STUDIES IN THE GLOSSOPTERIS FLORA OF INDIA—
32. ON THE GENUS GANGAMOPTERIS McCoy

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ABSTRACT

The genus Gangamopteris McCoy is an important constituent of the Glossopteris flora. Several views have been expressed in past for its specific delimitation but none of them have so far been proved to be very satisfactory. In the present paper some suggestions are proposed for the specific delimitation of the genus on the basis of external morphology of leaves.

INTRODUCTION

Gangamopteris McCoy is an important member of the Glossopterideae. It was first described by McCoy (1847) from Australia. Since then a large number of leaves have been assigned to it from various Lower Gondwana formations of the Southern hemisphere. In recent years Srivastava (1956), Höeg & Bose (1960) and Maithy (1965) have described the epidermal structure. Gangamopteris fructifications have been described by Plumstead (1960, 1963) from South Africa, viz. Ottokaria duriaica, Ottokaria transvaalensis and Vannus gondwanensis. Ottokaria type of fructification are also known to be attached to Glossopteris indica. Plumstead (1958: 65) opined that Ottokaria may be the fructification of both the genera, Gangamopteris and Glossopteris.

So far very little is known about the habit and growth of Gangamopteris. Some clusters of leaves belonging to G. obovata and G. indica were recorded from Wankie, South Rhodesia, by Plumstead (1958a) and on the basis of these specimens, she concluded that they were mainly deciduous, woody plants of arborescent habit with leaves growing at short shoots, in clusters at fairly wide intervals from the woody stems.

DISTRIBUTION OF GANGAMOPTERIS

Gangamopteris is widely known from India (Feistmantel, 1879, 1881, 1882, 1886; Seward, 1907), Australia (Feistmantel, 1890a, b; McCoy, 1847; Arber, 1902; Walkom, 1922, 1938; Teicheret, 1943), South Africa (Seward et al., 1908; Du Toit, 1927, 1929; Plumstead, 1956, 1958), Belgian Congo (Höeg & Bose, 1960), Angola (Krishnan, 1960); Rhodesia & Nyassaland (Lacey, 1961); Brazil (White, 1908; Carruthers, 1869; Lundqvist, 1919; Dolianiti, 1954a, b); Argentina (Archangelsky, 1957, 1958) and Antarctica (Plumstead, 1962). Some species of Gangamopteris have been described from Angara flora (Zalessky, 1918). The assignment of these leaves to Gangamopteris is not free from doubts, because so far the relationships between the two flora, i.e. Angara flora and Glossopteris flora is not well established.

Gangamopteris is probably the oldest member of the Glossopteris flora and in every country is first to appear, sometimes alone or with Glossopteris. In comparison to its wide geographical distribution the vertical range is limited, therefore, the genus is of considerable stratigraphical importance. The genus is more common in the Lower Permian and is rare or absent in the Upper Permian. In India Gangamopteris is dominant in Talchirs and Karharbaris, whereas in Damudas it is represented by only one definite species. From Raniganj stage about six species of Gangamopteris are known but the identity of some seems doubtful. In Australia it has been recorded along with marine fossils in the Lower Marine series about 2000 feet above its base and it reaches to the maximum development in the Lower Series of Coal Measures and gradually declines during the Upper Coal Measures. In Africa it occurs both in the Dwyka and Ecca series of the Karoo system and had been found by Leslie (1921) at Vereening below the Dwyka Tillite. Above the Tillite it is is common in Middle Ecca, but not higher. It is found both in Brazil, Argentina and Antarctica from beds regarded as Lower Permian in age.

Gangamopteris was first described by McCoy (1847) from New South Wales as
Cycloptenis angustifolia for a leaf showing netted venation as in Glossopteris, but without a midrib. This specimen was referred to Cycloptenis with some hesitation by McCoy but at the same time he thought that the difference in the venation is of the generic value. Later McCoy (1860) examined a large number of specimens from the Bacchus-Mars Sandstone, Victoria and came to the conclusion that the anastomosing of veins and the absence of a midrib are constant feature and hence, he proposed the generic name Gangamopteris.

The original diagnosis given by McCoy was later modified by Feistmantel (1879) and Arber (1905). In recent years the epidermal structure has been described by Srivastava (1956), Heg & Bose (1960) and Maithy (1965). Thus, in view of the above addition to our knowledge the genus Gangamopteris is redefined as below:

"Leaves simple, entire, symmetrical or asymmetrical; linear, lanceolate, elliptical, spatulate or obovate in shape; apex broadly rounded, obtuse, acute, acuminate or mucronate; base petiolate or contracted. Midrib absent; median region occupied by subparallel veins with anastomoses of elongate or hexagonal outline. Secondary veins arise from median veins by repeated dichotomy, arched, bifurcating and anastomosing network."

"Cuticle differentiated into two surfaces, stomata present on one or both the surfaces, stomatal apparatus haplocheilic, monocyclic, or dicyclic, distribution and orientation of stomata regular to irregular, papillae present or absent."

The genus Gangamopteris is closely allied to Glossopteris. Gangamopteris differs from Glossopteris in that it has no midrib and the veins are either radiating from lower median portion of the leaf or forming a group of almost parallel anastomosing veins occupying the position of a midrib. In past several workers have expressed doubts on the generic status of Gangamopteris. Seward (1910: 513) opined "the presence or absence of a midrib is not in itself a character of real taxonomic importance." Arber (1902) on the basis of the discovery of 'Scale leaves' of Glossopteris expressed his opinion "that the midrib is no longer a necessary characteristic of that genus" and he further stated, "it is, therefore, in the absence of full knowledge of the fructification of the either type, extremely doubtful whether the genus Gangamopteris should not be merged in Glossopteris". This has also been supported by Walkom (1922). Surname & Srivastava (1956) favoured this view on the basis of the cuticular studies and stated "it is thus evident that Glossopteris, Gangamopteris and Paldeovillaria cannot be regarded as natural genera" and supported further splitting of these genera. However, the separate retention of Gangamopteris from Glossopteris seems to be essential because in only few cases the specimens with a fructification or cuticle are found.

In certain case the generic identification between Glossopteris and Gangamopteris becomes difficult. Several of the Glossopteris specimens with striations on their midrib superficially appear to belong to Gangamopteris. Therefore, one must take due precaution for generic identification. It must be worth while to mention here that most of the Gangamopteris species described earlier from the Raniganj stage seems to be Glossopteris.

**PROBLEM OF SPECIFIC DELIMITATION**

The leaves of Gangamopteris are known to be commonly preserved in the form of impressions and sometimes as compressions. In the former case the study is limited to externally recognizable characters of the impressions. While in the latter case, in addition to the external morphological study, there is a scope for cuticular study. Till a decade or two back the specific identification and comparison were in a large majority of cases based solely on external features of the frond. In recent years the general trend has largely shifted on the epidermal studies and the results have proved that the epidermal structures are a more constant and reliable character for the proper identification and circumscription of a species. In this connection Sahni as early as 1923 (p. 277) has stated that "a special advantage of such studies is that, once we have learnt to associate certain epidermal character with certain species, it would thenceforth be easy to identify even small fragments which may otherwise be unrecognizable". It is generally presumed that the leaves with similar morphological feature will yield one type of cuticles. But cuticular evidence of the Glossopteridean remains have shown that
leaves resembling superficially differ in their epidermal structures, e.g. *Glossopteris indica*. Schimper-type of leaves have yielded three different types of cuticles, viz., *Glossopteris indica* Zeiller (1896), *Glossopteris arberii* Srivastava (1956) and *Glossopteris jamotii* Hegg & Bose (1960). On the other hand leaves with different morphological features viz., *Palaeovittaria kurzi* and *Glossopteris intermittens* have similar cuticles. Thus, these cuticular evidences leads us to the conclusion that these homogenous looking leaves are heterogenous in nature and their number of species is comparatively much more larger than originally thought to be on external morphological character. This is also supported by the recent discoveries of fructifications (Plumstead, 1956). The study of the morphology of dispersed spores from the Lower Gandwans of India (Bharadwaj, 1960) also supports this view.

Thus, these evidences raises the problem for specific identification of those similar looking leaves, one with a cuticle and the other without a cuticle? The most suitable course for the present seems to describe the leaves with a cuticle and without cuticle under two different specific names. In the latter the circumscriptio of species will be mainly based upon the external morphological characters, i.e. impression species whereas in the former the cuticular structure will form the main basis for specific identifications, i.e., cuticular species. Although, this method of approach might result into a nomenclatural duplication, but it will nevertheless resolve much confusion between the cuticular and non-cuticular forms.

The occurrences of *Gangamopteris* leaves in the form of impressions are in such a large number that one cannot neglect their study for stratigraphical purpose. Several views have been expressed in past for specific delimitation, but till now none seems to be very satisfactory. McCoy (1874) and Feistmantel (1879, 1881, 1890) instituted number of species from Australia and India on the basis of the leaf shape and venation. However, Arber (1905) adopted a broad definition of species and regarded many of the species described by McCoy and Feistmantel irrelevant and merged them together under one species. This broad-based concept of specific delimitation was later followed by Seward (1910) and supported by Walkom (1922). The recent evidences of cuticular studies of Glossopteridae and related remains go against Arber's contention and support more to the liberal species concept of Feistmantel. The studies of Lele & Maithy (1964) on the genus *Neoggerathopsis* has amply shown that the combination of the external morphological features, i.e. Leaf shape, apex, base and venations can more advantageously be used for specific delimitation. This has also been supported by the epidermal studies of these leaves.

On the basis of the above evidences a critical morphological study of several hundred *Gangamopteris* leaves from the Talchir— Karharbari beds was undertaken to evaluate a system for specific delimitation. From an analysis of this study it seems that the combination of the following characters can be applied with greater reliance for the specific circumscription.

1. Shape:

   a. Symmetry: Leaves either bilaterally symmetrical (*G. major*, *G. cyclopteroides*) or asymmetrical (*G. angustifolia*, *G. buriadica*, var. acrodeltoides).

   b. Outline of leaf: Various types of outlines are known among *Gangamopteris* leaves. They may be linear, lanceolate, elliptical, spatulate or obovate.

2. Apex:

   The apex seems to be an important feature and great reliance on this character can be stressed for specific delimitation. The apex may be acute, acuminate, obtuse, broadly rounded and mucronate.

3. Base:

   The base of the leaves may be petiolate or contracted. This can also be used in combinations with other characters.

4. Venation:

   a. Median veins

      (i) Median region has a prominent groove (*G. stephansoni* Plumstead).

      (ii) Median region occupied by sub-parallel prominent veins from base to apex forming elongate rectangular meshes (*G. kashmirensis* Seward)

      (iii) Median region occupied by sub-parallel veins, prominent at the
base and gradually becomes evanescent at the apex (G. cyclopteroides Feistm.).

(iv) Median region occupied by obscure or diffused veins (G. major Feistm.).

(v) Median region occupied by polygonal or hexagonal meshes from base to apex (G. obliqua McCoy).

b. Secondary veins:

(i) Course of veins: The courses of veins depend upon the angle of emergence. The veins are erect-straight (G. buria diea), erect-oblique (G. angustifolia) or arched (G. cyclopteroides). Secondary veins may be straight or flexuous.

(ii) Meshes: The forms of meshes are trapezoid, rectangular, hexagonal or polygonal. The size of the meshes may be more or less uniform, longer and broad near the median region and narrow and short near the margins or the formations of meshes are rare. The enclosed mesh area are more or less smooth or may have fibers like structures. In addition to this, statistical datas can be also taken into consideration, viz, density of veins, angle of emergence of secondary veins and the maximum width region of the leaf from apex.

Taking into consideration the above morphological characters, the Gangamopteris leaves published by early workers needs redefinition. A number of species appears to be synonymous while several others appear to be morphologically distinct. Feistmantel (1879, 1886) instituted a number of varieties of G. cyclopteroides from the Lower Gondwana formations of India. A careful examination shows that most of them are superfluous (viz. G. cyclopteroides var. subauriculata, G. cyclopteroides var. acrolata) except one viz. G. cyclopteroides var. acuminata, which should be considered as a distinct species due to the acute apex and ± erect veins. Gangamopteris buriadia var. acrodelloides Dolianiti (1954) should also be separated under a new species. The species is characterized by asymmetrical shape and deltoid apex whereas Gangamopteris buria diea Feistmantel (1879) has truncate apex. Feistmantel (1879) described under Gangamopteris major two types of leaves. One rhomboidal in shape with ± acute apex (Pl. 14, Fig. 3) and the other spathulate in shape with obtuse apex (Pl. 26, Fig. 2). On the basis of recent morphological evidences the latter type of specimens needs a separation from G. major under a distinct specific name.

Several views have been expressed in past and in recent years to consider Gangamopteris cyclopteroides Feistmantel (1879) as synonymous to G. obovata (Carr.) White (1908) and the latter name has also been used by several workers in view of priority. The recent morphological studies show that the two species should be kept separate. G. obovata (Carr.) White has elongate obovate shape and ± broadly rounded apex whereas G. cyclopteroides has lanceolate shape and obtuse apex. In the former the median veins are ± diffused at the base whereas in the latter it is prominent at the base and evanescent at the apex.

The survey of past literatures on Gangamopteris shows that new species have been established, even though the leaves are incomplete. As a result of which in some cases the apical and the basal portion of the same leaf have been designated under two distinct specific names. Feistmantel described two species of Gangamopteris from the Permian beds of Tasmania, viz. G. conspicua and G. mersyensis. The former species is based on the apical part whereas the later on the basal part. These two species which are based on two different portions of the leaves appears to be synonymous in view of the close similarity in their venation. Thus, in view of this fact for further morphological establishment of new species one should take only complete specimens under consideration and due care should be taken for incomplete leaves.

So far about twenty species of Gangamopteris are known from the Lower Gondwana of Southern hemisphere. Recent cuticular studies and records of fructification have pointed that these number of genera amongst these homogenous forms are far greater than what it was originally thought to be. In the present study an attempt has been made whether it is possible to segregate further the leaves of Gangamopteris in groups on the basis of morphology. A critical analysis of the various characters of
Gangamopteris leaves present that it could be further splitted into two main groups and several sub-groups. A scheme for the classification and synopsis for identification is presented here. This scheme is tentative and can be modified when more details are available.

Group I: Median region occupied by subparallel veins forming elongate-rectangular meshes. Leaves linear, lanceolate, elliptical or spathulate in shape.

A. Leaf Asymmetrical:
   Linear shape, acute apex.
   1. G. angustifolia McCoy
      Lanceolate—spathulate shape, apical portion deltoid, apex acuminate.
   2. G. buriadica var. acrodeltoides Dolianiti

B. Leaf Symmetrical:
   (i) Leaf has a distinct median groove rounded-oval shape, apex obtuse.
   3. G. stephensoni Plumstead
   (ii) Median region occupied by subparallel veins. Median veins prominent from base to apex. Lanceolate shape, acute apex.
   4. G. kashmirensis Seward
      Median veins prominent at the base and gradually get diffused.
      a. Fibres present in between the meshes. Lanceolate shape, obtuse apex, secondary veins flexuosus.
   5. G. fibrosa Maithy
      b. Fibres absent in between the meshes.
      (i) Apex pointed mucronate
         a. Elliptical shape, veins course oblique forming elongate rectangular meshes.
   6. G. mucronata Maithy
      b. Lanceolate shape, veins erect oblique forming rectangular meshes.
   7. G. mosesi Dolianiti
      (ii) Apex acuminate
         a. Lanceolate shape.
         Secondary veins forming meshes broad and elongate near median region.
   8. G. cyclopteroides var. acuminata Feistm.
      Secondary veins forming polygonal meshes of more or less uniform size.
   9. G. conspicua Feistm.
      (Syn. G. mersysensis Feistm.)
      b. Spathulate shape
      Secondary veins arched forming elongate rectangular meshes.
   10. G. spathulata McCoy
       Secondary veins erect, forming elongate rectangular meshes.
   11. G. major Feistmantel
      (iii) Apex obtuse
         a. Lanceolate shape
   12. G. cyclopteroides Feistmantel
      b. Elongate obovate shape
   13. G. obovata (Carr.) White
      (iv) Apex broadly rounded
         a. Spathulate shape
   14. G. ? major (Feistm.) Maithy
      b. Obovate shape
   15. G. clarkeana Feistmantel
      (v) Apex truncated
         a. Lanceolate shape
   16. G. buriadica Feistm.
   Group II. Median region is occupied by veins more or less hexagonal in shape. Leaves mostly obovate in shape.
      (i) Apex broadly rounded
         a. Oblong shape
   17. G. castellanosoi Archangelsky
      b. Obovate shape
   18. G. intermedia Maithy
      (ii) Apex acute
         a. Obovate shape
   19. G. obliqua McCoy
REFERENCES


