

Evolution of *Sida* L. (*Malvaceæ*) in West Africa

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Summary : The evolution and interrelationship between the different species of *Sida* L. in West Africa were considered. It was shown that the chromosome numbers and structure could be a contributive factor to the evolution of the genus. Other important factors which could have contributed to the high degree of variation and evolution of *Sida* are ecogeographic distribution, reproductive systems, gene recombination and natural selection through hybridization.

Résumé : L'évolution et les interrelations entre les différentes espèces de *Sida* L. d'Afrique Occidentale sont considérées. On savait que le nombre et la structure des chromosomes pouvaient être un facteur de l'évolution du genre. D'autres facteurs importants qui peuvent avoir contribué à faire parvenir le genre *Sida* à un haut niveau de variation et d'évolution sont : la répartition écologique et géographique, les systèmes de reproduction, les recombinaisons génétiques et la sélection naturelle par hybridation.

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INTRODUCTION

Sida L. is one of the most variable and widely distributed genera of the family *Malvaceæ* in West Africa. A detailed survey of *Sida* specimens in a number of herbaria in Africa, Europe and North America showed that the genus is mainly distributed in the tropical and warmer regions of the World. Similar observations have also been reported by several plant researchers like OLIVER (1868), HOOKER (1872), GLEASON (1952) and HUTCHINSON (1967).

The long list of synonyms recorded in Index Kewensis and in my taxonomic papers (UGBOROGHO, 1980a, b & c) confirm the complex nature of this genus. HOOKER (1872), in his Flora of British India, reported 80 species. GLEASON (1952) reported 150 species which he described as natives of the tropical and warm-temperate zones of both hemispheres. According to HUTCHINSON (1967), there are 250 species of *Sida* distributed in America and warmer regions of both hemispheres. HUTCHINSON & DALZIEL (1958) reported eleven species of this critical genus for West Africa. According to UGBOROGHO (1980a, b & c), all the eleven species reported by HUTCHINSON & DALZIEL are widely distributed in Nigeria.

TABLE I : WEST AFRICAN COUNTRIES WHERE SIDA SPECIES WERE COLLECTED

Country Species	Sénégal	Gambia	Guinea	Sierra Leone	Liberia	Ivory Coast	Ghana	Togo	Bénin	Nigeria	Cameroun
1. <i>linifolia</i>	+ ●	+ ●	+ ●	+ ●	+ ●	+ ●	+ ●	●	+ ●	+ ●	
2. <i>cordifolia</i>	+ ●		+ ●	+ ●	+	●	+ ●	+ ●	+ ●	+ ●	●
3. <i>pilosa</i>				+ ●	+ ●	+ ●	+ ●	●	●	+ ●	+ ●
4. <i>wrens</i>	+ ●			+ ●	●	●	+ ●	+ ●		+ ●	●
5. <i>spinosa</i>	+ ●	+ ●		+ ●			+ ●			+ ●	
6. <i>ovata</i>	+ ●					+				+ ●	
7. <i>rhombifolia</i> complex			+ ●	+ ●	+ ●		+ ●	+		+ ●	+ ●
8. <i>scabrida</i>				+ ●	+					+ ●	
9. <i>acuta</i> complex			●	+ ●	+	●	+ ●	+		+ ●	+ ●
10. <i>garckeana</i>				+	+					+ ●	

+ : Cited collections in Flora of West Tropical Africa by Hutchinson & Dalziel, 1958.

● : Collections studied by the Author at (K).

MATERIALS AND METHODS

In order to appreciate the complexity of this critical genus and thus suggest its possible origin and, or, the relationship between the species, all the specimens deposited in the following herbaria were studied : Ahmadu Bello University Herbarium, Zaria, Nigeria (HABU) ; BM ; CGE ; FHI ; Lagos University Herbarium, Lagos, Nigeria (LUH) ; MANCH ; OXF ; K ; LIV ; LIVU ; UCI ; IFE ; UNN.

Some varieties of the eleven *Sida* species in West Africa were also sent through the Keeper of the Herbarium of British Museum, or directly to me from the following herbaria : PH ; FBC ; G-DC ; CAL ; NAI ; L ; SOTON ; MHU ; HAW ; KHU ; FTG. Type specimens or phototypes were also studied at or received from the following herbaria : B ; C ; U ; MA ; LINN ; P ; LD.

Morphological data were obtained from both live plants and herbarium specimens. Observations on mitotic and meiotic chromosomes as well as hybridization experiments were carried out on live specimens from different parts of Nigeria and a few other countries including Sierra Leone and United States of America.

RESULTS AND DISCUSSION

As the results of this investigation reveal, *Sida* is wide spread in West Africa (Table 1). UGBOROGHO's (1978 ; 1980a-d) detailed studies on the biogeography and taxonomy of the species of *Sida* in Nigeria showed that the plants are widely distributed in that country. His observations which confirmed the high degree of variation exhibited by this genus in Nigeria is no doubt linked up with the presence of a large gene pool in the complex.

According to LÖVE & LÖVE (1966), investigation in biogeography in general and studies on the distribution of species in particular form one of the main pillars on which the theory of evolution rests. UGBOROGHO (1977) showed the importance of ecogeographic studies in the evolution of *Cerastium arvense* L. in North America. According to UGBOROGHO (1977), "in North America, the diploid fared better and simply moved up and down the continent with the changing climate. However, subsequent development of forest on the eastern side of the continent, and on the main mountain ranges of the West and Centre, has broken the distribution into a large series of isolated and often very small populations". It could therefore be stated that distribution of *Sida* species into various ecological habitats in West Africa has contributed largely to the evolution of the genus which probably attained its distribution in that part of Africa during the early tertiary period.

Cytologically, *Sida* has four ploidy levels of chromosome complements in West Africa. These are $2n = 14, 28, 32$ and 56 . The chromosomes are of about the same size in all the taxa except in *S. pilosa* where there is an appreciable variation in chromosome size. According to STEBBINS (1950), the commonest type of change in chromosome number found in the higher plants is polyploidy. This type of change is an irreversible one, so that in any polyploidy series, the oldest and most primitive members are those with the lowest chromosome numbers. He also stated that in many genera of higher plants, a change in chromosome number at diploid level may occur without multiplication of chromosome sets or even of whole chromosomes. Table 2 shows the summary of the cytological data of the Nigerian *Sida* species which are the representatives of all the known taxa of *Sida* in West Africa.

TABLE 2 : Summary of Cytological data of *Sida* species in Nigeria.

Taxon	Collector's No.	Origin	n	2n	×	Ploidy
1. <i>S. linifolia</i> Juss. ex Cav.	590	Calabar, Cross River state	7	14	7	Diploid
2. <i>S. cordifolia</i> L.	667	Badagry, Lagos state	14	28	7	Tetraploid
3. <i>S. pilosa</i> (Retz.) Ugbor.	663	Akoka, Lagos state	28	56	7	Octoploid
4. <i>S. urens</i> L.	493	Bauchi, Bauchi state	16	32	8	Aneuploid
5. <i>S. spinosa</i> (L.) Ugbor.	488	Zara Village, Kano state	14	28	7	Tetraploid
6. <i>S. ovata</i> Forskål	483	Nr. Gainawa Village, Kano state	14	28	7	Tetraploid
7. <i>S. rhombifolia</i> L. subsp. <i>rhombifolia</i>	357	Warri, Bendel state	7	14	7	Diploid
8. <i>S. rhombifolia</i> subsp. <i>retusa</i> (L.) Ugbor.	277	Epe, Lagos state	7	14	7	Diploid
9. <i>S. rhombifolia</i> subsp. <i>alnifolia</i> (L.) Ugbor.	179	Lagos, Lagos state	14	28	7	Tetraploid
10. <i>S. scabrida</i> Wight & Arnott	315	Badagry, Lagos state	14	28	7	Tetraploid
11. <i>S. acuta</i> Burman f. subsp. <i>acuta</i>	318	Badagry, Lagos state	14	28	7	Tetraploid
12. <i>S. acuta</i> subsp. <i>carpinifolia</i> (L. f.) Borssum Waalkes	578	Calabar, Cross River state	14	28	7	Tetraploid
13. <i>S. garcheana</i> Polak.	666	Akoka, Lagos state	14	28	7	Tetraploid

Considering the number (Fig. 1), morphology and sizes of the chromosomes in the species of *Sida* in Nigeria which are representative specimens of the species in West Africa, one could suggest that the evolution of the different taxa of this critical genus is through polyploidy, mutation of chromosomes and genes and gene recombination. The three types of polyploidy could have come to play in the evolution of this genus. The three subspecies of *S. rhombifolia* have chromosomes of about the same size and morphology (UGBOROHO, 1981). The tetraploid subspecies could have evolved from one of the diploid subspecies by autopolyploidy. *S. urens* has a mitotic chromosome number of 32. This is an increase of 4 chromosomes over the tetraploid species with $2n = 28$. Since the chromosomes are similar in size and morphology, *S. urens* could have originated from two or more tetraploid taxa with similar chromosome complements by aneuploidy. *S. pilosa*, an octoploid species, has chromosomes of about three different sizes ranging from about 1.5-3.5 μm . This is an indication that the species could have originated by allopolyploidy. In this case, hybridization and doubling of chromosomes could have involved two or more taxa with different chromosome sizes. Such taxa may probably include *S. cordifolia* with chromosome sizes of 3.0-3.5 μm , *S. spinosa* and *S. ovata* both with chromosome sizes of about 1.5-2.0 μm or any extinct species with chromosomes similar to those of the above species.

The genus *Sida* is very variable in its morphological character to such an extent that it is a taxonomic problem in West Africa as well as in several other parts of the world. This morphological variation has therefore made it difficult to trace the evolution of this genus.

From the results of the morphological investigations, the leaves have been found to be specially useful in differentiating the different taxa of *Sida*. The leaves of *Sida* show four distinct shapes — linear, cordate, rhombic and lanceolate — which are often modified by the environment (UGBOROHO, 1980e). Consequently, the thirteen taxa of *Sida* treated here have been separated basically into four groups.

The first group is made up of a single taxon, *S. linifolia*. Because of the linear shape of the leaves, this taxon can be easily separated from the other taxa. This plant could have differentiated from the rest of the taxa at the early stage of the evolution of the genus.

The taxa in the second group with cordate leaves are different from each other in chromosome number, size and morphology and also in micro-morphological features. For example, of the five taxa in this group, *S. cordifolia* ($2n = 28$) has the largest stomata (MM = 36.75) followed by *S. pilosa* ($2n = 56$) with MM = 33.00, *S. urens* ($2n = 32$) with MM = 30.66, *S. ovata* ($2n = 28$) with MM = 30.21 and *S. spinosa* ($2n = 28$) with MM = 26.55. Also while *S. pilosa*, *S. urens* and *S. spinosa* have 5 carpels per fruit, *S. ovata* has between 6 and 9 carpels per fruit and *S. cordifolia* has between 9 and 11. From these results coupled with the differences in chromosome sizes and morphology, it could be concluded that the five species did not evolve directly from the same diploid ancestors.

The third group, also made up of only one species which has been divided into three subspecies, is characterized by rhombic leaves. Though these leaves may be modified by the environment, the rhombic shape of the leaf is usually shown at one stage or another in the life history of this complex species. This is an evidence of genetic relationship. Some micro-morphological features like stomata, anthers and pollen grains — which are

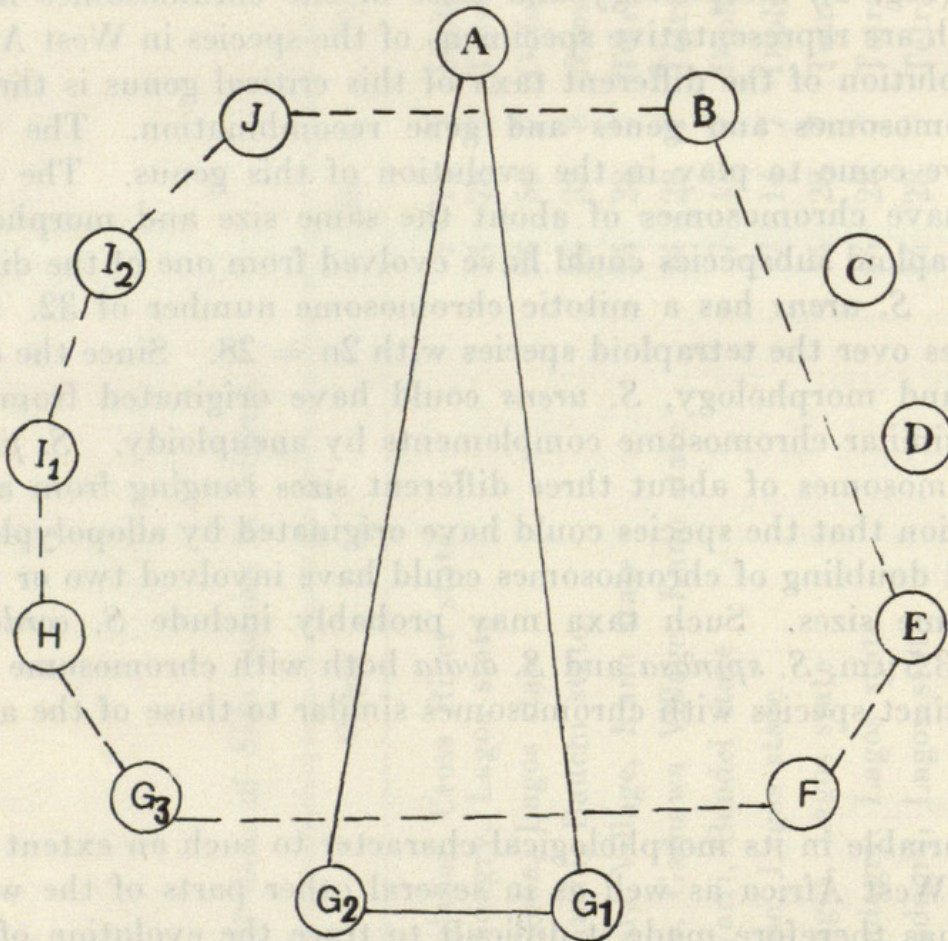


Fig. 1

CHROMOSOME NUMBERS OF THE
DIFFERENT TAXA OF SIDA

— : TAXA WITH $2n = 14$

- - : TAXA WITH $2n = 28$

C : TAXON WITH $2n = 56$

D : TAXON WITH $2n = 32$

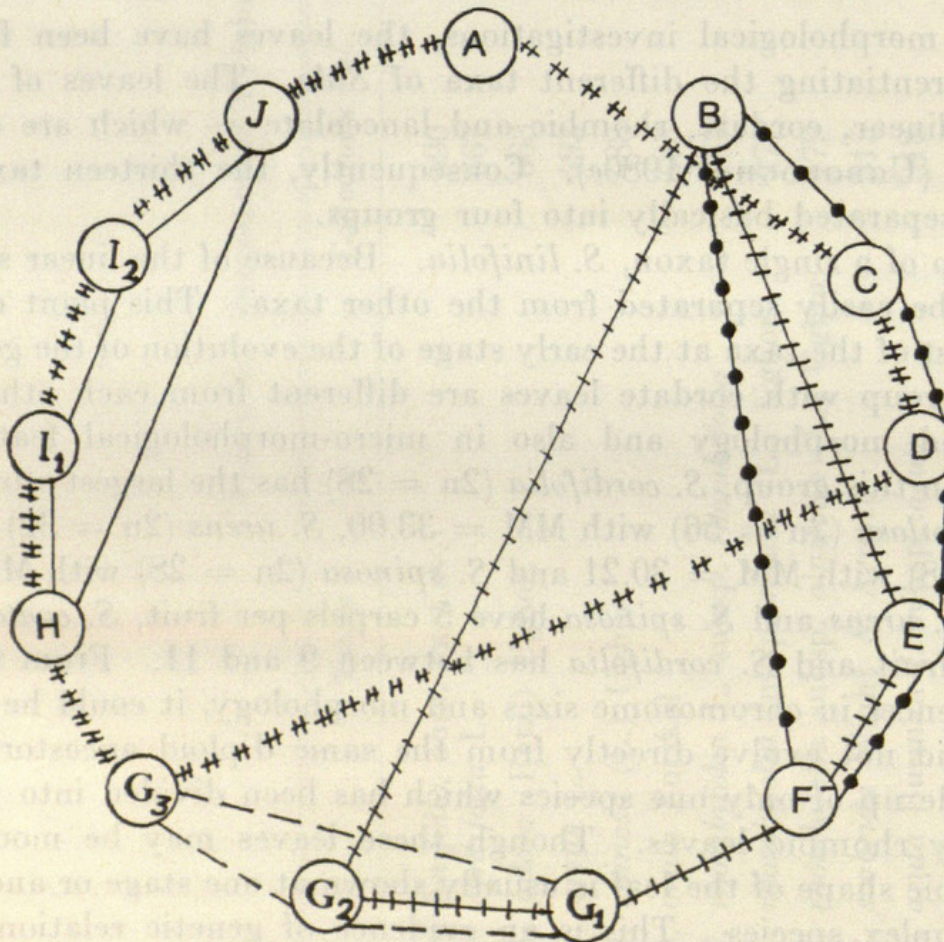


Fig. 2

MORPHOLOGICAL SIMILARITIES
AMONG THE TAXA OF SIDA WITH
RESPECT TO PUBESCENCE AND
THE SHAPES OF THEIR LEAVES

● ● ● ● : TAXA WITH CORDATE
LEAVES ON THE STERILE SHOOTS

- - - : TAXA WITH MOSTLY
RHOMBIC LEAVES ON THE STERILE
SHOOTS

— : TAXA WITH BROADLY
LANCEOLATE TO OVATE-LANCEOLATE
LEAVES ON THE STERILE SHOOTS

A : TAXON WITH LINEAR
LEAVES ON THE STERILE SHOOTS

++++ : LEAF MARGIN WITH
STELLATE HAIRS

: LEAF MARGIN WITH
SIMPLE HAIRS

rarely affected by the environment — are greater in size in the tetraploid forms than in the diploid plants (UGBOROGHO, 1982). These facts show that the tetraploid plant, *S. rhombifolia* subsp. *alnifolia*, could have evolved from one of the diploid subspecies, probably subsp. *retusa* by autopoloidy. Similar observations were also made by UGBOROGHO (1973) on *Cerastium arvense* complex in North America. STEBBINS (1950) also observed that the micro-morphological features of autotetraploids are often greater in dimension than those of their diploid ancestors.

In the case of allotetraploid plants, their chromosomes may be different in size and/or morphology from those of their diploid ancestors. Thus their micro-morphological features may not necessarily be bigger in size than those of their diploid ancestors. This is seen in OYEWOLE'S (1972) work on *Albucca*. According to OYEWOLE, "in the case of the West African species of *Albucca*, morphological features especially of the floral parts, are largest in the diploid species, followed by the hexaploid species, and finally by the tetraploid species. The pollen diameter also follows the same pattern, while the size of the stomata does not follow any definite pattern that could be associated with levels of polyploidy". Thus he concluded that the hexaploids have not directly evolved from the tetraploids and the known West African diploid.

The four tetraploid taxa which form group four are much closer in morphological features than the plants of group two. I therefore feel that the four taxa could have originated from closely related diploid forms.

Two other morphological characters which reveal genetic relationship within the genus are hairs and awns. The margins of the leaves of eight taxa possess simple hairs, while the remaining five taxa have stellate hairs on the margins of their leaves (Fig. 2). This feature is therefore of evolutionary importance. Like the hairs, the presence or absence of awns on the carpels of the different taxa separates the taxa into two groups. Seven taxa produced carpels with awns while six taxa are characterized by awnless or beaked carpels (Fig. 3). These two characters (hairs and awns) show genetic relationship between the taxa with cordate leaves and the only taxon with linear leaves as well as the taxa with lanceolate leaves.

It is now known that reproductive biology is an important factor in any consideration of the origin and pattern of variation in any group of sexually reproducing plants. It is a major factor affecting evolutionary success and greatly influences the type of habitat in which a plant can compete and survive. In recent years, the work of BAKER (1959, 1961), STEBBINS (1950), DAVIS & HEYWOOD (1963) and many others have established the role of breeding systems in directing evolution and affecting variation. While outbreeding tends to create and retain a large reservoir of variability, much of it in the form of recessive genes which buffer the species against the effects of changing environments, inbreeding provides a much more stable pattern of variation which enables the plant to take advantage of stable environmental conditions by displaying selectively advantageous features.

As the results of the compatibility tests reveal, *Sida* species are all strongly self-compatible (UGBOROGHO, 1978). However, hybridization experiments have shown that some

Fig. 3

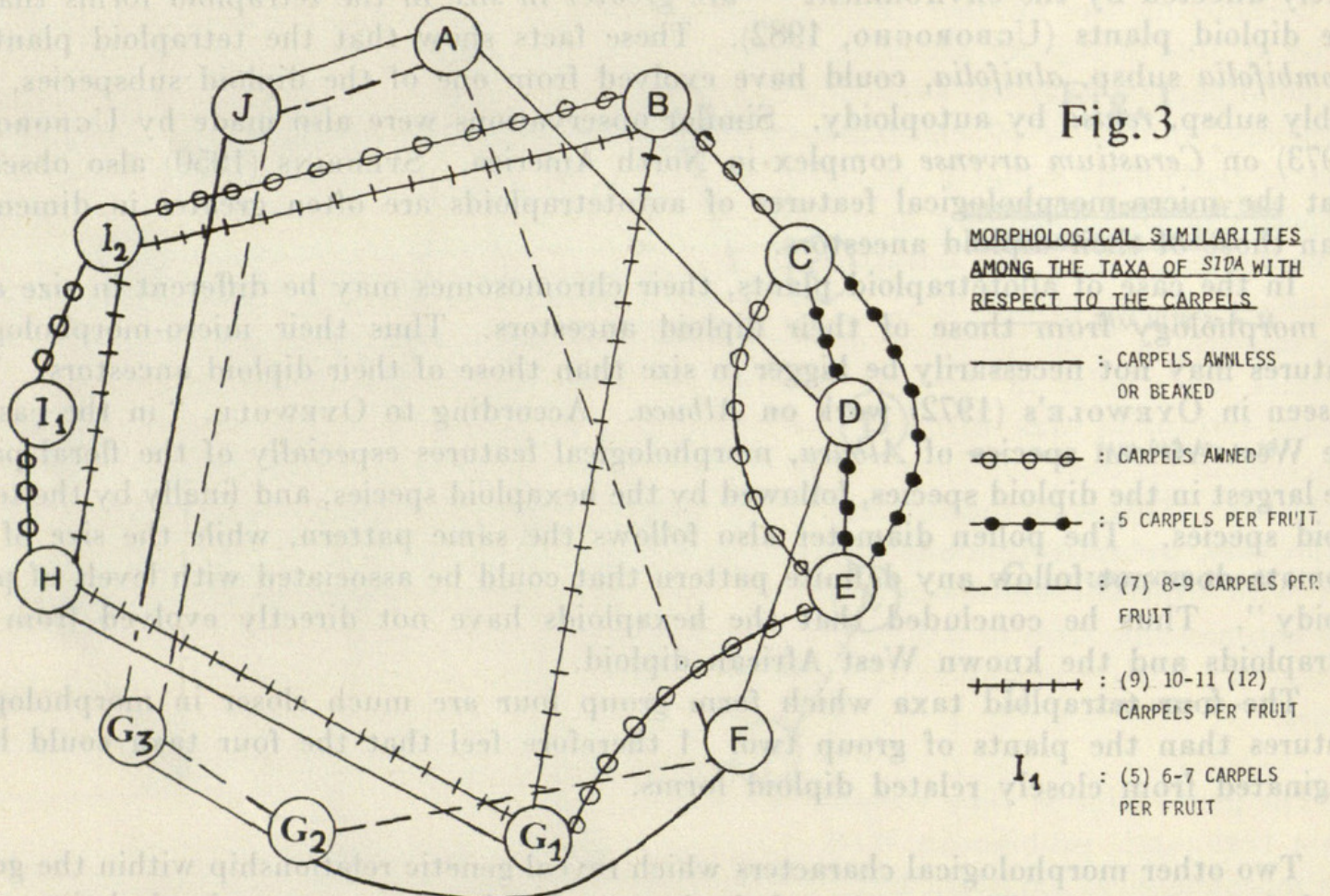
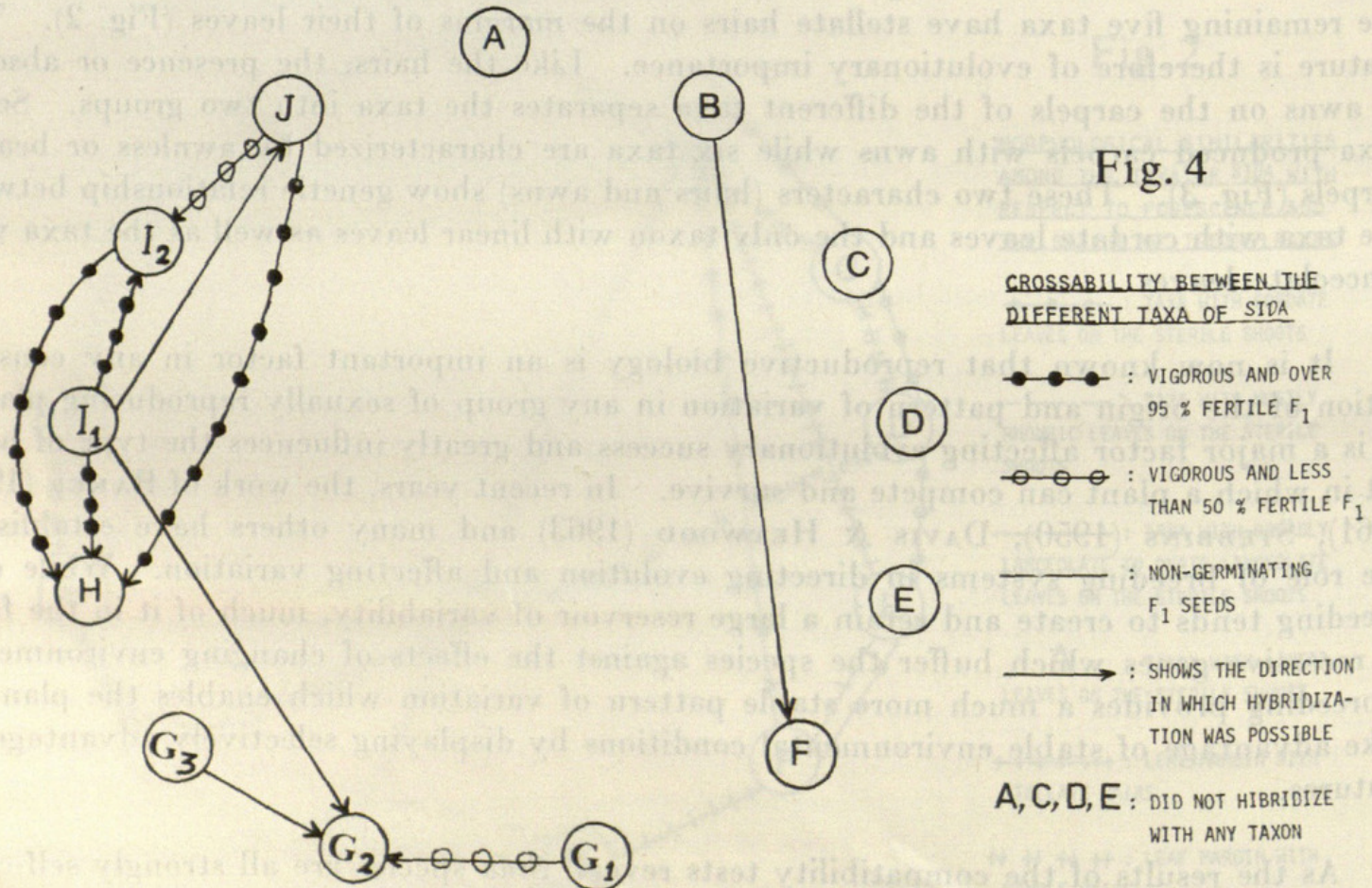


Fig. 4



of the species, especially those in group IV (SCOTT-EMUAKPOR & UGBOROGHO, 1980), hybridize relatively more easily with one another, while many others, e.g. the species in groups I and II, rarely hybridize with one another (Fig. 4).

Of the three subspecies of *S. rhombifolia* (Group III), only the two diploid subspecies produced viable seeds when they were artificially crossed with each other. The F_1 seeds obtained from three out of the nineteen crosses between the tetraploid plant (subsp. *alniifolia*) and subsp. *retusa* did not germinate when sown. These results show that the two diploid subspecies are closer genetically than the tetraploid with either of them. The taxa in group II are much more genetically distinct from one another than plants in the other groups, apart from group I which is made up of only one taxon. However, it should be mentioned that *S. cordifolia* and *S. ovata* are closer genetically than any other members of the group. This is because the two species were the only species which when brought together artificially produced seeds at all. However, the seeds did not germinate. It can therefore be concluded that the plants which are genetically related could have originated from the same or closely related ancestors.

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