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# Indication for the Presence of Mixed Modes of Sporogenesis in *Lindsaea Heterophylladryand.* (Lindsaeaceae: Pteridophyta)

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## Abstract

*Morphological studies on sporangia and spores of the hybrid fern *Lindsaeaheterophylla Dryand.* (*L. ensifolia Sw. x L. bonii Christ.*) from South India indicates the presence of mixed mode of sporogenesis with the occurrence of 8 spored sporangia during peak winter (December) and 32 spored sporangia during late winter (January). This kind of reproductive flexibility in this fern is attributed to environmental adaptation. Both morphological and reproductive flexibility in this species also proved the hybrid origin of this species. Further cytogenetical studies are required on this hybrid fern along with its parents to confirm the ploidy level of this fern, *LindsaeaheterophyllaDryand.**

**Keywords:** *Lindsaeaheterophylla*, Mixed sporogenesis, South India.

## Introduction

The largest lindsaeoid genus, *Lindsaea* (Lindsaeaceae) is with about 180 species. In PPG system of classification, the monophyletic family Lindsaeaceae, with seven distinct genera (*Lindsaea*, *Sphenomeris*, *Odontosoria*, *Osmolindsaea*, *Nesolindsaea*, *Tapeinidium* and *Xyopteris*) and 234 species, has been included under the suborder Lindsaeineae of the order Polypodiales. Of the eighteen species of *Lindsaea* from India (Fraser-Jenkins et al. 2017), seven species are in record from South India (Manickam & Irudayaraj 1992, Fraser-Jenkins et al. 2017, Benniamin & Shunmuga Sundari 2020). *Lindsaea* species are mostly small or medium sized terrestrial herbs specialized in having marginal continuous or discontinuous sori with bilippedindusia. As concluded by Lin et al. (1990) 32-spory life cycle in Lindsaeaceae is considered to be a derived character state, indicating the monophyletic origin, because 64-spory is widespread

in primitive to advanced groups of the leptosporangiate ferns, with various systematic affinities (Lin et al. 1990). The same is true in the recent PPG system of classification in which the two suborders Saccolomatineae and Lindsaeineae have been placed more or less in the middle of the phylogenetic tree of leptosporangiate ferns without affinity towards any other groups.

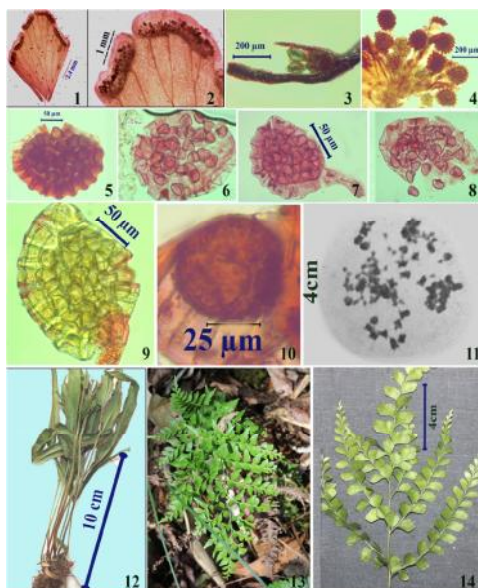
Most of the leptosporangiate ferns reproduce sexually by producing 64 haplospores from 16 spore mother celled sporangia or apogamously by producing 32 diplospores from 8 (Dopp & Manton system) or 16 (Braithwaite system) spore mother celled sporangia (Verma & Irudayaraj 2019). All the Lindsaeoid ferns operate a special type (Lindsaeoid 32 spore type) of sexual reproduction with the production of 32 haplospores in eight spore mother celled sporangia (Lin et al. 1990). The details on reproductive biology of Lindsaeoid species are almost nil except the reports of either gametophytic or sporophytic chromosome numbers only for about 60 species without any valid report for the occurrence of apogamy (<http://ccdb.tau.ac.il/>). Lin et al. (1990) have made a special effort to know the mode of reproduction in 21 species under three genera (*Sphenomeris*, *Lindsaea* and *Tapeinidium*) of Lindsaeaceae. All the 21 species are strictly with 32 normal spores in each sporangium. Exceptionally they have also observed 16-spored sporangia in two species of *Sphenomeris* (*S. clavata* & *S. deltoidea*) and 8-spored sporangia in two species of *Lindsaea* (*L. ensifolia* & *L. heterophylla*) with a note that the mode of reproduction of these four species is uncertain due to the lack of detail about the type of spores (haplospores/diplospores) and the sporogenetic process. Out of eighteen species of *Lindsaea* (Fraser-Jenkins et al. 2017) from India, only four species (*L. cultrata* (Willd.) Sw., *L. ensifolia* Sw., *L. heterophylla* Dryand. & *L. odorata* Roxb.) are cytologically known (Bir & Verma 2010) and all are gametophytic counts only with a single report of irregular meiosis in *L. heterophylla* (Manickam & Irudayaraj 1988) (Plate I, Figs. 11). All the reports for the four species of *Lindsaea* from India have been interpreted as sexual species without the confirmation of both gametophytic and sporophytic chromosome counts and also without checking the number of spores in the sporangia. The report of molecular evidence (Lehtonen 2013) for the hybrid origin of *L. heterophylla* Dryand. between the simply pinnate *L. ensifolia* Sw. and the bipinnate *L. orbiculata* var. *commixta* (Tagawa) K.U. Kramer = *Lindsaeabonii* Christ., the presence of irregular meiosis (Manickam & Irudayaraj 1988) and 8-spored sporangia (Lin et al. 1990) in *Lindsaeaheterophylla* Dryand. raise several questions on the mode of reproduction of *L. heterophylla* Dryand. which has so far been considered as a sexual species. In order to find out the mode of reproduction, spore number was checked on this species collected from the Western Ghats, Tirunelveli Hills, South India. The results of detailed observations on the number and nature of spores/tetrads in the sporangia of fresh specimens collected during peak winter (Second week of December 2019) and late winter (Fourth week of January 2020) in consequent months are presented here.

## Materials and Methods

Specimens of *Lindsaeaheterophylla* Dryand. with young, submature and mature sporophylls were collected from the Shola forest near the Forest-Guest house in Kakachi (on the way to Upper Kothayar), Tirunelveli Hills, Western Ghats, South India. The suspected simply pinnate and bipinnate parents *Lindsaeaensifolia* Sw. and *L. bonii* Christ. were also collected from the same locality. Initial observations were made on fresh specimens and for confirmation, specimens preserved in 4% Formalin and dry herbarium specimens were used. Soral, sporangia and spore morphology were observed under advanced digital compound light microscope and digital stereo microscopes of Lawrence and Mayo Company. For counting the number of spores per sporangium, the sporophylls were boiled/softened in 5-10% Potassium hydroxide solution for few minutes. Approximately 500 sporangia were observed on more than 100 microscopic slides.

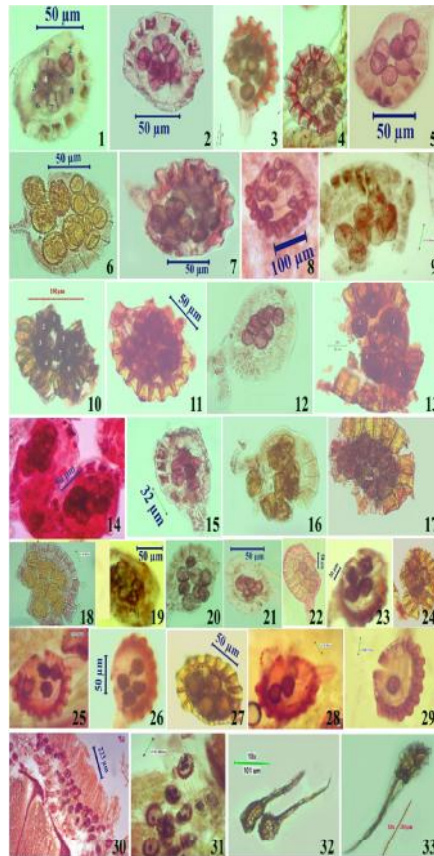
## Results and Discussion

The collected specimen *Lindsaea heterophylla* Dryand. is a terrestrial fern growing along fully shaded roadside inside the shola forest with short creeping rhizome, partially bipinnatellaminae (Plate I, Fig.13) and continuous or discontinuous, marginal indusiate sori (Plate I, Figs.1, 2). The sori are mixed type with the presence of young, mature sporangia of different stages present on the horizontal commissural vein in between bilipped indusia (Plate I, Figs.3, 4). The sori and sporangia are without any paraphyses or appendages. Sporangia are with a long, thick, multiseriate stalk and 125 x 100  $\mu\text{m}$  ovate or globose head and with 14-16 celled annulus (Plate I, Fig.7). More than 99 % sporangia are normal in shape and size with rare occurrence of aborted sporangia (Plate I, Fig. 3). Most of the sporangia are filled with different number of tetrads and/or different number of normal and aborted spores (Plate II, Figs. 1, 3, 21, 22, 28, 29, 31 & 32). Rarely some sporangia of normal shape/size are empty without any content. Normal sporangia are filled with 1, 2, 4, 6, 8 spores/tetrads or 16/32 spores. More than 58 % sporangia are filled with eight spores (Plate II, Figs.3-20) with the rare occurrence of eight tetrads (Plate II, Figs.1,2). 17%, 15% and 8% are with 4-spored (Plate II, Fig. 22-27), 32-spored (Plate I, Figs.5-9) and 2-spored (Plate II, Fig. 28), sporangia respectively. The remaining less than 2% sporangia are with 1, 6 or 16 spores (Plate II, Fig. 29,31). Rarely few sporangia are with mixture of young spores and mature tetrads with the indication for the asynchronised sporogenesis. The 32 normal spored sporangia are common (Plate I, Figs.5-9) in specimens collected during late winter (4th week of January, 2020) in contrast to 8 spored sporangia which are abundant (Plate II, Figs.3-20) in specimens collected during peak winter (2nd week of December, 2019). In the meantime, some 32 spored sporangia are present along with 8-spored sporangia, but 8-spored sporangia were not observed along with the normal 32-spored sporangia. Usually, in 8-spored sporangia the spores are somewhat larger with rough and irregular sporoderm pattern (Plate II, Fig.13), in contrast to 32-spored sporangia with uniform, normal sized, trilete, dark brown and smooth surfaced spores (Plate I, Figs.6,8,10). Most of the 2, 4 or 8-spored sporangia are with different sized spores (Plate II, Figs.23,25,28).



**Plate I.** 1-2. Sporophylls with marginal indusiate sori, 3.L.S of sorus showing upper and lower indusia, 4.Group of sporangia in a sorus, 5-9.Sporangia with 32 normal spores in each, 10. Mature trilete spore, 11. Irregular meiosis with in *Lindsaea heterophylla* Dryand.with univalent, bivalents

and multivalents indicating the presence of high number of chromosomes (After Manickam & Irudayaraj 1988), 12. Simply pinnate *Lindsaeaensifolia* Sw., 13. Partially bipinnate lamina of *L. heterophylla* Dryand. 14. Bipinnate *L. bonii* Christ.



**Plate II.** 1-2. 8 Tetrad sporangia, 3-20.8 Spored sporangia, 21.4 Tetrad sporangium, 22-27.4 Spored sporangia, 28.2 Spored sporangium, 29.1 Spored sporangium, 30. Sporangia on commissural veins, 31. Sporangia with mixed spore numbers, 32-33. Aborted sporangia.

From the present observation, it is clear that *Lindsaea heterophylla* Dryand. from the present study area shows the presence of 32 normal spored sporangia and 8-spored abnormal sporangia along with some 2, 4 and 16-spored sporangia. Abortion of sporangia and spores is very meager. The presence of 8-spored sporangia in *L. heterophylla* Dryand. has already been reported by Lin et al. (1990). Out of 21 taxa under three genera (*Sphenomeris*, *Lindsaea* & *Tapeinidium*) of Lindsaeoid ferns, 19 are with strictly 32 spored sporangia and two species of *Sphenomeris* are with 16 spored sporangia along with the exceptional occurrence of eight spored sporangia both in *L. ensifolia* and in *L. heterophylla* in addition to the normal 32 spored sporangia (Lin et al. 1990).

As Lindsaeoid type of sexual reproduction is with only 32 haplospores in each sporangium, the presence of both 32-spored and 8-spored or less than eight spored sporangia clearly indicates the mixed sporogenesis in this hybrid species. Similar type of mixed sporogenesis and mixed mode of reproduction has already been reported in the pentaploid hybrid species *Dryopteris affinis* agg., in which the presence of both abortive and normal spores has been observed in the same sporangium and in different sporangia of same individual. In the meantime, production of both sexual haplospores and apomictic diplospores has also been reported in the above pentaploid hybrid

between triploid apomictic *Dryopterisborreri* and tetraploid sexual *Dryopterisfilix-mas* (Ekrt & Koutecky 2016). Thus, in the hybrid between apomictic and sexual parents, both apomictic diplosporogenesis and sexual haplosporogenesis have been reported. Similarly the present hybrid, *LindsaeaheterophyllaDryand.* between *L. ensifolia* Sw. and *L. orbiculata* var. *commixta* (Tagawa) K.U.Kramer (= *Lindsaeabonii* Christ.), with the presence of both normal 32 haplospored sporangia and abnormal 8-spored sporangia indicates the presence of mixed mode of reproduction with both diplosporogenesis and haplosporogenesis. As the knowledge about the cytology and reproductive biology of *Lindsaeaspecies* in India is very meager, the details about ploidy level and mode of reproduction of two parents (*L. ensifolia* Sw. and *L. orbiculata* var. *commixta* (Tagawa) K.U.Kramer) of the hybrid *LindsaeaheterophyllaDryand.* is uncertain. All the cytological reports of the common parent *L. ensifolia* Sw. have been reported as tetraploid sexual species and there is no cytological report for another parent *L. orbiculata* var. *commixta* (Tagawa) K.U.Kramer(*L.bonii* Christ.) from India. *Lindsaeaorbiculata* var. *commixta* from Japan has been proved to be of hexaploid sexual with  $n=150$  and  $2n = 300$  (Lin et al. 1990).

Commonly the apogamous species like *Pterisbiaurita* L., *Dryopterisjuxtaposita* Christ. etc. are triploid in nature (Manickam & Irudayaraj 1988) originated by hybridization between diploid and tetraploid sexual parents. Occasionally some apomictic species are pentaploids (*Diplaziumtravancoricum* Beddome) as a result of crossing between tetraploid and hexaploidsexual parents. The hybrid, *Lindsaeaheterophylla* Dryand. of the present study might have originated by the cross between the two parental species *L. ensifolia*Sw. and *L. orbiculata* var. *commixta* (Tagawa) K.U.Kramer (*L.bonii* Christ.) with different higher-ploidy levels.

In general, most of the apomictic ferns produce both normal 32 diplospores in 8 Spore Mother Celled sporangia and 64 abnormal haplospores from 16 Spore Mother Celled sporangia in different proportion. Usually most of the leptosporangiate ferns produce 64 haplospores in sexual mode of reproduction and some can produce 32 diplospores in apomictic mode of reproduction. On other hand, the peculiar *Lindsaeoid* ferns can produce only 32 haplospores from 8 Spore Mother Celled sporangia in sexual reproduction and there is no valid evidence for apogamy. But the hybrid species taken for the present study, *Lindsaeaheterophylla* Dryand. produces 32 haplospores through sexual pathway and exceptionally produces 16, 8 and 4 diplospores through apomictic pathway of reproduction. Thus, it is concluded that the present interspecific hybrid *Lindsaeaheterophylla* Dryand.is with mixed type of sporogenesis with the formation of majority of 32 haplospored sporangia and 8 diplospored sporangia along with 4 or 2spored sporangia also. The ploidy variation and the fertility of different types of spores of this hybrid *Lindsaeaheterophylla* Dryand. have yet to be confirmed by modern techniques like Fluorescent flow cytometry. In the meantime, it is yet to be confirmed that whether the 8 spores are with 8 single haploid or diploid spores or with group of haploid or diploid spores. The later condition i.e. occurrence of group of spores as single unit is called as "Synaptospory" (Kramer 1977). Moreover in the present study, it has been observed that the 8-spored sporangia are dominant during the peak of winter season and 32-spored sporangia are dominant in the late winter season.

The occurrence of 8 spored sporangia during the peak winter season raises a question on the influence of cold stress on sporogenesis. There are large number of reports on the interruption of microsporogenesis in angiosperms by cold stress leading to total male sterility (Oliver et al. 2005; Sharma & Nayyar 2014; Liu et al. 2017). But in the present hybrid fern *Lindsaeaheterophylla* Dryand., some kind of adaptive reproductive pathway is followed during the peak winter by producing 8 spores per sporangium, instead of 32 spores, and by retaining them within the sporangium as a whole in the form of synaptospore until the favourable condition arise. Spore maturation and release are highly correlated with the climate factors. Spore release is related to

temperature and dryness. Some ferns postpone their spore release as they grow at higher elevation, where the temperature is lower but the humidity is higher than the lower elevation (Arosae et al. 2009). The correlations between spore maturation/release and annual mean temperature/annual mean precipitation are positively significant (Lee et al. 2016). So, it is a kind of environmental adaptation of this fern by reproductive flexibility depend on seasonal variation. The same kind of seasonal wise reproductive flexibility has already been reported in the common species *Pteris vittata* L. (Verma & Irudayaraj 2019). It is important to mention that, Lindsaeoid ferns with 32 spored Lindsaeoid type of sexual reproduction are not suitable for typical temperate climate with the evidence that none of the Lindsaeoid ferns is present in the Western Himalayas (Fraser-Jenkins et al. 2017, Benniamin & Shunmuga Sundari 2020) with temperate climate. Morphological plasticity and flexibility has also been reported in this species. *L. heterophylla* Dryand. is a highly plastic and highly variable species from plants with less lobed pinnae (towards *L. ensifolia* Sw.) to plants with larger segments, and some apical ones fused together and others becoming tall plants with smaller, very separate segments (similar to the type of *L. cuneata* Willd.) (Fraser-Jenkins 2017). Kramer (1971, 1972) has also described its continuous variation in venation from all free to mostly anastomosing veins. Variation in pinnule-morphology and in venation is also evident in plants from China (<http://www.efloras.org/>). Now it is very clear that all the above morphological and reproductive plasticity are due to the hybridization between one parent with simply pinnate lamina (Plate I, Fig.12) and copiously anastomosing veined pinnae (*L. ensifolia* Sw.) and another parent with bipinnate lamina (Plate I, Fig.14) and free veined pinnae (*L. bonii* Christ.) as evidenced from molecular study in which *L. heterophylla* is very close to both the above parents in the cladogram (Lehtonen 2013). The stomatal size (area) is minimum ( $1112 \mu\text{m}^2$ ) in *L. ensifolia* Sw., maximum ( $1494 \mu\text{m}^2$ ) in *L. bonii* Christ. and intermediate ( $1410 \mu\text{m}^2$ ) in the hybrid *L. heterophylla* Dryand. There are several problems to find out the correct parents for this interspecific hybrid due to the presence of incomplete and doubtful reports on cytology. Both the parents and the hybrid are present in India, Sri Lanka, China, Japan, Cambodia, Malaysia,

**Table 1: Cytology of the Hybrid *Lindsaea heterophylla* Dryand. and its parents, *L. ensifolia* Sw. and *L. bonii* Christ**

| Cytology                               |       | Country   | Reference  | Remark                                   |
|--|-------|-----------|--|--|
| (n)                                    | (2n)  |           |  |  |
| <b><i>L. Lindsaeaensifolia</i> Sw.</b> |       |           |  |  |
| 86                                     | -     | India     | Manickam & Irudayaraj (1988)   |  |
| 87                                     | -     | India     | Abraham et al. (1962), Mahabale & Kamble (1981), Irudayaraj & Manickam (1987), Irudayaraj (1998) | n=86-88<br>(4x Sexual, India, Sri Lanka) |
| 88                                     | -     | India     | Sankariammal (1990)  |  |
| -                                      | c.174 | India     | Abraham et al.(1962)   | n=47 (2x Sexual, Australia)              |
| -                                      | c.174 | Sri Lanka | Manton & Sledge (1954)   |  |
| 88                                     | -     | Sri Lanka | Manton & Sledge (1954)   |  |



|   |        |           |                                   |   |
|---|--------|-----------|-----------------------------------|---|
| -   | c. 130 | China     | Lin, Iwatsuki & Kato(1996)        | 2n=c.130 (3x? China - Uncertain),<br>2n=c.174<br>(4x Sexual, India & Sri Lanka),<br>2n= c.176<br>(4x Sexual, China).                                      |
| -   | c.176  | China     | Lin & Iwatsuki (1996)             |   |
| c.47  | -      | Australia | Tindale (2002)                    |   |
| <b>2. <i>Lindsaeaorbiculata</i> var. <i>commixta</i> (Tagawa) K.U.Kramer (=L. <i>bonii</i> Christ.)</b> |        |           |                                   |   |
| -   | 204    | Japan     | Nakato (1990)                     | Tetraploidsexual ? based on<br>x=50   |
| c.130   | -      | Japan     | Mitui (1976)                      | Hexaploidsexual ? based on<br>x=45  |
| c.150   | c.300  | Japan     | Lin et al. (1990)                 | Hexaploid sexual based on<br>x=50   |
| <b>3. <i>Lindsaea heterophylla</i> Dryand (L. <i>ensifolia</i> Sw. xL. <i>bonii</i> Christ.)</b>        |        |           |                                   |   |
| 86  | -      | India     | Kuriachan & Ninan (1976)          | Regular bivalents is doubtful in this hybrid.   |
| Irregular meiosis   | -      | India     | Manickam & Irudayaraj (1988)      | The only report of irregular meiosis in this hybrid. Photomicrograph is with mixture of univalents, trivalents and multivalents with a total of 2n=c. 220 |
| 90  | -      | India     | Sankariammal & Bhavanandan (1991) | Regular bivalents is doubtful in this hybrid  |
| -   | c.120  | China     | Lin & Iwatsuki(1996)              | 3x ??? Uncertain  |
| -   | c.130  | China     | Lin & Iwatsuki(1996)              |   |
| 92  | -      | India     | Vijayakanthet al. (2018)          | Photomicrograph given is with the mixture of bivalents, univalent and multivalents.   |

Philippines, Thailand, Taiwan, Vietnam (Fraser-Jenkins et al. 2017). But from none of the above countries cytological reports are available for both the parents and the hybrid. Cytological reports for one parent (*L. ensifolia* Sw.) and for the hybrid (*L. heterophylla* Dryand.) are available from India and China only (Table I). In general, the parent *L. ensifolia* Sw. is with three cytotypes (2x, 3x & 4x) from India, Sri Lanka, China and another parent *L. bonii* Christ. is with two cytotypes (4x, 6x) from Japan only. So it is very difficult to find out the suitable cytotype of both the parents for the hybrid *L. heterophylla* Dryand. Thus it is very difficult to ascertain the ploidy level of the parents and the hybrid with the availability of incomplete data along with several doubtful reports. At this uncertainty condition, the present finding of mixed sporogenesis in the hybrid *L. heterophylla* Dryand. may give some ideas for further research on reproductive biology based on cytogenetical studies.

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