A New Order of Tertiary Zalambdodont Marsupials

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***Yalkaparidon coheni* and *Yalkaparidon jonesi* are described here as the first-known members of the marsupial family Yalkaparidontidae and order Yalkaparidontia. Before discovery of these zalambdodont marsupials in unnamed Tertiary sediments from northwestern Queensland, only five orders of australidelphian marsupials were known. Dental and basicranial morphology suggest that notoryctids and yalkaparidontids, which both have highly specialized zalambdodont molars, are dentally convergent. Yalkaparidontids lived in lowland rainforests of northern Australia and appear to have vanished, with the rainforests, sometime in the middle to late Tertiary. Discovery of yalkaparidontids demonstrates a significantly greater breadth of diversity for Australian marsupials.**

DISCOVERY OF NEW AND AS YET unnamed fossiliferous deposits on Riversleigh Station in northwestern Queensland, Australia, has led to recovery of more than 200 new species of Tertiary vertebrates. Of these, the materials described here as *Yalkaparidon coheni* and *Yalkaparidon jonesi* represent a new family and a new order of marsupials, thereby adding significantly to the previously known diversity of Australian marsupials (*1*). They also represent the first fossil record of Australian zalambdodont marsupials (*2*). The living *Notoryctes typhlops*, the only known member of the order Notoryctemorphia (marsupial moles), is a zalambdodont marsupial of decidedly uncertain interordinal affinities (*1, 3, 4*). Discovery of yalkaparidontians does not appear to clarify the relationships of notoryctemorphians but does indicate the once greater diversity of zalambdodont marsupials.

Dental nomenclature follows Archer (*5*). Basicranial nomenclature follows Archer (*6*) and Aplin and Archer (*1*). Local faunal names and stratigraphic concepts other than those used before (*7–9*) are noted here for the first time. Suprafamilial nomenclature is that used and justified by Aplin and Archer (*1*). Catalog numbers with the prefix QM F are registered in the Queensland Museum paleontological collections.

Class Mammalia
Supercohort Marsupialia
Cohort ?Australidelphia

Order: Yalkaparidontia new.

Included family: Yalkaparidontidae new.

Etymology: *Yalkapari* is a northwestern Queensland aboriginal word meaning "boomerang" (*10*) and alludes to the boomerangshaped molars; *odous* is Greek for "tooth."

Diagnosis: Yalkaparidontians differ from all other marsupials in the following combination of features: extreme zalambdodonty, no trace of protocone or talonid; adult dental formula—three upper and one lower incisors, one upper and no lower canine, three upper premolars and one to possibly three lower premolars (P_3, P_{2-3}, or P_{1-3}), three upper and lower molars (M^{2-4} and M_{2-4}); ever-growing and rodent-like upper and lower first incisors; relatively enormous, procumbent lower incisor; diastema separating the third upper incisor from the third upper premolar; very large posterolateral palatal foramen; very small maxillary palatal vacuities; no squamosal epitympanic si-

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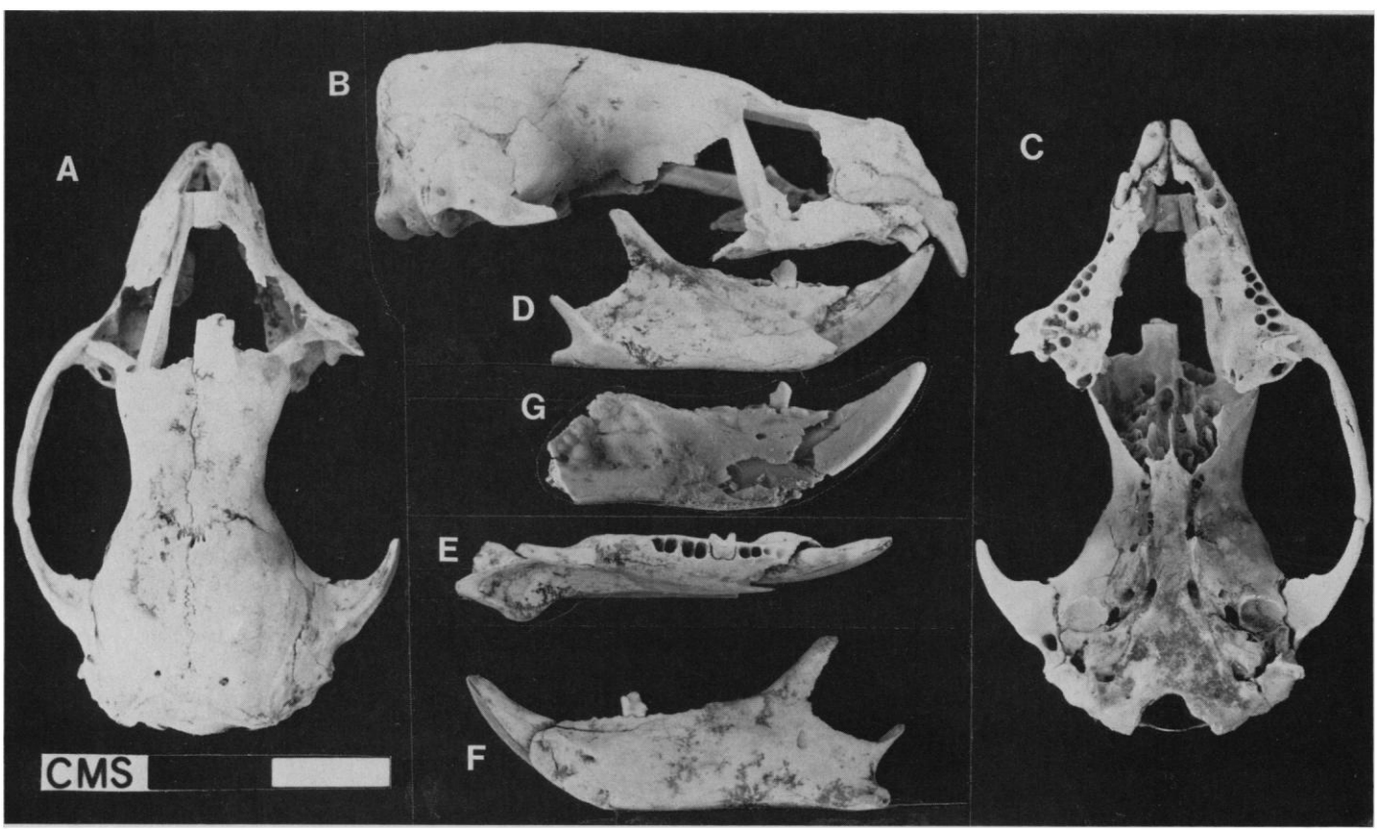

Fig. 1. *Yalkaparidon* spp. skull and dentaries. (**A** to **C**) *Yalkaparidon coheni*, dorsal, right lateral, and ventral views of the skull with left and right first incisor, right second and third incisors, and left fourth molar. (**D** to **F**) *Yalkoparidon coheni*, buccal, occlusal, and lingual views of the right dentary with second molar. (**G**) *Yalkaparidon jonesi*, buccal view of right dentary with third premolar.

nus; middle ear roofed only by alisphenoid and petrosal; small alisphenoid tympanic process; prominent ventral crest above promontorium but no petrosal tympanic process; foramen pseudovale; transverse canal foramina posterior to those for entocarotid; broad squamosal-alisphenoid contact; vestige only of squamosal postglenoid process; ectotympanic free.

Family: Yalkaparidontidae new.

Included genus: *Ƴalkaparidon* new.

Family diagnosis: That of the order Yalkaparidontia until additional families are recognized.

Genus: *Ƴalkaparidon* new.

Included species: *Ƴalkaparidon coheni* new, *Ƴalkaparidon jonesi* new.

Generic diagnosis: That of family Yalkaparidontidae until additional genera are recognized.

Species: *Ƴalkaparidon coheni* new (Fig. 1, A to F, and Fig. 2).

Etymology: Named in honor of the former Australian Minister of Arts, Heritage and Environment, the Hon. Barry Cohen.

Holotype: QM F13008, partially disarticulated skull recovered from limestone matrix as associated mass consisting of isolated cranium, left squamosal, left premaxilla, maxilla and jugal, right premaxilla and maxilla, and right dentary. Holotype has right upper three incisors, left upper first incisor, left upper posterior molar (M^4), right lower incisor, and right anterior molar (M_2).

Type locality: CS Site (CS Local Fauna), Godthelp Hill, Riversleigh Station, northwestern Queensland.

Paratypes: QM F13010, right dentary with lower incisor, from Upper Site (Upper Local Fauna), Godthelp Hill; QM F13011, right maxillary fragment with second upper premolar and posterior molar (M^3), from CS site.

Stratigraphy: All Riversleigh local faunas and collection sites noted here come from unnamed freshwater limestones that may be approximate equivalents of the middle Miocene Carl Creek Limestone. They form complex stratified sequences of spring and lake deposits. Some Riversleigh taxa (for example, *Wakiewakie* and *Namilamadeta*) closely resemble taxa in the Kutjamarpu and Tarkarooloo Local Faunas of central Australia interpreted (*11*) to be middle Miocene in age.

Diagnosis: *Ƴalkaparidon coheni* differs from *Ƴ. jonesi* in being slightly larger and in consistently exhibiting two alveoli for either a well-formed double-rooted second lower premolar or a single-rooted second lower premolar plus a single-rooted first premolar.

Description: Basic dental and cranial morphology are shown in Figs. 1 and 2. In the skull reconstruction, slight distortion has resulted in maxillary tooth rows being restored approximately 2 mm too far apart. Lower incisors in centric position rest on crowns of upper second and third incisors. First incisors enamel-free on dorsal (proximal) surface. Three-rooted upper molars have enamel-free areas buccal to crescentic cutting crests of teeth. Enamel on all teeth is thin and, in combination with enamel-free areas, functions through thegotic wear to maintain sharp leading cutting edges. Although upper molar cusp homology is in doubt, dominance of metacone in marsupials suggests this to be homology of lingual cusp. Two bucally directed crests that terminate as buccal corners of single selene emanate from metacone. No stylar cusps or other conules are evident. Degree of divergence of two crests of selene (as determined from isolated teeth) appears to decrease from second to third upper molars. Two-rooted lower molars have single large lingual cusp which we interpret as protoconid from which emanate two lingually directed crests. Although the corners at which these crests terminate could be homologs of paraconid and metaconid, they do not form discrete cusps. Planar glenoid fossa and presence of vestigial postglenoid process suggest a lower jaw capable of unusually extensive horizontal translation. Mandibular symphysis is unfused, and two dentaries are evidently capable of independent movement.

Species: *Ƴalkaparidon jonesi* new (Fig. 2G).

Etymology: Named in honor of the Australian Minister of Science, the Hon. Barry Jones.

Holotype: QM F13009, a partial right dentary with lower incisor and third premolar.

Type locality: Gag Site (Dwornamor Local Fauna), Gag Plateau, Riversleigh Station, northwestern Queensland.

Paratypes: QM F13012, an isolated first upper molar, Last Minute Site (Last Minute Local Fauna), Ray's Amphitheatre, Riversleigh Station.

Diagnosis: *Ƴalkaparidon jonesi* differs from *Ƴ. coheni* in being slightly smaller and in lacking any trace of teeth in diastema between third premolar (P_3) and incisor.

Description: So far as known, apart from diagnostic differences, *Ƴ. jonesi* resembles *Ƴ. coheni*.

Discussion: Although the cranial and rostral sections were fossilized together and are plausibly reconstructed as shown in Fig. 1, because there is no actual contact point between the root of the zygomatic arch on the cranial fragment and the left jugal (which is attached to the maxilla containing a yalkaparidontian molar), we do not have unreserved confidence about the association. In terms of basicranial structure, it is remotely possible that the cranial portion represents an otherwise unknown plesiomorphic bandicoot (peramelimorphian; many of which occur in the Riversleigh deposits) accidentally associated with the rest of the skull. However, this seems unlikely because of (i) the intimate association of similar-sized and non-duplicated skull fragments, (ii) the morphological compatibility of all of the fragments, and (iii) some non-bandicoot-like features of the basicranium.

We have concluded that the species of *Ƴalkaparidon* are marsupials because of the derived structure of the middle ear (for example, the alisphenoid and presumed ectotympanic floor) and the overall general resemblance of cranial morphology to the otherwise most plesiomorphic of Australian marsupials, the bandicoots. Independent support for this conclusion comes from studies of ultrastructure of the enamel, dentine, and enamel-dentine junction (*12*). Hence, although the molars of *Ƴalkaparidon* superficially resemble those of placental tenrecids (such as *Hemicentetes*), this similarity appears to be the result of convergence. There is no comparable similarity in canine, incisor, or cranial morphology between yalkaparidontids and tenrecids.

Consequently, we determined cheekteeth homology in terms of the plesiomorphic tooth number for marsupials (*5*) and presume adult yalkaparidontids display the second to fourth molars. Analogous reasoning leads us to conclude that the posterior premolar of yalkaparidontians is the third.

Molar cusp homology is in doubt because of the lack of structurally intermediate conditions that might serve as a guide to the history of molar specialization in the group. However, because other incipiently zalambdodont marsupials (for example, undescribed Riversleigh marsupial moles) suppress the paracone as do marsupials that have become carnivorous (for example, dasyurids and thylacinids), we interpret the single upper cusp as a metacone. Similarly, we presume that the single cusp of the lower molars is the protoconid.

Because *Ƴalkaparidon* exhibits many features such as the lack of a squamosal epitympanic sinus that are plesiomorphic for marsupials in general and none that would unambiguously relate it to some other particular group of marsupials, we are uncertain about whether yalkaparidontians are australidelphian or ameridelphian marsupials. However, the overall similarity of their basicranial anatomy to that of bandicoots and their geographic occurrence in Australia persuade us that it is most probably an australidelphian group.

The most recent revision of marsupial phylogenetic understanding and classification (*1*) has resulted in recognition of five

orders of australidelphian marsupials: Microbiotheria (containing the South American microbiotheriids); Dasyuromorphia (thylacinids, dasyurids, and myrmecobiids); Peramelemorphia (peroryctids, peramelids, and thylacomyids); Notoryctemorphia (notoryctids); and Diprotodontia (all previously known diprotodont Australian marsupials), each of which is comparable in diversity, antiquity (as judged in part by molecular divergence dates), and distinction to placental orders. In fact, the structural diversity in Diprotodontia is exceeded by few if any other orders of mammals. Each of these australidelphian orders is fundamentally distinct such that none is unambiguously more closely related to any of the other five (*1*). Yalkaparidontia represents yet a sixth category of this kind, the only one that has left no living descendants.

In the striking feature of its zalambdodonty, it superficially resembles marsupial moles (notoryctemorphians), but there are reasons for concluding that this similarity is the result of convergence. First, it is the only feature that suggests a possible relationship between the two groups and it must be seen in the context of comparable but counterindicative resemblances, based on single features, to non-notoryctid groups (for example, its diprotodonty resembling that of diprotodontians or its evergrowing first incisors resembling in this feature the teeth of wombats). Second, although *Yalkaparidon* molars are zalambdodont, there is no trace of protocones, talonids, metaconids, paraconids, or stylar cusps that are prominent features in molars of *Notoryctes*. Further, unlike the crowns of notoryctids, those of *Yalkaparidon* exhibit open selenes that undergo marked meristic change in the tooth row and trigonid basins that are lingually wide open. Third, although the zalambdodont condition of *Yalkaparidon* is far more derived than it is in *Notoryctes*, *Yalkaparidon* exhibits a strikingly more plesiomorphic basicranium that suggests no similarity let alone relationship to that of *Notoryctes*. Fourth, *Yalkaparidon* is diprotodont in its antemolar dentition in contrast to the more polyprotodont condition in *Notoryctes*. Fifth, although fossorially specialized marsupial mole-like postcranial elements occur in the Riversleigh deposits, they are all referable to much smaller incipiently zalambdodont marsupial moles that do show many notoryctid-like features. Zalambdodonty in the loosest sense of the word would then appear to be the only justification for placing *Yalkaparidon* within Notoryctemorphia. Considering the fact that zalambdodonty has developed convergently many times within different mammal groups (for example, necrolestids, chrysochlorids, and notoryctids), there seems little reason to presume that it could not have done so independently within Marsupialia.

Comparable reasons exist for being unable to place *Yalkaparidon* within or even near any of the other known orders of marsupials. For example, despite superficial similarities to diprotodontians including diprotodonty and three upper incisors, molar and basicranial structure as well as ultrastructure of enamel preclude placement of yalkaparidontians within Diprotodontia. Its essentially plesiomorphic basicranial morphology combined with its extraordinarily specialized dentition suggest that it represents a distinct ordinal lineage at least as venerable as any other order of marsupials.

Considering dental function, the species of *Yalkaparidon* could not eat foods that required crushing (incussion) during mastication. The small, delicate premolars, if they functioned at all, might have helped to hold objects in the diastemal space prior to their transfer to the molar region. The molars were clearly used primarily if not exclusively for vertical shearing. In this sense, they are superficially similar to the molars of some symmetrodonts and dryolestoids.

In terms of paleoecology, we interpret the vegetation of the Riversleigh area at the time of the presence of *Yalkaparidon* species to have been dense species-rich lowland rainforest (*9*). The reasons for this conclusion include the very high diversity of obligate tree-leaf–eating possums (with at least five species of pseudocheirid ringtail possums including species of *Pseudochirops*, living species of which occur only in rainforests) and the presence of species of *Hypsiprymnodon* (a potoroid kangaroo) and *Strigocuscus* (a cuscus), living species of which are only found in Australasian rainforests.

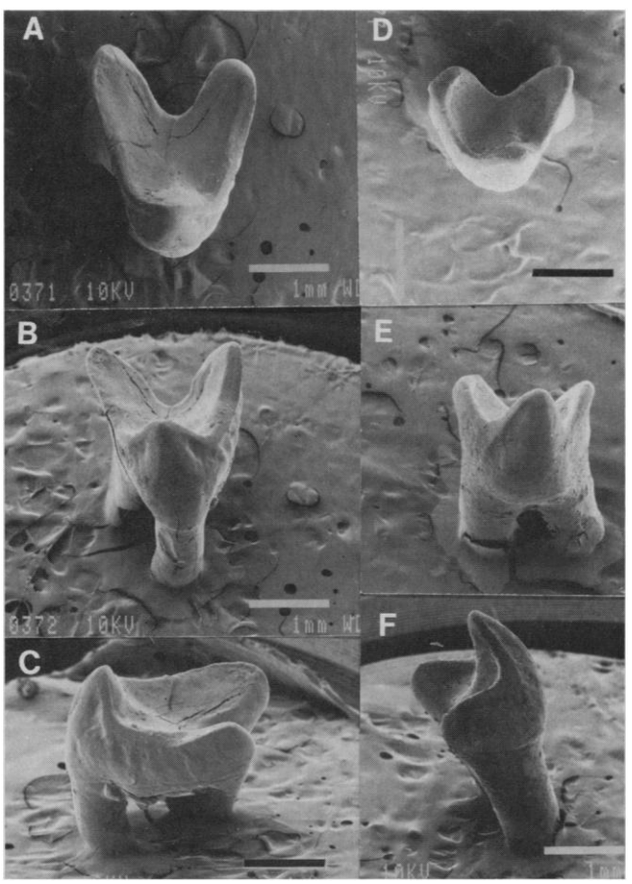

Fig. 2. *Yalkaparidon coheni*. (**A** to **C**) Right third molar (occlusal, lingual oblique, and anterior views). (**D** to **F**) Left ?third molar (occlusal, buccal oblique, and anterior views).

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The DNA-Binding Properties of the Major Regulatory Protein α4 of Herpes Simplex Viruses

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The transition from the expression of α, the first set of five herpes simplex virus genes expressed after infection, to β and γ genes, expressed later in infection, requires the participation of infected cell protein 4 (α4), the major viral regulatory protein. The α4 protein is present in complexes formed by proteins extracted from infected cells and viral DNA fragments derived from promoter domains. This report shows that the α4 protein forms specific complexes with DNA fragments derived from 5′ transcribed noncoding domains of late (γ_2) genes whose expression requires viral DNA synthesis as well as functional α4 protein. Some of the DNA fragments to which α4 binds do not contain homologs of the previously reported DNA binding site consensus sequence, suggesting that α4 may recognize and interact with more than one type of DNA binding site. The α4 proteins can bind to DNA directly. A posttranslationally modified form of the α4 protein designated α4c differs from the α4a and α4b forms with respect to its affinity for DNA fragments differing in the nucleotide sequences of the binding sites.

THE HERPES SIMPLEX VIRUS 1 AND 2 (HSV-1 and HSV-2) genes form several groups whose expression is coordinately regulated and sequentially ordered in a cascade fashion (*1*). The α genes are expressed first, and functional α proteins and especially the major regulatory protein, infected cell protein 4 (ICP4) or α4, are required for the expression of the β and γ genes later in infection (*2–6*). Previous studies have also suggested that the α4 protein may negatively regulate α gene expression (*3, 6–8*). The mechanism by which α4 protein positively regulates some genes and negatively regulates others is not known. The α4 protein in crude cellular extracts binds to DNA (*9*) and forms complexes that decrease the electrophoretic mobility in nondenaturing gels of specific DNA fragments from promoter domains of HSV genes (*10*). Monoclonal antibodies to the α4 protein further decrease the electrophoretic mobility of these complexes (*10*), and deoxyribonuclease (DNase) I footprints of some binding sites have suggested a DNA-binding consensus sequence (*10, 11*). In the studies described here on the interaction of the α4 proteins with DNA fragments derived from α genes and from late, γ_2 genes whose expression requires viral DNA synthesis as well as functional α proteins, we used three sets of fragments. The first was derived from the $\gamma_2$42 gene specifying ICP42, a γ_2 protein (*12, 13*), and consisted of 11 fragments designated D′1 to D′11 spanning the region of −179 to +104 relative to the transcription initiation site at +1 (Fig. 1, A and B). The second set contained a fragment extending from nucleotide +8 to nucleotide +194 relative to the transcription initiation site at +1 of the gene specifying the α-trans-inducing factor (αTIF), the infected cell protein 25 (ICP25), which is packaged in the virion and induces α genes after infection (*14–16*). The third set consisted of two DNA fragments from the α4 gene, which was previously shown to contain two α4 protein binding sites (*10, 17*). Fragment α4-2 spans the transcription initiation site, whereas fragment α4-1 is located between −140 and −199 relative to the transcription initiation site (*18*). The DNA fragments were terminally labeled with ^{32}P and mixed with mock-infected or infected cell nuclear extract in the presence of excess synthetic competitor DNA [poly(dI)·poly(dC)], and the reaction mixture was electrophoretically separated in a nondenaturing gel. To demonstrate the presence of α4 protein in the labeled DNA–protein complex, the binding of proteins in the nuclear extract with the labeled DNA was also done in the presence of monoclonal antibody H640 to α4 protein. The results were as follows.

1) The location and the number of α4 protein binding sites vary from one gene to another. The major and readily detected binding site in the αTIF gene is located in the 5′ transcribed noncoding leader sequence (Fig. 2, lanes 37 to 39). In the $\gamma_2$42 gene (Fig. 2), we detected at least four binding sites, two in the promoter domain and two in the leader sequence. The first binding site is in fragment D′1. The position of the second binding site is defined by fragment D′11, which binds, and fragment D′10, which does not, though the complete binding domain may extend into D′10. The location of the third site is unambiguously defined by D′8 and D′9, which bind, and D′10, which does not. The fourth site is contained in D′6, which binds; failure of D′7 to bind may be due to the Rsa I cleavage of the binding site. DNase I protection studies on the D′5 fragment, which contains the third and fourth sites, do not support the hypothesis that the third and fourth binding sites are components of a single extended binding site (*19*). The decrease in the mobility of the DNA-protein complexes caused by the monoclonal antibody to α4 confirmed the presence of the α4 protein in the complexes obtained with these fragments (Fig. 2).

2) In instances where the α4 protein–DNA probe formed multiple bands, all of the bands were shifted to a slower migrating position by the monoclonal antibody to α4. The same fragment formed both single and double bands (Fig. 2, lanes 2, 3, 5, and 6). Whereas fragment D′2 formed a strong, slow migrating band and a weak, fast migrating band, the two bands formed by the slightly larger D′3 fragment were of equal intensity. For a given nuclear extract and reagent concentration, the results were reproducible.

3) Faber and Wilcox (*11*) derived the consensus sequence ATCGTCnnnnYCGRC for the DNA binding site of the α4 protein on the basis of analyses of one binding site of this protein to the promoter domain of the HSV-1 glycoprotein D gene and two binding sites in the pBR322 plasmid DNA. Homologs of this sequence are present in the promoter domain of the α0 gene (ATCGTCactgCCGcC) (*10*). In our assays, homologs were present in the αTIF gene

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