

Critical review of Pseudocucurbitidae (Miliolina, Foraminifera) from the Late Triassic reef environments of the Tethyan area

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ABSTRACT – The Late Triassic foraminiferal genera *Amphorella*, *Spiriamphorella*, *Urnulinella*, *Pseudocucurbita*, *Paratintinnina*, *Costifera* and *Siculocosta* are considered junior synonyms of the genus *Cucurbita*. Consequently, the number of families of the Milioliporacea (Miliolina) is significantly reduced. The valid species of the genus *Cucurbita* are considered to be *Cucurbita infundibuliforme* Jablonský, 1973, *C. subsphaerica* (Borza & Samuel, 1977a) comb. nov., *C. longicollum* Senowbari-Daryan, 1983, *C. battagliensis* (Senowbari-Daryan, 1983) comb. nov., *C. cylindrica* (Senowbari-Daryan, 1983) comb. nov. and *C. floriformis* (Altiner *et al.*, 1992) comb. nov.. *J. Micropalaeontol.* 31(2): 179–186, July 2012.

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INTRODUCTION

A Late Triassic expansion of modern-type reefs (Flügel, 2002; Stanley, 2003; Bernecker, 2005; Kiessling, 2010) provided a wide range of habitats occupied by benthic foraminifera. Calcareous forms with barrel-shaped chambers positioned in an irregular line and having funnel-shaped apertures are regularly present in reefs of the Tethyan (e.g. Borza & Samuel, 1977a; Zaninetti *et al.*, 1982a, b; Senowbari-Daryan, 1983, 1986, 1987; Miconnet *et al.*, 1983; Di Stefano *et al.*, 1990; Bernecker, 1996; Bérczi-Makk, 1996; Senowbari-Daryan & Flügel, 1996; Martini *et al.*, 2004, 2009; Carillat & Martini, 2009) and Panthalassan (Chablais *et al.*, 2011) domains. The first generic name for this type of foraminifera was introduced by Jablonský (1973). In the following years, a multitude of new genera were introduced by several authors (Borza & Samuel, 1977a, b, 1978; Senowbari-Daryan, 1983, 1993; Senowbari-Daryan & Zaninetti, 1986), followed by as many revisions (see reviews by Senowbari-Daryan, 1983, 1993; this work). The final outcome is a somewhat confusing array of genera, subfamilies and families. According to the latest suprageneric revision (Zaninetti *et al.*, 1992) the foraminifera in question belong to several families of the Milioliporacea superfamily – Costiferidae, Siculocostidae, Siphoniferidae and Pseudocucurbitidae – with the family Spiriamphorellidae only questionably assigned to the same superfamily. In this paper, we aim to present a complete review of the past research on these reef-dwelling foraminifera. We then critically assess genera and species. The final outcome is the removal of several genus and species names. The new suprageneric classification differs considerably from previous classifications, is much simpler and biostratigraphically significant.

PREVIOUS RESEARCH

At the beginning of a long line of research and taxonomic debate on reef-dwelling foraminifera (see also reviews by Senowbari-Daryan, 1983, 1993) stands Jablonský (1973) with the description of the new genus *Cucurbita* (type species *Cucurbita infundibuliforme* Jablonský, 1973) from the Carnian (originally Cordevolian) beds of the Western Carpathians. Jablonský believed that cylindrical forms ending in a wide funnel represent individual species that form non-obligatory groups in colonies. The suprageneric position of his new genus was at the time unknown, but Jablonský (1973) believed it to be related to tintinnids.

Borza & Samuel (1977a) later introduced three new genera and nine new species *incertae sedis* from the Carnian and Norian strata of the Western Carpathians. As already mentioned by Zaninetti (1977), Zaninetti & Altiner (1981) and Zaninetti *et al.* (1982a), they failed to recognize different sections of the same form. Instead, they attributed different shapes and numbers of chambers to different evolutionary stages. To recapitulate, their first genus, *Amphorella*, was seen to consist of two chambers, the first smaller than the second. In *Spiriamphorella*, the evolution was thought to progress with an enlargement of the first chamber and reduction of the apertural neck. A spirally coiled initial part of the test was also recognized. The multilocular forms were referred to a third genus, *Urnulinella* (Borza & Samuel, 1977a). The new species they created, *Amphorella bicamerata* (subspecies *A. bicamerata bicamerata*, *A. bicamerata intermedia*), *A. bilongicamerata* (subspecies *A. bilongicamerata bilongicamerata*, *A. bilongicamerata minuta*), *A. lageniformis*, *A. subsphaerica*, *Spiriamphorella carpathica* (subspecies *S. carpathica carpathica*, *S. carpathica gemerica*), *S. rectilineata* (subspecies *S. rectilineata rectilineata*, *S. rectilineata districta*), *S. ovata*, *S. irregularis*, and *Urnulinella andrusovi*, were distinguished by the shape and size of their chambers, necks and caudal processes (Borza & Samuel, 1977a). Borza & Samuel (1977a) did not recognize the similarity of the individual chambers of their genera and species with *Cucurbita* Jablonský, 1973. However, they recognized this similarity for a fourth new genus, introduced (but not formally described until later!) in a separate paper in the same volume (Borza & Samuel, 1977b). According to that paper, *Paratintinnina tintinniformis* and *P. tulipaformis* were supposed to differ from *Cucurbita infundibuliforme* Jablonský in a ‘single-walled test in the collar part, and in the test surface which is – in contrast to *C. infundibuliforme* – smooth, without uneven projections (except the caudal projection)’ (Borza & Samuel, 1977b, p. 144) and in ‘having lesser dimensions of the test and wider dimension of the collar’ (Borza & Samuel, 1977b, p. 145), respectively.

Zaninetti (1977) almost immediately recognized the genera *Amphorella*, *Spiriamphorella* and *Urnulinella* as different sections of the same genus. However, she believed that they belong to the foraminiferal genus *Galeanella* Kristan, 1958 (indeed, in our experience, oblique sections of this genus cannot be distinguished

from single-chamber sections of these genera). She thus placed part of the thirteen species and subspecies of Borza & Samuel (1977a) into the synonymy of *Galeanella panticae* Zaninetti & Brönnimann in Brönnimann *et al.*, 1973 (see Brönnimann *et al.*, 1973 for comparison), *Galeanella? carpathica* (Borza & Samuel, 1977a) and *Galeanella? districta* (Borza & Samuel, 1977a). Zaninetti (1977) considered the latter two species valid and distinct species of the genus *Galeanella* (the question mark denotes the lack of pores due to the recrystallization of the wall). Certain subspecies and species were further considered to be too obliquely cut to receive species attribution. For the same reason, i.e. an unsuitable orientation, she marked *C. infundibuliformis* [sic] as *nomen dubium non conservandum* and placed the genus *Cucurbita* in the synonymy of the older genus *Galeanella*. Note, however, that Zaninetti (1977) did so in the belief that Jablonský's (1973) specimens also belong to the genus *Galeanella*.

In 1978, from the same locality as in 1977, Borza & Samuel described another new genus with four new species, which they again placed into *incertae sedis*, i.e. *Pseudocucurbita* (with species *Ps. globosa*, *Ps. subglobosa*, *Ps. campanulaformis* and *Ps. fusani*). They considered the new genus as a unilocular form. Gaździcki *et al.* (1978) followed Zaninetti's (1977) opinion but considered Jablonský's (1973) species as valid; they placed *Galeanella? infundibuliforme* among the foraminifera. Samuel & Borza (1981) validly described the genus *Paratintinnina*, introduced in Borza & Samuel (1977b). They declined the attribution of their (Borza & Samuel, 1977a, b, 1978) species to the genus *Galeanella* because of the lack of perforations and the different type of morphology. They also proposed the important notion that *Paratintinnina*, *Amphorella*, *Cucurbita* and *Pseudocucurbita*, but not *Urnulinella*, belong to the same higher taxonomic unit. The attribution to foraminifera was still considered too uncertain. Zaninetti & Altiner (1981) made another revision of the genera and species described at the time and removed *Spiriamphorella* (pars) from the synonymy of *Galeanella* because of its lack of pores. They viewed *Spiriamphorella* as a possible evolutionary link between *Ophthalmidium* and *Galeanella* (see also Zaninetti & Altiner, 1982) and considered its attribution to Milioliporidae questionable. The genera *Amphorella*, *Urnulinella*, *Pseudocucurbita* and part of the *Spiriamphorella* material were retained within the genus *Galeanella*: (1) *A. subsphaerica*, *S. irregularis* and *U. andrusovi* as synonyms of *G. panticae*; (2) *Ps. globosa*, *Ps. subglobosa*, *Ps. campanulaformis* and *Ps. fusani* as synonyms of *G. globosa*. The genus *Spiriamphorella* (synonyms *Cucurbita*, *Paratintinnina* and partly *Amphorella*) was taken to contain the species *S. carpathica* (synonyms *S. carpathica gmerica*, *S. rectilineata rectilineata*, *G.? carpathica*) and *S. districta* (synonyms *S. rectilineata districta*, *S. ovata* and *G.? districta*). As in Zaninetti (1977), certain species and subspecies could not be placed in either of the genera because of the randomness of the sections (Zaninetti & Altiner, 1981). Sadati (1981) reconstructed *S. districta* based on various sections of the test.

New Carnian reef material from the Taurus in Turkey stimulated Zaninetti and co-authors to make further revisions of this group of foraminifera (Zaninetti *et al.*, 1982a). The family Milioliporidae has been revised and divided into three subfamilies on the basis of perforations, the shape of the aperture, the general test morphology and the presence/absence of a secondary material enveloping and partly supporting the chambers ('secondary thecal mass'). The genus *Spiriamphorella* (with synonyms ?*Cucurbita*, pars *Amphorella*, *Paratintinnina*) was doubtfully placed in

Milioliporinae. Genera ?*Cucurbita*, *Spiriamphorella* (pars) and *Urnulinella* were considered junior synonyms of *Galeanella* of the subfamily Galeanellinae. *Galeanella irregularis* (former *Spiriamphorella*) joined the list of valid *Galeanella* species (already in Zaninetti & Altiner, 1982), with *Urnulinella andrusovi* considered its junior synonym. Their material also allowed the recognition of perforations. The genus *Pseudocucurbita* Borza & Samuel, 1978 was again made available, emended and put into the new subfamily Pseudocucurbitidae. It was distinguished from *Galeanella* on the basis of a thinner wall and distal narrowing of chambers, a wide collar and the presence of the 'secondary thecal mass' enveloping and partly supporting the chambers. The genus *Pseudocucurbita* was taken to contain one valid species, i.e. *Pseudocucurbita subsphaerica* (formerly *Amphorella*), with junior synonyms *Ps. globosa*, *Ps. subglobosa*, *Ps. fusani* and *Ps. campanulaformis*. Perforations were found in the wall and in the 'secondary thecal mass' as well (Zaninetti *et al.*, 1982a).

Although the publication appeared at a later date, Senowbari-Daryan (1983; submitted in 1982) did not consider the opinions expressed in Zaninetti *et al.* (1982a, b). Nevertheless, Senowbari-Daryan's (1983) work represents an extremely important contribution to the study of this type of foraminifera, as a large amount of material from the Upper Triassic of Greece, Sicily and Slovenia had been investigated. Several important points were made. Senowbari-Daryan (1983) rejected the name *Cucurbita* because it was supposed to be preoccupied by a bivalve. As *Pseudocucurbita* was considered synonymous with *Cucurbita*, it became its valid substitute as the next available name. Furthermore, the genus description was emended and several taxa from Borza & Samuel (1977a, b, 1978) were assigned to it. Of the already described species, Senowbari-Daryan (1983) considered as valid taxa *Pseudocucurbita infundibuliformis* (synonyms *C. infundibuliformis* [sic], *Ps. globosa*, *Ps. subglobosa*, *Ps. campanulaformis*, *Ps. fusani*), *Urnulinella andrusovi* (synonym *Amphorella subsphaerica*), *Spiriamphorella carpathica* (synonyms *S. carpathica carpathica*, *S. carpathica gmerica*, *S. rectilineata rectilineata*), *Spiriamphorella districta* (synonym *S. rectilineata districta*) and *Spiriamphorella ovata*. New species introduced for the genus *Pseudocucurbita* were *Ps. longicollum*, *Ps. laticollaris* and *Ps. brevicollum*. The new genus and species *Hydrania dulloi* was introduced. This species has chambers similar to those of taxa known previously, but with markedly different construction, with chambers added at a 90° angle to form a square test. The distinguishing character of the new genus *Costifera* is the presence of costae. Its construction is otherwise the same as that of *Pseudocucurbita sensu* Senowbari-Daryan (1983). The new species *Costifera cylindrica* and *Co. battagliaensis* were distinguished on the basis of the size and shape of the chambers and smooth or rugged chamber outline (i.e. the wall directly passes into costae or is separated from costae by a smooth line) (Senowbari-Daryan, 1983). *Costifera battagliaensis* also has a greater number of more closely spaced costae. Finally, the third new genus of Senowbari-Daryan (1983), *Siphonophora* (with new species *Si. pilleri*), differs noticeably from other known species in having a test constructed of a single tube, at first streptospirally enrolled, later uncoiled and surrounded by 'ringlike chambers' (Loeblich & Tappan, 1987).

Miconnet *et al.* (1983) questioned the assignment of the species '*Ps.*' *longicollum* and '*Ps.*' *brevicollum* to the genus *Pseudocucurbita* due to the lack of proof for the presence of the 'thecal mass'. They suggested that these species should occupy a position among the

Ophthalmidiinae rather than Pseudocucurbitinae. *Pseudocucurbita infundibuliformis* was, in their opinion, *Ps. subsphaerica*, and *U. andrusovi* should be put in synonymy with *G. irregularis*.

In 1986, Senowbari-Daryan & Zaninetti (p. 82) considered *Costifera battagliaensis* the type species of their new genus *Siculocosta* based on 'longitudinal ribs not separated from the test by distinct wall'. The same authors also proposed a new suprageneric classification, subdividing Miliolacea into five families: (1) Nubeculariidae (subfamilies Nubeculariinae, Nodobaculariinae, Ophthalmidiinae, Spiriamphorellinae nov. subfam., and Costiferinae, nov. subfam.); (2) Pseudocucurbitidae (rank elevated from subfamily); (3) Milioliporidae (subfamilies Milioliporinae, Galeanellinae); (4) Siphoniferidae; and (5) Altinerinidae. The genera in question have been placed in the following subfamilies/families: *Hydrania* in Ophthalmidiinae, *Spiriamphorella* in Spiriamphorellinae, *Costifera* and *Siculocosta* in Costiferinae, *Pseudocucurbita* in Pseudocucurbitidae, and *Siphonofera* in Siphoniferidae.

Senowbari-Daryan (1986) demonstrated the occurrence of spines in well-preserved specimens of *Pseudocucurbita infundibuliformis* from Sicily. The perforated 'secondary thecal mass' reported by Zaninetti *et al.* (1982a) was considered the result of sediment entrapment between the spines.

Loeblich & Tappan (1987) further modified the suprageneric classification of Senowbari-Daryan & Zaninetti (1986) by retaining Milioliporidae and Siphoniferidae at the family level but degrading Altinerinidae and Pseudocucurbitidae to the subfamily level under family Milioliporidae. The family Nubeculariidae, retaining subfamilies Costiferinae and Spiriamphorellinae, was moved under the superfamily Cornuspiracea. *Hydrania* was placed among Ophthalmidiidae (superfamily Cornuspiracea). Genus *Cucurbita* was again declared valid because the mollusc name was considered a *nomen nudum*. However, the subfamily name retained the name Pseudocucurbitinae due to the ICZN rule (Loeblich & Tappan, 1987).

In 1992, Loeblich & Tappan elevated Costiferinae to the rank of family. Costiferidae and Nubeculariidae were placed in the superfamily Nubeculariacea (Loeblich & Tappan, 1992).

Zaninetti *et al.* (1992) offered a new proposal for the division of Miliolina. The subfamilies listed above were elevated to the family rank and two new families were introduced – Hydraniidae and Siculocostidae. Costiferidae, Siphoniferidae, Milioliporidae, Pseudocucurbitidae and Siculocostidae were included in the superfamily Milioliporacea. Hydraniidae were placed in Nubeculariacea, whereas the position of Spiriamphorellidae was not clear – it could belong to either of the two superfamilies mentioned.

Based on new forms, Senowbari-Daryan (1993) considered specimens from Sicily previously determined as *C. longicollum* or *Hydrania dulloi* to belong to a new genus and species *Tignumparina zeissi* of the Pseudocucurbitidae family. *Tignumparina* differs from other genera in having chambers supported by beam-like elements.

Zaninetti & Martini (1992) redescribed the genera *Cucurbita* and *Urnulinella*. *Pseudocucurbita*, *Amphorella* and *Paratintinnina* were treated as their junior synonyms. The family Pseudocucurbitidae was redefined according to a new interpretation. *Cucurbita infundibuliformis* was treated as a valid species with junior synonyms *P. tulipaformis*, *Ps. globosa*, *Ps. subglobosa*, *Ps. campanulaformis* and *Ps. fusani*. *Spiriamphorella irregularis* was placed in synonymy with *U. andrusovi*. Altiner *et al.* (1992) introduced a new species of the

genus *Siculocosta*, i.e. *Siculocosta floriformis*, from the Norian strata of Turkey. Senowbari-Daryan & Flügel (1996) retained *Siculocosta* and *Costifera* in the same family, i.e. in Siculocostidae. Bérczi-Makk (1996) treated *Cucurbita infundibuliformis* as a valid species with junior synonyms *A. subsphaerica*, *A. bicamerata bicamerata*, *P. tulipaformis*, *Ps. globosa*, *Ps. subglobosa*, *Ps. campanulaformis* and *Ps. fusani*. *Urnulinella andrusovi* was awarded priority over *S. irregularis*, which was considered its synonym. The problem of neomorphic changes of the test wall was addressed by Sadati (1981), Zaninetti & Altiner (1982) and Zaninetti & Martini (1992).

SYSTEMATIC PALAEONTOLOGY

Class **Foraminifera** J.J. Lee, 1990

Order **Miliolina** Delage & Horouard, 1896

Suborder **Soritina** Ehrenberg, 1839

Superfamily **Milioliporoidea** Ehrenberg, 1839

Discussion. In contrast to the latest suprageneric position of Late Triassic reef-dwelling forms with amphora-like chambers (Zaninetti *et al.*, 1992), we reduce the list of existing families by not recognizing Spiriamphorellidae Senowbari-Daryan & Zaninetti, 1986, Costiferidae Senowbari-Daryan & Zaninetti, 1986, and Siculocostidae Zaninetti, Martini & Altiner, 1992. In this paper, these families are considered junior synonyms of Pseudocucurbitidae Zaninetti, Altiner, Dager & Ducret, 1982.

Family **Pseudocucurbitidae** Zaninetti, Altiner, Dager & Ducret, 1982 (Pseudocucurbitinae Zaninetti, Altiner, Dager & Ducret, 1982a, p. 97; Spiriamphorellinae Senowbari-Daryan & Zaninetti, 1986, p. 81; Costiferinae Senowbari-Daryan & Zaninetti, 1986, p. 81; Siculocostidae Zaninetti, Martini & Altiner, 1992, p. 216)

Discussion. Although *Cucurbita* holds priority as the genus name, Loeblich & Tappan (1987) argued that the suprageneric priority belongs to Pseudocucurbitidae Zaninetti *et al.*, 1982a, despite the invalidity of the genus *Pseudocucurbita*. As no family-group name has been established on the basis of the genus *Cucurbita*, and because no valid family-group names based on genera from the synonymy list older than Pseudocucurbitidae exist, we also retain the family name Pseudocucurbitidae according to Article 40.1 of the ICZN rules. The family currently contains only two genera (see discussion on the validity of the genera below): *Cucurbita* Jablonský, 1973 and *Tignumparina* Senowbari-Daryan, 1993. We also suggest the addition of the genus *Hydrania* due to its similarity with the genus *Tignumparina*, although additional research on this genus is yet to be conducted.

Genus *Cucurbita* Jablonský, 1973

(type species: *Cucurbita infundibuliforme* Jablonský, 1973)

(*Cucurbita* Jablonský, 1973, p. 420; *Amphorella* Borza & Samuel, 1977a, p. 100; *Spiriamphorella* Borza & Samuel, 1977a, p. 110;

Urnulinella Borza & Samuel, 1977a, p. 118; *Pseudocucurbita* Borza & Samuel, 1978, 69; *Paratintinnina* Samuel & Borza, 1981, p. 68; *Costifera* Senowbari-Daryan, 1983, p. 208; *Siculocosta* Senowbari-Daryan & Zaninetti, 1986, p. 82).

Discussion. It is evident that an extensive set of genera and species was reduced in subsequent years to yield a considerably simpler scheme. However, our view of the group differs significantly from the previous reinterpretations of the specimens figured in the

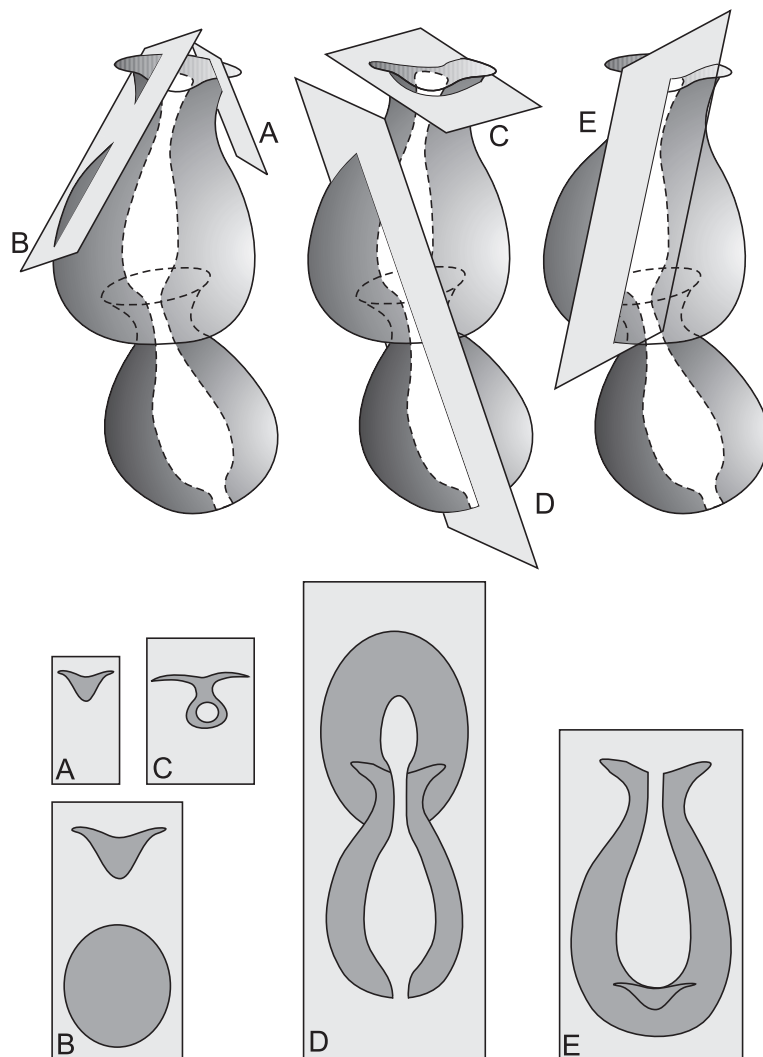


Fig. 1. A demonstration of some possible sections of the *Cucurbita* test (see also Sadati, 1981; Senowbari-Daryan, 1983).

literature, resulting in a further reduction of the previously proposed taxonomic groups (Tables 1, 2). In this paper, we refrain from discussing the genus *Hydrania* until additional specimens become available. From the specimens illustrated in Senowbari-Daryan (1983), we cannot confirm the reconstruction given by the author (Senowbari-Daryan, 1983, text-fig. 10).

CLASSIFICATORY DISCUSSION

Arguments for the placement of genera *Amphorella*, *Spiriamphorella*, *Urnulinella*, *Paratintinnina* and *Pseudocucurbita* under genus *Cucurbita*

As indicated by several authors, Borza & Samuel (1977a, b, 1978) over-split their material into a large number of species due to the different orientations of the sections (see Fig. 1). Our deviation from later revisions begins with this point. In our opinion, the material of Borza & Samuel (1977a, b, 1978) belongs to only two species, as discussed below.

Although the genus name *Cucurbita* was initially rejected (Zaninetti, 1977; Senowbari-Daryan, 1983) and replaced by

Pseudocucurbita (Senowbari-Daryan, 1983), Loeblich & Tappan (1987) re-established its validity. In our opinion, the Borza & Samuel species (subspecies included) *Amphorella bicamerata*, *A. bilongicamerata*, *A. lageniformis*, *Spiriamphorella carpathica*, *Paratintinnina tintinniformis*, *Pa. tulipaformis* and all the species of the genus *Pseudocucurbita* (*Ps. globosa*, *Ps. subglobosa*, *Ps. campanulaformis* and *Ps. fusani*) belong to *C. infundibuliforme* Jablonský, 1973 and are thus its junior synonyms (Fig. 2). In our opinion, the second species group of the genus *Cucurbita* comprises synonymous *Amphorella subsphaerica* (very oblique sections), *Spiriamphorella irregularis* and *Urnulinella andrusovi*. This species also has the body plan of the genus *Cucurbita* but has a chamber shape different from that of *C. infundibuliforme*, i.e. the chambers are stockier, with a shorter neck and a relatively less pronounced collar (Fig. 2). We suggest that the species priority should be given to *A. subsphaerica*. The principle of the first reviser (ISCZ, 1999, Article 24.2.2) does not apply in this case because *A. subsphaerica* has not previously been considered synonymous with *S. irregularis* and *U. andrusovi* (see ICZN, 1999, Article 24.2.5). By contrast, previous revisions awarded the priority either

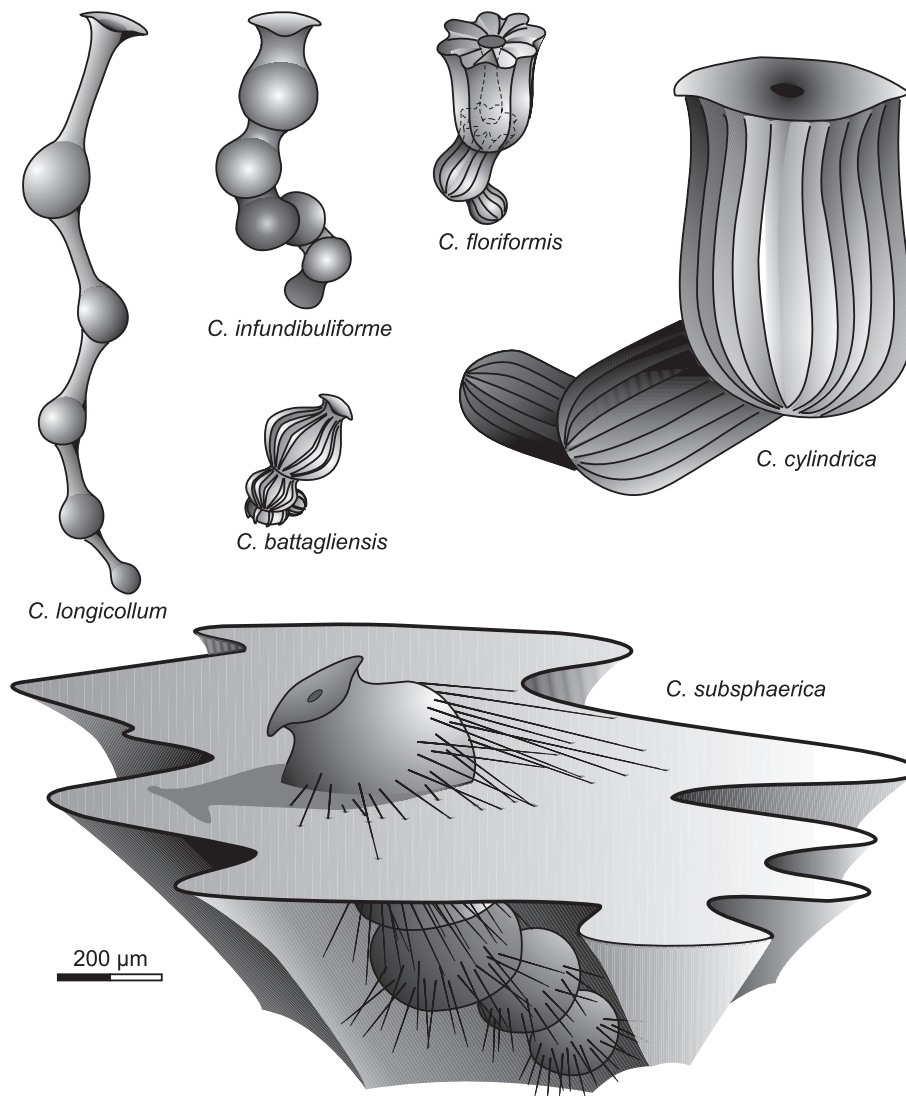


Fig. 2. Different (and considered valid in this paper) species of the genus *Cucurbita*. The presumed life position is demonstrated for *Cucurbita subsphaerica*. The spines (bristles), hypothesized by Senowbari-Daryan (1986) are shown only in *C. subsphaerica*, although they were probably present in all species. Reconstructions are based on drawings and material in Samuel & Borza (1981), Senowbari-Daryan (1983, 1986), Loeblich & Tappan (1987), Altiner *et al.* (1992). Tests' sizes are based on the reported lengths of individual chambers.

to *U. andrusovi* (e.g. Zaninetti & Martini, 1992; Bérczi-Makk, 1996) or to '*Galeanella irregularis*' (e.g. Zaninetti *et al.*, 1982a; Miconnet *et al.*, 1983). *Spiriamphorella rectilineata rectilineata*, *S. rectilineata districta* and *S. ovata* could form a third, longer-necked species group of the genus *Cucurbita*, but it is probable that these three species also belong to *C. infundibuliforme*. Given these considerations, we can dismiss all the genera introduced by Borza & Samuel (1977a, b, 1978) as junior synonyms of the genus *Cucurbita*, and the long list of their species is now reduced to *C. infundibuliforme* Jablonský, 1973 and *Cucurbita subsphaerica* (Borza & Samuel, 1977a). *Cucurbita longicollum* (Senowbari-Daryan, 1983) is, in our opinion, also a valid species (Fig. 2), whereas *Ps. laticollaris* and *Ps. brevicollum* represent junior synonyms of *C. infundibuliforme* and *C. subsphaerica*, respectively. The specimens determined by Senowbari-Daryan (1983) as *Ps. ovata* could belong instead to *C. longicollum*.

Arguments for the placement of genera *Costifera* and *Siculocosta* under genus *Cucurbita*

The body plan of the genera *Costifera* and *Siculocosta* is the same as that of the genus *Cucurbita*. The only difference is the presence of ribs (costae) on the outer surface of the test (Fig. 2). *Siculocosta* was separated from *Costifera* on the basis of the continuity of the wall, i.e. the lack of a distinct wall between the test and the costae (Senowbari-Daryan & Zaninetti, 1986).

Our first point is the invalidity of the genus *Siculocosta*. The specimens figured by Senowbari-Daryan (1983, pl. 21, fig. 6) may or may not (e.g. Senowbari-Daryan, 1983, pl. 21, figs 1, 2) display the diagnostic line between the test and costae. Thus, we believe that the absence/preservation of the line is due to neomorphic changes of the wall (e.g. Zaninetti & Altiner, 1982; Zaninetti & Martini, 1992) and is not a generic feature.

Genus	Zaninetti (1977)	Zaninetti et al. (1982a)	Senowbari-Daryan (1983)	Loeblich & Tappan (1987)	This work
<i>Cucurbita</i> Jablonský, 1973	Synonym of <i>Galeanella</i>	Synonym of <i>Galeanella</i> ?, <i>Pseudocucurbita</i> ?, <i>Spiriamphorella</i> ?	Name preoccupied	Valid	Valid
<i>Amphorella</i> Borza & Samuel, 1977a	Synonym of <i>Galeanella</i>	Name preoccupied; pars Synonym of <i>Pseudocucurbita</i>	Invalid; <i>Pseudocucurbita</i> or <i>Spiriamphorella</i> or <i>Urnulinella</i>	Synonym of <i>Spiriamphorella</i>	Synonym of <i>Cucurbita</i>
<i>Spiriamphorella</i> Borza & Samuel, 1977a	Synonym of <i>Galeanella</i>	Pars valid, pars Synonym of <i>Galeanella</i>	Valid	Valid	Synonym of <i>Cucurbita</i>
<i>Urnulinella</i> Borza & Samuel, 1977a	Synonym of <i>Galeanella</i>	Synonym of <i>Galeanella</i>	Valid	Valid	Synonym of <i>Cucurbita</i>
<i>Pseudocucurbita</i> Borza & Samuel, 1978		Valid, emended	Valid, emended	Synonym of <i>Cucurbita</i>	Synonym of <i>Cucurbita</i>
<i>Paratintinnina</i> Samuel & Borza, 1981		Valid	Invalid; <i>Pseudocucurbita</i> or <i>Spiriamphorella</i>	Synonym of <i>Cucurbita</i>	Synonym of <i>Cucurbita</i>
<i>Costifera</i> Senowbari-Daryan, 1983				Valid	Synonym of <i>Cucurbita</i>
<i>Siculocosta</i> Senowbari-Daryan & Zaninetti, 1986				Valid	Synonym of <i>Cucurbita</i>

Table 1. Validity of the genera introduced by Jablonský (1973), Borza & Samuel (1977a, b, 1978), Samuel & Borza (1981), Senowbari-Daryan (1983) and Senowbari-Daryan & Zaninetti (1986) according to the different authors and to this paper.

Second, we consider the presence of ribs a species character and not a generic feature. *Costifera battagliensis*, *Siculocosta cylindrica* and *Siculocosta floriformis* should be viewed as ornamented specimens of the genus *Cucurbita*. The first species differs in having more numerous costae, whereas the latter two differ in having pointed and well-rounded ribs, respectively (Fig. 2).

Description of the genus *Cucurbita* and palaeoecology

We agree with the description given by Zaninetti & Martini (1992), which differs slightly from the original description (Zaninetti et al., 1982a) in denying the presence of the secondary thecal mass. The morphology of *Cucurbita* suggests an unattached, free-living form, passively floating in the muddy substrate (see Senowbari-Daryan, 1987). The irregular juxtaposition of chambers is due to corrections of the test's orientation, which should be open towards the surface of the substrate, whereas bristles (spines, *sensu* Senowbari-Daryan, 1986) helped to anchor the test (Fig. 2). A robust shape with a short neck (as in *C. subsphaerica*) or a gracile form with a long neck (as in *C. longicollum*) are two different adaptations to a suspended mode of life. A spherical chamber shape produces increased buoyancy, so a long neck is unnecessary, whereas slimmer forms needed their long necks to keep the apertures above the substrate.

CONCLUSIONS

Genera *Amphorella*, *Spiriamphorella*, *Urnulinella*, *Pseudocucurbita*, *Costifera* and *Siculocosta* are junior synonyms of the genus *Cucurbita* (Table 1). Consequently, the number of families in the superfamily Milioliporacea is reduced by the removal of Spiriamphorellidae, Costiferidae and Siculocostidae. Genera *Cucurbita* and *Tignumparina* instead belong to the family Pseudocucurbitidae. The status and the suprageneric position of the genus *Hydrania* is not yet resolved.

The valid species of the genus *Cucurbita* are (Fig. 2; Table 2):

- *C. infundibuliforme* Jablonský, 1973 (junior synonyms *Amphorella bicamerata bicamerata* Borza & Samuel, 1977a, *Amphorella bicamerata intermedia* Borza & Samuel, 1977a, *Amphorella bilongicamerata bilongicamerata* Borza & Samuel, 1977a, *Amphorella bilongicamerata minuta* Borza & Samuel, 1977a, *Amphorella lageniformis* Borza & Samuel, 1977a, *Spiriamphorella carpathica carpathica* Borza & Samuel, 1977a, *Spiriamphorella carpathica gemerica* Borza & Samuel, 1977a, ?*Spiriamphorella rectilineata rectilineata* Borza & Samuel, 1977a, ?*Spiriamphorella rectilineata districta* Borza & Samuel, 1977a, ?*Spiriamphorella ovata* Borza & Samuel, 1977a, *Paratintinnina tintinniformis* (Borza & Samuel, 1977b), *Paratintinnina tulipaformis* (Borza & Samuel, 1977b), *Pseudocucurbita globosa* Borza & Samuel, 1978, *Pseudocucurbita subglobosa* Borza & Samuel, 1978, *Pseudocucurbita campanulaformis* Borza & Samuel, 1978, *Pseudocucurbita fusani* Borza & Samuel, 1978, ?*Pseudocucurbita laticollaris* Senowbari-Daryan, 1983);
- *C. subsphaerica* (Borza & Samuel, 1977a) *comb. nov.* (junior synonyms *Spiriamphorella irregularis* Borza & Samuel, 1977a, *Urnulinella andrusovi* Borza & Samuel, 1977a, ?*Pseudocucurbita brevicollum* Senowbari-Daryan, 1983);
- *C. longicollum* (Senowbari-Daryan, 1983);
- *C. battagliensis* (Senowbari-Daryan, 1983) *comb. nov.*;
- *C. cylindrica* (Senowbari-Daryan, 1983) *comb. nov.*;
- *C. floriformis* (Altiner et al., 1992) *comb. nov.*.

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Species	Zaninetti (1977)	Zaninetti & Altiner (1981)	Zaninetti <i>et al.</i> (1982a)	Senowbari-Daryan (1983)	Zaninetti & Martini (1992)	Bérczi-Makk (1996)	This work
<i>Cucurbita infundibuliforme</i> Jablonský, 1973	<i>Nomen dubium</i>	Not determinable		Valid	Valid	Valid	Valid
<i>Amphorella bicamerata bicamerata</i> B. & S., 1977a	Not determinable	Not determinable		<i>S. carpathica</i> and/or <i>S. districta</i>	Pars <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>
<i>A. bicamerata intermedia</i> B. & S., 1977a	Not determinable	Not determinable		<i>S. carpathica</i> and/or <i>S. districta</i>			Synonym of <i>C. infundibuliforme</i>
<i>A. bilongicamerata bilongicamerata</i> B. & S., 1977a	Not determinable	Not determinable		<i>S. carpathica</i> and/or <i>S. districta</i>			Synonym of <i>C. infundibuliforme</i>
<i>A. bilongicamerata minuta</i> B. & S., 1977a	Not determinable	Not determinable		<i>S. carpathica</i> and/or <i>S. districta</i>			Synonym of <i>C. infundibuliforme</i>
<i>A. lageniformis</i> B. & S., 1977a	Not determinable	Not determinable		<i>S. carpathica</i> and/or <i>S. districta</i>			Synonym of <i>C. infundibuliforme</i>
<i>A. subsphaerica</i> B. & S., 1977a	Synonym of <i>G. panticae</i>	Synonym of <i>G. panticae</i>	<i>Ps. subsphaerica</i>	Synonym of <i>U. andrusovi</i>	<i>C. infundibuliforme</i> & <i>U. andrusovi</i>	Synonym of <i>C. infundibuliforme</i>	<i>Cucurbita subsphaerica</i> comb. nov.
<i>Spiriamphorella carpathica carpathica</i> B. & S., 1977a	<i>G.? carpathica</i>	<i>S. carpathica</i>		<i>S. carpathica</i>			Synonym of <i>C. infundibuliforme</i>
<i>S. carpathica gemerica</i> B. & S., 1977a	Synonym of <i>G.? carpathica</i>	Synonym of <i>S. carpathica</i>		Synonym of <i>S. carpathica</i>			Synonym of <i>C. infundibuliforme</i>
<i>S. rectilineata rectilineata</i> B. & S., 1977a	Synonym of <i>G.? carpathica</i>	Synonym of <i>S. carpathica</i>		Synonym of <i>S. carpathica</i>			? Synonym of <i>C. infundibuliforme</i>
<i>S. rectilineata districta</i> B. & S., 1977a	<i>G.? districta</i>	<i>S. districta</i>		<i>S. districta</i>			? Synonym of <i>C. infundibuliforme</i>
<i>S. ovata</i> B. & S., 1977a	Synonym of <i>G.? districta</i>	Synonym of <i>S. districta</i>		Valid			? Synonym of <i>C. infundibuliforme</i>
<i>S. irregularis</i> B. & S., 1977a	Synonym of <i>G. panticae</i>	Synonym of <i>G. panticae</i>	<i>G. irregularis</i>	<i>Galeanella?</i> or <i>Urnulinella?</i>	(pars?) Synonym of <i>U. andrusovi</i>	Synonym of <i>U. andrusovi</i>	Synonym of <i>C. subsphaerica</i> comb. nov.
<i>Urnulinella andrusovi</i> B. & S., 1977a	Synonym of <i>G. panticae</i>	Synonym of <i>G. panticae</i>	Synonym of <i>G. irregularis</i>	Valid	Valid		Synonym of <i>C. subsphaerica</i> comb. nov.
<i>Paratintinna tintinniformis</i> B. & S., 1977b		Not determinable		<i>Pseudocucurbita</i> and/or <i>Spiriamphorella</i>			Synonym of <i>C. infundibuliforme</i>
<i>P. tulipaformis</i> B. & S., 1977b		Not determinable		<i>Pseudocucurbita</i> and/or <i>Spiriamphorella</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>
<i>Pseudocucurbita globosa</i> B. & S., 1978		<i>G. globosa</i>	Synonym of <i>C. subsphaerica</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>
<i>Ps. subglobosa</i> B. & S., 1978		Synonym of <i>G. globosa</i>	Synonym of <i>C. subsphaerica</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>
<i>Ps. campanulaformis</i> B. & S., 1978		Synonym of <i>G. globosa</i>	Synonym of <i>C. subsphaerica</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>
<i>Ps. fusani</i> B. & S., 1978		Synonym of <i>G. globosa</i>	Synonym of <i>C. subsphaerica</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>	Synonym of <i>C. infundibuliforme</i>

Table 2. Differing views on the validity of some species of the genus *Cucurbita*.

B. & S., Borza & Samuel.

Note that of the extensive list of species established by Jablonský (1973) and Borza & Samuel (1977a, b, 1978), only two are considered valid by the authors of this paper. These two, i.e. *C. infundibuliforme* Jablonský, 1973 and *C. subsphaerica* (Borza & Samuel, 1977a) comb. nov., are joined by *C. longicollum* (Senowbari-Daryan, 1983) comb. nov., *C. cylindrica* (Senowbari-Daryan, 1983) comb. nov., *C. battagliaensis* (Senowbari-Daryan, 1983) comb. nov. and *C. floriformis* (Altiner *et al.*, 1992) comb. nov.. Of the species not listed, *Ps. laticollaris* Senowbari-Daryan, 1983 is considered a junior synonym of *C. infundibuliforme*, and *Ps. brevicollum* Senowbari-Daryan, 1983 is considered a junior synonym of *C. subsphaerica* (Borza & Samuel, 1977a) comb. nov. .

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