A phylogenetic assessment of *Endocalyx* (Cainiaceae, Xylariales) with *E. grossus* comb. et stat. nov.

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Abstract

The phylogenetic affinities of four representative *Endocalyx* taxa at the species and variety levels are studied based on materials collected on different palm hosts in Japan and the states of Hawaii and Texas, USA. They include specimens and their isolates belonging to *E. cinctus*, *E. indumentum*, *E. melanoxanthus* var. *grossus*, and *E. melanoxanthus* var. *melanoxanthus*. Phylogenetic analyses of nuclear ribosomal DNA sequence data (ITS-LSU nrDNA) confirmed that *Endocalyx* belongs to the order Xylariales (Sordariomycetes) where all species and varieties treated form a strongly supported monophyletic lineage within the family Cainiaceae. They were also phylogenetically well resolved and consistent with their morphological and ecological circumscription. Species status is proposed for *E. melanoxanthus* var. *grossus* under the name *E. grossus* comb. et stat. nov. on the basis of its distinct morphological, molecular, cultural, and ecological characteristics. The putative placement of *Endocalyx* within the family Apiosporaceae (Amphisphaeriales), based on the presence of basauxic conidiophores, is rejected considering that all species treated clustered within the distant Cainiaceae (Xylariales). This characteristic mode of conidiophore elongation is determined to have evolved independently within distantly related ascomycetous lineages. Novel morphological and cultural features of *Endocalyx* taxa based on new isolates are described and commented. The recently described *E. metroxyli* is reduced to a synonym with *E. melanoxanthus*.

Keywords Anamorph (asexual/mitotic morph) · Palm fungi · Taxonomy · Xylariomycetidae

Introduction

The genus *Endocalyx* Berk. & Broome is characterized by sporodochial or synnematous, funnel-shaped, cupulate, cylindrical to pancake-shaped conidiomata arising from an annulus and containing a mass of conidia that is enclosed by yellow or brown sterile peridial hyphae (Petch 1908; Hughes 1953a; Morris 1963; Ellis 1971; Okada and Tubaki 1984; Seifert et al. 2011). Conidiophores are basauxic, hyaline to subhyaline, thread-like and branched, bearing monoblastic or polyblastic, integrated, terminal and intercalary filamentous conidiogenous cells. They produce dry, unicellular, lentil-shaped or elliptical conidia, almost round in one plane but sometimes slightly angular. They range from dark brown, blackish brown to almost black in color, with a smooth or minutely to moderately echinulate surface, rarely with hair-like projections, and often with a hyaline so-called germ slit. Some *Endocalyx* species such as *E. melanoxanthus* (Berk. & Broome) Petch var. *melanoxanthus* and *E. cinctus* Petch are pantropical in distribution and saprobic on dead plant materials. They are usually found colonizing palm tree debris apparently showing a strong specificity for these hosts, whereas others also grow on dead vines, lilies or twigs of woody trees (Hughes 1953a, 1978; Okada and Tubaki 1984).

The type species, *E. thwaitesii* Berk. & Broome (= *E. psilostoma* Berk. & Broome (Berkeley and Broome 1877)), was first described according to Petch (1908) on dead leaves...
of *Oncosperma* sp. (Arecales) from Sri Lanka (formerly Ceylon). Hughes (1953a), however, expressed doubts whether the scanty collection deposited in IMI was a palm, originally referred to as “dead sticks” in the protologue where no generic type was designated. Petch (1908) lectotypified the genus with *E. thwaitesii* and amended the original description based on a duplicate of the original specimen. He also described *E. cinctus* and transferred *Melanconium melanoxanthus* Berk. & Broome to *Endocalyx*, collected as well in Sri Lanka on petioles of another palm tree, *Car yota arenaria* L. (Berkeley and Broome 1875). Subsequently, four more species and a variety of *E. melanoxanthus* have been described: *E. indicus* J.N. Kapoor & Munjal on dead twigs of a woody dicotyledoneous plant in India (Kapoor and Munjal 1966); *E. indumentum* G. Okada & Tubaki and *E. melanoxanthus* var. *grossus* G. Okada & Tubaki on petioles of *Livistona chinensis* var. *boninensis* Becc. and *Trachycarpus fortunei* (Hook.) H.Wendl. (Arecales), respectively, in Japan (Okada and Tubaki 1984); *E. collantensis* J. Men & Mercado on dead branches of *Smilax* sp. (Smilacaceae) in Cuba (Mena and Mercado 1984); *E. amarkantakensis* U.S. Patel, A.K. Pandey & R.C. Rajak on dead twigs of *Shorea robusta* C.F. Gaertn. (Dipterocarpaceae) in India (Patel et al. 2002). Vitoria et al. (2011) accepted these seven species and two varieties although Seifert et al. (2011) recognized only five species and considered *E. collantensis* a synonym of *E. cinctus* [see also Index Fungorum (http://www.indexfungorum.org) and MycoBank (https://www.mycobank.org/)]. In a comprehensive study of the genus based on several Japanese specimens collected on palm trees, Okada and Tubaki (1984) described and isolated in pure culture *E. melanoxanthus* var. *melanoxanthus*, *E. melanoxanthus* var. *grossus*, *E. cinctus* and *E. indumentum*. They also conducted detailed morphological investigations on conidiogenesis and conidiomata of these and a representative collection of *E. thwaitesii* from Ghana (Hughes 1953a) using light and scanning electron microscopies (LM, SEM). These morphological studies on *Endocalyx* species and other conidioma-producing fungi were later expanded to assess the taxonomic implications of conidiomatal anatomy in synnematous hyphomycetes (Okada and Tubaki 1987; Seifert and Okada 1990). Recently, the eighth species, named *E. metroxyli* Konta & K.D. Hyde, was described from a dead petiole of the palm tree *Metroxy lon sangu* Rottb. in Thailand using both morphological and molecular data (Konta et al. 2021).

The phylogenetic position of *Endocalyx* has been the subject of speculation since the introduction of the genus. Berkeley and Broome (1877) first considered it was closely allied to *Alwisia* Berk. & Broome, a genus of myxomycetes (Mycetozoa, Amoebozoa). Later, Petch (1908) rejected this hypothesis and compared *Endocalyx* with *Graphiola phoen iscus* (Moug. ex Fr.) Poit. to conclude that in all essential details they were dissimilar although he did not exclude some reminiscences with other *Graphiola* species. Corte (1963), however, included the genus within the family Graphioliaceae, at that time belonging in the now defunct “Fungi Imperfecti”, and provided a key for the three species known at the time. This genus and particularly *G. phoeni cus* are now well resolved within the Exobasidiales (Ustilaginomycotina, Basidiomycota) based on morphological, ultrastructural, life cycle and molecular data (Begerow et al. 2006). Hyde et al. (1998), on the other hand, suggested that *Endocalyx* as well as other genera may belong to the family Apiosporaceae (Amphisphaeriales) due to the presence of basauxic conidiophores. The criterion for this tentative placement probably followed Hughes (1953b) who included *Arthrinium Kunze, Endocalyx, Dictyoarthrinium S. Hughes, Spegazzinia Sacc., Graphiola and Papularia Fr.* in his section VIII. This group was characterized by basauxic conidiophores that elongate at a basal growing point and arise from a swollen “conidiophore mother-cell”, with the oldest conidia towards the apex and the youngest towards the base of the conidiomata. Minter (1985) reviewed conidial development in *Arthrinium* and morphologically related genera such as *Endocalyx* and *Nigrospora* Zimm. to conclude that they were indeed closely related. He predicted that any teleomorphs found in fungi belonging to the “*Arthrinium* group” will occur in and around the genus *Apiospora* Sacc. Similarly, von Arx (1985) considered that genera with basauxic conidiogenesis and pigmented, often oblate or bilaterally flattened conidia growing mainly on litter of monocotyledons such as grasses and palms, represented a phylogenetic entity. Kendrick and Murase (1994), on the other hand, assembled informal groups of anamorphs with shared features. They speculated whether the relatively rare basauxic development in conjunction with other unusual features such as thick, darkly pigmented septa of the conidiogenous axis arising from a phialide-like mother cell and conidia with germ slits represented a monophyletic group. Nevertheless, they considered that their putative groupings may ultimately have to be confirmed or rejected by molecular data. The hypothetical placement of *Endocalyx* in Apiosporaceae and its close relationship with *Arthrinium* has been widely accepted (Taylor and Hyde 2003; Senanayake et al. 2015; Wijayawardene et al. 2017, 2018, 2021; Hyde et al. 2020). However, Konta et al. (2021) recently reassigned *Endocalyx* to the family Cainiaceae (Xylariales) employing molecular data for the first time. Their study was based on a limited taxon sampling including only two sequences of *E. cinctus* available in GenBank (http://www.ncbi.nlm.nih.gov/genbank/) and those of a novel species named *E. metroxyli* described from Thailand.

During recent surveys of saprobi c microfungi carried out by one of the authors (G.D.) in subtropical Texas, USA, specimens of *E. melanoxanthus* var. *melanoxanthus* were collected on palm tree debris and isolated in pure culture. In
order to confirm the phylogenetic placement and taxonomic status of *Endocalyx* on the basis of a more extensive taxon sampling, DNA sequence data was generated from these and the morphologically and culturally well-characterized voucher specimens and strains described by Okada and Tubaki (1984) in their seminal paper about the genus. Further unpublished specimens and cultures obtained by another author (G.O.), mainly in Japan (Sato et al. 1991), were also included for a more comprehensive assessment. Results are presented here and a new combination at the species level is introduced based on morphological and molecular evidence.

**Materials and methods**

**Morphological and cultural studies of specimens and isolates**

Two fresh specimens of *E. melanoxanthus var. melanoxanthus* were collected on dead inflorescences of the palm tree *Sabal minor* (Jacq.) Pers. (Arecales), the dwarf palmetto, during fieldwork carried out by G.D. in southeastern Texas in 2020. Conidiomata were recognized in the field using a hand lens and pieces of substrate showing colonies were brought to the lab for processing. They were briefly washed off under tap water and incubated in a moist chamber at room temperature (23–25 °C) for three weeks followed by periodical examinations under the stereoscope to observe the development of conidiomata and to take images. Single conidium isolations from conidiomata were made following Choi et al. (1999). Germinated conidia were transferred aseptically to 2% Malt Extract Agar with 0.01% chloramphenicol (MEA: Hardy Diagnostics, Santa Maria, California, USA) and incubated at 25 °C. Colony features were recorded after two weeks under similar conditions. Fungal structures were mounted in lacto-cotton blue for examination under an Olympus BX45 microscope (Olympus, Tokyo, Japan). Minimum, maximum, 5th and 95th percentile values were calculated based on 50 measurements of each structure at 1000× magnification and outliers are given in parenthesis. Images of conidiomata in Japanese specimens or isolates, a Z16 APO macroscope (Leica Microsystems, Wetzlar, Germany) with installed CombineZP software was used. An ORTHOPLAN microscope with a phase contrast device (Leitz, Wetzlar, Germany) and a BIOPHOT microscope with a differential interference contrast device (Nikon, Tokyo, Japan) was mainly used for isolating and culturing these strains. To attempt sporulation, some Japanese isolates were incubated on autoclaved wet petioles of suitable palm hosts placed on thick water agar plates in an unsealed glass Petri dish (or similar with high sides) at room temperature under prolonged incubation for several months or over a year. To obtain focus stacking composite images of conidiomata in Japanese specimens or isolates, a Z16 APO macroscope (Leica Microsystems, Wetzlar, Germany) with installed CombineZP software was used. An ORTHOPLAN microscope with a phase contrast device (Leitz, Wetzlar, Germany) and a BIOPHOT microscope with a differential interference contrast device (Nikon, Tokyo, Japan) were also employed (PC & DIC; abbr. used in figure legends). Photos were recorded using Leica MC190 HD and Nikon DS-5 M/DS-Fi1 digital cameras, and some photos were prepared as composite images (CI; abbr. used in figure legends). Voucher specimens collected by G.O. are deposited mainly in TNS and partly in ILLS. Strains are available for search at the JCM On-Line Catalogue of Strains (https://jcm.brc.riken.jp/en/catalogue_e). A total of twenty-six *Endocalyx* strains were included in this study (Table 1). Fungal names follow MycoBank and host plant names follow the International Plant Names Index (https://www.ipni.org).

**DNA extraction, PCR amplification, and sequencing**

Genomic DNA was extracted from fungal mycelia grown on MEA using a modified NaOH extraction method
Table 1 *Endocalyx* species, strains, and specimens used in this study including palm host, country and sequence information whenever relevant. GenBank accession numbers in bold correspond to sequences generated during this study.

| Species | Host/Country       | Strain and status (including original TKBC no.) | Voucher specimen no. and status | GenBank accession no. |
|---------|--------------------|-------------------------------------------------|---------------------------------|-----------------------|
|         |                    |                                                 |                                 | ITS       | LSU      |
| *Endocalyx cinctus* | Phoenix canariensis / Japan | NBRC/IFO 31306 (TKBC 1290) | TNS-F-18242, TNS-F-18265, IMI 287889 | MZ313191 | MZ313152 |
| E. cinctus | Livistona chinensis var. boninensis / Japan | JCM 7946<sup>c</sup> | TNS-F-91424 (G. Okada Ogasawara-191), TNS-F-91425 (ex-JCM 7946) | LC228648 | LC228704 |
| E. cinctus | Livistona chinensis var. boninensis / Japan | – | ILLS00121502 (G. Okada Ogasawara-192) | – | – |
| E. grossus | Trachycarpus fortunei / Japan | JCM 5164 = NBRC/IFO 31308 (ex-holotype) = CBS 105.86 (= TKBC 1286) | TNS-F-18281 (holotype), CBS H-12419 (isotype), IMI 287881 (isotype) | MZ313160 | MZ313138 |
| E. grossus | T. fortunei / Japan | JCM 5165 = NBRC/IFO 31309 (= TKBC 1287) | TNS-F-18252, CBS H-3951 | MZ313159 | MZ313158 |
| E. grossus | T. fortunei / Japan | JCM 5166 = NBRC/IFO 31310 (= TKBC 1292) | TNS-F-18248, CBS H-3952, IMI 287883 | MZ313179 | MZ313171 |
| E. grossus | T. fortunei / Japan | JCM 5167 = NBRC/IFO 31311 (= TKBC 1293) | TNS-F-18246, CBS H-3953 | MZ313169 | MZ313174 |
| E. grossus | T. fortunei / Japan | JCM 5168 = NBRC/IFO 31312 (= TKBC 1294) | TNS-F-18237 | MZ313165 | MZ313164 |
| E. grossus | T. fortunei / Japan | JCM 5169 = NBRC/IFO 31313 (= TKBC 1296) | TNS-F-18245, CBS H-3954 | MZ313172 | MZ313178 |
| E. grossus | T. fortunei / Japan | JCM 5170 = NBRC/IFO 31314 (= TKBC 1297) | TNS-F-18244, CBS H-3955 | MZ313166 | MZ313170 |
| E. grossus | T. fortunei / Japan | JCM 32411<sup>c</sup> | TNS-F-91426 (G. Okada 1763) | MZ313163 | MZ313168 |
| E. grossus | T. fortunei / Japan | – | ILLS00121505 (G. Okada 1764) | – | – |
| E. grossus | T. fortunei / Japan | JCM 32997<sup>c</sup> | TNS-F-91427 (G. Okada 1766), TNS-F-91428 (ex-JCM 32997) | MZ313136 | MZ313167 |
| E. grossus | T. fortunei / Japan | – | ILLS00121504 (G. Okada 1767) | – | – |
| E. grossus | T. fortunei / Japan | JCM 32998<sup>c</sup> | TNS-F-91429 (G. Okada 1769), TNS-F-91430 (ex-JCM 32998) | MZ313176 | MZ313177 |
| E. grossus | T. fortunei / Japan | – | ILLS00121506 (G. Okada 1770) | – | – |
| E. grossus | T. fortunei / Japan | JCM 33339<sup>c</sup> | TNS-F-91431 (G. Okada 1772) | MZ313175 | MZ313173 |
| E. indumentum | Phoenix canariensis / Japan | – | ILLS00121501 = G. Okada Ogasawara-80 | – | – |
| E. indumentum | L. chinensis var. boninensis / Japan | JCM 5171 = NBRC/IFO 31307 (ex-holotype), CBS 104.86 (= TKBC 1285) | TNS-F-18280 (holotype), IMI 287888 (isotype) | MZ313153 | MZ313161 |
| E. indumentum | L. chinensis var. boninensis / Japan | – | ILLS00121503 = G. Okada Ogasawara-194 | – | – |
| E. indumentum | L. chinensis var. boninensis / Japan | JCM 8042<sup>c</sup> | TNS-F-91432 (G. Okada Ogasawara-200), TNS-F-91433 (ex-JCM 8042) | MZ313162 | MZ313157 |
| E. melanoxanthus | Sabal minor / Texas, USA | CBS 147393 = JCM 39196 | ILLS00121433 | MW718201 | MW718204 |
| E. melanoxanthus | S. minor / Texas, USA | CBS 147394 | ILLS00121434 | MW718203 | MW718203 |
| E. melanoxanthus | L. chinensis var. subglobosa / Japan | JCM 5156 = NBRC/IFO 31298 (= TKBC 1281) | TNS-F-18239, CBS H-3945, IMI 287873 | MZ313137 | MZ313135 |
Table 1 (continued)

| Species* | Host/Country | Strain and status b (including original TKBC no.) | Voucher specimen no. and status | GenBank accession no |
|----------|--------------|--------------------------------------------------|--------------------------------|---------------------|
| *E. melanoxanthus* | L. chinensis var. subglobosa / Japan | NBRC/IFO 31299 = CBS 107.86 (= TKBC 1282) | TNS-F-18253 | MZ313147 MZ313148 |
| *E. melanoxanthus* | Washingtonia robusta / Japan | JCM 5158 = NBRC/IFO 31300 (= TKBC 1283) | TNS-F-18262, CBS H-3946, IMI 287875 | MZ313139 MZ313143 |
| *E. melanoxanthus* | L. chinensis var. boninensis / Japan | JCM 5159 = NBRC/IFO 31301 (= TKBC 1284) | TNS-F-18240, CBS H-3947 | MZ313146 MZ313145 |
| *E. melanoxanthus* | L. chinensis var. subglobosa / Japan | JCM 5160 = NBRC/IFO 31302 (= TKBC 1288) | TNS-F-18268, CBS H-3948, IMI 287877 | MZ313144 MZ313142 |
| *E. melanoxanthus* | P. roebelenii / Japan | JCM 5161 = NBRC/IFO 31303 (= TKBC 1289) | TNS-F-18247, CBS H-3949, IMI 287878 | MZ313150 MZ313151 |
| *E. melanoxanthus* | L. chinensis var. subglobosa / Japan | JCM 5163 = NBRC/IFO 31305 (= TKBC 1295) | TNS-F-18251, CBS H-3950 | MZ313155 MZ313141 |
| *E. melanoxanthus* | L. chinensis var. boninensis / Japan | JCM 7948 c | TNS-F-91434 (G. Okada Ogasawara-61) | MZ313140 MZ313149 |
| *E. melanoxanthus* | Cocos nucifera / Hawaii, USA | JCM 13432 c | ILLS00121495 | MZ313156 MZ313154 |
| *E. melanoxanthus* | Metroxylon sagu / Thailand | MFLUCC 15-0723A | MFLU 15-1454 | MT929162 MT929313 |
| *E. melanoxanthus* | Metroxylon sagu / Thailand | MFLUCC 15-0723B | MFLU 15-1454 | MT929163 MT929314 |
| *E. melanoxanthus* | Metroxylon sagu / Thailand | MFLUCC 15-0723C | MFLU 15-1454 | MT929164 MT929315 |
| *Endocalyx* sp. | L. chinensis var. boninensis / Japan | MAFF 244025 | HHUF 30261 | –

*Species names of *Endocalyx* including *E. grossus* and *E. melanoxanthus* (=*E. metroxyli*) proposed in this paper

bCBS, CBS-KNAW Culture Collection, Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands. *IFO*, Institute for Fermentation, Osaka, Japan (collection transferred to NBRC). *HHUF*, Herbarium of Plant Pathology Laboratory, Faculty of Agriculture and Life Science, Hirosaki University, Hirosaki, Japan. *ILLS*, Illinois Natural History Survey Fungarium, Champaign, USA. *IMI*, Herbarium of CABI Bioscience UK Centre, Surrey, UK. *JCM*, Japan Collection of Microorganisms, RIKEN BioResource Research Center, Tsukuba, Japan. *MAFF*, NARO Genebank, Microorganism Section, Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Japan. *MFLU/MFLUCC*, Herbarium/Culture Collection, Mae Fah Luang University, Chiang Rai, Thailand. *NBRC*, NITE Biological Resource Center, Kisasazu, Japan. *TKBC*, Culture Collection of Mycology Laboratory, Institute of Biological Sciences, University of Tsukuba, Tsukuba, Japan (collection closed). *TNS*, National Museum of Nature and Science, Tsukuba, Japan

cFor further strain details, see the JCM on-line catalogue of strains (https://jcm.brc.riken.jp/en/catalogue_e)

dAvailable from NARO Genebank database (https://www.gene.affrc.go.jp/databases_en.php)

(Osmundson et al. 2013), which consisted of adding 200 μL 0.5 M NaOH to ~75 mg of tissue, grinding with a micropette, centrifugation at 14,000 RPM for 2 min, and adding 5 μL of the resulting supernatant to 495 μL 100 mM Tris-HCl buffered with NaOH to pH 8.5–8.9 (Tris–HCl–DNA extraction solution). The complete nrDNA internal transcribed spacer (ITS) region and the first 1,100 bp of the 5′ end of large subunit nrDNA (LSU nrDNA) were amplified as two overlapping regions. PCR amplification using a GoTaq® Green Master mix (Promega, Madison, Wisconsin, USA) consisted of the following: 12.5 μL GoTaq® Green Master mix, 2.5 μL BSA, 2.5 μL 50% DMSO, 2 μL of each 10 μM primer ITS1F/LR3 or LR0R/LR6, and 3 μL DNA. PCR amplification was completed on a Bio-Rad PTC 200 thermal cycler under the following parameters: initial denaturation at 94 °C for 2 min, followed by 40 cycles of 94 °C for 30 s, 47 °C for 30 s, 72 °C for 1 min with a final extension step of 72 °C for 10 min. Gel electrophoresis (1% TBE agarose gel stained with ethidium bromide) was used to verify the presence of a PCR product. PCR products were purified using a Wizard® SV Gel and PCR Clean-Up System (Promega), and template DNA was used in 10 μL sequencing reactions with BigDye® Terminator v3.1 (Applied Biosystems, Foster City, California, USA) using a combination of the following primers: ITS1F, ITS4, LR0R, LR3, LR3R and LR6 (Vilgalys and Hester 1990; White et al. 1990; Gardes and Bruns 1993). Sequences were generated on an Applied Biosystems 3730XL high-throughput capillary sequencer at the W.M. Keck Center at the University of Illinois Urbana-Champaign. In the case of the JCM strains, they were first grown on PDA, and genomic DNA extraction, PCR amplification and sequencing were performed following the previously reported method (Hashimoto et al. 2021). Consensus ITS–LSU sequences were assembled with Sequencher 5.4 (Gene Codes Corp., Ann Arbor, Michigan, USA) and deposited in GenBank.
| Taxon                                      | Strain           | GenBank accession no |
|--------------------------------------------|------------------|----------------------|
| Achaetomium macrosporum                    | CBS 532.94       | KX976574             |
| Acrocordiella occulta                      | CBS 140500       | KT949893             |
| Acrocordiella occulta                      | CBS 140501       | KT949894             |
| Alishanica miscanthi                        | FU 31025         | MK503821             |
| Amphibambusa bambusicola                   | MFLUCC 11-0617   | KP744433             |
| Amphiphaeria sorbi                         | MFLUCC 13-0721   | KP744475             |
| Amphiphaeria thailandica                   | MFLU 18-0794     | MH971225             |
| Amphiphaeria umbrina                        | CBS 172.96       | FJ176863             |
| Anthostomelloides brabeji                  | CBS 110128       | EU552098             |
| Arecophila bambusae                         | HKUCC 4794       | AF452038             |
| Arecophila muroiana                        | GZUCC 0122       | MT742127             |
| Arthrinium arundinis                        | CBS 450.92       | AB220259             |
| Arthrinium arundinis                        | CBS 145128       | MK014868             |
| Arthrinium hysterinum                       | CBS 145135       | MK014877             |
| Arthrinium hysterinum                       | ICMP 6889        | MK014874             |
| Arthrinium marii                            | CBS 497.90       | AB220252             |
| Arthrinium phaeospermum                     | CBS 114318       | KF144907             |
| Arthrinium sacchari                         | CBS 301.49       | KF144917             |
| Atrotorquata lineata                        | HKUCC 3263       | AF009807             |
| Barrmaelia macrospora                       | BM               | KC774566             |
| Barrmaelia moravica                         | Cr1              | MF488987             |
| Barrmaelia oxyacanthae                      | CBS 142769       | MF488988             |
| Barrmaelia riciputz                        | CBS 142770       | MF488989             |
| Barrmaelia rhamnica                         | CBS 142771       | MF488990             |
| Cainia anthoxanthi                          | MFLUCC 15-0539   | KR092787             |
| Cainia desmazieri                           | WU 33597         | KT949896             |
| Cainia globosa                              | MFLUCC 13-0663   | KX822127             |
| Cainia graminis                             | CBS 136.62       | MH858123             |
| Cainia graminis                             | MFLUCC 15-0540   | KR092793             |
| Chaetomium elatum                           | CBS 374.66       | KC109758             |
| Collydiscola japonica                       | CBS 124266       | JF440974             |
| Daldinia palmensis                          | CBS 113039       | MH862912             |
| Daldinia placentiformis                     | MUCL 47603       | AM749921             |
| Daldinia pyrenica                           | MUCL 53969       | KY610413             |
| Daldinia rainundi                           | CBS 113038       | JX658517             |
| Daldinia theissenii                         | CBS 113044       | KY610388             |
| Entonaema liquescens                        | ATCC 46302       | KY610389             |
| Entosordaria perfudiosa                     | BW3              | MF488992             |
| Entosordaria perfudiosa                     | CBS 142773       | MF488993             |
| Hypocorea rostrata                          | NRRL 66178       | KM067909             |
| Hypoxylon fragiforme                        | DMS 9335105      | MT644893             |
| Hypoxylon haematostroma                     | MUCL 47600       | AM749924             |
| Hypoxylon investiens                        | CBS 118183       | KC968925             |
| Hypomontagnella monticulosa                 | MUCL 54604       | KY610404             |
| Hypoxylon perforatum                        | CBS 115281       | KY610391             |
| Hypoxylon pulicidum                         | CBS 122622       | JX183076             |
| Lepteutypa sambuci                          | CBS 131707       | KT949904             |
| Lepteutypa uniseptata                       | CBS 114967       | MH553979             |
Taxon sampling and datasets

The novel *Endocalyx* sequences obtained from the Japanese, Hawaiian and Texan strains were subjected to megablast searches in GenBank database to first explore their identity and phylogenetic position. The closest hits from blast searches were representatives of Xylariales, particularly members of the families Cainiaceae and Xylariaceae, which were selected and downloaded to assemble individual datasets. One exception was the only available LSU sequence of *Seynesia erumpens* (Berk. & M.A. Curtis) Petr. (AF279410), which produced incongruent results during subsequent analyses and was removed from the final dataset. One ITS and one LSU sequence of *E. cinctus* JCM 7946 available in GenBank and those belonging to the recently described *E. metroxyli* (Konta et al. 2021) were also added to the datasets. An additional ITS sequence from a specimen identified as *Endocalyx* sp., collected in the Ogasawara (Bonin) Islands (Tanaka et al. 2017) and currently deposited in MAFF, was retrieved from NARO Genebank database (https://www.gene.affrc.go.jp/databases_en.php) and added to the ITS
Phylogenetic analyses

Sequences were aligned with MAFFT v.7.475 (Katoh and Standley 2013) on the online server which automatically selected the FFT-NS-i iterative refinement strategy (Katoh et al. 2002) for both the ITS and LSU datasets. Maximum Likelihood (ML) and Bayesian inference (BI) approaches were first conducted for each individual dataset using RAxML v.8.2.12 (Stamatakis 2014) and MrBayes v.3.2.7a (Ronquist and Huelsenbeck 2003; Ronquist et al. 2012), respectively, on the CIPRES Science Gateway server (Miller et al. 2010). ML analyses were run under the GTR + CAT model using the rapid bootstrapping algorithm and 1,000 bootstrap iterations to estimate branch support with bootstrap support (BS) values ≥ 70% considered significant (Hillis and Bull 1993). BI analyses consisted of two independent runs of 10 million generations with four (one cold and three heated) Markov Chain Monte Carlo chains each starting from different random trees with default prior values and trees sampled every 100th generation. The first 25% of trees were discarded as burn-in prior to convergence and the remaining trees were used to compute a 50% majority rule consensus tree and estimate posterior probabilities (BPP) for each node. Analyses were set to stop when the standard deviation of split frequencies decreased below 0.01 and convergence of runs was further confirmed in Tracer v.1.6.0 (Rambaut et al. 2014). Clades were considered statistically significant when BPP ≥ 0.95 (Alfaro et al. 2003). No significant topological differences were observed between individual ITS and LSU trees (see Results). Therefore, datasets were concatenated in MEGA v.6.06 (Tamura et al. 2013) for further ML and BI analyses using the above settings. The best-fit substitution model for individual and concatenated datasets, as determined in MEGA using the corrected Akaike Information Criterion, was the GTR + G + I. Trees were edited in MEGA and further refined using Inkscape (https://inkscape.org). All alignments and resulting trees are deposited in TreeBASE (https://treebase.org/, study number S19717).

Results

Morphology on the hosts and in culture

On the hosts and in culture, the morphology of conidiomata and conidia of the Endocalyx species newly collected in Japan and USA agreed well with those in previous descriptions (Petch 1908; Hughes 1953a; Okada and Tubaki 1984). A synopsis of key diagnostic features is provided in Table 3. In addition to a new taxonomy for E. melanoxanthus var. grossus (proposed below as “E. grossus”) and the description of E. melanoxanthus var. melanoxanthus (reported below as E. melanoxanthus) based on the Texas specimens, novel observations and comments on other Endocalyx species are also included below. As a general remark, all species treated produced subspherical pycnidial conidiomata on autoclaved palm/wooden chips and agar media such as PDA and others (Okada and Tubaki 1984; this paper; Figs. 3C, D, G, 4). These conidiomata lacked ostioles on growth media (Table 3), and conidia were released by random cracking of the conidiomatal outer walls (Fig. 4C, F).

Molecular analyses

Intraspecific pairwise comparisons of the ITS and LSU sequences belonging to the Japanese, Hawaiian and Texan specimens of E. melanoxanthus var. melanoxanthus showed they are nearly identical except for one C-T transition at position 421 of the ITS alignment in strains JCM 5156, JCM 5159, JCM 5161, JCM 7948 and NBRC 31299, and one G-A transition at position 396 of the LSU alignment in strain JCM 5159. Similarly, strains MFLUCC 15-0723A, B and C belonging to E. metroxyli collected in Thailand differed only by one T-C transition at position 49 of the ITS alignment, whereas their LSU sequences were identical to those of the studied E. melanoxanthus var. melanoxanthus strains. In contrast, the strain Endocalyx sp. MAFF 244025 showed a total of 15 bp and one gap differences compared with the remaining ITS sequences. In the case of E. melanoxanthus var. grossus, all sequences were identical except for the LSU of JCM 5167 which contained a C-T transition at position 430 of the alignment. The ITS and LSU sequences of E. cinctus strains each showed three nucleotide differences between them, whereas they were identical between E. indumentum strains.

The combined ITS-LSU alignment consisted of 102 sequences and 1,683 positions including the outgroups, 897 from the ITS alignment and 786 from the LSU. The single best RAxML tree (ln = −17725.715920) generated
| Species          | Conidiomata                                      | Conidia/chlamydospores                                      | Host                  | References                  |
|------------------|-------------------------------------------------|-------------------------------------------------------------|-----------------------|-----------------------------|
| **E. cinctus**   | Consisting of two parts: (1) a basal hyphal cylinder covering a central column, black, rough-walled, carbonaceous; (2) a central column, synnematous, expanding radially and apically, funnel-shaped, holding the black conidial mass at the capitulum, enclosed by the yellowish peridial hyphae. With a bilayered cortex.³ | Conidia one-celled, flattened, 10–13(–17)×6–12 µm in face view, 7–8 µm thick, dark brown to fuscous black, guttulate, verrucose (LM), sparsely covered with evenly distributed coarse-relief islets (SEM)² | Conidia on growth media: Produced very rarely, almost identical to the natural ones | Some variety of palms including *Trachycarpus fortunei* | Petch (1908); Okada and Tubaki (1984); this study |
| **E. grossus**   | Cupulate or rarely cylindrical; peridial hyphae enclosing the inner conidial mass, mostly brown. With a monolayered cortex.² | Conidia one-celled, flattened, 9–16×9–15 µm in face view, 6–9 µm thick, brown to dark brown, guttulate, almost smooth to tuberculate (LM), with a thin surface layer that cracks in evenly distributed coarse-relief islets (SEM) | Conidia on growth media and sterilized palm chips: Almost identical to the natural ones | T. fortunei | Okada and Tubaki (1984); this study |
| **E. indumentum** | Cupulate to cylindrical, larger than those of *E. melanoxanthus* and *E. grossus*; peridial hyphae coarsely interwoven, dark brown. With a monolayered cortex | Conidia one-celled, at first flattened, later almost spherical, 8–12 µm in diam., dark brown, with a thick layer of densely packed, curved or straight, hair-like (LM), filamentous, somewhat flexuous and irregularly adherent (SEM) projections (up to 2.5 µm long) | Conidia on growth media: Produced very rarely, immature and without ornamentations | Some variety of palms³ | Okada and Tubaki (1984); this study |

² On growth media: Immersed or superficial, pycnidioíd, spherical at first, cupulate once bursting, dark brown to black

³ On sterilized palm chips: Somewhat similar to the natural, cylindrical ones, but produced very rarely under prolonged incubation

⁴ On growth media: Usually not produced

⁵ On sterilized palm chips: Immersed or superficial, pycnidioíd, spherical at first, closed, bursting for conidium dispersal under prolonged incubation, dark brown to black

⁶ Chlamydospores on growth media: Absent

⁷ Chlamydospores on sterilized palm chips: Produced quite often, almost identical to the natural ones

⁸ Chlamydospore-like conidia present
| Species       | Conidiomata                                                                 | Conidia/chlamydospores                                                                 | Host                  | References                      |
|--------------|-----------------------------------------------------------------------------|---------------------------------------------------------------------------------------|----------------------|---------------------------------|
| *E. melanoxanthus* | Cupulate to long cylindrical; peridial hyphae mostly vivid yellow. With a monolayered cortex | On growth media: Usually not produced. Immersed or superficial, sclerotium-like, pycnidial, spherical, closed, black | Conidia one-celled, flattened, 12–17×10–14 µm in face view, 7–9(−10) µm thick, dark brown to fuscous black, guttulate, almost smooth (LM), with a thin surface layer that cracks in evenly distributed islets (SEM) | Conidia on growth media: Usually not produced, somewhat irregular in shape | Conidia on sterilized palm chips: Produced very rarely, somewhat similar to the natural ones | Chlamydospores on growth media: Terminal or intercalary, solitary or catenate, non-deciduous, 1-celled, globose to cylindrical, dark brown, rarely with a longitudinal hyaline slit, smooth (LM) | Wide variety of palms including *T. fortunei* | Petch (1908); Okada and Tubaki (1984); this study |

*a* cf. Seifert and Okada (1990)  
*b* Growth media used: Czapek-Dox agar, malt extract agar, potato dextrose agar, cornmeal agar, and sterilized wooden chips. Details mentioned in Okada and Tubaki (1984) and this study  
*c* *LM*, light microscope. *SEM*, scanning electron microscope  
*d* Found very rarely on bamboos in Brazil (Okada, unpublished)
Fig. 1 Maximum-likelihood (ML) phylogenetic tree inferred from concatenated ITS-LSU nrDNA sequences belonging to the orders Xylariales and Amphisphaeriales showing the placement of treated Endocalyx species within Cainiaceae. The Endocalyx clade is highlighted in a yellow color box and the family Apiosporaceae in a blue color box. Bootstrap support values ≥ 70% are shown at the nodes and Bayesian posterior probabilities ≥ 0.95 are indicated by thickened branches from the ML analysis is shown in Fig. 1. The ML tree topology was similar in topology to the 50% majority rule consensus tree of the 6,688 sampled trees from the Bayesian analysis. Effective sample size values of all relevant parameters were > 200 as verified in Tracer, indicating adequate sampling of the posterior distribution (Drummond et al. 2006; Drummond and Rambaut 2009). The twenty-six Endocalyx strains formed a strongly supported monophyletic group (97% BS, 1.0 BPP) within the family Cainiaceae. Each species and variety were well resolved, and they split in two subclades: one including E. melanoxanthus var. melanoxanthus, E. indumentum
and *E. cinctus* and the other containing only *E. melanoxanthus* var. *grossus*. The Japanese, Hawaiian and Texan strains of *E. melanoxanthus* var. *melanoxanthus* formed a strongly supported monophyletic group (100% BS, 1.0 BPP). The three strains belonging to *E. metroxyli* from Thailand (MFLUCC 15-0723A, B and C, obtained from the same single specimen) and the strain *Endocalyx* sp. MAFF 244025 from Japan also clustered within this clade indicating they are conspecific with *E. melanoxanthus* var. *melanoxanthus*. They grouped sister to the two available strains of *E. indumentum* including the ex-type strain (JCM 5171) without significant BS support but showing significant BPP = 0.98. Strains of *E. indumentum*, *E. cinctus* and *E. melanoxanthus* var. *grossus* including the ex-type strain (JCM 5164) each formed highly supported clades (99% or 100% BS, 1.0 BPP). The four taxa of *E. melanoxanthus* var. *melanoxanthus* and *E. melanoxanthus* var. *grossus* should be treated as *E. melanoxanthus* and “E. grossus” and a new taxonomic treatment is proposed below for the latter. *Endocalyx metroxyli* is synonymized under *E. melanoxanthus*. The *Endocalyx* lineage was sister to a moderately supported monophyletic group including *Cainia graminis* (Niessl) Arx & E. Müll., the type species of *Cainia* Arx & E. Müll., and other members of Cainiaceae (Xylariales) belonging to three different genera. The family was recovered as a highly supported monophyletic clade (99% BS, 1.0 BPP). *Arthrinium* and *Nigrospora* species grouped together in a highly supported clade (98% BS, 1.0 BPP) representing the family Apiosporaceae in the distant order Amphipholiales sensu Wijayawarde et al. (2018). In general, phylogenetic reconstructions between individual loci (ITS/LSU) recovered similar topologies despite some minor differences in position for families in Xylariales such as Lopadostomataceae and Xylariaceae. Nevertheless, the *Endocalyx* clade and the family Cainiaceae grouped with strong support and identical consistency in all analyses (Figs. S1, S2).

**Taxonomy**

*Endocalyx cinctus* Petch, Ann. Bot. (London) 22: 394 (1908). (Figs. 2F, G, 3A).

For a detailed description on natural substrates and in culture together with key diagnostic features see Okada and Tubaki (1984) and Table 3.

**Materials examined:** Japan, Tokyo, Ogasawara Islands, Anijima Island, on peduncle of dead inflorescence of *Livistona chinensis* var. *boninensis*, 18 Mar. 1990, leg. & det. G. Okada [TNS-F-91424 = G. Okada Ogasawara-191; strain JCM 7946; TNS-F-91425 (dried culture of JCM 7946 incubated on autoclaved petiole of *L. chinensis* var. *subglobosa* (Hassk.) Becc.); idem [ILLS00121502 = G. Okada Ogasawara-192 (together with *E. melanoxanthus*)].

**Notes:** Morphologically, the specimen studied (TNS-F-91424) agrees well with the description provided by Okada and Tubaki (1984). In culture, strain JCM 7946 produced conidiomata and conidia (Figs. 2G, 3A) on autoclaved petioles of *L. chinensis* var. *subglobosa* after a 3-month incubation period that were almost the same as those on palm hosts (Fig. 2F). The conidial surface was slightly rough especially in young conidia (Fig. 3A). Conidiomata of *E. cinctus* are unique in morphology among *Endocalyx* species and consist of synnemata with a bilayered cortex on natural substrate (Fig. 2F) or with a spherically swollen carbonaceous base in culture (Okada and Tubaki 1984, 1987; Seifert and Okada 1990). *Endocalyx cinctus* is also the best species for inducing conidiomata and conidia on autoclaved petioles of palms (Okada and Tubaki 1984; this paper). After further prolonged incubation on an autoclaved petiole of *L. chinensis* var. *subglobosa*, irregularly shaped conidiomata including subspherical ones were produced (TNS-F-91425). These morphologically unique features of *E. cinctus* might become the subject of a future research project analyzing its whole genome available in GenBank (BCKC00000000).

*Endocalyx grossus* (G. Okada & Tubaki) G. Delgado & G. Okada, *comb. et stat. nov.* (Figs. 2B–D, 3G–I, 4A–E). MycoBank MB817907.

**Basionym:** *Endocalyx melanoxanthus* var. *grossus* G. Okada & Tubaki, Mycologia 76: 303 (1984).

For a detailed description on natural substrate and in culture together with key diagnostic features see Okada and Tubaki (1984) and Table 3.

**Typification:** Japan, Ibaraki, Tsukuba, Higashioka, 36°05′ N, 139°07′ E, on dead petiole of *Trachycarpus fortunei*, 6 Aug. 1982, leg. G. Okada, TNS-F-18281 = JCM 5164 = CBS 105.86 = G. Okada OFC 1116.

**Materials examined:** Japan, Saitama, Ogawa-machi, Otsuka, 36°03′28.4″ N, 139°15′03.3″ E, on dead petiole of *T. fortunei*, 2 Sep. 2017, leg. & det. G. Okada [TNS-F-91426 = G. Okada 1763; strain JCM 32411]; idem (ILLS00121505 = G. Okada 1764); idem, Koshigoe, near Tatekawa Dam, 36°01′13.8″ N, 139°12′40.0″ E, on dead petiole of *T. fortunei*, 23 Aug. 2018, leg. & det. G. Okada [TNS-F-91427 = G. Okada 1766; strain JCM 32997; TNS-F-91428 (dried culture of JCM 32997 incubated on autoclaved petiole of *T. fortunei*); idem (ILLS00121504 = G. Okada 1767); Ibaraki, Bando, Oguchi, 36°02′26.5″ N, 139°56′09.6″ E, on dead petiole of *T. fortunei*, 23 Jul. 2018, leg. & det. G. Okada [TNS-F-91429 = G. Okada 1769; strain JCM 32998; TNS-F-91430 (dried culture of JCM 32998 incubated on autoclaved petiole of *T. fortunei*); idem (ILLS00121506 = G. Okada
1770); Saitama, Chichibu, Hinoda-machi, Business office of the University of Tokyo Chichibu Forest, 35°59′19.1″ N, 139°04′48.3″ E, on dead petiole of *T. fortunei*, 13 Sep. 2018, leg. & det. G. Okada (TNS-F-91431 = G. Okada 1772; strain JCM 33339).

Notes: Okada and Tubaki (1984) morphologically distinguished *E. melanoxanthus* var. *grossus* from *E. melanoxanthus* var. *melanoxanthus* based on the brown to yellowish brown color of the peridial hyphae enclosing the conidial mass, which is vivid yellow to greenish yellow in the latter, and the verrucose conidial wall ornamentation. This is relatively smooth to tuberculate under LM, but SEM clearly revealed a thin outer layer that cracks and forms coarse-relief islets evenly distributed over the conidial surface. Moreover, the color of the conidial mass in *E. melanoxanthus* var. *melanoxanthus* is somewhat more glistening blackish than in the variety *grossus*. Differences in conidiomata were less evident, except the color of the peridial hyphae, but the variety *grossus* forms mostly cupulate, rarely cylindrical and usually smaller conidiomata, 0.2–0.3 mm and up to 3 mm high, whereas those of the variety *melanoxanthus* are 0.5–1 mm and can reach up to 7 mm high. Ecologically, this taxon is apparently restricted and known so far only from *T. fortunei*, the windmill palm, one of the best-known, cold-hardiest species of Arecaceae. Conidia of the variety *grossus* developed readily in culture compared to the variety *melanoxanthus* (Okada and Tubaki 1984). Clavate chlamydospore-like conidia were also formed in culture, but more obvious in the variety *melanoxanthus*, and growth was observed at 5 °C after 3 months, whereas other *Endocalyx* taxa did not grow under these conditions. In addition to these differences, the eleven strains belonging to the variety *grossus*, including the ex-type strain, grouped together with high support in our individual and concatenated analyses of ITS and LSU sequence data distant from those of the variety *melanoxanthus*. The variety *grossus* is therefore elevated.
here to the species rank distinct from *E. melanoxanthus* and the remaining *Endocalyx* taxa following the guidelines and recommendations outlined for description of fungal species (Seifert and Rossman 2010; Aime et al. 2021).

In culture, strain JCM 32998 produced conidial columns (Fig. 3G arrows) on an autoclaved petiole of *T. fortunei*. They consisted of almost rough conidia (Fig. 3I) and emerged from an annulus-like structure (Fig. 3G white arrowheads) associated with hemispherical to subspherical conidiomata (Fig. 3G black arrowheads). In the case of strain JCM 5164 (ex-type) and JCM 32997, many smaller conidiomata were produced on the autoclaved substrate under prolonged incubation. Moreover, it was observed that under the same conditions JCM 32997 developed a few conidial columns with brown peridial hyphae from an annulus-like structure (Fig. 3H). This conidiomatal structure is basically the same as that on the palm host. On the other hand, strain JCM 5166 abundantly developed similar subspherical conidiomata of various sizes on PDA under prolonged incubation and without any autoclaved substrate (Fig. 4A). Dark brown conidial masses appeared from broken conidiomata (Fig. 4B, C arrowheads), and conidial columns (Fig. 4D, E arrows) were produced from the lower part of broken conidiomata (Fig. 4D, E arrowheads), which were very similar to the annulus-like structure formed on the autoclaved petiole of *T. fortunei* (Fig. 3G white arrowheads).
**Endocalyx indumentum** G. Okada & Tubaki, Mycologia 76: 305 (1984). (Figs. 2E, 3B–F, 4F).

For a detailed description on natural substrates and in culture together with key diagnostic features see Okada and Tubaki (1984) and Table 3.

**Materials examined**: Japan, Tokyo, Ogasawara Islands, Chichijima Island, Suzuki, on dead petiole of *Phoenix canariensis* H. Wildpret, 12 Mar. 1990, leg. & det. G. Okada [ILLS00121501 = G. Okada Ogasawara-80 (together with *E. melanoxanthus*, no isolate)]; idem, Anijima Island, on peduncle of dead inflorescence of *Livistona chinensis* var. boninensis, 18 Mar. 1990, leg. & det. G. Okada [ILLS00121503 = G. Okada Ogasawara-194]; idem [TNS-F-91432 = G. Okada Ogasawara-200; strain JCM 8042; TNS-F-91433 (dried culture of JCM 8042 incubated on autoclaved petiole of *L. chinensis* var. *subglobosa*)].

**Notes**: Morphological details of the specimen studied (TNS-F-91432) agree well with the description of Okada and Tubaki (1984). In culture, strain JCM 8042 formed primordium-like structures of conidiomata on an autoclaved petiole of *L. chinensis* var. *subglobosa* after a 3-month-incubation period. Hemispherical to subspherical conidiomata were produced on the surface of the substrate after further prolonged incubation, and dark brownish conidial masses sometimes in columns emerged from inside of burst conidiomata (Fig. 3C, D arrow & arrowheads; TNS-F-91433). Conidia with hair-like projections (Fig. 3E, F) were the same as those on palm hosts (Okada and Tubaki 1984, Fig. 23). The strain JCM 5171 (ex-type) did not produce conidiomata under the same conditions. On the other hand, strain JCM 8042 developed subspherical conidiomata on PDA under prolonged incubation and without any autoclaved substrate (Fig. 4F). In the broken conidiomata (Fig. 4F arrowheads), small immature conidia without filamentous ornamentation were observed as reported by Okada and Tubaki (1984, Fig. 24).

**Endocalyx melanoxanthus** (Berk. & Broome) Petch, Ann. Bot. (London) 22: 390 (1908). (Figs. 2A, 5).

≡ *Melanconium melanoxanthum* Berk. & Broome, J. Linn. Soc. Bot. 14: 89 (1875).

= *Endocalyx metroxyli* Konta & K.D. Hyde, Life 11(486): 18 (2021).

Conidiomata scattered or aggregated in small to large groups and emerging from annulus-like, black, circular pustules, at first short-cylindrical or short-cupulate becoming long cylindrical, subcylindrical, long conical or cup-shaped after incubation for several days, reaching up to 3 mm high in well-developed fructifications and consisting of a black, glistening mass of conidia enclosed by a yellow to greenish yellow or orange yellow, annular mass of sterile peridial hyphae which remain at the base once the conidioma expands and grows upwards surrounding the column.
of conidia. Conidiophores micronematous, filiform, flexuous, hyaline, septate, smooth, anastomosing, 1–2.5(3.5) µm wide. Conidiogenous cells holoblastic, monoblastic, integrated, terminal or intercalary, cylindrical, minutely denticulate. Conidia solitary, dry, globose, subglobose or broadly ellipsoidal, slightly polygonal and flattened in front view, (10–)12–16 × 9–12(–13) µm, ellipsoidal, lenticular or rarely oblong in lateral view, (7–)8–9(–10) µm thick, with a paler equatorial germ slit, aseptate, brown, dark brown or blackish brown, thick-walled, smooth to finely roughened, often with a central or nearly central attachment scar.

Colonies on MEA moderately fast growing reaching 25–35 mm diam. after 10 days at 25 °C (A. Surface view; B. Reverse). C. Upper view of short conidiomata on the natural substrate. D–F. Lateral view of conidiomata after incubation, FSCI. G. Conidia. H. Conidia mixed with yellow peridial hyphae. I. Conidiophore with attached conidium. J–L. Chlamydospores on MEA. Scale bars: C–F = 500 µm; G, I–L = 10 µm; H = 15 µm

Materials examined: USA, Texas, Harris County, Spring, Meyer Park, 30°00’15.9” N, 95°31’35.7” W, 33 m a.s.l., on peduncle of dead inflorescence of Sabal minor, 20 Sep. 2020, leg. & det. G. Delgado (ILLS00121433; strains CBS 147393 = JCM 39196); idem, on spathe of dead inflorescence of S. minor, 20 Sep. 2020 (ILLS00121434; strain CBS 147394).

Other materials examined: Japan, Tokyo, Ogasawara Islands, Chichijima Island, Suzuki, on dead petiole of Livistona chinensis var. boninensis, 12 Mar. 1990, leg. & det. G. Okada (TNS-F-91434 = G. Okada Ogasawara-61; strain JCM 7948); USA, Hawaii, Hawaii Island, Hilo, around Liliuokalani Park and Gardens, on dead petiole of Cocos nucifera L., 2 Aug. 2005, leg. & det. G. Okada (ILLS00121495;
strain JCM 13432); ILLS00121502 and ILLS00121501 (see the above sections of *E. cinctus* and *E. indumentum* for collection details).

**Notes:** The description above refers to the freshly collected Texas specimens and serve to document the presence of *E. melanoxanthus* for the first time in the state. These materials agree well with previous descriptions of the fungus in having distinct annular, vivid, greenish yellow fructifications surrounding a black mass of subglobose, more or less angular, dark brown to blackish brown, aseptate conidia with a paler germ slit. Conidomia readily developed after incubation for a few days and the conidial mass together with the yellow peridial hyphae expand upward forming long cylinders up to 3 mm high in the longer fructifications. Okada and Tubaki (1984) also obtained morphologically similar, well-developed conidomata in a moist chamber that reached up to 7 mm high. The moisture conditions induced abundant sporulation that cannot be held by the outer layer of peridial hyphae, which tears laterally in several places or apically, opening up and releasing spores on the substrate (Fig. 5D–F). Wall ornamentation of conidia was confirmed to be very finely roughened and more visible around the paler wall of the germ slits in agreement with Okada and Tubaki (1984), who reported a fine dust-like layer covering conidia that cracks and creates islets as seen under SEM. In culture, the Texas strains did not sporulate after 3 months incubation on MEA, but they produced abundant chlamydospores in the same time period (Fig. 5J–L). This also agrees with Okada and Tubaki (1984) who reported solitary or catenate, terminal or intercalary, dark brown, chlamydospores similar in size and shape, with a paler germ slit and superficially resembling conidia. They also obtained immersed or superficial, pycnidial conidomata on sterilized wooden chips that produced conidia similar to those on the natural substrates, but this technique to induce sporulation was not attempted in this study for the Hawaiian and Texan strains. Additional details of Japanese specimens growing on the natural substrates and in culture are also found in Okada and Tubaki (1984), and key diagnostic features given in Table 3.

**Discussion**

This study represents a comprehensive assessment of the phylogenetic affinities of four *Endocalyx* taxa employing molecular data obtained from the specimens and strains collected in Japan, Hawaii and continental USA. Our phylogenetic analyses using a more extensive taxon sampling than that of Konta et al. (2021) confirmed that *Endocalyx* belongs to the order *Xylariales* (*Sordariomycetes*) and its familial position is resolved within the *Cainiaceae*. All species formed a distinct monophyletic lineage and they grouped with representative members of the family including *Cainia* *graminis*, the type species of *Cainia* and type genus of *Cainiaceae*. Molecular data along with distinct morphological, cultural and ecological features support the recognition of *E. grossus*, originally described as a variety of *E. melanoxanthus*, as a separate species. The remaining three taxa, *E. cinctus*, *E. indumentum* and *E. melanoxanthus*, were also phylogenetically well-resolved (Figs. 1, S1, S2) and all treated *Endocalyx* species were consistent with their morphological circumscriptions mainly based on conidiomatal morphology, presence or absence of a carbonaceous hyphal cylinder at the base of conidomata, color of the peridial hyphae and conidial mass, conidial wall ornamentation, and palm host preferences (Okada and Tubaki 1984).

Although *Endocalyx* is revealed as a phylogenetically, morphologically and ecologically well-defined genus based on the sampled specimens and isolates, *E. twaithesii*, the generic type species, lacks sequence data. Therefore, the generic position revealed by Konta et al. (2021) and this study, although including the ex-type strains of species such as *E. grossus* and *E. indumentum*, still requires confirmation by the inclusion of sequences from *E. twaithesii*. An online search on the IMI database ([http://www.herbiminfo/heriti info/heriti info/home.htm](http://www.herbiminfo/heriti info/heriti info/home.htm)) shows that two specimens of *E. twaithesii*, one a type specimen from the original collection (Thwaites 1408 in Sri Lanka; IMI 48588a) and another authentic specimen collected by S. Hughes in Ghana (formerly Gold Coast) (IMI 43614c, on twigs of *Cissus oerophila* Gilg & M. Brandt (Vitaceae)), are currently deposited in IMI. Future collection of fresh authentic material of *E. twaithesii* at the type locality (Sri Lanka) is needed to further evaluate the phylogenetic position of the genus.

The recently described *E. metroxyli* collected in Thailand on a dead petiole of *M. sagu* (Konta et al. 2021) clustered within the *E. melanoxanthus* clade (Fig. 1), and therefore it was reduced to its synonym (see the taxonomic part of *E. melanoxanthus*). Morphologically, the authors recognized that *E. metroxyli* was very close to *E. melanoxanthus* in having similar black annulus-like pustules, the fertile center enclosed by yellow peridial hyphae, and conidia nearly identical in size. The only distinctive features used to separate both species were the lack of cupulate or cylindrical conidomata and the absence of thread-like conidiophores in *E. metroxyli*. In our experience, however, after examining several specimens of *E. melanoxanthus* on natural substrate before and after incubation in moist chamber, conidomata of the Thailand specimen MFLU 15-1454 (Konta et al. 2021, Figs. 3C–E) seem to be poorly developed and sporulated probably due to its surrounding environmental conditions. This is confirmed by the specimen collection date that took place during the tropics drier season (December) and no mention of subsequent incubation was made by the authors. The expansion and development of fully cupulate, cylindrical or funnel-shaped conidomata in *E. melanoxanthus*,
E. grossus and E. indumentum seem to be enhanced under conditions of high moisture (Okada and Tubaki 1984; this paper). An example in this paper is the clear differences in conidioma development seen in the specimen E. melanoxanthus ILLS00121433 on the host before and after incubation in a moist chamber [Fig. 5C (before), D–F (after)]. Moreover, thread-like conidiophores are usually difficult to find especially in a poorly sporulated specimen, but they can be detected with due diligence (Fig. 5I). Prior to Konta et al. (2021) and the present work, only two unpublished nrDNA sequences and the master record of a whole genome shotgun sequencing project belonging to E. cinctus JCM 7946 (BCKC00000000) were available in GenBank. A large number of anamorphic genera such as Endocalyx currently lack molecular data, and therefore thorough review of past literature together with careful examination of authentic specimens and cultures is still essential to avoid redescribing old and well documented taxa as new (Koukol and Delgado 2021).

In general, isolates of E. melanoxanthus showed a surprisingly low genetic divergence despite originating from three disjunct tropical or subtropical locations in Japan, Hawaii and Texas. Sequences belonging to “E. metroxylí” from Thailand, synonymized here under E. melanoxanthus, were also nearly identical to the Japanese, Hawaiian and Texan collections. The only exception was the strain Endocalyx sp. MAFF 244025 which showed a considerable genetic variation in its ITS and may represent a distinct population of the fungus growing on the same palm host in the Ogasawara Islands, although further conclusions remain pending in the absence of additional molecular data or specimens examination. The Ogasawara Islands is an isolated archipelago in the northwestern Pacific Ocean 1000 km south of Tokyo with a high level of endemism of its flora and fauna (Kobayashi and Ono 1987; Ito 1998). Endocalyx melanoxanthus is a common colonizer of palm debris with a wide distribution that has been recorded so far from several tropical or subtropical countries including Taiwan (Okada, unpublished) on many different palm hosts (Ellis 1971; Taylor and Hyde 2003; Vitoria et al. 2011; Konta et al. 2021). An online search in MyCoPortal (MyCoPortal 2021) shows a total of 106 records of the fungus in seventeen countries. In USA, E. melanoxanthus has been previously recorded only in the states of Florida and Hawaii and now for the first time from Texas. Its long-distance dispersal is probably favored by its peculiar conidioma morphology as well as its host association (including tree planting), but previous knowledge about its intraspecific variability was lacking. However, G.O. collected in Brazil in 1993 some E. melanoxanthus-like fungi on bamboos, as well as E. melanoxanthus on palms (cf., Vitoria et al. 2011), in which the colors of peridal hyphae of the former were slightly different from the latter (Okada, unpublished).

Other species of Endocalyx apparently have more restricted hosts and distributions. Endocalyx grossus, elevated here to the species rank, is known only from T. fortunei, a cold-hardy palm native to Japan and other Asian countries. We speculate that probably E. grossus evolved independently from other studied tropical or subtropical Endocalyx species (Fig. 1). Similarly, E. indumentum, a species distinct in having conidia densely covered by a hair-like, filamentous ornamentation and dark brown, relatively larger conidiomata (Okada and Tubaki 1984), is so far only known from the endemic palm tree L. chinensis var. boninensis in the Ogasawara Islands. However, G.O. collected this species in Brazil in 1993 on bamboos and in Indonesia in 2011 on Carpentaria acuminata Becc. (Okada, unpublished; E. melanoxanthus was also found coexisting on the same sample of C. acuminata), suggesting that more collections will show a wider host range, distribution and genetic divergence. On the other hand, E. cinctus has been collected also from distant locations such as Argentina (Capdet and Romero 2012), Ghana (Hughes 1953a), Japan (Okada and Tubaki 1984), Sri Lanka (Petch 1908, type locality) and Brazil (Okada, unpublished). It is interesting to note that E. melanoxanthus was found growing together with E. cinctus (e.g., ILLS00121502) and E. indumentum (e.g., ILLS00121501 and an Indonesian collection) on the same palm debris. In contrast, Endocalyx grossus only colonizes T. fortunei as far as we know, although E. melanoxanthus rarely occurs on this host (Okada and Tubaki 1984). Future morphological, ecological and phylogenetic studies using more specimens, isolates and additional molecular markers will increase our limited knowledge of Endocalyx intraspecific variability as well as their species boundaries.

The putative placement of Endocalyx within the family Apiosporaceae (Hyde et al. 1998, 2020; Taylor and Hyde 2003; Senanyake et al. 2015; Wijayawardene et al. 2021) was not supported in our analyses. The four Endocalyx species treated in this paper clustered within the distant family Cainiaceae in Xylariales in agreement with Konta et al. (2021). Okada and Tubaki (1984) previously pointed out that the term “basauxic” refers to the nature of conidiophores, and conidiogenesis in Endocalyx was not the same as in Arthrinium or Spegazzinia. They even rejected the term “sympodial proliferation”, applied by Ellis (1971) to conidiogenesis in Endocalyx, and based on LM and SEM studies they only found basauxic elongation of conidiophores and holoblastic conidiogenesis, but no conidiophore mother-cells. These structures were not found during examination of the Texas specimens. Neither Hughes (1953a) nor Ellis (1971) described conidiophore mother-cells in Endocalyx. They stated that conidiophores are continuations of the core of hyphae at the base of the fructifications which elongate and anastomose to produce thread-like geniculate conidiophores. Other anamorphic genera having conidiophore
mother cells and considered also putative members of Api-
osporaceae were Spegazzinia Sacc. and Dictyoarthrinium
S. Hughes. However, recent phylogenetic studies assigned
them to the phylogenetically distant family Didymospha-
eriaceae in Pleosporales (Dothideomycetes) (Tanaka et al.
2015; Samarakoon et al. 2020a, 2020b). It is well known
that anamorphs having basauxic conidiophores are clearly
not a monophyletic group (Hashmi 1973). The absence of
conidiophore mother-cells in Endocalyx is therefore phylo-
genetically significant in a similar manner to the differences
noted by Kirschner et al. (2017) between modes of conidi-
genesis in Spegazzinia and Arthrinium. Anamorphic fungi
with this mode of conidiophore elongation do not represent
a natural group and this feature is shown to have evolved
independently within unrelated or even distant ascomycet-
ous lineages.

The family Cainiaceae (Krug 1978) has been previously
redefined (Kang et al. 1999; Jeewon et al. 2003; Smith et al.
2003) and recently accepted within Xylariales along with
fifteen other families in the class Sordariomycetes (Hyde
et al. 2020). Konta et al. (2021) keyed out eight genera in
Cainiaceae including Endocalyx but refrained from compar-
ing the genus with other members of the family described
solely based on their teleomorphs. However, a morpho-
logical connection between some of them and Endocalyx
is supported by the presence of germ slits in both their
ascosporas and conidia. Other features such as the very
dark brown ascospores at maturity, globose to ellipsoidal
shape, unicellular to 1-septate with ornamented walls hav-
ing reticulations or longitudinal striations (Kang et al. 1999;
Senanayake et al. 2015) may also be considered reminiscent
of conidia of some Endocalyx species. Seynesia erumpens,
for example, has two-celled ascospores with a full-length
germ slit in each cell (Hyde 1995). Together with S. nobilis
(Welw. & Curr.) Sacc., the type species of the genus cur-
rently lacking molecular data, they are also pantropical in
distribution and found as saprobes colonizing petioles and
stems of various palm trees and bamboos. Other Arecophila
species without available sequence data are also known to
colonize rachides or dead trunk and wood of palm species
(Hyde 1996). In contrast, Cainia species are mainly sapro-
bic or pathogenic on grasses (Poaceae) (Senanayake et al.
2015), whereas Amphibambusa bambusicola D.Q. Dai &
K.D. Hyde occurs on dead culms of bamboo species (Umali
et al. 1999; Liu et al. 2015). Anamorphs are poorly known
in the family, but Hyde (1995) reported the production of
pycnidial, globose conidiomata in S. erumpens on oatmeal
agar which is morphologically dissimilar from Endocalyx in
having falcate to lunate, unicellular, hyaline conidia. Müller
and Curbaz (1956) also reported that C. desmazeri C.
Moreau & E. Müll. [= C. incarcerata (Desm.) E. Müll. &
Arx] produced an anamorph in culture referred to Rhab-
dospora (Durieu & Mont.) Sacc. at a time when formally
naming different morphs of a pleomorphic fungus was stand-
ard practice but unnecessary today under the provisions of
the current code (Turland et al. 2018). Nevertheless, they
remarked this generic placement was doubtful and succes-
sive authors have been unable to reproduce this anamorph
in culture (Krug 1978; Kang et al. 1999; Senanayake et al.
2015). Rhabdospora is a poorly defined, Septoria-like genus
in need of revision with most of its accepted species cur-
rently placed in Septoria Sacc. (Mycosphaerellaceae, Cap-
nodiales, Dothideomycetes) (Quaedvlieg et al. 2013; Verk-
ley et al. 2013) and therefore it would be phylogenetically
unrelated to Cainia and Endocalyx in the Sordariomycetes.

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G.O. Field work, morphological and cultural studies: G.O., G.D.
Molecular work: A.H., A.N.M., T.I. Phylogenetic analyses: G.D.,
A.N.M. Writing and reviewing the paper: G.D., G.O. Editing the draft:
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Data availability Sequence data are available in the NCBI GenBank
(https://www.ncbi.nlm.nih.gov) under the accession numbers given in
Table 1; sequence alignments are available in TreeBASE (https://www.
treebase.org/); new combination name was registered in MycoBank
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Declarations

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