Article title: Speciation and infrageneric classification in the planktonic dinoflagellate *Tripos* (Gonyaulacales, Dinophyceae)

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**Speciation and infrageneric classification in the planktonic
dinoflagellate *Triplos* (Gonyaulacales, Dinophyceae)**

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Abstract The genus *Tripos*, formerly marine species of *Ceratium*, is the dinoflagellate with the greatest number of species and infraspecific taxa (~800) due to the high morphological intraspecific variability of numerous species. In the past, the species of *Tripos* were proposed into distinct genera. A re-instatement of this generic split is not justified due the difficulties to circumscribe the basal subgenera *Amphiceratium* and *Archaeoceratium*, and the polyphyletic character of *Biceratium*. A new infrageneric classification is proposed. The subgenus *Amphiceratium* is dismembered after the classification of the sections Inflata and partially Fusiformia into *Archaeoceratium*. The subgenus *Tripos* (autonym) replaces other names such as *Tripoceratium* or *Orthoceratium*. Based on the original descriptions, the records of *T. furca* and *T. lineatus* correspond to *T. eugrammus* and *T. furca*, respectively, and *T. macroceros* has been reported as *T. contrarius*. The names *T. belone* and *T. carriensis* have been misapplied for *T. pacificus* and *T. volans*, respectively. *Tripos arcuatus*, *T. gracilis*, *T. inclinatus*, *T. scapiformis* and *T. subcontortus* are revived to replace *T. euarcuatus*, *T. declinatus*, *T. horridus*, *T. longirostrum* and *T. contortus*, respectively. The species *T. ramakrishnae* and *T. fusus* var. *schuettii* were described from individuals infected by endoparasites. *Tripos rotundatus* comb. nov. is proposed for *C. digitatum* var. *rotundatum*. As a result of taxonomic revision, *Tripos* is restricted to 57 correct species, although the speciation and synonymy is largely incomplete due to lack of studies in the life cycle and molecular data.

Key words *Ceratium*; Dinoflagellata; Dinophyta; phytoplankton; plankton; systematics

Abbreviations:

auct. mult.: auctorum multorum = subsequent authors used the name in a different sense to the original author.

bp: base pairs

I.C.N.: International Code of Nomenclature for algae, fungi, and plants.

ITS rRNA: Internal Transcriber Spacer of the ribosomal RNA.

LSU rRNA: large subunit of the ribosomal RNA.

nom. illegit.: nomen illegitimum = illegitimate name. A validly published name that is not in accordance with specified rules of the I.C.N.

nom. inval.: nomen invalidum = invalid name. A name not validly published in accordance with specified rules of the I.C.N.

sensu auct.: sensu auctorum = in the sense of certain authors.

SSU rRNA: small subunit of the ribosomal RNA.

1. Introduction

The family Ceratiaceae within the Gonyaulacales contains a few freshwater species classified in the genus *Ceratium*, and numerous marine species classified in *Triplos*. The species are typically large and robust, often with horns, facilitating the net sampling. In addition, the apparently easy identification using only gross morphology (i.e. outline, including horns) has facilitated abundant information on the distribution, using the species as ecological indicators. Due to the morphological variability, *Triplos* is the dinoflagellate genus with the greatest number of species and infraspecific taxa (~800) with an embroiled synonymy and unresolved species circumscriptions. The taxonomy is largely reported in the dinoflagellate literature (Balech, 1988; Schiller, 1937; Steidinger and Tangen, 1997; Taylor,

1976), and monographic studies (Graham and Bronikowsky, 1944; Jørgensen 1911, 1920; Peters 1932; Sournia, 1968; Steemann Nielsen, 1934; Subrahmanyam, 1968).

In the late XIX century, the species were classified in several genera (*Amphiceratium*, *Archaeoceratium*, *Biceratium*, *Ceratium*, *Euceratium*), but since 1908 were unified into *Ceratium* (Kofoid, 1908b). The marine and freshwater species showed morphological and ecological differences, and they clustered into distinct clades in the molecular phylogeny (Gómez *et al.*, 2010). The genus *Triplos* was re-instated to encompass the marine species, while the genus name *Ceratium* remains for the freshwater species that contained the type species (Gómez, 2013). The infrageneric classification of the genus *Triplos* has remained almost invariable in the last century. In this study, the infrageneric classification is updated based on the molecular data, the synonymy is revised, and a list of correct species names is provided.

2 Materials and methods

Observations of *Triplos* were carried out from the North, equatorial and South Pacific Ocean, Caribbean Sea off Puerto Rico, Atlantic South off Brazil, European North Atlantic and the Mediterranean Sea following the methods in Gómez *et al.* (2010). DNA sequences were retrieved from GenBank. The LSU rRNA gene phylogeny is poorly represented because sequences of only nine species are available. The sequence JQ638944 retrieved as *T. balechii* is labelled as a SSU, LSU and ITS sequence, although it only contains a LSU rRNA gene sequence fragment. The sequence JQ638947 retrieved as *T. balechii* is unrelated to the genus. Other sequence retrieved as *T. balechii* (KT389993) is an environmental sequence, and more closely related to *T. massiliensis* than *T. balechii*. There are two short sequences retrieved as *T. massiliensis* (MF928001, 317 bp; MF928002, 371 bp). There are two short sequences

retrieved as *T. furca* (MF927997–8, 366 and 368 bp, respectively). A longer sequence retrieved as *T. furca* (AY027908) belongs to an undetermined species of *Protogonyaulax*.

After Gómez *et al.* (2010), there are no new documented SSU rRNA gene sequences longer than 1100 bp, with the exception of environmental sequences. The phylogenetic tree was built including new sequences that were short ~700 base pairs or less (MF927973–MF927990). The sequence with accession number JQ638929 identified as *T. balechii* has been excluded because it is too short (339 bp), and there is other longer sequence of the same species. The sequence MF927977 (425 bp) identified as *T. candelabrum* is excluded because there are other longer sequences of the same species. The sequence MF927978 identified as *T. dens* is discarded because it contains numerous undetermined nucleotides. SSU- and LSU rRNA gene sequence alignments were accomplished by ClustalW (Larkin *et al.* 2007) and the evolutionary history was inferred by using the Maximum Likelihood method based on the General Time Reversible model with the default settings (uniform rates, complete deletion of gaps/missing data) in MEGA7 software (Kumar *et al.*, 2016). Bootstrap values were obtained after 1000 replications. Sequences of *Protocerratium reticulatum* were used for rooting the SSU- and LSU rRNA gene phylogenetic trees.

3 Results and discussion

3.1 Molecular phylogeny of *Tripes*

The LSU rRNA gene sequences of *Tripes eugrammus* (retrieved as *T. furca*) clustered in the most basal position with full support, followed by *T. fusus*, type of the subgenus *Amphiceratium* (Figure 1). It should be noted that sequences of representatives of *Archaeoceratium* are missing. In the SSU rRNA gene phylogeny, the sequences of *T. eugrammus* are intermediate between the most basal position of the clades of *Archaeoceratium*

and *Amphiceratium*, and a more distal clade containing the rest of the species (Fig. 2). The molecular data suggest that the members of *Archaeoceratium* and *Amphiceratium* evolved from a hypothetical common ancestor with a morphology closer to *T. eugrammus*, with short antapical horns directed posteriorly. The species with antapical horns directed anteriorly, the typical anchor-like shape, are considered more recently evolved forms. The morphology of *T. pacificus* (commonly misidentified as *T. belone*) is intermediate between *T. eugrammus* and *Amphiceratium*, and *T. belone* (= *T. incisus*) between *T. eugrammus* and the species of *Archaeoceratium*. Unfortunately, DNA sequences of *T. pacificus* and *T. belone* are missing to test the hypothesis. The basal topology of the sequences of *Archaeoceratium* and *Amphiceratium* reminds the Dinophysales, other specious group of dinoflagellates. The basal genera of the Dinophysales *sensu stricto* are *Tripodosolenia* and *Amphisolenia* (Gómez *et al.* 2011). *Tripodosolenia* and the typical species of *Archaeoceratium* are characterized by a flattened and expanded midbody and they live preferentially at sub-photic depths. The species of *Amphisolenia* and *Amphiceratium* are characterized by a strong body elongation. This evolutionary parallelism between *Tripodos* and the Dinophysales is striking.

Fig. 1. Phylogenetic tree based on LSU rRNA gene sequences, showing the position of the sequences of *Tripos* and *Ceratium* by Maximum Likelihood (ML). The section and subgeneric names are based on the classical taxonomical schemes. A sequence of *Protoceratium reticulatum* is used as outgroup. Numbers near branches denote ML bootstrap probability value. Bootstrap values <70 are omitted. Scale bar denotes 0.05 substitutions per site.

The resolution of the most extended molecular markers for phylogeny of dinoflagellates (SSU- and LSU rRNA gene) is insufficient to solve the relationships in the distal clade. It encompasses most of the species that were classified in the subgeneric names *Euceratium*, *Macroceratium*, *Orthoceratium* or *Tripoceratium*, and also included some species classified in *Biceratium* (Fig. 2). The subgeneric name *Ceratium* must be applied for the freshwater species and the name *Euceratium* is invalid (article 21.3 of the International Code of Nomenclature, I.C.N.). This distal clade contains the type, *T. muelleri*, therefore these species

belong to the subgenus *Tripes* that is an autonym (I.C.N., art. 22.1) replacing *Orthoceratium* sensu Sournia or *Tripoceratium*.

Authors have admitted four subgenera, and Kofoed (1908c) also added *Macroceratium*. The distinctive characteristic of *Macroceratium* is the postindentation, with the bases of the antapicals projected more or less posteriorly beyond the midbody. This trait seems to be supported by the molecular data, and these species cluster together, and in a basal position of the distal clade in some phylogenies. However, the support is insufficient to consider *Macroceratium* as independent from the subgenus *Tripes*.

Fig. 2. Phylogenetic tree based on SSU rRNA gene sequences, showing the position of the sequences of *Tripos* and *Ceratium* by Maximum Likelihood (ML). The section and subgeneric names are based on the classical taxonomical schemes. A sequence of *Protoceratium*

reticulatum is used as outgroup. Numbers near branches denote ML bootstrap probability value. Bootstrap values <70 are omitted. Scale bar denotes 0.01 substitutions per site.

3.2 Subgenus *Biceratium*

3.2.1 Section of *Tripes eugrammus* (= *T. furca* auct. mult.).

Ehrenberg (1834) described *Peridinium furca* from samples collected at Kiel, Baltic Sea, illustrated in his figure 2 (Fig. 3a, available at <https://www.biodiversitylibrary.org/page/29725176>). Ehrenberg (1860) described *P. eugrammus* from Trieste, Mediterranean Sea, with his figure 4 published in 1873 (Fig. 3b, available at <https://digital.zlb.de/viewer/image/15818596/15/>). Ehrenberg (1854a) described *P. lineatum* from the Newfoundland, boreal North Atlantic Ocean, and Ehrenberg (1854b) figure it in his figure 25c in the plate 35 (Fig. 3c, available at <https://www.biodiversitylibrary.org/page/50932859>). The epithecae of *P. furca* and *P. lineatum* are triangular with the apical horn distinct from the rest of the epitheca (Fig. 3a, c), while the epitheca of *P. eugrammus* is gradually tapering into the apical horn (Fig. 3b). The bases of the hypothecae of *P. furca* and *P. lineatum* are almost parallel to the cingulum, while the basis of the hypotheca of *P. eugrammus* is more inclined. The antapical horns of *P. eugrammus*, especially the left one (Fig. 3b), are more robust than those in *P. furca* and *P. lineatum* (Fig. 3a, c). *Peridinium lineatum* showed shorter antapical horns than *P. furca*, although this feature may vary intraspecifically as occur in the anterior-most daughter cells. The lateral contour of the hypotheca is almost perpendicular to the cingulum in *P. lineatum* (Fig. 3c), while more inclined in *P. furca* (Fig. 3a). The comparison of the original illustrations (Fig. 3a–c) evidences that *P. furca* described from subarctic waters and *P. eugrammus* described from a late summer proliferation in the Mediterranean Sea are independent species. More difficult is to solve the identity of *P. lineatum*.

Fig. 3. Line drawings and micrographs of *Triplos eugrammus*, *T. furca*, and *T. hircus*. (a) *Peridinium furca* by Ehrenberg (1834). (b) *P. eugrammus* by Ehrenberg (1873). (c) *P. lineatum* by Ehrenberg (1854b). (d) *Ceratium furca* by Claparède and Lachmann (1859). (e) *C. furca* by Bergh (1881). (f) *C. triplos* by Lohmann (1908). (g) *C. furca* by Stein (1883). (h) *Biceratium furca* by Vanhöffen (1897). (i) *B. debile* by Vanhöffen (1897). (j) *C. lineatum* by Jørgensen (1911). (k) Immature cell. (l–n) *T. furca*. (o–x). *T. eugrammus*. (p–s). Aberrant forms. (t–v) Infected by an endoparasite. (w–x) Individuals with long antapical horns. (y–ab) *T. hircus*. (z) *C. hircus* by Schröder (1909).

Ehrenberg's illustrations of *P. furca* and *P. eugrammum* were realistic and enough to facilitate further identifications, but they have been neglected by further authors. The reasons could be problems to access to the Ehrenberg's huge scientific production, with the diagnosis and figure of each new species in distinct publications. Ehrenberg reported the diagnosis of *T. eugrammus* in 1860 and figured it in 1873. Claparède and Lachmann (1859) considered *P. furca* and *P. lineatum* as synonyms, and they reported an unfortunate illustration of their new combination *Ceratium furca*. In addition to the excessively thin horns, they figured a chimeric cell with the epitheca of *P. furca* and the hypotheca with the parallel antapical horns that characterizes *P. eugrammum* (Fig. 3d), the latter species undescribed at that time. Further studies did not help to solve this. From the Baltic Sea, Bergh (1881) admitted a high variability of *C. furca* that included individuals with the morphology of *P. lineatum* in his figures 13–14, *P. furca* in his figures 1–2, 15–19, and *P. eugrammum* in his figure 20 (Fig. 3e). From the Baltic Sea, Lohmann (1908) reported the morphological variability of *C. tripos* (Fig. 3f) with forms close to Bergh's illustrations of *C. furca* or Ehrenberg's *P. lineatum* and *P. furca*. Lohmann proposed new taxa such as *C. tripos* var. *subsalsum* f. *lineatum* that resembled Ehrenberg's *P. furca*. After the supposed high intraspecific variability in Bergh (1881), Stein (1883) considered *P. furca*, *P. eugrammum* and *P. lineatum* as a single species named '*C. furca* Dujard.' (Fig. 3g). Stein was a lumpner taxonomist and he illustrated three species as *C. furca*. He figured unrealistic epithecae in most of the illustrations, especially in his figure 11, but the hypothecae were more realistic. Stein's figures 7–10 illustrated individuals with parallel antapical horns that unequivocally correspond to *P. eugrammus*. Stein's figure 11 showed an individual with divergent antapical horns and the shape of the hypotheca of *P. furca*. Stein's figures 13–14 showed individuals with very short antapical horns that fit with

Ehrenberg's *P. lineatum* (Fig. 3g). Vanhöffen (1897) from samples collected near Newfoundland, type locality of *P. furca*, illustrated '*Biceratium furca* Dujard.' in his figure 15 (Fig. 3h), and the new species *Biceratium debile* in his figure 16 (Fig. 3i). Both taxa are synonyms (Fig. 3h–i). The basionym of the type species of the genus and subgenus *Biceratium* is the boreal species *P. furca*, and Vanhöffen (1897) did not report *P. eugrammus*. Lemmermann (1899) proposed *C. furca* var. *berghii* for the individual of Bergh's figure 20 (Fig. 3e) that corresponds to the morphology of *P. eugrammus* (Fig. 3e). Jørgensen (1911) considered '*Ceratium furca* (Ehrenberg) Dujardin' and *C. lineatum* as independent species. Jørgensen's illustration of *C. lineatum* showed divergent antapical horns (Fig. 3j) similar to Ehrenberg's *P. furca* (Fig. 3a). Jørgensen (1911) split *C. furca* into two subspecies: *berghii* for *C. furca* var. *berghii*, and *eugrammus* for *P. eugrammus*. This is unfortunate because *C. furca* var. *berghii* is *P. eugrammus*, and none of these two subspecies correspond to the morphology of Ehrenberg's *P. furca* (Fig. 3a). Jørgensen (1920) reported for *C. furca*: "This cosmopolitan species was noted from the Mediterranean Sea already by Ehrenberg who described it, 1859, from Trieste as a new species, *Peridinium eugrammus*". Jørgensen's synonymy has prevailed up to date and *T. eugrammus* remains as a junior synonym of *T. furca*. Based on Ehrenberg's illustrations, *T. furca* (Fig. 3k–n) and *T. eugrammus* (Fig. 3o–y) are independent species. The records in the literature and the DNA sequences (AJ276699, FJ402966, MF927997–8) reported as *T. furca* corresponded to *T. eugrammus*. The records in the literature reported as *T. lineatus* corresponded to *T. furca*. The DNA sequence (AF260391) retrieved as *T. lineatus* is not documented, but very likely it corresponds to *T. furca*. *Tripus eugrammus* has a wide distribution including tropical seas, while *T. furca* has a preferentially boreal-temperate distribution. *Tripus eugrammus* reaches high abundances in neritic waters, being common to observe aberrant individuals (Fig. 3p–s) or infected by endoparasites (Fig.

3t–v). Some individuals of *T. eugrammus* may show longer antapical horns (Fig. 3w–x). In warm oceans, *T. eugrammus* often co-occurred with individuals with antapical horns of almost similar length and slightly divergent as in *T. furca*. These individuals identified *T. hircus* (Fig. 3y–ab) are classified in the section Furciformia.

3.2.2 Section Furciformia (including Pentagona)

Tripos furca is the type species of the subgenus *Biceratium* and the section Furciformia. There is only one available LSU rRNA gene sequence (AF260391) retrieved as *T. lineatum* and it does not cluster with the basal sequences of *P. eugrammus* (Fig. 1). With the current available data, *T. eugrammus* is classified in its own section, and *T. furca* in the section Furciformia. We cannot study the relationship among the members of the sections Furciformia and Pentagona based on the LSU rRNA gene sequences because a single sequence is available (Fig. 1). Based on the SSU rRNA gene phylogeny, the members of Furciformia and Pentagona cluster in distinct clades (Fig. 2). Within this context, the sections Furciformia and Pentagona are merged until further molecular data will clarify this matter.

Fig. 4. Line drawings and micrographs of species of the section Furciformia (including Pentagona), and an autotomized cell of the section Macroceros. (a) *Ceratium furca* by Kofoed (1908a). (b) *C. lineatum* by Kofoed (1908a). (c) *C. eugrammum* by Kofoed (1908a). (d) *C. eugrammum* by Kofoed (1908c). (e) *C. minutum* by Jørgensen (1920). (f) *C. minutum* redrawn from Lebour (1925). (g–i). *Tripus minutus*. (j) Tentative microgamete. (k) *C. kofoidii* by Jørgensen (1920). (l) *C. setaceum* by Jørgensen (1911). (m) *C. setaceum* by Jørgensen (1920). (n) *C. boehmii* redrawn from Graham and Bronikovsky (1944). (o–q). *T. setaceus*. (r) Autotomized cell of the section Macroceros, tentatively *T. trichoceros*. (s–w). *T. teres*. (s) *C. teres* by Kofoed (1907b). (x) *C. lineatum* var. *longisetum* by Ostenfeld and Schmidt (1901). (y–ag) *T. pentagonus*. (y) *C. pentagonum* by Gourret (1883).

From individuals collected in the coast of southern California, Kofoed (1908a) tried to clarify the identity of *Peridinium eugrammum* with questionable results. Kofoed (1908a, his figure 1) as *C. furca* (Fig. 4a) illustrated a cell that corresponded to Ehrenberg's *P. eugrammum* (Fig. 3b). Kofoed (1908a, his figure 2) as *C. lineatum* (Fig. 4b) illustrated a cell of *C. pentagonum* (Fig. 4y). Kofoed (1908a, his figure 3) as *C. eugrammum* (Fig. 4c) illustrated a cell closer to Ehrenberg's *P. lineatum* with longer antapical horns. In other publication, Kofoed (1908c, p. 351, his figure 7) reported as *C. eugrammum* (Fig. 4d) as cell with short antapical horns that fit with Ehrenberg's *P. lineatum* (Fig. 3c). Jørgensen (1911) proposed the new species *C. kofoedii* for the figure 3 reported as *C. eugrammum* by Kofoed (1908a) (Fig. 4c). The illustrations of *C. kofoedii* in Jørgensen (1911) (Fig. 4k), *C. setaceum* in Jørgensen (1911) (Fig. 4l) and Jørgensen (1920) (Fig. 4m) very likely correspond to a single species (Fig. 4o–q). Graham and Bronikovsky (1944) described *C. boehmii* (Fig. 4n) that is similar to Jørgensen's illustrations of *C. kofoedii* and *C. setaceum*, and the slightly longer antapical horns resembled Ehrenberg's *P. furca* (Fig. 3a). We have to be careful to mistake the species of the subgenus *Biceratium* and individuals of *T. trichoceros* or other members of the section *Macroceros* which have undergone autotomy of the antapical horns (Fig. 4r). In Jørgensen (1911), the basionym of *C. kofoedii* is *C. eugrammum* in the figure 3 by Kofoed (1908a) (Fig. 4c), but later Jørgensen (1920) proposed the new species *C. minutum* (Fig. 4e) citing again as basionym the figure 3 by Kofoed (1908a) (Fig. 4c). Jørgensen's *C. kofoedii* is a distinct species from Ehrenberg's *P. eugrammum* and Kofoed's *P. eugrammum*. *Ceratium kofoedii* (Fig. 4k–l) is here considered conspecific with *C. setaceum*. Then, we can use *T. setaceus* (Fig. 4o–q) for *C. kofoedii* and *C. boehmii*.

Jørgensen (1920) described *C. minutum* with three illustrations of individuals collected in the European Atlantic, including two individuals collected off west Brittany (Fig. 4e). From

samples collected in the English Channel, Lebour (1925) illustrated as *C. minutum* with individuals showing very short antapical horns (Fig. 4f). The comparison of the original illustration of *C. minutum* (Fig. 4e) and Ehrenberg's *P. lineatum* (Fig. 3c) suggest that these taxa may be conspecific. A doubt is whether *P. lineatum* is a morphotype in the life cycle of other species. Short antapical horns are commonly observed in the anterior-most daughter cells of other species. However, *T. minutus* is not an immature cell because it divides with that morphology (Fig. 4g–i). The sexual life cycle of the species of *Tripes* is characterized by male microgametes with short horns. It cannot be discarded that developing gametes of *T. muelleri* or other species could be mistaken as *T. minutus* (Fig. 4j). Ehrenberg's *P. lineatum* and *T. minutus* are considered provisionally as independent species until further research will solve the relationship.

Gourret (1883) described *C. pentagonum* with a short apical horn (Fig. 4y). In neritic waters, it usually exhibited a short apical horn (Fig. 4z–ab) and sometimes formed colonies (Fig. 4ac). In the open ocean, a long apical horn is more commonly observed (Fig. 4ad–ag), being identified in the literature as *C. lineatum* var. *longisetum* (Fig. 4x). Kofoed (1907b) described *C. teres* (Fig. 4s) with short antapical horns and an intermediate shape of the epitheca between *T. pentagonus* (Fig. 4y) and *T. setaceus* (Fig. 4m). *Tripes teres* (Fig. 4t–w) showed a pentagonal cell body more antero-posteriorly elongated than *T. pentagonus* (Fig. 4ad–ag).

3.2.3 Section Candelabra

The general appearance of *Tripes eugrammus* (Fig. 3O) resembles the freshwater relatives such as *Ceratium hirundinella* (Fig. 5a–b), and more especially *C. furcoides*. The latter taxon

was also described from a lake as *C. furca* var. *lacustre*. That similarity is more evident between *T. candelabrum* (not ‘*candelabrus*’) (Fig. 5c) and *C. hirundinella* (Fig. 5a–b). *Triplos candelabrum* is a chain-forming species (Fig. 5d–e), while this feature is rare in *T. eugrammus* and the freshwater *Ceratium*. *Triplos eugrammus* is a euryhaline species that often reaches high abundance in low salinity coastal waters. The species of the freshwater genus *Ceratium* are characterized by the formation of cysts. Resting cysts have been only reported for *T. eugrammus* and *T. candelabrum* (Gómez *et al.*, 2010). The SSU rRNA gene sequences of *T. candelabrum* cluster with an unresolved relationship with other taxa (Fig. 2), and LSU rRNA gene sequences are not available. *Triplos candelabrum* and its section *Candelabra* remains in the subgenus *Biceratium* based on the superficial resemblance to *T. furca*. Other molecular markers of *T. candelabrum* are also a priority to clarify the evolution of the genus.

Fig. 5. Line drawings and micrographs of *Ceratium hirundinella*, and the section Candelabra of *Tripos*. (a–b) *C. hirundinella*. (c) *Peridinium candelabrum* by Ehrenberg (1873). (d–f) *T. candelabrum*.

3.3. Subgenus *Archaeoceratium*

3.3.1 Section *Poroceratium*

The members of *Archaeoceratium* inhabit preferentially in warm oceanic waters and at subphotic depths (>50 m). The records are rare because most of the samplings are carried out in the surface of temperate coasts. The cell division occurred during the night, and samplings are usually carried out during the day light. Observations of cells under division allow tracking the development of the daughter cells. The anterior- and the posterior-most daughter cells have temporally incomplete antapical and apical horns, respectively. When the cell development is unknown, it is more probable that recently divided cells with incomplete theca could be described as independent species.

The type species of *Archaeoceratium* is *Tripos gravidus* (Fig. 6a). The records of the close relatives *T. cephalotus* (Fig. 6b) and *T. praelongus* (Fig. 6d–g) are less frequent. Are *T. cephalotus* and *T. praelongus* morphotypes of *T. gravidus*? When a cell divides, the anterior-most daughter cell receives most of the epitheca of the parent cell, and it regenerates the antapical horns and a part of the hypotheca, and vice versa for the posterior-most daughter cell (Fig. 4h–i, aa–ab). Then, at least the epitheca or the hypotheca of the daughter cell should be similar to the parent cell. It is highly probable that we are dealing with an independent species when both epitheca and hypotheca are distinct from the tentative parent cell. The epitheca of *T. cephalotus* is round (Fig. 6b), while more or less ellipsoidal in *T. gravidus* or *T.*

praelongus. The hypotheca of *T. cephalotus* has short antapical horns, while *T. gravidus* or *T. praelongus* has longer antapical horns. This suggests that *T. cephalotus* is an independent species. The distinction between *T. gravidus* and *T. praelongus* is more difficult because they are varieties such as *T. gravidus* var. *obovatus* with intermediate characteristics (Fig. 6c). I have observed daughter cells that split during the sample treatment. One cell showed a large epitheca of *T. gravidus* and other cell showed a small epitheca with the shape of *T. praelongus* (Fig. 6d). However, other cells kept the morphology of *T. praelongus* even when they divide (Fig. 6e). The epitheca is incomplete in the posterior-most daughter cells (Fig. 6f–g). *Tripus praelongus* is considered a morphotype of *T. gravidus*, and the observations should be reported as *T. gravidus* var. *praelongus*.

Fig. 6. Line drawings and micrographs of species of the subgenus *Arhaeceratium*. (a) *Triplos gravidus*. (b) *Ceratium* sp. (= *T. cephalotus*) in Schütt (1892). (c) *T. gravidus* var. *obovatus*. (d–e). Daughter cells of *T. gravidus*. (d–g) *T. gravidus* var. *praelongus*. (h–i) *T. lanceolatus*. (j) *C. lanceolaum* by Kofoid (1907a). (k) *C. lanceolaum* by Gaarder (1954). (l) *Ceratium* sp. by Schütt (1892). (m–n) *T. digitatus*. (o) *C. digitatum* by Schütt (1895). (p–r) *T. rotundatus* comb. nov. (s) *C. digitatum* var. *rotundatum* by Jørgensen (1920). (t) *C. tasmaniae* redrawn from Wood (1963). (u–v) *T. schroeteri*. by Schröder (1906). (w) *C. schroeteri* by Kofoid (1907a). (x–ac) *T. belone*. (x) *C. belone* by Cleve (1900). (y) *C. belone* by Schröder (1906). (z) *C. furca* var. *incisum* by Karsten (1906). (aa) *C. incisum* by Jørgensen (1920). (ab) *C. brunellii* redrawn from Rampi (1942). (ac–an). *T. pacificus*. (ae) *C. furca* var. *longum* by Karsten (1906). (af) *C. pacificum* by Schröder (1906). (ag) *C. pacificum* by Kofoid (1907a). (ah) *C. pacificum* by Stüwe (1909). (ai) *C. belone* by Jørgensen (1920). (aj) Smaller cells of *C. belone* redrawn from Graham and Bronikovsky (1944). (ak) *C. furca* var. *belonoides* by Jørgensen (1920). (al) *C. pacificum* E.J.F. Wood redrawn from Wood (1963). Scale bars: 50 µm.

3.3.2 Section Lanceolata

The members of the section *Poroceratium* are characterized by a pore in the epitheca (Fig. 6a–b). The pore has not been reported in the rare species *Triplos lanceolatus*. Its morphology is intermediate between *T. praelongus* with a pointed epitheca and a straight cell of *T. schroeteri* with shorter antapical horns. My observations from the tropical Eastern Pacific (Fig. 6h) fit well in shape and size with the original description of *C. lanceolatum* by Kofoid (1907a) that described it from the same region (Fig. 6i). Gaarder (1954) identified as *C. lanceolatum* a

large cell (285 μm long) with long and bent antapical horns (Fig. 6j), already illustrated by Schütt (1892) with a pore in the epitheca (Fig. 6k). These observations resembled individuals of *T. gravidus* var. *praelongus* with an atypical lanceolate epitheca. *Tripes lanceolatus* remains in its own section because it is difficult to decide placing it in the sections Poroceratium or Digitata. Other tentative member of Lanceolata could be *T. brunellii*, only known from the original description by Rampi (1942) (Fig. 6ad).

3.3.3 Section Digitata

Tripes digitatus, classified in the earlier taxonomical schemes in the subgenus *Biceratium*, is classified in *Archaeoceratium* based on the molecular data (Fig. 2, Gómez *et al.*, 2010). It has one antapical horn laterally directed (Fig. 6l–n) that does not strictly fit with Kofoed's diagnosis of the subgenus: "Antapical horns subequal, directed posteriorly". Both, the epitheca and hypotheca of *T. digitatus* var. *rotundatus* (Fig. 6o) are distinct from those in *T. digitatus* (Fig. 6l–n). The epitheca of *T. digitatus* is strongly reflected towards the dorsal side, the left antapical horn is anteriorly directed and the apex showed a short projection (Fig. 6l–n), while *T. digitatus* var. *rotundatus* showed an epitheca less bent towards the dorsal side, the short projection in the apex is missing, and the left antapical horn is directed laterally (Fig. 6o–r). *Tripes tasmaniae* (Fig. 6p) is a synonym of *T. digitatus* var. *rotundatus* that Wood (1963) described without citing the similarity. *Tripes tasmaniae* is the earliest available name at the species rank (I.C.N. art. 11.2), but it is not a validly published name (I.C.N. art. 39.1). The classification of *T. digitatus* var. *rotundatus* at the species rank is proposed in this study.

In the earlier taxonomical schemes, *Tripes schroeteri* (non *T. schroederi*) was classified in the subgenus *Biceratium* based on the superficial resemblance with *T. eugrammus*. *Tripes schroeteri* is classified in *Archaeoceratium* because the epitheca is wide and flat, and the

antapical horns are unequal, robust and bent (Fig. 6s–u). Cleve (1900) described *Ceratium belone* (Fig. 6v), further illustrated by Schröder (1906) (Fig. 6w), and Karsten (1906) that described it as *C. furca* var. *incisum* (Fig. 6x). Cleve's illustrations are sketchy and the description of *C. belone* was scarcely detailed. The cell shape of Schröder's and Karsten's illustrations were similar to Cleve's taxon, but their illustrations showed more clearly that the left antapical horn is slightly bent. *Triplos incismus* is a junior synonym of *T. belone*. However, Jørgensen (1920) considered *C. incisum* and *C. belone* as independent taxa. Jørgensen's figures of *C. incisum* (Fig. 6ac) and *C. belone* (Fig. 6ai) corresponded to Cleve's *C. belone* (Fig. 6v–x) and Schröder's *C. pacificum* (Fig. 6af), respectively.

3.3.4 Section of *Triplos pacificus* (subsection Beloniformia in part)

Karsten (1906) described *C. furca* var. *longum* (Fig. 6ae) and Schröder (1906) described the same taxon as *C. pacificum* (Fig. 6af). Kofoed (1907a) reported a wider cell as *C. pacificum*, but it is closer to *C. belone* sensu Cleve (Fig. 6ag). Stüwe (1909) illustrated individuals that fit with the original description of *C. pacificum* (Fig. 6ah). Jørgensen (1920) under the name *C. belone* (Fig. 6ai) figured an elongated cell that corresponded to Schröder's *C. pacificum* (Fig. 6af). Jørgensen's interpretation of *C. belone* was questioned by Pavillard (1931, p. 71), but it has prevailed up to date. Graham and Bronikovsky (1944) admitted a high morphological variability of the epitheca of *C. belone*, ranging from individuals that fit with *T. pacificus* to smaller individuals with a thinner epitheca than in the original description of *T. belone* (Fig. 6aj). There are warm water taxa such as *C. furca* var. *belonoides* that can be mistaken for *C. belone* (Fig. 6ak). Wood (1963) added confusion when he proposed the later isonym *C. pacificum* (Fig. 6ao) for individuals of *T. geniculatus* (Fig. 7a–c). The evolutionary

origin of *T. pacificum* can be interpreted in two ways: 1) an elongated cell evolved from a common ancestor with *T. eugrammus* or *T. belone*, or 2) a cell with a developed right antapical horn evolved from a common ancestor with *T. fusus*. *Tripes pacificus* has a flattened epitheca gradually tapering towards the apex that suggests an affinity with *Archaeoceratium*. *Tripes pacificus* is here considered a link between *Archaeoceratium* and *Amphiceratium*. A new section should be proposed for *T. pacificus* if it is confirmed by the molecular data.

3.3.5 Section Inflata

The support to re-classify the members of the section Inflata and most of the members of section Fusiformia into *Archaeoceratium* is based on the molecular data of *T. falcatus*, a species currently classified in the section Fusiformia of *Amphiceratium*. The SSU rRNA gene sequence retrieved as *T. falcatus* (MF927979) showed a percentage of similarity of 99.86 and 99.71% when compared to the sequences of *T. digitatus* and *T. gravidus*, respectively, while the similarity was lower than 99% when compared to *T. fusus*. The sequence of *T. falcatus* clustered with high support with *T. digitatus* and *T. gravidus* (Fig. 2). This suggests that *T. falcatus* and its relatives should be classified in the subgenus *Archaeoceratium*.

Kofoed (1909, p. 219) defined the subgenus *Archaeoceratium* (as *Poroceratium*) as: “Antapical horns subequal, directed posteriorly. Midbody extends to apical pore. Apical horn not differentiated”. The species of the section Inflata of *Amphiceratium* (i.e., *T. geniculatus*, Fig. 7a–c), showed a flattened midbody and antapical horns closer to *Archaeoceratium*. *Tripes bigelowii* (Fig. 7d) is a rare species with an expanded midbody (Fig. 7d). In the current taxonomical schemes, *T. geniculatus* and *T. bigelowii* are classified in the section Inflata, while *T. inflatus* in the section Furciformia (Jørgensen 1911, Sournia 1968). Individuals of *T.*

inflatus (Fig. 7e–f) infected by the endoparasite *Amoebophrya* could be mistaken for *T. bigelowii* (Fig. 7d).

Gourret (1883) described *Ceratium longirostrum* (Fig. 7g) as a cell with straight horns and the right antapical horn was not visible as typical in *T. fusus* or *T. extensus*. Kofoed (1907a, his figure 12) described *C. pennatum* f. *propium* with slightly bent horns and the right antapical horn very reduced, but visible (Fig. 7h). Despite the significant differences, Jørgensen (1920) reported that *C. longirostrum* (Fig. 7g) and *C. pennatum* f. *propium* (Fig. 7h) are synonyms. Jørgensen's illustration (Fig. 7i) identified as *C. longirostrum* corresponded to Kofoed's *C. pennatum* f. *propium* (Fig. 7h), and not to Gourret's *C. longirostrum* (Fig. 7g). Gourret (1883) did not report any curvature of the horns in the diagnosis and he reported that his figure 65 showed the dorsal view. Jørgensen (1920) considered that Gourret's illustration showed the side view, but this option is highly improbable. Jørgensen (1920, p. 37) reported the figure 13 of *C. pennatum* f. *propium* in Kofoed (1907a) as synonym of *C. longirostrum*, but Kofoed's figure 13 corresponded to *C. pennatum* f. *inflatum*. Further authors have followed Jørgensen's interpretation using the name *C. longirostrum* for *C. pennatum*, and the latter name has disappeared from the literature. The name *T. pennatus* is here revived for *C. longirostrum* auct. mult. (Fig. 7i). Jørgensen (1920) proposed *C. falcatum* for *C. pennatum* f. *faltacum* (Fig. 7k–o). Jørgensen (1920, p. 35) reported that *C. fusus* var. *concavum* Gourret (Fig. 7q) is a synonym of *C. inflatum*, but it is closer to *C. falcatum* with a bent apical horn (Fig. 7p). Jørgensen (1911, p. 25) cited "*C. concavum* auct. p. p.)", but I am unable to find the proposal of *C. fusus* var. *concavum* at the species rank. Jørgensen (1920) proposed the new species *C. falcatifforme* (Fig. 7r) for a cell with a wider epitheca than *C. falcatum* (Fig. 7s–t). Kofoed (1907a) described *C. scapiforme* characterized by a wide epitheca (Fig. 7u). Jørgensen (1911) proposed *C. pennatum* var. *scapiforme*, and later reported "*C. pennatum* v. *scapiforme*

Jørgensen 1911, non *C. scapiforme* Kofoed” as synonyms of *C. longirostrum* (Jørgensen 1920). As occurred with *C. pennatum*, *C. scapiforme* (Fig. 7v) has disappeared from the literature after Jørgensen.

Fig. 7. Line drawings and micrographs of species of *Archaeoceratium*: section Inflata and some species formerly classified in Fusiformia of the. (a–c) *Tripes geniculatus*. (d) *Ceratium bigelowii* by Kofoed (1907a). (e–f) *T. inflatus*. (g) *C. pennatum* f. *inflatum* by Kofoed (1907a, fig. 13). (h) *C. longirostrum* by Gourret (1883). (i) *C. pennatum* f. *propium* by Kofoed (1907a, fig. 12). (j) *C. longirostrum* by Jørgensen (1920). (k) *T. pennatus*. (l) *C. pennatum* f. *falcatum* by Kofoed (1907a, fig. 14). (m) *C. falcatum* by Jørgensen (1920). (n–p) *T. falcatum*. (q) *C. fusus* var. *concauum* by Gourret (1883). (r–t) *T. falcatiformis*. (u) *C. faltatum* by Jørgensen (1920). (v–w) *T. scapiformis*. (x) *C. scapiforme* by Kofoed (1907a, fig. 23). Scale bars: 50 µm.

3.4 Subgenus *Amphiceratium*

3.4.1 Section Fusiformia

Amphiceratium is dismembered after the classification of the section Inflata and most of the species of the section Fusiformia in *Archaeoceratium*. *Amphiceratium* is here restricted to *T. fusus* and very closely allied taxa with an elongated cell body along the antero-posterior axis with almost straight horns, and a reduced or almost invisible right antapical horn (Fig. 8a). The type species *T. fusus*, is together with *T. eugrammus*, one of the more common species in temperate coastal waters. In addition to the individuals under division (Fig. 8b), it can be observed teratogenic or aberrant forms (Fig. 8c–e). Schütt's (1895) illustrated an individual of *C. fusus* with a wide epitheca (Fig. 8f) that was later reported as the variety *C. fusus* var. *schuettii*. It corresponds to individuals of *T. fusus* infected by the endoparasite *Amoebophrya* (Fig. 8g). Claparède and Lachmann (1859) reported illustrations identified as *C. furca* (Fig. 3d) and *C. biceps* (Fig. 8h) with atypical morphologies that have not been further reported.

Most of the authors have considered that they correspond to a single species, placing *C. biceps* as a synonym of *T. eugrammus* (= *C. furca* auct. mult.). As illustrated by Stein (1883), *C. biceps* resembles the lateral view of *T. eugrammus* (Fig. 8i) or its anterior-most daughter cell (Fig. 8j). Gourret (1883) described *C. fusus* var. *extensum* as a very elongated cell (Fig. 8l). Jørgensen (1911, p. 27) considered *C. biceps* sensu Kofoed 1908c as *C. strictum*, and Taylor (1976) considered *C. biceps* as an immature cell of *C. extensum*. Kofoed (1908c, his figure 21–23) induced the error when he assumed a high variability for *C. biceps* (Fig. 8j). During the cell division of *T. extensus*, the anterior-most daughter cell received the apical horn from the parent cell, and the posterior-most cell received the long left antapical horn (Fig. 8r–v). The daughter cell that receives the short right horn from the parent cell has been identified as *C. strictum* (Fig. 8t–v). Kofoed (1908c) illustrated a cell with short apical and antapical horns (Fig. 8j). This is atypical and Kofoed very likely misidentified an anterior-most daughter cell of *T. eugrammus* (Fig. 8k) with a life stage of *T. extensus*. *Tripus extensus* (Fig. 8m–n) is a thermophilic species unreported for the North Sea, and Claparède and Lachmann (1859) did not observe it (Fig. 8h) in the cold waters of a Norwegian fjord where *T. eugrammus* is present (Fig. 8i). *Ceratium biceps* (Fig. 8h) is an immature cell of *T. eugrammus* (Fig. 8k). The molecular data confirmed that *T. extensus* is distinct from *T. fusus* (Gómez *et al.*, 2010), but there are individuals with intermediate characteristics between both species that need research. The species diagnoses based on the length of the horns are risky because it depends of the degree of maturation after the division or the potential autotomy (Fig. 8r–s). The name *T. longirostrum* is available for a species with intermediate characteristics between *T. fusus* and *T. extensus* (Fig. 8o–q).

Fig. 8. Line drawings and micrographs of species of the section Fusiformia of the subgenus *Amphiceratium*. (a–g) *Tripus fusus*. (b) Cell under division. (c–e) Aberrant forms. (f) *Ceratium fusus* by Schütt (1895). (g) Cell infected by endoparasite *Amoebophrya*, known as *Ceratium fusus* var. *schuettii*. (h) *C. biceps* by Claparède and Lachmann (1859). (i) *C. furca*

by Stein (1883). (j) *C. biceps* by Kofoed (1908c, fig. 23). (k) Immature cell of *T. eugrammus*. (l–n) *Tripus extensus*. (k) *C. fusus* var. *extensum* by Gourret (1883). (o–q) *Tripus longirostrum*. (p) *C. longirostrum* by Gourret (1883). (r–v) Immature individuals of *T. longirostrum* or *T. extensus*. (u–v). The arrow points the right antapical horn. Scale bars: 50 μm .

3.5 Subgenus *Tripus*

Based on the SSU rRNA gene sequence phylogeny, the species of the clade that contains the type, *T. muelleri*, and distantly related to the sequences of the types of *Archaeoceratium*, *Amphiceratium* and *Biceratium*, should be grouped into a single subgenus named *Tripus*, an autonym (Fig. 2). Most of the authors have split the species of *Tripus* into four subgenera: *Amphiceratium*, *Archaeoceratium* (= *Poroceratium*), *Biceratium* (= *Ceratium*, *Orthoceratium* Meunier) and *Tripoceratium* (= *Euceratium*, *Orthoceratium* Sournia). Kofoed (1909) proposed the subgenus *Macroceratium* for some species formerly classified in *Tripoceratium* (*C. macroceros*, *C. gallicum*, *C. vultur*) which “bases of the antapicals projected more or less posteriorly beyond midbody forming a postindentation”, while *Tripoceratium* was restricted to species with “postmagin rounded, no postindentation”. Kofoed (1909) was fortunate and the postindentation is a trait supported by the molecular phylogeny, although the molecular divergence is not high to support the classification of *Macroceratium* as independent from the subgenus *Tripus* (Fig. 2). The antapical horns of the species of *Amphiceratium*, *Archaeoceratium* and *Biceratium* are directed posteriorly, while there is more variability in the species of the subgenus *Tripus*. In the asexual life cycle, anterior-most daughter or

autotomized cells show posteriorly directed antapical horns, while they bent and were anteriorly directed in the mature cells. This feature, together with the variability in the length of the horns due to environmental conditions (i.e., seasonality) are factors that induce a high variability of outlines. Consequently, it is even more difficult to establish the synonymy and species circumscriptions in the subgenus *Tripos* due to the numerous intermediate morphologies.

3.5.1 Section *Macroceros* (=Protuberantia)

Ehrenberg (1840, p. 201) described *Peridinium macroceros* with a brief diagnosis. Ehrenberg's illustration of *P. macroceros* (Fig. 9p) from an individual collected at Cuxhaven, German North Sea, is available at the Ehrenberg's collection at: <http://download.naturkundemuseum-berlin.de/ehrenberg/Ec%20Drawings/Ec%20draw%20001-999/Ec%20draw%20900-999/ECdraw950.jpg>). Further authors have interpreted *P. macroceros* as the species illustrated by Claparède and Lachmann (1859). This time, Claparède and Lachmann's illustration is realistic (Fig. 9a), but it is not conspecific with Ehrenberg's *P. macroceros* (Fig. 9p). *Ceratium tripos* var. *macroceros* by Claparède and Lachmann showed a prominent postindentation (Fig. 9a), while Ehrenberg's *P. macroceros* showed a scarce postindentation (Fig. 9p). In further literature, the species with the prominent postindentation have been assigned to *C. macroceros* (Fig. 9a–c, e–f). Only, the illustration of '*Ceratium tripos* var. *macroceras* f. *armata*' (Fig. 9d) by Karsten (1905, his plate 19, figs 7, 8) fit with Ehrenberg's *P. macroceros*, but Karsten (1905) was no coherent because his '*C. tripos* var. *macroceras* Ehrenberg' (his plate 22, figure 29) showed a prominent postindentation and it is not conspecific with his form '*armata*'. To the best of my knowledge, nobody has interpreted correctly Ehrenberg's *P. macroceros* because the diagnosis was not enough detailed, and the

illustration could not be accessible. What to do? The basionym of *T. macroceros* is *P. macroceros* as described by Ehrenberg (1840), and the diagnosis corresponds to the species figured by him (Fig. 9p), and not further interpretations. Then, *C. macroceros auct. mult.* needs other species name. The earlier name at the rank level for this species could be *C. gallicum* (Fig. 9e). *Ceratium deflexum* was later ranked at the species level (Fig. 9f). Under the name *T. gallicus* are included individuals with a progressive curvature of the antapical horns as *C. macroceros* sensu Claparède and Lachmann (Fig. 9g–j), and individuals with a more abrupt deflection angle of the antapical horns (Fig. 9k) that fit better with the original description of *C. gallicum*. Further research is needed to confirm if both forms are conspecific. *Tripes massiliensis* is a closely related species to *T. gallicus*, but with a less prominent postindentation (Fig. 9l–n). Ehrenberg's *P. macroceros* (Fig. 9p, u–w) shows a scarce postindentation when compared to *C. gallicum* and *C. massiliense*. Junior synonyms of *P. macroceros* also described from the North Sea are *C. batavum* (Fig. 9r) and *C. intermedium* (Fig. 9s), and from other regions are *C. contrarium* (Fig. 9q) and *C. protuberans* (Fig. 9t).

From the coasts of Marseilles, Gourret (1883) described *C. tripes* var. *inflexum* (Fig. 9x), *C. tripes* var. *typicum* (Fig. 9y) and *C. carriense* (Fig. 9z). Gourret's illustration of *C. carriense* is the anterior-most daughter cell of *C. tripes* var. *typicum*, and *C. tripes* var. *inflexum* is an aged cell of the same species that was further described as *C. flagelliferum* (Fig. 9aa). Gourret used 'typicum' to remark that this form was common in the coasts of Marseilles, and this should not be interpreted as the typical morphology of *C. tripes* (now *T. muelleri*). Based on my experience after one year of daily plankton samplings at the coasts of Marseilles, this species is common and abundant there (Fig. 9ab). Individuals of *T. carriensis* infected by an endoparasite showed an inflated midbody (Fig. 9ac–ad), and they have been described as *C. ramakrishnae* (Fig. 9ae). *Tripes carriensis* is characterized by antapical horns that bent at

the same height (Fig. 9x–ae). *Tripus trichoceros* is more slender and an oceanic species which antapical horns bent at different heights (Fig. 9af–ah). Gourret (1883) proposed *C. carriense* for an immature individual and this may induce confusion. Jørgensen (1920) and further authors misinterpreted the identity of *C. carriense*. Jørgensen illustrated an individual with the antapical horns bent at different heights, with a short curvature of the proximal region of the left antapical horn (Fig. 9ai, al–am). The tentative earlier name for Jørgensen's *C. carriense* is *T. volans* (Fig. 9aj), and it is also closely related to *T. tenuis* (Fig. 9ak). Questionable species are *C. uncinus* (Fig. 9an) or *C. californiense* (Fig. 9ao–ap) that can be considered aberrant forms of species of the section *Macroceros*.

Fig. 9. Line drawings and micrographs of the species of the section *Macroceros*. (a–c, e–k) *Tripus gallicus*. (a) *Ceratium tripos* var. *macroceros* by Claparède and Lachmann (1859). (b) *C. tripos* var. *macroceros* by Gourret (1883). (c) *C. macroceros* by Paulsen (1908). (d) *C.*

tripos var. *macroceros* f. *armatum* by Karsten (1905). (e) *C. gallicum* by Kofoed (1907b). (f) *C. macroceros deflexum* by Kofoed (1907b). (h) Aberrant form. (l–o) *T. massiliensis*. (l) *C. tripos* var. *massiliense* by Gourret (1883). (p–w) *T. macroceros*. (p) *Peridinium macroceros* by Ehrenberg. (q) *C. tripos* var. *contrarium* by Gourret (1883). (r) *C. batavum* by Paulsen (1908). (s) *C. intermedium* by Paulsen (1908). (t) *C. tripos* var. *macroceroides* by Karsten (1906). (x–ae) *T. carriensis*. (x) *C. tripos* var. *inflexum* by Gourret (1883). (y) *C. tripos* var. *typicus* by Gourret (1883). (z) *C. carriense* by Gourret (1883). (aa) *C. flagelliferum* by Cleve (1900). (ac–ad) Cell infected by an endoparasite. (ae) *C. ramakrishnae* redrawn from Subrahmanyam (1968). (af–ah) *T. trichoceros*. *Peridinium trichoceros* by Ehrenberg (1873). (ai) *C. carriense* by Jørgensen (1920). (aj) *C. volans* by Cleve (1900). (ak) *C. tenue* by Ostenfeld and Schmidt (1901). (al–am). *T. volans*. (an) *C. uncinum* redrawn from Sournia (1972). (ao) *C. californiense* by Kofoed (1907b). (ap) Individual which have undergone autotomy. Scale bars: 50 µm.

Jørgensen (1920) proposed *Ceratium pavillardii* for the illustration identified as *C. vultur* by Pavillard (1905) (Fig. 10a–e). This is fortunate because Pavillard (Fig. 10b) showed a cell with scarce postindentation when compared to *C. vultur* (Fig. 10f–g). *Tripes pavillardii* is more closely related to *T. volans* (Fig. 9aj). The main issue is the synonymy among the tropical taxa *T. vultur*, *T. robustus* (Fig. 10h–i), *T. japonicus* (Fig. 10j–k) and *T. sumatranus* (Fig. 10l–m). *Tripes sumatranus* and *T. recurvus* are interpreted as colonial or atypical forms of *T. vultur*, respectively. *Tripes vultur* and *T. robustus* are not considered synonyms because the postindentation is more marked in the latter taxon. *Tripes robustus* described by Ostenfeld and Schmidt (1901) (Fig. 10h) [non *C. robustum* (Cleve) Cleve)] is interpreted as individuals

of *T. japonicus* which have undergone autotomy. *Tripes reflexus* may correspond to an aberrant form (Fig. 10n–o). The section Reflexa is then merged in the section Vultur.

Fig. 10. Line drawings and micrographs of the section Macroceros of the subgenus *Tripes*. (a–e) *Tripes pavillardii*. (b) *Ceratium vultur* by Pavillard (1905). (f–g, l–m) *T. vultur*. (f) *C. vultur* by Cleve (1900). (h–k) *T. robustus*. (h) *C. robustum* by Ostenfeld and Schmidt (1901). (j) *C. japonicum* by Schröder (1906). (n–o) *T. reflexus*. (n) *C. reflexum* by Cleve (1900). Scale bars: 50 μ m.

3.5.2 Subsection Tergestina

Triplos arcticus (Fig. 11a–d) and *T. longipes* (Fig. 11e–j) are psychrophilic species co-occurring in arctic-boreal regions. *Triplos arcticus* was also described as *Ceratium labradoricum* (Fig. 11b–c). *Peridinium arcticum* was transferred into *Ceratium* as *C. arcticum* (Ehrenberg) Vanhöffen 1897, and not as *C. arcticum* Vanhöffen 1897 as commonly interpreted in the literature, and *C. arcticum* (Ehrenberg) Cleve 1900 is a later isonym. Vanhöffen's illustration identified as *C. arcticum* (Fig. 11e) corresponded to *C. longipes*. *Ceratium longipes* was first illustrated as *Peridinium triplos* by Ehrenberg (1834, pl. 2, figure 1f), later described as *P. longipes* by Bailey (1855) (Fig. 11f) and illustrated as *C. triplos* var. *tergestinum* by Schütt (1892). The DNA sequences obtained from the strain CCMP1770 have been identified as *T. longipes*. There is an image available at <https://ncma.bigelow.org/ccmp1770>, but it shows an aberrant cell that makes difficult to verify the identification.

3.5.3 Section Palmata

Cleve (1897) described *C. triplos* var. *horridum* with antapical horns that diverged from the apical horn (Fig. 11h). Based on the original description, *C. triplos* var. *horridum* can be considered conspecific with *C. longipes* (Fig. 11f–g). Other interpretation is that Cleve (1897) illustrated an immature individual, and the antapical horns will be parallel to the apical horn in the mature individuals. Based on the original description, the name *C. horridum* which basionym is *C. triplos* var. *horridum* is also a synonym of *C. longipes* (I.C.N. art. 7.3). Gran

(1902) and other authors reported individuals with antapical horns parallel to the apical horn for *C. horridum* (Fig. 11p–q), differing from Cleve’s basionym. *Ceratium intermedium* is a name for *C. horridum sensu auct.* (Fig. 11k–l). The original illustration of *C. buceros* is unfortunate because the shape of the hypotheca is unrealistic, probably reported from an aberrant individual (Fig. 11m–o). Jørgensen (1920) reported as *C. buceros* (Fig. 11n) a cell with the morphology of *C. tenue* (Fig. 9ak), and he classified *C. inclinatum*, *C. tenuissimum*, *C. molle* and *C. denticulatum* as varieties of *C. buceros*. This is unfortunate due the uncertainties on the identity of *C. buceros*. *Triplos intermedium* is common in temperate waters. *Ceratium clavigerum*, not ‘claviger’ is recorded in warmer waters. It exhibited long antapical horns, often inflexed (Fig. 11r–s), or with a dilated distal end of the antapical horns (Fig. 11t).

Fig. 11. Line drawings and micrographs of the species of the section Tergestina (a–j) and section Palmata (k–t). (a–d) *Triplos arcticus*. (a) *Peridinium arcticum* by Ehrenberg (1854b). (b) *C. triplos* var. *labradoricum* by Schütt (1892). (c) *C. labradoricum* by Vanhöffen (1897). (e) *C. arcticum* by Vanhöffen (1897). (f) *Peridinium longipes* by Bailey (1854). (g) *C. triplos* var. *longipes* by Cleve (1897). (h) *C. triplos* var. *horridum* by Cleve (1897). (i–j) *T. longipes*. (k) *C. horridum* (Cleve) f. *intermedium* by Jørgensen (1899). (l) *C. intermedium* f. *frigida* by Paulsen (1908). (m) *C. buceros* by Zacharias (1906). (n) *C. buceros* by Jørgensen (1920). (o) Aberrant cell. (p–q) *T. intermedium*. (r–t) *Triplos clavigerus*.

Triplos platycornis is characterized by the flattening of the distal part of the antapical horns which tips are never pointed (Fig. 12a–n). The main controversy in the identification is when the flattening is missing. The cell body of *T. compressus* is similar to *T. platycornis*, but the pointed tips of the antapical horns of Gran's (1902) original illustration (Fig. 12a) are unreported for *T. platycornis* (Fig. 12b–n). Authors such as Paulsen (1908) or Balech (1988) have considered *T. compressus* as an independent species, but their illustrations showed blunt tips of the antapical horns as in *T. platycornis*. These pointed tips of the horns in Gran's illustration is the main obstacle to consider these species as synonyms. A closely related species is *T. ranipes* (Fig. 12o–x). *Triplos platycornis* and *T. ranipes* are the type species of the sections Platycornia and Palmata, respectively. These sections are here merged with *T. intermedium* (= *C. horridum sensu auct.*) and *T. clavigerus* in a single section, and Palmata is the earlier available name.

3.5.4 Section Reticulata

The SSU rRNA gene sequence of *Triplos hexacanthus* clustered as an independent lineage that could be a link between the section *Macroceros* and other sections of the subgenus *Triplos* (Fig. 2). It is difficult to find relatives for *T. hexacanthus*. This is a peculiar species by characterized with strong surface reticulation of the theca and twisted antapical horns (Fig. 12y–ab).

Fig. 12. Line drawings and micrographs of the specie of the section *Palmata*, including *Platycornia*. (a) *Ceratium compressum* by Gran (1902). (b–m). *Triplos platycornis*. (g) *C. platycorne* by Daday (1888). (o–x) *Triplos ranipes*. (o) *Ceratium* sp. by Schütt (1882). (p) *C. ranipes* by Cleve (1900). (y–ab) *Triplos hexacanthus*. Scale bars: 50 μ m.

3.5.5 Section *Tripes* (=Rotunda)

The type species of *Tripes*, *T. muelleri*, and allied taxa show the typical anchor-like shape lacking the postindentation in the posterior contour (Fig. 13a–e). The species are distinguished based on the relative length and orientation of the antapical horns. When the antapical horns are short, it is not easy to decide whether the morphology is due to autotomy, an immature cell, seasonal variant or a true distinct species. Examples are *T. brevis*, *T. pulchellus*, *T. schmidtii* among others (Fig. 13f–i). This variability is a nightmare for the species circumscription, but it is interesting from the ecological point of view as it could be interpreted as responses to the environmental conditions. An example is *T. egyptiacus* that was described from the Canal of Suez (Fig. 13j). This is not an endemism because the Canal was inaugurated in 1869 and there is no time for the evolution of a new species. Then, the extreme and fluctuant environmental conditions (temperature, salinity) in the Canal of Suez induce an anomalous configuration of the antapical horns. The variable morphology of *C. egyptiacum* could correspond to stressed individuals of *T. muelleri* or even *T. dens*, the latter first described from the Red Sea (Fig. 13k). Even more problematic is when the antapical horns are very short or almost absent as observed in *T. dens* (Fig. 13k) and *T. divaricatus* (Fig. 13m). Böhm (1931) already reported the morphological variability of *T. dens*, including the example of a heteromorphic chain (Fig. 13l). One of the daughter cells corresponded to the morphology recently described as *T. balechii* (Fig. 13o). Lemmermann (1899, p. 345) proposed *C. tripes* var. *divaricatum* citing a basionym an illustration by Bergh (1881). That individual from the

Baltic Sea showed the anterior-most daughter cell of *T. muelleri* with an incomplete hypotheca (Fig. 13m). Based on observations near the USA-Mexico border, Kofoed (1908c) ranked *C. tripos* var. *divaricatum* at the species level and he figured a high intraspecific morphological variability (Fig. 13n). The immature cell of *T. muelleri* from the cold Baltic Sea (Fig. 13m) is not conspecific with Kofoed's taxon from the subtropical Pacific (Fig. 13n). The species name *C. divaricatum* is a synonym of *T. muelleri* (I.C.N. article 7.3) and Kofoed's taxon needs other name that could be *T. dens* or *T. balechii*, the latter described from the Mexican Pacific in 2003 (Fig. 13o, Meave del Castillo *et al.*, 2003). The molecular data should solve whether *T. dens* and *T. balechii* are or are not conspecific. There are several DNA sequences identified as *T. balechii* from the Mexican Pacific (Figs 1, 2), and a single DNA sequence identified as *T. dens* from Mexico (accession number MF927978). Anomalously, this sequence is full of indeterminate nucleotides that make impossible the comparison. With the current knowledge, *T. dens* is the correct name for this highly polymorphic taxon from warm oceans (Fig. 13j–p).

Fig. 13. Line drawings and micrographs of species of the section *Tripos*. (a–e) *T. muelleri*. (a) Note the different coloration. (f) *C. pulchellum* by Schröder (1906). (g) *C. schmidtii* redrawn from Jørgensen (1911). (h–i) *T. pulchellus*. (j) *C. egypticum* redrawn from Halim (1963). (k) *C. dens* by Ostenfeld and Schmidt (1901). (l) Heteromorphic chain of *C. dens* redrawn Böhm (1931). (m) A variety of *C. tripus* by Bergh (1881). (n) *C. divaricatum* by Kofoed (1908c). (o) *C. balechii* redrawn from Meave del Castillo *et al.* (2003). (p) Tentatively *T. dens*. (q) *C. tripus* var. *gracile* by Gourret (1883). (r) *C. tripus* var. *gracile* by Schröder (1906). (s) *C. tripus* var. *gracile* by Ostenfeld and Schmidt (1901). (t) *C. tripus* by Pavillard (1905) = *C. gracile* in Pavillard (1907a). (u) *C. gracile* by Jørgensen (1920). (v–w, aa, ac) *T. gracilis*. (x) *C.*

declinatum f. *majus* by Jørgensen (1920). (y) *C. declinatum* by Karsten (1907). (z) *C. declinatum* var. *debile* by Jørgensen (1920). (ab) *C. declinatum* f. *brachiatum* by Jørgensen (1920).

Some of the earlier illustrations of new species were too sketchy or were unprecise to represent the real morphology of the species. The illustration of *Ceratium tripos* var. *gracile* by Gourret (1883) was unfortunate. Gourret showed a cell with a bent apical horn that is atypical for the members of this section, and the midbody was anomalously elongated along the anterior-posterior axis. An important feature is that the apical horn arose close to the left side of the body and the left side of the epitheca is less convex (Fig. 13q). Gourret (1883) described *C. tripos* var. *gracile*, and he cited *C. tripos* var. *gracile* Pouchet as synonym. Then, *C. tripos* var. *gracile* Gourret is an invalid name because it is a later isonym. The description of *C. tripos* var. *gracile* by Pouchet (1883) did not include illustration, and he only reported that the cell showed long and thin double-curved horns. This suggests that it is unrelated to Gourret's taxon. Pavillard (1905) proposed the new species name *C. gracile* without apparently illustration. He reported that the species corresponded to *C. tripos* var. *gracilis* by Schröder (1900, his figures 17b,d,e) (Fig. 13r), and Ostenfeld and Schmidt (1901) (Fig. 13s). The illustration by Ostenfeld and Schmidt (1901) is close to *C. tripos*. Later, Pavillard (1907a) reported that the figures 5 and 7 in Pavillard (1905) (Fig. 13t) and Gourret's *C. tripos* var. *gracile* (Fig. 13q) corresponded to *C. gracile*. These illustrations showed the apical horn arising close to the left side of the midbody. Karsten (1907) described *C. tripos declinatum* with individuals showing a distinctive loop in the longer left antapical horn (Fig. 13y). Karsten (1907) illustrated the apical horn arising from the middle of the epitheca (Fig. 13y), but it arose closer to the left side in that species (Fig. 13aa). A long left antapical horn with a distal

loop is typically observed in oceanic individuals (Fig. 13aa). *Ceratium gracile* Pavillard 1905 and ‘*C. tripos declinatum* Karsten n. sp. 1907’ are synonyms. In this study, *C. gracile* Pavillard 1905 (Fig. 13t, u–w, aa, ac) is revived because it has the priority over *C. declinatum* (Fig. 13y). Jørgensen (1911, 1920) proposed *C. gracile* (Gourret) Jørgensen interpreting that *C. tripos* var. *gracile* was Pavillard’s *C. coarctatum* and *C. symmetricum* (Fig. 14a–d). Jørgensen (1920) proposed the new varieties *C. gracile* var. *coarctatum* and *C. gracile* var. *symmetricum* for the two species described by Pavillard (1905). Jørgensen’s illustration (Fig. 13u) under the name *C. gracile* corresponded to *C. coarctatum* (Fig. 14a–b). *Ceratium gracile* (Gourret) Jørgensen is a later isonym of *C. gracile* Pavillard. *Ceratium gracile* showed an asymmetric epitheca with the apical horn arising close to the left side, while the epithecae of *C. symmetricum* and *C. coarctatum* are symmetric with the apical horn arising from the middle (Fig. 14a–d). Jørgensen (1920) proposed the infraspecific taxa *C. declinatum* f. *majus* (Fig. 13x), *C. declinatum* f. *brachiatum* (Fig. 13ab), and *C. declinatum* var. *debile* (Fig. 13z). *Ceratium declinatum* f. *majus* and *C. declinatum* var. *debile* were unnecessary varieties because they fit well with the original descriptions of *C. gracile* (Fig. 13t) and *C. tripos* var. *declinatum* (Fig. 13y), respectively. *Ceratium declinatus* f. *brachiatum* strongly resemble to Jørgensen’s *C. euarctatum* (Fig. 14i).

Fig. 14. Line drawings and micrographs of species of the section *Limulus* of the subgenus *Tripus*. (a) *Ceratium coarctatus* by Pavillard (1905). (b) *Tripus coarctatus*. (c) *C. symmetricum* by Pavillard (1905). (d) *T. symmetricus*. (e) *C. filicorne* by Steemann Nielsen (1934). (f) *C. tripos* var. *arcuatum* by Gourret (1883). (g) *C. arcuatum* by Cleve (1900). (h) *C. arcuatum* by Pavillard (1905). (i) *C. euarcuatum* by Jørgensen (1920). (j–l) *T. arctuatus*. M. *C. karstenii* by Pavillard (1907a). (n) *C. schrankii* by Kofoed (1907b). (o) *T. karstenii*. (p) *C. tripos* var. *hiemale* by Paulsen (1908). (q) *C. aultii* redrawn from Graham and Bronikovsky (1944). (r) *T. aultii*. (s–t). *T. longissimus*.

3.5.6 Section *Limulus*

The resolution of the SSU rRNA gene phylogeny is insufficient to resolve the divergence among the species of the subgenus *Tripus* (Fig. 2), and the LSU rRNA gene phylogeny only

contains sequences of three species of the section *Tripes* (*T. muelleri*, *T. brevis* and *T. balechii*) that clusters together with moderate support (Fig. 1). The strain CCMP1770 identified as *T. longipes* is the only strain with sequences in both SSU- and LSU rRNA gene phylogenies. Independently of the correct species identification, the LSU rRNA gene sequence of the strain CCMP1770 is distantly related to the clade of the section *Tripes*. In the SSU rRNA gene phylogeny, the sequence of the strain CCMP1770 clusters with three species with similar morphology retrieved as *T. symmetricus*, *T. arietinus* and *T. euarcuatus*, and more distantly related to representatives of the section *Tripes* (Fig. 2). This suggests that these three species should not be classified in the section *Tripes*, and the classification in the section *Limulus* appears as the first choice.

Tripes symmetricus (Fig. 14a–b) and *T. coarctatus* (Fig. 14c–d) are classified in the section *Limulus*, and more distantly related to *T. gracilis* (= *C. declinatum* auct. mult.). *Tripes filicornis* (Fig. 14e) exhibited intermediate characteristics between *T. symmetricus* and *T. arcuatus*. As occurred with *C. gracile*, the name *C. arcuatum* (Gourret) Cleve has disappeared in the literature. Gourret (1883) described *C. tripes* var. *arcuatum* (Fig. 12f), and Cleve (1900) under the name *C. arcuatum* illustrated a cell (Fig. 14g) that differed from Gourret's taxon. Cleve (1900, p. 13) cited Gourret's taxon as basionym, and even if Cleve's illustration corresponds to a distinct species, *C. arcuatum* is the Gourret's taxon at the species rank (I.C.N. article 7.3). Pavillard (1905) illustrated *C. arcuatum* (Fig. 14h) as similar to Gourret's taxon (Fig. 14f). Jørgensen (1920) noted Cleve and Gourret illustrated distinct species. However, instead to propose a new species name for Cleve's species, Jørgensen (1920) proposed *C. euarcuatum* for "this characteristic species as already detected by Gourret 1883 (pl. 2, fig. 42, *C. tripes* var. *arcuatum*)". Jørgensen was citing the same basionym for *C. arcuatum* and *C. euarcuatum*, then these species names are synonyms (I.C.N. article 7.3). What is the name for

C. arcuatum sensu Cleve? Pavillard (1905, p. 51) noted that *C. arcuatum* sensu Cleve was distinct from the Gourret's taxon. Later Pavillard (1907a) proposed the species name *C. karstenii* (Fig. 14m) citing that it corresponded *C. arcuatum* sensu Cleve. That year, Kofoed (1907b) proposed *C. schrankii* (Fig. 14n) that is conspecific, although he did not cite Cleve's *C. arcuatum*. Pavillard published *C. karstenii* three weeks before than Kofoed's taxon. Then, the names for Gourret's and Cleve's taxa are *T. arcuatus* ($\equiv T. euarcuatus$) (Fig. 14j–l) and *T. karstenii* (Fig. 14o) ($=T. schrankii$), respectively. A taxon related to *T. karstenii* is *T. muelleri* var. *hiemale* (Fig. 14p). It has not been ranked at the species level, and it is doubtful its assignation as variety of *T. muelleri*. It is here considered conspecific with *T. aultii* (Fig. 14q–r). Other closely related taxon is *T. longissimum* which long antapical horns are directed parallel to the apical one (Fig. 14s–t).

Cleve (1900) described *Ceratium arietinum* (Fig. 15a) that is closely related to species such as *Tripus symmetricus* and *T. arcuatus*. *Ceratium tripus* f. *heterocamptum* (Fig. 15b) and *C. bucephalum* (Fig. 15c) are synonyms of *T. arietinus*, although the distinctive bent of the right apical horn is less evident (Fig. 15e–g). Graham and Bronikovsky (1944) described *C. carnegiei* with an inflated midbody (Fig. 15d). It cannot be discarded that it corresponds to individuals of *T. arietinus* infected by an endoparasite. Gómez *et al.* (2008) reported micrographs of an individual identified as *C. carnegiei*, but it corresponded to *C. ramakrishnae* (Fig. 9ae) that is a cell of *C. carriense* (non *C. carriense* auct. mult.) infected by an endoparasite (Fig. 9ac–ad). *Tripus lunula* is a thermophilic colony-forming species, with a semicircular contour of the antapical horns (Fig. 15h–j). Taxa of easy identification are *T. paradoxides* (Fig. 15k–p) and *T. limulus* (Fig. 15q–w). In contrast, it is difficult to solve whether *T. azoricus* (Fig. 15x–z) and *T. petersii* (Fig. 15aa–ae) are or are not conspecific. The section *Limulus* is here enlarged to include *T. arcuatus*, *T. arietinus*, *T. aultii*, *T. azoricus*, *T.*

carnegiei, *T. coarctatus*, *T. limulus*, *T. longissimus*, *T. lunula*, *T. karstenii*, *T. paradoxides*, *T. petersii*, *T. subcontortus* (non *T. contortus*) and *T. symmetricus*.

Fig. 15. Line drawings and micrographs of members of the section *Limulus*. (a) *Ceratium arietinum* by Cleve (1900). (b) *C. tripos* f. *heterocamptum* by Jørgensen (1899). (c) *C. tripos* var. *bucephalum* by Cleve (1897). (d) *C. carnegiei* redrawn by Graham and Bronikovsky (1944). (e–g) *Tripos arietinus*. (h–j) *T. lunula*. (k–p) *T. paradoxides*. (k) *C. paradoxides* by Cleve (1900). (q–w) *T. limulus*. (q) *C. tripos* var. *limulus* by Pouchet (1883). (x–ab) *T.*

azoricus. (x) *C. azoricus* by Cleve (1900). (aa) *C. petersii* by Steemann Nielsen (1934). Scale bars: 50 μm .

3.5.7 Subsection *Gibbera*

As occurred with *T. hexacanthus* classified in its own section, *T. gibberum* (not ‘gibberus’) is other species with atypical configuration of the antapical horns that makes difficult to find affinities with other taxa. The midbody is wide and the right antapical horn is bent and crossing the apical horn (Fig. 16a–d, i–m). *Tripus gibberum* is classified as the only member of its subsection. The available molecular data, retrieved as *T. concilians*, do not show any supported relationship with other species (Fig. 2). *Tripus gibberum* is morphologically close to the members of section *Tripus* because the posterior body margin is rounded, but the antapical horns are deflected with distinct lengths. Gourret (1883) described *C. gibberum* (Fig. 16a), *C. gibberum* var. *sinistrum* (Fig. 16c), and *C. gibberum* var. *contortum* (Fig. 16b). *Ceratium curvicone* (Fig. 16e) resembled the anterior-most daughter cell of *C. gibberum* (Fig. 16i–j). Cleve (1900) proposed *C. contortum* for *C. gibberum* var. *contortum* that was illustrated in Gourret’s figure 33. Jørgensen (1920, p. 72) proposed *C. concilians* (Fig. 16f) for “*C. tripus* var. *contortum*, Gourret 1883, plate 2, fig. 33”, but Gourret’s figure 33 is labelled as *C. gibberum* var. *contortum* (Fig. 16b). Independently of whether *C. contortum* sensu Cleve and *C. concilians* are or are not taxonomical (heterotypic) synonyms, these two species are homotypic (nomenclatural) synonyms that share the same basionym. Steidinger and Tangen (1997, p. 474) reported for *T. gibberum*: “can be confused with *C. concilians* which has proximally bent apical horn and rounded right epithecal shoulder. *C. concilians* is less reticulate”. Observations of the cell division of *T. gibberum* suggest that

reticulation or the bent of the apical horn have little diagnostic value because it depends on the degree of maturation of the cell (Fig. 16i–m). The illustration of *C. gibberum* var. *contortum* by Gourret (1883) suggests that it is a morphotype of *T. gibberus*, and consequently *T. contortus* is a synonym (I.C.N. art. 7.3). *Ceratium contortum* sensu Cleve (Fig. 16g), already illustrated by Schütt (1892) (Fig. 16h), and *C. gibberum* var. *contortum* differed in several aspects. The difference in the apical horn is irrelevant because Gourret illustrated unrealistic tilted apical horns as he did for *C. tripos* var. *gracile* (Fig. 13q). The apical horn of *C. gibberum* var. *contortum* arise from the middle of the epitheca (Fig. 16b), while in *C. contortum* sensu Cleve arise from the left side (Fig. 16g). Cleve's illustration showed a cell with a straight proximal part of the right antapical horn (Fig. 16g), while it is bent since the proximal part in Gourret's taxon (Fig. 16b). All the varieties of *C. gibberum* are neritic forms and common in the coast of Marseille, but the species misidentified as *C. contortum* has preferentially an oceanic and tropical distribution. I have observed it in the open Pacific (Fig. 16r–s), but not in the coasts of Marseilles. *Ceratium contortum* sensu Cleve needs other species name. Certainly, *C. contortum* sensu Cleve is close to *C. karstenii*, but the proposal of *C. contortum* var. *karstenii* (Pavillard) Sournia is unfortunate because *C. contortum* sensu Gourret is not closely related to *C. karstenii*. The available names for Cleve's *C. contortum* are *C. subcontortus* (Fig. 16n) and *C. saltans* (Fig. 16o) by Schröder (1906), or *C. longinum* (Fig. 16p) by Karsten (1906). Beyond the discussion on the priority of the publication, the illustration of *C. longinum* (Fig. 16p) does not fit well *C. contortum* sensu Cleve (Fig. 16g). The records reported in the warm waters as *T. contortus* are usually Cleve's taxon and they should be referred as *T. subcontortus* (Fig. 16r–s). Steidinger and Tangen (1997, p. 472) reported *C. arcuatum* (Gourret) Cleve as a posterior synonym of *C. contortum* (Gourret) Cleve. The comparison of the basionym's original illustrations evidences that they are

independent species (Figs 14f, 16b). *Triplos gibberum* (Fig. 16i–m), *T. contortus*, *T. curvicornis* and *T. concilians* are different names for a single species and classified in own subsection with affinities to the sections *Triplos* and *Limulus*. *Triplos subcontortus* is classified in the section *Limulus*. The figure 17 reports a tentative evolutionary scheme of the family Ceratiaceae.

Fig. 16. Line drawings and micrographs of species of the subsection *Gibbera*, and *T. subcontortus* of the section *Limulus*. (a) *Ceratium gibberum* var. *sinistrum* by Gourret (1883). (b) *C. gibberum* var. *contortum* by Gourret (1883). (c) *C. gibberum*. (d, i–m) *Triplos gibberum*. (e) *C. curvicorne* by Daday (1888). (f) *C. concilians* by Jørgensen (1920). (g) *C. contortum* by Cleve (1900). (h) *Ceratium* sp. by Schütt (1892). (n–o) *C. subcontortum* and *C. saltans* by Schröder (1906). (p) *C. triplos* var. *longinum* by Karsten (1906). (r–s) *T. subcontortus*. Scale bars: 50 μ m.

Fig. 17. Tentative evolutionary scheme of the family Ceratiaceae.

3.6. List of correct species

About 165 species names of marine species of *Ceratium* have been proposed. Numerous species (i.e., *Tripos muelleri*) have tens of described varieties and forms and the genus accounted for a total of about 800 infraspecific taxa. The diagnostic criteria for the species identification such as the relative length and orientation of the antapical horns varies according

the cell maturation, autotomy and environmental conditions. There are studies on the sexual life cycle of the freshwater *Ceratium*, but very few on *Tripes* (Apstein, 1911). The nature of the gametes will be useful to solve the controversy in the identity of species with short antapical horns such as *T. lineatus* and *T. minutus*, and the infraspecific taxa of *T. muelleri* (Lohmann 1908). The cultures will help investigate the intraspecific variability, but aberrant forms are often observed in culture conditions, and they should not be confused with ‘natural’ life stages.

We are far to solve the speciation of *Tripes* based on molecular data with sequences of only 30 and 9 species in the SSU- and LSU rDNA phylogenies, respectively. The species circumscription can be resolved with the sequences of the complete rDNA gene, including more variable regions (i.e., ITS). Currently, there are ITS sequences of only 3 species. For example, there is no a complete of the SSU rDNA sequence of *T. muelleri*, one of the first described dinoflagellates and abundant next door of the specialized laboratories in molecular phylogeny. The melting of Arctic sea ice has increased the research interest in the region. However, a documented DNA sequence of *T. arcticus* is not available. We cannot expect significant advances in a near future, especially for the tropical and deep water species, that are essential to understand the evolution of *Tripes*.

Tripes is the dinoflagellate genus with more infraspecific taxa, with species with several varieties, and these varieties with several forms. Each author will decide to use a given variety or form, and Gómez (2013) transferred all the species and infraspecific taxa of the marine *Ceratium* into *Tripes*. However, the publication of these alternative names in single publication invalidate all the new combinations (I.C.N., art. 36.3). Some of new combinations of *Tripes* at the species rank are here proposed again. A species list with the correct species names and their synonyms is below proposed.

Genus *Tripus* Bory 1823 (*Bursaria* O.F. Müller 1773 in part, *Ceratium* Schrank 1793 in part, *Cercaria* Michaelis 1830 in part, *Ceratophorus* Diesing 1850 in part, *Peridinium* Ehrenberg 1833 in part, *Dimastigoaulax* Diesing 1866 in part, *Amphiceratium* Vanhöffen 1896, *Biceratium* Vanhöffen 1896, *Poroceratium* Vanhöffen 1896, *Euceratium* (Gran 1902) Ostelfeld 1903, *Neoceratium* F.Gómez, D.Moreira et P.López-García, *nom. illegit.*

Subgenus *Biceratium* (Vanhöffen 1896) Jørgensen 1911, genus *Biceratium* Vanhöffen, subgenus *Orthoceratium* Meunier 1919 (non Schrank 1803, nec Sournia 1968).

Section of *Tripus eugrammus*

Tripus eugrammus (Ehrenberg 1860) F.Gómez, *comb. nov.* Basionym: *Peridinium eugrammum* Ehrenberg 1860, *Monatsber. K. Akad. Wiss. Berlin* 1859: 792. Synonyms: *Ceratium eugrammum* (Ehrenberg) W.S.Kent 1881, *C. biceps* Claparède et J.Lachmann 1859 (non *C. biceps* sensu Kofoid 1908c), non *Tripus furca* auct. mult.

Sectio *Furca* Pavillard 1907b, sectio *Furciformia* Jørgensen 1911, sectio *Biceratium* (Vanhöffen 1896) Gran 1902, including sectio *Pentagona* Jørgensen 1920.

Subsectio *Eufurca* Jørgensen 1911

Tripus furca (Ehrenberg 1833) F.Gómez 2013. Synonyms: *Peridinium furca* Ehrenberg, *C. furca* (Ehrenberg) Claparède et J.Lachmann 1859, *Biceratium furca* (Ehrenberg) Vanhöffen 1897, *B. debile* Vanhöffen 1897, non *Tripus eugrammus* auct. mult.

Tripus hircus (Schröder 1909) F.Gómez, *comb. nov.* Basionym: *Ceratium hircus*
Schröder 1909, *Ber. Deutsch. Bot. Ges.* 27: 213, fig. 2.

Tripus lineatus (Ehrenberg 1854) F.Gómez 2013, *comb. nov.* Basionym:
Peridinium lineatum Ehrenberg 1854. *Ber. K. Akad. Wiss. Berlin* 1854: 240
(≡*C. lineatum* (Ehrenberg) Cleve 1899, *Biceratium lineatum* (Ehrenberg)
S.T.Moses 1929).

Subsectio Pentagona Jørgensen 1911

Tripus minutus (Jørgensen 1920) F.Gómez 2013 (≡*C. minutum* Jørgensen 1920).

Tripus pentagonus (Gourret 1883) F.Gómez, *comb. nov.* Basionym: *Ceratium*
pentagonum Gourret 1883. *Ann. Mus. Hist. Nat. Marseille* 1(8): 45, pl. 4,
fig. 5. Synonym: *C. subrobustum* (Jørgensen 1920) Steemann Nielsen 1934,
C. lineatum auct. mult.

Tripus setaceus (Jørgensen 1911) F.Gómez 2013. Synonyms: *C. setaceum*
Jørgensen 1911, *C. kofoidii* Jørgensen 1911, *C. boehmii* H.W.Graham et
Bronikovsky 1944.

Tripus teres (Kofoid 1907b) F.Gómez 2013 (≡*C. teres* Kofoid)

Sectio Candelabra Jørgensen 1911

Tripus candelabrum (Ehrenberg 1859a) F.Gómez 2013. Synonyms: *P.*
candelabrum Ehrenberg 1859a, *C. candelabrum* (Ehrenberg) F.Stein 1883,
C. depressum Gourret 1883, *C. obliquum* Gourret 1883, *C. globatum*
Gourret 1883, *C. allieri* Gourret 1883, *C. dilatatum* Gourret 1883 [non *C.*
dilatatum (G.Karsten 1905) Kofoid 1907a].

Subgenus *Archaeoceratium* Jørgensen 1920, subgenus *Poroceratium* (Vanhöffen) Jørgensen 1911, genus *Poroceratium* Vanhöffen 1896.

Sectio *Poroceratium* (Vanhöffen 1896) Jørgensen 1911, subsectio *Annulifera* Jørgensen 1920.

Tripes gravidus (Gourret 1883) F.Gómez 2013. Synonyms: *C. gravidum* Gourret, *C. oviforme* Daday 1888, *C. praelongum* (Lemmermann 1900) Kofoed 1907 *ex* Jørgensen 1911, *Poroceratium gravidum* (Gourret) Vanhöffen 1896.

Tripes cephalotus (Lemmermann 1899) F.Gómez, *comb. nov.* Basionym: *Ceratium gravidum* var. *cephalotum* Lemmermann 1899. *Abh. Naturw. Ver. Bremen* 16: 349, pl. 1, fig. 16. Synonym: *C. cephalotum* (Lemmermann) Jørgensen 1911.

Sectio *Lanceolata* Jørgensen 1911

Tripes lanceolatus (Kofoed 1907a) F.Gómez 2013 ($\equiv$ *C. lanceolatum* Kofoed).

Sectio *Digitata* Jørgensen 1911, subsectio *Beloniformia* Jørgensen 1911, subsectio *Incisa* Jørgensen 1911.

Tripes belone (Cleve 1900) F.Gómez, *comb. nov.* Basionym: *Ceratium belone* Cleve 1900, *K. Svenska Vet.-Akad. Handl.*, [ser. 4] 34(1): 13, pl. 7, fig. 13. Synonym: *C. incisum* (G.Karsten 1906) Jørgensen 1911, non *C. pacificum* Schröder 1906.

Triplos brunellii (Rampi 1942) F.Gómez 2013 ($\equiv$ *C. brunellii* Rampi).

Triplos digitatus (F.Schütt 1895) F.Gómez 2013 ($\equiv$ *C. digitatum* F.Schütt).

Triplos rotundatus (Jørgensen 1920) F.Gómez, *comb. nov.* Basionym:

Ceratium digitatum var. *rotundatum* Jørgensen 1920. *Rep. Dan.*

Oceanogr. Exped. 1908–10 2(J.1): 7, fig. 2. Synonym: *Ceratium*

tasmaniae E.J.F.Wood 1963, *nom. inval.*

Triplos schroeteri (Schröder 1906) F.Gómez 2013 ($\equiv$ *C. schroeteri* Schröder).

Section Inflata Jørgensen 1911, subsectio Geniculata Jørgensen 1911, subsectio Jørgensen Bigelowia 1911.

Triplos bigelowii (Kofoed 1907a) F.Gómez 2013 ($\equiv$ *C. bigelowii* Kofoed).

Triplos inflatus (Kofoed 1907a) F.Gómez 2013. Synonyms: *C. inflatum* (Kofoed) Jørgensen 1911, *C. nipponicum* Okamura 1912.

Triplos falcatifomis (Jørgensen 1920) F.Gómez, *comb. nov.* Basionym:

Ceratium falcatiforme Jørgensen 1920. *Rep. Dan. Oceanogr. Exped. 1908–10* 2(J.1): 40, fig. 29.

Triplos falcatus (Kofoed 1907) F.Gómez, *comb. nov.* Basionym: *Ceratium*

pennatum f. *falcatum* Kofoed 1907a. *Bull. Mus. Comp. Zool. Harvard Coll.* 50: 172, pl. 2, fig. 14. Synonym: *C. falcatum* (Kofoed) Jørgensen 1920.

Triplos geniculatus (Lemmermann 1899) F.Gómez, *comb. nov.* Basionym:

Ceratium fusus var. *geniculatum* Lemmermann 1899. *Abh. Naturw.*

Ver. Bremen 16: 349, pl. 1, fig. 17. Synonyms: *C. geniculatum* (Lemmermann) Cleve 1900, *C. tricarinatum* Kofoed 1907a, *C. pacificum* E.J.F.Wood 1963, *nom. illegit.*

Tripes pennatus (Kofoed 1907a) F.Gómez, *comb. nov.* Basionym: *Ceratium pennatum* f. *propium* Kofoed 1907b. *Bull. Mus. Comp. Zool. Harvard Coll.* 50: 172, pl. 2, fig. 12, non figs 13–14. *C. longirostrum auct. mult.*

Tripes scapiformis (Kofoed 1907a) F.Gómez, *comb. nov.* Basionym: *Ceratium scapiforme* Kofoed 1907a. *Bull. Mus. Comp. Zool. Harvard Coll.* 50: 173, pl. 3, fig. 23.

Sectio of *Tripes pacificus*, subsectio Beloniformia Jørgensen 1911 in part.

Tripes pacificus (Schröder 1906) F.Gómez, *comb. nov.* Basionym: *Ceratium pacificum* Schröder 1906. *Vierteljahrsschr. Naturf. Ges. Zürich* 51: 368, fig. 42. Synonym: *C. belone auct. mult.* Non *C. pacificum* E.J.F.Wood 1963, *nom. inval.*

Subgenus *Amphiceratium* (Vanhöffen 1896) Ostensfeld 1903, genus *Amphiceratium* Vanhöffen.

Sectio *Fusus* Pavillard 1907b, sectio Fusiformia Jørgensen 1911, sectio *Amphiceratium* (Vanhöffen 1896) Gran 1902.

Tripes fusus (Ehrenberg 1833) F.Gómez 2013. Synonyms: *P. fusus* Ehrenberg, *C. fusus* (Ehrenberg) Dujardin 1841, *Amphiceratium fusus* Vanhöffen 1896, *P. seta* Ehrenberg 1859a, *C. seta* (Ehrenberg)

W.S.Kent 1881, *C. berghii* Gourret 1883, *C. pellucidum* Gourret 1883.

Tripus extensus (Gourret 1883) F.Gómez, *comb. nov.* Basionym: *Ceratium fusus* var. *extensum* Gourret 1883. *Ann. Mus. Hist. Nat. Marseille* 1(8): 52, pl. 4, fig. 56. Synonyms: *C. extensum* (Gourret) Cleve 1900, *C. strictum* (Okamura et Nishikawa 1904) Kofoed 1906, non *C. biceps* Claparède et J.Lachmann 1859.

Tripus longirostrum (Gourret 1883) F.Gómez, *comb. nov.* Basionym: *Ceratium longirostrum* Gourret 1883. *Ann. Mus. Hist. Nat. Marseille* 1(8): 55, pl. 4, fig. 65. Non *Ceratium pennatum* f. *propium* Kofoed 1907.

Subgenus *Tripus* autonym, subgenus *Euceratium* (Gran 1902) Ostenfeld 1903, *Tripoceratium* Kofoed 1909, *Macroceratium* Kofoed 1909, *Macroceratium* Böhm 1931, *Orthoceratium* Sournia 1968, non *Orthoceratium* Meunier 1919.

Sectio *Macroceros* Ostenfeld 1903, subgenus *Macroceratium* Kofoed 1909, sectio *Macroceros* Pavillard 1907b, sectio *Protuberantia* Karsten 1907, subsectio *Deflexa* Jørgensen 1911, subsectio *Volantia* Jørgensen 1911, subsectio *Flagellifera* Jørgensen 1911, subsectio *Tenuia* Jørgensen 1911, sectio *Trichoceros* Böhm 1931.

Tripus carriensis (Gourret 1883) F.Gómez, *comb. nov.* Basionym: *Ceratium carriense* Gourret 1883. *Ann. Mus. Hist. Nat. Marseille* 1(8): 38, pl. 4, fig. 57. Synonyms: *C. inflexum* (Gourret 1883) Schröder 1906, *C.*

flagelliferum Cleve 1900, *C. ramakrishnae* Subrahmanyam 1968, non *C. carriense* auct. mult.

Tripus gallicus (Kofoed 1907b) F.Gómez, *comb. nov.* Basionym: *Ceratium gallicum* Kofoed 1907b. *Univ. Calif. Publ. Zool.* 3: 302, pl. 24, figs. 10–12. 1907. Synonyms: *C. californiense* Kofoed 1907b, *C. deflexum* (Kofoed 1907b) Jørgensen 1911, *C. uncinus* Sournia 1972, *C. macroceros* auct. mult.

Tripus longissimus (Schröder 1900) F.Gómez, *comb. nov.* Basionym: *Ceratium tripus* f. *longissimum* Schröder 1900. *Mitt. Zool. Stat. Neapel* 14: 16, pl. 1, fig. 17i. Synonym: *C. longissimum* (Schröder) Kofoed 1907b.

Tripus macroceros (Ehrenberg 1840) F.Gómez, *comb. nov.* Basionym: *Peridinium macroceros* Ehrenberg 1840. *Ber. K. Akad. Wiss. Berlin* 1840: 201. Synonyms: *C. macroceros* (Ehrenberg) Cleve 1899, *C. contrarium* (Gourret 1883) Pavillard 1905, *C. batavum* Paulsen 1907, *C. intermedium* (Jørgensen 1905) Jørgensen 1911, *C. protuberans* (G.Karsten 1906) Paulsen 1930, ?*C. shameelii* Ghazala 2009. Non *C. macroceros* auct. mult.

Tripus massiliensis (Gourret 1883) F.Gómez, *comb. nov.* Basionym: *Ceratium tripus* var. *massiliense* Gourret 1883. *Ann. Mus. Hist. Nat. Marseille* 1(8): 27, pl. 1, figs. 2, 2a). Synonyms: *C. massiliense* (Gourret) G.Karsten 1906, *C. aequatoriale* Schröder 1906, *C.*

undulatum Schröder 1906, *C. ostenfeldii* Kofoed 1907b, ?*C. recurvatum* Schröder 1906, non *C. volans* Cleve 1900.

Tripes pavillardii (Jørgensen 1911) F.Gómez, *comb. nov.* Basionym: *Ceratium vultur* sensu Pavillard 1905. *Trav. Inst. Bot. Univ. Montpellier Stat. Zool. Cette, ser. mixte, Mém.* 2: 54, pl. 1, fig. 2; *C. pavillardii* Jørgensen 1911. *Int. Rev. Hydrobiol. u. Hydrogr., Biol. Suppl.* 2(1): 74, figs. 157, 158.

Tripes tenuis (Ostenfeld et Johannes Schmidt 1901) F.Gómez, *comb. nov.* Basionym: *Ceratium tenue* Ostenfeld et Johannes Schmidt 1901. *Vid. Medd. Naturh. For. Kjøbenhavn* 1901: 166, fig. 18. Synonym: *C. inclinatum* Kofoed 1907b.

Tripes trichoceros (Ehrenberg 1859a) F.Gómez 2013 ($\equiv$ *P. trichoceros* Ehrenberg 1859a, *C. trichoceros* (Ehrenberg) W.S.Kent 1881).

Tripes volans (Cleve 1900) F.Gómez, *comb. nov.* Basionym: *Ceratium volans* Cleve 1900. *K. Svenska Vet. Akad. Handl.*, [ser. 4] 34(1): 15, pl. 7, fig. 4. Synonyms: *C. patentissimum* Ostenfeld et Johannes Schmidt 1901, *C. ceylanicum* Schröder 1906, *C. elegans* Schröder 1906, *C. hundhausenii* Schröder 1906, *C. carriense auct. mult.*

Sectio Palmata Pavillard 1907b, sectio Platycornia Jørgensen 1911, subsectio Intermedia Jørgensen 1911.

Triplos claviger (Kofoid 1907) F.Gómez, *comb. nov.* Basionym: *Ceratium claviger* Kofoid 1907a. *Bull. Mus. Comp. Zool. Harvard Coll.* 50: 170, pl. 4, fig. 27.

Triplos compressus (Gran 1902) F.Gómez, *comb. nov.* Basionym: *Ceratium compressum* Gran 1902. *Rep. Norw. Fish. Mar. Invest.* 2(5): 54, 193, 196, fig. 16. *Triplos platycornis* is probably a senior synonym.

Triplos intermedius (Jørgensen 1899) F.Gómez, *comb. nov.* Basionym: *Ceratium triplos* f. *intermedium* Jørgensen 1899. *Bergens Mus. Aarb.* 1899(6): 42: pl. 1, fig. 10. Synonyms: *C. intermedium* (Jørgensen 1899) Jørgensen 1905, *C. denticulatum* (Jørgensen 1920) Paulsen 1931, *C. molle* Kofoid 1907b, *C. tenuissimum* Kofoid 1907b, *C. buceros* Zacharias 1906, *C. patentissimum* Ostenfeld et Johannes Schmidt 1901, *C. leptosomum* Jørgensen 1911, ?*C. inversum* G.Karsten, 1907, *C. horridum sensu auct.*

Triplos platycornis (Daday 1888) F.Gómez, *comb. nov.* Basionym: *Ceratium platycorne* Daday 1888. *Természetr. Füzet.* 11: 78, 101, pl. 3, figs. 1, 2. Synonyms: *C. lamellicorne* Kofoid 1908d, *C. dilatatum* (G.Karsten 1905) Kofoid 1907a (non *C. dilatatum* Gourret 1883). *Triplos compressus* is probably a junior synonym.

Triplos ranipes (Cleve) F.Gómez, *comb. nov.* Basionym: *Ceratium ranipes* Cleve 1900. *K. Svenska Vet. Akad. Handl.*, [ser. 4] 34(1): 13, pl. 7, fig. 1. Synonym: *Ceratium palmatum* (Schröder 1900) Cleve 1901.

Subsectio Tergestina Karsten 1907

Tripus arcticus (Ehrenberg) F.Gómez, *comb. nov.* Basionym: *Peridinium arcticum* Ehrenberg 1853. *Ber. K. Akad. Wiss. Berlin* 1853: 528. Synonyms: *C. arcticum* (Ehrenberg) Cleve 1900, *C. labradoricum* (F.Schütt 1892) Vanhöffen 1897, non *C. arcticum* sensu Vanhöffen 1897 (= *T. longipes*).

Tripus longipes (Bailey 1854) F.Gómez, *comb. nov.* Basionym: *Peridinium longipes* Bailey 1854. *Smithson. Contrib. Knowl.* 7(3): 12, fig. 35. Synonyms: *C. longipes* (Bailey) Cleve 1900, *C. arcticum* sensu Vanhöffen 1897, *C. horridum* (Cleve 1897) Gran 1902, non *C. horridum* sensu Gran 1902, non *C. horridum sensu auct.* (= *Tripus intermedius*).

Sectio Vultur (Jørgensen 1911) Böhm 1931, subsectio Vultur Jørgensen 1911, sectio Reflexa Jørgensen 1911, subsectio Reflexa (Jørgensen) P. Reinecke.

Tripus reflexus (Cleve 1900) F.Gómez (≡ *C. reflexum* Cleve)

Tripus robustus (Ostenfeld et Johannes Schmidt 1901) F.Gómez, *comb. nov.*

Basionym: *Ceratium robustum* Ostenfeld et Johannes Schmidt, 1901.

Vid. Medd. Naturh. For. Kjøbenhavn 1901: 166, fig. 17. Synonym: *C. japonicum* Schröder 1906.

Tripus vultur (Cleve 1900) F.Gómez, *comb. nov.* Basionym: *Ceratium vultur* Cleve 1900. *K. Svenska Vet.-Akad. Handl.*, [ser. 4] 34(1): 15, pl. 7, fig. 5. Synonyms: *C. sumatranum* (G.Karsten 1907) Jørgensen 1911, *C. recurvum* (Jørgensen 1911) P.Reinecke 1973.

Sectio Reticulata (Jørgensen 1911) Böhm 1931, subsectio Reticulata Jørgensen.

Tripus hexacanthus (Gourret 1883) F.Gómez 2013. Synonyms: *C. hexacanthum* Gourret 1883, *C. reticulatum* (Pouchet 1883) Cleve 1903, *C. aestuarium* Schröder 1911, ?*C. obesum* Pavillard 1930.

Sectio Tripus autonym, sectio Tripus Ostenfeld 1903, Pavillard 1907b, sectio Euceratium Gran 1902, sectio Rotunda G.Karsten 1907, subsectio Eutripus Jørgensen 1911, sectio Dens Jørgensen 1911.

Tripus brevis (Ostenfeld et Johannes Schmidt 1901) F.Gómez, *comb. nov.*
Basionym: *Ceratium tripus* var. *breve* Ostenfeld et Johannes Schmidt 1901. *Vid. Medd. Naturh. For. Kjøbenhavn* 1901: 164, fig. 13.
Synonym: *C. breve* (Ostenfeld et Johannes Schmidt) Schröder 1906.

Tripus dens (Ostenfeld et Johannes Schmidt 1901) F.Gómez 2013.
Synonyms: *C. dens* Ostenfeld et Johannes Schmidt 1901, *C. balechii* Meave del Castillo, Okolodkov et Zamudio 2003, *C. divaricatum* sensu Kofoed 1908c, non *C. divaricatum* (Lemmermann 1899) Kofoed 1908c.

Tripus gracilis (Pavillard 1905) F.Gómez 2013. Synonyms: *C. gracile* Pavillard 1905, *C. declinatum* G.Karsten 1907, *C. varians* Mangin 1922, *C. declinatum auct. mult.*

Tripus muelleri Bory 1825. Synonyms: *Cercaria tripus* O.F.Müller 1777, *Peridinium tripus* (O.F.Müller) Ehrenberg 1833, *C. tripus* (O.F. Müller) Nitzsch 1817, *C. neglectum* Ostenfeld 1903, *C. subsalsum* (Ostenfeld 1903) Apstein 1911, *C. dalmaticum* Schröder 1911, *C. divaricatum* (Lemmermann 1899) Kofoed 1908c, non *C. divaricatum*

sensu Kofoed 1908c, *C. schmidtii* Jørgensen 1911, *C. humile* Jørgensen 1911, *C. porrectum* (G.Karsten 1907) Jørgensen 1911, *C. tripodoides* (Jørgensen 1920) Steemann Nielsen 1934, *C. schroderi* D.S.Nie 1936, *C. truncatum* (Lohmann 1908) Apstein 1911, ?*C. egyptiacum* Halim 1963.

Tripus pulchellus (Schröder 1906) F.Gómez, *comb. nov.* Basionym: *Ceratium pulchellum* Schröder 1906. *Vierteljahrsschr. Naturf. Ges. Zürich* 51: 358, fig. 27. Synonym: *C. semipulchellum* Steemann Nielsen 1934.

Subsectio Arcuata Karsten 1907, subsectio Arcuata Jørgensen 1911.

Tripus arcuatus (Gourret 1883) F.Gómez, *comb. nov.* Basionym: *Ceratium tripus* var. *arcuatum* Gourret 1883. *Ann. Mus. Hist. Nat. Marseille* 1(8): 25, pl. 2, fig. 42. Synonyms: *C. arcuatum* (Gourret) Vanhöffen 1897, *C. euarcuatum* Jørgensen 1920, *C. filicorne* Steemann Nielsen 1934, *C. angusticorne* (Peters 1932) Steemann Nielsen 1939, *C. okamuræ* B. Schröder 1906.

Tripus axialis (Kofoed 1907a) F.Gómez 2013 ($\equiv$ *C. axiale* Kofoed 1907a).

Tripus coarctatus (Pavillard 1905) F.Gómez, *comb. nov.* Basionym: *Ceratium coarctatum* Pavillard 1905. *Trav. Inst. Bot. Univ. Montpellier Stat. Zool. Cette, ser. mixte, Mém.* 2: 52, pl. 1, fig. 6.

Tripus karstenii (Pavillard 1907a) F.Gómez, *comb. nov.* Basionym: *Ceratium karstenii* Pavillard 1907a. *Bull. Soc. Bot. France* 54: 152. Synonym: *C. schrankii* Kofoed 1907b.

Tripus longinum (G.Karsten 1906) F.Gómez, *comb. nov.* Basionym:

Ceratium tripus var. *longinum* G. Karsten 1906. *Wiss. Ergeb. Deutsch. Tiefsee-Exped. 1898–1899*, 2(2): 143, pl. 21, fig. 18.

Tripus subcontortus (Schröder 1906) F.Gómez, *comb. nov.* Basionym:

Ceratium subcontortum Schröder 1906. *Vierteljahrsschr. Naturf. Ges. Zürich* 51: 358, fig. 28. Synonym: *C. saltans* Schröder 1906, *C. contortum auct. mult.*

Tripus symmetricus (Pavillard 1905) F.Gómez, *comb. nov.* Basionym:

Ceratium symmetricum Pavillard 1905. *Trav. Inst. Bot. Univ. Montpellier Stat. Zool. Cette, ser. mixte, Mém.* 2: 52, pl. 1, fig. 4. Synonym: *C. orthoceras* (Jørgensen 1911) Pavillard 1931.

Sectio Limulus Jørgensen 1911, subsectio Lunulae Jørgensen 1911.

Tripus arietinus (Cleve) F.Gómez, *comb. nov.* Basionym: *Ceratium*

arietinum Cleve 1900. *K. Svenska Vet.-Akad. Handl.*, [ser. 4] 34(1): 13, pl. 7, fig. 3. Synonyms: *C. arietinum* Cleve 1900, *C. bucephalum* (Cleve 1897) Cleve 1900, *C. heterocamptum* (Jørgensen 1899) Ostenfeld et Johannes Schmidt 1901.

Tripus azoricus (Cleve 1900) F.Gómez 2013 ($\equiv$ *C. azoricum* Cleve 1900).

Tripus carnegiei (H.W.Graham et Bronikovsky 1944) F.Gómez 2013 ($\equiv$ *C. carnegiei* H.W.Graham et Bronikovsky 1944).

Tripus limulus (C.H.G.Pouchet 1883) F.Gómez, *comb. nov.* Basionym:

Ceratium tripus var. *limulus* C.H.G.Pouchet 1883. *J. Anat. Physiol.*

19: 424, pl. 18+19, fig. 4. Synonym: *C. limulus* (C.H.G.Pouchet) Gourret 1883.

Tripes lunula (A. Schimper in Chun 1900 ex G.Karsten 1906) F.Gómez 2013 ($\equiv$ *C. lunula* A. Schimper in Chun 1900 ex G.Karsten 1906).

Tripes paradoxides (Cleve 1900) F.Gómez 2013 ($\equiv$ *C. paradoxides* Cleve 1900).

Tripes petersii (Steemann Nielsen 1934) F.Gómez 2013 ($\equiv$ *C. petersii* Steemann Nielsen). Probably a synonym of *T. azoricus*.

Subsectio Gibbera Jørgensen 1911.

Tripes gibberum (Gourret 1883) F.Gómez, *comb. nov.* Basionym: *Ceratium gibberum* Gourret 1883. *Ann. Mus. Hist. Nat. Marseille* 1(8): 34, pl. 2, fig. 35. Synonyms: *C. curvicornis* (Daday 1888) Cleve 1900, *C. contortum* (Gourret 1883) Cleve 1900, *C. concilians* Jørgensen 1920, non *C. contortum auct. mult.*

4 Conclusions

About 165 species and 800 infraspecific taxa of *Tripes* have been proposed. The current molecular data with sequences of 30, 9 and 3 species for the SSU-, LSU- and ITS rRNA gene markers, respectively, are insufficient to solve the speciation of the genus. In the SSU- and LSU rRNA gene phylogenies, the sequences of the subgenera *Amphiceratium*, *Archaeoceratium* and *Tripes eugrammus* ($\equiv$ *T. furca auct. mult.*) were the basal clades, while the sequences of the typical anchor-shaped species clustered in the distal groups. The

reinstatement of the genera *Amphiceratium*, *Biceratium* and *Poroceratium* have several problems. The diagnostic characters to circumscribe *Poroceratium* are unclear, especially after encompassing most of the species of *Amphiceratium* (section Inflata, and most of the species of the section Fusiformia). There are no molecular data of key species such as *T. belone* and *T. pacificus* that could be a link between *Archaeoceratium* and *Amphiceratium*, and there is no any LSU rRNA gene sequence of species of *Poroceratium*. For the reinstatement of *Biceratium*, LSU rRNA gene sequences of only two species are available and they did not cluster together. The SSU rRNA gene sequences of *T. eugrammus* and the members of the sections Furciformia, Pentagona and Candelabra did not cluster as a monophyletic group. Consequently, a tentative split of *Tripos* needs more molecular data and morphological studies to define the diagnostic characters of the tentative segregated genera.

The review of the original species descriptions reveals that the names *T. eugrammus* and *T. furca* should be used for the species currently identified as *T. furca* and *T. lineatus*, respectively. The names *T. pacificus* and *T. carriensis* have been misapplied for *T. belone* and *T. volans*, respectively. The species names *T. arcuatus*, *T. gracilis*, *T. inclinatus*, *T. scapiformis* and *T. subcontortus* are revived to replace *T. euarquatus*, *T. declinatus*, *T. horridus*, *T. longirostrum* and *T. contortus*, respectively. Rare species were described from autotomized individuals such as *C. californiense* or *C. ehrenbergii*. Other species were described from aberrant individuals such as *C. deflexus*, *C. obesus*, *C. reflexus*, *C. shameelii* or *C. uncinnus*. The individuals infected by an endoparasites exhibit an expanded midbody, being described as distinct species such as *C. ramanskiniae* or *C. fusus* var. *schuettii*. Fifty-seven correct species are considered from the 165 names of marine species of *Ceratium* proposed in the literature. Our knowledge of the speciation and evolution of the genus *Tripos* is largely incomplete due to lack of studies in the life cycle and molecular data.

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