

---

**Nomenclatural errors in the Thraustochytriales (Heterokonta/Staminipila), especially with regard to the type species of *Schizochytrium***

Robert A. Andersen, *Friday Harbor Laboratories, University of Washington, Friday Harbor, Washington 98250, USA (corresponding author: raa48@uw.edu)*

Eneko Ganuza, *Heliae Development, 578 East Germann Road, Gilbert, Arizona 85297, USA*

The Phycmycetes, or algal fungi, have been known to science for over 150 years (Sparrow 1960), beginning with the description of *Labyrinthula vitellina* Cienkowski (Cienkowski 1865). Molecular studies have shown that the “true” fungi are more related to animals (e.g., Baldauf & Palmer 1993) whilst the “aquatic fungi” were heterokonts or stramenopiles (e.g. Gunderson *et al.* 1987, Dick 2001). Recent molecular phylogenetic studies have revealed considerable diversity masked by morphological similarity (e.g., Marchan *et al.* 2017, Pan *et al.* 2017). Numerous names have been published, but nomenclatural errors are common, i.e., errors contrary to the International Code of Nomenclature (ICN) rules. The main purpose of this paper is to correct names that are now, or were previously, assigned to the genus “*Schizochytrium*” (Goldstein & Belsky 1964).

The *Thraustochytriaceae* is anchored by the nomenclatural type for *Thraustochytrium proliferum* Sparrow (1936), a valid and legitimate species name. Bennett *et al.* (2017) placed the following eight genera in the *Thraustochytriaceae*: *Aurantiochytrium*, *Japonochytrium*, *Monorhizochytrium*, *Parietochytrium*, *Schizochytrium*, *Sicyoidochytrium*, *Thraustochytrium* and *Ulkenia*. *Althornia* was placed in the *Althornidiaceae* and together, these two families constitute the Thraustochytriales (Bennett *et al.* 2017). *Japonochytrium* was the second valid and legitimate genus name, with the type species *Japonochytrium marinum* Kobayashi & Ookubo (Kobayashi & Ookubo 1953). Goldstein & Belsky (1964) proposed the name “*Schizochytrium*”, but they failed to designate a nomenclatural type for “*Schizochytrium aggregatum*”. Accordingly, “*Schizochytrium*” and “*Schizochytrium aggregatum*” are not valid names (ICN Art. 40.1, Melbourne Code, McNeill *et al.* 2012). Specifically, Art. 40.1 states “Publication on or after 1 January 1958 of the name of a new taxon of the rank of genus or below is valid only when the type of the name is indicated (see Art. 7 - 10; but see Art. H.9 Note 1 for the names of certain hybrids).” Goldstein & Belsky (1964) explicitly stated that they were using the International Code of Botanical Nomenclature (ICBN). A few years later Gaertner (1981) also overlooked Art. 40.1 when he proposed “*Schizochytrium minutum*”, and the name is also invalid.

Raghu-Kumar (1988a), when naming *Schizochytrium octosporum* Raghu-Kumar 1988a, specifically designated a holotype specimen: he stated “Holotypus: Figs 1-13, *ex cultura* 3283 (15) *ex* Rosfjord, Norway, June, 1980”. That is, the holotype is Figs 1-13, and the holotype is based upon study of culture strain 3283 isolated from Rosfjord, Norway. In 1988, an illustration was allowed as the nomenclatural type (see Arts 40.4, 40.5, Melbourne Code, McNeill *et al.* 2012), and because Raghu-Kumar's figures (Raghu-Kumar 1988, figs 1-13 represent a single plate based upon a single-cell culture isolate, this qualifies as a gathering or illustration (Art. 8.1, Art. 8.2). If we examine Art. 40.6, it states in the last sentence “But in the case of the name of a monotypic (as defined in Art. 36.6) new genus or subdivision of a genus with the simultaneously published name of a new species, indication of the type of the species name is sufficient”. Thus, Raghu-Kumar (1988a) inadvertently validated the name *Schizochytrium* when he described *Schizochytrium octosporum* Raghu-Kumar 1988a. That is, because the name “*Schizochytrium*” was not validly published and thus it was not recognized by the ICN, Raghu-Kumar could use the generic name.

Not realizing that Raghu-Kumar (1988a) had validly published the name *Schizochytrium*, Dick (2001) designated a nomenclatural type for two additional names: *S. aggregatum* S. Goldstein &

Belsky ex M.W.Dick 2001 and *S. minutum* A.Gaertner 1981 ex M.W.Dick 2001. Accordingly, these constitute five valid and legitimate names in the genus *Schizochytrium*.

In 2007, Yokoyama & Honda (in Yokoyama *et al.* 2007) proposed the name *Oblongichytrium*; however, the authors explicitly included *Schizochytrium octosporum* Raghu-Kumar 1988a as a species within *Oblongichytrium*, and they designated *Schizochytrium minutum* Gaertner 1981 ex M.W.Dick 2001 as the type species for *Oblongichytrium*. This rendered *Oblongichytrium* superfluous and thus illegitimate because one cannot include the nomenclatural type of a valid and legitimate genus (i.e. *Schizochytrium* Raghu-Kumar) within a newly proposed genus that has a different nomenclatural type (ICN Art. 11.3). As a consequence, while the name *Oblongichytrium* was validly published, it was an illegitimate name and it is to be rejected (Art. 52.1). When FioRito *et al.* (2016) described *Oblongichytrium porteri* FioRito & Leander, they did not realize that *Oblongichytrium* was illegitimate and they chose an illustration as the holotype (Art. 40.5 ICN). *Oblongichytrium porteri* is not available (=invalid) under the International Code of Zoological Nomenclature (ICZN) because there is no explicit fixation of a holotype (ICZN Art. 16.4.1) and no statement of depository (Art. 15.4.2). If we assume that the authors had technical difficulties preserving a biological specimen, then we can accept their holotype designation (ICZN Art. 40.5). Here, the name is combined based upon ICN Art. 55.1.

***Schizochytrium porteri*** (FioRito & Leander) R.A.Andersen & Ganuza *comb. nov.*

Basionym: *Oblongichytrium porteri* FioRito & Leander in FioRito *et al. Marine Biology* 163: 170. 2016.

*Schizochytrium octosporum* was described based upon material collected from Rosfjord, Norway, in the 1980s. The culture no longer exists (Raghu-Kumar pers. comm.), and there are no thraustochytrid cultures that are from the same geographic area. As a consequence, there are no known DNA sequences for *S. octosporum*. Even though Yokoyama *et al.* (2007) were in error nomenclaturally, one may choose to accept their taxonomic arguments, i.e. using different strains to represent the species (Honda *et al.* 1999, Yokoyama *et al.* 2007). Similarly, we can exclude *S. limacinum* (now included in *Aurantiochytrium*, Yokoyama & Honda 2007), and we can tentatively place *S. porteri* in *Schizochytrium* on molecular grounds (FioRito *et al.* 2016). This would tentatively limit *Schizochytrium* to four species in a taxonomic sense: *S. octosporum* Raghu-Kumar 1988a (type species), *S. minutum* Gaertner ex M.W.Dick, *Thraustochytrium multirudimentale* Goldstein ex M.W.Dick 2001 (see Yokoyama *et al.* 2007) and *S. porteri* (FioRito & Leander) R.A.Andersen & Ganuza, *comb. nov.* (see FioRito *et al.* 2016). However, these taxa cannot be placed in the family *Oblongichytriaceae* Cavalier-Smith 2012 (in Anderson & Cavalier-Smith 2112); an illegitimate generic name cannot be used as the basis for a family name unless conserved (ICN Art. 18.3). Furthermore, the family name must be typified using one of the included generic names in the family (ICN Art. 10.6). Because *Thraustochytrium* is the basis for the *Thraustochytriaceae*, the only available generic name for the new family is *Schizochytrium*. Here, we propose the name:

**Family *Schizochytriaceae*** R.A.Andersen & Ganuza, *fam. nov.*

Description: Swimming cells biflagellate, heterokont, somewhat elongate; ectoplasmic nets well developed; resting stages not known.

Type species: *Schizochytrium octosporum* Raghu-Kumar 1988a, *Transactions of the British Mycological Society.*, 90: 273, figs 1-13 (holotype).

The family *Schizochytriaceae* is placed in the order Thraustochytriales, or, if one follows the classification of Bennett *et al.* (2017), the order Labyrinthulales.

Conversely, Yokoyama & Honda (in Yokoyama *et al.* 2007) did validly and legitimately publish the name *Aurantiochytrium*, and the genus may possibly contain at least two species in a taxonomic sense: *Aurantiochytrium limacinum* (D.Honda & Ookochi) Yokoyama & D.Honda 2007 (type species) and *A. mangrovei* (Raghu-Kumar) Yokoyama & D.Honda 2007. Both are validly published as species of *Schizochytrium*, and both were transferred to the new genus. Yokoyama *et al.* (2007a) provided the incorrect year when citing the basionym for *S. mangrovei* Raghu-Kumar 1988b, but this error is automatically corrected (see Arts. 41.6, 41.8) and did not invalidate the name. More significantly, the *S. mangrovei* combination was based on culture isolate RCC893 from Hong Kong. The original material for *S. mangrovei* was from a mangrove in India (Kumar 1988b) and this organism is likely a different species from the organism in the Hong Kong culture strain RCC893. Yokoyama *et al.* (2007a) provided no morphological data that demonstrated the identity of the Hong Kong strain RCC893 with *S. mangrovei*. Therefore, the inclusion of *Schizochytrium mangrovei* in *Aurantiochytrium* is questionable. We suggest retaining the name in the genus *Schizochytrium* until further information is available.

The name *Botryochytrium* Yokoyama, Salleh & D.Honda 2007 was proposed as a separate genus, and the nomenclatural type was specified by the basionym *Ulkenia radiata* A.Gaertner (Gaertner 1977; Yokoyama *et al.* 2007). This is an interesting nomenclatural problem because initially *Ulkenia radiata* Gaertner was not validly published (no nomenclatural type was designated; ICN Art. 40.1) (Gaertner 1977). However, M.W.Dick (2001) validated the name *Ulkenia radiata* A.Gaertner 1977 ex M.W.Dick 2001, and this validation preceded the proposal of the name *Botryochytrium* (Yokoyama *et al.* 2007) (Art. 41.8). The same argument applies to *Parietichytrium* Yokoyama, Salleh & D.Honda 2007 and to *Sicyoidochytrium* Yokoyama, Salleh & D.Honda 2007 because the type species for these new genera were not validly published until validated by Dick (2001).

Returning to *Ulkenia*, a complex nomenclatural picture is apparent. Originally, Ulken (1965) proposed the name "*Thraustochytrium visurgense*" but no nomenclatural type was provided, and the name is thus not valid. Gaertner (1977) proposed the new generic name "*Ulkenia*" but he used the invalid "*Thraustochytrium visurgense*" as the type; therefore "*Ulkenia*" was invalid at that time. Gaertner (1977) included *Thraustochytrium amoeboideum* Bahnweg & Sparrow 1974 and "*Ulkenia sarkariana*" as an additional species of "*Ulkenia*", but because Gaertner (1977) included more than one species, the name was not inadvertently validated (ICN Art. 40.6, last sentence, see above). Dick (2001) validated the name *Thraustochytrium visurgense* Ulken ex M.W.Dick, and in turn this validated the generic name *Ulkenia* A.Gaertner ex M.W.Dick and Gaertner's combination *Ulkenia visurgensis* (Ulken) A.Gaertner ex M.W.Dick.

The taxonomic position of *Pyrrhosorus marinus* Juel (Juel 1901) is somewhat uncertain, but we here include it in the *Thraustochytriaceae* so that future workers do not overlook this taxon. The name was valid even though no holotype was designated; a holotype was not required prior to 1958 (ICN Art. 40.1). As far as we know, no lectotype or other nomenclatural type has been designated. Therefore, we designate a nomenclatural type as follows:

*Pyrrhosorus marinus* Juel 1901: **Lectotype here designated: pl. 1: fig. 1**, in Juel 1901, *Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar* 26, Afd. III, No. 14.

The name Thraustochytridiales was first proposed validly by Sparrow (1973), who provided a Latin description. There is some controversy regarding the family name *Thraustochytriaceae*. Sparrow (1942) simply listed the name without a description or diagnosis, and the name is consequently invalid. The following year, Sparrow (1943) provided a description in English. However, because the ICBN at the time required a description or diagnosis in Latin for fungal names (ICN Art. 39.1),

this name was also invalid as a fungal name. The fungal family name was subsequently validated by Cejp (1959) when he provided a Latin description in a taxonomic key (Cejp 1959: 419).

Interestingly, if one were to consider the *Thraustochytriaceae* as algae, then the name *Thraustochytriaceae* Sparrow 1943 would be valid, i.e., algal names were not required to have Latin descriptions prior to 1958 (ICN Art. 44.1). The genus *Thaustochytrium* was divided into four sections (Charkavarty 1979b).

To aid those scientists who may be less familiar with nomenclatural rules, we have assembled below the names of Thraustochytriales that are valid and legitimate. It should be stressed that this is a list of names, not a taxonomic classification, and thus some names appear more than once. It is difficult or impossible to provide a full taxonomic revision in a short note as original cultures have been lost, names have been assigned to DNA sequences even though the DNA originated far from the type localities, and incomplete life stages exist for some taxa. Our main aim is to clarify nomenclatural issues, and we hope that others address potential taxonomic issues in the future.

Please note that names with "ex" preceding an author name follow Art. 46.10. For example, it is correct to cite the name *Schizochytrium aggregatum* Goldstein & Belsky ex M.W.Dick or *Schizochytrium aggregatum* M.W.Dick, but the name *Schizochytrium aggregatum* S.Goldstein & Belsky is incorrect because it refers to an invalid binary designation.

#### Order Thraustochytriales Sparrow 1973

##### Family Althorinidiaceae E.G.B.Jones & Alderman 1972

*Althornia* E.G.B.Jones & Alderman 1971

*A. crouchii* E.G.B.Jones & Alderman 1971 - type species

##### Family Schizochytriaceae R.A.Andersen & Ganuza fam. nov.

*Schizochytrium* Raghu-Kumar 1988a

*S. aggregatum* S.Goldstein & Belsky ex M.W.Dick 2001

*S. limacinum* D.Honda & Yokochi 1998

*S. mangrovei* Raghu-Kumar 1988b

*S. minutum* A.Gaertner ex M.W.Dick 2001

*S. octosporum* Raghu-Kumar 1988a - type species

*S. porteri* (FioRito & Leander) R.A.Andersen & Ganuza

##### Family Thraustochytriaceae Sparrow 1943 (see text for an alternative)

*Aurantiochytrium* Yokoyama & D.Honda 2007

*A. limacinum* (D.Honda & Yokochi) Yokoyama & D.Honda 2007 - type species

*A. mangrovei* (Raghu-Kumar) Yokoyama & D.Honda 2007

*Botryochytrium* Yokoyama, Salleh & D.Honda 2007

*B. radiatum* (A.Gaertner ex M.W.Dick) Yokoyama & D.Honda 2007 - type species

*Elina* N.J.Artemchuk 1972 ex M.W.Dick 2001

*E. marisalba* N.J.Artemchuk ex M.W.Dick 2001 - type species

*E. sinorifica* N.J.Artemchuk ex M.W.Dick 2001

*Japonochytrium* Kobayashi & Ookudo 1953

*J. marinum* Kobashisi & Ookudo 1953 - type species

*Monorhizochytrium* Doi & D.Honda 2017

*M. globosum* (Kobashisi & Ookudo) Doi & D.Honda 2017 - type species

*Parietichytrium* Yokoyama, Salleh & D.Honda 2007b

*P. sarkarianum* (A.Gaertner ex M.W.Dick) Yokoyama & D.Honda 2007 - type species

*Pyrrhosorus* Juel 1901

- Pyrrhosorus marinus* Juel 1901 - type species  
*Sicyoidochytrium* Yokoyama, Salleh & D.Honda 2007b  
*S. minuta* (Raghu-Kumar ex M.W.Dick) Yokoyama & D.Honda 2007b - type species  
*Thraustochytrium* Sparrow 1936  
*T. aggregatum* Ulken ex M.W.Dick 2001  
*T. amoeboideum* Bahnweg & Sparrow 1974  
*T. antarcticum* Bahnweg & Sparrow 1974  
*T. aureum* S.Goldstein ex M.W.Dick 2001  
*T. benthicola* Raghu-Kumar ex M.W.Dick 2001  
*T. caudivorum* Schärer, Knoflach, D.B.Vizoso, Rieger & Peintner 2007  
*T. gaertnerium* Ru.Jain, Raghu-Kumar, Bongiorno & Aggarwal (in Bongiorno et al. 2005)  
*T. globosum* Kobayashi & Ookudo 1953  
*T. kerguelense* Bahnweg & Sparrow 1974  
*T. kinnei* A.Gaertner ex M.W.Dick 2001  
*T. motivum* SGoldstein 1963b ex M.W.Dick 2001  
*T. multirudimentale* Goldstein 1963b ex M.W.Dick 2001  
*T. proliferum* Sparrow 1936 - type  
*T. roseum* S.Goldstein 1963c  
*T. rossii* Bahnweg & Sparrow 1974  
*T. striatum* Joa.Schneider ex M.W.Dick 2001  
*T. visurgense* Ulken ex M.W.Dick 2001  
*Ulkenia* A.Gaertner ex M.W.Dick 2001  
*U. amoeboidea* (Bahnweg & Sparrow 1974) A.Gaertner 1977 ex M.W.Dick 2001 - type  
*U. minuta* Raghu-Kumar ex M.W.Dick 2001  
*U. profunda* A.Gaertner ex M.W.Dick 2001  
*U. radiata* A.Gaertner ex M.W.Dick 2001  
*U. sarkiana* A.Gaertner ex M.W.Dick 2001  
*U. visurgensis* (Ulken ex M.W.Dick 2001) A.Gaertner 1977 ex M.W.Dick 2001

While we did not examine the Order Labyrinthulales, we noticed that the name *Aplanochytrium kerguelensis* Bahnweg & Sparrow 1972 was validly published, and the original publication stated that the holotype was deposited in MICH. However, when inquiring about the holotype, MICH could not find the holotype (Michael Wynne, pers. comm.). Therefore, we designate a lectotype as follows:

*Aplanochytrium kerguelensis* Bahnweg & Sparrow 1972

**Lectotype here designated: Fig. 1** in Bahnweg & Sparrow 1972 *Archiv für Mikrobiologie* 81: page 46.

### Invalid binary designations

The following binary designations are invalid. We recommend that these names be validated using biological material for the nomenclatural type rather than illustrations (as permitted by ICN Art. 40.5) to facilitate further taxonomic studies.

“*Thraustochytrium arudimentale*” - see Artemchuk (1972); no nomenclatural type.

“*Thraustochytrium indicum*” - see Charkravarty (1979a); no nomenclatural type.

“*Thraustochytrium pachydermum*” - see Scholz (1958); no nomenclatural type.

“*Thanatostrea polymorpha*” - see Franc & Arvy (1969); no nomenclatural type.

We thank Drs Paul Kirk (*Index Fungorum*, Royal Botanic Gardens, Kew, U.K.), John McNeill (Royal Botanic Garden Edinburgh, U.K.), Richard Moe (*Index Nominum Algarum* University of

---

California, Berkeley, U.S.A.) and Dr Gary Rosenberg (The Academy of Natural Sciences of Drexel University, U.S.A.) for help with nomenclatural issues. We are grateful to Dr Michael Wynne (University of Michigan, U.S.A.) for a holotype search and for help obtaining several research publications, we thank Dr Pavel Škaloud (Charles University, Prague, Czech Republic) for help obtaining the Cejp publication, and we thank Dr Raghu-Kumar (Myko Tech Pvt. Ltd, Goa, India) for information about his old, now lost, cultures. We are very grateful to Dr Paul Kirk and an anonymous reviewer for greatly improving the manuscript.

- Anderson, O.R. & Cavalier-Smith, T. (2012) Ultrastructure of *Diplophrys parva*, a new small freshwater species, and a revised analysis of Labyrinthulea (Heterokonta). *Acta Protozoologica* 51: 291-304.
- Artemtchuk, N.J. (1972) The fungi of the White Sea. III. New phycomycetes, discovered in the Great Salma Strait of the Kandalakshial Bay. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* 13: 231-237.
- Bahnweg, G. & Sparrow, F.K. (1972) *Aplanochytrium kerguelensis* gen. nov. spec. nov., a new phycomycete from subantarctic marine waters. *Archiv für Mikrobiologie* 81: 45-49.
- Bahnweg, G. & Sparrow, F.K. (1974) Four new species of *Thraustochytrium* from Antarctic regions, with notes on the distribution of zoosporic fungi in the Antarctic marine ecosystems. *American Journal of Botany* 61: 754-766.
- Baldauf, S.A. & Palmer, J.D. (1993) Animals and fungi are each other's closest relatives: congruent evidence from multiple proteins. *Proceedings of the National Academy of Sciences, USA* 90: 11558-11562.
- Bennett, R.M., Honda, D., Beakes, G.W. & Thines, M. 2017. Labyrinthulomycota. pp. 507-542. In (Archibald, J.M., Simpson, A.G.B. & Slamovits, C.H. Eds.) *Handbook of the Protists*. 2nd Edition, Volume 1. Springer, Cham, Switzerland. 822 pp.
- Bongiorni, L., Jain, R., Raghukumar, S. & Aggarwal, R.K. (2005) *Thraustochytrium gaertnerium* sp. nov., a new thraustochytrid stamenopilan protist from mangroves of Goa, India. *Protist* 156: 303-315.
- Cejp, K. 1959. *Flora CSR*. Czechoslovak Academy of Sciences. 475 pp. [*Flora of Czechoslovakia*, Series B, Volume 2, Oomycetes I].
- Chakravarty, D.K. (1979a) A new marine phycomycete from Adyar Estuary of Madras (*Thraustochytrium indicum* sp. nov.). *Nova Hedwigia, Beiheft* 63: 27-32.
- Chakravarty, D.K. (1979b) A critical note on the genus *Thraustochytrium*. *Nova Hedwigia, Beiheft* 63: 325-332.
- Cienkowski, L (1867) Über den Bau und die Entwicklichen der Labyrinthuleen. *Archiv für Mikroskopische Anatomie und Entwicklungsmechanik* 3: 274-310.
- Dick, M.W. (2001) *Straminipilous Fungi. Systematics of the Peronosporomycetes including accounts of the marine straminipilous protists, the plasmodiophorids and similar organisms*. Kluwer Acad. Publ., Boston 670 pp + XV
- Doi, K. & Honda, D. (2017) Proposal of *Monorhizochytrium globosum* gen. nov., comb. nov. (Stramenopiles, Labyrinthulomycetes) for former *Thraustochytrium globosum* based on morphological and phylogenetic relationships. *Phycological Research* 65: 188-201.
- FioRito, R., Leander, C. & Leander, B. (2016) Characterization of three novel species of Labyrinthulomycota isolated from ochre sea stars (*Pisaster ochraceus*). *Marine Biology* 163: 170. DOI 10.1007/s00227-016-2944-5.
- Franc, A. & Arvy, L. (1969) Sur *Thanatostrea polymorpha* n.g., n.sp., agent de destruction des branchies et des palpes de l'Huître portugaise. *Compte Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris, Série D* 268: 3189-3190.
- Gaertner, A. (1967) Ökologische Untersuchungen an einem marinen Pilz aus der Umgebung von Helgoland. *Helgolander Wissenschaftliche Meeresuntersuchungen* 15: 181-192.

- Gaertner, A. (1977) Revision of the Thraustochytriaceae (Lower Marine Fungi) I. *Ulkenia* nov. gen., with description of three new species. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* 16: 139-157.
- Gaertner, A. (1981) A new marine phycomycete, *Schizochytrium minutum*, sp. nov. (Thraustochytriaceae) from saline habitats. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* 19: 61-69.
- Goldstein, S. (1963a) Development and nutrition of new species of *Thraustochytrium*. *American Journal of Botany* 50: 271-279.
- Goldstein, S. (1963b) Morphological variation and nutrition in a new monocentric marine fungus. *Archiv für Mikrobiologie* 45: 101-110.
- Goldstein, S. (1963c) Studies on a new species of *Thraustochytrium* that displays light stimulated growth. *Mycologia* 55: 799-811.
- Goldstein, S. & Belsky, M. (1964) Axenic culture of a new marine phycomycete possessing an unusual type of asexual reproduction. *American Journal of Botany* 51: 72-78.
- Gunderson, J.H., Elwood, H., Ingold, A., Kindle, K. and Sogin, M.L. (1987) Phylogenetic relationships between chlorophytes, chrysophytes, and oomycetes. *Proc. Natl. Acad. Sci. USA*, 84:5823-5827.
- Honda, D., Yokochi, T., Nakahara, and Higashihara, T. 1998. *Schizochytrium limacinum* sp. nov., a new thraustochytrid from a mangrove area in the west Pacific Ocean. *Mycological Research* 104: 439-448.
- Honda, D., Yokochi T., Nakahara, T., Raghukumar, S., Nakagiri, A., Schaumann, K, & Higashihara, T. (1999) Molecular phylogeny of labyrinthulids and thraustochytrids based on sequencing of 18S ribosomal RNA gene. *Journal of Eukaryotic Microbiology* 46: 637-647.
- Jones, E.B.G. & Alderman, D.J. (1971) *Althornia couchii* gen. et sp. nov, a marine biflagellate fungus. *Nova Hedwigia* 21: 381-399.
- Juel, H.O. (1901) *Pyrrhosorus*, eine neue marine Pilzgattung. *Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar* 26, Afd. III, No. 14. 1-16 + 2 plates.
- Kobayashi, Y. & Ookubo, M. (1953) Studies on marine phycomycetes. *Bulletin of the National Museum (Tokyo)* 33: 53-65.
- Marchan, L.F., Chang, K.J., Nichols, P.D., Mitchell, W.J., Polglase, J.L. & Gutierrez, T. 2017. Taxonomy, ecology and biotechnological applications of thraustochytrids: a review. *Biotechnology Advances*. <http://dx.doi.org/10.1016/j.biotechadv.2017.09.003>
- McNeill, J., Barrie, F.R., Buk, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen P.S., Knapp, S, Marhold, K., Prado, J., Prud'Homme van Reine W.F., Smith G.F., Wiersema, J.H., and Turland, N.J. (2012) International Code of Nomenclature for algae, fungi and plants (Melbourne Code). *Regnum Vegetabile* Vol. 154, Koeltz Scientific Books. 208 pp.
- Pan, J. del Campo, J. & Keeling, P.J. (2017) Reference tree and environmental sequence diversity of Labyrinthulomycetes. *Eukaryotic Microbiology* 64: 88-96.
- Raghu-Kumar, S. (1977) A new species of the genus *Ulkenia* Gaertner (lower marine fungi) from the North Sea. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* 16: 159-165.
- Raghu-Kumar, S. (1980) *Thraustochytrium benticola* sp. nov.: a new marine fungus from the North Sea. *Transactions of the British Mycological Society* 74: 607-614.
- Raghu-Kumar, S. (1988a) *Schizochytrium octosporum* sp. nov. and other thraustochytrids from the North Seas (Rosfjord, Norway). *Transactions of the British Mycological Society* 90: 273-278.
- Raghu-Kumar, S. (1988b) *Schizochytrium mangrovei* sp. nov., a thraustochytrid from mangroves in India. *Transactions of the British Mycological Society* 90: 627-631.
- Schärer, L., Knoflash, D., Vizoso, D.B., Rieger, G. & Peintner, U. 2007. Thraustochytrids as novel parasitic protists of marine free-living flatworms: *Thraustochytrium caudivorum* sp. nov. parasitizes *Macrostomum lignano*. *Marine Biology* 152: 1095-1104.

- 
- Schneider, J. (1967) Ein neuer mariner Phycomycet aus der Keiler Bucht (*Thraustochytrium striatum* spec. nov.). *Kieler Meeresforschungen, Institut fuer Meereskunde der Universitat Kiel* 23: 16-20.
- Scholz, E. (1958) Über morphologische Modifikationen bei niederen Erdphycomyceten und Beschreibung zweier neuer Arten von *Rhizopodium* und *Thraustochytrium*. *Archiv für Mikrobiologie* 29: 354-362.
- Sparrow, F.K. (1936) Biological observations on marine fungi from the Woods Hole waters. *Bulletin of the Marine Biological Laboratory, Woods Hole* 70: 236-363.
- Sparrow, F.K. (1942) A classification of the aquatic Phycomycetes. *Mycologia* 34: 113-116.
- Sparrow, F.K. (1943) *The Aquatic Phycomycetes, Exclusive of the Saprolegniaceae and Pythium*. University of Michigan Press, Ann Arbor. 785 pp.
- Sparrow, F.K. (1960) *Aquatic Phycomycetes*. 2<sup>nd</sup> Ed. University of Michigan Press, Ann Arbor. 1187 pp.
- Sparrow, F.K. (1973) Mastigomycotina (zoosporic fungi). vol. 4b, pp. 61-73. In (G.C. Ainsworth, F.K. Sparrow, & A.S Sussman, Eds) *The Fungi, an Advanced Treatment*. Academic Press, New York.
- Ulken, Annemarie (1965) Zwei neue Thraustochytrien aus der Aussenweser. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* 9: 289-295.
- Yokoyama, R. & Honda, D. (2007a) Taxonomic rearrangement of the genus *Schizochytrium sensu lato* based on morphology, chemotaxonomic characteristics, and 18S rRNA gene phylogeny (Thraustochytridaceae, Labyrinthulomycetes): emendation of *Schizochytrium* and erection of *Aurantiochytrium* and *Oblongichytrium* gen. nov. *Mycoscience* 48: 199-211.
- Yokoyama, R., Salleh, B. & Honda, D. (2007) Taxonomic rearrangement of the genus *Ulkenia sensu lato* based on morphology, chemotaxonomic characteristics, and 18S rRNA gene phylogeny (Thraustochytriaceae, Labyrinthulomycetes): emendation for *Ulkenia* and erection of *Botryochytrium*, *Parietichytrium* and *Sicyoidochytrium* gen. nov. *Mycoscience*, 48: 329-341.