



Scientific Names and Authors of current Tribes in the red algal family Rhodomelaceae (Ceramiales, Rhodophyta): a nomenclatural analysis

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Summary

This paper deals with the correct citation of names of authors of Tribes formed from genus names currently assigned to the Rhodomelaceae. Unfortunately, nomenclatural problems and incorrect author citations have occurred for various Tribe names currently placed in the Rhodomelaceae. According to Díaz-Tapia & al. (2017: 920), the Rhodomelaceae is the largest family of red algae with over 1000 currently recognized species and over 140 currently recognized genera. A nomenclatural overview dealing with the scientific naming of taxa, the citation of authors of scientific names and a nomenclatural analysis of the taxonomic ranks utilized by some previous authors, is followed by a detailed account of the correct Tribe names, author citations and associated information. A glossary of nomenclatural terms and phrases used in this account is also included.

Keywords: Nomenclature; Rhodophyta; Scientific naming; Codes of Nomenclature; Tribes of Rhodomelaceae; Author citations.

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Nomi scientifici e autori delle attuali Tribù delle alghe rosse appartenenti alla famiglia Rhodomelaceae (Ceramiales, Rhodophyta): un'analisi nomenclaturale

Riassunto

Questo lavoro tratta della corretta citazione dei nomi degli autori di Tribù formate da nomi di generi attualmente assegnati alle Rhodomelaceae. Sfortunatamente, si sono verificati problemi di nomenclatura e citazioni di autori errate per vari nomi di Tribù attualmente inserite nelle Rhodomelaceae. Secondo Díaz-Tapia & al. (2017: 920), le Rhodomelaceae sono la più grande famiglia di alghe rosse con oltre 1000 specie attualmente riconosciute e oltre 140 generi attualmente riconosciuti. Una panoramica nomenclaturale che tratta della denominazione scientifica dei taxa, la citazione degli autori dei nomi scientifici e un'analisi nomenclaturale dei ranghi tassonomici utilizzati da alcuni autori precedenti, è seguita da un resoconto dettagliato dei nomi corretti delle Tribù, delle citazioni degli autori e delle informazioni associate. È incluso anche un glossario dei termini e delle frasi nomenclaturali utilizzati in questo lavoro.

Parole chiave: Nomenclatura; Rhodophyta; Denominazione scientifica; Codici di nomenclatura; Tribù di Rhodomelaceae; Citazioni degli autori.

1. Introduction

The scientific naming of algae, fungi and plants has been governed by a *Code of rules* since 1867 when the first official version (Candolle, 1867b), of what is now the *International Code of Nomenclature for algae, fungi, and plants* (e.g. Turland & al., 2018), was published in French after adoption by the August 1867 International Botanical Congress in Paris. A preliminary French version (Candolle 1867a) was discussed and assessed during the Congress, and voted changes were made before final adoption and publication. H.A. Weddell, who was a member of the Committee that finalized the publication of Candolle (1867b), prepared and published an English translation of the official French version the following year (Weddell, 1868).

Further details on proceedings are in Candolle (1867b: 5-7) and in the English translation (Weddell, 1868: 5-7). Additional historical data are provided by McNeill & Greuter (1986: 4).

Prior to 1867, nomenclatural decisions were based on individual author judgements. There were no set guidelines. By contrast, ICN Principle VI now mandates that the rules of nomenclature are retroactive unless expressly limited. For algae, (Art. 13.1(e)), this means that, with certain exceptions (e.g. see Art. 13.1(e)), ICN rules apply to all algal names and nomenclatural acts published from 1 May 1753 onwards, even though authors such as J. Agardh (1863), Gifford (1853), Decaisne (1841, 1842) and Trevisan (1848) had no *Code* of rules for guidance, and authors such as Schmitz (1889), Schmitz & Falkenberg (1897), Falkenberg (1901) and De Toni (1903) had guidelines that have long been superseded by those in the current ICN.

The italicized word *Code* refers here to the *International Code of Nomenclature for algae, fungi, and plants* (ICN) (Turland & al., 2018) as well to any edition/version of its predecessors. The pending Madrid *Code*, an update of Turland & al. (2018), was not formally published at the time of manuscript submission. Changes to the Shenzhen Code (Turland & al., 2018) were approved at the IBC in Madrid on 27 July 2024 and were being dealt with by the Editorial Committee (ICN Div. III, Prov. 7.4) when this manuscript was submitted.

The cover of the first *Code* (Candolle, 1867b) includes the words “Deuxième Édition”. This refers to the fact that there was an earlier preliminary printed document (Candolle, 1867a) that was used for discussions and changes at the August 1867 Congress. Candolle (1867b), however, is the officially adopted first nomenclatural *Code* of ‘Laws of Botanical Nomenclature’. The words “Deuxième Édition” (Second Edition) do not appear in the translated English version (Weddell, 1868).

The *Code*, which has evolved through subsequent assessments and changes, is now organized into Articles, Notes and Recommendations, and is accompanied by Examples, a Glossary, and Name and Subject indices. The word *Code* did not appear in the publication title until 1952 (Lanjouw & al., 1952); the word “Laws” (Lois) was used in the Paris 1867 edition (Candolle, 1867b); and the Word “Rules” was used in the Vienna edition (Briquet, 1906), the Brussels edition (Briquet, 1912), and the Cambridge edition (Harms, 1935). The *Code* was titled *International Code of Botanical Nomenclature* from 1952 (Lanjouw & al., 1952) until 2012 (McNeill & al., 2012), when it was

changed to *International Code of Nomenclature for algae, fungi and plants*.

According to Díaz-Tapia & al. (2017: 920), the Rhodomelaceae Horaninow nom. cons. (1847: 238) is the largest family of red algae, with over 1000 currently recognized species and over 140 currently recognized genera. Earlier, Kylin (1928: 123) and Abbott (1999: 351) indicated that almost half of all known Florideophyceae belonged to the Rhodomelaceae, and Scagel (1953: 1) stated that of all families of the Florideophyceae, the Rhodomelaceae was the richest in species. Within the family, Díaz-Tapia & al. (2017: Fig. S1, Fig. S2 in the Supporting Information) listed 18-19 Tribes. The electronic resource AlgaeBase (<https://www.algaebase.org/>), searched on 28 November 2024, listed 7 subfamily names, 22 Tribe names and 232 Genus names for the Rhodomelaceae. The family is distributed in all oceans and seas throughout the world (Kamiya & al., 2017: 74).

Part I of the present paper includes nomenclatural overviews relating to the scientific naming of taxa and to the citation of authors of scientific names, and a nomenclatural analysis of the taxonomic ranks utilized by Schmitz (1889), Schmitz & Falkenberg (1897), Falkenberg (1901), De Toni (1903), and Hommersand (1963) for taxa between the principal ranks of family and genus within the Rhodomelaceae. Part II contains an account of the correct scientific names, author citations and associated information for Tribe names formed from genus names currently assigned to the Rhodomelaceae. Accounts of several informal names also are included. The Schmitz, Falkenberg, and De Toni publications provided the foundation for subsequent work on the recognition of subfamilies, tribes, and subtribes in Rhodomelaceae, as noted by Fritsch (1945: 543, 746), Scagel (1953: 1), Hommersand (1963: 165), and Díaz-Tapia & al. (2017: 921). In Part III a summary of nomenclatural outcomes is reported.

Internal evidence from the Schmitz, Falkenberg and De Toni publications, relevant versions of the *Code*, and other pertinent sources have been used to determine the nomenclaturally correct rank, authorship and orthography of taxon names. Information on type genus, type species, and related matters also are included.

This account is limited to the assessment of the application of correct taxon names and author citations for taxa and associated nomenclatural matters; it is not concerned with the classification and circumscription of taxa, both of which lie within the realm of taxonomy and outside the realm of nomenclature. Like other

scientific disciplines, the nomenclatural results and conclusions presented here are subject to future updating as further data become available from new research, revised *Codes* of nomenclature, and the discovery of hitherto obscure or overlooked publications.

Table 1 contains a glossary of nomenclatural terms and phrases used in this account. Herbarium acronyms (denoted in bold face), are taken from the electronic database Index Herbariorum (<https://sweetgum.nybg.org/science/ih/>). In Table 2, a chronological list of currently recognized Tribes and author citations of Rhodomelaceae, is provided.

2. Results

Part I. Nomenclatural and Taxonomic Overviews

Unless otherwise indicated, citations of *Code* Articles and other provisions in Parts I-III are those in the Shenzhen Code (Turland & al., 2018).

Scientific naming of taxa

The *Code* governs scientific naming of taxa at all taxonomic ranks (ICN Preamble 1). Each successive edition of the *Code* supersedes all previous editions (ICN Preamble 14).

Each family or lower ranked taxon with a particular circumscription, position, and rank can have only one correct scientific name (ICN Art. 11.1, 11.3, 11.4).

The principal and secondary ranks of taxa are listed in Art. 3 & Art. 4, respectively. 'Family' and 'Genus' are examples of principal ranks (Art. 3.1); 'Tribe' is a secondary rank between Family and Genus (Art. 4.1); and Subfamily is a further rank situated between the principal rank of Family and the secondary rank of Tribe (Art. 4.2).

Words used for ranks of taxa (e.g. Family, Subfamily, Tribe, Genus) are referred to as rank-denoting terms (see Art. 37.7, 37.8).

The sequence of ranks specified in Art. 4.2 must not be altered (Art. 5.1). Taxon names with misplaced rank-denoting terms are regarded as not validly published (Art. 37.6) and thus have no status under the ICN (Art. 12.1). To achieve a proper sequence of ranks, misplaced rank-denoting terms and taxon names must be removed from the sequence (see Art. 37.7).

Taxon names published with a rank-denoting term used at more than one non-consecutive position represent informal usage of that rank-denoting term, and taxon names published with such terms are treated as unranked (Art. 37.8).

Except as noted in Art. 37.3, a presumed taxon name published on or after 1 January 1953 without a clear indication of rank is not validly published (Art. 37.1) and thus is not a scientific name. It has no status under the ICN (Art. 12.1).

The phrase “subdivision of a family” refers to any taxon at a rank between family and genus (Art. 4, Note 2; also see definition in ICN Glossary). ‘Subfamily’, ‘Tribe’, and ‘Subtribe’ are the most frequent ranks used for subdivisions of a family.

Names of families, subfamilies, tribes and subtribes are formed from the name of an included genus (Art. 18.1, 19.1, 19.3).

A taxon name published before 1 January 1953 without a clear indication of rank but which otherwise meets all requirements for valid publication is validly published, but it has no status in questions of priority (Art. 37.3, including Ex. 3), except for purposes of homonymy under Art. 53.3. Such a taxon name, however, can serve as a basionym or replaced synonym for a subsequent new combination, name at new rank or replacement name (all defined in the ICN Glossary) at a definite rank (Art. 37.3).

For a suprageneric taxon name published on or after 1 January 1887, the use of a specified termination listed in Art. 37.2, footnote 1 is accepted as an indication of the corresponding rank unless:

- a) the taxon name has an explicitly designated rank (which takes precedence); or
- b) the indication would result in a rank sequence contrary to Art. 5.1; or
- c) the indication would result in a rank sequence in which the same rank-denoting term occurs at more than one hierarchical position.

Art. 37.2c is applied to take account of the historical situation in which the (Latin) termination *-eae* was specified for taxon names in both the ranks of Subfamily and Tribe in the 1867 *Paris Code* (Candolle, 1867b, Art. 23, 24), and this was not updated until adoption of the 1905 *Vienna Code* (Briquet, 1906). Thus, for presumed taxon names of subfamilies or Tribes ending in *-eae* and published between 1 January 1887 and 17 June 1905, additional evidence is needed to determine which rank applies.

Suprageneric taxon names published prior to 1887 without a clear indication of rank (Table 1) are treated as unranked (Art. 37, Ex. 1).

The phrase “name at new rank” is used for a legitimate name whose rank has been changed. In terms of rank, the name has a new status, denoted as stat. nov. (status novus) (see Art. 32, Recommendation 32A). The name on which the name at new rank is based is its basionym (see ICN Art. 6.10). For names of families and of subdivisions of families, both the new name and the name on which it is based (the basionym) have the same stem and thus are formed from the same genus name and have the same nomenclatural type. Example: Tribe Bostrychieae Womersley, stat. nov. (2003: 361). Basionym: Bostrychioideae Falkenberg (1901: 700, 714, 747, as Bostrychieae). ICN Art. 41 deals with the nomenclatural requirements for valid publication of a name at new rank. Parenthetical author citations of the basionym [e.g. (Falkenberg) Womersley] are not used for suprageneric names (ICN Art. 49.2).

Author citations of scientific names

Rules for the citation of authors of scientific names occur in ICN Art. 46-50 (also see Art. 22.1, 26.1, 38.14, 41.3, 41.5). Accurate author citation data for names of taxa, including bibliographic data, provides important information about the original source and date of a name that is highly desirable or essential in monographic, floristic, and various other published accounts, particularly accounts in which nomenclatural novelties occur. These include name of a new taxon, a new combination, name at new rank, and replacement name, all defined in the ICN Glossary. Also see Table 1 in this paper.

Author citations may be required for valid publication. For example, ICN Art. 41.5 reads: “on or after 1 January 1953, a new combination, name at new rank, or replacement name is not validly published unless its basionym or replaced synonym is clearly indicated and a full and direct reference given to its author and place of valid publication, with page or plate reference and date...”. Art. 41.5 also specifies that on or after 1 January 2007, the actual basionym or replaced synonym also must be cited for valid publication to occur. For names published before 1 January 1953, see Art. 41.3.

Author citations and associated bibliographic data can also help to clarify issues of name priority (Art. 11), help to distinguish between apparent homonyms (Art. 53), help to identify basionyms (Table 1), isonyms (Art. 6, Note 2), and homotypic synonyms (Table 1), help to locate obscure publications in which names first appeared, and help to determine whether or not a document containing putative names

is effectively published (Art. 29-31). Author citations are not part of a scientific name; rather they are appended to a name (see definition of 'author citation' in Table 1 and in the ICN Glossary).

Author information also is important for identifying what appear to be scientific names but are not validly published; these supposed names are referred to as designations (Table 1; see definition in ICN Glossary; also see Art. 20.4 & 23.6). Names that are not validly published have no status under the ICN (Art. 12.1).

Isonyms result when same name based on the same type is published independently at different times perhaps by different authors (ICN Art. 6, Note 2 including Ex. 1-3). Only the earliest isonym of a group has nomenclatural status (Art. 6, Note 2); the other isonyms are without nomenclatural status (see Art. 6, Ex. 1-3) and may be disregarded (Art. 6, Note 2) except for conserved family names, as noted in Art. 14.14. For other aspects involving author documentation, consult the ICN Subject index entry "Author citation". In this account, genus names and author citations were checked against entries in the electronic resource *Index Nominum Genericorum*.

Contributions of Schmitz, Falkenberg & De Toni: general information

The accounts of Schmitz (1889), Schmitz & Falkenberg (1897), Falkenberg (1901), and De Toni (1903) were published when the 1867 Paris Code (Candolle 1867b) was in effect from 23 August 1867 to 17 June 1905 (when the Vienna Code became effective). The current hierarchy of taxonomic ranks (see ICN Art. 4.2, Turland & al., 2018) was standardized in Art. 8-10 of the 1867 Paris Code; the specified ranks from family (Ordo) to genus in descending order are Family, Subfamily (subordo), Tribe (tribus), Subtribe (subtribus) and Genus.

Terminations for Latin names also were specified in the 1867 Paris Code: *-aceae* for family names (Art. 21) with certain exceptions (specified in Art. 22); *-eae* for both subfamily names (Art. 23) and (Art. 24) Tribe names; and (Art. 24) *-ineae* for subtribes. The use of the same termination (*-eae*) for subfamily and Tribe names led to confusion in publications such as Schmitz (1889), Schmitz & Falkenberg (1897) and Falkenberg (1901) where the rank was not clearly and consistently specified before each name, as was done, for example, in De Toni (1903).

Use of the same Latin termination (*-eae*) for both subfamily names and tribe names was updated in Art. 23 of the 1906 Vienna Code (Briquet 1906); for subfamilies, the termination was changed to *-oideae*, while for tribes, the termination remained unchanged (*-eae*).



Fig. 1. Portrait of Friedrich Schmitz.

The significance of this is that until adoption of the 1906 Vienna Code, names that end in “*-eae*” could indicate either a subfamily or a tribe name. Consequently, for suprageneric taxon names published between 1 January 1887 and 17 June 1905 (when the Vienna Rules became effective; see Shenzhen Code Art. 14, Note 4), one cannot automatically assume under Shenzhen Code Art. 37.2 that the termination *-eae* is really an unequivocal indication of the rank of Tribe unless the rank-denoting term ‘Tribe’ accompanies the taxon name. Thus, any decisions as to the intended rank must be based on other internal evidence (Table 1) in the relevant publication.

In the context of the Rhodomelaceae, internal evidence is required to determine the rank intended by Schmitz (1889), Schmitz & Falkenberg (1897) and Falkenberg (1901) for names of subdivisions (Table 1) of the family Rhodomelaceae. De Toni (1903), by contrast, specified the rank (subfamily) for each subdivision of the family Rhodomelaceae that he recognized.

Treatment of names between family and genus in Schmitz 1889

When (Carl Johann) Friedrich Schmitz (8 March 1850–28 January 1895) published his 1889 account *Systematische Übersicht der bisher bekannten Gattungen der Florideen* (Systematic overview of the hitherto known genera of Florideophyceae), he was based at the Universität Greifswald in Greifswald, Germany, where he was Professor of Botany and Director of the Botanical Gardens.

The portrait in Fig. 1 was reproduced from Bryant & Irvine (2002); the original is housed at the Universitätsarchiv Greifswald (UAG), Fotosammlung in Greifswald, Germany. Bryant & Irvine (2002) provided biographic data and a detailed account of the microscope slide collection of Schmitz and his assistant, Paul Hauptfleisch, housed in the herbarium at the Natural History Museum, London (BM). The collection contains over 7000 slides (mostly of red algae) and was purchased by the BM in 1899.

Hauptfleisch (1895), Falkenberg (1896), and Stafleu & Cowan (1985: 262–264) provided further information on Schmitz; additional information on P. Hauptfleisch is in Stafleu & Cowan (1979: 102–103). Both Falkenberg and Hauptfleisch finalized work on the red algae for *Die natürlichen Pflanzenfamilien* 1(2) [Rhodophyceae: 298–544] Engler & Prantl, (eds.) (1897) after the death of Schmitz in January 1895.

Schmitz (1889: 437, 446) acknowledged Falkenberg for help with the Rhodomelaceae. Schmitz (1889: 446–449) recognized seven suprageneric taxa within the Rhodomelaceae: Rhodomeleae, Laurenciaeae, Amansieae, Polysiphonieae, Pollexfenieae, Dasyeae, Polyzonieae. Schmitz did not specify ranks before each name, all of which terminate in *-eae*, thus creating uncertainty as to whether he was treating these taxa as taxonomic tribes or as subfamilies in the context of Art. 23 & Art. 24 of the 1867 Paris *Code*, which was in effect in 1889. On p. 436, however, Schmitz wrote:

“Ebenso auch wird die Eintheilung der einzelnen Familieu in Tribus voraussichtlich noch mehrfach abgeändert werden müssen.” (Likewise, the division of individual families into tribes probably will have to be modified several times.).

This statement provides internal evidence that Schmitz actually regarded his names to apply to tribes (not subfamilies).

Author citations (with bibliographic data), while informative, are not generally required by the current ICN (see Art. 46.1). Of the seven tribes included by Schmitz, the Tribe Dasyeae J Agardh (1863: 793–794), is validly published and has been transferred from the Rhodomelaceae. Currently, dasyoid algae either are treated as a

distinct family, the Dasyaceae (e.g. Parsons & Womersley in Womersley 1998; Norris & al 2017; Huisman 2018; Nielsen & al. 2022) or as a distinct subfamily in the Delesseriaceae (e.g. Choi & al., 2002; Díaz-Tapia & al., 2019; Cormaci & al., 2023; Kang & al., 2024).

The 'Tribe' name "Polyzonieae Schmitz" (1889: 449) is a designation; it lacks a description and was not validly published in 1889. Subsequently, however, Falkenberg (in Schmitz & Falkenberg, 1897: 461) validly published it as the name of a Tribe; the Tribe is dealt with in Part II.

The remaining five Tribe names were validly published, namely the Rhodomeleae J. Agardh (1841: 23); the Laurencieae Gifford (1853: 155); the Amansieae Horaninow (1847: 238); the Polysiphonieae J. Agardh (1863: 792-3) and the Pollexfenieae J. Agardh (1863: 793). These Tribe names also are dealt with in Part II.

Treatment of names between family and genus in Schmitz & Falkenberg 1897

When Schmitz died (28 January 1895), his manuscript on the Rhodophyceae for *Die natürlichen Pflanzenfamilien* (Engler & Prantl, 1897) was not completed. This task was undertaken by Paul Hauptfleisch (1861-1906) with support from Paul Falkenberg. Hauptfleisch (in Schmitz & Hauptfleisch, 1896: 298, footnote) thanked Falkenberg for his support and noted that Falkenberg had taken over the reworking of the Rhodomelaceae.

Paul Falkenberg (2 September 1848 – 1 November 1925) was based at the Universität, Rostock, Germany where he was Professor of Botany and Director of the Botanical Garden from 1887-1923. Falkenberg's major research interest was the morphology and taxonomy of the red algal family Rhodomelaceae.

The portrait in Fig. 2 was supplied courtesy of Dr. Svenja Heesch, Institute of Biosciences, University of Rostock. Further information on Falkenberg is in Gassner (1927), Dorr & Nicolson (2008: 28-30) and at the University of Rostock

(https://cpr.uni-rostock.de/resolve/id/cpr_person_00002500).

Falkenberg (in Schmitz & Falkenberg, 1897: 421, footnote) reported that the manuscript left by Schmitz for his family was from 1892 and had not been touched since; that data for 16 of the 78 genera of Rhodomelaceae were not yet included; and that the "Einteilung der Familie" (Classification of the Family, meaning the key to family subdivisions and genera) (Schmitz & Falkenberg, 1897: 425-430),

likewise was not present, probably (according to Falkenberg) because Schmitz might have been waiting until the publication of the monograph of Falkenberg (which did not occur until 1901).

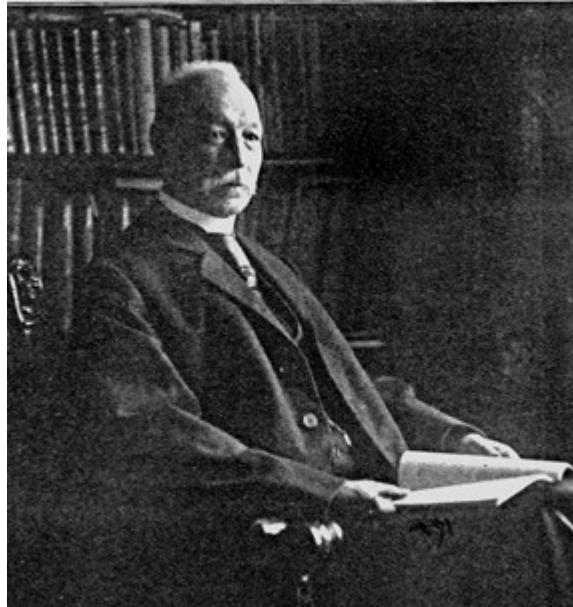


Fig. 2. Portrait of Paul Falkenberg.

Falkenberg (in Schmitz & Falkenberg, 1897: 421, footnote) also noted that Schmitz had completed only one illustration (Fig. 241 in Engler & Prantl 1897) and that Falkenberg added a number of unpublished figures from his forthcoming monograph with the permission of the zoological Station at Naples (in whose series *Fauna und Flora des Golfes von Neapel* the Falkenberg treatise was published in 1901).

These comments, particularly the absence of the taxonomic key, provide evidence that it was Falkenberg, not Schmitz, who authored the key and made the final decisions on the taxonomic rank used for family subdivision names in the taxonomic key and elsewhere in the 1897 account.

Falkenberg (in Schmitz & Falkenberg, 1897) recognized nine suprageneric taxa within the family Rhodomelaceae: the Laurencieae (p.430), Chondrieae (p.432), Polysiphonieae (p.436), Lophothalieae (p.445), Rhodomeleae (p.453), Herposiphonieae (p.457), Polyzonieae (p.461), Amansieae (p.465), and Dasyeae (p.471). All these names

have the Latin termination –eae, but lack a rank-denoting term, thus creating uncertainty as to whether they were names of tribes or subfamilies in the context of Art. 23 & Art. 24 of the 1867 Paris Code (Candolle 1867b), which was in effect in 1897.

In the paragraph immediately preceding the taxonomic key on p. 425, however, the above taxa are repeatedly referred to as Tribes, thus providing unequivocal internal evidence that Tribe is the rank to which Falkenberg assigned them. There is no mention of the rank of subfamily in this paragraph.

Additional direct evidence occurs on p. 461 where Falkenberg states:

“Die Gattung *Herpopteros* zeigt einen Typus dorsiventraler Organisation, der unter den R. bisher ganz allein steht und keiner der 3 Tribus der Herposiphonieae, Polyzonieae und Amansieae sich direct anschließt.” (The genus *Herpopteros* shows a type of dorsiventral organization that is so far unique among the Rhodomelaceae and does not directly join any of the three Tribes Herposiphonieae, Polyzonieae and Amansieae”).

In addition, on p. 472, Falkenberg states:

“Die Dasyeae sind unter allen Tribus der Rhodomelaceae wohl am schärfsten abgegrenzt” (The Dasyeae are probably the most clearly defined of all the tribes of the Rhodomelaceae).

Falkenberg was definitely using the rank of Tribe.

However, several anomalous/contradictory inconsistencies occur elsewhere in Schmitz & Falkenberg (1897). In a footnote on p. 421, Falkenberg refers to Schmitz' names as “seiner Unterfamilien” (his subfamilies); and on p. 430, just after the taxon key, Falkenberg again refers to “der Schmitz'schen Unterfamilien” (Schmitz's subfamilies) followed by some generic names (not subfamily names). We have found no instance in which Schmitz assigned the rank subfamily to a taxon of Rhodomelaceae.

On p. 437 (just prior to the account of *Digenia*), Falkenberg refers to the Polysiphonieae as a subfamily in one paragraph, but as a Tribe in the very next paragraph, resulting in a direct contradiction in ranks. On p. 446, in comments under the genus *Brongniartella*, Falkenberg refers to the ‘Polysiphonieen and the Lophothalieen as Unterfamilien in direct contradiction with explicit references to these taxa as Tribes on p. 425.

These anomalous/contradictory referrals, unfortunately, were apparently missed in proofreading and editing prior to publication; they are inconsistent with the more definitive statements of

Falkenberg on p. 425, 461 & 472. In our view, such inconsistencies/contradictions constitute errors in Schmitz & Falkenberg (1897) that should have been eliminated before publication. As a result, they are best disregarded. The current ICN also allows for the disregarding of later isonyms (ICN Art. 6, Note 2) and of admixtures for typification purposes (Art. 8.2, ICN Glossary).

If one accepts the definitive use of the rank of tribe by Schmitz & Falkenberg (1897: 425), then the Laurenciae (p. 430), Chondrieae (p. 432), Polysiphoniae (p. 436), Lophothalieae (p. 445), Rhodomeleae (p. 453), Herposiphoniae (p. 457), Polyzoniae (p. 461), Amansieae (p. 465), and Dasyeae (p. 471) are Tribes. This conclusion is consistent with the evidence-based conclusion that Schmitz (1889) regarded his family subdivision names to be Tribes.

Treatment of names between family and genus in Falkenberg 1901

The monumental morphoanatomical and taxonomic treatise *Die Rhodomelaceen des Golfes von Neapel und der angrenzenden Meeres-Abschnitte* by Falkenberg (1901), is centred on taxa in the Mediterranean Sea, but is world-wide in scope and includes taxa from as far away as Australia and New Zealand. Unfortunately, the nomenclature of suprageneric taxon 'names' in Falkenberg (1901) is complex and at times confusing.

Falkenberg was inconsistent in the use of Germanic and Latin names for supergeneric groups of Rhodomelaceae and in the use of apparent rank-denoting terms for particular groups. In the Index, Falkenberg (1901: 746-754) included the following Latinized names with the Latin termination *-eae*, but without an explicitly designated taxonomic rank: Amansieae (p. 746); Bostrychieae (p. 747); Chondrieae (p. 747); Dasyeae (p. 748); Herposiphoniae (p. 750); Heterocladieae (p. 750); Laurenciae (p. 750); Lophothalieae (p. 751); Polysiphoniae (p. 752); Polyzoniae (p. 752); Pterosiphoniae (p. 752); and Rhodomeleae (p. 753). In the Index, each Latin name included referrals to two bold-faced page numbers: one to an extended description in the text, and one to a page in the taxonomic key; the key contains diagnostic features used for identification and circumscription. These Latin names also were included as a list in the diagram on p. 700 showing perceived phylogenetic relationships but were not used elsewhere in Falkenberg (1901).

By contrast, in the Inhalt (Contents) (pp. XIII-XVI), the main text (especially pp. 110-699 & 701-713), and the Synoptische Uebersicht (Synoptic overview; essentially a taxonomic key) (pp. 714-732),

Falkenberg used Germanic names, with the non-Latin termination *-een*. Thus, the Latin Amansieae became the Germanic Amansieen (p. 402), the Bostrychieae became the Bostrychieen (p. 504), the Chondrieae became the Chondrieen (p. 187) and so forth. The Germanic names with the *-een* termination were employed much more frequently.

ICN Art. 19.7 specifies that if a name of a subdivision of a family is published with a non-Latin termination, it is not validly published. Thus, Falkenberg's Germanic names with the non-Latin termination *-een* are not validly published and have no status under the ICN (Art. 12.1).

Falkenberg also was inconsistent in the use of the rank-denoting terms family and subfamily for the same taxonomic group. For example, in the first paragraph of his comments on phylogeny, Falkenberg (1901: 698) provided unequivocal evidence that he was grouping the genera of Rhodomelaceae into subfamilies. Thus:

“Bei der Darstellung der speciellen morphologischen Verhältnisse einer Reihe von Rhodomelaceen-Typen ist oben so verfahren worden, dass einzelne grössere Gruppen von zweifellos nahe verwandten Gattungen direct zu Unterfamilien vereinigt worden sind...”. (In presenting the special morphological relationships of a number of Rhodomelaceae groups, the procedure above was such that individual larger groups of undoubtedly closely related genera were directly combined into subfamilies...”).

On p. 84, Falkenberg used the phrase **“den übrigen Unterfamilien der Rhodomelaceen”** (the other subfamilies of the Rhodomelaceae), and on p. 714, Falkenberg's first sentence in the Synoptic overview of the genera and species of Rhodomelaceae stated:

“Während die p. 700 gegebene Darstellung die Absicht hat, den inneren Zusammenhang zwischen den einzelnen Unterfamilien darzulegen, wie er sich aus den oben niedergelegten Detailuntersuchungen mir als das allgemein wissenschaftliche Resultat ergeben hat, sucht dieser Schlussabschnitt den Wünschen derer gerecht zu werden die den Werth einer Abhandlung mehr nach ihrer praktischen Brauchbarkeit bemessen.” (While the diagram on p. 700 has the intention of presenting the internal connection between the individual subfamilies that emerged as the general scientific result from the detailed investigations set out above, this final section seeks to do justice to the wishes of those who value that a Treatise is measured more according to its practical usefulness.)

The diagram on p. 700 includes the list of 12 names with the Latin termination *-eae*. These names with Latin terminations also occur in the Index. It is clear from these examples that Falkenberg was treating these groups as subfamilies.

Falkenberg's treatment differs markedly elsewhere in the main text where he refers to his groups as families in major headings and in the subsequent text, where taxon names have the Germanic termination *-een*. For example, on p. 402, the major section heading reads: **"Die Familie der Amansieen"** (The Amansien family), and the first sentence reads:

"Die Amansieen bilden eine äusserst scharf umgrenzte Familie der Rhodomelaceen." (The Amansiens form a very clearly defined family of Rhodomelaceae.).

Similarly, on p. 359, the major section heading reads: **"Die Familie der Polyzonieen"** (The Polyzonien family), and the first sentence reads:

"Die Familie der Polyzonieen zeigt den dorsiventralen Typus der Herposiphonieen weiter entwickelt." (The Polyzonien family exhibits the dorsiventral type of the Herposiphonieen further developed.).

All major section headings for the groups have the same format, as is evident in the Inhalt (Contents) (Falkenberg, 1901: xiii-xvi).

As mentioned above, and in accord with Art. 23 and Art. 24 of the 1867 Paris Code (Candolle, 1867b), which was in effect in 1901, the Latin termination *-eae* was used both for subfamily names and tribe names. Unfortunately, Falkenberg (1901) did not specify a rank in the Index or the Synoptische Uebersicht (Synoptic Overview) descriptions, but it is clear from numerous references to these names (including ones with German terminations) elsewhere in the text that, in 1901, Falkenberg was treating all of these as subfamily names (e.g. see Falkenberg, 1901 pp. 8, 71, 84, 93, 103, 110, 164, 184, 187, 188, 287, 299, 318, 591, 698, 705, 714). This is especially clear in comments on p. 698 and p. 714.

The use of *'-eae'* as the termination for two ranks was rectified in the 1906 Vienna Code (Briquet, 1906, Art. 23) when the subfamily termination was changed to *'-oideae'*

On several pages (p. 31, 181, 300) of the main text, however, Falkenberg (1901) referred to one or two particular groups as tribes, but elsewhere in the publication, the same groups are treated as subfamilies. On p. 31, for example, Falkenberg refers to "die ganze Tribus der Laurencieen und Chonrdrieen" (the entire tribes of the

Laurencieen and the Chondrieen) but on p. 187 and p. 235 these become Die Familie der Chondrieen and Die Familie der Laurencieen respectively. These inconsistencies seem likely to be uncorrected errors missed during proofreading and editing prior to publication.

Based on the above evidence, it is our opinion that the names Amansieae, Bostrychieae, Chondrieae, Dasyeae, Herposiphonieae, Heterocladieae, Laurencieae, Lophothalieae, Polysiphonieae, Polyzonieae, Pterosiphonieae, and Rhodomeleae were being treated as subfamily names in Falkenberg 1901. The treatment of names with the Latin termination *-eae* as subfamily names persisted for many years after 1905 (e.g. Mazza, 1909; Lucas, 1909; Børgesen, 1915-20, 1918; De Toni & Forti, 1922; Børgesen, 1937; Lucas & Perrin, 1947; Scagel, 1953, 1962a) even though under Art. 32.2 names with improper terminations but otherwise in accordance with the *Code* must be updated in accord with Art. 23 & 24 without change of authorship or date. A detailed analysis of the nomenclature of subfamily names is outside the scope of the current publication.

Treatment of names between family and genus in De Toni 1903

Giovanni Battista De Toni (2 January 1864 – 31 July 1924) was based at the Università degli Studi di Modena e Reggio Emilia, Modena, Italy, where he served as a Professor of Botany and Associate Director of the Botanical Garden. Further information on De Toni is in Béguinot (1925), Forti (1925; 1926), Stafleu & Cowan (1976: 637-638) and Stafleu & Mennega (1998: 240-248).

The portrait in Fig. 3a originally appeared as the frontispiece in Vol. 4(3) of *Sylloge Algarum* (De Toni, 1903). The portrait in Fig. 3b originally appeared in Forti (1926).

In taxonomic works, Giovanni Battista De Toni should not be confused with Giuseppe De Toni (his son). In the literature, Giovanni Battista De Toni is correctly abbreviated to De Toni, while his son is abbreviated G. De Toni. Further data are in Stafleu & Mennega (1998: 240, 248). Two years after Falkenberg (1901) published his treatise, De Toni (1903) published Volume 4 (Section 3) of his multivolume work *Sylloge Algarum*, subtitled *Sylloge Floridearum*. The volume contains accounts of taxa in the families Rhodomelaceae and Ceramiaceae.

Within the Rhodomelaceae, De Toni recognized 14 subfamilies. His “Conspectus subfamiliarum consists of a key and brief descriptions of each subfamily. The subfamilies Endosiphonieae De Toni (p. 776bis, 1001) and Pachychaeteae De Toni (p. 776bis, 1005) are

newly described; the remaining 12 subfamilies are those recognized by Falkenberg (1901), although there are a number of authorship errors. De Toni did not recognize Tribes.

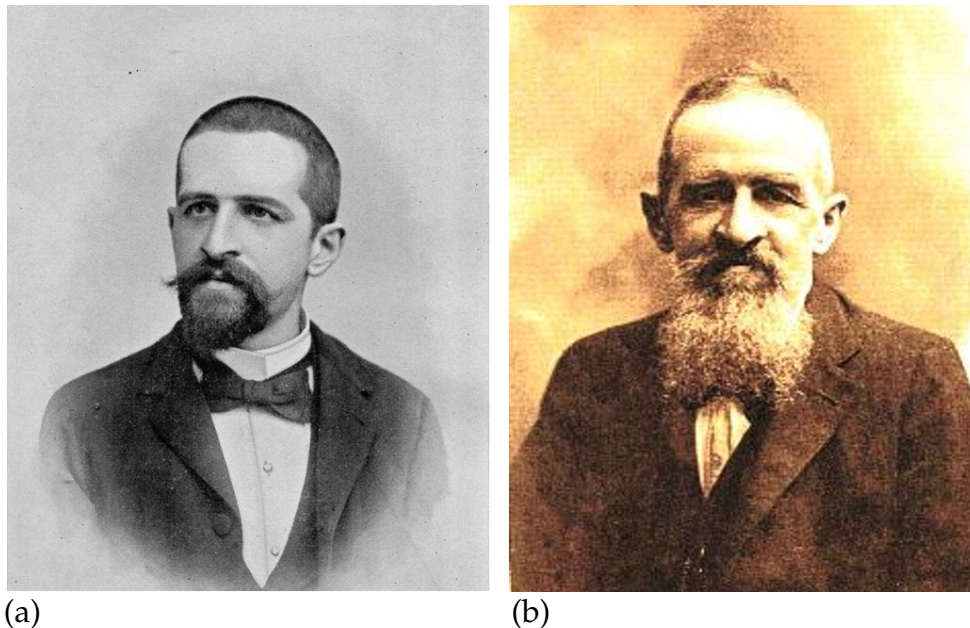


Fig. 3. Portraits of Giovanni Battista De Toni appeared in (a) De Toni (1903) and (b) Forti (1926).

The fact that both Falkenberg (1901) and De Toni (1903) subdivided the Rhodomelaceae into subfamilies almost certainly prompted various subsequent authors (e.g. Mazza (1905, 1909; Lucas 1909; Børgesen 1915-20, 1918; De Toni & Forti 1922; Børgesen 1937; Lucas & Perrin 1947; Scagel 1953, 1962a, 1962b) to do the same, all with the incorrect Latin termination *-eae*.

By contrast, Kylin (1956: 494-501) did not recognize formal taxonomic subfamilies or tribes, but instead informally subdivided the Rhodomelaceae into a series of 'Groups' based on generic names. These Gruppen (Groups) do not have nomenclatural status under the ICN (Art. 12.1); they are not validly published names of taxa.

Treatment of names between family and genus from 1963

Hommersand (1963) examined representative species of a considerable number of genera of Rhodomelaceae (and Ceramiaceae) as well as some Delesseriaceae and Dasyaceae to acquire a better

understanding of the relationships among families of Ceramiales and of the classification of the Ceramiaceae and Rhodomelaceae.

With respect to the Rhodomelaceae, Hommersand (1963: 334-335) concluded that the family was best subdivided into three subfamilies (the Bostrychioideae, Rhodomeloideae, & Polysiphonioideae) and that most of the remaining subfamilies recognized by earlier authors were best treated as Tribes.

Hommersand (1963: 334) also concluded that groups within subfamilies of the Rhodomelaceae corresponded in rank to the tribes of the Ceramiaceae, and, consequently, he referred to them as tribes. Hommersand (1963: 343, fig. 52; 346-348) listed names of 13 tribes, eight of which (Amansieae, Chondrieae, Laurencieae, Lophothalieae, Pleurostichidae, Polysiphonieae, Polyzonieae, Rhodomeleae) were validly published previously, and five (Bostrychieae, Heterocladiaceae, Lophosiphonieae, Pterosiphonieae, Streblocladiaceae) which, unfortunately, were not validly published by Hommersand. Further comments are below in the relevant accounts of Tribes.

In *Seaweeds of the British Isles*, Maggs and Hommersand (1993) subdivided the Rhodomelaceae into two subfamilies (the Bostrychioideae for the Tribe Bostrychieae; and the Rhodomeloideae for 12 tribes with British representatives).

In the *Marine Benthic Flora of Southern Australia*, Womersley (2003: 168-169) subdivided the Rhodomelaceae into Tribes, but he also informally recognized the Lophosiphonia Group and the Placophora Group of Kylin (1956) because (Womersley, 2003: 168) noted that they "...have not been designated as tribes...".

In *Phycologia Europaea Rhodophyta*, a compilation of European red algal literature records for the Baltic Sea, the Arctic Ocean, the NE Atlantic Ocean and the Mediterranean Sea, Athanasiadis (2016) subdivided the Rhodomelaceae into eight subfamilies: Bostrychioideae, Chondrioideae, Herposiphonioideae, Laurencioideae, Lophothlioideae, Polysiphonioideae, Rhodomeloideae, and Rytiphloideae (including the Tribe Amansieae); and he subdivided the Polysiphonioideae into four Tribes: Alsidieae, Lophosiphonieae, Polysiphonieae (including the subtribe Digeneinae), and Pterosiphonieae.

Díaz-Tapia & al. (2017: 923) reported that proposals to subdivide the Rhodomelaceae into three (Hommersand, 1963) or two subfamilies (Maggs & Hommersand, 1993) were not supported in a genome-scale phylogeny, and that results from their analysis of data from 89 genera and 497 species, supported recognition of 16 Tribes,

including five newly described Tribes. Díaz -Tapia & al. (2017) apparently were unaware of the treatment of Athanasiadis (2016).

Díaz -Tapia & al. (2017: 932) also cautioned that further investigations are needed and that there are at least 647 species and 60 genera of Rhodomelaceae for which molecular data were not present in 2017. It seems clear that our understanding of the biodiversity and phylogeny of the Rhodomelaceae requires considerably more research and refinement.

The nomenclatural results and conclusions presented in the present account also are subject to updating as further data become available from new research, and from revised *Codes* of nomenclature, and through the discovery of hitherto obscure or overlooked publications.

Part II. Nomenclatural Updates of Tribe Names Currently Placed in the Rhodomelaceae

During preparation of the account of the red algal family Rhodomelaceae for the *Flora marina bentonica del Mediterraneo* (Cormaci & al., 2025), it became apparent that incorrect author citations were being used in the literature for a number of Tribe names currently placed in that family, and in some cases, other nomenclatural problems also were evident.

The nomenclatural significance of correct author citations for scientific names, considered above in Part I, prompted a new nomenclatural analysis of Tribe names and associated author citations to ensure that each Tribe name and each author citation was correct and in accord with the *International Code of Nomenclature for algae, fungi, and plants*, namely the 'Shenzhen Code' (Turland & al., 2018). Other nomenclatural problems also have been addressed.

The current edition of the *Code* supersedes all previous editions (ICN Preamble 14). Although nomenclatural actions of previous authors may have been in accord with the *Code* in effect at the time of publication (e.g. Schmitz, 1889, Falkenberg, 1901), or may have preceded publication of the first *Code* (Candolle, 1867b) (e.g. Horaninow, 1847, J. Agardh, 1863), current nomenclatural Rules must prevail when assessing nomenclatural actions in previous publications.

Outcomes are provided below. Names of Tribes (formed from genus names currently placed in the Rhodomelaceae) are dealt with in alphabetical order. Table 2 lists names in chronological order for purposes of priority determination (ICN Art. 11). The application of

names at the rank of family or below is determined by means of nomenclatural types (Art. 7.1). All tribe names dealt with here are based on non-fossil types.

For purposes of designation or citation of the type of any subdivision of a family, the generic name alone suffices (Art. 10.9). In turn, **the type of a genus name is the type of a species name in accord with Art. 10.1 - 10.7; and the type of a species name is a specimen or illustration (Art. 8.1).**

Names of type species were checked in the *Index Nominum Genericorum* (online at <https://naturalhistory2.si.edu/botany/ing/>) in January-February 2025 and against original publications. According to statements on the ING website, "This electronic version must be considered a draft edition. The database is constantly being revised as new information becomes available." ING upload dates are given for each entry.

Code Appendices are online at <https://botany.si.edu/references/codes/props/>. The family name Rhodomelaceae is listed in ICN Appendix IIA as a conserved family name. Conserved genus names are listed in ICN Appendix III. Names can be conserved in accord with ICN Art. 14 to avoid disadvantageous nomenclatural changes resulting from the strict application of ICN rules (Articles, Principles, etc).

Accounts of currently recognized Tribes of Rhodomelaceae follow. Each account includes point-form statements which can be cross-compared and Additional Remarks usually pertaining only or mainly to the taxon in that particular account. Some accounts also have Background information.

In the accounts that follow, phrases such as "...Falkenberg (in Schmitz & Falkenberg, 1897: 435)" or "...Díaz-Tapia & Maggs (in Díaz-Tapia & al., 2017: 932)" mean that the person(s) cited before the word "in" authored some information in the publication cited in parentheses. For example, the statement "*Cladurus* Falkenberg (in Schmitz & Falkenberg, 1897: 435)" means that Falkenberg authored the genus name *Cladurus* on p. 435 in the 1897 publication of Schmitz & Falkenberg. Similarly, the statement "Tribe **Cladureae** Díaz-Tapia & Maggs (in Díaz-Tapia & al., 2017: 932)" means that Díaz-Tapia & Maggs authored the Tribe name Cladureae on p. 932 in the 2017 publication of Díaz-Tapia & al. Further information on citations using "in" is provided by Turland (2019: 97).

A phrase such as "*Bostrychia kelanensis* Grunow *ex Post*" means that Post authored the species name but ascribed it to Grunow as an "honorary" author. Further information on citations using "ex" is provided by Turland (2019: 96).

Taxon names published with improper Latin terminations have been corrected in accord with Art. 18.4, 19.7. or 32.2 without change of authorship or date; the improper version used by an author is noted in parentheses. Examples include “the Bostrychioideae (as Bostrychieae)”; “the Heterocladiaceae (as Heterocladieae)”; “Heterocladioideae (as Heterocladieae)”; “the Tribe name Laurencieae (as Laurenciaceae)”; “Subfamily Pterosiphonioideae (as Pterosiphonieae)”; “Polyzonioideae (as Polyzonieae)”, etc.

Tribe **Alsidieae** J. Agardh (1863: 792).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (J. Agardh, 1863: 792).
- Genera included in the Tribe Alsidieae by J. Agardh (1863: 792): *Alsidium* C. Agardh; *Bostrychia* Montagne (in Sarga 1842: 39) nom. cons.; *Bryothamnion* Kützinger; *Digenea* C. Agardh; *Odonthalia* Lyngbye, nom. cons.; *Rhodomela* C. Agardh, nom. cons.. Conserved genus names listed in ICN Appendix IIIA.
- Tribe name Alsidieae formed from the Genus name *Alsidium* C. Agardh (1827: 639) in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Alsidieae is the type of the genus name *Alsidium* (Art. 10.9). *Alsidium* is typified by the type of *A. corallinum* C. Agardh, according to the *Index Nominum Genericorum* (9 Feb 1996).
- Tribe name Alsidieae assigned by J. Agardh (1863: 792) to the family Rhodomelaceae. Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. Díaz-Tapia & al. (2017: 933) concluded that the Tribe name Alsidieae was not validly published by J. Agardh (1863: 792) but rather was validly published by Ardissonne (1883: 352). Díaz-Tapia & al. (2017: 933) stated that:

“although J. Agardh (1863) provided a diagnosis for the Tribe Alsidieae, he included this “tribus” and other tribes as sections of the Ordo Rhodomeleae so it is not valid under ICBN Art. 37.6–8 which states that names of taxa with misplaced rank are invalid. Therefore, the first valid publication of the Tribe Alsidieae was by Ardissonne (1883).”

Unfortunately, this statement is incorrect.

J Agardh (1863: 792) introduced the Tribe name Alsidieae in *Species, genera et ordines algarum*, a three-volume work published in

nine instalments from 1848-1901. The ranks to which J. Agardh assigned the Tribe Alsidieae and the genus *Alsidium* are explicitly indicated partly in Vol 1 (J. Agardh, 1848) and partly in Vol. 2 (J. Agardh, 1851) as follows:

Regnum Algarum – J. Agardh (1848: Vol. 1: Title page).

Classis Floridearum – J. Agardh (1851: Vol. 2. Title page for Vol 2(1) just after the main title page for Vol 2).

Series Desmiospermeae – J. Agardh (1851: Vol. 2(1), p. VII).

Subseries Corynospermeae – J. Agardh (1851: Vol. 2(1), p. XI).

Ordo Rhodomeleae - J. Agardh (1851: Vol. 2(1), p. XI; 1863: Vol. 2(3), p.787).

Tribus Alsidieae – J. Agardh (1863: Vol. 2(3), p.792).

Genus *Alsidium* – J. Agardh (1863: Vol. 2(3), p. 838).

Contrary to Díaz-Tapia & al. (2017: 933), Agardh (1863: 792) did **not** treat the Tribe Alsidieae or other Tribes as ‘Sections’ of the “Ordo Rhodomeleae”. ‘Ordo Rhodomeleae’ is correctable to ‘Family Rhodomelaceae’ under ICN Art. 18.2 of the Shenzhen Code (Turland & al., 2018). This correctability stems from the original Paris Code (Candolle, 1867b: Art. 8, 10, 21, Commentaire, item 8) (also see Weddell, 1868 for English translation) where *ordo* and *familia* were considered interchangeable. In addition, J. Agardh (1863) did **not** use the rank-denoting term “Section” (a rank between Genus and Species; see Art. 4.1); as evidenced above, he used the descending sequence Ordo (correctable to Family), Tribus, Genus, which is in accord with ICN Art. 5 as well as Art. 3 and Art. 4). There is **no misplaced term** involving the rank of Tribe; thus, **ICN Art. 37.6 is not relevant** to the valid publication of the Tribe Alsidieae J. Agardh.

Furthermore, Art. 37.7 & 37.8 do not render the Tribe name Alsidieae invalid. Recognition by J. Agardh (1863) of “**Series** Desmiospermeae” and “**Subseries** Corynospermeae” between the ranks of Class (Classis) and Family (Ordo, Familia) with misplaced rank-denoting terms does not affect the valid publication status of the Tribe Alsidieae J. Agardh because J. Agardh correctly placed the Tribe Alsidieae between the ranks of Family and Genus, as required by ICN Art. 37.6.

However, because the ranks of Series and Subseries are specified ranks between species and variety (Art. 4.1, 4.2), the use of Series and Subseries by J. Agardh between the principal ranks of Class (Classis) and Family (Ordo) **does** involve misplaced rank-denoting terms (Art. 37.6). Consequently, in accord with ICN Art. 37.7 (Turland & al., 2018), the misplaced rank-denoting terms “Series” and “Subseries” of J. Agardh **must be removed** so as to achieve a proper rank sequence

[Class-Family ('Ordo')-Tribe-Genus]. Therefore, in accord with Art. 37.7, the names "Desmiospermeae" and "Corynospermeae" are to be regarded as not validly published and thus have no status under the ICN (Art. 12.1).

Art. 37.8 is not relevant because J. Agardh (1863) did not use a rank-denoting term (e.g. Tribe; Section) at more than one non-consecutive position in his taxonomic sequence.

Thus, J. Agardh (1863: 792) validly published the Tribe name Alsidieae. However, the name was (initially) superfluous under Art. 52.1 because J. Agardh (op. cit.) included the genus *Rhodomela* C. Agardh, nom. cons., the type of the earlier Tribe name Rhodomeleae J. Agardh (1841: 23) in the Alsidieae. In accord with ICN Art. 11.3, the Tribe Rhodomeleae (J. Agardh, 1841) has nomenclatural priority against the Tribe Alsidieae (J. Agardh, 1863) (Art. 11.3) when *Rhodomela* and *Alsidium* are placed in the same Tribe.

Although superfluous when published, the Tribe name Alsidieae is not illegitimate because (Art. 52.4, last part of first sentence & Art. 52, Ex. 17) it is formed from a legitimate generic name (*Alsidium*). Thus, as noted in the last sentence of Art. 52.4, the Tribe name Alsidieae, when published was incorrect, but it may become correct later. Another example of a name that was initially superfluous but not illegitimate and became correct later is the Family name Rhodomelaceae (see Silva 1980: 87).

Subsequently, J. Agardh (1892: 142) placed *Alsidium* in the Tribe Polysiphonieae J. Agardh. This implies that J. Agardh concluded that the Tribe Alsidieae was a heterotypic synonym of the Tribe Polysiphonieae; however, J. Agardh (1892) did not mention the Tribe Alsidieae. As a result of J. Agardh's 1892 treatment, and in accord with ICN Art. 11.5, the Tribe name Polysiphonieae J. Agardh (1863: 792) has priority over the Tribe name Alsidieae J. Agardh (1863: 792).

To become correct again in the context of Art. 52.4, the Tribe name Alsidieae would need to be treated as a distinct taxon, while, at the same time, the type of the Tribe Rhodomeleae, *Rhodomela*, would need to be excluded from the Tribe Alsidieae, either explicitly or by implication (Art. 52.2(e), including Ex. 5, 6).

Díaz-Tapia & al. (2017: 927, 928, 931) treated the Tribe Rhodomeleae, including the genus *Rhodomela*, and the Tribe Alsidieae (p. 931, 933), including the genus *Alsidium*, as distinct tribes of Rhodomelaceae (no subfamilies), thus rendering the Tribe Alsidieae correct again. Both tribe names and both generic names are

validly published and legitimate, and thus are in accord with the ICN.

The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1 in the Supporting Information) did not include data from any species identified as *Alsidium*. Consequently, even though *Bryothamnion* and *Digenea* have resolved in a single clade with strong support (Díaz-Tapia & al., 2017: 927), the nomenclatural application of the Tribe name Alsidieae to a clade that does not include data from the type species or any other species of *Alsidium* is tenuous and requires further assessment once samples of the type and other species of *Alsidium* become available.

The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig. S2 in the Supporting Information) analysis included 5 samples from 5 species representing 3 genera among which was one sample and 2 sequences identified as *A. corallinum* (Table S4), the type species of *Alsidium*. *Alsidium*, *Bryothamnion*, and *Digenea* were resolved in a moderately supported clade (Díaz-Tapia & al., 2017: 927).

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae. Díaz-Tapia & al. (2017: 933) provided an emended description of the Tribe.

Tribe **Amansieae** P. Horaninow (1847: 238).

- Validly published as a legitimate name of a Tribe. Description provided (Horaninow, 1847: 238); taxonomic rank explicitly indicated in book title (*Characteres Essentiales Familiarum ac Tribuum Regni Vegetabilis et Amphorganici...*).
- Genera included in the Tribe Amansieae by Horaninow (1847: 238-239): *Amansia* J.V.F. Lamouroux; *Carpoblepharis* Kützing; *Dictyomenia* R. Greville; *Odonthalia* Lyngbye, nom. cons.; *Ornomenia*, nomen; *Pollexfenia* W. Harvey; *Polyzonina* Suhr; *Rytiphlaea* C. Agardh. Conserved genus name listed in ICN Appendix IIIA.
- Tribe name Amansieae formed from the Genus name *Amansia* J.V.F. Lamouroux (1809: 332), in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Amansieae is the type of the genus name *Amansia* (Art. 10.9). *Amansia* is typified by the type of *A. multifida* J.V.F. Lamouroux, the only species included in the genus protologue (Lamouroux, 1809: 332); listed in *Index Nominum Genericorum* (9 Feb 1996).

- Tribe name *Amansieae* assigned by Horaninow (1847: 238) to the Family Rhodomelaceae. Family name conserved listed in ICN Appendix IIA.

Additional Remarks. The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1 & Table S3 in the Supporting Information) include single samples of *Kuetzingia canaliculata* (Greville) Sonder and *Osmundaria fimbriata* (J.V.F. Lamouroux) R.E. Norris but no samples of *Amansia*. Consequently, even though *Kuetzingia canaliculata* and *Osmundaria fimbriata* have resolved in a single clade with strong support (Díaz-Tapia & al., 2017: 927), the nomenclatural application of the Tribe name *Amansieae* to a clade that did not include data from the type species or any other species of *Amansia* is tenuous and requires further assessment once samples of the type and other species of *Amansia* and of additional related genera become available.

The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig. S2 in the Supporting Information), included 35 samples representing 14 genera (11 of which were type species samples) and a further 9 samples identified as *Amansia* (including five samples identified to three species). Although the *Amansieae* was resolved as monophyletic with strong support (Díaz-Tapia & al., 2017: 927), the fact that the genus *Amansia* apparently is not monophyletic suggests that the application of the Tribe name *Amansieae* to the clade needs to be confirmed by including data from several samples of the type species, *A. multifida*, as well as additional species of the genus.

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae. Díaz-Tapia & al. (2017: 927) provided an updated description of the Tribe and noted that while their clade is resolved as monophyletic with strong support, relationships among species are in general not well supported, and revision is needed at generic level because *Amansia*, *Osmundaria* J.V.F. Lamouroux, and *Vidalia* J.V.F. Lamouroux ex J. Agardh apparently are not monophyletic.

Tribe name **Bostrychieae**: background information.

The algal Tribe Bostrychieae (Rhodomelaceae, Ceramiales, Rhodophyta), although widely attributed to Falkenberg (1901: 504) in the recent literature and in a number of online resources, was actually first validly published (inadvertently) as a taxon name by Womersley (2003: 361).

Extensive evidence from within Falkenberg (1901), detailed in Part I of the current account, demonstrates that Falkenberg validly published a series of Subfamily names (not Tribe names), including the Bostrychioideae (as Bostrychieae) using the Latin termination *-eae* which was in accord with (Candolle, 1867b: Art. 23), the *Code* in effect in 1901. In accord with ICN Art. 19.7, the Latinized subfamily name “Bostrychieae Falkenberg” (1901: 700, 714, 747) with the improper termination *-eae* must be changed to subfamily Bostrychioideae Falkenberg (1901: 700, 714, 747) with the proper termination *-oideae* without change of authorship or date.

In Candolle (1867b: Art. 23), the Latin termination *-eae* was specified for **both** subfamily names and tribe names, and this has caused considerable subsequent confusion and misinterpretation. As mentioned above, this situation was rectified in the Vienna Code (Briquet, 1906: Art. 23) where the specified Latin termination for subfamily names was changed to *-oideae* while the Latin termination *-eae* was retained for tribe names.

We are unaware of the use of a suprageneric taxon formed from the genus name *Bostrychia* Montagne (in Sagra, 1842) that was explicitly called the “Tribe Bostrychieae” prior to 1963 when Hommersand (1963: 311; 317; 334; 335; 343, Fig. 52; 346) did so, thereby effectively publishing the Tribe Bostrychieae as a taxonomic name in accord with ICN Art. 29 – 30.

Hommersand (1963), however, did **not** validly publish the ‘Tribe Bostrychieae’ as the name of a new taxon because he did not provide a Latin description or diagnosis or a reference to a previously and effectively published Latin description or diagnosis as required by ICN Art. 44.1. Hommersand (1963) also did not publish the ‘Tribe Bostrychieae’ as a name at new rank (defined in ICN Glossary) because he did not provide a full and direct reference (Art. 41.5) to its basionym.

As explained below, valid publication first occurred in Womersley (2003: 361) as a name at new rank (stat. nov.) (defined in the ICN Glossary; also see Table 1 in the present account), not as the name of a new taxon.

The intended name ‘Tribe Bostrychieae’ in King & Puttock (1989: 8) and in Maggs & Hommersand (1993: 286) cannot be interpreted as a new name of a taxon (no Latin descriptions are provided) or as a stat. nov. based on the name Subfamily name Bostrychioideae Hommersand (1963: 334) because the Hommersand ‘subfamily name’ is an isonym (defined in ICN Art. 6, Note 2 & ICN Glossary &

in Table 1 in this account) of the earlier Subfamily name *Bostrychioideae* Falkenberg (1901, as *Bostrychieae*). Later isonyms have no status under the *Code* and thus are not legitimate and cannot serve as a basionym for a name at new rank.

Tribe **Bostrychieae** Womersley (2003: 361, stat. nov.).

Basionym: Subfamily **Bostrychioideae** Falkenberg (1901: 700, 714, 747, as *Bostrichieae*). Improper Latin termination (defined in ICN Glossary) *-eae* corrected to *-oideae* in accord with ICN Art. 19.7, 32.2, 37.2 (footnote) without change of authorship or date.

- The **Tribe** *Bostrychieae* validly published by Womersley (2003: 361) as a legitimate name of a Tribe. Taxonomic rank explicitly indicated and description provided. As explained below, Womersley (2003: 361) actually inadvertently validly published the Tribe name *Bostrychieae* as a stat. nov. for the subfamily name *Bostrychioideae* Falkenberg (1901, as *Bostrychieae*). The name ‘Tribe *Bostrychieae*’ (Hommersand, 1963: 334, 335, 346) is not validly published (see background information above).
- Genera included in the Tribe *Bostrychieae* by Womersley (2003: 371): *Bostrychia* Montagne (in Sagra 1842: 39), nom. cons.; *Stictosiphonia* W.H. Harvey & J.D. Hooker (1847: 483). Conserved genus name listed in ICN Appendix IIIA. Subsequently, Zuccarello & West (2006: 31) proposed, on the basis of a phylogenetic analysis, that all species placed in *Stictosiphonia* by King & Puttock (1989) be returned to *Bostrychia*. The Zuccarello & West (2006: 27) analysis, however, did not include material of the lectotype species of *Stictosiphonia*, *S. hookeri* (W. H. Harvey) W. H. Harvey & J.D. Hooker (1847: 483) (basionym: *Bostrychia hookeri* W. H. Harvey (in J.D. Hooker & W.H. Harvey 1845: 269).
- Tribe name *Bostrychieae* Womersley formed from the genus name *Bostrychia* Montagne nom. cons. in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe *Bostrychieae* (and Subfamily *Bostrychioideae*) is the type of the genus name *Bostrychia* (Art. 10.9). *Bostrychia* is typified by the type of *B. scorpioides* (Hudson) Montagne (typ. cons.) (basionym: *Fucus scorpioides* Hudson), according to the *Index Nominum Genericorum* (9 Feb 1996).
- Tribe name *Bostrychieae* assigned by Womersley (2003) to the family Rhodomelaceae. Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. To determine whether the Tribe Bostrychieae Womersley (2003: 361) qualifies as a name at new rank (stat. nov.), the requirements of relevant provisions of ICN Art. 41 (Turland & al., 2018) must be considered. Art. 41.5 reads:

41.5. On or after 1 January 1953, a new combination, name at new rank, or replacement name is not validly published unless its basionym or replaced synonym is clearly indicated and a full and direct reference given to its author and place of valid publication, with page or plate reference and date (but see Art. 41.6 and 41.8). On or after 1 January 2007, a new combination, name at new rank, or replacement name is not validly published unless its basionym or replaced synonym is cited.

Art. 41.5 itself does not explain what is precisely different between a basionym being “clearly indicated” and a basionym actually being “cited”. This, however, is clarified by Ex. 16 which reads:

Ex. 16. The new combination *Conophytum marginatum* subsp. *littlewoodii* (L. Bolus) S. A. Hammer (Dumpling & His Wife: New Views Gen. *Conophytum*: 181. 2002), because it was made prior 10 January 2007, was validly published even though Hammer did not cite the basionym (*C. littlewoodii* L. Bolus) but only indicated it by giving a full and direct reference to its place of valid publication.

Thus, based on Ex. 16, a clear indication of the basionym involves giving a “full and direct reference to its author and place of valid publication, with page or plate reference and date”.

Womersley (2003: 361) provided the following text information: “Tribe Bostrychieae Falkenberg 1901: 504”, and the following entry occurs in the References (Womersley 2003: 504):

“FALKENBERG. P. 1901. Die Rhodomelaceen des Golfes von Neapel und der angrenzenden Meeres-abschnitte. Fauna und Flora des Golfes von Neapel. Monogr. 26 (Friedlander: Berlin).”

Collectively, these two pieces of information constitute a clear indication of a full and direct reference to the basionym data required by Art. 41.5, namely: author (P. Falkenberg), place of valid publication (Fauna und Flora des Golfes von Neapel. Monogr. 26, Friedlander: Berlin), and page reference and date (1901: 504). There are no omissions (Art. 41.6) from the requirements of a ‘clear indication’.

The Womersley (2003) format does not strictly agree with ICN Recommendation 41A.1 which states that all this information “should immediately follow a name at new rank. It should not be provided by mere cross-reference to a bibliography...”. However, Turland (2019: 39)

pointed out that such split references still are full and direct. By meeting the requirements of Art. 41.5, the requirement of Art. 41.1 and the conditions mentioned in Art. 41.6 also are satisfied.

Art. 41.2(a) requires that “for a name of a family or subdivision of a family, the basionym or replaced synonym must be a name of a family or subdivision of a family”.

Womersley’s (2003: 361) reference to Falkenberg (1901: 504) refers to the original description of the Subfamily Bostrychioideae Falkenberg (as Bostrychieae). Womersley (2003: 361) changed the rank of that name to Tribe Bostrychieae and thus effectively and validly published a name at new rank. This meets the requirement in Art. 41.2(a). Remaining provisions of Art. 41 are not relevant.

We unaware of any earlier publication in which the Tribe Bostrychieae was effectively and validly published as a stat. nov. with the explicitly stated rank of Tribe. The intended name Tribe Bostrychieae (Hommersand, 1963) was not validly published, as explained in the background information above. The name Tribe Bostrychieae likewise is not validly published in King & Puttock (1989) or in Maggs & Hommersand (1993) as explained in the background information above.

Based on DNA sequences from the nuclear-encoded 26S ribosomal RNA gene and plastid-encoded *rbcL* gene, Zuccarello & West (2006) concluded that all species be returned to the genus *Bostrychia* due to as yet a not fully resolved or supported phylogeny. Within the genus, two clades occurred and differed in attachment structure anatomy. Their data also showed that many of the currently circumscribed species were not monophyletic.

The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1 and Table S3 in the Supporting Information) contained information from single samples of three species of *Bostrychia* but did not include the type species *B. scorpioides*. A confirming analysis is needed once samples of the type species and several additional species of *Bostrychia* become available.

In the constrained taxon-rich tree (Díaz-Tapia & al. 2017: Fig. S2 & Table S4 in the Supporting Information), they found (p. 926) that all *Bostrychia* samples, including two of the type species, *B. scorpioides*, were placed together in an unsupported clade that consisted of two larger groups (clades) of 17 and eight species of *Bostrychia*, as well as the Heterocladieae, and a single species (*Bostrychia kelanensis* Grunow *ex Post*) without close relatives. The two larger groups corresponded to the two groups reported by Zuccarello & West (2006) that are

based on differences in the anatomy of attachment structures. Díaz-Tapia & al. (2017: 926) also thought that the positioning of the Heterocladieae among the Bostrychieae was likely to be an artefact due to the lack of overlapping markers in the dataset. Further assessments obviously are needed.

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae.

Tribe **Chondrieae** J. Agardh (1841: 20).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (J. Agardh, 1841: 20).
- Genera included in the Tribe Chondrieae by J. Agardh (1841: 20): “*Huic tribi adnumero...*” (I add to this tribe...)” *Bonnemaisonia* C. Agardh; *Calocladia* Greville; *Champia* Desvaux, *Chondria* C. Agardh, nom. cons.; *Laurencia* J.V.F. Lamouroux nom. cons.; *Lictoria* J. Agardh, gen. nov.; and *Mammea* J. Agardh, gen. nov. Conserved genus names listed in ICN Appendix IIIA.
- Tribe name Chondrieae formed from the genus name *Chondria* C. Agardh (1817: xviii), nom. cons., in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Chondrieae is the type of the genus name *Chondria* (Art. 10.9). *Chondria* is typified by the type of *C. tenuissima* (W. Withering) C. Agardh (basonym: *Fucus tenuissimus* W. Withering), according to the *Index Nominum Genericorum* (9 Feb 1996). According to Wynne (1991), the oldest correct name for *Chondria tenuissima* (W. Withering) C. Agardh is *Chondria capillaris* (Hudson) M. Wynne (basonym: *Ulva capillaris* Hudson (1778: 591)). The nomenclatural type of *Chondria*, however, remains the type of *Chondria tenuissima* (W. Withering) C. Agardh under ICN Art. 10.2 because the Hudson species was **not** definitely included in the protologue of *Chondria* by C. Agardh (1817: xviii) and has not been conserved as nomenclatural type of *Chondria* under Art. 14.9 (also see Art. 10.4). Withering (1796: 117) did not list the Hudson species as a synonym of his *Fucus tenuissimus*.
- Tribe name Chondrieae assigned by J. Agardh (1841: 7, 20) to a ‘familia’ (p. 7) called the ‘Florideae’, a ‘name’ **not** formed from the name of an included genus (Art. 32.1(c)), as required by Art. 18.1, and thus, ‘Florideae’ not validly published as a family name for nomenclatural purposes. This does not affect the validity of the tribe name Chondrieae.

Additional Remarks. Horaninow (1847:238) included *Chondria* in the Tribe Rhodomeleae (see below), thereby rendering the Tribe Chondrieae a heterotypic synonym of the Tribe Rhodomeleae. The two tribe names were published simultaneously by J. Agardh (1841). Horaninow's treatment established nomenclatural priority for the Tribe Rhodomeleae against the Tribe Chondrieae in accord with ICN Art. 11.5 when both genera are placed in the same Tribe.

Schmitz (1889: 448) included *Chondria* in the Tribe Polysiphonieae J. Agardh (1863: 794-795), whose type is *Polysiphonia*. *Chondria*, however, typifies the Tribe name Chondrieae J. Agardh (1841: 20), which has priority against the Tribe name Polysiphonieae J. Agardh (1863: 794-795), so when *Chondria* and *Polysiphonia* are placed in the same Tribe, the correct name for the Tribe is Tribe Chondrieae.

Subsequently, Falkenberg in Schmitz & Falkenberg (1897: 426) recognized the Chondrieae and the Polysiphonieae and distinct tribes in the Rhodomelaceae, as did Hommersand (1963: 347, 348), Maggs & Hommersand (1993: 308, 384), Womersley (2003: 169, 170, 407) and Díaz-Tapia & al. (2017: 927, 930).

The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1 and Table S3 in the Supporting Information) included three samples of *Chondria* sp. but no samples of the type species, *Chondria tenuissima*, and no samples of other genera assigned to the Chondrieae (Table S2). Further assessment is needed, especially in view of the finding in the constrained taxon-rich tree that *Chondria* was not monophyletic.

The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig. S2 in the Supporting Information) involved 45 samples from 9 genera currently assigned to the Tribe Chondrieae, including samples of the type species of *Chondria* and five other genera. The Tribe Chondrieae was resolved as a monophyletic clade with moderate support (Díaz-Tapia & al., 2017: 927). Within the clade, however, Díaz-Tapia & al. (2017: 927) also concluded that the evidence necessitates a revision at the genus level because *Chondria* and *Acanthophora* J.V.F. Lamouroux were not monophyletic.

Díaz-Tapia & al. (2017: Table S5) contains a summary of the "Key morphological characters" used by those authors to delineate tribes of Rhodomelaceae.

Tribe **Cladureae** Díaz-Tapia & Maggs (in Díaz-Tapia & al. 2017: 932).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (Díaz-Tapia & al., 2017: 932).
- Only genus included in the Tribe Cladureae by Díaz-Tapia & al. (2017: 932): *Cladurus* Falkenberg (in Schmitz & Falkenberg, 1897: 435).
- Tribe name Cladureae formed from the Genus name *Cladurus* Falkenberg (in Schmitz & Falkenberg, 1897: 435), in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Cladureae is the type of the genus name *Cladurus* Falkenberg (Art. 10.9). *Cladurus* is typified by the type of *C. elatus* (Sonder) Falkenberg (in Schmitz & Falkenberg, 1897: 435) (basonym: *Rhodomela elata* Sonder), according to the *Index Nominum Genericorum* (9 Feb 1996). *C. elatus* is the only species included in the genus protologue.
- Tribe name Cladureae assigned by Díaz-Tapia & al. (2017: 927) to the Family Rhodomelaceae. Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. Díaz-Tapia & al. (2017) did not include the Cladureae in their chloroplast phylogenomics analysis, presumably because complete chloroplast genome data were not available. The Tribe includes a single genus with two species.

The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig. S2 and Table S4 in the Supporting Information) included one sample of the type species, *Cladurus elatus*. It was resolved as a distinct clade and treated as a new tribe, the Cladureae Díaz-Tapia & Maggs in Díaz-Tapia & al. (2017: 932).

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae.

Tribe **Dipterosiphonieae** Díaz-Tapia & Maggs in Díaz-Tapia & al. (2017: 932).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (Díaz-Tapia & al., 2017: 932).
- Only genus included in the Tribe *Dipterosiphonieae* by Díaz-Tapia & al. (2017: 932-933): *Dipterosiphonia* Falkenberg (in Schmitz & Falkenberg, 1897: 463).

- Tribe name Dipterosiphonieae formed from the Genus name *Dipterosiphonia* Falkenberg (in Schmitz & Falkenberg, 1897: 463), in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Dipterosiphonieae is the type of the genus name *Dipterosiphonia* (Art. 10.9). *Dipterosiphonia* is typified by the type of *D. dendritica* (C. Agardh) Schmitz (in Schmitz & Falkenberg, 1897: 464) (basonym: *Polysiphonia dendritica* C. Agardh), according to the *Index Nominum Genericorum* (21 May 2006).
- Tribe name Dipterosiphonieae assigned by Díaz-Tapia & al. (2017: 924, 932) to the Family Rhodomelaceae. Family name conserved; listed in Appendix IIA.

Additional Remarks. The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1 & Fig. S1, & Table S3 in the Supporting Information), included two samples identified as *D. dendritica*, the type species of *Dipterosiphonia*. It was resolved as a distinct clade and (p. 932) newly described as Tribe Dipterosiphonieae Díaz-Tapia et Maggs (in Díaz-Tapia & al., 2017: 932).

The constrained taxon-rich tree (Díaz-Tapia & al. 2017: Fig. S2 and Table S4 in the Supporting Information) included two samples identified as *D. dendritica*, the type species of *Dipterosiphonia*, one sample of *D. australica* Womersley and four samples of unidentified species of the Tribe Dipterosiphonieae. The samples were strongly resolved as a distinct clade (noted on p. 929).

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae.

Tribe Herposiphonieae Falkenberg (in Schmitz & Falkenberg, 1897: 457).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in the protologue (Falkenberg in Schmitz & Falkenberg, 1897: 457, 459). Author of Tribe name not explicitly indicated but likely to be Falkenberg, who completed the manuscript after the death of Schmitz, as noted in Part I of this account.
- Genera included in Tribe by Falkenberg (in Schmitz & Falkenberg, 1897: 428-429; 457-461): *Cliftonaea* W.H. Harvey; *Herposiphonia* Nägeli; *Herpoteros* Falkenberg; *Lophosiphonia*

Falkenberg; *Microcolax* Schmitz; *Ophidocladus* Falkenberg; *Streblocladia* Schmitz (in Schmitz & Falkenberg, 1897: 457).

- Tribe name Herposiphonieae formed from the genus name *Herposiphonia* Nägeli (1846: 238), in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Herposiphonieae is the type of the genus name *Herposiphonia* (Art. 10.9). *Herposiphonia* is typified by the type of *H. tenella* (C. Agardh) Ambronn (1880: 197) (basonym: *Hutchinsia tenella* C. Agardh), according to the *Index Nominum Genericorum* (31 May 2006).
- Tribe name Herposiphonieae assigned by Falkenberg in Schmitz & Falkenberg (1897: 457) to the Family Rhodomelaceae. Family name conserved; listed in Appendix IIA.

Additional Remarks. Of the seven genera included in the Herposiphonieae by Falkenberg (in Schmitz & Falkenberg, 1897: 428-429; 457-461), three (*Herposiphonia* Nägeli; *Ophidocladus* Falkenberg; *Streblocladia* Schmitz) now typify distinct tribes recognized by Díaz-Tapia & al. (2017); *Cliftonaea* is considered a distinct genus in the Tribe Polyzonieae (Womersley, 2003: 317, 325; Díaz-Tapia & al., 2017: 923); *Herpopecteros* was retained in the Herposiphonieae (Womersley, 2003: 289, 312) but not included in Díaz-Tapia & al. (2017) due to lack of molecular data; *Lophosiphonia* was placed in the ‘Lophosiphonia Group’ by Womersley (2003: 169, 332) but referred to the Polysiphonieae by Díaz-Tapia & al. (2017: 930); and *Microcolax* was not dealt with by Womersley (2003, not recorded for southern Australia) or by Díaz-Tapia & al. (2017, due to lack of molecular data).

The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1, & Table S3 in the Supporting Information), included one sample identified as *Herposiphonia versicolor* (J.D. Hooker & W.H. Harvey) Reinbold but no samples of the type (*H. tenella*) or other species of *Herposiphonia*, and no samples from the other eight genera currently assigned to the tribe. According to Díaz-Tapia & al. (2017: 929), *Herposiphonia* contains 56 species. Further assessments are needed once samples from the type species (*H. tenella*), other species of *Herposiphonia*, and some or all of the other eight genera in the tribe become available.

The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig. S2 in the Supporting Information), included three samples of the type species, *Herposiphonia tenella*, and 23 other samples identified as *Herposiphonia*, six of which were identified to species. In Fig. S2, this

group was resolved as a distinct clade to which the Tribe name *Herposiphoniae* was applied. Further assessments are needed once samples of the other eight genera (Díaz-Tapia & al., 2017: 923) currently assigned to the tribe become available.

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae, and Díaz-Tapia & al. (2017: 933) provide an emended description of the Tribe.

Tribe name **Heterocladieae**: background information.

Hommersand (1963: 338) effectively published the name ‘Tribe Heterocladieae’, provided brief diagnostic information, included (p. 347) the genera *Heterocladia* Decaisne and *Trigenea* Sonder, stated (p. 338) that “These two genera comprise a separate tribe...”, included the intended tribe name in a diagram (p. 343, fig. 52) that depicted phylogenetic relationships of the tribes and subfamilies of Rhodomelaceae, and (p. 347) placed the Heterocladieae in his list of Tribes of Rhodomelaceae, Subfamily Rhodomelioideae.

Hommersand (1963), however, did **not** validly publish the intended name ‘Tribe Heterocladieae’ either as the name of a new taxon because he did not provide a Latin description or diagnosis or a reference to a previously and effectively published Latin description or diagnosis as required by ICN Art. 44.1; or as a name at new rank (defined in ICN Glossary) because he did not provide a full and direct reference (Art. 41.5) to its basionym. Valid publication occurred in Womersley (2003: 282) as a name at new rank rather than the name of a new taxon.

Considerable confusion occurs in the literature due to the improper use of the Latin termination – *ae*, now mandated (ICN Art. 19.3, 37.2, footnote) for Tribe names (e.g. Tribe Heterocladieae Womersley (2003)). The same name, Heterocladieae, with the same termination, also has been used incorrectly for taxa at the rank of Family (e.g. [Family] Heterocladieae Decaisne (1842: 359), correctable (Art. 18.4) to Family Heterocladiaceae), or at the rank of Subfamily (e.g. Subfamily Heterocladieae Falkenberg (1901: 750) and De Toni (1903: 1123), correctable (Art. 19.1, 19.7) to Subfamily Heterocladioideae), or at the rank of Subtribe (e.g. Subtribe Heterocladieae Trevisan (1848: 107), correctable (Art. 19.3, 19.7) to Subtribe Heterocladinae).

Decaisne (1842: 359) did not explicitly assign the rank of family to his name Heterocladiaceae, but it is clear from comments on p. 305-306 that he divided the Algae into four divisions or subclasses, one of which was the Choristosporeae (note the Latin termination on p. 359), and it is clear from a sentence on pp. 356-357 that within the Choristosporeae he recognized a number of families including (p. 359) the Heterocladiaceae (as Heterocladiaceae). The Latin termination –*ae*, is correctable to –*aceae* for a family name. The sentence on pp. 356-357 reads:

Je vais essayer de disposer, d'après ces principes, la série des familles qui composent l'ensemble des Algues Choristosporees (I will try to arrange, according to these principles, the series of families which make up all of the Choristosporean Algae.).

We have been unable to verify the statement in Phillips & al. (2000: 199) that:

"Decaisne (1842, p. 364) regarded *Heterocladia* as constituting the "subfamily" Heterocladiaceae of the "family" Choristosporeae, ...".

This statement does not occur on p. 364 of Decaisne (1842) and is contrary to Decaisne's comments on pp 305-306 and 356-357.

Decaisne (1842: 359) included a single genus (*Heterocladia*) with a single species (*H. australis* Dne.) in the Heterocladiaceae (as Heterocladiaceae). The family name is validated with comments on p. 364; the generic name *Heterocladia* was validated in Decaisne (1841: 177-178) with a description that also pertains to the species name *H. australis*. Decaisne (1841: 177) noted that the herbarium sheet was annotated *D. ruscifolia* var. *firmior* (*D.* = *Delesseria*) by J. Agardh.

The family name Heterocladiaceae Decaisne (1842: 359, as Heterocladiaceae) is now a 'rejected name' listed in ICN Appendix IIA (online at: <https://botany.si.edu/references/codes/props/>) opposite the conserved family name Rhodomelaceae Horaninow (1847).

The more recently published bryophyte family name Heterocladiaceae Ignatov & Ignatove (2004: 942), formed from the bryophyte genus name *Heterocladium* Schimper is an illegitimate later homonym (Art. 53.1) of the Heterocladiaceae Decaisne (1842). Because the bryophyte name is illegitimate, it cannot serve as the correct name (as defined in the ICN Glossary) of a family.

As explained in Part I of the present account, Falkenberg (1901), despite inconsistencies, treated his subdivisions of the Rhodomelaceae as subfamilies. This includes the Subfamily (Unterfamilie) Heterocladioideae (as Heterocladiaceae), which is based

on the Latin name *Heterocladiaceae* listed in the Index (p. 750) with references to p. 532 and 737 where validating descriptions occur. Falkenberg (1901: 714) unequivocally treated the *Heterocladioideae* (as *Heterocladiaceae*) as a subfamily (Unterfamilie) and referred to the diagram on p. 700, which includes a list of the subfamilies he recognized, all with the Latin termination *-eae*. In Candolle (1867b), the Code in effect in 1901, the Latin termination *-eae* was specified as the correct termination for both subfamily names (Art. 23) and tribe names (Art. 24).

De Toni (1903: 775bis, 776, 776bis) explicitly listed his subdivisions of the *Rhodomelaceae* as subfamilies; the heading **Subfamilia IX *Heterocladiaceae*** Decne. is on p. 1123, where he lists Falkenberg (1901: 582) as a reference. The Latin termination *-eae* and authorship citation Decaisne (Decne.) are incorrect; the correct termination for a subfamily is *-oideae* (Art. 19.2), and the correct author citation (Art. 49.2) is Subfamily *Heterocladioideae* Falkenberg (1901, as *Heterocladiaceae*).

Trevisan (1848: 107) inadvertently validly published the “Subtribe *Heterocladiaceae*” as a name at new rank by providing a reference (Art. 41.1) to the family name *Heterocladiaceae* Decaisne (as *Heterocladiaceae*) which is the basionym. In the context of the current Code, Trevisan’s Latin termination *-eae* is improper, and in accord with Art. 19.3 and 19.7, has to be corrected to Subtribe *Heterocladinae* without change of authorship or date.

The Bryophyte names *Heterocladiaceae* (unranked group) Brotherus (in Engler & Prantl, 1907: 978-979) and Subfamily *Heterocladiaceae* (Britton 1908: 24, 25; Lotsy 1909: 359), formed from the genus name *Heterocladium* are later homonyms of algal names but are not illegitimate because, as noted in Art. 53, Ex. 5, the provisions on homonymy do not apply to subdivisions of families. Whether this sort of homonymy can cause confusion in this case seems unlikely.

Tribe ***Heterocladiaceae*** Womersley (2003: 282, stat. nov.).

Basionym: Subfamily *Heterocladioideae* Falkenberg (1901: 700, 714, 750, as *Heterocladiaceae*). Improper Latin subfamily termination (defined in ICN Glossary) *-eae* corrected to *-oideae* in accord with ICN Art. 18.4, 32.2, 37.2 (footnote) without change of authorship or date.

- Validly published by Womersley (2003: 282) as the legitimate name of a Tribe. Taxonomic rank explicitly indicated and description provided. As explained below, Womersley actually inadvertently

published the Tribe Heterocladieae as a stat. nov. (name at new rank) for the subfamily name Heterocladioideae Falkenberg (1901, as Heterocladieae). As noted above, the name "Tribe Heterocladieae" was effectively but not validly published by Hommersand (1963).

- Only genus included in the Tribe Heterocladieae by Womersley (2003: 282): *Heterocladia* Decaisne (1841: 177-178, pl. V, figs 18-22).
- Tribe name Heterocladieae Womersley formed from the genus name *Heterocladia* Decaisne (1841), in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Heterocladieae is the type of the genus name *Heterocladia* (Art. 10.9). *Heterocladia* is typified by the type of *H. australis* Decaisne, according to the *Index Nominum Genericorum* (9 Feb 1996).
- Tribe name Heterocladieae assigned by Womersley (2003: 168, 282) to the family Rhodomelaceae. Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. Phillips & al. (2000) provided a detailed account of the nomenclatural type specimen in **PC** and correctly noted that Decaisne (1841: 177-178) based his description on that one specimen, which, therefore, is accepted as the holotype (ICN Art. 9.1). According to Decaisne (1841: 177), the specimen was annotated by J. Agardh with *D. ruscifolia* var. *firmior* (*D.* = *Delesseria*), but the varietal name was not validly published as a scientific name and thus is a 'designation' as defined in the ICN Glossary.

Although Phillips & al. (2000: 199, 217) referred to the "Tribe Heterocladieae" in the publication title and in the text, they did not realize that the name had **not** been validated by Hommersand (1963), and they did not validate the name as a new taxon or as a name at new rank (see Table 1 and definition in ICN Glossary).

Womersley (2003: 282) inadvertently validated the Tribe Heterocladieae as a name at new rank; the requirements for validation as a name at new rank (ICN Art. 41) were met in the same manner as occurred for the Tribe Bostrychieae (Womersley 2003: 361), as explained in the account of that Tribe.

For the Heterocladieae, Womersley (2003: 282) provided the following text information: "Tribe HETEROCLADIEAE Falkenberg (1901), p. 731"; and in the References Womersley (2003: 504) provided the following: "FALKENBERG. P. 1901. Die Rhodomelaceen des Golfes von Neapel und der angrenzenden Meeres-abschnitte. *Fauna und Flora des Golfes von Neapel*. Monogr. 26 (Friedlander: Berlin)."

Collectively, these two pieces of information constitute a clear indication of a full and direct reference to the basionym data required by Art. 41.5, namely: author (P. Falkenberg), place of valid publication (Fauna und Flora des Golfes von Neapel. Monogr. 26, Friedlander: Berlin), and page reference and date (Falkenberg 1901: 731). There are no omissions (Art. 41.6) from the requirements of a 'clear indication', but there is one correctable citation error: Womersley cited p. 731 (where the basionym has a non-Latin termination) rather than p. 750 (where the basionym has a Latin termination). As noted in Art. 41.6, errors of this sort do not preclude valid publication of a name at new rank.

The name at new rank can be correctly cited as Tribe Heterocladieae Womersley (2003: 282) stat. nov. Parenthetical author citations (such as Heterocladieae (Falkenberg) Womersley) are not used for suprageneric names (ICN Art. 49.2).

The Womersley (2003) format does not strictly agree with ICN Recommendation 41A.1, which states that all this information "should immediately follow a name at new rank. It should not be provided by mere cross-reference to a bibliography...". However, Turland (2019: 39) pointed out that such split references still are full and direct. By meeting the requirements of Art. 41.5, the requirement of Art. 41.1 and the conditions mentioned in Art. 41.6 also are satisfied.

Womersley (2003) changed the rank of the name from Subfamily to Tribe, thus satisfying the requirement of Art. 42.2(a). Remaining provisions of Art. 41 are not relevant.

Díaz-Tapia & al. (2017: 922) excluded the Heterocladieae from their chloroplast phylogenomics analysis because they could not collect new material for sequencing. The Tribe includes a single genus with three species (Phillips 2000; Womersley 2003).

The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig. S2 in the Supporting Information) included five samples representing all three known species of Heterocladieae, but the relationship of the Heterocladieae to other tribes of the Rhodomelaceae was considered unresolved (p. 926). Although the Heterocladieae was resolved as monophyletic (p. 925-926), it was placed together with members of the Bostrychieae in an unsupported clade that Díaz-Tapia & al. (2017: 926) thought was an artefact resulting from the lack of overlapping markers. Further comments are in the account of the Tribe Bostrychieae.

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae.

Tribe **Laurencieae** I. Gifford (1853: 125, as “Laurenciaceae”).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (Gifford, 1853: 124-125). Improper Latin termination *-aceae* corrected to *-ae* in accord with ICN Art. 19.7, 32.2, 37.2 (footnote) without change of authorship or date.
- Genera included in the Tribe Laurencieae by Gifford (1853: 124-125): *Bonnemaisonia* C. Agardh; *Chrysymenia* J. Agardh; *Chylocladia* Greville (in W.J. Hooker, 1833) nom. cons.; *Laurencia* J.V.F. Lamouroux, nom. cons. Conserved genus names listed in ICN Appendix IIIA.
- Tribe name Laurencieae formed from the genus name *Laurencia* J.V.F. Lamouroux, nom. cons. (1813a: 130; 1813b: 42), in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Laurencieae is the type of the genus name *Laurencia* J.V.F. Lamouroux, nom. cons. (Art. 10.9). *Laurencia* is typified by the type of *L. obtusa* (Hudson) J.V.F. Lamouroux (basonym: *Fucus obtusus* Hudson), according to the *Index Nominum Genericorum* (9 Feb 1996). Designation of type species: Schmitz (1889: 447); also see Schmitz & Falkenberg (1897: 431).
- Tribe name Laurencieae assigned by Gifford (1853: 97-99) to the “Series Rhodospermeae”; see additional remarks below.

Additional Remarks. Gifford (1853: 97-99) assigned the Tribe name Laurencieae (as Laurenciaceae) to the “Series Rhodospermeae” in the descending rank sequence **Series** Rhodomelaceae → **Tribe** Laurencieae (as Laurenciaceae) → **Genus** *Laurencia* → **Species**. Gifford (1853: 129-134) provided accounts of five species of *Laurencia*, including the type species, *L. obtusa*. As indicated below, the “Series Rhodospermae” is not a validly published name and thus has no status under the ICN Art. 12.1.

Gifford (1853: vii-viii) incorrectly stated that her classification was in accord with that of W.H. Harvey (1849). W.H. Harvey (1849: 4-5, 64), however, treated the Rhodospermae as one of three subclasses of

the *Natural Class* Algae (W.H. Harvey, 1849: p. x) and did not refer to the group as “Series Rhodospermae”.

The Gifford descending rank sequence **Series** → **Tribe** → **Genus** → **Species** predates the first version of the ICN (Candolle 1867a, 1867b) and does not comply with Art. 3-5 of the current *Code* (Turland & al., 2018).

The rank-denoting term “Series” now denotes a secondary rank (ICN Art. 4.1) between the principal ranks (Art. 3.1) of Genus and Species, not a rank higher than Tribe, as suggested by the Gifford (1853) sequence. Gifford’s rank sequence differs from that specified in ICN Art. 3.1 & 4.1 and thus is not in accord with Art. 5.1. In accord with ICN Prin. VI, Art. 3-5 are retroactive to 1 May 1753 unless expressly limited, as occurs in Art. 13.1.

In the context of ICN Art. 37.6, Gifford (1853) misapplied the rank-denoting term “Series” to a taxon above the rank of Tribe and then subdivided the “Series Rhodomelaceae” into Tribes, Genera and Species. Thus “Series Rhodomelaceae” is not a validly published name under Art. 37.6 and must be removed under Art. 37.7 to achieve a proper descending sequence of ranks, namely **Tribe** → **Genus** → **Species**. With removal of the non-valid ‘Series Rhodomelaceae’, the Tribe Laurencieae constitutes a validly published name.

In email correspondence, the above interpretation was confirmed as correct by Nicholas Turland (Chair) and John Wiersema (Secretary) of the Editorial Committee of the Shenzhen *Code* (Turland & al. 2018).

Although the Tribe Laurencieae Gifford (1853: 125) is validly published, it was (initially) superfluous under Art. 52.1 because Gifford (1853: 134) included *Laurencia tenuissima* (Withering) Greville, whose basionym, *Fucus tenuissimus* W. Withering (1796: 117), is also the type species of *Chondria* C. Agardh (1817: xviii). *Chondria* is the nomenclatural type of the earlier Tribe name Chondrieae J. Agardh (1841: 20), and thus the tribe name Chondrieae has nomenclatural priority against the tribe name Laurencieae (Art. 11.3) when *Laurencia* and *Chondria* are placed in the same Tribe.

Despite being superfluous when published, the Tribe name Laurencieae Gifford is not illegitimate because (Art. 52.4, last part of first sentence, & Art. 52, Ex. 17) it is formed from a legitimate generic name (*Laurencia*). Thus, as noted in the last sentence of Art. 52.4, the Tribe name Laurencieae, when published was incorrect, but it may become correct later. Another example of a name that was initially

superfluous but not illegitimate and became correct later is the Family name Rhodomelaceae (see Silva, 1980: 87).

To become correct in the context of Art. 52.4, the Tribe name Laurencieae would need to be treated as a distinct taxon (Tribe) while at the same time, no nomenclatural type (e.g. *Chondria*) of another earlier validly published tribe name (e.g. the Tribe Chondrieae) is included in the Laurencieae.

An example of this occurs in W.H. Harvey (in J.D. Hooker 1855: 233), who recognized the Tribe Laurencieae as a validly published Tribe and at the same time implicitly excluded the Tribe Chondrieae by explicitly referring the nomenclatural type of the genus, *Chondria tenuissima*, to the Tribe Rhodomeleae (see pp. 222, 223). Harvey did not mention Gifford (1853), where the Tribe Laurencieae was first validly published. Further information on the nomenclatural type of *Chondria* is in the account of the Tribe Chondrieae.

Recent examples in which both the Laurencieae and the Chondrieae are simultaneously and correctly treated as distinct tribes include Maggs & Hommersand (1993: 384, 393), Womersley (2003: 169, 407, 452) Díaz-Tapia & al (2017: 924, fig. 1; 925, fig. 2; 928; Table S2) and Nielsen & al. (2022: 211, 213).

The apparent earlier name Laurencieae [J.D.] Hooker & W.H. Harvey (1845: 539) lacks a description or diagnosis or reference to a previously and effectively published description or diagnosis as required by Art. 38.1, and thus, is not validly published. It is treated as a designation (as defined in the ICN Glossary)

The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1 & Table S3 in the Supporting Information), included four samples in the 'Laurencieae clade' (one each identified as *Laurencia marilzae* Gil-Rodríguez & al. [= *Laurenciella marilzae* (Gil-Rodríguez & al) Gil-Rodríguez & al.], *L. snackeyi* (Weber-van Bosse) M. Masuda, *Palisada* sp. and Laurencieae sp.) but no samples of the type species, *Laurencia obtusa*. In the absence of data from the nomenclatural type species of the genus *Laurencia* (ICN Art. 10.1) and thus the Tribe Laurencieae (Art. 10.9), nomenclatural application of the Tribe name Laurencieae is rather uncertain and requires further assessment once samples of the type and other species of *Laurencia* and of additional related genera become available.

The constrained taxon-rich tree (Díaz-Tapia & al. 2017: Fig. S2 in the Supporting Information) included 75 samples representing seven genera (five of which were type species samples); 37 of the 75 samples were identified as *Laurencia*, and 33 were identified to

species. However, the tree did not include any samples of *L. obtusa*, the type species of *Laurencia*. Consequently, the application of the Tribe name Laurenciaeae to the group needs to be confirmed by including data from several samples of the type species, *L. obtusa*.

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae. Díaz-Tapia & al. (2017: 927-928) also provided further comments on the Laurenciaeae and noted that the constrained taxon-rich tree included representatives of seven genera and that all included members resolved as a single clade that received high or moderate support.

Lophosiphonia-informal putative names.

The following putative suprageneric groups/names associated with the Genus name *Lophosiphonia* Falkenberg are not validly published in accord with Art. 38.1 (and relevant provisions of Art. 32-45) and thus have no status under ICN Art. 12.1:

- **Lophosiphonia Group** (e.g. Womersley 2003: 168, 169, 332) is an informal name explicitly (Womersley 2003: 168) not designated as a Tribe (see Art. 37.1), and lacks a Latin description as required by Art. 44.1, and thus is not validly published. Womersley (2003: 332) provided an English description and included two genera (*Lophosiphonia*; and *Ophidocladus* Falkenberg). *Lophosiphonia* was listed as type genus, but this has no status because it does not typify a validly published suprageneric scientific name. The name Lophosiphonia-group is also used by Díaz-Tapia & Bárbara (2013) who commented (p.372) that the Lophosiphonia group is artificial and that probably the genera assigned to it would be better accommodated in other tribes. Díaz-Tapia & al. (2017: 934) subsequently included the type species of *Lophosiphonia* in the Tribe Polysiphonieae.
- **Lophosiphonia Gruppe** (e.g. Kylin 1956: 498-99, 538) is an informal name lacking a clear indication of rank (Art. 37.1) and thus not validly published. Features characterizing the group can be determined from the identification key (Kylin 1956: 494-501). Genera included: *Ctenosiphonia* Falkenberg, *Falkenbergiella* Kylin, *Lophosiphonia* **Falkenberg**, *Oligocladus* Weber-van Bosse nom. illeg. ($\equiv$ *Oligocladella* P.C. Silva nom. nov), *Ophidocladus* Falkenberg, *Stichothamnion* Børgesen. P. Silva (in Silva & al., 1996: 530) reported that *Oligocladus* Weber-van Bosse (1911) was a later illegitimate

homonym of *Oligocladus* R. Chodat & Wilczek (1902) and proposed the replacement name *Oligocladella* P. Silva.

- **“Tribe Lophosiphonieae”** (e.g. Hommersand, 1963: 335, 338, 341 (characters indicated), 343 fig. 52, 348 (list of genera identical to that of Kylin)). A designation (see Table 1 and the ICN Glossary); no Latin description or diagnosis or reference to a previous description or diagnosis provided and thus not validly published. Athanasiadis (2016: 1238 & footnote 2) listed the name as “Tribe Lophosiphonieae Kylin (1956: 498, 538, 586, 591) nom.” but noted that it is ‘invalid’ because it lacks a Latin description or diagnosis. Norris & al. (2017:43) listed the name as “Tribe Lophosiphonieae Kylin ex Athanasiadis (2016: 1238)” apparently unaware of the fact that Athanasiadis (2016:1238, footnote 2) correctly indicated that the name was invalid.
- **Lophosiphonieae** Fritsch (1945: 746). A designation (see ICN Glossary). Fritsch (1945: 566) provided a series of comments about “several creeping dorsiventral Rhodomelaceae which show points of contact with the Herposiphonieae but resemble the Polyzonieae in their endogenous branching”, provided some examples in particular genera, and then stated “Although the exact affinities of these genera, which for convenience may be grouped as Lophosiphonieae, are difficult to assess, they help to emphasize the relationship between Herposiphonieae and Polyzonieae.” Neither a description or diagnosis of the Lophosiphonieae, nor a reference to a previous and effectively published description or diagnosis were provided by Fritsch, and he did not indicate a taxonomic rank. Without a proper description or diagnosis the Fritsch ‘name of convenience’, Lophosiphonieae, is not validly published in accord with Art. 38.1 and, thus, has no status under the ICN (Art. 12.1).
- **“Subfamily Lophosiphonieae”** (Børgesen 1918: 294). Designation (see ICN Glossary); Børgesen listed “Subfam. 5. Lophosiphonieae” with no further information.

We are unaware of any publication in which the Tribe name Lophosiphonieae was validly published. In the protologue account of *Lophosiphonia*, Falkenberg (in Schmitz & Falkenberg, 1897: 459-460), placed *Lophosiphonia* in the Tribe Herposiphonieae. Nearly a century later, Maggs & Hommersand (1993: 381) also included *Lophosiphonia* in the Tribe Herposiphonieae (compare with the treatment of Hommersand 1963, mentioned above).

Díaz-Tapia & al. (2017: 931) reported that a ‘Tribe Lophosiphonieae’ was not supported in their phylogenetic analysis,

and placed the genus *Lophosiphonia* in the Tribe Polysiphonieae (p. 934). The constrained taxon-rich tree analysis of Díaz-Tapia & al. (2017: Table S4) included one sample identified as *L. obscura* (C. Agardh) Falkenberg, the type species of *Lophosiphonia*.

Given the above, there seems little merit in recognizing a subfamily Lophosiphonioideae (see Athanasiadis 2016: 1238, footnotes 1 & 2). Scagel (1953: 13, 20-21) listed the “Lophosiphonieae” (correctable to Lophosiphonioideae in accord with Art. 19.7) as a subfamily of Rhodomelaceae (p. 13), and stated (p.20) that it “...is rather poorly defined, and its phylogenetic position is difficult to assess”, and commented (p. 20-21) that the “members” show more or less pronounced dorsiventrality, had main axes that usually were prostrate, had trichoblasts that usually were produced only at the tips of erect branches and that each fertile segment had only two tetrasporangia.

There is no mention in Scagel (1953) of *Lophosiphonia*, the genus from which the ‘subfamily name’ presumably was formed, and the genera that are mentioned by Scagel (1953) are said to show affinities with members of other ‘subfamilies’ *sensu* Scagel (1953). We have doubts as to whether Scagel’s comments satisfy the requirements of Art. 38.1(a) for a “description or diagnosis” and suggest that this could be formally determined using the procedure specified in Art. 38.4.

Tribe **Lophothalieae** Falkenberg (in Schmitz & Falkenberg, 1897: 445).

- Validly published as a legitimate name of a Tribe. Taxonomic rank explicitly indicated by Falkenberg (in Schmitz & Falkenberg, 1897: 425) in last paragraph before the taxonomic key. Description provided by Falkenberg (in Schmitz & Falkenberg, 1897: 445). Author of Tribe name not explicitly indicated but likely to be Falkenberg, who completed the manuscript after the death of Schmitz, as noted in Part I of this account.
- Genera included in Tribe Lophothalieae by Falkenberg (in Schmitz & Falkenberg, 1897: 427-428; 446-452): *Bostrychia* Montagne (in Sagra, 1842: 39) nom.cons; *Brongniartella* Bory de St-Vincent; *Chamaethamnion* Falkenberg (in Schmitz & Falkenberg, 1897); *Colaconema* Schmitz (in Schmitz & Falkenberg, 1897) (non Batters 1896); *Holotrichia* Schmitz (in Schmitz & Falkenberg, 1897); *Lophocladia* Schmitz (1893); *Lophothalia* (W.H. Harvey) Kützing; *Murrayella* Schmitz (1893) (non Kofoid 1907, a later illegitimate homonym); *Pteronia* Schmitz (in Schmitz & Falkenberg, 1897) (non *Pteronia* Linnaeus 1763, nom. cons.); *Wilsonaea* Schmitz; *Wrightiella* Schmitz. Conserved genus names listed in ICN Appendix IIIA.

Colaconema Schmitz (in Schmitz & Falkenberg, 1897: 452) is a later illegitimate homonym (Art. 53.1) of *Colaconema* Batters (1896: 8); De Toni (1903: 1170) published the replacement name *Colacopsis* for the Schmitz taxon. *Pteronia* Schmitz (in Schmitz & Falkenberg, 1897: 452) is a later illegitimate homonym (Art. 53.1) of *Pteronia* Linnaeus (1763: 1176). G. De Toni (1936: [4]) published the replacement name *Picconiella* for the Schmitz taxon. The author citation De Toni refers to Giovanni Battista De Toni; the author citation G. De Toni refers to Giuseppe De Toni.

- Tribe name Lophothalieae formed from the genus name *Lophothalia* (W.H. Harvey) Kützing (1849: 797), in accord with Art. 19.3 (including references to Art. 19.1 & 18.1). Basionym of genus *Lophothalia* (W.H. Harvey) Kützing: *Dasya* Subgenus *Lophothalia* W.H. Harvey (1847: 64).
- The nomenclatural type of the Tribe Lophothalieae is the type of the genus name *Lophothalia* (Art. 10.9). *Lophothalia* is typified by the type of *L. verticillata* (W.H. Harvey) Kützing (basonym: *Dasya verticillata* W.H. Harvey, 1844: 434), according to the *Index Nominum Genericorum* (9 Feb 1996).
- Tribe name Lophothalieae assigned by Falkenberg (in Schmitz & Falkenberg, 1897: 445) to the Family Rhodomelaceae. Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. Subsequently, Falkenberg (1901: xv, 732) transferred *Bostrychia*, *Colaconema* Schmitz (non Batters), and *Wilsonaea* to his newly described Subfamily Bostrychioideae (as Subfamily Bostrychieae). Falkenberg (1901) also referred to this group as the “Bostrychieen” or as “Die Familie der Bostrychieen” or as “die Gruppen der Bostrychieen...”, all of which have the German termination *-een* and, thus, are not validly published (Art. 19.3) and have no status under the ICN (Art. 12.1). Falkenberg (1901: 567, 579) moved *Chamaethamnion* to a group of three genera (*Chamaethamnion* Falkenberg (in Schmitz & Falkenberg, 1897), *Endosiphonia* Zanardini, *Pachychaeta* Kützing) whose systematic placement was very problematic.

Falkenberg (1901) referred *Brongniartella* Bory, *Holotrichia* Schmitz, *Lophocladia* (J. Agardh) Schmitz, *Lophothalia* Kützing, *Murrayella* Schmitz, *Pteronia* Schmitz (non Linnaeus), and *Wrightiella* Schmitz to a single group variously called “Die Familie der Lophothalieen” (p. xv, 533; German termination *-een* and thus not validly published), the “Lophothalieen” (p. 725, not validly published) or the “Lophothalieae Schmitz” (p. 751, a name with the Latin termination *-eae* and with references back to pp. 533 & 725).

In the first paragraph of the “Synoptische Uebersicht...”, Falkenberg (1901:714) refers to the “Unterfamilien” (subfamilies) listed in the diagram on p. 700, among which is the “II. Lophothalieae”. Because the termination –eae applied both to subfamily names and to tribe names under the 1867 Paris Code (Candolle, 1867b: Art. 23, 24), which was in effect in 1901, and because Falkenberg (1901: 751) provided page references (p. 533, 725) where the features of the Lophotalieae were mentioned, the name “Lophothalieae Falkenberg” (1901: 714, 751) can be regarded as the validly published name of a subfamily under Art. 37.2 & 37.3 of the Shenzhen Code (Turland & al., 2018).

The correct author citation is Subfamily Lophothalioideae Falkenberg. Because Falkenberg (1901: 751) listed Schmitz as an “honorary” author (without commenting), an optional author citation (Turland, 2019: 96) could be Subfamily Lophothalioideae Schmitz ex Falkenberg (1901: 751). This however seems inappropriate because, as noted in Part I, Schmitz had died in 1895, and no instance has been found in which Schmitz assigned the rank of subfamily to a taxon of Rhodomelaceae; and because Falkenberg (e.g. p. 110, 714) explicitly referred to the “Lophothalieen” as a subfamily without reference to Schmitz.

Unequivocal nomenclatural treatment as a subfamily occurs in De Toni (1903: 776 bis, 1007) where De Toni explicitly names the Lophothalieae as a subfamily and provides a description and a reference back to the 1897 protologue of the Tribe Lophothalieae, the basionym of the Subfamily. In effect, De Toni has raised the taxon to the rank of subfamily; it is a name at a new rank (stat. nov.) under ICN Art. 41. Nomenclaturally, the De Toni treatment is to be listed as Subfamily Lophothalioideae De Toni, stat. nov. (1903: 1007).

Hommersand (1963: 337, 343, fig. 52; 346) treated the Lophothalieae as a distinct tribe with 24 recognized genera, including nine of the eleven genera originally assigned to the Tribe by Falkenberg (in Schmitz & Falkenberg 1897). The two genera not included are *Bostrychia*, which Hommersand referred to the Bostrichioideae and *Wilsonaea*, which is not mentioned by Hommersand (1963). The replacement names *Colacopsis* G. De Toni and *Picconiella* De Toni were listed by Hommersand in place of *Colaconema* Schmitz (non Batters) and *Picconiella* in place of *Pteronia* Schmitz (in Schmitz & Falkenberg) (non Linnaeus).

The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1 & Table S3 in the Supporting Information),

included one sample identified as *Lophocladia kuetzingii* (Kuntze) P.C. Silva but no samples of any species of *Lophothalia*, and no samples from any of the other 27 genera (Díaz-Tapia & al., 2017: 926) that currently encompass the Lophothalieae. Consequently, the nomenclatural application of the Tribe name Lophothalieae to a clade that lacks samples from the type species and from any other species of *Lophothalia* is tenuous. Moreover, Díaz-Tapia & al. (2017: 926, 927) state that the phylogenetic relationships of the Lophothalieae within the Rhodomelaceae are still unclear, that it is not yet possible to provide an accurate delineation for the Lophothalieae, and that further morphological and molecular studies are needed to clarify the systematics of the Lophothalieae. We fully agree with these comments.

The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig. S2 in the Supporting Information) included 11 samples representing six genera (four involving type species samples) with *Lophothalia* represented by one sample of *Lophothalia hormoclados*, but no samples of the type species, *Lophothalia verticillata*, no samples of other species in the genus, and only six of the other 27 genera were represented. The concerns attending the chloroplast phylogenomics trees also apply to the constrained taxon-rich tree. Díaz-Tapia & al. (2017: 931) also indicate that the Lophothalieae is not monophyletic and its delineation is problematic. Considerably more research relating to the Lophothalieae is required.

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae. These also will need to be reconsidered once further research is conducted.

Tribe **Neotenophyceae** Kraft & Abbott (2002: 277).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (Kraft & Abbott, 2002: 277).
- Only genus included in the Tribe Neotenophyceae by Kraft & Abbott (2002: 277): *Neotenophycus* Kraft & Abbott (2002: 272).
- Tribe name Neotenophyceae formed from the Genus name *Neotenophycus* Kraft & Abbott (2002: 272) in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Neotenophyceae is the type of the genus name *Neotenophycus* Kraft & Abbott (Art. 10.9). *Neotenophycus* is typified by the type of *N. ichthyosteus* Kraft & Abbott, according to the *Index Nominum Genericorum* (25 May 2006).

- Tribe name Neotenophyceae assigned by Kraft & Abbott (2002) to the Family Rhodomelaceae. Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. Díaz-Tapia & al. (2017: 922) excluded the Neotenophyceae from their phylogenetic analyses because they could not collect new material for sequencing. To date, the Tribe includes a single genus with a single species.

Kraft & Abbott (2002: 277, footnote) noted the nomenclatural anomaly that the algal Tribe name Neotenophyceae could potentially be mistaken for the putative name of an algal Class because in both ranks the name would have the same spelling. The Latin termination for a tribe name is *-eae* and the termination for an algal class name is *-phyceae*. Both names are formed from the genus name *Neotenophycus* by replacing the *-us* with the correct termination as specified in Art. 37.2 footnote. A separate Class name based on the genus name *Neotenophycus* has not been formally proposed to date.

Tribe **Ophidocladeae** Díaz-Tapia & Maggs (in Díaz-Tapia & al., 2017: 933).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (Díaz-Tapia & al., 2017: 933).
- Only genus included in the Tribe Ophidocladeae by Díaz-Tapia & al. (2017: 933): *Ophidocladus* Falkenberg (in Schmitz & Falkenberg, 1897: 461).
- Tribe name Ophidocladeae formed from the Genus name *Ophidocladus* Falkenberg (in Schmitz & Falkenberg, 1897: 461), in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Ophidocladeae is the type of the genus name *Ophidocladus* (Art. 10.9). *Ophidocladus* is typified by the type of *O. simpliciusculus* (H. M. & P. L. Crouan) Falkenberg (basionym: *Polysiphonia simpliciuscula* H. M. & P. L. Crouan), according to the *Index Nominum Genericorum* (9 Feb 1996).
- Tribe name Ophidocladeae assigned by Díaz-Tapia & al. (2017: 924, 933) to the Family Rhodomelaceae. Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. Díaz-Tapia & Maggs (in Díaz-Tapia & al., 2017: 933) validly published the Tribe Ophidocladeae for a single genus (*Ophidocladus*) with a single species (*O. simpliciusculus*). According to Díaz-Tapia & al. (2017: 928) the Tribe was proposed based on

morphology and molecular evidence. The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; & Fig. S1, & Table S3 in the Supporting Information), included a single sample of *Ophidocladus simpliciusculus*, the only known genus and species in the Tribe Ophidocladeae. It resolved as a distinct clade. The constrained taxon-rich tree (Díaz-Tapia & al. 2017: Fig. S2 and Table S4 in the Supporting Information) also included a single sample of *Ophidocladus simpliciusculus*, and it resolved as a distinct clade. Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae. Further comments on the Ophidocladeae occur in Díaz-Tapia & al. (2017: 928).

Placophora-informal putative names.

The following putative names have no status under ICN Art. 12.1 because they are not validly published in accord with Art. 38.1 (and relevant provisions of Art. 32-45):

- **Placophora Group** (e.g. Womersley, 2003: 168, 169, 359), an informal name explicitly (Womersley 2003: 168) not designated as a Tribe (see Art. 37.1) and without a Latin description as required by Art. 44.1, and thus not validly published. Womersley (2003: 359) provided an English description, included two genera (*Amplisiphonia* Hollenberg, *Placophora* J. Agardh) and provided further historical data for *Placophora*, a genus represented in southern Australia by the type species *P. binderi* (J. Agardh) J. Agardh.
- **Placophora Gruppe** (e.g. Kylin 1956: 497, 527-529), an informal name lacking a clear indication of rank (Art. 37.1) and thus not validly published. Features characterizing the group can be determined from the identification key (Kylin, 1956: 494-501). Genera included: *Amplisiphonia*, *Periphykon* Weber-van Bosse, *Placophora* J. Agardh, *Pollexfenia* W.H. Harvey.
- **“Placophoreae”** (e.g. Scagel 1962b: 239). A designation (defined in Table 1 and the ICN Glossary); no Latin description or diagnosis or reference to a previous description or diagnosis provided and thus not validly published. No rank explicitly stated but likely to have been regarded as a subfamily from other comments in Scagel (1962b: 239). Genera included in the “Placophoreae” by Scagel (1962b: 239): *Amplisiphonia*, *Placophora*.

Tribe Pleurostichidiace Hommersand (1963: 342, footnote).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (Hommersand 1963: 342, footnote).
- Only genus included in the Tribe Pleurostichidiace by Hommersand (1963: 342): *Pleurostichidium* Heydrich (1893: 344).
- Tribe name Pleurostichidiace formed from the Genus name *Pleurostichidium* Heydrich (1893: 344) in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Pleurostichidiace is the type of the genus name *Pleurostichidium* Heydrich (Art. 10.9). *Pleurostichidium* is typified by the type of *P. falkenbergii* Heydrich, according to the *Index Nominum Genericorum* (9 Feb 1996).
- Tribe name Pleurostichidiace assigned by Hommersand (1963) to the Family Rhodomelaceae. Family name Rhodomelaceae conserved; listed in ICN Appendix IIA.

Additional Remarks. Heydrich (1893: 344-348, Taf. XVI) validly published the genus *Pleurostichidium*, recognized a single species, *P. falkenbergii*, provided an account of antheridial, cystocarpic and tetrasporangial material collected from the Bay of Islands, New Zealand in June 1892, and thought that it was allied to the Amansieae of Schmitz (1889). Subsequently, Hommersand (1963) validly published the Tribe Pleurostichidiace for a single genus (*Pleurostichidium*) with a single species (*P. falkenbergii*). In a detailed study of new field-collected and culture material, including the lectotype specimen (MEL 698765), Phillips (2000) provided a thorough study of the vegetative thallus and of male, female, carposporangial and tetrasporangial structures, and reported that the species was an obligate epiphyte lacking cellular connections with host cells. Phillips also reviewed the placement of *Pleurostichidium* in the Rhodomelaceae and concluded from morphoanatomical data and a molecular analysis based on the 18S rRNA gene that recognition of the Tribe Pleurostichidiace by Hommersand (1963) was justified, and provided an emended description (p. 785). By contrast, Díaz-Tapia & al. (2017: 922) excluded the Pleurostichidiace from their chloroplast phylogenomics analysis because they could not collect new material for sequencing. The constrained taxon-rich tree of Díaz-Tapia & al. (2017: Fig. S2 and Table S4 in the Supporting Information) included a single sample of the type and only known species, *Pleurostichidium falkenbergii*, and it resolved as a distinct clade. Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters”

used by those authors to delineate tribes of Rhodomelaceae. Further comments on the Pleurostichidieae occur in Díaz-Tapia & al. (2017: 929).

Tribe **Pollexfenieae** J. Agardh (1863: 792).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (J. Agardh, 1863: 792).
- Genera included in the Tribe Pollexfenieae by J. Agardh (1863: 792): *Jeannerettia* J. D. Hooker & W. H. Harvey (in W. H. Harvey, 1847: 20); *Martensia* Hering, nom. cons.; *Pollexfenia* W.H. Harvey. Conserved genus name listed in ICN Appendix IIIA.
- Tribe name Pollexfenieae formed from the genus name *Pollexfenia* W.H. Harvey (1844: 431), in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Pollexfenieae is the type of the genus name *Pollexfenia* (Art. 10.9). *Pollexfenia* is typified by the type of *P. pedicellata* W.H. Harvey, according to Womersley (2003: 352). Designation of type species: Schmitz (1889: 448) (typification statement at bottom of p. 436); also see Schmitz & Falkenberg (1897: 455). *P. pedicellata* was one of two species included in the protologue of *Pollexfenia*.

According to Womersley (2003: 352), *P. pedicellata*, which based on southern Australian material, is the correct name of the type species of *Pollexfenia*, and the name *P. laciniata* W.H. Harvey, which is based on South African material (see Papenfuss, 1942), is correctly known as *Papenfussia laciniata* (W.H. Harvey) Kylin. According to Wynne (2014: 143-145), *Papenfussia* Kylin belongs to the Tribe Papenfussieae within the family Delesseriaceae, subfamily Delesserioideae. In the *Index Nominum Genericorum*, *Papenfussia laciniata* is incorrectly listed as the type species of *Pollexfenia* based on an entry dated 9 Feb 1996.

- Tribe name Pollexfenieae assigned by J. Agardh (1863: 792) to the family Rhodomelaceae. Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. Schmitz (1889: 448), who had advice from P. Falkenberg (see Schmitz, 1889: 437 & 446, footnote 2), and J. Agardh (1892: 142), retained the Pollexfenieae as a distinct Tribe within the Rhodomelaceae. In 1897, however, recognition of the Tribe Pollexfenieae as a distinct taxon appears to have abruptly stopped. Without mention of the Tribe Pollexfenieae, Schmitz & Falkenberg

(1897: 425, 428, 454) assigned *Pollexfenia* to the Tribe Rhodomeleae. Subsequently Falkenberg (1901: 723, 724, 752) assigned *Pollexfenia* to the newly described Subfamily Pterosiphonioideae (as Pterosiphonieae on p. 752) without mention of the Tribe Pollexfenieae.

Various subsequent authors (e.g. De Toni 1903: 776, 976, 978; Lucas 1909: 34, 1929: 53; Lucas & Perrin, 1947: 245, 277) also referred *Pollexfenia* to the Subfamily Pterosiphonioideae without mention of *Pollexfenia* or the Tribe Pollexfenieae. Fritsch (1945: 746) did not specify the rank to which his 'subdivisions' of the Rhodomelaceae belonged, while Kylin (1956: 497, 529), who did not recognize subfamilies or tribes, referred *Pollexfenia* to the "Placophora group" within the Rhodomelaceae. Later, Hommersand (1963: 334-344 & fig. 52) recognized three subfamilies of Rhodomelaceae (Rhodomelioideae, Bostrychoideae, Polysiphonioideae), and (Fig. 52, p.343) he placed *Pollexfenia* in the Tribe Polysiphonieae without further comment.

Strangely, Hommersand (1963: 346-348) did not mention *Pollexfenia* in his List of genera of Rhodomelaceae. More recently (e.g. Womersley, 2003: 338, 351; Díaz-Tapia & al., 2017: 933, 934), *Pollexfenia* has again been assigned to the Tribe Pterosiphonieae without mention of the Tribe Pollexfenieae. These authors apparently were unaware that when the legitimate name *Pollexfenia* (which typifies the Tribe Pollexfenieae) and the legitimate name *Pterosiphonia* Falkenberg (in Schmitz & Falkenberg, 1897: 443), (which typifies the Tribe Pterosiphonieae) are assigned to the same Tribe, the tribe name Pollexfenieae (J. Agardh 1863) has nomenclatural priority (ICN Art. 11.3) against the Tribe name Pterosiphonieae Falkenberg (in Schmitz & Falkenberg, 1897). The term 'legitimate name' is defined in Table 1 & in the ICN Glossary. Additional comments occur in the account of the Tribe Pterosiphonieae. J Agardh (1863: 792) validly published the Tribe name Pollexfenieae, at the same time as the Tribe names Alsidieae and Polysiphonieae, in *Species, genera et ordines algarum*. The evidence for valid publication provided for the Tribe Alsidieae above also applies to the Tribe name Pollexfenieae. Díaz-Tapia & al. (2017: 933) incorrectly concluded that the Tribe Alsidieae was not valid. There are no misapplied rank-terms as thought by Díaz-Tapia & al. (2017: 933), and removal of the "Series" and "Subseries" data for the rank sequence of the Tribe Alsidieae under Art. 37.7 (see comments in the account of the Tribe Alsidieae above) also applies to the Tribe Pollexfenieae. Díaz-Tapia & al. (2017)

did not mention the Pollexfenieae as a distinct tribe. Instead, Díaz-Tapia & al. (2017: 934) indicated that *Pollexfenia* was one of the genera in the Tribe Pterosiphonieae in their molecular analyses. The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1 & Table S3) did not include any samples identified as *Pollexfenia*, and therefore, those analyses provide no data relating to relationships between the Tribes Pollexfenieae and Pterosiphonieae. By contrast, a single sample identified as *Pollexfenia* sp. was included in the constrained taxon-rich analysis (Díaz-Tapia & al., 2017: Fig. S2; Table S4 in the Supporting Information). No samples of the type species, *Pollexfenia pedicellata* W.H. Harvey, however, were included. In the resulting tree (Díaz-Tapia & al., 2017: Fig. S2), *Pollexfenia* and *Pterosiphonia* were resolved as genera in the clade to which Díaz-Tapia & al. (2017: 934; Fig. S2) assigned the Tribe name Pterosiphonieae. The Tribe Pollexfenieae was not included in Díaz-Tapia & al. 2017: Table S5 (in the Supporting Information), which contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae. The placement of the genus *Pollexfenia* in same clade as the genus *Pterosiphonia* based on data from a single sample of an unidentified species of *Pollexfenia* is very tenuous, and further investigation clearly is required. As noted above, and in accord with ICN Art. 11.3, the Tribe name Pollexfenieae has nomenclatural priority against the Tribe name Pterosiphonieae when *Pollexfenia* and *Ptersosiphonia* are placed in the same Tribe. Further comments occur in the account of the Tribe Pterosiphonieae below.

Tribe **Polysiphonieae** J. Agardh (1863: 794-795).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (J. Agardh, 1863: 794-795).
- Genera included in the Tribe Polysiphonieae by J. Agardh (1863: 795): *Amansia* J.V.F. Lamouroux; *Cliftonia* W.H. Harvey (1859) (= *Cliftonaea* W.H. Harvey, 1863) (non *Cliftonia* Banks ex C.F. Gaertner 1807); *Dictyomenia* R. Greville (1830) (as *Dictymenia*); *Kuetzingia* Sonder; *Lenormandia* Sonder, nom. cons.; *Neurymenia* J. Agardh; *Placophora* J. Agardh; *Polyphacum* C. Agardh (1820) (= *Osmundaria* J.V.F. Lamouroux); *Polysiphonia* R. Greville, nom. cons.; *Polyzon* Suhr; *Rytiphlaea* C. Agardh; *Vidalia* J.V.F. Lamouroux ex J. Agardh, nom. cons. Conserved genus names listed in ICN Appendix IIIA.

- Tribe name Polysiphonieae formed from the Genus name *Polysiphonia* R. Greville, nom. cons. (Greville, 1823: text for taf. 90), in accord with Art. 19.3 (including references to Art. 19.1 & 18.1). Genus name and its type conserved; listed in ICN Appendix IIIA.

A conserved name of a genus is conserved against all other names at the same rank with the same type (homotypic synonyms, which are to be rejected) whether or not they are cited in the corresponding list (in Appendix IIIA) as rejected names (ICN Art. 14.4).

According to data in the electronic resource *Index Nominum Genericorum* (consulted on 8 February 2025), the following names are superfluous (Art. 52.1) because they included (or are based on) the same type (noted below) as the conserved genus name *Polysiphonia* Greville and thus are to be rejected (as defined in Table 1 and the ICN Glossary): *Carradoria* C.F.P. Martius; *Grammalia* B.C. Dumoriter; *Hutchinsia* C.A. Agardh; *Oligosiphonia* J.E. Gray; *Polychetum* Chevallier; and *Polyoestea* Ruprecht.

In ICN Appendix IIIA, three heterotypic names are listed as rejected names opposite the entry for *Polysiphonia*: *Grammita* Bonnemaison; *Gratelupella* Bory; *Vertebrata* S.F. Gray.

- The nomenclatural type of the Tribe Polysiphonieae is the type of the genus name *Polysiphonia* R. Greville (Art. 10.9). *Polysiphonia* is typified by the type of *P. urceolata* (Lightfoot ex Dillwyn) R. Greville (basionym: *Conferva urceolata* Lightfoot ex Dillwyn) (typ. cons.), according to the *Index Nominum Genericorum* (30 Nov 2023). In the species protologue, Dillwyn (1809: 82) credited Lighthouse for the specific epithet by noting that Dawson Turner saw specimens in some herbaria that Lightfoot marked with “*C. urceolata*. M.S.”. Based on evidence from the designated types and recently collected material, Kim & al. (2000) concluded that *Conferva urceolata* Lighthouse ex Dillwyn (1809: 82, pl. G), the basionym of *Polysiphonia urceolata*, is a later heterotypic synonym of *Conferva stricta* Dillwyn (1804: pl. 40) and that, thus, the correct name (defined in the ICN Glossary) of the type species of *Polysiphonia* is *P. stricta* (Dillwyn) Greville.

The lectotype of the conserved genus name *Polysiphonia*, however, remains the conserved lectotype of *Conferva urceolata*, namely **LD** 39962 typ. cons (designated by Kim & al., 2000: 85), not the lectotype (BM specimen catalogue number **BM** 000530490) of *C. stricta*, namely *Conferva stricta* (designated by Maggs & Hommersand, 1993: 355), who cited the specimen as **BM-K**, Glamorgan (Swansee), undated, coll. *Dillwyn*).

LD 39962 is the nomenclatural type of *Polysiphonia urceolata* (*Conferva urceolata*), the genus *Polysiphonia*, and the Tribe Polysiphonieae.

- Tribe name Polysiphonieae assigned by J. Agardh (1863: 787, 794) to the family Rhodomelaceae (as Ordo. Rhodomeleae). Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. J Agardh (1863: 792) validly published the Tribe name Polysiphonieae (as well as the Tribe name Alsidieae, noted above) in *Species, genera et ordines algarum*; full publication details are in Stafleu & Cowan (1976: 19-20). The evidence for valid publication provided above for the Tribe name Alsidieae also applies to the Tribe name Polysiphonieae.

Díaz-Tapia & al. (2017: 933) incorrectly concluded that the Tribe Alsidieae was not valid. There are no misapplied terms involving the rank of Tribe, and, thus, ICN Art. 37.6 & Art. 37.8 do not apply. Removal of the “Series” and “Subseries” data for the rank sequence of the Tribe Alsidieae under Art. 37.7 also applies to the rank sequence for the Tribe Polysiphonieae. Although the Tribe Polysiphonieae J. Agardh (1863: 792) was validly published, it was (initially) superfluous under Art. 52.1 because J. Agardh (op. cit.) included the genus *Amansia* J.V.F. Lamouroux. As noted above, *Amansia* is the type of the earlier Tribe name Amansieae Horaninow (1847: 238), and thus the Tribe name Amansieae has nomenclatural priority against the Tribe name Polysiphonieae (Art. 11.3) when *Polysiphonia* and *Amansia* are placed in the same Tribe. Despite being superfluous when published, the Tribe name Polysiphonieae is not illegitimate because (Art. 52.4, last part of first sentence & Art. 52, Ex. 17) it is formed from a legitimate generic name (*Polysiphonia*). Thus, as noted in the last sentence of Art. 52.4, the Tribe name Polysiphonieae, when published was incorrect, but it may become correct later. To become correct again in the context of Art. 52.4, the Tribe name Polysiphonieae would need to be treated as a distinct taxon while at the same time, *Amansia*, the type of the Tribe Amansieae, would need to be excluded from the Polysiphonieae, either explicitly or by implication (Art. 52.2(e), including Ex. 5, 6). Exclusion occurred when J. Agardh (1892: 142-143) recognized both the Polysiphonieae and the Amansieae as distinct Tribes of the Rhodomelaceae (“Familiam Rhodomelearum” p. 129). Schmitz & Falkenberg (1897: 426, 429, 436, 465) and various subsequent authors including Hommersand (1963), Womersely (2003) and Díaz-Tapia & al. (2017) also recognized the Polysiphonieae and Amansieae as

distinct tribes. The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1 & Table S3 in the Supporting Information), included single samples identified as *Polysiphonia stricta* (the current correct name for the type species *P. urceolata*), *P. scopulorum* Harvey [= *Bryocladia scopulorum* (Harvey) Díaz-Tapia (in Díaz-Tapia & Verbruggen, 2024: 55)] and *Lophosiphonia teges* (Womersley) Díaz-Tapia & Maggs (in Díaz-Tapia & al., 2017: 934). The three samples were resolved as a distinct clade (Díaz-Tapia & al., 2017: 924, text Fig. 1). Given that the Polysiphonieae is the largest clade of the Rhodomelaceae (Díaz-Tapia & al., 2017: 930), describing a clade in a tree (Díaz-Tapia & al., 2017: 924) that includes only three samples as being resolved with high support (p. 930) seems rather odd. Obviously, further studies are needed. The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig. S2 & Table S4 in the Supporting Information) included 24 samples, among which was one sample of *Polysiphonia stricta* (the current correct name for the type species, *P. urceolata*). These samples formed a clade labelled Polysiphonieae in Fig. S2 within which four groups were identified using generic names (*Bryocladia*/*Falkenbergiella*; *Polysiphonia*; *Lophosiphonia*; and *Epizonaria* Díaz-Tapia & Maggs gen. nov.). The *Bryocladia*/*Falkenbergiella* group included 11 samples identified as *Bryocladia* Schmitz or *Polysiphonia* but not *Falkenbergiella*; all nine samples in the *Polysiphonia* group were identified as species of *Polysiphonia*; the three samples in the *Lophosiphonia* group were identified as species of *Lophosiphonia*; and one sample constituted the *Epizonaria* group. Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae. There is no mention in Table S1 of the groups delimited in Fig. S2. Díaz-Tapia & al. (2017: 934) provide an emended description of the Tribe. A subsequent molecular assessment of species diversity and generic boundaries in the Polysiphonieae and Streblodladieae is provided by Savoie & Saunders (2018). Savoie & Saunders (2018: 16-19) commented on the inclusion of the type species of *Lophosiphonia* in the Tribe Polysiphonieae, confirmed that *Polysiphonia* was polyphyletic, concluded (p. 4) that *Polysiphonia stricta* (Dillwyn) Greville (the current correct name for the type species of *Polysiphonia*) was a complex of several genetically distinct yet overlooked species, and stated that (p. 22) “Expanded phylogenetic analyses with more collections and additional taxa will be necessary to resolve the outstanding uncertainties”. Nomenclatural changes also will likely occur.

Tribe **Polyzonieae** J. Agardh (1892: 136).

- Validly published as a legitimate name of a Tribe. Description provided on p. 136 and taxonomic rank explicitly indicated on pp 133 & 142 in J. Agardh (1892).
- Genera included in Tribe Polyzonieae by J. Agardh (1892: 143): *Cliftonaea* W.H. Harvey nom. nov.; *Leveillea* Decaisne; *Placophora* J. Agardh; *Polyzonia* Suhr. *Cliftonaea* W.H. Harvey (1863: pl. 279) is a replacement name (*nomen novum*) for *Cliftonia* W.H. Harvey (1859: pl. 100), a later illegitimate homonym of *Cliftonia* Banks ex C. Gaertner (1807: 246). J. Agardh (1892: 143) misspelled the name as *Cliftonea*.
- Tribe name Polyzonieae formed from the Genus name *Polyzonia* Suhr (1834: 739) in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Polyzonieae is the type of the genus name *Polyzonia* (Art. 10.9). *Polyzonia* is typified by the type of *P. elegans* Suhr, according to the *Index Nominum Genericorum* (9 Feb 1996).
- Tribe name Polyzonieae assigned by J. Agardh (1892: 129) to the Family Rhodomelaceae. Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. The “Polyzonieae” first appeared as a *nomen nudum* (name without a description and thus not validly published) in Schmitz (1889: 449). In the context of the ICN, “Polyzonieae Schmitz” 1889 is a designation (as defined in the ICN Glossary). Schmitz (1889: 437) thanked Falkenberg for special assistance with work on the Rhodomelaceae; this indicates that in 1889 Falkenberg was contemplating a tribe for *Polyzonia* and other genera placed by Schmitz in the “Polyzonieae”. J. Agardh (1892: 136) subsequently validly published the Tribe name Polyzonieae.

Falkenberg in Schmitz & Falkenberg (1897: 425, 461) explicitly referred to the Polyzonieae as a Tribe in comments on p. 425 in the paragraph preceding the taxonomic key and on p. 461 in comments about the genus *Herpopteros* Falkenberg.

As noted in Part I, Falkenberg (1901) treated the Polyzonieae as a subfamily, and this treatment was adopted by various authors from

De Toni (1903) to Scagel (1953; 1962a: 1031). Hommersand (1963: 334; 335; 338; 342, fig. 52; 347), however, concluded that Falkenberg's subfamilies, including the Polyzonioideae (as the Polyzonieae) were best treated as tribes, and this conclusion was adopted by most subsequent authors including Womersley (2003: 169, 317) and Díaz-Tapia & al. (2017: 921, 923).

Díaz-Tapia & al. (2017: 923) included five genera in the Polyzonieae: *Cliftonaea* W.H. Harvey, *Dasyclonium* J. Agardh, *Echinosporangium* Kylin, *Leveillea* Decaisne, and *Polyzonia* Suhr.

The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1 and Table S3 in the Supporting Information) include single samples of *Cliftonaea pectinata* (W.H. Harvey) W.H. Harvey and *Dasyclonium flaccidum* (W.H. Harvey) Kylin but no samples of any species of *Polyzonia*. Thus, even though *Cliftonaea pectinata* and *Dasyclonium flaccidum* have resolved in a single clade with strong support (Díaz-Tapia & al., 2017: 927), the nomenclatural application of the Tribe name Polyzonieae to a clade that did not include data from the type species or any other species of *Polyzonia* is tenuous and requires further assessment once samples of the type and other species of *Polyzonia* and of all five genera mentioned by (Díaz-Tapia & al., 2017: 927) become available.

The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig. S2 in the Supporting Information), included 10 samples representing 4 genera among which was one sample identified as *Polyzonia elegans* (Table S4), the type species of *Polyzonia*. In this analysis, the Tribe Polyzonieae was resolved (Díaz-Tapia & al., 2017: 924) as monophyletic but with low support. Additional morphoanatomical data are provided by Díaz-Tapia & al. (2017: 923-924).

Díaz-Tapia & al. (2017: Table S5) contains a summary of the "Key morphological characters" used by those authors to delineate tribes of Rhodomelaceae.

Tribe name **Pterosiphoniae**: background information.

Hommersand (1963: 339) effectively published the name 'Tribe Pterosiphoniae', provided brief diagnostic information, included (p. 347) 10 genera (*Amplisiphonia* Hollenberg, *Carradoria* Martius, *Dictyomenia* Greville, *Melanocolax* M.T. Martin & Pocock, *Pterochondria* Hollenberg, *Pterosiphonia* Falkenberg (in Schmitz & Falkenberg), *Rhodomelopsis* Pocock, *Symphyocladia* Falkenberg (in Schmitz & Falkenberg), *Tayloriella* Kylin, *Vertebrata* S.F. Gray, nom.

rej.), included the intended tribe name in a diagram (p. 343, fig. 52) that depicted phylogenetic relationships of the tribes and subfamilies of Rhodomelaceae, and (p. 347) placed the Pterosiphonieae in his list of Tribes of Rhodomelaceae, Subfamily Polysiphonieae.

Hommersand (1963), however, did **not** validly publish the ‘Tribe Pterosiphonieae’ as the name of a new taxon because he did not provide a Latin description or diagnosis or a reference to a previously and effectively published Latin description or diagnosis as required by ICN Art. 44.1. Hommersand (1963) also did not publish the ‘Tribe Pterosiphonieae’ as a name at new rank (defined in ICN Glossary) because he did not provide a full and direct reference (Art. 41.5) to its basionym. Valid publication (see below) occurred inadvertently in Maggs & Hommersand (1993: 367) as a name at new rank (stat. nov.) rather than the name of a new taxon.

Falkenberg (in Schmitz & Falkenberg, 1897: 427, 443) initially placed the newly described genus *Pterosiphonia* in the Tribe Polysiphonieae. Subsequently, however, Falkenberg (1901: 700, 714, 752) placed *Pterosiphonia* in the newly described subfamily Pterosiphonioideae (as Pterosiphonieae). Falkenberg (1901: 714) unequivocally treated the Pterosiphonioideae (as Pterosiphonieae) as a subfamily (Unterfamilie), not a Tribe as suggested by some authors including Díaz-Tapia & al. (2017: 928, 929). Falkenberg (1901: 714) also referred to the diagram on p. 700, which includes a list of the subfamilies he recognized, all with the Latin termination *-eae*. In Candolle (1867b), the Code in effect in 1901, the Latin termination *-eae* was specified as the correct termination for both subfamily names (Art. 23) and tribe names (Art. 24), something apparently not realized by Maggs & Hommersand (1993). Falkenberg’s recognition of subfamilies is dealt with further in Part I of the present account.

We are unaware of anyone who treated Falkenberg’s subfamilies as tribes between 1901 and 1963. Indeed, if the name Pterosiphonieae had been validated as a Tribe by Fritsch (1945:746), it would have been superfluous (Art. 52.1) because *Pollexfenia*, the type of the older Tribe name Pollexfenieae J. Agardh (1863: 792) was included by Fritsch (1945: 746) in his Pterosiphonieae

Tribe Pterosiphonieae Maggs & Hommersand (1993: 367, stat. nov.).

Basionym: Subfamily Pterosiphonioideae Falkenberg (1901 700, 714, 752, as Pterosiphonieae). Improper Latin subfamily termination

(defined in ICN Glossary) *-eae* corrected to *-oideae* in accord with ICN Art. 18.4, 32.2, 37.2 (footnote) without change of authorship or date.

- Validly published by Maggs & Hommersand (1993: 367) as the legitimate name of a Tribe. Taxonomic rank explicitly indicated and description provided. As explained below, Maggs & Hommersand actually inadvertently published the Tribe Pterosiphonieae as a stat. nov. (name at new rank) for the subfamily name Pterosiphonioideae Falkenberg (1901, as Pterosiphonieae). As noted above, the name ‘Tribe Pterosiphonieae’ was effectively but not validly published by Hommersand (1963), and it was not published as a Tribe by Falkenberg (1901).
- Only genus included in the Tribe Pterosiphonieae by Maggs & Hommersand (1993: 367): *Pterosiphonia* Falkenberg (in Schmitz & Falkenberg, 1897: 443). None of the other genera mentioned by Hommersand (1963; see above) occur in the British Isles and thus were not mentioned in Maggs & Hommersand (1993).
- Tribe name Pterosiphonieae Maggs & Hommersand (1993: 367) formed from the genus name *Pterosiphonia* Falkenberg (in Schmitz & Falkenberg, 1897: 443), in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Pterosiphonieae is the type of the genus name *Pterosiphonia* (Art. 10.9). *Pterosiphonia* is typified by the type of *P. cloiophylla* (C.A. Agardh) Falkenberg (basonym: *Rhodomela cloiophylla* C.A. Agardh), according to the *Index Nominum Genericorum* (31 May 2006). Designation of type species occurred in the generic protologue (Falkenberg, in Schmitz & Falkenberg, 1897: 443).
- Tribe name Pterosiphonieae assigned by Maggs & Hommersand (1993: 283) to the family Rhodomelaceae. Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. As noted above, valid publication of the Tribe Pterosiphonieae occurred inadvertently in Maggs & Hommersand (1993: 367) as a name at new rank (stat. nov.) rather than the name of a new taxon. The requirements for validation as a name at new rank (ICN Art. 41) were met in the same manner as occurred for the Tribe Bostrychieae, explained in the account of that Tribe.

For the Pterosiphonieae, Maggs & Hommersand (1993: 367) provided the following text information: “Tribe PTEROSIPHONIEAE FALKENBERG (1901) p. 261” and in the References, Maggs & Hommersand provided the following: “Falkenberg. P. 1901. *Die*

Rhodomelaceen des Golfes von Neapel und der angrenzenden Meeres-abschnitte. Berlin.”.

Collectively, these two pieces of information constitute a clear indication of a full and direct reference to the basionym data required by Art. 41.5, namely: author (P. Falkenberg), place of valid publication (*Die Rhodomelaceen des Golfes von Neapel und der angrenzenden Meeres-abschnitte.* Berlin), and page reference and date (Falkenberg, 1901: 261). There are no omissions (Art. 41.6) from the requirements of a ‘clear indication’, but there is one correctable citation error: Maggs & Hommersand (1993: 367) cited p. 261 (where the “basionym” has a non-Latin termination) rather than p. 752 (where the basionym has a Latin termination, with a bold-face reference to p. 261 and p. 723 where descriptions occur). As noted in Art. 41.6, errors of this sort do not preclude valid publication of a name at new rank.

The name at new rank can be correctly cited as Tribe Pterosiphonieae Maggs & Hommersand stat. nov. (1993: 367). Parenthetical author citations (e.g. Pterosiphonieae (Falkenberg) Maggs & Hommersand) are not used for suprageneric names (ICN Art. 49.2).

The Maggs & Hommersand (1993) format does not strictly agree with ICN Recommendation 41A.1 which states that all this information “should immediately follow a name at new rank. It should not be provided by mere cross-reference to a bibliography...”. However, Turland (2019: 39) pointed out that such split references still are full and direct. By meeting the requirements of Art. 41.5, the requirement of Art. 41.1 and the conditions mentioned in Art. 41.6 also are satisfied.

Maggs & Hommersand (1993) changed the rank of the name from Subfamily to Tribe, thus satisfying the requirement of Art. 42.2(a). Remaining provisions of Art. 41 are not relevant.

Subsequent accounts involving multiple genera assigned to the Tribe Pterosiphonieae include Womersley (2003: 337-361), Savoie & Saunders (2016: 920), Norris & al. (2017:46) Díaz -Tapia & al. (2017: 234), and Díaz -Tapia & al. (2023, Fig. 2).

If, however, *Pollexfenia* (the genus from which the Tribe name Pollexfenieae is formed; see Art. 10.9) and *Pterosiphonia* (the genus from which the Tribe name Pterosiphonieae is formed; see Art. 10.9) are assigned to the same Tribe (e.g. as occurs in Womersley 2003, Savoie & Saunders 2016 and Díaz -Tapia & al. 2017, 2023), the correct name (Art. 11.1 & Art. 11.3) of that Tribe is the Pollexfenieae J.

Agardh (1863: 792), not the Pterosiphonieae Maggs & Hommersand (1993: 367). Tribe names are typified by the type of the genus from which the Tribe name is formed (Art. 10.9), and Pollexfenieae is the earlier legitimate name (Art. 11.3) and thus has nomenclatural priority when *Pollexfenia* and *Pterosiphonia* are assigned to the same Tribe. The Tribe Pterosiphonieae then becomes a heterotypic synonym of the Tribe Pollexfenieae.

Díaz-Tapia & al. (2017: 934) emended (the heading *Amended descriptions of tribes* is on p. 933) the description of the Tribe Pterosiphonieae, but the Tribe Pterosiphonieae as emended is still superfluous because *Pollexfenia*, nomenclatural type of the Tribe Pollexfenieae (J. Agardh 1863: 792), was definitely included (p. 934) and has priority against the Tribe Pterosiphonieae Maggs & Hommersand (1993: 367).

The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1 and Table S3 in the Supporting Information) did not include data from any species identified as *Pterosiphonia* or *Pollexfenia*. Without data from these genera, the nomenclatural application of the Tribe name Pterosiphonieae or the Tribe name Pollexfenieae to a clade that did not include data from the type species or any other species of *Pterosiphonia* or of *Pollexfenia* is tenuous and requires further assessment once samples of the type and other species of the type genus become available.

The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig. S2 in the Supporting Information) included one sample of an unidentified species of *Pollexfenia*, one sample of *Pterosiphonia cloiophylla*, the type species of the genus, single samples of three other species identified as *Pterosiphonia* and one sample of an unidentified species of *Pterosiphonia*. The analysis (Díaz-Tapia & al., 2017: 929) resulted in a moderately supported clade comprising 31 samples involving *Pterosiphonia* and seven other genera previously assigned to the Pterosiphonieae. The inclusion of *Pollexfenia* and *Pterosiphonia* samples in the same clade suggests that the two genera belong to the same taxonomic Tribe for which the name Pollexfenieae has priority, but the absence of any samples of the type species of *Pollexfenia*, *P. pedicellata* W.H. Harvey, strongly suggests that additional confirming studies are needed.

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae. In Table 5, from the nomenclatural point of view, the tribe name Pterosiphonieae requires change to Pollexfenieae.

Tribe **Rhodolachneae** Womersley (in Womersley & Bailey, 1970: 331).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (Womersley, in Womersley & Bailey, 1970: 331). Required Latin description (Art. 44.1) present.
- Only genus included in the Tribe Rhodolachneae by Womersley (in Womersley & Bailey, 1970: 331); *Rhodolachne* Wynne (1970a: 1780).
- Tribe name Rhodolachneae formed from the Genus name *Rhodolachne* Wynne (1970a: 1780) in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Rhodolachneae is the type of the genus name *Rhodolachne* (Art. 10.9). *Rhodolachne* is typified by the type of *R. decussata* Wynne, according to the *Index Nominum Genericorum* (9 Feb 1996).
- Tribe name Rhodolachneae assigned by Wynne (1970a) to the Family Rhodomelaceae. Family name conserved; listed in Appendix IIA.

Additional Remarks. Wynne (1970a, 1970b) provided detailed accounts of the type species. A second species, *R. radicata* Itono (1985: 53) described from Japan has subsequently been referred to *Bostrychia* by West & al. (2006).

Díaz-Tapia & al. (2017: 932) noted that *Rhodolachne* had very unusual morphological characteristics and stated that further investigations were needed to unravel its phylogenetic relationships and reassess its classification, but they did not include *Rhodolachne* in their phylogenetic analyses because molecular data were not available.

Tribe **Rhodomeleae** J. Agardh (1841: 23).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (J. Agardh, 1841: 23).
- Genera included in the Tribe Rhodomeleae by J. Agardh (1841: 24-29): *Alsidium* C. Agardh; *Amansia* J.V.F. Lamouroux; *Claudea* J.V.F. Lamouroux; *Dasya* C. Agardh, nom. et orth. cons.; *Dictyomenia* R. Greville; *Dictyurus* Bory de Saint-Vincent; *Odonthalia* Lyngbye, nom. cons.; *Polysiphonia* R. Greville, nom. cons.; *Polyzonia* Suhr; *Rhodomela* C. Agardh, nom. cons.; *Rytiphlaea* C. Agardh. Conserved genus names listed in ICN Appendix IIIA.

- Tribe name Rhodomeleae formed from the Genus name *Rhodomela* C. Agardh (1822: 368), nom. cons., in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Rhodomeleae is the type of the genus name *Rhodomela* (Art. 10.9). *Rhodomela* is typified by the type of *R. subfusca* (Woodward) C. Agardh (1822: 368) (basionym: *Fucus subfuscus* Woodward 1791: 132), according to the *Index Nominum Genericorum* (12 Jan 2021). Designation of type species: Schmitz (1889: 446); also see Schmitz & Falkenberg (1897: 456) and Silva (1952: 269).

In accord with ICN Art. 9.19, *R. subfusca* remains the type species even though the earliest correct name for *Rhodomela subfusca* is, as noted by Silva (1952: 269), considered to be *Rhodomela confervoides* (Hudson) P.C. Silva (basionym: *Fucus confervoides* Hudson 1762: 474). The nomenclatural type of *Rhodomela subfusca* also typifies the genus name *Rhodomela*, the Tribe name Rhodomeleae, the Subfamily name Rhodomeloideae, and the Family name Rhodomelaceae.

- Tribe name Rhodomeleae assigned by J. Agardh (1841: 7, 23) to a 'familia' (p. 7) called the 'Florideae', a 'name' **not** formed from the name of an included genus (Art. 32.1(c)), as required by Art. 18.1 and, thus, not validly published for nomenclatural purposes. Horaninow (1847: 238) placed the Rhodomeleae in the newly described family Rhodomelaceae, now a conserved family name listed in ICN Appendix IIA.

Additional Remarks. Maggs & Hommersand (1993: 289) recognized *Rhodomela subfusca* as the lectotype species of the genus *Rhodomela* and indicated that it was a heterotypic synonym of *R. confervoides*. Maggs & Hommersand (1993: 293) also neotypified the basionym, *Fucus confervoides* Hudson, with a **BM** specimen in the Herb. E. Forster. Whether this specimen and the type of *Fucus subfuscus* are conspecific apparently remains to be determined. We also are uncertain whether *Fucus subfuscus* has been lectotypified. Woodward (1791) based the species on material from Cromer on the coast of Norfolk (England) and provided a plate of illustrations, but we have not found any information as to whether any specimens used by Woodward still exist. The only original material we are aware of is the protologue illustration (Woodward, 1791: pl. 12, figs 1-5).

Five of the ten genera (other than *Rhodomela*) originally included in the Rhodomeleae by J. Agardh (1841) (*Alsidium*; *Amansia*; *Polysiphonia* nom. cons.; *Polyzonia* nom. cons.; *Rytiplhaea*) now typify other Tribes currently assigned to the Rhodomelaceae. In addition,

Díaz-Tapia & al. (2017) placed *Dictyomenia* in the Rhodomelaceae, Tribe Pterosiphonieae (p.929, 934) and retained *Odonthalia* and *Rhodomela* in the Tribe Rhodomeleae (p. 928). *Dasya* typifies the subfamily Dasyoideae, now assigned to the Delesseriaceae (Díaz-Tapia & al., 2019: 79; Cormaci & al., 2023: 451), while *Dictyurus* is now placed in the Delesseriaceae, subfamily Heterosiphonieae (Díaz-Tapia & al., 2019: 79; Cormaci & al., 2023: 450). Thus, of the eleven genera originally referred to the Tribe Rhodomeleae, only *Rhodomela* and *Odonthalia* have been retained in that Tribe.

The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1 in the Supporting Information), included single samples identified as *Choreocolax polysiphoniae* Reinsch and *Rhodomela confervoides* (Hudson) P.C. Silva, the earliest known correct name for *Rhodomela subfusca*, the nomenclatural type species of *Rhodomela* and the Tribe Rhodomeleae. The samples were resolved as a distinct clade with full bootstrap support to which the Tribe name Rhodomeleae was applied. When chloroplast genome data become available for the other four genera placed in the Tribe by Díaz-Tapia & al. (2017: Table S2 in the Supporting Information), and data from several additional samples of *Rhodomela confervoides* become available, further analyses should be undertaken to confirm the conclusions of Díaz-Tapia & al. (2017).

The constrained taxon-rich tree (Díaz-Tapia & al. 2017: Fig. S2 in the Supporting Information) included 16 samples from 14 species representing all 6 genera included by Díaz-Tapia & al. (2017), among which was one sample identified as *Rhodomela confervoides* (Table S4), the earliest known correct name for the type species, *Rhodomela subfusca*. The analysis resolved a highly supported clade (Díaz-Tapia & al., 2017: 928) to which the name Rhodomeleae was applied. Interestingly, the type species of *Odonthalia*, *O. dentata*, grouped with the type species of *Neorhodomela*, *N. munita* (Perestenko) Masuda rather than with the other samples identified as species of *Odonthalia*. Díaz-Tapia & al. (2017) did not comment on this.

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae.

Tribe **Sonderelleae** L.E. Phillips (2001: 498).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (L.E. Phillips, 2001: 498).

- Genera included in Tribe Sonderelleae by L.E. Phillips (2001): *Lembergia* Saenger (in Saenger & al., 1971: 110); *Sonderella* F. Schmitz (in Schmitz & Hauptfleisch, 1897: 415).
- Tribe name Sonderelleae formed from the Genus name *Sonderella* Schmitz (in Schmitz & Hauptfleisch, 1897: 415) in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Sonderelleae is the type of the genus name *Sonderella* (Art. 10.9). *Sonderella* is typified by the type of *S. linearis* (W.H. Harvey) F. Schmitz (basionym: *Amansia linearis* W.H. Harvey nom. illeg. (1859: pl. 108), according to the *Index Nominum Genericorum* (9 Feb 1996). *Amansia linearis* W.H. Harvey (1859: pl. 108) is a later illegitimate homonym of *Amansia linearis* Bory de Saint-Vincent (in Bélanger & Bory de Saint-Vincent, 1834: 173).
- Tribe name Sonderelleae assigned by L.E. Phillips (2001) to the Family Rhodomelaceae. Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. L.E. Phillips (2001) concluded from a detailed morphoanatomical study combined with a molecular analysis based on the 18S rRNA gene that *Sonderella* and *Lembergia* represented a distinct tribe within the Rhodomelaceae. Both genera contain single known species (L.E. Phillips, 2001: 487; Díaz-Tapia & al., 2017: 923).

The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924; text Fig. 1; Fig. S1 & Table S3 in the Supporting Information), included one sample identified as *S. linearis*, the type species of *Sonderella*. It was resolved as a distinct clade. Further comments are in Díaz-Tapia & al. (2017: 923). When chloroplast genome data become available for *L. allanii* (Lindauer) Saenger, the type and only known species of *Lembergia*, a further analysis is needed to confirm that it groups with *Sonderella* in a single clade.

The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig. S2 and Table S4 in the Supporting Information) included one sample identified as *Sonderella linearis*, the type species of *Sonderella*, and one sample of *L. allanii*, the type species of *Lembergia*, the two known species of the Sonderelleae. The samples were strongly resolved as a monophyletic clade (the Sonderelleae) with high support (noted on p. 923).

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae.

Tribe **Strebloladiaceae** Díaz-Tapia & Maggs (in Díaz-Tapia & al., 2017: 933).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (Díaz-Tapia & al., 2017: 933).
- Genera included in the Tribe Strebloladiaceae by Díaz-Tapia & al. (2017: 933): *Aiolocolax* Pocock, *Lampisiphonia* H.G. Choi, Díaz -Tapia & Bárbara (in Bárbara & al. 2013); *Leptosiphonia* Kylin; *Melanothamnus* Bornet & Falkenberg (in Falkenberg 1901); *Pterochondria* Hollenberg; *Polyostea* Ruprecht; *Strebloladia* F. Schmitz (in Schmitz & Falkenberg 1897); *Tolypiocladia* F. Schmitz (in Schmitz and Falkenberg 1897); *Vertebrata* S.F. Gray.
- Tribe name Strebloladiaceae formed from the Genus name *Strebloladia* Schmitz (in Schmitz & Falkenberg, 1897: 457) in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Strebloladiaceae is the type of the genus name *Strebloladia* (Art. 10.9). *Strebloladia* is typified by the type of *S. neglecta* Schmitz (in Schmitz & Falkenberg, 1897), according to the *Index Nominum Genericorum* (9 Feb 1996). According to Papenfuss (1964: 63-64, Note), *Strebloladia glomerulata* (Montagne) Papenfuss (1964: 63) (basonym: *Rhodomela glomerulata* Montagne, 1842: 4) is the earliest correct name for the type species of *Strebloladia*, *S. neglecta* Schmitz (in Schmitz & Falkenberg, 1897). This synonymy was indicated earlier by Falkenberg (1901: 354), but in our opinion, needs confirmation via a comparison of the type specimens of the two names. As correctly noted by Papenfuss (1964: 63-64, Note), the genus name *Strebloladia* is based on [the type of] *S. neglecta*.
- Tribe name Strebloladiaceae assigned by Díaz-Tapia & Maggs in Díaz-Tapia & al. (2017: 933) to the Family Rhodomelaceae. Family name conserved; listed in Appendix II A.

Additional Remarks. Hommersand (1963: 339-340) effectively published the 'Tribe Strebloladiaceae', provided brief diagnostic information, included the genera *Strebloladia* and *Microcolax*, stated that it "... should probably be recognized as a separate tribe", included the tribe in his diagram (p. 343, fig. 52) representing phylogenetic relationships of the tribes and subfamilies of Rhodomelaceae, and (p. 347) placed it in his list of Tribes of Rhodomelaceae.

The putative name Strebloladiaceae, however, was **not** validly published because Hommersand (1963) did not provide a Latin description or diagnosis or a reference to a previously and effectively

published Latin description or diagnosis as required by ICN Art. 44.1. Valid publication of the Tribe Streblocladieae occurred in Díaz-Tapia & al. (2017: 933).

The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; Fig. S1 & Table S3 in the Supporting Information), did not include samples from the type species of *Streblocladia*, *S. neglecta* Schmitz, or from *S. glomerulata* (Montagne) Papenfuss (the earliest known correct name for the type species), or indeed from any species of *Streblocladia*. Consequently, the nomenclatural application of the name Streblocladieae to this clade is tenuous and requires further assessment once chloroplast genome data become available for the type species and other species of *Streblocladia*.

The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig S2 in the Supporting Information) contained 81 samples from 10 genera including samples from the type species of all nine genera listed by Díaz-Tapia & al. (2017: 933), among which was one sample of *Streblocladia glomerulata* (Montagne) Papenfuss (Table S4), the earliest known correct name for the type species of *Streblocladia*, *S. neglecta* F. Schmitz, according to Papenfuss (1964: 63-4, Note). The Streblocladieae resolved as a distinct clade (Fig. S2 in Supporting Information).

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes of Rhodomelaceae. A diagnosis of the Tribe Streblocladieae Díaz-Tapia & Maggs occurs on p. 933, and Díaz-Tapia & al. (2017: 931) provide additional comments, and suggest (p. 932) that an integrative review at genus level is needed. A subsequent generic level analysis (Bustamante & al., 2021) has clarified generic boundaries and the boundary between the Tribe Streblocladieae and the Tribe Polysiphonieae.

Tribe *Thaumatelleae* Díaz-Tapia & Maggs (in Díaz-Tapia & al., 2017: 933).

- Validly published as a legitimate name of a Tribe. Description provided and taxonomic rank explicitly indicated in protologue (Díaz-Tapia & al., 2017: 933).
- Only genus included in the Tribe *Thaumatelleae* by Díaz-Tapia & al. (2017: 933): *Thaumatella* (Falkenberg) Kylin (1956: 511) (basonym: *Brongniartella* subgenus *Thaumatella* Falkenberg, 1901: 550).

The distinctive features of the subgenus are included in the first paragraph following the heading Subgenus *Thaumatella* (Falkenberg, 1901: 550).

- Tribe name Thaumatelleae formed from the Genus name *Thaumatella* (Falkenberg) Kylin (1956: 511), in accord with Art. 19.3 (including references to Art. 19.1 & 18.1).
- The nomenclatural type of the Tribe Thaumatelleae is the type of the genus name *Thaumatella* (Art. 10.9). *Thaumatella* is typified by the type of *T. disticha* (Falkenberg) Kylin (basionym: *Brongniartella disticha* Falkenberg, 1901: 550), according to the *Index Nominum Genericorum* (9 Feb 1996).
- Tribe name Thaumatelleae assigned by Díaz-Tapia & al. (2017: 933) to the Family Rhodomelaceae. Family name conserved; listed in ICN Appendix IIA.

Additional Remarks. Based on morphoanatomical data, Kylin (1956: 495, 511) placed the genus *Thaumatella* in his “Lophothalia Gruppe” within the Rhodomelaceae. By contrast, Womersley (2003: 240) treated *Thaumatella* as a heterotypic synonym of *Veleroa* Dawson (1944: 335) based on morphoanatomical data. The type species, *Thaumatella disticha*, was treated as a heterotypic synonym of *Veleroa adunca* (J. Agardh) Womersley & Parsons.

Thaumatella adunca (J. Agardh) Parsons & Womersley comb. nov., based on *Dasya adunca* J. Agardh (1890: 112), appears in Womersley (1998: 479) but then becomes *Veleroa adunca* (J. Agardh) Womersley & Parsons comb. nov. (in Womersley, 2003: 240).

Subsequently, Díaz-Tapia & Maggs (in Díaz-Tapia & al., 2017: 924, 933), based mainly on molecular analyses, established the Tribe Thaumatelleae for the single genus *Thaumatella* that (p. 928) was “resurrected” for the single species *Thaumatella adunca*.

The chloroplast phylogenomics trees of Díaz-Tapia & al. (2017: 924, text Fig. 1; & Fig. S1, & Table S3 in the Supporting Information), included a single sample of *Thaumatella adunca*, the only known species and genus in the Tribe Thaumatelleae. It resolved as a distinct clade (Díaz-Tapia & al., 2017: 924, text Fig. 1; & Fig. S1 in the Supporting Information).

The constrained taxon-rich tree (Díaz-Tapia & al., 2017: Fig. S2 & Table S4) in the Supporting Information) also included a single sample of *Thaumatella adunca*, the only known species and genus in the Tribe Thaumetelleae, and it resolved as a distinct clade.

Díaz-Tapia & al. (2017: Table S5) contains a summary of the “Key morphological characters” used by those authors to delineate tribes

of Rhodomelaceae. Further comments on the Thaumatelleae occur in Díaz-Tapia & al. (2017: 928).

Part III. Nomenclatural Outcomes

This account has provided a nomenclatural analysis of the scientific names and authors of current Tribes assigned to the red algal family Rhodomelaceae (Ceramiales, Rhodophyta). We have investigated whether Tribe names are validly published, determined the correct name for each Tribe, determined the correct author citation for each name, determined the priority of names, and provided other pertinent nomenclatural information.

As noted by McNeill & Turland in Mc Neill & al. (2006: vii) “Unambiguous names for organisms are essential for effective scientific communication; names can only be unambiguous if there are internationally accepted rules governing their formation and use”.

We fully agree with Díaz-Tapia & al. (2017: 932) that much work remains to fully understand the systematics of the most diverse family of the red algae. We also agree with (Díaz-Tapia & al., 2017: 931) that “integrative analyses of broad-based tested phylogenies and scrutinized morphoanatomical characters provides the strongest combination for evaluating previous classification schemes and proposing revisions supported by both molecular and non-molecular evidence.” Accurate nomenclature is an essential component of sound taxonomic research.

From the nomenclatural point, the application of scientific names, in our view, is attended by uncertainty when conclusions are based on analyses in which data from the type species of the relevant genera, tribes or subfamilies are lacking. Inclusion of type species data are needed to more confidently clarify taxon concepts and assess infraspecific genomic variability. Type species data also are needed to elucidate with greater certainty taxon circumscriptions, diagnostic characters, and other molecular and non-molecular evidence associated with monophyly.

3. Conclusions

Nomenclatural Basics

- Biological nomenclature deals with the application of scientific names to organisms. The scientific naming of algae, fungi and plants

is now governed by rules in the ICN (*International Code of Nomenclature for algae, fungi and plants*). The latest edition available online and in print (Turland & al., 2018) is superseded by the forthcoming Madrid edition now in preparation and due out in print in July 2025. The first version of what is now the ICN (Candolle, 1867b) was in effect from August 1867 until superseded by Briquet (1906).

- Every individual organism is treated as belonging to a series of taxa at consecutive ranks which in descending sequence include Family, Subfamily, Tribe, Genus, and Species (ICN Art. 3, 4). The rank of species is basic (Art. 2.1). In this sequence, the principal ranks are Family, Genus and Species; Tribe is a secondary rank and Subfamily is a further intermediate rank between Family and Tribe (Art. 3.1, 4.1, 4.2). Not all secondary and further ranks need to be used (Art. 4, Note 1). Each species, however, is assignable to a genus and each genus is assignable to a family (Art. 3.1).
- In accord with the ICN, the application of scientific names to taxonomic groups at the rank of family and below is determined by means of nomenclatural types (ICN Prin. II; Art. 7.1). A nomenclatural type is that element to which the name of a taxon is permanently attached (Art. 7.2). The term 'element' (see ICN Glossary) refers to a specimen or illustration eligible to serve as nomenclatural type, or to a name considered to be the full equivalent of its type (specimen or illustration) for purposes of designation or citation of a type.
- The nomenclatural type of the name of a family, subfamily or tribe is the same as that of the generic name from which it is formed (Art. 10.9). The nomenclatural type of the name of a genus is the nomenclatural type of the name of a species (Art. 10.1), and the nomenclatural type of the name of a species is either a single specimen or an illustration as specified in Art. 8.1.
- Accurate author citation data for names of taxa, including bibliographic data, provides important information about the original source and date of a name, and is essential to determine whether a name is validly published, whether it has priority against other names, etc.

Nomenclatural Outcomes

- Before the 1906 Vienna Code (Briquet, 1906), the specified use (Candolle, 1867b: Art. 23) of the Latin termination *-eae* for both subfamily names and tribe names has resulted in considerable

confusion, which has persisted ever since, particularly for names published after 1 January 1887 (ICN Art. 37.2).

- Internal evidence elucidated during the present study from each of the following publications shows that names of subdivisions of the family Rhodomelaceae were ranked as Tribes in Schmitz (1889) and in Schmitz & Falkenberg (1897) but were ranked as Subfamilies in Falkenberg (1901) and De Toni (1903).
- Falkenberg (1901) was inconsistent in the use of Germanic and Latin names for supergeneric groups of Rhodomelaceae. Falkenberg's extensive use of Germanic names with the non-Latin termination *-een* are not validly published (ICN Art. 19.7) and have no status under the ICN (Art. 12.1). Falkenberg's limited use of the Latin termination *-eae* for subfamily names was in accord with the *Code* then in effect (Candolle, 1867b), but after the change to *-oideae* for subfamily names in the 1906 Vienna Code (Briquet, 1906) led to inadvertent misinterpretations by various subsequent authors (e.g. Hommersand, 1963: 334; Phillips, 2000: 773; Zuccarello & West, 2006: 24; Díaz-Tapia & al., 2017: 921, 922, 931, 932) that Falkenberg's names denoted tribes, or families, or "Familien" equivalent to tribes.
- Our investigations encompassed the names of 22 currently recognized Tribes of Rhodomelaceae and two informal groups. Table 2 provides a chronological list of these names and the correct authorship citations resulting from this study. Names originally published in the same account are grouped together.
- Hommersand (1963) effectively published the intended Tribe names Bostrychieae, Heterocladieae and Pterosiphonieae but did **not** validly publish these intended names.
- The Tribe names (Pterosiphonieae Maggs & Hommersand, stat. nov.; Bostrychieae Womersley stat. nov.; Heterocladieae Womersley stat. nov.) were each identified as a name at new rank (stat. nov.). All three were inadvertently validated with that status.
- As of 9 February 2025 (based on data in the *Index Nominum Algarum* and in *AlgaeBase*), nine Tribe names (Bostrychieae Womersley, stat. nov.; Cladureae Díaz-Tapia & Maggs; Dipterosiphonieae Díaz-Tapia & Maggs; Heterocladieae Womersley, stat. nov.; Neotenophyceae Kraft & Abbott; Ophidocladeae Díaz-Tapia & Maggs; Pleurostichidieae Hommersand; Rhodolachneae Womersley; Thaumatelleae Díaz-Tapia & Maggs) include only one currently recognized genus.
- As of 9 February 2025 (based on data in the *Index Nominum Algarum* and in *AlgaeBase*), four tribes (Neotenophyceae;

Ophiocladieae; Pleurostichidieae; Thaumatelleae) include only one currently recognized species.

- The Tribe name Pollexfenieae J. Agardh (1863: 792) has nomenclatural priority against the Tribe name Pterosiphonieae Maggs & Hommersand (1993: 367) stat. nov. when the genera *Pollexfenia* and *Pterosiphonia* are placed in the same Tribe (as occurs, for example, in Womersley (2003) and Díaz-Tapia & al. (2017).
- Outcomes of chloroplast phylogenomics analyses and constrained taxon-rich analyses in Díaz-Tapia & al. (2017) have been summarized for Tribes for which outcomes are available. These provide valuable phylogenetic and taxonomic information, but caution is required in cases where samples were not included for the type species and in some cases for any species in the genus from which the Tribe name is derived. It is important to remember (ICN Art. 7.1) that “The application of names of taxa at the rank of family or below is determined by means of nomenclatural types (types of names of taxa)”.

We look forward to future studies of algal biodiversity and their associated nomenclature in the context of striving for an increasingly stable system of applying scientific names to taxa that includes data from relevant nomenclatural types.

Tab. 1. Glossary of nomenclatural terms and phrases used in this account. References to the ICN are given where appropriate. ICN Articles cited are those in the Shenzhen Code (Turland & al. 2018); the ICN Glossary referred to is also that in the Shenzhen Code.

author citation: the name(s) of author(s) appended to the scientific name of a taxon that they established or introduced in accord with ICN Art. 46-50. Examples: Tribe Alsidieae J. Agardh (1863: 792); <i>Alsidium corallinum</i> C. Agardh (1827: 639). Author citations are not part of a scientific name; they are appended to it. basionym: the legitimate, previously published name on which a new combination or name at new rank is based. (see entry in the ICN Glossary). clear indication of rank: the meaning of this term is not explained in Art. 37.1 or Art. 37.3 or in the definition of rank in the ICN Glossary, but is presumed here to mean that a rank must be specified or a taxon name must have one of the terminations listed in Art. 37.2, footnote. Also see indication of rank below. Code: any edition/version of the <i>International Code of Nomenclature</i> for algae, fungi and plants and its predecessors. correct name: the scientific name that must be adopted in accordance with the Shenzhen ICN. (see ICN Glossary entry and Art. 11.3 & 11.4). designation: a term used for what appears to be a scientific name but has not been validly published (see ICN Glossary). Designations are not scientific names and hence have no status under the <i>Code</i> (Art. 12.1). Also see Art. 23.6. effectively published name: a name that meets the requirements for effective publication specified in ICN Art. 29-31. To be validly published, a scientific name must also be effectively published. herbarium acronym: a specified 2-several letter designation for a registered herbarium (see the online database Index Herbariorum (https://sweetgum.nybg.org/science/ih/)). hierarchy: see taxonomic hierarchy homonym: each of two or more identically spelled scientific names of the same rank based on different types. (ICN Art. 53.1; also see ICN Glossary). The later homonym (meaning the most recently published homonym) of the name of a family, genus or species is illegitimate unless conserved, sanctioned or protected (Art. 53.1), and is unavailable for use. The provisions on homonymy do not apply to names of subdivisions of families, as noted in Art. 53, Ex. 5. homotypic synonym: each of two scientific names of the same rank based on the same type. (ICN Art. 14.4; ICN Glossary). IBC: International Botanical Congress ICN: acronym for the <i>International Code of Nomenclature for algae, fungi, and plants</i>. indication of rank: the use of Latin terminations (listed in Art. 37.2, footnote) as evidence of the rank of a scientific name published on or after 1 January 1887 in lieu of using a particular rank-denoting term (e.g. Order, Family) (Art. 37.2 including Ex. 1). From 1 January 1887 to 17 June 1905 (when the Vienna Rules were adopted) (Briquet 1906), the termination <i>-eae</i> was used both for subfamily and tribe names. Consequently, additional internal evidence is needed to determine which rank was intended. internal evidence: evidence within a publication in support of the validity of a scientific name established or introduced in the same publication. Scientific names are names that are validly published in accord with the ICN (see definition below). isonym: the same name based on the same type published independently at different times perhaps by different authors. (ICN Art. 6, Note 2 & ICN Glossary). Only the earliest isonym has nomenclatural status. The earliest isonym is to be cited from its original place of valid

publication; later isonyms may be disregarded, except for conserved names of families as noted in Art. 14.14.

Latin termination: see **specified Latin termination**.

legitimate name: a validly published name that is in accordance with the Rules (Art. 6.5).

misplaced rank: an out-of-sequence rank-denoting term. The sequence of ranks specified in Art. 4.2 must not be altered (Art. 5.1)

name at new rank: a new name based on a legitimate previously published name of a different rank (see entry in ICN Glossary). The previously published name is the basionym for the name at new rank. Note the restrictions in Art. 41.2 concerning the ranks of the two names. Also see entry for stat. nov. below.

name of a new taxon: a validly published name that is not based on a previously published valid name (ICN Art. 6.9). It is not a new combination, name at new rank or a replacement name.

new combination: a new name for a taxon below the rank of genus based on a legitimate, previously published name, which is its basionym (ICN Art. 6.10).

nom. cons. (= nomen conservandum): a name conserved for use under ICN Art. 14 in order to avoid disadvantageous nomenclatural changes resulting from the strict application of the rules. See entry for **conserved name** in the ICN Glossary.

nomenclature: the biological discipline of establishing, assigning, and governing the application of scientific names to taxonomic groups.

nomenclatural act: an act that results in a validly published name of a new taxon, new combination, name at new rank, replacement name or affects such a name (see ICN Glossary).

nomenclatural novelty: a phrase used in the *Code* to refer to any or all of the following categories: name of a new taxon, new combination, name at new rank, replacement name (Art. 6, Note 4).

nomenclatural type:

a. the specimen or illustration to which the scientific name of a taxon is permanently attached (ICN Art. 7.2).

b. the type of the name of a genus or any subdivision of a genus is the type of the name of a species (Art. 10.1). For purposes of designation or citation of a nomenclatural type, the species name alone suffices; it is considered as the full equivalent of its type.

c. the word element as used in the ICN applies to a specimen, illustration or name (see *element* in the ICN Glossary) that involves the designation or citation of the type of a name of a genus or subdivision of a genus.

principal ranks: the “main” taxonomic categories to which taxa belong: in descending order, these are kingdom; division or phylum; class; order; family; genus; and species. (ICN Art. 3.1).

priority: the use of dates of valid publication or other criteria specified in ICN Art. 11.1-11.10 to help determine the correct name of taxon of family rank or lower with a particular circumscription position and rank. The principle of priority does not apply above the rank of family (Art. 11.10).

rank: a term for any of the named positions in the taxonomic hierarchy (Art. 4.2); named positions include Family, Subfamily, Tribe, Genus, Species. Principal ranks are listed in Art. 3.1; secondary ranks are listed in Art. 4.1; and further ranks are listed in Art. 4.2.

rank sequence: the hierarchical order of rank denoting terms, specified in Art. 4.2.

rank-denoting term: a word used to denote the rank of a taxon (Examples: Family, Tribe, Genus).

rejected name (nom. rej.): a name (nomen rejiciendum) rejected in favour of a name conserved under ICN Art. 14 (see full definition of nomen rejiciendum and definition of rejected name in ICN Glossary); rejected names are ruled not to be used.

replaced synonym: the legitimate or illegitimate previously published name on which a replacement name (nomen novum) is based (Art. 6.11 & ICN Glossary).

replacement name (nomen novum; nom. nov.): a new name published as an explicit substitute for a legitimate or illegitimate previously published name, which is its replaced synonym (Art. 6.11 and ICN Glossary). Note the examples 14-16 after Art. 6.11. A replaced synonym, if legitimate, does not provide the final epithet, name, or stem of the replacement name. Also note Art. 6.12-6.13 for special situations.

scientific name: a validly published name that is applied to a taxonomic group (ICN Preamble 1). Scientific names are treated as Latin regardless of their derivation (ICN Principle V). Requirements for valid publication of a scientific name are specified in ICN Art. 32.1; also see Art. 60.4 & 60.7. The *Code* includes an Index of Scientific Names mentioned in the volume.

secondary rank: any of the subordinate ranks specified in ICN Art. 4.1: examples are **tribe** between family and genus; **section** and **series** between genus and species; and **variety** and **form** below species.

specified Latin termination: the stipulated ending of a suprageneric name for each particular rank. Art. 37.2, footnote, summarizes the stipulated ending used for each rank.

stat. nov. (status novus): a Latin phrase used to indicate a **name at new rank**: e.g. Tribe Pterosiphoniae Maggs & Hommersand, stat. nov. (1993: 367). The use of stat. nov. is not required for valid publication but an indication is recommended (Art. 32, Recommendation 32A).

subdivision of a family: any taxon at a rank between family and genus (ICN Art. 4, Note 2).

suprageneric taxon name: the name of a taxon at any rank above the rank of genus.

taxon (taxa): a taxonomic group at any rank (ICN Art. 1.1).

taxon name: the scientific name of an organism or group of organisms at any rank. Examples: *Alsidium corallinum* C. Agardh; Genus *Alsidium* C. Agardh; Tribe Alsidieae J. Agardh; Subfamily Endosiphoniae De Toni; Family Rhodomelaceae Horaninow.

taxonomic hierarchy: the sequence of taxonomic ranks specified in ICN Art. 4.2. Principal ranks are specified in Art. 3.1; secondary ranks are specified in Art. 4.1. Further ranks may be added to those listed in Art. 4.2 provided no confusion results (Art. 4.3).

taxonomic rank: see entry for **rank** above.

termination: see **specified Latin termination**.

type genus: The genus name from which the name of a suprageneric taxon is formed. Example: *Alsidium* is the genus name from which the tribe name Alsidieae was formed.

type species: the species name chosen or designated as the type of a genus.

unranked name: a taxon name without a known rank.

valid publication: published in accord with the requirements of ICN Art. 29-31 and Art. 38.1.

validly published name: an effectively published name that, in accord with Art. 38.1, also meets the requirements of the relevant provisions of ICN Art. 32-45. Validly published names are termed scientific names (ICN Preamble 1, Principle V).

Tab 2. Chronological list of currently recognized Tribes and author citations of Rhodomelaceae. Names of new taxa validated in the same publication have equal priority when first published.

Tribe **Chondrieae** J. Agardh (1841: 20).
 Tribe **Rhodomelaeae** J. Agardh (1841: 23).
 Tribe **Amansieae** P. Horaninow (1847: 238).
 Tribe **Laurencieae** I. Gifford (1853: 125, as Laurenciaceae).
 Tribe **Alsidieae** J. Agardh (1863: 792).
 Tribe **Pollexfenieae** J. Agardh (1863: 792).
 Tribe **Polysiphoniae** J. Agardh (1863: 794-795).
 Tribe **Polyzonieae** J. Agardh 1892: 136.
 Tribe **Herposiphoniae** Falkenberg in Schmitz & Falkenberg (1897: 457).
 Tribe **Lophothalieae** Falkenberg in Schmitz & Falkenberg (1897: 445).
 Tribe **Pleurostichidieae** Hommersand (1963: 342, footnote).
 Tribe **Rhodolachneae** Womersley in Womersley & Bailey (1970: 331).
 Tribe **Pterosiphoniae** Maggs & Hommersand (1993: 367, stat. nov.)
 Tribe **Sonderelleae** L.E. Phillips (2001: 498).
 Tribe **Neotenophyceae** Kraft & Abbott (2002: 277).
 Tribe **Bostrychieae** Womersley (2003: 361, stat. nov.).
 Tribe **Heterocladieae** Womersley (2003: 282, stat. nov.).
 Tribe **Cladureae** Díaz-Tapia *et* Maggs in Díaz-Tapia & al. (2017: 932).
 Tribe **Dipterosiphoniae** Díaz-Tapia *et* Maggs in Díaz-Tapia & al. (2017: 932).
 Tribe **Ophidocladeae** Díaz-Tapia *et* Maggs in Díaz-Tapia & al. (2017: 933).
 Tribe **Streblocladieae** Díaz-Tapia *et* Maggs in Díaz-Tapia & al. (2017: 933).
 Tribe **Thaumatelleae** Díaz-Tapia *et* Maggs in Díaz-Tapia & al. (2017: 933).

Lophosiphonia – informal group name.

Placophora – informal group name

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Electronic resources

The following online resources have been consulted in conjunction with the research presented in this account. These sites are aids to scientific research and are subject to updating; the accuracy and permanency of information/evidence obtained should be verified prior to use.

AlgaeBase: <https://www.algaebase.org/>

Biodiversity Heritage Library: <https://www.biodiversitylibrary.org/>

Index Herbariorum: <https://sweetgum.nybg.org/science/ih/>

Index Nominum Algarum: <https://ucjeps.berkeley.edu/INA.html>

Index Nominum Genericorum: <https://naturalhistory2.si.edu/botany/ing/>

International Code of Nomenclature for algae, fungi, and plants

Code text: <https://www.iapt-taxon.org/nomen/main.php>

Code Appendices: <https://botany.si.edu/references/codes/props/>

Overview of previous editions of the Code

<https://www.iapt-taxon.org/historic/index.htm>

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