

THE PHYLOGENY OF TERMITE
GENERA BASED ON IMAGO-
WORKER MANDIBLES

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INTRODUCTION

THE STUDY OF PHYLOGENY aims at the recognition of the relationships of organisms within a group based upon their descent. There are various lines of approach to the understanding of such relationships. Using any of the phases of biology, such as comparative morphology, physiology, embryology, ecology, genetics, zoogeography, or paleontology, one can arrive at phylogenetic interpretations. In a study like the one presented in this paper, in which a large number of genera are involved and access to all species in the living condition is difficult, comparative morphology is perhaps the best tool of attack. Sound studies of comparative morphology can be of great value in elucidating some of the important principles of biology. This paper attempts to lay a foundation for such interpretations.

The mandibles of the imago and the worker castes in termites provide a very useful morphological character for the study of phylogeny. This character is conservative and is almost identical in the two castes. Holmgren (1911, 1912) was the first investigator to take cognizance of this character in building his classification. Many years later, Hare (1937), while establishing the phylogeny of termites on the basis of soldier mandible development, also made frequent use of the imago-worker mandibles in the support of her conclusions. The present work is the first thorough study of the relationships of virtually all the living genera of

termites based primarily upon the imago-worker mandibles, though not entirely excluding other characters. In some cases the imago-worker mandibles alone have proved inadequate for the establishment of exact relationships. The phylogenetic series in such groups has been built upon information concerning other aspects of their biology. In this connection zoogeography has been of particular help.

The imago-worker mandibles of generitypes, when available, have been studied with the assumption that there is no fundamental variation within the genus. In some instances, a comparison of the imago-worker mandibles of the generitype with those of the other species of the same genus was made to determine the degree of variation. Except in a few cases, where there is some indication of variability, this character was found to be fairly constant. Genera showing large variation need revision and reassignment of the species, but such a study is beyond the scope of this paper. In the future, with better knowledge of these complexes, the phylogenetic scheme presented here (figs. 1-4) may still be improved.

I am greatly indebted to Dr. Alfred E. Emerson for suggesting the problem and taking keen interest in the progress of the work. Dr. James A. G. Rehn of the Academy of Natural Sciences of Philadelphia has been kind in lending me representatives of some genera of roaches.

MATERIAL AND TECHNIQUE

Except for three genera of roaches lent me by the Academy of Natural Sciences of Philadelphia, the entire study is based upon the termites in the collection of the American Museum of Natural History, now in the custody of Dr. Emerson. When the generitype was not available or was poorly represented in the collection, other species in the genus were substituted. In the majority of cases the species were metatypes (compared with type specimens). A total of 140 species (see Appendix) representing three genera of roaches and 137 genera and subgenera of termites was studied. Two genera of termites, viz., *Euscatotermes* and *Rostrotermes*, which were not available in the collection have been

incorporated into this study on the basis of the descriptions alone.

The mandibles were dissected in 80 per cent alcohol, and drawings made with the help of a camera lucida. Usually the mandibles of the worker caste were drawn because they were numerically better represented in the collection than the imago caste. Several workers, depending upon the availability of the material, were dissected and their mandibles compared in order to avoid any mistake resulting from the mixture of species in the field or in the vial. Whenever the imagoes were available their mandibles were compared with those of the worker.

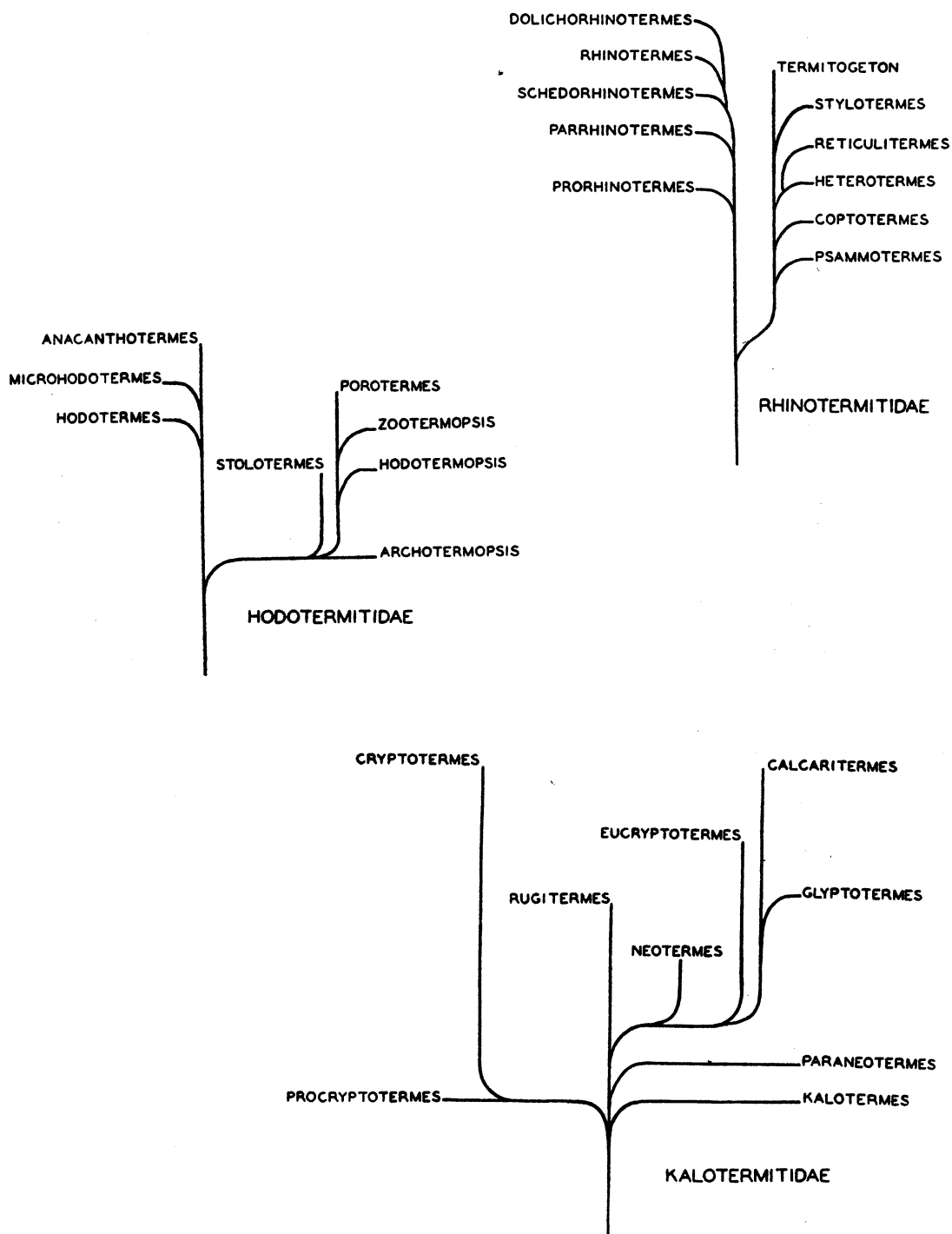


FIG. 1. Hypothetical phylogenetic tree of the families Kalotermitidae, Hodotermitidae, and Rhinotermitidae.

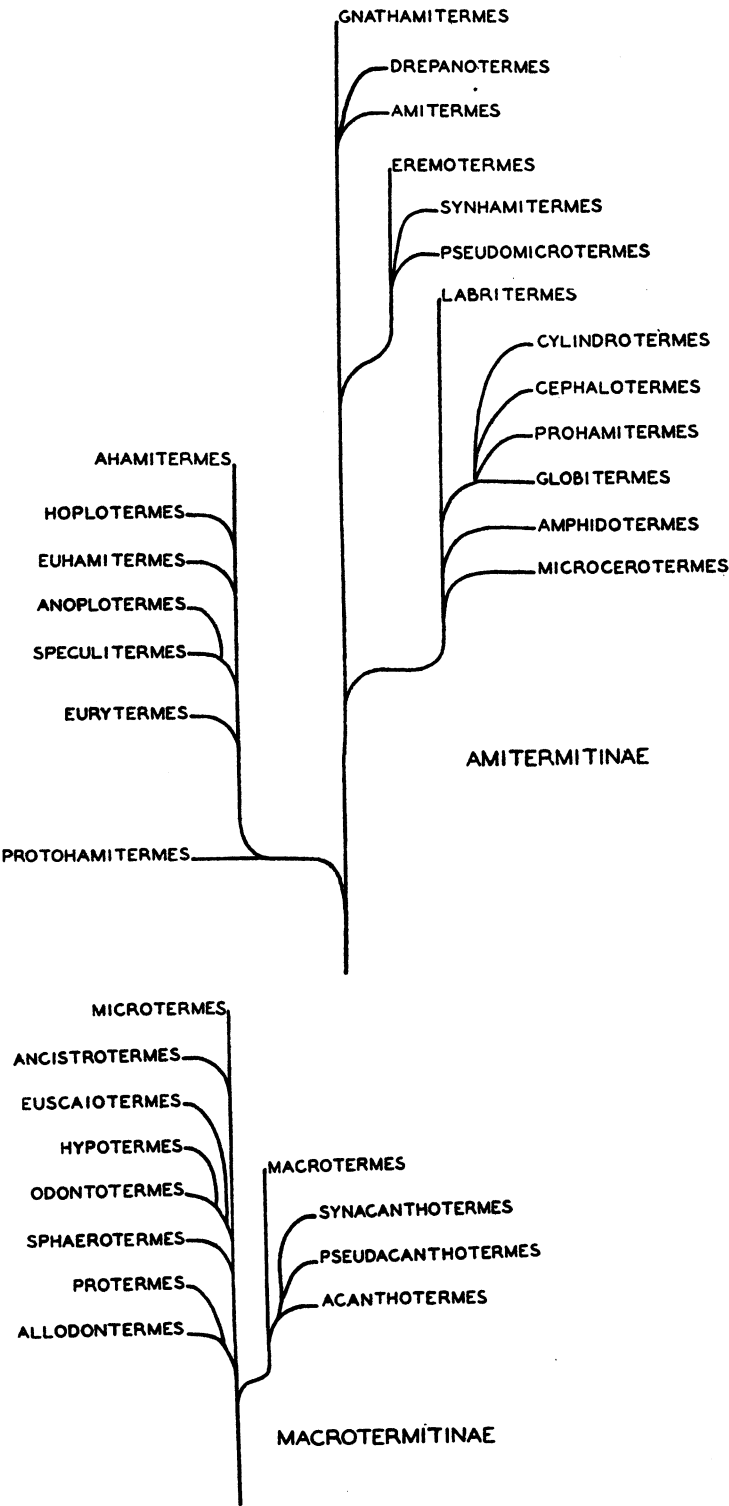


FIG. 2. Hypothetical phylogenetic tree of the subfamilies Macrotermittinae and Amitermitinae.

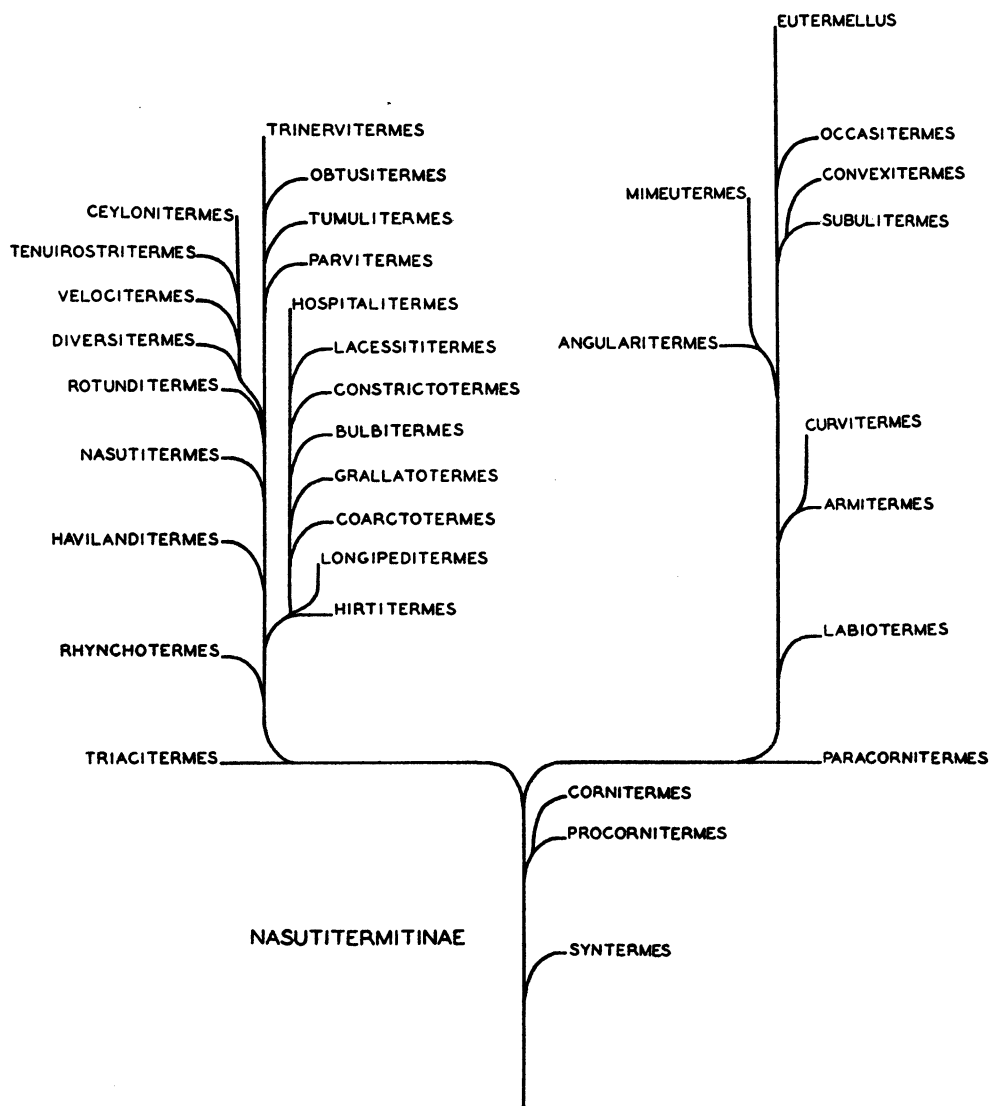


FIG. 3. Hypothetical phylogenetic tree of the subfamily Nasutitermitinae.

TERMINOLOGY

Snodgrass (1935) refers to the distal part of the mesal surface of the mandible with teeth as the incisor lobe and the proximal part as the molar lobe. Emerson (1933) designates the first tooth of the incisor lobe of Snodgrass as the apical tooth and the rest as the marginal teeth which in primitive mandibles like those of *Cryptocercus* (fig. 5) are further distinguished as the first, second, and third marginal teeth. He refers to the molar surface posterior to the marginals as the "molar plate." Because of the ease in comparing the individual homologous teeth

Emerson's terminology has been adopted. The two sides of the marginals will be referred to as the anterior and posterior edges. The entire edge is single from the apical to the last marginal, whereas the molar area is hollowed out into a cavity into which fits the corresponding part of the mandible of the opposite side. The under side of the molar plate is wedge shaped which, when seen from above, looks like a tooth in some mandibles. The latter should not be mistaken for any of the marginals.

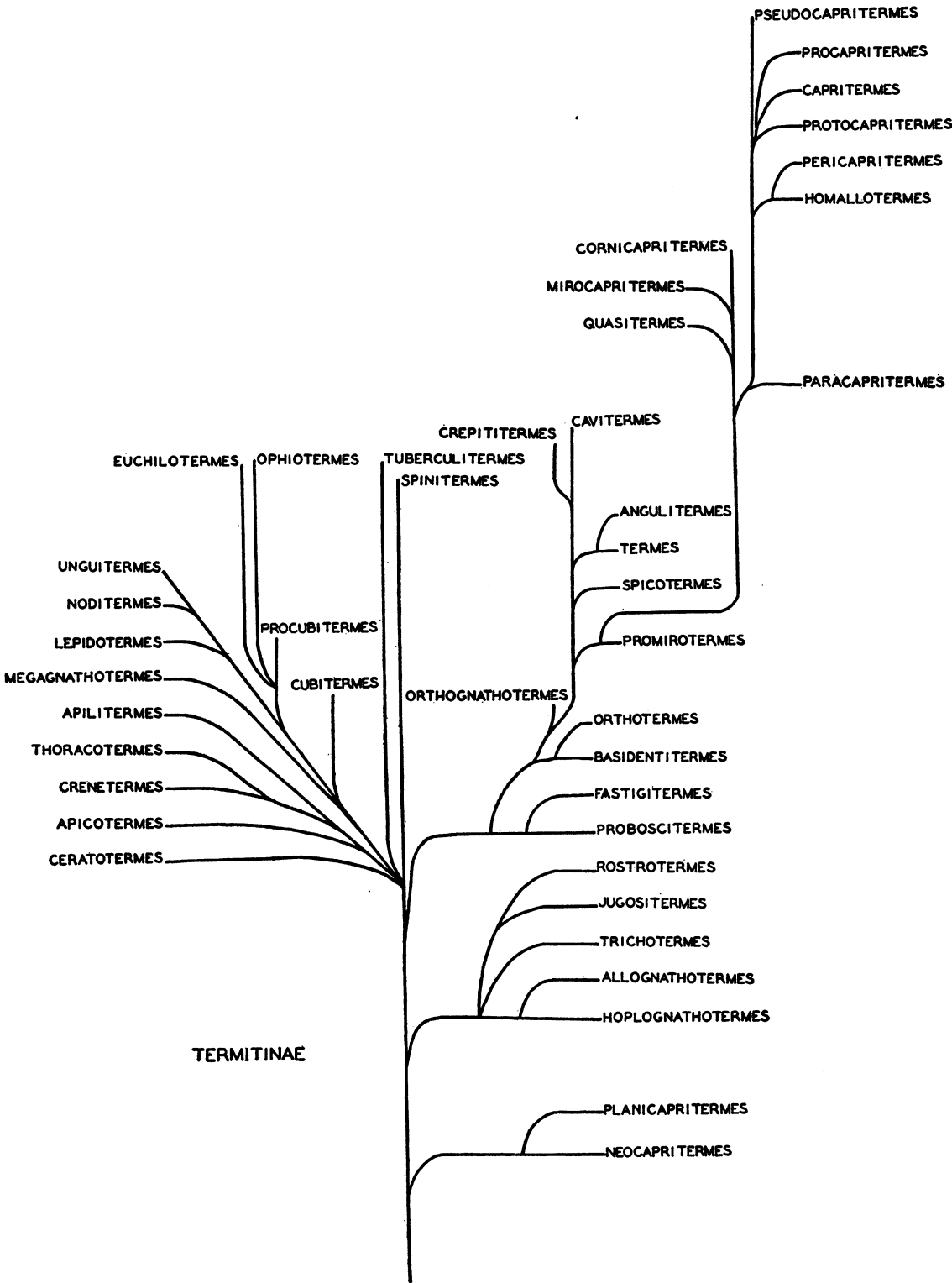


FIG. 4. Hypothetical phylogenetic tree of the subfamily Termitinae.

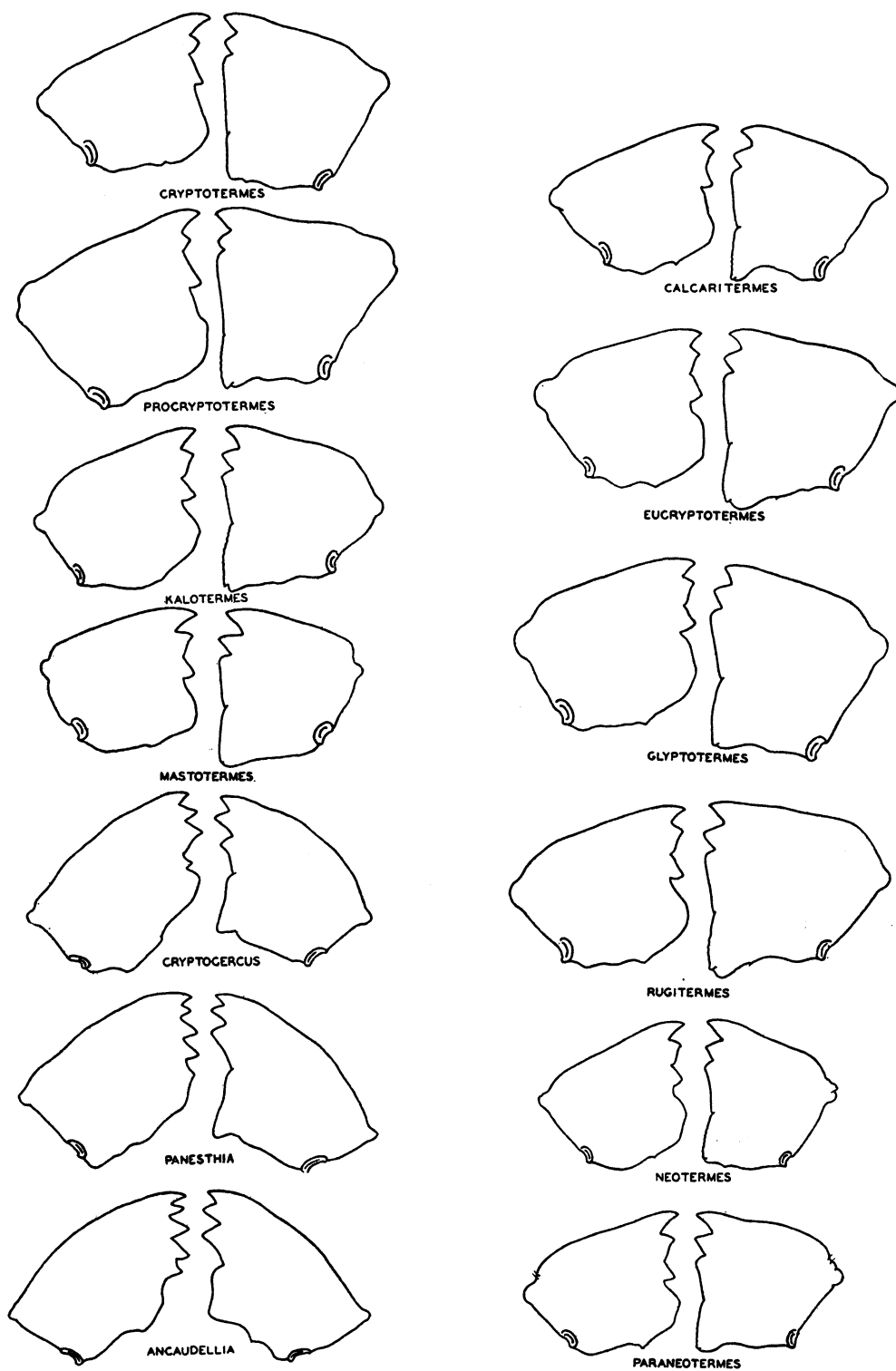


FIG. 5. Imago-worker mandibles of the families Blattidae, Mastotermitidae, and Kalotermitidae.

PHYLOGENETIC STUDY

MASTOTERMITIDAE

THE FAMILY MASTOTERMITIDAE is represented by a single living species, *Mastotermes darwiniensis* Froggatt, from Australia. In general it is considered to be the most primitive of all the modern termites, although in a few respects it shows specialization over some of the otherwise higher termites belonging to the Kalotermitidae and the Hodotermitidae.

Mastotermes shares with roaches a large number of characters, of which the most remarkable is the presence of an anal lobe in the hind wing. Another important blattoid feature in the hind wing is the absence of a basal suture which is present in all other termites. Crampton (1923) reports many other structural resemblances between *Mastotermes* and roaches, such as the origin of the pygidium from the tenth abdominal segment, the well-developed paraprocts, and the partial fusion of the styli-bearing organs. These homologies have been studied further and confirmed by Browman (1935). The egg masses of *Mastotermes* are similar to the oöthecae of roaches. There is therefore little doubt about the blattoid ancestry of *Mastotermes*.

None of the modern roaches can be considered to be the ancestor of termites. All alate modern roaches have horny forewings. The membranous wings of termites are more primitive. Moreover, Tillyard (1931) doubts the exact homology of the anal lobe of the hind wing of *Mastotermes*. He thinks that it is not complete as it includes only the second anal vein and its branches and that the line of folding does not correspond with that in the blattids. Among the modern blattids, *Cryptocercus punctulatus* Scudder, the sub-social, wingless, wood-feeding roach, bears closest relationship to termites. This rela-

tionship is borne out by the findings of Cleveland *et al.* (1931, 1934) who report a striking similarity of the cellulose-digesting flagellates of *Cryptocercus* to those of termites. Discussing the bearing of this relationship on the evolution of termites, the authors in their 1934 paper remark, "the evidence is overwhelming that this roach is either the ancestor of termites or is closely related to the ancestor which is extinct." While agreeing fully with the second part of their remark, I take exception to the view that *Cryptocercus* could be the ancestor of termites. Some earlier blattoid stock which had wings and had already acquired the symbiotic Protozoa may be considered as the common ancestor of *Cryptocercus* and termites.

In the imago-worker mandibles, *Mastotermes* (fig. 5) shows a much higher specialization than *Cryptocercus*. The marginals of the left mandible are reduced from three in *Cryptocercus* to two in *Mastotermes*, a condition more specialized than in some of the hodotermitids. The reduction was probably brought about either by complete regression of one tooth or by the fusion of the first marginal with the second or of the second with the third. Judging from the condition in the Termopsinae where a gradual reduction of the fully developed second marginal of *Archotermopsis* (fig. 6) to a rudimentary condition in *Zootermopsis* (fig. 6) has occurred, it is quite likely that the second marginal in the Mastotermitidae might have undergone further regression. In the biology the Mastotermitidae is more advanced than the next family, the Kalotermitidae. Probably after the separation from the ancestral stock it has continued specialization in a direction not exactly in line with other termites, although retaining some primitive characters.

KALOTERMITIDAE

There is strong evidence that the Kalotermitidae arose from *Mastotermes*-like ancestors. The imago-worker mandibles (fig. 5) are essentially the same as in the Mastotermitidae. The presence of the ocelli and the

arolium in both the families further strengthens their relationship. Kirby's study (1945) on the distribution of the termite flagellates belonging to the genus *Metadevescovina* provides additional evidence in support of this

affinity. These flagellates are known only from the Kalotermitidae and the Mastotermitidae, and interestingly enough more than half of the species, 10 out of 15, reported from the Kalotermitidae are confined to *Kaloterмес*, the most primitive genus of the family. None of the higher kalotermitids, such as *Cryptotermes*, *Eucryptotermes*, and *Calcaritermes*, are known to harbor these flagellates.

In the light of this evidence there is little doubt that the Kalotermitidae arose from mastotermitid-like ancestors. However, their direct origin from *Mastotermes* seems rather improbable. The large size of the colony and the fairly highly evolved nesting behavior of *Mastotermes* indicate its higher specialization compared to the kalotermitids. The latter have comparatively small colonies; their nest architecture is primitive, consisting of excavations in wood and the construction of simple partitions. Perhaps the Kalotermitidae arose as an offshoot from the early termite stock before evolution had gone far in the direction of *Mastotermes*.

The presence of a large number of transitory forms in the Kalotermitidae creates a great difficulty in the sharp differentiation of the genera. The imago-worker mandibles have not proved of much help in understanding the phylogenetic relationships within the family except for indicating two diverging lines of evolution. The first line, represented by *Procryptotermes* and *Cryptotermes*, is characterized by a comparatively marked elongation of the anterior edge of the second marginal and shortening of the posterior edge of the first marginal of the left mandible (fig. 5). The posterior edge of the second marginal of the right mandible is also conspicuously elongated. The second line, ending in *Calcaritermes*, does not show much marked elongation of the edges of the marginals. The terminal ends of these two lines of evolution, represented by *Cryptotermes* and *Calcaritermes*, show convergence in the evolution of the phragmotic head of the soldier caste.

Kaloterмес is the most primitive genus of the Kalotermitidae, as evidenced by its wing venation (the median being midway between the cubitus and the radial sector) and the elongate shape of its soldier head. There is an

indication of some variability in the imago-worker mandibles of this genus. It needs revision and reassignment of its species.

Probably the *Procryptotermes*-*Cryptotermes* branch arose from the *Kaloterмес* stem. *Cryptotermes* is more advanced than *Procryptotermes*, as indicated by its more highly developed phragmotic head and the less elongated anterior edge of the second marginal of the left mandible. *Neotermes* is closely related to *Kaloterмес*. The wing venation of *Neotermes* is a little more specialized than that of *Kaloterмес*. The median has shifted nearer to the radial sector, as compared to the position midway between the cubitus and the radial sector in *Kaloterмес*. This difference is, however, not absolute. The wing venation of *K. jouteli* is similar to that of *Neotermes*.

Paraneotermes shares many characters with both *Kaloterмес* and *Neotermes*. I am rather doubtful of the generic validity of *Paraneotermes*. With a more detailed study it may prove to be another intermediate form like *K. jouteli*. At present I am treating it as a genus as originally erected by Light (1937) and assigning it to a position intermediate between *Kaloterмес* and *Neotermes*.

Rugitermes shows a further advance over *Neotermes* through the coalescence of the median with the radial sector in the outer half.

Glyptotermes shows some distinct advance over *Neotermes*. The wing venation is more consolidated in that the median vein is entire, unlike that in *Neotermes* in which the median vein is joined to the radial sector by four to six cross veins. The soldier shows the beginning of the development of the phragmotic head.

In the remaining two genera, viz., *Eucryptotermes* and *Calcaritermes*, the soldier has a well-developed phragmotic head. While it is probable that *Calcaritermes* arose from *Glyptotermes*, the origin of *Eucryptotermes* seems to have taken place earlier. This conclusion is based upon the fact that the wing venation of *Eucryptotermes* is more primitive than that of *Glyptotermes*. In the development of the phragmotic head, *Eucryptotermes* is even more advanced than *Calcaritermes* and represents a convergent evolution of this adaptation.

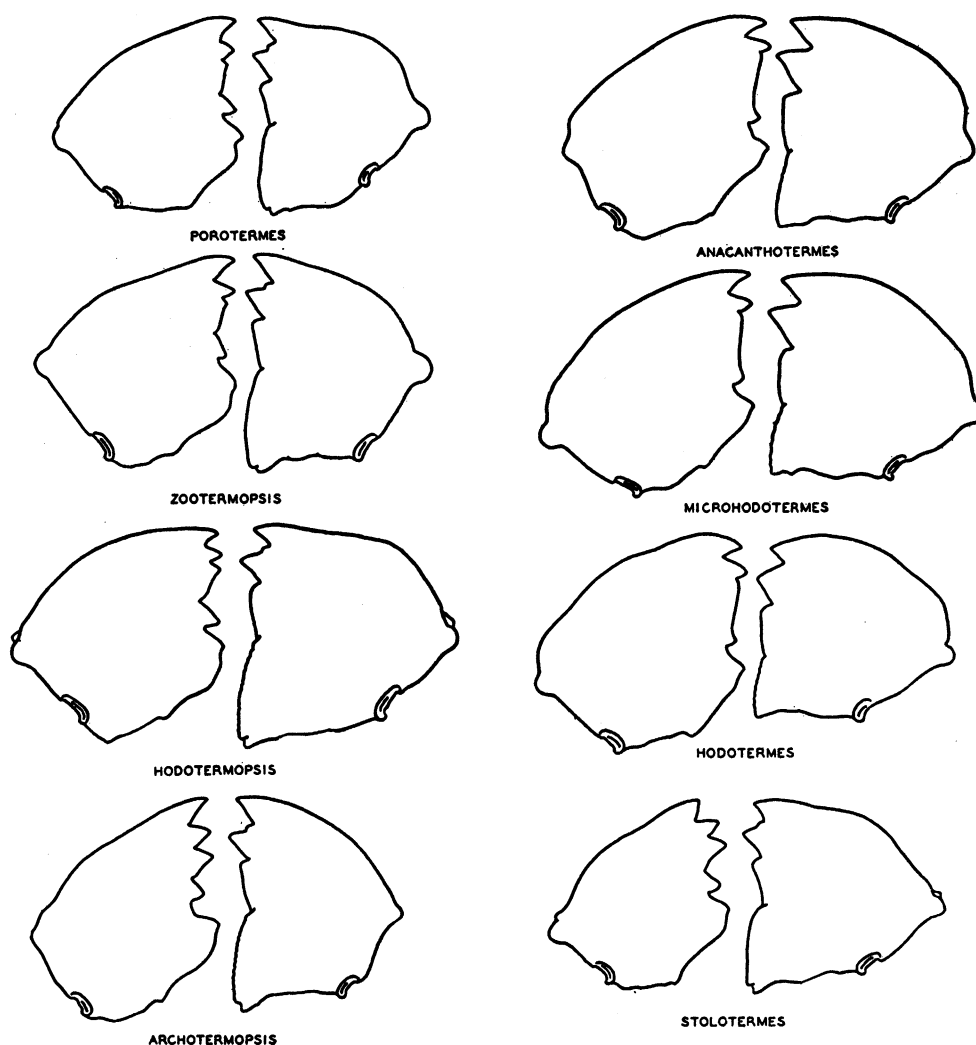


FIG. 6. Imago-worker mandibles of the family Hodotermitidae.

HODOTERMITIDAE

The Hodotermitidae seem to be an offshoot from primitive Isoptera possessing the characters common to the Mastotermitidae and the Hodotermitidae. While still maintaining a very close similarity to the blattids in the imago-worker mandibles (fig. 6) this group has evolved a higher social organization. Some of the hodotermitids, so far as is known, have an adult worker caste which is absent in the Kalotermitidae. One new character of phylogenetic importance which appears here for the first time in the

imago-worker mandibles is the small subsidiary tooth at the base of the anterior edge of the first marginal of the right mandible. This small tooth is found throughout the Rhinotermitidae and in some of the primitive fungus-growing genera belonging to the subfamily Macrotermitinae of the Termitidae. So far the studies of *Cryptocercus* and related genera such as *Ancaudellia* and *Panesthia* (fig. 5) reveal the absence of the subsidiary tooth in the Blattidae.

Among the subfamilies of the Hodoter-

mitidae, the Termopsinae are the most primitive. Their imago-worker mandibles come closest to the blattoid type. Of the three genera included in this subfamily, *Archotermopsis* is least specialized. In the possession of six-jointed to eight-jointed styli and the large reniform eyes, it is even more primitive than *Mastotermes* (Imms, 1919). A linear arrangement of the genera of the Termopsinae is possible (Emerson, 1933). There is a gradual reduction of the second marginal of the left imago-worker mandible. This tooth is most reduced in *Zootermopsis*. *Hodotermopsis* presents an intermediate condition between *Archotermopsis* and *Zootermopsis* in the development of the second marginal. Correlated with the reduction of this character is the corresponding widening of the angle between the second and the third marginals. This relationship is further borne out by other morphological characters, such as reduction in the size of cerci and styli from *Archotermopsis* to *Zootermopsis*.

The Stolotermitinae are represented by a single genus, *Stolotermes*. Their relationship has been discussed at some length by Emerson (1942). Their mandibles are homologous to those of the Termopsinae and come closest to those of *Archotermopsis*. Their specialized characters as compared to *Archotermopsis* are: the four-jointed tarsi, the four- to five-jointed cerci, the shorter styli, and the absence of the arolium. On the basis of these and other characters Emerson (*loc. cit.*) thinks that "we should place *Stolotermes* as a genus of the Hodotermitidae somewhat more specialized than *Archotermopsis* and best considered as an offshoot from the Hodotermitid base and not ancestral to any other living termites but possessing many characteristics that are ancestral in type to other termite groups, notably the Rhinotermitidae."

The Porotermitinae are likewise represented by a single genus, *Porotermes*. Their imago-worker mandibles are comparable to those of the Termopsinae and are very close to those of *Zootermopsis*. Browman (1935) concludes from his studies of the abdominal

structures of some female termites that *Porotermes* is "a possible branching off from the *Kalotermes* stem early in its history." This is not possible because the mandibles of the Hodotermitidae cannot be derived from those of any kalotermitid. Though showing resemblance to *Zootermopsis* in its imago-worker mandibles, *Porotermes* cannot be placed in the same subfamily because of the presence of several specialized characters. Emerson (1942) considers *Porotermes* to be at the same evolutionary level as *Stolotermes*.

The Hodotermitinae are the most highly evolved among the subfamilies of the Hodotermitidae. The imago-worker mandibles show a distinct advance over those of the *Archotermopsis-Zootermopsis* type. The second marginal of the left mandible is almost completely reduced and in many cases it is hardly visible. Other advances that the hodotermitids exhibit are the presence of a worker-like caste and a high degree of social organization. They are commonly called "harvester termites." The worker-like individuals pile up grass bits in the nests which consist of large globular excavations made in the soil. These cavities are filled with papery shelvings and are supported by cylindrical columns. This is a great architectural advance over the other hodotermitids which make simple partitions from their pellets of excrement in rotten logs in shady, moist localities (Imms, 1919). In respect to the imago-worker mandibles, all three genera of the Hodotermitinae are essentially similar and present the same evolutionary stage. With the help of other characters it is possible to trace their phylogenetic relationships. *Hodotermes* and *Microhodotermes* have lateral tibial spines which are lost in *Anacanthotermes*. The presence of the lateral tibial spines in the first two genera indicates their primitive condition compared with *Anacanthotermes*. *Microhodotermes* has more specialized wing venation than *Hodotermes*, as indicated by the loss of the branches from the radial to the subcosta.

RHINOTERMITIDAE

The Rhinotermitidae are more primitive than the Kalotermitidae in the character of the imago-worker mandibles (fig. 7) as evidenced by the possession of the full complement of three marginals and the subsidiary tooth, a pattern seen in roaches, *Archotermopsis*, and *Stolotermes*. It is therefore probable that the Rhinotermitidae arose from termites possessing mandibles of the *Archotermopsis-Stolotermes* type and not from the Kalotermitidae as suggested by Holmgren (1911) and Hare (1937). The exact ancestor can, however, be neither *Archotermopsis* nor *Stolotermes*, but is some common ancestor of both having ocelli. Primitive hodotermitids, after having lost the ocelli, could not give rise to forms with ocelli.

The study of the imago-worker mandibles reveals the presence of two distinct categories in the Rhinotermitidae. One has the second marginal of the left mandible longer than the first and the other has this tooth shorter (except in *Reticulitermes* in which it is as long as the first). This grouping of the rhinotermitid genera, except for the inclusion of *Prorhinotermes* in the first category and of *Stylotermes* in the second, is in line with the existing knowledge of their phylogenetic relationships. The first category (excluding *Prorhinotermes* and comprising four subfamilies, the Psammotermitinae, the Coptotermitinae, the Heterotermitinae, and the Termitogetoninae) is more primitive than the second category (excluding *Stylotermes* and comprising the Rhinotermitinae). The imago-worker mandibles, though conforming to the type characteristic of this family as a whole, have been of some help in indicating two main lines of evolution in the Rhinotermitidae.

The Psammotermitinae, represented by a single genus, *Psammotermes*, are the lowest among the Rhinotermitidae in the evolutionary scale. The soldier mandibles are primitive, as evidenced by the presence of a large number of teeth. They bear some resemblance, though not close, to the soldier mandibles of the Termopsinae. Holmgren (1911) shows *Psammotermes* arising from the Kalotermitidae stem in his phylogenetic tree, but, on the grounds discussed earlier, the Rhino-

termitidae cannot be derived from the kalotermitid stock.

The Coptotermitinae come next to the Psammotermitinae in the evolutionary sequence. The second marginal of the left mandible of *Coptotermes*, the only representative of this subfamily, is less stout and is shorter than in *Psammotermes*, and there is also a similar reduction of the first marginal of the right mandible. The soldier mandibles show a still greater departure from the *Psammotermes* type. The teeth are almost lost save for the slight sinuation or serration at the base. The frontal gland has undergone considerable development. This creates a big gap between the Psammotermitinae and the Coptotermitinae. The latter have closer relationships with the next subfamily, the Heterotermitinae, than with the Psammotermitinae.

The Heterotermitinae, though close to the Coptotermitinae, possess several distinct higher revolutionary features, such as the reduction of antennal articles, pronotum, anterior wing scales, and the 3:2:2 tibial spurs (3:3:3 in the Coptotermitinae). No soldier in the Heterotermitinae is known to possess eye spots. There is one record of the presence of rudimentary eyes in the soldier caste in the Coptotermitinae. Hill (1942) reports that the eye spots are visible in *Coptotermes grandiceps* Snyder. Before giving weight to this character it should be verified by anatomical study. A broad clypeus in the Heterotermitinae is another specialized character.

Heterotermes and *Reticulitermes* are the two genera included in the Heterotermitinae. *Reticulitermes*, while still sharing with *Heterotermes* such characters as the parallel-sided soldier head and the flat pronotum of the worker which justify its inclusion in the Heterotermitinae, has undergone great specialization in many other characters. Its ecology and protozoan relationships, together with some morphological characters (small anterior wing scale, second marginal of the left mandible as long as the first), separate it widely from *Heterotermes*.

The phylogenetic position of the Stylotermitinae is rather problematic. The imago-worker characters present a considerable advance over those of the three subfamilies dis-

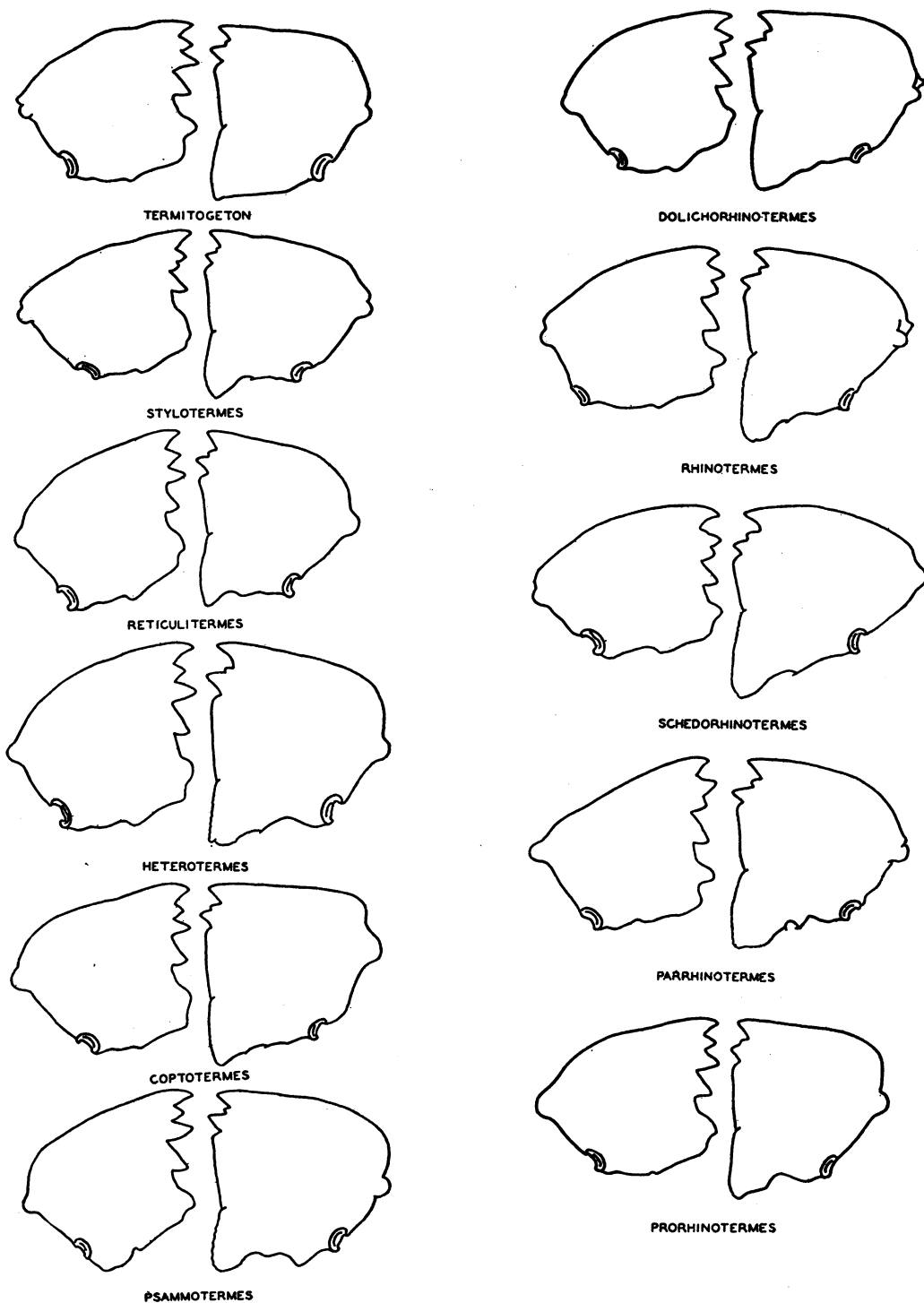


FIG. 7. Imago-worker mandibles of the family Rhinotermitidae.

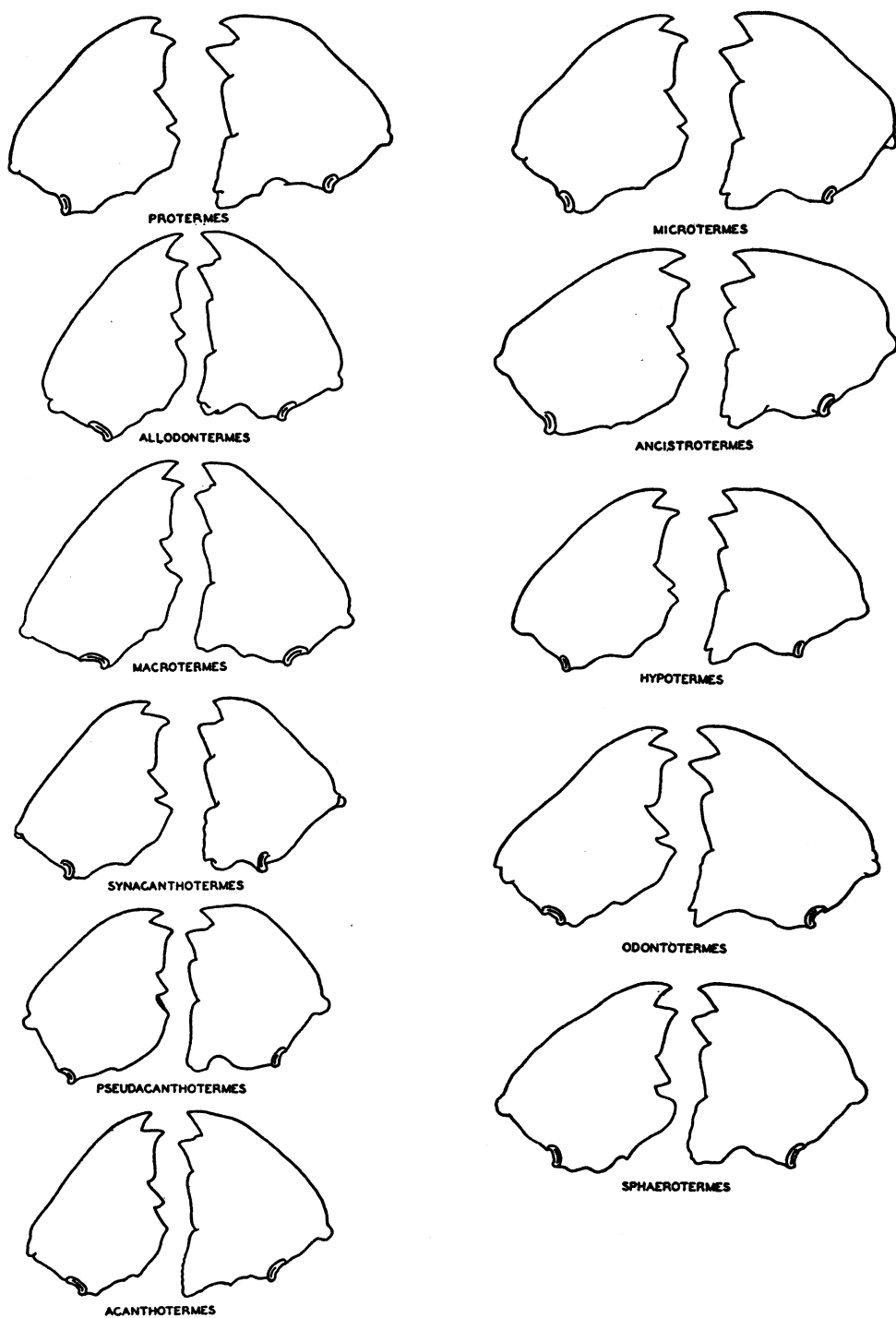


FIG. 8. Imago-worker mandibles of the subfamily Macrotermitinae.

cussed above, whereas the soldier caste possesses several primitive characters which bear superficial resemblance to those of some kalotermitids. It was on the basis of this superficial relationship that Holmgren and Holmgren (1917) suggested a *Kaloterмес* ancestry of *Styloterмес*. Snyder (1931) also agrees with their view. They remark, "*Styloterмес* is of particular interest since it exhibits characters which are connecting links between the lower termites in the family Kalotermitidae and those in the intermediate family Rhinotermitidae." Being a rhinotermitid, *Styloterмес* cannot be derived from the Kalotermitidae. I place *Styloterмес* next to *Heteroterмес* because it has the same type of wing venation and tibial spur arrangement but is more specialized in the imago-worker mandibles which are of the Rhinotermitinae type.

The Termitogentoninae are the highest evolved subfamily in the series in which the second marginal is longer than the first. Their specialized characters, not shared with any other of the subfamilies of the Rhinotermitidae hitherto considered, are the reduction of the wing venation (the radius and the median either absent or faintly present), the 2:2:2 tibial spurs, and the anteriorly narrowed soldier head.

The Rhinotermitidae have well-defined diagnostic characters such as the large forewing scale, the swollen clypeus of the imago, the second marginal shorter than the first (except in *Prorhinoterмес*), the anteriorly narrowed soldier head, and the saddle-shaped pronotum of the worker.

Prorhinoterмес is the most primitive genus of the Rhinotermitinae. Its imago-worker mandibles are still of the *Psammoterмес*-

Termitogeton type. Holmgren (1911) includes *Prorhinoterмес* (= *Arrhinoterмес*) under the Coptotermitinae, but such characters as the large clypeus of the imago, the reticulation of the wing membrane, the shape of the soldier head and its elongate labrum and the saddle-shaped pronotum of the worker leave no doubt of its close affinity to the other genera of the Rhinotermitinae. *Prorhinoterмес* represents the basic stock from which other genera of the Rhinotermitinae have arisen. Some of the diagnostic characters of the subfamily, for example the swollen clypeus and the saddle-shaped pronotum of the worker, are still not so pronounced in *Prorhinoterмес* as in the higher genera.

Parrhinoterмес shows a distinct advance over *Prorhinoterмес*. Its second marginal is distinctly smaller than the first, and the soldier is devoid of faceted eyes which are so distinctly seen in *Prorhinoterмес*. The reduction of the antennal articles and the saddle-shaped pronotum of the worker are some other specialized characters of *Parrhinoterмес*.

The remaining three genera, *Schedorhinoterмес*, *Rhinoterмес*, and *Dolichorhinoterмес*, have dimorphic soldiers. Of these, *Schedorhinoterмес* is more primitive. The minor soldiers have mandibles with teeth. The clypeus of the imago is swollen but does not yet appear to be elongate. The mandibles of the minor soldier of *Rhinoterмес* are very delicate and devoid of any tooth. The labrum is much more elongate, as is the clypeus of the imago. In *Dolichorhinoterмес* the major soldier has a more elongated labrum than either *Schedorhinoterмес* or *Rhinoterмес*.

TERMITIDAE

The Termitidae are the largest and most highly evolved family of termites, comprising five subfamilies—the Macrotermitinae, the Nasutitermitinae, the Amitermitinae, the Termitinae, and the Serritermitinae. These subfamilies cannot be arranged in any linear order. After emerging from the ancestral stock each has followed a different course of evolution. Regarding the origin of the family Termitidae, it is very probable that it arose from some rhinotermitid-like ancestor. The

presence of the subsidiary tooth in some of the primitive genera of the fungus-growing termites of the subfamily Macrotermitinae and in one genus, *Protohamiterмес*, of the Amitermitinae supports the postulation of such an origin of the Termitidae. *Protohamiterмес* still has all the three marginals of the left mandible (fig. 12) which seem to be homologous with those of the Rhinotermitidae.

MACROTERMITINAE

The subfamily Macrotermitinae, while possessing some primitive morphological features compared to other subfamilies of the Termitidae, exhibits specialization in its biology. All its genera and species have evolved an intricate instinct of fungus growing. The imago-worker mandibles (fig. 8) have essentially the same pattern throughout the subfamily except for the presence of the subsidiary tooth in some of its primitive genera. The second marginal of the left mandible is considerably reduced and is represented only by the broadly rounded lower end of the posterior edge of the first marginal. In this character and in the reduction of the forewing scale, the Macrotermitinae exhibit a higher specialization compared to the Rhinotermitidae.

Acanthotermes is the most primitive genus of the subfamily. Its primitive characters not shared with other genera are the prominent lateral spines of the mesothorax and metathorax and the trimorphic soldiers. *Pseudacanthotermes* has a poorly developed subsidiary tooth, and the thorax is devoid of the lateral spines. The soldiers are dimorphic. *Synacanthotermes* is closely related to *Pseudacanthotermes* as it has, in common with the latter, the subsidiary tooth and the trilobed hyaline tip of the soldier labrum, but in its monomorphic soldier and in the absence of the prothoracic processes it is more advanced.

Hare (1937) considers *Macrotermes* to be the most specialized genus of the Macrotermitinae on the basis of the "nearly smooth condition" of the third marginal. The depth of the cut between the third marginal and the molar plate is considered by the author as a phylogenetic character. Giving more weight to the fact that *Macrotermes* has a distinct subsidiary tooth in the imago, I am inclined to think that this genus arose from a much earlier stock than Hare postulates. The stock that gave rise to *Acanthotermes* was probably ancestral to *Macrotermes* also. The somewhat laterally produced margins of the mesothorax and metathorax and the trilobed hyaline tip of the soldier labrum in some species of *Macrotermes* further suggest its relationship to *Acanthotermes*.

My placement of *Protermes* also is different from that of Hare. An examination of a large

number of specimens of *Protermes* reveals the presence of the subsidiary tooth which apparently seems to have been missed by Hare. I therefore assign *Protermes* to a lower position in the phylogenetic tree of the Macrotermitinae (fig. 2). In this respect I am more in agreement with Holmgren (1912) than with Hare. Holmgren, however, puts *Protermes* at the base of the tree, which does not seem to be justifiable. Though it shares the subsidiary tooth with *Acanthotermes* it has many characters more specialized, such as fewer articles in the antennae, the thorax of the soldier without lateral spines, and the monomorphic soldiers. *Allodotermes* is very closely related to *Protermes*, though somewhat more primitive as indicated by the presence of the hyaline tip of the soldier labrum and the larger number of the antennal articles. The soldier mandibles also are more primitive than those of *Protermes*.

The genus *Sphaerotermes* has been placed at a lower level than *Macrotermes* by both Holmgren and Hare, but I, again on the basis of the relative degree of the development of the subsidiary tooth, assign it to a position next to *Macrotermes*.

The remaining three genera, viz., *Odontotermes*, *Ancistrotermes*, and *Microtermes*, have essentially the same type of imago-worker mandibles. The subsidiary tooth is lost completely. The stoutly built soldier mandible of *Odontotermes*, with its distinct tooth, is a primitive character compared to the condition in *Ancistrotermes* and *Microtermes*. If the depth of the cut between the third marginal and the molar plate of the left mandible studied by Hare is used, it is possible to arrange the subgenera of *Odontotermes* in a linear fashion. They fall in the sequence of *Odontotermes*, *Hypotermes*, and *Euscaiotermes*. The drawings of the worker mandibles of *Euscaiotermes* as given by Silvestri (1923) show the third marginal to be the least deeply cut.

Ancistrotermes and *Microtermes* have soldier mandibles more delicate than *Odontotermes*, and in some species of *Microtermes* the tooth of the soldier mandible is weakly developed. The fungus gardens of *Microtermes* are simple, possibly because they are reduced in size and the convolutions of the surface are not necessary. This would be an evolutionary

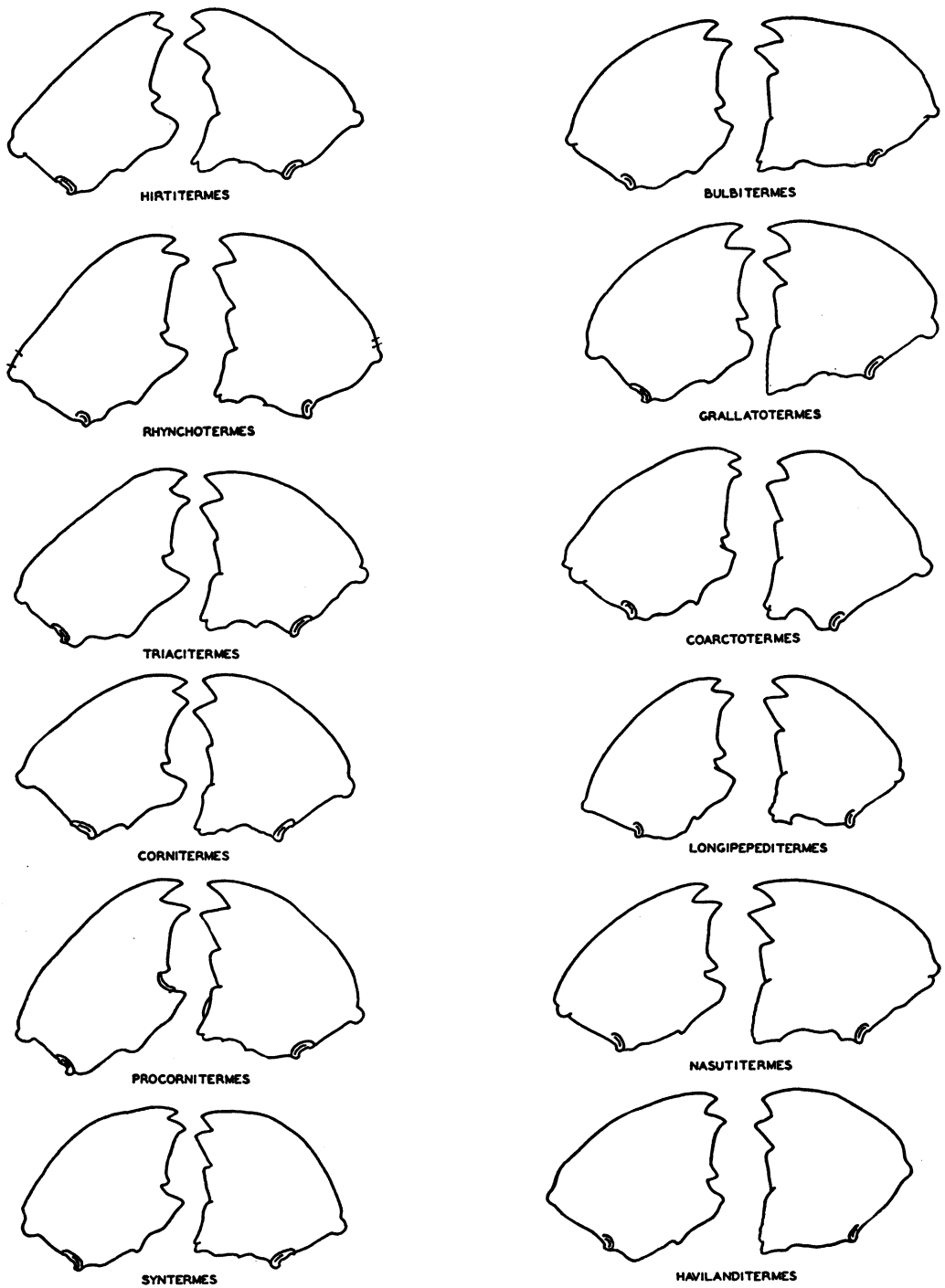


FIG. 9. Imago-worker mandibles of the subfamily Nasutitermitinae.

reduction. *Microtermes* has monomorphic soldiers, with the head narrowed anteriorly, and should be considered to be more advanced than *Ancistrotermes* which has dimorphic soldiers.

NASUTITERMITINAE

There is little doubt that the Nasutitermitinae and the Macrotermitinae arose from a common stock. The subfamily Nasutitermitinae presents some of the best cases for the study of the phylogenetic sequence because of the existence of many intermediate forms. A gradual evolution of the nasute soldier from the typically mandibulate type can be traced. Correlated with the evolution of the nasus and the frontal gland is the accompanying degeneration of the soldier mandibles. The phylogenetic positions of many of the nasute termites are not wholly clear from the available evidence. The following discussion must be considered indicative rather than exhaustive.

The relationship of *Syntermes* (fig. 9) has been discussed by Emerson (1945) in some detail. He says: "*Syntermes* is the most primitive genus of the Nasutitermitinae and is closest to the genus *Cornitermes*. The relative primitiveness is indicated by the large size of the imago and soldier, the relatively small frontal tube of the soldier, the 19 to 21 articles in the antennae of the imago and soldier, the proportionately large mandibles of the soldier, the lateral spines or the pointed sides of the thoracic nota of the soldier, the three apical spurs on the tibiae of the forelegs, and the short R_1 joining the costal border a little beyond the wing suture.

"The closest relative outside of the subfamily Nasutitermitinae would seem to be the genus *Acanthotermes* of the Macrotermitinae. The similarities of *Syntermes* and *Acanthotermes* include what seem to be homologous lateral spines on the soldier mesothorax and metathorax, vestiges of the lateral spines on the sides of the prothorax of *Acanthotermes* (these spines are very small on the worker of *Acanthotermes* but are present on most of the species of *Syntermes*), the white tip on the labrum of the soldier in both genera (the tip of the imago labrum has a white lip in *Syntermes* and *Pseudacanthotermes*), the postmentum of the soldier in

both genera is not particularly wide in the middle in contrast to the wide postmentum in the higher Macrotermitinae, and both *Syntermes* and *Acanthotermes* possess three spines near the tip of the tibiae of the foreleg and two spines on the tibiae of the other legs (3:2:2)." After discussing the specialized characters of *Syntermes* he comes to the conclusion that "Inasmuch as each of these primitive genera of the Macrotermitinae and Nasutitermitinae has generalized characters not found in the other subfamily, we must suppose that neither developed directly from the other, but both are descended from an extinct group possessing the primitive characters of both of these subfamilies."

The next higher genus is *Procornitermes* (fig. 9). Some of the characters of this genus are so much more specialized than in *Syntermes* that a big gap is left between the two genera. The reduction of the antennal articles, the absence of the lateral spines on the thorax, and the pronounced frontal tube of the soldier are the specialized features of *Procornitermes*. The genus *Cornitermes* (fig. 9) is very close to *Procornitermes*. Several characters overlap between them. *Procornitermes* has four to seven long spines on the inner side of the fore tibiae, whereas *Cornitermes* has 10 or more short spines. In this character *Cornitermes* is more specialized than *Procornitermes*. In the tibial spurs also, *Cornitermes* is more specialized, as all its species have 2:2:2 spurs in contrast to *Procornitermes* in which some species have 2:2:2 and some have 3:2:2 tibial spurs.

From *Procornitermes* onward there are two main branches of the phylogenetic tree of the Nasutitermitinae (fig. 3), one represented by *Triacitermes* and the other by *Paracornitermes*. The *Triacitermes* branch is characterized by the narrow angle between the apical and the first marginal and a long, more or less straight, cutting edge between the two marginals, a pattern also present in *Syntermes-Cornitermes*. In the entire series the apical is equal to, or shorter than, the first marginal. The *Paracornitermes* branch (fig. 11), on the other hand, has a long apical with a broad angle between it and the first marginal, and exhibits a short but sinuate cutting edge between the marginals. Each branch illustrates various stages of evolution,

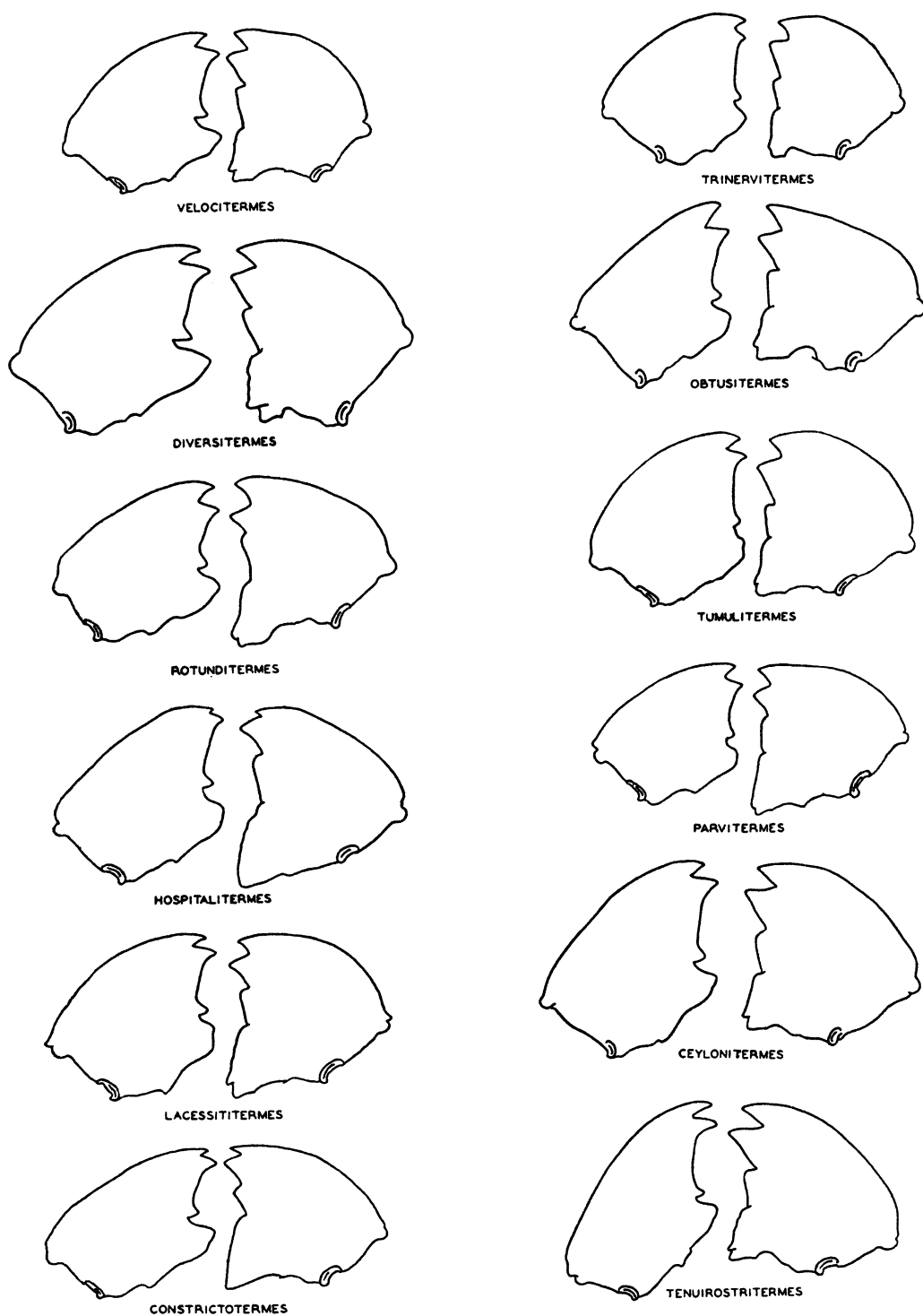


FIG. 10. Imago-worker mandibles of the subfamily Nasutitermitinae.

beginning in each case with soldiers that have a poorly developed nasus and biting type of mandible and independently evolve the typical nasute soldier. Inasmuch as *Procornitermes* has fewer tibial spines (spines not to be confused with spurs) than *Cornitermes* and that the rest of the nasute genera do not possess spines it is likely that the dichotomy of the phylogenetic tree arose from *Procornitermes*.

THE *Triacitermes* BRANCH

Figures 9, 10

Triacitermes is the most primitive genus of this branch. Its generitype was originally described under *Cornitermes* (Silvestri, 1901) and is closely related to *Procornitermes*. In the next genus, *Rhynchotermes*, the nasus of the soldier is much more prominent than in *Triacitermes*. The soldier mandibles are also more slender. In the imago-worker mandibles of *Rhynchotermes* the apical tooth is shorter than the first marginal, a character becoming more pronounced in the higher nasutes of the *Triacitermes* branch.

The rest of the genera of this branch have a fully developed soldier nasus and frontal gland, and the soldier mandibles are degenerate and non-functional. In this complex, *Hirtitermes* is the most primitive genus, as evidenced by the two small teeth at the base of both soldier mandibles.

I am inclined to place *Havilanditermes* between *Hirtitermes* and *Nasutitermes*. A possible primitive character shared by all these rather closely related genera and also by the *Constrictotermes* group of genera is the broad clypeus of the worker. The absence of any tooth on the soldier mandible of *Nasutitermes*, together with the greater proximity of the apical to the first marginal, indicates its higher evolutionary status compared to either *Hirtitermes* or *Havilanditermes*. *Havilanditermes* has more reduced points on the soldier mandible than are found in *Hirtitermes*.

There is an indication that the *Constrictotermes* group of nasute termites has arisen from *Hirtitermes*-like ancestors. One of the constricted-headed genera, *Longipeditermes*, has a small marginal tooth on the soldier mandible. In this character it shows relationship to *Hirtitermes* which has two small teeth

at the base (Holmgren, 1912). Moreover, *Hirtitermes* has a somewhat constricted head, though not so conspicuous as in the *Constrictotermes* group proper. Also the zoogeography of the latter is in conformity with its *Hirtitermes* origin in the Oriental region. All the members of the group have the soldier head greatly produced and elevated behind with a constriction at the base of the nasus.

Longipeditermes is the most primitive among the constricted-headed genera, as the marginal tooth on the soldier mandible would suggest. In the unusually long antennae and legs this genus exhibits convergence with *Hospitalitermes* and *Lacessititermes*. *Coarctotermes* (fig. 9) probably occupies the lowest position among the rest of the members of this group. The apical and the first marginal of the imago-worker mandibles are of the same size. The next higher genus is *Grallatotermes* (fig. 9). Its apical is distinctly shorter than the first marginal. *Bulbitermes* (fig. 9) is placed next to *Grallatotermes*, as it has a little more acute angle between the apical and the first marginal. *Lacessititermes* and *Hospitalitermes* both have markedly elongate antennae and legs. *Hospitalitermes* (fig. 10) has undergone extreme reduction of the apical. *Constrictotermes* (fig. 10) comes close to *Hospitalitermes* in so far as the reduction of the apical is concerned. In the length of the antennae and legs, however, it is like *Coarctotermes*-*Bulbitermes*.

The rest of the nasute termites of the *Triacitermes* branch have a swollen clypeus (length half or more than half the breadth) in the worker caste. Because in the primitive genera like *Hirtitermes* the clypeus is not markedly swollen (length less than half the breadth), I am inclined to regard the swollen clypeus as a more specialized character. The genus *Rotunditermes* is relatively more primitive in this grouping, as indicated by the large eyes of the imago. From *Rotunditermes* onward there are two series of the nasute genera; in one the points on the mandibles of the soldier are prominent, and in the other they are undergoing degeneration, leading to their complete disappearance in *Trinervitermes*.

In the first series (fig. 10), with the prominent points on the soldier mandible, *Diversitermes* has trimorphic, *Velocitermes* has

dimorphic, and *Tenuirostritermes* and *Ceylonitermes* have monomorphic, soldiers. This sequence in the polymorphism possibly indicates the sequence in their evolution also. *Tenuirostritermes* (fig. 10) has an unusually long cutting edge between the marginals of the left mandible. In the relative size of the apical this genus is more primitive than *Ceylonitermes* (fig. 10).

The second series (fig. 10) presents various stages of soldier mandible degeneration. The loss of points on the soldier mandible begins in some species of *Parvitermes*. In some individuals within the species, for example, *Parvitermes pallidiceps*, the loss of the point on the soldier mandible is noticeable, while others still possess the point in a rudimentary condition. Further degeneration of this char-

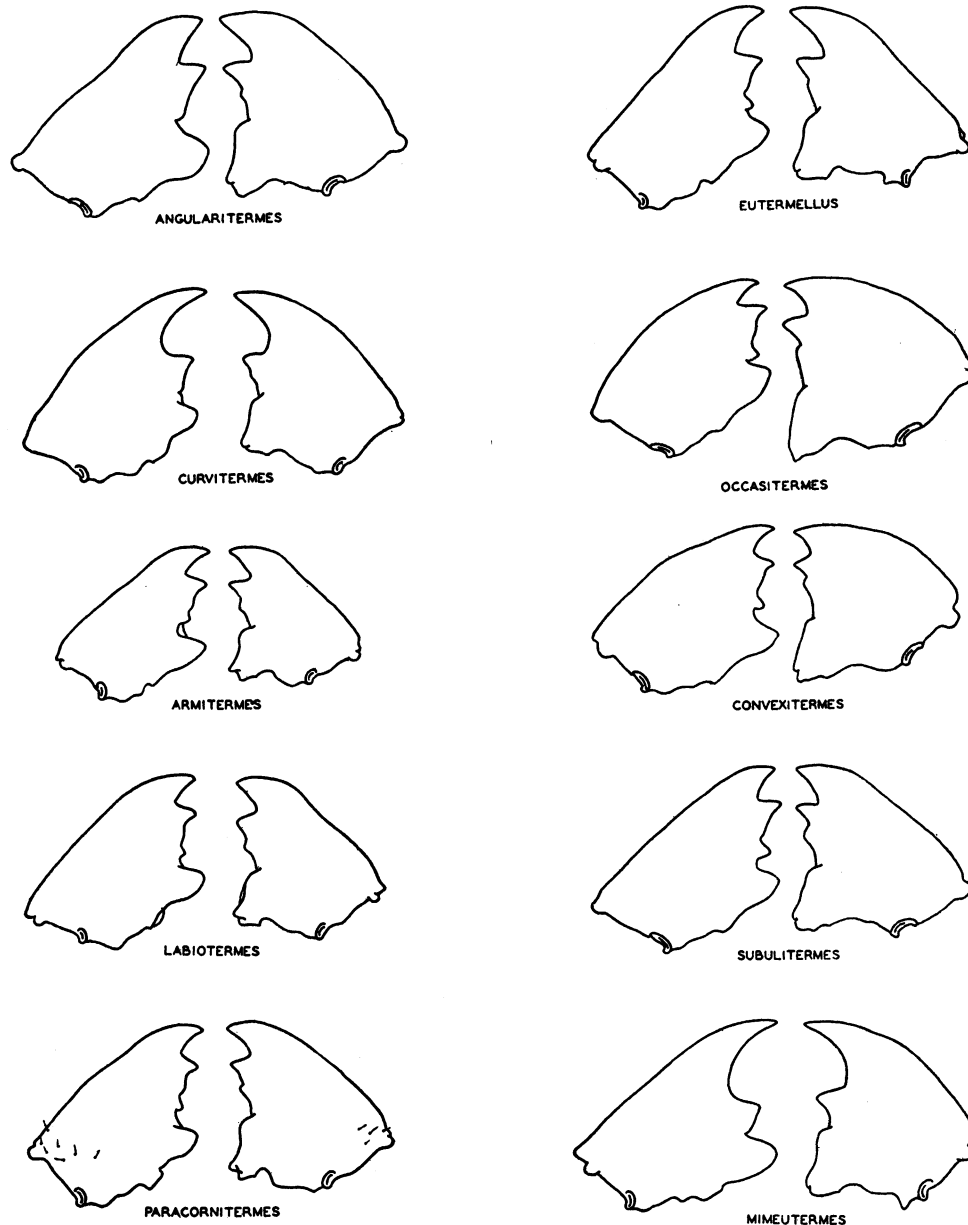


FIG. 11. Imago-worker mandibles of the subfamily Nasutitermitinae.

acter is seen in the next genus, *Tumulitermes*, in which all members of some species have lost the point. In the proximity of the apical to the first marginal, *Tumulitermes* is further advanced compared to *Parvitermes*. In *Obtusitermes* all the species have completely lost the point. *Trinervitermes* exhibits extreme degeneration of the soldier mandibles which are reduced to minute knobs.

THE *Paracornitermes* BRANCH

Figure 11

The evolutionary trend in the imago-worker mandibles of the members of this branch is in a direction opposite to that of the *Triacitermes* branch. Here the apical tooth is undergoing gradual enlargement, with the accompanying widening of the angle between the first marginal and the apical. The nasute soldiers, as in the first branch, have evolved from the mandibulate forms. The *Paracornitermes* branch is more highly evolved than the *Triacitermes* branch, because the imago-worker mandibles are much more specialized and indicate a parallelism with the Termitinae.

Paracornitermes is the lowest in the scale and occupies a position corresponding to *Triacitermes* in the first branch. The next genus is *Labiotermes*. *Armitermes* manifests further advance over *Labiotermes*. The species of *Armitermes* are relatively smaller. The nasus of the soldier is more highly developed, and the mandibles are more slender and delicate.

Curvitermes occupies a unique position. Originally it was regarded as a subgenus of *Armitermes* and was placed close to *Rhynchotermes* (*Rhynchotermes* was also considered a subgenus of *Armitermes*) by Holmgren (1912), but the presence in *Curvitermes* of a combination of both primitive and specialized characters makes its placement in a linear order with the more advanced nasute genera impossible. The soldier caste indicates a close relationship to *Armitermes*, but its imago-worker mandibles have undergone great specialization and show a superficial resemblance to those of *Mimeutermes*, a much more highly evolved genus. Most probably *Curvitermes* arose from the same stock as *Armitermes*.

The genera following *Armitermes* have a

typical nasute soldier with functionless mandibles. Among these genera there is further indication of two lines of evolution; in one the soldier mandibles still possess sharp points, and in the other these points have been lost.

Angularitermes and *Mimeutermes* comprise the first category possessing points. While the soldier mandibles are comparatively more primitive than the second series without points, the imago-worker mandibles are more specialized. On the basis of these characters it is postulated that *Angularitermes-Mimeutermes* arose from the main branch at a point earlier than *Subulitermes*. The ancestral stock must have possessed well-developed points on the soldier mandibles. The small marginal tooth on the right soldier mandible of *Angularitermes* is indicative of its primitiveness relative to *Mimeutermes*. The imago-worker mandibles of *Mimeutermes* are more specialized. The apical is larger and more curved, and the second marginal of the right mandible is lost completely.

The rest of the genera in the *Paracornitermes* branch exhibit a complete loss of the points on the soldier mandibles. *Subulitermes* and *Convexitermes*, the two most closely related genera, have rather primitive imago-worker mandibles. The apical is as long as, or a little shorter than, the first marginal, and the second marginal of the right mandible is comparatively more prominent and thus approaches a condition somewhat like that in the *Triacitermes* branch. But in the distinctly sinuate cutting edge between the marginals and in the comparatively broad angle between the first marginal and the apical in the left mandible, these genera should belong to the *Paracornitermes* branch.

There is some variability in *Subulitermes*. The generitype, *S. microsoma*, and a group of other species of this genus have a large apical and broad angle between the first marginal and the apical, while other species have the *Convexitermes*-type of imago-worker mandible, with a little more sinuate cutting edge between the marginals of the left mandible and more reduced second marginal of the right mandible. *Occasitermes* has a still more sinuate cutting edge. The width of the angle between the apical and the first marginal of the right mandible is comparable

to *Convexitermes*, but the same angle of the left mandible is narrower. *Eutermellus* is the highest evolved genus in this series. The apical tooth is much larger than the first marginal, and the second marginal of the right mandible is inconspicuous.

AMITERMITINAE

The subfamily name of Amitermitinae was given to the "*Hamitermes-Reihe*" of Holmgren by Kemner (1934). At first I was doubtful of the subfamily status of the Amitermitinae, but the study of the imago-worker

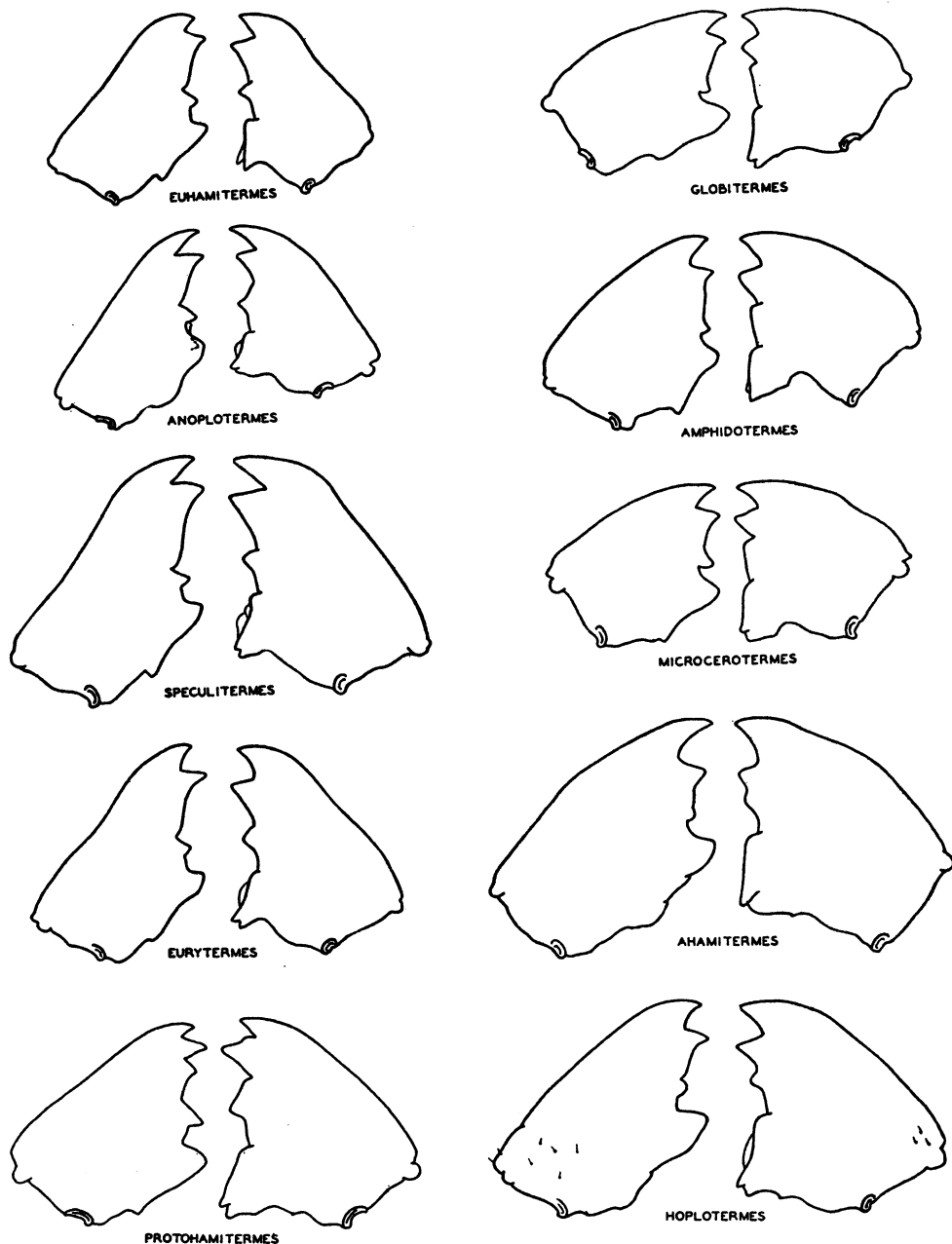


FIG. 12. Imago-worker mandibles of the subfamily Amitermitinae.

mandibles (figs. 12, 13) clearly indicates that their members form an assemblage distinct from the Termitinae. The imago-worker mandibles of all the genera of the Amitermitinae, except the series consisting of *Pseudomicrotermes*, *Synhamitermes*, and *Eremitermes*, have the apical as long as, or shorter than, the first marginal. On the other hand, in the Termitinae all the genera (excepting *Neocapritermes* and *Planicapritermes*) have the apical distinctly longer than the first marginal. The exceptional cases in both the subfamilies could possibly be the result of convergence.

The imago-worker mandibles of the Amitermitinae may be grouped into four main series based primarily upon the left mandible. The right mandible is essentially the same throughout except that in some genera the posterior edge of the second marginal is curved and in others it is straight.

THE *Protohamitermes* SERIES

Figure 12

The imago-worker mandibles of this series are primitive, as indicated by the three well-developed marginals of the left mandible of *Protohamitermes* and a distinct cut in front of the last marginal of the left mandible in the rest of the genera. The right mandible, however, is more specialized in the curved posterior edge of the second marginal. Homologizing the various parts of the mandible I think that the last marginal of the left mandible is comparable to the third marginal, and the deep cut in front of it is probably indicative of the second marginal. The tooth following the apical is unquestionably the first marginal.

Protohamitermes is the most primitive genus of this series. In spite of the primitive imago-worker mandibles resembling those of the Rhinotermitidae it should be regarded as a member of the Amitermitinae, as originally suggested by Holmgren (1911). The absence of reticulation in the wing venation, the small forewing scales, and the short pronotum of the imago and worker, together with the specialized condition of the posterior edge of the second marginal of the right mandible, are some of the characters indicative of a closer relationship to the Termitidae than to the Rhinotermitidae.

When the soldier caste is also known we may be in a better position to understand the exact relationship of *Protohamitermes*. As this genus is the most primitive member of the Termitidae and as the latter arose from rhinotermitid-like ancestors, it is not surprising to find three marginals on the left mandible and an indistinct subsidiary tooth on the right mandible.

The next genus, *Eurytermes*, and the genera following it are more specialized than *Protohamitermes*. The second marginal of the left mandible is indicated only by a cut in front of the third marginal. The 3:2:2 arrangement of the tibial spurs in *Eurytermes* is a primitive character similar to the condition in *Protohamitermes*.

Anoplotermes is an interesting genus. This is the only known termite without a soldier caste. Not a single collection of this large genus made in the Ethiopian, the Neotropical, or the Nearctic regions has so far revealed the presence of the soldier, and it would therefore be safe to presume that *Anoplotermes* has lost the soldier caste. Goetsch (1939), however, reports a nasute-like soldier in his captive colony of *Anoplotermes*. Inasmuch as the mandibles of the molting nymph are not figured or discussed (the mandibles of the worker only are listed in the author's table) I am constrained not to subscribe to Goetsch's interpretation. It seems likely that the colony he had belonged to *Armitermes*, which is known to occur in the same areas in South America as *Anoplotermes*. A study of the mandibles of this colony would easily solve this question.

Holmgren (1912) includes *Anoplotermes* in the Nasutitermitinae, but because of the close similarity of its imago-worker mandibles to those of *Eurytermes* I am following Hare (1937) in placing this genus in the Amitermitinae. The mandibles in the two genera are almost identical. *Anoplotermes* needs to be revised; until then the relationships of its subgenus, *Speculitermes*, remain questionable. From the evidence at hand *Speculitermes* appears to be more primitive than *Anoplotermes*. The short third antennal article and less conspicuous second marginal of the right mandible of *Anoplotermes*, *sensu stricto*, indicate its higher evolutionary status in relation to *Speculitermes*.

I am placing *Euhamitermes* next to *Anoplotermes* on the basis of the imago-worker mandibles alone. The fact that the imago caste of *Euhamitermes* is unknown and the soldier of *Anoplotermes* does not exist makes it difficult to understand the exact relationships of the two genera. *Hoplotermes* is considered by Light (1932) to be very close to *Eurytermes*, but the study of its imago-worker mandibles indicates its closer relationship to the next genus, *Ahamitermes*, than to *Eurytermes*. The reduction of the second marginal of both the mandibles and also the reduction of the length of the posterior edge of the first marginal of the left mandible in *Euhamitermes* are in contrast to the condition in *Eurytermes*. In *Ahamitermes* a further reduction of these characters is seen.

THE *Microcerotermes* SERIES

Figures 12, 13

The left imago-worker mandible in this series is more specialized than in the *Protohamitermes* series, whereas the right mandible is more primitive. The specialized character of the left mandible is the absence of the cut in front of the third marginal, leaving a straight edge between the marginals. The primitive feature of the right mandible is the straight posterior edge of the second marginal.

Microcerotermes is least specialized among the members of this series. This is indicated by the shape of the cutting edge of the left mandible. The rest of the genera have a more or less straight edge between the marginals of the left mandible, and in this respect they are more specialized than is *Microcerotermes*.

Amphidotermes, on the basis of its primitive soldier mandible, occupies the lowest position among the genera, with the straight edge between the marginals of the left mandible. The next four genera have essentially the same type of imago-worker mandible as *Amphidotermes*. *Globitermes*, *Prohamitermes*, *Cephalotermes*, and *Cylindrotermes* are shown as radiating from the same stock (fig. 12). *Cephalotermes* and *Cylindrotermes* are more closely related to each other than to *Globitermes* or *Prohamitermes*. The shape of the soldier head is almost the same in the first two genera. In the soldier mandible, however,

Cephalotermes is more primitive than *Cylindrotermes* because it possesses two small but distinct teeth in contrast to the one in *Cylindrotermes*.

Labritermes seems to be highly specialized in its soldier mandibles, but the imago-worker mandibles are still in line with the other genera of the *Microcerotermes* series, though they too have some specialized features such as the curved posterior edge of the second marginal of the right mandible.

THE *Pseudomicrotermes* SERIES

Figure 13

The genera belonging to this series form a well-defined group with a characteristic imago-worker mandibular pattern. The apical is large and broadly separated from the first marginal; the cutting edge of the left mandible is proportionately longer than in the *Microcerotermes* series, and the third marginal of the same mandible is more reduced.

Pseudomicrotermes is referred to the "*Pseudomicrotermes-Reihe*" by Holmgren in his classification of the family Termitidae. In his discussion of the systematic position of *Pseudomicrotermes* he says that it bears relationship to both the Coptotermitinae and the Heterotermitinae of the family Rhinotermitidae, though at the same time possessing several characters in common with *Microcerotermes* of the family Termitidae. The present study clearly indicates its close relationships with *Synhamitermes* and *Eremotermes*, as evidenced by the imago-worker mandibles. *Synhamitermes*, with a little shorter and slightly curved posterior edge of the second marginal of the right mandible, might be considered a little more specialized than *Pseudomicrotermes*. In *Eremotermes* the right imago-worker mandible is even more specialized than in *Synhamitermes*. However, the linear sequence of the soldier mandible is *Synhamitermes*, *Eremotermes*, and *Pseudomicrotermes*. Because of the small number of characters showing the phylogenetic sequence, I am tentatively placing these genera as radiating from a common ancestor.

THE *Amitermes* SERIES

Figure 13

The highest degree of specialization in the imago-worker mandibles of the *Amitermes*

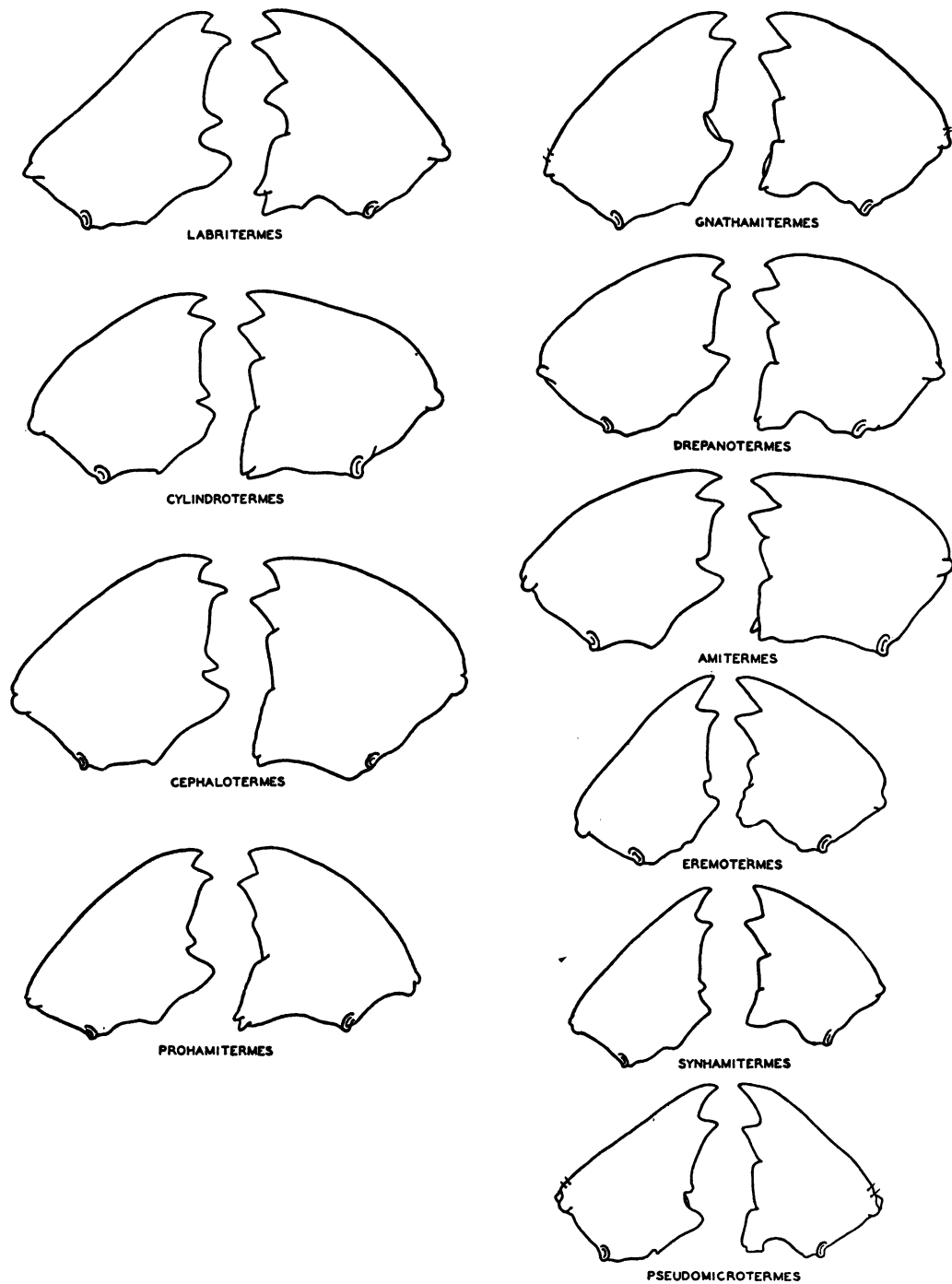


FIG. 13. Imago-worker mandibles of the subfamily Amitermitinae.

tinæ is seen in the *Amitermes* series. The third marginal of the left mandible is represented only by the rounded end of the long cutting edge. The three genera comprising this series are *Amitermes*, *Drepanotermes*, and *Gnathamitermes*, radiating from the same stock. Because of its zoogeographical distribution, the widely distributed *Amitermes* is probably ancestral to the Australian *Drepanotermes* and the Nearctic *Gnathamitermes*.

TERMITINAE

This subfamily comprises the largest number of termite genera. The imago-worker mandibles (figs. 14-17) exhibit a gradual reduction of their marginals, with the accompanying enlargement of the apical and the widening of the angle between the apical and the first marginal. The soldier mandibles are evolving from the biting type to the snapping type. The latter have convergently evolved twice in the subfamily.

Neocapritermes and *Planicapritermes*, though possessing soldiers with strongly asymmetrical snapping mandibles, have the most primitive imago-worker mandibles (fig. 14) in the subfamily. These are the only two genera of the Termitinae in which the apical of the imago-worker mandible is small and is as long as the first marginal. The other primitive features are the straight posterior edge of the second marginal of the right mandible and a deep cut in front of the third marginal of the left mandible. The deep cut in front of the third marginal of the left mandible is present in some of the *Amitermitinae* genera, such as *Eurytermes*, *Anoplotermes*, and other members of the *Protohamitermes* series, but in these genera the right mandible is more specialized in the curved posterior edge of the second marginal. The fungus-growing termites of the subfamily Macrotermitinae have imago-worker mandibles somewhat as in *Neocapritermes-Planicapritermes*, but the fungus growers should not be considered ancestral to any other group of termites because of their extreme biological specialization. As the possibility of the evolution of the Termitinae from the Nasutitermitinae is also ruled out (because of the highly specialized soldier caste in the nasute genera), we may postulate that *Neocapritermes* and *Planicapritermes* arose

from the stock that was ancestral also to the other subfamilies of the Termitidae.

The marked flatness of the soldier head, with its lobed posterior end, is indicative of a higher specialization of *Planicapritermes* compared to *Neocapritermes*.

All the other genera of the Termitinae fall into two main groups, one with the biting type of soldier mandible and the other with the snapping type.

GENERA WITH BITING TYPE OF SOLDIER MANDIBLE

More than half of the Termitinae genera possess the biting type of soldier mandible. In this group the imago-worker mandibles show various degrees of specialization. These genera lend themselves to further subgrouping. In some cases it is possible to trace a linear relationship within a subgroup; in others this cannot be done.

Hoplognathotermes (fig. 14) is the most primitive among the genera with biting type of soldiers. The soldier mandible is distinctly dentate. The imago-worker mandibles, however, are more specialized than those of even some of the higher genera. The second marginal of the right mandible is greatly reduced. The next genus, *Allognathotermes* (fig. 14), is very closely related to *Hoplognathotermes*. In the more reduced teeth of the soldier mandible and the more reduced second marginal of the right imago-worker mandible, *Allognathotermes* is more specialized than *Hoplognathotermes*.

Trichotermes, *Jugositermes*, and *Rostritermes* form another closely related group (fig. 14). The last two genera have almost identical imago-worker mandibles. The comparison of the mandibles of *Rostritermes* was made from the drawings given in Grasse's paper (1943). *Trichotermes* has somewhat more primitive imago-worker mandibles than do *Jugositermes* and *Rostritermes*. The soldier characters do not enable me to place *Trichotermes* in a linear arrangement with *Jugositermes* and *Rostritermes*, because *Trichotermes* possesses a prominent frontal projection without any ridges above the base of the antennae, whereas *Jugositermes* has very prominent ridges but no frontal projection. Because of the close similarity in the imago-worker mandibles and the short but stoutly

built soldier mandibles, *Trichotermes* is shown arising from the same point as *Jugositermes*-*Rostritermes* (fig. 4). Between the latter two genera, *Rostritermes* is more advanced, as evidenced by the shape of the head and the labrum of the soldier.

Next we consider a large complex of five radiating branches. *Ceratotermes* (fig. 14)

forms the first branch. The soldier as well as the imago-worker mandibles are relatively primitive. The second marginal of the right mandible is well developed.

Apicotermes, *Crenitermes*, *Thoracotermes*, and *Apilitermes* form the second branch (fig. 14). Of these genera, *Apicotermes* is most primitive. The soldier mandibles are

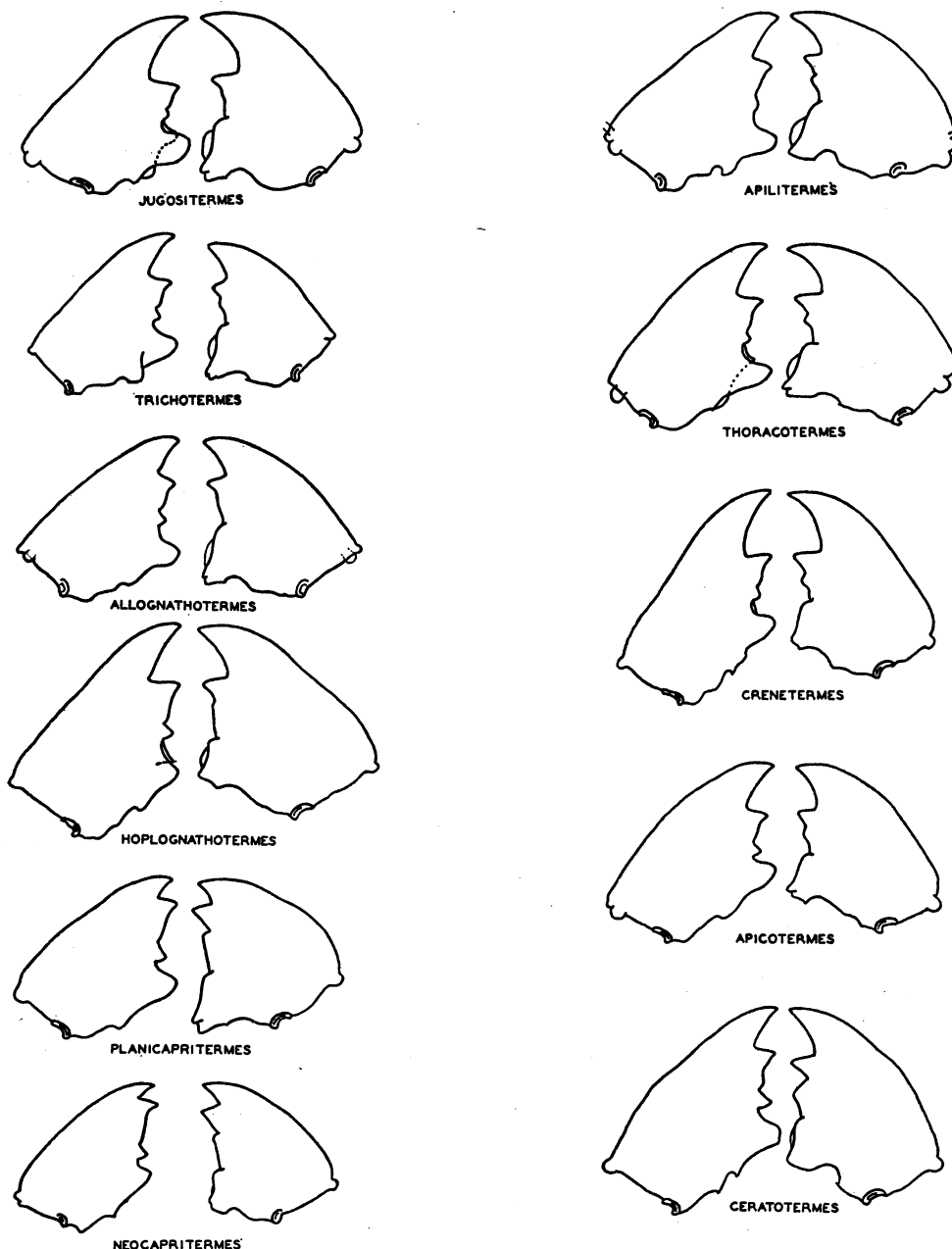


FIG. 14. Imago-worker mandibles of the subfamily Termitinae.

stout and possess small teeth. The imago-worker mandibles are more specialized compared to those of *Ceratotermes*, but the soldier mandibles are more primitive. The imago-worker mandibles of *Crenetermes* have the apical more elongated than in *Apicotermes*. In the length of the apical and also in the stouter soldier mandibles, *Thoracotermes* is a little more primitive than *Crenetermes*, but in the shape of the soldier labrum it is more specialized. *Apilitermes* has a still more slender soldier mandible than either *Thoracotermes* or *Crenetermes*.

The third branch is the largest and includes eight genera. Some of its members possess highly specialized imago-worker mandibles. The shape of the soldier labrum is, with slight variation, the same in all these genera. It is large, with broadly rounded to somewhat elongate lobes at the anterior end. *Cubitermes* and *Megagnathotermes* (fig. 15) are shown arising from the same stock. The large apical tooth of the imago-worker mandible and the more slender soldier mandible of *Megagnathotermes* are indicative of higher specialization compared to those of *Cubitermes*, but in the shape of the labrum and the more pronounced frontal projection of the soldier head, *Cubitermes* is more advanced than *Megagnathotermes*. *Procubitermes* has more slender mandibles and a more reduced soldier labrum than *Cubitermes*. In *Lepidotermes* the labrum is shorter than in *Procubitermes*, is more or less flat instead of being curved, and the frontal projection is better developed. *Noditermes* has a distinct tubercle-like projection on the postmentum. This character probably indicates specialization. The most specialized genus in the *Procubitermes* group is *Unguitermes*. The soldier mandible is curved in the middle, and the tip is claw shaped (Sjöstedt, 1926).

Ophiotermes and *Euchilotermes* probably arose from *Procubitermes*-like ancestors. This relationship is indicated by the similarity of the soldier labrum. The imago-worker mandibles of these two genera (fig. 15) have undergone considerable specialization. The apical is comparatively long and broadly curved, the second marginal of the right mandible is completely lost and of the left mandible is weakly developed. Of these two genera, *Ophiotermes* is more closely related

to *Procubitermes*. Some of the species of *Procubitermes*, for instance, *P. undulans* Schmitz, show a tendency towards the evolution of the *Ophiotermes* type of soldier mandible. The left mandible of *P. undulans* is elbowed (Emerson, 1928), a character more pronounced and present in both the mandibles of the *Ophiotermes* soldier. The imago-worker mandibles of *Euchilotermes* are more primitive than in *Ophiotermes*, but its soldier mandibles are more specialized in the absence of the tooth which is present in *Ophiotermes*.

Tuberculitermes and *Spinitermes* are shown, each by a separate branch. *Tuberculitermes* has the most highly specialized imago-worker mandibles (fig. 15). The apical is very long, slender, and curved. The mandibles of *Tuberculitermes* may be regarded as a further specialization of the *Ophiotermes* type, but the labrum character is so different that it seems justifiable to indicate this genus by a separate branch. *Spinitermes* (fig. 15) has imago-worker mandibles similar to those of *Ophiotermes*, but because of its geographical distribution it is unlikely that it belongs to the same group as *Ophiotermes*.

Basidentitermes, *Fastigitermes*, and *Proboscitermes* form another well-defined group. They are shown arising from the main stem at a level slightly lower than the origin of the *Ceratotermes*-*Spinitermes* branches. Their imago-worker mandibles (fig. 16) are more primitive than those of any other genus with a biting soldier. The second marginal of the right mandible is well developed and is as long as the first marginal. However, in the characters of the soldier, these genera are highly advanced. The soldier mandibles are delicate. *Basidentitermes* occupies the lowest position in the group. There is no distinct frontal projection of the soldier head except for a slight elevation surrounded by a bunch of hairs. The species of *Fastigitermes* are much smaller than those of *Basidentitermes*, and the soldier head has a prominent frontal projection. *Proboscitermes* is extremely specialized in the development of its frontal tube. The same phylogenetic sequence is manifest in the labrum of the soldier.

Orthotermes (fig. 16) appears to be an offshoot from *Basidentitermes*. The imago-worker mandibles and the soldier labrum are

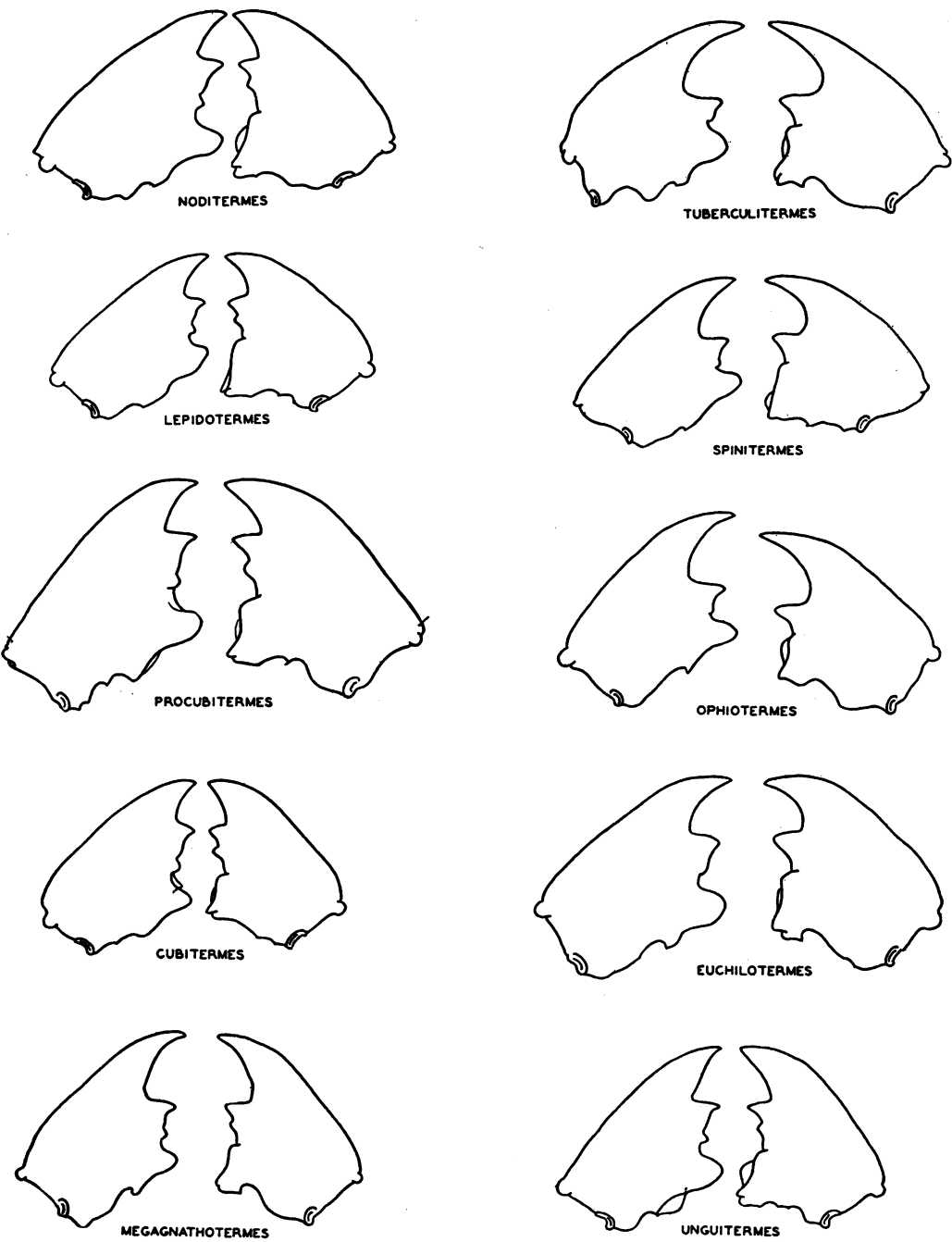


FIG. 15. Imago-worker mandibles of the subfamily Termitinae.

slightly more specialized than in *Basidentitermes*.

GENERA WITH SNAPPING TYPE OF SOLDIER MANDIBLE

The snapping type of soldier probably arose from the biting type. The close similarity of the imago-worker mandibles of *Promirottermes* (fig. 16), the most primitive genus possessing snapping soldiers, and those of *Basidentitermes* with biting type of soldier, is suggestive of an evolutionary sequence. The snapping group is further branched into two main lines, one with relatively symmetrical snapping mandibles and the other with various degrees of asymmetrical snapping mandibles.

Orthognathotermes appears to be an early offshoot from the branch which later gave rise to the termites with symmetrical snapping soldier mandibles. The soldier mandibles of this genus still serve the function of biting as well as snapping. It should not, however, be considered ancestral to other snapping forms because its imago-worker mandibles (fig. 16) are more specialized than those of the next genus, *Promirottermes*, which has typical snapping soldier mandibles. The well-developed second marginal of the right mandible and the equally well-developed third marginal with an anterior deep cut in the left mandible are indicative of the primitiveness of *Promirottermes*.

Spicotermes comes next to *Promirottermes* in the phylogenetic sequence. It has more specialized imago-worker mandibles (fig. 16) and a more pronounced frontal projection of the soldier head. In *Termes* (= *Mirottermes*) the frontal projection of the soldier head is more pronounced than in *Spicotermes*. Also in the imago-worker mandibles (fig. 16) *Termes* shows advance over *Spicotermes*. The second marginal of the right mandible is more reduced and the cutting edge between the two marginals of the left mandible is shortened. The same mandibular pattern is seen in *Angulitermes* (fig. 16) also, which suggests the possible origin of this genus from *Termes*. The soldier mandibles of *Angulitermes* are more slender than those of *Termes*, and the frontal projection is also more prominent.

Cavitermes (fig. 16) is much more special-

ized than *Angulitermes*, as evidenced by the loss of the second marginal on both of the imago-worker mandibles. In the soldier the highly developed frontal projection with a depression in the middle of the head is a further indication of the higher evolutionary status of *Cavitermes*.

Crepititermes has imago-worker mandibles (fig. 16) very much as in *Cavitermes* except that the apical is not so long. *Crepititermes* probably represents a side branch from the main branch leading to *Cavitermes*. Because of the flat soldier head without any frontal projection this genus cannot be considered ancestral to *Cavitermes*.

The genera with various degrees of asymmetrical soldier mandibles are most probably derived from the group with symmetrical soldier mandibles. Among the latter the closest relative appears to be *Promirottermes*. This relationship is indicated by the close similarity of the imago-worker mandibles of *Promirottermes* and *Paracapritermes* (fig. 17).

Paracapritermes, *Quasitermes*, *Mirocapritermes*, and *Cornicapritermes* still share the frontal projection of the previous group. *Paracapritermes* and *Quasitermes* have essentially the same type of imago-worker mandible (fig. 17), except that *Quasitermes* has a little more reduced second marginal on both the mandibles and a shorter posterior edge of the first marginals of the left mandible. The imago-worker mandibles of *Mirocapritermes* (fig. 17) are more specialized than in *Quasitermes*. *Cornicapritermes* has still more specialized imago-worker mandibles, as indicated by the reduction of the second marginal of the right mandible, but it is more primitive in the presence of a distinct cut in front of the third marginal of the left mandible.

The last six genera, viz., *Homallotermes*, *Pericapritermes*, *Capritermes*, *Procapritermes*, *Protocapritermes*, and *Pseudocapritermes*, have lost the frontal projection, but the strongly asymmetrical mandibles of the soldier are retained. This group is shown arising from *Paracapritermes* because of the resemblance of the imago-worker mandibles to those of *Homallotermes*. The loss of the frontal projection may have occurred secondarily. Judging from the shape of the

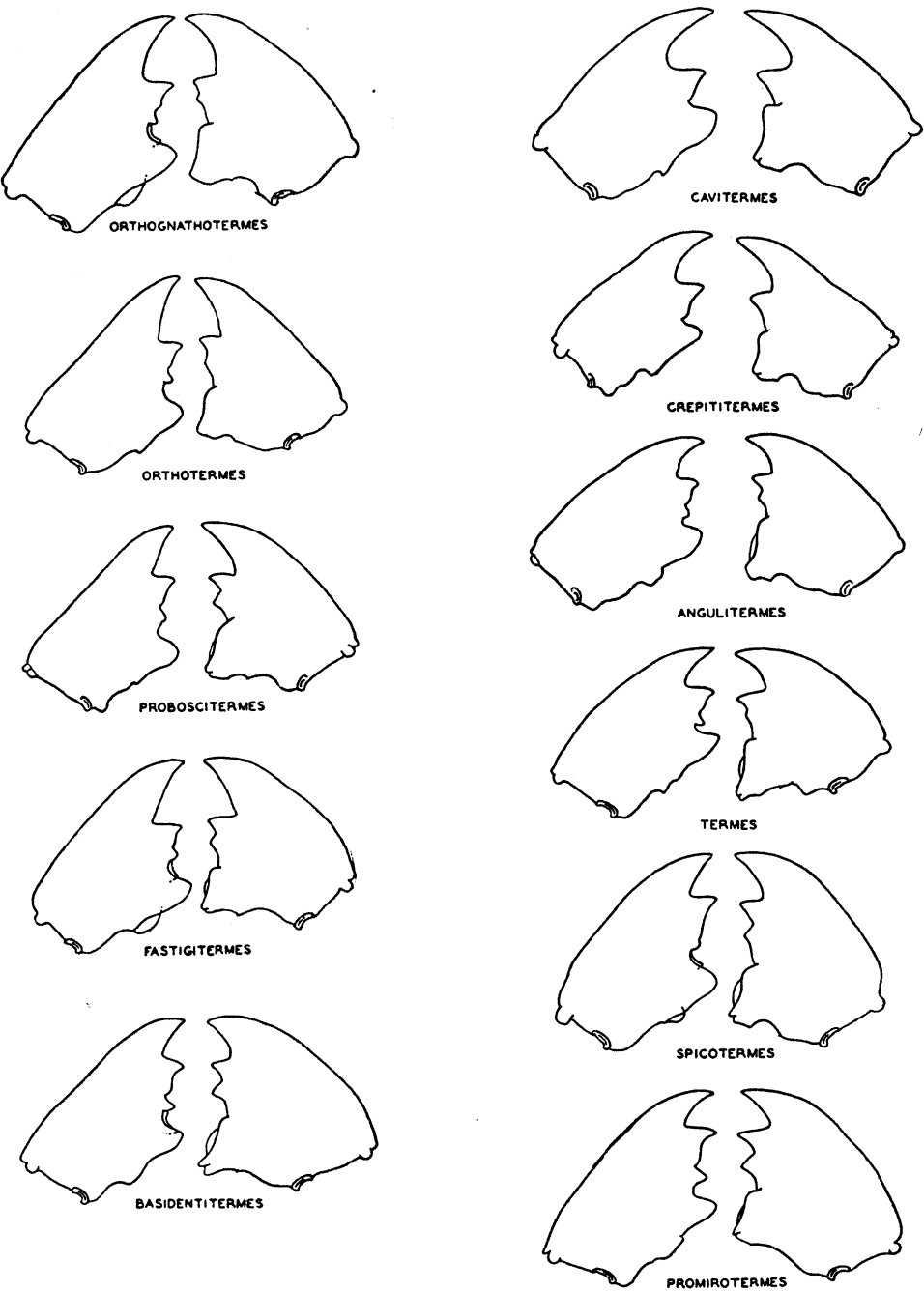


FIG. 16. Imago-worker mandibles of the subfamily Termitinae.

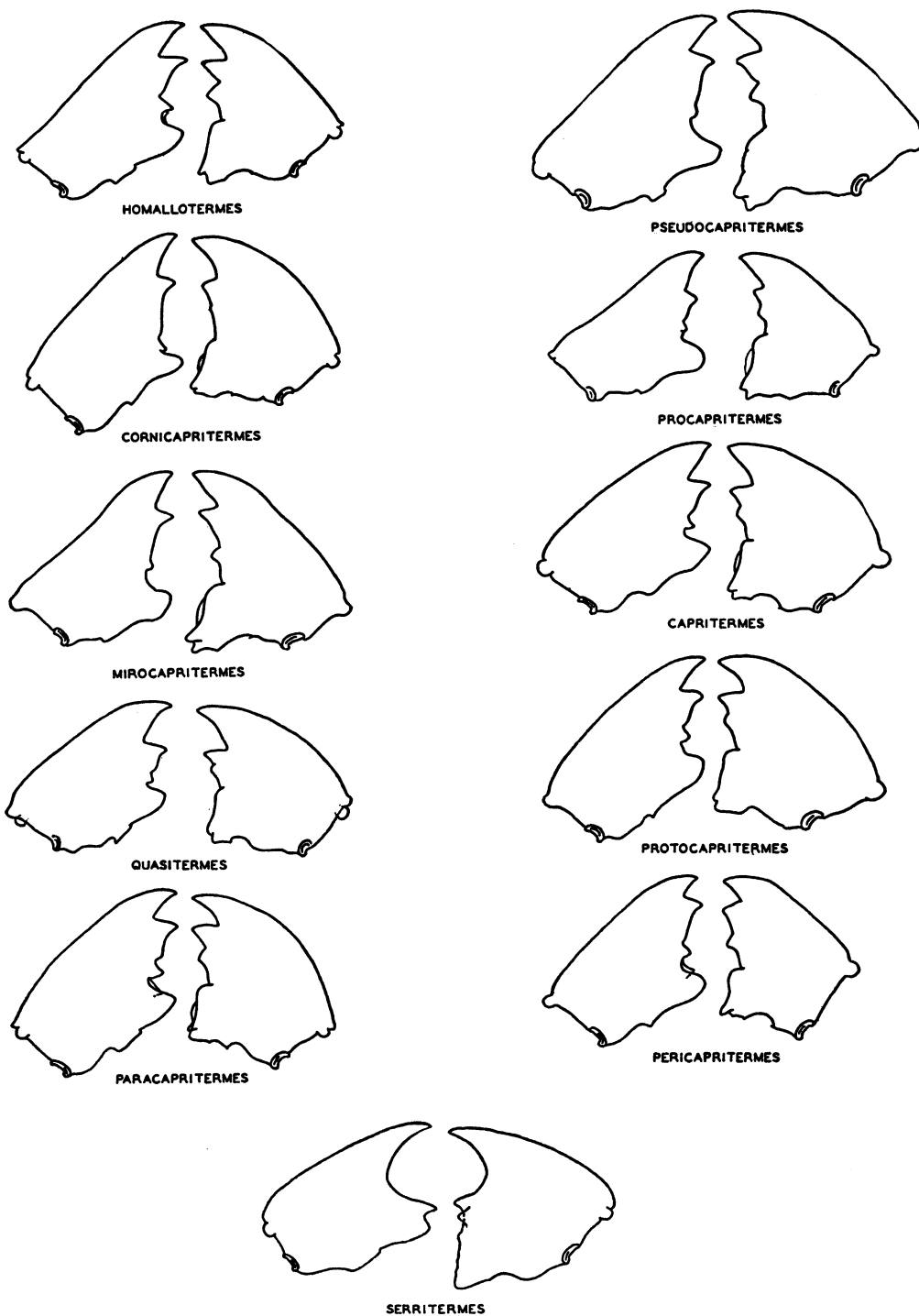


FIG. 17. Imago-worker mandibles of the subfamilies Termitinae and Serritermitinae.

second marginal of the right mandible of *Pericapritermes*, it seems likely that this genus is derived from *Homallotermes*. The next genus is *Protocapritermes*. The second marginal of the right mandible of *Protocapritermes* is less prominent than in *Pericapritermes*. The following two genera, *Capritermes* and *Procapritermes*, are very closely related to each other. In the rather straight posterior edge of the first marginal of the left mandible, *Pseudocapritermes* appears to be a little more advanced than *Procapritermes*.

SERRITERMITINAE

The Serritermitinae, represented by a single genus, *Serritermes*, were regarded as a subfamily of the Rhinotermitidae by Holmgren (1911). The primitive characters of the Serritermitinae, which probably led Holmgren to include them in the Rhinotermitidae, include the large pronotum, the large forewing scales, and the reticulated appearance of the wing membrane. Holmgren considers the serration of the soldier mandible to be primitive. Within the Rhinotermitidae he thinks the Heterotermitinae are the closest relatives of the Serritermitinae, on the basis of the large clypeus of the imago, and the serration of the soldier mandible, but because of the presence of the rudimentary eyes in the soldier caste, he shows this subfamily as an early branch from the Heterotermitinae stem. I am, however, inclined to

treat the Serritermitinae as a subfamily of the Termitidae because of the highly specialized imago-worker mandibles (fig. 17). I consider the soldier mandibles also to be highly specialized. The serration of the mandibles is quite distinct from the condition in *Heterotermes* and even in *Microcerotermes*, the only other genera having serrated soldier mandibles. Other specialized characters of the Serritermitinae are the 2:2:2 tibial spur arrangement, the absence of styli, and the reduction of the median in the wing.

Most of the Termitidae have a 2:2:2 tibial spur arrangement and lack styli. The large pronotum and the forewing scales of the Serritermitinae that in the opinion of Holmgren justify their inclusion in the Rhinotermitidae also are present in some of the primitive members of the Termitidae such as *Protohamitermes*. Moreover, not all the Rhinotermitidae possess these characters. *Psammotermes* and *Reticulitermes* have short pronota and short forewing scales. The inclusion of the Serritermitinae in the Rhinotermitidae would mean a sudden and an extreme specialization of the otherwise fairly fixed pattern of the imago-worker mandibles.

On the basis of this discussion I am transferring the Serritermitinae to the Termitidae. The characters of *Serritermes* are distinctive enough to retain a subfamily rank. The more primitive relatives of *Serritermes* that might clarify its evolution seem to have become extinct.

DISCUSSION

LONG BEFORE THE BIRTH of the theory of evolution it was recognized by naturalists that organisms could be grouped on the basis of their common anatomic and morphologic attributes. The question as to why members of such a "natural" group possess these common characteristics remained unanswered until 1859 when Darwin in his theory of evolution provided the plausible explanation. According to the theory of evolution the similarity among the members of a natural group is the result of their descent from a common ancestor. "Structural similarity due to common ancestry" is the underlying idea behind the concept of homology. The phylogenetic attribute of homology was, however, not implied by Owen (1843) who originally coined this term. The science of genetics has contributed a great deal towards the understanding of the phylogenetic implications of homology. Wright (1934), giving the genetic interpretation of homology, says: "The same, or similar, gene complexes may be expected to come into play wherever sufficiently similar conditions arise in different parts of the developing pattern, giving bilateral, metameric or other replicative homologies within the organism. In different but phylogenetically related organisms, more or less similar gene complexes tend to come into play in corresponding parts of the growth patterns, which are thereby kept developing along similar lines."

Recently Boyden (1947) has advocated the restriction of the idea of homology to that originally conceived by Owen. He comments: "The original and necessary concept in homology is essential structural similarity. The secondary meaning for homology of common phylogenetic origin has no place in serial homology and a role of secondary importance in special homology." By special homology is meant "the structural agreement of corresponding parts of the bodies of different organisms." In the light of the genetic interpretations given by Wright there appears to be no difficulty in deducing phylogenetic relationships from the study of serial homology as well. Similarity of gene complexes must be assumed in explaining homology whether serial or special.

In an approach to the study of phylogeny via morphology the chances of error are greatly minimized if we base our study on conservative characters. In termites the mandibles of the imago and worker provide such a character. There is no indication that the various types of mandibular pattern discussed here have any adaptive value. Termites eating the same kind of food may have different types of imago-worker mandibles. For example, *Hodotermes* (Hodotermitinae), *Trinervitermes* (Nasutitermitinae), and *Amitermes* (Amitermitinae) may eat the same grass, yet they possess dissimilar mandibular patterns. The three genera of the Termopsinae feed on damp, rotten logs, but their imago-worker mandibles are different. On the other hand we find the same mandibular pattern in some termites with different food habits. *Syntermes* and some species of *Nasutitermes* having entirely different ecological adjustments, one excavating soil and feeding on leaves, the other constructing arboreal nests and feeding on wood, both possess the same type of imago-worker mandible. It is therefore obvious that the different sizes of the cutting edges or the angles between them have no direct adaptive value. The development of the mandibular pattern of the imago and worker castes is most likely initiated by complex gene pattern that also influences the growth of other characters, some of which may have adaptive values. A change in the genetic complex under the stress of selection pressure need not necessarily result in a corresponding adaptive change in the mandibular pattern. Adaptive changes in the soldier caste, i.e., the evolution of the nasute soldier from the mandibulate soldier in the Nasutitermitinae or the evolution of the minor soldier in the Rhinotermitinae, are not correlated with changes in the mandibular pattern of the imago-worker. Here we have a character which is under the least direct selection pressure. Change, when it does occur, is consequently of great phylogenetic significance.

A character like that of the soldier mandible has strikingly different functions in different groups of termites. Any phylo-

genetic conclusions based on such a character might be erroneous because the exact phylogenetic relationship would be obscured by convergent adaptation. Sometimes serious mistakes have been made by confusing analogy with homology. A distinction between the two phenomena is by no means easy, particularly in closely related organisms. "The separation of analogous from homologous morphological characters through the maze of genetic modifications, physiological influences, growth patterns, degenerative changes, and convergent adaptations, is a difficult task" (Emerson, 1938).

The present study reveals several cases of convergence in the phylogeny of termites. The phragmotic head is a defense adaptation in plugging the holes of the nest. The evolution of the extreme phragmotic head in the family Kalotermitidae has taken place three times (*Cryptotermes*, *Eucryptotermes*, and *Calcaritermes*). On the basis of the soldier characters these three genera could easily be grouped together, but the imago-worker mandibles and the wing venation indicate that *Cryptotermes* has evolved independently of the *Glyptotermes* branch, and extreme phragmosis has appeared twice from the less specialized *Glyptotermes*-like ancestry.

Such a convergent evolution of the phragmotic head also has taken place in unrelated ants (*Colobopsis* and *Cryptocerus*; Wheeler, 1928).

Some of the best examples of convergence among the termites are found in the subfamily Nasutitermitinae. The two main branches of the tree have independently evolved the characteristic nasute soldiers. In previous classifications a large number of subgenera were included under *Nasutitermes* (Holmgren, 1912), and Hill (1942) was so confused about the status of these subgenera that he treated all of them as *Nasutitermes* (= *Eutermes*). This uncertainty with regard to the status of the various subgenera of *Nasutitermes* has been solved, to some extent, by the study of the imago-worker mandibles. All Holmgren's subgenera should now be treated as genera. Many of them belong to different phylogenetic lineages (fig. 3).

Another very striking example of convergence is seen in the subfamily Termitinae. *Neocapritermes* and *Planicapritermes* have

evolved the strongly asymmetrical soldier mandibles similar in function to those in the *Capritermes* group. An examination of their imago-worker mandibles indicates the extreme primitiveness of the *Neocapritermes* branch not seen in any other genus of the subfamily.

Parallelism, which means the evolution of the "adaptive characters" among the "members of different families of the same ordinal heritage" (Gregory, 1936), has also occurred in termite evolution. The soldier caste of *Stylotermes* (of the family Rhinotermitidae) bears a close resemblance to the soldier caste of *Kalotermes* (of the family Kalotermitidae). It was this parallelism which led Holmgren and Holmgren (1917) to think that "*Stylotermes* can be connected directly to *Kalotermes*, and exhibits an essentially distinct link" between the families Kalotermitidae and Rhinotermitidae.

The imago-worker mandible in termites exhibits various stages of regressive evolution from the roach-like mandible to the highly specialized type seen in the Serritermitinae in which an extreme reduction of the marginals of both the mandibles has occurred. Such a reduction also has taken place in the soldier mandibles of the nasute termites. The best example of progressive regression in the imago-worker mandibles is furnished by the subfamily Termopsinae, in which a gradual regression of the second marginal of the left mandible has taken place. This regression is most probably due to the slow accumulation of many small mutations. In other cases where no progressive regression is exhibited, one need not necessarily conclude that the reduction has been brought about in a single step, although somewhat similar instances of morphological modifications are not rare in *Drosophila* bred in the genetics laboratory. Next to *Armitermes* with biting type of soldier mandible in the *Paracornitermes* branch of the Nasutitermitinae is placed *Angularitermes* with degenerate mandibles characteristic of a nasute soldier. This big gap between the two genera is best explained as the result of extinction of the intermediate forms or the lack of their discovery.

When the phylogeny of the family Hodo-termitidae was discussed, mention was made

of the subsidiary tooth at the base of the anterior edge of the first marginal of the right imago-worker mandible. This character, apparently functionless, has probably existed in some termites for millions of years. It may therefore be logical to think in terms of the persistence of genes and gene patterns, an idea originally conceived by Emerson (unpublished). This property of some genes may also be inferred from the genetic explanation given to the phenomenon of atavism. In connection with the appearance of the little toe in the hind foot of the guinea pig, Wright (1934) remarks that this character "if not wholly novel in the phylogeny at least has emerged from the depth after millions of years." The genes responsible for this character have persisted through long geological time. "A change of timing within the development system, a change which might remain intact over eons" (Goldschmidt, 1946) causes the suppression of an organ or part of an organ. If this change is itself under the control of genes, which is most probably true, then we must believe in the persistence of genes during long evolutionary periods.

Throughout this study Dollo's rule of irreversibility of evolution has been found applicable. An organ, after having undergone regression, does not appear again. However, if the character is genetically simple it is possible that reappearance may occur. Reverse mutations have been demonstrated by geneticists. On the other hand if the character is under the control of a gene complex, as most taxonomic characters are, the probability of reappearance after loss would be very slight. In such cases full reversion can take place only if many genes mutate back at the same time, thus restoring the original homologous gene complex. Such an event seems to be an impossibility for genetically complex characters. Discussing irreversibility from the viewpoint of genetics, Muller (1939) says: "There can be apparent reversal of evolution with respect to given characters brought about by selection of mutations as well as by the genetic disintegration attendant upon mere removal of selection. But in neither case will the final product be genetically identical or even very similar to the archetype."

In some respects the social insects provide better material for phylogenetic studies than non-social organisms. In termites, for instance, one has at his disposal a large number of morphological characters in the differentiated castes upon which to base his phylogenetic conclusions. The soldier, worker, and the imago, which are so different morphologically and could be comparable in this respect to three unrelated organisms, are nevertheless members of a single unit, or supraorganism (Emerson, 1939). We can draw material for study from any of the castes, and we shall still be dealing with the same organism unit.

The polymorphism of the soldier caste has been of help in understanding the relationships of some termite genera. Dimorphic soldiers appear first in the family Rhinotermitidae. Among the entire Order Isoptera these genera (*Schedorhinotermes*, *Rhinotermes*, and *Dolichorhinotermes*) exhibit the most obvious functional dimorphism. The minor soldier has evolved a gas-defense mechanism. The labrum is considerably elongated and the mandibles are very much reduced as compared to the major soldier which possesses the biting type of mandible. The minor soldiers of these genera and the nasute termites of the subfamily Nasutitermitinae exhibit a convergent reduction of the mandibles in association with the evolution of an enhanced defense function.

In the subfamilies Macrotermitinae and Nasutitermitinae many genera have trimorphic or dimorphic soldiers. The relationships of these have been determined by a comparison of numerous morphological characters, and it may be assumed that derived monomorphic forms are more specialized than the polymorphic forms.

In many genera a better understanding of the relationships was made possible by the study of the zoogeographical data. *Spinitermes* and *Tuberculitermes* have very similar imago-worker mandibles, on the sole basis of which a close phylogenetic lineage might have been assumed, but their geographical distribution is hardly compatible with such a relationship. *Spinitermes* is known from South America and *Tuberculitermes* from Africa. Again, in the evolution of the *Constrictotermes* group of the nasute termites from the *Hirtitermes* branch, assistance was

sought from the zoogeographical data. The distribution of some of the primitive termites, such as *Mastotermes*, *Stolotermes*, and *Porotermes*, conforms to Matthew's theory of distribution of the primitive forms. Schmidt (1943), explaining Matthew's theory, says, "Australia, South America and the southern half of Africa project southward from the northern continents like great peninsulas, and as the more primitive forms enter them at the north, they have necessarily accumulated in these peninsulas from successive waves of dispersal, and of evolution." The most primitive termite, *Mastotermes*, is now confined to Australia. Its fossil history reveals its former much wider distribution in Europe and North America. *Porotermes* is recorded from Australia, Tasmania, New Zealand, the Cape Province in South Africa, and Chile. There is, however, a large

number of cases which are difficult to explain by means of the known principles of animal geography. The present study has, in a few cases, cleared some difficulties; others still remain a problem for those interested in zoogeography.

The phylogenetic scheme of the termite genera presented in this paper gives a broad perspective of relationships and is an improvement over previous schemes. No phylogenetic conclusions can approach perfection unless based upon evidence derived from various phases of biology, such as embryology, genetics, physiology, behavior, ecology, and zoogeography. Future discoveries will doubtless result in the modification of the phylogenies here postulated, but it is hoped that the relationships suggested by this study will be verified far more often than they will be refuted.

SUMMARY

1. THE PHYLOGENY of 139 out of a total of 142 genera and subgenera of termites based primarily upon the imago-worker mandibles has been studied.

2. The imago-worker mandibles of termites provide a conservative morphological character significant for the study of phylogeny.

3. The families Kalotermitidae and Rhinotermitidae have a relatively fixed mandibular pattern in the imago and worker castes. The Hodotermitidae and the Termitidae exhibit a great variation in the imago-worker mandibles. The variation of this character within a genus is negligible.

4. In the main, this study corroborates the termite classification proposed by Holmgren. In some cases, however, he has misinterpreted the phylogeny because of convergent adaptation. The study of the imago-worker mandibles has cleared some of these errors.

5. The subfamily Serritermitinae, hitherto included under the family Rhinotermitidae, is transferred to the family Termitidae.

6. It is concluded that the Rhinotermitidae arose from a stock which had *Archotermopsis*-like imago-worker mandibles and possessed ocelli and not from the Kalotermitidae as suggested by Holmgren and Hare.

7. There are several phylogenetic lineages in the Nasutitermitinae, and Holmgren's

subgenera are best raised to generic rank.

8. *Pseudomicrotermes*, whose exact relationship has thus far remained obscure, is now assigned to the subfamily Amitermitinae in which it forms a distinct group with *Eremotermes* and *Synhamitermes*.

9. There are several instances of convergence in termite evolution. The phragmotic head in the Kalotermitidae has evolved three times. The nasute soldier in the Nasutitermitinae has arisen twice independently. The evolution of the asymmetrical soldier mandibles in the Termitinae has occurred in two distantly related groups of genera.

10. Zoogeography has been of some help in understanding the phylogenetic relationships of several genera. The distribution of some primitive termites belonging to the families Mastotermitidae and Hodotermitidae conforms to Matthew's theory of distribution of primitive forms.

11. The worker caste, usually considered of little importance in termite taxonomy, can be of great value for generic identification, particularly by the study of its mandibles.

12. A discussion of the concepts of homology, conservative characters, convergence, Dollo's rule of irreversibility of evolution, regressive evolution, and the persistence of genes and gene patterns has been included.

APPENDIX

THE DRAWINGS of the imago-worker mandibles (figs. 5-17) are based on the following species:

ROACHES

1. *Ancaudellia serratissima* (Brunner), Firschen Haven, New Guinea, coll. Hebard.
2. *Panesthia angustipennis* (Illig), Solka boeni, Java.
3. *Cryptocercus punctulatus* Scudder, Glendale, Douglas County, Oregon.

TERMITES

4. *Mastotermes darwiniensis* Froggatt, nymph, det. G. F. Hill, metatype, comp. A. Emerson, Townsville, north Queensland, Australia, coll. F. H. Taylor.
5. *Kaloterme flavicollis* (Fabricius), imago, det. N. Holmgren, Italy, from Light collection, no. 240 It.
6. *Procryptotermes fryeri* Holmgren, imago, det. N. Holmgren, cotype from type colony, Takamaka, Aldabra Island, coll. J. C. F. Fryer, 6. X. 1908.
7. *Cryptotermes cavifrons* Banks, imago, det. and coll. T. E. Snyder, metatype, comp. A. Emerson, Florida, 24. III. 1917.
8. *Paraneotermes simplicicornis* (Banks), imago, det., coll., and comp. A. Emerson, Edoni, California, 8. IX. 1929.
9. *Neotermes castaneus* (Burmeister), imago, det. A. Emerson, Pine Crest, Monroe County, Florida, coll. E. M. Miller, 12. X. 1940.
10. *Rugitermes nodulosus* (Hagen), imago, det. A. Emerson, Ilha Grande, Brazil, coll. H. Muth and H. Sick, IX. 1944.
11. *Glyptotermes tuberculatus* Froggatt, imago, det. G. F. Hill, metatype, comp. A. Emerson, Takapuna, Auckland, New Zealand, coll. J. M. Kelsey.
12. *Calcaritermes nigriceps* (Emerson), imago, autotype, metatype, det. and comp. A. Emerson, Salybia Bay, Trinidad, coll. A. M. Adamson, 12. X. 1940.
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14. *Archotermopsis wroughtoni* Desneux, nymph, autotype, metatype, det. and comp. J. Desneux, Kashmir Valley, India, coll. E. Radcliff.
15. *Hodotermopsis japonicus* Holmgren, nymph, det. N. Holmgren from type colony, Loo-Choo Archipelago, coll. Watase, 16. IV. 1909.
16. *Zootermopsis angusticollis* (Hagen), imago, det. T. E. Snyder, Redwood, California, coll. R. Hopping, 29. VIII. 1918.
17. *Porotermes quadricollis* (Rambur), imago, det. A. Emerson, Talcahuana, Chile, coll. Steindachner, IV. 1873.
18. *Stolotermes brunneicornis* (Hagen), dealate, det. G. F. Hill, comp. A. Emerson, Adventure Bay, Brunns Island, Tasmania, 14. IV. 1935.
19. *Hodotermes mossambicus* Hagen, worker, det. F. Silvestri, Windhuk, southwest Africa.
20. *Microhodotermes viator* (Latreille), worker, det. F. Silvestri, redet. A. Emerson, Steinkop, Little Namaland, Africa.
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22. *Psammotermes hybostoma* Desneux, imago, det. and comp. A. Emerson, Temassinini, Algeria, coll. v. Geyr, 29. I. 1914.
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26. *Stylotermes fletcheri* Holmgren, worker, cotype, det. N. Holmgren, Coimbatore, India, coll. T. B. Fletcher, 11. X. 1912.
27. *Termitogelon umbilicatus* (Hagen), worker, det. H. Hagen, Rambodda, Ceylon.
28. *Prorhinotermes simplex* (Hagen), worker, det. A. Emerson, Miami, Florida, coll. W. Murphy, 10. II. 1935.
29. *Parrhinotermes aequalis* (Haviland), worker, det. N. Holmgren, metatype, comp. A. Emerson, Selangor, Malacca, coll. H. v. Buttel-Reepen, III. 1912.
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31. *Rhinotermes marginalis* (Linné), worker, plesiotype, det. and comp. A. Emerson, Kartabo, British Guiana, 20. IX. 1920.
32. *Dolichorhinotermes longilabius* (Emerson), worker, paratype, det. and coll. A. Emerson, Kartabo, British Guiana, 23. VI. 1920.
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37. *Allondonitermes rhodesiensis* (Sjöstedt), imago, det. F. G. M. Westropp, Msugaa, Tanganyika, coll. E. Burt, 3. XII. 1935.
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39. *Sphaerotermites sphaerotherax* Sjöstedt, metatype, morphotype, det. and comp. A. Emerson, near Stanleyville, Belgian Congo, coll. H. Kohl.
40. *Odontotermes (Odontotermes) vulgaris* (Haviland), worker, metatype, det. and comp. A. Emerson, Tylden, Cape Province, Africa.
41. *Odontotermes (Hypotermes) xenotermitis* Holmgren, worker, metatype, det. and comp. A. Emerson, Shillong, Assam, India, coll. C. C. Ghosh.
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52. *Longipeditermes longipes* (Haviland), worker, metatype, det. and comp. A. Emerson, Sandakan, Borneo, coll. K. P. Schmidt, 8. VII. 1929.
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72. *Angularitermes nasutissimus* Emerson, worker, paratype, det. and coll. A. Emerson, Kartabo, British Guiana, 11. VII. 1920.

73. *Mimeuterms giffardii* Silvestri, worker, cotype, det. and coll. F. Silvestri, Camayenne, French Guiana, 28. X. 1912.
74. *Subuliterms oculatissimus* Emerson, imago, paratype, from holotype colony, det. and coll. A. Emerson, Kartabo, British Guiana, 26. IX. 1920.
75. *Convexitermes manni* Emerson, worker, metatype, autotype, det. and comp. A. Emerson, Oronoque River, British Guiana, coll. N. Weber, 30. VII. 1936.
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77. *Eutermellus convergens* Silvestri, worker, cotype, det. F. Silvestri, Fernando Po River, Africa, coll. Fea.
78. *Protohamitermes globiceps* Holmgren, imago, cotype, det. N. Holmgren, Sarawak, Borneo, coll. G. D. Haviland.
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84. *Ahamitermes hilli* Nicholls, worker, paratype from type colony, det. and coll. Nicholls, Kalgoorlie, Australia, 20. III. 1928.
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87. *Globitermes sulphureus* (Haviland), worker, metatype, det. and comp. A. Emerson, Phoc-Son, Annam, coll. H. Fruhstorfer.
88. *Prohamitermes mirabilis* (Haviland), worker, cotype, det. and coll. G. D. Haviland, Mt. Lambir, Sarawak, Borneo.
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97. *Gnathamitermes perplexus* (Banks), worker, metatype, det. and comp. A. Emerson, Arizona, 18. IV. 1937.
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106. *Crenotermes albotarsalis* (Sjöstedt), imago, cotype, det. Y. Sjöstedt, Kribi, Cameroon, coll. Morgen, XII. 1888.
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worker, autotype, det. Y. Sjöstedt, Belgian Congo, coll. Laman.

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117. *Spinitermes nigrostomus* Holmgren, imago, metatype, det. and comp. A. Emerson, Courantyne River, Dutch Guiana, coll. N. Weber, 11. VII. 1936.

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coll. A. Emerson, Kartabo, British Guiana, 5. V. 1924.

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