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NOTES ON THE GENERA *NORDGAARDIA* AND *USCHAKOVIA* (BRYOZOA: BUGULIDAE)

PATRICIA L. COOK

Honorary Associate, Museum Victoria, GPO Box 666E, Melbourne, Victoria 3001, Australia

Abstract

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The rare deep-water bryozoan genera *Nordgaardia* and *Uschakovia* share important similarities in budding patterns and zooid structure together with a type of avicularium which has an extended subrostral chamber. Ovicells are known only in *Nordgaardia* and are here described in Australian specimens of *N. cornucopioides* for the first time. The remarkable spines of *Uschakovia gorbunovi* are described from a colony from the Faroe Islands; they are extensions of the frontal body wall, and each has a modified parietal muscle at its base.

Introduction

Two species of the genus *Nordgaardia* Kluge, 1962 have been described in some detail: *N. pusilla* (Nordgaard, 1907), type species, by Hayward (1978), and *N. cornucopioides* by d'Hondt (1983). The type and only species of Uschakovia Kluge, 1946, *U. gorbunovi* Kluge, 1946, has been described solely from Russian Arctic specimens by Kluge (1946, 1962). Deep-water bryozoans often have delicate colonies with thinly calcified zooids and the opportunity to examine well-preserved specimens is rare. A single almost complete colony of *U. gorbunovi*, together with 18 colonies of *N. cornucopioides*, seven of which possessed both ancestrulae and ovicells, are here compared directly from material in the collections of Museum Victoria. The relationships of the two genera with each other and with some other genera of the superfamily Buguloidea are assessed.

The specimen of *U. gorbunovi* is part of a collection including several colonies of this species, collected as part of the Undersøgelsor af den marine bunddyrfauna omkring Faerøesne (BIOFAR, Investigations of the marine benthic fauna of the Faroe Islands). The other specimens are stored at the Marine Station, Vidskridvbakka, FR-180, Kaldbak, Førøyar. The figured specimen, was presented to Museum Victoria by Dr P.J. Hayward (Marine Research Group, University of Swansea, UK), who investigated the Bryozoa from this collection (Hayward, 1994). The specimens of *N. cornucopioides* were among material sorted by P.E. Bock from Museum Victoria's SLOPE stations (taken on the south-eastern Australian slope from RV *Franklin* using a WHOI epibenthic sled) and are stored in Museum Victoria (NMV).

Nordgaardia Kluge

Nordgaardia Kluge, 1962: 437.

Type species. Synnotum pusillum Nordgaard, 1907.

Diagnosis. Colony erect, arising from an ancestrula anchored by numerous rhizoids, followed by a short chain of uniserial autozooids. Autozooids thinly calcified, elongated, tubular; proximal gymnocyst expanding to surround an extensive opesia with an almost terminal operculum. Distal part of zooids free, projecting from branch surface. Autozooids arranged in alternating pairs or in triads. Avicularia arising proximal to opesia, subrostral chamber greatly extended, expanded terminally into an acute, beaked rostrum. Ovicell with partially membranous ectooecium, surrounding a thinly calcified capsule of entooecium, attached to distolateral end of the brooding zooid, with a laterally directed aperture which partially obscures the brooding zooid operculum.

Remarks. Nordgaardia pusilla, originally introduced for material from 1000 m in the northern Atlantic, was redescribed in detail by Hayward (1978: 215, Figs 3d–h), who had 12 samples from the western European continental slope from a depth range of 610–1400 m. This material included colonies with ancestrulae and ovicells which he described for the first time. D'Hondt (1983) introduced a second species, *Nordgaardia*

cornucopioides from Brazil which differs from *N. pusilla* in having a greater proportion of each zooid freely projecting from the branch surface and in having more robust avicularia. D'Hondt's specimens possessed neither ancestrulae nor ovicells. The colonies described below from the continental slope of eastern Tasmania and Victoria appear to be referable to *N. cornucopioides* and allow description of both these features, and comparison with *N. pusilla*.

Camptoplites marchemarchadi Redier and d'Hondt (1976) was assigned to *Nordgaardia* by d'Hondt (1983: 82). Although d'Hondt (1983) distinguished the two genera from each other on the basis of their avicularian types, that of *N. marchemarchadi* having an elongated subrostral chamber, not a flexible 'stalk' as is present in *Camptoplites*, he mentioned that avicularia occurred only on the secondary branches. The development of these secondary branches is a characteristic found only in *Camptoplites*, and was fully described by Hastings (1943). The generic position of *C. marchemarchadi* is therefore equivocal. The type specimen was from West Africa, and it is possible that the fragmentary specimen from Senegal assigned to *Kinetoskias* sp. by Cook (1968: 63), which had similar avicularia, may have belonged to the same species.

Nordgaardia cornucopioides d'Hondt

Nordgaardia cornucopioides d'Hondt, 1983: 80, pl.1, figs 3–4 (off Brazil, 770–805 m).—Harmelin and d'Hondt, 1992: 31 (Gulf of Cadiz, 281 m).—d'Hondt and Gordon, 1996: 85, fig. 11D (New Caledonia, 1175–1950 m).

Material examined. Stn SLOPE-32, 38°21.90'S, 149°20'E, 23 Jul 1986, S of Point Hicks, Vic., 1000 m. stn SLOPE-33, 38°19.60'S, 149°24.30'E, 23 Jul 1986, S of Point Hicks, Vic., 930 m. stn SLOPE-34, 38°16.40'S, 149°24.30'E, 23 Jul 1986, S of Point Hicks, Vic., 800 m. stn SLOPE-45, 42°2.20'S, 148°38.70'E, 27 Jul 1986, off Freycinet Peninsula, Tas., 800 m. All NMV F74868.

Description. Nordgaardia with at least half the distal part of each zooid free and projecting from the branch surface. Avicularia expanded and truncate distally, with a hooked rostrum. Ovicells very large.

Remarks. The four colonies from Tasmania (stn SLOPE-45) and three of those from Victoria (stn SLOPE-32) have ancestrulae and rhizoids present, and branch three to four times. Ovicells are present in all these colonies, which include, on average, more than 100 zooids each. The ancestrula is tubular, attached by 10–12 proximal rhizoids, and has a narrow opesia extending nearly the whole of its length. It gives rise to one distal zooid which bears 15–20 rhizoids along its entire length. The first pair of autozooids follows. Subsequent autozooids are arranged in alternating pairs or in triads with frontals inclined to one side of the branch so that the long tubular proximal parts of the zooids tend to be visible only on the basal side. Hayward (1978) described the slightly different budding and branching patterns of *N. pusilla* in detail and also noted the difficulty in understanding the morphology of the ovicells because their delicate calcification was distorted by collection and preservation. The ovicells of *N. cornucopioides* are also very thinly calcified and are somewhat distorted. The ovicells are larger than those of *N. pusilla* (Table 1) and have an almost completely membranous ectooecium which surrounds a distinctly smaller calcified capsule of entooecium. The two layers merge at a small attachment area on the basal side of the distolateral wall of the brooding zooid which has a wider border of gymnocyst on the outer side. The large aperture of the ovicell opens laterally above the operculum of the brooding zooid which is

Table 1. Measurements in mm of *Nordgaardia pusilla*, *N. cornucopioides*, and *Uschakovia gorbunovi* from specimens and literature.

	N. pusilla	*N. cornucopioides*	*U. gorbunovi*
Length of ancestrula	1.30–1.50	1.70–1.85	1.00–1.70
Length of autozooids	1.40–1.80	0.90–1.20	0.76–0.83
Length of opesia	0.76–1.00	0.65–0.75	0.50–0.54
Length of subrostral chamber	0.54–0.85	0.67–0.74	0.45–0.66
Length of rostrum	0.12–0.19	0.19–0.30	0.12–0.27
Length of ovicell	0.36	0.45–0.50	—
Width of ovicell	0.28	0.39–0.45	—
Length of tentacles	—	0.40–0.45	0.25–0.29

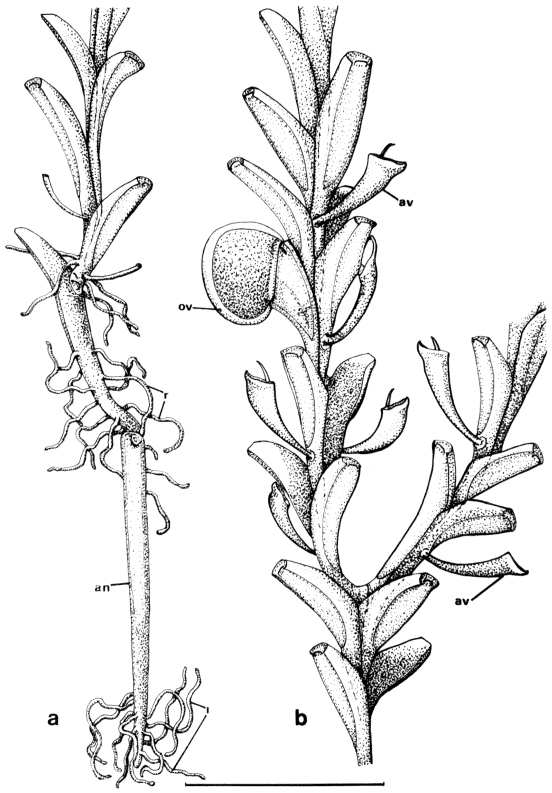

Figure 1. *Nordgaardia cornucopioides* d'Hondt, Tasmania. a, primary astogenetic zone: ancestrula (*an*), rhizoids (*r*). b, later astogenetic zone: avicularia (*av*), ovicell (*ov*). Scale = 1 mm.

therefore partially obscured (Fig. 1b). Ovicells with an uncalcified ectooecium were figured in *Bugula longissima* Busk by Hastings (1943: Fig. 39D) and ovicells with a laterally facing aperture obscuring the brooding zooid operculum were figured in *Kinetoskias mitsukurii* by Yanagi and Okada (1918: 425, Fig. 7a) and in *K. elongata* by Harmer (1926: 469, pl. 34, fig. 11). The closely similar ovicelled zooids of *Euoplozoum cirratum* (Busk) were illustrated by d'Hondt and Gordon (1996: 86, fig. 9D).

A few autozooids have partially protruded tentacle crowns. The tentacles are closely opposed and contracted in most cases but in a few zooids they are slightly expanded with an estimated total of 14–16 tentacles in the crown. The avicularia do not reach the largest rostral dimension given by d'Hondt (1983, i.e. length of rostrum 0.30 mm) but are within the range he figured. They are more robust than those of *N. pusilla* and their rostra are hooked terminally. The extensive muscle systems occupy nearly all the distal, expanded part of the elongated subrostral chamber.

D'Hondt's specific name refers to the similarity of the avicularia with those occurring in some species of the genus *Cornucopina* Levinsen. Harmer (1926) described several species including *C. moluccensis* (Busk) which has large avicularia almost exactly like those of *N. cornucopioides*. The extended proximal parts of the autozooids and the complex budding patterns of the two genera are also somewhat similar but *Cornucopina* differs completely in the expanded shape of the distal part of its autozooids and in the occurrence of numerous marginal spines.

The locality of the Tasmanian specimens of *N. cornucopioides* is remote from most other records of *Nordgaardia* which are all from the Atlantic. However, recently, specimens from very deep water from New Caledonia have been recorded by d'Hondt and Gordon (1996). It is just

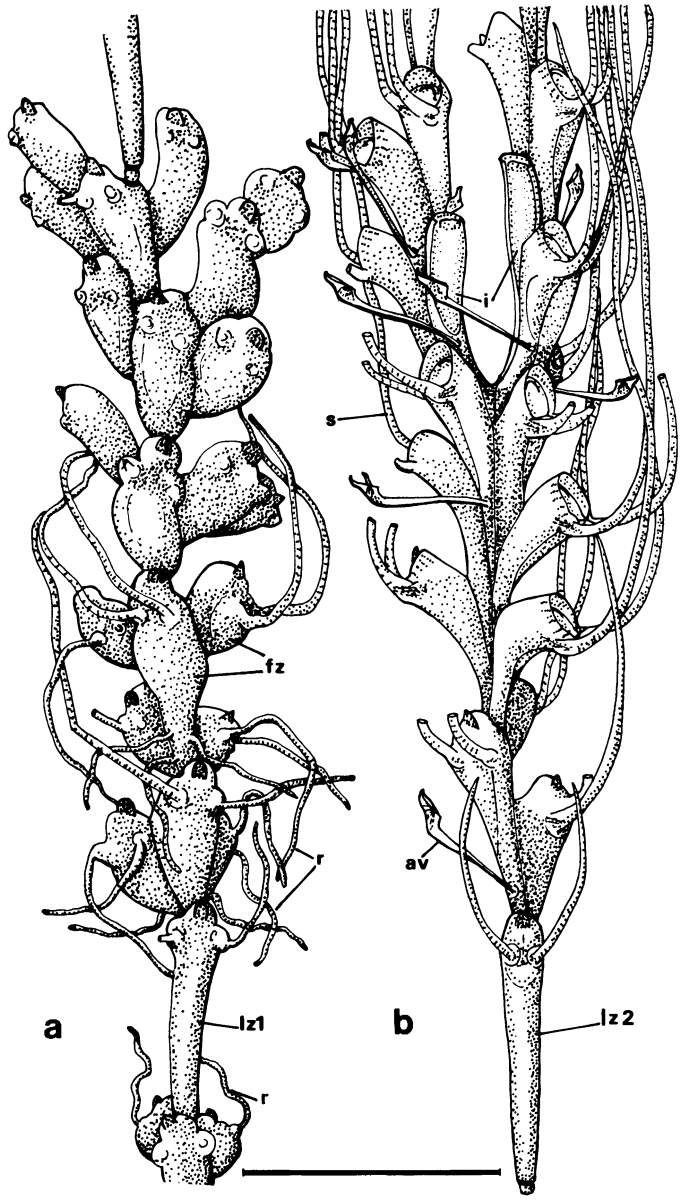

Figure 2. *Uschakovia gorbunovi* Kluge, Faroe Islands. a, primary astogenetic zone: founding zooids (fz), rhizoids (*r*), primary linking zooid (*lz 1*). b, later astogenetic zone: secondary linking zooid (*lz 2*), spines (*s*), inward-facing zooids (*i*), avicularia (*av*). Many spines not shown completely. Scale = 1 mm.

possible that a single rather variable taxon is concerned. Harmelin and d'Hondt (1992) noted that their colonies from the north-eastern Atlantic (off Cadiz, 35°43.5', 6°18.2'W, 281 m) had some avicularia which approached the more slender type found in *N. pusilla*. The avicularia of the Tasmanian population of *N. cornucopioides* are generally less robust than those originally described by d'Hondt (1983) from Brazil, and the very delicate, slender avicularia described for *N. marchemarchadi*, from Senegal, suggest that a direct comparison of all the available material might reveal a continuum of character states.

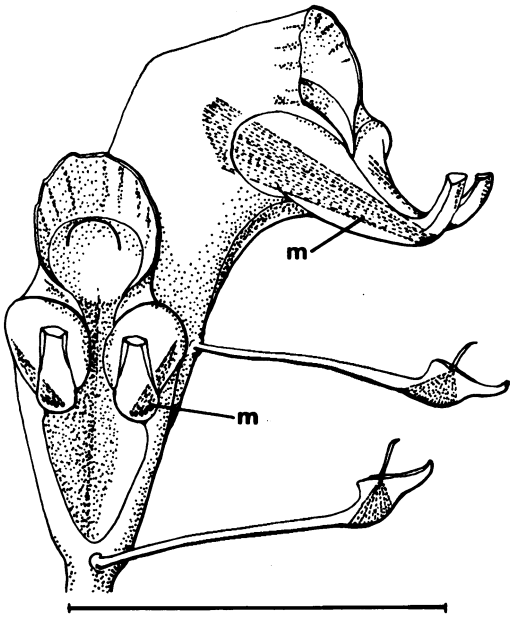

Figure 3. *Uschakovia gorbunovi* Kluge, Faroe Islands. Two autozooids and avicularia, showing modified parietal muscles (*m*). Spines not shown completely. Scale = 0.5 mm.

Uschakovia Kluge

Uschakovia Kluge, 1946: 196.

Type species. Uschakovia gorbunovi Kluge, 1946 (monotypic).

Diagnosis. As for *U. gorbunovi*.

Uschakovia gorbunovi Kluge

Uschakovia gorbunovi Kluge, 1946: 196 , pl. 1, figs 1–4.—Kluge, 1962: 438, Figs 228A–D (Arctic, Kara and East Siberian Seas, 64–648 m).—Hayward, 1994: 183 (Faroe Islands, 610–1400 m).

Material examined. BIOFAR stn 095, 060°41.51'N, 05°18.63'W, south-east Faroe Islands, 23 Jul 1987, 803 m, NMV F74869.

Description. Colony erect, arising from an ancestrula anchored by rhizoids which gives rise to a series of 'founding' zooids which also develop rhizoids. Erect branched part of colony originating from one zooid, or a short uniserial chain of 'linking' zooids which are extremely elongated. Branches of autozooids in alternating pairs and triads, becoming quadriserial before a bifurcation. Primary branch bifurcating several times to form a cluster of 4–6 branches. Autozooids with very long tubular proximal gymnocyst expanding distally to surround an elongated opesia. Outward-facing zooids with bipartite opesia, distal part covered by frontal membrane which surrounds operculum, the proximal part formed by the swollen bases of pair of long partially cuticular spines. Inward-facing zooids without spines, opesia elongated. Avicularia arising from proximal gymnocyst of both kinds of zooids; the subrostral chamber considerably elongated and expanded distally to form a terminally hooked acute rostrum. Ovicells unknown.

Remarks. The colony examined here does not differ materially from those described from the high Arctic by Kluge (1962). Colonies attain a height of 10–15 mm and a width of 5–8 mm, and are composed of two groups of distinctly different zooids, each group connected by a single elongated linking zooid (length 1.00–1.14 mm). The colony from the Faroes has no ancestrula; those figured by Kluge (1962) have ancestrulae which are more elongated than, but which otherwise resemble, the succeeding founding zooids. The groups of founding zooids (length 0.50–0.55 mm) alternate with one or two linking zooids and this succession may be repeated. The colony from the Faroes has a few founding zooids followed by a linking zooid which has no calcification. A further group of approximately 20 triserially budded founding zooids, the more proximal with rhizoids,

is then followed by a second, single calcified linking zooid. The remainder of the colony is formed by bifurcation of a biserial-to-quadriserial branch which is budded distally to the linking zooid (Fig. 2). The resulting colony has six branches. All zooids are very thinly calcified early in astogeny at least. The tubular proximal gymnocysts are closely apposed and each expands distally to surround the opesia; the terminal third of this upper part of the zooid is free and projects from the branch surface. The founding zooids appear to have passed through ontogenetic changes including resorption of calcification and they have completely cuticular body walls. A line marking the presumed former position of the edge of the gymnocyst is present in some zooids and all are swollen, irregularly orientated, and have open opercula. The underlying orifices are however sealed by cuticle. The more distal zooids have paired cuticular tubercles near the distal ends of the former opesia; the more proximal zooids have long uncalcified, spinous processes, or paired rhizoids in the same position. Other rhizoids arise from the proximal part of these zooids. The more proximal of the two linking zooids is more slender and longer than the neighbouring founding zooids but also has cuticular walls. The more distal linking zooid is separated from the nearest proximal founding zooid by two cuticular nodes with an intervening small calcified internode (Fig. 2b). The gymnocyst is thinly calcified and very elongated and tubular, expanding distally to surround a bipartite opesia which is divided by lateral constrictions formed by the swollen bases of paired spinous processes. The opesia proximal to the constriction is short and both parts of the frontal membrane form an angle at the constriction. The distal part is almost circular and the small almost semi-circular operculum has a marginal sclerite. The autozooids of the next three to four astogenetic generations resemble the linking zooid but have a shorter, tubular gymnocyst and longer narrower proximal opesia. The operculum and the circular distal part of the frontal membrane are sunken with a cowl-like raised rim of semitransparent gymnocyst with a crenulated border.

After four to five astogenetic generations the first bifurcation occurs and branches become tri- to quadriserial; they are close to each other and the autozooids facing inward differ from those facing outward which are in the majority. The inward-facing zooids are flattened and have a wide elongated opesia without any trace of spines or lateral constrictions; a distal pair of parietal muscles is visible in many zooids. The outward-facing zooids all have paired spines and laterally constricted bipartite opesiae. The spines are 1.55–3.50 mm long and are direct expansions of the body wall. On the proximal face they are derived from the cuticle of the frontal membrane; on the distal face they are thinly calcified and continuous with the lateral gymnocyst which forms a curved shoulder round the base of each spine. The spines are curved at their origin but extend distally and are numerous and long enough to obscure the underlying zooids completely. Although flattened and partially calcified at first, they become tubular and completely cuticular. At the base of each spine the frontal cuticle is expanded to form a tubercle and muscles extend through this from the cuticular frontal face to the interior of the shoulder and the lateral part of the gymnocyst (Fig. 3). These muscles appear to be modified and enlarged parietal muscles. All the zooids are so thinly calcified that they are somewhat shrunken by preservation in alcohol. In life the frontal membranes would be convex especially when the tentacle crowns were retracted. The base of the spines would therefore not constrict the opesia as much as they do in the preserved state. However, contraction of the parietal and other muscles during tentacle protrusion would presumably cause the proximal part of the frontal membrane to become concave. This would alter the position and direction of the elongated frontal spines. The avicularia which arise from the proximal gymnocyst are similar to but much less robust than those of *N. cornucopioides*; the elongated proximal part of the subrostral chamber is narrower and the 'head' more elongated.

Discussion

In colony form and budding patterns, and in the possession of erect rhizoid-bearing ancestrulae and elongated avicularia, *Nordgaardia* and *Uschakovia* resemble each other closely. Kluge (1962) suggested that the founding zooids of *Uschakovia* might function in nutrient storage as well as in attachment of colonies. The swollen, cuticular zooids resemble the basal vesicular kenozooids of *Caulibugula* (Hastings, 1939) which may also function in both of these ways. The greatly extended cuticular peduncle of *Kinetoskias* (see Kluge, 1962) which has rhizoids at its base is analogous to the founding zooid of *Uschakovia* but is an extrazooidal structure in direct contact with all autozooids. It presumably expands continuously with growth in the same manner as the peduncle of the ascophoran genus *Parmularia* (Cook and Chimonides, 1985). The

apparent resorption of calcification in *Uschakovia* seems to be an ontogenetic change which proceeds distally from the ancestrular region. The earliest founding zooids and the more proximal linking zooid bear only rhizoids, the more distal founding zooids bear long uncalcified spines and show traces of cuticle which may mark the former position of a gymnocyst. The distal linking zooid and first pair of autozooids have completely calcified gymnocysts but like all the founding zooids their open opercula have an underlying orifice sealed by cuticle. This gradient of ontogenetic change suggests that the resorption of calcification is a successive process which, in the larger colonies figured by Kluge (1962), may have proceeded further than in the specimens from the Faroes.

Nordgaardia and *Uschakovia* exhibit an interesting mosaic of characteristics of other genera within the Bugulidae. Both genera have similar avicularia which also closely resemble those of several species of *Cornucopina* (Harmer, 1926) as noted above. However, *Cornucopina* differs in autozooid morphology although its budding pattern does resemble that of *N. pusilla*. The avicularia of some species of *Kinetoskias* although less elongated are similar to those of *Nordgaardia* in structure and position (Yanagi and Okada, 1918; Harmer, 1926). As noted above, the ovicells of *Nordgaardia* resemble those of *Kinetoskias* which has however a very different colony form (Kluge, 1962). The modified parietal muscles at the base of the spines in *U. gorbunovi*, are, like the spines themselves, apparently unique. However, the 'flexor zooecii' muscles of both *Kinetoskias* and *Euoplozoum* (Busk, 1881; Harmer, 1926) are analogous in some ways although certainly not homologous.

An elongated ancestrula attached by long rhizoids is found in several genera of Bugulidae. Hastings (1943) illustrated the ancestrulae of several species of *Camptoplites* in detail. The zooid shape and to a certain extent the budding patterns and the avicularia of all the deep-water genera, including *Nordgaardia*, *Uschakovia*, *Kinetoskias* and some forms of *Camptoplites*, show a large number of similarities with one another which cannot all be ascribed to the common features of their environments. In all respects, the extensive continuum of character correlations found in the family Bugulidae (Gordon, 1984) seems to accommodate all four genera. Hayward (1978) considered that the budding and bifurcation patterns of *Nordgaardia* were so close to those of the genera *Epistomia* and *Synnotum* that both *Nordgaardia* and *Uschakovia* could be retained within the family Epistomiidae (Hastings, 1943; Ryland and Hayward, 1977). The members of this family do not however possess elongated avicularia or hyperstomial ovicells. Kluge (1962) introduced the family Sadkoidae to include *Nordgaardia* and *Uschakovia*. *Nordgaardia* has been included in this family by d'Hondt (1983) and by Harmelin and d'Hondt (1992). However, as noted by Ryland (1982: 760), the family name is invalid as no genus *Sadkoa*, from which the family name should have been derived, seems ever to have been described. In any case, the family is unnecessary as both genera are assignable to the Bugulidae.

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