The genus *Heterocapsa* is composed of armored dinoflagellates represented by relatively small planktonic species. 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
body scale ultrastructure, have not been reported in all the described species. For taxonomic assignment of unidenti-
fi ed species and unambiguous identification of H. circular-
isquamula, 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 cov-
ering 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 rec-
ognized as possessing morphological characters common to
Heterocapsa. In the present paper, the taxonomic history and
present status of the genus Heterocapsa are summa-
rized 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. quadritentata F. Stein, were simultaneously de-
scribed 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 micro-
scope. As Stein (1883) could find the sutures only on the
epithea of G. triquetrum and the other two taxa, he tenta-
vatively established a new genus Heterocapsa, to include the
species having a sutured epitheca and a flimsy hypotheca.
The original etymology of the genus Heterocapsa, there-
fore, 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 Hete-
rocapsa pacifica Kofoid (Kofoid 1907). The cell shape of
this species was somewhat similar to H. triquetra, but it dif-
fered 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) re-
ported a new species Heterocapsa quinquescipidata Mass-
sart. The cell of H. quinquescipidata resembled H. quadri-
dentata 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. quinquescipidata have not been re-
ported 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.
tripetra 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 pe-
riod, cell shape was treated as the most fundamental or con-
served 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=Hetero-
capsa) with the thecal plate arrangement illustrated as p.p.
(apical pore plate=Po), 5’, 3a, 7’, 6c, 4s, 5”, 2”. Subse-
sequently, von Stosch (1969) reanalyzed the entire thecal 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 frus-
tration over its classification. The thecal plate tabulation of
C. illdefina was identical to C. niei; however, the configu-
ration of the sulcal series and cell size were different. Trans-
mersion 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 de-
tail 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 (Pen-
nick & Clarke 1977). They then transferred C. niei and C.
illdefina to Heterocapsa based on these common characters
with two new nomenclatural combinations, H. niei (Loe-
blich III) Morrill et Loeblich III, and H. illdefina (Herman
e t Sweeney) Morrill et Loeblich III (Morrill & Loeblich III
1981). Since their proposal of these taxonomic combina-
tions, the genus Cachonina has been considered to be a ju-
nior synonym of Heterocapsa (Morrill & Loeblich III 1981,
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 (8a.s., r.s., l.a.s., l.p.s., [? a.a.s. and p.a.s.] p.s.), 5", 2". They might exist between the scales of each species.

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 & 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. illidifera*, 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.


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. quinquecuspis*, *H. kollmeriana*, and *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 amphiesmal 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. illedefina* (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.
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. triqueta* 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 characters, 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. pseudotriqueta* 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-

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