the contraction mechanism may be a rigid attachment of the globular head of the myosin molecule to the actin filament and an active change in the angle of attachment associated with the splitting of adenosine triphosphate. The availability of purified preparations of "head" subunits now opens up the problem to detailed attack.

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Evolutionary History of the Elephant

A tentative phylogeny of Elephantidae based on morphological and quantitative analysis is given.

Emiliano Aguirre

Elephants, which are among the most popular and decorative of animals, stand as a witness of prehistory, having been a part of the environment of our ancestors. The dinosaur was not contemporary with early man, as many films and stories insist, but the mammoth was. Although prehistoric or extinct elephants are frequently referred to as mammoths, such a designation is not always correct. The true mammoth is but one of many species of extinct elephants; furthermore, it belongs to one of a few genera, which include four or five species that have affinities with the woolly elephant. These different genera and species are grouped by zoologists into a family, Elephantidae. Because this family originated by the beginning of the Pleistocene period, elephants can be considered contemporary with man.

Anthropologists and prehistorians have often attempted to establish a chronology of sites of fossil man through correlations based upon the species of elephant associated with them (*1*), but the systematics of the Elephantidae is quite confused. The documented monograph of Osborn (*2*) established 10 genera and some 59 species of elephants; to these Garutt (*3*) added two more genera. However, many taxonomists have recognized only one genus and no more than five or six valid species. In the museum collections from most major sites there are many samples with dubious identifications and many intermediate forms labeled either with two names or with a composite or new name. It has been assumed that many different species have lived contemporaneously in a single area, as was the case for the sample excavated in the railway trench of San Paolo, Italy, in the first years of this century. Explanations of the phylogeny of elephants have had one feature in common: the patterns for the phyletic trees have agreed with the fashionable evolutionary theories

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of the particular period. Thus all the trees are dichotomic and linear from 1881 to 1888 (*4*), fairly dichotomic from 1888 to 1912 (*5*), and polyphyletic until 1923 (*6*). After 1940 dichotomic (*7*) patterns are again found.

A review of the evolutionary history of the Proboscidea before the appearance of the elephants may help us to understand the significance of the evolving character in the latter. For Proboscidea since the Old Tertiary period, two major characteristics have been defined: the anterior teeth are missing except for one or two pairs of tusks; and there is an increasing number of rows of cusps, with every new transversal row appearing behind the other and elongating the molar teeth.

Trends in Late Tertiary and Pleistocene Proboscideans

During the Middle Tertiary period the most important branch of Proboscidea, the Mastodontoidea, evolved into some differentiated groups or families (*8*, *9*). It is difficult to identify fossil mastodonts by skeletal remains; on the other hand, fossil molars are very plentiful, and these exhibit definite sequences of variations in the morphological features of the molar crown which are important in the origin and evolution of elephants.

In a major division, the family Gomphotheriidae Cabrera, the main cusps are only slightly subdivided or not subdivided and are round and breastlike in shape; well-differentiated central conules are detached from the wall of the rows of cusps and invade the transversal valleys between them. A longitudinal or median sulcus that separates the lingual cusps or cones in each row or ridge from the labial ones is always conspicuous. *Trilophodon* Falconer, *Tetralophodon* Falconer, and the American *Cuvieronius* Osborn are representative genera of this family.

A second group, the family Mastodontidae Girard, is characterized by molar teeth with cusps (cones) subdivided into conelets which are fused transversally into acute ridges; these are thereby transformed into linear crests, and the valleys between them are V-shaped and open. Only the primitive forms have regressive central conules, which are missing in most of this family as is the median sulcus. Some of the representatives of this family are *Mastodon* Cuvier and *Turicius* Osborn.

In addition to morphological characteristics, we must also consider several measurable traits, which vary in the mastodonts, as well as in the Pleistocene proboscideans, stegodonts, and elephants, in more or less the same way, but with different "tempo"; that is, there are some common biometrical trends in the different evolutionary branches of these animals. These traits include the following characteristics.

1) Multiplication of the transversal ridges of cusps, which is exceptional among other mammals and very peculiar to most proboscideans.

2) Increasing height of the ridges (hypsodonty), an allometric characteristic present in many other orders of mammals, which is expressed as a ratio, relating the height to the length or width of the crown. The best formula for elephants seems to be

$$K = H/A$$

where K is the index of hypsodonty, H is the height of a complete ridge, and A is the maximum width of the molar tooth.

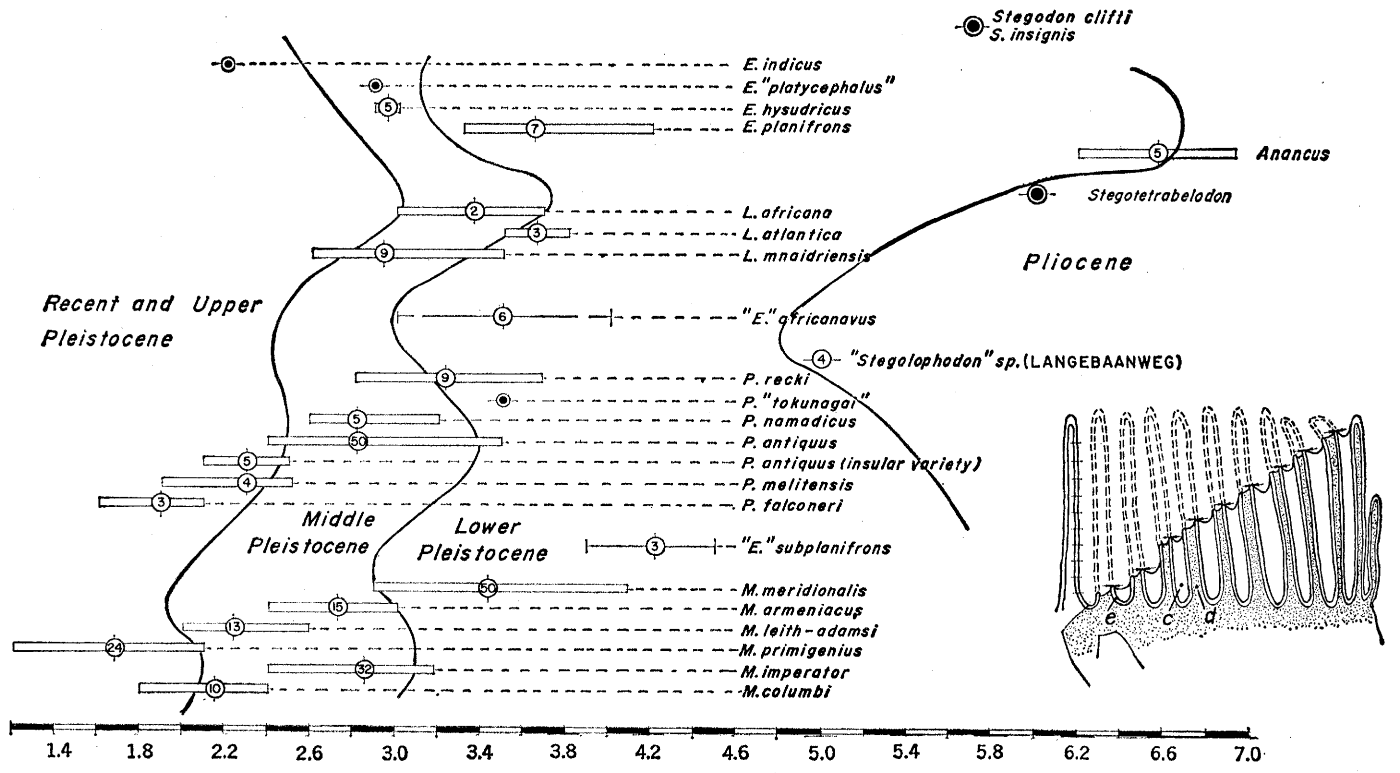

Fig. 1. Trend of diminishing thickness of enamel (in millimeters) in different species of elephants arranged in hypothetical phyletic groups. Size of the sample is shown by a circle superimposed on the mean value; double lines indicate range of variation; single lines show doubtful samples; solid circles represent single individuals or two of the same value. Wavy lines separate geological periods. Different tempos in evaluation appear through stratigraphical divisions. The inset illustrates the basis of the method; *e*, enamel; *c*, cement; *d*, dentine.

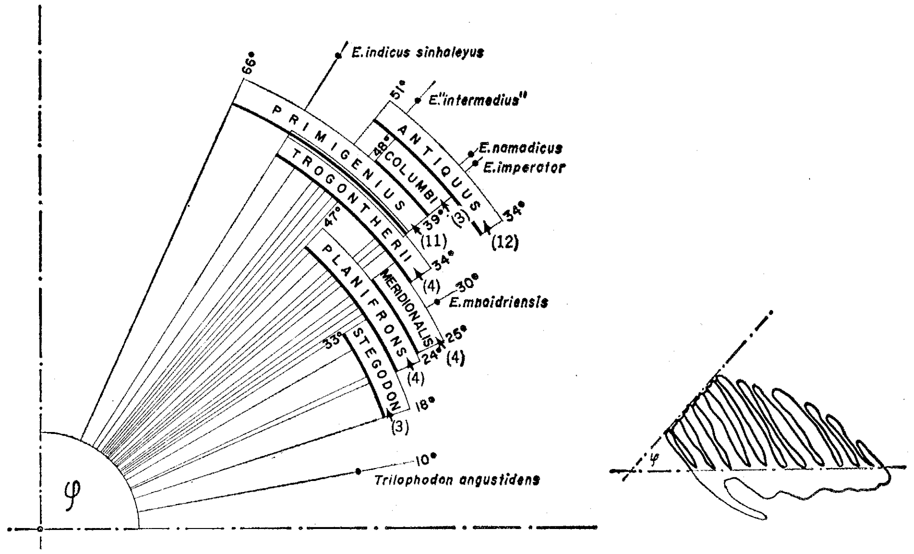

Fig. 2. Variation of the erupting angle ψ. The large degree of overlap of *Elephas trogontherii* with *E. primigenius* is the result of difficulties associated with the identification of the advanced forms of the former species, which may be considered as transitional forms or a pool of mutant populations. Sample size is indicated by the number in parantheses.

3) Diminishing thickness of the enamel, which is very conspicuous and constant. Almost every book and museum exhibition is illustrated with a series of outlines in which the thickness of the enamel in a mastodont, a stegodont, a primitive elephant, and a mammoth is represented with an ever-thinner black line. Nevertheless, this measurement is very seldom used in elephants because the variability of the enamel cover in the molars of proboscideans is great; the thickness varies noticeably not only among teeth of individuals in one species, but also among the ridges of one molar and along the section of a single ridge. Since statistics are the only valid representative figures for any magnitude in biological species, a mean of a random series of measurements in a molar would give a valid representative figure for the thickness of its enamel. This method (*10*) seems to be useful in permitting one to differentiate between species within an evolutionary branch and to make comparisons among different genera (Fig. 1).

4) Reduction of the total length of the grinding surface (the brevirostrine trend), which occurs in many mastodonts, and, most remarkably, in mammoths and their relatives. It is in harmony with the multiplication of ridges by their mesiodistal shortening. Thus the ridges become plate and are named ridge-plates in elephants. In classifying elephants the usual practice has been to use the number of plates or the length of the molar. The ratio of the number of plates to the length of the molar is a better means of identifying the genera and species of elephants than either of these characteristics separately. Many formulas have been proposed for this particular ratio, and it would be safer not to introduce a new formula. However, since evolutionary trends follow measurable variations in function, it is more effective to take into account the length of the grinding surface (*LF*) at the time of the animal's death and the number of plates actually working at that time (*U*). In this way data for two different species plotted in a scatter diagram show less dispersion and slightly less overlap than data plotted for the conventional total length and total number of plates (which is almost always approximate). The ratio of the functional density of the plates (Q) is given by

$$Q = 100U/LF$$

5) The brevirostrine trend and a trend to longevity which are related to a general quality of mammal dentition exaggerated in Proboscidea: namely, a delay in tooth eruption at definite intervals, which permits recognition of an individual's age. In mammals generally, the whole potential chewing surface works completely at an adult age, all teeth being present but in slightly different degrees of wear. However, in Proboscidea the anterior teeth are completely worn before eruption of the posterior ones. Thus in mastodonts and stegodonts, but particularly in elephants, every tooth is worn out and its roots are ejected before the one just posterior to it is even half-worn and long before the more posterior tooth has erupted. Thus elephants have only one grinding tooth in each half series at a given time (or have the rear of one and the front of the next, which is equivalent). Such a delay in tooth eruption in mastodonts and elephants is favored by the inclination of the erupting tooth relative to the occlusal surface; this inclination can be measured as an angle between the occluding surface and the base of the molar crown; it is progressive in every species of both mastodonts and elephants (Fig. 2). With the increase of this angle, a smaller length of the grinding surface is exposed to wear; as the functional length is reduced, the life of each tooth is increased and, consequently, the longevity of the animal is favored.

6) The width of the molars which evolves differently in elephants; this trait is for the most part constant in the different species related to mammoth (*Mammuthus*) whereas the molars tend to be narrow in the less brevirostrine living elephants and in the extinct *Elephas antiquus* Falconer (Fig. 3). The pattern of variation of width in the different plates of a single elephant molar is also peculiar for each phyletic group.

Each group reflects different evolutionary trends. Since some trends are expressed by a single measurement and some by a ratio (simple and constructed variable, respectively), we can separate not only species but also evolutionary branches in scatter diagrams according to a pair of those ratios or measurements more easily than we can by simple measurements alone (Figs. 4 and 5) (*11*).

Other trends in the evolution of tusks, skull, and the postcranial skeleton are known in elephants as well as in stegodonts and in Tertiary mastodonts. Most mastodonts have two pairs of highly specialized incisors, upper and lower. The upper incisors are developed as tusks, which vary in section, curvature, and divergence in their basal portion (the portion included in premaxillar bones) and may or may not have a longitudinal band of enamel. The lower incisors in mastodonts have very peculiar and different adaptations; these disappear in some advanced species such as Anancinae Hay. In all known stegodonts and elephants there are no lower tusks.

The skull of proboscideans varies

widely among individuals of each species and in different species and genera; similar trends in evolution and differentiation occur in separate families such as Elephantidae and Stegodontidae. Such trends aid in the characterization of species and genera, if these are carefully established, because the sexual dimorphism and the ontogenetic and phenogenetic variations are very wide. Long, low skulls are interpreted as primitive. Shortening of the cranial base and the palatal bones; depressing, elevating, or expanding the frontoparietal region; pneumatization; and development of the torus are trends exhibited by stegodonts and elephants as specializations. Some of these cranial formations are apparently correlated with the specializing curvature, size, and direction of the erupting tusks. If this hypothesis is sound, some of the most striking features of elephant skulls could have a biomechanical interpretation and could be subject to a large ontogenetic variation (Fig. 6). The skeleton of the proboscideans is not as well known and cannot contribute to phylogenetic studies, because the specialized features are less remarkable and the fossil record is largely insufficient to permit estimation of the range of individual variation.

Origin of Elephants and the Plio-Pleistocene Boundary

During the Pliocene (the latter portion of the Tertiary period), several lines of mastodonts evolved in Africa, Asia, and Europe, among which were the ancestors of elephants. Anancinae Hay, with the genera *Anancus* Aymard, *Pentalophodon* Falconer, and *Synconolophus* Osborn (in addition to the American representatives) are advanced in the loss of lower tusks, somewhat advanced in hypsodonty, diversified in the multiplication of ridges and the folding of the enamel in molar teeth, and advanced in the brevirostrine trend that delays the substitution of molars. Species of these genera are contemporaneous with most of the *Hipparion* faunas from Spain (Alfacar, Teruel), the Danube Valley, and India, and they may have evolved later in Africa. The anancoid molars have a particularly oblique disposition, half of the cusps of each ridge overlapping the other half; this pattern cannot develop into the morphology of elephant molars.

Stegodon Falconer and Cautley is

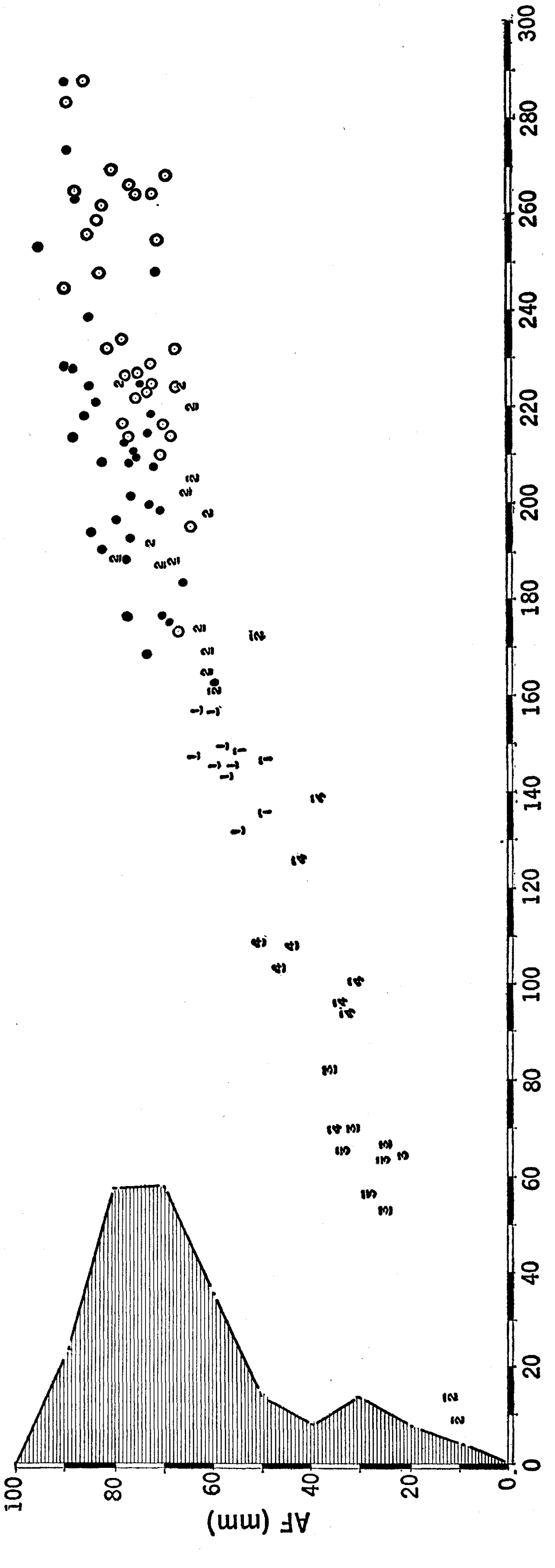

Fig. 3. Dispersion of well-preserved, half-worn molars of *Elephas antiquus* from Swanscombe, Torralba and Ambrona, Madrid, Toledo, Solilhac, Mauer, Steinheim, Rome, and Elisievich based on the width and length of their grinding surface at the time of death; *AF* represents functional width, that is, the widest section of a plate in the grinding surface, measured on the enamel; *LF* represents length of the grinding surface. Underlined numbers, upper molars; barred numbers, lower molars; open circles, lower last molars; solid circles, upper last molars. Numbers 2 to 4 in lower values, milk molars; numbers 1 to 2 in higher values, young adult molars.

an Asiatic genus that appears in the Early Pliocene. Its members are characterized by a short skull and short maxillar bones. The molars have crowns with a high number of ridges; these are roof-shaped and consist of little conules that are regularly multiplied; these ridges are separated by large V-shaped valleys. No longitudinal valley is marked; no central conules are visible. Elephant molars cannot derive from such teeth; thus the stegodonts are classified as a separate family, Stegodontidae Young and Hopwood (not a superfamily). Their ancestors reside in the Mastodontidae, where this peculiar morphology appears in an advanced form.

Since the Early Pleistocene, elephants have possessed parallel and rapidly multiplying plates in their molar teeth and very hypsodont crowns; however, over a long period, many have preserved in their former ridge-plates the longitudinal medial valley and a kind of residual central conule, which are typical features of the Gomphotheriidae Cabrera of the Miocene period. These features are still present to some extent in elephants and in several forms referred to as *Stegolophodon.* The elephant could have originated within or derived from this group.

Stegolophodon Schlessinger is a genus that appears in the Late Middle Miocene in Spain (*12*) and in the Siwalik Hills of India. It cannot be the transitional form between Mastodontidae in the narrow sense and *Stegodon* (*2, 9*), because *Stegolophodon* is less advanced in mastodontine trends. It has round or bunodontlike cusps and the mark of a longitudinal valley and central conules at least in the anterior ridges. Rather it could represent a branch of Gomphotheriidae, having characteristics convergent or isomorphic with those of the Mastodontidae-Stegodontidae; on the other hand, several African forms of *Stegolophodon* apparently display true elephantine characteristics such as higher hypsodonty, thinner enamel, a rapidly increasing number of plates, and irregular multiplication of median conelets on the transversal ridge-plates.

Stegolophodon sahabianus Petrocchi has central conules in the two anterior valleys, a remarkable hypsodonty ($K = 0.62$), very thin enamel, and a dense subdivision of median conelets that resembles enamel folding. As with the elephants, the anterior portion of the molar teeth in this species, including a few plates, is gomphotheriumlike in morphology, whereas the rest is more characteristically elephantlike; the former trait is inherited or conservative, and the latter is new and progressive. This Libyan species has lateral conules that are half-developed and that occlude the transversal valleys, a feature which appears later with characteristic frequency in *Elephas atlanticus* and *E. mnaidriensis,* and less frequently in other species (*13*).

Stegotetrabelodon Petrocchi is an important genus of Sahabi, also of the Pliocene age, and is represented by two species (*14*). Although it is not worthy of designation as a new family, it may represent a subfamily, Stegotetrabelodontinae, because of its particular position with reference to some evolutionary characteristics. This species has four tusks, the lower ones being regressive; the ridges of its molar teeth are gomphotheriumlike, with central conules in almost every transversal valley and with a longitudinal sulcus; there are eight ridges, which are hypsodont, with the conelets fusing near the top so that in half-worn ridges the enamel

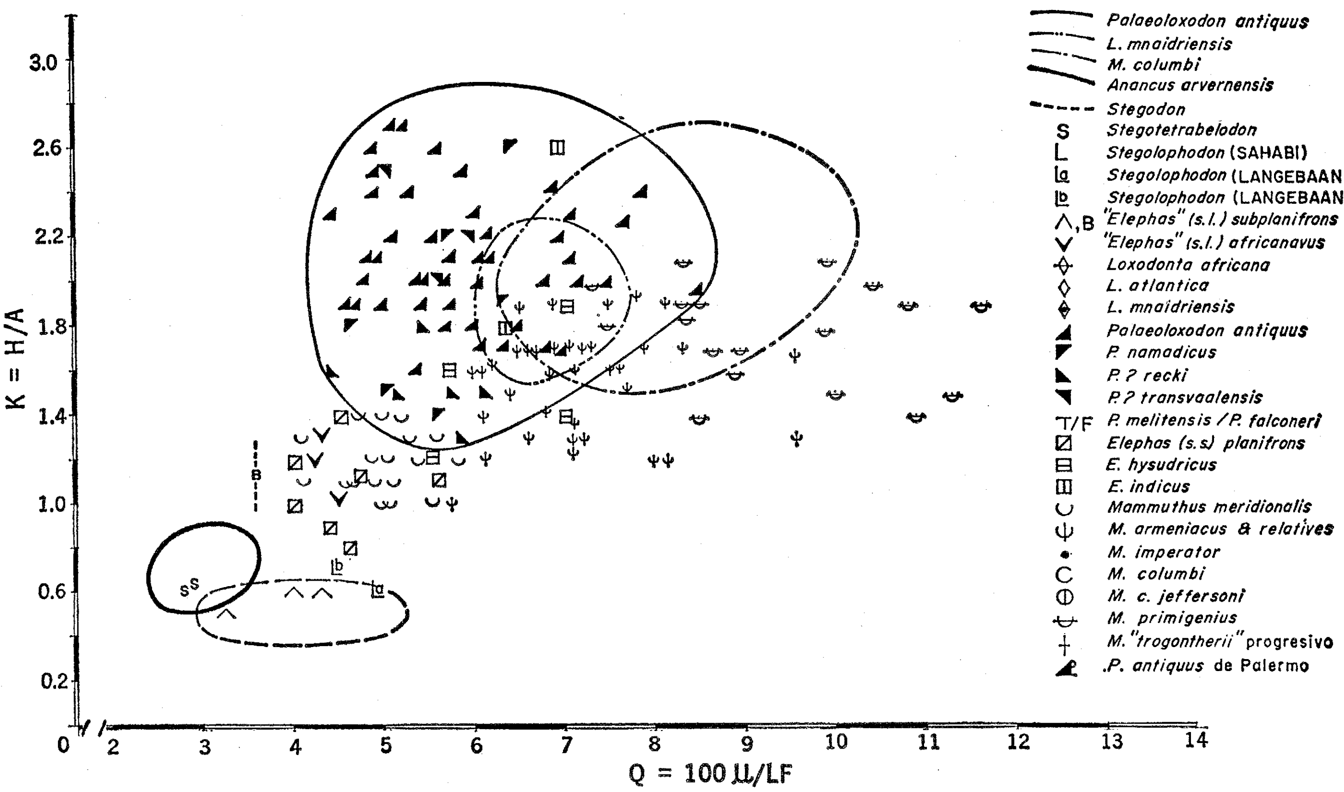

Fig. 4. Dispersion of 12 species of elephants and other proboscideans, relative to hyposodonty (K) and functional density of plates (Q). Data for the last upper molars of 170 specimens, half-worn and well-preserved, were plotted; U represents the number of plates actually functioning in the occlusal surface; LF, length of occlusal surface; H, altitude of a complete plate; A, maximum width. *Mammuthus imperator* and *M. columbi* not plotted.

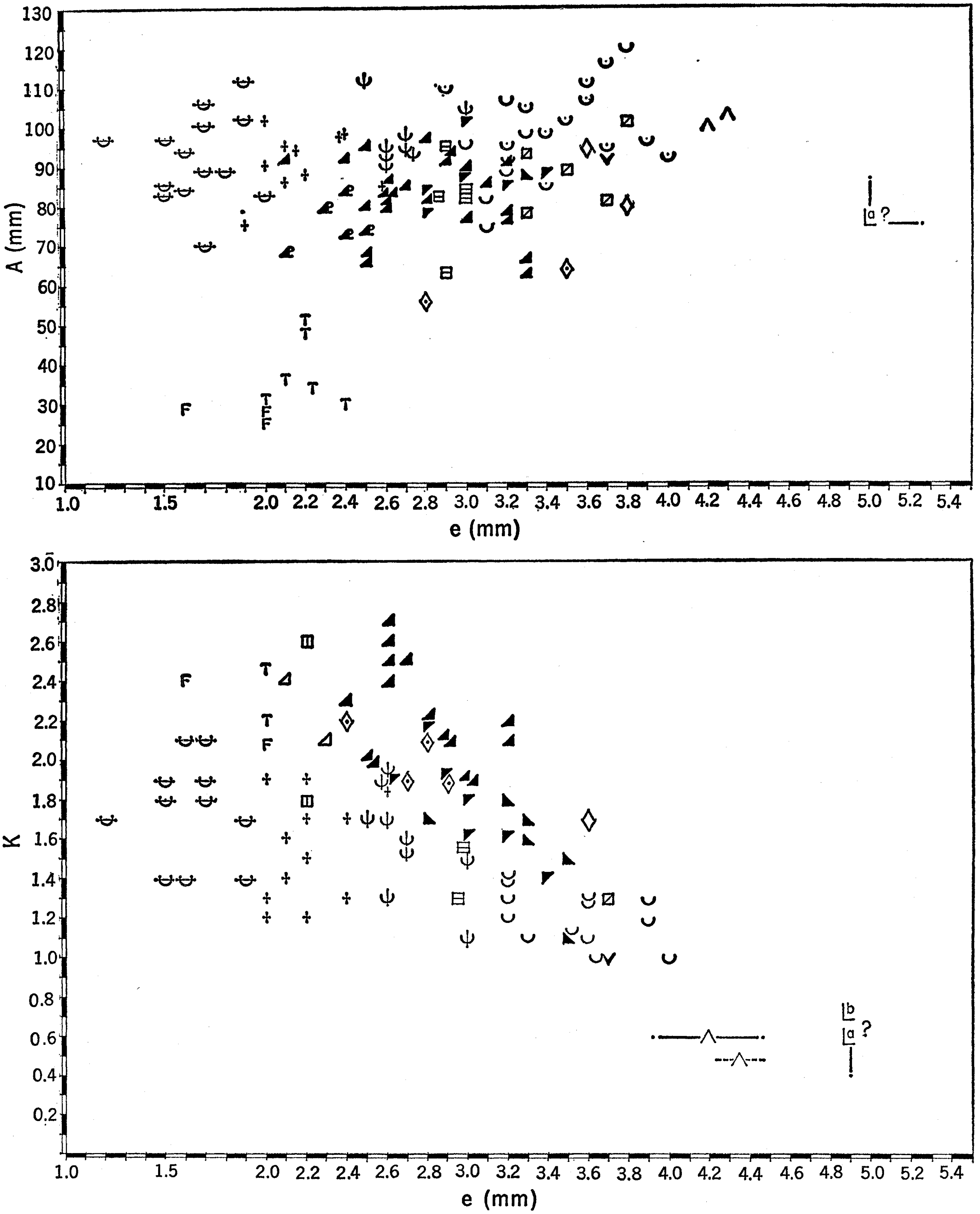

Fig. 5. (Top) Dispersion of grinding teeth of elephant according to absolute width (*A*) and mean thickness of the enamel (*e*) cover of plates. (Bottom) Dispersion of grinding teeth according to hypsodonty (*K*) and thickness of enamel. Symbols are those used in Fig. 4; *a* and *b*, two distinct forms of the Langebaanweg site known only by little fragments.

cover resembles the plates of primitive elephants. The section of its lower tusks is elliptic. In Granada I recovered the skull of a female *Elephas meridionalis* with elliptic section in both the proximal and distal portion of its upper tusks (*15*). Arambourg reports finding an elliptic-sectioned tusk among a population of *E. africanavus* in North Africa (*16*).

In Langebaanweg, South Africa, two forms have been collected, represented by very fragmentary remains. One form has been designated *Stegolophodon* sp. (*17*). I shall refer to it as form *a* and to the other as *b*. Three fragments of form *a* have ratios that fall within the dispersional area of *Elephas subplanifrons* and synonyms (*18*). These ratios might be slightly biased because they represent estimates on a fragment; no significant error is made in comparing a fragment of what is probably a second adult molar with a third molar, for such characteristics as mean thickness of enamel and hypsodonty; however, the functional densities of the plates (*Q*) in molar 2 (M2) and molar 3 (M3) are somewhat different (*10*) (Figs. 1, 4, and 5). The second form, *b*, is represented by three minor fragments that appear to be relatively hypsodont, having a thin cover of enamel apparently similar to that of elephantine plates.

In South Asia there are several forms of *Stegolophodon* which are imperfectly known. As judged from the morphology of molar teeth, it is more reasonable to attribute the ancestry of Asiatic elephants to these than to any other proboscidean; however, there is no close evidence for such a descent. A preserved skull of a juvenile *Stegolophodon cautleyi* Lydekker very much resembles that of a juvenile *Elephas hysudricus* in almost every detail; however, the parietal bones are greatly expanded and elevated in the latter (*19*). Only minor changes are required to permit derivation of the skull of either *Elephas planifrons* or *E. hysudricus* Falconer and Cautley from this kind of skull with its narrow premaxillae and convergent alveoli, orbital rings in advanced position, high lateral parietal bones with a medial V-shaped valley, and a frontal bone that is laterally narrowed and dorsally flat.

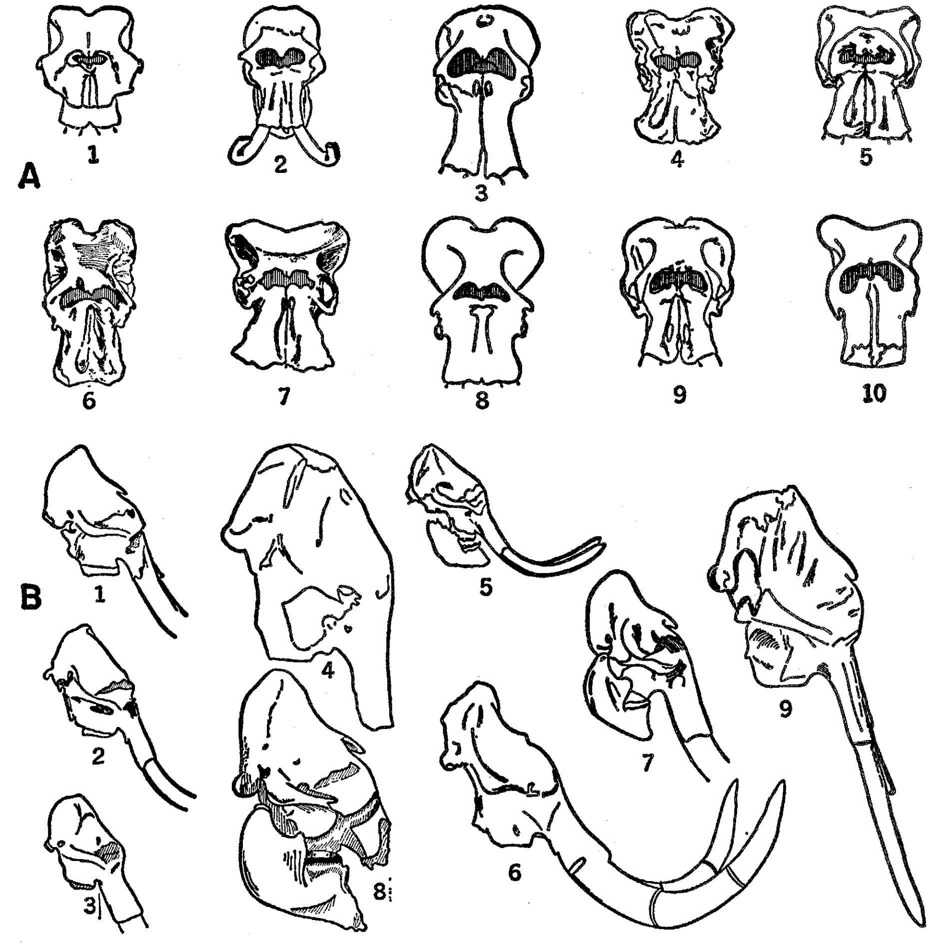

Fig. 6. Front view of the skull of various elephants (not to scale). (A) 1, *Elephas planifrons*; 2, *E. meridionalis*; 3, *E. primigenius*; 4, *E. antiquus "germanicus"*; 5, *E. africanus*; 6, *E. platycephalus*; 7, *E. mnaidriensis*; 8, *E. hysudricus*; 9, *E. indicus "dauntela"*; 10, *E. recki* (*26*). Lateral view of elephant skulls showing individual and sex variation within a phylum. (B) *Elephas primigenius* (1, male, 2, female); 3, *E. jeffersoni;* 4, *E. "primigenius hungaricus"*; 5, *E. "primigenius-trogontherii"*; 6, *E. primigenius "fraasi"*; 7, *E. jeffersoni* (*27*); 8, *E. primigenius* (*27*); 9, *E. primigenius "compressus."*

The question of the presence of true elephants in the Pliocene period of Europe is associated with that of the Plio-Pleistocene boundary. If this boundary is defined as the time of the first appearance of the faunal association of *Elephas, Leptobos,* and *Equus,* the entry of *Equus* is the closest identification of this boundary since *Equus* was the last to arrive in the Old World. Great complexity characterizes the Villafranchian fauna; but the name Villafranchian had been used formerly as the latest division of the Pliocene, and since 1948 it has been used synonymously with the Lower Pleistocene. Now its older beds, including the stratotype and the type locality for *Elephas meridionalis* Nesti, is recognized as Late Pliocene. Some remains from La Malouteyre and Rézols, France, and from Grosni, U.S.S.R., as well as *E. meridionalis gromovi* Garutt and Alexeieva from Rostov, U.S.S.R., also derive from the Late Pliocene (*20*). Elephants consequently originated some 4 million years ago, as judged by present standards, and are polyphyletic, having originated from separate lines of Stegolophodontinae, at least one Indian and another African.

Differentiation of Elephants

A few long-living species of elephants are known to have existed in the Early Pleistocene, and in the faunal revolution of the Early Middle Pleistocene these evolved into new species. These species extended from transitional forms to highly specialized forms which have become extinct. The two living forms are conservative and polymorphic representatives of a big family with many extinct branches or species.

Elephas meridionalis Nesti appears in Europe as a primitive species in the Late Pliocene. A sampling of 72 well-preserved, half-worn molars from Italy, Spain, England, Austria, France, and the U.S.S.R. exhibits a normal distribution and dispersion in diagrams, thus testifying to the unity of the species. The reported variations of the skull do not exceed the limits of the probable variability of a common specific pattern. The tusks of this species are known for their incurvature in two different planes, there being sexual dimorphism of this trait (*15*). The molars of *E. meridionalis* are heavy with thick cement and thick enamel, which is irregularly and randomly folded; the digitations of enamel (conelets) are deeply divided, a central section being more deeply separated; in occlusal figures of abrasion, a noticeable bend of enamel in an almost central position (a vestige of gomphotheriine central conules) is inconstant and irregular. The origin of this species is unknown. *Elephas planifrons* Falconer and Cautley has been assumed as its ancestor; however, *E. meridionalis* with its high, rounded skull could not have a contemporary ancestor such as the Indian elephant with its flattened frontal and parietal bones which tend to expand upward and sideward. *Elephas planifrons* has, on the average, higher values for the angle of eruption, which is an advanced characteristic. These two primitive forms originated independently. Notwithstanding the similarities in morphology of molar teeth and a wide overlapping in scatter diagrams for these two species, all remains attributed to *E. planifrons* in Europe have been shown to be those of *E. meridionalis* (*10*).

By the Early Middle Pleistocene, a new form appeared close to the geographical dominion of *E. meridionalis* which was better adapted to graze in the gramineous steppe. A higher number of plates, increased hypsodonty, thinner and narrowly folded enamel, reduced functional length, and wider angle of molar eruption are characteristic of *Elephas armeniacus* Falconer. That this form is identical with *E. trogontherii* Pohlig of the Danube River and Western Europe and with *E. wusti* of the U.S.S.R. is confirmed by the fact that in Capellini's Collection (Museum of Geology, Bologna, Italy) there are some specimens formerly identified by Falconer as *E. armeniacus*, whose cards have been corrected by Pohlig himself to *E. trogontherii.* The former name has priority, but the second has wider use. The species ranges from Seville, Spain, and southern England to Japan, and from central U.S.S.R. to Israel. The descent of *E. trogontherii* from *E. meridionalis* is suggested by their morphological and biometrical affinities and by their geographical distribution and chronology. It is difficult to distinguish some evolved forms of this species from the former steppe elephant in Hungary, northern Italy, and Voigstedt, East Germany. The transition from one species to the other could probably occur by way of isomorphic evolutionary trends through

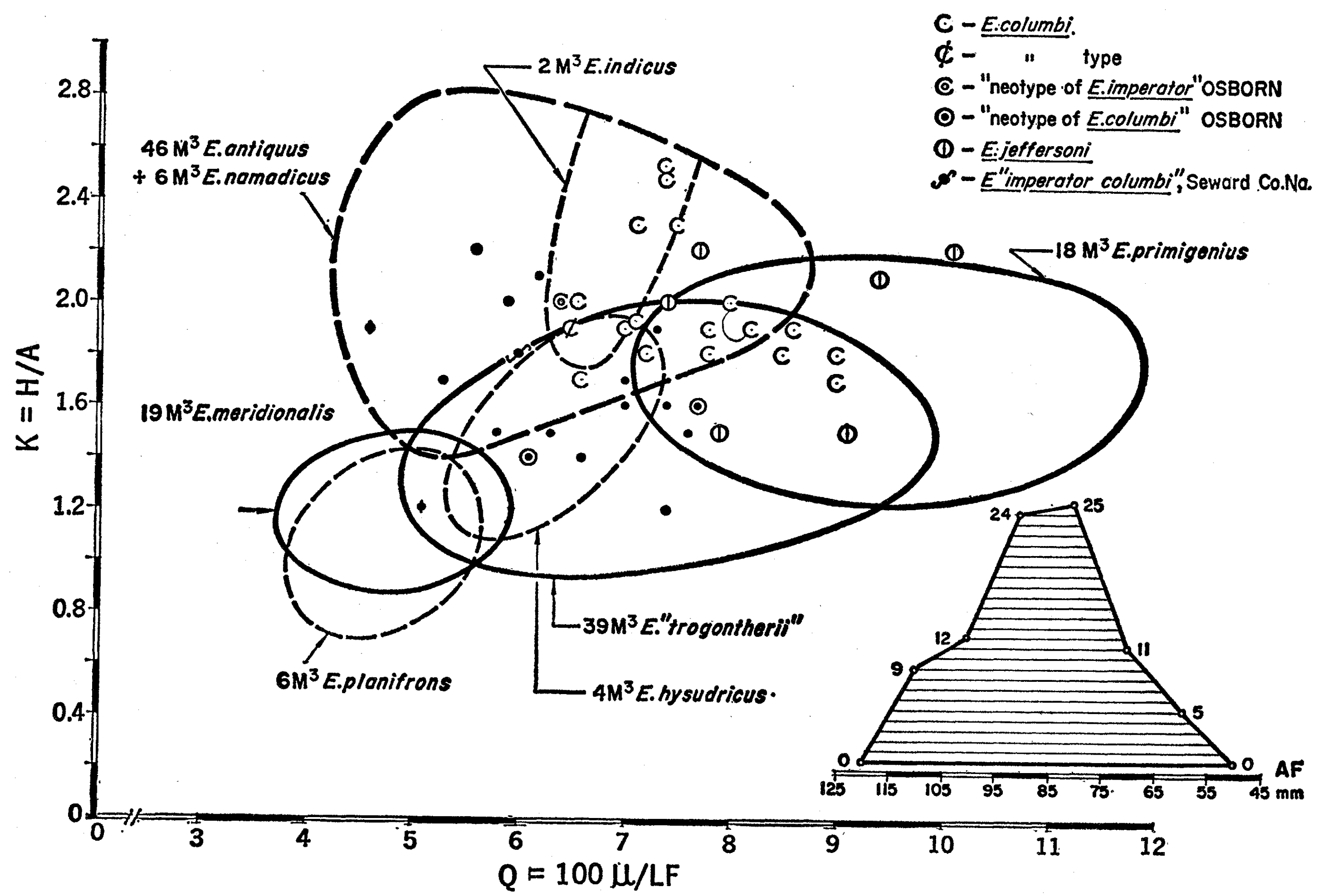

Fig. 7. Plotting of 43 specimens of the last (some penultimate) molars of American elephants (*Elephas primigenius* excluded), relative to hypsodonty (*K*) and functional plate-density (*Q*), compared to dispersional areas of the main species of the Old world (Fig. 4). American elephants are midway in the scale of those with high dispersion. Two species can be separated with transitional forms between them; there is also a late branching of *E. columbi*, with the characteristics of *E. jeffersoni* not consistently understood. The inset shows the histogram for the width of 86 adult molars of American elephants classified at present under two generic and ten specific names. The figures preceding the specific names indicate the size of the sample; for instance, 46 M^3 *E. antiquus* represents the dispersional area of 46 specimens of the last adult molar of *E. antiquus.* [*Elephas trogontherii* includes *Mammuthus armeniacus* and relatives, that is, the "progressive forms," as discussed in the text.] Simple dots: *E. imperator.*

natural selection in several contemporary populations.

In the Middle Pleistocene, this species rapidly progressed in the number of plates, hypsodonty, erupting angle, shortness of occlusal surface, and thinness of enamel. It split into various forms, maintaining a position midway between *E. armeniacus* and *E. primigenius* Blumenbach, which differed in the frequency of plates and hypsodonty, among others. All these represent a pool of forms from which *E. primigenius* originated by selection; thus it could be considered as a transient and polymorphic species. If so, the prior valid name for this group is *E. intermedius* Jourdan (names such as *E. trogentherii-primigenius* or *primigenius-trogontherii* are confusing). Its range is the same as that for the preceding species; this is also the original area for *E. primigenius,* which has an exceedingly high number of plates and a minimum thickness of enamel, but is not substantially advanced in hypsodonty. The result is an adaptation to the soft vegetation of the taiga and of the ephemeral warm season during the last glacial age; the new species extended to North America and was actively hunted by man on both continents. Evidence is lacking to support the existence of any valid subspecies of *E. primigenius,* which is everywhere a widely variable species (Figs. 4 and 5).

Immigration of elephants to North America did not occur frequently. The most primitive form was found in Pecos, New Mexico. The Irvington fauna, Gilliland formation, Seymour, Texas, contains a form of elephant which is advanced in several significant characteristics such as hypsodonty; a *K/A* age of 1.36 million years (*21*) consequently poses some questions. The skull and tooth morphology of all American elephants is decidedly similar to that of the whole phyletic group *E. meridionalis* to *E. primigenius,* the differences being irrelevant for a genus. The most primitive forms surpass *E. armeniacus* in significant trends as hypsodonty and could be the offspring of rapidly evolving immigrants derived from a population of *E. meridionalis.* If we recall the high individual variability of elephants and take into account the dispersion in scatter diagrams based on evolutionary trends, we can distinguish only two valid species of American elephants (Figs. 4 and 7)—*E. imperator* Leidy and *E. columbi* Falconer (*22*), both more or less polymorphic. *Elephas columbi jeffersoni,* since it has the highest number and frequency of plates, can be retained as a subspecies of the latter. The large Central Plains of North America seem more favorable to the preservation of species, through migration southward and northward following the advancement and retreat of ice, than do Europe and Asia, where the latitudinal disposition of geographical barriers favored instead evolution through selection. All forms mentioned above, from *E. meridionalis* through *E. primigenius* and *E. columbi jeffersoni,* thus belong to a phylogenetically well-defined genus, *Mammuthus* Burnett 1830.

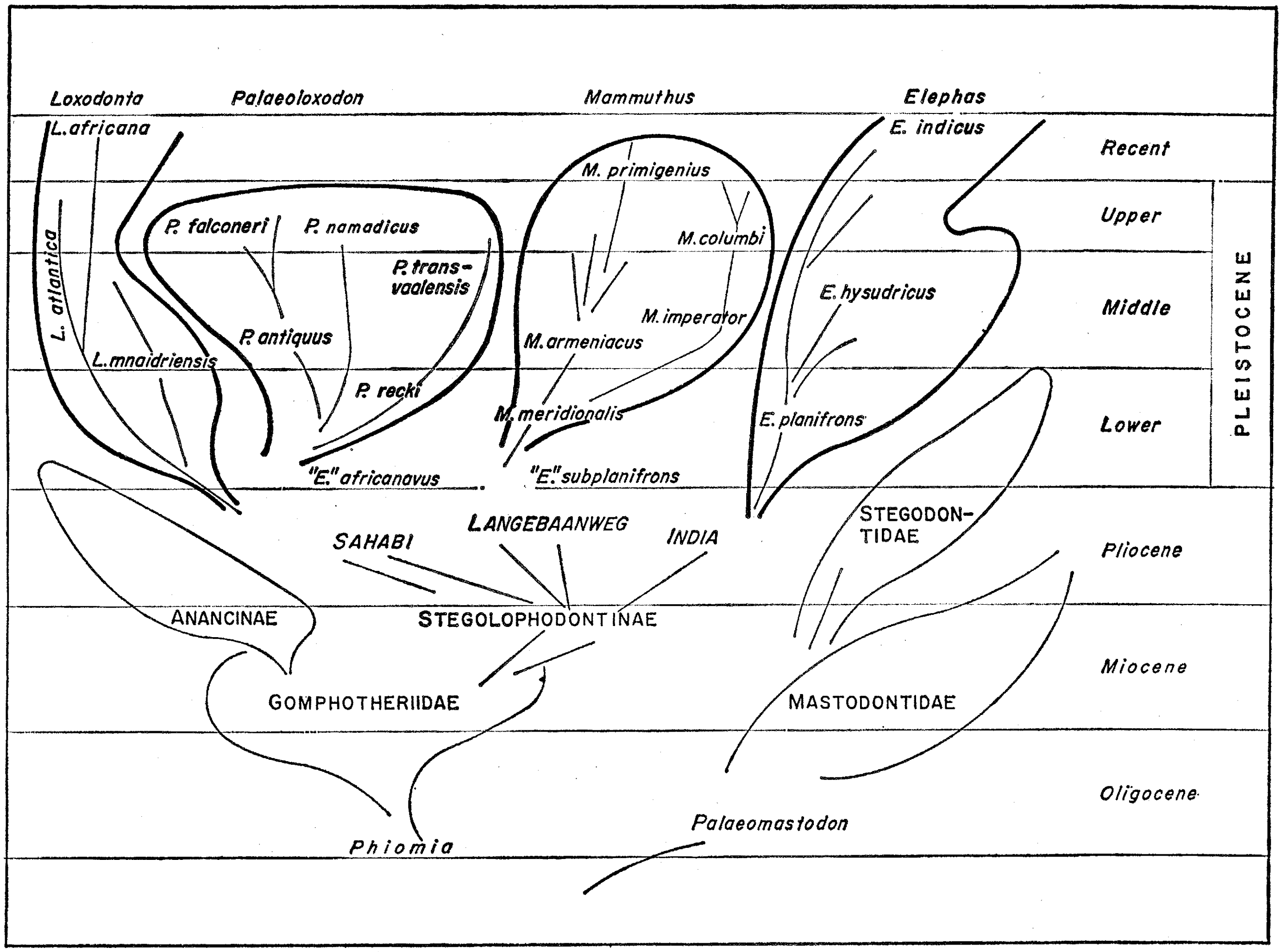

Fig. 8. Proposed phylogeny of Elephantidae.

Elephas antiquus Falconer, a European elephant certainly not known east of the Volga River, has affinities with the Asiatic *E. namadicus* Falconer, which has a similar original pattern of distribution and folding of enamel, general morphology of molar teeth and their plates, parietal expansion and frontal torus, and wide premaxillae with divergent tusks. Both are attributed to a different genus *Palaeoloxodon* Matsumoto. The oldest forms are difficult to distinguish as species. Later *P. antiquus* developed high, long, narrow molars with rather thick plates, a constant median fold of enamel (different from the typical loxodont sinus of the African elephant), and separate lateral rings of enamel at a stage of medium wear in the abrasional surface. Its ancient representatives with large molars and a primitive morphology seem to suggest a descent from *Elephas meridionalis*, but both the morphology and the ontogenic and sexual variations of the skull as well as the tusks and the evolutionary trends in some significant ratios fail to support the idea of a close common ancestor (Figs. 4 and 5). The same criteria seem to conflict with the idea that a close relation exists between *Elephas recki* of East Africa and *E. hysudricus*, as a result of a spectacular convergence of high lateral expansions of the skull; rather, the large forehead of *E. recki* and its rather flat parietal expansions and frontal torus, as well as its dental ratios and morphology, seem to relate it to *Palaeoloxodon* (Fig. 6). There is a list of specific names given to different specimens of an evolved form of *Palaeoloxodon* in South Africa: according to Cooke (*23*), these must be referred to *P. transvaalensis* Osborn. The Upper Pleistocene dwarf elephants from Sicily and other islands of the Mediterranean (*E. melitensis, E. falconeri*) derive from peninsular Italian populations of *P. antiquus* and consequently belong to the same genus.

An interesting African fossil elephant is *E. atlanticus* Pomel, which lived in the Early and Middle Pleistocene; it appears to be the unchallenged ancestor of the recent African elephant *Loxodonta africana*. The pattern of enamel distribution in the latter is oversimplified, and the enamel remains rather thick; forms transitional to it have been preserved from the Early Middle Pleistocene from *L. atlantica* (Pomel). This species is also characterized by a high frequency of individuals with lateral conelets detached from the ridge-plates that most frequently alternate with them and obliterate the transversal valleys; frequently deep angular folds of rather thick enamel concentrate in the median part of the plate, sometimes in a radiating pattern. Such features also occur in the half-size elephant of Sicily, *E. mnaidriensis* Adams, whose general morphology of grinding plates and thick enamel cover could never have originated from either *Palaeoloxodon antiquus* or *P. namadicus*. In some individuals the characteristics resemble those of the living elephant. Therefore I suggest that *E. mnaidriensis* Adams be included in the genus *Loxodonta* Cuvier. Its record in Sicily starts in the Sicilian stage (*24*) (the African continent and the central islands of the Mediterranean were probably linked in the Late Lower Pleistocene, that is, before the late main tectonic activity in the Mediterranean and East Africa). *Elephas mnaidriensis* is contemporaneous with *P. antiquus*, if not older, and its specialized skull morphology is strikingly similar to that of *P. antiquus* and its Asian relative. Still its affinity with *Loxodonta africana* cannot be denied. A close common heritage is very probable. On the other hand, it is very questionable whether and to what extent these species could hibridize.

Until new data (*25*) is published, we can tell very little about *E. africanavus* Arambourg, a primitive species of elephant in North Africa. The ratios for the few samples known to me fall in the range characteristic of *Mammuthus meridionalis*. Laminar density in the grinding surface is minimum; hypsodonty, being higher in numbers, represents a primitive stage as the larger section of the crown is in its basal part, with a conspicuous cingulum; the width is rather small; digitations of enamel are deeply separated; central conules are constant. All this closely resembles the gomphotheriine morphology of the North African Stegolophodontinae. This form can be related to the origin of *Loxodonta* or *Palaeoloxodon* more than to *Mammuthus*, and it overlaps in time with *P. recki*. It cannot be assigned to a genus at present. Let us call it "*Elephas*" in a wider sense. The same is true for *"Elephas" subplanifrons* Osborn (including *E. proplanifrons, E. andrewsi*) from South Africa, of an uncertain age, for which there are but a few specimens. These seem to represent the most primitive elephants both in morphology and in measurable trends (Figs. 1, 4, and 5) and could be related to a *Stegolophodon* in South Africa, such as one of those found at Langebaanweg.

In India and southeast Asia, *E. hysudricus* is probably a side-branch of a unique evolutionary line which corresponds to the phyletic group *Elephas* Linnaeus in the strict sense; its highly specialized skull with lofty parietal expansions and narrow frontal bone with lateral constrictions cannot mask a complex series of affinities with the living forms of *E. indicus* and also with the Lower Pleistocene *E. planifrons* (Fig. 6). *Elephas platycephalus* Osborn is a variation of this polymorphic phyletic group.

Summary

Polymorphism within each evolving branch, a wide range of variation, convergent adaptiveness, common heredity, large size, and overlapping of measurements make difficult the systematics of elephants. Only the identification of evolutionary trends may enable us to identify genera and species with sufficient reliability for regular samples.

It is uncertain to what extent many of the quantitative differences can be explained as simple variations resulting from local conditions of climate and food supply. Morphological variations are large; thus the affinities and trends in form have to be established carefully. It is probable that the diversification of elephants summarized in Fig. 8 relies on a genetic basis, and it is very difficult to decide at what moment the interbreeding of different forms has terminated.

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NEWS AND COMMENT

CBW: Pressures for Control Build in Congress, International Groups

The highly classified issue of chemical and biological warfare (CBW) is under intense public scrutiny this year as pressures build up to bring germ and gas weapons under stricter control. Several Congressional subcommittees have recently held hearings on aspects of the U.S. Army's CBW program and have subjected the Army's gas warfare experts to the most hostile questioning from Capitol Hill in a decade or more. A spate of books, television shows, and "educational" meetings held by scientific groups have tried to enlighten the public on the dangers of CBW. And at least three major international organizations, including the United Nations, are preparing detailed reports on the nature and effects of germ and gas weapons. These reports are expected to be the most comprehensive and authoritative analyses of CBW ever made public.

The net result of all this activity is that the public and its political leaders will be better informed about this secrecy-ridden subject than ever before, and the groundwork will have been laid for a serious drive to bring CBW under a strict arms-control agreement.

The recent inquiries on Capitol Hill are notable for their reflection of deep-seated hostility and skepticism among congressmen toward the military CBW program. The hearings have not yet produced a full-scale review of the entire CBW program. Indeed, they seem to have been launched almost by accident and have focused on convenient targets of opportunity, such as the safety of outdoor CBW testing and of dumping surplus gas weapons into the ocean. Nevertheless, persistent prodding by hostile congressmen has forced the Army to release new information about the American CBW effort.

Congressional concern this year has largely been sparked by Representative Richard D. McCarthy, a Democrat from Buffalo, N.Y., who happened to be sitting at home watching television with his wife in early February when he saw an NBC-TV documentary on CBW. McCarthy found the program "rather gripping and shocking" and, at the urging of his wife, set out to inform himself about the weapons. He first arranged a Pentagon briefing for 19 congressmen and senators. Then, finding that unsatisfactory, he fired off letters asking further questions of the Defense Department and other agencies.

In response to McCarthy's queries, the Pentagon, for the first time in several years, publicly revealed the dollar magnitude of the American CBW program. Expenditures for fiscal year 1969, according to John S. Foster, Jr., director of defense research and engineering, will total $350 million. The bulk of this—$240 million—is for procurement of smoke, flame, and incendiary weapons; tear gas; herbicides; and defensive equipment—all used primarily in the Vietnam War. Some $20 million has been spent for operation and maintenance of CBW facilities, and about $90 million has financed research, development, and testing activities, including work on the lethal agents that arouse the most fear and controversy. Foster stated categorically that the Pentagon is no longer procuring lethal chemical or biological agents for the weapons stockpile.

The Pentagon's figures have been disputed by some CBW critics. Congressman McCarthy finds it "difficult to accept" the $350 million estimate. And journalist Seymour M. Hersh, author of a book on CBW, has asserted that "CBW spending exceeds $650 million a year."

McCarthy has raised a number of broad policy issues during his crusade. He has questioned the tight secrecy