nearly 60% of all cyclopinid genera are monotypic (Boxshall & Halsey 2004; Karanovic 2008; Suárez-Morales & Almeyda-Artigas 2015; Walter & Boxshall 2019) clearly indicates that we are not even close to discovering the major extent of their diversity. Previously unobserved morphological features, such as the spermatophore flap in *Koreacyclopina*, are not uncommon with descriptions of many new species (Ivanenko & Defaye 2004; Defaye & Ranga Reddy 2008; Karanovic 2008; Suárez-Morales & Almeyda-Artigas 2015; Ohtsuka *et al.* 2016). Clearly, we will have to look for alternative characters when trying to reconstruct phylogenetic relationships between cyclopinids. Cuticular organs on somites were recently suggested as suitable micro-characters for reconstructing phylogenetic relationships between some harpacticoid copepods (Karanovic & Kim 2014b) and also for distinguishing closely related species using geometric morphometrics (Karanovic *et al.* 2016).

However, in cyclopoids they seem to be more numerous, variable, and difficult to homologize (Karanovic & Blaha 2019). They are certainly different between the two new Korean species described here, but some of them could easily be homologized and very little intraspecific variability was observed.

# Acknowledgments

This work was supported by a grant from the National Institute of Biological Resources (NIBR), funded by the ministry of Environment (MOE) of the Republic of Korea (NIBR201904101). I am very grateful to Prof Gi-Sik Min (Inha University, Incheon) for a continuous support through the research project 'Discovery of Korean Indigenous Species'. Several PhD students from Prof Min's lab were also very helpful with handling the specimens, and I am especially grateful to Mr Chi-Woo Lee. Finally, I would like to thank Prof. Ivana Karanovic and Ms Pham Thi Minh Huyen (both from the Hanyang University, Seoul) for their generosity in sharing research facilities and providing administrative help. The scanning electron microscope was made available through the courtesy of Prof. Jin Hyun Jun (Eulji University, Seoul), and I also want to thank Mr. Junho Kim (Eulji University, Seoul) for the technical help provided.

# References

Armonies, W. & Reise, K. (2000) Faunal diversity across a sandy shore. *Marine Ecology Progress Series*, 196, 49–57. https://doi.org/10.3354/meps196049

- Boxshall, G.A. & Halsey, S.H. (2004) An Introduction to Copepod Diversity 1 & 2. The Ray Society, London, xv + 966 pp.
- Boxshall, G.A. & Jaume, D. (2012) Three new species of copepods (Copepoda: Calanoida and Cyclopoida) from anchialine habitats in Indonesia. *Zootaxa*, 3150 (1), 36–58.

https://doi.org/10.11646/zootaxa.3150.1.2

- Brown, A.C. & McLachlan, A. (2006) *The Ecology of Sandy Shores*. Elsevier, Amsterdam, 328 pp. https://doi.org/10.1016/b978-012372569-1/50001-x
- Burmeister, H. (1835) Beschreibung einiger neuen oder weniger bekannten Schmarotzerkrebe, nebst allgemeinen Betrachtungen uber die Gruppe; welcher sie angehoren. Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum (Acta der Kaiserlichen Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher), Halle, 17, 269–336, pls. XXIII, XXIV, XXIVA, XXV.
- Chang, C.Y. (2009) Inland-water Copepoda. Illustrated Encyclopedia of Fauna and Flora of Korea, 42, 1-687.
- Chang, C.Y. (2010) Continental Cyclopoids I. Invertebrate Fauna of Korea, 21 (19), 1-92.
- Chang, C.Y. (2011) First record of the genus *Cyclopinoides* (Copepoda, Cyclopoida, Cyclopinidae) from the Pacific. *Animal Cells and Systems*, 15, 63–72.
  - https://doi.org/10.1080/19768354.2011.555132
- Claus, C. (1862) Untersuchungen über die Organisation und Verwandtschaft der Copepoden. (Im Auszuge zusammengestellt). Verhandlungen der physikalisch-medizinischen Gesellschaft zu Würzburg, 3, 51–103.
- Defaye, D. & Ranga Reddy, Y. (2008) A new Allocyclopina species (Copepoda, Cyclopoida, Cyclopinidae) from a hyporheic zone of the River Godavari, India, and comments on the morphological characters of the genus. Crustaceana, 81, 1119– 1141.

https://doi.org/10.1163/156854008X360851

Elwers, K., Martínez Arbizu, P. & Fiers, F. (2001) The genus *Pseudocyclopina* Lang in Antarctic waters: Redescription of the type-species, *P. belgicae* (Giesbrecht, 1902) and the description of four new species (Copepoda: Cyclopinidae). *Ophelia*, 54, 143–165.

https://doi.org/10.1080/00785236.2001.10409462

- Giere, O. (1993) *Meiobenthology, the Microscopic Fauna in Aquatic Sediments*. Springer-Verlag, Berlin, 328 pp. https://doi.org/10.1007/978-3-540-68661-3
- Giesbrecht, W. (1900) Mittheilungen über Copepoden 12–14. *Mittheilungen aus der Zoologischen Station zu Neapel*, 14, 39–82.
- Giesbrecht, W. (1902) Copepoden. In: Résultats du voyage du S.Y. Belgica en 1897-1898-1899, Zoologie. Rapports scientifiques publiés aux frais du Government Belge, 1902, 1–49.
- Gray, J.S. (1997) Marine biodiversity: patterns, threats and conservation needs. *Biodiversity and Conservation*, 6, 153–175 https://doi.org/10.1023/A:1018335901847

Gray, J.S. (2002) Species richness of marine soft sediments. *Marine Ecology Progress Series*, 244, 285–297. https://doi.org/10.3354/meps244285

Herbst, H.V. (1953) Weitere Cyclopoidea Gnathostoma (Crustacea Copepoda) des Küstengrundwassers. Kieler Meeresforsc-

hungen, 9, 257–270.

Herbst, H.V. (1955) Cyclopoida Gnathostoma (Crustacea Copepoda) von der brasilianischen Atlantikküste. *Kieler Meeresforschungen*, 11, 214–229.

- Ho, J.-S. (1986) Phylogeny of Cyclopoida. *In*: Schriever, G., Schminke, H.K. & Shih, C.-T. (Eds.), Proceedings of the Second International Conference on Copepoda, Ottawa, Canada, 13–17 August, 1984. *Syllogeus*, 58, pp. 177–183
- Ho, J.-S. & Thatcher, V.E. (1989) A new family of cyclopoid copepods (Ozmanidae) parasitic in the hemocoel of a snail from the Brazilian Amazon. *Journal of Natural History*, 23, 903–911. https://doi.org/10.1080/00222938900770471
- Huys, R. & Boxshall, G.A. (1990) The rediscovery of *Cyclopicina longifurcata* (Scott) (Copepoda: Cyclopinidae) in deep water in the north Atlantic, with a key to genera of the subfamily Cyclopininae. *Sarsia*, 75, 17–32. https://doi.org/10.1080/00364827.1990.10413438
- Huys, R. & Boxshall, G.A. (1991) Copepod Evolution. Ray Society, London, 468 pp.
- Ivanenko, V.N. & Defaye, D. (2004) A new genus and species of deep-sea cyclopoids (Crustacea, Copepoda, Cyclopinidae) from the Mid-Atlantic Ridge (Azores Triple Junction, Lucky Strike). *Zoosystema*, 26, 49–64.
- Jeong, C.-B., Lee, M.C., Lee, K.-W., Seo, J.S., Park, H.G., Rhee, J.-S. & Lee, J.-S. (2015) Identification and molecular characterization of dorsal and dorsal-like genes in the cyclopoid copepod *Paracyclopina nana*. *Marine Genetics*, 24, 319–327. https://doi.org/10.1016/j.margen.2015.08.002
- Karanovic, T. (2008) Marine interstitial Poecilostomatoida and Cyclopoida (Copepoda) of Australia. *Crustaceana Monographs*, 9, 1–331.

https://doi.org/10.1163/ej.9789004164598.i-332

Karanovic, T. (2014) On the phylogeny of Euryteinae (Crustacea, Copepoda, Cyclopoida), with description of one new species from Korea. *Zoologischer Anzeiger*, 253, 512–525. https://doi.org/10.1016/j.jcz.2014.07.002

Karanovic, T. (2017) Two new *Phyllopodopsyllus* (Copepoda, Harpacticoida) from Korean marine interstitial. *Journal of Species Research*, 6, 185–214.

https://doi.org/10.12651/JSR.2017.6(S).185

- Karanovic, T. & Blaha, M. (2019) Taming extreme morphological variability through coupling of molecular phylogeny and quantitative phenotype analysis as a new avenue for taxonomy. *Scientific Reports*, 9, 1–14. https://doi.org/10.1038/s41598-019-38875-2
- Karanovic, T. & Cho, J.-L. (2012) Three new ameirid harpacticoids from Korea and first record of *Proameira simplex* (Crustacea: Copepoda: Ameiridae). *Zootaxa*, 3368 (1), 91–127. https://doi.org/10.11646/zootaxa.3368.1.5
- Karanovic, T. & Cho, J.-L. (2016) Four new *Schizopera* (Copepoda, Harpacticoida) from marine interstitial habitats in Korea. *Zootaxa*, 4114 (1), 1–32.

https://doi.org/10.11646/zootaxa.4114.1.1

- Karanovic, T. & Cho, J.-L. (2017) Second member of the harpacticoid genera *Pontopolites* and *Pseudoleptomesochra* (Crustacea, Copepoda) are new species from Korean marine interstitial. *Marine Biodiversity*, 48, 367–393. https://doi.org/10.1007/s12526-017-0731-2
- Karanovic, T., Cho, J.-L. & Lee, W. (2012a) Redefinition of the parastenocaridid genus *Proserpinicaris* (Copepoda: Harpacticoida), with description of three new species from Korea. *Journal of Natural History*, 46, 1573–1613. https://doi.org/10.1080/00222933.2012.681316
- Karanovic, T., Djurakic, M., & Eberhard, S.M. (2016) Cryptic species or inadequate taxonomy? Implementation of 2D geometric morphometrics based on integumental organs as landmarks for delimitation and description of copepod taxa. *Systematic Biology*, 65, 304–327.

https://doi.org/10.1093/sysbio/syv088

- Karanovic, T., Grygier, M. & Lee, W. (2013) Endemism of subterranean *Diacyclops* in Korea and Japan, with descriptions of seven new species of the *languidoides*-group and redescriptions of *D. brevifurcus* Ishida, 2006 and *D. suoensis* Ito, 1954 (Crustacea, Copepoda, Cyclopoida). *ZooKeys*, 267, 1–76. https://doi.org/10.3897/zookeys.267.3935
- Karanovic, T. & Kim, K. (2014a) New insights into polyphyly of the harpacticoid genus *Delavalia* (Crustacea, Copepoda) through morphological and molecular study of an unprecedented diversity of sympatric species in a small South Korean bay. *Zootaxa*, 3783 (1), 1–96.

https://doi.org/10.11646/zootaxa.3783.1.1

- Karanovic, T. & Kim, K. (2014b) Suitability of cuticular pores and sensilla for harpacticoid copepod species delineation and phylogenetic reconstruction. *Arthropod Structure and Development*, 43, 615–658. https://doi.org/10.1016/j.asd.2014.09.003
- Karanovic, T., Kim, K. & Lee, W. (2014) Morphological and molecular affinities of two East Asian species of *Stenhelia* (Crustacea, Copepoda, Harpacticoida). *ZooKeys*, 411, 105–143. https://doi.org/10.3897/zookeys.411.7346
- Karanovic, T., Kim, K. & Lee, W. (2015) Concordance between molecular and morphology-based phylogenies of Korean *Enhydrosoma* (Copepoda: Harpacticoida: Cletodidae) highlights important synapomorphies and homoplasies in this genus

globally. Zootaxa, 3990 (4), 451–496.

https://doi.org/10.11646/zootaxa.3990.4.1

- Karanovic, T., Lee, S. & Lee, W. (2018) Instant taxonomy: choosing adequate characters for species delimination and description through congruence between molecular data and quantitative shape analysis. *Invertebrate Systematics*, 32, 551–580. https://doi.org/10.1071/IS17002
- Karanovic, T. & Lee, W. (2012) A new species of *Parastenocaris* from Korea, with a redescription of the closely related *P. biwae* from Japan (Copepoda: Harpacticoida: Parastenocarididae). *Journal of Species Research*, 1, 4–34. https://doi.org/10.12651/isr.2012.1.1.004
- Karanovic, T. & Lee, W. (2016) First records of *Hemicyclops tanakai* Itoh and Nishida, 2002 and *Tisbe ensifer* Fisher, 1860 (Crustacea, Copepoda) in Korea. *Journal of Species Research*, 5, 289–299. https://doi.org/10.12651/JSR.2016.5.3.289
- Karanovic, T., Yoo, H. & Lee, W. (2012b) A new cyclopoid copepod from Korean subterranean waters reveals an interesting connection with the Central Asian fauna (Crustacea: Copepoda: Cyclopoida). *Journal of Species Research*, 1, 155–173. https://doi.org/10.12651/JSR.2012.1.2.156
- Khodami, S., McArthur, J.V., Blanco-Bercial, L. & Martínez Arbizu, P. (2017) Molecular phylogeny and revision of copepod orders (Crustacea: Copepoda). *Scientific Reports*, 7, 1–11. https://doi.org/10.1038/s41598-017-06656-4
- Kim, I.-H. (2008) Sea Lice. *Invertebrate Fauna of Korea*, 21 (1), 1–66. https://doi.org/10.1038/s41598-017-06656-4
- Kim, K., Trebukhova, Y., Lee, W. & Karanovic, T. (2014) A new species of *Enhydrosoma* (Copepoda: Harpacticoida: Cletodidae) from Korea, with redescription of *E. intermedia* and establishment of a new genus. *Proceedings of the Biological Society of Washington*, 127, 248–283.

https://doi.org/10.2988/0006-324X-127.1.248

- Lang, K. (1946) Einige für die schwedische Fauna neue marine Cyclopoida Gnathostoma, nebst Bemerkungen uber die Systematik der Unterfamilie Cyclopodinae. *Arkiv för Zoologi A*, 38, 1–16.
- Lee, B.-Y., Kim, H.-S., Choi, B.-S., Hwang, D.-S., Choi, A.Y., Han, J., Won, E.-J., Choi, I.-Y., Lee, S.-H., Om, A.-S., Park, H.G. & Lee, J.-S. (2015) RNAseq based whole transcriptome analysis of the cyclopoid copepod *Paracyclopina nana* focusing on xenobiotics metabolism. *Comparative Biochemmistry and Physiology D*, 15, 12–19. https://doi.org/10.1016/j.cbd.2015.04.002
- Lee, S.-H., Lee, M.-C., Puthumana, J., Park, J.C., Kang, S., Han, J., Shin, K.-H., Park, H.G., Om, A.-S. & Lee, J-S. (2017) Effects of temperature on growth and fatty acid synthesis in the cyclopoid copepod *Paracyclopina nana*. *Fish Science*, 83, 725–734.

https://doi.org/10.1007/s12562-017-1104-2

- Lee, W., Park, E. & Song, S.J. (2012) Marine Harpacticoida. Invertebrate Fauna of Korea, 21 (11), 1–276.
- Lindberg, K. (1952) La sous-famille des Cyclopininae Kiefer (Crustacés Copépodes). Arkiv för Zoologi, New Series, 4 (16), 311–325.
- Lindberg, K. (1961) Une *Cyclopina* nouvelle du sable de la côte Atlantique de Portugal. *Kunglige Fysiografiska Sällskapets i Lund Förhandlingar, Proceedings of the Royal Physiographic Society at Lund*, 31 (13), 127–132.
- Lotufo, G.R. (1995) Psammic *Procyclopina* (Copepoda, Cyclopoida) from the coast of Brazil. *Zoologica Scripta*, 24, 245–255.

https://doi.org/10.1111/j.1463-6409.1995.tb00402.x

- Martínez Arbizu, P. (2000a) A new species of *Cyclopetta* from the Laptev Sea (Arctic Ocean), with the recognition of Cyclopettidae fam. nov., a new monophylum of free-living Cyclopoida (Copepoda). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie*, 70, 91–101.
- Martínez Arbizu, P. (2000b) Giselinidae fam. nov., a new monophyletic group of cyclopoid copepods (Copepoda, Crustacea) from the Atlantic deep sea. *Helgoland Marine Research*, 54, 190–212. https://doi.org/10.1007/s101520000051
- Martínez Arbizu, P. (2001a) Hemicyclopinidae n. fam., a new monophyletic group of marine cyclopinid Cyclopoida, with description of one new genus and two new species (Crustacea, Copepoda, Cyclopoida). *Senckenbergiana biologica*, 81, 37–54.
- Martínez Arbizu, P. (2001b) Psammocyclopinidae fam. n., a new monophyletic group of marine Cyclopoida (Copepoda, Crustacea), with the description of *Psammocyclopina georgei* sp. n. from the Magellan Region. *Senckenbergiana biologica*, 81, 37–54.
- Martínez Arbizu, P. (2006) Phylogenetic relationships within Schminkepinellidae fam. n., a new monophyletic group of marine cyclopinids (Cyclopoida: Copepoda), description of two new genera and four new species. *Zoologiya Bespozvonochnykh*, 3, 185–207.

https://doi.org/10.15298/invertzool.03.2.04

Mohammed, A.A. & Neuhof, V. (1985) Arctocyclopina pagonasta, a new genus and species of the family Cyclopinidae (Cyclopoida, Copepoda) from the annual sea ice in the Canadian Arctic. Canadian Journal of Zoology, 63, 2389–2394. https://doi.org/10.1139/z85-353

Oatley, C.W., Nixon, W.C. & Pease, R.F.W. (1965) Scanning electron microscopy. Advances in Electronics and Electron Phys-

ics, 21, 181-247.

https://doi.org/10.1016/S0065-2539(08)61010-0

- Ohtsuka, S., Tanaka, H. & Boxshall, G.A. (2016) A new species of hyperbenthic cyclopoid copepod from Japan: First record of the genus *Cyclopicina* in the Indo-Pacific Region. *Zoological Science*, 33, 659–666. https://doi.org/10.2108/zs160094
- Pesce, G.L. & Pandourski, I. (2002) *Pseudocyclopina livingstoni* sp. n. (Copepoda, Cyclopinidae) from the Livingston Island (Antarctica). *Biologia Bratislava*, 57, 133–137.
- Pleșa, C. (1969) Un nouveau Cyclopoïde interstitiel de la mer de Chine: *Heterocyclopina vietnamensis* n.g., n.sp. (Crustacea, Copepoda). *Vie et Milieu (A)*, 19, 329–344.
- Pruett, L. & Cimino, J. (2000) Coastal length based on the World Vector Shoreline, United States Defense Mapping Agency, 1989. Global Maritime Boundaries Database (GMBD), Veridian—MRJ Technology Solutions, Fairfax, Virginia, pp. [database]
- Sars, G.O. (1913) Copepoda Cyclopoida. An Account of the Crustacea of Norway with short Descriptions and Figures of all the Species, 6, 1–56, pls. I–XXXII.
- Scott, T. (1894) Additions to the fauna of the Firth of Forth. Part VI. *Reports of the Fishery Board for Scotland, Edinburgh*, 12 (3), 231–271, pls. V–X.
- Shen, C.-J. (Ed.) (1979) Fauna Sinica, Crustacea Freshwater Copepoda. Fauna Editorial Commission, Academia Sinica. Science Press, Beijing, 450 pp.
- Smirnov, S.S. (1935) Zur Systematik der Copepoden-Familie Cyclopinidae G.O. Sars. Zoologischer Anzeiger, 109, 203–210.
- Soh, H.Y., Moon, S.Y. & Wi, J.H. (2010) Marine Planktonic Copepods II. Invertebrate Fauna of Korea, 21 (28), 1–157.
- Stock, J.K. & Von Vaupel Klein, J.C. (1996) Mounting media revisited: the suitability of Reyne's fluid for small crustaceans. *Crustaceana*, 69, 749–798.

https://doi.org/10.1163/156854096x00826

- Suárez-Morales, E. & Almeyda-Artigas, R.J. (2015) A new genus and species of cyclopoid (Crustacea, Copepoda, Cyclopinidae) from a coastal system in the Gulf of Mexico. *ZooKeys*, 534, 17–34. https://doi.org/10.3897/zookeys.534.6019
- Thrush, S.F., Grey, J.S., Hewitt, J.E. & Ugland, K.I. (2006) Predicting the effect of habitat homogenization on marine biodiversity. *Ecological Applications*, 16, 1636–1642.

https://doi.org/10.1890/1051-0761(2006)016[1636:PTEOHH]2.0.CO;2

- Ueda, H., Ohtsuka, S., Seike, Y. & Ohtani, S. (2001) Second record of *Cyclopina kiraensis*, a small, brackish-water cyclopoid copepod, in Japan. *Limnology*, 2, 49–50. https://doi.org/10.1007/s102010170016
- Walter, T.C. & Boxshall, G. (2019) World Copepoda database [Database]. Retrieved from: http://www.marinespecies.org/copepoda (accessed 21 June 2019)
- Wells, J.B.J. (1965) Copepoda (Crustacea) from the meiobenthos of some Scottish marine sub-littoral muds. Proceedings of the Royal Society of Edinburgh, Section B, Biological Sciences, 69, 1–33. https://doi.org/10.1017/S0080455X00010110
- Wells, J.B.J. (1967) VII. The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. Transactions of the Royal Society of Edinburgh, 67, 189–358.

https://doi.org/10.1017/S0080456800024017

Wells, J.B.J. (2007) An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). Zootaxa, 1568 (1), 1–872.

https://doi.org/10.11646/zootaxa.1568.1.1

Zeppilli, D., Sarrazin, J., Leduc, D., Marinez Arbizu, P., Fontaneto, D., Fonanier, C., Gooday, A.J., Kristensen, R.M., Ivanenko, V.N., Sorensen, M.V., Vanreusel, A., Thebault, J., Mea, M., Allio, N., Andro, T., Arvigo, A., Castrec, J., Danielo, M., Foulon, V., Fumeron, R., Hermabessiere, L., Hulot, V., James, T., Lanfonne-Augen, R., Le Bot, T., Long, M., Mahabror, D., Morel, Q., Panralos, M., Pouplard, E, Raimondeau, L., Rio-Cabello, A., Seite, S., Traisnel, G., Urvoy, K., Van Der Stegen, T., Weyand, M. & Fernandes, D. (2015) Is the meiofauna a good indicator for climate change and anthropogenic impacts? *Marine Biodiversity*, 45, 505–535.

https://doi.org/10.1007/s12526-015-0359-z