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STUDIES IN THE HIPPOCASTANACEAE,
I. VARIATION WITHIN THE MATURE
FRUIT OF AESCULUS

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A WIDE variation in fruit size and shape is readily noticeable from observations of an *Aesculus* tree or shrub in late summer (Fig. 1). Upon closer examination it becomes apparent that this variation is due in part to the number of maturing seeds in the ovary.

The ovary is typically 3-locular and 3-carpellate with two ovules in each locule. These ovules are oriented differently, the lower descending with a dorsal raphe, and the upper horizontal or more often ascending with a ventral raphe. Each fruit, therefore, is potentially six-seeded.

The literature is not clear in regard to the number of seeds usually found in the mature fruit. Gray (1849) stated that the locules are one seeded by the abortion of one ovule in each, and by suppression the fruit is often 1- to 2-celled and 1- to 2-seeded. Pax (1895) said that the mature fruit is mostly 1-seldom 2-locular with one seed. Rendle (1925) also stated that only one seed per fruit develops due to the crushing of two out of three cells by the considerable growth of the one ovule. Chapman (1897) on the other hand described the fruit as being 1- to 3-seeded. The more recent literature presents the same information: Fernald (1950)—3-seeded or usually by abortion 2- or 1-locular and 2- or 1-seeded; Lawrence (1951)—usually 1-locular and 1-seeded; Gleason (1952)—seeds by

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abortion only one and subglobose, or 2 and semiglobose, or rarely 3 with flattened sides. Summarizing this information then, one might expect to find usually one, or possibly up to three, seeds per fruit.

Since there seems to be as much variation in the literature as in the fruit, and more than three seeds per capsule are often found, it was thought necessary to make some actual counts in conjunction with a much broader study of the entire genus.

Collections of fruit from six species were made during the summer of 1954 and studied from the point of view of the number of mature seeds, the position of these seeds within the capsule and the number of locules present. The result of this analysis is presented here.

Each fruit was examined and the number of mature seeds and their position recorded. In Table 1, "top" and "bottom" refer to the ascending and descending ovules respectively. The fifteen position-combinations were determined from the abortive ovules more easily than from the mature ones since the former more nearly retain their original position after the great enlargement of the seeds. More combinations could be recognized if, e.g. with 3 and 4 seeds, it were determined whether one or both ovules mature within the same locule. This information was kept only for 2-seeded combinations—both seeds in the same or different locules. Also given in Table 1 is the number of fruits found with a particular combination and the percentage based on the total fruits examined for each species.

From three trees of *A. hippocastanum* L. growing on the University of Michigan Campus and from two trees along a highway in Franklin County, Ohio, a total of 107 fruits was collected and examined. Table 1 indicates that the 1-seeded fruit was the most common type and that the ratio of "top" to "bottom" was essentially 1:1. In the 2-seeded type the most frequent combination was the 1 — 1 diff., meaning one ascending and one descending seed but in different locules.

An analysis was made of 153 fruits of *A. glabra* Willd. which were collected from a small population in Washtenaw County, Michigan. The 1-seeded capsule was again found to be the most common (Table 1) and maturation of ovules occurred in essentially the same numbers for ascending and descending.

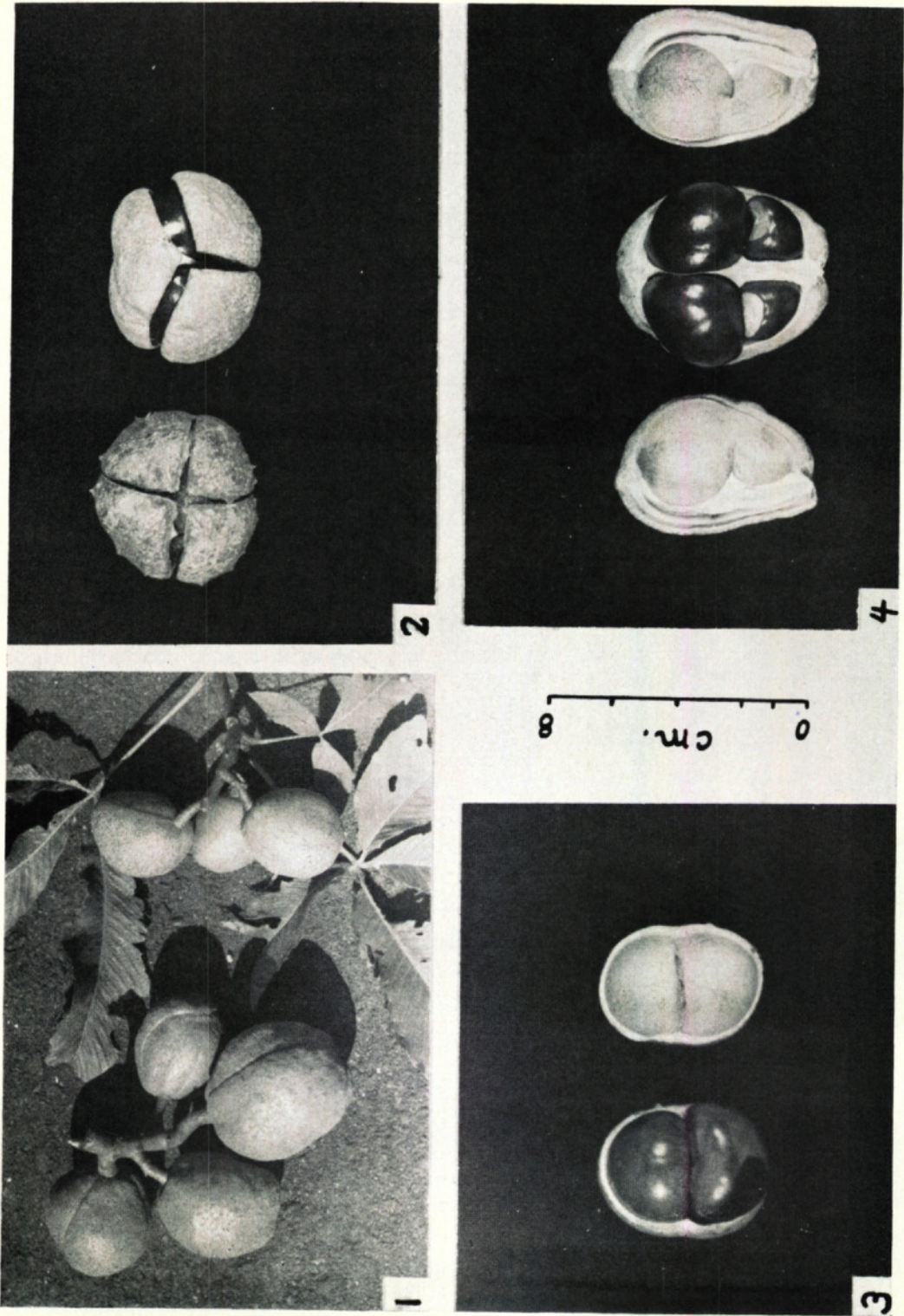


PLATE 1205. FIG. 1, Variation in size and shape of *Aesculus octandra* fruit. FIG. 2, Anomalous 4-locular capsule (left) and typical 3-locular capsule (right) of *A. hippocastanum*. FIG. 3, Anomalous 2-locular, 2-seeded and bi-valved capsule of *A. sylvatica*. FIG. 4, Fruit of *A. octandra* showing suppression of lower two ovules. Scale applies only to Figures 2, 3 and 4.

TABLE 1. NUMBER AND POSITION OF MATURE SEEDS IN CAPSULES OF SIX AESCULUS SPECIES

Number seeds in capsule	Position-combination	Hippo- castanum		Glabra		Octandra		Sylvatica		Parviflora		Discolor		Genus %
		Number	%	Number	%	Number	%	Number	%	Number	%	Number	%	
1	top	45	81.3	35	49.0	15	56.3	31	44.8	13	100			56.7
	bottom	42		40		16		34		15				
2	2 top	5		12		5		10						27.8
	2 bottom	2	16.8	11	35.3	2	32.7	9	28.3					
	1 top, 1 bottom different	7		8		5		15				9	56.3	
	1 top, 1 bottom same	4		23		6		7						
3	2 top, 1 bottom			10		4		13						11.9
	1 top, 2 bottom	2	1.9	8	13.1	1	9.1	10	20.0			4	25.0	
	3 top			2				2						
	3 bottom							4						
4	3 top, 1 bottom													2.6
	1 top, 3 bottom			1	1.3		1.9	1	4.8				3	
	2 top, 2 bottom			1		1		6						
5	3 top, 2 bottom													0.8
	2 top, 3 bottom			1	0.65			2	2.1					
6	3 top, 3 bottom			1	0.65			1						0.2

Aside from percentages which differ between *A. hippocastanum* and *A. glabra*, the most obvious difference is the occurrence in *A. glabra* of fruit with four, five and six mature seeds. Only one fruit each of the 5- and 6-seeded type was found, but it is significant that this condition does occur, even though seemingly rare for the species as well as the entire genus.

Fifty five capsules of *A. oclandra* Marsh., from a population in Haywood County, North Carolina, were studied. Over half were of the 1-seeded type, although 2-, 3- and 4-seeded forms were found in decreasing frequencies.

A total of 145 capsules of *A. sylvatica* Bartr. were examined from two populations, one from Clarke County, Georgia and the other introduced from Georgia and now growing at the University of Michigan Botanical Garden. Again there was a high percentage of 1-seeded fruits, but also relatively high percentages of 2- and 3-seeded forms were found.

A very small and probably clonal population of *A. parviflora* Walt. was visited in Early County, Georgia during June 1954. Mature fruits were not available, but a population sample of partially mature fruits was collected. Analysis of these showed only the one-seeded type. This lack of variation is of interest since the population is probably one clone which occupies an area of nearly 400 square feet and includes approximately 75 trees.

Sixteen capsules were kindly sent from a small population of what is tentatively considered *A. discolor* Pursh growing near Old Sutherland Springs, Wilson County, Texas. It was unusual to find no 1-seeded fruits among this collection. Over half were of the 2-seeded type and the rest 3- and 4-seeded.

Considering all six of these species together, percentages are given (Table 1) for the genus based upon the random samples totaling 504 capsules. The emphasis which previous authors have placed upon the 1-seeded type is not justified on the basis of these figures which show that this form is present in barely more than one half of the total. Over one quarter of all fruit was of the 2-seeded form and just under one eighth had three seeds. The most significant deviation from the literature is the nearly 4% of the total which contained four to six seeds.

Correction should be made of the error found in the literature regarding the interpretation of the number of locules present

in the mature fruit. Regardless of the number of seeds maturing, and the crushing of the locules by the excessive growth of the seeds, each of the locules remains at least partially distinct with its abortive ovules in their original position. The typical fruit then, is always 3-locular regardless of whether 1-seeded or 2- to 6-seeded.

Exceptions to this 3-locular condition were found in two of the species. Four-carpellate, 4-locular and in maturity 4-valved fruits of *A. hippocastanum* were found among the collections (Fig. 2). Also 2-locular and 2-valved fruits of *A. sylvatica* were found (Fig. 3). Of the 107 capsules of *A. hippocastanum* examined, thirteen of them, or 12%, were 4-locular. The majority of these were of the 1-seeded type, only a few having 2 seeds. Each of the four locules was distinct at maturity and each contained the expected two ovules. Only two capsules of *A. sylvatica* out of the 145 examined were 2-locular. One of these was 1-seeded and the other 2-seeded. The expected total of four ovules was present in both cases. The anomalous condition of 2 or 4 locules is rare, or at least infrequent in *A. hippocastanum*. Just what evolutionary significance these conditions have, if any, is not yet known.

At the outset of this study, the question arose as to whether only the ascending or descending ovules matured, or if both, in what proportions. The answer is shown in Table 1. A 1:1 ratio was found in the 1-seeded forms. In the 2-seeded and 3-seeded capsules only slightly more of the ascending ovules matured. These ratios show that the position of the maturing ovule in respect to ascending or descending is entirely random, and abortion is not due to a morphological degeneration of a portion of the ovary or placenta.

The cause of abortion in the majority of ovules is not known. According to Gray (1849) and Rendle (1925) the pressure from the maturing ovules is the important factor. If this were true, one would expect to find some degree of enlargement in all six ovules. Fig. 4 illustrated one of the few cases seen where pressure was effective in retarding the growth of ovules. In this case the lower two ovules did enlarge greatly until presumably stopped by pressure from the top. The smaller two were not true abortives since they expanded to full size after the capsule was opened. In practically every other case, the abortive



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