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Rhaeto-Liassic Mammals from Switzerland and West Germany

BY

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With 5 text figures and plates 10—12

ABSTRACT

European mammals and advanced mammal-like reptiles of Rhaeto-Liassic (Late Triassic-Early Jurassic) age are now known from localities in Switzerland, West Germany (BRD), France, and Great Britain. The Rhaetic bonebeds at Hallau, Switzerland, and in Baden-Württemberg, southwestern West Germany, contain samples of the animals that lived on the deltas and other coastal regions along the northwestern flank of the Vindelizian High, a continental area covering parts of northern Switzerland and southern West Germany. During the Rhaetian and early Liassic large parts of northwestern Europe were inundated by marine transgressions from the west and south creating an ephemeral archipelago that was largely submerged later in the Jurassic. Differences in known representation of mammals in Rhaeto-Liassic local faunas of northwestern Europe probably reflect: 1) small sample sizes of some local faunas, 2) differences in age within the Rhaeto-Liassic interval, and 3) the evolutionary diversification of insular faunas. Rhaetic bonebed local faunas of Hallau and Baden-Württemberg are known to include haramiyids, vertebrates of uncertain but probably mammalian affinities. *Morganucodon* (Mammalia, Triconodonta) is represented at Hallau by a new species. Two other new mammalian species in the Hallau local fauna are referable to new genera. One is provisionally allocated to the Morganucodontidae; the other is not referable to any previously known family or order. *Tricuspes* (?Mammalia) is recorded from Rhaetic bonebeds at Hallau and in Baden-Württemberg. Tritylodontids (Reptilia, Synapsida), present in several Rhaetic bonebed local faunas of Baden-Württemberg, are not part of the Hallau local fauna.

The taxonomic diversity of mammals now known from a very few samples of Rhaetian and Liassic age strongly suggests the time of origin of the Mammalia was significantly earlier in the Triassic.

KURZFASSUNG

Europäische Säugetiere und fortschrittliche säugetierähnliche Reptilien des Räto-Lias (Obertrias — Unterjura) sind jetzt von Lokalitäten in der Schweiz, Westdeutschland (BRD), Frankreich und Großbritannien bekannt. Die Rät-Bonebeds von Hallau (Schweiz) und Baden-Württemberg (Südwest-Deutschland) enthalten Reste von Wirbeltieren, die in Delta- oder anderen Küstengebieten entlang der Nordwest-Flanke des Vindelizischen Landes, eines kontinentalen Gebietes im Bereich der heutigen Nordschweiz und des südlichen Westdeutschland lebten. Während des Rät und tieferen Lias waren weite Teile von Nordwesteuropa durch marine Transgressionen von Westen und Süden überflutet. Sie schufen einen vorübergehenden Archipel, der im höheren Jura weitgehend wieder versank. Unterschiede innerhalb der bisher bekannten Vorkommen von Säugetieren in den rätoliassischen Lokalfaunen von Nordwest-Europa spiegeln wahrscheinlich wider: 1. kleine Probengröße einiger Lokalfaunen, 2. Altersunterschiede innerhalb der Zeitspanne des Rätolias und 3. eine stammesgeschichtliche Differenzierung in Inselfaunen.

Lokalfaunen aus den Rät-Bonebeds von Hallau und Baden-Württemberg enthielten nach bisheriger Kenntnis Haramiyiden und Wirbeltiere von unsicherer, aber wahrscheinlicher Säugetierzugehörigkeit. *Morganucodon* (Mammalia, Triconodonta) ist in Hallau durch eine neue Art vertreten. Zwei weitere neue Säugetierarten werden auf neue Gattungen bezogen. Eine wird

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vorläufig zu den Morganucondontidae gestellt; die andere ist mit keiner anderen bisher bekannten Familie oder Ordnung vergleichbar. *Tricuspes* (?Mammalia) wird aus den Rät-Bonebeds von Hallau und Baden-Württemberg nachgewiesen. Tritylodontiden (Reptilia, Synapsida), die in einigen Lokalfaunen der Rät-Bonebeds Baden-Württembergs vorkommen, fehlen in Hallau. Die taxonomische Vielfalt von Säugetieren, die bis jetzt von sehr wenigen Proben des Rät und Lias bekannt sind, spricht sehr dafür, daß die Entstehungszeit der Säugetiere auf jeden Fall in einen deutlich früheren Abschnitt der Trias fällt.

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INTRODUCTION

Mesozoic mammals were for the most part minute creatures in comparison to the dinosaurs and their other reptilian contemporaries. Even under the best of conditions their tiny bones and teeth are rarely seen as they weather out of the entombing sediments. About the middle of the 19th Century two vertebrate paleontologists, Prof. T. Plieninger of Stuttgart and Charles Moore of Bath, undertook research on natural concentrations of fragmentary small bones thought to be of Late Triassic age. Each of them washed the fossiliferous sediments in screens to remove as much of the associated sand and mud as possible. This separated the fossils and produced an even richer concentrate for sorting. Thus the screen washing technique of collecting fossil vertebrates got its start.

With rare exceptions, in the following years of the 19th and early 20th centuries collectors focused their attention on the mighty and gigantic vertebrates of the past. Remains of smaller, mouse-sized animals were found, but frequently these were almost accidental by-products of the search for larger animals. Almost a century later Profs. W. Kühne, C. W. Hibbard, and a few others championed the inclusion of screen washing in the basic repertoire of collecting techniques. Modern modifications of these techniques and improvement of equipment now permit recovery of minute fossils even when they occur in very low densities in the sediments.

After Plieninger's work many years elapsed before additional specimens of mammals and advanced mammal-like reptiles were recovered from the Rhaetic bonebeds of Baden-Württemberg. The next collecting programs were those carried out by E. von Huene and, later, Prof. O. H. Schindewolf. The entire collection of mammalian fossils from Hallau was obtained by Prof. B. Peyer who devoted many years to the processing of screen washing concentrates obtained from rock collected in 1942.

In 1956 Prof. Peyer published a monograph on mammals and reptiles from the Rhaetic bonebed at Hallau. This was an interim report based on the collection available in 1951. Sorting of the screen washing concentrates from Hallau was continued and, ultimately, almost doubled the size of the sample.

My involvement in research on the mammals from Hallau began in 1961. A postdoctoral fellowship from the National Science Foundation made it possible for me to visit Zürich where Prof. Peyer introduced me to his work. Unfortunately Prof. Peyer died in 1963 before he could complete his projected study. In 1974-75, thanks to a fellowship from the John Simon Guggenheim Memorial Foundation, I was able to return to Europe. Prof. E. Kuhn-Schnyder graciously made the collections from Hallau available for my study. Also it was possible to review the pertinent collections of Rhaetic mammals and advanced mammal-like reptiles from sites in adjacent parts of Baden-Württemberg. These, like the collections from Hallau, had yet to be analyzed in light of the flood of new data coming from research on the Rhaeto-Liassic local faunas of southern Wales. An award from the Alexander-von-Humboldt-Stiftung, the hospitality of the Institut für Paläontologie und historische Geologie, Universität München, and a leave of absence from the University of California Berkeley made it possible for me to return to Europe in 1978-79 and provided the freedom and support necessary to finish my research.

Designation of specimens

The fossils considered here are elements of several different collections and, over the years of the past century, some have been left without specific museum catalogue designations; others have been given several different catalogue numbers. The following are utilized in this paper:

Fossils in the Charles Moore collection, Bath Geology Museum, Bath, England, are identified by a three digit number with the letter C or M as a prefix.

Elements of the collections of the Institut und Museum für Geologie und Paläontologie, Universität Tübingen, have the prefix G. I. T.

In his monograph Peyer (1956) identified fossils from Hallau in the collections of the Paläontologisches Institut und Museum der Universität Zürich with Roman numerals. The same numerical designations, although written in arabic numerals, were used to identify the figures in the plates of his monograph. Fossils collected after the completion of the monograph were numbered separately and sequentially with arabic numerals. These designations are recorded here as NC (= new collection) 1, 2, etc. Subsequently the entire collection was recurated and the fossils given sequential numbers, in arabic numerals, with the prefix AIII.

In the descriptions of the fossils from Hallau these catalogue data are summarized at least in the lists of referred material. In parentheses after the current catalogue number the reader will find either Peyer's designation of the specimen in Roman numerals followed by a reference to the Tafel in his monograph (Peyer, 1956) on which it is illustrated, or its NC number in the new, hitherto unpublished collection.

Abbreviations

The following abbreviations have been used:

CV = coefficient of variation
M = mean
N = number
OR = observed range of variation
S = standard deviation

Acknowledgements

My involvement in studies of European Mesozoic mammals began in the academic year 1960-61 when, supported by a National Science Foundation postdoctoral fellowship, I was able to work with Dr. Kenneth Kermack at University College London. In following years I have been fortunate in being able to return to Europe and continue my research and education. Many colleagues and institutions have contributed to this and to all those named here and many others I am deeply grateful.

This paper is focused on the collections of mammalian fossils from northern Switzerland and Baden-Württemberg. For permission to study the collection from Hallau, information and advice, and provision of excellent research facilities during my visits, I wish to thank Prof. Drs. B. Peyer, E. Kuhn-Schnyder, and H. Rieber, and Dr. K. A. Hünermann of the Paläontologisches Institut und Museum der Universität Zürich. Dr. R. Schlatter, Museum zur Allerheiligen, provided considerable information concerning the geological setting of the Hallau bonebed.

At the Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Drs. F. Westphal and W.-E. Reif assisted me in my review of the collections. Dr. C. Hemleben arranged for preparation of scanning electron microscope pictures of several fossils. Dr. R. Wild, Staatliches Museum für Naturkunde, Stuttgart, helped me in both recapitulating the history of the type of *Thomasia antiqua* and exploring the possibility that some of the minute teeth found in Rhaetic bonebeds might be from the dentitions of pterosaurs. Also, my sincere thanks go to Dr. Denise Sigogneau-Russell, Institut de Paléontologie, Paris for discussions and the opportunity to review her recent discoveries at Saint-Nicolas-du-Port.

Many British colleagues have helped me, in particular I would acknowledge Drs. K. A. and D. M. Kermack, Frances Mussett, and Patricia M. Lees not only for the opportunity to study material in the collections of University College London, but also for the many days spent with them at fossil localities in southern Wales and southwestern Britain. Drs. R. Parrington and K. Joysey gave me access to collections in the Zoology Museum, Cambridge University. Prof. P. M. Butler, Royal Holloway College — my host during a year spent in England on a John Simon Guggenheim Fellowship — and Dr. R. J. G. Savage, University of Bristol, gave me access to collections and provided stimulating discussions. Mr. R. F. Pickford, Bath Geological Museum, helped in my review of the Charles Moore collection.

The shaded drawings in the plates are the work of Mr. A. J. Lee. Their preparation was made possible by a grant from the Annie M. Alexander Endowment, Museum of Paleontology, University of California Berkeley.

It is a great pleasure to acknowledge my hosts who made it possible for me to work at the Institut für Paläontologie und historische Geologie, Universität München during the 1978-79 acadmic year. Prof. Drs. Volker Fahlbusch and Richard Dehm invited me to work at the institute. I am deeply greatful to them and to Prof. Dr. Dietrich Herm and Dr. Peter Wellnhofer not only for professional assistance that greatly advanced my studies, but also the warm hospitality they extended to me and my family making it a memorable stay. Finally, I wish to express my sincere thanks and deep appreciation to the Alexander von Humboldt-Stiftung for both providing me with a "Senior U. S. Scientist Award" and their continuing interest that added highlights to our year in Germany.

GEOLOGY AND PALEOGEOGRAPHY

In a recent review of the Mesozoic records of mammalian evolution (Clemens et al., 1979) several fossil localities in northwestern and central Europe that have yielded the remains of primitive mammals and advanced mammal-like reptiles were grouped under the heading of sites of Late Triassic or Early Jurassic age. These included the Rhaetic bonebeds at Hallau, Switzerland, and in the Tübingen-Stuttgart area of West Germany (BRD), a locality in the vicinity of Nancy, France, and fossiliferous fissure fillings in western England and Wales. Goals of the research project reported here included reevaluation of the data available in the literature concerning the German and Swiss localities in order: 1) to arrive at a more precise determination of their relative ages and their temporal relationships to the French and British sites; 2) to summarize what is known of their taphonomy; and 3) to place these local faunas in the context of the major and rapid changes that occurred in the paleogeography of Europe during the Late Triassic and Early Jurassic. In following sections of this chapter these data on the Swiss and German sites are summarized and followed by a brief resumé of information concerning the French and British localities. For various reasons it was not possible to reopen and restudy the geological settings of the localities in Switzerland and Germany.

The results of this review were far from satisfactory. Clearly the period of earth history under consideration is of short duration. The fossiliferous deposits of interest are within the so-called Germanic geological province (e. g., see BRINKMAN, 1960) that during the Late Triassic was a largely continental area and primarily a site of erosion or deposition of terrestrial or shallow-water marine sediments. Contemporaneously, to the south in Tethys, considerable thicknesses of marine sediments accumulated. The Rhaetian was typified in this Tethyian (or Alpine) province.

Development of understanding of the evolution of the Germanic province and its faunas has been impeded by several obstacles. Possibly the most basic is the proclivity of many workers to avoid distinguishing between lithologic, biostratigraphic, chronostratigraphic, and chronologic units (see AGER, 1970). Thus Mittlerer Keuper, or Middle Keuper, for example, can be a designation for a very specific sequence of deposits in the Keuper basin of southwestern Germany (BRD), a chronostratigraphic designation for rocks deposited during the middle of the Late Triassic, a designation for middle Late Triassic time, or some mixture of these concepts (note PEARSON, 1970). Currently many workers utilize a sequence of stages/ages based upon studies of the Tethyian Triassic sequence as a standard scale of reference (note papers in ZAPFE, 1974a, for example). However there are uncertainties and disagreements concerning the definition of Rhaetian and Norian in the Tethyian province and utilization of these units in the Germanic province (note PEARSON, 1970, TOZER, 1974, ZAPFE, 1974a, and references cited). Palynological studies (note SCHUURMAN, 1979) and research on ostracods (note WILL, 1969) offer promise of surmounting correlation problems, but their resolution remains a goal for future research. Without precise correlations it is impossible to closely interrelate the evolution of the terrestrial fauna with the physical changes in the Germanic province, which was largely submerged during the Rhaeto-Liassic transgression. What has emerged from this work is a cloudy, hypothetical picture of their coevolution.

For the purposes of this paper the following concepts and units will be utilized with limited meanings. These choices reflect a geographic bias. The Swiss and German bonebed sites, which are the focus of this report, were formed as the Keuper basin of southwestern Germany and northern Switzerland was being filled and then flooded during the close of the Triassic and beginning of the Jurassic. Definitions of these concepts and units currently utilized by some workers in this part of central Europe are favored with the recognition that they can have significantly different meanings in other areas and for other workers.

Hettangian: The base of the Hettangian (frequently equated with the beginnings of the Liassic and Jurassic) will be taken as the beginning of the *Psiloceras planorbis* Zone. In this and in choice of subsequent, younger units of the Liassic the scale presented by ULRICHS (1977) for use in southwestern Germany is followed. This definition of the base of the Hettangian (or Lias) differs from that used by other workers in northwestern Germany (e. g., WILL, 1969) and suggested for international adoption (e. g., PEARSON, 1970) in which a Pre-*planorbis* Zone or Beds is recognized as the basal unit of the Hettangian.

Rhaetian: The complex history of the concept of the Rhaetian has been reviewed by PEARSON (1970, also see TOZER, 1974, WIEDMANN, 1974, ZAPFE, 1974b, and SCHUURMAN, 1979). Currently there is an unresolved debate over whether the Rhaetian is properly recognized as an age between the older Norian and the Hettangian or is simply coeval with part of the Norian.

Correlations have been attempted between the type region of the Rhaetian in the Tethyian province and sections containing shallow water to brackish marine deposits formed in a different faunal realm in northwestern Germany (see WILL, 1969, and SCHUURMAN, 1979). In Baden-Württemberg Rhaetic, Rät, or Upper Keuper, appear to have been used most frequently to designate the sediments, contained faunas, and/or an interval of time between the termination of deposition of the Middle Keuper and the lowest stratigraphic occurrence of beds containing a Liassic marine fauna. GEYER and GWINNER (1968) present a generalized Rät section for Baden-Württemberg dividing it into an Oberrät or *Triletes*-Schichten and an Unterrät or *contorta*-Schichten. On lithologic grounds the bonebeds of the Tübingen-Stuttgart area might be included in the Unterrät (AEPLER, 1974). How the times of formation of the Rhaetic bonebeds in the Tübingen region relate to the times of deposition of the Hallau bonebed, the Lower Rhaetic of the Nancy region, and the Rhaetian sections of northern Germany, Britain, and the Tethyian province remain open questions.

Rhaetic: This term is used here in the limited sense of a lithostratigraphic name. As will be argued below, the time of formation of some Rhaetic bonebeds might not be Rhaetian.

Middle Keuper: The uppermost lithostratigraphic unit of this sequence in Baden-Württemberg is the Knollenmergel. BRENNER (1973) argued that it can be considered as an essentially isochronous unit of Norian age. How the time(s) of termination of deposition of the Knollenmergel relate to the Rhaetian-Norian boundary (or the Hettangian-Norian boundary for those who reject the Rhaetian Age) is not yet determined.

Rhaetic local faunas of the Tübingen-Stuttgart area

Although varying in thickness and sporatic in occurrence Rhaetic bonebeds are common elements of the Rhaetic Sandstone (Rhätsandstein) in the vicinity of Tübingen and Stuttgart and as far southwest as the region of Täbingen and Balingen (Fig. 1). Within this area the Rhaetic Sandstone is not a continuous unit but consists of a group of usually thin, lenticular bodies of sandstone separated by areas of Rhaetic Clay (Rhätton) or regions where Rhaetic deposits are lacking. Formation of the Rhaetic Sandstone has been attributed to the development of prograding deltas modified by longshore currents (AEPLER, 1974).

In 1847, after a painstaking search of minute fossils concentrated by washing bonebed samples from exposures south of Stuttgart at Degerloch and Steinenbronn, PLIENINGER announced his discovery of two mammal-like teeth. One is now the type of the haramiyid *Thomasia antiqua*; the other is a fragment of a tritylodont cheek tooth. For the following 86 years, until 1931, discoveries of specimens of Rhaetic mammals or advanced mammal-like reptiles in bonebeds of Baden-Württemberg appear to have been limited to the recovery of fragmentary teeth of tritylodontid therapsid reptiles. *Tritylodon fraasi* Lydekker, 1887, was typified on a tooth from Schlößlesmühle bei Steinenbronn; the type of *Chaleopotherium plieningeri* Ameghino 1903, might have come from the same site. HENNIG (1922) used a tooth from either Schlößlesmühle or Olgahain as the basis of his concept of *Oligokyphus triserialis* and a second specimen, certainly from Olgahain, was informally named *O. biserialis* (see KÜHNE, 1956). BRANCA (1915), HENNIG (1922) and SCHMIDT (1928) reviewed various aspects of the vertebrate fauna of the bonebeds. Finally, SIMPSON (1928) presented a thorough analysis of the small, pertinent sample in his monographic study of the Mesozoic mammals of Europe.

During the summer of 1931 E. VON HUENE prospected a series of natural and man-made exposures of Rhaetic bonebeds. Apparently she limited herself to those that could be easily disaggregated and utilized a binocular microscope to search through the material. Rhaetic bonebeds at Sonnenberg bei Degerloch, Gais-

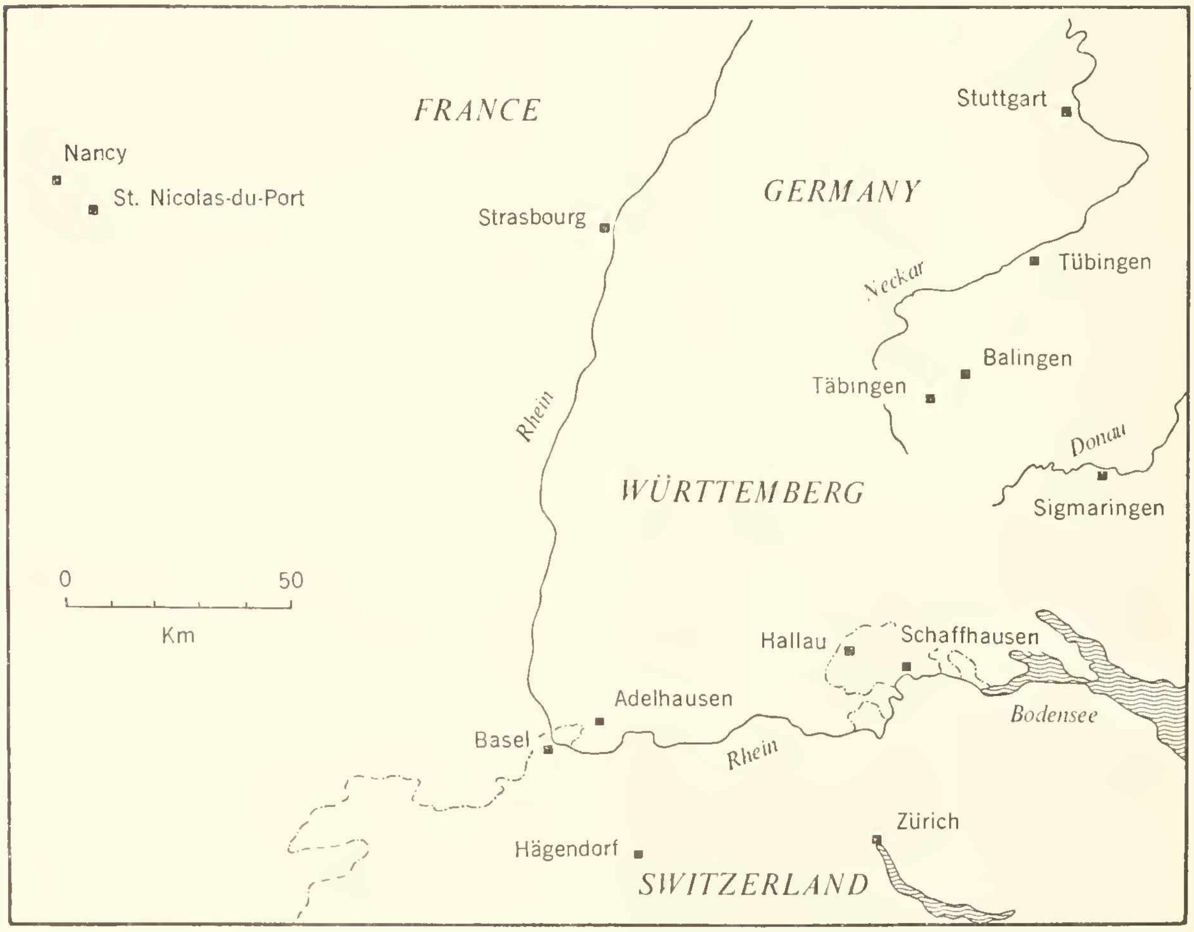

Figure 1: Sketch map of parts of northern Switzerland, southwestern Germany, and eastern France.

brunnen, and Olgahain proved to be the most productive. The results of her research were published two years later (E. VON HUENE, 1933).

Subsequently, the only major attempt to sample the microvertebrates of the Rhaetic bonebeds in the Tübingen-Stuttgart area appears to have been that undertaken by Prof. O. H. SCHINDEWOLF of Tübingen. Bonebed material was collected at Gaisbrunnen in 1947 and at Olgahain in 1948. Material from Olgahain was disaggregated and a fossiliferous fraction concentrated by use of heavy liquid flotation. This concentrate was subdivided by use of a series of screens; the smallest was 0.5 mm mesh. Only part of these concentrates have been sorted.

Since 1933 a few publications have dealt with the mammals or advanced mammal-like reptiles from the Rhaetic bonebeds of Baden-Württemberg. BUTLER (1939) and KÜHNE (note particularly 1950, 1956) considered the morphology and taxonomy of European tritylodonts. KÜHNE (1950) concluded that *Mucrotherium cingulatum* E. VON HUENE and *Uniserium enigmaticum* E. VON HUENE were based on fragmentary teeth of a tritylodont, probably *Oligokyphus*. Currently the specimens from the Rhaetic bonebeds of Baden-Württemberg appear to document the presence of no more than one species for which the name *Oligokyphus triserialis* is appropriate. It should be noted that KÜHNE (1956) justified recognition of two new species of *Oligokyphus*, *O. major* and *O. minor*, members of the Windsor Hill local fauna of England, on apparent differences in the geological ages of the English and German sites and absence of sufficient data demonstrating identity. HAHN (1973), in his review of the haramiyids found in Germany (BRD and DDR), described two teeth found in the collections made under the direction of Prof. SCHINDEWOLF.

As discussed in the following section on haramiyids, Schlößlesmühle bei Steinenbronn, once thought to be the type locality of *Thomasia antiqua*, can no longer be listed among the Rhaetic bonebed sites of Baden-Württemberg yielding remains of mammals or advanced mammal-like reptiles other than tritylodonts. HENNIG (1922, Section D) reported additional discoveries of "mammalian teeth" from various localities, some known e. g., Hohenheim and the valley of Goldersbach near Bebenhausen, and others not recorded. For various reasons — the specimens were not described in sufficient detail and now are lost or were shown to be referable to other kinds of vertebrates — these will not be considered further. However, they, other lost fossils (e. g., ZAHN G_2, E. VON HUENE, 1933), and the small number of specimens of mammals and mammal-like reptiles now available for study suggest that the current sample surely does not document the diversity of these animals in the Rhaetic bonebed fauna. These rare fossils of mammals and mammal-like reptiles (excluding teeth of tritylodonts) are now known certainly from just three localities in Baden-Württemberg:

Gaisbrunnen: The collecting locality was in a quarry in the Rhaetic Sandstone lying between Bebenhausen and Waldhausen, approximately 3.5 km north of Tübingen. Although giving a description of the lithology of the Rhaetic Sandstone, E. VON HUENE (1933) did not pay equal attention to the subjacent and superjacent strata. She noted the occurrence of four pelycepods *(Pecten acutauritis, ?Myoconcha beyrichi, Modiola minima,* and *Cardita praecursor)* and two ammonites, both represented by specimens of juvenile individuals *(Psiloceras [Waehneroceras]* sp. and *?Psilophyllites* sp.) in the bonebed. The lithology of the Rhaetic Sandstone was analyzed by AEPLER (1974).

The Geologische Karte von Tübingen und Umgebung (1969, 1:50,000, Geol. Landesamt Baden-Württemberg) shows that in the immediate vicinity of Gaisbrunnen the Rhaetic Sandstone lies on the Knollenmergel and is overlain by Lias α_{1+2}. ALTMAN (1965) described two nearby sections. In one (Section 35) approximately 2 km southsoutheast of Gaisbrunnen, a limestone directly above the Rheatic Sandstone yielded a fragment of *Psiloceras (Curviceras)* aff. *subangulare*. In a second (Section 37) approximately 1 km northwest of Gaisbrunnen the Rhaetic Sandstone is overlain by 2—5 cm of unfossiliferous marl. On top of the marl is a limestone. Altman (ibid.) reported the occurrence of *Psiloceras planorbis* and *Psiloceras plicatulum* in the lower part of the limestone. At higher levels he found *Psiloceras (Caloceras) johnstoni* and *Psiloceras (Curviceras?)*.

Olgahain: E. VON HUENE (1933) noted that her collections came from part of the Rhaetic bonebed exposed by the toppling of a large tree on the slopes of Kirnberg above Olgahain, approximately 1 km east of Gaisbrunnen. Again, although discussing the lithology of the bonebed and Rhaetic Sandstone, she did not review its geological setting. Probably it is similar to that of Gaisbrunnen. Shells of two kinds of pelecypods *(Modiola minima* and *Leda deffneri)* were identified but she did not recover any remains of ammonites.

Sonnenberg bei Degerloch: This collecting area is approximately 25 km northnortheast of Tübingen in the suburbs of Stuttgart. HAAG (1928) relocated the site where PLIENINGER presumably discovered the type of *Thomasia antiqua* and described a second section exposed about 500 m to the southsouthwest near Sonnenberg. A few years later E. VON HUENE (1933) noted that this second section was covered over but the overburden was removed in order to collect a sample. Thus the type of *Thomasia antiqua* and the fragment of a tooth collected by E. von Huene and here very tentatively referred to *Tricuspes tubingensis* probably came from different localities in the region of Degerloch.

E. von Huene (1933) gives a geological section that, though less detailed, can be reasonably correlated with Haag's (1928). Haag noted that the lowest unit exposed in the section was the Knollenmergel. The bonebed is shown to be overlain by: 1) a thin (1 cm) red-brown to yellow-brown earthy mass, 2) Liasmergel (up to 1 m) and, finally, 3) the first limestone of the Lias α. E. von Huene (ibid.) reported the discovery of a pelecypod, *Pecten actauritis*, and a juvenile individual of the ammonite *Psilophyllites* at Sonnenberg bei Degerloch.

At these three bonebed localities the Rhaetic Sandstone rests on the Knollenmergel, the stratigraphically highest unit of the Middle Keuper. The upper Middle Keuper was studied recently and intensively by Brenner (1973, 1978a, 1978b) from whose publications the following summary is drawn.

During deposition of the upper Middle Keuper, in the late Carnian and Norian, Baden-Württemberg and Kanton Schaffhausen lay in the southern part of the slowly but irregularly sinking German Keuper Basin (note Brenner, 1973, Abb. 19). One area of relatively greater subsidence within this basin was centered in the region just north of Sigmaringen (Fig. 1). The sites of the fossil localities in the Tübingen-Stuttgart area considered here lay in the northern part of this area of subsidence; Hallau (Kt. Schaffhausen) in the southern part. Sheet floods transported sediments to the most rapidly sinking parts of the basin, which apparently was quickly leveled. Brenner (1978a) suggested annual precipitation increased during the deposition of the Knollenmergel and the climate became semiarid to subhumid (annual precipitation 250 to 450 mm). Also, he (Brenner, 1973, note Tab. 2) treated the Knollenmergel as an essentially isochronous unit within the basin.

The genesis of bonebeds was studied in detail by Reif (see 1976), Aepler (see 1974), and their colleagues. These studies based on thorough sedimentological analyses, include a wide range of taphonomic considerations. In this work bonebeds were simply and generally defined as sediments with high concentrations of greatly fragmented and, usually, heavily rolled bones. Frequently the fragments of bone are well sorted and lie in the range of fine to coarse pebbles. Three categories of bonebeds were differentiated on the basis of their place and mode of origin:

Condensation bonebeds formed in shelf areas where the rate of sedimentation was low and fine sediments were winnowed away from the bones.

Placer bonebeds deposited in deltas and other sites of prograding sedimentation (e. g., channels).

Transgression bonebeds developed as lag deposits during marine transgressions.

Of the German and Swiss bonebeds considered in this report Gaisbrunnen and Sonnenberg bei Degerloch (Aepler, 1974) and, probably, Olgahain are placer bonebeds. Most likely the Hallau bonebed is a combination of a placer bonebed in part reworked during a marine transgression, but its genesis needs further analysis. Aepler's (ibid. and reports in preparation) studies focus on the genesis of the Rhaetic Sandstone and its bonebeds in the Tübingen area. The following points directly pertinent to this analysis were extracted from his work.

As already noted, the Rhaetic Sandstone occurs in lenticular bodies, each probably the deposit of a prograding delta modified by coastal longshore currents. The Rhaetic Sandstone delta in the vicinity of Tübingen is reconstructed as having had a low relief with its terrestrial area broken up by many channels and shallow lagoons. The streams forming these deltas are thought to have had their headwaters in low source areas to the south and/or east and carried a relatively small load of sediment, even in times of flood. They flowed generally northward emptying into the shallow sea that covered northwestern Germany during the Rhaetian. During development of this and other deltas sea level appears to have remained relatively constant.

Aepler (ibid., p. 147, also see Brenner, 1978a) summarized evidence suggesting that after the intensive aridity characteristic of most of Middle Keuper times annual precipitation increased and the climate became characterized by seasonal periods of intense rainfall resulting in occasional flooding. Although dune sands formed immediately along the coast, most of the delta surface and coastal area was well vegetated with major forests occurring upstream.

Formation of the placer bonebeds appears to have been a two-stage process. As the animals living in and around the streams and lagoons on the delta died their skeletons settled in or were brought into these water bodies. Initial fragmentation was primarily the result of the activities of carnivores and scavengers. Once submerged, the bones and teeth permineralized by uptake of phosphates provided by decay of organic material. The water in streams and lagoons on the delta usually was either calm or slow moving. Only the finest particles were winnowed away and a relatively low amount of sediment was brought in from source areas. Condensation bonebeds formed on the delta surface. At times of flooding the permineralized bones and teeth were transported and further fragmented, hydrodynamically sorted, and then deposited as placer bonebeds in the channels or on the delta front. Possibly the process of reworking on the delta surface occurred several times before the bones and teeth were entombed in the foreset beds of the prograding delta.

This reconstruction of the sedimentary regime indicates the fossils concentrated in the placer bonebeds are a thanatocenose of the remains of aquatic (both freshwater and, possibly, marine) and terrestrial organisms.

Although the possibility that some of the heavily abraided fossils might be parts of mammals or mammal-like reptiles that lived along the upper reaches of the tributary streams and were washed down at times of flood cannot be entirely ruled out, it seems more likely they are parts of the inhabitants of the delta.

Determination of the geological age of the mammals and mammal-like reptiles whose remains are preserved in the bonebeds of the Rhaetic Sandstone in terms of the standard European time scale remains an unattained goal. This is not simply the result of problems of correlation between the Tethyian and Germanic provinces already noted, although these are major contributing factors. AEPLER (1974) argued that the development of a Rhaetic Sandstone delta was a slow, complex process; probably one encompassing tens if not hundreds of thousands of years. In this multistaged process many years might have passed between the time an animal died and parts of its skeleton were finally entombed in a bonebed. Thus, determination of the age of a bonebed only sets a minimum age for the time of existence of the animals represented in the deposit.

On the basis of data currently available maximum and minimum ages of the bonebeds at Gaisbrunnen, Olgahain, and Sonnenberg bei Degerloch can be established within a limited range. All three bonebeds are parts of deposits laid down upon the Knollenmergel. This is the uppermost unit of the Middle Keuper and, following BRENNER (1973), can be assigned a Norian age.

At the other extreme, the Tübingen-Stuttgart area was largely if not fully submerged by marine waters during the Hettangian. Although his geological sections do not include those of the Gaisbrunnen and Olgahain localities, ALTMAN (1965) reports *Psiloceras planorbis* and, slightly higher stratigraphically, *P. johnstoni*, from a nearby section. HAAG (1928) did not record what, if any, ammonites were recovered in the section at Sonnenberg bei Degerloch, but reported the bonebed was capped by strata of Lias α, i. e., early Hettangian.

AEPLER (1974) considered the implications of the discovery of fragments of juvenile ammonites in some bonebeds (e. g., those reported by E. VON HUENE (1933) from Gaisbrunnen and Sonnenberg bei Degerloch), and suggested that the time of formation of these bonebeds might be correlative with the Pre-*planorbis* Zone as recognized by WILL (1969) in the Liassic section of northwestern Germany.

Restudy of the Rhaetic bonebeds, particularly investigations focused on recovery of ostracods and palynological samples, might permit more refined correlations. However, currently available data only warrant delimitation of a range of possible ages. The mammals and advanced mammal-like reptiles represented in the bonebeds at Gaisbrunnen, Olgahain, and Sonnenberg bei Degerloch most likely are no younger than Hettangian. They might be of earliest Hettangian (Pre-*planorbis* or *Psiloceras planorbis* Zone), Rhaetian, or latest Norian age. Probably they are no older than Norian.

Hallau local fauna

The mammals and mammal-like reptiles of the Hallau local fauna are known from fossils found at a single locality in the Klettgau region of northern Switzerland to the west of Lake Constance (Fig. 1). The site, sometimes called Breitelen, is near the crest of the Hallauerberg immediately to the northwest of the town of Hallau (formerly designated Unter-Hallau), in the western part of Kanton Schaffhausen. Here the Rhaetic bonebed is not now exposed at the surface, but probably occurs over an area of at least 1 kilometer's length in a southwest to northeast direction above the vineyards of Hallau. Apparently this bonebed has only been seen in man-made excavations.

Knowledge of the geology of the Hallau and adjacent areas stems from and in many respects still is directly based upon results of the research of Bergrat Dr. Ferdinand SCHALCH. SCHALCH's interest in strata adjacent to the boundary between the Keuper and Lias is illustrated in his dissertation (SCHALCH, 1873). Then and for many years thereafter it was commonly held that Rhaetic bonebeds, or other Rhaetian deposits, were absent from geological sections in a large part of southwestern Germany (Baden-Württemberg) and northern Switzerland. However, to the northeast of a line drawn through Täbingen and Balingen in Baden-Württemberg (Fig. 1) deposits of Rhaetian age, including the Rhaetic bonebeds of the Tübingen-Stuttgart area, were known to be well developed. To the southwest of a line through Adelhausen in Baden-Württemberg and Hägendorf bei Solothurn in Switzerland Rhaetian deposits were also known to be present in the geological sections.

SCHALCH was attracted to the section on Hallauerberg by a paper by Prof. MERKLEIN (1809), a professor of natural history in the gymnasium in Schaffhausen, who noted that a Herr HENSLER reported a Keuper bonebed was encountered during construction of a road below the poor houses of Unter-Hallau (now the site of a Bürgerheim, a home for the aged). In 1915 this site had long been covered over but the widening of a farm road opened new exposures of Liassic deposits less than a kilometer from the spot where Hensler reported the bonebed. Schalch had a shaft sunk to a depth of approximately 3 m and exposed the geological section down to the Upper Triassic deposits. Part of this section included the following units (from Peyer, 1956, with emendations):

Schalch's alphabetic designations	Thickness (meters)	Unit
m	2.5	Arietenkalk
l	0.23	Angulatusbank
k	5.35	Schwaichel (an ugly colored, dark gray to brownish green, irregularly stratified, marly shale with many finely dispersed, calcareous, sandy inclusions
i	0.20	Upper Psilonotenbank
h	0.70	marly shale, resembling the Posidonienschiefer
g	0.14—0.17	Lower Psilonotenbank
f	0.04—0.05	black, impure marl with abundant Liassic fossils
e	1.00	loose marl bonebed with the same (vertebrate) fossils as unit d
d	0.25	compact Zanclodonmergel breccia with bonebed
c	0.80	Zanclodonmergel resembling unit a
b	0.20	beds with loaf-like calcareous nodules
a	2.00+?	ordinary, green and red-spotted Zanclodonmergel

At Schalch's invitation Peyer undertook analysis of the vertebrate fossils found in the bonebeds (units d and e). The blocks of compact bonebed (unit d) were broken mechanically for inspection. Portions of the friable sediment of unit e were spread out on tables, carefully sprayed with water, and then sorted with the aid of an eight or ten-power magnifying glass. Not surprisingly fragments of very small mammals or mammal-like reptiles were not discovered during this project, although the remains of many larger vertebrates were recovered (see Schalch and Peyer, 1919, and Peyer, 1944a, 1944b, 1956).

In the autumn of 1942 a second shaft was sunk in the vicinity of the earlier excavation. Over eight metric tons of bonebed (probably this weight is for material from unit e and excludes blocks of unit d [Peyer, 1944 b, p. 306]) was collected and taken to Zürich for preparation. The friable bonebed (unit e) was dried, washed through screens (the smallest with a 1 mm mesh [ibid.]) and the concentrates divided according to grain size prior to sorting. Samples of the material that passed through the smallest screen were checked without the discovery of indentifiable fragments of bones or teeth. The compact bonebed (unit d) was left outdoors over winter to break down and then processed and sorted. Sorting was carried out with a binocular microscope and, in later phases of the work, heavy liquids were employed to further concentrate the bone fragments. The first report on the mammalian and mammal-like reptile remains (Peyer, 1956) was based on material found up to 1951, prior to completion of sorting of the concentrates. Peyer began preparation of a second report dealing with materials collected subsequently, but unfortunately this study was not completed before his death. Except for a small amount of material preserved as lithological samples in the Paläontologisches Institut und Museum der Universität Zürich, all the rock collected by Peyer has now been broken down, processed and the concentrates sorted.

Schalch and Peyer (1919) present the most thorough, available analysis of the geological section exposed in the Hallau excavations. Peyer (1944b) added observations made during the 1942 excavation. The basal units (a through c) were first referred to the Zanclodonmergel, which is now considered an alternative name for the Knollenmergel (see Schalch, 1916, Peyer 1944 b, Brenner, 1973). This allocation was made on the basis of: 1) the position of the strata at the top of the extensive Middle Keuper section, which except for the Jurassic strata at the crest, forms most of the Hallauerberg, and 2) their lithology. Other than a small fragment of bone and another scrap of carbonaceous material (jet) no fossils were encountered in these units during the 1915 excavation. However, during the 1942 excavation bones of *Gresslyosaurus* were found in unit c of the Zanclodonmergel (Peyer, 1944 b). The Zanclodonmergel is interpreted as a unit deposited in nonmarine conditions and no evidence from the Hallau site is contradictory.

The bonebed (units d and e) lies directly on the Zanclodonmergel. Schalch and Peyer's (1919) initial basis for separating the two units was difference in the degree of cementation, the particles of unit d being bound together with a calcite or, rarely, barite cement while those of unit e were not cemented. Dominant particles of the bonebed are fragments of limestone and marl (usually small, 1 to 2 mm in diameter, but some were reported to reach a diameter of 16 mm). Almost all these appeared to be derived from the Zanclodonmergel. Only a few were lithologically distinct, but these could have been derived locally from lower units in the Middle Keuper. The absence of quartz was noteworthy.

In addition to fragments of limestones and marls SCHALCH and PEYER (ibid.) noted the bonebeds contain abundant carbonaceous fragments, pieces of bone, fish and reptilian vertebrae, teeth, and coprolites. PEYER (ibid.) provided the following list of genera and species identified from the collections made in 1915 (many fragments were not identifiable at the generic or specific levels):

Ceratodus parvus
Sargodon tomicus
Hybodus sp.
Hybodonchus sp. ?
Gresslyosaurus sp.
Termatosaurus albertii
Megalosaurus sp.

Also recovered were scales of ganoid fishes and bones of nothosaurids and labyrinthodonts.

Later work by PEYER (1956) demonstrated that the bonebed units (d and e) do not differ solely in hardness but also in faunal content. Unit d, the compact bonebed, lacks fragments of marine invertebrates and probably was formed in a freshwater or brackish environment prior to the time of the marine transgression of the Hallau area. In contrast, in addition to the vertebrate fossils, during the sorting of the concentrates obtained from the upper unit (e) fragments of shells of mollusks, parts of crinoid stems, and various skeletal elements of echinoderms were found. PEYER (ibid.) concluded these fossils represent animals that were part of a typical lower Liassic marine fauna. Unfortunately the presence of these fossils was not recognized during collection of the rock. Some of the invertebrates found in the concentrate might be contaminants, fossils that fell or were washed down from exposures of unit f within the shaft. Although aware of this possiblity, PEYER (1944 b) suggested that many if not most of them were derived from unit e.

Unit e now appears to be the product of partial reworking of unit d with addition of more material from the Zanclodonmergel during the transgression of the sea. Reworking of the Keuper deposits and bonebed continued in other regions providing sediment to the Hallau area until the beginning of deposition of the Upper Psilonotenbank (SCHALCH and PEYER, 1919, and PEYER, 1944 b).

I could not find any record distinguishing the fossils of mammals or mammal-like reptiles that came from unit d from those derived from unit e. Because rock from both units was processed by PEYER, it is reasonable to assume the rare teeth of these animals occurred or appeared to occur in both. If the simplifying, but not particularly justified assumption is made that these teeth occurred in a random distribution throughout units d and e, then probably the majority of the fossils collected came from unit e for a much greater volume of this unit was available and processed.

The structure and composition of the bonebeds give ample testimony to transport of material from other areas and reworking of the fragments of rock and vertebrate fossils. SCHALCH and PEYER (1919) and PEYER (1944 b) tried to assess the degree to which these process might have mixed materials from different geological or biological sources. In the first paper they note that some fragments of limestone and marl show heavy abrasion suggesting considerable movement in transportation or at the site of deposition, others do not. There is equal diversity in the preservation of the fossils. STROMER and PEYER (1917, p. 18) commented that material of *Ceratodus* from Hallau showed greater morphological detail and was more complete than the heavily water-worn specimens found in British Rhaetic deposits, e. g., Aust Cliff near Bristol, or bonebeds in the Tübingen-Stuttgart area.

In this study of the mammals and mammal-like reptiles from Hallau no consistent differences in mode of preservation or postmortem wear suggested a heterogeneous sample derived from two or more sources of distinctly different ages or distances from the site of deposition. Lacking evidence to the contrary it is tentatively assumed that these fossils can be treated as representing members of a single local fauna (sensu TEDFORD, 1970).

Although not a substitute for a thorough taphonomic analysis, which definitly is needed, the following scenario is suggested. The formation of the Hallau bonebed started with reworking of the uppermost Zanclodonmergel by fresh or brackish water. Remains of terrestrial and aquatic vertebrates, probably parts of the local riparian and aquatic fauna, were concentrated in a bonebed. What is left of this deposit is now designated unit d. During the transgression of the sea the upper part of the bonebed was reworked. Fragments of marine invertebrates and, possibly, freshwater or terrestrial organisms were introduced to produce unit e.

Expression of the time of deposition of the Hallau bonebed in terms of the units of a standard European chronological scale cannot be made directly or with great precision. SCHALCH and PEYER's (1919) assignment of a Rhaetian age sparked considerable debate (see PEYER, 1944 b). The second excavation at Hallau provided some new information, but still did not permit precise correlation. The currently available data pertinent to this question can be outlined as follows:

The Knollenmergel, traditionally termed the Zanclodonmergel in reports on the Hallau bonebed, is the uppermost unit of the Middle Keuper and thought to have been deposited in the Norian (Brenner, 1973). The discovery of bones of *Gresslyosaurus* in unit c is in accord with this view. Thus the age of the Hallau bonebeds appears to be no greater than Middle Keuper (Norian).

The compact, lower bonebed (unit d) lacks large invertebrates that could be the basis for a correlation. Fragmentary invertebrate fossils found in unit e included no specimens that have been identified as representing species of sufficient biostratigraphic utility for the refined correlations needed. Also, they might well represent organisms that lived after most or all of the vertebrates represented in the bonebed.

Peyer (1956) suggested the ganoid fish *Sargodon tomicus*, the dipnoan *Ceratodus parvus*, and haramiyids might serve as Rhaetian index fossils. Haramiyids are now known to have existed from the Middle Keuper (Hahn, 1973) into the Jurassic, possibly as late as Bathonian (see Clemens and Kielan-Jaworowska, 1979). Considering the kind of data on the biostratigraphic ranges of the fishes available to Peyer, their utility as index fossils must be regarded as warranting further testing. To the best of my knowledge studies of ostracods, other microinvertebrates, or paleobotanical material from the Hallau bonebeds have not yet been attempted and the results published.

The bonebed is overlain by a black, impure marl containing many fossils of Liassic marine invertebrates (fide Peyer, 1956). Shells of ammonites identifiable at the specific level were not discovered. However, in the overlying Lower Psilonotenbank (unit g) an ammonite referable to *Psiloceras* was discovered during the 1915 excavation. Prof. Pompeckj (quoted in Schalch and Peyer, 1919) identified it as an Laqueolusform of the *Psiloceras johnstoni* group. Allocation to *Psiloceras johnstoni* (or *P. [Caloceras] johnstoni)* apparently has not been subsequently modified.

Urlichs (1977) in his review of the Lower Jurassic of southwestern Germany recognized the *Psiloceras planorbis* Zone as the lowest zone of the Jurassic. In stratigraphic sequence it is followed by the *Psiloceras (Caloceras) johnstoni, Psilophyllites hagenowi,* and *Alsatites laquens* zones. These four zones comprise the Lower Hettangian. The Lower Psilonotenbank (unit g) is the lowest unit in the Hallau bonebed section whose age of deposition can be correlated with this sequence. The occurrence of *Psiloceras johnstoni* indicates an early but not earliest Hettangian age.

In summary, on the basis of the data currently available all that can be said is that the Hallau bonebed local fauna might be of Rhaetian age. It is probably no older than Middle Keuper (Norian) and no younger than the *Psiloceras johnstoni* Zone, early but not earliest Hettangian.

Saint-Nicolas-du-Port local fauna, France

The occurrence of vertebrate fossils in Triassic and Liassic deposits of northeastern France has been known for many years, but until recently none of these fossils documented the presence of mammals or advanced mammal-like reptiles. It should be noted that instead of including it within the Triassic most French stratigraphers usually classify the Rhétien as the initial stage of the Jurassic arguing that it is the time of the beginning of the major marine transgressions of Europe that characterize the Liassic (note Ricour, 1961, Pearson, 1970).

In 1975 G. Wouters, screening sands in an old quarry at Saint-Nicolas-du-Port, discovered a curious, two-rooted tooth that might be an element of the dentition of an advanced mammal-like reptile (Russell et al., 1976). Prompted by this discovery D. Sigogneau-Russell (1978) undertook screen washing of a large quantity of the fossiliferous sand. This unit is part of a thick sequence of sandstones locally designated as Rhétien inférieur (note geological section given by Laugier, 1961). However, as Schuurman (1977) cautioned such stratigraphic assignments have been made on the basis of local lithostratigraphy and might not have chronostratigraphic significance.

In a preliminary report Sigogneau-Russell (1978) announced the discovery of isolated teeth of morganucodontids, possibly a docodont, kuehneotheriids, and haramiyids. This work is being continued and gives promise of providing the first large sample of a Rhaetic mammalian fauna from continental western Europe.

The systematic affinities of some of the mammals reported to date will be discussed after description of the materials from the Tübingen-Stuttgart area and the Hallau local fauna. However, it is appropriate to point out here that the only genera in common to two or all three of the French, Swiss, and German faunas are the haramiyids *Thomasia* and *Haramiya*. These haramiyid "genera" are probably loosely defined typological units for different kinds of teeth and might bear little relationship to the genera of animals represented. Thus, at our present state of knowledge, it is only at the family or higher levels that common occurrences of taxa in two or all three of these faunas are recorded with some degree of certainty. Most likely these differences in faunal composition reflect both differences in age and the evolution of insular faunas as the European continent was subdivided by epicontinental seas during the Rhaetian and early Liassic.

Late Triassic - Early Jurassic local faunas from fissure fillings, western Great Britain

In recent years most of our knowledge of Late Triassic-Early Jurassic mammals has come from fossils found in remarkable abundance in fissure fillings in Wales and southwestern England. Three groups of fissure fillings have yielded mammalian and advanced mammal-like reptile remains that are of concern here. First, the fissure fillings near the town of Bridgend in Glamorgan, South Wales, include deposits that are the source of immense samples of *Morganucodon* and *Kuehneotherium*. These were exposed during operation of commercial quarries in Carboniferous limestones. During the Rhaeto-Liassic this limestone plateau is thought to have been an island, which ROBINSON (note 1971) dubbed St. Brides Island. Most of the field research has been carried out by Dr. K. A. KERMACK and his associates at University College London (see KERMACK et al., 1973, for a history of research).

A second group of fissure fillings are those exposed in Holwell Quarry near Frome in Somerset, England. In 1858 a fossiliferous fissure filling was discovered in the quarry and Charles MOORE had over 3 tons of the matrix transported to his home in Bath. Sorting this matrix required over three years and yielded a wealth of vertebrate material including a few isolated teeth of haramiyids (note DUFFIN, 1978, and PICKFORD, 1971). Subsequently fissures at Holwell were worked by KÜHNE (1946) and SAVAGE and WALDMAN (1966, also see SAVAGE, 1971). Finally, another fissure filling in Somerset, "Mendip 14", at Windsor Hill Quarry near Shepton Mallet has yielded an extensive sample of *Oligokyphus* that was collected and studied by KÜHNE (1956).

As is the case with bonebeds, establishment of the time of deposition of a fissure filling only sets a minimum age for the contained fossils. Many of the processes that have led to the concentration of bones in fissure deposits are still poorly understood (note KERMACK et al., 1973). There is evidence suggesting that some of the fissure deposits just cited might have had developmental histories as long and complex as the placer bonebeds (REIF, 1976).

The age of the fissure fillings and contained fossils found near Bridgend, Wales, has been discussed recently by ROBINSON (1971) and KERMACK et al. (1973). ROBINSON dealt primarily with age determinations based upon a reconstruction of the physical evolution of the Bristol Channel region. During a later part of the Late Triassic (Norian), St. Brides Island and several other areas composed largely of Carboniferous limestones deformed by Hercynian folding still rose as plateaus above extensive piedmonts (note TUCKER and BURCHETTE, 1977). At this time the plateaus could have been ecological islands supporting faunas and floras different from those of the surrounding piedmont.

Starting in the Rhaetian and continuing in the Liassic seas flooded the area and, apparently, during the Sinemurian (*Arietes bucklandi* Zone) fully inundated St. Brides Island. When during the period Norian to Sinemurian the fissure fillings were formed remains an unresolved question. ROBINSON (1971) argued that the narrow, slot fissures containing the vertebrate fossils appear to be elements of a relatively immature system of underground water courses. She suggested this fissure system was cut after the seas had isolated the island, raised the base level, and promoted the evolution of new drainage patterns. "Just before submergence sedimentation, rather than solution, became the dominant process in these fissures (ibid., p. 136)". She concluded that the fauna of the fissures is largely of Liassic age.

KERMACK et al. (1973) present a broader discussion of the problem of age determination. They note that the local faunas including *Morganucodon* and *Kuehneotherium* occur in deposits containing other vertebrates, occasionally invertebrates, and plants, particularly remains of the conifer *Hirmeriella (Cheirolepis) muensteri*. To date this assemblage of organisms, the *Hirmeriella* association, is only known from fossil localities on St. Brides Island. Although little help in precise correlations with other mammal-bearing deposits, the distinctive composition of this association supports the hypothesis that beginning with ecological islands formed by highlands in arid to semiarid environments and later isolated by Rhaeto-Liassic seas many different insular faunas evolved.

KERMACK et al. (1973) cite evidence suggesting the fissure-filling local faunas are not as old as "Keuper", *i. e.*, pre-Rhaetian. They conclude, "the age of the *Hirmeriella* association in these fissures must be either the Lower Lias (Hettangian and Lower Sinemurian) or the Rhaetic. There is insufficient evidence to decide between them." To this can only be added the observation that differences in composition of individual concentrations of bone within various fissures might not be just a product of variations in taphonomy but also reflect differences in age. The chronological duration of the *Hirmeriella* association could encompass a significant fraction of the Rhaetian to Lower Sinemurian interval.

The specimens of haramiyids and *Eozostrodon* found at Holwell Quarry were discovered in at least two fissure fillings. These deposits are thought to be neptunian dikes, submarine fillings of fissures opening beneath the sea and, in some instances, close to shore (KÜHNE, 1956, ROBINSON, 1957, SAVAGE and WALDMAN, 1966). KÜHNE (1946) reviewed faunal and geological evidence and came to the conclusion that the fissure fillings could have been formed sometime in the interval from Rhaetian to Bajocian but favored a Rhaetian age for the haramiyids and *Eozostrodon.*

In his monograph on *Oligokyphus* Kühne (1956) presented thorough studies of the taphonomy and age of the fossiliferous fissure filling in the Windsor Hill Quarry, "Mendip 14". Although a year or two might have elapsed between the time of death of the individuals of *Oligokyphus* and the burial of their remains in the submarine fissure, there is strong evidence this interval was not significantly greater. Kühne (ibid.) concluded that the age of the fissure filling and the specimens of *Oligokyphus* was Charmouthian (Lias γ or Pliensbachian).

In summary, except for "Mendip 14", currently available data only warrant estimations of age ranges of the fissure fillings and their faunas. (Both D. Pacey and C. Duffin, University College London, have undertaken studies of different aspects of the problems of determination of the ages of these and other British Rhaeto-Liassic vertebrate localities). In the cases of both the fissure fillings of St. Brides Island and Holwell, the minimum ages of the vertebrate fossils are well within the Liassic. If, following Robinson's interpretation that sedimentation became the dominant process in the development of the fissures late in their history, then there is a possibility that their local faunas are younger than the Rhaetic bonebed local faunas of Switzerland, Baden-Württemberg, and France. The sample of *Oligokyphus* from "Mendip 14" appears to be distinctly younger than the genotypic species from Baden-Württemberg.

Paleogeography

During the early Mesozoic northwestern Europe was of approximately triangular outline (see Ziegler, 1978). The base of the triangle was formed by extension movements leading to the development of a complex graben system flooded by the Triassic, Tethyian seas. Contemporaneously, to the west, the active rift zones that would later produce the basin of the North Atlantic Ocean and link it to the Arctic Ocean formed the other side. The third side of the triangle was delimited by the edge of the stable Russian platform (Fig. 2).

In the Triassic the system of Permian basins within northwestern Europe was modified by the development of a new trough and graben complex. It was an area largely characterized by erosion and, except for the geographically limited transgression of the Middle Triassic seas, deposition of terrestrial sediments. Toward the close of the Triassic most of northwestern Europe had been reduced to an area of relatively low relief, extensive flood plains, tidal flats, and shallow basins separated by low hills and pla-

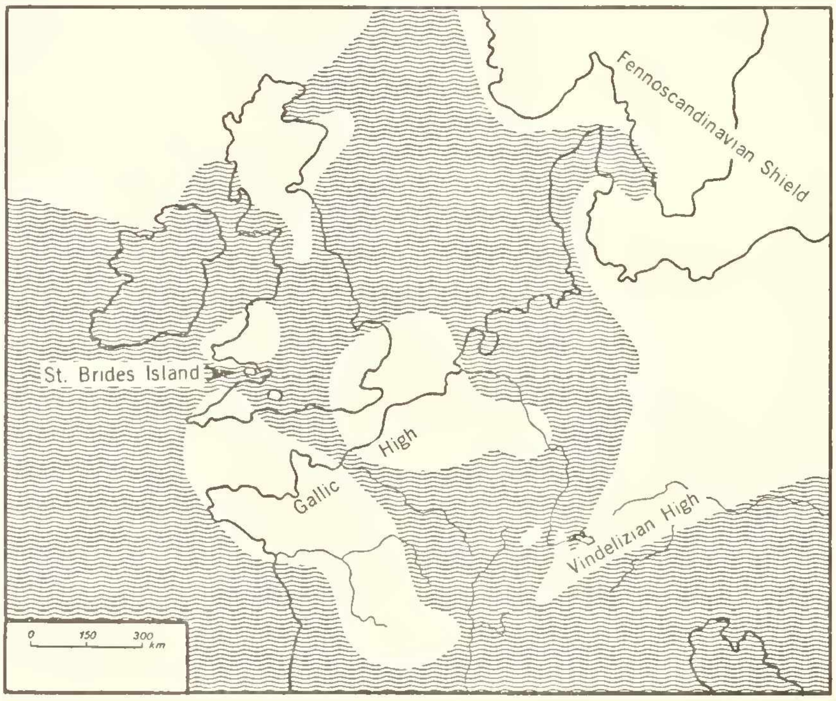

Figure 2: Schematic reconstruction of northwestern Europe showing areas covered by seas during the Rhaetian transgression (Based on data from Will, 1969, Ziegler, 1978, Muller, 1974, and T. R. Owen, 1976).

teaus. The arid climatic conditions characteristic of most of the Late Triassic (note ROBINSON, 1973) were ameliorated by increasing amounts of rainfall during the Norian and Rhaetian.

At the beginning of the Rhaetian marked regional extension movements, the Early Kimmerian tectonic pulse, affected not only the North Atlantic to Arctic and Tethyian rift systems but also northwestern Europe (ZIEGLER, 1978). This period of extension was the prelude to the Rhaeto-Liassic marine transgression that ultimately covered most of northwestern Europe.

Among the three areas of interest possibly the first to be affected by marine transgressions were the parts of Wales and southwestern England bordering the Bristol Channel. Although the range of variation in elevation was not great, the British Isles was an area of relatively varied relief that waters from the proto-North Atlantic probably quickly transformed into an archipelago (note AUDLEY-CHARLES, 1970 a und 1970 b, DONOVAN et al., 1979, and summary in T. R. OWEN, 1976). By early Hettangian (*Psiloceras planorbis* Zone), if not earlier, St. Brides Island could have been fully encircled by marine waters (ROBINSON, 1971). Its fossiliferous fissure fillings were formed sometime after the beginning of the Rhaetian but before final submergence of the island in the Lower Sinemurian. The fissure fillings at Holwell might also have been formed during this interval, but the "Mendip 14" fissure filling is younger (Pliensbachian).

During the Rhaeto-Liassic transgression what are now the continental parts of northwestern Europe were characterized by three major areas of erosion (note WILL, 1969, Figs. 47—49, ZIEGLER, 1978, Figs. 3 and 5, and Fig. 2). The Gallic High included, in varying combinations, parts of southeastern England, Belgium, and northwestern France (i. e., London-Brabant Massif, Ardennes High, Armorican High, and adjacent areas). To the northeast was the stable area of the Russian Platform (including the Fennoscandinavian Shield). Finally, in the southeast the Vindelizian High occupied parts of what are now northwestern Switzerland and southern West Germany. To the northeast it was linked to the Bohemian Massif.

Marine waters flooding the basins of northwestern Europe came primarily from the proto-North Atlantic Ocean. They transgressed in a generally eastward direction from the area of the British Isles flooding the basins between the Gallic High and the Russian Platform. A lobe of this sea expanded from the northeast toward the west and south into the Paris Basin. Early in the Rhaetian it breached the Gallic High in the vicinity of the modern Seine River valley and established a connection with seas in southern England (MULLER, 1974). Farther to the south a connection with Tethys was established (WILL, 1969).

The transgression of northern Germany came to a halt or slowed toward the end of the Rhaetian providing a stable sea level, one condition thought to be requisite for the development of the Rhaetic Sandstone deltas of the Tübingen-Stuttgart area (AEPLER, 1974). The streams forming these deltas had their headwaters in the Vindelizian High. Surface outcrops of the Rhaetic Sandstone containing bonebeds are known from the region of Stuttgart southwest to the Täbingen-Balingen area. Wells drilled in the vicinity of Lake Constance have encountered Rhaetic sediments that thin westward (BÜCHI et al., 1965). An approximately north-south trending high from the Aar Massif in the south, through the region of Zürich and into the Schwarzwald of southwestern Baden-Württemberg formed a peninsula into the Rhaetic sea. On the western side of this peninsula, *i. e.*, west of the Adelhausen-Hägendorf line (Fig. 1), sediments including bonebeds were also deposited during the Rhaetian (note TANNER, 1978).

AEPLER (1974) developed two working hypotheses concerning the chronology of development of the Rhaetic Sandstone deltas in Baden-Württemberg. One (note ibid., Abb. 12) suggests that the deltas were deposited in sequence as the seas transgressed, and, therefore, from the oldest in the Stuttgart area the Rhaetic deposits become progressively younger southwestward. The Rhaetic Sandstone in the Tübingen area is overlain by sediments of the *Psiloceras planorbis* Zone. However, the first Liassic ammonite found above the Hallau bonebed is *P. johnstoni*. It is tempting to hypothesize the bonebeds of the Tübingen-Stuttgart area are somewhat older than the Hallau bonebed. This might be the case. But, as AEPLER (ibid.) noted, the available data from Baden-Württemberg are also in accord with a hypothesis that the Rhaetic Sandstone deltas developed at about the same time throughout this area.

How the time of deposition of the bonebeds at Saint-Nicolas-du-Port relates to that of the Swiss and German bonebeds remains unclear. If the assignment of a Lower Rhaetian age proves correct and Will's paleogeographic map of the area for the time of the *contorta*-Schichten (WILL, 1969, Fig. 49) is reasonably accurate, the bonebeds of Saint-Nicolas-du-Port were formed on the eastern margin of the Gallic High. This area was then separated by a marine strait from the shores of the Vindelizian High.

In summary, a review of biostratigraphic studies of Rhaeto-Liassic stratigraphy of northwestern Europe does not result in a marked increase in precision of correlation of the vertebrate localities. In recent years detailed palynological research and studies of ostracods have added to development of a biostratigraphic framework. However these research techniques have yet to be applied in renewed investigations of the vertebrate fossil localities and the results published. The fissure fillings of St. Brides Island and Holwell Quarry, and the Rhaetic bonebeds of Saint-Nicolas-du-Port, the Tübingen-Stuttgart area and Hallau can be correlated with no more precision than to say that they all are of Rhaeto-Liassic age.

To speculate, making use of the probabilities and educated guesses of specialists, it can be argued that the oldest occurrence of a haramiyid is that from the probably Norian, *Plateosaurus* beds of Halberstadt (Hahn, 1973). If the assignment of Rhétien inférieur has more than local significance, the Saint-Nicolas-du-Port local fauna would be the oldest assemblage of mammals yet found in Europe, and possibly the world. The mammals from the bonebeds of Germany and Switzerland might be slightly younger but no younger than early Hettangian. Heavily weighting Robinson's (1971) argument that the filling of the fissures at St. Brides Island occurred close to the time of the island's final inundation in the Sinemurian, these local faunas could have a Hettangian-Sinemurian age. The Holwell local fauna might fall in this interval. The differences in faunal composition distinguishing it from those on St. Brides Island could be a product of insular evolution rather than differences in age. Probably both factors are involved. Finally, the rich accumulation of bones of *Oligokyphus* at the "Mendip 14", Windsor Hill quarry appears to be even younger, Pliensbachian.

FOSSILS FROM THE TÜBINGEN-STUTTGART AREA BADEN-WÜRTTEMBERG, WEST GERMANY

Introduction

Unlike the sample of the Hallau local fauna that was collected at one site, the fossils described here come from various exposures of the Rhaetic bonebeds in the Tübingen-Stuttgart area. Currently available data, reviewed in a preceding section, suggest they are derived from approximately contemporaneous sites formed under similar depositional regimes. For these reasons, and convenience, the systematic analyses of these few fossils are grouped in the following section. Whether they actually document members of one faunal unit remains to be determined.

Systematics

Class ?Mammalia
Order and Family incertae sedis
Tricuspes E. von Huene, 1933

Type species: *Tricuspes tubingensis* E. von Huene, 1933

Revised diagnosis: In comparison to the approximately contemporaneous morganucodontids, cheek teeth are of larger size and simpler morphology consisting of only three main cusps. The median or principal cusp is larger than the anterior and posterior accessory cusps. These cusps are not aligned directly behind one another, but the apex of the principal cusp is slightly buccal(?) to a line drawn through the apices of the anterior and posterior accessory cusps. A small cusp may be present on the presumed posterobuccal side of the crown. Directly below the crown the root is bilobed in cross section and might have been fully subdivided farther from the crown.

Distribution: Type locality: Gaisbrunnen, Baden-Württemberg, West Germany. Referred material from the following localities: Sonnenberg bei Degerloch, Baden-Württemberg; Hallau, Kanton Schaffhausen, Switzerland; and Saint-Nicolas-du-Port district of Meurthe-et-Moselle, France (pers. comm., D. Sigogneau-Russel).

Tricuspes tubingensis E. von Huene, 1933

Revised diagnosis: As for the genus until additional species are recognized.

Type specimen: An isolated tooth tentatively identified as a right lower molariform now in the collections of the Geologisch-Paläontologischen Institut der Universität Tübingen (see E. von Huene, 1933, Taf. I, Fig. 7, and Pl. 1:1—2).

Orientation: On the basis of several tenuous assumptions the type specimen is identified as a lower right molariform tooth (Pl. 1:1—2). A survey of teeth of the known Triassic and Jurassic mammals shows that usually, but not always, the lower molariform teeth have crowns higher (maximum cusp height relative to crown height) than those of the uppers. In many species cingula or cusps lateral to the main cusps are found on only one side of the lowers but on both sides of the uppers. These criteria, assumed to be applicable to *Tricuspes*, are the basis for identification of the type specimen as an element of the lower dentition.

In many molariform teeth of triconodont-type and known orientation, the anterior accessory cusp is lower than the posterior. Also, the anterior slopes of the main cusps tend to be more gradual and slightly convex in lateral outline. These two lines of evidence are the basis for the designation of the anterior end of the crown.

Identification of the type specimen as a right, rather than a left lower cheek tooth is almost an arbitrary choice. Two criteria are available for consideration, the angulation of the row of main cusps and the orientation of the small lateral cuspule. On lower molariform teeth of a tribosphenic or pre-tribosphenic pattern and some triconodont-like teeth (note *Amphilestes*, see Mills, 1971, p. 53-4), the apex of the principal cusp lies labial to the anterior and posterior accessory cusps. Second, lateral cingula or cusps are usually on the lingual side of the crown of lower molars. Thus, by the first criterion, the type of *Tricuspes tubingensis* is probably from the right dentition, by the second it is a left molariform. The first criterion is slightly favored because it might prove to be a more stable feature. A very similar tooth in the collection from Hallau lacks the lateral cusp, but shows the angulation of the main cusps.

Description: The root(s) are broken away leaving a fracture surface with a figure-eight outline showing subdivision of the pulp cavity. The crown appears to be well preserved and lacks evidence of wear facets of post-mortem abrasion (Pl. 1:1—2). A high principal cusp dominates the relatively simple crown. The anterior accessory cusp is lower than the posterior and both are separated from the principal cusp by distinct notches. A slight bulge at the base of the crown extends from the posterior end of the tooth around the presumed lingual side of the posterior accessory cusp. This swelling does not appear to have been the base of a distinct cingulum nor did it support cingular cusps. The fourth cusp on the crown is a small but distinct cuspule on the posterobuccal slope of the principal cusp. If the assumed orientation is correct, this is not a kühnecone, a cusp on the lingual margin of the crown.

Dimensions of the type specimen are as follows: crown length = 2.64 mm, width = 1.12 mm.

Discussion: A fragment of tooth described and illustrated by E. von Huene (1933, p. 84—5, Taf. I Fig. 9), found in the Rhaetic bonebed at Sonnenberg bei Degerloch, might be referable to *Tricuspes tubingensis*. The fossil appears to be less than half of a two-rooted tooth slightly larger than the type. Although having suffered some further damage since its original description, what little remains of the crown is not strikingly different from the posterior part of the crown of the type of *T. tubingensis*. If this identification is correct, then the specimen shows that some teeth of *T. tubingensis* were supported by two separate roots.

In her study E. von Huene (1933, Taf. III, Figs, 40, 41, 42, 44, 48) figured five fossils and described several more from the collections of Charles Moore, now housed in the Bath Geology Museum, Bath, England (see Pickford, 1971, Duffin, 1978). The figured specimens — a tooth, three vertebrae, and a phalanx — were identified as coming from the Rhaetic site "Vallis bei Frome" and not from the fissure fillings in Holwell Quarry. Of these fossils E. von Huene referred the tooth to *Tricuspes*; the bones were tentatively allocated to an undescribed, primitive crocodilian. Catalogue numbers were not recorded and, because of the turbulent history of the collection during and after World War II (see Pickford, 1971), these bones cannot now be certainly identified.

The illustration (E. von Huene, 1933, Taf. III, Fig. 40) of the tooth referred to *Tricuspes* shows a three-cusped crown supported by a single, blunted root. Crown length, measured from the illustration, is on the order of 1.4 mm. The accuracy of this drawing cannot be directly assessed, but clearly its shading is not rendered with the same care and detail used in the drawings of the type of *Tricuspes* or teeth of *Oligokyphus*.

Search of the Moore collection in 1975 resulted in discovery of only one tooth that could possibly have been the model for E. von Huene's illustration. It (C108) is a single-rooted tooth with a transversely flattened crown of 1.6 mm anteroposterior length. On either side of the principal cusp are small anterior and posterior accessory cusps. Below each accessory cusp, at the level of maximum length of the crown, are minute cusps, only easily visible with magnification. This fossil is identified as coming from Holwell Quarry. It resembles those from Hallau described by Peyer (1956, p. 56—59) as, "Zähne von wahrscheinlich Synapsiden Reptilien, Gruppe a".

Thus, the tooth from "Vallis bei Frome" allocated to *Tricuspes* by E. von Huene cannot be certainly relocated. The only fossil in what remains of the Moore collection that might have served as the model for her drawing is C108, which is recorded as coming from Holwell Quarry, not from the site at Vallis. It differs from the type of *Tricuspes* in its smaller size, morphology of cusps, proportions of the crown and undivided root. If found at Hallau, C108 would be included in "Gruppe a" of the teeth tentatively allocated to synapsid reptiles by Peyer (1956). However, the possibility that C108 was not the model for her drawing and the illustrated tooth was lost when the Moore collection was rapidly packed for storage cannot be dismissed. In summary, there is no unequivocal evidence that *Tricuspes* was part of the British Mesozoic fauna.

Family Haramiyidae

In addition to being represented in local faunas of the Tübingen-Stuttgart area and the Hallau local fauna, haramiyids are members of other continental European and British local faunas. Most of these records of haramiyids come from sites of Rhaetic or Liassic age, but a tooth is known from a locality in the Late Triassic, Keuper (Norian), *Plateosaurus*-Schichten (Hahn, 1973). Freeman (1976) reported the occurrence of an isolated tooth in Bathonian (mid-Jurassic) deposits in England that might have been part of the dentition of a late haramiyid or an early multituberculate. In spite of their widespread geographic and stratigraphic distribution in Europe, at no site yet discovered has a large sample of haramiyids been recovered. The group remains known from only isolated, usually fragmentary teeth. If only complete teeth or major fragments are counted, the total haramiyid sample consists of approximately fifty specimens (see Clemens and Kielan Jaworowska, 1979, for review).

The currently utilized classification of haramiyid genera and species has not changed greatly from that proposed by Simpson (1928). Two genera are recognized, *Haramiya* (= *Microlestes, Microcleptes)* and *Thomasia*, which are distinguished on the basis of number and relative size of cusps. In addition to the four species formally recognized by Simpson (1928) — *Haramiya moorei, H. fissurae, Thomasia antiqua*, and *T. anglica* — several unnamed "taxa" have been noted (see Hahn, 1973) or morphological variants described (Parrington, 1947). Currently there is no basis for determining whether these formal and informal groupings represent collections of teeth of different species or are simply associations of morphologically similar teeth. Prof. P. M. Butler and Dr. Giles MacIntyre (pers. comm.) are now engaged in research on occlusal patterns of haramiyid dentitions that might contribute to the resolution of some problems of classification. For the limited purposes of this analysis the "taxa" of haramiyids are treated as though they are based on collections of morphologically similar teeth that might be samples of different biological species. The difficulties encountered in assignment of some fossils strongly suggest they are not, but do not clearly offer the basis for an alternative classification.

In the following descriptions the terminology suggested by Hahn (1973) is employed. Briefly, Row A is the row of cusps of higher average height, which usually are three in number. Row B, usually consists of four or more cusps most of which are smaller than the cusps in Row A. The "U-shaped rim" is the low ridge connecting the two rows of cusps at one end of the central basin. At the other end of the crown, the higher cusps of Rows A and B are frequently linked by a saddle marking a terminus of the central basin. *As a convenience in preparing descriptions*, the "U-shaped rim" is assumed to be at the posterior end of the crown.

Thomasia Poche, 1908

The diagnosis of this genus currently utilized is that proposed by Simpson (1928, p. 63):

> "Microcleptidae [= Haramiyidae] with one rim of basined molar teeth [Row A] with three tubercules of which the anterior is markedly the largest and the posterior one may be much reduced. The anterior cusp of the other side [Row B] is not as high as that just mentioned, and is followed by four or more smaller cusps, the most posterior of which forms part of the posterior closure of the basin ["U-shaped rim"].

Currently two species of *Thomasia, T. antiqua* (Plieninger, 1847) and *T. anglica* Simpson (1928), are formally recognized, but Hahn (1973) also described teeth under the rubrics of *Thomasia* sp. 1 and sp. 2. As the name suggests, *T. anglica* is typified on and was known only from specimens found at Holwell Quarry, England.

Thomasia antiqua (Plieninger, 1847)

Simpson (1928) reviewed the confused history of the fossils originally referred to *Thomasia antiqua* by Plieninger (1847). In 1979, with the assistance of Dr. Rupert Wild, I reviewed the Rhaetic bonebed material in the collections of the Staatliches Museum für Naturkunde, Stuttgart. The original descriptions of the two teeth allocated to what is now *Thomasia antiqua* are in a paper (Plieninger, 1847) dealing with fossils from the bonebeds at Degerloch and Steinenbronn. Plieninger did not record which of the localities yielded the specimens of *Thomasia*. Henning (1922) argued that the type specimen probably came from Schlößlesmühle bei Steinenbronn and was followed in this by Simpson (1928), Hahn (1973), and Clemens et al. (1979). However a note now with the fossils that apparently was written by Prof. Dr. F. Berckhemer, the former curator of the Stuttgart paleontological collections, indicates that this is not the case. Berckhemer cites the autobiography of Herr Eser, a contemporary and friend of Plieninger, in which it is stated that the type was found at Degerloch. Also, in his study of *Belodon* Plieninger (1852, p. 428, footnote) notes that the fossils came from the Grenzbreccia (= Rhaetic bonebed) at Degerloch. As pointed out in the section on Geology and Paleogeography, Plieninger's locality is approximately 0.5 km away from Sonnenberg bei Degerloch a site worked by E. von Huene.

In addition to the type PLIENINGER (1847) described a second, similar, but somewhat larger tooth. Currently the collection contains several small pieces of bonebed that are labled, "*Microlestes antiquus* Plien., verletztes Orig. z-PLIENINGER, Jahresb. 1847, Taf. I, fig. 4". A cusp and part of the base of a tooth are preserved in one of the fragments. The size and configuration of the cusp suggests it is part of the second specimen and part of a tooth of *Oligokyphus*.

The hypodigm of *Thomasia antiqua*, as revised by HAHN (1973), consists of two isolated teeth, the type specimen and GIT 1430/1. Their dimensions are as follows:

	Length (anteroposterior)	Width
Type	2.1	1.3
GIT 1430/1	1.7	1.0

E. VON HUENE (1933) referred two teeth found at Gaisbrunnen to "*Microcleptes?*" One (see ibid., Taf. I, Fig. 6) now is lost. The illustrations of this specimen suggest some similarities to teeth that have been tentatively identified as haramiyid incisors. The second specimen, which she identified as "*Microcleptes* (?) sp.", is a heavily worn haramiyid molariform (see ibid., Taf. I, Fig. 4) that is designated ?*Thomasia* sp. and described below.

Collections from the Rhaetic bonebed exposed at Olgahain, made in 1948 under the direction of Prof. O. H. SCHINDEWOLF, contain three teeth of haramiyids. Two were described by HAHN (1973) and identified, respectively, as *Thomasia antiqua* (GIT 1430/1) and *Thomasia* sp. 2 (GIT 1430/2). The third specimen (GIT 1541/1), described below, is another heavily worn molariform that can be tentatively referred to *Thomasia*.

Thomasia sp. 1 is based on a single molariform found in the *Plateosaurus*-Schichten of the upper middle Keuper near Halberstadt (HAHN, 1973). At the moment this fossil provides the oldest record of the Haramiyidae, and possibly the Mammalia.

? *Thomasia* sp.

Description: The crown of the haramiyid found at Gaisbrunnen and described by E. VON HUENE (1933, Taf. I, Fig. 4) is heavily abraided (Pl. 1:4). Except for the lining of its basin and small parts of the margin of the crown, most of the enamel has been removed. However, large parts of the two roots are preserved. The almost complete root under the basin is transversly broader than the other. Starting at about the vertical midpoint of the broader (?posterior) root and continuing to the base of the crown, a bony septum links the roots. Dimensions of the crown are as follows: length = 1.17 mm, width = .99 mm.

The enamel-lined basin occupies less than half of the occlusal surface of the tooth. Its rim is not complete but interrupted by a notch near the end of the crown over the broader root. The cusps have been worn away. What remains of their bases suggests the basin was closed at the other end of the crown by a major cusp or cusps. It can be argued, but not forcefully, that the basin was situated toward the posterior end of the tooth, its "U-shaped rim" was breached by wear, and the mound at the other end of the crown was formed by the bases of the anterior cusps of Rows A and B. This orientation would place the smaller root at the anterior end of the crown.

The third haramiyid specimen (GIT 1541/1, Pl. 1:3) collected under the direction of Prof. SCHINDEWOLF at Olgahain is more heavily worn than the others. Dimensions of its crown are as follows: length = 1.63 mm, width = 1.35 mm.

Large, apical wear facets mark the positions of the anterior two cusps of Row A. Unlike typical molariform teeth of *Thomasia* the first cusp of this row was about the same basal diameter and not significantly larger than the second, and these cusps are well separated. The third cusp of Row A appears to have been much smaller, a character of some teeth referred to *Thomasia* (SIMPSON, 1928).

The cusps of Row B are almost completely obliterated by a wear facet that slopes laterally at a low angle and is likely the result of greater development of facets of the kind illustrated by HAHN (1973, Fig. 1d). A small shelf at the front of the crown could be what remains of an anterior cusp. The enamel has been removed from the anterior end of the median valley. This appears to have been initiated by a wear facet that did not breach the "U-shaped rim". Only their bases are preserved, but these suggest the tooth was supported by a larger, broader, anterior and a smaller, posterior root.

Discussion: In summary, the current record of haramiyids from the Tübingen-Stuttgart area includes fossils from the Degerloch, Gaisbrunnen, and Olgahain localities. The taxa, or morphologically defined units, recognized are: *Thomasia antiqua*, *Thomasia* sp. 2 (HAHN, 1973), and ?*Thomasia* sp. The small collection contains no evidence of the presence of *Haramiya*, but this could easily be an artifact of the small sample size.

HALLAU LOCAL FAUNA, KANTON SCHAFFHAUSEN SWITZERLAND

All the fossils from the Rhaetic bonebed at Hallau discussed here are in the collection of the Paläontologischen Institut der Universität Zürich, and are part of the material obtained in a project carried out under the direction of Prof. Bernhard Peyer. To the best of my knowledge this is the only collection of small vertebrate fossils to be assembled from this locality. Descriptions of more than half the fragments of teeth of mammals or mammal-like reptiles in the collection were presented in a major monograph by Peyer (1965); the remainder is described here.

Systematics

Class Reptilia

No attempt has been made to thoroughly review the records of reptiles in the sample of the Hallau local fauna. However in going through the collections two points worthy of note became apparent.

Order Pterosauria

The teeth of most known pterosaurs are simple, conical structures that probably are only certainly identifiable when found in association with larger elements of the skull (see Wellnhofer, 1978). In contrast, the dentitions of the few pterosaurs discovered in strata of Late Triassic (Norian) age include multicusped cheek teeth. Some of the cheek teeth of the Norian pterosaur *Eudimorphodon* Zambelli, 1973 (and see Wild, 1979) have crowns made up of as many as five cusps aligned anteroposteriorly and on first inspection resemble teeth of members of the mammalian order Triconodonta.

Dr. Rupert Wild, who has just completed a detailed study of *Eudimorphodon,* reviewed the illustrations of triconodont-like teeth in Peyer's (1956) monograph. He noted (pers. comm.) that some of the teeth Peyer designated "wahrscheinlich synapside Reptilien, Gruppe b" showed striking resemblances to cheek teeth of *Eudimorphodon* [for example: AIII-301 (Peyer, 1956, Taf. 12, Fig. 47), AIII-312 (ibid., Taf. 2, Fig. 58), and AIII-321 (ibid., Taf. 10, Fig. 67)]. Other teeth from Hallau that Peyer included in "wahrscheinlich synapside Reptilien, Gruppe a" resemble cheek teeth of a new, second genus of Norian pterosaur (Wild, 1979) and the Hettangian genus *Dimorphodon* [for example: AIII-272 (ibid., Taf. 9, Fig. 18), AIII-288 (ibid., Taf. 9, Fig. 34), AIII-320 (ibid., Taf. 5, Fig. 66), and AIII-322 (ibid., Taf. 10, Fig. 68)].

These teeth from Hallau share several morphological differences from the primitive conical pattern. In lateral view their crowns are relatively high (height of central cusp relative to anteroposterior basal length) and generally triangular in outline. Two, four, or possibly six (AIII-321, Peyer, 1956, Taf. 10, Fig. 67) cusps are symmetrically arranged on the anterior and posterior edges of the main cusp. On some teeth ridges on the lateral slopes of the cusps extend toward, but do not reach the base of the crown. No basal cingula are present. In occlusal view the teeth exhibit relatively little lateral expansion. As far as known all were supported by a large, single root (for example, AIII-320, ibid., Taf. 5, Fig. 66).

Dr. Wild's notations of morphological resemblance should not be interpreted as positive identifications of different genera of pterosaurs in the Hallau local fauna. Much more detailed research on the morphology and patterns of variation (both ontogenetic and individual) must be completed before identification of different pterosaur genera on the basis of isolated teeth can be attempted. Peyer (1956) is not alone among vertebrate paleontologists faced with the problem of identifying isolated, somewhat triconodont-like teeth of Late Triassic or Early Jurassic age who asked the question, are they teeth of primitive mammals or advanced mammal-like reptiles? Dr. Wild's observations require that the question now be phrased, are they teeth of primitive mammals, advanced mammal-like reptiles, or pterosaurs?

Order Therapsida

Family Tritylodontidae

The absence of identifiable remains, particularly fragments of teeth, of tritylodonts in the sample of the Hallau local fauna warrants special emphasis. These advanced mammal-like reptiles are common members of several Late Triassic and Early Jurassic local faunas. The possibility that their absence is the result of post-mortem sorting of skeletal elements according to size, either during deposition of the bonebed or collection, probably can be dismissed. A survey of part of the collection of bone fragments picked from the washing concentrates obtained at Hallau and samples of the original bonebed matrix revealed pieces of bone much larger than the cheek teeth of any known tritylodont. At the other end of the size range, isolated, individual cusps of teeth of morganucodontids and haramiyids, much smaller than the major cusps of tritylodontid cheek teeth were recovered. No fragments of teeth preserving the easily recognizable, selenodont-like cusps of tritylodonts are present in the collection. Thus, it seems most likely that the absence of tritylodontids is the result of biogeographic or ecological factors rather than postmortem sorting of the bone.

Class ?Mammalia
Order and Family incertae sedis
Tricuspes E. von Huene, 1933
Tricuspes cf. *tubingensis*

Referred material:

AIII-351 (NC 23), crown lacking root(s).

Description: One isolated tooth in the collection from Hallau closely resembles the type of *Tricuspes tubingensis,* but is slightly larger: crown length = 2.82 mm, crown width = 1.47 mm. Like the type, the central cusp is by far the largest and the three main cusps are not directly aligned one behind the other. Comparsion of occlusal views (Pl. 1:2a & 1:5a illustrates the more bulbous outline of the Hallau specimen and the absence of a cusp near the base of the presumed posterolabial side of the principal cusp. On the anterior base of the anterior accessory cusp, at the level of the maximum length of the crown, is a minute but distinct conule.

The apex of the anterior accessory cusp was lost by breakage, the apices of the other two main cusps appear to have been blunted by wear. No other wear facets can be unequivocally identified. Comparison of the lateral views of the two fossils (Pl. 1:2 b—c & 1:5 b—c) suggests the crown of the tooth from Hallau has a slightly more prominent basal constriction. Particularly on the lingual side of the tooth, what remains of its root shows a deep indentation indicative of at least the beginnings of subdivision.

Discussion: Reference of AIII-351 from Hallau to *Tricuspes* is based on similarities to the type in size and gross morphology; there are no unique, shared derived characters indicative of special phylogenetic relationship. Features distinguishing the two teeth would easily fall within the range of dental variation of a polyphyodont, advanced mammal-like reptile or of the diphyodont or monophyodont cheek teeth of an early mammal. Tentative allocation of *Tricuspes* to the Mammalia is also made on inconclusive evidence. The complexity of the morphology of the crown, particularly the slight angulation in alignment of the main cusps, and evidence suggesting the crown was supported by a partially divided root suggest, but do not demonstrate, mammalian affinity.

Family Haramiyidae

To date all fragmentary teeth of haramiyids found in the Tübingen-Stuttgart area that preserve enough of the crown to warrant identification at the generic level are referable to *Thomasia* with some degree of certainty. None show characters diagnostic of *Haramiya.* In contrast the larger sample from Hallau includes some teeth referable to *Thomasia* and *Haramiya* as well as a large collection of fragments that can only be identified as haramiyid. Again it should be stressed that as used here, *Haramiya* and *Thomasia* are names for different types of teeth that are assumed, primarily for the sake of convenience of description, to represent biological taxa. The conventions for orientation and terminology employed are those proposed by Hahn (1973).

Thomasia Poche, 1908
cf. *Thomasia antiqua* (Plieninger, 1847)

Referred material:

AIII-371 (NC 43), anterior end of Row B.
AIII-372 (NC 44), anterior end of Row B.
AIII-377 (NC 49), anterior end of Row B.
AIII-436 (NC 106), anterior end of Row B.

Revised diagnosis of *Thomasia antiqua:* Following Simpson (1928, p. 63—64), but recast in the terminology of Hahn (1973):

> The posterior cusp of Row A is small but distinct (minute to indistinct in *T. anglica*). Anterior cusp of Row B preceded by a well marked basal cuspule (a slight anterior cingulum not forming a distinct cusp in *T. anglica*). Anterior cusp of Row B followed by three well-differentiated, small cusps and then by a fourth, which is obscurely bifid (in *T. anglica* followed by 4 to 6 cusps, the last of which are posteromedial).

Description: The referred specimens include one or more cusps posterior to the largest cusp of Row B, but in none is the entire row preserved. Of the three AIII-371 is the most inclusive preserving what appears to be most of the basin-like depression anterior to the saddle, as well as the two cusps on either side of the largest cusp of Row B, which are of approximately the same size. Only part of the basin anterior to the saddle is preserved in AIII-372 and the cusp anterior to the largest cusp of Row B is distinctly smaller than that immediately behind this cusp. AIII-377 is smaller but otherwise very similar to this tooth.

AIII-436 requires special notice. It differs from the specimens just described in the smaller difference in size between the largest cusp of Row B and the two immediately adjacent to it. Discrete, in echelon wear facets are present on the lateral sides of the largest cusp of Row B and the cusp behind it. These facets are not in the same plane so could not have been produced by propalinal wear.

Discussion: Designation of these four specimens as cf. *Thomasia antiqua* rests solely on the basis that this is the only one of the four recognized haramiyid "species" in which a basal cuspule is thought to constantly occur anterior to the highest cusp of Row. B. A cusp in this position is usually not developed on teeth allocated to the other three "species". However, note that on AIII-309+314, described below and designated *Haramiya* sp., the anterior cingulum has a cusp-like terminus in front of Row B. The projection is admittedly much smaller than the cusps on the four specimens referred to cf. *Thomasia antiqua*. Also PARRINGTON (1947, p. 712—713) noted that a small cusp was present anterior to the largest cusp of Row B on the lectoholotype of *Haramiya moorei* (M211), but apparently is not a constant feature of the crowns of the other eight teeth referred to this species by SIMPSON (1928). The difficulty in taxonomic assignment of these four specimens from Hallau not only reflects their fragmentary condition but also stems from the typological nature of the named taxa of haramiyids. It underscores our lack of understanding of even the basic morphology and ranges of variation of haramiyid dentitions.

Thomasia anglica SIMPSON, 1928

Referred material:

AIII-295 (XLI, Taf. 1), anterior end of crown.

Description: AIII-295 (PEYER, 1956, Taf. 1, Fig. 41) appears to be the anterior end of the crown of a haramiyid molariform. The largest cusps of both rows are at the preserved end of the crown, those posterior to them are of lesser height. The highest cusp is taken to be the anterior cusp of Row A. It and the second cusp of Row A are larger and more widely spaced than their counterparts in Row B. Low but distinct, irregular ridges are present on the medial sides of the cusps of Row A and the posterior sides of cusps of Row B.

Anterior to the largest cusp of Row B is a narrow cingular ledge that is abruptly terminated laterally producing a small conule. This cingulum continues across the crown onto the anterior slope of the first cusp of Row A where there is a cusp-like irregularity in the crest. Unfortunately the posterior end of the crown of this tooth is missing and the number of cusps in the two rows cannot be determined. Maximum width of the crown is 1.72 mm.

Discussion: Reference of this tooth to *Thomasia* is based on the distinctly smaller size of the second cusp in Row A relative to the first. Allocation to *T. anglica* recognizes the absence of a distinct basal or cingular cusp at the anterior end of Row B. In PEYER's (1956, Taf. 1) Figure 41 b of the anterior end of the crown, the end of the anterior cingulum in front of Row B is given an unwarranted cusp-like appearance. Figures 41a and 41c (ibid.) are more accurate representations of its morphology. The other two characters in the diagnosis of *T. anglica* require knowledge of the total number of cusps in each row and the morphology of the posterior end of the crown. Neither can be determined because of damage to the specimen. Thus, the reference of this tooth to a "species" otherwise known only from England rests solely on the absence of a distinct basal cusp anterior to Row B. The presence or absence of such a cusp could easily be a matter of individual variation.

The small, irregular ridges in the enamel on the medial slopes of cusps of Row A and posterior slopes of cusps of Row B of AIII-295 are a minor exception to a criterion for distinguishing the teeth of haramiyids from those of multituberculates noted by HAHN (1973). Prior to this study ridges in the enamel had not been observed on teeth of haramiyids. Whether or not this occurrence should be interpreted as the first indication of a derived character better developed in members of the Multituberculata and evidence of an ancestor-descendant relationship of these groups remains to be determined.

?*Thomasia* sp.

Referred material:

AIII-308 (LIV, Taf. 2), posterior end of crown.

Discussion: AIII-308 (PEYER, 1956, Taf. 2, Fig. 54) is a fragment of the posterior end of a molariform possibly slightly smaller than AIII-295, which is allocated to *Thomasia anglica*. Identification beyond the level of haramiyid is based on the following tenuous interpretations. As oriented in Figure 54 a (ibid.) the cusps of the upper (in the figure) row are identified as part of Row A, which extends almost to the posterior end of the crown. If this identification is correct, the posterior cusp of Row A appears to have been much smaller than the middle cusp, a characteristic distinguishing *Thomasia* from *Haramiya*.

cf. *Thomasia* sp.

Referred material:

AIII-323 (LXIX, Taf. 12), posterior end of crown.

Description: Probably AIII-323 (PEYER, 1956, Taf. 12, Fig. 69) consists of at least half of the posterior end of the crown of a molariform. A row of one complete and half of another cusp (to the left in

Fig. 69, ibid.) appears to be what remains of Row A. Row B is represented by four cusps of approximately the same basal diameter and individual height but increasing anteriorly in elevation on the crown. At the preserved end of the crown a small basal cusp is present on the slope of the terminal cusp of Row A. It is linked to a small central cusp and that to the terminal cusp of Row B by low crests. Maximum width of the preserved part of the crown, measured perpendicular to the central basin is 2.12 mm.

Discussion: The absence of a low crest or higher saddle directly linking the terminal cusps of the two rows, the consequent absence of any indication of an anterior cingulum or basin and, in occlusal view, the sinuous outline of the crown all support Peyer's view that the fragment preserves the posterior end of the crown. Comparison of the specimen to *Thomasia* is suggested because of the apparent decrease in size of the last two cusps in Row A and closure of the central basin by two small cusps.

The tooth is large for a haramiyid molariform and its sides are not parallel. On the outside of Row A the crown had prominent lateral bulges around the slopes of the last two cusps. In contrast, on the outside slope of Row B there is a noticeable bulge around the base of only one cusp. This irregularity in occlusal outline broadly resembles that of the type of *Haramiya fissurae*, but on detailed comparison many differences become apparent.

Haramiya Simpson, 1947

Teeth allocated to this genus differ from those of *Thomasia* in the following respects (a formal diagnosis is given by Simpson, 1928, p. 55): The three cusps of Row A are of approximately equal size or the presumed anterior cusp is smaller than the other two. Row B consists of a single, large anterior cusp followed by three or four progressively smaller cusps.

Haramiya moorei (R. Owen, 1871)

Referred material:

AIII-269 (XV, Taf. 1), anterior end of crown.

AIII-309+314 (LV & LX, Taf. 1, Fig. 3), crown of molariform.

Two fragments of a haramiyid molariform were described separately by Peyer (1956): AIII-314 (ibid., Taf. 1, Fig. 60) is the anterior end, AIII-309 (ibid., Taf. 1, Fig. 55) is the posterior end. The fragments are now glued together and form the most complete haramiyid tooth in the Hallau sample.

Description: Row A of AIII-309+314 consists of three cusps of approximately equal height; the anterior is only slightly lower in height than the other two. This row of cusps is not fully aligned, the apex of the middle cusp is slightly lateral to those of the terminal cusps (Fig. 3). In occlusal view the edge of the crown lateral to Row A is bowed outward. Below and posterior to the anterior cusp of Row A is a distinct expansion of the crown forming an almost cusp-like basal cingulum (note Peyer, 1956, Taf. 1, Figs. 60a & 60c). Row B consists of four cusps of which the first is distinctly higher and larger than the other three. The lateral side of Row B is expanded and bulbous except for the groove separating the third and fourth cusps, which is deep and forms a cup-like depression.

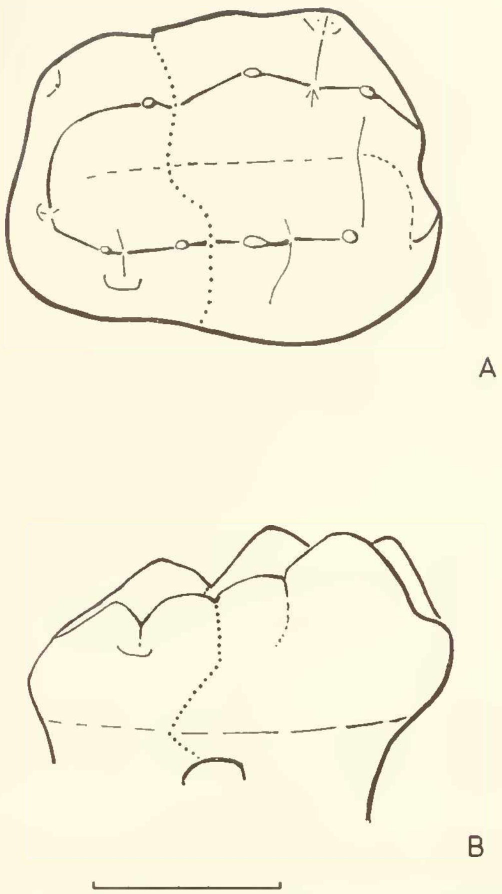

Figure 3: Outline drawing of AIII-309+314, *Haramiya moorei*, Hallau local fauna, Switzerland. Regularly dotted line marks the trace of the fracture. A. occlusal view, B. lateral view. Scale equals 1 mm.

The central valley is straight from the relatively low saddle linking the anterior cusps of Rows A and B to the "U-shaped rim". Anterior to the saddle is a small basin limited anteriorly and laterally by crests but extending without interruption to the edge of the crown (ibid., Fig. 60a). In front of Row B the crest is expanded but a distinct cusp does not appear to have been present. The anterior basin appears to be larger and better defined, at least laterally, than that of the molar of *H. moorei* illustrated by SIMPSON (1928, Fig. 14), but the morphology of this area of the crown differs among the teeth in SIMPSON's hypodigm (ibid., p. 58). At the posterior end of the crown a crest extends from the base of the last cusp of Row A posteriorly then medially to meet the base of the last cusp of Row B. At the posterior end of Row A the side of the crown has lost some chips of enamel, but clear evidence of a small basal cusp posterior to the last cusp of Row A (PEYER, 1956, Taf. 1, Fig. 55a) is present.

In occlusal view the tooth has an irregularly rectangular outline (Fig. 3). Crown dimensions are as follows: length = 2.23 mm, maximum width of crown across anterior cusps of Rows A and B = 1.83 mm, width at posterior end of Row A = 1.58 mm. The crown was supported by two transversely expanded roots. Just below the crown the broken surfaces of the roots have figure-eight outlines suggesting that at a greater distance from the crown both would have bifurcated.

Discussion: The relative proportions of the cusps of both Rows A and B clearly justify reference of AIII-309+314 to *Haramiya*. Morphologically the specimen appears to be easily encompassed within the range of variation of *H. moorei*.

Bases for reference of AIII-269 (PEYER, 1956, Taf. 1, Fig. 15) to *H. moorei* are very tenuous. If the complete cusp and the partial cusp shown above and to the right in PEYER's Figure 15 a (ibid.) are taken to be cusps of Row A and the other partial cusp identified as the first cusp of Row B, comparison of AIII-269 to the slightly smaller AIII-309+314 reveals some similarities. The first cusps of the two rows are linked by a saddle that is only slightly higher than the saddle of AIII-309+314. On AIII-269, anterior to the first cusp of Row A, what is preserved of a small basal cingulum could be part of the margin of an anterior basin. Resembling AIII-309+314 lateral to the presumed cusps of Row A are several small basal cusp-like expansions.

Haramiyid ?gen. et sp.

Referred material:

AIII-307 (LIII, Taf. 2), fragment of crown with Row A.

AIII-370 (NC 42, Fig. 4), fragment of crown with Row B.

Description: AIII-307 (PEYER, 1956, Taf. 2, Fig. 53) has been damaged since it was illustrated. It appears to have consisted of an entire Row A of a small molariform, crown length = 1.3 mm (measurement from figure). The three cusps of Row ?A were not well separated and of strikingly similar size and height. One cusp of Row ?B appears to have been preserved. It is illustrated as being linked to a terminal cusp of Row ?A by a low crest, possibly the anterior saddle.

AIII-370 consists of one row of cusps of another small haramiyid molar (Fig. 4), crown length = 1.98 mm. Apparently it was part of a relatively wide tooth. The maximum width of the fragment measured from the midline of the central valley to the edge of the crown is approximately 0.8 mm. One terminal cusp is decidedly higher than the other three cusps suggesting Row B is preserved. A saddle linking the anterior cusps of Rows A and B, if present, must have been small. A small fragment of a shelf-like cingulum suggests the anterior basin was also small.

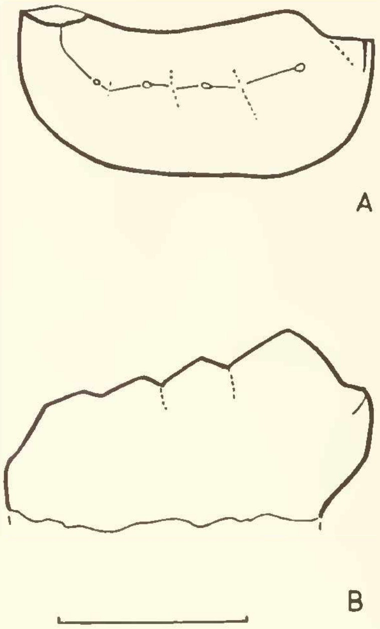

Figure 4: Outline drawing of AIII-370, haramiyid ?gen. et sp., Hallau local fauna, Switzerland. A. occlusal view, B. lateral view. Scale equals 1 mm.

Discussion: These two fragments are parts of relatively small haramiyid molariforms. If AIII-307 is correctly identified as preserving Row A, the cusps show the morphology characteristic of *Haramiya*, but the tooth was smaller than the smallest molariform referred to *H. moorei* by SIMPSON (1928; M217, crown length = 1.7 mm). If AIII-370 preserves Row B it preserves no characters allowing a choice in allocation to either *Thomasia* or *Haramiya*. The two specimens are grouped here simply to recognize their similar, relatively small size.

Other fossils possibly representing haramiyids: For the sake of completeness the following, slightly annotated list of fragments of haramiyid or haramiyid-like molariforms is included:

AIII-256 (II, Taf. 12), several cusps. PEYER (1956, p. 9) thought this was not a fragment of a mammalian or mammal-like reptile tooth. The cusps resemble those of some haramiyid or morganucodontid teeth. The morphology of the base of the crown is now obscured by glue.

AIII-257 (III, Taf. 12), a cusp. Possibly this is part of a large haramiyid molariform.

AIII-285 (XXXI, Taf. 7), possibly a side of a haramiyid molariform.

AIII-299 (XLV, Taf. 2), two small cusps, probably haramiyid.

AIII-306 (LII, Taf. 2), a large cusp and parts of two others that might be a fragment of a large haramiyid molariform.

AIII-315 (LXI, Taf. 2), a row of two complete and two fragments of cusps, possibly the posterior end of Row B of a tooth the size of AIII-309+314, *Haramiya moorei.*

AIII-374 (NC 46), part of a row of large cusps from a haramiyid molariform.

AIII-388 (NC 58), one and a half cusps, possibly haramiyid.

AIII-417 (NC 87), one and a half cusps, possibly haramiyid.

AIII-429 (NC 99), a large cusp, possibly haramiyid.

AIII-461 (NC 131), heavily abraided crown of a haramiyid molariform. Probably the posterior end is preserved. The root is transversely broad and has a figure-eight cross section.

AIII-491 (NC 161) probably preserves part of Row B. The cusps are large, inflated, closely approximated, and separted by deep, narrow clefts. The longitudinal crest connecting the apices of the cusps is sharp and forms carnassial notches where it passes from one cusp to another.

Isolated teeth that might include incisors or canines of haramiyids are noted below in the section on *Helvetiodon schutzi,* sp. et gen. nov.

Class Mammalia
Order Triconodonta
Family Morganucodontidae

The taxonomy and nomenclature of the Morganucodontidae has been reviewed elsewhere (CLEMENS, 1979). The conclusions of this review are that the known morganucodontids can be allocated to four genera of which the following three are monotypic: *Eozostrodon parvus* from Somerset, England, and *Erythrotherium parringtoni* and *Megazostrodon rudnerae* from Lesotho. *Morganucodon* includes three named species: *M. watsoni,* the common but possibly not the only species represented in the fissure fillings in Wales, Great Britain, and *M. oehleri* and *M. heikuopengensis* from China. A molariform of a morganucodontid from the Bathonian (mid-Jurassic) Forest Marble of England was illustrated by FREEMAN (1976, Fig. 1 g) and later allocated to a new genus and species, *Wareolestes rex* (Freeman, 1979).

Among the vertebrates in the Hallau local fauna currently only the morganucodontids and morganucodontid-like species can be classified as members of the Mammalia with reasonable confidence. For the most part this is not based upon the evidence provided by the fossils from Hallau, but on the close resemblances of these isolated teeth to those of morganucodontids from other areas that are known from much more complete material.

Morganucodon KÜHNE, 1949
Morganucodon peyeri, sp. nov.

Etymology: Dedicated to the late Prof. Bernhard PEYER.

Type specimen: AIII-329 (NC 1, Pl. 2:1), slightly damaged, probably left, lower molariform preserved in a fragment of dentary.

Type locality: Hallau bonebed, Kanton Schaffhausen, Switzerland.

Diagnosis: A small morganucodontid with molariform teeth smaller than those of *Morganucodon oehleri* but approximately the same size as those of *M. watsoni,* however, their crowns appear to be relatively narrower than those of the latter species. Buccal and lingual cingula of upper molariforms tend to be more weakly developed than those of *M. watsoni* and *M. oehleri* and the buccal more frequently interrupted across the base of the principal cusp. Resembling *M. watsoni,* but not *M. oehleri,* the lingual cingulum of the lower molars of *M. peyeri* is relatively well developed. Possibly the presence of a large, anterolingual cingular cusp, almost as large as the anterior accessory cusp, might separate *M. peyeri* from the other species. No evidence of buccal cingula, present on a very few lower molars of *M. watsoni* (PARRINGTON, 1971) and on some of the few described molars of *M. oehleri* (MILLS, 1971), has been found in the small sample of *M. peyeri.*

Referred material:

Upper molariform teeth

AIII-255 (I, Taf. 3), principal and posterior accessory cusp, left.

AIII-264 (X, Taf. 4), anterior accessory cusp, left.

AIII-267 (XIII, Taf. 4), posterior accessory cusp and part of principal cusp, right.

AIII-279 (XXV, Taf. 4), fragment of last molariform, left.

AIII-283 (XXIX, Taf. 4), posterior accessory cusp, left.

AIII-292 (XXXVIII, Taf. 4), anterior accessory cusp, right.

AIII-310 (LVI, Taf. 3), principal and posterior accessory cusp in fragment of maxilla, left.

AIII-324 (LXX, Taf. 12), principal and posterior accessory cusp, left.

AIII-428 (NC 98), posterior accessory cusp?

Lower molariform teeth

AIII-266 (XII, Taf. 4), principal cusp and kühnecone, left.

AIII-273 (XIX, Taf. 4), posterior accessory cusp and kühnecone, right.

AIII-280 (XXVI, Taf. 4), fragment with kühnecone, left.

AIII-284 (XXX, Taf. 4), possibly fragment of anterior end of crown, right.

AIII-296 (XLII, Taf. 4), anterior accessory cusp, right.

AIII-319 (LXV, Taf. 5), principal cusp, kühnecone, and posterior accessory cusp, left.

AIII-380 (NC 50), principal cusp, kühnecone, and posterior accessory cusp, left.

AIII-480 (NC 150), anterior accessory cusp and part of principal cusp, left.

Premolariforms

AIII-258 (IV, Taf. 6), posterior lower premolariform, left.

AIII-261 (VII, Taf. 2), posterior lower premolariform, left.

AIII-263 (IX, Taf. 6), upper premolariform, right.

AIII-277 (XXIII, Taf. 6), premolariform.

AIII-278 (XXIV, Taf. 6), premolariform.

AIII-282 (XXVIII, Taf. 6), premolariform.

AIII-335 (NC 7), posterior lower premolariform, left.

AIII-336 (NC 8), upper premolariform, left.

AIII-350 (NC 22), premolariform.

AIII-368 (NC 40), upper premolariform, left.

AIII-423 (NC 93), premolariform.

AIII-441 (NC 111), premolariform.

AIII-460 (NC 130), upper premolariform.

AIII-509, upper premolariform.

Upper molariforms: The available sample from Hallau lacks examples of complete upper molariform teeth, and the problems of identification and orientation of the fossils are challenging. Criteria developed for orientation of isolated teeth of *Morganucodon watsoni* (see, for example, Mills, 1971) stem from studies of teeth found in maxillary fragments, but unfortunately do not always go into the detail necessary for analysis of isolated teeth. In the following paragraphs the criteria for orientation of the upper molariform teeth are evaluated in a description of the dental morphology. The position in the dentition and orientation of many of the fragments proposed here (see list of referred specimens) differ from those suggested by Peyer (1956). Although usually in agreement on identification of specimens as upper and lower molariforms and on determination of their bucco-lingual orientation, we frequently differ on identification of the anterior and posterior ends of the crowns.

Resembling *M. watsoni*, teeth identified as upper molars of *M. peyeri* have three main cusps aligned mesiodistally with the principal (central) cusp larger and higher than either the anterior or posterior accessory cusp. Differences in their height are not as great as those distinguishing the main cusps of the lower molars. A second criterion applied in identification of upper molars is the presence of both buccal and lingual basal cingula. Mills (1971, p. 37) noted, "although the cingulum is continuous around the unworn tooth [upper molars of *M. watsoni*], it rapidly wears away on the lingual side". Upper molars of *Erythrotherium* and *Megazostrodon* are also characterized by the presence of both cingula but they show greater variation in development. A central break or gap interrupts the buccal cingula of M^{1-2} of *Megazostrodon* and M^1 of *Erythrotherium*. Fragments of molariform teeth allocated to *M. peyeri* with both buccal and lingual cingula (structures more extensive than simply cusps on the sides of the anterior and posterior ends of the crown) have been identified as upper molariforms. Apparently unlike *M. watsoni*, but similar to *Megazostrodon* and *Erythrotherium*, the buccal, and less frequently lingual cingula of unworn upper molariforms of *M. peyeri* are not always continuous along the total length of the crown. In the few instances where the principal and one accessory cusp are preserved and their relative size and height can be determined, the teeth having the cusp proportions taken as characteristic of upper molariforms always have both lingual and buccal cingula.

Parrington (1973, 1978) noted another criterion for differentiating upper from lower molars of *M. watsoni*; this is a feature of the morphology of their roots. The anterior root of an upper molar of *M. watsoni* tends to be oval in cross section with its long axis oriented anteroposteriorly while the posterior root has the long axis of its oval cross section oriented transversely. The long axes of cross sections of both roots of lower molars are oriented anteroposteriorly. This criterion does not appear to be fully applicable to upper molariforms of *M. peyeri*. On some (e. g., AIII-310) the posterior root, identified on criteria of crown morphology, is transversely expanded, but on others (e. g., AIII-283 and the posterior root of the tooth preceding the molar preserved in AIII-310 [Peyer, 1956, Taf. 3, Fig. 56 e]) it is not. These dissimilarities might reflect differences in ontogenetic stage, transverse expansions being a characteristic of older animals; position in the dentition; or perhaps the expansion is a derived morphology that did not characterize all members of *M. peyeri*.

On the basis of the morphology of AIII-310 (Peyer, 1956, Taf. 3, Fig. 56), the only fragment of an upper molariform preserved in a bit of the maxillary bone and, where applicable, comparisons with *M. watsoni*, *Erythrotherium*, and *Megazostrodon*, several criteria appear to be available for distinguishing the buccal and lingual sides of the crown. First, the buccal cingulum is usually wider than the lingual and surmounted by more and larger cusps. The degree of difference in these features, if any, varies between teeth. Mills (1971) noted that in *M. watsoni* development of the buccal cingulum varies along the tooth row being proportionately widest on the anterior molars. The few available fossils of *M. peyeri* suggest its buccal cingulum is more frequently interrupted across the slope of the principal cusp than the lingual.

Secondly, when viewed in transverse section, the apices of the principal and accessory cusps are not situated over the midpoint of the crown but are displaced lingually. Likewise the lingual slope of these cusps rises more steeply and is less convex than the buccal. Particularly on the slopes of the principal cusp, the labial cingulum is situated higher (nearer the apex of the cusp) than the buccal.

Finally, the general occlusal pattern of therapsids and mammals suggests that wear facets might be found on the lingual side of the upper molars, produced by contact with the labial sides of the lowers. Unfortunately, there is clear evidence that the bones concentrated in the Hallau bonebed underwent considerable post-mortem abrasion. Although some teeth show apical facets on the cusps that were most likely formed by abrasion with food, I have not been able to unequivocally identify wear facets on sides of any molariform upper teeth. The only possible exceptions are AIII-267 (Peyer, 1956, Taf. 4, Fig. 13) where one side of the crown is heavily abraided, and possibly AIII-310 (ibid., Taf. 3, Fig. 56), where cusps of the lingual cingulum might be blunted by wear.

Criteria utilized for identification of the anterior and posterior ends of the crown are even more uncertain for the fragment of maxillary preserved with AIII-310 does not give any information about its anteroposterior orientation. Usually in cheek teeth of early mammals the anterior edges of the main cusps do not rise as steeply, are more convex, and are longer than the posterior. This criterion usually appears to be applicable to at least the principal and anterior accessory cusps.

Mills (1971) noted that the anterior accessory cusp is lower than the posterior on M^{1-2}, almost equal on M^3, and quite equal on M^4 and presumed M^5 of *M. watsoni*. Unfortunately none of the fragments of teeth from Hallau preserve both accessory cusps. However the relative depths of the notches separating the main and accessory cusps can be determined. Like upper molars of *Morganucodon watsoni* the notch separating the anterior accessory cusp from the principal cusp appears to have been slightly deeper than that separating the principal and posterior accessory cusp.

In triconodontids the cheek teeth are interlocked by a projecting cusp on the posterior end of one tooth and a groove or basin, usually bounded by buccal and lingual cusps, on the anterior end of the following tooth. This mechanism is weakly developed in *M. watsoni* (Mills, 1971) where the anterior end of a molariform can slightly overlap the buccal side of the preceding tooth. On some upper molariforms of *M. peyeri* (e. g., AIII-310) the end of the crown with a projecting cingular cusp is supported by a transversely wide root; in others (e. g., AIII-283) the root at this end of the crown is elongated in an anteroposterior direction.

In his attempts to distinguish the anterior and posterior ends of the crown Peyer (1956) considered the position of the edge of the crown relative to the underlying root. He thought that characteristically the "anterior" end of the crown juts forward, balcony-like, in advance of the "anterior" face of the root, while the "posterior" accessory cusp is more directly situated over the "posterior" root and the back of the crown is almost in line with the back of the root. On the basis of the other criteria adopted here some of the anteroposterior orientations proposed by Peyer must be reversed and the balcony-like projections of the crowns of some teeth (e. g., AIII-255) are considered to be at the posterior end of the crown. However, the projections of the crown on what are thought to be posterior ends of other teeth are not as extreme and match those of fragments of the anterior end of the crown (e. g., AIII-292). As is the case with orientation of the maximum diameter of the root, the relationship of the margins of the root to the crown in *M. peyeri* might be diagnostic in some instances, but the morphology of the roots could be more variable than morphology of the cusps, and might require information on ontogenetic stage of the tooth before being applied.

In summary, most of the smaller fragments appear to pertain to molariform teeth similar to AIII-255 and AIII-310. A composite upper molariform can be briefly characterized as being dominated by three main cusps, of which the principal is higher than either the anterior or posterior accessory cusps. Probably on any tooth the posterior accessory cusp is as large as, if not larger than, the anterior and separated from the principal cusp by a shallower notch. The apices of these cusps are displaced toward the lingual side of the crown. Cusp development on the broad buccal cingulum varies, but usually the cusps are larger and more numerous than those on the narrower lingual cingulum. Apparently, the larger buccal cingular cusps are situated on the posterior part of the cingulum. When viewed in a transverse section, the lingual cingulum is higher (closer to the apices of the main cusps) than the buccal and the lingual slopes of the cusps are steeper than the buccal. At the posterior end of the crown a cingular cusp projects distally to form a weak interlocking mechanism with the depression in the anterior end of the next (posterior) molariform tooth. Two well separated, slightly diverging roots support the crown. In at least a few specimens the anterior root is anteroposteriorly elongated while the posterior is transversely widened.

One fragmentary tooth differs from this generalized pattern. AIII-279 (Peyer, 1956, Taf. 4, Fig. 25) is heavily damaged and beyond the presence of a large central cusp and anterior and posterior accessory cusps, little can be said about the morphology of its crown. However, the crown appears to have been supported by two closely approximated roots. As Peyer (1956, p. 26—27) suggested, what remains of the tooth is not unlike the posterior upper molars of triconodonts and, in a general way, resembles last upper molariform teeth of *M. watsoni.*

Lower molariforms: A fossil consisting of a damaged molariform and fragment of a mandible (AIII-329, Pl. 2:1) is the most complete mammalian specimen in the collections made by Prof. Peyer after he prepared his 1956 monograph and has been chosen as the type specimen of *Morganucodon peyeri.* This and AIII-319 (Peyer, 1956, Taf. 5, Fig. 65), a fragment consisting of the principal cusp and posterior end of the crown, are the basis for reconstructing the morphology of the lower molariform teeth. Fortunately the bone associated with AIII-329 is clearly a fragment of dentary and both these molariforms preserve the kühnecone, which identifies both the lingual and posterior sides of the crown. Unlike upper molariforms referred to *M. peyeri,* there appears to be little question concerning the anteroposterior and lateral orientation of the lowers.

Resembling the upper molariform teeth, the crown of the lowers consists of three main cusps essentially aligned anteroposteriorly with the principal (central) cusp distinctly larger and higher than the anterior and posterior accessory cusps. Of the two accessory cusps the posterior is the larger. In one fragment (AIII-380) the notch separating the principal and posterior accessory cusps ends in a deep cleft similar to the carnassial notch of therian carnivores. AIII-319 demonstrates the presence of a posterior cingular cusp behind and in line with the posterior accessory cusp; AIII-329 (Pl. 2:1) is damaged in this region but almost certainly had a distinct posterior cingular cusp. The posterior cingular cusp of AIII-273 (Peyer, 1956, Taf. 4, Fig. 19) is slightly more prominent than that of AIII-319.

The buccal side of the crown lacks any indication of basal cusps or cingula. In contrast, on the anterolingual side of the crown there are two cusps on AIII-329. The anterior is the larger of the two and is situated beside but slightly in advance of the only somewhat larger anterior accessory cusp. In occlusal view the anterolingual cingular cusp and anterior accessory cusp bound a shallow concavity in the anterior end of the crown, which probably received the posterior cingular cusp of the preceding molar. If correctly referred to *M. peyeri,* AIII-296 (Peyer, 1956, Taf. 4, Fig. 42) demonstrates the development of an interdentinal wear facet on the front of the crown below and between the anterolingual cingular cusp and anterior accessory cusp.

On both AIII-319 and AIII-329 part of the lingual slope of the principal cusp extends to the base of the crown without interruption by a cingulum. The kühnecone of AIII-329 is relatively larger than that of AIII-319, but both are distinct cusps separated by a cleft from the posterolingual side of the principal cusp.

Behind the kühnecone of AIII-319 are four cingular cusps generally increasing in height and size posteriorly. The most posterior of these lies lingual to the largest posterior cingular cusp, which is situated behind the posterior accessory cusp. The area of the crown between the kühnecone and the posterior cingular cusp shows considerable variation in the development of small cingular cusps. AIII-319 has a high number of cusps while, at the other extreme, on AIII-380, although a cingulum links the kühnecone with the posterior cingular cusp, no individual cusps are present between them.

The crown is supported by two roots but AIII-319 and AIII-329 give little information concerning their morphology. Peyer (1956) identified AIII-280 (ibid., Taf. 4, Fig. 26) as a last upper molariform but more likely it is a fragment of a lower molariform. His figures of the root of this specimen show the suggestion of a blunderbuss-like expansion of the tip of the root.

As was the case with the upper molars, the only unambiguous traces of dental wear are facets on the apices of some cusps (e. g., AIII-266, Peyer, 1956, Taf. 4, Fig. 12). The fragment of dentary of AIII-329 is heavily damaged. A groove along its ventrolingual edge might be what remains of a trough for accessory mandibular bones or, with equal uncertainty, it might be simply an artifact of postdepositional crushing.

Dimensions of molariforms: An accurate assessment of the size of the upper molariforms cannot be made on the basis of the present sample because of the lack of complete teeth. Several specimens are made up of the principal cusp, one accessory cusp, and, infrequently, part of the base of the missing accessory cusp. The range of variation in length of the preserved parts of their crowns is from approximately 1.2 to 1.5 mm. The longest fragment of crown is that of AIII-310, which is the least damaged tooth. Probably it had a maximum crown length of approximately 1.6 to 1.7 mm.

Width of the crown of the upper molars of *M. watsoni* varies according to the relative development of the buccal and lingual cingula and the amount of wear on the lingual side of the crown. The same sources of variation could influence measurements of the width of molars of *M. peyeri*. In order to get an approximation of average crown width of the upper molariforms of the latter species, the maximum widths of the fragments were measured with the following results: N = 7, OR = .48—.70 mm, M = .58 mm.

Only slightly more data on the dimensions of the lower molariforms of *M. peyeri* are available. The perimeter of the crown of one lower molariform, AIII-329, is intact and its dimensions are: length = 1.65 mm, width = .62 mm. Maximum widths of the fragments of lower molariforms were measured with the following results: N = 6, OR = .59—.66 mm, M = .64 mm.

While making comparisons of the fragmentary teeth of *M. peyeri* with a small reference collection of teeth of *M. watsoni* it appeared that the teeth of *M. peyeri* were longer (anteroposteriorly) and relatively narrower (transversely). With so little data available on the dimensions of the teeth of *M. peyeri* it is, of course, impossible to make any rigorous comparisons. However, to see if there was any basis for this impression of differences in proportions, a series of teeth of *M. watsoni* were measured. These teeth are all from Pontalun Quarry, Wales (see Kermack et al., 1973) and are preserved in mandibles so that their position in the dental arcade could be determined on criteria other than the individual morphology of their crowns. These specimens are in the collections of the British Museum (Natural History); Department of Zoology, University College London; and Museum of Zoology, Cambridge University. My analysis was focused on the question, to what extent, if any, do the teeth of the species of *Morganucodon* represented at Hallau differ in coronal dimensions from those of the sample of *M. watsoni* recovered from Pontalun Quarry? It is not a substitute for a still needed, thorough taxonomic study of the species of *Morganucodon* represented in the collections from Pontalun and other fossil localities in southern Wales.

As has been recognized by others (e. g., see Mills, 1971, Parrington, 1971) the longest molariform teeth of *M. watsoni* are M^2 and M_2. The data on the dimensions of these teeth obtained from a study of the Pontalun sample are given in Table 1. Their coefficients of variation are high. This could reflect taxonomic heterogeneity, the mechanical difficulties of obtaining precise measurements of such small teeth, or both.

Table 1

Comparisons of dimensions of molariform teeth of *Morganucodon watsoni*, Pontalun Quarry, and *M. peyeri*, Hallau local fauna.

	N	OR	M	S	CV
Morganucodon watsoni					
M^2					
Length	16	1.10-1.61	1.37	.15	10.7
Width	11	.55- .84	.68	.09	13.8
M_2					
Length	14	1.17-1.65	1.43	.13	9.1
Width	14	.59- .81	.69	.07	10.1
Morganucodon peyeri					
Lower molariform, AIII-329					
Length	1.65				
Width	.62				

Comparison of the dimensions of AIII-329 with the data on M_2 of *M. watsoni* (Table 1) shows that its crown is as long as the longest M_2 in this sample from Pontalun, but its transverse width, 0.62 mm, is less than the mean value. The mean breadths of the fragments of molariforms of *M. peyeri*, 0.58 mm for the upper and 0.64 mm for the lower, are smaller than the means of M^2, M^3, M_2 and M_3, but larger than means of M^1 and M_1 of *M. watsoni*. However, the first molariforms of *M. watsoni* are short (anteroposteriorly) with mean lengths of only 1.13 mm and 1.20 mm respectively.

Visual comparisons of apparently homologous parts of fragments of teeth of *M. peyeri* and *M. watsoni* suggest the molariform teeth of *M. peyeri* tend to be longer and relatively narrower than those of *M. watsoni*. When compared to a sample of *M. watsoni* from Pontalun, Wales, the few dimensions that can be obtained from the fossils from Hallau appear to substantiate this impression.

Premolariform teeth possibly referable to *Morganucodon peyeri:* Considering the relative abundance of its molariform teeth, most likely premolariform teeth of *M. peyeri* are included in the collection from Hallau. The small premolariform teeth described in this section are all of the simple, trenchant morphology that would be expected in the dentition of a morganucodontid. However, *M. peyeri*, is not the only morganucodontid present in the sample from Hallau and there are several other kinds of animals, be they mammal-like reptiles or mammals, represented that might also have had such simple, premolariforms in their dentitions. Grouping the descriptions of these teeth in this section is primarily a literary convenience and only secondarily a suggestion of possible zoological affinities.

AIII-258 (Peyer, 1956, Taf. 6, Fig. 4), AIII-261 (ibid., Taf. 2, Fig. 7), and AIII-335: Assuming the pattern of variation in length of the postcanines of *M. peyeri* is similar to that of *M. watsoni*, these premolariforms are of a size appropriate for posterior lower premolariforms of *M. peyeri* (OR length = 1.15—1.25 mm). The principal cusp of each tooth has a high trenchant crown suggesting it is part of the lower dentition. Two of the three specimens had a low anterior basal cusp. Basal cingula are lacking on the buccal and lingual side of the crown. Two low posterior cusps are present, one directly behind the principal cusp, the other more posterior and lingual in position. To this extent these premolariforms resemble P_4's of *M. watsoni*, but the premolars of *M. watsoni* usually (Mills, 1971) have two anterior basal cusps, a short anterolingual cingulum, and a small kühnecone. No premolariforms resembling P_4's of *M. watsoni* in these details have yet been discovered at Hallau. Whether the absence of additional anterior basal cusps and a kühnecone on P_4 of *M. peyeri* is a characteristic of this species or whether the lower posterior premolariform of *M. peyeri* has not been discovered, of course, cannot yet be determined.

One of the premolariforms, AIII-258 (Peyer, 1956, Taf. 6, Fig. 4) lacks enamel on the buccal side of the posterior accessory cusp. This might be the result of occlusion with an upper tooth.

Five premolariform teeth, AIII-263 (Peyer, 1956, Taf. 6, Fig. 9), AIII-336, AIII-368 (Pl. 2:2), AIII-460, and AIII-509 could be upper premolariforms of *M. peyeri*. Principal cusps of all these teeth are relatively low in comparison to those of the group of premolariforms just described. Similar differences in proportions distinguish upper and lower premolars of *M. watsoni*. Among these premolariforms from Hallau there is variation in development of the basal cingula from absence to presence of an almost complete lingual and a posterior buccal cingulum (Pl. 2:2), a range of variation like that found in *M. watsoni*. Dimensions of the crowns of these premolariforms are as follows: OR length = 0.70—0.95 mm, OR width = 0.44—0.55 mm. Major sections of the roots of AIII-368 (Pl. 2:2) are preserved and show that the posterior was slightly larger and transversely wider than the anterior.

Other premolariforms exhibit some differences in proportions but all have simple, trenchant crowns and might also be referred to *M. peyeri*. Three, AIII-277 (Peyer, 1956, Taf. 6, Fig. 23), AIII-278 (ibid., Taf. 6, Fig. 24) and AIII-423 are of small size (OR length = 0.77—1.03 mm). Their crowns are simple consisting of a principal cusp, a small posterior basal cusp and, on one, an anterior basal cusp. The crowns of AIII-277 and AIII-278 are supported by two, well separated roots; the roots of AIII-423 are missing. Two other small premolariforms, AIII-350 and AIII-441 (OR length = 0.82—1.00 mm) have similar crown morphologies but the roots are not fully divided. Finally, AIII-282 (Peyer, 1956, Taf. 6, Fig. 28) is a single-rooted premolariform with a large principal cusp and a small posterior accessory cusp.

Discussion: The systematic relationships of *Morganucodon peyeri* are considered in a later section following the descriptions of the other morganucodontid and morganucodontid-like mammals of the Hallau local fauna.

?*Morganucodon* sp.

Referred material:

AIII-305 (LI, Taf. 7), fragment of upper molariform, left.

AIII-333 (NC 5, Pl. 2:3) fragment of upper molariform, left.

AIII-340 (NC 12, Pl. 2:4) fragment of lower molariform, left.

Description: These three teeth are approximately the same size as the molariforms of *Morganucodon peyeri* and resemble them in general configuration. However, they are easily distinguished by the absence or relatively weak development of buccal and lingual cingula, and symmetry in length and curvature of the anterior and posterior slopes of the main cusps. Also, if the projecting cingular cusp is at the posterior end of the crown then the posterior roots of these teeth do not show the distinct transverse broadening typical of posterior roots of the upper molars of *M. watsoni* and some teeth from Hallau referred to *M. peyeri* (e. g., AIII-255 and AIII-310).

Of the three, AIII-340 (Pl. 2:4) is the most complete preserving most of the crown and part of one root. Its smallest cusp is assumed to be at the posterior end of the crown. This cusp is slightly offset in what is taken to be a lingual direction from the line of the three main cusps. The other end of the crown is damaged and the presence of an anterior basal cusp cannot be excluded. Except for a minor cingulum bordering a basin between the posterior basal and posterior accessory cusp, no other cingula are present on the crown. This essential absence of cingula and relative size of the cusps suggests AIII-340 is a lower molariform. Other than apical blunting of the main cusps there is no indication of wear facets. The crown was supported by two, well separated roots. The anterior root appears to have been longer anteroposteriorly than the posterior. The posterior probably was slightly wider than the anterior, but the difference might not have been great. A curious rugose area on the presumed buccal side of the posterior root probably is a growth on the root and not a thickening of its wall. A color change on the broken end of the root appears to demark the "normal" wall of the root from the exostosis. Dimensions of the crown of AIII-340 are as follows: length = 1.54 mm, width = 0.48 mm.

The relatively smaller difference in height of their main cusps and presence of basal cingula on one or both sides of their crowns suggest AIII-305 (PEYER, 1956, Taf. 7, Fig. 51) and AIII-333 (NC 5, Pl. 2:3) are upper molariforms. Neither specimen is complete. Both have lost one accessory cusp, which on both teeth teeth appears to have been the anterior. The degree of cingular development on the two teeth differs but, in transverse section, the apices of the main cusps of both are set to one side of the midlines of the crowns. Their steeper slopes are assumed to be on the lingual side of the crown. If so oriented the buccal cingulum of AIII-305 would be relatively better developed and more continuous than the lingual. AIII-333 lacks a lingual cingulum and the buccal is not continuous. Both teeth were supported by two, well separated roots. The widths of the crowns are as follows: 0.37 mm (AIII-333); 0.66 mm (AIII-305).

Discussion: Several interpretations of taxonomic affinity of these teeth are immediately apparent. First, they are teeth of a small morganucodontid that retain a primitive condition in only modest development of basal cingula. Or that the simplicity of their crowns indicates they are posterior premolariforms, deciduous premolariforms, or posterior molariforms of *Morganucodon peyeri*. Finally, and with equal uncertainty, it might be argued that these teeth document the presence of an early representative of the triconodontine triconodontids. Thus designation of these teeth as ?*Morganucodon* sp. is no more than a device to highlight their distinctive morphology. It is recognized that most of the similarities of these fossils to teeth of species of *Morganucodon* probably are the result of shared plesiomorphous characters.

Order ?Triconodonta
Family ?Morganucodontidae
Helvetiodon gen. nov.

Etymology: Helvetia, Switzerland; Odontos, Greek, tooth.

Type species: *Helvetiodon schutzi* sp. nov.

Diagnosis: As for the type and only species.

Helvetiodon schutzi sp. nov.

Etymology: Named for Herr Emil SCHUTZ of Neunkirch who assisted Prof. PEYER in his research in the Hallau area.

Type: AIII-348 (NC 20, Pl. 3:1), a damaged molariform, tentatively identified as a right, upper molariform.

Type locality: Hallau bonebed, Kanton Schaffhausen, Switzerland.

Diagnosis: Based on isolated teeth thought to be upper molariforms. Premolariforms probably are present in the sample, but lower molariforms are either missing or are unrecognized. Molariforms are large, approximately one and a half times the size of those of *Morganucodon*, *Megazostrodon*, and *Erythrotherium*, and in the size range of *Tricuspes* and *Wareolestes*. They differ from molariforms of *Tricuspes* in more complex morphology of the crown with extensive development of labial and lingual cingula and cusps. Presumed upper molariforms of *Helvetiodon* differ from those of *Megazostrodon* in absence of an anterior accessory cusp, more massive and bulbous morphology, and different pattern of development of cingular cusps. *Wareolestes* is known from a tooth that in number and disposition of cusps is little more than an enlarged edition of a lower molar of *Morganucodon*. In contrast, the presumed upper molariforms of *Helvetiodon schutzi* are not as close in their morphological resemblance to the upper molars of any known species of *Morganucodon*.

Referred materials:

Molariforms

AIII-268 (XIV, Taf. 4), fragment of posterior end of upper molariform.

AIII-270 (XVI, Taf. 4), fragment of posterior end of upper molariform.

AIII-303 (XLIX, Taf. 7), fragment of posterior end of upper molariform.

AIII-354 (NC 26, Pl. 3:2), crushed crown lacking posterior end, upper right.

AIII-390 (NC 60), fragment of posterior end of upper molariform.

AIII-437 (NC 107), fragment of an end of a molariform.

Premolariforms (reference to *Helvetiodon schutzi* tentative, see text)

AIII-259 (V, Taf. 11), anterior premolariform or incisiform.
AIII-265 (XI, Taf. 7), principal and anterior basal cusp.
AIII-291 (XXXVII, Taf. 8), anterior premolariform.
AIII-302 (XLVIII, Taf. 7), principal and accessory cusp.
AIII-325 (LXXI, Taf. 12), principal cusp.
AIII-334 (NC 6), principal and accessory cusp.
AIII-359 (NC 31), slightly damaged, principal and accessory cusp.
AIII-360 (NC 32), fragment with principal and accessory cusp.
AIII-393 (NC 63), fragment of crown.
AIII-402 (NC 72), principal and small, ?anterior basal cusp.
AIII-424 (NC 94, Pl. 3:3), anterior premolar.
AIII-439 (NC 109), anterior premolar.
AIII-458 (NC 128, Pl. 3:4), principal and accessory cusp.
AIII-459 (NC 129), principal and small, ?anterior basal cusp.

Incisiforms and caniniforms (reference to *Helvetiodon schutzi* tentative, see text).

AIII-260 (VI, Taf. 6)
AIII-271 (XVII, Taf. 6)
AIII-274 (XX, Taf. 8)
AIII-294 (XL, Taf. 6)
AIII-304 (L, Taf. 11)
AIII-311 (LVII, Taf. 11)
AIII-316 (LXII, Taf. 8)
AIII-326 (LXXII, Taf. 12)
AIII-330 (NC 2)
AIII-341 (NC 13)
AIII-345 (NC 17)
AIII-347 (NC 19)
AIII-349 (NC 21)
AIII-365 (NC 37)
AIII-416 (NC 86)
AIII-477 (NC 147)

The hypodigm of this taxon consists of two nearly complete molariforms and several fragments. None are of typical haramiyid morphology, and they show some resemblance to teeth of morganucodontids. The teeth are large, about one and a half times the size of teeth of similar morphology referred to *Morganucodon peyeri*, and lie in the estimated size range of *Tricuspes tubingensis*. A number of premolariforms ranging from essentially complete teeth to fragments of crowns, as well as incisiforms and caniniforms are also described here. These are the large premolariforms, incisiforms, and caniniforms found at Hallau and for the sake of convenience are described as a unit. Some could well be elements of the dentition of *Helvetiodon*, but the possibility that others are parts of dentitions of *Tricuspes*, haramiyids, or other mammals or mammal-like reptiles cannot be excluded.

Description: Both the type specimen of *Helvetiodon schutzi* and the complete referred molariform (AIII-354) are elements of the new collection assembled after 1956. The two fossils preserve a large part but not all of the crown. As a result of abrasion and/or chemical attack the type (AIII-348) has lost large segments of its enamel cap (in Pl. 3:1 enamel-covered areas are rendered in darker tones). More of the crown of AIII-354 (Pl. 3:2) is preserved, but the tooth has been crushed laterally (buccolingually) and distorted. The crowns of both teeth are dominated by a large principal cusp. When viewed laterally, the longer, slightly steeper slope of the principal cusp is assumed to be its anterior slope, and the accessory cusp a posterior accessory cusp.

In comparison to known morganucodontids and triconodontids the relative height of the principal cusp of these two teeth would be extreme but not inappropriate for an upper molariform (e. g., note the M^2 of *Morganucodon oehleri* [Mills, 1971, Pl. 5A]) or the last, upper premolariform (note *M. watsoni* [ibid., Pl. 1D; Parrington, 1971, Fig. 16f] or *M. oehleri* [Mills, 1971, Pl. 5A]). However, the relative proportions of height of principal cusp to length of crown more frequently would be matched by lower molars of *Morganucodon*. This characteristic suggesting the two teeth are lower molariforms is contradicted by the presence of both lingual and buccal cingula on the type and, probably, the referred specimen. With few exceptions (e. g., note *Hallautherium* gen. nov., described below) development of basal cingula on both sides of the crown is a definitive characteristic of upper molariform teeth of advanced mammal-like reptiles and early mammals. Provisionally, this character is given greater weight. But it must be stressed that both teeth are isolated and their tentative identification as upper molariforms is not substantiated by association with recognizable fragments of the maxillary bone.

Finally, and again essentially arbitrarily, degrees of completeness and complexity of the basal cingula are used to distinguish buccal and lingual sides of the crown. In morganucodontids, if there is any difference in complexity or completeness of the basal cingula of upper molars, usually the buccal cingulum is not as completely developed as the lingual, but it can be wider and carry larger cusps.

In summary, all the molariforms and fragments of molariforms allocated to *Helvetiodon schutzi* are isolated specimens lacking associated segments of maxillary or dentary bones. Their identification as elements of the upper dentition and determination of anteroposterior as well as lateral orientations are based primarily on comparison with molariform teeth of morganucodontids, to which they show some resemblance. All these determinations of position and orientation must be regarded as tentative.

Posterior to the dominant, principal cusp of the type (Pl. 3:1) is a small, low accessory cusp, which is now missing most of its enamel cap. An anterior accessory cusp, similar to those found on molars of *Morganucodon* was not present. The two major cusps at the anterior end of the crown are set laterally; the anterolingual is larger and positioned more anteriorly than the buccal. Configuration of the dentine core of the anterobuccal cusp suggests a ridge connected its apex with the crest along the anterior edge of the principal cusp.

On the lingual side of the preserved part of the crown the basal cingulum becomes lower from both ends toward the midpoint where it is interrupted for a short distance. The anterior segment carries two small cusps behind the large anterior cusp. On the posterior segment a large cingular cusp is present lingual to the notch separating the principal and posterior accessory cusps. What remains of the rest of the posterior end of the crown has been stripped of most of its enamel covering. There appears to have been a small, posterolingual basin enclosed by the posterior accessory cusp, large posterolingual cingular cusp, and the rising posterior end of the crown. The posterior crest of the posterior accessory cusp could have interrupted the cingulum across the posterior end of the crown.

Except around the apex of the principal cusp, most of the enamel is missing from the buccal side of the crown. The configuration of the remaining dentine indicates the presence of at least two, distinct posterior cingular cusps. There is no evidence of a buccal cingulum connecting the posterior and anterior cingular cusps. Dimensions of what remains of the crown of AIII-348 are as follows: length = 2.67 mm; width = 1.39 mm. The crown was supported by two, large but well divided roots.

Although somewhat crushed and distorted, AIII-354 (Pl. 3:2) also appears to be a right, upper molariform that in most respects is a duplicate of the type. The few morphological differences most likely reflect individual variation or difference in positions in the dentition. Like the type, the anterobuccal cingular cusp apparently was smaller than the lingual, but in AIII-354 it is clearly a terminus of the midline crest of the principal cusp.

The posterior slope of the principal cusp is transversely narrower than the body of the cusp and demarked from it by symmetrical vertical, buccal and lingual depressions. These might be the result of postmortem distortion, but more likely are original features of the tooth. Another possible difference from AIII-348 is the apparent absence of posterobuccal cingular cusps. The enamel is preserved over the buccal side of the principal cusp, and a cingulum is not present. Probably the two roots supporting the crown were well separated.

Dimensions of the crushed crown of AIII-348 are now: length = 2.85 mm; width = 1.09 mm. This tooth and the type of *Helvetiodon* are larger than would be expected for elements of the dentition of *Morganucodon peyeri, M. watsoni,* or *Hallautherium* (gen. nov., described below) and are in the predicted size range of *Tricuspes.*

In his description of the fossils from Hallau PEYER (1956) noted the presence of several fragments of large, molariform, triconodont-like teeth. These, and a specimen in the new collection appear to be too large to be parts of teeth of *Morganucodon peyeri* and *Hallautherium* (gen. nov., described below), but have a more complex morphology than would be expected in teeth of *Tricuspes tubingensis.* Comparisons with the more complete molariforms just described suggest that AIII-268 (PEYER, 1956, Taf. 4, Fig. 14) and AIII-303 (ibid., Taf. 7, Fig. 49) could be fragments of the posterior ends of crowns of molariforms of *Helvetiodon schutzi.* AIII-390 (NC 60) and AIII-437 (NC 204) might have had a similar origin.

AIII-270 (PEYER, 1956, Taf. 4, Fig. 16) preserves part of the slope of what probably was the principal cusp, posterior accessory cusp, and a cingular cusp. On one side of the crown a crenulated cingulum extends at least part way around the base of the accessory cusp; the full extent of this cingulum and morphology of the base of the other side of the crown are unknown. PEYER (ibid., p. 43) noted the "symmetrodont-like" disposition of the cusps of this fragment. If what remains of the posterior crest of the principal cusp is assumed to have extended directly to its apex, then the cingular cusp does not lie on a line defined by the apices of the principal and accessory cusps. The angulation is not as great as that at the junction of the anterior crest of the principal cusp and the crest of the anterobuccal cusp of AIII-354 and, probably, AIII-348. AIII-270 (PEYER, 1956, Taf. 4, Fig. 16) might be part of either an upper molariform or an otherwise unknown (or unrecognized) lower molariform of this species.

Premolariforms tentatively referred to *Helvetiodon schutzi:* The collection from Hallau contains several large premolariform teeth, probably too large to have been parts of the dentition of *Morganucodon peyeri.*

Some of these have accessory and basal cingular cusps suggesting they are elements of the dentition of *Helvetiodon schutzi;* others lacking such cusps might be parts of the presumably morphologically simpler dentition of *Tricuspes tubingensis.* For the sake of convenience all are briefly considered here.

Many of the large premolariform teeth resemble AIII-458 (Pl. 3:4). The principal cusp is not at the center of the crown, but is offset toward the assumed anterior end. Strong anterior and posterior crests from the edges of the principal cusp whose relatively great height suggests the tooth might be a lower premolariform. Near the base of the crown the anterior crest is deflected laterally to join a basal cingulum, which is truncated by a fracture. Probably the tooth lacked an anterior basal cusp. From comparisons with premolars of *Morganucodon watsoni* it appears likely that the basal cingulum is on the lingual side of the crown. The notch between principal and posterior accessory cusps is not particularly deep. On either side of this notch depressions extend basally; the lingual depression is larger. Buccal and smaller, lingual basal cusps are linked by a distinct, low crest. The crown was supported by two, well separated roots. Its dimensions are as follows: length = 1.47 mm, width = 0.77 mm.

The distal end of the crown of AIII-359 (NC 31) is damaged but the tooth appears to be essentially a duplicate of AIII-458 (width of crown = 0.84 mm). AIII-334 (NC 6) is similar to but smaller (length of crown = 0.99 mm, width = 0.48 mm) than the two teeth just described and its posterior basal cusps are not as large. It was supported by two distinct roots.

Proportions of the crown of AIII-302 (Peyer, 1956, Taf. 7, Fig. 48) are slightly different from those of AIII-458, but easily could be encompassed within the range of individual variation of homologous teeth. The apex of the principal cusp of AIII-302 has been blunted; apparently by contact with foodstuffs and not post-mortem abrasion. Dimensions of the crown are as follows: length = 1.42 mm; width = 0.77 mm.

Peyer (1956) thought AIII-265 (ibid., Taf. 7, Fig. 11) was part of the posterior end of a premolariform. The fragment is in the same size range as most of those premolariforms just described (crown width = 0.84 mm). Configuration of what is preserved of the crown suggests it is a fragment of the anterior end of a premolariform differing from AIII-458 in the presence of a anterior basal cusp. A weakly developed lateral cingulum extending to the apex of this basal cusp might be on the lingual side of the crown.

AIII-402 (NC 72) and AIII-459 (NC 129) appear to be fragments of large, two-rooted premolariforms each having a small, ?anterior basal cusp but lacking lateral basal cingula. A large segment of the root of AIII-459 is preserved and exhibits a slight but distinct curvature toward the midpoint of the crown. There is no evidence of expansion of the root but part of its tip is missing.

Although what little is preserved of its crown does not closely resemble those of any of the other large premolariforms, one of the roots of AIII-393 (NC 63) is preserved. It is curved, strongly diverging from the presumed vertical axis. Again, the tip is broken, but there is no sign of expansion.

AIII-325 (Peyer, 1956, Taf. 12, Fig. 71) is a small fragment of what appears to have been a large premolariform. One side of the crown (the side not illustrated by Peyer, ibid.) is heavily damaged. The width of the remaining part of the crown is 0.73 mm. If the preserved basal region of the crown is its anterior end, which seems more likely, then AIII-325 differs from AIII-458 in the greater complexity of cingular development. If it is part of the posterior end of the crown, it is of much simpler construction than AIII-458.

AIII-360 (NC 32) is a complete premolariform but is sligthly smaller than most of those described above (crown length = 1.06 mm; width = 0.62 mm). Its crown consists essentially of the principal cusp. A small basal cusp is present at the posterior end of the crest of the posterior ridge of the principal cusp. Just lateral to this basal cusp on the slightly more bulbous, convex side of the crown is a short basal cingulum. Most of the root(s) of the tooth is missing. What remains shows some indication of subdivision but does not clearly demonstrate whether the tooth was double or single rooted.

AIII-424 (NC 94, Pl. 3:3) is a small premolariform that, except for its large size (crown length = 0.73 mm; width = 0.40 mm) is similar to P_1 or P_2 of *Morganucodon watsoni.* The crown is simple consisting of an anteriorly canted principal cusp, two cusps on the lower part of the posterior crest of the principal cusp, and a simple cingulum along the anterobasal (?lingual) side of the crown. Although there is a vertically oriented depression on the ?buccal side of the root, a similar depression is lacking from the opposite side. The crown of AIII-439 (NC 109) is similar to that of AIII-424 but slightly larger (crown length = 0.92 mm, width = 0.44 mm). A depression on one side of the root of this tooth, which also is probably an anterior premolar, separates it into two lobes. The crown of AIII-291 (Peyer, 1956, Taf. 8, Fig. 37) is similar to those of the two premolariforms just described but it is significantly larger (length = 1.47 mm; width = 0.73 mm). AIII-259 (ibid., Taf. 11, Fig. 5) might be the crown of an anterior premolariform or an incisor.

Incisiforms and caniniforms: Finally, and primarily for the sake of completeness, teeth that might be incisiforms or caniniforms of *Tricuspes* or *Helvetio-*

don are noted in the list of referred material. All appear to be too large to be referable to either *Morganucodon* or *Hallautherium* (gen. nov. described below). If haramiyids were not multituberculate-like in the morphology of the anterior part of their dentitions (a common working assumption based on no conclusive evidence), the derivation of some of the teeth from dentitions of these animals is also possible.

Discussion: The possibility that teeth allocated to *Helvetiodon* might be parts of the dentition of *Tricuspes* was considered. It can be suggested that *Tricuspes* is based on lower molariforms and *Helvetiodon* on upper molariforms of the same taxon. However, the difference in degree of development of their basal cingula and of the separation of their roots argue against this possibility. Another hypothesis is that *Tricuspes* is typified on premolars of *Helvetiodon*, which could explain the differences in cingular structure. Again the differences in morphology of the roots (those of *Tricuspes* being only incipiently divided while the molariforms of *Helvetiodon* were supported by two well-divided roots) and the presence in the sample of several large, two-rooted premolariforms more likely referable to *Helvetiodon* argue against this hypothesis. On the limited data available a third hypothesis, that *Tricuspes* and *Helvetiodon* are distinct taxa, appears to be slightly more probable.

Order and Family incertae sedis
Hallautherium gen. nov.

Etymology: Hallau; Ther, Greek, beast.
Type species: *Hallautherium schalchi* sp. nov.
Diagnosis: As for the type and only species.

Hallautherium schalchi sp. nov.

Etymology: Named for Ferdinand Schalch whose studies of the Triassic-Jurassic boundary resulted in the discovery of the fossil locality near Hallau.

Type specimen: AIII-318 (Peyer, 1956, LXIV, Taf. 5, Fig. 64 & Text-figs. 2a—b; Fig. 5), left lower molariform preserved in a fragment of dentary.

Diagnosis: Only known from lower molariforms with a main row of four cusps and one or more anterior and posterior lingual cusps. These molariforms lack a basal, lingual cingulum or kühnecone. Unlike any known morganucodontids a large, posterior buccal basin is present on the type (a small depression on the referred specimen). Teeth are in the size range of *Morganucodon watsoni* and *M. peyeri*, but are smaller than those of *Tricuspes* and *Helvetiodon*.

Referred material:

AIII-337 (NC 9, Pl. 3:5), isolated lower molariform, right.

Description: The orientation of the type specimen (Fig. 5) suggested here differs from that proposed by Peyer (1956) and utilized by Hopson and Crompton (1969) and Parrington (1978). That the tooth is a lower molariform is clearly demonstrated by the fragment of dentary in which it is implanted. The principal cusp is anterior to the midpoint of the crown length (anteroposteriorly).

Two lines of evidence suggest the tooth is a left rather than a right lower molariform. The fragment of dentary of AIII-318 preserves essentially a full cross section of this bone (see Peyer, 1956, Taf. 5,

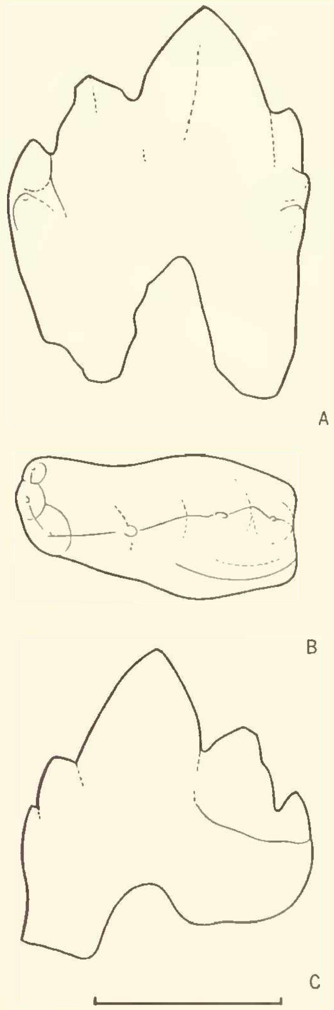

Figure 5: Outline drawing of AIII-318, *Hallautherium schalchi*, Hallau local fauna, Switzerland. A. lingual view, B. occlusal view, C. buccal view. Scale equals 1 mm.

Fig. 64, and Text-figs 2a—b). Directly behind the molariform there is a deep depression in the dentary. If this is part of the wall of a dental crypt, it suggests that at time of death the preserved molariform was near the posterior end of the horizontal ramus of the dentary. In support of this interpretation, a low ridge along the posterior part of the top of the dentary lateral to the molariform appears to be the anterior end of the coronoid process. As far as known the coronoid process of the dentary of advanced mammal-like reptiles and early mammals lies either in line with or, usually, buccal to the posterior teeth. A second line of evidence is the apparent development of buccal wear facets on AIII-318 and presence of a large wear facet on the referred specimen (AIII-337, Pl. 3:5).

If identification of AIII-318 as a posterior molariform is correct, the absence of indications of a lingual groove to house the splenial and, possibly, the prearticular and angular, as well as "Crompton's groove" (see PARRINGTON, 1971) is of some significance. In a homologous section of a dentary of a young individual of *Morganucodon watsoni* both grooves, particularly the former would be expected to be present (note PARRINGTON, ibid., fig. 10e—f). Enough of the surface of the dentary of AIII-318 is preserved to suggest the apparent absence of these grooves is not a result of post-mortem abrasion. Thus, possibly the mandible of *Hallautherium schalchi* was more mammal-like in construction than that of *Morganucodon watsoni* and other approximately contemporaneous morganucodontids.

The crowns of the lower molariforms are dominated by the relatively high principal cusp, situated anterior to the midpoint of the crown. Of the two accessory cusps the posterior is distinctly larger. The central row of cusps is completed by a small, posterior cusp set slightly buccal to the line formed by the other three. On AIII-318 there are two cusps lingual to the anterior accessory cusp. Of these the cusp in the most lingual position is the smaller. On AIII-337 only one major cusp is present lingual to the anterior accessory cusp, but a small cuspule is developed on its posterior slope (Pl. 3:5). Both teeth have a small posterolingual cusp lingual to the last cusp of the main row. There is no evidence of even slight development of either a cingulum between the anterior and posterior lingual cusps or a kühnecone.

Although closely similar in all characters described so far, AIII-318 and AIII-337 differ in structure of the buccal side of their crowns. On AIII-318 a distinct basin is present low and buccal to the posterior accessory cusp and the last (posterior) cusp of the main row. The buccal rim of this basin is smooth, but in comparison to adjacent parts of the crown differences in the texture of the rim and internal surface of the suggest the presence of wear facets. The degree to which attrition could have modified the configuration of the basin and its buccal rim cannot be assessed. Anterior to this basin the buccal surface of the crown is not interrupted by a cingulum or cusps. In contrast, AIII-337 lacks a distinct posterior buccal basin. A well-defined elongate wear facet lies along the buccal surface of its posterior accessory cusp. Posterior to it is a small basin-like depression.

Both teeth appear to have been supported by two, well separated roots. Of the two fossils, AIII-318 is distinctly the larger, length = 1.39 mm, width = 0.66 mm. Dimensions of AIII-337 are length = 1.08 mm, width = 0.44 mm. As long as the positions of these teeth in the dental arcade remain unknown, it is impossible to directly compare the size of *Hallautherium schalchi* with the known species of morganucodontids. However, assuming that AIII-337 is not the most posterior of the lower molariforms their dimensions suggest the dentition of *H. schalchi* was approximately in the size range of that of *Morganucodon watsoni* and *M. peyeri* but smaller than *Tricuspes*.

Discussion: Several paleontologists (e. g., PARRINGTON, 1978) have noted the differences between the type specimen of *Hallautherium schalchi* and the large samples of teeth of *Morganucodon watsoni* from localities in Wales. Size and/or configuration of cusps also clearly distinguish *Hallautherium* from *Megazostrodon* and *Erythrotherium*. However, there is a basic similarity in the overall configuration of their crowns, which are dominated by a central row of three or more cusps. This similarity is interpreted to be a common trait of many advanced mammal-like reptiles and early mammals in which increased complexity of the crown was achieved simply by multiplication of cusps along an anteroposterior (mesiodistal) axis.

The key difference between *Hallautherium* and known morganucodontids is the extreme development of the posterobuccal basin on at least one of the lower molariforms. Posterobuccal cusps occur on a few lower molars of *M. watsoni* (PARRINGTON, 1978), and MILLS (1971) noted the presence of a "suggestion of a cingulum on the buccal surface" of M_3 of *M. oehleri*. However, the presence of such a large buccal basin, which appears to have occluded with a cusp(s) of an upper molariform, is unknown in any species of *Morganucodon*, *Erythrotherium*, *Megazostrodon* or *Eozostrodon*. By the admittedly subjective standards employed in the taxonomy of early mammals, recognition of a new genus and species appears warranted. Whether the differences are indicative of a degree of phylogenetic separation that might be recognized through establishment of a new family is an assessment that should await collection of additional material.

SYSTEMATIC RELATIONSHIPS

The data currently available suggest that during the Middle and Late Triassic a number of lineages of cynodont therapsid reptiles diversified and independently underwent selection for decrease in body size, reduction in relative size of many elements of the lower jaw, increased complexity of dental morphology and occlusal pattern, and other characters of the mammalian grade of organization (see Crompton and Jenkins, 1979). If better known evolutionary radiations of other groups of vertebrates can be used as models, probably many characters now taken as diagnostic of mammals evolved in parallel in distinct lineages. Also the models would suggest that most of these lineages became extinct and were not represented by descendants in Middle or Late Jurassic faunas. Finally, if these assumptions are correct, the occurrence of species with a mosaic of a primitive grades of mammalian dental morphology and function but reptilian grades in other skeletal traits must be expected. Proper taxonomic allocation of such species has to await discovery of specimens yielding more than just information on dental morphology.

The class and ordinal affinities of many of the vertebrates in the local faunas of the Tübingen-Stuttgart area and Hallau that are known only from mammal-like teeth cannot be established on the meager data available. *Tricuspes* is an excellent case in point. The genus is now represented by isolated, fragmentary teeth found at Gaisbrunnen, Hallau, and, possibly, Sonnenberg bei Degerloch (D. Sigogneau-Russell, pers. comm., has found teeth referable to *Tricuspes* at Saint-Nicolas-du-Port). These teeth have some mammal-like features: presence of three cusps that are not aligned anteroposteriorly; development of a fourth, ?postero-buccal cusp; and at least incipient, if not full subdivision of the root. However, beyond these there is nothing suggesting mammalian affinity of the animal that bore these teeth. Among the few known Middle or Late Jurassic mammals or cynodonts none appear to be descendants of *Tricuspes.* However, the available samples of Jurassic faunas probably give us only limited documentation of their diversity. Though descendants might be identified in the future, most likely *Tricuspes* is a member of an advanced cynodont or cynodont-derived mammalian lineage. Querried allocation of *Tricuspes* to the Mammalia recognizes the few mammal-like features of its teeth.

Although ranging from the Middle Keuper (Norian) to possibly the Bathonian (see (Clemens and Kielan-Jaworowska, 1979), the Haramiyidae remains a poorly represented group in the fossil record. Haramiyids are known only from isolated teeth found at localities in Great Britain, France, West Germany, and Switzerland. A jaw fragment containing two or more teeth, an edentulous jaw, or any other skeletal material of a haramiyid have yet to be discovered or recognized. Current hypotheses concerning the systematic relationships of haramiyids were reviewed by (Clfmens and Kielan-Jaworowska (1979) but can be summarized here as follows: Many workers, emphasizing the mammal-like complexity of cusp morphology and root structure, tentatively include the Haramiyidae in the Mammalia. Some argue that haramiyids might be ancestral or closely related to the ancestors of multituberculates, but there is division of opinion on these hypotheses. Most likely the formally named taxa and informal taxonomic groupings are based simply on associations of morphologically similar teeth, and the current intrafamilial classification primarily reflects degrees of morphological similarity.

Review of the haramiyid teeth in the samples of local faunas of the Tübingen-Stuttgart area and Hallau revealed considerable morphological diversity. *Thomasia antiqua*, *Thomasia* sp. 2 (Hahn, 1973), and ?*Thomasia* sp. were identified in the collections from the German localities. Specimens referable to *Haramiya* have yet to be found, but this could easily be a product of the small sample sizes. Both form genera are represented in the Hallau local fauna. Isolated teeth of cf. *Thomasia antiqua*, *T. anglica*, ?*Thomasia* sp., cf. *Thomasia* sp., *Haramiya moorei*, as well as fragments of haramiyid teeth of uncertain specific or generic affinity are present in this sample. Unfortunately these fossils do not provide a key to understanding the composition of the haramiyid dentition or the systematic affinities of the group, but only document greater diversity in dental morphology.

Since publication of Peyer's (1956) monograph many workers have recognized that at least one species of morganucodontid was present in the Hallau local fauna. Detailed analyses of the material supports this view revealing the presence of a species closely resembling *Morganucodon watsoni*, *M. oehleri*, and *Erythrotherium parringtoni.* In order to distinguish specimens of *Morganucodon* and *Erythrotherium* data on the relative proportions and sequential morphologic differences of the cheek teeth are required (Crompton, 1974). These are not available for the Swiss species. Its allocation to *Morganucodon*, known from localities in Europe and Asia, rather than *Erythrotherium,* known only from South Africa, is based solely on the biogeographic probabilities.

The known molariforms of *Morganucodon peyeri* do not show particularly close resemblances to the morganucodontid recently described by Sigogneau-Russell (1978) in her preliminary report on the mammals found at Saint-Nicolas-du-Port. Full evaluation of the relationships of this animal must await further study of the new material from France.

Molariforms of *Morganucodon peyeri* differ from those of *M. watsoni* and *M. oehleri* in several morphological details that warrant recognition of a new species. The possibility that the Hallau local fauna is older than the local faunas from Rhaeto-Liassic fissures in Wales invited testing the hypothesis that *M. peyeri* was either ancestral to *M. watsoni* or documented a more primitive grade of evolution. Some features tend to support these speculations. The buccal and lingual cingula of the upper molariforms of *M. peyeri* are not as large as those of *M. watsoni.* Possibly the lower frequency in development of expansions of the roots of the molariforms of *M. peyeri* is a primitive trait. Also, the relative rarity of wear facets might be interpreted as indicating a more primitive grade in evolution of precise occlusal patterns

Although suggestive, none of these observations strongly supports the hypothesis and all can be interpreted in other ways. The geological evolution of western Europe during the Rhaeto-Liassic involved reduction in size and subdivision of land areas. The fossil record suggests *Morganucodon* or its ancestors were wide spread over what is now Eurasia. During the marine transgressions populations of terrestrial vertebrates were subdivided and isolated. They appear to have evolved independently to produce a series of distinct insular faunas. *Morganucodon watsoni* and *M. peyeri* probably represent different lineages formed during this radiation.

Three isolated teeth from Hallau are identified as ?*Morganucodon* sp. Although illustrating some features also found in morganucodontids, for example the presence of three principal cusps aligned anteroposteriorly, their crowns lack others, such as distinct cuspidate lateral cingula and kühnecones. The teeth are of the proper size to have been elements of the dentition of *M. peyeri*, perhaps posterior premolariforms, deciduous premolariforms, or posterior molariforms. Also, it is quite possible that they are molariform teeth of a primitive triconodontid or a hitherto unknown family of mammals.

Two new genera and species of vertebrates, probably mammals, are recognized in the Hallau local fauna. The teeth used to typify *Helvetiodon schutzi* are relatively large and bulbous for elements of the dentition of a Rhaeto-Liassic mammal. Although in approximately the same range of size as *Tricuspes*, the possibility that they are elements of the dentition of this or a closely related genus appears unlikely at the moment. As currently known, the molariforms of *Helvetiodon* had two, large principal cusps, the central being the larger. An anterior accessory cusp similar to those found on molars of *Morganucodon* is not present on the available teeth. Like *Morganucodon* upper molars, the molariforms of *Helvetiodon* had buccal and lingual cingula, but the morphology of the cingular cusps differs.

Recently FREEMAN (1979) described *Wareolestes rex* from a single tooth found in deposits of Bathonian age (Middle Jurassic) in the Forest Marble of Oxfordshire, England. The type is a large tooth (crown length = 2.31 mm; width = 1.24 mm, ibid.) comparable in size to the type and referred molariform of *Helvetiodon schutzi.* However, the type of *Wareolestes* appears to be an "enlarged" or "inflated" version of a lower molar of *Morganucodon watsoni.* As pointed out by FREEMAN (ibid.), the points of resemblance include occurrence of a principal row of four cusps and, although positioned somewhat anteriorly opposite the principal cusp, presence of an apparent homologue of the kühnecone. However, unlike most molars of *Morganucodon*, a subdued, noncuspidate cingulum is present on the buccal side of the crown. In contrast, although exhibiting some similarities, the molariforms of *Helvetiodon* are not so closely comparable to the upper molars of *Morganucodon.*

Hallautherium schalchi, the second new genus of mammals recognized in the Hallau local fauna, is based on lower molariform teeth smaller than the molariforms of *Helvetiodon.* The type specimen, AIII-318, was described by PEYER (1956). As has been argued above, the data suggest that PEYER's identification of the buccal and lingual sides of the tooth was in error. At least one of the lower molariforms of *Hallautherium* had a distinct posterior buccal basin that might well have received and been worn by a cusp of an upper molariform. Also, both the type and referred specimens, apparently also a lower molariform, lack kühnecones. Finally, the morphology of the small fragment of dentary preserved in the type suggests it was more mammal-like in construction than that of *Morganucodon watsoni.* These characters set *Hallautherium* well apart from any known morganucodontid or other Rhaeto-Liassic mammal.

Although following PEYER (1956) in orientation of AIII-318, HOPSON and CROMPTON's (1969) comments on this fossil are still pertinent to the problem of unraveling the ancestry of the multituberculates. Among the known, non-therian mammals of the Rhaeto-Liassic the general pattern of dental morphology is one of molariform teeth dominated by an anteroposteriorly oriented row of three or more cusps. The buccal side of the lower molariforms occluded against the lingual side of the uppers. Basal cusps or cingula normally occur on both sides of the upper molariforms, but only on the lingual side of the lowers.

Multituberculates first certainly appear in the fossil record in the Kimmeridgian (Late Jurassic), but might be recorded by a specimen of Bathonian age (Middle Jurassic, FREEMAN, 1976) from Britain or an Early Jurassic fossil found in India (DATTA et al., 1978). Like other non-therians the cusps of the molars of multituberculates are arranged in anteroposteriorly oriented rows. Although yet to be documented, it appears most likely that their molar pattern originated through the addition of basal cingula, which evolved into rows of cusps lateral to the main row of cusps. Evidence provided by the structure of their premolars and relative development of cusp rows on their molars suggests that multituberculate lower molars and M^1 evolved through addition of a buccal row of cusps to the primitive row while M^2 appears to have originated by the addition of a lingual row of cusps (see CLEMENS and KIELAN-JAWOROWSKA, 1979). Currently this presumed pattern of addition of cusp rows stands as the key apomorphy of the Multituberculata.

The importance of the dental morphology of *Hallautherium* in considerations of the ancestry of multituberculates is not that these teeth exhibit apomorphies hitherto only known in multituberculates. They do not. However, in being an exception to what has been regarded as the standard pattern of cingular development on molariform teeth of non-therians, they add to the documented range of morphological variation among these mammals. Thus they strengthen the plausibility of the hypothesis calling for origin of molars of multituberculates through a unique pattern of cingular development. Unless there were major reversals in the evolutionary trend in development of these additional cingula and rows of cusps, a correlary of this hypothesis is that the common ancestors of multituberculates and other non-therian mammals would be animals whose molariform teeth lacked basal cingula. Clearly such a grade in dental evolution would be appropriate for very early non-therian mammals or cynodont reptiles.

In summary, the available collections of Rhaeto-Liassic mammals from Switzerland and West Germany add to the documented diversity of mammalian lineages at this time. These collections, and that being assembled by SIGOGNEAU-RUSSELL from a locality in eastern France, clearly show that Rhaeto-Liassic mammals can no longer be easily classified in just three families, Morganucodontidae, Kuehneotheriidae, and Haramiyidae. Distinctly different mammalian lineages were present during this interval. Their diversity tends to support the view that the first members of the Mammalia are to be sought in older, Late Triassic or possibly Middle Triassic faunas.

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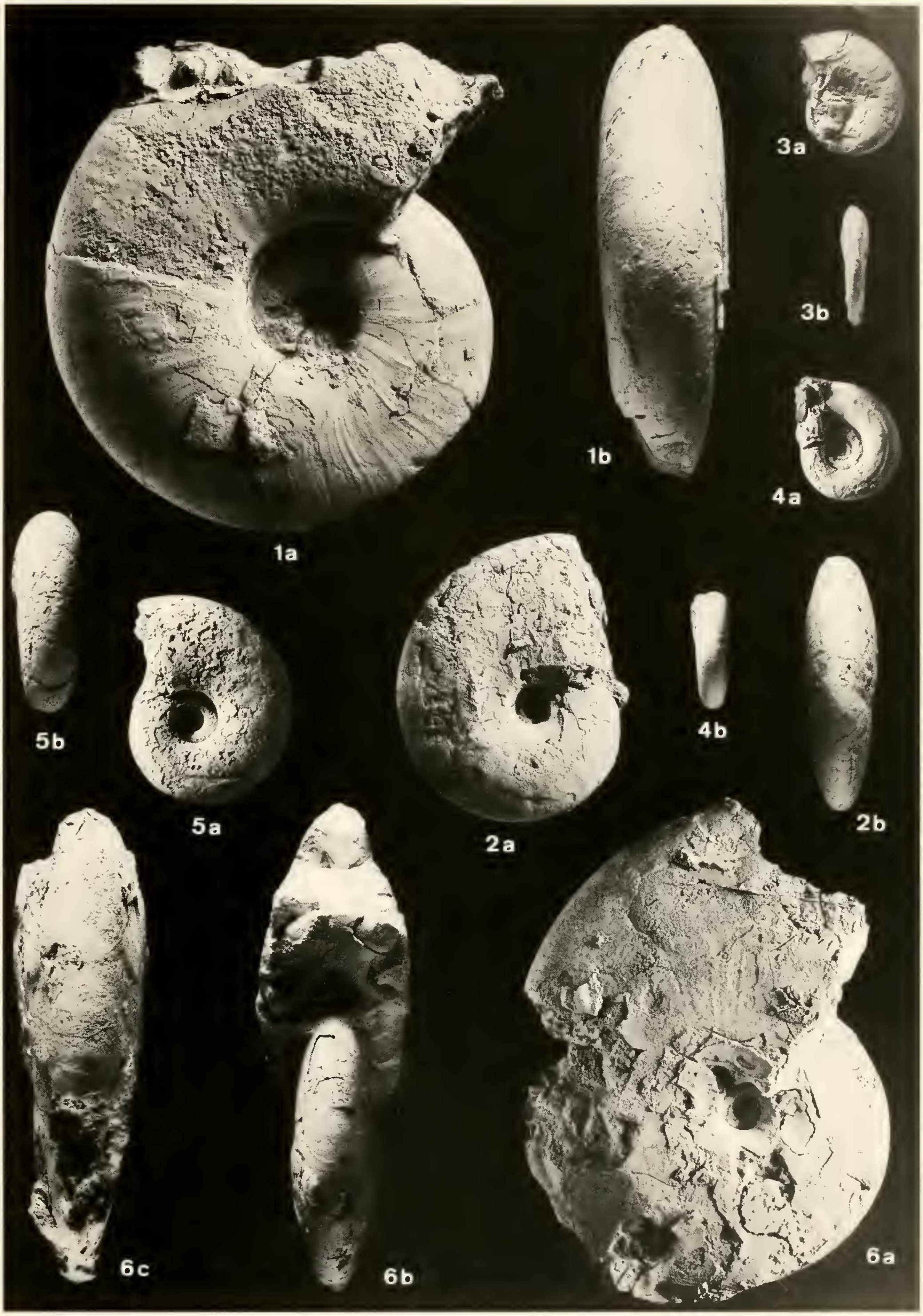

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1b

1a

2

3

4a

5a

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5b

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1b


1a


2


4b


3b


3a


4a


5a


5b

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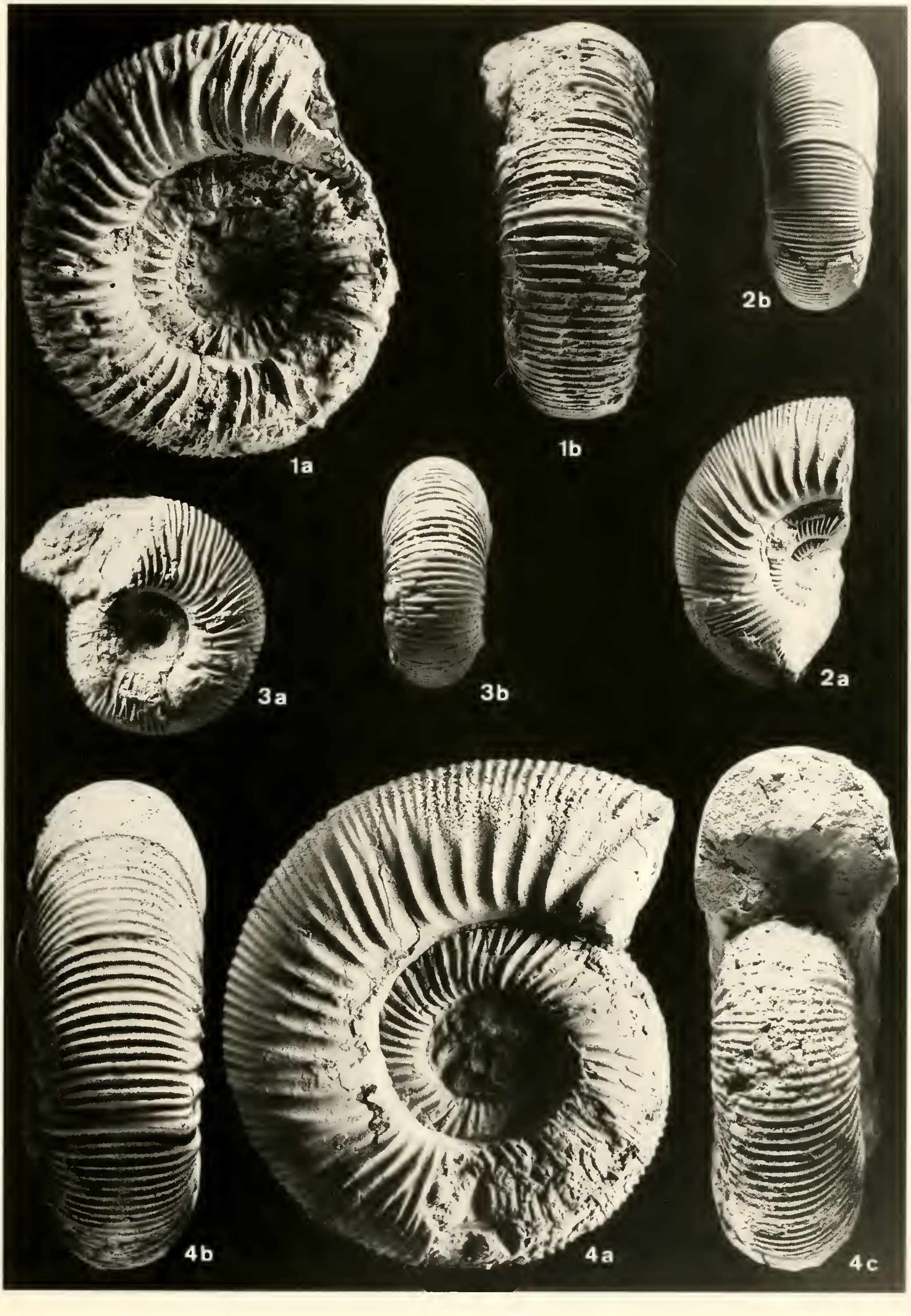

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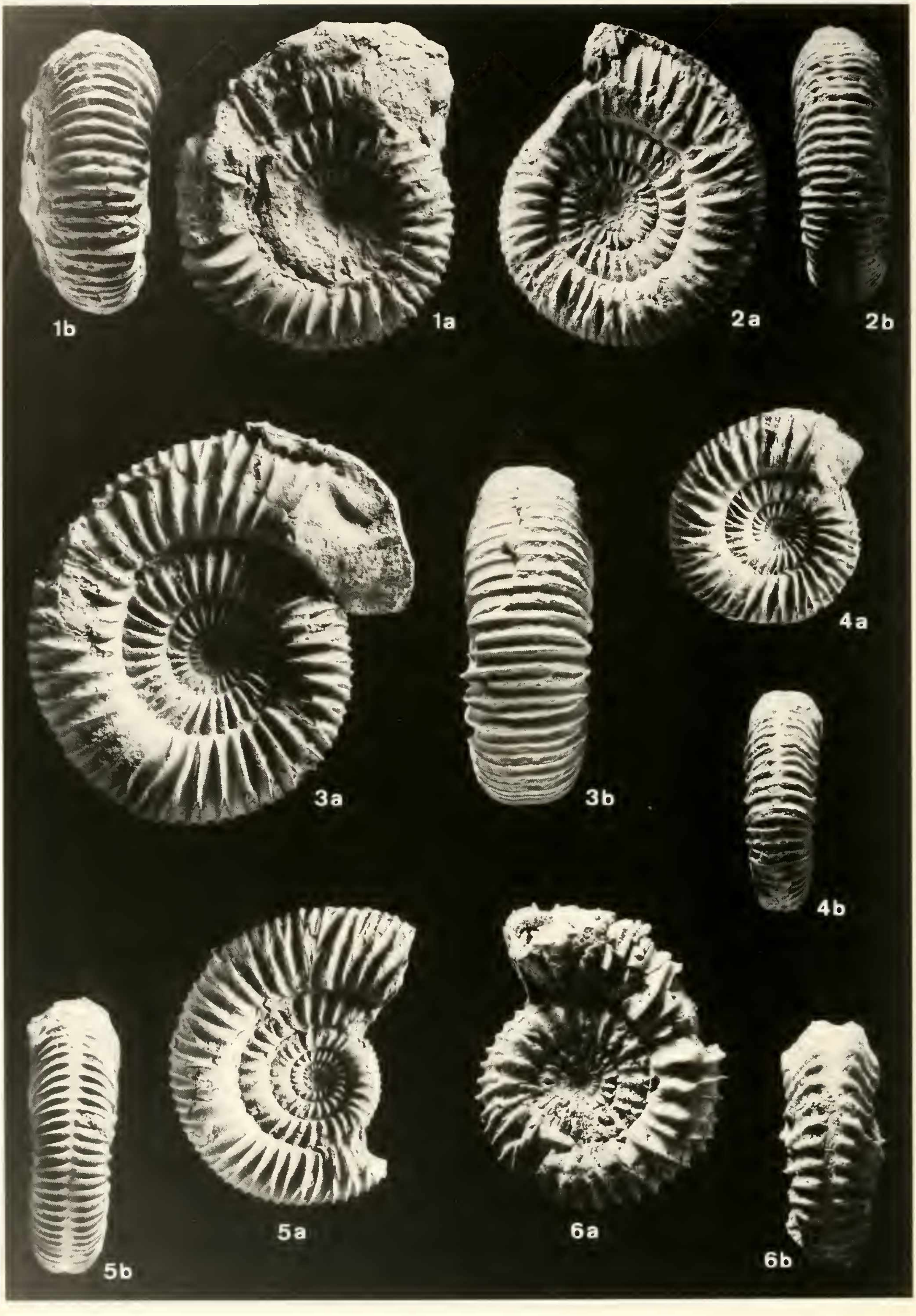

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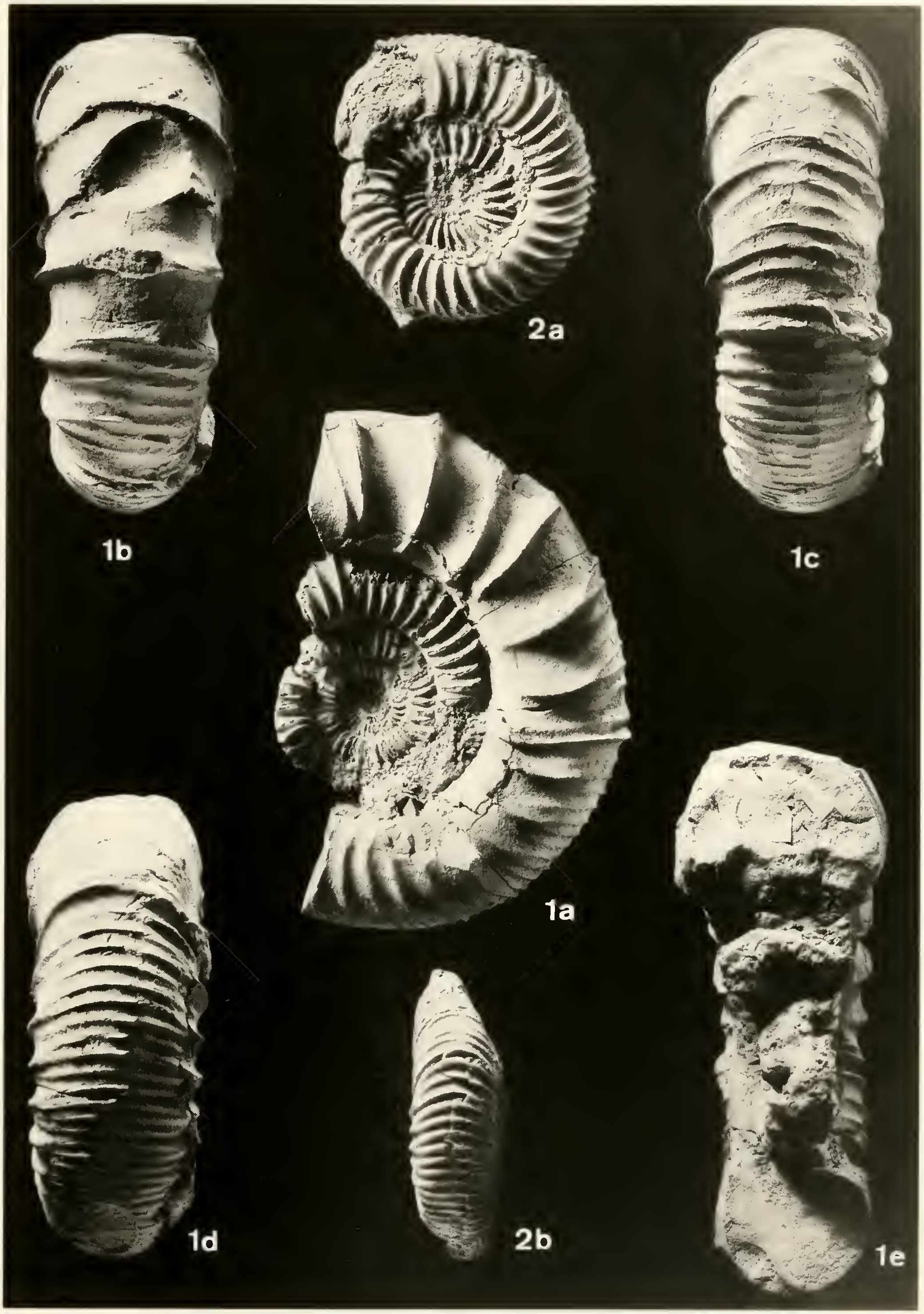
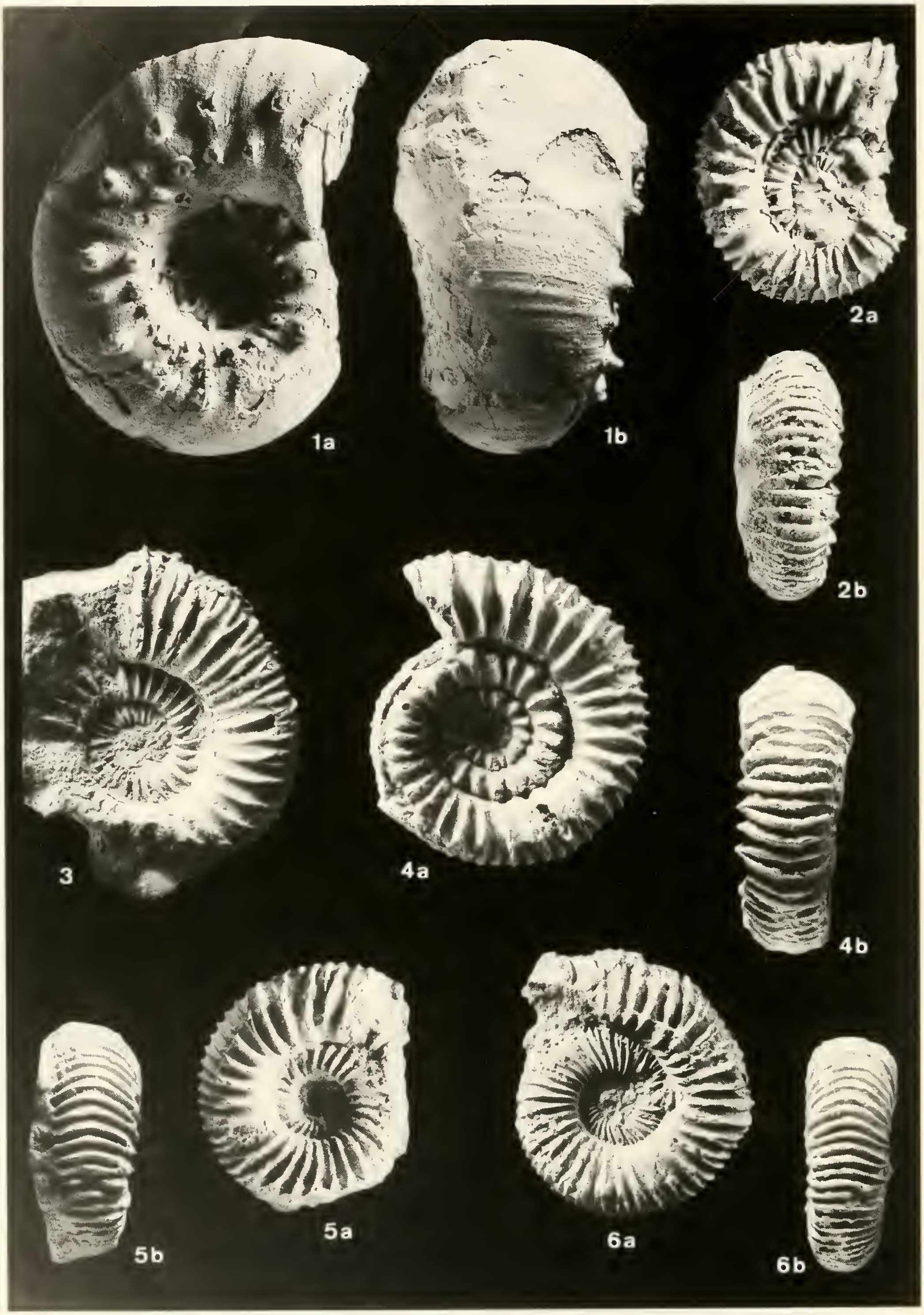
2: *Parapallasiceras* sp. indet. 40
2a—b, phragmocone and damaged body chamber: lateral and ventral views (S. G. N. 8942/4). Vaca Muerta Formation. Cerro Lotena. Upper Middle Tithonian. *W. internispinosum* Zone.



Leanza, H. A.: Lower and Middle Tithonian Ammonite Fauna.



Leanza, H. A.: Lower and Middle Tithonian Ammonite Fauna.

Plate 8

All figures natural size

Figure | Page

1: *Aspidoceras euomphalum* Steuer 41
1a—b, phragmocene with remains of body chamber: lateral and ventral views (S. G. N. 8931/15). Vaca Muerta Formation. Cerro Lotena. Upper Middle Tithonian. *W. internispinosum* Zone.

2: *Subdichotomoceras windhauseni* (Weaver) 36
2a—b, complete specimen: lateral and ventral views. (S. G. N. 8940/2). Vaca Muerta Formation. Cerro Lotena. Upper Middle Tithonian. *W. internispinosum* Zone.

3: *Parapallasiceras* aff. *P. pseudocolubrinoides* Oloriz 38
3, lateral view of an incomplete specimen. (S. G. N. 8947/1). Vaca Muerta Formation. Cerro Lotena. Upper Middle Tithonian. *W. internispinosum* Zone.

4: *Windhauseniceras internispinosum* (Krantz) 43
4a—b, inner whorls of the phragmocene: lateral and ventral views. (S. G. N. 8940/4). Vaca Muerta Formation. Cerro Lotena. Upper Middle Tithonian. *W. internispinosum* Zone.

5: *Subdichotomoceras* sp. juv. indet. 38
5a—b, phragmocone of a young specimen: lateral and ventral views (S. G. N. 8942/2). Vaca Muerta Formation. Cerro Lotena. Middle part of the Middle Tithonian. *A. proximus* Zone.

6: *Parapallasiceras* aff. *P. recticosta* Oloriz 39
6a—b, phragmocene with remains of body chamber: lateral and ventral views. (S. G. N. 8942/5). Vaca Muerta Formation. Cerro Lotena. Upper Middle Tithonian. *W. internispinosum* Zone.

Plate 9

All figures natural size

Figure Page

1: *Windhauseniceras internispinosum* (KRANTZ) 43
1a—b, complete specimen: lateral and ventral views. (S. G. N. 8941/1). Vaca Muerta Formation. Cerro Lotena. Upper Middle Tithonian. *W. internispinosum* Zone.

2: *Hemispiticeras* aff. *H. steinmanni* (STEUER) 43
2a—b, phragmocone: lateral and ventral views. (S. G. N. 8950/1). Vaca Muerta Formation. Cerro Lotena. Upper Middle Tithonian. *W. internispinosum* Zone.

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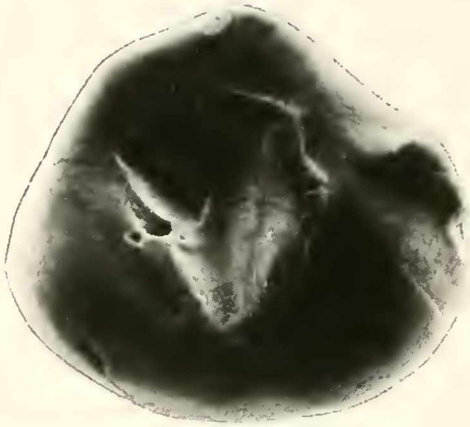
1


2a


2b


2c


3


4


5a


5b


5c

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Plate 10

Fig. 1: *Tricuspes tubingensis,* type specimen, tentatively identified as a right lower molariform, slightly retouched scanning-electron microscope photograph of lateral, probably buccal side. Also, see E. von Huene, 1933, Taf. 1, Fig. 7. Scale below photograph equals 1 mm.

Fig. 2: *Tricuspes tubingensis,* type specimen, tentatively identified as a right lower molariform: a, occlusal view, tentative orientation anterior to left, buccal upwards; b, lateral, probably buccal view, anterior to right, and c, lateral, probably lingual view, anterior to left. Scale above Fig. 2c equals 1 mm.

Fig. 3: ?*Thomasia* sp., Olgahain locality, GIT 1541/1, slightly retouched scanning-electron microscope photograph of occlusal view. Scale below photograph equals 1 mm.

Fig. 4: ?*Thomasia* sp., Gaisbrunnen locality, first described by E. von Huene (1933, see Taf. 1, Fig. 4). Slightly retouched scanning-electron microscope photograph of occlusal view. Scale below photograph equals 1 mm.

Fig. 5: *Tricuspes* cf. *tubingensis,* Hallau local fauna, AIII-351 (NC 23), tentatively identified as a right, lower molariform: a, occlusal view, tentative orientation anterior to left, buccal upwards; b, lateral probably buccal view, anterior to right; and c, lateral probably lingual view, anterior to left. Scale below Figs. 5b-5c equals 1 mm.

Plate 11

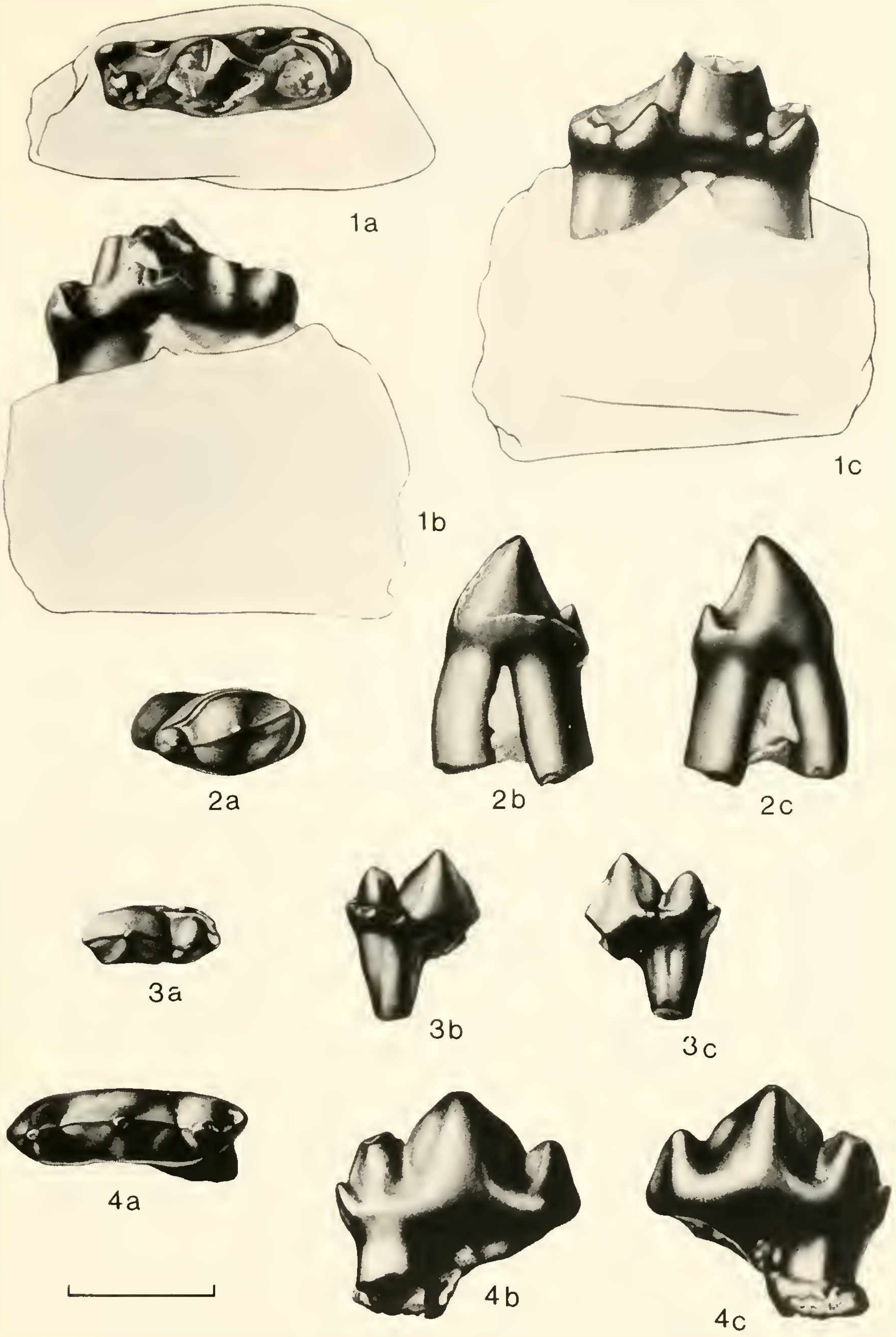
All figures drawn same scale. Scale below Fig. 4a equals 1 mm.

Fig. 1: *Morganucodon peyeri,* type, Hallau local fauna, AIII-329 (NC 1), tentatively identified as a right, lower molariform preserved in a fragment of dentary: a, occlusal view, tentative orientation anterior to left, lingual upwards; b, lateral, probably buccal view, anterior to left; and c, lateral, probably lingual view, anterior to right.

Fig. 2: ? *Morganucodon peyeri*, Hallau local fauna, AIII-368 (NC 40), tentatively identified as a left, upper premolariform: a, occlusal view, tentative orientation anterior to right, lingual upwards; b, lingual view; and c, buccal view.

Fig. 3: ? *Morganucodon* sp., Hallau local fauna, AIII-333 (NC 5), tentatively identified as a left, upper molariform: a, occlusal view, tentative orientation anterior to left, buccal upwards; b, lateral, probably buccal view, anterior to right; and c, lateral, probably lingual view, anterior to left.

Fig. 4: ? *Morganucodon* sp., Hallau local fauna, AIII-340 (NC 12), tentatively identified as a left, lower molariform: a, occlusal view, tentative orientation anterior to left, lingual upwards; b, lateral, probably lingual view, anterior to right; and c, lateral, probably buccal view, anterior to left.



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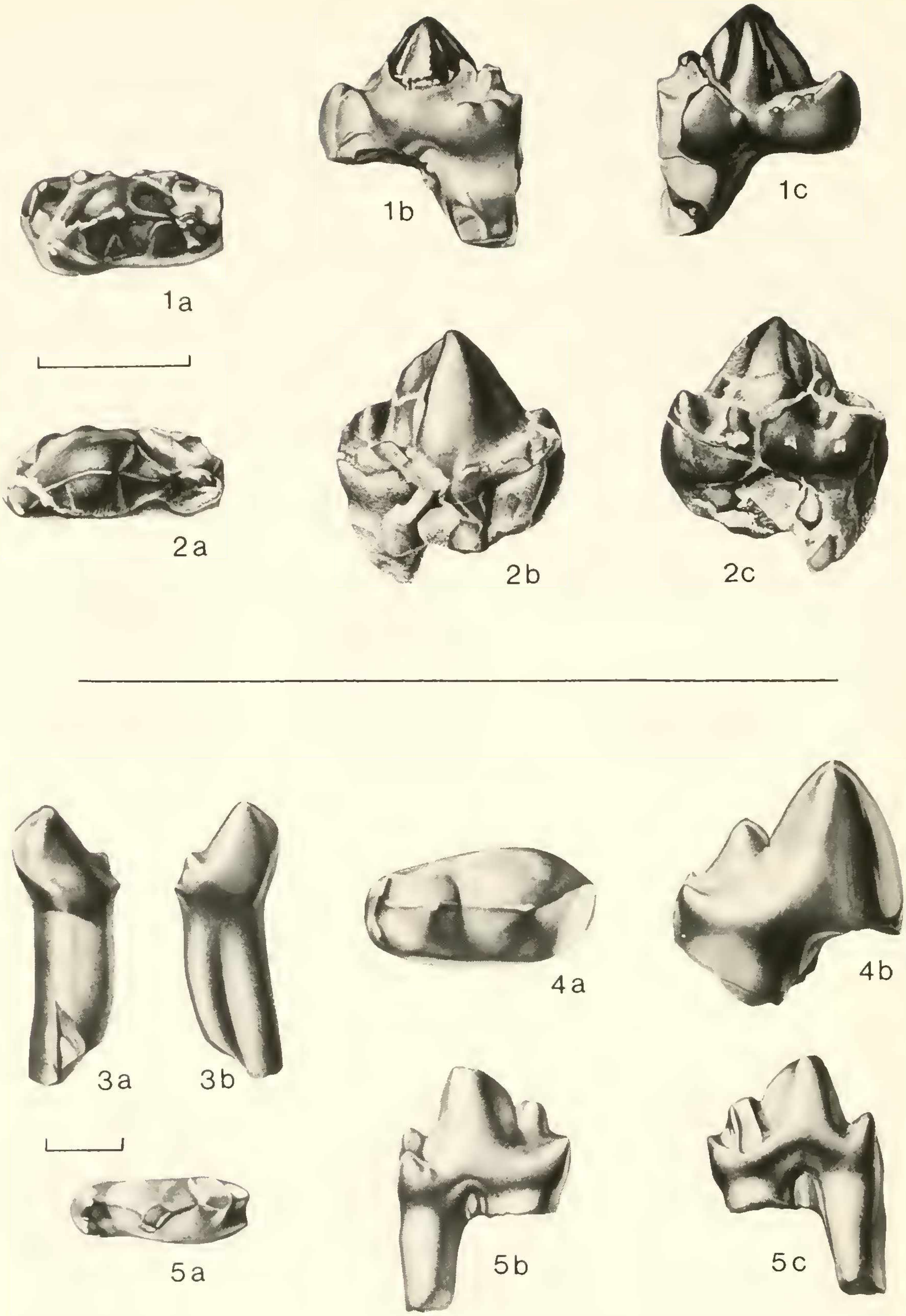

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Plate 12

Figures 1 and 2 drawn to same scale. Scale below Fig. 1a equals 1 mm. Figures 3 to 5 drawn to a different scale. Scale below Fig. 3a equals 1 mm.

Fig. 1: *Helvetiodon schutzi,* type, Hallau local fauna, AIII-348 (NC 20), tentatively identified as a right, upper molariform, enamel-covered areas rendered in darker tones: a, occlusal view, tentative orientation anterior to left, lingual upwards; b, lateral, probaly buccal view, anterior to left; and c, lateral, probably lingual view, anterior to right.

Fig. 2: *Helvetiodon schutzi,* Hallau local fauna, AIII-354 (NC 26), tentatively identified as a right, upper molariform: a, occlusal view, tentative orientation anterior to left, lingual upwards; b, lateral view, probably lingual view, anterior to right; and c, lateral view, probably buccal view, anterior to left.

Fig. 3: ? *Helvetiodon schutzi,* Hallau local fauna, AIII-424 (NC 94), tentatively identified as a right, lower, anterior premolariform: a, lateral view, probably lingual view; and b, lateral view, probably buccal view.

Fig. 4: ? *Helvetiodon schutzi,* Hallau local fauna, AIII-458 (NC 128), tentatively identified as a left, lower, posterior premolariform: a, occlusal view, tentative orientation anterior to right, buccal upwards; and b, lateral view, probably lingual view.

Fig. 5: *Hallautherium schalchi,* Hallau local fauna, AIII-337 (NC 9), tentatively identified as a right lower molariform; a, occlusal view, anterior to left, buccal upwards; b, lateral view, probably lingual view, anterior to left; and c, lateral view, probably buccal view, anterior to right.

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