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A PROPOSAL FOR A STANDARD TERMINOLOGY OF ANATOMICAL NOTATION AND ORIENTATION IN FOSSIL VERTEBRATE DENTITIONS

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ABSTRACT—There is little consistency in the notation and orientation terminology used in discussions of non-mammalian fossil vertebrate dentitions. The standardization of this terminology, as done in the medical and dental sciences, would facilitate all future research on fossil teeth. For mammals, we recommend following convention, where incisors, canines, premolars, and molars are abbreviated as In, Cn, Pn, and Mn (n = tooth number) in upper jaws and as in, cn, pn, and mn in lower jaws. Right, left, and deciduous teeth are indicated by **R**, **L**, and **D** (e.g., DP4, Rp2). For non-mammals, which can have dentigerous premaxillae, maxillae, and dentaries, as well as additional tooth-bearing bones (e.g., vomers, palatines, pterygoids, ectopterygoids, sphenoids, splenials, and even parasphenoids), we encourage identifying teeth using the bone abbreviation (e.g., pmn, mxn, dn, vn, paln). A number and slash (/) combination can be used to distinguish between multiple tooth rows (e.g., Pal1/n, Pal2/n), and specimen-specific maps can be created for very complicated dentitions. We suggest the use of the terms mesial and distal to designate tooth surfaces and directions facing toward and away from the mandibular symphysis. Labial is offered for those surfaces and directions facing the lips or cheeks and lingual for those facing the tongue. We offer the terms basal for the direction toward crown bases, apical for the direction toward crown tips, occlusal for views of the occlusal surfaces, and basal and root apical for views of crown bases and roots, respectively.

INTRODUCTION

Discussions of fossil vertebrate dentitions (mostly non-mammalian) generally lack a standard terminology of anatomical notation and orientation. Though this is largely an historical problem, it continues to plague recent works. To cite some recent examples, the ‘‘forward’’ facing surfaces of crowns have been described as both labial and anterior in osteichthyians (Purdy et al., 1996); as anterior in theropod dinosaurs and holotherian mammals (Erickson, 1995; Y. Wang et al., 1998); as mesial in hadrosaurid dinosaurs (Rodriguez-de la Rosa and Cevallos-Ferriz, 1998), and as medial in ornithopod dinosaurs (Lu, 1997). ‘‘Foreword’’ and ‘‘rearward’’ facing crown surfaces have been referred to as anterior and posterior in alligators (Williamson, 1996), elephants (Froelich and Kalb, 1995), creodonts (Lavrov and Emry, 1998), ursids (Stiner et al., 1998), squamates (Gao and Hou, 1996), marsupials (Goin and Candela, 1996), perissodactyls (Qi and Beard, 1996), theropods (Currie, 1987, 1995; Currie et al., 1990; Kirkland et al., 1993; Fiorillo and Currie, 1994; Rauhut and Werner, 1995; Hutt et al., 1996; Martill et al., 1996; Sereno et al., 1996; Carpenter, 1997; Dong, 1997a), prosauropod dinosaurs (Benton et al., 2000), ornithischian dinosaurs (Horner and Weishampel, 1988; Galton, 1995; Russell and Zhao, 1996; Lu, 1997), and in various other mammals and archosaurs (Biknevicius et al., 1996; Szalay and Trofimov, 1996; Kellner and Mader, 1997; MacFadden and Shockey, 1997; Kelly, 1998). These same crown surfaces have been referred to as both mesial and distal and anterior and posterior in armadillos (Vizcaíno and Bargo, 1998); as rostral and caudal in theropods (Harris, 1998); and as mesial and distal in toothed birds (Elanzowski and Wellnhofer, 1992), ichthyosaurs (Motani, 1996), suoids (Fortelius et al., 1996), argyrolagids (Sánchez-Villagra and Kay, 1997), sauropod dinosaurs (Dong, 1997b), hadrosaurids (Head, 1998), theropods (Bakker et al., 1988; Rowe, 1989; Britt, 1991; Farlow et al., 1991; Pérez-Moreno et al., 1994; Charig and Milner, 1997), phytosaurs (Hungerbühler, 2000), and various other reptiles (Willis and Molnar, 1997). ‘‘Outward’’ facing lateral crown surfaces have been described as lingual in ornithopods (Lu, 1997) and as both labial and buccal in hadrosaurids (Y. Wang et al., 1998). ‘‘Inward’’ lateral facing crown surfaces have been described as lingual in hadrosaurids (Rodriguez-de la Rosa and Cevallos-Ferriz, 1998). ‘‘Outward’’ and ‘‘inward’’ facing lateral crown surfaces have been described as either being external and internal or labial and lingual in theropods (Dong, 1997a); as lateral and internal in sauropods (Dong, 1997b); as labial and lingual in artiodactyls (Lucas and Emry, 1999), cervids (Azanza and Montoya, 1995), insectivores (X. Wang and Zhai, 1995), marsupials (Cifelli and de Muizon, 1998), armadillos (Vizcaíno and Bargo, 1998), feliforms (Albright, 1996), theropods (Hutt et al., 1996; Kellner and Campos, 1996; Charig and Milner, 1997), ornithischians (Dong, 1997c), sauropods (Upchurch, 1999), and osteichthyians (Kemp, 1997). These same surfaces have been described as buccal and lingual in marsupials (Muirhead and Filan, 1995; Kappelman et al., 1996; Wroe, 1996; Sánchez-Villagra and Kay, 1997), theropods (Kirkland et al., 1993), mosasaurs (Lingham-Soliar, 1998), hadrosaurids (Head, 1998), and ursids (Stiner et al., 1998); as labial and medial in ceratopsian dinosaurs (Dong and Azuma, 1997); and as medial and lateral in carnivores (Biknevicius et al., 1996), alligatoroids (Williamson, 1996), ornithischians (Hunt and Lucas, 1994; Galton, 1995, 1996; Russell and Zhao, 1996; Xu, 1997), sauropods (Sereno et al., 1994), and theropods (Sereno et al., 1996). There has been more consistency recently regarding the ‘‘top’’ or ‘‘working’’ surfaces of crowns: they have been generally referred to as the occlusal surfaces (Azanza and Montoya, 1995; Froelich and Kalb, 1995; Muirhead and Filan, 1995; Silverson, 1995; Albright, 1996; Renaud et al., 1996; Szalay and Trofi-

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mov, 1996; Cerdeño and Bond, 1998; Cifelli and de Muizon, 1998; Hand et al., 1998; Miller and Carranza-Castañeda, 1998; Prado et al., 1998; Vizcaíno and Bargo, 1998; Sankey, 2001). However, the presumed anatomical homologs of these surfaces (not necessarily the same functional surfaces) in theropods and ceratopsians have been referred to as coronal and apical (Erickson, 1995; Xu, 1997; Harris, 1998).

A review of volume 20 (issue 1) of the Journal of Vertebrate Paleontology (JVP) clearly illustrates a lack of nomenclatural standard in descriptions of fossil vertebrate dentitions. Of nine papers that discuss teeth and use some orientation terminology in this one issue of a single journal, four use the terms anterior and posterior (Benton et al., 2000; Gow, 2000; Norell et al., 2000; Peigné et al., 2000) and five use mesial and distal (Hungerbühler, 2000; Ortega et al., 2000; Rasmussen and Simons, 2000; Rose and Lucas, 2000; Weston, 2000) to discuss the same crown surfaces.

A lack of adherence to a strict anatomical nomenclature, of which the above examples are a symptom, can result in misapplications of terminology and confusion. This is exemplified in the description of *Probactrosaurus mazongshanensis* Lu, 1997, an iguanodontian ornithopod dinosaur for which two isolated maxillary (IVPP V. 11334-10, 11) and four isolated dentary crowns (IVPP. 11334-12–15) are known. Lu (1997) figured the ''outward facing'' surface of IVPP V. 11334-10 as the lingual view. However, while describing the primary ridge (Lu, 1997:35), an iguanodontian character that occurs on the ''outward facing'' surfaces of the maxillary and on the ''inward facing'' surfaces of the dentary crowns, he simply referred to this surface as lateral. Lu (1997) cited Norman and Weishampel's (1990) discussion of iguanodontid dentition, in which they explicitly addressed the primary ridge in the Iguanodontidae, and discussed *Probactrosaurus* Rozhdestvensky, 1966 specifically (although they used ''buccal'' for the ''outward facing'' surface). We therefore presume that Lu (1997) understood that he was discussing the ''outward-facing'' surface of IVPP V. 11334-10 when he applied the labels lingual and lateral. Additionally, Lu (1997) referred to the ''forward facing'' surface of IVPP V. 11334-12 as medial (Norman and Weishampel, 1990 used mesial) and then discussed the dentary primary ridge of *P. mazongshanensis*, referring to the surface in question (the ''inward facing'' surface) as both lingual (Lu, 1997:fig. 4d) and medial (p. 35). Lu's (1997) description of the dentition of *P. mazongshanensis* could be confusing to those unfamiliar with the details of iguanodontian dental anatomy (which is more than a simple matter of terminological preference). However, we believe the error here lies within language rather than anatomy and illustrates quite well the need to maintain a strict anatomical nomenclature.

The adoption of a standard terminology of anatomical notation and orientation for fossil dentitions, such as used for extant animals, would improve communication, reduce confusion, and facilitate all future comparative work done on teeth. Such a standard is generally followed in veterinary medicine (Getty, 1975; England, 1984; Dyce et al., 1996), anthropology (Brothwell, 1963; Swindler, 1976; Cruwys and Foley, 1986; Hillson, 1986), and oral biology (Peyer, 1968; Dahlberg, 1971; Phillips, 1971; Butler and Joysey, 1978; Scott and Symons, 1982; Fuller and Denehy, 1984; Tortora, 1995). If both the neontological and paleontological disciplines all used the same or very similar nomenclatural schemes (which is logical as fossil dentitions are the antecedents of modern ones), it would increase the interdisciplinary impact of the work done on teeth by all those involved and streamline our understanding of evolution as exemplified through dentitions. Indeed, we do not propose that everyone who works on dentition should adopt a new system. Rather, we simply recommend that what is, in most cases, current anatomical convention (e.g., see the **NA**, **NAV**, **NAA**) is followed. Again, this is less of a problem in works that address mammal teeth than those that are concerned with non-mammals.

It is ironic that vertebrate paleontology has not standardized dentition terminology and that the medical sciences have, as much of the anatomical terminology currently used in the latter fields was originated by Henry Fairfield Osborn, a vertebrate paleontologist. It is largely this vernacular that is most common in the veterinary, anthropological, and dental sciences, which will be discussed below. By indicating ''most common,'' we refer to the references cited above as well to a brief review conducted by Smith (2002) of dental nomenclature used in the 1999 editions of a number of biological journals that are concerned with dentition and compared with **JVP** and Journal of Paleontology (see Smith, 2002, for cited articles and data). While relying on established terminology as much as possible, we offer terms for those instances for which we have not found a satisfactory model in the literature.

Anatomical Abbreviations—**C**, canine, maxilla; **c**, canine, mandible; **d**, dentary; **D**, deciduous; **ect**, ectopterygoid; **I**, incisor, premaxilla; **i**, incisor, mandible; **M**, molar, maxilla; **m**, molar, mandible; **mx**, maxilla; **P**, premolar, premaxilla or maxilla; **p**, premolar, mandible; **pal**, palatine; **pm**, premaxilla; **ps**, parasphenoid; **pt**, pterygoid; **sph**, sphenoid; **spl**, splenial; **v**, vomer.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, USA; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MNHN-Bol-V**, Museo Nacional de Historia Natural, La Paz, Bolivia; **NMC**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **P**, Royal Saskatchewan Museum, Saskatoon, Saskatchewan, Canada; **QM**, Queensland Museum, Queensland, Australia; **TMP**, Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

Literature Abbreviations—**JM**, Journal of Mammalogy; **JP**, Journal of Paleontology; **JVP**, Journal of Vertebrate Paleontology; **NA**, Nomina Anatomica; **NAA**, Nomina Anatomica Avium (Handbook of Avian Anatomy, 2nd Edition, Publications of the Nuttall Ornithological Club 23, Cambridge, MA); **NAV**, Nomina Anatomica Veterinarina (Fourth Edition, prepared by the International Committee on Veterinary Gross Anatomical Nomenclature, Gent Belgium, 1992).

PROPOSED TERMINOLOGY OF DENTAL NOTATION

Mammals

Scientists who work on mammalian dentitions, whether in oral biology, the medical sciences, or paleontology, generally use one of two systems of notation terminology (e.g., Dyce et al., 1996). One system (Fig. 1a), which is more commonly applied to fossil mammals, identifies individual teeth using the abbreviation of incisors, canines, premolars, and molars as In, Cn, Pn, and Mn (where n equals tooth number), respectively, for upper jaws, and as in, cn, pn, and mn, respectively, for lower jaws. **D** can be used as a modifier (DP4, Di2, etc.) when discussing deciduous teeth in mammals that have an ontogenetic deciduous phase, and **R** and **L** can be used to indicate right or left (RP2, LDi2, etc.). In the second system, capital letters indicate permanent teeth and lower case letters indicate deciduous teeth. Additionally, the upper and lower tooth rows are indicated by superscripts and subscripts, respectively (I^1, P_2, i^2, etc.). This second system is often used in veterinary medicine (see Dyce et al., 1996). These systems are both effective and are almost universally employed. While a single standard of notation terminology for mammal teeth for all workers is desirable, there is no problem with either of the above notation schemes and the choice between them is rather arbitrary, al-

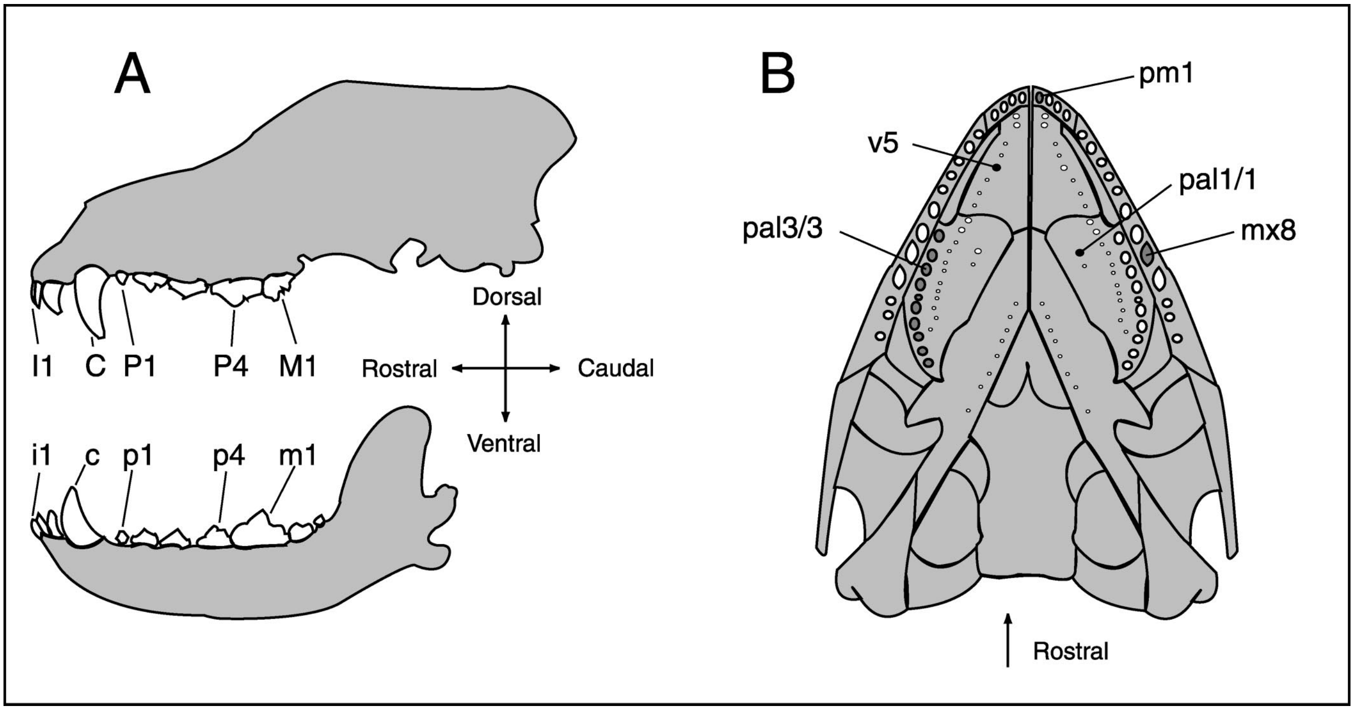

FIGURE 1. **A**, schematic canid skull in lateral view showing examples of proposed mammalian dental notation terminology. **B**, schematic sphenodontian skull in palatal view showing examples of proposed notation terminology for taxa with teeth on various bones besides the premaxilla, maxilla, and dentary (**A** modified from Dyce et al., 1996; **B** modified from Wu, 1994).

though there are some journals that prohibit the use of the superscript/subscript notation scheme (e.g., **JVP**, **JM**).

"Non-mammals"

For principal functional tooth rows of the vast majority of dentulous vertebrates (both mammal and non-mammal alike), tooth rows often begin on one bone and end on another (see Hillson, 1986; Carroll, 1988). A good example is the Permian tetrapod *Diadectes* Cope, 1878 (Fig. 2), which has two upper tooth rows, both covering multiple bones. However, whereas mammals have marginal dentitions situated exclusively in the premaxilla, maxilla and dentary, many non-mammals have additional tooth- and denticle-bearing bones such as the vomer, palatine, pterygoid, ectopterygoid, sphenoid, parasphenoid, or the splenial (Fig. 1b). We have not found an effective system of notation in the literature for such dentitions and thus propose numbering the teeth or denticles using the abbreviation for the bone, such that tooth number n increases from rostral to caudal on the bone (e.g., pmn, mxn, dn, vn, paln, ectn, ptn, sphn, psn, spln). As in mammalian taxa, **R** and **L** can be used to indicate right or left (Rpm2, Lpt4, etc.). Moreover, as such taxa often have multiple rows of teeth on individual bones (normally these are palatal teeth, but there are taxa with multiple rows of premaxillary, maxillary, or mandibular teeth), we would more precisely suggest using an additional number that would identify the specific tooth row. We propose having this number increase from the most medial tooth row. It is an arbitrary, but reasonable choice to number out from the midline (more important is standardizing the choice between numbering from medial or lateral). The row number is separated from the tooth number with a slash (/) (e.g., pal1/n, pal2/n; Fig. 1b), and again, crowns are numbered sequentially from the rostral end of the bone and **R** and **L** can be used to indicate right or left. It is also reasonable, though not essential, to designate upper jaw teeth using a capitalized bone abbreviation (Pmn, Paln, etc.) as is done for mammals (although all bones should be indicated with lower case abbreviations if non-dentigerous bones are also being discussed). This proposed notation terminology also works for taxa with highly derived tooth-bearing elements, such as the palatopterygoids and maxillopalatines of lissamphibians (Taylor, 1977) or the metapterygoids and dermopalatines of some fishes (e.g., amiids, see Grande and Bemis, 1998).

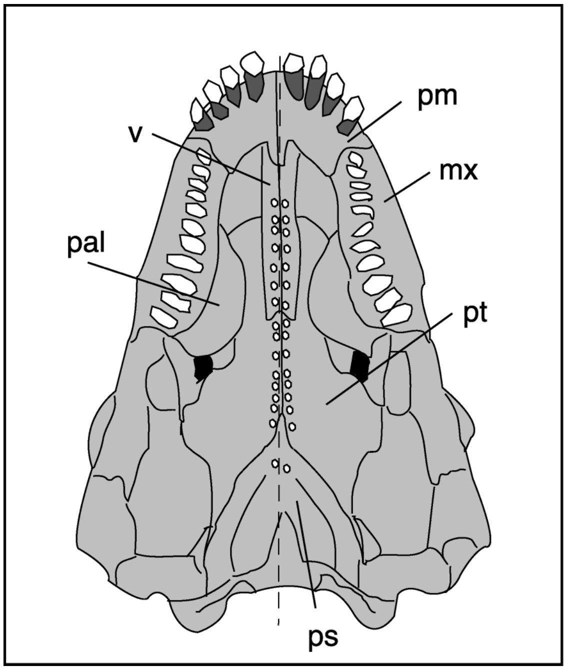

FIGURE 2. The skull of *Diadectes* in palatal view, illustrating how single tooth rows often cross multiple bones. Dashed line indicates sagittal plane (modified from Carroll, 1988).

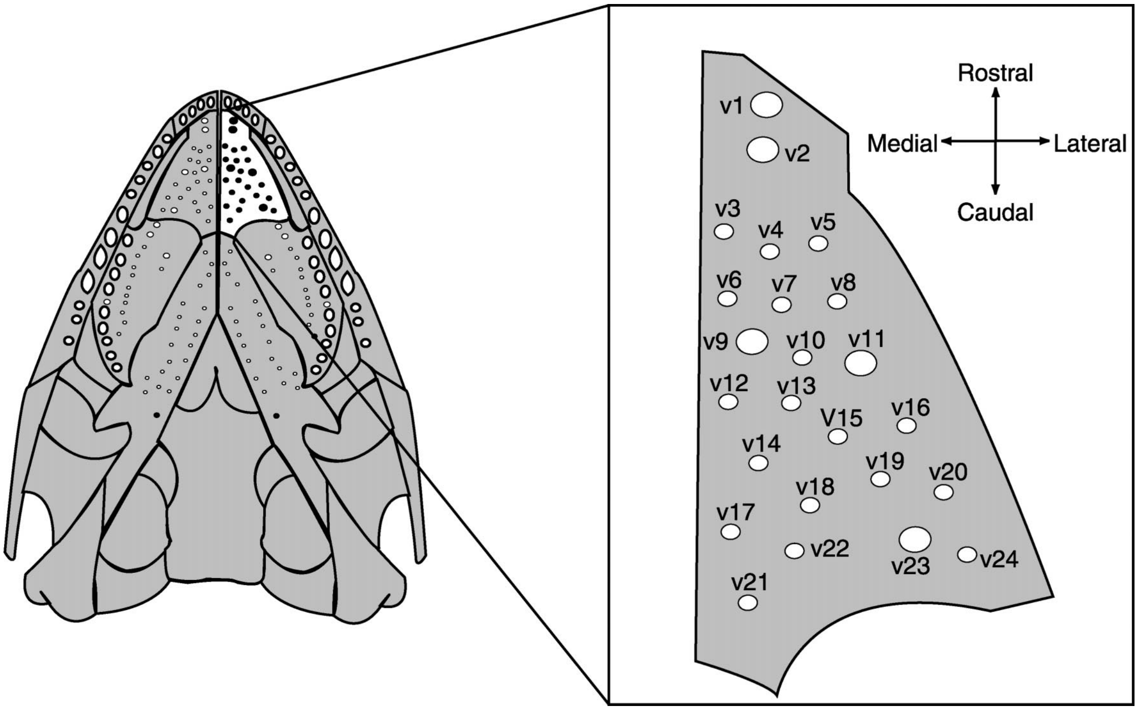

FIGURE 3. Schematic map of the left vomerine dentition in a sphenodontian skull (modified from Wu, 1994).

We have not found a reliable system of notation for those taxa with very complicated dentitions, such as multiple rows of premaxillary teeth or irregular or oblique rows of palatal teeth or denticles (odontoids) that have little symmetry and that involve multiple bones. These dentitions are common in actinopterygians, elasmobranchs, sphenodontians, sarcopterygians, and captorhinomorphs. For example, Trueb (1993) described a ''proliferation'' of teeth on the vomer of sirenid salamanders and Grande and Bemis (1998) discussed the buccal cavity of the actinopterygian *Amia calva* Linnaeus, 1766 as an ''impressively toothed region'' with dental elements on the parasphenoid, vomers, maxillae and premaxillae, and numerous palatal and mandibular bones (see Grande and Bemis, 1998:figs. 50, 52, 54, 58 for illustrations of other aspects of *Amia* dentitions). In instances when it is desirable to discuss a single tooth row or crown in such a dentition, visual representation is probably the most effective method of communication. The simplest system of notation might be to create and figure specimen-specific maps of a complicated dentition, such as a tooth patch in Figure 3 (see also Lewis et al., 1999:fig. 7). Welman (1998:fig. 1) figured the palatal dentition of the Triassic proterosuchian *Proterosuchus fergusi* Broom, 1903 in a similar way. He clearly showed the positions of the palatal dentitions, and used a numbering scheme to divide the pterygoidal teeth into four separate groups (Fig. 4a). With the addition of tooth numbers to his excellent figure (Fig. 4b), Welman (1998) could have additionally discussed within-row variation or even the details of a specific crown (e.g., one with an interesting paleopathological aspect).

PROPOSED TERMINOLOGY OF ANATOMICAL ORIENTATION

Concise, accurate, and effective orientation nomenclature is perhaps even more important than anatomical notation terminology. In paleontology, ''anterior'' is often the term that is used for that area of the tooth row or direction that is towards the front of the skull, and ''posterior'' for the area or direction that is towards the rear of the skull (Currie, 1987, 1995; Sereno and Novas, 1993; Fiorillo and Currie, 1994; Rauhut and Werner, 1995; Biknevicius et al., 1996; Dawson, 1996; Carpenter, 1997). However, these terms are problematic when applied to dentition. Anterior and posterior are terms from human anatomy that are designed to discuss bipedal animals such as primates. In primates, anterior designates the direction or region toward the front (i.e., abdomen and chest), and posterior refers to those areas toward the back (see Tortora, 1995). However, in quadrupeds the abdomen and chest face the ground rather than the direction of travel. Thus, in a quadruped, the direction toward the head is equivalent to the biped term superior, not anterior. To quote the **NAV** (p. 8), ''*Anterior*, *Posterior*, *Superior*, *Inferior*. These terms cannot be generally applied to quadrupeds because of the confusion arising from their meaning in human anatomy. The use of these terms is restricted to some structures of the head (see also **NAA**:1; Peyer, 1968:10).'' Indeed, it is current anatomical convention to use the terms cranial and caudal (and rostral and caudal within most parts of the cranium) as more effective descriptors than anterior and posterior when dealing with tetrapods (see Peyer, 1968; Dahlberg, 1971; Getty, 1975; Butler and Joysey, 1978; Tortora, 1995; Dyce et al., 1996). A discussion of whole body anatomical terminology is beyond the scope of this work, but we feel that there is generally less ambiguity and greater precision in the terms cranial, rostral, and caudal, as applied to quadrupeds, than there is in anterior and posterior.

Additionally, discussions of dentition are often at a scale of centimeters or millimeters, whereas cranial discussions are commonly at a scale of centimeters to decimeters and treatments of postcrania are typically at scales of centimeters to meters. Although cranial and postcranial elements can be as or more complicated than dentitions, cranial and caudal are generally effective directional terms at the scale that discussions of cranial and postcranial elements take place. However, when ap-

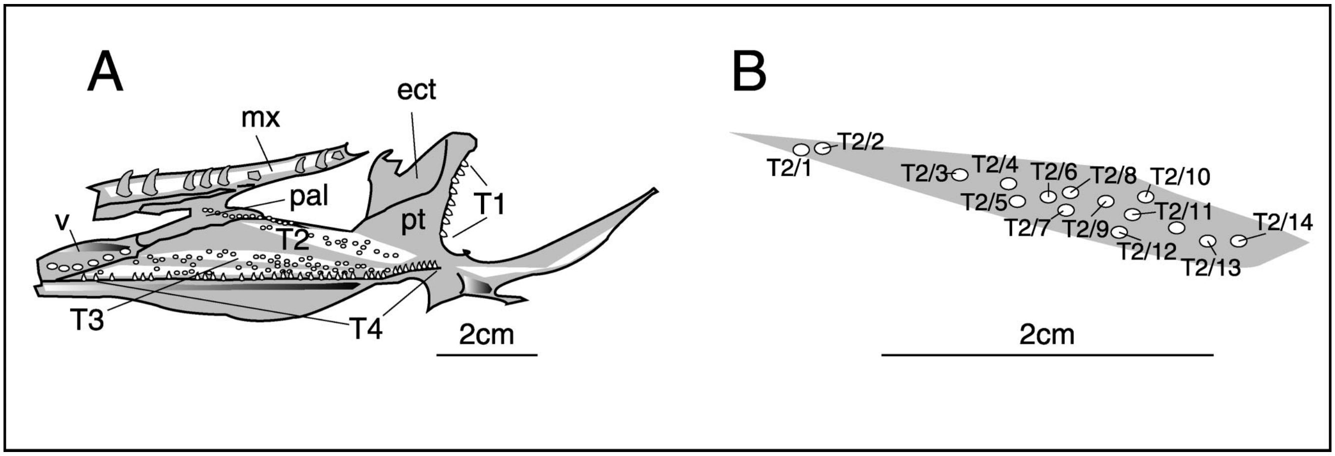

FIGURE 4. Reconstruction of the palate of *Proterosuchus*. **A**, Welman's 1998 figure, showing the distribution of the palatal teeth (T1–T4). **B**, map of the T2 tooth pavement with the addition of a numbering scheme, allowing for individual teeth to be identified (**A** redrawn from Welman, 1998).

plied to a small, complicated dentition where a high degree of precision is desirable, the effectiveness of whole-body terms decreases. Indeed, Dyce et al. (1996:109) made particular mention that ''the usual terms of relative position'' are inadequate to describe dentition and that a separate system is necessary. This is often true even for simple dentitions because jawbones frequently form parabolic curves and because palatal bones can be fairly complicated structures, resulting in jaws where the more caudal teeth are much farther from the midline than are the more rostral teeth. It is not very precise at this scale to describe a tooth as rostral to another when the two teeth are actually adjacent to one another, as are I1 and P1 in the phyllostomid bat *Mimon cozumelae* Schaldach, 1965 (Fig. 5a) or in the maxillary dentition of the Late Triassic rhynchosaur *Paradapedon* Chatterjee, 1974 (Fig. 5b). Referring to the teeth of *Paradapedon* as rostral to one another is clearly not appropriate and is potentially confusing. Incidentally, *Paradapedon* has a dentition that is well suited to the type of map illustrated in Figure 3.

There is an additional complication in that in many vertebrates, teeth change their orientations or their shapes across the length of the tooth row (we will use the long axis of the crown

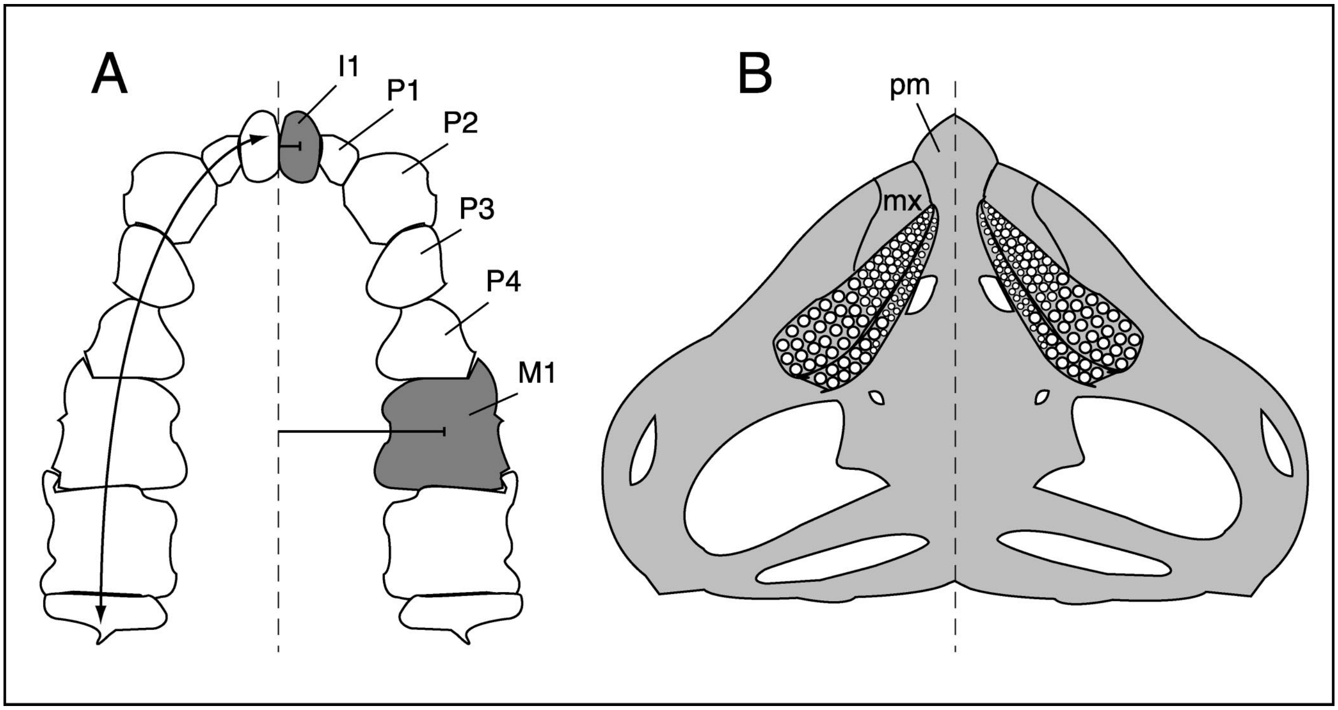

FIGURE 5. Examples of relative tooth positions within tooth rows. **A**, dental arcade of the phyllostomid bat *Mimon cozumelae* in occlusal view, showing the parabolic shape of the premaxillary and maxillary tooth rows (arrows). Notice that the center of the occlusal surface of M1 is 7.5× further from the sagittal midline (dashed line) than the center of the occlusal surface of I1. **B**, the skull of the rhynchosaur *Paradapedon* in palatal view, showing that the more caudal maxillary teeth are as much as 6× farther from the sagittal plane than the more rostral maxillary teeth (**A** modified from Cifelli, 1996; **B** modified from Carroll, 1988).

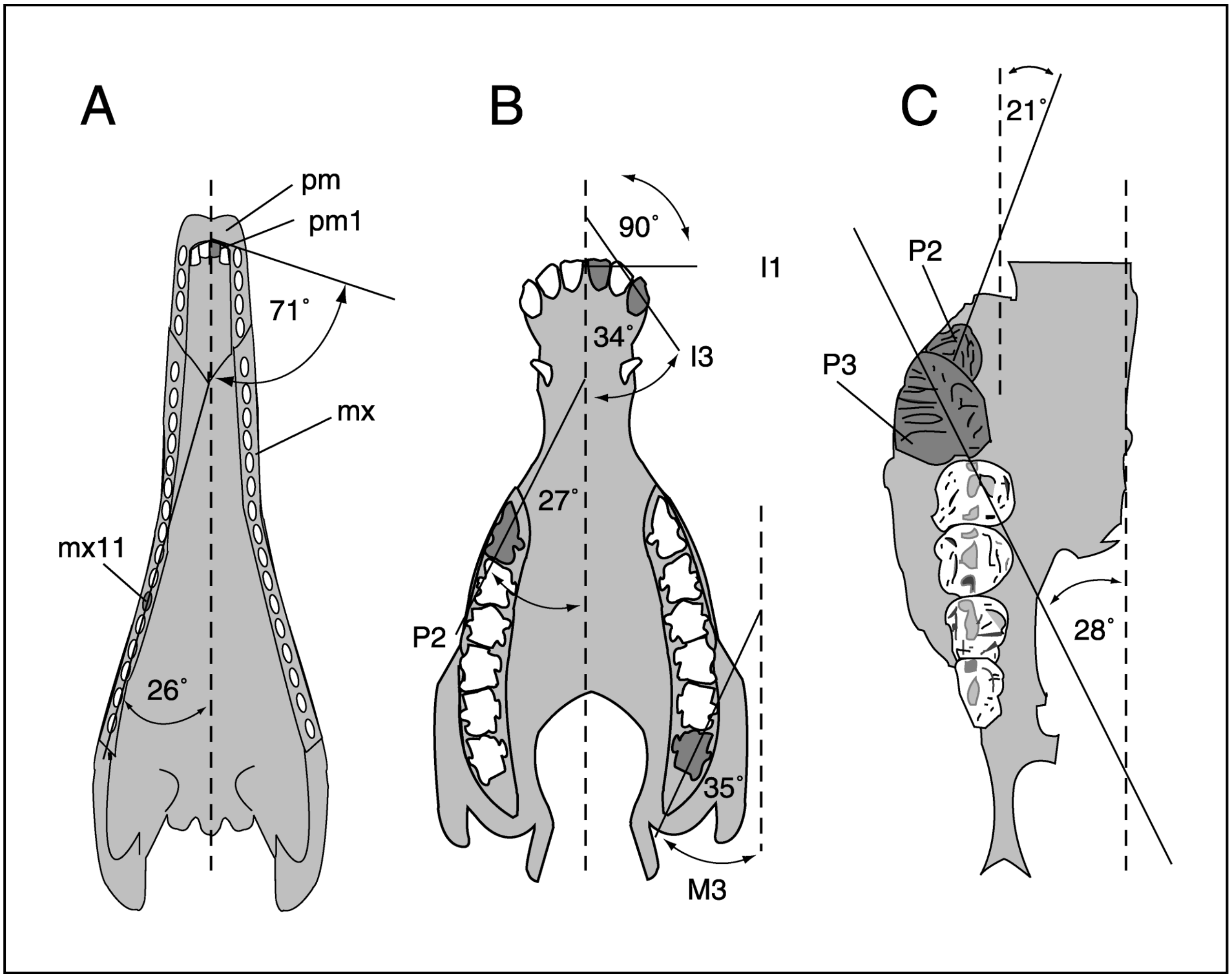

FIGURE 6. Intertaxonomic variation in crown long-axis orientation, compared against the median sagittal plane (dashed lines). **A**, the skull of *Proterosuchus* in palatal view, showing the 97° variation in long-axis orientation between Pm1 and Mx11 (71° + 26°). **B**, schematic upper dentition of an equid, showing the dramatic variation possible in long-axis orientation in some dentitions. **C**, right maxilla and palatine of the marsupial *Ekaltadeta ima* (QM F12436), showing the 49° difference in long-axis orientation between P2 and P3 Note: angle measurements are based from the illustrations and are schematic; they are not necessarily the exact values that exist on the specimens; **A**, modified from Carroll, 1988; **B**, modified from Dyce et al., 1996; **C**, modified from Wroe, 1996. All measurements are approximations.

base oriented in a horizontal plane and measured against the sagittal plane of the skull as the reference for this discussion). In a number of taxa, tooth rows curve enough that the crown long axes can significantly change orientation depending on where they are in the dental arcade. In homodont dentitions, this situation can result in the same faces of different crowns actually facing different directions across the length of the row. For example, the premaxillary and maxillary tooth rows in *Proterosuchus* form two distinct curves along their length such that there is a 97° difference in long-axis orientation between pm1 and mx11 (Fig. 6a). In heterodont dentitions, the situation is similar. In the equid in Figure 6b, it is obvious that long-axis orientations can change depending on where the tooth is located within the mouth. This schematic shows that not only can different teeth be located in significantly different relative positions from the midline (such as I1 and I3), but also that the long axis orientations can be significantly different (56° in Fig. 6b). Figure 6b also shows that these orientations can change so that teeth in the same tooth row can face both toward and away from the sagittal plane (the long-axis of P2 is orientated 27° toward the sagittal plane while the axis of M3 is orientated 35° away from it). The variation in long axis orientation is extreme in the Miocene marsupial *Ekaltadeta ima* Archer and Flannery, 1985 (QM F12436). In the palatal view of this specimen shown in Figure 6c, P2 is oriented 14° towards the midline and P3, the *next tooth* in line in the dentition, is oriented 28° away from it. Although P2 and P3 are in a fairly rostrocaudal relationship, the center of P3 is 1.19× further from the sagittal plane than the center of M1, the next tooth in line. With such variation in long-axis orientation possible in a single animal, relating tooth orientations either to the sagittal plane or to the rostral end of the skull is imprecise and potentially confusing.

The problem of crown orientation within tooth rows has been dealt with quite well in veterinary medicine (Getty, 1975; Dyce et al., 1996), in physical anthropology (Brothwell, 1963; Hillson, 1986), and in oral biology (Dahlberg, 1971; Butler and Joysey, 1978; Tortora, 1995) by relating the long axis of the tooth to the premaxillary and mandibular symphyses rather than to the median sagittal plane. Using this system (which arose from the early days of human dentistry because of the parabolic shape of the dental arcade), the more rostral direction along the tooth row and generally toward the jaw symphysis, regardless

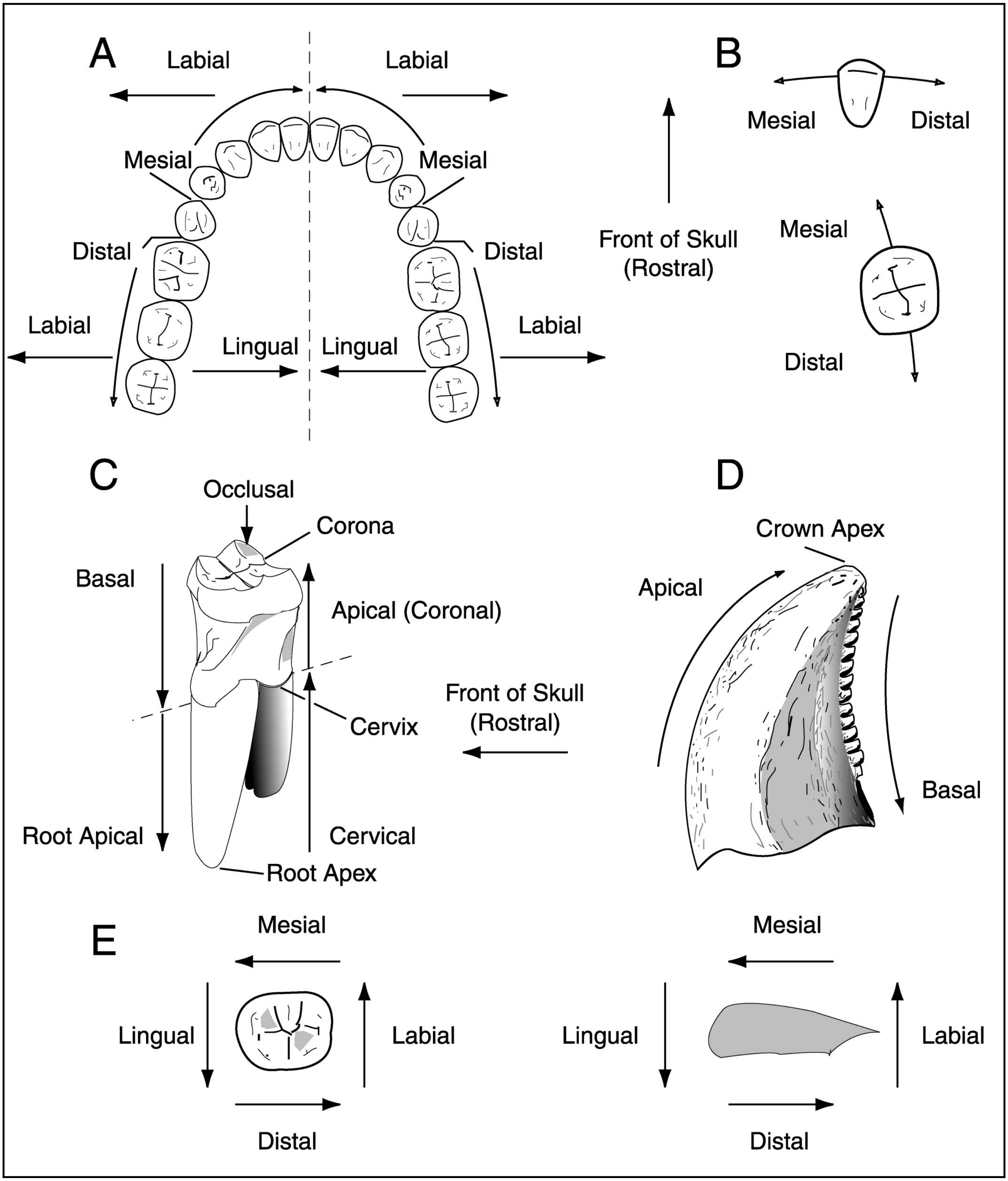

FIGURE 7. Proposed orientation terminology. **A**, idealized human dental arcade, in palatal view (dashed line represents median sagittal plane (concept from Hillson, 1986)). **B**, idealized I1 and M1 of a human in occlusal view, showing the mesial and distal surfaces. **C**, mammalian molariform tooth in lingual view. **D**, maxillary crown of the theropod *Saurornitholestes* Sues, 1978 (TMP 82.19.180) in lingual view (modified from Currie et al., 1990). **E**, corona of **C** in occlusal view (left) and mid-crown cross-section of idealized theropod maxillary tooth (right).

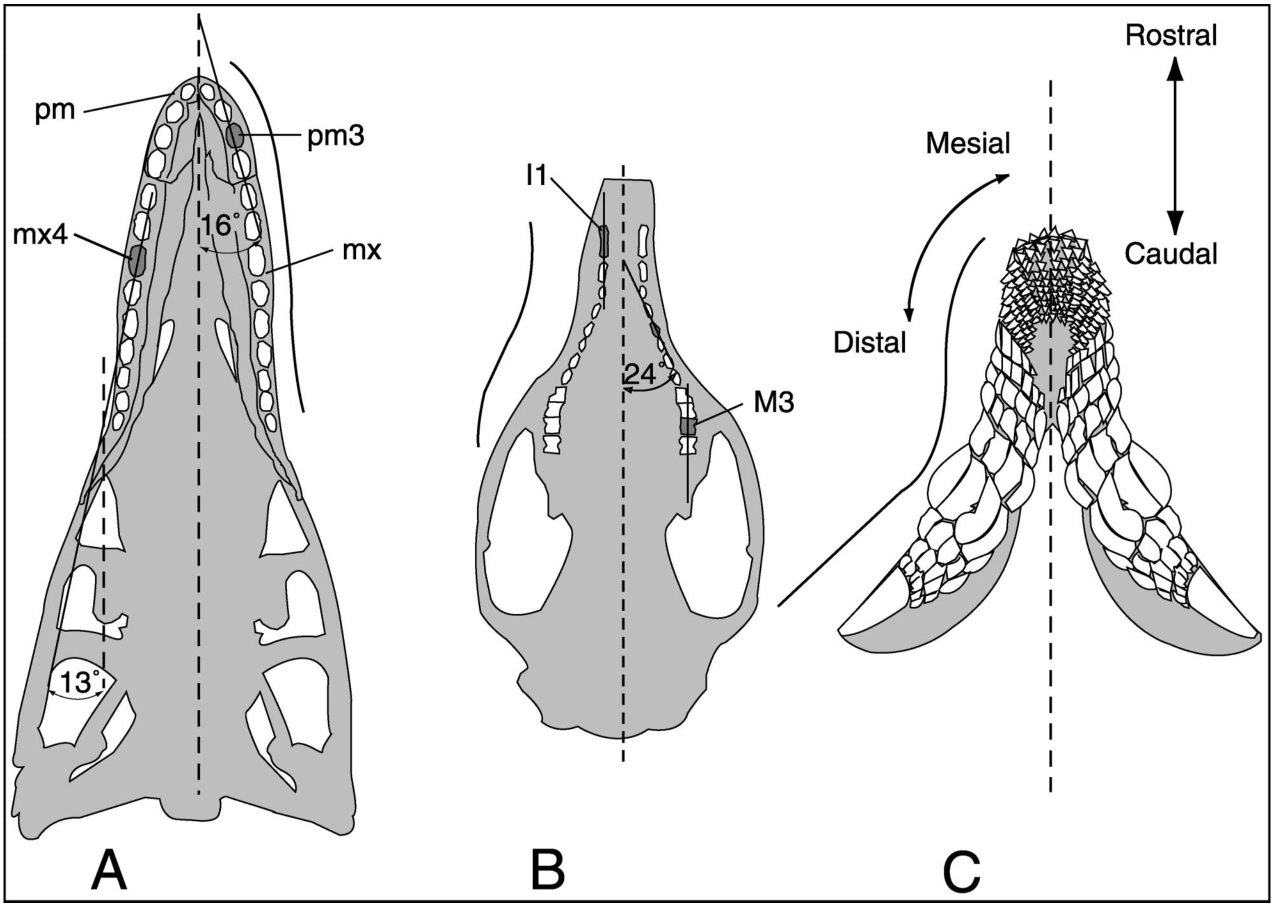

FIGURE 8. Applicability of the proposed terminology. **A**, reconstruction of the skull of *Dromaeosaurus* (AMNH 5356) in palatal view, showing the approximately 3° variation in long-axis orientation over the length of the tooth row. **B**, the dentition of the argyrolagid *Proargyrolagus* (MNHN-Bol-V-003454), where the tooth row curves such that while the incisors and molars are approximately parallel with the midline, the premolar axes are orientated about 24° towards it. **C**, the jaw of the elasmobranch *Heterodontus*. Black lines, traced along the tooth row, represent the curve of the row. Note that, at any point on these lines, the ''rostral'' facing crown surface is roughly toward the premaxillary symphysis and the ''caudal'' facing crown surface is away from it (**A** modified from Currie, 1995; **B** modified from Sánchez-Villagra and Kay, 1997; **C** modified from Carroll, 1988).

of the row's shape, becomes mesial and the more caudal direction, generally away from the symphysis, becomes distal (Fig. 7a–c). As such, the third premolar of a human is described as being mesial to the fourth premolar while the canine lies distal to the second incisor. Moreover, the carina on a theropod maxillary crown that faces toward the symphysis is the mesial carina and its opposite fellow is the distal carina (Fig. 7d, e).

The surfaces of the crown that face the lips and the tongue (or the corresponding directions in those taxa which lack these structures) are often referred to as labial and lingual, respectively, within veterinary anatomy and oral biology. Hillson (1986) preferred the commonly used term buccal (referring to cheek) instead of labial, which works just as well. Peyer (1968) mentioned that the term vestibular has also been used as a synonym for buccal, but this appears to have largely fallen out of favor. Although we are calling for a standard of terminology, there are enough taxa that lack both labiae and buccae to make both terms imprecise at times and the choice between them rather arbitrary. Labial and lingual have been used in paleontology (e.g., Cifelli and de Muizon, 1998; MacFadden and Dobie, 1998), but the term lateral is also known (e.g., Murry, 1986; Russell and Dong, 1993; Lee, 1997). Because lateral is defined in anatomy as the direction away from the midline and toward the latus or side (Tortora, 1995; Dyce et al., 1996), it is a poor choice for dentition both for the tooth-row curvature issues discussed above and because it is not always possible to determine which side of the animal an isolated tooth is from (see Lee, 1997). However, labiae (and to some degree buccae) often ''mold'' around tooth rows, following their general morphology and orientation, and linguae sit within the oral or buccal cavities (''inside'' of the dental arcade). Labial and lingual are thus precise descriptive and directional terms. Ambiguous mediolateral surfaces of shed tooth crowns can perhaps better be referred to simply as sides.

The bases and ends of tooth crowns are often described as the proximal or distal portions, as if they extend out from the axis of the animal the way limbs do, which is not the case. In the dental sciences, the base of the crown becomes the basal portion or direction, while the end of the crown (near the tip, which is often referred to as the apex or corona in molariform crowns) becomes the apical (or coronal) portion or direction (Fig. 7c, d). This terminology can also be used to refer to features toward or away from the crown surface, such as denticles or other crown ornamentation. The neck of the tooth, at the transition between the base of the crown and the top of the root, is referred to as the cervix dentis or simply the neck (Fig. 7c). The direction towards the cervix from the root can be called the cervical direction and thus distinguished from basal.

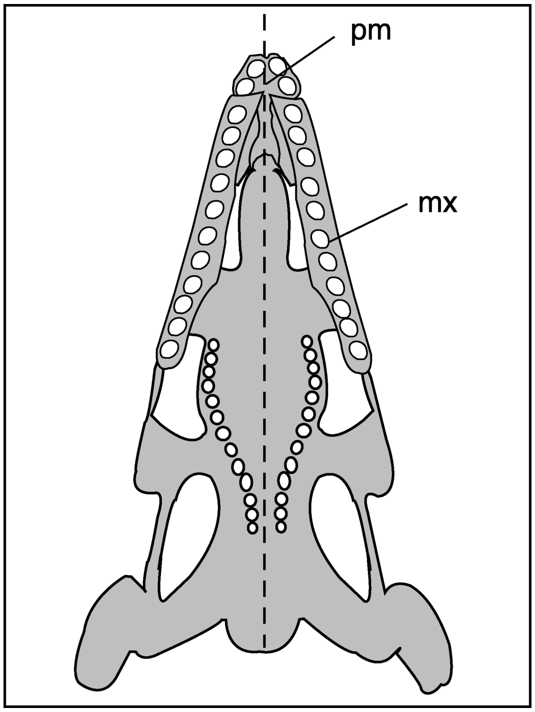

FIGURE 9. The skull of *Plioplatecarpus* (composite reconstruction of NMC 11835, 11840, and P 1756.1) in palatal view, showing the difficulty in describing long-axes for crowns with circular cross-sections. Note the curved nature of the pterygoidal tooth rows (modified from Holmes, 1996).

The presence of roots in mammalian dentition complicates the situation. Tips of conical crowns are often referred to as apices. However, the root tip in the mammalian dens is also called the apex (or specifically, the apex radicis dentis). As such, and as we have not found good terminology for the direction from the cervix dentis to the apex radicis dentis, we propose using the term root apical for this direction to distinguish it from apical, coronal, basal, and cervical.

The final directions to be accounted for are the views of the top of the crown and of the base of the root. The top surface of the crown is the surface that commonly occludes with its opposing tooth row in mammaliform dentitions (Fig. 7c, e). As anatomical terminology arose in mammals, occlusal is probably the most common term for crown top surfaces, even in conical dentitions that do not generally occlude (e.g., Fortelius et al., 1996; Kemp, 1996; Cifelli and de Muizon, 1998; MacFadden and Dobie, 1998; Miller and Carranza-Castañeda, 1998). Similarly, we suggest using the common term basal view for the view of the base of the crown in shed crowns. As we have found no model for the view of the root apex, we propose that this view can be termed root apical (or perhaps the less desirable term radical) in teeth for which a root is present.

The proposed terminology works for both simple and complicated dentitions as is shown in Figure 8. For example, the dentition of the Cretaceous theropod dinosaur *Dromaeosaurus albertensis* Matthew and Brown, 1922 (Fig. 8a) is fairly simple, with the premaxillary and maxillary tooth rows forming a continuous curve toward the midline such that there is a shallow angle (~3° based on Currie's 1995:fig. 1c) difference in long-axis orientation between pm3 and mx4. However, at any given point along the tooth row, the mesial direction is toward the premaxillary symphysis. In the Oligocene marsupial *Proargyrolagus* Wolff, 1984 (Fig. 8b), the dentition forms a curve such that the incisor axes are orientated essentially parallel to the sagittal plane. The tooth row curves at its middle so that the long axis of C1 is orientated 24° from the midline, and then the curve shallows toward the rear such that the long axes of the molars are again about parallel with the midline. The curve is significant enough so that the center of the occlusal surface of M4 is 2.5× farther from the midline than the center of I1, but at any point along the curve, the mesial direction is toward the premaxillary symphysis and the distal direction is away from it. Figure 8c shows a dramatic case, where the jaw of the elasmobranch *Heterodontus* Blainville, 1818 forms an S-shaped curve and tooth shape changes dramatically from ''rostral'' to ''caudal'' in the dentition. It should be noted in Figure 8c, however, that while it is clearly incorrect to discuss any of the crowns in a given row as being rostral or caudal to one another, the tooth rows themselves are most certainly in rostrocaudal relationships and should be discussed as such. Indeed, while crowns within rows are generally situated in some sort of parabolic arc, tooth rows in complicated dentitions are often orientated rostrocaudally.

The proposed terminology outlined above also works for those homodont dentitions with simple, cone-shaped crowns, although the situation becomes a bit complicated here, particularly when discussing the crown surfaces. Describing distinct mesial, distal, labial, or lingual faces on such teeth tends to be ambiguous. Truly cone-shaped crowns have no clear demarcations between faces and no distinct long-axes, as their cross-sections are often near circular (e.g., the Late Cretaceous mosasaur *Plioplatecarpus* Dollo, 1882:fig. 9). Specific crown faces for these morphologies can be difficult to ascertain, and orientation terms only apply in the broad sense, although many taxa with homodont dentitions do have carinae of some sort, which can partially alleviate the problem.

The examples illustrated in Figures 6a, c, and 8 also call attention to another point. Crown long axes in lower vertebrates are often referred to as the fore-aft basal length (commonly abbreviated as the FABL, see Currie et al., 1990; Farlow et al., 1991; Hungerbühler, 2000). As Farlow et al. (1991:163) defined FABL it refers to the mesiodistal base length of a crown. However, the terms fore and aft imply rostrocaudal relationships, and we have seen above that the ''fore–aft'' axis of a crown can describe a parameter that is completely different from the mesiodistal axis, as the two are often not coincident (e.g., compare the maxillary crowns of *Diadectes* in Figure 2 those of the *Dromaeosaurus* skull in Fig. 8a). Additionally, the mesiodistal length of a crown does not have to be the longest axis of the crown base, as in *Ekaltadeta* (Fig. 6c). This is an important point, as FABL was defined on the bases of the long axes of theropod dinosaur lateral crowns and is generally used to describe that parameter (e.g., Currie et al., 1990; Farlow et al., 1991; Brinkman et al., 1998; Harris, 1998). We therefore discourage the use of FABL and propose erecting the terms crown basal length (CBL) and mesiodistal axis (MDA) to decrease potential confusion. The CBL is self-explanatory. The MDA is the axis of the crown that is orientated toward and away from the premaxillary or mandibular symphyses, along the tooth row. In many cases, the CBL and MDA are the same. However, Figure 6c again illustrates that this does not have to be the case. In Figure 6c, there is a 49° difference between the CBL and MDA orientations between P2 and P3 (the MDA of P3 is parallel to the CBL of P2).

CONCLUDING THOUGHTS

There are many scientists that are concerned with dentition. In the current scientific climate, a high degree of specialization is the accepted (indeed expected) norm. As a consequence, there is not as much interdisciplinary communication as there could be. An intradisciplinary vocabulary is necessary, but we see no purpose in the various anatomical sciences all using different notation and orientation terminology for the same elements. The adoption of a standard terminology for fossil vertebrate dentitions, such as has been proposed here, would put the paleontological community back in the company of anthropologists, veterinary scientists, and medical and oral biologists, at least for dentigerous elements, and would facilitate the communication of information between these groups. Ideally, the standardization of dentition terminology could be a catalyst to continue moving towards the standardization of all anatomical terminology.

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