Vol. 38, pp 149–166 November 13, 1925

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

NOTES ON FOSSIL TERMITES WITH PARTICULAR REFERENCE TO FLORISSANT, COLORADO.

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Introduction.

By means of the study of Paleontology—the study of fossils that have been preserved in rocks, and of the fauna and flora that these imply—it is possible to reconstruct the world, not only in our imagination, but also by the arrangement of fossil skeletons of mammals, reptiles and birds grouped in museums and by paintings on canvas, as it existed in prehistoric times. It is also possible to trace geologic time and the evolution of plant and animal life by a study of successive strata of rocks and the fossils embedded in their layers. By means of such fossils and also fossil plants and insects, it is even possible to form an idea as to the character of the climate of the different prehistoric periods.

In those far distant days the fauna and flora of Europe and North America and the world in general were quite different from what they are to-day. There has been an age when reptiles were the dominant form of animal life, preceding the ages of mammals and of man. Species and genera of plants and animals now of an exceedingly restricted distribution or even entirely extinct, were formerly widely distributed.

This is due to the fact that there have been profound changes during the earth's history. The climate of the temperate zone at the present time is much cooler than that which existed through the longer part of the earth's history.

"Prehistoric" Termites.

No insects from the Silurian period are known. The ancestors of our present insect fauna must have had a long ancestry and

doubtless appeared earlier than the last part of the Carboniferous or the coal measures or during the Age of Amphibians and Lycopods. The roaches or Blattidae were among these fossils and are, therefore, among the oldest insects; the Paleodictyoptera of Scudder are the oldest insects (Paleozoic). Indeed, the Pennsylvanian period might be termed the Age of Roaches. These prehistoric insects were not the immediate ancestors of our living species. Termites, while they have a close systematic relationship with the roaches, are younger or more recently evolved. No termites are known from the Mesozoic or the Age of Reptiles, but may have then existed.

Termites have been collected from all deposits from the Lower Tertiary on (Handlirsch, 29); that is from the end of the Age of Reptiles and the beginning of the Age of Mammals. Holmgren (31) states that he believes that both groups, the termites and the Blattidae (the roaches) are offshoots of a more primitive group, the Protoblattidae. The "oldest Blattoideen" occur in the first part of the middle upper Carboniferous (Pottsville, North America); the "oldest Protoblattoideen" in the last part of the coal measures (Allegheny, North America); but the "youngest Protoblattoideen" occur in the Lower Permian formation of Europe (Germany).

Fossil termites are very well represented in the fauna of the Old World, and quite a number have been described from Europe. Many of the best preserved of these have been obtained in Baltic and other ambers—resins from coniferous trees; during the swarm, winged termites were entombed in the resin. Others fell into the shallow water or soft mud of prehistoric lake beds of accumulating fine volcanic ash from dust showers, mud flows—from feeder streams and sand, which, upon drying, hardened into rock. Fossil termites in the highly specialized family Termitidae are not found in Baltic amber! Fossil termites are also found in gum copal, an exudation from a tropical tree (*Trachylobium mossambicense* Klotsch), (a tree still extant and occurring in Africa) geologically, of comparatively recent formation (Pleistocene). The Termitidae or higher termites are well represented in gum copal. (Chart I.)

One might imagine several million years ago twilight on a warm evening in June or July, possibly after a heavy rain, in the Florissant Basin, with fairly large numbers of strong flying large

colonizing termites or "white ants" flitting about near the shores of the lake, seeking in dead coniferous trees, logs or stumps, crevices in which the males and females could establish new colonies. Many of these adventurous winged adults were carried out over the lake by the wind and their romance was ended by falling into the water.

Although they thus perished, their life was not in vain, for to-day they have been exhumed from their tombs in the Tertiary shales and, together with the fossil plants and other animals, they enable scientists to unfold the drama of the period in which they lived. The story is incomplete, indeed, far from a Pepys's diary, but there is sufficient to show the general topography and the mountain fauna and flora of the region.

Conditions in the Rocky Mountain Region in the Tertiary Period and To-day.

The Miocene shales of Florissant, Colorado, in North America have yielded many fossil termites. Fossil termites, as well as other animals and the plants, found in both the Tertiary beds at Oeningen and Radoboj in Europe and during the (upper?) Miocene epoch at Florissant, Colorado, indicate that the climate of these localities must have been very much warmer at that period than at present.

At Florissant, for instance, during the early Tertiary period, the vegetation was almost subtropical—including the fig and magnolia. The majestic redwood tree (*Sequoia haydeni* (Lesquereaux)) and incense cedar (*Heyderia* or *Libocedrus coloradensis* Cockerell) also occurred at Florissant during Tertiary times. The fossil termites and other insects of Florissant suggest a warm climate, such as that which is to-day found in the southwestern states, adjacent to the Mexican border. A fig insect has also been found in Florissant shales by Brues (5), apparently of the South American genus *Tetrapus* Mayr.

Prof. Cockerell believes that at Cathedral Bluff (west of Rifle, Colo.) fossil termites might possibly be found in older strata—Eocene; so far termites have not been found in the Eocene in Colorado. To-day the Rocky Mountain region of Colorado is in the Transition and Canadian Life Zones, although also containing Hudsonian, Arctic and Upper Sonoran. Florissant, notwithstanding its elevation of 8,193 feet above sea level, be-

longs to the upper part of the Transition Zone (Cockerell, 10). The fossil termite fauna, together with many of the fossil plants at Florissant, indicate that in the Miocene epoch of the Tertiary period this region must have been in the Lower Austral. Probably, however, the climate was more humid than the Sonoran or arid portion of the Lower Austral.

At Florissant, Colorado, the living *Sequoia* tree does not now exist; this tree disappeared with the decrease in humidity, during the later Tertiary period. No scrub oak and also, no living termites occur; the elevation is too great. Spanish Bayonet occurs on warm sites—sunny hillsides—at Florissant and elsewhere in Colorado.

Termites do not occur even on mountains in Arizona at such a great altitude as Florissant (8,193 feet), although colonies of *Reticulitermes tumiceps* Bks. occur sparsely at an elevation of 8,200 feet on the northern rim of the Grand Canyon, at Bright Angel Pt. In the Rocky Mountain region of Colorado 7,000 feet is approximately the altitude above which colonies of *Reticulitermes tibialis* Banks,—which is to-day the only living termite in Colorado,—are not found.

It is interesting to study the history of the redwood or *Sequoia* tree and its past and present distribution. To-day, there are only two living species, *S. sempervirens* (Lamb) Endlicher and *S. washingtoniana* (Winsl.) Sudworth; the latter of these trees is almost entirely restricted to the coast mountains and the former to Sierras of California; the coast species extends a few miles into Oregon. Thus there has been a gradual retreat until the present isolated groves are all that remain. Glaciers, fire, man and insects have greatly decimated their numbers.

In the vicinity of living *Sequoia* forests of to-day four species of termites occur; three of these species have been found living in the sapwood of this tree, namely *Termopsis angusticollis* Hagen, *T. nevadensis* Hag. and *Reticulitermes hesperus* Bks. Another species of *Reticulitermes* (*tibialis* Bks.) occurs in the same region in which the redwood (*S. sempervirens*) grows, but has not as yet been found infesting the wood of this tree.

Although grand and majestic to-day, towering above all other trees in the forest, in their past history they have played a more dominant rôle.

Berry (4) states that: "During the three to five million years

this would probably soon kill the *Sequoia* trees, since conifers can not withstand a clogging of the stomata of the leaves,—which results in suffocation. The climate became colder and more dry—too dry for *Sequoia* in the later Tertiary.

The writer has a specimen of a large winged adult fossil termite, probably *Parotermes scudderi* Cockerell, embedded in Florissant Miocene shale; these shales are wholly composed of volcanic sand and ash from a nearby source. In this identical specimen of shale—at a corresponding depth and on the same surface are embedded small twigs of *Sequoia*. These twigs were deposited at approximately the same time as the termite. *Parotermes* has no living representative and is an extinct genus. Twigs of *Sequoia* occur throughout the layers of this specimen of shale—on both faces; the specimen of shale is 4 mm. in thickness. At the time the shales were deposited the climate was warm but moist.

Arid conditions could have existed beyond this lake—which was in a deep, long, narrow valley (elevation unknown but lower than at Florissant to-day)—and its surrounding mountains on the plains. Old World (African) termites—species of ?*Hodotermes* Hagen or closely similar primitive termites—were present with the tsetse-fly (four species of *Glossina*) now exclusively African, indicating invasion of fauna from Eurasia. This is interesting in connection with the introduction of African mammals (*Mastodon*) into the Miocene of North America (Osborn, 37). Finally the lake was drained by shifting of the land and there came about an increasing aridity and lengthening droughts.

This would render an adaptation to such arid conditions necessary for survival. To-day species of *Hodotermes* (l. s.) and "*Eutermes*" Fritz Müller are so adapted; living species of "*Eutermes*," now placed in *Tenuirostritermes* Holmgren, a subgenus of *Nasutitermes* Banks, inhabit arid plains in southwestern Texas; surviving peccaries and the armadillo live in the same general region. In Arizona, a species of *Tenuirostritermes*, namely *tenuirostris* Desneux, occurs in the foothills and canyons of the Santa Catalina Mountains, where conditions are more or less desert-like.

With the draining of the Tertiary lake and general conditions of drought, the *Sequoia* tree doubtless made its last stand around the borders of Lake Florissant.

Similar conditions were caused by the slow reduction in size and gradual drying up of the ancient Lake Bonneville, to the present Great Salt Lake, which, however, was due to the increasing aridity of the country.

It is more probable that the fossil termite described by Scudder (47) as *Hodotermes? coloradensis* was a species more primitive and more generalized than *Hodotermes* of to-day. Von Rosen (52) has erected a new genus *Miotermes* for European fossil species, formerly considered to be *Hodotermes*, and places *coloradensis* in *Miotermes*. To the present writer it seems more probable that the species *H. ? coloradensis* was similar in habit to the primitive termite species of *Termopsis* Heer and *Archotermopsis* Desneux, rather than to *Hodotermes* Hagen, with its highly specialized worker caste adapted for foraging above ground in the sunlight, as do the dominant ants. Species of *Termopsis* have no true worker caste and apparently *Archotermopsis* likewise has none. But these termites possess a pigmented, worker-like third form reproductive type; these species are also adapted to mountain life, often being found at high altitudes, where the logs which they inhabit are covered with snow and ice for long periods of winter cold.

If a *Hodotermes*, it is odd that the worker is not found as a fossil! Also if a *Hodotermes*, it is very probable that this worker caste was developed in the late Tertiary period, in case of certain of these large primitive termites and was the factor that enabled them to survive.

None of the fossil termites are more generalized or more primitive than living termites. Indeed, a living species of the genus *Mastotermes* Froggatt of Australia is the most primitive; this termite has a wing structure similar to the roaches, and the egg mass is in an oötheca, indicating at least common ancestry. However, species of *Mastotermes* have also been found fossil in the Tertiaries of Great Britain (Von Rosen, 52). Nevertheless, in prehistoric times, there were naturally a greater prevalence of primitive termites than at present.

In the vicinity of the fossil forests of central eastern Arizona, termites of the same genus *"Eutermes"—Nasutitermes* Banks which occur as fossils with cones of Sequoia at Florissant, *may* occur living to-day. However, this is doubtful; unfortunately,

the writer has no termite specimens from the petrified forests of this section of Arizona.

The present termite fauna of southern Arizona, however, is numerous and rich in species; 14 species and 1 variety occur, representing 6 genera. The same number of species occur in Texas, but one more genus is represented. The southwestern portion (Sonoran) of the United States to-day has a larger number of termites in its fauna than any other section of this country. It is interesting to note that no living termite extends its range from coast to coast—across the continent.

On the following pages will be given an account of: The fossil termites of Florissant; the present meagre termite fauna of the Pikes Peak region of Colorado; the present geographical distribution of living species in the termite genera represented at Florissant by fossil species and of species of the two primitive genera *Termopsis* Heer and *Kalotermes* Hagen, which while they have not as yet been recognized as occurring in Colorado either as fossil or recent species, for the sake of comparison these latter genera will be treated here.

Genus **Kalotermes** Hagen.

This primitive genus is closely related to the genera *Termopsis* Heer and *Hodotermes* Hagen. Ocelli are present—a primitive character. Hagen considered *Kalotermes* to be the most primitive genus known in 1858. No fossil termites as yet have been found at Florissant, Colo., which are considered to belong in this genus. Fossil species of *Kalotermes* occur in the Tertiaries of Europe.

The living species of *Kalotermes* all have a southern habitat. To-day species of *Kalotermes* are restricted to the southern portions of North America; occurring in southeastern United States—north to Cape Henry, Va.; in southwestern United States (Texas, Arizona and southern California); also in Mexico and Lower California. The region in the vicinity of San Francisco is the northern limit of species of this genus on the Pacific Coast. The Siskiyou range of mountains, which is unusual in that it runs east and west, together with the colder climate is probably the barrier that prevents their extension into southern Oregon. This mountain range shuts off many southern insects from Oregon.

A very primitive and the largest known species of *Kalotermes*, namely, *K.* (*"Termes"*) *occidentis*, was described in 1853 by Walker from the West Coast of Central America. One of the types is in the British Museum, another in the Museum of Comparative Zoology at Cambridge, Mass. This termite has recently been found in Lower California on Angel Guardia Island, in the Gulf of California and in the Santa Catalina Mountains of

southern Arizona. Every specimen of soldier which has been found has vestiges of wings or rudimentary wing pads. This is a primitive or ancestral character; or a reversion to the time when all social insects were winged and there were no sterile worker or soldier castes. Holmgren (31) established a new subgenus (*Pterotermes*) for this termite.

Soldiers of other primitive termites have commonly been found with these vestigal wings, but only a very small proportion of the soldiers of any colony were so characterized. No other termite except the large primitive *Kalotermes occidentis* has been found in which all the soldiers in a colony have such wing pads.

Genus **Termopsis** Heer.

This genus was established by Heer for a fossil termite from the Miocene of Croatia, and Banks (1) considers *T. insignis* Heer to be the genotype. Von Rosen (52), however, places *insignis* in *Miotermes*. Another fossil species of *Termopsis* described by Cockerell (22) as *Termopsis? swinhoei* is from "burmite" or Burmese amber; "the stratum in which the amber is found is *Miocene*." Cockerell later (24) believed this amber to be older than Miocene. This species resembles *Termopsis? procerus* Heer, now the genotype of *Miotermes* Von Rosen. Hagen described as *Termopsis* three species from amber, i. e., *T.? bremii* Heer (placed in *Xestotermopsis* n. gen. by Von Rosen), *gracilicornis* Pictet and *deciduus* Hagen; Von Rosen believes all three represent but one species.

The only living species of *Termopsis* are three from North America; their distribution is rather limited. *Termopsis angusticollis* Hagen occurs along the coast in British Columbia, Washington, Oregon and California. A closely related species *T. nevadensis* Hagen occurs in British Columbia, Washington, Montana, Oregon, California and Nevada. As previously stated, both of these species of *Termopsis* are able to live at high altitudes and in regions where snow and ice cover the logs which they inhabit for long periods of winter cold. In this respect they are unlike most species of termites. According to Imms (34), *Archotermopsis wroughtoni* Desneux has similar habits in the Garwhal Himalayas (India).

T. laticeps Banks, a more distinct species, however, is confined to two southwestern states, i. e., Arizona and New Mexico.

It has been shown that no species of *Termopsis* either recent or as yet as fossils has been found in Colorado. It is possible, however, that fossil specimens occur at Florissant. Von Rosen believes *Parotermes insignis* Scudder to be a *Termopsis*.

Species of *Termopsis* are our largest living North American termites; they are also the most primitive Nearctic species. The genus *Termopsis* is more primitive than the genus *Kalotermes* Hagen, because the contained species are not as well defined in *Termopsis* as in *Kalotermes*. In the latter genus, some species are very distinct and the species are more numerous. In species of *Kalotermes* there is a reduction in the number of antennal joints. However, ocelli are present in *Kalotermes* and absent in *Termopsis;* the presence of ocelli is a primitive character.

Genus **Hodotermes** Hagen.

The genus *Hodotermes* (l. s.) is both recent and fossil. The species of this rather primitive genus, at present in the same subfamily as the genus *Termopsis* Heer, the *Hodotermitinae* Holmg., are grass or leaf-cutting termites but in their structure and pigmentation they show a progressive development. While they nest in subterranean galleries, they are termed "wander-termites," since both the workers and soldiers of some of the species are darkly pigmented, have faceted eyes, long legs and forage above ground exposed to the light. It is unusual for a generalized primitive termite to have a true worker caste and C. Fuller of South Africa believes that the worker caste has later been lost in the less primitive *Kalotermitidae* (*Termopsis*, *Kalotermes*, etc.). The presence of this highly specialized worker caste indicates that *Hodotermes* should be in a distinct family the *Hodotermitidae*.

Considering *Hodotermes* as being classified in the family *Kalotermitidae* where the worker caste is absent, it was believed that this worker of *Hodotermes* might prove to be an apterous third form reproductive type. The late Dr. (Miss) C. B. Thompson, Professor of Zoology at Wellesley College, Wellesley, Mass., was inclined to this view, from a study of the brain and eyes of two types of workers in *Macrohodotermes* (*Hodotermes*) *mossambicus* Hagen (?), but was unable to thoroughly study the sex organs due to lack of fresh material and hence could not confirm or disprove this. However, a superficial study indicated to Miss Thompson and the writer that these forms were sterile and not reproductive forms; the optic lobe is small, as is normal in the worker caste.

Furthermore, Fuller has kindly sent to the writer specimens of a yellowish, apterous caste, larger than the worker, that is found with species of *Macrohodotermes* Fuller; this caste has black pigmented eyes and may be a third form reproductive adult.

It is interesting to note in connection with the studies of blind animals that these workers of the diurnal, wandering termite *Hodotermes*, which forage for themselves above ground in the sunlight, have a deep body pigment and both compound (faceted) and simple eyes (ocelli). The apterous, ergatoid reproductive caste in termites which live entirely in underground galleries or hidden in tunnels in wood,—such as in species of the genus *Reticulitermes* Holmgren of subterranean habitat—have but little body pigment and have only traces of eyes.

An apterous queen of *Hodotermes* (*Anacanthotermes*) *ahngerianus* Jacobs. of Turkestan is figured by J. V. Vasiljev (Revue Russe d' Entomologie XI, 1911, pp. 235–245). The color of the head is brown and the eyes are black-brown.

Approximately two dozen living species in the genus *Hodotermes* (l. s.) occur in Africa (reaching furthest north in Egypt), Transcaspia, Turkestan, Persia and India.

No living species in the genus *Hodotermes* occurs at Florissant, Colo., or anywhere else in America, but as previously stated fossil species, doubtfully in this genus, have been found at Florissant.

The four fossil species of this genus found in Europe are *Hodotermes? procerus* Heer and *H.? haidlingeri* Heer, from Radoboj; also *H.? spectabilis* Heer and *H. insignis* Heer from Oeningen; all are placed in *Miotermes* by Von Rosen. In America at Florissant, Colo., *Hodotermes? coloradensis* Scudder occurs in Miocene shale. In the case of the species *coloradensis*, as other species, it is doubtful if this is a *Hodotermes;* however, it is a primitive species of huge size. Cockerell (19) states: "The presence of the subcostal (sub-marginal) vein, which was supposed to separate *Paroter-mes* from *Hodotermes*, is not diagnostic, this vein being present in true *Hodotermes*. It is *Porotermes* [Hagen], formerly considered a subgenus of *Hodotermes*, which has the subcosta absent or rudimentary. * * * The indications are, then, that *Parotermes* differs little from *Hodotermes*, so that it may be a matter of opinion whether it is really separable. * * * Its (*Hodotermes*) occurrence at Florissant affords a case parallel to those of the Nemopterids and Nemestrinids."

Cockerell described a new species from Miocene shale at Florissant, *Parotermes scudderi*, which is of great size and has the subcostal vein well developed and the abdominal appendages very small. The termite described by Scudder from the Florissant shales as *Hodotermes? coloradensis* is of great size and has unusually long abdominal appendages and the subcostal vein is totally absent. "It is therefore apparently not a true Hodotermes" (Cockerell, 19).

It is not definitely known whether the sections of all the countries which the living species of the genus *Hodotermes* (l. s.) inhabit are arid or humid; probably, however, they are usually arid and desert-like. The habit of these termites of wandering above ground in the sun is indicated by the true (faceted) eyes of the soldier and the worker.

The records written by fossil termites are at best very imperfect! While it has not been proved that *wingless* termite castes occurred in the Tertiary period, they doubtless occurred and were probably evolved during the late Cretaceous period. Polymorphism among the social insects may not have been as highly developed as at present, especially in the case of the reproductive forms, but it can not be stated that the sterile castes and colony or social habits developed *since* Tertiary times because of lack of fossil forms. Due to their habits, such sterile forms would be less liable to be preserved as fossils. Both mandibulate soldiers and nasuti have been found embedded in gum copal from the Pleistocene period.

Genus **Parotermes** Scudder.

Parotermes Scudder is a genus established from fossil termites alone and is peculiar to the American Tertiaries of Colorado; there are no living representatives; the genotype is *insignis* Scudder. The genus is closely allied to *Hodotermes, Termopsis* and *Kalotermes*.

At Florrisant, Colo., four species have been found, namely *Parotermes insignis* Scudder (placed in *Termopsis* by Von Rosen), *hagenii* Scudder, *fodinae* Scudder (both placed in *Kalotermes* by Von Rosen) and *scudderi* Cockerell. The replacement of some of these American species in this new fossil genus is doubtful; they might easily be assigned to recent genera.

Cockerell (19) states that *Parotermes* differs little from *Hodotermes* and may not be really separable.

Genus "Eutermes" Fritz Müller.

In the genus "*Eutermes*"—which has by recent classification been divided into several subgenera of the genus *Nasutitermes* Banks—the soldiers or "nasuti" have a nose-like process of the head, a nasus or "beak." The mandibles are merely vestigial or absent, but from this nose-like process is secreted a viscous fluid, which serves as a means of defense.

This genus is represented by both fossil and recent species. *Eutermes? obscurus* Heer and *E.? croaticus* Heer occur in the Radoboj of Europe; Von Rosen believes that they are in the family Termitidae. In the Miocene of Europe also occurs *Eutermes fraasi* Von Rosen; this is considering the genus "*Eutermes*" in its broad sense (s. l.), not in the more recent restricted meaning (s. str.).

In the Miocene of Florissant, Colo., occur two species, namely, "*Eutermes*" *fossarum* Scudder and "*E.*" *meadii* Scudder. Of these two species it may be said that their position in the present genus "*Eutermes*," that is, that they are either species of *Nasutitermes* Banks or *Tenuirostritermes* Holmgren, is doubtful.

According to Von Rosen "*Eutermes*" *meadii* might be a species of *Leucotermes* Silvestri close to *L. Hartungi* Heer from Oeningen. In a subgenus of *Leucotermes*, *Reticulitermes* Holmgren, a species to-day occurs in Colorado, namely, *R. tibialis* Banks. The present writer is unable to place *meadii*. The genus *Leucotermes* is not so highly specialized, as is "*Eutermes*" (s. l.). "*E.*" *fossarum* Scudd. is without doubt, even if not a "*Eutermes*," that is *Nasutitermes* (s. str.), one of the higher more specialized termites, not to-day represented by living species in the Rocky Mountain region. An examination of the type by the writer showed that the third joint of the antennae is apparently longer than the second or fourth, and that the wing scale is short, so it may really be a *Tenuirostritermes*,—species of which to-day occur in Arizona and Texas.

Living species of "*Eutermes*" (i. e., *Nasutitermes* or *Tenuirostritermes*) inhabit both humid and arid regions. The Lower Austral (Sonoran region) of Texas and Arizona is the present habitat of species of *Tenuirostritermes* in the United States. Living species of "*Eutermes*" (both *Nasutitermes* and *Tenuirostritermes*) occur in the West Indies or Antilles but not in either Florida or southern California; both these regions have, however, an environment *apparently* favorable.

Of course, the islands of the West Indies have a more diverse topography —including high mountains—than has Florida. Possibly the absence of these termites may be explained by disconnection by submergence in the Tertiary period of Florida and California from the extensive Niobrara Basin, when animals of this basin were moving southward due to the coming colder climate; or, previous to this change in climate, they had invaded the Florissant Basin from more southerly regions. Florida was probably elevated and definitely connected with North America towards the end of the Miocene (Dall, 25).

On the other hand, the presence of species of *Nasutitermes* "*Eutermes*" on the islands of the West Indies may be explained by a connection with the mainland through Yucatan, in the Tertiary period.

However, cycads,[1] which occur as Tertiary flora, to-day are living in Florida.

It is very difficult to generalize because of the doubtful identity of many of the fossil termites.

Summary and Conclusions.

It is evident from the foregoing that during the Tertiary period there was a relatively larger proportion (more genera) of primitive termites than of the higher species at Florissant, Colo., and than there is at present in North America. The same is also true of the termites of the Tertiaries of Europe. But none of the Florissant fossil termites exhibit exceptionally primitive characters except *Hodotermes? coloradensis* Scudder. The large size, the great length of the abdominal appendages (cerci), and wing venation of this termite are distinctive. Species of *Parotermes* Scudder are also characteristically primitive termites. The "excessive area of the externo-median vein, and the course of the latter, which is approximated much more closely than usual to the scapular vein and emits branches having an unusual longitudinal course" (Scudder, 47) are unusual.

Certain living termites—species of *Mastotermes* Froggatt of Australia, *Archotermopsis wroughtoni* Desn. of India—are generalized, primitive termites. Both of these genera are found as fossils.

In North America *Kalotermes occidentis* Walker—the largest species of *Kalotermes*—and species of *Termopsis* Heer, exhibit primitive characters. *K. occidentis* shows evidence—in the soldier with wing pads—of reversion to the winged ancestral condition when there were only the winged sexual adults.

Although there were a relatively larger proportion of the lower termites than higher at Florissant than at present found in North America, there were also representatives of the higher termites, such as species of "*Eutermes*" Fritz Müller. The presence of these termites—and *E. fossarum* Scudder from the Miocene appears to be a species of the subgenus *Tenuirostritermes*, genus *Nasutitermes*—indicates a warmer, more arid climate during the Tertiary period.

This, however, need not conflict with the presence of the humidity-loving *Sequoia* tree as a Miocene fossil at Florissant.

Species of *Tenuirostritermes*, while confined at present to the Sonoran portion of the Austral zonal region of the United States, are present in the more humid Antilles.

While there are no authentic paleontological records of termites before the Tertiary, Wheeler has stated (55) that "in all probability the termites, like the ants, reached their complete structural and social development in the late Cretaceous or early Tertiary and have since undergone very little modification."

[1] Zamia spp.

Fossil soldier and worker termites (sterile castes) have been found in gum copal, a resin which is of comparatively recent formation (Pleistocene). However, it is not probable that there was the elaborate polymorphism during the Tertiary period that exists to-day; this is especially true in the case of the reproductive forms, where polymorphism has probably come about since the Tertiary.

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GEOLOGICAL AGE AND GEOGRAPHICAL LOCATION OF DEPOSITS.

Middle Eocene "Burmite," Burmese amber.	Upper Eocene Bartonian Bagshot Beds, Bournemouth, Hampshire, England.	Upper Eocene or Lower Oligocene Baltic Sea amber.	Middle Oligocene Brunstatt in Elsass.	Middle Oligocene Gurnet Bay Isle of Wight Bembridge limestone, England.	Upper Oligocene Rott, Rheinlande.	Upper Oligocene Hasgita, Silesien.	Lower Miocene Radoboj, Croatia.	Miocene Randeck, Würtemberg.	Miocene Shale Florissant, Colo., North America.	Upper Miocene Oeningen, Baden.	Upper Miocene Gabbro, Italy.	Pleistocene Gum copal, Africa.

FAMILY, SUBFAMILY, GENUS AND SPECIES, ISOPTERA.

MASTOTERMITIDAE.

Mastotermes bournemouthensis Von Rosen

Mastotermes anglicus Von Rosen

Mastotermes bathei Von Rosen

Mastotermes (Hodotermes) heeri Assmann

Mastotermes (Termopsis) heeri Goepp.

Mastotermes croaticus Von Rosen

KALOTERMITIDAE.

HODOTERMITINAE.

"*Hodotermes*" sp. Von Rosen

Ulmeriella bauckhorni Meunier [1]

Miotermes ("Termes") proceras Heer
Miotermes ("Termes") haidlingeri Heer

Miotermes randeckensis Von Rosen

Miotermes (Hodotermes) coloradoensis Scudder

Miotermes ("Termes") insignis Heer
Miotermes ("Termes") spectabilis Heer

Xestotermopsis (Termopsis) bremii Heer

Archotermopsis torquisti Von Rosen

Paratermes scudderi Cockerell
Termopsis (Paratermes) insignis Scudder

Termopsis sunnhoei Cockerell

Proclectrotermes (Kalotermes) berendtii Pictet

Electrotermes (Kalotermes) affinis Hagen
Electrotermes (Kalotermes) girardi Giebel

KALOTERMITINAE.

Kalotermes rhenanus Hagen (2 species represented?)

Kalotermes (Paratermes) fodinae Scudder
Kalotermes (Paratermes) hageni Scudder

Kalotermes ceningensis Von Rosen

Kalotermes boantiokii Handlirsch

Kalotermes (K.) reinatus Von Rosen (MS) Gold Coast. Imagos.
Kalotermes (K.) erythrops Von Rosen (MS) East Africa. Imagos.
Kalotermes (K.) sp. (without pulvillus). German East Africa. Imagos.

Kalotermes (Neotermes) sp. = *pallidicollis* Sjöst.? East Africa. Imagos.

Kalotermes (Cryptotermes) batheri Von Rosen (MS) (= *brevis* Walker?) East Africa. Imagos.

Kalotermes (Glyptotermes) pusillus Heer. Gold Coast, East Africa, Sansibar. Imagos.

RHINOTERMITIDAE.

Leucotermes (Reticulitermes) antiquus Germar
Leucotermes (Reticulitermes) borussicus Von Rosen
Leucotermes (Reticulitermes) robustus Von Rosen

Leucotermes ("Eutermes") meadii Scudder

Leucotermes ("Termes") hartungi Heer

Coptotermes 3-4 sp. Various localities.

Rhinotermes sp. = *Rh. lamanianus* Sjöst.? Sansibar.

TERMITIDAE.

"Termes" eroticus Heer
Termes gigandeus Heer

Odontotermes ("Eutermes") pristinus Charpentier

"Eutermes" obscurus Heer

"Termes" buchii Heer

"Eutermes" fossarum Scudder

"Eutermes" (l. s.) *fraasi* Von Rosen

Termes (T.) omicus Von Rosen. East Africa. Minor soldier and worker.
Termes (T.) sp. = *goliath* Sjöst. German East Africa. Major soldier.

Odontotermes 2 sp. Gold Coast, German East Africa. Imagos.

Microtermes sp.? East Africa. Imagos.
Eutermes (Trinervitermes) handlirschi Von Rosen (MS). Gold Coast.
Eutermes (Trinervitermes) sp. Sansibar.

Mirotermes reinatus Von Rosen. East Africa. Imagos.
Mirotermes sp. East Africa. Imagos.

Microcerotermes (Eutermes) debilis Heer. Imagos.
Microcerotermes latinotus Von Rosen (MS) East Africa. Imagos.
Microcerotermes sp. East Africa. Worker.

ISOPTERA INCERTAE SEDIS.

"*Termes*" *rutati* Meunier (Worker?)
("*Termes*")—Burmeister
("*Termes*")—Guérin
("*Termes*")—Schlotheim
("*Termes*")—Smith

("*Termes*") Förster

("*Termes*")
Species Schöbherlin
"*Termes*" sp. Scudder

"*Eutermes*" sp. Scudder (worker?)
"*Eutermes*" sp. Scudder

[1] Cockerell and Snyder, Proc. Biol. Soc. Wash., Vol. 38, p. 80.