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A Revision of the Fossil Genus *Ulmeriella* (Isoptera, Hodotermitidae, Hodotermitinae)

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INTRODUCTION

All the species of Tertiary fossil termites that the author has been able to examine, through loans or by visits to various institutions where they are deposited, have been described or redescribed in previous papers (Emerson, 1933, 1965), are treated herein, or will be dealt with in papers to be published subsequently. He has discovered that many new characters may be found in these specimens and that former errors of both fact and interpretation can often be corrected. He has added new interpretations of the phylogeny, biogeography, paleoecology, and taxonomy, together with new synonymies. With the present available information, the conclusions must remain tentative in part, but at the same time it is possible to add many data that enable a far more consistent pattern of phylogenetic relationships and distributions. The genus *Ulmeriella* was formerly inadequately described and figured and was consequently given a doubtful or incorrect systematic position.

The study of fossil termites is both rewarding and frustrating (Emerson, 1965). The specimens are often rare, fragmentary, preserved in such a position that comparative characters cannot be accurately described or measured, or are unavailable for re-examination by a competent taxonomist of the order. Several institutions are either difficult

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to reach or are loath to loan specimens, particularly unique holotypes. It is impossible for any individual to monograph the fossil species in scattered small collections around the world, and some collections were destroyed during World War II. Some specimens seem to have been lost. Nevertheless, many institutions and individuals have cooperated to such an extent that the author has been able to study about two-thirds of the known species of fossil termites.

ACKNOWLEDGMENTS

The nearly complete collection of fossil termites described by G. Statz (1930, 1939, 1941) from the Oligocene beds of Rott, Germany, is in the Los Angeles County Museum of Natural History. The present author was permitted to borrow this collection; all the species are either redescribed herein or will be redescribed in later papers. He is indebted to Dr. Charles L. Hogue, Curator of Entomology, and to Dr. Herbert Friedmann, Director, for this privilege.

Drs. Thomas E. Snyder and Oliver S. Flint have allowed the author to study specimens of fossil termites in the United States National Museum of the Smithsonian Institution. The author is especially indebted to his old friend Dr. Thomas E. Snyder who has given freely of his time and knowledge since our first meeting in 1919, and for the extensive exchange of specimens that has contributed to the excellence of the termite collections in both the United States National Museum and the American Museum of Natural History.

Dr. Kumar Krishna has given critical discussions and greatly helped by copying numerous articles from journals in the splendid library of the American Museum of Natural History. He has also lent many specimens for comparative study from the collection of the American Museum.

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FAMILY HODOTERMITIDAE DESNEUX

The earliest higher taxon based on the genus *Hodotermes* was the tribe Hodotermitini Desneux (1904a, p. 284; 1904b, p. 14). Desneux originally included the genera *Hodotermes*, *Stolotermes*, and *Porotermes* in the tribe Hodotermitini, placed in the subfamily Calotermitinae of the family Termitidae. He also named the tribe Termopsis, omitting the formal ending, and included *Termopsis* and *Archotermopsis* in this tribe in the

Calotermitinae and Termitidae. Emerson (1933) described the living and fossil genera of the Termopsinae and has not redescribed the fossils in this paper. However, he classified the Termopsinae as a subfamily of the Kalotermitidae and treated *Ulmeriella* as a synonym of *Hodotermes*, mistakes that were corrected by Emerson (1942, pp. 10, 11).

A large bibliography deals with the Hodotermitidae, much of which can be found in Snyder (1949a, pp. 54, 360), Ahmad (1950, pp. 44, 51), and Emerson (1955b, pp. 499, 505, 506, 507, 509). The present author includes four subfamilies within the family Hodotermitidae, namely, the Termopsinae, Stolotermitinae, Porotermitinae, and Hodotermitinae. At present several authors have raised the subfamily Hodotermitinae as used here to family rank (Grassé, 1949, p. 531; 1952, p. 70) and treat various groupings of genera related to *Termopsis* as the family Termopsidae (Weidner, 1955a; Harris, 1961). The taxon Hodotermitinae in this article is usually the exact equivalent of the Hodotermitidae of those authors who separate the family Termopsidae from the Hodotermitidae. Emerson (1942, pp. 10, 11) treated the Hodotermitidae and the Hodotermitinae as he does in this article, and Snyder (1949a, pp. 54, 360) included the genera in family and subfamily groups in exactly the same way. Snyder (1949a, p. 363) included the fossil genus *Ulmeriella* in the Hodotermitidae and the Hodotermitinae as the present author does in the following pages.

In spite of the differences in the rank of taxa, all recent authors recognize the phylogenetic relationships between the genera and subfamilies as used in this paper. The Hodotermitidae are doubtless very primitive and probably evolved very early, possibly in late Paleozoic or early Mesozoic times. The mandibles of the most primitive genera, *Archotermopsis*, *Stolotermes*, and *Ulmeriella*, are similar to those of most of the cockroaches (Ahmad, 1950, figs. 5, 6), whereas the Mastotermitidae have a fused first and second marginal tooth of the left mandible, as is also the case in the Kalotermitidae. A convergent reduction of the point of the second marginal tooth of the left mandible, together with a corresponding elimination of the sharp notch separating the first and second marginal teeth, occurs in all the Termitidae except *Protohamitermes*. It seems best, therefore, to refer to the fused marginal teeth of the left mandible of derived genera as the first plus second marginal tooth, and the marginal tooth in front of the molar plate is thus the third marginal tooth in all genera in which it is not reduced. A number of recent authors confuse the homologies of the teeth by failing, by appropriate nomenclature, to recognize the fusion of marginal teeth in the left mandible.

The primitive left mandible of *Archotermopsis* and *Ulmeriella* is associated with the lenticular shape of the eye, the large numbers of lateral spines on the tibiae, the long and many-jointed cerci, and a primitive wing venation. The anal lobe of the hind wing of the Mastotermitidae is, however, more primitive than any hind wing of the Hodotermitidae. In numerous other respects, including the genitalia, the Mastotermitidae are more primitive than the Hodotermitidae. It may be surmised that a more primitive group of termites, as yet unknown, was ancestral to the Mastotermitidae and Hodotermitidae, and that this unknown group combined the primitive hind wing, ocelli, wide pronotum, and five-jointed tarsus of the Mastotermitidae with the primitive left mandible and five-jointed tarsus of the primitive genera of the Hodotermitidae. The derived families from this ancestral group each evolved in somewhat different directions. The Mastotermitidae have a more specialized dentition and the Hodotermitidae have more specialized hind wings, genitalia, loss of ocelli, and narrower pronota. It may also be surmised that the most primitive termites had many antennal articles, many lateral spines and terminal spurs on the tibiae, many-jointed cerci and other characteristics resembling cockroaches, but that the forewing had a humeral suture not present in any cockroaches, and that a soldier caste had appeared with the origin of the order Isoptera.

Although the Rhinotermitidae retain the primitive mandibles of the Hodotermitidae and show relationship in several other characters, they have retained the ocelli in the more primitive genera that were lost in the Hodotermitidae. It may be assumed, therefore, that the unknown ancestor of the Mastotermitidae and Hodotermitidae gave rise to the Rhinotermitidae before the loss of the ocelli in the presently known Hodotermitidae, and before the fusion of the first and second marginal teeth of the left mandible in the Mastotermitidae and Kalotermitidae.

The Rhinotermitidae seem to have given rise along two separate lines of greater specialization to the Serritermitidae (Emerson, 1965, p. 17) on the one hand, and to the Termitidae on the other. The recently named family Stylotermitidae, which should be treated as a subfamily of the Rhinotermitidae, and the family Indotermitidae, of which the type genus *Indotermes* should be included in the subfamily Amitermitinae of the Termitidae, do not deserve family rank in the opinions of several investigators and the present author.

SUBFAMILY HODOTERMITINAE DESNEUX

The genera *Ulmeriella*, *Hodotermes*, *Microhodotermes*, and *Anacanthotermes* are included in the Hodotermitinae. The last three genera are clearly

related in structure and behavior and constitute the desert and steppe harvester termites of Africa and Asia. Several species are found in subtropical or warm temperate climates, but a few species are tropical in their distribution in both the Ethiopian and the Oriental zoogeographical regions, in contrast to the temperate distribution of the large majority of the species of the Hodotermitidae. The wholly fossil genus *Ulmeriella* has been found only in temperate Tertiary deposits. Emerson (1942, p. 11) and Snyder (1949a, p. 363) placed *Ulmeriella* in the subfamily Hodotermitinae, but the descriptions of the fossils did not allow any termite specialist to be positive of its relationships. The redescription in the following pages, with many added characters, now makes it fairly clear that *Ulmeriella* is a very primitive genus of the Hodotermitidae, sharing with *Archotermopsis* its primitive dentition, lenticular eye, and long many-jointed cercus, but also sharing with other genera of the Hodotermitinae the conspicuous inferior branches of the radial sector. Because of the wing venation, the author agrees with Snyder (1949a) in placing the genus in the Hodotermitinae, but it is also indicated that the genus bridges the gap between the Termopsinae and the Hodotermitinae in numerous structures. Even without the newly discovered characters of *Ulmeriella*, we were already aware that the Hodotermitinae often possessed a larger number of antennal articles than the species of the Termopsinae, and the direction of evolution of the antennae is always toward reduction of numbers of articles in the imago and other castes. Besides the rather distinctive behavior, geographical distribution, ecology, and the possession of what is generally regarded to be an analogous worker caste with comparatively large pigmented and faceted eyes, this group of living genera is separated from its more remote relatives and provides a sound basis for the opinion that it constitutes a distinct phylogenetic branch symbolized by some as a subfamily and by others as of family rank. Although the author has placed *Ulmeriella* at the base of the Hodotermitinae, the genus serves to connect the Termopsinae and the Hodotermitinae in numerous important characters and, in the opinion of the author, justifies the inclusion of these two subfamilies within the single family Hodotermitidae. We still have no notion of the sterile castes of *Ulmeriella*, and little indication of the ecological adjustments, but the temperate distribution of the known fossils (fig. 1), with no evidence that they were confined to desert or steppe environments, provides a hint that *Ulmeriella* may not have been a harvester termite with similar behavior and ecology to those of the living genera of the Hodotermitinae. Numerous structural characters of the fossils indicate that the Hodotermitinae and Termopsinae evolved from

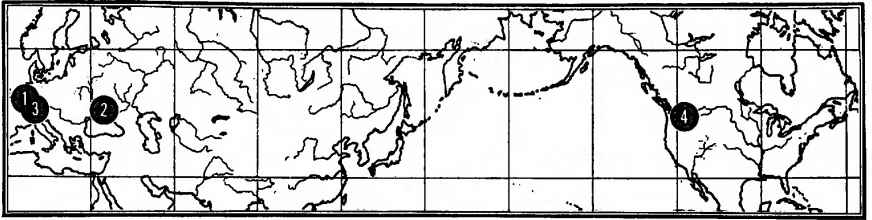


FIG. 1. Fossil localities of the genus *Ulmeriella*. 1. *Ulmeriella bauchhorni* Meunier, upper Middle Oligocene, Rott, Siebengebirge, Germany. 2. *U. cockerelli* Martynov, Upper Oligocene, Ashutas, Saisan district, Siberia, U.S.S.R. 3. *U. martynovi* Zeuner, Lower Miocene, Biebrich, Germany. 4. *U. latahensis* Snyder, Upper Miocene, near Spokane, Washington. A fifth species, *U. willershausensis* Weidner, Pliocene, Willershausen, West Germany, has recently been added.

the same ancestral hodotermitid. With our present knowledge, it would seem unwise to erect a new subfamily for *Ulmeriella* alone.

GENUS *ULMERIELLA* MEUNIER

- = *Ulmeriella* MEUNIER, 1920, p. 728.
- = *Ulmeriella*: COCKERELL AND SNYDER, 1925a, p. 22.
- = *Ulmeriella*: COCKERELL AND SNYDER, 1925b, p. 86.
- = *Ulmeriella*: FULLER, 1925, p. 4.
- > *Ulmeriella*: MARTYNOV, 1929, pp. 176–178.
- > *Diatermes*: MARTYNOV, 1929, p. 178.
- > *Ulmeriella*: ZEUNER, 1938, pp. 113, 116.
- > *Diatermes* ZEUNER, 1938, p. 116.
- > *Ulmeriella*: STATZ, 1939, pp. 14, 34–39, table 4.
- > *Diatermes*: STATZ, 1939, p. 32, table 4.
- > *Ulmeriella*: EMERSON, 1942, pp. 9–11.
- > *Diatermes*: EMERSON, 1942, p. 10.
- > *Ulmeriella*: SNYDER, 1949a, p. 363.
- > *Diatermes*: SNYDER, 1949a, pp. 352, 354.
- > *Ulmeriella*: SNYDER, 1949b, p. 164.
- > *Ulmeriella*: SNYDER, 1950, pp. 191–193.
- > *Ulmeriella*: EMERSON, 1955b, pp. 490, 499, 507.
- > *Diatermes*: EMERSON, 1955b, p. 507.
- = *Ulmeriella*: KRISHNA, 1961, pp. 314, 315.
- > *Diatermes*: EMERSON, 1965, pp. 14–15.
- > *Ulmeriella*: EMERSON, 1965, pp. 14, 34.
- = *Ulmeriella*: WEIDNER, 1967, pp. 65–75.

TYPE SPECIES: *Ulmeriella bauchhorni* Meunier (1920, p. 728).

INCLUDED SPECIES: *Ulmeriella cockerelli* Martynov (1929); *U. martynovi* Zeuner (1938); *U. latahensis* Snyder (1949b); *U. willershausensis* Weidner (1967).

Meunier (1920) named the genus and placed it in the Tricoptera.

Because of this error of classification, it is the only recognized termite genus that does not incorporate the root *termes*, derived from Greek and Latin, in the generic name. Cockerell and Snyder (1925a) placed *Ulmeriella bauckhorni* in the order Isoptera but were unable to assign it to a subfamily. From the wing fragment alone, Cockerell and Snyder (1925b, p. 86) thought that *Ulmeriella* might be the same genus as *Macrohodotermes* (currently synonymous with *Hodotermes*), but they preferred to keep the genera separate because of inadequate material. In spite of the descriptions, photographs, and drawings of the imagoes by Statz (1939), who placed the genus in the tribe Termopsini, the relationships of the genus were not well understood, even though Emerson (1942) placed the genus in the Hodotermitinae.

Fortunately the large collection of fossil termites made by Statz (1939), now in the Los Angeles County Museum, and the redescription of the genus and type species in the present article, remove nearly all doubts of its phylogenetic relationships or its taxonomic position.

The species distinctions, however, are not as yet precise or sure. Inasmuch as the underlying principles of the species concept are often misunderstood by many modern taxonomists of both living and fossil termites, a brief discussion of the concept is given below, particularly those aspects that are relevant to the species problem within the genus *Ulmeriella*.

SPECIES LIMITS AND DEGREE OF VARIATION

The question of the definition of species and the determination of the distinctions between closely allied species are old problems and continue to be controversial at the present time. There is, of course, a voluminous literature on the subject, both from the viewpoint of the abstract biological principles involved and of their practical application to cases. The present paper is not the place to review this problem in detail. Many authors and Emerson (1955a, 1956, 1961a, 1961b, 1962a, 1962b; Allee, Emerson, Park, Park, and Schmidt, 1949, p. 625; Schmidt and Emerson, 1960, pp. 853-855) have discussed the species problem and have given references to opposing viewpoints. Sokal and Sneath (1963) have discussed the problem with reference to modern biometrical techniques which, if used in connection with biological principles based on objective data and presumably operating at the time of speciation, may enable a mathematically more refined concept of species and species relationships. Unfortunately much controversy stems from the tendency of "modern" taxonomists to use words implying contempt for the "traditional" taxonomists, and for the latter to uphold the values of their

studies by means of polemics against the so-called "modernists." The present author believes there is much value to be gained from both the older studies and the modern mathematical and computer techniques, and that much of the controversy indicates a lack of broad perspective on both sides.

For the purposes of this discussion the author reiterates his earlier definition of a species as an evolved or evolving, genetically distinctive, reproductively isolated, natural population, all criteria being necessary and no one of which is sufficient alone. The taxonomist, particularly one dealing with fossil specimens, must usually rely on structural phenotypic characters, both qualitative and quantitative, to indicate the genetic basis of taxonomic categories. Separation in time and space may indicate reproductive isolation. Gross structural variation within population systems without genetic differences and reproductive isolation does not indicate species distinctions, the most obvious examples being the morphological differences between the sexes or between the castes of social insects. It is, therefore, not valid to use structural variation as the only criterion for species distinction, as some taxonomists often do. However, structure is often a very sensitive indication of genetic, developmental, and physiological processes, so the attitude that it is unimportant may result in gross errors.

Numerous modern numerical taxonomists often assume that variance of multiple characters is more "objective" than an emphasis on certain chosen characters that are termed "arbitrary." The present author believes that certain characters (for example, the dentition of the imago left mandible) are far more important for taxonomic and phylogenetic interpretation than others (for example, the branching of the medial vein) in the total phenotype, and that valid phylogenies may be constructed that are consistent with soundly based principles of genetics, development, and evolution. Thus he differs from some of the statements of leading numerical taxonomists who oppose the choice of characters deemed more important than others for taxonomic and phylogenetic relationships.

In the particular case under consideration at present, in which a fair number of fossil termites from the same locality and geological stratum have been given two names (*Ulmeriella bauckhorni* and *U. rottensis*), it is seen that the specimens in general fall into two size groups (table 1), although some measurements overlap. If such groups were separated clearly by time or space, one might consider them reproductively isolated, with no genetic exchange. Numerous instances occur of several species of the same genus of termites found in the same locality, with

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF IMAGOS OF *Ulmieriella bauchhorni* (MEUNIER)

	<i>U. bauchhorni</i> ^a			<i>U. rottensis</i> ^a			<i>U. bauchhorni</i> ^b		
	No.	Range	Aver.	No.	Range	Aver.	No.	Range	Aver.
Length of head to tip of mandibles	1	3.07	3.07	2	3.50-3.54	3.52	3	3.07-3.54	3.37
Length of postmentum	—	—	—	1	0.73	0.73	1	0.73	0.73
Width of postmentum	—	—	—	1	0.78	0.78	1	0.78	0.78
Width of head	5	2.56-2.87	2.68	6	2.75-3.35	3.07	11	2.56-3.35	2.90
Maximum length of eye	4	0.62-0.69	0.64	6	0.61-0.78	0.67	10	0.61-0.78	0.66
Width of eye in middle	4	0.41-0.46	0.45	6	0.34-0.44	0.37	10	0.34-0.46	0.40
Length of postclypeus	1	0.23	0.23	1	0.35	0.35	2	0.23-0.35	0.29
Width of postclypeus	—	—	—	1	1.07	1.07	1	1.07	1.07
Length of left mandible	1	1.22	1.22	—	—	—	1	1.22	1.22
Length of pronotum	3	0.87-1.12	1.03	5	1.16-1.58	1.37	8	0.87-1.58	1.24
Width of pronotum	5	1.97-2.43	2.22	7	2.26-3.35	2.67	12	1.97-3.35	2.50
Length of front tibia	—	—	—	2	1.83	1.83	2	1.83	1.83
Length of hind tibia	—	—	—	1	3.41	3.41	1	3.41	3.41
Length costal margin forewing scale	1	0.93	0.93	3	1.59-2.01	1.83	4	0.93-2.01	1.60
Length forewing from costal suture	9	9.96-13.16	11.41	9	12.03-13.91	12.92	18	9.96-13.91	12.17
Width of forewing	7	2.74-3.76	3.45	8	3.95-4.57	4.16	15	2.74-4.57	3.83
Length costal margin hind wing scale	1	0.64	0.64	2	0.87-1.34	1.10	3	0.64-1.34	0.95
Length of hind wing from costal suture	1	11.64	11.64	9	11.93-13.54	12.67	10	11.64-13.54	12.56
Width of hind wing	4	3.29-3.90	3.68	7	3.76-5.17	4.35	11	3.29-5.17	4.10
Length of stylus	—	—	—	1	0.33	0.33	1	0.33	0.33
Length of cercus	1	0.81	0.81	—	—	—	1	0.81	0.81

^a Determination by Statz.

^b Determination by Emerson.

little ecological distinction. However, these are rare among the more primitive termites, particularly among the Hodotermitidae. *Zootermopsis angusticollis* and *Z. nevadensis* provide an example, but these so-called species share the same set of intestinal flagellates, and there is some overlap in their measurements (although no marked differences in their structure), and a more thorough study of large numbers of specimens of all castes may show that these two names should be placed in synonymy.

The sexes of termites often show a smaller size of the male and a larger size of the female. The sex of the fossils of *Ulmeriella* from Rott cannot be determined for many specimens. The lack of distinctive structures, the overlap of some measurements, the possibility that the size groups may be associated with sex, and the lack of separation either chronologically or spatially make it seem more probable that the species should be placed in synonymy under the older name of *Ulmeriella bauckhorni* Meunier, and they are tentatively treated here as one species. In case much more evidence than is at present available may show this tentative hypothesis to be less probable, the measurements of the two groups are separated for comparative purposes (table 1). With the number of fragmentary specimens available for study, it does not seem worth while to make a more thorough statistical analysis. Computer processing of the data would be inappropriate, although the importance of this "traditional" study and the new information discovered is obvious, at least to the specialists investigating the taxonomy, classification, and phylogeny of groups within the order Isoptera.

Ulmeriella bauckhorni Meunier, new synonymy

Hodotermes sp. ROSEN, 1913, p. 323 (imago).

Ulmeriella bauckhorni MEUNIER, 1920, p. 728, fig. 1, pl. 1, fig. 1 (forewing).

Phryganidenflügel MEUNIER, 1920, p. 727 (wing).

"*Hodotermes*" sp.: SNYDER, 1925, chart.

Ulmeriella bauckhorni: SNYDER, 1925, chart.

Ulmeriella bauckhorni: COCKERELL AND SNYDER, 1925a, p. 21, pl. 1, figs. 1, 2 (wing).

Ulmeriella bauckhorni: COCKERELL AND SNYDER, 1925b, p. 86 (genus possibly synonymous with *Macrohodotermes* [= *Hodotermes*]).

Ulmeriella bauckhorni: FULLER, 1925, p. 4 (imago compared to *Hodotermes*).

Calotermes rottensis STATZ, 1930, p. 12, fig. 2 (imago).

Calotermes sophiae STATZ, 1930, p. 13, fig. 3 (imago).

Hodotermes bauckhorni: EMERSON, 1933, p. 190 (remarks).

Ulmeriella bauckhorni: ZEUNER, 1938, p. 116 (wing).

Ulmeriella bauckhorni: STATZ, 1939, pp. 3, 4, 15, 34, 35 (imago), pl. 6, figs. 26-29 (wings), table 4 (Termopsini).

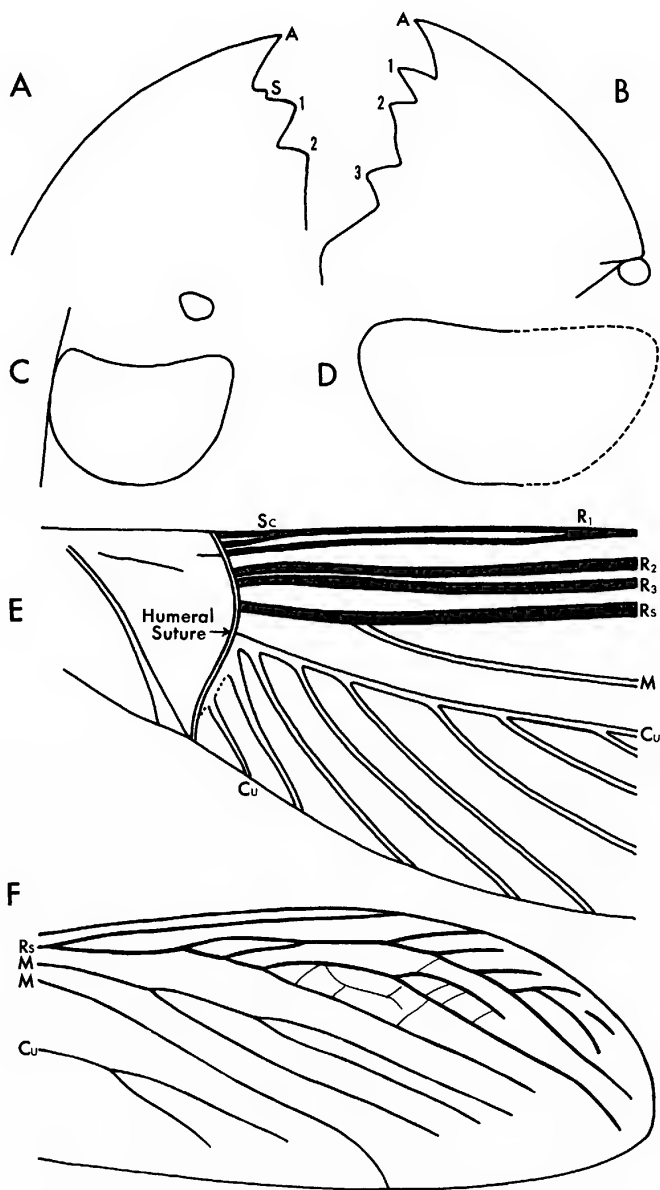


FIG. 2. *Ulmeriella bauckhorni* Meunier, imago, with different magnifications of parts. A. Right mandible from below (IV-7). B. Left mandible from below (IV-7). C. Estimated shape of eye and antennal fossa (I-7). D. Pronotum with estimated right side (IV-6). E. Basal portion of forewing, semidiagrammatic composite of several specimens (I-2, I-6, and others). F. Outer portion of forewing, semidiagrammatic outline of visible veins and reticulations (I-11).

Symbols: A, apical tooth; Cu, cubitus; M, media; R_1 , first radius; R_2 , second radius; R_3 , third radius; Rs, radial sector; S, subsidiary tooth of right mandible; Sc, subcosta; 1-3, first, second, and third marginal teeth.

Ulmeriella rottensis: STATZ, 1939, pp. 3-5, 16, 34, 35 (imago), pl. 7, figs. 30-32, pl. 8, fig. 33 (imago), table 4 (Termopsini).

Ulmeriella sp. STATZ, 1939, p. 37 (discussion).

Ulmeriella bauckhorni: STATZ, 1941, figs. 1, 2 (imago).

Ulmeriella rottensis: STATZ, 1941, figs. cover, 3, 4, 7 (imago).

Ulmeriella bauckhorni: SNYDER, 1949a, p. 363 (synonymy).

Ulmeriella rottensis: SNYDER, 1949a, p. 363 (synonymy).

Ulmeriella sp.: SNYDER, 1949a, p. 364 (synonymy).

Ulmeriella rottensis: WEIDNER, 1955a, pp. 45, 53, fig. 30 (imago); descriptions and captions of *Eotermes grandaeva* and *Ulmeriella rottensis* mixed or transposed.

Ulmeriella bauckhorni: WEIDNER, 1967, pp. 72-74, fig. 12 (wings).

Ulmeriella rottensis: WEIDNER, 1967, pp. 72-74, figs. 9-11 (wings).

IMAGO (FIG. 2): Y-suture distinct in many specimens, angle of arms in front about 110 degrees. Eye (fig. 2C) flat, not projecting much if any beyond side of head from above, concave in front, resembling eye of *Archotermopsis wroughtoni* (Desneux) (Emerson, 1933, figs. 8, 9), but front margin not so concave and eye proportionally smaller compared to size of head than in *A. wroughtoni* and *A. tornquisti* Rosen (Emerson, 1933, p. 178). Ocelli absent. Antennal fossae often distinct (fig. 2C). Small marks near eyes or in front of eyes possibly artifacts or muscle insertions, but pattern not sufficiently clear or consistent to warrant description. Antennal articles in some cases fairly distinct; in one case 27-29 counted, but exact number not certain; third and fourth articles very short and gradually lengthening beyond fourth article. Postclypeus visible in some cases and apparently about one-fourth to one-third as long as wide, proportionally longer than in Kalotermitidae (exact shape not clear in any specimen). Dentition of mandibles excellently preserved in numerous specimens. Left mandible (fig. 2B) with apical, first marginal, and second marginal teeth similar in size and length, in general resembling those of *Archotermopsis* and *Stolotermes* (Emerson, 1933, fig. 11; 1942, fig. D; 1961b, fig. 5) among living genera; posterior cutting edge of second marginal tooth longer than in *Archotermopsis*; third marginal tooth somewhat shorter and more bluntly pointed than other marginal teeth; angles between apical, first marginal, and second marginal teeth sharp, angle between second and third marginal teeth close to right angle; base obscure. Right mandible (fig. 2A) similar to that of *Archo-*
termopsis and that of *Stolotermes*, with subsidiary tooth at front base of first marginal tooth near angle with apical tooth (see Emerson, 1961b, pp. 122-123 for discussion of significance of this character). Although related to *Archotermopsis* more closely in dentition, apparently mandibles of *Ulmeriella* slightly more advanced in a few particulars, but definitely more primitive than those of living genera of Hodotermitinae (Ahmad, 1950, fig. 6) that have a much-reduced second marginal tooth in left

mandible. Pronotum (fig. 2D) narrower than head; front margin fairly evenly and moderately concave, with slight or insignificant notch in middle; front lobes near middle slightly convex and angular in some specimens, but in none so prominent as in *Archotermopsis* (Emerson, 1933, fig. 8); side angles somewhat sharply rounded as in *Parotermes* (Emerson, 1933, fig. 6); sides somewhat converging toward rear; hind margin with slight or no median notch. Portions of three legs visible in some specimens but not sufficiently clear for complete and accurate description. Front leg with four fairly distinct terminal thick spurs; three or four lateral spines fairly distinct, possibly others present in two rows, unsure of outer and inner regions, possibly some thick bristles confused with lateral spines; in one leg at least two and possibly three outer lateral spines present. At least two distinct terminal tibial spurs close together visible in what is apparently the middle leg, possibly another one present, more separated; tibia with apparently four fairly distinct lateral spines (one 0.18 mm. long) and several more on possibly inner side, one distinct spine on what may be outer edge, with possibly two or three additional indistinct spines; some spines apparently large and long, in one case five to eight spines and some coarse bristles visible but their orientation not clear; tarsal claws distinct, reasonably certain that arolium present; five tarsal joints apparently present, but somewhat indistinct and their orientation difficult to judge. Hind leg with three to four terminal tibial spurs and one to six thick indistinct spines on two specimens, one distinct lateral spine close to spurs almost as long and thick as spurs; two other lateral spines fairly distinct in one row in one specimen, and one spine in another row; possibly other spines present, but indistinct and difficult to see; orientation not clear, but impression probably showing both sides so that spines of one side show through to other side. Although only a few specimens have rather indistinct impressions of legs, general conclusion is that spurs and spines are present and that tarsus seems to have five articles and an arolium. These descriptions of legs should be taken as indications only, not to be interpreted too rigorously. Forewing scale longer than hind wing scale and overlapping base of hind wing; slightly convex or nearly straight costal border anterior to suture; notch at costal end (fig. 2E) of suture either slight or not visible in most specimens. Humeral suture (fig. 2E) somewhat but not strongly curved baseward from Rs to costal border, moderately or slightly curved from Rs to inner border where possibly slightly curved toward apex of wing in some specimens; suture not very angulate near Rs and often rather evenly curved or slightly sinuate. Forewing (fig. 2F) costal border somewhat convex or nearly

straight in middle, depending on preservation and amount of distortion, fairly strongly convex toward apical end; tip below middle of wing strongly convex; inner border moderately and fairly evenly convex throughout its length. Reticulations between veins visible, particularly in outer half of well-preserved wings. Venation at humeral suture (fig. 2E) seldom distinct, but in best specimens apparently a separate short Sc (0.85–0.95 mm. from suture), a long R_1 (2.80 mm. from suture), R_2 and R_3 separate or joined to form R_{2+3} , Rs, and Cu. Rs with three to five superior branches from main stem and one to four inferior branches, with secondary branches in some specimens; branches of Rs reaching both above and below tip of wing; space occupied by Rs and its branches comparatively large in outer fourth of wing; conspicuous inferior branches of Rs typical of *Hodotermitinae*, but occasionally occurring in other subfamilies (see hind wing of *Archotermopsis tornquisti* Rosen determined by Weidner, 1955b, pl. 1, fig. 4). In all wings well preserved in this region, M definitely joining Rs about 0.55–0.85 mm. from suture, a character usually present in hind wings but occasionally also present in forewings of *Microhodotermes viator* (Fuller, 1919, pl. 7, fig. 84A) and *Archotermopsis tornquisti* (Emerson, 1933, p. 178); M having two to four branches reaching inner border of wing well below tip. Cu having four to eight branches, in some specimens with secondary branches, reaching inner border in basal half or two-thirds of length of wing. Hind wing scale shorter than forewing scale, a character common to nearly all termites but forewing scale proportionally much longer than hind wing scale in primitive termites of which *Ulmeriella* is an example. Humeral suture of hind wing shorter than that of forewing, evenly curved from costal to inner border. In most specimens costal border slightly concave near middle. Shape, size, and general venation of hind wing similar to those of forewing, reticulations between veins, particularly in outer half of wing, alike. Sc absent from hind wing, a short anal vein invariably present near inner border beyond suture. R_1 (3.66 mm. long in one specimen), R_{2+3} , Rs, M joined to base of Rs beyond suture (2.07 mm. in one specimen), Cu, and A all seen in some specimens. Superior and inferior branches of Rs present, with about same degree of variation as in forewing. In one specimen, space occupied by Rs and its branches 2.16 mm. wide in outer portion of wing. Rs having possibly as many as six superior branches and one to three inferior branches, some secondarily branched. M a little closer to Cu than to Rs in middle of wing. Cu having seven to nine primary branches and none to three secondary branches reaching inner border well toward base from tip. Anal vein single and about 0.96–2.44 mm. long.

Styli visible in a few specimens (0.33 mm. long in one specimen), possibly indicating male sex although styli occur in both sexes in some genera of Hodotermitinae. Articles of cercus usually indistinct and difficult to count, but virtually certain that cerci long, with more articles than in other families of termites; when visible, four to nine articles counted, in a few cases eight to nine articles present resembling situation in *Archotermopsis*.

MEASUREMENTS: Even with a fair degree of variation, which is generally greater in primitive termites, measurements are very important for the identification of species. Particularly in shale or rock fossils, the position of the specimen and the lack of clarity of outlines of parts often make the measurements inaccurate, and they should not be interpreted too rigidly. There is little doubt in the mind of the author that the outline of some structures has been misconstrued, so that the extreme measurements sometimes may be in error. At the same time, there is a degree of consistency, and when large numbers of specimens have been examined, the approximate measurements have taxonomic value. Forty-one specimens of *Ulmeriella bauckhorni* are included in the description and measurements, but all these were fragmentary. The numbers of specimens for which a description and a measurement of any single structure are given range from one to 18, the latter number unusually large.

SPECIMENS: The holotype is a forewing reported by Meunier (1920, p. 728) and possibly deposited in Siegburg, Germany. The present description combines characteristics of 13 specimens of imagoes and wings from upper Middle Oligocene beds at the type locality of Rott (latitude 50° 44' N., longitude 7° 15' E.), east of Bonn, West Germany, determined by Statz (1939) as *Ulmeriella bauckhorni* Meunier, and 28 specimens from the same deposits and locality determined by Statz (1939) as *U. rottensis* Statz. All the collections were made by G. Statz, with dates ranging from December, 1931, to March, 1934. The labels on the 28 specimens of *U. rottensis* are assigned to "Meunier Statz," but the present author has found no reference in any of the articles by Meunier to this name, so the author of the name seems to be Statz alone. It is not known whether Statz compared his specimens with the holotype of *U. bauckhorni* or not, but there seems to be no doubt of the species identification, at least of those specimens determined as *U. bauckhorni*. Statz spent many years collecting fossil specimens at Rott, and his collection was acquired by the Los Angeles County Museum of Natural History after his death soon after the close of World War II. All specimens drawn or photographed by Statz (1939, 1941) and possibly by Statz (1930) are in the

collection with his labels, some labeled "Original" and some with the dates of the collection. All specimens are fragmentary or lack some details that are present in others. Without exact information about the existence or deposition of the type specimen of *U. rottensis*, a male specimen of an imago labeled "*Ulmeriella rottensis* Statz original" (I-9, which is a reverse impression of the same specimen figured by Statz (1939, pl. 7, figs. 30, 31) has been chosen as the lectotype or neotype. The reverse specimen in the figures by Statz (1939) and photographed for the cover illustration (Statz, 1941) was not found. The specimen has styli and has been determined tentatively as a male by the present author, although Statz labeled it as a female.

The 13 specimens determined by Statz as *U. bauckhorni* Meunier include one male imago (IV-6), five other imagos (IV-7-IV-11), four forewings (I-2, I-3, IV-12, IV-13), and three hind wings (I-1, IV-14, IV-15). Of these, IV-6, a male imago, is the best preserved and was illustrated by Statz (1939, pl. 6, figs. 26, 27), although his drawings are poor and inaccurate. Statz labeled 28 specimens "*U. rottensis* Meunier Statz," which are considered synonymous with *U. Bauckhorni* and included in the combined description and measurements in the present article. The best-preserved specimen is a male imago (I-9). Another specimen of an imago (I-6) may be a female. Other specimens include an imago (I-5), two dealates (I-4, I-7), one head (I-8), seven forewings (I-11, I-14, III-1, III-2, III-3, III-5, III-11), two somewhat questionable forewings (I-10, I-16), seven hind wings (I-12, III-7, III-8, III-10, III-12, III-13, III-15), one questionable hind wing (III-4), and five wings not certainly determined as either forewings or hind wings (I-13, I-15, III-6, III-9, III-14).

In general this series collected by Statz is among the most notable collections of fossil termites, and the description of the combination of characters from all specimens enables us to place the genus and species very close to its true phylogenetic position among the Hodotermitidae for the first time. Statz should be honored for his life-time devotion to the collecting and recording of the fossil insects of Rott, even though his descriptions and taxonomic judgments include numerous errors.

Ulmeriella cockerelli Martynov, new synonymy

Ulmeriella cockerelli MARTYNOV, 1929, p. 175, figs. 1, 2 (forewing).

Diatermes sibiricus MARTYNOV, 1929, p. 179, text fig. 3, pl. 1, fig. 1 (wing).

Ulmeriella cockerelli: ZEUNER, 1938, p. 116 (wing).

Ulmeriella cockerelli: STATZ, 1939, pp. 5, 34, 37, 38, pl. 1, fig. 5 (wing), table 4.

Diatermes sibiricus: STATZ, 1939, table 4.

Diatermes sibiricus [sic]: SNYDER, 1949a, p. 354 (synonymy).

Ulmeriella cockerelli: SNYDER, 1949a, p. 363 (synonymy).

Diatermes sibiricus: EMERSON, 1965, pp. 14, 15 (discussion).

Ulmeriella cockerelli: WEIDNER, 1967, pp. 73-74, fig. 15 (forewing).

The holotype forewing from Upper Oligocene rocks from Ashutas (latitude 47° 30' N., longitude 34° 57' E.), Saisan District, Siberia, has not been re-examined, and its location is unknown to the author. The figure of the forewing (Martynov, 1929) indicates a shape roughly similar to that of *U. latahensis* Snyder in the position of the tip. The length of the wing is given as 14 mm., and its width as 4.7 mm., but the base is not figured, and the true length from the humeral suture is probably longer. The size of the wing is therefore probably larger than that of *U. bauckhorni* and may be close to that of *U. latahensis*. The inferior branches of Rs are somewhat less sharply separated from the main stem, so that it is more difficult to decide whether a branch is inferior or superior, although the width of Rs with its branches is similar to that of the other species of *Ulmeriella*. The locality and geological horizon may be presumed to indicate a separate species, but the specimen is too fragmentary for precise classification. It is left in the genus *Ulmeriella* for the present.

A wing from the same locality and stratum was given the name *Diatermes sibiricus* by Martynov (1929) and has been a puzzle to the author (Emerson, 1965, p. 14). With the variation in the venation of *Ulmeriella bauckhorni* and *Microhodotermes viator* (Latreille) illustrated by Fuller (1919, pl. 7, figs. 84a-d), it now seems probable that *Diatermes sibiricus* is a synonym of *Ulmeriella cockerelli*, and tentatively it seems best to treat it as such. If the vein that fuses some distance from the base of Rs is considered to be M, then there is an inferior branch of Rs that ends or fuses with M toward the end of the wing. The venation is not typical of the Hodotermitinae, but it is by no means impossible that this degree of variation occurs within the same species. Zeuner (1938, p. 116) thought that *Diatermes* was closely related to *Ulmeriella*. Martynov (1929) estimated the length of the wing of *Diatermes sibiricus* as 16.5 mm., and the width as 5.5 mm. In no case is the base of the wing intact in the figures, so that these slightly larger measurements are unlikely to indicate a species difference from *Ulmeriella cockerelli*.

Ulmeriella martynovi Zeuner

Ulmeriella martynovi ZEUNER, 1938, p. 113 (imago), figs. 2-5 (imago, wings).

Ulmeriella martynovi: SNYDER, 1949a, p. 363 (synonymy).

Ulmeriella martynovi: EMERSON, 1965, p. 16 (wing).

Ulmeriella martynovi: WEIDNER, 1967, pp. 73-74, figs. 13, 14 (forewings).

This species was described from Biebrich (latitude 50° 02' N., longitude 8° 20' E.) near Mainz, West Germany, from Lower Miocene beds. The type specimen has not been re-examined by the author, nor does he know its location. The forewing length is given as 12.3 mm., but whether the length includes the scale or not is not known. The position of the wing tip (Zeuner, 1938, fig. 3) seems to be nearer to that of *U. bauckhorni* than to that of *U. cockerelli* or *U. latahensis*. In general the venation is in conformity with that of *U. bauckhorni*, including the coalition of Rs and M at the base of the forewing. The figure of the head (Zeuner, 1938, fig. 2) does not show the lenticular shape of the eye as in *U. bauckhorni*, but the lack does not indicate that the eye is actually round or oval. In numerous specimens of *U. bauckhorni* it is necessary to examine many eyes and to interpret carefully other lines in the vicinity of the eye before one can be sure of this primitive lenticular shape. The pronotum of *U. martynovi*, although distorted and possibly a little wider in proportion to the head than in other species of Hodotermitidae, does not differ significantly from that of *U. bauckhorni*. The general tentative conclusion is that *U. martynovi* should be left in the genus *Ulmeriella* until the type specimen can be re-examined or more specimens from the same deposits are described in greater detail. The placement of *U. martynovi* in the Mastotermitidae by Zeuner is certainly incorrect; it should be placed in the Hodotermitinae following Snyder (1949a, p. 363) and Emerson (1965, p. 16).

Ulmeriella latahensis Snyder

Ulmeriella latahensis SNYDER, 1949b, p. 164, fig. 1 (hind wing).

Ulmeriella latahensis: SNYDER, 1950, p. 191 (discussion).

Ulmeriella latahensis: WEIDNER, 1967, pp. 73-74 (hind wing).

LEFT HIND WING (HOLOTYPE): Humeral suture moderately and evenly curved from costal to inner border. Costal margin of apical portion of wing fairly straight in basal half and convex in outer half; tip strongly convex and ending about halfway between costal and inner borders rather than more toward inner border as in *U. bauckhorni* (see Snyder, 1949b, fig. 1). Reticulations between veins in outer half of wing. Base may be folded somewhat so that exact relationships and number of veins at suture somewhat obscured. Apparently a long single R_1 joining Rs near first superior branch. Rs having four superior branches from main stem and three inferior branches; main stem reaching tip of wing, all superior branches joining costal margin and all inferior branches, one of which is secondarily branched, reaching inner margin, with exception of one inferior branch that ends in membrane. M joined to Rs near

base and not reaching tip of wing; two branches of M clear. Cu with 10 inferior branches, at least one branched secondarily; branches at base numerous and fanlike. Anal apparently present and may be branched, but possibly branches of Cu converge and join each other or join A. Length of hind wing from costal suture, 16.06 mm.; width of hind wing, 5.17 mm.

Three fragments of hind wings are in the same box with the holotype and have the same catalogue number in the United States National Museum. The bases and tips of the wings are lacking, but the superior and inferior branches of Rs and the reticulations between the veins in general conform to those of the holotype. The widths of these wings are 3.30 mm., 3.41 mm., and 3.63 mm. Although narrower than the holotype, the range is within that of *Ulmeriella bauckhorni*, and it may be presumed that the specimens belong to *U. latahensis*.

Although genera and species based on wings alone must remain somewhat tentative, there is no reason for questioning the taxonomic validity of the species with our present information. The shape of the holotype differs slightly from that of *Ulmeriella bauckhorni* in the position of the tip of the wing, but the venation conforms in generic characters. The length of the hind wing is distinctly longer than that of *U. bauckhorni*, and the locality and geological stratum also indicate species separation.

SPECIMENS: The holotype hind wing and three fragments of hind wings are impressions in rock from the Latah Formation, Upper Miocene, at Cut No. 1, Portland and Seattle Railroad, near Spokane (latitude 47° 40' N., longitude 117° 25' W.), Washington. All specimens are deposited in the United States National Museum (U.S.N.M. No. 59181).

Ulmeriella willershausensis Weidner

Ulmeriella willershausensis WEIDNER, 1967, pp. 65-75, figs. 1-4 (forewing and hind wing).

Weidner (1967) described forewings and hind wings of *U. willershausensis* from Pliocene shales of Willershausen (latitude 51° 47' N., longitude 10° 06' E.), east of Einbeck, West Germany. The forewing of *U. willershausensis* is slightly longer (15.40 mm.) than that of *U. cockerelli* (14.00 mm.), and the width (4.50 mm.) is close to that of *U. cockerelli* (4.70 mm.). The shapes of the tips of the forewing and hind wing of *U. willershausensis* are similar to those of *U. cockerelli* and *U. latahensis*, and are more rounded and more median in position than those of *U.*

bauckhorni and *U. martynovi*, although distinctions in the wing shapes of different species of *Ulmeriella* have not been established with certainty. The generic assignment of *U. willershausensis* is in conformity with the redescription of *Ulmeriella* in the foregoing pages. The geological extension of the genus into the Pliocene of warm-temperate Europe is noteworthy. The holotype forewing and the paratype forewing and hind wings are in the collection of the Geologisch-Paläontologischen Institutes, Universität Göttingen.

SUMMARY

The fossil genus *Ulmeriella* is redescribed. Five species from temperate Tertiary deposits of Europe, Asia, and North America are included. *Ulmeriella* is considered to be the most primitive member of the Hodotermitinae and partially bridges the gap between the Termopsinae and Hodotermitinae within the family Hodotermitidae. Phylogenetic, biogeographical, and paleoecological interpretations are included. A brief discussion of the degree of variation and the limits of species among fossil termites is presented. *Ulmeriella bauckhorni* Meunier from upper Middle Oligocene beds, Rott, Germany, is redescribed and figured, and *U. rottensis* (Statz) is placed in synonymy. *Ulmeriella cockerelli* Martynov, known from a forewing from Upper Oligocene beds of Ashutas, Siberia, is discussed, and *Diatermes sibiricus* Martynov is placed in synonymy. *Ulmeriella martynovi* Zeuner known from an imago from Lower Miocene beds of Biebrich, Germany, is discussed. *Ulmeriella latahensis* Snyder from Upper Miocene beds of Washington is redescribed. *Ulmeriella willershausensis* Weidner from Pliocene beds of Willershausen, Germany, is discussed.

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