Taxonomic interrelations of holothurians *Cucumaria frondosa* and *C. japonica* (Dendrochirotida, Cucumariidae)

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Abstract

Morphological features, distribution, ecology and some of the chemical characters of *Cucumaria frondosa* and *C. japonica* are described. The two species are well distinguished by the spicule-shaped body wall, the structure of the introvert, tentacles and ambulacral podia, the colour of internal organs, the size of ova and the chemical structure of triterpene glycosides. The data points to the taxonomical independence of these species. Previous opinion that *C. japonica* is a subspecies of *C. frondosa* is not supported.

1. Introduction

Cucumaria frondosa and *C. japonica* belong to the largest and most abundant order of holothurians, order Dendrochirotida, and have great commercial value (especially *C. japonica*). Their systematic relations and biology are described in numerous publications, yet their taxonomic relations are still disputed.

Species independence of *Cucumaria japonica* has been repeatedly doubted since Britten (1906–1907). Many scientists considered *C. japonica* as a sub-species of *C. frondosa* (Saveljeva, 1941; Lambert, 1984) or a variety (Mortensen, 1932; Panning, 1949; 1955).

Mortensen (1932, p. 45) suggested that '...it may be rather a matter of personal choice whether *C. japonica* should be regarded as a separate species or only as a variety of *C. frondosa.* However, new data, important for the taxonomy of the two species, has emerged. These data include a new type of information – chemical composition of triterpene glycosides, helpful for solving taxonomic problems (Kalinin *et al.*, 1994). This helps the present understanding of the taxonomic relations between *C. frondosa* and *C. japonica.*

2. Material

Material examined includes original samples of *C. japonica* from different areas of the Peter the Great Bay (Japanese Sea), the Busse lagoon and the Gulf of Aniva (Sakhalin Island); original samples of holothurians preliminary identified as *C. japonica* from east and west Kamchatka; the collection at the Zoological Institute (St Petersburg) from the Kuril and Commander Islands (several thousand specimens in total); holothurians preliminarily identified as *C. frondosa japonica* from the west coast of Canada and the Aleutian Islands (the Royal Museum of British Columbia, Victoria, Canada – 12 specimens); and original collection from the Barents Sea (mainly from the Kanin area and the Seven Islands – several hundred specimens).

3. Comparison of *Cucumaria frondosa* and *C. japonica*

3.1. Gross morphology

In external appearance there is practically no difference between *C. frondosa* and *C. japonica.* The body of these holothurians is dense, cylindrical or barrel-shaped, slightly curved dorsally, especially in live animals, with a rounded or slightly stretched posterior end. The body is almost globular when the animals contracts.

The tube feet are large and retractile; in adults they are located usually on the ventral radials in two to four rows. On the dorsal side, the tube feet are smaller and very often transformed into papillae. The tube feet location varies greatly: in some specimens there are few feet and they are absent in the middle part of the body, even on the radii. In other animals, the feet are found and located in the interradii. In general, the tube feet location has no taxonomic value. In young holothurians the tube feet are spread in more regular bands, either in zigzags or in single rows. Tentacles are 10; they are large and similar in size, however two ventral tentacles can be smaller.

Data on the size of cucumarians are rather conventional since it depends greatly on the degree of the body contraction. For *C. japonica* maximum known

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length is 40 cm, whereas for *C. frondosa*, maximum known length is 50 cm (Deryugin, 1915), but most animals are much smaller (≈ 20 cm). Body mass of large animals comes up to 1.5–2.0 kg, but average weights are 500 g.

The colour of the body varies greatly: dark brown, dark purple, brown, greyish, yellowish, with the dorsal side clearly lighter. Completely white animals in both species are known; in some populations of *C. japonica* the ratio of white animals is large.

The structure of viscera is also similar. The body wall is thick and its mass constitutes up to 20 per cent of the total mass of the animal. We failed to find difference in the form, location and dimension of the stone canal, retractor muscles, polian vesicle, gonads and other structures, only the attachment of mesentery is an exception (see below).

In both species a strong reduction (up to absence) of body spicules is typical in the adults. Spicules are found more often in the posterior end of the body. The literature often mentions that spicule reduction is more expressed in *C. frondosa* than in *C. japonica*, however our observations did not confirm that: this character is strongly variable in both species.

Spicule changes during somatic growth are similar in *C. frondosa* and C. *japonica.* Spicules in *C. frondosa* are mainly round plates with regular perforations. The plate edge is smooth or slightly wavy; in large specimens the plates may have a spinous edge and rounded knobs on the surface. Buckle-shaped plates with four perforations are also found (Edwards, 1910a, pl. 13, fig. 8–11; Deichmann 1930, pl. 12, fig. 6–9). Spicule changes during somatic growth in C. j*aponica* are discussed in detail by Levin and Gudimova (1997 a, b).

The difference between spicules in young and adult specimens is so great that juvenile *C. frondosa* is often considered as a separate species, usually as *C. fucicola* (McKenzie, 1991). At the same time, spicules in young cucumarians can be similar to those in adults of another species and even genus. Thus, some plates of young *C. japonica* are almost identical to spicules of *Leptopentacta sachalinica.*

Similarities also exist in the type of spicules in adult cucumarians. Some spicules are almost rectangular plates with numerous regularly-located perforations: large holes are closer to the narrow end, whereas small ones are at the opposite, usually more spinous end (according to Panning these are *japonica*-type spicules). Besides, there are plates with more or less developed processes and irregularly located perforations (*frondosa*-type after Panning).

The calcareous ring of *C. frondosa* and *C. japonica* has a typical form, as all the species of the genus *Cucumaria*, with radial pieces lacking posterior processes. Radial and interradial pieces of the ventral side do not merge. The ring is very flexible owing to the mobile joint of the pieces and their elasticity. The form of the pieces varies greatly depending on the state of the animals before preparations and their age (Levin & Gudimova, 1997b).

Therefore, the calcarous ring is of no taxonomic value for this genus. The degree of development of the calcareous ring in the two species also varies with age and between individuals.

Based on the features discussed, some of the authors distinguished between *C. frondosa* and *C. japonica.* However, according to our data the range of variation is interspecific. At the same time, a number of important features vary greatly between *C. frondosa* and *C. japonica.*

3.2. Spicules

Cucumaria frondosa

Body wall – Irregular, square, rounded or slightly elongated perforated plates. Some spicules bear processes and lobes of various shapes. The surface of plates is either smooth or scattered with spines. In the central part of the plates, especially in large ones, an irregular perforated process is often formed. Plates are 170–320 µm in size.

Introvert – The plates are elongated or irregular, with a smooth or spinous margin. Usually plates have two to three layers with pronounced irregular central process. Plate size ranges from 160 to 370 µm (see Fig. 1, next page).

Tentacles – The tentacle spicules in large specimens are complicated, often with a secondary meshwork; some also are straight or curved rods, sometimes with single holes present. The surface of both types of spicules is with knobs. The size of plates ranges from 160 to 350 µm (Fig. 1).

Tube feet – Spicules are wide plates, with one end narrow and usually bearing round processes, and the other end notched or spinous. The endplate in adults is always complex and is formed by numerous (up to 70) small plates and rosettes. Figures of spicules of *C. frondosa* are given in Edwards (1910a, pl. 13, fig. 8–19; 1910b, pl. 19, fig. 2–4); Cherbonnier (1951, pl. 16, 17); Panning (1955, Abb. 1, 2).

Cucumaria japonica

Body wall – Mainly elongated perforated plates with a spinous edge and one end usually narrowing. Round irregular and triangular plates are also common. Perforations are numerous and round. The surface is covered with knobs or spines. The size of plates ranges from 190 to 280 µm (Fig. 2).

Introvert – Usually the spicules are perforated plates of different shapes with a notched margin. Spicules become thicker during development; 'bridges' and spinous projections may appear on the surface (at any place of file plate, not only in file centre, as shown by Ohshima, 1915). Elongated plates during development may transform into 3-dimensional, perforated spindle-like or conical structures (Fig. 2).

Tentacles – Three main spicule forms were found in the tentacles: 1) Elongated plates with double-sided or unilateral central bulb. The size of these plates is 240–320 µm; 2) Small, thin perforated plates of different shape and a size of 80 to 120 µm; 3) Large, elongated massive plates with a smooth surface or 3-dimensional meshwork of projections in the centre; and a size of 300 to 420 µm.

Tube feet – Spicules resemble those of the body wall, but are smaller. In the original description of *C. japonica* Semper (1866) pointed to very large plates with numerous small perforations radially spread around the cloacal opening. These types of spicules are absent in *C. frondosa.* These plates were also noticed by Augustin (1908) and Edwards (1910b, pl. 19, fig. 16), however other authors (Britten, 1906-1907; Mitsukuri, 1912) failed to find them. In our material, these plates were absent. Illustrations of spicules of *C. japonica* are given in: Semper (1868, Taf. 39, Fig. 18), Edwards (1910a, pl. 19, fig. 150, Mitsukuri (1912, fig. 48), Djakonov *et al.* (1958, fig. 2) and Baranova (1971, fig. 1).

3.3 Mesentery attachment

In *Cucumaria frondosa* the intestine mesentery passes from the anterior end in the dorsal interambulacrum, crosses the left dorsal and ventral longitudinal muscles (being perforated by the retractors), and finally runs along the left side of the midventral muscle and its median line to the cloaca (Deichmann, 1930; personal observations). In *C. japonica*, the attachment of mesentery in file posterior part of the body is significantly different: the mesentery crosses the midventral muscle at the basis of a correspondent retractor, then forms a loop in the interradius and approaches the cloaca along the median line of the midventral muscle (Fig. 3).

3.4. Colour of visceral organs

The colour of some visceral organs differs greatly between the two species, as shown in the following table.

Visceral organs	*C. frondosa*	*C. japonica*
Stone canal	Bright-red	Light-orange
Madreporite	Pink	Light-orange
Polian vesicle	Orange	Pink
Female gonad	Dark red, brownish	Dull-green
Eggs	Bright or cherry red	Green

3.5 Reproductive system

Significant differences are found between the female reproductive organs in the two species. Besides the difference in coloration of gonads and eggs, there is also a significant difference in file egg size between *C. frondosa* and *C. japonica:* the ripe oocytes reach 875–900 µm and 500–600 µm, correspondingly. The gonads in both *C. frondosa* and *C. japonica* are composed of two tufts of tubules.

3.6 Chemical composition

The chemical composition of specific triterpene dycosides in *C. frondosa* and C. *japonica* indicate (Kalinin *et al.*, 1994) that the general feature of these compounds is the presence of pentasaccharide branched at the second monosaccharide link (quinovose) of carbohydrate chain, the sulphate group in the position 4 of the xylose residue and 7(8)-double link in aglycone. For *C. japonica* the composition of 11 dycosides (cucumariosides) has been described. Cucumariosides contain glucose as the third monosaccharide residue of carbohydrate chain and the 16-ketogroup in the aglycone. The main component of the glycoside sum of *C. japonica* is cucumarioside A_2-2. The glycosides of *C. frondosa*, in contrast to those of *C. japonica* are frondosides, and they contain xylose in the carbohydrate chain and 16-beta-acetate in the aglycone. The main component of the glycoside fraction in *C. frondosa* is frondoside A (Fig. 4).

3.7 Distribution

C. frondosa is widely distributed in the Arctic region: it is known from the Hardanger fjord in the Norwegian Sea to the Novaya Zemlya and Franz Joseph Land in the Barents Sea, and in the southwestern part of the Kara Sea (probably farther to the east, although no reliable data are available). Near the British Isles it is known in the North Sea,

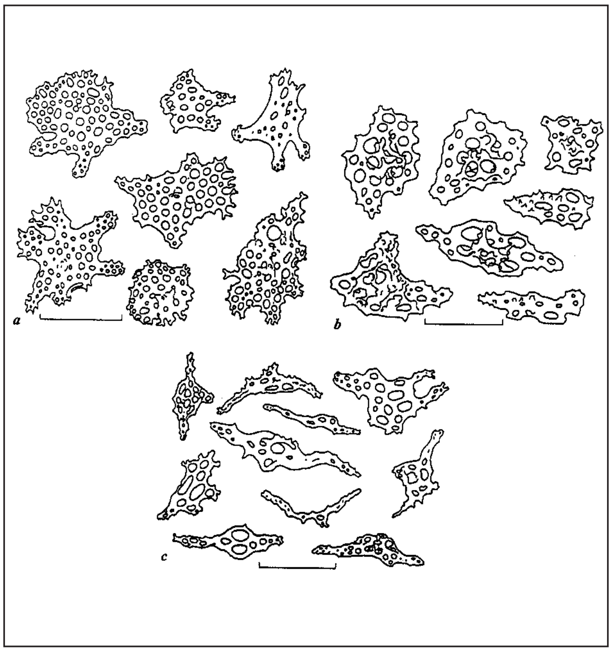

Figure 1.

Ossicles of *Cucumaria frondosa*:
a - body wall; b - introvert; c - tentacles.
Scale bar = 200 µm

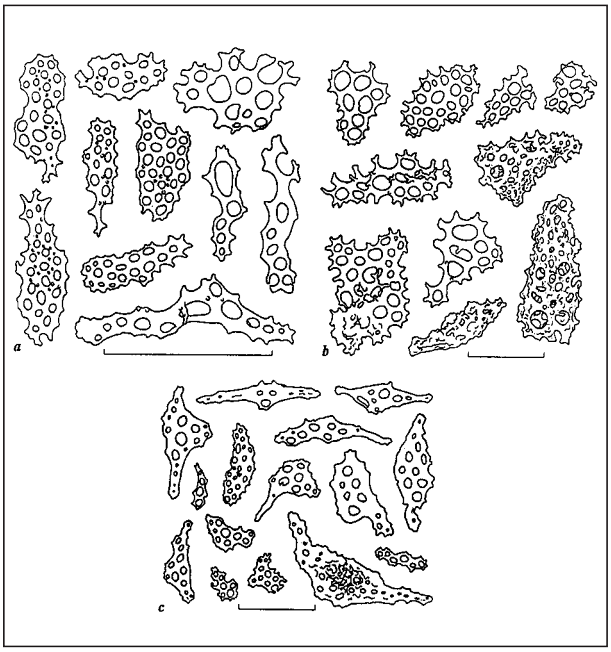

Figure 2.

Ossicles of *Cucumaria japonica*:
a - body wall; b - introvert; c - tentacles.
Scale bar = 200 µm

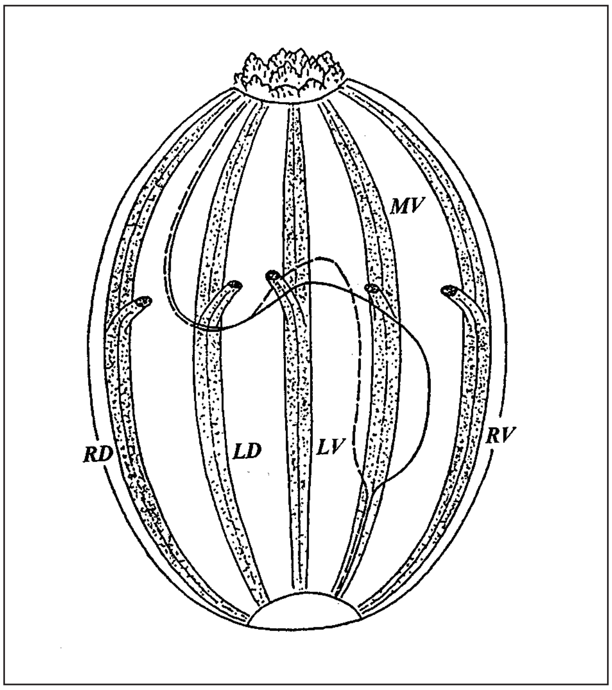

Figure 3.

Arrangement of mesentry in *Cucumaria frondosa* (solid line) and *C. japonica* (broken line).
Radii: LV - left ventral; RV - right ventral;
MV - midventral; LD - left dorsal; RD - right dorsal.

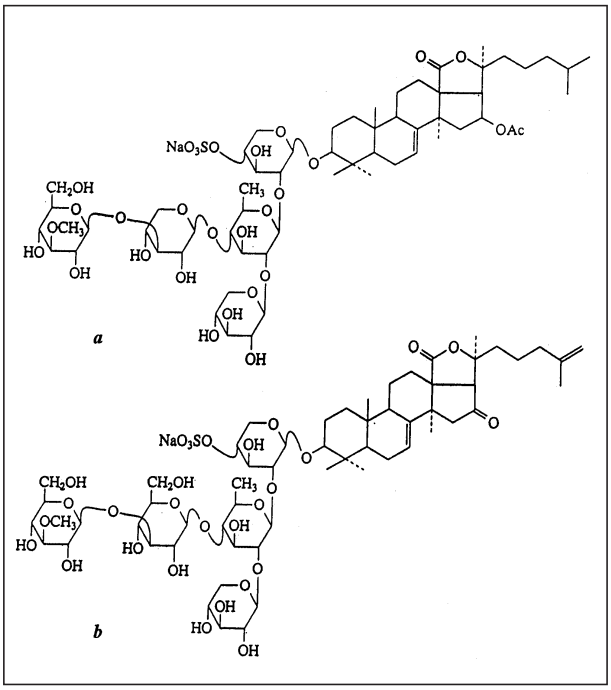

Figure 4.

Structure of triterpene glycosides:
a - frondoside A from *Cucumaria frondosa*;
b - cucumarioside A_2-2 from *C. japonica*

up to Dogger-bank in the south and near the Shetland and Orkney Islands. This species was earlier observed near the west coast of Scotland and Hebrides as far south as the Clyde, however, there is no recent data (McKenzie, 1991). In North America, the southern border of its distribution is the Cape Cod Peninsula and Nantucket Island (Edwards, 1910a; Smith *et al.*, 1964).

The report on species occurrence in Florida (Pourtalés, 1869) is obviously erroneous (see Deichmann, 1930). Semper (1868) has described *C. frondosa* var. *mediterranea*. Since there were no other data on species occurrence in the Mediterranean and the description was based on the museum specimens, it is not reliable.

In the Pacific, *C. frondosa* has been observed by Ayres (1855), but this record was questioned by Verrill (1867), Ludwig (1901) and Clark (1904). Edwards (1910a) indicated in 1907 that this species was reported from the west coast of North America; however, after studying a large collection from the National Museum he came to the conclusion that at least four species, similar but not identical to *C. frondosa*, inhabit the Pacific Ocean. One of them is *C. japonica*, although the specimen identified under this name by Lampert (1885), Clark (1904) and Edwards (1907) appeared to belong to *C. miniata* Brandt.

C. japonica. In the literature, the species range of *C. japonica is* usually given as the northeastern part of the Yellow Sea; the northeastern coast of the Honshu Island; along the continental coast of Russia in the Sea of Japan; the Sea of Okhotsk, the Kuril Islands, the Kamchatka Peninsula; and in the Bering Sea at least to the north of Kamchatka; near the Commander Islands; and along the northwestern coast of North America, from Sitka Island to Vancouver Island (Baranova, 1957, and others). However, according to present data, the real range of this species is much smaller.

The early opinion that this species is distributed up to the Bering Sea is apparently erroneous, as noticed first by Baranova (1980) who assumes that specimens from the north Kuril Islands and Kamchatka, earlier referred to as *C. japonica*, in fact belong to two new species: *C. savelijevae* (Paramushir Island, Shumshu Island, Achomten Bay on the east coast of Kamchatka) and *C. djakonovi* (Cape Olutorsky, Bering Island, in the Bering Sea,). Species composition and distribution of *Cucumaria* from the north Kuril Islands, Kamchatka, Commander Islands, Aleutian Islands and western Alaska appeared to be very complicated. The taxonomic status and the species range of *C. savelijevae* and *C. djakonovi* remains unknown (material is in work), although we agree with Baranova that large *Cucumaria* from this region are not *C. japonica*. Our preliminary results have shown that this species does not occur to the north of southern Kuril Islands.

The presence of *C. japonica* to the south of Sendai is unlikely. Sluiter's report of this species in the Molucca Strait has been most likely a mistake as was first noticed by Mitsukuri (1912).

C. japonica has been reported from the coast of northeast Pacific (Clark, 1902; Edwards, 1907; Baranova, 1971). Some authors, in particular Lambert (1984), believe that the species occurring south from Alaska, near the Vancouver peninsula, is *C. frondosa japonica*.

However, examination of specimens of '*C. japonica*' has revealed erroneous identification. '*C. japonica*' collected near Sitka Island, Alaska (Clark, 1902) appeared to be *C. miniata* (Brandt) (Mortensen, 1932). Specimens from the Royal British Columbia Museum (Canada), identified as *C. frondosa japonica*, appeared to be neither *C. frondosa* nor *C. japonica*. Thus, it is almost certain that *C. japonica* does not occur near the coast of America.

It is much more difficult to interpret the record by Mortensen (1932) of *C. japonica* (he considered this species a variety of *C. frondosa)* from the high-Arctic, near the northwestern coast of Greenland (Thule-Jones Sounds and Devis Strait). Taking into account a great number of intermediate forms between *C. frondosa* and *C. japonica* recognised by this author, it can be suggested that the specimens of *C. frondosa* from Greenland have an increased number of the *japonica*-type plates. Recent data have shown a possible parallelism of morphological features in the populations of the two species inhabiting the area of extreme temperatures, north-west Greenland and Kamchatka. Ecophysiological interpretation of this phenomenon has been suggested by Kafanov (1977; pers. comm.).

3.8 Ecology

C. frondosa and *C. japonica* live in similar conditions. They are known from the intertidal zone down to approximately 300 metres depth, with the peak in abundance at depths of 30 to 60 metres. Juveniles prefer kelp forests and shallow areas warmed up in the summer. Adults keep in relatively open and deeper water, on the loose gravel, shell debris, rocks or mud. In general, any solid substrate may be utilised if other conditions are favourable. The lower temperature range for both species is –1.8°C; upper temperature range is about +18.0°C for *C. japonica*, and about +8.0°C for *C. frondosa*.

Thus, the data show that *C. frondosa* and *C. japonica* are well-defined separate species. The synonymy summarising the data discussed is as follows:

Cucumaria frondosa (Gunner, 1767)

Holothuria frondosa Gunner, 1767: 114, t. 4, fig. 1-2; Muller O.F., 1788: 36;
- *pentactes* Fabricius, 1780: 352; Muller O.F., 1776: 71, t. 1; 1788: 36, pl_. 31, fig 8;
- *grandis* Forbes and Goodsir, 1839: 647;
- *fucicola* Forbes and Goodsir, 1839: 647 (erroneous *fusicola*)

Pentacta frondosa Jaeger, 1833: 12;
Cucumaria fusicola Forbes, 1841: 227;
Botryodactyla grandis Ayres, 1851: 52;
- *affinis* Ayres, 1851: 145.

Cucumaria frondosa Forbes, 1841; 209; Selenka 1867: 347; Semper, 1868: 234-235 (excepted *T. frondosa* var *mediterranea);* Norman, 1869; 316; Ludwig, 1901: 141; Michailovskij, 1904: 463, 1904: 159; H. Clark, 1904: 564; A. Clark, 1920: 12; Edwards, 1910a: 333-358, pl. 13, figs. 1-26; Hérouard 1923: 108, taf. 7, fig. 5, 6; Mortensen 1927: 398-399, fig. 236; Koehler, 1927 : 151, pl. 14, fig. 12a-c, Deichmann, 1930: 161-162, pl. 12, fig. 6-9; Gorbunov, 1932: 96; Engel 1932: 61, fig. 23, 24; Djakonov, 1933: 141, fig. 71B; Grieg, 1935: 7; Keys…, 1948, tab. 123, fig. 5; Ivanov *et al.*, 1946: 580-586, fig. 782-788, colour tab. (anatomy); Panning, 1949: 417-418 (partly), Abb. 4; 1955: 34-38 (partly), Abb. 1, 2; Ivanov & Strelkov, 1949: 39-41, tab. 28, fig. A-G, Cherbonnier, 1951: 37, pl. 16, fig. 1-23, pl. 17, fig. 1-10; Smith *et al.*, 1964: 188; Rowe, 1970: 683, 686; Baranova, 1977: 439-440; Pawson, 1977: 7; Ivanov *et al.*, 1985: 339-348, fig. 342-349 (anatomy); McKenzie, 1991: 146-147, fig. 8d; Gudimova & Denisenko, 1995: 1-44; Gudimova, 1998: 453-528 (non Pourtalés, 1869; non Edwards, 1907).

Non *Pentacta frondosa* Ayres, 1855; non *C. frondosa* var. *mediterranea* Semper, 1868; non *C. frondosa japonica* Lambert, 1984.

Cucumaria japonica Semper, 1868

Cucumaria japonica Semper, 1868: 236, Taf. 39, Fig. 2, 3, 7, 18; Lampert, 1885: 143; Theel, 1886: 110; Ludwig, 1901: 143; Britten, 1906 (1907): 133-135; Augustin, 1908: 25-26, fig. 18; Edwards, 1907: 61, 1910b: 603-604, pl. 19, fig. 1516, Mitsukuri, 1912: 242-246, pl. 8, figs. 67, 68, textfig. 48; Oshima, 1915: 255; Saveljeva, 1933: 44; Djakonov, 1938: 484; 1949: 70-71; Djakanov *et al.*, 1958: 266-268, fig. 1, 2; Panning, 1949: 417-418 (partly), Abb. 4, 1955: 34-38 (partly), Abb. 1, 2; Pogankin 1952: 183 (ecology); Ushakov, 1953: 298 (distribut., partly); Strelkov, 1955: 217, Tab. 64, fig. 1; Baranova, 1962: tab. 1 (distribut.); 1971: 243-245; 1976: 115, fig. 266; 1980: 109-120 (comparison); Djakonov *et al.*, 1958: 367; (non Lampert, 1885; non Baranova, 1957).

C. frondosa japonica Saveljeva 1941: 80; (non Lambert 1984). *C. frondosa* var. *japonica* Mortensen, 1932: 44-48, 52; Panning 1949: 417-418 (partly), Abb. 4; 1955: 34-38 (partly);.

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