

Taxonomy and identification of the armored dinoflagellate genus *Heterocapsa* (Peridinales, Dinophyceae)

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Abstract: The armored dinoflagellate genus *Heterocapsa* is composed of relatively small species, including a species responsible for harmful red tides, *H. circularisquama*. Some *Heterocapsa* species such as *H. rotundata* and *H. triquetra* have been well documented as red tide-forming species, but are not recognized as causing harmful effects. Following sequential shellfish mass mortalities in the coastal waters of western Japan due to *H. circularisquama* red tides, this species has attracted considerable interest. Many properties of this species, such as its distribution and growth characteristics, have been investigated to better understand the mechanisms involved in harmful red tide formation. Related to the need for unambiguous identification of *H. circularisquama*, several unidentified (or undescribed) *Heterocapsa* species, which must be distinguished from the harmful taxon, have been detected sympatrically in regions where *H. circularisquama* blooms occur. However, the taxonomic affiliation of these *Heterocapsa* species have not yet been determined because several characteristics of *Heterocapsa* (e.g. body scale ultrastructure) have not yet been reported from all described species due to the changing taxonomic criteria. After the taxonomic ambiguities in this genus were resolved, cellular and body scale morphology of *Heterocapsa* were reinvestigated and several new species were described. In the present paper, the taxonomic history and morphological characters of the genus *Heterocapsa* are summarized.

Key words: body scale, dinoflagellate, *Heterocapsa*, morphology, nucleus, pyrenoid, red tide, taxonomy, thecal plates

Introduction

The genus *Heterocapsa* is composed of armored dinoflagellates represented by relatively small planktonic species. Some *Heterocapsa* species such as *Heterocapsa rotundata* (Lohmann) Hansen and *Heterocapsa triquetra* (Ehrenberg) F. Stein have long been recognized to be cosmopolitan, red tide-forming taxa. In 1988, *Heterocapsa circularisquama* Horiguchi was first found in Uranouchi Inlet, Kochi Prefecture, Japan, and has since spread along the coast of western Japan accompanied by tremendous damage to bivalve aquaculture (Horiguchi 1995, Matsuyama 1999). Since this harmful species and its noxious effects, specifically on bivalves, had never been reported it was described as the new species *H. circularisquama* (Horiguchi 1995). The previous distribution of this novel harmful species remains unclear, however, its relatively higher optimum temperature for growth and a report of its occurrence from Hong Kong imply a recent transfer from tropical or subtropical waters

to Japan (Yamaguchi et al. 1997, Honjo et al. 1998, Iwataki et al. 2002b, Iwataki & Matsuoka 2007). The continued harmful impacts on aquaculture have promoted numerous investigations of the distribution and optimum conditions for growth of this species (e.g. Matsuyama et al. 1997, Yamaguchi et al. 1997, Nagai et al. 2000, Yamaguchi et al. 2001, Shiraishi et al. 2007). During previous studies of *H. circularisquama*, several undescribed species superficially resembling *H. circularisquama* had been observed; however, it was difficult to define their taxonomic status at that time.

The genus was originally described more than one hundred years ago (Stein 1883), and about 20 species have so far been assigned to *Heterocapsa*. Since the presence of a resting cyst is unknown in *Heterocapsa* (Fensome et al. 1993), species have been distinguished based on the morphology of the motile cell. Nonetheless, the generic criteria for species assignment within *Heterocapsa* have continued to change, resulting in some species descriptions unsuitable for inclusion the genus, according to our present knowledge. Moreover, some of the morphological characters of *Heterocapsa* that should be compared and contrasted, e.g.

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body scale ultrastructure, have not been reported in all the described species. For taxonomic assignment of unidentified species and unambiguous identification of *H. circularisquama*, reliable criteria are required. Reinvestigations of common morphological characters for the genus such as typical thecal plate arrangement (Po, cp, 5', 3a, 7", 6c, 5s, 5"', 2''') and ultrastructure of the triradiate body scales covering the cell surface have been carried out recently, and the taxonomy of this genus was reassessed (Iwataki et al. 2003, 2004). As a result of this work, fifteen species are now recognized as possessing morphological characters common to *Heterocapsa*. In the present paper, the taxonomic history and present status of the genus *Heterocapsa* are summarized and this reliability of morphological characters for species identification is discussed.

Taxonomic history of *Heterocapsa*

The genus *Heterocapsa* was originally established by Stein in 1883 with the proposal of a new combination of the type species *H. triquetra* from *Glenodinium triquetrum* Ehrenberg (Stein 1883). Two species, *H. umbilicata* F. Stein and *H. quadridentata* F. Stein, were simultaneously described as new species (Stein 1883). In the systematics of dinoflagellates at this time, two thecate genera, *Peridinium* and *Glenodinium*, were distinguished based on whether the thecal plates (or sutures) were visible under a light microscope. As Stein (1883) could find the sutures only on the epitheca of *G. triquetrum* and the other two taxa, he tentatively established a new genus *Heterocapsa*, to include the species having a sutured epitheca and a flimsy *hypotheca*. The original etymology of the genus *Heterocapsa*, therefore, denoted different types of the hemitheca. The cell shapes and thecal plate arrangements of the epitheca were sufficiently different to distinguish each of these three species from the other. These morphological and thecal plate variances represent the generic differences that are presently accepted.

The next description of a *Heterocapsa* species was *Heterocapsa pacifica* Kofoid (Kofoid 1907). The cell shape of this species was somewhat similar to *H. triquetra*, but it differed in several ways, including having a broader cell width, in the position of the nucleus and in possessing a prominent antapical spine. However, it contradicted the original description of *Heterocapsa*, as the thecal plates were not illustrated at all. Subsequently, Massart (1920) reported a new species *Heterocapsa quinquecuspidata* Massart. The cell of *H. quinquecuspidata* resembled *H. quadridentata* in possessing five spines on the hypotheca. Only the thecal plates of the dorsal epitheca were illustrated. Four *Heterocapsa* species *H. umbilicata*, *H. quadridentata*, *H. pacifica* and *H. quinquecuspidata* have not been reported from any location since their original description, with only *H. triquetra* being reported by several authors (e.g. Schütt 1895, Lindemann 1924). The type species *H. triquetra* was re-examined and sutures were found also on

the hypotheca (Lindemann 1924), but this plate tabulation still differed from later reports that have more recently been accepted (e.g. Morrill & Loeblich III 1981). During this period, cell shape was treated as the most fundamental or conserved character of *Heterocapsa* and the original criterion of the genus was neglected.

In the 1960s, all thecal plates were investigated in detail by light microscopy and their arrangements were adopted as a criterion of the genus. Loeblich III (1968) described the new species *Cachonina niei* Loeblich III as the type species of a new genus *Cachonina* (*Cachonina*=*Heterocapsa*) with the thecal plate arrangement illustrated as p.p. (apical pore plate=Po), 5', 3a, 8", 6c, 4s, 5"', 2'''. Subsequently, von Stosch (1969) reanalyzed the entire plate arrangement of *H. niei*; Po, 6', 3a, 8", 6c, 4s (s.a. (anterior sulcal plate), t (transitional plate), s.l. (left sulcal plate), s.p. (posterior sulcal plate)), 5"', 2'''. A tiny canal plate was then discovered and mentioned as the sixth apical plate 6' (von Stosch 1969). This was the first report of a complete thecal plate tabulation to be worked out in detail for a member of the genus *Heterocapsa* (Loeblich III et al. 1981). Thereafter the generic affiliation of each species was discussed based on its thecal plate arrangement.

The next *Cachonina* species, *C. illdefina* Herman et Sweeney, was described from a red tide sample collected in California (Herman & Sweeney 1976). This species name was based on the English term "ill-defined" due to the frustration over its classification. The thecal plate tabulation of *C. illdefina* was identical to *C. niei*; however, the configuration of the sulcal series and cell size were different. Transmission electron microscopy then revealed that *C. illdefina* had tubular cytoplasmic invaginations within the pyrenoid matrix, resembling those of *H. triquetra* as reported by Dodge & Crawford (1971). In 1977, Balech analyzed in detail the thecal plates of *C. illdefina*, and considered it to be synonymous with *C. niei* based on the similarity of their arrangements. In contrast to the opinion of Balech (1977), Morrill & Loeblich III reported a difference in cell size range between *C. niei* and *C. illdefina* (Morrill & Loeblich III 1981). They also re-observed the complete thecal plate arrangement of *H. triquetra*, 2pr, 5', 3a, 7", 6c, 7s, 5"', 1p, 2''', and argued that the arrangements of *Heterocapsa* and *Cachonina* were almost identical. Moreover they indicated the presence of organic body scales in these *Cachonina* species, a character already observed in *H. triquetra* (Penick & Clarke 1977). They then transferred *C. niei* and *C. illdefina* to *Heterocapsa* based on these common characters with two new nomenclatural combinations, *H. niei* (Loeblich III) Morrill et Loeblich III, and *H. illdefina* (Herman et Sweeney) Morrill et Loeblich III (Morrill & Loeblich III 1981). Since their proposal of these taxonomic combinations, the genus *Cachonina* has been considered to be a junior synonym of *Heterocapsa* (Morrill & Loeblich III 1981, Fensome et al. 1993, Hansen 1995, Horiguchi 1995, 1997). During the same year, a new species *Heterocapsa pygmaea* Loeblich III, Schmidt et Sherley was proposed (Loeblich III

et al. 1981). The thecal plate arrangement of *H. pygmaea* was given as; apical pore plate, canal plate, 5', 3a, 7", 5–7c (a.s., r.s., l.a.s., l.p.s., [? a.a.s. and p.a.s.] p.s.), 5"', 2'''. They regarded the eighth precingular plate (8") as the anterior sulcal plate (as), which is a commonly accepted interpretation at present. In the same paper, they also mentioned that the presence of body scales was a generic feature of *Heterocapsa*, and that scale sizes were a significant characteristic at the species level (Morrill & Loeblich III 1981).

Organic body scales, the distinctive feature of the genus *Heterocapsa*, were first reported from the type species *H. triquetra* (Pennick & Clarke 1977). Scales of *H. triquetra* were observed in detail using TEM of both thin sections and whole mounts, and the three-dimensional structure was illustrated. Thereafter, the presence of delicate organic body scales on the cell surface was reported from *Heterocapsa* species by several authors (Morrill & Loeblich III 1981, 1983, Bullman & Roberts 1986). Subsequently, the detailed structure of the scales of *H. niei* was examined and this clearly illustrated the difference of this species from *H. triquetra* (Morrill & Loeblich III 1983). They mentioned that the body scales were not only a common character of the genus *Heterocapsa*, but also that subtle differences might exist between the scales of each species.

During the 1970s, two species were assigned to *Heterocapsa*, yet they have not been reported since. *Heterocapsa kollmeriana* Swift et McLaughlin was reported from a bloom in Phosphorescent Bay, Puerto Rico (Swift & McLaughlin 1970). The thecal plate arrangements and position of the nucleus were unclear, and a detailed species description with a Latin diagnosis was not provided. Campbell (1973) transferred *Peridinium chattonii* Biecheler to the genus *Heterocapsa*, proposing a new combination *H. chattonii* (Biecheler) Campbell. He also observed *H. triquetra* and considered its short first apical plate 1' as an important taxonomic character of *Heterocapsa*. Another species of the genus, *Heterocapsa minima* Pomroy, was reported from the Celtic Sea, England (Pomroy 1989). This species was described mainly based on its small cell size and observations by scanning electron microscopy clearly revealed a thecal plate arrangement identical to *Heterocapsa*, although body scales were not shown. *H. minima* is a rare species of *Heterocapsa* occurring in offshore waters.

In 1989, body scales similar to those in *Heterocapsa* were observed on the unarmored dinoflagellate *Katodinium rotundatum* (Lohmann) Loeblich III, and their detailed structure was reported (Hansen 1989). The scale structure was not identical to previously reported scales in *Heterocapsa*. Several years later, rather thin thecal plates with an arrangement similar to those of *Heterocapsa* were found on *K. rotundatum*, leading Hansen (1995) to propose a new combination, *H. rotundata*. He also examined a culture of *Heterocapsa* cf. *minima* and noted the differences in cell shape and body scale ultrastructure between *H. rotundata* and *H. cf. minima*. Thus the morphology of body scales has been generally accepted to be the most important species

character. In the same year, the causative species of shellfish mass mortalities, *H. circularisquama*, was described (Horiguchi 1995). Cell shape, size and thecal plate arrangement of *H. circularisquama* were rather similar to those of *H. illedefina*, although the body scales clearly differed from the latter taxon. The species name of *H. circularisquama* means circular scale and it was the first species established based on body scale ultrastructure.

In the last decade, following the description of the harmful species *H. circularisquama* (Horiguchi 1995), seven *Heterocapsa* species, *H. arctica* Horiguchi, *H. horiguchii* Iwataki, Takayama et Matsuoka, *H. lanceolata* Iwataki et Fukuyo, *H. orientalis* Iwataki Botes et Fukuyo, *H. ovata* Iwataki et Fukuyo, *H. psammophila* Tamura, Iwataki et Horiguchi, *H. pseudotriquetra* Iwataki, Hansen et Fukuyo, were described according to body scale morphologies (Horiguchi 1997, Iwataki et al. 2002a, 2003, 2004, Tamura et al. 2005). Based on a comparison of morphological characteristics, common characters of the genus *Heterocapsa* were reexamined and the generic diagnosis was emended by Iwataki & Fukuyo as: unicellular photosynthetic dinoflagellate with thecal plates arranged as Po, cp, 5', 3a, 7", 6c, 5s, 5"', 2''' and three-dimensional triradiate body scales (Iwataki et al. 2003). Iwataki et al. (2004) reanalyzed body scale fine structures of reported *Heterocapsa* species and demonstrated the utility of scale structure for reliable species identification.

Armored dinoflagellates belonging to the genus *Heterocapsa* are summarized in Fig. 5. Twenty species have so far been described or transferred to *Heterocapsa*. Of these taxa, five species without the characteristics of *Heterocapsa*, *H. umbilicata*, *H. quadridentata*, *H. quinquecuspidata*, *H. kollmeriana*, *H. chattonii*, are not treated as *Heterocapsa* at present. The other fifteen species (Figs. 3–5) are presently recognized as valid *Heterocapsa* species.

Identification of *Heterocapsa* based on cellular morphology

Species of *Heterocapsa* are relatively small and share congruous morphological characters such as thecal plate arrangement and reticulated chloroplasts located peripherally, making species difficult to identify using light microscopy. Even though body scale fine structure (Figs. 1, 2) is required for the unambiguous identification of *Heterocapsa* species (Iwataki et al. 2004), cellular characteristics such as cell size, shape, and the positions of the nucleus and pyrenoid are different in some species and they are also useful for tentative species identification. Cell shapes, with the positions of the nucleus and pyrenoid, of recently recognized *Heterocapsa* are summarized in Figs. 3 and 4.

The average cell size of different *Heterocapsa* species is variable, ranging from 7.4 μm for *H. minima* to 45 μm for *H. pacifica* (Kofoid 1907, Pomroy 1989). Size ranges of most species often overlap each other; therefore, it is difficult to identify taxa based only on their cell sizes. On the

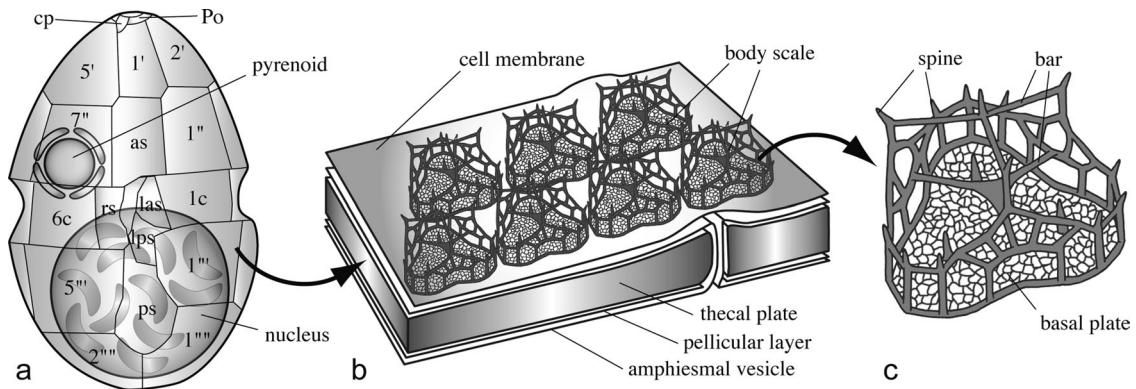


Fig. 1. Schematic illustrations of *Heterocapsa niei*, a motile cell with thecal plates including the apical pore plate (Po), canal plate (cp), apical plates (1', 2', 5'), precingular plates (1'', 7''), cingular plates (1c, 6c), sulcal plates (as, rs, las, lps, ps), post cingular plates (1''', 5''') and antapical plates (1''', 2''') (a), cell surface structure covered with body scales (b), and body scale structure (c). Thecal plates are located in amphiasmatal vesicles underlying the cell membrane. Body scales are positioned on the cell membrane and covering the cell.

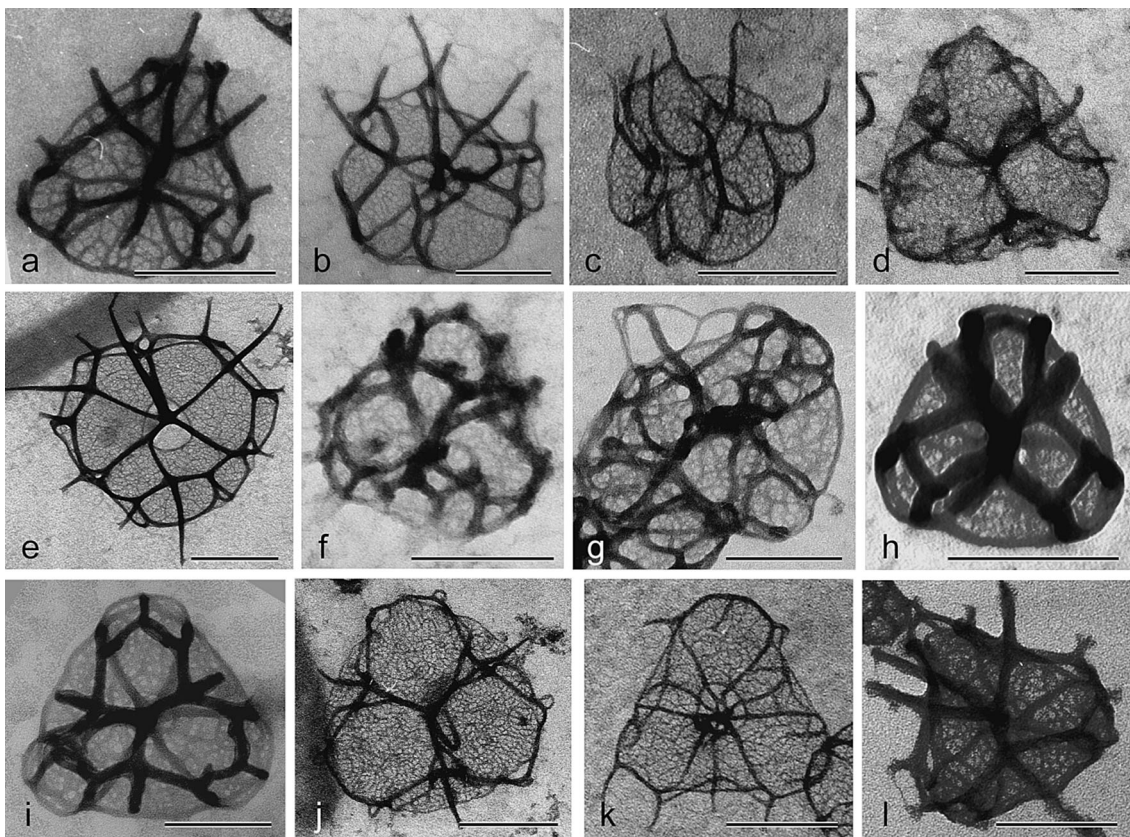


Fig. 2. Body scales of *Heterocapsa* species, whole mounts observed by TEM. *H. arctica* (a), *H. circularisquama* (b), *H. horiguchii* (c), *H. illdefina* (d), *H. lanceolata* (e), *H. niei* (f), *H. orientalis* (g), *H. ovata* (h), *H. psammophila* (i), *H. pygmaea* (j), *H. rotundata* (k), and *H. triquetra* (l). Body scale is composed of a reticulated triradiate basal plate and a three dimensional ornament composed of bars and spines; each species can be distinguished based on the scale structure, the shape of the basal plate, and the number of bars and spines. Scale bars=200 nm.

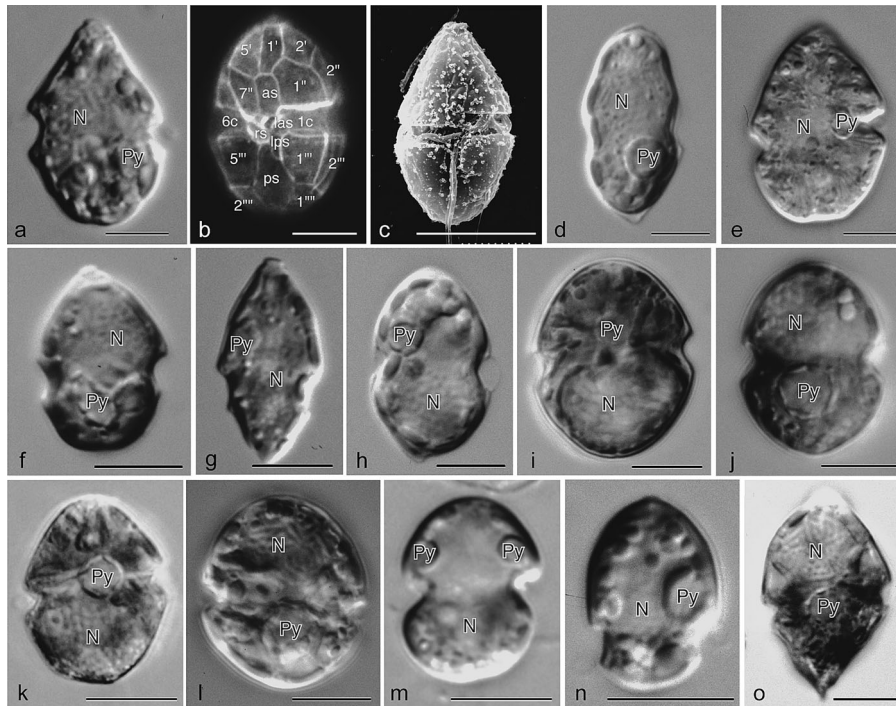


Fig. 3. Photomicrographs of *Heterocapsa* species. *H. circularisquama*, light microscopy (a), fluorescence microscopy showing thecal plate arrangement (b), SEM (c), *H. arctica* (d), *H. ildefina* (e), *H. horiguchii* (f), *H. lanceolata* (g), *H. niei* (h), *H. orientalis* (i), *H. ovata* (j), *H. psammophila* (k), *H. pseudotriquetra* (l), *H. pygmaea* (m), *H. rotundata* (n), and *H. triquetra* (o). N and Py indicate positions of the nucleus and pyrenoid, respectively. Scale bars = 10 μm .

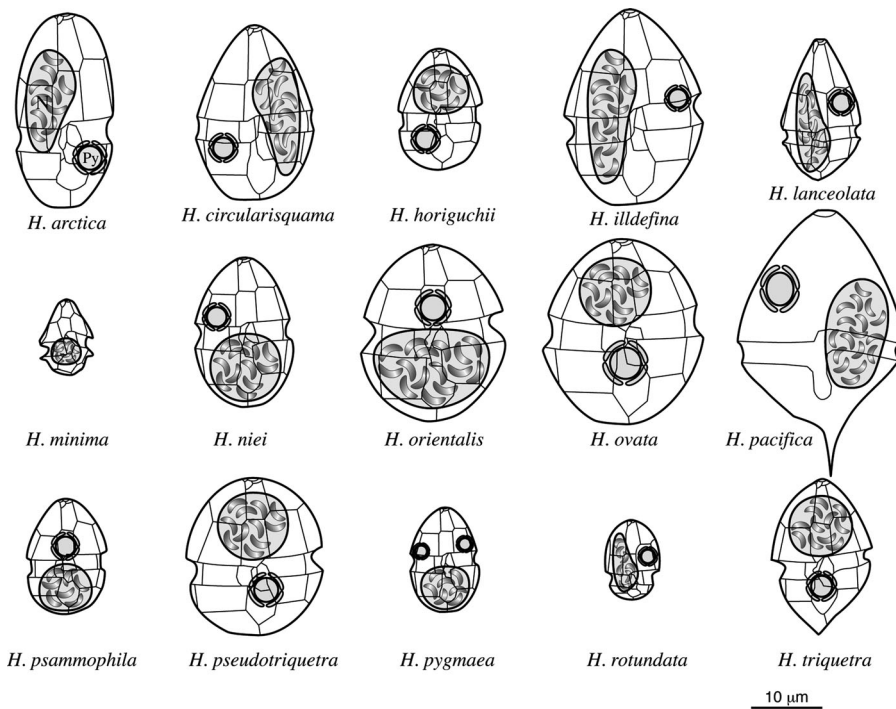


Fig. 4. Schematic drawings of species assigned to the genus *Heterocapsa* at present, showing cell shape and the positions of the nucleus (containing chromosomes: N) and pyrenoid (surrounded by starch sheaths: Py). Drawings of *H. minima* and *H. pacifica* are modified from Pomroy (1989) and Kofoid (1907), respectively; others are from Iwataki (2002) and Iwataki et al. (2002a, 2003, 2004). Pyrenoid position of *H. minima* and thecal plate arrangement of *H. pacifica* are unknown.

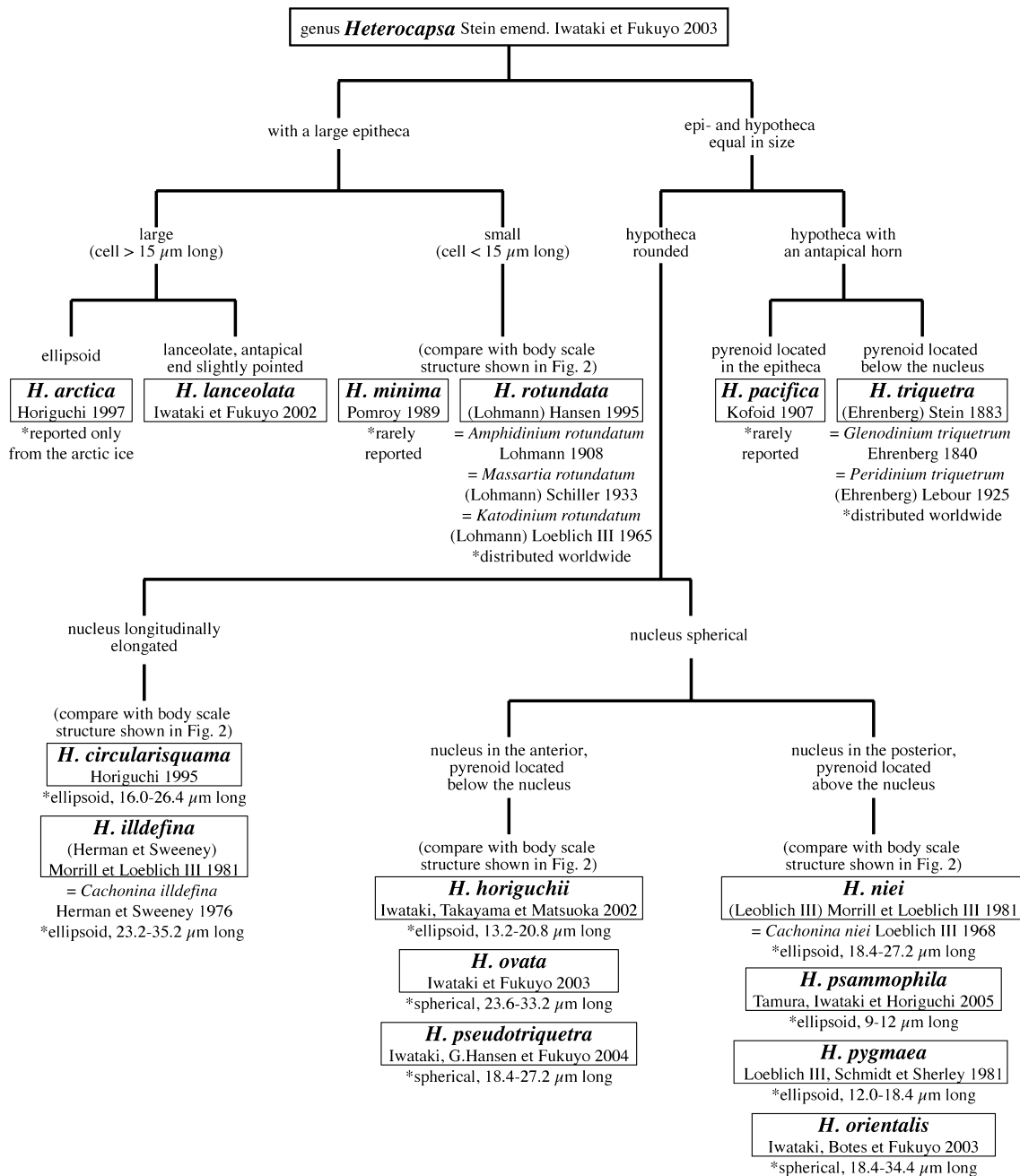


Fig. 5. A flow diagram for species identification of the genus *Heterocapsa* based on cell morphologies. Cell length is referable to Iwataki (2002).

other hand, cell shape seems to be stable in each species. Many *Heterocapsa* species exhibit an ellipsoidal or spherical outline in the dorsal view and it is difficult to discern. However, several species possess specific features such as an apparently large epitheca compared to the hypotheca and an antapical horn. For example, the cell shape of *H. triquetra* is rhomboid with an antapical horn, *H. arctica* is elongated with a large epitheca, *H. lanceolata* is lanceolate with a large epitheca and an antapical horn, and *H. rotundata* is rather small with a large epitheca (Hansen 1995, Horiguchi 1997, Iwataki et al. 2002a). Based on these specific charac-

ters, these four species can be identified under a light microscope (Figs. 3–5). On the other hand, cells of *H. orientalis*, *H. ovata* and *H. pseudotriquetra* are almost spherical (Iwataki et al. 2003, 2004). They can be discriminated from other ellipsoidal species, but are difficult to distinguish from each other. Other ellipsoidal species including *H. circularisquama* are also hard to identify under a light microscope.

Presence of a pyrenoid, surrounded by conspicuous starch sheaths, which are visible under a light microscope, is one of the common characters of the genus (Fig. 3). Be-

cause the positions of the nucleus and pyrenoid are stable among *Heterocapsa* species, their differences can be useful for differentiation of some species. Namely, for species with the nucleus located in the epitheca, the pyrenoid is usually positioned below the nucleus and vice versa (Figs. 3, 4). Using this characteristic combined with its cell shape, several rather nondescript species such as ellipsoidal and spherical species can be distinguished from each other. For example, *H. orientalis*, *H. ovata* and *H. pseudotriquetra* are spherical and quite similar to each other, but only *H. orientalis* has its nucleus in the hypotheca (Iwataki et al. 2003, 2004). Among the ellipsoidal species, the nuclei of *H. niei*, *H. psammophila* and *H. pygmaea* are located in the hypotheca, whereas that of *H. horiguchii* is positioned in the epitheca (Loeblich III et al. 1981, Morrill & Loeblich III 1984, Iwataki et al. 2002a, Tamura et al. 2005). The nuclei of *H. circularisquama* and *H. illdefina* are elongated through the cell (Herman & Sweeney 1976, Horiguchi 1995); therefore, they are difficult to distinguish from each other based on the nuclear position.

Consequently, about a half of all known *Heterocapsa* species can be distinguished based on the morphological characters such as cell shape and position of the organelles (Fig. 5). Since these characters can be observed under the light microscope, they are quite useful for identification of *Heterocapsa* species.

After harmful red tides of *H. circularisquama* appeared, morphological characters of *Heterocapsa* were reexamined and the generic criteria were emended. Moreover, following a detailed morphological evaluation, the presence of six new species, *H. horiguchii*, *H. lanceolata*, *H. orientalis*, *H. ovata*, *H. psammophila* and *H. pseudotriquetra*, was revealed recently only from Japanese coastal waters (Iwataki et al. 2002a, 2003, 2004, Tamura et al. 2005). Since the cells of *Heterocapsa* are rather small and often hard to identify, many undiscovered *Heterocapsa* species with unknown body scale structure are likely present in coastal waters worldwide. Based on future comparisons, including the description of such species, a more comprehensive taxonomic system will be constructed for the genus *Heterocapsa*.

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