ANTOLOGIA PALEONTOLOGICA
TOMO 4
ISMAEL FERRUSQUIA VILLAFRANCA

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ANTOLOGIA PALEONTOLOGICA

SOCIEDAD MEXICANA DE PALEONTOLOGIA, A. C.

ANTOLOGIA PALEONTOLOGICA - LECTURAS SELECTAS COMENTADAS SOBRE CONCEPTOS RECIENTES DE PALEOBIOLOGIA.

ISMAEL FERRRUSQUIA VILLAFRANCA, COMP.

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TOMO IV

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PRESENTE.

Estimado Dr. Ferrusquía-Villafranca:

Me es grato saludarlo y hacer de su conocimiento, que el trabajo titulado:

"Antología Paleontológica-Lecturas Selectas Comentadas Sobre Conceptos Recientes de Paleobiología".

En fecha reciente se sometió a la consideración de la Sociedad Mexicana de Paleontología para su publicación, se ha recibido el dictamen aprobatorio del Comité Editorial, quien ha recomendado por el tamaño de la obra (702 cuartillas), se le presente como una "Publicación Especial", ya que no podría incluirse en la Revista; relacionado con lo anterior, cabe destacar que el costo de la publicación excede la capacidad económica actual de la SOMEXPAL, por lo que ya se busca la implementación de mecanismos de financiamiento adicional, que permita a la brevedad posible publicar su interesante trabajo, que estamos seguros será de gran utilidad en la docencia y en la investigación paleontológica y de disciplinas científicas afines.

Sin otro particular, al despedirme hago propicia la ocasión para expresarle mi consideración y aprecio.

Atentamente,

Biól. Beatriz Contreras y Montero
Presidenta

PROLOGO

La formación de recursos humanos de alto nivel, es la labor prioritaria de un país, ya que su riqueza y grandeza son en gran medida una función del número y calidad de gente preparada que posee.

En el caso de México esta actividad es todavía de mayor importancia, por la obligación que se tiene de superar el enorme rezago que muestra, con respecto a otros paises, en muchos de los campos de la cultura y la economía, así como la imperiosa necesidad de elevar en términos reales el nivel de vida de todos los mexicanos, apoyándose, claro está, en un desarrollo integral, armonioso y plenamente adecuado a la naturaleza del territorio nacional y a la idiosincracia de su población.

En este sentido resulta muy acertado el esfuerzo que realiza la UAM-Iztapalapa, para alentar a su personal académico a la preparación de textos y obras de índole diversa, que sean coadyugantes eficaces en la docencia a nivel profesional y de posgrado y que subsanen, aunque sea sólo en forma parcial, la necesidad que existe de estas obras en el país.

La presente **ANTOLOGIA PALEONTOLOGICA**, se inserta como una contribución en este noble esfuerzo universitario. El conjunto de trabajos comentados que la integran reflejan los avances recientes en torno al origen y evolución de los seres vivos y su diversificación cronoespacial que los llevó a ocupar todos los ámbitos disponibles integrando así el componente más dinámico del Sistema Tierra, la Biósfera.

La antología pretende ser un vehículo hacia una mejor comprensión de este sistema al que pertenecemos, lo cual sin duda, nos permitiría enfrentar el reto y responsabilidad de conservarlo. En ello va en juego no sólo la supervivencia del hombre como una bioespecie más, sino su misión de hacerlo de una nueva era y una nueva forma de vivir.

La preparación de la obra en si se inició en 1991, cuando el suscrito, investigador del Instituto de Geología, UNAM, y profesor del Departamento de Biología, División CBS, UAM-I, realizó una estancia sabática como docente en la Facultad de Ciencias Biológicas de la Universidad Autónoma del Estado de Morelos, con objeto de proporcionar apoyo al Area disciplinaria de Paleontología, y entre otras cosas, se le encomendó la responsabilidad de preparar una Antología Paleontológica que complementara en lo posible, la formación académica de los estudiantes, poniendo a su alcance, literatura científica especializada y relevante, organizada de manera temática y comentada, para facilitar su comprensión. Esta obra subsanaría parcialmente el gran vacío que al respecto acusa nuestro país, haciendo posible el acceso de material bibliográfico a usuarios potenciales, que difícilmente podrían estar en contacto con él.

La aceptación de tal responsabilidad se hizo de buen grado, ya que como paleóntologo profesional y docente en el área, se tenía plena conciencia de esta necesidad. La realización de la obra constituyó un reto y una experiencia enriquecedora. Pero también implicó un esfuerzo y un tiempo mucho mayores de los considerados, ya que se anlizaron unas 5000 referencias bibliográficas, consultándose casi 900 trabajos diversos, seleccionándose de manera preliminar unos 200 e incluyéndose finalmente sólo 60; aun así, la obra consta de 700 cuartillas. El trabajo académico principal se desarrolló en las bibliotecas de los Institutos de Geología (UNAM) y Mexicano del Petróleo, en México, así como en las del Department of Geological Sciences, The University of Texas-Austin, y el Natural History Museum, Los Angeles, California, en Estados Unidos. No sólo se examinó la literatura, sino que se duplicaron o adquirieron los trabajos más relevantes, muchos de ellos en ese país, por no estar disponibles en México. Posteriormente, la duplicación xerográfica definitiva, la redacción de la obra y la preparación de la bibliografía respectiva, se realizó en el Instituto de Geología.

Con la elaboración de la versión xerográfica de la obra, concluyó la responsabilidad del suscrito ante la Universidad Autónoma del Estado de Morelos, cuyas autoridades ante la la imposibilidad de publicarlo, dejaron ala autor en libertda de buscar los mecanismos para hacerlo, ya que a todas luces los resultados del esfuerzo realizado, merecían ser compartidos con la comunidad académica y quedar a disposición de los estudiantes y maestros en las áreas de Biología y de Geología. De la misma opinión fueron los colegas a quienes se les mostró el trabajo, incluídas las autoridades de la División de Ciencias Biológicas y de la salud, UAM-I, quienes recomendaron presentarla en el CONCURSO DE LA ELABORACION DE LIBROS DE TEXTO Y MATERIAL DIDACTICO DE APOYO A LA DOCENCIA que ofrece esta división cuya convocatoria se publicó el 22 de marzo de 1993.

La adecuación de la obra a los requisitos y lineamientos de la convocatoria, conllevó un esfuerzo adicional enorme consistente en su transcripción completa a un formato de de procesador de palabras. Al efecto el suscrito solicitó y recibió el entusiasta apoyo de sus alumnos de biogeografía, Trimestre 93I, quienes lo ejecutaron en las instalaciones de la UAM-I.

AGRADECIMIENTOS

Una obra como la presente, implica la colaboración y el apoyo de diversas instituciones y personas; a todas ellas el autor les queda muy reconocido. En la fase inicial, la Universidad Nacional Autónoma de México, al través de las instancias del caso -Instituto de Geología y H. Consejo Técnico de la Investigación Científica- autorizó la estancia sabática; la Facultad de Ciencias Biológicas y la Dirección de Investigación y Postgrado de la Universidad Autónoma del Estado de Morelos, amablemente extendieron la invitación para realizar la estancia, ejecutaron las gestiones académico-administrativas correspondientes, y durante ella, tuvieron con el suscrito únicamente amabilidades, brindándole todo su apoyo; por ello, este se encuentra muy agardecido, especialmente con los profesores Biól. Luciano Vargas Mendoza y M. en C. Gerado Avila García, Directores respectivos de esas instituciones. La subsecretaría de Educación Superior e Investigación Científica de la SEP, y el Consejo Nacional de Ciencia y Tecnología, proporcionaron el apoyo económico que posibilitó la estancia.

El trabajo académico conducente a la preparación de la presente Antología, se benefició ampliamente con las discusiones sostenidas con los Doctores James Sprinkle, Keith Young, Jhon A. Wilson y Ernst L. Lundelius, de la University of Texas-Austin; Edward C. Wilson y Craig C. Black, del Natural History Museum, Los Angeles; y Robert Douglas, de la University of Southern, California, quienes compartieron sus experiencias y conocimientos, así como permitieron el acceso a sus bibliotecas particulares, ofreciendo además valiosas sugerencias.

ADVERTENCIA

Aunque la presente Antología se encuentra terminada y se dispone de prototipos, su duplicación xerográfica preliminar multiple, y desde luego, su eventual publicación, requieren la consecución de los permisos pertinentes, que deberán otorgar en su caso, los tenedores de los derechos respectivos -copy right-. Por tanto, deberán realizarse las gestiones necesarias.

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8.5 (a)

The earliest known ants: an analysis of the Createaceous species an inference concerning their social organization. *

E. O. Wilson

Abstract.- The known CReatceous formicoids are better interpreted from morphological evidence as foring single subfamily, the Shecomyrminae, and even a single genus, Sphecomyrminae , ranthe than multiple families and genera. The females appear to have been diferentiated as queen and worker castes belonging to same colonial species instead of winged and wingless solitary females belonging to different species. The former conclusion is support ed by the fact that the abdomens of workers of modern ant species and extinct MIocene ant species are smaller relative to the rest of the body than is case for modern wingless solitary wasps. The wingless Cretaceous formicoids conform to the proportions of ant workers rather than to those of wasps (Figs. 1-2) and hence are reasonably interpreted to have lived in colonies.

The Cretaceous formicoids are nervertheless anatomically primi tive with reference to modern ants and share some key traits nonsocial aculeate wasps. They were distributed widely over Laurasia and appear to have been munch less much abundant than modern ants.

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Introduction

This article attempts to resolve a problem in systematics thsn bears significantly on the origin and early evolution of the ants and hence the antiquity of advanced social behavior in insects generally. Studies of four mid-Crataceous amber ant subfamily Sphecomyrminae across a wide porttion of present-day North America: Sphecomyrma freyi from New Jersey (WILson et al. 1967 a,b) and S. canadensis from Alberta (WIlson 1985a) Dlussky (1975,1983) has described an important additional collection of ant like forms from the Upper Cretaceous of the Taymyr Peninsula (extreme north-central Siberia), southern Kazakh S.S.R.,and the Magadan region of extreme eastern Siberia. He erected 10 new genera to accommodate this material. In his more recent article, he also created a new family, the Armaniidae, to accommodate some of thje genera while elevating the Sphecomyrminae to family rank (hence Sphecomyrmidae)to receive others. This classification is summarized in Table 1.

Dlussky's taxomonic interpretation, which is based careful and descriptions of the new material, has sweeping consequences for our conception of the ants. First, it presents a picture of an extensive radiation of ants-like forms by the earle part of the Upper Cretaceous- in other words, by no later than 80 ma B.P. Second, Dlussky suggested that the Shecomyrmidae are not true ants or even precursors of the Formicidae but a closely related side branch, while the Armaniidae are the true ancestors of the ants. He doubted are the true antecestors of the ants. He doubted that either the Sphecomymidae or the werre eusocial; in other words he questioned whether they possessed the most ad vanced mode of social organization in which distintc queen and worker castes from overlapping adult generations and care for the developing young (see Wilson 1971).

Because of the ligth that the aerly fossil can shed on the origin of the ants and their distinctive social systems, which are matters hitherto largely unexplored due to the exclusively euso cial status of modern ant species, I decided to reexamine closely the morphological and biogeographic evidence provided by the Cretaceous material. I have arrived at a wholly different conclu sion from that of Dlussky. In essence, the differences among the fossil cannot support the separation of the two new families, the Sphecomymidae and Armaniidae, from the Formicidae. It is diffi cult to justify even the recognition of any genus other

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than Sphecomyrma on the basis of the morphological evidence. The most parsimonious explanation of the data is that the winged females and males from the Soviet deposits are queen and males of euso cial colonies of which the wingless Shecomyrma and wingless Soviet species sre the workers.

In proposing this view, I wish to emphasize sembled earlier by Dr. Dllussky and myself. There is only one eexception, the sup posed divided condition of the hind trochanter in the Armaniidae, to be discussed later. Instead, the dispariy is due to a differ ence of interpretetion of the facts with reference to higher classification and phylogeny. This is all to the good. By such contrasts the basic issues can be better clarified and the gath ering of new data stimulated.

Materials and Methodos

AAll of the characters known to vary among the Cretaceous species were firs broke into character states. Each genus and species was then redescribed character by character in matrix form to allow close comparison of taxa. THe holotypes of two of the best pre served and taxonomically most importan Soviet species, Armania robusta and Pseudarmanis rasnitsyni, were stuides closey in comparison with the descriptions. I also worked with all of the four known specimens of the North american formicoids, placed in **Sphecomyrma** (Wilson 1985a).

In addition, measurements were of a wide range of contemporary queen and worker ants and the winged and wingless females of other, nonsocial aculeate families deposited in the Museum of Comparative Zoology, in order to detect consistent differences in body proportions between social and nonsocial females. A single representative specimen was take from the series available in each species, and the species in turn were selected to provide a large amount of phyletic diversity.This information was needed to infer the lavel of social evolution of the earliest fossil. Further measurements were utilized from the monograph of Miocene ants of North America by Carpenter (1930). ALl of these fossil belog to extinct species but surviving subafamilies and in some cases surviving genera. They were considered useful because as rock fossils theeir shapes wee likely to have been distorted in the same menner as some of the Soviet specimens, which had been similarly preservedsk.

In particular, it was important to take into account the possible increase in length of the abdomen, which tends to occur when this softest of body parts is crushed laterally or dosrsoventtrally.

Head length was adopted as a reliable as a index of body size as a whole (se Wilson 1971). The size of the abdomen is critiacl as an indicaator of reproductives as appoosed to nonreproductive status in females, because it is the main part of the body con taining the ovaries, organs that are proportionately large in full social hymenopterans.

The abdomen in turn was defined in two ways for the present study. Firstt, a "functional" definition marks the abdomen aas the posteriormost discrete body part, commonly called the gaster by ant specialists-the ovary-bearing portion behind the oone or two segments of the waist. In addition, a strictly homologous definition of the abdomen (or, more precisely, posteriormost major body tagma) was used: all of the true abdominal segments of the waist in ants and a few aculeate wasps. The first, functional definition is intuitively the because the waist has by definition been reduced to a relatively thin, largely musculated portion that increases the mobility of in order to evaluate the situa tions as fully as possible.

The results were evaluated whith reference to the following criteria derived from standard systematic practice on mode faunas of insects and other animals. Individual taxa, whether species, genera, or representative of higher taxa, should be distingui sheed and made only if they differ by character states.The states can relatively minor in the case of species, but should be more subtantial in the case of genera (e.g., in ants they in clude the number of antannal and palpal segments, precence or absence of antannal scrobes; and they preferably should exist in multiples). In the case of fmilies, traits should be truly major, as for example the presence or absence of the petiole, presence or absence of principal exocrine glands, and the pattern of wing folding -again preferably accurring in multiples. Dussky (1975, 1983) appears to have used lighter criteria of the kind more commonly accepted in paleontology, in which it is recognized that fossils separated by large geographic distances and stretches of geological time are more likely to belong to different genera or higher categories. Add to this the fact that charactets are often obscured due to imperfections in fossilization, and reliance is therefore placed on minor character states.

Because of the importance of the evolutionary issues involved, I believe the criteria employed in issues involved, I believe the criteria employed in assessing the early ant fossils must be the stricter ones used in neontology. That is, it is preferablle not to recognize taxa unless the character states separating them can be seen and. are of approximately the same magnitude used in recognizing contemporaty taxa of same rank.

Results

The result of the character-state analysis for all of the Creta ceous formicoid genera are summarized in Table 2 and 3 . An inspections shows that no single character state or combination of states can be used to separate a distinct family, the Armanii dae, if neontological standars are applied. Moreover, almost none of the genera can be unambiguosly supported from the existing evidence. The only exception is Cretomyrma ,possessing prot\uberance onthe propodeum (in C.unicornis) more compact gaster, and proportionately longer legs; a second, weaker possi bility is DOlichomyrma , with an elongate head and slight con striction of gaster (Dlussky 1975, 1983, and new details provide the author in litt.).It cannot be denied that still other genera migth be represented by the Soviet fossils;we are only sure that few can be defined by neontological standards with existing data Hence the synonymy suggested in Table 4 is for the moment the appropiate nomenclatura arrangement.

Figure 1 and 2 show that the measurable, relatively undistorted wingless females among the North American and Soviet fossils, in other words Shecomyrma freyi and Dolichomyrma longiceps, have small abdomes in proportion to the remainder of the body, by both the functional and strictly homologous definitions of the abdo men. In this respectthey resemble the worker caste of modern ants more than they do the wingless females of moden nonsocial aculee ate wasps. Moreover, the winged female type of Pseudarmania rasnitsyni , a relatively undistorted specimen, is within the range of the queens of moden ants (as well as the females of nonsocial aculeate wasps), as shown in Fig.3. In sum, the wing less females among the Cretaceous fossils are best interpreted as worker ants rather than wingless reproductive aculeate wasps beloging to solitary species while the winged females are proba bly the queens.

Several additional observations support this conclusion. In his description, Dlussky (1983) state that a diagnostic traity of the Armaniida is the aproximately equal length of the scape and second funicular segments. Although ythis is quite correcty, another and more revealing way of putting the matter is to say that scape is quite short relative to the funiculus, while the second finicular segment is long lelative to the first nd third funicular segments. It turns out that these are precisellly the Sphecomyrminae. Hence both the winged and wingless Cretaceous females share the same another reason for associating them close ly.

Dussly (1983) gives as another diagnostic trait of the Armaniidae the possession of a second, free trochanter on the middle and hind legs. This conditions is weakly indicated in the drawing of Pseudarmania aberrans , but is wholly lacking in the drawing of all of the other armaniids and by direct examination I confirmed that it is indeed absent in the holotypes **Armania robusta**(the type genus species of the family and Pseudarmania rasnitsyni .

In the winged females of rmaniidae the petiole are more broadly attached posateriorly to the gaster than in the sphecomyrmine wingless females. But this is not a subfamilial or even species- level character. It is a common difference between the queens and wrkers belonging to the same species among ants, and taxonomic cahracter to separate higher formicoid taxa.

Discussion

The most parsimonious interpretion of the Cretaceous formicoid fossil neatly joinig the facts we kwon, is that bthey all belong to the subfamily Sphecomyrminae of the family Formi dae, or true ants. Furthermore, so long as contrary evidence is lacking the Cretaceous fossil should all be placed provisionally in the genera Sphecomyrma and Cretomyrma . It is entirely possi ble that other genera, and even taxa in additional subfamilies or still higher categories, existed in Cenomanian to Santonian times and might be representedd by the existing times and might be represented by the exixtenting fossils, but until supporting evidence emerges, the conservative taxonomic arrangemet suggested here (Table 4) is both more accurate and heuristtic.

This interpresented among the Cretaceous fossil are most reasona bly interpreted to be queen, worker, and male formicoids, repec tivclyu, in other words, what we would call ants as apposed to wasps. This hypotesis is more clearly depicted by juxtaposing the best preserved representatives of the three phases as though they are mambers of the same colony (see Fig. 4). The hypotesisi recervesconsiderable support from the size diferences between the best-preserved winged fossils and the best-preserved wigless ones, consistent with their being queens aand workers. It receives aditional support from the fact that the proportionate size of the abdomen in the Cretaceous ants is closter to modern ants than to modern aculeate waps (Figs. 1,2).

Dlussky (1983) made two inferences connecting anatomy to bahavior inclining him to the hypotesis that the cretaceous formicoids were not eusocial. The first is that the tips of antennal funicu li are too far removed from the mandibles to allow the precise coordination requiered for social behaviour: "The antennae in these insects did not permit them to control the manipulation of small objets, so that they could the manipulation of small ob jets, so that they could not have transported their brood or entered into trophallaxis with their larvea-that is, they could not have been true social insects." This supposition is surely incorret. The eusocial vespid wasps have similary proportioned antennae yet experience no difficulty in transporting all prey objets and placing them on the larvae. They also engage in tro phallaxis, or liquid food exchange. The flexibility of the funic uli contribute to these skills, and the twists and curves of the Cretaceous ant antennae suggest that their funiculi were likewise flexible. To this may be added the fact that some modern ants, such as the primitive Amblyiopone pallipes (Traniello 1982) and more advenced Pogonomyrmex badius (wilson 1971)do not engage in trophallaxix. Hence this form of food exchange was not essential for the evolution of eusocial behavior in ants.

Dlussky also inferred that the short, wasplike mendibles of the Cretaceous formicoids "indicates that these insects did not build true nests, and could have used only pre-existing hollows.' But tjis ovelooks the fact that some primitively eusocial wasps and bees use similar mandibles to build quite elaborate nests, mostly from carton and wax. a few, such as the halictid bess, excavate soil in a very antlike fashion.

Tosummarize, nothing in the observable anatomy of the Cretaceous formicoids precludes their having possessed a eusocial organiza tion, characterized by brood care, overlaap of adult generations, and division of labor between reproductive and nonreproductive castes. Although deirect evidence either way is lacking on the matter, these insects could also have constructed nests in the soil, rotting wood, or arboreal cavities.

The low accumulation rate of CRetaceous formicoids to date indi cates that they occurred in low densities compared wwith modern ants. Only two individuals (Sphecomyrma canadensis have been found so far aamong thousands of insects in amber from Alberta Province, Canada (Carpenter et al. 1939; J.F. McAlpine, pers. comm.).Formicoids constituted just 13 of the 1200 insect imprees sions in tthe Magadan collection and 5 of the 526 impressions in the Kazakhstan colection, in other words about 1% in both cases (Dllussky 1983). These figures contrast sharply wi th Oligocene and Miocene deposits. In the Florissant and other shales of North America (Carper 1930), as well as the Baltic amber of northerm Europe (Wheeler 1914) and amber of the Dominican Republic (Wilson 1985b), the ants are among the most abundant insect specimens. Thus the adaptive radiation that took place in the late Creta ceous or early Tertiary, yielding at least three of the dominant modern subfamilies (Myrmicinae, Dolichoderinae, Formicinae) by mid-Eocene times (Wilson 1985a) was accompanied by a maarked increase in abundance.

The ants are seen to have paralleled the mammals by achieving dramatic increases in diversity and abundance around tthe close of the Mesozoic Era. How they accomplished this breakthrouggh and managed to sustain a dominant position in the insect world to the present time is a matter of unusual interest, which additional paleontological studies should help to illiminate.

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WILSON, O. E.

TABLE I

E.O. WILSON

Taxon	Sex	Locality	Formation and age before present (million years B.P.)
Superfamily Formicoidea			
Family Sphecomyrmidae Dlussky 1983			
Sphecomyrma Wilson and Brown 1967	Female (wingless)	New Jersey, U.S.A.; Alberta, Canada	New Jersey: Santonian (80)
Cretomyrma Dlussky 1975	Female (wingless)	Taymyr Peninsula	Santonian (80)
Paleomyrmex Dlussky 1975	Male	Taymyr Peninsula	Santonian (80)
Family Armaniidae Dlussky 1983			
Archaeopone Dlussky 1975	Male	Southern Kazakh S.S.R.	Turonian (90)
Armania Dlussky 1983	Female (winged)	Magadan	Cenomanian (100)
Armaniella Dlussky 1983	Female (winged)	Magadan	Cenomanian (100)
Dolichomyrma Dlussky 1975	Female (wingless)	Southern Kazakh S.S.R.	Turonian (90)
Poneropterus Dlussky 1983	Male	Magadan	Cenomanian (100)
Pseudarmania Dlussky 1983	Female (wingless)	Magadan	Cenomanian (100)
Incertae Sedis (unplaced to family)			
Cretopone Dlussky 1975	Female (wingless?)	Southern Kazakh S.S.R.	Turonian (90)
Petropone Dlussky 1975	Female (wingless)	Southern Kazakh S.S.R.	Turonian (90)

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TABLA 3

Character	Species (Male)			
	Paleomyrmex zherichini	*Archaeopone kzylzharica*	*Archaeopone taylori*	*Ponerapterus sphecoides*
Ratio, length of 3d antennal segment to 2d segment	2–3	?	5	3
Genitalia covered by terminal abdominal tergite, or not	Not covered	Not covered	Not covered	Covered
Petiole trapezoidal (or nearly cubical) versus tapered anteriorly (delimiting a node)	Trapezoidal	Trapezoidal	Trapezoidal	Tapered
Trochanter	1-jointed	?	?	?
Source of data	Dlussky (1975)	Dlussky (1975)	Dlussky (1983)	Dlussky (1983)

TABLA 4

Superfamily Formicoidea Latreille 1802
Family Formicidae Latreille 1802

Formicidae Latreille 1802, *Hist. Nat. Gen. Part., Crust. & Ins.* 3:352. Type genus: *Formica*.

Sphecomyrmidae Dlussky 1983, *Paleontol. Zhurn.* 1983, no. 3, p. 65. Type genus: *Sphecomyrma* Wilson and Brown 1967. NEW SYNONYMY.

Armaniidae Dlussky 1983, *Paleontol. Zhurn.* 1983, no. 3, p. 66. Type genus: *Armania* Dlussky 1983. NEW SYNONYMY (tentative).

Subfamily Sphecomyrminae Wilson and Brown 1967
Sphecomyrma Wilson and Brown 1967

Sphecomyrma Wilson and Brown 1967, *Psyche* 74:8. Type species: *S. freyi* Wilson and Brown 1967.

Dolichomyrma Dlussky 1975, *Trans. Paleontol. Inst.* 147: 121. Type species: *D. longiceps* Dlussky. NEW SYNONYMY (tentative).

Paleomyrmex Dlussky 1975, *Trans. Paleontol. Inst.* 147:118. Type species: *P. zherichini* Dlussky. NEW SYNONYMY (tentative).

Archaeopone Dlussky 1975, *Trans. Paleontol. Inst.* 147:120. Type species: *A. kzylzharica* Dlussky. NEW SYNONYMY (tentative).

Armania Dlussky 1983, *Paleontol. Zhurn.* 1983, no. 3, p. 67. Type species: *A. robusta* Dlussky. NEW SYNONYMY (tentative).

Pseudarmania Dlussky 1983, *Paleontol. Zhurn.* 1983, no. 3, p. 69. Type species: *P. rasnitsyni* Dlussky. NEW SYNONYMY (tentative).

Armaniella Dlussky 1983, *Paleontol. Zhurn.* 1983, no. 3, p. 71. Type species: *A. curiosa* Dlussky. NEW SYNONYMY (tentative).

Poneropterus Dlussky 1983, *Paleontol. Zhurn.* 1983, no. 3, p. 73. Type species: *P. sphecoides* Dlussky. NEW SYNONYMY (tentative).

Cretomyrma Dlussky 1975

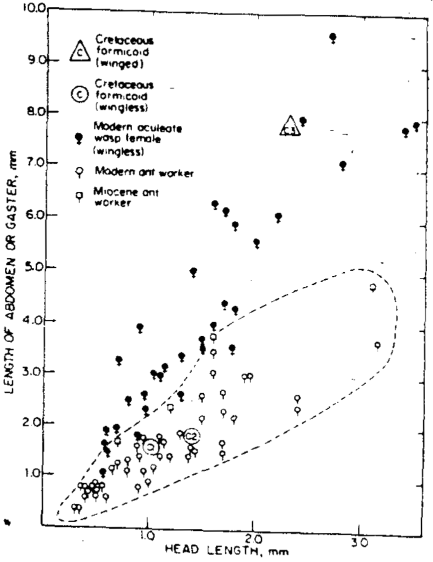
Cretomyrma Dlussky 1975, *Trans. Paleontol. Inst.* 147:115. Type species: *C. arnoldii* Dlussky.

Incertae Sedis

Petropone Dlussky 1975, *Trans. Paleontol. Inst.* 147:119. Type species: *P. petiolata* Dlussky.

Cretopone Dlussky 1975, *Trans. Paleontol. Inst.* 147:119. Type species: *C. magna* Dlussky.

FIGURA I



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PAUL FIGURA 1

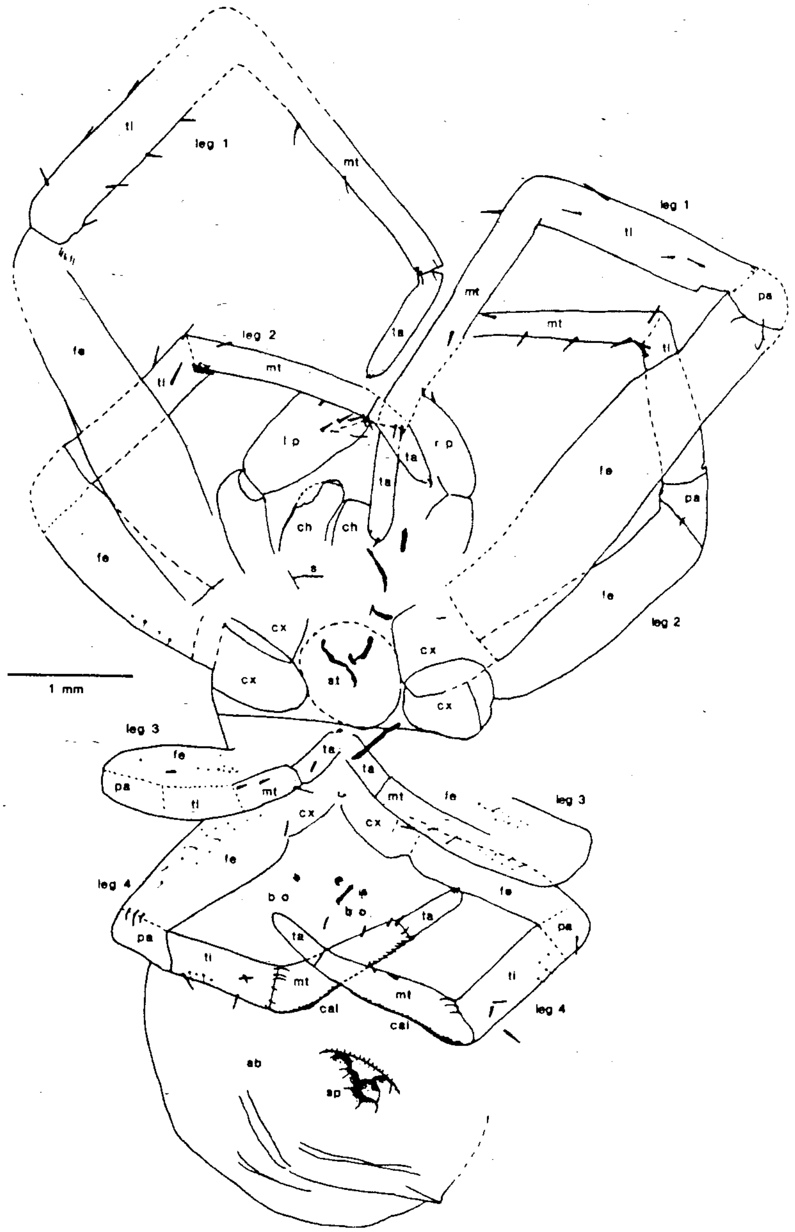

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PLATE I

PLATE I

SELDEN. *Palaeouloborus*

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WILSON, O. E.

PLATE 2

PLATE 2

SELDEN, *Palaeouloborus*, *Philoponella*

8.5 (b)

LOWER CRETACEOUS SPIDERS FROM THE SIERRA DE MONTSECH, NORTH- EAST SPAIN

by PAUL A. SELDEN

Abstract. Four specimens of spiders (Chelicerata: Araneae) from Lower Createaceous (Berriasian- mVAlanginian) lithographic lime stones of the Sierra de Montsech, Lerida Province, north-east Spain, are described, as Crataceous vilaltae gen. et sp nov. All delong to the infraorder Araneomorphae. Palaeuloborus is the oldes representative of the superfamily Deinopoides, Creataceus is referred to the superfamily Araneoides and Macryphantes isthe oldest record of the superfamily Araneoidea , family Tetrag nathidea (metine-tetragnathine-nephiline group). All three spiders were web weavers;Macryphates and Palaeouloborus wove orb webs, and may have used a wrap attack to prey on the abundant contemporaneous insect life preserved in tje Montse deposit.

SPIDERS are rare rocks of Mesozoic age. Only two specimenes, Juraraneus rasnitsyni Eskov, 1984, and Jurarchea zherikhini Eskov, 1987, from the Jurassic of the USSR, have been adequately described. THree specimenes from the Lower Createaceous of New South Wales (Jell and Duncan 1986) and twelve from the Trias of Frances (Gall 1971) were not identified to a taxonomic rank below that of order. Spiderts reported from Canadian Createaceous amber (McAlpine and Martin 1969), the Jurassic and Cretaceous of Siberis and MOngolia (reportes in Eskov 1984), and Cretaceous of Botswana (Waters 1989) await description. The four specimens described here are sufficiently well presrerved for their taxonomic affinities to be determined with some presion, and thus they represeent only the third find of Mesozoic spiders to be described and named. The fossil spiders described here are placed in extant superfamilies or families but closer assignation is considered unwise pending the of current studies on living and fossil members of these groups.

GEOLOGICAL SETTING

Locality . The Sierra de Montesech lies in the earstern Py rennes, between Balaguer and Temp in Lepida Provice, north-east Spain (see Schairer and Janicke (1970) for delails and location map). Three quarries in the vicinity of the abandoned village of Rubies, in the eastern part of the sierra, yield remarkable fossills. La Pedrera de Meia and La Cabrua have been worked for many years, and El Reguer' is currently under investigation.

Stratigraphy The 50m succession of limestones exposed quarries the Calcaires lithographiques a Plantes et Vertebres de la Pe drera de Rubies , is a facies development of the 100m Calcaices a Charophytes du MOntsech (Peybernes 1976). The deposit has been determined as late Berriasian to early Valangian in age on the evidence of ostracodes (Peybernesw and Oertli 1972; Brenner, Goldmacher and Schroeder 1974; Wahalley and Jarzembowski 1985), a conclusion consistet with evidence from palynology (Barale et al. 1984; R. Porter, personal communication 1988).

Sedimentology The Calcairesa Charophytes du Montsech is a se quence of mostly pale, fine grained thinly-bedded limestones. Sedimentary structures include laminations, fine grading minos deformation, and roll marks; trace fossil include arthopod track ways (Schairer and Janicke 1970). The enviroment of deposition deduced from the sedimentological and palaeontological evidence (see lbelow) is that of coastal lagooms within a large area of algal flats saparating marine conditions to the north from the Ebro continet to the south (Barale et al. 1984). Thjje spider- bearing sequence the Lithographic Limestones, represents a par ticularly tranquil lacustrine depositional episode (Lacasa and Martinez 1986) .

History of the fauna and flora. The exceptionally preserved biota of the Montsech lithographic limestone has received attention from paleontologists since the beginnig of this century. In the last few years, renewed insert in the deposit has brought new material to light, including the specimens described here, and avian fossils of phylogenetic importance from a locality of similar age and lithology in the neighbouring province of Cuenca (Sanz et al. 1988). LIsts of fauna and flora were given by Barale et al. (1984), with the most recent summary, especially of the insects, provide by Lacasa and Martinez (1986). All the indigenous microflora is of terrestial or non-marine aquatic provenances; the macroflora includes a wide range of gymnosperms, progymnosperms, a few ferns and horsetails, and other, unclassi fied, plants. Animals include ostracodes, few decapod crusta ceans, larval and mature insects belonging to eight extant or ders, a wide variety of fish, a few frogs and reptiles, and some dird remain. The spiders were first mentioned by Lacasa (1985. p. 2228) and a preliminary report of the results presented here was given by Selden (1989).

MATERIAL AND METHODS

Preservation. The spiders are preserved on thin slabs of pale buff-grey llimestone. Grains are not visible in the rock, and the hackly frature and vitreous appearnce under high-powewr micropy suggest cystallization from a lime mud. Calcite-fi;;ed cracks cross some specimens. The spider are preserved as pieces of cuticle on the debbing surface. The cuticle is brittle and brown: thicker parts are deep brown and the thinnest cuticle pale buff. The cutilce has not been chemicaly analysed; it is presumed still to be organic, but probablly not of the origina; composition. The best-preserved parts are visible through a thin layer of translu cent limestone, but their morphological details are hazy due to the presence of the overlying matrix. In such intalces, 22-4% hydrochloric acid are used, sparingly and with care, to remove the matrix and thus to reveal fine structural details. The spid ers are in varying state of original decay: for examplle in LC 1753 AP the podomeres ,of leg 1 in particular, are crowded with subcircular objects along the cebtral parts of the shaft . Thse objeticts are interpreted as the decvayed remmants of muscle . LC 1754 AP is very pooly preserved: mainly a mould remains, and this is interpreted as a specimen in which decay has progressed futher.

Both part and counterpart of especimens LC 1753 AP and LC 1754 AP are preserved, but only the psrt of specimens LC 1150 IEI and LP 1755 AP was collested. Specimens LC 1753 AP B, LC 1754 AP A, LC 1150 IEI and 1755 AP represent lower slabs preserving mainly ventral features of the specimenes ; LC 1753 AP A and LC 1754 AP B are upper slabs preserving mainly ventral features of the specimens ; LC 1753 AP A and LC 1754 AP B are upper salbs with dorsal features. However, aplitting the rock has not resulted in perfect separation of dorsall and ventral, and due to the mode of preservations within the limestone (described above), most of both dorsal and ventral parts are preserved on LC 1753 AP B, and LLC 1150 IEI. LC 1754 AP is mainli an external mould with little cuticle ramaining, but on LP 1755 AP ventral parts body and both dorsal and ventral sides of the distal parts of the legs are preserved. On all specimens, the legs an abdomen (when present) are crushed flat. The carapace has sufficiet convexity to produce relief in the fossil , so that on LP 1755 AP, for exam ple, the carapace shape can be determined by the relief of the sternum and cocae are outlined by seta and cuitle. The malle pals of LC 1753 AP, LC 1754 AP, and LC 1500 IEI appear to occupy depressions in the matrix. This is probably because they were bulbous structures in life therefore created a concavity in the sediment into whith the palp collapsed during burial.

The spiders were studies under aa Wild M 7S stereomicroscope, with the specimens immersed in ethanol or glicerine to enchance their constrast agains the pale rock backgroup. Camera lucida drawing were photographs were under same conditions. In additon, a Zeiss photautomat microspe was used, in reflected lingt mode with oil imm ersion objecttives, ,to view and photographic de tails at higher magnifications. The computer programs MacClade, version 2.1 (Manddison and Mandison 1987) poved very uself for exploring relationships.

Terminology Setal terminologyis somewhat problametioc, since different author have the same terms in different ways. Futher more, thre is a completa gradation in size between setae (small and may be or long thick or thin), bristles, and spine (large). Macroseta is a tterm use, for example by Opell (1979), to de scribe a large seta, which is smooth apart from few minute accessory spine wich are no longer than the mean thickness of the seta (see Lehtinen 1967, fig. 10a; Kullmann 1972, fig. 7). Two fairly distrintc setal types are commonly called plumose (e.g. by Forters and Wilton 1973; Forster and Blest 1979). The first, which is here called plumose, is generally thicker than the serrate seta, and has helical ridger beearing samall accessory spine which are much shorte tahn the width of the seta (see Lehtinen 1967, fig. 8; Kullmann 1972. fig . 8). The second, which is here called feathrey, is fine, smooth, and has long accessory branches which are much longe than width of seta (see Lehtinen 1967, fig. 9) Many other types of sate and spine exist; there may be complete gradations between them, and the extent of their phylogetic importance unknown.

Terminology of sclerites of male palps differs between workers in different group of spiders due to a lack of undersatanding of the homologies between the sclerites. Thus the task of recogniz ing palpal sclerites in fossil spiders problametical. Uselful descriptions of the contituent parts of male palpa oegans are found in Cromstack (1948), Levi (1961), Merrett (1963) and Millidge (1977). In leg formule (e.g. 1243), the leg lengths are renked in order longest (fist) to shortes (last). Abbreviations used in the text and tex-figures are as follows:

ab	abdome n
l	labium
s	serrula
bo	book-lug operculum
lp	letf palp
st	sternum
ca	cephalic are
m	maxilla
t	tegulum
cal	callamistrum
ma	median apophysis
ta	tarsus
ch	cheliacera
mt	metatarsus
ti	tibia
cx	coxa
pa	patella
ti	tibial apophy sis
e	embolus
pc	paracymbium
tr	trochganter
f	fovea
pe	pedicel
fe	femur
rp	rigth palp

Provenance and depository. Three of fossil specimens, LC 1150 IEI, LC 1753 AP, and LC 1754 AP, come from the quarry of La Cabrua, the fourth, LP 1755 AP, is from the locality of La Ped rera de Meia. Exact stratigraphical provenance is not known, but both of these localities are in the same 50m sequence of lito graphic limestones, the Calcaries lithographiques a Plantes et Vertebres de la Pedrera de Rubies, described above. The speci menes are deposited in the Institut d'Estudis llerdencs , Lerida.

Preserved specimens of extant spiders were studies for compara tive purposes, and in addition to those in the author's collec tion of mainly British species, the following specimens wereeex amined. Uloboridae:yptiotes flavidus,female, Funchal Madeira, M. J. Jones Collection No. 119. M-Archester Meseum; Philoponella ap., male and female, Lake Naivasha. mature and immature males, Nairobi, Kenya, J. Murphy Collection NOs 1302, 1363. Deinopidae: Deinopsis guianesis, females British Guiana, British MUseum, (Natural History) (BM(NH)) No. 1939.3.24.228;Deinopsis staunto ni, female Durban, South Africa, BN (NH) No.1903.8.20.1: Deinop sis sp., female and immature, KIlifi, Kenya, J. Murphyy Collec tion; Mennus camelus, femalles (types), Durban, South Africa BM (NH) No. 1903.7.10.22; Mennus sp., male, Kitale, and females Nairobi, Kenya, J. Murphy Collection Avella angulata,Gayndah,Aebutina binotata, Aguas Negras near Tarapu, Napo, Ecuador, British Museum (Natural History) Arachnid Collec tion.

SYSTEMATIC PALEONTOLOGY

Order ARANNEAE Clearck, 1757

Suborder OPHISTHOTHELAE Pocock 1892

Infraorder ARANNEOMORPHAE Smith, 1902

Remarks. The phylogenetic scheme for the higher classification of spiders which is currently widely accepted originated with Pocock (1892). In this scheme, the liphistiomorphae (Mesothe lae) is the sistter group to the Opisthothelae (Mygamorphae + Araneomorphae). The morphology of liphistiomorphs distinctive (Platnick and Gertsch 1976, fig. 5) The fossil spiders de scribed here synapomorphies: scelrite opf the first abdominal segment (Platnick and Gertsch 1976), and labium as wide as or wider than the sternum (Raven 1985) Thus they are referred to the Ophisthothellae.

Mygalomorph synamopomorph include the following external morpho logical feature: cheliceral fang which operates in the sagittal plane (orthognathous), complete loss of expression of the anterior median spinnerets, three or four articles in the poste rior latel spinnerets (Raven 1985). The alternative charcter states typity the Araneomorphae, and it is to this latter group that the Montesech spiders are referred. In particular, the chelicerae of Crataaraneus gen. nov. is more complex than the mygalomorph palp; and Palaeouloborus gen. nov. passesses a calamistrum and a cribellum; the latter is homologue posterior madian spinneret. Neither labial or maxillary cuspules nor three -or four segamnted posterios latel spinner are known in any of the Mostsech spiders, and each of them showns greater affinity to araaneomorph families than to mygalomorphos.

Assginment of the Cretaceous spiders to lower taxonomic categori presents greaater difficulty.

A competent anraneologits canm palce most living spiders seen in the field into a family with a high degree of certainty. Even in the absence of field characters, such as web type aand habitat, spider familial keys are relatively straightforward, onlly re quiring the use of a binocular microscope and normally no dissec tion. Spider families are diagnosed on unique combinations of morphological characters such as number and position of eyes, spinnert pattern, and number of tasal claws. However, research has shown that many of the characters on which the families are based are plesiomprphic at higher taxonomioc levels, convergent with other group , or are loss craracteristicas (Lehtinen 1978). A calssis example of this is the recognitiuon of the criblum as a synapomorphy for Araneomorphae: it precense in lower categories ie merely the expression of the plesiomorphoc state, and its absence illustrate convergence of the apomorphy in many araneo morph families. Whilst unique combinations of plesiomorphiesmay work as familial descriptions in practice, theycannot reflect true relationship between families. Of necessity, therefore, recent cladistic analysers have sought new or previosuly over looked characters as a apomorphies. These cahracters are commonly behavioural or anatomical, and may be pooly known in group out side those under particular study. More important in the present work, such characters are most unlikely tobe preserved in the fossil record.

An additional concern encountered when working rare fossils which have Recent relatives aarises from the possibility that the fossils may be ancestors of Recent species. Should the fossils be classifying fossils may be ancestors of Recent species. Should the fossils be classified in the same as their Recent relatives or in a separaste scheme ? Such problems have been discussed by Crowson (1970), Farris (1981) and others. A Uself device for classifing fossils with their Recent relatives is the plesion (Patterson and Rosen 1977): This prewsupposes, however, that the Recent classification is soundly based shared derived characters.

In spider systematics this is not yet true. IN this paper, the new taxa are taxa arre classified as

,close as posible to their presumed position in the Recent classification. Inevitably this entails palcemetn within ,taxa yet to be defined by synapomor phies or defined on shared derived characters which cannot be seen easily i n fossils. Because these are among the first Mesozoic spiders to be described, and because of the paucity of diagnostic feactures in the fossils, and the present lack of knowledge of synapomorphies in living families, the spiders are assinged to superfamilies, and in one case to family, but to no extant lower taxa. (Note that among Cretaceous insect, classifi cation to modern genera is not unusual). More specimens of Meso zoic spiders which are becoming available for study may hepl to elucidate further the taxonomic positions of the specimens de scribed here, and assist in unravelling the complexitieds of spider phylogeny phylogeny and evolution. The consensus' spide5 calssificat ion scheme given in Shear (1986b) is folowed here in general, but with discussion concerning the status of groups assingned to the Araneidae following recent work by Coddington (1989a,b, 1990).

Superfamily DEINOPOIDEA Koch, 1851

Remarks .. This superfaly consists of the two cribellate fami lies Uloboridae and Deinopidae, which weave orb webs (most Uloboriae) or spin modified orb webs which are then thrown re tiarius- like at their prey (Deinopidae). Much more is known about ulloboris than deinopids, though work on the latter is currently in progress. Although these two families have benn considered closely related for nearly a century (Simon 1892), Coddington (1986, p. 359), with reference to his cladogram (p. 358), remarked that: the monophyly of the uloborid -deinopid linages is baased on only three characteriters, primarily because so little is known about deinopids. The three characters Codding ton accepted as deinopoid synapomorphies are: puffed cribellate silk, pseudoserrate plumose hairs, and fourth-tarsal macrosetae; however, he qualified this by suggesting that the first two characters may actully be synapomorphies for all orb-web wweavers (Deinopoidea and Araneoidea) (Coddington 1986, pp. 327, 359). Recnt work by Coddington (1989a,b, 1990)has resolved the appar ent trichotomy between Araneoidea, Uloboridae, and Deinopidae (reported in Pllatnick 1986); Deinopoidae and Araneoidea being seen as sister group of orb- web weavers: the Orbicularie Wallck enaer, 1802.

Paleoeuloborus gen. nov., described below, possesses three tarsal claws accessory claws typical of web weavers aand lacks the tarsal adaptations of the superfamilies Thomisoidea, Philo dromoidea, Lycosoidea, Clubionoidea, Salticoidea and Pholcodea. The fossil genus also lacks the synapomorphies of Scytodoidea (Lehtinen 1986), Dysderoidea (Forster and Platnick 1985), Palpi manoidea (Forster and Platnick 1984), Hersiliodea, Hypochiloidea (Patnick 1977), Eresoidea, and Agelenoidea. Dictynoidea are cribellates, and the deinopoid families haves, at one time or another, been referred to this superfamily, and to the family Dicynidae in paarticular, However, dictynids are generally samll spiders, with short legs of approximately equall length, and lack femoral trichobothia (see below) ; thus they are quite unlike Palaeoulobus.

The characters which are most usefl in placing Palaeouloborus are: femoral trichobothria on legs 22,3, and 4, leg 1 more than five times the length of the carapace and more than twice the length of leg 3, all leg tarsi with large accessory claws and apparently non-pectinate paired claws, presence of calamistrum and cribellum, and presence of plumose hairs.

Femoral trichobothria occur in only two groups of araneomporph spiders: the metine- tetragnathine lineage of the superfamily Araneoidea, and the family Uloboridae (Opell 1979); Lehtinen 1980: Levi 1981). In both of these groups there is great dispari ty in length betwween the elongate anterios legs (1 and 2) and the short third pair (Pl. 22. fig . 9). a fecture also found in some other Araneoidea (Argiopinae Levi 1983). Palaeouloborus is cribellate, and since only the Deinopoidea, but not the AAran eoidea, are cribellate, this genus must be referred to the former superfamily. The calamistrum of Palaeouloborus is situated in a curved depression on the superior surface of fourth metatarsus. Such a curvature a curvature occurs in uloborids (PI. 2, fig. 10), to a much lesser degree in deinopids (

Shear 1986a), and also in Aebutina a poorly Knokwn genus tentatively referred to the Dictydae (Only females and immatures of this genus are Known). Additionally.

Paleouloborus bears plumose setae, which plumose setae, which are found in Deinopoidea but not Araaneoidea but not Araneoidea. Thje characteristic tarsal macrosetae of deinopoids (se below) appear to be absent from Palaeoloborus .

Palaeouloborus is referred to be the superfamily Deinopoidea, on the evidence give above. The fossil clearly resembles members of the family Uloboridea more closely than Deinopidae; the latter letgs all of a similar length, web- throwing ans lacks the femoral trichobothria typical of the Uloboridae and tthe fossil genus.

The position of Palaeouloborus within the Deinopoidea is nowdiscussed. In a recent revision of the Uloboridae, Opell (1979) gave the following characters as diagnostic of the family: (1) lack of poison gllads, (2) cribellate orb-web weavers, (3) femoral trichobothria, and (4) row of macrosetae (short spines) on metatarsus and tarsus of leg 4. The tarsal spine cannot be a synapomorphy for the Uloboridae since they also occur in Deinopidae (se below). Coddington (1986) added characters of the silk- glands described by Kovoor (1977), and some behavioural traits, to the list of uloborid synapomorphies, but omitted femoral trichobothria. Coddington's cladograms (1986, p. 358; 1989b,fig.108) show the metine-tetragnathines, which also have femoral trichobothria, far from the dichotomy of Araneoidea with Deinopoidea which presumes that femoral trichobothriam are a convergent phenomenon in uloborids and metines- tetragnathines. The alternattive hypothesis (that they are a synapomorphy for all orb-weavers) would require their loss in many separate lines.

The row tarsal and metatarsal macrosetae of uloborids was considered to be a synapomorphy of the family by Opell (1979), but in a later paper , Opell (1982) mentioned finding a poorly developed row on leg 4 of deinopids as well. My own observations confirm that macrosetae are present on the inferior surface of the distal half of the meatatarsus and the tarsus of leg 4, and to a lesser extent on leg 3, in the deinopids Deinopis, Menneus and Avella . These macrosetae are rather similar to the comb of serrate bristles seen in the Theridiidae in a similar position on the legs. HOwever, they differ from theridiid bristles in being plumose, not serrate. As in the Thjeridiids, they may need to be searched for, since blend into the general hirsuteness of the tarsus. The macrosetae are not greatly different from the curved bristles normally present on the inferior surface of the distal end of the tarsus. Also, as in theridiids, they are not strictly confined to mt4 and ta4, also being present on leg 3, and they vary form species to species. In all deinopids I studied they were quite unlike the comb of short, upstanding spines of the uloborid Zosis geniculatus illustrated by Opell (1979, pl. 1, figs, A and C). Rather they resemble the row of macrosetae of the the uloborid Hyptiotes cavatus figured by Opell (1982, pl. 1, fig. C.) The similariry between theridiids and deinopids in this feature is presumably due to convergence in their prey-wrapping strategies rather than synapomorphy. Clearly a comb of macrosetae on the fourthj leg is a derived character of uloborids and deinopids which is not present in Palaeouloborus.

The legs of uloborids bear fine feathery setae amongst setae; neither deinopids nor Palaeouloborus bear them.

Palaeouloborus cannot be included in the family Uloboridae because it has nweither feathery setae nor fourth tarsal macrosetae. The fossil lacks the many specializations of deinopids, and in addition the fourth tarsal macrosetal comb is absent. Rather than redefining the family Uloboridae to accommodate the fossil genus, it is left here within the superfamily Deinopodea., closer to the Uloboridae than the Deinopidae, but not placed in either family. This placement indicates that the loss of a fourth tarsal macrosetal comb is autapomorp[hic for the fossil genus.

Diagnosis . Deinopoid with ovate carapace bearing marked break of separating anterior of carapace from sloping posterior area; leg 1 more than five length of carapace and more than twice length of the 3; many trichobothria on superior? retrolateral surface of femur of leg 2 and superior? prolateral surfaces of femora of legs 3 and 4: paired tyarsal claws small, without teeth, median claw long, without teeeh, pair of large accesory claws; superior surface of metatrsus of leg 4 in gentle S-shape proximally convex and the concave, straightenin out about half- way along podomere, bearing calamistrum which becomes row of bristles towards distal end of podomere; plumose present. Row of macrosetae absent from tarsusk.

Palaeouloborus lacasae sp. nov.

plate1; plate 2, fig 1-5,7,8,10; text fig. 1

Derivation *of name After Antonio Lacasa - Ruiz Pallaeontologist at the Institut d' Estudis Ilerdencs. Lerida Spain.

Types specimen Holotype LP 1755 AP, freom the quarry of La Pedrera de Meia Sierra de Montsech, noth- east Spain, and held in the collections of the Institut d' Estudis Ilerdencs, Spain.Diagnosis As for the genus.

Description The carapace shape is determined from fragmentes of cuticle from the relief of the matrix. Thes craps of cuticle in the carapace region mainly represent coxae and sternum. However on the left side between legs 2 and 3, cut icle of the carapace edge can be seen lying in a depression by pressure of the edge into the matrix . Fain traces of cuticle from the posterior eedges of the crapace can also be discerned between the tarsi of legs 3. These cuticle remants and the faint deepression by the carapace margin suggests an ovatee carapace with truncated anterior margin. The carapaces is 1.73 mm log, and 1.50 mm wide. It is widest just posterior to its midpoint. There does not appear a well defined cephalic area., nor an obvious fovea. There is a marked transverse break transverse break of slope just posterior to the widest part of thge carapace and separating the raised foveal region from the backwardly sloping part of the carapace. This slope is found in some living spiders (e.g., the uloborid Phillonella , Pl. 2, fig 8), and accommodates an abdomen which extenceda forwards beyond the pedicel. Eyes not seen, no obvious turbercles.

Thechelicerae are large, 0.67 mm log, and 0.33 mm wide and somewhat forwardly direted, with parallel sides. The Fangs cannot be seen, since the anterios edges of the chelicerae are obscured by overlying matrix .

The palps are clothed with setae, and short spines occur on the superior surface of thee tarsus. The tarsus is oval, indicating that it was tumid in life. The distal end is not seen, so the presence of a claw cannot be confirmed. The specimens is therefore not a manute male, and could be an immature or a females. Very little of the basal parts of the palp can be seen, but supeerimposed on the anterior part of thhe carapacve area is a dark line which, under high magnifications, is seenb to be serrate (Pl 2, fig. 1). This interpreted as the serrulla of the left maxillla: cuticle is absent is absent where the serrula of the maxilla would have been preserved.

The leg formula is 1243. The coaxe measure approximately 0.58mm log and the trochanters 0.18mm Lengths of the more distal podomerws, in mm are as follows: leg 1 : fe 3.27, pa 0.77. ti 1.64,mt 2.50. ta 0.96. total 9.14: leg 2.11. pa 0.48, ti 1.35, mt 1.44, ta 0.77. total 6.15: leg 3: fe 1.35. pa 0.48, ti 1.06. mt 0.48. tal 0.48. total 3.85; leg 4: fe 1064, pa 0.48, ti 0.87, mt 1025, ta 0.552, total 4.76.

The legs are clothed with setae of the plumose type. Under high magnification, they are seen to bear a sculpture of striations srranged in a helical in a pattern, with abundant minute serrae (Pl. 2. fig 7). No feathery satae can be seen on the legs. The femoraa are only sparsely setose, setae and bristles becoming more abundant on distal parts of the legs. Groups of tricobothria re certaainly present on the femoraa of legs 2-4 and on the tibia of leg 4. These trichobothria are not feathered (Pl 2. 2, fig, 2). Isolated trichobothria are more difficult to see, and their presence elsewhere onthe legs cannot be confirmed. The leg spines are not large, and because see, and their presence elsewhere on the legs cannot be confirmed. The leg spines are not large because only part their presence elsewhere on the legs cannot be confirmed. The leg spinees are not large, and because only part of the specimen is preserved, the numbers of spsines given below are not the maximun number which may be present onthe legs. All tarsi are spinelless and bera two small, non-pectinate paired claws, a large madian claw which appears to be non-pectinate or if pectinate then with only minute teeth and two large accesory claws (Pl. 2. fig. 3). Fel beras few setae, mainly on the inferior surface (where they are curved) and on the superior surface, especially proximally and distally. Trichobothria may be present on fel (two possible trichobothrial bases can be seen fel on the right side) but cannot be confirmed. Fel and pal are spineless.

Till bears four inferior spines and three superior spines along the shaft of the podomere, one proximal lateral spine, one lateral subdistal spine, and one superior subdistal spine. Mtl bears three inferior and two lateral spines down the shaft of the ppopodomere. Proximally, mtl bears one superior one lateral, and one inferior spine, and two inferior distal spines are present. Fe2 is spineless and bears few setae, principally on the inferior and superior surfaces. Both second femora are pooly preserved but a few trichobothrial bases can be seen proximally, apparently on the retrollateral surface. Pa2 is spineless. Ti2 bears bristles proximally and along the inferior surface. Ti2 bears two inferior distal spinesw, one lateral subdistal spine subdistral spine, and one superrior distal spine. More spines are probably present on ti2 but on both sides specimen and bears brsitles, especially along the inferior surface. Mt2 bears superriopr ans inferior proximal spine, two median inferior spine and one lateral and two inferior distal spines. Fe3 bers few setae, one tiny spine laterally, and many trichobothria (Probably 20-40 in life) over a large are of tthe? prlateral surfase Pa3 is spineless. Ti# is poorly preserved on both sides of the specimen, but beears many bristles. Mt3 bears two short inferior spines and one lateral distal spine Fe4 is spineless, bears strong, curded bristles distally, and many tricchobothria (as may as on fe3) over a large area of the superior? prolateral surface. Pa4 bears large bristles laterally. Ti4 beras one superior proximal spine, and prolateral, retrolateral and superior spines subdistally. Ti4 beras about four trichobothria on the proximal; superior surface, and long curved bristles distally. The superior surface of mt4 follows a geentle S-shape , proximally convex and then concave, before sttraigghtening out about Half-way along the podomere. The superior surface of mt4 bears a calamistrum composed of curved setae , apparently in one row, running fro the proximal end of the podomere for about two- thirds of its length, where it passes indistinctlyu into a row of curved bristles which continues to the distal end of the podomere (Pl 2, figs. 5 and 8). Mt4beears two short inferior median spines, at least two very short spines inferodistally, and large bristlees distally.

The abdomen meausres 3.67 mm long, and 2.89mm wide. It is ovate, wrinkled posteriorly , and compressed to the right , indicating thant it was globose in life. The abdomen is sparsely setose, the setae becoming thicker, butnot longer, posteriorly, where they show plumose under high magnification (Pl.2, fig. 7) Apair of subtriangular areas of darker cuticle each weith a small dark patch anteriorly, is situated at the anterior end of the abdomen. These are interpreted as book-lung opercula. Three pairs of spinnerets are visible in the postterior half of the abdom,en. They are compressed to the right. Their position indicates that they weree not terminal, but ventral, in possition in life. A recured line immediately anterior to the anterior pair of spinnerets represents the cribellum. Little detail can be discerned the cribellar plate is nott preserved (this is presumably on the counterpart) only the fold of cuticle anterior to the plate. (In living spiders the cribellum is commonly ivaginated into a fold in front of spinnerets when not in use, see Pl. 2, fig. 6) Along this fold there are numerous short, blunt setae of setae a types not seen elsewhere on the spider (Pl. 2, fig. 4).

Superfamily ARANEOIDEA latreille 1806

Ramarks Cretaneusgen. nov. and Macryphantes gen. nov., describe below, are assigned to this superfamily. Both genera lack a calamisttrum and cribellum. This does not, by itself, exclude them from cribellate superfamily because mature males of many living cribellate genera commoly abandon web weaving with the concomitant degeneration of the cribellum and calamistrum, and the preserved specimens of both genera are matiure males, However, evidence is presented below that Crataraneus and Macryphantes show greater resemblance to araneoids than to any cribellate group.Tarsal adaptions (two claws, scopulae, Tarsomeres, etc.) for cursorial, saltatorial, and other specialized locomotory habits, as foud in the superfamilies rejected Cretaraneus .

Cretaeaneus palp appears to be relatively simple for an ara neoid, palps are variable within spider famillies. Therefore Cretaraneus , Though apparently lacking a comb of setae on the fourth tarsus, cannot be ecxluded with confidence form the Ther iddidae.

Stridulatory ridges are commonly present on the chelicerae of male linnyphiids but be obscure in some species, and the labim is usually rebordeded. Neither stridulatory ridger nor a rebordered labium is seen in Cretareneus. A link between Cretaneusand linyphiids is provided by the raised cephalic ., a feature common in linyphiid malrs. However, a presumed laterall condyle on the chelicera and accessory tarsal claws (serrate bristle) are features not found in the Lynyphiidae, but characteristic of the Araneidae.

The rotation but characteristic of the Araneidae.

The rotation of the male palpal sclerites in some Araneidae mentioned by Levi (1983) cannot be confirmed in Cretaneus be cause of the rotation produced during fossilization, although the general appearance of the palp in fossill genus is not reminis cent of the araneid palp. The apparent precence of a median apophysis in the palps of the fossil may provide information on its placement, but at present this character is unresollved (Codding 1989b). The wide labium, presumed cheliceral condyle, and accessory tarsal claws of Cretaneu are characteristic of most araneoids (Levi 1980). TThe rather large, forwardly directed chelicerae, and relatively simple palp of Cretaneus sugges the metine- tetraganthien lineage, but thge fossil lacks orther characteristics of some linyphiids also possess enlarged chelic erae. Male palps with a superficially simple appearence are characteristic of the genus Nephila (Schult 1983), but Cretaraneus bears few other similarties to the genus.

The Jurassic spide Juraraneus rasnitsyni Eskov, 1984 was placed a monospecific family, the JUraraneidae Eskov, (1984) defined the family on a unique combination of araneoid charac ters and could find no apomonphies foe the family. Cretaraneus resembles Juraraneus is many ways, including averall size shape ; leg (but not tarsal) lengths; approximate shapes of sternum, labium and maxillae ; general shape of chelicerae. py Cretaraneus differs from py Jurarneus in lacking the irreg gulsr group of denticles on the inner margin of the chelicera, and the palpal characters ionterpreted by Eskov (1984) as a large, hook-like paracymbiu, a large, pointed median apophysis, and a long straight conductor (=embolus?).

The family Archaeidae is includes in the Araneoideaa by many arachnologists but, in a radical revison of archaeids and some other samll families (for example Mimetidae, previously always placed in Araneoidea), Forter and Plantnick (1984) removed them to the Palpimanoidea. They also creater the monogeneris families Prachaneidae and Holarchaeidae for genera previosly included in the Archaeidae. Fortes and Platnick (1984, p. 99) proposed two synapomorphies for the superfamily Palpimanoides: cheleceral peg-teeth (modified setae as oppossed to cuticular teeth) , and an elevated cheliceral gland mound. They also mentioned that peg-teeth are found in some unrelated thomisoid and scytodoid genera, as convergent phenomena and have been seconfdarily lost in membres of six families assiggned by them tto the palpima noids. Cretaraneus possesses true teeth on the chelicerae, but mentioned here becausee of saome similarities with the Pararchaeidae.

The Pararchaeidae differ from the other papimaniods in having serrate, rathe than pulmose, hairs, and show similarity with Cretaraneus in the enlarged chelicerae with a prominent keel and large bristles on the tarsus. acheliceral keel is also found in other groups, for example the Leptonetidae (Gestsch 1974). The male palp of pararchaeids has a strongly developed embolus and a large tegular plate (Forster and Platnick 1984, p. 70), feature also apparent in the palp of Cretaraneus It sis possible, thefore, that some relationship exixts between Cretaneus and the Paararchaeidea, which may or may not be an araneoid family. An archaeid spider has been described from the Jurassic (Eskov 1987).

Since it seems imposible to refer Cretaraneus to an araneoid family, thre are two available options. First, a new be diffi cult,give the lack of specialized features displayed by fossil, and would not provide any additional phylogenetic information. The second optin, and the one chosen here, is leave the genus unplaced within the superfamily Araneoidea. It is possible that future discoveries will reveral that Juraraneus and Cretaraneus belong to the same group of Mesozopic araneoidos.

Genus CRETARANEUS gen. nov.

Derivation of name creta, chalk , and araneus, a spider.

Type and only known species Cretaraneus vilaltae sp. nov.

Diagnosis. Araneoid spider with subelliptical carapace bearing raised cephalis are and no fovea; subtrigular aternum; small, subtriangulsr labium; serrate setae convering all parts of body.

Chelicerae relatively large (0.4 x length of carapace), for wardly directed (at least in adult male), with inner and outer row of denticles (not peg-teeth), and mesal ridge; male palp with long embolus, and small, proximal? paracymbyum; leg rela tively equal in length, about three times the length of cara paces; femora, tibiae and meetatarsi with spines; tarsi with pectinate paired claws, small median claw, and associated serrate bristle; not true trichobothria; globose abdomen.

Derivation the name . Ramon Vilalta-Oliva. President of the Institut d' Estudis Ilerdenes Lerida.

Type specimen Holotype and only known specimen. LC 1150 IEI. complete specimen on single piece of limestone from of L a Ca brus. Sierra de Montsech. north-east Spain: held in collections of Intitut d;Estudis Ilerdenes, Spain.

Diagnosis. As for the genus.

Description . A well-preserved spider, and smallest fo the specimen known from Montsech. The carapace cuticle is preserved and is golden brown in colorur. The carapace is 1.73 mm long and 1.37 mm wide , and pyriform: its greatest width occurs at four- fifth of the length behind the anterior margin from greatest width.

Carapace is covered in setae. At the anterior of the carapace, these forwardly directed setas and long curved bristles. At the anterior of the carapace two circular structures are niterpreted as meddian eyes. Just posterior. At the anterior margin of the carapace, adeep, drop-shaped depression, with its blun endf anteriormost, marks the fovea. The shape is eomfirmed by specimen LC 1754 AP, in which the caparace is 3.25 mm wide.

A pair of deep depressiona just to the anterior median eyes are surrounded by dark cuticle. Thee structures are interpreted as the proximal ends of the chelicerae which are directed ventally; the chelicerae pre sumably disappear into the matrix beneth the specimen. The sternum appears to be circular; its shape is suug ested by the arrangement of the coxae, as seen on both LC 1753 AP and LC 1754 AP. The coxae of legs 4 meet in the midline ,and on both the holotype and paratype some remnats of the anterior edge of the aternum can be discerned.

The palp on the rith side of LC 1753 AP B (the left side of LC 1753 AP A) is preserved (Pl. 4, fig. 3), and confirms than the specimen is an adult malre. he palpal tarsus is subcircular in outline with a mesal bulge. This bulge represents either the mesal patrt of a circular cymbium or a mesally situated cresentic cymbium. The bulges extends beyond the oval dark oval band which is interpreted as the embolus (this structure cxould be the conductor or some other sclerite functioning as a guide for the embollus (this structure could be the conductor or some other sclerie funtioning as a guide for the embolus). The enbolus is coided in a horizontal viewed from above. On the proximalateral side,a thick, reniform lobe is interpreted as a median apophysis.A dark area can be seen on the proximal edge of the cymbium within the embolus; this is inferior in position ; this dark area belong to a clerie of the palp. A smaller dark patch occurs just anterior to the midpoit of the palp, onb the inferi or surface; this represents par of anothere sclerite. Numerous long bristles run right laterally from tjhe base of the tarus, and some curved bristles are present on its superior surface.

Larger, curved spinew are present around the base of the tarsus; the appear to originate proximal to the tarsus, that is, on tibia, which is otherwise pooly preserved.

The leg length formula is 1243. The legs are very unequal in legth, leg I being more than twice the length of leg 3.The coxea are aproximately equidimensional, each about 0.58 mm long . The trochanters are not easily visible, but each measures about 0.25 mm in length. Lengths of the more distal poodomeres and total leg lengths, in mm, are as follows: leg 1 : fe 4.33, pa 1.35, ti 3.00, mt 4.55, ta 1.70, total 15.76; leg 2: fe 3.17, pa 1.00 1.64, mt 3.00, ta 1.15, total 10.79; leg 3: fe 2.01, pa 0.39, ti 1.15, mt 1.64, ta 0.85, total 6.78: leg 4: fe 3.00, pa 0.81, tri 2.04, mt 1.98, ta not preserved (m presumed to be C. 0.95 by comparison with ratio of mt4 to ta4 seen in LC 1754 AP, see below), totaL c. 9.61 lc 1754 AP is poorly preserved, and slightly larger than LC 1753 AP, and its leg measurements are as folows (in mm but with a lessr degree of certainty than in LC 1753 AP): coaxe 0.9, trochanters 0.3; leg 1: fe 4.7, pa 1.4, ti 3.1, mt 5.0, ta 1.8, total 17.2; leg 2 : fe 3.8; leg 3: fe 2.3, pa 0.6, ti 1-4, mt 1.3, ta 0.9, total 7.7; leg 4 : fe 2.8, pa 0.9, ti 1.9, mt 2.1, ta 1.8, total 17.2; leg 2: fe 3.17, pa 1.00, ti 1.64, mt 1.64, ta 0.85, total 6.87: leg 4: fe 3.00, pa 0.81, ti 2.04, mt 1.98, ta not preserved (presumed to be c. 0.95 by comparison with ratio of mt4 to ta4 seen in LC 1754 AP, see below), total c. 9.61. LC 1754 AP is poorly preserved, and slightly larger than LC 1753 AP and its leg measurements are as follows (in mm but with a lesser degree of certaintly larger than LC 1753 AP): coaxe 0.9 trochanters 0.3; leg 1: fe 4.7, pa 1.4, ti 3.1, mt 5.0, ta 1.8, total 17.2; leg fe 3.8; leg 3 fe 2.3, pa 0.6, ti 1.4, mt 1.3, ta 0.9, total 7.7, leg 4: fe 2.8, pa 0.9, mt 2.1, ta 1.0, totalk 9.9.

All legs are thickly clothed with long appear amoth. but high magnification reveals minute accessory spines, especially distally, thus they are the serrate type. No plumose or feathery hairs can be seen. Spines are mostly large and numerous, ocurring on all podom,eres excerpt the coxae and trochantes. Some spines show a helical pattern of longitudinal lines. Most spine are quite large(mean length 0.48 mm) and straight (Pl. 4, fig 6), but spines end at the distal end of podolomeres are commoly curved and/or short. Fel bears five pairs of spines along the superior saurface and an inferoanterior distal spine (this may be one of a pair. Fel also has many very short, fine hairs on the inferior surface of the distal of the poodomere. Pal bears a prominent posterior spine, and antero- and posteroinferior distal spines.Til bears a awhorl of bout the spine proximally, two pairs of spines inferiorly and two single spines superior along the inferior surface, including and distal pair. Fe 2 bears four pairs of superior spines along the shaft, and poste ro- and anteroinferior distal spine. Pa2 bears one lateral and antero-and posteroinferior distal spiners. Ti2 bears ten long spines along the shaft of the podomere, and two short distal spine. Mt2 bears a pair proximally, a whorl of four spines and then five more along the salf, with a whorl of five spine dis-tally. Ta2 on the right side of LC 1753 AP B is particularly well preserved (Pl.4, fig. 5 and 7), and shows curves paired claws each with six teeth, an equally long curved median claw, and numerous serrate accessory claws (i.e. hypertrophied bristles, as seen in living Araneidae see Foelix 1970a). Ta2 bears two small spine on is inferior surface. Along the superior prolater al side of the proximal three-quarters of fe3 are about 24 trichobothria arranged mainly in two rows (Pl. 4, fig. !). The trichobothrial hairs are not feathered. This podomere bears may fine, curved hairs inferiorly, two median superior spine. Pa3 appears to be spineless. Ti3 bears long, stiff seta, and one madian and two subdistal apines. Pa appears to be spineless.Ti3 bears long, stiff setae, and one median and two subdistal spines. Mt 3 has three inferior and one superior proximal spines, one superior, antero-and posterolateral, and two short inferior and one lateral and three curved inferior spines and a whorl of five distal spines. Ta3 bears two small spines on its inferior sur face, like those which occur on. Ta2. Fe4 bears at least one superior prolateral row of about sixteen trichobothria, fine, curved hairs inferiorly, three superior, two inferior, and two posterios subdistal spines. Pa4 bears one distal spines. Mt4 bears antero- and two inferior and posterolateral spines proxi mally, two inferior median spines, one small curved superior median spine, two small curved distal spines, and two small and one large inferior distal spines. The numerous setae on the supeiro surface of mt4 are gently curved, giving the appearence of. weak calamistrium (Pl. 4, fig. 6). However, the high denssity of setae may be an artefact of compression, since a similar density of curved setae are no different in structure freom any otjhers. Thus mt4 does not bear a calamistrum.

No trace of the abdomen is preserved on LC 1753 AP, but it is preserved on LC 1754 AP ; it is oval, and measures 4.80 mm lo9ng and 4.20 mm wide. The greatest width is in the anterior half.The abdomen is eloganted, and form a compact group in a subterminal poosition on the abdomen.

MODES OF LIFE

Paleouloborus can be compared most closely the U,loboridae. Uroborids are orb-web weavers which use a characteristic'wrap attack' to subdue prey (Robinson 1975). In Uloborus and hyptiotes (Niels 1932 the tarsal claw is relatively large, the paired claws are fine and bear few (Hyptiotes) or no teeth (Uloborus), and in both genera there are large, accessory claws. A similar pattern of tarsal claws occurs in Palaeouloborus , and it is unlike taht found in araneids, in which the paired claws are large and pectinate (see, for exam ple, Levi 1978). Nielsen (1932, pp. 26-28) described the method of silk handling by Hyptiotes using this claw pattern. Whilst accessory claws are widespread among web-spinning spiders, and are used for silf handling they are particularly well developed in orb-web weavers; the pattern in the uloborisds studied seems distintive, and these genera are orb-web weavers.

Trichobothria occur on the femora of Palaeouloborus and ulobo rids. The functiuon of these is not known, but it is interesting than among living araneomorph sppiders they are only in tetragna thines and uloborids, both of whichh are orb- web wervers. Femo ral trichgobothria are absent from some adult Pachygnatha, tetragnathines which make no web adult (Levi 1980). Many orb-web weavers have no femoral trichobothria, but their presence in ttetragnathines uloborids appeards to bew liked with the habit. Another behavioral similary between tetragnathies and uloborisd is in resting postures (Levi 1980). Tetraganathies and many metines rest with their long legs 1 and 2 stretched out forwards, the fourth legs outstreched behind, and short third legs pointing backwards and where necessary gripping the twig on which the spider is resting. Opell and Eberhard (1983) distanguished four types of resting posture in uloborisd; in tree, legs 1 and 2 are streched forwads in some manner, whereas in the legs 12 and 2 are helf folded with the femora projecting at right angles to the long axis of the body. Opell and Eberhard (1983) remarked on the close similaritiues of redsting postures between uloborids and araneids. The femoral trichobothria are generally on the superior or retrolateral sides of femoral 1 and 2 on the prolateral sides of femoral 3 and 4 (Opell 1979) . Thus they point laterrally when the animal is in the normal resting posture. It is likely that the preserce of femoral trichobothria is linkede with the-uloborid and tetragnathine-metine resting postures. These beha vioural characters maay be due to convergence, but could conceiv ably be synapomorphies for all orb-web weavers (Shear 1986a). The great similarity in leg lengths, femoral trichobothrial pattern, and tarsal claws between Palaeouloborus and the Ulobori dae suggests that the web-building and resting behaviour of the fossil genus resembled that of typical member of the living family.

The wrap-attack prey capture in uloborids was described by Opell (1979) and Lubin (1986). In it. the spider hangs by the first and second pairs of legs whilst throwing silk over prey using the fourth leg-pair. Afer further entanglement of the prey in these threads, the appoaches closer to the prey and, holding it now with the second and third leg-pairs wraps it more tightly with silk combed by the row of macrosetae on the fourth legs. A wrap attack is found in a number of spider groups, such as the Ther idiidae and Nesticidae (both which have a comb of setae on the fourth legs). Metinae, Tetragnathinae, Araneidae, Oecobiidae, Hersilidae, and Pholcidae n(Coddinton 1986). The wrap attack of uloborids differs from that other spider families because ulobo rids lack poison glands and the prey is killed digestive enzymes during (Opell 1979). Since a wrap attack is fround in families whiuch do not have a comb of setae on the legs, such a comb is not essential for this method of prey capture. Wrap attack is therefore a possible method of prey captuire in Palaeouloborus.

Macryphantes compares most closely in general appearance with large long legged araneoids such as the argiopine araneids, tetragnathines, and nephilines. Argiopines are similar in geeral appearencc and habits to uloborids (both are orb- web weaving wrap-attack predators) but they lack femoral trichobothria. Macrophantes has an araneoid pattern of tasal claws, and bears femoral trichobothria. Thefore, it is suggested tha Macrophantes wove an orb web, rested in a posture like that of uloborids or metines-tetragnathines and may have used a wrap-atrack method of prey capture.Cretaraneus has few positive feature which its possible mode of . The fossl genus is small, short- legged, and bears pectinate, paired claws and serrate accessory claws, which indicate that it is a web-legged, and bears pectinate, paired claws and serrate accessory clwas, which indicate that it is a web-weaving spider. Small, short-legged araneoids, such as Creta ceousand most theridiids and linyphiids, are weavers of sheet webs in litter, undergrowth, or bushes; such webs catch pedestri an or small flying prey . It iis likely that cretaraneus occupied a similar ecological niche.

A gereat variety of orb webs are woven by uloborid and araneoid spiders, each designed to capture a specific type of prey. They are put up for short periods or longer, day or ninghy, and in open or secluded situations (Riechert and Gillespie 1986; Stowe 1986; Lubin 1986). They vary from massive, collective structures to minimalist device hardly recognizable as orb web derivatives. It is impossible to suggest what type of prey acrophantes and Palaeouloborus captured with their orb webs. There was a wide diversity of insect in the Montsech area during the early Createceous. Which suggests taht prey specializacion may have been practised by orb-web weavers at that time.

CONCLUSIONS

Described here the oldest known representatives of the spider superfamily Deinopoidea family Tetragnathidaer, and the second olds record of the superfamily Araneoidea in the fossil record. The Deinopoidea and the Araneoidea both contain weavers of orb webs of ramarkable similarity. Indeed, these is continuing debate about whether the orb webs of remarkable similarity. Indeed, these is continuing debate about whether the orb webs of remarka ble similarity. Indeed, there is continuing debate about whether the orb web evoled only once, in the common ancestror of the Deinopoidea and Araneoidea, or is a convergent phenomenon in these two groups. Shear (1986a) comprehensively reviewed the evidence for and against these conflicting hypotheses, and ara neoids in the LOwer Cretaceous indicates that, whichever hypothe sis is favoured, both group of orb-web weavers were in extence at time, and suggests that the orb web originated earlier in the Mesozoic it not before.

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AP. Explanatory drawing for Pl. 1.. See Terminology for explana tion of Abbreviations.

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TEXT FIG 1 Paleouloborus lacasa gen. et sp. nov. holotype, LP 1755 AP. Expalnatory Drawing for Pl. 1. See Terminology for explaanation of abbreviations.

EXPLANATION OF PLATE 1

Paleouborus lacasa gen. et. sp. nov. , holotype ; Lithographic Limestone Lower Cretaceous; Sierra de Mointsech, Lerida Province, Spain LP 1755 AAP , whole specimen. lower slab, under ethanol, 21. See text- fig 1 for explanation.

Figs 1-5, 7, 8. Paleouloborus lacasaae gen et sp. nov., holotypr; Lithographic Limestone, Lower Cretaceous: Sierra de Montsech, Lerida Providence, Spain, Lp 1755 AP, oil immersion. I. Serrula of left maxilla, bristle at left end , 240. 2, Femoral trichobo thria, x 150. 3., Claws on distal end of tarsus of left leg 4 ; note long median claws and accessory claws, x 100.4. Spinnerets: anterior pair (at top), median pair , and posterios pair (Part); recurved line of short setae (Seen at left) in front of anterior spinnerts mark approximate possition of cribellum; compare with fig 6, x85.5 Proximal part of metatarsus ofrigth leg 4 showing curvatuire of superior surface calamistrum note long, curved bristle at distal end of tibia (bottom left) compare with fig. 10x 60.7 Plumose seta, x 625.8 Distal end of metatarsus of leg 4 showing calamistrum (overlying tarsus of 4 right leg 4 on right) terminating in of curved bristle to ieft x 85.

Figs 6, 9, 10. ilopponella sp . , Lake Naivasha, Kenya;M JMurphy Coll. No. 1363. under ethanol. 6. Ventral view of poste rior end of abdomen of immature male, Showing spinnerets and cribellum in front, x 36.9 Left lateral view of immature male, x 13. 10 Metatarsus of right leg 4 of mature female, showing curva ture of superior surface calamistrium, x 50.

TEXT-FIG 2 Cretaraneus vilaltae gen. et. sp. nov. holotype, LC 1150 IEI, Explanatory drawing for tex fig 3 See Terminology for explanation of abbreviations

TEXT-FIG 3. Cretaceous vilatae gen. et sp. nov., holotype Litho graphic Lismestone Lower Cretaceous: Sierra de Montesech, Lerida Province Spain LC 1150 IEI . See test-fig 2 for explanation x 13.

TEXT FIG. 4 Cretaceous vilaltae gen. et. sp. nov. , holoty'pe Lithographic Limestone Lower Cretaceous : Sierra de Monsetsech: Lerida Province Spain LC 1150 IEI , a tarsal claws on left leg 2 note large pectinate paired clwas, small, uncinate, median claw (bottom centre) and curved serrate bristles, especiallu inferiorly x 2200, b, tyical spine, on tibia of left palpal tarsus: see f for explanation. x .88 e, tarsal claws on right leg 4. x 200 f, explanatory drawing of d, g. explanatory drawing of see Terminol ogy for expalnation abbreviations.

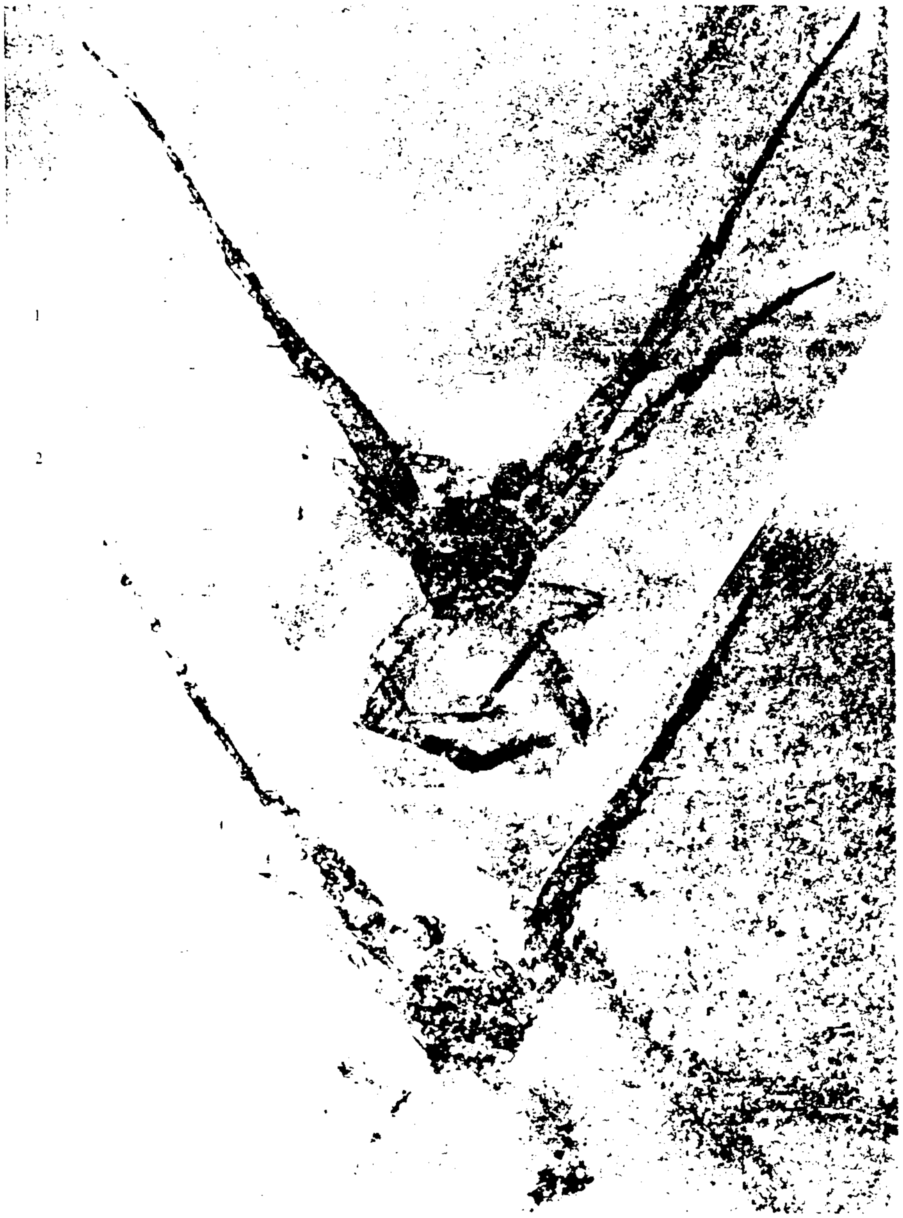
TEXT-FIG 5 Macrophantes cowdeni gen. et sp. nov.- holotype, LC 1753 AP B. Explanatory drawingf for Pl. ., Fig 1 See Terminology For explanation of abbreviations.

EXPLANATION OF PLATE 3

Figs.1 and 2 Macrophantes cowdeni gen. et. et sp nov., holotype: Lithographic Li8mesto0ne, Lower Cretaceous :, Sierra de Montsech Lerida Province, Spain under ethanol. 1, LC 1753 AP B , lower slab, x 7, see text fig 5 for explanation 2, LC 1753 AP A , uppeu slab, x 7.

TEXT- FIG 6. Macrophantes cowdeni gen.et sp .nov.,paratype,LC1754AP A. Explanatory drawing for PI.4,fig 4.See Terminology for explanation of abbreviations.

Figs 1-7 Macrophantes cowdeni gen. et sp. nov., holotype: Lime stone, Lowqer Cretaceous; Sierra de Montsech, Lerida Province, Spain 11,3, 5-7, LC 1753 AP B , hiolotype, oil immersion 1, Trichobothria setae and spines on prolateral ssurface of femur of right leg 3, x 85.3 Right paLP, SHOWING APOPHYSIS ON RIGHT SIDE, X 47.5 Distal end of tarsus ofd right leg 2, showing paired pectinate claws, long median claw, and curved, serrate bristles (accessory claws), x 320.6 Spines and setae on shaft of matatarsus of left leg 4, superior surface to top, x 85.7 Distal half of tarsus of right leg 2 showing terminal claws and short spine on inferior ssurface of podomere, x 130.2 LC 17654 AP B , paratype upper slab, x 4.54 LC 1754 AP A, PARATYPE, LOWER SLAB, X 3.6; See text-fig . 6 for explanation . Both under ethanol.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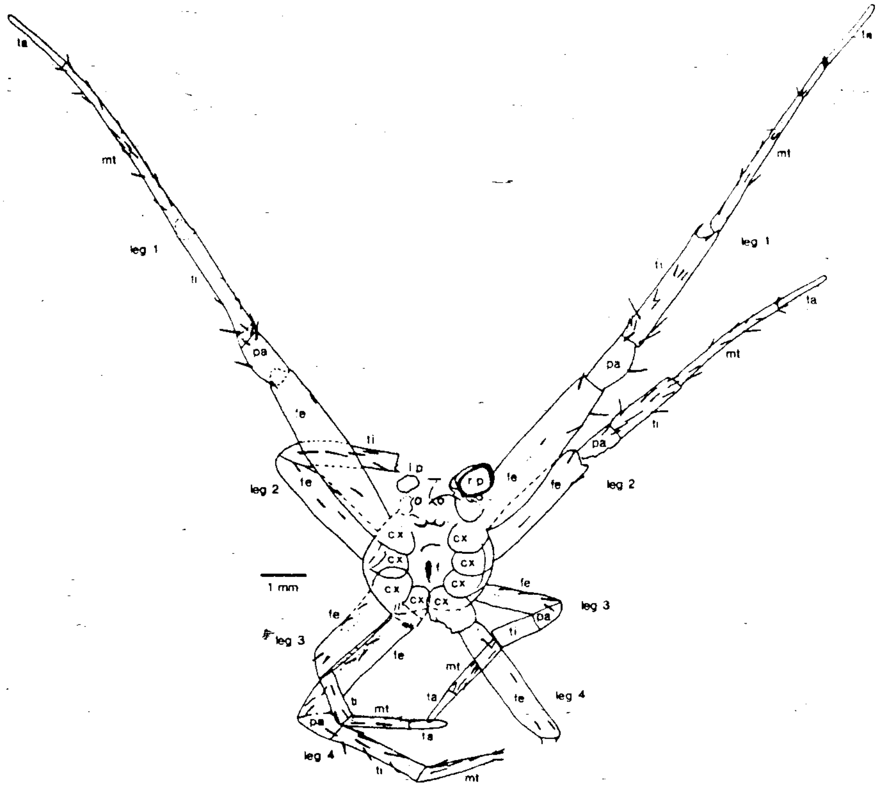
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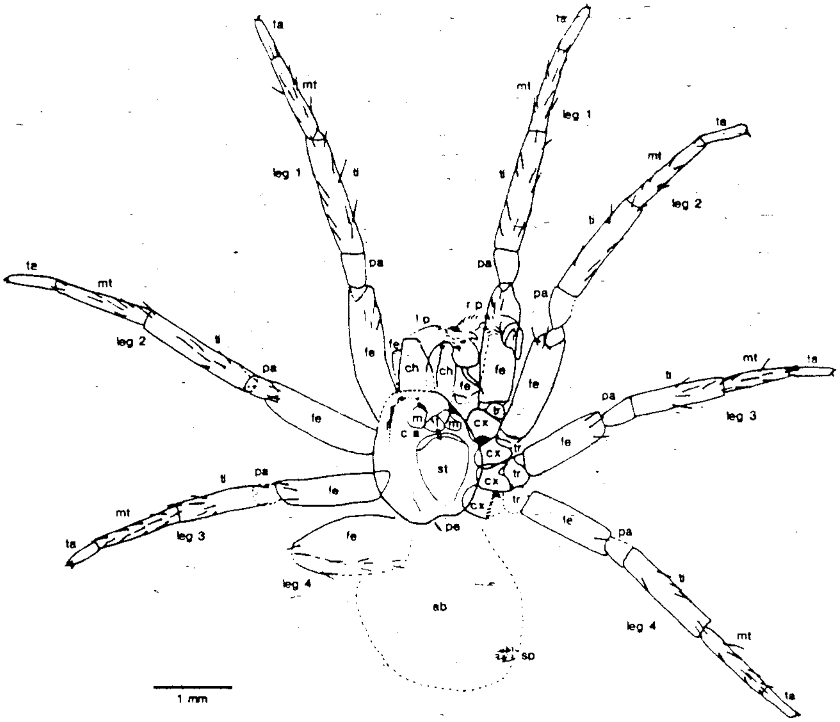
P.A.Selden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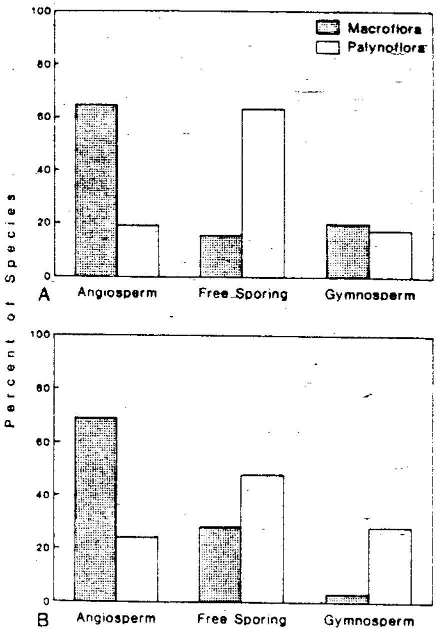

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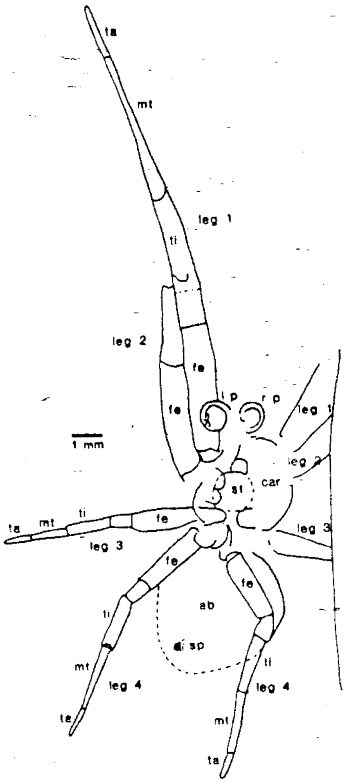
						MORPHOLOGY	LEAVES
		■	■	■	■	Simple[1]	
			■	■	■	Pinnate[2]	
			■	■	■	Palmate[3]	
						MARGIN	
		■	■	■	■	Entire[4]	
		■	■	■	■	Chlor. teeth[5]	
						VENATION	
		■	■	■	■	Pinnate[6]	
		■	■	■	■	Parallel[7]	
						STOMATA	
		■	■	■	■	Anomocytic[8]	
		■	■	■	■	Paracytic[9]	
						SEX DISTRIBUTION	FLORAL ORGANIZATION
			■	■	■	Hermaphrodite[10]	
			■	■	■	Unisexual[11]	
						ARRANG. OF PARTS	
			■	■	■	Acyc.-Hemicyc.[12]	
				■	■	Cyclic[13]	
						INSERT. OF PARTS	
			■	■	■	Hypogynous[14]	
				■	■	Epigynous[15]	
						CARPEL NO./ARRANG.	GYNOECIUM
			■	■	■	Many apocarpous[16]	
			■	■	■	Five apocarpous[17]	
			■	■	■	Three apocarpous[18]	
			■	■	■	Six syncarpous[19]	
				■	■	Five syncarpous[20]	
				■	■	Three syncarpous[21]	
				■	■	One[22]	
						OVULE TYPE	
			■	■	■	Anatropous[23]	
			■	■	■	Orthotropous[24]	
						STAMEN NO./ARRANG.	ANDROECIUM
				■	■	Numerous free[25]	
				■	■	Nine free[26]	
			■	■	■	Five free[27]	
			■	■	■	Three fused[28]	
						ANTHER ATTACHMENT	
			■	■	■	Basifixed[29]	
			■	■	■	Dorsifixed[30]	
						ANTHER DEHISCENCE	
			■	■	■	Simple[31]	
			■	■	■	Valvate[32]	
						POLLEN APERTURES	POLLEN
■	■	■	■	■	■	Monosulcate[33]	
		■	■	■	■	Tricolpate[34]	
			■	■	■	Tricolporate[35]	
				■	■	Triporate[36]	
						EXINE SCULPTURE	
		■	■	■	■	Psilate[37]	
■	■	■	■	■	■	Reticulate[38]	
						EXINE STRUCTURE	
		■	■	■	■	Granular[39]	
		■	■	■	■	Acol. semi-tect.[40]	
■	■	■	■	■	■	Col. semi-tect.[41]	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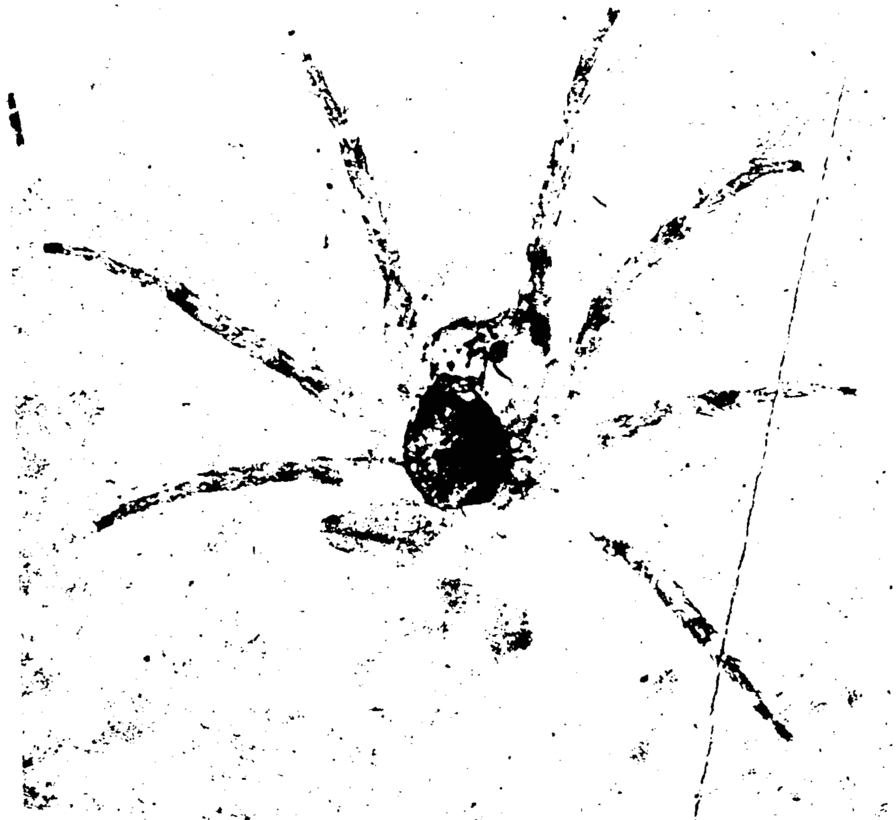

8.6 MACROFAGOS VERTEBRADOS

8.6 (a)

PALAEOCOLOGY, TAPHONOMY, AND DATING OF PERMO-TRIASSIC * REPTILES FROM ELGIN NORTH-EAST SCOTLAND.

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ABSTRACT Three Permo-Triassic reptile and one footprint fauna are known from the are of Elgin,north-east Scotland. The foot prints are probably Permian in age and they indicate an assem blege of mammalike reptiles. The mammals-like reptiles, pareia saur and procolophonoid from the Cutties Hillock Sandstone Forma tion (new name) are probably latest Permian in age. They were found at the base of an aeolian unit, just above pebbly sheet- flood deposits. The Lossiemounth Sandstone Formation is dated as Lower Norian on the basis of its varied reptile fauna. This fauna shows affinities with northern and southern hemisphere faunas of its time, and contains Britain's oldest dinosaur, the coeluro saurSaltopus . The Loossiemonth reptiles (c. 130 individual animals from four or more localities) were apparently preserved at the bases of barchan dunes and many of them just above flood plain deposits.Most of the skeletons are well preserved in arti culatier and only a few show disturbance, possibly by scavenging. The fauna consited of Hyperodapedon and Stagonolepis , two moder ate-sized herbivores (25% each), a selection of small omnivores: Leptopleuron (23%), Brachyrhinodon (9%), Scleromochlus (5%), and Erpetosuchus (2%) , and medium-large carnivore, Ornithosuchus (10%) and small canivoroSaltopus (1%), some of the smaller animals show adaptations to living on sand. The last reptile fauna, from the Rhaetic of Linksfield, consist of odd bones of marine reptiles.

VERTEBRATE

Palaeontologist who study Mesozoic reptiles often concentrate on individual genera and do not record information on faunas. This paper present information on the Elgin reptile faunas that we have gathered by personal observation of the specimens and the geology, and by studying unpublished documents and the scattered published literature.

Two main faunas of fossil reptiles are known from the neighbour hood of Elgin, north-east Scotland. The easrlier, from the Cut ties Hillock Sandstone Formation (defined below; probably latest Permian) consists of two genera of mammals-like reptiles, a pareiasaur and a procolophonid and the later, from the Lossie mounth Sandstone Formation (late triassic) comprises at latest four genera of thecodontians, a rhynchosaur, a sphenodontid, a procolophonid, and a coelurosaur dinosaur. A third fauna from the Rhaetic of Linksfield constains a few marine reptile bones. The Hopeman Sandstone Formation (in the restricted sense proposed in this paper, see below) has also yield a fauna consisting of two-ot three kinds of footprints. Both main faunas are unusual in showing close affinities with those of southern continents as well as with those of the rest of western Europe and North Ameri ca. Both faunas are also unusual in that the remains are pre served in aeolian deposits, clearly not the natural habitat of the majority of the animals.

The aims of this paper fivefold: to review the compposition of the faunas to consider the sedimentology and environments of the reptiles beds: to discuss the taphonomy of the remains: to assess the ecology of the late Triassic reptiles; and to review the relationships and age of the faunas. Most ofthe data have never been published before, and it is hoped that this paper will provide a useful summary of the Elgin reptiles and their

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environ ments. The tophonomic observations are original and should be of value for comparision-with other aeolian deposits. Most attention will be devoted to the late Triassic fauna because of the larger number of remains, and its greater impoortance in Triassic faunal development.

Repository abbreviations used in this work are: BMNH, British Museum (natural History); EM, Elgin Museum; GSE, Geological Survey Museum (Edinburgh), GSM, Geological Survey Museum (London); MM, Manchester Museum; NUGD, Newcastle University, Geology Department; RSM, Royal Scottish Museum, Edinburgh.

THE FAUNAS.

Footprints fromt he Hopeman Sandstone Formation.

At least two kinds of footprint have been identified from the Hopeman Sandstone Formation. Type A (text-fig 1A) (roughly circu lar, impressions 30-40mm long, stride length 110-120 mm, width of track way 80-90 mm, no sing of toe marks) is presented by a slab collected in 1850. This was the fisrt fossil from Elgin rocog nized as reptilian, and the tracj way was initially interpreted as having been formed by a tortoise (Brickended 1850, 1852).

Numerous slabs of larger footprints (TypeB, text-fig. 1B) were collected afterthat (Beckles 1859; Huxley 1859b; Hickling 1909). The fore-and hind-foot were clearly different. The print od the forefoot is semicircular, about 40 mm long and 60 mm wide, with traces of four or five claws at the front. The print of the hind-foot is larger, about 90 mm long and 80 mm wide, with traces of five claws at the front.The prints overlap in pairs, and stride lengh was 300-400 mm. These were named helichnus megach erius Huxley 1877. Larger specimens (print 170 mm long. 140 mm wide) were figured by Huxley (1877, pl 15, fig 6)and some simi lar trcks may still be seen on a large slab at Clashach Quarry (NJ 163702) These large tracjs measure 150-250 mm long and 100- 150 mm wide, and the stride length is 700-800 mm (text-fig 1c). A possible third kind of track was described from the coast by Huxley (1877) and Hickling (1909, pl 2 fig, 7. 8) and from Cut ties Hillock (Watson and hickling 1914).This is supposedly dis tinguished by having broader toes than types A or B, but the generally smudged preservation of most specimes makes such a distinction inadvisable. The Hopeman footprints were probably formed by two or more mammal-like reptile genera, possibly ducy nodonts (Haubold 1971).

Reptiles from the Cutties Hillock Sadstone Formation.

Reptiles bones were collected from a quarry on Cutties Hillock in 1884, and some nearly complete skeleton were objet in 1881 and 1885 (Judd 1885, 1886a, b, Traquiar 1886). Three genetic de scribed by E.T. Newton (1893);Gordian, Geika and Elginia.

Gordinia and Geikia are dicynodonts, a group of herbivorous mammals-like most of wich had no teeth except for a tusk Gordinia (text-fig 2A) is represented by remains of the skulls and skele tons of eight to thirteen individuals, and four species were originally described, although they are perhaps all synonymous (Walker 1973). Gordinia had a heavy broad skull, 100-180 mm long, and it was clearly provided with powerful jaw muscles. The rela tionships of Gordonia are uncertain; Cluver and king (1983, p 268) state possibly related to Kingoria or Dicynodon . The single specimen of Geikia has no teeth at all and the snout is box-like. Rowe (1980) has redescribed the specimen Africa and Zambia. He also placed Dicynodon locusticeps from Tanzania in the genus Geikia and in the new Family Aulacephalodontidae, and Cruick shank and Keyser (1984) have confirmed this assigment of Geikia.

Elginia was a pareiasaur with a remarkably spinescent skull (tex-fig. 2c). The 210mm long holotype skull is broad and covered with rough pits and spines of various sizes. The teeth are leaf like in shape, and Elginia was probably a herbivore. Other pare iasaur remains include vertebrate and a sacrum probably belonging to the holotype as well as and undescribed partial skeleton and skull.

A fourth reptile from Cutties hillock is represented by a speci men that was described by Newton (1893,pp 461-462, pl 33 fig 5) as a tail of?

Gordonia. This specimen consist of seven dorsal vertebrate, the blades of two scapulae and the blade of an ilium of a procolophonid (Walker 1973). Finally; remains of an un-named dycynodont were collected from nearby Knock of Alves (or York Tower) Quarry in 1953 by A.D.W.

Reptiles from the Lossiemounth Sandstone Formation (table 1).

A slab containing scutes of the thecodontian reptile Stagonolepis (text-fig 3A) was the first fossil found in the Elgin Permo- Triassic, but it was initially interpreted as a large ganoid fish (Agassiz 1984). later finds of limb-bones led to its interpreta tion as a reptile (Huxley 1859a,b), and in particular as an ancestral crocodile (Huxley 1875, 1877). More recent study (Walker 1961) has shown that it was an aestosaur- a probable herbivore. Stagonolepis is represented by skull and skeletal remains of thirty or more individuals which up to 2-7 m long. The snout had a curious blunt end, probably for digging, and the teeth were peg-like, Stagonolepis was shaped rather like a crocodile and had an extensive armour around its body.

The first Elgin reptile tobe recognized as such was Leptopleuron lacertinum Owen 1851 (objetive synonym, Telerpeton elginense Mantell 1852), based on a small skeleton collected at Spynie (Benton 1983c). Further finds (Huxley 1867; Boulenger 1904; Huene 1912a, 1920) showed it to be a procolophoind, a small omnivorous or herbivorous reptile with a triangular, spiked skull (text-fig. 3E). The skull was about 52 mm long. and the body may have been up to 400 mm in total length.

The third animal to be obtained from the Lossiemount Sandstone Formation was named Hyperodapedon by Huxley (1859a). It was interpreted as a rhynchosaur (Huxley 1869, 1887; Burckhardt 1900; Boulenger 1903; Huene 1929; Benton 1983d, 1984), a group of diapsid reptiles that were abundant in many faunas worldwide in the middle and late Triassic. its closest relative is H. huxleyi from the Maleri formation of India. Hyperodapedon was a bulky 1-3 m long quadruped with strong limbs- the hind-foot had large claws and was probably adapted for scratch digging. The skull was the most remarkable feature (text-fig. 3B). It was 100-200 mm long and very broad at the back-three was an anterior premaxillary beak and the teeth were arranged in multiple rows on the maxilla. the dentary had a sharp edge and it cut into a groove in the maxillary toothplate, provinding a strong shearing bite.

Remains of the medium sized carnivore Ornithosuchus (text-fig 3C) were described by Huxley (1877), Newton (1894), Boulenger (1903), Broom (1913), Huene (1914), and Walker (1964). This animal was probably partly quadrupedal and partly bipedal, and it had sharp dagger-like teeth. Several specimens are known and these indicate a range in skull length of 50 to 450 mm and in body lengh of 0.5-3.5 m. Ornithosuchus was regarded by Walker (1964) as an ancestral carnosaur, but comparison with Riojasuchus (Bonaparte 1969) suggests that it had a crocodile-reserved type of ankle joint (Cruick shank 1979) rather than the mesotarsal joint typical of dinosaurs, and was thus a thecodontian closely related to some South American forms (Bonaparte 1969).

A second small carnivore (or insectivore) is Erpetosuchus which was collected from a block built into a wall in Lossiemounth in the early 1890's (Newton 1894). The specimens includes a skull (text-fig 3D), the fore-limbs and shoulder girdle, and the armour plates, which indicate a total body lengh of about 600 mm. It seemed to have some crocodilian characters (Walker 1968) but these were later considered to be the result of convergence. Erpetosuchus is another advanced pseudosuchian thecodont with a narrow 75 mm long skull which has a huge antorbital fenestra and a broad square posterior skull roof (Walker 1970, pp 364, 367- 368; Krebs 1976, pp 87-89).

Extensive collecting by William Taylor, a local naturalist, beetwen 1890 and 1920, produced abundant remains of these animals from Lossiemounth and Spynie, as well as the holotypes of three new genera: Scleromochlus, Saltopus, and Brachyrhinodon.

Scleromochlus was based on several skeleton which an animal with a short body, short forelimbs, but long hindlimbs and long tail (Woodward 1907; Huene 1914). The skull (text-fig 3G) is relative ly thecodontian whose skull specialization suggest a relationship to the aetosaurs (Walker 1970, p 361; Krebs 1976, p 90) One specimen (BMNH R3146) shows transverse bands of thin dorsal scutes, figured by Woodward (1970) as abdominal ribs.

Saltopus (text-fig. 6A), represented by only one skeleton, and unfortunately lacking the skull, is Elgin'sonly dinosaur (Huene 1910a). the vertebrate and limbs are rather poorly preserved in ounline, and the total body length was probably about 600 mm. It is a coelurosaur (Walker 1970, p 359), and may be a podokesaurid (Huene 1914; Steel 1970) or a procompsognathid (Romer 1966).

One small undescribed thecodontian is represented by a somewhat obscure skeleton in Manchester Museum (MM L8270; Watson 1909a). This consist of a disarticulated skull, some of the skeleton, and some scutes. It is probably a new form, but is too poor tobe described.

He record of a lungfish tooth-plate from Spynie, identified as Ceratodous (Traquair 1895, p 280) is an error. This record is attributed by Taylor (1920) to Huxley, but he gives no references and we have been unable to find that Huxley mentions it. The earliest references appears tobe that of Judd (1866a). The error was caused by confusions between tha Triassic locality Spynie and New Spynie (now called Quarrywood), which lies on Upper Old Red Sandstone 4km to the west. The tooth-plate is probably of anero pleuron (T.S.Westoll, pers. comm:) and the locality is most likely Leggat Quarry (NJ 176635),850m to the south-west of Quar rywood, as suggested by Taylor (1901, p 48).

Reptiles from the Rhaetic of Linksfield

A large glacial erratic at Linksfield, near Elgin (NJ 222641) has yielded some reptile remains, as well as fish. The sediments were originally determined as Puebeck or Wealden (Duff 1842), but they were later dated as Rhaetic (Moore 1860, Jones 1863, Anderson 1964) on the basis of the fish and ostracods. Duff (1842, pl 4.5) figured spines , scales and teeth of such fish as Hybodus, Lepi dotes, Sphenochus, and Acrodus, as well as a plesiosaur vertebra and teeth, and femur of a chelonian reptile which seeley (1891) later described as the femur of a crocodile Saurodesmus rodertso ni.

STRATIGRAPHICAL TERMINOLOGY.

The Permo-triassic of the Elgin area outcrops in two belts, one along the coast between Burghead and Lossiemounth, and the other in theregion of Elgin itself (text-fig 4). The beds near Elgin occur in small fault-blocks within petrologically similar Upper Old Sandstone.

The nomenclature of the Hopeman and Cutties Hillock sandstones.

Formal lithostratigraphical terms for the main units of the Permo-Triassic of the Elfin are were introduced by Warrington et al (1980). the Hopeman Sandstone Formation was proposed to in clude predominantly aeolin sandstone some 60 m thick cropping out along the coast between Cummingstown and Covesea Skerries Light house, and also for a separate strip of similar rocks, 30-45 m thick, lying on top of Quarry Wood ridge and in the Knock of Alves area to the west of Elgin. Although there is some evidence which suggest that the sadstones of these two regions are broadly equivalent, and while it is true that the coastal sandstonesare much better exposed (although the base is not seen). The most important of these is that the name Cutties Hillock for a wold- famous fossil vertebrate locality and set of beds has disap peared. To be replaced by an unfamiliar name. Furthermore, apart from a small scrap of bone (Peacock et al 1968, p 59) the coastal sandstone have yield nothing but reptilian tracks, whereas the reptilian fauna entirely from the inland localities. thus the accurate determination of the age of this formation has to be obtained from a study of the reptiles, none of which occurs in the type area.

The tracks from the coastal sandstones are believed to have been made by dycinodont reptiles, but this is a group which ranges in time from the middle of the Permian until late in the riassic. Hickling (1909) considered that the closest comparisions of these tracks were to be made with those from Magnesian Limestone and is thus early Uppear Permian in age, while the tracks from Penrith are late Lower Permian. In Contrast, the Cutties Hillock fauna is probably very late Permian in age (see below). Tracks were also seen at Cutties Hillock Quarry itself in 1878 before the reptiles were discovered (Peacock et al 1968, p 73) and have occasionally been seen since. A single small print from a nearby quarry, the position of which is now uncertain, was figured by Watson and Hickling in 1914. However, these tracks can surely only be used as evidence of a brad time-equivalence between the sandstone of the two areas.

While we do not gree with the conclusions of glennie and Buller (1983) concerning the subdivisions of the Hopeman Sandstone on the coast, These diferences of interpretations serve to underline the necessity for a separate formal lithostratigraphical unit to include the reptile-bearing beds, to avoid confusion, and until such time as definite correlations shall have beenestablished. It is proposed, therefore, that these inlad beds be termed the Cutties Hillock Sadstone Formation.

Peacock et al (1968) preferred to used the name Sandstone of Cutties Hillock (Quarry Wood) instead od Cutties Hillock Sand stone because Cutties Hillock does not occur on Ordnance Survey maps (it does actually appear on a map by Gordon (1982)). Howev er, this is not a strong objection since the position of the quarry is given by Judd (1886a, pp 397-398) and is well estab lished by local tradition. The term Cutties Hillock Sandstone Formation has in fact already been used by smith et al (1974, p 25), although not formally defined.

Origin and correct form of the name cutties hillock

_Although var ious suggestions have been made, including shorth hillock and witches hillock, it seems most likely that the name derives from a Gaelic original. It does not seem to have appeared in printun til after the discovery of the reptiles in 1884. Mackie, an important worker on the local geology and discoverer of the Rhynie Chert, always used the form Cuttieshillock in several papers (e.g. 1897) and in articles in local mewspapers. Other local writers tended to do tha same; furthermore, the old labels onthe specimens frpom this locality in Elgin Museum also use this form. Maxwell (1894) mentions, among other similar names Kitty shalloch in Galloway and Cuttyshallow in Ayrshire. In the last instance he gives the derivation as the Gaelic ceide sealghe, pronounced to sound something like ked-dyshalluh and meating hill-brow of the huting. It appears. Therefore, that originally tha name had nothing to do with the words cutty or hillock, but when it was written down, authors tended to split it into two words, transferring the 's to first of these and sometimes adding a siungular or plural apostrophe as seemed appropriate.

Cutties hillock Sandstone Formation .

Type area. Quarries and natural exposures o Quarry Wood ridge, the Knock of alves and Carden Hill west of Elgin. The formation is seen to rest unconformably on Rosebrae Beds of the Upper Old Red Sansdtone in Rosebrae Quarry (NJ 173633) and York Tower Quarry (NJ 162629). The reptile fauna comes mainly from Cutties Hillock Quarry (NJ 185638).

OCCURRENCE OF THE REPTILES.

Sedimentology of the Hopeman Sandstone Formation(s.s.)

The hopeman Sandstone Formation of the coast between Cummingstown and Covesea Skerries and Halliman Skerries, somes 60 m thick, shoiws evidence of largely aeolian deposition; large-scale cross bedding is common, and the sandstone are generally composed of well-rounded grains of quarz and felspar, often of high spherici ty, with only a little mica (Peacock et al 1968, p 59) However, the action of water is indicated in places by lenses of coarse sandstone and well-rounded pebbles with only a little mica (Peacock et al, 1968, p 59). However, the action of water is indicated in places by lenses of coarse sandstone and well-round ed pebbles with small-scale cross-bedding, as well as contorted beds (Peacock 1966). Willliams (1973) identified four phases of dunes; seif dunes at the base, fallowed by three phases of barch an dunes. Each of the first three phases is topped by contorted beds and sheet flood or playa lake deposit. The fossil tracks have been obtained principally from Masonshaugh Quarry, Cummings town (NJ 125692). Occasional footprints have been observed in Greenbrae Quarry (NJ

137692) and Clashach Quarry (NJ 163 7902), and Peacock et al (1968, p. 59) report an unidentifiable bone fragment from Greenbrae.

TAPHONOMY OF THE HOPEMAN SANDSTONE fORMATION FOOTPRINTS.

The footprints of the Hopeman Sandstone Formation may be pre served on low-angle dune foreset, but this has only been observed in a few in situ occurences. The slabs collected in the nine teenth century may include some from horizontal bedding planes. However, there is usually a mound of sand behind each print (Brickenden 1852; Huene 1913; Watson and Hickling 1914), and this would suggest that the animals were moving uphill. These mounds are seen also behind the large footprints at Clashach (text-fig. 1 c).

Sedimentology of the Cutties Hillock Sandstone Formation

The Cutties Hillock Sandstone Formation is between 30 and 45m thick. It may be divided into two units (Peacock et al, 1968; William 1973): a lower phase consisting of a series of pebbly sandstone that lie discordantly on the Old Red Sandstone, and an upper phase which consists of about 30 m of large-scale light brown and yellow cross-bedded sandstone. The lower pebly beds have been interpreted as sheet flood deposits, but the presence of dreikanter pebbles with rounded edges suggests that they were exposed to wind erosion before being reworked by water (Mackie 1902; watson 1909b; Watsonand Hickling 1914; Williams 1973) The upper phase shows well-rounded quarz grains and unidirectional forests which indicate fossil barchan dunes. The reptiles Elgin ia, Gordonia, and Geikia came fromCutties Hillock Millstone Quarry (NJ 185638) and an isolated footprint and other trackways were found nearby (Linn 1886, Hune 1913; Watson and Hickling 1914). An unidentified bone in Forres Museum was found in Crown head Quarry (NJ 183630) on the sounth side of Quarry Wood hill and is of interest as the only bone recorded from this part of the outcrop. A slab in Elgin Museum showing footprints with a tail-drag on top of ripple-marks probably came from Robbies Quarry, the position of which is uncertain.but it was probably one of the Crownhead group of quarryes.

Taphonomy of the Cutties hillock Sandstone Formations reptiles.

The reptiles from the Cutties Hillock Sandstone Formation appear to have been collected from the base of the upper phase, just above the pebbly sandstone. Judd (1886a, pp 400-401) noted that 20 feet of the reptiliferous Sandstone was to be seen above the pebbly layers, and that the remainsof five reptiles all came from one horizon and that a sixth came from the bead below. Phillips (1886) confirmed this Gordon (1892, p 242) referred to a portion of this conglomerate containing reptilian remains. Newton (1893, pp 462, 466) also noted that the specimens of Gordonia juddiana also pebbles in the specimen of Gordonia duffiana. These blocks (E:M 1978. 559.1.2) show quarz pebbles up to 20 mm and up to 7 mm in diameter respectively.

Individual bones may be distorted. The bones are represented by cavities inthe rock from which black material containing iron, manganese, and cobalt (Newton 1893, p 435) The cavities may be compressed with opposite impressions almost touching. Limb bones may be particularly flattened, and the ends may be hard to inter pret either because of poor preservations and compresion, or bacause the ends were largely cartilaginous in life. The centra of the dicynodont vertebrate are usually missing or very poorly preserved, alhough neural arches and ribs may be easy to cast. By constrast, the centra of Elginia are well preserved. Skulls are often vertically compressed (Newton 1893; Walker 1973; Rowe 1980), and in G. duffiana most of the squamosals and the righ half of the occiput are missing, which presumably indicates post-mortem, pre-fossilization damage.

Sedimentology of the Lossiemouth Sandstone Formation

He is distributed in several small fault-bounded blocks at Lossiemonth, Spynie, and Findrassie (Peacock et al 1968, pp 67- 69; Williams 1973) The thickness of the unit varies from 7 to 30 m. It is underlain by strata which have been interpred as thin representative of the Burghead Sandstone Formation. Peacock et al (1968) suggested that the Burghead Sandstones (mainly point bars in their typearea, according to Williams (1973)) interdigetate with the Lossiemounth as a reduced lateral equivalent of the Burghead Sandstone Formation.However, this interpretation is hard to prove because there is a large geographic gap between the qutcrops of typical Burghead Sandstones intheir type area. The Lossiemounth Sandsatone Formation is overlain by the Cherty Rock (sandy limestone and chert).

The sandstone may be finely laminated, but more usually they show large-scale cross-beds on well-wethered surfaces. These features, aswell as the absence of pebbles, the rarity of micas and heavy minerals, strongly suggest aeolian depositions.

Forest analysis of the cross-beds indicates a preaviling south westerly wind forming barchan dunes. These have been interpreted as reworked sand from the underlying Burghead Sandstone Forma tion, which he regards as composed of floffd-plain sadstones at Lossiemouth. Dunes up to 20 m high migrated across the flood plain during arid periods, and theaeolian deposition was termi nated by large-scale flooding and the deposition of silicified and calcareous sandstone (Sago Pudding Sandstone Formation).

The reptiles were obtained from Lossiemouth East Quarry (NJ 236707), Lossiemont West Quarry (NJ 231704), Spynie (NJ 223657), and others), and Findrassie (NJ202650). Taylor (1920) reported a specimen of Leptopleuron (EM 1920.5) from a glacial erratic of Triassic beds on the Hill of Meft, north-west of Urquhart (NJ268642).

Taphonomy of the Lossiemounth Sandstone Formation reptiles

The skeletons of Stagonolepis and Hyperodapedon were apparently found just above the base of the Lossiemounth Sandstone Forma tion. Murchison (1859, p 428) stated that the bones faound then were collected in the lowest part of the freestones being quar ried at Lossiemounth. Gordon (1859, p 46) confirmed this, stating that the lowest beds at Lossiemounth were red clay, succeded by yellowish soft sandstone and then harder sandstone. The red clay may be equivalent to that reported by Peacock et al (1968, p. 65) as micaceous siltstone, the yellowish soft sandstone may be the Burghead Beds equivalent and the harder sandstone is probably the Lossiemounth Sandstone Formation. The bones were found immediate ly under this hard siliceous sadstone in a quarry half-way to the new harbour from Rockhouse, and in the face of the wall of rock that overhangs tha houses froting the old harbour... This refers to the east end of Lossiemounth East Quarry (NJ 237707). Judd (1873, p 137) stated that the reptiles were found 100 ft, below thelop of the sandtones, which would imply abount tha base of the Lossiemounth Sandstone Formation, if its complete thickeness is taken into account. Judd (1886a, pp 397, 403) added that the reptile remains all came from a single band of soft rock Further, Gordon (1892, p 245) suggested that if any excavation were to be made for fossils alone, it should be, in the first place, in the Lossiemouth quarries, and in the platform left by the quarrymen.

They did not go further down, because the bed was softish and rubbly, but it was at this horizont more than elsewhere in the quarry that most fossil were found.

At Spynie the reptiles also appear to have been found low in the Lossiemounth Sandstone Formation. The type specimen of L. lacer tinum was fpound by Mr. William Young at the botton of a sahft whitch had been sunk through 51 feet of sandstone down to a soft rubbly bed (Duff in Muschison 1859, p 435) Gordon (1859, pp 45- 46) added that the specimen was extracted from the living rock, deep in a quarry opened on the west end of the hill and Martin (c, 1860) stated that the specimen was found low down, in the bottom of the quarry. The quarry has been identified as an old pit at NJ 2206 6557 (Peacock et al 1968, p 68). Hyperodapedon apparently came from another pit nearby: the most westerly of the Spynie quarries (NJ 2192 6555) (Gordon in Huxley 1877; Linn 1886; Peacock et al 1968, p. 68) These openings were probably abandoned over 100 years ago, judging by the large trees growing in them, and Ornithosuchus , collected in 1891, may have come from the large quarry still in operation (NJ 2225 6565). Thios was the sites of two fine skulls of Hyperodapedon collected in about 1948 (now in RSM).

The first finds of Stagonolepis from Findrassie were made near the east entrance to Findrassie House, and among the debris of a pit opened up for road material (Gordon 1859, p 44). The East Londge of the Fidrassie Estate is situated at NJ2074 6545, and the pit could be one of the remaning Findrassie quarries which lie south and south-west of the entrance (Peacock et al. 1968, p 69), or it could have been filled (Walker 1961, p 106). On the original geological survey of the Elgin area, Linn (1886) record ed that Stagonolepis was found in the more westerly of a line of three quarries (NJ 2015 6495). Peacock et al (1968, p 137) sug gest a more easterly pit at NJ 205651 as the source of the rep tiles. Most of the Findrassie specimens figured by huxley (1877) are in the form of well preserved moulds. Howerver, some specimens in Elgin Museum labelled Findrassie look different and have bone preserved-this may indicate a different locality. There are ocasional pebbles inb the matrix, and the early specimens at least ocurred at the base of the reptiliferous sandstone, just above the Upper Olde Red Sandstone (Gordon 1859; Walker 1961).

Outline sketches of the more complete skeletons of Hyperodapedon (text-fig. 5) show that most were fossilized flattened in a horizontal plane, although it is hard to say whether they are lying on their bellies or on their backs. Only the type specimens lies partially on its side (tex-fig 5). The vertebral column is usually unbroken and the ribs and gastralia retain their association. The limbs are often ina natural resting pose, with the forelimbs flexed and pointing forwards, the hindlimbs are often in a natural resting pose, with the forelimbs flexed and pointing forwards, the hindlimbs pointing forwards or backwards. The shoulder girdle and pelvis may retain their original positions but they ussually collapse. The skull is often present undamaged and in close articulation with the vertebral column., In these specimens there is no evidence of disarticulation by water currents, wind, or moving sand. The animals generally appear to have died naturally and to have been covered by sand fairly rapidly. One or two isolated bones, sueh as tooth-bearing elemnts (EM 1926.6; BMNHR3151, R4780; MM L8272), show that some skeleton were broken up before fossilization.

The remains of the other meduium-sized reptiles, Stagolepis and Ornithosuchus, are also generally preserved with vertebrate, lims, and skull in articullation. Even ythe double row of dermal scutes above thevertebrate of Ornithosuchus often occurs in its original position.,However, scutes of Stogonolepis are very often found isolated, and small bones may be slightly sattered in some casee (e.g. foot of Orinithusuchus; Walker 1964, p 95). the type specimen of O. woodwardi (BMNH R 2409-24190) is preserved with the skeleton lying on its side and the skull in a horizontal plane. The head is turned back close to the sacrum presumibly by drying out of the neck ligaments after death. The Ornithosuchus skull, BMNH R3143, is preserved on its side. However, it should be stressed that there are no complete specimens available of Stagonolepis and Ornithosuchus . IN fact, only a few specimens od Stogonolepis show more that small group of associated bones, and it is clearly not possible to say a great deal about the attitude and completeness of the specimens. The mains reasons for the lack of complete specimens were that there was usually no one with sufficient professional interest around at the time ofd dicovery to make sure that everything was picked up, and it was clearly difficult to collected large fossil which were preserved as moulds in a virtually structureless sediments. This is particularly true ofStagonolepis which also had hundreds of scutes around its body; these would have made careful collection even more difficult.Many acutes were doubtless removed from their proper associatio because they made attractive specimens on their own. Only specimens od Stagonolepis and Ornithusuchus from Findrassie show signs of transport. They are disarticulated and slightly damaged, and Walker (1961, p 106) noted that pebbles are occasionally present in the Findrassie matrix. These facts may indicate some reworking by water.

The small reptiles of the Lossiemounth Sandstone Formation are often preserved in an undisturbed well-articulated state and flattened in a horizontal plane (text-fig. 6). The skull is in place, the back bone may be straight or curved, and the limbs are in natural squatting pose, as with the specimens of Hyperodapedon. However, there are about ten partial skull of Leptopleuron-isolated mandibles, maxillae, parts of the cheek region. In one specimens the skull roof behind the orbits has been lost, and probably also the upper part of the braincase. One Brachyrhinodon has also lost the skull roof. The type specimens of Erpetosuchus (BMNH R 3139) has the jaws wide open and tha forelimbs in a standing pose. Two individuals of Scleromochlus are preserved together on ene slab (BMNH R 3146) with the head of ene lying partly over the anterior trunk of the other.

In detail most bones are excellently preserved and they show little sign of crushed or distorted, even in association with other unaffected elements. A right ilium (BMNH R 4788) and a posterior caudal vertebra (GSM 90884) of Stagonolepis became distorted without fracturing, and this led to problems of identification (Walker 1961, pp 106-107) A skull of Ornithosuchus (BMNH R 4782; RMS 1967. 10.1A) are rather compressed (text-fig. 7a, B) and the skull of BMNH R 4782 has also collapsed slighly. The compression of all of these bones has probably been caused by the weight of superincumbent sediment, unusual in a sandstone matrix. Delicate skulls, like those of scleromochlus, may be completely flattened.Various specimens of Hyperodapedon (e.g. BMNH R 4782; RSM 1967. 10.1A, 2; GSM 90932/5) show fine cracks or larger fractures on the surface of the bone (tex.fig. 7c) wich may be connected with the same process. The cracks have not oponet in any way, and they are probably not suncracks.

Signs of predation or scaveging appear to be rare, but this hard to assess because of collection failure in many cases. Walker (1964, pp. 129-131) described a specimen of Ornithosuchus (BMNH R 3562) in which an articulated skeleton of a large individual has been crushed and broken in certain areas. The anterior scutes of the left side are damaged, the transverse processes of the associated vertebrate are boken off short, the anterior edge of the left scapula, which lies immediately below these vertebrate, is also broken and incomplete. The humerus is broken at the some point and the ribs of the left side are missing. The body has been considerably disturbed in the region or the left shoulder and side, but the rest of the skeleton is not affected, so that the damage was almost certainly caused by a predator or scavenger.

Two isolated skulls of Hyperodaoedon (RSM GY 1984. 20.1.2) show similar localized damage. In one the parietal is broken off just behind the attachment of the epipterygoids, and small displaced bone chips are preserved, and the top of the braincase is slightly crushed. This damage occurred before fossilization and probably at, or afyter, death since the breaks are clean, but there are no tooth or claw marks on the bone. The damage was probably not caused by physical processes since fine sclerotic lates are preserved, only slightly displaced, in the orbit. In the other specimens the brancaise has been completely removed, and it is represented by only two fractured, displaced bones slivers. The atlas, axis, and two anterior cervical vertebrae are preserved in articulation, but pushed in between the quadrates. Ossified hyoid elements are preserved in place, so the disarticulation is unlikely to have been caused by sedimentary processes.

The bone material is either absent (some Fidrassie specimens), or very soft and sometimes partly replaced by iron oxide (goethite) and fluorite (Spynie, Lossiemouth). When original material is preserved the structure of bones and teeth may be extremely clear, and the cavities highlighted by the replacemented sandstone. Positive preparation in the study of some specimens of Stagonolepis and Ornithosucus. Normally, cts have been made from the natural moulds left as cavities in the rock, and various methods that involve flexible synthetic rubbers have been developed in order to preserve the rock mould and produce a high-fidelity copy or the bone (walker 1961, 1964, 1973; Benton and Walker 1981).

ECOLOGY OF THE LOSSIEMOUTH SANDSTONE FAUNA (text-fig. 8)

The composition of the fauna of the Lossiemouth Sandstone Forma tion and the average sizes of its constituents are summarized in Table 2. The absence of plants, invertebrates, and fish, and the relatively small numbers of specimens make it futile to draw up food-chains and calculate biomass and productivity.

Stagonolepis and Hyperodapedon dominate the faunas as medium- sized herbivores that must have fed in relatively well-vegetated and watered areas distinct from the dune-fields in which they are preserved. Stagonolepis had strong dorsal and ventral armour and a heavy tail. It may have grubbed for plants or invertebrates with its shovel-like snout, and masticated them with its small pointed teeth by means of a slicing jaw action. The structure of the forelimb and shoulder girdle show that Stagonolepis normally walked on all fours, and the forelimb may have been used for digging also. For fast movement it may have been able to hold its limbs under the body for short for short periods, as in croco diles. Stagonolepis was a throughly terrestrial animal (Walker 1961).

Hyperodapedon was a shorter more bulky terrestrial reptile which had powerful limbs. The massive laterally flattened claws of the foot and the construction of the hinlimb strongly suggest that it was used for scratch-digging. Hyperodapedon may have fed on buried roots and tubers and other lowlevel vegetation which it raked up with its premaxillary beak and manipulated with a large tongue.

The jaws operated like a penknife, with the dentary cutting into a deep groove onthe maxilla. there were multiple rows of teeth that were not replaced from below. There were massive spaces for adductor mucles at the back of the skull, and Hyperodapedon probably probably cut up tough plant material with a poweful precision.shear bite (Benton 1983b, d, 1984)

Stagonolepis and Hyperodapedon were probalby preyedupon, or their carcasses scavenged, by large Ornithosuchus, Ornithosuchus may have been capable of bipedal locomotion for short spell, as well as quadrupedal locomotion. The long, curved teeth were clearly those of a carnivore, and the spinose scutes along the back may have necessary for protection against cannibalistic attack (Walker 1964, 1977).

Erpetosuchus was a rare small carnivore and/ ir insectivore. The dentition was peculiar, with long sharp recurved teeth at the front of the jaws and toothless longitudinal ridges behind which may have been used for crushing theprey. There was also an incip ient secondary palate, which may have been connected with the need to masticate the food.

Saltopus Elgin's only dinosaur, was a small presumably carnivo rous coelurosaur. It is more primitive than Huene (1910a) indi cated, having three rather than four sacral vertebrate, and the anterior blade of the ilium is not very long. Further, Saltopus shows no particular adaptations to hopping, as he suggested. Huene also suggested that it had elongate cervical vertebrae, but these are not preserved: tha anterior portion and the skull of the only skeleton in missing.

Saltopus , small individuals of Ornithosuchus, and possibly Erpetosuchus, probably fed on the small herbivores of the Lossie mouth Sandstone Formation; Leptopleuron, Brachyrhinodon, and Scleromochlus. Leptopleuron may be seen as a reptilian rodent. It had traversely broad back teeth consisting of two cusps linked by a narrow cross ridge, that were probably used for grinding up and chopping tough plants sliced off by its sharp, chisel-like front teeth. The teeth were set well foward in tha jaws, the lower jaw was deep with a strong (coronoid) process, and the temporañl area of the skull was spiny which may have acted to deter predators, to break up the animals against a background of spiny vegetation, and/or to form part of an interespecific combat display. The size and form of Leptopleuron and its inferred habitat, are reminis cent of two deswert-dwelling lizard; the Coast horned lizard, Phrynosoma cornutum from North America, and the Moloch, Moloch horridus from Australia.

Brachyrhinodon a tiny sphenodontid with acrodont teeth on the jaw margins and on the palate, and a very short snout, was probably also a herbivore that could chop up tough vegetation with ease. It was much smaller than the living Sphenodon (Brachyrhinodon had a skull lengh of 20-30mm; Sphenodon has a 70 mm skull), and its habits need not have been the same.

Scleromochlus is equipped with long hindlimbs that have been interpreted (Woodward 1907; Huence 1914) as adaptations to jumping, and it may have sought ots foot on the dunes in wich it is preserved, Jumping animals (saltators) have lengthened hindlimbs, the distal segmen in particular, several tarsal, or metatarsal, bones may lengthen, the tail is long (for balance), and the dorsal vertebral column may be shortened and the pelvis strengthened in order to withstand the impact of landing (Hildebrand 1974, pp. 512-515). Scleromochlus displays all of these features and in addition, it has a deep intercondylar fossa (patellar groove) at the distal end of the femur (Huene 1914, p 10), a feature seen in jumping mammals to accommodate a strong quadriceps femoris tendon. Scleromochlus may be compared with the jerboa and kangaroo rat which are similarly adapted and live in hot, sandy deserts. The suggestion by Huene (1914) that Scleromochlus climbed trees and made bold leaps from a branch or even glided, is not likely since the feet hardly appear to be adapted for grasping branches. Likewise, the suggestion by Wilfarth (1949, pp 7-9) that Scleromochlus lived underwater and used its powerful hindlimbs to propel itself to the surface for air, seems even less probalbe Scleromochlus also appears to have some specific adaptations for living on sand, like the North America desert-living iguanid lizards uma and Dipsosaurus the nares are nearly closed by lateral flanges, there is posterior flanges from the squamosal and quadratojugal protecting the tympanic region, the lower jaws is countersunk, and the metatarsus is flattened.

The sedimentological and taphonomic data suggest taht most of the Lossiemoutn Sandstone Formation animals normally lived in well- vegetated areas, possibly around interdune pools or close to water outside the dune-field. During arid periods, large sand dunes migrated across the floodplain, and many of the animals may have been overwhelmed by the sand. Others died from natural causes within the area of dunes. Nevertheless, it is strikings that no fossils have been preserved in the underlying water-laid beds, of animals like fishes, labyrinthodont amphibians, or phytosaurs.

The cadavers were normally buried rather rapidly by drifting sand dunes, which is suggested by their relatively well-articulated state. There may have been some scavenging of the carcasses by Ornithosuchus and the smaller carnivores.

AGE VARIATION AND SEXUAL DIMORPHISM.

Stagonolepis, Ornithosuchus, Hyperodapedon, and Leptopleuron are represented by enough specimens to permit some observations on variation in size and proportions.

The material of Stagonolepis segregates into two size groups, each containing similar numbers of specimens. Individuals within each group are remarkably uniform insize, and all measurements differ by 25-30% between the groups. Proportions are similar i both groups and morphological differences slight. These groups have been interpreted as male and female animals (Walker 1961), Romer and Prince (1940) found two size-groups in material of Dimetrodon limbatus and they also explained these in terms of sexual dimorphism. Among living reptiles, male crocodiles and alligators tend to be larger than females of the same age (Guggisberg 1972, p.127). Male lizard and tuataras also tend to be larger than females, but snakes often show exactly the opposite relationship (Goin and Goin 1971, pp. 115-116; Porter 1972, p.309). Both situations may be found in chelonians.

Ornithosuchus displays a broad range of size, with estimated skull lengh ranging from 125 to 210 mm. with the majority in he range 170-180mm. One small fragment (RSM 1966.43.2) represents the tip of a juvenile dentary, but the other specimens cannot be segregated into distinct size-groups (Benton 1983d). Thus, as with Ornithosuchus, the size distributions corresponds to age alone. As is general among living reptiles, age size-classes may be apparent among juveniles, but they are usually blurred in older animals because of individual differences ingrowth rate (Gibbons 1976).

However, the material of Hyperodapedon may be divided into two classes according to proportions. For example, if two skull of identical length are compared, certain important elements (toothplate, occipital condyle, glenoid and quadrate facets) have tha same dimensions, but bone bars and sheets between skull opening may differ markedly. Forms may be classified as gracile or robust on the basis of measurements of interorbital width, thickness of postorbital, or jugal, which differ by 20-70%. There is no relationship between these proportions and overall skull- size. It has been suggested (Benton 1983d) that the robust forms may be male, and the gracile forms female by analogy with certain living and fossil reptiles. The extant lizard Lacerta jacksoni shows sexual differences in the shape of the snout, nares, fron tails, and occiput (Degen 1911). Proposed males and females of the dinosaur P-Orotoceratops achieve the same maximum size, but differ in certain secondary sexual characters (frill, horn), as well as in the nasal height of the skull, size of the parietal fenestra, size of nares, height of the coronoids process, and other features (Dadson 1976). Similarly, differents skull pat terns have been ascribed to sexual dimorphism in Dimetrodon limbatus (Romer and Prince 1940), Seymouria baylorensis (Vaughn 1966), and Tetragonias (Cruickshank 1967).

DATING THE FAUNAS

The Hopeman Sandstone Formation

The footprints from the Hopeman Sandstone Formation (s.s.) are regarded as those of mammal-like reptiles, probably dicynodonts, and they closely resemble tracks from strata close to the Lower/Upper Permian boundary of Dumfriesshire, Penrith, and Mansfield (Hickling 1909; Watson 1909b; Watson and Hickling 1914; Haubold 1971; Smith et al 1974). As noted already (p215), Glennie and Buller (1983) divided the Hopeman Sandstone Formation into two units, assuming that the contorted sandstones are confined to one horizont at a about the same topogrphical level in the cliffs. However, since Williams (1973) recognized three well- separated horizons of contorted strata in upward succession from east to west, this assumption is open to question. Furthermore. the Clarkly Hill bore hole (Peacock et al 1968, p 130) encoun tered pebbly sandstone at the base of the Hopeman Sandstone, many of the pebbles being faceted. This pebbly sandstone would natu rally be taken to be the equivalent of the dreinkanter bed at the base of the Cutties Hillock Sandstone Formation, whereas Glennie and Buller correlate the upper of their two units with this formation. In addition Glennie and Buller (p.57) imply that the reptilian tracks occur in the lower of their two units, again if anything suggesting a correlation of this unit with the Cutties Hillock beds. The latter, however, areof very late Permian age. In fact, if we interpret Gleinnie and Buller correctly, the tracks would come predominantly from the upper of their two units, since they were most common in Masonsshaugh, Greenbrae, and Clashach quarries. However, the evidence of the footprints cannot be regarded as very strong (see above), and the uncertain ty over the succession within the Hopeman Sandstone Formation simply amphasizes the necessity for separate Cutties Hillock Sandstone Formation in order to avoid confusion.

The Cutties Hillock Sandstone Formation

The reptiles from the Cutties Hillock Sandstone Formation were initially assumed to be of the same age as those from the Lossie mounth Sandstone Formation (Judd 1885, 1886a). However, Newton (1893) hinted that the faunas were distinct, and Taylor (1894) suggest a Permian age. idependently, huene (1902) and Boulenger (1904) made the same suggestion. Walker (1973) discussed the age of the Cutties Hillock reptiles in detail, comparing Elginia and Geykia with animals from South Africa and Tanzania. He concluded that the Elgin formation was to be placed very close to the Permo-Triassic boundary, as had Watson and Hickling before him (1914), tentatively suggesting that it mitting lie at the very base of the Triassic, equivalent to a possition low in the Lys trosaurus Zone of South Africa. The main evidence for this sug gestion was that both Elginia and Geikia are more advanced than their closest relatives from-tha late Permian of South Africa and Russia, particular stress beinng laid on the specialization of the skull of Elginia. This view was not only based on the high degree of the spinescence, as stated by Rowe (1980), but refer ence was made to other skull characteristics. Rowe (1980) consid ered that the relationships of Geikia point to an uppermost Permian (i.e. Daptovephalus zone) horizont for the Cutties Hil lock Sandstone Formation. Using different evidence from the late Permian of Tanzania, is close to the ancestry of Geikia, the cryptodontid dicynodonts, all come from the late Permian of South Africa or Zambia. On the other hand, pareiasaurs less specialized in the skull that Elginia persist into the higher part of the Daptocephalus zone (Kitching 1977) and there seems no reason why this group should have become exytinct wold-wide at the Permo- Triassic boundary. On balance, it seems best best to take a conservative course, and regard the Cutties Hillock Sandstone Formation as lying at the extreme summit ot the Permian, but bearing in mind that elginia may represent a relict line which lingered on rather later in Scotland than elsewhere.

The Lossiemouth Sadstone Formation

The dating of the Lossiemouth Sandstone Formation has an even more involved history. The Elgin sadstone were all initially considered to be Devonian in age, until finds of reptile foot prints ans bones in the period between 1850 and 1860 convinced most palaecologists that some of them must be regarded as young er. Local geologist long considered that that the Lossiemounth sadstone were Devonian because they wanted to have the oldest reptiles in the world (e.g. Phillips illips 1886; Gordon 1892). Also, certain geologist(e.g. Sir R.I.Murchison, Charles Lyell) had their own reason for preferring to assign the reptiles to the Old Red Sandstone (Benton 1983 c.). However, Hxley (1867) argued convincingly for a Triassic age, and Mrchison (1867, p. 267) accepted an Upper Triassic assigment.

Huene (1980) correlated the Lossiemounth sandstone with the German Lettenkohle (Late Ladinian) on the assumption that Hypero dapedon also occured in the Lower keuper sandstone of the English Midlands together with amphibians and plants typical of the German formation.

There is now stronge evidence for a lower Norian (Upper Triassic) assigments for the Lossiemouth Sandstone Formation. Walker (1961) pointed out that Stagonolepis is very closely similar to Aetosau rus from the german Stubensandstein (Middle Norian: Anderson and Cruickshank 1978; Tucker and Benton 1982). Aetosaurs occur also in the German Blasensandstein (Ebrachosaurus Lower Norian), the Dockum Group of Texas and the Chinle Formation of Indian (un- named: L.Norian) the Ischigualasto Formation and Los Colorados Formation of Argentina (Aetosauroides and Neoaetosauroides, respectively; L. Norian and U. Norian /Rhaertian), and tha new Haven Sandstone of Cunnecticut (Stegomus: M.Norian). Aetosau roides is slightly more primitive than Stagonolepis (Walker, in discussions to Warrington 1970, p 218). Ornithosuchus is most closely related to Riojasuchus from the los Colorados Formation or Argentina (Norian; Bonaparte 1978). H. gordoni is remarkabli similar to H. huxleyi from the Maleri Formation of India, and Scaphonyx from the Santa Maria Formation of Brazil and Ischigua lasto Formation of Argentina (all late Carnian or early Norian). The Elgin procolophonid Leptopleuron appears to be very close to Hypsognathus from the Newark Group of new Jersey (latest Triassic or earliest Jurassic; Olsen and Galton 1977). Brachyrhinodon is most like Polysphenodon from the Gipskeuper (Carnian) of East Germany (Walker 1966). The other Elgin reptiles do not appear to have had relatives elsewhere, as far as we know.

The close relationship of PyHyperodapedonPy from Elgin and India is important. The Maleri Formation has also yield a primitive phytosaur close to Francosuchs from the german Blasensandstein (Lower Norian). the Maleri Formation fauna also contains speci mens of the Labyrinthodont Metoposaurus which is restricted to horizons in Germany ranging from the Schilfsandstein to the Blasensandstein (Upper Carnian-Lower Norian). The Maleri Formati is very probably lower Norian in age, and the Lossiemouth Sand stone Formation also. Unfortunately the age of the Lossiemouth beds cannot be confirmed independiently by means of pother fossil groups.

The Lossiemouth Sandstone fauna shows some affinity with other northern hemisphere faunas of the late triassiz. it shares aetosaurs, Sphenodontids, procolophonoids and, coelurosaur with the North America and German faunas. however, the Elgin beds lack the metoposaur amphibians and phytosaurs that dominate all of these faunas. The other elements of the Lossiemouth Sandstone fauna show affinities with India and the southern continents; similar late Triassic rhynchosaurs are known from Indian and South America (a few scraps from Borth America), the closest relative of Ornithosuchus comes from South America, the South America and Indian faunas also have aetosaurs.

It is hard to find palaeogeographic reasons for these apparent distributional anomalies. The solution may depend on the environments in which tha animals lived. The sediments i which the German. North America, and India fsaunas are found are largely water-laid, and metoposaurs and phytosaurs are clearly aquatic or semi-aquatic animals. However, the sediments of the South America formations are also largely water-laid, and amphibian are rare and phytosaurs are absent. The distiction between these two kinds of faunas is probably environmental, however, and they have been distinguished as a Metoposaur/Phytosaur Empire (germany, North America) and a Rhynchosaur/Diademodoind Empire (South America, Africa, India) (Tucker and Benton 1982; Benton 1983a) an interesting problems is the virtual absence of rhynchosaurs in North SAmerica, and their complete absence in Germany which is hard to explain in view of their overwhelming abundance alsewhere.

SUMMARY

1.- Fossil reptile remains are known from four horizonts in the region of Elgin, North-east Scotland: the Hopeman Sandstone Formation, the Cutties Hillock Sandstone Formation, the Lossiemounth Sandstone Formation, and the Rhaetic.

2.-The remains from the Hopeman Sandstone Formation of the coastal region are footprints of several kinds. These indicaste a range of two or three genera of mammal-like reptiles as the producers, and they resemble other mid-to late-Permian trackways from elsewhere.

3.- The reptiles from the Cutties Hillock Sandstone Formation include two dicynodonts, Geikia and Gordonia,a pareiasaur, Elginia, and an un-named procolophonid. These reptiles indicate a date in the late Permian near the Permo-Triassic boundary.

4.- The reptiles from the Lossiemounth Sandstone Formation include the rhynchosaur Hyperodapedon, the thecodontians Stagonolepis, ornithosuchus, Erpentosuchus, and Scleromochlus, the procolophonid Leptopleuron the sphenodontian Brachyrhinodon, and the early dinosaur saltopus these reptiles individually suggest a late Triassic age, and jointly a lower Norian age.

5.- The reptiles from the Rhaetic of Linksfield include plesiosaurs and crocodiles, represented by odd teeth, vertebrae, and limb bones.

6.- The Cutties Hillock Sandstone Formation is formally defined here, and it is distinguished from the Hopeman Sandstone Formation. There is litle evidence for a direct correlation of the two, and the new name is requiered to show the distinctness of the two formations.

7.- The reptiles of the Cutties Hillock Sandstone Formation and the lossiemouth Sandstone Formation occur in aeolian sediments. the skeleton are preserved fairly completely, and with only occasional disturbance (by predators). The bones is sometimes preserved, and sometimes completely lost, so that casts can be made. There is good evidence that the skeleton occurred low intheir respective formations, at the base of large aeolian dunes.

8.- The lossiemouth fauna includes medium-sized herbivores that must have fed in well-watered areas, as well as smaller lizard- shaped animals taht show adaptations for running around in the dunes. For some genera there are enounigh specimens to shown age variations and sexual dimorphism.

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Text-fig 1.- Reptile footprints from the Hopeman Sandstone Forma tion, near A small prints, after Brinckenden (1952; B, medium prints. Chelichmus megacheirus after Huxley (1877, pl. 14); c, large prints, field photograph. A. B. from Masonshaugh Quarry; c grom Clashach Quarry, scales are shown for A and B; c, shows tracks which are 100-150mm wide and have a stride lengh of 700-800.mm.

Text-fig. 2. The reptiles of Cutties Hillock Sandstone Formation of Cutties Hillock Quarry, near Elgin. Skull of A. Gordonia; b Geikia; and c, Elginia, all drawn to the same scale.(A, Newton 1893; B, after Newton 1893 and Rowe 1980; C, after Newton 1893 and original.)

Tabla 1.- Classification of the reptiles of the Lossiemouth Sandstone Formation.

Text.-fig. 3. The reptiles of the lossiemouth sandstione Forma tion, near elgin (late triassic; early Norian). Skull of A, stagonolepis, B, Hyperodapedon; c; Ornithisuchus; D, Erpetosu shus; E, Leptopleuron, F, Brachyrhinodon, and G, scleomochlus, drwan to three different scales (A-C, D, E-G). The skull of Saltopus is not known, (A, after Walker 1961; B, after Benton 1983 d; C. after Walker 1964; D, original; E, original; F, after Huene 1910b, G, original).

Text-fig 4 The distribution of the Permo-Triassic beds around Elgin, north-east Scotland. The formations are indicated by shading, and the main reptile and footprint localities are named.

Text-fig. 5 skeleton of Hyperodapedon as preserved to show typi cal position of fossilization. Vertebrate and ribs are shaded black, and all other elements are shown in outline.

Tex-fig. 6 Skeleton of some smaller reptiles from the lossiemouth sandstone formation to show the positions of fossilization. Vertebrate ribs are shaded black, and all other elements are shown in outline.

Text-fig.7 Compression and pre fossilization damage to bones of Hyperodapedon from the Lossiemouth sandstone Formation, A,, lateral view of distorted partial left scapula, compared with B, lateal view of left scapula, restored from cast, both from ani mals of similar size, C, crushed distal end of a femur , showing pre-fosilization damage.

Tabla 2.- The Lossiemouth Dandstone Formation fauna, composition. Information from Walker (1961, 1964) Benton (1977, 1983 d), and original.

Text-fig. 8 A scene at elgin, noth -east scotland, in Lossiemouth Sandstone Formation times showing reconstruction of the reptiles in an imaginary scene with typical late Triassic plants. Three Hyperodapedon feed on seed.ferns in the foreground. Behind them on Ornitosuchus runs towards the armoured stagonolepis which is looking over its shoulder. Behind Stagonolepis two Erpetosuchus feed on a small carcass. On the rocks in the left the side of the pond. In and around the pond there are horsetails, cycads, and ferns, and there are tall lycopods in the distance. Based on a colour painting by Jenny Halstead in Benton (1983b).

M.J.Benton and A. D. Walker.

Figura 1

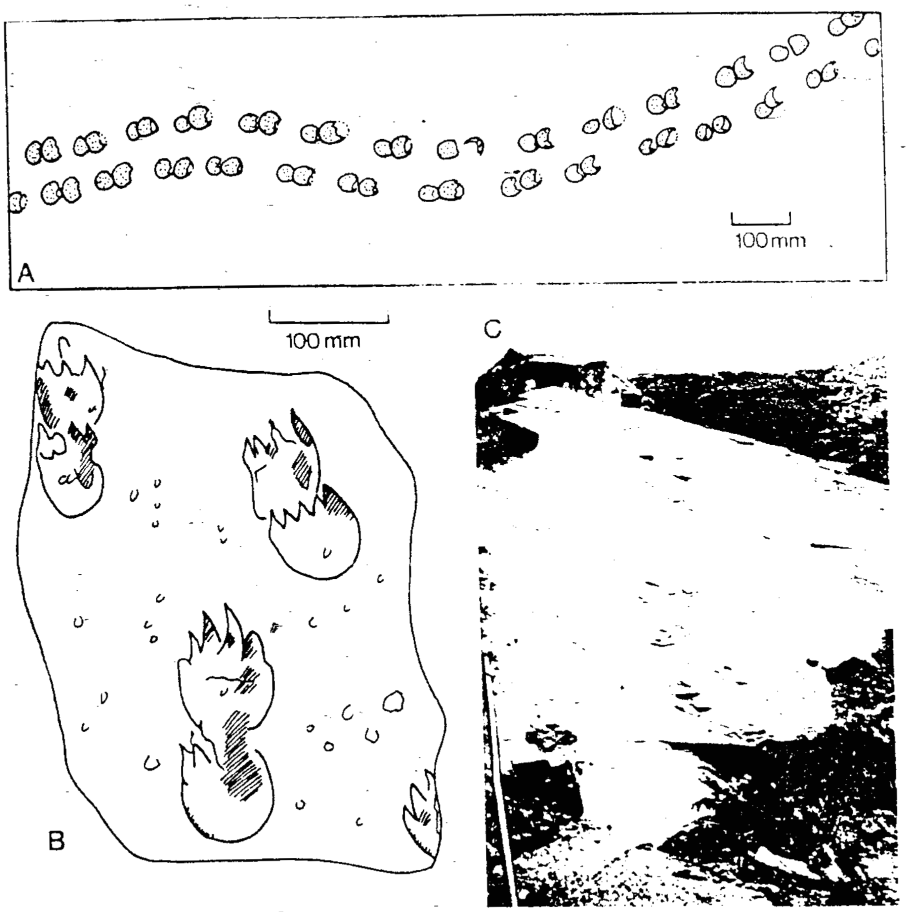


Figura 2

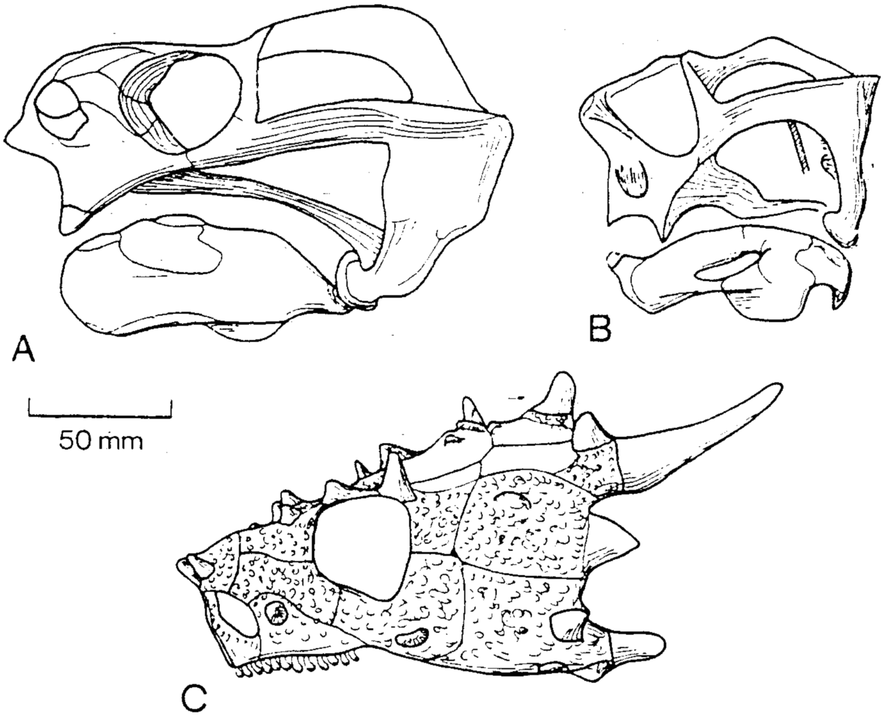


Tabla 1.

SUBCLASS ANAPSIDA
Family Procolophonidae Cope 1889
Leptopleuron lacertinum Owen 1851 (objective junior synonym, *Telerpeton elginense* Mantell 1852)
SUBCLASS DIAPSIDA
Cohort Archosauromorpha Huene 1946
Superorder Rhynchosauria Osborn 1903
Family Rhynchosauridae Huxley 1887
Hyperodapedon gordoni Huxley 1859 (subjective junior synonym, *Stenometopon taylori* Boulenger 1903)
Superorder Archosauria Cope 1869
Order Thecodontia Owen 1859
Family Stagonolepididae Lydekker 1887
Stagonolepis robertsoni Agassiz 1844
Family Ornithosuchidae Huene 1908
Ornithosuchus longidens (Huxley 1877) (subjective synonyms, *Dasygnathus longidens* Huxley 1877; *O. woodwardi* Newton 1894; *O. taylori* Broom 1913)
Family Erpetosuchidae Watson 1917
Erpetosuchus granti Newton 1894
Family Scleromochliidae Huene 1914
Scleromochlus taylori Woodward 1907
Order Saurischia Seeley 1888
Family [illegible]idae Huene [illegible]
Saltopus elginensis Huene 1910
Cohort Lepidosauromorpha Benton 1983
Superorder Lepidosauria Haeckel 1866
Order Sphenodontia Williston 1925
Family Sphenodontidae Cope 1870(?)
Brachyrhinodon taylori Huene 1910

Figura 3

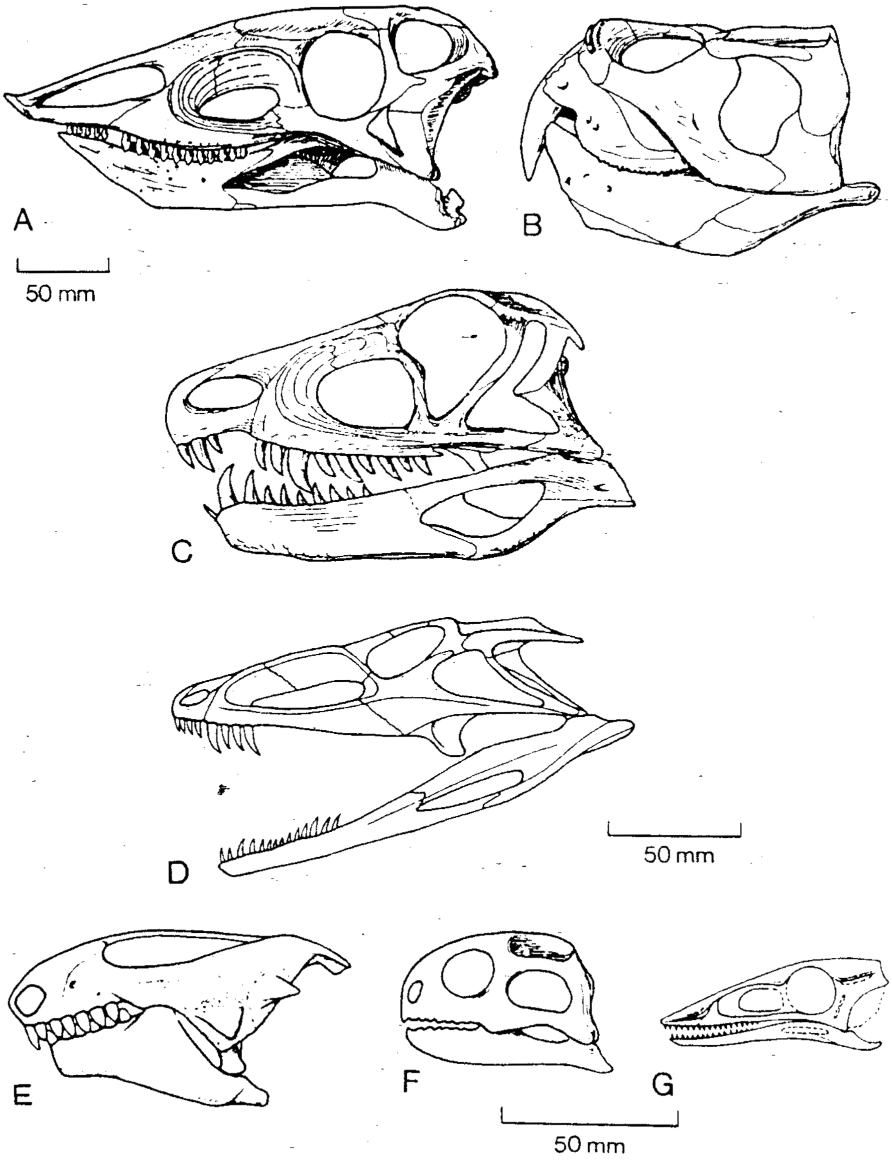


Figura 4

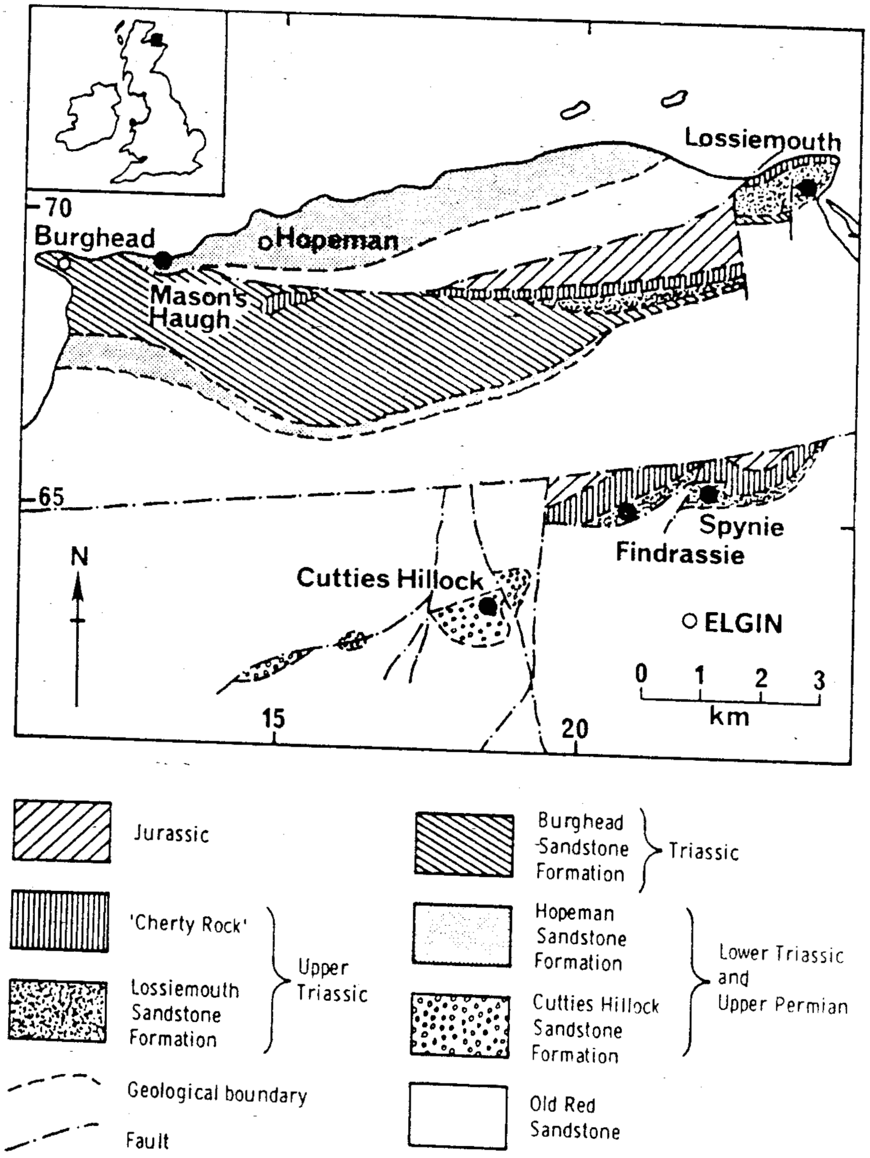

70
65
15
20
Burghead
Hopeman
Mason's Haugh
Lossiemouth
Cutties Hillock
Spynie
Findrassie
ELGIN
N
0 1 2 3
km
Jurassic
'Cherty Rock'
Lossiemouth Sandstone Formation
Upper Triassic
Geological boundary
Fault
Burghead Sandstone Formation
Triassic
Hopeman Sandstone Formation
Cutties Hillock Sandstone Formation
Lower Triassic and Upper Permian
Old Red Sandstone

Tabla 2

	Body length	Approx. number of individuals
Herbivores		
Stagonolepis	2·1-2·7 m	30(+)
Hyperodapedon	1·0-1·5 m	35
Carnivores		
Ornithosuchus	1·0-3·7 m	12
Saltopus	600 mm	1
Carnivore/insectivore		
Erpetosuchus	?700 mm	2/3
Small omnivores		
Leptopleuron	110-250 mm	?30
Brachyrhinodon	150 mm	?11
Scleromochlus	200 mm	7
		128

The classification of the Permo-Triassic rocks around Elgin, using the new terminology (Warrington *et al.* 1980), and as recommended here, is:

Cherty Rock (?Norian-Rhaetian)

Lossiemouth Sandstone Formation (Carnian-Norian)

(Synonyms: Reptiliferous Sandstone (pars) (Symonds 1860; Harkness 1864; Judd 1873, 1886*a*, *b*; Gordon 1892; Traquair 1895; Mackie 1897; Boulenger 1903); Elgin Sandstone (Newton 1894); *Stagonolepis* Beds (Boulenger 1904; Huene 1910*a*); *Stagonolepis* Sandstone (Watson 1909*b*; Huene 1910*b*, 1912*a*, *b*, 1913, 1914); Sandstones of Lossiemouth, Spynie, and Findrassie (Westoll 1951); Sandstones of Spynie, Lossiemouth, and Findrassie (Peacock *et al.* 1968)).

Burghead Sandstone Formation (??Anisian-Carnian)

(Synonyms: Burghead Sandstones (Westoll 1951); Burghead Beds (Peacock *et al.* 1968)).

Hopeman Sandstone Formation (Late Permian)

(Synonyms: Sandstones of Cummingstone (Huxley 1859*b*, 1877); Cummingstone Beds (Hickling 1909; Watson 1909b; Watson and Hickling 1914); Reptiliferous Sandstone (pars) (Symonds 1860; Harkness 1864; Judd 1873, 1886*a*, *b*; Traquair 1895); Sandstones of Cutties Hillock and Hopeman-Cummingstone (pars) (Westoll 1951); Sandstones of Cuttie Hillock (Quarry Wood) and Hopeman (pars) (Peacock *et al.* 1968)).

Cutties Hillock Sandstone Formation (Late Permian)

Reptiliferous Sandstone (pars) (Judd 1886*a*, *b*; Traquair 1895; Mackie 1897); Elgin Sandstone (Gordon 1892; Newton 1893); Cutties Hillock Beds (Watson 1909*b*; *Gordonia* Beds (Boulenger 1904); *Gordonia* Sandstone (Huene 1913); Sandstones of Cutties Hillock and Hopeman-Cummingstown (pars) (Westoll 1951); Sandstones of Cutties Hillock (Quarry Wood) and Hopeman (pars) (Peacock *et al.* 1968); Cuttie's Hillock Sandstone (Walker 1973)).

Figura 5

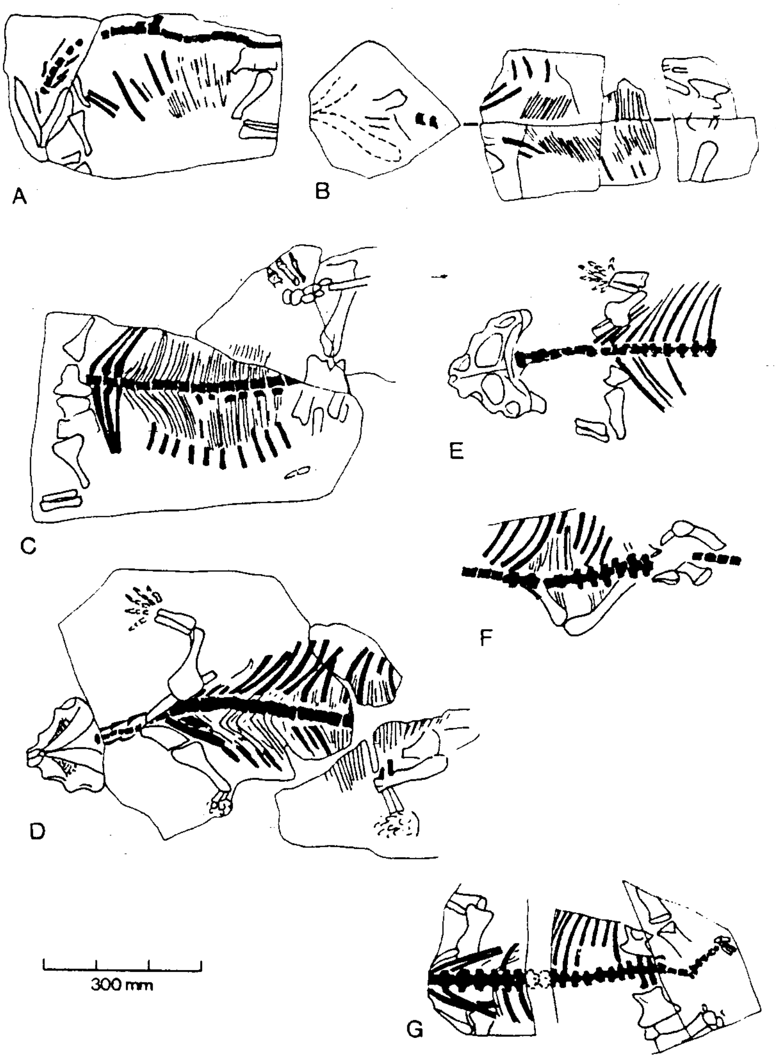


Figura 6

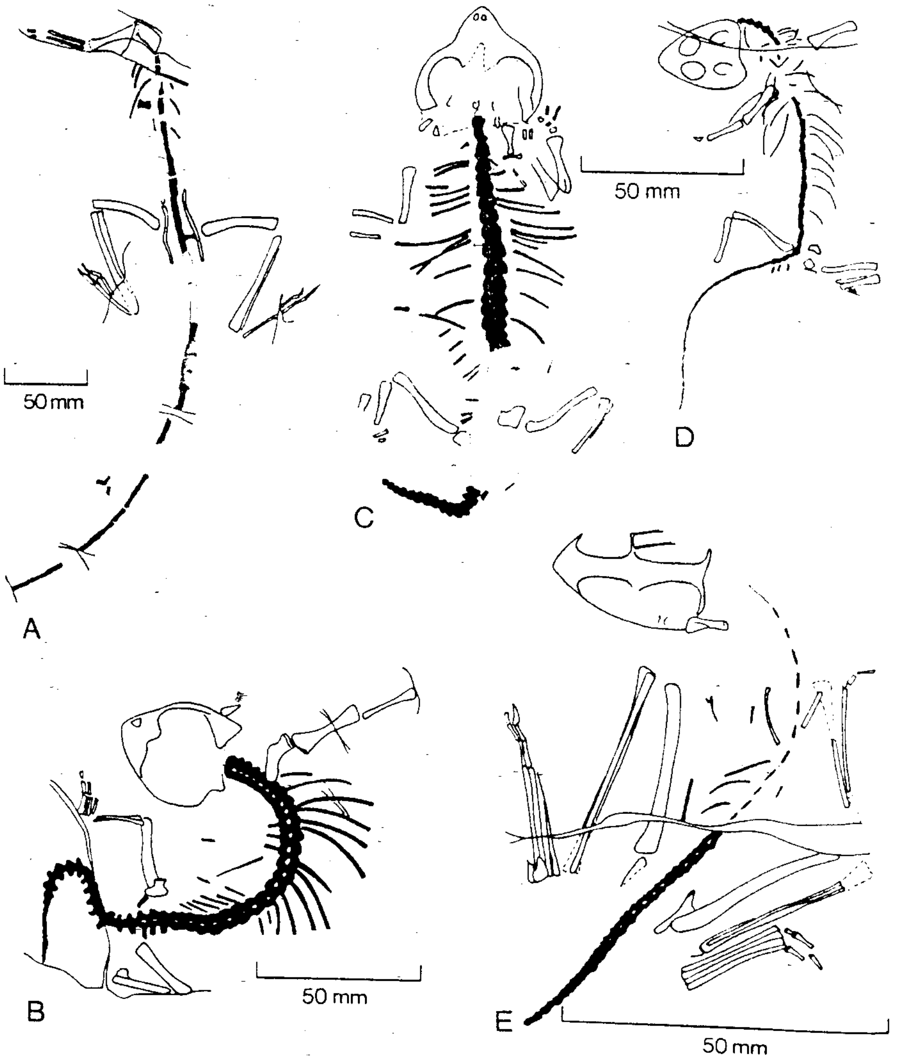


Figura 7

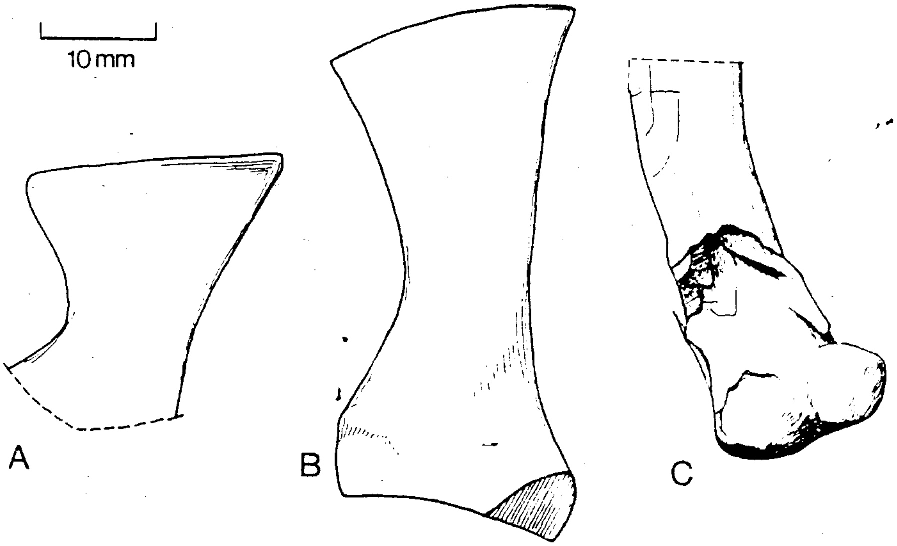
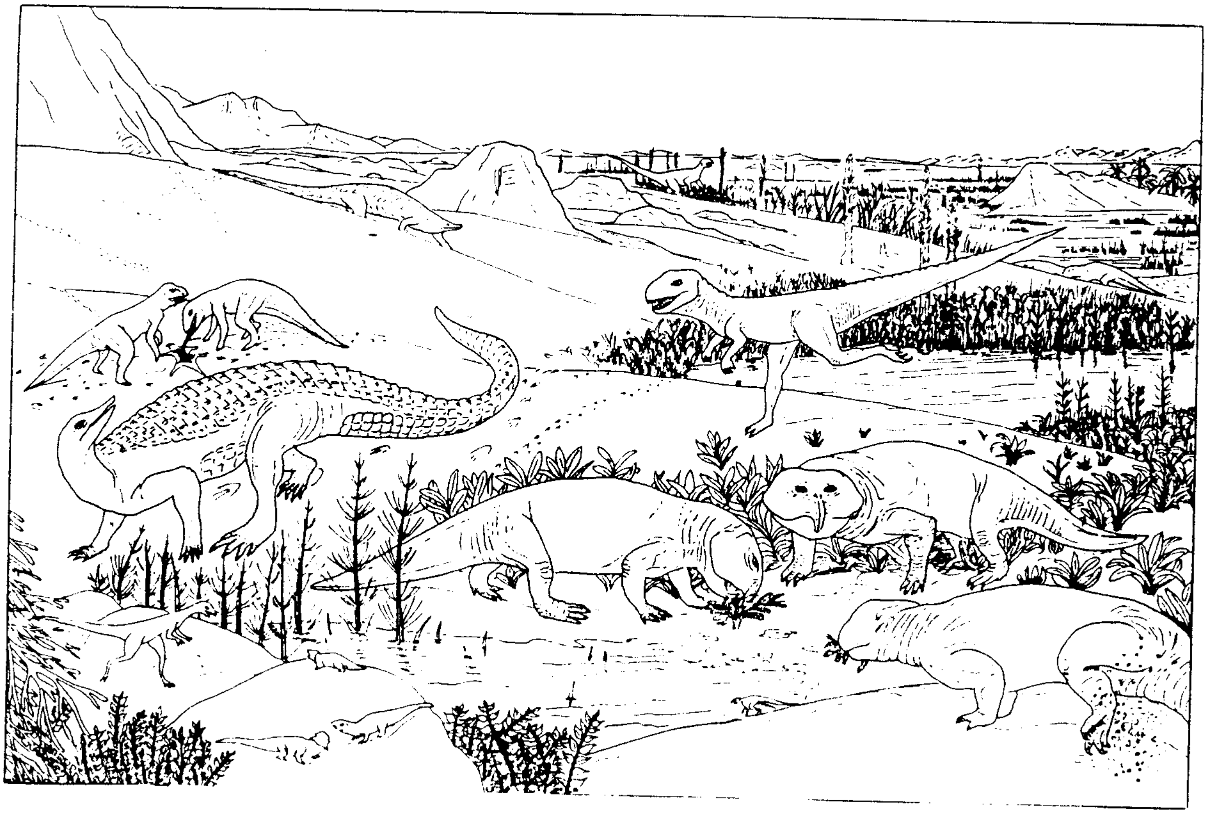


Figura 8



In PADIAN, K. & CHURE. D.J., CONVENERS, 1989. THE AGE OF DINO SAURS, SHORT-COURSES IN PALEONTOLOGY NUMER2: KNOXVILLE, TENN., THE PALEONTOLOGICAL SOCIETY, p. 7-21

8.6 (b)

THE ORIGIN of DINOSAURS and the BEGINNING of the AGE of DINOSAURS

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INTRODUCCION

What are dinosaurs? what fauetre charactteristize them ? Who were their closest relatives? What were the times like when the dino saurs fisrt evolveds? How did their appaerance change the balance of diversity in terrestrial ecosystems? During the past decade we have come to know much more about these topic than ever before. What follows is only a brief review. For more extensive informa tion, readers are referred to the chapters in Padian (1986a), particularly the Introduction, on questions of the Late Triassic- Early Jurassic transition; and to Gauthier (1984-1986) on the characteristics of dinosaurs and their relations. Because this is meant to be a general account, like the other papers in this book, it is impossible to cite every worker, discovery, or relev aant paper in the fielld, and some personal judgments must be exercised.

THE DINOSAURIA

The first remain of dinosaurs to be recognized as fossils of extinct reptiles were found in England in the 1820s (for good accounts, see Desmond 1975 and Charing, 1979). Megalosaurus was a giant carnivore; Iguanodon, vegetarian with leaf-shaped teeth and a curiors spike for a thumb. Neither animal was preserved and early restorations perhaps understandably made both cretuares quadrupedal (after all, who had ever seen a bipedal reptiles?) : pyIguanodon's spike was a first stuck on its nose. In the fol lowing decades several new taxa were added to the problematic giant land-going reptil;es of southern England, as well asd new discoveries of the unreleted marine forms, the ichthyosaurs and plesiosaurs, and the flying pterosaurs. In 1841 Richard Owen, the consummate genius of Vistorian zoology, created a new group of reptiles, the Dinosauria, to encompss the half-dozen forms and to set them apart from other reptiles by virtue of their erect llimbs, their pelvees that incorparated at least five sacral vertebrae, and their terrestrial habits. In so doing. Owen also to drive another nail into the coffin of the transmuttional evolutionists by denying evolutionary progress.

In a brilliant article, Desmond (1979)_ argued that Owen's purpose was to shown that ancient reptiles were more sophisticat ed in form and physiology than their living counterparts. Ironi cally, he creted a grade of evolutionaril advanced reptriles in order to deny evolution.

The conceptt of Dinosauria has shifted over the ayers, and ques tions of dinosaur monophylly and membership have persisted had a common origin and can be diagnosed by a suite of feature,. Gauthier (1984, 1986) listed sosme of these shared by mthe commonancestor of all known dinosaurs (Figures 1 and 2). The vertebrall column waas highly regionalized, and there were at least three sascral vertebrae. Digits 4 and 5 on the hand were reduced in size and number of phalanges, and the distall end of the first metacarpalll (the base of the trumb) is offset so that digit is somewhat opposable to the others. The hip bones have reduced their contact around the socket (acetabu;lum), so that the socket is at least partly open. The upper rim of the ssocket is buttressed, and there is along, depp channel on the lower part of the pelvis behind the socket that housed the cau dofemorallis brevis muscle. This tibia (shin bone) has a cre cent-shaped knee crest and is widened ast its snkle end. Tibia is much more robustthan the fibula, the other lower leg bone, much as in humans; and the proximal ankle bones that they contac (the astragalus and callcaneum, respectively) are similarly disparate in size (in crocodiles, lizards,and turtles, they are more nearly equal because there is more rotation in the lower leg during walking). The astragalus has large ascendinmg process against the tibia. The two proximal ankel bones together form a double roller jopint (as on the drumstick of the cjhicken) for the main articulayion of the hinge of tthe ankle. The metatyarsal (sole bones) are longg and closed appressed; the foot is functionally tridactyl, and the stance is digitigrade. This is what the first dinosaurs were like.

Some of these characters are shaared by the closest relatives dinosaurs, including pterosaurs and the small archosaur Lagosuchus (Figure 3B; Bonaparte, 1975), but the unique combination of all these characters is known only in the dinosaurs. Pterosaurs, of course, are highly modified for flight, so it is difficult to know whether they passed through any or all of the dinosaurian' characteris states before becoming so modified. Lagosuchus and other related forms of the South American Triassic are not yet welll enough known to say just how many dinosaurian charactes they sharew. Clearly all these groups had a common ancestror in the Middle Triassic and pursued closeed related evolutionary paths. The available evidence indicates tat thier common ancestor was a small, agile, lightly built, bipedal archosaurian reptile, predaceous rather than herviborous, that used its forelimbs (now freed from locomotion) for avariety of functions. This seems to have been the great invention of the dinosaurs. Many reptiles of today, including crocodiles and lizards, can achieve an erect stance when they nwant to. In its' high walk,' for example, the crocodile pulls its hind limbs underneath the body and proceeds, instead of sprawling These reptiles are versatile in this respect.

But dinosaurs had no choice: their hip and joints telll us that they had to stand fully erect, limbs tucked under and moving under the body. This suggests two things: first, that they had the enrgetic capability to be habbitually erect; and second, that they were using their hands for other things, as their offset trumbs attest. Just what those uses were is not entirely clear; seizing prey and manipulating objects come to mind. But one could reasonably infeer that some selective force must have contributed to the switch from the energically less costtly and more versatile stance retained by other reeptiles. It also must have played an important role in respiration, and thereby in the metabolism necessary to sustain activity, as Carrier (1987) has elegantly shown.

I will return to the relationsps of dinosaurs to other Mesozoic reptiles after explaining abit about the time period that wi nessed their origin.

THE AGE OF DINOSAURS

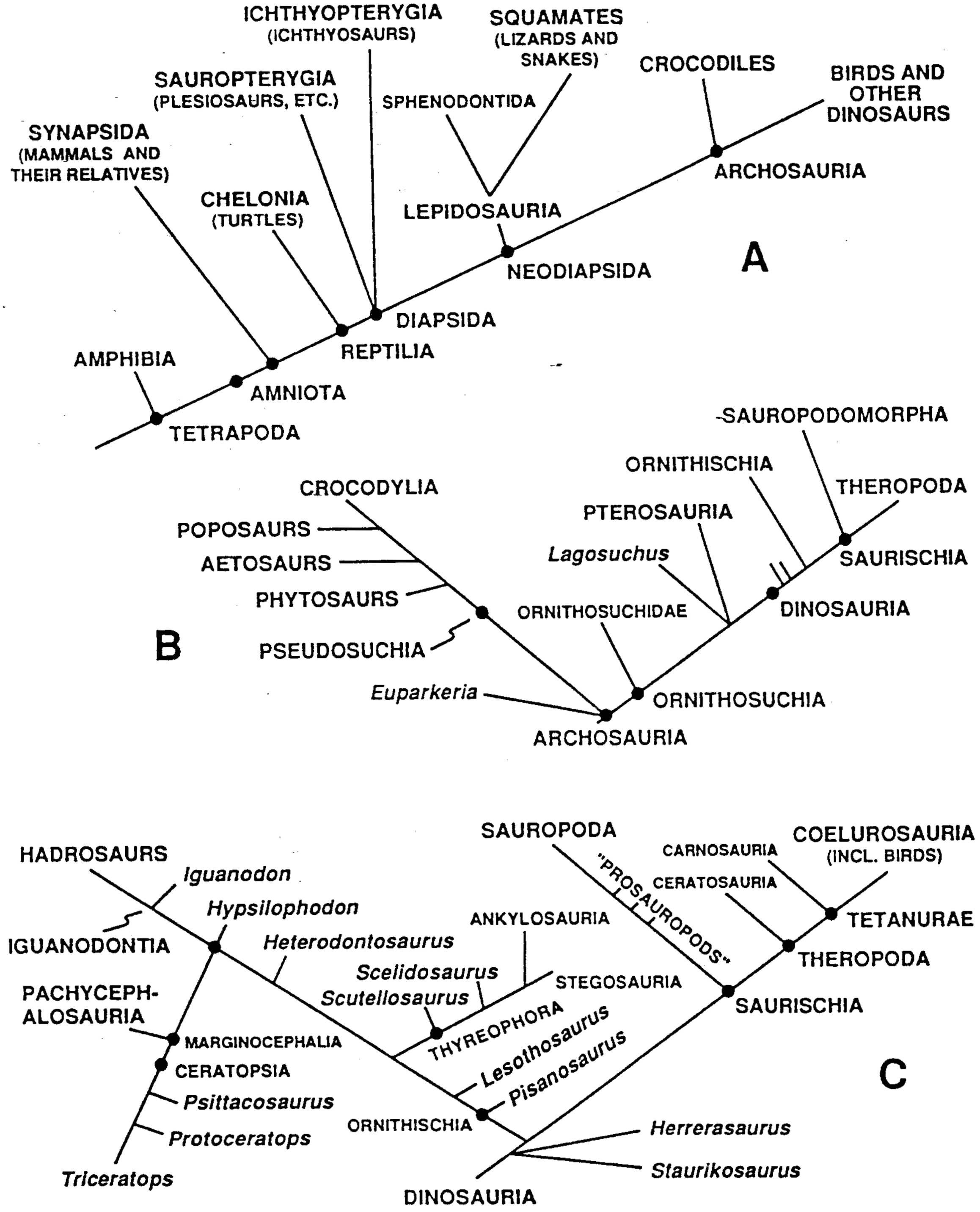
The first known dinosaurs appeared in the latest Middle Triassic or earliest Late Triassic of South America, and are known from only a few incomplete skeletons (Staurikosausus, Herrerasausus, Ischisaurus, Pisanosaurus, and Trialestes;see Gluy 1982 for illusttion of some ot these). Pisanosaurus appaers to be an ornithischian dinosaur but the rest are neither ornithischians nor saurischians prope, as Gauthier (1984) showed. There are a couple of apocryphal Middle Triassic records of dinosaur footprintts (Haubold 1986), aand certainly there must have been dinosaurs at some poiont in the Middle Triassic, but it is really in the Cranian and Norian that the first good records of dinosaurs occur, and Africa (Padian 1986b). The "Age of Dinosaurs," therefore, does not precisely concide with the Mesozic Era, Because the dinosaurs ggot a late strat.

Moreover they did not disappear by the end of the Cretaceous. As the chapter in this book by Gauthier and Padian demonstrates, the birds are descwnded from small carnivorous dinosurs, and so by the criterion of morpholyly sre formally to be considered dinosaurs(see also Gauthier, 1984, 1986; Gauthier and Padian, 1985.)

The Triassic was an exceptionally busy time in vertebrte history (Padian 1986a, pp. 3-4; see also Padian and Clemens, 1985). More recognized taxonomic orders of tetrapods lived at one point or another during the Triassic than at any other time in vertebrate histtory, with the exception of the Tertiary (the explosion of mammals and the addition of the taxonomically inflated birds does this) This is because Triassic terrestriall life really consists of three major faunal elemts: (1) group that survived from earlier periods, (2) group that lived only during the Triassic, and (3) group that appeared at the end of theee Triassic but reached their greatest diversities in later periods.

The first group wich I call "Paleozoic holdoveras" comprises mostly llarge, flatskulled amphibians that proweled the water ways, plus the ttherapsid relatives of mammals (often misnamed " mammal like reptiles" see below). Thesee group were on the wane and had nearly all disappeared by the end of the Triassic. The second group includes tetrapods, mostly reptiles, that arose and outt died out during the Triassic, in most cases the Late Triasic. Many of their names are not generally familiar but they include metropposaurs, phytosaurs, eatosaurs, rtauisuchids, poposaurs, lagosuchids, triphosaurs, rhynchosaurs, and tanys tropheids [Some of these will be encontered later; skeletons and restorations of many of them can be found in Colbert (1972- 1985), Charig et al. (1976) Carroll (1987), and Long and Houk (1989).] The reasosns sujggested for their demise range from competition with the dinosaurs (not readily demostrable, and anyway dinosaurs were few in number and diversity back then) toecological catastrophe (difficult to se what could have af fected them that would have spared the dinosaurs) to simple luck of the draw (possible, but a non explanation in that respect).

Kevin P.


ICHTHYOPTERYGIA
(ICHTHYOSAURS)
SQUAMATES
(LIZARDS AND SNAKES)
SAUROPTERYGIA
(PLESIOSAURS, ETC.)
SPHENODONTIDA
CROCODILES
BIRDS AND OTHER DINOSAURS
SYNAPSIDA
(MAMMALS AND THEIR RELATIVES)
CHELONIA
(TURTLES)
LEPIDOSAURIA
ARCHOSAURIA
NEODIAPSIDA
A
DIAPSIDA
REPTILIA
AMPHIBIA
AMNIOTA
TETRAPODA
SAUROPODOMORPHA
ORNITHISCHIA
CROCODYLIA
THEROPODA
PTEROSAURIA
POPOSAURS
AETOSAURS
Lagosuchus
SAURISCHIA
PHYTOSAURS
ORNITHOSUCHIDAE
DINOSAURIA
B
PSEUDOSUCHIA
Euparkeria
ORNITHOSUCHIA
ARCHOSAURIA
SAUROPODA
COELUROSAURIA
(INCL. BIRDS)
HADROSAURS
CARNOSAURIA
"PROSAUROPODS"
CERATOSAURIA
Iguanodon
Hypsilophodon
TETANURAE
ANKYLOSAURIA
IGUANODONTIA
Heterodontosaurus
THEROPODA
Scelidosaurus
STEGOSAURIA
PACHYCEPHALOSAURIA
Scutellosaurus
SAURISCHIA
THYREOPHORA
MARGINOCEPHALIA
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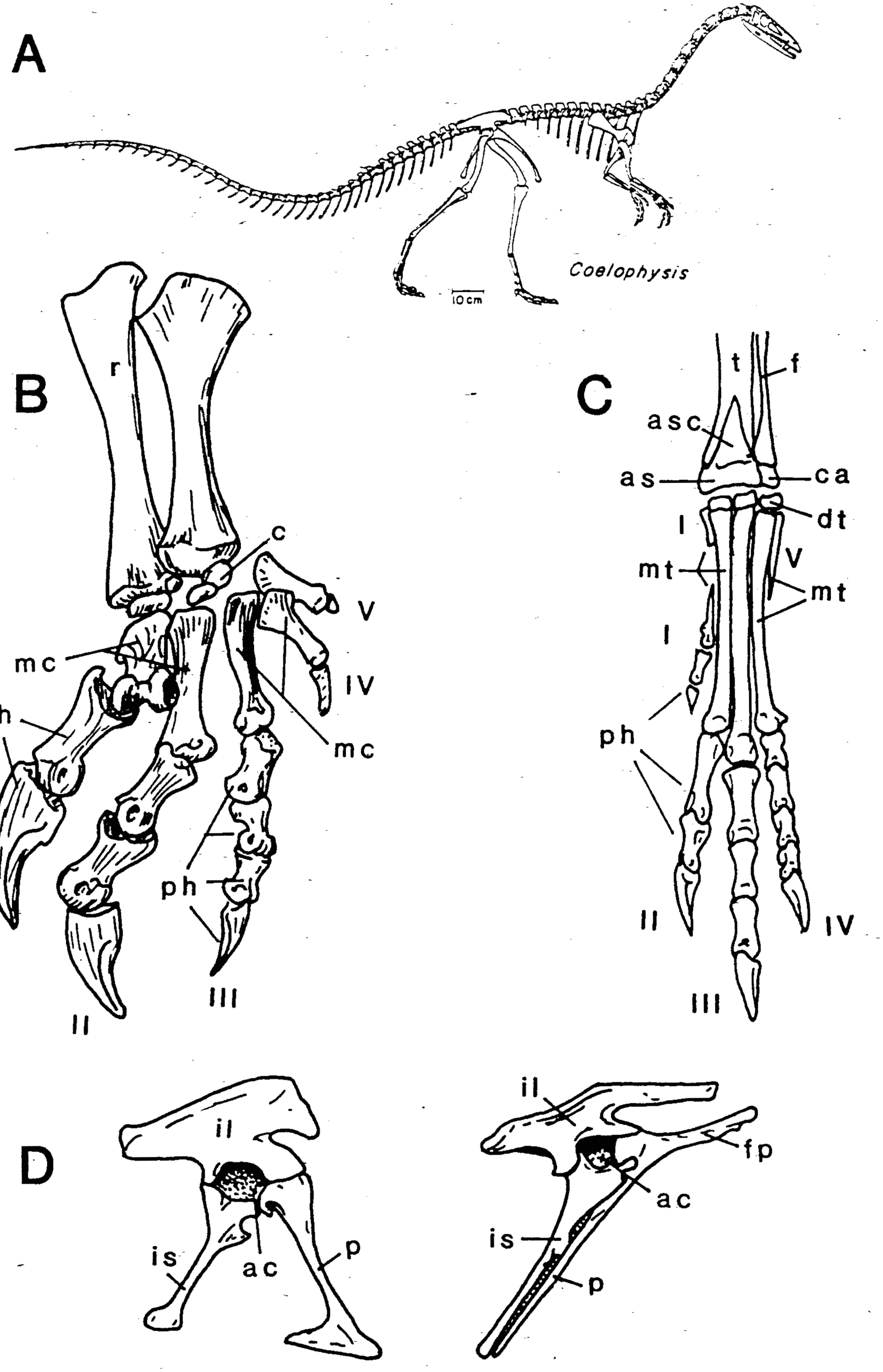
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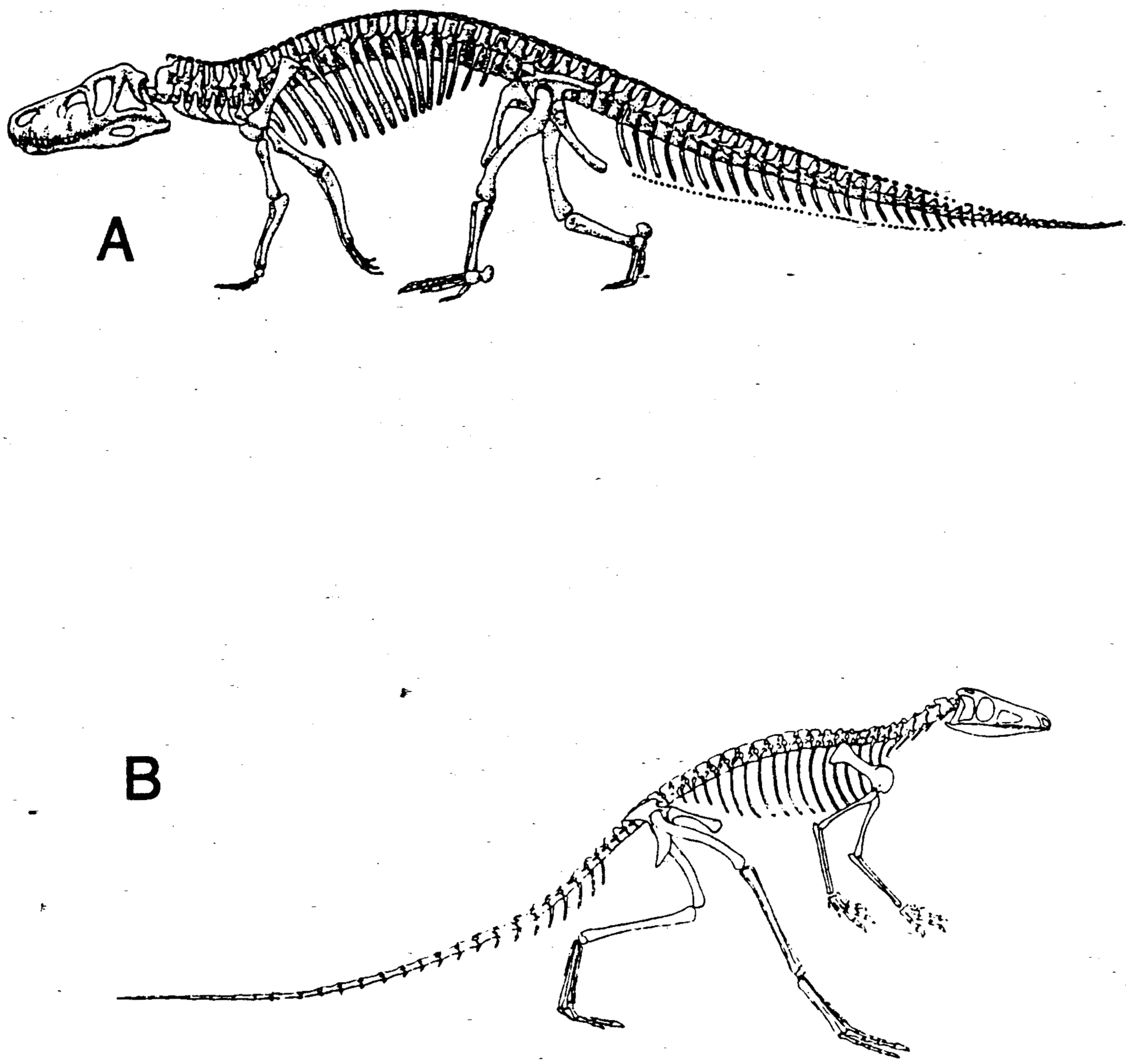
Kevin P.



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PALEONTOLOGY NUMER 2: KNOXVILLLE, TENN .,
THE PALEONTOLOGICAL SOCIETL ,p. 12-133.

The Origin of birds and the Evolution of Flight

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INTRODUCTION

One of the most salient advances in vertebrate paleontology in recent has been the settling of the question of the origin of birds,a problem that has vexed evolutionary biologists since well before Darwin. To be sure, the consensus is not unanimous, and many details of this branch this branch of the phylogenetic tree are yet to be worked out, but we now have a much clearer picture of this problem than we had a decade ago .Less settled, but equally stimulating, has been the controversy over the origin of flight in birs and other flying vertebrates. Was there a gliding stage? Did flight beggin from the ground up or from the trees down? Were birds initially arboreal? What selective pressures drove the ancestors of birds to take advantege of the aerial opportunity?

The overarching interest in such questions, it us that they get at the heart of the study of "macroevolution," in its fullest sense.Macroevolution can mean the origin of " major groups " of taxa , such as the birds. It can also mean the origin the of " major adaptations " as they are assembled, piece , through the phylogenetic sequence.Fortunately, new evidence on these ques tions and new methods of analysis have come to predominate scien tific work of the past decade.They have brought us to the point where the origin of birds, once the most problematic of evolu tionary " missing links." is now probably the best resolved major evolutionary transition known in all of paleontology.

New evidence has come mostly from the discovery of new theropod dinosaurs of the Mesozoica, including many very closely related to the first birds .Among new methods of analysis, certainly the use of phylogenetic analysis (cladistics) has had the biggest impact, for two major reasons. First, it insists on setting out taxa that are diagnosed only by shared derived characters, and linked witht ohther taxa only on the basis of such characters.Second ,it forms a phylogenetic framework against which other questions of the early history of brids and their adaptations must be measured. After all , there is no limit to the nember of hypotheses one can generate about an evolutionary event ,but there is only one true history .Working with the best supported phylogenetic hypothesis constrains to some degree many of the limitless possibilities of adaptive and other historical explanations . It also provides the best opportunity for evolu tionary understandings that are based on a concordance of inde pendent lines of evidence.

The various questions surrounding the origin of birds and flight are reviewed in the volumen of proceedings of the first Interna tional Archaeopteryx conference , held in Einchstatt, West Germa ny , in 1984 (Heecht ,Ostrom, Viohl, and Wellnhofer, 1985). [Copies of this book are still availabe , and at a generous discount,from the the Freunde des JuraMuseum, Willibaldsburg , D-8078 Einchstatt] This book is a very good compendium of recent work on these questions, with extensive and historical reviews; for the sake of economy we will tend to these later papers , to which readers may turn for more background on the questions . Another source of information is a volumen of preceedings of a AAAS symoposium held at the California Academy of Sciences in June, 1984 (Padian 1986e ;copies availeble from the Publications office of the Academy).

In the following pages we provide a review of some of the major advances in the study of the origin of birds and the evolution of flight and some comments onother related questions.

THE ORIGIN OF BIRDS

By the late 1860s, T. H. Huxley had deduced that dinosaurs were the closest relatives of the birds

(Huxley,1868, 1870), on the basis of extensive examination of large living ratite birds and comparison to Mesozoic theropod dinosaurs (review in Desmond, 1975; Gauthier, 1986). He presented his conclusions to the Geolo gicalSociety of London in 1869, providing a list of 35 charcters to upport this relationship. In the audience was H. G. Seelley, an accomplished if maverick paleontologist who had made his reputationthe unlikely combination of South African dicynodont synapsids and British pterosaurs; he would later (1888) sunder Owen's (1841) concept of Dinosauria by proposing the two compo nent orders Ornithischia and Saurischia, based mainly on hip structure.

Seeley, who had a great range of largely self taught knowledge, was known for expressing the odd and heterodox view that was prone to put in fly in the ointment.On this date his reaction to Huxley's lecture was no exception. Seeley 'thought it possible that the peculiarstructure of the hinder limbs of the Dinosauria was due to the functions they performed rather than to any actual affinity with birds. That is to saay, why could not the similar ities be convergences, inasmuch as these dinosaurs and birds both wal on their hind limbs? With these words , Seelley effec tively neutralized Huxley's hypothesis of relationships and his list of 35 charcters, without providing a single character of his own nor any alternative hypothesis of relationship. Today we would take a different tack. We would say that convergence has to be demosntrated by proving an alternative hypothesis that more parsimoniously explains all the available evidence. This has been the primary probllem with all hypotheses of relationships of birds (Gauthier, 1984, 1986; Gauthier and Padian, 1985). It is lless question of evidence than of method.

Regardless of the merits of Huxley's or Seeley's arguments, the fact is tha Huxley's idea was bypassed by history. Perhaps this shoulld not surpriese us. In Victorian Era it was common for anttransmutationists such as Richard Owen to invoke convergence as an explanation of why groups that supposed to be taxonomically distinct had certain morphological similarities: these were seen as necessary to fuction or development. It is indeed difficult to counter this point of view, unless one insists that convergebce be demosmnstrated , not merely asserted. Although we like to think that the transmutationists won the battle over evolution in the 19th Century, in fact Owens's archetypal trascendentalism has had much more influence on biological education. If you find this hard to accept, pick up your child's life science textbook and see wheter its presentation of biology accords more with Darwin's sweeping evolutionary view or with Owen's eessentially sattic , topological comparative approach.

In the following decades, candidates for the closest relatives of birds included pterosaurs, ornithischian dinosaurs, mammals, thecodonstian archosaurs, crocodylomorphs, and theropod dinosaurs (not to mention a variety of less likely candidates). Of these groups, pterosaurs are indeed birdlike in many respects (Padian, 1983, 1985) but their wings are formed of completely different morphological structures, as are those of bats. Ornithischian dinosaurs, like birds, have a pubis that has migrated backwards tlie alonside the ischium, but few other birdlike features that are convergent or shared r shared by most archosaurs. A bird- mammal link has been recently resuscitated by Gardineer (1982), but effectively falsified by Gauthier, Kluge, and Rowe (1988a), among other respondants.

Heilman (1926), in a book of seminal influence on all later workers, reviewed evidence in favor of these various possible relationships, using anatomy, development, integument, stratigra phy, and many othr\\er lines of evidence. He, too, approachead the conclusion that small carnivorous dinosaurs were the most relatives of birds. But he drew back from this conclusion because these Mesozoic theropods apparently lacked clavicles, the bones that represent the furcula (wishbone) of birds. Heilmann reasoned from a rather literal interpretation of Dollo's law that struc tures once lost in evolution could not be regained, and so he rejected the theropod ancestry of birds. Instead, he argued, the origins of birds must be from a more distant archosaurian rela tive, and he pointed to the thecodontians as the most likely source of candidates. This is really a failsafe argument: while rejecting all specific candidates for ancestry, one can throw an evolutionary origin farther back into the obscured lower branches of the phylogenetic tree. And like the argument from the asserted convergence, Heilmann's won favor with biologists. Until nearly the present day it has been the standard textbook story.

Since the early 1970s, three diferent taxa have been advanced as the principal candidates as the closest relatives of, and ulti mately the phylogenetic source of, Archaeopteryx and the rest of the birds. These are (1) crocodylomorphs; (2) thecodontians; and (3) ttheropod dinosaurs.

The crocodylomorph hypothesis.-- The principal exponent of this view has been Dr. Alick Walker, who based his reasoning on a series of extremely careful and detailed studies of the skull (especially the braincase and ear region) of an early crocodyllo morph from the Triassic-Jurassic boundary sediments of South Africa, Sphenosuchus. There is no doubt that the early crocody lomorphs were much more gracile and lightl built than their extant counterparts, and they show a number of adaptations for an active life-style reminiscent of similar features in brids and dinosaura (see discussion of early crocodylomorphs in Chapters 2 and 14). Unfortunately , until very recently there was very litttle available skull material of small carnivorous dinosaurs that could also be compared to the skulls of Archaeopteryx (which is not rich un such details) and extant birds. So a full comparison comparison could not be made.

Walker mas followed in his view by L.D. Martin and K.Whetstsone(see e.g.,Whetstone and Martin 1979, 1981) who argued on the basis of characters in the teeth, tarsus, and braincase that brids and crocodiles shared a very clase common acees-tor to the exclusion of other groups. However, no specific taxon for closest relationship was proposed, and the majority of hypothe sized synapomorphies were eventually shown to be convergences or more generally distributed than these authors suggested (Gauthi er, 1986: 3-4).In 1985, Walker criticized Whetstone's (1983) interpretation of the braincase of Archaeopteryx, and in the light of new evidence rejected his previous view of a close crocodile--bird relationship in favor of the theropod hypothesis(Walker,1985;Gauthier, 1986).

The thecodontian hypothesis. Following Heilmann's reasoning , the principal advocates of this view in recent yaers have been S.F.Tarsitano ans M.K. Hecht (e.g.,1980).Again,without pointing to any specific thecodontian, they have made the case that the birdlike characters of all known Mesozoico theropods are too specialized or too late in time to qualife these dinosaurs as the srem group from which birds evolved.And indeed there are several small, lightly, agile-look ing Triassic archosaurs from which one could derive birds by further transmutation of the skeleton.(However , we would agree with P.E Olsem [pers.comm.] that one would really hove to go through a theropod to do so.) The probllem is that every state ment of the" thecodontian" hypothesis has had to rely on an "unknown thecodont"(Tarsitano and Hecht,1980). Certainly , com plete knowledge of all fossil forms will never be available ,and we must be mindful of the incompleteness of our knowledge.On the other hand,an appeal to that ignorance as the incompleteness of our knowledge.On the hand , an appel to that ignorance as the basis of a phylogenetic or anti-phyogenetic statement appear to restrict severely any attempt to reconstruct evolutionary histo ry.An additional difficulty for the "thecodontian " hypothesis is the concept of "thecodontians" itself has come under heavy criticism in recent years .As Gauthier and Padian (1895) stressed,"Thecodontia has been a convenient term for archosaurs that are not crocodiles, pterosaurs, dinosaurs, or birbs, but its use has obscured relationships more than clarified them.In phylogegetic analysis, this admittedly paraphyletic grouping is useless."Instead, Gauthier (1980; summarized in Gauthier and Padian , 1985)used morphological synapomorphies to show that the supposedly "basal archosaurs"usually called thecodontians could be neatly divided into those that were closer to crocodiles(Pseudosuchia; Crocodylotarsi of Benton and Clark , 1988), closer to birds (Ornithosuchia; Ornithotarsi of Bentopn and Clark, 1988),closer to birds common ancestry of brids and crocodiles (Archosauria sensu stricto).

The "thecodontian " hypotesis thus becomes problematic.With the dissolution of this assemblage, it is no longer possible to pick and choose birdlike characters from among a range ao taxonomical ly separated,primitive archosaurs . The "Thecodontia ", a group of " Flying Dutchmen " of uncertain phylogenetic relationships that do not belong to any well-defined monophyletic taxon , is not a natural taxon , and its use should de abandoned (Gauathier and Padian, 1985; Padian, 1989b;see Chapeter 2) .Without any specific hypottesis of relationship, the "thecodontian" hypotesis appears to have no material basis, and reduces to a denial of other hypotheses.

The theropod hypothesis.-Huxley's original idea was based on a far smaller range of dino saurian material than is avaible to us today , and he drew his phylogenetic inferences from the whole spectrum of dinosaurs known to him then. In the early 1970s, the small Early Cretaceous ceolurosaur Deinonychus and its relative provided J.H.Ostrom with a more specific insight onot the origin of brids .In a series of papers,Ostrom(1969, 1973,1975a,b,1976) used detailled osteological comparisons to show unique feature shared only by coelurosaurs and brids, and to demonstrate possible morphological transitions that occurred between these basaj coelurosaurs and Archaeopteryx and the brid .Gauthier (1984, 1986 ; reviewed in Gauthier and Padian, 1985; see also Rowe , this volume) used cladistic analysis to arrange Ostrom's hypothesized synapomor phies and dozens of others in a fuller sequence that placed brids squarely within the coelurosaurian, theropod, saurischian dino saurs.

The conclusion reached by these studies is birds are dinosaurs , not just descended from them, by the principles of group member ship that are required by the monophyly criterion of phylogenetic systematics.This realization is an especially effective one to bring to students , who delight that they eat dinosaur at Thankasgiving, have dinosaur in their backyards, and occasionally go out for dinosaur McNuggets .Thedinosaurs are not extinct; living dinosaurs are restricted to a fragment of their former morphological diversity, but their extant representatives coprise thousands of living species.Furthermore, following the same principles of group membership discussed above , and reviewing the basic dichotomy of amniotes into Synapsids (mammals et al.) and Reptiles (see Chapter 2), birds belong to the Reptilia . The living species of birds and other reptiles, in fact ,outnumber mammals.So, despite allegations that the Cenozoic is the Age of species diversity the reptiles still have the edge.

Who are the coelurosaurs?-- As Gauthier (1986) has redefined them, Coelosau ria includes A ves as well as all other tetanurine theropods that are more closely related to living birds than they are to carno saurs (Tetanurae = Carnosauria + Coelosauria). As used here, Coelosauria is a monophyletic taxon, including birds. Coelosaurs have not always been treated in this way, for that name has traditionally been aplied to all small theropods aside from birds (e.g., Ostrom, 1969). Recent analyses have demonstrated the inadequacy of dividing theropods on the basis of size alone. For example, it is now clear that the huge carnosaurs are more close ly related to birds than are several of the small theropods formerlu referred to Coelosauria (Gauthier, 1984, 1986). More over, the usually small coelosaurs contain both large forms, such as Dromornis (a ratite estimated to weigh some 500 kg) and Dein ocheirus (a giant ornithomimid known only from its eight foot long arms), as well as small forms, such as the pigeon-sized Archaeopteryx and the diminutive hummingbirds.

Gaps in the fossil record complicate our understanding of the initial radiation of Coelosauria. The oldest coelosaurs currently known are from the Late Jurassic. Some of the species, such as Ornithlestes hermanni and Elaphosaurus bambergi, are known from single, partial skeletons, and others, such as Coelurus fragilis, have been reported only from incomplete skeletons. Ironically, the most completely known early coelosaur is Archaeopteryx litho graphica, and it is already a bird. That is unfortunate because it implies that coelosaurs that are even less closely related to living birds must have diverged still earlier in the Jurassic. Terrestrial sediments of mid-Jurassic age are very rare, and as a consequence we have yet to discover a truly archaic coelosaur. The situation is further complicated because many groups of coelosaurs that diverged before the origin of birds, such as ornithomimids, caenagnathids, dromaeosaurids, and troodontis, are best known from their highly modified Late Cretaceous representa tives, which may be removed from the ancestral coelosaur by as much as 70 milion years (see Currie, this volume).

Despite these complications, it is relatively easy to distinguish coelosaurs from other theropod dinosaurs (Gauthier, 1986). For example, the quadrate bone, which suspends the jaw on the skull, is set close to the braincase in birds, with an inner attachment to the prootic bone and an outer articulation with the opisthotic (braincase). The head of the quadrate in other coelosaurs is not so modified, but it is intermediate in form in that the quadrate attaches near the base of the opisthotic, rather than near the outer edge of that element as in other theropods. But the most obvious of the diagnostic characters of Coelosauria are several modifications in the neck, forelimbs, and hindlimbs that are normally thought of as peculiarly avian. In contrast to other theropods, coelosaurs have very long arms and hands, and their long neck bones join another in a distinctively avian fashion, with flexed zygapophyses and incipiently heterocoelus centra. Their hindlimbs are equally diagnostic in having an enlarged ascending process of the ankle that firmly binds it to the shank, and in having compressed the metatarsal bones connecting the toes to the ankle (see Rowe, this volume).

The Manuraptoran Coelosaurs.-- Manuraptora (Gauthier, 1986) is a subgroup of coelosaurs that is even more markedly birdlike. It includes such well-known coelosaurian groups as Caenagnathenidae, Dromaeosauridae, Troodontidae, and , of course birds (Norman, 1985; Currie this volume). Manuraptorans can be distinguished from such coelosaurs as ornithomimids by several evolutionary novelties, the most noteworthy of which involve the forelimbs and hsoulder girdles. It is clear that the earliest manuraptorans were unable to fly, yet they had most of the modifications that are essential to flight in living birds (Ostrom, 1969).

The hand in living manuraptorans (bird) is reduced and nearly fingerless, with the remaining elements largely fused to one another .But the elements of the hands of early manuraptorans, including early brids,are virually indentical, down to the pro portions of the individual bones comprising esch of three (Ostrom , 1976). The preyseizing hands that arose in the ancestral theropod bacame finely tuned, raptorial organs un manuraptorans .These huge, grasping handes have long , slender fingers;the shorter thumb converges slightly on the linger outer fingers during grasping, and the third fringer has a sllender and bowed at its base whose joint surfaces may have enabled that finger to oppose the others as well(Russell and Seguin,1982).The fingertips aresupplied with very large , sharply pointed,tren chantly margined, deeply trenchantly margined, deeply recurved claws reminiscent of on the prehensile feet of hawks and owls. The wrist is formed by a halfmoon-shaped bone that enables the hand to move in a broad arc upon the forelimb(Ostrom,1969,1976; Gauthier and Padian ,1985).The forelimbs in manuraptorans are very log ,and they are operated by comparatively powerful muscles arising from a prominent breastbone.The clavicles are fused, forming the "wishbone"so characteristic of birds, in order to brecxe the shoulder against the froces imposed by struggling prey (Barsbold, 1983). And the lower part of the shoulder girdle is girdle is modified in such a was as to indicate that a chest muscle that formerly swung the arm down is now beginning to lift it up, thus is now beginning to lift it up, thus providing great er power on the recovery stroke when seizing prey. Such muscle scars as remain on the forelimbs and girdles suggest that the arms coul be folded against the body at rest in much the same manner seen in living birds (Ostrom,1974). Moreover , the entire forelimb and shoulder apparatus operated as in living birds: the arms swung downand forward , then up and back , thus describing the classic figure-eight motion that characterizes the flight stroke in brids and all other animals that fly, whether through the air or in the weter (Gauthier and Padian,1985; Padian 1985; Rayner, 1988).The manuraptoran foot, with its hyperextendable and sickle-clawed second toe , is equally diagnostic (Ostrom, 1969). Living cariamid birds have similarly modified feet, with sickle claws that are used for defense as well as for killling prey. More or less prominently developed raptorial second toes are present in Archaeopteryx, Ornitholestes, dromaeosaurids, and troodontids, and perhaps in caeanagnathids. Ornithurine birds (all those post-Archaeopteryx birds with reduced tails) generally lack such a specialized toe, so its presence in some llater birds is probably secondary. Manuraptoran feet are often portrayed as didactyl, with the raptorial claw held aloft so as not to blunt its tip during locomotion. However, Cariama walks on all its toes and the tip of its deeply arched sickle claw touches the ground, so it seems reasonable to assume the earlier manuraptorans did likewise.

In manuraptorans, the tail is shorter than in other theropods, and it is stiffened by aa combination of modified invertebral articulations and (in forms such as Deinonychus) a network of stiffened zygapophyseall extensions similar to the ossified tendons of ornithischians (see papers by Norman and Sereno, this volume). Ostrom (1969) suggested that this tail acted as a dynam ic stabilizer for the animal when slashing at prey with its feet; in running, it would also provide greater maneuverability, and this function seems to have been retained in birds (in which the function became more aerial than terrestrial).

Although the origin of birds from among coelurosaurs has become a fairly settled issue in the systematic community, there is stil much to be known about the specific relationships of the early manuraptoran groups, and which of these is the closest to birds. One problem has been that not all skeletal partsof all manurapto ran forms are known, so detailed comparisons are difficult. As new forms constantly turn up (see Currie this volume), the weight of evidence shifts. Part of the reason is that the group is subject to extensive convergences (e.g., the auditory recess in ornithurines and troodontids, the reversed pubes in Avialae and Dromaeosauridae, the bulbous parasphenoid in Troodontidae and Ornithomimidae, the large sickle -claws in Dromaeosauridae and Troodontidae, and the extensive pneumatization of the skull in troodontids, caenagnathids, and Ornithurae). Moreover, there are problematic age-related characters (such as ossified uncinates and ventral ribs, the calcified sternum, fused metatarsal bones) that make it difficult to tell whether the features shown by an individual specimen are characteristic of its taxonomic group or its ontogenetic stage. For the present, it is perhaps best to take Currie's conservative, open-minded view of the interrela tionships of these theropods (this volume), because the state of our knowledge is rapidly changing with new evidence and new analyses.

THE EARLY EVOLUTION OF BIRDS

Definition of birds.-- Birds have feathers and no other organisms do. This unistes birds as a group .On the basis of feathers, Archeopteryx is usually classifies as a bird.Over the years there has been dispute about whether it could fly or not, but it was clearly doing something aerial with its has no feotures that debar it was clearly doing something aerial with its feathers, and it has no features that debet it from ancestry or very close relationship to later-birds.Of course, it is possible that we might find other,non-flying coelurosaurs with feathers, which may have evolved initially for functions other than flight(see papers in Hecht et al.,1985) This raises the question of how to define birds.Let us say that we found a deinonychosaur , very close toArchaepteryx,with cotour or downy feathers, but no flight feathers, but couldn't fty , and presumbabaly nome of its ances tors could .How would we classify this animal?.Guathier (1984,1986)suggested that the term A ves be restricted to the living groups of birds and all the descendants of their common ancestro .This suggestion would provide stability to the defini tion of A ves, regardless of any future fossil discoveries that would fill in the evolutionary gaps and muddy the clean break between birds and ather reptiles . However, recognizing that Archaepteryx represents a decicive step toward living birds ,and has several crucial avian features such as fligght feathers, Gauthier proposed the taxon Aviales to include it and all more derive birds .In consequence,Archaeopteryx(and other primitive birds like Hesperornis an Ichthyornis) is a "bird ". But not a member of no Aves .This provides both recognition and stability to the taxon.

Archaeopteryx.-- The six known specimens of Archaeopterix litho graphica (Welllnhofer, 1974, 1988a, b; Ostrom, 1975a, b, 1976) represent the oldest winged, or avialan coelosaurs. They are still the earliest known bird specimens. Molnar (1985) has ably reviewed other early birds or would-be birds; for further comment see Jensen and Padian (1989) and Padian (1988b), and other papers in Hecht et al. (1985).

For over a century Archaeopteryx has been seen as the "missing link" between reptiles and birds, though until recently it was far from clear which reptiles were being linked. The appereance of Archaeopteryx in the fossil record has been essentially equat ed with the origins of birds and of flight. However, given the advances of recent years, it is now apparent that Archaeopteryx has far more obvious link with other Mesozoic, non-flying thero pods than it does with the living groups of birds. This statement may seem ironic, but it turns out that nearly every characteris tic of Archaeopteryx is shared by non-flying Mesozoic theropods, and very feew link it to later birds. It is perhaps for this reason that the Eichstatt specimen of Archaeopteryx, which has only the faintest of feather impressions, was initially classified as a juvenile specimen of Compsognathus. Only when Ostrom (1972a) recognized the feather impressions on the Teyler specimen, a discovery that changed its taxonomic assignement instantly from Pterodactylus to Archaeopteryx, did curators in museums all over the world with holdings from the Solnhofen limestones re-examine their collections assiduosly -- with the result of the announcement of the "new" Eichstatt speecimen., so beautifully described by Wellnhofer (1974).

The cited papers by Ostrom, Wellnhofer, Gauthier and Padian have laid out in detail the evidence that Archeopteryx retains characters that mostly have a distribution among theropod dinosaurs that indicates a much more ancient origin -- for examples, the fused clavicles, the tridactyl hand reduced first finger and bowed third, the halfmoon-shaped carpal, the calcified breastbones, the long arms and legs, the backwards-pointing pubis, the shortened, stiffened tail, and the reversed hallux on the tridactyl foot. Most of these characters have been explained by evolutionists as adaptations for flight or arboreal life. These modifications may facilitate flight, but it is now clear that their persistence in non-flying theropods requires a more general explanation than the particular role(s) that they currently play in avian biology (Padian, 1985; Gauthier and Padian, 1985; Gauthier, 1986). Most of these characters have been introduced previously, and further explanations of their roles in avian evolution can be gleaned easily from the references just cited and from the papers in Hecht et al. (1985).

Birds after Archaeopteryx.-- In addition to the being the earliest known bird, Archaeopteryx is the one known from the most complete material until one gets to Hesperornis and its flightless, dividing relatives from the Late Cretaceous (Marsh, 1880). In the Late Jurassic and Early Cretaceous there are many fragmentary bird bones, as well as impressions of feathers, on which taxa have been based. Molnar (1985) has thoroughly reviewed most of these taxa and some other would-be middle Mesozoic birds. To his reviewed we append only a few updated comments. Marsh's Laopteryx is probably a pterodactiloid (Ostrom, 1986). Palaeopteryx (Jensen, 1981) is a nomen nudum (Jensen and Padian, 1989), and most of the "Dry Mesa" (Uncompahgre) material originally considered avian or avian-like is pterodactyloid, with a few probable manuraptoran pieces. Cosesosaurus is an aquatic archosauromorph (see discussion in Evans, 1988) and has nothing to do with birds.

Olson (1985) has reviewed many occurrences of Cretaceous birds, particularly those supposed to represent extant families, and has rejected every case. Cretaceous birds, it seems, had specializations that converged on many of toes seen in living birds (for example, the loon-like diver Hesperornis and the ternlike Ichtiornis), but in Olson's view the supposed phylogenetic affinities to living bird families are wishful thinking. Particularly important early bird discoveries of the past decade include C.A.Walker's (1981) report o the very unusual Enantiornithes from the Cretaceous of South America, and the report by Sanz et al. (1988) of Early Cretaceous ornithurine birds and feathers from Spain. The latter bird has strong coracoids braced to the sternum, a wishbone with a hypocleidium, a long, fused foot, an expanded pelvis, and a reduced tail with pygostyle.

The presence of a palaeognath bird, Gobipteryx, in the Late Cretaceous sediments of Mongolia (Elzanowski, 1981) indicates that the primary avian clades, Palaeognathae and Neoggnathae, had already diverged from their last common ancestor by the close of the Mesozoic Era (Cracraft, 1986). It follows further that the full suite of evolutionary novelties underlaying the level of flight performance fundamental to extant birds was already in place more than 75 million years ago. Even at that early date, the ancestor of Aves could be distinguished from the ancestor of Archosauria by at least 213 synapomorphic modifications in the skeleton alone (Gauthier, 1986). systematists looking to link birds with other groups, matters were only made worse by the extinction of the few remaining nonavian archosaur group till extant at the end of the Cretaceous. The disppearance of intermadiate forms, groups still extant at the end of the Cretaceous.

The disappearance of intermediante froms, together with an astronishing diversification of birds and the nesuing Cenozoic Era, has further accentuated the differences between birds and their nearets living relatives, the crocodiles. We still have large gaps in the early history of birds, eespecially in the Jurassic and Cretaceous, and because of problems with presevation, we may never have a very complete record of some episodes in early avian history. Using what we have, however, the fossil record is surprisingly good for answering some central questions about the origins of birds and flight.

Before moving to a consideration of flight, the recent announcement of a Triassic bird, to be named "Protavis " by its discoverer, Dr. Sankar Chatterjee, deserves mention. To date this discovery is not only an announcement, and no scientific report on it has appeared. we will not consider here the various claims and counterclaims made about it in the press to date. It is worrth noting that occasionally a Triassic or other pre-Jurassic fossil emerges and is reported to knock Archaeopteryx off its perch, and " Protoavis" is the most recente candidate. But the "Protoavis" question, so far reduce to one major issue. We alrededy have a well already have a well documented phylogeny of theropod evolution.

Presumably if it is correctly interpreted, "Protoavis" will fit somewhere on this evolutionary tree. But it does not promise, on basis of claims made so far, to alter this tree in any major way. If the claims are correct, then bids would simply have a more ancient geologic recod than usually thought. Skeptics and supporters alike now need to wait a published report before further comment; already the cretionist press has seized upon Dr. Chatterjee's preliminary claims to mock the competence of paleontologists and their inferences about the fossil record.

Final question is Archaepteryx a forgery, as Hoyle and Wickramasinhe (Hoyle et. al. 1985) have claimed ? Obviosuly not, as Rietschel (1985) and Charigg et al. (1986) have shown; these claims, of course, is to replece convertional evolutionary theory. The motivation for these claims, of course, is to replace conventional evolutionary theory, which Hoyle and Wickramasinghe reject, with their own notion of "germens from space" periodically bringing new viral material to infect the DNA of Earth's organisms, thus causing bursts of evolution. But then, these workers have also testified that insects are smarter than we are they're just not letting on.

CAPITULO 9 ACTUALIZACION BIOTICA: LA DOMINANCIA DE LOSMAMIFEROS.

9.1 PREAMBULO

Este capítulo se dedica al grupo que durante todo el Cenozoico, y desde luego, en la actualidad, ha dominado el ambiente terrestre, diversificándose ampliamente y explotándolo con una amplitud y diversidad que no tienen paralelo en toda la historia de la Tierra. Se decidió no incluir información sobre productores, esto es sobre plantas, ya que las angiospermas que han dominado la escena desde el Cretácico fueron ya consideradas.

En el primer trabajo, Farish Enkins sumariza la información sobre el origen del grupo, a partir de terápsidos muy avanzados, discutiendo las modificaciones craneales y postcranales, así como algunas de las anatomía blanda, que son discernibles en el registro fósil en esta fase de transición , y les da una interpretación morfológico-funcional, básicamente mediante un avance gradual, pero contínuo en el control de la homotermia como clave de sobrevivencia en un ambiente arbóero confinado. Discute también el surgimiento de linajes independientes de mamíferos, y su radiación adaptativa temprana, conducente al surgimiento de numerosas líneas paralelas. Cabe destacar que durante dos terceras pates de la duración geológica del grupo desde el Tríasico Temprano al Reciente los mamíferos constituyeron un grupo subordinado, "marginado" por los dinosaurios en el Mesozoico, y es al exttingirse estos, que los mamíferos rápidamente adquieren esa dominancia ecológica, que tienen al presente.

En el segundo trabajo Dave Krause describe la evolución mamiferiana durante el Paleoceno, primera de las épocas o subdivisiones formales del Cenozoico, y que testifica la radiación adaptativa de los "nuevos amos" del dominio terrestre, que les permitió ocupar ampliamente el ecoespacio dejado por los dinosaurios. Esta radiación produjo una mastofauna arcáica, esto es, constituida por organismos diferenciados desde el Cretácico y que acusaron cambios mínimos en el Paleoceno, o bien, organismos que aparecen en esta época, pero cuyo linajes se extingen en el Terciario Temprano. La diversidad alcanzada por esta fauna es considerable, e incluye formas herbívoras, carnívoras, insectívoras y otras; modalidaes de locomoción también variados, cursores, corredores, fosoriales, etc. hábitos terrestres, arbóreos; y tamaños desde unos pocos gramos, hasta tal vez 152kg. Todo ello evidencia la rápida ocupación de nichos ecológicos asombrosamente variados, que desarrollaron estos mamíferos, ocurrida en un lapso geológico breve, tal vez de 5 Ma.

En el tercer trabajo, Dave relata algunos aspectos de la historia evolutiva de los mamíferos modernos , usando como apoyo o tema central, lo que él designa como la "sabanización " de los continentes, es decir el surgimiento y extensión del bioma de sabanas 791 (praderas, pampa, estampa, son designaciones de variedades de este bioma), resultado de la tendencia general Cenozoica hacia condiciones de sequedad y enfriamiento creciente. Este fenónomeno tuvo repercusiones muy profundas en la evolución delos mamíferos, ya que diversos grupos desarrollaron adaptaciones que les permitían "prosperar" en estas condiciones y aprovechar a la vegetación dominada por gramíneas o a los consumidores primarios, como alimento principal, tal es el caso de los caballos , los elefantes y los roedores cricétidos. Webb también discute aspectos biogeográficos de estos mamíferos, relacionados con procesos de intercambio faunístico; así como patrones de reemplazamiento faunístico.

En el último trabajo, Catherine Badgley sumariza la información paleontológica disponible sobre la ancestría de nuestra propia especie, enfatizando los aspectos filogenéticos, así como el escenario geográfico ambiental en que ocurrió el surgimiento del hombre, es decir el marco paleoecológico de la evolución humana.

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9.3

ORIGINS

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9.3 (a)

A Survey of Mammalian Origins.

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INTRODUCTION

The origin of mammals, often treated as a discrete but obscure event that took place sometime between the Late Triassic and Early Jurassic, can also be viewed as the product of many transitions-from the early synapsid radiations during the Pennsylvanian and Early Permian through the emergence of placentals and marsupials in the Cretaceus (see Hopson, 1969). A fundamental dichotomy appeared early in the evolution of amniotes; sauropsids (represented today by living reptiles and birds)constituted one lienage, synapsids (which includes the mammalian descendants) the other. Thus, mammalian ancestry may be traced to pelycosaurs that fisrt appear in the fossil record as part of the earliest known reptilian fauna (Carroll, 1982). And mammalian bony and dental structures continued to undergo substantial modification throughout the Mesozoic, long after the appearance of forms technically classified as Mammalia. Given these phylogenetic changes, the suggestion that there ocurred a point when mammals "originated" seems simplistic. Yet the major evolutionary stages may still be evaluated whith the purpuse of identifying the inception of features and functions basic the radiation of modern mammals. Accordingly, this survey summarizes our current understanding of the evolution of mammals whit full acknowledgment that an account of mammalian origins has neither a definitive beginning nor a climactic end.

SYNAPSID EVOLUTION: GENERAL TRENDS.

Several features of the skull of a representative primitive synapsid (the pelycosaur Dimetrodontl; Figure 1A) represent the beginning of two trends in mammmalian development: the evolution of the masticatory complex and the middle ear (see Hopson and Barghusen, in press). Typical features of these primitive mammalian predecessors are an expanded maxilla (mx, Figure 1), enlarged caniniform teeth (presaging the dental differentiation of therapsids, and a single temporal fenestra (tf, Figure 1) related to the jaw adductor muscles. Although not all synapsids appear to have been carnivorous, it is clear that a predaceous habit and specialization of the jaws, teeth and associated muscles represented adaptations fundamental to the bennings of mammalian history. Mammal-like reptiles, especially, elaborated an array of tooth forms and skull shapes virtually unequalled by any tetrapod group save mammals (Figure 2). The two most obvious aspects of the trend are the increased size of the dentary (dn, Figure 1) in the lower jaw, and the expansion of the temporal fenestra to accommodate an enlarged mass of jaw adenctors (tf,Figure 1B-D). In synapsids, the postdentary bones established early a distinctive configuration (including a flage, or reflected lamina, of the angular, and a ventrally oriented retroacticular process of the articular) that was to undergo progressive modification in relation to the development of the mammalian middle ear (see MIDDLE EAR, below).Figure 1 Stages in the evolution of the mammalian skull. A, The pelycosaur Dimetrodon limbatus 1, after Romer and Price, 1940, plates 6 and 15. B, The gorgonopsid Lycaenops ornatur 1, modifed after Colbert, 1948, Figure 1.C, The cynodont Thrinaxodon liorhinus 1, modified after Hopson, 1969, Figure 8. D. the mammal sinoconodon changchiawaensis1, from Crompton and Sun, in press.

ADVANCED MAMMAL-LIKE REPTILES: CYNODONTS.

The latest radiation of mammal-like reptiles, beginning in the Late Permian, gave rise to the cynodonts which, considered together, represent transitional stages in the establishment of definitive mammaalian features (Figure 3). Among these the procynosuchids are the most primitive. Procynosuchus 1 exhibits numerous characters, many of which are related to the masticatory apparatus, that were further elaborated among later cynodonts (Kemp, 1979; Hopson and Barghusen, 1968); the zygomatic arches are bowed laterally and the coronoid is centered in the temporal fosas (rather than close to a Zygomatic arch); and the pstcanine teeth have anterior and posterior accessory cusps, as well as cuspules along the lingual (internal) margin of the crown.

In various cynodont families (e.g., Thrinaxodontidae, Probainognathidae and Chiniquodontidae) are found further refinements of cranial features that established the basic plan inherited by the earliest mammals (Hopson and Barghusen, in press). Differentiation of the teeth into incisors, canines, and post canine (molariform) teeth in clearly evident. The number of upper and lower incisor teth are lost. The estructure of the postcanine molariforms, in which there were three or four cusps aligned anteroposterioly and a central primary cusp (Figure 6A), established the primitive pattern for mammals. However, in most cynodonts (excluding the so -called gomphodonts in the families Diademodontidae and Traversodontidae, and the Tritylodontidae) the reptilian mode of tooth replacement persisted (postcanine teeth were replaced continuously throughout life in an alternathing sequence) and the roots were single (not multiple, as in mammals). Modifications of the skull and jaw related to mastication are apparent in several lineages: the braincase consolidated as an enclosed structure with the epipterygoid suturally joinin the prootic, and thus provided for an extensive origin of the temporalis muscle (Hopson, 1969). A secondary palate completely separated the oral and nasal cavities. This structure has been interpreted as evidence that cynodonsts undertooks some oral processing of food, although the original function of the secondary palate may have been as a structural cross-brace (A. W Crompton, personal communication) It is worth nothing in this context that among carnivorous cynodonts (those with trir -or quadricuspid postcanine teeth of the pattern typical of mammals occlusion (tooth - to- tooth contact did not develop, it is therefore unlikely that "mastication" of the mammalian type was present. Occlusion did develop, however, in certain herbivorous cynodonts, such as the traversodontids and tritylodontids, clearly indicating that oral processing of food was important in some forms.

In their postcranial skeleton (Figure 4) cynodonts exhibited a number of features intermediate between "reptilian" and mammalian grades of organizacion , and in this sense were truly transitional forms (Jenkins, 1971: Kemp, 1980). The cynodont atlas-axis complex retained a reptilian arrangement of its contitute ossicles, but in the paring of the occipital condyles, the differentiation of a dens (a neomorphic, anterior outgrowth of the atlas body) and the reduction of the prezygapophyses of the axis, showed incipient specializations to permit atlanto-occipital flexion and extension as well as atlanto- axial rotation (Jenkins, 1969).The unique specializations of mammals at these two joints for mobility of the head were already underway among cynodonts. Similarly, the remainder of the vertebral column extnbited certain- modifications toward a mammalian level of organization but without attaining the distinctive feactures that uniquely characterize mammals. Both cervical and lumbar ribs were retained; only a subtle gradational change ocurred between the toracic and lumbar series in the shapes of neural spines and articular processes. It is unilikely that cynodonts flexed and extended the vertebral column in a sagittal plane as do mammals; the principal movements were probably lateral undulation, as in reptiles, facilitated in some forms by an enlarged iliocostalis system of muscles inserting on imbricating costal plates.

The shoulder girdle of cynodonts was comprised of a trough-shaped scapula, and anterior and posterior coracoids; a robust clavicle articuled with the anterior margin of the scapula (the homologue of the scapular spine/ acromion of mammals). This primitive arrangement was inherited virtually unchanged by the early mammals and persists today among monotremes in an only slightly modified form. Propulsive movement of the humerus appear to have involved a significant amount of elevation long axis rotation, a primitive characteristic, was retained. The cynodont hyndlimb and pelvic girdle also showed a mosaic of feactures that represented an intermediate stage in the development of a mammalian pattern. Among these were an ilium with a substantially elongated and broadened anterior portion (figure 4), s socket- like acetabulum and a bulbous, inflected femoral head. The femur, held at angles of about 55 grads to a sagital plane, was posturally intermediate between the more sagittal orientation of early mammals. Cynodonts possessed a well- developed calcareal tuberosity for insertion of the triceps suare, indicating that at this stage the major pedal plantarflexors acted directly on the calcareus. Cynodonts likewise exhibit the beginning of the mammalian condition in wich the astragalus is superimposed on the calcaneus. In mammals the astragalus has no "plantar contact" but lies entirely between the tibia above and the calcaneus below. In cynodonts this condition is incipient, for the astragalus still has a partial plantar contact along its medial half; the lateral half of the astragalus was suported by the calcaneus through a rudimentary sustentaculum tali.Figura 4. Reconstruction of the cynodont Thrinaxodon liorhinus1.Figura 5. Reconstruction of a Liassic morganucodontid. From Jenkins and Parrington, 1976, Figura 18.

THE EARLIEST KNOW MAMMALS.

Given the nature of the reptile-mammal transition, it is not surprising that there have been varied opinions on defining the Class Mammalia (for a review, see Crompton and Jenkins, 1973). The most widley accepted criterion is the presence of dentary condyle on the jaw articulating with a glenoid in the squamosal, although many other features may be cited (Cromton and Sun, in press).

Fossil remains of the earliets known mammals are now known from a number of localities throughout the world (Clemens et al., 1979). Of particular imortance are the fissure deposits in Wales and southwest England, and the bone beds of continental Europe (Germany, Switzerland). More recently, a fauna of early mammals has been discovered in north-eastern France (Sigogneau-Rusell, 1976,1983). In Africa, isolated but important mammalian specimens have been recovered from the Stomberg Group in Lesotho (Crompton 1974). From the Lufeng beds of the Yinnan Province of china are known a number of important specimens that are (Sigogneau-Rusell and Sun, 1981; Crompton and Sun, in press; Zhang, 1984). IN North America, an early mammal fauna has been discovered in the Kayenta Formation of northeastern Arizona (Jenkins et al ., 1983). Following the biostratigraphic analyses of Olsen and Galton (1977) and Clemns (1980), the preponderance of evidence favors an Early Jurassic (Liassic) age assignment for these faunas, reather than Late Triassic (Rhaetian) or "Rhaeto-Liassic" as was equivocally stipulated in earlier papers.

Nearly all the earliest Known mammals were an order of magnitude smaller than any of the Middle Triassic cynodonts. In Head- body length, they perhaps reached ten centimeters and a body weight estimated between 20 to 30 gr. Only Sinocodon 1 appears to have been larger; its skull length is about 5 cm, compared to 3 cm in morganucodontids (Crompton and Sun, in press).

MORGANUCODONTIDS.

Among the different kinds of early mammals known from Liassic deposits, the family Morganucodontidae is Known in greatest detail by virtue of the many isolated skeletal elements or Morganucodon1, and a nearly complete skeleton each of the related forms Megazostrodon 1. On dental evidence, the morganucodontids appear to have been allied to certain "nontherian" families of mammals of the later Mesozoic, such as the tricinodontids. and docodontids. With the possible exception of the monotrems, this group ef early mammals left no living descendants. Nevertheless, they clearly had attained a mammalian grade of organization, and in terms of our present knowledge of the fossil record offer the best view of the adaptations of early mammals. The following summarizes their most important features.Figure 6. Representative postcanine teeth of thrinaxodon 1(from Crompton, 1963, Figure 4) and molars of-Morganucodon 1and Kuehneotherium 1(from Hopson and Crompton, 1969, Figure 7). Anterior ends of the teeth are to the left.

The jaw joint was transitional in estructure, comprising a dentary-squamosal contact as well as primitive, reptilian quadrate-articular contact. Post dentary bones persisted in close relation to the lower jaw (Figure 8; see MIDDLE EAR, below). Teeth were well diferentiated into incisors, canines, premolars and molars, and the postcanine teeth were double rooted. During occlusion, the lower jaw moved dorsomedially and a consistent pattern of wear facets formed as the outer surface of the lower molars sheared against the inner surface of the upparatus, and wasfuther elaborated among later "nontherian" as well as therian mammaks. The typical morganucodontid cusp pattern (with a primary central cusp (A,a), an anterior secundary cusp (B,b), and two posterior secondary cusp (C,c;D,d), all aligned anteposterioly) is clearly reflective of a cynodont heritage (Figure 6B). Other feactures include the ossification of the braincase and the development of the internal ear: an anterior lamina of the prootic established a lateral wall to the cavum epiptericum (lodging the trigeminal ganglion) and provided a foramen for the maxillary and mandibular divisions of the trigeminal nerve; a bony "floor" enclosed the cavum epiptericum, and separated two foramina for the exit of the anterior (greater petrosal) and posterior (primary, or Hyomandibular) of the facial nerve; and the cochlear region became relatively enlarged (Kermack et al., 1973, 1981; Crompton and Jenkins, 1979; Crompton and Sun, in press.

The structure of the postcranial skeleton in morganucodontids gives evidence of the early establishment of many typically mammalian features (Jenkins and Parrington, 1976). The specializations of the atlas-axis complex begun among cynodonts (i.e., double occipital condyles, a dens, reduction of the atlanto-axial zygapophyses) were further elaborated to the poin that these early mammals apparently employed as much flexion-extension at the atlanto-occipital joint and rotation at the atlanto-axial joint as do modern forms. Clear diferentiation of the cervical vertebrae in Megazostrodon1, which included norrow laminae and pedicles, broadly spaced zygapophyses, and rod-like, posterioly throughout later mammalian evolution. The enlargement of the cervical vertebral foramina, evidence of a spinal cord intumescence corresponding to the origin of the branchial plexus, has been interpreted as eividence of greater neuromuscular control of the forelimb. Evidence of a cervico- thoracic flexure indicates an upright posture to the head and neck as in modern forms (figure 5). In Morganucodon 1a series of three mid-dorsal vertebrae exhibit "anticlinal" and "diaphragmatic" characteristics indicanting a sharp transition between the thoracic and lumbar series. This differentiation is related to musculoskeletal specialization for axial flexion and extension typical of the locomotor movements and posture of mammals. The pelvic girdle, with a narrow, rod-like ilium directed anterodorsally, a large obturator foramen, and a reduced pubis, was fully advanced to a mammalian grade of organization (Figure 5). Aspects of the limbs and particularly the joints are consistent with an interpretation of well- developed mobility. The hallux appears to have been somewhat divergent, and extension independent of the other digits were possible. This feature, together with sharp, trenchant claws, supports the interpretation that these early mammals were active forogers with climbing alilities similar to those of many small mammals today.

As in the skull, where primitive features (such as the postdentary bone) persist despite the development of structure that established the mammalian plan, the postcranial skeleton alsois a mosaic. The morganucodontid shoulder girdle in particular is little modified from thet in cynodonts (cf,Figure 4,5); the scapula remains a trough-shaped blade, both caracoids persist, and the glenoid is a semilunar, posterioly direscted concavity. The only major difference is that the anterior coracoid has been reduced in size. The humero-ulnar joint is composed of a condyle on the distal end of the humerus and a corresponding cup on the ulna; this condition, inherited from cynodonts, is retained by monotremes and other nontherian mammals, and contrast with the trochlear joint typical or more advance forms (Jenkins, 1973).

KUEHNEOTHERIIDS

Kuehneotherium (Kermack et al., 1968) and Woutersia (Sigogneau- Russell, 1983) represent an entirely different family of early mammals that is known only on the basis of isolated teeth and jaws. Despite this, the group appears to occupy a singularly important position in mammalian ancestry on the basis of the pattern of the cusps and the occlusal relations between molar teeth. Unlike the condition in other early mammals in which the cusps are aligned anteroposteriorly, in kuehneotheriids the secondary cusps are arranged in a triangular pattern (Figure 6C). Cusps B and C of upper molars are buccally positioned (toward the tongue). This pattern of "reversed triangles" presages the more complex interlocking mechanism of tribosphenic molars that developed later in mammalian evolution (Kernack et al 1968). Although the shear facets created by this type of occlusion were relatively simple in comparison to those in later mammals, the occlusal pattern (including the talonid-like fuction of cusp d and the fact that cusp E is positioned as a primitive parastyle(has the fundamental features of a primitive therian dentition (Crompton, 19711). However, as in morganucodontids,the quqdrate and articular remained in the primitive configuration (Figure 7E), and thus kuehnetheriids also had a double jaw joint.

THE DIVERSITY OF EARLY MAMMALS

Until recently, representatives of the families Morganucodontidae and Kuehneotheriidae were the primary fossil evidence on which to base interpretations of the earliest known stage in mammalian evolution. A third family, the Haramiyidae, had long been known from European deposits; represented only by rare, isolated teeth with paired roots and with multiple cusps arranged around the margins of a broad crown, these fossils provided more of a puzzle than any solution to interpreting mammalian origins (although Hahn, 1973, has asvanced credible arguments for a relationship to multituberculates). On this limited evidence,Crompton and jenkins (1973, 1979) interpreted morganucodontids and kuehneotheriids as representing a subtle but importat dichotomy between closely related forms leading to "nontherian" and therian mammals, respectively. Recent discoveries, however, have shown that these early mammalian faunas were more diverse than previously thought, and it is now clear that the earliest known mammals include representatives of families other than haramiyids, morganucodontids and kuehneotheriids (Clemens, 1980; Jenkins et al., 1983). These findings not only create new systematic problems, but they also provide evidence that substantial diversification of mammals occurrend before the "earlies known" faunas of Liassic age. More importantly, however, morphological studies of the new specimens alter revious conception of how mammalian structural and functional features arose. These new findings can be summarized as follows:

Dinnetherium. Jenkins et al. (1983) described molar wear facets in this genus (from the Kayenta Formation of northeastern Arizona) that are inicative of medial translation and rotation of the mandible during the occlusal phase. These movements appear to have ben more highly developed that in anyy other contemporaneous mammal. The structure of the jaw is also unusual in possessing an angular process (a neomorphic outgrowth of the dentary) that expanded laterally over the postdentary bones and created a new insertion area for a superficial masseter muscle (Figure 7). Oron and Crompton (in press) have shown that in the modern insectivore Tenrec 1and in other mammals the combined activity of the temporalis (acting dorsomedially) and superficial masseter (acting dorsolaterally) are instrumental in effecting medial translation and rotation of the jaw. The ocurrence of a neomorphic angle in Dinnetherium 1 is evidence that a superficial masseter was positioned and functioned as in modern mammals, an interpretation consistent with the reconstruction of jaw movements based on wear facets. This finding challeges the previous supposition that the therian angle arose by posterior migration of the pseudangular process that took place as certain postdentary bones (i.e., the articular and angular) were incorporated into the middle ear. Thhis would imply that rhe evolution of the mammalian masticatoty apparatus and middle ear were not so tightly coupled either masticatory apparatus and middle ear were not so tightly coupled either structurally or functionally as previously had been supposed.

Figure 7. The lower jaw of Dinnertherium nezourum showing the pseudangular (psang) and angular (ang) processes.

Sinoconodon. Crompton and Sun (in press) provide an analysis of new and better preserved material of this important genus originally described by Patterson and Olso (1961). There is no quiestion that Sinoconodon 1(Figure 1D) is a mammal by the conventional definition, for it clearly possesses a dentary-squamosal joint; the dentary condyle is large and bulbous, and the apposing glenoid is deeply concave (as opposed to the morganucodontid condition in which it is very shallow). The dentary itself is large and robust, and the postdentary bones appearto have been smaller than in other early mammals. But Crompton and Sun also point out that, in addition to these distinctly mammalian features, Sinoconodon 1 retains some characteristics of a cynodont such as Thrinaxodon1. Among these are the massive, angular nature of the symphysial region of the mandible, and the fact that the condyle lies below the level of the postcanine alveoli (cf. Figure 1C,D). Postcanine teeth do not appear to have been clearly differentianted into premolars and molars by structural differences and, even more surprising, precise occlusal relations between upper and lower postcanine teeth are absent. It is even possible that these teeth did not actually come into occlusal contact during jaw closure. Thus it appears that a load-bearing dentary- squamosal joint does not necessarily entail occlusion, although in every known case where precise, unilateral occlussal relations occur the dentary-squamosal joint is well developed. The different occlusal patterns known among other early mammals (Crompton, 1974; Jenkins et al., 1983) may well have arisen subsequent to a "Sinoconodon 1stage" in which the dentary-squamosal joint was present but occlusion was not yet established.

Gobiconodon. This late surviving representative of the family Amphilestidae,known from the Early Cretaceous Cloverly formation of western North America and also from deposits of comparable age in Mongolia, would not otherwise be pertinent to this account of mammalian origins except for one unusual feature. The two Cloverly specimens, both of which appear to be adult on the basis epiphyseal funsion, clearly show "molar" teeth in the process of being replaced. The long accepted definition of a molar is that it is not preceded by a deciduous ("milk") tooth a relation initially established on the basis of observations of living mammals and the heretofore found consistent with the fossil record. Diphyodonty and the nondeviduous nature of molars have been widely accepted as unique mammalian characteristics. Hopson (1973) has argued cogently that the rapid growth rate of juvenile mammals and their dependence upon maternal milk for nourishment is related to this type of tooth replacement. As in the case Sinoconodon 1, Gobiconodon 1 upsets our conception of a standard. By definition, its molariform teeth cannot be "molars" although in all other structural and functional respects they functioned as mammalian molars. Hallautherium. Clemens (1980) erected this new genus on the basis of several isolated teeth from Hallau, Switzerland. Although the general proportions and alignment of the cusps are comparable to those in morganucodontids certain details, including an enlarged posterobuccal basin, are so divergent from any pattern previously known that Hallautherium 1is appropriately considered "Mammalia incertae sedis." it is clear, however, that Hallautherium 1 adds to our growing appreciation of dental diversity among the earliest known mammals.

THE MIDDLE EAR

The auditory apparatus of mammals is characterized by an articulated chain of there bones: the malleus, incus and stapes conduct vibrations from the tympanum, a membrane sensitive to airborne sound, to the inner ear which lodges that part of the VIIIth (vestibulo-cochlear) nerve associated with the Organ of Corti. On embryological evidence, it was established well over a century ago that certain structures of the reptilian jaw and jaw joint were homologous with bones in the mammalian middle ear (Figure 8B, C). More recently, major phylogenetic aspects of this trasformation have been clarifided, principally through a landmark study by allin (1975). Allin traced the evolution of the synapsid middleear to its beginnings among pelycosaurs, and demonstrated convincingly that auditory structure in this lineage was fundamentally different from that in other reptiles. The reflected lamina (rl) of the angular (an) is a persistent and dominant feature (Figure 1). In primitive forms, the reflected lamina was probably associated in part with an oral-pharyngeal diverticulum (the recessus mandibularis), and in therapsids developed as a principal support for a membrane (tympanum) with true auditory fuction (Figure 8A). The residual homologue of the angular, the ectotympanic bone, retains this same function in mammals (Figure 8B). The retro-articular process of the articular, lying posteriorly and medially to the tympanum, persists as the manubrium of the malleus: and the primitive reptilian jaw joint between the articular and quadrate, although reduced to miniscule size, serves to link the mammalian incus and malleus.

Figure 8-A, the posterior half of the skull in a cynodont (Thrinaxodon1) shows that the jaw joint (between the articular in the lower jaw and the quadrate lodged in the squamosal) also was part of the auditory apparatus. Vibrations of the tympanum, largely supported by the reflextec lamina of the angular, were conducted via the articular and quadrate to the stapes. B, the posterior half of the skull in a Virginia opossum (Didelphis) shows the typical mammalian jaw join formed by a dentary-squamosal articulation. The tympanum and middle ear ossicles, much reduced in size, lie behind the jaw joint but retain the same relations as in cynodonts. C, the lower jaw joint of a fetal mammal (medial view) reveals that the middle ear ossicles develop in position and form comparable to those in cynodonts (see inset, B). D, reconstruccion of the destition and jaws of the liassic mammal Morganucodon1; E, the lower jaw is shown in medial view. In this and other early mammals the auditory apparatus persisted in its association with the lower jaw although the quadrate and articular were relieved of their fuction as the primary jaw joint. F, in Morganucodon 1a distintive pattern of wear facets on the molars was developed as a result of occlusal contact. In order to display these relations, the internal surface of the upper molar (which wears against the external surface of the lower) is represented as if transparent. The relative positions of upper and lower molars varied among genera of early mammals, and thus produced generically distinctive facet patterns. (From Crompton and Jenkins, 1979, Figure 3-2).

Figure 8 (See legend on opposite page).

NEEONTOLOGICAL PERSPECTIVES ON PALEONTOLOGICAL PROBLEMS

Anatomical and physiological studies of modern mammals and reptiles have provided complementary approaches to questions concerning the early evolution of mammals. A few examples may be cited:

How this mammalian homeothermy arise? Crompton et al. (1978), on the basis of energetic studies of a monotreme, a marsupial and several insectivore species, posed the hypothesis that mammalian temperature regulation developed in two stages. At first, a body temperature of 28 - 30 C allowed early mammals to occupy a "nocturnal insectivore" niche was largely unexploited. Subsequently, higher metabolic rates enabled mammals to maintain higher body temperature (38 - 40 C, comparable to those of most modern mammals) and thus permitted diurnal activity. The fisrts stage was modelled on the finding that three insectivores (tenrec, setifer and hedgehog) possess a relatively low, reptile-like metabolic rate. From additional studies of other mammals, Oron et al, (1981) concluded that the unusual energetic regime found in the three insectivores may not represent a primitive condition, but rather "a specialization for the conservation of energy" Nonetheless, it is clear that homeothermy is possible in mammals at lower metabolic rates than are present in most forms today (Taylor, 1980).

To what degree do mammalian and reptilian limb muscles differ? Jenkins an Goslow (1983) compared the results of a cineradiographic and electromygraphic analysis of the shoulder muscles in the Savannah monitor lizard with those from an earlier study on the Virginia opossum (Jenkins and Weijs, 1979). A large number of putatively homologous muscles in two species were found to be comparable in attachments, in activity patterns with respect to phases of the step cycle, and in apparent actions; these muscles, desingnated as "functional equivalents." were interpreted as a representation of the pattern inherited from the common tetrapod ancestor of living mammals and lizards. The muscles yhat were found not to be equivalent in attachment, activity or action were considered "Functionally divergent"; such divergence could be interpreted as a specialization peculiar to either mammals or lizards, but in any case provides a basis on wich to stipulate the fuctional, rather than simply anatomical, differences that separate mammals and reptiles. A major diference lies in the propotion of muscles used in the propulsive phase (limb in contact with the substrate) versus the swing phase (limb not in contact with the substrate). The opossum uses only about a quarter of its shoulder muscles for swing phase activity, the remainder being active during propulsion; monitors, in contrast, activate half of their total shoulder musculature during the swing phase. Parallel studies of the pelvic musculature now in progress are revealing a similar pattern: a mammal employs more of its musculature during the propulsive phase than does a reptile.

How did the mammalian tibio-astragalar joint evolve? A radiographyc study of tarsal relations and movements in a variety of climbing mammals (Jenkins and McClearn, in press) has provided the basis for reinterpreting the origin of mammalian ankle structure. Two primary patterns have been identified among living mammals: in didelphids and phalangerids, the prosimal surface of the astragalus bears two sulci to receive apposing tibial condyles (the extinct multituberculates have a nearly identical arrangement), whereas in other marsupials (such as macropodids) and in eutherians the astragalus is of a distictive trchlear shape. This structural diversity is explicable in terms of parallel evolution from the tibio-astragalar joint of advanced mammal-like reptiles and the earliest known mammals in which the bulbous, hemispheroidal proximal surface of the astragalus bears two indistinct facets for the tibia.These facets are represented in didelphis and multituberculates as sulci, and in macrodids and eutherians as the proximal and medial surface of the trochlea. Monotremes alone among living mammals appear to have retained the basic features of the primitive mammalian condition, and in echidnas it occurs with slight modification as a ball and socket joint.

ACKNOWLEDGMENTS.

My attempt to summarize our knowledge of mammalian origins is quite obviously a compedium of the observations and ideas of many workers. I should like especially to acknowledge the major contributions made by A. W. Crompton and James A. Hopson, and to thank them for their criticisms and suggestions in preparing this presentation. Edgar F. Allin reviewed the account of the MIDDLE EAR, a subject to which he has substantially contributed. Figures 2 and 3, modified from Hopson (1969), indicate relationships that were specifically suggested by J. A. Hopson based on his paper (in pree) with H. R. Barghusen. The reconstruction of Sinoconodon 1(Figure 1D) was generously contributed by A. W. Crompton and Sun Ai-Lin in advence of their publication. Figure 8 is reproduced with permission of the University of California Press. I am also very grateful to Lillian L.W. Maloney for her special assistance, to L. Laszlo Meszoly for rendering Figures 1-4, 6 and 7, and to Deedra McClearn for editorial review.

FIGURA 1

Jenkins A.Jr.

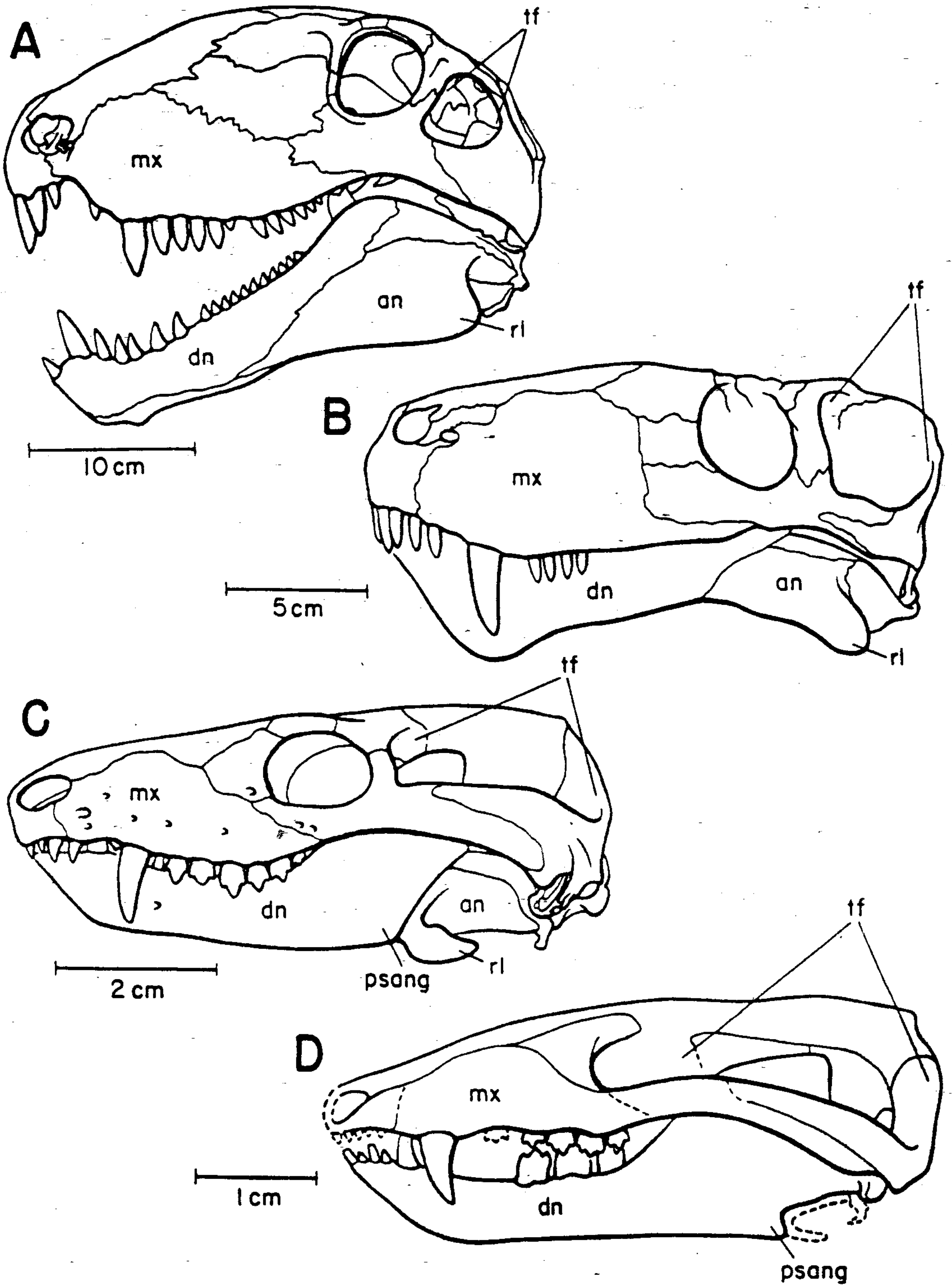


FIGURA 2 Jenkins A. Jr.

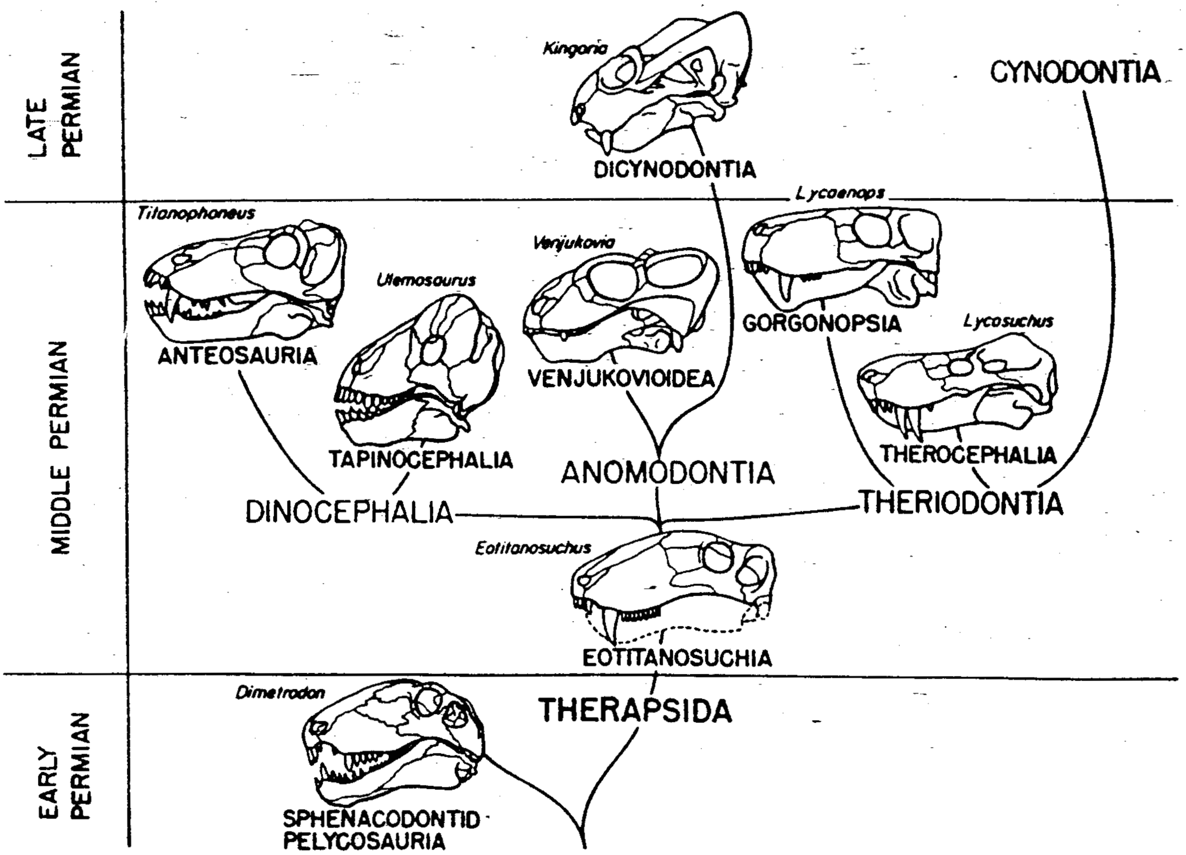


FIGURA 3

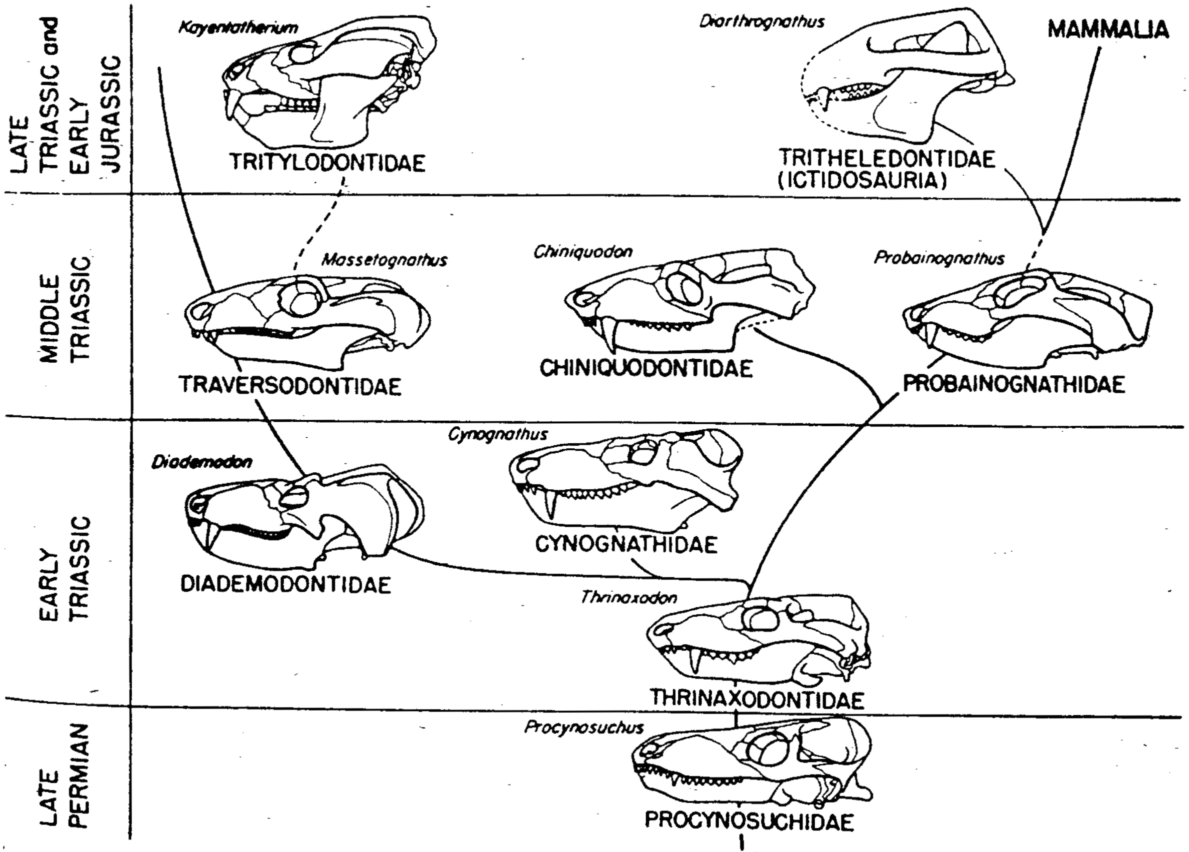


FIGURA 4

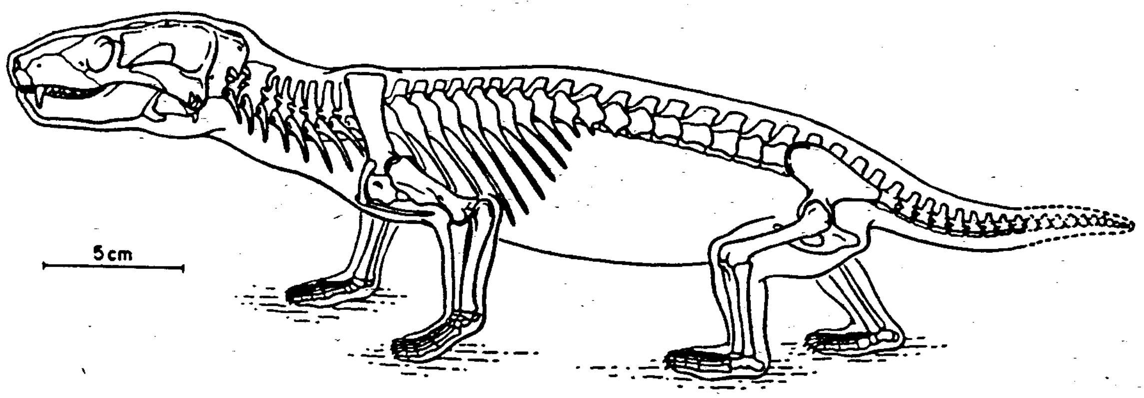


FIGURA 5

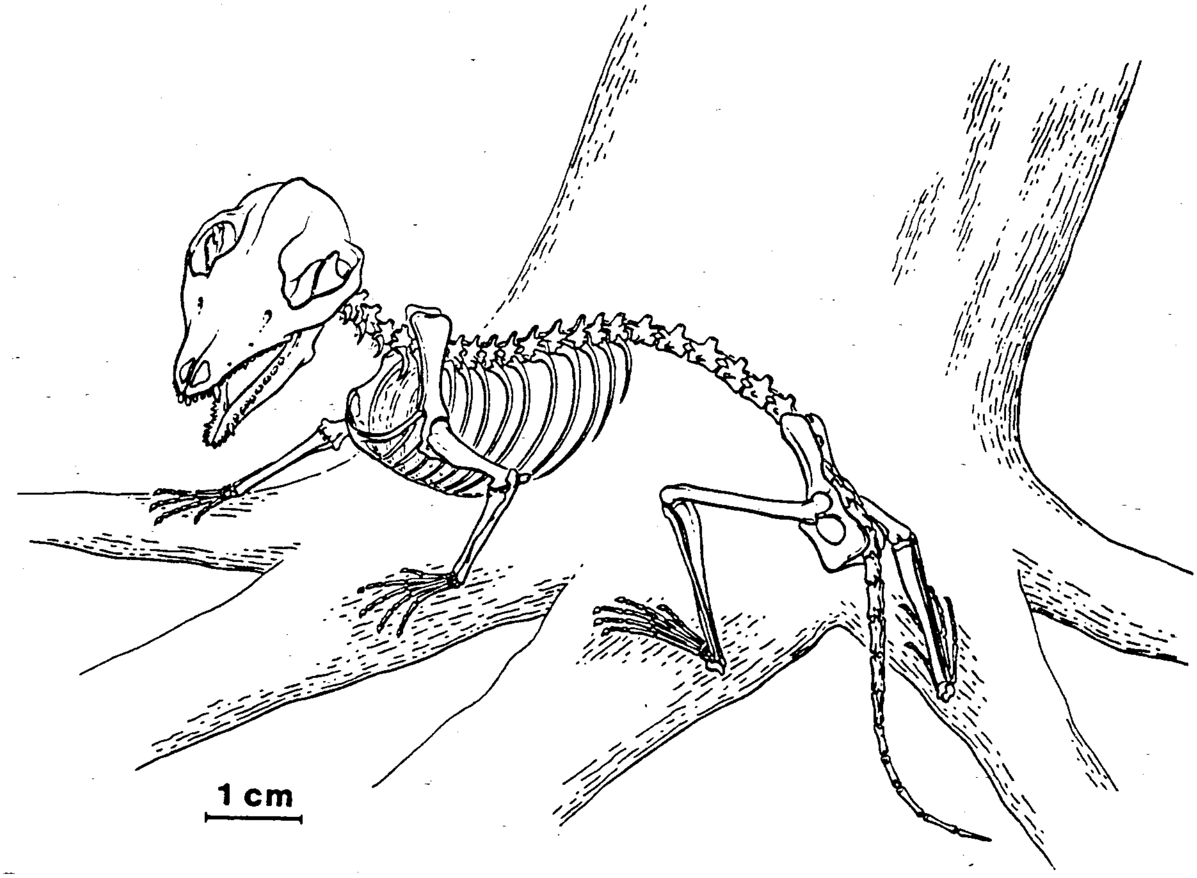
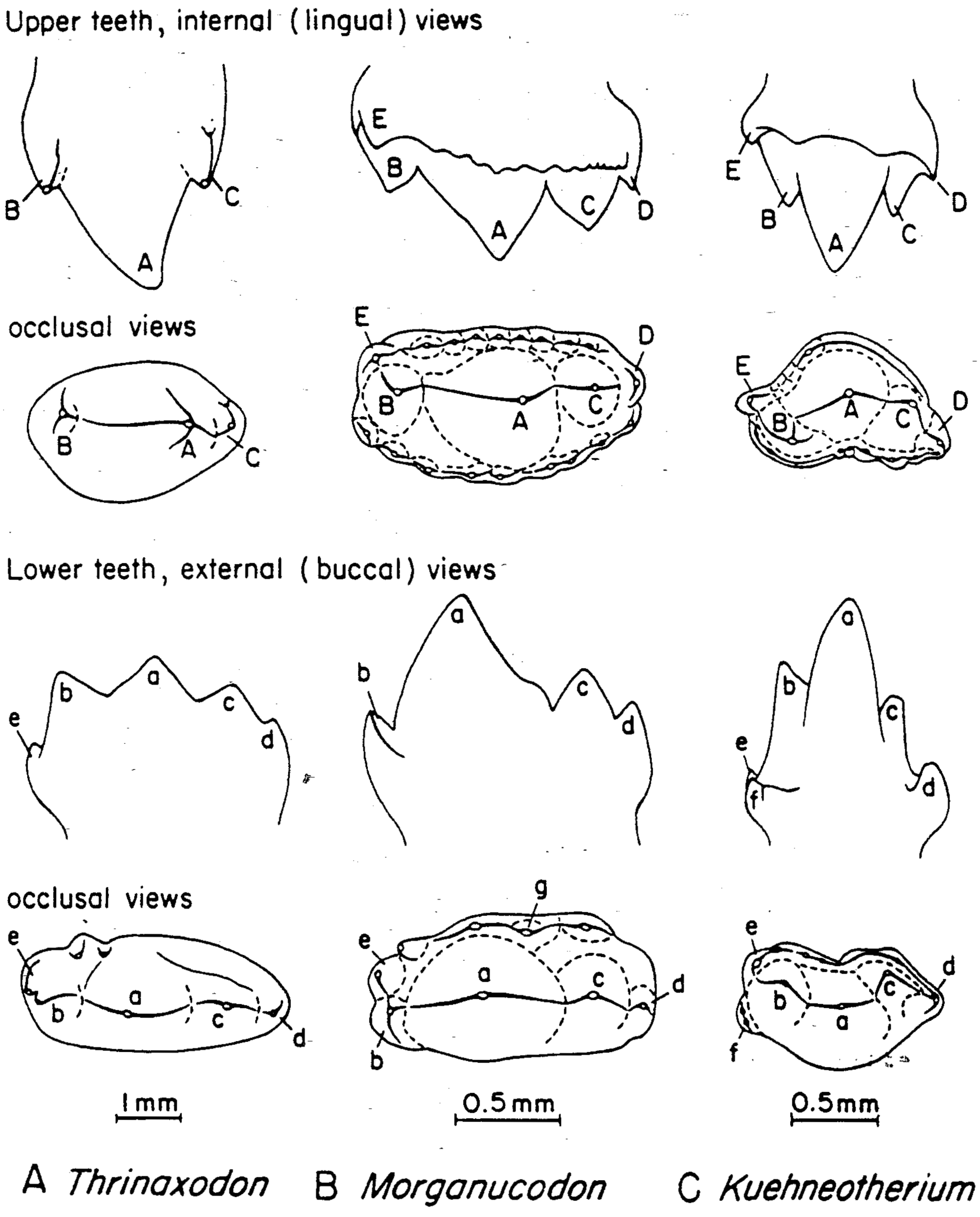


FIGURA 6


Upper teeth, internal (lingual) views
B
C
A
E
B
A
C
D
E
B
A
C
D
occlusal views
B
A
C
E
D
B
A
C
E
B
A
C
D
Lower teeth, external (buccal) views
e
b
a
c
d
b
a
c
d
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b
c
e
f
d
occlusal views
e
b
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g
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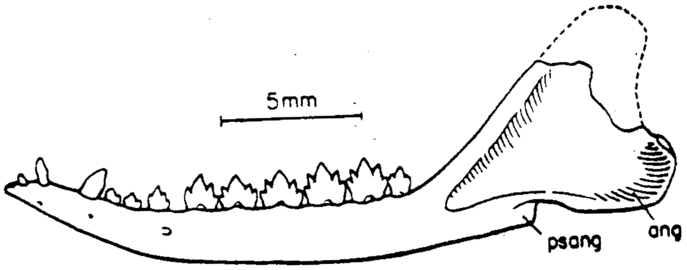
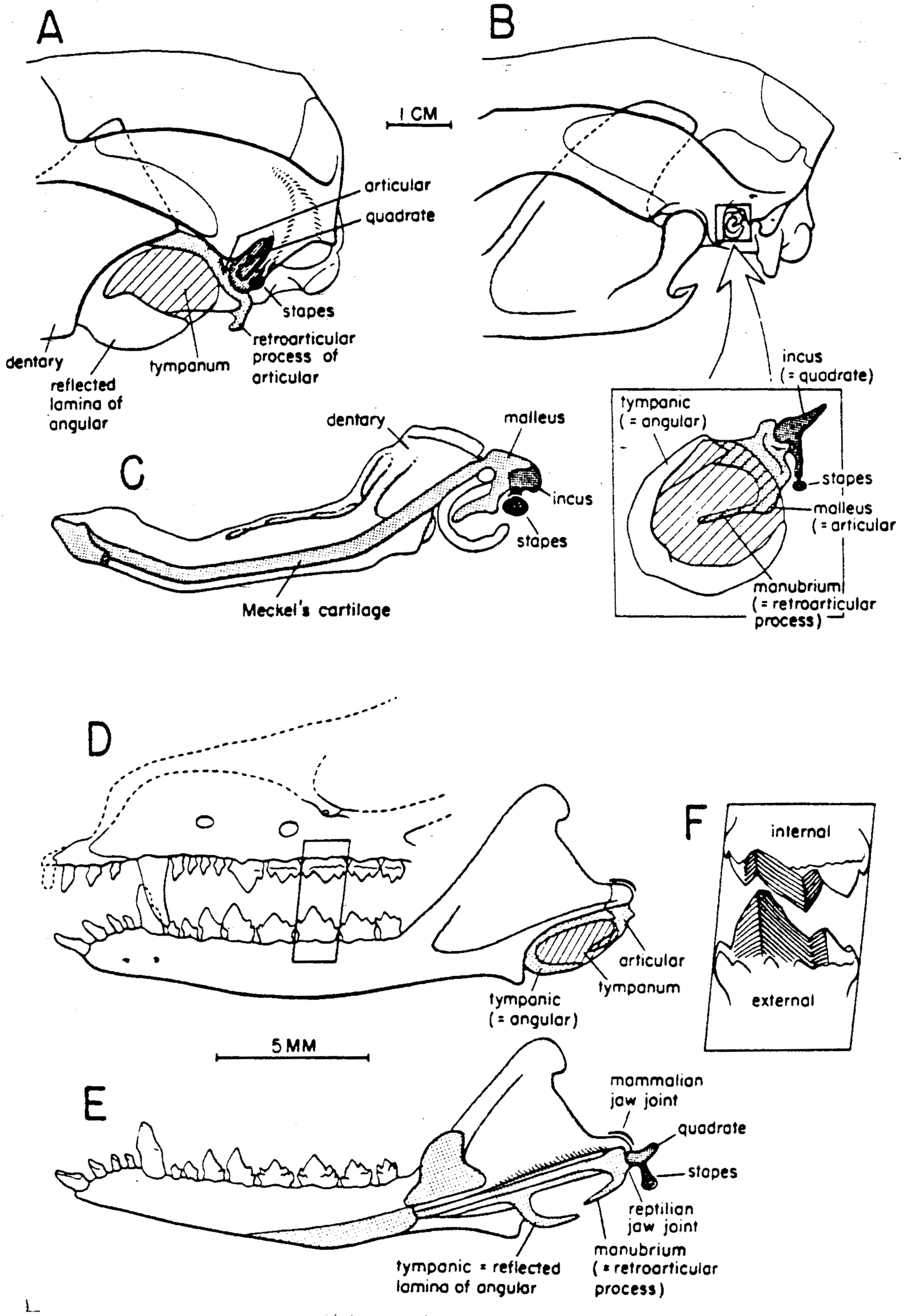
a
c
d
b
e
b
c
d
a
f
1 mm
0.5 mm
0.5 mm
A Thrinaxodon
B Morganucodon
C Kuehneotherium

FIGURE 7



Jenkins, A. Jr.

FIGURE 5



IN GINGERICH, P.D. 7 BADGLEY, C., ORGANIZERS, 1984. MAMMALS, NOTES FOR A SHORT COURSE: KNOXVILLE, TENN., UNIV. TENNESSEE DEPT. GEOL. SCE. STUDIES IN GEOLOGY 8, AND THE PALEONTOLOGYCAL SOCIETY, p 87-109.

9.4 (a)

Mammalian Evolution in the Paleocene: Beginning of an Era.

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INTRODUCTION

The Paleocene (approximately 65 to 55 million year ago) is the first epoch of the Cenozoic Era; it is also the beginning of an era in which mammals underwent a major adaptative radiation and became dominant land animals. It was a fascinating and exciting era of transition in mammalian evolution between the dark ages of the Cretaceous, when mammals were few and small and lived in the shadown of the great, "ruling reptiles", and the explosive ages of the Eocene, when mammals were dicerse and in full blossom. In the Late Cretaceous there were approximately eigth families of marsupials and placentals; by the early Eocene over 70 had come into being. Were mammals from the Paleocene totally unknown, creationists would surely have plenty of grist for their missing-link mills. But paleocene mammals are now known from five continents and they give evidence of archaic groups of mammals that wereunleashed from the constraining supression of dinosaurs. Paleocene mammals evolved rapidly and included "evolutionary experiments" that failed soon thereafter but also groups that were at the base of enormously successful adaptative radiations later in the Cenozoic. In fact, more than one-third of the known orders of the Cenozoic had their beginnings, or origins, in the Paleocene. Origins are captivating. At one time or another every one of us has pondered the origin of the universe, the origin of life, the origin of humankind, etc. Without knowledge of Paleocene mammals, many basic questions concerning the origin and evolution of mammalian adaptations woulld not be answerable.

Although a great deal has been learned about Paleocene mammals since G. G. Simpson's excellent review in 1937 (c), less is still knownabout mammalian evolution during the Paleocene than for any of the later epochs of the Cenozoic. The prime reasons for this discrepancy in availability oof information are 1) Paleocene mammals are older and therefore have had a greater chance of being destroyed by various geological agents; 2) Paleocene mammals are generally smaller and therefore more difficult to find and collect (and to prepare and study once collected); and 3) historycally, fewer paleontologists have studied Paleocene mammals.

In the limited space available, I will attempt to provide a brief overview of geographic, climatic, and temporal setting in which Paleocene mammals lived and died, as well as symposis of some of the better known fossil mammal localities on each continent. This will be followed by a limited survey of some of the more important archaic groups of Paleocene mammals, More progressive groups (such as rodents, bats, artiodactyls, perissodactyls, and primates of modern aspect ("euprimates")) will be treated by K. D. Rose in the following chapter even though the earliest representatives of some of these groups may have had their first appearance in the Paleocene boundary and at the Paleocene-Eocene boundary. For general information on mammalian taxa that lived during the Paleocene the reader is referred to Kurten (1971), Romer (1966, 1968), and Savage and Russell (1983).

PALEOCENE GEOGRAPHY AND CLIMATE

During the Paleocene the positions of the continents and the size and distribution of eperic seas were different from those of today. A useful distillation of the relationships between areas of land and sea during the Paleocene, and its relevance to mammalian biogeography is provided by Savage and Russell (1983:50). The salient aspects of these relationsships are illustrated in Figure 1 and can be summarized as follows:

1) North America and western Europe were contiguos and provided a variably developed avenue for mammalian dispersal until possibly as late as the early Oligocene (McKenna, 1983). Terrestrial Paleocene mammalian faunas of North Amarica and western Europe show many similarities (but not as many as during the early Eocene).

2) Partial or complete epicontinental seaways appear to have separeted northwestern Europe (Great Britain and part of Scandinavia) from central and southeastern Europe and European USSR from Asian USSR. The latter seway, the Obik Sea, projected southwars from the Arctic Basin and may have connected with the Tethyan Sea, which trended in an northwest-southeast direction and separated Africa from Europe and Asia.

Figure 1 --Positions of the continents and ditribution of epicontinental seas approximately 60 millions years ago (modified from Savage and Rusell, 1983).,

3) A high latitude land connection through Berigia (between northerastern Asia and northwestern North America) was developed in the Late Cretaceous and persisted in to the Paleocene.

4) South America was separated from both Africa and Central America.

5)The Indo-Pakistan region was still an island heading northward in the present Indian Ocean.

6) Australia was not yet and island continent and was still joined to Antarctics, wich may or may not have been contiguous with the southern tip of South America.

7) Large floodingseas constricted the aerial extent of several continent. In North America, for example, large parts of both the east and west coasts of the United Stages were flooded and one seaway extended northward from the Gulf of Mexico to near the present-day Canadian border.

Paleoclimatic evidence from several areas in North America suggest that temperature decreased toward the end of the Cretaceous and that these relatively cool temperature pprevaile into the early Paleocene. During the Paleocene climates fluctuated: mean annual temperatures and equability were relatively low during the early and late Paleocene and high during the middle Paleocene and early EOCENE (Sloan,1969); Wolf and Poore, 1982). Much of the evidence for these changes derives from information on the composition and diversity of both the fauna (Rose, 1981 a, b) and flora (Hickey, 1980) in the Bighorn Basin of Wyoming. The relatively high humidity apparent during the Paleocene is shown by the morphology of fossil leves from North America (Wolf, 1978),western Europe (Dorf, 1964), and Australia (Kemp, 1978). The temperature fleuctuations postulated above have been corroborated by evidence from oxygen osotopes in the North Sea (Buchardt, 1978) and calcareous plankton in the Alantic Ocean (haq et al., 1977).

BIOSTRATIGRAPHY AND IMPORTANT PALEOCENE MAMMAL LOCALITIES.

The 10 million year duration of the Paleocene epoch can be, and has been, subdivided on the basis of its mammalian faunas. It was, however, first defined by a paleobotanist, W. P. Schimper, in 1874 on the basis of floras from the Paris Basin, France. The boundaries of Schimper's Paleocene have been modified in the light of later work and a history of these modifications can be gleaned from the works of Gingerich (1975) and Savage and Rosell (1983). The estimated ages for the lower and upper boundaries of the Paleocene are 65 and 55 million years ago, respectively (Berggren et al., 1978).

Paleocene mammals are best known from North America but they are also now well represented in collections from Europe, Asia, and South Americ. Only one locality in Africa has so far yielded Paleocene mammals and none have yet been recovered from the continents of Australia and Antarctica. Some of the more important Paleocene mammal localities from each continent are listed below and their positions are indicated on Figure 2. Figure 3 provides a tentative intercontinental correlation of the paleocene on the basis of its contained mammalian faunas.

Figure 2--Map the world showing localities that have yielded Paleocene mammals.

Figure 3-- Tentative intercontinental correlation of Paleocene ages. Shaded areas reflected uncertainties concerning precise correlations with Noth American Land-Mammal Ages.

North Americal.-- (Major references: Rusell, 1967; Sloan, 1969).

Paleocene mammals are know from more specimens, more species, more localities and more levels in North America than on any other continent. This has, iin turn, resulted in a relatively precise biostratigraphic zonacion of the Paleocene. The North American Paleocene has been divided into four Land-Mammal Ages: the Puercan, Torrejonian, and Tiffanian corrspond roughly to early, middle, and late Paleocene. The fourth Land-Mammal Age, the Clarkforkian, straddles the Paleocene-Eocene boundary. The Dragonian Land-Mammal Age, proposed by Wood et al. (1941), Is now generaly recognized as early Torrejonian (Tomida, 1981) and tha Mantuan, recently proposed by Van Valen (1978), is considered to be early Puercan (Gingerich et al., 1980; Archibald, 1982).

Each of the North American Land-Mammal Ages has been further subdivided into a series of zones bases on mammalian species that make their first appearance in each zone. The most recent species -level biostratigraphic framework for the Paleocene has been summarizad by Gingerch (1983 b), who subdivided the Puercan in three zones, the Torrejonian into four, the Tiffanian into five, and the Clarkforkian in three. The Paleocene-Eocene boundary is drawn between the first and second zones of the Clarkforkian(Rose, 1980, 1981 a)

Paleocene mammals were first discovered in North America in 1879 by David Baldwin, who then collected for the renowned O.C.March, in the San Juan Basin of New Mexico and Colorado (Simons, 1963). This Basin contains the type localities for the Puercan, orrejonian, and Tiffanian Land-Mammal Ages. Fossil mammals from the San Juan Basin have been described in a large number of papers, the most important being Matthew's classic overview of the Puercan and Torrejonian collections. The late Paleocene iffany fauna was described by Simpson (1935). A survey of recen work on Paleocene mammals from the San Juan Basin is contained in Lucas et al. (1981). Paleocene mammals are also known from numerous localities in several other large intermontane basin scattered along and to the east of the Rocky Mountains in western North America. Sediments within these structural depresions were deposited during a major period of mountain-building in latest Mesozoic and earliest Cenozoic time. This is the so-called Laramide orogeny. Broad regional uplift of the western Inerior during the late Cenozoic resulted in the rejuvenation of streams and large-scale erosion that has culminated in the highly dissected topography in the atrea today. Although important and exciting field work is being carried out in many area, two basins requiere special mention: the Bighorn Basin of northwestern Wyoming and the Crazy Mountain Basin of south-central Montana. In addtion to work in the San juan Basin, collection from these two basin are largely responsible for our concepts of Paleocene mammalian evolution in North America. The Bighorn Basin, in the Polecat Bench - Clark ^ s Fork Basin area, contains a demostrable stratigrafic succesions containg Puercan, Torrejonian, Tiffanian, and Clarkforkian mammals (Gingerich et al., 1980). The Crazy Mountain Basin is noteworthy because it contains some of the largest and best documented samples of Torrejonian and Tiffanian mammals. Recent work in the Crazy Mountain Basin and Tiffanian mammals. Recent work in the Crazy Mountain Basin (Krause and Ginberich, 1983b; Gingerich et al., 1983) is attempting to build on the early studies by Simson (1936, 1937 a, b) and others.

Europe.-- (Major Reference: Russell, 1964, 1975).

In 1841 de Blainville described the bear-like arctocynid condylarth Artocyon primaveus 1and he thus became the first person to ever decribe a Paleocene mammal. Arctocyon primaveus 1is a member of the Cernay fauna, which is know from two areas in the northeastern part of the Paris Basin: Cernay-les-reims and Mont de Berru. The Cernay fauna is Thanetian (late Paleocene) in age and is correlative with the late Tiffanian of North America (Gingerich, 1976b). A slightly early fauna, from near the town of Walbeck in Germany, is a peculiar, unbalanced assemblage that was deposited in a fissure fill. The Walbeck fauna is probably equivalent to the early or middle Tiffanian of North American (Gingerich 1976 b). The recent discovery of the peculiar plesiadapiform primate Saxonellal, previously only known from Walbeck, in a middle Tiffanian fauna from Alberta, Canada, lends additional support to this correlation (Fox, 1984). A third locality, at Manat in the south of France, has yielded only three species of mammals and is thought to be equivalent to the earliest of the Tiffanian zones in North America (Gingerich, 1976 b). Finally, a very important Paleocene fauna was recently discovered at the Montain (middle Paleocene)type locality near Hainin (southwest of Brussells) in the Mons Basin of Belgium (Godifriaux and Thaler, 1972). Tha sample from the hainin locality represents theoldest known Paleocene mammalian fauna from Europe. Only the multituberculates, marsupials, and condylarths from the Hain fauna have been described in detail (Vianey-Liaud, 1979; Crochet and Sige, 1983; Sudre and Rusell, 1982). The multituberculates and condylarths are dominated by genera that are unknown from elsewhere in Europe, North America, or Asia.

Approximately 50% of the genera of Europe were shared with North America during the early Eocene. During the late Paleocene less than 10% of the genera were shared but, nonetheless, they still provide strong evidence of a land connection between the two continents.

Asial.--(Major Reference: Chow and Zheng, 1980; Li and Tong, 1983; South China "Redbeds" Reserch Group, IVPP, 1977).

The discovery of Paleocene mammals in the Xinjiang Region of the People's Republic of China in 1960 signalled the beginning of one of the most important recent advances in vertebrate paleontology (Crow, 1960). Since 1960, new and very productive localities yielding Paleocene mammals have been sicovered in numerous basins in Xin-jiang, Guandong, Jiang-xi, Hu-nan, An-hui, He-nan, and Shaan-xi provinces and in the Nomogen area of Inner Mongolia (Chow and Zheng, 1980; Li and Tong, 1983). More than 125 species of Paleocene faunas have been tentatively divided into two groups; those from the early and middle Paleocene (Shanghuan Provincial Age) and those from the laete Paleocene (Nungshaanian Provbircial Age). The ubiquitous pantodont Bemalambda 1is restricted to the Shanghuan while Archaeolamda 1is characterisatic of the Nungshanian.

A series of faunas from the Inner Mongolian Gashato Formation, discovrered by American Museum of Natural History expeditions in the 1920's and formely regarded as late Paleocene in age (e.g., Szalay and McKenna, 1971), are now thought to be earliest Eocene, correlative with the North American Clarkforkian Land- Mammal age (Dashzeveg and McKenna, 1977; Gingerich and Rose, 1977; Rose, 1981 a).

South America.-- (major References: McKenna, 1980a; Patterson and Pascual, 1968; Simson; 1948, 1967, 1978, 1980).

Paleocene mammals have long been known from two major areas in South America: 1) The Itaborai locality in Brazil, and 2) east-central Chubut province in Patagonia. The faunas from these areas were generally considered to belong to the late Paleocene Riochican Land-Mammal Age. Rodrigues Francisco and Sounza Cunha (1978), however, recently suggested an early Paleocene age for the Itaborai fauna and Marshall et al. (1981) now believe taht the Riochican spans the middle and late Paleocene. Mammals of probable Paleocene age have recently been discovered in nortwestern Argentina, in the provinces of Salta, Jujuy (Marshall et al., 1981), and Tucuman (Soria and Pwell, 1981), but these faunas are incompetely described. Conservatively, the mammals from all of the known South American Paleocene localities are here treated as Riochican in age. The Riochican mammals consist of marsupials, xenarthrans, and several different kinds of ungulatres. The ordinal diversity of Paleocene mammals from South America (7) is considerably less than from North

America (15, or even Asia (11). The mammalian fauna from Itaborai is dominated by marsupials, that from Patragonia by ungulates. Peculiarly, the known Riochican faunas exhibit a strong imbaalnce of mammalian carnovores and herbivores, only three small marsupial carnivores are known from Itaborai and none from Patagonia.

Africa.--Paleocene mammals are known from only one locality in Africa (Cappetta et al., 1978). The locality is in the Quarzazate Basin of Morocco and is thougth to be early Paleocene in age. The few specimens from there are isolated teeth of paleoryctid proteutherians, creodonts, and carnivorans.

THE CAST OF CHARACTERS

The familial and ordinal distribution of Paleocene mammals in space and time is summarized in Table 1. Even the briefest synopsis of every family, or e3very order, of Paleocene mammals is impossible in this forum. My intent, Therefore, is to provide a conspectus of only some of the most diverse and spectacular orders represented in the Palecene, although a brief discussion of the unexpected recent discovery of a possible xenarthran in China os appended to this section. Table 2 lists the most diversas (species rich) orders of Paleocene mammals within each recognized temporal subdivision on each continent. It is immediately apparent that,archaic orders predominated. Two types of mammalian orders can be characterized as "archaic": 1) those that were represented in the Cretaceous and did not change signidicantly during the Paleocene, and 2) those that are quite highly specialized, evolved just prior to or during the Paleocene, but became extinct soon thereafter.

Condylarths were the most, or one of the most, diverse Paleocene groups pf mammals on every continent. Multituberculates, proteutherians, and, toward the latter half of the epoch, plesiadapiform primates achived high species diversities in North America and Europe. The Paleocene mammalian fauna of Asia was dominanted by anagalids and pantodonts while marsupials and notoungulates comprised the majority of species on South America. Each of these major Paleocene groups will be discuassed individually below; groups that are represented by excellent cranial or posteranial material are illustrated in Figures 4-10.

TABLE 1--Mammalian higheeer taxa the Paleocene of North America, Europe, Asia, and South America. Subdivisiona of the Paleocene are abbreviated as follows: Pu, Puercan; To Torrejonian;, Ti, Tiffanian; Cr, Clarkforkian; D-M, Dano-Montian; T, Thanetian; E-M, Early-middle Paleocene; L, Late Paleocene; R, Riochican. Temporal distributions of taxa are modified from lists provided by Savage and Russell (1983) and Li and Ting (1983).

TABLE 2 -- The most diverse orders of Paleocene mammals. Only the three most diverse ordens in each temporal subdivision on each-continent are listed. The porcentages indicate tha ratio of the numbert of species per order to total number of species in each temporal subdivision times 100.Also listed is the total number of known species in each temporal subdivision on each continent.

Order Multituberculata 1.- General references: Clemens and Kielan-Jaworowska, 1979; Sloan, 1979].

Multituberculata, whose closest living relatives are the monotremes, comprise one of the oldest, longest-lived orders of mammals. They are known from the Late Jurassic to the early Oligocene and were among the most diverse and abundant mammals in the Paleocene. Their geographic distribution is confined to North,, America, Europe, and Asia and is therefore entirely Holarctic. Multituberculates are currently divided into three suborders: Plagiaulacoidea, Ptilodontoidea and Taeniolabidoidea. Plagiaulacoids are generally considered to include , or to be representative of, the ancestral stocks from which later multituberculates evolved. Only ptilodontoids and taeniolabidoids are present in Paleocene faunas.

Ptolodontois were small (shrew-to rat-sized), whereas taeniolabidoida, although also having shrew-sized members, included forma as large as modern beavers (Figure 4). Like most fossil mammals, multituberculates are best known from dental remains. Ptilodontoids possessed a pair of long, slender procumbent lower incisors, the crowns of which are completely covered wich enammel, and an enlarged, blade-like fourth lower premolar that functioned as a slicing wedge (Krause, 1982a.). Taeniolabidoids, on the other hand, are united as a group by the common possession of an enlarged pair of lower incisors bearing a ventrolabially restricted band of enamel. This morphology produced through wear, a self-sharpening tool for gnawing, as in the incisors of rodents. Taeniolabidoid lower,, fourth premolars were generally reduced although a few genera (such as Eucosmodon and Neoliotomus) retained large, ptilodontoid-like blades All multituberculates have distinctive molars with many cusps arrranged in mesiodistal rows -- hence the name Multituberculata.

Figure 4.- Cranial and dental morphology of Ptilodus (low. left. modofied from Krause, 1982a) and Taeniolabis 1(upper left, modified from Katthew. 1937). On roght, reconstruction of multituberculate skeleton based primarily on the skeleton of Ptilobus 1(from Krause and Jenkins, 1983; reproduced with permission from Museum of Comparative Zoology, Harverd University).

The ptilodontid Ptilobus known from Puercan Through Clarkforkian levels in wersten North America, is the most completely known of any multituberculate. Excellent skull and skeletal material of this rat-sized genus has been recovered. Ptilobus 1appears to have been an omnivore, possibly specializing in a diet of small body size suggests that these forms were less herbivorous than previously thought; they almost certainly supplemented their diet with protein-rich foods such as insects, worms, seeds or nuts and were thus quite omnivorous (Krause, 1982a). An analysis of dental function in Ptilobus 1has revealed that ptilodontoids had two distinct masticatory cycles:- a slicing-crushing cycle in wich the posterior premolars were used to open and initially break down large, hard food items and a grinding cycle in which the mandible was retracted while the molars, with their reciprocally concavo-convex cups, were held in thight occlusion (Krause, 1982a). This pattern of occlusion, particularly the posteriorly-directed power stroke of the grinding cycle, appears to be unique among mammals. Taeniolaboids, with their rodent-like incisors, reduced premolars, and anlarged molars de-emphasized the slicing-crushing cycle and placed a greater emphasis on gnawing and grinding.

The postcranial skeleton of Noth American multiberculates also reveals a number of unusual and even unique specialization including the presence of a post-obturator foramen, an enlarged prepollex and parafibula, a large, lateral flange proximally on the fibula, and a deep excavation posteriorly beneath the proximal articular surface of the tibia (Krause and Jenkins, 1983). The recently-descovered skeleton of Ptilodus 1exhibits several adaptations indicating that it, and all other Nort American multituberculates for which postcranial material is known, were arboreal. These adaptations include a distinctive tarsal construction for a range of pedal mobility characteristic of mammals that descend trees headfirst, a hallux that could be abducted and adducted for prehension in a plane independent of the other digits, and a long, robust, and prehensile tail (Jenkins and Krause, 1983).

Why did this great group of mammals, which was undoubtedly one of the most successful, long-lived taxa in all of mammalian history, go extinc? It is impossible to specify the exact cause of such an event but strong inverse correlations of abundance and diversity between North American multituberculates and rodents suggest possible diffuse competition between the two groups (Van Valen and Sloan, 1966). Multituberculates may also have competed earlier with plesiadapiform primates and conddylarths. Reconstruction of diets, body sizes, activity patters, habitats, and locomotion in multituberculates indicates that the resource space occupied by the group may have overlapped broadly with that of rodents (Krause, 1981, 1982b). The most rapid decline in multituberculates occurred at the Tiffanian- Clarkforkian boundary, the precise time at which rodents are thougth to have immigrated to North America from Asia.,Order Marsupialia [General references: Crochet, 1977, Marshall, 1982a; Paterson and Pascual, 1968; Paula Couto, 1952; Simpson, 1980].

Almost every continent has been suggested as the area of origin for marsupials but the most defensible include North America, South America, Australia, and Antarctica (Marshall, 1980b). Although Australia is known as the "Land of Marsupials," the earliest record of marsupials on that continent in late Oligocene. Records of marsupials on North and South America extend back to the Late Cretaceous and in Antarctica to the late Eocene (Woodburne and Zzinsmeister, 1982). Despite their early diversity in the Cretaceous of North America (at least 9 genera), only one genus (Paradectes 1; Family Didelphidae) survived into the Paleocene. Moarsupials became extinct in North America in the middle Miocene although Didelphis1, the Virginia opossum, re- invaded from South America in the Pleistocene and is thriving today. In the Paleocene, marsupials achieved their greatest diversity in Souch America where they are represented by 14 genera of didelphids (more than in the Recent fauna), one genus of Borhyaenidae, and three genera of Polydolopidae (Marshall, 1982a). Didelphids include the opossums and are regarded as the stem family of the Marsupialia; its most primitive members lie near the ancestry of all other marsupial groups. Didelphids of the Paleocene, asnow, were mostly omnivores although the smaller species undoubtedly fed largely on insects. Borhyaenids are a groups of "dog- like" marsupials that included short-legged carnivorous and omnivorous forms. Its most spectacular member is the saber- toothed marsupial Thylacosmilus 1of the Miocene and Polydolopids. such as the best-known Paleocene genus Epidolops 1(Figure 5), have pincer-like incisors, bunodont, multi-cusped molars, and enlarged, laterally compresses posterior lower premolars with serrate edges reminiscent of those in ptilodontoid multituberculates.

Figure 5 -- Cranial and dental morphology of Epidolops 1. Left, ventral view of skull (modified from Paula Couto, 1952). Right, lateral view of left dentary (modified from Marshall, 1980b)."Insectivores1" [General references: Butler, 1972; Novaceak, 1982]

The general notion that most early mammals were tiny, primitive insectivores is incorrect. The archanis ungulate groupo. the Condylarthra, had already assumed a position of dominance by the early Paleocene and other groups were also in abundance. Nonetheless, insectivores were present and, if anything, are under-represented in the Paleocene fossil record because of their small size. Screen-washing techniques utilized in the past 20 years have, of course, rectified this situation to some extent.

Mammals generally referred to as insectivores have long been placed in a waste-basket taxon, the Insectivora. The waste- basket has been partly emptied by removing a group now referred to by some as Lipotyphla and by others as Insectivora sensu strictol. Lipotyphla of the Paleocene include a hedgehog-like group (the Erinaceoidea) and a shrew-like group (the Soricoidea). The waste-basket, however, still contains various groups of placental mammals that have diverged little from the ancestral stock. This new waste-basket and primarily early Cenozoic taxon, the Proteutheria, was coined by Romer (1966) and elevated to ordinal status by Butler (1972). McKenna (1975a) attempted to dissolve the Proteutheria and to re-assing its component families to various ,eutherian "super-groups." The Proteutheria, for obvious reasons, is a group that particularly defies brief characterization. Suffice it to say that, during the Paleocene, there were at least six families present, none of which were particularly diverse or abundant. Some of the more important famillies include the relatively large and aquatic Pantolestidae and two superficially rodent-like groups, the Apatemyidae and Mixodectidae.

Order Primates - Suborder Plesiadapiformes (Major references: Gingerich, 1976b; Kay and Cartmill, 1977; Rose and Fleagle, 1981).

The earliest primate, Purgatorius, belongs to the diverse radiation of primates placed in the Suborder Plesiadapiformes, representatives of which are known from both North America and Europe. Purgatorius 1may have been presented in the latest Cretaceus (Van Valen and Sloan, 1965) but is best known from the early Paleocene (Puercan) of Montana (Clemens, 1974). Purgatorius 1is so generalizad in its dental morphology that it is difficult to determine its relationships to later primates. However, in the middle and late Paleocene, presiadapiform primates became very common and were represented by a number of families with divergent specialization. These include microsypids, plesiadapids, carpolestids, paramomyids, picrodontids, and saxonellids. Like most Paleocene mammals, plesiadapiforms are known primarily from jaws and teeth, although relatively complete skulls are known for a few genera (e.g., Palaechthon, Plesiadapis, Zanycteris) 1and partial postcranial skeleton are known for the closely related genera Plesiadapis and Nannodectes.

Plesiadapis, the best know of the Plesiadapiformes, had a rodent-like skull with a small braincase, long snout, laterally-directed eyes, and a distinct diastema between the enlarged lower incisors and the cheek teeth (Figure 6). The skull lacked a post-orbital bar, a very primitive condition among primates. The partial postcranial skeleton of Plesiadapis includes most of the limbs (Figure 7). Plesiadapis 1was a heavily-built animal but no consensus has yet beet reached on whether it was an arboreal or terrestrial form (Szalay et al., 1975; Gingerich, 1976b). The Plesiadapidae included probable omnivores, hervirores, and granivores (Gingerich, 1976b). Figure 6-- Cranial and dental morphology of representatives of four fmilies of plesiadapiform primates. Top left, Palaechthon 1(Family Microsyopidae, modified from Szalay and Delson, 1979). Top right, Plesiadapis (Family Plesiadapidae, modified from Gingerich, 1976b). Bottom left, Ignacius (Family Paromomyidae, modified from Szalay and Delson, 1979). Bottom right, Carpodaptes 1(Family Carpolestidae, modified from Szalay and Delson, 1979). Stippled areas indicate parts that are still unknown. Scale bars each represent 1cm.Figure 7-- Skeletal reconstruction of Plesiadapis1. Solid black areas indicate parts pf the skeleton that are still unknown. (Modified from Tattersall, 1970).

The Mocrosyopidae are the most primitive family of Plesiadapiformes. The earlier, small microsyopids, such as Palaechton, were predominantly terrestrial insect-eaters that used primarily tactile, auditory, and olfactory cues to locate their prey (Kay and Cartmill, 1977). The Paromomyidae include small primates with long snouts, lonh slender lower central incisors, and a pointed lower fourth premolar (Simpson), 1955). Carpolestids and saxonellids are more specialized Plesiadapiformes. Both groups consist of small, mouse-sized animals that had enlarged, transversely compressed, and multituberculate-like posterior premolars (Rose, 1975). Picrodontids, another highly specialized group, have peculiarly-expanded first molars that are reminiscent of those in some bats (Szalay, 1968). These resemblances led to early suggestions of bat relationships but later workers have instead regarded the similarities as convergent and simply indicative of a bat-like diet of friut and nectar. The relationship of plesiadapiform primates to other mammals and, in fact, to other primates is obscure. Plesiadapiformes were probably derived from some insectivoran sometime in the Late Cretaceous, but the ancestrial insectivoran stock has so far been elusive (Novacek et all., 1983). Plesiadapiform primates are allied with later forms primarily on the basis of detailed resemblances in the cheek teeth, although some postcranial characters have also been used. The pattern of carotid circulation in plesiadapiformes, however, has recently been found to be non-homologous with that in later primates and re-establishes the uncertainty concerning the phylogenetic relationships of this early radiation (MacPhee et all., 1983).,[Order Condylarthra -- [General references: Cifelli, 1983; Matthew, 1937; Simpson, 1937a].

The Condylarthra is an extinct radiation of primitive mammals,that arose during the Late Cretaceous and flourished during the Paleocene. The order is thought to have been involved, either directly or indirectly, in the ancestry of as many as 18 other orders of mammals includings all living hoofed mammals, or ungulates, "subungulates" (hyraxes, proboscideans, sirenians, desmostylans), whales, and tubulllidentates (aardvarks). In reality, however, few clear-cut commections to later groups have been documented. Condylarths exhibit a tremendous diversity in morphology and undoubtedly occupied a wide range of adaptive zones.

The composition of the Condylarthra has changed, and will indubitably change, numerous times. For instance, arctocyonids and mesonychdis (the groups dealt with in greatest detail here) were once placed in the Suborder Creodonta of the Order Carnivora along with three other families: Miacidae, Oxyaenidae, and Hyaenodontidae. With additional study, vertical classifications have resulted in the elevation of the Creodonta to separate,ordinal status but including only the Oxyaenidae and-Hyaenodontidae. The Miacidae have been allied with "true" carnivores in the Order Carnivora and arctocyonids and mesonychids are now included within the Condylarthra by some and given separate ordinal status (Arctocyonia and Acreodi, respectively) by others. Likewise, some of the earliest whales were originally described as condylarths. The changings concept of the Condylarthra is indicative of a broader, more interesting phenomenon concerning " archaic" mammals. With increasing efforts to trace modern ungulate or ungulate-like clades to their "roots" in the Paleocene, various taxa are removed from the Condylarthra is therefore a grade because abailable evidence does not permit its sibdivision. For the present purpposes, I have adopted a conservative classification and thus at least 10 families o condylarths are identified as having been present in the Paleocene.

The earlies condylarths are the Arctocyonidae, known from the Late Cretaceous of North America (Sloan and Van Valen, 1965) and probably South America. They were one of the most diverse families of the Paleocene and were probably at the base of the subsequent condylarth radiation (Van Valen, 1969). Early Paleocene arctocyonids were of small to neduim size. They generally had long, low skulls with prominent canines and low-crowned, primitively tribosphenic molars. Salient features in the postcranial skeleton include short limbs, clawed feet, and long tails. Larger forms, the size of small bears, evolved later in the Paleocene and are present in both North America and Europe. typical of these later forms is Arctocyon (Figure 8), which, like most bears, probably had an omnivorous diet.Figure 8--Cranial and dental morphology of Arcotocyon (left, modified from Russell, 1964) and Dissacus (rigth, modified from Matthew, 1937).

Mesonychids were more common in the Eocene but at least one genus, Dissacus, attained a broasholarctic distribution in he late Paleocene. Dissacus had simple, triangular molars and high-crowned shearing lowers (Figure 8). Unlike arctocyonids, mesonychids had hooves but they were of unusual construction in that terminal phalanges that supported them were narrow and fissured. Mesonychids were probably carnivorous or piscivorous (Szalay, 1969b) and probably gave rise to whales (Gingerich et al., 1983).

The remainigs families of Paleocene condylarths were primarily herbivorous forms. Included here are such divergent forms as the small, generalized hyopsodontids, the periptychids, with their characteristic wrinkling of molar enamel, meniscotheriids, with had molarized premolars and selenodont cheek teeth, and the only ,family family represented in South America, the Didolontidae. Space restrictions preclude a detailed treatment of each of the herbivorous condylarth families.Order Pamtodonta-- [General referencen: Chow et al., 1977; Simons, 1960].

The Pantodonta include the largest of Paleocene mammals. They were generally large, heavy-bodied herbivores with small brains, short, stout limbs, and pentadactyl feet. They had an entirely holarctic distribution and presumably filled several of the ecological niches vacated by dinosaurs at the end of the Cretaceous. Pantodonts are present ion the early Eocene of North America and Europe and survived into the early Oligocene in Asia, but their greatest radiation was in the Paleocene of North America and Asia. Pantodonts have not yet been dicovered from the moderate to large size. The smallest form is the recently described Cyriacotherium, wich was probably about the size of a small sheep (Rose and Krause, 1982). Two of the best-known North American genera are Pantolambda and Titanoides (Figure 9). Pantolombda was slightly larger than Cyriacotherium and had simple, conical canines and W-shaped crests on the molars. Its digits terminated in small hooves.

Titanoides, a rhinoceros-sized animal, is one of the few examples among ungulates that possessed clawn rather than hooves. It was also unusual in the development of large, sabre-like upper canines, presumably an adaptation for digging up roots. The Asian radiation included, in addition to several large forms, a host of small pantodonts that were as small as a rat. Until recent collecting in the People's Republic of China, the magnitude of this radiation of pantodonts that were as small was largely unknown. One of the Chinese forms, Bemalambda, is known from both cranial and postcranial material and is thus among the best-known Paleocene mammals from Asia (Chow et al., 1977). It appears to be even more primitive than the earliest North American form, Pantolombda, but already shows the characteristic w-shaped molar crests. It, like Barylambda from North America (Gingerich and Childress, 1983), was sexually dimorphic.Figure 9-- Cranial and dental morphology of Pantolambda (left, modified from Matthew, 1937) and Titanoides (rigth, modified from Simons, 1960). [Order Anagalida--[General references: Szalay and McKenna, 1971; Li and Ting, 1983].

The Anagalida is comprised of a large radiation of Late Cretaceous and early Tertiary Asian mammals that was first given ordinal status in 1971 by Szalay and McKenna, despite the fact that menbers of the order were known since the 1920's. Early workers regarded anagalidans as tree shrews but Knowledge of the relationships and diversity of the Anagalida has increased tremendously in the past few years with the discovery of many new species in the Paleocene of China. In their recent tally of anagalid taxa, Li and Ting (1983) list five families (Anagalidae, Pseudictopidae, Zalambdalestidae, Eurymylidae, and Mimotonidae), 23 genra, and 33 species. A greay deal remains to be learned of the Anagalida and pf their relationschips to other mammals. Symptomatic of this gap in our knowledge is the general confusion concerning the composition of the order. Kielan- Jawoeowska et al. (1979), for instance, would not include the Zalambdalestidae in the order, while Sych (1971) erected a separate order (Mixodontia) for the Eurymylidae, Savahe and Russelll (1983) did not recognize the Mimotonidae as a family distinct from the Eurymylidae, and Gingerich (1981e) removed the Didymoconidae, a family originally regarded by Szalay and McKenna (1971) as possibly belongig to the Anagalida, to the Condylarthra.

The destition of anagalidana tends to include molariform posterior premolars, hypsodont and easilyworn upper cheek teeth, and procumbent incisors. The postcranium was apparently lagomorphlike. agomorph characteristics have long been noted in the Anagalida and the group is now regarded as having been near the ancestry of both the agomorpha and Rocentia (Hartenberger, 1980; McKenna, 1982).

Order Notoungulata [General references: Patterson and Pascual, 1968; Simpson, 1980].

Notoungulates were a diverse group of South American ungulates that reached their acme in the Oligocene but survived into the Pleistocene. They also archieved a modest diverity in the late Paleocene and early Eocene of Asia and are represented by rare specimens of a single genus in the late Paleocene and early Eocene of North America (in the Bighorn Basin of Wyoming only). This geographic distribution has led to much speculation about centers of origin for the group. The most recent view is based on the reidentification by Marshall et al. (1983) of Perutherium (from late Cretaceous beds at aguno Umayo in Peru). previously thought to be a condylarth, as a notoungulate. Because of the early record of Perutherium, is South American, Marshall et al. argue that notoungulates originated on that continent and subsequently migrated to North America and then Asia. Perutherium1, however, is known from only isolated lower molar fragments and is so primitive that allocation to the Notoungulata may be premature. It has, in fact, previously been referred to three different condylarth families and Hoffstetter (1981), followed by Cifelli (1983), even questioned its status as a eutherian.

There are, conservatively 14 families of notoungulates, only seven of which occur in the Paleocene. Of these, only the Arctostylopidar occur in North America and Asia; all other notoungulate orders are restricted to Souch

America. Notoungulates exhibit a characteristic pattern of crests, or lophs, on both the upper and lower molars. Also typical of creats, or lophs, on both the upper and lower molars. Also typical of notoungulates is the peculiar osseous construction of the middle ear cavity, the most significant deature of which is that the epitympanic recess is greatly enlarged into a sinus. [Order Xenarthra 1-- [General reference: McKenna, 1980; Patterson and Pascual, 1968; Simpson, 1978, 1980].

The evolutionary history of xenarthrans, the order of mammals to which armadillos, sloths, glyptodonts and anteaters belog, is largely confided to South America. Toward the end of the Cenozinc, however, several forms mograted northward as far as Alaska, and possible xenarthrans posses a suite of purportedly primitive featureatures (e.g., presence of septomaxillary bones, a monotreme-like stapes, complete ossification of ribs, poorly differentiated vagina and uterus, and poor thermoregulation) that has led some workers to belive that they were the earliest group to diverge from the Eutheria. The polarity of most of these characters, however, has yet to be documented (McKenna, 1975a. 19880a; Novacek, 1982).

Rlevant to this discussion is a group of fossorial, early Cenozinc mammals from North America, the Palaeanodonta. Palaeanodonts, including the families Epoicotheriidae and Metacheiromydae, have long been regarded as primitive menbers or ancestors of the Xenarthra. Emry (1970), however, argued that palaeanodonts were related to pangolins (Order Pholidota) and not Xenarthrans. The recent discovery of morphologically primitive palaeanodonts from the late Paleocene of the Bighorn Basin, Wyoming, however, suggests that palaeanodonts may have been ancestral to both pholidotans and xenarthrans (Rose, 1978, 1979; but see Storch., 1978b). Palaeanodonts, in turn may have been derived from pantolestid or pantolestid-like proteutherians (Rose, 1978).

One of the most extraordinary Paleocene mammals discovered in recent years is Ernanodon1, a possible xenartharan from the late Paleocene of China (Ting, 1979). Ernanodon 1was a collie.sized animal that had very powerful jaws and a dentition consisting of vestigial incisors, large canines, and reduced, peg-like cheek teeth. Its postcranial skeleton is very robust and powerfully-built and the forefeet had large claws. These deatures suggest that Ernanodon 1represents an early, "experiment" in ant- or termite-eating (Radinsky and Ting, 1984). The discovery of Ernanodon 1in China is intriguing from a biogeographical point of view. The evolutionary history of undoubted xenarthrans is almost entirely restricted to Souch America (beginning in the Riochican) and if Ernanodon 1is indeed a xenarthran its presence in China becomes very difficult to explain. Figure 10 -- Cranial and dental morphology of Ernanodon (modified from Radinsky and Ting, 1984).

FAUNAL TURNOVER

One of the most pronounced intervals of early Cenozoic faunal turnover occurred near the Paloecene-Eocene boundary in North America (Rose, 1980, 1981, b). Other mejor turnovers surely occurred, in North America and elsewhere, but none is as well documented as that near the beginning of the Eocene. The change in faunal composition took place in two stages, both presumably a result of major immigrations. The first coincides with the Tiffanian-Clarkforkian boundary when rodents and tillodonts, as well as the genera Haplomylus 1(a hyopsodontid condylarth) and Coryphodon 1(a pantodont) all apper simultaneously. The second stage, at the Clarkforkian-Wasatchian boundary, is heralded by the first appearance in North America of artiodactyls, perissodactyls, primates of the families Adapidae and Omomyidae, and probably hyaenodontid creodonts and meniscotheriid condylarths. Correspondingly, major groups that were previously diverse and abundant during most of the Paleocene are drastically reduced or become extinc altogether. Thus, for example, multituberculates decline sharply at the end of the Tiffanian, as do phenacodontid condylarths and plesiadapid and carpolestid primates at the end of the Clarkforkian.

The reasons for these turnovers must remain speculative but they were probably owing to a combination of changing climates and competition between native and immigrant taxa. Where the immigrant taxa came from is also inferential but paleogeographic considerations as well as new informarion on the Paleocene fossil records on other continents show that the first wave of newcomers probably came fron Asia (Chow et al., 1977; Hartenberger, 1980) whereas the second came fron Europe (Godinot, 1981)., [By constrast, earlier transitions in faunal composition, such as at the Torrejonian-Tiffanian boundary, appear to have been a result of intracontinental evolution and dispersal. Concerning the Torrejonian-Tiffanian turnover, Soloan (1969) and Gingerich (1976b) noted that, in many respects, mammals of the middle Paleocene and early Eocene were more similar to one another than those of the late Paleocene and early Eocene. They observed that there were a large number of early Eocene taxa that had more suitable structural ancestors in the middle Paleocene that in the immediately precending late Paleocene. They therefore hypothesized that, during the relatively cool late Paleocene, the lineages of mammalas representd at Torrejonian horizons in the Western Interior migrated southern stock then gave rise to the late Paleocene ancestors of early Eocene forms that migrated northward again as climates ameliorated. The character of the late Paleocene - early Eocene faunal transtion has now been documented through an intensive field program carried out by P. D. Gingerich and colleagues. No similar work, however, has been done on the middle- late Paleocene transition in western North America and the intriguing Sloan-Gingerich hypothesis therefore remains to be adequately tested.

OVERVIEW

Dinosaurs met their demise at the end of the Cretaceous and their role in terrestrial ecosystems appears to have been quickly occupied by mammals. The Mesozoic-Cenozoic boundary therefore marks the geologically sudden transition from the "Age of Dinosaurs" to the "Age of Mammals." Wheter or not dinosaurs were the direct ecological vicars of some Cenozoic mammals, there is no doubt that Paleocene mammals were vastly different from those of the Mesozoic. Nonetheless, mammals of the Paleocene are typically characterized as "archaic" -and they certainly were relative to those of the Eocene, when many orders with living representatives made their first appearance in the fossil record. The primitive nature of Paleocene mammals, as well as their generally fragmentary condition, makes them particulary difficult to study. More so than in the later Cenozoic, they are largely represented only by dental remains. Also, since many of them had not yet diverged a great dental from their ancestral stocks, the most minute of differences become significant. Although an overstatement, there is some truth to Romer's (1966; 29) proclamation: "Were we living in the late Cretaceous we would probably include all placentals then existing in a single family, and even in the Paleocene most forms could be reasonably placed in a single order."

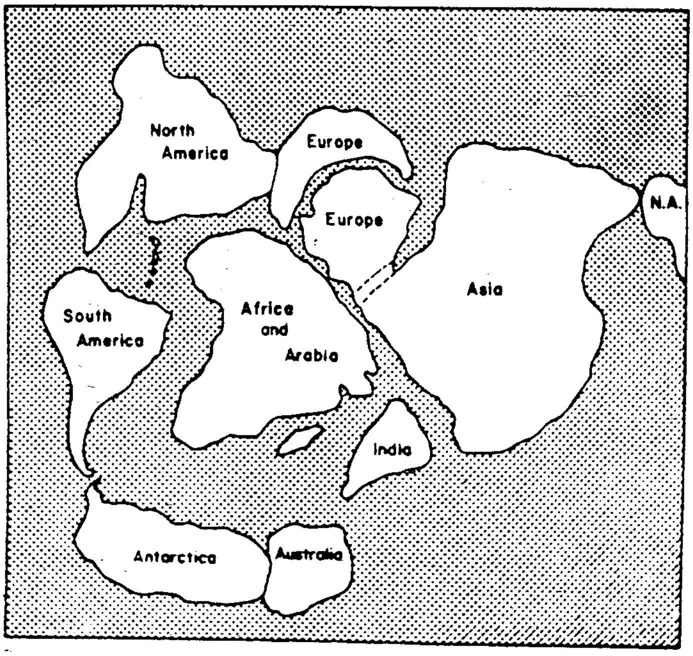


FIGURA 1

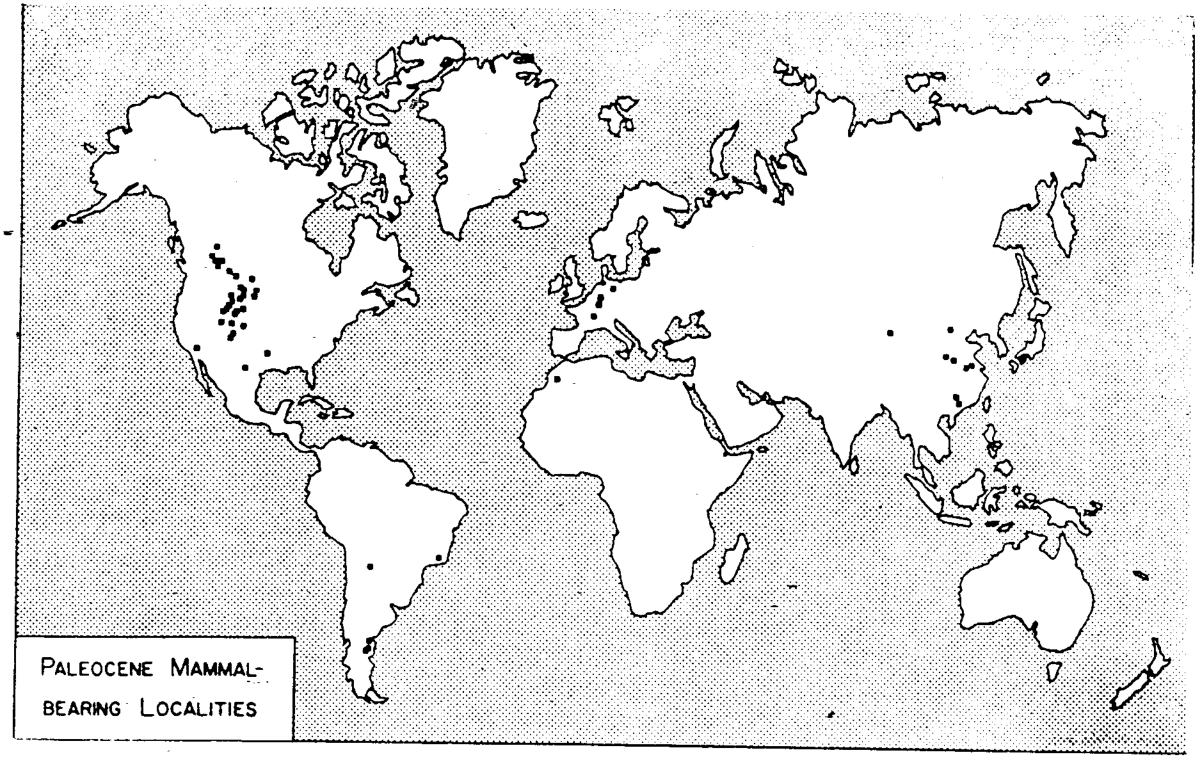


FIGURA 2

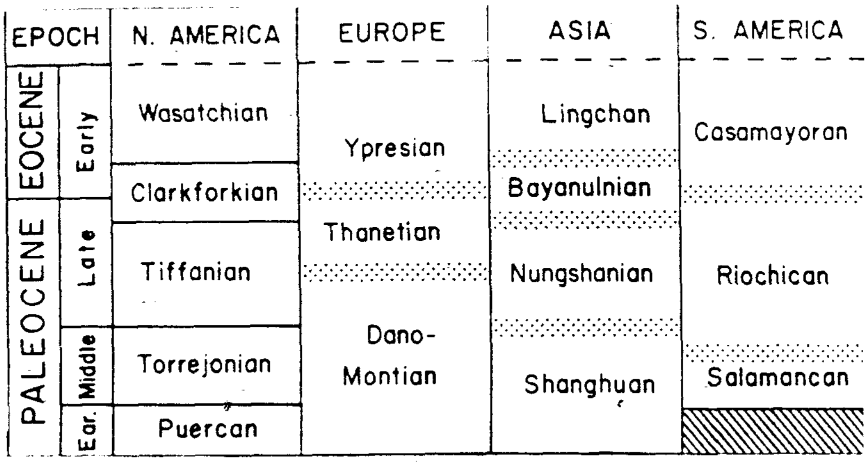

EPOCH
N. AMERICA
EUROPE
ASIA
S. AMERICA
EOCENE
PALEOCENE
Early
Late
Middle
Ear.
Wasatchian
Clarkforkian
Tiffanian
Torrejonian
Puercan
Ypresian
Thanetian
Dano-
Montian
Lingchan
Bayanulnian
Nungshanian
Shanghuan
Casamayoran
Riochican
Salamancan

FIGURE 3

TABLE 1

TAXON	NORTH AMERICA				EUROPE		ASIA		SOUTH AMERICA
	Pu	To	Ti	Cf	D-M	T	E-M	L	R
Order MULTITUBERCULATA									
Family Ptilodontidae	●	●	●	●					
Family Neoplagiaulacidae	●	●	●	●		●			
Family Cimolodontidae		●	●			●			
Family Boffiidae					●				
Family Eucosmodontidae	●	●	●	●					
Family Taeniolabididae	●	●	●					●	
Order MARSUPIALIA									
Family Didelphidae	●		●	●					●
Family Borhyaenidae									●
Family Polydolopidae									●
Order PROTEUTHERIA									
Family Palaeoryctidae	●	●	●	●		●			
Family Micropternodontidae								●	
Family Leptictidae	●	●	●	●		●			
Family Pantolestidae		●	●	●		●			
Family Pentacodontidae		●	●	●	●				
Family Apatemyidae	●	●	●	●	●	●			
Family Mixodectidae		●	●			●			
Order LIPOTYPHLA									
Soricoidea	●	●	●	●	●	●			
Erinaceoidea		●	●	●	●	●			
Order DERMOPTERA									
Family Plagiomenidae	?	●	●	●					
Order PRIMATES									
Family Microsyopidae	●	●	●	●		●			
Family Plesiadapidae		●	●	●		●			
Family Carpolestidae		●	●	●					
Family Paromomyidae		●	●	●					
Family Picrodontidae		●	●						
Family Saxonellidae			●			●			
Order CONDYLARTHRA									
Family Arctocyonidae	●	●	●	●		●			
Family Periptychidae	●	●	●				●	●	
Family Mioclaenidae	●	●	●						
Family Phenacodontidae		●	●	●					
Family Hyopsodontidae	●	●	●	●		●	●	●	
Family Mesonychidae		●	●	●		●	●	●	
Family Didymoconidae							●	●	
Family Menisocotheriidae				●		●			
Family Tricuspiodontidae						●			
Family Didolodontidae									●
Order TAENIODONTA									
Family Stylinodontidae	●	●	●	●					
Order TILLODONTIA									
Family Esthonychidae			●	●			●		

Continued TABLE 1

TAXON	NORTH AMERICA				EUROPE		ASIA		SOUTH AMERICA
	Pu	To	Ti	Cf	D-M	T	E-M	L	R
Order PANTODONTA									
Family Pantolambdidae		●	●						
Family Titanoideidae		●	●	●					
Family Barylambdidae			●	●					
Family Cyriacotheriidae			●	●					
Family Coryphodontidae				●					
Family Archaeolambdidae							●	●	
Family Bemalambdidae							●		
Family Harpyodidae							●	●	
Family Pantolambdodontidae								●	
Family Pastoralodontidae							●	●	
Family Phenacolophidae								●	
Order DINOCERATA									
Family Uintatheriidae			●	●				●	
Order NOTOUNGULATA									
Family Arctostylopidae			●	●				●	
Family Henricosborniidae									●
Family Notostylopidae									●
Family Oldfieldthomasiidae									●
Family Isotemnidae									●
Family Archaeohyracidae									●
Family Interatheriidae									●
Order TRIGONOSTYLOPOIDEA									
Family Trigonostylopidae									●
Order LITOPTERNA									
Family Proterotheriidae									●
Family Macraucheniidae									●
Order CARNIVORA									
Family Miacidae	●	●	●	●	?	?	●		
Order CREODONTA									
Family Oxyaenidae			●	●					
Order ANAGALIDA									
Family Anagalidae							●	●	
Family Pseudictopidae							●	●	
Family Eurymylidae							●	●	
Family Mimotonidae							●	●	
Family Zalambdalestidae							●		
Order RODENTIA									
Family Paramyidae				●				?	
Order XENARTHRA									
Family Ernanodontidae								●	
Family Dasypodidae									●
Family Glyptodontidae									●
Order Uncertain									
Family Epoicotheriidae			●						
Family Metacheiromyidae			●	●					
Family Carodniidae									●

TABLE 2

NORTH AMERICA	EUROPE	ASIA	SOUTH AMERICA
Puercan Condylarthra - 69% Multituberculata - 13% Proteutheria - 8% Total species - 84 Torrejonian Condylarthra - 40% Proteutheria - 20% Multituberculata - 16% Total species - 159 Tiffanian Condylarthra - 29% Primates - 19% Multituberculata - 15% Total species - 167 Clarkforkian Condylarthra - 22% Primates - 16% Creodonta - 9% Total species - 88	Thanetian Condylarthra - 50% Proteutheria - 17% Multituberculata - 14% Primates - 14% Total species - 36	E.-M. Paleocene Anagalida - 35% Pantodonta - 27% Condylarthra - 23% Total species - 48 L. Paleocene Pantodonta - 30% Anagalida - 27% Condylarthra - 15% Total species - 71	Riochican Marsupialia - 39% Notoungulata - 32% Condylarthra - 11% Total species - 57

FIGURA 4

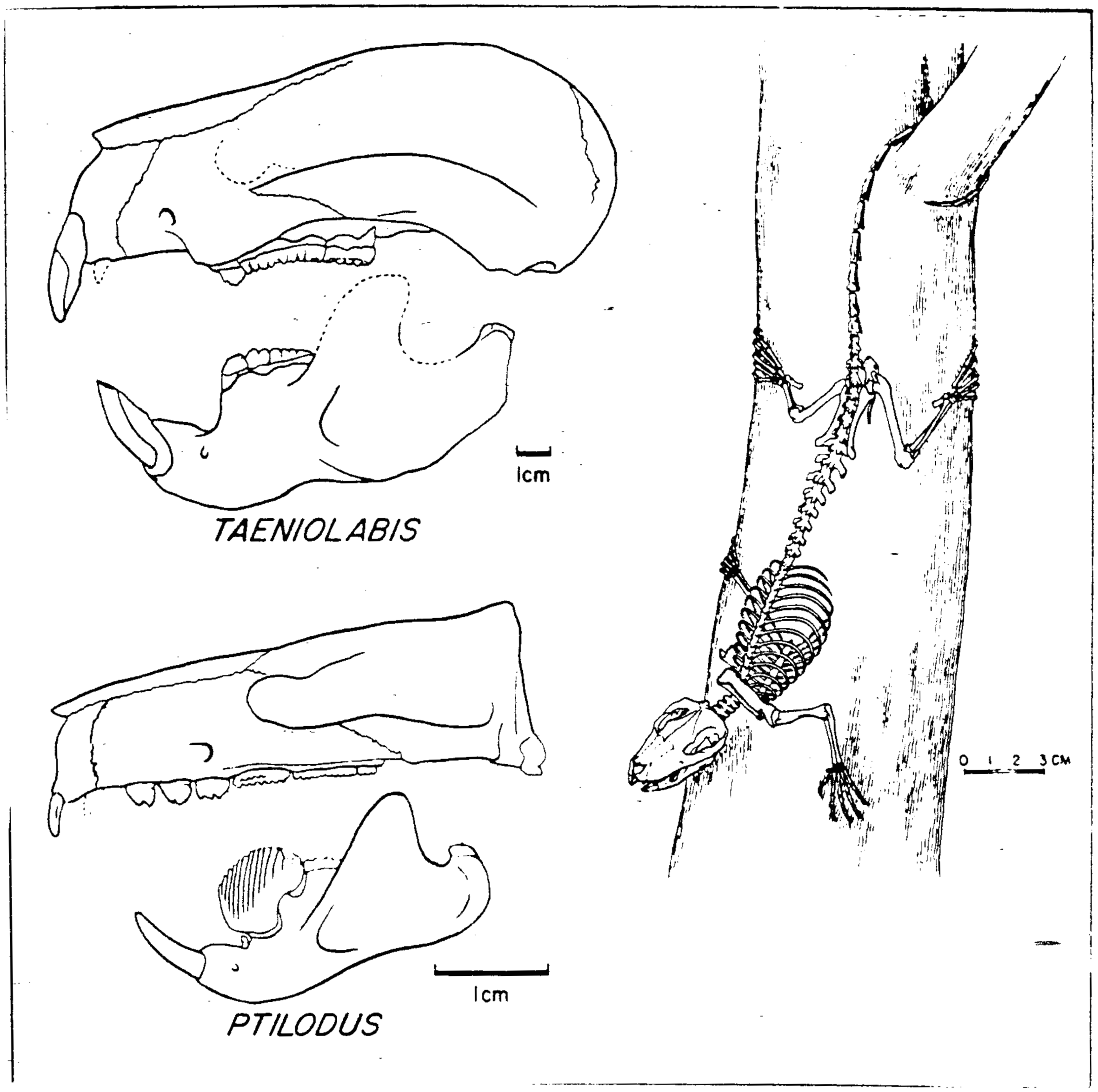


FIGURA 5

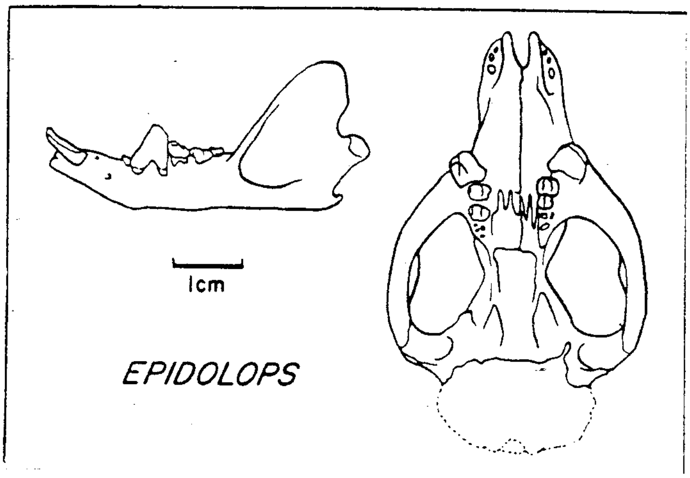


FIGURA 6

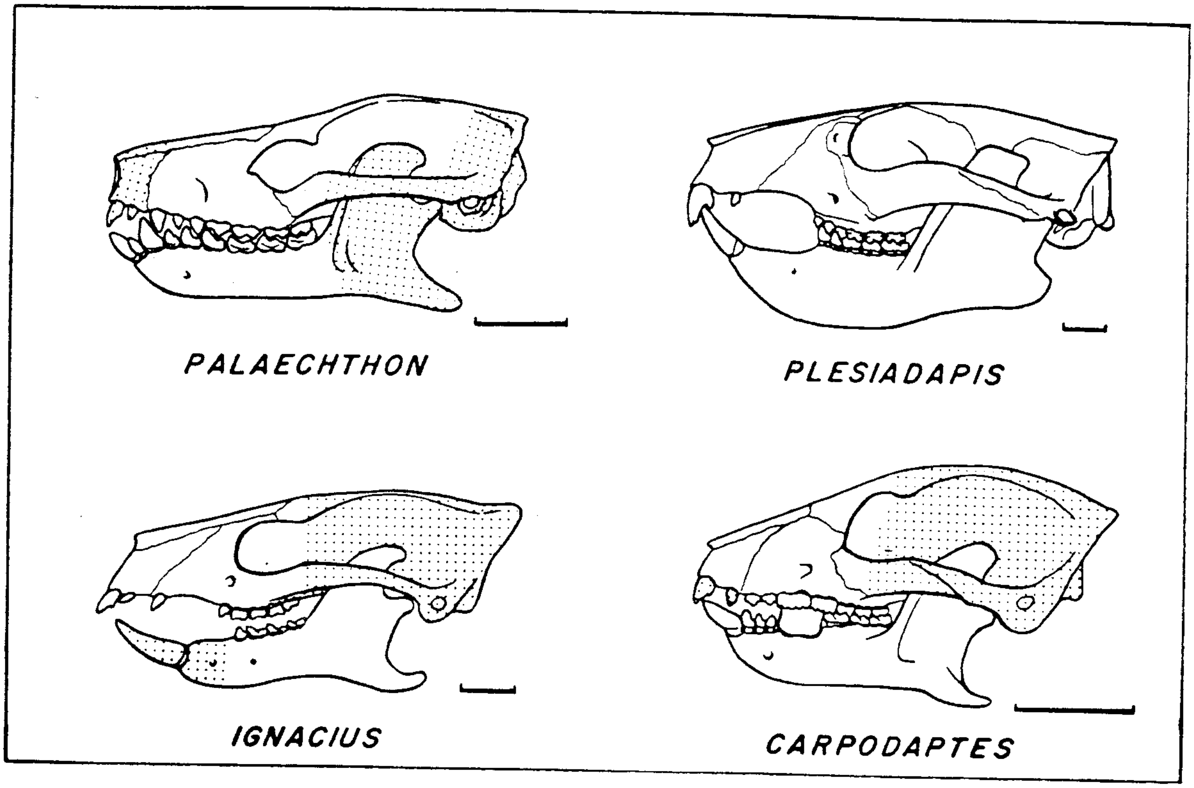


FIGURA 7

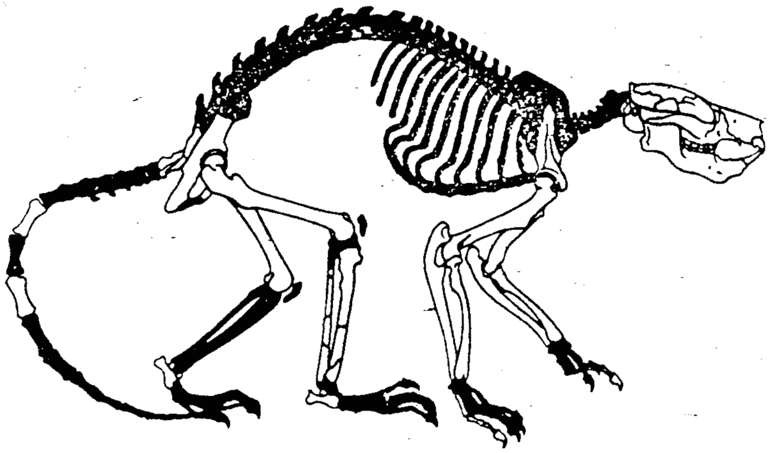


FIGURA 8

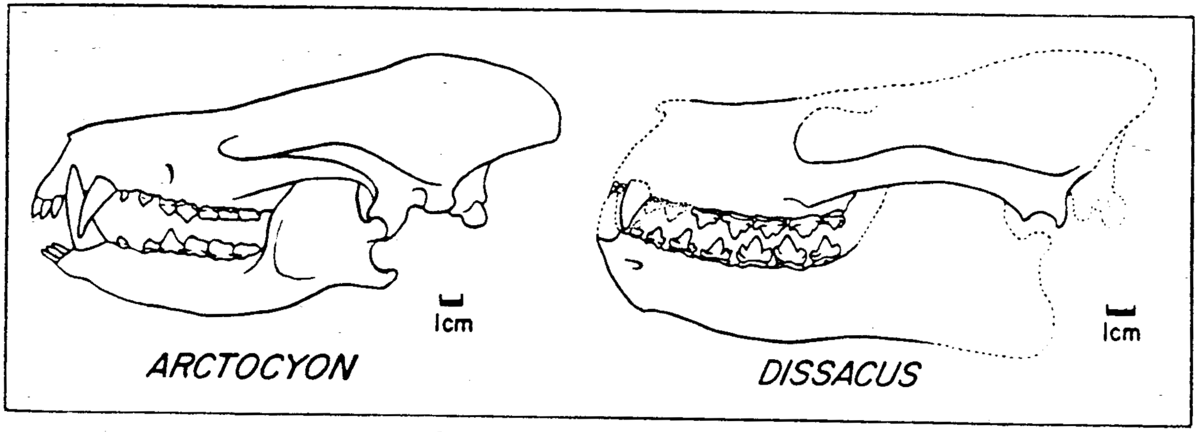


FIGURA 9

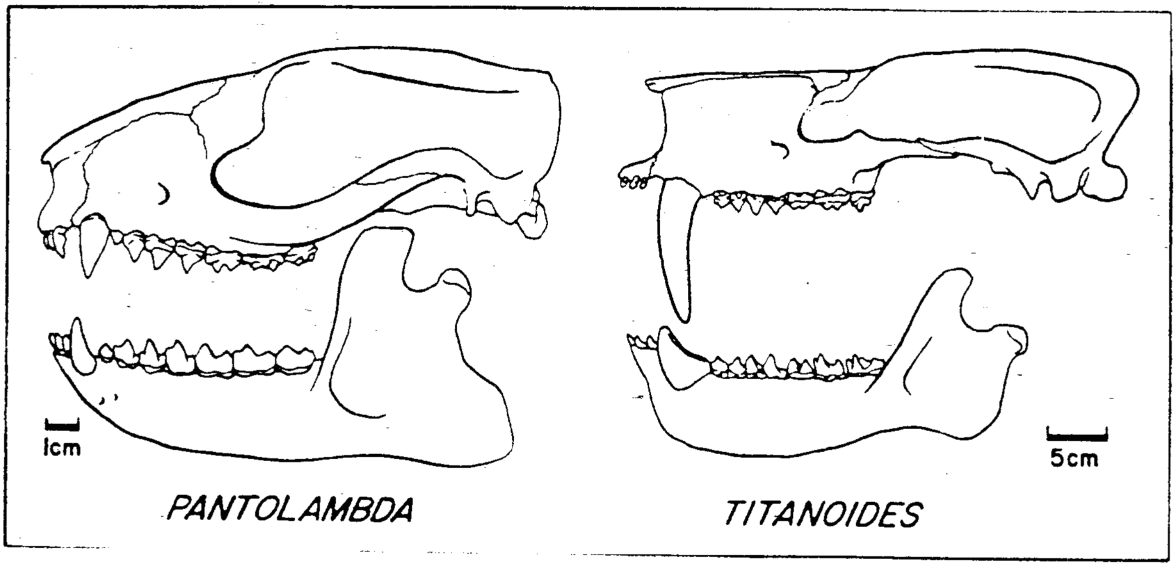
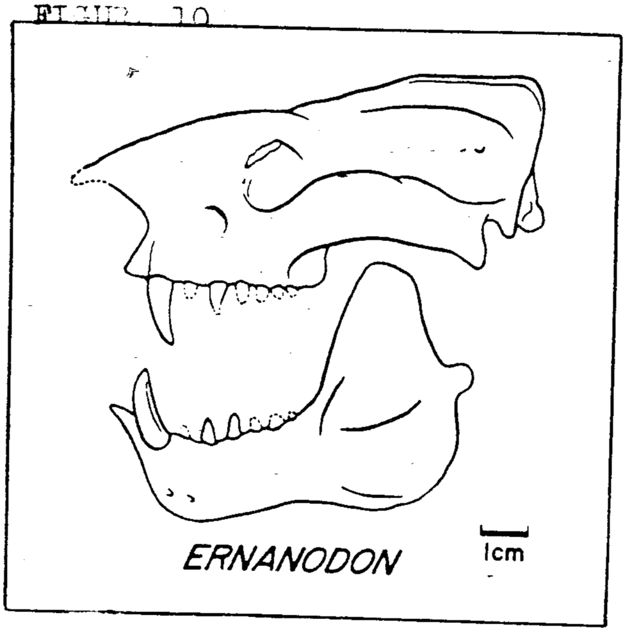


FIGURA 10



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9.5(a)

NEOGENE FAUNAS OF NORTH AMERICA

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INTRODUCTION.

The second half of the Age of Mammals yields ,any stories worth telling. The one that I find grandest and most central, however is the "Savanna Story." While featuring it as the principle theme, I hope to weave in the following secondary subjects:

1) the adaptive radiation of four representatives groups, namely hypsodont horses, camels, elephants and cricetid rodents;

2) intercontinental dispersal patterns cross Beringia and between the American continents;

3) and faunal turnover patterns.

A good general reference on these and related topics is Kurt5win (1971).

SAVANNA STORY

The major clomatic trend during the last fifty-million years appears to have been toward cooler and drier conditions, or less equability. And in the centers of continents, behind cordilleras in the zone of prevailing westerlies, or on coasts of cold-water upwelling, this trend has beeen accelerated. During the mid-Cenozoic on every continent except Antarctica, predominantly forest settings gave way to mosaics of forest and nonforest biomes; savanna, scrub and steppe vegetation expanded, and the importance of grasses increased.

The opening of savannas had a profound affect on mammal faunas (Webb, 1977). Some of the most distinctive groups of the Neogene epoch originated in such settings and some of the most rapid evolutionary outbursts were fomented there. The governing mechanism seems ro have been the prevailing climate which controlled the dominant vegetation which in turn provided the principal selecticve force on land vertebrate faunas. These notions are represented in Figure 1.

HYPSODONT HORSES

The rise of hypsodont horses is a familiar history which illustrates several features of savanna adaptation. In their dentitions, Oligocene horses of the genera Mesohippus and Miohippus developed a complete cheek series of six molariform teeth wich lophate (rether than cuspidate) patterns. Within the early Miocene genus Parahippus the crown height of each molariform tooth neared completion by addition of a crochet and elaboration of the hypostyle. From early species such as P. pristinus to late species such as P. congatus body size doubled. Presumably these animals shifted from browsing to mixed feeding. The next step in this horse history is the genus Merychippus wich appears in the medial Miocene. The late Heningfordian transition to primitive species such as M. primus from advanced Parahippus sucha as P. leonesis is distinguished by the final connection of the crochet from the protoloph to the metaloph, and increasing crown height. From mixed feeding Merychippus had moved to grazing. The genus Merychippus rapidly gave rise to a major radiation of hypsodont horses in the middle and late Miocece (Figure 2). It should be noted that this radiation took place entirely within North America. Only or two hipparionine genera did reach the Old World in the late Miocene; and of course Equus so dispersed in the late Pliocene. In the early Miocene, however, the only equid genus that entended its range to Eurasia was Anchitherium, a ,browsing form derived with little change except size increase from Miohippus. Likewise in North America, such primitive browsing genera as Hypohippus and Megahippus persisted as contemporaries ,of the progressive grazing genera through most of the Miocene.

HYPSODONT CAMELS

The camels also experienced a Miocene radiation as the savanna biome expanded across the midcontinent of North America. They also developed hypsodont cheek teeth wich copious cement and longer, deeper-faced crania to accommodate such dentitions. The most peculiar characteristics of progressive camelids, however are found in their postcranial skeletons. The limbs which even in the Oligocene had quiteclongate proportions, became larger and in many groups atill longer. The most remarkable were the giraffe camels Aepycamelus of the mid to late Miocene, which were closely convergent in size and shape with modern Giraffa. In foot structure the hypsodont camelids experienced a peculiar reversal: instead of remaining unguligrade (on tip toes), as do all other progressive cursorial ungulates, they "fell" to a digitigrade stance, reduced their hooves, and developed a large pad around each digit. (The subordinal name for camels, Tylopoda, refers to this distinctive "cushion foot".) This and a number of related adaptation evidently provided camels with an unusually efficient mode of locomotion in open country.Figure 1. The dominant vegetation in midcontinental North America shifted from forest to savanna to steppe as rain fall declined. Savanna settings were optimum for diverse terrestrial herbivores including grazers and browsers. See text for fuller discussion. Ungulates, especially horses and camels, reached their acme in the late Miocene.Figure 2. Successive genera of horses in the Miocene of North America. Grazers, derived from Parahippus and Merychippus diversified greatly in the later half of the epoch as savanna settings expanded. With the expansion of steppe in latest Miocene and Pliocene the browsers were lost and grazers severely declined. As with hyposodonth Equidar the radiation of Camelidar was confined to North America in the medial to late Miocene (Fig.3). The more primitive browsing genera survived alongside the progressive mixed-feeding and grazing genera until about the end of the Miocene. Camelids disporsed outside of North America only in the late Pliocene when large camelines reached the Old World and medium-sized lamines reached South America.Figure 3. Successive genera of camels in the Miocene of North America. Grazers and mixed-feedrs diversified in the later half of the epoch as savanna settings expanded. With the expansion of steppe environments in the latest Miocene and Pliocene the browsers became extinct and the grazers and mixed-feeders declined.

ELEPHANTIDAE

When one speaks of large mammals images of elephants almost inevitably come to mind. And no better example of savanna adaptations can be found than amon the Proboscidea. The gomphotheres had evolved from the pig-sized Oligocene genus Phiomia in North Africa to the rhino- sized genus Gomphotherium in the mid Miocene of Europe. And this groups was paralleled in its history by the mammutids. Indeed both groups reached North America in the late medial Miocene together. But these early groups were mainly large browsers, not yet true savanna beasts.

The elephantids appear rather suddenly in the late Miocene of Africa; intermediate forms (souch as Stegotetrabelondon) document the rapid transition between long-jawed gomphotheres and short-jawed elephants. The most evident changes are in the dentition and involve markedly increased hypsodonty in the molariform teeth plus the addition of copious cement. As the gomphothere lophids are modified to elephant plates, the plate height, plate compression (from front to back) and late number per tooth increase very rapidly. Meanwhile the cranium becomes markedly deeper and, unlike horses and camels, markedly shorter. ,Elephantids develop "rotary eruption", an unique dental adaptation, in which only one (or parts of two) molariform teeth in each jaw half come into wear at a time, thus permittind a short jaw to accommodate a succession of massive grinders.

The limbs also became proportionally longer in elephantids. They were well-adapted to grazing or mixed-feeding in open-country. The elephants (mammoths) dispersed throughout the Old World during the late Pliocene and early Pleistocene, and reached North America in the early Pleistocene. Gomphotheres reached South America, radiated there and produced some elephant-like adaptations, but elephantids never entered that continent.

CRICETID RODENTS

No order of mammals has proved more successful in distributing widely and diversifying explosively than the Rodentia, and within this order the most successful families have been the Cricentidae and their derivatives, the Microtidae (Voles), and the Muridae (rats and mice). From their Oligocene origins the cricetids diversified in every northern continent; and by the end of the Tertiary, one group had reached South America (with its own subfamilial radiation) and another group had reached Africa and then Madagascar (with another subfamilial radiation). Meanwhile by the mid-Miocene in southern Asia, the Muridae appeared and spread to Australia by the late Pliocene.

The remarkable success of these "mice" has been attributed partly to their efficient chewing mechanism, with lophate teeth and masseter muscles extended forward onto the rostrum, and partly to their very efficient reproductive system with large litters on a monthly basis. The cheek teeth consisted of only there molars in each jaw half. Each molar progresses from a simple four-cuspid patters (as in Eumys) to a lophate pattern with wide reentrant valleys (as in Peromyscus), and finally to a tall (sometimes rooted, often ever-growing) multiprismatic pattern with heavy cement (as in Microtidae) of the Pliocene in north temperate steppe and tundra environments. Both in their appearance and in their function, microtid teeth can be compared to elephantid teeth. Both represent grazing adaptations.

INTERCONTINENTAL DISPERSALS

Each group of savanna-adadpted organisms originated and radiated in the heartland of a single continent. Only later did some members of the group disperse to other continents. One can envision the savanna fauna of each continent as a deep reservoir and the land bridges between them as spillways well up on their sides. As the reservoirs fill up or as the spillways are lowered somewhat, the contents of adjacent reservoirs mix. In such a manner intercontinental dispersals between savanna faunas took place. The secular trend toward climatic deterioration through the late Cenozoic increased the possibilities of such dispersals.

In Figure 4, I have attempted in summarize the Neogene intercontinental dispersals between North and South America, and also between North America and the Old World. In this simplified scheme only two North America and Asia and the Isthmian Link between North and South america. We may focus firs on Beringian interchanges and secondly on Isthmian interchanges.

BERINGIAN INTERCHANGES

The Bering Land Bridge permitted several sets of dispersals between the New World and the Old World. Although the exact tabulation of land mammals genera will be subject to further improvements, the following general points seem secure:- 1) a major set of dispersals reached North Ameri from Asia in , the Hemingfordian (about 20 million years ago);

2) another major set of dispersals moved reciprocally in both , directions during the Hemphillian especially in the late , Hemphillian (about 5 million years ago);

3) the rest of the Pliocene and Pleistocene saw frequent, nearly continuous dispersal events;

4) the direction of movement changed markedly from a nearly balanced reciprocal flow in the Mio-Pliocene to a predominance of taxa moving from Asia to North America in the Pleistocene; and,

5) the habitat prefence of the mammals moving through Beringia shifted from forest and savanna in the Miocene and Pliocene to steppe and in the Pleistocene.

THE GREAT AMERICAN INTERCHANGE

The history of South America's mammals fauna took place almost entirely in isolation, and because of that, the few limited episodes of immigration take on great importance. By the beginning of the Cenozinc three major groups of mammals are recorded, in South America, namely marsupials, edentates, and ungulates. A second introduction of new mammals, evidently by island-hopping or "Noah's Ark" across the Caribbean, brought ceboid primates and hystricognath rodents in the late Oligocene. A third invasion concisted solely of the procyonid (raccoon) Cyonasua 1in the late Miocene. To account for the entire Tertiary mammal fauna of Souch America, one need postulate only six immigrant taxa, there at the beginning two in tla late Oligocene and one in medial Miocene.

Figure 4. Neogene immigrants to North America. From the left, land mammal genera from Eurasia; from the right, land mammal genra from South America. An early peak of Asiatic immigrants marks the Hemingfordian (20 million years ago); nearly continuous peaks also mark the Pliocene and Pleistocene record.

The Great American Interchange produced late Pliocene and Pleistocene immigrations from South America. The great American Interchange introduced new species of mammals into South America on a dramatically augmented scale. In the late Pliocene a continuous land bridge through Panama was produced by convergence of the Cocos Plate and central America, and this rapidly led to a dozen species of land mammals moving in each direction between the American continents. The results in South America included extensive replacemnts of native fauna and intense radiation of immigrant groups, including, canids, llamas, and most notably, cricetid rodents. Half of the present land mammal genera of South America are descendants of Plio-Pleistocene immigrants (Marshall et al., 1982). The reciprocal side of the interchange was less impressive, although it carried South American mammals into North America for the first time since the beginning of the Cenozoic. Most emigrants from South America diversified little, all but three became extinct, and none extended beyond North America into the Old World. They did, however, overwhelmiingly colonize Central America, which is now assigned by zoogeographers to the Neotropical Realm.

FAUNAL EQUILIBRIUM PATTERNS.

The species-equilibrium theory was introduced by MacArthur and Wilson for island biotas over ecological time, but it has since found wide application in tracking the biota of continents, ocean basin, or the whole globe. The faunal equilibrium hypothesis can be put to an especially striking test by the Suth American fauna. The turnover rates and numbers of genera may be compared before, during and after the interchange. Generic diversity, which had been near 72 for at least 6 million years, rose to 84 in the Uquian (at the peak of the interchange) and to 107 in the Ensenadan (also during the interchange); turnover rates also increased markedly as predicted by equilibrium theory.

Equilibrium theory also predicts that the number of immigrants moving from a source fauna to an "island" will depend on the diversity of that source fauna. The same principle applies to a reciprocal intercontinental interchange. For example North America contributed 60 percent more genera o the great American interchange than South America, and that is the aproximate difference in their respective faunal diversities in the Pliocene. A similar imbalance occurs across the Bering Strait in the latest Miocene and Pliocene, with Asia contributing a larger number of immigrants o North Amerca than the reverse.

Equilibrium theory recognizes a dynamic interrelationship between the immigration rate (supplemented by new cladogenetic taxa) and the extinction rate. It thus predicts that waves of new immigrant taxa will surelly produce waves of extinct taxa. In unequal interchanges between continents of different sizes and carrying capacities, the smaller continents will suffer more. Thus the theory predicts many extinctions throughout the Pliocene and Pleistocene, and proportionally heavier impacts in South America and in North America than in the Old World.

LATE CENOZOIC EXTINCTIONS.

Increasing severe and frequent extinctions swept through the land mammal faunas of the late Cenozoic. The largest episode in North America came in the late Hemphillian when nearly 40 genera vanished.The final late Pleistocene extinction waver was more intense than the others of the late Cenozoic, and thus seems to demand a more direct explanation than the others. The two regularly cited causal hypotheses are human predation and climatic change, and the new book by Martin and Klein (1984) still does not wholly resolve this debate between them. I mill conclude by criefly advocating the climatic hypothesis of the Pleistocene extinctions.

Several difficulties beset the human hunting theory. Most of the Pleistocene extinctions in Europe, Asia, and Beringian parts of north America came long after they were inhabited by bans of hunting peples well equipped with lithic toll kits. In temperate North America, however, dere is close coinsidence betwen the firts extensive Pale-Indian records an the last recors of most species of mega fauna. Even so major faunal and floral reorganization indicate severe climatic shifts atr the time, and several groups disappesred at high latitudes but survive at low latitudes. In a longer view, it is quite clear that several major extinction events resulted from climatic deteriotations of the last ten million year. The increasingly severe climates of the late Cenozoic led to the remplacemen of the old native savanna faunas by an increasingly cosmopolitan steppe fauna, especially rich in grazing microtine rodents and remarkably impoverished in large mammmals.

FIGURE 1

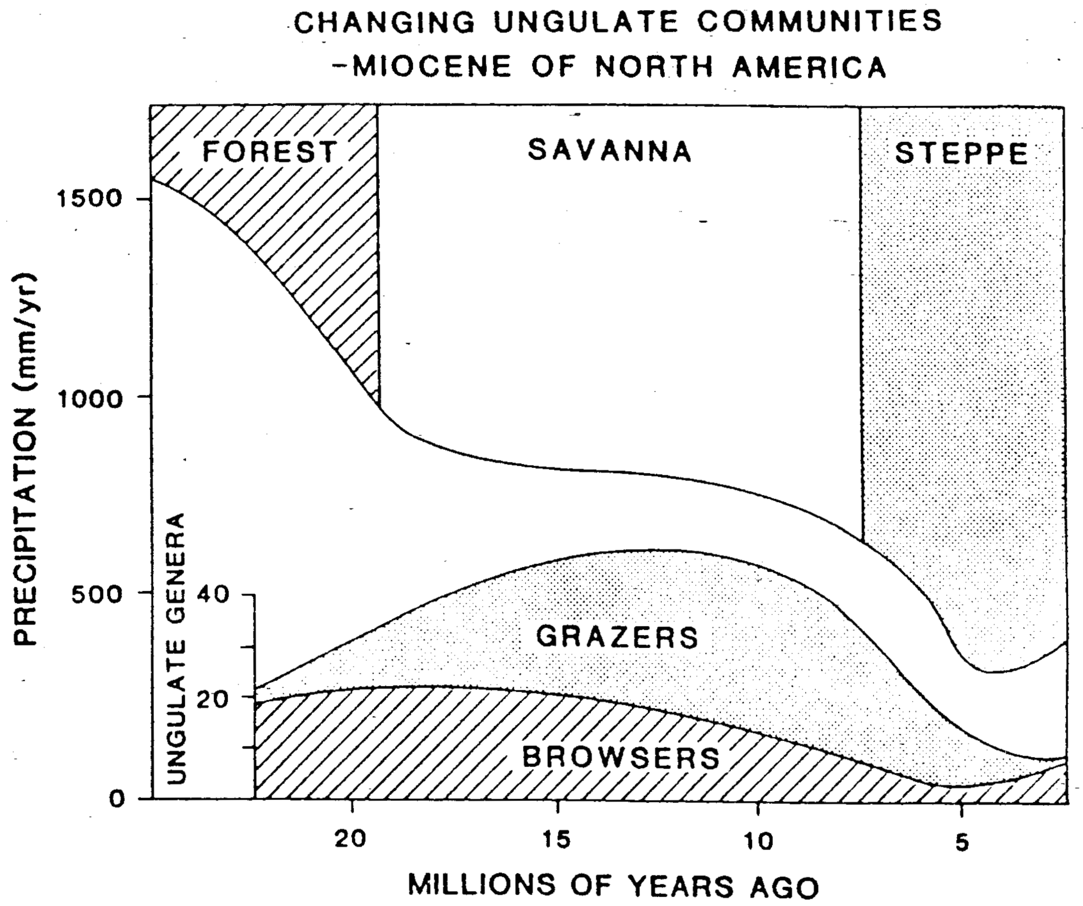

CHANGING UNGULATE COMMUNITIES
-MIOCENE OF NORTH AMERICA
FOREST
SAVANNA
STEPPE
GRAZERS
BROWSERS
PRECIPITATION (mm/yr)
1500
1000
500
0
UNGULATE GENERA
40
20
20
15
10
5
MILLIONS OF YEARS AGO

FIGURA 2

MIOCENE EQUIDAE OF NORTH AMERICA

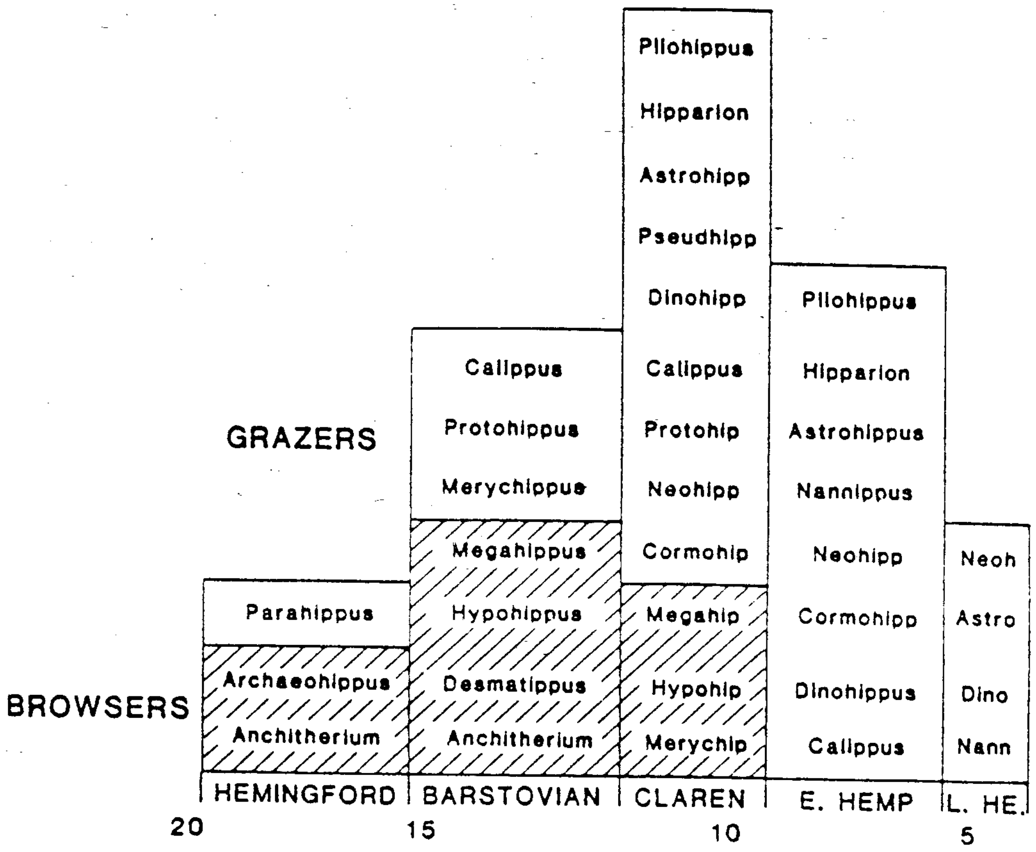


FIGURA 3

MIOCENE CAMELIDAE OF NORTH AMERICA

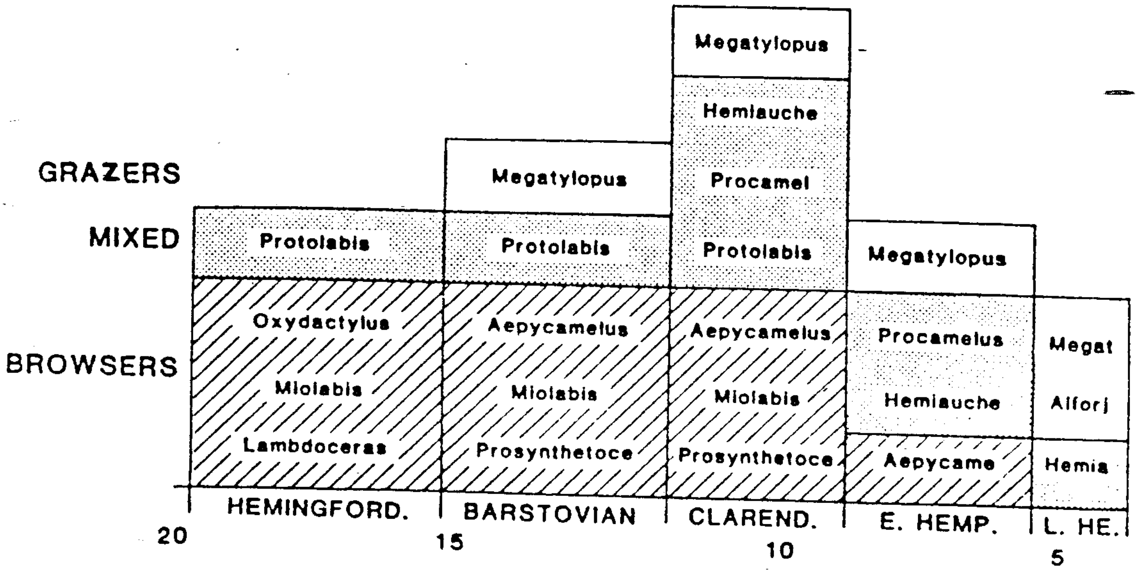
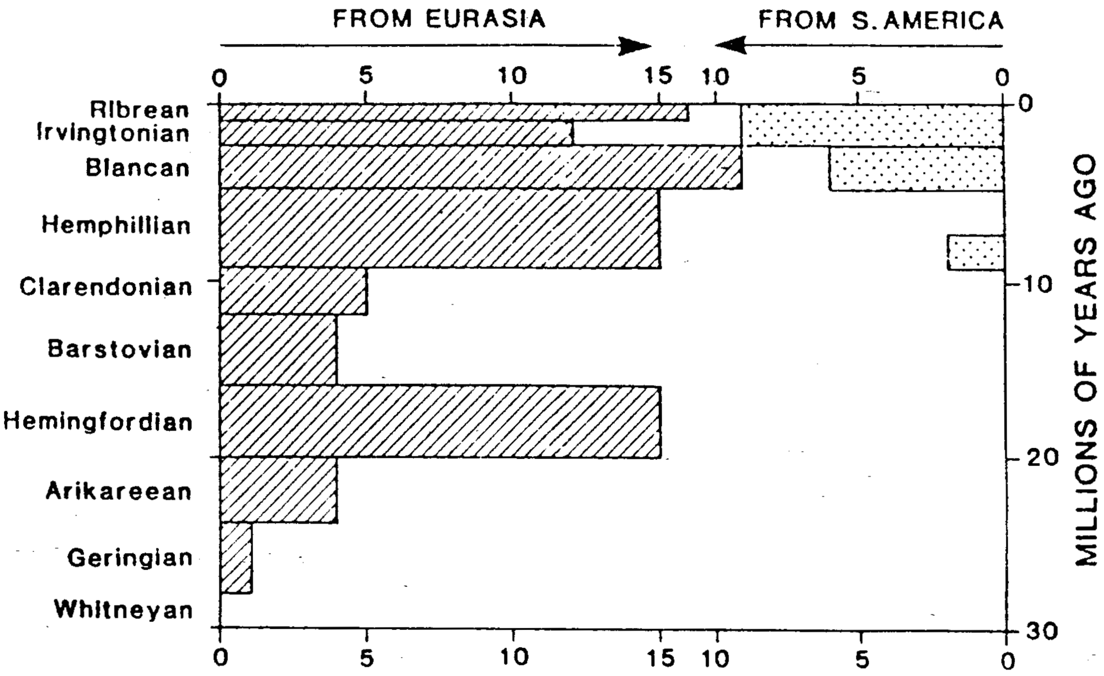


FIGURA 4

IMMIGRANT LAND-MAMMAL GENERA IN NORTH AMERICA



9.6

LA ASCENDENCIA DEL HOMBRE UNA INTRODUCCION.

In: GINGERICH, P.D. BADGLEY, C., ORGANIZER, 1984. MAMMALS. NOTES FOR A SHORT COURSE: KNOXVILLE, TENN., UNIV. TENNESSEE DEPT. GEOL. SCI.STUDIES IN GEOLOGY 8, AND THE PALEONTOLOGICAL SOCIETY, P.182-198.

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INTRODUCTION.

The evolutionary history of humans is well understood in outline, compared to that of many other groups of mammmals. But human evolution remain enigmatic in its details, and these are compelling both scientifically and personally because they relate to the biological uniqueness of humans. Humans are placed in the primate family hominidae, which, in traditional classifications, contains a single living spoecies, Homo sapiens. The closest living relatives of humans are great apes: the chimpanzees Pan paniscus and Pan troglodityes1, the gorila Gorilla gorilla, 1and the orangutan Pongo pygmaeus. 1these apes habve tradiotionally been placed in the family pongidae as the sister group of hominidae. Living Hominidae and Pongidae, together with Hylobatidae (gobbons) comprise the modern representatives of the primate suborder Hominoidea.

In the last two decades, interpretations of the fossil record pertaining to human evolution have changed significantly (Pilbeam, 1980); and there is no consensus viewpoint even now (Ciochon, 1983). A dramatic increase in the recovery of vertebrate fossils from continental, Old World sites has revealed the presence of moderate taxonomic diverity of hominid since the early Miocene. Nonetheless, the hominoid fossil record is fragmentary- in terms of the completeness of individual specimens, the number of body part represented, and the distribution of fossil through geologic time. Studies in molecular evolution of proteins and nucleic acids have provided a consistent "molecular" view of the relative divergence times of livging hominoids Curret general agreement about broad cladistic patterns among the hominoidea reflects a synthesis of thre branching pattern indicated by compatative anatomy and molecular systematic, with absolute divergence times loosely bases on the temporal distribution of fossil.

It is difficult to place humans in the proper perspective of mammalian biology, for both cultural and biological reasons. Religious views adcating a separate origin and purpose of huumans versus the rest of "nature are deeply embedded in western belief systems. Even though these views no longer prevail intellectually, they are still widesoread implicitly in culture and politics. For over a century, scientific view of hominid origins and of man's place in nature have reflected preconception and prejudice as much as natural history and fossils (Pilveam, 1980; Landau et al, 1982). From the standpoint of anatomy and behaviour, humans possess the shatred derived features of mammals and many characterustic primate features. But, humsans are unquestionably strinking and typicsal mammmals. Both the evolutionary anhancement of typical primate attributes and the evolution of features unique to hominids have resulted in a primate lineage of extraordinary behavioral and ecological character.

Below, I review the comparative biology of living hominids to examinhe similarities ans differences betwwen humans and their close relatives, then outline ther homininoids fossil record to document where and when characteristically human features were acquired. Aphylogeny follows that combies information from hominoid molecular systematic and fossil. This review concludes with a brief consideration of the environmental context of human evolutiopn. Useful general references on human evolution include Lee and Devore (1968), Butzer and Izacc (1975),. Jolly and Plog (1976), Legros Clark (1978), Wolpoff (1980), Zohlman (1982), Ciochon and Corrúccini (1983), and Pilbeam 1984).

HUMANS AND PRIMATES.

Humans exhibit many anatomical and behavioral features characteristic of primates in general. Manual dexterity, high visual acuity, diurnal activity patterns, relatively long maturacion times and life spsns, relatively large brain volumens, and elaborate social behavior are common among living primates. Many features viewed as characteristically human--e.g., intellligence, language, culture, tool-malking, and long-lasting social boads- arebut extensions of trends already widespread within the primate order. It is important here to distinguish attributes that are original in human evolution from those that are not original but are nonetheless fundamental.

Skeletal feature thet humans share with most primates include the retention of five digits on both the hand and the foot, an opposable thumb (many primates also possess and opposable big toe), flat nails insteated of claws on the terminal phalanges, short faces, and a high ratio of brain size to body size relative to other mammals. All catarrhines (Old Wold monkeys, apes, and humans) share the same dental formula: 2/2,1/1,2/2,3/3. The premolars retained are considered to be the third and fouth premolars. Hominoids lack tails and possess relatively larger brains than other primates. Their cheek teeth are low-croened; hypoconulids are present on the lower molars, although these are occasionally, with attendant anatomical modifications in the habitually bipedal, with attendant anatomical modifications in the pelvis,hip knee, ankle, foot, vertebral column, ande skull. Dentally hominids differ from pongids (figure 1) in having a less heterodont dentition, with the anterior teeth (incisor and caninos) smaller in relation to cheek teeth than in pongids. Pongids, hylobatids, and Old Wold monkeys have sexually dimorphic canines: males have larger canines in relations to cheek-tooth size than females. The canines of modern humans exhibit little dimosphism in this trait. Finally, hominids are distinguished by large brain sizes relative to body sizes. Living humans have a ratio of brain size to body size over twince that of a chimpanzee (Jerison, 1973; Zihlman, 1982).,Figure1. The skull of male gorilla (a) and of modern Homo sapiens (B) 1(not to scale), to illustrate. differences in dentition and relative brain size (After LeGros Clark, 1978).

Living primates vary in many aspects of natural history, and in some instance, humans represent a departure from the prevailing tred. Most living and extonct primates are associated with forested habitats in tropical to sub-tropical climatic regimes. Hominids, including the earliest austrolopithecines, occur in more open, seasonal habitats. By the end of the pleistocene, humans had come to inhabitat all the climatic extremes of the terrestrial environment.

Most primate diets are opportunistic and omnivorous in terms of the range of foods easten, but are heavily vegetarian in terms of the volume of food sonsumed. Primate foods include friuts, flowers, seeds, leaves, stems, gumm tubers, bird eggs, and insects. Among the hominoids, gobbons, orangutans, and chimps are predominantly frugivorous with leaves and other plant part as secundary component. Gorillas rely mainly on leaves, shoots, and stems, with fruit as a smaller dietary component. Chimps are known to eat meat on occasion (Teleki, 1975). Humans depart from all of these dietary pattern in being omnivorous: their diets are still predominantly vegetarian, but a significant portion is also meat. Living hunter-gastherers have diverse vegetarian diets that include nuts, fruits, berries, leafy greens, tubers, and resins; hunted meat rarely exceeds 40% of the diet (Lee,1968). Many sedentary societies rely havily on grains (the sees product of the Graminae, tha Grasses), such as wheat, rice, and corn. This dietary dependence is distinctive among the hominoid and would not be possible among humans without food preparation such as grinding and cooking. Primates are very selective forangers and consume food on the spot. Humans differ in transporting, storing, and sharing a significant portion of their foor.

Most primates live year-round social groups, comprising one ore more adult of both sexes and the offspring of the female(s). Most species are polygamous, although styles of polygamy and the amount of interaction among males and females varies widely. For many species, females remain in their natal groups and breeding males are inmigrants from other groups. Wrangham (1980) porporses an ecological model for these female-bonded groups in which the primary deteriminats of group size is feeding ciompetition. Species that are polygamous are also sexually dimorphic in body size, with males always the larger sex. Size dimorphism rearches its gretes extreme in the orangutan and gorilla; males may weigh twince axs much ads females (Zihlman, 1982). Size dimorphism may have been even more extreme mong some miocene hominoids, similar cheek teeth of Ramapithecus 1and Sivapithecus 1at several late Miocene fossil sites (de Bonis, 1983).

Among living hominoids, the great apes sre polygamous and gibbons are monogamous. Orangs are the most solitary of the apes. Groups consist of adults females and their offspring in adjacent feeding areas. The territory of a dominant male typically overlaps the smalller territories of several females. Gorillas leive in small groups comprising a domiannt male, several femares, and their offspring. Chimps live in multi- male, multi-female groups, in which males tend to be motre closely related than females (Nishida,1979). chimp intermale aggression is highest asmong the apes:aggression is greatest in inter groups conflicts, and next over intra-group dominace hierarchies. Gibbons live in small social units of adults male and female plus offspring. Human are usually monogamous, with a similar social unit. But these families typically aggregate in loose or tight social, economic, and political units. These units may shift composition and size, depending on resource distribution including seasonal variation.

Relative to other primates, humans infants are altricial (underdeveloped) at birth. Both the central nervrvous system and the inmune system are inmature, and there in long period of postnatal brain growth. Chimp and human have approximately equal ratios of brain weight to body weight in newborns. But, brain advancement (newborn) world. The African apes inhabit forest of central Africa; no fossils are known for Pan 1and Gorilla1. Gibbons live today only in southeast Asia; they have a sparse and ambiguous fossils record in Africa and Eurasia. The Orangutan lives today only in Indonesia; the only fossils attributable to Pongo 1are from the Pleistocene of southeast Asia. With the exception of homo sapiens1, homonoids are less "successful""-- in terms of taxonomic diversity, abundance, and distribution- now than during most of the Neogene.Figure 2 The distribution of Neogene Homonoid localities in the Old world.

The distribution of Neogene hominoid fossil localities (figure 2) exhibits a distinctive geographic and temporal pattern. Early Miocene hominoids of the Proconsul 1group are known exclusively from East Africa, primarily from sites located in the western Rift Valley (Andrews and Van Couvering, 1975). During the middle Miocene, the East African record is vry poor, but hominoids (the Dryopithecus 1group and Ramapithecus 1group) occur widely through Eurasia, from Spain to China. Hominoids persist until about 7 mybp in eastern and southern Asia, then are unkown in Eurasia until the middle Pleintocene. In Africa, a few hominoidd fossils of uncertain affinity are known at the end of the Miocene. Then, the fossil record is fairly dense from about 3.7 mybp on in East Africa, mainly from the eastern Rift Valley, and from about 3.0 mybp on in southern Africa (figure 3). The temporal distribution of hominoid fossils from East Africa matches that of other vertebrate fossils and reflects mainly the disparate times of rifting and rapid sedimentation in the two arms of the Rift Valley, with the eastern Rift Valley experiencing more recent tectonic activity (Beherensmeyer, 1982). The virtual absence of hominoid and other vertebrate remains in East Africa from 14-4 mybp cannot be taken as evidence for the absence of living hominoid. In Eurasia, however, vertebrate faunas are known through the Neogene, hence, the absence of hominoids from the late Miocene until the Pleistocene apparently reflects the disappearence of the Miocene forms.Figure 3 The temporal and geographic distribution of Neogene hominoid localities.

Much of the hominoid fossil record consist of jaws and isolated teeth, although cranial and post-cranial elements are finally becoming known for a few taxa. With the rare esception, hominoid fossils are uncommon at the sites where they are known. The predominance of dental material, especially cheek teeth, has not permitted unambiguous evaluation of taxonomic diversity at the genus and species levels (Badgley et al., 1984; Pilbeam, 1984). For the present discussion, I employ the taxonomically neutral terms ""drymorph" and "ramamorph," after Ward and Pilbeam (1983), with reference to the miocenen Homonoids. The relationships of these terms to a conventional taxonomy is given below. It should be stressed, however, that no taxonomic scheme in in general agreement, and this one can be considered a representative frequency distribution rather than a definitive scheme. Information is drawn from Freagle and Kay (1983) and Kelly and Pilbeam (in press).

SYSTEMATICS OF FOSSIL AND LIVING HOMINOIDEA

Propliopithecidae: *Aegyptopithecus, Propliopithecus, Pliopithecus.*

Proconculidae (African dryomorphs), proconsul, Rangwapithecus, Dendropithecus, Limnopithecus, Micropithecus.

Dryopithecidae: (European dryomorphs), *Dryopithecus, Rudapithecus, Bodvapithecus.*

Ramapithecidae:(ramamorphs), *Ramapithecus, Sivapithecus, Renyapithecus, Ouranopithecus, Gigantopithecus*

Hylobatidae: *Hylobates, Symphalangus*

Pongidae, Pongo, Pan, Gorilla

Hominidae: *Australopithecus, Homo*

A morphologically distintive suite of early to middle Miocene hominoids, the dryomorphs, is known from East Africa and Europa. the East African recird begins at bout 23 mybp with the earliest specimens of Proconsul 1from Meswa Bridge, Kenya, and continues until about 14 mybp at ft. Ternan (Andrews, 1981). The African material includes al least eight species: three small-bodies ones the size gibbons (Linmopithecus, Dendropithecus, Micropithecus) 1and five medium sized forms (2kg) three species of Proconsul 1and two species of Rangwapithecus1. IN dental features, the African dryomorphs exhibit variable enamel thickness (most forms have thin enamel); canines are dimorphic; incisors are large relative to cheek teeth; molars bear cingula. Thesre hominoids had moderately long faces; they moved quqdrupedally in an arboreal setting (Rose, 1983). The European dryomorphs, including Dryopithecus, Rudapithecus 1and Bodvapithecus 1(Kelley and Pilbeam, iin press), have thin enamel, molar cingula, dinorphic canines, small to moderate incisors, and a sectorial P . The earlies Old World monkeys are known from about 19 mybp. probably, the earliest dryomorph materiales postdates the split of hominoids and cercopithecoids (Pilbeam, 1984).

A second distinctive suite of miocene hominoids, the ramamorphs, is known primarily from the middle to late Miocene of Eurasia. Common taxa in this group are Ramapithecus 1and Sivapithecus1, although there is currently dispute and ambiguity about the taxonbomic diversity represented by these taxa (Kay, 1982; Badgley at al., in press). The earliest ramamorph material consists of recently discovered specimens attributed to Sivapithecus 1from Bylux in Northen Kenia (Walter and leakey,1984); this sites is dated at 17 mybp and is thus constemporaneus with the period of maximum diversity of the African Dryomorphs. The body size range of ramamorphs is 15-17 kg, with "Ramaphitecus" 1referring to the smaller form (15-20 kg) and "Sivapithecus" 1referring to material mainly in the range of 40-50 kg. (pilbeam, 1980). These hominoids exhibits very thick enamel on the cheek teeth, moderate canine dimorphism, megadonty (cheek teeth very large in relation to body size) and a some what molarized. Molar cingula are absent. Insisors and canines are relatively small in Ramapithecus 1and larger in Sivapithecus 1represent female and males, respectively small in Ramapithecus 1and larger in SIvapithecus1. It is plausible, at some sites, that Ramapithecus 1and Sivapiythecus represent females and males, respectively, of one species; if so, then the sexusal dimorphism in body size is greather than that of any living primates (DeBonis, 1983; Wu et al.;

1983). Postcranially, ramamorphs are not well known, except for unassociated skeletal elements of the forelimb, hidlimb, and foot of Sivapithecus1, from Siwalik sites of pakistan (Pilbeam el tal , 1980) The f unctional interpretation of these elemnsts indicates that Sivapithecus moved quadrupedally, with the main emphasis on climbing, and lacked the locomotory specialization for knuckle-walking, sus pension, or bipedalism of living large hominoids (Rose, 1983, in press). The only cranial material known form ramamorphs is from Lufeng, a late Miocene sites in southwest China; nearly complete skulls of both the large and small homonoid have been recovered (Lu et al 1981; Wu et al 1982). They are crushed flat and it is not possible to estimate brain volumes.

The hominoid fossil record is almost blank between 7 and 4 mybp. The earliest undisputed hominoid fossil come fdrom Laetoli in northern Tanzania, at 3.7 mybp and Hadar in Ethiopia at around 3.0 mybp, and are considered represent one taxon, Austrolopithecus afarensis 1(Johanson and White, 1980). This homind is fully bepedal, as evidenced not only by the morphology of hindlimb elements, but also by a remarkable set of three hominid trackways at Laetoli (Leakey and Hay, 1979; hay and Leakey, 1982). Recently, Stern and Susman (1983) have argued that this hominid was also capable of considerable arboreal maneuverability as well. Austrolopithecines are known from East Africa and South African localities, from 3.7 - 1.0 mybp. At least four species are known (A. Afarecnis, A. Africanus, A robustus, and A. boisei)1, with precise ancestor-descendant relationships unresolved at present. One of the major controversies is Whether A. afarencis or A. africanus 1is at the base of the split between later australopithecines and Homo 1(white et al; 1983) The yougest austrolopithecine, A. boisei1, robustus form from East Africa,m disappeared around 1 mybp. Brain volumes of the early austrolopithecines are 450 - 550 cc, 20 - 30 % larger than that of ape of similar body size. Cheek teeth are megadont with thick enamel, and the P is molarized. Canines are small, incisiform, and exhibit little sexualdimorphism. Size dimorphism is moderate, greter than in modern humans.

The first stone tools are known from Koobi Fora and Olduvai Gorge at about 2.1 mybp. While tools have considered to be associated only with Homo,1, their appearance antedates the earliest record of Homo 1by about 0.3 my. The distribution of vertebrate remains and stone toools at these early sites suggests that hominids used tools for food- processing, possibly for hunting, and may have established long-term occupation sites (Isaac, 1978).

The first appearance of *homo* (*H. habilis*) is from koobi Fora at about 1.8 mybp. The earliest Homo is distinguished by a considerably larger brain (700 cc) and by different tooth proportions; cheek teeth are smaller relativel to the anterior dentition, compared to Australopithecus1. By abouth 1.75 mybp,H: habilis 1had disappeared and was replaced by H. erectus in East Africa. H. erectus 1is characterized by larger body size and greather robustness than H habilis 1, a further expansion of brain size (850-1000 cc=, and a further diminution of cheek tooth size. This species was the first to leave Africa and bevcome widely distributed throughout the Old Worl. Fossils attributed to H. erectus 1are known from Java abouth 1 mybp and from China at about 0.8 mybp. Around 0.3 mybp, H erectus 1was succeeded by "Archaic" H. sapiens, 1including the neanderthals. "Modern H. sapiens 1appeared about 40 000 years bp. succeeding archaic H sapiens sbruptly. Morphological trends in the lineage leading from H erectus 1to modern H sapiens 1include an increase in brain size, a decreace in tooth size, and in the robustness of skeletons and skulls. Changes in distintive stone-tool industries from Africa and Europe match.

Figure 4 represente an attempt to synthesize the hominoid fossil record and molecular systematics into a provisional phylogeny. In this scheme, hominoid evolutionary history contains multiple radiations from the early Miocene onward. The radiation of large hominoids begins around 16 mybp, with a split into a predominantly Eurasian clade (ramamorphs + Pongo 1) and predominantly African calde (leading to hiomo, Pan1, and Gorilla1). The common ancestor of the clades leading to Pongo 1and Homo 1is undocumented by fossils, as is the common ancestor of Homo 1and the African apes. Thus, much remains to be learned, even of this well studied case of mammalian evolutionary histry.Figure 4. Phylogeny of Neogene Hominoids, incorporating molecular and anatomical data with the temporal and geographic distribution of fossils. Based of information in Pilbeam (1984) and (Kelley and Pilbeam, in press).

THE ENVIRONMENT AND HUMAN EVOLUTION.

The ecological significance of the changes in geographic distribution and morphology of hominoids can be understood, in part, in terms of global paleoenvironmental history. In the last two decedes, there has been considerable progress in reconstructing the positions of land masses and oceans, ocean temperatures and circulation patterns. These physical factors are important determinants of climate. Geological, floral, and faunal studies of the continental Neogene of the Old Wold indicate changes in geographic barriers and in the distribution and composition of terrestrial plant and animal comunities.

Hominoids probably arose in Africa, since they are known only in Africa from the time of Aegyptopithecus 1through the radiation of the african Dryomorphs. The first hominoids outside Africa are known from Arabia and Turkey in the middle Miocene (Figure 3). Until the early Miocene, Afro-Arabia was an isolated land mass, lying South of its present position and separated from Eurasia by the Thetyan seaway. During the period 19 - 16 mybp, contact ocurred between Arabia and Eurasia in a pattern of intermittent land bridges, large island, and narrow seways througj what is now the eastern Mediterranean and the Middle East. somewhat leter, contact ocurred in the western Mediterranean. These land connections facilitated the dispersal of land animals from Eurasia into Europe and vece versa. Two main dispersal phases are recognized for mammals, one around 18 mybp and another around 15 mybp. In the first dispersal, more taxa moved from Asia to Africa; in the second, more taxa moved from Africa to Asia (H. Thomas, paper presented April 6, 1984, at the " Ancestors" conference, American Museum of natural History, New York). Hominoids may have expanded into Eurasia in multiple dispersal events. The existence of morphologically heterogeneous hominoids--i.e. the european dryomorphsd and the ramamorphs- both with morphological counterparts in Africa- suggests that large hominoids dispersed from Africa more than once.

Within East Africa, tectonic activity centered in the western Rift Valley and orogenic uplift of the East African Highlands led to the establishement of complex biogeographic provincialism in the early Miocene (Andrews and Van Couvering, 1975). Mammalian faunal endemism occurs as early as 18 mybp between sites in the western Rift Valley (e.g., Rusinga) and the eastern Rifth Valley (e.g.,Buluk), with dryomorphs of the Proconsul 1group to the west and the earliest fossils with ramamorph affinities to the east. Climatic, floral, and faunal differences occur as well (A. Walker, paper presented April 6, 1984, at the "Ancestors" conference, American Museum of Natural History, new York), whith the western sites being closer to the lowland tropical forest block (Andrews and Van Couvering, 1975).

Once out of Africa, the hominoids of the mid-late Miocene dispersed throughout Eurasia. the earliest record of ramamorphs in siwalik localities of the Indian subcontinent is 12 mybp, from the type Chinji Formation of northen Pakistan (s.m.. Raza and N:M: Johnson, pers. comm.). Ramapithecus and Sivapithecus 1persist in Siwalik localities until about 7 mybp. From this time on, fossils of the ramamorph group disappear from Eurasia, although it now apppears likely that an eastern population of ramamorphs gave rise to Pongo 1(Andrews and Cronin, 1982; Ward and Pilbeam, 1983). What these thick-enamelled hominoids ate is an unresolved issue, although their diet is probably in the general domain of large homonoid herbivory. The bioestratigraphic association of Siwalik ramasmorphs whit presumed forest-dewelling mammals such as tragulids and deinotheres (Barry et al, 1982) suggests that the almost simultaneous disappearance of all these taxa is related to a dwindling vegetation association such as the South Asian tropical forest that today occupies the Malay region (Badgley et al., in press).

Substantial changes in global climates occurred during the Miocene. The northward movement of the Africa plate brought about both the gradual closing of the Tethys Sea and the opening of Drake's passage, the latter leading to the formation of the circum-Antartic ocean current. The establishement of this current led to a pronounced intensification of latitudinal temperature differentiation. From the early Miocene until the present, ocean surface temperatures have declined by 10 c (Kennett, 1977). The consequence of this climatic cooling on the forest and eventually by woodland and grassland (Bonnefille, 1979). By the and of the miocene, the vegetation type known as savannah-a grassland with less than 20% forest canopy--prevailed in much of east Africa. Modern savannah environments are characterized by higly sesonal rainfall; as a result of the seasonal availability of primary productivity, many species of savannah mammmals migrate.

At Laetoli, where the first undisputed hominids occur, is a series of ash layers containing thousand of vertebrate footprints. This secuence, known as the Footprint Tuft, was deposited over a period of a few weeks spanning the end of the dry seson and beginning of the rainy season (Hay and Leakey, 1982). In the footprint record, thre hominid trackways occur with mammals whose modern counterparts are the earliest wet-season inmigrants in a savannah environment. The "cause" of bipedalism is an ancient and unresolved puzzle in human evolution. The Footprint Tuft offers a plausible ecological hypotesis-- that bipedalism enabled these large hominoids to migrate among food resources that displayed an increasingly heterogeneous spatial and temporal distribution.

In the PLio-Pleistocene, intense climatic fluctuations--related to the growth of the Antartic ice cap and the onset of continental gleciation in the northern hemisphere--were added to the global tred in climatic cooling. For primates with a dentition inherited from frugivorous and folivorous ancestors, the savannah must have posed a seriois clallenge in terms of diet. One of the most curious aspects of humans evolution us how, throught the hominoid-hominid transition, diets changed from the inferred more typical antropoid diet of the Miocene hominoids to a condition of omnivory in wich meat and diverse plant part other than leaves and fruit are significant component. This dietary shift is puzzling because its is not reflected in modification of the dentition to the extent thet is present in other mammals. The hominid dentition possesses noither high-crowned nor sectorial teeth. The development of tools-probably first in wood, later in stone and bone--may have served the roles of food-gathering and processing that are served by the dentition in other mammals.

Tools may have been developed initiali for procurement of plant foods or for defese or for scavenging carcasses or for some combination of these activities. The tamphonomy of eatrly artifact sites indicates that hominids carried the raw materials considerable distances (up to 20 km) from their geological sources to the location where tools were manufactured and employed (Isaac, 1976;1978). The reapeaded associations of stone-tool concentrations with concentrations of vertebrate remains suggest that many tools were created for the procesing, although not necessarily the hunting, of animals food.

The expansion of the range of Homo 1through the Old World occurred during the intense climatic fluctuations of the Pleistocene and is perhaps related to the divversity of potential food resources facilitated by the development of tools. Human populations, while spreading rapidly through the Old Wold and into the New World around 13,000 bp, remained relatively small untill quite recently. The rapid increase in polulation size achieved by modern Homo sapiens is coincident with the control of fool production, manifest ultimately in the cultivation of plants and domestication of animals. With these measure, human populations were no longer depent on following the ever-changing food resources on a sessonal or longer basis.

Agriculture permitted sedentism and sedentism prodeced cites.

CONCLUSION

The ecological perspective offered in the preceding section is based primarily on the relation of hominoids and hominid to food resources. Although this synthesis is plausible, it is speculative and will probeably remain so. Two aspect of the hominoid fossil record hinder the resolution of some of the major issues in human evolution. The first is a sampling problem as pertains mainly to the Miocene portion of the fossil record: the fossil record, althougt much improved compared to twenty years ago, is still scant. The worldwide gap from 7-4 mybp, the larger gap in the agrican record,and the absence of fossils of the african apes obcure the transition from hominoid to hominid. The Plio.Pleistocene record, by comparition, is rich. But, the development of most characteristically hominid features are not documented in skeletal remains. Most of these features are behavioral-- e.g., the emergence of language, art, and ranked societies. Even the changing ralationship to food resources is not reflected in dental feature as much as in population sizes and social organization.

Since most aspect of behavioral are unobservable in fossils, many essential transition in becoming human must be reconstructed--if at all-- on the basis of the information from other living systems. It is for this reason that the study of human origin has forested so much research on the ecology and behavior of diverse human populations, non-human primates, and other mammals. These efforts to examine human ecology and behavior by analogy have made substantial contributions to the biology of mammals in general, as well as to our own evolutionary history.

ACKNOWLEDGMENTS

B. Holly Smith and Philip Gingerich provided helpful discution and comments on this manuscript. Figures 2-4 were drafted by Karen Klitz.

FIGURA 1

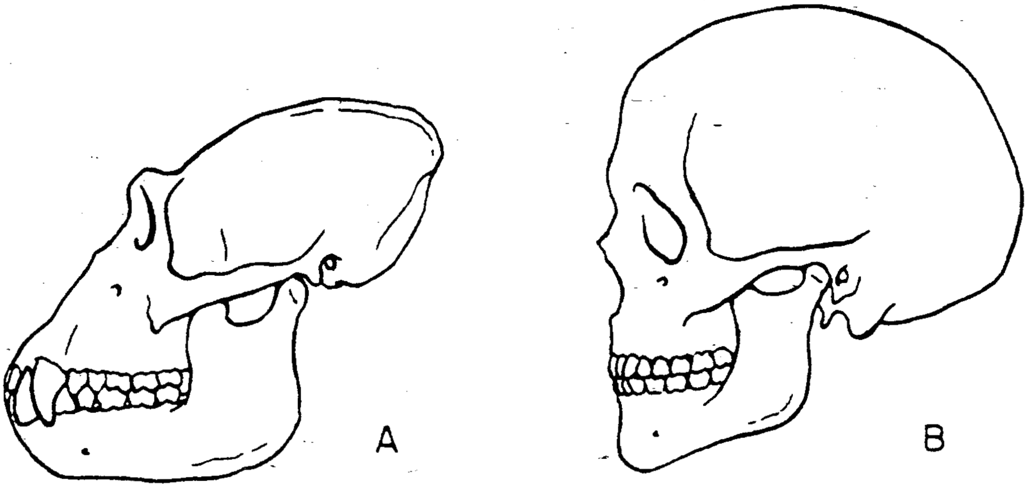


FIGURA 2

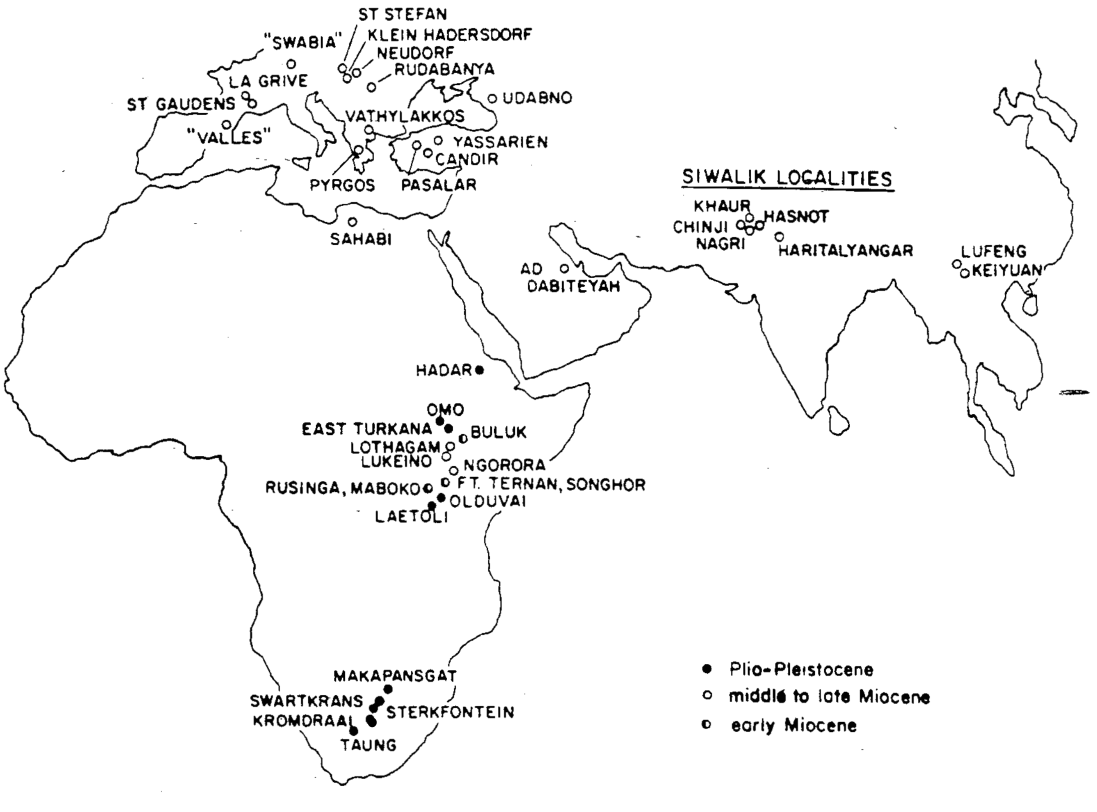
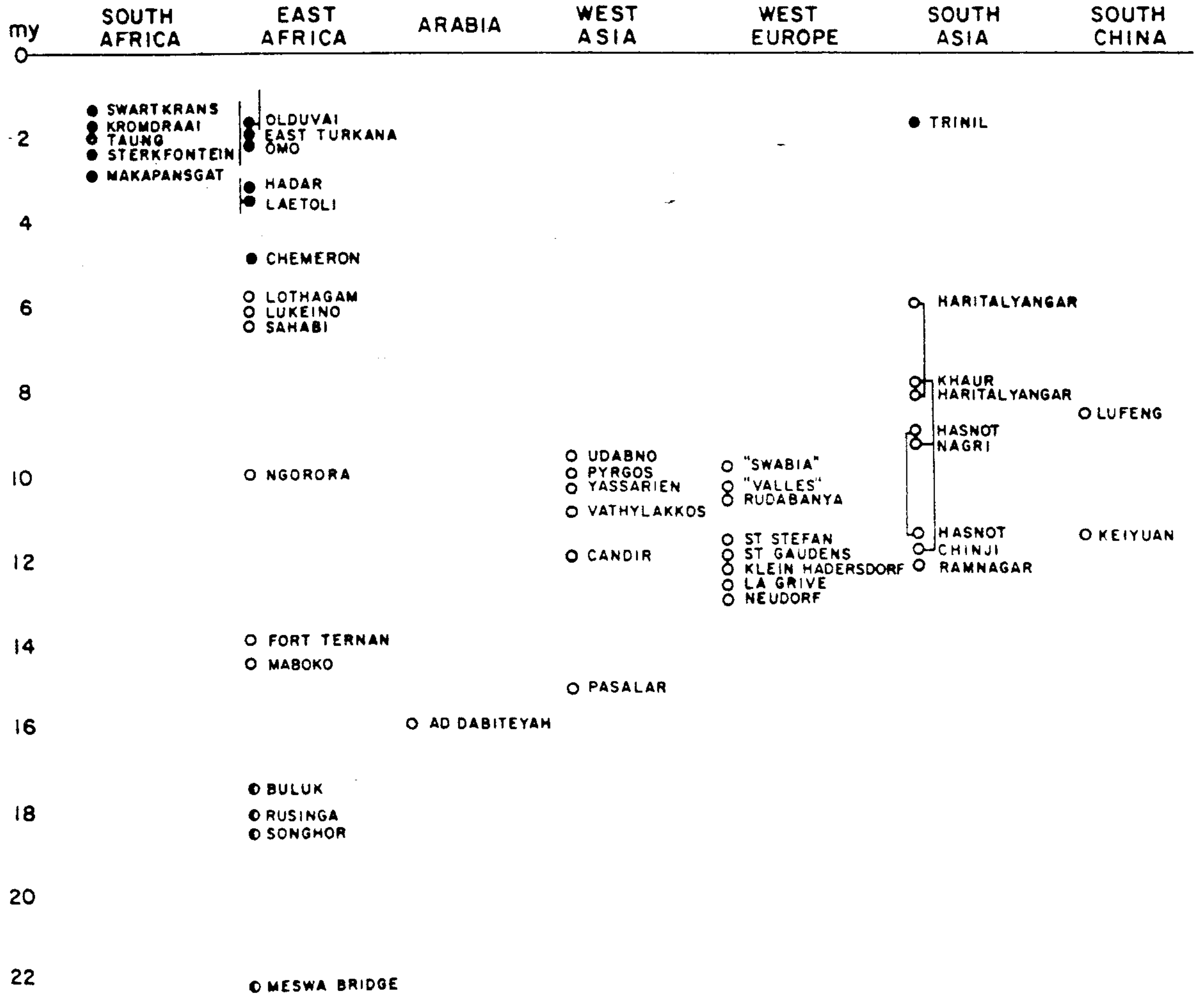


FIGURA 3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SWARTKRANS
KROMDRAAI
TAUNG
STERKFONTEIN
MAKAPANSGAT
OLDUVAI
EAST TURKANA
OMO
HADAR
LAETOLI
CHEMERON
LOTHAGAM
LUKEINO
SAHABI
NGORORA
FORT TERNAN
MABOKO
BULUK
RUSINGA
SONGHOR
MESWA BRIDGE
AD DABITEYAH
UDABNO
PYRGOS
YASSARIEN
VATHYLAKKOS
CANDIR
PASALAR
"SWABIA"
"VALLES"
RUDABANYA
ST STEFAN
ST GAUDENS
KLEIN HADERSDORF
LA GRIVE
NEUDORF
TRINIL
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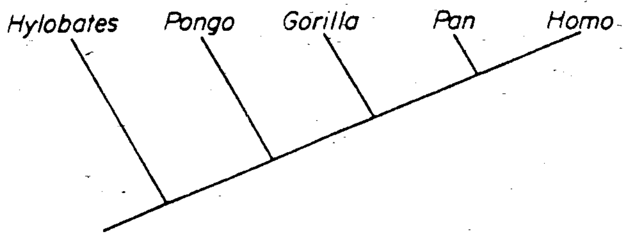
CHINJI
RAMNAGAR
LUFENG
KEIYUAN

FIGURA 4


Hylobates
Pongo
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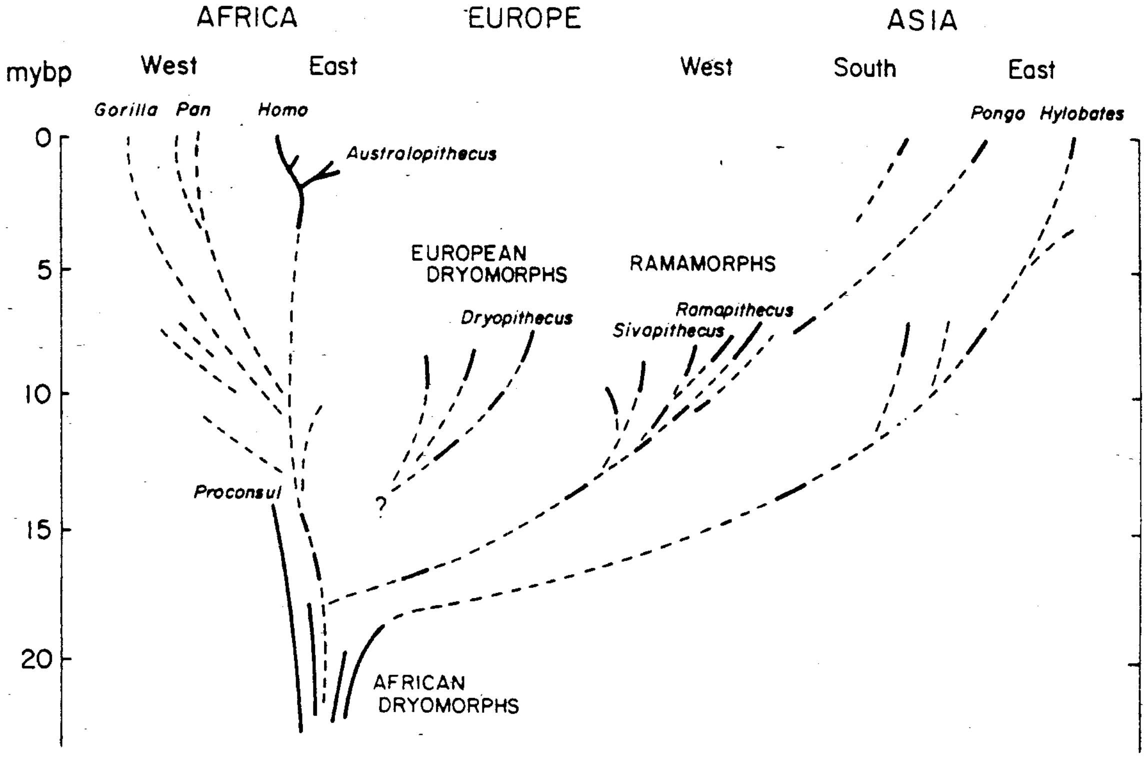
Homo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EUROPEAN DRYOMORPHS
RAMAMORPHS
Dryopithecus
Ramapithecus
Sivapithecus
Proconsul
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AFRICAN DRYOMORPHS

SECCION IV: RELEVANCIA DE LA INFORMACION PALEONTOLOGICA EN LA TEORIA BIOLOGICA.

Capítulo 10. Contribuciones teóricas diversas.

10.1 PREAMBULO

El propósito de esta sección, es destacar la relevancia que ha tenido la información paleontológica en la formulación de nuevas ideas, conceptos o teorías biológicas, así como en la reformulación de otras. las contribuciones han sido muy numerosas, en campos variados que se extienden desde la Biología Evolutiva, hasta la Ecología; Todas tienen en comun que constituyen una reflexión o interpretaciómn del registro fósil- frecuentemente en relación estrecha con el registro estratigráfico- vehículo que permite asomarnos al pasado y que muestra la secuencia de cambios que han tenido el intrincado camino de la evolución organica. Esta posibilidad es privativa de las ciencias Histórico-geológicas, y no puede tenerse en las neontológicas, por lo que debe aprovecharse al máximo.

En el capítulo que nos ocupa, se han seleccionado sólo algunos topicos en donde las contribuciones han sido importantes, sin pretender mostrar completo, el amplio espectro conceptual que han cubierto. La primera parte del mismo está dedicada a cuestiones de Biología Evolutiva, e incluye estos artículos: En el primero, David Raup diserta sobre el origen geológico temprano de los grandes taxas, señalando mediante un analisis probabilistico de la distribución de los tiempos de divergencia (que es el tiempo transcurrido desde que existió el ancestro común) teóricos en comparación co los observados, que el surgimiento temprano de los grandes grupos es un rasgo derivado de la geometria del árbol evolutivo, es decir una propiedad topológica de los conjuntos sucesivamente divergentes. En cambio, la interpretación de la individualización morfológica de los distintos phyla, todavia no ha sido ecológicamente explicada de manera satisfactoria.

En el segundo trabajo, Douglas Erwin discute el tema de relojes moleculares, filogenias moleculares y el origen de los phyla, señala que aunque las secuencias de proteínas, RNA y DNA se han usado ampliamente para elaborar filogenias o para determinar el timepo de divergencia, en especial cuandio la información paelontológica es insuficiente o falta del todo, los resultados cpon frecuencia son ambiguos, equívocos o peor aun, conducen a errores, debido a que la redundancia inherente del código genético, frecuentemente enmascara la homoplasia, imposibilitando as5h 1recostruir inequiívocamente las secuencias de divergencia.Concluye indicando que un uso mas afortunado de esta técnica sería su aplicación en el discernimiento de los patrones de la estructunización genómica de caracteres.

En ello para explicar como la evolución direccional de caracteres a nivel específico, puede surgir a darse por heterocronia (que es el cambio en la regulación del desrrollo morfológico, p. ej. pedomorfosis.). Argumenta que las discontinuidades morfologicas- a lo largo de un gradiente- han surgido por sef heterocronia. A s5h 1mismo señala que el establecimiento de gradientes morfológicas heterocrónidos, sólo es posible en un gradiente ecológico adecuado.

En el cuarto y último trabajo de este apartado, Jack Sepkoski presenta el concepto de faunas evoluciponarias; las describe como conjuntos de taxa de alta jerarquia- pareticularmente clases- que tienen historias similares de diversificación y que conjuntamente han dominado la biota por un lapso geológico extenso. A su vez este concepto (la expansión y declinación de las faunas evolucionarias en particular) puede aplicarse para describir megavariacionres en la dominancia faunistica y en la interpretación de los cambios cronológicos en la diversidad taxonómica global. Se han identificado tres de estas faunas en el dominio marino y la aplicación de este concepto se han extendido al dominio terrestre con éxito moderado.

Cabe destacar que Sepkoski le da una formalización y cierta caracterización matemática, a una idea que ha estado en el campo de la Paleontologia desde el siglo pasado: La singularidad de "faunas cronologicas", es decir de faunas caracterizadas por ciertos grupos dominantes, claro están restringidas geocronologicamente, y que por tanto a su vez permite definir o caracterizar bioestratigráficamente a tales lapsos geocronológicos; por ej. es del dominio público que la fauna marina del Paleozoico Temprano, es significativamente diferente de la del Paleozoico Tardío, y que cada una de ellas tiene ua composición taxonómica particular. Para los fines que nos ocupan, cada una de ellas sería una fauna evolucionaria.

En el resto de la seccion, se abordan dos topicos más, biodiversificación y extinción El primero es trata do por Jack Sepkoski y Mike Hulver, quienes han compilado un extenso conjunto de diagrams sobre diversidad paleontologicamente registrada de clases o linajes fileticas (familias a clases), tanto de organismos marinos como terrestres, para el Fanerozoico; ellos presentan esta rica información en un atlas de indudable valor.

En el ultimo artículo Antoni Hoffman diserta sobre las diversas concepciones o puntos de vista que han tenido sobre el fenomeno de las extinciones masivas. Señala, que aunque este tema en la última década (sin duda como resultado del interes que sobre este fenomeno desperto la hipotesis del impacto meteorico como causa de la extincion maciova dek Cretasico terminal), y la historia de la invedstigacion sobre el mismo, es compleja y se remomnta al nacimiento miosmo de las ciencias geológicas. La concepción catastrofista ha sufrido un ciclo en la responsabilidad y aceptación que han tenido en el mundo cientifico. Originalmente, Cuvier y otros, invocaron catástrofes diversas, para explicar la desaparición de especies y aún de linajes complejos, observables en el registro fósil. Este punto de vista resultó respetable, tanto por la autoridad académica de Cuvier y de los otros proponentes de esta tesis, como por su aparente concordancia biblica, que hacía del llamado diluvio universal, una de tales catástrofes.

Poco antes en Inglaterra, James Huntton propuso una tesis esencialemente gradualista, ordinaria y común para describir a los procesos geologicos y poara explicar los resultados de los mismos, observables en el registro rocoso de la historia dse la Tierra. esta tesis fe ampliamente desarrollada por Charles Lyell y potros, quienes mostraron que aún los grandes cambios observables en este registro, podían explicarse gradualísticamente, concibiéndolos como el resultado de la acumulación de muchos "microcambios" al través de un largo tiempo geologico-sin que se le vea principio o fin, según escribía el propio Huntton.

Puntos de vista tan opuestos ocasionaron la controversia principal del primer tercio del Siglo XIX. La concepcion gradualista se fue imponiendo y constituyo uno de los apoyos fundamentales de la teoría.

103 BIOLOGIA EVOLUTIVA

103 (a)

On the early origins of major biologic groups

Paleobiology, vol. 9, num. 2, 1983, p. 107-115

NOTA: Información temporalmente extraviada.

Paleobiology, 9(2), 1983, pp. 107–115

10.3 BIOLOGIA EVOLUTIVA

10.3(a) On the early origins of major biologic groups

David M. Raup

Abstract.—The commonly observed fact that the principal biologic groups appear early in an adaptive radiation is shown to be an artifact of the geometry of the evolutionary tree. For marine invertebrates of the Phanerozoic, total diversity and species turnover rates combine to make early origins of major groups inevitable. This is demonstrated through an analysis of the theoretical probability distribution of divergence time (time to most recent common ancestor) in comparison with observed distributions. Whereas the fact of early origins does not require ecological explanations, the interpretation of the morphologic distinctness of major groups when they first appear remains an ecological problem.

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Introduction

Students of evolutionary history have observed repeatedly that in an adaptive radiation, the major subgroups appear early and at about the same time. In a review of this phenomenon, Nicol et al. (1959, p. 351) said, "The major subdivisions of a group (e.g., classes of a phylum or orders of a class) generally originate early in its history, whereas new subdivisions of lesser rank (e.g., genera and species) may arise at any time throughout the group's geologic history."

Documentation of the generality of early origins of major groups is straightforward. The phenomenon is most striking in marine invertebrates. Nearly all living phyla of marine invertebrates that have reasonably good fossil records have first occurrences either in the late Precambrian or early to middle Cambrian. At the class level there are 27 paleontologically important living groups and all have documented occurrences which are Silurian or older (data from Sepkoski 1982). The mean geologic age of first occurrence for these 27 classes is 533 Myr with a standard deviation of only 51 Myr. Fully 20 of the 27 have first occurrences earlier than 500 Myr (Cambrian or older). These data are shown graphically in Fig. 1. For orders of marine invertebrates, the mean time of first occurrence is 328 Myr BP and there is a strong frequency peak at about 500 Myr (Fig. 2).

The same relative pattern can be seen in the geologic records of vertebrates and land plants although origins are generally displaced in time toward the Recent. For example, nearly all orders of living mammals have origins during a fairly narrow interval between 50 and 70 Myr BP.

An important consequence of the foregoing is that standing diversity at the higher taxonomic levels (phyla, classes, and orders) tends to be stable or to decline through geologic time following the initial radiation. Curves for standing diversity of marine shelf invertebrates prepared by Valentine (1969) show that the number of phyla is essentially constant, with virtually no origination or extinction. The standing diversities of classes and orders decline steadily so that present-day levels are 25%–35% lower than in the late Ordovician. This is due to a substantial excess of extinctions over originations and it further supports the generalization that originations of the higher-level groups are concentrated early in geologic history.

These generalizations have been the subject of considerable theoretical analysis. Interpretations have varied greatly. At one extreme, Willis (1940, p. 191) said "evolution goes on in what may be called the downward direction from family to variety, not in the upward, required by the theory of natural selection." In other words, the general phenomenon of early origins has been considered by some workers to be counterintuitive or against general Darwinian theories of evolution. Many of the interpreta-

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tions have been largely ecological, and much excellent analysis of this aspect has been carried out by Valentine (1973, 1980). Valentine and others have argued that the phenomenon results from the exploration of the empty adaptive zones that exist early in a radiation. Valentine postulates that a few distinctive bauplans invade, or originate in, empty niche space, thus establishing the major classes and orders and only later is diversity filled out at the lower levels. The general observation that major groups increase in genus/family ratios through geologic time has been used to support ecological explanations.

In this paper I will explore an alternate view: that the early origin of major groups is an inevitable product of the geometry of the branching evolutionary tree. I will argue that the simple fact of early origins is an artifact and requires no biological explanation. The analysis will be confined to purely cladogenetic aspects of the problem. Consideration of the morphologic distinctness of groups when they first appear, important to Valentine's analysis, will not be investigated.

Divergence Time as an Appropriate Metric

The analysis of early origins could be developed from purely empirical data on the ranges in time of higher taxa. This has been done by others, especially Nicol et al. (1959), but is somewhat less than satisfactory. There is no rigorous mathematical basis for differentiation of the several levels in the taxonomic hierarchy. Also, the geologic range data for higher taxa are often subject to considerable uncertainty, due in part to the ever-present problems of definition of particular taxa. In the present analysis, I will use divergence time as a metric, and this will avoid many of the problems of definition of higher taxa.

Divergence time is defined as follows. Given two living species, how far must one go back in geologic time to find the single species which is the most recent common ancestor of both living species? This time, in millions of years, is the divergence time for that pair of species.

Hypothetical evolutionary trees are shown in Figs. 3–4. Let us assume that they are correct and complete representations of the evolution of imaginary biologic groups through time. In these trees, each vertical line is a species lineage. We need not be concerned with questions of punctuated equilibrium or gradualism. In Figs. 3–4, the vertical lines may be unchanging species enjoying complete stasis or they may be lineages undergoing phyletic transformation through a succession of chronospecies. In either case, the end of the vertical line indicates complete extinction of a genome, and the start of a vertical line indicates a speciation event. What happens in between is not relevant to the present analysis. In the diagrams, the arrangement of lineages left to right has no significance.

In a real-world situation, nested sets of taxonomic groups could be superimposed on each of the trees. Clusters or clades could be recognized, and their number would depend on the methods used and on the morphologic differences between the species. Probably no two classifications developed by different workers would be exactly the same. Fortunately, divergence time can be used as a convenient proxy, thereby avoiding many problems.

Divergence times for a few cases are indicated in Fig. 3. Figures 5–6 show frequency distributions of the divergence times for all possible pairs of surviving species in the trees. The phenomenon of early origins under consideration in this paper is manifested by a concentration of divergence times early in the time scale. The link between early origins and divergence time will be developed below.

Behavior of Divergence Time

The divergence time distributions in Figs. 5–6 are very different, but they have an important characteristic in common. The distributions are not smooth. Rather, they are dominated by spikes representing the points of common ancestry for major clusters. This spikiness has been noted by Sibley and Ahlquist (1982) and by others working with genetic distance data. It is logically inevitable that if we have two distinct branching clusters with a single common ancestor, any species pair that draws one species from each cluster will have the same divergence time. This is illustrated in Fig. 3 by the fact that any pair of species involving cluster A and cluster C shows a divergence time of precisely 47 time units before present. This produces a major spike in the frequency distribution of divergence times at 47. The spikes are present throughout the hierarchy of taxonomic levels. Sibley and Ahlquist have suggested that concentrations of genetic distances reflecting these spikes can be used to delimit taxonomic rank.

Although both divergence time distributions in Figs. 5–6 show the spikiness just discussed, the distributions differ. Figure 5 has a concentration of young divergence times and Fig. 6 has a concentration of older ones. Both distributions are highly skewed and would appear even more so were the vertical scale not logarithmic. The obvious difference between the trees in Figs. 3–4 is in species turnover rate. Turnover rate is a function of two quantities: speciation rate and extinction rate. Mean divergence time is also influenced by the total elapsed time, but this can be subsumed in the turnover rate. In other words, the important element is the geometric fabric of the tree: the relationship between turnover rate and elapsed time. The contrast between the trees in Figs. 3–4 suggests that a multitude of relatively short branches leads to a low mean divergence time (Fig. 5). As will be shown later, standing diversity is also an important element determining the divergence time distribution.

Figures 3–6 present some of the characteristics of the divergence time distribution in relation to branching trees, but they can tell us nothing about the real world because they are not scaled to approximate natural rates of turnover or real world diversity. As Stanley et al. (1981) have emphasized, scaling for diversity is often important in the analysis of the dynamics of evolutionary trees.

An Equation for Divergence Time Distribution

Assume that at some time, t, before present there are S species lineages. In Fig. 3, eight such lineages exist at the bottom of the diagram. During the 90 time units leading to the top of the diagram ("Recent"), all of the starting lineages die out but their progeny persist for varying lengths of time as clusters or clades. In the case of Fig. 3, only the starting lineage on the extreme left has descendants surviving to the Recent. Thus, all living species must have divergence times less than 90 time units. In Fig. 4, on the other hand, several of the starting lineages have living descendants, so that divergence times for many living species pairs will exceed the 90 time units.

The problem is to develop an equation which will predict the expected divergence time distribution for randomly chosen pairs of living species. The relevant constants are S_0, the standing diversity at time = 0 ("Recent"); p, the average rate of branching, expressed as speciation events per lineage per time unit; and q, the average rate of extinction, expressed as terminations per lineage per time unit. In deriving an equation, I will use the mathematics of random branching processes and assume time homogeneity. That is, it will be assumed that p and q do not change through time. This does not prejudge the question of whether speciation and extinction rates are constant; it is only a convenient way to describe differences in branching patterns. The resulting equation could be elaborated to include changing p and q values.

Where branching rate is greater than extinction rate ($p > q$), standing diversity increases through time. This is the general condition in evolution over long periods of geologic time, and for evolutionary radiations in particular. If we look backward in time from the Recent, standing diversity will appear to decay. Given p and q and an assumption of time homogeneity (above), we can compute the expected value of diversity (S_t) at some time = t before present (BP) as follows:

$$S_t = S_0 e^{-(p-q)t} \tag{1}$$

It should be noted that S_t is an expected value and has a high variance where samples are small. Therefore, the estimate of past diversity, S_t, in the derivation that follows is a reasonable approximation only for situations in which one is dealing with thousands or tens of thousands of species, and the reader should be cautioned that application to cases with smaller samples should be avoided.

Now let us specify two Recent species at random and imagine the evolutionary tree that produced these two (and all other surviving species). Each of the two specified species can be traced back along a unique path from lineage to lineage until the base of the tree is reached. At some point the ancestral paths of the two species will meet, and this point represents the divergence time for the species pair. The two paths will meet at a speciation event, that is, a cross-link in the tree. In each small time interval, the total number of possible cross-links is

$$_{S_t}\mathbf{C}_2 = \frac{S_t!}{(S_t - 2)!(2)} = \frac{S_t(S_t - 1)}{2} \tag{2}$$

The expected number of cross-links (speciation events) that actually occur in a given time interval is the expected diversity times the speciation rate. If we consider a time interval of 1 Myr, the expected number of speciation events, N, is

$$N = pS_t = pS_0 e^{-(p-q)t}. \tag{3}$$

Any one of these speciation events has a probability of successfully connecting the two ancestral paths of interest, and this probability is the reciprocal of the number of possible different cross-links (2). And the probability of not making a successful link is one minus the reciprocal of (2). Consequently,

$$\text{probability of no cross-links in } n \text{ tries} = \left[1 - \frac{2}{S_t(S_t - 1)}\right]^n. \tag{4}$$

The probability of at least one successful cross-link in t successive time units is one minus the product of a series developed from (4). This may be written as follows:

$$W_t = 1 - \prod_{j=1}^{t}\left[1 - \frac{2}{S_j(S_j - 1)}\right]^n.$$

In this equation, S is defined as in (1) an as in (3). W_t is the probability that a rando chosen pair of Recent species has a diverg time less than some time = t before present. numerical value of W_t approaches 1.0 as base of the evolutionary tree is approache single ancestor for all Recent species).

Given values of the three constants (p, q, S), the equation can be solved for a series values to develop the distribution of W_t f which a predicted frequency distribution o vergence times can be developed.

Divergence Time Distributions

The W_t distribution depends on the partic combination of p, q, and S, but some gen izations are possible. All other things b equal, increasing diversity increases mean vergence time. Thus, although the tree in 3 yields a fairly low mean divergence time 5), a tree with the same overall fabric (relat low p and q) but higher diversity would s a higher mean divergence time. This mak especially important that divergence time putations be scaled properly for number species. It also means that computer simula is totally impractical for most real-world si tions.

Increasing turnover rate (numerical valu p and q) decreases mean divergence time, a be seen from a comparison of the trees in 3–4. Increasing the rate of growth of dive ($p - q$) decreases mean divergence time by ing more of the divergence points to be con trated higher in the tree.

The divergence time distributions show Figs. 5–6 are monotonic and highly skewed. this is not typical. It is logically true that frequency of divergence times must drop to as the Recent is approached (time = 0) and go to zero as the ancestor of the entire grou approached (high t). All complete, ideal di butions are unimodal. This can be seen if ulations such as those in Figs. 3–4 are run peatedly with the same input constants and results summed. Whether the frequency di butions are skewed toward or away from Recent depends on p, q, and S.

It was noted above that empirical divergence time distributions are collections of spikes (Figs. 5–6). This will be true of any distribution based on a single tree. Equation (5) does not produce spikes because it describes a generalized probability density distribution which approximates the combined result of many separate trees built from one set of constants.

Predicted Divergence Times for Marine Invertebrates

To use W_t to predict the divergence time distribution for a real-world situation, we must have good estimates of final diversity and of branching and extinction rates.

The literature contains a variety of estimates of present-day diversity (see Valentine 1970; Valentine et al. 1978). We will be concerned here with numbers of readily fossilizable marine invertebrates on the continental shelf. Estimates of present-day diversity range from roughly 100,000 to 300,000 living species, and I will use 150,000 as the standard for this paper although, as will be shown, the effects of changes in this number are relatively minor in the context of divergence time distributions.

Extinction rate estimates are on reasonably firm ground, but the uncertainties are such that we must also consider a range of values. Raup (1978) used data on generic survivorship to develop an average species extinction rate of $q = .09$. Since the average duration of a species in geologic time is the approximate reciprocal of q, the mean duration for shelf invertebrate species should be about 11 Myr. For a variety of reasons this estimate may be high, but it may be used as a starting point for analysis.

An estimate of mean speciation rate can be obtained from the extinction rate and modern diversity estimates. If diversity has increased over the Phanerozoic (Sepkoski et al. 1981), then speciation rate, p, must exceed the extinction rate, q. The fundamental quantity is $(p - q)$ in (1). Equation (1) can be rearranged as follows:

$$S_0/S_t = e^{-(p-q)t} \qquad (6)$$

The ratio S_0/S_t is the factor by which diversity decreases as one goes backward in time. Thus

$$(p - q) = -\frac{\ln(S_0/S_t)}{t} \qquad (7)$$

and

$$p = (p - q) + q. \qquad (8)$$

Solving equations (7) and (8) yields an estimate for mean p.

Table 1 shows a set of calculated values for W_t for q ranging from .05 to 5.0 (equivalent to species durations from 20 to 0.2 Myr) and for $(p - q)$ from .00019 to .00461 (equivalent to factors of diversity increase from Cambrian to Recent of from 1.1 to 10). All computations in Table 1 use an estimate of 150,000 species for present-day standing diversity and $t = 500$. The important result of the computations is that the numbers in Table 1 are all extremely small. This means that for any randomly chosen pair of living species, the probability is very low that they belong to the same clade. Or, to put it another way, the probability is high that the common ancestor of the two species is to be found in rocks older than 500 Myr. Only in the lower right-hand corner of the table are the numbers significantly different from zero. One would have to postulate a mean species duration of 200,000 yr or less and also postulate a Paleozoic to Recent diversity increase approaching an order of magnitude to find more than a few percent of the divergence times less than 500 Myr.

Parallel computations based on modern diversities of 100,000 and 300,000 species did not give appreciably different results. The computations were also done for $t = 400$. The resulting W values were slightly higher, but the basic pattern was unchanged.

The computations resulting in Table 1 show that an evolutionary tree that has the basic geometry of the real tree for marine invertebrates will be one in which the overwhelming percentage of randomly chosen species pairs will have pre-Ordovician common ancestors. This says, in turn, that randomly chosen pairs of living species are most likely to involve intergroup comparisons, where the constituent groups have Cambrian or Precambrian origins. Although this is in qualitative agreement with the general observation that most major groups have early origins, it must be checked with actual distributions of divergence times of living marine invertebrates.

It should be noted in passing that equation (5) could be used to predict the time of the start of the whole radiation or the origin of the tree itself ($W_t = 1.0$). If this is done for the range of p and q values used for Table 1, the predicted start of the invertebrate radiation is deep in the Precambrian. But to carry the computations this far would be invalid because there is ample evidence that the major invertebrate radiation was a late Precambrian phenomenon (Valentine 1973, 1980; Sepkoski 1979). The early stages of the radiation were characterized by much higher branching rates than those used here, and they represent a significant departure from time homogeneity of the branching process.

Divergence Times in the Real World

Surveying divergence times with real species is extremely difficult, even though in theory it should be simple. One could select pairs of living species at random and determine from the paleontological literature an estimate of the time to most recent common ancestry for each pair. But problems abound because of the many uncertainties in reconstruction of phylogenetic patterns, of missing stratigraphic records, and other problems. But we can get a general picture of actual divergence time distributions and set some general limits.

Let us consider the 27 paleontologically important classes of marine invertebrates that are living today. Rough estimates of the numbers of living species in each are available, and they can be grouped into four categories: 20,000–30,000 species (Rhizopodea and Gastropoda), 10,000–20,000 species (Bivalvia and Malacostraca), 1000–10,000 species (9 classes), and fewer than 1000 species (14 classes) (data from Valentine [1970] and Van Valen [1973]). These numbers are generalized in Table 2. If we assume for simplicity that the average number of species in each of the size groups is the midpoint of its range, then the total number of species is 136,500 (see Table 2).

As we have seen (Fig. 1), all of the 27 classes have first occurrences in the geologic record in rocks of 400 Myr BP (top of the Silurian) or older, with a mean time of first occurrence of 533 Myr BP. The common ancestors of many of the younger classes (Ordovician and Silurian) are in the Cambrian or Precambrian. Let us generalize that 500 Myr BP is the minimum divergence time for a species pair drawn from any two of the classes. It may be that this is actually a conservative estimate because experience has shown that as more fossils are discovered, the first occurrences of major groups tend to be pushed back in time.

Consider a class that has 15,000 living species. Any one of these species can join with another living species to form a species pair. Some pairs will be intraclass and some will be interclass, depending on whether they have species from the same class or different classes. The number of possible intraclass pairs for a class having 15,000 species is $\{(15{,}000)(14{,}999)\}/2 = 1.125 \times 10^8$. Extending this procedure to all 27 classes, the total number of intraclass pairs is 9.86×10^8 (Table 2). The total possible pairs (intraclass and interclass) is $[(136{,}500)(135{,}499)]/2 = 9.32 \times 10^9$.

The ratio of the two totals just given is the proportion of intraclass pairs: 0.106. Thus, only about 10% of all possible species pairs are intraclass. If the minimum age of origin of the 27 classes is taken as 500 Myr, then it follows that at least about 90% of the possible pairs of living species have divergence times greater than 500 Myr and only 10% are less than 500 Myr. But because many of the subgroups within classes have divergence times as old, or almost as old, as the classes themselves, simple counts of numbers of intraclass pairs almost certainly underestimate the number of pairs with high divergence times. This means that the actual proportion of divergence times greater than 500 Myr is almost certainly greater than 90%.

Let us now turn to a somewhat higher resolution analysis and consider divergence time distributions within a single class, the class Echinoidea. Using the data set of Raup (1975), there are approximately 1000 living echinoid species classified into about 15 orders and 50 families. Using the reasoning that was applied above, there are about 500,000 possible species pairs of living echinoids. Some of these are pairs within families or within orders, some are between families or between orders. Obviously, species related at the lower taxonomic ranks are more likely to have lower divergence times. Consider a family such as the Arbaciidae. There are 31 living species and thus 465 intrafamily comparisons are possible. But there are about 30,000 possible comparisons between arbaciid and nonarbaciid echinoids. Thus, of all the possible pairs of living echinoid species involving arbaciids, only about 1.6% are within-family pairs. Now, the Arbaciidae is the only living family in the order Arbacioida, and thus 98.4% of echinoid pairs involving at least one arbaciid are also interordinal and imply high divergence time. Mean divergence time for echinoid orders ranges between 190 and 345 Myr. Therefore, if we were to pick an arbaciid species at random and pair it with any other echinoid species, the overwhelming probability (0.984) is that this pair is an interordinal pair and has a divergence time measured in hundreds of millions of years.

We can go somewhat further and consider randomly selected pairs which include an arbaciid echinoid and any other marine invertebrate. As we have seen, the total number of possible pairs of invertebrate species is about 9.3×10^9. If one member of a species pair is an arbaciid echinoid, there are only 465 possible pairs which would also include a second arbaciid. It is clear that if we were to choose an arbaciid echinoid at random and link it with any other marine invertebrate, the probability is negligible that the second species is even an echinoid. More likely, it will be in another invertebrate class, which again gives us a high divergence time.

Discussion

The theoretical predictions of divergence time distribution for marine invertebrates (Table 1) indicate that nearly 100% of divergence times should be 500 Myr or older. Even allowing for considerable error in our estimates of turnover rates and past diversities, it is difficult to lower this estimate to less than 98% or 99%. The analysis of empirical divergence times gives minimum estimates of these old divergence times of about 90% (Table 2). While both the theoretical and empirical analyses support the basic contention that major groups appeared early, there remain several interesting questions. One of these is the significance of the disparity between 99% and 90% for theoretical and empirical analyses, respectively. There are two possible explanations for this. The first is purely artifactual. The estimated numbers of high divergence times in the real world are probably too low because the numbers of intraclass pairs with high divergence times have been underestimated. The other possible interpretation is that the real-world estimate of 90% is actually valid and represents a real departure from the theoretical predictions of the stochastic model used as a basis for the equations.

The derivation of the equations assumed that speciation and extinction rates are constant through time. We know that this is not the case. In particular, we know that the evolutionary system is occasionally perturbed by mass extinction. That is, there are short intervals of time wherein the extinction rate, q, rises markedly. This results in a drop in standing diversity. Following the mass extinction there is a fairly rapid recovery of diversity, which implies that speciation rate is much higher relative to extinction rate for the time necessary to bring diversity back up to pre–mass extinction levels (Sepkoski 1979). The recovery from a mass extinction often is associated with adaptive radiations; that is, bursts of cladogenetic activity which either produce new major groups (families and orders) or which see the rapid diversification of groups that already existed. One of many examples is the rapid and extensive evolutionary radiation of the scleractinian corals following extinctions at the end of the Cretaceous. Mass extinctions have the effect of forcing the biota through a bottleneck and, to some degree, "restarting the clock" in the branching system of evolution. One effect of such a perturbation should be that modern taxa originate at a time later in evolutionary history than would be predicted by the purely stochastic model. And this may well explain a mean divergence time which is less than predicted. Any sequence of mass extinction and recovery will produce a new spike in the divergence time distribution and lower the overall mean divergence time for the group as a whole. This explanation of the observations is speculative, of course, because we do not know for sure how much the real-world mean divergence times are underestimated. This is a direction for research which has considerable potential. One can even imagine that major adaptive radiations are expressed as spikes in the divergence time distribution and that this could be a useful way to detect major bursts of cladogenetic activity.

Conclusions

The combination of theoretical and empirical analyses presented in this paper demonstrates that the early origin of major groups is the expected condition. This would not be true for any evolutionary tree, for there are many combinations of p, q, and S which produce a divergence time distribution quite different from what we observe in the real world. Therefore, we can conclude that the fact of early origins of major groups does not require an ecological or other biological explanation beyond accommodating the simple inputs of starting diversity, speciation rate, and extinction rate.

This paper has been devoted entirely to the cladogenetic or branching aspects of the problem. The fact that new groups are usually distinct morphologically as soon as they appear in the fossil record has been completely ignored. The distinct morphology suggests an unusually rapid diversification early in the history of a biologic group, and this may well result from the ecological causes suggested by Valentine. Thus, whereas the present analysis indicates that early origins are a nonbiological artifact, the analysis cannot speak to the most intriguing problem of the morphologic divergence that takes place so quickly in an adaptive radiation.

Acknowledgments

I thank J. John Sepkoski, Jr., Stephen M. Stigler, and James W. Valentine for many helpful discussions during the development of this research.

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FIGURA 1

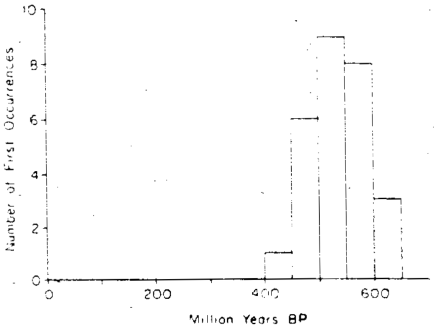

FIGURE 1. First occurrences of 27 modern classes of paleontologically important marine invertebrates. Stratigraphic range data from Sepkoski (1982).

FIGURA 2

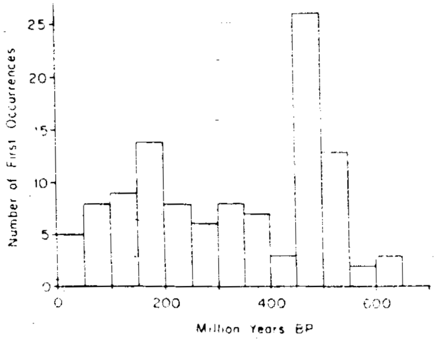

FIGURE 2. First occurrences of the modern orders in the 27 classes represented in Fig. 1. Stratigraphic range data from Sepkoski (1982).

FIGURA 3

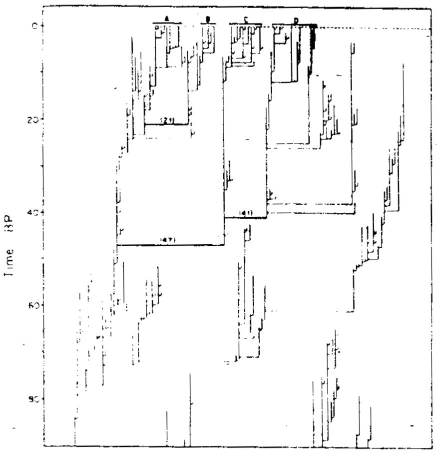

FIGURE 3. Hypothetical evolutionary tree based on relatively high rates of species turnover. A few divergence times are indicated, such as 47 for any species pair involving clusters A and C.

FIGURA 4

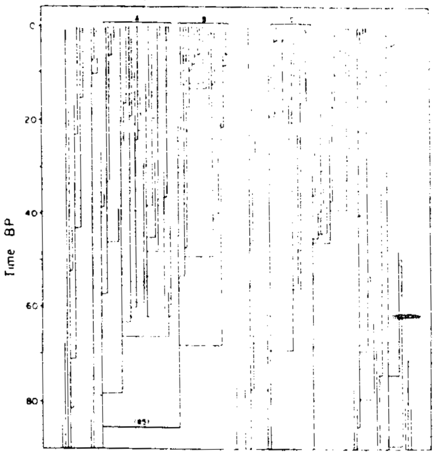

FIGURE 4. Hypothetical evolutionary tree based on relatively low rates of species turnover

FIGURE 5

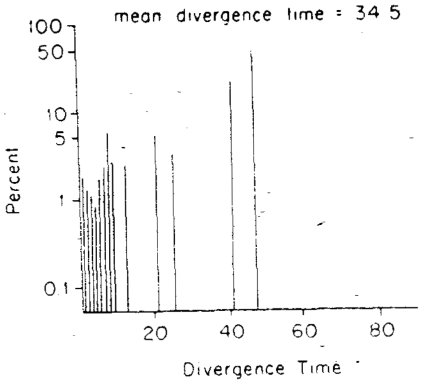

FIGURE 5. Frequency distribution of divergence times for all possible pairs of surviving species in Fig. 3. Spikes at 41 and 47 reflect concentrations of those divergence times in Fig. 3.

FIGURE 6

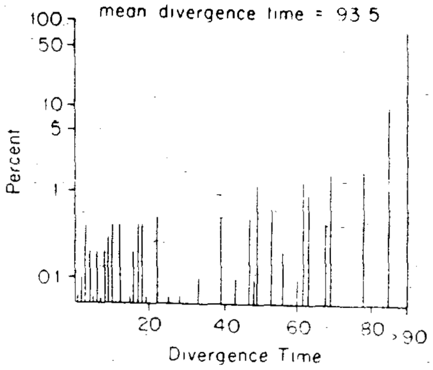

FIGURE 6. Frequency distribution of divergence times for all possible pairs of surviving species in Fig. 4. High frequency of divergence times greater than 90 reflects the fact that many of the common ancestors of surviving species existed at the base of Fig. 4.

TABLE 1

Duration of species (Myr)	Diversity increase factor (Cambrian–Recent)					
	1.1	2	3	4	5	10
20	.000	.001	.001	.001	.001	.002
10	.001	.001	.001	.002	.002	003
5	.002	.002	.003	.003	.003	005
2	.004	.005	.006	.007	008	.013
1	.007	.010	.012	.014	.017	.026
0.5	.014	.019	.024	.029	.033	.051
0.2	.034	.047	.059	.070	.080	122

TABLE 1. Predicted proportion of divergence times less than 500 Myr. Equation (5) for W_t is solved with an assumed modern diversity of 150,000 and various combinations of p and q. Extinction rate (q) is the reciprocal of species duration, and speciation rate (p) is determined by the rate of diversity increase, extinction rate, and modern diversity (eq. [7] and [8]).

TABLE 2

Classes	Median species per class	Total species	Total intraclass pairs
2	25,000	50,000	6.24×10^8
2	15,000	30,000	2.24×10^8
9	5,500	49,500	1.36×10^8
14	500	7,000	1.75×10^8
27		136,500	9.86×10^8
Total species pairs (intra- and interclass):			9.32×10^9
Proportion of intraclass pairs:			0.106
Proportion of interclass pairs:			0.894
			1.000

TABLE 2. Generalized numbers of intraclass species pairs for modern classes of marine shelf invertebrates (limited to groups generally recognized as fossilizable).

10.3 (b)

MOLECULAR CLOCKS, MOLECULAR PHYLOGENIES AND THE ORIGIN OF PHYLA.

Douglas H. Erwin

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Protein, RNA sequences have been widely used to construct phylogenies and to calculate divergence times using a molecular clock. Reliance on molecular information is particularly atractive when fossil evidence is missing or equivocal, as in the Cambrian metazoan radiation. I consider the aplicability of molecular clocks and phylogenetic analysis of molecular data to the origin of metazoan phyla, and conclude that molecular information is often ambiguous or misleading. Amino acid sequences are limited use because the redundancy of the genetic code masks patterns of descendent, while of a nucleotide sequnces only four potential states exist each site (the four nucleotide bases). In each case, homoplasy may often go undetected. The application of a molecular clock to resolve the timing of the metazoa radiation is unwarranted, while molecular phylogenetic reconstruction should be approached with care. A potential more useful technique for phylogenetic reconstruction wuold be the use of patterns of genome structure and organization as characters. Molecular clock, phylogenetics, metazoan radiation, origin of phyla.

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The explosive growth of molecular biology has led to the estimation of the time of divergence events using a molecular clock and the determination of phylogenetic patterns by comparision of amino acid sequences (from proteins) or nucleotide sequences (from RNA and DNA). such tecniques have been applied to paleontological problems where the fossil evidence is either missing or equivocal in an attempt to resolve the timing and pattern of divergence. Runnegar (1982a, b, 1986) has suggested that molecular information may resolve the question of the timing and duration of the Cambrian Metazoa radiation. I adress here the reliability of the molecular clock as well as other aplications of molecular data (phylogenetic analysis using protein, DNA or RNA sequences) to resolve the rate and timing of the Cambrian radiation. It is not the goal of this paper to discuss more restricted (either temporally or phylogenetically uses of molecular data, or to argue that such data is without interest, but rather to discuss the application of molecular data to a particular paleontological problem.

THE MOLECULAR CLOCK.

Zuckerkandl & Pauling (1962, 1965) noted that the substitution of amino acids within a protein follows a Poisson process. They suggested the characteristic substitution rate for individual sequences is related to absolute time rather than generation length,, which led to an absolute time scale by calibrating substitution rates for individual amino acid sequences against known divergence times determinated from the fossil record. The molecular clock model has been applied to both amino acid and nucleotide sequences to estimate phylogenies and divergence times (for reviews se Wilson et al 1977; Thorpe 1982; Gillespie 1986; Li et al 1987; Andrews 1987, and papers in junkes 1987. particularly Zuckerkandl 1987).

Applications of the clock to globins, cytochrome C and 5S RNA sequences produced a date of 1000 to 900 millions yaers ago (Ma) for the initial radiation of the animal phyla (Fig. 1 Runnegar 1982 a, b, 1986) this work supports claims of a lengthy period of metazoa diversification prior to the appearence of late Precambrian metazoa body fossils (runnegar 1982 a, b, 1986) and cats doubt upon arguments for a more rapid origination of phyla during tha latest Precambrian (valentine 1986; valentine & Erwin 1987 and references therein).

The molecular clock model can only be applied when certain assumtions ~~are~~ met. these are: constancy of substitutions rate for the genes under investigation within lineages, and dependence of substitutions rate on absolute rather than generation times. Procedures which test the validity of these assumptions for individual studies are in wide use. However, the reliability of the molecular clock model has been questioned by the discovery of highly variable substitution rates while broad phylogenetic analyses indicate that substitution rates may be more closely effected by generation length than previously appreciated.

The questions of rate constancy.- A constant substitution rate requieres incorporation of mulations into a population at a rate equal to their rate of mutations (Kimura 1983; constant is in terms of a Poisson process). the number of variable sites (NVS) constrols the number of sites at which substitutions is permissible, and produces a characteristics substitutions rate for each sequences (Kunisawara et al 1987). Since each protein differs in NVS, the rate of substitutions varties between sequences. Furthermore, NVS may vary through time. Consequently, deviations from rate cosntancy may reflected changes in the rate of incorporations or production of mutations, in the selective value of substitutions or in NVS.

Statical studies have revelated deviations from rate constancy, but until recently these desviations have been considered insufficient to reject the clock (Langley & Fich 1974; Fitch & Langley 1976; Hudson 1983). More recent studies suggest the desviations are significat. Moo-Lee et al (1985) compared amino acid substitutions rates of superoxide dismutase in Drosophila and mammals, indicating a highly erratic clock. However, Moo-Lee et al. may have misinterpreted the saturation effect of substitutions and the data may be equally consistent with a generation time effect. A comparison of echinoid and vertebrate mithochondrial and nuclear DNAs nuclear DNA substitutions rates while mithochondrial rates have been stable. other studies have reather similar conclusions (Gingerich 1986; Britten 1986).

Variations in the rate of substitution in SS RNA were detected in a comparison of arthropod sequences with variety of metazoa species (Hendricks et al 1986). The authors concluded that tha rtadom deviations in the evolutionary rate 5S RNA are too great to used in analyzing metazoa phylogeny. Field et al (1988) have succeful used 18S RNA to analyze metazoan phylogeny (see below). Gillespie's statical analysis of substitutions rates (1984 1986) demostrates a highly episodic pattern of substitution, with short, with short periods of rapid change interspersed with longer periods of slower replacement. He suggests that the clock cannot be modeled using a Poisson process in which the rate of the process is itself randomly changing.

Support for rate-constancy has been provided by a determination of the number of variable sites (NVS) in cytochrome C and hemoglobin by Kunisawa et al. 1987. they calculated tha square root of the variance and the average number of amino acid substitution differences for about 100 different amino acid sequences of each protein demostrated little variation in NVS. They concluded that the substitution rate per variable sites is close to uniform from bacteria through mammals, although a combination of rapid and slow sites is required to explain the substitution rates of cytochrome C. A constant NVS does not preclude a hidghly episodic substitution pattern poroducing a long-term appearance of rate-constancy.

Goodman (1981) has argued that sequence comaprision reveal increased rates of protein evolution inmediately following establishment of new clades, followed by a decrese in substitutions rates as adaptations to a new roles increases. In particular. Goodman claims evidence for inicreased selections during the initial appearance of jawed fish and tetrapods and later during the early Cenozoic mamalian radition. Increased selective preassure would cause a change in the substitutions immediately following gene duplication (as in hemoglobins and citochrome C), are also discussed by Ohta (1988) and Li (1985). junkes (1987) noted and increased rate of transitions (purine- purine or pyrimidine changes) relative to transversions (purine- pyrimidine changes) during the early stages is clearly greather than anticiped by early proponents of the clock, yet whether this variation invalites the clock entirely, as suggestedd by some authors (Hudson 1983; Gillespie 1984), is unclear.

The problems generations times.- If tha rates of substitutions is dependent on generation time rather than absolute time, calculed substitutions rates may differ simply because of differences of generation times between lineages, or within a single lineages over time. Wu & Li 1985), Li et al. 1987 and Li et al 1985) compared nucletide substitution rates for 11 genes (including globins) using a relative-rates test and compared the result several out groups (differents outgroups were requiered because of insufficient sequence information). They concluded that the substitution rate in rodents has been higher that is man since the slit between lineages leading to rodents and primates. Synonimous substitutions rates (those in wich there is no change in the amino acid) occured two times more frequently in mice than in humans, while non-synimous changes occurred 1.3 times more often. Comparision of homologous genes formed by gene duplication provided a directed test of the role of generation time, with only a weak effect if large change in generation time occur. However, the generation time effect is significant for synonimous changes (see also Easteal 1985; Li & Wu 1987; Wu & Li 1985; Easteal 1987; Fisch 1987).

THE MOLECULAR CLOCK AND THE ORIGIN OF ANIMAL PHYLA.

Runnegar's molecular clock date for the origin of animals phyla is based largely on amino acid sequences from vertebrate and invertebrate globins and to a lesser extent cytochrome C and 5S RNA nucleotide aequences (Runnegar 1982 a 1986) The gene duplication event following the separation of the agnatha (jawless fish) from jawed fish (and alll other vertebrates; Fig. 2) established two related sequences, the alfa globins and beta globins, with independent evoltiinsary histories. This duplication provides a claibration point for the clock at 45o Ma from fossil evidence. Since the alpha and beta sequecnes diverged at the same point in all vertebrates. Runnegar has made pairwise comparisions of the amount of substitution in alpha and beta aminoa acid sequences and demostred an approximately normal distribution of percentage differences (Runnegar 1982a, 1986) Rate-constancy of substitutions in vertebrate globins was examined through pairwise comparisions of alpha and beta chains within species to the appropiate human globin chains. this suggests that while the rate of substitutions has varied between lineages, the rates has been approximately constant within a lineage, as required by the clock. Between-phylum comparisons were then used to calculate... an approximate minimum date for the initial radiation of the animal phyla (Runnegar 1986; 13; Fig. 1).

By assuming that the rate of globin substitutions has been uniform for the past 450 Ma and than this uniform rate may be extrapolated an additional 450 Ma, Runnegar (1982a, 1986) calculated a date for the origin of phyla. Three-way comparisions of annelid, molluc and vertebrate sequences desmotrate that between phyla differences are greater than those within vertebrates (as excepted). Corrected values (wich account for superimposed substitutions) are used to calculate the initial radiation of animal phyla and the divergence between alpha globin and myoglobin and beta globin and myoglobin.

There are several reasons for questions the 1000-9000 Ma date. First. the annelid, mollusc, and vertebrate divergence dates the actual divergence of the phyla only in molluscs, annelids and vertebrates are eachj others closest relatives, or if all three diverged simultaneously (perhaps along with other taxa) from a common ancestor. Other wise, the date, if correct, may simply reflect tyhe divergence of pre annelid, pre-molluscs and pre vertebrtate lineages during the evolutions of metazoa. In this case the date is for an earlier event in metazoa phylogeny and may not reflect the radiations of exinsting animal phyla. More importantly, this aplications of the molecular clock extrapolation of evolutionary rates beyond calibration points rather than interpolatiopn between known points (W.M. Fitch, pers. Comm., 1988) Since there are not methods to test te accuracy of such extrapolations, the result of such studies are unreliable. third, as discussed above, substitutions rates appear to be highly episodic, a feature which will be masked by the sort of long-term analysis used by Runnegar. As noted, increased substitutions rates are particularly common during gene duplication rates is likely to have greater than calcule rate, and the divergence times less.

A more telling problem lies in the cellular role and early evolutionary history of the globins are likely to have been under intense selective preassure during the metazoa radiation and again during the early evolutions of the vertebrates. These pressure stemmed from the conversion from diffusion to active respiratory transport as body size increaced (Runnegar 1983), from increases in metabolic activity and from possible increases in atmosferic O2 (Runnegar 1982 a, 1982c; see also Towe 1981; Berkener & Marshall 1964).

MOLECULAR PHYLOGENIES

The use of molecular sequence data in phylogenetic analysis is in principle no different from using any other characters. homologous sequences of amino acid, DNA, or RNA are compared and the differences noted, a transformation series (describing the sequences of changes) constructed and the rtesulting character matrix analyzed using must have a substitutions rate appropiate for the question being addressed, slow for comparisions of phyla and classes with long divergence times, but fast for species within a genus.

A major source of difficulty is constructiong transformation series and resolving potential homoplasies. Table 1 contains a portion of the flanking (non-coding) and coding region of the H4 histone gene from an echinoid and an asteroid. Noted than the amino acid sequence of the coding region is constant, despite seven changes in the nucleotide sequence. Each of the nucleotide changes occurred at the third codon position, and due to the redundancy of the genetic code no changes in amino acid sequence occured. more realistically the sequence is highly conserved and changes in amino acid sequence were selected against.

The imposibility of determining the actual nucleotide sequence from amino acid data is demostrated by the number of posibble nucleotides which could produce most amino acid. When changes in amino acid sequence do occur, it is frecuently difficult to determine the transformation series. In the lower postion of Table 2 the most parsimonius nucleotide changes are listed which would produce the change from the alpha chain to the beta chain. Note that there is no reason to believe that the shortest possible transformation route was actually followed, not that the transformation route was actually followed, nor than the transformation occurred in the direction illustrated. the final residue, Tryptophan, is rthe only one also found in myoglobin and thus presumably conserved from the ancestral sequence of myoglobin and hemoglobin. [These and other problems are discussed at length by Patterson (1987)].

Field et al. (1988) recently proposed a set of phylogenetic relationships for the metazoa based on 18S ribosomal RNA Their result suggest three radiations of metazoa (the first actually a radiations of protist lineage, since the multicellular animals appear to be polyphyletic), and rapid phylogenetic splittiing of major groups soon after their appearance. While Field et al's, result may well correct, no phylogeny can be based on a single sequence, any more than a biological systematist would used external patterns or internal morphology but ignore developmental patterns or internal morphology. Their work needs to be substantiated using sequences other than 18S RNA and which have substitution rates apprpiate for phylum-level comparisions. Finally, the braching order within major groups probably lies within the levels of resolution of the technique and may well be modified by future studies.

DISCUSSION.

The inherent ambiguity in most molecular phylogenetic techniques limits their ability to resolve outstanding evolutionary problems, particularly those involving broad phylogenetic analyses. DNA_DNA hybridization has been used in the phylogenentic studies of birds (Sibley & Ahlquist 1983) and hominoids (Sibley & Ahlquist 1984). Hybridization studies are less informative than sequences studies since the former anly produces a measure of everall similarity from the temperature of dissociation. They produce no information on the patterns of evolutionary change within sequence, nor do they provide any means of separating convergence from shared descent.

Despite the comments above, molecular data may prove enormously impoortant in future broad phylogenetic studies. Phylogenethic characters are presents within the structure and organization of the genome itself, and like morphometric characters have a large number of possible states, are easly distinguished and transformation series constructed. The divergence history of human globin in Fig. 2. was derived from comparative molecular studies and can easly be used as a series of phylogenetic characters. This aplications of molecular data has been relatively infrequent, but has greath potential. the major obstacle preventing wider application is tha lack sufficiently diverse information on genome structure and organization.

Determining tha rate and duration of major radiation events is an important paleontological problem, butg the difficulties inherent in variable substitutions rates requiere substantial input from the fossil recor. It is not clear taht tha tweo fundamental assumption of the molecular clock; rate-constancy and generation-time independence, are vaild in general. nor is it clear that Runnegar's data are applicable to the origin of phyla, or data their extrapolations actually dates the appearance of the extant phyla. The clock may be valuable in analyses of restricted phylogenetic groups with a similar generation lengh, but ist extention to the broad sweep of metazoan history is clearly unwarranted. jan Bergstrom pointed out that if there is a strong differential in substitutions rates during a divergence event, as suggested by Goodwin (1981), use of the molecular clock within a single clade may be flawed as well. Runnegar's conclusion that the initial divergence of metazoa phyla occurred 900-1000Ma (Runnegar 1982 a, b, 1986) appars insuportable. Molecular evidence does not presently allow us to discriminate between a lengthy. precambrian divergence of metazoa and a rapid burst of the diversification close to the actuall appearance of fossil (Valentine & Erwin 1987; Valentine 1986).

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Fig. 1. Molecular clock dates produced by Runnegar for the divergence of metazoa phyla as determined from amino acid sequences of vertebrate globins, cytochrome C and nucleotide sequences of 5S RNA Calibration points are taken from the divergence between the alpha and beta vertebrate globins, a pairwise comparisions of divergences in amino acid sequences of invertebrate globins between mollusc classes (M), annelid classes (A), and echinoderms clases (E). The point F-A is derived from the everange difference between fungal and animal sequence of 5S RNA. The soild region denotes the range of points derived from between phylum comparisions cytochrome C. Since several substitutions may occur at the same site, percentage divergence may be greater than 100%.Fig 6 from Runnegar (1986).

Fig. 2. The evolutionary relationships between members of the human globin gene cluster based on comparisons with other vertebrate groups. The present human globins genes were derived by gene duplication events. The fossil record provides an estimate of the time of the split between the Agnatha and all other fish (and thus all other vertebrates) thus calibrating this duplications even. The remaining gene duplication events have been calibrated in a similar fashions.

Tabla 2. Comparison of initial portion of N-Terminal ends of a lpha and beta chains of humans hemoglobins. The upper portion of the figure shows the DNA triplet codons which could produce the amino acid in the alpha chain, illustrating the redundancy of the genetic code. In the lower portion the shortest possible transformations series are indicated, assuming the alpha chain is primitive. The variety of possible transformations indicates that transformations series cannot be constructed from amino acid data. Capitalized amino acid are identical in each chain. the final residue, tryptophan also occurs in myoglobins. A- adenine, T-thyamine, C- Cytosine, G- guanine, X- any nucleotide.

FIGURA 1

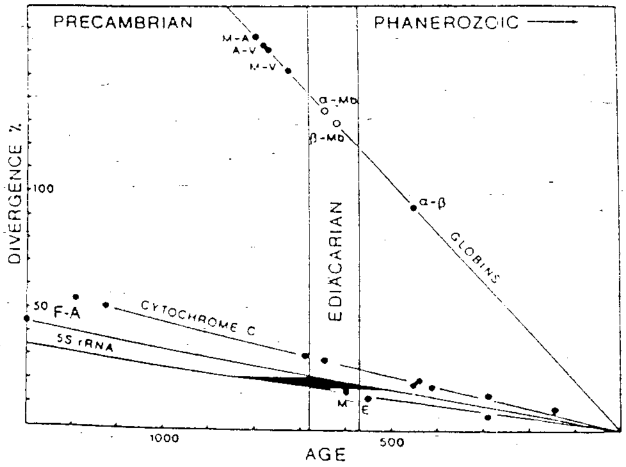

FIGURA 2

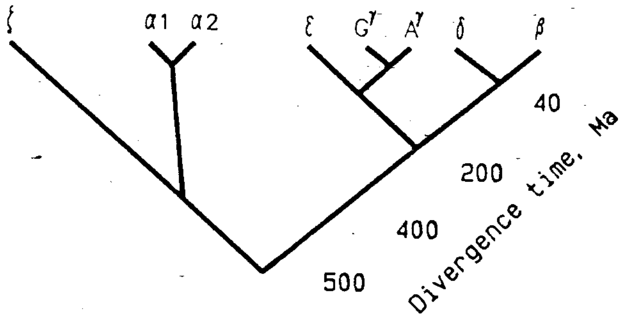

Tabla 1

5′										3′					
	−10	0				5					10				
	•• ••	••		•	•		•			•		•		•	
Sp	CATCATCATG	TCA	GGT	CGA	GGA	AAA	GGA	GGA	AAG	GGA	CTC	GGA	AAA	GGT	GGT
Po	CACAACTATG	TCT	GGT	CGC	GGT	AAA	GGT	GGA	AAG	GGG	CTC	GGC	AAA	GGG	GGT
		ser	gly	arg	gly	lys	gly	gly	lys	gly	leu	gly	lys	gly	gly

Tabla 2

N-terminal end α	β	
		Possible nucleotides for α-chain:
VAL	VAL	GTT GTC GTA GTG
	His	CAC
LEU	LEU	TTA TTG CTT CTA CTG CTC
Ser	Thr	AGU AGC TCT TCA TCG TCC
PRO	PRO	CCT CCC CCA CCG
Ala	Glu	GCT GCC GCA GCG
Asp	Glu	GAT GAC
LYS	LYS	AAA AAG
		Possible transformation series:
Thr	Ser	ACX → AGT. AGC or ACX → TCX
Asn	Ala	AAT. AAC → GCX
VAL	VAL	
Lys	Thr	AAA. AAG → ACA. ACG
ALA	ALA	
Ala	Leu	GCX → CTX or GCX → TTG. TTC
TRP	TRP	

10.3 (c)

HETEROCHRONY AND PHYLOGENETIC TRENDS. *

Kenneth J. McNamara

INTRODUCTION.

Morphological evolution has been considered by some authors (Schindewolf 1936; Goldscmidt 1940; Waddington 1962; Zuckerkandl 1968, 1976; Van Valen 1974; Stanley 1975, 1979, Gould 1977; Alberch 1980) to occur as the result of changes in the regulation of morphological development (heterochrony). Such developmental changes may from part of normal phenotypic variation (Cock 1966; Larson 1980; Travis, 1981), but if the resultant morphological novelities are adaptative significance, selection may favor the establishment of the variant as a genetic isolate, and speciation may result.

Aphylogenetic trend may be defined as directional morphological change between more than two species. Such trends have been interpreted in a number of ways; as little mor than elemts in the fossil record, chosen by investigators as they apparently conform to a morphologically graded series (Eldredge and Gould 1974); as the result of directional speciation (Grant 1963; Stanley 1979); as due to the action of species selection (Stanley 1973, 1979); or as the rusult of evolution toward increased speciation i species-specific characters-the effect hypothesis (Vrba 1980).

Ede (1978), Gould(1980), Alberch (1980) and Levinton and Simon (1980) have suggested that heterochrony may direct morphological variation of a species along particular pathways. It is the aim of this paper to purpusue this line of argument by examining a series of recently described examples, mainly from the fossil record, which have been interpreted as phylogenetic trends, in which heterochrony has been ythe principal factor in directing the course of the morphological evolution (Ruckards 1977; Mcnama ra 1978; in press a, b; McNamara and Philip 1980a; Wright and Kennedy 1980).

Amodel is proposed in wich directional morphological change at the species level arieses by repeated selection of phenotypic variants which develop by heterochromic processes. In the model, selection for adaptively significant heterochronic morphological novelties along an environmental gradients resulting in the establishment of a phylogenetic trend.

HETEROCHRONY

Changes in ontogenetic sequences through time occur by contrac tion, extension, or a shift in timing of rates of morphological development. Reduction in morphological developments through successive ontogenies (paedomorphosis) can occur by neoteny, thet is, a reduction in rate of development; progenesis, in which precocious sexual maturation reduces the period of juvenile allometric growth; or by post-displacement, a retardation in onset of growth of particular organs. Increased morphological development during ontogeny (termed peramorphosis by Alberch et al 1979) can occur by; acceleration, an increase in growth rate; hypermorphosis, in wich delay in onset of maturity legthens the period of juvenile allometric growth; or by pre- displacement, that is the earlier onset of development of particular struc tures.

As Alberch et al (1979) have noted, an ontogenetic trajectory is regulated by a number of parameters; onset age of growth; cessa tion of growth (generally at onset of maturity); growth rate during the growing period; and size at the commencement of the growth period. Growth through the juvenile phase of development often occurs by allometry, and growth rates are generally much higher than in the adult. Large scale morphological changes may therefore occur during an organism's ontogeny, Consequently any alteration in growth rate or timing of onset of growth, particu larly early in the ontogeny, will profundly changes the adult morphology.This will result in the rapid development of thescend ant morphological novelties without the development

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of intermedi ate morphotypes between the ancestor and descendant.

The morphological characteristic of an individual are generally appropiate for the mode of life of its particular stage in devel opment. The environment occupied by the juvenile may be very different from that occupied by the adult. For example, many marine invertebrates have free-living planktic larval stages, but immobile denthic adult. As the ontogeny of an individual in purely directional, the evolution of descendant paedomorphs or peramorphs provides an inbuilt, pre-existing directional compo nent. If selection of such morphtypes occurs periodically along an environmental gradient this will result in directional specia tion and the development of a phylogenetic tred.

PAEDOMORPHOCLINES AND PERAMORPHOCLINES.

Let us first consider a series of ontogenies which change with time by paedomorphosis.The ancestral apaedomorph (i.e. non- paedomprphic form) may be said to pass through morphological stages A to M during its development to an adult (fig 1) If a descendant species which evolvesfrom the ancestral form is neo tenic or progenetic, the descendant will pass through fewer morphological stages during growth, say only A to K. By the postulates of the model there will subse quently be selection of a paedomorph which passes througj fewer stages still during its ontogeny, say A to I. Similary, this form may then itself give rise to a descendant species which passes only through stages A to G, and so on to the last species to evolve, the most paedomor phic with respect to the ancestral apaedomorph, which passes only through morphological stages A to C.

It can be see by considering just the adult morphological stages of the six hypothetical species that they constitute a morpholo- gical stages of the six hypotetical species that they constitute a morphological gradient through time: M-K-I-G-E-C. This temporal morphological change between adults thus follows the opposite pathway to the ontogenic developement of the earliest species, the apaedomorph, which passes through all morphological stages, A to M. The sequence of adult morphologiest displaying such a temporal morphological gradient will be a phylogenetic trend; it is herein termed a paedomorphocline.

The evolution of a descendant paedomorphic species need not result in the extinction of its direct ancestor, Ineed, in the situation described above all six species could coexist temporal ly, though not spatially (see below); the paedomorphocline could then be cponsidered on a single time plane as a purely ecological phenomenon.

As Gould (1977) has ponted out, there is no reason why paedomor phosis should occur any more often than peramorphosis. Thus one can evisage the converse to the paedomorphocline in the peramor phocline. This, by definition, will possess the opposite pattern of morphological change to the paedomorphocline. An ancestral species passing through morphological stages. A to C during ontogeny may give rise by one of the peramorphic processes tpo a descendant species which passes through morphological stages A to E durin id ontogeny (fig 2); this is turn may give rise to a species passing through morphological stages A to G, and so on if the resultant morphologies are adaptatively successful along the environmental gradient which the peramorphocline in invading. For a similar reason to those for the paedomorphocline, if the ances tral species persists in its particular niche and if siutable niche are available along the environmental gradient, specietion will be unidirectional (see discussion).

THE TEGULORHYBCHIA-NOTOSORIA PAEDOMORPHOCLINE.

The earliest known species of the rhynchonellide brachiopod Tegulorhynchia, an undescribed species from the Early Paleocene to Early Eocene of Western Australia (Mcnamara in Press a), may be considered to be the ancestral apaedomorph and the earliest member of the Tegulorhynchia-Notosaria paedomorphocline (fig 3). This ancestral species of Tegulorhrynchia undergoes more morpho logical change during its ontogeny than any other sppecies on the paedomorphocline. Small juveniles possess a narrow shell with shallow valves of similar depth; a rectimarginate commissure; 25 costellae at a shell legth of 2 mm; and long, pointed beak with a large foramen, and widely disjunct, small deltidial plates. Through the ontogeny, during which the shell grows to a maximum legth of abouth 18 mm, the principal morphpological changes involve a broadening of the shell; a large increase in valve depth; developemtn of a strongly uniplicate commissure; an increase in the number of castellae by frequent branching early in ontogeny, producing up to 80 fine costellae in the adult; reduction in height of beak and increase in umbonal angle; and diminution in size of foramen by the deltidial plates becoming conjunct, then almost closing the forament.

The second species in the paedomorphocline is the New Zeland Late Eocene to Early Miocene T squamosa (hutton 1873), Lee (1980)considers the living T. Doederleini (Davidson 1886) to be a separate species from T. squamosa on account of stratigraphical (ranging from the pliocene o the present day)and geographic discontinuities, even though morphologically there seems little to warrant their separation. These species may be considered to be neotenic with respect to the apaedomotph, as they have fewer ribs in the adult (up to 60); slightly narrower shell; less strongly developed uniplication; lerger forament, though the deltidial plates remain conjuct; and larger shell size (legth up to nearly 25 mm).

The Australian Tertiary species T. coelata (Tenison Woods 1878) and T thomsoni Chapman and Crespin 1923 continue this paedomorphic trend. They have fewer costellae than T. squamosa; norrower shell; disjunct deltidial plates; larger formen; more pointed beak; and weaker uniplication of the commissure. Stratigraphically T. coelata and T. thomsoni appeared later than T. squamosa, T. coelata being first recorded from the Early Miocene. The younger of the two, T. thomsoni, has fewer costellae than T, coelata (28 as opposed to 36-40); more prominent beak; valves of similar depth and larger foramen, consistnt with its position further along the paedomorphocline.

The end members of the paedomorphocline, Notosaria anipoda (Thomson 1918), which first appeared in the Late Oligocene, and N. nigricans (Sowerby 1846), which ranges through to the present day, possess the most juvenile characters in the adult; norrowest shell; weakest uniplication; fewest costellae (25); most disjunct deltidial plates; and largest foramen.

These end members seem to have appeared before the proceding species on the paedomorphocline, T. thomsoni, illustration that, on occasions, some paedomorphs may not necessarily have evolved from the immediately preceding species on the paedomorphocline. In other words, the position of T. thomsoni on the paedomorphocline was bypassed by species of Notosaria, which probably evolved from T squamosa, T. thomsoni is morphologically close to Notosaria, and taxonomic revision of the species might even result in its emplacement within that genus. Geographic separation of Notosaria and T. thomsoni indicates evolution of similar morphotypes from different ancestors, which have different position on the paedomorphocline. THe southern Australian T. thomsoni evolved from T. coelata; the new Zeland spoecies of Notosaria evolved from T, squamosa. There is greater morphological separation between Notosaria and T. squamosa than between tha Australian species, T. thomsoni and T. coelata. Be tant sas it may, the overall phylogenetic tred has favored selection of paedomorphs.

Ecological significance of the paedomorphocline. The living species of Tegulorhynchia, T. doederliini, occurs only in water deeper than 100m (Lee 1980) and to as deep as 635m (Dall 1920). Lee (1980) considers that fossil Tegulorhynchia inhabited deep or relatively quiet water. The paedomorph Notosaria, However commonly occurs in the intertidial zone (Allen 1960); Percival 1960; Rudwick 192; Richardson 1981) and is most commonly found in water less than 200m deep (Lee 1978), although it has been recorded from deper water. Lee and Wilson (1979) consider the extinct N. antipoda also to have inhabited a shallow water, high hydrodinamic environment.

I believe that the neotenic retention by species of Notosaria of a large foramen and, consequently, a large, muscular pedcle (Richardson 1981), which permits strong sttachment of the animal to its substrate (Richardson 1979), enabled this morphotype to inhabit a much shallower water, thus higher hydrodinamic, environment than Tegulorhynchia. The latter, in its quiet water environment, can obtain adequate attachment with a smaller tethering pedicle. The juvenile Tegulorhynchia, with its relatively large formen, would possess a relatively thicker pedicle to provide secure attachment to the substrate, as the smaller juveniles are more susceptible to dislodgement by current activity and requiere form attachment (Richardson 1981).

Other morphological character possessed by the paedomorphic Notosaria, such as fewer, much coaser costellae, are also suited to occupation of a shallow water environment. The relatively shallower valves of Notosaria indicate possetion of a shallower sphirolophos lophophore than Tegulorhynchia. Such a lophophore would be adequate in higer hydrodynamic environment. Ocupation of quieter water by Tegulorhynchia necessitates possession of a deeper spirolophous lophophore. This correlation of habitat water depth with lophophore size, deduced from shell depth, has been noted by Hurst and Watkins (1978).

The intermediate species of Tegulorhynchia along the paedomorphocline may be predicted to have been adapted to intermediate conditions along the environmental gradient between the predominantly nearshore, high hydrodynamic habitat of Notosoria, and the deep water, low hydrodynamic environment occupied by the apaedomorph.

The apaedomorph shows no indication of any morphological drift during its 10 Myr range from the Early Paleocene to the Early Eocene (McNamara in press a). Lee (1980) has similary noted that the morphotype T,suqmosa-doederleini. although exhibiting a certain degree of phenotipic variarion, underwent no directional morphological change for over 40 Myr from the Late Eocene to the present day. The same is true for Notosaria, lee and Wilson (1979) having absерved that there is, indeed, less variation between population means from the Miocene to presentr day than between extremes of living populatios of N. nigricans.

Olenellus Paedomorphocline.

A paedomprphocline may be observed in the fossil record on what is, essentially, a single time plane. In the Early Cambrian Fuciud Beds of northwest Scotland, five species of the trilobite Olenellus have been identified, and interpreted as having arosen by paedomorphosis (mcNamara 1978). In constrast to the neotenic Tegulorhynchia-notosaria paedomorphocline which is observable both spatially and temporally, the Olenellus paedomorphocline is an example of a spatial progenetic paedomorphocline show a slight increase in zise, the progenetic nature of the Olenellus example, discused in detail by McNamara (1978), is demostrated by the progressive reduction in maximum adult size along the paedomorphocline

Although all five species of Olenellus occur in the same rock unit, O. lapworthi Peach and Horne 1892, is considered to be tha ancestral apaedomorph, because its morphology is typical ot that of most other areas. Even within the Fucoid Beds it is a wide spresd species, whereas O. armatus Peach 1974, which lies at the other end of the paedomorphocline (fig 4), occurs at only one locality. This restricted distribution of O. armatus is characteristic of progenetics species (mcNamara 1981). O.lapworthi os followed along the paedomorphocline by O. reticulatus Peach 1894, O. hamolucus, Cowie and McNamara 1978, O. intermedius Pach 1894 and finally, O. armatus.

Although the detailed ontogeny of the apaedomorph, O. lapworthi, which would have undergone most morphological development during its ontogeny, is incompletely known, its adult form is very similar to that of other species of Olenellus in wich ontogenies have been well document (Palmer 1957; Hu 1971). Essentially, the apaedomorph would have undergone large-scale morphological change involving; an appreciable broadening of the cephalon, largely due to widening of the extraocular area; posterior migration of the the frontal lobe, resulting in increased glabellar furrow sinuosity; posterior migration of eye lobe and genal angle, resulting in a rounding of the anterior cephalic margin; migration of the intergenal spine toward the geneal angle, and its degeneration; and an increase in thorasic pleural width as new segments were added (McNamara 1978).

AS a trilobites, like other arthropods, grew by perioduc moult ing, their ontogeny consited of periods of morphological stasis, interspersed by rapid saltations to new morphologies. This is quite unlike the morphological development of the branchiopods which proceeded continuously through to the adult phase. Even so, species of both groups of the animals appear to have periodically evolved along paedomorphocline by morphological saltations. The potential exited for precocious maturastion to have occurred in species of Onellus at any moulthing event. However, only five paedomorphs appear to have become establisihing as separate species, each occupyng and adaptative peak on the paedomorpho cline. Palmer (1957) estimates that Olenellus underwent ecdysis at least twenty-nine times during intogeny-twenty-nine potential opportinities for progenesis. If the fossil record in the Fucoid Beds is a reasonably accurate indication of the number of the species, can occur only when sufficient morphological distance is established between the ancestral and descendant morphotypes such that an adaptative threshould is crossed. Competition for re sources is thus avoided.

ECOLOGICAL SIGNIFICANCE OF THE PAEDOMORPHOCLINE.

The environmen tal gradient along which this paedomorphocline is considered to have developed is again a deep to shallow marine situation. In this case, however, it is believed that higer water temperatures in shallows water mithing have triggered premature maturation in the pelagic larvae of the benthic adult apaedomorph, which is thought to have inhabited deeper water (McNamara 1978) Control by temperature in inducing and inhabited maduration in vertevbrates is well documented (Singh-Pruthi 1924; Newell 1948; Wigglesworth 1954; Boner 1968). If Jell 1978 is correct in interpreting the function of genel caeca, wich cover the extrao9cular area of the apaedomorph, as a secundary repiration base, the progressive reduction in extraocular area along trhe paedomorphoclinemay have restricted the successive paedomorphocline may have restricted the successive paedomorphs to progressively more oxigenated waters, this interpretation is supported by the character of the last paedomorph, Olenellus armatus, It retains many overt larvcal characteristic, suggesting it led an entirely pelagic existence in shallower, warmer, more oxygenated waters than its progenitor.

OTHER PAEDOMORPHOCLINES.

The living spatangoid Breynia. Spatial paedomorphocline can be observed not only species. A recent study (McNamara in press b) of living Auatralian species of the span tangoid echinoid Breynia indicates the presence of a paedomorfo cline incolving three living species. Despite its widespread occurrence in Miocene and Pliocene rocks of the Indian Subconti nent, Japan, Taiwan and Indonesia, Breynia is recorded in Austra lia only from Miocene rocks in the nortwest of the continent and is absent from the miocene deposit of the southern part. The three living species which occurs along the western coast, are B desorii Gray 1851, which occurs along the western coast and the western part of the northern coast; B, australasie (Leach 1815), which occurs along the eastern coast and in the Arafura Sea.

The three species form a paedomorphocline. The western species, B.desorii, which is known to have existed at least as far back as the ate Pleistocene and was derived from the Indian Ocasn genetic pool, is considered to be tha apaedomorph.It shares more features in common with Miocene species of Breynia than either of the other two living Australian species, principally in its greater aboral tuberculation, longer petals and smaller peritome. Some variants even possess a lambrum which is separated from the plastrom by ambulacral plates, a featured otherwise found only in Miocene species of Breynia.

B.australaside is interpreted as having evolved by paedomorphosis from B. desorii and spread to the east coast; absence of both fossil and living Breynia from southern Australian sugests that Breynia spread around the northern part of the continent, B. asutralasiae attains maturity later than B. desorii and retains juvenile characters B. desorii into the adult phase; it is there fore neotenic. Yhe juvenile characters retained include fewer primary tubercles;shorter petals; broader, shorter internal faciole; relatively larger peristome and periproct; and fewer subanal pore pairs, B. n.sp. is the end member of the paedomoor phocline. It is an uncommon species and retains earlier juvenile characters into the adult than B australasie, from which it is believed to have evolved. It has a low test: fewer primary tuber cles; shorter petals; smaller plastron; broader periplastranal area; and fewer subanal pore pairs within a narrower fasciole.

Phenotypic variation between adults of species of Breynia in volves slight changes inrates of development of particular struc ture. For instance, in a population of the apaedomorph B, desorii from off Dirk Hartong Island, Western Australia, many adult specimens possess a wider internal fasciole and fewer primary tubercles than is normal for the species. in retention of these more juvenile characters, the individuals are reminiscent of the paedomorphic B. australasie. However, in all other characters, such as peristome and periproct shape, the Dirk Hartog population is like B. desorii from elsewhere. It seems likely that such phenotypic variation led to the evolution of B. australasiae from B. desorii.

The evironmental gradient along which this paedomorphocline has developed, is not known.There are insuffient data on the life habits of tha adults, and nothing is known of the mode of life of the juveniles. The differences between species could be related to differences in depth of burial in the sediment; preference for different sediment type; or perhaps occupation of benthic habi tats at different water depths. Development of a larger plastron and more subanal tuber feet in B. desorii suggest that it may burrow deeper than either of the other two species.

The cenomamian ammonite Protacanthoceras. Wright and Kennedy's(1980) study of the acanthoceraid ammonite genus Proto canthoceras has revealed the evolution of a number of paedomor phic species through the Middle to Upper Cenomanian Protacathoc eras tuberculatum Thomel 1972-P.T. mite Wright and Kennedy 1980- P.arkelli- Wright and Kennedy1980 p. a. arkelli Wright and Kennedy 1980-P. tegulicium Wright and Kennedy 1980 form the early Middle Cenomanian costatus Zone to the mid Upper Cenomanian naviculare zone. Wright and Kennedy (1980) revcord that while speciation appears to have occurred by series of saltations, there is also evidence in the P. tuberculatum tootstock of some apparently gradual phylogenetic changes between the successive paedomorphs involved a reduction in strength of ornament and developement of a compressed shell. The final species in the paedomorphocline, P. tegulicium. lacks siphonial and outer ventroleteral tubercles. These are present from the nuclei of P arkelli which preceds P. tegulicium. Tuberculation is most strongly developed in the ancestral apaedomorph of the paedomorphocline, P. tuberculatum tuberculatum.

Evolution of the small (15-30 mm diameter) Protacanthoceras from the large (up to 500 mm) Acanthoceras was by progenies.The small species P. asgerri Wright and Kennedy 1980, Which does not lie on the paedomorphocline, probably arose from P. tuberculatum by progenies. The environmental gradients along which the paedomor phocline developed is not known, although Dr. Kennedy (litt. comm., 10 jun 1981) suggest that the adaptative significance of the paedomorphosis may have lain either in the shorter juvenile phase, reducing the time between hatching and spawning, or in development of a smaller size, allowing exploitation of new niches.

The silurian graptolites. Petalograptus and Cephalograptus. Rick ards (1977) has described a serioes of paedomorphs in the mono graptis Petalograptus and Cephalograptus, which evolved from P. onatoelongatus through three intermediate distimct paedomorphs with overlapping times ranges, along a paedomorph is a apecies with much enlarged early thecae. The progresive increase thecal size along the paedomorphocline implies neoteny was the paedomor phic process. Again, the environmental gradient associated with the paedomorphocline is not known, although the development of progressively longer thecae along the paedomorphocline may indi cate adaptation to differenct feeding strategies

THE PARASTER-SCHIZASTER PERAMORPHOCLINE.

The spatangoid echinoid genus Schizaster is generally considered to consist of two subgenera: Schizanter and Paraster. Which lie at oposite ands of a morphological gradient (McNamara and philip 1980 a) The paraster morphotype appeared before the Schizaster morphotype and has, like Schizaster, persisted to the present day. The basic Paraster morphological characteistics of relative ly small test; centrally positioned apical system and apex shal low ambulacrum III, which aborally bears few, widely spaced, pore pairs; shallow anterior notch; widely divergent anterior petals; short labrum, which projects little anteriorly; and relatively small plastrom, are siutable for living in coarse sediment. Chesher (1966has noted that living P. florinfiensin Kier and grant 1965 burrows in coarse calcareus sand to a depth of 25 cm .Fossil species of Paraster from the Tertiary of Australia occur in calcarenites (McNamatra and Phillip 1980a), suggesyting they had similar subtrate preferences.

A series of the species occurs througs the Australian Tertiary which I interpret as a peramorphocline from the Paraster morpho type to the Schizarter morphotype (Fig 5). The Middle Miocene S. Sphenoides Hall 1907 developed at the end of a peramorphocline which comprises the ancestral aperamorph (i.e. non-peramorphic from) P. carinatus McNamara and Phillip 1980a (Middle to Late Paleocene), followed by P. tatei McNamara and Philip 1980a(Late Oligocene to Early Miocene) and S. abductus Tate 1981 (early Miocene, The principal morphological changes which occur along the peramorphocline involve; the attainment of a larger, longer test; a more posteriorly situated apex and apical system; less anteriorly divergent anterior petals; deeper petals; deeper anterior notch and ambulacrum III, which bears an increasing number of more closely spaced funnel-building tube feet (McNamara and Philip 1980a, Fig 8); more anteriorly positioned and sunken peristome; more anteriorly projecting labrum; and relatively larger plastrom. The extreme Schizaster morphology developed in the Middle Miocene by S. sphenoides has persisted to the present day.

Ontogenetic study of a living species of Schizaster, S.myorensis, from Moreton Bay, Queensland (McNamara and Philip 1980b) revealed that small juveniles of the Schizaster morphotype posses the same morphological characteristics as juvenileParaster and are very similar to adult Paraster. Ontogenetic development of Schizaser therefore parallels phylogenetie development of the Schizaser morphotype from the Paraster morphotype through the Tertiary. Species possessing the extreme Schizaster morphotype are well adapted to living in very fine-grained sediments. Indeed, S. myorensis burrows to at least 10 cm depth i the muddiest sediment in Moreton Bay. Furthermore, extinct forms such as S. sphenoides occur only in fine-grained marly beds.

By what is believed to be a combination of hypermorphosis (the Schizaster species becoming mature later than paraster) and acceleration in development of some features, particularly the rate of production of funnel-building tube feet, the Schizaster morphotype is capable of occupying a very fine-grained sediment. Living buried in such a sediment would necessitate the possession of morphological characteristics which can most efficiently utilize a single source of water drawn down the funnel. Paraster, al though building a funnel (chesher 1966) which also assists in surface feeding, would have its test bathed by water percolating through the much coarser sediment which in inhabitats.

The peramorphic developement in Schizaster of deep petals, poste riorly positioned apex and apical system (which enabled length ening of the anterior patels and ambulacrum III), deper peristome and elongation of the labrum, all reflect developement of adapta tions wihich contributed toward efficent utilization of a local ized water source, and consequently permited colonisation of a much finer.gradined sediment than that inhabited by ancestral morphotypes. The increse in area of palastron, which was accompa nied by an iincrease in number of burrowing plastonal spines, facilitatres burrowing in a fine-grained sediment. The ability of the evolving peramorphs to inhabit progressively finer sediments reflects tha adaptations of the species on the morphological gradient to the environmental gradient of coarse to fine-grained sediment. Explotation of new sedimentary environments by morpho types evolving along the peramorphocline resulted in apatial separation of the peramorphs and resultant geographic and genetic isolation.

DISCUSSION.

The model of paedomorphoclines and peramorphoclines developed from the example disscussed above, proposes that directional morphological evoliution may arise by heterochrony How can such a model be recoinciled with evoliutionary theory which predicts that speciation is an essentially random event? What are the principal factors controlling the speciation? Why should the speciation be directional? The following discussion will deal with paedomorphoclines, but equivalent arguments apply to pera morphoclines.

The establishment of an extreme paedomorphic phenotype as a separate species is ultimately dependent upon its possession of morphological novelties adaptative in a environment which thsa ancestral from is unable to occupy because of its unsuitable morphological characteristics. The morphological novelties aris ing from paedomorphosis may be regarder as preadaptations (sensus Simpson 1944) which enable colonization of a new wnvironment.

Larson et al. (1981) have discussed how presadaptations arising in plethodointid salamanders arose by developmental alterations. Once initiated, complex morphological changes were able to be archived relatively rapidly. The morphology of a descendant paedomorph must therefore be sufficiently different from its ancestor to ovoid competitive exclusion and allow ecological separation of the ancestor and descendant. The extreme paedomor phic phenotype may be regarder as heving tha ability to overcome an adaptative threshould in order to attain the ecological sepa ration. This is likely to ensure reproductive and genetic isola tion of morphotypes, so facilitating the evolution of a new species. As a consaequence, the ancestral species would be ex pected to persist temporally, through not spetially, with the paedomorph.

If sellection act only on morphotypes derived by changes in regulation of developemnt, the peristing ancestral species ewf frectively inhabit reverse speciation to ancestral morphologies, by competitive exclusion, and so direct speciation along the paedomorphocline (fig. 6). Selection os successive paedomorphs along a paedomorphocline can only occur if the adaptations that are developed are siuted to the environmental gradient, such as a relatively larger pedicle and coaser ribs in the Tegulorhynchia- Notosaria paedomorphocline developed in response to an environ mental gradient of deep to shallow water.

The importance of asn environmental gradient in controlling directional speciation has been recognized by Grant (1963), who observed the presence of five species of the herbaceous plant Polemonium along an environmental gradient toward lower tempera tures at higher elevation. The possition occupied by each species on a paedomorphocline may be equated to an adaptative peak (Wright 1932). Variation in gene regulation will provide the changeable genetic composition of adaptative peaks. Only some of the paedomorphic phenotypes will reach the adaptative peaks. These will be the few extreme paedomorphs which are capable of overcoming tha adaptative threshould, The position of the adapta tive threshold will depend upon the adaptative significance of the morphological novelty and the nature of the morphological novelty and the nature of the environmental gradient; and the nature of the environmental grasdient; buit in need not remain static through time. Consequently, if the same range of paedomor phic phenotypes were to exist over a period of time, it is only when there is a shift in the position of the adaptative threshould that extreme paedomorphic phenotypes would be able to cross it (Fig.6). In all probability, however, the range of paedomorphic phenotypes will also be a variable factor through time. The coincidence of the two, perhaps both by as slight shift in the adaptative threshould and by an extension of the range of paedomorphic phenotypes, will be necessary for the succesful occupation of the next adaptative peak along the paedomorpho cline.

A paedomorphocline may therefore be considered as a series of adaptative peaks lying along a unidirectiônal morphological axis. The model predicts that these peaks generally become established sequentially along an environmental gradient. The possition of each peak on the environmental gradient will be dictated by the position of the ancestral apaedomorph, and the degree of morpho logical separation beween each descendentan and ancestor pair necessary for them to avoid significant competition for re sources.

Variation ion rates of morphological development i the apaedo morph, or changes in the timing of onset of maturity, might be expected to be sufficient to produce enough morphotypes to occupy all the adaptative peaks on the heterochronic gradient. In such a situation the last species in the paedomorphocline could there fore potentially develop directly from the apaedomorph by a large change inthe timing of onset of maturity. Other, intemediate, forms onthe heterochronic gradient would subsequently develop at radom. It is clear, however, from the examples of temporal paedo morphoclines and paedomorphoclines described above, that the adaptative peaks are not occupied in this radom fashion.

The clearly sequential evolution of species indicates that there are constraints imposed on the developemtn or the heterochronic phenotypes. Either each species can undergo only a limited degree of developmental raterdation or acceleration, sufficient only to produce occasional phenotypes capable of overcomieng the adapta tive threshould and occupying the next adaptative peak along the paedomorphocline, or ecological constraints may restrict more than a limited distance along the environmental gradient. The most probable situation in that both of these factors operate.

It might be expected that the model of heterochronic directional speciation would only fit a gradualistic interpretation, as both tha ontogeny and the environmental gradient along which tha spoecies is developing may be gradually changing, through space and timem respectively. However, as has been outlined above, this does not appear to be the case. of thsa almiost intinite number of morphotypes which could potentially develop along the paedo morphocline, only a small number, those able to cross the adapta tive threshould and occupy new adaptative peaks, become estab lished as viable species. All are separated by significant mor phological unit, whit little or no morphological shift through time once established as a separated species.

THe species which lie long a paedomorphocline arte therefore characterized by their temporal morphological stability, their temporar morphologicial stsability, Their distinct morphological separation from one anohther and by their sudden, generally sequential, apperarance in the fossil record. The pattern of evolution of species along heterochronic morphological gradients is therefore consistent with the "punctuated equilibria" model of macroevolution (Eldredge end Gould 1972; Gould and Eldredge 1977), rather than the gradualistic model.

The importance of heterochrony in rapid speciation has been discussed by Valentine and Cambell (1975); Gould (1977); McNamara (1978); and Stidd (1980). However, trhe role of heterochrony in the development of phylogenetic trends and assimilation intpo the "puntuated equilibria" fremework has recived little attention, Stanley (1975,1979) has stressed the importance of "species selection" in the punctuational model and its role in the devel opment of a phylogenetic trends. He coinsider that the direction takes by specietion has a strong radom element, a view taken by Rensch (1959), Wright (1956, 1967) and Mayr (1963), Speciation, if essentially radom, would have equal probalities of moving in either direction along an environmental or morphological axis. STANLEY (1979) considers that apparently directional speciation occurs as a consequence of environmental factors acting on ini tial radom speciation. Recently, however, Goul (1980) and Alberch (1980) have questioned the validity of the concept of radom speciation in all situation and streed the non-radom appearance of some morphological novelties. Maynard Smith (1981) has gone so far as to state that "there is no evidence to show that the direction of punctuational changes is random with respect to major trends".

When selection acts only on descendant paedomorphs it is immedia ly restricted to a single morphological axis of the organim's own antogeny. As outlined above, peristence of the ancestral morphotype on the paedomorphocline blocks evolution back to the ancestral from by competitive exclusion. Selection in that situation is chanelled in one direction: away from the ancestral morphology. Directional speciation will thus ensue, as long as the environmental gradient persists. Terminationof the gradient will result in the cessation of the phylogenetic trend.

CONCLUSIONS.

A number of recently described examples of heterochrony in diverse groups of theorganims indicate that directional specietion, resulting in phylogenetic trends, may develop because the ontogeny of an individual can provide anbuilt, directional component. Any heterochronic variation, by extention, contraction, or change in timing of onset, of morphological effects onthe descendant adult. Paedomorphs or peramorphs may thus be morphologically quite distinct from their progenitors and can potentially evolve rapidly. Selection for these morphotypes can lead to rapid speciation and the evolution of morphologically distinct descendants, without the appearence of intermediate morphotypes.

Provinding that the descendant morphotypes are siutably adapted to considitions along an environmental gradient, a phylogenetic trend, in the form of a paedomorphocline or peramorphocline, can become established. Persistence of the ancestral form with little or no directional morphological drift through time limits selection along the heterochromic morphological gradient to one direction; that is, along the environmental gradient, away from the ancestral species. Over a period of time dictrional speciation may thus occur and result in the development of a phylogenetic trend.

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Fig. 1. The paedomorphocline; a discontinuous morphological gradient of progresively more paedomorphic species through time. Time 1 represents a situations whereby all paedomorphs and the apaedomorphs could coexist temporally; ecological separation of morphotypes will eosure they do not coexist spatially, A to M represent arbitrary ontogenethic stages. Species time range is for the adult morphology.

Figure 2: The peramorphocline a discontinuos morphological gradi ent of progressively more peramorphic species through time; successive species evolving along the peramorphocline pass through more morphological stages during ontogeny. A to M repre sent arbitrary ontogenetic stages. Species time range is for the adult morphology.

Fig 3. Tegulrhynchia.Notosaria, paedomorphocline by neoteny; illustrating temporal narrowing of shell, reduction in number of costellae, decrease in beak angle and increase in relatively foramen size by progressive reductionh in rate of growth of deltidial plates. These adaptations enabled colonisation of progressively shallower water environment. All adult recostruc tion x 2(after McNamara in press a, tex-fig 3).

Fig 4 A spatial paedomorphocline by progenesis in species of olenellus from the lower Cambrian of north west scotland. The paedomorphocline is considered to have followed as environmental gradient of increasing temperature and oxygen content into shal lower water. Bars by recosntruction represent Imm, illustrating the progressive reduction in maximum adult size as a consequence of progenesis.

Fig 5. Peramorphocline from Scrizater (paraster) to Schizaster (schizaster) through the Australian Tertiary to recent. Paramor phic establishment of the Schizaster ss. morphotype is thought to reflect adaptation to occupation of finer grained sediments. S. (paraster) adult recosntruction X 1; S (schizaster) adult recon struction x 0.5; juvenile recosntruction x 1.

Figure 6. Suggested mechanism for the development of a paedomor phocline. It is not until a population of species 1. Such as population B, has paedomorphic phenotypes capables of crossing the adaptative threshould and occupying a new adaptative peak, that a paedomorphic species may arise. Shiftihing adaptative threshoulds and variation inrange of paedomorphic phenotypes affects timing of evolvolution of species 2. Fpor instance, even though the range of paedomorphic phenotypes is greater in opula tion A thain B, the position of the adaptative threshould is such that it is not crossed by phenotypes of population A. Extreme paedomorphs of population C of species 1 are limited by compara tive exclusion. There is no adaptative threshould. The persist ence of such population, however, effectively blocks reverse speciation fom species 2 to species 1. Selection of extreme paedomorphic phenotypes of species 2 Which can cross and adapta tive threshould results in the establishment of a further paedo morphic species, species 3. The paedomorphocline is therefore established and uniderctional speciation ensus. Broken lines represent adaptative thresholds.

M. J. McNamara

FIGURA 1

64

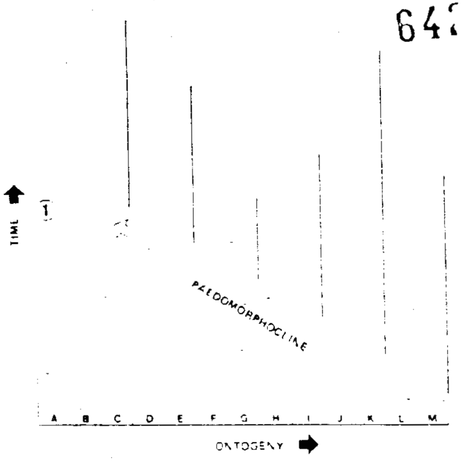


FIGURA 2

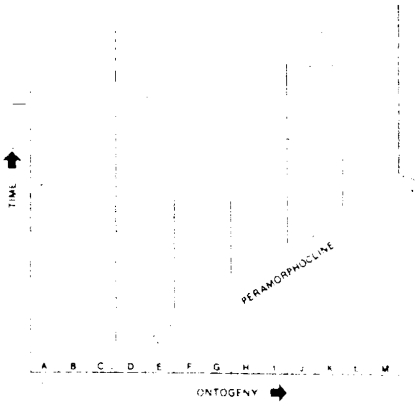


FIGURA 3

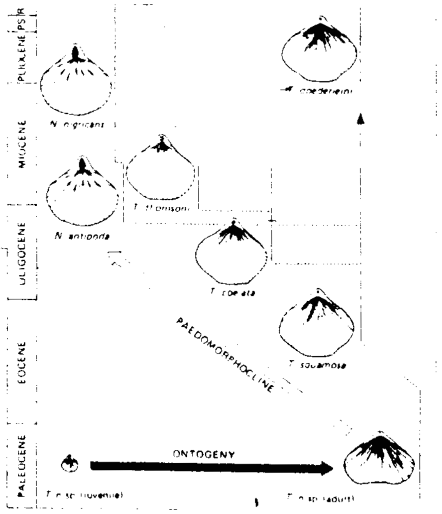


FIGURA 4

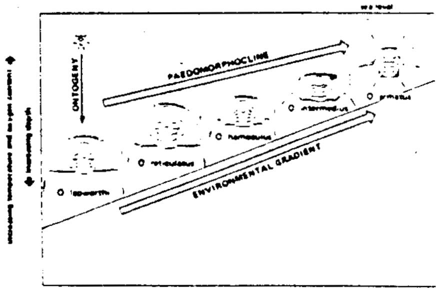


FIGURA 5

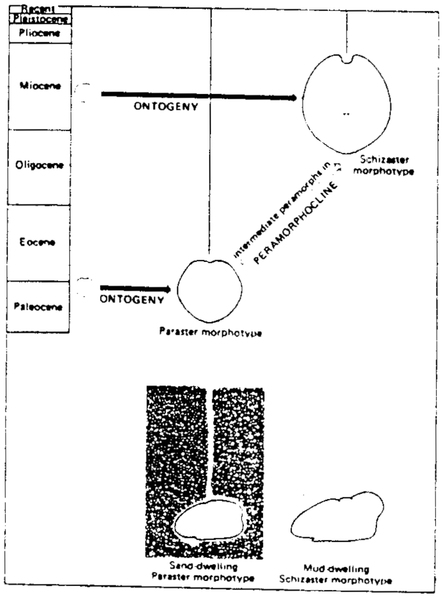
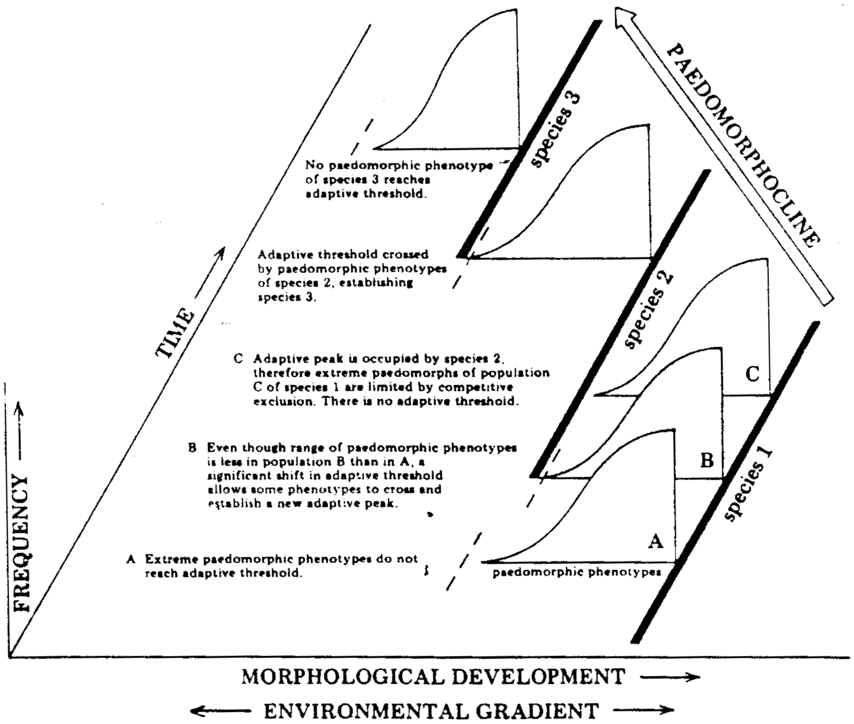


FIGURA 5


PAEDOMORPHOCLINE
species 3
No paedomorphic phenotype of species 3 reaches adaptive threshold.
Adaptive threshold crossed by paedomorphic phenotypes of species 2, establishing species 3.
species 2
TIME
C Adaptive peak is occupied by species 2, therefore extreme paedomorphs of population C of species 1 are limited by competitive exclusion. There is no adaptive threshold.
C
B Even though range of paedomorphic phenotypes is less in population B than in A, a significant shift in adaptive threshold allows some phenotypes to cross and establish a new adaptive peak.
B
species 1
A
A Extreme paedomorphic phenotypes do not reach adaptive threshold.
paedomorphic phenotypes
FREQUENCY
MORPHOLOGICAL DEVELOPMENT
ENVIRONMENTAL GRADIENT

10.3 (d)

EVOLUTIONARY FAUNAS.

J.J. Sepkoski, Jr.

In: D.E.G.BRIGGS & P.R. CROWTHER, EDITS., 1990.
PALEOBIOLOGY, A SYNTHESIS, OXFORD, INGL.,
BLACKWELL SCIENT. PUBLIC., P 37-41.

Evolutionary faunas are sets of higher taxa (especially classes) that have similar histories of diversification and together dominate the biota for an extended interval of geological time. The expoansion and decline of evolutionary faunas can be used to describe large-scale variations in faunal diminance and to inter pret temporal changes in global taxonomic diversity in the fossil record. The concept was introduced by Sepkoski (1981), who iden tified three'great evolutionary faunas' in the Phanerozoic marine record. These faunas were defined statically in a factor analysis of familial diversity within taxonomic classes, which grouped together classes that attained their maximum diversities around the same time. The nalysis permitted the histories of the aggre gate faunas to be traced from initial diversification through dominance and into decline. This treatment of the faunas as units throughout their histories distinguishes the concept of evolu tionary faunas from that of "dynasties", used by some authors for assemblages of dominant taxa during specified intervals of geo logical time.

MARINE EVOLUTIONARY FAUNAS.

Characteristics. The three evolutionary faunas identified in the marine fossil record are the Cambrian fauna, important during the Cambrian Period, the Paleozoic Fauna, diminant from Ordovician to Permian, and the Modern, or Mesozoic-Cenozoic Fauna, dominant in the post-Paleozoic (fig. 1A). The classes in each faunas share a number of characteristics, or central tendencies, suggesting that they are not randomly assembrled groups of taxa. The most strink ing characteristic is that the classes tend to diverisuty togeth er, each successive fauna displaying a slower rate of diversifi cation but higher level of maximum diversity than those preceding it. These poroperties lead to a sequential expansion of evolu tionaryfaunas and resultant step-like pattern of increase in global marine diversity (with the step betwenn the Paleozoic and Modern faunas dusrupted by the Paleozoic and Modern faunas di scrupted by the massive Late Permian extinction event-Section 2.13.4). This pattern is present even though most marine classes originated early in the Phanerozoic and the total number of classes has remained virtually constant since.

The expansion of each evolutionary fauna is associated with the decline of the previously dominant fauna. The declines are much slower than the initial diversifications, giving tha faunas very asymmetrical histories. Such a pattern is difficult to simulate in 'radom' models of diversification (Sepkoski 1981) but can be described with coupled logistic equation of the form:

$$dDi/dt = riDi(1- Dj/Di)$$

where Di is the diversity of the ith evolutionary fauna at time t,rj, is its initial diversification rate, Dj is its maximum or èquilibrium' diversity, and Dj is the summed diversity of all faunas at time t (Sepkoski 1984; Kitchell & Carr in Valentine 1985). This equation states that an evolutionary fauna only if its initial diversification rates is lower and equilibrium diver sity is higher. If ri is higher, the evolutionary fauna will expand so rapidluy that the evolutionary fauna will expand so rapidly that the preceding fauna will never appear to diversity; if Di is lower, the evolutionary fauna will never be able to expand and replace the preceding one. Thus, the coupled logistic equation suggests a certain inevitability in the sequential diversification of evolutionary faunas, althoug it does not specify their timing or relative differences in maximum diversi ty.

Classes within evolutionary faunas tend to have similar mean rates of taxonomic turnover. Classes in the Cambrian Fauna tended to have high turnover rates, those in the Paleozoic Fauna compar atively low rates (with some exceptions in all cases). These differences are reflected in the responses of the faunas to mass extinctions (Sepkoski 1984): The Cambrian Fauna suffered large proportional reductions in diversity relative to the Palaeozoic fauna during mass extinctions in the Ashgillian and Frasnian, and the Paleozoic Fauna suffered more than the Moder at all major mass extinctions of the Phanerozoic. This differential reaction seems to have led to the great change in faunal dominance associ ated with the Late Permian mas extinction (section 2.13.4.).

Evolutionary faunas also seem to have differing ecological char acteristics. The Cambrian Fauna tended to be assembled into broadly intergrading communities that were dominated by general ized deposit feeders and grazer and had low epifaunal and infau nal tiering (Bottjer & Ausich 1986; see also Section 1.7.1). Comunities of the Paleozoic Fauna were dominated by epifaunal suspension feeders with complex tiering; many other ecological guilds were also represented so that the faunal as a whole seems to have occupied more èscopace'than tha Cambrian Fauna (Bambach in Tevesz & McCall 1983). Finally, the Modern Faunas is repre sented by yet more guilds and is characterized by large numbers of durophagous predators (Vermeij 1987) and mobile deep infauna (Trayer in Tevesz & McCall 1983); epifaunal tiering is reduced inmost communities.

Sepkoski and Miller in Valentine (1985) demonsttrated that evolu tionary faunas tend to form coherent assemblages within shelf environments throughout the Paleozoic Era. Members of the Cambri an Fauna were spread across the entire shelf early in the Paleo zoic Era but became progressively restricted to deeper-water environments during the Ordovisican as members of the paleozoic Fauna expanded across the middle and finally outer shelf. At the same time, early members of the modern Fauna came to dominat inner shelf environments and later, deeper, low-oxygen environ ments. The Late Premian mass extinction eliminated dominance of the Paleozoic Fauna from middle and outer shelf environments and led to expansion of the Modern Fauna across the entire shelf.

It must be emphasized that none of these evolutionary and ecolog ical differences betwwen the faunas is absolute. In a sense, the faunas are 'fuzzy bouned sets'with their characteristics overlap ping and some members of each fauna mimicking members other. The characteritics thus represent node on a continuum. Major unsolved problems are why such nodes should exist and why they seem to change so little through the Phanerozoic.

COMPOSITION AND HISTORY. The individual histories of the marine evolutionary faunas are illustrated in Fig 2. The cambrian Fauna was dominated by trilobites along with inarticulate brachiopods, on the placophorans, hyoliths, and eocrinoids; most of the prob lematical taxa of the so-called 'small shellyfaunas'of the Tommo tian are also included. Various of these classes are paraphylet ic, with descendent monophyletic taxa belonging to other evolu tionary faunas; however, in most cases the paraphyletic classes either declined long before their descendent taxa diversified (e.g. Monoplacophora) or contained monophyletic subtaxa that diversidied in parallel with the rest of the evolutionary fauna (e.g. the inaticulata) Tha Cambrian Fauna diversified very rapid ly from the laest Vendian into the early Cambrian and was the principal constituend of the evolutionary explosion across the precambrian-cambrian boundary (see also section 1.5). Its maximum diversity was attained in the late Middle and early late Cambri an. Beginning in the latest cambrian, the fauna began a long, gradual decline, accentuated by the Ashgillian and Frasnia mass extinctions (section 2.13.2, 2.13.3).

The paleozoic Fauna initiated its expansion as the cambrian fauna began to decline; this combination resulted in nearly stable global diversity throughout the late cambrian. The paleozoic faunawas dominated by articulate brachiopods whit important contributions from crinoids, corals, ostracodes, cephalapods, and stenolaemate bryozoans. These groups were major components of the ordovician radiations, which tripled global taxonomic diversity over a 50 milion year interval. The Paleozoic fauna attained its maximum diversity from the late ordovician to devonisn and then begán decline. During the Carboniferous and Permian, this decline was matched by a slow expansion of the modern fauna so that again global diversity remained nearly constant. The Paleozoic Fauna was severely reduced by the late Permian mass extinction (srection 2.13.4) but in the mesozoic underwent two radiations: one in the Triassic, terminated by the Norian mass extinction (2.13.5), and a second, slower expansion in the jurassic. The Jurassic expansion was reversed in the Cretaceous when global diversity exceeded Paleozoic levels, and the remnants of the Paleozoic fauna again went into decline.

The modern fauna is dominated by gastropod and bivalve molluscs, osteichthyan and chondrichthyan fishes, gymnolaemate bryozoans, malacostracans and echinoids. Most of these classes appeared but diversified only sliwly through the Paleozoic era. they suffered minor extinction relative to the paleozoic fauna during the late permian and became the domiant fauna in the triassic. through the mesozoic and cenozoic, the modern fauna continued the rather slow and steady diversification initiated earlier, producing the long post paleozoic increase in global taxonomic diversity.

Throughout their histories, the three great evolutionary faunas experinced considerable internal turnover, with continuos change in otdinal and lower-level taxonomic composition. This was particulary true of the Cambrian fauna, which underwent very rapid changes during its initial radiation. It may prove useful to subdivide this fauna and define two more evolutionary faunas: and ediacaran fauna, ecompassing the distintive soft-bodied animals fossil of the vendian (section 1.3.1.5), and a tommotian fauna, comprising the mostly problematical skeletal taxa of the earliest cambrian (sections 1.4, 1.5, 5.2.5). These possible faunas seem to fit iinto the general progression of evolutionary rates and diversity levels observed for the three great evolutionary fauna. The Ediacaran and especially Tommotian taxa appear to have had higher diversification rates and more rapid evolutionary turnover than the remainer of the Cambrian Fauna, and seem to show successive increases in diversity leading into the cambrian period. Further analysis of diversity pattern and faunal change in the Vendian and early Cambrian are needed to assess whether such addtional evolutionary faunas are useful for describing tha early metazoa radiation.

TERRESTRIAL BIOTAS.

The concept of evolutionary faunas has proved useful for organising faunal turnover and diversity change in the marine rcord and has been extended with varying success to other evolutionary systems, specifically terrestrial vascular plants ans tetrapod vertebrates. Niklas et al (1983) identified four major plant groups, which can be termed evolutionary floras, in species- level data on tracheophyte diversity (fig 1B) there are: (1) an initial silurian.devonian flora of early vascular plants that radiated and then disappeared during the devonian; (2) a pteridophyte dominated lora, including ferns, lycopods, sphenopsids, and progymnosperms, that diversified in the Latre devonian and early carboniferous and dominated plant communities to the end of the Paleozoic era; (3) a gymnosperm-dominated flora of seed planta that apperade in the late devonian and rose to dominance in the Mesozoic; and (4) an angiosperm flora that originated in the early cretaceous and rapidly radiated to dominance thereafter, repalcing the preceding gymnosperm flora. As in the marine system, each of these floras (excepting the angiosperms) originated early in the history of vascular plants and radiated sequentially to produce step-like increases in global tracheophyte diversity.

Three assemblages of terrestrial tetrapod families have been identified by Betnton (1985) in the vertebrate fossil record (fig 1C). These comprise: (1) the labyrinthodonts, anaspids, and synapsids, which appeared during the middle paleozoic and completely dominated the terrestrial vertebrate record to the end of the paleozoic; (2) the early diapsid, dinosaurs, and pterosaurs, which arose in the triassic, attained maximum diversity in the late jurassic and cretaceous, and disappeared at the terminal cretaceous mass extinction (section 2.13.7); and (3) the lissamphibians, turtles, crocodiles, lizard, birds and mammals, which originated in the Triassic and jurassic, expanded through the cretaceus, and then diversified to very high levels in the cenozoic. Although these assemblages have some similarities to marine evolutionary faunas, there are some important differences: the assembleges do not all appear early in the history of tetrapods and their sequential diversifications are not all associated with step-like increases in global diversity. It remains to be seen whether such paterns could be identified if more terrestrial taxa (e.g. the arthropods) were included and analyses performed at lower taxonomic levels. If so, evolutionary faunas and floras would appear to be a general propietary of the development of Phanerozoic biotas.

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Fig 1. Diversity curves, A, marine animal families. B terrestrial vascular plant species; C terrestryal tetrapod families. Each curve is divided into fields that illustrate the diversities of the constituent evolutionary faunas and floras, A, After Sepkoski (1984); Cm = cambrian evolutionary fauna, Pz = Paleozoic fauna, Md = modern fauna; stippled field represents known diversity of families with rarely preserved members that lack heavily mineralized skeletons, B, After Niklas et al (1983); numbered fields as in text. C. After Benton (1985) numbered fields as in text.

Fig 2. histories of the three great evolutionary faunas of the marine fossil records as represented by their familial diversities through the Phanerozoic Representatives of the important classes in each fauna are illustrated above the diversity curves (After sepkoski 1984).

Figure 1

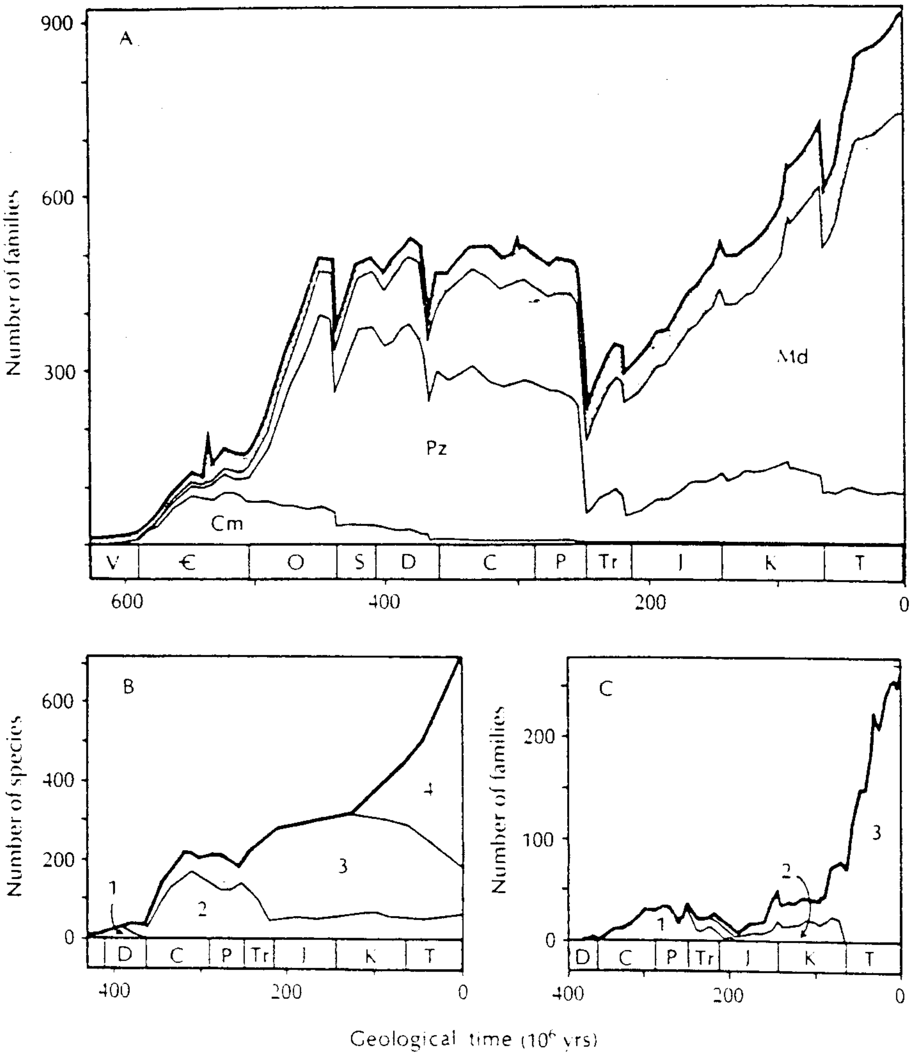
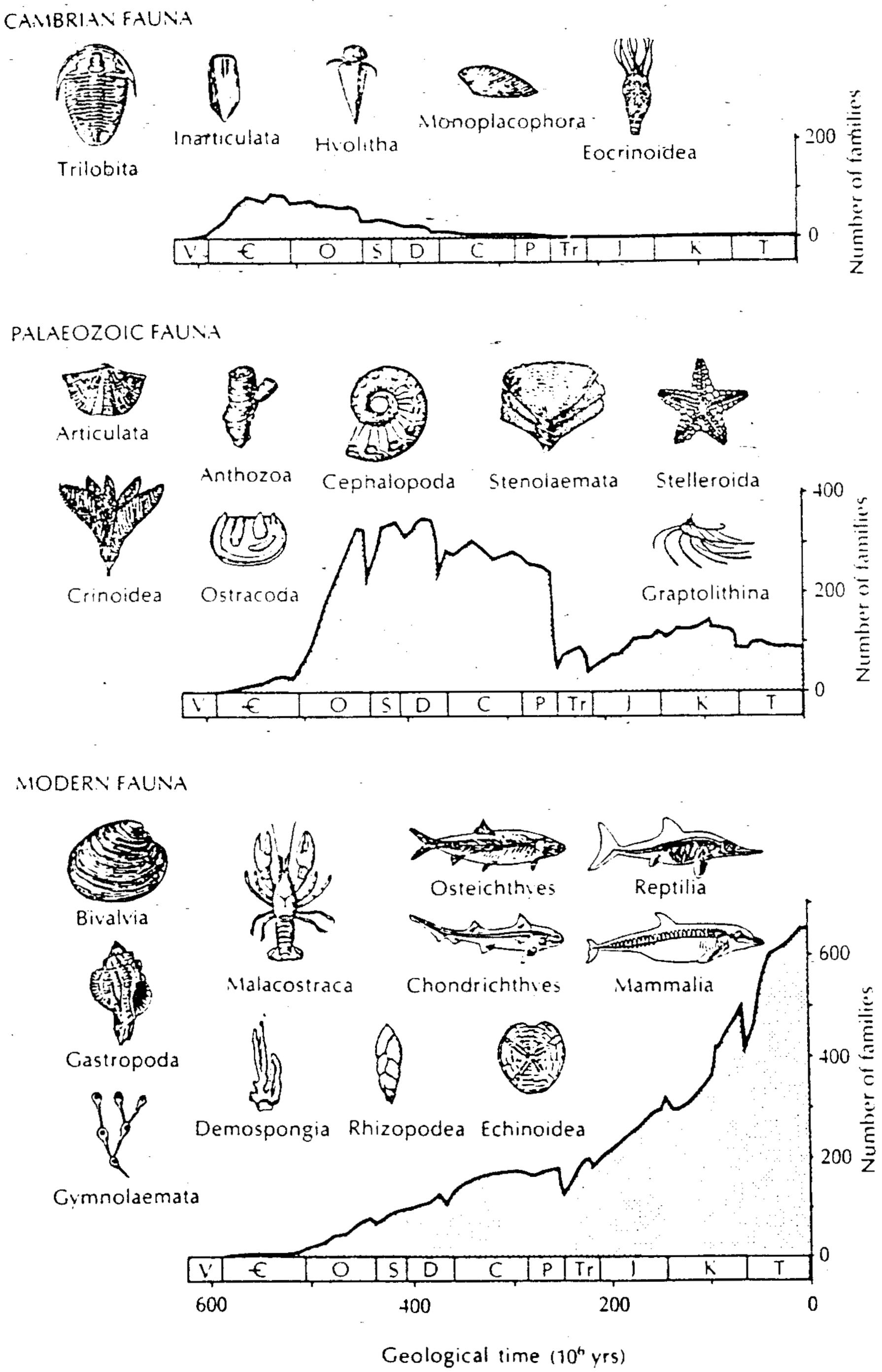

A
Number of families
900
600
300
Md
Pz
Cm
V
€
O
S
D
C
P
Tr
J
K
T
600
400
200
0
B
Number of species
600
400
200
0
1
2
3
4
D
C
P
Tr
J
K
T
400
200
0
C
Number of families
200
100
0
1
2
3
D
C
P
Tr
J
K
T
400
200
0
Geological time (10⁶ yrs)

Figure 2


CAMBRIAN FAUNA
Trilobita
Inarticulata
Hyolitha
Monoplacophora
Eocrinoidea
200
0
Number of families
V
€
O
S
D
C
P
Tr
J
K
T
PALAEOZOIC FAUNA
Articulata
Anthozoa
Cephalopoda
Stenolaemata
Stelleroida
Crinoidea
Ostracoda
Graptolithina
400
200
0
Number of families
V
€
O
S
D
C
P
Tr
J
K
T
MODERN FAUNA
Bivalvia
Malacostraca
Osteichthyes
Reptilia
Chondrichthyes
Mammalia
Gastropoda
Demospongia
Rhizopodea
Echinoidea
Gymnolaemata
600
400
200
0
Number of families
V
€
O
S
D
C
P
Tr
J
K
T
600
400
200
0
Geological time (10⁶ yrs)

In: Valentine, J.W. Edit., 1985 Phanerozoic diversity pat-terns. profiles in macroevolution: Princeton, N.J:& San Fco., Cal Princeton univ. Press, Chapt 1, p 11-39.

10.4 BIODIVERSIFICACION.

10.4 (A)

An Atlas of Phanerozoic Clade Diversity Diagrams.

J. John Sepkoski, Jr. and Michael L. Hulver.

Department of the Geophysical Sciences, University of Chicago.

Clade diversity diagrams are spindle-shaped graphs that summarize patterns of taxonomic evolution within higher taxa through geo logic time. Most clade diversity diagrams are contructed about a central axis that represents time (scaled either metrically or ordinally, by stratigraphic interval). Some measure or estimate of taxonomicx diversity (or rinchness) is then plotted symetri cally abouth the axis to give the diagram on everall spindle shape (e.g., Fig 1).

Diversity diagrams for individual clades convey information about their size, shape and variability in the fossil record (ef, Gould et al, 1977). Such morphologic information is valuable for as sessing how evolutionary rates (that is, rates of origination and extinction) vary within the taxa through geologic time. Clade diversity diagrams for groups of higher taxa hypothesized to be related by phyñlogeny or by function are useful for comparisons of the histories of the taxa. Common pattern of expansion or contrction may relate to general factors governing all taxa, whereas reciprocal patterns may be interpretable as negative interactions between pairs of ecologically similar taxa (e.g. Simpson, 1953; Banbach, this volumen) Sets of clade diversity diagrams also are useful for summarizing variation among largew numbers of clades for the purpose of testing general maroevolu tionnary models (e.g., Raup et al, 1973; Gould etr al., 1977).

This chapter presents a collection of clade diversity diagrams which we hope well be usefull for examining the general histories of a wide variety of animal taxa, The main body of the chapter is a series of 12 figures displaying spindle diagrams for orders, classes, and phyla of both marine and nonmarine (or continental) animals for the whole of the phanerozoic (including the Vendian). Nearly all of the diagram are plotted at a uniform taxonomic and temporal resolution, specifically that of familial diverisity per stratigraphic stage. The taxonomic rank of family is used simply because comprehensive data with good stratigraphic resolution can be obtained for all animal groups at this level. Although families do not display all of the detail of the fossil record they should be sufficiently sensitive to show major evolu tionary trends and patterns with characteristic timescales of fives to tens of million years (see also Sepkoski, 1979, 1982a; Raup and Sepkoski 1982),

The clade diversity diagrams inmost of the figures are formatted in strips that have time in the vertical dimension. Most of the strips are scaled from 625 myr at their bottoms to aproximately 1myr BP at their tops. (No data on Recent diversity are directly included in the diagrams). Geologic eras and systems are indicat ed at the lefthand ends of the strips, with eras denoted by Cz = cenozoic, Mz Mesozoic, Pz Paleozoic and pe = lates precambrian; syatems are denoted by standart symbiols, with V = vendian The widths of the clade diversity diagrams ineach strip indicate the numbers of families konown from direct fossil evidence or from interpolation between known occurrences to be present inthe clades ineach of 80 stratigraphic stages or comparable intervals (see Table 1 in Sepkonski, 1982b for a listing of the stages used) A scale for the familial diversities appears in the lower righthand part of most of the figures. All of the diagrams were produced with an IBM personal computer and Epson dot-matrix printer.

The first two figures in this chapter constain class-level sum maries of the entire Phanerozoic fossil record. Figure 1 displays clade diversity diagrams for the 87 classes and 15 unique, prob lematic genera that have representatives in the marine fossil record. This illustration is an updated version of figure 1 i Sepkoski (1981) with corrections based on new data in Sepkoski

(1982b). The second figure in this chapter summarizes the conti nental fossil record The diversity diagrams displays numbers of freshwater and terrestrial families whitin the 39 animal classes known from the nonmarine fossil record; data on the classes were compiled from the literature sources listed in table 1. Also shown at the bottom of figures 2 are clade diversity diagrams for numbers of species within the 13 taxonomic divisions of the tracheophytes and bryophytes; the data for these diagrams were taken from Niklas, Tiffney and Knoll (this volume), same relative scale as in fig 1 and 2 in order to facilitate comparision. Figures 3 and 4 display family-level clade diagrams for orders within the moderrately diverse marune phyla: the protozoa, porif era, coelenterata, bryozoa, brachiopoda, annelida and hemichorda ta. (the set of clade diversity diagrams for the Annelida in cludes several taxa of questionable affinities wich micht best be considered incertae sedis; these are in the group of diagramss begining with Cribricyathida and ending with Cournulitidae) The more diverse marine phyla are represented in Figura 5 to 8. Figures 5 displays orders of marine mollucs. Figure 6 orders marine arthropods; Figure 7 orders of echinoderms; and Figure 8 orders of marine vertebrates.

The two largew phyla of cpontinental animals, the nonmarine Arthropoda and chordata, are featured in fig 9 and 10. Nonmarine taxa have been segreged from their marine relatives because we believe that tha land and ses arte best treated as separate major arenas of evolution (see also Boucot, 1983) Despite the fact that some continetal clades contain secondary species which alternate between marine and nonmarine habitats and that all clades ultimately had their origins in the ocean, the great majoritarity of continetal animals evolved in situ, isolated from evolutionary activity in the seas. Thus, the segregations of marine and continental taxa enhances assessment of evolutionary patterns within axes for the continental clade diversity diagrams in figures 9 and 10 have been truncated below the silurian; this is because there is virtually no nonmarine fossil record prior to the mid Paleozoic (see Boucot and janis, 1983).

The final pair of figres in this chapter (fig 11 and 12) con tains 14 diversity diagrams for families within entire phyla, split between marine and continetal. These diagrams are formatted somewhat differently than in the preceding figures. The splindles have been cut in half and rotated so that the time axix runs horizontally. This arrangement permits easier assessment of the times and magnitudes of diversity change but impeds comparisons of changes between groups.

The use of a single level of taxonomic and stratigraphic resolu tion in all clade diversity diagams is intended to aid interpre tation and comparision of patterns among the various taxa. Howev er, the consatancy of resolution does not imply a uniformity of quality throughout the data. The accuracy of the taxonomic and stratigraphic information varies considerably among the taxonomic and stratigraphic information varies considerably among the taxonomix groups. In general, the quality in much better for marine taxa than for nonmarine taxa. Also, as should be expected, the fossil data are much better (and much more complete) for heavily skeletonized animals than for softbodied and lightly sclerotized animals. In fact, many of the diagrams for the latter groups reflected litte more than the geologic distribution of Largerstatten that preserve unusual fossil. This is particularly evidence in the long. thin clade diagrams for such exant groups as the Nemertinea and Priapulida (figure 1); these diagrams show only the extension of stratigraphic ranges from the recents to the one ormore Largerstatten thsat happen to contain the groups‘ early members.

Much of the characters of the diversity diagrms for same large clades, such as insect (figure 2 and 9), also represents the effects of Lagerstatten. For the insects, the more important Largestatten include the upper Carboniferous siderite concretion deposits of North American and Europe, the mid-permian lake deposits od Kansas and Kazakhstan, the Eocene Green River depos its of Wyoming, and especially the Oligocene Baltioc Amber of northern Europe. The Baltic Amber alone contributes most of the cenozoic bulge in the clade diversity diagrams for both insects and other lightly sclerozed terrestrial arthropods (figures 2, 9, and 12). The effects of Largestatten, or of their non.ocur rence, are even seen in some well-skeletonized groups with fairly extensive fossil records. The drop in the diversity of continen tañ vertebrates in the jurassic (fig 12), for example, probably reflects largely a paucity of fossoliferous continental deposits between the Raethian and Tithonian (see also Carroll, 1977; Padian and Clemens, 1985, this volumen).

These shortcomings of the fossil record, along with the problems associated with family-level data and 5 to 10 myr-long stages, do limint the value of the clade diversity diagrams presented here. However, we belive that a great deal still can be learned from them about the apparent order, or disorder, in their radiations and extinctions. Thus we hope that this atlas will aid in the assessment and interpretation of evolutionary history as well as serve as a baseline for the compilation of more accurate and detailed diversity data.

ACKNOWLEDGEMENTS.

We thank K.J.Niklas, B.H. Tiffney, and A.H.Knoll for permission to reproduce their data on contineta1 plant diversity infigure 2. We also thank J. Cracraft, P.Crane, and J.A. Hopson for help and advice during compilation of data on continantal animals. Produc tion of this paper received partial support from NSF Grant DEB81-08890 to J.J.S.

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Fig, 1. THE MARINE FOSSIL RECORD Families whitin classes of fossil marine mammals.

TABLE 1. principal literature sources of information on the taxonomy and stratigraphy of continental animal families..

Fig, 2. THE CONTINENTAL FOSSIL RECORD. Families within classes of continental (i.e. terrestrial and freshwater) fossil animal and species within divisions of continental plants.

Fig. 3. Families within orders of fossil Protozoa, Porifera and Coelenterata.

Fig. 4. Families within orders of fossil Bryozoa, Brachiopoda, Annelida, and Hemichordata.

Fig. 5. Families within orders fossil marine Mollusca.

Fig. 6. Families within orders of fossil marine Arthropoda.

Fig. 7. Families within orders of fossil Echinodermata.

Fig. 8. Families within orders of marine Vertebrata.

Fig. 9. Families within orders of fossil nonmarine Arthropoda.

Fig. 10. Families within orders od fossil nonmarine vertebrata.

FIg. 11. Familial diversity of selected marine animals phyla.

Fig. 12. Familial diversity of selected marine and continental animal phyla.

FIGURA 1

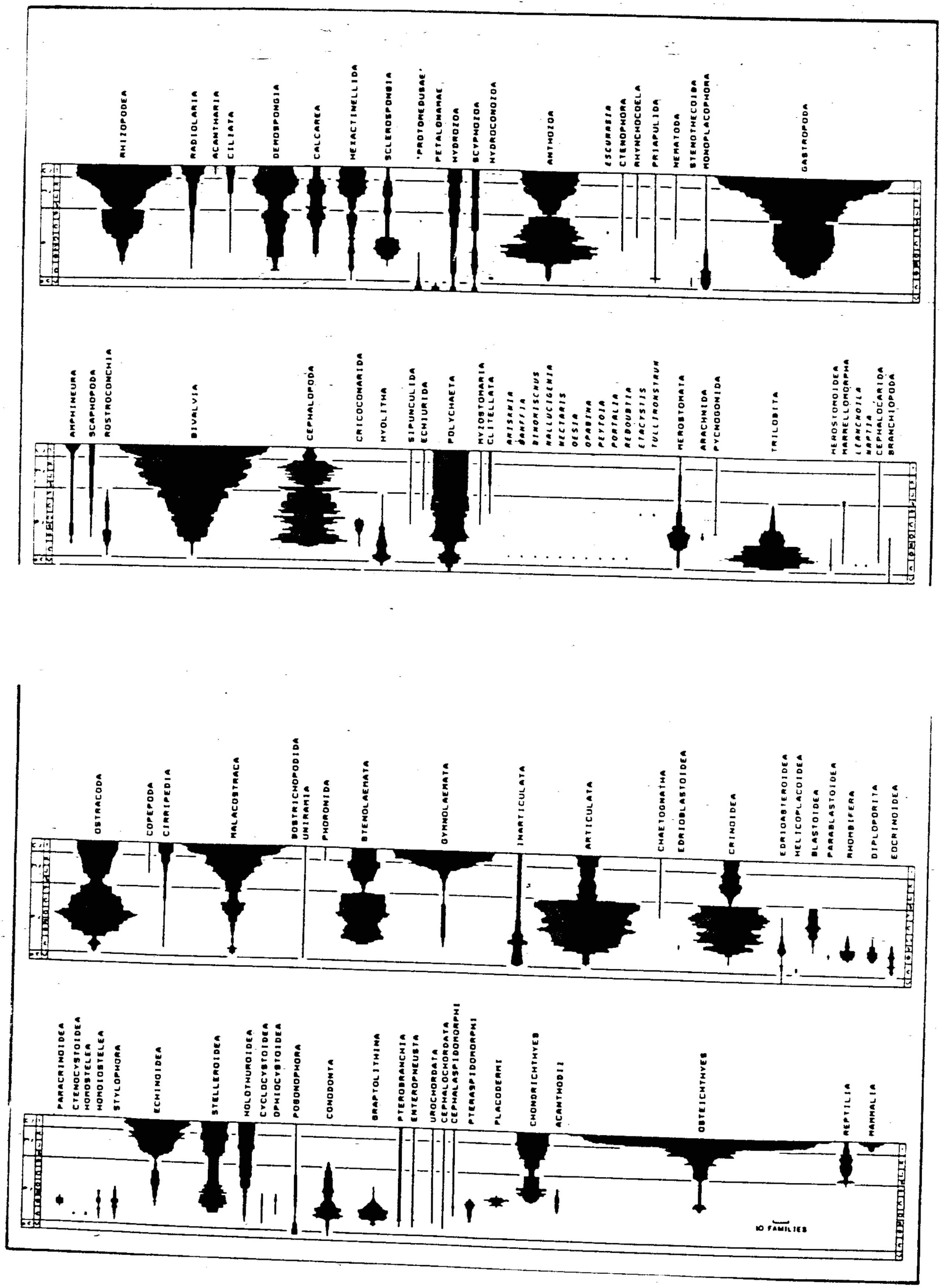

RHIZOPODEA
RADIOLARIA
ACANTHARIA
CILIATA
DEMOSPONGIA
CALCAREA
HEXACTINELLIDA
SCLEROSPONGIA
'PROTOMEDUSAE'
PETALONAMAE
HYDROZOA
SCYPHOZOA
HYDROCONOZOA
ANTHOZOA
ESCUMASIA
CTENOPHORA
RHYNCHOCOELA
PRIAPULIDA
NEMATODA
STENOTHECOIDA
MONOPLACOPHORA
GASTROPODA
AMPHINEURA
SCAPHOPODA
ROSTROCONCHIA
BIVALVIA
CEPHALOPODA
CRICOCONARIDA
HYOLITHA
SIPUNCULIDA
ECHIURIDA
POLYCHAETA
MYZOSTOMARIA
CLITELLATA
AMISKWIA
BANFFIA
DINOMISCHUS
HALLUCIGENIA
NECTARIS
OESIA
OPABINIA
PEYTOIA
PORTALIA
REDOUBTIA
ETACYSTIS
TULLIMONSTRUM
MEROSTOMATA
ARACHNIDA
PYCNOGONIDA
TRILOBITA
MEROSTOMOIDEA
MARRELLOMORPHA
LEANCHOILA
NARAOIA
CEPHALOCARIDA
BRANCHIOPODA
OSTRACODA
COPEPODA
CIRRIPEDIA
MALACOSTRACA
BOSTRICHOPODIDA
UNIRAMIA
PHORONIDA
STENOLAEMATA
GYMNOLAEMATA
INARTICULATA
ARTICULATA
CHAETOGNATHA
EDRIOBLASTOIDEA
CRINOIDEA
EDRIOASTEROIDEA
HELICOPLACOIDEA
BLASTOIDEA
PARABLASTOIDEA
RHOMBIFERA
DIPLOPORITA
EOCRINOIDEA
PARACRINOIDEA
CTENOCYSTOIDEA
HOMOSTELEA
HOMOIOSTELEA
STYLOPHORA
ECHINOIDEA
STELLEROIDEA
HOLOTHUROIDEA
CYCLOCYSTOIDEA
OPHIOCYSTOIDEA
POGONOPHORA
CONODONTA
GRAPTOLITHINA
PTEROBRANCHIA
ENTEROPNEUSTA
UROCHORDATA
CEPHALOCHORDATA
CEPHALASPIDOMORPHI
PTERASPIDOMORPHI
PLACODERMI
CHONDRICHTHYES
ACANTHODII
OSTEICHTHYES
REPTILIA
MAMMALIA
10 FAMILIES

FIGURA 2

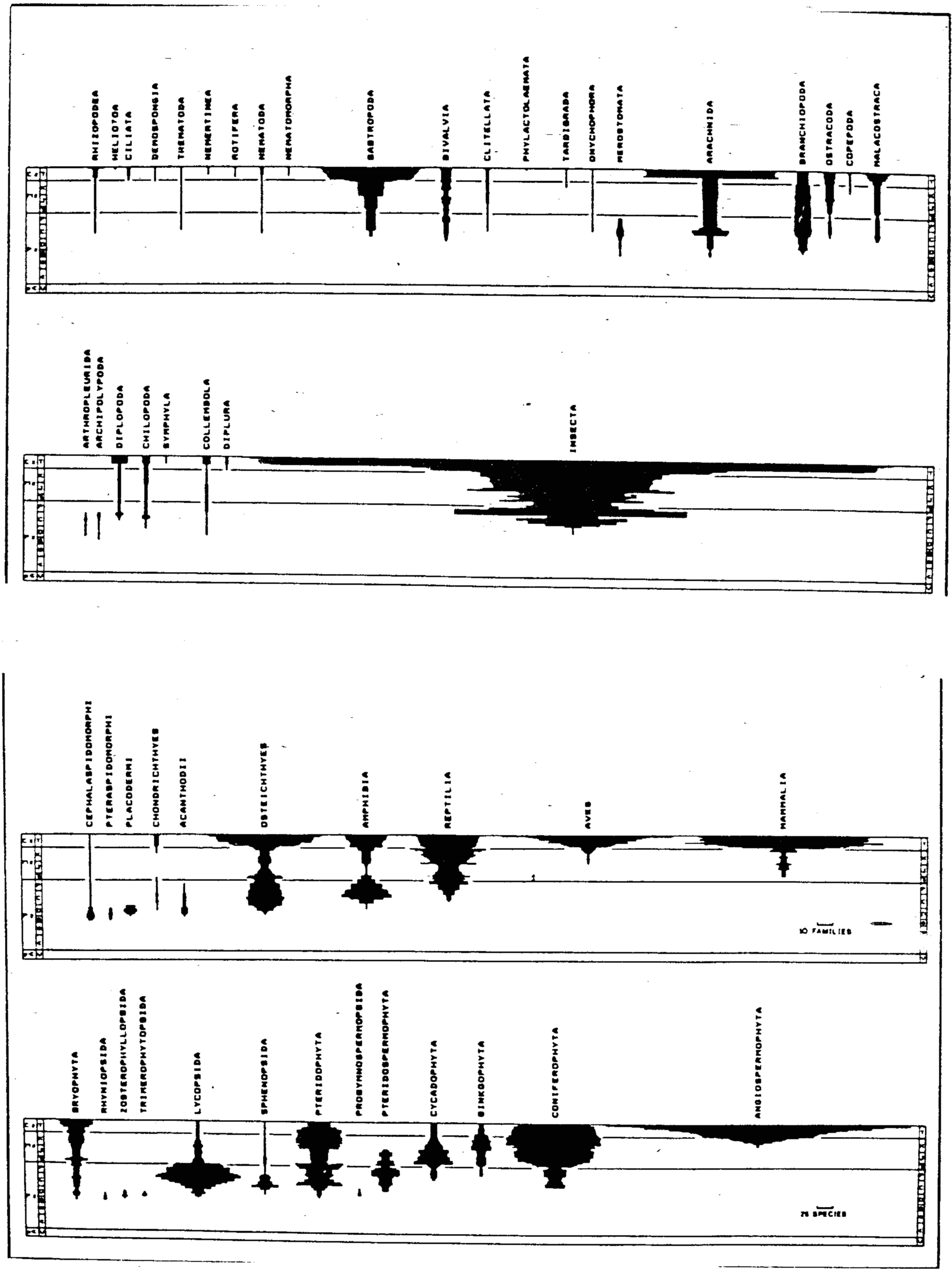

RHIZOPODEA
HELIOZOA
CILIATA
DEMOSPONGIA
TREMATODA
NEMERTINEA
ROTIFERA
NEMATODA
NEMATOMORPHA
GASTROPODA
BIVALVIA
CLITELLATA
PHYLACTOLAEMATA
TARDIGRADA
ONYCHOPHORA
MEROSTOMATA
ARACHNIDA
BRANCHIOPODA
OSTRACODA
COPEPODA
MALACOSTRACA
ARTHROPLEURIDA
ARCHIPOLYPODA
DIPLOPODA
CHILOPODA
SYMPHYLA
COLLEMBOLA
DIPLURA
INSECTA
CEPHALASPIDOMORPHI
PTERASPIDOMORPHI
PLACODERMI
CHONDRICHTHYES
ACANTHODII
OSTEICHTHYES
AMPHIBIA
REPTILIA
AVES
MAMMALIA
10 FAMILIES
BRYOPHYTA
RHYNIOPSIDA
ZOSTEROPHYLLOPSIDA
TRIMEROPHYTOPSIDA
LYCOPSIDA
SPHENOPSIDA
PTERIDOPHYTA
PROGYMNOSPERMOPSIDA
PTERIDOSPERMOPHYTA
CYCADOPHYTA
GINKGOPHYTA
CONIFEROPHYTA
ANGIOSPERMOPHYTA
25 SPECIES

FIGURA 3

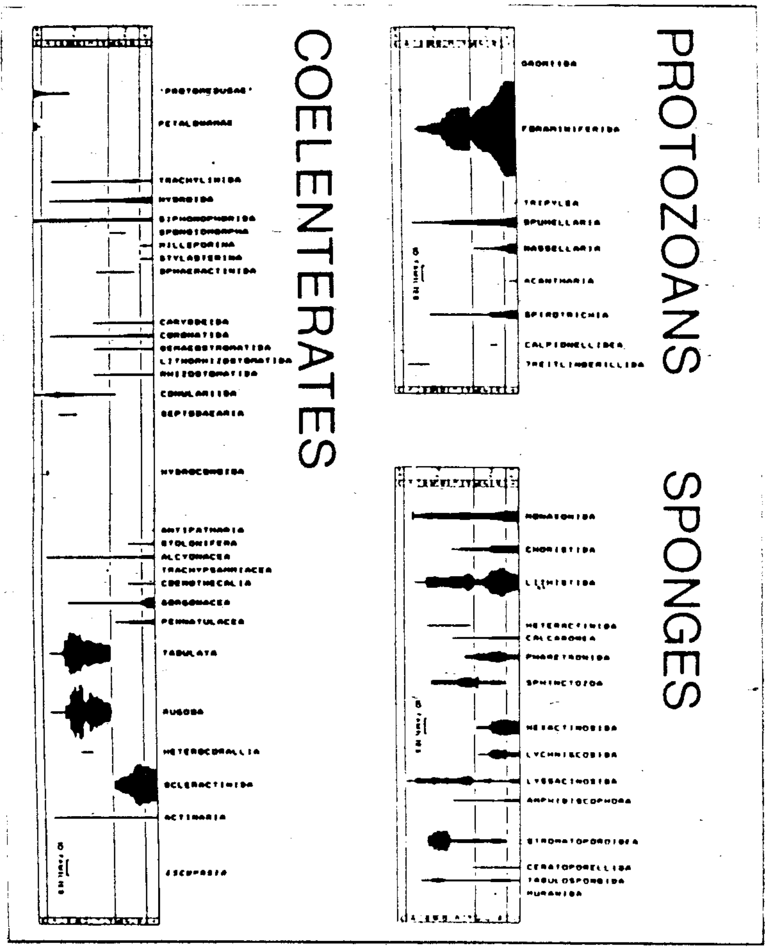


FIGURA 4

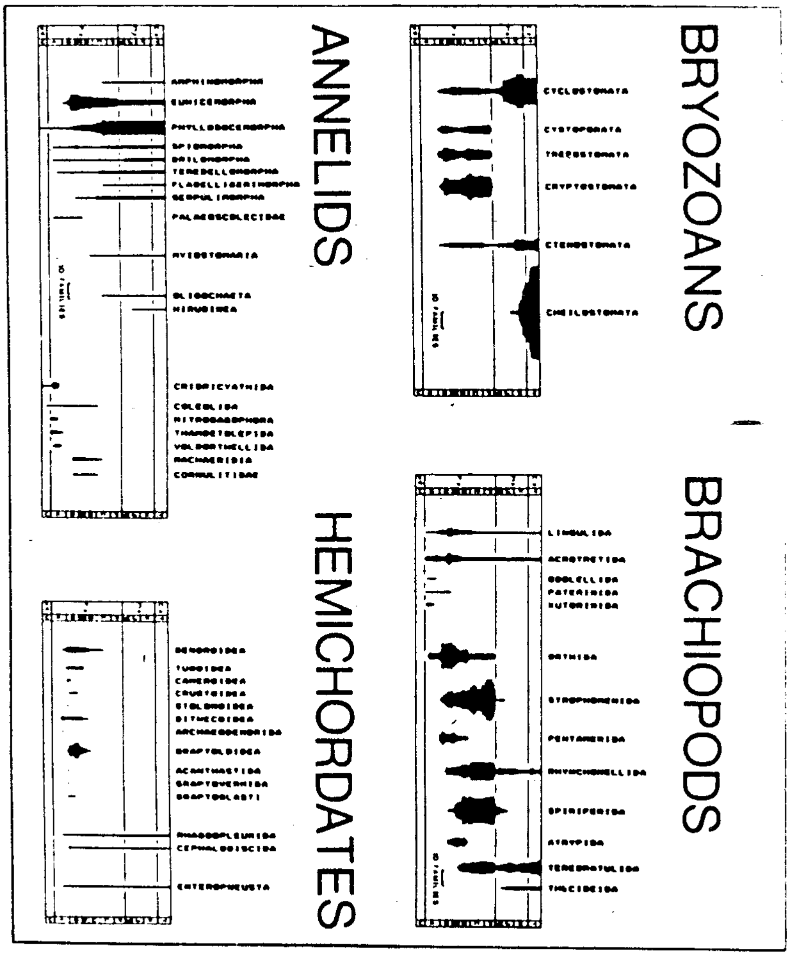


FIGURE 5

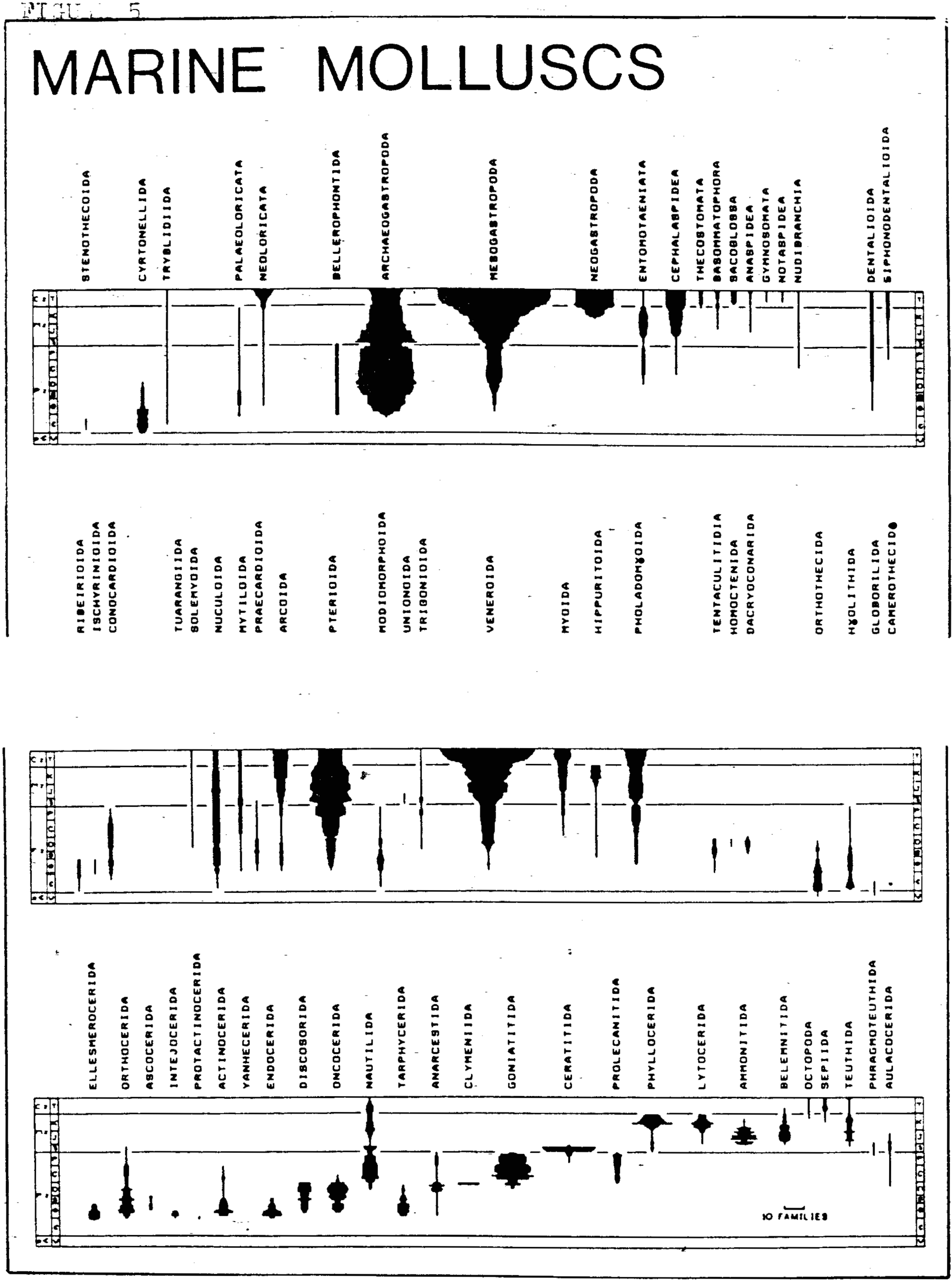

MARINE MOLLUSCS
STENOTHECOIDA
CYRTONELLIDA
TRYBLIDIIDA
PALAEOLORICATA
NEOLORICATA
BELLEROPHONTIDA
ARCHAEOGASTROPODA
MESOGASTROPODA
NEOGASTROPODA
ENTOMOTAENIATA
CEPHALASPIDEA
THECOSOMATA
BASOMMATOPHORA
SACOGLOSSA
ANASPIDEA
GYMNOSOMATA
NOTASPIDEA
NUDIBRANCHIA
DENTALIIDA
SIPHONODENTALIIDA
RIBEIRIOIDA
ISCHYRINIOIDA
CONOCARDIOIDA
TUARANGIIDA
SOLEMYOIDA
NUCULOIDA
MYTILOIDA
PRAECARDIOIDA
ARCOIDA
PTERIOIDA
MODIOMORPHOIDA
UNIONOIDA
TRIGONIOIDA
VENEROIDA
MYOIDA
HIPPURITOIDA
PHOLADOMYOIDA
TENTACULITIDA
HOMOCTENIDA
DACRYOCONARIDA
ORTHOTHECIDA
HYOLITHIDA
GLOBORILIDA
CAMEROTHECIDA
ELLESMEROCERIDA
ORTHOCERIDA
ASCOCERIDA
INTEJOCERIDA
PROTACTINOCERIDA
ACTINOCERIDA
YANHECERIDA
ENDOCERIDA
DISCOSORIDA
ONCOCERIDA
NAUTILIDA
TARPHYCERIDA
ANARCESTIDA
CLYMENIIDA
GONIATITIDA
CERATITIDA
PROLECANITIDA
PHYLLOCERIDA
LYTOCERIDA
AMMONITIDA
BELEMNITIDA
OCTOPODA
SEPIIDA
TEUTHIDA
PHRAGMOTEUTHIDA
AULACOCERIDA
10 FAMILIES

FIGURE 6

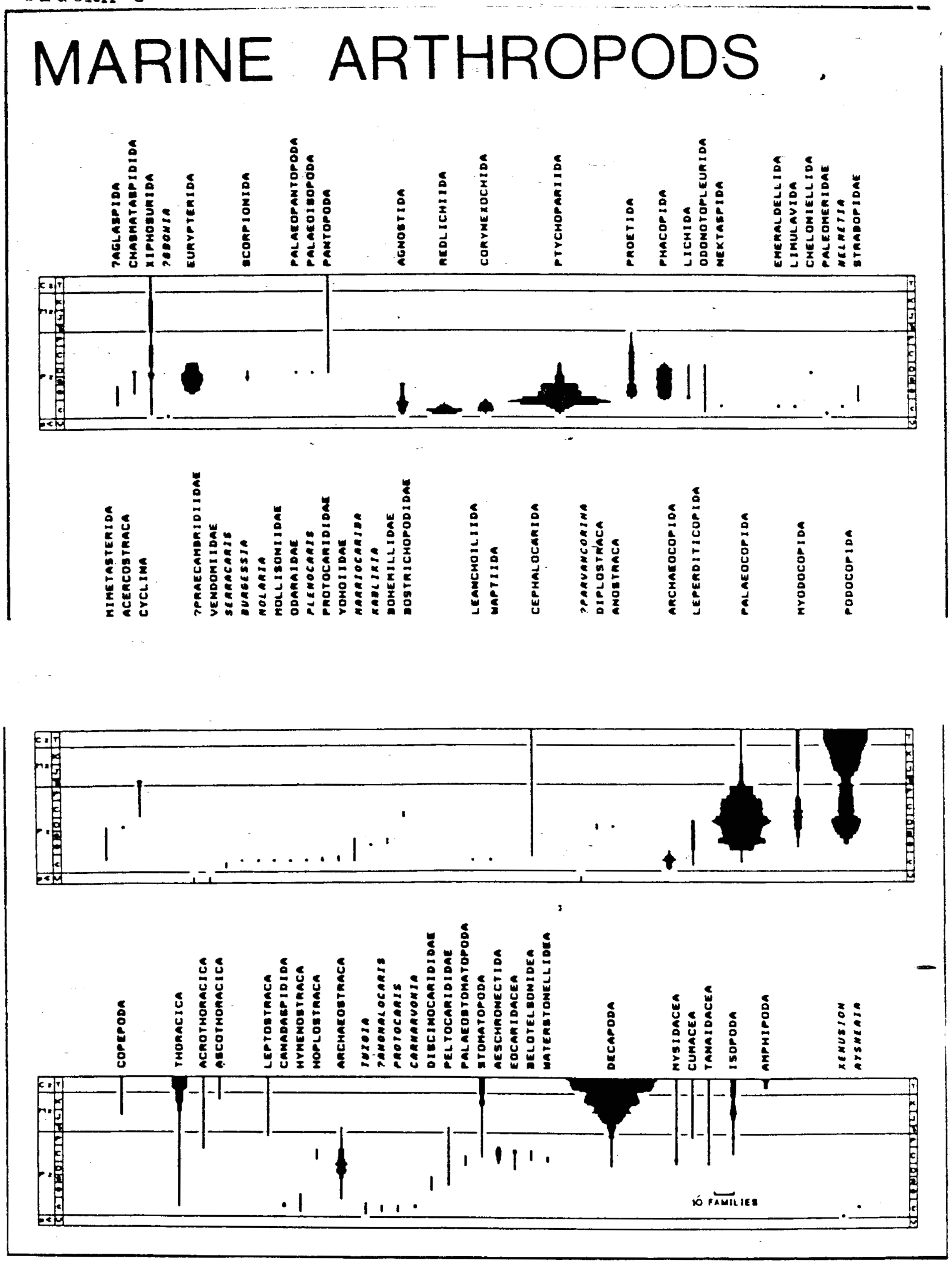
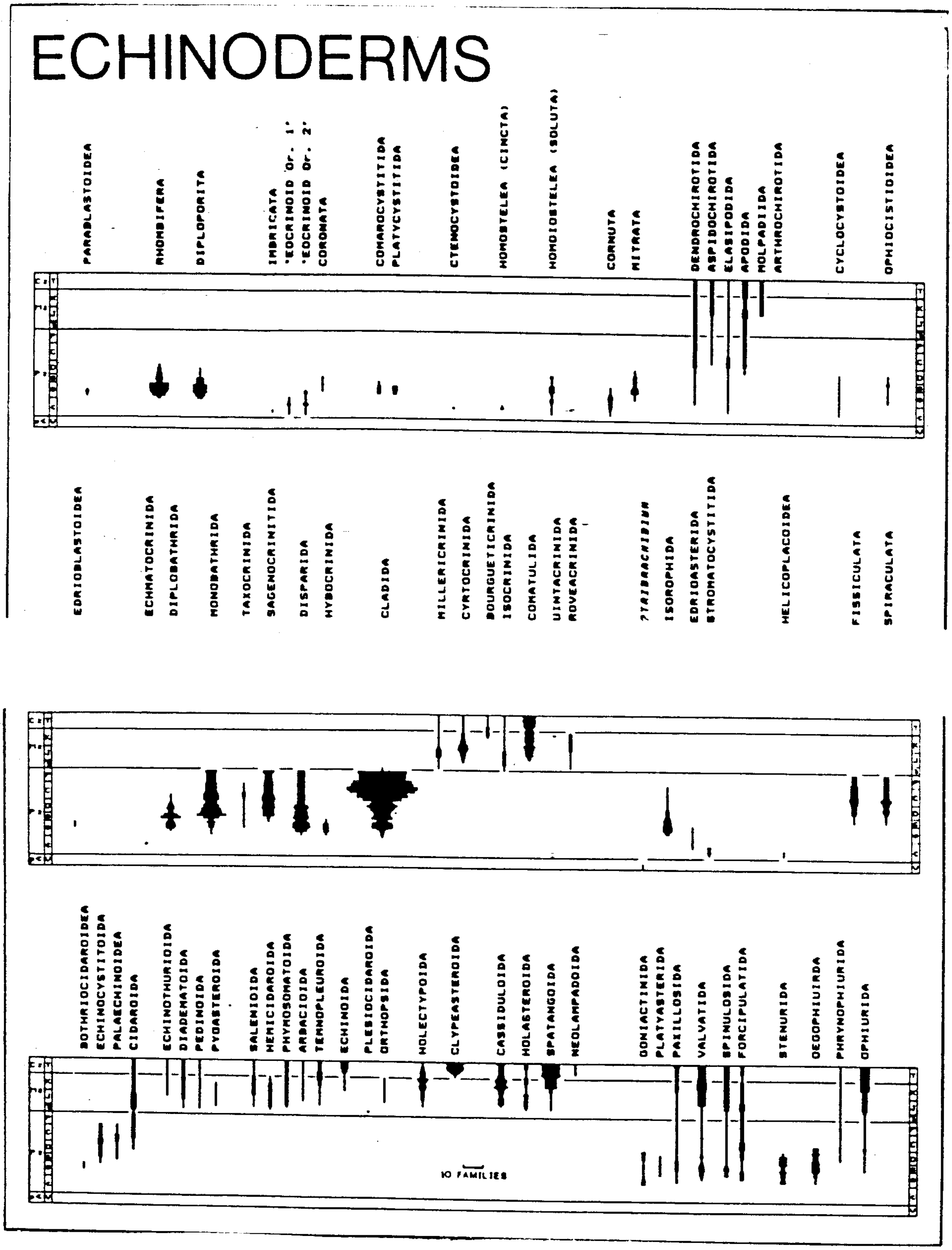
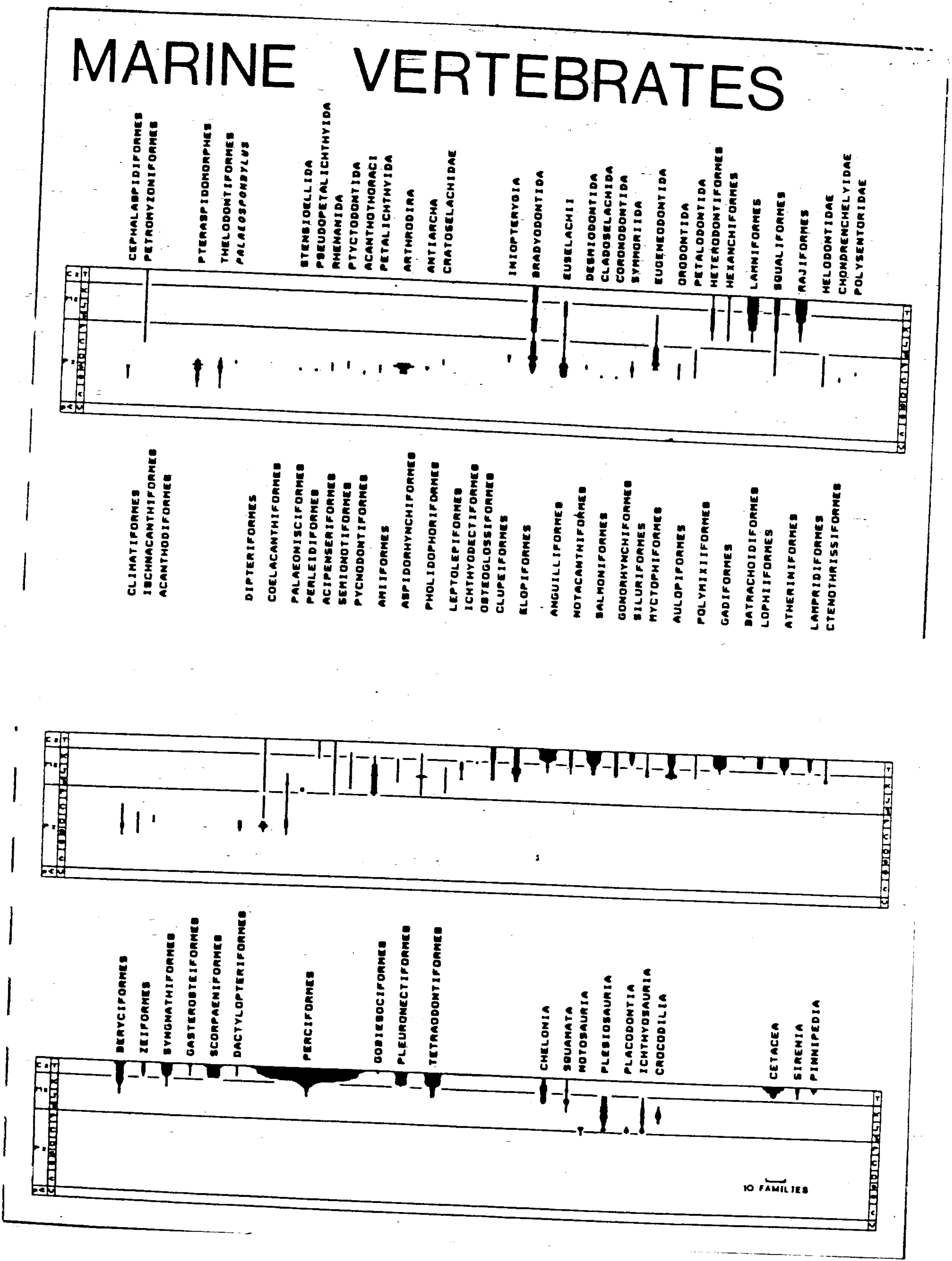

MARINE ARTHROPODS
?AGLASPIDA
CHASMATASPIDIDA
XIPHOSURIDA
?SBONIA
EURYPTERIDA
SCORPIONIDA
PALAEOPANTOPODA
PALAEOISOPODA
PANTOPODA
AGNOSTIDA
REDLICHIIDA
CORYNEXOCHIDA
PTYCHOPARIIDA
PROETIDA
PHACOPIDA
LICHIDA
ODONTOPLEURIDA
NEKTASPIDA
EMERALDELLIDA
LIMULAVIDA
CHELONIELLIDA
PALEOMERIDAE
HELMETIA
STRABOPIDAE
MIMETASTERIDA
ACERCOSTRACA
CYCLINA
?PRAECAMBRIDIIDAE
VENDOMIIDAE
SERRACARIS
BURGESSIA
MOLARIA
MOLLISONIIDAE
ODARAIDAE
PLENOCARIS
PROTOCARIDIDAE
YOHOIIDAE
MARRIOCARIDA
KABLIKIA
BOHEMILLIDAE
BOSTRICHOPODIDAE
LEANCHOILIIDA
NAPTIIDA
CEPHALOCARIDA
?PARVANCORINA
DIPLOSTRACA
ANOSTRACA
ARCHAEOCOPIDA
LEPERDITICOPIDA
PALAEOCOPIDA
MYODOCOPIDA
PODOCOPIDA
COPEPODA
THORACICA
ACROTHORACICA
ASCOTHORACICA
LEPTOSTRACA
CANADASPIDIDA
HYMENOSTRACA
HOPLOSTRACA
ARCHAEOSTRACA
TUZOIA
?ANOMALOCARIS
PROTOCARIS
CARNARVONIA
DISCINOCARIDIDAE
PELTOCARIDIDAE
PALAEOSTOMATOPODA
STOMATOPODA
AESCHRONECTIDA
EOCARIDACEA
BELOTELSONIDEA
WATERSTONELLIDEA
DECAPODA
MYSIDACEA
CUMACEA
TANAIDACEA
ISOPODA
AMPHIPODA
XENUSION
AYSHEAIA
10 FAMILIES

FIGURA 7


ECHINODERMS
PARABLASTOIDEA
RHOMBIFERA
DIPLOPORITA
IMBRICATA
'EOCRINOID Or. 1'
'EOCRINOID Or. 2'
CORONATA
COMAROCYSTITIDA
PLATYCYSTITIDA
CTENOCYSTOIDEA
HOMOSTELEA (CINCTA)
HOMOIOSTELEA (SOLUTA)
CORNUTA
MITRATA
DENDROCHIROTIDA
ASPIDOCHIROTIDA
ELASIPODIDA
APODIDA
MOLPADIIDA
ARTHROCHIROTIDA
CYCLOCYSTOIDEA
OPHIOCISTIOIDEA
EDRIOBLASTOIDEA
ECHMATOCRINIDA
DIPLOBATHRIDA
MONOBATHRIDA
TAXOCRINIDA
SAGENOCRINITIDA
DISPARIDA
HYBOCRINIDA
CLADIDA
MILLERICRINIDA
CYRTOCRINIDA
BOURGUETICRINIDA
ISOCRINIDA
COMATULIDA
UINTACRINIDA
ROVEACRINIDA
?TRIBRACHIDIUM
ISOROPHIDA
EDRIOASTERIDA
STROMATOCYSTITIDA
HELICOPLACOIDEA
FISSICULATA
SPIRACULATA
BOTHRIOCIDAROIDEA
ECHINOCYSTITOIDA
PALAECHINOIDEA
CIDAROIDA
ECHINOTHURIOIDA
DIADEMATOIDA
PEDINOIDA
PYGASTEROIDA
SALENIOIDA
HEMICIDAROIDA
PHYMOSOMATOIDA
ARBACIOIDA
TEMNOPLEUROIDA
ECHINOIDA
PLESIOCIDAROIDA
ORTHOPSIDA
HOLECTYPOIDA
CLYPEASTEROIDA
CASSIDULOIDA
HOLASTEROIDA
SPATANGOIDA
NEOLAMPADOIDA
GONIACTINIDA
PLATYASTERIDA
PAXILLOSIDA
VALVATIDA
SPINULOSIDA
FORCIPULATIDA
STENURIDA
OEGOPHIUIRDA
PHRYNOPHIURIDA
OPHIURIDA
10 FAMILIES

330

FIGURA 5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PETROMYZONIFORMES
PTERASPIDOMORPHES
THELODONTIFORMES
PALAEOSPONDYLUS
STENSIOELLIDA
PSEUDOPETALICHTHYIDA
RHENANIDA
PTYCTODONTIDA
ACANTHOTHORACI
PETALICHTHYIDA
ARTHRODIRA
ANTIARCHA
CRATOSELACHIDAE
INIOPTERYGIA
BRADYODONTIDA
EUSELACHII
DESMIODONTIDA
CLADOSELACHIDA
CORONODONTIDA
SYMMORIIDA
EUGENEODONTIDA
ORODONTIDA
PETALODONTIDA
HETERODONTIFORMES
HEXANCHIFORMES
LAMNIFORMES
SQUALIFORMES
RAJIFORMES
HELODONTIDAE
CHONDRENCHELYIDAE
POLYSENTORIDAE
CLIMATIFORMES
ISCHNACANTHIFORMES
ACANTHODIFORMES
DIPTERIFORMES
COELACANTHIFORMES
PALAEONISCIFORMES
PERLEIDIFORMES
ACIPENSERIFORMES
SEMIONOTIFORMES
PYCNODONTIFORMES
AMIIFORMES
ASPIDORHYNCHIFORMES
PHOLIDOPHORIFORMES
LEPTOLEPIFORMES
ICHTHYODECTIFORMES
OSTEOGLOSSIFORMES
CLUPEIFORMES
ELOPIFORMES
ANGUILLIFORMES
NOTACANTHIFORMES
SALMONIFORMES
GONORHYNCHIFORMES
SILURIFORMES
MYCTOPHIFORMES
AULOPIFORMES
POLYMIXIIFORMES
GADIFORMES
BATRACHOIDIFORMES
LOPHIIFORMES
ATHERINIFORMES
LAMPRIDIFORMES
CTENOTHRISSIFORMES
BERYCIFORMES
ZEIFORMES
SYNGNATHIFORMES
GASTEROSTEIFORMES
SCORPAENIFORMES
DACTYLOPTERIFORMES
PERCIFORMES
GOBIESOCIFORMES
PLEURONECTIFORMES
TETRAODONTIFORMES
CHELONIA
SQUAMATA
NOTOSAURIA
PLESIOSAURIA
PLACODONTIA
ICHTHYOSAURIA
CROCODILIA
CETACEA
SIRENIA
PINNIPEDIA
10 FAMILIES

FIGURA 9

Sepkoski and Hulver

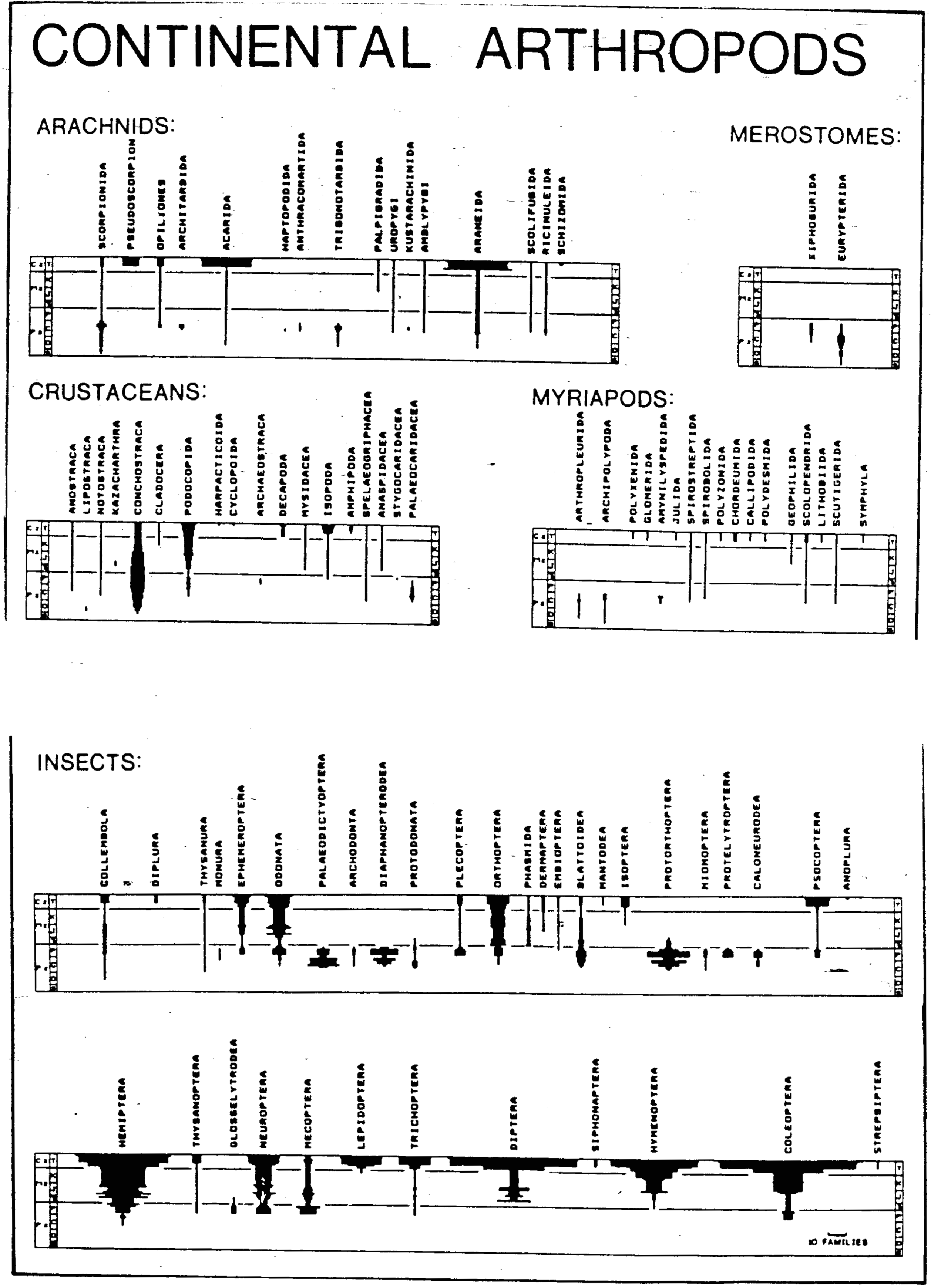

FIGURE 10

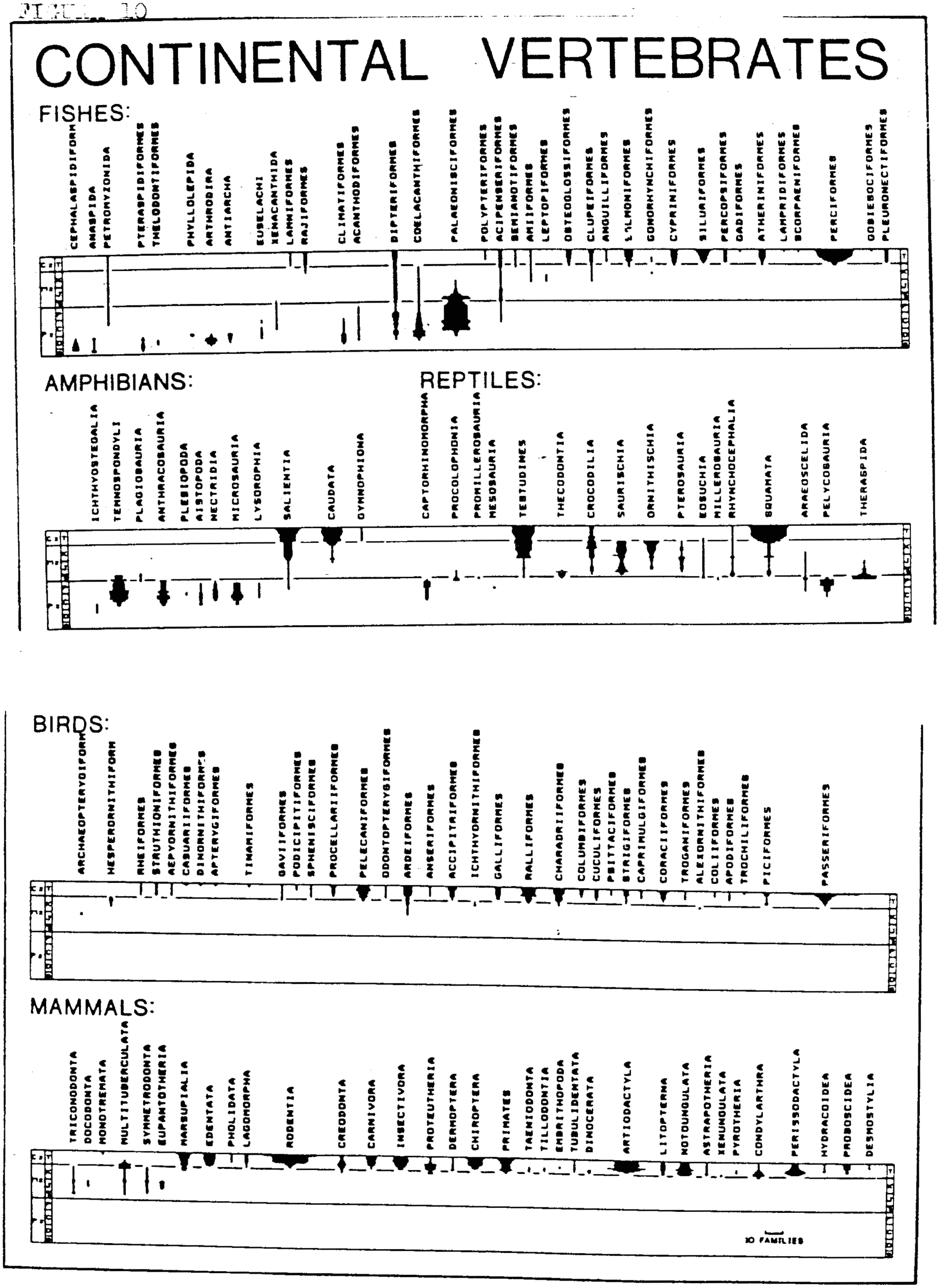
CONTINENTAL VERTEBRATES
FISHES:
CEPHALASPIDIFORM
ANASPIDA
PETROMYZONIDA
PTERASPIDIFORMES
THELODONTIFORMES
PHYLLOLEPIDA
ARTHRODIRA
ANTIARCHA
EUSELACHI
XENACANTHIDA
LAMNIFORMES
RAJIFORMES
CLIMATIIFORMES
ACANTHODIFORMES
DIPTERIFORMES
COELACANTHIFORMES
PALAEONISCIFORMES
POLYPTERIFORMES
ACIPENSERIFORMES
SEMIONOTIFORMES
AMIIFORMES
LEPTOPIFORMES
OSTEOGLOSSIFORMES
CLUPEIFORMES
ANGUILLIFORMES
SALMONIFORMES
GONORHYNCHIFORMES
CYPRINIFORMES
SILURIFORMES
PERCOPSIFORMES
GADIFORMES
ATHERINIFORMES
LAMPRIDIFORMES
SCORPAENIFORMES
PERCIFORMES
GOBIESOCIFORMES
PLEURONECTIFORMES
AMPHIBIANS:
ICHTHYOSTEGALIA
TEMNOSPONDYLI
PLAGIOSAURIA
ANTHRACOSAURIA
PLESIOPODA
AISTOPODA
NECTRIDIA
MICROSAURIA
LYSOROPHIA
SALIENTIA
CAUDATA
GYMNOPHIONA
REPTILES:
CAPTORHINOMORPHA
PROCOLOPHONIA
PROMILLEROSAURIA
MESOSAURIA
TESTUDINES
THECODONTIA
CROCODILIA
SAURISCHIA
ORNITHISCHIA
PTEROSAURIA
EOSUCHIA
MILLEROSAURIA
RHYNCHOCEPHALIA
SQUAMATA
ARAEOSCELIDA
PELYCOSAURIA
THERAPSIDA
BIRDS:
ARCHAEOPTERYGIFORM
HESPERORNITHIFORM
RHEIFORMES
STRUTHIONIFORMES
AEPYORNITHIFORMES
CASUARIIFORMES
DINORNITHIFORMES
APTERYGIFORMES
TINAMIFORMES
GAVIIFORMES
PODICIPITIFORMES
SPHENISCIFORMES
PROCELLARIIFORMES
PELECANIFORMES
ODONTOPTERYGIFORMES
ARDEIFORMES
ANSERIFORMES
ACCIPITRIFORMES
ICHTHYORNITHIFORMES
GALLIFORMES
RALLIFORMES
CHARADRIIFORMES
COLUMBIFORMES
CUCULIFORMES
PSITTACIFORMES
STRIGIFORMES
CAPRIMULGIFORMES
CORACIIFORMES
TROGONIFORMES
ALEXORNITHIFORMES
COLIIFORMES
APODIFORMES
TROCHILIFORMES
PICIFORMES
PASSERIFORMES
MAMMALS:
TRICONODONTA
DOCODONTA
MONOTREMATA
MULTITUBERCULATA
SYMMETRODONTA
EUPANTOTHERIA
MARSUPIALIA
EDENTATA
PHOLIDATA
LAGOMORPHA
RODENTIA
CREODONTA
CARNIVORA
INSECTIVORA
PROTEUTHERIA
DERMOPTERA
CHIROPTERA
PRIMATES
TAENIODONTA
TILLODONTIA
EMBRITHOPODA
TUBULIDENTATA
DINOCERATA
ARTIODACTYLA
LITOPTERNA
NOTOUNGULATA
ASTRAPOTHERIA
XENUNGULATA
PYROTHERIA
CONDYLARTHRA
PERISSODACTYLA
HYRACOIDEA
PROBOSCIDEA
DESMOSTYLIA
10 FAMILIES

FIGURE 11

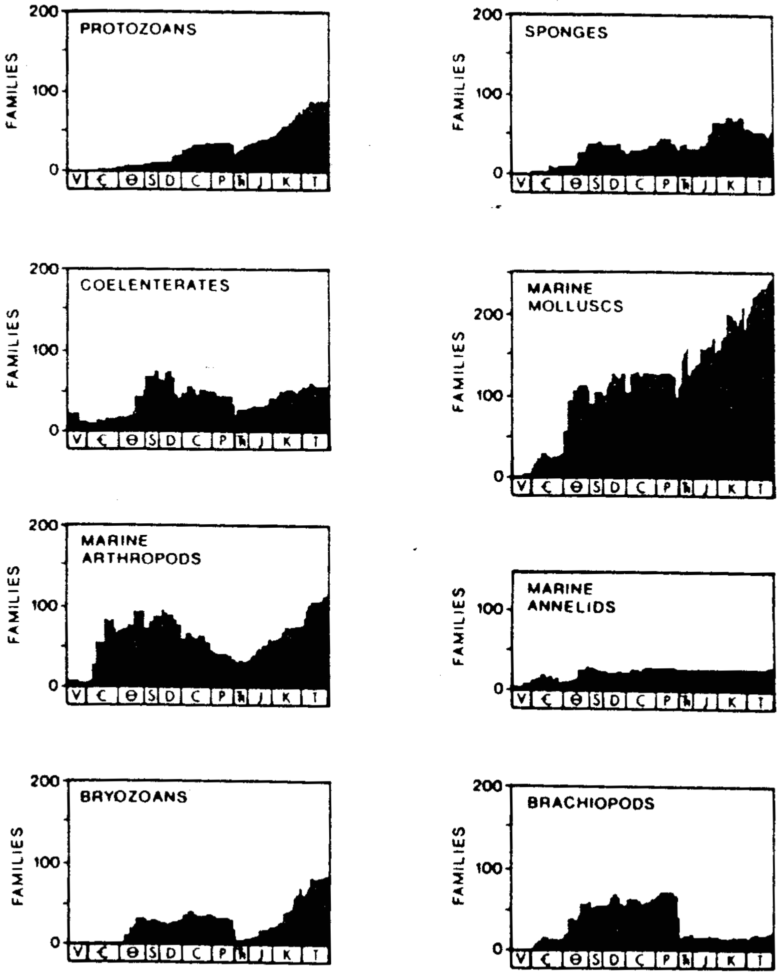
PROTOZOANS
SPONGES
COELENTERATES
MARINE MOLLUSCS
MARINE ARTHROPODS
MARINE ANNELIDS
BRYOZOANS
BRACHIOPODS
FAMILIES
200
100
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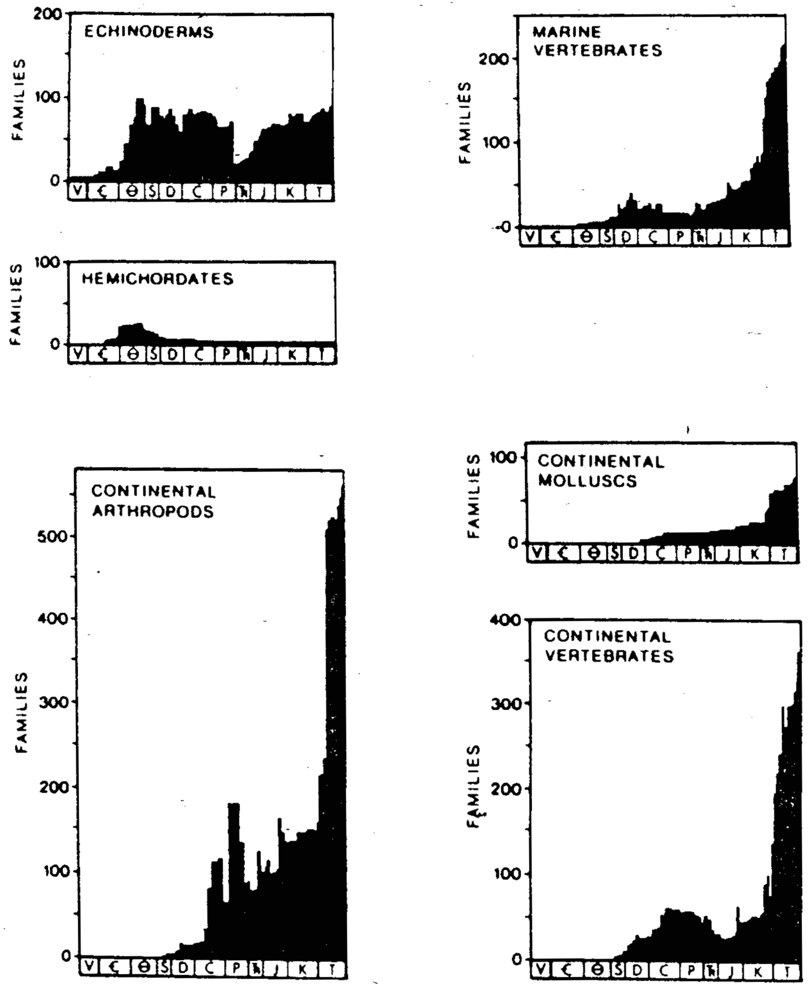
FIGURE 12


ECHINODERMS
HEMICHORDATES
MARINE VERTEBRATES
CONTINENTAL ARTHROPODS
CONTINENTAL MOLLUSCS
CONTINENTAL VERTEBRATES
FAMILIES
0
100
200
300
400
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10.5 EXTINCION.

10.5(a)

CHANGING PALEONTOLOGICAL VIEWS ON MASS EXTINCTION PHENOMENA.

Antoni Hoffman

In: DONOVA, S.K., EDIT., 1989. MASS EXTICTIONS: PROCESSES AND EVIDENCE: nEW YORK, COLUMBIA UNIV. PRESS, CHAPT. 1, P 1-18.

A HISTORICAL SKETCH.

Even a quick perusal of the Nature and science magazine over the last decade or two early indicates that problem of mass extic tions- that is to say, the search for an adequate causal explana tion of the disappearence of a large number of fossil groups within reartively short periods periods of geological time at such stratigraphic intervals as the Permian-Triassic, Cretaceous-Tertiary, Ordovician-Silurian, and Frasnian-Famennian transition-has only recently become an important topic in the earth and life sciences. The history of research in this area is nenertheless quite long and rather complex.

The ancient Greek concepts of plenitude, or fullness of the natural world, implies that no organisms that ever existed on the Earth could ultimately disappear fom ists surface, because their final extinction would leave an unbridgeable gap in the Great Chain of Being. Species extinction, therefore, was for long considered impossible. Eighteeth-century naturalist kenw, of course, that a wide variety of fossil had no counterparts among living organisms, but this apparent anomaly was commoly explained by an as yet inadequate knowledge of life on the Earth. It ap peared perfectly reasonable to asume at the time that ammonites or trilobites could still be discovered alive somewhere in tha world ocean, as Neopilina molluscs and Latimeria fishes indeed have been in the twentieth century. It is only after Cuvier (1799) had fisrt described fossil proboscideans that species extiction was eastablished as fact, for it was hard to believe that such large and prominent mammals could roam the Earth with out being ever observed by travellers. Yet tha concept of plkeni tude could still be reconciled with the fact of species extinc tion by assuming-as in fact Lamarck (1809) did man is the sole agent responsible for species extinction. According to Lamarck, species are essentially inmortal because they are alway able to adapt perfectly to any environmental configuration and man alone is capable of violationg the order of the natural world. Under this assumption is was fully understable that the species that underwent extinction were such large animals as the woolly mam moth, which could be easly considered as a valuable prey for human hunters.

With rapidly grwing knowledge of the inventory of living animal species, however, and also with rapidly increasing awareness that fossils such as ammonites or trilobites, without known living counterparts, were by no means oddities but rather very common phenomena, it become undeniable in the early nineteenth century that species extinction did indeed often take place inthe geolog ical past. Within a few decades three main causal explanations for this phenomenon were put forth. Brocchi (1814) proposed that each species was created with a specified, predetermined life- span, in close analogy to individual longevity, He believed that the extiction of species simply marks the end of their life time and is therefore essentially independent of extrinsic, environ mental factors-just as death will inevitably and the life of each person, regardless of fatal accidents or disease. Lyell (1832), in turn, regarded species extinction as a fully natural process caused primarily by the unescapable effects of continuosly chang ing environmental conditions. In his view, each species must sooner or latter encounter such a hostile configuaration of environmental factors that it will become extict, simply because its individuals will be unable to cope succefully with this new environment context.

Both these concepts implied that species extiction should gener ally occur independent of one another, whithout a clear-eut, orderly pattern in time. Cuvier (1825) observed, however, that fossil species in the Paris Basin disappear from the record in large clusters at certain horizons-all or at least a great many of them, at once, as if wiped out by a single catastrophic agent at each horizon. He therefore interpreted species extinctions as due to local catastrophes which destroyed life entirely in an area, thus vacanting the ecological space neccessary for the are's repopulation by immigrants that survived the cataclysm elsewhere.

Cuvier's perspective on species extinction was developed into a more extreme position by Buckland (1923), who regarded the faunal breaks such as those described by Cuvier as a clear sign of world-wide catastropes, and particularly by D'Orbigny (1852), who established a whole times series of such global holocaust as providing the main reference points for stratigraphy and the history of life. This emphasis on environmental catastrophes as the main causes of species extinction could, of course, be con tested or even rejected outright, but even the most devoted followers of the Lyellian gradualism had to agree that some major events did indeed occur in life's physical envirnment on the Earth and must have had some impact one the fate of organic species. Darwin (1846), for example, noted that many large terrestrial mammals had lived until recently in South America and he attibuted their extinction to the effects of rapid climatic changes during the ice age.

In the Origin of species Darwin (1859) wrote very little of species extinction which he regarded, very much in the same vein as Lyell, as due to various environmental factors which drive species first to rarity and then to extinction. He was inclined to emphasize the role of biotic factors, foremost among them interspecific competition, much more strongly than Lyell disd, but he was also explicit in his scepticism about our insight into the nature of extinction of any particular species. In spite of his gradualistic prejudice. Darwin was ready to admit that some extinctions of large taxonomic groups-for instance, the trilo bites at the end of the Paleozoic and the ammonites at the close of the Mesozoic-were wondefully sudden'Countray to the Cuvierani an tradition, however, which viewed these phenomena as an incon testable indication of mass extinction events when many organic groups had been exterminated simultaneously, Darwin suggested that their apparent rapidity migh really be only artefactual, due to wold-wide gaps in the fossil record which clumped together events that had actually been quite widely stretched over geolog ical time.

This view was generally shared by the most othodox Darwineans among paleontologist-for example, Neumayr (1889), Andrusov (1891) and Davitashvili (1969)-who conceived of species extinction as caused primarily by interespecific competition, various physical factors, and regional environmental catastrophes, whereas thay regarded the so-called mass extinctions as nothing but artefacts of the fossil record. In turn, the follower of Brocchi-for exam ple, Beurlen (1933), Zunini (1933) and especially Schindewolf (1950)-tended to interpret the extinction of individuals species in terms of their specific life cycle. Though they certainly dis not deny the occurrence of regional environmental catastrophes and their implications for species extinction, they largely agreed with the Darwinians that mass extinction phenomena are wildly exaggerated by the notorious imperfection of the fossil record.

The idea of the specific life cycle was later rejected by modern evolutionary biology. The interpretation of mass extinctions- in particular the Paleozoic-Mesozoic and Mesozoic-Cenozoic ones- as possible artefacts of gaps in the fossil record, however, has become one of the two rival perspectives on these phenomena. the other has, of course, envisaged mass extinctions as caused by real environmental catastrphes and it has been based on a more literal reading of the fossil record. The contrast between these two interpretations has largely shaped the history of debate about mass extictions, but it has always hinged on divergent views on the precision and reliability of stratigraphic correla tion among very distant areas.

For so long as the fossil record was only poorly knowm. Darwin's gradualist perspective appeañled to the majority of geologists and palaeontologist. The subsequent progress in stratigraphy, however, has led in the twentitn century to the idea of mass extinction processes operating over the entire Earth instead to being confied to single geographical regions, Marshall (1928) and Henning (1932), for example, regarded the Cretaceous-Tertiary boundary extinctions as a pronounced and abrup catastrophe of global dimensions and explained them by involking a sudden wave of cosmic radiation as the appropriately catastrophic causal factor. The stratigraphic record, however, still could be inter preted both ways abd hence several workers-For example, Povlova (1924) and Sobolev (1928)- considered the same extinctions as extended over millions of years; therefore, they referred to more mundane causal processes, such as the various geographic, climat ic and biotic effects of diastrophic cycle.

This divergence in palaeontological interpretations of the com pleteness of the record at various stigraphic boundaries, and consequently of the rapidity and nature of mass extinction phe nomena, has persited until today. One the one hand, several prominents geologists and palaentologists accepted the catastr phic nature of mass extinctions; in fact, even Schindewolf (1954) and Beurlen (1956) became at some point convinced that these phenomena could not be reasonably accounted for by an accidental clustering of the ends of the life cycle in a great number of species. As a result, a ever more imaginative narrative scenar ious were presented which invoked a very wide variety of terres trial and extraterrestrial causal factors as the ultimate cul prits of extinction. Thus, Schindewolf (1954), Krasovsky and Shklovskiy (1957, Liniger (1961), and Russell and Tucker (1971) proposed hat mass extinctions are caused by waves of cosmic radiation produced by supernova explosion in relative proximaty to our planetary system. Dyssa et al. (1960) claimed that intense vaolcanism could cause earthly radioactivity to exceed lethal levels and thus lead to extinctions. De Laubenfels (1956) invoked a bolide impact on the earth at the Cretaceous-Tertiary boundary to explain the demise of the dinosaur. McLaren (1970) put forth the hypothesis that a whole siute of environmental consequnece of a solide impact i the ocean could best account for the pattern of Frasnian-Famennian extictions. Hays (1971) seggested that mass extinctipons could the causally related to geomagnetic field reversals. Beurlen (1956) thought that a dramatic and vitually instantaneous change in sewater chemistry had poisoned and thus exterminated the majority of marine organims could at the end of the Paleozoic. Gartner and Keany (1978) claimed that a billover of could brckish water from the previously isolated Arctoc Basin on the wold ocean had happened at the Cretaceous-Tertiary transi tion and caused mass mortality among the pelagic plankton; ac cording to McClean (1978), this event should have led to a green house effect due due to carbon dioxide buildup in the atmosphere, and hence ot further extinctionson a dramatic climatic change. There were no limits to imaginations, simply because there was no hard empirical evidnece either firmly to corroborate seroiusly to contradict any of these stories. Schindewolf (1954), indeed, esplicitly wrote that his hypothesis was merely a 'desperate move'to splain the mystery he could not resolve in a more scien tific way.

On the other hand, the advocates of more gradualistic interpreta tions of mass extinction phenomena could at least base their explanatary scenarios on the apparent coincidence between these large-scale biotic changes and various major geological process es. Following from such evidence, global marine regressions were often regarded as the prime causes of mass extinctions (Lichkov, 1945; Newell, 1967), even though a clear mechanism of species extinction by regresion was not identified. It is only after the advent of the theory of island biogeography that Schopf (1974) could causally interpret the striking correlation he observed between the pace of Permian- Triassic extinctions in the sea and the decline in the total area of continental shelves inhabitable by shallow-water marine organims of the time. The island biogeo graphic theory predicts that the smaller the available area, the smaller the number of species it can harbour; hence, the origin of the single supercontinent at the end of the Paleozoic should lead to numerous extinctions. Given this mechanism of extinction, however, mass extinctions should be very protacted in time and thay should also nonselectyve affect all the organic groups present in the ocean; and Schopf was very emphatic on this point. Other authors suggested other extictions machanisms triggered by marine regressions. For inatance, Johnson (1974) suggested that the Frasnian-Famennian extinction of reef biotas had been caused by their particyulary vulnerable palaeogeographic position on broad shalves where even a minor regresion must have led to major enviromental consequences of global sea-levels fluctuations-from climatic to oceanographic to purely biogeografic ones.

Global marine regressions, however, are of course not the only sort of large-scale environmental phenomenon that could be correlated with mass extinctions. Many geologist and paleoecologists have always regarded climatic change, and particularly cooling or even glaciation, as the main cause of mass extinction. The empirical evidence in support of this view is best presented by Stanley (1987; 1988). The trouble is that, given the protacted duration of mass extinctions phenomena-as requiered by this kind of explanatory scenario- and given also the apparently great potential of various marine organisms to adapt rapidly to changes in seawater temperature, a climatic cooling hardly seems to be a sufficient cause for mass extinction; except, that is, for such unusual palaeographic situations as the West Atlantic or the Mediterranean in the Neogene.

As clearly shown by Jablonski (1986), however, in his comparative analysis of the phenomena traditionally recognized for the main mass extinctions in the history of life on the Earth-that is, the Ordovician-Silurian, Frasnian-Famennian, Permian-Triassic, Triassic-Jurassic, and Cretaceous-Tertiary transitions-neither eustatic sea-level falls, nor global climatic changes, nor any phases of the diastrophic cycle are consistently associated with mass extinction; and none of these explanantions is adequqte to explain all these five mass extinctions, let alone all the other geological time intervals that are sometimes interpreted to include events belonging to this category (the Eocene-Oligocene, Cenomanian-Turonian, earliest Toarcian, letest Precambrian, and so on). As theories aimed to explain all mass extinctions, these traditional gradualist scenarios appear, then, also unsatisfactory. This is perhaps why new empirical developments were necessary substantially to rejuvenate this field of research in the 1980s.

THE CURRENT CONTROVERSY.

The finding by Alvarez et al. (1980) and Smit and Hertogen (1980) that greochemical anomalies, including a pronounced iridium spike, are associated with the mass extinction horizon of pelagic plankton at the Cretaceous-Tertiary boundary has for the first time provided hard evidence that could be interpreted as indicative of a causal link between biotic events and extraterrestrial influences. Iridium is a very rare element in the Earth's crust and its considerable concentrations at widely distant locations in the same stratigraphic horizonts could be best explained as fallout from the dust cloud raised by impact of iridium-enriched bolide on the Earth, Such an impact, in turn, would also have a wide variety of environmental consequences, beginning with an initial shock and heat wave and ending with nuclear winter-type events (pollack et al 1983) and seawater intoxication by trace elements (Erickson and Dickson, 1987), wich could casily explain mass extinction of marine as well as terrestrial organism. The hypothesis of Cretaceous-Tertiary mass extinction by a huge bolide impact is, therefore, very appealing. Its proposal hasdramatically changed the pace od research, and the tone of debate, onmass exticntions (for critical reviews of ideas andevidence see Sepkoski and Raup, 1986; Jablonski, 1986; Hoffman, 1989).

The hypothesis of an impact at the Cretaceous-Tertiary boundary is strongly supported by literally dozens of reports on geochemical (iridium and other siderophile element enrichment) and mineralogical (shocked quarz, fluffy carbon, microspherules comparable to altered impact droplets)fingersprints associated with either the marine or the palynological Cretaceous-Tertiary boundary. An iridium anomaly, associated in addition with microtektites, has also been discovered at the Eocene-Oligocene transition (Ganapathy, 1982). Therefore, when Raup and Sepkoski (1984) analysed the record of family extictions among marine animals and found that in may indicate a 26-million-year periodicity in extinction intensity of these taxa, it was logical to assume that the uni formity of extinction mechanism, suggested by the apparent periodicity of extinction events, points to extraterrestrial impacts as the culprits of mass extinction.

A search was immediately undertaken for astronomical mechanism that could cause such an impact periodicity, and astronomical mechanisms that could cause such an impact periodicity, and astronomer have rapidly come up with quite an impressive array of hypotheses; the Nemesis, a twin star of our Sun, could periodi cally disturb the Oort cloud of comets and throw some of them toward the inner planets; the same effect could be produced by the undetected tenth planet of our solar syatem; oscillations of the solar system about the galactic plane could also lead to increased frequency of our planet's encounters with comets, and so on.None of these hypoteses cred more or less serious troubles, but none of them could be ultimately refuted (Sepkoski and Raup, 1986). All of them hinge, however, on the assumption of a uniformity-of-mass-extinction mechanism by extraterrestrial impacts. This assumption is in turn substantiated by the argument that if the peaks of extinction known from the fossil record are periodic, and if one or even two of these peaks are caused by impacts, then all the other peaks are most likely to be also caused by impacts.

The argument has largely shaped the countroversy on mass extinc tions which has continued relantessly in the 1980's. For, on the one hand, it critically depends on the presumed validity of the hypotheses proposing the extinction periodicity and the impact causing of the Cretaceous-Tertiary(and to lesser degree also the Eocene-Oligocene) extinctions. One the other hand, it imples that all mass extinctions in the history of life on the Earth should be associated with impacts fingerprints and have a pattern compatible with a sudden and dramatic catastrphe. the latter impli cations has simulated several research projects that focused on the individual biotic events which could be construed as mass extinctions, but I shall not duscuss this topic here, since the evidence will be presented and evaluated in detail in the other chapters of this book. Suffice it to note here that no evidence has thus far been presented that would impacts; and the impact also is highly contentious. The question of extinction periodici ty, moreover, is no less controversial.

Raup and Sepkoski (1984,1986) conducted a series of statical analyses of rate and intensity of extinctions of marine animals families and genera during the Phanerozoic. They concluded that the observed pattern of temporal diustribution of extinction peaks is best explained by assuming a significant contribution from an approximately 26 million-year periodic signal in the later Phanerozoic, and perhaps a longer-period signal in the Paleozoic. This conclusion and my subsequent suggestion that this empirical pattern may in fact reflect nothing but a random varia tion in extinction intansity through time (Hoffman, 1985) have triggered a heated debate. It is important to realiza that the emphirical pattern of extinctions peaks evidently is not strictly periodic, so that the question of the likelihood that a random process leads to a strictly periodic pattern is irrelevant. What is actually at issue in this debate is whether the empirical pattern deviates so little from periodicity that it could only be obtained with the contribution of a strong periodic signal, or whether te observed amount of regularity is so small that the pattern could also result from a random process.

The issue is far from being ultimately resolved. On the one hand, Sepkoski and Raup (1986), sepkoski (1986) and Forx (1987) present new analyses to reinforce the hypotesis of extinction periodici ty, On the other

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On the other hand, a recent cathodoluminescence study of shecked quartz grains at the Cretaceous-Tertiary boundary demostrated their non-volcanic origin (owen and Anders, 1988); and the rhodi um distribution in the boundary clay is very different from that found in terrestrial rocks, but closely similar to the one re corded in metiorites (Bekov et al., 1988). Moreover, tsunami deposits have been recently discovered at the cretaceous-tertiary boundary (Bourgeois et al, 1988). These data, then strogly suggest that an impact dis indeed take place at the very end of the Cretaceous, presumably during, or very soon after, a period of extremely intense volcanic activity.

The relative contribution of the environmental consequences of impact and volcanism to the Cretaceous-Tertiary mass extinction can hardly be disentangled. The fossil record, however, documents a more complex pattern than just a severe across-the board extinction of many organic groups at the Cretaceous-Tertiary boundary. Among the pelagic plankton the foraminifer and coccolithophorid extinctions occur at demonstrably different stratigraphic horizont (Perch-Nielsen et al., 1982; Gartner and Jiang, 1984; Smit and Romein, 1985; Lindinger and Keller, 1987). Marine macroinvertebrates, in turn, were certainly undergoing significant extinctions over the last few million year of the Cretaceous (Birkelund and Hakansson, 1982; Kauffman, 1986; Ward et al., 1986; Hallam, 1987; Zinsmeister et al., 1987), thus ruling out their attributions solely to the terminal Cretaceous impact. This is parhaps why Alvarez et al. (1984) accepted the view that many organic groups, dwindling for whatever unidentified reasons toward the end of the Cretaceous, fell ultimately victim to the impact event at the Cretaceous-Tertiary boundary.

It thus appears that the Cretaceous-Tertiary mass extinction cannot beplausbly interpreted as caused solely by a bolide impact and its environmental consequences, and it is more feasible to invoke a coincidence of at least two different factors which were causally unrelated to each other (since the impact occurred at the end of a period of intense veolcanism and extinctions). Hence, even if there were good reasons to assume the uniformity of extinction mechanisms for all mass extinctions, there would be no reason to accept extraterrestrial impacts as the ultimate cause for'these biotic events. In the absence ofstrong evidence for extinction periodicity, however, the hypothesis of a uniform causation of all mass extinctions-either by impact, as envisaged by the hypothetical astronomical mechanism, or by episodes of extraordinary volcanism caused by mantle processes, as proposed recently by Loper et al (1988)-appears absolutely unsubstantiated.

This conclusion fully pertains to the recent article by Hut et al. (1987) who note thet the Cenomanian-Turonian. Cretaceous- Tertiary, and Eocene-Oligocene extinctions episodes, and who then propose that these mass extincion periods-and presumably also the others, for which they also hypothesize such stepwise nature-are caused by comet showers. The concept is derived from the fact that multiple impacts occurred during the Eocene-Oligocene transition and that an impact also took place during the extinctions at the Cretaceous-Tertiary boundary. The assumption of a uniformity of mass extinction mechanism then forces Hut et al. to envisage impact causation also for the Canomanian-Turonian episodes of extinction and for the several latest Cretaceous epidodes prior to the terminal event. There is, however, no evidence to justify this extrapolation. Moreover, both the Cenomanian.Turonian and Eocene-Oligocene data employednow by Hut et al. were previously explained by the same palaeontologists by reference to entirely were associated in time with the biotic events subsumed under the heading of mass extinction (Keller, 1983; Kauffman, 1984; Elder, 1987; Hansen, 1987).

It hus appears that all one can safely say at this pont about the Cretaceous-Tertiary, Eocene-Oligocene, and Cenomanian_Turonian extinctions is that they occurrred incluster of extinction episodes, some of them perhaps causally related to bolide impacts onthe Earth, but others apparently not. There is, moreover, strong evidence that some other extinction peaks, including thetraditionally recognized Ordovician-Silurian and Frasnian- Famennian mass extinction, are also clusters of extinction episodes rather than single catastrophes (Brenchley 1984; House, 1985; Benton, 1986; Farsan, 1986; Hallanm, 1986). This has led me to the conclusion that the major peaks of extinction may in fact be clusters of separate events more or less accidentally agregated in time (Hoffman, 1989). They may be caused by global environmental events of various sorts-palaeoceanographic, climatic, or volcanic ones, as well as bolide impacts, Undoubtedly, extraterrestrial impacts on the Earth, enormous volcanic eruptions, oceanic anoxic event, dramatic sea-level changes and climatic fluctuations ocurred repeatedly during the Phanerozoic; yet only very few of these phenomena were actually implicated in the causation of mass extictions. Perhaps then mass extinctions are not the biotic consequences of any single phenomenon of one or another sort, but rather rare incidences of more than one major changes in the physical environments accidntally cumpled together within relatively short intervals of geological time, say, 2-4 million years in duration.

This hypothesis of mass extinctions as coincidences of lesser episodes caused by a variety of physical factors may superficially resemble Schindewolf's (1954) desperate move to explain the mystery that could not be resolved in a more scentific way. Occurrence of such coincidences, however, is not all implausible or unlikely.

Consider, for example, w different kinds of physical events that occur at radom, each with the probability of 1-p per million years. The following formula:

$$[p^{wk} + wp^{(w-1)k}(1-p^{k})]^{n/k} = 1 - C$$

gives then the probability 1-C that, during the period of n million years. none of the consecutive k-million-year intervals will contain more than one event. of at least two wvwnts will occur within n million years. Assuming that, say, 5 different kinds of events may cause considerable extinctions (extraordinary volcanic eruptions, rapid climatic cooling, major transgressions and regressions, oceanic overturns, and large bolide impacts)and occur each with the average frequency of one every 50 millions year interval, C equals under such assumptions 0.73 for 100 million years and 0.96 for 250 million year. If the average frequency of events of each kind is decreased to only 1 per 100 million year, C still reaches 0.40 for at least one coincidence in a 4-million-year interval ocurring within 100 million years and 0.60 for one such coincidence within 250 million years.

Recall that C seriously underestimate the actual probability of coincidence of events, as it does not take into account the probability of coincidences that would span two consecutive time intervals. Clearly, then, coincidences (on the geological time- scale) of major environmental events accidentally aggregated within a few million years are quite likely to occur, and they may well account for at least some of the mass extinctions. This is not to say, however, that all mass extinctions are nothing but such clusters of separate extinction episodes.

For example, because of a major marine regression, the fossil record at the Permian-Triassic transition is so poor that the detailed pattern of extinction cannot be recognized on the global scale. In any event, however, no distinct episodes of extinctions ca be identified, and contrary to the traditional opinion that the extinctions were spreas ever as much as 10 million year (Schop, 1974), more recent studies on continuos stratigraphic sections suggest a much more rapid, though by no means catastrophic, process (Streng et al., 1984). The oceanic carbon and oxygen isotope records at the Permian-Triassic transition- spanning this greatest of all mass extinctions- indicate a dramatic oceanographic event, apparently more profund than any other observed thus far in the Phanerozoic. These isotopic records have been recently reviewed by Holser and Magaritz (1987, see also Magaritz et al., 1988), but Gruszczynski et al. (1989, Malkowski et al, 1989) present crucially important new data which demostrate that, after a rapid shift toward extremely positive values, the oceanic delta 13 C declined by more than 10 per mille, that is, down to distinctly negative values. The oceanic oxygen isotope essentially mimicks the carbon one.

The trigger for the latest Permian changes in delta 13 C trend id unknow. The mass balance vcalculations made by Gruszczynski et al. (1989; Malkowski et al, 1989) demostrate, however, that the late Permian rise in delta 13 C must have been caused by a rapid removal from the ocean-atmosphere system of huge amounts of organic carbon- more than 30 times tha total amount of carbon in the presently living biosphere. The subsequent drop in delta 13C indicates that the ocean received three times more of organic carbon than it had previoüsly lost. The amounts of organic car bon, which is refflected by the carbon isotopoe spike, must have left much oxygen free; the reducing conditions at the se-bottom contributed to nutrient recycling in the ocean and thus to an increase in the standing crop of the marine biosphere. Howver, the subsequent oxidation of organic matter, which is reflected by the carbon isotope records at the Permian-Triassic transition thus indicate a considerable decline in atmospheric oxygen and oceanic nutrient levels, which could well be the prime causes of mass extinction.

The isotopic records thus identify an oceanographic event as the cause of the Permian-Triassic extinctions, whereas no other causal factors have been recognized which could significantly contribute to these extraordinaryexotic phenomena. Perhaps, then, this is a rare case of mass extictions phenomenon that really deserves this name-triggered indeed by a single process and, consequntly, confined in duration to a reasonably coherent time interval. The other mass extinctions, however, may be caused by various independent processes. It seems though that, apart from the Cretaceous-Tertiary mass extinction, their palaeoceanography is too poorly known to rule out the possibility of their, at least partial, causation by processes similar to the one operat ing at the Permian-Triassic transition.Much more palaeoceano graphic effort, particularly on the Palaeozoic, is beeded to decopher the palaeoenvironmental context of those mass extinc tions.

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SECCION V: LA PALEONTOLOGIA EN MEXICO.

CAPITULO 11. EL PANORAMA PALEONTOLOGICO.

11.1. Preambulo.

A pesar de que la investigacioón paleontológica en nuestro país se remonta al primer tercio de siglo XIX, y de que a partir de 1986 existe una institución nacional dedicada a las ciencias geològicas-incluida la Paleontología no se ha escrito al presente una historia de la misma; por lo que resultaría imposible realizar aquí esa tarea. En consequencia, se ha preferido abordar algunos aspectos desu problemàtica, destacando el entorno socio académico en que se ha insertado eldesarrollo de esta ciencia en México.

Las fuentes bibliográficas específicas, son claro está muy reducidas, por lo que el presente autor se vió en la necesidad de echar mano de dos de sus propios trabajos y de notas que al respecto se han preparado con otros fines.

En el primero de ello, que fue una entrevista hecha al presente autor, se expone en lo general la gran importancia cinetífica nacional e internacional que tiene el registro fòsil con que cuenta nuestro país, y de la trascendente labor quese desarrolla en el Instituto de Geología, par darlo a conocer a la comunidad científica, por ser éste, el principal centro de investigación en esta especialidad que existe en México.

En el segundo, se aborda la problemática de la nvestigación paleontológica, mostrando que tanto el entorno socioacadémico de la profesión paleontológica, como la naturaleza geológica del territorio nacional, han influido poderosamente paraconformar la clase de investigación paleontológica que se hace en el país, con su marcado énfasis en el trabajo sistemático y bioestratigráfico.

Con el objeto de suplementar la información presentada, se ha decidido agregar lo siguiente:

_Docencia.- La paleontología General y algunas de sus especialidades como la Micro paleontología, Paleontología Estrafigráfica, Palinología, Paleontología de vertebrados y otras, así como ciencias afines, p. ej., la Geologìa Histórica, forman parte del curriculum académico de las licenciaturas de Biología, Ingeniería Geológia y Oceanografía entre otras. Cabe destacar que estas carretras se imparten en nstituciones de educación superior- principalmente universidades- ubicadas en 18 (Biologìa), 10 (Ingeniería Geológica) y 4 (Oceanografía) entidades federativas de la Rèpública. Ello teóricamente implica una amplia distribución geográfica de las instituciones educativas donde puede obtenerse cierta formación paleontológica. Sin embargo, las condiciones en términos de número de estudiantes, infraestructura de apoyo docente-colecciones, literatura, laboratorios, etc.- y nivel académico así como especialización de los profesores, son muy heterogéneas; siendo significativamente mejores en el Distrito Federal que en los Estados, y en conjunto, su calidad es de modesta a pobre, si se le compara conlas necesidades de la formación académica que se supone debe atender satisfactoriamente.

Por lo que respecta al perfil académico del Profesor de Paleontología en este país,es el de un Licenciado en Biología, que imparte esta disciplina por tiempo parcial, ya que se dedica profesionalmente a otras actividades; aunque en el Distito Federal, un nùmero relativamente alto de profesores, tienen un grado académico superior al de la Licenciatura y/o se dedica profesionalmente a la práctica paleontológica en la investigación y/o en la docencia.

En relaciòn a la formación académica de los paleontólogos, es necesario destacar que la Paleontologìa no es una especialidad formal en ninguna de las licenciaturas, y es una especialidad "informal" en los posgrados que se ofrecen en el país, restringidos a la Universidad Nacional Autónoma de México y en el Instituto Politecnico Nacional, en donde las maestrìas y doctorados más próximos, son en Ciencias, con la especialidad deBiología o Geología. En la Práctica, la mayor parte de los paleontólogos mexicanos con posgrado especializado en esta disciplina, lo han adquirido en el extranjero, y aùn persiste esta tendencia.

LA PROFESION PALEONTOLOGICA.

En el mercado profesional en esta disciplina se restringe principalmente a la docencia, a las pocas instituciones donde se realiza investigación científica formal, que son el Instituto de Geología, el Instototo Mexicano del Petróleo y el Instituto nacional de Antropología e Historia; así como a Petróleos Mexicanos, donde de manera cotidiana se realiza investigación aplicada y trabajo académico de servicio profesional. El desarrollo socioeconómico del país, no permite que existab de manera viable, empresas consultoras privadas, por lo que ningún paleontólogo profesional, podría subsistir conla prestación privada de susservicios técnicos o científicos. Las perspectivas en este terreno, tal vez mantengan esta misma tendencia en el futuro inmediato.

LITERATURA CIENTIFICA.- La literatura especializada que se produce en México, consiste de una serie reducidade revistas, entre las que destacan Paleontología Mexicana, y la Revista de la Sociedad Mexicana de Paleontología. En las publicaciones Geológicas, tales como el boletín de la Sociedad Geológica Mexicana, el Boletín de la Aociación Mexicana de Géologos Petroleros y las Revistas del Instituto de Geologìa y del Instituto Mexicano del Petroleo, aparecen frecuentemente trabajos paleontológicos. Mención aparte merece el esfuerzo de producir textos y obras de consulta, principalomente paradocencia universitaria; el trabajo apenas se inicia y merece una amplia oportunidad de desarrollo, para subsanar el vacio y la dependencia que ello implica. Esta Antologìa es un paso enesa direcciòn.

LA SOCIEDAD MEXICANA DE PALEONTOLOGIA.- En 1986, se organizó por vez primera en Mèxieo, una sociedad científica dedicada a promover el interès en la Paleontología, dotando por fin a la comunidad respectiva de un foro permanente, para realizar el necesario intercambio de ideas y experiencias que posibiliten undesempeño académico satisfactorio.

A la fecha, en esta sociedad, que se agrupa a la mayorìa de los profesionales del ramo en el país, así como a colegas extranjeros que tienen interés en México, ha desplegado una actividad inusitada, habiendo celebrado ya tres congresos nacionales, publicando varios números de su impprtante revista, así como otras labores académicas. Es de desearce que la Sociedad se fortalezca más, para que pueda incidir mejor en la solución de la compleja problemática que al respecto enfrenta el país.

EPILOGO.- La actividad paleontológica en México, acusa una problematica similar a la de muchas disciplinas científicas básicas, es decir dispone de un presupuesto limitado - más bien reducido- y el número de sus profesionales es pequeño. Empero ellos han realizado una amplia labor, dando aconocer una buena parte de la impoetantisima biota fósil presente en nuestro territorio. El avance real en este campo, requiere de la participaciòn entusiasta de toda la comunidad, tanto en el aspecto docente, como en el de investigación científica y aplicada, así como en el de la difusión; ello permitirá alcanzar y sostener el nivel de calidad que este país necesita y merece.

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11.3 ASPECTOS GENERALES.

11.3(A)

LA RIQUEZA PALEONTOLOGICA DE MEXICO, VALIOSA A NIVEL MUNDIAL. *

El registro fósil documenta la evolución orgánica, permite conocer como vivierón ciertas especies e inferis relaciones filogenéticas.

En México, la importancia de los hallazgos paleontológicod que se realizan y se desarrollarán en el futuro es enorme, tanto a nivel nacional como mundial, por la peculiar ubicación geográfica e historia geologica que tiene nuestro país: es decir, nuestro territorio ocupa una area clave para entender la historia geologica y biologica de America y de los continentes africano y Europeo.

El Dr. Ismael Ferrusquia Villafranca, miembro de la academia de la Investigación Cientifica y de la comunidad paleontologica, hablo sobre esta ciencia, asì como del esfuerzo permanente de la UNAM en el campo de la difusion cultural y de la actividad científica.

La paleontología es una ciencia natural y como tal, dijo el especialista del Inst. Geol. de la UNAM, rsponde a interrogantes que el hombre se plantea acerca de la naturaleza, particularmente en torno a los seres vivos que existierón en el pasado geologico: su pertenencia biólogica, su escenario geografico, su relación con los seres actruales y los vestigios que dejaron de su existencia etc.

Estas son algunas de las cuestiones que el paleontologo trata de resolver y las actuales constituyen el nucleo de su actividad profesional. En este sentido, agregò, las respuestas tienen un doble valor: por un lado intentan resolver interrogantes trascendentales que el hombre se hace como expresiones de su curiosidad innata.

Por otro lado, la información paleontologica contribuye a resolver problemas de otras ciencias, como la biología evolutiva, en donde el registró fósil documenta al fenomeno de la evolución orgánica, permite conocer cuándo y dónde vivierón ciertas especies, inferir sus relaciones filogenéticas y entender su distribución biogeografica, entre otras.

En el terreno de la geologia, por el hechomismo de la evolución orgánica, los seres vivos han dejadpo un registro fosil individualizable cronologicamente. Este posibilita que, en funciòn de los fósiles de algunas rocas, se pueda conocer su edad geologica relativa y conbase en ello establecer su correlación estratigrafica y, desde luego, conocer con relativa certidumbre la historia geologica de un lugar.

Los fósiles, aseveró el doctor Ferrusquia, profesor de la Facultad de Ciencias y autor de múltiples artículos publicados tanto a nivel nacional como internacional, son testimonios materiales de seres vivos, reconocibles como tales por su configuración y estructura, que existierón en el pasado. En términos convencionales se habla de una antigüedad minima de 10 mil a 20 mil años. Estos testimonios incluyen desde organismos completos hasta huellas de su actividad. Ello implica la existencia de una gran diversidad de fósiles y, en consequencia, métodos muy variados para estudiarlos. En función de su tamaño existen macroscópicos y microscópicos; y pueden tener una antigüedad de 3mil 500 millones de años. Por su naturaleza biológica incluyen representantes de los 5 reinos que se reconocen en el presente.En cuanto a su origen, los fósiles se generan con base en procesos que excluyen a ciertos individuos de la destrucción y reciclaje de material que naturalmente ocurre en los seres vivos. Este fenómeno se denomina como proceso de fosilización y en general involucra la cobertura rápida por sedimentos, evitandose asi la destrucción del resto orgánico.

Es de esperarse, afirmó el doctor Ferrusquía, que estos procesos sean más frecuentes en las cuencas sedimentarias que en otros medios, pues la presencia de un esqueleto mecanico mineralizado favorece la posibilidad de la fosilización. Por estas razones el registro fósil está

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*Entrevista al Dr. I. Ferrusquía V., publicada en la Gaceta de la UNAM, Num. 2,478, Junio 11, 1990.

cosntituido mayoritariamente por animales esqueletófosros marinos, que son los que tienen la máxima posibi lidad de fosilizarse. Aún así, es sólo una minima parte de los individuos que forman una especie dada los que se fosilizan y de ellos sólo unos cuantos son reconocidos, colectados, estudiados y eventualmente publicados.

Es por está razón, consideró el paleontólogo, que los fósiles constituyen un recurso patrimonial, cultural, natural finito y no renovable, que debe ser reconocido y apreciado por su oblación, así como protegido del abuso y la depredación.

Sobre la actividad que acerca de esta ciencia serealiza en nues tro país, el doctor Ismael Ferrusquía señalo que lacomunidad de paleontologos de México es relativamente pequeña - dada la magni tud y complejidad del registro fósil nacional- y labora princi palmente en el sector público, en especial en instituciones de educación superior, donde realiza actividades de docencia y en menor grado de investigación; en Petróleos Mexicanos se encuentra el mayor número de paleontólogos profesionales en areas de exploración geológicas-petrolera.

El desarrollo económico-industrial en México es tal que ningún paleontólogo podria subsistir en la practica profesional privada, pues no existiría suficiente demanda de sus servicios. Esta situación, consideró el investigador, ha ocasionado que el inves tigador, ha ocasionado que la investigación paleontologica en lo general se realice como una actividad dfe apoyo y que, en conse cuencia, no se haya gozado de liberatad de llevarla a cabo per se, Ello ha influido en el conocimientoque sobre el registro fósil se generado en México; se ha hecho enfasis en aquello que resulta de interés para la geologia petrolera, en dettrimento de las otras áreas.

En el país solamente el Instituto de Geología de la UNAM realiza de manera sistematica investigación paleontologica basica; por ello la importancia y trascendencia de la labor que aquí se practica. El Instituto, dijo, tiene ya una historia más que centenaria, y es junto con los Institutos de Biología y Astrono mia uno de los tres fundadores de la investigación científica profesional en la UNAM. En él se aloja la colección más extensa de fósiles de México y en su bibliotreca se encuentra el mayor aceryo bibliografico, mpo solo del país, sino de muchos de Lati noamerica. Sin embargo, no existe un servicio geológico o un museo nacionales especificamente encargadoa de mantener este tipode acervos, desarrollar y coordinar la investigación en este disciplina en todo el país. En la práctica el Instituto ha sumido esta especialidad a nivel nacional con las limitaciones del cadso y sin el apoyo legislativo cporrespondiente.

Sobre la legislación que rige en esta disciplina, el doctor Ismael Ferrusquia informó queen México el Estado considera a los fósiles como paete del patrimonio cultural y por decreto presidencial desde 1986 su cuiudado recae en el Instituto nacional de Antropologia e Historia de la Secretaria de Educación Pública, al mismo nivel que el material histórico o el Arqueologico. Entre otros aspectos, los fosiles mexicanos no pueden ser objeto de comercio; las colecciones privadas deben estar registradas ante el INAH y la exportacion del material fosil requiere del permiso respectivo. El establecimiento practico de este decreto esta lleno de dificultades y la comunidad de paleontologos cuestiona ya su conveniencia real para lograr los fines que se propuso el Estado al expedirlo.

Acercar el panorama actual de la paleontologia en Mexico, sus problematica y sus perspectivas, el especialista dijo que el registro fósil de nuestro pais es muy grande y variado. Incluye elementos de precambrico a pleistocenicos, burdamente de 1,700 millones a 5, 00 0 10,000 años de antiguedad; animales y vege tales, macroscopicos y microscopicos, marinos y continentales; pero en general aun es casi desconocido, dado que el tamaño de la comunidad cientifica, especializada es proporcionalemtne muy pequeño. Tal vez no exceda de 300 numeros de paleontologos profe sionales de México.

Por lo tanto, en el presente y en el futuro inmediato gran poarte del esfuerzo de esta comunidad se centrara en la necesidad de describir este registro. Debido al escaso numero de programas de investigacion, estrictamente palentologica, esta tarea tomara mas tiempo; por ello una de las responsabilidades principales de la comunidad sera lograr su incremento. la diversidad y complejidad del registro requiere de especialistas muy diversos que debera en n tiempo corto, si se pretende realizar la mencionada labor para paleontologos nacionales y en un lapso razonable. Atender esto es tambien una tarea prioritaria. Al igual que en otrosseg mentos de la comunidad cientifica que la tasade reemplazamiento es inferior a la necesaria para mantener su dinamismo y opera tividad; problema que implica, una situacion paradojica no se puede proporcionar un empleo satisfactoriamente remunerativo, en numero suficiente, a los escasos jovenes que atendiendo a su vocacion se esta formando academicamente en esta ciencia o que, piensan hacerlo, con todo para los entusiastas y los esforzados siempre habra unlugar, finalizado.

Jaime R. Villagrana.

II.4 INVESTIGACION

11.4 (a)

SOBRE LA INVESTIGACION PALEONTOLOGICA EN MEXICO. *

Ismael Ferrusquia Villafranca.

RESUMEN:

El marco y las características de la profesión geológica, deter minan la naturaleza de los estudios paleontológicos desarrollados en México. En el territorio nacional, las rocas calcáreas jurásicas, cretásicas y cenozoicas son las semimentarias más abundante; constituyen asimismo importantes rocas productoras o almacenado ras de petróleo. En consequencia, la mayor parte del trabajo pa leontológico se ha hecho sobre fósiles procedentes de rocas.

La estructura geológica-paleontológica es tal, que de las diuez instituciones principales solamente una realiza investigación paleontológica básica. Aproximadamente el 4% (unos 100) de los geólogos que trabajan en México, se dedica profesionalmente a la paleontológia; la mayoría de ellos está en petróleos mexicanos, Instituto Mexicano del Petróleo y el Instituto de Geología.

Debido a la gran necesidad de trabajo sistemático y bioestrati gráfico básico, el enfasis de las investigaciones se da en estos asp0ectos. Sin embargo se promueve también la investigación paleontológica avanzada sobre obtras cuestiones.

ABSTRACT

Mexico's geologic framework and the make up of the geologic profession are the main factors shaping the nature of the paleon tological work. The jurasic, cretaceous and cenozoic carbonates rocks are the most abundant sedimentary rocks, as well as the chief sources of oil. Hence the bulk of the paleontological works is done their fossil

The geological-paleontological community works for the most part in ten major institutions; eight arte devoted to aplied geologic studies and only two are cioncerned with basic research. About 4% (some 100) of the geologist working in the mexico takes up pale ontology as a profession. They work mainly for petroleos Mexicano s, Instituto Mexicano del Petroleo e Instituto de Geologia.

A large amount of straight systematics and biostratigraphic work remains to be done, therefore these aspects are and will be emphasized in the paleontologic research for a long time.Advanced research is promoted also, however.

Introduccion:

Para entender el alcance, la naturaleza y el desarrollo de la investigación paleontológica en méxico es necesario examinarla bajo la perspectiva dada por el marco geológico y la estructura de la comunidad y la profesión en México. Influye desde luego otros factores. Se sumariza a continuacion,las características de estos factores.

EL MARCO GEOLOGICO.

Una de las maneras màs sencillas de resumir descriptivamente la geología del país es el enfoque de provincialización morfotectón ica, esto es , dividir al país en amplias regiones que tengan rasgos e historia geológica similar. Hay varios arreglos posibles (cf. Guzman y de Cserna, 1963) el que se presenta a continuación (fig 1), es el mas apropiado para el objtetivo presente.

Se reconocen aqui diez provincias.

1.- PENINSULA DE BAJA CALIFORNIA.

La mitad norte está constituida por rocas instrusivas mesozoicas que intrusionaron y flaquearon rocas sedimentarias marinas y continentales. La mitad sur incluye principalemente andesita y basaltos cenozoicos, y rocas sedimentarias marinas y continen tales del

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jurásico al reciente, la punta de la península está formada por rocas intrusivas y sedimentarias que aparentemente tienen una historia geológica muy distinta al resto de la penín sula.

2.-CUENCAS Y SIERRA NOROCCIDENTALES

Es la extensión meridional de la provincia Basin and Ragen de Estados Unidos. Está constituida por rocas paleozoicas marinas fallados en bloques, que constituyen las sierras. Las cuencas están llenas de sedimentos continentales cenozoicos. El fallami ento en bloques ha expuesto en algunas partes alas rocas crista linas precámbricas; es aquí donde se encuentra las rocas más antiguas de México, que corresponden al proterozoico medio y tardío.

3.-SIERRA MADRE OCCIDENTAL

Esta constituida por rocas volcanicas de edad cenozoica media y tardía que incluyen principalmente tobas e ignibritas rioloticas a riodaciticas y derrames andesiticos.,La escases de caminos dificulta la cartografía geológica detallada esta provincia es la más grande de todas.

4.- FAJA NEOVOLCANICA TRANSMEXICANA

Está cosntituida principalmente por rocas andesíticas a basalti cas del cenozoico medio y tardio. La composición cambia cronológ icamente de andesitica a basaltica. Se aprecia un fallamiento en bloques y rifting moderado, dirigido de oriente a poniente que a producido pilares y fosas tectónicas, en donde se han desarrolla do lagos y sedimentos lacustres asociados. La interpretación de esta faja volcánica es incierta todavía, pero claramente consti tuye un rasgo geológico mayor.

5.- SIERRA MADRE DEL SUR

Es la provincia más complicada e incluye tres dominios, Guerrer ense, Oaxaqueño y C-Hiapaneco. Estos dominios coresponden a cuencas sedimentarias de compleja evolución geológica, desarrolladas sobre rocas cristalinas proterozoicas y paelozoicas de evolución geológica compleja tambien. Las rocas de esta provincia incluyen el espectro de litología y su edad va del proterozoico tardio al reciente.

En la región suroriental,las estructuras geológicas de las rocas mesozoicas cambian gradualmente su dirección principal de norte a sur noroeste-sureste.

6.- PLATAFORMA DE YUCATAN

E una plataforma clacarea cenozoica, acrecionada desde el Eoceno, donde se ha desarrollado una extensa topografia carstica.

7.- PLANICIE COSTERA DEL GOLFO

La mitad norteña está constituida por rocas clásticas marinas y transicionales que representan una fase regresiva relacionada con la genesis y evolución del golfo de México.La mitad oriental in cluye rocas calcáreas cenozoicas tardias en la superficie, que cubren a rocas cenozoicas y mosozoicas enel subsuelo,portadoras de hidrocarburos abundantes, de donde se desarrollan los nuevos e importante compos petroleros.

8.- SIERRA MADRE ORIENTAL.

ESTA constituida por rocas calcáreas marinas jurásicas y cretasi cas plegadas, falladas y levantadas durante la Orogenesis Lara mide. Lassierras que ocupan la región oriental, cambian gradual mente su orientación nore-sur hacia este-oeste, mediante una flexura mayor, que constituye uno de los grandes enigmas de la geologia mexicana. Las cuencas intermontanas estan rellenas de rocas clasticas cenozoicas.

9.- SIERRAS Y ALTIPLANICIES NORTEÑAS

Estan formadas por sierras orientadas noroeste-sureste, cosnti tuidas por rocas calcáreas jurasicas y cretasicas plegadas, falladas y levantadas, separadas entre si por cuencas intermontañas confluyentes, rellenas de clasticos cenozoicos. En la región occidental estan asociadas con rocas volcanicas andesiticas, silicias del cenozoico medio y tardio, que contienen yacimientos minerales economicamente importantes.

10.- ALTIPLANICIE CENTRAL

Es una cuenca endorreica, rellena parcialmente por clasticos cenozoicos derivados de las sierras que lo bordean. En su región meridional, esta asociada a rocas volcánicas andesiticas y siliceas en donde se han desarrollado yacimientos minerales muy importantes. En el subsuelo de esta provincia semiarida, se aloja extensos acuiferos.

Resumiendo la geología se tiene que, aproximandamente un tercio del país esta constituido por rocas volcánicas; otro tercio esta compuesto por rocas calcareas marinas, jurasicas y cretasicas en su mayoria plegadas y falladas complejamente,que forman la Sierra madre Oriental, parte de la sierra madre del sur y las sierras nortecentrales; 4el otro tercio incluyen los otros tipos litologicos, entre los que destacan por su abundancia, las rocas cristalinas plutonicas y metamorficas, que se representan un 60% de este tercio y, las rocas clasticas marinas y continentales que constituyen un 30% dfe este. Es notoria la escasez de rocas paleozoicas sedimentarias no metomorfizadas.

Con esto en mentre, reulta claro que el trabajo paleontológico en Méxido se centra volumetrivcamente en las rocas mesozoicas marinas, en menor escala en las rocas cenozoicas marinas y mucho menios enlas meso y cenozoicas continentales.

LA COMUNIDAD Y PROFESION GEOLOGICA.

Como en otros paises, los estudios geológicos en México se han encaminando principalmente a la busqueda de recursos naturales no renovalbles tales como, petróleo, yacimientos minerales de valor economico, acuiferos , uranio, fosfato, etc. Esto se ha logrado principalmente al traves de instituciones gubernamentales de diferente tipo. En Mexico trabajan al presente unos 2 mil a 2500 geológos (López Ramos, 1974), en varias institusiones mutuamente independiente, de rango equivalente, pero de tamaño, estructura y ojetivos diferentes, las siguientes diez son las principales:

PETROLEOS MEXICANOS (PEMEX)

Constituye el grupo mayoritario, dedicado obviamente a la exploracion geológica petrolera. Su personal incluye 1200 geólogos, (50%de la comunidad geológica nacional).

INSTITUTO MEXICANO DEL PETROLEO (IMP)

Es el grupo de investigaciòn de PEMEX, el trabajo geológico enfatiza la investigación básica orientada a la geológia petrolera. Su personal incluye unos 120 geòlgos.

CONSEJO DE RECURSOS MINERALES (CRM).

Es el segundo grupo mayoritario, dedicado principalemtne a estudios de geología economica. Su personal incluye 250 geòlogos.

SECRETARIA DE AGRICULTURA Y RECURSOS HIDRAULICOS (SARH)

Grupo dedicado a la prospección geohidrologica. Su personal incluye unos 200 geólogos.

COMISION FEDERAL DE ELECTRICIDAD. (CFE)

Grupo dedicado a estudios geológicos aplicado a la ingfenieria civil; recientmente han desarrollado estudios sobre carbón y recursos geotermicos, en un esfuerzo por encontrar fuentes alternativas de energía, su personal incluye unos 150 geólogos.

DIRECCION DE ESTUDIOS GEOLOGICOS Y GEOGRAFICOS DEL TERRITORIO NACIONAL (DEGGETENAL).

Este grupo esta haciendo el inventario de los recursos naturales del pais; presenta sus resultados en mapas dispuestos en cuadran gulos de 20'x 30', escala 1:50000. La serie topográfica es la mejor. Los mapas geológicos se apoyan apliamente en estudios fotogeologicos. Su personal incluye unos 80 geólogos.

URANIO MEXICANO (URAMEX).

Este grupo se dedica a la prospección geológica del uranio, etc., tiene unos 60 geólogos.

SECRETARIADE ASENTAMIENTOS HUMANOS Y OBRAS PUBLICAS. (SAHOP)

Su grupo de geólogos se dedica a estudios aplicados a la ingenie ria civil, Su personal incluye unos 50 geólogos.

FOMENTO MINERO (FM).

Este grupo realiza estudios de geología economica para la indus tria minera pequeña y mediana. Su personal incluye unos 50 geólo gos.

INSTITUTO DE GEOLOGIA, UNAM (IG)

Grupo pequeño dedicado a la investigación geológica básica. Su personal incluye 50 geólogos.

Existen otros grupos mas pequeños en las universidades estatales, enla industria privada, principalmente minera y en la consulto ria. Solamente las compañias minera grandes, tienen personal geologico de base.

RESUMIENDO:

Las diez instituciones geólogicas principales, donde presta sus servicios aproximadamente el 85% de los geólogos mexicanos, son de tipo gubernamental, de tamaño, estructura y objetivos muy distintos, mutuamente independientes y de rango equivalente. Su trabajo implica una sobreposición considerable; que dificíl de evitar, por lo nula coordinación, causada por la falta de una institución nacional rectora o de un programa maestro de trabajo geológico de alcance nacional. Unicamente dos instituciones, el IMP y el Ig, realiza sistematicamente investigación básica; los otros ocho desarrollan investigación aplicada. Aproximadamente un 4% de los geólogos que trabajan en México, estos es unos 100 aproximadamente, realizan trabajos paleontológicos; estos estudi os se desarrollan principalmente en PEMEX, IMP e IG.

OTROS FACTORES QUE INFLUYEN EN EL DESARROLLO Y NATURALEZA DE LA INVESTIGACION PALEONTOLOGICA EN MEXICO.

L.- Formación profesional.

No existe en México ninguna institución dedicada a la formación profesional paleontológica; debe mencionarse sin embargo, que en los tres ultimos lustros se han desarrollado programas de estudio de postgrado que incluyen especialización en paleontológia. En consecuencia, el profesional de la paleontológia ha adquirido su formación mediante estudios formales de postgrado en isntitu ciones extranjeras o nacionales; o bien se ha habilitado como tal, mediante un entrenamiento capacitatorio informal y un gran esfuerzo autodidacta. Por ende, el resultado del trabajo refleja en cierta medida esta formación . Aproximadamente un tercio de los paleontológos de México tienen estudios formales.

2.-SUBORDINACION DE LA INVESTIGACION PALEONTOLOGICA A OTROS OBJETIVOS.

Dedido a que el desarrollo historico y economico del país se ha centrado en torno a la exportación de materias primas y energenicos, y a que el desarrollo industrial que se está realizando requiere de estos insumos, la investigación geológica se ha encausado en gran medida a su busqueda. Consecuentemente, la labor paleontológica ha quedado subordinada a estos objetivos prioritarior, con la natiural falta de incentivos para desarrollar programas que tiendan a la solución de problemas paleontológicos que no tengan una relación directa con objetivos economicos. Solo recientmente se ha comprendido, que la busqueda y hallazgo de los recursos mencionados, es en realidad el resultado de una sintesis cognositiva apoyada en resultados de investigación básica de naturaleza muy diversa, y de las cuales la paleontológia pura es una parte importante.Aun asi, hay mucho camino por recorrer, para liberar a la paleontología de esta posición subordinada.

LA INVESTIGACION PALEONTOLOGICA EN MEXICO.

Tal es el marco en el cual se desenvuelve la investigacion paleontológica en México. Comprensible la mayor parte esta dedicada al estudio de las rocas mesozoicas marinas, una parte menor a las rocas cenozoicas marinas y continentales y aun una menor, a las rocas paleozoicas. Comprensiblemente tambien, los esfuerzos principales se desarrollan en el Instituto Mexicano del Petroleo y en el instituto de Geologia.

INSTITUTO MEXICANO DEL PETROLEO Y PEMEX.

Se señalo ya que el IMP es el grupo de investigacion de PEMEX. El personal incluye unos 35 paleontologos. De ellos, los micropaleontologos constituyen el grupo mayoritario. El enfasis esta en estudio sobre foraminiferos, tendientes a establecer zonacion bioestratigrafica detallada, parametros ambientales diversos, correlacion regional y otros aspectos.Existe tambien un importante grupo palinologico, asi como algunos especialistas en otros tasa de interes inmediato en la prospeccion petrolera, como son los amonitas y conodontes.

En PEMEX, la labor paleontologica es principalmente de tipo rutinario, tendiente a la ubicacion estratigrafica, apoyandose principalmente en el reconocimiento de foraminiferofaunas de las distintas zonas establecidas.Aproximadamente de 35 a 50 paleontologos desarrollan esta labor, realizandola en las Oficinas Regionales de PEMEX, localizadas en distintos estados de la republica.

Los resultados de los proyectos de investigacion del IMP y de PEMEX son confidenciales. Algunos de ellos se publican en el IMP boletin del IMP o en otras revistas. Sin embargo, a pesar del enorme interes que tienen las investigaciones sobre la bioestratigrafia de la mitad sur de la planicie costera del Golfo, de la sierra madre de Chiapas y de la region de Vizcaino en la peninsula de Baja California, debido a su relacion obvia con los recientemente desarrollados e importantes campos petroleros, los resultados de estas investigaciones son muy confidenciales.

INSTITUTO DE GEOLOGIA, UNIVERSIDAD NACIONAL AUTONOMA DE MEXICO.

Es la unica institucion dedicada a la investigacion geologica basica. Su objetivo es contribuir al conocimiento sobre la evolucion central geologica del pais. En ausencia de una institucion geologica central y de un museo nacional, el instituto ha adoptado informalmente estas dos responsabilidades, aunandolas a su funcion primaria como una institucion universitaria de investigacion científica, De suerte que su naturaleza es "sui generis". Este triple papel se refleja en los distintos departamentos que lo integran.

El departamento de paleontología tiene como objetivo central, estudios bioestratigraficos y paleontologicos de varias regiones y grupos. Se desarrollan programas de Paleontología de varias regiones y grupos.Se desarrollan programas de Paleontología de invertebrados, Vertebrados, Micropaleontología y Paleobotánica.

El Programa de Paleontología de Invertebrados incluye estudios sistemáticos de gasterópodos, pelecípodos, equinodermos, corales, amonitas y braquiópodos meso y cenozoicos principalmente, así como estudios bioestratigráficos en varias regiones tales como Baja California, La Cuenca Mixteca, el Sureste de Mèxico y la Planicie Costera.

El Programa de Paleontología de Vertebrados incluye estudios faunísticos, de tiburones y mamíferos principalmente y estudios bioestratigráficos en Baja California, La Añltiplanicie Mexicana el Sureste de México y algunas cuencas INtermontanas de la Sierra Madre Oriental. La naturaleza exploratoria y prospectiva del trabajo, obliga a la descripción de material muy diverso.

El Programa de Micropaleontología tiene sus énfasis en estudios faunísticos y bioestratigráficos sobre ostrácodos y foraminíferos cenozoicos de la Planicie Costera del Golfo y de la Península de Baja California.

El programa de Paleobotánica incluye estudios paleoflorísticos en las cuencas carboníferas cretácicas de Coahuila, Jurásicas de Oaxaca; paleofloras triásicas de Sonora e Hidalgo y reciente mente,ficoflora precámbricas en Sonora. En el Departamento de Geología, se desarrollan estudios palinoestratigráficos de Coa huila y Sonora, así como foraminiferoestratigráficos en Baja California y Sonora.

Además de estos, el Departamento de Paleontología tiene a su cargo el Museo, que funge como Depositario Nacional de facto de los fósiles mexicanos, particularmente de los tipos. El Museo de Paleontología aloja la colección de fósiles más extensa del país e incluye más de 500 000 ejemplares.

EVALUACION Y CONSIDERACIONES GENERALES.

Debido a que el número de paleontólogos ha sido siempre muy reducido y se ha visto obligado a laborar en condiciones y pro gramas de investigación, subordinados a otros objetivos, no se ha dispuesto ni de la masa crítica ni de la libertad de acción para desarrollar programas ambiciosos de Investigación paleontológica básica; en consecuencia, gran parte de la paleobiota mexicana es desconocida. De ahí que una gran cantidad de trabajo descriptivo-sistemático permanezca por hacer, que seguramente mantendrá ocupada a la comunidad paleontológica por mucho tiempo. Por ejemplo, el desarrollo de la Paleontología de Vertebrados, está principalemente en la fase prospectiva. El problema es importante, por que no se cuentan con especialistas en varios grupos importantes y la tasa de crecimiento de la comunidad es relativamente baja.

En cambio la Paleontología de Invertebrados es la más desarrolla da, principalmente debido a su relación ovia con la geología petrolera.

Se necesita desarrollar una gran cantidad de trabajo bioestrati gráfico, para producir cartas de correlación más confiables, esquemas detallados de zonación, mapas de bioespecies, etc. De hecho el Cenozoico Continental no ha sido subdividido estrati graficamente.

A pesar de la gran cantidad de trabajo descriptivo que de necesi dad se realiza, se está desarrollando investigación avanzada en algunas áreas tales como morfología funcional de tiburones, patrones de distribución en mamíferos y moluscos, modelos paleoe cológicos, taxonomia teórica y filogenia, entre otros.

La comunidad Paleontológica está consciente de la enorme signifi cación de México, para verificar hipótesis o buscar soluciones a problemas cienfíficos trascendentes tales como, biogeográfia regional de diversos grupos, rutas de dispersión; orígen radia ción adaptativa y dispersión de ciertos grupos, cambios climáti cos latitudinalmente relacionados, endemicidad y distribución extrema de ciertos grupos; evolución y tectónica regional, recon strucciones paleogeográficas y palinepásticas, etc.

Como un ejemplo de las amplias implicaciones del trabajo paleon tológico que se realiza actualmente, se resumirá uno (Ferrusquía et al., 1978 (1981)), en el que el autor estuvo directamente involucrado: "Las Huellas de dinosaurios más australes de Norteamérica y su significación geobiológica."

En Playa Azul, Michoacán aflora una secuencia volcanosedimentaria ¿Jurásica media-cretásica temprana? constituida por derrames andesíticos, piroclastitas riolíticas, biomicritas marinas someras y filovolcarenitas rojas inmaduras, buzan al SSE y están intrusionadas por mantos, "stocks" pequeños y diques que muestran plegamientos y fallamientos. Este es el primer hallazgo de rocas vulcanosedimentarias principalmente continentales de edad jurásico-cretásica en el margén pacífico de México.

La dinosaurichnofauna incluye siete morfotipos asignables a terópodos y ornitópodos; constituye un primer registro de sauricnitas en Méwxico y es el más meridional en Norteamerica; testifica la comunidad de dinosaurofauna Norteamericana del Jurásico Medio-Cretásico Temprano por lo menos hasta el Sur de Michoacan y concomitantemente, a la continuidad territorial que hizo posible esta extensión faunística.

Los resultados de estas investigaciones se publican principalmente en las series del Instituto: Revista, Boletín y Paleontología Mexicana, algunos estudios se publican en revistas extranjeras.

EL FUTURO DE LA PALEONTOLOGIA EN MEXICO.

Aunque es difícil hacer afirmaciones definitivas, examinando las necesidades principales, es posible plantear algunas expectativas plausibles:

1.- Considerando que hay deficiencias importantes de personal para cubrir algunos grupos, tópicos y áreas, resulta imprescindible generarlo.

2.- La gran cantidad de trabajo sistemático-descriptivo por hacer, mantendrá a la comunidad paleontológica ocupada por muchas décadas.Por tanto el trabajo futuro continuarà enfatizando este aspecto.

3.- El trabajo bioestratigráfico que falta también es enorme, consecuentemente, se enfatizarà en la futura labor tendiente a desarrollar y perfeccionar la zonación bioestratigráfica y la correlación.

4.- A pesar de esto, es deseable promover el desarrollo de investigación avanzada,para realizar una síntesis conceptual significativa y no quedar a la zaga en esta disciplina científica.

5.-Todo ello será posible en la medida que la comunidad paleontológica desarrolle una estrategia que libere de su papel subordinado entre las Ciencias de la Tierra, así podrá avocarse al planteamiento de programas ambiciosos de alcance nacional y cooperación internacional, que aseguren el desarrollo armonioso y balanceado de las distintas especialidades paleontológicas, el ataque de problemas relevantes por sí mismos o por su relación con el desarrollo socioeconomico del país y la generación del personal debidamente entrenado, al ritimo idóneo.

6.-Para ello se debe cambiar inteligentemente la importación de personal extranjero, el entrenamiento formal dentro y fuera del país, de personal nacional seriamente interesado y el establecimiento de programasde cooperación internacional, con países que cuenten con una comunidad paleontológica apmpliamente desarrollada. Los mejores programas incluirían entrenamiento e investigación suplementaria en áreas o tópicos en donde se han detectado problemas específicos relevantes, pero, no se cuenta con especialistas. Tambièn se podrían intercambiar especialistas, para resolver problemas inmediatos.

7.- En último término, pero no de menor importancia es el contar recursos materiales y una infraestructura adecuada, que permita a la comunidad paleontológica desarrollarse y enfrentar exitosamente el reto que representan las tareas señaladas. La cominidad debe avocarse a esto.

SUMARIO Y CONCLUSIONES.

1.-El marco geológico, la organización de comunidad geológica y el desarrollo socioeconómico del país, han determinado en gran medida la naturaleza de los estudios paleontológicos en México.

2.-Las rocas calcáreas jurásicsas y crétasicas son las más abundantes fosíliferas y también las de mayor interés petrolero, consecuentemente, en torno a ellas se ha desarrollado la mayoría del trabajo paleontológico.

3.-De las diez instituciones geológicas principales de México, solamente en dos se desarrolla investigación básica; ésta incluye Paleontología.

4.-Unicamente el 4% (unos 100) de los geológos que trabajan en México, se dedica profesionalmente a la Paleontología; la mayoría están en PEMEX, IMP y el IG.

5.- El Instituto de Geología desarrolla programas de investigación en Paleontología de Invertebrados, Vertebrados, Micropaleontología, Paleobótanica y Palinología; cuenta también con el Muse Nacional, poseedor de la más extensa colección paleontológica del país.

6.-Debido a la gran necesidad de trabajo sistemático y bioestratigráfico básico por hacer, las publicaciones actuales y futuras de la comunidad paleontológica mexicana enfatizarán estos aspectos.

7.-Un programa de cooperación internacional que involucre entrenamiento e investigación suplementaria, sería el más adecuado para desarrollar completamente y breve, la Ciencia de la Paleontología en México.

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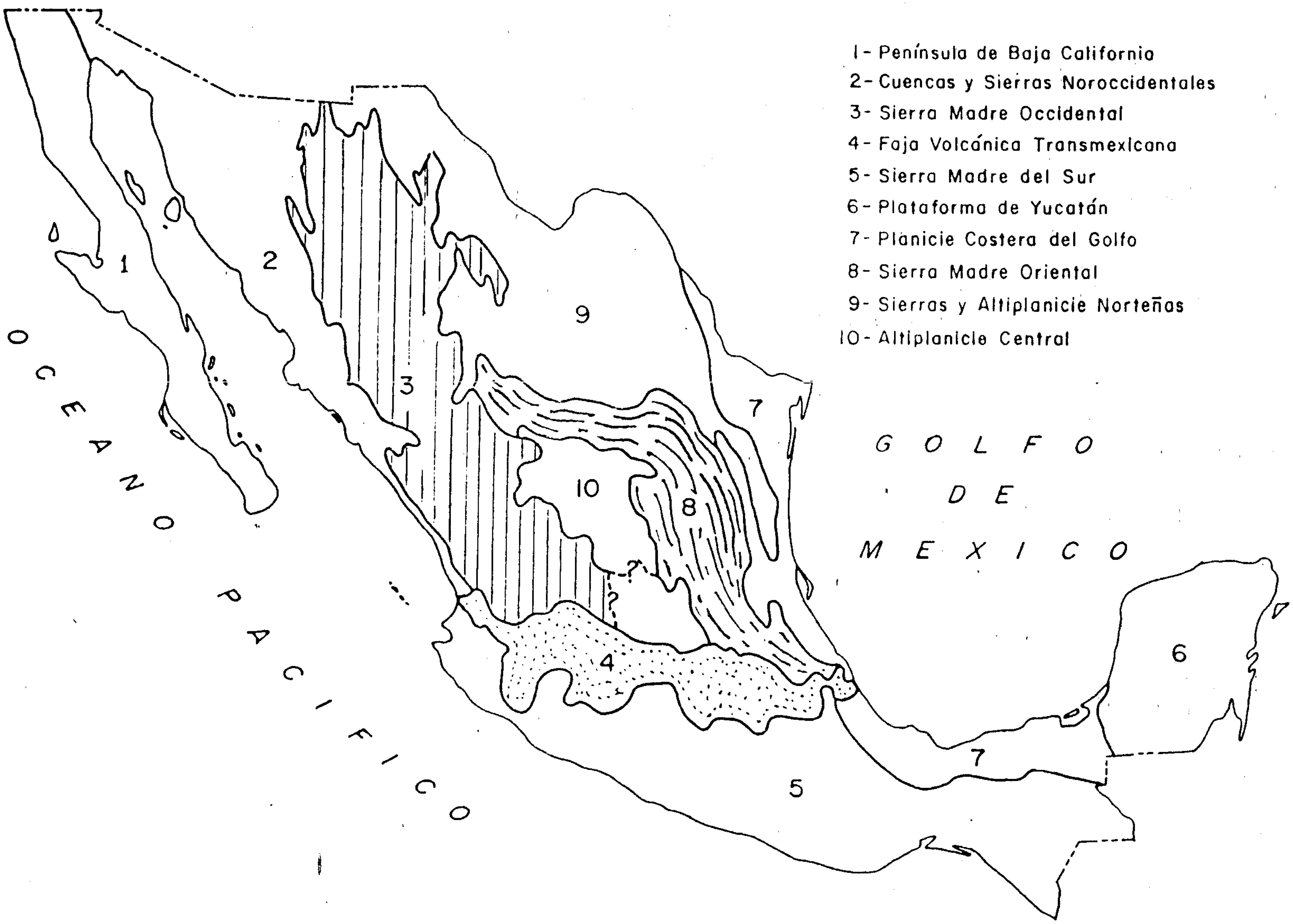
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