Taxonomic Studies of *Melampsora* Species on Willows in China Based on Morphology and Molecular Phylogeny

September 2013

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A Dissertation Submitted to

the Graduate School of Life and Environmental Sciences,

the University of Tsukuba

in Partial Fulfillment of the Requirements

for the Degree of Doctor of Philosophy in Agricultural Science

(Doctoral Program in Biosphere Resource Science and Technology)

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Chapter 1 Introduction

1-1 *Melampsora* species as causal agents of rust diseases on willows

Willows belong to the plant family *Salicaceae*, which comprises trees and shrubs with aggregated flowers in pendulous or erect catkins. Originally, Linnaeus (1763) described the family *Salicaceae* and divided it into two genera, *Populus* and *Salix*. The genus *Populus* is wind-pollinated and has pendulous catkins bearing flowers with numerous stamens, while the genus *Salix* is insect-pollinated and shows traits of catkins bearing two, three or five stamens (Azuma et al. 2000). Within genus *Salix*, some botanists segregated the genera *Chosenia* Nakai and *Toisusu* Kimura (Nakai 1920; Kimura 1928), but this taxonomic treatment was not widely accepted (Skvortsov 1972; Zheng 1983; Ohashi 2001; Chen et al. 2010; Hardig et al. 2010). In this study, the genera *Chosenia* and *Toisusu* are tentatively recognized as separate genera from the genus *Salix*, and "willows" refers to species belonging to all three genera. Of the three genera, *Chosenia* and *Toisusu* each contain one or two species, while *Salix* is estimated to be included 300 to 550 species according to various authorities (Argus 1997). The species diversity is highest in China (257 species) (Chen et al. 2010). There are 120 species in Russia (Skvortsov 1972) and 103 species in North America (Argus 1997), and 65 species in Europe (Bean 1980). A few species are indigenous species in India, Japan, and some countries in Africa and South America (McCracken and Dawson 1996; Karp and Shield 2008).

Currently, fast-growing woody crops are emerging as an attractive source of biomass, and willows, especially those that grow as shrubs with multiple small stems, have many characteristics desired for energy crops (Kuzovkina 2005). Due to its advantages of fast-growing and high yield property, willows have great potential as alternatives to fossil-based resources. The advancement of shrub willows is gaining worldwide interest and willow cultivars are grown widely in Europe and North

America to produce renewable energy and by-products (González-García et al. 2012). In addition, willows are also one of the best candidates for phytoremediation, ornamentation and fiber production, and so on (Verwijst 2001). In China, willows are used for multiple purposes, such as bioenergy crops, afforestation and environmental conservation (Wright 2006). Since the plantation included a limited number of genotypes, willows are susceptible to a wide range of fungal pathogens and leaf-eating insects. Among the former, the most important fungal pathogens are *Melampsora* rusts, which cause leaf rust diseases in both natural habitats and plantations grown to produce renewable energy on agricultural land (Royle and Hubbes 1992; Hunter et al. 1996). *Melampsora* rusts on willows belong to the genus *Melampsora* (Melampsoraceae, Pucciniales, Basidiomycota) of rust fungi, and these fungal pathogens are characterized by uredinia with capitate paraphyses and crust-like telia which comprise sessile, laterally adherent single-celled teliospores on willows (Pei 2005).

Melampsora species attack leaves, causing premature defoliation that leads to major defoliation in the worst cases. In some cases, the rust species can attack the stem and kill the plants. With heavy infestations, rust fungi can lower willow biomass production by up to 40% by damaging leaf tissues and reducing the photosynthesizing area (McCracken and Dawson 1998; Pei et al. 2003). Furthermore, damaged plants become more susceptible to frost, environmental hazards and other pathogens, such as willow scab (*Fusicladium saliciperdum* Lind.), branch cankers (*Glomerella miyabeana* Arx.), and stock-deforming fungi (*Cryptodiaporthe salicella* Petr.) (Royle and Hubbes 1992; Verwijst et al. 1996; Pei et al. 1999). Consequently, diseases caused by *Melampsora* species comprise one of the most important factors limiting the development of willow plantations.

Despite the ecological and economic importance of willow species, little information is available on the identity and diversity of *Melampsora* species on willows. The taxonomy of *Melmapsora* on willows has long been confusing and species identification is often very difficult because reliable morphological characteristics for distinguishing species in this genus are not clear. The precise

identification of host species is also difficult because their morphological characteristics are highly variable and they often intercross naturally (Verwijst 2001; Pei et al. 2004). In the absence of suitable morphological characteristics for delimiting *Melampsora* species on willows, comprehensive taxonomic studies need to be conducted.

1-2 Taxonomy and life cycle of *Melampsora* species on willows

The genus *Melampsora* was established in 1843, and *M. euphorbiae* on *Euphorbia exigua* L. was treated as the type species (Castagne 1843). This genus is well-defined in the 'Illustrated Genera of Rust Fungi' (Cummins and Hiratsuka 2003), and it has following morphological characteristics: Spermogonia group I (type 3, subcuticular; or type 2, subepidermal). Aecia subepidermal, erumpent, generally considered to be *Caeoma*-type, but some species have peridial cells adherent to the host epidermis; aeciospores catenulate, verrucose with rod-like columns or blocks. Uredinia subepidermal, erumpent, *Uredo*-type, bright yellow or orange when fresh, fading to nearly colorless, with abundant capitate paraphyses and in some species a partial peridium; Urediniospores borne singly on pedicels, wall colorless, echinulate, pores scattered or bizonate, obscure. Telia subepidermal or rarely subcuticular, remaining covered, consisting of laterally adherent crusts 1 spore deep; Teliospores 1-celled, sessile (some species have spore-like, presumably sterile, cells below the spores), wall brown or brownish, germ pore 1; basidia external. The definition of genus *Melampsora* is widely accepted by urediniologists. Recent molecular studies indicated that the genus *Melmapsora* is monophyletic and phylogenetically distinct from all other genera of rust fungi (Maier et al. 2003; Wingfield et al. 2004).

Within the genus *Melampsora*, about 90 species have been described worldwide, and over 50 species have been reported on willows (Kirk et al. 2001). These 50 species were described by various taxonomists in Asia, Australasia, Europe and North America, and they owned either heteroecious or autoecious life cycles (Wilson and

Henderson 1966; Ziller 1974; Hiratsuka and Kaneko 1982; Spiers and Hopcroft 1996; Pei 2005). In order to complete the life cycle, heteroecious species have their uredinia and telia on genus *Chosenia*, *Salix* or *Toisusu*, and spermogonia and aecia of these species occur on coniferous trees as *Larix*, *Abies*, *Pinus* and *Tsuga*, or on various herbaceous plants such as *Chelidonium*, *Corydalis*, *Saxifraga*, *Allium*, *Ribes*, several Orchidaceous genera or other dicotyledonous and monocotyledonous plants (Hiratsuka and Kaneko 1982; Pei et al. 1993). Autoecious species is only reported in *M. amygdalinae*, which can complete their life cycle only on genus *Salix*, such as *S. triandra* or *S. pentandra* (Gäumann 1959).

Among the five different spore stages (spermagonium, aecium, uredinium, telium and basidium) in the life cycle, morphological characteristics of the uredinial and telial stages were of significant importance for species recognition (Cummins and Hiratsuka 2003; Pei 2005). However, the taxonomy of *Melampsora* at the species level is still in a state of confusion, especially that of rust fungi on willows. Due to lack of comprehensive taxonomic studies, inconsistencies still remain in the descriptions of certain morphological characteristics, and the taxonomic criteria for species delimitation were also varied among different taxonomists in Europe, North America and Japan, where comprehensive studies have been conducted for many years. The differences in the taxonomic criteria for species delimitation among taxonomists were summarized in Table 1-1.

Since the genus *Melampsora* was established, the taxonomy of *Melampsora* species on willows has undergone four stages. Initially, species were recognized based on the symptoms they produced and the willow species they infected. The earliest study of *Melampsora* species on willows was reported in Europe, where *M. salicina* was recorded on willows for the first time by Léveillé (1847). This species was originially treated as *Sclerotium salicinum* by De Candolle (1815) based on the symptoms on the host leaves, but it was transferred to the genus *Melampsora* based on telial host information. In the second stage, Thümen (1879) first used the morphological characteristics of the uredinial and telial stages for species delimitation, and he reported six *Melampsora* species from Europe based on morphological

differences in the position of uredinia, the shape of urediniospores, the wall thickness of urediniospores, the length of urediniospores, the position of telia, the position of teliospores, the length of teliospores and the width of teliospores (Thümen 1879). Plowright (1889) followed the taxonomic treatment of Thümen (1879) and reported several *Melampsora* species in Britain based on morphology in uredinial and telial stages.

In the third stage, species were recognized mainly based on the morphological characteristics and the host range because the host alternation of *Melampsora* species on willows was discovered at the end of the 19th Century (Klebahn 1897). Based on extensive inoculation experiments, Klebahn redefined the taxonomy of *Melampsora* species on willows and first used the host ranges of the aecial and telial stages for species recognition. Based on the results of inoculation experiments, he recognized several species, e.g. *M. euonymi-capraearum*, *M. laricis-auritae*, *M. laricis-daphnoides*, *M. laricis-epitea*, *M. ribesii-epitea* and *M. ribesii-purpureae*, which had similar morphology but differed from each other mainly in host specificity of the aecial and telial stages (Klebahn 1899; 1902; 1914). The taxonomic treatments of Klebahn were generally accepted by Schneider (1905), Sydow and Sydow (1915), Arthur (1920) and other taxonomists at the beginning of the 20th Century, and many *Melampsora* species were described based on both the morphological differences in uredinial and telial stages and the host range in both aecial and telial stages. In Japan, Matsumoto (1915) reported several *Melampsora* species on willows based on both morphology and the telial host range, and such taxonomic treatment was subsequently followed by Ito (1938). Nevertheless, despite the fact that inoculation experiments demonstrated host alternation of several *Melampsora* species reported in Japan (Hiratsuka 1932), the host range and morphology in the aecial stage were not used to recognize Japanese species. The taxonomic treatment of Matsumoto (1915) was also followed by Russian taxonomists (Kuprevich and Tranzschel 1957).

In the fourth stage, the application of information on the aecial and telial hosts for taxonomic work was gradually abandoned in the middle of the 20th Century because ecological attributes, including virulence on host species, were used for infraspecific

recognition below the species rank based on the nomenclature regulations (Stearn 1953). In taxonomic studies of *Melampsora* species on willows, Hylander (1953) first applied the morphological species concept for species delimitation and lumped morphologically similar rusts with distinct aecial host range into one species, *M. epitea*. Several *Melampsora* species, e.g., *M. abietis-caparaerum*, *M. alpina*, *M. euonymi-capraearum*, *M. laricis-epitea*, *M. repentis*, *M. reticulatae* and *M. ribesii-purpureae*, were recognized as synonyms of *M. epitea* based on the similarity of morphology in the uredinial and telial stages although they had spermogonial and aecial stages on different host genera, such as *Abies*, *Euonymus*, *Larix*, *Ribes* and *Saxifraga*. Gäumann (1959) used the information of the telial host range for subspecies division, but he still used the aecial host range and morphology in the uredinial and telial stages for species delimitation. However, the taxonomic treatment of Hylander (1953) was widely accepted by Wilson and Henderson (1966) and Azbukina (1974) in Europe, Ziller (1974) in North America and Hiratsuka and Kaneko (1982) in Japan.

Species delimitation was relied on morphological characteristics in uredinial and telial stages, while the aecial and telial host ranges were served as important information for subspecies division in different taxonomic systems. Wilson and Henderson (1966) combined several described species into *M. epitea* based on morphological similarity, but they subdivided *M. epitea* into two varieties based on aecial host information: one variety had its aecial host on *Saxifraga aizoides*, and the other had its aecial host on *Saxifraga hypnoides*, *S. oppositifolia*, *Euonymus*, *Larix*, *Ribes* and Orchidaceae. However, Bagyanarayana (2005) lumped 21 described species into *M. epitea*, but he divided it into several *formae speciales* based on aecial host range on *Saxifraga*, *Euonymus*, *Larix*, *Ribes*, *Tsuga*, *Viola* and Orchidaceae, respectively.

Taxonomic studies on *Melampsora* species have long been conducted in Europe, North America and Japan, but species delimitation is still problematic due to lack of a consensus system. Although the aecial and telial host ranges have been abandoned for species recognition based on botanic nomenclature regulation, different taxonomic

systems have used different morphological characteristics as criteria for species delimitation (Table 1-1). Until now, morphological characteristics, including the size of uredinia, the position of uredinia, the length of urediniospores, the width of urediniospores, the wall thickness of urediniospores, the wall apex thickness of urediniospores, the shape of urediniospores, the position of germ pore, the existence of smooth regions in urediniospores, the apex thickness of paraphyses, the position of telia, the position of teliospores, the length of teliospores, the width of teliospores and the apex thickness of teliospores have been variously used for species delimitation (Thümen 1879; Klebahn 1914; Matsumoto 1915; Sydow and Sydow 1915; Arthur 1934; Kuprevich and Transhel 1957; Gäumann 1959; Hiratsuka and Kaneko 1982; Bagyanarayana 2005; Liu 2005). Although these morphological characteristics were used for species recognition, the effectiveness of those traditionally emphasized criteria has not been thoroughly evaluated. Due to the inconsistencies in the criteria used for the recognition and delimitation of *Melampsora* species on willows, no consensus exists on their number.

In recent years, DNA-based phylogenetic analyses have been used for taxonomy of rust fungi, such as species from genera *Puccinia*, *Pucciniastrum*, *Chrysomyxa*, *Phakopsora*, *Uromyces*, *Gymnosporangium*, together with morphological studies (Zambino and Szabo 1993; Virtudazo et al. 2001; Liang et al. 2006; Maier et al. 2007; Chatasiri and Ono 2008; Vialle et al. 2012). Specifically, the nuclear ribosomal RNA gene (rDNA) large subunit (LSU), small subunit (SSU) and internal transcribed spacer (ITS) have become one of the most popular loci for studying the rust fungi at the subgeneric level because of their successful application in a range of fungal groups, the availability of universal primers for PCR amplification, high copy numbers and high-resolution for revealing the phylogenetic framework to these cryptic fungal species (Maier et al. 2003; Wingfield et al. 2004). Molecular data for the rDNA LSU, SSU and ITS regions have already been used to clarify the relationship of *Melampsora* species with other rust fungi and interspecific relationships (Maier et al. 2003; Wingfield et al. 2004; Pei et al. 2005). The genus *Melampsora* was confirmed to be monophyletic and distinct from other rust fungi (Maier 2003; Pei et al. 2005).

Molecular phylogenetic results indicated that these molecular data could be informative for revealing the interspecific relationships, and they were also helpful to evaluate the principal morphological characteristics for species delimitation.

A few reports have examined the phylogenetic framework at interspecific levels within the genus *Melampsora*. Recent morphological and molecular phylogenetic analyses evaluated morphological characteristics, which were then used to recognize *Melampsora* species on poplars (Tian et al. 2004). In that study, besides traditional morphological criteria, several other morphological characteristics, such as the position of uredinia, the position of telia, the shape of urediniospores and the distance between spines, were found to be effective based on sequence information of rDNA ITS regions and D1/D2 region (Tian et al. 2004).

For *Melampsora* species on willows, Smith et al. (2004) first conducted morphological and molecular phylogenetic analyses of *M. epitea* from North America, and they recognized molecular divergence within *M. epitea* based on sequence data of rDNA ITS regions. Bennett et al. (2011) further revealed the genetic diversity of *M. epitea* in North America, and recognized 14 phylotypes based on rDNA ITS regions and LSU region. However, no clear morphological differences were recognized among these phylotypes. Similar results were obtained from molecular phylogenetic studies on *M. epitea* in Europe, which was also deemed to be polyphyletic (Pei et al. 2005; Milne et al. 2012). All of these studies revealed the existence of cryptic species in *M. epitea* in North America and Europe, and the discordance of morphology and molecular phylogeny was also recognized.

Although molecular phylogenetic studies have examined *Melampsora* species on willows, no comprehensive study was carried out to evaluate these reported morphological criteria based on molecular information. In addition, the polyphyly of *M. epitea* revealed by molecular data also indicated that reevaluation of previously used morphological criteria and the use of new morphological characteristics were required. For example, new characters, such as the spine density and the ultrastructure of urediniospores, were suggested to be effective for delineating of cryptic species in the *M. epitea* complex (Smith et al. 2004). Determination of whether these

morphological characteristics, together with other morphological features in the uredinial and telial stages, need to be explored to recognize *Melampsora* species on willows.

1-3 Taxonomic history of *Melampsora* species on willows in China

China has a long history of planting willows. According to historical documents and archaeological data, willows were cultivated from Xia and Shang dynasties (about 2033 BC) in China to protect the embankments and roads and to beautify gardens (Guan 2006; Shi 2008). Presently, 257 species, 122 varieties and 33 forma belonging to 37 willows sections have been reported in China (Zheng 1983; Wu et al. 2004). Some willow species have been cultivated widely for economical purposes (21000 ha) and ecological purposes to combat desertification (59000 ha) (Wright 2006). Leaf rust diseases often occur on these willow plantations and *Melampsora* species cause great economic and ecological losses in China. These diseases are difficult to control and no accurate information on the causal agents can be obtained due to the taxonomic discordance of *Melampsora* species on willows in China.

According to Zhuang (1994b), the earliest report on rust fungi in China was presented in 1886 based on specimens collected by Delavay in Yunnan in 1983. As to species in genus *Melampsora*, the first report was in 1908 and the species *M. hirculi* was found in Mongolia on *Saxifraga hirculus* L. (Liro 1908). Subsequently, investigations on the genus *Melampsora* gradually increased and many species were reported on willows. *Melampsora coleosporioides*, originally described in Japan (Dietel 1902), was recorded on *S. babylonica* in 1913 in northeastern China (Miyake 1913). *Melampsora ribesii-purpureae*, described based on rust fungus on European willows with the aecial host on *Ribes* species, was also reported on *S. purpurea* in China based on morphological characteristics and telial host range (Liou 1935). One year later, *S. wilsonii* was recognized as a new host of *M. ribesii-purpureae* in Jiangsu province in China (Tai 1948). Hiratsuka (1941) reported *M. laricis-epitea* and *M.*

salicis-warburgii in China. *Melampsora yezoensis*, which was described on *S. jessoensis* in Japan (Matsumoto 1915), was also reported by Cummins (1950) on *S. longiflora* in China. From then on, several taxonomists have described other *Melampsora* species on willows consecutively.

In 1979, Tai summarized the previous reports of *Melampsora* species on willows at the national level and listed 11 *Melampsora* species on genus *Salix* in his "*Sylloge Fungorum Sinicorum*" (Tai 1979). Although Tai summarized a species list based on previous reports in China, no comprehensive taxonomic system was provided. These 11 species were recognized mainly based on European or Japanese taxonomic systems proposed by different researchers. Among them, *M. coleosporioides*, *M. epiphylla*, *M. salicis-warburgii* and *M. yezoensis* were recognized using Japanese taxonomic systems (Matsumoto 1915; Ito 1938), while *M. farinosa*, *M. laricis-caprearum*, *M. laricis-eptiea* and *M. ribesii-purpureae* were first recorded in Europe based on both morphology and aecial and telial host information. However, these species were reported simply based on the morphology in the uredinial and telial stages or telial host information, and no host alternation was confirmed among these reported *Melampsora* species.

Subsequently, studies on local flora of rust fungi were conducted to explore the *Melampsora* species on willows in China. Since the 1980s, the rust flora in Fujian, Inner Mongolia, Gansu, Qinghai, Tibet and Xinjiang provinces has been investigated and several *Melampsora* species on willows were reported in these regions (Wang et al. 1980; Zhuang 1983; 1986; 1989; 1994; Zhuang and Wei 2002; 2003; Zhuang and Wang 2006). In all, 25 *Melampsora* species were reported on willows in China, and these reported species, host plants and locality were listed in Table 1-2.

Of these 25 *Melampsora* species on willows reported in China, most were mainly identified based on European or Japanese taxonomic systems proposed by different taxonomists. Two different taxonomic systems were used to recognize Chinese material during the regional investigation in the 20th Century. Cao (1999) provided a system during the survey of rust flora in Qingling Mountain of Shaanxi province in China. Morphological characteristics, such as the dimension and wall thickness of

urediniospores, the position of teliospores and the dimension of teliospores were used as important criteria for species recognition. The other taxonomic system was provided by Liu (2005) during the taxonomic studies of *Melampsora* species on willows in Inner Mongolia. Morphological characteristics, such as the position of uredinia and telia, the dimension of urediniospores and teliospores, the wall thickness and ornamentation, the apex thickness of urediniospores, the position and dimension of teliospores, were employed as important characteristics for species identification. These two taxonomic systems emphasized different morphological characteristics and the morphological circumscription of species was different.

As noted previously, regional investigations of *Melampsora* species on willows identified 25 species using different taxonomic systems, and the existence of several species was doubtful because they were identified simply based on willow species. These 25 reported species were variously circumscribed, and no taxonomic revision of *Melampsora* species on willows at the national level has been conducted in China. Thus, taxonomic discordance existed among these reported species due to lack of a consensus system, and comprehensive taxonomic studies of *Melampsora* species reported on willows in China are necessary.

1-4 Objective of this study

The purpose of this study was to clarify the relationship of morphological groups and phylogenetic groups, and to determine the species on willows in China based on morphological and molecular phylogenetic analyses. For this purpose, herbarium specimens of *Melampsora* on willows collected in China were used. These specimens covered the largest possible number of hosts and geographical span based on taxonomic literatures reported in China. Additional specimens from Europe, Japan and Russia were included for morphological and phylogenetic comparison. The numerical taxonomic methods were implemented to classify morphological groups based on qualitative and quantitative characters. Thereafter, phylogenetic groups were

detected among specimens based on multi-gene phylogenetic analyses. Species of *Melampsora* on willows were determined based on both morphological characteristics and molecular phylogeny. Finally, an enumeration of *Melampsora* species on willows in China was also described.

Table 1-1 Taxonomic criteria used for species delimitation in different taxonomic systems.

Taxonomic systems	Morphological characteristics in uredinial and telial stages															Telial host	Aecial host
	Uredinia					Urediniospores				Paraphyses	Telia	Teliospores					
	Size	Position	Shape	Length	Width	Wall thickness	Apex thickness	Smooth region	Germ pore	Apex thickness	Position	Postion	Length	Width	Apex thickness		
Thümen (1879)		●	●	●		●					●	●	●	●			
Plowright (1889)		●	●	●	●						●	●	●	●			
Dietel (1902)		●	●	●	●						●	●	●	●		●	●
Klebhn (1914)			●	●								●			●	●	●
Sydow and Sydow (1915)			●	●	●							●			●	●	●
Matsumoto (1915)				●	●							●	●	●		●	
Arthur (1934)		●	●	●	●	●					●	●	●	●		●	●
Ito (1938)	●		●	●	●	●		●				●	●	●	●	●	
Kuprevich and Tranzschel (1957)		●	●	●	●	●		●			●	●	●	●	●	●	

Table 1-1 Continued.

Gaümann (1959)		●	●	●	●						●	●	●	●		●	
Wilson and Henderson (1966)	●	●	●	●	●		●			●	●	●	●	●			
Ziller (1974)	●	●	●	●	●		●			●	●	●	●	●			
Hiratsuka and Kaneko (1982)		●	●	●	●	●	●	●	●		●	●	●	●			
Cao (199)		●	●	●	●		●				●	●	●	●			
Liu (2005)	●	●	●	●	●	●	●			●	●	●	●	●			
Bagyanarayana (2005)		●	●	●	●	●	●				●	●	●	●			

Table 1-2 *Melampsora* species, host range and locality reported in China.

***Melampsora* Species**	**Host**	**Locality**	**Reference**
Melampsora kamikotica Kaneko & Hiratsuka	*Chosenia arbutifolia* A. K. Skvortsov	Inner Mongolia	Liu (2005)
M. amygdalinae Klebahn	*Salix paraplesia* Schneid	Inner Mongolia	Zhuang and Wei (2002)
M. arctica Rostr.	*S. spathulifolia* Seem	Shaanxi	Cao and Li (1999)
	S. hylonoma Schneid	Shaanxi	Cao and Li (1999)
	Salix sp.	Inner Mongolia	Zhuang and Wei (2002)
M. capraearum Thümen	*S. caprea* L.	Xinjiang	Zhuang and Wei (2002)
	S. cheilophila Schneid	Inner Mongolia	Liu (2005)
	S. sinica C.Wang et C.F.Fang	Inner Mongolia	Liu (2005)
	S. wallichiana Anderss	Inner Mongolia	Liu (2005)
	S. xerophila Flod.	Inner Mongolia	Liu (2005)
	S. hsinganica Y. L. Chang et Skvortsov	Inner Mongolia	Liu (2005)
	S. ernesti Schneid	Shaanxi	Cao and Li (1999)
	S. starkeana Willd.	Inner Mongolia	Liu (2005)
M. coleosporioides Dietel	*S. bobylonica* L.	Hebei	Tai (1979)
		Shanxi	Tai (1979)
		Jiangsu	Tai (1979)
		Taiwan	Tai (1979)
		Sichuan	Tai (1979)
		Shaanxi	Cao and Li (1999)
		Inner Mongolia	Liu (2005)
	S. chaenomeloides Kimura	Hebei	Tai (1979)
		Shanxi	Tai (1979)
		Taiwan	Tai (1979)
	S. cheilophila Schneid	Henan	Tai (1979)

Table 1-2 Continued

M. coleosporioides Dietel	*S. gilgiana* Seem	Shanxi, Hebei	Tai (1979)
	S. heteromera Hand.-Mazz	Yunnan	Tai (1979)
	S. matsudana Koidz	Hebei	Tai (1979)
		Shanxi	Tai (1979)
		Inner Mongolia	Liu (2005)
	S. mesnyi Hancer	Jiangxi	Tai (1979)
	S. wilsonii Seem	Shaanxi	Tai (1979)
	Salix sp.	Liaoning	Tai (1979)
		Shaanxi	Tai (1979)
		Fujian	Tai (1979), Zhuang (1983)
		Gansu	Tai (1979)
M. epiphylla Dietel	*S. heterochroma* Seem	Shaanxi	Cao and Li (1999)
	S. sinica C. Wang et C. F. Fang	Shaanxi	Cao and Li (1999)
	S. hylonoma Schneid	Shaanxi	Cao and Li (1999)
	S. rehderiana Schneid	Shaanxi	Cao and Li (1999)
	S. wallichiana Anderss	Inner Mongolia	Zhuang and Wei (2002)
		Shaanxi	Cao and Li (1999)
	S. cheilophila Schneid	Shaanxi	Cao and Li (1999)
	S. rosmarinifolia L.	Inner Mongolia	Zhuang and Wei (2002)
	Salix sp.	Heilongjiang	Tai (1979)
M. epitea Thümen	*S. characta* Schneid	Inner Monglia	Liu (2005)
	S. psammophila C. Wang	Inner Monglia	Liu (2005)
	S. siuzevii Seemen	Hei longjiang, Inner Mongolia	Zhuang and Wei (2002)
	S. taraikensis Kimura	Hei longjiang	Zhuang and Wei (2002)
	S. triandra L.	Hei longjiang	Zhuang and Wei (2002)
	S. hypoleuca Seem	Shaanxi, Gansu	Cao and Li (1999)
	S. xerophila Floder	Hei longjiang	Zhuang and Wei (2002)
	S. daltoniana Andress	Tibet	Zhuang (1994a)
	S. delavayana Hand.-Mazz.	Tibet	Zhuang (1994a)

Table 1-2 Continued

M. epitea Thümen	*S. alba* L.	Xinjiang	Zhuang(1989)
	S. gyirongensis Zhao et Fang	Tibet	Zhuang (1994a)
	S. psilostigma Anderss	Tibet	Zhuang (1994a)
	S. radinostachya Schneid	Tibet	Zhuang (1994a)
	S. sericocarpa Anderss	Tibet	Zhuang (1994a)
	S. wallichina Anderss	Tibet	Zhuang (1994a)
	S. zayulica Wang et Fang	Tibet	Zhuang (1994a)
	S. insignis Anderss	Tibet	Zhuang (1994a)
	Salix sp.	Tibet	Zhuang (1994a)
		Xinjiang, Qilian	Zhuang and Wei (2003)
M. euonymi-capraearum Klebahn	*S. myrtilloides* L.	Inner Mongolia	Liu (2005)
	S. linearistipularis Hao	Inner Mongolia	Liu (2005)
M. farinosa Schröter	*S. wilsonii* Seem	Hunan	Tai (1979)
M. kupreviczii Zenkova	*S. rosmarnifolia* L.	Inner Mongolia	Liu (2005)
M. lapponum Lindfield	*S. starkeana* Willd.	Inner Mongolia	Liu (2005)
M. laricis-caprearum Klebahn	*S. caprea* L.	Henan, Jilin	Tai (1979)
	S. capraea L. var. *sinica* Hao	Shaanxi	Tai (1979)
	S. spathulifolia Seem	Shaanxi	Tai (1979)
	S. annulifera Marq.	Tibet	Zhuang (1986)
	S. hypoleuca Seem.	Sichuan, Hubei	Guo(1989)
	Larix griffithiana (Lindl. et Gord.) Hort. et Carr.	Tibet	Zhuang (1886)
	S. driophila Schneid	Tibet	Zhuang (1886)
	S. gilashanica C. Wang et P. Y. Fu	Tibet	Zhuang (1886)
	Salix sp.	Tibet	Zhuang (1886)
		Xinjiang	Tai (1979)
M. laricis-epitea Klebahn	*S. delavayana* Hand.-Mazz	Yunnan	Tai (1979)
	S. longiflora Anderss	Yunnan	Tai (1979)
	S. psilostigma Anderss	Yunnan	Tai (1979)

Table 1-2 Continued

M. laricis-epitea Klebahn	*S. purpurea* L.	Taiwan	Tai (1979)
	S. iliensis Rgl.	Xinjiang	Zhuang(1989)
	S. capsuii Fr.	Xinjiang	Zhuang(1989)
	S. tetrasperma Roxb.	Yunnan, Sichuan	Tai (1979)
	S. sericocarpa Anderss	Tibet	Zhuang (1986)
	S. wallichiana Anderss	Tibet	Zhuang (1986)
	S. psilostigma Anderss	Tibet	Zhuang (1986)
	S. insignis Anderss	Tibet	Zhuang (1986)
	S. viminalis L.	Dongbei	Tai (1979)
	Salix sp.	Jilin	Tai (1979)
		Heilongjiang	Tai (1979)
		Anhui	Tai (1979)
		Taiwan	Tai (1979)
		Yunnan	Tai (1979)
		Guizhou	Tai (1979)
M. laricis-pentandrae Klebahn	*S. pentandra* L.	Inner Mongolia	Liu (2005)
M.microsora Dietel	*S. fargesii* Burkill	Hubei	Zhuang (1994b)
	S. sinica C.Wang et C. F. Fang	Shaanxi	Cao and Li (1999)
M. repentis Plowright	*S. siuzevii* Seemen	Inner Mongolia	Liu (2005)
	S. triandra L.	Inner Mongolia	Liu (2005)
	S. rorida Laksch	Inner Mongolia	Liu (2005)
	Salix sp.	Inner Mongolia	Liu (2005)
M. ribesii-viminalis Klebahn	*S. viminalis* L. var. *gmelini* (Pall.) Anderss	Hei longjiang	Zhuang and Wei (2002)
	S. viminalis L.	Inner Mongolia	Liu (2005)
	Salix sp.	Inner Mongolia	Liu (2005)
M. ribesii-purpureae Klebahn	*S. matsudana* Koidz	Shaanxi	Tai (1979)
	S. opsimantha Schneid	Shaanxi	Tai (1979)
	S. purpurea L.	Hebei	Tai (1979)

Table 1-2 Continued

M. ribesii-purpureae Klebahn	*S. raddeana* Laksch ex. Nasarow	Inner Mongolia	Liu (2005)
	S. wilsonii Seem	Jiangsu	Tai (1979)
	Salix sp.	Shanxi	Tai (1979)
		Shaanxi	Tai (1979)
M. salicis-albae Klebahn	*S. alba* L.	Xinjiang	Zhuang (1989)
	S. babylonica L.	Sichuan, Shandong	Tai (1979)
	S. matsudana Koidz	Inner Mongolia	Liu (2005)
		Gansu	Tai (1979)
	Salix sp.	Sichuan	Tai (1979)
		Heilongjiang	Tai (1979)
		Yunnan	Tai (1979)
		Gansu	Tai (1979)
M. salicis-viminalis Wang et Guo	*S. viminalis* L.	Tibet	Wang (1980)
M. salicis-cavaleriei Tai	*S. cavaleriei* Levl.	Yunnan	Tai(1979)
M. salicis-cupularis Wang	*S. cupularis* Rehd.	Shaanxi	Tai(1979), Cao (1999)
		Inner Mongolia	Liu (2005)
	S. wilsonii Seem	Shaanxi	Tai (1979)
	Salix sp.	Shaanxi	Tai (1979)
		Qinhai	Tai (1979), Zhuang and Wei (2003)
M. salicis-warburgii Saw	*S. babylonica* L.	Shaanxi	Cao and Li (1999)
	S. warburgii Seem	Taiwan	Tai (1979)
M. tsinlingensis Z. M. Cao et J. Y. Zhuang	*S. paraplesia* Schneid	Shaanxi	Cao and Li (1999)
	S. koreensis Anserss	Inner Mongolia	Liu (2005)
M. yezoensis Miyabe et Matsumoto	*S. longiflora* Anderss	Guizhou	Tai (1979)
	S. dunnii Schneid	Fujian	Zhuang(1983)
	S. tetrasperma Roxb.	Fujian	Zhuang(1983)
	S. matsudana Koidz	Shaanxi	Cao and Li (1999)

Chapter 2 Morphological studies

In this section, the morphological characteristics in the uredinial and telial stages of herbarium specimens from China, Europe, Japan and Russia were examined by stereo microscope (SM), optical microscope (OM) and scanning electron microscope (SEM). The effectiveness of morphological characteristics in the uredinial and telial stages was evaluated by the numerical taxonomic method. Morphological groups were classified by hierarchical cluster analysis based on the effective qualitative and quantitative characters, and the diagnostic characters of morphological groups were also determined.

2-1 Materials and Methods

2-1-1 Specimens examined

Two hundred and six dried specimens (Table 2-1) from China were borrowed from several herbaria to cover the largest possible hosts and locality based on taxonomic literatures reported in China. Most of specimens were used for the species description in Liou et al. (1935), Tai (1948, 1979), Wang et al. (1980), Zhuang (1983, 1986, 1989, 1994a, 1994b), Zhuang and Wei (2002, 2003), Cao and Li (1999), Liu (2005) and Zhuang and Wang (2006) in China. Each specimen was chosen according to the name on the attached label and host information. These specimens contained all 25 *Melampsora* species reported in China. Additional 229 specimens (Table 2-2) from Europe, Japan and Russia were borrowed to make the morphological and phylogenetic comparison. These rust specimens were labeled either the same species

name of *Melampsora* or the same host plant species as reported in China.

Specimens were borrowed from following herbaria: Mycological Herbarium of Institute of Microbiology, CAS, China (**HMAS**), Inner Mongolia Agricultural University, China (**HNMAP**); Mycological Herbarium of College of Forestry, Northwest A & F University, China (**HMNWFC**); Systematic Mycology and Microbiology Laboratory, Agricultural Research Service, USDA, USA (**BPI**); Mycological Herbarium of the Graduate School of Life and Environmental Sciences, University of Tsukuba, Tsukuba, Japan (**TSH**); Hiratsuka Herbarium, Tokyo, Japan (**HH**); National Museum of Nature and Science, Tsukuba, Japan (**TNS**). In addition, 9 specimens from England were kindly supplied by Dr. Ming-Hao Pei (Rothamsted Research, Harpenden, Hertfordshire, UK).

Among these 435 dried herbarium specimens used for morphological observation, type specimens of the following species were included: *M. kamikotica* (HH-73060, holotype); *M. laricis-urbaniana* (HH-78307, neotype; HH-53302, isoneotype); *M. epiphylla* (HH-77578, isotype); *M. yezoensis* (HH-99463, neotype); *M. microsora* (HH-53150, isotype); *M. kiusiana* (HH-53157, holotype); *M. humilis* (HH-53278, isotype), *M. salicis-viminalis* (HMAS38658, holotype), *M. salicis-cavaleriei* (HMAS3607, holotype) and *M. tsinlingensis* (HMAS76119, holotype).

The ontogenic terminology of spore states and morphology in the uredinial and telial stages of rust fungi were followed by Cummins and Hiratsuka (2003).

2-1-2 Morphological observation

Morphological characteristics in the uredinial and telial stages were observed under SM, OM and SEM. For SM observation, the position of uredinia and telia was

examined and the size of sori was measured. For OM observation, the urediniospores, the hand sections of uredinia and telia of specimens were mounted in a drop of lactophenol solution on a microscopic slide. Morphology of uredinia, urediniospores, paraphyses, telia and teliospores were observed under OM. The length, the width and the wall thickness of urediniospores, the length, the width and the apex thickness of paraphyses, the length, the width and the apex thickness of teliospores were measured with a Q-Win Image analyzer (Leica, Tokyo, Japan). Fifty urediniospores and teliospores from each specimen were randomly measured.

In order to observe the position and the number of the germ pores in urediniospores, the method of Liang (2006) was used. The urediniospores on glass slides were stained with cotton blue in lactophenol and heated to the smoking point, and then a coverslip was placed while it was still warm. The coverslip was pressed hard onto the slide until the spore contents were expelled, and the spore walls were in one plane of focus. The distribution pattern of germ pores was categorized according to Cummins and Hiratsuka (2003).

In order to determine the shape of urediniospores, a numerical data, shape factor was used. This character is a dimensionless quantity used in image analysis and microscopy that numerically describe the shape of urediniospore independent of its size. It often represents the degree of deviation from an ideal shape, such as a circle, sphere or equilateral polyhedron. Shape factors are often normalized the value ranges from zero to one. A shape factor equal to one usually represents an ideal case or the maximum symmetry. Fifty urediniospores from each specimen were randomly selected, and the shape factor was measured by Sigma Scan Pro ver. 5.0 for Windows (SPSS Science, Chicago, IL).

The ultrastucutre of uredinia, the surface ornamentation of urediniospores and paraphyses was observed by SEM. Digital images were captured, and the distance

between spines was measured using the no-cost image analysis software Photoruler ver. 1.1. Samples were dusted on a double adhesive tape on a specimen holder and coated with platinum-palladium at 25 nm thick by a Hitachi E1030 Ion Sputter. The coated specimens were observed with an S-4200 scanning electron microscope (Hitachi, Tokyo, Japan) operated at 15 kV.

2-1-3 Character selection and cluster analysis

Totally 23 morphological characteristics in the uredinial and telial stages were observed (Table 2-3). These morphological characteristics were classified into two different types, qualitative character and quantitative character. In order to recognize morphological groups among specimens, cluster analysis was conducted with the software package SPSS ver. 20.0 for Windows (SPSS, Chicago, IL). Two hundred and thirty-one specimens, which had both uredinial and telial stages, were selected for cluster analysis. The status of qualitative characters was coded into different numbers (Table 2-4), and the data matrix was constructed together with the mean value of quantitative characters. In order to reduce the effect of different scales of measurement for different quantitative characters, the quantitative variables were transformed to standardized values and each value for the item being standardized was divided by the range of the values. Hierarchical clustering analysis was employed utilizing the Ward's method for each parameter. In the resulting dendrogram, similarity levels (Sneath and Sokal 1994) for a cluster with zero distance and for a final cluster with the maximum distance were defined as 100% and 0%, respectively. Specimens were separated into groups, and a dendrogram was established to recognize the possible groups of *Melampsora* species on willows based on similarity

of tested morphological data. According to the dendrogram, one-way analysis of variance (one-way ANOVA) was conducted in each recognized cluster to detect statistically significance of morphological characteristics at the different similarity level. Morphological groups were recognized based upon the results of cluster analysis. Diagnostic characters for each morphological group were determined based on the divisive method of cluster analysis.

2-2 Results

2-2-1 Qualitative characters in uredinial and telial stages

Qualitative characters in the uredinial and telial stages were recognized based on morphological observation of 435 specimens using SM, OM and SEM. In the uredinial stage, morphological observation under SM indicated that the positions of uredinia were recognized as amphigenous, epiphyllous and hypophyllous. Specimens were divided into two different types based on the existence of smooth regions in urediniospores. Some specimens had urediniospores with the smooth region at the apex, but the other specimens had urediniospores without the smooth region at the apex (Fig. 2-1). Based on observation by SEM, morphology of spines on urediniospores of the examined specimens was separated into three different forms: echinulate type 1, echinulate type 2, and echinulate type 3 (Fig. 2-2). Echinulate type 1 was characterized by even distribution of stout, sharp-pointed conical spines. The spine form of the majority of the specimens fell within this category. Echinulate type 2 was characterized by gradually decreased spines toward the smooth region on the urediniospores. Echinulate type 3 was characterized by conical, straight or blunt spines on the surface of urediniospores.

Based on ultrastructural observation of the uredinia, the position of paraphyses in uredinia was divided into two types: intermixed and peripheral paraphyses in uredinia and only peripheral paraphyses in uredinia (Fig. 2-3 IV-1 and IV-2). Paraphyses fell into two groups based on the apical wall thickness. One group had evenly thickened paraphyses at side and apex, and another group had paraphyses with apparently thickened at apex (Fig. 2-3 V-1 and V-2). Morphological observations of the surface of paraphyses by SEM revealed that all examined specimens had the smooth surface in paraphyses, and no difference was recognized among specimens.

The germ pores on the urediniospores were examined and two types of positions were recognized among specimens. Some urediniospores had scattered germ pores and the other specimens owned germ pore tending to biozonate (Fig. 2-4).

Morphological observation of the telia under SM indicated that the positions of telia were amphigenous, epiphyllous and hypophyllous. The positions of teliospores of all examined specimens were categorized as subepidermal, subcuticular or both subepidermal and subcuticular (Fig. 2-5).

2-2-2 Quantitative characters in uredinial and telial stages

Among these quantitative characters, the shape factor, which was used as a quantitative variable to describe the shape of urediniospores, was discrete (Fig 2-6 A). In addition, the apex thickness of urediniospores, was also discrete (Fig. 2-6 B). However, the other quantitative characters, including the length, the width and the wall thickness of urediniospores, the length, the width and the apex thickness of paraphyses, the length, the width and the apex thickness of teliospores and the mean distance between spines were continuous among specimens, and no apparent

distinction was recognized (Appendix 1). The uredinia and telia usually scattered or aggregated on leaves and the size of uredinia and telia ranged from 0.2 mm to 1.2 mm in each specimen. No apparent variation was recognized among specimens.

2-2-3 Cluster analysis

Based on morphological observation, totally 231 specimens with both uredinial and telial stages were selected for cluster analysis. The detailed morphological information of these specimens was listed in the Appendix 1. Morphological characteristics, such as the size of uredinia, the number of germ pores, the size of telia and the surface structures of paraphyses were excluded for cluster analysis because no apparent variation was recognized within the specimen and between specimens. Other 19 morphological characteristics were used for cluster analysis to detect possible morphological groups among specimens. Qualitative characters were transformed into numerical data, and they were used for hierarchical clustering analysis together with mean value of quantitative characters (Table 2-4). A dendrogram was produced by the Ward's method based on morphological data (Fig. 2-7). This figure showed that 231 specimens were separated into 23 groups, and these groups were designated as M1 to M23.

Based on the results of the dendrogram and morphological comparisons of each recognized cluster or groups at the different similarity levels using multivariate analyses, the key characters, which could be used to differentiate clusters or groups, were recognized. The dendrogram could be divided into two large clusters at the 10% similarity level (Fig. 2-7 A), and the shape factor of urediniospores was found to be a key character to separate the two major clusters. Although this character was

quantitative character, histogram indicated that this character was disjunctive (Fig. 2-6 A). The upper cluster included specimens in having mainly globoid or ellipsoid urediniospores with mean shape factor ranged from 0.86 to 0.89. The lower cluster included specimens having obovoid or broadly ellipsoid urediniospore with mean shape factor ranged from 0.81 to 0.85.

Three clusters were recognized at the 40% similarity level (Fig. 2-7 B), and groups from M1 to M13 were divided into two clusters based on the existence of intermixed paraphyses. Four clusters were distinguished at the 50% similarity level (Fig. 2-7 C), and the position of teliospores was the key character to separate groups from M1 to M11 into two clusters. Five clusters were recognized at the 60% similarity level (Fig. 2-7 D), and the position of teliospores was a key character to separate groups from M14 and M23 into two clusters.

Six clusters were recognized at the 70% similarity level (Fig. 2-7 E), and the position of germ pores was the diagnostic character to separate groups from M16 to M23 into two clusters. At the 76% similarity level (Fig. 2-7 F), eight clusters were recognized. The position of teliospores was the key characters to separate groups from M7 to M11 into two clusters, and the existence of intermixed paraphyses was diagnostic character to separate groups from M21 to M23 into two clusters.

Eleven clusters were distinguished at the 88% similarity level (Fig. 2-7 G). The position of telia was the key character to separate groups from M1 to M6 into two clusters. Based on the position of telia and spine forms of urediniospores, groups from M16 to M20 were separated into three clusters at the same similarity level.

Totally 15 clusters were recognized at the 92% similarity level (Fig. 2-7 H). The position of telia was the key character to separate group M7 from M8, and group M7 was separated from M10 and M11 based on the same character. At the same similarity level, groups M18, M19 and M20 were separated into two clusters based on the apex

thickness of urediniospores. Moreover, based on the position of telia, the position of teliospores and the spine form of urediniospores, group M22 was separated from M23.

Totally 23 groups were recognized at the 98% similarity level (Fig. 2-7I). The position of uredinia and the length of teliospores were key characters to divide M1, M2 and M3 into separate groups. M1 differed from M2 in the length of teliospores (Fig. 2-8 A), and they were differed from M3 in hypophyllous uredinia. At the same similarity level, the position of uredinia and the length of urediniospores were key characters to divide M4, M5 and M6 into different groups. M4 and M5 were separated from M6 in the position of uredinia, and two groups were further separated based on the length of urediniospores (Fig. 2-8 B). At the same similarity level, M10 was separated from M11 based on the length of urediniospores (Fig. 2-8 C), and M12 was also separated from M13 based on the length of urediniospores (Fig. 2-8 D). The position of uredinia, the length of urediniospores and teliospores were the key characters to separate M14 and M15. Based on the smooth regions of urediniospores, M19 and M20 were divided into separate groups.

Based on a hierarchical clustering analysis, totally 23 morphological groups were recognized, and morphological differences of these recognized groups were summarized in Table 2-5. Based on the divisive method in cluster analysis, the diagnostic characters for differentiation of each group and cluster were also determined, and these key characters were indicated on the node of the dendrogram in the Fig. 2-7.

2-3 Discussion

Numerical taxonomy has been proposed to implement quantitative assessment of trait variation used in species delimitation, but few researchers use numerical methods in fungal systematics because of the fear of the mathematical problems linked with the presence of mixed-type (continuous and categorical) data originating from their investigations (Dabinett and Wellman 1978; Nogrady 1998). However, numerical taxonomy can be more objective, because several characters are selected equally and used to evaluate the similarity of organisms by mathematical methods. Thus, it could avoid the limitation of the information on subjective factors during identification (Sneath 1995; Sieber et al. 1998). Cluster analysis is multivariate procedures routinely used in numerical taxonomy to detect groups based on the outcome which relies on the correct similarity/dissimilarity coefficients (Nogrady 1998). In order to conduct the taxonomic study of *Melampsora* species on willows in China, cluster analysis was implemented to detect possible groups in *Melampsora* species on willows based on qualitative and quantitative characters. Based on morphological observation and cluster analysis, 23 groups (M1 to M23) were recognized. It is the first time that the numerical method was used for the taxonomic study of *Melampsora* species on willows.

Based on the calculation of the frequency in the positive characters occurring in each group, cluster analysis is effective to determine one or several diagnostic characters, which should be selected as the main characters for species identification and taxonomy (Kampfer et al. 1991; Wieclaw and Koopman 2013). In this study, based on the morphological comparison and the dendrogram obtained from cluster analysis, 12 morphological characteristics in the uredinial and telial stages were recognized as significant diagnostic characters (Fig. 2-7). The shape factor of urediniospores, the existence of smooth regions in urediniospores, the existence of intermixed paraphyses, the length of urediniospres, the width of urediniospore, the

spine form of urediniospores, the apex thickness of urediniospores, the position of germ pore, the position of uredinia, the position of telia, the position of teliospores and the length of teliospores, appeared to be the more significant characters than other qualitative and quantitative traits in this study.

Among these effective morphological characteristics, the existence of smooth regions in urediniospores, the existence of intermixed paraphyses, the length of urediniospres, the width of urediniospore, the spine form of urediniospores, the apex thickness of urediniospores, the position of germ pore, the position of uredinia, the position of telia, the position of teliospores and the length of teliospores have been used in previous taxonomic studies (Ito 1938; Kuprevich and Tranzshel 1957; Wilson and Henderson 1966; Kaneko and Hiratsuka 1984; Cao 1999; Bagayananana 2005; Liu 2005). Additional morphological characteristics, such as the shape factor of urediniospores, the existence of intermixed paraphyses and the spine form of urediniospores, were new effective criteria to distinguish morphological groups of *Melampsora* on willows.

The spine morphology of urediniospores was previously used for species recognition in the taxonomic studies of *Gymnosporangium*, *Pucciniastrum*, *Phragmidium* on the genus *Rosa*, *Puccinia* on sugarcane and so on. The spine morphology was proved to be stable and was able to be used for differentiating species (Lee and Kakishima 1999; Wahyuno et al. 2001; Virtudazo et al. 2001; Liang 2006). Recent molecular phylogenetic studies of *Pucciniastrum* species also indicated that the spine form of urediniospores reflected the phylogeny and it was an important morphological characteristics to distinguish species (Liang 2006). Due to lack of SEM in the early taxonomic studies in genus *Melampsora*, little attention was paid on spine morphology. Although ultrastructure of spine morphology in urediniospores was investigated in the genus *Melampsora* in recent years (Smith et al. 2004; Spiers and

Hopcroft 1996; Tian et al. 2004), there was no report of spine morphology for species recognition. In this study, spine morphology was found to be a stable and promising character to differentiate *Melampsora* species on willows.

The shape of urediniospores was frequently used for species recognition and several different types, such as globoid, ellipsoid, ovoid and obovoid to broadly ellipsoid, were described in various taxonomic systems (Kuprevich and Tranzshel 1957; Hiratsuka and Kaneko 1982; Bagayananana 2005). However, it was difficult to recognize these different types because the terminology and definitions to describe the shape were not precise. In this study, the shape factor was used as a numerical quantity to determine the shape of urediniospores precisely. This quantitative character was proved as an effective character to determine the shape of urediniospores and to detect groups (Fig. 2-7). Although this character was suggested as an important character based on the results of molecular phylogenetic studies of *M. epitea* in North America (Smith et al. 2004), this character was first proved to be an important taxonomic criterion for species recognition in this study.

The uredinia of *Melampsora* were recognized as *Uredo*-type with intermixed paraphyses based on Cummins and Hiratsuka (2003). However, through the morphological observation, two different types of paraphyses were found based on the position of paraphyses in uredinia. One type was uredinia with both intermixed and peripheral paraphyses, and the other type was uredinia with peripheral paraphyses (Fig. 2-3 A and B). The first type is frequently reported in genus *Melampsora*. The other type is similar to *Calidion*-type, and this type has never been reported in genus *Melampsora*. The position of paraphyses in uredinia was proved to be a new and stable character for species recognition of *Melampsora* species on willows.

Based on cluster analysis of 19 morphological characteristics, 23 groups were recognized among 231 specimens. Moreover, 12 morphological characteristics in the

uredinial and telial stages, including 7 qualitative characters and 5 quantitative characters, were recognized as the diagnostic characters to differentiate these morphological groups according to the divisive method of cluster analysis and one-way ANOVA.

Table 2-1 Specimens of willow *Melampsora* rust from China used in this study.

***Melampsora* species (according to label)**	**Herbarium accession number**	**Spore stage[a]**	**Host species**	**Geographic locality**
Melampsora amygdalinae	HMAS42407	II, III	*Salix paraplesia*	Inner Mongolia
M. amygdalinae	HMAS67397	II	*S. subfragilis*	Ningxia
M. amygdalinae	HMAS89609	II	*S.trianadra*	Jilin
M. amygdalinae	NHNWFC-111	II	*Salix* sp.	Shaanxi
M. arctica	HMNWFC-TB96025	II	*S. hylonoma*	Shaanxi
M. arctica	HMNWFC-TB86003	II	*S. spathulifolia*	Shaanxi
M. arctica	HMAS42842	II, III	*Salix* sp.	Inner Mongolia
M. capraearum	HMAS52899	II, III	*S. alatavica*	Xinjiang
M. capraearum	HMAS67392	II	*S. alfredi*	Hebei
M. capraearum	HMAS52894	II, III	*S. argyracea*	Xinjiang
M. capraearum	HMAS67393	II, III	*S. caprea*	Hebei,
M. capraearum	HMAS58563	II	*S. caprea*	Xinjiang
M. capraearum	HMAS82380	II	*S. caprea*	Inner Mongolia
M. capraearum	HKAS 29594	II	*S. cathayana*	Yunnan
M. capraearum	HNMAP1330	II	*S. cheilophila*	Inner Mongolia
M. capraearum	HMAS48435	II, III	*S. dissa*	Sichuan
M. capraearum	HMNWFC-LC86080	II	*S. ernesti*	Shaanxi
M. capraearum	HMNWFC-F96010	II	*S. ernesti*	Shaanxi
M. capraearum	HNMAP3065	II, III	*S. hsinganica*	Inner Mongolia
M. capraearum	HMAS67394	II	*S. matsudana*	Hebei
M. capraearum	HMAS37814	II	*S. paraplesia*	Xinjiang
M. capraearum	HMNWFC-TB95002	II	*S. purpurea*	Shaanxi
M. capraearum	HNMAP1710	II, III	*S. sinica*	Inner Mongolia
M. capraearum	HNMAP1716	II, III	*S. sinica*	Inner Mongolia
M. capraearum	HNMAP1697	II, III	*S. sinica*	Inner Mongolia
M. capraearum	HNMAP3176	II, III	*S. starkeana*	Inner Mongolia
M. capraearum	HNMAP3167	II, III	*S. starkeana*	Inner Mongolia
M. capraearum	HNMAP1690	II, III	*S. wallichiana*	Inner Mongolia
M. capraearum	HNMAP1578	II	*S. wallichiana*	Inner Mongolia
M. capraearum	HNMAP3151	II	*S. xerophila*	Inner Mongolia
M. capraearum	HMAS652326	II	*Salix* sp.	Xinjiang
M. capraearum	HMAS132526	II	*Salix* sp.	Hebei
M. capraearum	HMAS56197	II	*Salix* sp.	Qinhai
M. coleosporioides	HMAS17721	II, III	*S. bobylonica*	Hebei
M. coleosporioides	HMAS56586	II	*S. bobylonica*	Hebei

Table 2-1 Continued.

M. coleosporioides	HMAS56986	II	*S. bobylonica*	Hebei
M. coleosporioides	HMAS8619	II, III	*S. bobylonica*	Beijing
M. coleosporioides	HMNWFC-L91054	II, III	*S. bobylonica*	Shanxi
M. coleosporioides	HMAS36728	II	*S. bobylonica*	Jiangsu
M. coleosporioides	HMNWFC-HD90015	II	*S. bobylonica*	Shaanxi
M. coleosporioides	HMNWFC-F96001	II	*S. bobylonica*	Shaanxi
M. coleosporioides	HMAS56160	II	*S. bobylonica*	Fujian
M. coleosporioides	HMAS52904	II	*S. bobylonica*	Xinjiang
M. coleosporioides	HNMAP3114	II, III	*S. bobylonica*	Inner Mongolia
M. coleosporioides	HNMWFC-HM13	II, III	*S. chaenomeloides*	Shaanxi
M. coleosporioides	HMAS35105	II	*S. cheilophila*	Henan
M. coleosporioides	HMAS25375	II	*S. gilgiana*	Shanxi, Hebei
M. coleosporioides	HMAS25374	II	*S. glandulosa*	Hebei
M. coleosporioides	HMAS530101	II	*S. heteromera*	Yunnan
M. coleosporioides	HMAS8629	II, III	*S. matsudana*	Hebei
M. coleosporioides	HNMAP3090	II, III	*S. matsudana*	Inner Mongolia
M. coleosporioides	HNMAP3135	II, III	*S. matsudana*	Inner Mongolia
M. coleosporioides	HMAS610331	II	*S. wilsonii*	Shaanxi
M. coleosporioides	HMAS25375	II	*S. wilsonii*	Shaanxi
M. coleosporioides	HMAS211224	II	*Salix* sp.	Liaoning
M. coleosporioides	HMAS24439	II	*Salix* sp.	Shaanxi
M. coleosporioides	HMAS41592	II	*Salix* sp.	Fujian
M. coleosporioides	HMAS24440	II	*Salix* sp.	Gansu
M. coleosporioides	BPI1109521	II	*Salix* sp.	Gansu
M. epiphylla	HMNWFC-TB95013	II	*S.cheilophila*	Shaanxi
M. epiphylla	HMNWFC-LC86025	II	*S. heterochroma*	Shaanxi
M. epiphylla	HMNWFC-HD95040	II	*S. hylonoma*	Shaanxi
M. epiphylla	HNMAP2158	II	*S. microstachya*	Inner Mongolia
M. epiphylla	HMNWFC1121	II	*S. rehderiana*	Shaanxi
M. epiphylla	HMAS82376	II, III	*S. rosmarinifolia*	Inner Mongolia
M. epiphylla	HMAS82377	II	*S. rosmarinifolia*	Inner Mongolia
M. epiphylla	HMAS82378	II	*S. rosmarinifolia*	Inner Mongolia
M. epiphylla	HMAS82379	II, III	*S. rosmarinifolia*	Inner Mongolia
M. epiphylla	HMAS82381	II	*S. rosmarinifolia*	Inner Mongolia
M. epiphylla	HMAS82382	II	*S. rosmarinifolia*	Inner Mongolia
M. epiphylla	HMAS82406	II	*S. rosmarinifolia*	Inner Mongolia
M. epiphylla	HMNWFC-T93002	II	*S. sinica*	Shaanxi
M. epiphylla	MNWFC-BX88010	II	*S. sinica*	Shaanxi

Table 2-1 Continued.

M. epiphylla	HMAS82399	II	*S. wallichiana*	Inner Mongolia
M. epiphylla	BPI 1109484	II, III	*Salix* sp.	Hei Long Jiang
M. epitea	HMAS52905	II, III	*S. alba*	Xinjiang
M. epitea	HMAS55038	II, III	*S. alba*	Xinjiang
M. epitea	HMAS55037	II, III	*S. argyracea*	Xinjiang
M. epitea	BPI803204	II	*S. cathayana*	Sichuan
M. epitea	HKAS29399	II	*S. cathayana*	Yunnan
M. epitea	HNMAP3175	II	*S. characta*	Inner Monglia
M. epitea	HKAS29605	II	*S.chienii*	Yunnan
M. epitea	HMAS67400	II, III	*S. daltoniana*	Tibet
M. epitea	HMAS67421	II	*S. delavayana*	Tibet
M. epitea	HMAS64717	II, III	*S. gyirongensis*	Tibet
M. epitea	HMNWFC-HD83016	II	*S. hypoleuca*	Shaanxi
M. epitea	HMNWFC-HD95020	II	*S. hypoleuca*	Gansu
M. epitea	BPI745989	II	*S. insgnis*	Tibet
M. epitea	HMAS67419	II	*S. insgnis*	Tibet
M. epitea	BPI22942	II	*S. mongolica*	Inner Mongolia
M. epitea	BPI23006	II	*S. mongolica*	Inner Mongolia
M. epitea	HMAS136753	II	*S. paraplesia*	Gansu
M. epitea	HNMAP3136	II	*S. psammophila*	Inner Monglia
M. epitea	HMAS67407	II	*S. psilostigma*	Tibet
M. epitea	HMAS67408	II	*S. psilostigma*	Tibet
M. epitea	HMAS67409	II	*S. psilostigma*	Tibet
M. epitea	BPI23006	II	*S. purpurea*	Inner Mongolia
M. epitea	HMAS62584	II, III	*S. purpurea*	Shandong
M. epitea	HMAS64402	II	*S. radinostachya*	Xizang
M. epitea	HMAS67402	II	*S. sericocarpa*	Xizang
M. epitea	HMAS134712	II, III	*S. siuzevii*	Hei Long Jiang
M. epitea	HMAS82383	II	*S. siuzevii*	Inner Mongolia
M. epitea	HMAS135888	II	*S. taraikensis*	Hei Long Jiang
M. epitea	HMAS82387	II	*S. taraikensis*	Hei Long Jiang
M. epitea	HKAS29560	II	*S. tetrasperma*	Yunnan
M. epitea	HMAS82388	II, III	*S.trianadra*	Hei Long Jiang
M. epitea	HMAS67410	II	*S. wallichiana*	Gansu
M. epitea	HMAS82384	II, III	*S. xerophila*	Hei Long Jiang
M. epitea	HMAS82386	II	*S. xerophila*	Hei Long Jiang
M. epitea	HMAS67403	II	*S. zayulica*	Xizang
M. epitea	HMAS67404	II	*Salix* sp.	Xizang

Table 2-1 Continued.

M. epitea	HMAS67405	II	*Salix* sp.	Xizang
M. epitea	HMAS5208	II	*Salix* sp.	Xinjiang
M. euonymi-capraearum	HNMAP3149	II, III	*S. linearistipularis*	Inner Mongolia
M. euonymi-capraearum	HNMAP3140	II, III	*S. myrtilloides*	Inner Mongolia
M. farinosa	BPI30590	II	*S. babylonica*	Anhui
M.kamikotica	HNMAP3186	II, III	*Choseniaarbutifolia*	Inner Mongolia
M. kupreviczii	HNMAP3061	II, III	*S. rosmarnifolia*var. *brachypoda*	Inner Mongolia
M. kupreviczii	HNMAP3193	II, III	*S. rosmarnifolia*var. *brachypoda*	Inner Mongolia
M. kupreviczii	HNMAP3190	II, III	*S. rosmarnifolia*var. *brachypoda*	Inner Mongolia
M. lapponum	HNMAP1972	II, III	*S. starkeana*	Inner Mongolia
M. laricis-caprearum	HMAS46883	II	*S. annulifera*	Tibet
M. laricis-caprearum	HMAS46884	II	*S. annulifera*	Tibet
M. laricis-caprearum	HMAS987	II	*S. caprea*	Shaanxi
M. laricis-caprearum	HMAS25387	II	*S. caprea*	Henan
M. laricis-caprearum	HMAS42844	II	*S. caprea*	Jilin
M. laricis-caprearum	HKAS5579	II	*S.matsudana*	Xizang
M. laricis-caprearum	HKAS12368	II	*Salix* sp.	Sichuan
M. laricis-caprearum	HMAS92640	II	*Salix* sp.	Xinjiang
M. laricis-epitea	HMAS52918	II	*S. capsuii*	Xinjiang
M. laricis-epitea	HMAS55747	II	*S. hypoleuca*	Ningxia
M. laricis-epitea	HMAS52919	II	*S. iliensis*	Xinjiang
M. laricis-epitea	HMAS55161	II	*S. koreensis*	Jilin
M. laricis-epitea	HMAS356	II, III	*S. longiflora*	Yunnan
M. laricis-epitea	HMAS55179	II, III	*S. matsudana*	Guizhou
M. laricis-epitea	HMNWFC-668	II	*S. matsudana*	Shanxi
M. laricis-epitea	BPI 1109442	II, III	*S. raddeana*	Jilin
M. laricis-epitea	BPI 1103840	II, III	*S. tetrasperma*	Sichuan
M. laricis-epitea	BPI1109484	II, III	*S. viminalis*	Hei Long Jiang
M. laricis-epitea	BPI23207	II, III	*Salix* sp.	Hei Long Jiang
M. laricis-epitea	BPI023209	II, III	*Salix* sp.	Anhui
M. laricis-epitea	BPI023210	II, III	*Salix* sp.	Anhui
M. laricis-epitea	BPI023212	II, III	*Salix* sp.	Anhui
M. laricis-epitea	TSH-R9843	II, III	*Salix* sp.	Taiwan
M. laricis-epitea	HMAS55179	II, III	*Salix* sp.	Guizhou
M. laricis-epitea	BPI023208	II, III	*Salix* sp.	Guizhou
M. laricis-epitea	BPI023211	II	*Salix* sp.	Guizhou
M. laricis-pentandra	HNMAP3059	II, III	*S. pentandra*	Inner Mongolia

Table 2-1 Continued.

M. laricis-pentandra	HNMAP 3163	II, III	*S. pentandra*	Inner Mongolia
M. laricis-pentandra	HNMAP3171	II, III	*S. pentandra*	Inner Mongolia
M. laricis-pentandrae	HMAS58575	II, III	*S. alba*	Xinjiang
M. repentis	HNMAP3168	II, III	*S. rorida*	Inner Mongolia
M. repentis	HNMAP3060	II, III	*S. rorida*	Inner Mongolia
M. repentis	HNMAP1594	II, III	*S. siuzevii*	Inner Mongolia
M. repentis	HNMAP1959	II, III	*S. siuzevii*	Inner Mongolia
M. repentis	HNMAP3181	II, III	*S. trianadra*	Inner Mongolia
M. repentis	HNMAP3184	II	*Salix* sp.	Inner Mongolia
M. ribesii-viminalis	HMAS82389	II, III	*S. viminalis* var. *gmelini*	Hei Long Jiang
M. ribesii-viminalis	HNMAP1698	II, III	*Salix* sp.	Inner Mongolia
M. ribesii-purpureae	HMAS37818	II, III	*S. magnifica*	Xinjiang
M. ribesii-purpureae	HMAS965	II	*S.matsudana*	Shaanxi
M. ribesii-purpureae	HMAS8629	II, III	*S. purpurea*	Hebei
M. ribesii-purpureae	BPI23006	II	*S. purpurea*	Hei Long Jiang
M. ribesii-purpureae	HNMAP1587	II, III	*S. raddeana*	Inner Mongolia
M. ribesii-viminalis	HMAS58573	II, III	*S. iliensis*	Xinjiang
M. ribesii-viminalis	HNMAP3208	II, III	*S. viminalis*	Inner Mongolia
M. ribesii-viminalis	HNMAP1967	II, III	*S. viminalis*	Inner Mongolia
M. ribesii-viminalis	HNMAP3058	II, III	*S. viminalis*	Inner Mongolia
M. salicis-albae	HMAS52924	II, III	*S. alba*	Xinjiang
M. salicis-albae	HMAS56267	II	*S. babylonica*	Sichuan
M. salicis-albae	HNMAP3138	II, III	*S. matsudana*	Inner Mongolia
M. salicis-albae	HNMAP3094	II, III	*S. matsudana*	Inner Mongolia
M. salicis-albae	HNMAP3137	II	*S. matsudana*	Inner Mongolia
M. salicis-albae	HNMAP3183	II	*S. matsudana*	Inner Mongolia
M. salicis-albae	HNMAP3173	II	*S. matsudana*	Inner Mongolia
M. salicis-albae	BPI1109650	II, III	*Salix* sp.	Guizhou
M. salicis-albae	BPI25363	II, III	*Salix* sp.	Hei Long Jiang
M. salicis-cupularis	HMNWFC-TB85040	II, III	*S. cupularis*	Shaanxi
M. salicis-cupularis	HNMAP3152	II, III	*S. cupularis*	Inner Mongolia
M. salicis-cupularis	HMAS76122	II, III	*S. cupularis*	Shaanxi
M. salicis-cupularis	HMAS24455	II	*S. wilsonii*	Shaanxi
M. salicis-cupularis	HMAS24457	II	*Salix* sp.	Qinhai
M. salicis-cupularis	BPI199071	II	*Salix* sp.	Qinhai
M. salicis-cupularis	HMAS24773	II	*Salix* sp.	Qinhai
M. salicis-viminalis	**HMAS38658(holotype)**	II, III	*S. viminalis*	Xizang
M. salicis-warburgii	HMNWFC-LG91054	II, III	*S. babylonica*	Shaanxi

Table 2-1 Continued.

M. salicis-warburgii	HH-53135	II, III	*S. warburgii*	Taiwan
M. salicis-warburgii	HH-53136	II	*S. warburgii*	Taiwan
M. salicis-warburgii	HH-53137	II	*S. warburgii*	Taiwan
M. salicis-warburgii	HH-53138	II	*S. warburgii*	Taiwan
M. salicis-warburgii	HH-53139	II	*S. warburgii*	Taiwan
M. salicis-warburgii	HMAS56075	II, III	*Salix* sp.	Fujian
M. tsinlingensis	HNMAP3257	II, III	*S. koreensis*	Inner Mongolia
M. tsinlingensis	HNMAP3185	II, III	*S. koreensis*	Inner Mongolia
M. tsinlingensis	HMNWFC-T95008	II	*S. paraplesia*	Shaanxi
M. yezoensis	HMAS71118	II, III	*S. cathayana*	Sichuan
M. yezoensis	HMAS41605	II, III	*S. dunnii*	Fujian
M. yezoensis	HMAS41606	II, III	*S. dunnii*	Fujian
M. yezoensis	HMAS71119	II, III	*S. glandulosa*	Shaanxi
M. yezoensis	HMNWFC-TB94003	II	*S.matsudana*	Shaanxi
M. yezoensis	HMAS41607	II	*S. tetrasperma*	Fujian
M.microsora	HMAS55414	II	*S. fargesii*	Hubei
M.microsora	HMAS55396	II, III	*S. fargesii*	Hubei
M.microsora	HMNWFC-TB82008	II	*S. sinica*	Shaanxi
M. salicis-cavaleriei	**HMAS3607(holotype)**	II, III	*S. cavaleriei*	Yunnan

a: II refers to uredinial stage; III refers to telial stage.

Table 2-2 Herbarium specimens of *Melampsora* specimens on willows from other countries used in this study.

***Melampsora* species (according to label)**	**Herbarium accession number**	**Spore stage[a]**	**Host species**	**Locality**	**County**
Melampsora arctica	HH-53261	II	*Salix subreniformis*	Middle Kuriles	Japan
M. arctica	HH-53262	II	*S. aquilonia*	Middle Kuriles	Japan
M. bigelowii	TNS-F-191264	II	*S. humboldtiane*	Jujuly	Argentia
M. capraearum	HH-52982	II	*S. bakko*	Hokkaido	Japan
M. capraearum	HH-77932	II	*S. bakko*	Hokkaido	Japan
M. capraearum	HH-53317	II	*S. bakko*	Hokkaido	Japan
M. capraearum	TSH-R10194	II, III	*S. bakko*	Aomori	Japan
M. capraearum	TSH-R3877	II	*S. bakko*	Shizuoka	Japan
M. capraearum	TSH-R9606	II	*S. bakko*	Niigata	Japan
M. capraearum	TSH-R9607	II, III	*S. bakko*	Niigata	Japan
M. capraearum	TSH-R13471	II	*S. bakko*	Yamagata	Japan
M. capraearum	TSH-R1598	II	*S. bakko*	Gunma	Japan
M. capraearum	TSH-R12127	II	*S. bakko*	Gunma	Japan
M. capraearum	TSH-R10222	II	*S. bakko*	Tochigi	Japan
M. capraearum	TSH-R10223	II	*S. bakko*	Tochigi	Japan
M. capraearum	TSH-R10727	II, III	*S. bakko*	Tochigi	Japan
M. capraearum	TSH-R13425	II, III	*S. bakko*	Akita	Japan
M. capraearum	TSH-R13426	II, III	*S. bakko*	Akita	Japan
M. capraearum	TSH-R10731	II	*S. bakko*	Ishikawa	Japan
M. capraearum	TSH-R12057	II, III	*S. bakko*	Yamanashi	Japan
M. capraearum	HH-52984	II	*S. bakko*	Yamanashi	Japan
M. capraearum	TSH-R2763	II	*S. bakko*	Nagano	Japan
M. capraearum	TSH-R3043	II	*S. bakko*	Nagano	Japan
M. capraearum	TSH-R7490	II, III	*S. bakko*	Nagano	Japan
M. capraearum	TSH-R7489	II, III	*S. bakko*	Nagano	Japan
M. capraearum	HH-77841	II	*S. bakko*	Gifu	Japan
M. capraearum	TSH-R1467	II	*S. bakko*	Toyama	Japan
M. capraearum	TSH-R15004	II	*S. bakko*	Ibaraki	Japan
M. capraearum	TSH-R17516	II	*S. bakko*	Kagawa	Japan
M. capraearum	TNS-F-107383	II, III	*S. caprea*	Valkeakoski	Finland
M. capraearum	TNS-F-1468	II, III	*S. caprea*	Turku	Finland
M. capraearum	BPI22628	II, III	*S. caprea*	Marayong	Australia
M. capraearum	TNS-F-222866	II, III	*S. caprea*	Thuringia	Germany

Table 2-2 Continued.

M. capraearum	NWC-0943	II, III	*S. caprea*	Rothamsted	England
M. capraearum	THS-R7693	II	*S. hutenii*	Hokkaido	Japan
M. capraearum	THS-R7696	II	*S. hutenii*	Hokkaido	Japan
M. capraearum	THS-R7699	II	*S. hutenii*	Hokkaido	Japan
M. capraearum	THS-R7702	II, III	*S. hutenii*	Hokkaido	Japan
M. capraearum	HH-78362	II	*S. leucopithecia*	Ibaraki	Japan
M. capraearum	TSH-R7614	II	*S. leucopithecia*	Miyagi	Japan
M. chelidonii-pierotii	TSH-R10771	II, III	*S. chaenomeloides*	Ibaraki	Japan
M. chelidonii-pierotii	TSH-R7339	II	*S. chaenomeloides*	Ibaraki	Japan
M. chelidonii-pierotii	TSH-R7463	II, III	*S. chaenomeloides*	Iwate	Japan
M. chelidonii-pierotii	TSH-R7518	II	*S. chaenomeloides*	Kagawa	Japan
M. chelidonii-pierotii	TSH-R7519	II	*S. chaenomeloides*	Tottori	Japan
M. chelidonii-pierotii	TSH-R7513	II	*S. chaenomeloides*	Hiroshima	Japan
M. chelidonii-pierotii	TSH-R7510	II, III	*S. pierotii*	Miyagi	Japan
M. chelidonii-pierotii	TSH-R7511	II	*S. pierotii*	Miyagi	Japan
M. chelidonii-pierotii	TSH-R7512	II, III	*S. pierotii*	Miyagi	Japan
M. chelidonii-pierotii	TSH-R7365	II, III	*S. pierotii*	Kagoshima	Japan
M. coleosporioides	TSH-R17881	II	*S. babylonica*	Tokyo	Japan
M. coleosporioides	TSH-R7538	II, III	*S. babylonica*	Miyagi	Japan
M. coleosporioides	TSH-R7501	II	*S. babylonica*	Miyagi	Japan
M. coleosporioides	TSH-R7465	II	*S. babylonica*	Ibaraki	Japan
M. coleosporioides	TSH-R9849	II, III	*S. babylonica*	Ibaraki	Japan
M. epiphylla	HH-53112	II	*S. kinuyanagi*	Iwate	Japan
M. epiphylla	HH-53113	II	*S. kinuyanagi*	Niigata	Japan
M. epiphylla	TSH-R7541	II, III	*S. kinuyanagi*	Miyagi	Japan
M. epiphylla	TSH-R7611	II	*S. kinuyanagi*	Miyagi	Japan
M. epiphylla	HH-53114	II	*S. kinuyanagi*	Ishikawa	Japan
M. epiphylla	HH-53098	II	*S. pet-susu*	Hokkaido	Japan
M. epiphylla	TSH-R7643	II	*S. pet-susu*	Hokkaido	Japan
M. epiphylla	TSH-R7649	II, III	*S. pet-susu*	Hokkaido	Japan
M. epiphylla	TSH-R7661	II, III	*S. pet-susu*	Hokkaido	Japan
M. epiphylla	TSH-R7660	II	*S. pet-susu*	Hokkaido	Japan
M. epiphylla	TSH-R7666	II	*S. pet-susu*	Hokkaido	Japan
M. epiphylla	TSH-R7691	II	*S. pet-susu*	Hokkaido	Japan
M. epiphylla	TSH-R7695	II	*S. pet-susu*	Hokkaido	Japan
M. epiphylla	TSH-R7684	II, III	*S. pet-susu*	Hokkaido	Japan
M. epiphylla	TSH-R12126	II	*S. pet-susu*	Gunma	Japan
M. epiphylla	HH-53064	II	*S. rorida*	Hokkaido	Japan

Table 2-2 Continued.

M. epiphylla	HH-53063	II	*S. rorida*	Hokkaido	Japan
M. epiphylla	TSH-R7641	II	*S. rorida*	Hokkaido	Japan
M. epiphylla	TSH-R7651	II, III	*S. rorida*	Hokkaido	Japan
M. epiphylla	TSH-R7654	II	*S. rorida*	Hokkaido	Japan
M. epiphylla	TSH-R7689	II, III	*S. rorida*	Hokkaido	Japan
M. epiphylla	TSH-R7660	II	*S. rorida*	Hokkaido	Japan
M. epiphylla	TSH-R7698	II	*S. rorida*	Hokkaido	Japan
M. epiphylla	TSH-R7560	II	*S. rorida*	Miyagi	Japan
M. epiphylla	HH-53044	II	*S. sachalinensis*	Hokkaido	Japan
M. epiphylla	HH-55840	II	*S. sachalinensis*	Hokkaido	Japan
M. epiphylla	HH-77931	II	*S. sachalinensis*	Tottori	Japan
M. epiphylla	TSH-R10210	II, III	*S. sachalinensis*	Aomori	Japan
M. epiphylla	HH-53031	II	*S. sachalinensis*	Aomori	Japan
M. epiphylla	HH-77954	II	*S. sachalinensis*	Aomori	Japan
M. epiphylla	TSH-R9837	II	*S. sachalinensis*	Nagano	Japan
M. epiphylla	TSH-R10234	II	*S. sachalinensis*	Tochigi	Japan
M. epiphylla	TSH-R9836	II	*S. sachalinensis*	Tochigi	Japan
M. epiphylla	**HH-77578 (isotype)**	II, III	*S. sachalinensis*	Gifu	Japan
M. epiphylla	HH-77391	II	*S. sachalinensis*	Tottori	Japan
M. epiphylla	HH-52997	II	*S. sachalinensis*	Tottori	Japan
M. epiphylla	TSH-R16766	II	*S. sachalinensis*	Yamanashi	Japan
M. epiphylla	TSH-R1537	II, III	*S. sachalinensis*	Toyoma	Japan
M. epiphylla	TSH-R12088	II, III	*S. sachalinensis*	Fukushima	Japan
M. epiphylla	TSH-R9608	II	*S. sachalinensis*	Niigata	Japan
M. epiphylla	TSH-R53034	II	*S. sachalinensis*	Shimane	Japan
M. epiphylla	TSH-R10207	II, III	*S. sachalinensis*	Akita	Japan
M. epiphylla	TSH-R12280	II	*S. sachalinensis*	Yamagata	Japan
M. epiphylla	TSH-R18333	II	*S. sachalinensis*	Yamagata	Japan
M. epiphylla	TSH-R3884	II, III	*S. sachalinensis*	Shizuoka	Japan
M. epiphylla	TSH-R10186	II, III	*S. sachalinensis*	Shizuoka	Japan
M. epitea	NWC-KNW-1	II, III	*S. burjatica*	Rothamsted	England
M. epitea	NWC-06419	II, III	*S. daphnoides*	Rothamsted	England
M. epitea	HH-53350	II	*S. futura*	Aomori	Japan
M. epitea	TSH-R9618	II, III	*S. futura*	Niigata	Japan
M. epitea	TSH-R9619	II, III	*S. futura*	Niigata	Japan
M. epitea	TSH-R9620	II, III	*S. futura*	Niigata	Japan
M. epitea	TSH-R9621	II	*S. futura*	Niigata	Japan
M. epitea	TSH-R9622	II	*S. futura*	Niigata	Japan

Table 2-2 Continued.

M. epitea	TSH-R9623	II, III	*S. futura*	Niigata	Japan
M. epitea	TSH-R10730	II	*S. futura*	Ishikawa	Japan
M. epitea	TSH-R7492	II, III	*S. gilgiana*	Nagano	Japan
M. epitea	TSH-R7494	II, III	*S. gilgiana*	Nagano	Japan
M. epitea	TSH-R7468	II	*S. gilgiana*	Nagano	Japan
M. epitea	TSH-R7475	II	*S. gilgiana*	Nagano	Japan
M. epitea	TSH-R7540	II, III	*S. gilgiana*	Miyagi	Japan
M. epitea	TSH-R7572	II	*S. gilgiana*	Miyagi	Japan
M. epitea	TSH-R7599	II, III	*S. gilgiana*	Miyagi	Japan
M. epitea	TSH-R7666	II, III	*S. gracilistyla*	Hokkaido	Japan
M. epitea	TSH-R7692	II, III	*S. gracilistyla*	Hokkaido	Japan
M. epitea	TSH-R7700	II, III	*S. gracilistyla*	Hokkaido	Japan
M. epitea	HH-78365	II	*S. gracilistyla*	Tottori	Japan
M. epitea	TSH-R7473	II	*S. gracilistyla*	Nagano	Japan
M. epitea	TSH-R7505	II	*S. gracilistyla*	Miyagi	Japan
M. epitea	TSH-R12217	II	*S. gracilistyla*	Miyazaki	Japan
M. epitea	TSH-R9611	II	*S. gracilistyla*	Niigata	Japan
M. epitea	HH-77885	II	*S. japonica*	Chiba	Japan
M. epitea	TSH-R7482	II, III	*S. japonica*	Chiba	Japan
M. epitea	HH-78273	II	*S. japonica*	Kanagawa	Japan
M. epitea	TSH-R3885	II, III	*S. japonica*	Shizuoka	Japan
M. epitea	TSH-R3886	II	*S. japonica*	Shizuoka	Japan
M. epitea	TSH-R3887	II	*S. japonica*	Shizuoka	Japan
M. epitea	TSH-R3889	II, III	*S. japonica*	Shizuoka	Japan
M. epitea	TSH-R1540	II	*S. japonica*	Fukushima	Japan
M. epitea	HH-53078	II	*S. miyabeana*	Hokkaido	Japan
M. epitea	HH-53060	II	*S. miyabeana*	Hokkaido	Japan
M. epitea	HH-78311	II	*S. miyabeana*	Hokkaido	Japan
M. epitea	HH-53077	II	*S. miyabeana*	Hokkaido	Japan
M. epitea	TSH-R7638	II	*S. miyabeana*	Hokkaido	Japan
M. epitea	TSH-R7653	II, III	*S. miyabeana*	Hokkaido	Japan
M. epitea	TSH-R7655	II, III	*S. miyabeana*	Hokkaido	Japan
M. epitea	TSH-R7659	II, III	*S. miyabeana*	Hokkaido	Japan
M. epitea	TSH-R7688	II, III	*S. miyabeana*	Hokkaido	Japan
M. epitea	TSH-R7694	II	*S. miyabeana*	Hokkaido	Japan
M. epitea	TSH-R7652	II	*S. miyabeana*	Hokkaido	Japan
M. epitea	TSH-R7680	II, III	*S. miyabeana*	Hokkaido	Japan
M. epitea	TSH-R7681	II, III	*S. miyabeana*	Hokkaido	Japan

Table 2-2 Continued.

M. epitea	BPI22984	II, III	*S. nigricans*	Petrozavodsk	Russia
M. epitea	TSH-R1489	II, III	*S. reinii*	Fukushima	Japan
M. epitea	TSH-R10228	II	*S. reinii*	Tochigi	Japan
M. epitea	TSH-R10306	II, III	*S. reinii*	Tochigi	Japan
M. epitea	TSH-R7487	II, III	*S. reinii*	Nagano	Japan
M. epitea	TSH-R18314	II	*S. reinii*	Yamagata	Japan
M. epitea	TSH-R12023	II, III	*S. reinii*	Yamanashi	Japan
M. epitea	HH-78294	II	*S. reinii*	Yamanashi	Japan
M. epitea	TNS-F-121034	II	*S. viminalis*	Berlin	Germany
M. epitea	VMP891-1	II, III	*S. viminalis*	Somerset	England
M. epitea	TSH-R10176	II, III	*S. vulpina*	Aomori	Japan
M. epitea	TSH-R10212	II, III	*S. vulpina*	Aomori	Japan
*M. euonymi-caprae*arum	TNS-F-186320	II	*S. aurita*	—	Germany
M. humilis	HH-77912	II	*S. integra*	Yamagata	Japan
M. humilis	TSH-R087	II	*S. integra*	Ibaraki	Japan
M. humilis	TSH-R6016	II	*S. integra*	Ibaraki	Japan
M. humilis	TSH-R086	II, III	*S. integra*	Ibaraki	Japan
M. humilis	TSH-R12333	II, III	*S. integra*	Yamanashi	Japan
M. humilis	HH-78294	II	*S. integra*	Yamanashi	Japan
M. humilis	TSH-R2453	II, III	*S. integra*	Nagano	Japan
M. humilis	TSH-R2452	II, III	*S. integra*	Nagano	Japan
M. humilis	TSH-R2454	II, III	*S. integra*	Nagano	Japan
M. humilis	TSH-R2475	II	*S. integra*	Nagano	Japan
M. humilis	TSH-R2476	II, III	*S. integra*	Nagano	Japan
M. humilis	TSH-R1468	II, III	*S. integra*	Toyoma	Japan
M. humilis	TSH-R12215	II	*S. integra*	Miyazaki	Japan
M. humilis	TSH-R9612	II, III	*S. integra*	Niigata	Japan
M. humilis	TSH-R10561	II, III	*S. integra*	Tochigi	Japan
M. humilis	TSH-R10220	II, III	*S. integra*	Tochigi	Japan
M. humilis	TSH-R10717	II, III	*S. integra*	Tochigi	Japan
M. humilis	TSH-R3893	II, III	*S. integra*	Shizuoka	Japan
M. humilis	**HH-53278 (isotype)**	II, III	*S. koriyanagi*	Tokyo	Japan
M. humilis	TSH-R7548	II	*S. koriyanagi*	Miyagi	Japan
M. humilis	TSH-R7563	II	*S. koriyanagi*	Miyagi	Japan
M. humilis	TSH-R7613	II	*S. koriyanagi*	Miyagi	Japan
M. humilis	TSH-R7650	II	*S. koriyanagi*	Miyagi	Japan
M. humilis	TSH-R13703	II	*S. koriyanagi*	Kochi	Japan
M. kamikotica	**HH-73060 (holotype)**	II, III	*Chosenia arbutifolia*	Nagano	Japan

Table 2-2 Continued.

M. kamikotica	HH-77944	II, III	*C. arbutifolia*	Nagano	Japan
M. kamikotica	HH-78366	II, III	*C. arbutifolia*	—	Russia
M. kiusiana	HH-53158	II, III	*S. subopposita*	Fukuoka	Japan
M. kiusiana	HH-77887	II	*S. subopposita*	Fukuoka	Japan
M. kiusiana	HH-53159	II, III	*S. subopposita*	Fukuoka	Japan
M. kiusiana	**HH-53157(holotype)**	II, III	*S. subopposita*	Oita	Japan
M. kiusiana	HH-99464	II, III	*S. subopposita*	Oita	Japan
M. laricis-pentandrae	NWC-0913	II, III	*S. pentandrae*	Rothamsted	England
M. laricis-urbaniana	TSH-R7419	II, III	*Toisusu urbaniana*	Hokkaido	Japan
M. laricis-urbaniana	TSH-R7420	II, III	*T. urbaniana*	Hokkaido	Japan
M. laricis-urbaniana	**HH-78307 (neotype)**	II, III	*T. urbaniana*	Hokkaido	Japan
M. laricis-urbaniana	**HH-53302(isoneotype)**	II, III	*T. urbaniana*	Hokkaido	Japan
M. laricis-urbaniana	TSH-R9834	II, III	*T. urbaniana*	Nagano	Japan
M. laricis-urbaniana	TSH-R9835	II, III	*T. urbaniana*	Nagano	Japan
M. microsora	TSH-R10779	II, III	*S. subfragilis*	Ibaraki	Japan
M. microsora	TSH-R7330	II, III	*S. subfragilis*	Ibaraki	Japan
M. microsora	TSH-R7333	II, III	*S. subfragilis*	Miyagi	Japan
M. microsora	TSH-R7335	II, III	*S. subfragilis*	Hiroshima	Japan
M. microsora	**HH-53150 (Isotype)**	II, III	*S. subgragilis*	Tokyo	Japan
M. microsora	HH-53225	II, III	*S. subgragilis*	Hokkaido	Japan
M. reticulata	TNS-F-107037	II, III	*S. reticulata*	Kuusamp	Finland
M. reticulata	TNS-F-120783	II, III	*S. reticulata*	Alaska	USA
M. ribesii-purpureae	TNS-F-107388	II, III	*S. daphnoides*	Turku	Finland
M. ribesii-purpureae	NWC-06843	II, III	*S. purpureae*	Rothamsted	England
M. ribesii-purpureae	TNS-F-186369	II, III	*S. purpureae*	—	Germany
M. ribesii-purpureae	BPI23007	II, III	*S. purpureae*	Tudent	Italy
M. ribesii-purpureae	BPI23008	II, III	*S. purpureae*	Latvia	Russia
M. ribesii-purpureae	BPI23009	II, III	*S. purpureae*	Zurich	Switzerland
M. salicis-albae	NWC-06210	II, III	*S. alba*	Rothamsted	England
M. salicis-albae	NWC-09234	II, III	*S. alba*	Rothamsted	England
M. salicis-warburgii	TSH-R7529	II	*S. pierotii*	Tottori	Japan
M. salicis-warburgii	TSH-R7545	II	*S. pierotii*	Miyagi	Japan
M. salicis-warburgii	HH-53339	II	*S. pierotii*	Shimane	Japan
M. salicis-warburgii	HH-53343	II, III	*S. pierotii*	Hokkaido	Japan
M. yezoensis	TSH-R10193	II, III	*S. jessoensis*	Aomori	Japan
M. yezoensis	TSH-R1504	II, III	*S. jessoensis*	Nagano	Japan
M. yezoensis	TSH-R1507	II, III	*S. jessoensis*	Nagano	Japan
M. yezoensis	TSH-R1510	II	*S. jessoensis*	Ibaraki	Japan

Table 2-2 Continued.

M. yezoensis	TSH-R7341	II, III	*S. jessoensis*	Hokkaido	Japan
M. yezoensis	**HH-99463 (neotype)**	II, III	*S. jessoensis*	Hokkaido	Japan
M. yezoensis	HH-53165	II	*S. jessoensis*	Hokkaido	Japan
M. yezoensis	TSH-R7397	II, III	*S. jessoensis*	Iwate	Japan

a: II refers to uredinial stage; III refers to telial stage.

Table 2-3 Qualitative and quantitative characters in uredinial and telial stages of *Melampsora* species on willows examined and measured in this study.

Spore stage	Qualitative characters	Quantitative characters
Uredinial stage	Position of uredinia	Size of uredinia
	Existence of smooth regions in urediniospores	Shape factor of urediniospores
	Spine form of urediniospores	Length of urediniospores
	Existence of intermixed paraphyses	Width of urediniospores
	Existence of thickened apex in paraphyses	Wall thickness of urediniospores
	Position of germ pore	Distance between spines
	Surface structure of parpahyses	Number of germ pore
		Length of paraphyses
		Apex width of paraphyses
		Apex thickness of paraphyses
Telial stage	Position of telia	Size of telia
	Position of teliospores	Length of teliospores
		Width of teliospores
		Wall thickness of teliospores

Table 2-4 Qualitative character with character states used for cluster analysis.

I: Position of uredinia
1: hypophyllous; 2: epiphyllous; 3: amphigenous
II: Existence of smooth regions in urediniospores
1: with smooth regions at apex; 2: without smooth regions
III: Spine form of urediniospore
1: echinulate 1; 2: echinulate 2; 3: echinulate 3
IV: Existence of intermixed paraphyses
1: intermixed; 2: peripheral
V: Existence of thickened apex in paraphyses
1: thickened at apex; 2: evenly thickened
VI: Position of germ pore
1: bizonate; 2: scattered
VII: Position of telia
1: hypophyllous; 2: epiphyllous; 3: amphigenous
VIII: Position of teliospores
1: subepidermal; 2: subepidermal or subcuticular; 3: subcuticular

Table 2-5 Twelve key characters of 23 morphological groups recognized by cluster analysis.

Morphological group	Morphological characters[a]											
	PU	SF[b]	GP	SF	SRA	LU	WU	ATU	IP	PT	PTs	LT
M1	H	0.8768c	S	T1	E	15.93a	13.78a	1.86	I	E	SE	27.06b
M2	H	0.8788c	S	T1	E	13.69a	12.07a	1.67	I	E	SE	42.92d
M3	A	0.8635c	S	T1	E	20.16c	13.52ab	2.18	I	A	SE	46.95e
M4	H	0.878c	S	T1	E	16.69ab	13.9ab	1.89	I	A	SE	26.08b
M5	A	0.8768c	S	T1	E	17.97ab	15.49ab	2.17	I	A	SE	28.95bc
M6	H	0.8732c	S	T1	E	22.96cd	16.25b	2.43	I	A	SE	26.28b
M7	H	0.876c	S	T1	E	18.12bc	15.64ab	2.34	I	A	SC	28.56bc
M8	H	0.8754c	S	T1	E	18.72bc	15.81b	2.6	I	E	SC	31.30c
M9	H	0.8727c	S	T1	E	14.41a	12.50a	1.64	I	E	SE & SC	29.19c
M10	H	0.8802c	S	T1	E	14.01a	12.36a	1.45	I	A	SE & SC	26.51b
M11	H	0.8834c	S	T1	E	20.32c	17.64c	2.07	I	A	SE & SC	28.88bc
M12	H	0.8778c	S	T1	E	19.05bc	15.93b	2.01	P	H	SE	30.63c
M13	H	0.8769c	S	T1	E	15.42a	12.98a	1.49	P	H	SE	24.85b
M14	A	0.8277a	S & B	T2	S	20.67c	15.36ab	1.92	I	A	SE & SC	30.48c
M15	E	0.8239a	S & B	T1	E	25.46d	20.46d	2.19	I	E	SE & SC	17.84a
M16	H	0.8205a	S & B	T2	S	24.32d	16.60bc	2.43 (Apex: 5.75)	I	H	SE	30.83c

Table 2-5 Continued.

M17	H	0.8233a	S & B	T1	E	23.09cd	15.52ab	2.22 (Apex: 6.68)	I	H	SE	28.31bc
M18	H	0.8277a	S & B	T1	S	22.11cd	16.36b	2.08	I	A	SE	24.47b
M19	H	0.8173a	S & B	T1	S	25.83d	17.82c	2.12 (Apex: 6.18)	I	A	SE	23.83b
M20	H	0.8207a	S & B	T1	E	22.55cd	16.64bc	2.13 (Apex: 9.83)	I	A	SE	24.21b
M21	H	0.8437b	S	T1	S	19.84bc	13.44a	1.64	P	E	SC	23.82b
M22	H	0.826a	S	T2	S	23.46cd	14.76ab	1.68	I	H	SE	28.49bc
M23	H	0.8407b	S	T1	S	22.16cd	15.29ab	1.92	I	E	SC	28.65bc

a: PU: Position of uredinia (A: amphigenous, E: epiphyllous, H: hypophyllous). SF: Shape factor of urediniospores. GP: Position of germ pore. (S: scattered, S & B: scattered or tending to bizonate). SF: Spine form (T1: echinulate type 1, T2: echinulate type 2, T3: echinulate type 3).SRA: Smooth regions at apex (E: echinulate; S: smooth at apex). LU: Length of urediniospores (μm). WU: Width of urediniospores (μm). ATU: Wall apex thickness of urediniospores (μm). IP: Position of parpahyses (I: intermixed; P: peripheral). PT: Position of telia (A: amphigenous, E: epiphyllous, H: hypophyllous). PTs: Position of teliospores (SE: subepidermal, SC: subcuticular, SE & SC: subepidermal or subcuticular). LT: Length of teliospores (μm).

b: Small letter behind the mean value of quantitative variables in the column denote significantly different at the 0.05 level according to Duncan's multiple range test.

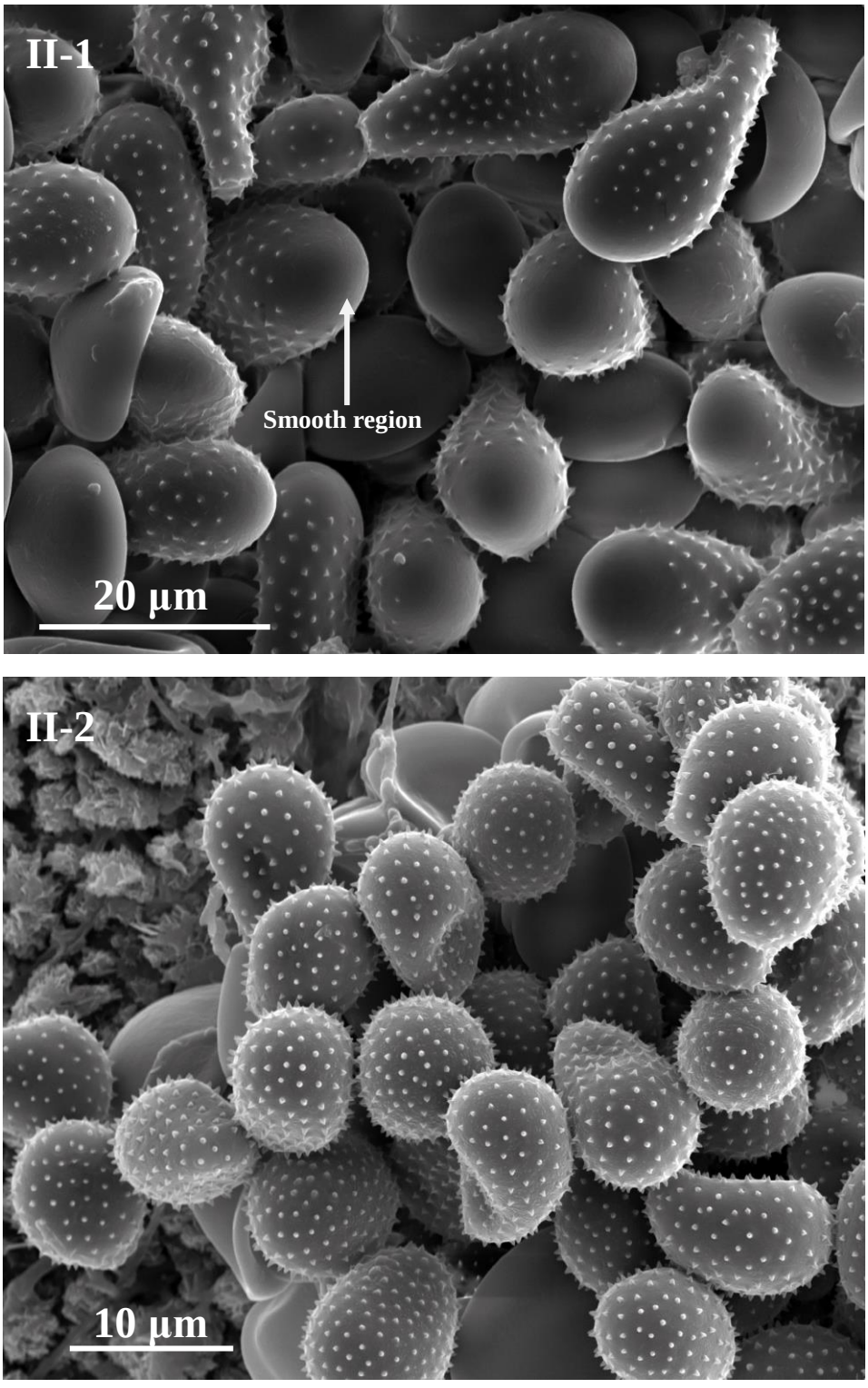


Fig. 2-1 Ornamentation of urediniospores. Based on smooth region in urediniospores, three types were divided: II-1: Urediniospores with smooth region or smooth spot at apex; II-2: No smooth region in urediniospores.

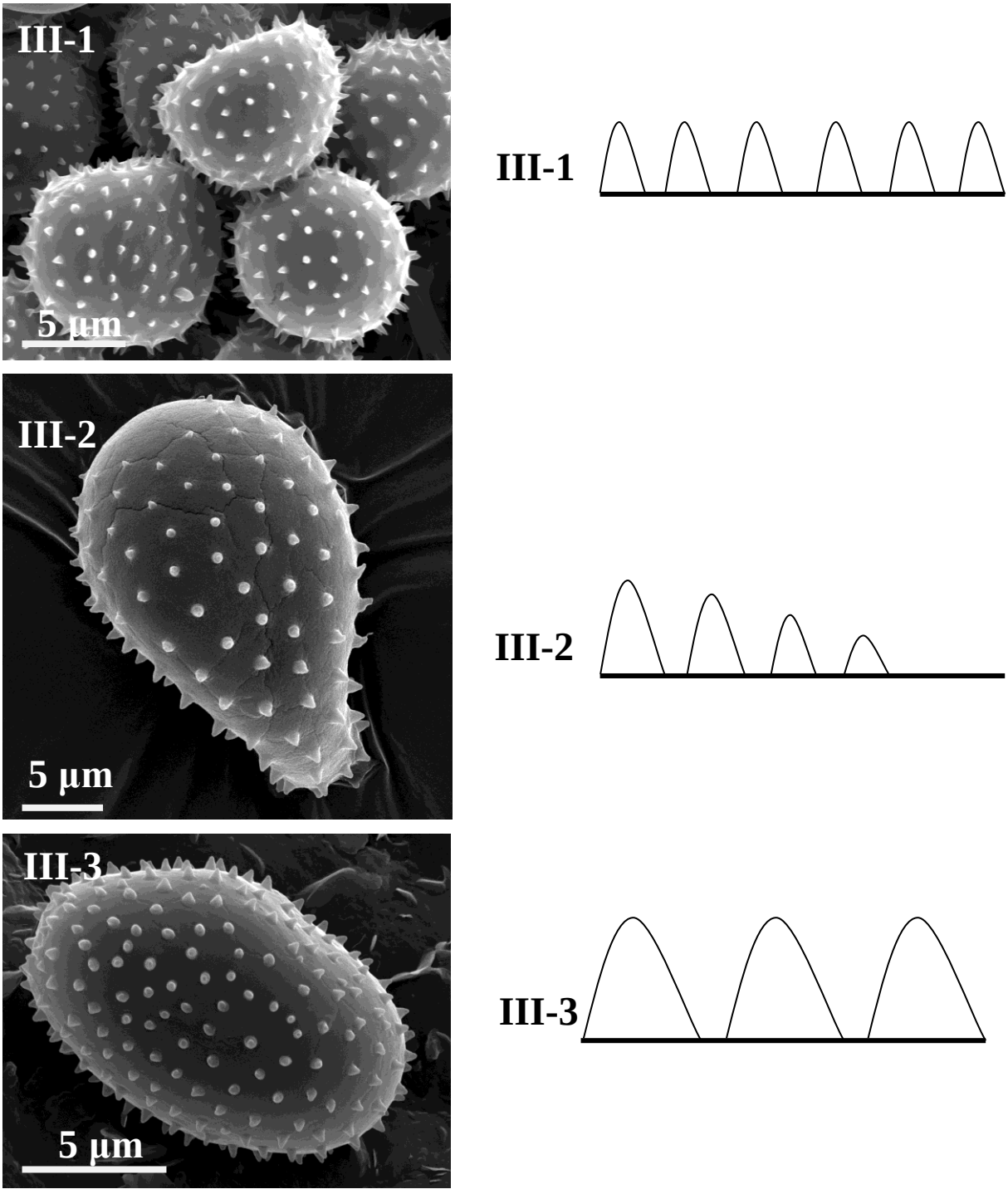


Fig. 2-2 Morphology of spines on the surface of urediniospores. Based on spine characteristics, three types of spines were recognized: III-1: Echinulate type 1; III-2: Echiulate type 2; III-3: Echinulate type 3.

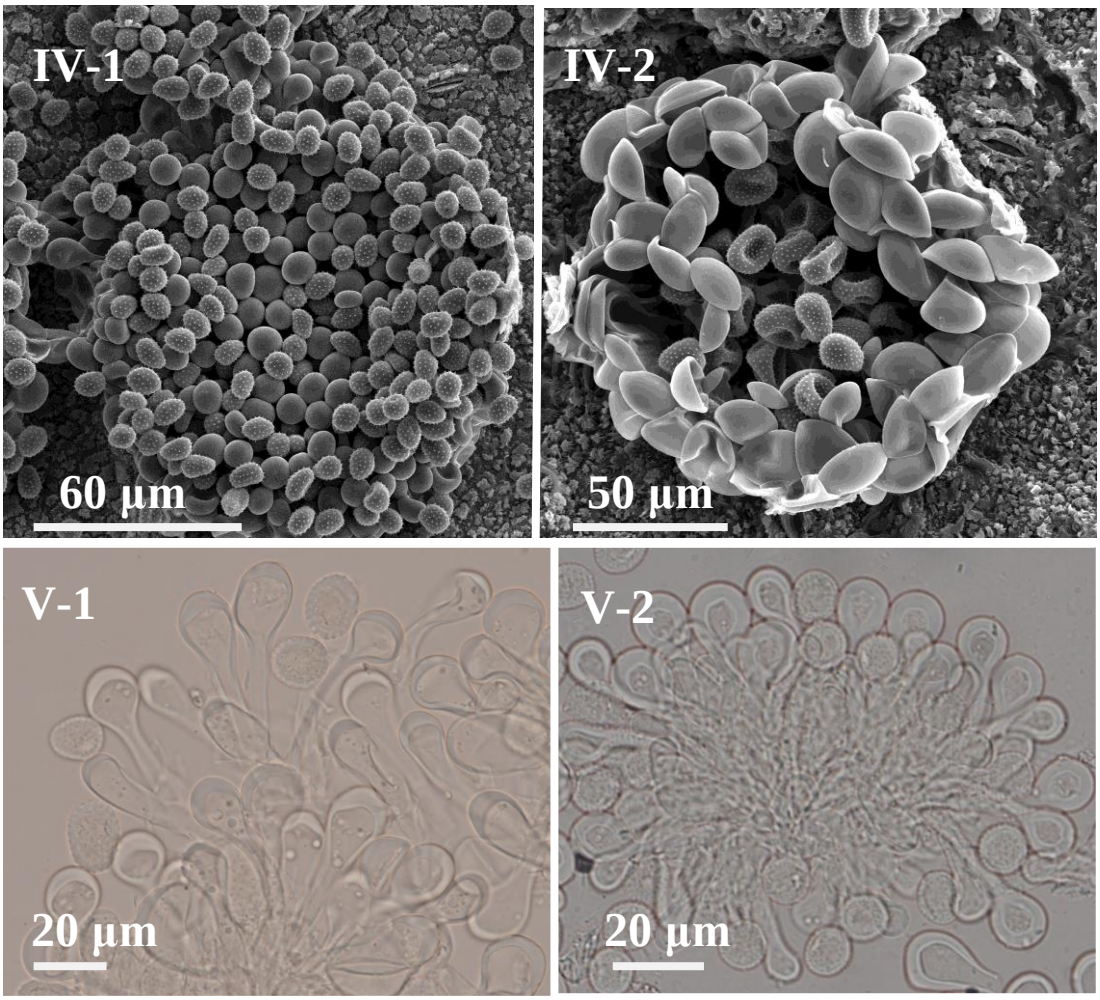


Fig. 2-3 Morphology of paraphyses in the uredinium. IV-1: Both intermixed and peripheral paraphyses were found in the uredinium. IV-2: Peripheral paraphyses were found in uredinium and no intermixed paraphysed were recognized. V-1: Paraphyses with apparently thickened apex. V-2: Paraphyses with evenly thickened apex.

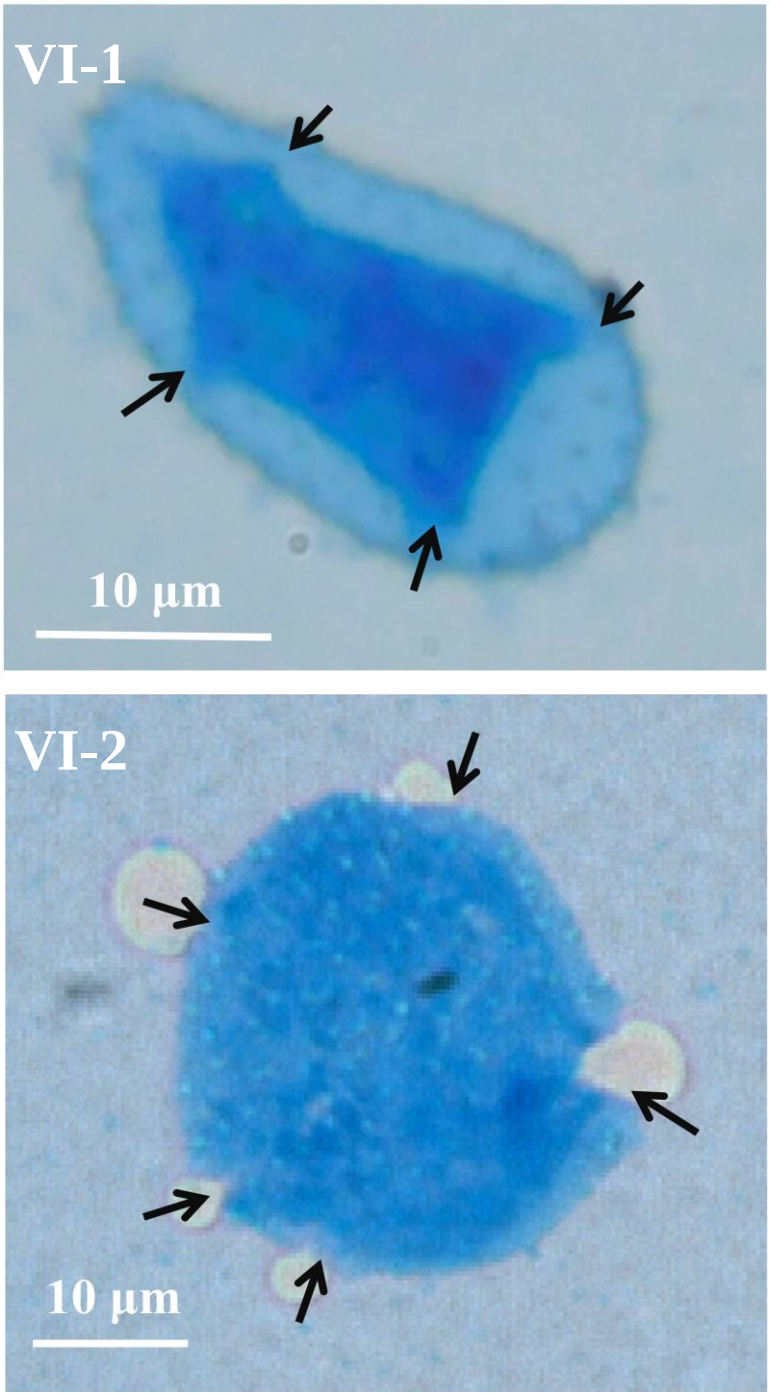


Fig. 2-4 Position and number of germ pores on urediniospores. Two types of position of germ pore (black arrows): VI-1: bizonate; VI-2: Scattered.

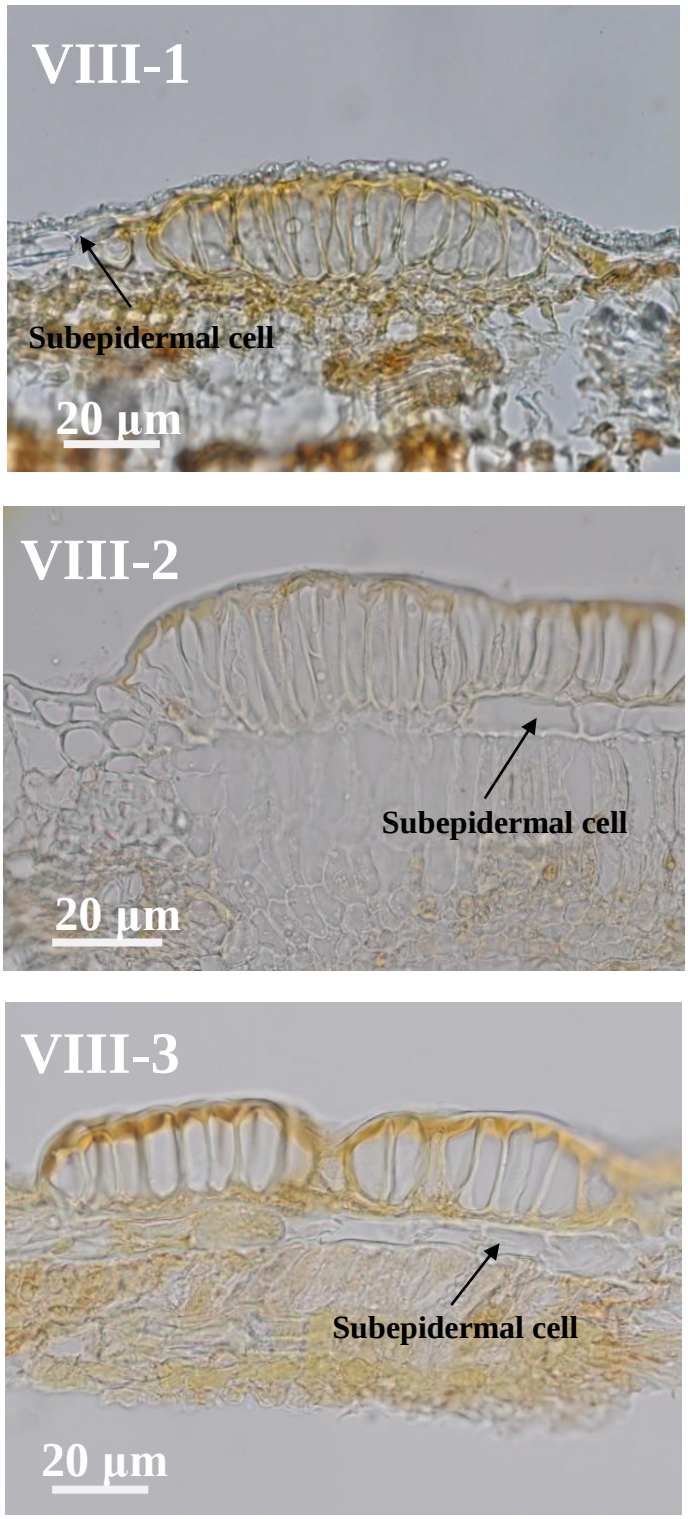
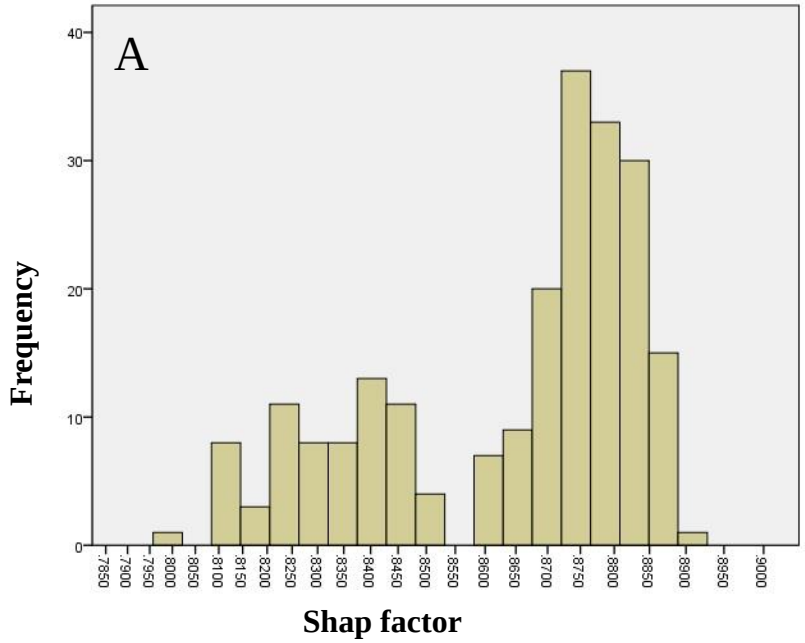


Fig. 2-5 Three types of position of telospores recognized: VIII-1: Subepidermal; VIII-2: Subepidermal or subcuticular; VIII-3: Subcuticular.



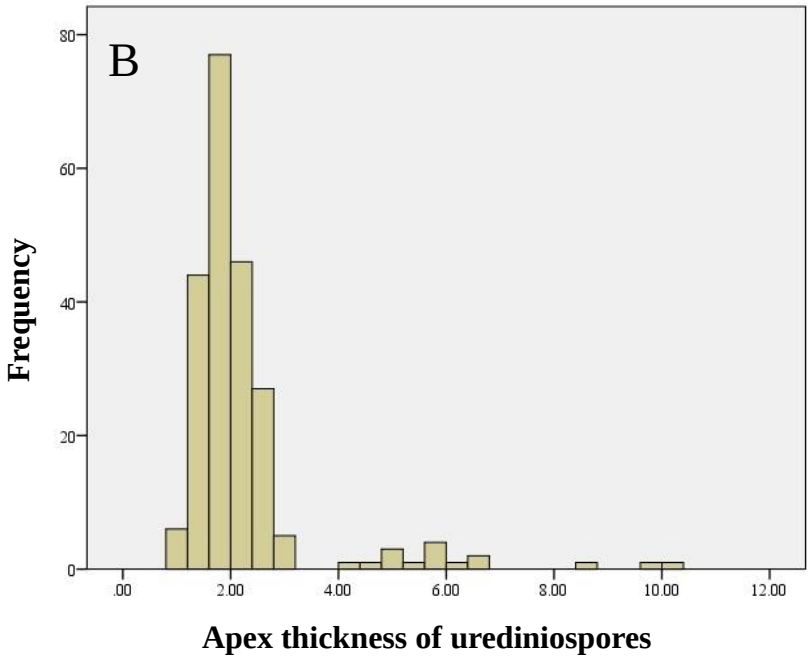


Fig. 2-6 Histogram of shape factor (A) and apex thickness of urediniospores (B) from specimens used for cluster analysis.

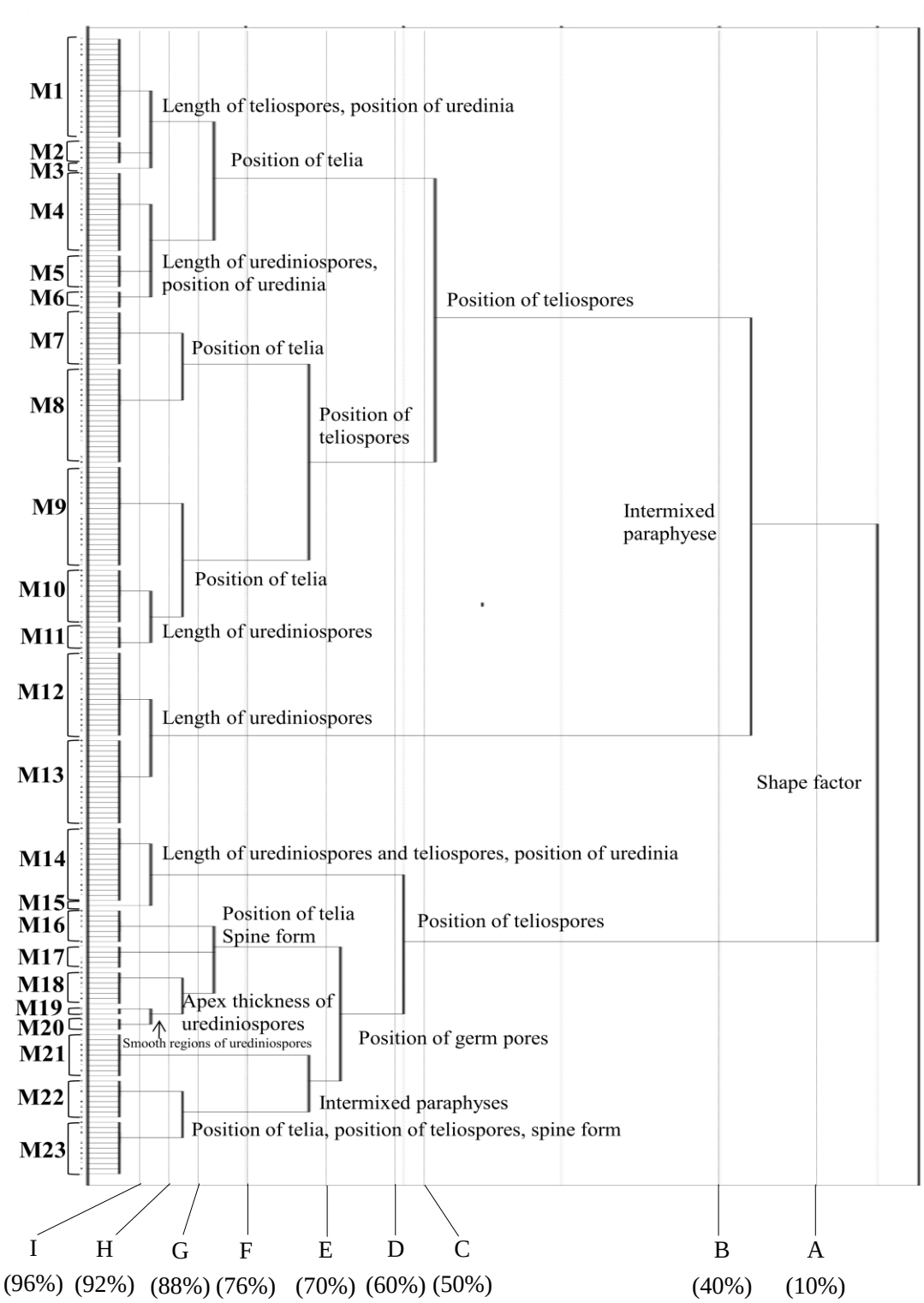


Fig. 2-7 Dendrogram resulted from 19 morphological characteristics of 231 *Melampsora* specimens on willows. Specimens were divided into 23 groups (M1 to M23) based on diagnostic characters on each node. Detailed information of specimens in each group was demonstrated in the Appendix 1. The dash lines indicated separation points at different similarity level, which was indicated in the parentheses.

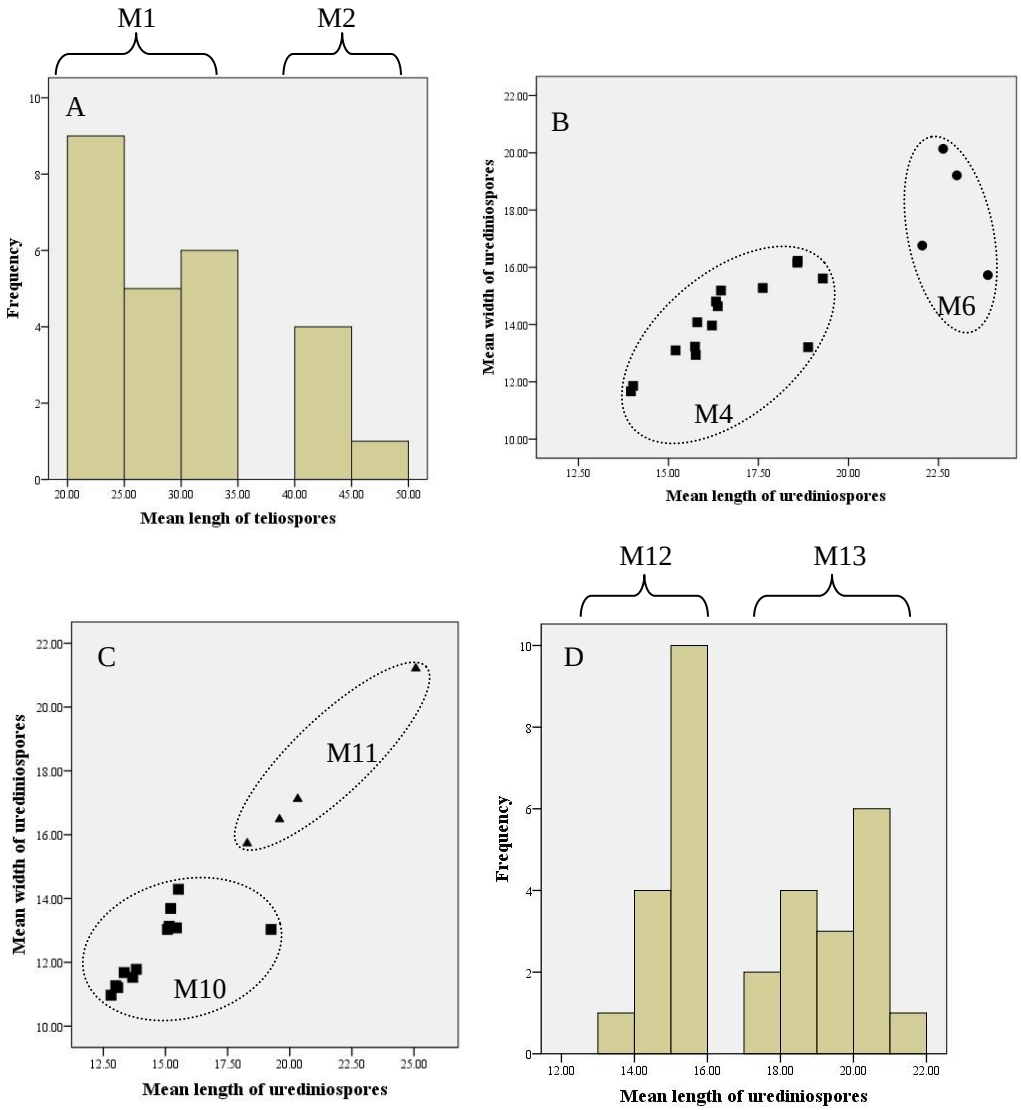


Fig. 2-8 Morphological differences recognized by quantitative variables. A: Differences in the teliospores in M1 and M2 indicated by a histogram. B: Differeces in the dimension of urediniospores of M4 and M6 revealed by scattered diagram. C: Differeces in the dimension of urediniospores of M10 and M11 revealed by scattered diagram. D: Differeces in the length of urediniospores in M12 and M13 indicated by a histogram.

Chapter 3 Molecular phylogenetic analyses

In this chapter, molecular phylogenetic studies were conducted to determine the phylogenetic relationships among the *Melampsora* rusts on willows used in this study. The D1/D2 region of the LSU and ITS regions of the nuclear ribosomal RNA gene, which was found to be useful in resolving relationships at the generic and species level in the rust fungi, were analyzed. In addition, three proteins coding genes, β-tubulin gene, elongation factor 1α gene (EF-1α) and M277, were tried to analyze from all herbarium specimens used in this study.

3-1 Materials and Methods

3-1-1 Materials

In this study, all herbarium specimens, which were used for morphological examination, were also used for molecular phylogenetic analyses. Detailed information of specimens was shown in Table 2-1 and Table 2-2.

3-1-2 DNA extraction, PCR amplification and Sequencing

Genomic DNA was extracted from a single uredinium on each specimen. Spores from a single uredium were crushed between two sterilized glass slides and suspended in the 20 μl extraction buffer [10 mM Tris-HCI pH 8.3, 1.5 mM $MgCI_2$, 50 mM KCI, 0.01% sodium dodecyl sulfate (SDS), 0.01% Proteinase K]. The suspensions were incubated at 37ºC for 60 min and then at 95ºC for 10 min, followed by a 4ºC soak (Virtudazo et al. 2001). From the crude extract, 1 to 3 μl samples were used directly for each polymerase chain reaction (PCR) amplification. DNA extracts from these older herbarium specimens were diluted into 10 fold before the PCR amplification to successfully amplify the target fragment, and DNA templates of some dried

specimens needed to be diluted into 50 fold or 100 fold.

Five loci were tried to amplify from all examined specimens. Two nuclear ribosomal RNA gene regions, rDNA D1/D2 region and the ITS regions, were tried to amplify from all specimens. Two protein-coding genes, the β-tubulin gene and the EF-1α gene, which were occasionally used for phylogenetic analyses in the rust fungi (van der Merwe et al. 2007), were also amplified. In addition, MS277, which is required for rRNA accumulation during biogenesis of the ribosome, was selected as one of the candidate genes for phylogenetic analyses because this gene was one of the best-performing genes for phylogenetic studies of fungi retrieved by Aguileta et al. (2008).

rDNA D1/D2 region and ITS regions were amplified using the primer pairs NL1 (5′-GCATATCAATAAGCGGAGGAAAAG-3′) and NL4 (5′-GGTCCGTGTTTCAAGACGG-3′) (O' Donnell and Cigelnik 1997), and ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) (Gardes and Bruns 1993) and ITS4 (5′-TCCTCCGCTTATTGATATGC-3′) (White et al. 1990). DNA was amplified using a GeneAmp PCR System 9700 (Applied Biosystems, Foster City, CA, USA). 25 μl reaction mixtures comprised 1 unit of Taq DNA polymerase (TaKaRa, Tokyo, Japan), a commercial deoxynucleoside triphosphate (dNTP) mixture (containing 2.5 mM of each dNTP), Taq reaction buffer (containing 2 mM Mg^{2+}), and 0.2 μM of each primer. PCR was performed followed by Alaei et al. (2009) with 40 cycles of the following profile: 1 cycle of 94°C for 5 min, 40 cycles of denaturation at 94°C for 1 min, annealing at 45°C for 1 min, and extension at 72°C for 1 min, followed by a final extension at 72°C for 10 min.

Partial sequences of the EF-1α gene were also tried to amplify using a nested PCR method based on van der Merwe et al. (2007). Two primers, EF1-526F (5′-GTCGTYGTYATYGGHCAYGT-3′) and EF1-1567R (5′-ACHGTRCCRATACCACCRATCTT-3′), were used for the first round PCR. PCR was performed in following profile: 8 min at 98°C followed by 3 cycles of 45 s at 94°C, 1 min 40 s at 55°C and 2 min at 72°C, followed by 10 cycles of 45 s at 94°C, 1 min at 56°C (decrease of 1 degree with every cycle) and 1 min 40 s at 72°C,

followed by 10 cycles of 30 s at 94°C, 45 s at 52°C and 2 min at 72°C and a final extension for 8 min at 70°C. For the second PCR, two primers, EFbasidF (5′-GTGCGGTGGTATCGACAAGC-3′) and EFbasidR (5′-CATGTTGTCACCGTGCCATCC-3′), were use to amplify a fragment of 700 base pairs. PCR products of the first round PCR were diluted into 100 fold, and the second round PCR amplification was performed in 30 μl reactions with 2 μl dilutions. The thermal cycling conditions were: 1 cycle at 96°C for 7 min, 32 cycles of 40 s at 94°C, 40 s at 56°C and 1 min 40 s at 72°C with a final extension of 10 min at 72°C.

For the amplification of partial sequence data of the β-tubulin gene, a semi-nested PCR procedure was conducted according to van der Merwe et al. (2007). The first round PCR thermal cycle was carried out with two primers, B-tub 1317F (5′-GAGMGRATYAGYGTTTATTAC-3′) and B-tub 2662bR (5′-GAACTCCATCTCGTCCATTCTA-3′). The PCR condition was as follows: 8 min at 98°C followed by 3 cycles of 45 s at 94°C, 1 min 40 s at 58°C and 2 min at 72°C, followed by 10 cycles of 45 s at 94°C, 1 min at 58°C (decrease of 1 degree with every cycle) and 1 min 40 s at 72°C, followed by 10 cycles of 30 s at 94°C, 45 s at 58°C and 2 min at 72°C and a final extension for 8 min at 70°C. After the first round PCR, the products were diluted into 100 fold and 2 μl of diluted PCR products were used for second round PCR. Two primers, B-tub 1442F (5′-AGAAYGAGGTYGCTGSCAAC-3′) and B-tub 2662bR (5′-GAACTCCATCTCGTCCATTCTA-3′), were used, and the thermal cycling conditions of second round PCR were: 1 cycle at 96°C for 7 min, 32 cycles of 40 s at 94°C, 40 s at 58°C and 1 min 40 s at 72°C with a final extension of 15 min at 72°C.

The MS277 was amplified based on the PCR procedure of Vialle et al. (2013). Two primers, MS277_EX1F2 (5′-GCAGATGATCTGGTCTCCGAGAA-3′) and MS277_DR (5′-TTCCCATACTCCGCAGGTAG-3′), were used to amplify the MS277 of *Melampsora* species. The PCR procedure was followed by Vialle et al. (2012) and MS277 was amplified with thermocycling conditions as follows: denaturation for 3 min at 95°C, 50 cycles at 95°C for 45 s, 30 s at 56°C, and 1 min 30 s at 72°C with a final extension of 10 min at 72°C.

After amplification, 3 μl microliter of the product from each reaction was run on an agarose gel (1% agarose) stained with ethidium bromide and visualized under UV light. Amplified bands were cut from the gel, and they were purified by Wizard® SV Gel and PCR Clean-Up Kit (Promega, WI, USA). Purified PCR products were sequenced directly using BigDye^{TM} Terminator Cycle Sequencing Ready Reaction Kit (PE Applied Biosystems, USA) with the same amplification primer sets used for PCR. The reaction was set up as 25 cycles of 96°C for 10 s, 50°C for 5 s, 60°C for 4 min. Cycle sequencing reaction products (20 μl) were purified by ethanol precipitation and sequences were analyzed on a 3130 Automated DNA Sequencer (PE Applied Biosystems, USA).

3-1-3 Phylogenetic tree construction

The specimens, which were used for molecular phylogenetic studies, were listed in Table 3-1. The raw sequence data were manually aligned using Bioedit ver. 7.0.9 (Hall 1999), and multiple alignments were performed in Clustal X ver. 1.8 (Thompson et al. 1997). Topologies were first constructed based on individual gene datasets. Because most of the previous studies on *Melampsora* species on willows were mainly focused on rDNA ITS regions (Smith et al. 2004; Pei et al. 2005; Yamaoka et al. 2010; Damadi et al. 2011; Samils et al. 2011; Milne et al. 2012), rDNA ITS sequence data from previous phylogenetic studies were used for comparison. Detailed information of these sequence data was listed in Table 3-2. The introns of the EF-1α gene were excluded from analyses due to alignment problems caused by highly variable characters within each intron. The alignment of individual datasets used for phylogenetic analyses were presented in the Appendix 2, 3 and 4. Secondly, the individual datasets were combined to construct phylogenetic trees. Sequence data of *M. laricis-populina* were retrieved from GenBank and served as outgroups.

Maximum parsimony (MP) analysis and maximum likelihood (ML) analysis were performed to all data matrices using PAUP* ver. 4.0b10 (Swofford et al. 2001).

Moreover, Bayesian Markov chain Monte Carlo (MCMC) analysis was performed by MrBayes ver. 3.1.2 (Huelsenbeck and Ronquist 2001). MP analysis was performed using the heuristic search option with 1000 random taxa additions and tree bisection and reconstruction (TBR) as the branch-swapping algorithm. All sites were treated as unordered and unweighted, with gaps treated as a fifth state. The strength of the internal branches of the resulting tree was tested with bootstrap analysis using 100 replications. In ML and Bayesian analyses, the best-fit substitution models for different datasets were estimated in Modeltest ver. 3.7 based on implementation of Akaike information criterion (AIC) (Posada and Crandall 1998). ML analysis was conducted with 100 bootstrap replicates under the best-fit evolutionary model. In Bayesian analysis, four Markov chains were run for twice from random starting trees for 2 million generations, and trees were sampled every 100 generations. The initial 25% of MCMC samples were discarded as burn-in and a majority rule consensus tree of all remaining trees was calculated to determine the Bayesian posterior probabilities (Bpp) for the individual branches. The procedure of molecular phylogenetic analyses was illustrated in Fig. 3-1. All phylogenetic trees were visualized using Dendroscope ver. 3.2.7 and annotation was carried out using TreeDyn ver. 198.3 (Chevenet 2006; Huson and Scornavacca 2012).

3-2 Results

Sequence data of rDNA ITS regions and D1/D2 region were successfully amplified from 135 specimens belonging to 22 morphological groups, and sequence data of EF-1α gene were obtained from 43 specimens. The information on herbarium number, host species and locality of these 135 specimens was listed in Table 3-1. Due to failures in DNA extraction of the specimen from a morphological group M15, this group was not included in molecular phylogenetic analyses. Although sequence data of the β-tubulin gene and MS277 were tried to amplify from all examined specimens, these two loci were failed to amplify from most examined specimens. Thus,

phylogenetic analyses were conducted using sequence data of rDNA ITS regions, D1/D2 region and EF-1α gene.

The sequence data of rDNA ITS regions ranged from 546 bp to 568 bp. Besides 135 sequence data from this study, additional 78 sequence data of *Melampsora* species on willows from GenBank were used for comparison (Table 3-2). The data matrix included 185 variable sites with 139 informative sites. In the topology generated from rDNA ITS regions, MP, ML and Bayesian inference obtained consistent topology. The best-fit evolutionary model was K81uf+I+G. Totally, 33 phylogenetic groups were recognized, and they were designated as I1 to I33 (Fig. 3-2; Fig. 3-3). Specimens obtained from this study were located in 28 phylogenetic groups. Twenty-five groups included specimens from one morphological group, but groups I1, I4 and I14 contained more than two morphological groups. Phylogenetic group I1 included specimens from morphological groups M4 and M7, and I4 included specimens from M12 and M13 (Fig. 3-2). Group I14 included specimens from M11 and M14 (Fig. 3-3).

In the topology obtained from rDNA D1/D2 region, sequence from these specimens ranged from 505 bp to 560 bp. In the final data matrix, 460 sites were constant and 65 sites were parsimony informative. HKY+I+G was selected as a best-fit evolutionary model. The phylogenetic trees obtained from MP, ML and Bayesian inference were largely congruent although MP showed low resolution at the basal and inter-branch of major clades. In the phylogeny obtained from rDNA D1/D2 region, 21 phylogenetic groups were recognized, and they were designated as D1 to D21 (Fig. 3-4; Fig. 3-5). Except for two phylogenetic groups, D2 and D7, the other 19 phylogenetic groups were proved to be monophyletic because they included specimens from one distinct morphological group. Phylogenetic group D2 was weakly supported and it included 52 specimens from morphological groups M1, M4, M7, M8, M10, M12, M13 and M17 (Fig. 3-4). D7 included 18 specimens from morphological groups M2, M4 and M9 (Fig. 3-5).

Sequence data of EF-1α gene were obtained from 43 specimens from 13 morphological groups and the final alignment of sequence data varied from 341 bp to

368 bp after excluding three introns. Totally, 47 sites were variable and 37 sites among these variable sites were parsimony informative, and the best-fit evolutionary model was TrNef+G. Phylogenetic trees were constructed with sequence data of *M. laricis-populina* (GenBank No. EU487220) as outgroups. Totally 18 phylogenetic groups were recognized, and they were designated as E1 to E18 (Fig. 3-6). Although some of phylogenetic groups were weakly supported by Bpp and Bootstrap values, they were proved monophyletic because each group included specimens from one morphological group.

The combined dataset had high resolution of phylogenetic relationship. The EF-1α gene sequence data were failed to combine with rDNA sequence due to limited numbers of data. Thus, sequence data of rDNA ITS regions and D1/D2 region were combined together. The alignment data matrix of combined data varied from 1058 bp to 1077 bp after excluding the ambiguous sites. Totally 232 sites were variable and 156 sites of these variable sites were parsimony informative. TVM+I+G was chosen as the best-fit evolutionary model. In the phylogeny of combined dataset, 29 phylogenetic groups were recognized with high bootstrap values and Bpp and they were designated as G1 to G29 (Fig. 3-7; Fig. 3-8). Except for G1 and G4, other phylogenetic groups were proved monophyletic and they were composed of specimens from one morphological group. G1 included specimens from two morphological groups, M4 and M7, and G4 included specimens from M12 and M13.

3-3 Discussion

In this study, 29 phylogenetic groups were recognized based on the combined dataset of rDNA ITS regions and D1/D2 region, and these groups were designated as G1 to G29. Although EF-1α gene was unable to combine with rDNA sequence data due to limited sequences, EF-1α gene phylogeny revealed that specimens in G1 in the combined dataset of rDNA phylogeny were located in two distinct groups, E5 and E7. Thus, phylogenetic group G1 was divided into two groups based on the results of

EF-1α gene phylogeny, and they were tentatively designated as G1-1 and G1-2. Based on the phylogeny obtained from sequence data of rDNA ITS regions, D1/D2 region and EF-1α gene, totally 30 phylogenetic groups were recognized in this study. The detailed information on phylogenetic groups in the different DNA loci was summarized in Table 3-3.

Previous studies of *Melampsora* species on willows have frequently focused on the analysis of the data from rDNA ITS regions (Smith et al. 2004; Yamaoka et al. 2010; Damadi et al. 2011; Samils et al. 2011; Milne et al. 2012), because this locus is easy to be amplified and contains a large number of informative variables. In this study, rDNA ITS regions showed better phylogenetic resolution among specimens than D1/D2 region because more phylogenetic groups were recognized in the rDNA ITS phylogeny (Table 3-3). The ITS locus contained a high level of phylogenetic signal, and two phylogenetic groups (D2 and D7) from D1/D2 locus were split into several phylogenetic groups in the rDNA ITS phylogeny. Although these two target regions were frequently used as promising fragments in rust taxonomic studies based on consensus analysis on trees estimated from data partitions of two fragments (Tian et al. 2004; Liang et al. 2006; Chatasiri and Ono 2008), it can be indicated that the concordance of genealogies from these two loci did not reflect the real phylogeny of *Melampsora* species on willows because two fragments owned different percentage of informative sites and showed different phylogenetic resolution among these specimens.

Although rDNA ITS locus was proposed as an effective DNA barcode for species recognition in the fungi kingdom (Schoch et al. 2012), three phylogenetic groups (I1, I4 and I14) in the rDNA ITS phylogeny were composed of morphologically distinct groups in this study. Among these three phylogenetic groups, I14 was further split into two phylogenetic groups (G11 and G12) in the combined data of rDNA ITS regions and D1/D2 region, and each group included specimens from one morphological group. I1 was further split into two phylogenetic groups (E5 and E7) in the phylogeny of EF-1α gene (Table 3-3), and these two groups were proved to be monophyletic. These results indicated that the rDNA ITS regions had insufficient variation to reveal the

phylogenetic relationship of sibling species with distinct morphological characteristics and the variability of the ITS region among species did not appear to be uniform.

Therefore, combined the results of rDNA ITS regions, D1/D2 region and EF-1α gene yielded the best results of phylogeny among all these datasets used in molecular studies. Previously, Kluge (1989) proposed that phylogenetic analysis should be performed on a combined dataset using all possible evidence because a slowly evolving gene might be useful in resolving older evolutionary splits but be of little use for younger groups, whereas rapidly evolving genes might be best for accurately resolving recent speciation events (Huelsenbeck et al. 1996). On the other hand, Talyor et al. (2000) proposed the genealogical concordance phylogenetic species recognition (GCPSR) method to determine the species boundaries in the fungi, and the GCPSR method uses the concordance between the genealogies of several unlinked genes to identify the evolutionary independent lineages and recognize phylogenetic species. This GCPSR was widely used in fungi taxonomic studies, especially in rust fungi (Tian et al. 2004; Liang et al. 2006; Chatasiri and Ono 2008; Vialle et al. 2012). Molecular phylogenetic results in this study supported the propose of Kluge based on total evidence of information because differences in these sequences were correlated well with morphological groups. Moreover, different target regions reinforced and complemented one another to a considerable degree and yielded a well-resolved and well-supported tree although they provided different resolution in topologies obtained from individual dataset (Table 3-3).

In this study, three protein-coding genes, partial β-tubulin gene, partial EF-1α gene and MS277, were selected for molecular phylogenetic analyses. Although these genes were widely used in fungi phylogenetic studies, a limited numbers of studies of three loci were reported in rust fungi (van der Merwe et al. 2007; Vialle et al. 2012). In this study, three loci were tried to amplify from herbarium specimens, and only a limited numbers of sequence data were obtained from EF-1α gene. The failures of amplification protein-coding genes might be caused by the existence of introns in these three loci, which has already been reported in species from *Puccinia*, *Melampsora* species on poplar and other rust fungi (van der Merwe et al. 2007; Feau

et al. 2011; Vialle et al. 2012). In addition, low quantity of DNA template and long-time storage of herbarium specimens also caused failures in amplification. These three fragments were one of the promising gene candidates for phylogenetic studies in the rust fungi, but it is very important to explore a novel method to obtain these sequence information from older herbarium specimens. Moreover, other target regions, which were proved to be effective in the fungi phylogeny, need to be investigated.

Table 3-1 Morphological groups, host plant, locality and herbarium number of rust specimens used for molecular phylogenetic analyses.

Morphological group	Voucher specimens	Host plants	Host Section	Locality	rDNA ITS regions*	D1/D2 region*	EF-1α*
M1	HMAS64717	*S. gyirongensis*	Unknown section	China, Tibet	○	○	○
	HMAS42842	*Salix* sp.	Unknown section	China, Inner Mongolia	○	○	×
	HNMAP1972	*S. starkeana*	Vetrix	China, Inner Mongolia	○	○	×
	HNAMP3190	*S. rosmarnifolia*	Incubaceae	China, Inner Mongolia	○	○	○
	HNAMP3193	*S. rosmarnifolia*	Incubaceae	China, Inner Mongolia	○	○	×
	HNMAP3061	*Salix* sp.	Unknown section	China, Inner Mongolia	○	○	×
	TSH-R7689	*S. rorida*	Daphnella	Japan, Hokkaido	○	○	×
	TSH-R7654	*S. rorida*	Daphnella	Japan, Hokkaido	○	○	×
	TSH-R7613	*S. koriyanagi*	Purpurea	Japan, Miyagi	○	○	×
	TSH-R7550	*S. koriyanagi*	Purpurea	Japan, Miyagi	○	○	×
	HNMAP3060	*S. triandra*	Amygdalinae	China, Inner Mongolia	○	○	○
	HNMAP3181	*S. triandra*	Amygdalinae	China, Inner Mongolia	○	○	○
	HMAS82388	*S. triandra*	Amygdalinae	China, Inner Mongolia	○	○	×
	TSH-R8778	*Salix* sp.	Unknown section	Russia	○	○	×
	HMAS52984	*S. argyracea*	Argyraceae	China, Xinjiang	○	○	○
	BPI1108633	*S. argyracea*	Argyraceae	China, Tibet	○	○	×
M2	HH-77887	*S. subopposita*	Incubaceae	Japan, Fukuoka	○	○	×
	HH-53157	*S. subopposita*	Incubaceae	Japan, Fukuoka	○	○	×
M3	HMAS38658	*S. viminalis*	Viminales	China, Tibet	○	○	×
M4	HMAS67392	*S. alfredi*	Unknown section	China, Hubei	○	○	×
	HNMAP3175	*S. characta*	Viminales	China, Inner Mongolia	○	○	×
	HMAS52904	*Salix* sp.	Unknown section	China, Xinjiang	○	○	×
	HMAS82376	*S. rosmarinifolia*	Incubaceae	China, Inner Mongolia	○	○	○
	HMAS67393	*S. caprea*	Vetrix	China, Hubei	○	○	×
	HMAS82380	*S. caprea*	Vetrix	China, Inner Mongolia	○	○	×
	HMAS37818	*S. magnifica*	Magnificae	China, Xinjiang	○	○	×
	HMAS48435	*S. dissa*	Denticulatae	China, Sichuan	○	○	×
	HNMAP1594	*S. siuzevii*	Viminales	China, Inner Mongolia	○	○	×
	HNMAP3140	*S. myrtilloides*	Myrtilloides	China, Inner Mongolia	○	○	○
	HNMAP3149	*S. linearistipularis*	Helix	China, Inner Mongolia	○	○	○
	BPI22984	*S. nigricans*	Nigricantes	Russia	○	○	×
	HMAS135888	*S. taraikensis*	Glaucae	China, Hei Long Jiang	○	○	×
	HMAS58573	*S. iliensis*	Unknown section	China, Xinjiang	○	○	×
	NWC891-1	*S. viminalis*	Viminales	England, Rothamsted	○	○	○
	NWC-9533	*S. viminalis*	Viminales	England, Rothamsted	○	○	×
	NWC-KNW-1	*S. burjatica*	Unknown section	England, Rothamsted	○	○	○
	TSH-R2552	*S. integra*	Purpurea	Japan, Nagano	○	○	×
	BPI23007	*S. viminalis*	Viminales	England, Rothamsted	○	○	×
M5	HMAS62584	*S. purpurea*	Purpurea	China, Shandong	○	○	○
	HMAS52905	*S. alba*	Salix	China, Xinjiang	○	○	○

Table 3-1 Continued.

	NWC-06843	*S. purpurea*	Purpurea	England, Rothamsted	○	○	○
	TNS-F-186369	*S. purpurea*	Purpurea	Germany	○	○	×
M6	TNS-F-107037	*S. reticulata*	Chameaetia	Finland, Kuusamp	○	○	○
	TNS-F-120783	*S. reticulata*	Chameaetia	Finland, Kuusamp	○	○	×
	TSH-R10306	*S. reinii*	Arbuscella	Japan, Tochigi	○	○	×
	HH-53248	*S. reinii*	Arbuscella	Japan	○	○	×
M7	HNMAP3065	*S. hsinganica*	Unknown section	China, Inner Mongolia	○	○	×
	HNMAP1716	*S. sinica*	Vetrix	China, Inner Mongolia	○	○	○
	HNMAP1697	*S. sinica*	Vetrix	China, Inner Mongolia	○	○	○
	HNMAP1710	*S. sinica*	Vetrix	China, Inner Mongolia	○	○	○
	HMAS82384	*S. xerophila*	Vetrix	China, Heilongjiang	○	○	○
	HNMAP3111	*S. xerophila*	Vetrix	China, Inner Mongolia	○	○	○
	HNMAP1690	*S. wallichiana*	Vetrix	China, Inner Mongolia	○	○	×
	HNMAP1339	*S. wallichiana*	Vetrix	China, Inner Mongolia	○	○	○
	HNMAP3176	*S. starkeana*	Vetrix	China, Inner Mongolia	○	○	×
M8	TSH-R9832	*S. bakko*	Vetrix	Japan, Nagano	○	○	○
	TSH-R10727	*S. bakko*	Vetrix	Japan, Nikko	○	○	○
	TSH-R10194	*S. bakko*	Vetrix	Japan, Aomori	○	○	○
	TSH-R3879	*S. bakko*	Vetrix	Japan, Shizuoka	○	○	○
	TSH-R10513	*S. bakko*	Vetrix	Japan, Gunma	○	○	○
	TSH-R7489	*S. bakko*	Vetrix	Japan, Nagano	○	○	○
	TSH-R7702	*S. hultenii*	Unknown section	Japan, Hokkaido	○	○	×
	TNS-F-107383	*S. caprea*	Vetrix	Finland	○	○	×
	BPI22628	*S. caprea*	Vetrix	Australia	○	○	○
	TNS-F-222866	*S. caprea*	Vetrix	Germany	○	○	○
M9	TSH-R9836	*S. sachalinensis*	Viminales	Japan, Tochigi	○	○	○
	TSH-R9837	*S. sachalinensis*	Viminales	Japan, Nagano	○	○	○
	TSH-R7643	*S. pet-susu*	Unknown section	Japan, Hokkaido	○	○	○
	TSH-R7684	*S. pet-susu*	Unknown section	Japan, Hokkaido	○	○	○
	HMAS134712	*S. siuzeuii*	Viminales	China, Hei Long Jiang	○	○	×
	HNMAP3208	*S. viminalis*	Viminales	China, Inner Mongolia	○	○	×
	HNMAS82389	*S. viminalis*	Viminales	China, Inner Mongolia	○	○	○
	HNMAP3058	*S. viminalis*	Viminales	China, Inner Mongolia	○	○	○
	HNMAP3218	*S. viminalis*	Viminales	China, Inner Mongolia	○	○	×
	HNMAP3108	*S. viminalis*	Viminales	China, Inner Mongolia	○	○	○
	HNMAP1698	*S. viminalis*	Viminales	China, Inner Mongolia	○	○	×
M10	TSH-R3884	*S. sachalinensis*	Viminales	Japan, Shizuoka	○	○	×
	TSH-R10186	*S. sachalinensis*	Viminales	Japan, Shizuoka	○	○	×
	TSH-R12280	*S. sachalinensis*	Viminales	Japan, Yamagata	○	○	×
	BPI023212	*Salix* sp.	Unknown section	China, Anhui	○	○	×
M11	HMAS76122	*S. cupularis*	Sclerophyllae	China, Shaanxi	○	○	×
	HNMWFC-T85040	*S. cupularis*	Sclerophyllae	China, Shaanxi	○	○	×
	HNMAP3152	*S. cupularis*	Sclerophyllae	China, Inner Mongolia	○	○	×
M12	TSH-R9831	*S. gilgiana*	Purpurea	Japan, Nagano	○	○	×
	TSH- R7492	*S. gilgiana*	Purpurea	Japan, Nagano	○	○	×

Table 3-1 Continued.

M12	TSH-R3885	*S. japonica*	Cordatae	Japan, Shizuoka	○	○	×
	TSH-R9618	*S. futura*	Unknown section	Japan, Niigata	○	○	○
	TSH-R13426	*S. futura*	Unknown section	Japan, Akita	○	○	○
	TSH-R7731	*S. miyabana*	Purpurea	Japan, Hokkaido	○	○	×
	TSH-R7681	*S. miyabana*	Purpurea	Japan, Hokkaido	○	○	×
	TSH-R12023	*S. reinii*	Arbuscella	Japan, Yamanashi	○	○	×
	TSH-R7487	*S. reinii*	Arbuscella	Japan, Nagano	○	○	×
M13	TSH-10561	*S. intergra*	Purpurea	Japan, Tochigi	○	○	×
	TSH-R1468	*S. intergra*	Purpurea	Japan, Toyoma	○	○	×
	TSH-R10176	*S. vulpina*	Unknown section	Japan, Aomori	○	○	×
	TSH-R10212	*S. vulpina*	Unknown section	Japan, Aomori	○	○	×
	HMAS71118	*S. cathayana*	Denticulatae	China, Sichuan	○	○	×
	BPI199071	*Salix* sp.	Unknown section	China, Qinghai	○	○	×
	HMNWFC915094	*Salix* sp.	Unknown section	China, Shaanxi	○	○	×
M14	HMAP3114	*S. babylonica*	Salix	China, Inner Mongolia	○	○	○
	TSH-R9849	*S. babylonica*	Salix	Japan, Nagano	○	○	×
	TSH-R10771	*S. chaenomeloides*	Denticulatae	Japan, Ibaraki	○	○	×
	TSH-R7339	*S. chaenomeloides*	Denticulatae	Japan, Ibaraki	○	○	×
	HMAS55396	*S. fargesii*	Psilostigmatae	China, Hubei	○	○	×
	HMAS71119	*S. glandulosa*	Denticulatae	China, Shaanxi	○	○	×
	HMAS8619	*S. matsudana*	Salix	China, Hubei	○	○	×
	HNMAP3094	*S. matsudana*	Salix	China, Inner Mngolia	○	○	×
	HNMAP3135	*S. matsudana*	Salix	China, Inner Mngolia	○	○	×
M16	NWC-0913	*S. pentandra*	Pentandrae	England, Rothamsted	○	○	○
	HNMAP3201	*S. pentandra*	Pentandrae	China, Inner Mongolia	○	○	○
	HMAS42407	*S. paraplesia*	Pentandrae	China, Inner Mongolia	○	○	×
	HNMAP3163	*S. pentandra*	Pentandrae	China, Inner Mongolia	○	○	×
	HNMAP3059	*S. pentandra*	Pentandrae	China, Inner Mongolia	○	○	×
M17	TSH-R7420	*Toisusu urbaniana*		Japan, Hokkaido	○	○	○
	TSH-R9834	*T. urbaniana*		Japan, Nagano	○	○	○
	TSH-R9835	*T. urbaniana*		Japan, Nagano	○	○	×
	HH-78366	*Chosenia arbutifolia*		Russia	○	○	×
M18	NWC-09234	*S. alba*	Salix	England, Rothamsted	○	○	○
	NWC06210	*S. alba*	Salix	England, Rothamsted	○	○	○
	HMAS52924	*S. alba*	Salix	China, Xinjiang	○	○	×
M19	HNMAP3185	*S. koreensis*	Pentandrae	China, Inner Mongolia	○	○	×
	HNMAP3257	*S. koreensis*	Pentandrae	China, Inner Mongolia	○	○	×
M20	HNMAP3186	*C. arbutifolia*		China, Inner Mongolia	○	○	×
	HH-73050	*C. arbutifolia*		Japan, Nagano	○	○	×
M21	TSH-1504	*S. jessoensis*	Subalbaceae	Japan, Nagano	○	○	×
	TSH-R1507	*S. jessoensis*	Subalbaceae	Japan, Nagano	○	○	×
	HH-99463	*S. jessoensis*	Subalbaceae	Japan, Hokkaido	○	○	×
M22	TSH-R10079	*S. subfragilis*	Amygdalinae	Japan, Ibaraki	○	○	×
M22	TSH-R7330	*S. subfragilis*	Amygdalinae	Japan, Ibaraki	○	○	×
	TSH-R7335	*S. subfragilis*	Amygdalinae	Japan, Hiroshima	○	○	×

Table 3-1 Continued.

	HH-53150	*S. subfragilis*	Amygdalinae	Japan, Tokyo	○	○	×
	HH-53135	*S. warburgii*	Wilsonianae	China, Taiwan	○	○	×
M23	TSH-R7510	*S. pierotii*	Salix	Japan, Miyagi	○	○	×
	TSH-R7512	*S. pierotii*	Salix	Japan, Miyagi	○	○	×
	TSH-R7365	*S. pierotii*	Salix	Japan, Kagoshima	○	○	○

*(○) indicated that sequence data were successfully obtained from specimens; (×) represented that sequence data were failed to obtain from specimens.

Table 3-2 Details of reference sequences of *Melampsora* species on willows that were retrieved from GenBank database.

Species	Host plants	GenBank accession no.	Reference
M. amygdalinae	*Salix triandra*	AY444776.2	Pei et al. (2005)
M. abietis-caprearum	—[a]	GQ479202.1	—
M. arctica	—	GQ479203.1	—
M. bigelowii	—	GQ479205.1	—
M. bigelowii	—	GQ479206.1	—
M. capraearum	*S. caprea*	AY444779.1	Pei et al. (2005)
M. capraearum	—	GQ479207.1	—
M. capraearum	—	GQ479208.1	—
M. capraearum	—	GQ479209.1	—
M. coleosporioides	*Salix* sp.	AY652949.1	Pei et al. (2005)
M. chelidonii-pierotii	*S. pierotii*	AB646769.1	Yamaoka et al. (2010)
M. epiphylla	*S. viminalis*	AY652947.1	Pei et al. (2005)
M. epitea	*S. viminalis*	AY444778.2	Pei et al. (2005)
M. epitea	*S. acutifolia*	AY444777.2	Pei et al. (2005)
M. epitea	*S. arctica*	AY471620.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471621.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471622.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471633.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471624.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471625.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471626.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471627.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471628.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471629.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471630.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471631.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471632.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471633.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471634.1	Smith et al. (2004)
M. epitea	*S. arctica*	AY471635.1	Smith et al. (2004)
M. epitea	*S. interior*	AY471636.1	Smith et al. (2004)
M. epitea	*S. interior*	AY471637.1	Smith et al. (2004)
M. epitea	*S. interior*	AY471638.1	Smith et al. (2004)
M. epitea	*S. interior*	AY471639.1	Smith et al. (2004)
M. epitea	*S. nigra*	AY471640.1	Smith et al. (2004)
M. epitea	*S. nigra*	AY471641.1	Smith et al. (2004)
M. epitea	*S. nigra*	AY471642.1	Smith et al. (2004)
M. epitea	*S. nigra*	AY471643.1	Smith et al. (2004)
M. epitea	*S. bebbiana*	AY471644.1	Smith et al. (2004)
M. epitea	*S. bebbiana*	AY471645.1	Smith et al. (2004)
M. epitea	*S. bebbiana*	AY471646.1	Smith et al. (2004)
M. epitea	*S. bebbiana*	AY471647.1	Smith et al. (2004)
M. epitea	*Salix* sp.	AY471648.1	Smith et al. (2004)
M. iranica	*S. elbursensis*	FJ386432.2	Damadi et al. (2011)
M. laricis-epitea	*S. viminalis*	JF825968.1	Samils et al. (2011)
M. laricis-epitea	*S. viminalis*	JF825969.1	Samils et al. (2011)
M. laricis-epitea	*S. viminalis*	JF825970.1	Samils et al. (2011)
M. laricis-pentandrae	*S. pentandra*	AY444771.2	Pei et al. (2005)
M. paradoxa	—	GQ479269.1	—
M. paradoxa	—	GQ479270.1	—

Table 3-2 Continued.

M. paradoxa	—	GQ479271.1	—
M. paradoxa	—	GQ479272.1	—
M. paradoxa	—	GQ479273.1	—
M. ribesii-purpureae	*S. purpureae*	AY444770.2	Pei et al. (2005)
M. ribesii-purpureae	—	GQ479900.1	—
M. ribesii-purpureae	—	GQ479275.1	—
M. ribesii-purpureae	—	GQ479274.1	—
M. salicis-albae	*S. alba*	AY444775.2	Pei et al. (2005)
M. salicis-albae	*S. alba*	FJ455127.1	—
M. yezoensis	*S. jessoensis*	AB646768.1	Yamaoka et al. (2010)
Melampsora sp.	*S. arbuscula*	JN646136.1	Milne et al. (2012)
Melampsora sp.	*S. arbuscula*	JN646138.1	Milne et al. (2012)
Melampsora sp.	*S. aurita*	JN646169.1	Milne et al. (2012)
Melampsora sp.	*S. herbacea*	JN646119.1	Milne et al. (2012)
Melampsora sp.	*S. herbacea*	JN646120.1	Milne et al. (2012)
Melampsora sp.	*S. herbacea*	JN646121.1	Milne et al. (2012)
Melampsora sp.	*S. lanata*	JN646173.1	Milne et al. (2012)
Melampsora sp.	*S. lanata*	JN646174.1	Milne et al. (2012)
Melampsora sp.	*S. lapponum*	JN646205.1	Milne et al. (2012)
Melampsora sp.	*S. lapponum*	JN646206.1	Milne et al. (2012)
Melampsora sp.	*S. myrsinites*	JN646193.1	Milne et al. (2012)
Melampsora sp.	*S. myrsinites*	JN646199.1	Milne et al. (2012)
Melampsora sp.	*S. myrsinifolia*	JN646233.1	Milne et al. (2012)
Melampsora sp.	*S. reticulata*	JN646253.1	Milne et al. (2012)
Melampsora sp.	*S. reticulata*	JN646254.1	Milne et al. (2012)
M. laricis-populina	*Populus simonii*	AB116839.1	Tian et al. (2004)
M. laricis-populina	*P. simonii*	AB116841.1	Tian et al. (2004)

[a]No information available in GenBank.

Table 3-3 Phylogenetic groups recognized by sequences of rDNA ITS regions, D1/D2 region and EF-1α gene.

Phylogenetic groups	ITS +D1/D2	D1/D2 region	ITS regions	EF-1α gene
G1-1[a]	G1	D2	I1	E7
G1-2[a]	G1	D2	I1	E5
G2	G2	D1	I2	E9
G3	G3	D2	I3	—[b]
G4	G4	D2	I4	E4
G5	G5	D8	I7	E6
G6	G6	D2	I6	E12
G7	G7	D2	I5	—[b]
G8	G8	D2	I8	E11
G9	G9	D7	I9	E1
G10	G10	D7	I10	E3
G11	G11	D6	I14	—[b]
G12	G12	D9	I14	—[b]
G13	G13	D4	I12	—[b]
G14	G14	D7	I11	—[b]
G15	G15	D20	I17	—[b]
G16	G16	D19	I18	E8
G17	G17	D21	I20	—[b]
G18	G18	D2	I19	—[b]
G19	G19	D3	I28	E13
G20	G20	D10	I25	E17
G21	G21	D11	I26	—[b]
G22	G22	D5	I24	E14
G23	G23	D12	I29	—[b]
G24	G24	D13	I30	E18
G25	G25	D16	I25	—[b]
G26	G26	D15	I27	E16
G27	G27	D17	I16	E10
G28	G28	D14	I21	E2
G29	G29	D18	I32	—[b]

[a]Phylogenetic group G1 of rDNA phylogeny was divided into two phylogenetic groups, G1-1 and G1-2, based on phylogenetic result of EF-1α gene.

[b]Data did not obtained from this study.

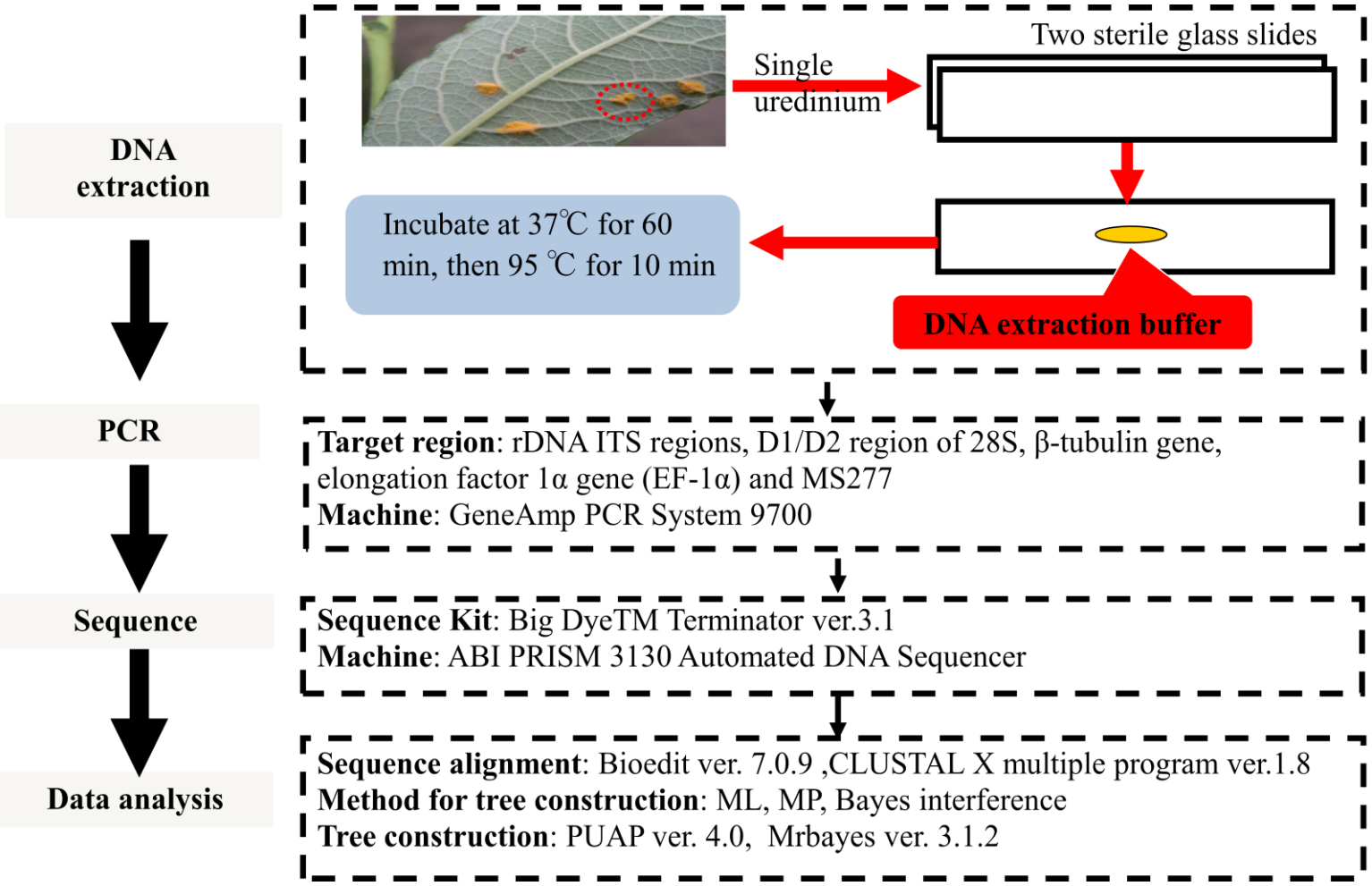
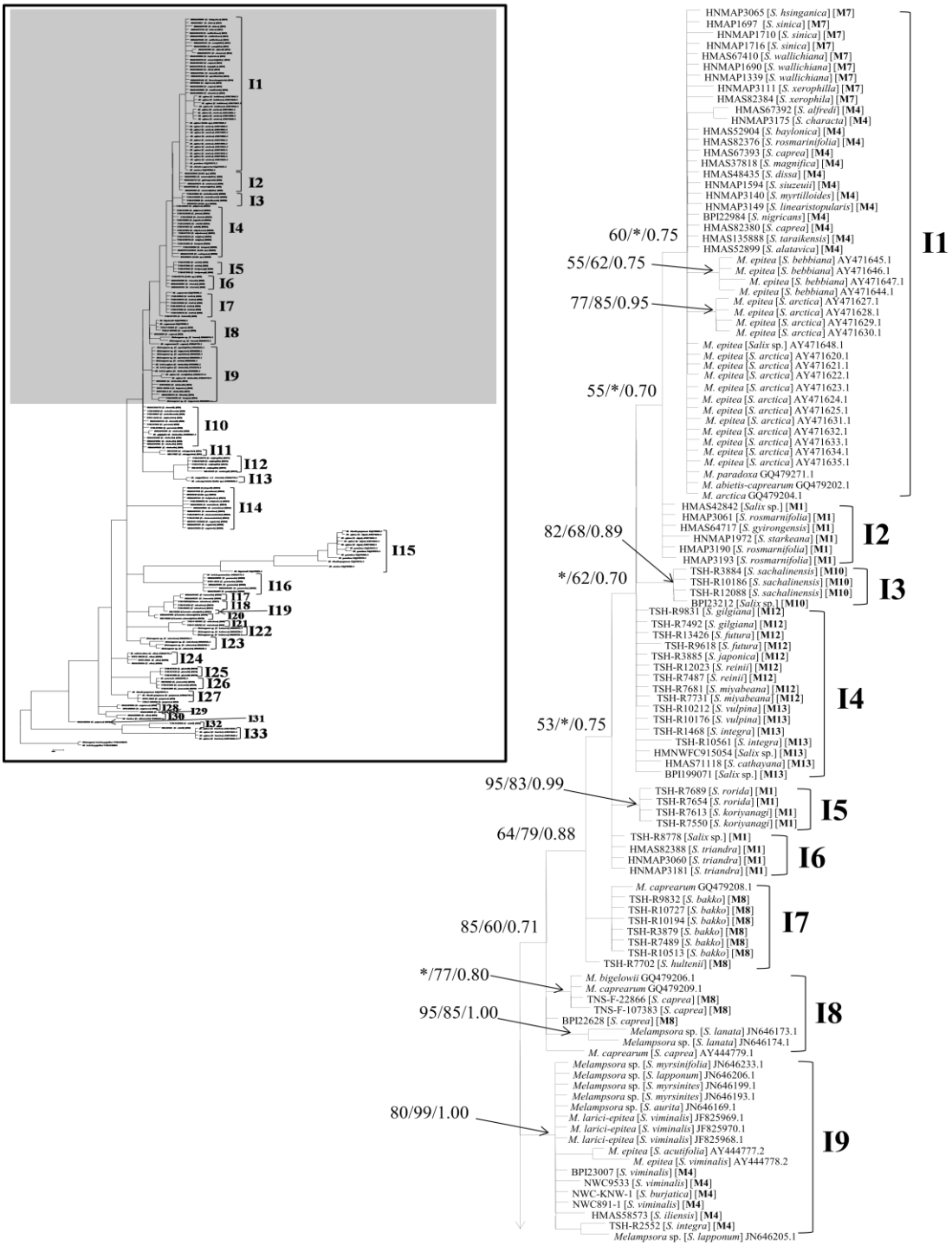


Fig 3-1 Procedure of molecular phylogenetic analyses.



(Continued on Fig. 3-3)

Fig. 3-2 Phylogenetic relationships of *Melampsora* on willows based on Bayesian analysis of rDNA ITS regions. Bayesian posterior probabilities (Bpp) were followed by the bootstrap values of MP and ML on the nodes in the topology. Asterisk (*) represented bootstrap values less than 50% or Bpp less than 0.75 in the topology. Letters in the parentheses after each specimen was indicated morphological group recognized by cluster analysis.

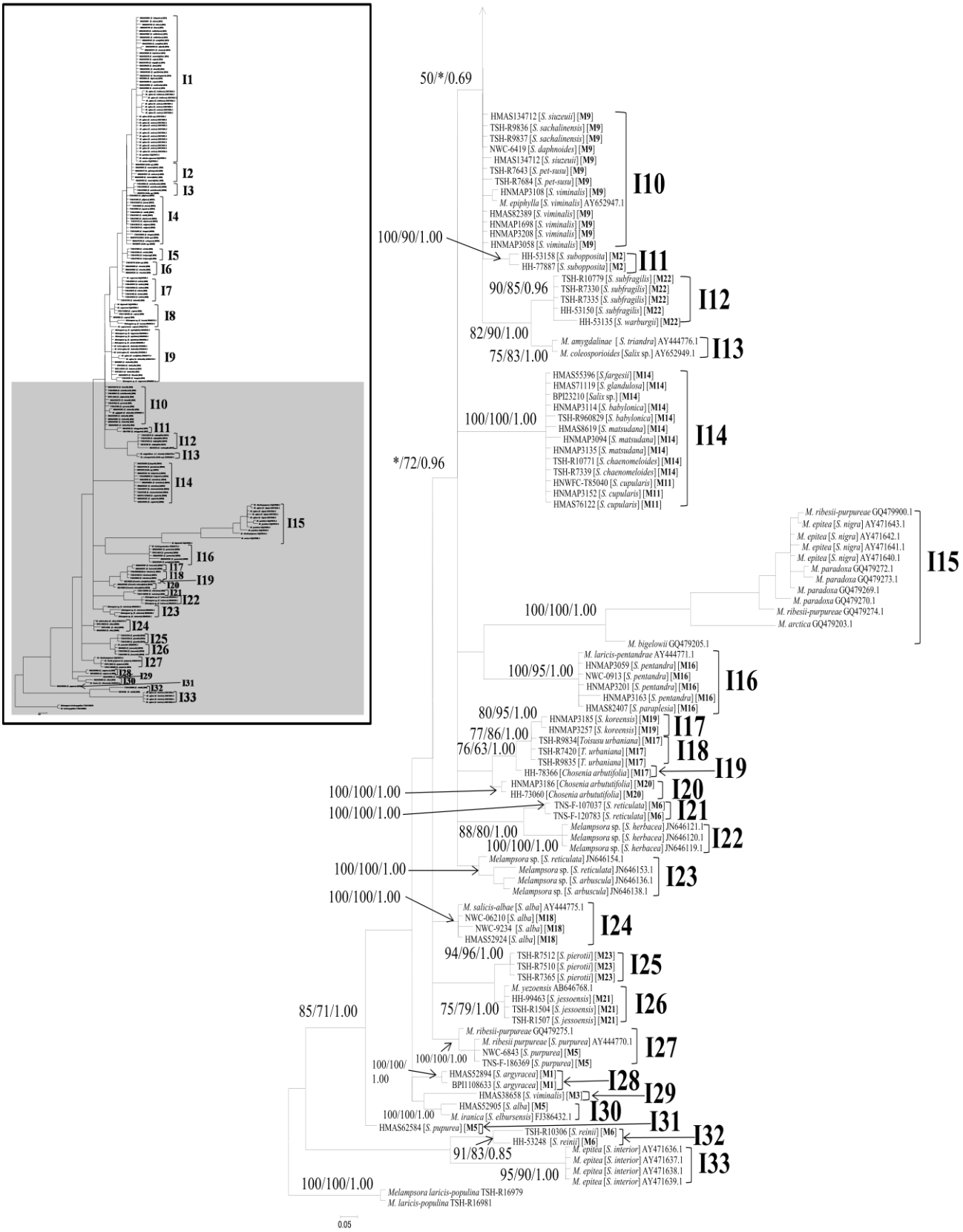
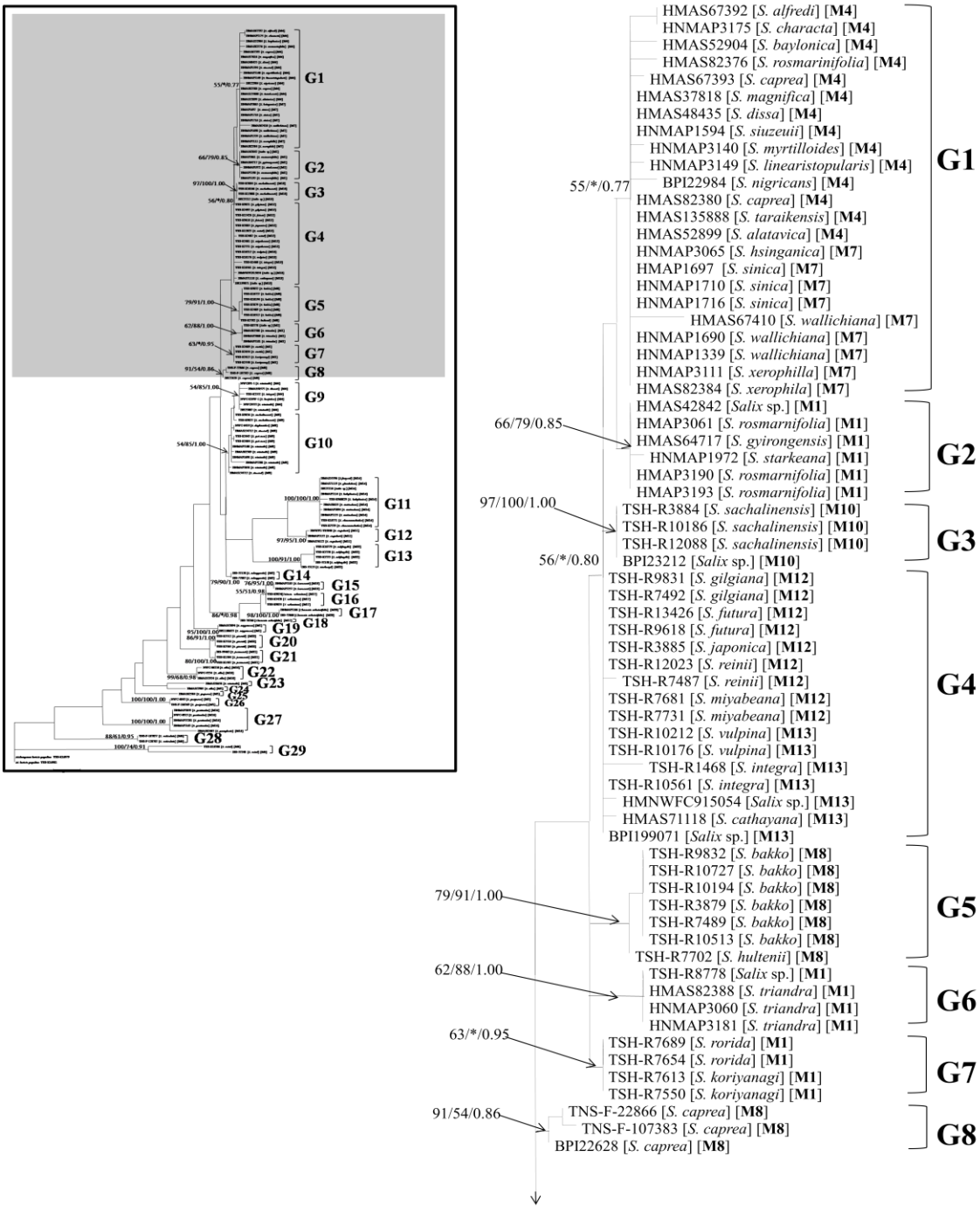


Fig. 3-3 Phylogenetic relationships of *Melampsora* on willows based on Bayesian analysis of rDNA ITS regions. Continued from Fig. 3-2.



(Continued on Fig. 3-5)

Fig. 3-4 Phylogenetic relationships of *Melampsora* on willows based on Bayesian analysis of rDNA D1/D2 region. Bayesian posterior probabilities (Bpp) were followed by the bootstrap values of MP and ML on the nodes in the topology. Asterisk (*) represented bootstrap values less than 50% or Bpp less than 0.75 in the topology. Letters in the parentheses after each specimen was indicated morphological group recognized by cluster analysis.

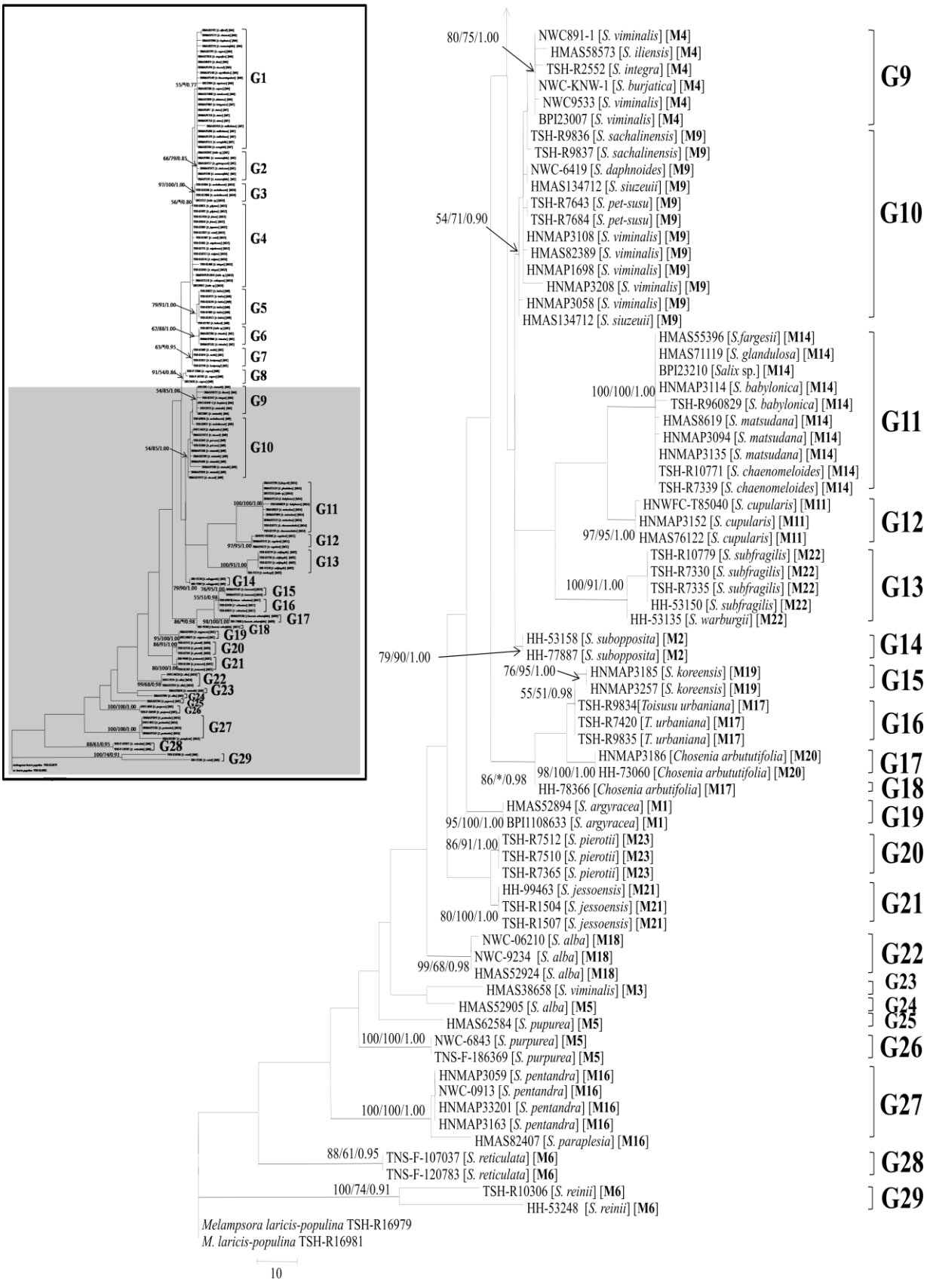


Fig. 3-5 Phylogenetic relationships of *Melampsora* on willows based on Bayesian analysis of rDNA D1/D2 region. Continued from Fig. 3-4.

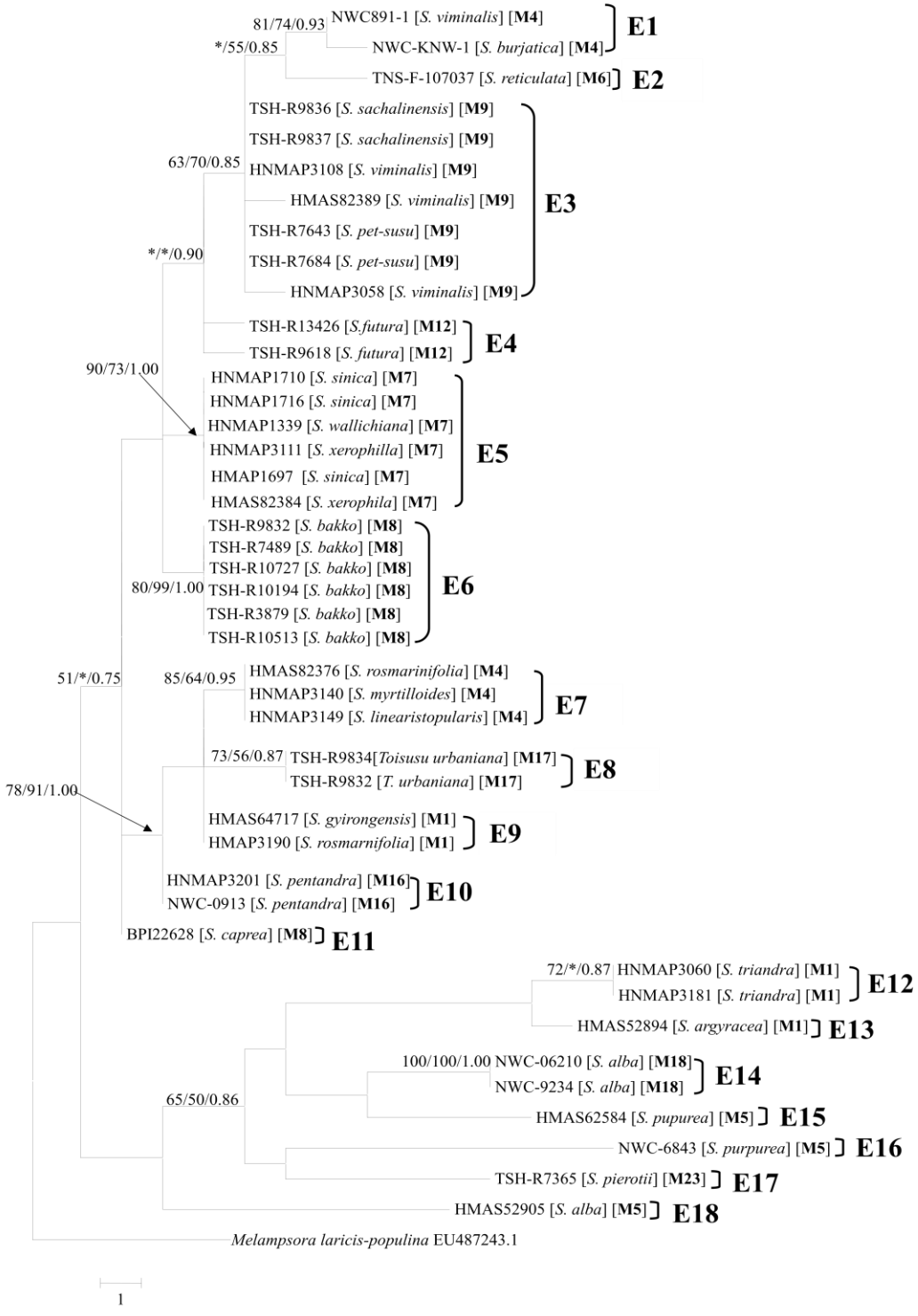
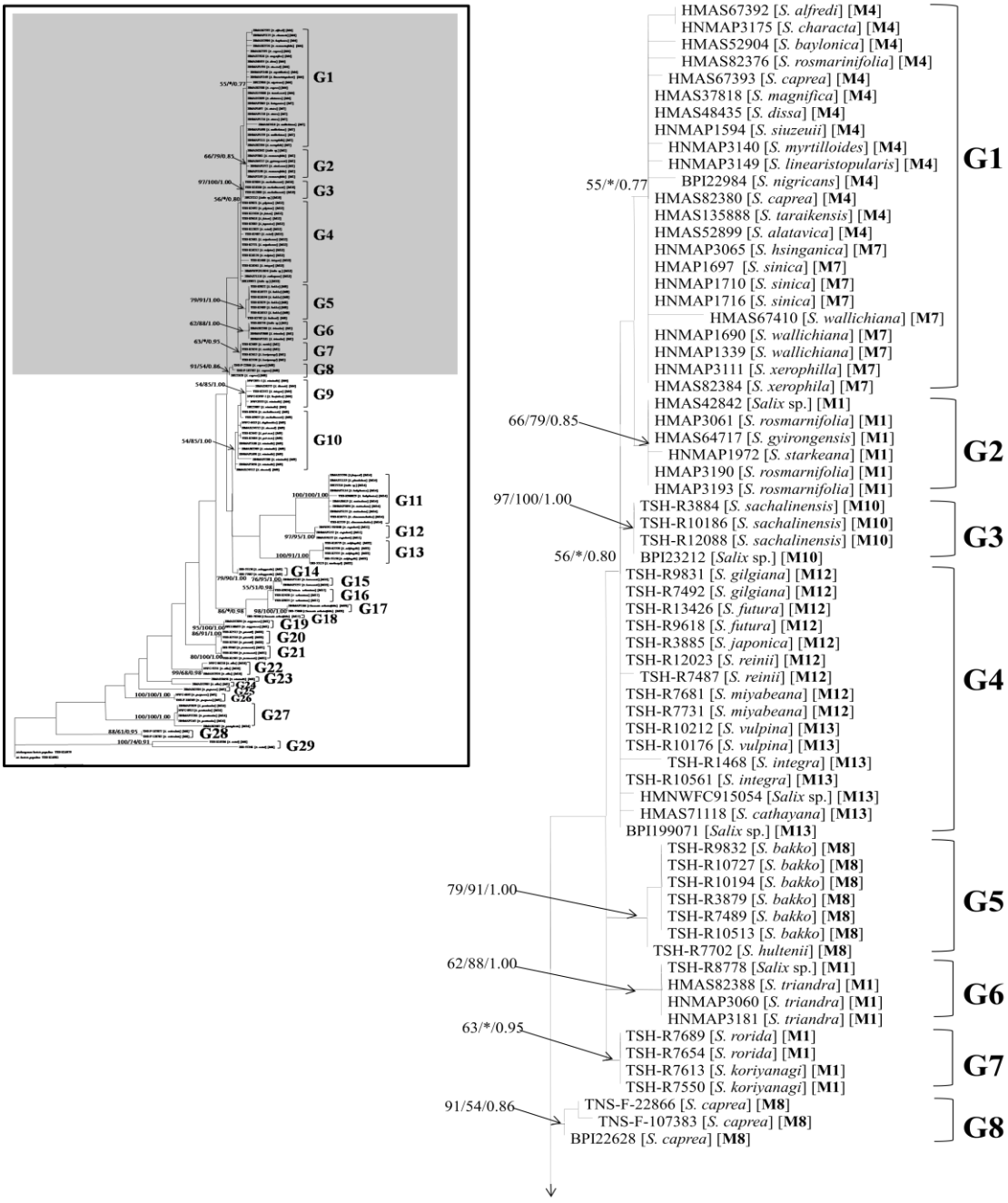


Fig. 3-6 Phylogenetic relationships of *Melampsora* on willows based on Bayesian analysis of EF-1α gene. Bayesian posterior probabilities (Bpp) were followed by the bootstrap values of MP and ML on the nodes in the topology. Asterisk (*) represented bootstrap values less than 50% or Bpp less than 0.75 in the topology. Letters in the parentheses after each specimen was indicated morphological group recognized by cluster analysis.



(Continued on Fig. 3-8)

Fig. 3-7 Phylogenetic relationships of *Melampsora* on willows based on Bayesian analysis of the combined data of rDNA ITS and D1/D2 regions. Bayesian posterior probabilities (Bpp) were followed by the bootstrap values of MP and ML on the nodes in the topology. Asterisk (*) represented bootstrap values less than 50% or Bpp less than 0.75 in the topology. Letters in the parentheses after each specimen was indicated morphological group recognized by cluster analysis.

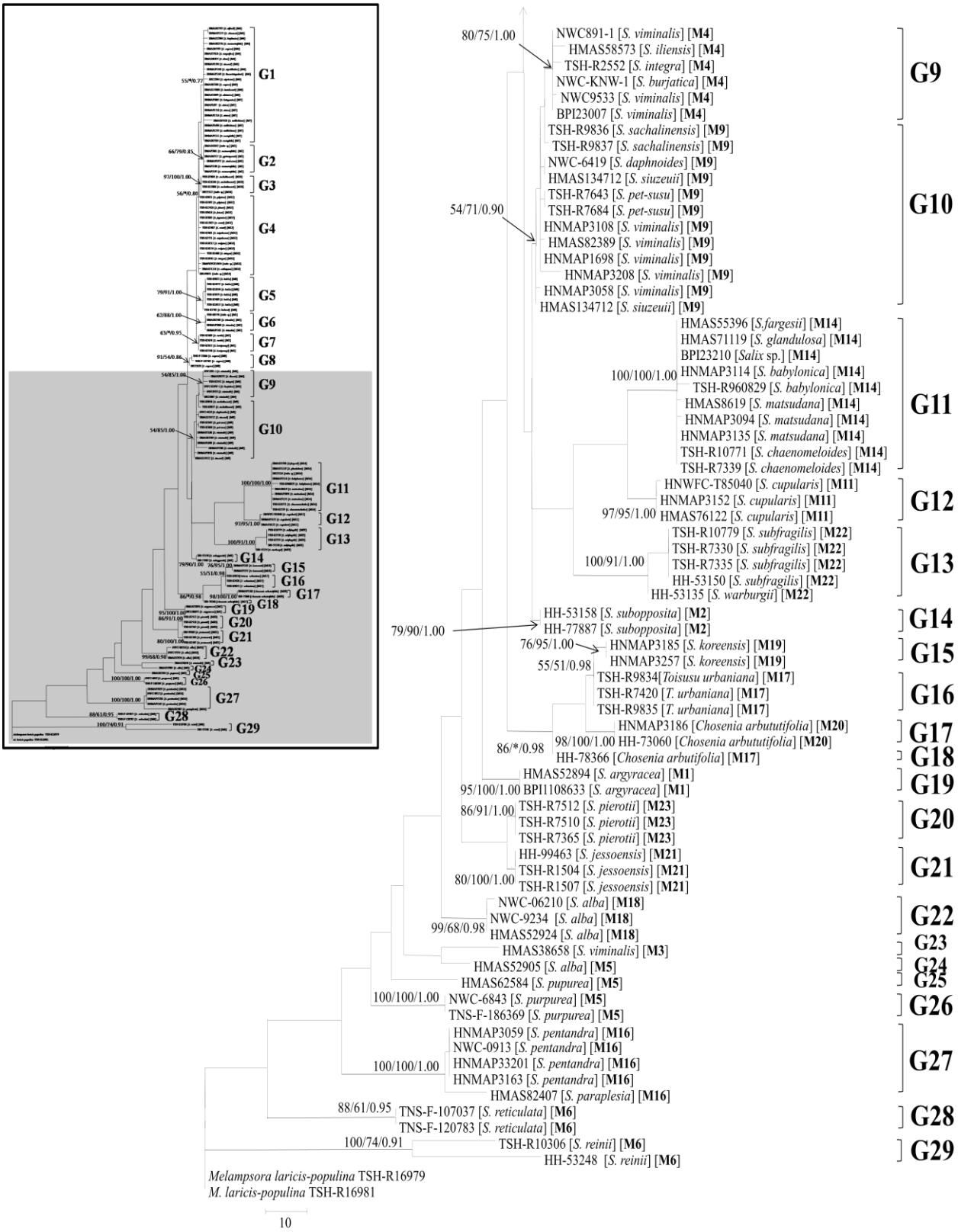


Fig. 3-8 Phylogenetic relationships of *Melampsora* on willows based on Bayesian analysis of the combined data of rDNA ITS and D1/D2 region. Continued from Fig. 3-7.

Chapter 4 Taxonomic discussion

4-1 Correlation of phylogenetic groups and morphological groups

Based on morphological characteristics in the uredinial and telial stages, numerical taxonomy was conducted to classify specimens using numeric algorithms including cluster analysis and one-way ANOVA. Hierarchical clustering analysis recognized 23 groups (M1 to M23) based on overall similarities of 19 morphological characteristics (Fig. 2-10). Molecular phylogenetic studies on sequence data of rDNA ITS regions, D1/D2 region and EF-1α gene recognized 30 phylogenetic groups from specimens of 22 morphological groups (except M15). The correlation of morphological groups and phylogenetic groups was shown in Fig. 4-1.

Among these 30 phylogenetic groups, fourteen groups, G1-2, G3, G10～G15, G17, G20～G23, G27 were consistent with the morphological groups M7, M10, M9, M14, M11, M22, M2, M19, M20, M23, M21, M18, M3 and M16, respectively (Fig. 4-1 red line). Morphological comparisons of 19 morphological characteristics within above-mentioned morphological groups indicated that no apparent difference was recognized among specimens in each morphological group. Thus, these groups were recognized as separate taxa.

However, the other 16 phylogenetic groups were not consistent with the morphological groups recognized by cluster analysis. Among them, four phylogenetic groups, G2, G6, G7 and G19 were corresponded to a morphological group, M1 (Fig. 4-1 blue line). Specimens in these phylogenetic groups owned globoid or ellipsoid urediniosores, epiphyllous telia, subepidermal teliospores without thickened apex. Liu (2005) reported *M. epitea*, *M. lapponum*, *M. kuprevicizii* and *M. repentis* as separate species in China based on the differences in the shape and the dimension of urediniospores and the dimension of teliospores. All the specimens used by Liu (2005) were included in M1. Morphological comparison with the other morphological group indicated that the above-mentioned characteristics did not show clear differences

among specimens in M1. However, detailed examination of other morphological characteristics showed that these specimens were able to be classified into four morphological groups (Fig. 4-2 A) based on the difference in the distance between spines and the length of paraphyses (Fig. 4-2 B). These four morphological groups corresponded to G2, G6, G7 and G19, and they were recognized as separate taxa.

Two phylogenetic groups, G5 and G8, were corresponded to M8, which was characterized by hypophyllous uredinia, globoid or ellipsoid urediniospores, epiphyllous telia, subcuticular teliospores with apparently thickened apex. Based on taxonomic systems provided by Wilson and Henderson (1966), Hiratsuka and Kaneko (1982) and Bagyanarayana (2005), specimens in M8 were regarded as *M. capraearum* due to its subcuticular teliospores with apparently thickened apex. However, detailed comparison of specimens in M8 indicated that it could be divided into two groups based on the distance between spines (Fig. 4-3). These two groups corresponded to G5 and G8, and they were recognized as separate taxa.

Two phylogenetic groups, G16 and G18, were corresponded to M17, which was characterized by having hypophyllous uredinia, obovid or ellipsoid urediniospores germ pore tending to bizonate, hypophyllous telia and subepidermal teliospores without thickened apex. Although the above-mentioned morphological characteristics did not show apparent differences, M17 could be classified into two groups based on the apex thickness in urediniopsores. One group was found on *Toisusu urbaniana* with apparently thickened apex up to 6.7 μm and another group was found on *Chosenia arbutifolia* with evenly thickened walls in urediniospores (Appendix 1). These two groups corresponded to two phylogenetic groups G16 and G18, and they were recognized as separate taxa.

Three phylogenetic groups, G24, G25 and G26, were corresponded to a morphological group M5 (Fig. 4-1 blue line), which was characterized by having amphigenous uredinia, globoid and ellipsoid urediniospores, amphigenous telia and subepidermal teliospores without thickened apex. Except these above-mentioned characteristics, specimens in M5 could be divided into three morphologically distinct groups in the length of teliospores and the distance between spines (Fig. 4-4). These

three groups corresponded to phylogenetic groups G24, G25 and G26, and they could be recognized as separate taxa. Among them, G25 could differentiate from G24 and G26 in distance between spines (Fig. 4-4 A), and G24 differed from G25 and G26 in the length of teliospores (Fig. 4-4 B).

Two phylogenetic groups, G28 and G29, were corresponded to M6 (Fig. 4-1 blue line), which had hypophyllous uredinia, globoid, ellipsoid or obovoid urediniospores, amphigenous telia and subepidermal teliospores without thickened apex. Specimens in M6 were able to be recognized as *M. epitea* according to Hiratsuka and Kaneko (1982) and Bagyanarayana (2005). However, detailed analyses of morphological characteristics in the present study revealed that M6 was able to be divided into two morphological groups based on differences in the distance between spines and the length of paraphyses (Fig. 4-5 A, B and C). These two groups were corresponding to G28 and G29, and they could be recognized as separate taxa.

Two phylogenetic groups, G1-1 and G9, were corresponded to a morphological group M4, which was characterized by having hypophyllous uredinia, globoid or ellipsoid urediniospores with evenly thickened walls, without thickened apex in urediniopsores, paraphyses and teliospores, amphigenous telia with subepidermal teliospores. Although *M. euonymi-capraearum* and *M. ribesii-purpureae* were treated as synonym of *M. epitea* in Europe (Wilson and Henderson 1966), Liu (2005) separately reported these species from *M. epitea* in China based on the difference in the dimension of urediniospores and the dimension of teliospores. Specimens used by Liu (2005), were included in M4, and no distinguishable morphological difference was recognized among specimens. Recent molecular phylogenetic studies have already revealed the presence of cryptic species in *M. epitea* (Bennett et al. 2011; Milne et al. 2012). These taxa embedded within one morphospecies might have been genetically isolated for a long time to lose the ancestral shared polymorphism, but they did not accumulate obvious synapomorphic morphological characters to discriminate these cryptic species at the same time period (Stefani et al. 2013). Thus, G1-1 and G9 were tentatively recognized as discrete taxa based on molecular information.

Phylogenetic group G4 was composed of two morphological groups, M12 and M13 (Fig. 4-1 green line) although two morphological groups differed from each other based on the length of urediniospores. They were tentatively treated as two distinct taxa based on morphological evidence, and they were designated as G4 (M12) and G4 (M13).

Based on the combination of molecular groups and morphological groups, 31 taxa were recognized. Although morphological group M15 was not included in the molecular phylogenetic analyses due to the failures in DNA extraction, specimens in this group had unique morphological characteristics, such as epiphyllous uredinia and telia, which had never found in other taxa in this study. Moreover, this group included only one type specimen of *M. salicis-cavaleriei*, which was reported by Tai (1979). It was tentatively treated as a separate taxon. Thus, totally 32 taxa were recognized based on morphological and molecular evidence in the present study.

Morphological studies using hierarchical clustering analysis revealed 12 morphological characteristics appeared to be significant characters for classification and these characters were proved as informative by molecular data. In addition to these characters, two additional new morphological characteristics, the distance between spines and the length of paraphyses, were found as the important characters based on correlation of morphological groups and phylogenetic groups. The distance between spines has already been used for taxonomic studies in the rust fungi, but the effectiveness of this character varied in different rust fungi (Smith et al. 2004; Tian et al. 2004; Liang 2006). In the *Pucciniastrum* species, Liang (2006) recognized that the distance between spines was not an effective character based on morphological and molecular information. However, through comprehensive studies of *Melampsora* species on poplar in China, Tian et al. (2004) indicated that this character was effective to distinguish species and the molecular data also proved this character to be phylogenetically informative. In the *Melampsora* species on willows, Smith et al. (2004) first evaluated this character and suggested that this character was effective to distinguish the cryptic species in *M. epitea*. However, the conclusion was not drawn due to limited samples in their study. In this study, based on comprehensive analyses

of morphological and molecular information, the distance between spines was proved to be an effective character and it is a new character for species recognition in the *Melampsora* species on willows. Although the morphology of paraphyses was used for taxonomic studies in other rust fungi, only the apex thickness of paraphyses was used for species delimitation in *Melampsora* species on willows (Hiratsuka and Kaneko 1982). The length of paraphyses was first proved to be an effective character for species delimitation.

4-2 Taxonomy and nomenclature of 32 taxa identified in this study

The present study recognized 32 taxa based on morphological and molecular phylogenetic analyses. Taxonomy and nomenclature of these taxa were discussed in the following paragraph.

4-2-1 *Melampsora epitea* and the related species

Melampsora epitea Thümen was first established by Thümen (1879) on *S. alba*, but this name was questionable due to lack of the type specimen information and no credible records of this species until now (Pei 2005). Since the aecial and telial host ranges were excluded for species recognition, Hylander (1953) first included six Scandinavian species with indistinguishable morphology into *M. epitea* although these species had different aecial host range. This taxonomic treatment was widely accepted, and morphologically similar European, North American and Asian *Melampsora* species with different aecial host ranges were lumped into this species complex (Wilson and Henderson 1966; Ziller 1974; Hiratsuka and Kaneko 1982). Until now, this species complex included up to 21 previously reported species as synonyms, which had similar morphology with different host alternation on *Abies*, *Euonymus*, *Larix*, *Ribes*, *Saxifraga*, *Viola* and some Orchidaceae (Bagyanaryana

2005). However, recent molecular phylogenetic studies revealed high genetic divergences within this species complex (Pei et al. 2005; Benette et al. 2011; Milne et al. 2012).

In this study, specimens, which labeled as *M. arctica*, *M. euonymi-capraearum*, *M. humilis*, *M. kiusiana*, *M. lapponum*, *M. reticulatae*, *M. laricis-epitea*, *M. repentis* and *M. ribesii-purpureae* as well as *M. epitea* were borrowed from China, Europe, Japan and Russia. These former 9 *Melampsora* species were recognized as synonyms of *M. epitea* by Bagyanaryana (2005). All specimens were found in 14 separate taxa, including G1-1, G2, G4 (M12), G4 (M13), G6, G7, G9, G14, G19, G24, G25, G26, G28 and G29.

G1-1 was characterized by having hypophyllous uredinia, globoid or ellipsoid urediniospores with evenly thickened walls, echinulate type 1, without thickened apex in urediniopsores, paraphyses and teliospores, amphigenous telia with subepidermal teliospores. This taxon included specimens on *S. alfredii*, *S. caprae*, *S. character*, *S. dissa*, *S. purpureae*, *S. linearistopularis*, *S. myrtilloides*, *S.magnifica*, *S. taraikensis*, *S. rorida* and *S. rosmarinifolia*, which were previously identified as *M. epitea*, *M. euonymi-capraearum*, *M. repentis*, *M. laricis-epitea* or *M. ribesii-purpureae* in China based on differences in the shape of urediniospores, the dimension of urediniospores, the position of teliospores, the dimension of teliospores and telial host range (Tai 1979; Zhuang 1994a; Zhuang and Wei 2002; Liu 2005). In this study, no apparent difference was found among the specimens in this taxon. Phylogenetic studies using rDNA ITS regions revealed that this taxon was close to North American *M. epitea* on *S. arctica* and *S. bebbiana* (I1 in Fig. 3-2). The present fungus seemed to be one of the members of *M. epitea* or the new species close to them. Since the type specimens of the above-mentioned species were not included in the present analyses, the specific name of the present fungus was not able to be determined. Therefore, G1-1 was designated as *Melampsora* sp.1.

G2 was characterized by having hypophyllous uredinia, globoid or ellipsoid urediniospores, epiphyllous telia and subepidermal teliospores without thickened apex. This taxon included specimens from *S. gyirongensis*, *S. rosmanifolia* and *S. starkeana*,

which was previously named as *M. epitea*, *M. lapponum* or *M. kuprevicizii* in China by different taxonomists (Zhuang 1994b; Liu 2005). This taxon differed from *M. epitea* in its epiphyllous telia, but it resembled to *M. lapponum* and *M. kuprevicizii* in the position of telia, dimension of urediniospores and teliospores (Pei 2005). Although *M. kuprevicizii* was originally reported on *S. rosmanifolia* (Azbukina 1974), it was still difficult to determine the name of this taxon because type specimens of these three species were not included in analyses. This taxon was tentatively designated as *Melampsora* sp. 2.

G4 (M12) had hypophyllous uredinia, globoid or ellipsoid urediniospores, peripheral paraphyses, hypophyllous telia and subepidermal teliospores without thickened apex. This taxon included specimens on *S. futura*, *S. miyabeana*, *S. japonica* and *S. reinii* from Japan. Based on Hiratsuka and Kaneko (1982), rust fungi on these willows were recognized as *M. epitea*. But fungi on *S. miyabeana* were described as *M. laricis-miyabeana* based on the dimension of urediniospores, the dimension of teliospores and telial host range (Matsumoto 1919). This species was treated as a synonym of *M. epitea* (Hiratsuka and Kaneko 1982). Because no type specimen was designated in *M. laricis-miyabeana*, relationship of *M. epitea*, *M. laricis-miyabeana* and present taxon was unknown. This taxon (I4 in Fig. 3-2) was phylogenetically distinct from *M. epitea* from Europe and North America. Because the existence of peripheral paraphyses was not reported neither in *M. epitea* nor in its synonyms in the former taxonomic studies, comprehensive studies on *M. epitea* and related species are required. Thus, this taxon was tentatively designated as *Melampsora* sp. 3.

G4 (M13) had similar morphology as G4 (M12) except for its relatively shorter length of urediniospores. This taxon included specimens on *S. futura*, *S. integra* and *S. vulpina* from Japan, and it also included specimens on *S. cathayana* and several unknown *Salix* species from China. According to Hiratsuka and Kaneko (1982), Japanese rust fungi on *S. futura* was identified as *M. epitea*, and the rust fungi on *S. integra* could be identified as *M. humilis*. Although the type specimen of *M. humilis* was included in this study, it was found in another taxon, G7. This taxon seemed to be

closely related with *M. epitea*, and it was designated as *Melampsora* sp. 4 due to the reason mentioned above.

G6 resembled to G2 (*Melampsora* sp. 2) but differed in the distance between spines and the length of paraphyses. This taxon included specimens from *S. triandra* in China and one unidentified *Salix* species from Russia. Liu (2005) identified the rust fungus on *S. triandra* in China as *M. repentis*, which was widely accepted as a synonym of *M. epitea* (Wilson and Henderson 1966; Bagyanarayana 2005). Liu (2005) did not make comparisons with the type specimens of *M. epitea* and *M. repentis*. Although G6 was proved to be a distinct taxon, the name of this taxon could not be determined because the type specimen of *M. repentis* was not included in this study. This taxon was tentatively designated as *Melampsora* sp. 5.

G7 resembled to G2 and G6 but differed in the distance between spines and the length of paraphyses. This taxon included Japanese specimens on *S. koriyanagi* and *S. rorida*. Although the rust fungus on *S. rorida* was recognized as *M. epiphylla* according to Hiratsuka and Kaneko (1982), no apparent thickened apex was recognized in teliospores. The rust fungus on *S. koriyanagi* was recognized as *M. humilis*, and the isotype specimen (HH-53278) of *M. humilis* was included in G7. Thus, this taxon was identified as *M. humilis.*

G9 resembled to G1-1 and no apparent morphological difference was recognized between two taxa although they were phylogenetically distinct. G9 included specimens from *S. iliensis* from China, *S. burjatica* and *S. viminalis* from Europe and *S. integra* from Japan. The rust fungus on *S. integra* in Japan was usually regarded as *M. humilis* (Hiratsuka and Kaneko 1982), but *M. humilis* was recognized in another taxon (G7) and differed from this taxon in the position of telia. Zhuang (1989) identified rust fungus on *S. iliensis* as *M. laricis-epitea* in China and suggested that *M. laricis-epitea* was able to be separated from *M. epitea* based on differences in the apex thickness of paraphyses (Zhuang 1989). The rust fungus on *S. burjatica* and *S. viminalis* from Europe was recognized as *M. epitea* based on morphology although it was previously treated as *M. laricis-epitea* based on both morphology and host range (Plowright 1889). It was still difficult to determine the name of this taxon because the

type specimens of these three species were not included in this study. Thus, this taxon was designated as *Melampsora* sp. 6.

G14 had hypophyllous uredinia, globoid or ellipsoid urediniospores, epiphyllous telia and subepidermal teliospores and slender teliospores up to 60 μm. This taxon was found on *S. subopposita* from Japan, and rust fungus on this willow species was recognized as *M. kiusiana*. Type specimen (HH-53157, holotype) was included in this taxon based on the present morphological and phylogenetic studies, and this taxon was identified as *M. kiusiana*. Although *M. kiusiana* was suggested as a synonym of *M. epitea* by Bagyanarayana (2005), this species was distinguished from *M. epitea* and other *Melampsora* species in its epiphyllous telia and slender teliospores up to 60 μm.

G19 differed from G2, G6 and G7 in its distance between spines and the length of paraphyses, moreover, this taxon was distinguishable from G2, G6 and G7 in its teliospores with slightly thickened apex. This taxon included specimens from *S. argyracea* in China, and there was no record of *Melampsora* species on this willow species in China before. The rDNA ITS phylogeny indicated that this taxon formed a well supported lineage (I28 in Fig. 3-3), which was distinct from other *Melampsora* species. Thus, this taxon is regarded as a new species, *M. salicis-argyraceae* P. Zhao & Y. Yamaoka, sp. nov., based on both morphological and molecular evidence.

G24 was characterized by having amphigenous uredinia, globoid and ellipsoid urediniospores, amphigenous telia and subepidermal teliospores without thickened apex. This taxon included specimens from *S. alba* in China, and it was recognized as *M. epitea* (Zhuang 1989). In the rDNA ITS phylogeny, this taxon formed a highly supported group (I30 in Fig. 3-3) with the holotype specimen of *M. iranica* (GenBank accession No. FJ386432.2). Morphological characteristics of this taxon in the present study fitted well with the taxonomic description of the holotype specimen of *M. iranica* provided by Damadi et al. (2011). Although the type specimen was not included in this study, this taxon was identified as *M. iranica* based on morphological and molecular information. This species was new to China.

G25 resembled to G24 except for the distance between spines and the length of teliospores. This taxon included specimens on *S. purpurea* from Europe. rDNA ITS phylogeny indicated that this taxon formed a well supported lineage (I27 in Fig. 3-3) together with sequence data of *M. ribesii-purpureae* from GenBank. *Melampsora ribesii-purpureae* was reported on *S. purpurea* in Europe (Klebahn 1914; Sydow and Sydow 1915), and it was treated as a synonym of *M. epitea* according to Wilson and Henderson (1966) and Pei (2005). Although this taxon seemed to be one of the members of *M. epitea*, the specific name of this taxon was still uncertain because the type specimens of *M. epitea* and *M. ribesii-purpureae* were not examined in this study. Thus, this taxon was tentatively named as *Melampsora* sp. 7.

G26 resembled to G24 and G25 except for the distance between spines and the length of teliospores. This taxon included specimens on *S. purpurea* from China and they were named as *M. ribesii-purpureae* (Tai 1979). In this study, this taxon formed a distinct lineage (I31 in Fig. 3-3) in the rDNA ITS phylogeny, which was phylogenetically distinct from other members of *M. epitea*. Both morphological and molecular evidence supported that this taxon is a new species, and it was named as *M. salicis-purpureae* P. Zhao & Y. Yamaoka, sp. nov.

G28 had hypophyllous uredinia, globoid, ellipsoid or obovoid urediniospores, amphigenous telia and subepidermal teliospores without thickened apex. This taxon was found on *S. reticulata* from Europe. The rust fungus on *S. reticulata* was described as *M. reticulatae* based on morphology and host range (Klebahn 1914), but this species was treated as a synonym of *M. epitea* (Wilson and Henderson 1966; Bagyanarayana 2005). Because the type specimens of *M. epitea* and *M. reticulatae* were not included in this study, the name of this taxon is still not confirmed although it formed a distinct group in the rDNA ITS phylogenies (I21 in Fig. 3-3). Thus, it was tentatively named as *Melampsora* sp. 8.

G29 resembled to G28 but differed in the distance between spines and the length of paraphyses. This taxon was found on *S. reinii* from Japan, and the rust fungus on this willow species was regarded either as *M. epitea* or *M. arctica* (Hiratsuka and Kaneko 1982). In the molecular phylogeny, this taxon formed a distinct group (I32 in

Fig. 3-3). Because the type specimens of *M. arctica* and *M. epitea* were not included in this study, G29 was designated as *Melampsora* sp. 9.

4-2-2 *Melampsora capraearum* and the related species

Melampsora capraearum Thümen was first reported on *S. caprea* in Europe (Thümen 1879), and this species was characterized by its subcuticular teliospores with predominantly thickened apex. In Europe, this species was reported on *S. aurita*, *S. caprea*, *S. cinerea* and their hybrids (Wilson and Henderson 1966), and Japanese rust fungus on *S. bakko*, *S. hultenii* and *S. leucopithecia* was treated as *M. capraearum* (Hiratsuka et al. 1990). In China, *M. capraearum* and its synonym (*M. laricis-caprearum*) were reported on 13 willow species. In this study, specimens on *S. hsinganica*, *S. sinica*, *S. starkeana*, *S. wallichiana* and *S. xerophila* from China, specimens on *S. bakko* and *S. hultenii* from Japan and specimens on *S. caprea* from Europe owned subcuticular teliospores with predominantly thickened apex were used. These specimens were located in three phylogenetically distinct groups, G1-2, G5 and G8.

G1-2 was characterized by having hypophyllous uredinia, globoid or ellipsoid urediniospores, amphigenous telia, subcuticular teliospores with apparently thickened apex. This taxon included specimens collected in China which were identified as *M. capraearum* or its synonym (*M. laricis-caprearum*) due to its subcuticular telia with apparently thickened apex (Tai 1979; Cao and Li 1999; Zhuang and Wei 2002; Liu 2005). However, this taxon differed from *M. capraearum* (Wilson and Henderson 1966; Hiratsuka and Kaneko 1982; Bagyanarayana 2005) in the position of telia, the distance between spines, the length of teliospores and the apical wall thickness of teliospores. Furthermore, it phylogenetically differed from *M. capraearum* on *S. bakko* in Japan (G5) and on *S. caprea* in Europe (G8). Thus, this taxon was considered as a new species, *M. salicis-sinicae* P. Zhao, C. M. Tian & Y. J. Yao, sp. nov.

G5 was characterized by having hypophyllous uredinia, globoid or ellipsoid urediniospores, epiphyllous telia, subcuticular teliospores with apparently thickened apex. This taxon was similar to G1-2 except for its epiphyllous telia, thickness of the apical wall in teliospores and the distance between spines. G5 was found on *S. bakko* and *S. hultenii* from Japan and previously identified as *M. capraearum* because of its apparently thickened apex in teliospores (Hiratsuka et al. 1990). Although *M. capraearum* was first described in Germany with a type specimen on *S. caprea*, the rust fungus on *S. bakko* and *S. leucopithecia* Kimura in Japan was also considered to be conspecific with *M. capraearum* due to existence of thickened apex in teliospores (Ito 1938; Hiratsuka et al. 1992). In this study, G5 was distinct from the taxon on *S. caprae* from Europe. The rust fungus on *S. caprae* from Europe may be *M. capraearum* according to host information and geographic distribution, but conclusion was not able to be drawn because the lectotype specimen of this species was not included in this study. Here G5 was tentatively designated as *M. capraearum* 1.

G8 resembled to G5 but differed in the distance between spines. This taxon was found *S. caprae* from Europe and recognized *M. capraearum* based on subcuticular teliospores with apparently thickened apex (Wilson and Henderson 1966). Since *M. capraearum* was first reported on *S. caprae* in Europe (Thümen 1879), this taxon seemed to be *M. capraearum*. However, another taxon, G5, also owned similar morphology as *M. capraearum*. These two taxa differed mainly in the distance between spines, but this character was not used for previous taxonomic studies. Because the lectotype specimen of this species was not included in this study, here this taxon was tentatively designated as *M. capraearum* 2.

4-2-3 The other *Melampsora* species

G3 was characterized by having hypophyllous uredinia, globoid or ellipsoid urediniospores, epiphyllous telia and subcuticular or subepidermal teliospores with thickened apex. This taxon was constituted of specimens from *S. sachalinensis* from

Japan and one unidentified willow species from China, and morphologically it could be identified as *M. epiphylla* according to Hiratsuka and Kaneko (1982). In addition, morphological examination confirmed that the isotype specimen (HH-77578) was included in this taxon although DNA was failed to extract from the isotype specimen. Thus, this taxon was identified as *M. epiphylla*.

G10 was characterized by having hypophyllous uredinia, globoid or ellipsoid urediniospores, epiphyllous telia and subepidermal or subcuticular teliospores with slightly thickened apex. This taxon resembled to *M. epitea* in the dimension of urediniospores and teliospores but differed in its subepidermal or subcuticular teliospores. This taxon included specimens from *S. viminalis* in China, which were recognized as *M. ribesii-viminalis* due to its subcuticular teliospores (Zhuang and Wei 2002; Liu 2005). In addition, the rust fungus on *S. viminalis* from Europe, which was also recognized as *M. ribesii-viminalis* (Wilson and Henderson 1966), was also included in this taxon. Although the type specimen was not included in this study, morphological and molecular phylogenetic information indicated that this taxon was *M. ribesii-viminalis.*

G11 was characterized by having obovid or ellipsoid urediniospores with smooth spots at apex, echinulate type 2, germ pore bizonate, amphigenous telia, subepidermal or subcuticular teliospores without thickened apex. This taxon included rusts on *S. babylonica*, *S. chaenomeloides*, *S. fargesii*, *S. glandulosa* and *S. matsudana*. In China, the rust fungus on *S. babylonica*, *S. chaenomeloides*, *S. glandulosa* and *S. matsudana* were recognized as *M. coleosporioides* (Tai 1979; Zhuang 1994b; Liu 2005). The rust fungus on *S. fargesii* was reported as *M. microsora* in China (Zhuang 1994b), but differed from *M. microsora* in position of uredinia and telia, position of teliospores and the spine form of urediniospores. *Melampsora coleosporioides* was first described in Japan based on specimens on *S. babylonica* (Dietel 1902). The rusts on *S. babylonica* and *S. matsudana* were recognized as *M. coleosporioides* but rust on *S. chaenomeloides* was recognized as *M. chelidonii-pierotii* in Japan (Hiratsuka and Kaneko 1982). However, *M. chelidonii-pierotii* differed from this taxon in its

absolutely subcuticular teliospores. Therefore, this taxon was recognized as *M. coleosporioides* although type specimen was not observed in this study.

G12 was characterized by having hypophyllous uredinia, globoid or ellipsoid urediniospores with evenly thickened wall, echinulate type 1, amphigenous telia with subepidermal or subcuticular teliospores. This taxon was similar to *M. epiphylla* (G3) in its amphigenious telia with subepidermal or subcuticular teliospores, but this taxon did not own thickened apical walls in teliospores. In addition, the dimension of urediniospores of this taxon varied more than *M. epiphylla*. This taxon included specimens from *S. cupularis* in China, and they were recognized as *M. sacliscis-cupularis* according to Tai (1979). Although the type specimen was not found in this study, one specimen, HMNWFC-T85040, which was collected from the same location as the holotype specimen, was included in this taxon. Therefore, this taxon was recognized as *M. salicis-cupularis*.

G13 had obovid or ellipsoid urediniospores, smooth regions at apex, echinulate type 2, germ pore bizonate, hypophyllous telia and subepidermal teliospore. This taxon included specimens on *S. subfragilis* and *S. warburgii*. According to Hiratsuka and Kaneko (1982), the rust fungus on *S. subfragilis* was recognized as *M. microsora*, and the rust fungus on *S. warurgii* was recognized as *M. salicis-warburgii*. This two species differed from each other in the smooth regions at the apex and the dimension of urediniospores. In this study, SEM observation indicated that specimens from *S. subfragilis* including type specimen of *M. microsora* had a smooth apex in urediniospores although *M. salicis-warburgii* was characterized by its smooth apex in urediniospores. Molecular phylogeny also revealed specimens on *S. subfragilis* and *S. warburgii* formed a well supported group and the type specimen of *M. microsora* (HH-53150, isotype) was located in the same group. Thus, this taxon was designated as *M. microsora*. Moreover, specimens on *S. warburgii*, which were used to describe *M. salicis-warburgii* in Taiwan by Sawada (1931), were also found in this taxon. The type specimen was not designated in *M. salicis-warburgii* when Sawada first described this species. Morphological and molecular phylogenetic analyses in this study indicated that *M. salicis-warburgii* was a synonym of *M. microsora*.

G15 was characterized by having amphigenous uredinia with obovid or ellipsoid urediniospores, urediniospores with thickened apex, germ pore bizonate, amphigenous telia and subepidermal teliospores without thickened apex. G15 included specimens on *S. koreensis* in China, and these specimens were identified as *M. tinglinensis* by Cao (1999) and Liu (2005) in China. Although only uredinial stage was found on the type specimen of *M. tsinlingensis* (HMAS76119, holotype), morphological characteristics in uredinial stage fitted well with the other specimens in G15. Thus, G15 was designated as *M. tsinlingensis*.

G16 was characterized by having hypophyllous uredinia, obovid or ellipsoid urediniospores with thickened apex, germ pore bizonate, hypophyllous telia and subepidermal teliospores without thickened apex. This taxon resembled to *M. tsinlingensis* in the morphology of urediniospores and teliospores, but differed in its position of uredinia, the position of telia and the distance between spines. This taxon was found on *Toisusu urbaniana.* This taxon included the neotype specimens (HH-78307, neotype; HH-53302, isoneotype) of *M. laricis-urbaniana*. Thus, it was identified as *M. laricis-urbaniana*.

G17 had hypophyllous uredinia, obovid or ellipsoid urediniospores, urediniospores with apparently thickened apex, germ pore tending to bizonate, amphigenous telia and subepidermal teliospores without thickened apex. This taxon included specimens on *Chosenia arbututifolia*, and it was treated as *M. kamikotica* based on Hiratsuka and Kaneko (1982). Because the type specimen (HH-73060, holotype) was included in this taxon, it was named as *M. kamikotica*. This species was distinguishable from other *Melampsora* species in its urediniospores with thickened apex up to 10 μm, the position of uredinia and telia. In addition, this species was only found in the genus *Chosenia*.

G18 resembled to G16 except for its urediniospores with evenly thickened wall. This taxon included one specimen on *Chosenia arbututifolia*. On *Chosenia* genus, two species, *M. chosenia* and *M. kamikotica*, were reported until now (Azbukina 1974; Hiratsuka and Kaneko 1982). They were different from the apex thickness in urediniospores, and *M. chosenia* was reported without apparently thickened apex in

urediniospores (Azbukina 1974). In this study, this taxon differed from *M. kamikotica* (G17) in its apex thickness of urediniospores, and it phylogenetically differed from *M. kamikotica*. This taxon was identified as *M. chosenia* although the type specimen was not examined in this study.

G20 had hypophyllous uredinia, obovid or ellipsoid urediniospores, and smooth regions at apex, echinulate type 2, peripheral paraphyses with thickened apex and epiphyllous telia with absolutely subcuticular teliospores. This taxon included specimens on *S. raddeana*, *S. chaenomoloides* and some unidentified *Salix* species from China. Although *M. epitea* and *M. coleosporioides* were reported on these willow species in China (Tai 1979; Liu 2005), this taxon clearly differed from *M. epitea* in the shape of urediniospores, the existence of smooth regions in urediniospores, the spine form of urediniospores and the position of teliospores. This taxon also differed from *M. coleosporioides* (G11) in the position of telia and teliospores, the existence of intermixed paraphyses and the spine form of urediniospores. Japanese specimens on *S. pierotii*, which were recognized as *M. chelidonii-pierotii* based on Hiratsuka et al. (19902), were also included in this taxon. Although the type specimen of this species was not included, this taxon was designated as *M. chelidonii-pierotii* based on morphological information.

G21 was characterized by having hypophyllous uredinia, obovid or ellipsoid urediniospores, smooth regions at apex, echinulate type 2, intermixed and peripheral paraphyses with thickened apex, epiphyllous telia and subcuticular teliospores. This taxon resembled to *M. chelidonii-pierotii* (G20) except for its intermixed paraphyses and the distance between spines. This taxon included specimens on *S. longiflora* and *S. dunii* from China, and these specimens were identified as *M. yezoensis* (Tai 1979; Zhuang 1983). This taxon included the neotype specimen (HH-99463) of *M. yezoensis* on *S. jessoensis* from Japan, which was designated by Hiratsuka and Kaneko (1982). Thus, this taxon was identified as *M. yezoensis.*

G22 had hypophyllous uredinia, obovid or ellipsoid urediniospores, echinulate type 2, germ pore tending to bizonate, amphigenous telia and subepidermal teliospores. This taxon was composed of specimens on *S. alba* from China, and these

specimens were recognized as *M. salicis-albae* (Zhuang 1989). In addition, European specimens on *S. alba*, which were identified as *M. salicis-albae* (Pei 2005), were also included in this taxon. In addition, sequence data of *M. salicis-albae* (AY444775.1) from GenBank was found in the same group with this taxon in the rDNA ITS phylogeny (I24 in Fig. 3-3). Thus, this taxon was identified as *M. salicis-albae* although the type specimen was not examined in this study.

G23 was characterized by having amphigenous uredinia, globoid, obovid or ellipsoid urediniospores in large size, echinulate type 3, amphigenous telia and subepidermal teliospores without thickened apex. This taxon was distinguishable from other *Melampsora* species in its amphigenous uredinia and telia, dimension of urediniospores and spine form of urediniospores. Because this taxon included only a type specimen (HMAS38658, holotype) of *M. salicis-viminalis* (Wang et al. 1980), it was identified as *M. salicis-viminalis.*

G27 was characterized by having hypophyllous uredinia, obovid or ellipsoid urediniospores, echinulate type 2, urediniospores with apparently thickened apex, paraphyses with thickened apex, germ pore tending to bizonate, amphigenous telia and subepidermal teliospores. This taxon included specimens on *S. pentandra* and *S. paraplesia* in China, and they were recognized as *M. laricis-pentandrae* (Liu 2005) and *M. amygdalinae* (Zhuang and Liu 2002). This taxon morphologically fit well with *M. laricis-pentandrae*, but it differed from *M. amygdalinae* in its urediniospores with apparently thickened apex (Wilson and Henderson 1966; Bagyanarayana 2005). This taxon included specimens on *S. pentandra* from England, which was regarded as *M. laricis-pentandrae* by Pei et al. (2005). In addition, this taxon formed a well supported group (I16 in Fig. 3-3) together with sequence data of *M. laricis-pentandrae* (AY444771.1) in the rDNA ITS phylogeny. Although the type specimen was not checked in this study, morphological and molecular information indicated that this taxon was *M. laricis-pentandrae*.

M15 was characterized by its epiphyllous uredinia, ellipsoid or obovoid urediniospores, epiphyllous telia, subepidermal or subcuticular teliospores without thickened apex. This taxon was distinct from other *Melampsora* species especially in

its epiphyllous uredinia and telia. Only one type specimen (holotype, HMAS3607) of *M. salicis-cavaleriei* was found in this taxon, thus it was named as *M. salicis-cavaleriei*.

In the present studies, 14 taxa were recognized among *M. epitea* and related species. Among them, three taxa were identified as previously described species, *M. humilis*, *M. iranica* and *M. kiusiana*. Two taxa were described as new species, *M. salicis-argyraceae* P. Zhao & Y. Yamaoka, sp. nov. and *M. salicis-purpureae* P. Zhao & Y. Yamaoka, sp. nov. The other 9 taxa were recognized as distinct species, but the proper name of each taxon was not able to determine due to lack of data from the type specimens. They were designated as *Melampsora* sp. 1 to *Melampsora* sp. 9 in this study. Before this study, Smith et al. (2004), Pei et al. (2005), Benette et al. (2011) and Milne et al. (2012) conducted molecular phylogenetic studies on *M. epitea* complex and suggested the existence of cryptic species within this species complex. Among these recognized species in this study, *Melampsora* sp. 1 seemed to be the same taxon detected by Smith et al. (2004) in North America. *Melampsora* sp. 6 was the same taxon founded by Pei et al (2005) and Milne et al. (2012) in Europe. *Melampsora* sp. 7 was the same taxon founded by Pei et al (2005). However, the remain 6 species, *Melampsora* sp. 2, *Melampsora* sp. 3, *Melampsora* sp. 4, *Melampsora* sp. 5, *Melampsora* sp. 8 and *Melampsora* sp. 9 were found out in the present study for the first time. *Melampsora* sp. 2 was only detected in China, and *Melampsora* sp. 3 and *Melampsora* sp. 9 were only found in Japan. *Melampsora* sp. 8 was found on specimens from Europe. *Melampsora* sp. 4 was detected both in China and Japan, and *Melampsora* sp. 5 was found on specimens from China and Russia. Further studies were required to clarify the taxonomic condition of *M. epitea* complex by using specimens obtained from host plants from Asia, Europe and North America. Moreover, information on the life cycle and morphology of aecial stage was also required.

The present study also revealed that *M. capraearum* were separated into three species based on morphological differences and molecular phylogeny. These three species were correlated with geographic distribution. The fungus in China was treated

as a new species, *M. salicis-sinicae*, but the other two groups, one from Japan and another from Europe, were not completely identified. To determine their taxonomic condition, comparison with more specimens from Europe and Japan is desired, and the type specimen information of *M. capraearum* is also necessary.

The remaining 15 species were identified as distinct species which were described previously. Species name, phylogenetic groups, morphological groups and geographic origins of these 32 species were summarized in Table 4-1.

Table 4-1 *Melampspra* species recognized by the morphological characteristics and molecular phylogenies.

Species	Phylogenetic groups	Morphological groups	Geographic origins
Melampsora sp. 1	G1-1	M4	China, North America, Russia
M. salicis-sinicae	G1-2	M7	China
Melampsora sp. 2	G2	M1	China
M. epiphylla	G3	M10	China, Japan
Melampsora sp. 3	G4	M12	Japan
Melampsora sp. 4	G4	M13	China, Japan
M. capraearum 1	G5	M8	Japan
Melampsora sp. 5	G6	M1	China, Russia
M. humilis	G7	M1	Japan
M. capraearum 2	G8	M8	Europe
Melampsora sp. 6	G9	M4	China, Europe, Japan
M. ribesii-viminalis	G10	M9	China, Europe, Japan
M. kiusiana	G14	M2	Japan
M. coleosporioides	G11	M14	China, Japan
M. salicis-cupularis	G12	M11	China
M. microsora	G13	M22	China, Japan
M. tsinlingensis	G15	M19	China
M. larici-urbaniana	G16	M17	Japan
M. chosenia	G17	M17	Russia
M. kamikotica	G18	M20	China, Japan
M. salicis-argyraceae	G19	M1	China
M. chelidonii-pierotii	G20	M23	China, Japan
M. yezoensis	G21	M21	China, Japan
M. salicis-albae	G22	M18	China, Europe
M. salicis-viminalis	G23	M3	China
M. iranica	G24	M5	China
M. salicis-purpureae	G25	M5	China
Melampsora sp. 7	G26	M5	Europe
M. larici-pentandrae	G27	M16	China, Europe
Melampsora sp. 8	G28	M6	Europe
Melampsora sp. 9	G29	M6	Japan
M. salicis-cavaleriei	—	M15	China

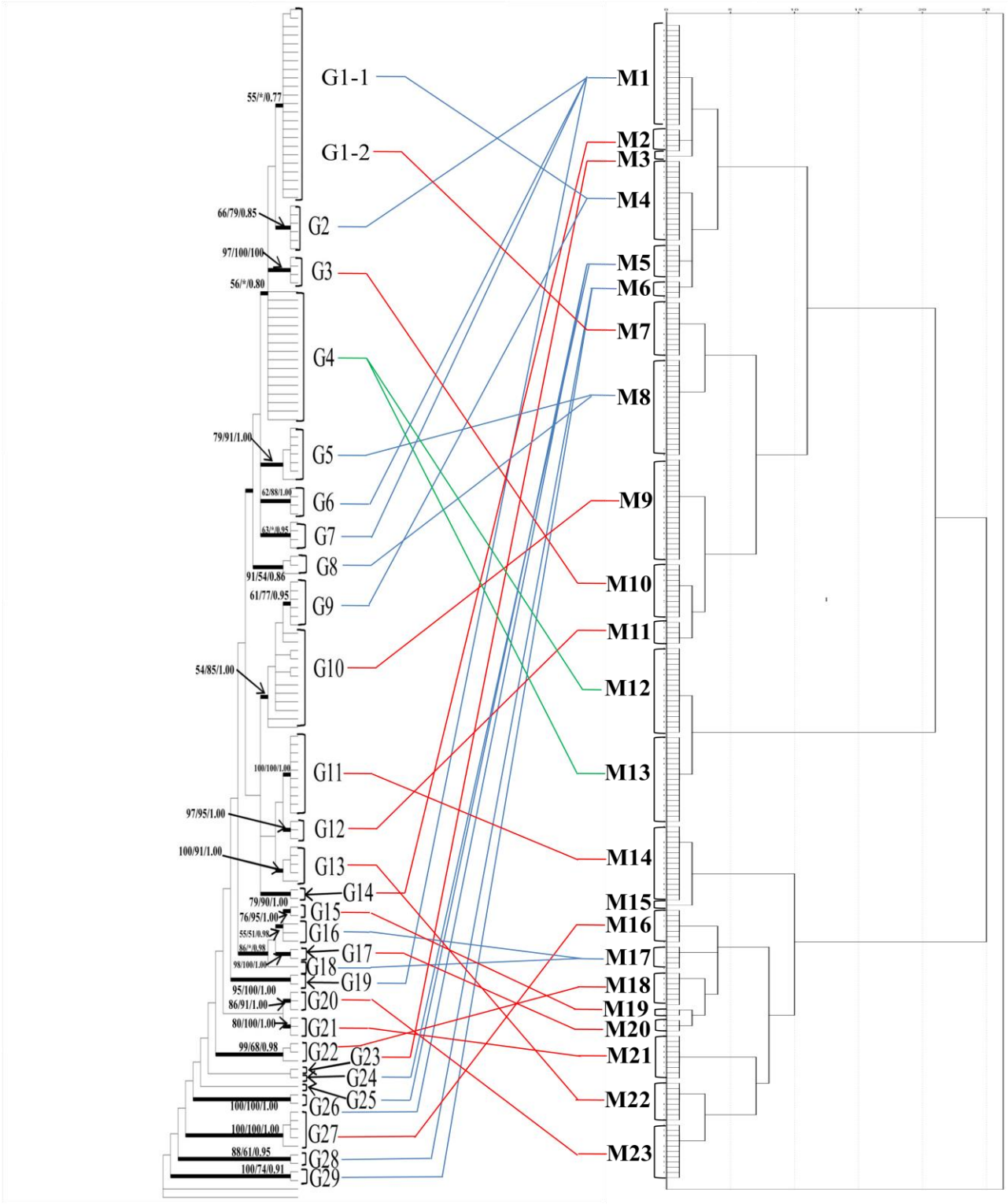


Fig. 4-1 Correlation of morphological groups and phylogenetic groups of *Melampsora* species on willows recognized in this study. Red line indicated that morphological groups were consistent with phylogenetic group. Blue line indicated that specimens in one morphological group located in several phylogenetic groups. Green line indicated that specimens in several morphological groups located in one phylogenetic group.

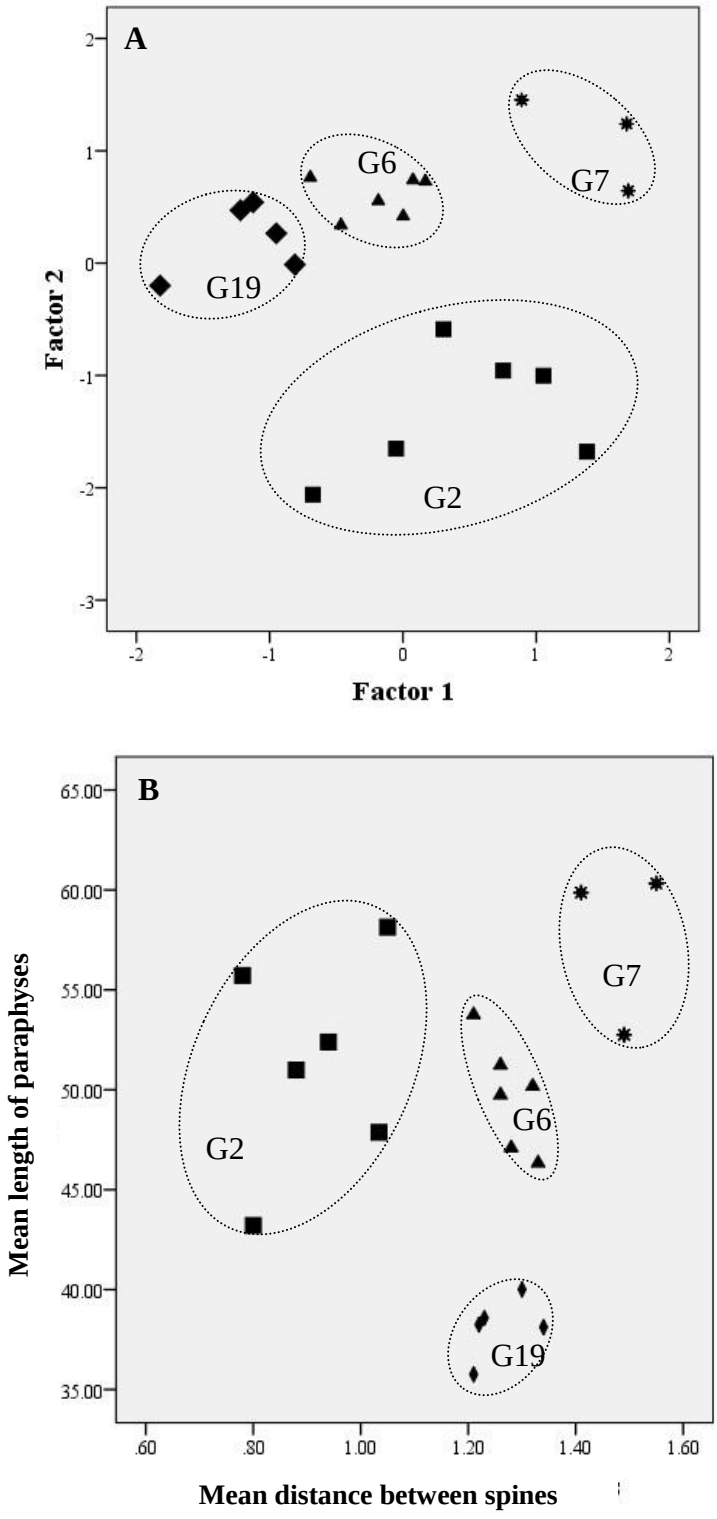


Fig. 4-2 Principal component analysis (PCA) of significant different variables determined by one-way ANOVA in M1 group (A). 2D scattered diagram was generated by the mean distance between spines against the mean length of paraphyses (B).

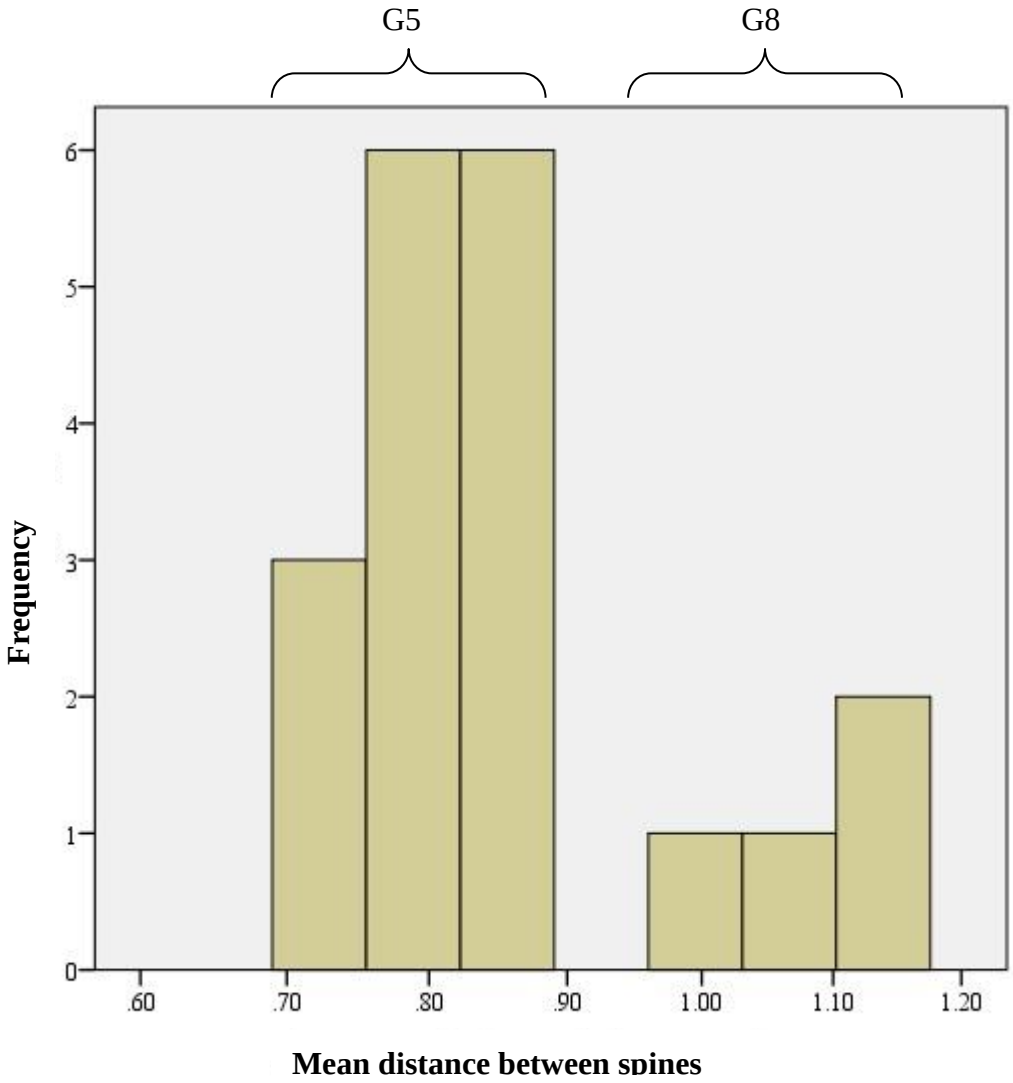


Fig. 4-3 Histogram of the distance between spines with statistical significant differences among specimens of G5 and G8 in M8.

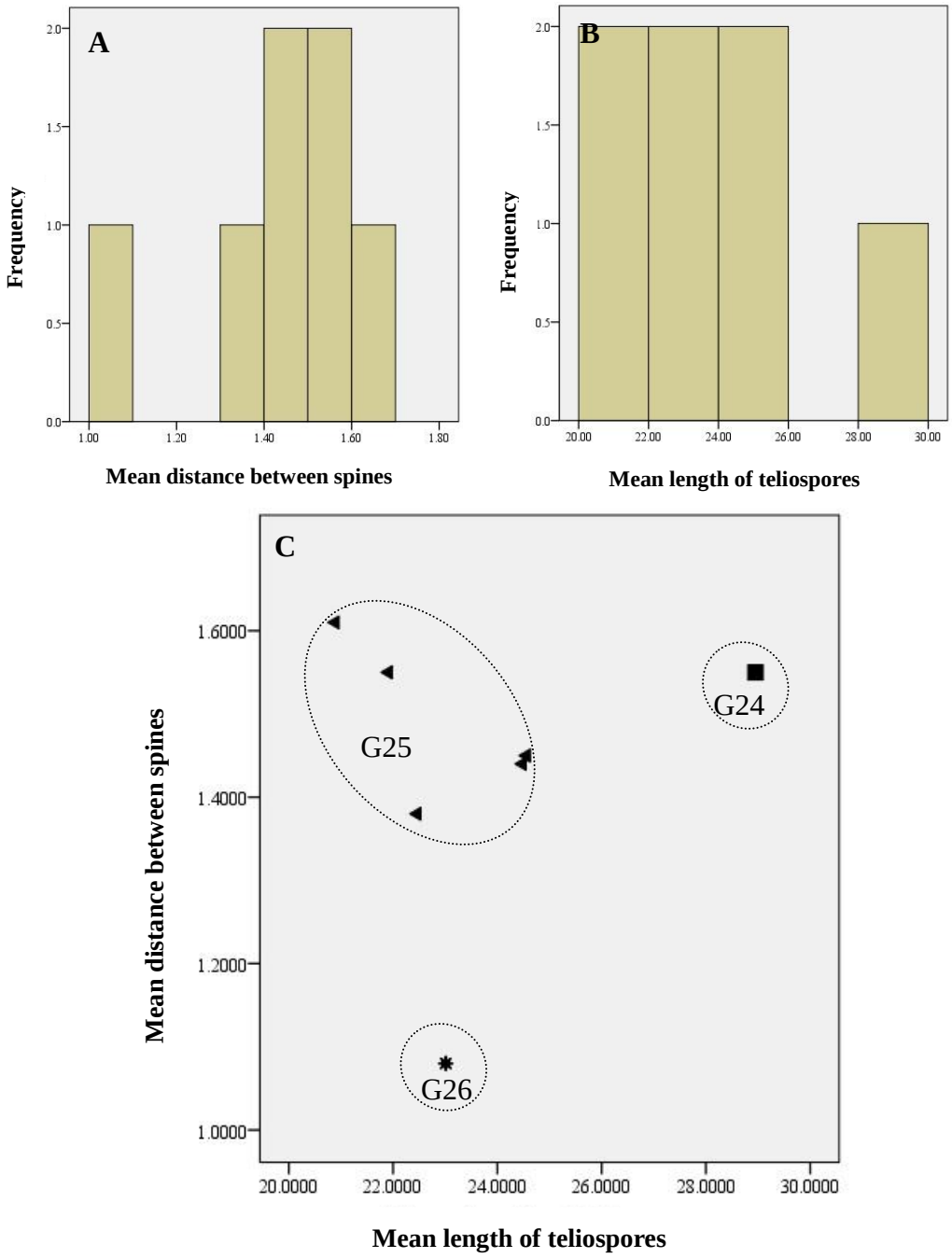


Fig. 4-4 Histogram and 2D scattered diagram of morphological differences among specimens in M5 corresponding to three phylogenetic groups, G24, G25 and G26. The histogram was generated based the distance between spines (A) and the length of teliospores (B) and the scattered diagram (C) was generated based these two quantitative characters.

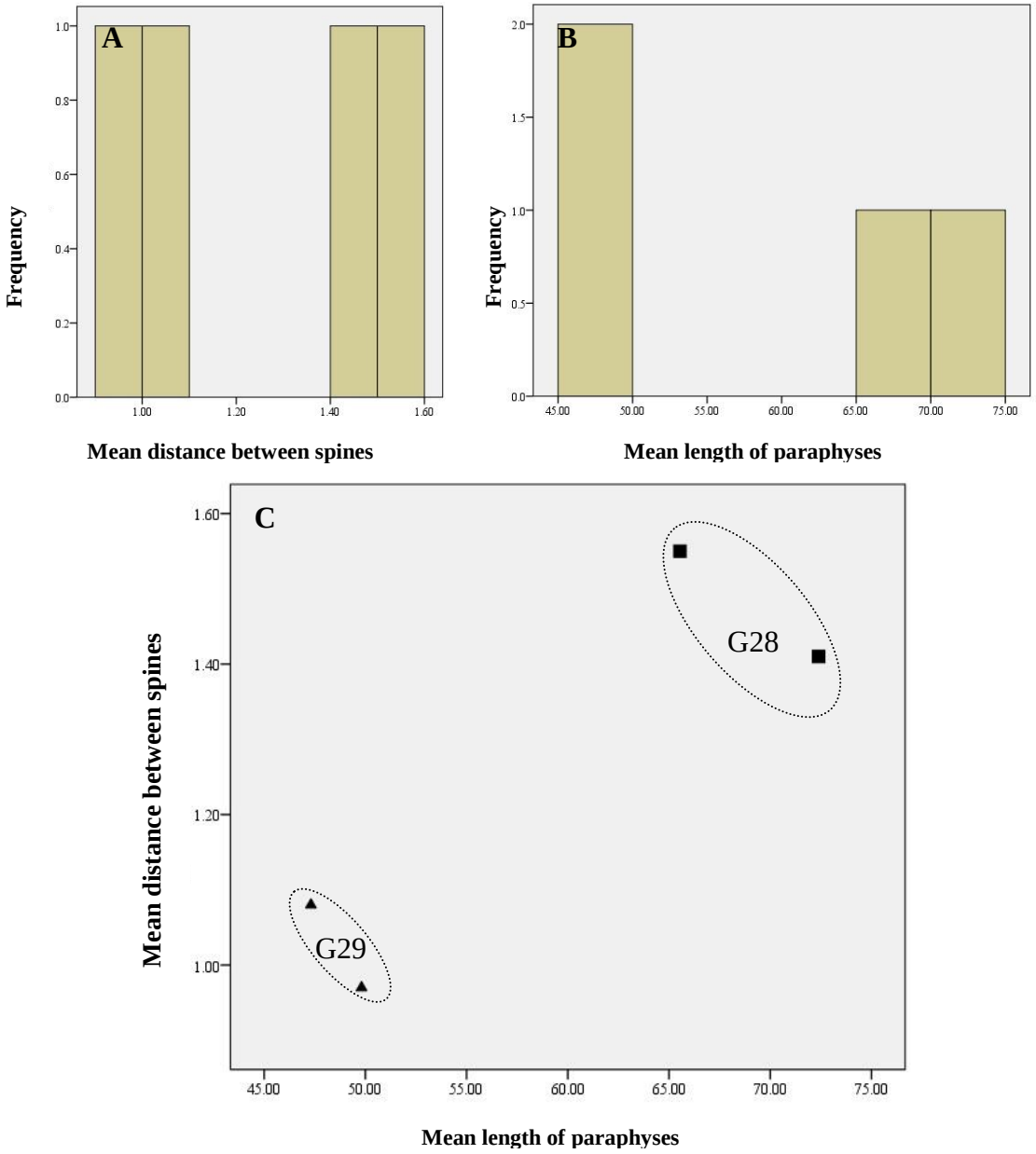


Fig. 4-5 Histogram and scattered diagram of quantitative characters with statistical significant differences among specimens in M6. The distance between spines (A) and the length of paraphyses (B) were indicated in histogram, and scattered diagram (C) was generated based two quantitative characters.

4-3 *Melampsora* species recognized in China in this study

Among 32 species recognized in this study, 22 species were confirmed in China as listed below:

1. *Melampsora chelidonii-pierotii* Tak. Matsumoto, Bot. Mag. Tokyo 40: 46, 1926
2. *Melampsora coleosporioides* Dietel, Botanische Jahrbücher für Systematik Pflanzengeschichte und Pflanzengeographie, 32: 50, 1903
3. *Melampsora epiphylla* Dietel, Botanische Jahrbücher für Systematik Pflanzengeschichte und Pflanzengeographie, 32: 50, 1902
4. *Melampsora kamikotica* S. Kaneko & Hirats. f., Report of the Tottori Mycological Institute, 20: 3, 1982
5. *Melampsora iranica* S. M. Damadi, M. H. Pei, J. A. Smith et M. Abbasi, For. Path., 41: 396, 2011
6. *Melampsora laricis-pentandrae* Klebahn, Forst. naturw. Zeitschr. 6: 470, 1897
7. *Melampsora microsora* Dietel, Botanische Jahrbücher für Systematik Pflanzengeschichte und Pflanzengeographie, 32: 50, 1902
8. *Melampsora ribesii-viminalis* Klebahn, Pringsheims Jb. Wissenschaftl. Botanik 34: 363; 1900
9. *Melampsora salicis-albae* Klebahn, Pringsheims Jb. Wissenschaftl. Botanik 35: 679, 1901
10. *Melampsora salicis-argyraceae* P. Zhao & Y. Yamaoka sp. nov.
11. *Melampsora salicis-viminalis* Wang et Guo, Acta Microbiologica Sinica 1: 1980
12. *Melampsora salicis-cavaleriei* F. L. Tai, Farlowia, 3: 102, 1947
13. *Melampsora salicis-cupularis* Y. C. Wang, Contributions from the Institute of Botany National Academy of Peiping, 6: 225, 1949
14. *Melampsora salicis-sinicae* P. Zhao, C. M. Tian & Y. J. Yao, sp. nov.
15. *Melampsora salicis-purpureae* P. Zhao & Y. Yamaoka, sp. nov.
16. *Melampsora tsinlingensis* Z. M. Cao et J. Y. Zhuang in Cao, Li & Zhuang,

Mycosystema 19: 19; 2000

17. *Melampsora yezoensis* Miyabe & T. Matsumoto: 8, 1915
18. *Melampsora* sp. 1
19. *Melampsora* sp. 2
20. *Melampsora* sp. 4
21. *Melampsora* sp. 5
22. *Melampsora* sp. 6

Among these 22 recognized species in China, three species, *M. salicis-argyraceae*, *M. salicis-sinicae*, and *M. salicis-purpureae*, were recognized as new species on willows based on morphological and molecular evidence. *Melampsora salicis-argyraceae* was found on *S. argyracea* in China first time in this study. *Melampsora salicis-sinicae* was previously recognized as *M. capraearum* or its synonym, *M. laricis-caprearum* (Tai 1979; Cao and Li 1999; Zhuang and Wei 2002; Liu 2005). *Melampsora salicis-purpureae* was formerly recognized as *M. ribesii-purpureae* in China (Tai 1979; Liu 2005).

In addition, two species, *M. chelidonii-pierotii* and *M. iranica* were recognized as new record in China. *Melampsora chelidonii-pierotii* were previously reported as *M. coleosporoides* (Tai 1979) and *M. ribesii-purpureae* (Liu 2005), respectively. *Melampsora iranica* were recognized as a new record on *S. alba*, and this species was previously reported as *M. epitea* in China (Zhuang 1989). *Salix alba* was added as one new host plant of *M. iranica.*

Among the 25 *Melampsora* species reported in China (Table 1-2), 11 *Melampsora* species were confirmed in China in this study. They were *M. coleosporioides*, *M. epiphylla*, *M. kamikotica*, *M. laricis-pentandrae*, *M. ribesii-viminalis*, *M. salicis-albae*, *M. salicis-viminalis*, *M. salicis-cavaleriei*, *M. salicis-cupularis*, *M. tsinlingensis* and *M. yezoensis*. However, the remaining 14 species appeared to be misidentification or taxonomic change was required. *Melampsora salicis-warburgii* reported in China and Japan (Tai 1979; Hiratsuka and Kaneko 1982) was recognized as a synonym of *M. microsora* in this study.

Melampsora amygdalinae reported on *S. paraplesia* by Zhuang and Wei (2002) was identified as *M. laricis-pentandrae*. In this study, although *M. capraearum* and its synonyms, *M. laricis-caprearum* was reported in China, the rust fungus on host species of these two reported species was recognized as *M. salicis-sinicae*. Specimens of *M. arctica*, *M. epitea*, *M. euonymi-capraearum*, *M. kupreviczii*, *M. lapponum*, *M. laricis-epitea*, *M. repentis* and *M. ribesii-purpureae*, which belonged to *M. epitea* complex, were identified as *M. salicis-argyraceae*, *M. salicis-purpureae*, *Melampsora* sp. 1, *Melampsora* sp. 2, *Melampsora* sp. 4, *Melampsora* sp. 5 and *Melampsora* sp. 6. The existence of *M. farinosa* was uncertain because specimen used for species description in China only had uredinial stage. Some synonyms of *M. epitea* complex need to be separated from this complex and species name may be recovered after further taxonomic studies. In addition, the presence of *M. capraearum* 1 and *M. capraearum* 2 on the other willows in China have to be confirmed in the future.

4-4 Description of *Melampsora* species on willows in China

4-4-1 Key to species

1. Urediniospores mostly obovoid or broadly ellipsoid……..…2

2. Teliospores subepidermal or subcuticular……..…..…3

3. Telia amphigenous, uredinia amphigenous…….....***M. coleosporioides*** Dietel

3. Telia epiphyllous, uredinia epiphyllous…….....***M. salicis-cavaleriei*** Tai

2. Teliospores subepidermal……..……..…..4

4. Germ pore scattered……...5

5. Uredinia without intermixed paraphyses, paraphyses thickened at apex, telia epiphyllous, teliospores subcuticular……...……...***M. yezoensis*** Miyabe et Matsumoto

5. Uredinia with intermixed paraphyses.....6

6. Telia hypophyllous, teliospores subepidermal, urediniospores echinulate type 2……...***M. microsora*** Dietel

6. Telia epiphyllous, teliospores subcuticular, urediniospores echinulate type 1……...……...***M. chelidonii-pierotii*** Tak. Matsumoto

4. Germ pores tending to bizonate…….……7

7. Telia hypophyllous, urediniospores echinulate type 2, with smooth apex, thickened at apex……***M. laricis-pentandrae*** Klebahn

7. Telia amphigenous, urediniospores chinulate type 1……...8

8. Urediniospores without thickened apex, paraphyses evenly thickened…….***M. salicis-albae*** Klebahn

8. Urediniospores with thickened apex, paraphyses thickened at apex…….9

9. Urediniospores thickened at apex, up to 10 μm, uredinia and telia on genus *Chosenia*…….**.....*M. kamikotica*** Kaneko et Hiratsuka

9. Urediniospores slightly thickened at apex, with smooth spots at apex, uredinia and telia on genus *Salix*……..…...***M. tsinlingensis*** Z. M. Cao et J. Y. Zhuang

1. Urediniospores mostly globoid, ellipsoid, ovoid…….…10

10. Uredinia without intermixed paraphyses……...11

11. Uredinia hypophyllous, telia hypophyllous, urediniospores 10–24×10–19 μm…….. ***Melampsora* sp. 4**

10. Uredinia with intermixed paraphyses…….……..12

12. Teliospores subepidermal.……...……...13

13. Telia epiphyllous, uredinia hypophyllous.....….14

14. Urediniospores with dense spines, mean value 0.83-1.15 μm, paraphyses comparatively long, 25–78×9–25 μm…….….***Melampsora* sp. 2**

14. Urediniospores with sparse spines, mean value 1.23-1.37 μm, paraphyses comparatively short, 24–67×7–24 μm…….....…***Melampsora* sp. 5**

14. Urediniospores with sparse spines, mean value 1.41-1.55 μm, paraphyses comparatively long, 38–85×9–29 μm, teliospores had slightly thickened apex……***M. salicis-argyraceae*** P. Zhao & Y. Yamaoka, sp. nov.

13. Telia amphigenous……15

15. Uredinia amphigenous……..16

16. Teliospores comparatively long, 29–63×5–12 μm, urediniospores

comparatively long, 15–28×10–18 μm, with dense spines, mean value 0.65 μm…….….***M. salicis-viminalis*** Wang et Guo

16. Teliospores comparative short, 16–32×5–11 μm, urediniospores comparatively short, 16–21×14–19 μm, spines mean value 1.08 μm……...***M. salicis-purpureae*** P. Zhao & Y. Yamaoka, sp. nov.

16. Teliospores 20–40×5–11 μm, urediniospores comparatively short, 14–21×12–19 μm, urediniospores with sparase spines, with mean value 1.55–1.63 μm……...…***M. iranica*** Damadi, Pei, Smith et Abbasi

15. Uredinia hypophyllous…….17

17. Urediniospores 11–27×8–19 μm, paraphyses 27–70×7–26 μm; teliospores 14–45×5–15 μm…… ……..……..***Melampsora* sp. 1**

17. Urediniospores 14–24×11–20 μm, paraphyses 30–61×9–26 μm; teliospores 18–34×6–14 μm…….……***Melampsora* sp. 6**

13. Teliospores subcuticular or subepidermal……18

18. Telia amphigenous, teliospores with apparently thickened apex…….…… ***M. salicis-sinicae*** P. Zhao, C. M. Tian & Y. J. Yao, sp. nov.

18. Teliospores sometimes slightly thickened at apex……19

19. Telia epiphyllous, urediniospores comparatively short, 10–20×8–19 μm..... ***M. ribesii-viminalis*** Klebahn

19. Telia amphigenous……20

20. Teliospores slightly thickened at apex, up to 5 μm, urediniospores comparatively short, 11–23×9–18 μm……...……...….***M. epiphylla*** Dietel

20. Teliospores evenly thickened, urediniospores comparatively long, 14–30×12–27 μm …….……***M. salicis-cupularis*** Wang

4-4-2 Description of species in China

1. ***Melampsora coleosporioides*** Dietel, Bot. Jb. 32: 50; 1903. (Fig. 4-6)

Spermogonia and aecia unknown. Uredinia amphigenous, 0.1–0.4 mm; urediniospores obovoid, ellipsoid or broadly ellipsoid, with smooth apex, 14–32×9–24 μm, wall 1.5–3 μm thick, wart spines, mean distance between spines 1.25–1.51 μm, germ pores 3–8, tending to be bizonate; Paraphyses mainly capitates, 21–66×8–21 μm, intermixed or surrounded in the uredinia, wall evenly thickened or slightly thickened at apex, up to 7 μm; Telia amphigenous, 0.3–1.2 mm; Teliospores subepidermal or subcuticular, 20–45×4–10 μm, wall 1 μm thick, not thickened at apex.

Host plant：II, III on *S. babylonica* L. (Inner Mongolia: HNMAP3114; Beijing: HMAS56896, HMAS17721); II, III on *S. matsudana* Koidz. (Guizhou: HMAS55179; Shaanxi: HMNWFC-15; Beijing: HMAS8619); (Inner Mongolia: HNMAP3135; HNMAP3138; HNMAP3094; HNMAP3173); II, III on *S. glandulosa* Seem. (Shaanxi: HMAS71119). II, III on *S. fargesii* Burk. (Hubei: HMAS55414, HMAS55396); II, III on *Salix* sp. (Anhui: BPI023210, Hei Long Jiang: BPI25363).

Distribution: China, Japan and Russia (Kuprevich and Transhel 1957).

2. ***Melampsora salicis-cavaleriei*** Tai Farlowia 3:102; 1947. (Fig. 4-7)

Spermogonia and aecia unknown. Uredinia epiphyllous, scattered, 0.2–0.4 mm; Urediniospores obovoid, ellipsoid or broadly ellipsoid, echinulate, occasionally with smooth spots, 21–32×15–26 μm, wall 1.5–3 μm, mean distance between spines 1.01 μm, germ pores scattered, 3–5; Paraphyses capitates, 30–51×11–24 μm, intermixed or surrounded in the uredinia, with evenly thickened or slightly thickened apex, up to 6 μm; Telia epiphyllous, mainly scattered, 0.2–0.4 mm; Teliospores subepidermal or subcuticular, 25–54×5–11 μm, wall 1 μm thick, not thickened at apex.

Host plant: II, III on *S. cavaleriei* H. Lév. (Yunnan: HMAS3607 holotype)

Distribution: China.

3. ***Melampsora yezoensis*** Miyabe et Matsumoto, Trans. Sapporo nat. Hist. Soc. 6(1): 8; 1915 (Fig. 4-8)

Spermogonia and aecia not seen in China. Uredinia hypophyllous, rounded or

irregular, 0.2–0.6 mm; Urediniospores obovoid, ellipsoid or broadly ellipsoid, 14–28×11–21 μm, wall evenly thickened, 1.3–3.5 μm, echinulate spines type 1, mean distance between spines 0.98–1.11 μm, sometimes with smooth spots at apex, germ pores 4–6, scattered; Paraphyses capitates or clavate, 28–57×9–20 μm, without intermixed paraphyses, thickened at apex, up to 10 μm. Telia epiphyllous, 0.2–10 mm; Teliospores subcuticular, 15–35×4–8 μm, wall 1.2 μm thickened, not thickened at apex.

Host pants: II, III on *S. longiflora* Anderss (Yunnan: HMAS356); II, III on *S. dunnii* Schneid. (Fujian: HMAS41605; HMAS41606).

Distribution: China, Japan and Russia (Kuprevich and Transhel 1957).

4. ***Melampsora microsora*** Dietel, Botanische Jahrbücher für Systematik Pflanzengeschichte und Pflanzengeographie, 32: 50, 1902 (Fig. 4-9)

Spermogonia and aecia not seen in China. Uredinia hypophyllous, 0.1–0.4 mm, scattered or grouped together. Urediniospores obovoid, broad ellipsoid or ovoid, 15–33×8–18 μm, wall 0.8–2.4 μm, evenly thickened, with smooth regions at apex, mean distance between spiens were 1.06–1.29 μm, germ pore 3–5, scattered; Paraphyses capitates, 28–69×10–22 μm, intermixed or surrounded in the uredinia, evenly thickened at apex. Telia hypophyllous, 0.2–0.6 mm; Teliospores subepidermal, 18–42×5–16 μm, wall 1 μm thick, no thickened at apex.

Host plant: II, III on *Salix warburgii* Seem. (Taiwan: HH-53135, HH-53150, HH-53225). II, III on *Salix* sp. (Fujian: HMAS56075)

Distribution: China and Japan.

5. ***Melampsora chelidonii-pierotii*** Matsumoto, Bot. Mag. Tokyo 40: 46, 1926. (Fig. 4-10)

Spermogonia and aecia not seen in China. Uredinia amphigenous, mostly hypophyllous, 0.4–0.8 mm; urediniospores obovoid, ellipsoid or broadly ellipsoid, 16–26×11–18 μm, wall 1.5–2.6 μm thick, echinulate, mean distance between spines 1.26–1.38 μm, germ pores 3–6, bizonate or tending to be scattered; Paraphyses mostly

pear- or lollipop-shaped and interspersed throughout uredinia, evenly thickened at apex or slightly thickened at apex, up to 7 μm. Telia epiphyllous, 0.2–0.4 mm; Teliospores subcuticular, 12–41×5–14 μm, wall 1.6 μm thick, not thickened at apex.

Host plant: II, III on *Salix chaenomeloides* Kimura (Shaanxi: HMNWFC13). II, III on *S. raddeana* Laksch (Jilin: BPI1109442; Inner Mongolia: HNMAP1587); II, III on *Salix* sp. (Shaanxi: HMNWFC-665; HNMWFC-L91054); II, III on *Salix* sp. (Hei Long Jiang: BPI23207; Anhui: BPI23209)

Distribution: China, Japan and Russia (Kuprevich and Transhel 1957).

6. ***Melampsora laricis-pentandrae*** Klebahn in Forst. naturw. Zeitschr. 6: 470; 1897 (Fig. 4-11)

Spermogonia and aecia not seen in China. Uredinia mainly hypophyllous, occasionally occurred on the upper side of leaves, 0.2–1.0 mm; Urediniospores obovoid, broad ellipsoid or ovoid, 16–35×11–20 μm, with smooth apex and the apex thickened up to 6 μm, wall 1.5–2.5 μm at sides, echinulate 3, mean distance between spines 1.33–1.51 μm, germ pores 3–7, scattered or tending to bizonate; Paraphyses mainly capitates, 33–87×10–24 μm, intermixed or surrounded in the uredinia, slightly thickened or evenly thickened at apex, up to 8 μm. Telia amphigenous, 0.1–0.4 mm; Teliospores subepidermal, 22–48×6–14 μm, wall 1–2 μm, not thickened at apex.

Host plant: II, III on *Salix pentandra* L. (Inner Mongolia: HNMAP3059, HNMAP3163, HNMAP3201, HNMAP3171 and HNMAP3207). II, III on *Salix* sp. (Inner Mongolia: HMAS42407)

Distribution: China, Europe and Russia (Kuprevich and Transhel 1957; Wilson and Henderson 1966; Bagyanarayana 2005).

7. ***Melampsora salicis-albae*** Klebahn, Pringsheims Jb. Wissenschaftl. Botanik 35: 679; 1901 (Fig. 4-12)

Spermogonia and aecia not seen in China. Uredinia amphigenous, rounded, 0.2–0.8 mm; urediniospores obovoid, ellipsoid or broadly ellipsoid, with smooth apex, 17–32×12–20 μm, wall 1.5–2.5 μm thick, wart spines, mean distance between spines

1.34–1.55 μm, germ pores 2–6, scattered or tending to be bizonate; Paraphyses capitates or clavate, 38–80×11–22 μm, intermixed or surrounded in the uredinia, the apex evenly thickened, up to 5 μm; Telia amphigenous, 0.4–1.2 mm; Teliospores subepidermal, 20–35×5–12 μm, wall 1 μm thick, not thickened at apex.

Host plants: II, III on *S. alba* L. (Xinjiang: HMAS55038, HMAS52925; HMAS52924; HMAS58575), II on *Salix* sp. (Guizhou: BPI1109650)

Distribution: China, Europe and India (Wilson and Henderson 1966; Bagyanarayana 2005).

8. ***Melampsora kamikotica*** Kaneko et Hiratsuka, in Hiratsuka et Kaneko, Rept. Tottori. Mycol. Inst. 20, 3, 1982 (Fig. 4-13)

Spermogonia and aecia not seen in China. Uredinia hypophyllous, scattered, rounded, 0.3-0.5 mm; Urediniospores obovoid, ellipsoid, or broadly ellipsoid, 20–31×14–21 μm, wall 2–2.9 μm at sides, 2.5–10 μm thick at apex, colorless, with echinulate spines, mean distance between spines 1.40–1.50 μm, germ pore 2–4, scattered, or tending to bizonate; Paraphyses numerous, intermixed or surrounded in the uredinia, mainly capitates, 50–72×12–22 μm, wall thickened at apex up to 10 μm. Telia amphigenous, rounded, 0.1–0.6 mm; Teliospores subepidermal, 15–33×6–13 μm, wall 1 μm thick, not thickened at apex.

Host plant: II, III on *Chosenia arbutifolia* (Pall.) A. Skvortz (Inner Mongolia: HNMAP 3186).

Distribution: China and Japan.

9. ***Melampsora tsinlingensis*** Z. M. Cao et J. Y. Zhuang in Cao, Li & Zhuang, Mycosystema 19: 19, 2000 (Fig. 4-14)

Spermogonia and aecia unknown. Uredinia amphigenous, scattered, rounded, 0.3–0.8 mm; Urediniospores obovoid, ellipsoid, ovoid. 19–33×15–22 μm, wall 1.5–2.6 μm thick at sides, apex thickened up to 6 μm, echinulate or sometimes slightly smooth at apex, mean distance between spines 1.70–1.88 μm, germ pore 4–7, scattered or tending to bizonate; Paraphyses intermixed or surrounded in the uredinia,

42–73×7–19 μm, wall 3–8 μm thickened at apex; Telia amphigenous, 0.4–1.0 mm; Teliospores subepidermal, 16–29×7–13 μm, wall 1 μm, not thickened at apex.

Host plant: II, III on *Salix paraplesia* C. K. Schneider (Shaanxi: HMAS76119, holotype), on *Salix koreensis* Andersson (Inner Mongolia: HNMAP3185; HNMAP3257).

Distribution: China.

10. ***Melampsora*** **sp. 4** (Fig. 4-15)

Spermogonia and aecia unknown. Uredinia hypophyllous, occasionally aggregated on stem, 0.2–0.4 mm, scattered or grouped; Urediniospores globoid or ellipsoid, 10–24×10–19 μm, wall 0.7–3.2 μm thick, echinulate, mean distance between spines 0.72–1.17 μm, germ pores 3–5, scattered; Paraphyses capitate, surrounded in the uredinia, 19–80×8–26 μm, with uniformly thickened membrane, up to 8.5 μm. Telia hypophyllous, 0.2–0.8 mm, scattered or aggregated; Teliospores subepidermal, 11–49×5–19 μm, wall 1.0–3.1 μm, evenly thickened without thickened apical wall.

Host plant: II, III on *S. cathayana* Diels (Sichuan: HMAS71118); II, III on *Salix* sp. (Shaanxi: HMNWFC915054).

Distribution: China and Japan

11. ***Melampsora*** **sp. 2** (Fig. 4-16)

Spermogonia and aecia unknown. Uredinia hypophyllous, occasionally aggregated on stem, 0.1–0.4 mm, scattered or grouped; Urediniospores globoid or ellipsoid, 11–21×10–19 μm, wall 1.0–3.0 μm thick, echinulate, mean distance between spines 0.83–1.15 μm, germ pores 3–7, scattered; Paraphyses capitate, intermixed or surrounded in the uredinia, 25–78×9–25 μm, with uniformly thickened membrane, up to 7.6 μm. Telia epiphyllous, 0.2–0.8 mm, scattered or aggregated; Teliospores subepidermal, 13–41×4–15 μm, wall 1.0–2.0 μm, evenly thickened without thickened apical wall.

Host plant: II, III on *S. rosmarinifolia* L. (Inner Mongolia: HNMAP3061,

HNMAP3190, HNMAP3193); II, III on *S. starkeana* Willd. (Inner Mongolia: HNMAP1972); II, III on *S. gyirongensis* S. D. Zhao et C. F. Fang (Tibet: HMAS64717); II, III on *Salix* sp. (Inner Mongolia: HMAS42842)

Distribution: China and Russia (Kuprevich and Transhel 1957).

12. ***Melampsora* sp. 5** (Fig. 4-17)

Spermogonia and aecia unknown. Uredinia hypophyllous, scattered, 0.1–0.4 mm; Urediniospores globoid or ellipsoid, 9–21×9–19 μm, wall 0.7–2.7 μm thick, echinulate, mean distance between spines 1.27–1.37 μm, germ pores 2–5, scattered; Paraphyses capitate, intermixed or surrounded in the uredinia, 24–67×7–24 μm, with uniformly thickened membrane, up to 7.8 μm. Telia epiphyllous, 0.4–0.8 mm, scattered or aggregated; Teliospores subepidermal, 13–41×6–15 μm, wall 0.6–2.8 μm, evenly thickened without thickened apical wall.

Host plant: II, III on *S. triandra* L.(Inner Mongolia: HNMAP3060, HMAS3160, HNMAP3181, HNMAP3169 ; Heilongjiang: HMAS82388)

Distribution: China and Russia (Kuprevich and Transhel 1957).

13. ***Melampsora salicis-argyraceae*** P. Zhao & Y. Yamaoka, sp. nov. (Fig. 4-18)

Spermogonia and aecia unknown. Uredinia hypophyllous, scattered, 0.4–0.8 mm; Urediniospores globoid, ellipsoid or ovoid, 12–21×7–18 μm, wall 1.7–3.65 μm thick, echinulate, mean distance between spines 1.41–1.55 μm, germ pores 5–7, scattered; Paraphyses capitate, intermixed or surrounded in the uredinia, 38–85×9–29 μm, with uniformly thickened membrane, up to 6.2 μm. Telia epiphyllous, 0.8–1.2 mm, scattered or aggregated; Teliospores subepidermal, 17–51×5–16 μm, wall 0.9–4.5 μm, thickened at apical wall.

Host plant: II, III on *S. argyracea* E. Wolf (Xinjiang: HMAS52894, HMAS55037; Tibet: BPI1108633)

Distribution: China

14. ***Melampsora salicis-viminalis*** Wang et Guo in Acta Microbiologica Sinica 1:

1980. (Fig. 4-19)

Spermogonia and aecia unknown. Uredinia amphigenous, scattered or densely aggregated, 0.4–0.8 mm; Urediniospores ellipsoid, globoid or ovoid, 15–29×10–18 μm, wall 1.7–3.0 μm thick, mean distance between spines 0.83 μm, germ pores scattered, 5–9; Paraphyses capitates, hyaline, 35–71×12–20 μm, intermixed or surrounded in the uredinia, apex wall evenly thickened or slightly thickened at apex, up to 5 μm. Telia amphigenous, scattered, 0.4–0.8 mm; Teliospores subepidermal, 29–63×6–12 μm, wall 1 μm thick, not thickened at apex.

Host plant: II, III on *S. viminalis* L. (Tibet: HMAS38658 holotype)

Distribution: China.

15. ***Melampsora salicis-purpureae*** P. Zhao & Y. Yamaoka, sp. nov. (Fig. 4-20)

Spermogonia and aecia unknown. Uredinia amphigenous, scattered, 0.4–0.8 mm; Urediniospores globoid or ellipsoid, 16–21×14–19 μm, wall 1.7–3.4 μm thick, echinulate, mean distance between spines 0.90–1.10 μm, germ pores 3–6, scattered; Paraphyses capitate, intermixed or surrounded in the uredinia, 37–62×10–20 μm, with uniformly thickened membrane, up to 5.8 μm. Telia amphigenous, 0.1–0.4 mm, scattered or aggregated, 0.4–0.8 mm; Teliospores subepidermal, 16–32×5–11 μm, wall 0.7–1.8 μm, evenly thickened without thickened apical wall.

Host plant: II, III on *S. purpurea* L. (Shandong: HMAS62584)

Distribution: China.

16. ***Melampsora iranica*** S. M. Damadi, M. H. Pei, J. A. Smith et M. Abbasi, For. Path., 41:396, 2011. (Fig. 4-21)

Spermogonia and aecia unknown. Uredinia amphigenous, occasionally aggregated on stem, 0.4–0.8 mm, scattered or grouped; Urediniospores globoid or ellipsoid, 14–21×12–19 μm, wall 1.5–3.2 μm thick, echinulate, mean distance between spines 1.55–1.63 μm, germ pores 4–6, scattered; Paraphyses capitate, intermixed or surrounded in the uredinia, 36–67×11–24 μm, with uniformly thickened membrane, up to 8.3 μm. Telia amphigenous, 0.4–1.2 mm, scattered or aggregated;

Teliospores subepidermal, 20–40×5–11 μm, wall 0.6–1.5 μm, evenly thickened without thickened apical wall.

Host plant: II, III on *S. alba* (Xinjiang: HMAS52905).

Geographical distribution: China and Iran (Damadi et al. 2011).

17. ***Melampsora* sp. 1** (Fig. 4-22)

Spermogonia and aecia unknown. Uredinia hypophyllous, occasionally aggregated on stem, 0.1–0.6 mm, scattered or grouped; Urediniospores globoid or ellipsoid, 11–27×8–19 μm, wall 1.0–3.5 μm thick, echinulate, mean distance between spines 0.97–1.13 μm, germ pores 3–7, scattered; Paraphyses capitate, intermixed or surrounded in the uredinia, 27–70×7–26 μm, with uniformly thickened membrane, up to 8.3 μm. Telia amphigenous, 0.1–0.8 mm, scattered or aggregated; Teliospores subepidermal, 14–45×5–15 μm, wall 1.0–5.0 μm, evenly thickened without thickened apical wall.

Specimens examined: II, III on *S. caprea* L. (Xinjiang: HMAS58563; Hebei: HMAS67393; Inner Mongolia: HMAS82380; Jilin: HMAS42844); II, III on *S. hypoleuca* Seemen (Ningxia: HMAS55747); II, III on *S. sinopurpurea* C. Wang et Ch. Y. Yang (Beijing: HMAS8629); II, III on *S. alfredi* Görz (Hebei: HMAS67392); II, III on *Salix* sp. (Xinjiang: HMAS52904). II, III on *S. wilsonii* Seemen (Shaanxi: HMAS25375); II, III on *S. magnifica* Hemsl. (Xinjiang: HMAS37818); II, III on *S. myrtilloides* L. (Inner Mongolia: HNMAP3140); II, III on *S. characta* Schneid. (Inner Mongolia: HNMAP3175); II, III on *S. dissa* Schneid. (HMAS48435); II, III on *S. siuzevii* Seemen. (Inner Mongolia: HNMAP1594); II, III on S. *delavayana* (Tibet: HMAS67421); II, III on *S. alatavica* Kar. et Kir. ex Stschegl. (Xinjiang: HMAS52899); II, III on *S. linearistipularis* (Franch.) Hao (Inner Mongolia: HNMAP3149)

Distribution: China, Europe and Russia (Wilson and Henderson 1966; Ziller 1974; Bagyanarayana 2005).

18. ***Melampsora* sp. 6** (Fig. 4-23)

Spermogonia and aecia unknown. Uredinia hypophyllous, occasionally aggregated on stem, 0.1–0.8 mm, scattered or grouped; Urediniospores globoid or ellipsoid, 14–24×11–20 μm, wall 1.5–3.5 μm thick, echinulate, mean distance between spines 0.97–1.38 μm, germ pores 3–6, scattered; Paraphyses capitate, intermixed or surrounded in the uredinia, 30–61×9–26 μm, with uniformly thickened membrane, up to 7.8 μm. Telia amphigenous, 0.3–0.8 mm, scattered or aggregated; Teliospores subepidermal, 18–34×6–14 μm, wall 0.8–1.7 μm, evenly thickened without thickened apical wall.

Specimens examined: II, III on *S. iliensis* Regel. (Xinjiang: HMAS58573).

Distribution: China, Japan and Europe (Wilson and Henderson 1966; Bagyanarayana 2005).

19. ***Melampsora salicis-sinicae*** P. Zhao, C. M. Tian et Y. J. Yao, sp. nov. (Fig. 4-24)

Spermogonia and aecia unknown. Uredinia hypophyllous, mostly scattered, occasionally grouped together, 0.2–0.8 mm; Urediniospores globoid or ellipsoid, 14–25×12–22 μm, wall 1.5–4.0 μm thick, echinulate, mean distance between spines 0.98–1.13 μm, germ pores 3–6, scattered; Paraphyses capitate, sometimes clavate, intermixed or surrounded in the uredinia, 39–86×10–26 μm, with uniformly thickened membrane, up to 8.7 μm; Telia amphigenous, 0.2–0.8 mm, scattered or aggregated; Teliospores subcuticular, 17–49×6–15 μm, wall 1.0–2.6 μm, thick with apex thickness up to 9.8 μm.

Host plant: II, III on *S. hsinganica* Y. L. Chang et Skovrtsov (Inner Mongolia: HNMAP3065); II, III on *S. sinica* C. Wang et C. F. Fang (Inner Mongolia: HNMAP1697, HNMAP1710; Shaanxi: HMAS987); II, III on *S. starkeana* Willdenow (Inner Mongolia: HNMAP3176; HNMAP3167; HNMAP3159); II, III on *S. wallichiana* Andersson (Inner Mongolia: HNMAP1690, HNMAP1339); II, III on *S. xerophila* Floder (Inner Mongolia: HNMAP3111; Hei Long Jiang: HMAS82384).

Distribution: China.

20. ***Melampsora ribesii-viminalis*** Klebahn, Pringsheims Jb. Wissenschaftl. Botanik

34: 363; 1900 (Fig. 4-25)

Spermogonia and aecia unknown. Uredinia hypophyllous, scattered, rounded, 0.1–0.8 mm; Urediniospores globoid, ellipsoid and ovoid, 10–20×8–19 μm, wall 0.66–4.26 μm, evenly echinulate, average distance between spines 1.02–1.26 μm; germ pore scattered, 2–6; Paraphyses capitates, intermixed or surrounded in the uredinia, wall evenly thickened at apex; Telia epiphyllous, 0.1–0.8 mm, scattered or grouped; Teliospores subepidermal or subcuticular, 14–45×5–13 μm, wall 1 μm thick, not thickened at apex or slightly thickened at apex.

Host plant: II, III on *S. viminalis* L. (Hei Long Jiang: HMAS82389; Heilongjiang: BPI1109484; Inner Mongolia: HNMAP3208, HNMAP3222, HNMAP3058, HNMAP3218, HNMAP1967); II, III on *S. siuzevii* Seemen. (Hei Long Jiang: HMAS134712; Inner Mongolia: HNMAP1959); II, III on *Salix* sp. (Inner Mongolia: HNMAP3184; HNMAP1698).

Distribution: China, Japan and Europe (Kuprevich and Transhel 1957; Wilson and Henderson 1966; Bagyanarayana 2005).

21. ***Melampsora epiphylla*** Dietel, Bot. Jb. 32: 50; 1902. (Fig. 4-26)

Spermogonia and aecia not seen in China. Uredinia hypophyllous, occasionally aggregated on stem, 0.1–0.5 mm, scattered or grouped; Urediniospores globoid or ellipsoid, 11–23×9–18 μm, wall 1.0–4.0 μm thick, echinulate, mean distance between spines 1.05–1.18 μm, germ pores 3–5, scattered; Paraphyses capitate, intermixed or surrounded in the uredinia, 29–66×9–25 μm, with uniformly thickened membrane, up to 7.1 μm; Telia amphigenous, 0.1–0.8 mm, scattered or aggregated; Teliospores subepidermal or subcuticular, 18–55×4–17 μm, wall 1.0–5.0 μm, evenly thickened without thickened apical wall.

Host plant: II, III on *Salix* sp. (Anhui: BPI23212).

Distribution: China and Japan.

22. ***Melampsora salicis-cupularis*** Wang Contr. Inst. Bot. Nat. Acad. Peiping 6: 225; 1949. (Fig. 4-27)

Spermogonia and aecia unknown. Uredinia hypophyllous, 0.2–0.6 mm; urediniospores globoid or ellipsoid, echinulate, 14–30×12–27 μm, wall 1.5–3 μm thick, mean distance between spines 1.01–1.12 μm, germ pores 3–5, scattered; Paraphyses mainly capitate, 41–93×16–37 μm, intermixed or surrounded in the uredinia, with evenly thickened or slightly thickened apex, up to 8 μm; Telia amphigenous, mainly hypophyllous, 0.2–0.8 mm; Teliospores subepidermal or subcuticular, 20–40×5–14 μm, wall 1 μm thick, not thickened at apex.

Host plant: II, III on *S. cupularis* Rehd. (Shaanxi: HMAS76122; HMNWFC-T85040; Inner Mongolia: HNMAP3152). II, III on *Salix* sp. (Guizhou: BPI23208).

Geographical distribution: China.

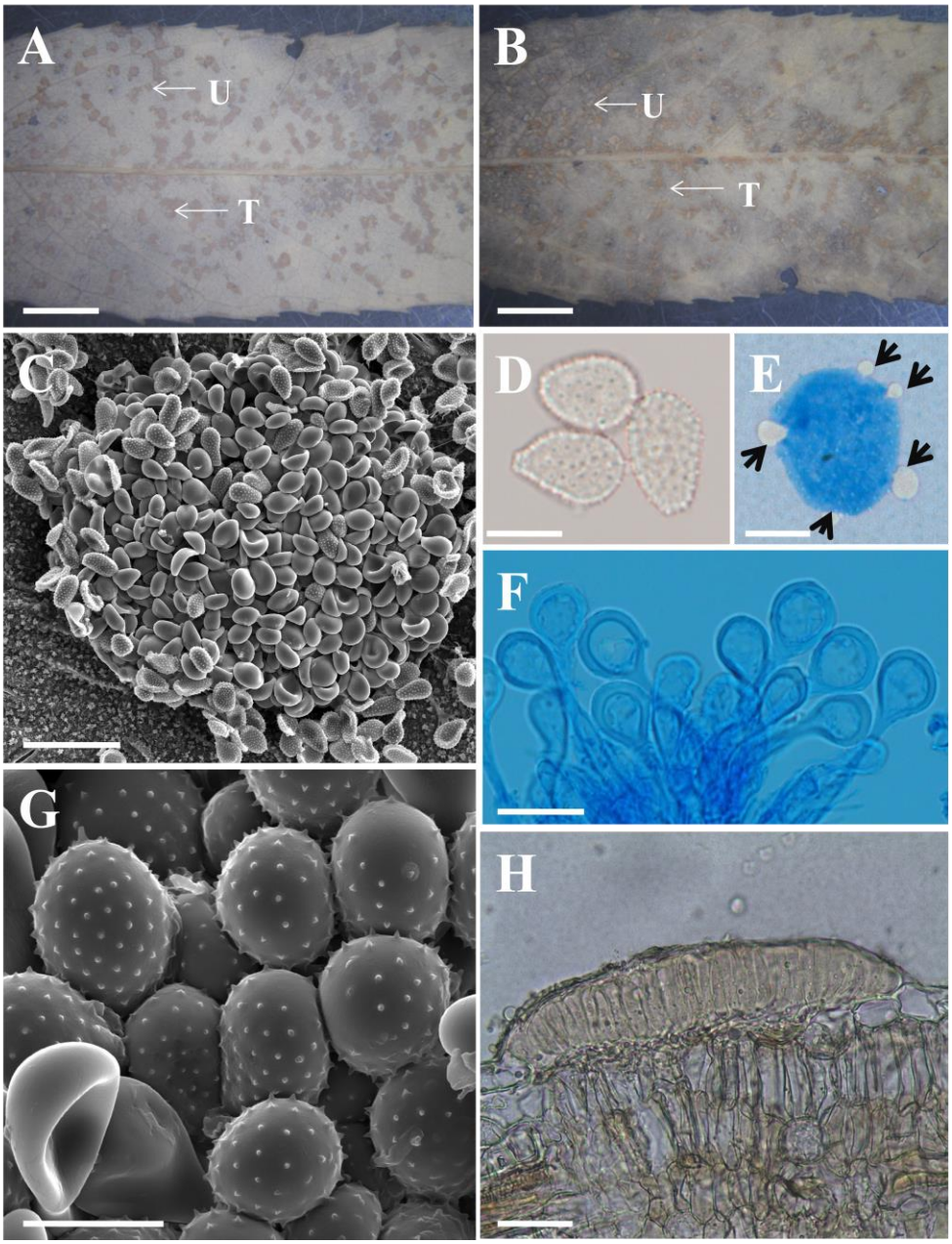


Fig. 4-6 Morphology of *Melampsora coleosporioides* (HNMAP3114). A: Uredinia (U) and telia (T) on the abaxial leaf surface. Uredinia scattered, telia intermixed with uredinia. B: Uredinia and telia on the adaxial leaf surface. C: Uredinia observed by SEM, with intermixed paraphyses. D: Obovoid, ellipsoid or ovoid urediniospores observed by OM. E: Scattered or tending to biozonate germ pores (black arrows). F: Capitate paraphyses without thickened apex. G: Ultrastructure of urediniospores, echinulate, with smooth spots at apex. H: Subepidermal or subcuticular teliospores without thickened apical wall. *Bars*: A, B 30 mm; C 50 µm; D 20 µm; E 10 µm; F 30 µm; G 10 µm; H 20 µm.

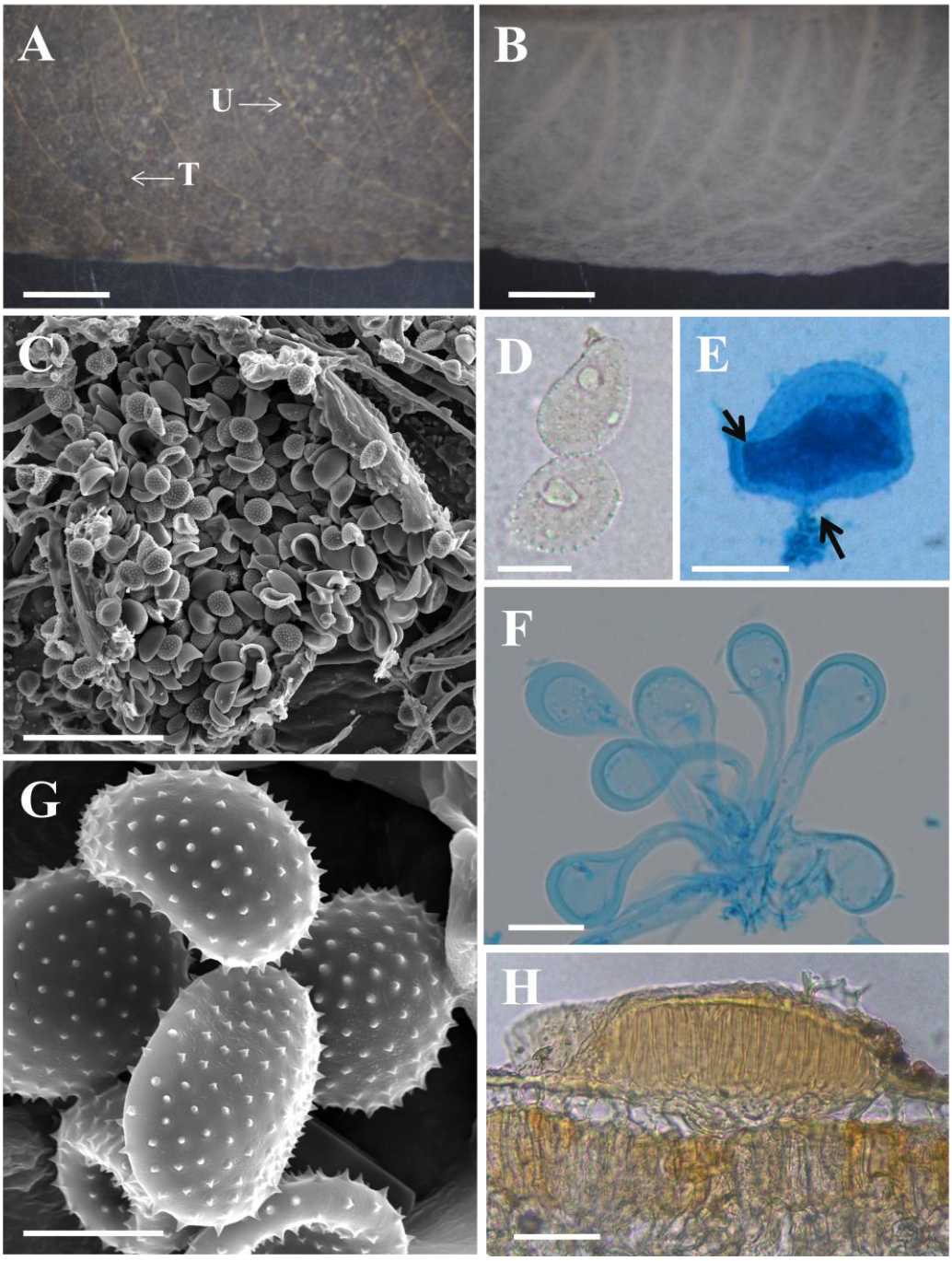


Fig. 4-7 Morphology of *Melampsora salicis-cavaleriei* (HMAS3607). A: Uredinia (U) and telia (T) on the abaxial leaf surface. Uredinia scattered, telia intermixed with uredinia. B: No uredinia and telia on the adaxial leaf surface. C: Uredinia observed by SEM, with intermixed paraphyses. D: Obovoid or ellipsoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses without thickened apex. G: Ultrastructure of urediniospores, echinulate. H: Subepidermal or subcuticular teliospores without thickened apical wall. *Bars*: A, B 30 mm; C 50 µm; D 20 µm; E 15 µm; F 20 µm; G 15 µm; H 20 µm.

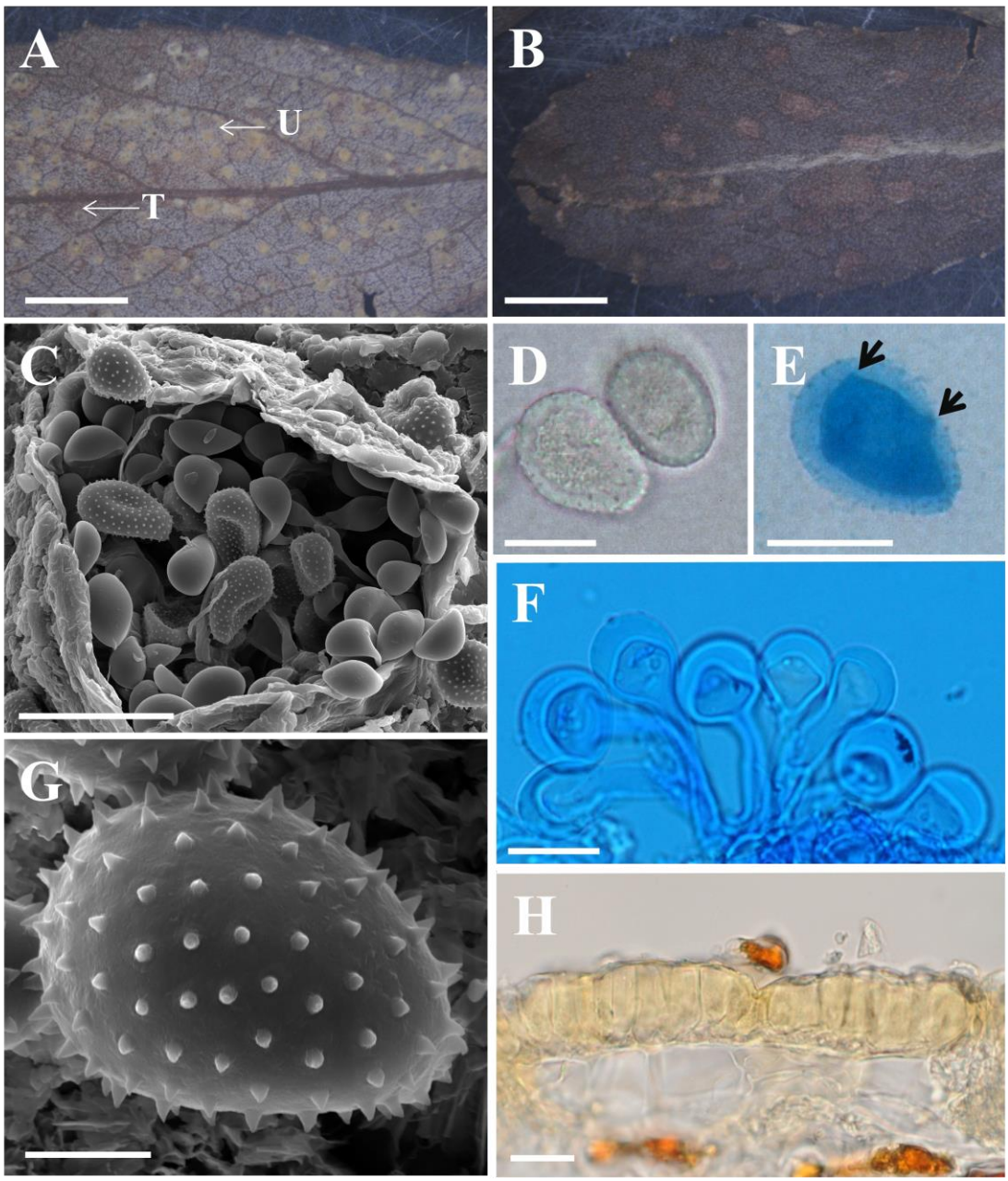


Fig. 4-8 Morphology of *Melampsora yezoensis* (HMAS356). A: Uredinia (U) and telia (T) on the abaxial leaf surface. Uredinia scattered, telia intermixed with uredinia. B: No uredinia or telia on the adaxial leaf surface. C: Uredinia observed by SEM, without intermixed paraphyses. D: Obovoid, ellipsoid or ovoid urediniospores observed by OM. E: Scattered or tending to biozonate germ pores (black arrows). F: Capitate paraphyses with thickened apex. G: Ultrastructure of urediniospores, echinulate. H: Subcuticular teliospores without thickened apical wall. *Bars*: A, B 15 mm; C 30 µm; D 20 µm; E 20 µm; F 20 µm; G 10 µm; H 20 µm.

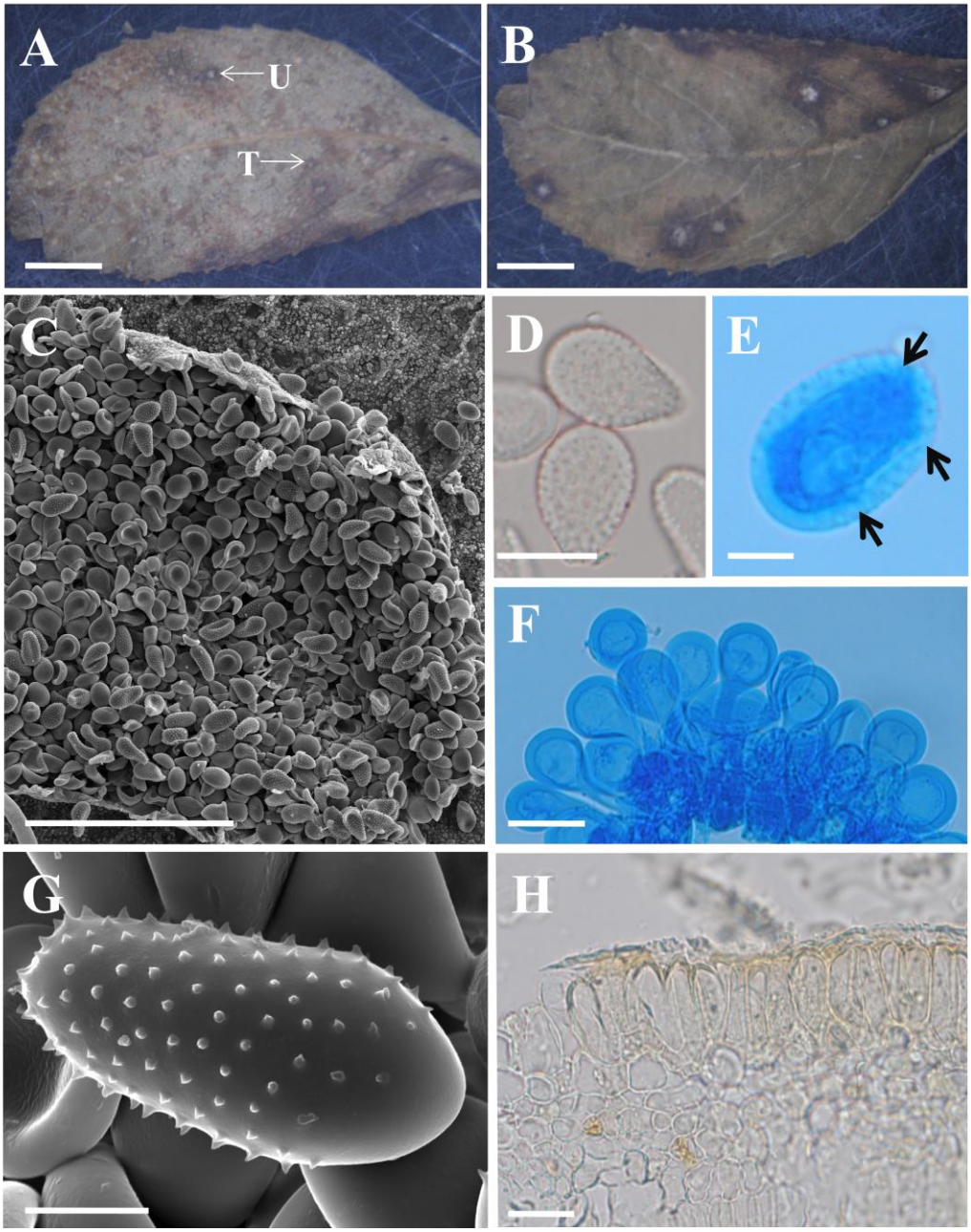


Fig. 4-9 Morphology of *Melampsora microsora* (HMAS56075). A: Uredinia (U) and telia (T) on the abaxial leaf surface. Uredinia scattered, occasionally gathered in groups, telia intermixed with uredinia. B: No uredinia or telia on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Obovoid, ellipsoid or ovoid urediniospores observed by OM. E: Scattered or tending to biozonate germ pores (black arrows). F: Capitate paraphyses. G: Ultrastructure of urediniospores, with smooth region at apex. H: Subepidermal teliospores without thickened apical wall. *Bars*: A, B 25 mm; C 120 μm; D 20 μm; E 10 μm; F 25 μm; G 10 μm; H 20 μm.

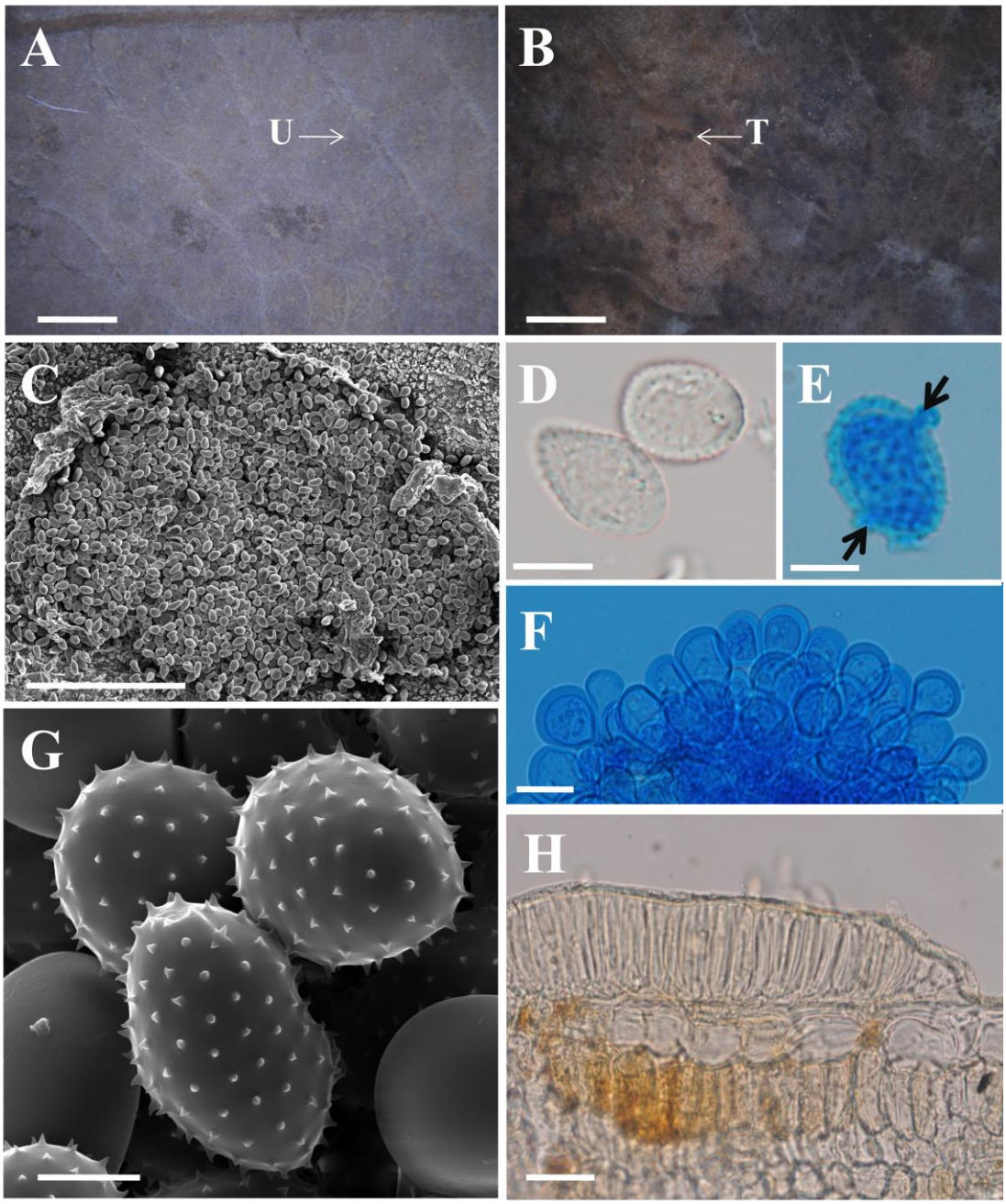


Fig. 4-10 Morphology of *Melampsora chelidonii-pierotii* (HNMWFC-L91054). A: Uredinia (U) on the abaxial leaf surface. Uredinia scattered. B: Telia (T) on the adaxial leaf surface. C: Uredinia observed by SEM, with intermixed paraphyses. D: Obovoid or ellipsoid urediniospores observed by OM. E: Scattered or tending to scattered germ pores (black arrows). F: Capitate paraphyses without thickened apex. G: Ultrastructure of urediniospores, echinulate. H: Subcuticular teliospores without thickened apical wall. *Bars*: A, B 15 mm; C 200 µm; D 20 µm; E 20 µm; F 20 µm; G 10 µm; H 20 µm.

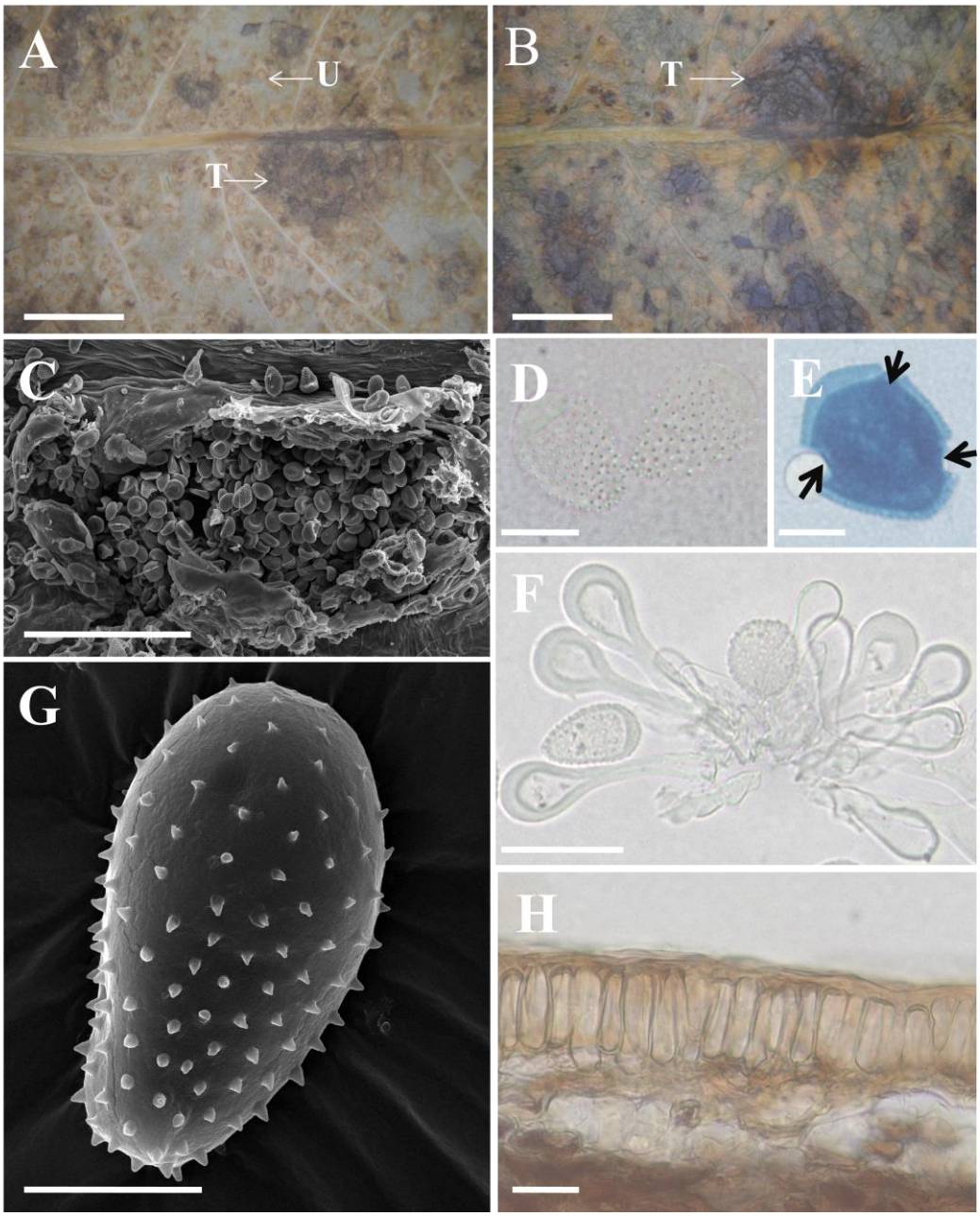


Fig. 4-11 Morphology of *Melampsora laricis-pentandrae* (HNMAP3163). A: Uredinia (U) and telia (T) on the abaxial leaf surface. Uredinia scattered, occasionally gathered in groups, telia intermixed with uredinia. B: Telia on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Obovoid, ellipsoid or ovoid urediniospores observed by OM. E: Scattered or tending to biozonate germ pores (black arrows). F: Capitate paraphyses intermixed with urediniospores. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal teliospores without thickened apical wall. *Bars*: A, B 20 mm; C 60 µm; D 20 µm; E 10 µm; F 30 µm; G 10 µm; H 20 µm.

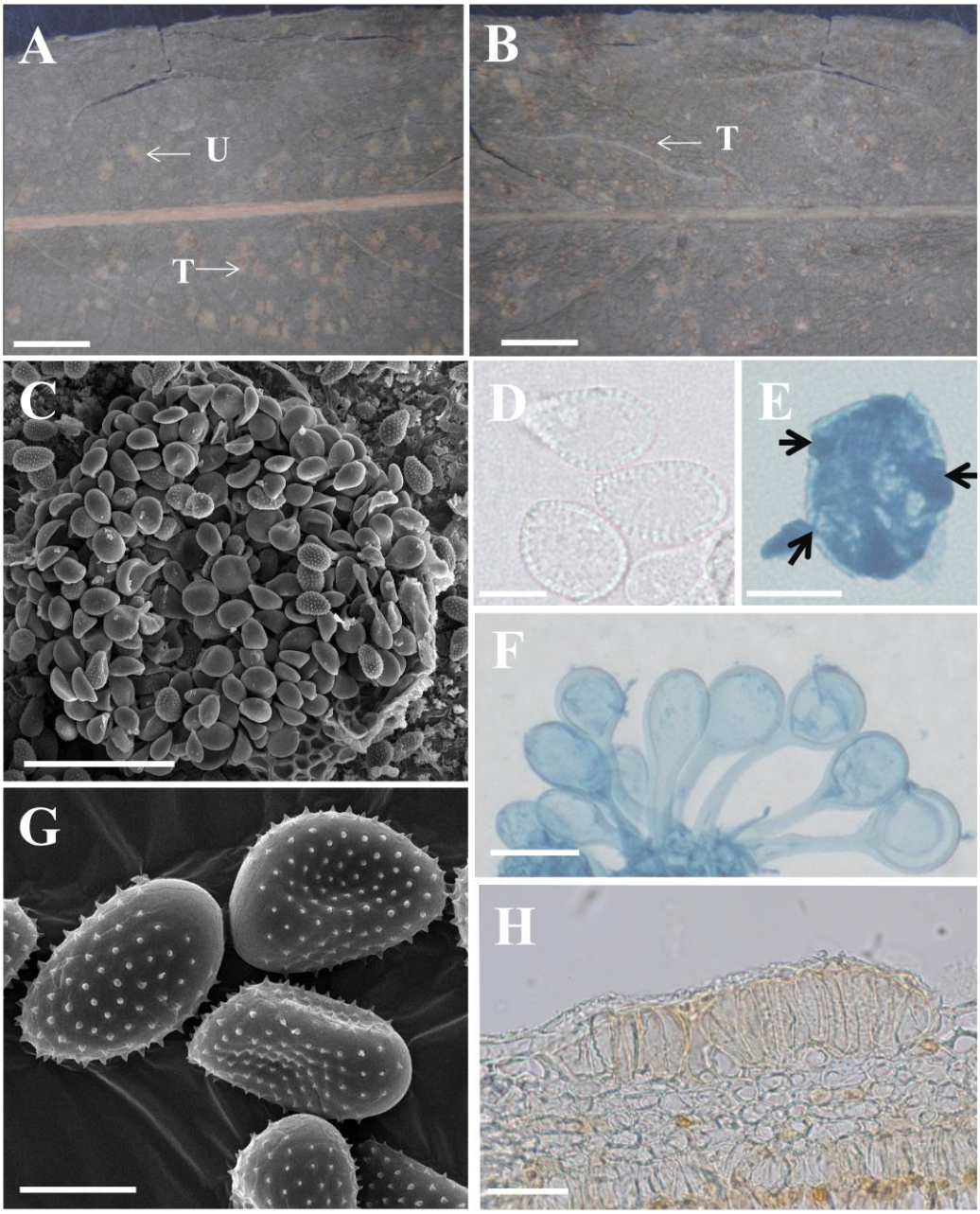


Fig. 4-12 Morphology of *Melampsora salicis-albae* (HMAS52924). A: Uredinia (U) and telia (T) on the abaxial leaf surface. Uredinia scattered, occasionally gathered in groups, telia intermixed with uredinia. B: Telia on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Obovoid, ellipsoid or ovoid urediniospores observed by OM. E: Scattered or tending to biozonate germ pores (black arrows). F: Capitate paraphyses. G: Ultrastructure of urediniospores, with smooth region at apex. H: Subepidermal teliospores without thickened apical wall. *Bars*: A, B 20 mm; C 60 μm; D 20 μm; E 20 μm; F 20 μm; G 10 μm; H 20 μm.

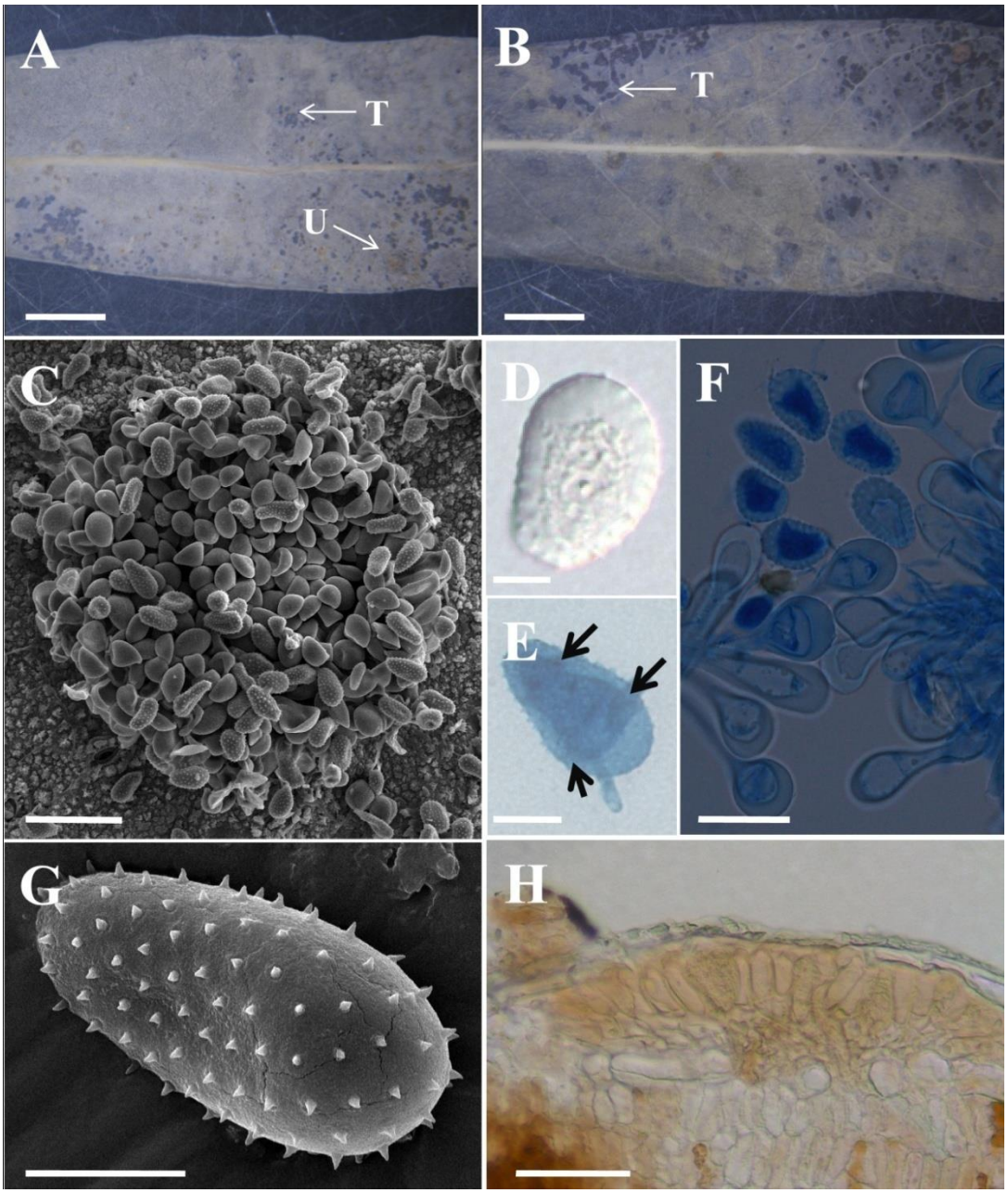


Fig. 4-13 Morphology of *Melampsora kamikotica* (HNMAP3186). A: Uredinia (U) and telia (T) on the abaxial leaf surface. Uredinia scattered, occasionally gathered in groups, telia intermixed with uredinia. B: Telia on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Obovoid or broadly ellipsoid urediniospores with thickened apex observed by OM. E: Scattered or tending to biozonate germ pores (black arrows). F: Capitate paraphyses with apparently thickened apex. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal teliospores without thickened apical wall. *Bars*: A, B 50 mm; C 50 µm; D 5 µm; E 10 µm; F 30 µm; G 10 µm; H 20 µm.

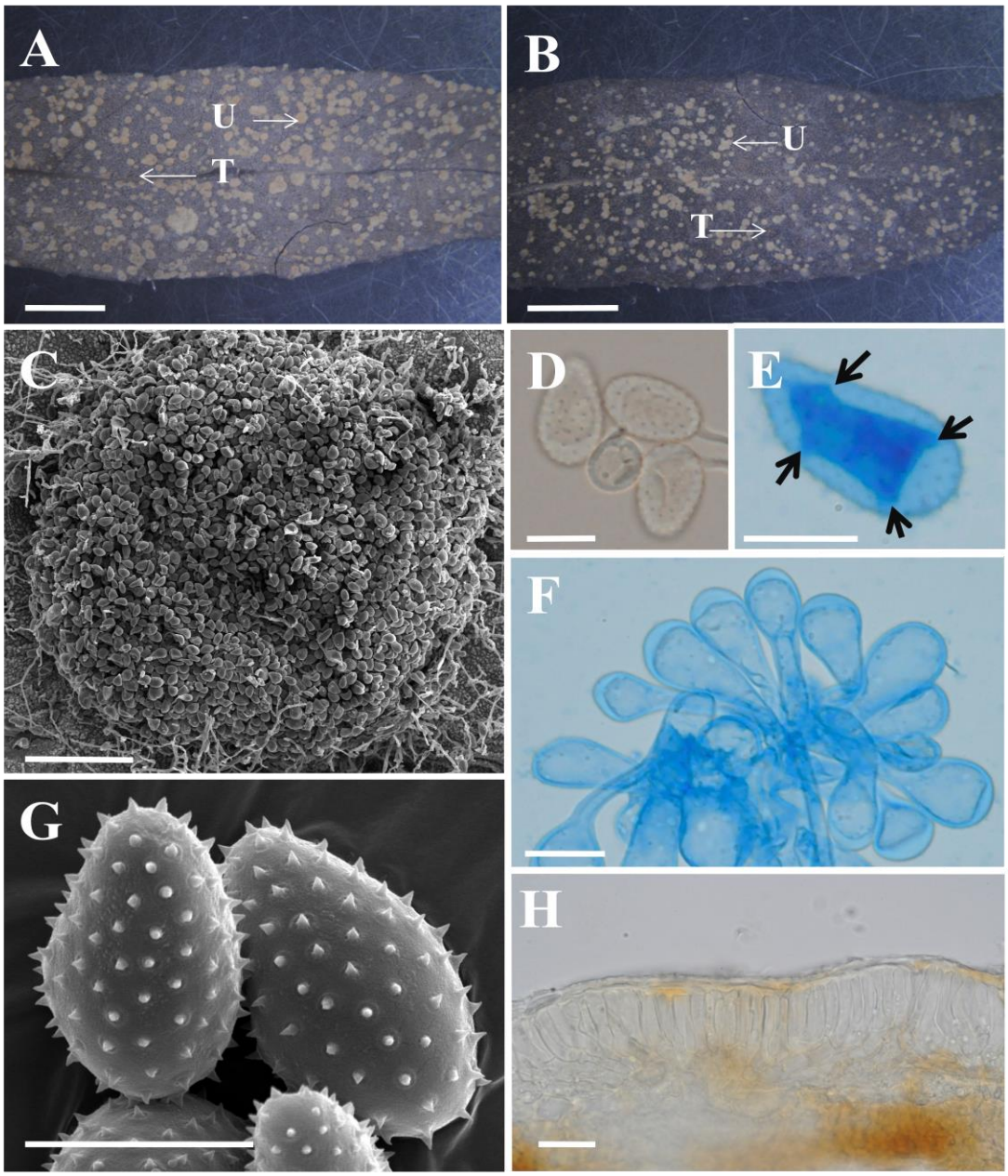


Fig. 4-14 Morphology of *Melampsora tsinlingensis* (HNMAP3185). A: Uredinia (U) and telia (T) on the abaxial leaf surface. Uredinia scattered, occasionally gathered in groups, telia intermixed with uredinia. B: Uredinia and telia on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Obovoid, ellipsoid or ovoid urediniospores observed by OM. E: Scattered or tending to biozonate germ pores (black arrows). F: Capitate paraphyses intermixed with urediniospores. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal teliospores without thickened apical wall. *Bars*: A, B 30 mm; C 100 μm; D, 15 μm; E 20 μm; F 30 μm; G 10 μm; H 20 μm.

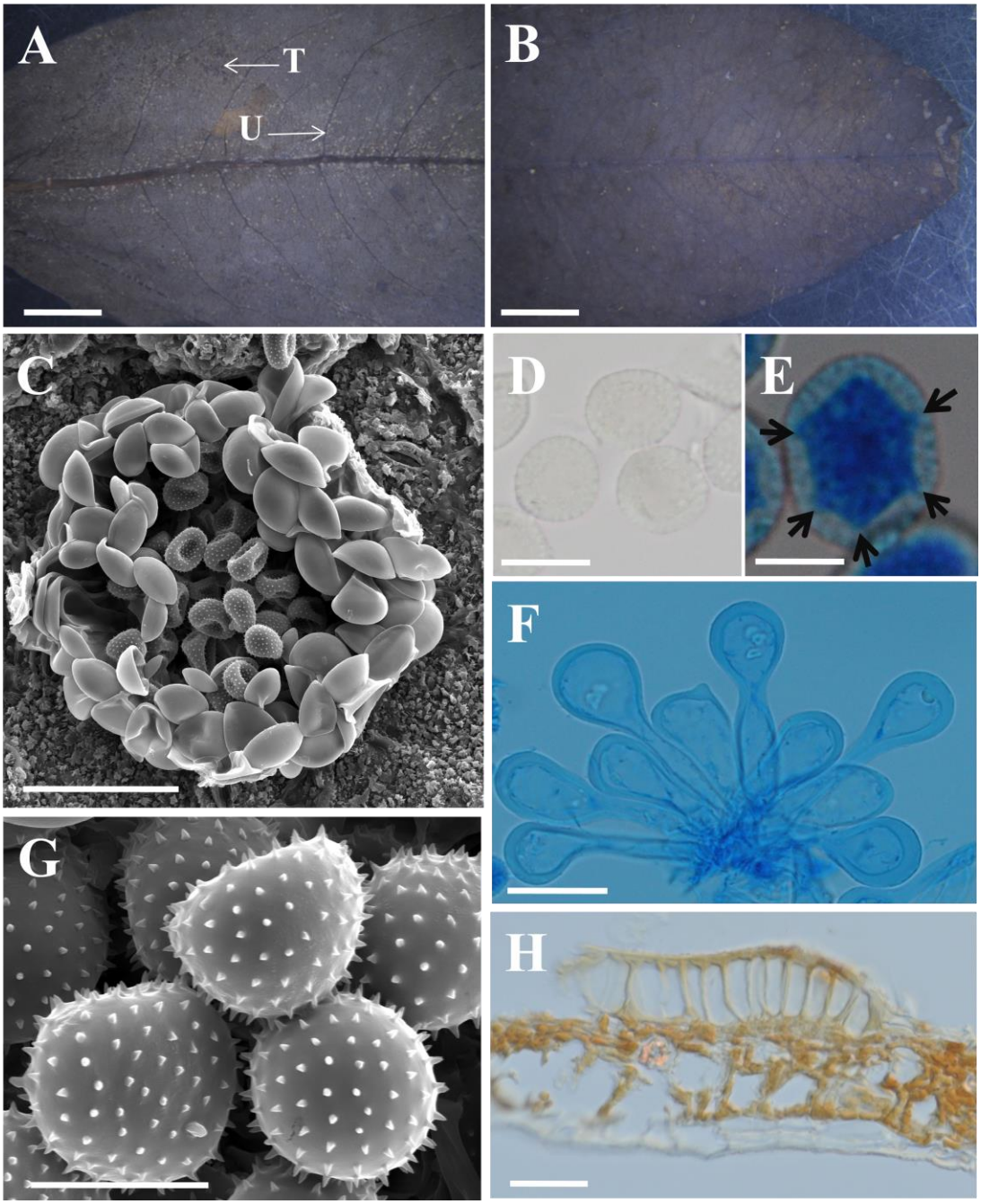


Fig. 4-15. Morphology of *Melampsora* sp. 4 (HMNWFC-L915054). A: Uredinia (U) and telia (T) on the abaxial leaf surface. Uredinia scattered, occasionally gathered in groups, telia intermixed with uredinia. B: No uredinia and telia on the adaxial leaf surface. C: Uredinia observed by SEM, peripheral paraphyses. D: Globoid, ellipsoid or ovoid urediniospores observed by OM. E: Scattered or tending to biozonate germ pores (black arrows). F: Capitate paraphyses. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal teliospores without thickened apical wall. *Bars*: A, B 30 mm; C 50 µm; D, 10 µm; E 10 µm; F 30 µm; G 10 µm; H 20 µm.

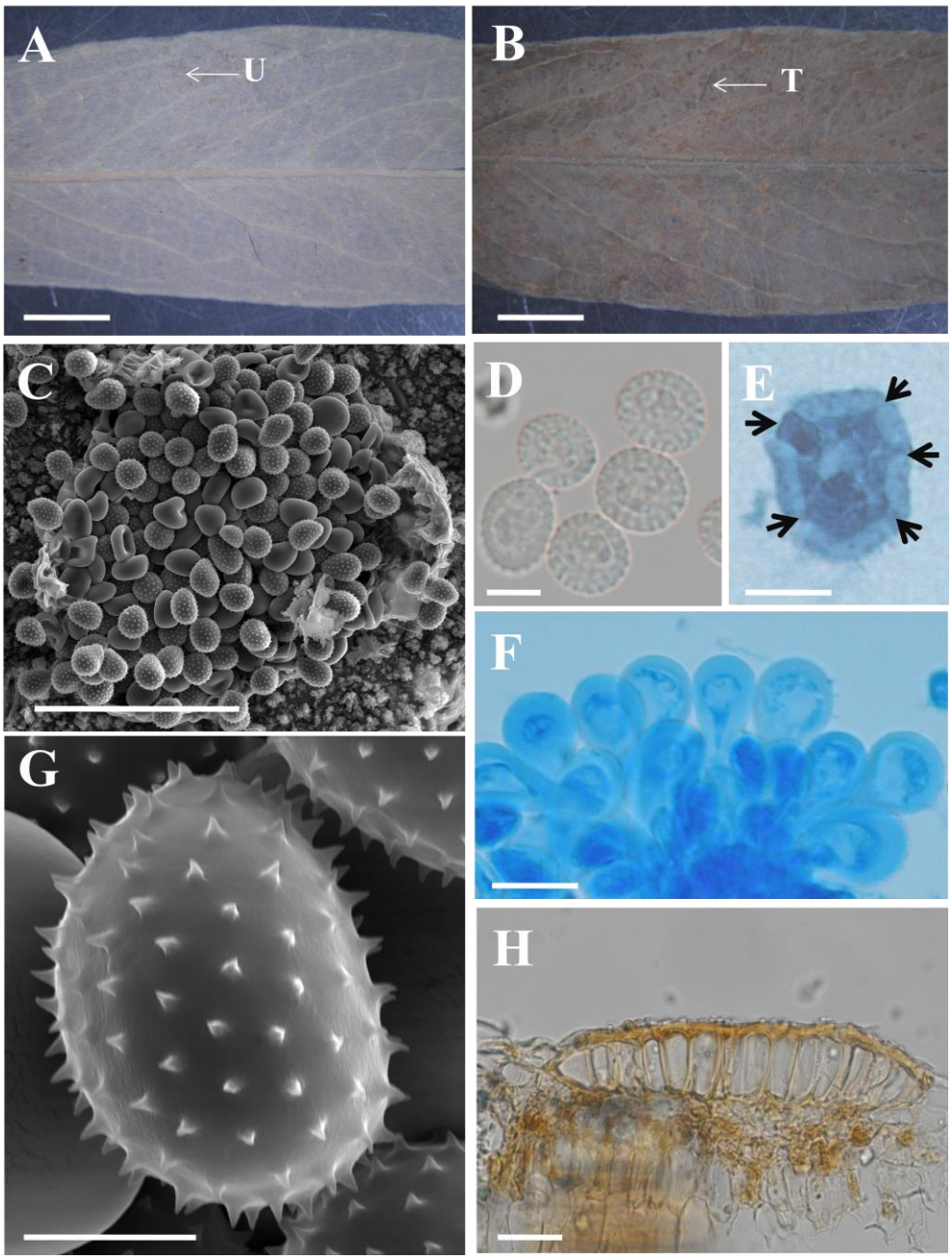


Fig. 4-16 Morphology of *Melampsora* sp. 2 (HNMAP3193). A: Uredinia (U) on the abaxial leaf surface. B: Telia (T) on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Globoid or ellipsoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses with evenly thickened apex. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal teliospores without apparently thickened apical wall. *Bars*: A 20 mm; B 20 mm; C 50 µm; D 10 µm; E 5 µm; F 20 µm; G 6 µm; H 20 µm.

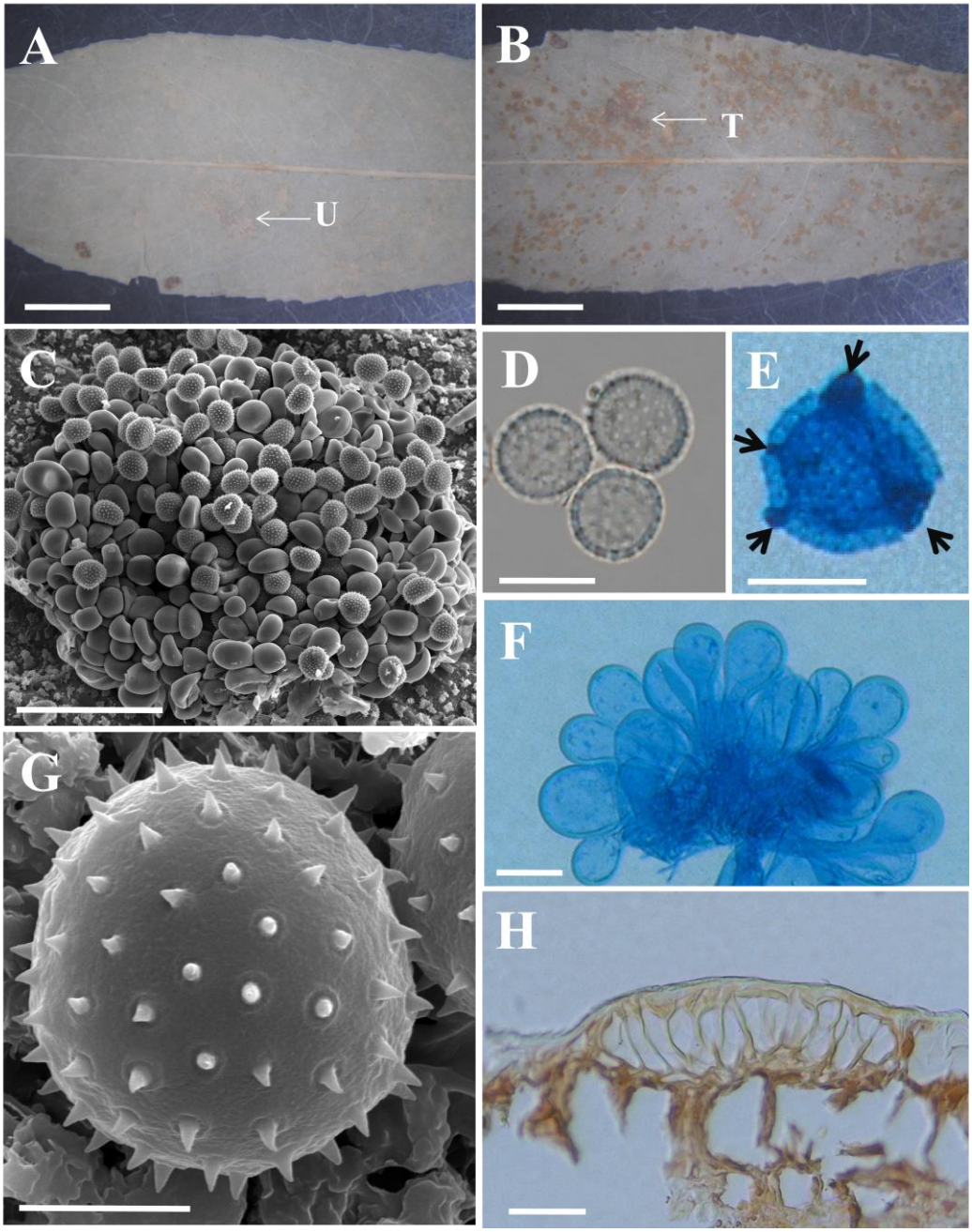


Fig. 4-17 Morphology of *Melampsora* sp. 5 (HNMAP3060). A: Uredinia (U) on the abaxial leaf surface. B: Telia (T) on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Globoid or ellipsoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses with evenly thickened apex. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal teliospores without apparently thickened apical wall. *Bars*: A 30 mm; B 30 mm; C 50 µm; D 10 µm; E 10 µm; F 20 µm; G 6 µm; H 20 µm.

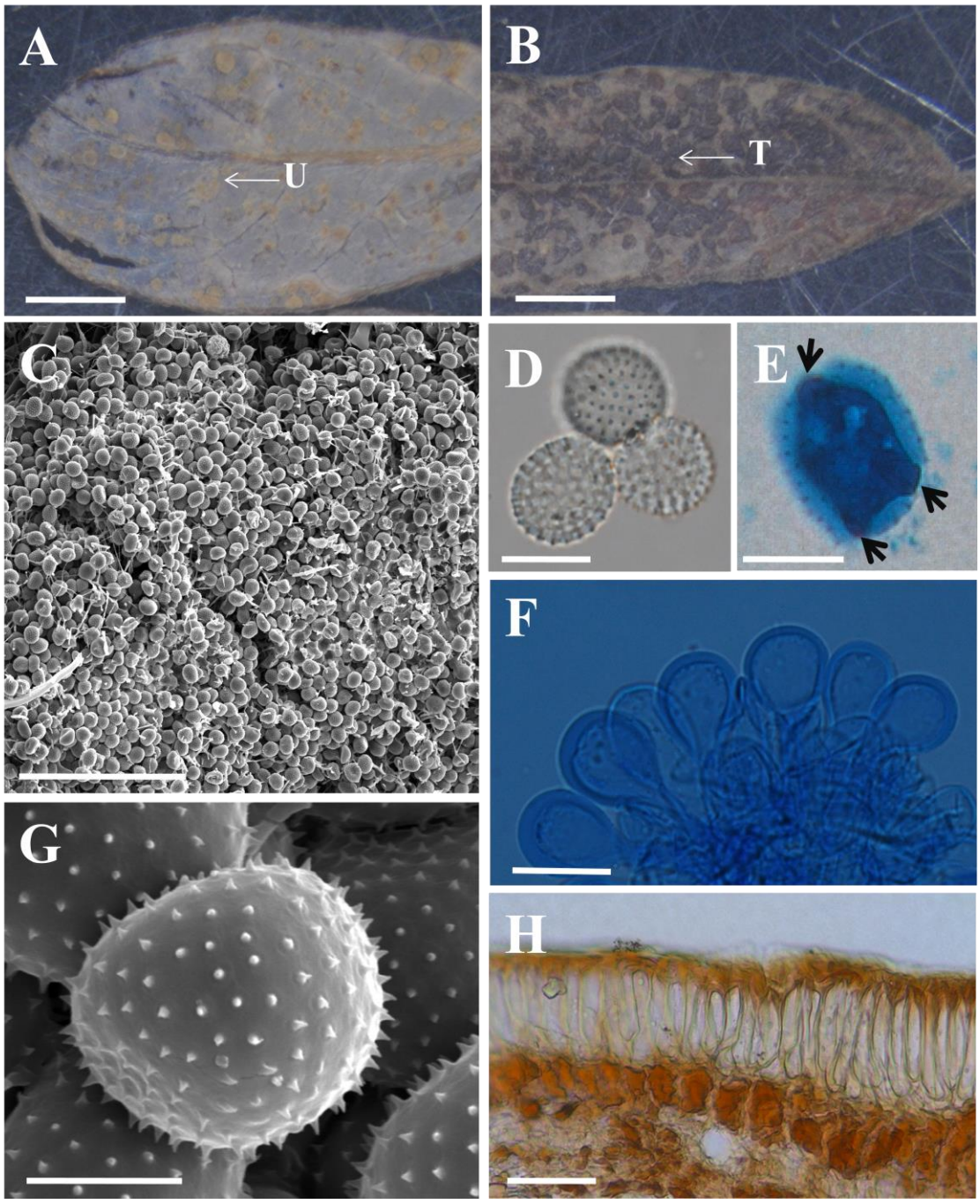


Fig. 4-18 Morphology of *M. salicis-argyraceae* (HMAS52894). A: Uredinia (U) on the abaxial leaf surface. B: Telia (T) on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Globoid or ellipsoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses with evenly thickened apex. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal teliospores with thickened apical wall. *Bars*: A 20 mm; B 20 mm; C 100 μm; D 10 μm; E 10 μm; F 25 μm; G 5 μm; H 20 μm.

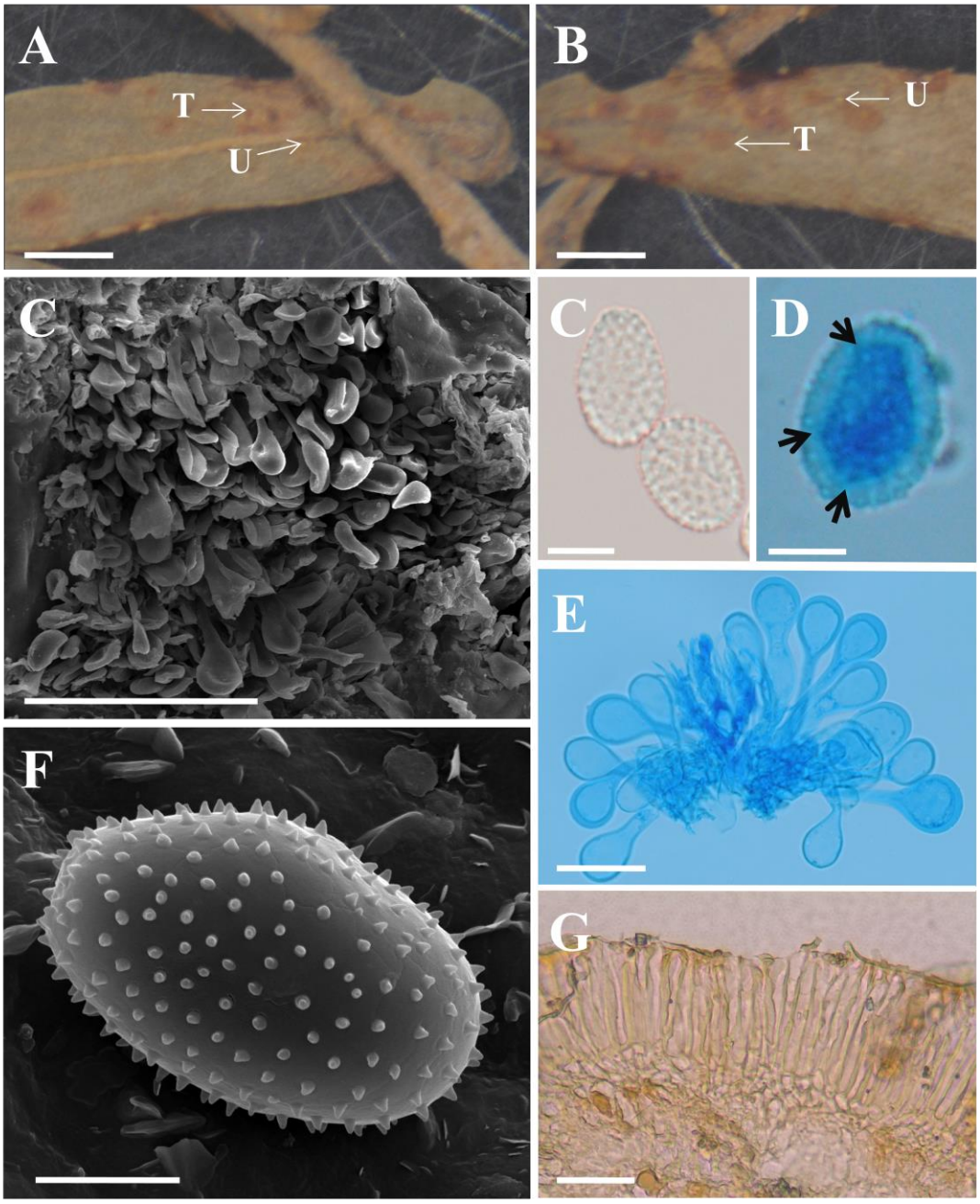


Fig. 4-19 Morphology of *Melampsora salicis-viminalis* (HMAS38658). A: Uredinia (U) and telia (T) on the abaxial leaf surface. Uredinia scattered, telia intermixed with uredinia. B: Uredinia and telia on the adaxial leaf surface. C: Uredinia observed by SEM, with intermixed paraphyses. D: Obovoid or ellipsoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses without thickened apex. G: Ultrastructure of urediniospores, echinulate. H: Subepidermal teliospores without thickened apical wall. *Bars*: A, B 25 mm; C 30 µm; D 10 µm; E 15 µm; F 30 µm; G 10 µm; H 20 µm.

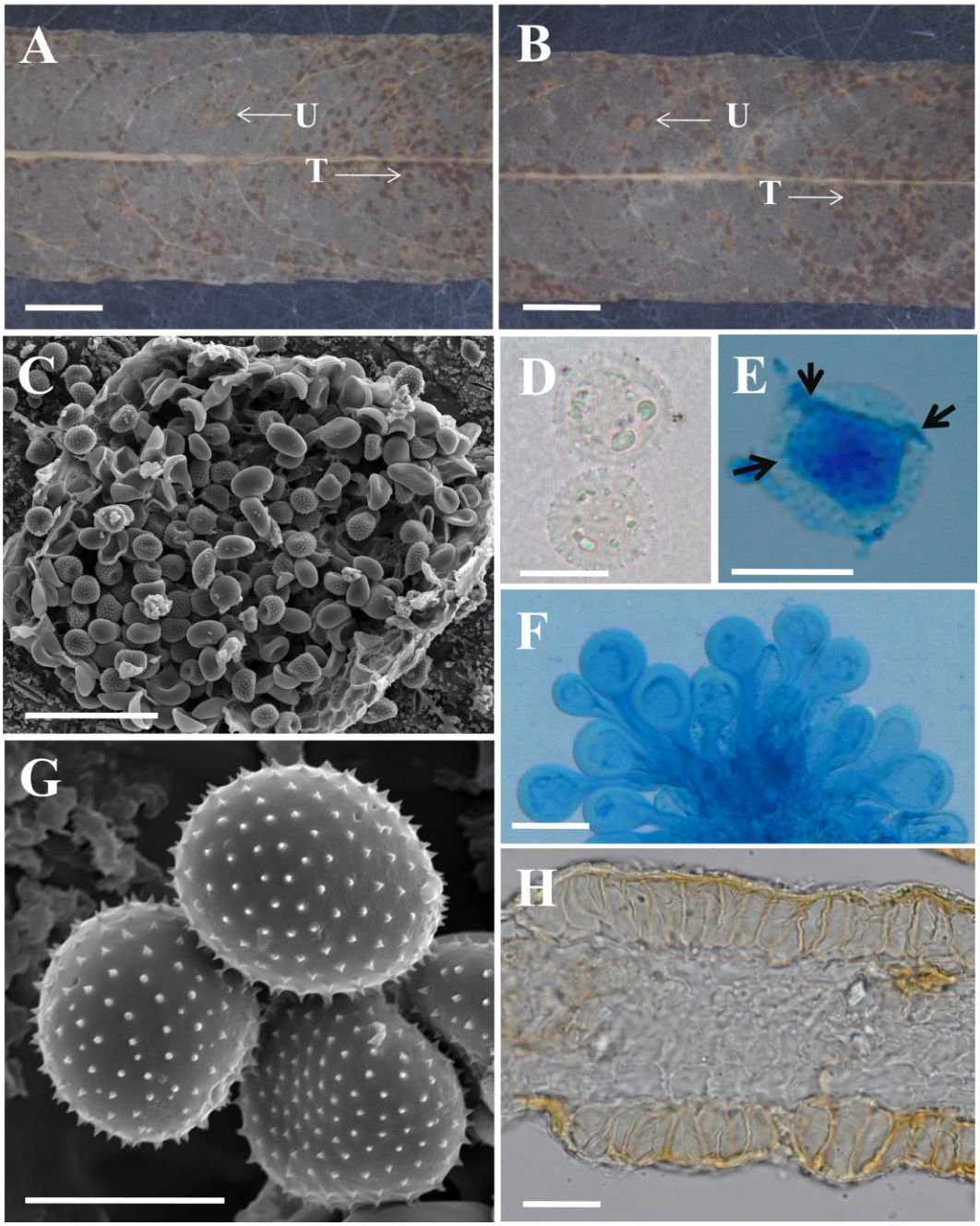


Fig. 4-20 Morphology of *M. salicis-purpureae* (HMAS62584). A: Uredinia (U) and telia (T) on the abaxial leaf surface. B: Uredinia (U) and telia (T) on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Globoid or ellipsoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses with evenly thickened apex. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal teliospores with thickened apical wall. *Bars*: A 15 mm; B 15 mm; C 50 µm; D 10 µm; E 10 µm; F 20 µm; G 15 µm; H 20 µm.

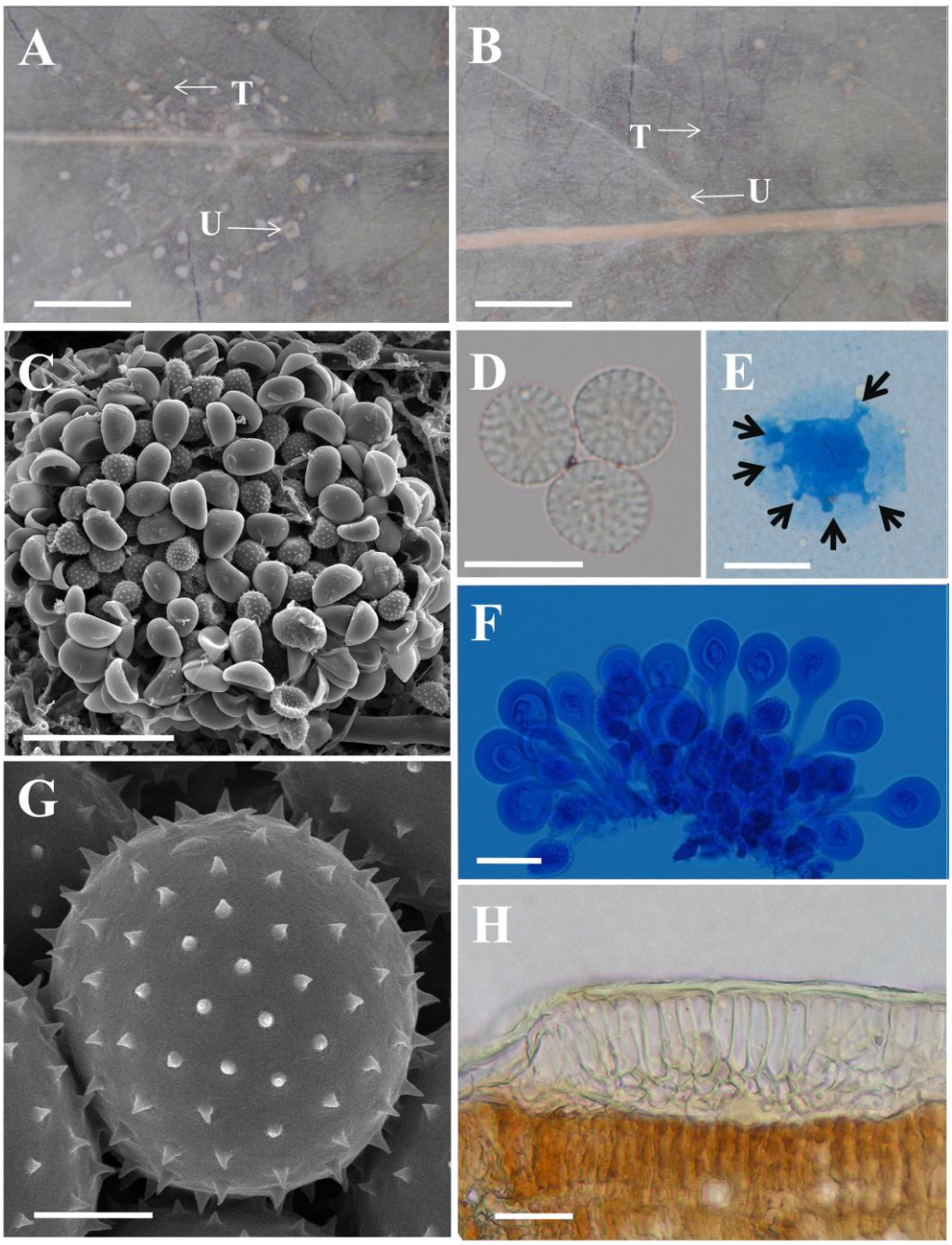


Fig. 4-21 Morphology of *Melampsora iranica* (HMAS52905). A: Uredinia (U) and telia (T) on the abaxial leaf surface. B: Uredinia (U) and telia (T) on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Globoid or ellipsoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses with evenly thickened apex. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal teliospores without distinct thickened apical wall. *Bars*: A 5 mm; B 5 mm; C 60 µm; D 20 µm; E 10 µm; F 20 µm; G 6 µm; H 20 µm.

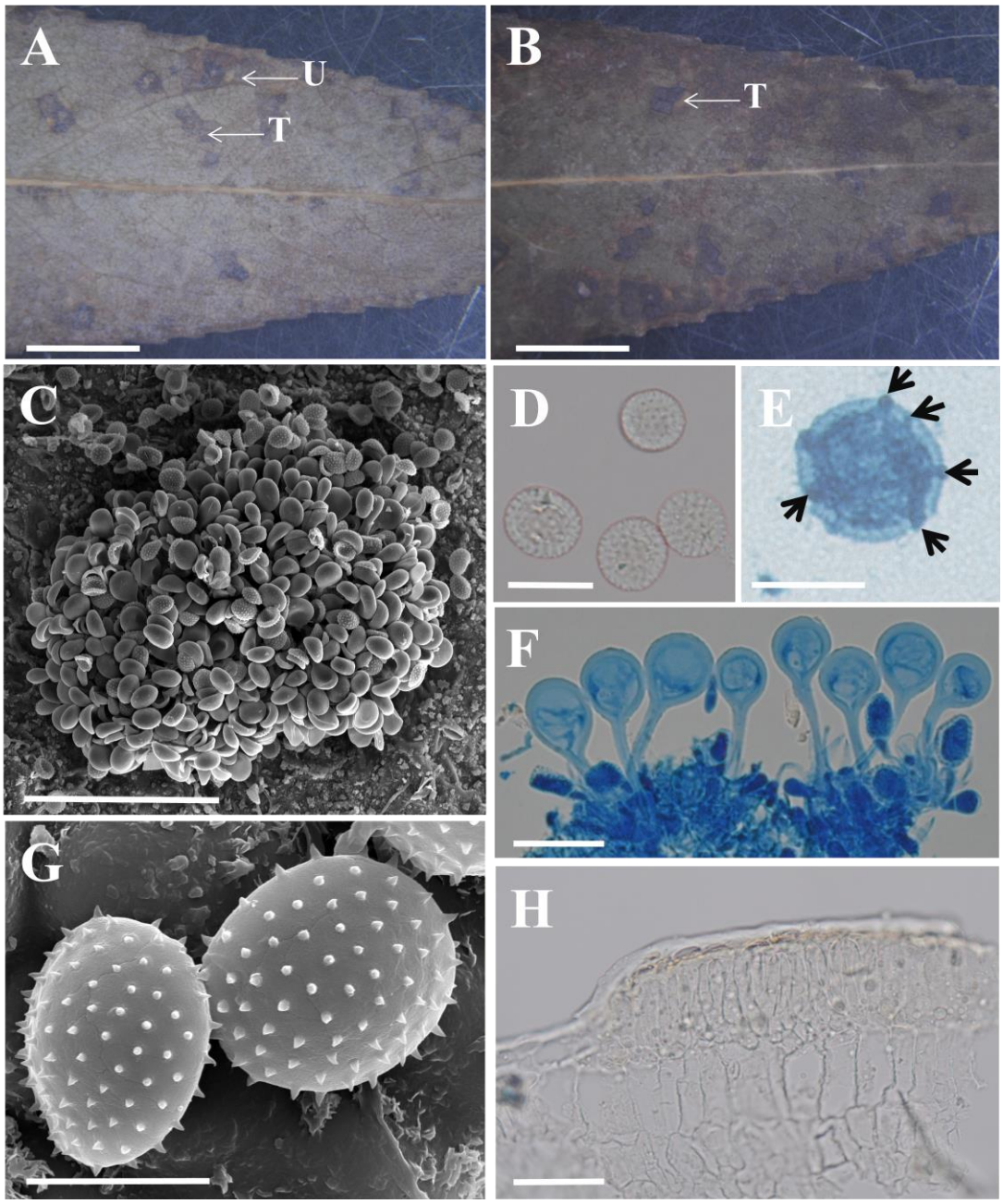


Fig. 4-22 Morphology of *Melampsora* sp. 1 (HNMAP3149). A: Uredinia (U) and telia (T) on the adaxial leaf surface on the abaxial leaf surface. B: Telia (T) on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Globoid or ellipsoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses with evenly thickened apex. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal teliospores without thickened apical wall. *Bars*: A 25 mm; B 25 mm; C 100 µm; D 20 µm; E 10 µm; F 20 µm; G 10 µm; H 20 µm.

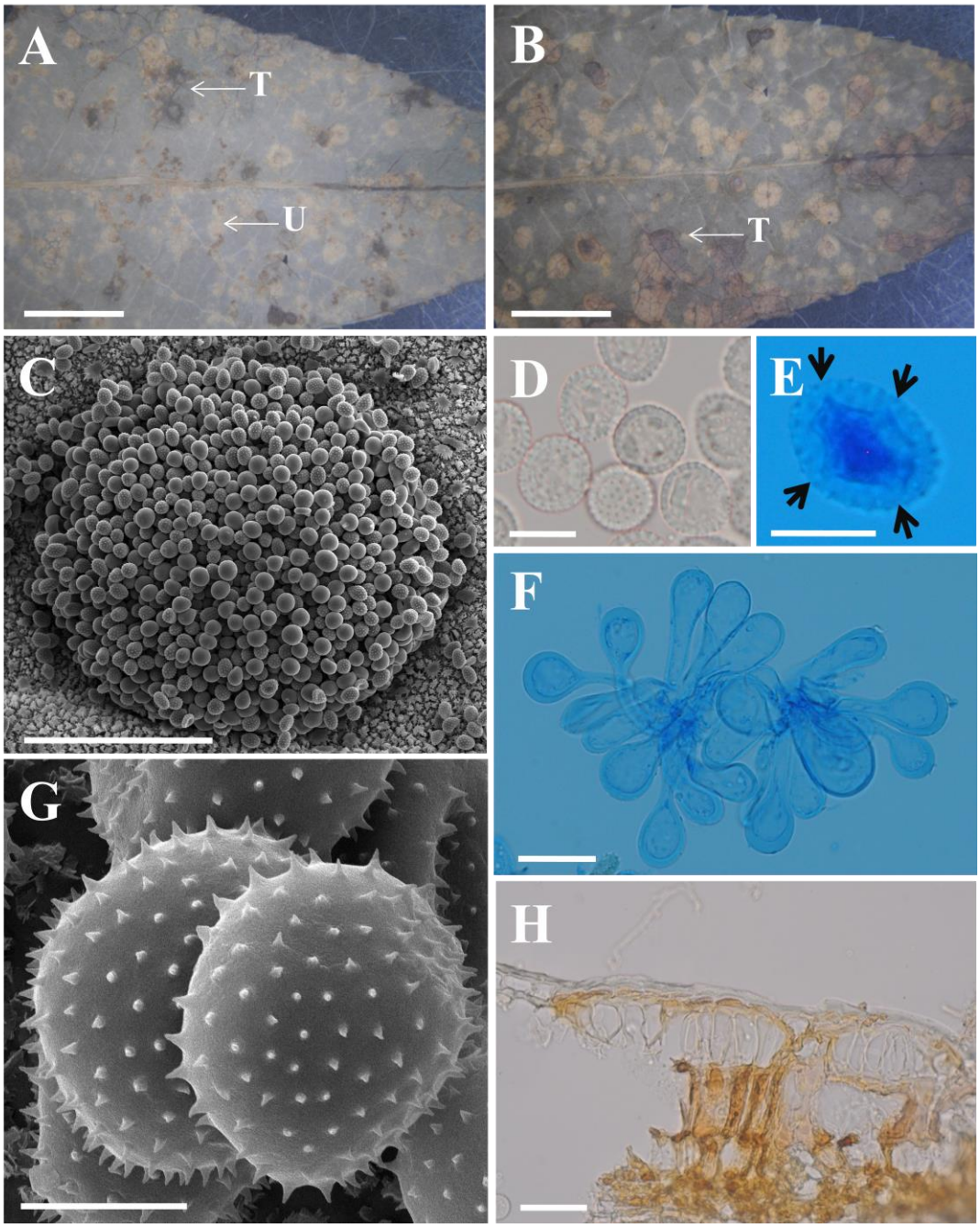


Fig. 4-23 Morphology of *Melampsora* sp. 6 (HMAS58573). A: Uredinia (U) and telia (T) on the adaxial leaf surface on the abaxial leaf surface. B: Telia (T) on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Globoid or ellipsoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses with evenly thickened apex. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal teliospores without thickened apical wall. *Bars*: A 20 mm; B 20 mm; C 100 μm; D 10 μm; E 10 μm; F 25 μm; G 5 μm; H 20 μm.

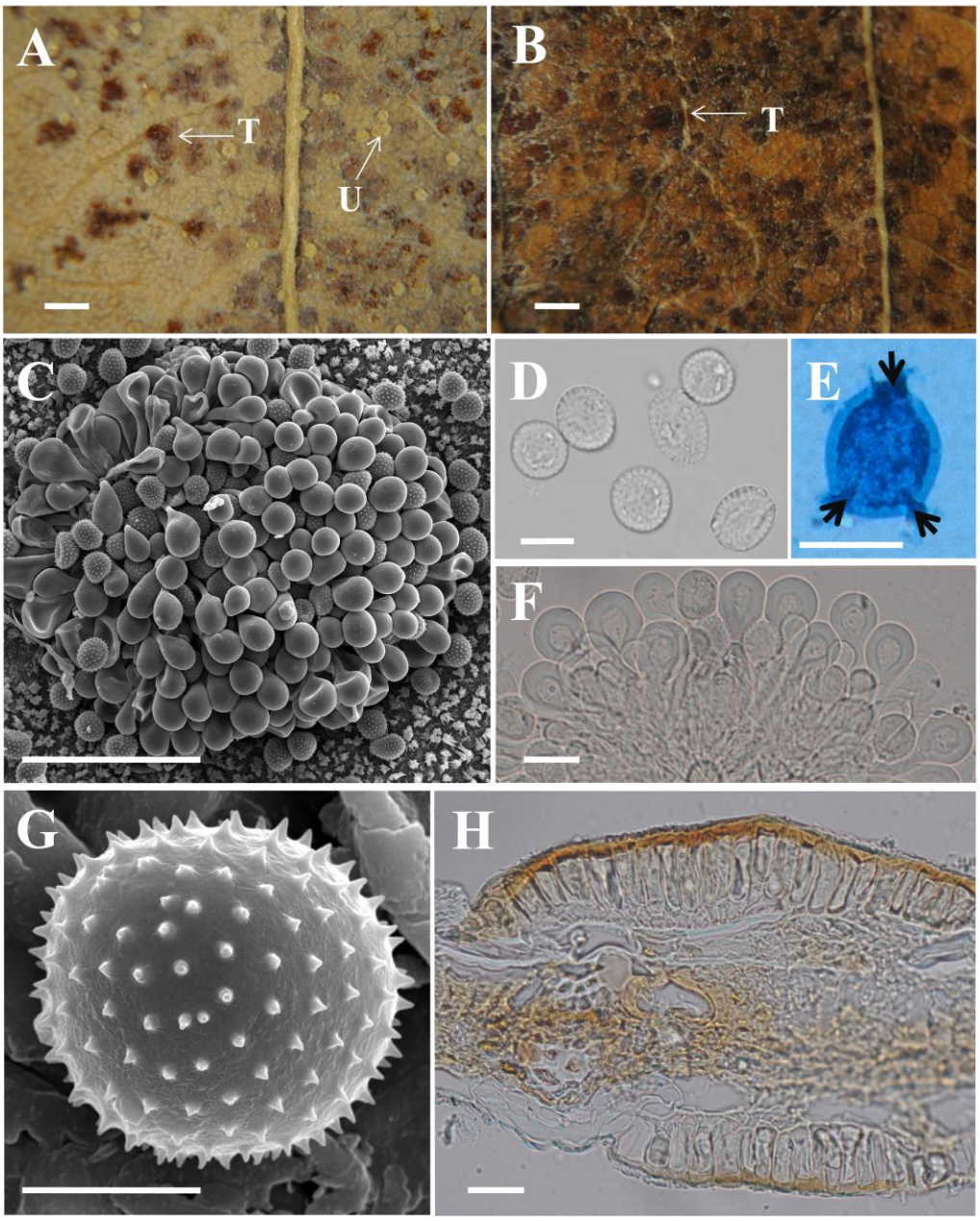


Fig. 4-24 Morphology of *Melampsora salicis-sinicae* (HNMAP1710). A: Uredinia (U) and telia (T) on the abaxial leaf surface. Uredinia scattered, occasionally gathered in groups, telia intermixed with uredinia. B: Telia on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Globoid, ellipsoid or ovoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses intermixed with urediniospores. G: Ultrastructure of urediniospores, with echinulate spines. H: Amphigenous, subcuticular teliospores with distinct thickened apical wall. *Bars*: A, B 20 mm; C 60 μm; D, E 15 μm; F 20 μm; G 6 μm; H 30 μm.

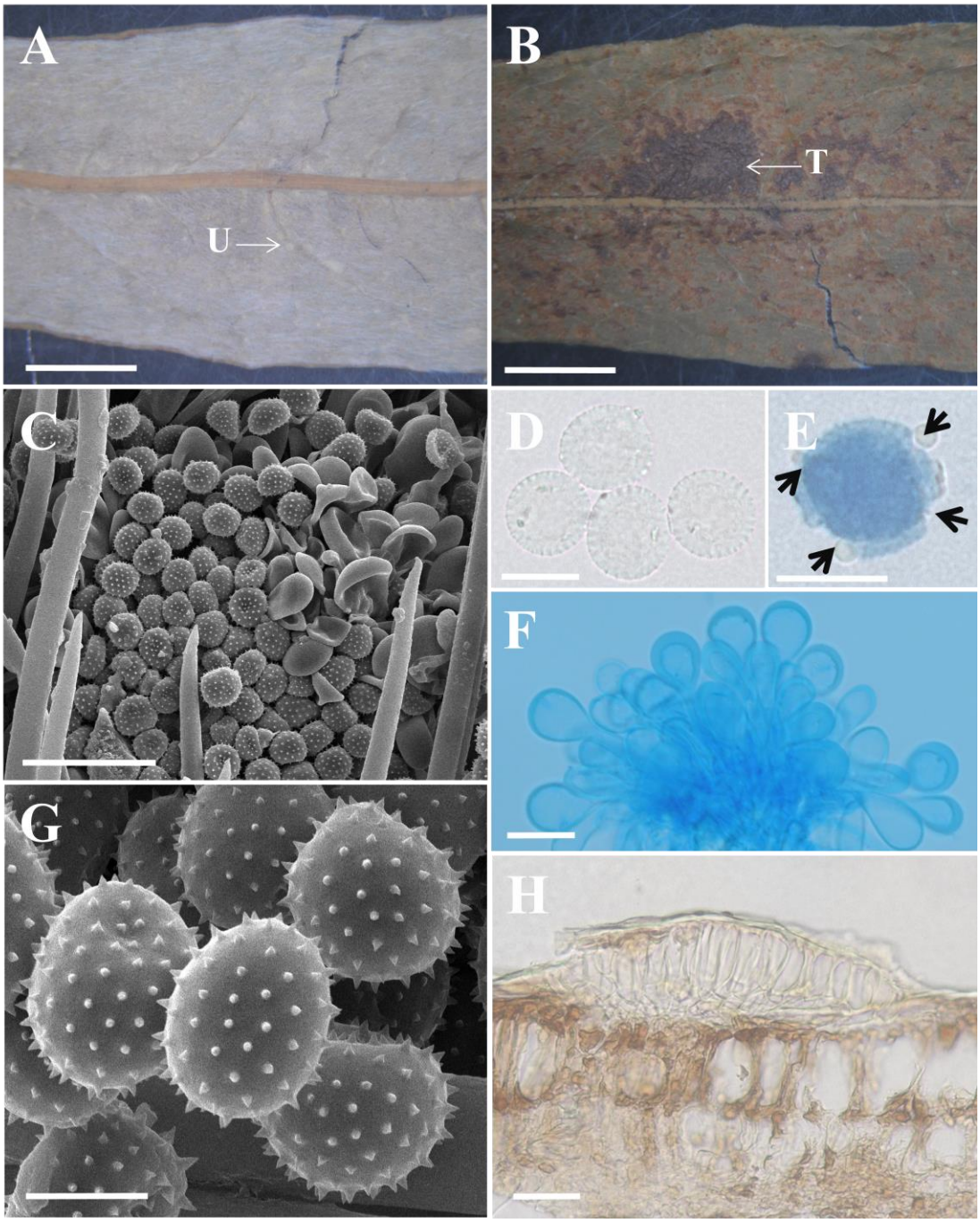


Fig. 4-25 Morphology of *Melampsora ribesii-viminalis* (HNMAP3222). A: Uredinia (U) on the abaxial leaf surface. B: Telia (T) on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Globoid or ellipsoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses with evenly thickened apex. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal or subcuticular teliospores with distinct thickened apical wall. *Bars*: A 15 mm; B 15 mm; C 50 μm; D 10 μm; E 10 μm; F 20 μm; G 6 μm; H 20 μm.

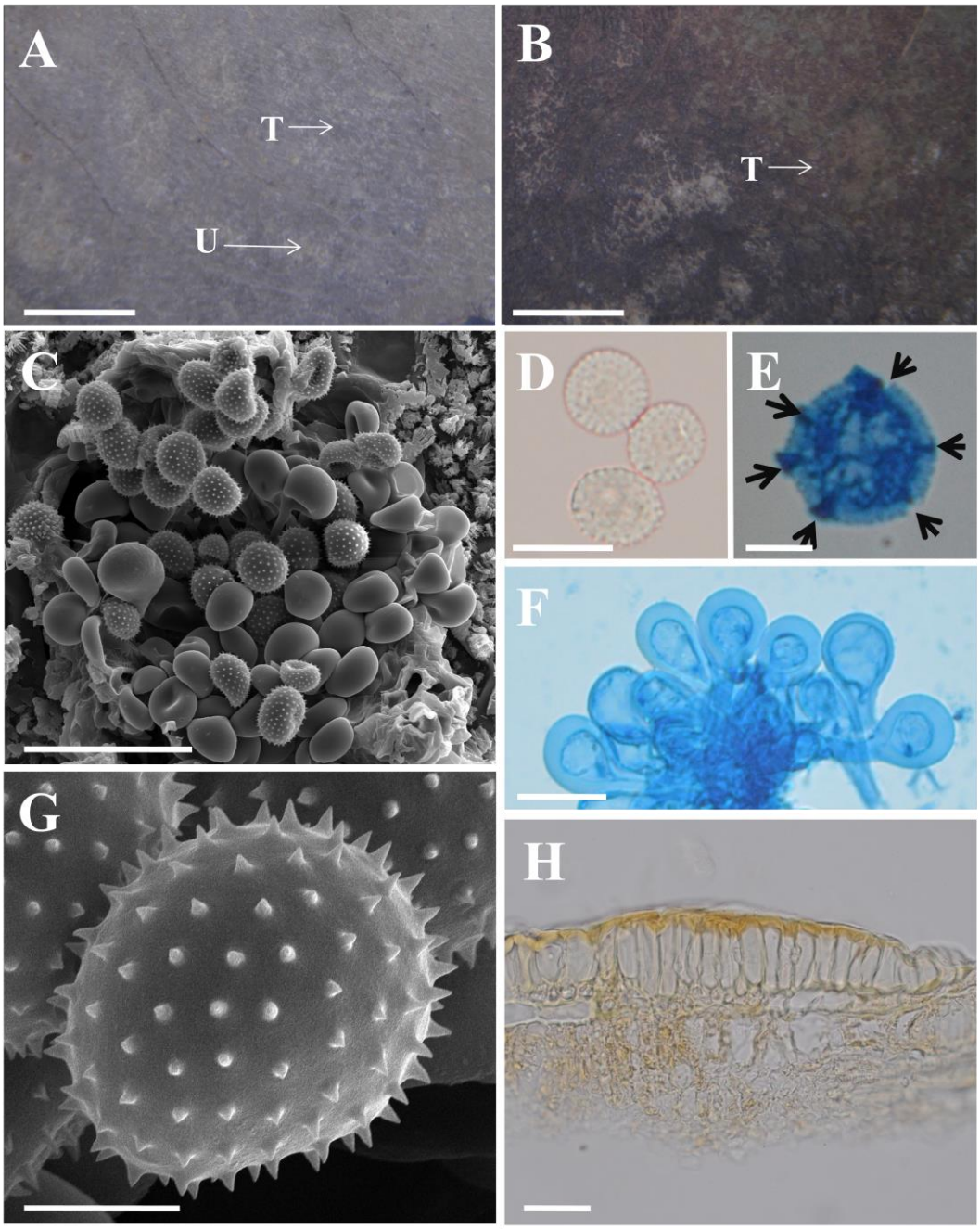


Fig. 4-26 Morphology of *Melampsora epiphylla* (BPI23212). A: Uredinia (U) and telia (T) on the abaxial leaf surface. B: Telia on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Globoid or ellipsoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses with evenly thickened apex. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal or subcuticular teliospores with distinct thickened apical wall. *Bars*: A 10 mm; B 10 mm; C 30 μm; D 20 μm; E 10 μm; F 20 μm; G 6 μm; H 20 μm.

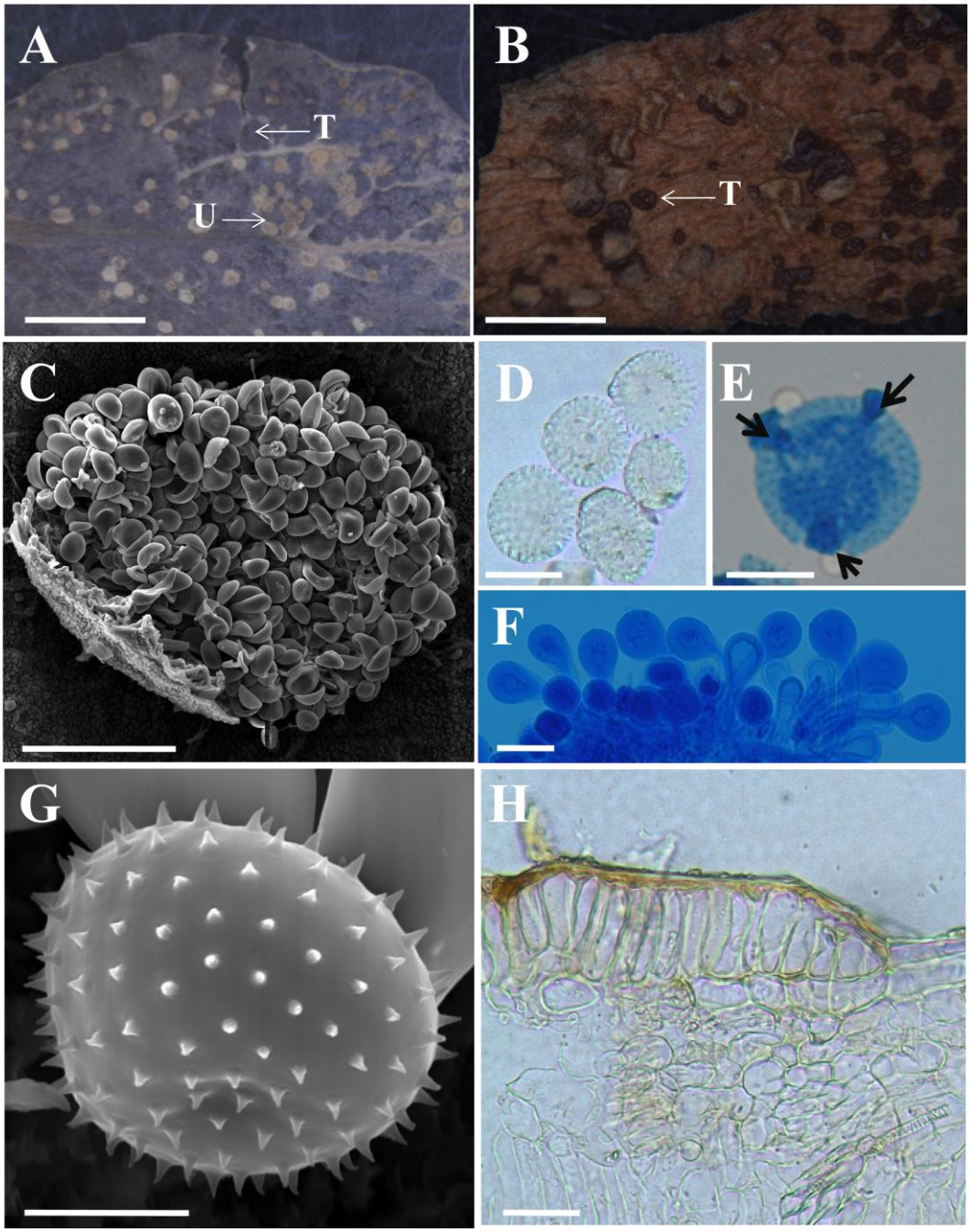


Fig. 4-27 Morphology of *Melampsora salicis-cupularis* (HNWFC-T85040). A: Uredinia (U) and telia (T) on the abaxial leaf surface. B: Telia (T) on the adaxial leaf surface. C: Uredinia observed by SEM, abundant paraphyses intermixed with urediniospores. D: Globoid or ellipsoid urediniospores observed by OM. E: Scattered germ pores (black arrows). F: Capitate paraphyses with evenly thickened apex. G: Ultrastructure of urediniospores, with echinulate spines. H: Subepidermal or subcuticular teliospores without distinct thickened apical wall. *Bars*: A 5 mm; B 5 mm; C 50 µm; D 20 µm; E 10 µm; F 20 µm; G 6 µm; H 30 µm.

Chapter 5 General discussion

5-1 Integrative taxonomic methods for species delineation and character selection

In this study, numerical taxonomy was used for morphological studies, and the cluster analysis was used to determine the morphological groups and to evaluate the morphological characteristics for species recognition. This method can provide an outcome based on correct similarity/dissimilarity coefficients (Sieber et al. 1998; Sneath 1995). Moreover, this method uses many of phenotypic characters, rather than only diagnostic ones with equal a priori weighting, and it emphasizes species as clusters derived from measures of overall similarity of qualitative and quantitative characters (Sneath and Sokal, 1973). In addition, the technique provides an effective way to evaluate the criteria used for classification, and several key characters were selected objectively based on the calculation of the frequency of positive characters occurring in each group (Kampfer et al. 1991; Wieclaw and Koopman 2013). Morphological results indicated that this approach was applicable and explicit for species recognition and character selection.

Nevertheless, numerical taxonomic method had some limitations when it came to distinguishing morphologically cryptic taxa with minute morphological differences. These limitations were further reflected by molecular phylogenetic studies, and relatively higher phylogenetic groups than the preliminary estimation of species richness based on morphological characteristics. Due to shortcomings of morphology-based taxonomy, a new taxonomic method, ‘integrative taxonomy’, which was first proposed by Dayrat (2005) and Will et al. (2005), were used to integrate various lines of evidence to estimate the species diversity.

Two different ways of integrative taxonomy exist: ‘integration by congruence’ and ‘integration by cumulation’ (Padial et al. 2010). The approach of ‘integration by congruence’ was adopted under the assumption that concordant patterns of divergence

among several taxonomic characters indicate full lineage separation. This method is widely used for taxonomic studies in rust fungi, such as taxonomic studies of *Melampsora* species on poplar, *Pucciniastrum* species, *Phakopsora* species, and so on (Tian et al. 2004; Liang 2006; Chatasiri and Ono 2008). However, this approach has the risk of underestimating species numbers because the process of speciation is not always accompanied by character change at all levels and the relative rates of character change during lineage divergence are heterogeneous (Padial et al. 2010).

Another approach of integrative taxonomy is 'integration by cumulation', which is based on the assumption that divergences in any of taxonomic characters can provide evidence for the existence of a species (de Queiroz 2007). The evidence from all characters is assembled cumulatively, and concordances and discordances are explained from the evolutionary perspective. The recognition of a species is decided based on the available information which is considered good indicators of lineage divergence (Padial et al. 2009; Schlick-Steiner et al. 2010). Because this method is probably most suitable to uncover recently diverged species in adaptive radiations, the most appropriate taxonomic characters for each group can be used for species recognition. Based on these advantages, the way of 'integration by cumulation' was used to determine the *Melampsora* taxa on willows based on existing morphological and molecular evidence. This approach was first used for taxonomic studies on rust fungi, and it provided the best resolution for distinguishing species based on both concordance and discordance of morphological and molecular data, which were caused by limited sampling of certain taxa or limited numbers of sequence data obtained from certain DNA locus.

5-2 Species delineation in *Melampsora epitea* complex based on morphological and molecular evidence

Before ecological attributes were abandoned for taxonomic study at the species level, many species were described mainly based on the telial and aecial host

dissimilarity although no significant differences in uredinial and telial morphology were recognized (Klebahn 1914; Matsumoto 1915; Sydow and Sydow 1915; Arthur 1934; Kuprevich and Transhel 1957; Gäumann 1959). Since the ecological attributes were not used for species recognition, these morphologically similar but ecologically dissimilar species were treated as synonyms of *M. epitea* (Hylander 1953). The species included in this species complex differed in number depending on the taxonomists, and up to 21 previously described species have been treated as synonyms of *M. epitea* (Bagyanaryana 2005). Recent phylogenetic analyses have already demonstrated the existence of cryptic species within this species complex (Smith et al. 2004; Pei et al. 2005; Milne et al. 2012), but no effective characters were recognized to delineate these recognized taxa although attempts were made based on the correspondence between the rDNA phylogeny and ultrastructure of urediniospores (Smith et al. 2004) or telial host specificity (Bennett et al. 2011; Milne et al. 2012).

In this study, 14 distinct species were recognized from specimens of the *M. epitea* complex based on numerical taxonomic method and molecular phylogenetic analyses. These 14 species were clearly distinguishable. In addition, five traditionally emphasized morphological criteria (the position of uredinia, the length of urediniospores, the width of urediniospores, the position of telia and the length of teliospores) and three newly recognized morphological criteria (the existence of intermixed paraphyses, the length of paraphyses and the distance between spines) were proved to be effective for recognizing cryptic species within the *M. epitea* complex after a comprehensive evaluation. These effective characters will be important for delineating the cryptic species in this species complex in the future.

Among these 14 species, *Melampsora* sp. 1 and *Melampsora* sp. 6 are morphologically indistinguishable in the uredinial and telial stages although they were phylogenetically distinct. Recent studies on cryptic species of the *Phakopsora ampelopsidis* complex have already revealed that morphological characteristics in the aecial stage were important for delineating cryptic rust taxa (Ono 2000). In addition, studies of *Melampsora* species on poplar revealed that the phylogenetic lineage corresponded to aecial host specialization (Vialle et al. 2012). Therefore, to delineate

these cryptic species with indistinguishable morphology in the uredinial and telial stages, such as *Melampsora* sp. 1 and *Melampsora* sp. 6, further studies on the life cyle and morphological characteristics in aecial stage need to be investigated.

Based on rDNA ITS phylogeny, sequence data of *M. epitea* from North America and Europe were located in seven phylogenetic groups. North American rust fungi on *S. arctica* and *S. bebbiana* were located in I1 together with G1-1, and these on *S. nigra* and on *S. interior* were located in two distinct phylogenetic groups, I15 and I33, respectively. GenBank sequence data of *M. epitea* from Europe were located in four phylogenetic groups, among them, only one phylogenetic group, I9, included data obtained from specimens in China and Japan (Fig 3-2). Although these rust fungi from different phylogenetic groups were previously recognized as populations or *formae speciales* of *M. epitea* (Smith et al. 2004; Pei et al. 2004; Pei et al. 2005; Milne et al. 2012), results obtained from this study indicated specimens from seven phylogenetic groups should be recognized as distinct species. To circumscribe these cryptic taxa in the *M. epitea* complex, detailed morphological examination of specimens from Europe and North America is required.

Melampsora epitea was first described by Thümen (1879), but no type specimen was designated. Among these synonyms of the *M. epitea* complex, many species were originally described by Klebahn (1889; 1914), Schneider (1905), Arthur (1920) and other taxonomists using morphology and host information, but type specimens were not designated in most species. Without recorded specimens under these species names and with the disappearance of the nomenclatural types, determine the proper name of species within the *M. epitea* complex is difficult. Although 14 species were clearly recognized within *M. epitea* complex in this study, species names of nine taxa were not able to confirm. To determine the specific name of these distinct species from specimens of the *M. epitea* complex, type specimens for *M. epitea* and related species must be designated.

5-3 Taxonomic conclusion used for agricultural purposes

Integrated disease management of willow rust disease needs understanding the identity and biology of the causal agents. Thus, accurate identification of fungal pathogens strengthens each part of plant pathology in agricultural practice, and disease diagnosis, quarantine and disease control need the fundamental information from basic taxonomic studies. Thus, taxonomic study provides a key prerequisite for identification and characterization of fungal pathogens in agriculture. In recent years, the world is facing an increasing demand for renewable energy to replace the use of fossil fuels, and short rotation coppice (SRC) willows are the main contributors for biomass production (Wright 2006). Willow species, such as *S. burjatica*, *S. caprea*, *S. dasyclados*, *S. daphnoides*, *S. exigua*, *S. interior*, *S. miyabeana*, *S. nigra*, *S. purpurea*, *S. reticulata* and *S. viminalis*, were widely cultivated in Europe and North America as good candidates for biomass production (Wright 2006; González-García et al. 2012). However, fungal diseases, especially rust diseases caused by species in genus *Melampsora*, can be devastating to willow plantation (Verwijst 2001). Due to discordance and confusion of previous taxonomic systems, the casual agents of above-mentioned SRC willows were recognized as *M. epitea* complex, which included morphologically similar rusts from Asia, Europe and North America (Hiratsuka and Kaneko 1982; Pei 2005). Although genetic divergences of *M. epitea* have already been reported based on amplified fragment length polymorphism (AFLP) and sequence data of rDNA ITS regions and D1/D2 region (Pei et al. 1993; Smith et al. 2004; Pei et al. 2005), these species were not able to be delineated in the absence of clear morphological characteristics.

In this study, based on a broad sampling of specimens belonging to *M. epitea* and its related species, 14 distinct species were recognized. Among them, *Melampsora* sp. 1, *Melampsora* sp. 3, *Melampsora* sp. 6, *Melampsora* sp. 7 and *Melampsora* sp. 8 were found on the above-mentioned SRC willow species. Previously, *Melampsora* sp. 1, *Melampsora* sp. 3 and *Melampsora* sp. 8 were recognized as *M. epitea* in Europe,

North America and Japan (Wilson and Henderson 1966; Ziller 1974; Hiratsuka and Kaneko 1982), and *Melampsora* sp. 6 and *Melampsora* sp. 7 were traditionally recognized as *M. epitea* f.sp. *laricis-epitea* and *M. epitea* f.sp. *ribesii-purpureae*, respectively (Pei 2005). However, they were distinct from *M. epitea* and well circumscribed based on morphological and molecular evidence in this study. Previously, *M. epitea* was reported to be alternated on a wide range of aecial host species (Hylander 1953; Pei 2005). In this study, *Melampsora* species, which were differentiated from *M. epitea* complex, may have completely different life cycles from each other based on the taxonomic description and previously inoculation experiments. Such information will provide fundamental information to clarify the disease cycle, which is essential to guide the application of adequate and accurate measures to control leaf rust diseases on SRC willows.

In recent years, the DNA barcoding, which has provided a rapid and accurate way to identify fungal pathogens based on standardized and species-specific DNA fragment, is gradually used instead of laborious and time-consuming conventional identification (Hebert et al. 2003). Until now, several important open access databases, such as Consortium for the Barcode of Life (CBOL, http://www.barcoding.si.edu), Plant Pathogen Barcode (PPB, http://www.plantpathogenbarcode.org) and Barcode of Life (http://www.barcodeoflife.org), have already been created to promote plant pathogen identification based on DNA barcoding. The gene region proposed for standard barcode of fungal species in these databases is rDNA ITS regions (Schoch et al. 2012), which had already been proved as the ideal locus for DNA barcode of *Melampsora* species on poplars (Feau et al. 2011). Based on morphological and phylogenetic results obtained from this study, it was indicated that rDNA ITS regions had some limitations for sufficient discrimination closely related taxa in *Melampsora* species on willows. By contrast, a combined dataset of rDNA ITS regions and D1/D2 region seemed to be much more promising because most of recognized phylogenetic groups were consistent with morphological results. Therefore, a fragment including partial rDNA ITS regions and D1/D2 region might be sufficient to separate these closely related species in the genus *Melampsora* on SRC willows, and it is a suitable

marker region for applications in DNA based species identification.

In conclusion, species were recognized based on consistence of phylogenetic groups recognized by rDNA D1/D2 region, ITS regions including 5.8S and EF-1α gene with morphological groups detected by numerical taxonomic method. In addition, *Melampsora* species on willows in China were re-circumscribed. Moreover, 14 distinct species were recognized from specimens belonging to *M. epitea* complex, and 3 distinct species were recognized in the population previously identified as *M. capraearum*. However, the proper names of several species were still uncertain due to lack of information of type specimens. To determine the proper name of each species, comprehensive studies of *M. epitea* complex from Asia, Europe and North America are required. In this study, five species were tentatively recognized due to lack of enough morphological and molecular data, thus, further studies need to be conducted to confirm the taxonomic status of these species.

Summary

Willows are cultivated worldwide due to their physiological and economic importance. Leaf rust diseases, which were caused by *Melampsora* species of the family Melampsoraceae in the order Pucciniales, are the most serious diseases occurred on willows in natural habitats and plantation. Up to date, 50 *Melampsora* species have been known on willows in the world. Among them, 25 species have been reported in China. These reported species were described by several taxonomists, and species identification was followed by different taxonomic systems. No consensus system was provided to recognize *Melampsora* rust on willows. Recently, molecular phylogenetic analyses have been used to assist taxonomy of rust fungi. However, no comprehensive morphological and molecular phylogenetic studies have been conducted on *Melampsora* species of willows in China. The purpose of this study was to clarify the relationship of morphological groups and phylogenetic groups, and to determine the species in China based on morphological and molecular phylogenetic analyses.

Morphological observations were carried out by stereo microscope, optical microscope and scanning electron microscope. Two hundred and six specimens from various regions in China and additional 229 specimens from Europe, Russia and Japan were used for the morphological observation. Twenty-three morphological characteristics in uredinial and telial stages were selected for analyses. Two hundred and thirty-one specimens out of 435 specimens had both uredinial and telial stages, and they were used for morphometric analysis using cluster analysis and multivariate analysis. These specimens were separated into 23 morphological groups (M1 to M23) and the diagnostic characters for each group were also determined. Among these morphological characteristics examined in this study, characters used in traditional taxonomy, such as the smooth regions in urediniospores, the length of urediniospres, the width of urediniospores, the apex thickness of urediniospores, the position of germ pore, the position of uredinia, the position of telia, the position of teliospores and the

length of teliospores were proved effective. Moreover, the shape factor of urediniospores, the existence of intermixed paraphyses, the spine form of urediniospores, were found as new diagnostic characters to distinguish morphological groups in this study.

Molecular phylogenetic analyses were conducted based on sequence data of the D1/D2 region of the large subunit of ribosomal RNA gene and the internal transcribed spacer (ITS) regions including 5.8S and partial elongation factor 1α (EF-1α) gene. Sequences were tried to obtain from all specimens used for morphological studies. However, sequence data of the D1/D2 region and ITS regions were successfully amplified from 135 specimens belonging to 22 morphological groups but not from a specimen of M15. Moreover, sequence data of EF-1α gene were only obtained from 43 specimens belonging to 18 morphological groups. Molecular phylogenetic analyses using a combined dataset of D1/D2 region and ITS regions distinguished 29 highly supported phylogenetic groups (G1 to G29). In the EF-1α gene phylogeny, G1 group was further divided into two phylogenetic groups, G1-1 and G1-2. Thus, totally 30 phylogenetic groups were recognized.

Based on correlation of morphological groups and phylogenetic groups, only 14 morphological groups were consistent with phylogenetic groups. The remaining morphological groups did not fit with phylogenetic groups. Among them, 5 morphological groups could be further divided into 13 morphological groups based on the distance between spines, the apex thickness of urediniospores, the length of paraphyses and the length of teliospores. These 13 groups were corresponding with phylogenetic groups. No apparent difference was recognized among specimens within M4, M12 and M13. M4 was corresponding to two phylogenetic groups, M12 and M13 were corresponding to one phylogenetic group. Totally 27 morphological groups were consistent with phylogenetic groups, and they were recognized as distinct taxa. Two phylogenetic groups in M4, M12 and M13 were tentatively treated as different taxa. M15, which lack of sequence information due to failure in DNA extraction, was tentatively treated as separate taxon.

Totally 32 taxa were recognized in this study and were treated as separate species.

Among them, 14 species, which were previously included in the *M. epitea* complex, were recognized as distinct species. In addition, 3 species were distinguished in the population previously identified as *M. capraearum*. Among 32 species, 22 species were recognized in China. Names of 11 species have already been reported in China. Three species, *M. salicis-argyraceae*, *M. salicis-sinicae* and *M. salicis-purpureae* were described as new species. Two species, *M. chelidonii-pierotii* and *M. iranica* were new to China. *Melampsora salicis-warburgii* was recognized as a synonym of *M. microsora*. Thus, *Melampsora* species on willows in China were determined.

Acknowledgements

I would like to express my deep and sincere gratitude to my supervisor, Professor Yuichi Yamaoka and Professor Makoto Kakishima. Their wide knowledge and logical way of thinking have been of great value for me. Their understanding, encouraging and continued support have provided a good basis for the present dissertation.

I wish to express my great appreciation to my committee members, Professor Hiroshi Honda, Laboratory of Applied Zoology, Institute of Agriculture and Forestry, University of Tsukuba; Professor Ryo Ohsawa, Plant Breeding Laboratory, Institute of Agriculture and Forestry, University of Tsukuba; Professor Ken-ichiro Ishida, Laboratory of Plant Diversity and Evolutionary Cell Biology, University of Tsukuba, for their numerous suggestions, comments, encouragement, and willingness to serve as my advisory committee members.

I wish to express my warm and sincere thanks to Dr. Hideo Ishii, for his detailed and constructive comments, for his important and continuous support throughout my study and also for his advices and friendly encouragement to my research and daily life in Tsukuba.

I also want to express my deep appreciation to Dr. Cheng-Ming Tian, professor in Beijing Forestry University in China, and his wife, Dr. Ying-Mei Liang, for their invaluable support and help in my life and my study for many years.

I want to thank Dr. Yi-Jian Yao, curator of Mycological Herbarium of Institute of Microbiology, CAS in China; Dr. Qi Wang, Jilin Agricultural University; Zhen-She Hou and Yan-Zhong Shang, Inner Mongolia Agricultural University; Professor Zhi-Min Cao, Northwest A & F University; Dr. Zhu-Liang Yang, Kunming institute of Botany, CAS in China; Dr. Tsuyoshi Hosoya, National Museum of Nature and Science for their invaluable assistance during the field collection and for providing material used in this study. I also want to express my deep appreciation to Hiratsuka Herbarium, Tokyo, for providing important herbarium specimens for my study.

I thank Dr. Izumi Okane and Dr. Junichi Peter Abe, Laboratory of Plant Parasitic

Mycology, Institute of Agriculture and Forestry, University of Tsukuba, for their suggestions and technical assistance in my research. I also thank the present and former member of the Laboratory of Plant Parasitic Mycology for their fruitful discussion and all the help extended and the thing I learned from them about the work in the laboratory and life in Japan.

I want to thank the Ministry of Education, Culture, Sports, Science and Technology (**MEXT**) and Japan International Cooperation Agency (**JICA**), for providing the opportunity to study at the University of Tsukuba in Japan.

Finally, I want to give my deepest gratitude to my family, especially my wife, Dr. Qing-Hong Wang, for their encouragement and their loving support in my life.

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Appendix

Appendix 1: Morphological characteristics of 231 specimens from 23 morphological groups recognized by cluster analysis.

MG[a]	SN[b]	PU[c]	SF[d]	GP[e]	SF[f]	SRA[g]	ADS[h]	LU[i]	WU[j]	ATU[k]	WP[l]	IP[m]	LP[n]	WP[o]	AP[p]	PT[q]	PTs[r]	LT[s]	WT[t]	WTT[u]
M1	HMAS64717	H	0.8742	S	T1	E	0.78	14.7-(18.28)-21.09	12.35-(15.19)-18.74	1.49-(2.01)-2.56	E	I	40.9-(55.72)-69.86	13.63-(17.73)-23.43	1.7-(3.71)-5.54	E	SE	13.63-(21.03)-30.89	6.39-(8.36)-12.99	1.49-(2.34)-4.05
	HMAS42842	H	0.8756	S	T1	E	1.05	13.42-(15.38)-18.1	11.08-(13.04)-15.55	1.49-(2.08)-2.59	E	I	44.73-(58.14)-77.76	14.06-(19.27)-24.71	2.98-(5.98)-7.24	E	SE	19.38-(30.95)-39.62	4.90-(7.51)-12.39	1.28-(2.29)-4.46
	HMAP1972	H	0.8822	S	T1	E	0.94	13.21-(17.60)-20.24	11.72-(15.41)-17.68	1.07-(1.82)-2.77	E	I	38.55-(52.39)-68.59	10.44-(14.68)-19.17	1.92-(3.76)-5.11	E	SE	17.89-(26.04)-36.85	5.75-(8.87)-12.78	0.85-(1.58)-2.34
	HAMP3190	H	0.8713	S	T1	E	0.8	10.86-(13.22)-15.12	9.59-(11.21)-12.31	1.49-(1.71)-2.59	E	I	28.18-(43.21)-53.41	9.61-(14.81)-20.45	1.7-(3.39)-6.6	E	SE	12.57-(22.79)-30.03	5.75-(8.55)-12.78	1.45- (2.07)3.13
	HMAP3061	H	0.8807	S	T1	E	0.88	11.93-(14.09)-18.1	9.8-(12.44)-14.27	1.07-(1.72)-2.56	E	I	32.59-(50.99)-67.1	9.16-(16.13)-22.58	1.49-(3.54)-7.67	E	SE	17.47-(31.30)--40.47	4.26-(7.32)-14.48	0.79-(1.33)-2.56
	HMAP3167	H	0.8841	S	T1	E	0.83	14.27-(17.03)-20.66	12.14-(15.39)-17.68	1.28-(1.79)-2.56	E	I	37.91-(47.87)-60.92	12.78-(17.83)-23.73	2.56-(3.11)-5.92	E	SE	16.61-(30.23)-41.53	6.18-(8.89)-12.99	1.07-(2.25)-5.11
	HMAP3181	H	0.8791	S	T1	E	1.23	8.95-(11.71)-15.12	8.95-(11.71)-15.12	1.07-(1.36)-2.13	E	I	27.48-(38.58)-47.29	9.8-(13.46)-17.89	1.7-(3.63)-7.45	E	SE	14.48-(20.18)-25.99	5.11-(8.35)-12.35	0.64-(1.13)-1.49
	HNMAP3060	H	0.8662	S	T1	E	1.3	9.8-(14.12)-18.32	9.8-(14.12)-18.32	1.07-(1.65)-2.03	E	I	27.9-(40.01)-50.69	10.22-(14.04)-17.25	3.19-(5.13)-7.88	E	SE	18.32-(28.27)-40.04	6.39-(9.13)-11.93	0.85-(1.47)-2.13
	TSH-R8778	H	0.8836	S	T1	E	1.21	13.61-(17.13)-20.37	12.56-(14.64)-17.38	0.75-(1.32)-2.38	E	I	24.34-(35.76)-43.59	8.83-(16.53)-22.39	1.04-(2.53)-4.6	E	SE	13.02-(20.19)-29.58	6.38-(9.84)-14.48	0.52-(1.45)-2.77
	HMAP3060	H	0.8741	S	T1	E	1.27	11.93-(14.09)-18.1	9.8-(12.44)-14.27	1.07-(1.72)-2.56	E	I	32.59-(50.99)-67.1	9.16-(16.13)-22.58	1.49-(3.54)-7.67	E	SE	17.47-(31.30)--40.47	4.26-(7.32)-14.48	0.73-(1.33)-1.56
	HNMAP3169	H	0.8809	S	T1	E	1.34	10.86-(13.94)-17.25	8.73-(11.57)-15.12	0.85-(1.57)-2.56	E	I	26.2-(38.12)-54.53	7.24-(11.94)-15.12	1.49-(3.03)-5.11	E	SE	15.34-(23.20)-32.38	5.96-(8.57)-12.96	1.7-(2.44)-3.62
	TSH-R7654	H	0.8701	S	T1	E	1.28	11.52-(15.13)-17.95	9.76-(12.12)-13.93	0.81-(1.55)-2.24	E	I	29.7-(47.09)-74.07	9.86-(14.92)-22.69	1.7-(3.94)-7.15	E	SE	14.75-(23.68)-35.61	7.1-(10.56)-15.98	0.63-(1.44)-2.43
	TSH-R7613	H	0.8847	S	T1	E	1.26	13.65-(18.17)-21.91	12.32-(15.56)-17.99	0.59-(1.44)-2.14	E	I	29.58-(49.74)-59.12	10.49-(16.47)-26.23	1.42-(3.05)-7.11	E	SE	14.06-(21.20)-25.77	5.11-(7.32)-10.44	0.85-(1.25)-2.13
	TSH-R7689	H	0.8676	S	T1	E	1.33	11.66-(15.73)-24.16	7.54-(11.97)-15.12	0.66-(1.35)-2.27	E	I	22.92-(46.34)-63.84	9.23-(13.82)-18.23	2.28-(4.56)-5.92	E	SE	16.75-(29.44)-41.62	7.44-(11.36)-15.22	0.77-(2.50)-4.16
	HNMAP3160	H	0.8847	S	T1	E	1.26	13.65-(18.17)-21.91	12.32-(15.56)-17.99	0.59-(1.44)-2.14	E	I	29.58-(51.74)-71.12	10.49-(16.47)-26.23	1.42-(3.05)-7.11	E	SE	17.25-(23.71)-30.08	5.75-(9.70)-12.55	1.49-(2.72)-3.19
	TSH-R7550	H	0.8836	S	T1	E	1.21	13.61-(17.13)-20.37	12.56-(14.64)-17.38	0.75-(1.32)-2.38	E	I	24.34-(53.76)-68.59	8.83-(16.53)-22.39	1.04-(2.53)-4.6	E	SE	13.02-(20.19)-29.58	6.38-(9.84)-14.48	0.52-(1.45)-2.77
	TSH-R7535	H	0.8821	S	T1	E	1.32	12.81-(15.63)-19.31	10.93-(13.25)-15.1	0.93-(1.56)-3.93	E	I	38.16-(50.18)-72.33	7.66-(17.76)-28.77	1.86-(4.03)-6.14	E	SE	14.89-(25.88)-35.18	6.04-(9.93)-14.06	0.71-(1.63)-3.27
	HNMAP3168	H	0.8773	S	T1	E	1.22	12.14-(14.81)-17.68	8.73-(11.98)-13.63	1.28-(1.73)-2.56	E	I	29.82-(38.25)-49.84	6.82-(13.94)-18.72	2.56-(4.77)-5.96	E	SE	21.3-(30.25)-44.52	5.75-(9.61)-16.19	0.89-(1.41)-2.98

Appendix 1: Continued.

	HMAS52894	H	0.8759	S	T1	E	1.41	12.78-(17.19)-20.66	7.88-(15.27)-17.47	1.7-(2.32)-3.62	E	I	39.83-(59.87)-85.2	9.59-(18.52)-28.33	2.77-(4.29)-6.18	E	SE	17.25-(33.77)-50.91	5.75-(8.01)-15.98	0.85-(1.99)-4.47
	BPI1108833	H	0.8771	S	T1	E	1.55	12.78-(16.13)-18.99	7.31-(13.21)-17.04	1.7-(2.32)-3.35	E	I	39.83-(60.33)-81.21	9.59-(19.12)-28.33	2.77-(3.05)-6.18	E	SE	16.41-(29.35)-45.33	4.44-(11.31)-19.81	1.03-(2.41)-4.33
	HMAS55037	H	0.8804	S	T1	E	1.49	11.5-(18.43)-22.58	10.44-(16.01)-18.96	1.49-(1.92)-2.77	E	I	38.34-(52.75)-70.5	11.29-(16.73)-20.87	1.28-(3.67)-5.11	E	SE	26.2-(37.08)-55.81	2.56-(4.96)-7.45	0.88-(2.56)-4.89
M2	HH-77158	H	0.8773	S	T1	E	1.03	10.85-(13.21)-15.33	8.34-(12.33)-15.83	0.86-(1.04)-2.34	E	I	25.47-(55.48)-78.75	10.09-(16.13)-21.85	0.99-(4.01)-8.41	E	SE	29-(44.33)-65.08	4.31-(6.77)-11.9	0.91-(1.33)-2.98
	HH-53158	H	0.8831	S	T1	E	0.96	12.7-(15.66)-19.5	12.17-(13.85)-16.4	0.92-(1.54)-2.84	E	I	29.55-(49.01)-73.84	11.08-(16.02)-26.47	1.92-(3.46)-5.54	E	SE	24.24-(42.43)-60.93	5.99-(8.55)-11.7	1.07-(2.35)-3.05
	HH-53157	H	0.8744	S	T1	E	1.11	11.29-(14.45)-18.1	7.67-(11.66)-15.55	1.07-(1.77)-2.34	E	I	41.03-(53.38)-72.63	9.37-(15.77)-18.32	1.92-(3.67)-5.75	E	SE	26.41-(41.73)-58.81	4.47-(5.80)-8.52	1.49-(1.90)-2.56
	HH-99464	H	0.8756	S	T1	E	1.03	9.93-(12.03)-15.04	9.17-(12.20)-14.27	1.49-(1.93)-2.56	E	I	33.84-(56.06)-73.73	10.01-(14.29)-20.24	2.13-(3.46)-5.32	E	SE	24.37-(40.95)-57.77	6.03-(8.87)-12.72	0.85-(1.12)-1.49
	HH-53159	H	0.8787	S	T1	E	0.89	12.14-(13.09)-15.33	7.44-(9.41)-12.19	1.07-(2.05)-2.56	E	I	38.17-(50.69)-69.88	10.86-(18.54)-30.03	1.7-(3.63)-7.03	E	SE	31.01-(46.22)-55.33	7.38-(9.07)-14.56	1.49-(2.60)-3.54
M3	HMAS38658	A	0.8635	S	T1	E	0.65	15.12-(20.16)-28.75	10.22-(13.52)-17.55	1.7-(2.18)-2.77	E	I	34.93-(48.74)-70.29	11.72-(15.46)-20.45	2.56-(3.29)-5.32	A	SE	28.97-(46.95)-62.62	5.11-(7.87)-11.72	0.85-(1.27)-1.49
M4	HMAS67393	H	0.8718	S	T1	E	1.05	13.63-(15.80)-18.74	11.29-(14.08)-16.61	1.49-(2.02)-2.77	E	I	42.6-(52.91)-66.8	11.29-(16.18)-22.15	2.13-(3.78)-7.03	A	SE	16.61-(21.20)-29.82	4.9-(8.92)-14.27	1.7-(2.23)-3.62
	HMAS82376	H	0.8853	S	T1	E	0.97	11.93-(13.96)-16.83	9.37-(11.67)-13.63	1.07-(1.62)-2.34	E	I	38.98-(55.61)-72.42	13.21-(17.58)-25.77	1.7-(3.01)-5.54	A	SE	14.06-(21.20)-25.77	5.11-(7.32)-10.44	0.85-(1.25)-2.13
	HMAP3140	H	0.8763	S	T1	E	1.11	13.7-(16.46)-20.45	8.41-(13.19)-18.47	1.67-(1.68)-2.56	E	I	38.55-(51.91)-68.22	11.08-(18.39)-22.58	1.92-(3.92)-6.18	A	SE	27.05-(33.37)-43.55	5.32-(8.11)-10.86	0.65-(1.31)-2.23
	HMAS8629	H	0.8754	S	T1	E	1.03	15.34-(19.29)-24.07	11.72-(15.61)-17.68	1.7-(2.54)-3.62	E	I	35.36-(47.43)-61.68	10.22-(15.59)-21.51	2.56-(5.15)-7.45	A	SE	12.14-(23.00)-35.36	5.75-(7.77)-11.93	0.64-(1.17)-1.28
	HMAS52899	H	0.8847	S	T1	E	1.1	10.65-(15.74)-18.74	7.67-(13.23)-16.61	1.07-(1.93)-2.77	E	I	26.84-(42.55)-61.13	10.44-(14.77)-19.17	2.34-(4.58)-7.67	A	SE	17.25-(23.71)-30.08	5.75-(9.70)-12.55	1.49-(2.72)-3.19
	HNMAP1594	H	0.8714	S	T1	E	1.2	13.42-(17.62)-21.73	10.86-(15.28)-18.74	1.28-(1.73)-2.56	E	I	30.03-(45.96)-60.92	9.8-(14.67)-25.13	2.13-(4.69)-8.31	A	SE	11.72-(21.28)-36	5.32-(9.38)-12.78	0.85-(1.38)-2.77
	HMAS48435	H	0.8811	S	T1	E	1.13	13.85-(18.88)-27.69	9.37-(13.21)-15.36	1.07-(1.64)-2.56	E	I	32.8-(50.15)-61.34	13.63-(17.45)-20.45	2.13-(4.34)-6.82	A	SE	23.64-(31.08)-38.55	4.47-(6.43)-10.44	1.7-(2.44)-3.62
	HNMAP3149	H	0.878	S	T1	E	0.98	11.30-(15.76)-19.1	8.95-(12.84)-16.48	1.7-(1.96)-2.56	E	I	39.71-(52.97)-70.08	11.5-(17.42)-25.66	1.7-(3.94)-5.54	A	SE	22.51-(32.51)-42.08	6.36-(7.86)-12.03	0.85-(1.12)-1.77
	TSH-R2476	H	0.8805	S	T1	E	1.21	14.22-(16.37)-18.83	12.58-(14.64)-16.41	0.81-(2.02)-3.62	E	I	29.88-(47.54)-80.64	11.71-(17.19)-23.27	1.47-(3.32)-6.06	A	SE	17.59-(25.07)-35.96	6-(10.94)-15.45	0.95-(1.92)-4.07
	TSH-R2454	H	0.8837	S	T1	E	1.1	11.43-(14.02)-18.29	9.22-(11.86)-16	0.47-(1.28)-2.6	E	I	24-(36.62)-49.03	10.9-(14.75)-18.38	1.8-(3.68)-5.21	A	SE	15.86-(27.3)-35.21	7.75-(10.3)-14.05	0.74-(2.2)-4.19
	TSH-R2453	H	0.8864	S	T1	E	1.07	12.08-(15.2)-18.04	11.17-(13.1)-15.33	0.82-(1.41)-2.01	E	I	34.18-(43.13)-61.97	13.02-(17.29)-23.86	2.04-(4.17)-7.13	A	SE	16.54-(22.2)-33.7	5.72-(9.54)-14.64	0.69-(1.51)-2.61
	NWC-9533	H	0.8728	S	T1	E	1.10	13.42-(17.52)-22.15	10.86-(15.42)-19.38	1.49-(2.48)-3.41	E	I	29.82-(44.38)-57.51	9.59-(16.18)-21.94	2.34-(3.97)-5.75	A	SE	21.33-(26.43)-34.18	4.67-(8.91)-11.78	0.62-(1.42)-1.9
	TSH-R2552	H	0.876	S	T1	E	0.86	13.63-(16.21)-19.6	10.44-(13.97)-16.83	1.49-(1.84)-2.34	E	I	32.38-(41.88)-54.74	9.8-(15.27)-19.38	1.49-(3.25)-5.96	A	SE	18.1-(25.72)-33.44	6.6-(8.77)-13.63	0.77-(1.56)-2.45
	HMAS58573	H	0.8728	S	T1	E	0.97	13.42-(18.59)-22.15	10.86-(16.22)-19.38	1.49-(2.48)-3.41	E	I	29.82-(44.38)-57.51	9.59-(16.18)-21.94	2.34-(3.97)-5.75	A	SE	20.24-(27.17)-31.31	7.67-(10.23)-11.08	0.85-(1.32)-1.7
	VMP891-1	H	0.8731	S	T1	E	1.29	13.91-(16.42)-20.96	13.21-(14.81)-16.29	1.7-(1.88)-2.56	E	I	37.91-(47.69)-53.41	14.06-(17.68)-21.73	1.7-(3.10)-4.05	A	SE	21.51-(27.17)-33.07	4.64-(7.34)-13.15	0.89-(1.17)-1.16
	NWC-KNW-1	H	0.885	S	T1	E	1.38	15.19-(18.58)-23.64	9.06-(12.33)-17.29	1.7-(2.11)-3.14	E	I	41.74-(56.21)-60.92	14.91-(20.89)-25.56	1.7-(4.69)-8.73	A	SE	17.29-(28.17)-36.01	7.44-(9.65)-11.23	0.75-(1.62)-2.45

Appendix 1: Continued.

M5	HMAS52905	A	0.8768	S	T1	E	1.55	14.27-(17.97)-21.09	11.5-(15.49)-18.53	1.49-(2.17)-3.19	E	I	35.78-(52.56)-66.24	10.65-(19.04)-23.64	2.34-(4.08)-8.31	A	SE	19.81-(28.95)-39.19	4.9-(8.01)-10.22	0.62-(1.05)-1.5
	HMAS62584	A	0.8607	S	T1	E	1.08	16.19-(19.09)-20.87	14.06-(16.28)-18.74	1.7-(2.55)-3.41	E	I	37.06-(48.17)-61.13	9.8-(15.16)-19.81	2.13-(3.44)-5.75	A	SE	16.83-(23.01)-31.52	4.69-(7.46)-10.86	0.71-(1.12)-1.79
	NWC-06843	A	0.8722	S	T1	E	1.45	16.61-(18.88)-22.15	12.78-(15.66)-17.89	1.92-(2.59)-3.62	E	I	35.85-(50.28)-71.36	11.05-(16.07)-22.36	2.56-(3.40)-5.32	A	SE	17.04-(22.46)-36.42	6.39-(8.22)-11.5	0.61-(1.03)-1.46
	TNS-F-185359	A	0.8765	S	T1	E	1.38	15.55-(18.31)-21.94	12.45-(14.67)-19.19	1.28-(1.70)-2.34	E	I	31.52-(47.52)-64.33	11.72-(15.46)-20.45	2.77-(4.29)-6.18	A	SE	17.47-(21.30)--35.47	6.6-(8.71)-12.78	0.88-(1.27)-1.51
	BPI23007	A	0.8823	S	T1	E	1.55	14.91-(19.92)-24.92	12.99-(14.77)-18.1	1.49-(1.85)-2.77	E	I	39.62-(57.61)-75.61	11.93-(16.81)-25.35	1.28-(2.34)-3.62	A	SE	28.54-(23.91)-38.76	5.32-(7.79)-11.72	0.64-(1.13)-1.49
	BPI23008	A	0.8799	S	T1	E	1.44	14.91-(17.84)-22.15	10.44-(15.42)-18.96	1.28-(1.99)-2.56	E	I	37.06-(48.17)-61.13	9.59-(18.52)-28.33	2.34-(4.56)-6.82	A	SE	17.47-(20.48)-40.09	5.75-(7.56)-10.65	0.85-(1.43)-2.56
	BPI23009	A	0.8801	S	T1	E	1.61	16.19-(21.7)-25.56	7.88-(15.27)-17.47	1.7-(2.55)-3.41	E	I	38.34-(52.75)-70.5	5.54-(14.44)-21.73	2.13-(3.44)-5.75	A	SE	16.82-(23.89)-37.24	4.26-(6.98)-13.21	0.93-(1.22)-1.49
M6	TNS-F-107037	H	0.8768	S	T1	E	1.41	18.97-(22.63)-26.37	14.36-(20.14)-23.62	1.23-(2.91)-5.09	E	I	44.89-(72.39)-93.80	13.79-(23.31)-30.98	2.93-(4.99)-5.62	A	SE	22.08-(34.08)-47.71	6.45-(8.88)-10.54	0.84-(1.02)-1.65
	TNS-F-120783	H	0.888	S	T1	E	1.55	17.85-(23.01)-27.88	13.39-(19.21)-22.55	1.56-(2.68)-4.93	E	I	40.11-(65.54)-93.04	15.08-(21.11)-28.97	3.57-(5.06)-7.44	A	SE	18.39-(29.57)-48.51	6.97-(9.94)-13.35	0.99-(1.44)-1.87
	TSH-R10306	H	0.8613	S	T1	E	0.97	17.37-(22.05)-24.55	10.19-(16.76)-20.62	1.83-(2.36)-3.29	E	I	29.02-(49.81)-62.81	14.89-(21.84)-28.29	2.74-(4.41)-7.18	A	SE	21.15-(27.11)-36.61	5.57-(8.17)-10.46	0.82-(1.55)-2.57
	HH-53248	H	0.8659	S	T1	E	1.08	16.31-(23.87)-26.31	11.03-(15.73)-22.11	1.56-(2.49)-3.11	E	I	27.39-(47.31)-66.07	12.54-(19.07)-25.05	2.56-(5.19)-8.34	A	SE	18.34-(25.44)-35.17	4.21-(7.33)-12.07	0.76-(1.22)-2.78
M7	HMAP1710	H	0.8756	S	T1	E	0.96	16.14-(18.85)-23.03	8.5-(15.08)-16.84	1.70-(2.07)-2.56	E	I	34.29-(45.56)-62.83	12.57-(15.79)-20.45	1.07-(4.30)-6.39	A	SC	17.73-(30.54)-42.41	3.75-(8.79)-15.63	1.77-(3.90)-7.45
	HMAP3111	H	0.8672	S	T1	E	1.12	12.98-(18.22)-25.35	13.15-(16.42)-19.68	1.49-(2.06)-2.77	E	I	43.5-(51.49)-74.76	14.48-(18.77)-26.2	2.13-(3.89)-7.45	A	SC	21.74-(33.15)-43.49	3.7-(10.19)-16.63	1.75-(4.57)-7.07
	HNMAP3176	H	0.8682	S	T1	E	0.98	15.36-(17.28)-24.11	10.7-(16.32)-19.02	1.49-(1.94)-2.77	E	I	37.28-(52.24)-61.13	14.48-(18.88)-23.28	2.98-(5.27)-7.45	A	SC	16.79-(31.24)-41.2	4.6-(11.27)-14.57	2.53-(3.85)-6.79
	HNMAP3065	H	0.876	S	T1	E	1.03	14.91-(18.17)-24.45	11.35-(15.65)-20.47	1.92-(2.56)-3.41	E	I	41.32-(53.76)-71.99	11.5-(17.25)-24.07	2.77-(4.02)-6.39	A	SC	18.91-(28.27)-37.28	6.12-(9.83)-14.64	2.26-(4.49)-9.61
	HNMAP1716	H	0.8759	S	T1	E	0.96	15.04-(18.84)-27.15	10.85-(17.12)-24.09	1.92-(3.09)-4.05	E	I	33.87-(49.28)-61.98	13.63-(18.99)-25.77	1.7-(5.16)-8.52	A	SC	22.47-(31.35)-38.98	5.06-(10.33)-14.85	1.88-(4.14)-7.42
	HMAS82384	H	0.881	S	T1	E	1.17	10.78-(16.93)-22.96	10.44-(15.31)-19.47	1.28-(1.84)-2.98	E	I	38.77-(47.69)-66.88	10.01-(14.29)-20.24	1.7-(3.63)-7.03	A	SC	23.74-(29.65)-39.49	4.7-(8.49)-14.33	2.45-(3.87)-6.57
	HNMAP1690	H	0.8793	S	T1	E	1.14	15.12-(17.68)-20.99	13.05-(16.67)-20.89	1.92-(2.78)-3.83	E	I	35.15-(48.30)-61.98	11.29-(16.25)-20.45	3.19-(5.17)-7.45	A	SC	19.96-(28.31)-39.31	6.82-(10.93)-14.27	1.7-(4.42)-6.05
	HMAP1697	H	0.877	S	T1	E	1.03	12.91-(16.70)-22.45	8.72-(15.13)-19.32	1.49-(2.13)-2.77	E	I	26.84-(43.82)-52.19	10.82-(14.83)-19.17	2.56-(3.91)-5.54	A	SC	22.63-(35.83)-48.92	5.96-(9.29)-12.78	2.07-(4.10)-8.31
	HMAS987	H	0.8787	S	T1	E	0.99	17.68-(21.84)-25.56	15.76-(19.23)-23.43	1.49-(2.90)-3.62	E	I	40.04-(62.93)-90.1	13.42-(18.61)-25.35	2.77-(4.24)-6.18	A	SC	12.99-(24.55)-37.51	4.47-(6.26)-8.52	2.76-(5.67)-7.97
	HNMAP1479	H	0.8744	S	T1	E	0.94	13.21-(17.63)-22.15	11.72-(15.69)-19.38	1.49-(2.16)-3.19	E	I	37.49-(50.76)-73.49	12.35-(18.35)-22.58	2.56-(4.78)-9.37	A	SC	21.09-(30.32)-41.96	7.24-(9.63)-12.35	1.7-(3.39)-5.75
	HMAP1339	H	0.8778	S	T1	E	1.07	14.2-(17.11)-21.66	13.08-(15.60)-18.32	1.49-(2.18)-3.19	E	I	36.64-(46.39)-62.83	10.44-(14.41)-21.99	2.34-(4.03)-6.82	A	SC	23.85-(33.23)-42.47	6.18-(9.66)-12.35	188-(3.63)-9.69
M8	TSH-R9832	H	0.8843	S	T1	E	0.81	12.56-(19.76)-26.65	12.19-(17.42)-22.45	1.7-(2.92)-4.44	E	I	43.1-(65.87)-88.82	10.78-(22.17)-29.02	2.39-(4.76)-7.33	E	SC	16.33-(24.18)-29.28	6.08-(10.51)-14.82	2.93-(5.25)-7.92
	TSH-R10194	H	0.8775	S	T1	E	0.72	14.75-(16.25)-21.09	13.16-(16.12)-16.93	0.88-(2.07)-3.27	E	I	35.42-(53.23)-73.09	12.91-(19.38)-26.43	0.84-(2.2)-3.94	E	SC	17.33-(27.12)-34.13	6.5-(10.61)-14.44	4.11-(6.79)-10.29
	TSH-R3879	H	0.8851	S	T1	E	0.81	14.12-(17.85)-22.56	12.27-(15.26)-19.45	1.46-(2.62)-4.18	E	I	29.96-(49.23)-68.77	9.86-(17.89)-24.12	0.87-(2.18)-4.99	E	SC	22.29-(30.22)-36.78	5.62-(8.13)-10.42	4.82-(6.61)-9.39

Appendix 1: Continued.

	TSH-R7489	H	0.8724	S	T1	E	0.87	15.38-(19.61)-26.78	13.09-(16.15)-20.89	1-(1.84)-3.03	E	I	25.8-(42.78)-72.29	6.34-(12.66)-17.45	0.78-(2.04)-4.73	E	SC	21.08-(26.94)-36.04	6.1-(7.99)-10.34	3.68-(8.52)-10.3
	TSH-R10727	H	0.8869	S	T1	E	0.78	13.76-(16.30)-21.71	10.21-(15.62)-18.96	1.49-(2.28)-4.05	E	I	31.52-(53.18)-61.75	11.72-(18.78)-23.64	2.13-(3.93)-7.45	E	SC	14.38-(27.71)-35.38	6.45-(11.39)-16.89	3.67-(5.77)-8.12
	TSH-R10513	H	0.8791	S	T1	E	0.82	14.04-(16.55)-22.39	10.69-(14.44)-17.81	1.72-(3.04)-4.31	E	I	34.32-(49.49)-69.59	14.31-(17.76)-23.53	1.71-(3.73)-6.82	E	SC	18.22-(26.42)-27.92	7.33-(10.69)-14.41	2.85-(4.86)-7.58
	TSH-R7702	H	0.8644	S	T1	E	0.88	15.17-(18.26)-21.19	11.66-(16.06)-18.29	1.03-(2.11)-2.93	E	I	48.43-(63.19)-85.86	13.85-(16.05)-18.18	1.98-(2.66)-3.11	E	SC	18.44-(24.67)-30.88	8.57-(12.03)-14.48	2.83-(4.64)-7.71
	TSH-R3879	H	0.8654	S	T1	E	0.89	14.62-(17.85)-20.56	13.27-(15.96)-18.45	1.46-(2.62)-4.18	E	I	29.96-(49.23)-68.77	9.86-(17.89)-24.12	0.87-(2.18)-4.99	E	SC	22.29-(30.12)-36.38	5.62-(9.93)-15.42	4.85-(6.7)-9.39
	TSH-R10513	H	0.8831	S	T1	E	0.86	14.04-(17.55)-20.39	12.69-(15.74)-18.81	1.72-(3.04)-4.31	E	I	34.32-(49.49)-69.59	14.31-(17.76)-23.53	1.71-(3.73)-6.82	E	SC	18.92-(24.02)-27.92	7.33-(10.69)-14.41	3.82-(6.16)-8.08
	TSH-R10208	H	0.8627	S	T1	E	0.87	14.92-(17.62)-20.59	12.92-(15.38)-17.43	0.99-(2.42)-3.21	E	I	25.31-(48.36)-68.11	10.22-(17.25)-23.17	0.85-(3.11)-5.38	E	SC	24-(27.20)-33.82	7-(10.47)-15.07	3.21-(4.81)-7.06
	TSH-R18249	H	0.8779	S	T1	E	0.88	12.29-(17.95)-21.43	10.31-(15.74)-19.22	1.04-(2.52)-4.64	E	I	28.28-(44.93)-68.29	11.47-(17.36)-23.26	0.76-(2.4)-4.59	E	SC	15.33-(24.88)-30.28	6.68-(11.11)-16.82	3.73-(5.85)-8.02
	TSH-R18248	H	0.8656	S	T1	E	0.85	15.71-(18.57)-22.16	8.9-(14.88)-20.97	1.4-(2.12)-3.16	E	I	32.9-(56.67)-78.79	8.09-(17.80)-23.14	1.84-(3.35)-7.21	E	SC	15.02-(22.01)-27.62	8.05-(11.42)-16.88	2.89-(5.31)-7.68
	TSH-R7480	H	0.8691	S	T1	E	0.79	14.94-(17.89)-21.56	11.18-(15.46)-18.19	0.96-(1.96)-3.18	E	I	29.67-(60.33)-76.83	12.24-(18.74)-24.29	0.96-(3.02)-6.02	E	SC	12.58-(20.2)-26.21	5.32-(9.86)-14.11	2.69-(5.25)-7.88
	TSH-R13425	H	0.8713	S	T1	E	0.83	15.11-(19.77)-24.69	12.91-(16.3)-18.97	1.22-(2.19)-3.3	E	I	36.83-(52.09)-76.31	12.52-(20.22)-26.24	1.58-(4.43)-6.93	E	SC	16.86-(26.15)-33.52	7.24-(9.63)-12.96	3.69-(4.18)-5.84
	TSH-R10194	H	0.8724	S	T1	E	0.89	11.75-(17.25)-21.09	10.16-(14.72)-18.93	0.88-(2.07)-3.27	E	I	35.42-(53.23)-73.09	12.91-(19.38)-26.43	0.84-(2.2)-3.94	E	SC	16.33-(18.62)-20.13	3.5-(7.11)-10.44	3.31-(4.49)-5.91
	TSH-R9607	H	0.8631	S	T1	E	0.71	14.8-(17.71)-22.66	12.8-(15.54)-18.13	0.64-(1.28)-1.86	E	I	31.41-(40.37)-54.56	8.27-(16.97)-24.38	1.45-(2.84)-5.18	E	SC	11.58-(21.12)-27.81	5.34-(8.70)-12.57	3.71-(4.81)-7.06
	TSH-R13427	H	0.8799	S	T1	E	0.75	14.42-(19.13)-23.16	10.47-(16.03)-18.42	1.18-(2.17)-3.77	E	I	38.85-(46.24)-77.02	14.41-(19.79)-28.43	1.34-(4.34)-7.13	E	SC	18.51-(22.89)-28.83	7.85-(10.65)-13.31	3.13-(6.84)-9.53
	TSH-R21982	H	0.8728	S	T1	E	0.82	13.44-(17.98)-20.21	12.08-(16.26)-19.93	1.17-(2.7)-4.28	E	I	25.3-(44.52)-67.89	12.79-(17.32)-23.31	0.92-(3.14)-5.17	E	SC	14.87-(20.36)-26.31	8.53-(11.25)-14.56	4.12-(7.69)-10.54
	NWC9467	H	0.8752	S	T1	E	0.96	13.48-(18.04)-23.22	12.14-(15.81)-17.89	1.92-(2.60)-4.69	E	I	38.55-(56.38)-69.22	11.29-(16.39)-22.15	1.28-(2.85)-6.6	E	SC	28.97-(33.40)-48.14	6.39-(9.92)-14.48	3.56-(5.60)-8.81
	TNSF-22866	H	0.8807	S	T1	E	1.13	15.76-(19.54)-22.36	10.91-(16.78)-19.82	1.75-(2.55)-3.71	E	I	40.21-(48.06)-67.01	12.91-(19.33)-23.56	2.74-(5.05)-8.70	E	SC	21.63-(27.51)-39.99	5.43-(8.22)-11.05	3.33-(7.21)-9.59
	TNSF-107383	H	0.8769	S	T1	E	1.15	14.28-(16.80)-24.48	13.89-(16.98)-19.62	0.99-(1.86)-3.24	E	I	46.43-(61.38)-75.95	20.35-(21.87)-27.07	4.23-(5.40)-7.18	E	SC	20.24-(30.72)-38.13	5.32-(8.32)-12.14	2.56-(4.13)-8.09
	BPI22628	H	0.8688	S	T1	E	1.07	15.88-(17.96)-20.85	12.91-(16.11)-19.86	1.49-(2.94)-4.46	E	I	34.51-(50.04)-66.75	9.69-(17.77)-22.83	2.75-(3.85)-6.45	E	SC	27.05-(33.57)-43.45	5.32-(8.01)-10.86	2.98-(4.33)-9.59
M9	HMAS134712	H	0.8761	S	T1	E	1.02	11.08-(13.12)-15.76	9.16-(11.89)-13.42	1.28-(1.68)-2.13	E	I	27.26-(36.49)-44.58	9.59-(13.13)-16.19	1.92-(2.79)-4.05	E	SE & SC	14.06-(21.55)-28.12	6.6-(9.18)-11.93	0.64-(1.24)-1.98
	HMAP3208	H	0.8698	S	T1	E	1.26	10.22-(13.09)-17.47	9.16-(11.58)-14.91	0.85-(1.61)-2.56	E	I	29.82-(42.41)-54.85	8.52-(13.99)-20.87	1.92-(2.74)-3.41	E	SE & SC	28.54-(31.91)-41.76	6.6-(8.71)-12.78	0.87-(1.33)-1.79
	HMAP3058	H	0.8768	S	T1	E	1.15	14.91-(17.59)-20.45	12.99-(15.59)-18.74	1.28-(1.70)-2.34	E	I	42.39-(50.35)-57.51	14.27-(18.36)-22.79	1.7-(2.86)-4.26	E	SE & SC	17.47-(31.48)-44.09	6.39-(8.78)-12.14	0.89-(1.6)-2.33
	HMAP3218	H	0.8723	S	T1	E	1.08	11.29-(14.45)-18.1	9.59-(12.44)-14.91	1.07-(1.65)-2.34	E	I	32.59-(48.60)-60.07	8.95-(15.39)-21.73	1.92-(3.14)-5.96	E	SE & SC	21.94-(29.48)-39.62	4.47-(6.79)-8.73	0.66-(1.03)-1.59
	BPI1109484	H	0.8727	S	T1	E	1.22	9.8-(12.23)-16.4	8.73-(10.59)-12.78	0.85-(1.50)-2.56	E	I	41.96-(47.68)-53.68	12.35-(15.67)-20.87	1.7-(2.74)-3.83	E	SE & SC	16.19-(22.91)-27.26	4.47-(7.28)-10.44	0.84-(1.27)-1.48

Appendix 1: Continued.

	HMAP3222	H	0.869	S	T1	E	1.01	11.5-(13.88)-17.04	10.01-(12.19)-13.68	1.07-(1.72)-2.56	E	I	32.59-(42.90)-52.89	9.59-(13.64)-16.83	1.49-(3.25)-5.32	E	SE & SC	21.73-(29.98)-38.55	5.32-(7.79)-11.72	1.09-(1.45)-1.94
	HMAP3218	H	0.8769	S	T1	E	1.16	11.29-(14.45)-18.1	9.59-(12.44)-14.91	1.07-(1.65)-2.34	E	I	32.59-(48.60)-60.07	8.95-(15.39)-21.73	1.92-(3.14)-5.96	E	SE & SC	21.94-(31.55)-39.62	4.47-(6.79)-8.73	0.67-(0.89)-1.48
	HMAP1967	H	0.8711	S	T1	E	1.03	11.93-(15.03)-17.04	10.22-(13.04)-15.55	1.49-(1.88)-3.19	E	I	37.49-(51.49)-65.18	8.52-(16.68)-24.28	1.49-(2.76)-4.26	E	SE & SC	17.89-(20.85)-24.07	3.62-(5.1)-7.24	0.85-(1.27)-1.49
	TSH-R9836	H	0.8767	S	T1	E	1.13	12.09-(15.54)-16.74	10.65-(13.21)-16.34	1.92-(2.64)-4.26	E	I	37.7-(50.11)-76.04	10.44-(18.73)-27.48	2.13-(3.27)-4.16	E	SE & SC	15.92-(31.08)-44.52	5.06-(10.33)-16.98	1.62-(2.92)-5.22
	TSH-R10207	H	0.8699	S	T1	E	1.12	11.34-(13.0)-15.7	8.59-(11.27)-13.5	0.59-(1.07)-2.78	E	I	37.53-(53.05)-74.1	12.6-(17.7)-21.98	2.43-(4.32)-6.46	E	SE & SC	22.72-(30.94)-46.23	6.02-(10.82)-14.85	1.78-(2.33)-3.24
	TSH-R7668	H	0.8772	S	T1	E	1.17	9.82-(13.68)-16.75	8.37-(11.53)-13.43	0.84-(1.20)-2.38	E	I	30.45-(38.02)-50.38	11.38-(13.99)-16.49	1.13-(2.44)-4.1	E	SE & SC	18.62-(30.24)-41.25	7.86-(9.98)-15.09	1.61-(2.27)-3.59
	TSH-R9837	H	0.8833	S	T1	E	1.08	10.87-(15.17)-18.26	10.79-(13.22)-17.39	0.66-(1.38)-2.37	E	I	38.23-(50.4)-65.9	12.04-(16.19)-20.75	1.2-(3.22)-5.47	E	SE & SC	16.3-(28.46)-39.06	4.11-(9.46)-14.98	1.44-(3.33)-4.74
	TSH-R7661	H	0.8681	S	T1	E	1.05	8.7-(11.86)-14.5	8.17-(10.65)-13.4	0.92-(1.54)-2.84	E	I	25.47-(55.48)-78.75	10.09-(16.13)-21.85	0.99-(4.01)-8.41	E	SE & SC	18.24-(42.43)-45.93	3.99-(6.35)-7.71	1.87-(2.93)-4.29
	TSH-R7649	H	0.8731	S	T1	E	1.08	13.29-(17.57)-20.25	10.02-(14.7)-18.82	0.83-(1.62)-3.51	E	I	22-(42.54)-77.03	10.48-(16.63)-22.14	0.86-(1.54)-3.05	E	SE & SC	17.83-(30.37)-42.07	6.04-(9.32)-14.33	1.44-(2.86)-3.61
	TSH-R7643	H	0.8662	S	T1	E	1.04	7.01-(9.37)-11.77	5.64-(9.02)-10.59	0.84-(1.58)-2.72	E	I	27.69-(50.4)-73.88	11.73-(17.14)-22.35	1.08-(3.5)-5.41	E	SE & SC	22.34-(25.14)-42.62	4.46-(7.16)-8.92	2.16-(3.11)-4.09
	TSH-R7678	H	0.8709	S	T1	E	1.28	10.35-(13.36)-15.7	9.12-(11.26)-13.43	0.79-(1.31)-2.18	E	I	28.79-(45.44)-58.16	9.55-(15.19)-20.96	1.28-(3.15)-5.51	E	SE & SC	22.01-(33.67)-44.61	6.32-(8.77)-13.82	0.79-(2.09)-3.03
	HMAP3184	H	0.8766	S	T1	E	1.13	10.65-(13.48)-16.61	9.59-(12)-15.58	1.07-(1.73)-2.34	E	I	36-(44.54)-52.82	10.22-(14.95)-19.17	1.7-(3.45)-5.75	E	SE & SC	16.19-(20.13)-30.67	5.11-(8.1)-11.72	0.61-(1.03)-1.46
	HMAP1959	H	0.8673	S	T1	E	1.11	11.29-(14.13)-16.61	10.44-(12.41)-16.19	1.49-(1.79)-2.56	E	I	37.28-(45.46)-56.23	15.34-(18.23)-22.15	1.7-(3.01)-4.47	E	SE & SC	22.79-(38.71)-51.97	6.6-(9.3)-14.48	1.07-(1.36)-2.56
	HMAS82376	H	0.8853	S	T1	E	1.01	11.93-(13.96)-16.83	9.37-(11.67)-13.63	1.07-(1.62)-2.34	E	I	38.98-(55.61)-72.42	13.21-(17.58)-25.77	1.7-(3.01)-5.54	E	SE & SC	14.06-(21.20)-25.77	5.11-(7.32)-10.44	0.85-(1.25)-2.13
	NWC-6419	H	0.8601	S	T1	E	1.52	10.22-(13.35)-15.55	8.73-(10.95)-14.7	1.49-(1.60)-2.77	E	I	35.36-(49.39)-72.63	11.5-(17.01)-23.43	1.28-(2.25)-3.19	E	SE & SC	22.54-(28.37)-36.2	5.33-(9.14)-13.55	0.75-(2.33)-3.15
	HMAP1698	H	0.8675	S	T1	E	1.08	14.7-(16.59)-18.1	11.93-(14.68)-17.25	1.49-(1.93)-2.98	E	I	38.55-(45.90)-55.4	11.72-(16.07)-21.51	2.77-(3.99)-5.96	E	SE & SC	20.66-(24.73)-31.55	5.75-(7.56)-10.65	0.78-(1.34)-2.37
M10	TSH-R3884	H	0.8771	S	T1	E	1.09	13.18-(15.08)-17.21	11.23-(13.03)-16.25	0.88-(1.68)-2.99	E	I	35.77-(44.53)-56.45	13.35-(16.16)-20.41	1.05-(4.09)-7.02	A	SE & SC	15.71-(25.92)-33.99	9.25-(12.43)-16.78	1.38-(2.42)-3.08
	BPI23212	H	0.8834	S	T1	E	1.02	13.42-(19.25)-23.22	11.5-(14.24)-16.83	1.49-(1.95)-2.56	E	I	29.39-(40.20)-54.95	12.14-(15.61)-19.17	1.7-(3.02)-4.69	A	SE & SC	26.2-(37.08)-55.81	2.56-(4.96)-7.45	0.84-(1.03)-1.48
	TSH-R12088	H	0.8874	S	T1	E	1.18	12.16-(15.44)-19.11	10.25-(13.08)-17.15	0.99-(1.18)-4.01	E	I	42.79-(60.11)-85.76	10.43-(18.52)-25.31	1.7-(3.4)-5.58	A	SE & SC	17.54-(23.37)-29.33	3.37-(8.72)-16.85	1.08-(2.31)-4.08
	TSH-R10186	H	0.8724	S	T1	E	1.05	11.3-(13.83)-17.44	8.7-(11.78)-15.19	0.9-(1.54)-2.26	E	I	30.36-(42.33)-65.73	9.6-(14.06)-20.15	1.29-(3.17)-5.12	A	SE & SC	21.49-(27.38)-36.06	7.25-(9.28)-13.71	1.48-(3.02)-5.08
	TSH-R10471	H	0.8856	S	T1	E	1.2	11.92-(15.21)-17.88	10.98-(13.69)-16.9	0.73-(1.61)-2.61	E	I	31.7-(43.16)-56.77	11.98-(16.74)-21.27	1.58-(3.06).4.68	A	SE & SC	21.28-(28.21)-35.99	6.95-(9.91)-12.56	1.58-(2.59)-4.01
	TSH-R10381	H	0.8821	S	T1	E	1.19	12.1-(15.15)-18.16	9.12-(13.13)-15.02	0.97-(1.72)-2.73	E	I	31.18-(44.26)-61.01	8.32-(16.73)-22.91	1.74-(3.22)-4.71	A	SE & SC	17.06-(23.04)-27.66	5.83-(9.25)-19.59	1.27-(2.31)-4.19
	TSH-R10233	H	0.8833	S	T1	E	1.17	11.82-(15.52)-17.55	10.6-(14.29)-16.43	0.71-(1.42)-2.18	E	I	35.24-(49.77)-73.72	10.89-(17.61)-26.18	1.49-(3.49)-7.38	A	SE & SC	16.21-(24.74)-36.31	4.73-(9.49)-16.48	1.56-(2.83)-4.57
	TSH-R1537	H	0.8846	S	T1	E	1.09	12.01-(14.42)-17.98	9.07-(11.84)-14.45	0.7-(1.47)-3.06	E	I	41.47-(51.95)-69.09	11.73-(16.28)-21.71	2.41-(4.17)-6.03	A	SE & SC	19.43-(30.59)-47.02	6.01-(9.58)-15.35	1.67-(3.09)-6.06

Appendix 1: Continued.

	TSH-R10186	H	0.8871	S	T1	E	1.05	11.3-(13.83)-17.44	8.7-(11.78)-15.19	0.9-(1.54)-2.26	E	I	30.36-(42.33)-65.73	9.6-(14.06)-20.15	1.29-(3.17)-5.12	A	SE & SC	21.49-(27.38)-36.06	7.25-(9.28)-13.71	1.48-(3.02)-5.08
	TSH-R10230	H	0.8756	S	T1	E	1.12	8.9-(13.08)-17.45	8.07-(11.21)-15.33	0.75-(1.35)-2.01	E	I	28.23-(41.56)-68.41	11.13-(15.49)-24.45	1.44-(3.02)-8.05	A	SE & SC	14.07-(26.36)-32.99	7.59-(10.01)-13.24	1.18-(2.72)-4.69
	TSH-R10210	H	0.8769	S	T1	E	0.98	10.59-(13.34)-16.33	9.59-(11.68)-13.83	0.76-(1.33)-2.03	E	I	31.4-(45.62)-57.76	9.12-(14.87)-24.15	1.19-(2.67)-4.58	A	SE & SC	12.18-(23.81)-33.08	5.94-(9.95)-14.03	1.1-(2.38)-4.69
	TSH-R12088	H	0.8803	S	T1	E	1.18	12.16-(15.44)-19.11	10.25-(13.08)-17.15	0.99-(1.18)-4.01	E	I	42.79-(60.11)-85.76	10.43-(18.52)-25.31	1.7-(3.4)-5.58	A	SE & SC	17.54-(23.37)-29.33	3.37-(8.72)-16.85	1.08-(2.31)-4.08
	TSH-R10207	H	0.8731	S	T1	E	0.97	11.34-(13.0)-15.7	8.59-(11.27)-13.5	0.59-(1.07)-2.78	E	I	37.53-(53.05)-74.1	12.6-(17.7)-21.98	2.43-(4.32)-6.46	A	SE & SC	22.72-(30.94)-46.23	6.02-(9.82)-14.85	1.78-(3.7)-5.95
	TSH-R7668	H	0.8795	S	T1	E	1.17	9.82-(13.68)-16.75	8.37-(11.53)-13.43	0.84-(1.20)-2.38	E	I	30.45-(38.02)-50.38	11.38-(13.99)-16.49	1.13-(2.44)-4.1	A	SE & SC	18.62-(30.24)-41.25	7.86-(9.98)-15.09	0.96-(2.27)-5.59
	TSH-R7690	H	0.8744	S	T1	E	1.2	10.19-(12.81)-18.39	7.31-(10.97)-17.04	0.8-(1.5)-3.61	E	I	31.35-(45.89)-61.71	12.12-(16.28)-20.86	1.33-(2.59)-5.01	A	SE & SC	15.79-(26.46)-35.45	6-(9.57)-16.4	0.83-(2.12)-5.86
M11	HMAS76122	H	0.8851	S	T1	E	1.08	13.85-(18.29)-21.73	11.93-(15.73)-18.75	1.49-(1.98)-2.98	E	I	45.16-(61.41)-71.99	16.19-(20.76)-25.35	2.34-(4.59)-7.88	A	SE & SC	20.24-(30.72)-38.13	5.32-(8.32)-12.14	0.61-(1.03)-1.46
	HNMWFC-T85040	H	0.8771	S	T1	E	1.02	19.38-(25.07)-29.82	16.61-(21.21)-26.84	1.77-(2.22)-2.98	E	I	40.9-(70.13)-92.65	17.04-(26.41)-36.42	1.92-(4.04)-7.03	A	SE & SC	19.6-(30.13)-40.04	6.39-(9.92)-14.48	0.85-(1.33)-2.34
	HNMAP3152	H	0.888	S	T1	E	1.07	15.55-(17.59)-21.51	14.91-(16.48)-19.17	1.49-(1.99)-2.98	E	I	31.52-(50.36)-73.27	10.65-(15.91)-19.17	1.92-(3.41)-6.18	A	SE & SC	15.34-(24.67)-35.78	4.47-(8.8)-12.78	0.80-(1.35)-2.13
	BPI23208	H	0.8835	S	T1	E	0.98	16.83-(20.32)-30.57	14.91-(17.12)-20.87	1.7-(2.09)-2.98	E	I	41.32-(60.14)-85.63	12.78-(19.15)-26.87	1.92-(3.28)-5.11	A	SE & SC	17.45-(29.98)-38.05	4.56-(11.03)-14.85	1.28-(1.76)-2.56
M12	TSH-9831	H	0.8687	S	T1	E	0.92	11.63-(14.81)-18.14	10.01-(12.47)-14.16	0.7-(1.21)-1.72	E	P	22.69-(34.81)-47.75	11.22-(15.16)-18	0.63-(2.34)-4.87	H	SE	15.48-(25.4)-35.97	5.72-(9.15)-12.88	0.78-(1.43)-2.61
	TSH-R7492	H	0.8722	S	T1	E	0.82	12.78-(15.12)-22.36	11.72-(15.35)-19.38	1.28-(1.89)-2.56	E	P	28.33-(44.53)-56.87	9.59-(18.42)-25.35	1.49-(2.87)-4.05	H	SE	20.02-(26.07)-33.44	7.03-(9.61)-15.99	0.85-(1.63)-2.56
	TSH-R3885	H	0.8856	S	T1	E	1.07	11.99-(15.91)-18.84	11.38-(13.70)-15.34	0.71-(1.09)-1.48	E	P	24.68-(34.06)-44.29	8.19-(15.22)-22.85	0.99-(2.19)-3.86	H	SE	12.66-(20.07)-30.48	5.15-(8.28)-11.8	0.6-(1.46)-3.17
	TSH-R7540	H	0.8748	S	T1	E	1.03	12.02-(15.82)-20.3	9.81-(13.63)-18.64	0.84-(1.24)-2.75	E	P	19.02-(31.78)-42.39	8.79-(13.35)-20.58	1.25-(1.97)-3.37	H	SE	14.51-(19.99)-25.94	6.01-(7.94)-12.09	0.73-(1.21)-1.99
	TSH-R12023	H	0.8712	S	T1	E	0.87	11.29-(14.92)-18.53	9.59-(12.39)-14.48	1.07-(1.63)-2.56	E	P	35.57-(43.43)-49.63	12.35-(16.06)-19.6	2.13-(3.27)-4.47	H	SE	18.1-(26.4)-32.16	6.82-(10.44)-13.63	1.49-(1.99)-3.19
	TSH-R9618	H	0.8623	S	T1	E	0.92	14.18-(16.77)-23.23	11.04-(13.74)-15.28	0.73-(1.27)-1.71	E	P	38.59-(48.34)-60.73	11.2-(16.27)-20.82	1.55-(4.03)-6	H	SE	18.66-(25.41)-37.6	7.12-(10.26)-16.51	0.67-(1.66)-2.76
	TSH-R9619	H	0.8822	S	T1	E	1.09	12.61-(15.76)-19.56	9.74-(13.34)-16.23	1.4-(1.90)-3.2	E	P	29.12-(45.88)-60.46	10.49-(17.94)-24.15	1.66-(3.83)-8.48	H	SE	17.52-(23.54)-36.47	6.55-(10.16)-14.63	1.16-(1.86)-2.64
	TSH-R7492	H	0.8816	S	T1	E	1.07	10.75-(13.56)-16.29	9.29-(11.98)-14.04	0.87-(1.48)-2.35	E	P	31.69-(43.66)-79.2	12.95-(16.7)-24.08	0.96-(3.28)-4.67	H	SE	14.71-(21.36)-29.55	7.85-(11.60)-15.03	0.65-(1.46)-2.78
	TSH-R13426	H	0.8759	S	T1	E	1.15	12.81-(15.64)-21.89	10.11-(12.86)-15.97	0.82-(1.4)-2.04	E	P	24.07-(32.75)-46.19	7.82-(14.75)-20.12	0.99-(2.02)-2.88	H	SE	10.92-(19.66)-26.43	4.33-(9.22)-16.43	0.62-(1.46)-2.82
	TSH-R10220	H	0.8819	S	T1	E	1.15	12.14-(15.34)-18.53	10.86-(13.27)-15.76	1.49-(1.84)-2.98	E	P	38.98-(48.87)-66.2	12.99-(17.5)-22.87	2.13-(3.43)-4.47	H	SE	16.83-(23.54)-31.52	6.82-(10.32)-12.78	0.85-(1.32)-2.34
	TSH-R7487	H	0.8834	S	T1	E	0.91	12.27-(15.41)-18.96	11.43-(13.33)-15.82	1.25-(2.12)-2.95	E	P	20.61-(35.35)-44.41	9.02-(14.11)-19.80	2.56-(4.19)-6.28	H	SE	14.27-(24.64)-29.54	7.97-(11.73)-15.74	0.72-(2.24)-4.45
	TSH-R7655	H	0.8804	S	T1	E	1.17	11.31-(14.55)-18.41	9.28-(12.24)-14.17	1.02-(1.41)-2.53	E	P	25.4-(43.68)-74.28	10.62-(16.37)-20.91	1.28-(2.98)-6.26	H	SE	13.68-(29.43)-49.3	6.62-(11.49)-18.7	0.83-(1.43)-2.44
	TSH-R7688	H	0.8759	S	T1	E	1.05	13.5-(15.62)-18.78	9.07-(12.28)-16.66	0.81-(1.40)-2.22	E	P	26.74-(41.37)-51.04	11.99-(15.01)-19.15	1.65-(3.4)-5.85	H	SE	18.76-(31.99)-47.18	6.03-(11.06)-17.14	0.63-(1.81)-3.69

Appendix 1: Continued.

	TSH-R7731	H	0.8689	S	T1	E	1.1	11.46-(14.61)-17.87	9.33-(12.43)-15	0.69-(1.3)-2.16	E	P	33.28-(44.46)-57.71	11.66-(16.11)-20.15	1.65-(3.28)-5.19	H	SE	13.84-(25.71)-39.63	7.97-(10.65)-14.56	0.61-(1.5)-2.72
	TSH-R7681	H	0.8717	S	T1	E	1.06	11.33-(15.02)-19.33	8.34-(13.19)-16.51	0.69-(1.3)-2.16	E	P	30.54-(40.05)-59.34	13.59-(18.27)-23.70	1.37-(3.77)-6.45	H	SE	15.40-(22.55)-37.81	7.97-(10.65)-14.56	0.88-(1.34)-2.56
M13	TSH-R10212	H	0.877	S	T1	E	1.19	12.5-(20.82)-25.98	10.41-(17.34)-18.5	1.24-(1.87)-3.28	E	P	41.89-(48.74)-54.86	14.68-(18.98)-25.06	2.18-(3.63)-5.25	H	SE	17.14-(28.75)-36.04	7.12-(11.32)-15.07	0.55-(1.24)-1.92
	TSH-R3888	H	0.883	S	T1	E	1.12	11.5-(18.71)-20.87	9.16-(13.21)-17.68	1.07-(1.52)-2.03	E	P	31.74-(51.51)-70.98	11.08-(16.55)-23.22	1.7-(3.07)-5.96	H	SE	22.36-(34.33)-47.92	7.03-(9.27)-12.98	2.56-(3.14)-4.9
	HMAS71118	H	0.8756	S	T1	E	1.04	16.74-(20.47)-26.56	15.07-(17.94)-20.42	1.28-(2.24)-3.81	E	P	36.38-(53.36)-72.34	13.01-(19.78)-27.03	2.79-(4.82)-9.02	H	SE	23.45-(30.40)-40.47	8.23-(11.09)-16.03	1.42-(1.87)-3.96
	TSH-R7494	H	0.8624	S	T1	E	1.15	15.76-(18.37)-21.09	10.44-(14.99)-17.47	1.92-(2.65)-3.62	E	P	41.75-(52.97)-72.42	11.5-(16.56)-24.5	2.56-(5.19)-7.03	H	SE	20.2-(26.77)-39.62	5.96-(8.66)-12.99	1.49-(2.52)-4.47
	BPI199071	H	0.8813	S	T1	E	0.97	16.68-(21.23)-27.77	13.22-(16.68)-20.24	088-(1.98)-3.44	E	P	28.64-(38.17)-48.06	9.27-(14.09)-19.12	1.73-(3.23)-5.87	H	SE	21.6-(31.08)-49.92	5.39-(8.20)-12.01	0.88-(1.19)-1.95
	TSH-R7279	H	0.8876	S	T1	E	1.19	14.77-(17.97)-23.83	10.98-(14.40)-20.51	0.94-(1.70)-2.58	E	P	25.87-(41.47)-64.49	11.48-(17.66)-27.66	1.07-(2.53)-3.97	H	SE	21-(35.77)-44.73	4.75-(7.31)-10.12	0.72-(1.21)-1.56
	TSH-R10176	H	0.8728	S	T1	E	0.99	15.76-(19.78)-24.07	11.72-(16.25)-19.38	1.28-(1.68)-2.34	E	P	23.22-(41.93)-54.53	10.86-(18.04)-22.58	1.92-(3.07)-4.69	H	SE	19.81-(26.29)-32.8	5.54-(8.35)-11.29	1.07-(1.66)-2.98
	TSH-R9620	H	0.8851	S	T1	E	1.13	12.48-(18.16)-22.87	10.57-(15.92)-21.96	1.07-(1.73)-2.07	E	P	35.36-(49.6)-65.18	11.72-(19.56)-29.39	2.34-(3.62)-5.54	H	SE	26.91-(37.13)-46.23	5.54-(8.87)-11.98	0.55-(0.87)-1.37
	TSH-R9623	H	0.8828	S	T1	E	1.21	14.53-(17.72)-21.62	11.11-(13.72)-18.18	1.48-(2.54)-3.32	E	P	31.23-(46.12)-57.26	12.73-(17.71)-27.59	1.7-(3.62)-6.61	H	SE	18.81-(28.35)-36.11	6.9-(10.29)-15.54	0.86-(1.37)-2.83
	TSH-R1468	H	0.8757	S	T1	E	1.17	16.74-(20.47)-26.56	15.07-(17.94)-20.42	1.28-(2.24)-3.81	E	P	36.38-(53.36)-72.34	13.01-(19.78)-27.03	2.79-(4.82)-9.02	H	SE	23.45-(30.40)-40.47	8.23-(11.09)-16.03	1.42-(1.87)-3.96
	TSH-R3893	H	0.8877	S	T1	E	0.89	12.93-(15.95)-18.78	10.46-(13.60)-15.68	0.78-(1.17)-1.63	E	P	27.31-(37.79)-50.72	11.04-(16.8)-26.55	0.39-(1.35)-2.23	H	SE	13.78-(21.7)-29.27	5.07-(8.19)-11.35	0.39-(1.35)-2.23
	TSH-R950925	H	0.8723	S	T1	E	0.98	15.75-(20.49)-26.66	9.86-(15.20)-19.62	1.41-(2.59)-4.29	E	P	30.02-(50.20)-71.49	12.93-(16.74)-19.39	3.22-(4.56)-7.09	H	SE	30.88-(38.57)-44.79	9.08-(11.33)-13.24	1.83-(2.48)-3.12
	TSH-R12333	H	0.8893	S	T1	E	1.03	15.73-(20.93)-24.93	14.05-(17.28)-20.02	0.9-(1.62)-3.13	E	P	35.7-(52.65)-68.18	12.85-(21.82)-30.53	1.53-(3.58)-6.1	H	SE	23.66-(30.89)-40.51	4.79-(9.18)-13.09	0.79-(1.6)-2.85
	TSH-10561	H	0.8732	S	T1	E	1.04	11.29-(19.92)-18.53	9.59-(12.39)-14.48	1.07-(1.63)-2.56	E	P	35.57-(43.43)-49.63	12.35-(16.06)-19.6	2.13-(3.27)-4.13	H	SE	18.1-(26.4)-32.16	6.82-(10.44)-13.63	1.49-(1.99)-3.19
	TSH-R10717	H	0.868	S	T1	E	1.11	14.48-(18.16)-20.87	12.57-(15.52)-18.96	1.07-(1.73)-2.07	E	P	35.36-(49.6)-65.18	11.72-(19.56)-29.39	2.34-(3.62)-5.54	H	SE	14.91-(28.93)-37.7	5.54-(8.67)-12.98	0.85-(1.73)-2.77
	TSH-R12057	H	0.8833	S	T1	E	0.93	16.15-(19.83)-27.07	11.68-(15.38)-23.1	1.49-(2.34)-3.24	E	P	36.47-(48.95)-56.59	14.89-(19.86)-23.83	4.23-(6.45)-10.19	H	SE	28.57-(37.77)-49.03	7.99-(11.34)-16.19	0.91-(1.64)-2.34
	TSH-R86	H	0.8817	S	T1	E	0.89	15.45-(19.08)-22.14	13.92-(16.91)-19.27	0.96-(2.13)-3.93	E	P	31.47-(52.90)-70.42	16.18-(22.62)-30.94	2.04-(3.96)-5.46	H	SE	13.44-(25.75)-36.94	5.43-(9.56)-13.8	0.6-(1.94)-3.75
M14	HMAP 3114	A	0.8377	S & B	T2	S	1.43	15.98-(22.09)-31.52	9.16-(14.0)-17.68	1.28-(1.79)-2.77	E	I	21.33-(43.29)-58.15	8.52-(14.05)-18.32	1.49-(2.69)-3.83	A	SE & SC	20.02-(32.82)-44.30	4.26-(7.42)-10.64	0.85-(1.33)-2.34
	HMAP3138	A	0.8406	S & B	T2	S	1.21	16.83-(20.58)-25.13	11.93-(14.58)-17.04	1.49-(2.09)-2.98	E	I	34.93-(48.14)-60.07	11.93-(14.58)-17.04	1.49-(2.09)-2.98	A	SE & SC	17.47-(24.73)-31.74	3.41-(5.64)-8.95	0.74-(1.01)-1.32
	HNMWFC-HM15	A	0.8101	S & B	T2	S	1.35	17.89-(20.51)-23.86	13.21-(16.35)-19.71	1.77-(2.41)-3.19	E	I	29.82-(39.76)-53.89	13.21-(16.35)-19.71	1.77-(2.41)-3.19	A	SE & SC	16.83-(20.55)-33.23	3.76-(4.37)-5.42	0.67-(1.09)-1.48
	TSH-R9849	A	0.8583	S & B	T2	S	1.54	18.73-(23.92)-32.16	15.34-(18.64)-22.32	1.28-(2.05)-2.98	E	I	36.42-(46.48)-59.85	12.99-(16.71)-21.94	1.92-(2.95)-3.41	A	SE & SC	21.3-(27.08)-44.32	3.27-(8.54)-12.75	0.89-(1.13)-1.78
	HMAS55396	A	0.8477	S & B	T2	S	1.59	17.35-(21.33)-30.74	15.34-(18.64)-22.32	1.49-(2.33)-2.98	E	I	36.42-(46.48)-59.85	15.34-(18.64)-22.32	1.28-(2.05)-2.98	A	SE & SC	18.33-(25.71)-40.09	4.69-(7.69)-10.75	1.45-(1.77)-2.64

Appendix 1: Continued.

	HMAS56896	A	0.8356	S & B	T2	S	1.58	14.48-(19.92)-29.18	7.88-(13.44)-16.61	1.07-(1.77)-2.56	E	I	23.43-(38.82)-54.74	6.39-(13.05)-18.53	1.49-(3.26)-5.54	A	SE & SC	26.41-(31.73)-48.81	4.47-(5.80)-8.52	1.49-(1.96)-2.47
	BPI25363	A	0.8447	S & B	T2	S	1.45	14.15-(17.12)-28.33	7.88-(13.44)-16.61	1.28-(1.96)-2.56	E	I	20.97-(41.57)-59.11	7.88-(13.44)-16.61	1.28-(1.96)-2.56	A	SE & SC	26.41-(33.19)-45.74	4.33-(6.01)-11.32	1.49-(2.06)-2.47
	HMAS71119	A	0.8391	S & B	T2	S	1.71	16.61-(22.02)-27.48	12.78-(17.72)-23.22	1.7-(2.03)-2.56	E	I	39.04-(54.34)-66.24	13.31-(16.78)-21.09	2.77-(3.79)-6.34	A	SE & SC	22.35-(30.07)-41.33	5.89-(8.31)-13.04	0.89-(1.22)-2.56
	HMAP3094	A	0.8391	S & B	T2	S	1.3	19.17-(22.78)-30.46	11.72-(15.27)-18.32	1.07-(1.66)-2.77	E	I	42.6-(52.25)-73.91	12.78-(18.37)-25.13	2.77-(4.62)-7.67	A	SE & SC	29.82-(35.89)-43.24	4.26-(6.98)-13.21	0.76-(1.03)-1.98
	HMAP3135	A	0.8583	S & B	T2	S	1.38	15.76-(20.67)-25.99	10.86-(15.52)-18.53	1.07-(1.65)-2.13	E	I	35.78-(45.38)-66.24	11.73-(16.49)-23.64	2.34-(3.17)-5.11	A	SE & SC	23.43-(33.18)-42.81	4.68-(7.16)-11.02	0.89-(1.44)-2.56
	TSH-R10771	A	0.7682	S & B	T2	S	1.25	17.44-(23.33)-29.74	11.23-(14.08)-17.28	0.86-(1.51)-3.15	E	I	34.27-(47.26)-65	11.48-(15.84)-21.16	1.79-(3.44)-5.23	A	SE & SC	20.09-(36.02)-43.93	5.24-(8.27)-12.25	0.55-(1.37)-2.3
	HMAS8619	A	0.8517	S & B	T2	S	1.38	15.34-(19.33)-26.34	9.8-(15.99)-20.24	1.7-(2.04)-2.77	E	I	30.25-(42.93)-62.62	9.59-(15.79)-19.81	1.92-(2.86)-4.05	A	SE & SC	15.24-(27.20)-34.93	3.83-(5.51)-7.24	0.75-(1.27)-1.46
	TSH-R7538	A	0.8123	S & B	T2	S	1.3	19.17-(22.78)-30.46	11.72-(15.27)-18.32	1.07-(1.66)-2.15	E	I	42.6-(52.25)-73.91	11.72-(15.27)-18.32	1.07-(1.66)-2.77	A	SE & SC	29.82-(35.89)-43.24	4.26-(6.98)-13.21	0.98-(1.71)-2.56
	HMAS17721	A	0.8197	S & B	T2	S	1.28	15.34-(19.33)-26.34	9.8-(15.99)-20.24	1.7-(2.04)-2.98	E	I	30.25-(42.93)-62.62	9.8-(15.99)-20.24	1.7-(2.04)-2.77	A	SE & SC	15.24-(27.20)-34.93	3.83-(5.51)-7.24	0.98-(1.27)-1.46
	HMAS55179	A	0.8123	S & B	T2	S	1.37	14.91-(14.68)-18.32	9.16-(13.94)-15.55	1.07-(1.67)-2.13	E	I	30.67-(42.10)-50.69	9.16-(13.94)-15.55	1.07-(1.67)-2.13	A	SE & SC	16.83-(25.28)-36.93	5.62-(7.68)-10.35	1.13-(2.28)-2.69
	BPI23210	A	0.7682	S & B	T2	S	1.28	16.83-(20.28)-24.92	10.44-(12.96)-15.12	1.49-(2.13)-2.77	E	I	21.94-(35.95)-50.69	11.29-(14.72)-18.53	1.92-(2.89)-3.62	A	SE & SC	25.56-(34.54)-44.72	3.84-(6.72)-11.08	0.67-(0.89)-1.48
M15	HMAS3607	E	0.8239	S & B	T1	E	1.01	21.32-(25.46)-31.89	14.48-(20.46)-25.13	1.49-(2.19)-2.77	E	I	30.03-(40.45)-50.75	11.08-(16.47)-23.22	2.13-(2.96)-5.75	E	SE & SC	12.78-(17.84)-24.92	2.13-(4.97)-8.9	0.85-(1.13)-1.48
M16	HMAP3163	H	0.8455	S & B	T2	S	1.37	17.25-(22.68)-30.03	12.14-(15.91)-18.13	apex: 5.88 1.07-(1.87)-2.94	T	I	41.37-(56.65)-71.36	14.06-(19.02)-23.86	2.98-(4.45)-6.38	H	SE	21.49-(27.38)-36.06	5.07-(8.19)-11.35	0.52-(1.45)-2.77
	HNMAP3059	H	0.8234	S & B	T2	S	1.4	19.17-(23.18)-32.59	13.42-(15.92)-20.24	apex: 5.75 1.49-(2.43)-3.33	T	I	33.44-(49.43)-66.62	9.8-(16.13)-20.45	1.28-(3.64)-5.98	H	SE	22.58-(32.23)-41.53	7.67-(9.78)-13.42	0.85-(1.42)-2.13
	NWC-0913	H	0.8196	S & B	T2	S	1.51	19.6-(26.09)-34.51	14.48-(17.15)-19.38	apex:5.76, 1.28-(2.28)-2.98	T	I	42.52-(68.19)-87.62	11.5-(16.91)-23.22	1.7-(4.15)-7.67	H	SE	23.64-(33.40)-48.35	6.0-(8.99)-12.99	0.89-(1.21)-1.45
	HMAS42407	H	0.8245	S & B	T2	S	1.33	15.55-(23.85)-28.54	10.22-(14.77)-19.6	apex: 4.99, 1.28-(2.03)-3.19	T	I	37.06-(51.19)-68.88	13.63-(19.64)-24.04	2.77-(4.87)-6.18	H	SE			
	HMAP3201	H	0.8264	S & B	T2	S	1.41	17.25-(25.36)-34.29	14.27-(17.42)-19.6	apex: 5.11, 1.28-(1.63)-2.56	T	I	39.4-(49.46)-59.21	13.21-(18.08)-22.79	2.13-(3.92)-6.18	H	SE	25.77-(33.44)-44.3	5.54-(8.23)-12.99	0.99-(1.31)-1.58
	HMAP3163	H	0.8099	S & B	T2	S	1.36	17.25-(22.68)-30.03	12.14-(15.91)-18.13	apex: 4.89, 1.49-(2.01)-2.87	T	I	41.37-(56.65)-71.36	14.06-(19.02)-23.86	2.98-(4.45)-6.38	H	SE	25.43-(31.08)-47.21	6.61-(10.03)-12.11	0.84-(1.22)-1.56
	HMAP3171	H	0.8139	S & B	T2	S	1.57	21.73-(25.99)-31.67	14.48-(18.40)-21.51	apex: 5.54, 1.07-(1.69)-2.34	T	I	41.96-(55.59)-64.54	14.7-(20.24)-28.97	2.77-(5.07)-8.95	H	SE	20.33-(28.54)-39.31	6.01-(9.34)-14.03	0.85-(1.05)-1.21

Appendix 1: Continued.

	HMAP3207	H	0.8011	S & B	T2	S	1.34	18.74-(24.71)-30.25	12.99-(17.34)-20.45	apex: 5.96, 0.85-(1.85)-2.56	T	I	35.78-(52.44)-64.96	11.72-(17.45)-22.58	2.56-(3.54)-5.75	H	SE	21.51-(29.74)-43.67	4.47-(7.78)-10.44	0.71-(1.51)-2.13
M17	TSH-R9834	H	0.8323	S & B	T1	E	1.57	15.75-(20.49)-26.66	9.86-(15.20)-19.62	apex: 4.29.41-(1.79)-2.77	E	I	30.02-(50.20)-71.49	12.93-(16.74)-19.39	3.22-(4.56)-7.09	H	SE	30.88-(38.57)-44.79	9.08-(11.33)-13.24	1.83-(2.48)-3.12
	TSH-9835	H	0.8354	S & B	T1	E	1.23	16.55-(19.75)-28.63	10.22-(15.17)-18.32	apex: 6.59, 1.07-(1.52)-2.56	E	I	41.32-(54.35)-69.86	11.5-(17.04)-25.56	3.62-(7.61)-11.29	H	SE	27.05-(41.40)-48.14	7.88-(10.94)-15.12	1.28-(2.79)-4.56
	HH-78307	H	0.8241	S & B	T1	E	1.33	14.91-(20.50)-25.45	13.21-(15.50)-19.71	apex: 6.68, 1.7-(2.09)-2.98	E	I	37.95-(45.79)-67.95	14.7-(17.87)-22.52	2.98-(4.88)-7.03	H	SE	21.71-(27.03)-40.04	8.41-(10.64)-13.95	0.64-(2.13)-3.49
	HH-53302	H	0.8277	S & B	T1	E	1.49	17.04-(23.90)-28.99	11.48-(18.46)-22.13	apex: 4.55, 1.7-(2.19)-2.77	E	I	40.26-(57.86)-78.17	10.86-(16.42)-20.87	1.28-(3.67)-5.11	H	SE	19.38-(30.95)-39.62	6.76-(8.37)-12.42	0.85-(2.43)-3.54
	HH-78366	H	0.8233	S & B	T1	E	1.21	17.98-(23.09)-31.52	10.86-(15.52)-18.53	1.77-(2.22)-2.98	E	I	41.11-(53.08)-70.93	10.86-(16.08)-20.66	2.56-(3.91)-5.54	H	SE	17.28-(28.31)-36.56	5.01-(7.59)-12.22	0.82-(1.33)-1.86
M18	NWC-09234	H	0.8312	S & B	T1	S	1.34	17.25-(21.77)-25.35	11.93-(15.28)-17.47	1.49-(2.10)-2.77	E	I	37.28-(48.97)-71.36	11.08-(16.33)-21.94	1.28-(2.37)-4.26	A	SE	22.79-(29.49)-35.57	5.32-(7.73)-11.08	0.66-(1.04)-1.52
	NWC06210	H	0.8259	S & B	T1	S	1.55	20.87-(25.64)-31.31	13.27-(17.49)-19.17	1.28-(2.03)-2.98	E	I	39.62-(51.11)-79.85	14.91-(16.81)-21.09	1.49-(2.69)-3.62	A	SE	14.06-(21.55)-28.12	6.6-(9.18)-11.93	0.87-(1.21)-1.43
	HMAS52924	H	0.8387	S & B	T1	S	1.46	20.45-(25.34)-28.98	11.29-(17.46)-21.51	1.49-(1.93)-2.56	E	I	52.19-(65.86)-86.48	10.86-(18.29)-26.63	1.49-(2.99)-4.26	A	SE	15.34-(24.67)-35.78	4.47-(8.8)-12.78	1.01-(1.33)-1.81
	HMAS55038	H	0.8103	S & B	T1	S	1.5	14.7-(17.45)-20.45	14.7-(17.45)-20.45	1.92-(2.57)-3.41	E	I	37.91-(67.08)-102.24	14.91-(22.95)-31.74	1.92-(3.25)-5.11	A	SE	17.47-(24.73)-31.74	2.56-(4.96)-7.45	0.67-(0.89)-1.48
	HMAS58575	H	0.8351	S & B	T1	S	1.44	13.85-(17.49)-20.24	13.85-(17.49)-20.24	1.92-(2.63)-3.41	E	I	40.26-(57.86)-78.17	10.22-(16.62)-23.86	2.98-(4.57)-8.31	A	SE	16.83-(20.55)-33.23	1.92-(3.36)-5.54	0.64-(0.94)-1.28
	BPI25363	H	0.8211	S & B	T1	S	1.66	17.68-(24.26)-28.54	14.48-(15.98)-18.74	1.49-(1.66)-2.13	E	I	28.75-(40.19)-56.44	10.01-(13.42)-16.83	1.92-(2.50)-3.19	A	SE	17.55-(26.77)-35.98	6.01-(7.94)-12.09	0.78-(1.43)-2.61
	BPI1109650	H	0.8314	S & B	T1	S	1.57	15.76-(22.81)-27.69	10.65-(13.37)-15.76	1.49-(1.62)-2.56	E	I	41.11-(53.08)-70.93	10.86-(16.08)-20.66	2.13-(2.83)-4.35	A	SE	17.52-(23.54)-36.47	7.1-(10.56)-15.98	0.72-(1.21)-1.56
M19	HMAP3185	A	0.8143	S & B	T1	S	1.88	18.74-(25.83)-32.8	14.7-(17.82)-21.51	apex: 6.18, 1.49-(2.12)-2.52	T	I	41.96-(50.89)-71.99	6.6-(14.97)-18.74	2.98-(4.63)-6.72	A	SE	15.34-(20.83)-28.97	6.5-(9.08)-12.35	0.85-(1.43)-2.56
	HMAP3257	A	0.8203	S & B	T1	S	1.71	16.45-(23.66)-30.52	10.34-(18.89)-23.55	apex: 5.01, 1.49-(1.87)-2.56	T	I	32.59-(47.60)-67.1	11.73-(18.15)-22.07	3.01-(5.44)-8.96	A	SE	20.66-(26.13)-33.55	6.39-(9.92)-14.48	0.77-(1.55)-2.01
M20	HMAP3186	H	0.8121	S & B	T1	E	1.44	20.24-(24.06)-30.89	14.48-(16.75)-20.87	apex: 10.01, 1.56-(2.32)-2.90	T	I	49.20-(58.46)-71.57	11.72-(16.61)-21.94	2.71-(5.55)-10.23	A	SE	15.34-(23.20)-32.38	5.54-(8.15)-12.57	0.56-(1.33)-2.33
	HH-73060	H	0.8241	S & B	T1	E	1.55	16.55-(22.03)-28.56	15.76-(17.77)-23.43	apex: 9.83, 1.49-(2.13)-2.77	T	I	38.55-(51.91)-68.22	11.08-(18.39)-22.58	1.92-(3.92)-6.18	A	SE	18.2-(24.71)-33.02	7.45-(9.57)-12.8	0.89-(1.77)-2.56

Appendix 1: Continued.

	HH-77944	H	0.8259	S & B	T1	E	1.37	14.27-(21.56)-26.84	12.57-(15.39)-18.96	apex: 8.74, 1.28-(1.89)-2.56	T	I	43.24-(60.2)-75.4	10.86-(16.42)-20.87	3.41-(4.63)-8.19	A	SE	17.47-(24.73)-31.74	6.98-(11.03)-14.56	0.74-(1.47)-1.95
M21	TSH-R1504	H	0.8525	S	T1	S	1.1	16.83-(19.88)-24.92	12.79-(15.17)-19.17	1.28-(1.84)-2.56	T	P	31.95-(42.75)-56.44	10.22-(14.17)-18.96	2.56-(3.74)-7.03	E	SC	22.58-(26.51)-30.89	4.69-(7.62)-10.86	0.94-(1.23)-1.56
	TSH-R1507	H	0.8451	S	T1	S	1.03	14.41-(18.54)-25.03	13.35-(16.01)-18.53	1.28-(2.07)-2.78	T	P	29.95-(40.22)-53.05	9.54-(16.27)-20.01	4.01-(5.33)-9.53	E	SC	18.34-(24.09)-29.87	5.33-(8.74)-12.59	0.73-(1.28)-1.61
	HH-99463	H	0.8433	S	T1	S	0.98	17.31-(22.54)-27.03	11.07-(15.98)-20.55	1.28-(2.07)-2.56	T	P	28..33-(39.43)-56.87	11.04-(15.32)-19.54	5.98-(7.11)-8.96	E	SC	19.33-(27.55)-33.21	4.44-(9.93)-13.55	0.88-(1.03)-1.56
	TSH-R7341	H	0.8487	S	T1	S	0.88	14.27-(16.82)-23.23	9.51-(11.55)-13.42	0.84-(1.24)-2.75	T	P	26.84-(39.97)-54.31	9.16-(13.94)-18.32	2.34-(4.22)-7.88	E	SC	12.66-(20.07)-30.48	7.33-(10.69)-14.41	0.85-(1.32)-1.7
	TSH-R10193	H	0.8502	S	T1	S	0.94	15.38-(19.61)-26.78	9.12-(11.26)-13.43	0.81-(1.55)-2.24	T	P	37.95-(45.79)-67.95	10.44-(16.43)-25.51	1.92-(4.51)-7.03	E	SC	13.02-(20.19)-29.58	7.46-(10.53)-14.75	1.49-(1.72)-2.69
	TSH-R7397	H	0.8319	S	T1	S	1.13	16.74-(20.47)-26.56	11.45-(14.08)-16.73	0.92-(1.54)-2.84	T	P	26.09-(43.43)-60.83	9.55-(15.19)-20.96	1.65-(3.4)-5.85	E	SC	18.92-(24.02)-27.92	7.12-(11.47)-16.07	0.85-(1.35)-2.13
	HMAS41605	H	0.8377	S	T1	S	0.89	18.5-(20.85)-24.98	9.28-(12.24)-14.17	0.79-(1.31)-2.18	T	P	33.28-(44.46)-57.71	11.73-(17.14)-22.35	1.45-(3.16)-6.23	E	SC	15.33-(24.88)-30.28	6.04-(9.1)-13.65	0.84-(1.27)-1.48
	HMAS41606	H	0.8365	S	T1	S	1.06	15.75-(20.49)-26.66	8.08-(11.48)-15.04	0.84-(1.58)-2.72	T	P	26.74-(41.37)-51.04	10.09-(16.13)-21.85	0.78-(2.04)-4.73	E	SC	15.02-(22.01)-27.62	6.38-(9.84)-14.48	0.67-(0.89)-1.48
	HMAS365	H	0.8445	S	T1	S	0.97	14.88-(19.34)-25.03	9.17-(13.22)-19.76	0.92-(1.54)-2.84	T	P	29.7-(44.09)-59.07	10.99-(17.22)-24.33	1.11-(2.38)-3.45	E	SC	17.59-(25.07)-35.96	5.35-(9.11)-13.39	0.71-(1.12)-1.79
M22	TSH-R10779	H	0.8283	S	T2	S	1.29	15.31-(20.68)-33.26	9.53-(14.69)-17.69	0.79-(1.44)-2.35	E	I	32.35-(39.26)-47.79	12.12-(16.47)-21.13	1.27-(2.48)-3.71	H	SE	22.17-(31.37)-42.06	7.23-(9.91)-14.34	0.59-(1.21)-2.12
	TSR-R7330	H	0.8276	S	T2	S	1.33	15.25-(23.11)-32.15	8.31-(15.05)-17.6	1.03-(1.73)-2.55	E	I	28.31-(36.88)-51.29	11.03-(14.7)-20.51	1.67-(2.55)-3.05	H	SE	18.31-(32.05)-40.06	5.03-(8.61)-11.29	1.01-(1.33)-2.56
	TSH-R7335	H	0.8209	S	T2	S	1.15	17.33-(22.66)-30.06	11.59-(15.14)-17.6	1.03-(1.81)-2.72	E	I	33.98-(48.78)-68.58	10.55-(15.51)-22.55	1.57-(3.08)-4.94	H	SE	23.51-(29.88)-44.44	7.03-(11.03)-15.21	0.88-(1.21)-2.56
	TSH-R7333	H	0.8254	S	T2	S	1.36	18.74-(23.48)-29.56	11.93-(15.73`)-18.75	1.28-(1.57)-2.13	E	I	27.69-(37.99)-50.27	8.95-(12.76)-15.98	1.7-(3.01)-4.47	H	SE	17.89-(26.04)-36.85	5.75-(8.87)-12.78	0.87-(1.09)-1.56
	HH-53150	H	0.8301	S	T2	S	1.33	16.42-(24.06)-29.17	10.07-(13.23)-16.61	1.49-(1.64)-2.78	E	I	32.59-(50.99)-67.1	9.16-(16.13)-22.58	2.77-(5.07)-8.95	H	SE	22.14-(27.87)-35.36	4.33-(7.41)-11.93	0.64-(1.17)-1.28
	HH-53225	H	0.8239	S	T2	S	1.37	19.48-(26.76)-32.36	9.59-(14.63)-17.89	1.28-(1.88)-2.98	E	I	29.82-(42.41)-54.85	8.52-(13.99)-20.87	2.56-(3.54)-5.75	H	SE	17.25-(23.71)-30.08	5.60-(9.16)-12.55	1.49-(2.72)-3.19
	HH-53135	H	0.8403	S	T2	S	1.27	15.34-(24.03)-28.28	11.08-(14.99)-19.6	1.49-(1.84)-2.59	E	I	32.59-(42.90)-52.89	9.59-(13.77)-16.83	2.13-(3.13)-4.26	H	SE	18.31-(32.05)-40.06	5.03-(8.61)-11.29	1.01-(1.33)-2.56
	HMAS56075	H	0.8397	S	T2	S	1.39	17.89-(22.06)-25.35	10.86-(15.69)-18.74	1.49-(2.74)-2.77	E	I	31.52-(41.63)-53.46	9.8-(16.74)-23.22	1.7-(4.20)-8.95	H	SE	22.45-(33.58)-39.24	4.01-(8.74)-12.56	0.76-(1.24)-2.33
M23	TSH-R7512	H	0.8341	S	T1	S	1.34	17.68-(21.84)-25.56	11.29-(14.08)-16.61	1.49-(2.02)-2.77	E	I	33-(43.14)-58.71	11.22-(15.49)-19.21	2.31-(5.31)-8.37	E	SC	19..33-(35.31)-47.55	5.67-(10.33)-15.31	1.01-(1.44)-2.31
	TSH-R7510	H	0.8437	S	T1	S	1.21	18.74-(23.15)-29.39	11.29-(15.03)-18.96	1.28-(1.73)-2.77	E	I	43.45-(53.70)-64.96	10.01-(17.65)-22.15	1.92-(3.65)-5.75	E	SC	21.09-(32.98)-43.88	4.9-(6.58)-8.95	1.07-(1.57)-2.56
	TSH-R7365	H	0.842	S	T1	S	1.4	17.25-(23.26)-27.48	17.25-(19.38)-21.94	1.7-(2.26)-2.98	E	I	45.37-(63.68)-78.17	12.14-(22.34)-29.82	1.7-(2.96)-4.69	E	SC	22.78-(27.27)-42.36	1.92-(3.36)-5.54	1.07-(1.36)-2.13
	TSH-R7545	H	0.8438	S	T1	S	1.37	17.04-(21.90)-25.99	10.44-(14.46)-17.47	1.49-(1.88)-2.56	E	I	27.69-(42.24)-57.94	8.73-(13.25)-17.03	1.49-(3.62)-5.32	E	SC	21.3-(27.08)-44.32	4.69-(7.46)-10.86	0.64-(1.13)-1.49
	HH-53339	H	0.8385	S	T1	S	1.33	17.25-(23.26)-27.48	17.25-(19.38)-21.94	1.49-(1.77)-2.34	E	I	39.62-(51.11)-79.85	11.29-(14.72)-18.53	1.92-(2.89)-3.62	E	SC	18.32-(28.27)-40.04	5.11-(7.87)-11.72	0.72-(1.21)-1.56
	HH-53343	H	0.8431	S	T1	S	1.28	16.83-(20.28)-24.92	10.44-(12.96)-15.12	1.49-(2.13)-2.77	E	I	23.43-(38.82)-54.74	14.91-(18.96)-24.92	1.77-(2.49)-5.02	E	SC	17.47-(31.30)--40.47	3.76-(4.37)-5.42	0.65-(1.46)-2.78

Appendix 1: Continued.

HNMWFC-HM13	H	0.8427	S	T1	S	1.45	14.48-(19.92)-29.18	7.88-(13.44)-16.61	1.28-(1.75)-2.77	E	I	39.62-(51.11)-79.85	12.99-(16.71)-21.94	2.56-(3.31)-5.52	E	SC	18.74-(27.45)-37.49	4.47-(6.50)-10.22	1.83-(2.48)-3.12
BPI1109442	H	0.8388	S	T1	S	1.21	11.08-(20.99)-25.99	8.31-(13.40)-18.32	1.49-(1.73)-2.34	E	I	30.03-(40.45)-50.75	9.16-(13.94)-18.32	1.49-(3.58)-5.42	E	SC	19.38-(30.95)-39.62	5.11-(6.90)-9.16	0.62-(1.46)-2.82
HMAP1587	H	0.8344	S	T1	S	1.39	17.68-(24.26)-28.54	14.48-(15.98)-18.74	1.49-(1.62)-2.13	E	I	43.45-(53.70)-64.96	10.22-(14.17)-18.96	2.77-(4.27)-5.75	E	SC	12.14-(23.00)-35.36	7.67-(9.59)-11.08	0.69-(1.51)-2.61
HNMWFC-HM665	H	0.8461	S	T1	S	1.36	15.76-(22.81)-27.69	10.65-(13.37)-15.76	1.77-(2.22)-2.98	E	I	37.95-(45.79)-67.95	9.59-(18.42)-25.35	1.49-(3.15)-5.32	E	SC	11.72-(21.28)-36	5.75-(9.70)-12.55	0.74-(1.33)-1.32
HNMWFC-L91054	H	0.8409	S	T1	S	1.33	17.37-(22.05)-24.55	10.19-(16.76)-20.62	1.7-(2.04)-2.77	E	I	27.69-(42.24)-57.94	11.29-(15.70)-22.58	1.49-(4.35)-5.46	E	SC	16.61-(30.23)-41.53	4.47-(8.8)-12.78	0.64-(1.05)-1.28
BPI23209	H	0.8491	S	T1	S	1.4	15.54-(23.03)-27.71	11.33-(17.37)-21.03	1.28-(1.93)-2.56	E	I	46.94-(53.86)-67.73	12.99-(17.5)-22.87	1.49-(2.87)-4.05	E	SC	25.35-(33.29)-40.47	7.03-(9.27)-12.98	0.67-(1.09)-1.48
BPI23207	H	0.8338	S	T1	S	1.25	16.03-(24.47)-29.31	9.84-(15.54)-22.77	1.49-(1.66)-2.13	E	I	28.75-(40.19)-56.44	14.89-(21.84)-28.29	1.92-(3.62)-5.54	E	SC	16.83-(25.28)-36.93	6.82-(10.44)-13.63	0.64-(1.15)-1.49

a: Morphological group.

b: Specimen No.

c: Position of uredinia (A: amphigenous, E: epiphyllous, H: hypophyllous).

d: Shape factor of urediniospores.

e: Position of germ pore. (S: scattered, S & B: scattered or tending to bizonate).

f: Spine form (T1: echinulate type 1, T2: echinulate type 2, T3: echinulate type 3).

d: Smooth regions at apex (E: echinulate; S: smooth at apex).

e: Average distance between spines (μm).

f: Length of urediniospores (μm).

g: Width of urediniospores (μm).

h: Wall thickness of urediniospores (μm).

i: Wall of paraphyese (E: evenly thickened, T: thickened at apex).

j: Position of parpahyses (I: intermixed; P: peripheral).

k: Length of paraphyes (μm).

l: Width of paraphyese (μm).

m: Wall thickness of paraphyese (μm).

n: Position of telia (A: amphigenous, E: epiphyllous, H: hypophyllous).

o: Position of teliospores (SE: subepidermal, SC: subcuticular, SE & SC: subepidermal or subcuticular).

p: Length of teliospores (μm).

q: Width of teliospores (μm).

r: Wall apex thickness of teliospores (μm).

Appendix 2: Alignment of sequence data of rDNA ITS regions.

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                 ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                      5         15         25         35         45         55         65         75         85         95
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                   105       115       125       135       145       155       165       175       185       195
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HMAS76122        ATCAGTACGT ATCCCAAAGG C-AACTTTGA GTTACATTAC CCATCATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CC- -TATAAT--T
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NWC891_1         ATCAGTACGT ATCCCAAAGG C-AACTTTGA GTTACATTAC CCATAATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CC- -TATAAT--T
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TSHR1504          ATCAGTACGT ATCCCAAAGG C-AACTTTGA GTTACATTAC CCATCATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CC- -CAAAAC--C
TSHR7512          ATCAGTACGT ATCCCAAAGG C-AACTTTGA GTTACATTAC CCATCATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CC- CTAT-AT--T
NWC6843           ATCAGTACGT ATCCCAAAGG C-AACTTTGA GTTACATTAC CCATCATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CG- -TTTAAT--T
TNS_F_186369      ATCAGTACGT ATCCCAAAGG C-AACTTTGA GTTACATTAC CCATCATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CG- -TTTAAT--T
TSHR1507          ATCAGTACGT ATCCCAAAGG C-AACTTTGA GTTACATTAC CCATCATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CC- -CAAAAC--C
TSHR1504          ATCAGTACGT ATCCCAAAGG C-AACTTTGA GTTACATTAC CCATCATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CC- CTAT-AT--T
TNS_F_53150       ATCAGTACGT ATCCCAAAGG C-AACTTTGA GTTACATTAC CCATCATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CC- CTAT-AT--T
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HH53248           ATCAGTACGT ATGACAAAGG C-AACTTTGG CTTACATTAC ATATAAGTTA -CCCCCATTT ACACTTAAGA AGTTTTAAGA ATGATA-CC- -TATAAC--T
TNS_F_222866      ATCAGTACGT ATCCCAAAGG C-AACTTTGA GTTACATTAC CCATAATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CC- -TATAAT--T
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TNS_F_22628       ATCAGTACGT ATCCCAAAGG C-AACTTTGA GTTACATTAC CCATAATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CC- -TATAAT--T
TNS_F_107037      ATCAGTACGT ACTTCAAAGG C-AACTTTGA TTTACATTAC CCATCATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CC- -CATAAT--T
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JF825969          ATCAGTACGT ATCCCAAAGG C-AACTTTGA GTTACATTAC CCATAATTTA -CCCCCATTT ACACTTAATA AGTTTTAAGA ATGATA-CC- -TATAAT--T
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GQ479900          ATCAGTACGT ATTACAAAGT CTGACTTTGT TTTACATTAC ATATAAGTTA CCCCCTATTT ACACTTAAGA AGTTTTAAGA ATGATA-CC- CTATAAT--T
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GQ479274          ATCAGTACGT ATTACAAAGT CTGACTTTGT CTTACATTAC ATATAAGTTA CCCCCTATTT ACACTTAAGA AGTTTTAAGA ATGATA-CC- CTATAAT--T
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                      205        215        225        235        245        255        265        275        285        295
HMAS38658         ATATAACTTT CAGCAATGGA TCTCTAGGCT CTCACGTCGA TGAAGAACAC AGTGAAATGT GATACGTAAT GTGAATTGCA GAATTCAGTG AATCATCGAA
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HMAS52904         ATATAACTTT CAGCAATGGA TCTCTAGGCT CTCACGTCGA TGAAGAACAC AGTGAAATGT GATACGTAAT GTGAATTGCA TAATTCAGTG AATCATCGAA
HMAS82376         ATATAACTTT CAGCAATGGA TCTCTAGGCT CTCACGTCGA TGAAGAACAC AGTGAAATGT GATACGTAAT GTGAATTGCA TAATTCAGTG AATCATCGAA
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HNMAP3059         ATATAACTTT CAGCAATGGA TCTCTAGGCT CTCACGTCGA TGAAGAACAC AGTGAAATGT GATACGTAAT GTGAATTGCA TAATTCAGTG AATCATCGAA
HNMAP3108         ATATAACTTT CAGCAATGGA TCTCTAGGCT CTCACGTCGA TGAAGAACAC AGTGAAATGT GATACGTAAT GTGAATTGCA GAATTCAGTG AATCATCGAA
NWC6419           ATATAACTTT CAGCAATGGA TCTCTAGGCT CTCACGTCGA TGAAGAACAC AGTGAAATGT GATACGTAAT GTGAATTGCA GAATTCAGTG AATCATCGAA
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BPI23210          ATATAACTTT CAGCAATGGA TCTCTAGGCT CTCACGTCGA TGAAGAACAC AGTGAAATGT GATACGTAAT GTGAATTGCA GAATTCAGTG AATCATCGAA
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HMAS135888         TTTATAT--T TCATTGAGGC AGTCTTTGGT CTTTATGACT ATCCGCTAAT ---------- ---------- ---
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TSH_R16981         TTTATAT--T TCATTGAGGC AGTCTTTGGT CGCTCCGACT ATCCGCTAAT -AGGGCAACT TGAAGAATAG CTT
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Appendix 3: Alignment of sequence data of rDNA D1/D2 region.

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                 ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                      5         15         25         35         45         55         65         75         85         95
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HMAS52904        AATCTGGCAC TTTTTACAAG TGTCCGAGTT GTAATTTGTA GAGCTGTTAT CCGTACTGGA CCATGTACAA GTCTGTTGAA AAGCAGCATC ATTGAAGGTG
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NWC9234           GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
HNMAP1710         GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
HNMAP3111         GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
HNMAP3175         GATTCGAAAG -GATCTCCTT ---------- ---------- ---------- ----------
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TSHR10727         GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
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1690              GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
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HNMAP1698         GATTCGAAAG -GATCTCCTT ACTATGGATG T--------- ---------- ----------
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TSHR7510          GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
TSHR7365          GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
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BPI1108633        GATTCGAAAG -GATCTCCTT ACTATGGATG TAGGTGAAAT AACTATAAGC GACCCGTCTT
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TSHR10194         GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
TSHR3879          GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
TSHR7483          GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
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TSHR7613         GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
HMAS135888       GATTCGAAAG -GATCTCCTT ACTATG---- ---------- ---------- ----------
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HNMAP3065        GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
HNMAP1594        GATTCGAAAG -GATCTCCTT ACTATGGATG T--------- ---------- ----------
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TSHR8778         GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT ---------- ----------
HMAS82388        GATTCGAAAG -GATCTCCTT ACTATGGATG TTG------- ---------- ----------
HNMAP3140        GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
TSHR10513        GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
HNMAP3135        GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
HNMAP3152        GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
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TSHR10771        GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
TSHR10779        ---------- ---------- ---------- ---------- ---------- ----------
TSHR7731         GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAA- ---------- ----------
HNMAP3181        GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGGTAAAA ---------- ----------
TSH_R16979       GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACC------
TSH_R16981       GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACC------
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TSHR1504         ---------- ---------- ---------- ---------- ---------- ----------
HH53150          ---------- ---------- ---------- ---------- ---------- ----------
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HH78366          GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
HH53135          GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
BPI22984         GATTCGAAAG -GATCTCCTT ACTATGGA-- ---------- ---------- ----------
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HH53248          GATCAGAAAA TGATCTCCTT ACTATGGATG TTGGTGAAAT ATCTTTAAGC GACC------
TSN_F_222866     GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
TSN_F_107383     GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
TSN_F_22628      GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
TSN_F_107037     GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
NWC9467          GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
TSN_F_120783     GATTCGAAAG -GATCTCCTT ACTATGGATG TTGGTGAAAT AACTTTAAGC GACCCGTCTT
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Appendix 4: Alignment of sequence data of EF-1α gene.

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                  ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                       5         15         25         35         45         55         65         75         85         95
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HNMAP1710         ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
NWC891_1          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR9836          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
HNMAP3111         ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
HNMAP1716         ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
HNMAP1697         ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
HMAS82384         ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
HNMAP1697         ATATGCCTGG GTACTTGACA CGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR3879          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR9832          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR9837          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR10727         ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR10194         ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR7489          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR10513         ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR3879          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
HNMAP1339         ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR9620          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGGGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR7643          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCATATA CTTCGTTACC
TSHR7684          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCATATA CTTCGTTACC
TSHR9836          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR9837          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR3889          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGGGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR9834          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
TSHR9832          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
NWCKNW_1          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
NWC09535          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
HNMAP3140         ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
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HNMAP3149         ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
BPI22628          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
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HMAS52894         ATATGCCTGG GTACTCGACA AGCTCAAGGC CGAGCGAGAA CGTGGTATTA CCATCGACAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTTGTTACC
NWC09234          ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGACAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTCGTTACC
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HNMAP3181         ATATGCCTGG GTACTTGACA AGCTCAAAGC CGAGCGAGAA CGTGGTATCA CCATCGATAT TGCGCTCTGG AAATTCGAGA CCCCCAAATA CTTYGTTACC
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HNMAP1710         GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATTACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
NWC891_1          GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
TSHR9836          GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
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HMAS82384         GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATTACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
HNMAP1697         GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAA GCCGATTGTG CCATCTTGAT CATCGCCTCC GGTGTCGGTG
TSHR3879          GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
TSHR9832          GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
TSHR9837          GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
TSHR10727         GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
TSHR10194         GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
TSHR7489          GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
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HNMAP1339         GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATTACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
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TSHR9837          GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
TSHR3889          GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
TSHR9834          GTCATTGATG CTCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
TSHR9832          GTCATTGATG CTCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
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NWC09535          GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
HNMAP3140         GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
TSHR3885          GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
HNMAP3149         GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
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HMAS52894       GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
NWC09234        GTCATTGATG CTCCAGGACA TCGTGATTTC ATTAAAAACA TGATCACTGG AACATCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
HMAS62584       GTTATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACCGG AACCTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
HNMAP3181       GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
HNMAP3060       GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
NWC06210        GTCATTGATG CTCCAGGACA TCGTGATTTC ATTAAAAACA TGATCACTGG AACATCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
TSHR7635        GTCATTGATG CCCCAGGACA TCGTGATTTC ATTAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG
HMAS52905       GTCATTGATG CCCCAGGACA TCGTGATTTC ATCAAAAACA TGATCACTGG AACTTCCCAG GCCGATTGTG CTATCTTGAT CATTGCCTCC GGTGTCGGTG

                ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                    205        215        225        235        245        255        265        275        285        295
EU487243        AATTCGAAGC CGGTATCTCA AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT CCGTCAACTT ATCGTGGCCA TCAACAAGAT
HNMAP1710       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
NWC891_1        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR9836        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
HNMAP3111       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
HNMAP1716       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
HNMAP1697       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
HMAS82384       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
HNMAP1697       AATTCGAAGC CGGTATCTCC AAGGACGGTC AAACTCGTGA ACATGCTCTT CTCGCTTTCA CTCTCGGTGT CCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR3879        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR9832        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR9837        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR10727       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR10194       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR7489        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR10513       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR3879        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
HNMAP1339       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CTCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR9620        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR7643        AATTCGAAGC CGGTATCTCC AAGGACGGTC AAACTCGTGA ACATGCTCTT TTCGCTTTCA CTCTCGGTGT CCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR7684        AATTCGAAGC CGGTATCTCC AAGGACGGTC AAACTCGTGA ACATGCTCTT TTCGCTTTCA CTCTCGGTGT CCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR9836        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR9837        AATTCGAAGC CGGTATCTCC AAGGACGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR3889        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR9834        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR9832        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
NWCKNW_1        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
NWC09535        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
HNMAP3140       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR3885        AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
HNMAP3149       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
BPI22628        AATTCGAAGC CGGTATCTCC AAAGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
HNMAP3201       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
HMAS52894       AATTCGAAGC CGGTATCTCT AAGGATGGTC AAACTCGTGA ACATGCTCTC CTTGCCTTCA CTCTCGGTGT CCGTCAACTT ATCGTGGCCA TCAACAAGAT
NWC09234        AATTTGAAGC CGGTATCTCC AAGGACGGTC AAACTCGTGA ACATGCTCTT CTTGCCTTCA CTCTCGGTGT CCGTCAACTT ATCGTGGCCA TCAACAAGAT
HMAS62584       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACATGCTCTT CTTGCCTTCA CTCTCGGTGT CCGTCAACTT ATTGTGGCCA TCAACAAGAT
HNMAP3181       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCTTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
HNMAP3060       AATTCGAAGC CGGTATCTCC AAGGATGGTC AAACTCGTGA ACACGCTCTC CTTGCCYTCA CCCTCGGTGT TCGTCAACTT ATCGTGGCCA TCAACAAGAT
NWC06210        AATTTGAAGC CGGTATCTCC AAGGACGGTC AAACTCGTGA ACATGCTCTT CTTGCCTTCA CTCTCGGTGT CCGTCAACTT ATCGTGGCCA TCAACAAGAT
TSHR7635        AATTTGAAGC CGGTATCTCC AAGGACGGTC AAACTCGTGA ACATGCTCTT CTTGCCTTCA CTCTCGGTGT CCGTCAACTT ATCGTGGCCA TCAACAAGAT
HMAS52905       AATTCGAAGC CGGTATCTCC AAGGACGGCC AAACTCGTGA ACACGCTCTT CTTGCCTTCA CCCTCGGTGT CCGTCAACTT ATCGTGGCTA TCAACAAGAT

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                    305        315        325        335        345        355
EU487243        GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATACGAGGA AATTGTCAAG GAAACCT
HNMAP1710       GGACACCTGC AAGTGGTCCG AGCAGAGCCA GATACGAGGA AATTGTCAAG GAAACCT
NWC891_1        GGACACCTGC AAGTGGTCCG AGCAGAGCTA GATACGAGGA AATTGTCAAG GAAACCT
TSHR9836        GGACACCTGC AAGTGGTCCG AGCAGAGCTA AATACGAGGA AATTGTCAAG GAAACCT
HNMAP3111       GGACACCTGC AAGTGGTCCG AGCAGAGCCA GATACGAGGA AATTGTCAAG GAAACCT
HNMAP1716       GGACACCTGC AAGTGGTCCG AGCAGAGCCA GATACGAGGA AATTGTCAAG GAAACCT
HNMAP1697       GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATACGAGGA AATTGTCAAG GAAACTT
HMAS82384       GGACACCTGC AAGTGGTCCG AGCAGAGCTA GATACGAGGA ---------- -------
HNMAP1697       GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATACGAGGA AATTGTCAAG GAAACTT
TSHR3879        GGACACCTGC AAGTGGTCCG AGCAGAGCCA YATACGAGGA AATTGTCAAG GAAACCT
TSHR9832        GGACACCTGC AAGTGGTCCG AGCAGAGCCA YATACGAGGA AATTGTCAAG GAAACCT
TSHR9837        GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATA------ ---------- -------
TSHR10727       GGACACCTGC AAGTGGTCCG AGCAGAGCCA YATACGAGGA AATTGTCAAG GAAACCT
TSHR10194       GGACACCTGC AAGTGGTCCG AGCAGAG--- ---------- ---------- -------
TSHR7489        GGACACCTGC AAGTGGTCCG AGCAGAG--- ---------- ---------- -------
TSHR10513       GGACACCTGC AAGTGGTCCG AGCAGAGCCA YATACGAGGA AATTGTCAAG GAAACCT
TSHR3879        GGACACCTGC AAGTGGTCCG AGCAGAGCTA GATACGAGGA AATTGTCAAG GAAACCT
HNMAP1339       GGACACCTGC AAGTGGTCCG AGCAGAGCCA GATACGAGGA AATTGTCAAG GAAACCT
TSHR9620        GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATACGAGGA AATTGTCAAG GAAACTT
TSHR7643        GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATACGAGGA AATTGTCAAG GAAACTT
TSHR7684        GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATACGAGGA AATTGTCAAG GAAACTT
TSHR9836        GGACACCTGC AAGTGGTCCG AGCAGAGCTA GATACGAGGA AATTGTCAAG GAAACCT
TSHR9837        GGACACCTGC AAGTGGTCCG AGCAGAGCTA GATACGAGGA AATTGTCAAG GAAACCT
TSHR3889        GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATACGAGGA AATTGTCAAG GAAACTT
TSHR9834        GGACACTTGC AAGTGGTCCG AGCAGAG--- ---------- ---------- -------
TSHR9832        GGACACTTGC AAGTGGTCCG AGCAGAG--- ---------- ---------- -------
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NWCKNW_1          GGACACCTGC AAGTGGTCCG AGCAGAGCTA GATACGAGGA AATTGTCAAG GAAACCT
NWC09535          GGACACCTGC AAGTGGTCCG AGCAGAGCTA GATACGAGGA AATTGTCAAG GAAACCT
HNMAP3140         GGACACCTGC AAGTGGTCCG AGCAGAG--- ---------- ---------- -------
TSHR3885          GGACACCTGC AAGTGGTCCG AGCAGAG--- ---------- ---------- -------
HNMAP3149         GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATACGAGGA AATTGTCAAG GAAACTT
BPI22628          GGACACCTGC AAGTGGTCCG AGCAGAGCTA GATACGAGGA AATTGTCAAG GAAACCT
HNMAP3201         GGACACCTGC AAGTGGTCCG AGCAGAGCCA GATACGAGGA AATTGTCAAG GAAACCT
HMAS52894         GGACACCTGC AAGTGGTCCG AGCAGAGCCA GATACGAGGA AATCGTCAAG GAAACCT
NWC09234          GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATACGAGGA AATTGTCAAG GAAACCT
HMAS62584         GGACACCTGC AAGTGGTCCG AGCAGAGCCA GATACGAGGA AATTGTCAAG GAAACCT
HNMAP3181         GGACACCTGT AAGTGGTCCG AGCAGAGCTA GATACGAGGA AATTGTCAAG GAAACCT
HNMAP3060         GGACACCTGT AAGTGGTCCG AGCAGAGCTA GATACGAGGA AATTGTCAAG GAAACCT
NWC06210          GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATACGAGGA AATTGTCAAG GAAACCT
TSHR7635          GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATACGAGGA AATTGTCAAG GAAACCT
HMAS52905         GGACACCTGC AAGTGGTCCG AGCAGAGTCA GATACGAGGA AATTGTCAAG GAAACCT
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