A STEGODON FROM FLORES

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With pls. II - III

In December, 1956, the Raja of Nage Keo discovered fossil vertebrate remains at Ola Bula on the Soa plateau, between Ola Kile and Menge Ruda, lat. 8° 30′—8° 45′ S., long. 121° 00′—121° 15′ E. of Greenwich, in Central Ngada, Flores. These finds were reported by the Kepala Daerah of Flores to Dr. Th. L. VERHOEVEN, priest at Mataloko, who visited the site in January, 1957[1]). The fossil specimens were found lying on the grass-covered surface of a partially eroded sandstone layer, and occur over an area almost one kilometer long by a width of several hundred meters. Along the Ai Sissa, which intersects the upland plain, the fossils protrude from the river banks. Fossils were collected both by Dr. VERHOEVEN and by Mr. C. CASTILLIO from the surface of the plain as well as from the river banks and from the foot of a hill rising above the plain at Ola Bula. All these finds are apparently derived from the same fossiliferous sandstone, and most of them are more or less weather-worn.

Realizing at once the great importance of the finds, Dr. VERHOEVEN contacted the Museum Zoologicum Bogoriense, and in March, 1957, the Director of the Museum, Mr. A. M. R. WEGNER, accompanied by Mr. A. S. DYHRBERG, arrived in Flores to see the site, and to make further collections of fossils. All the specimens thus far recovered have been shipped to the Museum at Bogor, whence, by kind permission of the Indonesian authorities, Mr. WEGNER sent the entire collection to me for identification. It is a great pleasure to acknowledge my indebtedness to all concerned for their splendid cooperation, as a result of which these fossils, the first of their kind ever found in Flores, or in any of the Lesser Sunda Islands for that matter, are now available for study.

The collection of fossil remains from Ola Bula, which arrived at the Rijksmuseum van Natuurlijke Historie at Leiden in August, 1957, consists

1) Dr. VERHOEVEN's explorations in Flores are being supported by the WENNER-GREN Foundation for Anthropological Research.

of several hundreds of greater and smaller bone and tooth fragments. Most of these have corroded surfaces as a result of their having been exposed to the weather, but others are better preserved, and a certain number of fragments could even be matched, such as, e.g., a pair of mandibular rami and some fragments all of the same specimen that had evidently begun to disintegrate just before its recovery from the grass plain.

To my surprise, the Ola Bula collection proved to contain the remains of stegodonts, and of stegodonts only; there is not a single identifiable tooth or bone fragment in the entire collection that belongs to animals other than *Stegodon*. The material now at hand amply justifies the following diagnosis of a new race, peculiar to the island of Flores:

Stegodon trigonocephalus florensis nov. subsp.

Diagnosis: Smaller, on an average, than *Stegodon trigonocephalus* MARTIN from the Pleistocene of Java; molars relatively higher-crowned. Twelve or thirteen ridges in the lower last molar.

Holotype: The mandible with both M_3s in situ, described and figured in the present paper.

Locality: Ola Bula on the Soa plateau, Central Ngada, Flores.

Age: Middle or Upper Pleistocene.

The most diagnostic specimen is a mandible with both M_3s in situ (pl. II, figs. 1-2). The right horizontal ramus is better preserved than the left, of which the lingual surface is for the most part lost, exposing the lingual surface of the molar with its roots. The bone of the rami in front of the molars is much injured, but the two halves of the mandible fortunately make a good contact in the symphysial region. The ascending rami are missing; their anterior borders are on a level with the seventh ridges of the molars.

The molars are incomplete behind: the left M_3 is broken off behind ridge 7 from the front, and the right M_3 carries eleven ridges. From the backward taper of the posterior end of M_3 dext, it is, however, clear that one or at most two ridges only are missing, which makes for a total of twelve or thirteen ridges in the M_3. This is a figure that points to a highly progressive stegodont such as *Stegodon trigonocephalus* MARTIN from the Pleistocene of Java, in which the number of ridges in the last lower molar varies from 11 to 13. Of this species there is a wealth of material in the DUBOIS Collection, which has recently been described (HOOIJER, 1955). All the comparative data on *Stegodon trigonocephalus* given in the present paper are derived from this source.

The left M_3 of the Flores *Stegodon* mandible is entire in front, apart from a contact facet caused by interproximal wear with the M_2, of which no trace remains. The right M_3 is slightly more advanced in position than the left (a feature not uncommon in elephantids), and lacks the anterior talonid and part of the first ridge. In front of the right M_3 a small portion of the hind root of M_2 is still in situ. The anterior talonid is most developed on the labial side, as usual in lower molars; its enamel figure is confluent with that of the first ridge in the median line. The first three ridges are worn to single enamel figures, with wrinkled borders; that of the first ridge is sharply constricted in the middle, pointing to the presence of a median cleft that normally appears in the first ridges of *Stegodon* molars. The fourth ridge has the conelets barely worn out; there are about ten conelets. The fifth ridge shows the dentine cores of the central conelets only, and the sixth ridge has just been touched by wear. The seventh ridge is the foremost unworn ridge. The amount of cement on the crown increases markedly from front to back; in the front valleys there is hardly any cement whereas behind the ridges are fully bathed in cement, which covers the sides of the ridges up to the apices of the highest conelets.

As a whole the molars are curved and even slightly twisted lengthwise: their lingual surfaces are convex, their labial surfaces concave from before backward. The lower margin of the crown is convex rootward anteroposteriorly, and the ridges converge crownward: the hindmost ridges are progressively inclined forward and also inward. We find this peculiar curvature and twist in the long last molars of all progressive stegodonts.

The total length of the crown of M_3 cannot be exactly given, but would have been about 250 mm in a straight line, which brings the present Flores specimen within the range of variation of *Stegodon trigonocephalus* from Java, in which the length of M_3 varies from 240 to 304 mm. As the right ramus was broken into several fragments when I received the specimen it has been possible to measure every single ridge, and these measurements are recorded in table 1. It will be observed that the greatest width and the greatest height of the crown are at the seventh ridge from the front, which most often is the case in the M_3 of the Java *Stegodon trigonocephalus*, too. The ridges become progressively higher, relative to their basal width, when passing backward along the crown. The laminar frequency of the present Flores molars (the number of ridges per 10 cm of anteroposterior length, that is) is 4½ on the lingual, and 5½ on the labial side; it is 5 in the median line of the occlusal surface.

In the Java *Stegodon trigonocephalus* the laminar frequency of M_3 varies from 4 to 6. The root formation of the Flores *Stegodon* M_3 is also similar to that of the Java stegodont, with an anterior root supporting only the first two ridges, and the remainder of the root system fused into a single root.

TABLE 1

Measurements of ridges of M_3 of *Stegodon trigonocephalus florensis*

No. of ridge	1	2	3	4	5	6	7	8	9	10	11
Basal width	63	66	68	70	71	72	72	70	69	65	59
Total height	—	—	—	—	—	—	50	49	49	47	46
Height-width index	—	—	—	—	—	—	69	70	71	72	78

In table 2 the principal measurements of the Flores M_3 can be compared with those of its homologue in the Java *Stegodon trigonocephalus*. There is a great amount of variation in dimensions of M_3 of the Java stegodont, which includes the observations of the *Stegodon* M_3 from Flores; the latter appear to be to the lower side of the range of variation of the Java M_3s. However, in the relation between the greatest height and the greatest width of the crown, as expressed in the height-width index $\left(\frac{\text{height} \times 100}{\text{width}}\right)$ there is a difference between the Flores M_3 and those of Java: the Flores specimen is slightly higher-crowned than any of its counterparts from the Pleistocene of Java.

TABLE 2

Measurements of M_3 of *Stegodon trigonocephalus* subsp.

	Java	Flores
Greatest width of crown	68-98	72
Greatest height of crown	48-61	50
Crown height-width index	56-66	69

In the evolution of the stegodonts as we now know them (data assembled in OSBORN, 1942, pp. 805-909, pl. XX) the molars show an elevation from brachyodont to subhypsodont, culminating in *Stegodon trigonocephalus* (OSBORN, l.c., p. 853). A few years ago I described a pygmy stegodont from the Middle Pleistocene Djetis fauna of Java that represents the most progressive species of its genus, surpassing even *Stegodon trigonocephalus* in the great relative height of the molar ridges. Of this species, *Stegodon hypsilophus* HOOIJER (1954), M_3 is, however, unknown, the type being a pair of M^3s. It is, at any rate, evident, that the Flores tegodont described in the present paper is a more progressive type than 'tegodon trigonocephalus from Java, and, moreover, rather small in size. n these points the Flores *Stegodon* marks a step from *Stegodon trigonocephalus* proper to *Stegodon hypsilophus*.

Fortunately, there is also the posterior portion of a left upper last nolar in the Flores collection (pl. III, figs. 1-2). It comprises four ridges ınd the hind talon, all unworn. That it belongs to the upper jaw is evident 'rom the rootward concavity of the base of the crown as well as from the :rownward divergence of the ridges. Cement fills the valleys up to the :onelets, which vary from 9 to 10 in number per ridge. The talon consists of three subequal cones. The laminar frequency is 5. This specimen affords :he most welcome opportunity of comparing the Flores stegodont not only with *Stegodon trigonocephalus* from Java but also with *Stegodon hypsilophus*, as shown in table 3. The M^3 of *Stegodon trigonocephalus florensis* nov. subsp. is slightly smaller than that of the Java *Stegodon trigonocephalus*, and has relatively higher ridges, although the ridges are not elevated to the extent seen in *Stegodon hypsilophus*, which latter is moreover decidedly smaller than the Flores type. Thus, the M^3 of the Flores stegodont corroborates the conclusions already drawn from the study of the M_3 in a most satisfactory manner.

TABLE 3

Unworn ridges of M^3 of *Stegodon* species

	trigonocephalus (Java)	Flores	*hypsilophus*
Ridge 4 from behind,			
width	71-102	70	59
height	42-62	54	52
height-width index	46-69	77	88
Ridge 3 from behind,			
width	68-97	62	53
height	40-59	53	49
height-width index	44-71	85	92
Ridge 2 from behind,			
width	60-91	56	45
height	37-54	45	44
height-width index	45-73	80	98
Ridge 1 from behind,			
width	44-84	47	41
height	32-48	40	39
height-width index	46-89	85	95

The third best specimen of the molars of *Stegodon trigonocephalus lorensis* available at present is a portion of an upper molar with three ridges, two of which unworn. The first ridges are 77 mm wide at base, the third, 75 mm. The second ridge is 52 mm high, the last, 55 mm. The present specimen in all probability represents the fifth to and including the seventh ridge of an M^3 (the fifth usually is the widest ridge in the upper last molar of *Stegodon trigonocephalus*). An isolated ridge, not of the same individual, is intermediate: 76 mm wide at base, and 54 mm high in the unworm state. Table 4 shows that in greatest width and in greatest height the present M^3 is just within the variation limits of its homologue in the Java *Stegodon trigonocephalus*, but in the height-width index the Flores M^3, again, surpasses the large Java stegodont. The pygmy stegodont from Java (*hypsilophus*) has by far the highest crown height-width index.

TABLE 4

Measurements of M^3 of *Stegodon* species

	trigonocephalus (Java)	Flores	*hypsilophus*
Greatest width of crown	76-113	77	64
Greatest height of crown	49-59	55	57
Crown height-width index	46-68	71	89

The above mentioned ridges with a basal width of 77 mm are the widest in the collection from Flores now at hand; there remain a large number of molar portions, isolated ridges, and fragments the serial position of which cannot be exactly determined, and which, therefore, are of no value for purposes of comparison. Two specimens, however, clearly represent the hinder ends of M_3s, and these may be recorded in this place as they supplement the description of the M_3 of the mandible. The two specimens, one right and one left, most probably of the same individual but not belonging to the above recorded mandible (pl. III figs. 3-5), comprise the last two ridges and the talonids, heavily encrusted with cement. The talonids are ca. 34 mm high and wide, and consist of two cones each, the labial larger than the lingual. The measurements in table 5 indicate that the ridges are proportionally higher than the eleventh ridge of the M_3 first described above. The last (thirteenth) ridge of a small M_3 of *Stegodon trigonocephalus* from Trinil, Java, likewise is 45 mm wide, but only ca. 40 mm high. The Flores specimens are further interesting in showing large basal cusps at the labial entrances to the valleys. They are undamaged in the right molar, and are 18 mm high by a horizontal diameter of 10 mm. A very similar development of extra cusps is also shown in the hinder end of the Trinil specimen.

Three symphysial portions of the mandible, without teeth, conform well to those of *Stegodon trigonocephalus*, and need no special remarks. There are also fragmentary mandibular rami, one of which with root stumps. The postcranial material, which is rather well represented in the Flores collection,

TABLE 5

Unworn last ridges of M_3 of *Stegodon trigonocephalus florensis*

No. of ridge from behind	2		1	
	r.	l.	r.	l.
Basal width	52	54	45	46
Total height	46	47	45	44
Height-width index	88	87	100	96

again offers the means of comparison of the Flores stegodont with *Stegodon trigonocephalus* from Java. The following specimens are available: an atlas without the transverse processes, an injured epistropheus, a vertebra with one costal facet on each side of the corpus, and, hence, one of the posterior thoracics, an isolated spinous process of a thoracic vertebra with a median perforation (an anomaly also known in the large Java stegodont), a right humerus without the lateral distal condyle, its proximal portion broken off from the shaft but preserved, the medial distal condyle of a left humerus, the proximal part of a left ulna, part of a right os coxae, two proximal and two distal portions of femora, the distal portion of a left tibia, the shaft of an immature left tibia, and a metapodial. The measurements of these specimens may be compared with those of the series of homologous bones of the large Java *Stegodon* in table 6.

Most of the bones of the postcranial skeleton of the Flores *Stegodon* are below the ranges of variation of their homologues in the Java *Stegodon trigonocephalus*, and thereby confirm one of the results obtained from the study of the dentition: the Flores stegodont must have been smaller, on an average, than *Stegodon trigonocephalus* from Java.

Having established the relationships of the *Stegodon* from Ola Bula we have to consider the zoogeographic side of the question. The genus *Stegodon*, apart from its occurrence in the Lower Pleistocene of East

TABLE 6

Measurements of *Stegodon trigonocephalus* subsp. (in cm)

	Flores	Java
las, lateral length of corpus	7½	9
vertical diameter facies art. cranialis	8½	10
transverse diameter of idem	5½	6
vertical diameter facies art. caudalis	6½	9
diameter foramen transversarium	2½	3
total height	15	15½—18
ɔistropheus, ventral length	ca. 10	11½—12½
total height	ca. 18	20 —20½
ıoracic vertebra, length of corpus	5½	6¼— 6½
width of fossa	9½	10
height of idem	8½	7½— 8
umerus, width over caput and lat. tuberosity	15	ca. 18 —23½
anteroposterior diameter of caput	13	15½—ca. 20
transverse diameter of idem	10	12 —ca. 14
least diameter at middle of shaft	5	6 — 9
anteroposterior diameter medial condyle	ca. 12	13 —16½
lna, width of humeral articular surface	13	16 —21½
width of medial portion of idem	5	6½— 9½
emur, greatest distal width	16	18 —25½
anteroposterior diameter medial condyle	ca. 13	18½—25
ibia, greatest distal width	ca. 13	12 —19½

.frica (MACINNES, 1942)[1]) is exclusively Asiatic, ranging, through India ıto Burma, China, Japan, and Southward into Java, the Philippines, and 'elebes. The fossils described in the present paper indicate that *Stegodon* .as also been able to reach Flores. There can be little doubt as to the ispersal route it used. Flores is one out of the chain of volcanic islands xtending Eastward from Java and situated on the same geanticlinal belt. 'he Lesser Sunda Islands arc shows signs of recent upheaval; it was ıostly below sea-level during the Tertiary (KUENEN, 1935) but in post-'ertiary times, especially during times of glacially lowered sea-level, it ıust have provided the means for land animals to spread Eastward from 'ava. Students of the recent vertebrate fauna of Bali, Lombok, Sumbawa, .nd Flores agree that the fauna of these islands is predominantly Oriental, mpoverishing as we pass Eastward along the island chain (DE BEAUFORT, .926; MERTENS, 1930, 1936; RENSCH, 1931, 1936; MAYR, 1945). The sland arc, although it probably never formed a continuous land bridge at the height of the Pleistocene glaciations the straits between Java and

1) The record of *Stegodon* from Bethlehem, Israel, by BATE (in GARDNER and 3ATE, 1937) is erroneous; the supposed *Stegodon* remains are those of primitive ırchidiskodonts (HOOIJER, unpublished).

Bali, and between Lombok and Sumbawa may have formed land connections, but those between Bali and Lombok, and between Sumbawa and Flores remained open), was the most likely way for *Stegodon* to get to Flores from Java.

Stegodon trigonocephalus ranges in Java from Lower to Upper Pleistocene, and upon its colonization of Flores developed a local race on the latter island. It is impossible to determine the amount of time involved in this subspecific differentiation, but it may well have been in the order of a few thousand years only, a small fraction of the duration of the Pleistocene. Among the recent mammals of the island chain Bali-Flores there are very few endemic species (e.g., *Papagomys armandvillei* (JENTINK) of Flores); subspecific differentiation, mostly accompanied by a diminution in size, usually is all that can be recognized. These facts point to a relatively young age of the fauna of the Lesser Sunda Islands, and are in harmony with the geological data; there evidently was little, if any, opportunity for the mammals of the Greater Sunda Islands to spread along the Lesser Sunda Islands previous to the Pleistocene.

Each of the straits in the Lesser Sunda Islands is a zoogeographic barrier to some extent, but even Flores has a recent fauna comprising Oriental insectivores, bats, primates, rodents, carnivores, and ungulates. Of some of these a transportation by human agency cannot definitely be ruled out, but even so the living mammalian fauna of Flores is rather varied. It would seem very improbable that in the Pleistocene the fauna of Flores would not have been equally varied.

Therefore, if *Stegodon*, as we now know, has penetrated from Java to Flores sometime during Pleistocene, there seems to be no obvious reason why other herbivores (and carnivores!) would not have got around to using the means of getting there. The site of Ola Bula has been missed by EHRAT (1928), whose geological explorations in Flores included the upland plain of Soa (l.c., p. 257/258). EHRAT briefly describes the Neogene sediments, and merely states that the upper part of the plateau is Quaternary in age. A simplified version of the geological sketchmap of Flores by EHRAT (l.c., pl. IX a, b) will be found in VAN BEMMELEN (1950, pl. 10 fig. 208). The *Stegodon* reported upon in the present paper points to a Middle or Upper Pleistocene age of the deposits in which it was contained.

It is to be hoped that in the near future large-scale excavations will be made at Ola Bula. The Pleistocene fauna of nearby Celebes, an island that was definitely more effectively isolated from the Sunda Shelf during the Pleistocene than was Flores, contains beside *Stegodon* (HOOIJER, 1953), an *Archidiskodon*, an endemic suid *Celebochoerus*, an *Anoa*, as well as arks, a crocodile, turtles, and a *Testudo*. It is extremely unlikely that tensive searches for fossil vertebrate remains in the fossiliferous beds Ola Bula would not lead to at least as rich a paleontological harvest.

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EXPLANATION OF THE PLATES

Plate II

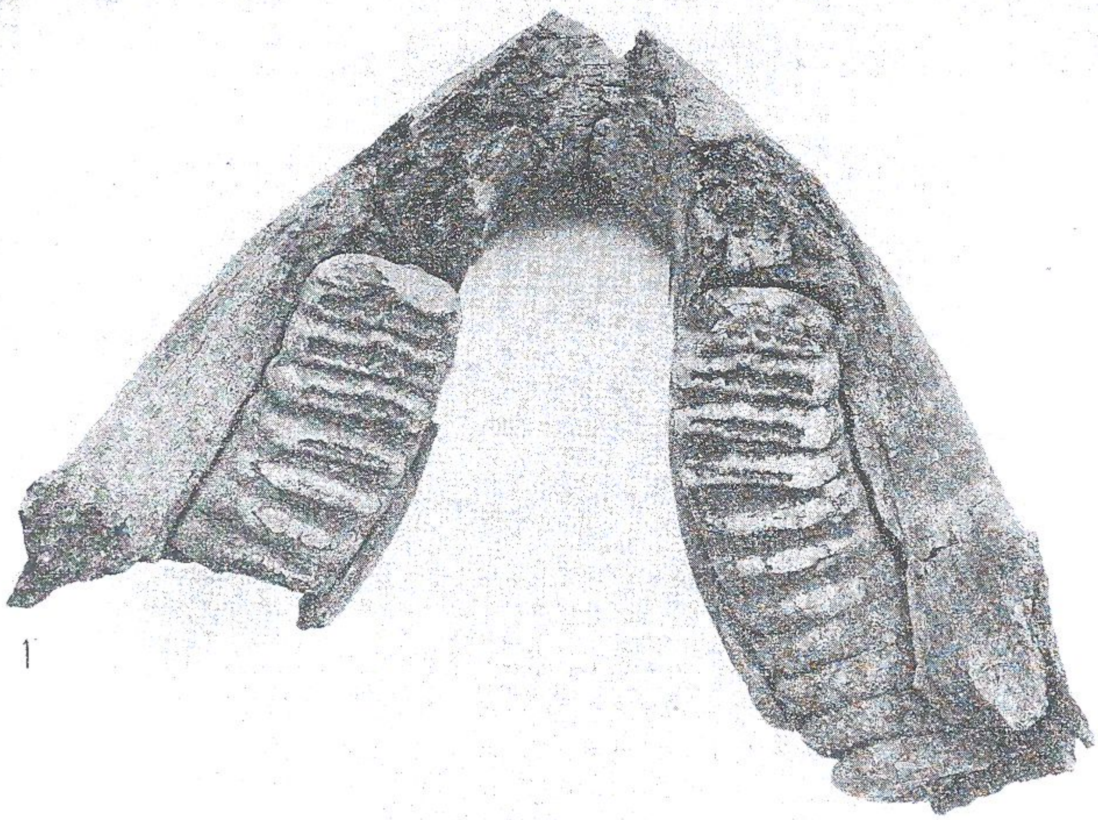
Stegodon trigonocephalus florensis nov. subsp., Ola Bula, Flores; fig. 1, mandible (holotype), top view; fig. 2, right ramus of mandible of fig. 1, lingual view.

Fig. 1, ¼ natural size; fig. 2, $^{3}/_{10}$ natural size.

Plate III

Stegodon trigonocephalus florensis nov. subsp., Ola Bula, Flores; figs. 1-2, posterior end of M^3 sin.; fig. 1, labial view; fig.2, anterior view, showing fourth plate from behind; figs. 3-4, posterior end of M_3 dext.; fig. 3, labial view; fig. 4, crown view; fig. 5, posterior end of M_3 sin., anterior view, showing second plate from behind.

Fig. 1, ⅔ natural size; figs. 2 and 5, ¾ natural size; figs. 3 and 4, $^3/_5$ natural size.



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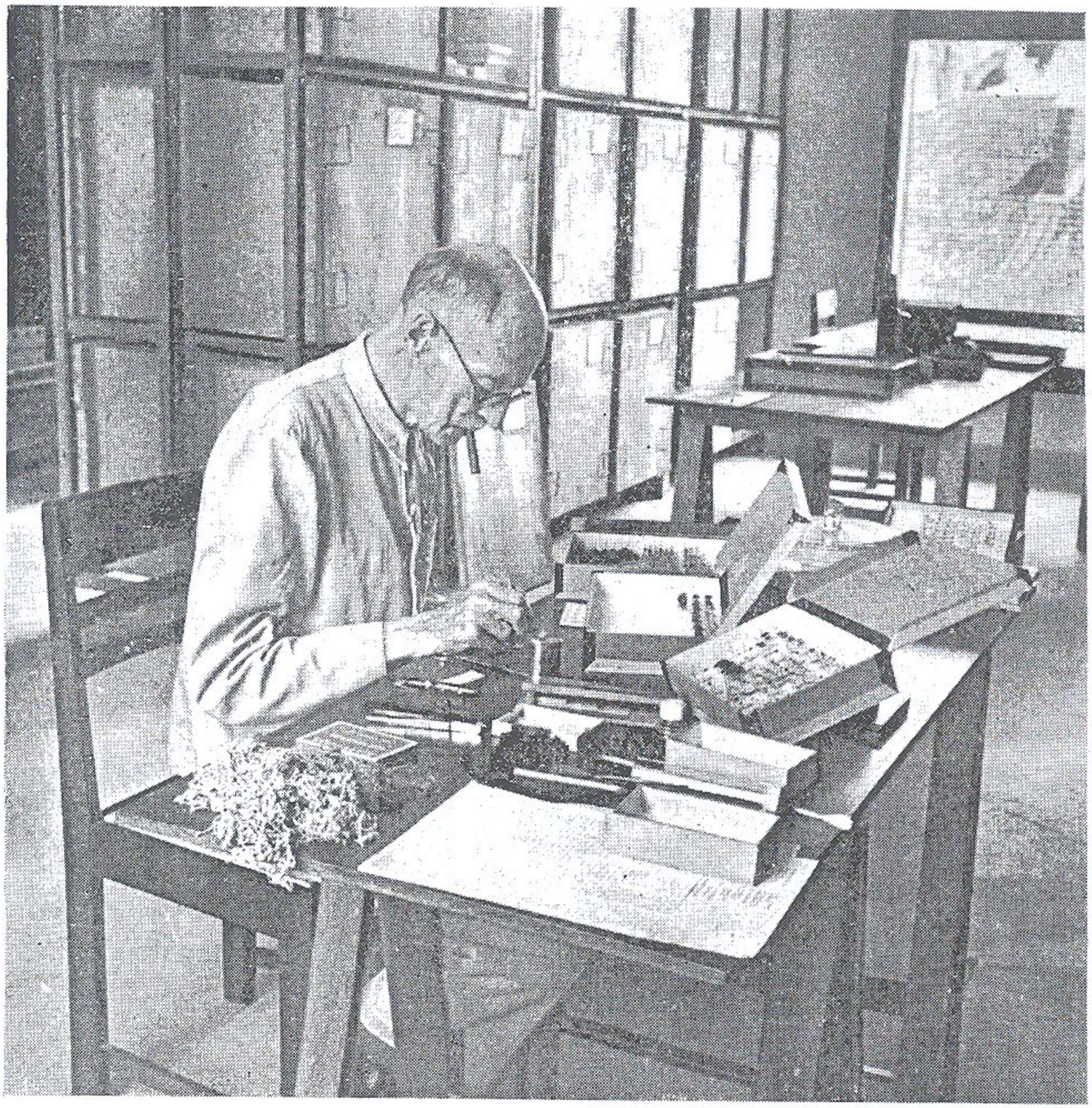

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