THE MICROSTRUCTURE OF PROBOSCIDEAN IVORY AND ITS APPLICATION TO THE SUBORDINAL IDENTIFICATION OF ISOLATED IVORY SPECIMENS

W. David Lambert[1]

Though relatively common as fossils, isolated proboscidean ivory fragments are difficult to identify below the ordinal level because of their lack of diagnostic gross morphological features. To help rectify this situation, the microstructure of ivory from a wide variety of proboscideans was surveyed, including *Zygolophodon*, *Mammut* (family Mammutidae), *Gomphotherium*, *Cuvieronius*, *Rhynchotherium*, *Amebelodon*, *Torynobelodon* (family Gomphotheriidae), *Elephas*, *Loxodonta*, and *Mammuthus* (family Elephantidae). On the basis of this survey, the following discoveries were made. 1) Medullar and cortical ivory of mammutids have microstructural features that allow them to be readily distinguished from those of gomphotheres and "typical" elephantids. 2) Gomphotheres and extant elephantids have identical medullar and cortical ivory. 3) *Mammuthus* medullar ivory is identical to that of extant elephantids and gomphotheres, but its cortical ivory strongly resembles that of mammutids; the two can be distinguished only by subtle features of the dentinal tubules. On the basis of these survey results, practical aspects of identifying isolated ivory fragments are discussed, as well as the evolutionary implications of observed ivory microstructural patterns.

Key Words: ivory microstructure; dentinal tubule; *Mammuthus*; *Mammut*; Gomphotheriidae

INTRODUCTION

Isolated proboscidean ivory fragments are among the most ubiquitous of late Cenozoic mammal fossils. However, though common, these specimens are generally difficult to identify to subordinal levels, except in some cases where biogeography provides extra clues (e.g., all fossil ivory from South America, where only a single proboscidean family is known, can be confidently referred to the family Gomphotheriidae [Simpson & Paulo-Couto 1957]). This difficulty in identifying isolated ivory fragments is unfortunate because such identification has a number of possible valuable applications, for example providing faunal and/or paleoecological information about a site otherwise unavailable, elucidating human hunting paleoecology from ivory artifacts, and aiding wildlife forensics in distinguishing legal *Mammuthus* fossil ivory from that of illegal extant elephants (Espinoza et al. 1990).

The basis for the difficulty in identifying proboscidean ivory below the ordinal level lies in the fact that, as a general rule, ivory fragments lack diagnostic morphological features at a gross scale. For example, unless one is fortunate enough to have at least a modestly complete specimen, even a large piece of *Mammuthus* tusk can be difficult to distinguish from that of *Mammut*. An enamel band on the upper tusk is considered diagnostic for typical gomphotheres sensu lato (e.g., *Gomphotherium*) and its absence diagnostic for mammutids such as *Mammut*. However, conservative mammutids like *Zygolophodon* may have enamel bands on their upper tusks, while upper tusks of some gomphotheres (as well as the elephantids as a whole) such as Old World *Anancus* and New World *Stegomastodon* may lack an enamel band altogether (Osborn 1936).

This lack of diagnostic gross features in proboscidean ivory has led some workers to look for subtler means of gleaning information from it. Espinoza et al. (1990) showed that the ivory of the living elephants *Loxodonta* and *Elephas* can be distinguished from that of extinct proboscideans, including a mammoth (*Mammuthus*), a gomphothere (*Gomphotherium*), and a mammutid (*Mammut*), by comparing the angles formed by the intersection of Schreger lines (often informally called cross-hatchings) common in proboscidean ivory. Similarly, Fisher et al. (1998) and Trapani and Fisher

[1]The Louisiana School for Math, Science, and the Arts, 715 University Parkway, Natchitoches, LA 71457; <dlambert@lsmsa.edu>

(2003) proposed that *Mammut* and *Mammuthus* ivory could be distinguished on the basis of differences in their Schreger line angles. Unlike the Espinoza et al. and Fisher studies where singular Schreger angle values were utilized to diagnose individual ivory specimens, Trapani and Fisher (2003) generated multiple angle measurements from individual ivory specimens that were subjected to discriminant factor analysis for identification.

Following a different approach, Saunders (1979) performed a comparative study of *Mammuthus* and *Mammut* ivory microstructure in which he showed that *Mammuthus* ivory could be distinguished from that of *Mammut* on the basis of differences in absolute dentinal tubule density, *Mammuthus* ivory having a greater density than *Mammut*.

The aforementioned methodologies have some practical limitations in their paleontological application. First, to different degrees they are restricted in their taxonomic scope. In all of these studies some proboscidean families are either represented by only a single genus (Mammutidae and Gomphotheriidae in the Espinoza et al. study, Elephantidae and Mammutidae in the Saunders study) or neglected altogether (Gomphotheriidae in the studies of Saunders, Fisher et. al., and Trapani and Fisher), so that there is a failure to account for the possibility of intrafamilial and/or intraordinal variation in ivory morphology. Secondly, potential practical difficulties exist in applying the results of these studies towards identifying small and/or isolated fossil specimens, since ivory properties can vary with position within a tusk and original positions of ivory fragments can be difficult to determine. For example, in the case of the Saunders methodology, which is based upon absolute dentinal tubule densities, dentinal tubule density in proboscidean ivory changes as one goes from the tusk medulla to the cortex (see below). Similarly, as noted by Fisher et al. (1998), Schreger line angles in tusks can vary significantly with both radial and linear location (for this reason, in their study they focused their examinations on the far cortical regions of the tusks). The factor analysis of Schreger line angles utilized by Trapani and Fisher (2003) can be used without such positional information, though this reduces the reliability of the resulting identifications significantly.

Considering the aforementioned difficulties with existing methods, a new, quick, and relatively simple method for identifying isolated pieces of ivory to subordinal or lower levels that does not require information about the original location of the specimen in the tusk could be valuable in a number of situations. One such promising method involves examination of ivory microstructure, particularly aspects of both dentinal tubule size and overall appearance that broadly and distinctively vary both with position within the tusk and between proboscidean taxa. This paper surveys this aspect of ivory microstructure over a significant though not exhaustive portion of proboscidean diversity, including the families Elephantidae, Gomphotheriidae, and Mammutidae, with examination of ivory from both the cortical and medullar regions of the tusks. In addition I discuss the specifics of how these ivory microstructural features can be used to identify ivory specimens to the ordinal level or below, as well as some implications of these features for the evolution of proboscidean tusk microstructure.

METHODS

Ivory from the following families and genera were examined, with each specimen reliably identified at least to the level of genus.

Mammutidae:
Zygolophodon proavus, SMNH P1665.1
Mammut americanum, UF 18505, and fig. 4 in
      Saunders (1979)

Gomphotheriidae:
Gomphotherium sp., UF 38262
Amebelodon britti, UF 135801
Torynobelodon sp. (uncatalogued specimen from the
      early Hemphillian Withlacoochee River 4A
      site in the collection of the Florida Museum of
      Natural History)
Rhynchotherium blicki, UF/FGS-5450
Cuvieronius sp., UF 6074

Elephantidae:
Elephas maximus, UF(M) 26156
Loxodonta africana, UF(M) uncatalogued
Mammuthus primigenius, UF/FGS 5357 and UF
      uncatalogued
Mammuthus columbi, fig. 3 in Saunders (1979)
Mammuthus sp., UF uncatalogued

All ivory fragments were examined under a scanning electron microscope (SEM) without a reflective coating, the hydroxyapatite in both fossilized and modern ivory being sufficiently electron reflective to allow sharp SEM images. The specimens were viewed in

longitudinal profile to provide a clear view of their dentinal tubules, dentinal tubules in proboscidean ivory radiate from the central region of the tusk roughly perpendicular to its long axis (Owen 1845; see below). In some, but not all cases, both medullar and cortical ivory from an examined tusk were observed to determine possible radial variation in morphology within the tusk. Medullar ivory samples were taken from the region near the tusk core, and when possible cortical ivory specimens were taken from the region approximately midway between the tusk core and its external surface. Because of logistical difficulties no attempt was made to systematically map ivory microstructural changes from the core to the external surface for any tusk, though a number of different medullar and cortical regions were examined for tusks of *Mammut*, *Mammuthus*, *Cuvieronius*, and *Rhynchotherium*.

Collection abbreviations are as follows: AMNH, American Museum of Natural History; SMNH, the Saskatchewan Museum of Natural History; UF, Florida Museum of Natural History, vertebrate paleontology collection; UF/FGS, Florida Geological Survey collection, now part of the UF collection; and UF(M), Florida Museum of Natural History, mammalogy collection.

THE STRUCTURE OF PROBOSCIDEAN IVORY

Before embarking on a descriptive survey of proboscidean ivory, it will be useful to briefly review its macro- and microstructure. Proboscidean ivory is largely composed of dentine, though it may have an external shell composed of cement. Ivory dentine, like that of vertebrate teeth in general, has a network of tubes called dentinal tubules that radiate from the central core of the tooth. In typical proboscideans these dentinal tubules are not structurally uniform throughout the tusk, but rather tend to branch dichotomously at acute angles as they extend from the central pulp cavity towards the external surface. They tend to be largest near the medulla and gradually become smaller as they extend outward into the cortex, becoming particularly small near the external cement shell. Thus, the absolute density and size of dentinal tubules varies with position within any given radial section of tusk (Owen 1845; Saunders 1979). In addition to the dentinal tubule, another important microstructural feature present in most if not all proboscidean ivory is a structure here referred to here as a dentinal ridge (Owen [1845] refers to this structure by the nondescriptive term opake cellule). A dentinal ridge is a tube of dentine that runs roughly parallel to the central pulp cavity of the tusk and perpendicular to the dentinal tubules, resembling a crudely linear ridge or swollen 'lake' in longitudinal profile.

SURVEY OF PROBOSCIDEAN IVORY MICRO-STRUCTURE

FAMILY MAMMUTIDAE

Medullar Ivory—*Zygolophodon* medullar ivory was unavailable for examination, so *Mammut* is the sole representative of the family for this type of ivory. The dominant feature of mammutid medullar ivory is a dense network of thick dentinal ridges (Fig. 1A). Dentinal tubules (appearing as distinct pits or pores in the dentinal ridge complex) are present, but highly scattered as compared with mammutid cortical ivory (see below). These dentinal tubules are relatively large compared to those of typical gomphotheroids, being easily visible at a magnification of only 300x (see below). This high relative density of dentinal ridges has not been observed in the medullar ivory of any other examined proboscidean taxa and appears to be a diagnostic feature, though whether for mammutids as a whole or *Mammut* in particular is as yet uncertain.

Cortical Ivory—At first glance the cortical ivories of *Zygolophodon* and *Mammut* appear distinctly different, with the surface of the *Mammut* specimen being much more regular in appearance than that of *Zygolophodon* (Fig. 1B-C). However, this difference is in all likelihood taxonomically insignificant, this aspect of ivory microsurfaces varying considerably among proboscidean individuals for unknown reasons. For example, the dentinal surface of a *Mammut americanum* specimen shown in Saunders (1979) is as irregular as the *Zygolophodon* ivory in Figure 1B, while similarly the *Mammuthus* ivory specimen shown in Saunders (1979) is much more irregular than that shown in Figure 3 below.

Surface regularity aside, the cortical ivories of *Zygolophodon* and *Mammut* are similar to each other and differ greatly from the medullar ivory described above in having a much higher density of dentinal tubules, with thick dentinal ridges embedded between them. Significantly, these dentinal tubules appear to be roughly the same size as those of the medulla. This dense packing of large dentinal tubules appears to be diagnostic for mammutid cortical ivory. Among the gomphotheroid taxa examined, a similar and possibly analogous condition was found only in the distantly related elephantid *Mammuthus* (see below).
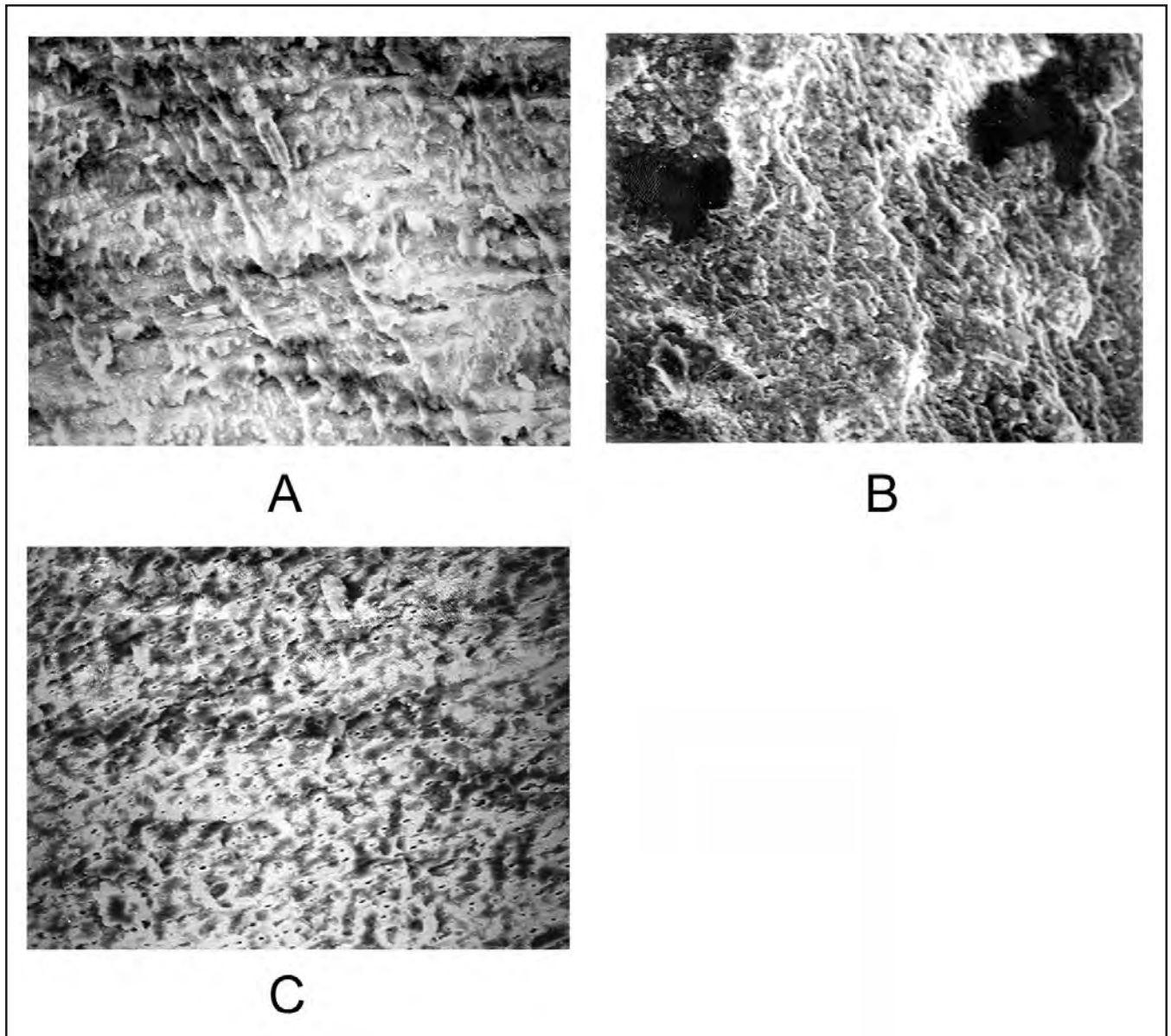
Figure 1. SEM photographs of mammutid ivory. A, *Mammut* medullar ivory, UF 18505, 300X; B, *Zygolophodon* cortical ivory, SMNH P1665.1, 300X; C, *Mammut* cortical ivory, UF 18505, 300X.

FAMILY GOMPHOTHERIIDAE

Medullar Ivory—The microstructure of typical gomphotheroid medullar ivory, including extant elephants (see below), differs considerably from that of the mammutids. In gomphotheres as in mammutids, the dominant microstructural feature of medullar ivory is a network of dentinal ridges (Fig. 2A-B). The density of these ridges however is significantly lower in gomphotheres, with fairly large expanses of featureless dentine present that are absent from mammutids (The careful observer will note that the dentinal ridge density is distinctly greater in *Gomphotherium* than in *Rhynchotherium*; however, this difference is presumably taxonomically insignificant, since the dentinal ridge density in gomphotheres for both medullar and cortical ivory varies as much as this or more across the surfaces of individual specimens). Another apparent difference between mammutid and gomphothere medullar ivory lies

in the size difference of their medullar dentinal tubules, the considerably smaller ones in gomphotheres being invisible at a magnification of 300x (Fig. 2A-B) and not appearing until a magnification over 1000x is attained (Fig. 2C). In addition to simple size, the medullar dentinal tubules of gomphotheres differ from those of mammutids in being more densely packed.

Cortical Ivory—Like the medullar ivory, cortical ivory microstructure is broadly consistent among the gomphothere taxa observed. Gomphothere cortical ivory is not dramatically different in appearance from that of the medulla. At a magnification of 300X, the primary visible difference between the two is a somewhat greater density in the dentinal ridges and smaller featureless dentinal expanses in cortical ivory (Fig. 3A-B). Considering the degree to which this feature varies in the figured specimens in both regions, it should be considered an unreliable basis for identifying the source tusk region
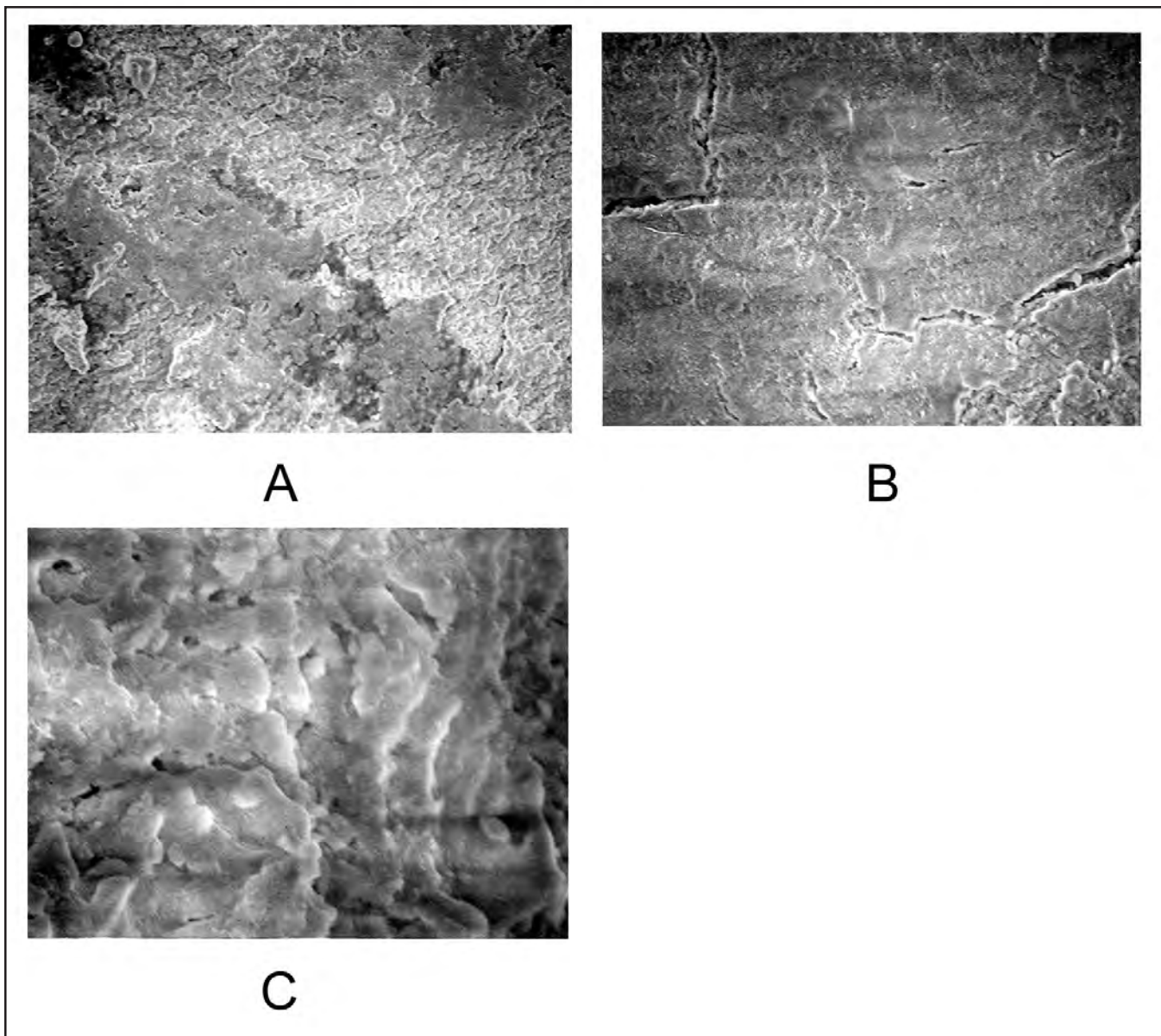

Figure 2. SEM photographs of gomphothere medullar ivory. A, *Gomphotherium*, UF 38262, 300X; B, *Rhynchotherium*, UF/FGS 5450, 300X; C, *Rhynchotherium*, UF/FGS 5450, 1500X.

for isolated specimens. Also, as in medullar ivory, the dentinal tubules in gomphothere cortical ivory are much smaller than those of mammutids (Fig. 3C-D), not being clearly visible below a magnification of 1500X in Figure 3C. It is noteworthy that while the specimens figured in Figure 3C and 3D both came from the same regions of their respective tusks, approximately halfway between the tusk core and the surface, there is a considerable difference between them in the relative development,

density, and size of their dentinal tubules. Specifically, those of *Torynobelodon* (Fig. 3D) are considerably more densely packed, better defined, and larger than those of *Gomphotherium* and typical gomphotheres (including modern elephantids; see below) as a whole. In evaluating the significance of these differences, it is worth considering that the gomphothere *Torynobelodon*, along with its sister genus *Platybelodon*, is characterized by the presence of unusual dentinal rods in its lower tusks
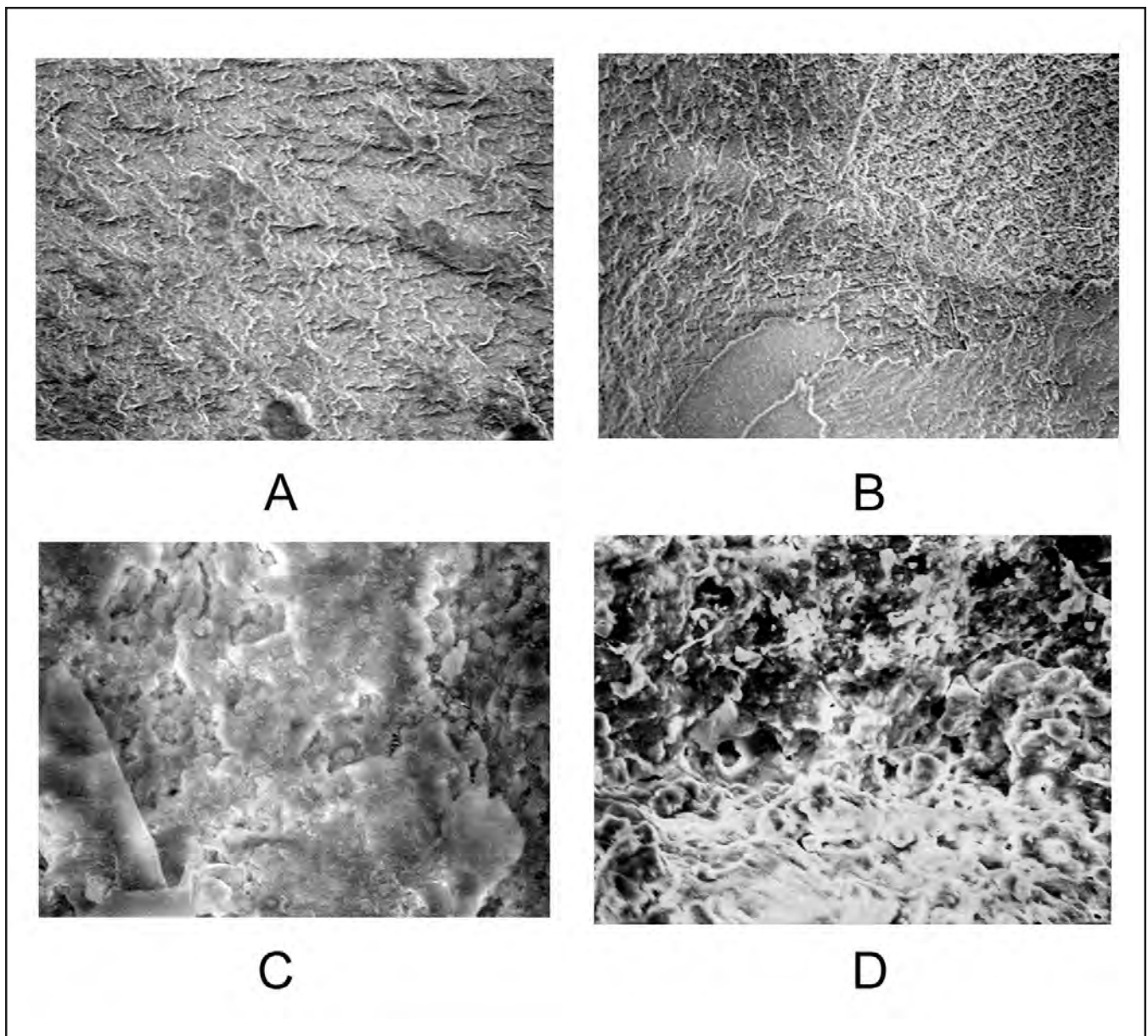

Figure 3. SEM photographs of gomphothere cortical ivory. A, *Gomphotherium*, UF 39050, 300X; B, *Amebelodon*, uncatalogued specimen in the Florida Museum of Natural History, 300X; C, *Gomphotherium*, UF 38255, 1500X; D, cf. *Torynobelodon*, uncatalogued specimen in the Florida Museum of Natural History, 1000X.
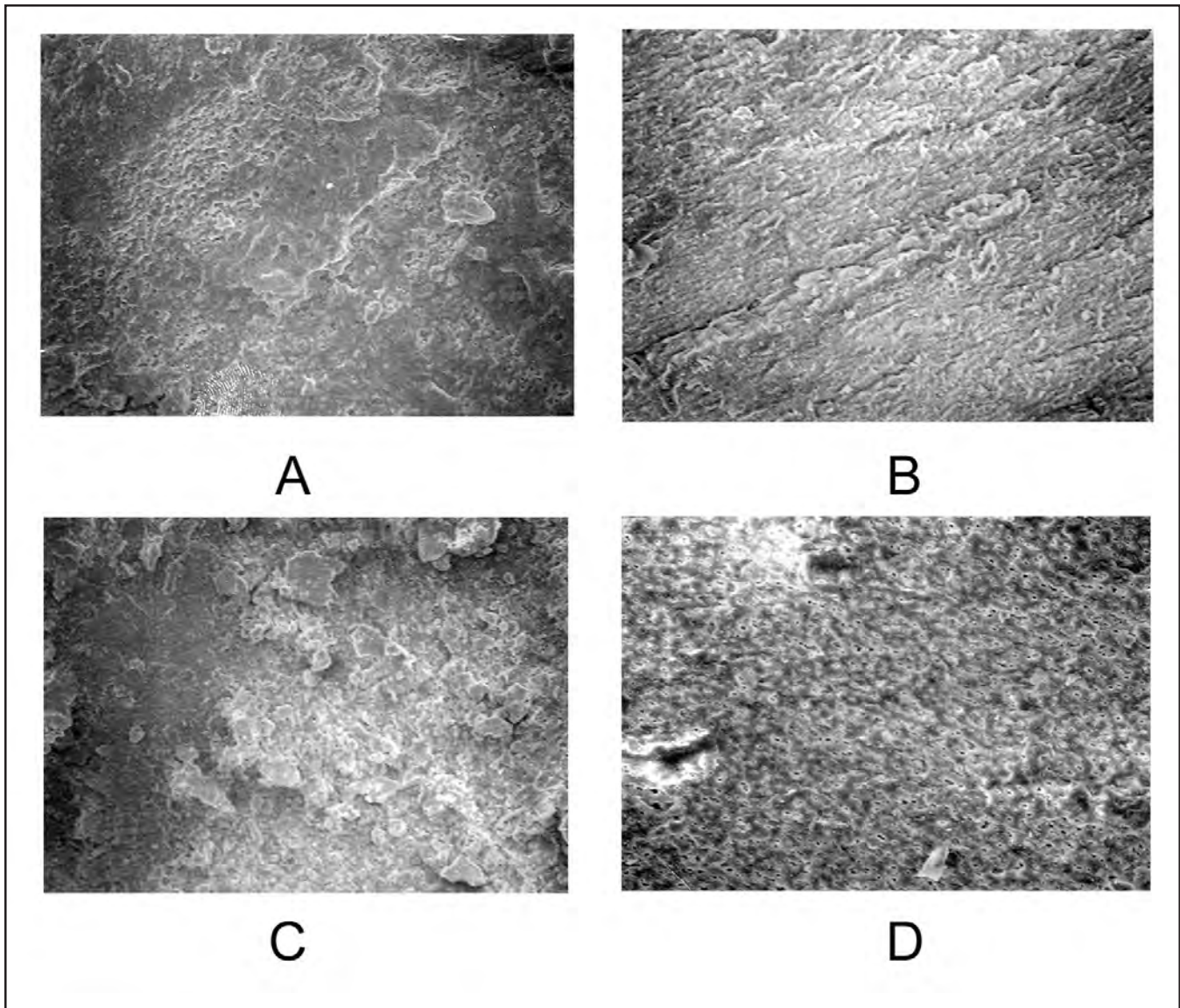
Figure 4. SEM photographs of elephantid ivory. A, *Elephas* medullar ivory, UF(M) 26156, 300X; B, *Elephas* cortical ivory, UF(M) 26156, 300X; C, *Mammuthus* sp. medullar ivory, uncatalogued specimen in the Florida Museum of Natural History, 300X; D, *Mammuthus primigenius* cortical ivory, UF/FGS 5357, 300X.

(Lambert 1990; Lambert 1996), the source of the ivory specimen in question. Thus, it is conceivable that the unusual features visible in the figured *Torynobelodon* specimen represent an autapomorphic, possibly adaptive, condition within this particular gomphothere lineage. An SEM examination of cortical ivory from other *Torynobelodon* and *Platybelodon* lower tusks would be useful in investigating this possibility.

Family Elephantidae

    Elephas maximus and *Loxodonta Africana*.—

In all aspects examined in this study, the medullar and cortical ivories of *Elephas* and *Loxodonta* are essentially indistinguishable from those of typical gomphotheres described above (Fig. 4A-B). Considering that the elephantids are direct descendents of gomphotheres (e.g., Coppens et al. 1978; Lambert & Shoshani 1998), I suggest that this condition is plesiomorphic for the group.

    Mammuthus—Of all the examined gomphotheroid proboscideans (i.e., gomphotheres and elephantids), only *Mammuthus* stands out as being significantly different in its ivory microstructure. The medullar ivory of

Mammuthus is basically indistinguishable from that of a typical gomphotheroid, with an abundance of dentinal ridges and relatively small dentinal tubules (Fig. 4C). However, its cortical ivory differs drastically from the gomphotheroid condition, and rather resembles the mammutids in having densely packed, relatively large dentinal tubules confluent with short, thick dentinal ridges (Fig. 4D). Nevertheless, despite their strong superficial similarity, *Mammuthus* and mammutid cortical ivories can be distinguished on the basis of subtle differences in their dentinal tubules. Neighboring dentinal tubules tend to be isolated in mammutids, with little tendency for their walls to touch. In *Mammuthus*, neighboring dentinal tubules tend to be distinctly contiguous, commonly merging to form large, often strangely shaped tubules. It should be noted that these characteristics do not apply to every single mammutid and *Mammuthus* dentinal tubule; some adjacent dentinal tubules in a mammutid may be in close contact (though few actually merge), while some *Mammuthus* dentinal tubules may be isolated from their neighbors. However, this overall trend is strong enough that ivory specimens of these two taxa can usually be reliably distinguished, a useful attribute since these two taxa commonly overlapped geographically in North America during the Pleistocene.

DISCUSSION

IDENTIFYING PROBOSCIDEAN IVORY

From the preceding discussion, it is apparent that identifying a proboscidean ivory fragment to family or below on the basis of microstructure is not merely a matter of viewing a specimen under a SEM and picking out a simple diagnostic feature from the image. For example, the medullar ivories of all of the observed gomphotheroids are essentially indistinguishable, as are the cortical ivories of gomphotheres and typical elephantids as represented by *Elephas* and *Loxodonta*.

Excluding mammutids, which are distinct in both their medullar and cortical ivories (assuming that the medullar condition observed in *Mammut* is indeed representative of the mammutids as a whole), the reliability of the identification of any given proboscidean ivory fragment to the family level or below hinges on two factors: the relative completeness of the specimen, and a knowledge of proboscidean biogeography. For example, consider the hypothetical situation of a piece of ivory found at a site of late Irvingtonian or early Rancholabrean age in the southeastern United States. Biogeography restricts the possible identity of this specimen to one of three families, each represented by a single known genus: Mammutidae (*Mammut*), Gomphotheriidae (*Cuvieronius*), and Elephantidae (*Mammuthus*) (Kurten & Anderson 1980; Lambert 1996). However, actual identification of the specimen by SEM analysis to one of these families and therefore by deduction genus could prove to be either straightforward or else very difficult depending on a number of factors. If the specimen was fairly complete radially, preserving both medulla and cortex, or else belonged to *Mammut*, then identification would be reasonably simple since both the medullar and cortical ivories of mammutids are distinct from gomphotheroids, and the cortical ivory of *Mammuthus* is readily distinguishable from that of a typical gomphotheroid such as *Cuvieronius*. However, if the specimen was identified as gomphotheroid medullar ivory, then the identification of the specimen would probably have to be limited to gomphotheroid proboscidean ivory, family indeterminate.

These same considerations would apply when identifying ivory from any site where members of more than one proboscidean family potentially coexisted, though the relative difficulty of the situations could vary considerably. For instance, identifying a piece of ivory from a North American site older than the Irvingtonian would at least in principle be a simpler task than in the aforementioned hypothetical situation, since during this time the only families present on the continent were the Gomphotheriidae and the highly distinctive Mammutidae (Kurten & Anderson 1980). In contrast, identifying isolated ivory fragments from late Miocene and Pliocene age sites in Africa would be potentially a very complex task, since mammutids, gomphotheres, elephantids, and the unexamined stegodonts and deinotheres all coexisted on the continent during this time (Coppens et al, 1978; Tassy & Shoshani 1987). Thus, in conclusion, the more radially complete a given ivory specimen and the smaller the potential familial diversity of proboscideans at the site at which it was found, the simpler is the task of identifying that specimen on the basis of its microstructure.

THE EVOLUTIONAY SIGNIFICANCE OF IVORY MICROSTRUCTURE

Based on the results of this study, elephantoid ivory microstructure can be divided into three basic categories, the mammutid, gomphotheroid, and *Mammuthus* morphotypes. Excluding *Mammuthus* for the moment, it appears that a dichotomy within the elephantoid proboscideans arose when the gomphotheroids and mammutids diverged from an unspecified common an-

cestor in Africa during the Oligocene (Tobien 1996). Mammutid ivory is characterized by a medullar region that is dominated by a dense network of dentinal ridges with the cortical region containing large, structurally isolated dentinal tubules, while in the gomphotheroids both the medulla and cortex are relatively uniform with the dentinal tubules small. Which of these two conditions represents the plesiomorphic condition is unclear based on the available evidence, and could be an interesting avenue for future research.

This leads to the peculiar case of *Mammuthus*. *Mammuthus* is without doubt a gomphotheroid, and yet, unlike any other observed gomphotheroid, including the modern elephants, it has extremely large dentinal tubules in its cortex, very much like those of mammutids. The independent appearance of this distinctive feature in two separate lineages suggests the possibility of convergent evolution, which in turn implies some shared functional advantage. But if indeed this situation represents convergent evolution, then this begs the question of the utility of this particular ivory microstructure.

One possible answer is increased structural strength. Saunders (1979) hypothesized that tusk shape could be related to microstructure, some microstructures giving large tusks the capacity to absorb shock and thus resist breaking under impacts or even their own weight better than others. Compared with those of the other gomphotheroids, *Mammuthus* tusks are unusual in being exceptionally long, strongly curved, and spirally twisted (Kurten & Anderson 1980). This unusual shape must have subjected *Mammuthus* tusks to stresses not encountered by those of other gomphotheroids, and as suggested by Saunders these new stresses may have required *Mammuthus* tusks to evolve an ivory microstructure able to withstand them, one similar to that found in mammutid cortical ivory. However, the Saunders hypothesis in this context raises an interesting new question. If a mammutid-like cortical microstructure is especially well suited for withstanding internal stresses, why then is it found in mammutids, whose tusks are not significantly different in shape from those of typical gomphotheroids? Addressing this question is difficult, in part because the polarity of the mammutid condition is unknown. Indeed, it is conceivable that this condition did not have the same functional significance in these two taxa (for example, the flattened lower tusks of the shovel-tusked gomphotheres *Amebelodon* and *Platybelodon* were shown by Lambert [1992] to have very different uses in feeding despite their superficial similarity). Hopefully future research, such as phyloge-

netic analyses, computer simulations of the physical properties of these different ivory microstructures, and so on will allow these questions to be answered more satisfactorily.

ACKNOWLEDGEMENTS

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