A REVISION OF THE GENUS *EURYCOPE* (ISOPODA, ASELLOTA) WITH DESCRIPTIONS OF THREE NEW GENERA

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ABSTRACT

Most of the genera in the important deep-sea isopod family Eurycopidae need revision. In this paper, the type-genus *Eurycope* is revised, and three new genera (*Disconectes*, *Tytthocope*, and *Belonectes*) are proposed to contain some of the species removed from it. The new genera are based on redescribed type-species, permitting more precise generic placement of other species. New records are given for *Disconectes phalangium* and *Belonectes parvus*.

Asellote isopods of the family Eurycopidae are important components of deepsea benthic assemblages in both diversity and numbers of individuals (Wilson and Hessler, 1980). Belying this importance, taxonomic revisions of this family and its type-genus, *Eurycope*, have been neglected. Previous systematists have been struck by the pervasive unity in the natatory body form of the Eurycopidae and often have been loathe to discriminate new forms. Hansen (1916) was the progenitor of this school of thought, and significantly influenced a number of later workers. For example, Nordenstam (1955), in describing the extremely modified bathypelagic *Bathyopsurus* for the first time, felt that this genus might eventually be transferred to *Eurycope* in accordance with the view of Hansen (1916). Consequently many eurycopine taxa, especially the type-genus *Eurycope*, have become extremely heterogeneous as new morphologies have been added to existing genera and species.

Eurycope is the most complex and troublesome eurycopid genus. Sars (1899) originally noticed the great differences in the species he included in it, predicting that *E. phalangium* and similar species, and *E. megalura* were likely to be placed in separate genera. Hansen (1916), who was an inveterate lumper, nevertheless recognized that *Eurycope* could possibly be separated into two "sections": species with natatory pereonites 5 and 6 dorsomedially fused, and species with free pereonal somites. Nierstrasz and Stekhoven (1930), who elevated Hansen's Eurycopini to the level of family, also recognized that *E. frigida* and similar species could be transferred to a new genus on the basis of their reduced seventh pereonite and pereopods, but believed "... on the whole *Eurycope* is a well-defined genus ..." (Wolff, 1956, p. 123).

In contrast to this latter statement, a survey of Atlantic species of *Eurycope* (Wilson and Hessler, 1980) reveals that this group can easily be broken into a number of genera which, in part, follow the recommendations of previous authors. In this paper we describe four newly formulated genera and include redescriptions of the type for each genus, drawn from previously described species. The diagnoses and remarks for the types provide characters by which species in each genus are identified. The central genus *Eurycope*, with *E. cornuta* as its type, is still large and contains recognizable subgroups, whose status is the subject of continuing research in this laboratory. Three new genera, *Disconectes*, *Tyt*-thocope, and Belonectes, are erected for the other large groups of species removed from *Eurycope*. There remain additional smaller groups of species (see Table 2) which will receive taxonomic treatment in future papers.

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Fig. 1. *Eurycope cornuta* Sars, 1864. A–B, lectotype female. A, lateral view with enlargement of the uropod. B, right frontal portion of cephalon showing antennula, basal part of antenna, rostrum, and frons. C, antennula of a paralectotype copulatory male.

Methods

The materials, methods, and taxonomic characters used herein are discussed in Wilson and Hessler (1980) and Wilson (1981). Following established styles of Wolff (1962) and Hessler (1970), appendages are counted with roman numerals, and somites with arabic numerals. Hemiplumose setae, found on eurycopid opercular pleopods, have only one row of long thin setules.

The lack of designated type specimens for the species described by G. O. Sars (publications from 1864 to 1899) deserves mention. Fortunately the specimens examined by Sars are retained in the Zoological Museum of the University of Oslo. We regard as syntypes any specimens in the Sars collection from the type locality (the first named locality in the original description), and have chosen a lectotype from them. No syntypes were dissected for the descriptions; the limb

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illustrations were drawn from specimens collected by Hessler in the Herdla and Hjelte Fjords of southwestern Norway (depths c. 250 m). Dissections of *Belonectes parvus* (Bonnier, 1896), new combination, were made from specimens collected in the Bay of Biscay near Bonnier's type locality (John Allen stations 40 through 65; see Table 7).

Taxonomy

FAMILY EURYCOPIDAE Hansen, 1916 Subfamily Eurycopinae Wolff, 1962 Eurycope G. O. Sars, 1864

Type-species.—Eurycope cornuta G. O. Sars, 1864 (Fig. 1).

Generic diagnosis.—Eurycopidae with deep, vaulted and rounded natasome; venter with no enlarged or recessed areas; body without dorsal or lateral spines. Tergal articulations of pereonites 5–7 distinct; pereonite 7 subequal or longer than pereonites 5 and 6. Rostrum and frons distinct; clypeus narrow strip; labrum longer than clypeus. Pleotelson posterolateral margin parallel to or angled downward in lateral view. Antennular first article broad, with well developed medial lobe. Mandibular molar triturating surface broad, oval, with tiny denticles and small setae on posterior edge; ventral edge flattened into angular blade. Mandibular condyle as long as or longer than molar process. Mandibular palp well developed and functional; flattened distal article strongly curled laterally. Bases of pereopods I–IV subequal to body depth. Bases of pereopods V–VII subequal, short, and robust. Uropods short, biramous; protopod broad or tubular, not leaflike; exopod subequal to or shorter than endopod.

Species included.—See Table 1.

Derivation of name.—Eurycope means "broad oar" (Greek, feminine), apparently referring to the natatory percopods.

Generic remarks.—Members of the genus Eurycope, as restricted here, are most easily recognized by their smooth, deep, dorsally rounded bodies, distinct rostra, unfused natasomites, short subequal bases of pereopods V–VII, and well developed medial lobes on the basal segment of the antennulae. Even in its restricted definition, this genus is speciose (Table 1). However, Eurycope contains subgroups of closely related species, such as the *E. complanata* subgroup. This subgroup also includes E. cryoabyssalis, E. hanseni, E. inermis, E. ratmanovi, E. *iphthima*, and a number of other undescribed species presently being described in our laboratory. Other such groups are typified by each of the following described species: E. brevirostris, E. galatheae, E. producta, and E. quadrata. A number of characters are useful in distinguishing these subgroups: the size and shape of the rostrum, the frons, the degree of strengthening and calcification of the condyle and molar of the mandible, the epipod on the maxilliped, the female pleopod I, the distal tip of the male pleopod I and the uropodal protopod. Formal recognition of these groups is not attempted here because some characters require further research in order to determine their stability within each subgroup.

A number of species formerly included in *Eurycope* do not fit into the new concepts of this paper's other new genera. Some can be placed in existing genera of the Eurycopidae, but others will require more taxonomic effort. These species are listed in Table 2 with their potential taxonomic placements. A few of these require further comment here.

There exists within the Eurycopidae, as presently defined, a complex of genera

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E. affinis Birstein, 1970	E. iphthima Wilson, 1981
E. brevirostris Hansen, 1916	E. lavis Schultz, 1978
E. californiensis Schultz, 1966	E. linearis Birstein, 1963
E. cornuta Sars, 1864 (type-species)	E. manifesta Menzies and George, 1972
E. complanata Bonnier, 1896	E. ochotensis Kussakin, 1979
E. cryoabyssalis Just, 1980	E. pavlenkoi Gurjanova, 1933
E. curtirostris Birstein, 1963	E. producta Sars, 1868
E. eltaniae Menzies and George, 1972	E. quadrata Barnard, 1920
E. galatheae Wolff, 1956	E. ratmanovi Gurjanova, 1946
E. gaussi Wolff, 1956	E. spinifrons Gurjanova, 1933
E. hanseni Ohlin, 1901	E. vicaris Vanhöffen, 1914
E. inermis Hansen, 1916	

having a facies reminiscent of the Ilyarachnidae. Described taxa in this group are *Lipomera lamellata* Tattersall, 1905, *Ilyarachna aspidophora* Wolff, 1962 (genus *sic*, placed in the Eurycopidae by Hessler and Thistle, 1975), *Eurycope frigida* Vanhöffen, 1914, *E. cf. frigida* Nordenstam, 1933, and *E. ovata* Birstein, 1970. Species belonging in this suprageneric group appear to be ilyarachnids, but examination reveals two important characters which indicate that they are evolutionarily independent of the Ilyarachnidae. Contrary to the diagnosis of this latter family (Wolff, 1962), the bases of pereopods III and IV are elongate, similar to pereopods II and I. More important, while much of the resemblance of the ilyarachnoid facies to the Ilyarachnidae stems from their strongly developed cephalic cheeks and mandibles, the former have a rounded *molar process* and the latter have a rounded *incisor process*. Because of these differences in the mandibles and ambulopods, other similarities must be independently derived.

Eurycope mutica and *E. pygmaea* appear to belong in *Disconectes*, new genus, but their facial structure and mandibles more closely ally them to *Munnopsurus* Richardson, 1912. However, the fusion of pereonites 5 and 6, and the shape of the pleotelsons prevent their inclusion in that genus.

Species	Potential assignment (nr. = nearest relative)		
Eurycope acutitelson Menzies, 1962	nr. Eurycope Sars, 1864		
Ilyarachna aspidophora Wolff, 1962	Ilyarachnoid facies		
(placed in Eurycopidae by			
Hessler and Thistle, 1975)			
Eurycope crassa Vanhöffen, 1914	Munneurycope Stephensen, 1913		
E. frigida Vanhöffen, 1914	Ilyarachnoid facies		
E. cf. frigida Nordenstam, 1933	Ilyarachnoid facies		
E. gibberifrons Wolff, 1962	?		
E. glabra Kensley, 1978	nr. <i>Eurycope</i> Sars		
E. magna Birstein, 1963	Munnicope Menzies and George, 1972		
E. mutica Sars, 1864	nr. Munnopsurus Richardson, 1912		
E. nobilii Richardson, 1911	?		
E. nodosa Menzies, 1962	nr. Eurycope Sars		
E. ovata Birstein, 1970	Ilyarachnoid facies		
E. pygmaea Sars, 1870	nr. Munnopsurus Richardson		
E. quadratifrons Birstein, 1969	?		
E. sarsi Beddard, 1886	nr. Munneurycope Stephensen		
(=E. acutiperaeons Schultz, 1978)			
E. scabra Hansen, 1897	Munnicope Menzies and George		

Table 2. Species excluded from *Eurycope* but not placed in new genera.

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Fig. 2. *Disconectes phalangium* (Sars, 1864), new combination. A–B, lectotype female, lateral and dorsal views. C–D, copulatory male, lateral and dorsal views. E, preparatory female, ventral oblique view, basal portions of pereopods in plane view. F, cephalon, frontal oblique view, cuticular ridges shown on rostrum and frons. G, left uropod, copulatory male, ventral view. H–J, left pereopods V–VII, lateral view, brooding female.

Type-species.—Eurycope cornuta G. O. Sars, 1864 (Fig. 1).

E. cornuta Sars, 1899, p. 145; Wilson and Hessler, 1980, p. 255; for a complete synonymy under this name, see Hult, 1941, p. 103.

E. robusta Harger, 1878, p. 375.

Lectotype.—Preparatory female, 3.5 mm, Straits of Drøbak, from Sars' collection, Zoological Museum of Oslo (ZMO) catalogue number F546a.

D. picardi (Amar, 1957)

D. antarcticus (Vanhöffen, 1914)	D. madseni (Wolff, 1956)
D. cavus (Menzies and George, 1972)	D. ovalis (Vanhöffen, 1914)
D. curtus (Vanhöffen, 1914)	D. ovaloides (Menzies, 1962)
D. furcatus (Sars, 1870)	D. phalangium (Sars, 1864); type-species

Table 3. Species included in Disconectes.

D. latirostris (Sars, 1882)

Paralectotypes.—16 individuals, ZMO cat. no. F546b.

Species diagnosis.—Body oval with light pigmentation at margins of body segments, length 2.2 width, depth 0.3 length. Rostrum narrowly quadrate with low cephalic keels anteriorly, with little or no overhang; from sloping abruptly to rounded inverted V ridge above clypeus. Peronites 1-4 lengths midsagittally subequal, short, combined length one-half to one-third that of pereonites 5-7. Pleotelson length approximately 0.65 width, rounded posteriorly; distal end angling downward approximately 30° in lateral view. Antennular medial lobe length subequal to second article length. Mandibular palp longer than body of mandible. Lacinia mobilis with 7 teeth decreasing in size dorsally. Maxilliped with large, flat, spinelike distolateral margins of basis and ischium; epipod with angular lateral projection. Pleopod I in mature male with lateral lobes broad, distally nonprotruding, constricting, and terminating short distance proximal to medial lobes; medial lobes approximately half pleopod width, distally rounded, laterally pointed. Male pleopod II stylet longer than protopod. Female pleopod II distally rounded, nonprotruding; keel deep, medially narrow, with obtuse apex approximately three quarters length from insertion; lateral fields not recurved. Uropod robust, with subequal rami; protopod not distally broadened, basal fringing setae shorter than protopod; both rami with distal rosettes of stout unequally bifid setae.

Remarks.—For a full description and illustration of this species see Wilson and Hessler (1980).

Disconectes, new genus

Diagnosis.—Eurycopidae with oval disklike body, with no large setae or spines, pereonites 5 and 6 lacking dorsal articulations. Pereonite 7 smaller than combined pereonites 5 and 6. Natatory pereonites' venter sloping upward from anterior margin; (Fig. 2A, C, E) venter of pereonites 1-4 bulging distinctly lower than level of anterior natasome. Clypeus very large, rounded, much larger than small labrum (Fig. 2F). Pleotelson posterolateral margin either sinuate or angled upward as seen in lateral view. Antennular first article short and squat, medial lobe distinct but protruding only slightly. Mandibular molar thin and tubular, distally truncate with sharp spines and denticles, lacking distinct flat angular blade, with several small setae on posterior margin. Mandibular condyle shorter than molar process. Mandibular palp large, robust; distal article very large, flattened, curled laterally approximately 45°. Bases of pereopods I-IV successive lengths showing small increase posteriorly. Basis of pereopod V shorter and thicker than pereopod VI; percopod VII basis subequal to or shorter than percopod VI, approximately same thickness. Uropods short, biramous, protopod tubular; exopod length greater or less than endopod, endopod less than twice length of protopod.

Species included.—10 species (Table 3).

Derivation of name.—Disconectes (Greek, masculine) means "disk-swimmer," referring to the disklike appearance of some members of the genus.

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Generic remarks.—Members of the genus Disconectes are characteristically small, broad, and flattened, although a few species are rotund. Shape of the natasome, large clypeus, very small labrum, and thin, sharp-toothed mandibular molar process are key characters for the identification of this genus. Interspecific variation occurs in the shape of the rostrum, frons, and uropods. These characters, in conjunction with the male pleopod I, the female pleopod II, and special features of the body shape, can be used to differentiate the species of this genus.

Supraspecific groups appear in *Disconectes*, although there is substantial intergradation. *Disconectes phalangium*, *D. furcatus*, *D. latirostris*, and *D. ovalis* typify four clusters of species, but some disconectid species are difficult to classify and seem to fall between groups. The species list given in Table 3 is somewhat limited, while a taxonomic survey of the Atlantic basins (Wilson and Hessler, 1980) shows that this geographic area alone has approximately 24 species, most of which are new.

Type-species.—Disconectes phalangium (G. O. Sars, 1864) (Figs. 2-3).

Eurycope phalangium: G. O. Sars, 1864, p. 210; Wolff, 1962, pp. 146, 257; for a complete synonymy under this name see Hult, 1941, p. 110.

Eurycope phallangium: G. O. Sars, 1899, p. 147.

Lectotype.—Preparatory female, 1.6 mm long, from the Straits of Drøbak, ZMO cat. no. F15478a.

Paralectotypes.-20 additional specimens, ZMO cat. no. F15478b.

Additional Norwegian material.—Approximately 100 specimens from Herdla and Hjelte Fjords, c. 250 m, collected by Hessler.

General distribution.—Shallow bathyal waters in or around the Bay of Biscay, the British Isles, Norway, the Davis Straits, and the Gay Head-Bermuda Transect off New England, U.S.A., 54–1,597 m (Table 4).

Species diagnosis.—Rostrum of cephalon narrowing rapidly from antennular insertions to anterior subquadrate projection only 0.1 width of cephalon, with small angular cephalic keels. Frons nearly perpendicular to body axis, height 0.42 cephalon height, with comparatively large, widely spaced cuticular ridges. Male pleopod I with indistinct lateral lobes, distolateral margin slightly indented, grading directly into rounded medial lobes. Female pleopod II deep, with obtusely angled apex: depth 0.54 length; apex 0.59 length of pleopod from insertion, with large seta. Preanal ridge not enlarged. Exopod of uropod 1.1 times longer than endopod.

Description.—Mature female body length 1.5–1.9 mm, copulatory males smaller, approximately 1.3 mm. Body length 1.7 width. Combined pereonites V–VI medial length 1.6 pereonite VII length. Pleotelson length 0.7 width, with approximately 11 setae on each ventrolateral margin.

Lateral spine on cephalon rounded, not pointed; no teeth or setae on lateral margins of antennal sockets (Fig. 2F).

Antennular (Fig. 3A, B) basal article broader than long. Second article only slightly shorter than medial length of basal article; broader in males than in females; second article 0.47 width of first article in copulatory males, 0.41 in mature females. Third article length 0.43 that of second article.

Antenna extremely long and thin; length 5.0 body length. Antennal scale small, less than half length of fourth article, with single small seta.

Left mandible (Fig. 3C-E) thin, curved ventrally. Incisor process with 5 teeth.



Fig. 3. Disconectes phalangium. A, right antennula, preparatory female. B, right antennula, copulatory male. C–E, left mandible, preparatory female. C, dorsal view, with enlargements of a palp cleaning seta and the spine row. D, anterior view of incisor and lacinia mobilis. E, ventral view of molar process. F, maxillula. G, maxilla. H, maxilliped with enlargement of specialized setae on the distal tip of the endite. I, left percopod I, preparatory female, lateral view. J, pleopod I of copulatory male with enlargement of distal tip. K, pleopod II, copulatory male. L, pleopod II, preparatory female. M–O, pleopods III–V.

Station	Median north latitude	Median west longitude	Median depth (m)	Number of individuals
WHOI 73	39°46′ 39°49′	70°43′	1,400	59
87	3 9°49′	70°40′	1,102	166
88	39°54′	70°37′	478	27
96	39 °55′	70°40′	498	5
105	39°57′	71°04′	530	7
207	39° 51′	70°55′	808	4
209	39°4 6′	70°49′	1,597	22
313	51°31′	12°36′	1,495	44
Allen 40	43°36′	03°25′	860	4
61	46°20′	04°35′	952	1

Table 4. New localities for Disconectes phalangium.

* More information on these stations in Wilson and Hessler, 1980.

Left spine row with 1 large spine and 2 denticles, all supplied with accessory setae. Molar process connected to spine row and incisor process by thin cuticular sheet. Dorsal condyle thin flap of cuticle, not heavily developed. Palp approximately same length as body of mandible; distal article with 5 branched setae, 5 long straight setae, and numerous cuticular combs on inside of curl; second article with 2 large and 2 small setae distally. Right mandibular incisor process with 4 teeth, most ventral tooth largest; right spine row with 3 large spines.

Maxillipedal (Fig. 3H) epipod pointed, narrow; length 3.6 width, with no lateral extension. Basis with 2 coupling hooks and 3 distal bifurcate fan setae. Palp article 2 (merus) lateral length 1.4 width, width 1.6 basis endite width. Palp article 3 (carpus) with only 3 recurved setae, each associated with marginal tooth. Palp article 4 (propodus) medial lobe very small, width less than basal width of article, with 2 large setae.

Pereopod I (Fig. 3I) large, subchelate. Carpus and propodus lengths subequal, 0.79 basis length, sharing subchelate joint, with two ventral rows of setae: one dense row of short fine setae and one sparse row of long setae lateral to previous row. Carpus with more setae in rows than propodus. Dactylus with dense ventral row of fine setae.

Percopods II–IV extremely long, nearly 3 body lengths, thin, subequal. Bases of percopods I–IV 0.35, 0.41, 0.42, 0.42 length of body, respectively.

Pereopods V–VII (Fig. 2H–J) dactyli elongate, flattened, longer than propodi, each with large terminal claws. Bases V–VII length: body length ratios 0.15, 0.22, 0.22, respectively. Ischium of pereopod VI lacking plumose setae; 2 plumose setae on ischia of pereopods V and VII. Propodus: carpus length ratios for pereopods V–VII 0.79, 0.70, 0.85, respectively; propodi of pereopods V and VII subequal, smaller than propodus VI. Length: width ratios for carpi V–VII, respectively, 1.6, 1.8, 1.7; 2.5 for propodi V–VII.

Male pleopod I (Fig. 3J) length 2.2 width, ventral surface convex, with no ventral setae.

Male pleopod II (Fig. 3K) protopod length 2.0 width; large setose lobe posterior to exopod, length 0.26 pleopod length. Endopod inserting 0.5 length from pleopod origin; stylet extending distally to tip of basal segment, length 0.59 protopod length.

Female pleopod II (Fig. 3L) length 1.04 width, with no large setae on lateral margins.

Uropodal protopod short, slightly wider than long, with 7–9 large setae in row on distal margin.



Fig. 4. *Tytthocope megalura* (Sars, 1872), new combination. A–C, lectotype female. A, lateral view. B–C, dorsal views of body and left antenna. D, antennula and basal segments of antenna, brooding female. E, antennula, copulatory male. F, cephalon, frontal oblique view, rugosity of cuticular surface shown. G–H, lateral and ventral cuticular fringe of pereonites 1–4, left to right, respectively. I, ventral oblique view of natasome, preparatory female, bases of natapods in plane view.

Remarks.—*Disconectes phalangium* differs from other members of the genus by its very long antennae, long ambulopods, narrow rostrum and elongate uropodal exopod. Because long appendages are usually lost in deep-sea samples, the former two characters are not included in the diagnosis. Of the described species, D. antarctica (Vanhöffen, 1914) is most closely related to *D. phalangium* on the basis of the general body shape and similarities in the frons. The width of the rostrum, the length of the uropodal exopod, and the medial lobe of the male pleopod I can be used to separate these two species, as well as similar undescribed species in the Atlantic deep sea.

Tytthocope, new genus

Diagnosis.—Eurycopidae with longitudinally compressed natatory pereonites and inflated pleotelson. Venter of pereonite 6 protruding abruptly downward (Fig.

4A, arrow), well below level of pereonite 5 which also protrudes downward. Tergum of pereonites 5 and 6 only partially fused medially; pereonite 7 greatly reduced in length compared to pereonites 5 and 6. Rostrum of cephalon broad, tapering anteriorly into sloping broad frons; clypeus nearly as broad as cephalon but narrow longitudinally; labrum approximately twice length of clypeus (Fig. 4F). Pleotelson posterolateral margin curved slightly downward in lateral view. Antennular first article roughly triangular or trapezoidal, lacking medial lobe or lateral flattened area. Mandibular molar thin, flattened, tapering distally to narrow spinose ridge with few setae. Mandibular condyle shorter than molar process but robust, with additional posterior ridge. Mandibular palp thin; distal article reduced, shorter than proximal article, curled laterally approximately 90°. Bases of percopods II-IV successive lengths increasing posteriorly, percopod I basis slightly longer than percopod II basis. Percopod VII greatly reduced compared to other natatory percopods; basis shorter and thinner than percopod V basis, area of carpus and propodus less than half that of pereopods V or VI. Pleopod II of female lacking keel. Uropods biramous, tiny, shorter than length of anal operculum.

Species included.—Six species (Table 5).

Derivation of name.—Tytthocope (Greek, feminine) means "small oar," referring to the reduced pereopod VII in the adult.

Generic remarks.—Sars (1899, p. 152) mentions in his description of Eurycope megalura that "this is a very distinct species, and ought perhaps to be regarded as the type of a separate genus . . ." The accumulation of five similar described species and five undescribed species from the Atlantic deep sea validates this prediction. The most characteristic features of Tytthocope, new genus, are broad sloping frons and rostrum, medial fusion of pereonites 5 and 6 (as distinct from complete fusion or unfused and freely articulated), ventrally protruding pereonite 6, reduction of pereonite 7 and its pereopods, and inflated pleotelson. Pereonite 6 is usually the largest and most muscular of the natatory segments, as opposed to pereonite 7 in most Eurycope and pereonite 5 in Disconectes and Belonectes.

As in the ilyarachnoid facies, *Tytthocope* has a reduced pereopod VII (Fig. 5G), although this reduction is only in size, not in swimming morphology. By contrast, the last pereopod of the ilyarachnoid facies is a walking leg or is absent altogether.

The mandibular molar in *Tytthocope* (Fig. 6C–D) parallels that of the Ilyarachnidae: in both taxa it is reduced and flattened, although the molar is more setose in the latter taxon. Other mandibular features, such as the incisor and the condyle, show no similarity.

Interspecies character variation in *Tytthocope* is most evident in the form of the rostrum, the size of pereonite 7 and the inflation of the pleotelson. In addition, setation on the body and rostrum, and the shape of the male pleopod I are sometimes important in species discrimination. This genus is more tightly defined than *Eurycope* and *Disconectes*; all the species in *Tytthocope* are very similar to one another and do not readily separate into subgroups.

The highly convoluted branchial pleopods (Fig. 6N-P) of *Tytthocope megalura* are unusual among the genera of the Eurycopinae. Pleopods V and IV form nested cups and pleopod III seems to function as a lid. The pleotelson of this species is enlarged, apparently to accommodate these pleopods. Because all members of *Tytthocope* have an enlarged or inflated pleotelson, this pleopod form may be characteristic of the genus. However, pleopods III-V are known in too few species.

Table 5. Species included in Tytthocope.

Type-species.—Tytthocope megalura (G. O. Sars, 1872) (Figs. 4-6).

Eurycope megalura G. O. Sars, 1872, p. 274; 1899, p. 151; Tattersall, 1905, p. 75; Nierstrasz and Stekhoven, 1930, p. 125; Gurjanova, 1933, p. 424; Wolff, 1962, pp. 146, 261.

?Eurycope megalura: Hansen, 1916, p. 148.

Lectotype.—Juvenile female, length 2.1 mm, from the outer part of Hardanger Fjord at Mosterhavn, 267–335 m, ZMO cat. no. F15332a.

Paralectotype.-Brooding female, ZMO cat. no. F15332b.

Additional Norwegian material.—6 specimens from Hjelte Fjord, c. 250 m, collected by Hessler.

General distribution.—Southwestern Norway; Hardanger, Stavanger, and Hjelte Fjords. West of Ireland (Tattersall) and southwest of Iceland (Hansen); this latter record may be another species. Depth range 250–365 m and ?1,461 m (Hansen).

Species diagnosis.—Rostrum lacking large setae; lateral margins angular, serrate, converging anteriorly without lobes. Serrate spination also on ventrolateral cephalic margin, anterior (ventral and dorsal) and lateral margins of pereonites 1–4, lateral margin of first article of antennula, and margins of coxae of pereopods I–IV. Body dorsal surfaces with fine setae. Pleon not especially inflated, narrower than natatory pereonites. Male pleopod I distally tapering to coalesced lateral and medial lobes; tip with small lateral recurved spinose projection.

Description.—Adults approximately 2.1–2.2 mm, maximum observed size brooding female 2.9 mm. Length : width ratio of juvenile female lectotype 2.2, in preparatory female 2.6. In preparatory and brooding females only pereonite 4 wider than pereonite 5; otherwise sexual dimorphism not evident. Anterior rostral width 0.57 posterior width, 0.24 cephalic width. Pleotelson medial length 0.90 width, widest at anterior marginal seta; height 0.45 length.

Antennula of large brooding female (Fig. 4D) 0.25 body length, with 11 articles; first article length 1.3 width; second article extending to tip of first article, longer than next two articles together; distal 5 articles bearing 1 aesthetasc each. Antennula of copulatory male (Fig. 4E) 0.31 body length with 14 articles, distal 7 articles bearing 1–3 aesthetascs each; second article larger and more robust than in female, extending one third its length beyond tip of article 1; more distal articles shorter and more robust than in female.

Antenna (Fig. 4C) total length approximately 1.7 body length, articles 5 and 6 together 0.7 body length, with approximately 30 thin flagellar articles; scale very small, rounded, with 2-3 unequally bifid setae (Fig. 4D).

Left mandible (Fig. 6A–F) incisor process with three teeth, central tooth rounded and much larger than outer teeth. Lacinia mobilis with 5 teeth, central tooth much larger than others. Spine row with 8 spines, each with 2 or 3 extremely fine accessory setae. Molar process with 3 sharp flattened teeth and 2 robust serrate setae. Condyle length 0.75 molar process. Palp length 0.79 mandibular body length; second article distal tip with 2 large setae; third article with 8 cleaning setae.



Fig. 5. *Tytthocope megalura*, copulatory male. A–G, left pereopods I–VII, all drawn to same scale in lateral view, enlargements of coxa, propodus, and dactylus shown for pereopod I. H, pleopod I, enlargement of distal tip shown. I–J, pleopod II. I, ventral view of whole limb. J, dorsal view of endopod and exopod.

Right mandible (Fig. 6G) with 4 teeth on incisor, one larger than others, very small dorsalmost tooth on side of adjacent tooth; spine row with 9 members.

Maxilliped (Fig. 6K) with 3 coupling hooks; endite width 0.43 basis width, 0.4 merus (palp 2) width, with 3 fan setae and one compound spinose seta distally. Merus distolateral corner acute, extending to level of insertion of propodus. Carpus (palp 3) with 5 stout recurved setae medially. Lobe of propodus (palp 4) 0.6 article width. Epipod distally pointed; length 2.6 width; width 0.89 basis width.

Pereopod I (Fig. 5A) small, thin, not subchelate, with few setae; propodus with row of minute setae on ventral margin; pereopod length 0.55 body length. Am-



Fig. 6. *Tytthocope megalura*, preparatory female. A–F, left mandible. A, dorsal view. B, palp, distal tip, enlargement of cleaning seta shown. C, edge view of lamellar molar process and condyle. D, anterodorsal plane view of molar process. E, posterior view of mandibular body with enlargement of lacinia mobilis and incisor process. F, spine row, lacinia, and incisor in ventral view. G, right mandibular spine row and incisor in dorsal view. H, paragnaths. I, maxillula. J, maxilla. K–L, maxilliped and an enlargement of the endite distal tip; fan setae in latter offset. M, dorsal and lateral views of pleopod II with detail of medial cuticular surface from lateral view. N–P, pleopods III–V. Q, pleotelson distal tip, ventral view, pleopod II removed. R, right uropod.

bulatory percopods II–IV (Fig. 5B–D) strong, robust, with long unequally bifid setae on dorsal and ventral margins and lacking propodal rows of fine setae; lengths relative to body length increase posteriorly: 0.93, 1.03, 1.19. Basis I 1.03 longer than basis II; bases I–IV lengths relative to body length, respectively: 0.19, 0.18, 0.19, 0.19.

Natatory pereopods V-VII (Fig. 5E-G) carpi and propodi broad and round; propodus VII almost circular; dactyli V-VII leaflike, with small serrations on

Length ratios	Pereopod V	Pereopod VI	Pereopod VII
Pereopod : body	0.66	0.65	0.42
Basis : body	0.14	0.15	0.10
Basis : ischium	1.06	1.25	1.42
Basis : basis V	1.00	1.06	0.72
Dactylus : propodus	0.56	0.56	0.78
		Width : length ratios	8
Carpus	0.85	0.85	0.84
Propodus	0.71	0.75	0.84

Table 6. *Tytthocope megalura*: relative article sizes of natatory percopods from a copulatory male (2.2 mm).

margin and no terminal claws. Basis V very robust, with several unequally bifid and broom setae, basis VI with only one each, basis VII with no unequally bifid or broom setae. See Table 6 for comparative article sizes of percopods V–VII.

Pleopod I (Fig. 5H) of copulatory male widest near insertion, width 0.32 length; orifice position 0.83 length from insertion. Pleopod ventral surface with simple setae only, lacking hemiplumose setae.

Pleopod II of copulatory male (Fig. 5I–J) protopod width 0.46 length, with flattened extension 0.23 total length past posterior tip of exopod. Stylet (endopod 2) short, 0.39 total pleopod length; endopod originating 0.69 pleopod length from insertion. Lateral margin with only 6 simple setae lacking hemiplumose setae.

Pleopod II of preparatory female (Fig. 6M) lacking marginal hemiplumose setae or stout, apical, unequally bifid seta; ventral surface with 2 rows of small simple setae. Width 0.85 length; depth 0.35 length; distal tip covering anal opening.

Pleopods III-V (Fig. 6N-P) highly convoluted: pleopod V deeply cupped dorsally; pleopod IV endopod also cupped, *in situ* inside pleopod V; exopod IV curled medially, inflated, inside endopod IV; pleopod III vaulted distally, covering concavity of pleopods IV and V. Exopod of pleopod III with two brush setae.

Uropod (Fig. 6R) only 0.047 total body length; protopod width 1.1 length; endopod length 2.0 protopod; exopod length 0.48 endopod, 0.95 protopod. Thin, recurved, unequally bifid setae on distal margins of uropod segments; broom setae only on endopod tip, only setal types absent.

Species remarks.—Tytthocope megalura is the only described species of the genus that has denticles on the rostral margins. Three other undescribed species in the Atlantic deep sea also have similar denticles but are different in the shape of the rostrum and pleotelson.

Hansen (1916, p. 148) reports two specimens of T. megalura collected by the Ingolf expedition southwest of Iceland at depths much deeper than most of the records for this species. He states that his specimens show a longer and broader "abdomen," and "the front cephalic area seems to differ from the figure of Sars in having no angles at the sides of the terminal emargination." Because these taxonomic characters vary at the species level, it is likely that the specimens examined by Hansen (1916) are a different species.

Belonectes, new genus

Diagnosis.—Eurycopidae with elongate, streamlined natasome; venter with pronounced medial bump at posterior margin of pereonite 5, becoming abruptly recessed dorsally posterior to bump (Fig. 7B, arrow). Pereonite 4 with distinct ventromedial bump. Pereonites 5 and 6 fused dorsally, pereonite 7 smaller and



Fig. 7. *Belonectes parvus* (Bonnier, 1896), new combination. A–B, E, lectotype male. A–B, dorsal and lateral views. C, rostrum, dorsal oblique view, copulatory male, showing cuticular ridges. D, cephalon, frontal oblique view, brooding female. E, ventral oblique view of natasome, bases of left natapods in plane view. F–G, copulatory male from Allen 56, dorsal view of body and left lateral view of pleotelson. H–I, preparatory female from WHOI 313, same views as F and G.

narrower than combined pereonites 5 and 6. Rostrum of cephalon broad, quadrate, sloping directly into very low frons (Fig. 7C, D); clypeus dorsally prominent, approximately half length of labrum. Pleon posterolateral margin angles distinctly upward in lateral view. Antennular first article trapedzoidal, lacking medial lobe. Mandibular molar thin, obliquely truncate distally; ventral margin flattened into



Fig. 8. A, antennula, preparatory female. B, proximal portion of antennula, copulatory male. C, anterior portion of cephalon and proximal parts of antennula and antenna, lateral view. D–G, left mandible, copulatory male. D, mandible and palp with enlargement of a cleaning seta, dorsal view. E, palp, lateral view. F, ventral view of distal parts. G, posterior view of lacinia mobilis and incisor process. H, incisor of right mandible, posterior view. I, paragnaths. J, maxillula. K, maxilla. L, maxilliped, epipod detached, enlargement of a fan seta shown. M–P, right pereopods I–IV, copulatory male from WHOI 188. Q, bases of pereopods I–IV in plane view.

Station		Median latitude	Median longitude	Median depth (m)	Number of individuals
*Allen	40	43°36′N	03°25′W	860	2
• •	50	43°46′N	03°37′W	2,379	1
	56	43°43′N	03°48′W	641	2
	65	46°15′N	04°49′W	1,922	2
*WHOI	313	51°31′N	12°36′W	1,495	3
	321	50°12′N	13°36′W	2,879	6
	326	50°05′N	14°26′W	3,859	1
**INCAL	1.3	57°58′N	10°52′W	2,075	3
	1.8	55°01′N	12°33′W	2,888	3
	2.1	50°19′N	13°08′W	2,550	5
	2.3	47°30′N	09°33′W	4,268	1
		Question	nable localities		
*WHOI	186	22°57′S	13°04'E	460	3
	188	23°00'S	12°58'E	620	301
	192	23°01′S	12°29'E	2,136	1
	200	09°42′S	10°55'E	2,699	1

Table 7. New localities for Belonectes parvus.

* More information on these stations in Wilson and Hessler (1980). ** Described in Sibuet (1979).

angular blade; posterior margin with tiny denticles and small setae. Mandibular condyle shorter than molar process. Mandibular palp distal article somewhat reduced, curled approximately 90° laterally. Bases of percopods I-IV elongate and subequal; bases of natatory percopods differing from one another: percopod V basis shortest and widest, percopod VI longest but intermediate width, pereopod VII basis thinnest but intermediate length. Uropods short, protopod biramous tubular; exopod tiny; endopod more than twice length of protopod.

Species included.—Belonectes parvus (Bonnier, 1896); B. latifrons (Menzies and George, 1972).

Derivation of name.—Belonectes (Greek, masculine) means "arrowswimmer," referring to the arrowhead-like dorsal appearance of members of this genus.

Generic remarks.—Belonectes is most easily distinguished by four diagnostic characters: a broad, sloping, quadrate rostrum; a labrum which is large compared to the clypeus; the fusion of pereonites 5 and 6 dorsally; and a pronounced bump on the posteroventral surface of pereonite 5. Disconectes resembles Belonectes in the fusion of the anterior natasomites, and some species of the former have a broad, quadrate rostrum. The shape of the natasomal venter and the size of the labrum allow an unambiguous separation of the two taxa.

There are only two described species in *Belonectes*: the type, *B. parvus*, and B. latifrons (Menzies and George, 1972). In addition, the Atlantic survey has revealed the presence of four additional species, making this genus somewhat species-poor compared to the much larger *Eurycope* and *Disconectes*. The lack of species in Belonectes is not an effect of taxonomic definition because, while Eurycope and Disconectes include more morphological variations, Tytthocope is even more rigidly defined but includes significantly more species. Therefore, species of *Belonectes* are rare in deep-sea faunal assemblages, both as taxa and as individuals.

The length and width of the rostrum, the male pleopod I distal tip, and the presence or absence of setae on the venter of the natasome have proven to be



Fig. 9. *Belonectes parvus*. A-C, percopods V-VII. Pleopod I: D, whole limb; E, enlargement of distal tip; F, lateral view; G, optical cross section from middle part. Pleopod II: H, right endopod and exopod, ventral view; I, whole limb, left side. J, pleopod II, brooding female, ventral and lateral views. K-M, pleopods III-V. N, uropod.

sensitive characters for distinguishing closely related belonectid species. Other species are more obviously different in the shape of the female pleopod II and the preanal ridge. All species of *Belonectes* have a keel-like form of the anterior pleopods, but some show this feature much more strongly, one even having an anteriorly jutting prow on the keel. These pleopods may or may not cover the anal plates, depending on the species. *Type-species.*—*Belonectes parvus* (Bonnier, 1896) (Figs. 7–9).

Eurycope parva: Bonnier, 1896, p. 600; Hansen, 1916, p. 149; Gurjanova, 1933, p. 424; Menzies, 1962, p. 142; Wolff, 1962, pp. 145, 263; Chardy, 1979, p. 81.

Lectotype.—Copulatory male, 2.4 mm, badly decalcified, ambulosome partially hyperextended. Caudan station 13, 44°17′N, 4°38′W, 950 m. Deposited in the Zoological Museum of the University of Claude Bernard, Lyon, J. Juget, curator.

Paralectotype.—Small male from Caudan 13, also at UCB, Lyon. See remarks concerning other individuals.

Additional material.—See Table 7.

General distribution.—Northeastern Atlantic and Bay of Biscay, 641–4,268 m. Questionable localities: Davis Straits, 2,623 m (Hansen, 1916); southeastern Atlantic, 460–2,699 m (Table 7).

Species diagnosis.—Pereonite 5 with transverse setal row on posteroventral margin. Ventral surfaces of female pleopod II convex anterior and posterior to apex; apex in posterior half of pleopod II. Male pleopod I with rounded distal tip, lateral lobe distinct, rounded, medial lobe subquadrate, with several setae. Rostrum length 1.1–0.9 width (measured at anterior extent of antennular first articles); width 0.43–0.49 cephalon width. Preanal ridge enlarged in male only, shorter than uropod, longer than uropodal protopod. Anus of male not covered by pleopods I–II, female anus covered.

Description.—Adults 2.3–2.7 mm; females larger than males. Females with more expanded ambulosome; body length : width and natasome : body length ratios for male and female, respectively, 2.4 (0.74), 2.5 (0.69).

Rostrum (Fig. 7C–D) midline slightly raised into broadly obtuse ridge; with regular cuticular ridges describing large u's open anteriorly. Cephalic keels rounded, thick, expressed only anteriorly.

Pleotelson posterolateral margin (Fig. 7G, I) concave, angled upward; distal tip curling downward.

Antennular basal article (Fig. 8A–B) with serrate lateral margin; length : width ratio 1.1, in males distally broader than in females; distal maximum width ratio 0.63, 0.53, respectively. Second article also broader in males than females. Third article shorter than second article. Copulatory male antennula with 52 articles; fifth article longer than basal article; distal 45 articles wider than long, each with single aesthetasc. Female antennula with approximately 12 articles; aesthetascs on distal 2 articles.

Intact antenna unknown; antennal scale (Fig. 8C) small, less than half length article 4, with one small distal seta.

Mandibles (Fig. 8D–H) dorsoventrally thin, with denticles posterolateral to insertion of palp. Left and right incisor processes with 4 teeth; second tooth from bottom largest. Lacinia mobilis with 4 teeth; ventral tooth largest, with several accessory setae ventrally. Left spine row with 6 spines, each with several accessory setae. Palp shorter than mandibular body; distal article with 8 thin cleaning setae.

Maxilliped (Fig. 8L) basis with 3 coupling hooks and 2 elongate fan setae on basis. Epipod length 3.1 width; length subequal to basis length. Ischium (palp 1) width 0.9 merus width, with lateral angular projection adjacent to similar projection on basis. Merus (palp 2) width 1.5 endite width. Carpus (palp 3) medial length 4.6 lateral length; 7–8 recurved setae on medial margin. Propodus (palp 4) medial lobe length 2.8 basal width, with 5–6 recurved setae. Dactylus (palp 5) short, length 0.81 propodal length.

Length ratios	Pereopod V	Pereopod VI	Pereopod VII
Pereopod : body	0.45	0.54	0.39
Basis : body	0.07	0.12	0.08
Basis : ischium	0.71	1.14	1.02
Basis : basis V	1.00	1.65	1.13
Dactylus : propodus	0.60	0.54	0.62
		Length : width ratio	s
Carpus	1.33	1.41	1.63
Propodus	1.57	1.51	1.35

Table 8. *Belonectes parvus*: relative segment sizes of natatory percopods from a brooding female (2.7 mm).

Pereopod I (Fig. 8M) simple, not grasping, lacking setae, 0.90 body length. Ambulatory pereopods II–IV (Fig. 8N–P) lengths increasing slightly posteriorly: 1.29, 1.33, 1.36 body length, respectively; article lengths heterogeneous: ischium II, carpus III, propodus II, dactylus IV longest of their respective articles. Pereopod II most robust; ischium II longer than I, III, IV, with distinct rows of setae on carpus and propodus. Bases I–IV (Fig. 8Q) subequal; lengths 0.24 body length. Ischia I–IV greatly reduced, less than one-third to one-half bases length.

Natatory percopods (Fig. 9A–C) with short, dorsally serrate, leaflike dactyli having tiny distal claws. Percopod VII ischium with no plumose setae. Percopod V basis with several broom setae. Comparative sizes of percopod segments shown in Table 8.

Male pleopod I (Fig. 9D–G) widest at insertion; length 3.7 width at dorsal orifice; length from insertion to dorsal orifice 0.77 total pleopod length; ventral surface with prominent keel; maximum pleopod depth 0.21 length; posterior surface of keel with several pairs of simple setae, no hemiplumose setae.

Male second pleopod (Fig. 9H–I) broad, length 1.3 width, ventral surface concave medially; distolateral margin with hemiplumose setae. Endopod inserting 0.77 total length from origin; stylet length 0.42 protopod length, no postexopod extension.

Female pleopod II (Fig. 9J) deep, keeled; length 1.29 width; depth 0.62 length. Pleopod covering anus; medial keel thin, with single apical seta.

Uropod (Fig. 9N) simple; length 0.063 body length. Protopod half length and exopod quarter length of endopod. Protopod not bulging medially; length 1.4 width, with approximately 6 unequally bifid setae.

Species remarks.—Belonectes parvus is, for the present, best distinguished from *B. latifrons* by the shape of the distal tip in the male pleopod I and the dorsal aspect of the pleotelson. Other closely related undescribed species are separated from *B. parvus* by the postapical shape of the female pleopod II, the presence or absence of setae on the natasomal venter, and the length : width ratio of the rostrum, especially in the males.

Bonnier (1896) attributes five specimens to *B. parvus*, but only four specimens were found in the type material, of which two belonged to another species. Bonnier completely dissected one specimen for his description, the parts of which subsequently became lost (as in *Munella*, according to Wilson and Hessler, 1974). He stated that this specimen was 3 mm long—larger than any of the specimens examined in the present study. This may be because Bonnier's animal was in fact exceptional, or he may have included the labrum in his measurement. The two remaining syntypes were of typical size, although in poor condition. Some of the differences seen in the chosen lectotype are due to its decalcified and partially distorted condition.

A southeastern Atlantic population of *Belonectes* is nearly indistinguishable from *B. parvus*, differing only in having fewer ventral setae and a slightly broader maxillipedal merus. Because the distribution is clearly disjunct, these specimens may represent a closely related sibling species. However, lacking any better evidence, it is prudent to include them tentatively in *B. parvus*. The females reported from Davis Straits (Hansen, 1916) are possibly not *B. parvus* because the description resembles a separate undescribed species from the Gay Head-Bermuda Transect. The specimens from the Davis Straits require re-examination.

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