During the sessions, the question of exactness in identifying and comparing homologues was discussed by several participants. Professor Butler stated that the thought held by some, that differences arise in going back along the jaw, might also be viewed alternatively to represent structures on anterior teeth as degenerate forms of those on the posterior ones. Patterson also thought that he could not place any great trust in premolar analogy and that, as he stated in the Brussels Conference in 1956, "it is a dangerous tool."

Butler and others also questioned identification of cusps by their relationship to crests. Butler asked, "How sharp does a convex surface have to be before it becomes a crest? . . . On a photograph a highlight on a slope is difficult of identification . . . in some cases I would say that there is not a crest where one is claimed." He also went on to say that having crests running across a tooth in the upper and lower jaws does not make the crests homologous, "Nor does it make the cusps at their lingual ends homologous."

—A. A. D.

Origin of the Cusps and Crests of the Tribosphenic Molar

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It is important to point out as clearly as possible what is known about the origin of the tribosphenic molar structures. This tooth is the principal milestone in the evolution of mammalian dentition. It has given rise to all known molars of placental mammals. Simpson,[11] who introduced the term "tribosphenic," said that "This is the most important and potent type of molar structure that has ever been evolved." The homology between the cusps and crest of the upper and lower molars, however, can be determined only if the origin of the different structures is established.

The primitive, haplodont teeth were shearing mechanisms. The dryolestoid dentitions had a cutting function. The tribosphenic dentition has, at the same time, shearing, cutting, and grinding action. It works as a double pestle and mortar.

A complete description of the tribosphenic molars will not be given here. A previously published description,[12] based on the study of the most ancient and primitive tribosphenic dentitions, those from the Upper Cretaceous and the Paleocene, is more complete than that given by Simpson.[11] The upper molar, for instance, bears more crests than described by him (Fig. 1). All the elements constituting the tribosphenic molars are indicated in the illustrations in the present report.

The pattern made by the crests and cusps is typical in the Mesozoic and Paleocene forms; only in later periods have the connections between crests and cusps changed.

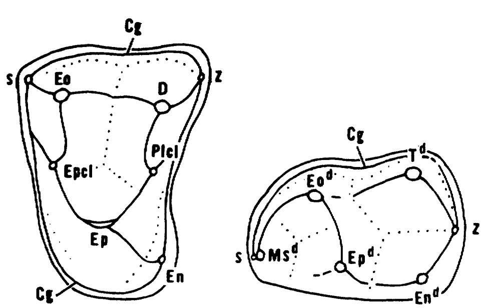

FIG. 1.—Diagram of the crown view of an upper and a lower tribosphenic molar (vestibular side, top; lingual side, bottom; mesial side, left; distal side, right). Cg = Cingulum; En = endocone; En^{d} = endoconid; Eo = eocone; Eo^{d} = eoconid; Ep = epicone; Ep^{c1} = epiconule; Ep^{d} = epiconid; Ms^{d} = mesioconid; S = mesiostyle or mesiostylid; T^{d} = teloconid; Z = distostyle or distostylid. (Vandebroek, 1964.)

The three main crests on the upper molar must be remembered: (1) A mesiodistal crest, the eocrista, which runs from the mesial to the distal cingulum, through the tops of both vestibular cusps; (2) a transverse crest, the epicrista, which descends from the top of the mesiovestibular cusp or eocone, passes through a conule, and reaches the main lingual cusp or epicone; (3) a second transverse crest, the plagiocrista, which is symmetrical to the eocrista and descends from the top of the distovestibular cusp or distocone, passes also through a conule, and reaches the epicone. The crests are blurred out near the top of the vestibular cusps when the latter are developed.

Origin of the Tribosphenic Pattern

In prior work,[12] it was shown that the identification of the elements composing a molar has to be carried out by comparison with the structure adjacent teeth. The various dentitions show, at least to some extent, a progressive gradation from a haplodont premolar to the molar. Even in the groups in which the transition from the premolars to the molars is reputed to be the most abrupt, enough indications can be found to establish the origin of each feature.

The homology of the cusps in different teeth of one row can be determined because of the existence of crests joining the cusps. Special attention must be paid to ensure that, as far as possible, the study is based on specimens with unworn teeth.

All the types of teeth are to be considered as being derived from a haplodont primary tooth that is characterized not only by a primary cusp and cingulum but also by a mesiodistal crest running through the top of the cusp. Styles arise at the contact point of this main crest with the cingulum.

The existence in all dentitions of a mesiodistal main crest is to be emphasized.

The presence in all the primitive orthotherian dentitions of a transverse, lingual or vestibular crest running from the apex of the main cusp to the cingulum is also to be stressed (Fig. 6, 7). Many Mesozoic (Docodonta and Dryolestoidea) premolars show lingual and vestibular transverse crests at the same time. Notwithstanding the strong development of a lingual transverse crest, a vestibular transverse one is easy to detect in the upper molars of the Docodonta and in some premolars of primitive Placentalia. It may be found again in some Eutherian first molars.

The identification of all the crown elements with the structures found in the adjacent premolars shows a progressive gradation, from a canine-shaped P^1 to a more or less molarized P^4 and, finally, to the M^1. The data are summarized for the upper molars (Fig. 2) and the lower molars (Fig. 3).

By following the molarization process in primitive dentitions, from haplodont upper premolar to the molar, it is easy to show that:

1. The main cusp of the haplodont tooth becomes the mesiovestibular molar cusp.
2. The distovestibular cusp arises on the eocrista, on the distal slope of the main cusp.
3. The eocrista remains more or less parallel to the vestibular border of the crown.
4. The main lingual cusp, the epicone, arises at the contact point of the epicrista with the lingual cingulum.
5. The labial part of the epicone is transversely elongated in a kind of bud or lobe and the epicrista describes a curve, from which the convex side is turned mesially, and the lingual part of this crest and the mesial ginfulum come to lie nearly parallel to each other and finally merge.
6. A conule, the epiconule, arises at the point where the primary cingulum and the eocrista join.
7. A secondary cingulum appears on the base of the epicone and epiconid.
8. A new cusp, the endocone, develops on the distal contact point of the secondary cingulum with the primary cingulum.
9. A figure, symmetric to that formed by the epicrista and its conule, appears on the distal half of the crown; the crest is the plagiocrista and the conule is the plagioconule.

The crest joining the epicone with the endocone has been called endocrista; the crests joining the conules with the cingulum are called simply medial and distal descending crests.

The functional aspect of the described modifications will be considered later.

It has been known for a long time that the primitive lower molar is formed by a high mesial half, the trigonid, and a lower distal half, the talonid. The trigonid bears

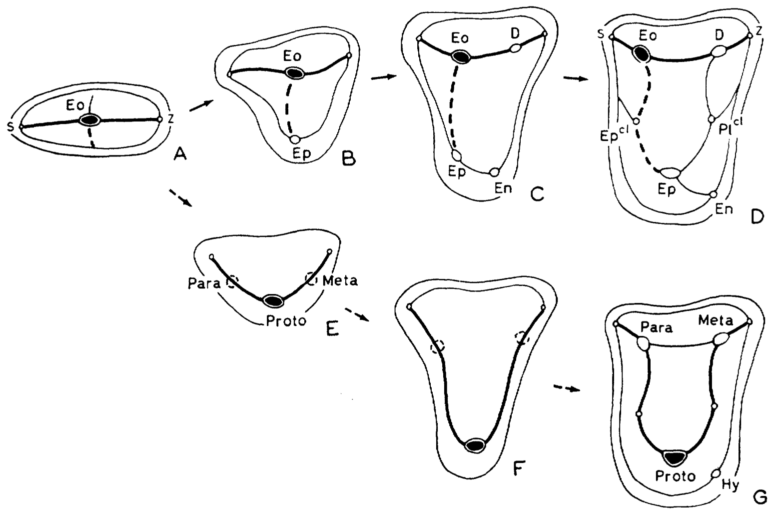

FIG. 2.—Diagrammatic representation of the development of the tribosphenic upper molar (vestibular side, top; lingual side, bottom; mesial side, left; distal side, right). A to D shows development as determined by the comparison of adjacent teeth; E to G shows development as supposed in the Cope-Osborn cusp rotation theory. The main cusp is shown in black. Thick line = main mesiodistal crest or eocrista; broken line = main transverse crest or epicrista. The plagiocrista runs from the distocone (D) to the epicone (Ep) via the plagioconule (Pl^{c1}); the endocrista runs from Ep to the endocone (En); descending crests run from epiconule (Ep^{c1}) or Pl^{c1} to the cingulum. The comparison between D and G shows the equivalents between the proposed nomenclature and the Osborn nomenclature.

three cusps, one on the vestibular side, the eoconid, and two on the lingual side, the mesioconid and the epiconid. The talonid is a large basin that is limited by an elevated rim bearing three cusps, one on the vestibular side, the teloconid, one on the lingual side, the endoconid, and a smaller distal style, the distostylid.

The molarization process in the lower dentition may be summarized:

1. The main cusp of the haplodont premolar becomes the vestibular cusp of the trigonid.
2. This eoconid, and with it the whole central part of the eocrista, shifts progressively toward the vestibular rim of the crown.
3. The medial style, on the contrary, shifts in the lingual direction.
4. The mesial lingual cusp of the trigonid, called here the mesioconid, arises by individualization form the mesiostyle.
5. The distal lingual cusp of the trigonid develops on the contact point of the transverse crista or epicrista with the lingual cingulum and is thus an epiconid.
6. The vestibular and main cusp of the talonid, called here the teloconid, arises also by individualization from the distostyle.
7. The vestibular cingulum ends distally on the growing teloconid in the first stages of its appearance but soon surrounds this still-developing cusp to again reach the distostyle.
8. The endoconid appears simply on the lingual cingulum.
9. The lingual cingulum disappears completely between the two lingual cusps of the trigonid.
10. Only parts of the vestibular cingulum remain visible.

It should be stressed that the preceding description of the origin of the elements constituting the tribosphenic upper and lower molars can be followed by comparison of unworn adjacent teeth in all the earliest placental dentitions known (Cretaceous, Paleocene, and Eocene).

The problem of the homology between upper and lower tribosphenic molars is easy to solve. Both molars derive from a haplodont primary tooth that bears a mesiodistal

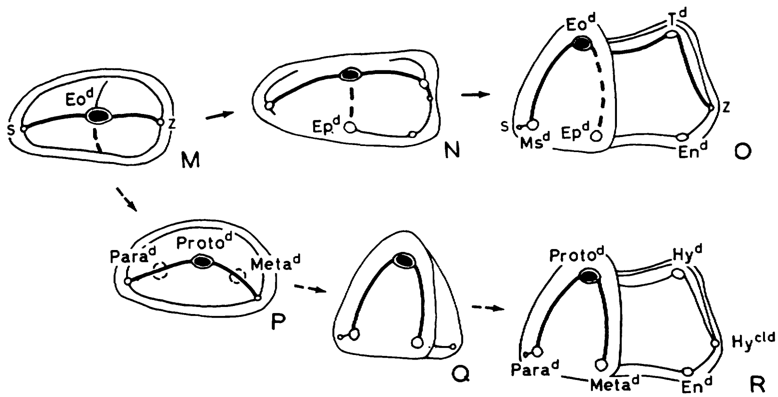

FIG. 3.—Diagrammatic representation of the development of the tribosphenic lower molar (vestibular side, top; lingual side, bottom; mesial side, left; distal side, right.) M to O shows development as determined by comparison of adjacent teeth; P to R shows development as supposed in the Cope-Osborn cusp rotation theory. The main cusp is shown in black. Thick line = main mesiodistal crest or eocrista; broken line = main transverse crest or epicrista. The endocrista runs from the epiconid (Ep^d) to the endoconid (En^d). The comparison between O and R shows the equivalents between the proposed nomenclature and the Osborn nomenclature.

eocrista and is surrounded by a cingulum. In both molars, a first step in the process of molarization is the development, on the lingual side, of a transverse crest, the epicrista, that runs from the primary cusp toward the internal cingulum. At the point of contact of the epicrista with this cingulum, the epicone or epiconid arises. In both molars, portion of the primitive internal cingulum joins the epicone or epiconid to a distal lingual cusp, the endocone or endoconid. This means that, in spite of differences in proportion and structure, many important features of the upper and lower molars have the same origin and are homologous. It means also that the internal, or lingual, side of an upper tribosphenic molar is homologous with the internal side of the lower molar. The external sides of both are also homologous.

During the molarization process in the tribosphenic dentition, the eocrista remains in straight line or is only slightly deformed. In 1961, the term "euthemorphic" was introduced to characterize such a disposition in opposition to the lambda-shaped or "zalambdomorphic" structure of the main crest in other dentitions.[12] Both terms should only have a descriptive value and do not pretend necessarily to express a relationship between all the forms having one of those structures.

Euthemorphic dentitions have been present in all the geologic periods, beginning with the Upper Jurassic.

The functional evolution in the development of the tribosphenic dentition (Fig. 4) can be explained as follows: (1) To the shearing effect of the main cusps, the development of strong epicristae adds a first cutting unit. (2) The shifting of the eoconid and the mesioconid in opposite directions gives an oblique direction to the mesial part of the eocrista that causes this portion of the lower eocrista to constitute a second cutting unit with the lingual part of the plagiocrista. (3) The symmetrization of the upper molar develops a basin that is limited by elevated rims, the epicrista and the epiconule on the mesial side and the plagiocrista and the plagioconule on the distal side. The teloconid fits in this basin as a kind of pestle. The epiconid, however, serves as a pestle for the talonid basin.

Mesioconid and Plesioconid

Concerning the origin of the cusps, the only modifications that were introduced in the 1961 report[12] refer to the mesioconid. This cusp is considered as arising from a bulge on the mesial slope of the eocrista, although it is added that "It is not certain that the mesioconid usually arises independently from the cingulum in placentals.

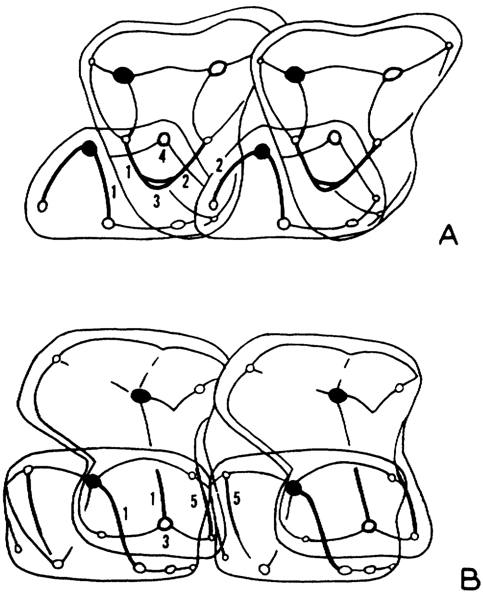

FIG. 4.—Occlusion diagrams of the tribosphenic (A) and docodont (B) molars (vestibular side, top; lingual side, bottom; mesial side, left; distal side, right). The eocone and eoconid are shown in black. 1 = Cutting unit made by both epicristae; 2 = cutting unit made by lingual part of the plagiocrista and the mesial part of the lower eocrista; 3 = epicone fitting in the talonid basin; 4 = teloconid fitting in the central basin of the upper molar; 5 = cutting unit made by the mesial transverse rest of the docodont upper molar and the lingual part of the distal cingulum of the lower tooth. (Vandebroek, 1961.)

I found at least one case in which the external cingulum seems to run to the top of a small mesioconid."

Quinet,[9] who studied an important lower Eocene placental material, has found clearer indications about the cingular origin of the mesioconid. One of my collaborators, Quintart, has investigated this problem in recent Carnivora; his study also led to the conclusion that the mesioconid is of cingular origin.

Those new studies show that the mesioconid is not homologous with the cusp that sometimes develops from a bulge of the eocrista on the mesial slope of the main cusp. It is proposed that the noncingular cusps (Fig. 5) be called plesiocone (plesio = near) or plesioconid.

Cope-Osborn Cusp Rotation Theory

For the sake of clearness in the present report, the new nomenclature introduced in 1961 [12] is used without referring to the equivalents in the traditional Osborn nomenclature, which is based on the Cope-Osborn cusp rotation theory. The fallacy of this conception should once more be stressed.

The Cope-Osborn cusp rotation theory may be summarized as follows: The tribosphenic molar, called the tritubercular molar by these authors, arises from a haplodont molar by addition of an anterior and a posterior cusp and by rotation of these cusps to the vestibular side of the primary cusp in the upper molar and to the lingual side in the lower molar (Fig. 2, E to G; Fig. 3, P to R).

This hypothesis, explained for the first time by Cope [3] in 1874, was developed in 1888 by Osborn,[8] who then introduced his well-known cusp nomenclature. It is evident that the conceptions of both authors were inspired from figures seen in dentitions of Dryolestoïdea and Symmetrodonta. The comparison of adjacent teeth proves indeed that, in those groups, the rotation of two additional cusps occurs. However, this is by no means true for the tribosphenic molar or for the zalambdodont dentitions deriving from the latter.[12]

The Cope-Osborn theory and the Osborn nomenclature have given rise to one of the most tangled situations in comparative anatomy. Scott,[10] by 1892, had found already that the comparison of adjacent teeth of Lower Eocene mammals (especially in the genera in which the last premolar is completely molarized) showed the evidence explained in the first part of the present report. However, because like Cope and Osborn he thought that the molar structure originated from that of the Dryolestoidea, he accepted the theory that the primary cusp corresponds to the main lingual cusp in the molars but to the mesiovestibular cusp in the last premolars.

This unfounded conclusion is especially astonishing as there are instances in which the last premolar is completely molarized and presents exactly the same structure as the first molar. This conception of a different origin for two adjacent identical teeth has been called "the premolar paradox" or "the premolar analogy theory." The efforts of Wortman [14] and Gidley [4] to redress the situation were in vain, probably because they made other errors of interpretation that

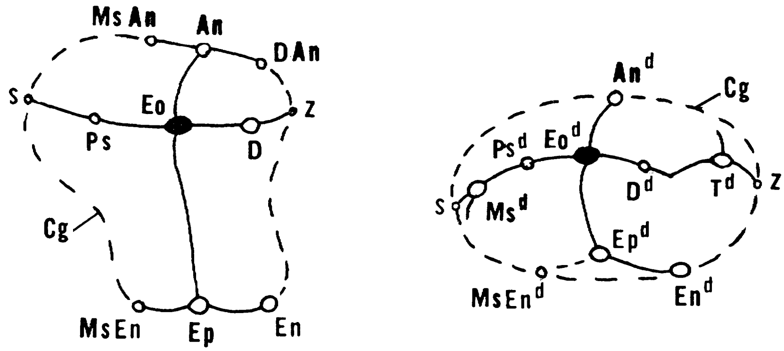

FIG. 5.—Diagram showing most of the cusps that can appear on primitive upper and lower teeth (vestibular side, top; lingual side, bottom; mesial side, left; distal side, right). These cusps are never simultaneously present. An = anticone; An^d = anticonid; D^d = distoconid; DAn = distoanticone; MsAn = mesioanticone; MsEn = mesioendocone; $MsEn^d$ = mesioendoconid; Ps = plesiocone; Ps^d = plesioconid. Other abbreviations are explained in the legend for Figure 1. (Vandebroek, 1964.)

must have ruined the credence they could have found. Gregory,[5] in 1934, still supported the premolar analogy theory.

If the correct identification of the eocone is now generally accepted, the idea that the tribosphenic molars originated from a more or less V-shaped type of tooth and that the tribosphenic talonid derives from the dryolestoïd talonid seems still to prevail.[2,7] One can only repeat what was declared in 1961: "The comparison of adjacent teeth shows that no trace of rotation or shifting of cusps, which should have been redressed during its formation, is to be found in recent or in fossil euthemorphic dentitions. On the contrary, the zalambdomorphic dentitions show a progressive deformation of a straight eocrista. There is no more reason to search for the origin of the primitive placental tooth whether in zalambdomorphic, dilambdomorphic or marsupial dentitions."[12]

If there is any Jurassic group more or less closely related to the Eutherians, it must surely be the Docodonta (Fig. 6, 7). The molars of *Docodon* exhibit many characteristics of the tribosphenic molar: a strong epicrista, epicone, and epiconid and the beginning of the development of a talonid with a basin that is limited vestibularly by a teloconid and into which the epicone fits as a kind of pestle. The patterns still resemble that of a last premolar or an incompletely molarized first molar of a tribosphenic dentition, however. In spite of their high degree of molarization, the upper molars of *Docodon* do not possess the typical elements of the tribosphenic upper molars; i.e., the plagiocrista and the conules. They are in some ways hypertrophied premolars. A great difference that indicates a diverging evolution, however, is the shifting of the mesioconid in a vestibular direction instead of in a lingual direction. The crest descending from this mesioconid toward the lingual border of the tooth makes a cutting unit with the lingual part of the upper molar distal cingulum.

A comparison of the functional shearing, cutting, and crushing units existing in the tribosphenic, docodont, and dryolestoïd dentition shows that, of the five functional units present in the first dentition, three are also present in the docodont dentition and only one, the eocone-eoconid shearing unit, is to be found in the dryolestoid dentition. The three docodont functional units are the eocone-eoconid shearing unit, the cutting unit made by the epicristae, and the crushing unit resulting from the epicone fitting in a talonid basin.

The only important cutting unit in the dryolestoïd dentition is realized through an eocrista-eocrista contact of the mesial rim of the upper molar with the distal rim of the trigonid. The opposite cutting unit, the distal rim of the upper tooth contacting the mesial rim of the trigonid, is much less important because the lower molar mesial rim is much lower than the distal one and the rims overlap each other in active occlusion.

None of the supposed homologies between the upper and lower tribosphenic mo-

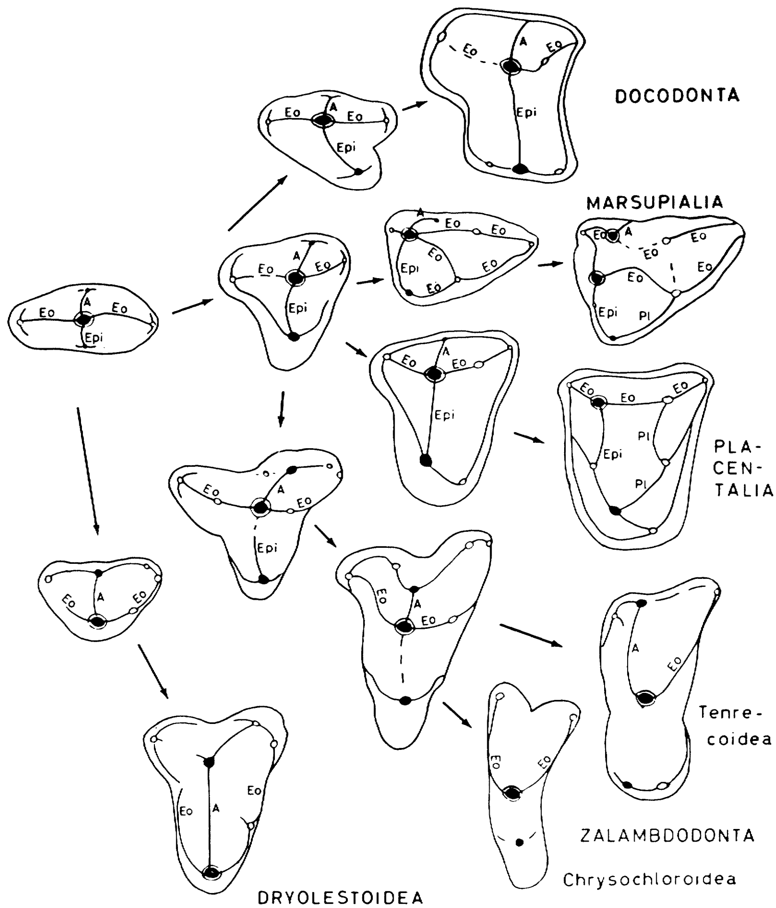

FIG. 6.—Principal types of upper orthotherian molars with a diagrammatic representation of their development (vestibular side, top; lingual side, bottom; mesial side, left; distal side, right). Each transition stage between the haplodont primitive premolar and the atypical molar is taken from an existing row of adjacent teeth. A = anticrista; Eo = eocrista; Ep = epicrista; Pl = plagiocrista. (Vandebroek, 1964.)

lars that are expressed by the nomenclature of Osborn [8] is correct. This nomenclature is therefore confusing in the highest degree and makes any comparative work on the structure of teeth practically impossible.

Morphologic Gradients

The comparison of adjacent teeth of a large material shows clearly the existence of four morphologic gradients: an incisor, a canine, a premolar, and a molar gradient, three of which have already been emphasized by Butler.[1] The idea of threshold was added in 1961 [12] to explain the morphologic jump between the different types of teeth.

Besides those main gradients, the existence of minor gradients is frequently shown by structural details such as small additional crests or cusps that extend across the limits of two types of teeth. A first indication of such a detail, for instance, may be barely visible in a second premolar, more clearly visible in the third premolar and strongly developed in the fourth premolar. The structure will be reduced but still detectable in the first molar and will have completely disappeared in the second molar.

Homology Between Permanent and Deciduous Teeth

The homology between permanent and deciduous teeth is evident. Progressive gra-

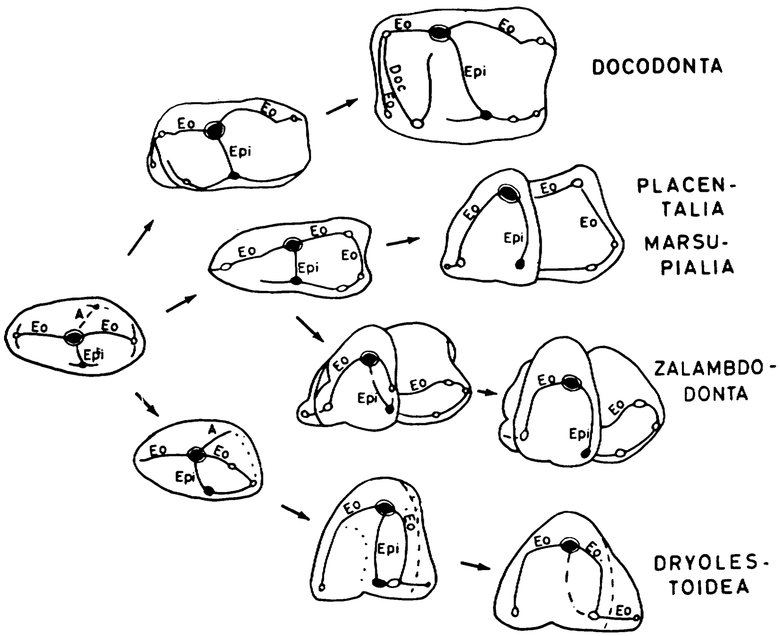

FIG. 7.—Principal types of lower orthotherian molars with a diagrammatic representation of their development (vestibular side, top; lingual side, bottom; mesial side, left; distal side, right). A = anticrista; Eo = eocrista; Ep = epicrista; Pl = plagiocrista; Doc = mesial transverse crest. In Docodon, the mesial transverse crest is strongly developed. (Vandebroek, 1964.)

dations in the structure are sometimes found between the premolars and the molars and sometimes between the deciduous and definitive teeth. The identity of structure between deciduous or permanent premolars on one side and molars on the other depends on the times of development of both groups of teeth.

The deciduous or permanent last premolars that develop almost simultaneously with the first molar are more or less similar to this molar. They are the expression of the same stage of development of gradients in two neighboring places on the tooth row. The last premolars that develop much earlier or later than the first molar are different from this molar, being the expression of another stage of development of the morphogenetic gradients at a determined place. A beautiful example of this principle in the dentitions of Zalambdodonta was described in the 1961 report.[12] The first molar shows a structure, each detail of which can be found again in the deciduous last premolar only in *Solenodon,* but in the permanent last premolar in *Setifer* and *Echinops*.[12]

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