

## FULL PAPER

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## *Heteroepichloë*, gen. nov. (Clavicipitaceae; Ascomycotina) on bamboo plants in East Asia

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**Abstract** The causal agents of witches' broom of bamboo plants in East Asia, *Epichloë bambusae* and *E. sasae*, were morphologically and phylogenetically examined. The phylogenetic studies were conducted using ITS 1, 2, and 5.8S rDNA regions. Both *Epichloë* species produce *Ephelis*-type conidia in artificial medium and are phylogenetically situated in different clades from *Epichloë* and *Parepichloë*. Here, we propose a new genus *Heteroepichloë* for these two bambicolous *Epichloë* species.

**Key words** *Aciculosporium take* · *Ephelis*-type conidia · *Epichloë bambusae* · *Epichloë sasae* · *Parepichloë*

### Introduction

Grass endophytes and a related fungal group have received widespread attention because they have peculiar relationships with their host plants. Among them *Epichloë typhina* (Pers.: Fr.) Tul., which causes choke disease of cool season grasses and related *Neotyphodium* Glenn et al. orphans, are extensively studied because of their economical importance and their ecological significance.

The members of *Epichloë* (Fr.) Tul. et C. Tul. have been described on various host species and considered miscellaneous assemblages to be reexamined (White 1994). The species on warm season grasses and bamboo plants are the pertinent quarries. Two *Epichloë* species on bamboos have been recorded in East Asia, namely, *E. bambusae* Pat. (Patouillard 1897) and *E. sasae* Hara (Hara 1922; Hino

1961), respectively; they cause witches' broom of bamboo plants. *Epichloë sasae* was originally described by Hara on *Sasa* spp. (Hara 1922), which are small bamboo plants grown in understories of Japanese beech forests in the Japanese archipelago. *Epichloë bambusae* was described by Patouillard on *Gigantochloa* spp. (Patouillard 1897), which are large and tall bamboo plants grown at roadsides or in cultivated stands in Indonesia and other tropical areas of Asia. Witches' broom of bamboo plants caused by *Aciculosporium take* I. Miyake (anamorph: *Albomyces take* I. Miyake, Clavicipitaceae) is also distributed in Japan and other East Asia regions. Numerous greatly shortened shoots emerge at the newly developing branchlets of the host bamboo plants. The newly developing tillers and leaves are deformed and dwarfed. Recently, *Aciculosporium take* has been rampantly breaking out in bamboo stands of commercial forests and ornamental and exhibitional gardens in the Japanese archipelago, especially *Phyllostachys bambusoides* Siebold et Zucc. It was confirmed that *A. take* infected 5 genera, 17 species of bamboos including *Sasa* spp. (Sect. *Sasa*) besides *Phyllostachys* spp. (Tsuda et al. 1997). The production of bamboo culms is reduced, and the scenery created by bamboo stands is severely damaged and disturbed in an unsightly manner.

The symptoms and signs caused by *E. bambusae* are considerably different from those caused by *A. take* (Gäumann 1927; Tsuda et al. 1997). The signs of *A. take* can be easily differentiated those of *E. bambusae* and *E. sasae* by the production of whitish minute anamorphic stroma, on which pale brown, wartlike teleomorphic stroma develops in summer. The signs of both *Epichloë* species on *Sasa* species (Hino 1961) and *Gigantochloa* species (Gäumann 1927), respectively, are almost the same in appearance. Unfortunately, the identity or taxonomical relationship between the two *Epichloë* species has not been revealed.

In 1998, White and Reddy (1998) examined the phylogenetic relationships of some *Epichloë* species, including both species on bamboo plants, and a *Balansia* species, *B. cynodontis* Syd., on grasses and proposed the new genus of *Parepichloë* typified by *E. cinerea* Berk. et Broome on

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*Eragrostis* and *Sporobolus* species. In their treatment, the two *Epichloë* species inhabiting bamboo plants are included in this new genus without considering molecular data but based only on the superficial morphological resemblance of herbarium materials.

In the course of our phylogenetic studies on clavicipitaceous fungi, we have been aware of the differences of the *Epichloë* species recorded on bamboos from those found on grasses. Fortunately, we were able to collect these *Epichloë* species on *Sasa* and *Gigantochloa* and *E. cinerea* on *Sporobolus* species. We examined their morphological characteristics using fresh materials and analyzed their phylogenetic relationships by comparing DNA sequences. Here, we present the taxonomic position of these two bambusicolous *Epichloë* species.

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## Materials and methods

### Collections

Sources, sample names, and GenBank accession numbers of the isolates used are indicated as follows.

*Epichloë sasae*: collected at Botanical Garden of Hokkaido University, Sapporo-shi, Hokkaido, on *Sasa* sp. (Sect. *Sasa*) (*E. sasae*-H; AB065432), Ashu Experimental Forest of Kyoto University, Miyama-cho, Kyoto on *Sasa* sp. (Sect. *Sasa*) (*E. sasae*-K; AB065430), and Shiga-Kogen, Yamanouchi-cho, Nagano on *Sasa* sp. (*E. sasae*-N; AB065431).

*Epichloë bambusae*: collected at Bogor Botanical Garden, Bogor, on *Gigantochloa* sp. (*E. bambusae* Bo-01; AB065428, Bo-02; AB065429), northern part of Bandung on *Gigantochloa* sp. (*E. bambusae* Ba-01; AB065426), and Lembang on *Gigantochloa* sp. (*E. bambusae* Le-01; AB065427), Java Island, Indonesia.

*Epichloë cinerea*: collected at Ilam, Eastern Nepal on *Sporobolus* sp. (*E. cinerea* Ne-01; AB065425).

*Aciculosporium takei*: collected at Uji-shi, Kyoto on *Pleioloblastus gramineus* (Bean) Nakai (Sect. *Nezasa*) (*A. takei* Nezasa; AB065422), Uji-shi, Kyoto on *Phyllostachys bambusoides* (*A. takei* Madake; AB065423), Chiyoda-ku, Tokyo on *Phyllostachys bambusoides* var. *castilloni-inversa* Houz. de Leh. (*A. takei* Ginmeichiku; AB065424), Ashu Experimental Forest of Kyoto University, Miyama-cho, Kyoto, on *Sasa* sp. (Sect. *Sasa*) (*A. takei* Chimakizasa; AB066293), and Yoro Bamboo Garden, Gifu on *Sasa* sp. (Sect. *Lasioderma*) (*A. takei* Nambusuzu; AB066292).

The specimens were dehydrated by silica gel drying for morphological observations and DNA analyses. Cultures were also obtained from both *Epichloë* species on bamboo plants. These species were cultured at 25°C on complete medium [CM: 0.15% Ca (NO<sub>3</sub>)<sub>2</sub>·4H<sub>2</sub>O, 0.05% KCl, 0.05% MgSO<sub>4</sub>·7H<sub>2</sub>O, 0.04% KH<sub>2</sub>PO<sub>4</sub>, 0.003% K<sub>2</sub>HPO<sub>4</sub>, 0.1% yeast extract, 0.1% tryptone, 1% glucose (w/v)] by the method of Nakada et al. (1994). All voucher specimens or isolates are deposited at the herbarium of the Kyoto University Museum (KYO).

### Morphological observations

Morphological observations were routinely conducted on dehydrated materials of silica gel-killed materials as well as on cultured materials.

### DNA sequencing and molecular phylogenetic studies

The fungal genomic DNA was extracted from silica gel-dried materials or liquid cultures on complete medium according to the method of Nakada et al. (1994). The extracted DNA were stored in tetraethyl (TE) buffer at -20°C. The ITS 4 and ITS 5 primers amplified the ITS 1, 2, and 5.8S rDNA regions, as described by White et al. (1990). Polymerase chain reaction (PCR) was conducted using Taq polymerase (Takara, Otsu, Japan) on a PCR Thermal Cycler (TP-3000; Takara). The PCR products were purified and cloned on plasmid vector pZErO<sup>TM</sup>-2 (Invitrogen, CA, USA). They were sequenced by the Sanger method using an ALFred DNA sequencer (Amersham Pharmacia Biotech, Uppsala, Sweden). The sequencing reaction was completed with the Amersham sequencing kit (Thermo sequenase fluorescent labeled primer cycle sequencing kit with 7-deaza-dGTP) using Cy-5 fluorescent primers, M13-20 and M13-Rvs (Amersham Pharmacia Biotech).

The sequence data were edited with the software package DNAsis-Mac (version 3.0; Hitachi Software Engineering, Tokyo, Japan). We used the newly analyzed sequences of *Epichloë bambusae*, *E. sasae*, *A. takei*, and *E. cinerea* (= *P. cinerea*), together with the sequences of other clavicipitaceous fungi used in our previous study (Tanaka et al. 2001). The sequences were aligned with CLUSTAL W (Thompson et al. 1994).

Phylogenetic analyses were performed with the software PAUP 3.12 (Swofford 1993) and PHYLIP (version 3.72; Felsenstein 1993), using DNADIT, NEIGHBOR, SEQBOOT, DNAML, and CONSENSE. Phylogenetic trees were constructed using parsimony with a heuristic search and maximum likelihood. The bootstrap analysis was implemented using 100 replicates of heuristic searches to determine the confidence levels of the inferred phylogenies (Felsenstein 1985).

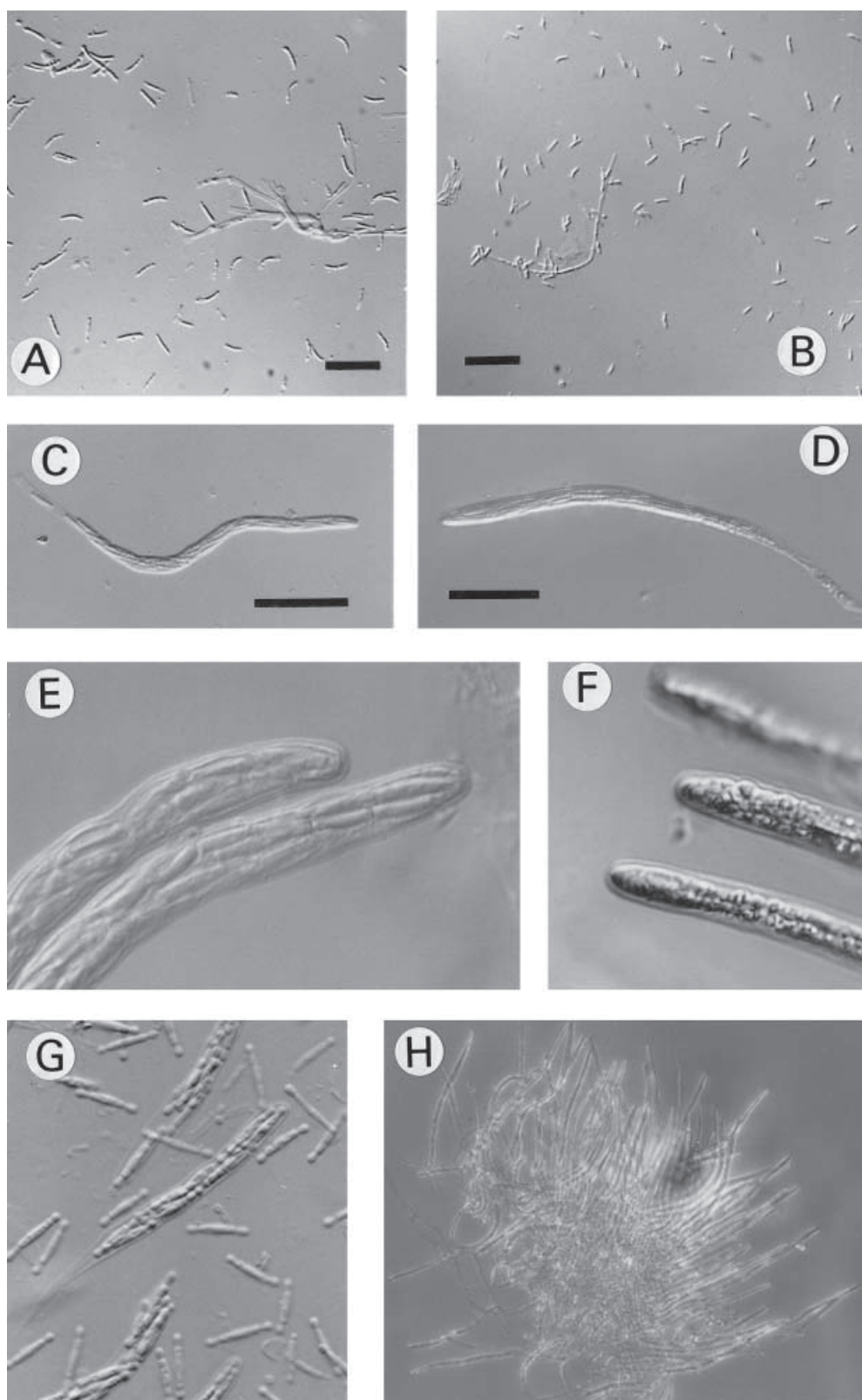
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## Results

### Morphological study

Some different characteristics were found between the two species on bamboo plants and *Parepichloë* species proposed by White and Reddy (1998). Those *Parepichloë* species have not been documented for the anamorph. However, *E. bambusae* and *E. sasae* produced anamorphic conidia on CM agar medium. They were morphologically similar to *Ephelis*-type conidia accommodated in some clavicipitaceous fungi. The conidia were unicellular, filiform, and hyaline,  $5.8 \pm 0.5 \times$  ca.  $1.5 \mu\text{m}$  for *E. bambusae* and  $8.5 \pm 0.8$

**Fig. 1.** Morphological characteristics of *Heteroepichloë sasae* and *H. bambusae*. **A** Conidia of *Heteroepichloë sasae* produced on CM agar medium. **B** Conidia of *Heteroepichloë bambusae* produced on CM agar medium. **C** Ascus of *Heteroepichloë sasae*. **D** Ascus of *Heteroepichloë bambusae*. **E** Ascus tip of *Heteroepichloë sasae* in an ascostromata. **F** Ascus tip of *Heteroepichloë bambusae* in an ascostromata. **G** Asci and part-spores of *Heteroepichloë sasae*. **H** Ascus arrangement of *Heteroepichloë bambusae*. Bars **A,B,G** 20  $\mu\text{m}$ ; **E,F** 10  $\mu\text{m}$ ; **H** 50  $\mu\text{m}$



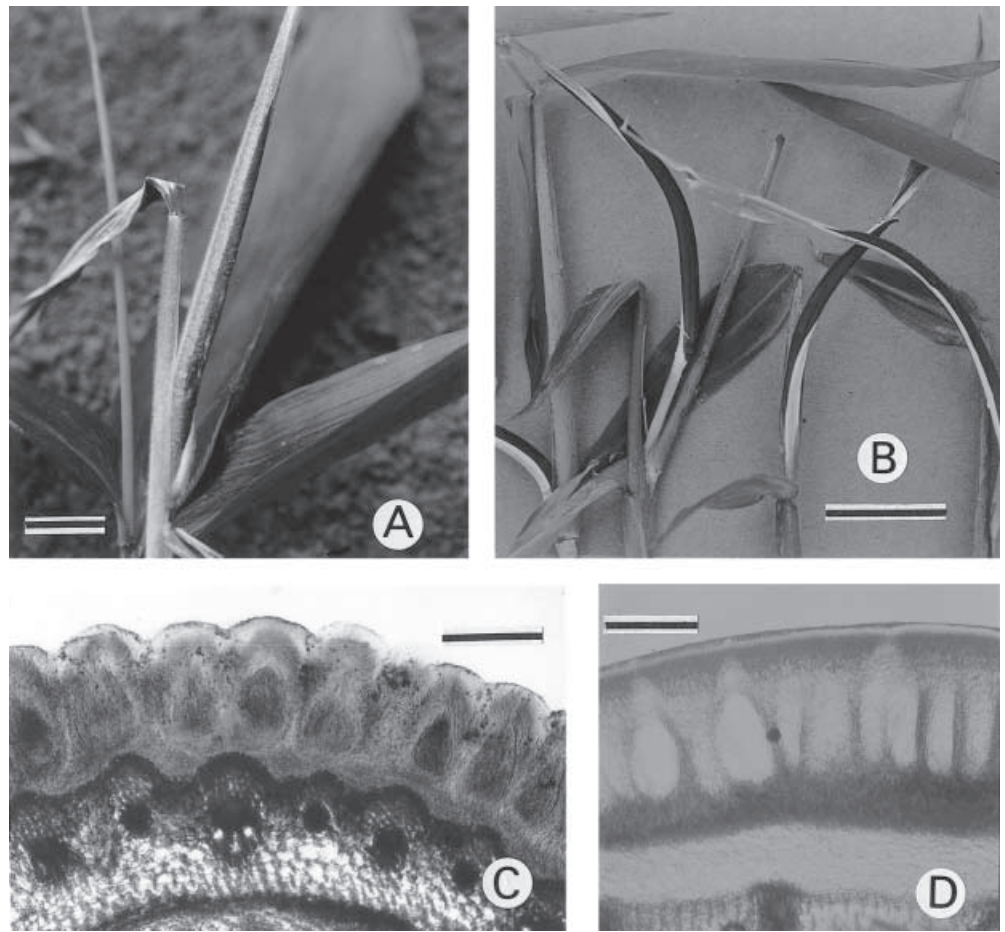
$\times$  ca. 1.6  $\mu\text{m}$  for *E. sasae* (Fig. 1A,B). They were holoblastically born on hyaline and simple conidiophores.

The ascostromata of the two *Epichloë* species on bamboo plants develop on the leaf sheath of host plants (Fig.

2A,B). At the young stage, the surface is yellowish in *E. bambusae* and purplish in *E. sasae*. The ascostromata are guided by the growth of the inrolled young leaves and protrude from the apex of the sheath or burst up from the



**Fig. 2.** Gross morphology of *Heteroepichloë sasae* and *H. bambusae*. **A** Ascostromata of *Heteroepichloë sasae* produced on *Sasa* sp. **B** Ascostromata of *Heteroepichloë bambusae* produced on *Gigantochloa* sp. **C** Perithecial arrangement of *Heteroepichloë sasae* in an ascostromata. **D** Perithecial arrangement of *Heteroepichloë bambusae* in an ascostromata. Bars **A,B** 1 cm; **C,D** 100  $\mu$ m



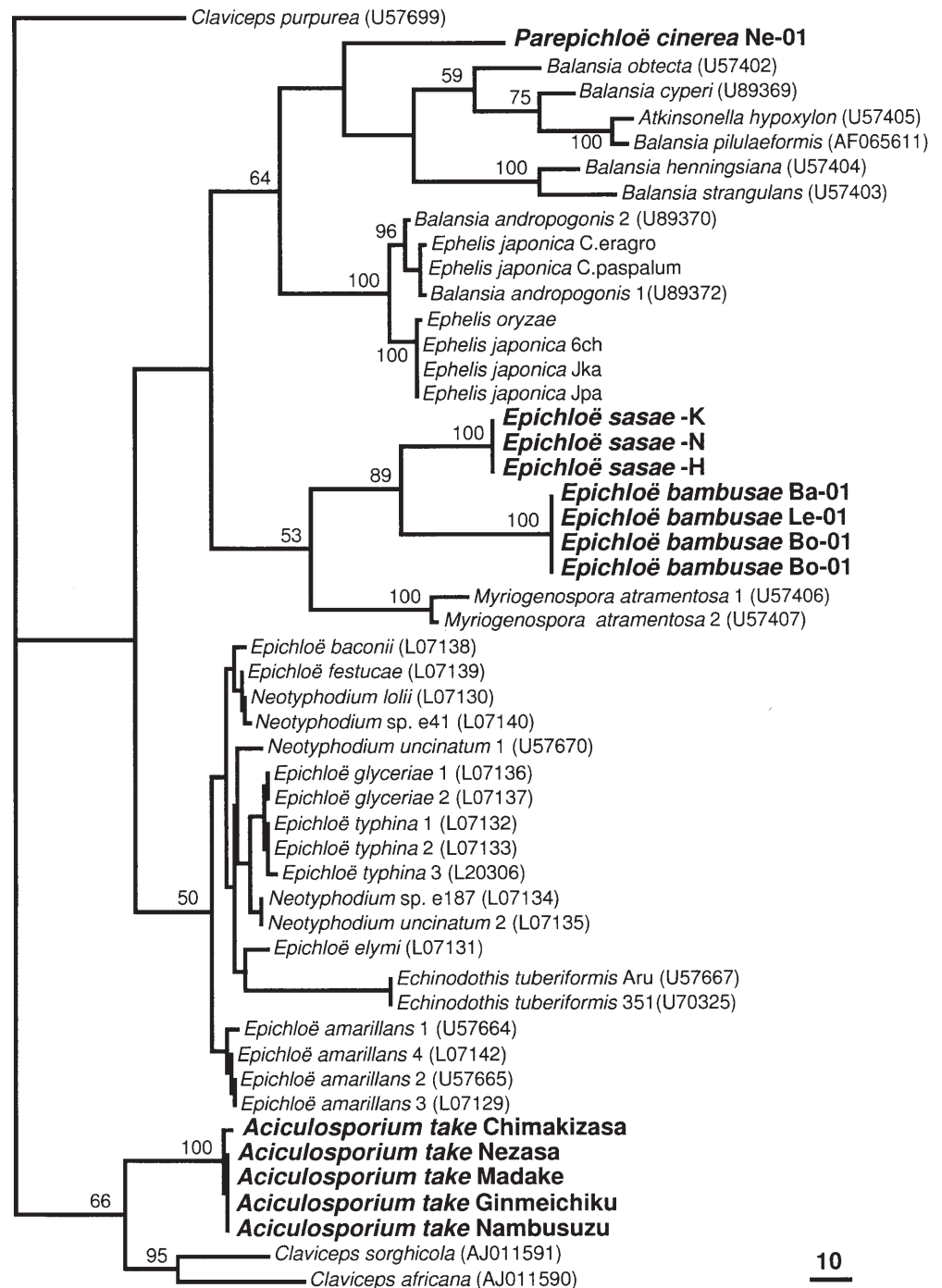
middle part of the sheath. They grow loosely twisted up to 10 cm long. They are soft and fleshlike in the sheath, and later become hard and glutinous. The perithecia are embedded and arranged regularly in the ascostromata (Fig. 2C,D). The asci are abundantly produced in the perithecium and spread when the perithecium is crushed (Fig. 1C,D,H). Their ascus tips are round and somewhat thickened (Fig. 1E,F), but their capitulation is not so prominent as *E. typhina* nor so flattened as *E. cinerea*, as depicted by Sharma and Tewari (1969) and White and Reddy (1998). Ascospores are hyaline, filiform, and multiseptated and easily fragmented to dumbbell shaped part-spores in the ascus (Fig. 1G). These figures concur with those given by Gäumann (1927) for *E. bambusae* and by Hino (1961) for *E. sasae*.

The type species of *Parepichloë* J.F. White et P.V. Reddy, *P. cinerea* (Berk. et Broome) J.F. White et P.V. Reddy (= *E. cinerea*), grows on the inflorescences of warm season grasses, *Eragrostis* and *Sporobolus* spp., and encircles the whole of the inflorescence. The ascostromata are brittle and perithecia are randomly and sparsely arranged in the ascostromata, as pointed out by White and Reddy (1998) and previous authors (e.g., Sharma and Tewari 1969). *E. cinerea* (= *P. cinerea*) materials from Nepal used in this work morphologically fit the previous descriptions (Mhaskar and Rao 1976; White 1994).

#### Phylogenetic studies

We found two base differences in the ITS 1 sequences between our collection and *P. cinerea* sequences obtained from GenBank. This variation is considered to occur at the intraspecific level, compared to the variation in *P. sclerotica* (Pat.) J.F. White et P.V. Reddy in which four base differences have been recognized. We could not find mature asci in our materials. The ascus tip of *P. cinerea* is clearly different from our bambusicolous species (cf. fig. 8 in White and Reddy 1998; fig. 6 in Sharma and Tewari 1969). Ascospores of *P. cinerea* are also easy to separate to part-spores; they are not dumbbell shaped but cylindrical.

The phylogenetic analysis using ITS 1, 2, and 5.8S rDNA sequences was also combined with our previous study (Tanaka et al. 2001). *Epichloë bambusae* and *E. sasae* formed a different independent group from *Parepichloë* or *Epichloë* group in a parsimonious and a maximum-likelihood tree (Figs. 3, 4). They showed some similarities to *Myriogenospora* species on *Andropogon virginicus* L. or *Erianthus contortus* Baldw. ex Elliot in the parsimonious tree. The *E. bambusae*-*E. sasae* group was clearly different from *P. cinerea*, which was located within the *Balansia* group. It was suggested that *Parepichloë* species were more closely related to *Balansia* than to *Epichloë* species (Tanaka



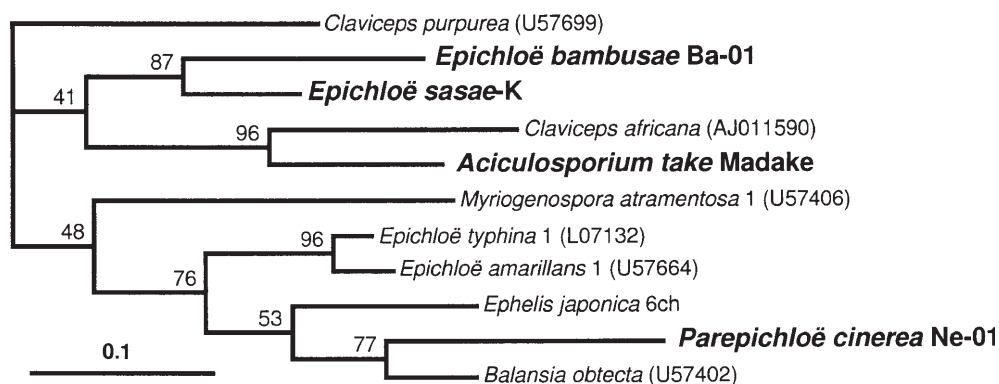
**Fig. 3.** One of 13 trees of bambusicolous *Epichloë* (*Epichloë sasae* and *Epichloë bambusae*) and other related clavicipitaceous fungi inferred from a parsimony analysis of ITS 1,-2, and 5.8S regions of rDNA. Heuristic search found 13 equally parsimonious trees. Topological differences among the 13 trees were intraspecific changes of *Ephelis* or *Epichloë* isolates. The values shown at the nodes are the confidence

levels from 100 replicate bootstrap samplings. The tree length was 789, the consistency index (CI) was 0.615, the homoplasy index (HI) was 0.385, the retention index (RI) was 0.833, and the rescaled consistency index (RC) was 0.512. Newly analyzed sequences are shown in boldface. The data obtained from GenBank are indicated with their accession numbers. Bar is branch length

et al. 2001). The results did not support the conclusions of White and Reddy (1998) that the bambusicolous *Epichloë* species belong to the genus *Parepichloë*. *Aciculosporium take* were included in an independent group related to *Claviceps africana* Freder., Mantle et De Miliario and *C. sorghicola* Tsukib., Shimam. et T. Uematsu.

## Discussion and taxonomy

Morphological characteristics of *E. bambusae* and *E. sasae* clearly bear little structural similarity to those of the genus *Epichloë*, typified by *E. typhina*. The recent treatment of



**Fig. 4.** Phylogenetic relationships of bambusicolous *Epichloë* (*E. sasae* and *E. bambusae*) and other related clavicipitaceous fungi inferred from a maximum-likelihood analysis of ITS 1,-2, and 5.8S regions of rDNA. The Ln likelihood was  $-2967.07132$  and the estimated transi-

tion/transversion ratio was 1.553007. The values shown at the nodes are the confidence levels from 100 replicate bootstrap samplings. Newly analyzed sequences are shown in **boldface**. The data obtained from GenBank are indicated with their accession numbers

White and Reddy (1998) for both fungi as members of *Parepichloë* is also considered to be incorrect. The genus *Parepichloë* was established mainly on the basis of the phylogenetic topology calculated from nucleotide sequences of the ITS 1 region of *E. sclerotica* Pat., *E. schumanniana* Henn. (treated as *E. sclerotica*), *E. cinerea*, and *Balansia cynodontis* by comparing to other warm season grass-inhabiting epibiont-related species. Unfortunately, the members included in the genus, such as *E. oplismeni* Henn. and *E. volkensii* Henn., together with *E. sasae* and *E. bambusae*, were only considered by comparing morphological characteristics of herbarium materials.

The morphology of hypothallus (or stromata) is believed to be important in these epibiotic clavicipitaceous fungi (Diehl 1950; White 1994). If so, whether the species encircle entire tillers or inflorescences or part of foliage of host plants or not might be one of the morphological characteristics that have some expression in the evolution process. The stroma of *P. cinerea* clearly encircle the whole inflorescence of host plants. The ascostroma of *P. cynodontis* (= *B. cynodontis*) also entirely encircles tillers of *Cynodon dactylon* (L.) Pers. Another species, *P. sclerotica* (= *E. sclerotica*), also has hornshaped ascostromata half-encircling the tillers or inflorescences of gramineous grasses. Their ascostromata are somewhat brittle. In contrast, the ascostromata of *Epichloë* species on the Bambusoides do not encircle the whole of the new leaves and are hard and glutinous. Thus, the difference among *Epichloë* species typified by *E. typhina*, *Parepichloë*, and *Epichloë* species on the Bambusoides is clear.

Judging from these results, it is wise to treat *Epichloë* species of the Bambusoides as belonging to a separate genus from both *Epichloë* and *Parepichloë*. Here we propose a new genus for these species hitherto treated as a member of *Epichloë* or *Parepichloë*.

***Heteroepichloë*** E. Tanaka, C. Tanaka, Abdul Gafur et Tsuda, gen. nov.

*Stromatibus* primum folium inevolutum in vagina folii circumdatis, postremo relaxtus spiralter emergentibus, atris, solitariis, primo carnosus, tandem coriaceis ad maturitatum vel in sicco; peritheciis in stromate immersis, oblongis vel ovato-oblongis, apice ostiolatis, aparaphysatis; ascis unitunicatis, cylindratis, apice rotundatis et incrassatis; ascosporis fasciculatis, filiformibus vel linearibus, in maturitate separatis. Forma anamorpha sporis filiformibus praedita *Ephelidis* similis.

Stromata primarily on leaves within a sheath, half encircling the leaves, later emerging from the sheath by loosely spiraled development, black, fleshy when young, becoming hard and glutinous when mature or on desiccation; perithecia embedded in stroma, ovate with nonemerged to slightly emerged ostioles; asci cylindrical, with thickened rounded apex; ascospores filiform, septate, hyaline. Anamorph, filiform, *Ephelis*-type spores present.

This genus is similar to *Epichloë* and *Parepichloë*, but differs most notably in possession of an epibiotic habit and stromata that have black surfaces with glutinous texture when mature.

Type species: ***Heteroepichloë bambusae*** (Pat.) E. Tanaka, C. Tanaka, Abdul Gafur et Tsuda, comb. nov. = *Epichloë bambusae* Pat., Ann. Jard. Buitenz. I (suppl):125–126, 1897.

Basionym: = *Parepichloë bambusae* (Pat.) J.F. White et P.V. Reddy, Mycologia 92:231, 1998.

Other species included in the genus: ***Heteroepichloë sasae*** (Hara) E. Tanaka, C. Tanaka, Abdul Gafur et Tsuda, comb. nov. = *Epichloë sasae* Hara, Shizuokaken-nokaiho 300:163, 1922 (basionym) = *Parepichloë sasae* (Hara) J.F. White et P.V. Reddy, Mycologia 92:231, 1998.

The two *Heteroepichloë* species on bamboo plants have very similar morphology but the phylogenetic comparison clearly separates them into different species (see Fig. 3). They share common characteristics such as scleroid stromata developing on the leaf sheath. When at the young

stage, the stomata are yellowish in *H. bambusae* and purplish in *H. sasae*.

Other species included in *Parepichloë* by White and Reddy (1998), such as *P. volkensis* and *E. oplismeni* without determining the molecular phylogenetic relationships, should await future examination. Thus, here we retained our comments for taxonomic treatments. More precise evidence on both a phylogenetic and morphological basis is needed.

The epibiont species of *Balansia* and its allied genera have been recorded on some bambusoid plants (Diehl 1950). *Balansia linearis* (Rhem) Diehl and *Balansiopsis gaduae* (Rhem) Höhn., both of which have several synonyms, are recorded from South America. They are clearly different from fungal species of the Asian bamboo in their morphology by lacking scleroid ascostromata. Some other species, such as *Epichloë warburgiana* Magnus and *Echinodothis tuberiformis* (Berk. et Ravenel) G.F. Atk., are reported as an epibiont of bambusoid grasses by White (1994). However, they may be different species judging from his descriptions. In the meantime, a fungus looking like *Heteroepichloë* on *Ochlandra tranvancoria* (Bedd.) Benth. was identified as *B. linearis* in India. The morphological characteristic of *B. linearis* cited by Diehl based on original descriptions and materials from South America is thin filmy stromata (Diehl 1950). Judging from the figures provided by Mohanan (Mohanan 1997; figs. 50, 52), the fungus on *O. tranvancoria* might not be *B. linearis* but rather a new member of *Heteroepichloë* or *H. bambusae* itself.

The host plants of *H. bambusae* are mainly distributed in tropical Asia and those of *H. sasae* are distributed in cool regions of the Japanese archipelago, where the host plants are covered with snow for several months. The hosts of the former are big bamboos and the hosts of the latter are *Sasa* species, which are considered to be indigenous to the northern part of northern Asia. Investigation on the origin of both species is therefore very interesting. However, the evolutionary differentiation of bamboo plants is not fully understood (Suzuki 1978). In the Japanese archipelago, *Aciculosporium take* seems to have an identical ecological niche as *H. bambusae* in large bamboo plants in tropical areas. The fungus sometimes has been wrongly cited as *Balansia take* (I. Miyake) Hara, and it frequently shares host species such as *Sasa* species with *H. sasae* in cool regions.

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